# Hidden Symmetry in Chains of Biological Coupled Oscillators

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We experimentally investigated spatiotemporal patterns in chains of coupled biological oscillators with boundaries and found hidden symmetric patterns that are not straightforwardly derived from explicit geometrical symmetry of the systems. We propose a model of coupled oscillators in chains with a hidden oscillator interconnecting its boundaries. The model can explain all observed patterns including the hidden symmetric ones, while other models such as discrete analogs of Neumann boundary conditions in continuous systems cannot.

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It is known that certain boundary conditions in spatially continuous systems with symmetry constrain their dynamical behavior to exhibit hidden symmetric patterns [1,2]. On the contrary, boundary effects in spatially discrete systems with symmetry, such as coupled nonlinear oscillator systems with boundaries where oscillators are symmetrically arranged, have not been investigated extensively with direct comparison to experimental systems. This is true despite the fact that coupled oscillator systems are known as fundamental models of practical systems in a wide range to explain dynamical behavior like synchronization in collectives of interacting elements [3]. Most of the practical systems have boundaries. Linear arrays of oscillators, i.e., chains of oscillators, are basic models for such discrete systems with boundaries. We investigated spatiotemporal patterns in chains of coupled oscillators constructed with living cells of plasmodium of the true slime mold, *Physarum polycephalum*. We analyzed their spatiotemporal symmetries using the group-theoretic bifurcation theory developed by Golubitsky and Stewart [2,4].

The plasmodium is an amoebalike multinucleated giant unicellular organism. It shows nonlinear oscillation phenomena in its cell thickness, etc., that generate spatiotemporal patterns throughout the whole body. Spatiotemporal patterns are considered to be related to information processing in this organism and have attracted interest [5,6]. We constructed living coupled oscillator systems in chains with the plasmodium by patterning cell shapes using microfabricated structures [Figs. 1(a) and 1(b)] [7–9]. Microfabricated structures consist of wells and channels. We observed thickness oscillation of plasmodium in the wells, each of which can be regarded as an oscillator. The coupling strength between oscillators is controlled systematically by channel width [7]. With this system, we have succeeded in elucidating well-characterized phenomena in coupled oscillator systems, e.g., time delay effects in two oscillator systems [8] and symmetric spatiotemporal patterns in rings of oscillators [9]. These phenomena can be found generally in other coupled oscillator systems and have also been reported in nonbiological systems, such as electric circuits [10], chemical oscillator systems [11], and so on. In addition to generality, this system is one of the most easily controlled biological systems. Therefore, its investigation would help us to better understand more complicated biological systems. To study boundary effects in a discrete system of slime mold, we constructed $N$-oscillator systems in chains ($N = 3, 4, 5, 6, 7$), where all oscillators are considered to be homogeneous; then, we observed their spatiotemporal patterns [12].

Group-theoretic bifurcation theory, used here to analyze spatiotemporal patterns, is a very powerful tool for analysis of coupled oscillator systems. The theory can provide catalogs of possible generic spatiotemporal patterns that are irrespective of their internal models and based merely on geometrical symmetries of systems. Using the theory, we can address spatiotemporal patterns in biological systems even when their detailed internal dynamics are unknown. Chains of coupled oscillators [e.g., Fig. 1(b)] are explicitly symmetric with respect to group $Z_2$, which is a group generated by reflection (equivalent to $\pi$ rotation) in the center of the system [shown as blue lines in Fig. 1(b)]. According to the theory, these systems are expected to show $Z_2$-symmetric spatiotemporal patterns.

First, spatiotemporal patterns in three-oscillator systems [Fig. 1(b)] were analyzed. Figure 1(c) shows the pattern most frequently observed when the coupling strength is strong. Oscillators at both ends showed antiphase synchronization; the oscillator in the center showed double frequency (pattern $A$). This pattern is invariant with respect to reflection in the center oscillator with $\pi$ phase shift; the same waveforms of oscillators 1and 3 are mapped to each other by reflection in the center oscillator

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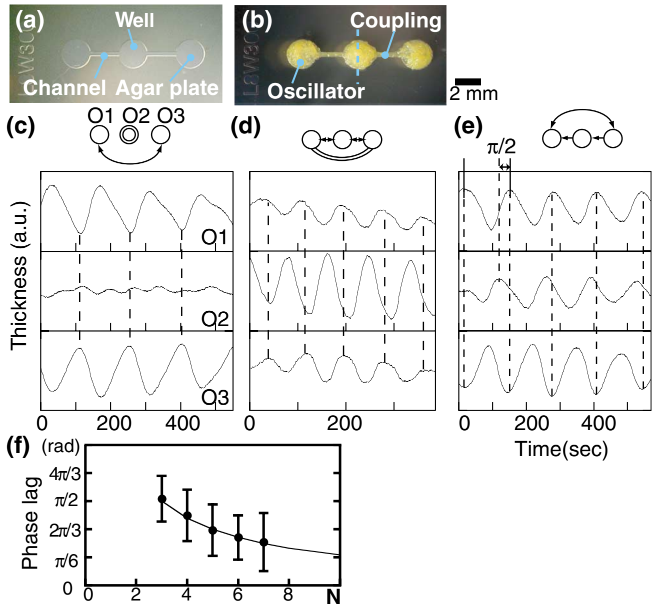


FIG. 1 (color). Three homogeneous oscillators in a chain constructed with plasmodium of *Physarum polycephalum*. (a) Microfabricated structure for cell shape patterning [7]. Coupling strength is controlled by channel width. (b) Living coupled oscillator systems with the plasmodium patterned by microfabricated structures [7]. The blue dashed line signifies a reflection axis of each system. (c)–(e) Typical oscillation patterns in chains of three oscillators with strong couplings. Schematic diagrams illustrate phase relations among three oscillators (O1, O2, and O3) denoted by circles. Double circles denote oscillators with double frequency. Bidirectional arrows, double lines, and unidirectional arrows show the phase relation of antiphase, in-phase, and $\pi/2$-phase lag, respectively. Graphs show time courses of thickness in each oscillator [7]. (c) Antiphase and double frequency pattern (pattern $A$). (d) All antiphase pattern (pattern $B$). (e) Traveling wave pattern (pattern $D$). (f) Phase lags between adjacent oscillators. Filled circles denote mean values of all phase lags irrespective of positions such as those between oscillators 1 and 2, 2 and 3, etc., obtained from more than ten samples for each $N$. The solid line denotes a theoretical curve for $2\pi/(N+1)$.

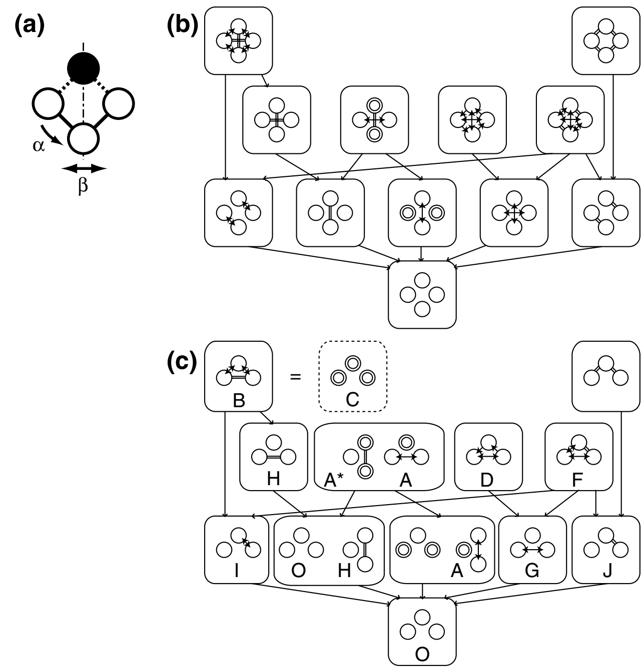


FIG. 2. Possible oscillation patterns. (a) A schematic diagram of a system with a hidden oscillator for a chain of three oscillators. $\alpha$ and $\beta$, generators of dihedral group $D_4$, denote $\pi/2$ rotation and reflection, respectively. (b) Rings of four oscillators [4]. (c) Chains of three oscillators. Unidirectional arrows connecting the patterns show containment of subgroups. Capital alphabet letters are names of the patterns that were experimentally observed. The names are consistent with those in the text and Fig. 3. The pattern encircled by dashed lines (pattern $C$) was observed in the experiment, but has not been predicted theoretically. Double circles in pattern $C$ denotes oscillators with double frequency. Other notations of oscillators and phase relations are same as those in Fig. 1.

with $\pi$ phase shift, while the waveform of oscillator 2 with double frequency is invariant itself. That is, this pattern maintains $Z_2$ symmetry. This multirhythmic pattern is noteworthy and has already been reported for a system of three oscillators in a ring [9]. Figure 1(d) shows another pattern where all adjacent oscillators are in antiphase (pattern $B$). This pattern also maintains $Z_2$ symmetry; the same waveforms of oscillators 1and 3 are mapped to each other by reflection in the center oscillator.

However, surprisingly, we also observed a pattern that does not maintain $Z_2$ symmetry. That is a pattern with traveling waves from one end oscillator to the other end, as shown in Fig. 1(e) (pattern $D$). Phase lags between adjacent oscillators were around $\pi/2$, irrespective of the coupling strength. The $\pi/2$-phase lags suggest that this system has a hidden symmetry of dihedral group $D_4$, a group generated by $\pi/2$ rotation $\alpha$ and reflection $\beta$ [Fig. 2(a)].

Traveling waves were generally observed in $N$-oscillator systems for $N = 3, 4, 5, 6, 7$ in the plasmodium. For $N$-oscillator systems, phase lags between adjacent oscillators in one directional traveling wave pattern were almost $2\pi/(N+1)$ for $N = 3, 4, 5, 6, 7$ [Fig. 1(f)], which implies the existence of $D_{N+1}$ symmetry in a chain of $N$ oscillators, generally. Traveling waves have been observed in other biological systems as well [13,14]. However, they cannot be explained by the simplest mathematical models with diffusion couplings, which leads to in-phase synchronization. To explain them, various modified models have been proposed with some assumptions in couplings or oscillators such as asymmetrical couplings [13], synaptic couplings [13], gradient of frequencies in the oscillators [14], a periodic boundary condition directly connecting both ends [15], and a "reflection trick" with a periodic boundary condition [16]. All these assumptions can explain the existence of traveling waves, but not of those with $2\pi/(N+1)$-phase lags that were experimentally observed here.

Although the chained systems explicitly have $Z_2$ symmetry, some of the observed patterns cannot be derived from $Z_2$ symmetry. The problem is that homogeneity among oscillators (without coupling) has not been reflected in $Z_2$ symmetry. Actually, this system should have additional symmetry corresponding to homogeneity among the oscillators. It can be introduced as translation symmetry by assuming a single hidden oscillator interconnecting the oscillators at both ends. It turns chains of $N$ oscillators into rings of $N+1$ oscillators with $D_{N+1}$ symmetry [Figs. 2(a) and 4(a)(below)]. This assumption permits translation of an oscillator at the end to inner positions, and vice versa, by $2\pi/(N+1)$ rotations, which correspond to $2\pi/(N+1)$-phase lags in traveling waves.

With the assumption of a hidden oscillator, spatiotemporal patterns observed in a chain of $N$ oscillators correspond to those of $N$ oscillators extracted from a ring of $N+1$ oscillators. As an example for $N=3$, Fig. 2(b) shows all possible patterns in a $D_4$-symmetric four-oscillator system in a ring [4]. Figure 2(c) shows those of three oscillators extracted from Fig. 2(b). This diagram, therefore, shows possible patterns for a chain of three oscillators. Indeed, we observed most of the patterns shown in Fig. 2(c) [for wave forms, see Figs. 1(c)–1(e)] except one with all in phase. Experimentally observed patterns are denoted by capital alphabet letters in Fig. 2(c). Some of them, including pattern $D$, could not be understood straightforwardly without the assumption of a single hidden oscillator. It should be noted that, for $N$ oscillators in chains ($N=4, 5, 6, 7$), we observed most of the possible patterns in $N$ oscillators extracted from $N+1$ oscillators in rings. This fact supports again the assumption that patterns in chains of $N$ oscillators can be understood via the hidden $D_{N+1}$ symmetry.

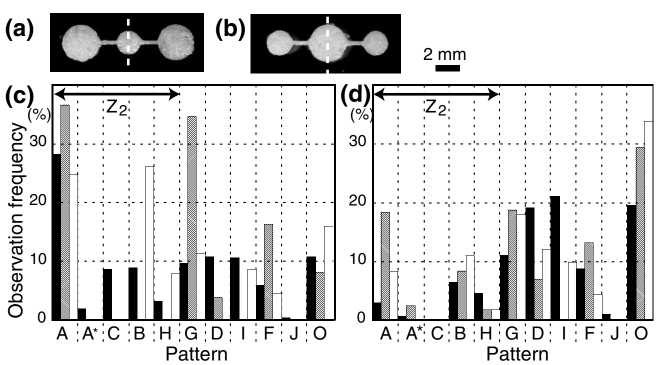


FIG. 3. Observation frequencies of patterns in homogeneous and inhomogeneous oscillator systems. (a),(b) Inhomogeneous oscillators, type I (a) and type II (b). Large and small oscillators have 3 and 2 mm diameters, respectively. Black bars show homogeneous systems; hatched and white bars are for inhomogeneous systems of types I and II, respectively. Patterns denoted by capital alphabet letters correspond to those in Fig. 2(c). (c) Strong coupling (channel width: 0.4 mm). (d) Weak coupling (channel width: 0.3 mm). Observation frequencies were calculated with the number of periods in each oscillation pattern against more than 250 periods obtained from more than five samples in each condition.

To support the hidden oscillator assumption deduced from homogeneity among oscillators, we analyzed oscillation patterns in two types of inhomogeneous-oscillator systems: one comprising two larger oscillators at both ends [type I, Fig. 3(a)], and the other comprising a single larger oscillator in the center [type II, Fig. 3(b)]. Breaking homogeneity among the oscillators at the ends and the ones in the center permits only $Z_2$-symmetric patterns as theoretically possible patterns. Figures 3(c) and 3(d) show observation frequencies of each pattern in the homogeneous- and inhomogeneous-oscillator systems. Inhomogeneous systems show significant decrease of observation frequency of $D_4$-symmetric pattern $D$ irrespective of coupling strength, from 10.8% to 3.9% (type I), or to 0.0% (type II) with strong coupling, and from 19.2% to 7.0% (type I), or to 12.2% (type II) with weak coupling. On the other hand, observation frequency of $Z_2$-symmetric pattern $A$ or $B$ increased. These results imply that homogeneity among oscillators is critical for observation of hidden symmetric patterns.

We show another simple way to look at $N$-oscillator systems in a chain as ones extracted from an $(N+1)$-oscillator system in a ring. Let the system of $N$ oscillators be given by the simplest linear form $\dot{\Delta} = A_N^{\text{type}} X$, where $X = (x_1, x_2, \ldots, x_N)$ is a state and $A_N^{\text{type}}$ is either $A_N^{\text{ring}}$ or $A_N^{\text{chain}}$ depending on its form of connection. For example,

$$A_3^{\text{chain}} = \begin{bmatrix} a & b & 0 \\ b & a & b \\ 0 & b & a \end{bmatrix},\ A_4^{\text{ring}} = \begin{bmatrix} a & b & 0 & b \\ b & a & b & 0 \\ 0 & b & a & b \\ b & 0 & b & a \end{bmatrix},\ A_3^{\text{ring}} = \begin{bmatrix} a & b & b \\ b & a & b \\ b & b & a \end{bmatrix},$$

where $a$ and $b$ denote dynamics of each oscillator and coupling, respectively. It is obvious that $A_3^{\text{chain}}$ is a submatrix of $A_4^{\text{ring}}$ (e.g., the parts surrounded by dashed lines). As $A_4^{\text{ring}}$ is invariant under all elements in group $D_4$, we can still extract a submatrix $A_3^{\text{chain}}$ from transformed $\sigma \cdot A_4^{\text{ring}}$, for all elements $\sigma$ of $D_4$. However, the $A_3^{\text{chain}}$ is not a submatrix of $A_3^{\text{ring}}$. Generally, $A_N^{\text{chain}}$ for all integers $N$ is a submatrix of $A_{N+1}^{\text{ring}}$ and can be extracted from $\sigma \cdot A_{N+1}^{\text{ring}}$ for all elements $\sigma$ of $D_{N+1}$. That is, symmetries in $N$ oscillators in chains can be identified with those in $(N+1)$ oscillators in rings, but not by those in $N$ oscillators in rings. A problem remains: why can it not be with $(N+2)$ or $(N+3)$ oscillators in rings?

Finally, we discuss other possible boundary conditions. One is periodic one and others are discrete analogs of Neumann boundary condition in continuous systems. The

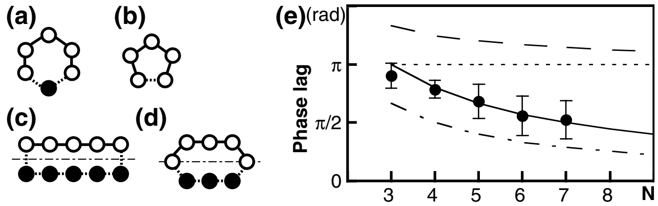


FIG. 4. Boundary conditions on chains of coupled oscillators. (a) $D_{N+1}$-symmetric ring of periodic type with a single hidden oscillator. (b) $D_N$-symmetric ring of periodic type without hidden oscillators. (c) $D_{2N}$-symmetric ring of Neumann type with $N$ hidden oscillators. (d) $D_{2N-2}$-symmetric ring of Neumann type with $N-2$ hidden oscillators. Open and filled circles denote real oscillators and hidden oscillators, respectively. Dashed lines are reflection axes. (e) Phase lags between real oscillators at both ends. Solid, mixed dashed, long dashed, and short dashed lines denote theoretical curves of $4\pi/(N+1)$, $2\pi/N$, $(N+1)\pi/N$, and $\pi$ corresponding to $D_{N+1}$, $D_N$, $D_{2N}$, and $D_{2N-2}$ symmetry, respectively. Filled circles denote experimental results with weak coupling obtained from more than ten samples for each $N$.

periodic condition requires a chain of $N$ oscillators to be either $D_{N+1}$ symmetric with a hidden oscillator [our assumption; Fig. 4(a)] or $D_N$ symmetric [Fig. 4(b)]. The Neumann type condition necessitates that a chain of $N$ oscillators be either $D_{2N}$ or $D_{2N-2}$ symmetric by a reflection trick [17] for the following reason. A $D_{2N}$-symmetric system with $N$ hidden oscillators is obtained by taking reflection axes between ends of real oscillators and those of hidden oscillators [Fig. 4(c)], which was first proposed for coupled chemical oscillators [16]. A $D_{2N-2}$-symmetric system with $N-2$ hidden oscillators is obtained by taking the reflection axes at both ends of real oscillators [Fig. 4(d)]. However, only the $D_{N+1}$-symmetric case fits the observation in the slime mold system. That fact is verified by checking phase lags between both ends of real oscillators for traveling wave patterns. For systems with $D_{N+1}$, $D_N$, $D_{2N}$, or $D_{2N-2}$ symmetry, the phase lags should be $4\pi/(N+1)$, $2\pi/N$, $(N+1)\pi/N$, or $\pi$, respectively, as shown in Fig. 4(e). In our observation, phase lags almost perfectly followed $4\pi/(N+1)$ for $D_{N+1}$. It has not been clarified whether our assumption of $D_{N+1}$ symmetry is generic for coupled oscillators in chains, if it is applicable only to the slime mold system because of system-specific reason such as characteristic coupling manner [8], which might be long-range couplings [18,19], for example, or how the hidden oscillator should be treated in real chains. Discovering other examples that support our assumption would help us to answer these questions.

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