Chapter 1
Modeling Fireflies Synchronization

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Abstract Albeit synchronous behavior of some fireflies species is one of the paradigmatic examples of synchronization, there are not many efforts to model in a realistic way this astounding phenomenon. One of the most important features of fireflies synchronization is the cooperative behavior of many fireflies giving rise to the emergency of synchronization without any leader, a fact that took a long time to be recognized. In this chapter, we review the main attempts to build models allowing the explanation of how and why fireflies synchronize. The starting point is qualitative models based on simple observations. The latter served to formulate original mathematical models enabling not only to explain fireflies synchronization but also some other collective phenomena. Integrate-and-fire oscillators (IFOs) constitute an emblematic model to describe the fireflies' synchronous behavior, and they have also inspired ones to build electronic circuits with similar features and adapted to fireflies in the sense that they communicate with each other by means of light-pulses. The above-mentioned electronic circuits received the name of electronic fireflies or more technically, light-controlled oscillators (LCOs). These en-

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gines allowed a systematic study of synchronization from experimental, theoretical and numerical viewpoints. They have also been used in a wide variety of situations ranging from simple cases of identical oscillators to scenarios where populations of dissimilar oscillators whose interaction does explain synchronization as well as the response to synchronization, a widespread phenomenon occurring in fireflies. The obtained results and the well-knowledge of the models allow introducing simplified versions. These simplifying ideas might be taken as toy models in the strict sense of the word because based on these models it is possible to construct a game. This minimalist model is called the "solitary flash" game (SFG), a game where fireflies are the players and they can synchronize thanks to simple rules. Finally, we discuss briefly the potentials of the fireflies synchronization paying particular attention to its application in communication networks.

1.1 Introduction

Synchronization defined as the adjustment of rhythms of self-sustained oscillators due to a weak coupling is one of the most widespread complex phenomena observable both in human-made systems and in natural ones [55]. In general, synchronization is attained via a mechanism similar to a phase transition implying the emergence of structural order [44]. From a historical viewpoint, it is stated that the first observation of synchronization was done by the Dutch scientist Christian Huygens, considered the most ingenious watchmaker of all time [71] and also one of the founders of the mathematization of nature [82]. Curiously, another Dutch naturalist, Engelbert Kaempfer, described for the first time the synchronous collective behavior of large populations of fireflies, a phenomenon that he observed during his voyage to Asia (1690–1692) as stated by Buck [10]. What are the differences between their two observations? Simply, the first one is the detection of synchronization in a small human-made system, and the other one is the manifestation of a natural self-organized system. Being the first system composed of two pendulums continuously coupled through a shared structure consisting of one or two wooden beams in a half-timber house [6]; and the second one consisting of hundreds or thousands of fireflies seen as self-sustained-oscillators coupled by light pulses, i.e., a noncontinuous coupling. Although the results of both observations aroused curiosity and were considered as paradigmatic examples of the phenomenon of synchronization, their formal description took more than two centuries to be formulated and still now some aspects are not completely unveiled such as what determines the stability of multiple types of limit behavior [34]. For pendulums synchronization, in the last years, several works were devoted to the reproduction [51] and improvements [53] of Huygens' experimental setup, the linear stability analysis of this system, the proper explanation of the results [35], and the extensions of the synchronization phenomenon for this type of system. Thus, the obtained results showed that not only anti-phase synchronization is possible as found by Huygens but also in-phase synchronization is possible. A system of n pendulums hanging from an elastic horizontal beam, where synchronization and clustering are manifested has been modeled [25], in the same line, the extension to multiple coupled Huygens' pendulums combined with a similar system but composed of metronomes deserved the attention in the last years [34]. Concerning the synchronization of fireflies, the phenomenon was not entirely accepted before 1918, and among the statements denying the fireflies synchronous behavior we mention that of W. Craig quoted [24]:

> Dr. Edward S. Morse [50] cites a case from memory in which he saw "fireflies flashing in unison," but he gives no exact details. He quotes a paper by Mr. Blair [7] mentioning the same phenomenon; but Mr. Blair states that he never observed the synchronism himself, and he does not cite any authority who has observed it. Dr. Morse in another paper [50] quotes R. Shelford as observing a tree full of fireflies pulsating "so that at one moment the tree would be one blaze of light, whilst at another the light would be dim and uncertain." This last clause makes it appear that some fireflies were not in synchronism with the others, and thus brings in the statistical fallacy to be mentioned presently.

Similarly, P. Laurent in this letter "The supposed synchronal flashing of fireflies" [37] quoted:

> I could hardly believe my eyes, for such a thing to occur among insects is certainly contrary to all natural laws. However, I soon solved the enigma. The apparent phenomenon was caused by the twitching or sudden lowering and raising of my eyelids. The insects had nothing- whatsoever to do with it. Many times in the past twenty years I have proved that my solution was correct.

Despite the devastating above-mentioned quotations against the fireflies synchronization which were denominated as anthropomorphic explanations [18]; these shortly after were forsaken due to the increasing of careful observations and improvements in measurements and used instruments. The latter allowed the confirmation that fireflies synchronization is entirely real and has a specific functionality. The aspects mentioned above were found and developed throughout this time. Among the main features which were unveiled we emphasize: chemical [2] and physical [5, 57, 75] mechanisms related to the fireflies light emission, genetic [4] and evolutionary [33, 45, 72] issues, the how and why fireflies synchronize in relation to the courtship and mating behavior observed in several species [42] behavior that constitutes the main functionality of synchronization [13]. The fireflies communication [40] deserved several systematic observations giving rise to establish the "language" of different species and the fact that in some species, males synchronization must be followed by the females response [83]. Among other interesting aspects, we mention the misleading courtship using some artificial light sources or LEDs to stimulate female response [48]. The tragic case of "devouring femme fatale" where a male looking for a conspecific female is deceived and devoured by a female of another species who imitates the response of the wanted partner has also been studied [43]. A catalog of communication codes in *Photinus* species [38] shows the diversity of these intercourse signals and also changes the traditional ideas that taxonomy is only possible by identifying the main morphological features, but it is also possible to identify fireflies species by knowing their courtship coding as found by Lloyd [41]. As we see, the diversity of themes and aspects that involve the synchronization of fireflies is very vast. However, from mathematical modeling, there were not many attempts to formally explain the synchronization in these insects. A. Winfree proposed a model of the collective behavior of a population of oscillators that could represent electronic oscillators, secretory cells, neurons or animals such as fireflies [80]. In the same line, other models were developed for populations of oscillators [36, 52]; in these studies, the oscillators are generic and not necessarily with the specific features of fireflies flashing. In 1990, inspired in a model of heart cells, Mirollo and Strogatz proposed a model for pulse-coupled oscillators that have the main characteristic of fireflies, i.e., the oscillator behaves in such a way that it has a charging stage until a threshold is attained and then it fires (flashes). The latter is the reason this type of oscillators are also called integrate-and-fire oscillators [47]. Thereafter, several works were devoted to study synchronization on IFOs [1]. The first qualitative model used to understand the fireflies synchronization were based upon the simple experiments exciting or inhibiting the flashing rhythm of a firefly (in particular with *Pteroptyx cribellata*). The latter allowed to formulate a resettable pacemaker model to explain the modifications on the rhythmic flash emission that eventually permits the synchronization [12]. This model facilitates the development of ideas conducting to postulate formal models from reset and threshold concepts. Precise models for fireflies were formulated for instance for *Pteroptyx malaccae* based on phase delay synchrony as a mechanism [28]. Another perspective for specific fireflies was constructed from some electronic devices called light-controlled oscillators (LCOs) or electronic fireflies due to their features that mimic real fireflies because they communicate through light-pulses and can synchronize [59]. The similarity between LCOs and IFOs could drive to think that the results obtained with these models are very similar but surprisingly, there are striking differences even with simplified LCOs versions [63]. It is important to remark that LCOs model can be extended to explain not only synchronization but also the response to synchronization [58] as occurring in several fireflies species, in particular, those of genus *Photinus* [38, 40]. Fireflies synchronization has multiple applications and just to mention some of them: the use of this concept to enhance the robustness of wireless communication networks [77], the better understanding of real task-execution scenarios for swarms of robots [22], the new techniques of light extraction for LEDs improvements are also inspired in fireflies luminescence [5]. The chapter is organized as follows: In Sect. 1.2, we describe the concept of entrainment and the qualitative resettable pacemaker models based on simple observations. The explanation of the first mathematical models to describe fireflies synchronization is pointed out in Sect. 1.3, including the paradigmatic IFOs, and the LCOs. The comparison of LCOs and IFOs is presented in Sect. 1.4. The generalization of LCOs model to explain the response to synchronization is exposed in Sect. 1.5. The depiction of the "solitary flash game" (SFG) is shown in Sect. 1.6. As a sort of conclusive remarks, in Sect. 1.7, we state the limitations of the models and the perspectives of the fireflies synchronization phenomenon.

1.2 Explanation of the entrainment in fireflies

The concept of entrainment constitutes the basis for understanding a myriad of oscillatory behaviors in living beings. Entrainment is related to the resetting of biological clocks introduced by Winfree in 1975 [81]. Among the key behaviors, circadian rhythms constitute perhaps the most known phenomena [76], in which are principally involved populations of neurons giving rise mostly to coherent oscillatory behavior and allow the adaptation to the environment [49]. In general, the entrainment of neurons is an essential aspect related to certain functionalities, and it has been widely studied for instance, on effects of regularly spaced synaptic input [54], and phase control of neural pacemakers. Cardiac cells and their entrainment are also considered in different contexts such as the spontaneous impulse generation in the pacemaker of the heart [74], effects of regularly spaced nervous input [66], a nonlinear analysis when the cells are periodically stimulated, and the generation of cardiac dysrhythmias [32]. Fireflies constitute an excellent example of the oscillatory control strategies exhibited by most living beings: temporal coordination, prediction and preparation for repetitive events, high efficiency in energy transduction and communication, and enhanced precision of control [65]. Thus, the synchronous rhythmic behavior of the fireflies' flashes must also be tackled with the concept of entrainment. We start from the fact that male fireflies can spontaneously flash in a regular rhythm. The entrainment of the flashing rhythm of these insects is related to neural aspects as pointed out in several works (see [20]) and a saga of papers explaining in detail several noteworthy aspects associated with the control of flashing in fireflies). The set of articles firstly included topics such as the lantern as a neuroeffector organ [16]; secondly, the role of central nervous system [21]; thirdly, the peripheral excitation [17], and also aspects linked to synchronization suchlike the free run pacemaking in a synchronic *Pteroptyx* [15], or the pacemaker synchronization in *Pteroptyx cribellata* [14]. They yielded the basis to propose formal models bringing out the most relevant aspects of fireflies flashing behavior. The knowledge of how entrainment works lets us see the problem of synchronization as mutual entrainment between oscillators being the reciprocal feedback decisive concerning the stability. One important aspect akin to the determination of how fireflies synchronize is related to the influence of other light sources on the rhythm of their light emission frequency. A careful observation of the influence mentioned above and the afterward simple experimental setup design, allowed to realize about the resettable feature of the luminescent control of fireflies [12]. The proposed resettable pacemaker model is depicted in Fig. 1.1, where the authors considered that the instantaneous flash emitted by the oscillator in Fig. 1.1(a) could reset instantaneously. The signal of oscillators shown in Fig. 1.1(b)-(c) produces a delayed flash (Fig. 1.1(b)) or advances according to the reception of a light pulse (Fig. 1.1(c)).

The schematic view of fireflies' waveform permits the understanding on the entrainment of flashing fireflies. The phase resetting model introduced by Buck is shown in Fig. 1.1 and it has been applied by himself to two fireflies species, namely *Photinus pyralis* and *Pteroptyx cribellata* [11] and based on these observations, it was possible to formulate some primary models to explain how fireflies synchro-

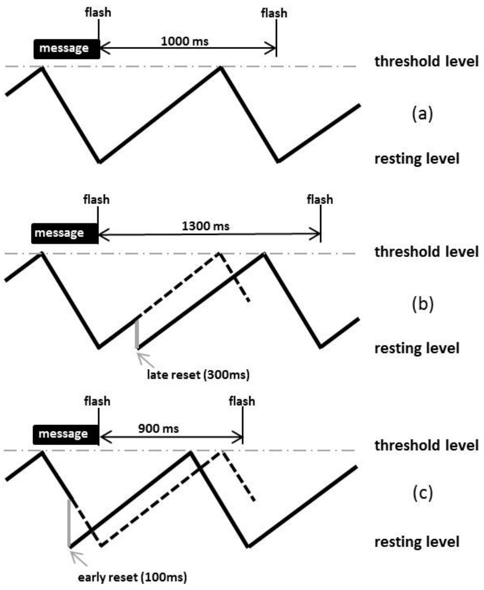


Fig. 1.1 Resettable pacemaker model suggested in [12]. (a) Normal or natural interflash period of one second. (b) delayed flash that in this case appears 300 ms later. (c) Advance flash (early reset) cropping up 100 ms before the standard flash.

nize. In Sect. 1.3, we focus on three simple models characterized by the fact that they intend to reproduce the oscillatory and synchronous features of fireflies species detailed in [11]. To conclude this section, we point out that many aspects were neglected such as temperature effects [26], chemical conditions [2, 19], or some behaviors related to competition or aggressive mimicry [43] that eventually could play a role in how synchronization is attained.

1.3 First models: How to explain collective behavior?

One of the first models arose to explain the synchronous behavior of biological oscillators is due to Winfree [80] who formulated a phase model based on relaxation oscillators whose analysis permits to solve exactly a particular situation under a mean field coupling with firing impulses [3]. Afterwards, some refinements of Winfree's model have been concocted [9] and especially, the formulation owed to Kuramoto became a paradigmatic model to study synchronization [36]. Finally, one of the few models dedicated mainly to fireflies is that formulated by Ermentrout who proposed an adaptive model for the synchronous behavior of *Pteroptyx malaccae* [27].

Before to start the analysis of IFOs and LCOs, it is imperative to mention a valuable tool to characterize the response of an oscillator to a periodic stimulus: the phase response curve (PRC). A PRC is a graphical representation of the magnitude of the phase shift produced in an oscillatory system by a pulse versus the time at which the pulse was applied. Let T_0 be the natural period of the oscillation and considering that $t = t_{F0}, 2t_{F0}, 3t_{F0}, \ldots$ are the times of successive firing events. Suppose that at $t = t_0 \in [0, T_0)$, we perturb the trajectory. Then, the new firing time is $T(t_0)$. A primary assumption is that the firing events occurring after $t = T(t_0)$ are at $t = T(t_0) + T_0, T(t_0) + 2T_0, \ldots$. Thus, the effect of the perturbation is only carried for one cycle; there is no memory of the perturbation once the event has occurred. The PRC is defined regarding the phase shift as [31]:

$$\Delta(\phi) \equiv \frac{T_0 - T(T_0\phi)}{T_0} , \tag{1.1}$$

where $\phi \equiv t_0/T_0 \in [0,1)$ is the phase at which the stimulus is applied. Thus, a perturbation applied to the oscillator will generate either an advance or a delay in the phase, and it is a function of the magnitude and the timing of the perturbation. In Eq. (1.1), $\Delta(\phi)$ is positive (negative) if the perturbation acts to advance (retard) the time of the next event. We use PRCs with the aim of describing the IFOs and LCOs.

1.3.1 Integrate-and-Fire Oscillators

The IFOs have been widely used in neural systems [28] and also they constitute an important model to describe synchronous fireflies [47]. Originally, they were featured by a voltage-like state variable V_i, whose dynamics is:

$$\frac{\mathrm{d}V_i}{\mathrm{d}t} = I - \eta V_i, \qquad 0 \le V_i \le 1, \qquad i = 1, \ldots, N. \tag{1.2}$$

With $I > 0$ being the input, and $\eta \ge 0$ is the leakiness; more concretely, $I > 1$ ensures the existence of a PRC as shown in Fig. 1.2(c). When the oscillator i reaches the threshold ($V_i = 1$), the oscillator "fires" and V_i is reset *instantaneously* to zero. The oscillators interact by a simple form of pulse coupling: when a given oscillator fires, all the other variables V_j, $j \ne i$ are increased by an amount β/N (the quotient by N is made to get reasonable behavior in the thermodynamic limit). That is,

$$\textbf{If} \quad V_i(t) = 1 \quad \Longrightarrow \quad V_j(t^+) = \min(1, V_j(t) + \beta/N), \quad \forall j \ne i. \tag{1.3}$$

Moreover, the oscillator at the state $V = 0$ (i.e. just after firing) cannot be affected by the others. The construction of an IFO's PRC starts by integrating Eq. (1.2) to find the IFO's natural period:

$$T_0 = \frac{1}{\eta} \ln \frac{I}{I - \eta} . \tag{1.4}$$

At $t = t_0$, due to the perturbation, the oscillator adds its voltage-like variable V by an amount β and then evaluates when the oscillator fires next. If t_0 is close enough to $t = T_0$ then the perturbation β will lift V past 1 and the oscillator will fire immediately so that $T(t_0) = t_0$. Otherwise, the fire event will be held at $t = T(t_0)$, and T is computed as follows

$$T \;=\; t_0 \;+\; \int_{V+\beta}^{1} \frac{\mathrm{d}V}{I - \eta V} \quad ,$$

that finally gives

$$T \;=\; \frac{1}{\eta} \ln \frac{I - \eta \beta \mathrm{e}^{\eta t_0}}{I - \eta} \quad . \tag{1.5}$$

Consequently, the PRC for the integrate-and-fire oscillator is

$$\varDelta\left(\frac{t_0}{T_0}\right) \;=\; 1 \;-\; \frac{\ln\left(\frac{I - \eta\beta\mathrm{e}^{\eta t_0}}{I-\eta}\right)}{\ln\left(\frac{I}{I-\eta}\right)} \quad . \tag{1.6}$$

The IFOs entrainment and some examples of PRCs are shown in Fig. 1.2.

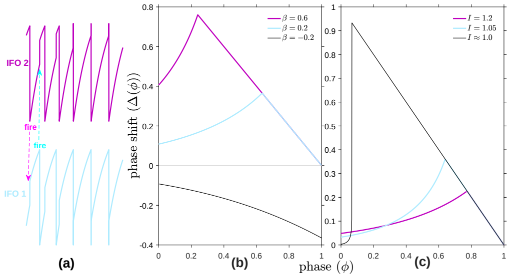


Fig. 1.2 (a) Entrainment and mechanism of synchronization of two coupled IFOs. PRCs for an IFO with $\eta = 1$. (b) Different strengths for $I = 1.25$. (c) Different values of I when the strength is $\beta = 0.1$.

We slightly modify this description with the aim of considering the characteristics related to fireflies, in particular to *Pteroptyx cribellata* whose oscillation period varies between 800 and 1600 ms [14]. The modified formulation considers two threshold values V^{upper} and V^{lower} not necessarily 1 and 0. When the oscillator i reaches the threshold ($V_i = 1$), the oscillator "fires" and V_i is reset *instantaneously* to zero. We slightly modify this description with the aim of considering the characteristics related to fireflies, in particular to *Pteroptyx cribellata* whose oscillation period varies between 800 to 1600 ms [14]. The modified formulation considers two threshold values V^{upper} and V^{lower} not necessarily 1 and 0. The mechanism when IFOs are coupled might be explained as follows: when IFO$_j$ reaches its upper threshold, it fires, and the variables V_i of all the other IFOs are modified by adding the quantity β'_{ij} but not exceeding V^{upper}. Thus, $V_i(t^+) = \min(V^{\text{upper}}, V_i(t) + \beta_{ij})$. A general coupling scheme in which it is possible that a set of $N_f < N$ IFOs achieve their thresholds simultaneously, implies that IFO$_i$ modifies its dynamics in the form:

$$\textbf{If}\left\{V_j(t)=V^{\text{upper}}\right\}\Longrightarrow V_i(t^+)=\min\left(V^{\text{upper}},V_i(t)+\sum_{j=1}^{N_f}\beta'_{ij}\right)\wedge\left\{V_j(t^+)=V^{\text{lower}}\right\}\ , \tag{1.7}$$

where $j=1,\dots,N_f$. The meaning of β'_{ij} is the coupling strength and represents the action of IFO$_j$ on IFO$_i$; and finally, the natural period of IFO$_i$ might be incorporated in the form:

$$\frac{\mathrm{d}V_i(t)}{\mathrm{d}t}=\frac{1}{T_{0i}}[V_{Mi}-V_i(t)],\quad V^{\text{lower}}\leq V_i(t)\leq V^{\text{upper}}\ , \tag{1.8}$$

with the same condition Eq. (1.7) when coupled with other IFOs.

1.3.2 Electronic fireflies: Light-Controlled Oscillators

Originally, LCOs were conceived with the aim of mimicking fireflies synchronous behavior through a simple electronic device. An LCO functions under the primary fireflies characteristics, i.e., with the ability to emit periodic light-pulses, and receiving light pulses of other(s) LCO(s); so that, its internal flashing rhythm can be modified thus enabling synchronization. The LCOs were widely studied in different contexts such as experimental characterization [23, 59, 68, 69], noise influence [60, 62], and other aspects related to stability and synchronization [67]. The model for LCOs was built regarding their electronic components (resistors, capacitors, diodes, a source voltage characterized by V_M, and LM555 chip). The latter flip-flop constitutes the LCO's heart because this simple chip confers the oscillatory features to the LCO, establishing two well-defined thresholds: lower ($V^{\text{lower}}=V_M/3$), and upper ($V^{\text{upper}}=2V_M/3$). The above-mentioned thresholds are associated with a binary variable $\varepsilon(t)$ that takes the values $\varepsilon(t)=1$ or $\varepsilon(t)=0$ during the charging stage (slow process) or discharging stage (fast process) respectively. The discharging stage changes to the charging one and vice versa when one of these thresholds is achieved. The dynamical equations describing a set of N coupled LCOs in terms of the natural charging time (T_{c0}) and the discharging or firing time (T_{d0}) are:

$$\frac{\mathrm{d}V_i(t)}{\mathrm{d}t}=\underbrace{\frac{\ln 2}{T_{c0i}}(V_{Mi}-V_i(t))\varepsilon_i(t)}_{\text{charging term}}-\underbrace{\frac{\ln 2}{T_{d0i}}V_i(t)[1-\varepsilon_i(t)]}_{\text{discharging term}}+\underbrace{\sum_{j=1}^{N}\beta_{ij}\delta_{ij}[1-\varepsilon_j(t)]}_{\text{coupling term}}\ , \tag{1.9}$$

where δ_{ij} indicates if 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 $\beta_{ij}=\beta_{ji}$.

A simple inspection of Eq. (1.9) shows that both charging and discharging stages might be modified by the effect of the coupling with other LCO(s). The charging and the discharging times might be shortened or lengthened, respectively, when the pulsatile action due to the light of other LCOs takes place.

Similarly to the IFOs' case, we specify in Fig. 1.3 how a perturbation acts on the LCO's waveform according to the region in which it is applied.

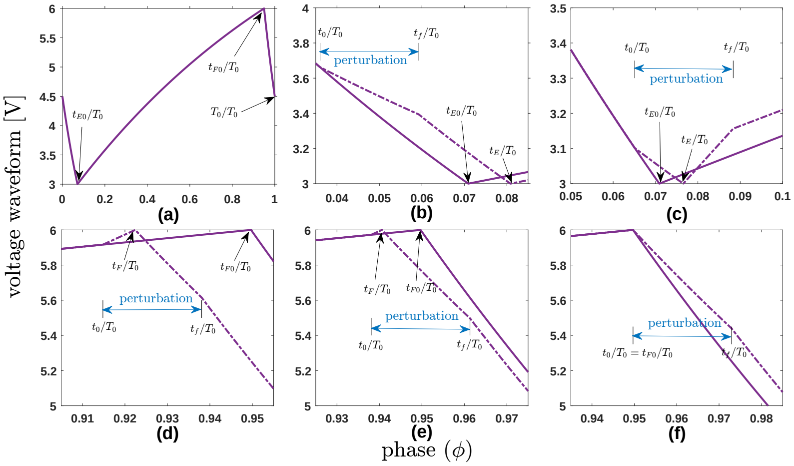
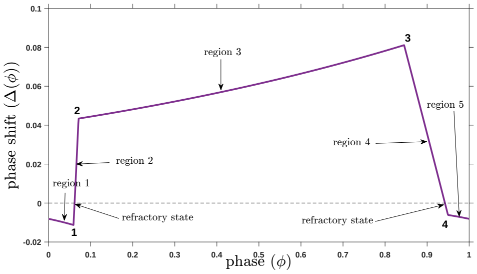


Fig. 1.3 Parameter definition to determine the LCO's PRCs. t_{E0} and t_{F0} represent the LCO's extinction time and the LCO's firing time, respectively, (without perturbation), t_0 and t_f represent the initial and the final time of the perturbation, respectively. Finally, t_E and t_F are the extinction and firing time of the perturbed LCO. (a) Whole unperturbed signal. (b) Region 1 with $t_0 = t_{E0} - 1.5\tau$. (c) Region 2 with $t_0 = t_{E0} - 0.25\tau$. (d) Region 3 with $t_0 = t_{F0} - 1.5\tau$. (e) Region 4 with $t_0 = t_{F0} - 0.5\tau$. (f) Region 5 with $t_0 = t_{F0}$. The unperturbed signal is represented with a solid line whereas the perturbed one with dash and dotted line. We have considered a coupling strength $\beta = 200$ and the duration of the pulse $\tau = 1.0$ ms.

In order to show clearly how the PRC can be obtained for an LCO, we define an arbitrary zero phase for the LCO's waveform. For convenience, we take it to be when the signal is just in the middle of the thresholds in the discharging stage so it has the voltage value $\frac{V_M}{2}$. This choice enables us to take into account the regions where there are transitions from one stage to another. These regions are particularly interesting because during a transition there can be both effects: advance or delay in the phase (Fig. 1.4).

Fig. 1.4 PRC obtained from analytical solution of the LCO's differential equations. Points 1,2,3, and 4 are related to $t_E^{(2)}$, t_{E0}, $t_F^{(4)}$, and t_{F0}, respectively. The phases corresponding to the refractory states are also shown.



To characterize the synchronous behavior attained by two mutually coupled LCOs with the oscillatory features of *Pteroptyx cribellata*, the Arnold tongues (synchronization regions) are shown in Fig. 1.5. These areas representing stability are obtained by considering the winding number $\rho = T_1/T_2$, where T_1 and T_2 are, respectively, the LCO$_1$ and LCO$_2$ natural oscillation periods. This result is significant because it shows in detail the phase-locking attained for two nonidentical mutually coupled LCOs which gives the possibility to have a deeper understanding of the synchronous behavior of such a system, including the possibility to control it.

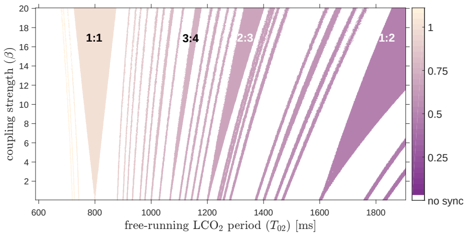


Fig. 1.5 Arnold tongues for LCOs oscillating with the features of *Pteroptyx cribellata* and considering a rapid flash. The color bar indicates the winding number or synchronization order. Some of these ratios (1:1, 2:3, 3:4, and 1:2) are explicitly shown.

Just to mention, there are other ways to model fireflies behavior. For instance using multi-agent systems (MAS), one of their most well-known platform is NetLogo [79] where employing simple interaction rules among the agents (fireflies), and some strategies such as advanced or delayed phase, the whole population is able to synchronize. A fireflies model is available in NetLogo [78], which is based on the flashing behavior of some species: *Pteroptyx cribellata, Luciola pupilla*, and *Pteroptyx malaccae*.

1.4 From ideal to real: Comparing IFOs and LCOs

Despite the similarities between IFOs and LCOs, there are some features that distinguish them markedly. An important difference is that the ideal IFO considers an instantaneous resetting or flashing, but of course, in real fireflies, the flashing lasts a specified time interval that is typical for each species (see Table 1.2). In order to quantitatively establish the differences between IFOs and LCOs, we consider the same form and features for all the oscillators. Thus, analyzing populations of coupled oscillators, for IFOs, we can consider Eqs. (1.7)–(1.8) taking into account that $V^{\text{lower}} = V_M/3$, and $V^{\text{upper}} = 2V_M/3$, i.e., the same as in the LCOs' case. On the other hand, the IFOs' and LCOs' coupling strengths are related by $\beta'_{ij} = \beta_{ij} T_{d0j}$. For LCOs, Eq. (1.9) and the threshold conditions govern their dynamics.

In what follows, we show some results evincing the differences between IFOs and LCOs. In order to characterize synchronization, we use the concept of probability of total synchronization (PTS), defined as the ratio of the number of trials in which all the oscillators achieve complete synchronization to the number of total trials. We also consider two types of coupling: (i) A *mean field* one where each one of the N oscillators is coupled to the others with a coupling strength given by $\beta_{ij} = \beta/N$, being β a constant. (ii) A *distance dependent* coupling, in which the coupling strength is $\beta_{ij} \propto 1/r_{ij}^{\alpha}$, where the exponent α was found to take the value 2.11 [59].

Finally, in our analysis, we allow for situations in which identical or nonidentical oscillators might compose the ensemble. We denote the unlikeness by a difference in the period ΔT tied up with the relative variance σ_{rel} of a normal distribution linked to the possible values of the period $T_i = T_{\mathrm{ref}} + \Delta T_i$. The quantity T_{ref} is a reference period proper to the fireflies species.

As a relevant aspect to point out the behavioral differences between IFOs and LCOs, we compute the transient to achieve total synchronization in our sets of oscillators. In order to study transients, we consider the fact that all the oscillators fire almost simultaneously as the criterion to determine whether or not a set of oscillators attains complete synchronization. When the coupling is a mean-field one, we observe in the scatter plots of Fig. 1.6 that for identical LCOs (Fig. 1.6(a)) and IFOs (Fig. 1.6(e)), mostly the whole population synchronizes. Note that circles' sizes are proportional to the PTS in percentage. The transient grows with N, but the mean values are small for both cases. On the contrary, when we consider the differences σ_{rel}, we observe for LCOs that transient escalates with N but also, PTS slumps with N. When the coupling depends on the distance between oscillators, synchronization

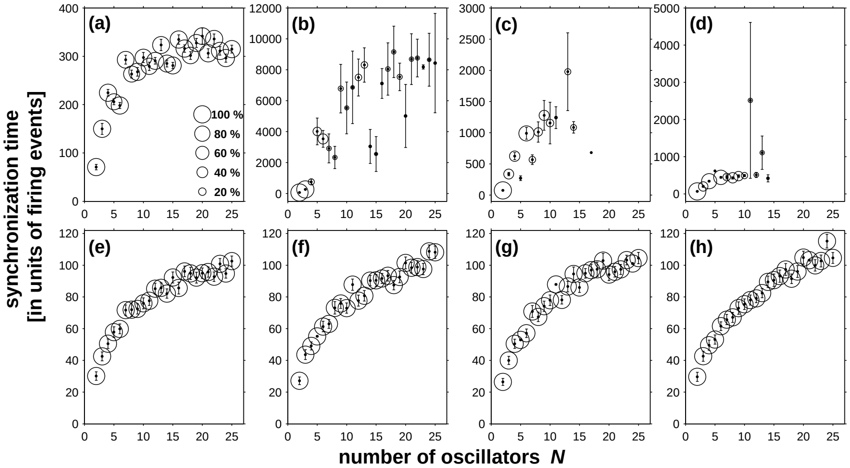


Fig. 1.6 Synchronization time as a function of N for globally coupled LCOs (top) and IFOs (bottom) being the coupling a mean-field one, when the differences σ_{rel} are: (a) and (e) 0 (identical), (b) and ((f) 0.10×10^{-4}, (c) and (g) 2.24×10^{-4}, and (d) and (h) 7.07×10^{-4}. The size of the circles are proportional to PTS and the error bars represent the standard deviation.

time escalates even when the oscillators are identical (Fig. 1.7(a) and (f)). The case of identical IFOs is dramatic inasmuch as populations with $N > 8$ imply noughts for the PTS. The same behavior in both kind of oscillators is observed when the dif-

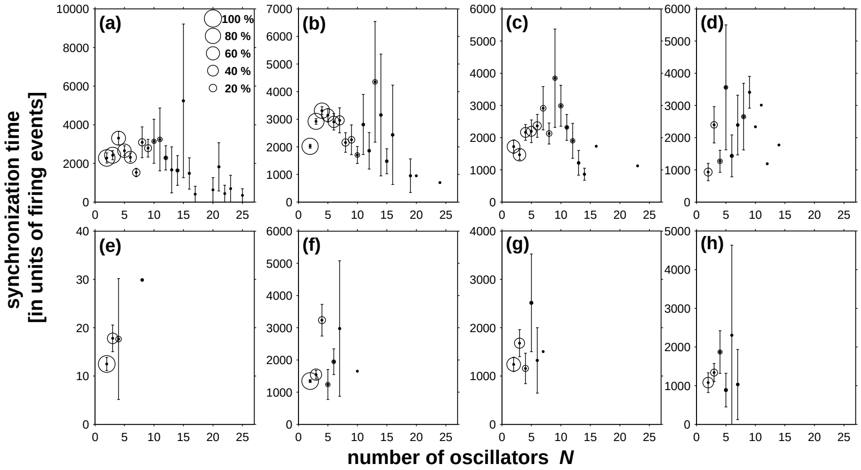


Fig. 1.7 Idem as Fig. 1.6 but for a distance-dependent coupling.

ferences are $\sigma_{\text{rel}} = 0.10 \times 10^{-4}$ (Fig. 1.7(b) and (f)), $\sigma_{\text{rel}} = 2.24 \times 10^{-4}$ (Fig. 1.7(c) and (g)), and $\sigma_{\text{rel}} = 7.07 \times 10^{-4}$ (Fig. 1.7(d) and (h)). It is remarkable that complete synchronization is not usual when the coupling is distance-dependent. A summary of the results is shown in Table 1.1. An exhaustive study on the differences between IFOs and LCOs can be found in [63]. As indicated above, we can affirm that despite IFOs and LCOs seem to be quite similar; the dynamical behavior might present very different behaviors. Evidently, LCOs are more realistic because they are experimentally based and validated. As a consequence, we choose LCOs as the more appropriate model for describing fireflies synchronization and as it is stated in Sect. 1.5, an extension of the LCOs might be applied not only to explain male fireflies synchronization but also the female response to synchronization what gives us more clarity concerning the functionality of fireflies synchronization.

Table 1.1 Comparison of different coupling configurations of LCOs and IFOs and the important changes concerning the $\langle PTS \rangle$, and synchronization time. The check mark points out the existence of an important change in the concerned variable.

configurations comparison	$\langle PTS \rangle$	sync. time
LCOs mean-field vs. LCOs distance-dependent	✓	✓
LCOs mean-field vs. IFOs mean-field	✓	✓
LCOs mean-field vs. IFOs distance-dependent	✓	✓
LCOs distance-dependent vs. IFOs mean-field	✓	✓
LCOs distance-dependent vs. IFOs distance-dependent		✓
IFOs mean-field vs. IFOs distance-dependent	✓	✓

1.5 Beyond the fireflies courtship: the response to synchronization

Courtship is the primary cause for which fireflies synchronize. Indeed, this behavior is known from more than a century ago [46]. The mechanisms for some species, in particular for those belonging to *Photinus* genus were disemboweled, and their oscillatory features were described by Lloyd [40] and improved by Lewis and Cratsley [38].

Fireflies courtship in most species belonging to *Photinus* genus is hallmarked by the females' response to males' synchronization. A first attempt to explain the response to synchronization has been made using a modified LCOs model, in which, males and females exhibit dissimilar features when they are interacting [58]. The model and the mechanisms of response to synchronization are described in [58, 61]. It is shown that, not only the experimental results presented in [48] are reproduced, but it is also capable of predicting more complex and realistic situations; in particular, the behavior of other species of the genus *Photinus* as it will be described later.

As explained in [61], to model the response to synchronization, it is necessary to consider the dissimilarity between males and females in which concerns their oscillatory features. In Fig. 1.8 the terminology used in the description of a male and a female is explained. Several fireflies' species exhibit a bursting behavior for the male with n_f flashes per burst (Fig. 1.8a) followed by a quiescent or silent time T_s, a parameter that remains constant even when the oscillators are coupled. On the contrary, the female generally emits only 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. 1.8(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 commonly two different time scales, i.e., within each cycle, there is a slow process followed by a firing one. Each process ends at its 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. (1.2). It is also important to note that in Fig. 1.8a, the parameters values and $n_f = 6$ correspond, 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:

$$\frac{\mathrm{d}V_i(t)}{\mathrm{d}t} = \frac{\ln 2}{T_{ci}}\left(V_{Mi} - V_i(t)\right)\varepsilon_i(t) - \frac{\ln 2}{T_{di}} V_i(t)\left(1 - \varepsilon_i(t)\right), \tag{1.10a}$$

$$V_i(t) = \left(V_i(t) - V_i^{\text{lower}}\right)\varepsilon_i(t) + V_i^{\text{lower}}. \tag{1.10b}$$

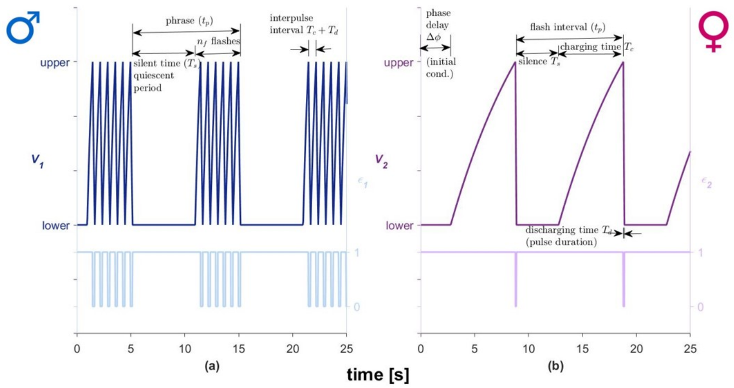


Fig. 1.8 Dynamic V and binary ε variables for the relaxation oscillators associated with (a) male, and (b) female fireflies of (*Photinus carolinus*). They are characterized by the quiescent period (silent time) T_s, the active phase with n_f flashes per burst, the charging and the discharging times T_c and T_d, respectively, the interpulse interval $T_c + T_d$, the flash interval or duration of a phrase T_p, and the phase delay $\Delta\phi$ that plays the role of initial condition. In this particular case, the parameter values are, respectively, for the male (♂) and female (♀): $T_{p♂}$=10.000 s, $n_{f♂}$=6, $T_{c♂}$=0.500 s, $T_{d♂}$=0.200 s, $T_{s♂}$=5.800 s and $\Delta\phi_{♂}$=0.603 rad $\equiv$ 0.960 s, $T_{p♀}$=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.

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:

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

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

$$\textbf{If} \quad V_i(t) = V_i^{\text{lower}} \quad \textbf{and} \quad \varepsilon_i(t) = 0 \quad \textbf{then} \quad \varepsilon_i(t_+) = 1; \tag{1.11a}$$

$$\textbf{If} \quad V_i(t) = V_i^{\text{upper}} \quad \textbf{and} \quad \varepsilon_i(t) = 1 \quad \textbf{then} \quad \varepsilon_i(t_+) = 0; \tag{1.11b}$$

$$\textbf{If} \quad V_i(t) = V_i^{\text{lower}} \quad \textbf{and} \quad \varepsilon_i(t) = 1 \quad \textbf{then} \quad \varepsilon_i(t_+) = 1, \tag{1.11c}$$

where t_+ in the condition given by Eq. (1.11c) is defined in the interval

$$t = [t_+ \quad (k-1)(T_p + n_f(T_c + T_d)) + \Delta\phi] \, , \tag{1.12}$$

for every k flash interval or phrase, i.e., for every complete cycle comprising the active phase and the silent time. Eq. (1.12) states for the successive silent intervals.

The main feature of the considered oscillators dwells on its flashing 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:

$$\frac{\mathrm{d}V_i(t)}{\mathrm{d}t} = \frac{\ln 2}{T_{c0i}}\left(V_{Mi} - V_i(t)\right)\varepsilon_i(t) - \frac{\ln 2}{T_{d0i}} V_i(t)\left(1-\varepsilon_i(t)\right) + \theta_i \sum_{i,j=1}^{N} \beta_{ij}(1-\varepsilon_j(t)), \tag{1.13}$$

where $i, j = 1, \ldots, N$. Conditions that are given by Eq. (1.10b) and Eqs. (1.11), which take into account the existence of a silent time, must also be followed by Eq. (1.13). The quantities T_{c0i} and T_{d0i} are the lasting time of the charge and the discharge, respectively, 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. (1.13) shows that both charging and discharging stages might be modified by the effect of 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 value 1 for males, and -1 for females. This factor is of particular importance because it determines the behavior of the oscillators when stimuli are applied to them.

Several studies have been carried out in [58] considering *Photinus carolinus* flash patterns. Here, we show in Fig. 1.9 the interaction between a set of four males and one female that according to their flashing patterns correspond to *Photinus collustrans* (Fig. 1.9(a)) and *Photinus greeni* (Fig. 1.9(b)). In the case of *Photinus collustrans*, the typical behavior of female response to synchronized males occurs at around 18 s. When considering *Photinus greeni*, it first appears a sporadic female response when the males are not completely synchronized and eventually, at around 28 s and when the males are in synchrony, the female response becomes persistent. To obtain the above-mentioned Figs., we use the oscillatory fireflies features pointed out In Table 1.2. *

1.6 Nice epilogue playing with fireflies: the “solitary flash” game

With the aim of explaining fireflies flashing behavior, a very simple algorithm has been proposed by Stewart and Strogatz [73]. Based on simple rules, it permits to capture main features of entrainment and synchronous behavior in fireflies. Originally, the rules are formulated as:

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.

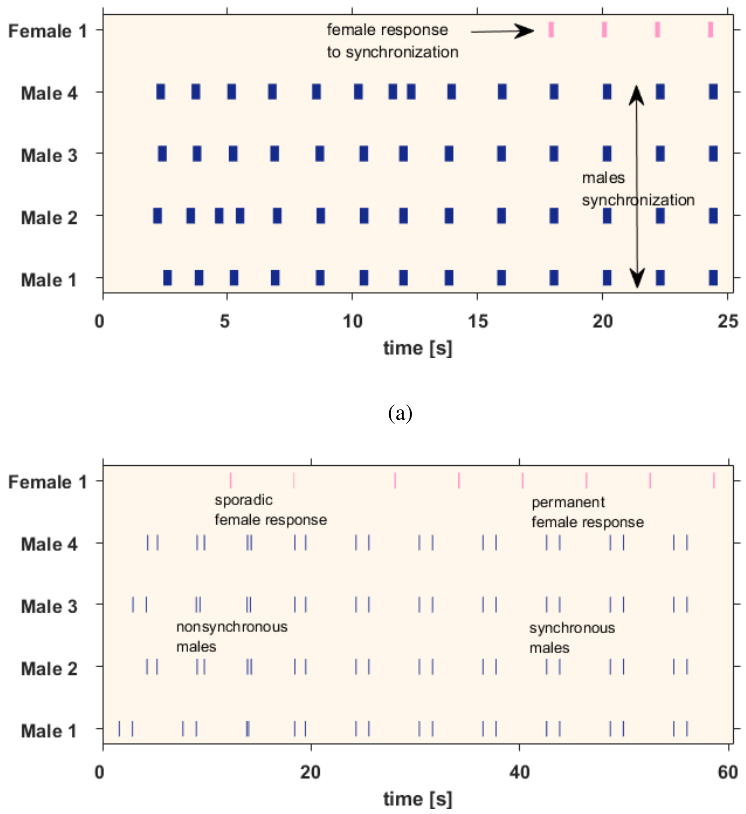
Table 1.2 Main oscillatory features of different *Photinus* species.

Species	Gender	Flashes	Flashing [s]	Interflash [s]	Quiescence [s]
P. collustrans	♂	1	0.343	2.200	1.843
	♀	1	0.443		
P. ignitus	♂	1	0.243	4.986	4.743
	♀	1	0.314		
P. marginellus	♂	1	0.385	2.871	2.486
	♀	1	0.114		
P. pyralis	♂	1	0.729	5.657	4.928
	♀	1	0.214		
P. sabulosus	♂	1	0.129	3.786	3.657
	♀	1	0.057		
P. umbratus	♂	1	0.557	6.786	6.229
	♀	1	0.343		
P. consanguineus	♂	2	0.171	0.500	4.643
	♀	1	0.243		
P. greeni	♂	2	0.100	1.271	3.571
	♀	1	0.157		
P. consimilis	♂	8	0.086	0.271	>4.914
	♀	2	0.129	0.286	

3. Each firefly starts the game in any box (initial condition) excepting the flashing one.
4. Each firefly advances clockwise one position per time step.
5. When a firefly flashes, it remains in the flashing 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 and simultaneously in the shortest possible time.

The rules mentioned above might allow or not the occurrence of complete synchronization. The dynamics of the game strongly depends on the initial conditions and also on rule 5 because it determines what happens to a firefly when it approaches, arrives or passes through the flashing box. We consider the following four complementary 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 flashing box and consequently without flashing in its cycle. This fact imposes a difficulty in attaining complete synchronization.
(b) When a firefly restarts a new cycle, it is mandatory that it arrives at the flashing box and as a result, it flashes in each cycle. This rule facilitates the achievement of complete synchronization.
(c) When two or more fireflies are nearby the flashing box, they wait until all of them are indeed in this box; at this time, all the fireflies advance one position.



(a)

(b)

Fig. 1.9 Flash sequences for males (blue) and females (pink) of two different *Photinus* species: (a) *collustrans* ($n_{f\text{♂}} = n_{f\text{♀}}$=1), and (b) *greeni* ($n_{f\text{♂}}$=2, $n_{f\text{♀}}$=1). In both cases, the female response to males synchronization is pointed out. We used the fireflies parameters shown in Table 1.2, coupling strength for each case $\beta_{ij} = 2.5$ and 15, and initial conditions (times for which the cycle of each oscillator starts): [1.91111, 0.1858, 0.8795, 0.5717, 8.0807] s, and [0.3848, 3.5573, 2.0924, 5.1107, 4.1023] s respectively.

This modification respect to (b) makes it easier to attain complete synchronization.

(d) Finally, if we consider a similar situation as in (c) but with the modification that when the fireflies are forced to be in the flashing 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. 1.10.

Time series for all cases (a)–(d) are presented in Fig. 1.11, where we considered four fireflies and a specified set of initial conditions $(n_{01}, n_{02}, n_{03}, n_{04}) = (4, 6, 11, 19)$. Examples of basins of attraction are depicted in Fig. 1.12 where the condition is

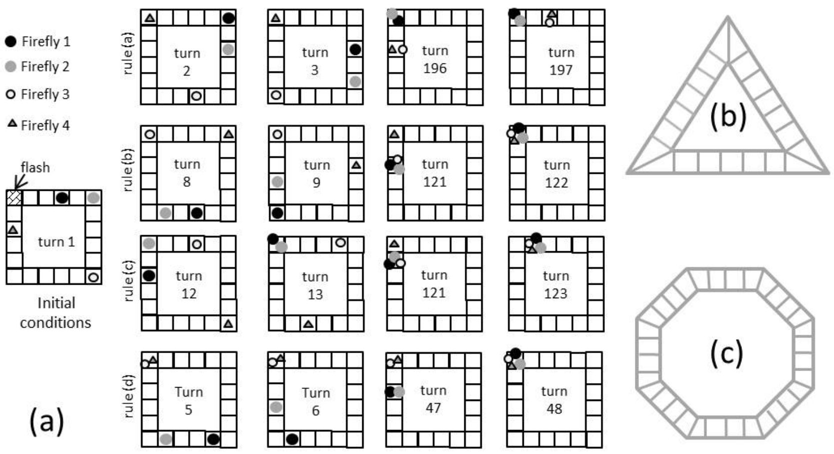


Fig. 1.10 (a) Frames of the game evolution for four players (fireflies) and the rules (a)–(d) considering for all the four cases the same initial conditions $(n_{01}, n_{02}, n_{03}, n_{04}) = (4, 6, 11, 19)$. Some other possibilities for the cardboard: (b) triangle, and (c) octagon.

related to the lasted time to achieve complete synchronization with collective simultaneous flashing. It is interesting to observe in Fig. 1.11(a) that the fireflies do

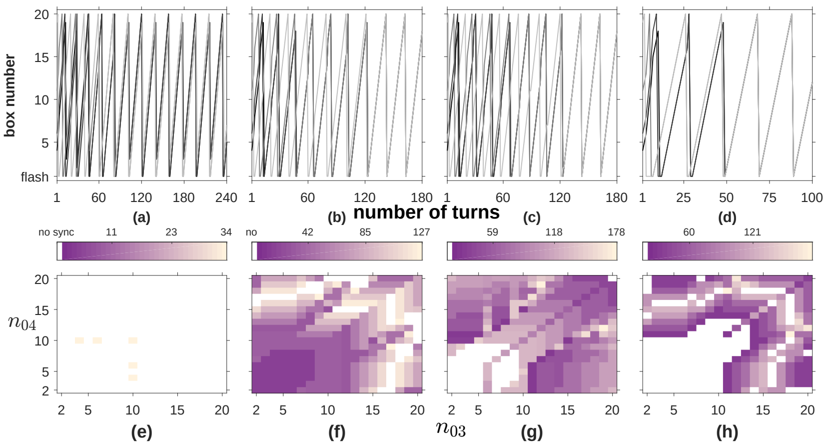


Fig. 1.11 First row: (a)–(d) Time series for the evolution of four fireflies following the rules (a)–(d) above mentioned. Second row: (e)–(h) Basins of attraction for the rules (a)–(d) considering that the initial condition for the first and second fireflies are (n_{01}, n_{02})=(4,6). White boxes represent situations in which simultaneous, collective, and persistent flashing (in every cycle) are not achieved, i.e., there is not complete synchronization.

not reach the complete 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 102nd turn; as a consequence, exhibiting synchronization but fireflies 1 and 2 do not flash in every cycle. On the contrary, Fig. 1.11(b)–(d) shows that simultaneous flashing is achieved, respectively, in 122, 142, and 48 turns (time steps). So that, in principle it indicates that in successive order the rules that facilitate synchronization are ,respectively, (d), (b), (c), and (a). With a view to sustaining the recent affirmation, we obtain some other basins of attraction for three and four fireflies. Indeed, we now consider a board in nonagon form, with 9 boxes per side, and initial conditions (n_{01}, n_{02})=(5,10); the basins of attraction for each rule are shown in Fig. 1.12(a)–(d) when the number of players is three, and in Fig. 1.12(f)–(i) when the number of players is four. The corresponding box plots displaying the medians, and the quartiles related to synchronization time as well as the percentage of complete synchronization events for each rule are shown in Fig. 1.12e and j for three and four fireflies, respectively. A visual and qualitative insight of the results set out that, as expected, rule (a) is the less favorable to attain complete synchronization. On the other hand, for three players, the results of rules (b), (c) and (d) seem to be very similar, but rule (d) is slightly more favorable to complete synchronization. Similarly, the visual inspection for four players shows us that for the rule (c), in almost all cases, complete synchronization is achieved (99.6%) but in contrast, the synchronization times are considerably longer than for rules (b) and (d).

A deeper statistical analysis corroborates in a certain way our previous assertions. Thus, for three players, the statistical analysis of both situations indicates that the median time of synchronization is the greatest for rule (a) and the shortest for rule (d). As the times of synchronization do not follow a normal distribution, a Kruskal-Wallis test was performed to look for differences in the distribution of the four rules ($\chi^2 = 436.7,\ df = 3,\ p < 2.2 \times 10^{-16}$). A Dunn's test for multiple comparisons showed that all pairwise comparisons between rules (a) to (d) are significantly different ($p < 0.001$), except between rule (b) and rule (c) ($p = 1.91 \times 10^{-1}$). The percentages of initial conditions for rules (a) to (d) leading to complete synchronization were respectively 11.3%, 93.0%, 93.8% and 93.0%. Thus, we can conclude that rule (d) is characterized by a very high number of initial conditions driving to complete synchronization, with the shortest times.

For the case of four players, the median time is also the greatest for rule (a) and the shortest for rule (d) (defining t_s as the synchronization time for achieving complete synchronization, t_s(a) $>$ t_s(c) $>$ t_s(b) $>$ t_s(d)). As the Kruskal-Wallis test was significant ($\chi^2 = 2361.7,\ df = 3,\ p < 2.2 \times 10^{-16}$), a Dunn's test of multiple comparisons was performed. All the pairwise comparisons were highly significant ($p < 0.001$). The percentages of initial conditions for rules (a) to (d) leading to complete synchronization were respectively 3.9%, 93.0%, 99.6% and 93.8%. As in the case of three players, rule (d) is characterized by a high number of initial conditions conducting to complete synchronization with the significantly shortest times.

This simple game with its four basic rules (algorithms) allows to explain complete synchronization in some species of fireflies, and it has an intrinsic richness,

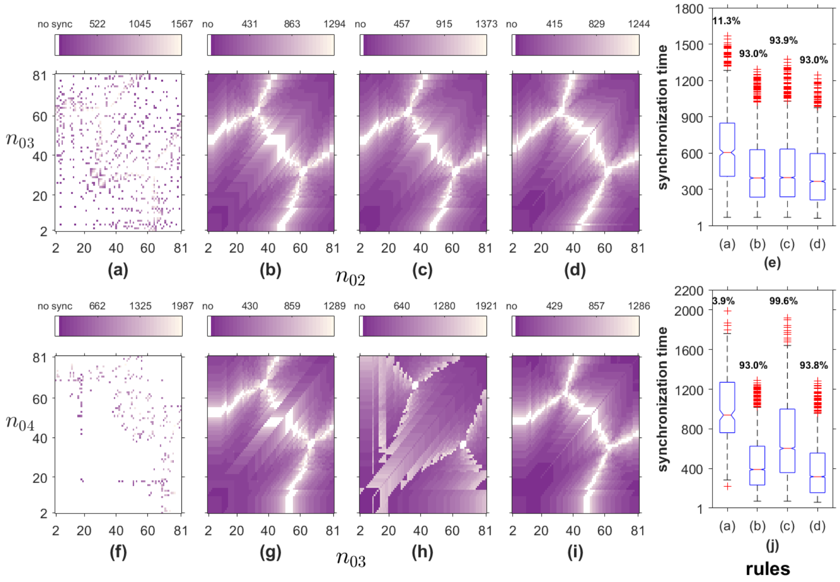


Fig. 1.12 Basins of attraction for rules (a)–(d) for (first row) three players with initial condition (n_{01}=5), and (second row) four players (fireflies) with a set of initial conditions (n_{01}, n_{02})=(5,10), when playing with a nonagon shape board (9 sides), with 9 boxes per side. (e) and (j), box plots (median and quartiles) of the synchronization times related to the basins (a)-(d) and (f)-(i). The percentage of the synchronous events is shown in the upper part, above the whisker.

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 fireflies (players). In some cases, an inhibitory coupling is also possible, as it is described in Sect. 1.5, for light-controlled oscillators (LCOs) and some species of fireflies. This type of coupling might be incorporated in the game considering that for some boxes on the game board, the player must go back a 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.) allows to extend the study of this model and analyze its isochronous dynamics as in [39].

1.7 What is missing in better understanding the fireflies synchronization and which are the potentials of this phenomenon?

Synchronization constitutes one of the central phenomena in nature, and a lot of advances have been gotten to understand how and why many systems exhibit synchronous behavior in different contexts. The case of fireflies synchronization is paradigmatic not only for the visual beauty that it represents but principally for the functionality that it typifies. Many efforts have been devoted to qualitatively describe synchrony in fireflies and also to decipher the “amorous language” that is involved with it. Mathematical models have been proposed to explain this behavior and thanks to physical-mathematical refinements, experimental work with mimicking systems, and computer simulations; nowadays it is possible to capture the main features of fireflies synchronization including the response of the female brought out by several species. Even though the models are based on rather simple ideas such as the consideration of each firefly as an oscillator and neglecting environmental influences (the weather conditions, the presence of external lights, the action of other species, the visual field of individuals, etc.), these models give the account of the main features and also have predicting power. The latter contributed to the development of applications of this phenomenon in different areas such as in the improvement of reliability and efficiency of mobile computer networks [8], in the solution of engineering problems [29], and in swarms of robots as a first approach for understanding real task-execution scenarios [22] among others. Some new impact applications are also remarkable, such as those leading to improve the efficiency of LEDs [5], or those conducting to a new method of medical diagnostics based on the way in which fireflies produce cold light [70].

Nevertheless, there are still some challenges concerning the fireflies synchronization. From a biological viewpoint, it is necessary to study more fireflies species and whether or not they exhibit synchronous behavior. A more detailed repertory of synchronous features could also be helpful. The latter might contribute to improve the models and consequently to envisage new concepts and applications. Though some works were devoted to the study of synchronization of mobile oscillators [30, 56], it is necessary to focus the studies on fireflies through a weighted mobile network approach for populations of coupled fireflies which seem to be adequate because of the individuals’ mobility, limitations on the fireflies visual field, existence of obstacles, and coupling strength dependence on the distance.

Response to synchronization deserves deeper studies and improved models allowing to characterize the females’ response patterns adequately and also consider control aspects. Finally, the ideaFinally, the idea of working with mingled (both genders: males and females) and mixed (natural and artificial fireflies) groups is also a great challenge because it involves insects-robots interaction which could have profound implications at the level of primary synchronous behavior.

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