Swimmer Suspensions on Substrates: Anomalous Stability and Long-Range Order

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We present a comprehensive theory of the dynamics and fluctuations of a two-dimensional suspension of polar active particles in an incompressible fluid confined to a substrate. We show that, depending on the sign of a single parameter, a state with polar orientational order is anomalously stable (or anomalously unstable), with a nonzero relaxation (or growth) rate for angular fluctuations, not parallel to the ordering direction, at zero wave number. This screening of the broken-symmetry mode in the stable state does lead to conventional rather than giant number fluctuations as argued by Bricard *et al.*, Nature **503**, 95 (2013), but their bend instability in a splay-stable flock does not exist and the polar phase has long-range order in two dimensions. Our theory also describes confined three-dimensional thin-film suspensions of active polar particles as well as dense compressible active polar rods, and predicts a flocking transition without a banding instability.

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Biological systems and their artificial analogues, such as vibrated granular layers [1] and self-propelled rollers [2], are powered by energy supplied directly at the level of constituent particles, which leads to macroscopic stresses and currents. "Active hydrodynamics" [3–8], which describes how nonequilibrium currents and forces affect the orientational order of anisotropic units, presents a general framework to study the large-scale dynamics in such systems.

Active phases frequently defy expectations rooted in equilibrium physics. Motile *XY* spins [3–5,9] on a substrate display long-range orientational order even in two dimensions, and anomalous number fluctuations with the standard deviation in number *N* of particles in a region growing more rapidly than \sqrt{N} [3,9–11]. Enhancing the noise in this system yields an isotropic phase via an instability towards an inhomogeneous, polarized banded phase ultimately rendering the transition discontinuous [12,13].

Much of our understanding of polar active systems [9,12,13] comes from studies that ignore any ambient solvent, but biological systems are typically suspensions in an incompressible fluid that mediates long-range hydrodynamic interactions. This aspect is well understood for *bulk* suspensions [3,14,15], but subtleties arise for systems confined to two dimensions by walls or adsorption on substrates. The Stokesian hydrodynamic interaction, although screened at leading order by the bounding surfaces, leaks through in a weakened form through the inescapable *nonlocal* constraint of incompressibility [16–19]. Although active variants of incompressible magnets [20] have been considered before [21,22], this does not directly relate to the physics of polar suspensions in which only the *joint* density of the active particles and fluid is incompressible but the concentration of the polar particles, while conserved, may fluctuate.

In this Letter we present a general theory of a suspension of motile polar particles in a thin film of incompressible fluid, or, equivalently, a polar active gel [3] bounded by planar solid walls, taking the effects of incompressible flow correctly into account. Our main results are as follows. (i) Through the interplay of motility and incompressibility, a flock is stable for all wave vector directions, with deformations of the orientational broken-symmetry variable relaxing on a finite, nonhydrodynamic timescale as the wave number $q \rightarrow 0$ for *almost* all wave vector directions. This contradicts the claimed generic bend instability [2] of confined incompressible flocks, and is, of course, contrary to conventional expectations [23] of a vanishing relaxation rate, in the long-wavelength limit, for Nambu-Goldstone modes [24]. The "gapping" of the orientational Nambu-Goldstone mode due to the active forcing of the velocity field of an incompressible fluid is closely akin to Anderson's original formulation [25] of the mechanism [26] for granting "mass" to such modes through the longrange character of the Coulomb interaction. (ii) Motility and incompressibility suppress the instability towards the inhomogeneous banded state that generically occurs in *compressible* polar systems between the ordered and the disordered states, implying that a direct transition from an isotropic state to a homogeneous flock is possible, without the intervention of a banded phase. (iii) The variance of orientational fluctuations is nondivergent for $q \rightarrow 0$, with a correlation length that is finite for any nonzero motility. As a consequence number fluctuations are normal, with variance proportional to the mean [27]. (iv) Our main results remain correct up to very large length scales even in weakly compressible systems [1,9,29]. Our theory is relevant to all current experiments on planar confined active polar suspensions [30–32], which we illustrate by showing how it emerges from the averaging of the dynamics of three-dimensional polar fluid confined in one direction.

We start by constructing the general dynamical equations for the polarization $\mathbf{p}(\mathbf{r}, t)$ and the concentration $c(\mathbf{r}, t)$ of a collection of active units suspended in a fluid with the total velocity field of the particles and the fluid being $\mathbf{u}(\mathbf{r}, t)$, where \mathbf{r} is a two-dimensional position vector. The joint density ρ of the particles and the fluid is incompressible, i.e., $\dot{\rho} = 0$ implying $\nabla \cdot \mathbf{u} = 0$. In the absence of activity and fluid flow, the equilibrium relaxation derives from a Landau–de Gennes free energy, which we write in the single Frank constant approximation for simplicity [33]:

$$\mathcal{H} = \int_{\mathbf{r}} \left(\frac{\alpha(c)}{2} |\mathbf{p}|^2 + \frac{\beta}{4} |\mathbf{p}|^4 + \frac{K}{2} |\nabla \mathbf{p}|^2 + \gamma \mathbf{p} \cdot \nabla c + c \ln c \right),$$
(1)

where the sign of $\alpha(c)$ determines the stability of the isotropic, flow-less phase. A negative $\alpha(c)$ gives rise to a nonzero polarization, which remains bounded due to the β term and whose heterogeneities are suppressed by the elastic constant *K*. The γ term describes the tendency of the polarity to align along or opposite to concentration gradients [34], while the last term is characteristic of an ideal solution (setting $k_BT = 1$).

To lowest order in gradients, the generic dynamical equation for ${\bf p}$ is

$$\partial_t \mathbf{p} = \Lambda \mathbf{u} - \frac{\delta \mathcal{H}}{\delta \mathbf{p}},\tag{2}$$

where the coefficient Λ , whose sign depends on the detailed shape of a polar particle [1,18], aligns the polarization vector with the local suspension velocity and is specific to systems in contact with a substrate [1,18,35]. We treat it as independent of the direction of **p**, which does not qualitatively modify our conclusions [36]. The coefficient in front of the second term of the right-hand side of Eq. (2) is set to 1 through a proper choice of time units. Advective and selfadvective terms, which are discussed in Ref. [36] are not displayed in Eq. (2) since they turn out to be less relevant than the terms retained in Eq. (2) even in the ordered phase. Ignoring inertia, Newton's second Law reduces to force balance which to lowest order in gradients is

$$\Gamma \mathbf{u} = v\mathbf{p} - \nabla \Pi - \Lambda \frac{\delta \mathcal{H}}{\delta \mathbf{p}},\tag{3}$$

where Γ is the coefficient of damping by the substrate and Π is the pressure that enforces incompressibility. *v***p** denotes the active polar force density of the particles. The final term on the right-hand side of Eq. (3) is required to ensure that the steady state in the limit of vanishing activity reduces to the equilibrium distribution. Finally, the continuity equation for the concentration field is

$$\partial_t c + \mathbf{u} \cdot \nabla c = -\nabla \cdot \left(v_p c \mathbf{p} - D_c c \nabla \frac{\delta \mathcal{H}}{\delta c} \right), \quad (4)$$

where $v_p c \mathbf{p}$ denotes an active concentration current due to the motility of the particles [3–5,9,44] [45]. The final term leads to standard diffusive dynamics. Equations (2)–(4) are similar to the ones for two-fluid polar active systems [1], with the only difference being the incompressibility constraint.

To determine the stability of a homogeneous isotropic $(|\mathbf{p}| = 0)$ state, we perform a linear stability analysis of Eqs. (2) and (3). For $\Lambda v > 0$, the state is destabilized when

$$\tilde{\alpha} = \alpha(c) - \frac{\Lambda v}{\Gamma + \Lambda^2} = \alpha(c) - w < 0.$$
(5)

Thus, for v > 0, a positive alignment parameter Λ reinforces the moving particles' alignment, thereby favoring the instability of the homogeneous disordered phase as in Ref. [18] (also see Ref. [36]). Following this instability, a homogeneous ordered phase with $\mathbf{p} = p_0 \hat{x}$, $c = c_0$, and $\mathbf{u} = u_0 \hat{x}$ may form, where $p_0^2 = |\tilde{\alpha}/\beta|$ and $u_0 = (w/\Lambda)p_0$. To study its stability, we project Eq. (3) transverse to the wave vector \mathbf{q} to eliminate the velocity field. Introducing the polarization fluctuations $\delta \mathbf{p} = (p_0 + \delta p)(\cos\theta \hat{x} +$ $\sin\theta \hat{y} - p_0 \hat{x}$, we obtain equations for small deviations from the ordered state: $\partial_t(\delta c, \delta p, \theta) = \mathbf{M} \cdot (\delta c, \delta p, \theta)$. The three eigenvalues of matrix M characterize relaxation modes of the system. Naively, the presence of a conservation law for the concentration and broken rotation symmetry would suggest that two of these modes should be "hydrodynamic"; i.e., the associated eigenvalues vanish in the $\mathbf{q} \rightarrow 0$ limit. A detailed calculation, however, reveals that this is not correct [36] in the presence of the motility-induced long-range interactions mediated by fluid incompressibility. Such long-range interactions suppress fluctuations in the ordered state, as in dipolar XYmodels [20,46] or superconductors [25]. Here, they imply that our system has only one hydrodynamic mode associated with the conserved concentration field with relaxation rate $\kappa_c \propto q^2$, the stability of which we discuss later. The remaining two eigenvalues, which govern the dynamics of the polarization fluctuations, are nonhydrodynamic, and go to a finite limit as $\mathbf{q} \rightarrow 0$:

$$\kappa_{\pm}(\phi) = -\frac{1}{2} \left[w + 2|\tilde{\alpha}| \left(1 + \frac{\Lambda^2}{\Gamma} \sin^2 \phi \right) \pm \sqrt{\left[w + 2|\tilde{\alpha}| \left(1 + \frac{\Lambda^2 \sin^2 \phi}{\Gamma} \right) \right]^2 - 8|\tilde{\alpha}| w \sin^2 \phi \left(1 + \frac{\Lambda^2}{\Gamma} \right)} \right], \tag{6}$$

where ϕ is the angle between **q** and $\hat{\mathbf{x}}$. For w < 0, one of the eigenvalues is always positive, implying a generic instability. For w > 0, both κ_{+} and κ_{-} are stabilising, though one of the two eigenvalues (κ_{-}) vanish for fluctuations with wave vectors precisely along the ordering direction. This implies that all components of the polarization vector have a finite exponential-decay time to their steady state value even in infinite systems, except for perturbations purely in ordering direction (i.e., $\phi = 0$), for which $\kappa_{-}(0) \sim$ $-K_p(0)q^2$ [the somewhat cumbersome form of $K_p(\phi)$ is displayed in Ref. [36]]. Crucially, K_p is not generically negative along any wave vector direction including along \hat{x} even at arbitrarily high activities [10]. Of course, K_p can turn negative along \hat{x} for certain choices of phenomenological parameters, leading to an instability of the polar phase. However, in this Letter we focus on the case in which K_p is stabilizing, leading to exceptional stability of the ordered phase to polarization fluctuations (since these fluctuations decay exponentially along almost all directions), a consequence of the interplay of active motility v, passive velocity response through Λ , and incompressibilityinduced long-range interactions.

While Eq. (6) demonstrates that two of the eigenvalues of the dynamical matrix **M** are stabilizing, its third and only hydrodynamic eigenvalue $\kappa_c(\phi)$ also has to be negative for the existence of a homogeneous polar phase (see Ref. [36] for the expression of κ_c deep in the ordered phase). Close to the transition (i.e., for $\tilde{\alpha} \to 0^-$), this eigenvalue is known to always turn positive for $\phi = 0$ in dry compressible systems [3], implying a generic instability towards an inhomogeneous, banded phase [12,13,47,48]. In our suspension of active particles in an incompressible fluid, however, the real part of this eigenvalue, in the limit $\tilde{\alpha} \to 0$, becomes isotropic and does not change sign suppressing this instability for all $-\gamma v_p < D_c w/c_0$, which is simply the condition for the stability of the homogeneous flock:

$$\lim_{\tilde{\alpha}\to 0} \kappa_c(0) = -\left[D_c + \frac{c_0 \gamma v_p}{w}\right] q^2.$$
(7)

As a result, the transition to the ordered state in this system may not necessarily proceed via a banded phase unlike in dry flocks.

To determine the effect of noise on the ordered phase of our system, we first compute the static structure factor of angular fluctuations in the presence of a zeromean Gaussian white noise $\xi(\mathbf{r}, t)$ in Eq. (2) with $\langle \xi(\mathbf{r}, t)\xi(\mathbf{r}', t')\rangle = 2B\delta(\mathbf{r} - \mathbf{r}')\delta(t - t')$. In the aligned phase, at small wave vectors, this yields

$$\lim_{q \to 0} S(q) = \lim_{q \to 0} \langle |\theta(\mathbf{q})|^2 \rangle = \frac{Bq^2}{K_p(0)q_x^4 + wq_y^2}.$$
 (8)

The integral of Eq. (8) over wave vectors \mathbf{q} converges, implying a finite amplitude for the angular fluctuations and thus the existence of a long-range ordered aligned polar phase. Furthermore, the dynamic structure factor of angular fluctuations [36] is also singularly modified due to the wave vector-independent relaxation rate—unlike usual systems which spontaneously break a continuous symmetry, it has no zero-frequency pole in the zero wave number limit except when this limit is approached along $\mathbf{q} = q\hat{x}$.

To verify that these conclusions, which we obtained by linearizing Eqs. (2)–(4), is not modified by the inclusion of nonlinearities, we consider the simple case of a flock in which number is not conserved [49]. In this simple case, our model exactly maps onto the polar flock with constraint $\nabla \cdot \mathbf{p} = 0$ studied in Refs. [21] [36]. This mapping ultimately yields exact equal-time exponents of the ordered phase via a transformation to the KPZ equation [36]. This implies that our model, in which there is no explicit constraint on **p**, also has long-range order in two dimensions with the same roughness and anisotropy exponents as in Ref. [21]. This relation between the nonlinear theory of polar swimmers without number conservation in incompressible polar fluid and a theory of a suspension of polar active particles with $\nabla \cdot \mathbf{p} = 0$ is unusual; for instance, an apolar system in an incompressible fluid [10] does not correspond to a theory in which $\nabla \nabla$: **Q** = 0, where **Q** is the apolar order parameter. In addition, removing the condition of fixed concentration introduces additional relevant nonlinearities and spoils the mapping, likely resulting in an ordered phase with distinct behavior.

Beyond the existence of an ordered phase in two dimensions, a hallmark of active matter physics is the possibility of anomalous number fluctuations. To assess their existence in our system, we calculate the static-structure factor of density fluctuations. We find that the number fluctuations scale as \sqrt{N} as in equilibrium systems [36], despite the presence of an active particle current $\propto \mathbf{p}$ in Eq. (4). Indeed, since all components of \mathbf{p} have fast, nonhydrodynamic relaxation rates [50], the polarization aligns with any gradient in concentration, i.e., $\mathbf{p} \sim \nabla c$. Therefore, the active current $\propto \mathbf{p}$ is equivalent to a passive diffusive current, implying equilibriumlike statistics for the concentration fluctuations. This is a result of the nonzero restoring torque for orientational distortions even in the limit of long wavelengths [27].

While the above results are directly relevant for the experiments on single layers of motile particles (such as a

more strongly confined variant of Refs. [2,28], which would have an effectively two-dimensional incompressibility constraint), our theory also describes the effective thickness-averaged dynamics of three-dimensional films of polar active particles in an incompressible fluid of lateral dimension L, confined along the z direction over a length scale $h \ll L$. To demonstrate this, we describe the threedimensional polar fluid by the three-dimensional polarization vector $\mathbf{\bar{p}}(\mathbf{\bar{x}}, t) = (\mathbf{\bar{p}}_{\perp}, \mathbf{\bar{p}}_z)$, velocity $\mathbf{\bar{u}}(\mathbf{\bar{x}}, t) = (\mathbf{\bar{u}}_{\perp}, \mathbf{\bar{u}}_z)$ and particle number $\bar{c}(\bar{\mathbf{x}}, t)$, where $\bar{\mathbf{x}}$ is a three-dimensional position vector, and $\bar{\mathbf{p}}_{\perp}$ and $\bar{\mathbf{p}}_{z}$ and $\bar{\mathbf{u}}_{\perp}$ and $\bar{\mathbf{u}}_{z}$ are the projections transverse to and along the confining direction of the three-dimensional polarization and velocity, respectively. We further denote the three-dimensional gradient by ∇ . The dynamics is described using a standard set of constitutive equations [51,52], on which we use the lubrication approximation of thin-film flows [53] to project our equations in two dimensions, exploiting the fact that the gradients along z are large, namely, $\partial_{\bar{z}} = \mathcal{O}(1/h) \gg \partial_{\bar{x}}, \partial_{\bar{y}}$ [36]. The thickness average of the three-dimensional viscous force density $\bar{\eta}\bar{\nabla}^2\bar{\mathbf{u}}$, with $\bar{\eta}$ being the viscosity of the three-dimensional fluid, yields the frictionlike force $-\Gamma \mathbf{u}$ in Eq. (3) to lowest order in h/L, where $\Gamma = 12\bar{\eta}/h^2$ and **u** is the thickness-averaged velocity in the xy plane, with the three-dimensional incompressibility condition translating into $\nabla \cdot \mathbf{u} = 0$. Beyond this standard viscous force and other passive terms reminiscent of classical hydrodynamics, our three-dimensional dynamical equations feature two three-dimensional active polar force densities, namely, $\overline{\nabla}^2 \overline{\mathbf{p}}$ and $\overline{\nabla} \cdot (\overline{\mathbf{p}} \overline{\mathbf{p}})$ [52]. The former characterizes the fore-aft symmetry around, and hence the motility of, an elementary active object. Upon thickness averaging it leads to the two-dimensional propulsive force \propto **p** of Eq. (3), where **p** is the thickness averaged transverse polarization $\bar{\mathbf{p}}_{\perp}$. The latter active term determines the contractile or extensile character of active units, and leads to a force $\propto \nabla \cdot (\mathbf{pp})$, which is subdominant at large lateral scales and is thus not included in our two-dimensional equations. We similarly obtain Eq. (2) for the polarization field by choosing walls forcing a nontrivial \bar{z} dependence on the polarization $\bar{\mathbf{p}}$ through the boundary conditions $\bar{\mathbf{p}}_{\bar{z}=0} = \hat{z}$ and $\bar{\mathbf{p}}_{\bar{z}=h} = -\hat{z}$. Polarization is generically affected by shear, which we describe through the symmetric strain rate tensor $\mathbf{\bar{U}} = (1/2) [\nabla \mathbf{\bar{u}} + (\nabla \mathbf{\bar{u}})^T].$ This gives rise to two different contributions to $\partial_t \bar{\mathbf{p}}$ in the three-dimensional polarization equation, namely, $\bar{\nabla} \cdot \bar{\mathbf{U}} = (\bar{\nabla} \cdot \bar{\nabla}) \bar{\mathbf{u}}$, which describes the alignment of the polarization vector with the local gradients of the shear rate, and $\mathbf{\bar{p}} \cdot \mathbf{U}$, which describes its alignment to a local shear flow. Again using lubrication arguments, we obtain the first term on the right-hand side of Eq. (2) from the former. The latter leads to the usual flow alignment, which orients the polarity along the two-dimensional velocity gradient and due to its subdominance is not included in

While strictly valid for incompressible systems, our conclusions regarding the nonhydrodynamic relaxation of angular fluctuations and nongiant number fluctuations are also applicable up to large length scales in weakly compressible systems such as fluidless collections of motile particles or active polar rods in a dense bead medium [1]. To characterize such systems, we reintroduce the dynamics of their overall density field ρ , which satisfies the conservation equation $\partial_t \rho = -\nabla \cdot (\rho \mathbf{u})$. We assume a linear relation between small changes in the pressure Π and the density $\rho: \Pi(\rho) - \Pi(\rho_0) \simeq \delta \rho / (\chi \rho_0)$, where χ is the fluid's compressibility, $\delta \rho = \rho - \rho_0$, ρ_0 is the average density and consider a system deep in the ordered phase, implying a fast relaxation of δp to zero. Here, we consider only the coupled dynamics of ρ and θ described by Eqs. (2)–(3) (consideration of fluctuations in c does not change our qualitative result [36]). Defining the nondimensional compressibility $\tilde{\chi} = \chi K_p \rho_0 \Gamma$, we check the fate of the relaxation rate of angular fluctuations in our weakly compressible fluid $(\tilde{\chi} \ll 1)$. Focusing on the direction $\phi = \pi/2$, which displays the strongest incompressibility-induced stabilization in the incompressible case, we calculate the eigenvalues associated with the coupled density and orientational dynamics $(\delta \rho, \theta)$:

$$\kappa_{\pm}' = -\frac{w\tilde{q}^2}{2\tilde{\chi}} \left[1 + \tilde{\chi} \pm \sqrt{(1 - \tilde{\chi})^2 - \frac{4\tilde{\chi}}{\tilde{q}^2}} \right], \qquad (9)$$

with $\tilde{q} = q\sqrt{K_p/w}$. $\kappa'_+ \sim -w\tilde{q}^2/\tilde{\chi}$ diverges as $\tilde{\chi} \to 0$ (see Fig. 1), indicating that the pressure homogenizes quickly in

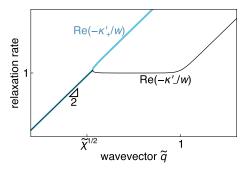


FIG. 1. A log-log plot of the dimensionless decay rates for the two eigenmodes associated with the coupled dynamics of the total density and angular fluctuations in a weakly compressible system [Eq. (9)]. While both modes display a diffusive (slope 2) relaxation for small dimensionless wave vector \tilde{q} , taking the dimensionless compressibility $\tilde{\chi}$ to zero shifts the blue curve to the left, implying that the relaxation rate associated with any finite \tilde{q} goes to infinity. Meanwhile, the second relaxation rate (black curve) develops a wide \tilde{q} -independent plateau, mimicking the nonhydrodynamic relaxation rate associated with a truly incompressible system.

a nearly incompressible medium and the orientation θ relaxes at a rate κ'_- . In an incompressible system, this relaxation rate went to a finite limit as $q \to 0$. This is not strictly the case here, as $\kappa'_- \propto -\tilde{q}^2$ for wave vectors $\tilde{q} < \tilde{\chi}^{1/2}$. However, κ'_- has a plateau for intermediate wave vectors $\tilde{\chi}^{1/2} < \tilde{q} < 1$ that extends to $q \to 0$ for $\tilde{\chi} \to 0$. As the smallest wave vector realizable in a system of size *L* is π/L , a weakly compressible polar fluid is indistinguishable from a truly incompressible one for $L \ll 1/\sqrt{\tilde{\chi}}$, and is, therefore, deprived of giant-number fluctuations, while larger systems display it.

While our discussion has thus far focused on polar particles that align with the local flow (w > 0), consistent with existing experiments [1,2], systems with w < 0 are conceivable [54]. One possibility would be particles that point opposite to the local flow ($\Lambda < 0$) while moving along their polarity (v > 0). In this case the homogeneous ordered phase is unstable and all perturbations with wave number smaller than $\sqrt{K/(|w| \sin^2 \phi)}$ grow exponentially. This instability, which leads to a finite correlation length for the polarization field, is distinct from the one that leads to a polarized, concentration-banded state in dry active systems [12]. Nevertheless, since the polarization correlation diverges precisely along the ordering direction, a banded chevron state with counterpropagating polar lines may be the steady state in this case.

The analysis presented here clarifies theoretical expectations on the structure of number fluctuations of motile systems in confined incompressible fluid, which have been a source of confusion [2]. It moreover provides a framework to analyze the dynamics of numerous guasi-2D biological systems, which are almost invariably immersed in an incompressible fluid, from the scale of the intracellular medium [30] to that of crawling cell layers [55]. Its predictions of nonhydrodynamic relaxation, the possible absence of a banded phase at the disorder-order transition, and normal number fluctuations should be testable in any of these contexts or in artificial chemotactic colloids [56]. Our results are also largely applicable to weakly compressible systems such as dense granular layer of polar rods or dense mixtures of rods and beads [1]. From a theoretical standpoint, our work establishes that hydrodynamic interactions singularly alter equal-time as well as time-displaced correlations of the orientation even when the long-wavelength fluctuations of the fluid momentum density are damped by friction with a substrate via a nonequilibrium analog of the classic Anderson-Higgs mechanism. Alongside the breaking of the Hohenberg-Mermin-Wagner theorem [4,9] and existence of anomalously large fluctuations [3,5,9], this finding constitutes another striking violation of equilibrium expectations in active matter.

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- N. Kumar, H. Soni, S. Ramaswamy, and A. K. Sood, Nat. Commun. 5, 4688 (2014).
- [2] A. Bricard, J.-B. Caussin, N. Desreumaux, O. Dauchot, and D. Bartolo, Nature (London) 503, 95 (2013).
- [3] M. C. Marchetti, J. F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, M. Rao, and R. Aditi Simha, Rev. Mod. Phys. 85, 1143 (2013).
- [4] J. Toner, Y. Tu, and S. Ramaswamy, Ann. Phys. (Amsterdam) 318, 170 (2005).
- [5] S. Ramaswamy, Annu. Rev. Condens. Matter Phys. 1, 323 (2010).
- [6] J. Prost, F. Jülicher, and J.-F. Joanny, Nat. Phys. 11, 111 (2015).
- [7] F. Jülicher, K. Kruse, J. Prost and J. Joanny, Phys. Rep. 449, 3 (2007).
- [8] F. Jülicher, S. W. Grill, and G. Salbreux, Rep. Prog. Phys. 81, 076601 (2018).
- [9] J. Toner and Y. Tu, Phys. Rev. E 58, 4828 (1998).
- [10] A. Maitra, P. Srivastava, M. C. Marchetti, J. S. Lintuvuori, S. Ramaswamy, and M. Lenz, Proc. Natl. Acad. Sci. U.S.A. 115, 6934 (2018).
- [11] S. Ramaswamy, R. A. Simha, and J. Toner, Europhys. Lett. 62, 196 (2003).
- [12] E. Bertin, M. Droz, and G. Grégoire, J. Phys. A 42, 445001 (2009).
- [13] J. B. Caussin, A. Solon, A. Peshkov, H. Chaté, T. Dauxois, J. Tailleur, V. Vitelli, and D. Bartolo, Phys. Rev. Lett. 112, 148102 (2014); A. Solon, H. Chaté, and J. Tailleur, Phys. Rev. Lett. 114, 068101 (2015).
- [14] R. A. Simha and S. Ramaswamy, Phys. Rev. Lett. 89, 058101 (2002).
- [15] D. Saintillan and M. J. Shelley, Phys. Rev. Lett. 100, 178103 (2008).
- [16] N. Liron and S. Mochon, J. Eng. Math. 10, 287 (1976).
- [17] S. Ramaswamy, Adv. Phys. 50, 297 (2001).
- [18] T. Brotto, J.-B. Caussin, E. Lauga, and D. Bartolo, Phys. Rev. Lett. **110**, 038101 (2013).
- [19] B. Cui, H. Diamant, B. Lin, and S. A. Rice, Phys. Rev. Lett. 92, 258301 (2004).
- [20] A. Kashuba, Phys. Rev. Lett. 73, 2264 (1994).
- [21] L. Chen, C.-F. Lee, and J. Toner, Nat. Commun. 7, 12215 (2016).
- [22] L. Chen, J. Toner, and C. F. Lee, New J. Phys. 17, 042002 (2015).

- [23] P. C. Martin, O. Parodi, and P. S. Pershan, Phys. Rev. A 6, 2401 (1972).
- [24] Y. Nambu, Phys. Rev. 117, 648 (1960); J. Goldstone and A. Salam, Phys. Rev. 127, 965 (1962).
- [25] P. W. Anderson, Phys. Rev. 130, 439 (1963).
- [26] P. W. Higgs, Phys. Rev. Lett. 13, 508 (1964); F. Englert and R. Brout, Phys. Rev. Lett. 13, 321 (1964); G. S. Guralnik, C. R. Hagen, and T. W. B. Kibble, Phys. Rev. Lett. 13, 585 (1964).
- [27] Bricard *et al.* [2] do find conventional number fluctuations, using a dynamical model that is essentially equivalent to ours, as a consequence of screened splay fluctuations but incorrectly conclude that this reference state is unstable thanks to the erroneous finding of a bend instability. Further, neither the theoretical treatment of Ref. [2] nor ours actually applies to the experimental systems considered in Refs. [2,28]. In particular, though Ref. [2] claims to find conventional number fluctuations in their experiment, this claim is incorrect, as is acknowledged in Ref. [28]; number fluctuations in both Refs. [2,28] are giant.
- [28] D. Geyer, A. Morin, and D. Bartolo, Nat. Mater. 17, 789 (2018).
- [29] V. Narayan, S. Ramaswamy, and N. Menon, Science 317, 105 (2007).
- [30] V. Schaller, C. Weber, C. Semmrich, E. Frey, and A. R. Bausch, Nature (London) **467**, 73 (2010).
- [31] T. Butt, T. Mufti, A. Humayun, P. B. Rosenthal, S. Khan, S. Khan, and J. E. Molloy, J. Biol. Chem. 285, 4964 (2010).
- [32] D. Kaiser, Nat. Rev. Microbiol. 1, 45 (2003).
- [33] P. G. de Gennes and J. Prost, *The Physics of Liquid Crystals*, 2nd ed. (Clarendon, Oxford, 1993).
- [34] W. Kung, M. C. Marchetti, and K. Saunders, Phys. Rev. E 73, 031708 (2006).
- [35] L. P. Dadhichi, A. Maitra, and S. Ramaswamy, J. Stat. Mech. (2018) 123201.
- [36] See Supplemental Material at http://link.aps.org/ supplemental/10.1103/PhysRevLett.124.028002 for detailed calculations, which includes Refs. [37–43].
- [37] L. Giomi, T. B. Liverpool, and M. C. Marchetti, Phys. Rev. E 81, 051908 (2010).
- [38] Y. Hatwalne, S. Ramaswamy, M. Rao, and R. Aditi Simha, Phys. Rev. Lett. 92, 118101 (2004).
- [39] S. Ramaswamy and G. F. Mazenko, Phys. Rev. A 26, 1735 (1982).
- [40] A Maitra, Ph. D. thesis, Indian Institute of Science, 2014.

- [41] P. M. Chaikin and T. C. Lubensky, *Principles of Condensed Matter Physics* (Cambridge University Press, Cambridge, England, 2000).
- [42] N. D. Mermin, Phys. Rev. 176, 250 (1968).
- [43] T. C. Lubensky, S. Ramaswamy, and J. Toner, Phys. Rev. B 33, 7715 (1986).
- [44] J. Toner, Phys. Rev. E 86, 031918 (2012).
- [45] The coefficient v_p is generally independent of v. The former describes the speed of active particle current and can be measured by imaging the flock while the latter leads to a force proportional to polarization, leading to a flow, and the ratio v/Γ can be measured by measuring the fluid flow due to a single motile unit using particle image velocimetry techniques.
- [46] V. Maleev, Zh. Eksp. Teor. Fiz. **70**, 2374 (1976) [V. MaleevSov. Phys. JETP **43**, 1240 (1976)]; V. L. Pokrovsky and M. V. Feigelman, Sov. Phys. JETP **72**, 557 (1977); Y. Yafet, J. Kwo, and E. M. Gyorgy, Phys. Rev. B **33**, 6519 (1986).
- [47] A. P. Solon et al., Phys. Rev. E 92, 062111 (2015).
- [48] A. P. Solon, H. Chate, and J. Tailleur, Phys. Rev. Lett. 114, 068101 (2015).
- [49] J. Toner, Phys. Rev. Lett. 108, 088102 (2012).
- [50] Except for a perturbation with a wave vector purely along \hat{x} , i.e., with $q_y = 0$, but the equations for θ and δc get decoupled for such a perturbation and δc has a purely diffusive dynamics.
- [51] A. Maitra, P. Srivastava, M. Rao, and S. Ramaswamy, Phys. Rev. Lett. **112**, 258101 (2014).
- [52] L. Giomi and M. C. Marchetti, Soft Matter 8, 129 (2012).
- [53] H. A. Stone, in *Nonlinear PDEs in Condensed Matter and Reactive Flows*, NATO Science Series C: Mathematical and Physical Sciences Vol. 569, edited by H. Berestycki and Y. Pomeau (Kluwer Academic, Dordrecht, Netherlands, 2002); A. Oron, S. H. Davis, and S. G. Banko, Rev. Mod. Phys. 69, 931 (1997).
- [54] R. Gupta and R. Gupta (unpublished).
- [55] M. Poujade, E. Grasland-Mongrain, A. Hertzog, J. Jouanneau, P. Chavrier, B. Ladoux, A. Buguin, and P. Silberzan, Proc. Natl. Acad. Sci. U.S.A. 104, 15988 (2007);
 L. Petitjean, M. Reffay, E. Grasland-Mongrain, M. Poujade, B. Ladoux, A. Buguin, and P. Silberzan, Biophys. J. 98, 1790 (2010); O. du Roure, A. Saez, A. Buguin, R. H. Austin, P. Chavrier, P. Silberzan, and B. Ladoux, Proc. Natl. Acad. Sci. U.S.A. 102, 2390 (2005).
- [56] S. Saha, R. Golestanian, and S. Ramaswamy, Phys. Rev. E 89, 062316 (2014).