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SYNCHRONOUS RHYTHMIC FLASHING OF FIREFLIES

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I. INTRODUCTION

ONE of the most interesting and complex types of group behavior in animals is that in which several organisms simultaneously repeat the same activity at regular intervals of time. In ordinary usage such behavior is called "synchronous," but, as pointed out by Craig (1916) and Alexander (1935), it actually involves two distinct factors, synchronism and rhythm.

Neither synchronism nor rhythm, alone, is uncommon. Synchronous behavior, for example, often occurs in a group of organisms as the result of a common response to the same stimulus. This stimulus may either be environmental, as in the synchronous responses observed in saw-fly larvae (Bennett, 1860), caterpillars (Beebe and Beebe, 1910), plant lice (Allard, 1917), fireflies (Allard, 1935), etc., or it may appear to originate in some individual in the group, as in the simultaneous behavior of birds (Annandale, 1900; Craig, 1916; Wheeler, 1917), pronghorned antelope (Wheeler, 1917), fish (Beebe, 1926), and frogs (Cunningham, 1903; Allard, 1917). Rhythm, likewise, is a common phenomenon in animals (Flattely, 1920), the chirping of crickets (Dolbear, 1897; Bessey and Bessey, 1898; Edes, 1899; *et al.*), and the beat of the heart being two examples among many. Lillie (1928) has pointed out several interesting analogies between physiological rhythms and those in inorganic systems.

The following pages deal primarily with types of behavior which involve both synchronism and rhythm. Such behavior has been reported in a wide variety of organisms, e.g., in ants (Peal, 1880, 1881; Forbes, 1881; Gounelle, 1900; *et al.*), Phalangidae (Newman, 1917; Wheeler, 1917), web-worm larvae (McDermott, 1916; Peairs, 1917), Orthoptera (Gould, 1895; Coues, 1895; Bostwick, 1895; Dolbear, 1897; Shull, 1907; Craig, 1916, 1917; E. S. Morse, 1916 a; Allard, 1917, 1918, 1930; Comstock, 1924; Fulton, 1925, 1928 a, 1928 b, 1934; *et al.*), caterpillars (Allard, 1917; Buxton, 1923; Minnich, 1925), bees (Burbidge, 1880; Evans, 1922), marine organisms (Herdman, 1903, 1903 a, 1905) wasps (Beebe, 1921), aphids (Williams, 1922; Tanner, 1930), termites (Conner, 1933), and many others. Since, however, by far the largest number of reports concern synchronous rhythmic flashing of fireflies, the subsequent discussion is confined primarily to these insects. There is presented a rather extensive review of the earlier literature, found in obscure journals and books of travel, and a more superficial review of the more recent literature, found in accessible journals. Among the many friends who have aided in the preparation of this paper, I wish in particular to thank Dr. E. W. Gudger who generously placed at my disposal a large number of references to synchronism.

The earliest account found is in Kaempfer's (1727) description of a trip down the Meinam River from Bangkok (Siam). He says:

The Glowworms (*Cicindelae*) 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.

Turpin, in a book on Siam (1771) says (translation): "Nothing gives a finer sight at night than to see a tree all covered with fireflies; it seems decked with many bright sparks which go out and rekindle almost at the same moment."

Goldsmith (1811) states: "The trees on the banks of the Meinam are finely illuminated with swarms of fireflies, which emit and conceal their light as uniformly as if it proceeded from a machine of the most exact contrivance." (See also Van Vleck, 1924.)

Bishop Pallegoix (1854) reports (translation):

The fireflies which are found in Siam are very common and are remarkable for the intensity of their light. One sees these insects fly separately from one tree to another and in all directions, but more often they are assembled by thousands on a great tree on the bank of the river. It is a magnificent spectacle to see spring out at one time from all the branches of this tree as it were, thousands of great electric sparks, because these fireflies emit not a continuous light but one interrupted by the effect of a sort of respiration. It is difficult to explain how this emission of light is simultaneous for several thousands of individuals.

Sir John Bowring (1857) poetically remarks of the Siamese firefly: "They have their favorite trees, round which they sport in countless multitudes, and produce a magnificent and living illumination: their light blazes and is extinguished by a common sympathy. At one moment every leaf and branch appears decorated with diamond-like fire; and soon there is darkness, to be again succeeded by flashes from innumerable lamps which whirl about in rapid agitation."

Cameron (1865) describes observations made in Burma:

The bushes literally swarm with fireflies, which flash out their intermittent light almost contemporaneously; the effect being that for an instant the exact outline of all the bushes stands prominently forward, as if lit up with electric sparks, and next moment all is jetty dark—darker from the momentary illumination that preceded. These flashes succeed one another every three or four seconds for about ten minutes, when an interval of similar duration takes place; as if to allow the insects to regain their electric or phosphoric vigor.

A very interesting discussion of Cameron's report is found in *The Transactions of the Entomological Society, London*, Ser. III, vol. 2, pp. 94–95, 1865, in which the Rev. H. Clark reports having seen synchronous flashing in the Organ Mountains (Brazil?).

Theobald (1866) gives a full description of a display witnessed along the banks of the Irawadi Delta in Burma; which is quoted here in part:

The bushes overhanging the water were one mass of fireflies. . . .The light of this great body of insects was given out. . . .in rhythmic flashes, and for a second or two lighted up the bushes in a beautiful manner; heightened, no doubt, by the sudden relapse into darkness which followed each flash. There are the facts of the case (and I may add that it was towards the end of the year) and the only suggestion I would throw out, to account for the unusual method of luminous emanation, is that the close congregation of large numbers of insects, from the small space afforded them by the bushes in question, may have given rise to the synchronous emission of the flash by the force of imitation or *sympathy*.

Collingwood (1868) says, concerning fireflies at Singapore:

. . . .on fine evenings and in favorable (that is, damp and swampy) localities, they present a very remarkable appearance. Clustered in the foliage of the trees, instead of keeping up an irregular twinkle, every individual shines simultaneously at regular intervals, as though by a common impulse; so that their light pulsates, as it were, and the tree is for one moment illuminated by a hundred brilliant points, and the next is in almost total darkness. The intervals have about the duration of a second, and during the intermission only one or two remain luminous.

Burbidge (1880) also describes a display near Singapore: "As we glided onwards their numbers increased, until we came upon them in thousands, evidently attracted by some particular kind of low tree, around which they flashed simultaneously, their scintillating brilliancy being far beyond what I could have imagined to be possible."

Severn (1881), referring to an Indian firefly, says:

The curious pulsation of flashing of their light is remarkable, the insects on the tree all act in perfect concert, i.e., five seconds of no light, then seven rapid flashes; five seconds no light, seven flashes; and so the game continues throughout the dark hours. It is also worthy of special notice that all the glow-insects on a dozen or more trees will continue to keep up the most perfect time to the flashing of their light and the interval of pause, and this for many consecutive hours; but this singular agreement as to the time relates to close clusters of trees only. Thus distinct groups of trees separated by one or more hundred yards may not agree, and do not do so as a rule.

Annandale (1900) has given us a rather detailed and careful description of a display witnessed in Malaya:

A large tree was covered with many hundreds of fireflies, the majority of which seemed, judging from the similarity of their lights, to belong to one species, or perhaps to one sex. There were three individuals seated together, however, whose lights were larger and bluer than those of the others. The lights of all the specimens of the more abundant variety flickered in unison with one another; those of the minority, the three individuals, flickered together also, but in different time. At one instant the tree was lighted up as if by hundreds of little electric lamps; at the next it was in complete darkness except for three blue points.

Cunningham (1907) says, in reference to Bengalese fireflies:

As the train panted slowly upwards, many of the trees alternately flamed out into dazzling splendor and vanished off in the gathering gloom of an impending storm, whilst hosts of insects resting in them lit and put out their lamps as though by common consent. The cause for such simultaneous action on the part of countless individuals is hard to imagine, but there can be no question of the fact that such displays do take place.

Shelford (1916), referring to a display in Borneo, says: "On the opposite bank was a small tree growing close by the water's edge, which was covered with thousands of Fire-Flies, small beetles of the family *Lampyridae*; and I observed that the light emitted by these little creatures pulsated in a regular synchronous rhythm, so that at one moment the tree would be one blaze of light, whilst at another the light would be dim and uncertain."

Wells (1924, 1925) describes a rather astonishing manifestation of synchronism in Malaya, although it is not clear whether this display involved rhythm also. He says:

About every fifteen minutes these flies separated into two armies, one settling on the trees growing on the left bank of the river and the other on the right bank. Then, when I had decided that they had gone to bed for the night, the whole army on the left bank gave one big flash in perfect unison, which was immediately answered by another big flash from the right bank. There must have been thousands of them stretching along the river bank for a hundred yards or more, but the flies at one end of the line flashed their lights exactly at the same time as the flies on the other end. . .

Guenther (1931) reports witnessing a display in Brazil. He says: "In Petropolis . . . I noted how hundreds of green lights blazed out *simultaneously* and were simultaneously extinguished; with so regular a rhythm that it seemed as though the sparks were blown upon by a huge mechanical bellows that gave a puff every second."

To pass more cursorily over the more accessible recent reports, rhythmic synchronous flashing of fireflies has been observed in the Philippines by Cox (1917), Purssell (1918), Barnes (1919), F. Morse (1918), and Brokenshire (1929); in New Guinea by Dodd (1918); in Siam by Reinking (1921), Morrison (1927, 1929), Smith (1935), and Alexander (1935); in Jamaica by Miller (1935); in India by Connor (1933); in Mexico by Merril (1930); in Borneo by Muir (1908, 1916); and in this country by E. S. Morse (1916), Allard (1916), Hudson (1918), Snyder and Snyder (1920), Hess (1920), and Rau (1932). In addition, there have appeared a considerable number of more or less circumstantial second-hand reports from various parts of the world. Some of these are cited in the reviews of Blair (1915), E. S. Morse (1916 a, 1916 b, 1918, 1924), Craig (1916), Allard (1917), Dahlgren (1917), Gudger (1919), Williams (1922), Allee (1927, 1931), Howard (1929), and Crawford (1934).

Of the 36 reports of synchronous flashing discussed above, 15 are from the Malay Peninsula (Siam, Burma, Malay States, etc.), 5 from the Philippines, 3 from Bengal, 3 from the East Indies, 6 from the United States, 2 from Brazil, and one each from Mexico and Jamaica. The preponderance of reports from the Oriental region (26) as compared with those from the rest of the world, is very striking.

The evidence presented leads to the following conclusions:

(1) It is reasonably certain that rhythmic synchronous flashing of fireflies occurs.

(2) Nearly all the Oriental reports state that the synchronism involved huge numbers of insects; that the displays occurred on trees growing in or near water; that synchronism is common in some regions and species; and that a given display persists unbroken sometimes for hours. The reports from the United States, markedly fewer and less consistent than those from the Orient, give the impression that synchronous flashing is exceedingly rare.

(3) In some displays observed the synchronism was reported to be "perfect," i.e. all the insects flashed at precisely the same instant (Kaempfer, Goldsmith, Bowring, Burbidge, Annandale, E. S. Morse (1916 a), F. Morse, Reinking, Wells, Morrison, Brokenshire, and Smith). In others the synchronism was not perfect: it either began at one or several foci among the aggregated insects and swept rapidly over the whole assemblage ("wave synchronism," Hudson, Hess, Williams, and Alexander), or a few insects flashed in the "dark" periods between mass synchronous flashes (Collingwood, Annandale, Purssell, Barnes, Hess, Miller, and Smith). Annandale, Hess, and Smith, however, maintained that the asynchronous flashes were produced by individuals of a different species, and Morrison suggested that they were due to the residual glow of the light organ after the synchronous flashes.

II. INTERPRETATIONS

The theories propounded to explain synchronous flashing are nearly as numerous and remarkable as the reports of the displays themselves. Some of these theories deal with synchronism, some with rhythm, and some with both. It will be convenient to separate them into five groups.

Obviously inadequate explanations

Included under this heading are the suggestions that puffs of wind influence the insects alternately to expose and conceal their lights (*Trans. Ent. Soc. Lond.*, 1865); that synchronism is due to twitching eyelids (Laurent, 1917); and that the synchronism is in some way connected with the sap of the trees on which the insects gather (Morrison, 1927).

Accident

The accident theory is based upon the common observation that fireflies tend to flash rhythmically and that the rhythm is of approximately the same frequency in all the individuals in a given region. The argument then is that if the fireflies once get into synchronism with one another they will continue to flash synchronously because of their equal rhythmicities. The supporters of the theory are thus concerned with suggesting ways by which the original synchronization might accidentally be brought about. Gates (1917), however, apparently believed not only that the first synchronous flash occurred entirely by accident, but, what seems statistically even more improbable, that each succeeding rhythmic synchronous flash also was accidental.

Several authors (Allard, 1916; Hudson, 1918; Rau, 1932) have noted that some displays of synchronism take place under unusual environmental conditions, such as exceptional humidity, calm, darkness, etc., and in a large open space crowded with insects. Snyder and Snyder (1920) maintain that such conditions insure the uniformity of the natural rhythmicity of flashing so that synchronism, once initiated, will continue. No mechanism for initiating synchronism, however, is suggested. McDermott (1916) and Rau (1932) similarly regard synchronous flashing as a rare phenomenon brought on by a fortuitous concatenation of atmospheric factors. Rau offers, for the display he observed, the following tentative explanation: "Perhaps the entire population was ready to rise in flight but was held back by the shower; when this suddenly ceased, they were all in equal readiness, and at the propitious moment took to wing and flashed together. Since their flashes are at a fairly uniform interval, they continued in unison quite by accident, and did not break step for a few minutes."

The "accident" theory would account for "perfect" synchronism, but not for "wave" synchronism. It should be noted, however, that the definition of synchronism is an academic question: The percentage of a population which must be performing a rhythmic action simultaneously in order for it to be called synchronous doubtless varies greatly depending on the type of behavior and the frequency of the rhythm. "Wave" synchronism, however, is fundamentally incompatible with "perfect" synchronism, since it seems clear the the former must involve a response of each individual to the flash of a near neighbor, so that the community flash occurs progressively, like an ignited gunpowder train, and it is equally clear that the latter could not be brought about by such a mechanism.

Whereas special environmental conditions might conceivably induce isolated instances of synchronism, it seems unlikely that they can account for the spectacular displays exhibited by Siamese fireflies, in which Smith (1935) asseverates that the synchronism continues hour after hour each night for months, "without regard to air currents, air temperature, moisture or any of the other meteorologic conditions which have been stated to influence firefly flashing." Moreover, it is open to question whether the basis of the accident theory, namely, that the synchronism, once initiated, would continue autonomously, is tenable. Thus Snyder and Snyder (1920) and Buck (1937c) have shown in an American species that there is a normal individual variation of from five to ten per cent in the mean duration of the rhythmic interval between successive flashes, even under uniform conditions, so that these individual variations would in all probability very soon carry the various individuals entirely out of phase with one another and disrupt the synchronism.

Illusion

Bates (1865) first suggested that synchronous flashing is an illusion. This notion has been strongly championed on psychological grounds by Craig (1916, 1917) and Ruckmick (1920). Craig contends that all synchronous rhythmic activities depend on a (perhaps unconscious) learned "conceptual awareness of the relation between one's own actions and the actions of others, and purposive imitation of the latter." This faculty, he says, is present only in man, although lower animals may exhibit an admirable synchronism (not rhythmic), which, under special conditions, may coincide with some powerful environmental rhythm. Craig then argues that the reports of synchronous flashing are illusions due to a "predisposition to perceive rhythm" in the accidental synchronism statistically to be expected in aggregations of flashing fireflies.

This thesis of illusion is amplified from the standpoint of experimental psychology in a remarkable contribution by Ruckmick (1920). From a study of the published reports Ruckmick concluded that most of the observations were made in an emotional attitude "bordering on the romantic" and that their accuracy was thus subject to suspicion. Supposing, then, that several coincidences should take place in a large number of flashing fireflies, the "well-known tendency of the human mind to integrate its experiences" would, according to Ruckmick, "tend to set the mind of the observer in the direction of subsequent groupings of the flashes into patterns, supplied, for the most part, by himself." Ruckmick accordingly tested this hypothesis in the darkroom, by exposing subjects to numerous electric lights flashed by machinery in a disorganized manner (no pattern or rhythm). These experiments resulted, first, in spontaneous (unsolicited) comments that the flashing lights reminded the subjects of fireflies flashing, and second, in likewise unprompted groupings of the flashes into spatial, and more especially, temporal patterns, the latter being described as "rhythmic." Ruckmick's conclusion is that under conditions simultating the natural there is a strong tendency for the mind to read order into disorganized experiences, and on this account reports of prolonged synchronous flashing are likely to be unreliable.

It seems unlikely that the evidence and arguments advanced by Craig and Ruckmick, cogent as they are, can serve to invalidate the multitudinous reports of synchronous flashing, many of which were made by experienced and careful observers, but at any rate there are at least two questionable features in Ruckmick's work: (1) His premise that not infrequently all the fireflies in a given large group would accidentally flash in unison is statistically very improbable. (2) Ruckmick's experimental setup was not an accurate imitation of the flashing of fireflies in nature, in that his lamps were not flashed rhythmically; whereas actually most of the fireflies in a given region flash rhythmically and with very nearly the same period (Snyder and Snyder, 1920; Buck, 1937 c). Moreover, the present writer was unable to detect any synchronism in the flashing of huge aggregations of tropical fireflies, in which each individual flashed with the same rhythm, but quite at random with respect to the others (Buck, 1937 b).

Sense of rhythm

Bowring (1857), Theobald (1866), and Wheeler (1917) consider the synchronous flashing to be due to a "sympathy" or "Einfühlung" among the insects. This principle apparently corresponds to the "conceptual awareness" of Craig, already discussed, and to the "organic law of rhythmic appreciation" of Allard (1935). This idea involves consciousness of one's own rhythm, consciousness of one's neighbor's rhythm, and deliberate imitation of the latter; or, in anthropomorphic terms, a "sense of rhythm."

The "sense of rhythm" or "sympathy" hypothesis is not so much an attempted explanation of synchronous flashing as it is a more or less gratuitous attempt to relate the phenomenon to similar behavior in higher animals and man. The reason for this attempt is, apparently, the conviction that displays of synchronism in which all the fireflies flash exactly in unison cannot be understood without postulating the existence in insects of some faculty similar to that which enables human beings to walk or sing in unison. It is, however, possible to explain such apparently exact synchronism in a simpler and more objective manner. Such an explanation is discussed below.

Leader or pacemaker

The most popular proposed explanation of rhythmic synchronism is the "leader" or "pacemaker" theory, espoused by Blair (1915), Allard (1917, 1918), Hudson (1918), Hess (1920), and Alexander (1935). The essential feature of this theory is that all the fireflies simultaneously respond to the flash of one (the leader), which flashes rhythmically. This theory is an improvement over the accident theory in that it provides a mechanism for keeping the flashes synchronous so that the normal individual variations in rhythm will not break up the synchronism, but it is nevertheless open to criticism on the following points:

(1) Most of the proponents of the leader theory maintain that the flashes take the form of a wave, whereas a communal response to a single leader would necessarily result in perfect synchronism.

(2) As pointed out by Annandale and by Morrison, a single leader could not possibly be visible to all of the members of such huge swarms of fireflies as are reported to exhibit synchronism. (The fact that the compound eyes of insects are situated on the sides of the head, and designed for perception over a very wide angle, makes this a less serious objection than it would be if applied to primates, where the field of view is greatly circumscribed. Furthermore, since so many of the reports emphasize the wetness of the localities in which the displays of synchronous flashing occur, it might be imagined that the flash of the leader could be relayed to the rest of the swarm by means of its reflection on the water below.)

(3) No mention is made of what determines which individual shall be the leader, or of why he should flash more regularly than the others. Unless the leader's flash is somehow different from all the others (of which there is no evidence) he would have to flash at a slightly faster rate than any of the other fireflies to prevent being anticipated by some individual which happened to flash a little sooner than the average rhythm interval. Moreover, if each collective flash depended on the leadership of a single individual the whole group would re-

main dark if the pacemaker missed a single beat.

(4) The contention of Alexander (1935) that "in the absence of a pacemaker mechanism we should be forced to postulate the existence of an accurate physiological chronometer, a mechanism to most of us quite inconceivable," seems scarcely germane, since it is precisely such a mechanism which must activate the "pacemaker" itself. Moreover, not only are we quite familiar with such chronometers, or their manifestations in higher animals (e.g., heartbeat, action potentials in nerve, peristalsis, respiratory rhythm, etc.; cf. Child [1924] pp. 184–186) but there is good reason to believe, from the work of Brown and King (1931), Snell (1931, 1932), and others, that such a mechanism exists in the firefly. Snyder and Snyder (1920), indeed, have compared the flashing rhythm to the rhythmic electrical discharges originating in the central nervous system of vertebrates. Further data on the physiology of pacemakers are contained in Hoagland's (1935) book.

Richmond (1930) has suggested a simplified form of the leader theory, which, because it eliminates the idea of a single fixed pacemaker, obviates some of the criticisms presented above. Richmond's theory postulates first, that all the fireflies flash rhythmically, with nearly the same period, due to the alternate discharge and recovery of some battery-like mechanism (cf. also Blair), and second, that each insect flashes immediately if stimulated by a flash which occurs at a time near that at which he would normally flash. The title "leader" thus would apply merely to the firefly which happened to flash first after the last concerted flash.

Richmond's postulation is supported by certain analogies in nerve physiology. If, for example, the flashing is under nervous control (which seems certain from the work of Lund [1911], Brown and King, Snell, *et al.*), it might be expected that following each flash there would be a "refractory" period during which the insect would not respond to the stimulus of a flash, and during which he would not flash of his own accord (inhibition?). After this period a potential of some sort would be built up which would result ultimately in a spontaneous flash, but which could be discharged meanwhile by the stimulus of a flash from some other individual (cf. Allee, 1931, p. 92, and Child, 1924, pp. 276–287). Certain experiments of Hess (1920) and Buck (1937 c), described below, indicate that a mechanism similar to that here postulated may be present in the firefly, although Snyder and Snyder assume that at a given temperature "the flashing mechanism discharges [spontaneously] as fast as it can." That the battery analogy is not an accurate one in the sense that it implies that some substance is used up during the flash, and another flash cannot occur until more substance appears, is indicated by the work of several investigators who induced fireflies to flash at a rate higher than normal by electrical stimulation, or treatment with chemicals.

Summary

It will be seen that none of the theories proposed to account for synchronous flashing of fireflies provides an adequate explanation of the phenomenon. Richmond's modified leader theory appears in general to present the fewest intrinsic difficulties, although, like the other theories, it is mainly speculative. It provides a reasonable explanation for perfect synchronism within a relatively small area, by postulating that all the fireflies in the area respond synchronously to the first individual within sight which flashes after the last preceding synchronous flash. It also can be adapted to explain synchronism over a larger area, providing that each synchronous flash passes as a wave over the assembled fireflies, by postulating that each firefly responds not to one particular individual, but to the flash of some member of the swarm, and that he, in turn, stimulates another, and so on.

Richmond's theory, however, like all the other theories, appears to be completely inadequate to explain displays of synchronism of the magnitude observed in Siam by Morrison (1927, 1929) and Smith (1935), who report that enormous numbers of fireflies, distributed along a half-mile of river front, all flash in exact unison. If the synchronism is really as absolute as reported, there seems to be no obvious escape from the necessity of referring the phenomenon to some abstract faculty like "sense of rhythm," since all the individuals obviously could not be responding to a single leader. However, the frequency of the flashing rhythm is reported to be very high (more than a hundred times per minute, according to several observers), and this ought to make it very difficult to distinguish between absolute synchronism and a very rapid wave flash of the type described by Alexander (1935), presumably in the same fireflies studied by Morrison and Smith. Assuming that the synchronism is in fact of the wave type, the Siamese displays are amenable to a simpler explanation than the above, by means of the Richmond leader theory. The reaction time between the flash of the leader and the response of the other fireflies, however, would have to be exceedingly short.

III. EXPERIMENTAL

Introduction

Gates (1917) was unsuccessful in attempts to produce synchronism or to alter the frequency or manner of flashing in *Photuris pennsylvanica* by means of a flashlight.

Morrison (1927, 1929) states that he inhibited the synchronous flashing of fireflies in a tree "by exposing them to a bright light for about a minute," and that "when the light is turned off the synchronism returns, having its origin apparently in some individual or group generally located in the central part of the tree."

Hess (1920) maintains that in observations on synchronous flashing in *Photinus consanguineus* he discovered that "by standing on the side of the valley and causing short flashes with a pocket flashlight, the fireflies of the entire valley responded," and that by flashing slightly sooner than the normal time for flashing he could increase the frequency of the synchronous flashes to some extent.

Allard (1935) induced several females of *Photinus scintillans* to respond synchronously to flashes from a flashlight. This has been observed many times by the present writer in females of *Photinus pyralis*, but since in both species the responses occur only following a stimulus they are not truly rhythmic.

Relation between the mating signals and synchronous flashing

It has been demonstrated (Buck, 1937 c) that the male and the female of the American firefly, *Photinus pyralis* are brought together for mating by a system of flashing signals of which the essential feature is that the responding female invariably flashes two seconds after each successive rhythmic flash of the male.

Earlier (Buck, 1935) it was shown that during the mating signals several males are often attracted simultaneously to the same female, and that these males flash in unison. It was further shown that synchronism on a larger scale can readily be induced by substituting a flashlight for the female in the mating signals, and a theory to explain how such synchronism could spread to include a large number of fireflies was presented, as follows: "A little group of synchronously responding males built up around one female, as described above, acts as a unit in stimulating another female a considerable distance away because the combined intensity of the several simultaneous flashes is greater than that of a single flash; the second female, then, in responding to the first group of males, gathers in to herself a coterie of males which flash in unison and are, of course, synchronized with the original group; they in turn stimulate a third female which "attracts" a third cluster of males, also synchronized with the original, and so on, until a large number of fireflies scattered over an extensive area are flashing in unison. The whole process depends on the fact that all the females reply to each of the flashes of the male at the same definite interval."

This theory is a reasonable explanation of synchronism in *P. pyralis*, but does not account for the synchronous flashing observed by Hess (1920) in *P. consanguineas*, if his contention that both males and females flash synchronously together is valid. In addition, Miller (1935) and Smith (1935) assert that it does not account for the displays which they saw in Jamaica and Siam, respectively, because no females were seen. Smith in fact maintains that the females remain in the jungle from which the male fireflies "have definitely flown for the purpose of engaging in this nightly display."

Relation between subjection to darkness and synchronous flashing in P. pyralis

Males of *P. pyralis* were put into a large mosquito-netting cage in the darkroom and subjected to a light intensity of about 65 meter candles (for details see Buck, 1937 a). It was found that sooner or later, depending on previous treatment, these fireflies began to fly about and flash in a manner typical of their behavior in the field. Under these circumstances, their flashes, although rhythmic for a given individual, showed no sign of synchronism. If these males were then suddenly subjected to total darkness the character of the flashing was immediately and strikingly altered. All the fireflies flashed synchronously: then this fulguration was followed by four or five seconds of complete darkness, after which another salvo of flashes ensued. This rhythmic synchronism persisted uninterrupted for a considerable time and then gradually died away. Careful observation showed that each community flash was initiated by a single flash, the others following almost instantaneously. Each individual apparently took his cue to flash from his more immediate neighbors, so that the mass flash took the form of a very rapid chain of overlapping flashes, the insect farthest from the "leader" flashing last, but so promptly as usually to light up before the leader's flash had faded. That the synchronism was truly due to a follow-the-leader system and not to accident or individual adherence to some fixed rhythm is shown by the following facts: (1) Different individuals acted successively as the leader, the first flash after the dark between period being the one followed, regardless of its source; (2) There was considerable variation in the time between successive concerted flashes during the later, more irregular phases of the process, in which as much as ten seconds sometimes elapsed before the signal for flashing was given. That the synchronism was not induced specifically by the unnatural conditions of complete darkness is indicated by the fact that the same phenomenon was occasionally seen in the field among males which were sufficiently close together. The total darkness thus seemed to serve only to increase the relative intensity of the flashes of the neighbors.

This synchronizing tendency in the males of *P. pyralis* probably could not in itself produce a mass synchronism among large numbers of specimens in the field, such as the display reported by Rau (1932), unless the insects were extremely crowded, and then the synchronism would be expected to take the form of waves spreading out from one or several foci. However, it may be the explanation of how several males which respond to the same female get into synchronism with each other (Buck, 1935).

The responses of the male of *P. pyralis* thus appear to be of two types: (1) To a stimulus occurring approximately two seconds after his flash he responds by orienting and proceeding toward the lure, whether female, flashlight, or another male (Buck, 1937 c). (2) To flashes which are close enough to him, i.e. of sufficient relative intensity, and which occur near the time at which he would be expected to flash, he responds by flashing synchronously with them (cf. Richmond, 1930).

IV. SUMMARY

The evidence presented in the preceding pages indicates clearly that rhythmic synchronous flashing of fireflies is a very complex phenomenon, and that it differs greatly in different localities and species.

The four principal theories formulated to explain synchronous flashing are analyzed in detail: (1) The "accident" theory, which postulates that synchronism is initiated by accident, and maintained by the normal rhythm of flashing of the members of the swarm. (2) The "illusion" theory, which holds that the human mind deceives itself into seeing rhythmic synchronism in the few accidental coincidences which would (allegedly) be expected to occur in large numbers of fireflies flashing at random. (3) The "sympathy" theory, which attempts to relate synchronous flashing to the human "sense of rhythm." (4) The "leader" theory, which maintains that synchronism is produced by the mass of fireflies responding to the flash of a leader.

None of these theories is adequate to explain fully all the features of synchronous flashing observed. In general, a modified form of the "leader" theory appears to be the most satisfactory.

Experimental evidence is presented which indicates that in the American firefly, *Photinus pyralis*, synchronism is sometimes a by-product of the flashing signals used in mating, and is sometimes due to a follow-the-leader response.

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