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Mechanism of Rhythmic Synchronous Flashing of Fireflies

Fireflies of Southeast Asia may use anticipatory time-measuring in synchronizing their flashing.

John Buck and Elisabeth Buck

The Dutch physician Engelbert Kaempfer, after a voyage downriver from Bangkok to the sea in 1680, wrote, "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 . . . " (*1*). Since then more than 30 similar reports of oriental firefly displays have appeared (*2*), and it has been claimed that the concerted flashing continues "hour after hour each night for months" (*3*).

Synchronous flashing has commanded attention as a spectacle and in relation to its function (*4*). However, the greatest interest in the flashing has centered on mechanisms by which synchrony might be attained and maintained. The complexity of this problem is shown by the fact that, even excluding the suggestion that the phenomenon is due to twitching eyelids of the observer (*5*), several quite different explanations have been proposed. The possibility that the synchrony is an illusion (*6*) needs also to be kept in mind because of certain human perceptual limitations that will be mentioned later, and because of experimental evidence that the mind tends to read order into a display of randomly flashed lights (*7*). In view of the variety of puzzles associated with concerted flashing we are glad to be able to describe some observations and measurements made recently in Thailand (*8*). In comparing these data with previous reports we exclude all single-episode or irregularly repeated synchrony, whether occurring mysteriously (*9*) or evoked by a clearly identified cause such as an explosion (*10*). We also exclude as trivial all rhythmically repeated mass flashing which is driven or cued from outside the participating congregation (*11*). However, because of the basic physiological interest of synchronization we include in our analysis related behavior in the only animals beside fireflies that seem able to perform endogenous mass acts of rhythmic synchronism—man and certain sound-producing insects (*12*).

Types of Synchronism

Mass rhythmic behavior implies alternation of times in which the individual acts are relatively frequent ("episodes") with times in which they are infrequent or absent. In the type of display seen in Thailand all the flashing may be concentrated within an interval shorter than 20 percent of each cycle length (see below) and is readily recognizable as synchronism. However, even a display in which the individual acts had a sinusoidal frequency distribution would be strikingly different from randomness and might well be construed as "synchronous." It is clear, therefore, that biological synchrony can only be defined in arbitrary quantitative terms. Similarly, a given range or span of coincidence with the communal flash can be attained by a variety of basically different processes. Hence, to indicate the types of information needed to analyze synchronization we outline below some mechanisms that have been observed or proposed in various organisms.

Inertial synchrony. In this mechanism the individual rhythms, after being put into synchrony by a single nonrecurrent triggering stimulus, continue in step because their natural periods are approximately equal. Such synchrony can occur, for example, in a population of microorganisms after an inhibitor of cell division has been washed out (*13*). It also occurs between runners during the first few strides after the starting gun. In fireflies the rhythmic flashing of individual flying males is well known (*14, 15*), and it has been suggested by several observers that some rare or accidental event, such as the sudden darkness preceding a late afternoon thunderstorm or the ending of a shower of rain (*16*), might set off the whole population in step. Transient synchronous flashing seen after an inhibitory sweep of bright artificial light (*17*) suggests that lightning could have a similar effect. Such inertial cycling might conceivably apply to certain rare and brief displays reported in American fireflies (*2*), but it is completely inadequate to account for the sustained nightly synchrony in oriental concerts. Even if one assumes that the start of flashing is triggered by, say, an exquisite sensitivity

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to a particular intensity of ambient illumination (*16, 18, 19*) or to a circadian "clock" (*19, 20*), a congregation that flashed at a frequency of more than 6000 per hour (*21, 22*), and with the degree of individual cycle variability observed in biological rhythms, would soon be hopelessly out of step unless a congregational entrainment mechanism were operating continuously.

Driven synchrony. This mechanism involves simultaneous responses to a rhythmic stimulus by an otherwise inactive congregation. In many American fireflies, several perched females may respond simultaneously to flashes of a male or of an artificial light (*23*). However, the displays are small-scale and temporary and involve no intrinsic rhythm in the responders. The mechanism seems inapplicable to concerts involving only males, as is reported for most sightings in which the sex of the flashers was ascertained, since males usually flash spontaneously.

Alternation synchrony. In certain species of grasshoppers a pair with similar periods may by accident chirp synchronously for a few cycles, but normally if individual A chirps shortly before the expected time of B's chirp it delays B's chirp by a little less than one cycle. When B's chirp then does occur it correspondingly delays A's next chirp. The result is that the frequency of chirping of each hopper is approximately halved, and the two sing alternately at an overall frequency slightly faster than that of a single male singing alone (*24*). Between members of a pair, therefore, this mechanism promotes alternate chirping and minimizes synchrony. However, "When a large number . . . are close enough together . . . to react to each other, the result is a sort of synchronized alternation in which each male is in alternation with the neighbor he hears most clearly and also in synchrony with other males alternating with his neighbor. The result is a great pulsing sound. . . ." (*25*). Analogous behavior in fireflies has not been suggested previously, but it can be tested easily by seeing whether each firefly participates in each mass flash.

Paced synchrony. According to this proposal all the fireflies normally flash rhythmically, with nearly the same period, but they can be triggered prematurely by sight of a neighbor's flash (*26*). The pacemaker is not qualitatively different from the other fireflies, as in driven synchrony, but can be either an individual with slightly faster flashing rhythm than any other or simply whichever firefly happens to flash next after a mass coruscation (*27*). Because of limited visibility it seems likely that several relays would be required to excite a large swarm and that the luminescence would spread as a wave as A triggered group B, B triggered C, and so on. Wave synchrony has been described in a few American reports (*28*) and has been induced experimentally on a small scale (*2, 29*), but it is seldom mentioned in accounts of oriental displays. However, with short response latency, relatively long flash duration, changing pacemaker individuals, and a dense population, it might be very difficult to detect local asynchronies.

Anticipatory synchrony. In most oriental firefly synchrony, consonance was reported to be "perfect," and neither driver nor pacemaker was seen. Such displays have been ascribed to "sense of rhythm," "an organic law of rhythmic appreciation," "sympathetic telepathy," and similar nonexplanations with anthroponomical overtones.

Among "sense of rhythm" behaviors in man the rhythmic synchronous handclapping that may break out spontaneously at sporting events, though not involving any preexisting rhythm in the participants, has some resemblances to firefly synchrony. Even in marching and in orchestral playing, ostensibly led activities, the participants seem to be modulating their individual endogenous pacemakers at least partly via a consensus or blend of multiple cues from the community. Though it is well known that players do not follow the conductor's downbeat but anticipate it, timing their rhythm to achieve exact coincidence, it could be argued that each individual is still making a direct and immediate response to the conductor's prior upbeat movement or some earlier phase of the beat cycle. However, the ability of groups of experienced players or singers to maintain excellent ensemble for a surprisingly long time with eyes closed or in the dark shows that they can synchronize from acoustic feedback alone, and the precision of the synchrony seems incompatible with waiting for a direct cue from a lead voice or instrument.

We have not found any published analysis of "sense of rhythm" synchronization within groups of animals, but the presumably similar process in which a human subject taps a key in time with rhythmic external sonic signals or light flashes has been studied extensively. Two findings may relate to the problem of mass endogenous synchrony. First, the subject, though believing himself to be in exact synchrony with the external signal, may actually be tapping consistently early or late (*30–32*). Second, in subjects who lag the signal, the delay between signal and tap is (for frequencies higher than one tap per second) much less than the physiological reaction time (*31*). This fact, plus the fact that most subjects actually lead the signal, shows that "the reaction is not to the stimulus with which it synchronizes but to the series of stimuli which precede it at relatively large intervals" (*30*). This retrospective aspect of "sense of rhythm" synchrony distinguishes it fundamentally from all other mechanisms for mutual entrainment (*33*).

By four-channel recordings from groups of four subjects instructed simply to tap their keys together we have confirmed the expectation that human beings use anticipation when synchronizing with each other as well as when they synchronize with a fixed external rhythm. Such quartets soon settle into a self-chosen rhythm, usually between two and three taps per second, in which the average span between the earliest and latest taps in each episode is less than 50 milliseconds (msec) (*34*). Since the minimum physiological latency for a finger response to sharp isolated sounds is usually at least 120 msec, even with practice (*35*), it is clear that none of the subjects can be tapping in response to a cue received in the same episode (*36*). Rather, some cue in the preceding cycle, or cycles, is being used to predict the proper time to tap in order to attain synchrony.

Firefly Synchrony in Thailand

Oriental synchronous flashing has been reported principally from mangrove trees along brackish rivers. Professor Kloom Vajropala of Chulalongkorn University and Dr. Boonsong Lekagul of the Association for the Conservation of Wildlife of Thailand kindly took us to stretches of the great Chao Phraya (Meinam) river south of Bangkok. This is the region where Kaempfer made his observations nearly 300 years ago, and it has remained the classic locality for synchronous displays. Since the tangled mangroves grow in deep mud, it is generally impracticable to approach them on foot. At high tide, however, the trunks are submerged, and it is possible to nose a boat in among the branches and observe the fireflies at close quarters. For this purpose the local water taxi (*rua-hang-yao*), a shallow-draft, canoe-like craft, seating four to six in tandem, served admirably. Some of the professional boatman, incidentally, are aware of the association between fireflies (*hing hoi*) and the mangrove *Sonneratia caseolaris (ton lampoo*). This association is not obligatory (*4*).

From the boat we were able to make photometer records of the flashing of individual fireflies and parts of the swarms (*37*), and to bag large numbers of specimens for later work. In addition, on one occasion Dr. Boonsong succeeded in taking motion pictures of the flashing for us (*38*).

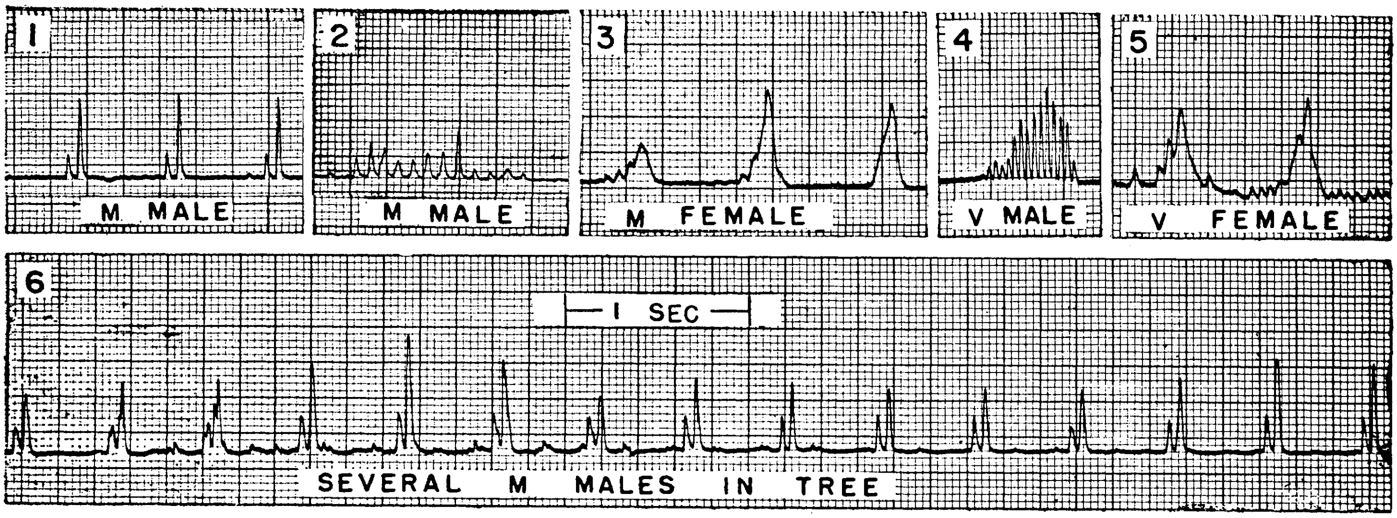
In Thailand we were able on several occasions to confirm earlier observers: Insofar as the naked eye is concerned, the fireflies do flash synchronously, and in spectacular fashion. Firefly trees were not common in regions we visited, nor were all swarms flashing in concert, but the synchronous displays stood out sharply. As we drew in toward the dark shoreline, pale nebulous patches began to resolve, at a distance of 30 meters or so, into bushes or trees spangled with hundreds of tiny lights pulsing steadily in a rapid rhythm of about two per second. Each time we saw this hurrying, soundless, hypnotic, enduring performance it impressed us anew as uniquely different from any behavior we had ever seen.

The individual fireflies produced very short and sharp flashes, between which the light extinguished completely. The insects were sitting motionless, mostly on the upper surfaces of leaves and usually distributed rather uniformly through the foliage. A given spatial pattern of flashes in a tree usually persisted for many consecutive episodes, and we confirmed directly that given individuals were each participating in each communal flash. However, the pattern was not invariable, since fireflies did occasionally fly to or out of the swarm or stop flashing for a period. On rare occasions a hovering firefly was seen keeping pace with the swarm flash at two per second, but ordinarily the flying individuals flashed in a fast twinkle (see below).

Sometimes we had the vague impression that part of a swarm had gotten slightly out of phase with the rest, creating a local swirling or wavelike effect, but those periods were so ephemeral that no clear idea of the aberration could be formed before full synchrony was restored. Possibly similar effects within and between trees have been described from Thailand (*22*) and New Britain (*39*).

In a given tree the vast majority of flashes were in phase with each other, and apparently exactly so, but there were also occasional flashes which seemed qualitatively different and unrelated to the prime rhythm. These emissions included (i) a rapid continuous flicker or twinkle seen occasionally in walking individuals but given usually by single fireflies in flight to, from, or within a tree, and also by individuals forced to fly when we beat the branches with our insect nets; (ii) occasional single fixed-position flashes much brighter and longer than those of the dominant (synchronized) fireflies; (iii) single dim flashes at irregular intervals from individuals apparently at rest. We emphasize that without deliberate attention these asynchronies were not noticeable in comparison with the overwhelming effect of the concerted display.

The asynchronies were traced to the presence in the trees of two firefly species, both of the genus *Pteroptyx*. The synchronously flashing specimens were found to be perching males of *P. malaccae*. Their flashes, which look single except when seen from only a few centimeters away, are really double (Fig. 1), each subflash lasting 40 msec and the two being about 60 msec apart peak-to-peak. The rapid twinkling in flight was also due to *P. malaccae* males: In our only photometric record (Fig. 2), flash frequency was 12 per second. Excited captive males at rest also flicker, but more irregularly. The long bright flashes in the trees were given by



Figs. 1–6. Photometer records of flashing in *Pteroptyx*. Reading from left to right; time scale equals 200 msec between major ordinate lines; vertical scale (light intensity) is arbitrary and not comparable from record to record. Fig. 1. Three successive flashes in a series from one of a synchronously flashing pair of *Pteroptyx malaccae* males, the other of which was shielded from the photometer. Recorded indoors. Flashing cycle length is about 560 msec (28°C). Fig. 2. Twinkle or flicker of *Pteroptyx malaccae* male in flight indoors. Fig. 3. Three flashes of captive *Pteroptyx malaccae* female. Fig. 4. Flash of *Pteroptyx valida* male at rest. (Recorded indoors to avoid *Pteroptyx malaccae* flashes in background of field records.) Fig. 5. Two flashes and glow of captive *Pteroptyx valida* female. Fig. 6. Fifteen consecutive mass flashes of undetermined number of *Pteroptyx malaccae* males flashing synchronously in bush.

males of a larger species, *P. valida*. The photometer shows that these are not single emissions but flickers of very high frequency (Fig. 4). The flashes of the females of the two species (Figs. 3 and 5) are rather similar in contour and are thought to account for the irregularly timed dim flashes in the trees (*40*). Counts of samples from four trees totaled: *P. malaccae* males, 285; *P. malaccae* females, 121; *P. valida* males, 25; *P. valida* females, 7 (*41*). All subsequent mentions of *"Pteroptyx"* in this paper refer to males of *P. malaccae.*

Regularity of Individual Flashing Rhythm

In the series of 22 successive flashes from which Fig. 1 was extracted the mean cycle length (main peak to main peak) was 557.3 ± 2.5 (standard deviation) msec. This implies that more than 95 percent of all flash cycles measured off by that individual would fall within ± 5 msec of the mean period. To get an idea of how the flashing of *Pteroptyx* compares in regularity with other conspicuously cyclic short-period biological activities, we computed coefficients of variation (*V*) for several diverse rhythms, *V* being a good comparative measure because it is independent of absolute cycle length. Roving males of the American firefly *Photinus pyralis* had *V* values of about 11 (*42*). The values of *V* for the chirping cycle lengths of the crickets *Oecanthus "niveus"* (=*fultoni*) and *Nemobius fasciatus tinnulus* were about 3 (*43*). Human heartbeat during various stages of sleep had *V* values ranging from 12 down to 1.5, with 3 to 4 being common (*44*). Human finger-tapping ranged from 7 down to 1.7, with 4 to 5 being typical (*45*). The frequencies of spontaneous firing of two free-running nonacoustic neurons in moth ears had *V* values of 5 and 2.7 (*46*). In the calling of the whippoorwill, familiar for its maddeningly persistent rhythm, *V* ranged from 7 to 3 with a mean of 4.5 (*47*). Therefore the flashing of entrained *Pteroptyx*, with *V* values ranging from 1.4 down to 0.6 (*48*), is only about a tenth as variable as the flashing of *Photinus pyralis* and seems to compare very favorably with the most regular of the other rhythms measured. Nevertheless, it is amply variable to preclude the possibility of prolonged inertial synchrony even between pairs of fireflies.

Degree of Synchrony

The best-coordinated swarm flashes seemed to us not to last appreciably longer than the flash of a single *Pteroptyx* male. Is such a judgment reliable? Nobody knows, because, even aside from subjective factors (*6*, *7*), nobody has tested human sequence-perception within a dispersed multitude of rapidly cycling point sources of short duration and low intensity. However, psychophysical data for "perceived motion" between spatially separate light sources plus the well-known decrease in flicker fusion frequency with increasing image distance from the fovea and decreasing source area and luminance (*49*) suggest that flashes in a swarm could be out of phase by perhaps as much as 50 msec and still appear simultaneous.

Figure 6 shows a typical photometric record from a synchronized swarm. This record resembles those from single fireflies (Fig. 1) except for slightly greater variability (*V* = 1.9), slight increase in duration of many of the flashes, and small shoulders on rise or decay phase of some; for example, flashes 2, 3, 4, 6, and 7. The maximum discrepancy in cycle coincidence in these single-trace integrative records was about 30 msec. The significance of this range in relation to precision of synchrony throughout the whole swarm clearly depends on how representative were the samples actually recorded. Many of the records were made under circumstances in which it appeared that 10 to 20 fireflies of equal brightness were within a distance ratio of 1.4 from the phototube (twofold intensity range). Concurrent cinema records made at comparable distances (see below) show up to a dozen flashes in one film frame. Hence, at face value, such records as Fig. 6 indicate that the congregation may depart from perfect synchrony by only about ± 15 msec from mean flash time. However, only two or three superimposed flashes can actually be resolved in the photometer records.

If we go to the opposite extreme and assume that each photometer record

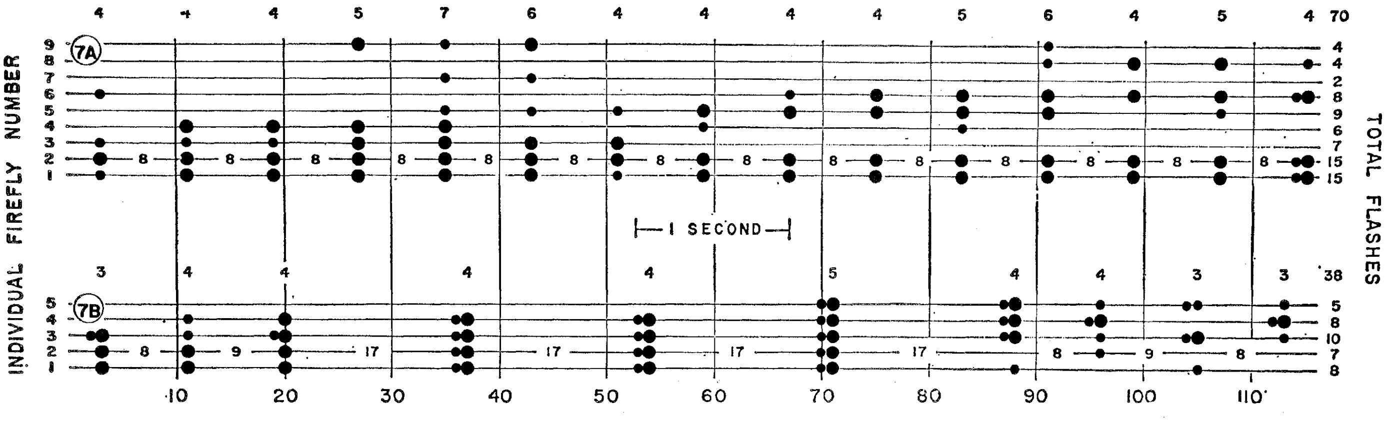


Fig. 7. Time distribution of flashes of *Pteroptyx malaccae* males in successive frames of 16-mm cinema film field record of synchronous flashing, exposed at nominal 16 frames per second. Sequence left to right. Each firefly numbered individually along left margin. The smaller and larger circles indicate "bright" and "dim" film images. Numbers along top are total flashes in each mass episode. The figure 8's between groups of flashes represent the number of frames in each successive cycle (seven blank plus one with flashes). (A) Seventy flashes of 9 fireflies in 113 consecutive frames. Same firefly swarm as in Fig. 7B, but recorded from greater distance (mean flash intensity much lower) and earlier in evening. (B) Thirty-eight flashes of 5 fireflies in 112 consecutive frames out of a series of 281. Four mass flashes skipped (see text).

of swarm flashing represents only a single individual, an indirect estimate of flash overlap can be derived from multiple records of different subpopulations within the congregation. Seven such records, averaging 32 consecutive flashes, were made from different points around a dense swarm in a small bush. The dominant rhythms ranged only from 556.8 ± 6.3 to 564.4 ± 6.0 msec, and the entire 223 cycles, considered as a single sample, had a mean duration of 559.8 ± 6.3 msec ($V = 1.1$). This implies that 95 percent of all flashes produced by the fireflies in question would fall within ± 13 msec of the mean period.

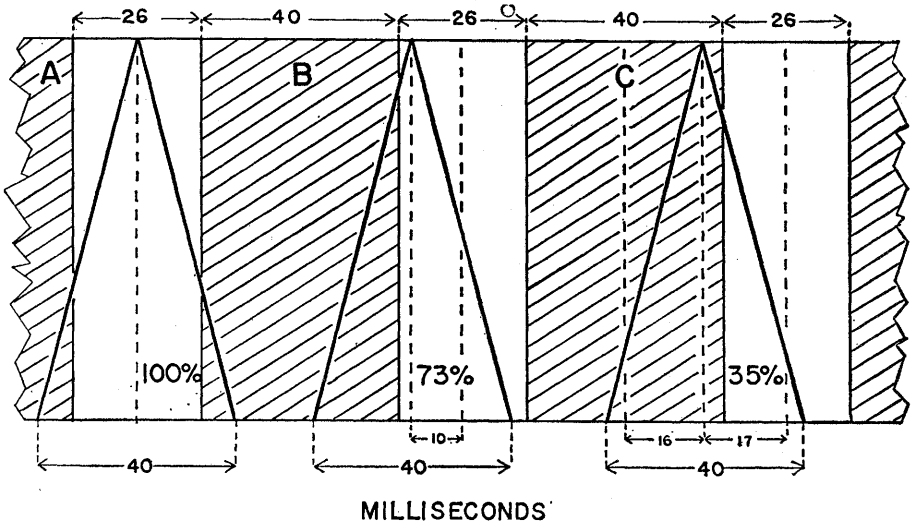


Fig. 8. Phase relations between camera shutter and flashing cycles. (A) Position of maximum light transmittance; flash indicated by triangle. (B) Flash peak displaced 10 msec from center of open shutter phase; 37 percent of potential light occluded. (C) Flash peak displaced 16 msec from center of closed-shutter phase; 65 percent of light occluded. The flash overlaps the open-shutter period 16 msec, which allows only 35 percent of the light to pass, not quite enough to expose the film detectably.

Cinematographic records from the same bush as the multiple photometer records permit an independent estimate of precision of synchrony. Ten series, ranging up to 34 consecutive flash cycles and involving 100 fireflies in 98 mass episodes in 958 film frames, were analyzed. Each frame was projected at a magnification of ×10 on finely ground glass in a Vanguard motion analyzer, and the position of each flash was plotted on an overlay of transparent plastic sheet. In this way it was possible to correct for any shift in field of view due to gentle rocking of the boat or unsteadiness of the hand-held camera and thus identify individual fireflies and follow their flashing in successive mass flashes throughout a film series. Two representative sequences, each spanning about 8 seconds, are diagramed in Fig. 7. The upper series was recorded from a distance of about 2 meters, the lower from about 1 meter.

Since the camera shutter cycle was in the range of 60 to 65 msec (for a nominal film speed of 16 frames per second) and the two peaks of the *Pteroptyx* flash are about 60 msec apart (Fig. 1), both peaks could potentially show in successive frames. In the series of flashes diagramed in Fig. 7A none of the minor (first) peaks was bright enough to be recorded, save for three barely visible spots in the last episode. In Fig. 7B many flashes in the series were amply bright, as shown by the numerous spot pairs in two consecutive frames.

The degree of flash coincidence in the cinema records is remarkable. Not one of the 70 individual flashes shown in Fig. 7A or the 38 flashes in Fig. 7B was out of phase with a mass flash by as much as a single camera shutter cycle. The regularity of the flashing rhythm is also noteworthy: In the series shown in Fig. 7A mass episodes occurred 8 frames apart "as if," to quote an old description of the flashing of ancestors of these same fireflies, "it proceeded from a machine of the most exact contrivance" (*50*). However, there seemed to be much variability in participation by different fireflies. Though two individuals contributed to all concerts, the others apparently missed from 6 to 13 flashes each. Such recorded skips are particularly striking in the 7B diagram, where four mass flashes are missing entirely, at approximately frames 28, 45, 62 and 79. As judged from the preceding and following parts of the record, four or five fireflies would have been expected to flash during each of these episodes.

We think that most of the apparently sporadic flashing and the variations in intensity of successive flashes of individual fireflies were due to slight phase differences between firefly and camera cycles. Thus, in Fig. 7A, though the flashes were comparatively dim because of distance, the shutter cycle apparently happened to be so nearly one-eighth of the congregational flash rhythm that two fireflies (Nos. 1 and 2) were recorded in all 15 mass flashes, and slightly more than half of the 135 flashes presumably produced by the nine fireflies during the period of photography overlapped open-shutter periods sufficiently to register on the film. In the much brighter series of Fig. 7B, made about an hour after Fig. 7A at slightly lower ambient temperature, the rhythm was slightly slower, so that the flashing cycle apparently coincided fully with an open-shutter period only at every other mass episode (every 17 frames). Consequently, most of the intervening mass flashes were occluded or much attenuated (*51*).

As judged from the concurrent time-calibrated photometer records, the camera was running at about 15.1 frames per second during the filming of the series in Fig. 7B. Since the shutter had a 143° open sector, this exposure frequency corresponds approximately to 66-msec shutter cycles of alternating 26-msec open periods and 40-msec closed periods. From these data, and from the double form of the *Pteroptyx* male's flash it is possible to deduce limits of asynchrony in mass flashing that are narrower than the limit of one shutter cycle apparent directly from the films.

If each subflash (Fig. 1) is considered to be an isosceles triangle with a 40-msec base (maximum subflash duration) and the open-shutter period is considered to be a rectangular window with a 26-msec base which moves laterally across the triangle, the percentage of the light from a flash that could pass the shutter at various phase differences between flash cycle and shutter cycle can be estimated graphically. For example, if a subflash peaks 10 msec before or after the midpoint of the open-shutter period only 73 percent as much light can go through as when the peak is exactly at the midpoint (Fig. 8, A and B).

For ten flashes in each of eight different photometer records the intensity of the major (second) subflash averaged 2.8 times that of the minor. In the flash series diagrammed in Fig. 7B the minor peaks, though only about 36 percent as intense as the corresponding major peaks (1 : 2.8), appear in nearly every instance in which the major peak is visible. This indicates that the major peak of any flash produced by these fireflies would have registered unless attenuated at least 64 percent. Thus the 17 to 20 flashes that presumably did occur at the times of the four mass skips, but were intercepted by the shutter, must have suffered more than 64 percent attenuation. However, flashes could not have peaked more than 16 msec from the center of a closed-shutter period without overlapping a contiguous open-shutter period sufficiently (more than 16 msec) to be visible in a frame just before or after the skip (Fig. 8C). Hence, the allowable deviation in flash peak position from either the center of an open-shutter period (to show) or from the center of a closed-shutter period (to be occluded) seems to be about 16 msec. This is less than 6 percent of mean cycle length. Insofar as these specific data go, this ± 16 msec coincidence range of synchrony between a dozen or so close neighbors would be a maximum, since most of the flashes in Fig. 7B are much brighter than necessary for the minor peak to be just visible when fully in phase with an open-shutter period. The maximum time range between flash peaks throughout a large, well-synchronized swarm of *Pteroptyx* is still uncertain, but it appears that ± 20 msec might be a fair estimate.

Process of Synchronization

Behavior of fireflies in our lodgings in Bangkok suggests how mass synchronism may be initiated and maintained in nature. Our experiments consisted of liberating males of *Pteroptyx malaccae* in groups of 50 into the nearly dark room, and were usually begun at about 11 p.m. after return from the river. When the fireflies first issued from the polyethylene bags into which they had been sorted, they flew upward in tight helical paths, twinkling at high frequency, and began bumping along the ceiling. We think that this behavior was due to unsuitability of the ceiling for perching and that had tree branches been available the insects would have come quickly to rest. However, the prolongation of flight did reveal the important fact that the fireflies at this stage were definitely attracted to one another. We saw and photographed numerous examples of one individual chasing another, or of two darting at each other from distances of a meter or more, sometimes with collisions in midair.

Eventually the insects began to alight on the walls. After some minutes of walking about, they settled down, and the rapid flickering light which is characteristic of flight changed to the steady cadence of two apparently single short flashes per second (Fig. 1). When thus at rest there seemed to be little or no tendency for these males to attract one another, and in fact it was rare for them to establish themselves closer together than 10 to 15 centimeters.

Then, as we watched, centers of synchrony began to build up slowly among the fireflies on the wall. In one area we would notice that a pair had begun to pulse in unison; in another part of the room a group of three would be flashing together, and so on. We never saw a synchronized group containing more than about a dozen fireflies but even such limited displays were extremely impressive, and the sparse and planar distribution of the insects made it easier to follow what seemed to occur as synchrony became established.

When two nearby fireflies began their sedentary flashing they appeared at first to flash independently. This is to say that although each was flashing rhythmically at a frequency close to two per second, the two rhythms did not seem to be coordinated. This apparent independence sometimes continued for half a minute or so, but eventually the flashes came into coincidence. From that instant the two fireflies continued to flash together in apparently perfect synchrony. Similarly, if a third male then alighted near the synchronously flashing pair, he seemed to flash independently until his rhythm coincided with theirs, then locked in.

It did not appear that the frequency of flashing of a synchronized group was different from that of the individual fireflies before entrainment, but separate recordings of each individual rhythm before, during, and after synchronization would be needed to settle this important point. The scope of entrainment was surprisingly short: individuals were observed to synchronize from about a meter apart but not from two.

We had observed in the field that if one cups his hands around a member of a synchronously flashing swarm, that individual becomes agitated, begins to twinkle, and soon flies off. In the "laboratory," we found that if an opaque screen was interposed between the members of an isolated synchronized pair on the wall, the consonance broke down immediately, and both insects began to move about nervously, flashing rapidly and irregularly. These observations confirm the expectation that synchronization involves visual feedback, but their principal importance is in suggesting that the flashing in unison requires continuous monitoring by each participating individual. There is no indication of a leader-follower relationship.

The initial positive phototaxis of these Thai fireflies and their ability to couple their individual flashing rhythms together thus provide a mechanism by which large, synchronously flashing arboreal swarms might build up from small-scale congregations stemming from chance propinquity. The point of most physiological interest, however, is the actual mechanism by which synchronization is attained.

Mechanism of Synchronization

Our records show that synchronous flashing in Thai fireflies is not an illusion.

Insofar as initiation of synchrony is concerned, we know that fireflies remain in the trees all day (*4*), but we never got to the river in time to see the buildup of synchrony under natural conditions. Our few indoor observations suggest that perching males that are initially flashing out of phase may take quite a number of cycles to get into step, after which a lock-in mechanism takes over. One possible explanation of the coming into step is chance coincidence due to variations in endogenous rhythmicity between and within individuals. Alternatively, the initial entrainment could involve progressive phase-shifting, operating either over the whole range of temporal separation or after the rhythms have drifted to within a certain degree of approximation.

In the maintenance of steady-state synchrony in *Pteroptyx* it is clear that the inertial, driven, and alternation mechanisms discussed in the introduction are excluded. The choice therefore seems to lie between the hypotheses of paced and anticipatory synchronization. In synchronization between members of a single pair of fireflies a critical distinction might be made on the basis (i) of whether the interval between flashes of the two tended either to exceed the physiological reaction time (pacemaking) or average considerably less (anticipation) (*52*), (ii) that it should not be possible to entrain an individual to a *slower* rhythm via the pacemaking mechanism, or (iii) that paced synchrony should be able to start at once whereas anticipatory or "sense of rhythm" synchrony might require a number of cycles for an out-of-phase individual to get into phase.

The potentially most important clue to the mechanism of synchronization among *Pteroptyx* males is the eye-lantern excitation delay or latency: This should correspond to the minimum period between flashes of two fireflies if the first flashed slightly faster than the second and acted as pacemaker. We were unable to measure this interval while we were in Thailand, for lack of electrophysiological apparatus. However, after this paper had been submitted, efforts of generous friends (*53*) provided us a few live *Pteroptyx* from Bangkok, from which, with the expert assistance of Dr. F. Hanson, we obtained the necessary data. We did not succeed in measuring directly the neural transit time between the eye and the (abdominal) lantern, but we did record latencies of 55 to 80 msec when stimulating electrically at various points in the ventral thorax and in the abdomen anterior to the lantern. When the electrodes were placed directly in luminous tissue, presumably exciting only peripheral nerve and adrenergic link (*54*), latency was still 42 to 50 msec. As judged from experiments on the American firefly *Photuris versicolor*, 15 to 25 additional milliseconds would be required for central nervous transmission from eye to lantern (*55*). Hence, in view of our photometric and cinematographic evidence that synchrony is exact to the order of ± 16 msec, it appears that the Thai fireflies cannot be entraining via visual responses in which each individual is cued in by seeing another flash or flashes in the same mass episode. Rather, their synchrony must depend on regulation with respect to a preceding mass flash.

Entraining fireflies to controllable rhythms of artificial light could provide an important test of the synchronizing mechanism. Inducing an individual to flash faster than his normal rhythm would not necessarily be decisive, at least if he then regularly lagged the signal, because the coupling might not be distinguishable from a direct sequential response; but a slowing of his preexisting rhythm could hardly occur via pacemaking. Because we had stupidly failed to recognize the importance of this question while in Thailand, we were forced to try the experiment on material available locally, the American firefly *Photinus pyralis* (*56*). This species is a far from ideal substitute for *Pteroptyx* since its period is much longer and it has roving rather than congregational habits (*15*), and particularly because it is active at too high an ambient light intensity to allow field recording. Also, sequence judgment by the observer is impeded by the fact that the *P. pyralis* flash lasts about 500 msec, so that even if the flash were delayed 150 msec after the signal, 150 msec being the latency to direct electrical stimulation of peripheral nerve in this species (*55*), a considerable flash overlap could occur. This species shows sequential (wave) synchrony when a group of males that has been flashing asynchronously in dim light is plunged into total darkness (*2*). However, when a male and female of *P. pyralis* are engaged in courtship signals, other males, originally out of phase, can readjust their rhythms so as to come into phase with the original male and thereafter flash synchronously with him (*57*).

By laying out on the ground a 2-meter circle of 20 miniature Christmas tree lamps flashed in rhythmic synchrony, we attempted to simulate a coterie of males clustering around a female (but without the female's response flash). At an ambient temperature of 30°C, at which the males flash with a mean period of about 4.2 seconds and females respond about 1.5 seconds after a male's flash, males cruising in the vicinity made two types of response when the lamps were flashed every 4 seconds. Individuals that had happened to flash about 1.5 seconds before the artificial flash oriented to the lamp-string and flew toward it stepwise for several flash cycles as if responding to the signals of a female. These pseudocourtships soon broke down because the lamp-string of course did not conform to the irregularities in flashing rhythm that occur normally, particularly in the late stages of courtship after the male has alighted and is making his way toward the female on foot. In the other type of response, males also approached the lamps but were flashing approximately in phase with them. These males did not go directly to a lamp and alight, as they do in responding to a female, but hovered over the string, reorienting and making short flights after each flash as if looking for an answering female's flash. This entrainment continued for a dozen or so episodes in some instances.

Entrainment to lamps could not be maintained long enough to test the same individual males at two cycle lengths, but males from the general population were able to get into approximate synchrony with lamp cycles of 3.0 and 5.0 seconds. With the 3-second signal, flashing appeared to be triggered by the lamp flash, as in the "paced" mechanism (*26*). The groups of males responding to the longer-than-normal cycle (5 seconds) often flashed slightly ahead of the signal, but their continuing duplication of the lamp cycle indicates ability to slow their endogenous rhythm and couple to the external signal (*58*).

The expectation that paced synchrony could reach phase coincidence in one step, whereas anticipatory coupling might require several cycles of phase-shifting, is based on the fact that the latency of each directly triggered response is independent of the preceding episode whereas anticipatory phasing depends on the relative temporal positions of two or more events in the preceding episode or episodes. This distinction is well shown, for example, by a human subject who is tapping synchronously with an external sound at two taps per second when signal frequency is suddenly increased to three per second. He is "caught" very late, makes a sudden and large shortening of his tap cycle, and then, having achieved approximate equality of rhythm with the signal (though lagging markedly), gradually shifts phase back to his original temporal position in advance of the signal by marking off a succession of tap cycles slightly shorter than the signal cycle (*34*). In other words, a considerable phase shift can be produced with only trivial shortening of the tap cycle because the successive differences are cumulative. What appears to be a

Table 1. Theoretical and observed mechanisms of synchronization. +, Present; —, absent; +(?), not fully measured.

Characteristic	Pacing	Anticipation	Cricket chirping	Human finger-tapping	Firefly flashing
Coincidence span $<$ reaction time	—	+	+(?)	+	+
Can lead external rhythm	—	+	+	+	+
Entrainable to slower rhythm	—	+	+	+	+
Phase shift cumulative	—	+	+(?)	+	+(?)

very similar phase shifting in the cricket *Oecanthus fultoni* is seen in a record in which an individual chirping 190 per minute was exposed to a recorded chirp series at 166 per minute: Cycle length was increased about 13 percent in one step, and then in seven additional cycles the phase lead between the entrained chirp and signal chirp was reduced progressively from about 100 msec to about 30 (*33*). A similar mechanism might explain how the Thai fireflies on the wall reached the lock-in point after each had independently adopted the stable rhythm of two flashes per second.

The evidence relating to the mechanism of synchronization in *Pteroptyx* is summarized in Table 1. The latency and entrainment data appear to rule out the pacemaker theory. If extrapolation from one insect to another, and from one anticipator to another, be allowed, an anticipatory mechanism appears to be favored.

If *Pteroptyx* synchronizes via the anticipatory type of phase-shifting used by human beings and probably by *Oecanthus fultoni*, each male must be able to distinguish the relative order of occurrence of his flash and that (those) of his influential neighbor (neighbors) and then to shorten or lengthen his next cycle according to whether he lagged or led, respectively, the other flash (flashes) (*59*). He needs, in other words, a "sequence discriminator" coupled to a device for modulating his endogenous pacemaker. It would be premature to propose any specific model for this machinery, but it is possible to guess that the firefly nervous system would be as capable of the necessary information-processing as that of a tree cricket (*33*) or weevil (*60*). Insofar as time-measuring goes, an ability to reproduce intervals of up to several thousand milliseconds is clearly shown not only by the endogenous ryhthms of spontaneous flashing by males of many species but by the fixed-length triggered response delays of females of courting species, delays that are usually far longer than the respective minimum physiological latencies. Many fireflies also have the ability to subdivide major intervals into fixed fractions (that is, to measure off several unequal intervals in sequence), as in flash patterns involving complex rhythmic "phrases" (*17, 61*). Ability to modify or inhibit the flashing rhythm is shown by males of many species while flying around obstacles or in the late stages of courtship, and, in a still more "voluntary" way, by the imitation of flash patterns of other species practiced by the predatory female of the American firefly *Photuris* (*62*).

Summary

In Thailand, male *Pteroptyx malaccae* fireflies, congregated in trees, flash in rhythmic synchrony with a period of about 560 ± 6 msec (at 28°C). Photometric and cinematographic records indicate that the range of flash coincidence is of the order of ± 20 msec. This interval is considerably shorter than the minimum eye-lantern response latency and suggests that the *Pteroptyx* synchrony is regulated by central nervous feedback from preceding activity cycles, as in the human "sense of rhythm," rather than by direct contemporaneous response to the flashes of other individuals. Observations on the development of synchrony among Thai fireflies indoors, the results of experiments on phase-shifting in the American *Photinus pyralis* and comparisons with synchronization between crickets and between human beings are compatible with the suggestion.

References and Notes

1. E. Kaempfer, *The History of Japan (with a description of the Kingdom of Siam)*, posthumous translation (Sloane, London, 1727; or reprint by McLehose, Glasgow, 1906).
2. For a general review see J. B. Buck, *Quart. Rev. Biol.* **13**, 301 (1938).
3. H. M. Smith, *Science* **82**, 151 (1935).
4. We suggested elsewhere [J. Buck and E. Buck, *Nature* **211**, 562 (1966)] that the firefly trees serve as a quasi-permanent rendezvous for mass mating and that synchrony increases their efficiency as beacons.
5. P. Laurent, *Science* **45**, 44 (1917).
6. W. Craig, *ibid.* **44**, 784 (1916); *J. Animal Behav.* **7**, 444 (1917).
7. C. A. Ruckmick, *Trans. Illinois Acad. Sci.* **13**, 103 (1920).
8. From 10 to 20 October 1965. We thank the American Philosophical Society and National Geographic Society for travel grants. Among the many colleagues who ministered to the manuscript we thank particularly Dr. J. T. Enright.
9. C. Wells, *Asia* **24**, 108 (1924).
10. R. Ruedemann, *Science* **86**, 222 (1937).
11. In extension of Ruedemann's (*10*) observation, response to repeated air-pressure waves might conceivably explain the otherwise scarcely credible report of Thai fireflies flashing in time with piano music [K. Eskelund, *My Danish Father* (Doubleday, New York, 1947), p. 147].
12. Buck (*2*) refers to synchronous head-tapping by ants and termites and several other insect synchronies. There appears to be a common impression that some birds can beat their wings synchronously [for example, W. M. Wheeler, *Science* **45**, 189 (1917), but see also Craig (*6*)], but consultation with nearly a dozen experts in bird behavior and study of numerous photographs of bird flight revealed no instance not easily explicable as "inertial" synchrony (see below) occurring soon after takeoff of a flock startled into flight. Horses are said to be unable to walk in step without cues from the riders [see also Craig (*6*)]. The word "synchronism" has also been misapplied to a type of chorusing in which a whole congregation bursts into song periodically but in which the individual calls are not synchronized. In frogs "there is no regular rhythmic expression within the group itself. Each frog croaks in its own way, until a perfect babel of noise is produced" [H. A. Allard, *Amer. Natur.* **51**, 438 (1917)]. In the 17-year locust *Magicicada cassinii* each of the "impressive crests and troughs of sound" [H. A. Allard, *Proc. Entomol. Soc. Wash.* **48**, 93 (1946)] is set off by a leader or leaders, builds to a peak in about 5 seconds, then dies away in an equal period, with a given individual buzzing for only 1 to 2 seconds of each 10-second chorus [R. D. Alexander and T. E. Moore, *Ohio J. Sci.* **58**, 107 (1958)]. Synchronous claw-waving in fiddler crabs has been reported [H. Gordon, *Anim. Behav.* **6**, 238 (1958)] but without quantitative details.
13. E. Zeuthen, Ed., *Synchrony in Cell Division and Growth* (Interscience, New York, 1964); I. L. Cameron and G. M. Padilla, Eds., *Cell Synchrony* (Academic Press, New York, 1966).
14. C. D. Snyder and A. V. Snyder, *Amer. J. Physiol.* **51**, 536 (1920); L. N. Edmunds, Jr., *Ann. Entomol. Soc. Amer.* **56**, 716 (1963).
15. J. B. Buck. *Physiol. Zool.* **10**, 412 (1937).
16. P. Rau, *Ecology* **13**, 7 (1932).
17. J. E. Lloyd, *Misc. Publ. Mus. Zool., Univ. of Michigan No. 180* (1966), p. 46.
18. H. A. Allard, *Proc. Entomol. Soc. Wash.* **33**, 49 (1931).
19. J. B. Buck, *Physiol. Zool.* **10**, 45 (1937).
20. L. Plate, *Z. Ges. Naturwiss.* **54**, 1 (1916); H. Pieron, *Feuill. Jeunes. Natur.* **21**, 186 (1925).
21. O. A. Reinking, *Science* **53**, 485 (1921); T. F. Morrison, *ibid.* **69**, 400 (1929).
22. G. Alexander, *ibid.* **82**, 440 (1935).
23. F. A. McDermott, *Can. Entomol.* **43**, 399 (1911); H. A. Allard, *Science* **82**, 517 (1935).
24. B. B. Fulton, *J. Elisha Mitchell Sci. Soc.* **50**, 263 (1934); M. D. R. Jones, *J. Exp. Biol.* **45**, 15 (1966). One species (*Ephippiger*) is even said to be able to alternate both at the single insect frequency and in such a way that each insect keeps its own original frequency and the final rhythm is doubled [R. G. Busnel, B. Dumortier, M. C. Busnel, *Bull. Biol. France Belg.* **90**, 219 (1956)].
25. R. D. Alexander, in *Animal Sounds and Communication*, W. E. Lanyon and W. N. Tavolga, Eds. (American Institute of Biological Sciences, Washington, D.C., 1960).
26. A popular theory, best described by C. A. Richmond, *Science* **71**, 537 (1930).
27. The mechanism by which many katydids synchronize their calling may be analogous. However, in pair interaction the leader-follower relationship seems fixed and the follower stops if the leader falls silent (*25*). Dumortier [in *Acoustic Behavior in Animals*, R. G. Busnel, Ed. (Elsevier, New York, 1964), p. 617], on the assumptions that

frequency of cricket chirping is normally maximum and that all individuals have the same "refractory period," has proposed that a premature chirp inhibits all listeners for one beat (one refractory period) after which all chirp in unison.

28. G. H. Hudson, *Science* **48**, 573 (1918); E. Porter, *Sci. Amer.* **151**, 159 (1934).
29. W. N. Hess, *Biol. Bull.* **38**, 39 (1920).
30. K. Dunlap, *Psychol. Rev.* **17**, 399 (1910).
31. H. Woodrow, *J. Exp. Psychol.* **15**, 357 (1932).
32. Such biases would seemingly operate to reduce the degree of coincidence obtainable with increasing consortium size. In this connection it is interesting that N. Wiener [*Cybernetics* (Massachusetts Institute of Technology Press, Cambridge, 1961), chap. 10] ; → A. T. Winfree [*J. Theoret. Biol.* **16**, 15 (1967)], by analogy with certain types of mutual entrainment in nonlinear oscillators, have suggested that the rhythm of flashing of a synchronized ensemble of fireflies might be more, not less, regular than that of any one of the fireflies in isolation. See also J. Barlow, *Cold Spring Harbor Symp. Quant. Biol.* **25**, 54 (1961).
33. Perfect synchrony has also been reported to occur in the chirping of numerous cricket species, particularly the snowy tree cricket, *Oecanthus fultoni (niveus)* (*2*). Unpublished records of individual responses in this cricket [T. J. Walker, thesis, Ohio State University (1957)] strongly suggest that *Oecanthus* uses anticipatory synchronization, although reaction time was not measured directly.
34. J. Buck, E. Buck, H. F. Brubach, in preparation.
35. R. S. Woodworth and H. Schlosberg, *Experimental Psychology* (Holt, Rinehart and Winston, New York, 1954).
36. This is shown also by the fact that in each of the episodes one, and usually two, of the subjects leads the mean group frequency. In most of our duets and quartets the subjects interchange relative positions many times in the course of a long serial record (*34*).
37. Photometer designed and constructed by Dr. F. E. Hanson, Jr. The photometer comprises an RCA 1P21 phototube, Cambridge Trans-Scribe electrocardiograph with a chart speed of 25 mm/sec; battery-driven transistorized electronics throughout; rated frequency response limit of 100 cycle/sec; acceptance angle to 50 percent attenuation, 30°.
38. Bolex 16-mm camera with 25-mm *f*1.8 lens; high-speed Ektachrome film and forced development to 800 ASA equivalent. Film and processing courtesy National Geographic Society.
39. Y. Haneda, *Kagaku Nanyo* **3**, 66 (1941); in *The Luminescence of Biological Systems*, F. H. Johnson, Ed. (AAAS, Washington, D.C., 1955), p. 361; *Sci. Rep. Yokosuka City Mus. No. 12* (1966), p. 4.
40. These females can also flicker, at least when disturbed in captivity, so the fireflies that flicker while flying to or out of trees may include *P. malacae* females as well as *P. malaccae* males.
41. A taxonomic and distributional paper on the genus *Pteroptyx* just completed by Mrs. L. Ballentyne of the University of Queensland and Mrs. M. McLean of our laboratory has turned up a close, but probably not exclusive, association of synchronous flashing with this genus. The species studied in New Britain by Haneda (*39*) is *P. cribellata*. The species seen synchronizing near Singapore appears to be *P. malaccae* (which we found also in Borneo), although flash frequency is reported to be only half that of the Thai race (*51*). Other species of *Pteroptyx* occur in New Guinea, Sumatra, Cambodia, and the Philippines in regions where synchrony has been seen.
42. Series of 72 and 40 consecutive flashes with mean cycle lengths of about 5.7 seconds at 23°C, measured to nearest 100 msec. Seventy-nine consecutive cycles of spontaneous flashing, measured in a pinned-down *Photuris versicolor* male, had a V value of 7 [J. Buck and J. F. Case, *Biol. Bull.* **121**, 234 (1961)].
43. Series of 47 and 87 chirps at frequencies of about two and five per second, respectively, measured to nearest 2 msec directly from the records in *The Songs of Insects* [G. W. Pierce (Harvard Univ. Press, Cambridge, Mass., 1949)].
44. From 35 1-minute electrocardiograph records on three subjects, kindly supplied by Dr. Jimmy Scott. The interval between R waves averaged about 1000 msec; recorded to nearest 5 msec.
45. Multiple tests on about 20 subjects with both endogenous and externally cued frequencies of one to five per second in runs of up to 300 successive taps (*34*). Measured to nearest 5 msec.
46. One beta cell from each ear, recorded simultaneously from the tympanic nerves of same specimen of *Feltia* sp. Series of 99 and 59 spikes, of cycle lengths 78 and 130 msecs, respectively. Recorded at a film speed of 100 cm/sec and measured to nearest 0.5 msec. Film record courtesy Dr. K. D. Roeder. [See A. E. Treat and K. D. Roeder, *J. Insect Physiol.* **3**, 262 (1959)].
47. Transcribed on chart paper from tape recordings kindly supplied by the Laboratory of Ornithology, Cornell University. Five records, apparently from three different birds and ranging from 32 to 71 consecutive calls, had cycle lengths of 960 to 1200 msecs. Measured to nearest 5 msec.
48. Six entrained individuals, all with cycle lengths close to 560 msec. Series ranging from 19 to 82 consecutive flashes. Measured to nearest 4 msec. Repeated measurement of particular records at long intervals indicated that most of the apparent variation, small though it is, is due to measurement error. The precision of the oriental type of synchrony might by promoted by the fireflies' habit of perching motionless in trees, because the fixed and repetitive pattern of flashes received by the participants' eyes might reinforce the effect of the community rhythm. Similarly, the rapid flashing of the oriental tree fireflies appears better adapted to synchronization than the several-second cycle of many roving species because it would not require as great proportional accuracy in time measurement to achieve the same absolute degree of coincidence.
49. C. H. Graham, Ed., *Vision and Visual Perception* (Wiley, New York, 1965). See also (*35*).
50. J. Goldsmith (pseudonym of Sir Richard Phillips), *An Easy Grammar of Geography* (Flint, London, ed. 31, 1811).
51. In a paper on a West Malaysian *Pteroptyx* [J. M. Bassot and I. Polunin, *Sci. Rep. Yokosuka City Mus. No. 13* (1967), p. 18] records made on slowly moving film with camera shutter constantly open strongly indicate that single "new" fireflies can appear suddenly, in phase with older members of a synchronizing "constellation," though the authors concede also the possibility of new individuals having moved into view. If this finding, which might apply also to some of our "unmasked" fireflies, is confirmed, it will be important in showing an ability of fireflies to "come in on the beat" as human beings can do if they first have the opportunity to observe a few cycles of the rhythm to be duplicated.
52. Actually, when a whole congregation, rather than a pair, is being considered, it is not clear that the mean temporal span of flash coincidence must be less than the response latency during anticipatory coupling nor that the mean interval may not be less than the latency in instances of pacemaking involving fireflies of closely similar periods, with interchange of lead. Likewise the supposition that the group rhythm in paced synchrony would be faster than the average of the individual periods before entrainment, because of the accelerating effect of premature triggering, may not in practice constitute a usable distinction from anticipatory synchrony since our human quartets showed a consistently greater acceleration of tapping rate than did the individual members tapping by themselves (*34*).
53. The fireflies were obtained by Dr. Douglas Gould of the Walter Reed Army Medical Center unit of the SEATO Medical Research Project, Thailand, and brought to Bethesda by Dr. Robert Gordon of our Institute.
54. J. Buck, J. F. Case, F. E. Hanson, Jr., *Biol. Bull.* **125**, 251 (1963); K. M. Smalley, *Comp. Biochem. Physiol.* **16**, 467 (1965).
55. J. F. Case and J. Buck, *Biol. Bull.* **125**, 234 (1963). Difficulties in direct measurement of eye-lantern latency are probably due to the delicate balance between inhibition and excitation. The closest measurement to a true photic latency yet available is the 90-msec flash delay for electrical stimulation in the brain of *Photuris versicolor.* In several other American species, and in the Italian *Luciola lusitanica* [F. Magni, *Arch. Ital. Biol.* **105**, 339 (1967)], even the direct lantern latency is longer than 90 msec.
56. J. Buck and F. E. Hanson, Jr., in preparation.
57. J. B. Buck, *Science* **81**, 339 (1935).
58. Hess (*29*) reported some success in slowing the flashing of *P. consanguineus* with a flashlight, but, since he claimed that both sexes were involved and since the response traveled as a wave, the type of entrainment is unclear.
59. Our data on finger-tapping indicate that, except with frequencies of the order of five per second, phase shifting is affected only by cues in the immediately preceding episode (*34*).
60. Drs. T. H. Bullock and J. Thorson have kindly called our attention to a sequence discriminator in the brain of the beetle *Chlorphanus* used in the perception of motion [B. Hassenstein and W. Reichardt, *Z. Naturforsch.* **11b**, 513 (1956)].
61. F. A. McDermott, *Z. Wiss. Insektenbiol.* **10**, 303 (1914); H. S. Barber, *Smithsonian Misc. Coll.* **117**, 1 (1951); F. A. McDermott and J. Buck, *Trans. Amer. Entomol. Soc.* **85**, 1 (1959); H. H. Seliger, J. Buck, W. G. Fastie, W. D. McElroy, *Biol. Bull.* **127**, 159 (1965).
62. J. E. Lloyd, *Science* **149**, 653 (1965).