The idea of Global Coordinating Result from the Incomplete Identification of a Local Site

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Abstract

We studied the chemo-tactical behavior of an amoeboid multinuclear cell, *Physarum polycephalum* plasmodium, and observed a local deviation within the organism played the key role to escape from a severe environmental condition. The organism has been studied as coupled nonlinear oscillators system, which is one of the famous self-organizing system for the study of morphogenesis. Such a model frequently concentrated on cohesive force that makes the non-differential organism maintain as a single individual avoiding from separation. Deviation from cohesion is frequently regarded as extrinsic perturbation. However, the drastic change of development of the organism shown in our experiments cannot explain by the external stochastic perturbation. From experimental facts, we, by contrast, focused on the duality of cohesive and deviational force. We have constructed a new model introducing such a duality by an interface of a self-similar transition map, which is temporally constructed by neighbors' states. Because of such a non-differentiable transition map, even if an initial state of one element would be close to another one, the state transition of them is not always similar each other. Such a duality thus implies the idea of incomplete identification for an element that has just the limited information. We tested our model and showed the possibility that such an incomplete identification, by contrast, could drive the global coordinating featuring the plasticity as a single system.

Keyword: *Physarum*; Self-organization; Nonlinear oscillator; Positional information; Pattern formation

1 Introduction

1.1 Plasmodium of *Physarum Polycephalum*

Physarum polycephalum, a plasmodial slime mold (myxomycete), lives in dark, moist environments such as under the bark of decaying logs and beneath decaying leaves on the forest floor. The vegetative form of this organism is plasmodium, a yellow mass of indefinite morphology. It can cover an area of several square centimeters, while the organism moves like a giant amoeba.

For more than 40 years, *Physarum polycephalum* has been a model research organism for the study of several biological problems including growth and differentiation, cell cycle dynamics, cytoplasmic streaming, self-organized dynamics and complex system (e.g. Kamiya,1959; Cummins,1968; Matsumoto,1986; Coggin,1996). In the plasmodium stage, *Physarum* forms a single giant cell in which plasmodial strands spread like a net (Fig.1).
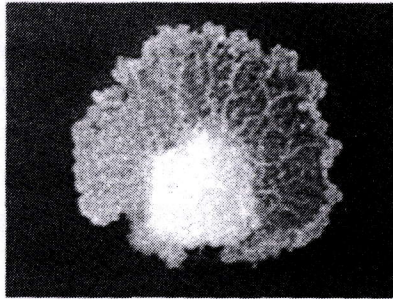

Fig.1: Physarum polycephalum plasmodium

The plasmodial strand consists of outer ectoplasmic gel layer and inner endoplasmic sol, and it forms anastomotic network within the plasmodium like that of blood vessel. Any parts of the organism always show thickness oscillation caused by the reversible streaming of the endoplasm (shuttle streaming), that is driven by periodic contraction and relaxation of the ectoplasm (Kamiya,1950; Komnic,1973; Ueda,1978). In the ectoplasmic gel layer, actin filaments and myosin-like molecules have been found, thus oscillation of ectoplasm is considered to be caused by the motional proteins (Kessler,1982). Depending upon environmental conditions, various types of global spatio-temporal patterns of the thickness oscillation are organized within the organism accompanying amoeboid locomotion. This rhythmic contraction pattern, thus, results in

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locomotion of the plasmodium (Kamiya,1968; Ueda,1990; Nakagaki,1996). Locomotion can be oriented by external stimuli of a local site within the organism, such as chemical gradients (chemotaxis) and temperature gradients (thermotaxis) (Ueda,1982; Matsumoto;1988). One of remarkable features of this creature is this tactical locomotion. For example, when both edges of a *Physarum* strand are stimulated spontaneously by Glucose, an attractive stimulus, with different concentration, it migrates toward the higher concentrated side as an individual (Miyake,1996). It is, therefore, considered that *Physarum* possesses some kind of information processing mechanism, although it is a giant amoeboid cell of indefinite morphology without nervous system like other higher animals.

1.2 Mechanical Model of *Physarum*

How does *Physarum* plasmodium coordinate its behavior as an individual? How can each local site without global bird-eyes acquire the information carrying the whole space and interpret it? Wolpert (1969) has first proposed the idea of the positional information for the questions. He suggested the policy such that it was necessary for an organism to organize some kind of a single polarity of positional information in advance by which each local site can know where it is within the whole organism

It was experimentally suggested that the information processing in the *Physarum* plasmodium is described to some extent in terms of a pattern of phase gradient vectors in a field of many nonlinear oscillators (Matsumoto,1986; Hu,1994). Some practical models were proposed standing upon the positional information theory as one-dimensionally coupled nonlinear oscillators system (e.g. Miyake,1993; Takahashi,1997), which is formed like as

$$\frac{d^2}{dt^2}X_i(t) - \varepsilon(1 - X_i(t)^2)\frac{d}{dt}X_i(t) + \omega^2 X_i(t) = C(X_{i+1}(t) + X_{i-1}(t) - 2X_i(t))$$

$$(i = 1,2,...,n) \qquad (1)$$

where the left and right term express van der Pol oscillator, which is the typical self-sustained nonlinear oscillator, and diffusion type coupling. $X_i(t)$ is the amplitude of i-th oscillator and n is the number of the oscillator in this system. ε is the strength of nonlinearity, ω is the intrinsic angular frequency and C is the strength of coupling.

In the model, an edge oscillator senses an environmental stimulus in the form of frequency modulation. For example, an attractive stimulus makes it faster and repulsive

slower. Then, the effect of modulation propagates to the whole system through diffusion type interaction with neighboring oscillators and finally a single polarity of the phase gradient vector is achieved.

The coupled nonlinear oscillators model mimics the experimental results in some simple situations. It provides important suggestion to the study of protist upon the aspect of mechanical system. Especially, the remarkable advantage of this model is to promise to achieve a single polarity, which yields each element (oscillator) the positional information. Therefore, it makes such a non-differential system possible to react as a whole. This remarkable advantage of the model can, by contrast, work at the sacrifice of the plasticity in a term of locomotion. In this system, a single polarity is achieved against any stimulus at edge part. In other words, the system is destined to converge into a single polarity because any environmental stimulus has to be interpreted only in the form of frequency modulation. So this system can react either positive or negative against any stimulus. Here a naïve question arises such that if the organism has only two choice of behavior, how can it be living under the complex situation of the real world? Or is there no chance to survive if it is surrounded by repellents?

In this paper, we, by contrast, experimentally observed an emergence of local deviation within the organism, which implied the existence of at least two polarities, and it drove global adaptable behavior as an individual. We then modified the previous model by introducing the idea of contraction map, in which both cohesive force and deviation from cohesive force involved, and successfully demonstrated our experimental results.

2. Method

2.1 Organism

We conducted two types of experiments (experiment Ⅰ and Ⅱ) using plasmodia of *Physarum polycephalum*. It was cultured on 1% agar gel sheet without lighting and feeding 10 hours in an incubator (25℃). We observed its behavior and thickness oscillation by taking video image and processing with a personal computer (IBM, Aptiva). When the organism was viewed through transmitted light, the brightness level varied due to the temporal thickness of the organism. The thickness oscillation was defined as the relative difference of such a brightness level for every 5sec. That is a common apparatus (e.g. Nakagaki,1990).

2.2 Experiment I and II

In experiment I and II, we focused on the chemo-tactical behavior of this animal. We made an anger gel sheet (1%) which contained Glucose, that is known as an attractant, in experiment I and KCl, a repellent, in experiment II. As shown in Fig2a and Fig2b, the distribution of those chemical substances was not uniformly distributed. It was distributed such that the projection in a particular section can form Gaussian-like concentration (0mM – about 100mM). The organism is put at the one side. Especially in experiment II, the *Physarum* plasmodium is surrounded by KCl and plastic wall of the Petri dish. According to nonlinear oscillators model, the single negative polarity can be formed inside the organism, which means that the organism never gets away from this side. Twenty individuals were tested for each experiment.
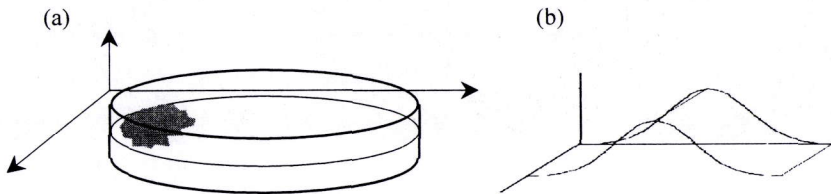
(a) (b)

Fig.2: (a)Apparatus of experiment I and II and (b)The schematic image the of distribution of the chemical substance.

3 Result of Experiments

3.1 Result of Experiment I

The result of experiment I is quite similar with the reaction predicted by the nonlinear oscillators model. The organism showed positive response as a single organism. The plasmodium developed concentric and sheet-like shape. It crawled toward the middle part where the concentration of Glucose was higher and finally reached another side of the Petri dish in preserving its front shape (Fig3). Fig.5a shows the transition of the period of the thickness oscillation at a front part. It was gradually decreasing until the front part reached the highest Glucose area. It took just about 250min after the experiment started, and it then slightly increased while it was keeping low value after that. This result supports the previous model because a positive migration of a whole organism emerged accompanying with the frequency modulation, getting faster in this case, at the front part.
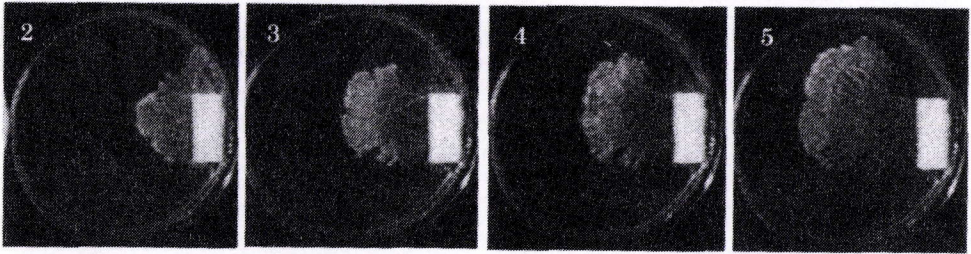
Fig.3: Developing of the *Physarum* in experiment I at each time indicated.
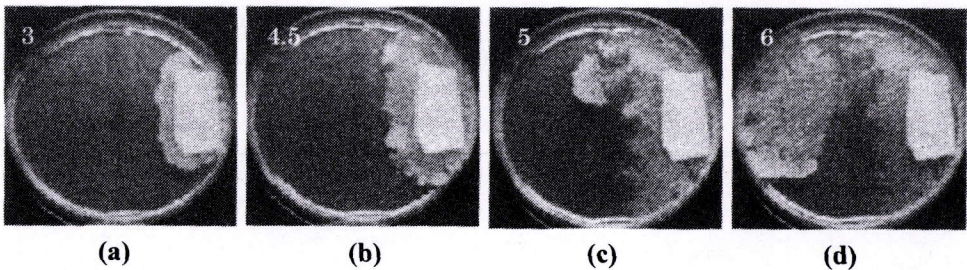

| (a) | (b) | (c) | (d) |

Fig.4: Developing of the *Physarum* in experiment II at (a) first, (b) second, (c) third and (d) forth stage. Photos were taken at time indicated.

3.2 Result of Experiment II

On the other hand, the result of experiment II is intriguing. We classified the result in this experiment into four stages according to the transition of the front shape for convenience. At the first stage, the plasmodium developed preserving its front shape like experiment I during crawling comparatively lower KCl area (Fig.4a). At the second stage, when the front part reached the higher KCl area, it split and divided rather small area and formed tiny strands (Fig.4b). In such strands, the amount of protoplasm was decreasing, which the brightness level of transmitted light suggested, and the organism as a whole seemed to stop developing forward. The period of the thickness oscillation got slower in this stage. The result thus mostly support previous model until this stage. However, after that, some tiny area suddenly developed and migrated rapidly forward over highest KCl area with forming small fan-like shape at the front and tiny strand at the end by which this advanced small area is connected with original part. (the third stage, Fig.4c). Finally, the forth stage, the organism as a whole successfully got over the high repellent area by sending the protoplasmic sol through the tiny strand of

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ectoplasmic gel layer that was formed at the third stage. So such a tiny strand worked like as the bridge over the repellent area (Fig.4d). The result at third and forth stage is inconsistent with the previous model at following two point.

1) The small part showed temporal positive reaction against repellent. Actually, when such a small part started to migrate forward, the period of thickness oscillation temporally got smaller (about 60sec) even compared with original level (about 80sec) as if it were stimulated by an attractant (Fig.5b). This sudden change of the period occurred only at the front part of tiny strand while the other parts of the organism preserved slower oscillation (about 90sec, Fig.5b) and it recovered the original level again soon. This type of temporal activation of the front area can be found at most of the parts which advanced against the repellent in experiment Ⅱ.

2) The emergence of local parts, while it was not separated from the original part, seemed to result from at least two polarities formed stably inside the organism. Actually, the branching part emerged at the third stage gradually isolated in keeping connecting with other parts. It continued developing, after that, by migration of protoplasm from original part and finally it has covered left side of the Petri dish.
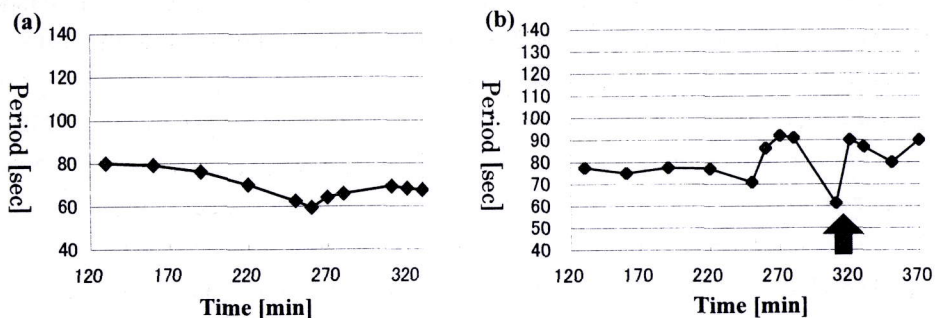

Fig.5: Transition of period of thickness oscillation at front part in (a) experiment I and (b) experiment Ⅱ in which strong modulation temporally emerged as if it resulted from an attractive stimulus (indicated by an arrow).

4 Our Model

4.1 Policy of Our Model

In experiment I, the period of an edge oscillation got faster and the organism migrated toward higher attractant area preserving its front shape. It suggests that a local

frequency modulation brought forth a global structure within the organism. On the other hand, according to the coupled nonlinear oscillators model, a global structure is achieved in the form of a spatio-temporal pattern of phase gradient by changing frequency of an edge oscillator. The model then provides important suggestion for the behavior of the animal on the aspect of mechanical system. However, the model is inconsistent with the result of experiment Ⅱ. As mentioned above, the model is destined to converge into a single polarity of a global structure. Such a property results from the nonlinear oscillators' nature of an entrainment under the diffusion type interaction. The previous model thus only introduces the mechanism of cohesive force that makes the non-differential organism maintain as a single individual avoiding from separation. The result of experiment Ⅱ shows, by contrast, that a particular part is differentiated as if it resulted from an attractive stimulus despite it was given repellent. Such a branching part elongates toward repellent in developing coherent relationship among other parts. This kind of controversial development suggests the existence of competition between cohesive and deviational forces hidden in local interactions. Langevin type equation in which deterministic (intrinsic) force is linearly coupled with stochastic (extrinsic) force cannot explain such a phenomenon because such an equation does not contain alternation of driving force between intrinsic and extrinsic forces. The alternation of driving force can result in dual interaction between coherence and deviation from coherent pattern. Considering the coherent development of the organism in experiment Ⅰ and the emergence of stable bi-polarity, in experiment Ⅱ, accompanying coherent development after that, the deviational force can be embedded in the cohesive interaction. We focus on this crucial duality and modify the previous model. The properties of frequency modulation against chemical stimuli are quite well observed in experiment Ⅰ, a first half of experiment Ⅱ and other experiments (e.g. Miyake,1994). We then modify just only the form of the interaction of the previous model, which means the right term of eq.1, because the cohesive force of is provided by its diffusion type interaction.

4.2 Our Model Introducing the idea of Contraction Map
4.2.1 Basic Assumption of Positional Information Theory

We propose the new model that implies the crucial duality of cohesive and deviational force mentioned above. We formalize such a duality as the competition within a local element (an oscillator) such that an identification of neighbors' states,

which implies the limited information, and perpetual choice of a transition rule for itself, which implies the anticipation of global semantics. In this context, perpetual anticipation drives the cohesive force and, at the same time, the incompleteness of anticipation drives the deviational force. The formalizing procedure is as follows.

For the sake of convenience, we take a system developing by a transition via the interaction among the nearest neighbors such as,

$$a_i^{t+\Delta t} = F(a_{i-1}^t, a_i^t, a_{i+1}^t) \qquad (i = 1, 2, ..., n) \tag{2}$$

The function F represents a particular transition rule. Developing along time is uniquely determined by this equation for each site, i. In the case of diffusion type interaction is expressed as

$$a_i^{t+\Delta t} = F(a_{i-1}^t, a_i^t, a_{i+1}^t) = C(a_{i+1}^t + a_{i-i}^t - 2a_i^t) \tag{3}$$

Remember that the hypothesis of positional information arises from the question, "how can each local site without global bird-eyes acquire the information carrying the whole space and interpret it?" This question is based upon the assumption that there is a succession from the term of genesis of positional information to the term of interpreting it. It leads that the following term can refer to the function or pragmatic semantics of the information carried at each site. As for the motion of slime mold, it corresponds to perpetual process involving continuous genesis of phase gradient and following differentiation with respect to function. The next question arises how each site can know the appearance of stable steady state of positional information. If all what each cell knows is restricted by finite information, each cell cannot identify the appearance of steady state because each site cannot detect infinite time series. This question is as same as the question, how each site can determine a particular correspondence between a finite set of states (i.e., $a_1^t, ..., a_{i-1}^t, a_{i+1}^t, ... a_n^t$) and a correspondence itself (i.e., a particular map, F in eq.2). Gunji et al. (1999) suggests that the correspondence between a set of states and a map (correspondence itself) cannot be uniquely determined in advance, and that such a correspondence is perpetually chosen in time development, per se. In general conditions, there is a situation in which perpetual choice of correspondence is stable, and it looks as if a system followed a particular unique correspondence (i.e., a particular map). However, if one takes the results of our experiments of slime molds into consideration in a term of a model of positional information, he has to construct a model in which perpetual choice of a function proceeds in time development.

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4.2.2 The Idea of Contraction Map

Gunji et al. (1997) proposed a system in which transition rule as a return map is perpetually determined by a finite set of states among nearest neighbors. The correspondence between a return map and the neighbor of a state (a_i^{t-1}, a_i^t) is defined in the form of self-similarity. It is expressed as a contraction map from a subset of Cartesian product to each neighbor of (a_i^{t-1}, a_i^t). If a state of the i-th local site at the t-th step is expressed by a_i^t, a temporal return map, f^t, is determined by a self-similar set such as

$$f^t = \bigcup c_j (f^t) \tag{4}$$

where c_j represents a contraction map assigned by $\boldsymbol{b}_j = (a_j^{t-1}, a_j^t)$ or (a_j^{t-2}, a_j^{t-1}) for all $j \in \{i-1, i+1\}$. As a result, transition is determined by

$$a_i^{t+1} = f^t (a_i^t) \tag{5}$$

Each contraction map as c_j is defined as shown in Fig.6. Whole subspace of Cartesian product of a set of state is self-similar with a subspace represented by each black square assigned by $\boldsymbol{b}_j = (a_j^{t-1}, a_j^t)$ or (a_j^{t-2}, a_j^{t-1}).
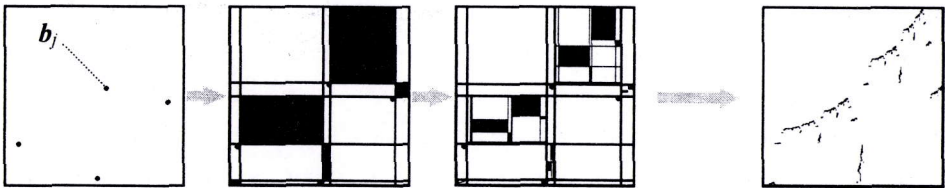

Fig.6: Procedure of producing contraction map ($j=2$)

4.2.3 Duality of Cohesive and Deviational Force

Because a return map perpetually changed by using a contraction map is destined to be a non-differentiable map, it contains both the force of stabilized coherent pattern and the force driving large deviation from coherence. As shown in Fig.7, the contraction map deduced from the neighbors works as a kind of rough estimation. On the other hand, even if an input, a_i^t, for this map would be close to a neighbor's point, an output, a_i^{t+1}, is not necessary to close to that of the neighbor's. It leads both coherent among neighboring sites and deviation from coherence. That is why time development is destined to be open-ended.
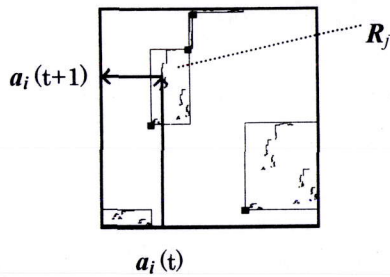
Fig.7: Schematic diagram showing dual force embedded in the contraction map. Any input-output is contained in a rectangular assigned by each element (denoted R_j for an element) . On the other hand deviational transition can occur because of non-differential map.

The competition of cohesive and deviational forces can reveal the duality of fast and slow information propagation. In our model, an interaction between nearest neighbors reveals slow information propagation on one hand, and a choice of a transition map by using a contraction map reveals fast information propagation on the other hand. Such a competition results in both robust coherence and the deviation from coherence. The significance of such a mechanism can be demonstrated by the collision of cars. Approaching drivers in two cars in opposite directions manages to prevent collision, while there are many kind of information to make a decision because drivers can anticipate in terms of various time spans. Both identification of the location of opposite car and anticipation of the motion of a car can entail to indefinite detection of car movements. The identification of location and anticipation of motion can be compared to slow and fast information propagation. That is why despite the intention of preventing the collision two cars can be collapsed (i.e., cohesive pattern appears).

We conducted the computer simulation introducing the idea of contraction map. It consists of nonlinear oscillators coupled with the interaction in the form of contraction map (contraction coupling model). We then compared our model and the previous diffusion coupling model under the same parameters. The number of oscillator is 15 for both simulations. The intrinsic angular frequency of an edge oscillator is changed gradually faster in S- I or slower in S- II, that is assumed as the reaction against the chemical stimuli of the organism which observed at experiment I and II .

5. Results of the Computer Simulation

We name here the previous model as diffusion coupling model and our new model as contraction coupling model for convenience.

5.1 The result of S- I

In this case, the intrinsic angular frequency of an edge oscillator is made gradually faster. Fig.8a shows the spatio-temporal phase pattern of each oscillator calculated by diffusion coupling model. The gradation of this figure represents phase of each oscillators. The phase gradient of position i at time t, $\Delta\theta_i^t$, is defined as

$$\Delta\theta_i^t = \theta_i^t - \theta_{i-1}^t \quad (i = 2,...,n) \tag{6}$$

where n is the number of oscillator. As Fig.8a shows, the influence of the edge oscillator's modulation gradually propagates from the edge to the whole system and the global pattern of the positive phase gradient achieved. The period of the edge oscillator, which is calculated by the phase transition in Fig.8a, decreases as the intrinsic angular frequency increases (Fig.9a). On the other hand, Fig.8b shows the typical phase pattern of our model. The positive phase gradient that strongly direct to the modulated oscillator emerges. But it has some discontinuous or negative phase gradient. So the synchronicity as a whole system is rather weak, compared with the previous model. The period of the edge oscillator is also disturbed but it decreases as a whole similarly to that of diffusion coupling model (Fig.9b). Compared with the result of experiment I , these two models can be assumed as a practical model regarding with the transition of the period of an edge oscillator and an emergence of the positive phase gradient that is assumed as the chemotaxis in the plasmodium.
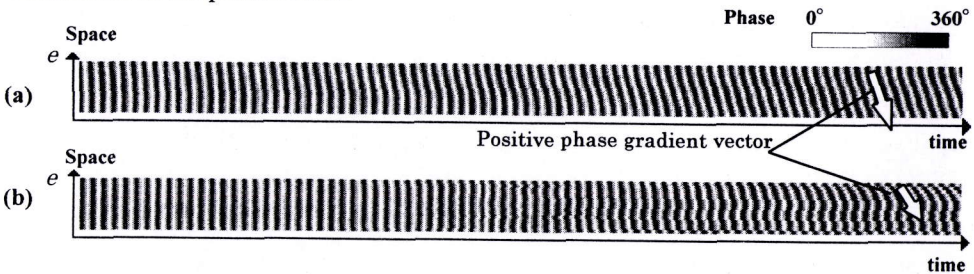

Fig.8: Spatio-temporal phase pattern of (a) diffusion coupling model and (b) our model in S- I . Oscillator at a terminal site, denoted by e, is modulated. White arrows represent the phase gradient vector, positive in this case, over position and time.
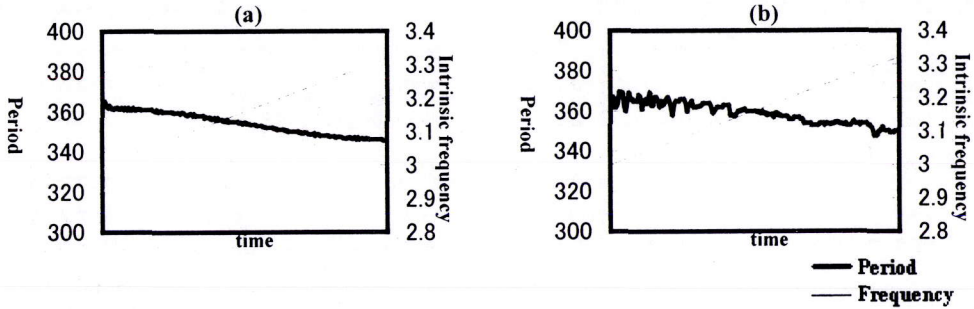
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Fig.9: Transition of period and intrinsic angular frequency of an edge oscillator of (a) diffusion coupling model and (b) our model in S- I .

5.2 The result of S- II

The intrinsic frequency of an edge oscillator is made gradually slower in this case. Fig.10a is the spatio-temporal phase pattern of diffusion coupling model. The local negative phase gradient is achieved and the influence of modulation is gradually propagated from the edge as like S- I of diffusion coupling model but it is not propagated to the whole. The period of the edge oscillator does not change unless the intrinsic frequency decreases (Fig.11a). On the other hand, as shown in Fig.10b, the phase pattern in our model unforeseenly changes which occurs anywhere in the system spontaneously and the positive and negative phase gradient strongly emerges at the same time. In addition, the period of the edge oscillator suddenly decreases for a moment just before the phase pattern changes (Fig.11b, denoted by an arrow). Regarding with the transition of the edge period and an emergence of two opposite phase gradients, the result of our model is quite mimic with the result of experiment II in contrast with diffusion coupling model.
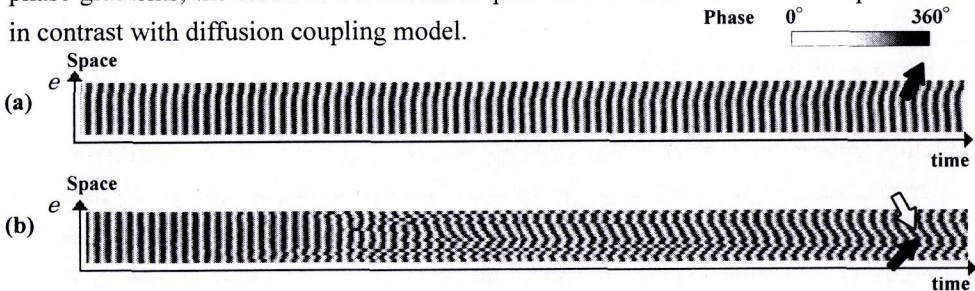

Fig.10: Spatio-temporal phase pattern of (a) diffusion coupling model and (b) our model in S- II . Oscillator at a terminal site, denoted by *e*, is modulated. Black and white arrow represents the negative and positive phase gradient vector.
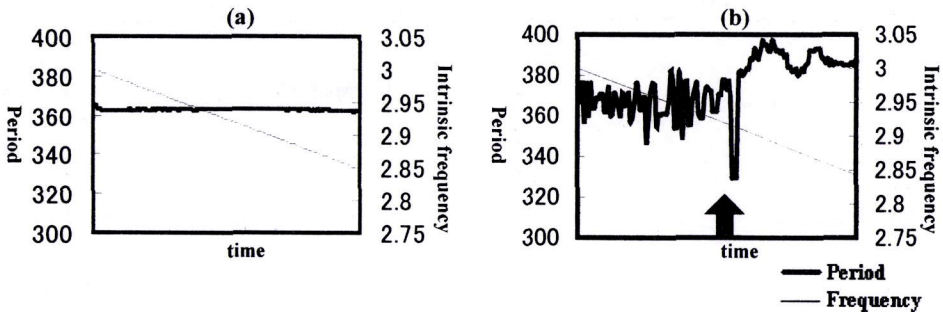
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Fig.11: Transition of period and intrinsic angular frequency of an edge oscillator of (a) diffusion coupling model and (b) our model in S- I .

6. Discussion & Conclusion

Our model of contraction coupling model can explain the results of experiment I and II. The appearance of bi-polarity accompanying sudden modulation of the period at terminal site shown in simulating result of our model in S- II may result from the property of a self-similar non-differentiable return map. In simulating result of our model in S- I , most initial conditions given attractant stimulus at the terminal site can generate positive polarity. It is considered that high intrinsic angular frequency as an attractant stimulus can compensate the effect of non-differentiable map. Because, as the results of diffusion coupling model that merely introduces cohesive force show, the cohesive force works more effective when the intrinsic angular frequency is higher, that is brought from the nature of a self-sustained nonlinear oscillator. Therefore it is considered that the effect of the rough estimation of cohesive force can conceal that of deviational force in our model.

We formalized an aspect of perpetual choice in this paper as a self-similar return map, which is temporally constructed at each site and each step by only its neighbors' state. No transition rule is given a priori unlike diffusion coupling model. Because the transition rule in our model is deduced by definitely limited information, it is not necessary to be corresponding with the transition rule at other sites and steps. Such a transition for a local site thus implies incompleteness in term of emulating the global semantics and identification in term of calculating its next state applying contraction map. As mentioned above, the simulating results of our model is quite mimic with the

experiments. Especially, in the simulating results of our model in S-II, the phase pattern unforeseenly disturbs at anywhere in the system spontaneously and the global bi-polar phase pattern emerges. It is remarked that such a property is formalized by perpetual choice of the (state-reaction)-correspondence. We thus suggest the possibility that such an incomplete identification of a local site drive the global coordinating featuring plasticity as a single system.

Coherent pattern is studied in broad research fields covering fish school and coherent firing of neurons, focusing on self-organizing process. The concept of such a self-organizing process is generally formalized by paying attention to intrinsic cohesive interactions. Deviation from cohesion is frequently regarded as extrinsic perturbation. By contrast we focus on duality of cohesive and deviational force resulting from fast and slow information propagation, and illustrate that it explains behaviors of slime mold involving singular reaction under singular conditions. If one does not neglect such a singular behaviors of a system, one has to construct a model by which both general behavior under general condition and peculiar behavior can be explained. As a result, we confirm the significance of perpetual choice of a map, per se. This study can be an initial step to the perspective of a dynamic system in the theory of morphogenesis and development.

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