No many-scallop theorem: Collective locomotion of reciprocal swimmers

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To achieve propulsion at low Reynolds number, a swimmer must deform in a way that is not invariant under time-reversal symmetry; this result is known as the scallop theorem. However, there is no many-scallop theorem. We demonstrate here that two active particles undergoing reciprocal deformations can swim collectively; moreover, polar particles also experience effective long-range interactions. These results are derived for a minimal dimers model, and generalized to more complex geometries on the basis of symmetry and scaling arguments. We explain how such cooperative locomotion can be realized experimentally by shaking a collection of soft particles with a homogeneous external field.

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Microorganisms rely on their ability to swim in order to achieve a variety of biological tasks, including sensing, targeting, or feeding [1]. Well-studied examples include bacteria, spermatozoa, and ciliated protozoa [1–3]. Given the recent advances in the construction of complex colloidal assembly [4,5] and in the coupling of biological machines to artificial microstructures [6], man-made functional microswimmers are expected to catch up with real microorganisms [7].

A fundamental challenge in designing artificial microswimmers lies in the constraints of the so-called scallop theorem [8]. Since at small scales, or at low Reynolds number, the Stokes flow equations are linear and time reversible, swimming can only be achieved by a sequence of shape deformations noninvariant under time reversal, or nonreciprocal; the prototypical reciprocal movement is that of a scallop which opens and closes its shell [Fig. 1(a), left]. However, there is no many-scallop theorem [9], and the sequence of deformations undergone by a collection of reciprocal swimmers is, in general, nonreciprocal [Fig. 1(a), right].

In this paper, starting from this simple observation, we reveal a new mode of locomotion for hydrodynamically coupled reciprocal active particles. We show that such active particles can modulate their relative distance by exploiting hydrodynamic coupling, thereby inducing on each other velocity fields which do not average out to zero and allowing for collective motion to occur. Such collective motion is quantitatively different from the more conventional propulsion of nonreciprocal swimmers as we emphasize below. In addition, we show that a set of nonidentical reciprocal active particles experiences long-range effective interactions which can either be attractive or repulsive depending on the particles geometry. These results are demonstrated rigorously for a pair of force-free reciprocal dimers, and a generalization to different geometries is offered on the basis of symmetry principles and scaling arguments. Experimentally, we show that simple elastic particles shaken by a homogeneous oscillating external field could be exploited to obtain collective locomotion.

Following the minimal framework introduced by Golestanian and co-workers [10,11], we consider a collection of prototypical active particles, force-free dimers, for which we neglect the flow disturbance created by the links joining them [see Fig. 1(b)]. The *i*th dimer is composed of two bodies, i_1 and i_2 , separated by the time-varying distance $\ell_i(t) = x_{i_2} - x_{i_1}$, where x_{α} denotes the position of body $\alpha = i_1, i_2$ along the *x* axis. The linearity of the Stokes equation implies that the motion of each body in a dimer is linearly related to the forces f_{β} , acting on the bodies from all dimers

$$\dot{x}_{\alpha} = \sum_{\beta} H_{\alpha\beta} f_{\beta}, \tag{1}$$

where the $\{H_{\alpha\beta}\}$ are the hydrodynamic mobilities of the bodies $(\beta=j_1,j_2)$. We assume that each dimer is force-free,



FIG. 1. (Color online) (a) A body deforming its shape in a reciprocal fashion, such as a scallop, cannot move on average at low Reynolds numbers (left, $\langle V \rangle = 0$), whereas nonreciprocal deformation leads to net propulsion (right, $\langle V \rangle \neq 0$). (b) Two force-free dimers interacting hydrodynamically. The dimers are composed of two solid spheres (more generally, bodies), of radii $\{a_1, a_2\}$ and $\{b_1, b_2\}$, have lengths $\ell_a(t)$ and $\ell_b(t)$, and are separated by the distance d(t).

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 $f_{i_1}+f_{i_2}=0$, and define $f_i \equiv f_{i_1}=-f_{i_2}$ [Fig. 1(b)]. The center of the *i*th dimer is denoted $x_i \equiv (x_{i_1}+x_{i_2})/2$.

(a) Single dimer. We first consider the case of an isolated active dimer, labeled a. In that case, we have $\dot{x}_a = H(\ell_a)f_a$ and the dimer elongation satisfies $\dot{\ell}_a = \mu_a(\ell_a)f_a$. Hence, we have $\dot{x}_a = H(\ell_a)\dot{\ell}_a/\mu_a(\ell_a)$, which is an exact derivative and therefore averages to zero over time, $\langle \dot{x}_a \rangle = 0$, for any periodic sequence of forces or deformations imposed to the dimer. This is the scallop theorem.

(b) Two dimers. We now consider the case of two dimers (a and b). Although the dimers are not able to swim when alone, we show how interactions through the viscous fluid enable collective motion. We restrain our analysis to wide and widely separated dimers in an unbounded fluid; if *d* is their relative distance, and *R* the typical size of the bodies in the dimers, we consider the limit $R \ll \ell_i \ll d$ for which the mobilities in Eq. (1) are given by the Green's function *H* of the Stokes equation in the appropriate geometry [12]: $H_{\alpha\beta} \equiv H(\alpha_\beta - x_\alpha)$ if $\alpha \neq \beta$, $H_{\alpha\alpha} \equiv H(\alpha)$ [13]. Performing a Taylor expansion for the dynamics of the four bodies, Eq. (1), we obtain at leading order in 1/d,

$$\dot{x}_a = M_a f_a - [\partial_x H(x_b - x_a)]\ell_b f_b, \qquad (2a)$$

$$\dot{x}_b = M_b f_b + [\partial_x H(x_b - x_a)]\ell_a f_a, \qquad (2b)$$

$$\dot{\ell}_a = \mu_a(\ell_a)f_a + \mu_{ab}\ell_a\ell_bf_b, \qquad (2c)$$

$$\dot{\ell}_b = \mu_b(\ell_b)f_b + \mu_{ab}\ell_a\ell_bf_a, \qquad (2d)$$

where we have defined the mobility coefficients associated with the position and the elongation of each dimer, respectively: $M_i = [H(i_1) - H(i_2)]/2$, $\mu_{ab} = \partial_{xx}H(d)$, and $\mu_i(\ell_i) = 2H(\ell_i) - H(i_1) - H(i_2)$. We further restrain our analysis to small amplitude reciprocal motion of each dimer around the time average length, $\overline{\ell_i} = \langle \ell_i \rangle$ (in all that follows brackets stand for time average). More precisely, if we write $\ell_i = \overline{\ell_i} + O(\epsilon, \epsilon^2)$ and $f_i = O(\epsilon, \epsilon^2)$, we keep terms up to $O(\epsilon^2)$ in Eqs. (2a)–(2d). We can then compute the average collective and relative swimming speeds of the dimers, $\langle V \rangle \equiv \langle \dot{x}_b + \dot{x}_a \rangle/2$ and $\Delta V \equiv \langle \dot{x}_b - \dot{x}_a \rangle$, respectively. To do so, we distinguish the two ways in which the dimers can be physically actuated.

(c) Force-driven motion. We first consider the case where the internal forces f_i are specified. This is analogous to biological swimmers possessing force-generating units (the axoneme for eukaryotic cells [14], the rotary motor for bacteria such as *E. coli* [15]). In that case, we assume the internal force to be known, $O(\epsilon)$, and time periodic. The forcedisplacement relation, Eqs. (2c) and (2d) can then be linearized, and after some straightforward algebra, we obtain $(\langle V \rangle, \Delta V/2) = \mu_{ab}/2[\bar{\ell}_a M_b(-, +)\bar{\ell}_b M_a]\langle f_a \int f_b \rangle$. In the case of spherical bodies in an unbounded fluid, this simplifies to

$$\langle V \rangle = \left[\frac{\overline{\ell}_a(b_2 - b_1)}{b_1 b_2} - \frac{\overline{\ell}_b(a_2 - a_1)}{a_1 a_2} \right] \frac{\langle f_a \int f_b \rangle}{48 \pi^2 \eta^2 d^3}, \quad (3a)$$

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$$\Delta V = \left[\frac{\overline{\ell}_a(b_2 - b_1)}{b_1 b_2} + \frac{\overline{\ell}_b(a_2 - a_1)}{a_1 a_2}\right] \frac{\langle f_a \int f_b \rangle}{24\pi^2 \eta^2 d^3}, \quad (3b)$$

where we have used the Oseen kernel $H(x)=1/(4\pi\eta x)$ (x>0), and $H(\alpha)=1/(6\pi\eta a_{\alpha})$, with a_{α} the radius of the sphere α . The results of Eq. (3) show that, generically, the scallop theorem breaks down for two active particles interacting hydrodynamically: taken individually, these particles cannot move, but when interacting through the fluid, they display collective motion $(\langle V \rangle \neq 0)$, and experience an effective long-range interaction $(\Delta V \neq 0)$, both of which decay in space as $1/d^3$. The direction and sign of the collective and relative speeds depend on the geometry and actuation of the dimers; for sinusoidal forcing $f_i(t)=\overline{f_i}\cos(\omega t+\phi_i)$, we have $\langle f_a \int f_b \rangle = \overline{f_a} \overline{f_b} \sin(\phi_b - \phi_a)/2\omega$, and locomotion occurs if the two particles are actuated with phase differences.

To emphasize the difference between this collective swimming mode and the (conventional) propulsion of nonreciprocal swimmers, we consider a "linked-spheres swimmer" [11,16] made of two rigidly connected dimers [d(t) is kept constant] and obtain $\langle V \rangle = 0$ at order $1/d^3$. This important difference reveals that, physically, locomotion of the pair of dimers occurs primarily because their relative distance is oscillating in time, and therefore the flow fields seen by each dimer does not average to zero. Hence fluid-mediated forces are the crucial ingredient leading to collective locomotion.

(d) Displacement-driven motion. We now assume the sequence of deformation of each dimer, $\ell_i(t)$, to be specified and time periodic, $\ell_i = \bar{\ell}_i + \delta \ell_i(t)$, with $\delta \ell_i(t) = O(\epsilon)$. This is the relevant limit for (robotic) man-made microswimmers. We invert the force-displacement relationship, Eqs. (2c) and (2d), and after some tedious but straightforward algebra we obtain locomotion and relative motion at speeds $(\langle V \rangle, \frac{\Delta V}{2}) = \frac{\bar{\ell}_a \bar{\ell}_b \mu_{ab}}{2 \mu_a \mu_b} [\frac{M_b}{\mu_b} \frac{\partial \mu_b}{\partial \ell_b} (-, +) \frac{M_a}{\mu_a} \frac{\partial \mu_a}{\partial \ell_a}] \langle \delta \ell_b \delta \dot{\ell}_a \rangle$. For spherical bodies in an unbounded fluid we now have

$$\langle V \rangle = \left[\frac{\overline{\ell}_a(b_2 - b_1)}{\overline{\ell}_b(b_1 + b_2)} - \frac{\overline{\ell}_b(a_2 - a_1)}{\overline{\ell}_a(a_1 + a_2)} \right] \frac{9\widetilde{a}\widetilde{b}\langle \delta\ell_b \delta\dot{\ell}_a \rangle}{4d^3}, \quad (4a)$$

$$\Delta V = \left[\frac{\overline{\ell}_a(b_2 - b_1)}{\overline{\ell}_b(b_1 + b_2)} + \frac{\overline{\ell}_b(a_2 - a_1)}{\overline{\ell}_a(a_1 + a_2)} \right] \frac{9\widetilde{a}\widetilde{b}\langle \delta\ell_b \delta\dot{\ell}_a \rangle}{2d^3}, \quad (4b)$$

where we have defined $\tilde{i}=i_1i_2/(i_1+i_2)$ (i=a,b).

Similarly to force-driven motion, the scallop theorem does not hold for a pair of reciprocal bodies, and locomotion arises if there is a nonzero phase difference between the deformation of each particle. To further stress on the difference with a nonreciprocal swimmer made of two mechanically connected dimers, we note that we would obtain in this case a $O(1/d^3)$ swimming velocity [17], but with a sign opposite to that arising from hydrodynamic interactions—Eq. (4a)—as shown in Fig. 2(d).

(e) Identical swimmers. In the particular case where the two dimers are identical $(a_i=b_i, i=1,2, \text{ and } \overline{\ell}_a=\overline{\ell}_b\equiv\ell)$, the results of Eqs. (3a) and (4a) cancel out. One needs to go to higher order in the asymptotic expansions to obtain the



FIG. 2. (Color online) Dynamics of identical dimers interacting hydrodynamically. Units are chosen so that $\delta \ell_a(t) = \cos(t), \ \delta \ell_b(t)$ $=\sin(t)$. (a) Mean displacement, $\langle \int V dt \rangle$, for two mirror-images polar dimers ($a_1 \neq a_2$, solid line); mean displacement for two mirrorimages apolar dimers $(a_1=a_2)$, dash-dotted line); mean distance, $\int \Delta V dt$, between the two dimers (polar and apolar cases, dashed line). (b) Mean displacement (solid line) and mean separation distance (dashed line) for two identical polar dimers pointing in the same direction. (c) same as (b) but for dimers pointing in the opposite direction; note the change in the sign of the dimer-dimer effective interaction. (d) Comparison between the swimming speed of two active dimers and a single swimmer made of two rigidly connected dimers (constant d). In all figures, the lengths ℓ_a and ℓ_b oscillate with the same amplitude and frequencies, and a relative phase of $\pi/2$. In the chosen units, $\overline{\ell}_a = \overline{\ell}_b = 10$, $d|_{t=0} = 100$, $a_1 = 3$, $a_2=3/2$ for the polar dimers and $a_1=a_2=2$ in the apolar case.

swimming kinematics, which is readily done, and locomotion is obtained at order $1/d^4$, with velocities

$$\langle V \rangle = \frac{\ell^2 \langle f_a \int f_b \rangle}{16\pi^2 \eta^2 \tilde{a} d^4} \quad \text{and} \quad \langle V \rangle = \frac{9 \tilde{a} \ell^2 \langle \delta \ell_a \delta \dot{\ell}_b \rangle}{4 d^4} \tag{5}$$

for force- and displacement-driven motion respectively.

In Figs. 2(a)-2(c) we highlight the main features of the collective dynamics of a pair of identical dimers in the case of displacement-driven motion, by integrating numerically Eqs. (4b) and (5); results for force-driven motion are similar. We first show in Fig. 2(a) that, on average, mirror-symmetric swimmers remain at the same relative distance and swim collectively with a constant velocity. When the swimmers do not display mirror-image symmetry, we show in Fig. 2(b) and 2(c) that they undergo a repulsive or an attractive effective interaction depending on their relative orientation. The dimers are separating or approaching at rate $d \sim \pm 1/d^3$, and therefore $d \sim (t_0 \pm t)^{1/4}$; accordingly, the mean speed decreases as $\langle V \rangle \sim (t_0 \pm t)^{-1}$, and the distance traveled by the swimmers can be arbitrarily (logarithmically) large, $\int \langle V \rangle dt$ $\sim \log(t_0 \pm t)$ [18]. Note that in the case of relative attraction, a proper description of the near-contact hydrodynamics would regularize the finite-time singularity displayed in Fig. 2(c); in an experiment, short-range surface forces (such as

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van der Waals) would lead to self-assembly of the two dimers into a four-spheres nonreciprocal swimmer.

(f) Generalization. The results above demonstrate the emergence of collective motion and of long-range interactions between two dimers embedded in a viscous fluid. A generalization of these results can be offered as follows. Firstly, our far-field results [above Eqs. (3) and (4)] are valid beyond the spherical-dimer infinite-fluid setup, in particular, in confined geometries such as Hele-Shaw cells or microfluidics systems, and for dimers composed of particles of any shape.

Secondly, Eqs. (3) and (4) also apply for stochastic fluctuations of the length of each dimer [11,16], and any correlation between the noisy shaking sources acting on each dimer is seen to lead to nonzero swimming velocities and effective interactions between the two active objects.

Thirdly, the $1/d^3$ spatial decay of the velocities with the interdimer distance in Eqs. (3) and (4) could have been anticipated since the locomotion arises from the rectification of interacting force dipoles decaying as $1/x^2$ at long distance [19]; this scaling argument also holds for any pair of active particles having a single deformation degree of freedom aligned with the *x* axis. In the small deformations limit, we expect their collective and relative swimming velocities to be of the form

$$\langle V \rangle \sim \left\langle f_a \int f_b \right\rangle \sum_{n \ge 3} \frac{\alpha_n}{d^n}, \quad \Delta V \sim \left\langle f_a \int f_b \right\rangle \sum_{n \ge 3} \frac{\gamma_n}{d^n}, \quad (6)$$

$$\langle V \rangle \sim \langle \delta \ell_b \delta \dot{\ell}_a \rangle \sum_{n \ge 3} \frac{\beta_n}{d^n}, \quad \Delta V \sim \langle \delta \ell_b \delta \dot{\ell}_a \rangle \sum_{n \ge 3} \frac{\delta_n}{d^n}$$
(7)

for force- and displacement-driven motion, respectively, and where $\{\alpha_n, \beta_n, \gamma_n, \delta_n\}$ depend solely on the shape of the particles [20]. Note from Eqs. (3b), (4a), and (4b) that for two mirror-image particles, $\gamma_3 = \delta_3 = 0$. This result is actually true at all orders, and two swimmers with mirror-image symmetry verify $\Delta V=0$. Indeed the flow and pressure fields induced by the beating of two mirror-image dimers are invariant under the combination of time-reversal and mirror symmetries. Consequently, ΔV , which has the symmetry of a velocity gradient, transforms into $-\Delta V$, and therefore $\Delta V=0$. Similarly, we have $\alpha_3 = \beta_3 = 0$ for identical dimers; this is a consequence of the two (rectified) dipoles having opposite contributions on each dimer, and will generally be true for a pair of identical particles.

Fourthly, beyond the one-dimensional models considered in this paper, we expect all types of reciprocal motion, including those with three-dimensional shape deformation, and with nontrivial relative orientation, to display collective motion induced by hydrodynamic interactions. Finally, although we have emphasized locomotion in this paper, our results could be extended to the dual problem of pumping fluid by anchored bodies.

(g) Soft swimmers. We now turn to a discussion of the experimental realization of these ideas. Actuating a collection of active particles with out-of-phase conformational changes is difficult, and it would be preferable to devise a framework where an homogeneous external field could pro-

duce directed locomotion. We show below that this is theoretically possible if the particles are soft: indeed, since soft particles in a viscous fluid possess relaxation times, different particles will naturally react to an external shaking with phase differences, and locomotion will ensue. Practical examples of soft-particle actuation could include bending of magnetic filaments by magnetic fields [7], temperature or light actuation of liquid-crystal elastomers [21,22], or selfsustained chemical reactions for swelling of gels [23].

We thus consider a pair of force-free apolar and identical dimers (radius a, average length ℓ) subject to a homogeneous external shaking. We write $f_i = f^{\text{shake}} + f_i^{\text{relax}}$, for i = a, b, where the force f^{shake} is externally produced and the same for each dimer (homogeneous forcing). The force f_i^{relax} is the internal (elastic) response of the dimer, and we write $f_i^{\text{relax}} = k_i \delta \ell_i$, where k_i is the dimer stiffness; in that case, the intrinsic dynamics of each active particle is characterized by a relaxation time scale $\tau_i = 3\pi \eta a/k_i$. Assuming a monochromatic shaking $f^{\text{shake}} = f_0 \cos(\omega t)$ for simplicity, integration of Eqs. (2c) and (2d) leads to collective motion with speed

$$\langle V \rangle = \left[\frac{(\tau_a - \tau_b)(\omega^2 \tau_a \tau_b)}{(1 + \omega^2 \tau_a^2)(1 + \omega^2 \tau_b^2)} \right] \frac{\ell^2 f_0^2}{16\pi^2 \eta^2 d^4 a},$$
(8)

and $\Delta V=0$ by (geometrical) symmetry. We see that, under homogeneous forcing, the only condition necessary to obtain locomotion is $\tau_a \neq \tau_b$. Locomotion always occurs in the direction of decreasing relaxation time, i.e., the stiff dimer is pulling the soft one; optimal locomotion occurs when the system is actuated with frequency $\omega \sim (\tau_a \tau_b)^{-1/2}$ and when the ratio of relaxation times is large.

- [1] D. Bray, Cell Movements (Garland Publishing, New York, NY, 2000).
- [2] J. Lighthill, SIAM Rev. 18, 161 (1976).
- [3] C. Brennen and H. Winet, Annu. Rev. Fluid Mech. 9, 339 (1977).
- [4] V. N. Manoharan, M. T. Elsesser, and D. J. Pine, Science 301, 483 (2003)
- [5] C. Goubault, P. Jop, M. Fermigier, J. Baudry, E. Bertrand, and J. Bibette, Phys. Rev. Lett. 91, 260802 (2003).
- [6] R. K. Soong, G. D. Bachand, H. P. Neves, A. G. Olkhovets, H. G. Craighead, and C. D. Montemagno, Science 290, 1555 (2000).
- [7] R. Dreyfus, J. Baudry, M. L. Roper, M. Fermigier, H. A. Stone, and J. Bibette, Nature (London) 437, 862 (2005).
- [8] E. M. Purcell, Am. J. Phys. 45, 3 (1977).
- [9] J. Koiller, K. Ehlers, and R. Montgomery, J. Nonlinear Sci. 6, 507 (1996).
- [10] A. Najafi and R. Golestanian, Phys. Rev. E 69, 062901 (2004).
- [11] R. Golestanian and A. Ajdari, Phys. Rev. E 77, 036308 (2008).
- [12] J. Happel and H. Brenner, Low Reynolds Number Hydrodynamics (Prentice Hall, Englewood Cliffs, NJ, 1965).
- [13] In all generality, H can include the effect of nearby walls, or model dimers composed of nonspherical bodies.
- [14] B. Alberts, D. Bray, J. Lewis, M. Raff, K. Roberts, and J. D. Watson, The Molecular Biology of the Cell (Garland, New York, 1994).
- [15] H. C. Berg, Annu. Rev. Biochem. 72, 19 (2003).

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A final relevant example is the case where one dimer is purely passive, i.e., its elongation is not coupled to the external field. Specifically, we assume dimer a to be actively shaken, with $f_a^{\text{shake}} = f_0 \cos(\omega t)$, while dimer b is passive, and $f_{b}^{\text{shake}} = 0$. In that case, the beating of the passive dimer arises from the hydrodynamic interactions with the active dimer, and its amplitude is a function of the distance d. Collective motion arises with speed

$$\langle V \rangle = -\left[\frac{\omega^2 \tau_a \tau_b}{(1+\omega^2 \tau_a^2)(1+\omega^2 \tau_b^2)}\right] \frac{3 \tau_a \ell^4 f_0^2}{32 \pi^2 \eta^2 d^7},\tag{9}$$

and the active particle is seen to "pull" the passive one even if the two dimers are geometrically and mechanically identical.

(h) Perspective. Using a simple model, we have shown in this paper how two bodies with reciprocal deformation can exploit hydrodynamic interactions to obtain collective locomotion and effective long-range interactions. Can one expect large scale directed motion, coarsening, or ordering to occur in suspensions of reciprocal active particles? Although such cooperative effects have already been demonstrated for coupled active (but non-self-propelled) particles in several different contexts [24-26], the generalization of our results to a large number of active particles remains an open challenge.

Note added. Recently, we became aware of a study submitted by Alexander and Yeomans on a similar problem [27].

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- [16] R. Golestanian and A. Ajdari, Phys. Rev. Lett. 100, 038101 (2008).
- [17] $\langle V \rangle = [\bar{\ell}_a(\frac{b_1 b_2}{b_1 b_2}) \bar{\ell}_b(\frac{a_1 a_2}{a_1 a_2})] 3a\tilde{b} \langle \delta \ell_b \delta \dot{\ell}_a \rangle / 4d^3.$ [18] If the dimers are not identical, we have the scaling $\langle V \rangle$ ~1/d³, resulting in $\int \langle V \rangle dt \sim t^{1/4}$ in the case of separating swimmers and $\int \langle V \rangle dt \sim O(1)$ otherwise.
- [19] C. M. Pooley, G. P. Alexander, and J. M. Yeomans, Phys. Rev. Lett. 99, 228103 (2007).
- [20] Linear and quadratic terms proportional to $\delta \dot{\ell}_i$ and $\delta \ell_i \delta \dot{\ell}_i$ have a zero mean. Thus, at lowest order, the only nonzero term has the antisymmetric form $\langle \delta \ell_b \delta \dot{\ell}_a - \delta \ell_a \delta \dot{\ell}_b \rangle = 2 \langle \delta \ell_b \delta \dot{\ell}_a \rangle$ for reciprocal deformations sequences [16].
- [21] A. Buguin, M. Li, P. Silberzan, B. Ladoux, and P. Keller, J. Am. Chem. Soc. 128, 1088 (2006).
- [22] M. Camacho-Lopez, H. Finkelmann, P. Palffy-Muhoray, and M. Shelley, Nature Mater. 3, 307 (2004).
- [23] S. Maeda, Y. Hara, T. Sakai, R. Yoshida, and S. Hashimoto, Adv. Mater. (Weinheim, Ger.) 19, 3480 (2007).
- [24] M. Badoual, F. Jülicher, and J. Prost, Proc. Natl. Acad. Sci. U.S.A. 99, 6696 (2002).
- [25] S. Ramaswamy, J. Toner, and J. Prost, Phys. Rev. Lett. 84, 3494 (2000).
- [26] V. Narayan, N. Menon, and S. Ramaswamy, J. Stat. Mech.: Theory Exp. 2006, P01005 (2006).
- [27] G. P. Alexander and J. M. Yeomans, Europhys. Lett. 83, 34006 (2008).