

**LETTER** *Special Section on Neural Nets, Chaos and Numerics*

# Environment-Dependent Self-Organization of Positional Information in Coupled Nonlinear Oscillator System —A New Principle of Real-Time Coordinative Control in Biological Distributed System—

Yoshihiro MIYAKE†, Yoko YAMAGUCHI††, *Members*, Masafumi YANO††\*  
and Hiroshi SHIMIZU††, *Nonmembers*

**SUMMARY** The mechanism of environment-dependent self-organization of "positional information" in a coupled nonlinear oscillator system is proposed as a new principle of real-time coordinative control in biological distributed system. By modeling the pattern formation in tactic response of *Physarum* plasmodium, it is shown that a global phase gradient pattern self-organized by mutual entrainment encodes not only the positional relationship between subsystems and the total system but also the relative relationship between internal state of the system and the environment.

*key words:* positional information, oscillation, entrainment, self-organization, coordination, real-time control, distributed system, *Physarum*

## 1. Introduction

Biological system is a good example of the distributed nonlinear system. One of the most interesting abilities is the real-time coordinative control by using emergent and flexible properties of the nonlinear dynamics among large degrees of freedom. What is the principle of information processing in such biological system control?

Recently, biological system oriented artificial models, such as neural networks,<sup>(1),(2),(11)</sup> multiagent system<sup>(3),(15)</sup> and genetic algorithm,<sup>(7),(10)</sup> are widely investigated. However, to realize a global coordinative control in these systems for obtaining optimal solutions, the information on the relationship between each subsystem and the total system is thought to be indispensable and it should be spontaneously generated according to the external conditions of the system in real-time.

In biological system, such information is self-organized in the pattern formation process and is called "positional information".<sup>(23)</sup> It provides a kind of space coordinate indicating the relative positional

relationship between parts and whole of the system. Interpreting this information, each subsystem is informed of its position within the whole system and it becomes able to coordinately differentiate into many different states in a position-dependent manner.

In this report, we focus our attention on the self-organization of the positional information as a typical example of the biological coordinative control. However, since the concept was mainly applied to the developmental system, its applicability has been restricted to the insulated systems.<sup>(6),(8),(9),(12),(20),(23)</sup> From the viewpoint of engineering realization, the important point is that the system can work in real time even under changing and unpredictable environment. Thus the concept should be generalized to the dynamical relationship between the system and the environment.

The pattern formation in tactic response of *Physarum* plasmodium would be a good model in such problem, because the reorganization of its body shape is coordinately achieved according to the environmental conditions in a whole body. Therefore, the purpose of this report is to elucidate the self-organization mechanism of the positional information contributing to the pattern formation in taxis. The obtained mechanism is thought to become available not only on the plasmodium but also on the coordinative control of artificial distributed systems.

## 2. Tactic Response of *Physarum* Plasmodium

The plasmodium is a large amoeboid cell. Though it has no nervous system, it exhibits highly coordinative tactic behavior as one whole system. As shown in Fig. 1, when a part of the organism is attached to an attractant, the migration toward the stimulated region accompanying with the pattern reorganization of its body shape are observed in every part.

In this process it is widely suggested that mutual entrainment between intracellular rhythms play important roles as intracellular communication. Tension<sup>(25)</sup> and chemical<sup>(18),(21)</sup> oscillations with a period of 2 to 3

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† The author is with the Department of Information and Computer Engineering, Kanazawa Institute of Technology, Ishikawa-ken, 921 Japan.

†† The authors are with the Faculty of Pharmaceutical Sciences, The University of Tokyo, Tokyo, 113 Japan.

\* Presently, with the Research Institute of Electrical Communication, Tohoku University, Sendai-shi, 980 Japan.

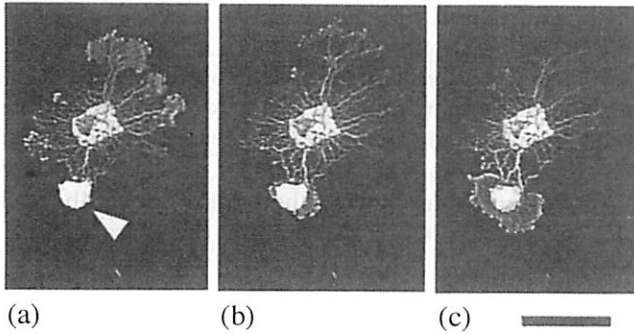


Fig. 1 Pattern reorganization in tactic response of *Physarum* plasmodium. (a) It migrates toward the top of its fan-shaped body. Then an attractant was applied to the rear part indicated by the arrow. (b) It started to change its body shape according to the stimulus. (c) Finally it was reorganized and its polarity reversed as a whole. Each photograph was taken by 1 hr interval. Bar: 5 cm.

minutes are observed at any regions of the plasmodium and they spatially synchronize. Attractants and repellents increase and decrease their frequencies, respectively.<sup>(5)</sup> A local application of stimulant induces global phase wave propagating between the stimulated site and the other regions, and its direction depends on whether the stimulus is an attractant or a repellent.<sup>(13),(19)</sup> Migratory direction coincides with that of the phase advance in the wave.<sup>(14)</sup> We further reported that such global phase waves and the coordinative pattern reorganization disappear when the mutual interaction between these rhythms is inhibited.<sup>(16),(24)</sup> These facts strongly suggest that the organization of coherent phase pattern has close correlations with the coordinative control in tactic pattern formation.

An essential problem is how the positional information for such environment-dependent coordination is encoded on the global phase patterns. Therefore, based upon the experimental evidences, we shall propose a simplified model of the plasmodium as a coupled nonlinear oscillator system and the environmental conditions are assumed to change its native frequencies. Our results will show that the characteristics of the global phase gradient pattern self-organized in such system are convenient to encode the environment-dependent positional information.

### 3. The Coupled Nonlinear Oscillator Model

We start from the model of intracellular rhythms in the plasmodium as the coupled nonlinear oscillators as shown in Fig. 2. Each oscillator stands for local chemical oscillation. The whole array of the oscillators is assumed to be one-dimensional, which is a model of the plasmodial strand as a minimum struc-

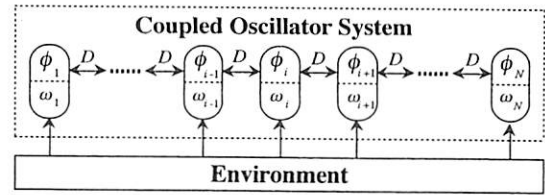


Fig. 2 Coupled nonlinear oscillator model. The internal state of each oscillator is described only by the phase, and they mutually interact through diffusionlike coupling. The environmental conditions change the native frequencies at each oscillator. See text for details.

ture. Diffusionlike coupling is applied to the interaction between nearest-neighbor oscillators, owing to the chemical interaction between intracellular rhythms. When we assume that the orbit of nonlinear oscillator is a ring for simplicity,<sup>(22)</sup> the evolution equation in each oscillator is given as the dynamics of phase only.

Thus the coupled oscillator model is expressed by using ring oscillators as follows:

$$\begin{aligned} d\phi_i/dt = \Delta\omega_i + D \sin(\phi_{i+1} - \phi_i) \\ + D \sin(\phi_{i-1} - \phi_i) \end{aligned} \quad \text{for } i=2, \dots, N-1, \quad (1a)$$

$$\begin{aligned} d\phi_i/dt = \Delta\omega_i + D \sin(\phi_{i+1} - \phi_i) \end{aligned} \quad \text{for } i=1, \quad (1b)$$

$$\begin{aligned} d\phi_i/dt = \Delta\omega_i + D \sin(\phi_{i-1} - \phi_i) \end{aligned} \quad \text{for } i=N, \quad (1c)$$

with

$$\Delta\omega_i = \omega_i - \omega_s \quad \text{for } i=1, \dots, N. \quad (1d)$$

Each of  $N$  oscillators is identified by the positional index  $i$ . Here,  $\phi_i$  and  $\omega_i$  denote the phase and the native angular frequency, which are characteristic of the  $i$ -th oscillator;  $t$  stands for the time. In Eqs. (1a)–(1c), the time evolution of the phase is described on a coordinate rotating with an arbitrary angular frequency  $\omega_s$ . The coupling constant  $D$  is positive and assumed to be common to the whole system for simplicity. The evolution equations at both ends of the system ( $i=1$  and  $N$ ) are given by Eqs. (1b) and (1c), which represent the free-end condition at the boundary.

How do the environmental conditions influence the above coupled oscillator system? Since in the plasmodium the attractants increase the frequency of intracellular rhythm while the repellents decrease it, the environment is assumed to change only the value of native angular frequency in the model.

### 4. Analyses of the Model

The important problems in the present model are

how the spatial phase pattern is organized under a given distribution of native angular frequencies corresponding with the environmental conditions and how the positional information is encoded on the self-organized pattern.

Let us analyze the steady state solution of the set of Eqs. (1a)-(1d). When the parameter  $\omega_s$  is given as the globally entrained frequency among all oscillators, the equations at the steady state are obtained by setting the term on the left hand side zero.

$$\sin \delta_i - \sin \delta_{i-1} = \Delta\omega_i/D \quad \text{for } i=2, \dots, N-1, \quad (2a)$$

$$\sin \delta_i = \Delta\omega_i/D \quad \text{for } i=1, \quad (2b)$$

$$-\sin \delta_{i-1} = \Delta\omega_i/D \quad \text{for } i=N, \quad (2c)$$

with

$$\delta_i = -(\phi_{i+1} - \phi_i) \quad \text{for } i=1, \dots, N-1. \quad (2d)$$

In these expressions, new parameter  $\delta_i$  is termed "phase gradient". It is introduced in order to describe the detail structure of the spatial phase relationship. The phase gradient denotes the phase difference between the  $i$ -th and  $(i+1)$ -th oscillators as is given in (2d). It is assumed to have a positive value when the oscillator with a smaller positional index has an advanced phase.

The necessary conditions for the set of Eqs. (2a)-(2d) have solutions are easily given as

$$|\Delta\omega_i| < 2D \quad \text{for } i=2, \dots, N-1, \quad (3a)$$

$$|\Delta\omega_i| < D \quad \text{for } i=1 \text{ and } N. \quad (3b)$$

Under the above conditions, Eqs. (1a)-(1d) have two kinds of steady state solutions. One is a stable phase locking and the other is an unstable one. When the conditions (3a) and (3b) are sufficiently satisfied such that  $\Delta\omega_i/D \cong 0$ , the stable solution is nearly equal to zero, i.e.  $(\delta_1, \dots, \delta_{N-1}) \cong (0, \dots, 0)$ , and the unstable one is nearly equal to  $\pi$ , i.e.  $(\delta_1, \dots, \delta_{N-1}) \cong (\pi, \dots, \pi)$ . In this limit, one can linearize Eqs. (2a)-(2d) around the stable steady state by using the approximation of  $\sin \delta_i \cong \delta_i$ . Then one obtains,

$$\delta_i - \delta_{i-1} = \Delta\omega_i/D \quad \text{for } i=2, \dots, N-1, \quad (4a)$$

$$\delta_i = \Delta\omega_i/D \quad \text{for } i=1, \quad (4b)$$

$$-\delta_{i-1} = \Delta\omega_i/D \quad \text{for } i=N. \quad (4c)$$

Thus summing up Eq. (4a) according to  $i$  from  $i=2$  to  $j$  on both sides, and further adding Eq. (4b) to the result in the same way, one can obtain the phase gradient at the position  $j$  as

$$\delta_j = (1/D) \sum_{i=1}^j \Delta\omega_i \quad \text{for } j=1, \dots, N-1. \quad (5)$$

Equation (5) explicitly shows that the spatial structure of phase gradient under the steady state is determined by  $\Delta\omega_i$ , i.e. the relationship between the globally

entrained frequency  $\omega_s$  and the local native frequencies  $\omega_i$  at each part.

The native frequencies of each oscillator are determined by the environmental conditions. However, the globally entrained frequency has been left unknown in the above analysis. Summing up Eq. (4a) from  $i=2$  to  $N-1$  on both sides, and further adding Eqs. (4b) and (4c) to the result, we can obtain the entrained frequency as

$$\omega_s = (1/N) \sum_{i=1}^N \omega_i. \quad (6)$$

This equation shows that the globally entrained frequency  $\omega_s$  is determined as a mean value among local native frequencies throughout the whole system.

From Eqs. (5) and (6), we can completely obtain the pattern of the phase gradient under the steady state. The self-organization mechanism of these phase gradient pattern is summarized as follows. The phase gradient is determined by the relationship between the local native frequencies and the globally entrained one, while the globally entrained frequency is obtained as the mean value among all of the local frequencies. Thus the phase gradient in each part is determined in comparison with the globally entrained state.

In order to clarify typical and significant characteristics of the above model, let us examine the solution under the following environmental conditions. That is, the native frequency at one end ( $i=1$ ) is modulated while those at other sites are kept constant at the same value. This means that the plasmodium first encounters a new environmental stimulus at the peripheral region of the body during migration. The conditions for the native frequency are given as

$$\omega_i = \omega_e \quad \text{for } i=1, \quad (7a)$$

$$\omega_i = \omega_0 \quad \text{for } i=2, \dots, N, \quad (7b)$$

where  $\omega_0$  and  $\omega_e$  denote the original and modulated frequency, respectively.

In this case, globally entrained frequency is easily calculated from Eq. (6) as

$$\omega_s = (1/N) \{\omega_e + (N-1)\omega_0\}. \quad (8)$$

Thus, by using the relationships (3a) and (3b), we can derive the necessary conditions for the entrainment as

$$\begin{aligned} |\Delta\omega_i| &= |\omega_e - \omega_s| \\ &= |\omega_e - (1/N) \{\omega_e + (N-1)\omega_0\}| < D, \\ \therefore |\omega_e - \omega_0| &< ND/(N-1) \quad \text{for } i=1, \end{aligned} \quad (9a)$$

$$\begin{aligned} |\Delta\omega_i| &= |\omega_0 - \omega_s| \\ &= |\omega_0 - (1/N) \{\omega_e + (N-1)\omega_0\}| < 2D, \\ \therefore |\omega_e - \omega_0| &< 2ND \quad \text{for } i=2, \dots, N-1, \end{aligned} \quad (9b)$$

$$\begin{aligned}
 |\Delta\omega_i| &= |\omega_0 - \omega_s| \\
 &= |\omega_0 - (1/N)\{\omega_e + (N-1)\omega_0\}| < D, \\
 \therefore |\omega_e - \omega_0| &< ND \text{ for } i=N. \quad (9c)
 \end{aligned}$$

Since the conditions (9b) and (9c) are included by (9a), the necessary condition for the global entrainment among all oscillators is regarded as

$$|\omega_e - \omega_0| < ND/(N-1). \quad (10)$$

Under the condition (10), substituting native frequencies (7a) and (7b) into Eq. (5), and further using entrained frequency (8), we can finally obtain the phase gradient as

$$\begin{aligned}
 \delta_j &= (1/D)\{\omega_e - \omega_s + (\omega_0 - \omega_s)(j-1)\} \\
 &= (1/D)[\omega_e - (1/N)(\omega_e + (N-1)\omega_0) + \{\omega_0 \\
 &\quad - (1/N)(\omega_e + (N-1)\omega_0)\}(j-1)] \\
 &= (1/D)(\omega_e - \omega_0)(1-j/N) \\
 &\quad \text{for } j=1, \dots, N-1. \quad (11)
 \end{aligned}$$

This equation explicitly gives the global pattern of phase gradient self-organized at the stable steady state corresponding to the above environmental conditions.

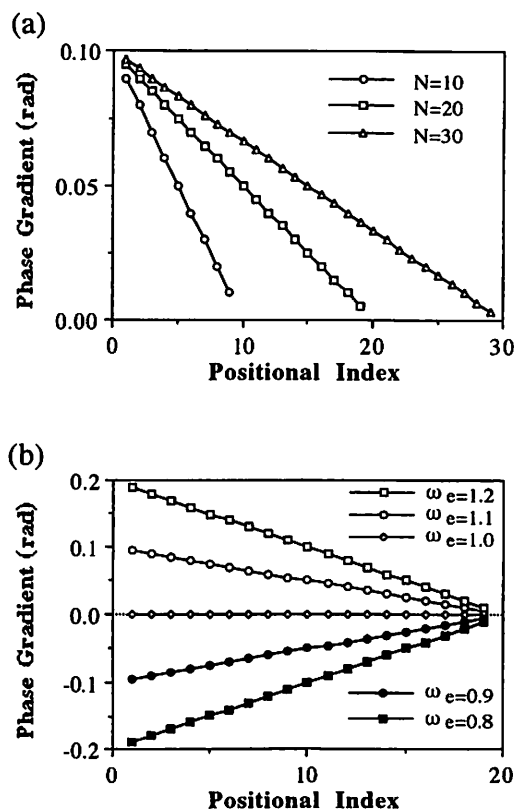


Fig. 3 Phase gradient pattern under the stable steady state. (a) Effect of the system size;  $\omega_e=1.1$ ,  $\omega_0=1.0$  and  $D=1.0$ . (b) Effect of the frequency modulation;  $\omega_0=1.0$   $N=20$  and  $D=1.0$ .

In some typical cases, the influences of system size and frequency modulation on the phase gradient pattern are calculated and shown in Figs. 3(a) and 3(b), respectively.

### 5. Characteristics of the Phase Gradient Pattern

When one considers the resultant pattern as a representation of the environment-dependent positional information, the following two characteristics should be stressed.

(i) One is the ability to code the positional relationship within the whole system. As shown in Fig. 3(a), since the magnitude of the phase gradient decreases linearly as the positional index  $j$  increases, the pattern shows global polarity from the stimulated site ( $j=1$ ) to the opposite end ( $j=N-1$ ). In addition, its spatial pattern is size-invariant as shown in the same figure, because the positional index  $j$  is normalized by the total system size  $N$  as in Eq. (11). Thus its magnitude at each part becomes proportional to the relative distance from the stimulated site under a fixed frequency modulation. Therefore, a kind of space coordinate indicating relative positional relationship between subsystems and the whole system is thought to be self-organized in the coupled oscillator model independent of the total system size.

(ii) The other is the ability to code the relative relationship between the internal state of the system and the environmental conditions. As shown in Fig. 3(b), when the modulated frequency  $\omega_e$  as the environmental stimulus is larger than the original one  $\omega_0$  within the system, the gradient becomes positive in every part and its direction points to the stimulated site, and *vice versa*. Since the gradient is determined by the difference between the two frequencies as in Eq. (11), it represents the relationship between the system and the environment, i.e., whether the environmental condition is relatively attractive or repulsive for the system, can be encoded on the phase gradient. Therefore, the frequency coding in the coupled oscillator model is thought to be advantageous for self-organizing the relevant positional information in changing and unpredictable environments.

These characteristics are in accordance with our experimental evidences in the plasmodium. The direction of the phase gradient depends on whether the stimulus is an attractant or a repellent,<sup>(19)</sup> and it is further clarified that its response is determined merely by relative change of the environmental conditions independent of the species of a stimulant.<sup>(16)</sup> In addition, we recently found that magnitude of the phase gradient decreases depending on the distance from the stimulated site.<sup>(17)</sup> Therefore, it is strongly suggested that the above positional information model is valid in the plasmodium.

Goodwin & Cohen proposed the phase shift

model to generate the positional information in coupled oscillator system.<sup>(6)</sup> However, since they used the phase difference between two phase waves having different propagation velocity, the model became very complicated to realize the size-invariant property and it could not include the environmental effects. On the other hand, Cohen et al. studied the relationship between the native frequencies and the phase patterns organized in coupled-oscillator system as a model of the spinal cord.<sup>(4)</sup> However, they could not find the above two characteristics as the positional information.

## 6. Conclusions

A mechanism of the environment-dependent self-organization of positional information was proposed as a new principle of real-time coordinative control in biological distributed systems. The results clarified that the emergent and flexible properties in the nonlinear dynamics are essential for such control. By the mutual entrainment between nonlinear oscillators, the positional information which encodes not only the positional relationship between subsystems and the total system but also the relative relationship between the internal state of the system and the environmental condition is self-organized as a global phase gradient pattern. Interpreting this information, each subsystem is informed of its position within the whole system and of the meaning of the stimulus. Thus, it is thought that biological systems become able to be coordinately controlled in a position-dependent and in an environment-dependent manners.

Owing to its simple and plausible assumptions, it is thought that one could widely apply the present model to many artificial distributed systems. Not only the information processing systems such as neural networks and multiagent system but also the large scale systems in society such as electric power supply networks and traffic control would be good examples of its application, because such systems should work coordinately under changing environment and changing system size. If each subsystem has the characteristics as a nonlinear oscillator, the positional information is thought to be easily self-organized by the mutual entrainment between subsystems.

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