

General Chemotactic Model of Oscillators

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We propose a general chemotactic model describing a system of interacting elements. Each element in this model exhibits internal dynamics, and there exists a nonlinear coupling between elements that depends on their internal states. From this model, we derive a simpler model describing the phases and positions of the chemotactic elements by means of center-manifold and phase-reduction methods. We find that, despite its simplicity, the model obtained through this reduction exhibits a rich variety of patterns.

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We consider a system of nonequilibrium elements whose internal degrees of freedom interact with their collective macroscopic or mesoscopic order [1–7]. In this study, the elements are regarded as simplified local units that capture the essence of the behavior of the actual local units existing in a wide variety of physical systems, such as an internal network of genes and proteins in a bacterium [8], reactive droplets in a reaction-diffusion system [9], neurons in a network [10,11], or some of the “microscopic components” that form a collective system [12–16]. In such systems, these elements exhibit not only spatiotemporal patterns but also collective functions. For instance, the cohort migration of mammalian cells forms tissue patterns [17,18], and the *Proteus mirabilis* invades human urothelial cells by swarming [19]. As another type of example, it has been found that collections of simple robots employing swarm intelligence are capable of performing complex tasks [20]. These very diverse systems share the important property that the spatiotemporal patterns exhibited by the assemblies of elements are directly linked to their functions. In this Letter, we derive a model to study this class of phenomena in a unified manner, ignoring system-specific details. For this purpose, rather than constructing an *ad-hoc* toy model, we propose a broad class of models from which we derive a simple model by means of center-manifold and phase-reduction methods [21–23].

A self-sustained (or limit-cycle) oscillator provides perhaps the simplest model that captures the essential features of such dynamical elements. Employing elements of this kind, we assume that each element in isolation is characterized by a supercritical Hopf bifurcation above which it exhibits oscillatory dynamics. We include a simple interaction among the elements, which, in the physical systems of interest, is mediated by a chemical that diffuses in space. We assume that the elements exhibit chemotaxis [24], i.e., that the motion of each element is driven by the local gradient of the chemical density, and the elements produce and consume this chemical in amounts that depend on its internal state. As perhaps the simplest model of such a system, we propose the following:

$$\dot{X}_i(t) = f(X_i) + kg(S(r_i, t)), \quad (1)$$

$$m\ddot{r}_i(t) = -\gamma\dot{r}_i - \sigma(X_i)\nabla S|_{r=r_i}, \quad (2)$$

$$\tau\partial_t S(\mathbf{r}, t) = -S + d\nabla^2 S + \sum_i h(X_i)\delta(\mathbf{r} - \mathbf{r}_i). \quad (3)$$

(This model can be further generalized, as discussed elsewhere). Here, the n -dimensional real vector X_i and the D -dimensional real vector r_i represent the internal state and the position of the i th element, respectively. The dynamics of X_i are driven by the intrinsic function f and influenced by the external chemical concentration, S . This influence is represented by the function g and the strength k . Without loss of generality, we assume that the S -independent part of $g(S)$ vanishes, i.e., $g(0) = \mathbf{0}$, because this part can be included in $f(X)$. The dynamics of r_i are driven by the spatial gradient of S in a chemotaxis manner, as represented by the term $\sigma\nabla S$, where σ is a $D \times D$ matrix. The constants m and γ represent the mass of each element and the kinematic viscosity coefficient, respectively. The time evolution of the chemical concentration, S , is determined by three types of processes, corresponding to the three terms in Eq. (3): spatially uniform decay, diffusion in space, and local consumption and production carried out by the elements. The constant d is the diffusion coefficient. We assume that the decay rate is equal to unity, without loss of generality. Because we consider the case in which each element produces and consumes the chemical in amounts that depend on its internal state, we reasonably assume that the X -independent part of $h(X)$ vanishes, i.e., $h(0) = 0$. To make the subsequent analysis as clear as possible, we include a time constant τ characterizing the dynamics of S and retain some constants that could be set to unity through suitable scaling transformations. Because we consider the case in which each element possesses some internal dynamical state, we assume that $f(X)$ depends on a parameter μ and exhibits a simple dynamical state consisting of limit-cycle oscillation, which appears through a supercritical Hopf bifurca-

tion at $\mu = +0$. We define \mathbf{X} such that $\mathbf{X} = 0$ corresponds to the steady state. When k is set to zero, \mathbf{X} can be approximated by $\mathbf{X}(t) = A(t)e^{i\omega t}\mathbf{U} + \text{c.c.}$, where A is the complex amplitude of the Hopf oscillation and ω is the Hopf frequency. c.c. is complex conjugate. \mathbf{U} is a right eigenvector of the Jacobian of \mathbf{f} at $\mu = 0$, and it satisfies the relation $L_0\mathbf{U} = i\omega\mathbf{U}$, where L_0 is the Jacobian. The slow temporal evolution of \mathbf{X} can be described by the equation $\dot{A} = e^{-i\omega t}\mathbf{U}^* \cdot (\dot{\mathbf{X}} - L_0\mathbf{X})$, where \mathbf{U}^* is a left eigenvector of L_0 , and it satisfies the relation $\mathbf{U}^*L_0 = i\omega\mathbf{U}^*$. Then, substituting $f(\mathbf{X})$ for $\dot{\mathbf{X}}$, and carrying out a center-manifold reduction, we derive the Stuart-Landau equation [21]:

$$\dot{A} = \mu\lambda_+A - \beta|A|^2A. \quad (4)$$

Here, λ_+ and β are complex constants of order μ^0 ($= 1$), with $\text{Re}\lambda_+$ and $\text{Re}\beta$ positive. Because Eq. (4) should be balanced, A and \dot{A} are order $\mu^{1/2}$ and $\mu^{3/2}$, respectively. Next, assume that \mathbf{f} is changed slightly to $\mathbf{f} + k\mathbf{g}$, with $k \neq 0$. It is then clear that the corresponding reduced equation must also be modified with the additive term

$$e^{-i\omega t}\mathbf{U}^* \cdot k\mathbf{g}. \quad (5)$$

Then, in order to balance this term with the remaining terms in Eq. (4), $k\mathbf{g}$ must be order $\mu^{3/2}$. Because Eq. (3) is linear, it is easily solved, and from it we obtain S as a functional of \mathbf{X} ,

$$S = \int \frac{dq}{(2\pi)^D} \int_0^t \frac{dt'}{\tau} \sum_i h(\mathbf{X}_i(t')) e^{iq \cdot [\mathbf{r}_i(t') - \mathbf{r}] + v(q)(t' - t)}, \quad (6)$$

where $v(q) \equiv \frac{1+dq^2}{2\pi^D}$. Here, we have omitted a term proportional to $\int \frac{dq}{(2\pi)^D} e^{-iq \cdot \mathbf{r}} e^{-v(q)t}$, because this term vanishes for the asymptotic state (i.e., for $t \rightarrow \infty$). Noting that $\mathbf{X} = O(\mu^{1/2})$ and $h(0) = 0$, we can use the linear approximation $h(\mathbf{X}) = \mathbf{h}_0 \cdot \mathbf{X}$, where $\mathbf{h}_0 \equiv \frac{dh}{d\mathbf{X}}|_{\mathbf{X}=0}$. Thus, we find that S is order $\mu^{1/2}$. It is thus seen that the forcing term $-\sigma\nabla S$ in Eq. (2) is extremely small in the limit $\mu \rightarrow +0$. Thus, $\dot{\mathbf{r}}_i$ is also extremely small; i.e., \mathbf{r}_i varies extremely slowly in the limit $\mu \rightarrow +0$. This slowness and the fact that $\dot{A}_i = O(\mu^{3/2})$ imply that $\mathbf{r}_i(t')$ and $A_i(t')$ in the time integral of Eq. (6) vary on time scales that are much longer than that characterizing the decay of $e^{v(q)(t' - t)}$. Thus, we can safely replace $\mathbf{r}_i(t')$ and $A_i(t')$ with $\mathbf{r}_i(t)$ and $A_i(t)$. After the integration over t' , we obtain

$$S = (\mathbf{h}_0 \cdot \mathbf{U}) e^{i\omega t} M(\mathbf{r}) + \text{c.c.}, \quad (7)$$

where $M(\mathbf{r}) \equiv \sum_i A_i \int \frac{dq}{(2\pi)^D} \frac{e^{iq \cdot (\mathbf{r}_i - \mathbf{r})}}{i\omega\tau + 1 + dq^2}$. Because S is small and $\mathbf{g}(0)$ is equal to zero, \mathbf{g} in the term (5) can be approximated by $\mathbf{g}_0 S$, where $\mathbf{g}_0 \equiv \frac{d\mathbf{g}}{dS}|_{S=0}$. Thus, we finally obtain

$$\dot{A}_i = \mu\lambda_+A_i - \beta|A_i|^2A_i + \eta M(\mathbf{r}_i), \quad (8)$$

where $\eta \equiv k(\mathbf{U}^* \cdot \mathbf{g}_0)(\mathbf{h}_0 \cdot \mathbf{U})$. Here, we require k to be order μ in order to balance the term (5) with the others in Eq. (4). Note that Eq. (8) ignores the contribu-

tion from the complex conjugate of M , which would give rise to a rapidly oscillating component. This introduces negligible error because such components would be averaged out in the equation describing the slow evolution of A_i . Solving Eq. (2) for $\dot{\mathbf{r}}_i$, we obtain $\dot{\mathbf{r}}_i = -\int_0^t dt' \sigma(\mathbf{X}_i(t')) \nabla S|_{\mathbf{r}=\mathbf{r}_i(t')} \frac{1}{m} e^{-(\gamma/m)(t' - t)}$. Here, we have omitted a term proportional to $e^{-\frac{2\sigma}{m}t}$, because it vanishes in the asymptotic (i.e., $t \rightarrow \infty$) state. Next, we expand $\sigma(\mathbf{X})$ in terms of \mathbf{X} , substitute Eq. (7), and replace $\mathbf{r}_i(t')$ and $A_i(t')$ with $\mathbf{r}_i(t)$ and $A_i(t)$. The validity of this replacement is insured by the fact that $\mathbf{r}_i(t')$ and $A_i(t')$ are nearly constant over the damping time $\frac{m}{\gamma}$ of $e^{-(\gamma/m)(t' - t)}$. Then after carrying out the integration over t' , we obtain

$$\dot{\mathbf{r}}_i = -\zeta A_i^* \nabla M|_{\mathbf{r}=\mathbf{r}_i} + \text{c.c.}, \quad (9)$$

where $\zeta \equiv \frac{1}{\gamma}(\mathbf{U}^* \cdot \sigma_0)(\mathbf{h}_0 \cdot \mathbf{U})$ and $\sigma_0 \equiv \frac{d\sigma}{d\mathbf{X}}|_{\mathbf{X}=0}$. A_i^* is c.c. of A_i . Note that Eq. (9) ignores the contribution from rapidly oscillating components, similarly to Eq. (8). It is noteworthy that Eq. (9) does not include m . This reflects the fact that the inertial motion relaxes very rapidly on the time scales of A_i and \mathbf{r}_i . In fact, Eq. (9) does not change even if m is set to zero in the original model. After carrying out the rescaling of time $t \rightarrow t' \equiv \mu \text{Re}\lambda_+ t$ and of the amplitude $A(t) \rightarrow A'(t') \equiv \sqrt{\text{Re}\beta/(\mu \text{Re}\lambda_+)} \times \exp(-i\mu \text{Im}\lambda_+ t) A(t)$, we rewrite A' and t' as A and t . Finally, we obtain the reduced model of the chemotaxis oscillators in the normal form

$$\dot{A}_i = A_i - (1 + ic)|A_i|^2A_i + \chi \mathcal{M}(\mathbf{r}_i), \quad (10)$$

$$\dot{\mathbf{r}}_i = -A_i^* \nabla \mathcal{M}|_{\mathbf{r}=\mathbf{r}_i} + \text{c.c.}, \quad (11)$$

where the local mean field \mathcal{M} with the coupling kernel G is given by $\mathcal{M}(\mathbf{r}) \equiv \sum_i A_i G(\mathbf{r}_i - \mathbf{r})$, with

$$G(\mathbf{r}) \equiv \int \frac{dq}{(2\pi)^D} \frac{b e^{iq \cdot \mathbf{r}}}{\rho^2 + q^2}, \quad (12)$$

which is evaluated over the entire wave number space. In the above relations, we have $c \equiv \text{Im}\beta/\text{Re}\beta$, $\chi \equiv \eta \text{Re}\beta/(\zeta \mu \text{Re}\lambda_+)$, $b \equiv \zeta/d\text{Re}\beta$, and $\rho \equiv \sqrt{(1 + i\omega\tau)/d}$. All these parameters are independent of μ , because η is order μ .

In order to further simplify the model represented by Eqs. (10) and (11), we treat the term $\chi \mathcal{M}$ as a perturbation and use a phase-reduction technique. Here, we assume that χ is sufficiently small that A_i remains in the neighborhood of the limit cycle. This assumption is reasonable, because if A_i is far from the limit cycle, the i th element will exhibit behavior that differs significantly from that exhibited when it is isolated; in other words, in this case, the element has lost its individuality. However, because this is not the type of system in which we are interested in this Letter, we ignore such a case. Hence, the dynamics projected onto the limit cycle $A(\phi) = e^{-ic\phi}$ are described by the following equations:

$$\dot{\phi}_i(t) = 1 + (\kappa P_i + \text{c.c.}), \quad (13)$$

$$\dot{\mathbf{r}}_i(t) = -\nabla_{\mathbf{r}_i} P_i + \text{c.c.}, \quad (14)$$

where $P_i \equiv \sum_j e^{-ic(\phi_j - \phi_i)} G(\mathbf{r}_j - \mathbf{r}_i)$ and $\kappa \equiv (1 + i/c)\chi/2$. Note that this model becomes a potential system when κ is large and $\phi_i - t$ is adiabatically eliminated. Here, we consider the coupling kernel G . In one-dimensional space, G can be simply expressed as $G^{D=1}(\mathbf{r}) = \frac{b}{2\rho} e^{-\rho|\mathbf{r}|}$. In two-dimensional space, we have $G^{D=2}(\mathbf{r}) = \frac{b}{2\pi} K_0(\rho|\mathbf{r}|)$, where K_0 is the modified Bessel function of the second kind with a complex argument. In a space with any number of dimensions, because ρ is a complex parameter, $G(\mathbf{r})$ oscillates and decreases rapidly when $|\mathbf{r}|$ increases, and $G(\mathbf{r})$ almost vanishes when $|\mathbf{r}|$ is greater than the coupling length, $r_c \equiv 1/\text{Re}\rho$, which can be seen from Eq. (12) by employing a rotating-wave approximation. Thus, the main characteristics of $G(\mathbf{r})$ —oscillation and decay—are qualitatively well described by $G^{D=1}(\mathbf{r})$, which we substitute for G in all cases for simplicity in the following. In fact, we have numerically confirmed that the spatiotemporal patterns displayed in the figure of this Letter, obtained using $G^{D=1}$, can also be observed using the original G by making slight adjustments to the parameter values. Using $G^{D=1}$ in place of G , we now rescale the phase equation. Introducing the variable ψ_i defined as $\psi_i \equiv c\{\phi_i - [1 + (\kappa G(0) + \text{c.c.})]t\}$, we rescale the spatiotemporal coordinates as $\mathbf{r} \rightarrow \mathbf{r}' \equiv \text{Re}\rho \mathbf{r}$ and $t \rightarrow t' \equiv |c\kappa b/\rho|t$. Then, omitting the prime, we obtain [25]

$$\dot{\psi}_i(t) = \sum_{j \neq i} e^{-|\mathbf{R}_{ji}|} \sin(\Psi_{ji} + \alpha|\mathbf{R}_{ji}| - c_1), \quad (15)$$

$$\dot{\mathbf{r}}_i(t) = c_3 \sum_{j \neq i} \hat{\mathbf{R}}_{ji} e^{-|\mathbf{R}_{ji}|} \sin(\Psi_{ji} + \alpha|\mathbf{R}_{ji}| - c_2), \quad (16)$$

where $\mathbf{R}_{ji} \equiv \mathbf{r}_j - \mathbf{r}_i$, $\hat{\mathbf{R}}_{ji} \equiv \mathbf{R}_{ji}/|\mathbf{R}_{ji}|$, and $\Psi_{ji} \equiv \psi_j - \psi_i$. These equations contain the four real parameters $c_1 \equiv \arg(c\kappa b/\rho) - \pi/2$, $c_2 \equiv \arg(-b) - \pi/2$, $c_3 \equiv \text{Re}\rho/|\rho/c\kappa| (>0)$, and $\alpha \equiv \text{Im}\rho/\text{Re}\rho (>0)$. Note that c_3 is equal to the ratio of the time scales of ψ_i and \mathbf{r}_i . Also, note that although the density of the elements does not appear explicitly in these equations, it is an important parameter.

Now, we demonstrate some of the richness of these models by presenting the results of numerical calculations carried out in two-dimensional space with periodic boundary conditions. [Note that the nature of the boundary conditions is not important in sufficiently large systems, because the coupling function $G(\mathbf{r})$ decays rapidly with increasing $|\mathbf{r}|$.] The initial conditions are such that the positions and phases are randomly distributed. The number of elements is 50. Figure 1 (left) displays a snapshot of the element distribution exhibited by Eqs. (15) and (16) with a particular set of parameter values after the transient has decayed. The colors represent the phases of the corresponding elements. This self-organized hierarchical struc-

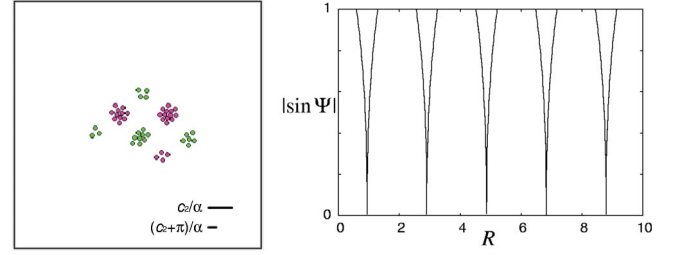


FIG. 1 (color). (left) *Clustered clusters* (or *modular networks*): snapshot of the element distribution in two-dimensional space exhibited by Eqs. (15) and (16), with $c_1 = c_2 = c_3 = 1.5$ and $\alpha = 1.6$. The colors represent the internal states ψ of the elements. The spatial size of the system is 30×30 , and it is shown in its entirety. The two scale bars represent c_2/α and $(c_2 + \pi)/\alpha$ (see main text). Although we have adopted a point element in this Letter, we plot its position with a finite size to facilitate visualization. (right) Invariant curve Eq. (17) with $E = 1.3$. The parameter values are the same as above. When the oscillators synchronize, i.e. $\sin\Psi = 0$, the distance R must be approximately 1, 3, 5, \dots . Because $|\sin\Psi| \leq 1$, values of R in the neighborhood of 0, 2, 4, \dots are avoided. In this way, an effective excluded volume (or zone) appears even though the elements are point objects.

ture is composed of synchronous clusters that exhibit antiphase synchronization with the neighboring clusters. This behavior is reminiscent of chemotactic cell sorting during biological development. The cohort of elements moves in the system while keeping an approximately constant shape.

In order to obtain an understanding of the pattern in analytical terms, we consider a two-oscillator system; this corresponds to the case in which for any given oscillator there exists only one oscillator in its neighborhood. Because $\dot{\mathbf{r}}_i$ is parallel to $\hat{\mathbf{R}}_{ji}$, the two oscillators move only along a line parallel to $\hat{\mathbf{R}}_{ji}$ that does not change with time. Thus, we use $r_i \equiv \hat{\mathbf{R}}_{21}|_{t=0} \cdot \mathbf{r}_i$ instead of \mathbf{r}_i . The differences between the variables representing the two oscillators, $\Psi \equiv \psi_2 - \psi_1$ and $R \equiv r_2 - r_1$, obey the equations $\dot{\Psi} = -2e^{-|R|} \cos(\alpha|R| - c_1) \sin\Psi$ and $\dot{R} = -2c_3 \frac{R}{|R|} e^{-|R|} \sin(\alpha|R| - c_2) \cos\Psi$. When the first equation is divided by the second equation, we can separate the variables Ψ and R . Then, integrating once, we derive the invariant curve

$$|\sin\Psi| = E e^{a_1|R|} |\sin(\alpha|R| - c_2)|^{a_2}, \quad (17)$$

where $a_1 \equiv \sin(c_1 - c_2)/c_3$ and $a_2 \equiv \cos(c_1 - c_2)/(c_3\alpha)$. (We can easily derive another curve in the case $\alpha = 0$ or $c_3 = 0$.) Here, E is a conserved quantity that is defined by the initial conditions $\Psi(0)$ and $R(0)$. Thus, $\Psi(t)$ and $R(t)$ move on this invariant curve. Figure 1 (right) presents an example of this curve. Equation (17) implies that if the two oscillators are synchronized (in-phase, $\Psi = 0$, or anti-phase, $\Psi = \pi$), the distance must be $R = c_2/\alpha \bmod (\pi/\alpha)$. In fact, this distance can be observed in Fig. 1, where the distance between the neighboring elements in

the synchronous cluster is c_2/α , and the distance between the neighboring clusters is $c_2/\alpha + \pi/\alpha$. Further, the distance cannot become such that the right-hand side of Eq. (17) becomes greater than 1. This implies an effective excluded volume; i.e., the elements spontaneously maintain a finite separation, even though there is no actual excluded volume. Note that α ($\equiv \text{Im}\rho/\text{Re}\rho$) introduces a spatial scale other than the coupling length, r_c ($\equiv 1/\text{Re}\rho$). Because we have $\rho \equiv \sqrt{(1 + i\omega\tau)/d}$, α is nonzero if and only if $\omega\tau \neq 0$. The quantity $\omega\tau$ is the ratio of the time scales of the intraelement dynamics ($1/\omega$) and the dynamics of the concentration of the chemical that mediates the interactions among elements (τ). We conjecture that living organisms utilize delays (corresponding to the case $\tau \neq 0$) in the interactions among elements when performing collective operations which require multiple spatial scales.

We cannot present all the observed patterns in this Letter. However, by simply changing the parameter values, we have found that our models can exhibit many types of patterns, including “fireworks,” a junction of three branches, stick-slip motion of clusters, train motion, and closed “membranes” that move through the system, unite with other membranes, grow, and divide into two membranes [26]. Further analysis of such patterns will be reported elsewhere.

The starting point of this Letter is a general class of chemotaxis oscillators, from which we derived simpler models. It is noteworthy that we assume only the condition $k = O(\mu)$ in the derivation [27]. We have found that our models exhibit a rich variety of patterns that can be realized by simply changing the parameter values. This richness is due to the fact that the interaction between elements can be attractive or repulsive, depending on the internal states of the elements. Considering this point, we conjecture that we can observe such richness in a more general class of systems that are characterized by this kind of varying interaction. We believe that if we properly combine such models and consider more complex conditions (including system-specific details), we should be able to predict a great variety of directly experimentally observable phenomena.

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 - [25] In these equations, \sum_j becomes $\sum_{j \neq i}$, because we have $\nabla G(\mathbf{r}_i - \mathbf{r})|_{\mathbf{r}=\mathbf{r}_i} = \mathbf{0}$, which can be easily seen from Eq. (12), in which the integrand of $\nabla G|_{\mathbf{r}=\mathbf{0}}$ is an odd function of \mathbf{q} .
 - [26] See EPAPS Document No. E-PRLTAO-99-050738 for a video of some patterns. For more information on EPAPS, see <http://www.aip.org/pubservs/epaps.html>.
 - [27] If k is not order μ , we can derive rather trivial models, e.g., the Stuart-Landau equation.