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Experimentally faithful model for synchronous flashing of Southeast Asia fireflies –Rigorous results and numerical observations–

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Abstract—In this study, we present an experimentally faithful model for synchronous flashing of Southeast Asia fireflies. This model is based on the data of integrate-and-fire mechanism of the synchrony in firefly flashing, obtained in the field experiments by Hanson et. al. [1]. Through systematic simulations and analysis, we obtain some rigorous results and numerical observations on perfect synchrony and wave-like patterns in synchrony. This suggests that our model accounts for the coexistence of perfect synchrony and wave-like pattern observed in New Guinea.

1. Background and purpose of this study

Synchronous flashing of Southeast Asia fireflies has fascinated people including scientists for over one hundred years. Data from recent fieldworks uncover that these fireflies often exhibit a certain traveling wave pattern of flashing, as well as a perfectly synchronized pattern, as schematically shown in Fig. 1. For the latter perfectly synchronized pattern, mathematical models have been developed, for example, by Mirollo and Strogatz [2], and by Ermentrout [3], etc. However, to our knowledge, none of such models account for the coexistence of perfect synchrony and traveling wave-like pattern.

In this study, we focus on the systematic data from fieldworks by F. Hanson, J. Case, E. Buck, and J. Buck [1], which explains how a single firefly is entrained to rhythms of certain artificial flashing. Based on this experimental observation, we are lead to a simple, but experimentally faithful mathematical model of firefly (*P. effulgens*) synchrony. Interestingly, this model exhibits both perfect synchrony and a certain wave-like pattern, depending on the natural frequency in flashing for each firefly, quite naturally. Then, we consider and clarify the following items, which are observed in the presented model for firefly synchrony.

(i) The global convergence to the perfect synchronization is proved for the all-to-all coupling case of N fireflies (in Sec. 3), and (ii) Some conditions for generating the wave-like flashing pattern are identified (in Sec. 4).

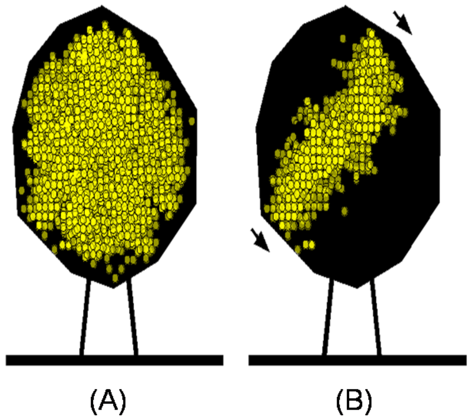

Figure 1 Two typical patterns of synchronous flashing of fireflies
(A) Perfect synchronization
(B) Wave-like flashing pattern

2. Experimentally faithful model for firefly synchrony

Now, we review conventional studies of mathematical modeling on firefly synchrony. So far, several mathematical models have been proposed for perfect synchronization of fireflies. Mirollo and Strogatz [2] is the first to explore such modeling. This has accomplished a rigorous account for perfect synchronization of 'fireflies' for the first time. However, in reality, as they mention clearly in their paper [2] their model is originally inspired by the Peskin's mathematical models for cardiac oscillators. Then, it is fair to mention that their model is NOT directly related to the observed firefly synchrony.

Later on, Ermentrout proposed an adaptive model for synchrony in a particular firefly [3]. This provides a reasonable mathematical insight as to why *P. malaccae* exhibits superior ability for wide range of frequency entrainment. However, some essential points in this model are due to a mathematical reasoning, which is not directly supported by the experimental data.

Further, Ermentrout analyzed a particular rotating firing pattern in pulse-coupled oscillators [4]. This provides some new mathematical treatments for rotating wave pattern in pulse-coupled oscillators. But, this also is not directly linked to the observed wave patterns in group synchrony of fireflies.

On the contrary, Hanson et. al. [1] have already obtained some experimental observations on the entrainment mechanism of an isolated firefly , which is briefly summarized in Fig. 2. To account for their observations, they set the following two assumptions. (1) Each firefly has a constantly incrementing 'timer' in its nervous system. If this timer reaches a certain threshold, the firefly flashes immediately and the timer is reset to the initial state of 0. Then, an isolated firefly flashes periodically in its own natural frequency, as in Fig. 3(a). (2) When a firefly receives a flashing pulse from other fireflies, it resets its timer to 0 and basically cancels its planned flashing as in Fig. 3(b). But, as shown in Fig. 3(c), if a firefly receives a pulse from other fireflies when its timer becomes more than around 80% of the above mentioned threshold, it resets its timer to 0 but flashes at it has planned, due to certain mechanism of its nervous system.

These assumptions seem quite natural and reasonable, although their description in [1] is a bit complicated. However, to our knowledge, this mechanism has never been considered to construct an experimentally faithful modeling of firefly synchrony. In this study, based on the above insights by Hanson et. al. [1], we propose an integrate-and-fire model for mutual synchrony of fireflies (schematically shown in Fig. 3). Through systematic simulations and analysis on this model, some properties of perfect synchrony and wave pattern of flashing are clarified.

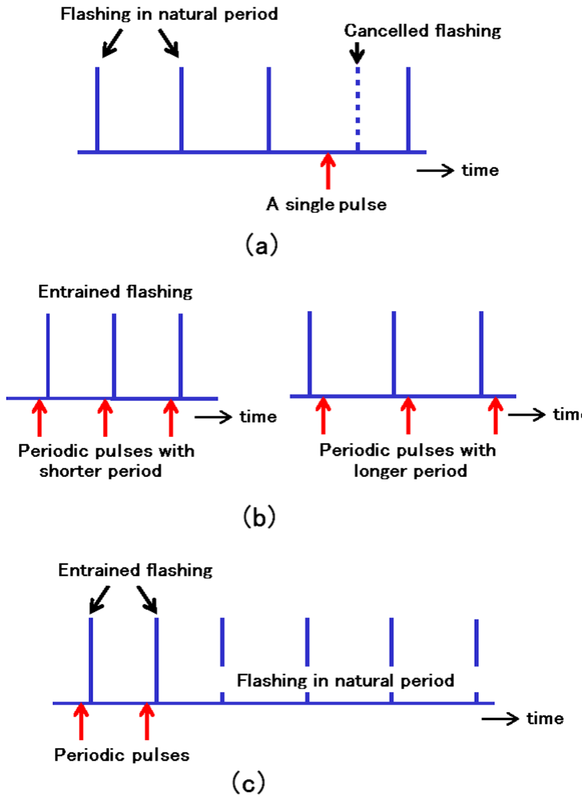

Figure 2 Summary of the observations in Hanson et. al.[1]
(a) Phase shift of flashing by a single pulse
(b) Entrainment to periodic pulses with shorter or longer period, respectively
(c) Process of losing entrainment after the periodic pulse is removed

3. An integrate-and-fire model and its global convergence to synchrony

Here, we consider an integrate-and-fire model for firefly group synchrony, based on the above mentioned entrainment mechanism. To model this group synchrony, we assume each firefly controls its timing of flashing by the above mentioned entrainment mechanism, as a first approximation. Then, we start from the most simple, all-to-all (global) coupling case of N fireflies, where each firefly equally interacts with each other. And, later we consider cases of local coupling within a certain distance, in Sec. 4.

3.1. Synchronization patterns for two fireflies

We start from the simplest case of mutually interacting two fireflies. As mentioned in Sec.2, we assume each firefly has a continuously incrementing timer, and for simplicity we further assume all fireflies have the same speed of increment ($\equiv 1$) and have the same maximum value of the timer ($\equiv 1$) where the firefly flashes. With this simplification, we can identify the state of the timer as a point on the span $[0, 1)$.

Now, we name the two fireflies as A and B. From the above assumption, their instantaneous state of timers are defined as ϕ_A and ϕ_B ($\in [0, 1)$) respectively. The time evolution of these phase variables $\phi_{A,B}$ is visualized as in Figs.4 and 5.

As shown in Fig. 4(a), when B receives a pulse from A, the timer of B is reset to 0 (; ϕ_B becomes 0) and B cancels its planed flashing if $\phi_B < \Theta$ holds. Then, in this case B is completely synchronized to A by the first pulse from A, and this synchronization remains after that. Thus, the process to complete synchronization is summarized as in Fig. 4(b).

On the contrary, as shown in Fig. 5(a), if B receives a pulse from A when $\phi_B \geq \Theta$, the situation becomes a bit complicated. In this situation, by the pulse from A, ϕ_B becomes 0 from ϕ_B^* but B flashes as it has planned. Then, by this pulse from B, ϕ_A becomes 0 and A cancels its flashing since $\phi_A = 1 - \phi_B^* < \Theta$. After the time of ϕ_B^* ($= 1-(1-\phi_B^*)$) from this event, when $\phi_A = \phi_A^* = \phi_B^*$, A receives a pulse from B. And this situation is the exactly the same to the beginning except for A and B being replaced. From the above

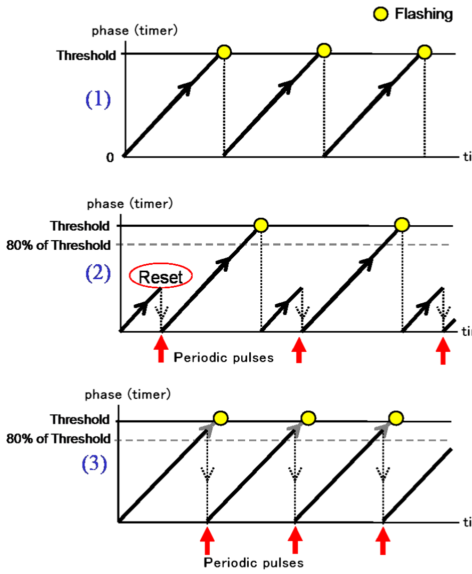

Figure 3 Schematic description of entrainment mechanism per Hanson et. al.[1]
(1) Case of no external stimuli ; periodic flashing in its own natural frequency
(2) Entrainment to periodic pulses with longer periods than the natural period of the firefly
(3) Entrainment to periodic pulses with shorter periods than the natural period of the firefly

arguments, the following property is proved.

[Prop. 1] For mutually interacting fireflies, perfect synchronization is realized if their initial phase difference, $|\phi_A - \phi_B| > 1.0 - \Theta$ (case 1). If the initial phase difference, $|\phi_A - \phi_B| \leq 1.0 - \Theta$, two fireflies flash alternatively with the phase difference $|\phi_A - \phi_B|$ $(= 1 - \phi_B^*)$ (case 2).

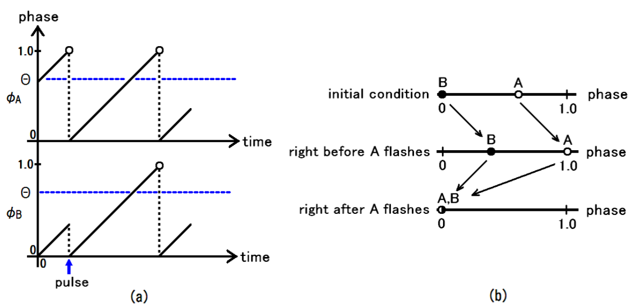

Figure 4 Complete synchronization for two fireflies

3.2. Synchronization patterns of N fireflies

Then, we generalize the above arguments for the case of two fireflies to N $(N \geq 2)$ fireflies.

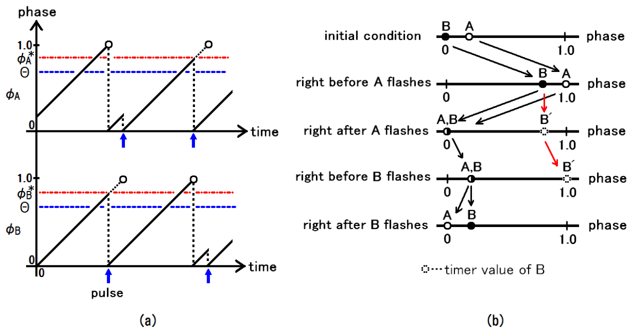

Figure 5 Alternative flashing pattern for two fireflies

First, we name the N fireflies respectively as from 1 to N, instead of A and B in the case of two fireflies. Then, the associated phase variables are defined by $\phi_1, \cdots, \phi_N$ $(\in [0, 1))$ and we assume

$$0 \leq \phi_1 < \cdots < \phi_k < \cdots < \phi_N < 1, \quad (1)$$

without loss of generality. (If any two fireflies k and l $(< k)$ has the same initial phase; $\phi_k = \phi_l$, then we identify these two fireflies as one firefly, say k, without loss of generality.)

For instance, we consider the initial condition of $\phi_1, ..., \phi_N$ as in Fig. 6(a). After the time of $1 - \phi_N$ from this situation, the firefly N flashes (; ϕ_N becomes 1 as in Fig. 6(b)). Then, the fireflies 1, ..., $k-1$ are synchronized to N from this point. On the other hand, the fireflies $k, ..., N-1$ are synchronized to N but they are going to flash as they has planned. This situation is shown in Fig. 6(c), where ○ denotes the firefly which is synchronized to N but still going to flash. Here, a key consideration is required; the number of ○ in Fig. 6(c). (It is noted that the instance of Fig. 6(c) is always realized for any initial conditions when the firefly N flashes.) If the number of ○ is zero, it implies the completion of perfect synchronization among the fireflies 1, ..., $k-1$, and N. Then, if the number of ○ is one, this situation falls into the case 1 (; perfect synchronization) in Prop. 1. Finally, if the number of ○ is more than 2, this falls into the case 2 (; alternative flashing) in Prop. 1. Thus, the synchronization patterns of N fireflies are completely classified into two cases; perfect synchronization and alternative flashing. From the above arguments, the following property is proved.

[Prop. 2] For mutually interacting N fireflies, depending on the initial conditions, perfect synchronization or an alternative flashing pattern of two clusters are eventually realized.

4. Numerical observations for synchronous patterns

We now consider a group of fireflies in lattice for simulation. Our simulation settings are described below. Each firefly equally responds to every pulse from other fireflies.

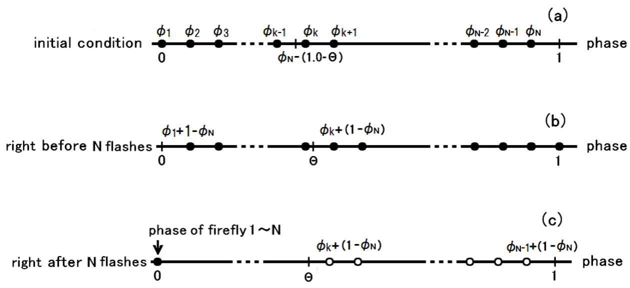

Figure 6 Synchronization process for N fireflies

Range of interactions are set to 4 (nearest neighbor), 8, 12, and all to all, respectively for each simulation (see Fig. 7). Network of mutual interaction is simplified as an array of network. Fixed or periodic boundary conditions are assumed. Natural frequencies of fireflies are set to constant and uniform. Initial timings are set to random, and then we observed some settled patterns in simulation.

As a result, both perfect synchronization pattern and rotating wave pattern are observed, depending on the initial timings (see Fig. 8). In the rotating wave pattern (Fig. 8(a)), it is observed that fireflies around the center have longer flashing periods than others. Actually, for a pacemaker with lower frequency, a concentric wave pattern is obtained (Fig. 8(b)).

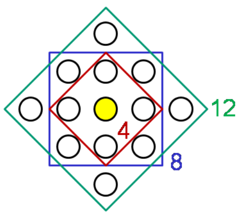

Figure 7 Range of interactions

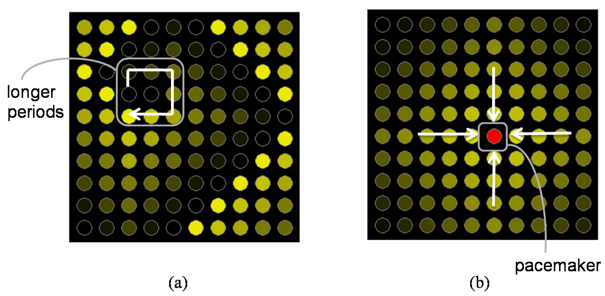

Figure 8 Simulation Results
(a) Rotating wave pattern
(b) Concentric wave pattern

5. Conclusions

We confirmed that the presented experimental faithful model per Hanson et. al. [1] generates both perfect (or partially) synchronization patterns and rotating wave pattern even in the case of constant and uniform natural frequency distribution in fireflies. One possible cause of wave pattern is existence of firefly which has even a slightly lower frequency than others.

The presented simple model reasonably explains the coexistence of perfect synchrony and wave-like patterns observed in New Guinea. Such features cannot be obtained by the conventional 'phase model' descriptions.

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