Pattern formation of reaction-diffusion system having self-determined flow in the amoeboid organism of *Physarum* plasmodium

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The amoeboid organism, the plasmodium of *Physarum polycephalum*, behaves on the basis of spatio-temporal pattern formation by local contraction-oscillators. This biological system can be regarded as a reaction-diffusion system which has spatial interaction by active flow of protoplasmic sol in the cell. Paying attention to the physiological evidence that the flow is determined by contraction pattern in the plasmodium, a reaction-diffusion system having self-determined flow arises. Such a coupling of reaction-diffusion-advection is a characteristic of the biological system, and is expected to relate with control mechanism of amoeboid behaviours. Hence, we have studied effects of the self-determined flow on pattern formation of simple reaction-diffusion systems. By weakly nonlinear analysis near a trivial solution, the envelope dynamics follows the complex Ginzburg-Landau type equation just after bifurcation occurs at finite wave number. The flow term affects the nonlinear term of the equation through the critical wave number squared. Contrary to this, wave number isn’t explicitly effective with lack of flow or constant flow. Thus, spatial size of pattern is especially important for regulating pattern formation in the plasmodium. On the other hand, the flow term is negligible in the vicinity of bifurcation at infinitely small wave number, and therefore the pattern formation by simple reaction-diffusion will also hold. A physiological role of pattern formation as above is discussed.

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I. INTRODUCTION

The plasmodium of *Physarum polycephalum* is a large amoeboid cell, showing contraction-relaxation cycles everywhere within an organism. These local contraction motivates intracellular transport of endoplasmic sol [1]. Therefore, the plasmodium can crawl when the local flow is appropriately arranged all through the organism. Some types of spatio-temporal pattern of the contraction have been observed after stimulation, and discussed in relation to development of its amoeboid behaviours [2,3,4,5]. Mechanism of the pattern formation is closely related to a mechanism of cellular behaviours in the plasmodium. Then we expect that a certain origin of biological fineness for controlling a system is in characteristic mechanism of the biological pattern formation. This paper is concerned with such character in a biological system.

Let us consider theoretical framework of the pattern formation in the plasmodium. Chemical oscillation is a clock of the rhythmic contraction. Possible candidates for the chemicals are, for example, Ca$^{2+}$ and/or ATP [6,7]. Since the contraction apparatus is located at outer layer of the plasmodium, called ectoplasm [8,9,10], it is proper to focus on chemical oscillations and diffusion in the ectoplasm. As above, the plasmodial contraction system can be regarded as diffusively coupled oscillators or a reaction-diffusion system in the ectoplasm. Actually, some experimental results can be explained using this framework [1,2].

But another effect of spatial interaction must be considered. That is the protoplasmic streaming in inner part of the plasmodium, called endoplasm, because the contraction pattern is modified by inhibition of the streaming [11,12]. Miyake *et al.* [13] proposed a model of the information processing system with two levels of subsystems corresponding to the endoplasmic oscillators with long-range interaction and the ectoplasmic ones with short-range interaction. From more physical viewpoints, some models based on hydrodynamics and chemical kinetics, have been presented [14,15,16]. However, we still have an issue that the streaming can be sometimes negligible, as mentioned in the former paragraph. To solve the pretence of this discrepancy, it is inevitable to study pattern formation including the streaming effect. For that purpose, we firstly suppose a physical model of reaction-diffusion-advection equations.

The oscillating chemicals are exchanged between endo- and ectoplasm, and flow out/in via the streaming [17,18]. The streaming is motivated by the gradient of contraction force [19]. Hence, the contraction pattern determines the streaming. That is to say, the protoplasmic streaming is a factor of the contraction pattern, and also inversely motivated by the pattern. Then the reaction-diffusion system having self-determined flow arises. The self-determined flow is just a characteristic of the biological system in the plasmodium. We analyze pattern formation of such a system by weakly nonlinear analysis, particularly noticing effects of the advection term on simple reaction-diffusion systems. The weakly nonlinear analysis is based on singular perturbation expansion, and therefore has an advantage that
model equations are free from details. Because, no matter how complex or uncertain the functions are in our model equations, expanded lower order terms are merely considered in the analysis. This advantage is valuable especially in analysis of biological model, which often includes uncertain assumptions in detail.

As the results of the analysis, a possible solution of the pretence discrepancy described earlier is found, and furthermore, one apparent character of the plasmodial pattern formation is shown. A possible role of the plasmodial pattern formation is discussed at a physiological point of view.

II. BASIC EQUATIONS

The plasmodium of Physarum has a cytoplasmic cortex (ectoplasmic gel) filled with endoplasmic sol. The ectoplasm makes periodic contraction and relaxation, and it causes intracellular streaming of the endoplasm. A sheet of cytoplasm becomes thick when the endoplasm flowing into it. Metabolic substances regulate contractile cycles, diffuse in the cytoplasm, and are transferred by the endoplasmic flow. Standing on these points, we present a dynamics of rhythmic







Where \( h \) denotes the thickness of the endoplasmic sol, and \( \bar{v} \) is the averaged velocity of the endoplasmic flow. \( u \) is \( N \) metabolic species in gel and sol, \((u_{\text{gel}}, u_{\text{sol}}) = (u^1, \ldots, u^N)\). \( F_{\text{gel}} \) and \( F_{\text{sol}} \) represent reaction kinetics among metabolic elements and exchanges of them between the ectoplasm and endoplasm. \( D_{\text{gel}} \) and \( D_{\text{sol}} \) are diagonal matrices of diffusion constants of metabolic elements. We note that Eq. (1) becomes the closed system if the dynamics of \( \bar{v} \), the equation of motion of endoplasmic flow, are given. Let us consider the small Reynolds number flow in a contractile vein and assume the intracellular pressure is determined by the concentration of the chemicals: 

\[
\bar{v} = -q(h)\nabla P(u).
\]

This means the stationary flow approximation that deformation of the ectoplasm is very slow compared with variation of the endoplasmic flow. It is hence not considered that the ectoplasmic cortex has viscoelastic features.

In Eq. (1), the sol-gel conversion is ignored, and thus the mass conservation of endoplasmic sol is satisfied. This implies the limitation of the model, such as the cell motility, the formation and reconnection of a network of protoplasmic strands. In the following, we assume that the thickness of the endoplasmic sol is almost constant all over the plasmodium, and that the diffusion constants of the metabolic elements are homogeneous in the plasmodium. The intracellular pressure \( P \) is expanded around the homogeneous static state \( u = u_s \) as

\[
P(u) = P(u_s) + \sum_j (u^j - u^j_s) \frac{\partial P}{\partial u^j}(u_s) + \text{higher order terms}.
\]

Hereafter, we ignore the higher order terms which have no effects on results deduced by the weakly nonlinear analysis. Under these assumptions, we rewrite Eq. (1) in the form of the reaction-diffusion-advection equations:

\[
\frac{\partial u}{\partial t} + M \nabla u \cdot \nabla u = F(u; \mu) + D\nabla^2 u,
\]

where \( F \) is reaction kinetics, \( M \) represents a tensor of advection coefficients induced by endoplasmic flow, and \( D \) is a diagonal matrix of diffusion constants.

We assume that the system (2) has a trivial homogeneous steady solution \( u = 0 \), and it is stable when the bifucation parameter is \( \mu < \mu_c \). Over the bifurcation point, \( \mu > \mu_c \), the trivial solution is unstable and local reaction kinetics becomes oscillatory. Reaction kinetics \( F(u; \mu) \) can be expanded around the trivial solution as

\[
F(u; \mu) = Lu + N_2 uu + N_3 uuu + \cdots,
\]

\[
L = \left( \frac{\partial F^i}{\partial u^j} \right), \quad N_2 = \left( \frac{\partial^2 F^i}{\partial u^j \partial u^k} \right), \quad N_3 = \left( \frac{\partial^3 F^i}{\partial u^j \partial u^k \partial u^l} \right) \ldots \text{ at } u = 0.
\]

Linearizing the system (2) near the homogeneous steady state, we obtain equations for spatial Fourier components,
\[ \dot{W}(t; k) = (L - k^2D)W(t; k), \quad u(t, x) = \int W(t; k)e^{ikx}dk. \]

The stability of \( W = 0 \) is given by the eigenvalue problem for the eigenvalue \( \lambda \) and eigenvector \( U \),

\[ (L - k^2D)U = \lambda U. \quad (3) \]

We obtain the eigenvalue \( \lambda = (U^*, (L - k^2D)U)/(U^*, U) \) from Eq. \( (3) \). On the bifurcation point, \( \text{Re} \lambda = 0 \) and \( \partial (\text{Re} \lambda)/\partial k = 0 \) are satisfied at some \( k = k_c \) for the maximal eigenvalue(s). In the vicinity of the bifurcation point \((\mu, k) = (\mu_c, k_c)\), the eigenvalue is

\[ \lambda = \lambda_c + \frac{\partial \lambda}{\partial \mu} \bigg|_{c} (\mu - \mu_c) + \frac{\partial \lambda}{\partial k} \bigg|_{c} (k - k_c) + \frac{1}{2!} \frac{\partial^2 \lambda}{\partial k^2} \bigg|_{c} (k - k_c)^2 + \cdots, \quad (4) \]

where the subscript \( c \) denotes the bifurcation point, and expansion coefficients are given as

\[ \lambda_c = \pm i\omega_c, \quad \frac{\partial \lambda}{\partial k} \bigg|_{c} = \pm i\epsilon g, \quad \omega_c, \epsilon g \geq 0. \]

Hence the bifurcation problem has four generic cases: (i) \( k_c = 0 \) and \( \omega_c = 0 \); (ii) \( k_c = 0 \) and \( \omega_c \neq 0 \) (Hopf bifurcation); (iii) \( k_c \neq 0 \) and \( \omega_c = 0 \) (Turing bifurcation); (iv) \( k_c \neq 0 \) and \( \omega_c \neq 0 \) (travelling-wave type). According to the weakly nonlinear analysis of Eq. \( (2) \), the advection term is expected to modulate its bifurcation behaviour in the case of (iii) and (iv).

### III. ENVELOPE EQUATION

Let us consider the envelope equation just after the bifurcation of travelling-wave type occurs, on a basis of weakly nonlinear analysis \[21\]. We denote the bifurcation parameter by \((\mu - \mu_c) \sim \epsilon^2\), and suppose that \( u^j \sim O(\epsilon) \) \((j = 1, \ldots, N)\) in the vicinity of the bifurcation point. In the following analysis, the envelope equation is derived for one spatial dimension system of Eq. \( (2) \) with the single travelling wave. We introduce perturbation expansions and multiple scales,

\[ u \sim cu_1 + \epsilon^2 u_2 + \epsilon^3 u_3 + \cdots, \quad L \sim L_0 + \epsilon^2 L_2 + \cdots, \]
\[ X = x - ct, \quad \xi = \epsilon(x - cg t), \quad \tau = \epsilon^2 t, \quad (5) \]

where \( c_g = \omega_c/k_c \) is the phase velocity and \( c_g \) is the group velocity. Substitution of Eq. \( (5) \) into \( (2) \) yields perturbation equations for each order in \( \epsilon \):

\[ O(\epsilon^m) \quad \left( L_0 + D \frac{\partial^2}{\partial X^2} + c_g \frac{\partial}{\partial X} \right) u_m = b_m, \quad m = 1, 2, 3, \ldots \quad (6) \]

where \( b_m \) denotes the inhomogeneous term of the \( m \)-th order equation.

For the first order equation in Eq. \( (5) \), the inhomogeneous term is \( b_1 = 0 \). Then we have a solution

\[ u_1 = W(\xi, \tau)e^{ik_c X}U + c.c., \]

where c.c. means complex conjugate. \( U \) is an eigenvector of an eigenvalue \( \lambda = -i\omega_c \) for the eigenvalue problem \( (3) \) on the bifurcation point.

For the second order equation, that is \( m = 2 \) in Eq. \( (3) \), we expand the solution and inhomogeneous term by the phase \( \phi = k_c x - \omega_c t, \)

\[ u_2 = \sum_l u_2^{(l)} e^{il\phi}, \quad b_2 = \sum_l b_2^{(l)} e^{il\phi}. \]

Then the solvability conditions for \( u_2 \) are

\[ (U^*, b_2^{(1)}) = (\bar{U}^*, b_2^{(-1)}) = 0, \quad (7) \]
\[ b_2^{(1)} = -\frac{\partial W}{\partial \xi}(c_g + 2ik_c D)U, \quad b_2^{(-1)} = \bar{b}_2^{(+1)}. \]
These conditions are obviously satisfied since

\[ c_g = \frac{\partial \lambda}{\partial k} \bigg|_e = -2ik_c \frac{(U^*, DU)}{(U^*, U)}. \]

Thus we must advance our calculation to the third order to obtain the envelope equation.

For the third order equation in \( \epsilon \), we expand \( u_3 \) and \( b_3 \) as

\[ u_3 = \sum_l u_3^{(l)} e^{il \phi}, \quad b_3 = \sum_l b_3^{(l)} e^{il \phi}, \]

then the solvability conditions for \( u_3 \),

\[ (U^*, b_3^{(+1)}) = (\bar{U}^*, b_3^{(-1)}) = 0, \quad \frac{\partial^{(2)}}{\partial \xi^2} W, \]

\[ b_3^{(+1)} = \frac{\partial W}{\partial \tau} U - c_g \frac{\partial u_2^{(1)}}{\partial \xi} + 2k_c^2 \bar{W} M (u_2^{(2)} \bar{U} + \bar{U} u_2^{(2)}) - WL_2 U \]

\[ -WN_2 (u_2^{(0)} U + u_2^{(0)} U) - \bar{W} N_2 (u_2^{(2)} U + \bar{U} u_2^{(2)}) \]

\[ -|W|^2 WN_3 (UUU + \bar{U} U + \bar{U} U) - 2ik_c \frac{\partial u_3^{(1)}}{\partial \xi} - \frac{\partial^2 W}{\partial \xi^2} DU, \]

\[ b_3^{(-1)} = \bar{b}_3^{(+1)}. \]

Thus we obtain the complex Ginzburg-Landau (CGL) equation:

\[ \frac{\partial W}{\partial t} = c_1 W - c_2 |W|^2 W + c_3 \frac{\partial^2 W}{\partial \xi^2}, \quad c_j = (U^*, V_j)/(U^*, U), \]

\[ V_1 = L_2 U, \]

\[ V_2 = -2k_c^2 M \left\{ \bar{U}, (L_0^{(2,2)})^{-1} (N_2^{(+1)} U) \right\} + N_2 \left\{ U, (L_0)^{-1} (N_2^{(+1)} \{ U, \bar{U} \}) \right\} \]

\[ + N_2 \left\{ U, (L_0^{(2,2)})^{-1} (N_2^{(+1)} U) \right\} - N_3 \left( UUU + \bar{U} U + \bar{U} U \right), \]

\[ V_3 = -(c_g + 2ik_c D)(L_0^{(1,1)})^{-1} (c_g + 2ik_c D) U, \]

where \( L_{0}^{(1,m)} = L_0 - ik_c^2 D + im\omega_c, N_2^{(+1)} = N_2 + ik_c^2 M, \) and \( \{ X, Y \} = XY + YX \). By means of the dispersion relation \( \frac{c_2}{2} \), \( c_1 = (\partial \lambda/\partial \mu)_e \), and \( c_3 = (1/2) (\partial^2 \lambda/\partial k^2)_e \), are generically complex constants.

The CGL equation \( 1 \) describes the small amplitude dynamics of the system near the bifurcation point, that is, \( W \) slowly and slightly modulates travelling wave with the wave number \( k_c \) and frequency \( \omega_c \). The coefficient of the nonlinear term, \( c_2 \), depends on the advection term in Eq. \( 1 \). Since the advection term has the form of the gradient of metabolic species, \( c_2 \) is including the term of \( k_c^2 \). It is known that \( c_2 \) determines the amplitude of plane wave solutions and the nonlinear dispersion relation. The signature of \( \text{Re}(c_2) \) decides the type of bifurcation at \( \text{Re}(c_1) = 0 \): a supercritical bifurcation occurs for \( \text{Re}(c_2) > 0 \), while subcritical one for \( \text{Re}(c_2) < 0 \). In the latter case, we will need higher order terms as \( |W|^4 W \) to the CGL equation.

The CGL equation has various type of solutions with relation to the coefficients \( 2 \), but we do not mention each of them. Because we have derived the CGL equation from Eq. \( 1 \) which has no concrete form of reaction and advection terms, it is impossible to give the coefficients of the CGL equation explicitly. In the next section, we discuss the advection effect implied by the CGL equation \( 1 \) and compare our results with ones of reaction-diffusion models without the endoplasmic flow.

We comment on the envelope equation of spatial two dimensions. Add a scaling of \( y \)-axis, \( \eta = \epsilon y \), to Eq. \( 1 \) and continue the similar calculation above, we obtain the CGL-type equation without rotational symmetry (see appendix).

**IV. CONCLUSIONS**

We have presented a reaction-diffusion-advection model of the *Physarum* plasmodium which makes rhythmic contraction. The local contraction determines intracellular transport of endoplasmic sol, and this motivates the crawling behaviour of the plasmodium. By means of the weakly nonlinear analysis of the model, we obtain the following results: (1) an advection effect arises to the slow dynamics when the travelling-wave type bifurcation occurs; (2)
the envelope equation has the form of the CGL equation; (3) the advection terms affect the nonlinear term of the CGL equation through $k_c^2$. In weakly nonlinear region of a reaction-diffusion-advection model, (2) implies that we can observe similar dynamical behaviour to conventional reaction-diffusion systems without flow. Thus it is expected that some experimental results of the rhythmic contraction in the plasmodium have been illustrated by such simple reaction-diffusion systems. The last result (3), however, shows possibility that the nonlinear effect near the bifurcation point stems from not only reaction kinetics but also the self-determined flow. In the remainder of this section, we attempt to discuss the effect of the self-determined flow on physiological behaviour.

In general, advection can play an effective role for pattern formation, as the flow of matter often causes instabilities of hydrodynamical systems [23,24]. For example, Rovinsky and Menzinger [25] have shown that a differential flow of is dominant across the bifurcation point.

In weakly nonlinear region of the self-determined advection causes the strong dependency of pattern formation on the critical wave number, $k_c$. The affected nonlinear term of the CGL equation is known to be closely related with bifurcation and size of amplitude. Because phase difference of the metabolic oscillation between neighbours tends to become larger as $k_c$ is larger, $k_c$ is regarded as an indicator that an oscillator is in step with its neighbouring oscillators. This point of view implies that phase difference in local plays an important role for pattern formation such as amoeboid behaviours in the Physarum plasmodium.

Real patterns observed by measuring thickness oscillation in the plasmodium show that the wave number is always about one or two in free locomotion under culture conditions. However, larger wave number more than ten appears transiently in relation to changes in behaviours induced by an appropriate stimulation. This phenomenon may relate to the $k_c$-dependency. Further analysis of the $k_c$-effect would be given if the model equations are concretely specified.

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APPENDIX: DERIVATION OF THE ENVELOPE EQUATION IN TWO DIMENSIONS

Before studying the envelope equation in two dimensions, we comment on counter propagating waves. For the bifurcation of travelling-wave type, counter propagating waves are possible in one spatial dimension, although we derived the envelope equation (CGL equation) for the single travelling wave in section II. The envelope dynamics of the counter propagating waves is the coupled equations of envelopes $W_+$ and $W_-$ of a linearized solution

$$W_+ e^{i(k_x x + \omega_t t)} U_+ + W_- e^{i(k_x x - \omega_t t)} U_- + c.c.$$

where $(L_0 - k^2 D) U_\pm = \pm i\omega_c U_\pm$. The time evolution of $W_\pm$ is governed by the dynamics like CGL equation, but is modulated by the interaction terms $|W_\pm|^2 W_\mp$.

In the case of two spatial dimensions, multimode travelling waves satisfying $|k_j| = k_c$, are neutrally stable on the bifurcation point. Although we can obtain the multimode envelope equations, it is not clear that the dynamics of them has structural stability. Such a problem has a relation to pattern selection, and we need more precise analysis on the bifurcation with symmetry. Hereafter we discuss the envelope equation for a single travelling wave of Eq. (2) in two spatial dimensions. We assume that a set of mode near the single plane wave travelling along $x$-axis, $\exp[i(k_c x - \omega_c t)]$, is dominant across the bifurcation point.

Introducing perturbation expansions and multiple scales,

$$u \sim \epsilon u_1 + \epsilon^2 u_2 + \epsilon^3 u_3 + \cdots, \quad L \sim L_0 + \epsilon^2 L_2 + \cdots,$$

$$X = x - c_g t, \quad \xi = \epsilon(x - c_g t), \quad \eta = \epsilon y, \quad \tau = \epsilon^2 t,$$

(A1)
and substituting Eq. (A1) into Eq. (2), we obtain perturbation equations,

\[ O(e^m) \left( L_0 + D \frac{\partial^2}{\partial X^2} + c_p \frac{\partial}{\partial X} \right) u_m = b_m, \quad m = 1, 2, 3, \ldots \]  

(A2)

The inhomogeneous term of the first order equation is vanishing, \( b_1 = 0 \). For the second and third order equations, the inhomogeneous terms are

\[
\begin{align*}
    b_2 &= -c_g \frac{\partial u_1}{\partial \xi} + M \left( \frac{\partial u_1}{\partial \tau} \frac{\partial u_1}{\partial X} - N_2 u_1 u_1 - 2D \frac{\partial^2 u_1}{\partial X \partial \xi} \right), \\
    b_3 &= \frac{\partial u_1}{\partial \tau} - c_g \frac{\partial u_2}{\partial \xi} + M \left( \frac{\partial u_2}{\partial \tau} \frac{\partial u_1}{\partial X} + \frac{\partial u_1}{\partial \tau} \frac{\partial u_2}{\partial X} + \frac{\partial u_1}{\partial \tau} \frac{\partial u_1}{\partial X} + \frac{\partial u_1}{\partial \tau} \frac{\partial u_1}{\partial X} \right) \\
     &\quad - L_2 u_1 - N_2 (u_2 u_1 + u_1 u_2) - N_3 u_1 u_1 u_1 - D \left( 2 \frac{\partial^2 u_2}{\partial X \partial \xi} + \frac{\partial^2 u_1}{\partial \xi^2} + \frac{\partial^2 u_1}{\partial \eta^2} \right).
\end{align*}
\]

We write a solution of the first order equations with the slowly varying envelope \( W(\xi, \eta, \tau) \),

\[ u_1 = W e^{ik_c X} U + c.c. \]

Since the solvability conditions for the second order equation are satisfied by the definition of \( c_g \), we advance our calculation to the third order:

\[
(U^*, b_3^{(+1)}) = (U^*, b_3^{(-1)}) = 0, \quad b_3^{(+1)} = \frac{\partial W}{\partial \tau} U - c_g \frac{\partial u_2^{(1)}}{\partial \xi} + 2k_c^2 \tilde{W} M (u_2^{(2)} U + \tilde{U} u_2^{(2)}) - WL_2 U \\
- WN_2 (u_2^{(0)} U + U u_2^{(0)}) - \tilde{W} N_2 (u_2^{(2)} U + \tilde{U} u_2^{(2)}) \\
- |W|^2 WN_3 (UU + \tilde{U} \tilde{U} + \tilde{U} U) - 2ik_c D \frac{\partial u_1^{(1)}}{\partial \xi} - \left( \frac{\partial^2 W}{\partial \xi^2} + \frac{\partial^2 W}{\partial \eta^2} \right) DU,
\]

\[ b_3^{(-1)} = b_3^{(+1)}. \]

From the solvability conditions (A3), we get the envelope dynamics,

\[
\frac{\partial W}{\partial \tau} = c_1 W - c_2 |W|^2 W + (c_3 + c_4) \frac{\partial^2 W}{\partial \xi^2} + c_4 \frac{\partial^2 W}{\partial \eta^2}, \quad (A4)
\]

where coefficients \( c_1, c_2, c_3 \) are the same in Eq. (A3) and \( c_4 = -ic_g / 2k_c. \) The coefficient \( c_4 \) implies dispersion waves which are observed in the nonlinear Schrödinger equation.

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