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Periodic rhythm and anti-phase synchronization in calling behaviors of Japanese rain frogs

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Abstract

We recorded and analyzed calls of Japanese rain frogs *Hyla japonica*. While a single frog called nearly periodically, a pair of frogs called alternately; namely we observed that after one frog called several times (3 to 39 times) alone, another frog began to call, and two frogs called alternately. The intervals of the calls when a frog called alternately with another frog is longer than those when the same frog called alone. We model these phenomena as the system of coupled phase oscillators; namely the calls of one frog as a periodic phase oscillator and the calls of two frogs as two coupled phase oscillators which synchronize in anti-phase. We also discuss a possible biological meaning of the calling behaviors.

1 Introduction

Mutual synchronization has been observed in many biological oscillators such as male fireflies in southeast Asia[1], pacemaker cells of hearts[2], and circadian rhythms[3]. For example, in certain parts of southeast Asia, thousands of male fireflies congregate in trees and flash in synchrony, night after night for weeks or even months, irrespective of air currents, air temperature, moisture or any other meteorologic conditions[1].

The answers to the question "What modes of temporal organization could result from weak interactions in a population of innately oscillatory elements?" are found mathematically and numerically as natural nonlinear phenomena of periodic processes and their interactions [3, 4]. Such theoretical analysis has been effective for understanding phenomena of synchronization in biological oscillators, including synchronous behaviors of living things.

In fact, synchronization of biological oscillators has been theoretically analyzed in many systems. For example, Ermentrout and Rinzel proposed a simple phase model for the entrainment of a firefly to stimuli[5]. They modeled the periodic stimuli with the phase variable Θ with $-\pi < \Theta \leq \pi$, namely $\Theta \in \boldsymbol{S}^1 = (\boldsymbol{R} \mod 2\pi) = [-\pi, \pi]/\{-\pi \equiv \pi\}$ [6] as follows:

$$\frac{d\Theta}{dt} = \Omega, \tag{1}$$

where Ω is an intrinsic frequency of the stimuli, and $\Theta = 0$ corresponds to the flash of the stimuli. Then, they modeled firefly's response to the stimuli with the second internal phase variable θ with $\theta \in \boldsymbol{S}^1$ as follows:

$$\frac{d\theta}{dt} = \omega + A\sin(\Theta - \theta), \tag{2}$$

where ω is an intrinsic frequency of the firefly, A is a positive coupling coefficient, and $\theta = 0$ corresponds to the flash of this firefly. This model of Eqs. (1) and (2) exhibits the property that if $|\Omega - \omega| < A$, the phase difference $\Theta - \theta$ locks to a fixed value, and if $|\Omega - \omega| \ll A$, these two oscillators synchronize in nearly in-phase. Mirollo and Strogatz also analyzed synchronization of pulse-coupled biological oscillators mathematically [7].

In particular, there have been some studies on synchronization of calls of frogs. Loftus-Hills studied the synchronization in calling behaviors of frogs *Pseudacris streckeri* [8], where tape-recorded calls were used to evoke responses of frogs. Lemon and Struger studied acoustic entrainment to randomly generated calls in frogs *Hyla crucifer* [9]. In the present paper, we study spontaneously calling behaviors of Japanese rain frogs *Hyla japonica*.

2 Methods

In the evening to night, male Japanese rain frogs *Hyla japonica* which were calling vividly were collected from breeding assemblages in paddy fields in Kyoto, Japan. Collected frogs were individually housed in small plastic cages with lengths 18cm and 8cm, and height 10cm, which were placed at intervals of about 40cm. Each cage was dipped about 1cm in water of the paddy fields where the frogs inhabited.

Experiments were performed immediately after collection. Spontaneous mating calls were recorded with a video camera (DCR-TRV18, SONY). Then, the data of the calls of a single frog or two frogs were picked up.

The time series data were analyzed with a digital computer (DynaBook T4, TOSHIBA) with respect to the waveforms and power spectrums (Raven Lite 1.0), the Fourier Transform (FFT), and nonlinear time series analysis [10, 11, 12].

3 Experimental Results

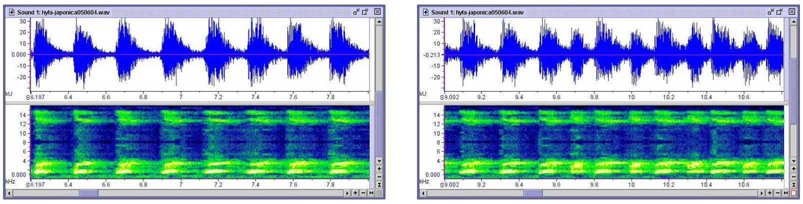
Figure 1 shows the calls recorded from (a) a single frog and (b) two frogs, where the upper and lower panels in (a) and (b) show the waveforms and the power spectrums in time windows of 1.8 s, respectively. A single frog called nearly periodically as shown in Fig. 1(a). In the experiment shown in Fig. 1 (b), after one frog called several times (3 to 39 times) alone, another frog began to call, and two frogs called alternately. Figure 1 (b) exhibits that the second frog began to call at 9.7s.

Figure 2 shows reconstructed orbits of the calls of (a) a single frog and (b) two frogs in delay coordinates [10, 11, 12]. The orbits of Fig. 2 are reconstructed from the data of amplitudes of the calls which are re-bined with 500 points, where the total time length is 3.8 s both in (a) and (b). Figure 2 shows that the calls of both a single frog and two frogs are nearly periodic.

In order to examine the change in intervals or the fundamental frequency of the calls of a single frog before and after the interactive calling of two frogs, we further analyze the longer data of waveforms of the calls. Figure 3 shows the power spectrums of (a) the calls of a single frog which called alone before two frogs started to call alternately and (b) those of two frogs which called alternately; the horizontal and vertical axes are the frequency and the power, respectively, where the total time length is 4.0s both in (a) and (b). There is the main peak around 4.2Hz in Fig. 3(a). That is, this frog called nearly periodically about 4.2 times in one second. On the other hand, there is the main peak around 7.0Hz in Fig. 3(b), which means that two frogs call alternately about 7.0 times in one second; namely, each frog call about 3.5 times in one second. The intervals of the calls of a single frog during the interactive calls of two frogs is longer than those of the same frog which called alone. At first this frog called about 4.2 times in one second, and then while two frogs called alternately, the same frog called about 3.5 times in one second.

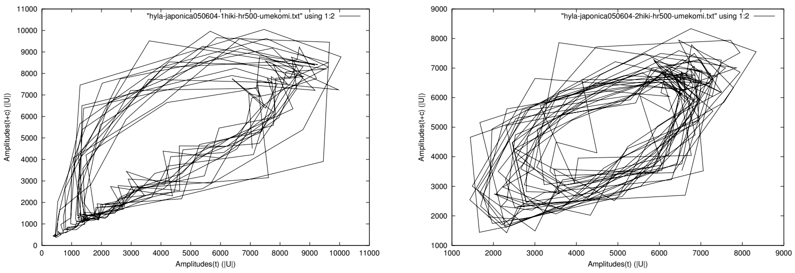
4 Discussion

In the experiment, a single frog called nearly periodically, and a pair of frogs called alternately. The intervals of the calls of a single frog during the interactive calls is longer than those of the same frog which called alone. Next, we model these phenomena as the system of coupled phase oscillators.



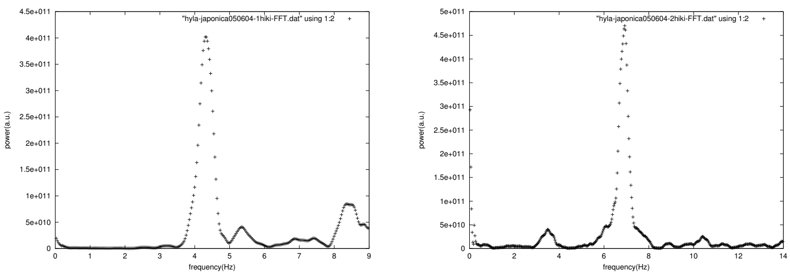
(a) (b)

Figure 1: The calls of (a) a single frog and (b) two frogs. The upper and lower panels in (a) and (b) show the waveforms and the power spectrums in time windows of 1.8s. Figure 1(b) shows that the second frog began to call at 9.7s.



(a) (b)

Figure 2: Reconstruction of orbits in delay coordinates of the calls of (a) a single frog and (b) two frogs, where the delay is set at 0.015s. The total time length is 3.8s both in (a) and (b).



(a) (b)

Figure 3: Fourier analysis of (a) the calls of a single frog which called alone before two frogs started to call alternately and (b) those of two frogs which called alternately, where the total time length is 4.0s both in (a) and (b). There are main peaks around 4.2Hz in (a) and 7.0Hz in (b).

Then, we discuss a possible biological meaning of anti-phase synchronization in the calls.

4.1 Analysis by phase oscillator models

We model the calls of frogs as a system of coupled phase oscillators, namely the calls of one frog is regarded as a phase oscillator which behaves periodically, and the calls of two frogs as two coupled phase oscillators which synchronize in anti-phase. The calls of a single frog is described as a phase oscillator with the phase variable θ with $\theta \in \boldsymbol{S}^1$ as follows:

$$\frac{d\theta}{dt} = \omega, \tag{3}$$

where ω is the intrinsic frequency. It is assumed that each call is generated at $\theta = 0$. This model represents the property that each frog calls periodically.

Then we model the calls of two frogs as the system of two coupled phase oscillators. In the experiment, after one frog called periodically (3-39 times) alone, another frog began to call, and two frogs called alternately. We consider these phenomena with two processes; namely (1) the first process that while one frog calls periodically, another frog hears the calls of the first frog without calling by itself, and (2) the second process that two frogs call alternately.

The first process is modeled by the system of two coupled phase oscillators with two phase variables θ_a and θ_b as follows [13]:

$$\frac{d\theta_a}{dt} = \omega_a, \tag{4}$$

$$\frac{d\theta_b}{dt} = \omega_b - g(\theta_a - \theta_b - \beta), \tag{5}$$

where $\theta_a \in \boldsymbol{S}^1$, $\theta_b \in \boldsymbol{S}^1$, ω_a and ω_b are the intrinsic frequencies of two frogs, g is a 2π-periodic function of the argument that describes the one-directional interaction, and β is a positive phase frustration parameter.

To examine whether two oscillators synchronize, we analyze the dynamics of the phase difference $\phi \equiv \theta_a - \theta_b$ with $\phi \in \boldsymbol{S}^1$. Subtracting Eq. (5) from Eq. (4) yields

$$\frac{d\phi}{dt} = (\omega_a - \omega_b) + g(\phi - \beta). \tag{6}$$

Here, we assume g to be a sinusoidal function for the sake of simplicity, according to models of Kuramoto [13] and Strogatz [14], namely $g(\phi - \beta) = K \sin(\phi - \beta)$ with a positive coupling coefficient K.

Then, if $|\omega_a - \omega_b| \ll K$, then this system has a stable equilibrium point $\phi^* \fallingdotseq \pi + \beta = -\pi + \beta$. Further, if $\beta \ll \pi$, a stable equilibrium point ϕ^* nearly equals to π, which represents nearly anti-phase synchronization. This result models the property that after one frog calls periodically, another frog begins to call in nearly anti-phase. Generally speaking, when the system is at a stable equilibrium point, the equation $\frac{d\phi}{dt} = 0$ holds. Hence, the equilibrium point ϕ^* of Eq. (6) satisfies the following equation:

$$\omega_a = \omega_b - K \sin(\phi^* - \beta). \tag{7}$$

Substituting Eq. (7) in Eq. (5) yields

$$\left.\frac{d\theta_a}{dt}\right|_{\phi=\phi^*} = \left.\frac{d\theta_b}{dt}\right|_{\phi=\phi^*} = \omega_a. \tag{8}$$

Next, we model the second process as the following system of two mutually coupled phase oscillators:

$$\frac{d\theta_a}{dt} = \omega_a - g_{ab}(\theta_b - \theta_a - \alpha), \tag{9}$$

$$\frac{d\theta_b}{dt} = \omega_b - g_{ba}(\theta_a - \theta_b - \beta), \tag{10}$$

where g_{ab} and g_{ba} are 2π-periodic functions that represent the mutual interactions, α and β are positive frustration parameters. Subtracting Eq.(10) from Eq. (9) gives

$$\frac{d\phi}{dt} = (\omega_a - \omega_b) + g_{ba}(\phi - \beta) - g_{ab}(-\phi - \alpha). \tag{11}$$

Here, we assume again as a simple model that $g_{ab}(\psi) = g_{ba}(\psi) \equiv K \sin(\psi)$ [13, 14]. Then, Eq. (11) can be represented as follows:

$$\frac{d\phi}{dt} = (\omega_a - \omega_b) + 2K \cos(\frac{\alpha + \beta}{2}) \sin(\phi + \frac{\alpha - \beta}{2}). \tag{12}$$

Thus, if

$$|\omega_a - \omega_b| \ll 2K \cos(\frac{\alpha + \beta}{2}), \tag{13}$$

then this system has the following stable equilibrium point:

$$\phi^* \fallingdotseq \pi - \frac{\alpha - \beta}{2}. \tag{14}$$

Further, if $\alpha \fallingdotseq \beta$, a stable equilibrium point ϕ^* nearly equals to π, which represents almost anti-phase synchronization. This result represents the property that two frogs call alternately. The stable equilibrium point ϕ^* of Eq. (12) satisfies the following equation:

$$\omega_a + K \sin(\phi^* + \alpha) = \omega_b - K \sin(\phi^* - \beta). \tag{15}$$

Substituting Eqs. (14) and (15) in Eqs. (9) and (10), we have

$$\left.\frac{d\theta_a}{dt}\right|_{\phi=\phi^*} = \left.\frac{d\theta_b}{dt}\right|_{\phi=\phi^*} = \omega_a - K\sin(\frac{\alpha+\beta}{2}). \tag{16}$$

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In the modeling analysis above, anti-phase synchronization results from the assumptions of $|\omega_a - \omega_b| \ll K$, $\beta \ll \pi$, $\alpha \fallingdotseq \beta$, and Eq. (13). It should be noted that these assumptions are equivalent to $|\omega_a - \omega_b| \ll K$, $\alpha \fallingdotseq \beta$, and $\alpha \ll \pi$. Hence, Eq. (16) can be approximately represented as follows:

$$\left.\frac{d\theta_a}{dt}\right|_{\phi=\phi^*} = \omega_a - K\alpha + O(\alpha^3) \tag{17}$$

$$\fallingdotseq \omega_a - K\alpha. \tag{18}$$

If $0 < K\alpha < \omega_a$, Eqs. (8) and (18) show the change of the frequency of the same frog before and after the synchronization. The frequency of the phase oscillator θ_a becomes smaller from $\frac{\omega_a}{2\pi}$ to $\frac{\omega_a - K\alpha}{2\pi}$ after the synchronization. In the experiment, the frequency of the single frog changed from 4.2Hz to 3.5Hz. Hence, we can approximately estimate the relation between the parameters K and α from the theoretical model and the experimental data as follows:

$$\frac{K\alpha}{2\pi} \fallingdotseq 0.7(\mathrm{Hz}). \tag{19}$$

4.2 Possible biological meaning

If one male frog mates with one female in a one-to-one manner, it is important for two males to make females distinguish them each other.

In fact, many kinds of frogs are known to mate in such a one-to-one manner [15]. Especially, the mating behavior in Japanese rain frogs is in this manner [16]. Thus, it is probable that Japanese male rain frogs call alternately for each of them to make females distinguish oneself from the nearest male.

5 Conclusion

5.1 Main results

We recorded and analyzed the calls of Japanese rain frogs. While a single frog called nearly periodically, a pair of frogs called alternately; after one frog called several times (3 to 39 times) alone, another frog began to call, and two frogs called alternately. The intervals of the calls of the first frog during the interactive calls of two frogs is longer than those of the same frog which called alone. We model these phenomena as the system of coupled phase oscillators; namely the calls of one frog as a periodic phase oscillator and the calls of two frogs as two mutually coupled phase oscillators which synchronize in almost anti-phase. We suppose that it is biologically important for two male frogs *Hyla japonica* to call alternately and make females distinguish them each other.

5.2 Future problems

In order to further improve our models of calling behaviors of Japanese rain frogs, we need to consider the following problems.

(1) In the mathematical models, we have assumed the coupling strength as constant. It is probable, however, that frogs interact not continuously but only when they call. If we modify the coupling strength to be dependent on timing of calls of another frog, the phase model may be more suitable as the model of calling behaviors of frogs.

(2) In the mathematical model, we described the interaction function as a sinusoidal function for the sake of simplicity. It is an important future problem to take real data of phase response curves experimentally, and define the interaction function of the calls peculiar to Japanese rain frogs.

(3) The relation between the coupling strength and the difference in the intrinsic frequencies of two frogs is important for the understanding of the dynamics of the system. We need to make an experiment to elucidate the relation. In other words, we should record the calls of each frog separately, and analyze intrinsic frequencies. Then, we change the distance between frogs to change the coupling strength; if frogs are put at a longer distance, the coupling strength should be weaker.

(4) A frog may respond to the calls of another frog with a certain time delay. We should explore the effects of time delay on the dynamics of the synchronization.

(5) In the real situation, the natural frequencies of calls are not necessarily very close. Then, we explore a possibility that one frog adjusts own intrinsic frequency to that of another frog.

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