Deterministic endless collective evolvement in active nematics

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We propose a simple deterministic dynamic equation and reveal the mechanism of large-scale endless evolvement of spatial density inhomogeneity in active nematic. We determine the phase regions analytically. The interplay of density, magnitude of nematic order, and nematic director is crucial for the long-wave-length instability and the emergence of seemingly fluctuated collective motions. Ordered nematic domains can absorb particles, grow and divide endlessly. The present finding extends our understanding of the large-scale and seemingly fluctuated organization in active fluids.

Assemblies of active particles, which may be a physical abstraction of running animals[1], flying birds[2], swimming bacteria[3], migrating cells[4] or even cytoskeleton[5], have been served as a new building block for physicists over the last decade or so to understand the common collective behavior in these non-equilibrium systems[6]. Active nematic, a recently proposed concept for a kind of apolar active particles, is formed by driven rod-like particles with head-tail symmetry through the randomly driving force along the rod orientation axis at the single-particle level[7(a)-7(f)]. The symmetry of the system is not broken by applying such micro-driven forces until spontaneous symmetry breaking occurs. Recently, simulations and experiments in active nematic system show well-organized collective motions with system-sized fluctuation[7(b)-7(e)]. For example, splitting and merging of large-scale self-organized structures are exemplified in the simulation on active nematics[7(c)]. Experiments also show large-scale collective swarming and swirling in driven granular rods monolayer[7(d),7(e)]. These observations lead us to think about the nature of such seemingly fluctuated collective motions. It is currently unclear whether these large-scale collective motions arise in a deterministic manner or as a result of noises applied upon the system. Moreover, are they genuinely restless on large scale and evolving without end? These important aspects are still not well addressed in previous studies.

In the present study, we start from a deterministic equation to study the mechanism of restless collective evolution in active nematics. We reveal a new phase that is characterized by the unattainability of stable steady state. We first identify that, if the steady state can be reached, the system investigated here favors spatially homogeneous state. On the other hand, by taking account of the interplay between particle density and local nematic order (i.e., magnitude and orientation), the linear stability analysis shows that homogeneous nematic state can be unstable to fluctuations of small wave number. Therefore, the system enters into a chaotic phase region with no stable steady state. Large-scale spatial inhomogeneity of density and nematic order is developed as a result of long-wavelength instability. The spatial inhomogeneity in turn changes the direction of the nematic director, leading to a non-ending evolvement of the system. Numerical flux analysis shows that the particle-rich nematic domains are surrounded by particles fluxes, and evolve via absorbing particles from low-density isotropic medium, growing, and extending itself and breaking into small pieces. More importantly, all these seemingly fluctuated collective motions giving rise to giant number fluctuations are governed by a deterministic equation which is essentially free of noises.

We notice that one salient feature of simulation rules for active nematics by Chate et al.[7(c)] is that particle rotations are governed through inter-particle nematic interaction while spatial translational movements are free of such interactions. Experimentally particles are driven along their long axis, inducing strong longitudinal diffusion, and they can thrust into the media with the supply of kinetic energy[7(e)]. A simple diffusion equation which follows these observations can be written as(see [8]):

$$\begin{aligned}\partial_t f(\mathbf{r},\mathbf{u},t) &= \nabla[D_{\parallel}\mathbf{uu}\nabla + D_{\perp}(\mathbf{I}-\mathbf{uu})\nabla]f(\mathbf{r},\mathbf{u}) \\ &+ \mathscr{R}[D_r\mathscr{R}f(\mathbf{r},\mathbf{u}) + D_r\mathscr{R}w(\mathbf{r},\mathbf{u})f(\mathbf{r},\mathbf{u})],\end{aligned} \tag{1}$$

where $D_{\parallel}$ and $D_{\perp}$ are the parallel and perpendicular components of the translational diffusion constants. D_r is the rotational diffusion constant, and the rotational operator $\mathscr{R}$ is defined by $\mathscr{R} = \mathbf{u}\times\partial_{\mathbf{u}}$[9]. $f(\mathbf{r},\mathbf{u},t)$ is the particle number distribution function where the spatial coordinate $\mathbf{r}$ and the unit vector $\mathbf{u}$ denote the center-of-mass position and long-axis direction of particles, respectively. $w(\mathbf{r},\mathbf{u})$ is a self-consistent interacting potential which has $\pm\mathbf{u}$-symmetry. In two-dimensional(2-D) case, the most common form of such interacting potential is the excluded-volume-like interaction $w(\mathbf{r},\mathbf{u}) = l^2\int \mathrm{d}\mathbf{u}'|\mathbf{u}\times\mathbf{u}'|f(\mathbf{r},\mathbf{u}')$, where l is the particle length.

The diffusion equation Eq.(1) for active nematics satisfies particle number conservation with the spatial translational current $\mathbf{J}^s(\mathbf{r},\mathbf{u}) = -D_{\parallel}\mathbf{uu}\nabla f(\mathbf{r},\mathbf{u}) - D_{\perp}(\mathbf{I}-\mathbf{uu})\nabla f(\mathbf{r},\mathbf{u})$ and the local rotational current $\mathrm{J}^r(\mathbf{r},\mathbf{u}) = -D_r\mathscr{R}f(\mathbf{r},\mathbf{u}) - D_r\mathscr{R}w(\mathbf{r},\mathbf{u})f(\mathbf{r},\mathbf{u})$, which are independent of each other. The translational current is purely diffusive. In the Fourier space as defined by $f(\mathbf{r},\mathbf{u}) = \int \mathrm{d}\mathbf{r}\tilde{f}(\mathbf{k},\mathbf{u})e^{-i\mathbf{k}\cdot\mathbf{r}}$, the spatial fluctuation modes are governed by diffusive decaying term

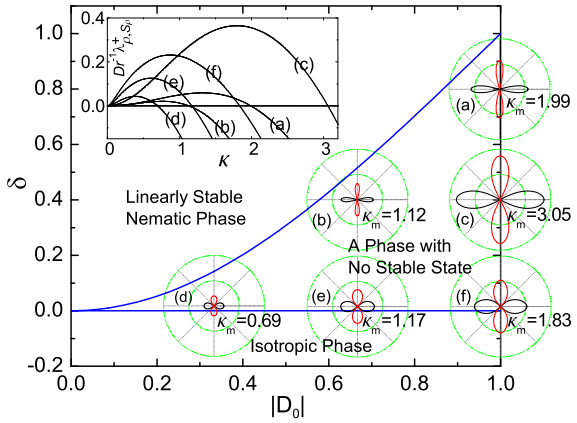

FIG. 1: Three phases are separated by the blue curves. Polar plots (a)-(f) indicate the instability regime for κ and θ. The locations (D_0, δ) of their origins are used as the parameters to produce these plots. (a) $|D_0| = 0$, $\delta = 0.8$, (b) $|D_0| = 2/3$, $\delta = 0.4$, (c) $|D_0| = 0$, $\delta = 0.4$, (d) $|D_0| = 1/3$, $\delta = 0.01$, (e) $|D_0| = 2/3$, $\delta = 0.01$, and (f) $|D_0| = 0$, $\delta = 0.01$. The black and red branches in polar plots represent the cases of positive and minus D_0, respectively. The inset shows the corresponding instability modes $D_r^{-1}\lambda^{+}_{\tilde{\rho},S_\rho}|_{\theta=0}$ for these polar plots.

$-k^2(D_\parallel \cos^2\varphi + D_\perp \sin^2\varphi)\tilde{f}(\mathbf{k},\mathbf{u})$, where φ is the angle $\mathbf{k}$ makes with $\mathbf{u}$. For positive $D_\parallel$ and $D_\perp$, all the spatial fluctuation modes decay except for $k = 0$ which indicates total particle number conservation. Therefore, as governed by these decaying diffusive modes, the spatial term suggests that only the spatially homogeneous state will probably be the stable steady state if there are no particle sources and sinks in the system and at the boundaries. However, when $D_\parallel \neq D_\perp$, we will show that the spatially homogeneous state may become unstable to fluctuations in the nematic state. Consequently, the system is deprived of all possible stable steady state and becomes restless and evolves endlessly, similar to the deterministic nonperiodic flow found in turbulence[10].

We first examine the spatially homogeneous dynamic equation derived from Eq.(1) by neglecting the spatial derivatives: $\partial_t f(\mathbf{u},t) = \mathscr{R}[D_r\mathscr{R}f(\mathbf{u}) + D_r\mathscr{R}w(\mathbf{u})f(\mathbf{u})]$. Determined by the integration kernal of the self-consistent interacting potential $w(\mathbf{u})$, $f(\mathbf{u},t)$ has $\pm\mathbf{u}$-symmetry. In spatially homogeneous nematic state, we assume that the nematic director $\mathbf{n}_0$ is in the x-axis, and thus the distribution function can be expanded as $f(\mathbf{u},t) = (2\pi)^{-1}\rho\sum_{n=0}^{\infty} a_n(t)\cos 2n\phi$, where ρ is the particle number density, ϕ is the angle of the unit vector $\mathbf{u}$, and $n = 0, 1, 2\cdots\infty$. The dynamic equation of the coefficient $a_n(t)$ is given by $(4D_r)^{-1}\partial_t a_n(t) = -n^2 a_n + \frac{\rho l^2 n^2 a_n}{(4n^2-1)\pi} + \rho l^2 \sum_{m=1}^{\infty} \frac{nm a_m (a_{|n-m|} - a_{|n+m|})}{(4m^2-1)\pi}$, where $a_0(t) = 1$ and $a_1(t) = 2S(t)$, since the number density $\rho = \int \mathrm{d}\mathbf{u} f(\mathbf{u},t)$ and the nematic order parameter $S(t) = \int \mathrm{d}\mathbf{u}\cos 2\phi f(\mathbf{u},t)/\rho$. By setting $a_n = 0$ for $n \geq 3$, the truncated dynamic equation for the nematic order parameter can be written as: $\frac{\partial_t S(t)}{4D_r} = (\tilde{\rho}-1)S - \frac{3\tilde{\rho}^2 S^3}{4(5-\tilde{\rho})}$, where $\tilde{\rho} = \rho/\rho^*$ is the rescaled number density, and the critical density $\rho^* = 3\pi/2l^2$, beyond which the system enters into a spatially homogenous nematic state.

Next, we examine the linear stability of such spatially homogeneous nematic state above ρ^*, by expanding the number distribution function $f(\mathbf{r},\mathbf{u}) = (2\pi)^{-1}\rho(\mathbf{r})[1 + 4(u_\alpha u_\beta - \delta_{\alpha\beta}/2)Q_{\alpha\beta}(\mathbf{r})]$ with the inclusion of the alignment tensor $Q_{\alpha\beta}(\mathbf{r}) = S(\mathbf{r})(\hat{n}_\alpha\hat{n}_\beta(\mathbf{r}) - \delta_{\alpha\beta}/2)$ where $\hat{\mathbf{n}}(\mathbf{r})$ is the unit vector of the nematic director. We assume that nematic director is along the x axis of the system. Small fluctuations of density and nematic director near the ordered nematic state are given by $\delta\tilde{\rho}(\mathbf{r}) = \tilde{\rho}(\mathbf{r}) - \tilde{\rho}_0$ and $S\delta n_y(\mathbf{r}) = Q_{xy}(\mathbf{r})$, respectively. Here, $\tilde{\rho}_0 = \rho_0/\rho^*$ is the reduced bulk particle density, and $\delta n_y(\mathbf{r})$ is the y-component of the deviated nematic director. Noting that $\mathbf{n}_0(\mathbf{r}) = \hat{\mathbf{x}}$ and $|\mathbf{n}| = 1$, $\delta n_y(\mathbf{r})$ is the only possible small fluctuation of nematic director $\mathbf{n}(\mathbf{r})$. The resulting hydrodynamic equations can be obtained from Eq. (1), yielding

$$\partial_t\delta\tilde{\rho} = \frac{D_p}{2}\partial_\alpha^2\delta\tilde{\rho} + \frac{D_n}{2}(\partial_x^2 - \partial_y^2)(\tilde{\rho}S) + 2D_n\tilde{\rho}_0 S\partial_x\partial_y\delta n_y, \quad (2)$$

$$\tilde{\rho}_0 S\partial_t\delta n_y = \frac{D_n}{4}\partial_x\partial_y\delta\rho + \frac{D_p}{2}\tilde{\rho}_0 S\partial_\alpha^2\delta n_y, \quad (3)$$

$$\partial_t[\tilde{\rho}S(\mathbf{r})] = \frac{D_n}{4}(\partial_x^2 - \partial_y^2)\tilde{\rho} + \frac{D_p}{2}\partial_\mu^2(\tilde{\rho}S) + 4D_r\tilde{\rho}(\tilde{\rho}-1)S - D_r\frac{3\tilde{\rho}^3S^3}{5-\tilde{\rho}}, \quad (4)$$

where $D_p = D_\parallel + D_\perp$ and $D_n = D_\parallel - D_\perp$. It is easy to see that the homogeneous state is stable to fluctuations of coupled nematic director and density field. Here we consider the stability of the modes that couple fluctuations of density $\delta\tilde{\rho}(\mathbf{r}) = \tilde{\rho}(\mathbf{r}) - \tilde{\rho}_0$ and magnitude of nematic order $\delta S_\rho(\mathbf{r}) = \tilde{\rho}(\mathbf{r})S(\mathbf{r}) - \tilde{\rho}_0 S_0$ with $\delta n_y = 0$ around the homogeneous state $(\tilde{\rho}_0, S_0)$, where $S_0 = \sqrt{4(5-\tilde{\rho}_0)(\tilde{\rho}_0-1)/3\tilde{\rho}_0^2}$. The mode of fluctuations in Fourier components with wave vector $\mathbf{k}$, defined by $\delta\tilde{\rho}(\mathbf{r}) = \int \mathrm{d}\mathbf{k}\tilde{\rho}_\mathbf{k} e^{-i\mathbf{k}\cdot\mathbf{r}}$ and $\delta S_\rho(\mathbf{r}) = \int \mathrm{d}\mathbf{k} S_{\rho\mathbf{k}} e^{-i\mathbf{k}\cdot\mathbf{r}}$, is governed by

$$\partial_t\begin{bmatrix}\tilde{\rho}_\mathbf{k}\\ S_{\rho\mathbf{k}}\end{bmatrix} = -\frac{1}{2}\begin{bmatrix} D_pk^2 & D_n\cos 2\theta k^2 \\ D_n\cos 2\theta k^2/2 & D_pk^2 \\ -8D_r\tilde{\rho}_0 S_0 & +16D_r\delta\end{bmatrix}\begin{bmatrix}\tilde{\rho}_\mathbf{k}\\ S_{\rho\mathbf{k}}\end{bmatrix}, \quad (5)$$

where $\delta = \tilde{\rho} - 1$, θ is the angle between wave vector $\mathbf{k}$ and nematic director $\mathbf{n}_0$. The eigenvalues of the coefficient matrix in Eq.(5) are given by $D_r^{-1}\lambda^{\pm}_{\tilde{\rho},S_\rho} = -(8\delta + \kappa^2)/2 \pm \sqrt{D_0^2\kappa^4\cos^2 2\theta/8 - 4\sigma D_0\kappa^2\cos 2\theta + 16\delta^2}$, where $\sigma = \sqrt{(4-\delta)\delta/3}$, the rescaled coefficient $D_0 = D_n/D_p$, and the wave number $\kappa = \sqrt{D_p/D_r}k$. The real part of $\lambda^{-}_{\tilde{\rho},S_\rho}$ is always negative, representing stable decaying

mode. However, the mode $\lambda^+_{\tilde{\rho},S_\rho}$ becomes positive when $32(D_0\sigma\cos2\theta+\delta)\kappa^2+(2-D_0^2\cos^2 2\theta)\kappa^4<0$. The coefficient of κ^4 is always positive since $|D_0|\leq 1$, signifying that for large enough wave numbers, the fluctuations are always stable. For small wave numbers which describe large-scale fluctuations, the stability is controlled by the coefficient of κ^2. Thus when $(D_0\sigma\cos2\theta+\delta)<0$, the system becomes unstable on large scale.

The phase map for (D_0,δ) is given in Fig. 1. Between the isotropic and linearly stable nematic phases, there is a region where spatially homogeneous nematic state is unstable. It is denoted as a 'phase with no stable state' to emphasize that the only possible form of steady-state solution is unachievable there. For different (D_0,δ) within the 'no stable state' region, the instability mode structures (κ,θ) are given by the polar plots whose central positions represent (D_0,δ). Here, each polar plot is composed of horizontal (black) and vertical (red) branches enclosing unstable fluctuation modes, corresponding to $D_0<0$ and $D_0>0$, revealing that spatial inhomogeneities are developed parallel and perpendicular to the nematic director, respectively. The maximum values κ_m of κ for the instability regimes are always in the directions $\theta=\pi/2,3\pi/2$ for $D_0>0$ and $\theta=0,\pi$ for $D_0<0$, respectively. Generally speaking, κ_m becomes larger when (D_0,δ) is far from the phase boundary. The inset of Fig. 1 shows the value of $D_r^{-1}\lambda^+_{\tilde{\rho},S_\rho}$, where for small κ, $D_r^{-1}\lambda^+_{\tilde{\rho},S_\rho}>0$ corresponds to the long-wavelength instability and the onset of large-scale spatial inhomogeneity.

What will happen in the phase region where there is no stable steady state? And how the system evolves in time? To answer these questions we directly integrate Eq. (1) numerically in this region using alternative implicit algorithm(see [8]). Starting from an isotropic and spatial-homogeneous initial condition, local ordered nematic domains form at the beginning, accompanied with quick development of density inhomogeneity. Further coarsening of these structures leads to the coexistence of particle-enriched nematic domains and particle-poor isotropic region where $\rho<\rho^*$ (Fig. 2a). However, such a large-scale spatially inhomogeneous structure is unstable, and it will evolve and become fragmented as shown in Fig. 2b. The fragmented structure will again coalesce and similar process will repeat aperiodically and endlessly (see [8] M1.mov). In Fig. 2c-2k, we show how a particle-rich nematic branch breaks into pieces and reunites into a structure with new morphology.

How does the fragmentation process occur? In Fig. 3a-c, we take a close look at the process that a nematic band breaks up(for a more continuous process, see [8] M2.mov). In Fig. 3a, after the spontaneous formation of a nematic band, initially, it is shown that the nematic director in the high-density ordered region is almost parallel to the density stripe boundary. In this case, the

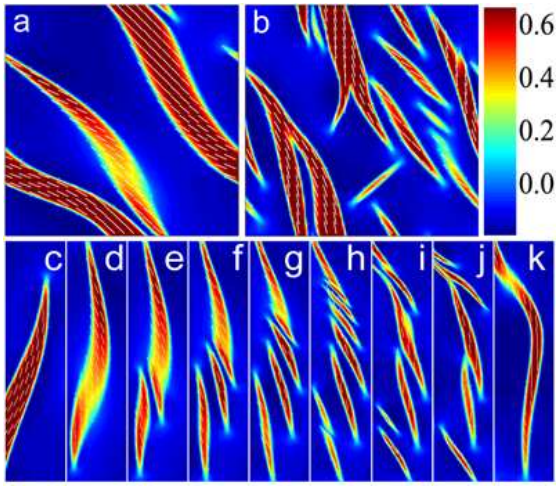

FIG. 2: Density and nematic order profiles are plotted. The color scale shows the local relative rescaled density value $\delta(\mathbf{r})=\tilde{\rho}(\mathbf{r})-1$. The length and angle of white segments show the magnitude and direction of nematic order, respectively. The dynamic parameters are $D_r=2$, $D_\perp=0.4$, and $D_\parallel=2.4$. The reduced instability dynamic parameter $D_0=5/7$ and $\delta=0.01$. The system size is 300×300 with the particle length $l=1$. Periodic boundary condition is implemented. Discrete time step $\Delta_t=0.018$ and spatial steps $\Delta_x=\Delta_y=\Delta_r=3$. (a)-(b) The snapshots are taken at times $1.7\times10^6\Delta_t$ and $2.3\times10^6\Delta_t$. (c)-(k) A close look of the breaking and coalescing processes of a nematic domain, at times 1.6×10^6, 1.7×10^6, 1.71×10^6, 1.72×10^6, 1.73×10^6, 1.74×10^6, 1.75×10^6, 1.76×10^6 and 1.8×10^6 in unit Δ_t.

nematic director is along the x-axis. For $D_n>0$, from our previous stability analysis, the term $-\frac{1}{2}D_n\partial_y^2(\rho S)$ in Eq.(2) is directly responsible for the development of such density inhomogeneity. Now, we are interested if such aligned director field is stable to small fluctuations $\delta\mathbf{n}_\perp(\mathbf{r})=\mathbf{n}(\mathbf{r})-\mathbf{n}_0=(0,\delta\hat{n}_{\perp y})$. To linear order, the dynamic equation for $\delta\hat{n}_{\perp y}(\mathbf{r})$ can be obtained from Eq.(1) as $\tilde{\rho}S\partial_t\delta n_{\perp y}=\frac{1}{2}D_p[\tilde{\rho}S\partial_x^2\delta n_{\perp y}+\delta n_{\perp y}\partial_y^2\tilde{\rho}S]$, where we have assumed that there is no spatial variation of $\tilde{\rho}S$ along x-axis. The spatial variation of $\tilde{\rho}S$ along the y-axis is significant since density inhomogeneity is developed in that direction. Near stripe boundaries, we always have $\partial_y^2\tilde{\rho}S>0$, which makes the fluctuations $\delta n_{\perp y}$ unstable. Such instability will induce the change of the nematic orientation, and this explains why the nematic directors in Fig. 2 and Fig. 3b are most likely to be oblique to the density profile boundaries. When the nematic directors become oblique to the boundary, as shown in Fig. 3b, there is a leakage of particles from the high-density region. As the particle density in the stripe falls into the 'no stable state' region as shown in Fig. 1, the spatial instability takes place again. This leads to a fragmentation event, as shown in Fig. 3c. It is shown that a density crevice forms parallel with the nematic director as spatial instability requires. In Fig. 3d, we show a

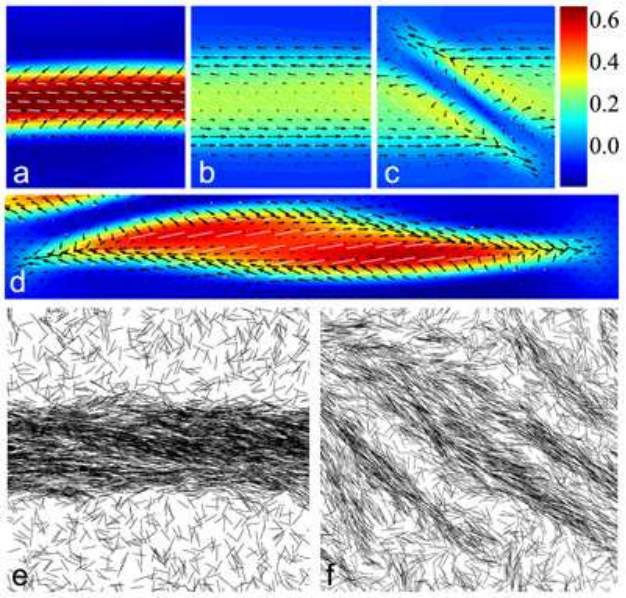

FIG. 3: (a)-(c) Three typical steps that an ordered stripe breaks, at times $30000\Delta_t$, $60000\Delta_t$ and $63000\Delta_t$ in sequent. (d) Twisted spindle shaped structure formed after it breaks off from a larger ordered structure. The color scale shows the local relative rescaled density value $\delta(\mathbf{r}) = \tilde{\rho}(\mathbf{r}) - 1$. The length and angle of white segments show the magnitude and direction of nematic order, respectively. The black arrow shows the direction and strength of particle fluxes. (e)-(f) Simulation result shows density inhomogeneity and similar restless evolvement in active nematics for 9.4×10^4 and 1.1×10^5 simulation sweeps.

twisted-spindle shaped high-density region with local nematic order, which is commonly formed after it breaks off from a larger ordered structure in Fig. 2e.

We also perform simulations to examine the stability of homogeneous nematic state on the basis of Eq.(1) (see [8]). Fig. 3e shows the formation of a particle-enriched nematic band. We find that such band is also unstable and undergoes similar process (see [8] M3.mov), where the nematic director changes its direction in time and the fragmentation event takes place afterward (Fig. 3f).

It is worth to notice that all these highly dynamic structures are surrounded by particle fluxes around the density profile boundaries. The density currents are defined as $\mathbf{J}(\mathbf{r}) = (J_x(\mathbf{r}), J_y(\mathbf{r}))$, with $J_\alpha(\mathbf{r}) = -\frac{1}{2}D_p\partial_\alpha\rho(\mathbf{r}) - D_n\partial_\beta[\rho(\mathbf{r})Q_{\alpha\beta}(\mathbf{r})]$ where the first term is just ordinary diffusive current and the second term is the current generated by coupling nematic directors. As we show in Fig. 3a, inward currents, generated by $(0, \frac{1}{2}D_n\partial_y(\rho S))$ which is included in the second term of $\mathbf{J}(\mathbf{r})$, are directly responsible for the development of density inhomogeneity. As the time evolves, in Fig. 3b, along the two sides of stripe boundaries the system generates anti-parallel currents which also originate from $-D_n\partial_\beta[\rho(\mathbf{r})Q_{\alpha\beta}(\mathbf{r})]$, and the particles seem to move under a self-organized rachet potential[11]. When the crevice forms in Fig. 3c, particles flow into the low density region as guided by the nematic directors, accompanied with the growth of nematicly ordered tips near the crevice. In Fig. 3d, as indicated by the density currents, the twisted-spindle shaped nematic region absorbs particles from the medium on both sides and generate outward flux on both tips. In this way it can grow and extend itself quickly into the low-density medium. With the presence of these density fluxes around the ordered structure, it behaves like a creature absorbing, growing, dividing and dissipating into isotropic medium endlessly.

In summary, the dynamic equation abstracted from previous simulations and experiments suggests a nematicly ordered phase with no stable steady state. Thus the system must evolve endlessly. We reveal the statistical mechanism that governs the large-scale and seemingly fluctuated collective evolution. We show that, as a result of long-wavelength instability, density and order inhomogeneity develops as guided by nematic director field. The spatial inhomogeneity in turn changes the directions of local nematic directors. The changed nematic directors further guide the fragmentation events, leading to endless evolution of the system. Finally, it would be interesting to extend our analysis to other active fluids.

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[1] J.K. Parrish and L. Edelstein-Keshet, Science **284**, 99 (1999); M. Ballerini *et al.*, Proc. Natl. Acad. Sci. USA **105**, 1232 (2008).
[2] T. Feder, Phys. Today **60**, 28 (2007).
[3] C. Dombrowski, L. Cisneros, S. Chatkaew, R.E. Goldstein, and J.O. Kessler, Phys. Rev. Lett. **93**, 098103 (2004); D. Volfson, S. Cookson, J. Hasty, and L.S. Tsimring, Proc. Natl. Acad. Sci. USA **105**, 15346 (2008).
[4] P. Rorth, Trends Cell Biol. **17**, 575 (2007).
[5] T. Surrey, F. Nedelec, S. Leibler, and E. Karsenti, Science **292**, 1167 (2001); P. Kraikivski, R. Lipowsky, and J. Kierfeld, Phys. Rev. Lett. **96**, 250813 (2006); V. Schaller, C. Weber, C. Semmrich, E. Frey, and A.R. Bausch, Nature **467**, 73 (2010); X. Shi, Y. Ma, Proc. Natl. Acad. Sci. USA **107**, 11709 (2010).
[6] T. Vicsek, A. Czirok, E. Ben-Jacob, I. Cohen, and O. Shochet, Phys. Rev. Lett. **75**, 1226 (1995); J. Toner and Y. Tu, Phys. Rev. Lett. **75**, 4326 (1995); R.A. Simha and S. Ramaswamy, Phys. Rev. Lett. **89**, 058101 (2002); G. Gregoire and H. Chate, Phys. Rev. Lett. **97**, 090602 (2006); A. Baskaran and M.C. Marchetti, Phys. Rev. Lett. **101**, 268101 (2008); A. Baskaran and M.C. Marchetti, Proc. Natl. Acad. Sci. USA **106**, 15567 (2008); D. Saintillan and M. J. Shelley, Phys. Rev. Lett. **100**, 178103 (2008); J. Toner, Y. Tu, and S. Ramaswamy, Ann. Phys. (N.Y.) **318**, 170 (2005); S. Ramaswamy, Annu. Rev. Condens. Matter Phys. **1**, 9.1 (2010).
[7] (a) S. Ramaswamy, R.A. Simda, and J. Toner, Europhys.

Lett. **62**, 196 (2003); (b) S. Mishra and S. Ramaswamy, Phys. Rev. Lett. **97**, 090602 (2006); (c) H. Chate, F. Ginelli, and R. Montagne, Phys. Rev. Lett. **96**, 180602 (2006); (d) V. Narayan, N. Menon, and S. Ramaswamy, J. Stat. Mech. P01005 (2006); (e) V. Narayan, S. Ramaswamy, and N. Menon, Science **317**, 105 (2007); (f) I.S. Aranson, D. Volfson, and L.S. Tsimring LS, Phys. Rev. E **75**, 051301 (2007).

[8] See supplementary information for supporting materials and movies.

[9] T. Shimada, M. Doi, and K. Okano, J. Chem. Phys. **88**, 7181 (1988); A. Ahmadi, M.C. Marchetti, and T.B. Liverpool, Phys. Rev. E **74**, 061913 (2006); A. Baskaran and M.C. Marchetti, Phys. Rev. E **77**, 011920 (2008).

[10] E.N. Lorenz, J. Atoms. Sci. **20**, 130 (1963).

[11] F. Jülicher, A. Ajdari, and J. Prost, Rev. Mod. Phys. **69**, 1269 (1997).