San Diego State University

Paper Review: Beyond a pacemaker's entrainment limit: phase walk-through

Opal Issan

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Abstract

Entrainment is a universal process where a system's frequency is synchronized with an external perceived rhythm. This process occurs in various physical and biological systems. Due to its appearance in nature, it is important to study simplified models of coupled oscillators. In the paper "Beyond a pacemaker's entrainment limit: phase walk-through", Ermentrout and Rinzel propose a simple nonlinear one-variable model of synchronized flashing fireflies [1]. In this paper review, the ideas presented by Ermentrout and Rinzel are explained, including a comprehensive analysis of the model and its contribution to understanding other oscillatory biological systems, including circadian pacemakers.

Keywords **- Nonlinear Dynamical Systems, Synchronization, Oscillators, Firefly.**

Introduction

Male Fireflies synchronously flash under active neurons generating pacemaker activity. The Male fireflies try to attract the attention of female fireflies as they cruise overhead [2]. This is an mesmerizing phenomena in nature (see Figure 1). The male fireflies send a pulse to one another as they cluster together and synchronously light up. In this process, as one firefly sees the flash of another it will shift its beat to match the other [2]. This shift in rhythm creates perfectly synchronized flashing. This can lead to thousands of fireflies lighting up perfectly together on one tree or bush. They light up about three times every two seconds [2]. The fireflies synchronization is categorized as "integrate and fire" oscillation, described by the oscillators interacting by a simple form of pulse coupling [3].

This paper review will refer to "Beyond a pacemaker's entrainment limit: phase walk-through" by Ermentrout and Rinzel as paper 1. In paper 1, the authors developed a simplified mathematical model that describes the system of flashing fireflies. The model is a simple one dimensional nonlinear differential equation. They derived the model by examining experimental data of *Pteroptx malaccae*, a common species of fireflies in Malaysia. From this dataset, it is visible that when the period of stimulus is around 770 ms entrainment is visible. Whereas, in slightly higher frequency, such as 750 ms, the entrainment no longer occurs [1]. Meaning, the fireflies will flash at different rhythms. This phenomena is called a *phase walk-through*, where firefly struggle to synchronize.

To reiterate, based on the expiremental dataset, the authors of paper 1, developed a simple one dimensional model to describe how a firefly flashing rhythm is effected by a stimuli (or in nature - the flashing of another firefly). In the following sections include introducing the model, its derivation, and an in-depth analysis of the system and its parameters.

Fireflies in Osaka, Japan. Credit: Asahi Shimbun Getty Images.

Figure 1: Fireflies in Osaka, Japan synchronously flash in the process of mating. More specifically, male fireflies flash in unison in attempt to attract surrounding females [2]. The male fireflies respond to light signals with a latency of about 1s, therefore it is difficult to capture this phenomena. To overcome this challenge, this image was taken using a long exposure shot.

Derivation of Firefly Synchronization Model

Oscillators are systems that exhibit periodic behavior, described as $\dot{\phi} = f(\phi)$ and $f(\phi + \lambda k) = f(\phi)$, such that the system is λ-periodic and k is an integer. *Phase space* is a coordinate system that describes the systems observables as they change in time. In the example presented in paper 1, the observables are the phase of the firefly's flashing denoted by θ. $\theta = 0$ is the instance when a flash occurs, and since the phase is periodic, $\theta = 2\pi n$ and $n \in Z$ is also an instance of a flash. In the case where the stimuli is absent, θ goes from 0 to 2π in T_0, measured in ms. T_0 is called the *period* of oscillation.

$$\frac{\partial \theta}{\partial t} = \frac{2\pi}{T_0} \tag{1}$$

As mentioned in paper 1, a point on the intrinsic cycle moves with an angular velocity of $\omega_0 = \frac{2\pi}{T_0}$ and the zeitgeber, the stimulus flash or the other firefly flash, velocity will be denoted by $\omega = \frac{2\pi}{T}$. Since the frequency increases when the stimuli flashes before the firefly and otherwise the frequency decreases, the authors of paper 1, propose a more complex yet one dimensional differential equation to describe synchronization of a firefly exposed to stimuli.

$$\frac{\partial \theta}{\partial t} = \frac{2\pi}{T_0} + \beta \sin(\omega t - \theta) \tag{2}$$

In equation (2), β measures the relative influence of the zeitbeger [1]. This equation can be manipulated and analyzed by the following steps. First, let us introduce a new variable ϕ, the *phase difference* between the stimulus and the firefly, such that $\phi = \omega t - \theta$ and $\frac{\partial \theta}{\partial t} = \omega - \frac{\partial \phi}{\partial t}$. Therefore, equation (2) can be rewritten as follows

$$\begin{aligned} \omega - \frac{\partial \phi}{\partial t} &= \frac{2\pi}{T_0} + \beta \sin(\phi) \\ \frac{\partial \phi}{\partial t} &= \omega - \frac{2\pi}{T_0} - \beta \sin(\phi) \\ \frac{\partial \phi}{\partial t} &= \frac{2\pi}{T} - \frac{2\pi}{T_0} - \beta \sin(\phi) \\ \frac{\partial \phi}{\partial t} &= \frac{2\pi}{TT_0}(T_0 - T) - \beta \sin(\phi) \end{aligned} \tag{3}$$

Where one can qualitatively analyze the behavior of the system using techniques from the mathematical branch of nonlinear dynamical systems. This equation can be solved numerically using a numerical scheme such as fourth order Runge-Kutta.

Qualitative Analysis

Most nonlinear systems are impossible to solve analytically due to nonlinearity. Therefore, there are mathematical techniques to overcome this challenge and analyze the behavior of system *qualitatively*. The qualitative steps employed in paper 1 include a geometric interruption of the differential equation phase space, finding fixed points, their stability, and classification of bifurcation points. The following section will analyze the fireflies system proposed by Ermentrout and Rinzel [1].

Fixed Points Analysis

Fixed points represent equilibrium solutions. An equilibrium is the state of which the system either converges or diverges from as t approaches ∞. In order to find the fixed points of equation (3) we set $\dot{\phi}$ equal to zero, and solve for ϕ.

$$\begin{aligned} \frac{\partial \phi}{\partial t} &= \frac{2\pi}{TT_0}(T_0 - T) - \beta \sin(\phi) \overset{set}{=} 0 \\ \sin(\phi_e) &= \frac{2\pi}{TT_0\beta}(T_0 - T) \\ \phi_e &= \arcsin\big(\frac{2\pi}{TT_0\beta}(T_0 - T)\big) \end{aligned} \tag{4}$$

The fixed points depend on the parameters β, T_0, and T. Let $c = \frac{2\pi}{TT_0\beta}(T_0 - T)$. Then, if $c = 0$, all trajectories flow toward the stable fixed point $\phi^* = 0$, therefore the fireflies will entrain (see figure 2 for a phase portrait). When $0 < c < 1$, then the stable fixed point is located at $\phi^* > 0$. Therefore, the fireflies will flash in the same frequency but they will not flash in unison [4]. The firefly's rhythm is *phase-locked* to the stimulus [4]. Strogatz describes the phenomena of phase locking as follows: "phase locking means that the firefly and the stimulus run with the same instantaneous frequency, although they no longer flash in unison" [4]. As c increases, the two fixed points merge and eliminate. Therefore, when $c > 1$ the phase difference grows infinitely and the fireflies will not be able to synchronize their flash, corresponding

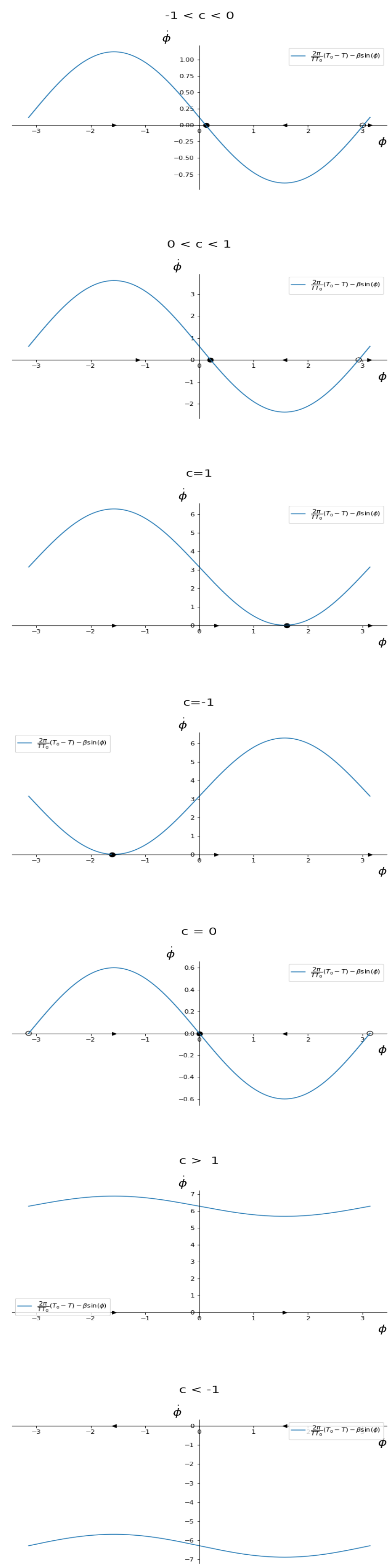

Figure 2: Let $c = \frac{2\pi}{TT_0\beta}(T_0 - T)$. There are three different cases of fixed points depending on the value of c. If $-1 < c < 1$, there is a stable fixed point (two to three fixed points total). If $c > 1$ or $c < -1$, there are no fixed points. Lastly, if $c = \pm 1$, there is one half-stable fixed point.

to a *phase-drift* [4]. Due to the symmetry of the problem, the same applies for when $c < 0$ (see figure [2]). Therefore, there are stable fixed points only when $-1 < c < 1$, this interval is called the *range of entrainment* [4].

Stability Analysis

Fixed points can be classified as stable, unstable, or half-stable. Stable, meaning the solutions converge to the equilibrium. Unstable equilibrium repels the solutions as time evolves. Lastly, a half stable system does not repel nor attract the systems solutions. In order to evaluate the stability of the fixed points, we need to first compute $\frac{\partial^2\phi}{\partial t^2}$.

$$\frac{\partial^2\phi}{\partial t^2} = -\beta\cos(\phi) \tag{5}$$

Then, evaluate $\frac{\partial^2\phi}{\partial t^2}$ at the fixed point ϕ_e. If $\frac{\partial^2\phi}{\partial t^2}(\phi_e) < 0$ the fixed point is *stable*. If $\frac{\partial^2\phi}{\partial t^2}(\phi_e) > 0$, the fixed point is *unstable*, and if $\frac{\partial^2\phi}{\partial t^2}(\phi_e) = 0$, it is possible the fixed point is *half-stable*.

In figure [1], the stable fixed points are marked by a full black circle and the unstable fixed points are marked by a hollow black circle. This is common in analyzing the phase portrait of a dynamical system.

Let $c = \frac{2\pi}{TT_0\beta}(T_0 - T)$. Notice, when $c = \pm 1$, there is an half stable fixed point. Otherwise, when $-1 < c < 1$, the fixed point closer to 0 is classified as stable (see figure [1]). The difference between the rhythm of the firefly and the stimuli will converge to the stable fixed point as time evolves.

Bifurcation

Bifurcation points are critical values of the systems parameter where small perturbations in the parameters can cause instabilities in the system. There are three types of bifurcation points: saddle node, transcritical, and pitchfork. In the fireflies system, there are two saddle node bifurcations where $c = 1$ or $c = -1$. A saddle node bifurcation point dictates if the system's fixed points collide or mutually annihilate.

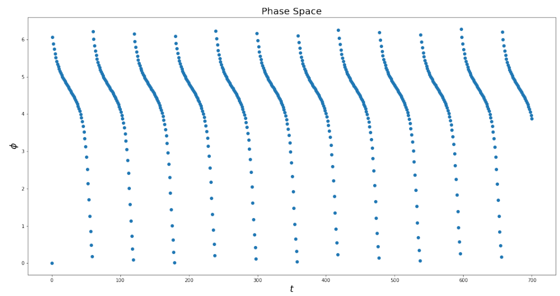

Figure 3: Phase Space of the numerical solution of equation (3) (mod 2π). The parameter values are set to be $\beta = 0.17$, $T = 2\pi/1.2$ and $T_0 = 2\pi$. Therefore, $c < -1$ and the system exhibits *phase-drift*. The resulted ϕ is plotted modular 2π. The numerical solution was obtained using 4th order Kutta-Runge solver in Python (see GitHub notebook for more details on how to implement the numerical scheme in Python.)

Oscillation Period

The oscillation period where $c > 1$ can be found analytically using integration.

$$T = \int dt = \int \frac{dt}{d\phi} d\phi \tag{6}$$

Then, use equation (3) to replace $\frac{dt}{d\phi}$.

$$T = \int_0^{\phi} \frac{1}{\frac{2\pi}{TT_0}(T_0 - T) - \beta\sin(\phi)} d\phi \tag{7}$$

Since time required for ϕ to change is given by 2π then

$$T_{beat} = \int_0^{2\pi} \frac{1}{\frac{2\pi}{TT_0}(T_0 - T) - \beta\sin(\phi)} d\phi \tag{8}$$

By substituting $u = \tan(\phi/2)$ we can solve the integral and the resulting T_{beat} is as follows

$$T_{beat} = \frac{2\pi}{\sqrt{(\frac{2\pi}{TT_0}(T_0 - T))^2 - \beta^2}} \tag{9}$$

By modifying the parameters T_0, T, and β (as long as $c > 1$), one can evaluate how the oscillator's period T_{beat} changes. Notice that when $\beta \to \frac{2\pi}{TT_0}(T_0 - T)^-$, T_{beat} blows up [4].

Summary and Discussion

This report analyzed the performance of the phase difference model developed by Ermentrout and Rinzel [1]. The simple nonlinear one dimensional model results had high correlation with experimental data of *Pteroptyx malaccae* fireflies in Malaysia that exhibit a weak stimulus. The model suggested that the beat periods for when the system experiences a phase walk-through are described by a nonlinear function and not a simple linear function as proposed by Pavlidis [1]. Paper 1 explains how to predict phase walk-through when the parameters are beyond the interval of entrainment. An experiment studying the beat frequency as a function of stimulus period has not been done yet [1] [4].

By analyzing the model proposed in paper 1 one is able to identify the three phenomena that can occur: phase synchronization, phase drift, and phase-locked. phased drift occurs when the parameters of the system are beyond the interval of entertainment, otherwise the firefly and the stimuli will flash in unison or in a uniform delay.

Understanding the synchronization and desynchronization of the fireflies flashing can provide knowledge about different biological oscillators. Hanson [6] discussed the similar properties of fireflies and circadian pacemakers. The mathematical theory behind oscillators can also be used to optimize sensor networks. The ideas proposed by Ermentrout and Rinzel [1] advanced our understanding of oscillators, their mathematical formulation, and appearance in nature.

Code Availability

The code used to generate the figures is available at `https://github.com/opaliss/synchronous_fireflies`.

References

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