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Call Alternation between Specific Pairs of Male Frogs Revealed by a Sound-Imaging Method in Their Natural Habitat

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Abstract

Male frogs vocalize calls to attract conspecific females as well as to announce their own territories to other male frogs. In the choruses, acoustic interaction allows the male frogs to alternate their calls with each other. Such call alternation is reported in various species of frogs including Japanese tree frogs (*Hyla japonica*). During call alternation, both male and female frogs are likely to discriminate calls of the male frogs because of small amount of call overlaps. Here, we show that call alternation is observed in natural choruses of male Japanese tree frogs especially between neighboring pairs. First, we demonstrate that caller positions and call timings can be estimated by a sound-imaging method. Second, the occurrence of call alternation is detected on the basis of statistical tests on phase differences of calls between respective pairs. Although our previous study revealed a global synchronization pattern in natural choruses of the male frogs, local chorus structures were not examined well. Through the observation of call alternation between specific pairs, this study suggests the existence of selective attention in the frog choruses.

Index Terms: Japanese tree frogs, selective attention, field recordings, animal calls, natural choruses

1. Introduction

Animals vocalize sounds for various purposes. For instance, bats emit ultrasounds to localize prey and obstacles by hearing echoes [1]; male birds sing complex songs to attract conspecific females [2]. Thus, the use of sounds is essential for animals to survive and breed in the wild.

Frogs are abundant nocturnal animals that use sounds during mating process. Male frogs construct choruses to attract conspecific females, and females approach one of the males by discriminating their calls [3, 4]. Because many male frogs join choruses at the same breeding site, they must compete with each other to mate with conspecific females.

In 1977, Wells surveyed the major features of behavior of anurans, i.e., frogs and toads, and suggested that future workers moved from a purely descriptive to a more quantitative approach [5]. 36 years after, Bee et al. followed the Wells's seminal paper to survey anuran behavior in historical context and importance, e.g., criteria for female mate choice, aggregation and spacing, calling energetics, parental care as well as acoustic interactions and chorus organization [6]. Future direction of acoustic interactions and chorus organization, as they pointed out, include new technologies for analyzing acoustic interactions, mechanism of chorus organization and female preference.

We studied calling behavior of male Japanese tree frogs (*Hyla japonica*) by applying audio-processing techniques both for indoor experiments and field recordings. Japanese tree frogs are observed widely in Japan, and breed mainly at paddy fields from April to July [7]. In our indoor experiments, three individuals of the male frogs were placed at stationery positions, and their calling behavior was recorded with three microphones. Independent component analysis of the audio data revealed various calling patterns, such as anti-phase synchronization of two frogs and tri-phase synchronization of three frogs [8]. In our field recordings, a sound-imaging method was applied to natural choruses of male Japanese tree frogs [9]. Then, analysis of video data revealed a global synchronization pattern of several male frogs, i.e., two-cluster synchronization that two groups of male frogs called alternately with each other [10]. As for the field observations, we speculated that such alternating behavior allowed both females and males to discriminate calls of the male frogs in their natural habitat [8, 10]. However, local chorus structures of the male frogs were not examined well.

This study aims at detecting call alternation among respective pairs of male Japanese tree frogs in their natural choruses by calculating phase differences of their calls. It should be noted that there are few studies on spatio-temporal structures of frog choruses because of the difficulty in localizing and separating their calls in dense distribution.

This paper is organized as follows: brief reviews of our previous studies on sound-imaging method and field recording (Sec 2.1 and 2.2), methods of time series analysis and statistical test (Sec 2.3), results (Sec 3), and discussion and conclusions (Sec 4).

2. Materials and Methods

2.1. Sound-Imaging Method

To reveal behavioral dynamics of animals emitting sounds, audio processing techniques are useful. In particular, sound-source localization based on time difference of arrivals among multiple microphones is conducted on several species of animals such as bats and dolphins [11, 12], revealing spatio-temporal dynamics inherent in their echolocating behavior. While bats and dolphins spatially distribute in low density, other species of animals show denser spatial distribution. Sound-source localization in such a dense distribution is a more chal-

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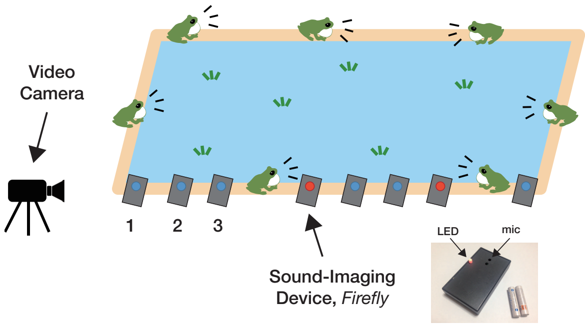

Figure 1: *Schematic diagram of a sound-imaging method.* 85 units of sound-imaging devices were deployed along a ridge of a paddy field where male Japanese tree frogs were calling. Lights of the devices were captured by an off-the-shelf video camera. The inset shows a photograph of the sound-imaging device.

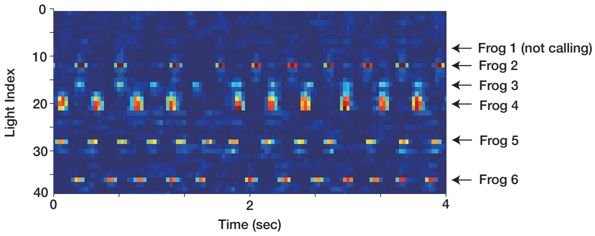

Figure 2: *Illumination pattern of sound-imaging devices.* Color represents light intensity of each device. Black arrows represent the positions of calling frogs. Note that Frog 1 did not join this chorus.

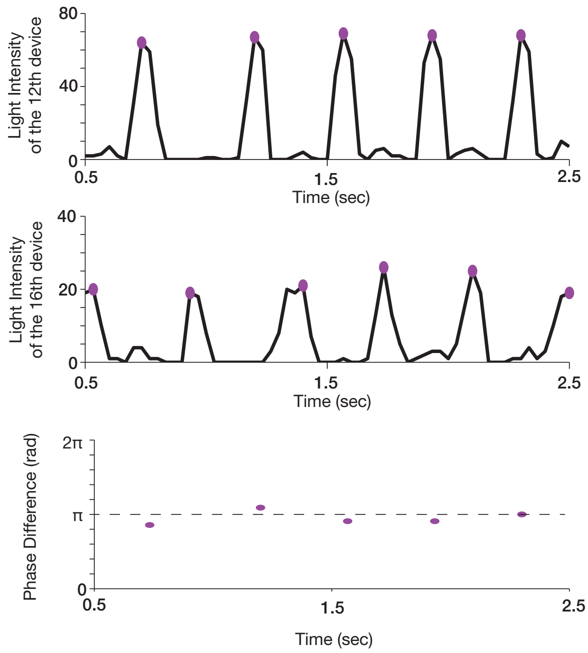

Figure 3: *Call alternation between a specific pair of male frogs.* Top and middle graphs show the light intensity of the 12th and 16th devices extracted from the data shown in Fig. 2. Pink dots represent call timings of respective frogs estimated by our method. Bottom graph shows the phase difference between calls of these two frogs, demonstrating that they call alternately at the phase difference of almost π.

lenging task, because frequent call overlaps deteriorate the performance of localization.

We proposed a sound-imaging method for localizing and discriminating multiple animal calls in a dense distribution in darkness [9]. The method is based on a sound-imaging device called *Firefly* (see the inset of Fig. 1). Each unit of *Firefly* consists of a microphone and a light-emitting diode (LED), and is illuminated when capturing nearby sounds. Sound-imaging devices are deployed for covering a space where target animals distribute (see Fig. 1). Illumination patterns of the devices are captured by an off-the-shelf video camera. Analysis of the video data allows us to localize the positions of calling animals as well as to discriminate their call timings.

We applied this method to the study on natural choruses of male Japanese tree frogs, and succeeded in visualizing spatio-temporal structures of the choruses [10].

2.2. Field Recording

In this study, we used the video data capturing illumination patterns of sound-imaging devices obtained from our previous field recording [10]. For the recording, we deployed 85 devices at the interval of 40 cm along a ridge of a paddy field where male Japanese tree frogs were calling (see Fig. 1). The lights of LEDs of the devices were recorded by an off-the-shelf video camera (HDR-XR550V, Sony) fixed on a tripod (VCT-80AV, Sony) at the sampling rate of 29.97 frames per second. This recording was conducted at Oki island in Japan on 15 th, June, 2011. The temperature and relative humidity were 20.5 $^{\circ}C$ and 53.5 %, respectively.

Video data was then analyzed according to the method proposed by Mizumoto et al. [9]. Since we confirmed that lights of 39 devices closer to the camera were stably captured, we restricted our analysis to the illumination patterns of those devices. From the illumination patterns, we can estimate the positions of calling frogs and also discriminate their call timings (see Figs. 2 and 3).

2.3. Data Analysis

Local structures of the frog choruses were examined on the basis of phase differences between calls of respective pairs. First, we carefully checked video data of 30 min and confirmed that 9 frogs were calling at our field site. Their call timings were then estimated according to the method proposed in [8]. The analysis showed that the total number of calls varied a lot depending on individuals; the maximum number was 2799 in 30 min while the minimum number was just 72. To examine the occurrence of call alternation with a sufficient sample size, we restricted our analysis to the frogs that called more than 500 times in 30 min. Consequently, we excluded three frogs from our analysis (they were located besides the 25th, 26th and 38th devices, and called 72, 133, and 405 times, respectively), and chose the other six frogs. The six frogs were positioned besides 8th, 12th, 16th, 20th, 28th, and 36th devices, and were indexed from Frog 1 to Frog 6, respectively. Call numbers and inter-frog distances estimated by the present method are summarized in Tables 1 and 2.

A phase difference between calls of two frogs is defined as

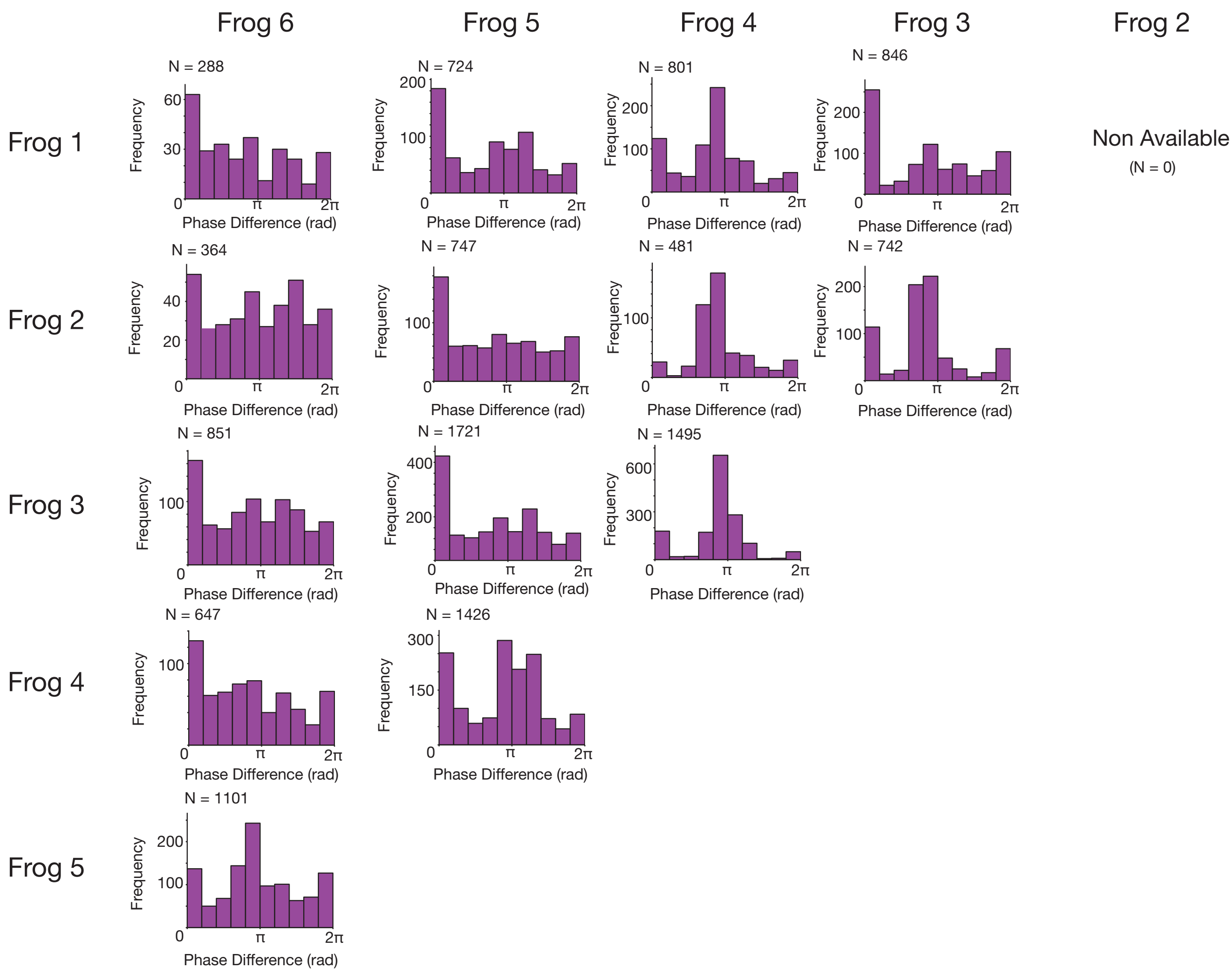

Figure 4: *Histograms of phase differences between each pair of the six male frogs that called more than 500 times in 30 min.* Here, N represents the sample size of the phase differences.

Table 1: *Total number of calls vocalized by six frogs in* 30 *min.* To examine the occurrence of call alternation with a sufficient sample size, we restricted our analysis to these six frogs that called more than 500 times in 30 min.

Frog ID	1	2	3	4	5	6
Call Number	1099	880	2213	1705	2799	1266

Table 2: *Inter-frog distances between neighboring pairs estimated by the present method.* We deployed sound-imaging devices at the interval of 40 cm along a straight line (see Materials and Methods). Therefore, the position of each frog was discretely estimated at the interval of 40 cm.

Frog Pair	1 and 2	2 and 3	3 and 4	4 and 5	5 and 6
Distance	160 cm	160 cm	160 cm	320 cm	320 cm

follows [8, 13]:

$$\phi_{nm} = 2\pi \frac{t_{m,j} - t_{n,i}}{t_{n,i+1} - t_{n,i}} \quad (1)$$

where ϕ_{nm} represents a phase difference between calls of the nth and mth frogs. $t_{n,i}$ represents the timing of the ith call vocalized by the nth frog. A phase difference is then calculated when both of the following conditions are satisfied:

$$t_{n,i} \leq t_{m,j} < t_{n,i+1} \quad (2)$$

$$0.2 < t_{n,i+1} - t_{n,i} < 0.5 \quad (3)$$

The first condition is required to restrict ϕ_{nm} between 0 and 2π. The second condition is assumed because inter-call intervals of male Japanese tree frogs are typically in this range [7, 14]. It should be noted that $\phi_{nm} = \pi$ means call alternation of two frogs while $\phi_{nm} = 0$ means call synchrony. We calculated ϕ_{nm} for all the pairs of the six frogs shown in Table 1.

To detect the occurrence of call alternation, we conducted modified Rayleigh test (V-test) with assuming its parameter μ_0 as π [15, 16]. The test was conducted independently on the phase difference between each pair. When P value was less than 0.001, the pair was determined to significantly alternate their calls with each other.

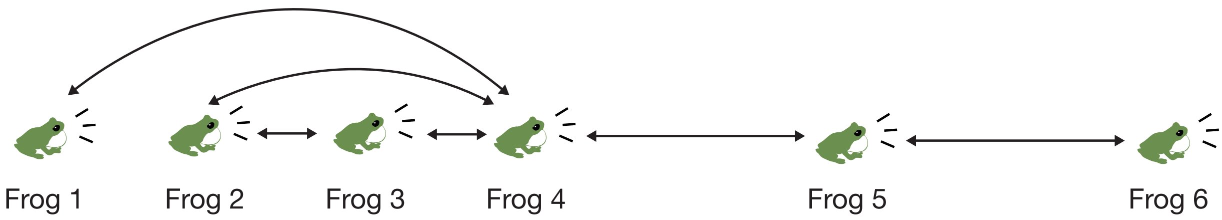

Figure 5: *Schematic diagram of frog pairs that alternated their calls with each other.* The occurrence of call alternation was detected by applying modified Rayleigh test (V-test) to the phase difference of each pair. For the test, we set a threshold of P value as 0.001. Total call number and inter-frog distances of the six frogs are summarized in Tables 1 and 2.

3. Results

Histograms of the phase differences are shown in Fig. 4. The histogram of Frogs 1 and 2 was not available because they did not join the same chorus. We have shown that several histograms have an obvious peak at π (e.g., the histogram of Frogs 3 and 4), indicating that specific pairs of the male frogs alternate their calls with each other.

Figure 5 shows the results of statistical tests on the phase differences, where the pairs that significantly alternate their calls ($P < 0.001$) are described by black arrows. This analysis reveals the following behavior:

1. All the neighboring pairs that joined the same chorus alternated their calls with each other.
2. Two pairs of non-neighboring frogs (i.e., Frogs 1 and 4, and Frogs 2 and 4) also alternated their calls.

The first result demonstrates that male Japanese tree frogs pay attention to their neighbors, suggesting that inter-frog distance is an important factor determining their selective attention (Note that Frogs 1 and 2 are also a neighboring pair, but they did not join the same chorus at all). The second result, however, suggests another possibility that inter-frog distance is not the only factor. We speculate that acoustic traits of their calls (e.g., call intensity and call frequency) also affect the selective attention.

4. Discussion and Conclusions

4.1. Advantages of Sound-Imaging Method

While our sound-imaging method can estimate caller positions and call timings of male Japanese tree frogs, a microphone-array system would work as an alternative method. For instance, Jones et al. used a 15-channel microphone array and localized six individuals of American green tree frogs (*Hyla cinerea*). They showed that neighboring pairs alternated their calls with each other [17]. Bando et al. recorded choruses of Schlegel's green tree frogs (*Rhacophorus schlegelii*) with a 7-channel microphone array and applied Bayesian nonparametric microphone array processing (BNP-MAP) [18] to the audio data. They succeeded in separating calls of two individuals of *R. schlegelii*, and revealed call alternation between them [19].

While a microphone-array system can also localize and discriminate frog calls, it has several difficulties when applied to field recordings. We consider that our method has the following advantages over a microphone-array system:

1. **Costs of Money:** Our method only needs sound-imaging devices and video camera that are inexpensive.
2. **Costs of Deployment:** No cable is required because each sound-imaging device is powered by rechargeable batteries.
3. **Synchronization of Recording System:** Each sound-imaging device independently responds to nearby sounds, and their illumination pattern is synchronously recorded by a video camera.

Thus, our system needs less money, time, and efforts to conduct recordings. We believe that such an inexpensive and tractable method is useful for field observation of animal calls.

4.2. Details in Temporal Chorus Structures

We performed statistical tests on the phase differences across the whole recording time, meaning that its temporal information was ignored. For instance, our analysis demonstrates that each pair among the three frogs of Frogs 2, 3, and 4 alternate their calls (see Fig. 5). However, such a chorus pattern is impossible when the three frogs join the same chorus: namely, if two pairs of Frogs 2 and 3, and Frogs 2 and 4 alternate their calls at the phase difference of π, the rest pair of Frogs 3 and 4 must synchronize their calls at the phase difference of 0 [8]. For these three frogs, we speculate that only two frogs joined the same choruses at one time. Such a population dynamics of the chorusing frogs needs to be further examined.

4.3. Call Synchrony

The histograms of Fig. 4 indicate the other type of behavior in addition to call alternation. For example, the histogram of Frogs 3 and 5 has an obvious peak at 0, indicating that these two frogs synchronize their calls with each other. We then conducted modified Rayleigh test with assuming its parameter μ_0 as 0 [16], and showed that call synchrony was detected in three non-neighboring pairs of Frogs 1 and 3, Frogs 2 and 5, and Frogs 3 and 5, respectively ($P < 0.001$).

While call alternation was reported in many species of frogs, call synchrony was reported in a few species. Cross-banded tree frogs (*Smilisca sila*) synchronize their calls with each other in an extremely short latency [20]. Their behavior is likely to be evolved as an antipredator purpose: namely, predators (e.g., frog-eating bats) have a difficulty for localizing the male frogs during call synchrony because of a large amount of call overlaps. Further studies with larger sample sizes are required to show the existence of call synchrony and reveal its behavioral meanings inherent in the choruses of male Japanese tree frogs.

5. Acknowledgements

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