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Coupled-oscillator model with a conservation law in rhythmic amoeboid movements of plasmodial slime mould

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Abstract

Experiments of cell fusion and partial separation of the plasmodium of true slime mold is demonstrated concentrating on the spatio-temporal phase patterns of rhythmic amoeboid movement. Motivated by these experimental results, we introduce a new model of coupled oscillator system which has one conserved quantity. Simulations will be shown using the model equation system, which reproduce the experimental results well.

Keywords: *Physarum polycephalum*, coupled oscillator system, amoeboid movement, cellular rhythm

PACS codes: 87.18.Hf, 87.17.Aa, 87.18.Ed

1 Introduction

The true slime mold "*Physarum polycephalum*" is the protozoan organism that eats bacterium and fungus. It has an amoeba-like stage of plasmodium in its life cycle. Now we consider behaviors of the plasmodium, which is a huge unicellular organism with many nuclei. In fact, the possible size is of tens centimeter according to circumstances. If it is cut into two parts by a knife, each behaves as a smaller plasmodium, independent from another. On the other hand, when two plasmodia come into contact, they fuse and coalesce to form a single larger plasmodium. As above, the plasmodium has unique characters on the control of system size and its individuality. Although being highly flexible in the system size, the plasmodium can behave in some smart ways: avoiding various dangerous conditions, approaching to nutrients and humidity, solving a maze [1]-[3], and designing an effective network of communication inside a cell [4]. These behaviors are based on amoeboid movement, which are formed by interacting homogeneous elements of

protoplasm because there is neither central nervous system nor such an special organ. In other words, the plasmodium is a typical example of decentralized autonomous system. Thus, mechanism of pattern formation is a main problem to be solved in order to understand how the smart behaviors are self-organized. To find a solution for this problem, mathematical modeling is inevitable. We propose here a mathematical model describing some basic behaviors of the plasmodium.

The plasmodium consists of the "sponge part" including distributed actin-myosin fiber and the "tube part" made up of the paries of the actin-myosin fiber. As illustrated in Fig.1, the sponge part consists of complicated network of canals, in which the protoplasmic sol (painted in gray) flows in from and out to the tube part. There are also some of canals opening to extracellular space at the cell surface (painted in white), which don't connect with the intracellular canals filled with the sol.

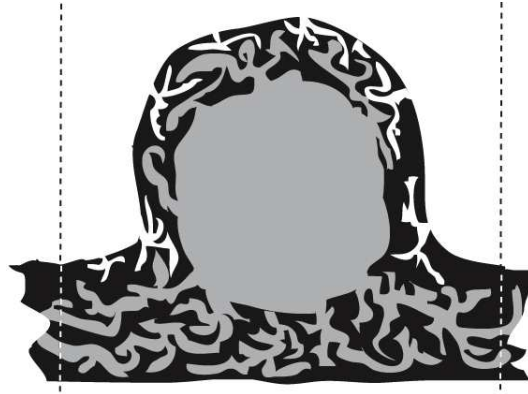


Figure 1: Schematic description of the cross section of the plasmodium, in which the gel part is painted in black and the gray part expresses the protoplasmic sol.

The actin-myosin fiber exhibits rhythmic contraction everywhere within the organism with the period of two minutes. This rhythmic contraction gives pressure to the protoplasmic sol, which leads to flow of the sol. The sol flows into the tube and runs through it, and exudes. The flow of sol in the tube is not unifold, but the flow direction is switched back and forth. Then we can observe periodic changes in the flow direction, known as protoplasmic shuttle streaming. Accompanying the shuttle streaming, periodic changes in cell thickness also takes place. The plasmodium shows spatio-temporal patterns of the thickness oscillation and the shuttle streaming in the tube. In this report, we focus on these patterns.

In order to describe the dynamic behavior of the plasmodium, we unify two different conventional lines of modeling framework: coupled oscillator system of cellular rhythms [5]-[9] and viscoelastic properties of protoplasm [10]-[11]. Our main idea is to require a constraint of a conserved quantity to coupled oscillator system. Roughly speaking, this constraint results from conservation law for total protoplasmic mass. It is shown that the model equations well reproduces the rhythmic contraction and shuttle streaming. In this paper we will present biological backgrounds, mathematical formulation and the simulation results of the model.

2 Experimental

In this section, we review the experimental results of the thickness oscillations in various conditions, and point out some characters to be noticed. Similar type of experiments have been reported [12], but our analysis here is more in detail, leading to findings of pattern characters.

2.1 Propagating circular plasmodium

Fig.2 shows the snapshots of the top view of the circular plasmodium propagating on the flat agar surface, which was measured by the conventional method [13].

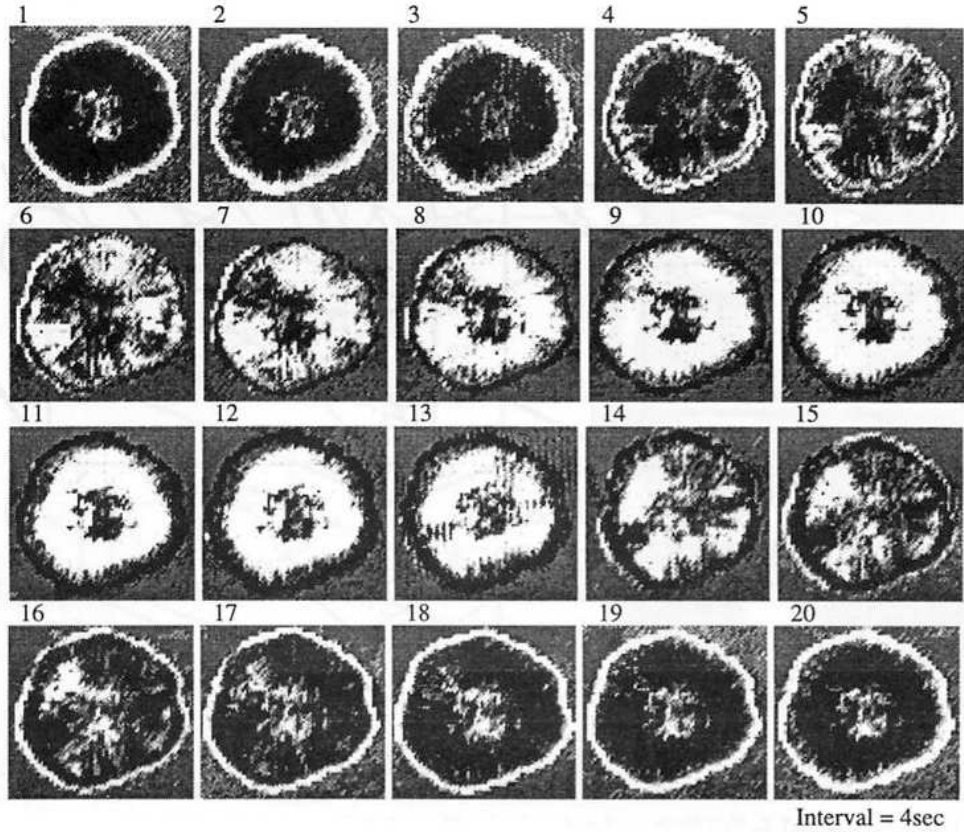


Figure 2: Top view snapshots of thickness oscillation in the circular plasmodium. The panels are numbered sequentially in time. The images are taken by using transmitted infrared rays, where the white part is thin and the black one is thick. The diameter of the circular plasmodium is about 4 cm.

Anti-phase oscillation is observed between the peripheral part and its rear of plasmodium. The inner part is thick when the periphery is thin, and vice versa, which is a direct consequence of the conservation of sol. Hereafter we will call this anti-phase oscillation "peripheral phase inversion". Peripheral phase inversion is very commonly observed

regardless of the size of the plasmodium when it propagates freely. However, it should be noted that peripheral phase inversion does not appear if the plasmodium is touching the wall, typically when it fully extends in the petri dish. By our interpretation, the fact that the periphery is softer than the central part is essential, and the details will be discussed in [14].

2.2 Cell fusion

Two plasmodia were initially placed in the rectangular vessel with 1cm width and sufficient length, and they extended and oscillated independently (Fig.3(a)), until they touched each other. In the early stage of coalescence, cell fusion was incomplete and two plasmodia were connected weakly and oscillated in anti-phase. In addition, peripheral phase inversion was taking place, therefore entire phase distribution was, for instance, thin at the left edge, thick in the left middle, thin in the right middle and thick in the right edge (Fig.3(b)). After a while from they contacted, the anti-phase pattern between two plasmodia disappeared, or exactly speaking, two plasmodia became one plasmodium and only peripheral phase inversion remained (Fig.3(c)). Fig.4 presents the

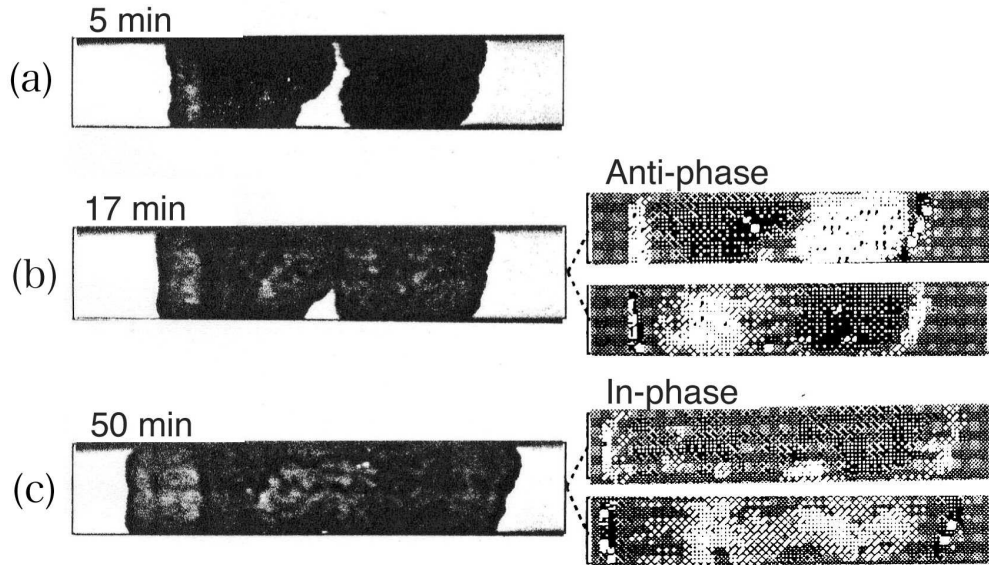


Figure 3: Real thickness patterns during the early stage of plasmodial coalescence. (a) At first two plasmodia expand and oscillate at their own. (b) They oscillate with anti-phase for several minutes since they meet. (c) Finally, they fuse completely and oscillate together.

spatio-temporal pattern of the thickness of plasmodium. Disappearance of the anti-phase oscillation between the two plasmodia (or the two parts of the coalesced plasmodia) and transition to the in-phase oscillation is clearly observed around 30 minutes after the contact.

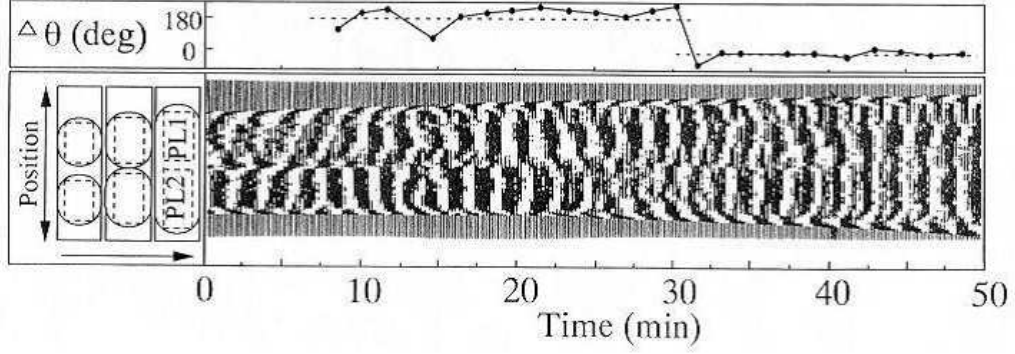


Figure 4: Spatio-temporal pattern of the thickness in the experiment of cell fusion, illustrated by the left schema in the lower panel. This schema consists of three sub-schemata corresponding to three time stages: before the contact of two plasmodia, soon after the contact and the final stage of coalescence. The final size of the plasmodium was about 1cm x 4 cm. The lower panel shows the thickness pattern of time and one dimensional space which is measured along the longitudinal line of the rectangular vessel. The line graph in the upper panel shows the time sequence of the phase difference between the two parts indicated by two boxes of dashed line (PL1 and PL2).

2.3 Partial separation

The results of the previous experiment suggest that the *weaker* connection between the two part of the plasmodium induces an anti-phase oscillation. In order to examine this idea, we divided the circular plasmodium into two halves by surgical operation leaving only a narrow connection as described in Fig.5(a). Then they behave stably like the pattern in Fig.5(b), more specifically they have anti-phase between main parts of left side and right side, and between middle and edge in each half, so whole pattern of thickness is described as thin-thick-thin-thick or thick-thin-thick-thin along a horizontal direction.

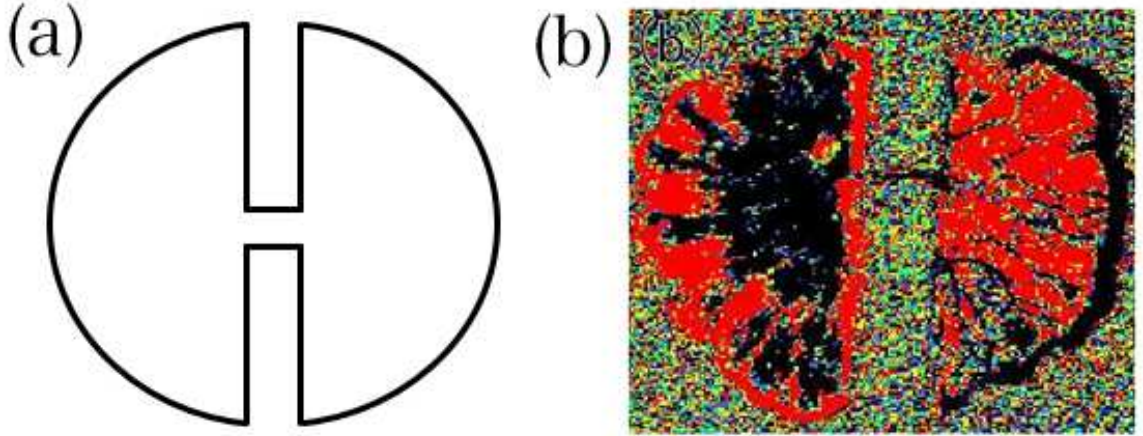


Figure 5: The experiment of partially separated plasmodium. The schematic illustration in the panel (a) shows a top view of the plasmodial shape just after the partial separation. A circular plasmodium was prepared at first and belt-shaped pieces of the plasmodium was cut and removed along a diameter except a narrow connection, then we obtained a bottlenecked shape. Before and after the partial separation, we observed thickness patterns. The panel (b) shows the typical pattern of anti-phase between inner parts of two halves and between the middle and the edge in each half. Thickness variations is visualized by the color chart: red and black indicate thin and thick, respectively. The diameter of the circular plasmodium was about 5 cm.

3 Model Equations

As mentioned in the introduction, the plasmodium does not have any central organ which governs its whole behavior, and its structure is almost uniform in the coarsened scale. If the plasmodium is cut into little pieces, each one soon starts oscillating with the same period with the one before cutting. These facts strongly suggest that the plasmodium is an aggregation of self-sustaining oscillators, thus it is quite plausible that our model is written in the form of a coupled oscillator system. In this section, we will derive a one dimensional model first as a model of the experiment of cell fusion, then extend it to a two dimensional one in order to simulate the experiment of partial separation.

Let us start from expressing the local oscillator (mechano-chemical oscillator) by the equation system

$$\frac{du}{dt} = f(u, v) \quad \text{and} \quad \frac{dv}{dt} = g(u, v), \quad (1)$$

where u is an amount of sol (or equivalently an amount of the vacancy of the sponge which is connecting not to the outside but to the tubes), and v is possibly a vector valued variable including all the other variables than u which consist of the oscillator, for example, concentrations of some chemicals. In this article, we will not discuss about the

details of the local oscillator itself (See, for example, [15]-[16].) and rather concentrate on the spatio-temporal patterns of oscillations when the form of $f(u, v)$ and $g(u, v)$ is appropriately fixed. Actually, their concrete form will be given in the simple form to execute simulations in the next section.

In order to construct a one dimensional model of the cell fusion, the x -axis is taken to be parallel to the longer edge of the vessel, and we handle the integrated values in the section $x = \text{const}$ (this section will be called " x -section" hereafter). The easiest way to make the local oscillator system (1) a one dimensional coupled oscillator system is just adding a diffusion term in each equation, as follows:

$$\frac{\partial u}{\partial t} = f(u, v) + \frac{\partial}{\partial x} \left(D_u \frac{\partial u}{\partial x} \right), \quad (2)$$

$$\frac{\partial v}{\partial t} = g(u, v) + \frac{\partial}{\partial x} \left(D_v \frac{\partial v}{\partial x} \right), \quad (3)$$

where $u = u(x, t)$ and $v = v(x, t)$. The diffusion term of (2) express the transportation of sol through the sponge in the x -direction, and the one of (3) does typically a diffusion of some chemical agent. However, such a simple extension does not give a good description of the behavior of the plasmodium in this case. Actually, the solutions of the equations (2)-(3) always converge to the uniform oscillation by the phase diffusion, which contradicts to the experimental results. It is mainly because the total mass of sol is conserved in the time scale considered here, which is not taken into account in the equations (2)-(3). Therefore, we have to design model equations expressing the *coupled oscillator system with one conserved quantity* instead of the conventional coupled oscillator system (2)-(3).

In order to achieve such a construction in the way which reflects the structure of actual plasmodium, we assume that the n tubes run along the x -axis which is surrounded by the sponge structure. Then another variable $w = w(x, t)$ is introduced, which is a small deviation from the total section W of the n tubes in natural (pressure free) state. We regard a tube as an elastic one whose radius in natural state is denoted by R . In this model, it is assumed that the n tubes are all identical, thus $W = n\pi R^2$ holds. When a tube is expanded to the size $R + r$ by the inner pressure p , the tension along the wall of the tube is written by $\xi \cdot 2\pi r$ where ξ is an elastic constant, thus we have

$$p = \frac{2\pi\xi}{R}r \quad (4)$$

by considering a balance of the forces perpendicular to the wall of the tube. On the other hand, $w = 2n\pi Rr$ holds for $r \ll R$ provided that all tubes equally expand, thus $p = \frac{\xi}{nR^2}w$ holds. By setting $k = \frac{\xi}{R^2}$, we have

$$np = kw. \quad (5)$$

Let us assume that the flow along the tube is approximately Poiseuille flow at each moment. Then the total flux Q across the x -section is expressed by the formula

$$Q = -n \frac{\pi R^4}{8\eta} \frac{\partial p}{\partial x}, \quad (6)$$

where η is a viscosity of the fluid filling the tube and $\frac{\partial p}{\partial x}$ is a pressure gradient along the longitudinal axis of the tube. Corresponding to the intermediate state in the experiment of cell fusion, we have to express how well the tubular structure is developed. There are several parameters relating to it, say R , n and ξ , where the former two are geometric parameters and the latter is associated with the strength of the bind of actin-myosin fibers in the wall of tubes. We here assume that the geometric parameters are constant and only ξ is changeable, for simplicity. Under such assumption the flux Q is written in the form

$$Q = -\frac{\partial}{\partial x}(D_w w), \quad (7)$$

where $D_w = k \frac{\pi R^4}{8\eta} = \xi \frac{\pi R^2}{8\eta}$. Note that the elastic constant ξ might have a spatial dependence, thus k and D_w do. The formula (7) permits us to express the transportation through the tubes in the x -direction by a kind of diffusion form.

The exchange of sol between the vacancy of sponge and the tubes must be taken into account in our model. Actin-myosin fibers distributed in the sponge supply the power of contraction, which pushes sol out of the vacancy into the tube. We can consider the minus of $f(u, v)$ gives the transportation rate of sol caused by the contraction of the sponge. On the other hand, the elastic recovering force of tubes will push sol from the tubes into the vacancy of the sponge. Here we introduce the stiffness β of the sponge, by which the transportation of sol from one tube caused by the tubular pressure is written in the form $\frac{p}{\beta}$. This expression implies that the softer the sponge is (the smaller β is), the easier sol is pushed out from the tube into the vacancy of the sponge. The transportation rate from the n tubes is given by $n \frac{p}{\beta} = \frac{k}{\beta} w$ from the equation (5). Note that $\frac{k}{\beta}$ is a ratio between the stiffness of the tube and the sponge.

Considering the above two types of transportation, the outflow rate from the tube within the x -section is expressed by $f(u, v) + \frac{k}{\beta} w$. Therefore the equation for the variable w is obtained as follows:

$$\frac{\partial w}{\partial t} = -f(u, v) - \frac{k}{\beta} w + \frac{\partial^2}{\partial x^2}(D_w w). \quad (8)$$

by combining the transportation rates of sol along the x -axis and within the x -section. Note that the sponge is regarded as an active element and the tubes as a passive element in our model.

Corresponding to the form of the exchange rate of sol in the x -section, the equation of u is to be modified as follows:

$$\frac{\partial u}{\partial t} = f(u, v) + \frac{k}{\beta} w + \frac{\partial}{\partial x} \left(D_u \frac{\partial u}{\partial x} \right). \quad (9)$$

Although it might be better to adopt a nonlinear diffusion in this equation since the sponge is a porous medium, we select a linear diffusion for simplicity in this model. (In

the other type of our models, the nonlinear diffusion is employed. [14]) We leave the equation (3) for v as it is here.

Our one dimensional model is finally constructed by coupling the u -equation (9), the v -equation (3) and the w -equation (8). Note that the parameters D_u , D_v , D_w , k and β might depend on the space variable x . The relation $D_u, D_v \ll D_w$ must hold since the transportation through the tube is much faster than the one through the sponge and the one by the diffusion of chemicals. By taking sums of both side of the equations (9) and (8), it is easily seen that the sum $u + w$ is a conserved quantity as long as the no flux boundary condition is adopted. This corresponds to the fact that the total mass of sol is constant in the time scale handled in this model.

We extend the one dimensional model to the two dimensional one by considering that the tubular structures are randomly oriented and distribute in sufficiently fine scale. By replacing the differential operator $\frac{\partial}{\partial x}$ in the one dimensional model by $\nabla = \mathbf{i}\frac{\partial}{\partial x} + \mathbf{j}\frac{\partial}{\partial y}$, we have the following two dimensional model;

$$\frac{\partial u}{\partial t} = f(u, v) + \frac{k}{\beta}w + \nabla \cdot (D_u \nabla u), \quad (10)$$

$$\frac{\partial v}{\partial t} = g(u, v) + \nabla \cdot (D_v \nabla v), \quad (11)$$

$$\frac{\partial w}{\partial t} = -f(u, v) - \frac{k}{\beta}w + \nabla^2(D_w w). \quad (12)$$

Similarly to the one dimensional case, the totality of $u + w$ is conserved under the no flux boundary condition.

4 Simulations

We will demonstrate several simulations using the one and the two dimensional models derived in the previous section. In order to carry out the simulations, the concrete form of the functions $f(u, v)$ and $g(u, v)$ must be fixed. We adopt the " λ - ω system" as a simple local oscillator, which is given by the formula:

$$f(u, v) = -\omega v + P(1 - u^2 - v^2), \quad (13)$$

$$g(u, v) = \omega u + P(1 - u^2 - v^2). \quad (14)$$

These functions give a limit cycle solution running along the unit circle $u^2 + v^2 = 1$ in the phase plane with an angular velocity ω . The parameter P expresses an extent how strongly the limit cycle solution is caught to the unit circle against fluctuations.

No flux condition is imposed at the boundary in all the simulations in this section. A simple explicit finite difference scheme is employed for solving the model equations numerically.

4.1 One dimensional simulations

In the experiment of cell fusion, we observed the two types of phase inversion. One is a peripheral phase inversion which always takes place, and another is a phase inversion

across the part of weaker connection which appears in the transitive state of fusion process. In the following, simulations are carried out according to each stage of the experiment together with the transition.

Peripheral phase inversion

As mentioned in the section 2, peripheral phase inversion is commonly seen when the plasmodium propagates freely, and we consider that it is caused by the existence of softer front. Following to this idea, we set the parameters β and D_u both of which relate to the stiffness of the sponge smaller in the periphery than the other part, meanwhile all the other parameters are set to be constant. The spatio-temporal pattern of the simulated solution is illustrated in Fig.6. As you can see, this simulation successfully reproduce the peripheral phase inversion, which is corresponding to the phase patterns observed in the final state of cell fusion (Fig.3(c) and the latter half of Fig.4). Note that the region where the simulation is performed is fixed and not extended, thus exactly speaking our simulation does not describe the *propagating* plasmodium. Nevertheless peripheral phase inversion clearly arises in the simulation, which strongly supports our idea concerning to its cause.

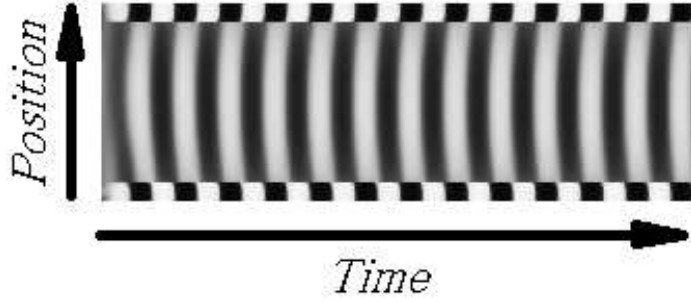


Figure 6: Spatio-temporal pattern of the variable u expressed in gray scale, where u is larger in the darker part and smaller in the lighter. Figs.7-9 are drawn in the same way with this figure. The value of u is almost equivalent to the thickness of the plasmodium. Parameters are set as follows: System size = 1.0, $\omega = 1.0$, $P = 1.0$, $k = 1.0$, $D_v = 1.0 \times 10^{-2}$ and $D_w = 8.0$. The parameters β and D_u have dependency on the space variable x such as

$$\beta(x) = \begin{cases} 2.5 \times 10^{-1} & \text{for } 0.1 \leq x \leq 0.9 \\ 2.5 \times 10^{-3} & \text{otherwise} \end{cases}, \quad D_u(x) = \begin{cases} 4.0 \times 10^{-2} & \text{for } 0.1 \leq x \leq 0.9 \\ 5.0 \times 10^{-4} & \text{otherwise} \end{cases}.$$

Phase inversion at the center

Next we try to simulate the phase inversion across the part of weaker connection by setting the parameters D_u , D_v , D_w and k small at the center. This parameter setting describe the situation in which the connection between the two plasmodia is not well established. Fig.7 clearly shows the desired result, where the phases are almost synchronized within each domain. Such an anti-phase oscillation is a good compromise between the phase diffusion and the conservation law under the existence of the weaker connection point.

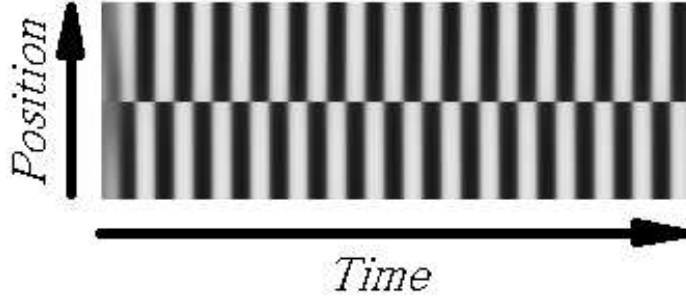


Figure 7: Parameters are set as follows: System size = 1.0, $\omega = 1.0$, $P = 1.0$, $k = 1.0$, $\beta = 2.5 \times 10^{-1}$, $D_u = 4.0 \times 10^{-2}$, $D_v = 1.0 \times 10^{-2}$ and $D_w = 8.0$. The parameters D_u , D_v , D_w and k have smaller values at the central point of the domain as follows: $D_u = 4.0 \times 10^{-4}$, $D_v = 1.0 \times 10^{-4}$, $D_w = 8.0 \times 10^{-1}$ and $k = 0.1$.

Coexistence of the two types of phase inversions

The above two simulations are combined to simulate a phase pattern including the two types of phase inversions observed in the earlier stage of cell fusion (Fig.3(b) and the former half of Fig.4). The result is shown in Fig.8, in which both types of phase inversion are well reproduced.

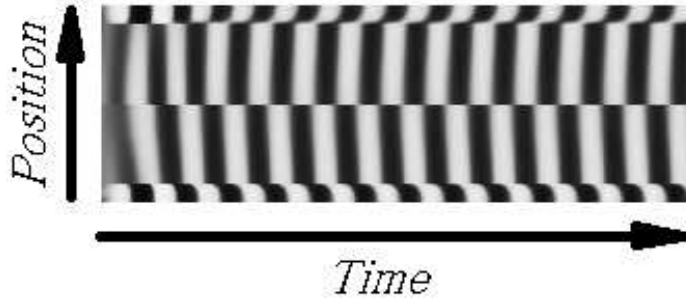


Figure 8: All the parameters are set to be the same with the ones in Fig.6 except for the central point where the parameters are taken following to the ones in Fig.7.

Transition of the phase pattern during cell fusion

Finally the whole procedure of the experiment of cell fusion is simulated by making the connection stronger at the center which was initially set to be weak. The parameters were changed so slowly that it takes more than 3 periods of the oscillation for the complete recovery of connection. Fig.9 illustrates the transition from the phase pattern in which both type of phase inversions arise simultaneously to the one in which only a peripheral phase inversion appears.

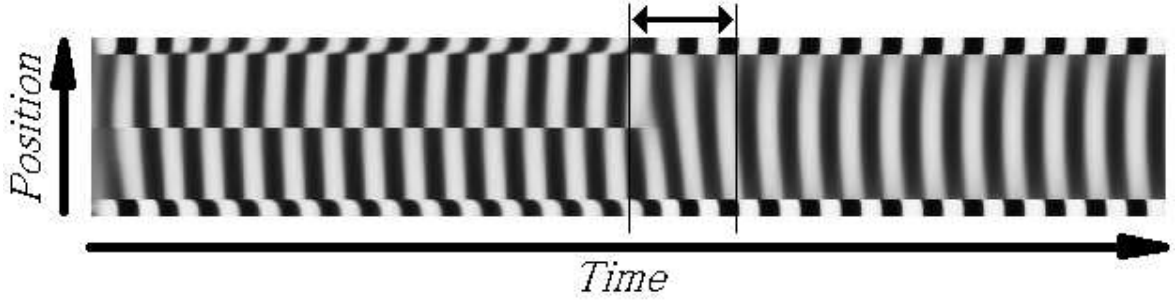


Figure 9: Initially all the parameters are set to be the same with the ones in Fig.8, then the values of D_u , D_v , D_w and k are linearly changed to the ones in Fig.6 in the time interval indicated above.

4.2 Two dimensional simulations

Two dimensional simulations are concerned with both of the experiments; propagating circular plasmodium and partial separation. In the following simulations the shape of the region filled with plasmodium is given by setting all the diffusion constants zero outside the region, which actually results in the no flux condition at the boundary. Also no oscillators are given outside the region, consequently the values of variables u , v and w are kept to be zero there as is initially set.

Peripheral phase inversion

In this simulation the shape of the region filled with the plasmodium is set to be a disk, and the parameters are taken to imply a softer periphery. Fig.10 exhibits a time sequence of simulated phase patterns. Peripheral phase inversion is clearly observed, which induces strong shuttle streaming between the center and periphery of the plasmodium. Consequently we have a flow of sol along radial directions in this experimental conformation.

Again we point out the fact that the simulation does not describe any propagation of the plasmodium but just assume the existence of softer periphery which, we think, is essential for the appearance of peripheral phase inversion.

Simulation of the experiment of partial separation

The final simulation is almost the same with the previous one but for the shape of the region which is designed corresponding to the experiment of partial separation (Fig.5). The parameters are set to be constant except for the vicinity of circumference where softer periphery is assumed. And the weaker connection of the two domains is geometrically realized by the bottlenecked shape of the region. Phase inversion across the path is successfully simulated together with a peripheral phase inversion as is shown in Fig.11. This result confirms the idea that the weaker connection between two domains of the plasmodium induces the phase inversion.

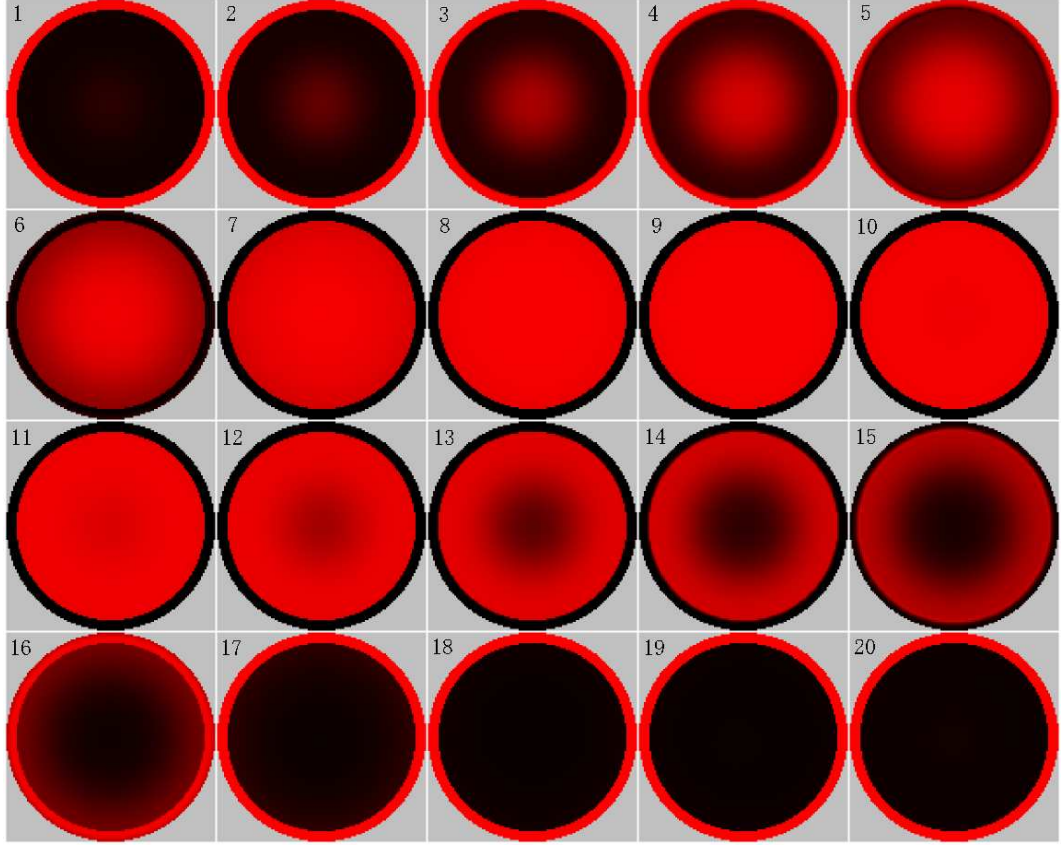


Figure 10: Snapshots of the variable u expressed by gray scale, where u is larger in the darker part and smaller in the lighter. Fig.11 is drawn in the same way. The parameters are taken as follows: System size = 1.0×1.0 , $\omega = 5.0$, $P = 4.0$, $D_v = 9.0 \times 10^{-2}$, $D_w = 6.0$. The parameters β and D_u have dependency on the position (x, y) such as

$$\beta(r) = \begin{cases} 1.0 \times 10^{-1} & \text{for } 0.0 \leq r \leq 0.4 \\ 1.0 \times 10^{-2} & \text{otherwise} \end{cases}, \quad D_u(r) = \begin{cases} 1.0 \times 10^{-1} & \text{for } 0.0 \leq r \leq 0.4 \\ 1.0 \times 10^{-3} & \text{otherwise} \end{cases},$$

where r is a distance from the center.

5 Summary

In this article, we first demonstrated the spatio-temporal oscillation patterns in several experiments, where the phase inversion were typically observed. Then we introduced one and two dimensional models written in the reaction diffusion equation system. The essence of these models is that they express coupled oscillator systems having one conserved quantity, which makes the models behave in a similar way to the actual plasmodium. The conservation is derived by considering the exchange of sol between the sponge and the tubes. If no diffusion in the x -direction is permitted, our model just gives the oscillation at each point exchanging sol between the vacancy of sponge and the tubes locally. However, our model includes the diffusion and especially D_w is much larger than D_u and D_v meaning the tube is acting as a highway for the transportation of sol, while the sponge is hard to move through. This character of transportation induces variety

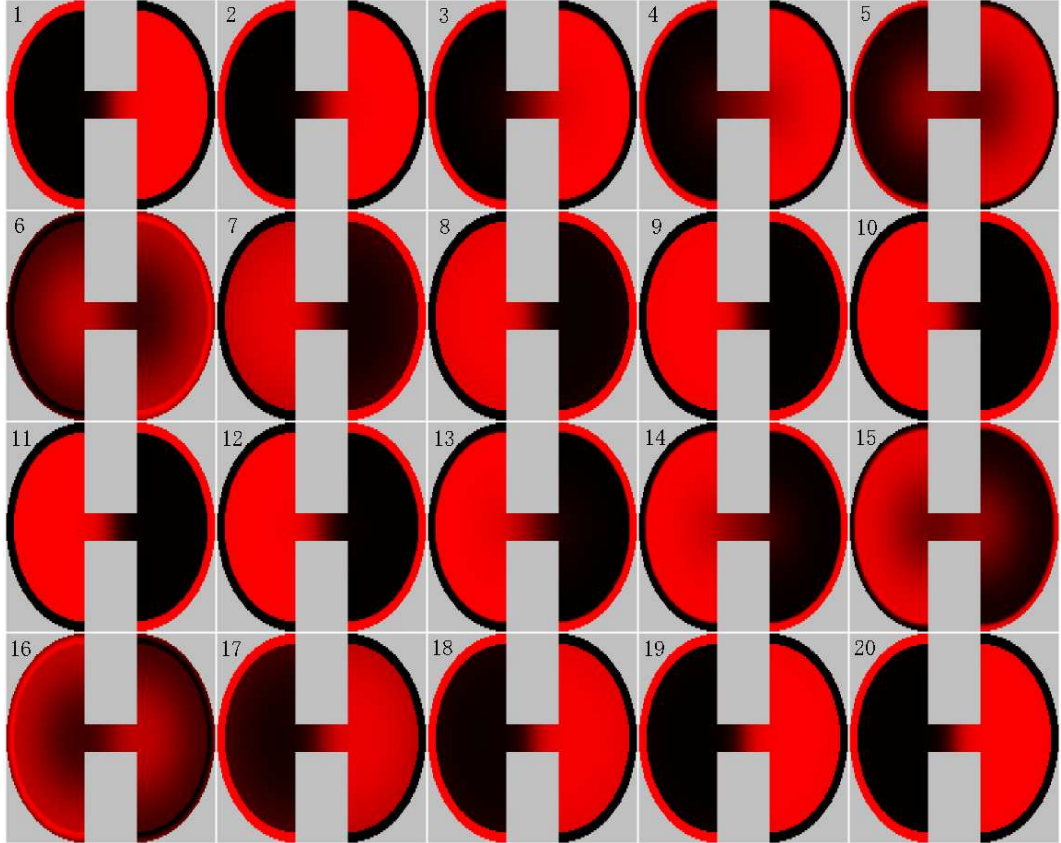


Figure 11: The region is obtained by cutting the disk so as to leave the narrow path with the length $1/3$ and the width $2/15$ connecting the left and right region. All the parameters are set to be the same with the ones in Fig.10 except for the shape of the region.

of spatio-temporal phase patterns. It was shown that our models are applicable to the various situations of the plasmodium by choosing the parameters appropriately. From the series of simulations of the models, we can claim that the stiffness of gel plays an important role to determine the phase patterns of oscillation and the flow induced by the phase distribution.

As already mentioned, our models are written in the fixed region and neither propagation nor migration of the plasmodium was not handled. Models including such factors will be discussed elsewhere [14]. Also no directional change of tubular structure is taken into account in our models. However, we already observed that the adaptive change of tubes takes place so that the fibers are strengthened in the direction of the flux of sol [17]. Models including such directional reconstruction of the tubular structure is left to the future study.

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