Chapter 1
Fireflies: a Paradigm in Synchronization

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Abstract Synchronous flashing in Fireflies is perhaps the first observed natural phenomenon displaying synchronization of a large ensemble. During a long time, this collective behavior was not recognized and validated as synchronous, but nowadays it constitutes a paradigmatic example of synchronization. In this chapter, we explain biological aspects related to fireflies flashing and their functionality. The response to synchronization observed in some firefly species is illustrated utilizing a model based on electronic fireflies, and we explore the consequences of the firefly courtship as a whole process including the males' synchronization and the corresponding females' response. Some other aspects are pointed out, such as fireflies inspired models for communication networks, and the use of firefly synchronization concept in mobile networks and other devices. Finally, we explore the actual applications inspired in fireflies synchronicity and also the perspectives both in biomedical issues and in technological systems including robotics. This chapter attempts to reveal the most important aspects related to firefly synchronization providing an extensive bibliography which allows the reader to deepen in all the exciting and fascinating issues linked to the firefly behavior.

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1.1 Introduction

All living beings exhibit oscillatory behavior manifested internally in metabolic, cellular, and molecular processes. Among those, glycolytic oscillations observed in muscles and yeast, oscillations of cyclic AMP found in *Dictyostelium* amoebae, mitotic oscillations leading to cell division cycle in eukaryotes, the pulsatile hormone signaling, the calcium oscillation observed at the level of internal part of cells, and circadian rhythms [37]. Nevertheless, the animated matter is also able to manifest oscillatory features that can be perceived by the senses of other living beings and especially by humans. Among the temporal patterns that humans can recognize in other species, we can mention the locust mass migration, and several synchronous behaviors such as in chewing, chirping, breeding, and flashing [15]. Synchronization is a widespread phenomenon both in nature and in artificial systems; it consists in the adjustment of the time scales among oscillators due to a weak coupling [73] implying the emergence of structural order analogous to phase transitions [63]. Synchronization has deserved a lot of interest in the last two decades in which, thousands of papers, extensive reviews, and books treated this phenomenon related to chaotic aspects [5], and its applications to living [69], communication [47], networks [61], and mechanical systems [70]. There is also an excellent popularization book dealing with the most important features of synchronization and surely with fireflies [91]. Perhaps, the human light perception is the primary and most important connection with the environment. The sunlight, the moonlight, the brightness of different objects in the sky, the fire, and the light of certain animals, have undoubtedly triggered an intense curiosity in the human beings. The above-mentioned phenomena were not only observed by humans, but they intended to explain how and why those events occur, and they also tried to manage them finding numerous applications leading to a better lifestyle, establishing in this way, a qualitative difference with other species. Among the light emitting animals, fireflies possibly constitute the most charismatic and typical behavior because of their proximity, accessibility, and innocuity for humans. Several works have been carried out to describe, classify and study fireflies originating publications about taxonomy [50, 60], geographical distribution of certain species [32], diverse issues on the light organ [11], and recently genetic analyses associated to phylogenetics and systematics of some species [3] or in evolutionary problems linked to the flashing [64]. Throughout this chapter, we explain many biological, chemical, physical and mathematical aspects to unravel the firefly flashing synchronization, its consequences and potentials. In Sect. 1.2, we cover the bioluminescent features such as flashes colors and spectra of the fireflies [32], describing them under different perspectives going from their chemical aspects related to enzymes [66] or oxidation mechanisms [8] to their physical ones in connection with the influence of static magnetic fields [43]. In Sect. 1.3, we give the basis to understand why the evolution drives the fireflies to synchronize and the functional interpretation of this behavior [59] mainly implying communication aspects [16] in flash pattern recognition [14] as a fireflies' "language" related to courtship [13]. The heart of this chapter constitutes the physical-mathematical approach attempting to explain how and why diverse species of fireflies synchronize, the latter is considered with certain detail in Sect. 1.4 where we start with a toy model called the “solitary flash” [90]; then, we consider multi-agent systems (MASs) based models using well-known platforms and dealing with features related to firefly-inspired synchronization [7]. Thereafter, the details of phase and relaxation oscillators as the first approach for understanding fireflies synchronization [1, 23, 99] are given. Before to end Sect. 1.4, synchronization of pulse-coupled oscillators (PCOs) are described [62, 67, 76] mainly from a biological application perspective emphasizing the family of integrate-and-fire oscillators (IFOs) [42]. In Sect. 1.5, a consistent explanation of the phenomenon of response to synchronization [31] as a complete process of courtship is done supported by experimental results using artificial flashes [14, 68] and by a formal model [75, 78]. Finally, in Sect. 1.6, we explore the firefly-inspired synchronization and its applications including evolvable systems [92], wireless and other technological networks [7, 34, 54, 95], electronic and robotic devices [7, 21, 28, 76, 85] or even in improving light extraction efficiency [4]. All the aspects mentioned above give us a large bundle of concepts, models, and applications related to fireflies’ collective behavior which constitutes a paradigmatic example of synchronization.

1.2 The light of fireflies

The first question that arises concerning the glowing insects is how and why fireflies emit light flashes. First of all, it is important to grasp the mechanisms leading to fireflies bioluminescence. We can approach this phenomenon considering three viewpoints: (i) Phenomenologically, in which, macroscopic aspects of the light are important such as the functionality of the emission comprising defense, offense, communication and propagation [98]. (ii) Chemically, as firstly stated by Dubois in 1887 [25], the processes involved in the production of light might be seen as a complex machinery, where two key substances luciferin (LH_2) and luciferase (Luc) allow the phenomenon to takes place in the presence of oxygen (O_2). This mechanism is common to several species exhibiting bioluminescence. (iii) Physically, the reactions in which single-electron-transfer seems to be essential for the mechanism leading to the production of the photon involved in bioluminescence [8].

The curiosity for the lightning innards of some living beings, in particular for fireflies that are the most accessible to the sense of sight triggered scientific work with the aim of deciphering the involved processes leading to firefly flashing. Detailed and systematic observations of flashing fireflies started perhaps with the experiences of Leconte in 1881, who described in detail the American Lampirydae [50]. Almost at the same time, in France, Dubois studied the bioluminescent beetles called *Pyrophorus* [24] and also the Pholadidae, a family of bivalve mollusks [25] trying to understand the “light production” in these animals through observing the mores, the morphological features, and the structure of the luminous organ. As above mentioned, Dubois identified the essential substances for the chemical reactions conducting to the light emission, and also generalized the idea that these chemical substances might be similar in different phosphorescent animals [26]. Several qualitative observations have been made in diverse fireflies species. Firstly, studying mating behaviors [65], then focusing on the control of flashing in fireflies [41], or on the effects of chemical compounds [36] and physical variables on the flashing features, such as temperature [27], light [20], static magnetic fields [44] or pulsed ones [43].

From a chemical point of view, the term bioluminescence introduced by Harvey in 1916 [40] is a fundamental concept to explain the cold light emission by living organisms, in particular by fireflies. The chemical aspects related to fireflies light emission had started to be developed since the origin of the identification of LH_2 and Luc. There were some works where these types of substances were extracted to show their phosphorescence properties [38]. After the discovery of these compounds in fireflies [39], scientists realized their importance and significant role in the production of light. The mechanisms of bioluminescence were unraveled both generically in all the living beings exhibiting this feature [88, 98], and particularly in fireflies [66]. It is possible to summarize the bioluminescent processes by simple chemical reactions as those shown below:

$$\mathrm{LH_2} + \mathrm{O_2} \xrightarrow{\mathrm{Luc}} \mathrm{Oxyluciferin} + \mathrm{CO_2} + h\nu \tag{1.1}$$

$$\mathrm{Photoprotein} + \mathrm{Ca}^{2+} \longrightarrow \mathrm{Protein{-}coelenteramide} + \mathrm{CO_2} + h\nu\,, \tag{1.2}$$

where the first reaction depicts the oxidation of luciferin giving place to the protein-bound Oxyluciferin and a photon with frequency ν. On the other hand, in the second reaction, a conventional Photoprotein activated by calcium ions results into protein-bound coelenteramide. Specifically for fireflies, the reactions are

$$\mathrm{LH_2} + \mathrm{ATP} + \mathrm{Luc} \longrightarrow \mathrm{Luc{\cdot}LH_2{-}AMP} + \mathrm{PP_i} \tag{1.3}$$

$$\mathrm{E{\cdot}LH_2{-}AMP} + \mathrm{O_2} \longrightarrow \mathrm{Luc} + \mathrm{AMP} + \mathrm{CO_2} + \mathrm{Oxyluciferin} + h\nu\,, \tag{1.4}$$

with a wavelength photon λ_{max}=560 nm (yellow-green).

Finally, from a physical viewpoint, apart from some variables susceptible to affect the firefly flashing (temperature, light, static and pulsed magnetic fields, etc.); there are microscopic aspects especially in relationship with the process of oxidation. More specifically, the oxygen supply mechanism [94] or the single-electron-transfer pathway for the critical oxidative process [8]. These microscopic studies are carried out using modern experimental techniques such as synchrotron phase-contrast microtomography and transmission x-ray microscopy.

Certainly, chemiluminescence and bioluminescence are closely related and although, in a first stage, the efforts were devoted to the explanation of the chemical processes giving rise to luminescence in some living beings. Nowadays, several works are contributing not only to unravel the mechanisms of bioluminescence but also to find applications in several fields including clinics, imagery, drug discovery, genetics, forensics, environmental monitoring, and conservation of cultural heritage among others. A detailed description of the above-mentioned applications is done in [81]. Recently, the relationship of firefly light-extraction efficiency [4], inspired similar mechanism for light-emitting diodes. The Nobel prize 2008 in chemistry awarded to Osamu Shimomura, Martin Chalfie, and Roger Y. Tsien for the discovery and development of the green fluorescent protein, GFP constitutes a milestone in bioluminescence and also a reward for the efforts performed in advance of the knowledge of the phenomenon firstly observed in fireflies.

1.3 Why fireflies synchronize?

The succession of observations made to conclude that the primary function of synchronization in fireflies is that of courtship has meant a long and tortuous road that has often led to incorrect interpretations. Fortunately, the scientific approach was imposed, and it is now possible to state that fireflies collective flashing is perhaps the most cited phenomenon as an example of synchronization.

1.3.1 First encounters with synchronous fireflies

As stated by Roda [82], the oldest known written document describing qualitative and nonsystematic observations on flashing fireflies and glow-worms were made in China, dating roughly from 1500 to 1000 BCE. The knowledge and observation of fireflies were common in several cultures such as the Mayas where they played a role in religious practices and also in mythology associated with the cigar smoking. However, there is no doubt that the most interesting phenomenon when sighting ensembles of fireflies, is the ability that certain species exhibit to attain collective synchronous flashing. The first reported observation on firefly-synchronization is due to Engelbert Kaempfer a Dutch physician, naturalist, and explorer born in Westphalia, in the present German territory. As a result of his observations during his voyage to Japan and Siam (1690–1692) he wrote (quoted in [10]):

> 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.

The latter constitutes the first description of synchronization in a large population of coupled oscillators. After that, several observations of firefly synchronization were reported among the most interesting; we only mention the citation due to Theobald [93] who based in a comment about the unison light of fireflies, wrote:

> In Pegu, however, I have witnessed the exhibition in question; myriads of fireflies emitting their light, and again relapsing into darkness, in the most perfect unison .... 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.

Buck in 1938 cited more than 30 reports on synchronous fireflies [10] with observations carried out in different locations of the planet (e.g. Siam, Burma, Singapore, Borneo, Malaya, Philippines, New Guinea, Jamaica, Mexico, United States, and Brazil). In this historic article, he also pointed out some explanations for firefly synchronization, including the insubstantial ones (the wind and other environmental influences, twitching eyelids [49], the effect of the sap of the trees, accident, illusion, sense of rhythm or "sympathy", and leader or pacemaker). None of these explanations were adequate to resolve the phenomenon of synchronous flashing. It is important to call attention to the fact that the statements mentioned above do not consider any functionality in the achievement of firefly synchronization. From an energetic point of view, the lack of functionality of synchronization could be regarded as an inefficient, useless and unjustified process. Evidently, a more detailed study of firefly synchronization showed that this phenomenon is significant for the survival of many of these species since, as it will be seen later, synchronization allows the identification of particular species as well as an intersexual communication language.

1.3.2 Synchronization for courtship and mating

During the first two decades of the twentieth century, several observations done principally by Mc Dermott had shown that the light emission in some American Lampyridae species, evinced the flashing (photogenic function) importance as a mating adaptation [65]. However, there is not any mentioning to the synchronous flashing already reported by numerous scientists as stated above. The discovery of the synchronization functionality in fireflies is due to Buck in 1935 who established that firefly synchronous flashing is related to the mating and it is persistent until copulation is produced or when there are no more unfertilized females capable of responding to synchronized males [9]. After that, the idea that synchronization is associated with processes of conspecific recognition and mating evolved until it was strongly accepted in the phenomenology of fireflies. A considerable number of studies and publications testified to the acceptance that the synchronization phenomenon is closely related to courtship and mating in fireflies. Concerning the topics discussed considering the aforementioned association, we highlight those related to mating protocols of synchronously flashing fireflies [14, 57], and to different aspects of flash communication [18, 59]. The well established and cumulated knowledge on firefly synchronization allowed a deeper qualitative understanding of this phenomenon and the popularization of these facts in excellent books such as those written by Lewis [51], and Ortler [71]. The formulation of mathematical models to explain firefly synchronization also played a significant role in improving the insight of the phenomenon; details of the most well-known ones are presented in Sect. 1.4.

1.4 Models to explain the fireflies' synchronous behavior

Several models intend to reproduce and explain the fireflies synchronous behavior. The basis of each model has different motivations that can go from simple guidelines of a game [90], via simple interaction rules [97] and mathematical considerations [67, 99] to more sophisticated analysis, where phase response curves (PRC) and Arnold's tongues are useful tools for describing dynamical features and synchronization.

1.4.1 A toy model

The so-called "solitary flash" game is a friendly and straightforward model leading to an explanation of firefly synchronous flashing behavior. Originally, the game has been proposed by Stewart and Strogatz [90] and its simple rules as they were raised:

1. The game board consists of a polygon of n sides, each of them containing r boxes, i.e. $N = n \times r$ boxes on the board.
2. The first box plays the role of the flashing box, i.e. when a player (firefly) arrives at this box, it flashes.
3. Each firefly starts the game in any box (initial condition) except the flash one.
4. Each firefly advances clockwise one position per time step.
5. When a firefly flashes, it remains in the flash box one-time step, while the other fireflies go forward according to the place in the board in which they are. For instance, if the firefly is on a box of the first side, it continues to advance one position; on the other hand, if the firefly is on a box of the second side, it advances two spaces, and three if it is on a box of the third side and so on.
6. The goal of the game is that all fireflies flash synchronously in the shortest possible time

The above-mentioned rules might allow or not the occurrence of synchronization. The dynamics of the game strongly depends on the initial conditions and also in rule 5 because it determines what happens to a firefly when it approaches, arrives or passes through the flash box. We consider the following four variants of rule 5:

(a) When a firefly is in a box located on the far side of the polygon, it could happen that it might overtake the flash box and consequently without flashing in its cycle. This fact imposes a difficulty in attaining of synchronization.
(b) When a firefly restarts a new cycle, it is mandatory that it arrives at the flash box and as a result, it flashes in each cycle. This rule facilitates the achievement of synchronization.

(c) When two or more fireflies are nearby the flash box, they wait until all of them are effective in this box; at this moment, all the fireflies advance one position. This modification respect to (b) makes it easier to attain synchronization.
(d) Finally, if we consider a similar situation than in (c) but with the modification that when the fireflies are forced to be in the flash box, the other fireflies advance according to rule 4 and not only one position as in the precedent case.

Some frames of the game evolution reflecting the rules (a)–(d), and some other possibilities for the cardboard are shown in Fig. 1.1.

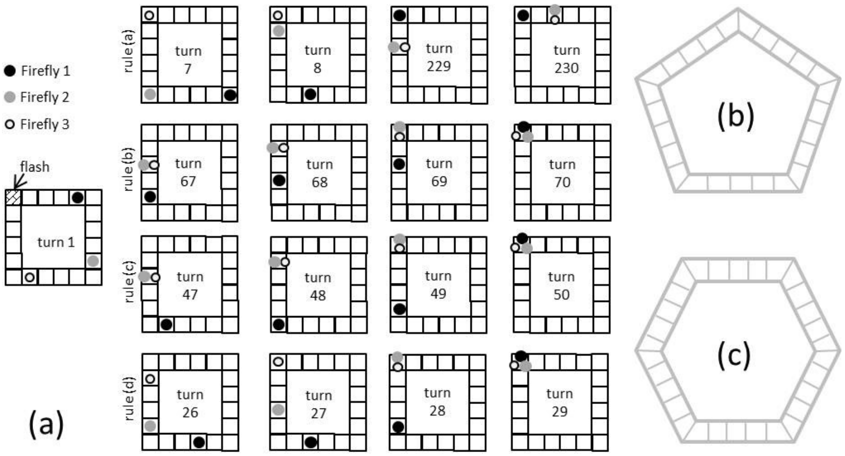


Fig. 1.1 (a) Frames of the game evolution for the rules (a)–(d) considering for all the four cases the same initial conditions $(n_{10}, n_{20}, n_{30}) = (5, 10, 15)$. Some other possibilities for the cardboard: (b) pentagon, and (c) hexagon.

Time series for all cases (a)–(d) are shown in Fig. 1.2, where we considered three fireflies and a specified set of initial conditions $(n_{10}, n_{20}, n_{30}) = (5, 10, 15)$. The basins of attraction for these cases are depicted in Fig. 1.2(e)–(h) where the condition is related to the lasted time to achieve synchronization with collective simultaneous flashing. It is interesting to observe in Fig. 1.2(a) that the fireflies do not reach the synchronization condition of simultaneous flashing of all the individuals of the system. Nevertheless, considering the formal definition of synchronization, the phase difference among the fireflies remains constant from the 228th turn; as a consequence, exhibiting synchronization but fireflies 1 and 2 do not flash in every cycle. On the contrary, Fig. 1.2(b)–(d) show that simultaneous flashing is achieved respectively in 70, 50, and 29 turns (time steps). So that, in principle it indicates that in successive order the rules that facilitate synchronization are respectively (d), (c), (b), and (a). With a view to sustaining the recent affirmation, we compute statistical parameters related to the synchronization time when all fireflies flash simultaneously, as well as the percentage of this situation in each basin of attraction for the

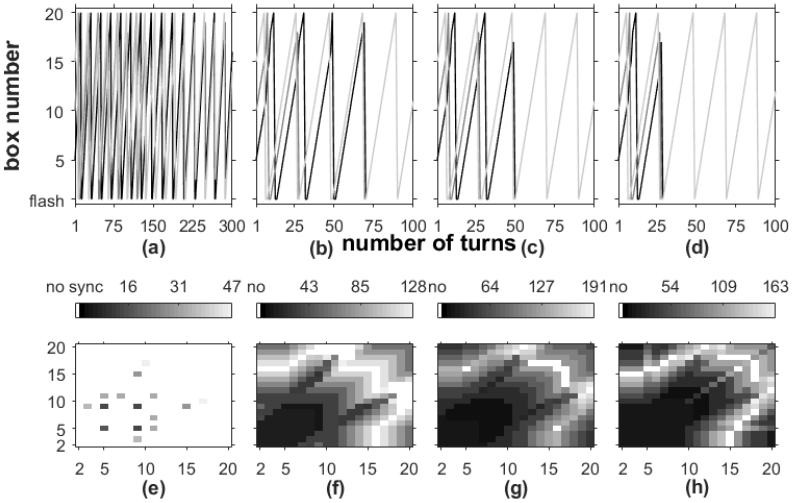


Fig. 1.2 First row: (a)–(d) Time series for the evolution of three fireflies following the rules (a)–(d) above mentioned. Second row: (e)–(h) Basins of attraction for the rules (a)–(d) considering that the initial condition for the first firefly is the box 5. White boxes represent situations in which simultaneous, collective, and persistent flashing (in every cycle) are not achieved.

indicated cardboard related to Fig. 1.2 (four sides and five effective boxes per side). The results are shown through a box plot in Fig. 1.3 where its information supports our assumption related to facilitated synchronization. This simple game with its four basic rules (algorithms) allows to explain synchronization in some species of fireflies, and it has an intrinsic richness since these simple rules can be translated to a more technical language belonging to synchronization theory. Thus, it is possible to find a relation between the number of sides and boxes per side with the type of coupling: in the case explained above, we have an excitatory coupling between the

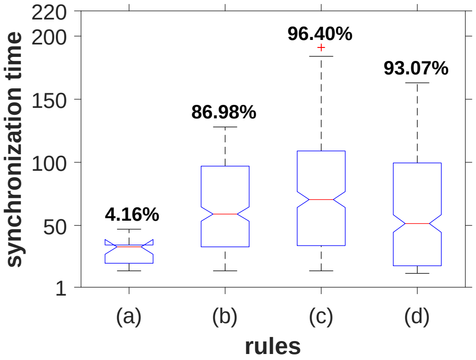


Fig. 1.3 Box plot of the statistical parameters (median and quartiles) related to Fig. 1.2 for the synchronization time associated with each of the rules. The percentage of the synchronous events are shown in the upper part, above the whisker. With all these information, it is possible to estimate which rule leads more often and quickly to synchronization.

fireflies (players). In some cases, as it is described in Sect. 1.4.5, for Light-controlled oscillators (LCOs) and for some species of fireflies, inhibitory coupling is also possible; this type of coupling might be incorporated in the game considering that for some boxes on the game board, the player must go back certain number of boxes according to its position. The high number of game choices (shape of the polygon, number of squares for each side of the polygon, the number of players, basic rules of the game, etc.) allow to extend the study of this model and analyze its isochronous dynamics as in [53].

1.4.2 Multi-agent based models

Conceptually, a MAS reflects one of the complex systems basis, namely the cooperativity due to the interactions among the components of the system giving rise to the accomplishment of a task or the emergence of a new property or functionality of the system. As stated in Sect. 1.1, several platforms are allowing to work with MASs. To explain the potentialities of MASs, we focus on the platform NetLogo [97] whose library contains a nice firefly model. This model is mainly based on the flashing behavior of some species: *Pteroptyx cribellata, Luciola pupilla*, and *Pteroptyx malaccae* described in [12], it has been built with simple interaction rules taking into account two main synchronization strategies (phase delay and phase advance) [96]. The agents of the model are fireflies having as a main feature that they have their own period, and a cyclic behavior, i.e. each firefly has an initial period and position as well as its position in the cycle; in most cases, the fireflies period are initially considered as identical for the whole population. The interaction of fireflies is done by means of the flashes that they can emit (influencing the rest of the individuals) or perceive (being affected in their dynamics). Synchronization might be achieved according to the rules and the parameter values. SpikingLab is another interesting application done in NetLogo and related in some way to fireflies; actually to the integrate-and-fire oscillators, a popular model describing synchronization in fireflies (explained in more detail in Sect. 1.4.4). This NetLogo project introduces a Spiking Neural Network (SNN) phenomenological model mimicking the neural dynamics regardless of the biophysical processes [46]. As a consequence, all the neural features such as membrane and resting potential, spike threshold, inhibitory and excitatory postsynaptic response, exponential decay rate and refractory and absolute periods are embedded in two possible states: open and absolute refractory. The model is used for simulating a virtual insect able to process three types of information: visual and sensations related to pleasure and pain.

One of the most important applications of firefly synchronization is that related to communication networks and algorithms allowing a synchronous behavior on certain devices. In general, the above-mentioned applications use MAS concepts and programming. For instance, another way to solve the firefly synchronization task was carried out by Teuscher and Capcarrere, using two-dimensional (2-D) cellular automata (CA) and random boolean networks [92], programming in such a way; the

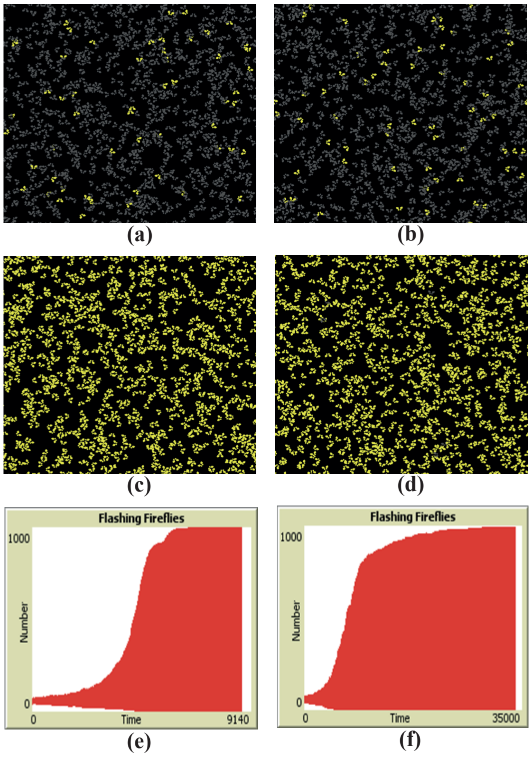

(a) (b)
(c) (d)
(e) (f)

Fig. 1.4 (Color online) Screenshots of NetLogo fireflies model interface using the strategy of phase delay (first column), and phase advance (second column). The general parameters are: number of fireflies = 1000, flash length = 2, flashes to reset = 2, and cycle-length = 35. (a) and (b) represent the arena showing the initial situation with few number of fireflies flashing simultaneously; (c) and (d) the final one where almost all fireflies are flashing in synchrony; and (e) and (f) the time series showing the number of fireflies vs. the time steps. In both cases, the program runs until synchronization is fully established. For the delay strategy, the synchronization time is around 6200-time steps, and for the advance one, it is around 31000-time steps.

performing computations are locally and based on co-evolution. They have also implemented employing an FPGA-Evolware. In other words, software and hardware implementation have been designed for solving the firefly synchronization task successfully. Other works dealing with synchronization in a framework of MAS have been mostly developed with PCOs. There are some other applications based on firefly synchronization and MAS that are pointed out in Sect. 1.6.

1.4.3 Phase and relaxation oscillators

After a systematic study of the biological and chemical properties of flashing fireflies and their synchronous behavior, Winfree attempted to build a mathematical model capable of describing synchronization in large populations of *phase oscillators* and considering that each firefly is represented by an oscillator of this type [99]. Let us start by understanding the features of these oscillators. A phase oscillator might be considered as an oscillator whose periodic solution travels around a circular limit cycle with angular velocity $\Omega(r^*)$. Winfree proposed a model of coupled phase oscillators characterized by a sensitivity and an influence function, depending only on the phase. Mathematically, the Winfree's model might be written as:

$$\dot{\theta}_i = \omega_i + \left(\sum_{j=1}^{N} X(\theta_j) \right) Z(\theta_i) \ , \ \ i = 1, \cdots, N \ , \tag{1.5}$$

where the phase and natural frequency of oscillator i are represented respectively by θ_i and ω_i. All the oscillators i are influenced by oscillator j through the phase by $X(\theta_j)$; as a result, oscillator i responds through the phase-dependent function $Z(\theta_i)$ called the sensitivity. Using this model applied to a population of oscillators, Winfree found that there is a sort of phase transition towards the synchronization. Some other works dealing with Winfree's model have been developed and in particular that of Ariaratnam and Strogatz [2] is very interesting because they obtain the phase diagrams showing the different regions of the dynamical behavior of this model: total and partial locking, total and partial oscillation death, and incoherence.

After the Winfree formulation, other phase oscillator based models were proposed, one consisting of 25 sawtooth coupled oscillators with an experimental realization. Each one of these oscillators consists of a neon tube N connected to a battery E through a resistance R and shunted by a capacitance C as shown in Fig. 1.5(a). The functioning of the oscillator is determined by the current-voltage characteristic (Fig. 1.5(b). The oscillation is produced as follows: the condenser charges until it reaches the voltage V_0 and the oscillator fires generating a current I_1 during the discharge of C until V_d and then restarting the charging process; so that, giving rise to oscillation.

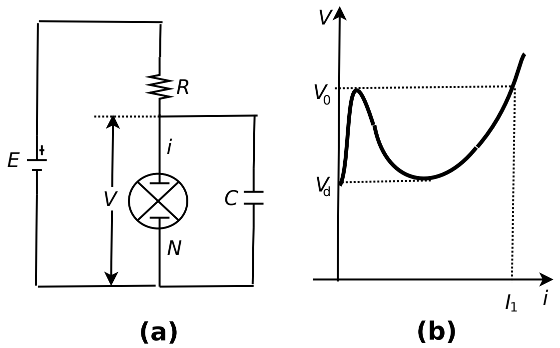


Fig. 1.5 (a) Scheme for the sawtooth oscillator, being the neon tube N the heart of the oscillator. (b) Current-voltage characteristic of N.

Following the intuitive model of Winfree, Kuramoto developed a more formal model carefully described in [48], where he used perturbation methods, weak coupling $K \geq 0$, almost identical oscillators, and the concept of mean field coupling to obtain its famous equation:

$$\dot{\theta}_i = \omega_i + \frac{K}{N}\sum_{j=1}^{N} \sin\left(\theta_j - \theta_i\right) \ , \ \ i = 1, \cdots, N \ . \tag{1.6}$$

The Kuramoto model with its purely sinusoidal coupling constitutes the simplest possible case of equally weighted, all-to-all coupled oscillators. The model can also be described in terms of the order parameters r and ψ, resulting:

$$r\mathrm{e}^{i\psi} = \frac{1}{N}\sum_{j=1}^{N} \mathrm{e}^{\theta_j} \ , \tag{1.7}$$

where $r(t)$ is a normalized function that is a measure of the oscillators population coherence, and ψ is the average phase. Using Eq. (1.7), the original model states:

$$\dot{\theta}_i = \omega_i + Kr\sin(\psi - \theta_i) \ , \ \ i = 1, \cdots, N \ , \tag{1.8}$$

indicating that each oscillator is coupled to the common average phase with coupling strength given by Kr [1]. Under the consideration of certain assumptions, it is possible to find a critical value for the intensity of coupling K_c denoting a bifurcation point and also that for $K > K_c$, there is a dramatic increase in the coherence of the oscillators population when the bifurcation is supercritical. There are several reviews of the importance of Kuramoto model for synchronization and networks [1, 83] and also some recent extensions including adaptive frequencies [72].

Another firefly-inspired model is due to Ermentrout [29] who proposed a mechanism that allows the fireflies to synchronize at a nearly zero phase difference. The model has a PRC that it is the same as the determined for *Pteroptyx malaccae*, but the behavior under a train of periodic stimuli is different due to the adaptive character of the model. Firstly, he considered a single periodically forced oscillator stated by:

$$\dot{\theta} = \omega + P(t/\tau)\Delta(\theta) \quad \mathrm{mod}\ (1) \ , \tag{1.9}$$

where ω is the oscillator's natural frequency, $P(\phi)$ is the periodic forcing stimulus, and $\Delta(\theta)$ is the oscillator PRC. All functions are one-periodic. Under certain assumptions, it is possible to average Eq. (1.9) and obtain:

$$\dot{\theta} = \omega + H(t/\tau - \theta) \ , \tag{1.10}$$

where H depends on the PRC as

$$H(\phi) = \int_0^1 P(s)\Delta(s - \phi)\mathrm{d}s \ . \tag{1.11}$$

The 1:1 phase-locked solutions of Eq. (1.9) are:

$$\theta_n \to \tilde{\theta} \ , \ \Delta(\tilde{\theta} + \omega\tau) = 1 - \omega\tau \ . \tag{1.12}$$

The latter can be solved considering that $1 - \omega\tau$ does not exceed the maximum of Δ or fall below the minimum of Δ, giving:

$$\tilde{\theta} = 1 - \omega\tau + \Delta^{-1}(1 - \omega\tau) \ . \tag{1.13}$$

If $\Delta(0) = 0$, then $\omega\tau \equiv 1$, means that the intrinsic frequency is the same than the forcing one. This model for N coupled oscillators might be written as:

$$\dot{\theta}_i = \omega_i + \sum_{j=1}^{N} H_{ij}(\theta_j - \theta_i) \ . \tag{1.14}$$

The main result of the analysis of Eq. (1.14) states that there can be phase-locking but with phase differences not necessarily close to zero.

Relaxation oscillators are one of the most suitable models to study systems susceptible to synchronize: neurons, cardiac cells, and fireflies. An important feature of these oscillators is that within each cycle, there are two time scales: a slow one where an integration process takes place, and a fast one where a firing process occurs. Contrarily to the common phase oscillators, the relaxation oscillators waveform is very different from a sinusoidal wave; rather it looks like a sequence of pulses. There is no universal model for relaxation oscillators, having each of one their proper characteristics [73].

Numerous examples of relaxation oscillators may be found in literature, ranging from electronic devices generating relaxation oscillations [74] to those applied to biology, especially in neurons [45]. One of the most classical examples of a self-oscillating system is the van de Pol equation described by the equation of motion

$$\ddot{x} - \mu(1 - x^2)\dot{x} + x = 0 \ , \tag{1.15}$$

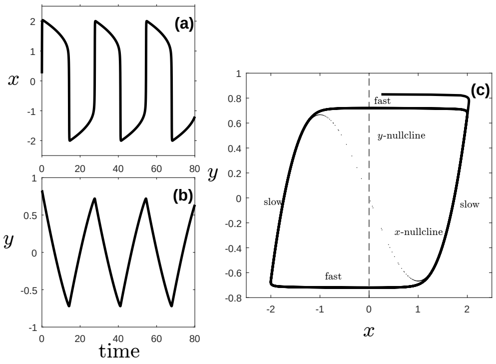
where for large μ behaves as a relaxation oscillator (Fig. 1.6(a)). Eq. (1.15) may be cast into a set of first-order differential equations:

$$\dot{x} = \mu\,[y - F(x)] \tag{1.16a}$$

$$\dot{y} = -\left(\frac{1}{\mu}\right)x \ , \tag{1.16b}$$

that allows us to observe the following: the x-nullcline given by the relation $y = F(x)$, has a cubic form and the y-nullcline, provided by the expression $x = 0$ is a vertical line. Both nullclines, as well as the corresponding limit cycle, are illustrated in Fig. 1.6(c). This system has one fixed point, located at the origin, where the two nullclines cross one another. The motion along the limit cycle trajectory involves two time scales, a fast horizontal movement, and a slow vertical motion. When y is near the x-nullcline, both $\mathrm{d}x/\mathrm{d}t$ and $\mathrm{d}y/\mathrm{d}t$ vary gradually, and the movement is slow. When the trajectory departs from the cubic nullcline $\mathrm{d}y/\mathrm{d}t$ is large, and the horizontal movement is fast. Another well-known relaxation oscillator is the IFO that deserves our attention in Sect. 1.4.4 because it is one of the most used models to describe synchronization in fireflies.

Fig. 1.6 van der Pol oscillator acting as a relaxation one when μ=10. Time series for the variable (a) x that shows a relaxation regime, and (b) y that shows a rotator regime. (c) Limit cycle trajectory and the accompanying fast and slow time scales.



1.4.4 Integrate and fire oscillators

These oscillators were extensively used to model a great variety of phenomena such as synchronization in fireflies [67] and several aspects of neuronal systems [30] among others. IFO models were also used to describe firing patterns [35] and critical phenomena [22] such as avalanches.

IFOs are principally used to describe collective behavior. To model self-synchronization of the cardiac pacemaker, Peskin considered a network of N IFOs, each characterized by a voltage-like state variable V_i, whose dynamics is:

$$\frac{\mathrm{d}V_i}{\mathrm{d}t} = I - \eta V_i, \qquad 0 \leq V_i \leq 1, \qquad i = 1, \ldots, N. \tag{1.17}$$

When the oscillator i reaches the threshold ($V_i = 1$), the oscillator "fires" and V_i is reset *instantaneously* to zero (Fig. 1.7(a)). The oscillators interact by a simple form of pulse coupling: when a given oscillator fires, all the other variables V_j, $j \neq i$ are increased by an amount β/N (the quotient by N is introduced in order to get reasonable behavior in the thermodynamic limit $N \to \infty$). That is,

$$\text{If} \quad V_i(t) = 1 \quad \Longrightarrow \quad V_j(t^+) = \min(1, V_j(t) + \beta/N), \quad \forall j \neq i\,. \tag{1.18}$$

Moreover, the oscillator at the state $V = 0$ (i.e., just after firing) cannot be affected by the others, so that the state $V = 0$ is absorbing. The latter ensures the possibility of perfect synchronization. To illustrate how this model works, we have numerically solved (1.18) for two mutually coupled IFOs and 500 globally coupled oscillators (see Fig. 1.7(b)), where we observe that at the beginning, each oscillator has its own natural frequency and as time goes by, groups of synchronous oscillators are formed, and finally, the entire population is synchronized, i.e. all the IFOs emitting their pulses simultaneously. Here, we have considered several phase oscillator models all of them related to the explanation of firefly synchronization in its simplest form. All

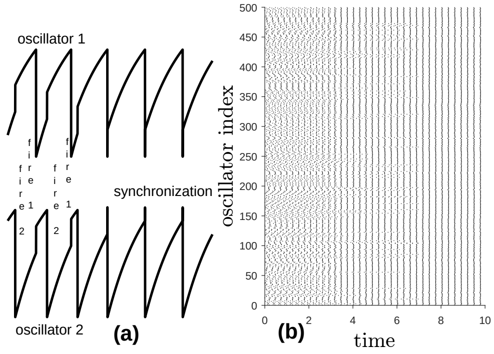


Fig. 1.7 (a) Synchronization mechanism in two coupled IFOs. (b) Points correspond to firing times to represent the dynamics of a population of 500 coupled IFOs showing the tendency towards complete synchronization. The parameter values used in both cases are $I = 2.5$, $\eta = 1$ and $\beta = 0.25$.

these models could be applied to other oscillatory systems, but their original goal was to understand how and why fireflies synchronize.

1.4.5 Light-controlled oscillators: Electronic fireflies

As it has been stated above, most of the analytical models of fireflies synchronization were based on mathematical equations driven the system of coupled oscillators to synchronize. Nevertheless, some experimental devices allow the study of synchronization by carrying out careful experiments. One of these devices is the LCO that also receives the appellation of *electronic firefly*. From a technical viewpoint, each LCO consists of an LM555 chip wired to function in its astable oscillating mode (Fig. 1.8(a)). The alternations of it are determined by a dual *RC* circuit in parallel with four photo-sensors that allow the LCO to interact with others by means of light pulses (Fig. 1.8(b)). Basically, an LCO is a relaxation oscillator in the sense that it has two time scales characterized by the binary variable $\varepsilon(t)$: within each cycle there are intervals of slow (charging stage, $\varepsilon(t) = 1$) and fast (discharging stage, $\varepsilon(t) = 0$) motion. The period is determined by the two external *RC* circuits and the output waveform takes the form of a pulse signal with minimum and maximum values set at $\frac{V_M}{3}$ and $\frac{2V_M}{3}$ respectively, V_M being the value of the supply voltage. These threshold voltages determine the value of $\varepsilon(t)$. If we consider a system composed of N LCOs, the equation we use to model the voltage evolution for the i^{th} LCO is:

$$\frac{\mathrm{d}V_i(t)}{\mathrm{d}t} = \underbrace{\lambda_i(V_{Mi} - V_i(t))\varepsilon_i(t)}_{\text{charging term}} - \underbrace{\gamma_i V_i(t)[1-\varepsilon_i(t)]}_{\text{discharging term}} + \underbrace{\sum_{j=1}^{N} \beta_{ij}\delta_{ij}[1-\varepsilon_j(t)]}_{\text{coupling term}}\ , \tag{1.19}$$

where

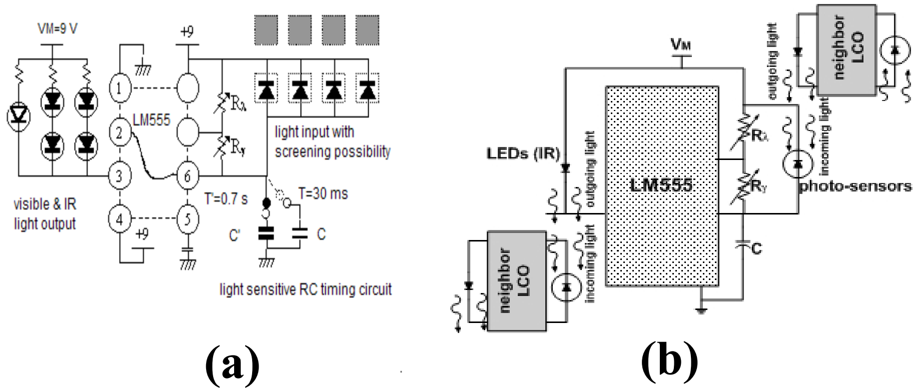


Fig. 1.8 (a) Block diagram of an LCO with the LM555 in its astable functioning mode. (b) Simplified diagram of the LCO and schematic view of the coupling between LCOs.

$$\delta_{ij} = \begin{cases} 1 \text{ , if } i \neq j \text{ and they may interact} \\ 0 \text{ , otherwise} \end{cases}$$

indicates whether or not LCOs i and j interact. Note that the interaction term is active only when at least one of the other LCOs is discharging. In this model, we consider symmetric coupling, such that $\beta_{ij} = \beta_{ji}$. Another important experimental fact is the coupling distance-dependent, i.e. the coupling strength β is almost quadratically inverse with the distance, being the measured dependence: $\beta_{ij} \propto \frac{1}{r_{ij}^{\alpha}}$, being the power α=2.11.

Several experiments have been carried out with LCOs such as measurements of phase-locking and phase differences in various sets of locally coupled LCOs [76], transients [85] and determination of synchronous regions [84, 86]; in all of them, the model described by Eq. (1.19) has been validated. On the other hand, locally and globally coupled LCOs were studied comparing their dynamical features, finding astonishing changes in their dynamics, despite very small differences between the oscillators [80]. Studies dealing with the influence of noise on LCOs have also been done using uniform [77] and Gaussian [79] distributions, resulting in some impressive results. Such as those showing that white noise can enhance synchronization on a set of two LCOs under the condition that the noise acting on each of one has different variances, i.e. various noise intensities acting on each LCO.

From a biological point of view, the use of LCOs as a fireflies model, allows to describe realistic situations in which, there is a population of 10 fireflies distributed randomly both spatially and in what concerns their initial condition V_{i0} and considering a distance-dependent coupling (Fig. 1.9(a) for identical, and (b) for nonidentical fireflies). It is possible to describe synchronization employing polar plots where the radial and angular coordinate are related to period and to phase difference measured with respect to a reference firefly (in this case, firefly 2). The frames corresponding to Fig. 1.9(a1)–(a4), and (b1)–(b4) display the dynamical situations after 2, 250, 500, and 1000 flashing events respectively. Thus, for identical fireflies and after 250 flashing events, there are two synchronous clusters, one constituted by fireflies 7, 9, and 10, and the other by the rest of fireflies; these two clusters are maintained over time until 1000 flashing events. According to the fireflies positions into the arena, it does not surprise the emergence of the cluster formed by fireflies 7, 9, and 10, although it could also be expected that firefly 3 be part of it; but undoubtedly, the initial conditions made it possible to arrive at the situation shown in Fig. 1.9(a4). On the other hand, for the configuration of nonidentical fireflies of Fig. 1.9(b), it is observed that after 250 firing events, there are four groups of fireflies with the following distribution: (i) 1 and 8, (ii) 5 and 9, (iii) 10 and (iv) 2, 3, 4, 6 and 7 (Fig. 1.9(b2)). Synchronous cluster formation is interesting because it reflects in some way the position of the fireflies in the arena. As time lasts, groups (i) and (ii) are “absorbed” by (iv) (Fig. 1.9(b3)), situation that persists up to 1000 firing events (Fig. 1.9(b4)). Even tough, Firefly 10 has a very similar period to that of the large synchronous bunch, its phase difference is different. Again, the position of the fireflies seems to play an important role in the emergence of the synchronization.

Throughout this Sect., we have considered all the models are attempting to explain synchronization in fireflies as a self-organization process but without specific details on the features of each firefly species (except for the Ermentrout model). In general, most of the models consider only the oscillators ability to synchronize and that all of them have similar features (associated with the oscillators identity, e.g. males). Nevertheless, if we desire to understand the firefly courtship as a whole, it is necessary to take into account not only the emergence of males’ synchronization but also the females’ response, considering that the oscillators associated to each of the sexes are dissimilar to the other sex. Precisely in the next Sect. we address this problem.

1.5 Response to synchronization

Already in the beginnings of the century, the courting behavior of *Photinus pyralis* has been described and even some simple experiments to reinforce the males’ behavior have been carried out. After that, the female response was observed and described in detail for *Photinus* fireflies [56], introducing the mechanism “flash-answer” that is part of a sexual function of bioluminescence and allows the conspecific identification, avoiding the interspecific one. Some exceptions must be pointed out that are related to the aggressive mimicry where females of the genus *Photuris* attract and devour males of the genus *Photinus* by mimicking the flash responses of *Photinus* females [55, 58]. The observation on *Photinus* flash-patterns describing their importance in fireflies communication, as well as their importance in courtship, deserved the attention and numerous publications came to light allowing a better understanding of the mating process as a whole [17, 19, 52, 59, 89].

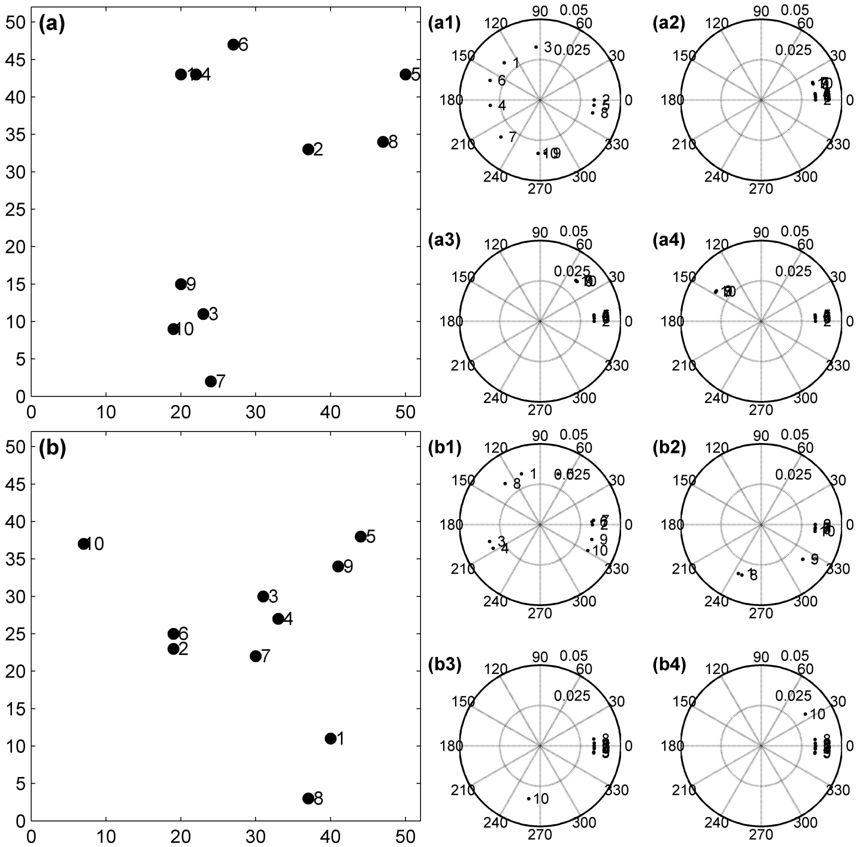


Fig. 1.9 Ensembles of 10 (a) identical and (b) nonidentical globally coupled fireflies with a distance-dependent coupling and randomly distributed in an arena consisting of 50×50 cells. Polar representation where the radial and angular coordinates are respectively related to the fireflies' period and phase difference. (a1)–(a4) Identical and (b1)–(b4) nonidentical LCOs. Frames showing the dynamical polar distribution after (a1) and (b1) 2, (a2) and (b2) 250, (a3) and (b3) 500, and (a4) and (b4) 1000 flashing events.

In 2010, Moiseff and Copeland reported a surprising finding issued from experiments carried out with virtual males and a real *Photinus carolinus* female; they showed that males' synchronization is associated with the female's response [68]. The latter improved the knowledge concerning the synchronous behavior of fireflies, enhancing the fact that both males and females participate actively in the courtship. In other words, when referring to fireflies courtship, we must consider the females' response to males' synchronization. A first attempt to explain the response to synchronization [75] has been made using a modified LCOs model, in which, males and females exhibit dissimilar features when they are interacting. The model described in [75] not only reproduces the experimental results shown in [68], but it is also capable of predicting more complex and realistic situations; in particular, the behavior of other species of the genus *Photinus*. As stated in [52], there are species differences in the courtship flash signals of *Photinus* fireflies; this special feature permits even to identify *Photinus* species just by recognizing their courtship flashing patterns. Some examples for these flashing patterns in the case of males are [52]: two flashes per phrase for *Photinus consanguineus* and *Photinus greeni*, six flashes per phrase for *Photinus carolinus* (the species considered in [68, 75], eight flashes per phrase for *Photinus consimilis*.

In order to model the response to synchronization, it is considered the dissimilarity in their oscillatory features between males and females. In Fig. 1.10 is explained the terminology used in the description of a male and a female. The first type (Fig. 1.10(a) fires a burst of n_f spikes (flashes) during the active phase, followed by a quiescent or silent time T_s, a parameter that remains constant even when the oscillators are coupled. The female has one flash in its fast discharging process T_d which is preceded by a long-lasting charging process T_c and followed by a silent time T_s (Fig. 1.10(b). We define the interburst period or the duration of a phrase T_p as the complete cycle comprising the active phase and the silent time. Consequently, the active phase takes $n_f(T_c + T_d) = Tp - Ts$. Males and females are individually considered as relaxation oscillators because they have two different time scales, i.e., within each cycle, there is a slow process followed by a firing process. Each process ends at its own threshold, being the lower and the upper thresholds at $V^{\text{lower}} = V_M/3$=3 and $V^{\text{upper}} = 2V_M/3$ =6 respectively. We take these threshold values in connection with the experimental aspects related to the LCO, namely, the oscillator serving as the basis of the model stated in Eq. (1.20). Note that we take V_M=9 which is the considered value from an experimental point of view and related to the value of a voltage source. It is also important to note that in Fig. 1.10(a), the parameter values and $n_f = 6$ which corresponds in biological terms to the *Photinus carolinus* flashing pattern. It is clear that the model could be adapted to other species just in changing the relevant parameters.

The equations describing the dynamical variable V_i of each oscillator i are given by:

$$\frac{\mathrm{d}V_i(t)}{\mathrm{d}t} = \frac{\ln 2}{T_{ci}}\left(V_{Mi} - V_i(t)\right)\varepsilon_i(t) - \frac{\ln 2}{T_{di}} V_i(t)\left(1 - \varepsilon_i(t)\right), \tag{1.20a}$$

$$V_i(t) = \left(V_i(t) - V_i^{\text{lower}}\right)\varepsilon_i(t) + V_i^{\text{lower}}. \tag{1.20b}$$

As stated above, V_M is a constant that determines the lower and upper thresholds and $\varepsilon_i(t)$ is a binary variable describing the state of the ith oscillator by:

$$\begin{array}{ll} \varepsilon_i(t) = 1 : \text{extinguished oscillator} & \text{(charging and silent stage)} \\ \varepsilon_i(t) = 0 : \text{fired oscillator} & \text{(discharging stage)}. \end{array}$$

The transition between the states determined by ε is described by the following relation:

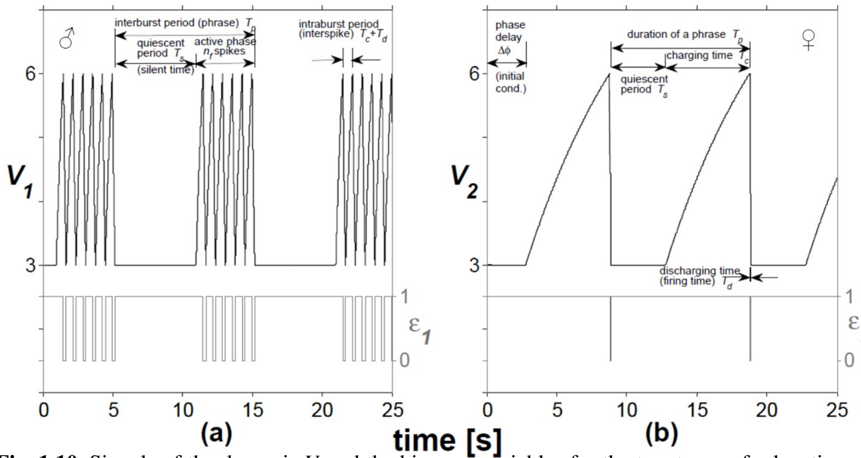


Fig. 1.10 Signals of the dynamic V and the binary ε variables for the two types of relaxation oscillators used in this work. They are characterized by the quiescent period T_s, the active phase with n_f spikes per burst, the interburst period or silent time T_s, the charging and the discharging times T_c and T_d respectively, the intraburst or interspike period $T_c + T_d$, the interburst period or duration of a phrase T_p, and the phase delay $\Delta\phi$ that plays the role of initial condition. (a) Male oscillator that in this case has the following parameter values: T_p=10.000 s, n_f=6 (*Photinus carolinus*), T_c=0.500 s, T_d=0.200 s, T_s=5.800 s and $\Delta\phi$=0.603 rad $\equiv$ 0.960 s. (b) Female oscillator having in this particular case the parameter values: T_p=10.000 s, n_f=1, T_c=6.000 s, T_d=0.100 s, T_s=3.900 s and $\Delta\phi$=1.750 rad $\equiv$ 2.785 s.

$$\textbf{If} \quad V_i(t) = V_i^{\text{lower}} \quad \textbf{and} \quad \varepsilon_i(t) = 0 \quad \textbf{then} \quad \varepsilon_i(t_+) = 1; \tag{1.21a}$$

$$\textbf{If} \quad V_i(t) = V_i^{\text{upper}} \quad \textbf{and} \quad \varepsilon_i(t) = 1 \quad \textbf{then} \quad \varepsilon_i(t_+) = 0; \tag{1.21b}$$

$$\textbf{If} \quad V_i(t) = V_i^{\text{lower}} \quad \textbf{and} \quad \varepsilon_i(t) = 1 \quad \textbf{then} \quad \varepsilon_i(t_+) = 1, \tag{1.21c}$$

where t_+ in the condition given by Eq. (1.21c) is defined in the interval

$$t = [t_+ \;\; (k-1)(T_p + n_f(T_c + T_d)) + \Delta\phi]$$

for every k interburst period or phrase, i.e., for every complete cycle comprising the active phase and the silent time.

The main feature of the considered oscillators dwells on its firing process which allows a pulsatile coupling with other oscillators that can receive these pulses or spikes leading to a modification in their oscillatory dynamics. The dynamical equations describing a generic group of N coupled oscillators are:

$$\frac{\mathrm{d}V_i(t)}{\mathrm{d}t} = \frac{\ln 2}{T_{c0i}} (V_{Mi} - V_i(t))\, \varepsilon_i(t) - \frac{\ln 2}{T_{d0i}} V_i(t)\, (1 - \varepsilon_i(t)) + \theta_i \sum_{i,j=1}^{N} \beta_{ij} (1 - \varepsilon_j(t)), \tag{1.22}$$

where $i, j = 1, \ldots, N$. Conditions that are given by Eq. (1.20b) and Eqs. (1.21), which take into account the existence of a silent time, must also be followed by Eq. (1.22). The quantities T_{c0i} and T_{d0i} are, respectively, the lasting time of the charge and the discharge when there is no action on the oscillator i by other oscillators. Furthermore, we consider that oscillators are mutually coupled with a coupling strength β_{ij} that represents the pulsatile action of the oscillator j spike during its discharge upon the oscillator i. Concurrently, β_{ij} are the elements of the weighted adjacency matrix of the set. A simple inspection of Eq. (1.22) shows that both charging and discharging stages might be modified by the effect of the coupling with other oscillator(s). The charging and the discharging times might be shortened or lengthened respectively when the pulsatile action due to the firing of other oscillator(s) takes place. The latter is determined by the value of θ that takes the values:

$$\theta = \begin{cases} 1\,, & \text{Males} \\ -1\,, & \text{Females} \end{cases}$$

This factor is significant because it determines the behavior of the oscillators when stimuli are applied to them.

Several studies have been carried out in [75] considering *Photinus carolinus* flash patterns. Here, we show in Fig. 1.11 the interaction between a set of eight males and four females that according to their flash patterns correspond to *Photinus consanguineus*. Fig. 1.11(a) shows how the males' flashes evolve until all the population is completely synchronized and how females trigger their responses, firstly sporadically and then permanently as shown in Fig. 1.11(b). This phenomenon that appears in *Photinus* fireflies might be extended to other types of oscillators under the con-

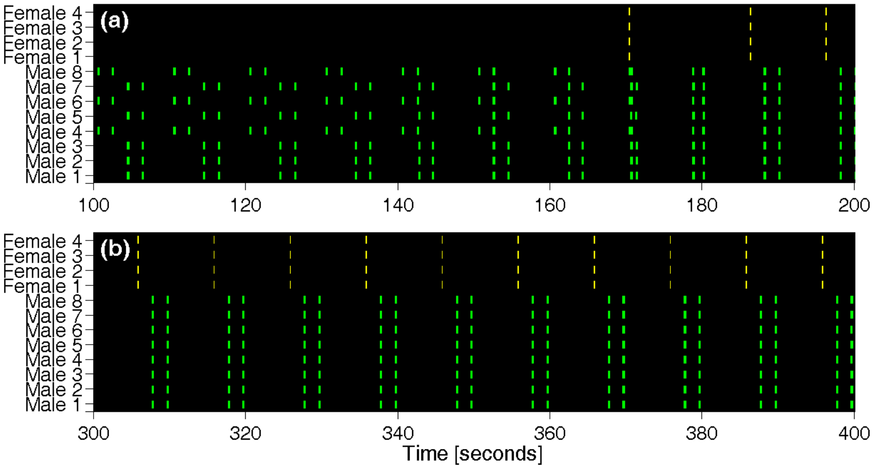


Fig. 1.11 (Color online) Evolution of the flashes in a population of 12 slightly different males and four slightly different females considering similar parameters and features as in Fig. 1.10. (a) Sequence from 100 s to 200 s in which, the males are not synchronized until around 180 s, and consequently, the females do not respond, or they do it sporadically as it appears for around 170 s. (b) Sequence from 300 s to 400 s in which, the males are completely synchronized, resulting in permanent and simultaneous females' responses.

dition that they are dissimilar as stated in [78] where the mechanisms of response to synchronization were unraveled. The response to synchronization phenomenon is illustrated in Fig. 1.12, where in (a) it is shown a set of males that can synchronize and, in (b) a set of females that their interactions do not lead to synchronization. Finally, when both populations are mingled as in Fig. 1.12(c), the males still synchronize, and as a result of this, females respond following different patterns being the most interesting the simultaneous and permanent responses, as they have acquired the property to synchronize. When extending the results to other types of oscillators and considering the role of network topologies, it is possible to deeply study the collective behavior of these interacting dissimilar oscillators both from a theoretical and experimental point of view, especially when the sets are composed of a considerable number of oscillators. The latter could contribute to a better understanding of systems that exhibit the phenomenon of response to synchronization, viz. fireflies, neurons, and possibly other animals and other types of cells.

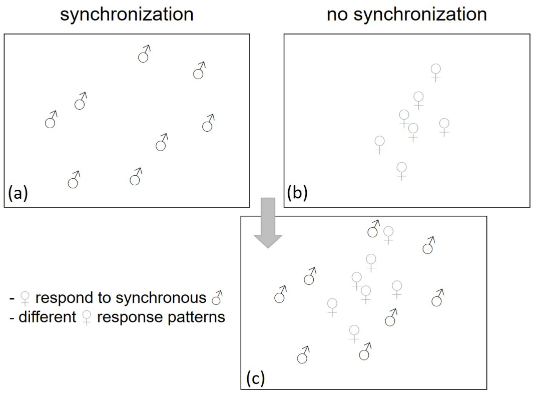


Fig. 1.12 Illustration of the response to synchronization event in *Photinus* fireflies. (a) A set of interacting males that can easily synchronize. (b) A set of interacting females that cannot synchronize. (c) Mingled set of males and females, where the males still synchronize and as a consequence, females respond exhibiting different response patterns according to the parameter values and initial conditions being one of the possible responses, the simultaneous and permanent females flashing in each cycle as shown in Fig. 1.11(b).

1.6 What have we learnt from fireflies?

Sometimes talking about fireflies seems to be very romantic and without any relationship to science and living well. Thus, it is not surprising to find some opinions published in newspapers such as that cited by Strogatz [91] and Bojic et al. [6]: On May 18, 1993, an article entitled “Govt. Blows Your Tax $$ to Study Fireflies in Borneo-Not a Bright Idea! published in the tabloid *National Enquirer* recorded the opinion of the Representative Tom Petri who said:

> Spending taxpayers money studying fireflies doesn’t sound like a very bright idea to me.

Certainly, is not a fortunate opinion and denotes a plain ignorance concerning how much the basic research can offer. As we have already mentioned, the knowledge acquired from fireflies is enormous and only referring to the most recent ones, we can mention the use of the firefly synchronization in the wireless network's world. Under the inspiration of the fireflies synchronous behavior, it is possible to argue that in communication processes, it is better to consider cooperation concepts rather than think in a system driven by a master. Hence, if all nodes cooperate, synchrony can be reached within few periods. Once nodes have agreed on a common time scale, they are then able to communicate in a synchronous manner using a slotted medium access protocol, benefiting from fewer collisions and higher throughput. When working with Wireless Sensor Networks (WSN), firefly synchronization is also exploited, and algorithms based on this concept are tested with the aim of giving greater robustness to the WSN. Other concepts such as the Meshed Emergent Firefly Synchronization (MEMFIS) that mitigates the acquisition phase by integrating synchronization into the communication phase have also been developed to enhance the robustness of the network [95]. Nowadays, the formulation of universal algorithms for WSNs is one of the main tasks. Other networks such as the cognitive radio ad hoc networks (CRAHNs) can also use a synchronization protocol based on fireflies and as a result, the convergence time to synchronization is shorter than convergence time using other protocols [54]. The use of fireflies as role models seems to have the best characteristics for synchronization mechanism related to Machine-to-Machine (M2M) systems (in general composed of networked computational devices) [6]. From the recent review of applications in networks, it is clear that firefly synchronization concept plays an important role and further development is also based on this fact.

Mobile networks or devices have also found significant developments with ideas issued from firefly synchronization. Thus, applications to the optimization of mobile networks have also been developed using firefly-synchronized agents [7]. On the other hand, the so-called firefly algorithm [100] is a swarm intelligence (collective behavior and decentralized systems) is a kind of stochastic, nature-inspired, metaheuristic algorithm that can be applied to solving the hardest optimization problems. It solves problems of continuous optimization, combinatorial optimization, constraint optimization, multi-objective optimization, as well as dynamic and noisy environments, and even classification. It is widely applied in engineering problems [33]. Algorithms based on firefly synchronization have also been used for swarms of robots as a first approach for understanding real task-execution scenarios [21]. In the same line, possible interactions between real and electronic fireflies (mixed populations) were proposed and even with the possibility of considering males and females differently (mingled populations) that could help to a deeper understanding of the underlying behavior of fireflies and also find potential applications based on the response to synchronization. A picturesque view of this kind of mixed and mingled sets of electronic and real fireflies is shown in Fig. 1.13. Finally, we could mention some new impact applications such as those leading to improve the efficiency of LEDs [4], or those to conduct a new method of medical diagnostics based on the way in which fireflies produce cold light [87]. In summary, fireflies not only delight

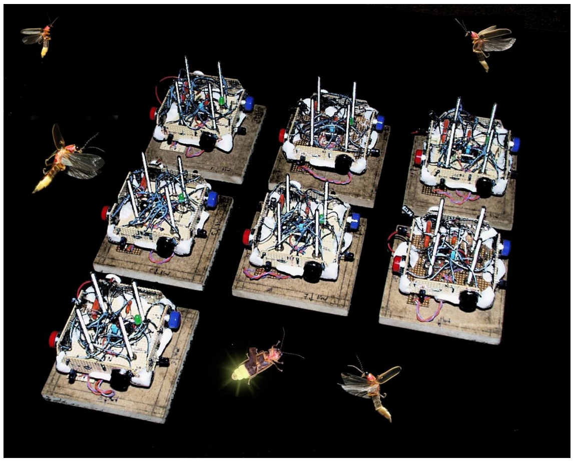


Fig. 1.13 (Color online) A picturesque view of the interaction between LCOs (electronic fireflies) and real fireflies. Electronic fireflies would be designed either to simulate the behavior of males or females, and real males and females would be part of the system as well. (Use of fireflies images with permission of Terry Priest.

us with their beautiful, hypnotic flashes but also they allow us to better understand nature in their many facets from basic phenomena such as self-organization to all the applications in a wide variety of fields. The emergence of functional synchronization due to the collective behavior without any leader, the response to synchronization, the biochemical mechanism of luminescence, are only a few of the issues that fireflies “illuminated” us.

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References

[1] Acebron, J., Bonilla, L., Vicente, C., Ritort, F., Spigler, R.: The kuramoto model: A simple paradigm for synchronization phenomena. Rev Mod Phys **77**(1), 137–49 (2005)

[2] Ariaratnam, J., Strogatz, S.: Phase diagram for the winfree model of coupled nonlinear oscillators. Phys Rev Lett **86**(19), 4278–4281 (2001)

[3] Ballantyne, L., Lambkin, C.: Systematics and phylogenetics of indo-pacific luciolinae fireflies (coleoptera: Lampyridae) and the description of new genera. Zootaxa **3653**, 1–162 (2013)

[4] Bay, A., Cloetens, P., Suhonen, H., Vigneron, J.: Improved light extraction in the bioluminescent lantern of a photuris firefly (lampyridae). Opt Express **21**(1), 764–780 (2013). DOI 10.1364/OE.21.000764

[5] Boccaletti, S., Kurths, J., Osipov, G., Valladares, D., Zhou, C.: The synchronization of chaotic systems. Phys Rep **366**(1-2), 1–101 (2002)

[6] Bojic, I., Nymoen, K.: Survey on synchronization mechanisms in machine-to-machine systems. Eng Appl Artif Intel **45**, 361–375 (2015). DOI 10.1016/j.engappai.2015.07.007

[7] Bojic, I., Podobnik, V., Ljubi, I., Jezic, G., Kusek, M.: A self-optimizing mobile network: Auto-tuning the network with firefly-synchronized agents. Inform Sciences **182**(1), 77–92 (2012). DOI http://dx.doi.org/10.1016/j.ins.2010.11.017

[8] Branchini, B., Behney, C., Southworth, T., Fontaine, D., Gulick, A., Vinyard, D., Brudvig, G.: Experimental support for a single electron-transfer oxidation mechanism in firefly bioluminescence. J Am Chem Soc **137**(24), 7592–7595 (2015). DOI 10.1021/jacs.5b03820

[9] Buck, J.: Synchronous flashing of fireflies experimentally induced. Science **81**(2101), 339–340 (1935)

[10] Buck, J.: Synchronous rhythmic flashing of fireflies. Q Rev Biol **13**(3), 301–314 (1938). DOI 10.1086/394562

[11] Buck, J.: The anatomy and physiology of the light organ in fireflies. Ann NY Acad Sci **49**(3), 397–485 (1948). DOI 10.1111/j.1749-6632.1948.tb30944.x

[12] Buck, J.: Synchronous rhythmic flashing of fireflies. ii. Q Rev Biol **63**(3), 265–289 (1988)

[13] Buck, J., Buck, E.: Flash synchronization as tool and as enabler in firefly courtship competition. Am Nat **116**(4), 591–593 (1980). DOI 10.1086/283649

[14] Buck, J., Case, J.: Physiological links in firefly flash code evolution. J Insect Behav **15**(1), 51–68 (2002)

[15] Camazine, S., Deneubourg, J.L., Franks, N., Sneyd, J., Theraulaz, G., Bonabeau, E.: Self-Organization in Biological Systems. Princeton University Press, Princeton (2001)

[16] Carlson, A., Copeland, J.: Flash communication in fireflies. Q Rev Biol **60**(4), 415–436 (1985). DOI 10.1086/414564

[17] Carlson, A., Copeland, J., Raderman, R., Bulloch, A.: Response patterns of female photinus macdermotti firefly to artificial flashes. Anim Behav **25**, 407–413 (1977). DOI http://dx.doi.org/10.1016/0003-3472(77)90015-X

[18] Carlson, A., Copeland, J., Shaskan, R.: Flash communication between the sexes of the firefly, photuris lucicrescens. Physiol Entomol **7**(2), 127–132 (1982). DOI 10.1111/j.1365-3032.1982.tb00280.x

[19] Case, J.: Flight studies on photic communication by the firefly photinus pyralis. Integr Comp Biol **44**(3), 250–258 (2004)

[20] Case, J., Trinkle, M.: Light-inhibition of flashing in the firefly photuris missouriensis. Biol Bull **135**(3), 476–485 (1968)

[21] Christensen, A., O'Grady, R., Dorigo, M.: From fireflies to fault-tolerant swarms of robots. IEEE T Evolut Comput **13**(4), 754–766 (2009). DOI 10.1109/tevc.2009.2017516

[22] Corral, A., Pérez, C., Díaz-Guilera, A., Arenas, A.: Self-organized criticality and synchronization in a lattice model of integrate-and-fire oscillators. Phys Rev Lett **74**(1), 118–121 (1995)

[23] Dörfler, F., Bullo, F.: Synchronization in complex networks of phase oscillators: A survey. Automatica **50**(6), 1539–1564 (2014). DOI http://dx.doi.org/10.1016/j.automatica.2014.04.012

[24] Dubois, M.: Note sur la physiologie des pyrophores. CR Soc Biol **36**, 661–664 (1884)

[25] Dubois, M.: Les elaterides lumineaux. CR Soc Biol **39**, 564–566 (1887)

[26] Dubois, M.: Nouvelles recherches sur la phosphorescence animale. CR Soc Biol **41**, 611–614 (1889)

[27] Edmunds, J.: The relation between temperature and flashing intervals in adult male fireflies, photinus pyralis1. Ann Entomol Soc Am **56**(5), 716–718 (1963). DOI 10.1093/aesa/56.5.716

[28] Ercsey-Ravasz, M., Srkzi, Z., Nda, Z., Tunyagi, A., Burda, I.: Collective behavior of electronic fireflies. Eur Phys J B **65**(2), 271–277 (2008). DOI 10.1140/epjb/e2008-00336-1

[29] Ermentrout, B.: An adaptive model for synchrony in the firefly pteroptyx malaccae. J Math Biol **29**(6), 571–585 (1991)

[30] Ermentrout, G., Chow, C.: Modeling neural oscillations. Physiol Behav **77**(4-5), 629–633 (2002)

[31] Faust, L.: Natural history and flash repertoire of the synchronous firefly photinus carolinus (coleoptera: Lampyridae) in the great smoky mountains national park. Fla Entomol **93**(2), 208–217 (2010). DOI 10.1653/024.093.0210

[32] Faust, L.: Fireflies, Glow-worms, and Lightning Bugs: Identification and Natural History of the Fireflies of the Eastern and Central United States and Canada. University of Georgia Press, Athens, Georgia (2017)

[33] Fister, I., Fister Jr, I., Yang, X.S., Brest, J.: A comprehensive review of firefly algorithms. Swarm Evol Comput **13**, 34–46 (2013). DOI http://doi.org/10.1016/j.swevo.2013.06.001

[34] Gielow, F., Jakllari, G., Nogueira, M., Santos, A.: Data similarity aware dynamic node clustering in wireless sensor networks. Ad Hoc Netw **24, Part A**, 29–45 (2015). DOI http://dx.doi.org/10.1016/j.adhoc.2014.07.008

[35] Goel, P., Ermentrout, B.: Synchrony, stability, and firing patterns in pulse-coupled oscillators. Physica D **163**(3-4), 191–216 (2002)

[36] Gohain Barua, A., Rajbongshi, S.: The light of the firefly under the influence of ethyl acetate. J Biosci **35**, 183–186 (2010)

[37] Goldbeter, A.: Biochemical oscillations and cellular rhythms. The molecular bases of periodic and chaotic behaviour. Cambridge University Press, Cambridge (1996)

[38] Harvey, E.: On the chemical nature of the luminous material of the firefly. Science **40**(1018), 33 (1914)

[39] Harvey, E.: The light-producing substances, photogenin and photophelein, of luminous animals. Science **44**(1140), 652 (1916)

[40] Harvey, E.: The mechanism of light production in animals. Science **44**(1128), 208 (1916)

[41] Hastings, J., Buck, J.: The firefly pseudoflash in relation to photogenic control. Biol Bull **111**(1), 101–113 (1956). DOI 10.2307/1539187

[42] Hopfield, J., Herz, A.: Rapid local synchronization of action potentials: toward computation with coupled integrate-and-fire neurons. Proc Natl Acad Sci USA **92**(15), 6655–6662 (1995)

[43] Iwasaka, M., Miyashita, Y., Barua, A., Kurita, S., Owada, N.: Changes in the bioluminescence of firefly under pulsed and static magnetic fields. J Appl Phys **109**(7), 07B303 (2011)

[44] Iwasaka, M., Ueno, S.: Bioluminescence under static magnetic fields. J Appl Phys **83**(11), 6456–6458 (1998)

[45] Izhikevich, E.: Resonate-and-fire neurons. Neural Networks **14**(6-7), 883–894 (2001)

[46] Jimenez-Romero, C., Johnson, J.: Spikinglab: modelling agents controlled by spiking neural networks in netlogo. Neural Comput Appl pp. 1–10 (2016). DOI 10.1007/s00521-016-2398-1

[47] Jovic, B.: Synchronization Techniques for Chaotic Communication Systems. Springer, Berlin (2012)

[48] Kuramoto, Y.: Chemical Oscillations, Waves, and Turbulence. Springer, Berlin (1984)

[49] Laurent, P.: The supposed synchronal flashing of fireflies. Science **45**(1150), 44 (1917)

[50] Leconte, J.: Synopsis of the lampyridæof the united states. T Am Entomol Soc **9**(1), 15–72 (1881). DOI 10.2307/25076399

[51] Lewis, S.: Silent Sparks: The Wondrous World of Fireflies. Princeton University Press (2016)

[52] Lewis, S., Cratsley, C.: Flash signal evolution, mate choice, and predation in fireflies. Annu Rev Entomol **53**(1), 293–321 (2008). DOI 10.1146/annurev.ento.53.103106.093346

[53] Li, P., Lin, W., Efstathiou, K.: Isochronous dynamics in pulse coupled oscillator networks with delay. Chaos **27**(5), 053,103 (2017). DOI 10.1063/1.4982794

[54] Lipa, N., Mannes, E., Santos, A., Nogueira, M.: Firefly-inspired and robust time synchronization for cognitive radio ad hoc networks. Comput Commun **66**, 36–44 (2015). DOI http://dx.doi.org/10.1016/j.comcom.2015.04.005

[55] Lloyd, J.: Aggressive mimicry in photuris: Firefly femmes fatales. Science **149**(3684), 653 (1965)

[56] Lloyd, J.: A new photinus firefly, with notes on mating behavior and a possible case of character displacement (coleoptera: Lampyridae). Coleopts Bull **22**(1), 1–10 (1968)

[57] Lloyd, J.: Model for the mating protocol of synchronously flashing fireflies. Nature **245**, 268–270 (1973)

[58] Lloyd, J.: Mimicry in the sexual signals of fireflies. Sci Am **245**, 138–145 (1981)

[59] Lloyd, J.: Evolution of a firefly flash code. Fla Entomol **67**(2), 228–239 (1984). DOI 10.2307/3493942

[60] Lloyd, J.: On research and entomological education vi: Firefly species and lists, old and now. Fla Entomol **86**(2), 99–113 (2003). DOI 10.1653/0015-4040(2003)086[0099:ORAEEV]2.0.CO;2

[61] Lu, X., Qin, B.: Synchronization in Complex Networks. Nova Science Pub Inc, New York (2011)

[62] Lyu, H.: Synchronization of finite-state pulse-coupled oscillators. Physica D **303**, 28–38 (2015). DOI http://doi.org/10.1016/j.physd.2015.03.007

[63] Manrubia, S., Mikhailov, A., Zanette, D.: Emergence of dynamical order. World Scientific Publishing Co. Pte. Ltd., Singapore (2004)

[64] Martin, G., Branham, M., Whiting, M., Bybee, S.: Total evidence phylogeny and the evolution of adult bioluminescence in fireflies (coleoptera: Lampyridae). Mol Phylogenet Evol **107**, 564–575 (2017). DOI http://doi.org/10.1016/j.ympev.2016.12.017

[65] McDermott, F.: Observations on the light-emission of american lampyrid: The photogenic function as a mating adaptation; 5th paper. Can Entomol **49**(2), 53–61 (1917). DOI 10.4039/Ent4953-2

[66] McElroy, W., Seliger, H., White, E.: Mechanism of bioluminescence, chemiluminescence and enzyme function in the oxidation of firefly luciferin*,. Photochem Photobiol **10**(3), 153–170 (1969). DOI 10.1111/j.1751-1097.1969.tb05676.x

[67] Mirollo, R., Strogatz, S.: Synchronization of pulse-coupled biological oscillators. SIAM J Appl Math **50**(6), 1645–1662 (1990)

[68] Moiseff, A., Copeland, J.: Firefly synchrony: A behavioral strategy to minimize visual clutter. Science **329**(5988), 181 (2010)

[69] Mosekilde, E., Maistrenko, Y., Postnov, D.: Chaotic synchronization: applications to living systems. World Scientific, Singapore (2002)

[70] Nijmeije, H., Rodriguez-Angeles, A.: Synchronization of Mechanical Systems. World Scientific Publishing, Singapore (2003)

[71] Ortler, B.: The Fireflies Book: Fun Facts About the Fireflies You Loved as a Kid. Adventure Publications, Inc., Cambridge (2014)

[72] Ott, E., Antonsen, T.: Frequency and phase synchronization in large groups: Low dimensional description of synchronized clapping, firefly flashing, and cricket chirping. Chaos **27**(5), 051,101 (2017). DOI 10.1063/1.4983470

[73] Pikovsky, A., Rosenblum, M., Kurths, J.: Synchronization : a universal concept in nonlinear sciences. Cambridge University Press, New York (2001)

[74] Van der Pol, B.: On relaxation oscillation. Phil Mag **2**, 978–992 (1926)

[75] Ramírez-Ávila, G., Deneubourg, J., Guisset, J., Wessel, N., Kurths, J.: Firefly courtship as the basis of the synchronization-response principle. Europhys Lett **94**(6), 60,007 (2011)

[76] Ramírez-Ávila, G., Guisset, J., Deneubourg, J.: Synchronization in light-controlled oscillators. Physica D **182**(3-4), 254–273 (2003)

[77] Ramírez-Ávila, G., Guisset, J., Deneubourg, J.: Influence of uniform noise on two light-controlled oscillators. Int J Bifurcat Chaos **17**(12), 4453–4462 (2007)

[78] Ramírez-Ávila, G., Kurths, J.: Unraveling the primary mechanisms leading to synchronization response in dissimilar oscillators. Eur Phys J Spec Top **225**(13), 2487–2506 (2016). DOI 10.1140/epjst/e2016-60033-5

[79] Ramírez-Ávila, G., Kurths, J., Guisset, J., Deneubourg, J.: When does noise destroy or enhance synchronous behavior in two mutually coupled light-controlled oscillators? Phys Rev E **82**(5), 056,207 (2010)

[80] Ramírez-Ávila, G., Kurths, J., Guisset, J., Deneubourg, J.: How do small differences in nonidentical pulse-coupled oscillators induce great changes in their synchronous behavior? Eur Phys J Spec Top **223**(13), 2759–2773 (2014). DOI 10.1140/epjst/e2014-02290-y

[81] Roda, A.: Chemiluminescence and bioluminescence: past, present and future. Royal Society of Chemistry, Cambridge (2011)

[82] Roda, A.: A History of Bioluminescence and Chemiluminescence from Ancient Times to the Present, pp. 1–50. The Royal Society of Chemistry (2011). DOI 10.1039/9781849732024-00001

[83] Rodrigues, F., Peron, T., Ji, P., Kurths, J.: The kuramoto model in complex networks. Phys Rep **610**, 1–98 (2016). DOI http://dx.doi.org/10.1016/j.physrep.2015.10.008

[84] Rubido, N., Cabeza, C., Kahan, S., Ramírez-Ávila, G., Marti, A.: Synchronization regions of two pulse-coupled electronic piecewise linear oscillators. Eur Phys J D **62**(1), 51–56 (2011). DOI 10.1140/epjd/e2010-00215-4

[85] Rubido, N., Cabeza, C., Marti, A., Ramírez-Ávila, G.: Experimental results on synchronization times and stable states in locally coupled light-controlled oscillators. Philos T Roy Soc A **367**, 32673280 (2009). DOI 10.1098/rsta.2009.0085

[86] Santillán, M.: Periodic forcing of a 555-ic based electronic oscillator in the strong coupling limit. Int J Bifurcat Chaos **26**(03), 1630,007 (2016). DOI 10.1142/S021812741630007X

[87] Schena, A., Griss, R., Johnsson, K.: Modulating protein activity using tethered ligands with mutually exclusive binding sites. Nat Commun **6**, 7830 (2015). DOI 10.1038/ncomms8830https://www.nature.com/articles/ncomms8830#supplementary-information

[88] Shimomura, O.: Bioluminescence: chemical principles and methods. World Scientific (2006)

[89] Stanger-Hall, K., Lloyd, J.: Flash signal evolution in photinus fireflies: Character displacement and signal exploitation in a visual communication system. Evolution **69**(3), 666–682 (2015). DOI 10.1111/evo.12606

[90] Stewart, I., Strogatz, S.: Synchronisation, rythmes et allures. Pour la science (dossier hors-série) **44**(July/September), 90–93 (2004)

[91] Strogatz, S.: Sync: The Emerging Science of Spontaneous Order. Hyperion Press, New York (2003)

[92] Teuscher, C., Capcarrere, M.: On Fireflies, Cellular Systems, and Evolware, pp. 1–12. Springer Berlin Heidelberg, Berlin, Heidelberg (2003). DOI 10.1007/3-540-36553-2_1

[93] Theobald, W.: Notes and queries. J Asiatic Soc Bengal **35**(2), 73–76 (1866)

[94] Tsai, Y.L., Li, C.W., Hong, T.M., Ho, J.Z., Yang, E.C., Wu, W.Y., Margaritondo, G., Hsu, S.T., Ong, E., Hwu, Y.: Firefly light flashing: Oxygen supply mechanism. Phys Rev Lett **113**(25), 258,103 (2014)
[95] Tyrrell, A., Auer, G., Bettstetter, C.: Emergent slot synchronization in wireless networks. IEEE T Mobile Comput **9**(5), 719–732 (2010). DOI 10.1109/TMC.2009.173
[96] Wilensky, U.: NetLogo Fireflies model. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL. (1997)
[97] Wilensky, U.: NetLogo. Center for Connected Learning and Computer-Based Modeling, Evanston, IL (1999)
[98] Wilson, T.: Bioluminescence: living lights, lights for living. Harvard University Press (2013)
[99] Winfree, A.: Biological rhythms and the behavior of populations of coupled oscillators. J Theor Biol **16**, 15–42 (1967)
[100] Yang, X.S.: Firefly Algorithm, pp. 221–230. John Wiley Sons, Inc. (2010). DOI 10.1002/9780470640425.ch17