



Figure 10.1 Artist's depiction of an aggregation of fireflies flashing synchronously in a tree in southeast Asia. (Illustration © Bill Ristine 1998)

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## Synchronized Flashing among Fireflies

The Glowworms . . . represent another shew, which settle on some Trees, like a fiery cloud, with this surprising circumstance, that a whole swarm of these Insects, having taken possession of one Tree, and spread themselves over its branches, sometimes hide their Light all at once, and a moment after make it appear again with the utmost regularity and exactness, as if they were in perpetual Systole and Diastole.

—Perhaps the earliest documented description of synchronous flashing, from the Dutch physician Engelbert Kaempfer's (1727) account of a trip along the banks of the Chao Phraya (Meinam) River in Thailand in 1680. (Quoted in J. Buck, *Quarterly Review of Biology*)

### Synchronous Rhythmic Flashing

Fireflies are a familiar sight on warm summer evenings. Flashing their abdominal lanterns as they fly over lawns and meadows, one generally discerns no pattern to the flickering display. Among the common North American genera *Photinus* and *Photuris*, the males rove about singly, searching for females that rest on low vegetation, and are thus called roving fireflies. Courtship involves a Morse-like code of alternating signals between the sexes. The male modulates the duration and intensity of his flash, as well as the rate and number of flashes in a species-specific pattern. This allows a female to recognize a conspecific male, to which she responds with a flash after a species-specific time delay. At about 24 °C, for example, the female *Photinus ignitus*, an eastern U.S. species, answers the male after three seconds (Lloyd 1981). Among the roving fireflies, successful mating often requires a period of continuous species-specific communication involving alternating, accurately timed flashes that guide a flying male to the sedentary female. (For reviews see Lloyd 1971, 1979, 1981.)

Fireflies are beetles (family Lampyridae), and occur as more than 2000 species worldwide. Not surprisingly different species have evolved a great variety of luminescent mating signals. However, one particular form of luminescent behavior, seen from India east to the Philippines and New Guinea, has particularly fascinated explorers and naturalists for hundreds of years. In

this vast region, enormous aggregations of fireflies gather in trees and flash in near-perfect synchrony (Figure 10.1). None of the authors has had the opportunity to see these fascinating displays in the wild, but films of synchronously flashing fireflies in Malaysia can be seen in the documentary nature program, "Talking to Strangers," in the "BBC Trials of Life" series of videos by David Attenborough, available from Time-Life Videos. The hypnotic excitement of witnessing such displays was described seventy years ago by Howard (1929) as "a strange sight... there in the darkness was a tree just filled with lightning bugs. The strange thing was that they all flashed at the same time. One second everything would be dark, the next second the whole tree would be aglow with a beautiful light!"

Adamson (1961) made similar observations:

It is then too that one sees the great belt of light, some ten feet wide, formed by thousands upon thousands of fireflies whose green phosphorescence bridges the shoulder-high grass. The fluorescent band composed of these tiny organisms lights up and goes out with a precision that is perfectly synchronized, one is left wondering what means of communication they possess which enables them to coordinate their shining as though controlled by a mechanical device.

In the same vein, Smith (1935) wrote:

Imagine a tree thirty-five to forty feet high thickly covered with small ovate leaves, apparently with a firefly on every leaf and all the fireflies flashing in perfect unison at the rate of about three times in two seconds, the tree being in complete darkness between the flashes. Imagine a dozen such trees standing close together along the river's edge with synchronously flashing fireflies on every leaf. Imagine a tenth of a mile of river front with an unbroken line of [mangrove] trees with fireflies on every leaf flashing in synchronism, the insects on the trees at the ends of the line acting in perfect unison with those in between. Then, if one's imagination is sufficiently vivid, he may form some conception of this amazing spectacle.

Recent descriptions of the phenomenon provide more specific details. In the firefly *Pteroptyx cribellata*, for example (Buck and Buck 1976, 1978; Lloyd 1973a), before sunset large numbers gather in certain swarm trees, having apparently arrived on previous evenings. Thousands of individuals begin flashing soon after sunset, while synchrony builds up slowly through the night. One can see a great variety of light emissions at these congregations. Most prominent are the males' rhythmic synchronous flashes. Perched males flash synchronously. Airborne males also synchronize with others as they move in a slow hovering flight up to several meters from the foliage, attracted to other females. Males that land on foliage can be seen approaching females. The males group in small clusters around a perched female.

Unsynchronized flashing also occurs. Females emit arrhythmic long-duration glows that are dimmer than the male's signal, males respond rapidly to the females with glows and twinkles, and other males emit continuous glows as they chase females in flight. These flashing displays continue through the night and successful encounters result in copulations.

As Buck and Buck (1976) remark, neither the beauty of such a spectacle nor its mesmerizing effect can entirely account for the fascination of these displays. During the past 300 years, not only have there been many dozen descriptions, but also lively debate over how fireflies accomplish their rhythmic flashing. Some early authors felt that the phenomenon was merely an illusion and adamantly denied its existence (see review by Buck 1938). Much of the fascination as well as disbelief during the early 1900s arose because people had difficulty imagining any mechanism to explain *how* fireflies coordinate their synchronous flashing. There was also the mystery of *why* fireflies flash in unison. Most of this chapter is devoted to answering the "how" question; however, we will first briefly explore the possible adaptive significance of this activity.

### Adaptive Significance of Synchronous Rhythmic Flashing

The reproductive significance of luminescence is well established for the roving fireflies and the consensus among entomologists is that collective synchronized flashing also is related to reproductive behavior (Figure 10.2). However, the significance of synchrony for mating is still not entirely clear. Even the most recent review of the subject (Buck 1988) presents a bewildering array of potential explanations, some of which are presented in the next section, but none of which is entirely convincing. Furthermore, the early functional interpretations of synchronous flashing suffered from erroneous group selectionist views and other misunderstandings concerning evolutionary theory. Some of that confusion persists in current discussions (see Buck and Buck 1978, 1980; Lloyd 1971, 1973a, 1973b; Otte 1980 for detailed discussions). Finally, we must emphasize that fireflies employ a variety of mating systems (Buck and Buck 1978; Lloyd 1966, 1973a; Otte and Smiley 1977), and so a single functional explanation may be inadequate to explain all instances of synchronous flashing.

Rather than review the entire literature, at this point we will outline what appears to be the most likely explanation for synchronized flashing in *Pteroptyx malaccae*, the Thai species, that Smith (1935) described. As in other species, synchronized flashing is performed entirely by males that maintain positions spaced on individual leaves or similar territories in trees for long periods. Females fly to these trees to mate with males. The females emit irregularly timed, longer-duration flashes that are dimmer than the male's. Mating pairs are commonly found in the trees (Buck and Buck 1978). The mating system does not

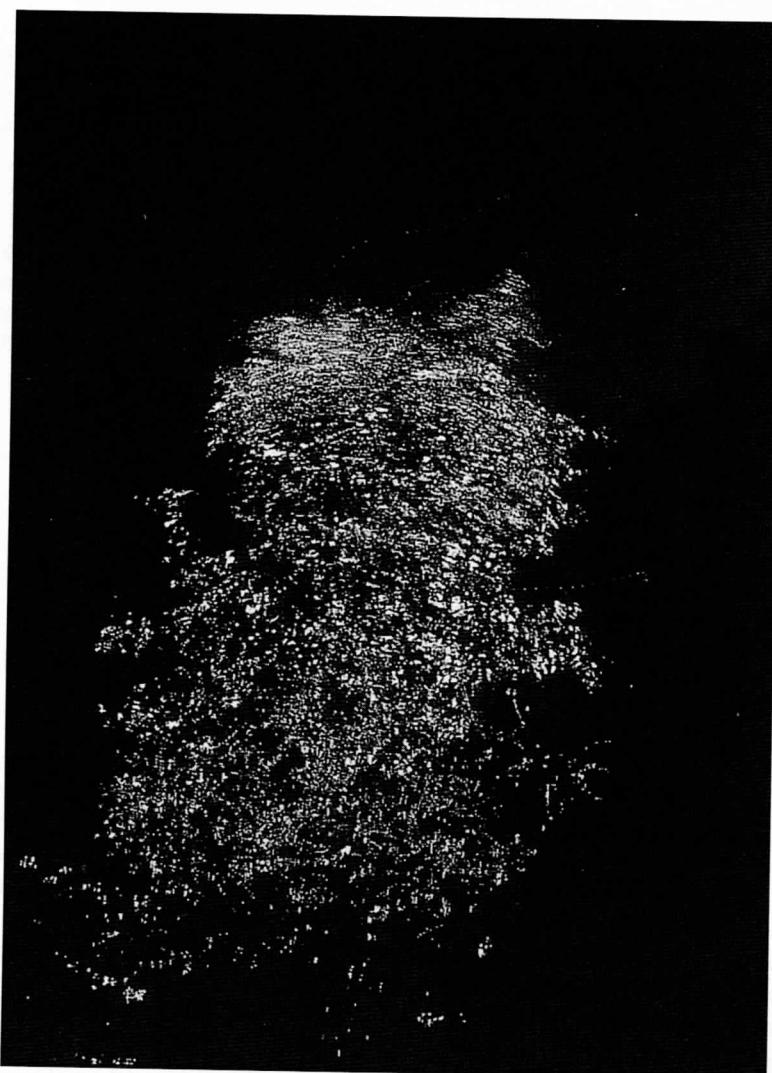


Figure 10.2 Thousands of fireflies flashing in synchrony as shown in a time exposure photo of a nocturnal mating display. (From Strogatz and Stewart 1993)

involve a repetitive male-female dialog as in the roving species, but rather a massed congregation of males that females visit for mating. In certain vertebrates and invertebrates, such male-mating assemblies are termed *leks* (Bradbury and Gibson 1983). According to Gibson and Bradbury (1986), "Lek systems are commonly defined by four criteria: absence of parental care by the

male, clusters of displaying males, location of mating aggregations away from resources required by females, and apparent freedom of females to choose mates."

The mating system of *Pteroptyx* may involve such a lek system (Buck and Buck 1976; Otte and Smiley 1977; Lloyd 1979), and it has been argued that synchrony among the males could serve at least three purposes in this context. First, synchrony could accentuate the males rhythm (Otte and Smiley 1977). If, as in *Photinus* (Lloyd 1966), females select males based upon a species-specific flash repetition rate, then the chaotic flashing of dense aggregations of males may thwart the female's ability to assess the males' flashing pattern. By mutually synchronizing their rhythm, each male benefits by allowing its flashing rate to be evaluated by a potential mate.

Second, a similar argument based on enhanced detection applies if mating requires that males visually detect females (Otte and Smiley 1977). If a portion of the mating sequence requires that males detect the flash of nearby females, synchronization could serve as a noise-reduction mechanism allowing males better to find females in the dark interflash periods.

Third, synchronization could be a signal enhancement mechanism (Otte and Smiley 1977) enabling small groups of synchronizing males to attract larger numbers of females. According to (Lloyd 1979), "Ability to keep the identifying species-specific rhythm with conspecific males is critical to a male's success because it permits him to enhance the attractiveness of his sublek in the swarm as it competes with others for incoming females...."

Note that these explanations operate within a rather localized environment. In this regard, Lloyd (1973a, p. 991) warns that the huge *mass* displays encompassing areas of one or many trees may not have adaptive significance. He states "Although mass synchronous flashing of fireflies is conspicuous and associated with mating behavior, it probably is of little reproductive significance. This phenomenon may merely be the gross consequence of individual males synchronizing with their neighbors as they compete in small clusters for females on an extremely localized level." In other words, synchronization among small groups of males in a local lek is likely to be adaptive, but *mass* synchrony may be an epiphenomenon that arises as local synchronies coalesce at higher male densities.

In summary, it seems reasonable to assume that among *Pteroptyx*, at least at the level of small clusters of males, synchronous flashing could serve adaptive functions related to mating. Similar arguments have been suggested to explain the synchrony occasionally seen in other species such as roving *Photinus* fireflies (Otte and Smiley 1977).

Whether or not we accept the thesis that synchronized flashing has adaptive value, the question we will address in this chapter is: What is the mechanism of synchronization? We will see that through the natural selection of certain

behavior and physiology, some firefly species evolved a simple, yet elegant self-organized mechanism for synchronous flashing.

## Some Early Hypotheses of the Mechanism

It is instructive to see how an adequate explanation of synchronous flashing emerged gradually over many decades. Many mechanisms were offered before 1938 to explain synchronous flashing (reviewed by Buck, 1938). Hypotheses based on leadership and templates were seriously considered and, for many years, were difficult to refute. Part of the problem of formulating a satisfactory explanation was the lack of experimental data to support or refute specific hypotheses. The absence of an adequate conceptual framework also hindered the development of good hypotheses. As a result, a variety of rather naive explanations were initially suggested. We will briefly review these early hypotheses, and see how they were supplanted only recently by a satisfactory explanation.

### *Anthropomorphic and Other Inadequate Explanations*

Several early writers refused to believe that synchronization occurred. Laurent (1917) was so skeptical of the phenomenon that he attributed synchronization to the rapid rhythmic twitching of the observer's eyelids! Craig (1917) reasoned that whenever a "large number of fireflies are flashing at slightly different rates there must be a great amount of accidental synchronism." Craig (1916) also contended that, "Viewing any large assortment of instances without statistical methods, one can see in them whatever one is predisposed to see; and we are always predisposed to perceive a rhythm—this is a well-known psychological fact."

Explanations denying the very existence of synchronization of course were abandoned as soon as recording photometers and high-speed movie cameras offered incontestable evidence that synchronized flashing was more than a quirk of human perception. However, such evidence was unavailable until 1965, when several expeditions to Borneo, Thailand, New Guinea, and Southeast Asia gathered data to verify centuries-worth of anecdotal observations by naturalists and explorers (Buck and Buck 1976).

Other early writers believed in the existence of synchronization, but invoked explanations that were clearly naive and anthropomorphic in their reliance on an animal's consciousness of its own rhythm. For example, Wheeler (1917) described pelicans in flight with their wings apparently beating in synchrony. He attributed this to a "fine sense of rhythm on the part of each individual." He went on to describe the synchronous flashing of fireflies in similar terms and stated, "In fireflies the initiation of the simultaneous flashes must be due to optic stimuli, as it is in people endeavoring to keep in step with one another, but the continuation of the established rhythm would seem to depend

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on a kind of ‘Einfühlung,’ which is German for “empathy.” (In the colloquial sense, the verb “einfühlen” means to be on someone’s wavelength.) Many years later, Buck and Buck (1968) observed that the mechanism was still believed to be analogous to certain human activities: “Among ‘sense of rhythm’ behaviors in man the rhythmic synchronous handclapping that may break out spontaneously at sporting events, though not involving a preexisting rhythm in the participants, has some resemblances to firefly synchrony.” The mechanism was termed *anticipatory synchrony* because the human participants seemed to be using information from the preceding cycle or cycles “to predict the proper time to [clap] in order to attain synchrony,” rather than to be acting in response to immediate cues from the handclapping of others (Buck and Buck 1968).

### No Environmental Influences Organize Synchronous Flashing

Nature provides many sources of rhythmic activity, such as seasonal temperature changes, daily tides, and diurnal light-dark cycles. Therefore, it is not surprising that someone would suggest an environmental trigger to explain the rhythmic flashing of fireflies. This is a hypothesis based on a kind of template, one of the commonly assumed alternatives to a self-organization mechanism. However, it is difficult to imagine an environmental stimulus of sufficient regularity and proper frequency to impose the observed synchrony. Buck (1938) cites a discussion in the *Transactions of the Entomological Society of America*, in 1865, in which the far-fetched suggestion was made that puffs of wind stimulate the fireflies alternately to expose and conceal their lights.

Eventually it was realized that *repetitive*, external rhythmic stimuli could not explain the phenomenon, so it was suggested that perhaps a *single* stimulus was responsible. It was argued that the synchrony might arise from a single triggering stimulus in combination with the fireflies’ regular flashing rhythm. If the rhythm were regular enough and if all the fireflies were to begin flashing at the same time, then synchrony might result automatically. This may appear to make sense, but cannot be the mechanism. Termed *inertial synchrony*, this slightly more sophisticated, but equally inadequate, explanation was convincingly discounted by Buck and Buck (1968). First, even if an abrupt event, such as a particular level of ambient light, a clap of thunder, or a bolt of lightning initiated flashing, the individuals would soon fall out of rhythm unless the rate of flashing were exceedingly regular, far more regular than that observed. Second, we know that aggregations of synchronously flashing fireflies are dynamic, with individuals arriving and leaving through the night (Lloyd 1973a), making it unlikely that all the participants could have been subjected to a common initiating stimulus. Finally, detailed observations by numerous observers have failed to reveal any evidence of a single triggering stimulus.

### **Leaders Control Synchronous Flashing**

Having discounted the possibility that synchronization is imposed by external stimuli, the only other logical explanation seemed to be that the organizing influence came from an individual within the group of fireflies itself—a hypothesis based upon a leader. In the early part of this century, Blair (1915) read a paper before the South London Entomological Society and Natural History Society. He believed that the “probable explanation of the phenomenon is that each flash exhausts the battery, as it were, and a period of recuperation is required before another flash can be emitted. It is then conceivable that the flash of a leader might act as a stimulus to the discharge of their flashes by the other members of the group, and so bring about the flashing concert by the whole company.”

Two valid objections make it unlikely that any leader coordinates the rhythmic flashing. First, it is inconceivable that a single leader could act as the pacemaker for the extensive mass congregations of the thousands of fireflies observed in species such as *Pteroptyx*. How could a single leader be visible to all the members of the congregation? The second objection is that even if one invokes a mechanism with several leaders relaying information through the system, experimental data readily rules out any sort of follow-the-leader mechanism. A critical finding was that among the Thai species *Pteroptyx malaccae*, the time interval beginning with the first flash of a member in the group and ending with the last flash in the group was extremely short, only about 30 ms. The minimum delay for flash generation, even by direct neural stimulation near the light organ, was experimentally measured at 55–80 ms. This proved that during group synchronization, fireflies cannot be using the sight of a neighboring flash to initiate their own flash in a follow-the-leader type of mechanism. Their reaction time is simply too slow (Hanson et al. 1971) (also see Box 10.2).

Of all these early hypotheses of synchronization, only one came close to what we now believe to be the correct mechanism. Richmond (1930), lacking any experimental data, but with surprising insight, theorized: “Suppose that in each insect there is an equipment that functions thus: when the normal time to flash is nearly attained, incident light on the insect hastens the occurrence of the event. In other words, if one of the insects is almost ready to flash and sees other insects flash, then it flashes sooner than otherwise. On the foregoing hypothesis, it follows that there may be a tendency for the insects to fall in step and flash synchronously.”

As discussed later, Richmond captured the essence of a self-organization system of interacting oscillators optically coupled to one another. We don’t know whether Richmond understood the full implications of his description, but it is clear that Buck (1938) did not, because he viewed the theory merely as a “simplified form of the leader theory,” and he remarked that, “Richmond’s theory... like all the other theories, appears to be completely inadequate to explain displays of synchronism of the magnitude observed in Siam....”

Although Richmond suggested that his mechanism could be extended to a system involving many flashing units, we do not know whether he simply envisioned the most rapidly flashing individual acting as a leader (the interpretation that Buck seems to have taken), or whether he truly conceived of a collective self-organizing mechanism for coupling large numbers of fireflies. Whatever the case, Richmond's insight, tucked away in the back pages of *Science*, appears to have been largely forgotten. However, Hanson et al. (1971) do cite Richmond's article in the introduction of their own *Science* article describing a mechanism for synchronization based on the photic resetting of a flash-timing oscillator in the brain.

Let us now examine some experiments that served as a prelude to the formulation of a mechanism for synchronized flashing.

## Neurophysiology of Individual Flashing

Experimental work on the mechanism of flashing began with neurophysiological studies of the central nervous system of fireflies (Case and Buck 1963). Hanson et al. (1971), Bagnoli et al. (1976), and Case and Strause (1978) reviewed the evidence suggesting that rhythmic flashing of male fireflies is controlled by a neural timing mechanism in the brain that oscillates at a constant frequency. Case and Buck (1963) and Buonomici and Magni (1967) found that each flash is triggered by nerve impulses in the brain that travel down the ventral nerve cord and lanternal nerves to the firefly's lantern. Experiments using ablation and local electrical excitation further supported the role of the brain as the central timer (Bagnoli et al. 1976).

Once the oscillator was identified, experiments revealed details of how it worked. Appropriate photic input could enhance or inhibit flashing (Buck 1937; Magni 1967). With systematic studies of the effect of exogenous light signals on the flash rhythm, a mechanism for synchronous flashing emerged. It was also discovered that different species use different synchronization mechanisms (Hanson 1978).

To avoid confusion, let us initially restrict our discussion to the synchronization mechanism of *Pteroptyx cribellata*, an extensively studied species from Papua New Guinea (Buck et al. 1981; Hanson 1978; Hanson et al. 1971). A set of experiments by Buck et al. (1981) revealed the effect of artificial pulses of light on the male rhythm. Individual fireflies were restrained and prevented from seeing their own flashes. In a darkened room, a fiberoptic system guided pulses of white light of 40 ms duration to the firefly's eye. The firefly flashed in response to the stimulus and each flash was recorded for analysis. In the absence of any stimulation, one male was found to flash regularly at a rate of nearly one flash per second (more precisely, its free run period was  $965 \pm 90$  ms). After measuring this spontaneous periodicity, single 40 ms pulses were interjected randomly within its spontaneous flashing cycle every

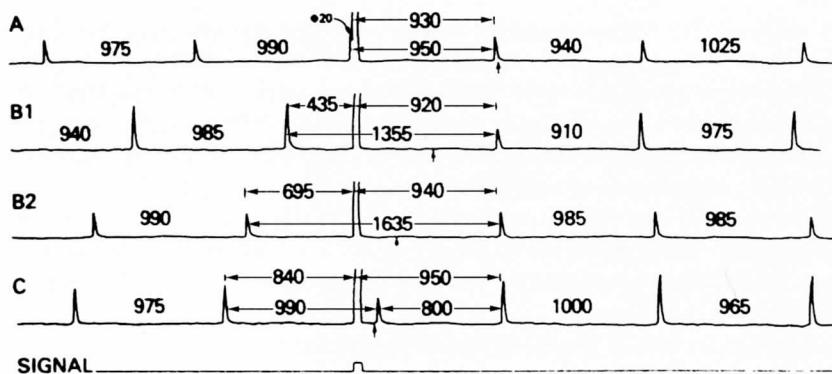


Figure 10.3 Responses of a firefly to single, artificial 40 ms pulses of light. See text for a discussion. (From Buck et al. 1981)

10 s or so. The firefly was tested with 21 pulses over a period of about 250 cycles. Three different responses to the artificial photic signals were observed, depending upon when the signal was imposed relative to the last preceding free run flash (Figure 10.3):

1. In response (A), one of the 21 signals happened to occur almost simultaneously with the firefly's own spontaneous flash (see response A). Since the first post-signal flash occurred 930 ms later—almost exactly when expected had there been no signal—this signal appeared to have no effect on the firefly's normal rhythm.
2. Each of the 17 signals that occurred between 110 and 840 ms after the firefly's own spontaneous flash inhibited the next expected free run flash responses (B<sub>1</sub> and B<sub>2</sub>). Instead of occurring when expected, the flash was delayed. It occurred approximately 1 s after the signal pulse. In response B<sub>1</sub>, the flash occurred 920 ms, and in B<sub>2</sub> 940 ms, after the signal pulse. Viewed another way, the signal inhibited the expected flash, delaying it by approximately the length of time into the cycle that the signal occurred. These relationships should be clear from careful examination of responses B<sub>1</sub> and B<sub>2</sub>.
3. Three signals fell late in the firefly's flash cycle, 840 ms or more after the previous flash but prior to the next expected flash. These late signals did not inhibit the next expected flash, which occurred when expected. In response C, the flash arrived 990 ms after the previous flash. However, the next flash arrived *early*, after 800 ms in response C.

In all cases, flashes occurring after the affected flash were followed by a series of flashes of normal free run duration. In other words, the signal pulse

did not stop the cycle.

At the end of the cycle, the firefly returned to its normal free run rhythm.

No matter what the signal was, the firefly always responded in the same way.

## A M

A firefly's rhythmic flashing is controlled by a pacemaker neuron in the *Pterothorax* ganglion. This pacemaker neuron has a normal timing pattern, but it can be triggered by external signals. For example, if a firefly is placed in a dark environment with a regular source of light, it will synchronize its flashes with the external light source.

To understand how a firefly's rhythmic flashing is controlled, we need to look at the individual components of the firefly's nervous system. The firefly's nervous system consists of a brain, a midbrain, a hindbrain, and a ventral nerve cord. The brain and midbrain are involved in processing sensory information and generating motor commands. The hindbrain is involved in controlling the firefly's circadian rhythms. The ventral nerve cord is involved in controlling the firefly's muscles and glands.

An adult firefly has a complex nervous system with many different types of neurons. Some neurons are involved in sensing light, others in generating light, and others in controlling the firefly's movements. Once a firefly has learned to flash, it can repeat the same pattern over and over again.

did not alter the firefly's normal period, but only affected the timing of the next flash (in B<sub>1</sub> and B<sub>2</sub>) or the timing of the flash after the next flash (in C).

At first this behavior must have seemed confusing, as it may seem confusing to the reader at first inspection. A perplexing feature was that identical light signals resulted in two very different effects on the flashing rhythm. The type B effects caused the expected flash to arrive late, and the type C effects caused the following flash to arrive early.

Nonetheless, based upon the results of this one set of simple experiments the authors were able to hypothesize a model mechanism that was consistent with all the data and explained synchronized flashing. Let us examine the proposed model.

### A Model Based on Coupled Oscillators

A breakthrough in our understanding of the mechanism of synchronous flashing actually came a decade earlier than the experiments just described when Hanson et al. (1971) presented results of preliminary experiments with *Pteroptyx cribellata*. The second sentence of their brief two-sentence abstract in *Science* succinctly states their hypothesis: "Since the interval between the pacer signal and the firefly's flash of the next cycle approximates the firefly's normal free-run period, it is suggested that the pacer signal resets the flash-timing oscillator in the brain, thus providing a mechanism for synchronization." This idea was suggested even earlier by Winfree (1967), who presented a theoretical paper on the behavior of populations of coupled oscillators. Referring to the "astonishing but persistent" reports of synchronizing fireflies in southeast Asia, he stated, "We will see . . . that innate individual rhythmicity with phase-dependent sensitivity to mutual influences can give rise to . . . striking community synchronization."

To understand the implications of Winfree's observation consider an individual firefly flashing at its normal free run period (a, in Figure 10.4). The pacemaker resetting model assumes that some property of the oscillatory center in the firefly brain—called "excitation"—gradually changes over time. Excitation of the brain's pacemaker rises from its baseline level to a threshold triggering level that elicits a flash. It is assumed that once a flash is triggered, the excitatory state spontaneously falls back to the baseline level and restarts the cycle of rising excitation. Although this excitation has never been directly measured in the firefly brain, there is a useful electrical analog of an oscillator that behaves similar to the firefly oscillator (Strogatz and Stewart 1993).

An oscillator can be modeled as circuit consisting of a resistor in parallel with a capacitor (Figure 10.5). A constant input current supplied by a battery charges the capacitor by increasing the voltage across the capacitor plates. Once the threshold voltage is reached, the capacitor discharges, and the cycle repeats.

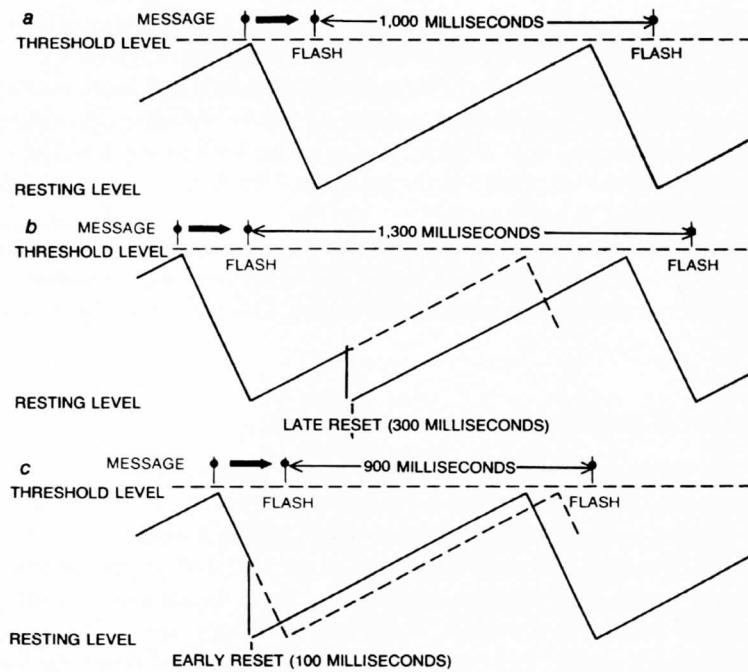


Figure 10.4 Model of a resettable pacemaker within a firefly. See text for discussion.  
(From Buck and Buck 1976)

Similarly, each time the oscillatory center in the brain reaches the triggering level, a volley of signals passes down the nerve cord to the firefly's lantern. The rising excitation (charging) phase of the cycle takes about 800 ms. The time it takes from the signal leaving the brain to the onset of flashing in the firefly's lantern is about 200 ms. During this same 200 ms the brain's oscillator is also reset (discharged) from its threshold level back to zero. As a result of these neurophysiological processes, the normal interflash period is about 1 s.

When no external stimuli are applied, the flashing remains regular and rhythmic. Now suppose the firefly receives a photic signal during the charging portion of its cycle (b, in Figure 10.4). A signal of sufficient intensity abruptly resets the excitation back to its zero baseline. If that happens, the flash does not occur at the expected time but is delayed until the excitation has again built up from zero to the triggering level. The flash is delayed by a period equal to the interval from the baseline level to the onset of the light signal.

Finally, suppose the firefly receives a signal shortly after the threshold level for triggering the flash has already been reached (c, in Figure 10.4). The model assumes that the impulse to trigger the next flash has already left the brain and is traveling down the ventral nerve cord. At this point, any light signal to

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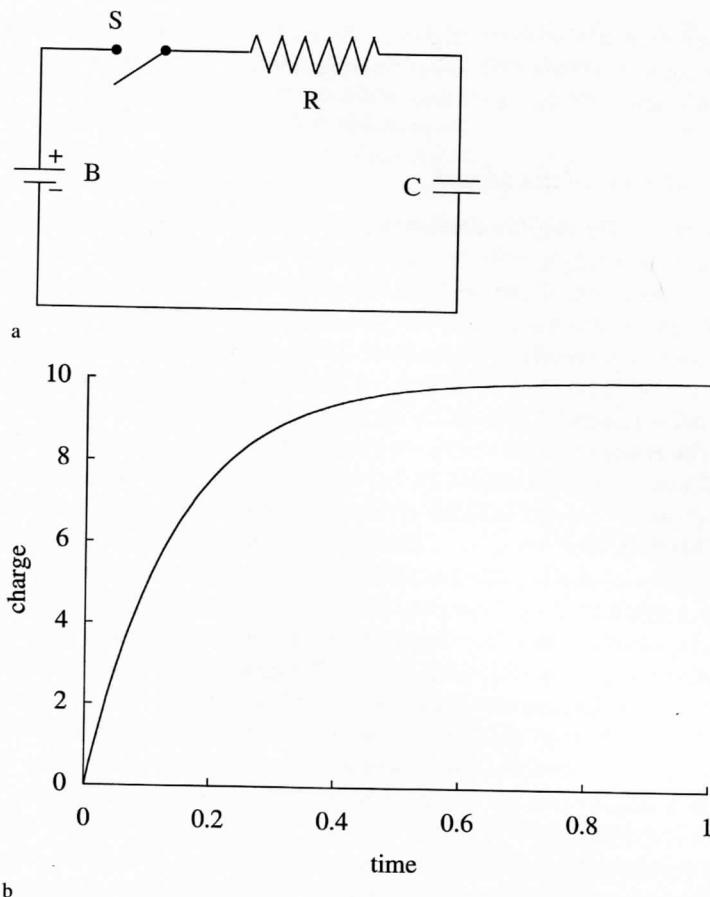


Figure 10.5 An oscillator modeled as a circuit (a) with a resistor (R) in parallel with a capacitor (C). The charge on the capacitor depends on the battery voltage, the resistance, and the capacitance, as shown in (b).

the brain cannot affect the timing of the flash cycle in progress and the flash occurs as expected. However, the light signal does affect the oscillatory center in the brain. Instead of taking the normal 200 ms to reset (discharge) back to the zero baseline, the light signal causes an immediate reset. As a result, the flash following the next flash occurs earlier by an amount of time equal to the time remaining for the normal reset.

Based on this single process of photic resetting of the neural oscillator in the brain, self-organizing synchronized flashing occurs. Each firefly acts as an intrinsic oscillator flashing at its own characteristic frequency. But in addition,

each firefly interacts with its neighbors. Each firefly is coupled to its neighbors through light perceived from other flashing fireflies; the sight of a neighbor's flash shifts the individual's rhythm.

### A Critical View of the Model

This model for synchronization seems consistent with experimental data showing how a single male firefly's flashing frequency rapidly becomes entrained to an artificial pacing flash. Data also show that a group of fireflies exhibits remarkable flash synchrony, so much so that recordings of light emission from a single firefly and a group of fireflies is practically indistinguishable (see figure on page 78 of Buck and Buck 1976). However, a crucial aspect of the model is missing. Although we now can understand how an artificial pacing signal can entrain a single firefly, we have not been shown that this mechanism is sufficient to explain what happens when a *group* of fireflies, all flashing out of phase, is brought together. The collective situation is far more complicated. Many flashes are emitted concurrently and there are reciprocal effects of one firefly on another. We must also consider the differing intensities of the flashes, a function of light intensity falling off inversely with the square of the distance from the source. In nature, during the incoherent initial stages of the process, each firefly sees a barrage of conflicting light emissions. Furthermore, each firefly has its own slightly different intrinsic rhythm which is somewhat variable from flash to flash. The problem is one of extrapolating the results of experiments in which a single artificial pacer flashing in a precise rhythm entrains a single firefly to the more general situation of a population of real fireflies in the field.

The problem of synchronization among a population of oscillators requires a more rigorous theoretical and mathematical approach. The problem has received considerable attention partly because of its intrinsic mathematical interest and partly because of the importance and ubiquity of such processes in biology. Some of the recent work (Miroollo and Strogatz 1990; Strogatz et al. 1992; Strogatz and Stewart 1993) is inspired by the medically important subject of the origin of synchronicity in the heart's natural pacemaker, a cluster of about 10,000 cells termed the *sinoatrial node* (Peskin 1975; Jalife 1984; Michaels et al. 1987). Miroollo and Strogatz (1990) have analyzed mathematically a population of oscillators interacting through a mechanism similar to that found in *Photinus pyralis* (See below: Flash Synchronization in Other Firefly Species.) Their model, however, makes a number of critical simplifying assumptions in the interest of mathematical tractability. They assume that all oscillators in the population are *identical*, that each oscillator is sensitive to incoming light impulses throughout its charging cycle, and that the increase in excitation is concave downward as in the electrical analog (Figure 10.5), rather than linear as assumed by Buck and Buck (1976) and Buck et al. (1981) (see Figure 10.4).

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Under these assumptions, a population will become synchronized under almost all initial conditions. The system synchronizes rather slowly at first, but then builds up more rapidly (Mirollo and Strogatz 1990). Although the assumption of identical oscillators makes the problem more tractable mathematically, we would really like to know the properties of a system of realistic firefly oscillators, with similar but not identical intrinsic flash frequencies.

Strogatz and Stewart (1993) discuss this more complicated situation in a recent article in *Scientific American*. (For a more technical presentation, see Strogatz et al. 1992 and Ermentrout 1991.) Their main conclusion is as follows: "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." (Strogatz and Stewart 1993, p.107). As the variation in frequencies of individual oscillators falls below a critical threshold, a portion of the system suddenly synchronizes. The combined signal of this synchronization cluster stands out above the background noise of random flashes and "captures" additional oscillators, further amplifying its collective signal. This infectious positive feedback results in an epidemic of synchrony.

Strogatz and Stewart's conclusions provide an excellent commentary on the relationship between self-organization and natural selection. (See Misconception #1 in Chapter 7.) If flash synchronization has adaptive value, as we assume it does, then natural selection should result in fireflies with the necessary strength of coupling among individual fireflies to achieve flash synchrony. By acting on the physiological "rules" of interaction among individual fireflies, evolution has determined the final structure of the self-organized process.

### ***Flash Synchronization in Other Firefly Species***

Based on comparative studies (Hanson 1978) (see also the review by Buck 1988) it appears that several different mechanisms for self-organized flash synchrony have evolved. Studies suggest that *Photinus pyralis*, for example, has a different pacemaker resetting mechanism than *Pteroptyx cribellata*. Instead of causing an immediate resetting of the pacemaker to its baseline level, a light signal appears to advance the flash by raising excitation to the threshold triggering level. A number of other species also appear to utilize flash-advance synchronization rather than the phase-delay synchronization seen in *Pteroptyx cribellata* (Buck 1988). In a detailed study by (Hanson 1978), *Luciola pupilla* (unlike *Pteroptyx cribellata*) required many cycles of an imposed light signal to become synchronized. This slow entrainment suggests that an external light signal does not advance the pacemaker of *Luciola* immediately to threshold but only raises the excitation level of the pacemaker partially towards a triggering level. Regardless of the details of each mechanism, the important feature is

that fireflies are optically coupled through their ability to reset their neighbor's pacemaker.

Even though an enormous amount of sophisticated neural circuitry and neurophysiology undoubtedly underly the firefly's central nervous system oscillator and lantern, this self-organizing mechanism is conceptually simple and can explain all the observed features of flash synchronization. With the pieces of this fascinating mystery laid out in front of us, and with the advantage of hindsight, perhaps the synchronization mechanism now appears rather trivial. This is often the case with mechanisms based on self-organization.

Even with the mystery largely solved, many unknown details still remain. For example, the actual timer in the brain has never been isolated. Bagnoli et al. (1976), on the basis of their surgical ablation and electrical stimulation studies conclude that "(a) the photomotor neurons of the firefly's brain are located in the deep protocerebral neuropile; (b) their rhythmic activity is the result of the interaction with an oscillator located in the optic lobes, possibly in the lobula." Isolating the firefly flash-control center and characterizing the presumed neural network responsible for its oscillatory properties will prove to be a formidable task. A comparable oscillatory system that has been well studied is the rhythmic bursting neuron of the sea mollusk, *Aplysia* (Pinsker 1977a, b). But as Buck et al. (1981) remark, "the firefly brain is not much larger than the largest *Aplysia* neuron." The difficulties of doing studies at the single-cell level within such a tiny brain make it unlikely that the system will be analyzed in detail, at least within the foreseeable future.

### Flash Synchronization as a Self-Organizing Process

In what ways is the mechanism of flash synchronization a self-organizing process? A key feature of the system is that the pattern emerges as a result of multiple interactions among the fireflies. Synchronization is not imposed by any influence outside the system, such as a leader, a supervisor or external physical cue. Synchronization arises from within, based on local interactions among fireflies that follow the simple rule: A neighbor's light emission shifts the timing of one's own light emission (Figure 10.6). The rule does not directly code for synchrony, as with a conductor's baton beating time in a predetermined cadence, yet this simple phase-shifting rule is sufficient to coordinate the rhythm of the group.

As discussed previously, the ability of a local group of synchronized individuals to capture additional oscillators is a form of positive feedback, a common feature of self-organizing systems. Negative feedback is also present, in the form of a physiological constraint that keeps positive feedback from self-perpetuating out of control: A firefly can be stimulated to flash only within a fixed range of frequencies. Although its normal period is about 1000 ms, it can be paced only at a rhythm of between 800 and 1600 ms. Within a certain range

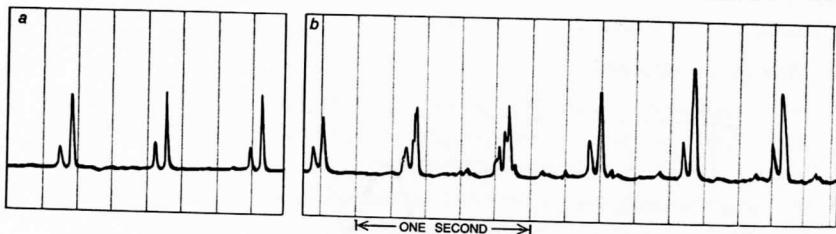


Figure 10.6 Solo and chorus flashing of *Pteroptyx malaccae* males are compared: a single firefly emits a two peaked flash every 500 ms in a pattern virtually duplicated by synchronized fireflies. (From Buck and Buck 1976)

the system is refractory, providing negative feedback that brakes and shapes the positive feedback, helping to create a precise temporal pattern.

How might this system have evolved? One possibility is that natural selection favored the basic oscillatory flash apparatus of male fireflies as a mating adaptation because it was inherently a self-organizing mechanism for group synchronization based on individual pacemaker reactions to light signals from local neighbors. A collective pattern emerges using an optical coupling mechanism to provide networks of local interactions among fireflies.

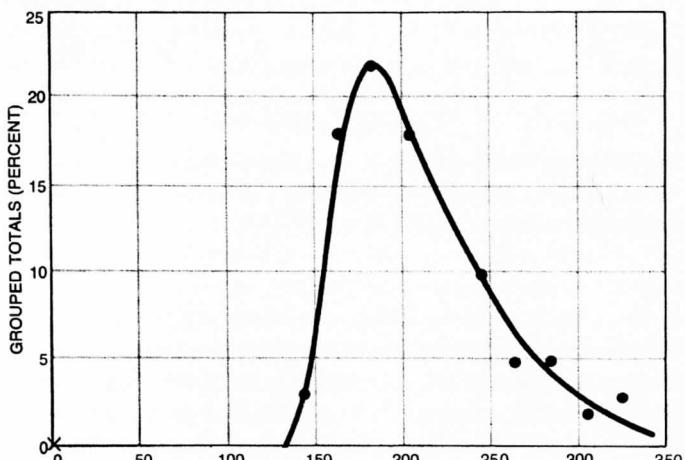
### Box 10.1 Demonstration of Synchronization in Humans

Buck and Buck (1976) describe two simple demonstrations of synchronized activity in humans that can be performed in the classroom. The first demonstration shows that synchronized finger-tapping in human subjects does not occur as a result of individuals reacting to one another in a follow-the-leader manner. The second demonstration suggests that the actual mechanism involves individuals listening to the tapping rhythm and adjusting their own frequency to the collective rhythm.

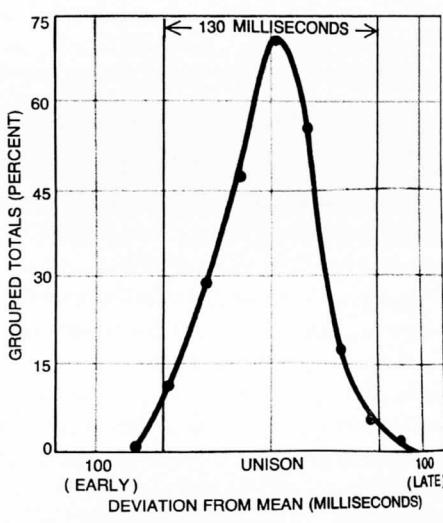
*Demonstration 1:* The person conducting the demonstration instructs participants to close their eyes and hold a coin in their fingers. Participants wait for the instructor to tap his or her coin on the tabletop. Participants then tap their coins as quickly as possible. This is a test of reaction time performed as a group. As the graph in Figure 10.7a shows, very few participants can respond in less than 150 ms.

*Demonstration 2:* The instructor gives the participants these simple instructions: "Close your eyes and start tapping your coin on the tabletop in a comfortable, regular rhythm trying to synchronize with your

*Box 10.1 continued*



(a)



(b)

Figure 10.7 Reaction-lag time and synchronized activity demonstrated with human subjects. (From Buck and Buck 1976)

*Box 10.1 continued*

neighbors.” As Buck and Buck point out, with these instructions an audience of several hundred people will synchronize within a few cycles, usually at a frequency of 2 to 3 taps/s. More remarkably, the time interval between the first taps and the last taps in a volley are generally less than 130 ms (Figure 10.7b), shorter than the reaction time just demonstrated!

What is the mechanism for synchrony in demonstration 2? As the reaction time data confirm, the participants cannot be waiting to hear a neighbor’s tap before initiating their own tap. The explanation offered by Buck and Buck (1976) is that each person must have “measured the passage of time up to the instant when it was necessary to initiate the neural message that caused his fingers to move in synchrony with the fingers of all the other participants.” Thus, based on the subject’s perception of the rhythm of the taps, the subject anticipates the time to the next tap and factors in the motor delay between the brain and finger. This is the “anticipatory time-measuring” or “sense of rhythm” explanation earlier suggested by Buck and Buck (1968) for the mechanism of rhythmic synchronous flashing of fireflies. We should now be better able to appreciate the difference between the mechanism of synchrony used by humans in finger tapping and the mechanism of firefly flash synchronization. The cognitive processes that humans use to synchronize finger tapping are not those used by fireflies. Among fireflies, the perception of a neighbor’s photic signal automatically resets an oscillator in the firefly’s brain and triggers a flash. Among humans, there is no oscillator for an arbitrary tapping rhythm. Humans do indeed have a sense of rhythm, they can measure time intervals and anticipate when to initiate a motor message to tap.

With a means for recording the sounds of subjects as they tap, and a device for displaying the recording, it is possible to generate graphs similar to those in Figure 10.7. This can be done with most personal computers using a microphone and the appropriate sound analysis software.

**Box 10.2 Temporal Patterns in Other Organisms**

The natural world abounds in examples of collective temporal patterns other than synchronized rhythmic activity in insects. The mechanisms for many of these examples are unknown, but we expect that many eventually will be shown to involve self-organizing mechanisms.

*Box 10.2 continued*

Three categories of synchronization and rhythmicity may be distinguished (Table 10.1). The simplest category (I in Table 10.1) involves a burst of synchronized activity based partly on mutual, positive feedback interactions. For example, many sea birds that nest in large colonies stimulate each other to breed earlier and within a shorter period of time compared to members of small colonies. Termed the *Fraser Darling effect* (Darling 1938) in herring gulls, for example, this results in higher survival of the chicks since the percentage mortality (due largely to predation) of offspring per unit time is relatively constant. The adaptive significance of such a collective phenomenon is obvious. It is the temporal equivalent of Hamilton's so-called selfish herd geometry (Hamilton 1971). In this situation a mother bird gains a fitness advantage by hiding her offspring from predation in a large crowd of conspecifics within a narrow window of time. The density-dependence of the effect indicates that it does not result solely from an external environmental influence, such as the change in day length, but suggests the additional role of a self-organized mechanism based on behavioral and physiological interactions among group members.

Another, similar example is the synchronous release of spermatozoa by marine sponges (Reiswig 1970). In this case, the spread of activity to nearby colonies when they come into contact with sperm-laden water suggests some form of communication, possibly chemical, among individuals rather than the sole influence of an environmental trigger. Many other examples in this category are known, such as synchrony of vocalizations in frog choruses or bird leks. Only a few examples are listed in the table.

A second category of synchronized rhythms (II in Table 10.1) involves activities for which individuals show no intrinsic rhythmicity but are rhythmic as a group. An example is *Leptothorax* ants, in which colonies exhibit synchronous rhythmic bursts of activity approximately every 20 min (Franks and Bryant 1987; Franks et al. 1990; Cole and Trampus 1991, 1998; Goss and Deneubourg 1988). Another example is pancreatic beta-cells that secrete insulin. These cells are electrically coupled by their gap junctions. In sufficiently large clusters, the cells exhibit regular electrical bursting activity whereas isolated cells show disorganized spiking activity (Sherman et al. 1988; Sherman and Rinzel 1991).

The third category (III in Table 10.1) involves rhythmic individual activity synchronized at the group level. Synchronization of flashing among fireflies is just one example. Others include the synchronized choruses of certain crickets, katydids, and cicadas; the synchronization of human fe-

*Box 10.2 continued*

**Table 10.1** Synchronized Rhythmic Activity (see Box 10.2 for an explanation of categories I, II, and III) among Groups of Organisms

*Box 10.2 continued*

**Table 10.1** Synchronized Rhythmic Activity (see Box 10.2 for an explanation of categories I, II, and III) among Groups of Organisms

Organism	Scientific Name	Process and Category	Coupling Mode	References
Hydrozoans (Many species)		Coordinated movements of zooids (I)	Mechanical, electrical	Mackie 1973
Tropical marine sponges	<i>Verongia archeri</i> , <i>Geodia</i> sp. <i>Neofibularia nolitangere</i>	Synchronized sperm release (I)	Unknown	Reiswig 1970
Red abalones	<i>Haliotis rufescens</i>	Synchronized sperm and egg release (I)	Chemical (prostaglan- dins)	Morse 1993
Fiddler crab	<i>Uca annulipes</i>	Synchronized claw waving (I)	Visual	Gordon 1958; Backwell et al. 1998
Harvestmen	Family Phalangidae	Synchronized group movements <sup>a</sup> (I)	? Mechanical (tactile)	Newman 1917; Wheeler 1917
Spiders	<i>Anelosimus eximius</i> (Theridiidae)	Synchronized prey capture activity (II)	? Web vibrations	Krafft and Pasquet 1991
Ants	<i>Leptothorax</i> spp.	Synchronized activity cycles (II)	? Mechanical (tactile)	Franks and Bryant 1987; Franks et al. 1990; Cole 1991
	<i>Eciton burchelli</i> (army ants)	Periodic foraging activity (II)	?	Schneirla 1949, 1956; Gotwald 1995
	<i>Campanotus</i> spp. and others	Synchronized alarm drumming (I)	Substrate vibrations	Fuchs 1976a,b; Hölldobler and Wilson 1990
	<i>Messor pergandei</i> (harvester ants)	Periodic foraging activity (II)	Pheromone	Rissing and Wheeler 1976; Goss and Deneubourg 1989
Honey bees	<i>Apis mellifera</i>	Synchronized respiration (I)	Unknown	Moritz and Southwick 1992
Saharan silver ant	<i>Cataglyphis bombycinus</i>	Synchronized foraging activity (I)	Unknown	Wehner et al. 1992

*Box 10.2 continued*

**Table 10.1** *continued*

Organism	Scientific Name	Process and Category	Coupling Mode	References
Hornet	<i>Vespa orientalis</i>	Synchronized vibrations (III)	Mechanical	Barenholz-Paniry et al. 1988
Migratory locust	<i>Schistocerca gregaria</i> and others	Mass migrations (I)	Visual, ? chemical, tactile	Uvarov 1928
Fall webworm larvae	<i>Hyphantria cunea</i>	Synchronized group movements <sup>a</sup> (I)	? Mechanical (tactile)	McDermott 1916; Peairs 1917
Aphids	None given	Synchronized body movements while feeding <sup>a</sup> (I)	?	Tanner 1930
Termites	Unidentified Indian species	Synchronized chewing <sup>a</sup> (I)	?	Connor 1933
Firefly	<i>Pteroptyx</i> spp., <i>Photinus</i> spp. <i>Luciola</i> spp., others	Synchronized flashing (III)	Photic (optical)	Buck 1988 and references therein
Snowy tree cricket	<i>Oecanthus fultoni</i>	Synchronized chirping (III)	Acoustic	Walker 1969
Katydid	<i>Mecopoda</i> sp., <i>Neoconocephalus spiza</i>	Synchronized chirping (III)	Acoustic	Sismondo 1990; Greenfield and Roizen 1993
Periodical cicada	<i>Magicicada</i> spp.	Synchronized chirping (III)	Acoustic	Alexander 1967, 1975
Springtails (collembola)	<i>Hypogastrura</i> spp.	Synchronized moulting (III)	? Olfactory (pheromonal)	Leinaas 1983
Herring gulls, & other colonial sea birds	<i>Larus</i> spp. and others	Synchronized breeding (I)	Unknown	Darling 1938
Human females	<i>Homo sapiens</i>	Synchronized menstrual cycles (III)	? Olfactory (pheromonal)	McClintock 1971; Russell et al. 1980

<sup>a</sup>Observations not well documented in the literature.

*Box 10.2 continued*

male menstrual cycles; and the synchronized molting of springtails. All probably involve interactions among coupled oscillators. Many other well-documented examples of this type of mutual synchronization in biological systems not listed in the table include those in which individual units are single cells, such as sinoatrial-node pacemaker cells (Jalife 1984; Michaels et al. 1987); *Saccharomyces* yeast cells undergoing glycolytic metabolism (Winfree 1980); the unicellular marine plant *Gonyaulax* with its circadian rhythm of bioluminescence (Winfree 1980, 1987); and the intensively studied example of oscillations in chemotactic cyclic AMP signals in the slime mold, *Dictyostelium*, described in Chapter 8.

Table 10.1 also lists examples of coordinated activity among groups of organisms that are not sufficiently documented to know whether the process is rhythmic and synchronized. These are the examples involving harvestmen, webworm larvae, aphids, ants, termites, and probably fall into the simplest category noted at the outset.

A type of mutual synchronization seen in honey bees (Southwick and Moritz 1987), deer mice (Crowley and Bovet 1980), and red wolf/coyote hybrids (Roper and Ryon 1977) was omitted from the table because the activities are circadian rhythms probably triggered largely by diurnal cues. They are of interest here, however, since experiments have shown them to be modulated by social interactions among group members.