

Complex and Transitive Synchronization in a Frustrated System of Calling Frogs

Ikkyu Aihara

Department of Physics, Graduate School of Sciences, Kyoto University

Ryu Takeda, Takeshi Mizumoto, Takuma Otsuka, Toru Takahashi, and Hiroshi G. Okuno

*Department of Intelligence Science and Technology,
Graduate School of Informatics, Kyoto University*

Kazuyuki Aihara

Institute of Industrial Science, University of Tokyo

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This letter reports new synchronization phenomena and mathematical modeling on a frustrated system of living beings, or Japanese tree frogs (*Hyla japonica*). While an isolated male Japanese tree frog calls nearly periodically, he can hear sounds including calls of other males. Therefore, spontaneous calling behavior of interacting males can be understood as a system of coupled oscillators. We construct a simple but biologically reasonable model based on the experimental results of two frogs, extend the model to a system of three frogs, and theoretically predict the occurrence of rich synchronization phenomena, such as tri-phase synchronization and 1:2 anti-phase synchronization. In addition, we experimentally verify the theoretical prediction by ethological experiments on calling behavior of three frogs and time series analysis on recorded sound data. Note that calling behavior of three male Japanese tree frogs is frustrated, because almost perfect anti-phase synchronization is robustly observed in a system of two male frogs. Thus, nonlinear dynamics of the three-frogs system should be far from trivial.

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I. INTRODUCTION

Synchronization is ubiquitous in real systems, and has been attracting a great deal of attention in physics as well as in many other disciplines since the seminal work on Huygens' clocks [1]. In addition, theoretical studies revealed plausible synchronization mechanisms for accomplishing cooperative phenomena in the real world, including phase-oscillator models [1], a phase-reduction method for a general class of noisy oscillators [2], feedback control [3] and co-evolution of phases and coupling strengths [4] in coupled oscillator systems, and a general chemotactic model of oscillators [5]. However, those theoretical studies mainly focused on in-phase synchronization, and nonlinear dynamics of anti-phase synchronization in a coupled system had not been sufficiently investigated [6]. In particular, anti-phase synchronization is widely observed in acoustic communications by a pair of living beings, including birds, mammals, crickets, and frogs [7–9]; such alternating calling behavior plays an important role in their communications to transmit sound information included in the interacting calling behavior by mutually avoiding overlaps of their calls.

From theoretical points of view, anti-phase synchronization between a pair raises an interesting fundamental problem in a coupled system with many oscillators [6]; anti-phase synchronization between a pair cannot be realized in every pair of three oscillators, because, when two pairs of the three synchronize in anti-phase respectively, the remaining third pair must synchronize in-phase. Thus, such a system of more than two oscillators

is generally frustrated. Note that a similar situation of the frustration can be seen in antiferromagnetic spin-systems [10]. From the viewpoint of frustration, however, the coupled-oscillator systems show an important difference from the spin systems; while the state of a spin is limited to up or down [10], that of a phase oscillator is described with a phase variable $\theta \in \mathbb{S}^1$ [6, 9].

To clarify possibly complex behavior in such a frustrated system of coupled phase oscillators, it is reasonable to first investigate the simplest case of the frustration. In this paper, we theoretically and experimentally study spontaneous calling behavior of three male Japanese tree frogs *Hyla japonica* shown in Fig.1A [6, 9] as a frustrated system of living beings, because our experimental observations revealed that, while a single male Japanese tree frog calls nearly periodically, a couple of males generate robust anti-phase synchronization [9] (see Figs.1B and C).

The paper is organized as follows: in Sec.II, we construct a possible phase oscillator model representing interactive calling behavior by three frogs and theoretically predict synchronization phenomena; in Sec.III, we empirically verify the theoretical prediction shown in Sec.II by ethological experiments and time series analysis; in Sec.IV, we discuss the relationship between the modeling and experimental results, biological implications by the model analysis, and possible biological meanings of synchronized behavior by frogs.

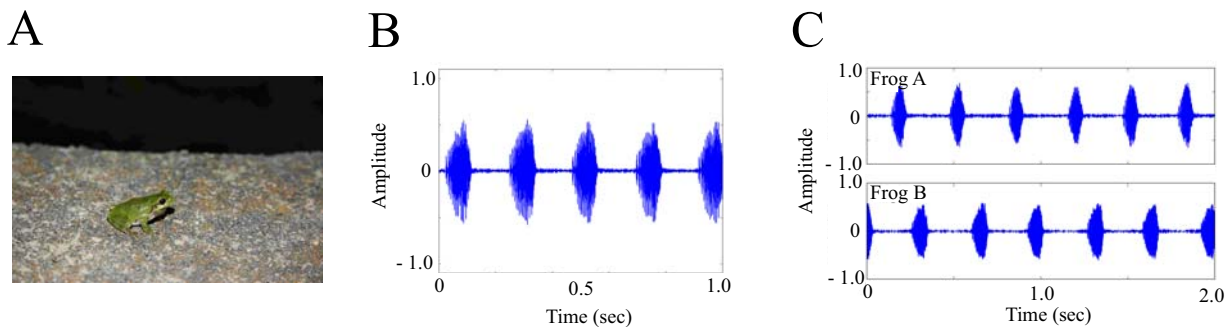


FIG. 1: (Color online) Calling behavior of one or two frogs. (A) Japanese tree frog *Hyla japonica*. (B) Periodic calling behavior of a single male frog. (C) Anti-phase synchronization of two frogs. Figures 1B and C represent sound data of a single frog and those of two frogs, respectively.

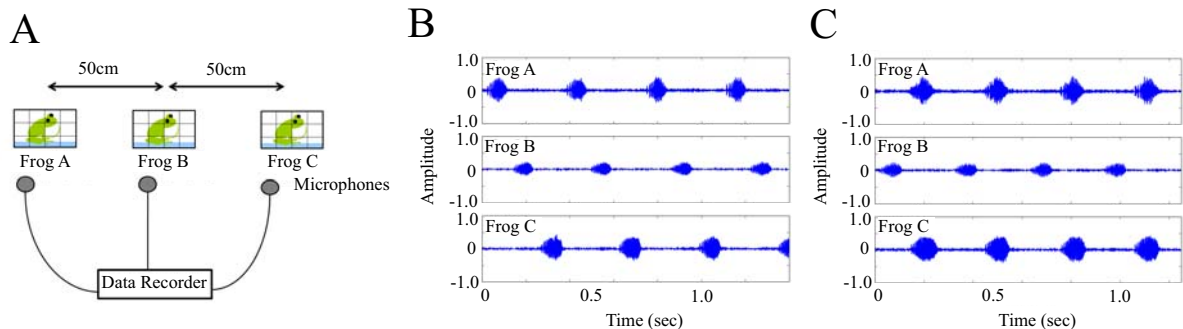


FIG. 2: (Color online) Calling behavior of three frogs. (A) Schematic diagram describing the experimental situation; three frogs were put in cages respectively, and set along a straight line at a distance of 50cm. Spontaneous calling behavior was recorded by three microphones placed close to each frog. (B) Tri-phase synchronization of $A \rightarrow B \rightarrow C$; the three frogs A, B and C call in turns with the phase difference of $2\pi/3$. (C) 1:2 anti-phase synchronization of B vs AC; the two frogs A and C synchronize in-phase of 0, and the remaining one of frog B synchronizes in anti-phase of π with the others. In Figs.2B and C, sound data of respective frogs are separated by independent component analysis.

II. MATHEMATICAL MODELING

To predict possible synchronized behavior of three Japanese tree frogs, we first construct a simple but biologically reasonable model based on the experimental results of two frogs shown in Fig.1C that two frogs robustly synchronize in anti-phase [9]. Let us model calling behavior of the two frogs α and β [1, 9], as follows:

$$\frac{d\theta_\alpha}{dt} = \omega_\alpha + K[\sin(\theta_\alpha - \theta_\beta) - \gamma \sin(2(\theta_\alpha - \theta_\beta))], \quad (1)$$

$$\frac{d\theta_\beta}{dt} = \omega_\beta + K[\sin(\theta_\beta - \theta_\alpha) - \gamma \sin(2(\theta_\beta - \theta_\alpha))], \quad (2)$$

where phases θ_α and θ_β represent the call timings of the frogs α and β (i.e., when $\theta_\alpha = 0$, we consider that the frog α calls), ω_α and ω_β are the natural frequencies of respective frogs (i.e., $2\pi/\omega_\alpha$ and $2\pi/\omega_\beta$ are the intrinsic inter-call intervals [8]), K is the positive coupling strength between the two frogs due to their acoustic communication, and γ is a positive parameter which represents the effect of the second-order component in the interac-

tion term or changes the stability between the anti-phase and in-phase states [9]. Our experimental observations on interactive calling behavior of two frogs show that, while anti-phase synchronization of two frogs is robustly observed, in-phase synchronization is detected only transiently [9]. Next, we introduce suitable parameter values in Eqs.(1) and (2) to explain the experimental results of two frogs. First, it is experimentally shown that the intrinsic frequencies ω_α and ω_β tend to take close values under the same experimental condition [9]. Hence, we assume $\omega_\alpha = \omega_\beta$ for the sake of simplicity. Note that, under this first assumption, both anti-phase and in-phase synchronization states, i.e., $\phi = \pi$ and $\phi = 0$ with $\phi \equiv \theta_\alpha - \theta_\beta$, become equilibrium points, namely $\frac{d\phi}{dt}|_{\phi=\pi} = 0$ and $\frac{d\phi}{dt}|_{\phi=0} = 0$. In addition, γ is assumed to take a positive value of less than 0.5. The linear stability of the anti-phase state and that of the in-phase state can be analyzed by $\frac{\partial}{\partial \phi} \frac{d\phi}{dt}|_{\phi=\pi} = -2K(1 + 2\gamma)$ and $\frac{\partial}{\partial \phi} \frac{d\phi}{dt}|_{\phi=0} = 2K(1 - 2\gamma)$, respectively. When $\omega_\alpha = \omega_\beta$ and $0 \leq \gamma < 0.5$, the former is negative and the lat-

ter positive. Therefore, under these two assumptions of $\omega_\alpha = \omega_\beta$ and $0 \leq \gamma < 0.5$, the experimental results on a two-frogs system [9] is qualitatively explained; namely, anti-phase synchronization of two frogs is represented as a stable equilibrium, and the in-phase synchronization is described as an unstable one.

Extending Eqs.(1) and (2) to a system of three coupled oscillators, we model spontaneous calling behavior of three frogs as follows:

$$\frac{d\theta_i}{dt} = \omega_i + \sum_{j=A,B,C} K_{ij}[\sin(\theta_i - \theta_j) - \gamma \sin(2(\theta_i - \theta_j))], \quad (3)$$

where θ_i ($i = A, B, C$) represents the timing of successive calls by the frog i , ω_i is its intrinsic frequency, and K_{ij} is the positive coupling strength between the frogs i and j with $K_{ij} = K_{ji}$ [6]. Let us consider suitable parameter values in Eq.(3) which qualitatively explain the experimental situation shown in Fig.2A, and perform bifurcation analysis with bifurcation parameters γ and K_{AC} to theoretically predict possible synchronized calling behavior of three frogs. First, we assume $\omega_A = \omega_B = \omega_C$, for the same reason as in a system of two frogs. Second, since male frogs interact through sounds, and the distance between the frogs A and B is identical to that between the frogs B and C in the experiments (See Fig.2A), we assume that the adjacent pairs interact with the same strength, i.e., $K_{AB} = K_{BC} = 1.0$, for simplicity. Then, we vary bifurcation parameters γ and K_{AC} within $0 \leq \gamma < 0.5$ and $0 \leq K_{AC} < 1.0$, and calculate stable phase differences of $\phi_{AB} \equiv \theta_A - \theta_B$ and $\phi_{AC} \equiv \theta_A - \theta_C$. The former assumption of $0 \leq \gamma < 0.5$ is consistent with that in the model analysis on a two-frogs system. In addition, since the distance between the frogs A and C is longer than that between the frogs A and B as shown in Fig.2A, K_{AC} is assumed to be less than $K_{AB} = 1.0$.

Results of the bifurcation analysis are summarized in Figs.3A and B. Note that, throughout the model analysis, we set the error bound of $\pi/6$ for detection on synchronization modes, the same as in the time series analysis performed on experimental data where the phase differences between frogs (i.e., ϕ_{AB} and ϕ_{AC}) can fluctuate even in almost synchronized states. As a result, it is theoretically predicted that, depending on values of K_{AC} and γ , two types of tri-phase synchronization ($A \rightarrow B \rightarrow C$ and $A \rightarrow C \rightarrow B$) and three types of 1:2 anti-phase synchronization (A vs BC , B vs AC , and C vs AB) can be observed under the experimental situation shown in Fig.2A. For example, tri-phase synchronization of $A \rightarrow B \rightarrow C$ means $\phi_{AB} \simeq 2\pi/3$ and $\phi_{AC} \simeq 4\pi/3$; 1:2 anti-phase synchronization of A vs BC means that, while the two oscillators B and C synchronize in nearly in-phase, the remaining one A synchronizes in nearly anti-phase with B and C . Details of the synchronization properties are explained in caption of Fig.3A and B.

III. EXPERIMENTS

We experimentally verified the model prediction. Spontaneous calling behavior of three male Japanese tree frogs was recorded with microphones placed close to each frog, as shown in Fig.2A. The experiments were carried out totally 44 times on May and June both in 2008 and 2009, and four trials where three frogs successively called were obtained, corresponding to Data(1)–(4) in Fig.4B–E and Table I. In those experiments, recording time for each trial was about 4 hours. Recorded sound data were analyzed to separate individual calling signals by the independent component analysis (ICA) [11]. During calling behavior of three frogs, various types of synchronization were robustly observed as typically shown in Figs.2B and C (Listen also to supplementary sound files): the first one in Fig.2B represents tri-phase synchronization of $A \rightarrow B \rightarrow C$ that the three frogs A , B and C called in turns with the phase difference of almost $2\pi/3$; the second one in Fig.2C is 1:2 anti-phase synchronization of B vs AC that two of the three frogs (Frogs A and C) synchronized almost in-phase, while the remaining one (Frog B) synchronized almost in anti-phase with the others.

Separated sound signals were analyzed to estimate the phase differences of three frogs, i.e., $\phi_{AB} \equiv \theta_A - \theta_B$ and $\phi_{AC} \equiv \theta_A - \theta_C$, according to the methods shown in Supplemental Materials [12]. Consequently, we stably observed various types of synchronized behavior and switching phenomena as shown in Fig.4B–E, including three types of 1:2 anti-phase synchronization (A vs BC , B vs AC , and C vs AB) and two types of tri-phase synchronization ($A \rightarrow B \rightarrow C$ and $A \rightarrow C \rightarrow B$); Figure 4B represents the occurrence of three types of 1:2 anti-phase synchronization (A vs BC , B vs AC , and C vs AB), Figure 4C represents that of mainly only one of the 1:2 anti-phase synchronization (A vs BC), Figure 4D shows that of three types of 1:2 anti-phase synchronization (A vs BC , B vs AC , and C vs AB) and two types of tri-phase synchronization ($A \rightarrow B \rightarrow C$ and $A \rightarrow C \rightarrow B$), and Figure 4E shows that of two types of tri-phase synchronization ($A \rightarrow B \rightarrow C$ and $A \rightarrow C \rightarrow B$) and one of the 1:2 anti-phase synchronization (A vs BC). Moreover, pink lines in Fig.4B–E show the existence of complex switching dynamics in this frogs' system.

Moreover, we categorize obtained phase differences, ϕ_{AB} and ϕ_{AC} , into synchronization modes to estimate the stability or durations of respective modes as shown in Table I (See also Supplemental Materials [12]). During calling behavior of two frogs, while anti-phase synchronization is robustly observed, in-phase synchronization is rarely detected. In addition, during total recording time of three frogs, tri-phase synchronization and 1:2 anti-phase synchronization can be robustly observed compared with the in-phase synchronization by all the three frogs.

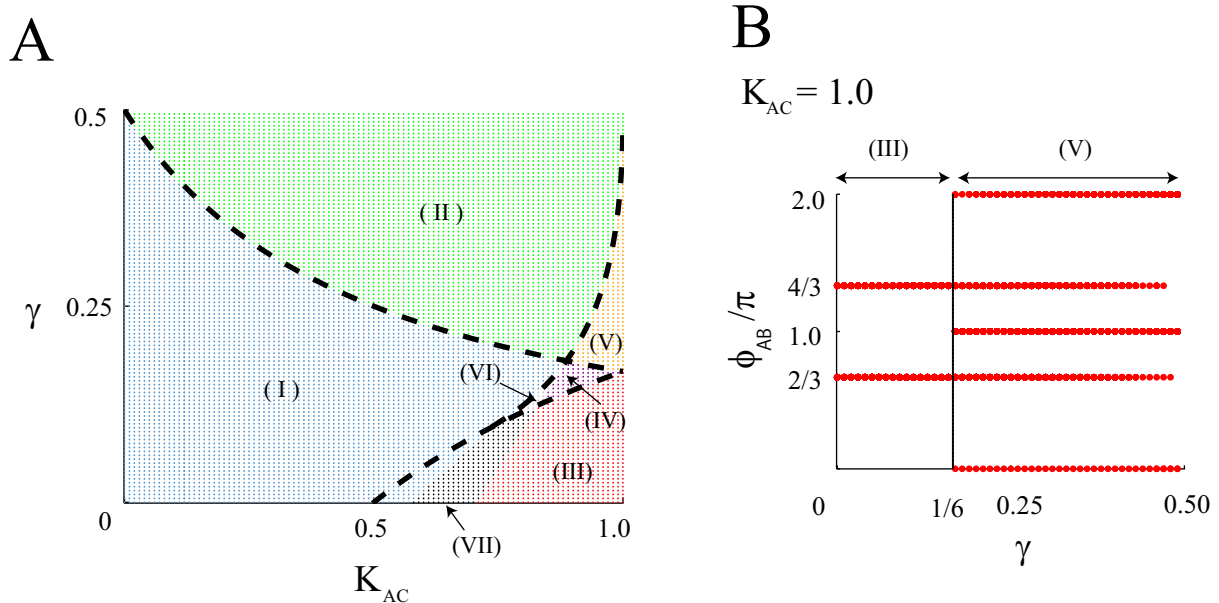


FIG. 3: (Color) Bifurcation analysis on the model of Eq.(3), with the bifurcation parameters K_{AC} and γ . (A) Phase diagram of synchronization states on the K_{AC} - γ plain. Here, we set the error bound of $\pi/6$ to detect synchronization modes and compare with the experimental data. Region(I) depicted with blue dots represents parameter values at which the 1:2 anti-phase synchronization of $(\phi_{AB}, \phi_{AC}) \simeq (\pi, 0)$ is stable, Region(II) with green dots is the multi-stable state for three types of 1:2 anti-phase synchronization $(\phi_{AB}, \phi_{AC}) \simeq (\pi, 0)$, $(0, \pi)$ and (π, π) , Region(III) with red dots is for two types of tri-phase synchronization $(\phi_{AB}, \phi_{AC}) \simeq (2\pi/3, 4\pi/3)$ and $(4\pi/3, 2\pi/3)$, Region(IV) with purple dots is for one of the 1:2 anti-phase synchronization $(\phi_{AB}, \phi_{AC}) \simeq (\pi, 0)$ and two types of tri-phase synchronization, Region(V) with yellow dots is for three types of 1:2 anti-phase synchronization and two types of tri-phase synchronization, Region(VI) with grey dots is for one of the 1:2 anti-phase synchronization $(\phi_{AB}, \phi_{AC}) \simeq (\pi, 0)$ and the synchronization states different from both tri-phase and 1:2 anti-phase synchronization, and Region(VII) with black dots is for the synchronization states different from both tri-phase and 1:2 anti-phase synchronization. Dotted lines give exact bifurcation sets obtained by the bifurcation stability analysis [6]. (C) Bifurcation structure along $K_{AC} = 1.0$ in Fig.3A, where the vertical axis represents a stable phase difference of ϕ_{AB} . While two types of tri-phase synchronization with $(\phi_{AB}, \phi_{AC}) = (2\pi/3, 4\pi/3)$ and $(4\pi/3, 2\pi/3)$ are bistable in $0 \leq \gamma < \gamma_*$, two types of tri-phase synchronization and three types of 1:2 anti-phase synchronization are multi-stable in $\gamma_* \leq \gamma < 0.5$ with $\gamma_* = 1/6$; the former state corresponds to Region(III) in Fig.3A, and the latter corresponds to Region(V).

IV. DISCUSSION

We show that mathematical modeling with Eq.(3) qualitatively explains the experimental results on synchronized calling behavior of three frogs summarized in Fig.4B–E, assuming $\omega_A = \omega_B = \omega_C$ and $0 \leq \gamma < 0.5$: multi-stability between three types of 1:2 anti-phase synchronization in Data(1), and stability of one of the 1:2 anti-phase synchronization (A vs BC) in Data(2), are qualitatively described with Region(II) in Fig.3A; multi-stability between two types of tri-phase synchronization and three types of 1:2 anti-phase synchronization in Data(3), and that between two types of tri-phase synchronization and one of the 1:2 anti-phase synchronization (A vs BC) in Data(4), are reproduced with Region(V) in Fig.3A. Note that, although mathematical modeling in our previous study [6] gives the similar

framework with only the first order component in the interaction terms of Eq.(3), that cannot explain the complicated multi-stability as shown in Fig.4B–E with fixed parameter values. Since an experimental condition in respective trials is almost stationary, parameter values in model analysis should be constant for describing each data. In this sense, mathematical modeling with Eq.(3) successfully explains complex synchronization phenomena by three frogs compared with our previous study [6]. From the viewpoint of mathematical modeling, however, it is an important future problem to clarify mechanisms responsible for the transitive and switching phenomena shown in Figs.4B–E, by considering effects such as background noise [2] and time delay [13] as well as those of chaotic dynamics [14]; note that chaotic systems also generate anti-phase synchronization [15].

Then, let us discuss biological implications from the

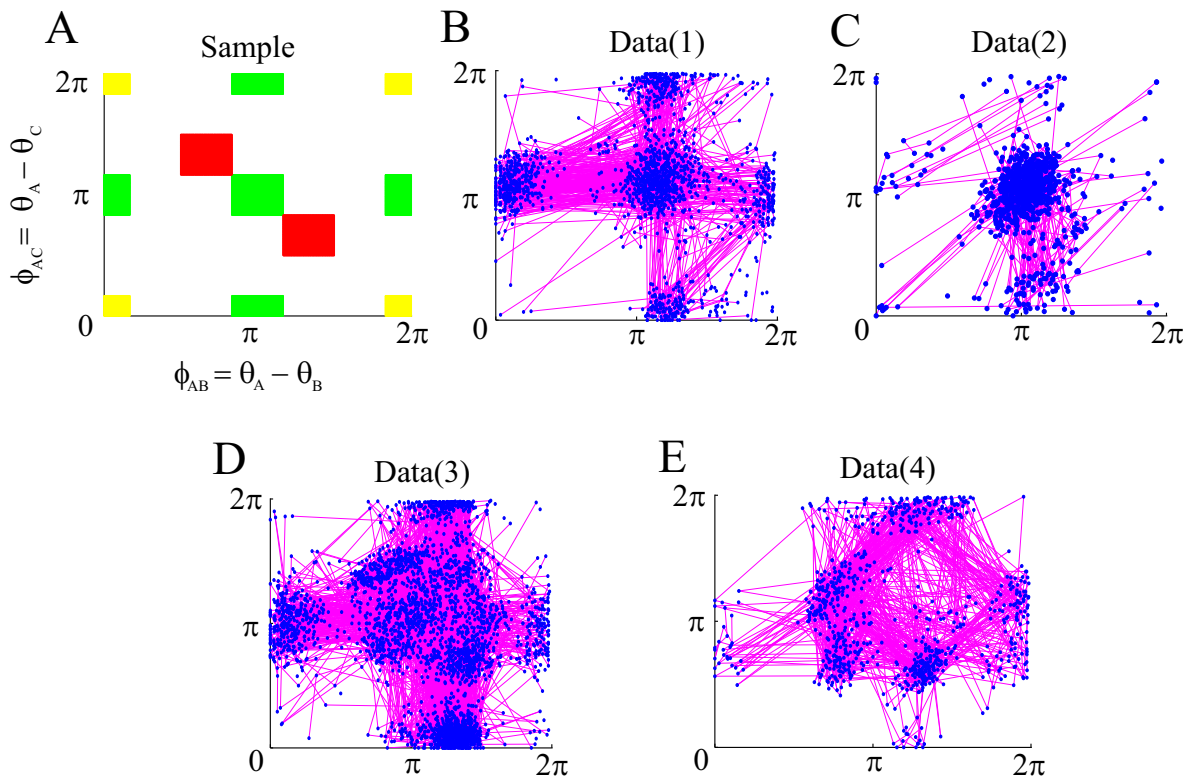


FIG. 4: (Color) Synchronization and switching-dynamics experimentally observed in a three-frogs system. (A) Definition of synchronization states on the phase plain of ϕ_{AB} (the abscissa) and ϕ_{AC} (the ordinate), setting the error bound of $\pi/6$. Regions of tri-phase synchronization, 1:2 anti-phase synchronization and in-phase synchronization are shown with red, green and yellow, respectively. (B)–(E) Plots of the phase differences ϕ_{AB} and ϕ_{AC} obtained from four experimental trials. Note that the phase plots shown by blue dots are localized not around the in-phase state but around the tri-phase and 1:2 anti-phase states. Transitions between different states are indicated by pink lines.

model analysis. The important point is that tri-phase synchronization of three frogs can be stably observed as shown in Data(3) and (4) and qualitatively explained with the model analysis by assuming the condition of $K_{AC} \simeq K_{AB} = K_{BC}$ such as Regions (III), (IV) and (V) in Fig.3A. Since the coupling coefficient of K_{ij} represents how strongly the frogs i and j interact, the condition of $K_{AC} \simeq K_{AB} = K_{BC}$ biologically implies that, during interactive calling behavior of three frogs in the straight setting of Fig.2A, everyone can equally recognize the other two individuals and then tri-phase synchronization is realized. It should be noted that the similar calling property is reported in another species of frogs, Puerto Rican tree frogs; a single frog avoids acoustic overlap with two neighbors [16].

From an ethological point of view, it is important that our experiment clearly shows the existence of complex synchronized behavior by three male frogs to maintain their mutual intercall intervals each other, i.e., the tri-phase synchronization and 1:2 anti-phase synchroniza-

tion. Such alternating phenomena by three frogs would be biologically meaningful both for males and females to keep their own territories and localize calling males, the same as discussed in our previous study on a two-frogs system [9].

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Data(1)

	Total	Anti-Sync	Tri-Sync	1:2 Anti-Sync	In-Sync
One Frog	173.1sec				
Two Frogs	378.2sec	138.7sec (36.6%)			11.7sec (3.1%)
Three Frogs	660.8sec		34.7sec (5.2%)	64.0sec (9.6%)	0sec (0%)

Data(2)

	Total	Anti-Sync	Tri-Sync	1:2 Anti-Sync	In-Sync
One Frog	732.2sec				
Two Frogs	1416.4sec	595.3sec (42.0%)			39.6sec (2.8%)
Three Frogs	298.3sec		15.5sec (5.2%)	60.4sec (20.2%)	2.5sec (0.8%)

Data(3)

	Total	Anti-Sync	Tri-Sync	1:2 Anti-Sync	In-Sync
One Frog	104.8sec				
Two Frogs	1088.2sec	396.7sec (36.4%)			41.3sec (3.8%)
Three Frogs	1265.8sec		91.4sec (7.2%)	33.2sec (2.6%)	0sec (0%)

Data(4)

	Total	Anti-Sync	Tri-Sync	1:2 Anti-Sync	In-Sync
One Frog	101.7sec				
Two Frogs	976.7sec	621.1sec (63.5%)			22.4sec (2.2%)
Three Frogs	350.6sec		52.8sec (15.0%)	4.2sec (1.1%)	0sec (0%)

TABLE I: **Summary of synchronized behavior obtained from the experimental data of calling frogs.** Total calling durations of a single frog, two frogs and three frogs, and temporal sums of detected synchronization modes are shown for four experimental trials (See Supplemental Materials [12]). As for calling of two frogs, anti-phase synchronization is robustly observed, but in-phase synchronization is rarely detected. During calling of three frogs, tri-phase synchronization and 1:2 anti-phase synchronization can be stably observed compared with the in-phase synchronization.

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