Soft active matter

M.C. Marchetti, J.F. Joanny, S. Ramaswamy, T.B. Liverpool, J. Prost, Madan Rao, and R. Aditi Simha

1 Physics Department and Syracuse Biomaterials Institute Syracuse University Syracuse NY 13244 USA
2 Physicochimie Curie (CNRS-UMR168 and Université Pierre et Marie Curie) Institut Curie Section de Recherche 26 rue d’Ulm 75248 Paris Cedex 05 France
3 Department of Physics Indian Institute of Science Bangalore 560 12 India
4 TIFR Centre for Interdisciplinary Sciences 21 Brundavan Colony Narsingi Hyderabad 500 075 India
5 Department of Mathematics University of Bristol Bristol BS8 1TW UK
6 Physicochimie Curie (CNRS-UMR168) Institut Curie Section de Recherche 26 rue d’Ulm 75248 Paris Cedex 05 France
7 E.S.P.C.I 10 rue Vauquelin 75231 Paris Cedex 05 France
8 Raman Research Institute Bangalore 560 080 India
9 National Centre for Biological Sciences (TIFR) Bangalore 560065 India
10 Department of Physics Indian Institute of Technology Madras Chennai 600 036 India

(Dated: May 2, 2014)

In this review we summarize theoretical progress in the field of active matter, placing it in the context of recent experiments. Our approach offers a unified framework for the mechanical and statistical properties of living matter: biofilaments and molecular motors in vitro or in vivo, collections of motile microorganisms, animal flocks, and chemical or mechanical imitations. A major goal of the review is to integrate the several approaches proposed in the literature, from semi-microscopic to phenomenological. In particular, we first consider dry systems, defined as those where momentum is not conserved due to friction with a substrate or an embedding porous medium, and clarify the differences and similarities between two types of orientationally ordered states, the nematic and the polar. We then consider the active hydrodynamics of a suspension, and relate as well as contrast it with the dry case. We further highlight various large-scale instabilities of these nonequilibrium states of matter. We discuss and connect various semi-microscopic derivations of the continuum theory, highlighting the unifying and generic nature of the continuum model. Throughout the review, we discuss the experimental relevance of these theories for describing bacterial swarms and suspensions, the cytoskeleton of living cells, and vibrated granular materials. We suggest promising extensions towards greater realism in specific contexts from cell biology to ethology, and remark on some exotic active-matter analogues. Lastly, we summarize the outlook for a quantitative understanding of active matter, through the interplay of detailed theory with controlled experiments on simplified systems, with living or artificial constituents.

CONTENTS

I. Introduction 2

II. “Dry” Active Matter 6
   A. Polar Active Systems: Toner and Tu continuum model of flocking 8
      1. Homogeneous steady states 8
      2. Properties of the isotropic state 8
      3. Properties of the ordered state 9
   B. Active Nematic on a substrate 12
      1. Active Nematic 13
      2. Self-propelled hard rods: a system of “mixed” symmetry? 15
      3. Current Status of Dry Active Matter 15
   C. Current Status of Dry Active Matter 18

III. Active gels: self-driven polar and apolar filaments in a fluid 19
   A. Hydrodynamic equations of active gels 20
      1. Entropy production 20
      2. Conservation laws 20
      3. Thermodynamics of polar systems 20
      4. Fluxes, forces and time reversal 21
   B. Active nematic gels 21
      1. Constitutive equations 21
      2. Microscopic interpretation of the transport coefficients 22
      3. Active currents in nematic and polar systems from fluxes and fluxes 22
      4. Viscoelastic active gel 23
      C. Active polar gels 23
      D. Active Defects 24
      E. Current status on active gels 25

IV. Hydrodynamic Consequences of Activity 26
   A. Instabilities of thin liquid active films 26
      1. Spontaneous flow of active liquid films 26
      2. Instabilities of thin films 28
   B. Polar active suspensions with inertia 30
   C. Rheology 31
      1. Linear rheology of active isotropic matter 32
      2. Linear rheology of active oriented matter 35
      3. Nonlinear rheology of active nematics 35
   D. Applying the hydrodynamic theory to phenomena in living cells 36

V. Microscopic descriptions of active matter 38
   A. Review of microscopic models 38
      1. Self-propelled particles 39
      2. Motors and filaments 39
   B. From stochastic dynamics to macroscopic equations 40
      1. Smoluchowski dynamics 41
      2. From Smoluchowski to hydrodynamics 41
      3. An example: derivation of continuum equations for aligning Vicsek-type particles 42
I. INTRODUCTION

The goal of this article is to introduce the reader to a general framework and viewpoint for the study of the mechanical and statistical properties of living matter and of some remarkable non-living imitations, on length scales from sub-cellular to oceanic. The ubiquitous nonequilibrium condensed systems that this review is concerned with (Joanny and Prost, 2009; Jülicher et al., 2007; Toner et al., 2005; Vicsek and Zafeiris, 2012) have come to be known as active matter (Ramaswamy, 2010). Their unifying characteristic is that they are composed of self-driven units – active particles – each capable of converting stored or ambient free energy into systematic movement (Schweitzer, 2003). The interaction of active particles with each other and with the medium they live in gives rise to highly correlated collective motion and mechanical stress. Active particles are generally elongated and their direction of self-propulsion is set by their own anisotropy, rather than fixed by an external field. Orientational order is thus a theme that runs through much of the active-matter narrative, as can be seen for instance in the image of a swarm of myxobacteria, shown in Fig. 1. The biological systems of our interest include in vitro mixtures of cell extracts with bio-filaments and associated motor proteins (Fig. 2), the whole cytoskeleton of living cells, bacterial suspensions (Fig. 3), cell layers (Fig. 4), and terrestrial, aquatic (Fig. 5) and aerial flocks. Non-living active matter arises in layers of vibrated granular rods, colloidal or nanoscale particles propelled through a fluid by catalytic activity at their surface (Fig. 6), and collections of robots. A distinctive – indeed, defining – feature of active systems compared to more familiar nonequilibrium systems is the fact that the energy input that drives the system out of equilibrium is local, at the level of each particle, rather than at the system’s boundaries as in a shear flow, for example. Each active particle consumes and dissipates energy going through a cycle that fuels internal changes, generally leading to motion. Active systems exhibit a wealth of intriguing nonequilibrium properties, including emergent structures with collective behavior qualitatively different from that of the individual constituents, bizarre fluctuation statistics, nonequilibrium order-disorder transitions, pattern formation on mesoscopic scales, unusual mechanical and rheological properties, and wave propagation and sustained oscillations even in the absence of inertia in the strict sense.

Living systems of course provide the preeminent example of active matter, exhibiting extraordinary properties such as reproduction, adaptation, spontaneous motion, and dynamical organization including the ability to generate and to respond in a calibrated manner to forces.

A theoretical description of the general properties of living matter is not currently achievable because of its overall complexity, with the detailed state of a cell determined by a hopelessly large number of variables. However, in a given living organism there are at most 300 different cell types, which an optimist could view as a very small number given the immensity of the accessible parameter space. Perhaps, therefore, global principles such as conservation laws and symmetries constrain the possible dynamical behaviors of cells or, indeed, of organisms and populations, such as collections of bacteria (Fig. 3), fish schools (Fig. 5) and bird flocks. Quantifying the spontaneous dynamical organization and motion of living
FIG. 3 Bacterial “turbulence” in a sessile drop of Bacillus subtilis viewed from below through the bottom of a petri dish. Gravity is perpendicular to the plane of the picture, and the horizontal white line near the top is the air-water-plastic contact line. The central fuzziness is due to collective motion, not quite captured at the frame rate of $1/30$ s. The scale bar is 35µm. Adapted with permission from Dombrowski et al. (2004).

FIG. 4 A disclination defect of strength $m = -1/2$ formed by human melanocytes on a plastic surface. The bars are 100µm. The three images show three different situations: (i) the core of the defect is an area free of cells (left); (ii) the core of the disclination is an area with isotropically distributed cells (center); and (iii) the core of the defect is occupied by a star-shaped cell (right). The cells that form the nematoid order are in an elongated bipolar state. Reproduced with permission from Kemkemer et al. (2000).

systems is a first step toward understanding in a generic way some of these principles, by focusing on specific questions that are accessible to theory. This has proved to be the case for the long wavelength behavior of active membranes (Manneville et al., 2001; Prost and Bruinsma, 1996; Ramaswamy and Rao, 2001; Ramaswamy et al., 2000); the general theory of flocking (Toner and Tu, 1995, 1998, Toner et al., 2005); or the macroscopic mechanical properties of the cytoskeleton as an active gel (Jülicher et al., 2007; Kruse et al., 2005). Agent-based models offer a minimal approach to the study of active systems, with an emphasis on order and fluctuations rather than forces and mechanics. In such a setting, seminal studies of flocking as a phase transition were first carried out by Vicsek et al. (1995) [see also the remarkable computer-animation work of Reynolds (1987)], with important modifications and extensions by Grégoire and Chaté (2004) and Chaté et al. (2008a, 2006). These models describe point particles with fixed speed moving on an inert background. The direction of motion changes according to a noisy local rule that requires particles to align with their neighbors at each time step. This family of models displays a well-defined transition from a disordered to an ordered phase with decreasing noise strength or increasing density. In the context of the cytoskeleton activated by motor proteins, detailed simulations of ensembles of semi-flexible filaments on which motor bundles can exert force dipoles have also been carried out by several authors (Head et al., 2011; Mogilner and Oster, 1996; Nédélec et al., 1997; Pinot et al., 2009).

In this article we will not review the agent-based models and the wealth of results obtained by numerical sim-
ulations, but rather focus on identifying generic aspects of the large scale behavior of active systems and characterizing their material properties. Many of the macroscopic properties of active systems are universal in the sense that systems operating at widely differing length scales, with significant differences in their detailed dynamics at the microscopic level, display broadly similar properties. Visually similar flocking phenomena are seen in fish shoals (Parrish and Hamner, 1997) and collections of keratocytes (Szabó et al., 2006). Contractile stresses are evident on a sub-cellular scale in the cytoskeleton (Fig. 7) (Bendix et al., 2008; Joanny and Prost, 2009), as well as on a scale of many cells in swimming algae (Rafai et al., 2010). The hope is to be able to classify active matter in a small number of universality classes, based on considerations of symmetry and conservation laws, each with a well-defined macroscopic behavior. We consider here four classes of active matter according to the nature of the broken symmetry of the ordered phase and the type of momentum damping. First the broken symmetry: elongated self-propelled objects are in general polar entities with distinct heads and tails, which can cooperatively order either in a polar (ferromagnetic) phase or in a nematic phase. In a polar phase, all the microscopic objects are on average aligned in the same direction; this is the case for bacteria or fish. The polar order is described by a vector order parameter $\mathbf{p}$, known as the polarization. Nematic ordering can be obtained in two ways, either in systems where polar self-propelled objects are parallel but with random head-tail orientations or in systems where the self-propelled particles are themselves head-tail symmetric such as the melanocytes that distribute pigment in the skin. The polar/apolar distinction in the context of living matter is brought out clearly by the broken symmetry and presence/absence of momentum conservation.

| symmetry | dry | wet |
|----------|-----|-----|
| nematic  | melanocytes | bipolar catalytic rods in suspension |
| polar    | migrating animal herds | cell cytoskeleton |
|          | migrating cell layers | cytoskeletal extract in bulk |
|          | vibrated asymmetric granular particles | swimming bacteria in bulk |
|          | vibrated granular rods | Au-Pt catalytic colloids |

Table I summarizes various examples of active systems classified according to symmetry and presence/absence of momentum conservation (wet/dry). Of course even in “dry” systems, where momentum is not conserved, hydrodynamic or medium-mediated interactions may in some cases be important, depending on the length scale of interest. For instance, for active particles in a viscous fluid of viscosity $\eta$ and experiencing a frictional drag $\gamma$, hydrodynamic flows can be neglected only on length scales larger than $\sqrt{\eta/\gamma}$.

A useful theoretical framework to describe the macroscopic properties of active matter is provided by the methods of nonequilibrium statistical mechanics. In a generalized hydrodynamic approach, a coarse-grained description of the large-scale, long-time behavior of the system is given in terms of a small number of continuum fields. The evolution of these fields is written in terms of a set of continuum or hydrodynamic equations that modify the well-known liquid crystal hydrodynamics (de Gennes and Prost, 1993; Martin et al., 1972) to include new nonequilibrium terms that arise from the activity. Generalized hydrodynamic theories have been very successful.
in the description of many condensed matter systems, such as superfluids (Dzyaloshinskii and Volovick, 1980), liquid crystals (Martin et al., 1972), polymers (Milner, 1993), as well as of course simple fluids.

One approach to obtain a hydrodynamic theory of active systems is to start from a microscopic model and use the tools of statistical physics to coarse-grain the model and obtain the long-wavelength, long-time scale equations (Ahmadi et al., 2005; 2006; Aranson and Tsimring, 2005; Kruse and Jülicher, 2003; Liverpool, 2003). This task is difficult if the microscopic description is realistic and it can only be carried out at the cost of approximations, such as low density or weak interactions. It allows one to relate the parameters in the macroscopic equations to specific physical mechanisms (albeit in a model-dependent manner) and to estimate them in terms of experimentally accessible quantities. The low-density limit has been worked out for several models, initially without and later including the effect of the embedding solvent. Some specific examples are discussed in section V.

An alternative, more pragmatic, approach is to directly write hydrodynamic equations for the macroscopic fields including all terms allowed by symmetry, as was pioneered for dry flocks by Toner and Tu (1995; 1998), and extended to the case of self-propelled particles suspended in a fluid by Simha and Ramaswamy (2002a) and more generally to active-filament solutions (Hatwalne et al., 2004). As one might expect in hindsight, novel terms, of a form ruled out for thermal equilibrium systems, appear in these “pure-thought” versions of the equations of active hydrodynamics.

A more systematic implementation of the phenomenological hydrodynamic approach is to treat the nonequilibrium steady state of an active system as arising through the imposition of a non-vanishing but small driving force on a well-defined parent thermal equilibrium state whose existence is not in question (de Groot and Mazur, 1984). For example, in the biological case of systems composed of cytoskeletal filaments and motor proteins, such as the cell cytoskeleton, the driving force is the difference $\Delta \mu$ between ATP and its hydrolysis products. If $\Delta \mu$ is assumed to be small, the macroscopic hydrodynamic equations can be derived in a systematic way following the Onsager procedure. One identifies thermodynamic fluxes and forces and writes the most general linear relation between them that respects the symmetries of the problem. The novel terms mentioned above that arise by directly writing down the hydrodynamic equations of active matter are then seen to be a consequence of off-diagonal Onsager coefficients and an imposed constant nonzero $\Delta \mu$. Generalized hydrodynamic theories have been very successful in the description of complex and simple fluids (Martin et al., 1972). The advantage is that the equations are expanded around a well defined state. The drawback is that many active systems, biological ones being particularly pertinent examples, are far from equilibrium and one might for example miss some important physics by the restriction to the linear nonequilibrium regime. This phenomenological approach can, however, be very useful, especially when coupled to microscopic derivations for specific model systems.

Regardless of the choice of hydrodynamic framework, the reasons for the choice of variables remain the same. When an extended system is disturbed from equilibrium by an external perturbation, its relaxation is controlled by the microscopic interactions among constituents. It is useful to divide the relaxation processes into fast and slow, and to build a theory of the slow dynamics in which the fast processes enter as noise and damping. Such a division is unambiguous when there are collective excitations with relaxation rates $\omega(q)$ that vanish as the wavevector $q$ goes to zero; these are the hydrodynamic modes of the systems (Forster, 1975; Martin et al., 1972). Familiar examples are diffusion and sound waves in fluids. A formulation in terms of hydrodynamic fields provides a generic description of the nonequilibrium large scale physics that relies only on general properties and local thermodynamics, and does not depend strongly on microscopic details of the interactions. In order to build a hydrodynamic theory, whether phenomenologically or by deriving it from a microscopic model, the first task is to identify the slow variables, which are the local densities of conserved quantities, the “broken-symmetry” variables which have no restoring force at zero wavenumber, and, in the vicinity of a continuous phase transition, the amplitude of the order parameter (Forster, 1975; Martin et al., 1972). From there on, the procedure is well defined and systematic. Conserved quantities are fairly easy to identify. Momentum conservation for “wet” systems means that the momentum density is a slow, conserved variable, while for “dry” systems it is a fast variable. Identifying the type of order – polar or nematic, in the cases that we will examine yields both the amplitude of the order parameter and the broken-symmetry modes.

Several useful reviews on various aspects of the behavior of flocks and active systems have appeared in the recent literature (Joanny and Prost, 2009; Jülicher et al., 2007; Ramaswamy, 2010; Toner et al., 2005; Vicsek and Zaferis, 2012), as well as on the properties of swimmers (Ishikawa, 2009; Koch and Subramaniam, 2011; Lauga and Powers, 2009) and bacterial suspensions and colonies (Ben-Jacob et al., 2000; Cates, 2012; Murray, 2003). The present review aims at highlighting the unity of various approaches and at providing a classification of active systems. It demonstrates the link between microscopic derivations and continuum models, showing that the hydrodynamic equations derived from different microscopic models with the same general symmetry have the same structure and only differ in the details of parameter values, and that the continuum models proposed and used in the literature can all be formulated in a unified manner. It is hoped that this review will provide a use-
ful and self-contained starting point for new researchers entering the field.

This review is organized as follows. We first consider dry active systems focusing on the ordering transition, the properties of the ordered phase and the differences between polar and nematic active matter. We also discuss in section II a system first analyzed theoretically by Baskaran and Marchetti (Baskaran and Marchetti 2008a,b) where the self-propelled particles are polar in their movement but nematic in their interaction and hence in the nature of their macroscopic order. In section III we discuss orientable active particles suspended in a fluid, or active gels, for short. We give a systematic derivation of the constitutive equations of a nematic active gel, for a system weakly out of equilibrium, and dwell briefly on the effects of polar order, viscoelasticity and the presence of multiple components. In section IV we present some applications of the hydrodynamic theory of active matter to specific geometries that could arise in experiments. We focus on instabilities of thin films and on the rheological properties of active matter. Section V gives a brief account of microscopic theories of active matter. We offer examples to show how microscopic theories allow one to determine in principle the phenomenological transport parameters introduced in the hydrodynamic theories and to estimate their order of magnitude. The concluding section VI presents open questions related to hydrodynamic theories of active matter and gives some perspectives.

II. “DRY” ACTIVE MATTER

In this section we consider active systems with no momentum conservation. This class includes bacteria gliding on a rigid surface (Wolgemuth et al. 2002), animal herds on land (Toner and Tu 1998) or, in the artificial realm, vibrated granular particles on a plate (Aranzon and Tsimring 2006; Designe et al. 2010; Kudrolli et al. 2008; Narayan et al. 2007; Ramaswamy et al. 2003; Yamada et al. 2003) in all of which momentum is damped by friction with the substrate. It is also plausible that models without an explicit ambient fluid contain the main physics of concentrated collections of swimming bacteria (Drescher et al. 2011) and motor-filament suspensions (Liverpool 2003), where steric and stochastic effects could for most purposes overwhelm hydrodynamic interactions. Minimal flocking models have also been tested against observations on aerial displays by large groups of birds where, despite the much lower concentration in comparison to bacterial suspensions, (presumably inertial) hydrodynamic effects seem negligible (Ballerini et al. 2008; Ginelli and Chaté 2010).

We refer to these systems as “dry” active systems. In this case the only conserved quantity is the number of particles (neglecting of course cell division and death) and the associated hydrodynamic field is the local density of active units. Over-damped active particles that can order in states with polar and nematic symmetries are described below. The first class consists of polar or self-propelled units with interactions that tend to promote polar order, i.e., explicitly align the particles head to head and tail to tail, as in the classic Vicsek model (Vicsek et al. 1995). The second class consists of active particles that may themselves be apolar, such as melanocytes, the cells that distribute pigments in the skin, where activity induces non-directed motion on each cell (Gruler et al. 1999) or polar, such as self-propelled hard rods (Baskaran and Marchetti 2008b; Peruani et al. 2006; Yang et al. 2010), but with interactions that tend to align particles regardless of their polarity, so that the ordered state, if present, has nematic symmetry. A cartoon of the different cases is shown in Fig. 8.

A. Polar Active Systems: Toner and Tu continuum model of flocking

A continuum effective theory for the flocking model of Vicsek et al. (1995) was proposed in 1995 by Toner and Tu (1995, 1998) (see also Toner et al. 2005). The Vicsek model describes a collection of self-propelled particles with fixed speed and noisy polar aligning interactions, and displays a nonequilibrium phase transition from a disordered state at low density or high noise to an ordered, coherently moving state at high density or low noise strength. Toner and Tu formulated the continuum model phenomenologically solely on the basis of symmetry considerations. Recently, the Toner-Tu model was derived by Bertin et al. (2006, 2009) and Ihle (2011) by coarse-graining the microscopic Vicsek model. These derivations provide a microscopic basis for the hydrodynamic theory, yielding explicit values for essentially all the parameters in the Toner-Tu model, except for the noise strength in the latter. The Boltzmann-equation approach of Bertin et al. (2006) and Ihle (2011) leads to a deterministic coarse-grained description, with the stochasticity of the Vicsek model reflected in an average sense through the diffusion and relaxation terms. In this section we introduce the continuum equations in their simplest form and analyze their consequences.

Since the particles are moving on a frictional substrate, the only conserved field is the number density $\rho(\mathbf{r}, t)$ of active particles. In addition, to describe the possibility of states with polar orientational order, one must consider the dynamics of a polarization vector field, $\mathbf{p}(\mathbf{r}, t)$. These continuum fields can be defined in terms of the position $\mathbf{r}_n(t)$ of each active particle and a unit vector $\hat{\mathbf{v}}_n(t)$ denoting the instantaneous orientation of the velocity of
where \( v_0 \) is the self-propulsion speed of the active particles, \( \gamma \) a rotational viscosity, and \( \lambda_1 \) a parameter controlling the strength of the advective term on the left hand side of Eq. (2b). The last term on the right hand side of Eq. (2b) captures the fluctuations and is taken to be white, Gaussian noise, with zero mean and correlations

\[
\langle f_\alpha(r,t) f_\beta(r',t') \rangle = 2 \Delta \delta_{\alpha\beta} \delta(r-r') \delta(t-t') .
\]

For simplicity, and consistency with Toner and Tu (1998) and with the derivation of Bertin et al. (2006) of the Toner-Tu equations from the model of Vicsek et al. (1995), we have neglected the diffusive current and the associated noise in the density equation in (2). In (2) and everywhere in the following we have taken the noise terms to be purely additive, ignoring dependence on the local values of \( \rho \) (see, e.g., Dean (1996)) or of the order parameter (here \( p \)). This approximation is adequate for the present purposes of calculating two-point correlators in a linearized theory, but is actively under discussion (Gowrishankar and Rao, 2012; Mishra et al. 2009; Mishra et al., 2012) for situations of strong inhomogeneity such as the coarsening of active nematics.

Note that in the continuum flocking model \( p \) plays a dual role: on the one hand \( p \) is the orientational order parameter of the system, on the other \( v_0 p \) represents the particle velocity field. This duality is crucial in determining the large scale behavior of this nonequilibrium system. The free energy functional used in (2) is given by

\[
F_p = \int_r \left\{ \frac{\alpha(\rho)}{2} |\mathbf{p}|^2 + \frac{\beta}{4} |\mathbf{p}|^4 + \frac{K}{2} (\partial_\alpha p_\beta) (\partial_\alpha p_\beta) - \frac{1}{\rho_0} \mathbf{v} \cdot \mathbf{p} + \frac{\lambda}{2} |\mathbf{p}|^2 \nabla \cdot \mathbf{p} \right\} .
\]

(4)

where \( \rho_0 \) is the average density and \( \delta \rho = \rho - \rho_0 \). The first two terms on the right hand side of Eq. (4) control the mean-field continuous order-disorder transition that takes place as the parameter \( \alpha \) goes through zero. In the derivation of Bertin et al. (2006), \( \alpha \) depends on local density \( \rho \) and the noise strength in the underlying microscopic model, and turns negative at sufficiently large \( \rho \). A reasonable phenomenological approach to describe the physics near the transition is to take \( \alpha(\rho) = D_r (1 - \rho/\rho_c) \), changing sign at a characteristic density \( \rho_c \). For stability reasons the coefficient \( \beta \) is positive. The ratio \( D_r/\gamma \) has dimensions of frequency. In the following we will use it to set our unit of time by letting \( D_r/\gamma = 1 \). We also divide implicitly all the coefficients in the free energy (4) by \( D_r \). The third term in the free energy describes the energy cost for a spatially inhomogeneous deformation of the order parameter. The Frank constant \( K \) is positive. For simplicity we employ a one-elastic constant approximation and use the same value for the stiffness associated with splay and bend deformations of the order parameter field, as also for gradients.
in its magnitude. Splay/bend anisotropy can however, play a very important role in active systems, as demonstrated for instance by Voituriez et al. (2006). The last two terms are allowed only in systems with polar symmetry [see, e.g., Kung et al. (2006)]; they give the density and $|p|^2$ contributions to the spontaneous splay. Upon integration by parts, they can be seen to enable gradients in $\rho$ or in the magnitude $|p|$ of the order parameter to provide a local aligning field for $p$. Alternatively, the $\lambda$ term can be viewed as a splay-dependent correction to $\alpha(p)$: splay of one sign enhances, and of the other sign reduces the local tendency to order.

By using Eq. [4] for the free energy, the equation for $p$ takes the form

$$\partial_t p + \lambda_1(p \cdot \nabla)p = -\left[\alpha(\rho) + \beta|p|^2\right]p + K \nabla^2 p - v_1 \nabla \frac{\rho}{\rho_0} + \frac{\lambda}{2} \nabla|p|^2 - \lambda p(\nabla \cdot p) + f,$$

(5)

It is instructive to compare Eq. (5) with the Navier-Stokes equation for a simple fluid. The term proportional to $\lambda_1$ is the familiar advective nonlinearicity. Unlike the fluid, the flocking model does not possess Galilean invariance as the particles are moving relative to a substrate. As a result, $\lambda_1 \neq v_0$ [which would have read $\lambda_1 \neq 1$ had we not extracted a velocity scale in (2a)]. If we think of $p$ as proportional to a flow velocity, the second term on the right hand side represents the effects of viscous forces. The third and fourth terms of Eq. (5) can be written in an approximate pressure-gradient form as $-(1/\rho_0) \nabla P$ with a pressure $P(\rho, |p|) \approx v_1 \rho - (\lambda \rho_0/2)|p|^2$. This highlights the parallel and the contrast with the Navier-Stokes equation: in the latter, an equation of state determines the thermodynamic pressure in terms of density and temperature and not the velocity field. The first term on the right hand side of Eq. (5) arises from the role of $p$ as order parameter for a polarized state and does not have an analogue in equilibrium fluid flow. There is, however, an equilibrium analogue in the context of electrostriction, a property of all dielectric materials that causes them to change their shape under the application of an electric field, although in this case polarization does not correspond to velocity, but rather to reactive polarity. General symmetry arguments given by Mishra et al. (2010) and Toner et al. (2005) allow for more general polar terms in Eq. (6): $\frac{1}{2} \nabla|p|^2 + \lambda_2 p(\nabla \cdot p)$. The derivation based on the free energy (4), using (2b) yields $\lambda_3 = -\lambda_2 = \lambda$. For the out-of-equilibrium system considered here the coefficients of these two terms are not generally related, but the microscopic derivation of Bertin et al. (2009) also yields $\lambda_3 = -\lambda_2$ as well as $\lambda_i \sim v_0^2$ and $v_1 = v_0/2$.

1. Homogeneous steady states

The dynamical model described by Eqs. (2a) and (2b) exhibits by construction, in a mean-field treatment of homogeneous configurations, a continuous transition from a disordered to an ordered state. For $\alpha > 0$, corresponding to an equilibrium density $\rho_0 < \rho_c$, the homogeneous steady state of the system is disordered or isotropic, with $p = 0$ and a corresponding zero mean velocity. For $\alpha < 0$, corresponding to $\rho_0 > \rho_c$, the system orders in a state with uniform orientational order, with $|p_0| = \sqrt{-\alpha_0/\beta}$, where $\alpha_0 = \alpha(\rho_0)$. In the ordered state, which is also a moving state, with $v = v_0 p_0$, continuous rotational symmetry is spontaneously broken. This mean-field analysis survives fluctuation corrections even in two dimensions (Toner and Tu, 1995, 1998), evading the Mermin-Wagner theorem forbidding – at equilibrium – the spontaneous breaking of a continuous symmetry in two spatial dimensions (Chaikin and Lubensky, 2000; Hohenberg, 1967; Mermin and Wagner, 1966). In the present nonequilibrium system, however, the theorem does not apply.

The escape from Mermin-Wagner is primarily due to the advective nonlinearities in (2) which effectively generate long-range interactions in the system, even if density variations are ignored as shown recently by Toner (2012). The ordered phase itself, especially near the transition, is exceedingly complex as a result of coupling to the density. Although the mean density is an important control parameter for the transition to a flock, the local propensity to order depends, via $\alpha(\rho)$ in (4), on the local density $\rho (r,t)$. This is analogous to the density-dependent exchange coupling in a compressible magnet in Milosevic et al. (1978). The analogy ends there: unlike in the magnet, the order parameter feeds back strongly into the density dynamics via the current on the right hand side of Eq. (2a). See section II.A.3 of Toner and Tu (1998), and the review by Toner et al. (2005) for a more complete discussion of this point.

2. Properties of the isotropic state

To study the linear stability of the homogeneous steady states we examine the dynamics of spatially inhomogeneous fluctuations $\delta \rho = \rho - \rho_0$ and $\delta p = p - p_0$ from the values $\rho_0$ and $p_0$ in each of the homogeneous states. The isotropic state is characterized by $\rho_0 < \rho_c$ and $p_0 = 0$. The equations for the dynamics of linear fluctuations about these values are

$$\partial_t \delta \rho = -v_0 \partial_0 \nabla \cdot p,$$

(6a)

$$\partial_t p = -\alpha_0 p - \frac{v_1}{\rho_0} \nabla \delta \rho + K \nabla^2 p + f,$$

(6b)

where $\alpha_0 > 0$. Fourier-transforming (6) in space and time to look at modes of the form $\exp(\mathbf{iq} \cdot \mathbf{r} - i\omega t)$ leads
to dispersion relations between frequency $\omega$ and wavevector $q$ for small fluctuations about the uniform isotropic phase. Polarization fluctuations transverse to $q$ decouple and decay at a rate $\alpha_0 + Kq^2$. The relaxation of coupled fluctuations of density and longitudinal polarization is controlled by coupled hydrodynamic modes with frequencies

$$\omega_\pm^2(q) = -\frac{i}{2}(\alpha_0 + Kq^2) \pm \frac{i}{2}\sqrt{(\alpha_0 + Kq^2)^2 - 4v_0v_1q^2}.$$  

(7)

Linear stability requires that fluctuations decay at long times so that $\text{Im}[\omega(q)] < 0$. The isotropic state is linearly stable for all parameter values, provided $v_0v_1 > 0$. The parameter $v_1$ enters like an effective compressional modulus. Microscopic derivations of the continuum model have yielded $v_1 = v_0/2$ at low density [Baskaran and Marchetti (2008b)] and $v_1 = v_0/2$ at high density [Baskaran and Marchetti (2011)]. In this case $v_1 > 0$ and the isotropic state is always stable. At high density, however, caging effects can result in a density dependence of $v_1$, which can in turn lead to a density instability of the isotropic state as shown by [Fily et al. (2012)] and [Tailleur and Cates (2008)]. Here we restrict our discussion to the situation where the isotropic state is linearly stable. Even in this case, it has unusual properties: approaching the mean-field ordering transition, i.e., decreasing $\alpha_0$, is like decreasing friction. As argued by [Ramaswamy and Mazenko (1982)] for equilibrium fluids on a substrate, the dispersion relations can acquire a real part for $\alpha_0 \leq v_0v_1/K$ and a range of wavevectors, $q_c <= q <= q_+ + 2\sqrt{v_0v_1}/K$ and the propagating waves resemble sound waves, with $\omega^2_\pm \approx \pm q\sqrt{v_0v_1}$. These propagating sound-like density waves are ubiquitous in collections of self-propelled particles. We stress, however, that if the limit $q \to 0$ is taken first, density fluctuations always decay diffusively.

### 3. Properties of the ordered state

We now examine the linear stability of the ordered state by considering the linear dynamics of fluctuations about $\rho_0 > \rho_c$ and $\rho_0 = \rho_0\hat{x}$. The detailed analysis below is for $d = 2$, but the general conclusions including the instability of the uniform ordered state just past threshold hold in all dimensions. It is useful to write the order parameter in terms of its magnitude and direction, by letting $p = \hat{n}p$, where $\hat{n}$ is a unit vector pointing in the direction of local orientational order. Fluctuations in the polarization can then be written as $\delta p = \hat{n}_0\delta p + \rho_0\delta n$. The condition $[\hat{n}]^2 = 1$ requires that to linear order $\hat{n}_0 \cdot \hat{n} = 0$. For the chosen coordinate system $\hat{n}_0 = \hat{x}$. Then in two dimensions $\delta n = \delta n\hat{y}$ and $\delta p = \hat{x}\delta p + \hat{y}\rho_0\delta n$. The linearized equations are

$$\begin{align*}
(\partial_t + v_0\rho_0\partial_x)\delta p &= -v_0\rho_0\nabla \cdot \delta p, \\
(\partial_t + \lambda_1\rho_0\partial_x)\delta p &= -2\alpha_0\hat{x}\delta p + ap_0\delta p + \lambda_2\rho_0(\nabla \cdot \delta p) \\
(\partial_t/v_0)\nabla \delta p + \lambda_3\rho_0\nabla \delta p + K\nabla^2 \delta p + f,
\end{align*}$$

(9a)

(9b)

where $a = -\alpha'\beta' = \alpha\beta'/\beta - \alpha' > 0$ and primes denote derivatives with respect to density, e.g., $\alpha'' = (\partial_\rho \alpha)_{\rho = \rho_0}$. For the analysis below it is useful to display explicitly the three coupled equations for the fluctuations. For compactness, we introduce a vector with elements $\phi = \{\delta p, \delta n, \delta \hat{n}\}$ and write them in a matrix form as

$$\partial_t \phi_q(t) = M(q) \cdot \phi_q(t) + F_q(t)$$

(10)

where the matrix $M$ is given by

$$M(q) = \begin{pmatrix}
-\alpha_0v_0\rho_0 & -iq_xv_0\rho_0 & -iq_xv_0\rho_0 \\
ap_0 - iq_xv_1/\rho_0 & -2\alpha_0 - iq_x\lambda_0 - Kq^2 & iq_y\lambda_2p_0^2 \\
-iq_yv_1/(\rho_0p_0) & iq_y\lambda_3p_0 & -iq_x\lambda_1p_0 - Kq^2
\end{pmatrix}$$

(11)

The sign of the combination $\lambda = \lambda_1 - \lambda_2 - \lambda_3$ is important in controlling the nature of the instabilities in the ordered phase. Notice that all microscopic derivations of the continuous equations for various systems of self-propelled particles [Baskaran and Marchetti (2008b)] [Baskaran and Marchetti (2011)] yield $\lambda > 0$. Finally, the noise vector $F_q(t)$ has components $F_q(t) = \{0, f_{k}^q(t), f_{l}^q(t)\}$, with $f_{k}^q(t) = \tilde{q}f_{k}^q(t), f_{l}^q(t) = f_{l}^q(t) - \tilde{q}f_{l}^q(t)$ and $\tilde{q} = q/q$. The dispersion relations of the hydrodynamic modes are the eigenvalues of the matrix $M$. The solution of the full cubic eigenvalue problem is not, however, very instructive. It is more useful to discuss a few simplified cases [Baskaran and Marchetti (2008b)] [Baskaran and Marchetti (2011)] [Mishra et al. (2010)].

### a. Linear instability near the mean-field order-disorder transition

We first consider the behavior of fluctuations as $\rho_0 > \rho_c$, i.e., decreasing $\alpha_0$, is like decreasing friction. As argued by [Ramaswamy and Mazenko (1982)] for equilibrium fluids on a substrate, the dispersion relations can acquire a real part for $\alpha_0 \leq v_0v_1/K$ and a range of wavevectors, $q_c <= q <= q_+ + 2\sqrt{v_0v_1}/K$ and the propagating waves resemble sound waves, with $\omega^2_\pm \approx \pm q\sqrt{v_0v_1}$. These propagating sound-like density waves are ubiquitous in collections of self-propelled particles. We stress, however, that if the limit $q \to 0$ is taken first, density fluctuations always decay diffusively.
the mean-field transition is approached from the ordered phase, i.e., for \( \alpha_0 \rightarrow 0^− \) and \( p_0 \rightarrow 0^+ \). Fluctuations \( \delta p \) in the magnitude of polarization decay at rate \( \sim |\alpha_0| \) and become long-lived near the transition. In fact in this limit one can neglect the coupling to director fluctuations and only consider the coupled dynamics of \( \delta p \) and \( \delta n \). This decoupling becomes exact for wavevectors \( \mathbf{q} \) along the direction of broken symmetry, \( \mathbf{q} = q \hat{\mathbf{x}} \). The decay of director fluctuations is described by a stable, propagating mode, \( \omega_n = -q\lambda_1 p_0^2 - i Kq^2 \). For small \( q \) the imaginary part of the frequencies \( \omega^\pm_\mathbf{q} (\mathbf{q}) \) of the modes describing the dynamics of density and order parameter magnitude takes the form

\[
Im[\omega^\pm_\mathbf{q}] = - \left[ s_2 q^2 + s_4 q^4 + O(q^6) \right]
\]

(12)

with \( s_2 = \frac{v_0 v_1}{4\alpha_0^2} \left[ 1 - \frac{v_0^2 a_0^2}{4\alpha_0} \right] \), implying an instability at small \( q \) when \( s_2 < 0 \), corresponding to \( |\alpha_0| \leq \frac{v_0^2 a_0^2}{4\alpha_0} \). Microscopic calculations yield \( \alpha_0 \sim v_0 \) and \( v_1 \sim v_0 \) (Bertin et al. 2009), indicating that the instability exists for arbitrarily small \( v_0 \) and in a narrow region of densities above the mean field order-disorder transition. The \( O(q^4) \) term in Eq. (12) stabilizes fluctuations at large wavevectors. In detail, near the mean-field transition (\( \alpha_0 \rightarrow 0^- \)) \( s_2 \approx -a^2/8\beta_0^2 \) and \( s_4 \approx 5a^4/128\beta^2 \alpha_0^2 \) and the mode is unstable for \( q < q_c \approx 4\sqrt[3]{3/|\alpha_0|^3}/(5a^2) \approx (\rho_c - \rho_0)^{3/2} \). Numerical solution of the nonlinear hydrodynamic equations with and without noise have shown that in this region the uniform polarized state is replaced by complex spatio-temporal structures.

In the absence of noise, one finds propagating solitary waves in the form of ordered bands aligned transverse to the direction of broken symmetry and propagating along \( \hat{\mathbf{x}} \) amidst a disordered background (Bertin et al. 2009; Mishra et al. 2010). As discussed below, these bands have been observed in numerical simulations of the Vicsek model (Chaté et al. 2008) and are shown in Fig. 10.

b. “Sound waves”. Deep in the ordered phase, i.e., for large negative \( \alpha_0 \), fluctuations \( \delta p \) in the magnitude of the order parameter decay on non-hydrodynamic time scales. We assume \( \delta p \) has relaxed to zero on the time scales of interest and let for simplicity \( p_0 \simeq 1 \). In addition, we include a diffusive current and the associated noise that were neglected in the density Eq. (2a). The coupled equations for density and polar director fluctuations, \( \delta p \) and \( \delta n \), take the form

\[
(\partial_t + v_0 \partial_x) \delta p = -v_0 \rho_0 \partial_x \delta n + D \nabla^2 \delta p + \nabla \cdot \mathbf{f}_p ,
\]

(13a)

\[
(\partial_t + \lambda_1 \partial_x) \delta n = -v_1 \partial_y \left( \frac{\delta p}{\rho_0} \right) + K \nabla^2 \delta n + f_y ,
\]

(13b)

where \( D \) is a diffusion constant and \( \mathbf{f}_p \) describes white, Gaussian noise. The hydrodynamic modes, obtained from Eqs. (13a) and (13b), are stable propagating sound-like waves, with dispersion relation

\[
\omega^\pm_\mathbf{q} = q c_\pm(\theta) - i q^2 K_\pm(\theta) + O(q^4) ,
\]

(14)

with speeds and dampings \( c_\pm(\theta) \) and \( K_\pm(\theta) \), whose detailed forms are given in the review by Toner et al. (2005) and depend on the angle \( \theta \) between \( \mathbf{q} \) and the direction \( \hat{\mathbf{x}} \) of broken symmetry. For \( \theta = \pi/2 \), i.e., \( \mathbf{q} \) along \( y \), we find \( c_\pm = \pm \sqrt{v_0 v_1} \) and \( K_\pm = (K + D)/2 \), while for \( \theta = 0 \), corresponding to \( \mathbf{q} \) along \( x \), the two modes are decoupled and \( \omega^\pm_\mathbf{q} = q v_0 - i q^2 K = q v_0 - i q^2 K^2 \).

The difference in the propagation speeds is due to the lack of Galilean invariance. In a normal fluid, sound waves propagate because of mass and momentum conservation and inertia. In contrast, the presence of propagating long-wavelength density disturbances here is a signature of the spontaneously broken orientational symmetry which renders \( \delta n \) “massless” (Ramaswamy 2010).

Going back to the full form of the matrix \( \mathbf{M} \) in (11), we notice that to leading order in \( q \) the relaxation of \( \delta p \) is governed by the equation

\[
\partial_t \delta p_{\mathbf{q} \omega} = -2|\alpha_0| \delta p_{\mathbf{q} \omega} + ap_0 \rho_{\mathbf{q} \omega} + O(q) .
\]

(15)

This reminds us to be precise about what it means for a mode to be “fast”: fluctuations in the magnitude of the order parameter cannot be neglected, but rather are slaved to density fluctuations on long timescales: \( \delta p_{\mathbf{q} \omega} \sim (ap_0/2|\alpha_0|) \delta \rho_{\mathbf{q} \omega} \). Inserting this into (10) yields an effective dynamics for \( \delta n \) and \( \rho \) with an instability of splay fluctuations if \( \lambda_3 > 2\rho_0^2 \omega_1^2/\delta p_{\mathbf{q} \omega} \) > 0 (Mishra et al. 2010). An analysis of the eigenvalues of the full matrix \( \mathbf{M} \) confirms this result.

c. Giant density fluctuations. The linearized equations with noise can also be used to calculate correlation functions. Of particular interest is the static structure factor

\[
S(\mathbf{q}) = \frac{1}{\rho_0 V} \langle \delta \rho_{\mathbf{q} \omega}(t) \delta \rho_{\mathbf{-q} \omega}(t) \rangle = \int_{-\infty}^{\infty} \frac{d\omega}{2\pi} S(\mathbf{q}, \omega) ,
\]

(16)

where

\[
S(\mathbf{q}, \omega) = \frac{1}{\rho_0 V} \int_0^\infty dt \exp(i\omega t) \langle \delta \rho_{\mathbf{q} \omega}(0) \delta \rho_{-\mathbf{q} \omega}(t) \rangle .
\]

(17)

is the dynamic structure factor. We are interested in calculating density fluctuations in the region away from the mean-field transition, where the ordered state is linearly stable. Eqs. (13a) and (13b) yield \( S(\mathbf{q}, \omega) \). For a reader wishing to work through the calculation, note that to leading order in the wavevector the noise \( \mathbf{f}_p \) in the density equations can be neglected, except for \( \mathbf{q} \) along the direction of broken symmetry (\( \theta = 0 \)). Integrating over frequency as in Eq. (16), again to leading order in \( q \), one obtains
For \( \theta = 0 \) the leading \( 1/q^2 \) singularity displayed in (18) vanishes; to determine the finite value of \( S(q) \) in that limit requires going to higher order in \( q \) which we will not do here. As we will see below, the divergence of the static structure function at large wavelengths (as \( 1/q^2 \) in the present linearized treatment) is a remarkable and robust property of uniaxially ordered active systems, whether polar or nematic, and follows generally from the orientational order that develops in a sufficiently dense collection of self-driven particles with anisotropic body shape (Ramaseswamy et al. 2003, Simha and Ramaseswamy 2002a,b, Toner and Tu 1995, 1998, Toner et al. 2005). The \( 1/q^2 \) is also a dimension-independent property of our linearized theory; the numerical prefactors \( d \) do, however, depend on dimensionality. The divergence of the static structure function for \( q \to 0 \) implies an important violation of the familiar scaling of number fluctuations in equilibrium. In the limit of vanishing wavevector the structure factor is simply a measure of number fluctuations, with

\[
\lim_{q \to 0} S(q) = \frac{\Delta N^2}{\langle N \rangle},
\]

where \( N \) and \( \langle N \rangle \) are the instantaneous and average number of particles in a region of size \( V \), respectively, and \( \Delta N^2 = \langle (N - \langle N \rangle)^2 \rangle \) is the variance of number fluctuations. In an equilibrium system \( \Delta N \sim \sqrt{\langle N \rangle} \), so that \( \Delta N / \langle N \rangle \sim 1 / \sqrt{\langle N \rangle} \to 0 \) as \( \langle N \rangle \to \infty \). The \( 1/q^2 \) divergence of \( S(q) \) for \( q \to 0 \) predicted by Eq. (18) implies that in an active system \( \Delta N \) grows faster than \( \sqrt{\langle N \rangle} \). To understand this we rewrite Eq. (18) as

\[
\Delta N \sim \sqrt{\langle N \rangle} S(q \to 0) \sim \sqrt{\langle N \rangle} \frac{\Delta N^2}{\langle N \rangle}.
\]

Assuming that the smallest accessible wavevector is of the order of the inverse of the system size \( V^{-1/d} \), with \( d \) the space dimension, we find \( S(q \to 0) \sim V^{2/d} \sim (\langle N \rangle^{2/d}) \). This gives

\[
\Delta N \sim \langle N \rangle^a, \quad a = \frac{1}{2} + \frac{1}{d}.
\]

The linear theory reviewed above predicts a strong enhancement of density fluctuations in the ordered state, with an exponent \( a = 1 \) in two dimensions (Toner and Tu 1995, Toner et al. 2005). We will see in section II.B that a similar linear theory also predicts the same scaling in the ordered state of active apolar nematic. In general, we expect the exponent to be substantively modified as compared to the theoretical value by fluctuation effects arising from the coupling of modes at different wavenumbers as a result of nonlinear terms in the equations of motion. “Giant density fluctuations” have now been seen experimentally in both polar (Deseigne et al. 2010) and apolar (Narayan et al. 2007) vibrated granular matter. See section II.B.3 for a more detailed discussion of the apolar case. The scaling exponents, although measured over a limited dynamical range, are consistent, for the apolar case, with the linearized treatment presented here and in (Ramaseswamy et al. 2003), and with the renormalization-group treatment (Toner and Tu 1995, 1998, Toner et al. 2005) in \( d = 2 \) for polar flocks. Giant number fluctuations have also been seen in simulations of Vicsek-type models by Chaté and collaborators (Chaté et al. 2008a,b, 2006). Much remains to be understood about number fluctuations in flocks, as revealed for instance by the experiments of (Zhang et al. 2010) (see Fig. 9). Recent work has also revealed other mechanisms that can yield large number fluctuations and even true phase separation in active systems in the absence of an ordered state (Cates 2012, Fily et al. 2012, Tailleur and Cates 2008). We refer the reader to section II.C for further discussion of this point.

Recall that in thermal equilibrium the thermodynamic sum rule relates \( S(q = 0) \) to the isothermal compressibility \( \chi_T = -\frac{1}{T} \langle \frac{\delta^2 p}{\delta T} \rangle_T \), according to \( S(q \to 0) = \rho_0 k_B T \chi_T \), with \( \rho_0 = \langle N \rangle / V \) the mean number density. One might then be tempted to say that orientationally ordered active systems are characterized by a diverging effective compressibility. This would in general be wrong. Augmenting the free-energy functional with a linear coupling \( \int U(r, t) \delta \rho(r, t) d^3 r \) and calculating the response function \( \langle \delta \rho(r) / \delta U \rangle_{q, \omega} \) can readily be shown to yield a finite result for \( q, \omega \to 0 \). The giant density fluctuations seen in the ordered state of active systems are an excess noise from the invasion of the density dynamics by the soft Goldstone mode of orientational order, not an enhanced response to perturbations.

**FIG. 9** (color online) Swimming *bacillus subtilis* bacteria exhibit strong polar order and fluctuations that are smaller at low density (A) than at high density (B). Nearby bacteria with arrows of the same color belong to the same dynamic cluster; the arrows indicate a bacterium’s speed and direction. Adapted with permission from (Zhang et al. 2010).
d. Long-range order of dry polar active matter in 2d. The ordered polar state is remarkable in that it exhibits long-range-order of a continuous order parameter in two dimensions. This has been referred to as a violation of the Mermin-Wagner theorem, although it is important to keep in mind that the latter only holds for systems in thermal equilibrium. From Eqs. (13a) and (13b) one can immediately obtain the correlation function of fluctuations in the direction $\delta n$ of polar order, with the result $\langle |\delta n(q)(t)|^2 \rangle \sim 1/q^2$. Taken literally, this result implies quasi-long-range order in two dimension in analogy with the equilibrium XY model. It has been shown, however, that nonlinearities in Eqs. (13a) and (13b) are strongly relevant in $d = 2$ and lead to a singular renormalization of the effective stiffness of the polar director at small wavenumbers $q$, so that $\langle |\delta n_q(t)|^2 \rangle$ diverges more slowly than $1/q^2$ for most directions of $q$, thus preserving long-range order (Toner and Tu, 1995, 1998; Toner et al. 2005). A qualitative explanation of how this happens can be given as in Ramaswamy (2010), but a remarkable, pictorial yet quantitative account can be found in lecture notes by Toner (2009). Exact arguments for scaling exponents in two dimensions are given by Toner (2012) in the limit where particle number is fast, i.e., not conserved locally.

e. Numerical simulation of Vicsek-type models. Although a review of numerical simulations of agent based models is beyond the scope of this paper, for completeness we summarize the main findings. Quantitative agreement has been found between numerical experiments on microscopic models and the predictions of the coarse-grained theory, including long-range order in $d = 2$, the form of the propagating modes, anomalous density fluctuations, and super-diffusion of tagged particles (Grégoire and Chaté 2004; Toner et al. 2005). Early numerical studies (Vicsek et al. 1995) and some later variants (Aldana et al. 2007; Baglietto and Albano 2009; Gönç et al. 2008) found a behavior consistent with a continuous onset of flocking, as a mean-field solution would predict. However, the currently agreed picture, in systems where particle number is conserved, is of a discontinuous transition (Chaté et al. 2007; 2008b; 2006; Grégoire and Chaté 2004). It was found in fact that in a large domain of parameter space, including the transition region, the dynamics is dominated by propagating solitary structures consisting of well-defined regions of high density and high polar order in a low-density, disordered background. The ordered regions consist of stripes or bands aligned transverse to the direction of mean order and traveling along the direction of mean motion with speed of order $v_0$, as shown in Fig. 10. Away from the transitions, for weak noise strengths, a homogeneous ordered phase is found, although with anomalously large density fluctuations. Numerical solution of the nonlinear continuum model described by Eq. (2) has also yielded traveling wave structures (Bertin et al. 2009; Gopinath et al. 2012; Mishra et al. 2010). Finally, traveling density waves have been observed in actin motility assays at very high actin density (Butt et al. 2010; Schaller et al. 2010), as shown in Fig. 11. Although it is tempting to identify these actin density waves with the traveling bands seen in simulations of the Vicsek model, the connection is at best qualitative at the moment. In particular, it remains to be established whether these actin suspensions can indeed be modeled as dry systems, or hydrodynamic interactions are important, as suggested in Schaller et al. (2011a).

B. Active Nematic on a substrate

Nematic order is the simplest kind of orientational order, with a spontaneously chosen axis which we shall designate the $\hat{x}$ direction, and no distinction between $\hat{x}$ and $-\hat{x}$. Lacking a permanent vectorial asymmetry, the system, although driven, has no opportunity to translate its lack of time-reversal symmetry into an average nonzero drift velocity. The reader would be forgiven for thinking that such a non-moving state cannot possibly display any of the characteristics of a flock. Remarkably, however, some of the most extreme fluctuation properties of ordered phases of active particles are predicted (Ramaswamy et al. 2003) and observed in experiments (Narayan et al. 2007) and earlier in simulations (Chaté et al. 2006; Mishra and Ramaswamy 2006) on this flock that goes nowhere on average. As with polar active systems, several levels of description are possible for an active nematic – minimal agent-based stochastic mod-
FIG. 11 Density waves in a dense actin motility assay. The left image is a snapshot of the traveling wavefronts of actin observed in motility assays for actin density above about 20 filaments/µm², adapted with permission from Schaller et al. (2010). The right image (courtesy of V. Schaller) is obtained by overlaying maximal intensity projections of 20 consecutive images, corresponding to a total time of 2.5 seconds. The time overlay allows one to trace the trajectory of the filaments, showing that filaments in the high-density regions move collectively with high orientational persistence, while filaments lying outside the bands perform uncorrelated persistent random walks. The elongated density modulation travels in the direction of the filaments’ long direction at a speed that remains approximately constant over the time scale of the experiment.

1. Active Nematic

In this section we construct the equations of motion for active apolar nematics and discover their remarkable properties. We continue to work in a simplified description in which the medium through or over which the active particles move is merely a momentum sink, without its own dynamics. Effects associated with fluid flow are deferred to a later section. We consider again a collection of elongated active particles labeled by \( n \), with positions \( \mathbf{r}_n(t) \) and orientation described by unit vectors \( \hat{\mathbf{n}}_n(t) \). As in the case of polar systems on a substrate, the only conservation law is that of number. The slow variables of such a formulation are thus the number density \( \rho(\mathbf{r}, t) \) at location \( \mathbf{r} \) and time \( t \), as defined in Eq. (1a) in section II.A and the apolar nematic orientational order parameter, a traceless symmetric tensor \( \mathbf{Q} \) with components

\[
Q_{\alpha\beta}(\mathbf{r}, t) = \frac{1}{\rho(\mathbf{r}, t)} \sum_n \left( \hat{\mathbf{n}}_{\alpha n}(t) \cdot \hat{\mathbf{n}}_{\beta n}(t) - \frac{1}{d} \delta_{\alpha\beta} \right) \delta(\mathbf{r}-\mathbf{r}_n(t))
\]

measuring the local degree of mutual alignment of the axes of the constituent particles, without distinguishing head from tail. In constructing the equations of motion we keep track of which terms are permitted in a system at thermal equilibrium and which arise strictly from nonequilibrium activity. As we are ignoring inertia and fluid flow, the dynamics of the orientation is governed by the equation

\[
\gamma_Q \partial_t \mathbf{Q} = -\delta F_Q / \delta \mathbf{Q} + \mathbf{f}_Q
\]

describing the balance between frictional torques governed by a rotational viscosity \( \gamma_Q \) and thermodynamic torques from a free-energy functional

\[
F_Q = \int_\mathcal{R} \left[ \frac{\alpha_Q(\rho)}{2} \mathbf{Q} : \mathbf{Q} + \frac{\beta_Q}{4} (\mathbf{Q} : \mathbf{Q})^2 + \frac{K_Q}{2} (\nabla \mathbf{Q})^2 + C_Q \mathbf{Q} : \nabla \nabla \frac{\delta \rho}{\rho_0} + \frac{A}{2} \left( \frac{\delta \rho}{\rho_0} \right)^2 \right]
\]

that includes a tendency to nematic order for \( \alpha_Q < 0 \) and \( \beta_Q > 0 \), Frank elasticity as well as variations in the magnitude of \( \mathbf{Q} \) via \( K_Q \), bilinear couplings of \( \mathbf{Q} \) and \( \rho \), and a compression modulus \( A \) penalizing fluctuations \( \delta \rho \) in the density about its mean value \( \rho_0 \). Note that all parameters in (23) can depend on \( \rho \), as indicated explicitly for \( \alpha_Q \). We also stress that this form of the free energy only applies in two dimensions. For active nematic in three dimensions terms of order \( \mathbf{Q}^3 \) also need to be included. We have included in (22) a spatio-temporally white statistically isotropic tensor noise \( \mathbf{f}_Q \) to take into account fluctuations of thermal or active origin. It is implicit that all terms in (22) are traceless and symmetric. We have ignored several possible terms in the equation of motion for \( \mathbf{Q} \) – additional couplings to \( \rho \) via off-diagonal kinetic coefficients, nonlinear terms not expressible as the variational derivative of a scalar functional, and terms of sub-leading order in gradients – none of which plays an important role in our analysis. The unique physics of the self-driven nematic state [Ramaswamy et al. 2003] enters through active contributions to the current \( \mathbf{J} \) in the conservation law

\[
\partial_t \rho = -\nabla \cdot \mathbf{J}
\]

There are several ways of generating these active terms: one can write them down on the grounds that nothing rules them out in a nonequilibrium state [Ramaswamy et al. 2003, Simha and Ramaswamy 2002a], derive them from specific microscopic models involving motors and filaments [Ahmadi et al. 2005, 2006], or apolar flocking...
spite the fact that (25) has one more gradient than the current in the polar case in (2). We will comment below on this subtlety after we summarize the calculation and the relevant experiments and simulations.

Using (23) in (22), and including in the current \( \mathbf{J} \) in (24) both the active contribution (23) and a purely passive diffusive part \( -\frac{1}{\gamma} \frac{\mathbf{S}}{\delta r_0} \), with a mobility \( \gamma^{-1} \), leads to

\[ \partial_t \rho = D \nabla^2 \rho + B \nabla^2 \mathbf{\nabla} : \mathbf{Q} + \zeta_Q \mathbf{\nabla} : \mathbf{Q} + \mathbf{\nabla} \cdot \mathbf{f}^\rho, \tag{26} \]

with \( D = A/(\rho_0^2 \gamma) \), \( B = C_Q/(\rho_0 \gamma) \). We have treated \( \zeta_Q \) as constant, and we have introduced number-conserving fluctuations through the random current \( \mathbf{f}^\rho \) which, again, we take to be statistically isotropic and delta-correlated in space and time.

Despite its apparent structural simplicity the apolar active nematic state has been explored less than its polar counterpart. The ordering transition appears numerically (Chaté et al., 2006) to be of the Kosterlitz-Thouless type, but analytical approaches must confront the difficulties of the coupling of order parameter and density and have not been attempted so far, beyond mean-field (Ahmadi et al., 2005, 2006) which predicts a continuous transition in two dimensions. Working with equations of a form similar to (22) and (26), Shi and Ma (2010) obtained in a Boltzmann-equation approach from the model of Chaté et al. (2006) with a finite-wavenumber instability of the uniform nematic state just past onset, and a “perpetually evolving state”. Note that similar behavior has been obtained by Giomi and collaborators for ”wet” nematic fluids (Giomi et al., 2011, 2012) and has been observed in very recent experiments on \textit{in vitro} suspensions of microtubule-kinesin bundles (Dogic, 2012). Finally, there are preliminary numerical indications (Mishra, 2009, Mishra and Ramaswamy, 2011) of anomalous growth kinetics of active nematic order following a quench from the isotropic phase, with a strong clumping of the density. We will not pursue these issues further in this review. In the remainder of this section we restrict ourselves to a simple understanding of the statistics of linearized density fluctuations deep in a nonequilibrium situation maintained by a nonzero activity must in general give a current

\[ \mathbf{J}_{\text{active}} = \zeta_Q \mathbf{\nabla} \cdot \mathbf{Q}, \tag{25} \]

where \( \zeta_Q \) is a phenomenological active parameter. Graphic experimental evidence of curvature-induced current can be found in Fig. 13 for details see Narayan et al. (2007). Supporting Material. As shown by Ramaswamy et al. (2003) and reiterated below, this \( \zeta_Q \) term leads to giant number fluctuations in active nematics. This is de-
It is straightforward to show that $\theta_q$ has equal-time correlations $S_0^0 = \int (d\omega/2\pi) S_{Q_0}^0 \propto 1/q^2$, and a lifetime $\propto 1/q^2$. The term $\nabla \cdot p$ through which $\theta_{Q_0}$ appears in the density equation (20) can be re-expressed as $\partial_t \partial_y \theta$. This autonomy of $\theta$ means that this term can be viewed as colored noise with variance $\propto q^2 q_0^2 / q^2$, and relaxation time $\propto 1/q^4$. The zero-frequency weight of this noise is thus $\sim q^2 q_0^2 / q^4$, i.e., of order $q^0$ but anisotropic. By contrast, the conserving noise $\nabla \cdot q$ has zero-frequency weight that vanishes as $q^2$ and is thus irrelevant in the face of the active contribution $\nabla \cdot q$, whose long-time, long-distance effects are now revealed to be analogous to those of a number-non-conserving noise. The deterministic part of the dynamics of $\rho$, on the other hand, is diffusive and hence number-conserving. This combination implies immediately that the equal-time correlator $S_0^0 \sim \text{noise strength} \times \text{relaxation time} \sim q_0^2 q_0^2 / q^4$, i.e., direction dependent but of order $1/q^2$, as argued in greater detail in section 11.A.3.c for a linearized description of density fluctuations in a polar flock.

There is a puzzle here at first sight. We remarked above that the apolar contribution to the active current (23) is one order higher in gradients than the polar term. Why then do density fluctuations in the linearized theory for polar and apolar flocks show equally singular behaviour? The reason is that in polar flocks density gradients act back substantially on the polarization $p$ through the pressure-like term $v_1 \nabla p/\rho_0$ in (4), reducing the orientational fluctuations that engendered them. The effect of density gradients on $\theta$ in the apolar case is far weaker, a quadrupolar aligning torque $\sim \partial_x \partial_y \rho$ which does not substantially iron out the orientational curvature that engendered the density fluctuations.

It should be possible to check, on a living system, the rather startling prediction that flocks that go nowhere have enormous density fluctuations. Melanocyte suspensions at high concentration show well-ordered nematic phases when spread on a substrate as seen by Gruler et al. (1999). However, we know of no attempts to measure density fluctuations in these systems. The prediction of giant number fluctuations has been tested and confirmed first in a computer simulation of an apolar flocking model by Chaté et al. (2006) and then in an experiment on a vertically vibrated monolayer of head-tail symmetric millimeter-sized bits of copper wire by Narayan et al. (2007). Of particular interest is the fact that the experiment observed a logarithmic time decay of the autocorrelation of the local density, a stronger test of the theory than the mere occurrence of giant fluctuations. Issues regarding the origin of the fluctuations in the experiment were nonetheless raised by Aranson et al. (2008), with a response by Narayan et al. (2008).

Faced with such large density fluctuations, it is natural to ask whether the active nematic state is phase-separated in the sense of Das and Barma (2000). This idea was tested by Mishra and Ramaswamy (2006) to a simulation model in which particles were advected by the nematic curvature (Lebowohl and Lasher, 1973), and indeed the steady state showed the characteristics of Das and Barma (2000)'s fluctuation-dominated phase separation.

2. Self-propelled hard rods: a system of “mixed” symmetry?

The Vicsek model contains an explicit alignment rule that yields an ordered polar, moving state. The alignment interaction is in this case explicitly polar, in the sense that it aligns particles head-to-head and tail-to-tail. A different model of self-propelled particles where the alignment interaction has nematic, rather than polar, symmetry has been studied in detail by Baskaran and Marchetti (2008a, b, 2010). These authors considered the dynamics of a collection of self-propelled hard rods moving on a frictional substrate and interacting via hard core collisions. Numerical simulations of self-propelled hard rods have also been carried out by Ginelli et al. (2010); Kraikivski et al. (2006); Peruani et al. (2006, 2008); and Yang et al. (2010) and have revealed a rich behavior. The model consists of rods interacting via excluded volume interactions and self-propelled at speed $v_0$ along their long axis. The detailed analysis by Baskaran and Marchetti (2010) of the collisions of two self-propelled hard rods (see Fig. 14) shows that although self-propulsion modifies the collision by enhancing longitudinal momentum transfer and effectively tends to align two colliding rods, the alignment is in this case “apolar”, in the sense that it tends to align particles without distinguishing head from tail. Baskaran and Marchetti (2010) used tools of nonequilibrium statistical mechanics to derive a modified Onsager-type theory of self-propelled hard rods, obtaining a Smoluchowski equation that is modified in several ways by self-propulsion. They then obtained hydrodynamic equations by explicit coarse-graining of the kinetic theory. One result of this work is that self-propelled hard rods do not order in a polar moving state in bulk. In spite of the polarity of the individual particles, provided by the self-propulsion, the symmetry of the system remains...
nematic at large scales. Self-propulsion does, however, enhance nematic order, as shown earlier by Kraikivski et al. (2006) in a model of actin motility assays, where actin filaments are modeled as rigid rods moving frictionally on a two-dimensional substrate and the propulsion is provided by myosin motors tethered to the plane. It is well known (in a mean field approximation neglecting fluctuations) that thermal hard rods of length \( \ell \) undergo a continuous isotropic-nematic transition in two dimensions at a density \( \rho_{\text{ons}} = 3/(2\pi\ell^2) \) (Doi and Edwards, 1986), as first shown by Onsager in 1949 (Onsager, 1949). Self-propelled rods perform a persistent random walk (ten Hagen et al., 2009; Kareiva and Shigesada, 1983; Kardar, 2010) consisting of ballistic flights randomized by rotational diffusion. At long time the dynamics is diffusive and isotropic, with effective diffusion constant \( D_e = D + v_r^2/2D_r \), where \( D \) is the longitudinal thermal diffusion coefficient and \( D_r \) the rotational diffusion rate. Self-propelled rods of length \( \ell \) then behave as rods with an effective length \( \ell_{\text{eff}} \approx \sqrt{D_e/D_r} = \ell \sqrt{1 + v_r^2/(2DD_r)^{1/2}} \) and undergo an isotropic-nematic transition at a density \( \rho_{1N} = \rho_{\text{ons}}/(1 + v_r^2/2D_r) \), where we have used \( D \sim \ell^2 D_r \). The microscopic derivation carried out in Baskaran and Marchetti (2008a) supports this estimate. This result has been verified recently via large scale simulations of self-propelled hard rods (Ginelli et al., 2010; Yang et al., 2010).

The statistical mechanics of self-propelled hard rods and the derivation of the modified Smoluchowski equations is described in detail in Baskaran and Marchetti (2010) and will not be repeated here. Instead the hydrodynamic equations for this system are introduced phenomenologically below and their consequences are discussed.

Once again, the only conserved field is the density \( \rho(r,t) \) of self-propelled rods. Theory and simulations have indicated that although self-propelled particles with apolar interactions do not order in polar states, their dynamics is characterized by an important interplay of polar order, described by the vector order parameter \( p \) defined in Eq. (11), and nematic order, characterized by the alignment tensor \( Q_{ij} \) of Eq. (21). In other words, although the polarization \( p \) does not describe a broken symmetry, it seems necessary to incorporate its dynamics to capture the rich physics of the system into a continuum description. We then consider coupled equations for the conserved particle density, \( \rho \), and the two coupled orientational order parameters, \( p \) and \( Q \). Once again, the equations can be written in terms of a “free energy” as

\[
\partial_t \rho = -\nabla \cdot (v_0 \rho p) + D \nabla^2 \rho + \frac{1}{\gamma} \nabla \cdot \nabla \cdot \frac{\delta F_{pQ}}{\delta Q} + \nabla \cdot f^p, 
\]

\[
\partial_t p + \lambda_1(p \cdot \nabla) p - \delta_1 Q \cdot Q + \frac{\delta_2}{\gamma_p} Q p = -\frac{1}{\gamma_p} \frac{\delta F_{pQ}}{\delta p} + f, 
\]

\[
\partial_t Q + \lambda_1(p \cdot \nabla) Q = -\frac{1}{\gamma_Q} \left[ \frac{\delta F_{pQ}}{\delta Q} \right]_{ST} + f^Q, 
\]

where the subscript \( ST \) denotes the symmetric, traceless part of any second order tensor \( T \), i.e., \( [T]_{ST} \) has components \( T_{ij}^{ST} = \frac{1}{2} (T_{ij} + T_{ji}) - \frac{1}{2} \delta_{ij} T_{kk} \), and

\[
F_{pQ} = F_Q + \int_r \left\{ \frac{\alpha_{pQ}}{2} |p|^2 + \frac{K}{2} (\partial_\alpha p_\beta) (\partial_\alpha p_\beta) 
+ P(\rho, p, S) (\nabla \cdot p) - v_2 \delta_{a\beta} (\partial_\alpha p_\beta) \right\}, 
\]

We have grouped several terms (including some that were made explicit for instance in Eq. (1)) by writing a local spontaneous splay in terms of a “pressure” \( P(\rho, p, S) \). The reader should note that it is essential to retain the general dependence of this pressure on \( \rho, p \), and \( S \) to generate all terms obtained from the microscopic theory. Here \( p = |p| \) and the magnitude \( S \) of the alignment tensor has been defined by noting that in uniaxial systems in two dimensions we can write \( Q_{\alpha \beta} = 2S (n_\alpha n_\beta - \frac{1}{2} \delta_{\alpha \beta}) \), with \( n \) a unit vector. Then \( Q_{\alpha \gamma} Q_{\gamma \beta} = S^2 \delta_{\alpha \beta} \). The kinetic theory of Baskaran and Marchetti yields \( \alpha_{pQ} > 0 \) at all densities, indicating that no isotropic-polar transition occurs in the system. In contrast, \( \alpha_Q(\rho) \) is found to change sign at a characteristic density \( \rho_{1N} \), signaling the onset of nematic order. The closure of the moments equations used in Baskaran and Marchetti (2008a) to derive hydrodynamics only gives terms up to quadratic in the fields in the continuum equations, but is sufficient to establish the absence of a polar state and to evaluate the renormalization of the isotropic-nematic transition density due to self-propulsion. Cubic terms, such as the \( \sim \beta_2 Q^3 \) needed to evaluate the value of the nematic order parameter in
the ordered state and the active $\sim \delta_2 Q : Q p$ can be obtained from a higher order closure and are included here for completeness. A higher order closure also confirms the absence of a term proportional to $p^2$ in the polarization equation, which could, if present, yield a bulk polar state. We note that a $p \cdot Q \cdot p$ term in the free energy is permitted and would yield both the $p \cdot Q$ term on the left hand side of the $p$ equation, as well as a $ppp$ term in the $Q$ equation, with related coefficients. The joint presence of these terms can lead to the existence of a polar ordered state. The hard-rod kinetic theory of Baskaran and Marchetti produces only the $p \cdot Q$ term. The fact that the theory does not generate the $p \cdot Q$ term, which would be obligatory had the dynamics been governed entirely by a free-energy functional, underlines the nonequilibrium nature of the dynamics we are constructing. It would be of great interest to find the minimal extension of self-propelled hard-rod kinetic theory that could produce a phase with polar order.

a. Homogeneous Steady States and their Stability. The only homogeneous steady states of the system are an isotropic state with $\rho = \rho_0$ and $p = Q = 0$ and a nematic state where $p = 0$, but $Q$ is finite. The transition occurs at $\rho_{1N}$ where $\alpha_{pQ} \sim (\rho_{1N} - \rho)$ changes sign. As in the case of the active nematic, we work in two dimensions denoted $x$ and $y$, so that $Q$ has components $Q_{xx} = -Q_{yy} = \cos 2\theta$, $Q_{xy} = Q_{yx} = \sin 2\theta$. In the nematic state $\alpha Q < 0$, $\beta > 0$ in (27b), yielding a phase with uniform nematic order and $S = \sqrt{-\alpha Q/(2\beta Q)}$. We choose our coordinates so that this reference state has $\theta = 0$. The phase transition line is shown in Fig. 15 as a function of density $\rho_0$ and self-propulsion speed $v_0$ for the microscopic hard rod model discussed in Baskaran and Marchetti [2008a,b].

As in the case of polar and nematic active systems, the isotropic state is stable. It can also support finite-wavevector propagating sound-like waves (Baskaran and Marchetti [2008b]). The properties of the ordered state, on the other hand, are more subtle, and not yet fully explored. If we consider a homogeneous perturbation of the nematic state, we find that fluctuations $\delta p$ of the polarization along the direction of nematic order are unstable if $\lambda_1 S_0 > \alpha_{pQ}$. This global instability occurs outside the hydrodynamic regime as it involves fluctuations in the polarization and its significance remains a bit of a puzzle. Deep in the nematic state, neglecting fluctuations of both polarization and magnitude of the nematic order parameter, the homogeneous nematic state is unstable above a critical self propulsion speed. The instability arises from a subtle interplay of splay and bend deformations and diffusion longitudinal and transverse to the direction of nematic order and has been discussed in detail in Baskaran and Marchetti [2008b].

Numerical simulations of collections of self-propelled rods with steric repulsion have recently revealed a rich behavior, quite distinct from that of polar Vicsek-type models. As predicted by theory, self-propelled rods with only excluded volume interactions do not order in a macroscopically polarized state, but only exhibit nematic order, which appears to be long-ranged in two dimensions. Again, simulations have also confirmed that self-propulsion enhances the tendency for nematic ordering as well as aggregation and clustering (Ginelli et al. [2010], Peruani et al. [2006], Yang et al. [2010]). After an initial transient, the rods form polar clusters that travel in a directed fashion. Large clusters can form by collisions of smaller...
ones and break up due to collisions with other clusters or due to noise. Eventually the system reaches a stationary state, in which the formation rate of any cluster size equals its breakup rate, and the rods aggregate in large stationary clusters. Above the order-disorder transition, phase separation manifests itself with the formation of nematic bands, consisting of high density regions where the particles are on average aligned with the long direction of the band, but move in both directions, exhibiting no polar order (Ginelli et al., 2010), as shown in Fig. 17.

Self-propulsion has also been shown to increase the segregation tendency in mixture of self-propelled rods with distinctly different motilities (McCandlish et al., 2012). In closing this section we remark that mixed-symmetry models of the sort just presented may well be the best description of the collective crawling of rod-like bacteria such as those studied by Wu et al. (2011). Cluster formation qualitatively similar to that observed in simulations of SP rods has been observed in recent experiments in myxobacteria Peruani et al. (2012).

C. Current Status of Dry Active Matter

Although much progress has been made in the understanding and classification of dry active matter, a number of open questions remain.

Clustering and phase separation, with associated giant number fluctuations, are ubiquitous in active systems. It was first suggested that giant number fluctuations may be a distinct property of the ordered state (nematic and polar) of active systems, intimately related with the existence of a spontaneously broken orientational symmetry (Ramaswamy et al., 2003; Simha and Ramaswamy, 2002a; Toner and Tu, 1998). In ordered states such large fluctuations can indeed be understood as arising from curvature-driven active currents unique to the ordered state of active systems (Narayan et al., 2007). More recently giant number fluctuations consistent with a standard deviation growing linearly with the mean number of particles, rather than with the $1/2$ exponent expected in systems where the central limit theorem applies, have been reported in active systems of symmetric disks with no alignment rule that do not exhibit any orientational broken symmetry (Fily et al., 2012). In this case large density fluctuations associated with strong clustering and phase separation seem to arise from the general mechanism proposed in Cates et al. (2010) and Tailleur and Cates (2008) and reviewed recently in Cates (2012) associated with the breaking down of detailed balance in systems that are driven out of equilibrium by a local input of energy on each constituent, as in self-propelled systems or bacterial suspensions. Strong density inhomogeneities leading to persistent clustering have also been seen in layers of vibrated granular spheres (Aranson et al., 2008; Prevost et al., 2004). Again, although in this case other mechanisms such as the inelasticity of collisions may play a role, more work is needed to elucidate the generic aspect of this ubiquitous phenomenon.

Although some controversy still remains (Aldana et al., 2007; Gönci et al., 2008; Vicsek et al., 1995), there is now strong numerical evidence (Chaté et al., 2007) that the order-disorder transition in dry active systems is discontinuous, with an associated wealth of coexistence phenomena. One unusual aspect of the transition is that density fluctuations destabilize the ordered state right at the mean-field order transition. This behavior seems to be associated with a phenomenon that has been referred to as “dynamical self-regulation” (Baskaran and Marchetti, 2012; Gopinath et al., 2012) associated with the fact that in this class of active systems the parameter that controls the transition, namely the density of active particles, is not tuned from the outside, as in familiar
equilibrium phase transitions, but rather it is dynamically convected or diffused by non equilibrium active currents controlled by the order parameter itself. It would of course be very interesting to attempt to use formal field theory and renormalization group methods to shed some light on this unusual non equilibrium transition.

The behavior of collections of self-propelled or active particles is strongly affected by the presence of boundaries and obstacles (Elgeti and Gompper 2009; Wensink and Löwen 2008). Ratchet effects have been demonstrated experimentally and theoretically for active particles interacting with asymmetric obstacles or on asymmetric substrates, without any external forcing (Angelani et al. 2009; DiLeonardo et al. 2010). For bacteria undergoing run and tumble dynamics or self-propelled particles performing persistent random walks, the guiding effect of asymmetric boundaries can yield a variety of rectifying effects (Wan et al. 2008), that can even power submillimeter gears, as demonstrated in recent experiments (DiLeonardo et al. 2010; Sokolov et al., 2010). Understanding the interaction of bacteria with obstacles and with passive particles is crucial for harnessing the collective power of these living systems and developing micron-scale mechanical machines powered by microorganisms. Whether these phenomena can be described in the dry limit discussed in this section or require a proper treatment of flow as introduced in the next section and even hydrodynamic interactions is still an open question.

Finally, there has been a surge of recent interest in the properties of dense active matter and the living crystalline or glassy states that may be formed in these systems. The nonequilibrium freezing of active particles may be directly relevant to the behavior of suspensions of self-propelled Janus colloids or other artificial microswimmers (Palacci et al., 2010). Recent work has demonstrated that active particles do form crystalline states, but the freezing and melting is in this case a true non equilibrium phenomenon that cannot be described simply in terms of an effective temperature for the system (Bialké et al. 2012). In vitro experiment on confluent monolayers of epithelial cells suggest that the displacement field and stress distribution in these living systems strongly resemble both the dynamical heterogeneities of glasses and the soft modes of jammed packings (Petitjean et al. 2010; Poujade et al. 2007; Trepat et al. 2009; Angelini et al. 2010, 2011). This observation has led to new interest in the study of active jammed and glassy states (Henkes et al. 2011) obtained by packing self-propelled particles at high density in confined regions or by adding attractive interactions. In these models the interaction with the substrate has so far been described simply as frictional damping. Although a rich and novel dynamical behavior has emerged, it has become clear that a more realistic description of stress transfer with the substrate will be needed to reproduce the active stress distribution observed experimentally (Trepat et al. 2009) in living cellular material.

III. ACTIVE GELS: SELF-DRIVEN POLAR AND APOlar FILAMENTS IN A FLUID

In this section we describe an alternative method for constructing hydrodynamic theories for a class of active materials. This approach involves a systematic derivation of the hydrodynamic equations based on a generalized hydrodynamic approach close to equilibrium following closely the work of Martin Parodi, and Pershan for nemato-hydrodynamics (de Gennes and Prost 1993; Martin et al., 1972). As in the previous sections, the theory is mostly based on symmetries and does not involve significant microscopic considerations; it is thus applicable to a whole range of systems, which share the appropriate polar or nematic symmetries and which are liquid at long times. We focus here on an ‘active gel’, defined as a fluid or suspension of orientable objects endowed with active stresses, with momentum damping coming from the viscosity of the bulk fluid medium, rather than from friction with a substrate or a porous medium (Julicher et al. 2007; Kruse et al. 2004; Simha and Ramaswamy 2002a, b). The equations that emerge are those proposed in Simha and Ramaswamy (2002a) for self-propelling organisms, but the development in Julicher et al. (2007) and Kruse et al. (2004) was carried out in the context of the cytoskeleton of living cells, a network of polar actin filaments, made active by molecular motors that consume ATP.

In section III.B we consider an active system with a polarization field \( \mathbf{p} \) but we suppose that the physics of this system is invariant under a change of \( \mathbf{p} \) to \( -\mathbf{p} \). We therefore consider an active nematic gel. The polarization vector can in this case be considered as the director field for the nematic order. An alternative approach is to describe the ordering not by a director field but by a nematic alignment tensor, \( \mathbf{Q} \). This approach, also part of the phenomenological treatment in Simha and Ramaswamy (2002a), is presented in Salbreux et al. (2009). A brief discussion of polar active gels and of the effects of polarity on the dynamics is given in section III.C.

A. Hydrodynamic equations of active gels

For the sake of simplicity in this section we only discuss a one component active polar gel considering therefore that the complex composition of active materials such as the cytoskeleton can be described by an effective single component. The original formulation of Simha and Ramaswamy (2002a) for the hydrodynamics of self-propelled orientable suspensions was already an explicitly multicomponent formulation of active liquid-
crystal hydrodynamics, but without a formal link to the nonequilibrium thermodynamic approach to active systems of Jülicher et al. (2007). Generalizations of the latter approach to multicomponent systems are possible and have been recently proposed by Callan-Jones and Jülicher (2011) and Joanny et al. (2007). The multicomponent theory takes properly into account the relative permeation between the various components which are neglected in the simpler one-component description. As in the previous sections, we retain as slow variables, the number density $\rho$, the polarization $p$, and the momentum density $g = pmv$ where $v$ is the local velocity of the gel and $m$ the (effective) mass of the molecules.

1. Entropy production

The derivation of generalized hydrodynamic equations is based on the identification of fluxes and forces from the entropy production rate $\dot{S}$ à la de Groot and Mazur (1984). We do not wish to consider heat exchange here; we will assume that the active gel has a constant temperature, meaning that it is in contact with a reservoir at a finite temperature $T$. In this case, the entropy production rate is related to the rate of change in the free energy of the active gel $T\dot{S} = -\frac{dF}{dt}$.

For a passive gel at rest, the free energy density $f$ is a function of the two intensive variables, the density $\rho$ and the polarization $p$ and its differential is $df = \mu d\rho - h_\alpha dp_\alpha$. The field conjugate to the density is the chemical potential $\mu$ and the field conjugate to the polarization is the orientational field $h$. For a passive system moving at a velocity $v$, the density of kinetic energy $\frac{1}{2}pmv^2$ must be added to the free energy.

For an active gel one must also take into account the fact that energy is constantly injected into the gel locally. A simple intuitive way to introduce the energy injection is to assume that as in the case of the cytoskeleton, this is due to a nonequilibrium chemical reaction such as the consumption of ATP. If the energy gain per ATP molecule is denoted by $\Delta\mu$, and the rate of advancement of the reaction (the number of ATP molecules consumed per unit time and unit volume) is denoted by $r$, then the associated rate of change of the free energy per unit volume is $-r\Delta\mu$. Taking into account all contributions, we find the entropy production rate of an active gel at a constant temperature $T$ (Kruse et al. 2004, 2005).

\[
T\dot{S} = \int d\mathbf{r}\left\{-\frac{\partial}{\partial t}\left(\frac{1}{2}pmv^2\right) - \mu\frac{\partial \rho}{\partial t} + h_\alpha p_\alpha + r\Delta\mu\right\}. \tag{29}
\]

2. Conservation laws

The two conserved quantities in an active gel are the density and the momentum. The density conservation law reads

\[
\frac{\partial \rho}{\partial t} + \nabla \cdot (\rho \mathbf{v}) = 0. \tag{30}
\]

The momentum conservation law can be written as

\[
\frac{\partial \rho v_\alpha}{\partial t} + \partial_\beta \Pi_{\alpha\beta} = 0, \tag{31}
\]

where the momentum flux in the system is $\Pi_{\alpha\beta} = \rho m v_\alpha v_\beta - \sigma^\alpha_{\alpha\beta}$, where the first term is associated with the so called Reynolds stress and $\sigma^\alpha_{\alpha\beta}$ is the total stress in the system. For most active gels, in particular for biological systems, the Reynolds number is very small and we ignore in the following the Reynolds stress contribution.

3. Thermodynamics of polar systems

For generality in this section we consider active gels in three dimensions. The polarization free energy of an active polar material is a functional of the three components of the polarization vector $p$. However, if the system is not in the vicinity of a critical point there are only two soft modes associated with rotations of the polarization. The modulus of the polarization is not a hydrodynamic variable and is taken to be constant. Without any loss of generality, we assume that the polarization is a unit vector, and that the effect of its modulus is integrated in the phenomenological transport coefficients. The polarization free energy of the active gel is then the classical Frank free energy of a nematic liquid crystal (de Gennes and Prost 1993).

\[
F_p = \int d\mathbf{r}\left[\frac{K_1}{2} (\nabla \cdot p)^2 + \frac{K_2}{2} (p \cdot (\nabla \times p))^2 + \frac{K_3}{2} (p \times (\nabla \times p))^2 + v \nabla \cdot p - \frac{1}{2} h_0^0 |p|^2 \right]. \tag{32}
\]

The first three terms correspond to the free energies of splay, twist and bend deformations. The three Frank constants $K_i$ are positive. We have also added in this free energy a Lagrange multiplier $h_0^0$ to insure that the polarization is a unit vector. This free energy is very similar to the free energy of Eq. (44), although in Eq. (44) we had made the additional approximation that the Frank constants are equal. In the case where the polarization is a critical variable, one would also need to add to Eq. (32) a Landau expansion in powers of the polarization modulus as done in Eq. (44).

The orientational field is obtained by differentiation of the free energy (32). It is useful to decompose it into a component parallel to the polarization $h_\parallel$ and a component perpendicular to the polarization $h_\perp$.

In the simple case where the system is two-dimensional, the polarization can be characterized by its polar angle
θ. In the approximation where the Frank constants are equal the perpendicular molecular field is \( h_\perp = K\nabla^2 \theta \).

In a non-isotropic medium the stress is not symmetric. There is an antisymmetric component of the stress associated to torques in the medium. As for nematic liquid crystals, this anti-symmetric component can be calculated from the conservation of momentum in the fluid \( \text{[de Gennes and Prost 1993]} \) and is equal to \( \sigma_{\alpha\beta}^A = \frac{1}{2}(h_\alpha p_\beta - p_\alpha h_\beta) \sim h_\perp \).

4. Fluxes, forces and time reversal

Using the conservation laws and performing integrations by parts, the entropy production can be written as

\[
T\dot{S} = \int d\mathbf{r} \left\{ \sigma_{\alpha\beta} v_{\alpha\beta} + P_\alpha h_\alpha + r \Delta \mu \right\},
\]

where \( \sigma_{\alpha\beta} \) is the symmetric deviatoric stress tensor defined by

\[
\sigma_{\alpha\beta}^A = \sigma_{\alpha\beta} + \sigma_{\alpha\beta}^A - \delta_{\alpha\beta} P,
\]

with \( \sigma_{\alpha\beta}^A \) the antisymmetric part of the stress tensor and \( P \) the pressure. We have also introduced the strain rate tensor \( v_{\alpha\beta} \) and the antisymmetric part of the velocity gradients associated to the vorticity \( \omega_{\alpha\beta} \), defined as

\[
v_{\alpha\beta} = \frac{1}{2}(\partial_\alpha v_\beta + \partial_\beta v_\alpha), \quad \omega_{\alpha\beta} = \frac{1}{2}(\partial_\alpha v_\beta - \partial_\beta v_\alpha).
\]

Finally, \( P_\alpha = \frac{\partial p_\alpha}{\partial t} \), with

\[
\frac{\partial p_\alpha}{\partial t} = \partial_\alpha v_\beta p_\alpha + \omega_{\alpha\beta} p_\beta,
\]

is the convected derivative of the polarization. Note that if the system is chiral, kinetic momentum conservation must be taken into account properly and the local rotation is no longer given by \( \alpha_{\alpha\beta} \) \( \text{[Furthauer et al. 2012]} \).

This form of the entropy production allows for the identification of three forces: \( v_{\alpha\beta} \) which has a signature \(-1\) under time reversal, \( h_\alpha \) which has a signature \(+1\) under time reversal and \( \Delta \mu \) which also has a signature \(+1\) under time reversal. The conjugated fluxes are respectively \( \sigma_{\alpha\beta} \), \( P_\alpha \) and \( r \). The fluxes and associated driving forces that control the hydrodynamics of active gels are summarized in Table II.

| Flux      | Force       |
|-----------|-------------|
| \( \sigma_{\alpha\beta} \) | \( v_{\alpha\beta} \) |
| \( P_\alpha \) | \( h_\alpha \) |
| \( r \) | \( \Delta \mu \) |

Table II Fluxes and associated forces controlling the entropy production in a one-component nematic active gel.

care must be taken in considering the time reversal symmetry. The fluxes must all be separated into a reactive component with a signature opposite to that of the conjugate force and a dissipative component with the same signature as the conjugate force. As an example, the reactive component of the stress is the elastic stress and the dissipative component is the viscous stress. Only the dissipative component of each flux contributes to the entropy production.

B. Active nematic gels

1. Constitutive equations

We first consider an active polar liquid for which the relationship between fluxes and forces is local in time.

It is convenient to split all tensors into diagonal and traceless parts: \( \sigma_{\alpha\beta} = \sigma \delta_{\alpha\beta} + \tilde{\sigma}_{\alpha\beta} \), with \( \sigma = (1/3)\sigma_{\alpha\alpha} \), \( \tilde{\sigma}_{\alpha\alpha} = 0 \), and \( d \) the dimensionality. Similarly, we let \( v_{\alpha\beta} = \frac{d}{2} \delta_{\alpha\beta} + \tilde{v}_{\alpha\beta} \), where \( u = \partial_\gamma v_\gamma \) is the divergence of the velocity field. Finally, all fluxes are written as the sums of reactive and dissipative parts,

\[
\sigma_{\alpha\beta} = \sigma^r_{\alpha\beta} + \sigma^d_{\alpha\beta}, \quad P_\alpha = P^r_\alpha + P^d_\alpha, \quad r = r^r + r^d.
\]

a. Dissipative fluxes. Only fluxes and forces with the same time signature are coupled and \( \sigma_{\alpha\beta} \) is only coupled to \( v_{\alpha\beta} \). This leads to the constitutive equations

\[
\sigma^d = \eta u \quad (38a)
\]

\[
\tilde{\sigma}^d_{\alpha\beta} = 2\eta \tilde{v}_{\alpha\beta} \quad (38b)
\]

We ignore here the tensorial character of the viscosity and assume only two viscosities, as for an isotropic fluid: the shear viscosity \( \eta \) and the longitudinal viscosity \( \tilde{\eta} \). The two other fluxes are coupled and the corresponding constitutive equations read \( \text{[Kruse et al. 2004]} \text{[2005]} \)

\[
P^d_\alpha = \frac{h_\alpha}{\gamma_1} + \epsilon_\alpha \Delta \mu, \quad (39)
\]

\[
r^d = \Lambda \Delta \mu + \epsilon_\alpha h_\alpha. \quad (40)
\]

\( \gamma_1 \) is the rotational viscosity and we use here the Onsager symmetry relation which imposes that the “dissipative” Onsager matrix is symmetric.
b. Reactive fluxes

The reactive Onsager matrix is antisymmetric and couples fluxes and forces of opposite time reversal signatures.

\[ \sigma^r = -\tilde{\gamma} \Delta \mu + \nu_1 p_a h_\alpha , \]
\[ \tilde{\sigma}_{\alpha\beta}^r = -\zeta \Delta \mu \nu_{\alpha\beta} + \frac{\nu_1}{2} (p_a h_\beta + p_\beta h_\alpha - \frac{2}{3} p_\gamma h_\gamma \delta_{\alpha\beta}) , \]
\[ P^a_r = -\tilde{\nu}_1 \rho p_a \frac{u}{3} - \nu_1 p_\beta \tilde{v}_{\alpha\beta} , \]
\[ r^r = \frac{\zeta u}{3} + \zeta q_{\alpha\beta} \tilde{v}_{\alpha\beta} . \]

In most of the following we consider incompressible fluids so that \( u = \nabla \cdot v = 0 \). In this case the diagonal component of the stress can be included in the pressure which is a Lagrange multiplier ensuring incompressibility and one can set \( \zeta = \tilde{\nu}_1 = \tilde{\eta} = 0 \).

To summarize, the hydrodynamic equations for an incompressible one-component active fluid of nematic symmetry are given by

\[ m \rho (\partial_t + v \cdot \nabla) v = -\nabla P + \nabla \cdot \sigma , \]
\[ \rho (\partial_t + v \cdot \nabla) p_a + \omega_{\alpha\beta} p_\beta = -\nu_1 v_{\alpha\beta} p_\beta + \frac{1}{\gamma_1} h_\alpha + \epsilon \Delta \mu p_a , \]
\[ h_\alpha = K \nabla^2 p_a + h^0_\parallel p_a , \]

with \( h^0_\parallel \) a Lagrange multiplier to be determined by the condition \( |p| = 1 \). Finally, it is convenient for the following to write the deviatoric stress tensor given by the sum of trace and deviatoric parts of the dissipative and reactive components by separating out passive and active parts as

\[ \sigma_{\alpha\beta} = \sigma^p_{\alpha\beta} + \sigma^a_{\alpha\beta} , \]

with passive and active contributions given by

\[ \sigma^p_{\alpha\beta} = 2\eta \tilde{v}_{\alpha\beta} + \frac{\nu_1}{2} (p_a h_\beta + p_\beta h_\alpha - \frac{2}{3} p_\gamma h_\gamma \delta_{\alpha\beta}) , \]
\[ \sigma^a_{\alpha\beta} = -\zeta \Delta \mu \nu_{\alpha\beta} . \]

The other active coefficient, \( \epsilon \), is an active orientational field that tends to align the polarization when it is positive. In the limit where the modulus of the polarization is \( p = 1 \) one can always consider that \( \epsilon = 0 \) and introduce an effective activity coefficient \( \zeta + \epsilon \gamma_1 \nu_1 \). In the following we therefore choose \( \epsilon = 0 \) and use this effective value of the activity coefficient \( \zeta \).

3. Active currents in nematic and polar systems from forces and fluxes

Let us take the opportunity to show that the active currents in nematic (section II.B) and polar (section II.A) systems follow naturally from the forces-and-fluxes framework. In this short treatment we ignore fluid flow. Consider a mesoscopic region in our active medium, in a chemical potential gradient \( \nabla \Phi \) corresponding to the concentration \( \rho \), and subjected to a nonzero chemical potential difference \( \Delta \mu \) between a fuel (ATP) and its reaction products (ADP and inorganic phosphate). For small departures from equilibrium, the fluxes \( r \) (the rate of consumption of ATP molecules) and \( J \) must be linearly related to \( \Delta \mu \) and \( \nabla \Phi \). The presence of local orientational order in the form of \( p \) and \( Q \) allows one to construct scalars \( p \cdot \nabla \Phi \) and \( Q \cdot \nabla \Phi \); thus \( r \) in general gets a contribution \( (\zeta_p p + \tilde{\zeta}_Q Q) \cdot \nabla \Phi \), where \( \zeta_p \) and \( \tilde{\zeta}_Q \) are kinetic coefficients depending in general on \( \rho \) and other scalar quantities. The symmetry of dissipative Onsager
coefficients then implies a contribution

$$J_{\text{active}} = (\zeta_p \rho + \bar{\zeta} \Omega \cdot \Omega) \Delta \mu$$

(47)

to the current. In the presence of a maintained constant value of $\Delta \mu$ the current (47) rationalizes, through the $\zeta_p$ and $\bar{\zeta} \Omega$ terms, the form of (23) (with $\zeta_p \Delta \mu \rightarrow \bar{\zeta}_\Omega$). In particular, it underlines the fact that active currents do not require an explicit polar order parameter. Even without $\rho$, the term in $\zeta_p$ in (47) tells us that curvature in the spatial arrangement of active filaments gives rise to particle motion. In retrospect this is not shocking: a splayed or bent configuration of a nematic phase has a vectorial asymmetry, as argued through Fig. 12. In a system out of equilibrium this asymmetry should reflect itself in a current. As shown by Ramaswamy et al. (2003) and discussed in section II.2, $\zeta_p$ leads to giant number fluctuations in active nematics.

4. Viscoelastic active gel

An active gel is not in general a simple liquid but rather a viscoelastic medium with a finite viscoelastic relaxation time, which is only liquid at long time scales. In a passive visco-elastic medium the constitutive relation between stress and strain is non local in time. The simplest description of a visco-elastic medium is the so-called Maxwell model where the system only has one relaxation time, which is only liquid at long time scales. In particular, it underlines the fact that active currents do not require an explicit polar order parameter. Even without $\rho$, the term in $\zeta_p$ in (47) tells us that curvature in the spatial arrangement of active filaments gives rise to particle motion. In retrospect this is not shocking: a splayed or bent configuration of a nematic phase has a vectorial asymmetry, as argued through Fig. 12. In a system out of equilibrium this asymmetry should reflect itself in a current. As shown by Ramaswamy et al. (2003) and discussed in section II.2, $\zeta_p$ leads to giant number fluctuations in active nematics.

The long time viscosity of the medium is then

$$\eta_v = \frac{1}{\tau E \tau}$$

(48)
The Maxwell model involves two material constants, the viscoelastic relaxation time $\tau$ and the shear modulus $E$. The long time viscosity of the medium is then $\eta = E \tau$. In order to respect rotational and translational invariance, we use here a convected Maxwell model with a convected time derivative of the stress tensor $D\bar{\sigma}_{\alpha\beta}/Dt = \partial \bar{\sigma}_{\alpha\beta}/\partial t + \nu_1 \partial \bar{\sigma}_{\alpha\beta} + \omega_1 \bar{\sigma}_{\alpha\beta} + \bar{\sigma}_{\gamma\mu} \omega_2 \gamma$. Note that there are several ways of defining the convective derivative of tensors. For simplicity we use the same notation $D\rho/Dt$ to denote convected derivatives of vectors and tensors.

The generalization of the Onsager hydrodynamic approach of the previous section to a viscous elastic polar passive medium lead to the constitutive equations for an active gel [Jülicher et al., 2007],

$$2\eta v_{\alpha\beta} = (1 + \frac{\tau}{\rho} D) (\delta_{\alpha\beta} + \zeta \Delta \mu q_{\alpha\beta} - \frac{\nu_1}{2} (p_{\alpha} h_{\beta} + p_{\beta} h_{\alpha})),$$

(49a)

$$D\rho_{\alpha}/Dt = \frac{1}{\gamma_1} (1 + \frac{\tau}{\rho} D) h_{\alpha} - \nu_1 v_{\alpha\beta} p_{\beta},$$

(49b)

where for simplicity we have only considered an incompressible active gel where the modulus of the polarization is unity. Note that the memory of the system not only plays a role for the stress but also for the dynamics of the orientation and that we have supposed that the two corresponding relaxation times are equal.

It is important to note that the dynamical equation for the polarization is very similar to Eq. (2b) used in section I which has been obtained using the same symmetry arguments; Eq. (2b) ignores memory effects and therefore the visco-elasticity of the polarization response; all the extra terms in Eq. (2b) do not appear here because the Onsager approach that we use only derives the linear hydrodynamic theory.

C. Active polar gels

For the sake of simplicity, we have only presented here the derivation of the hydrodynamic theory of active gels in the simplest case where the system is a single component fluid and has nematic symmetry, $\rho$ being the director, and ignore any type of noise. Several extensions of this theory have been proposed.

For a polar system, there is an extra polar term in the free energy $\frac{1}{2} F_p = \int d \rho \nu(\rho) (\nabla \cdot h)$. This spontaneous splay term is a surface term if the coefficient $\nu$ is a constant. If $\nu$ depends on the local density, this term, that was included in Eq. (1), yields a “pressure-gradient” proportional to $\nabla \rho$ in the equation for the polarization. Other non linear polar terms that can be added on the right hand side of the dynamical equation for the polarization (49) are proportional to $\rho \cdot \nabla \rho$, $\nabla \rho^2$ and $\rho \nabla \cdot \rho$. These terms have already been considered in Eq. (2b). The first of these terms cannot be derived from a free energy and is therefore an active term proportional to $\Delta \mu$. Its effect in a dynamics linearized about an ordered state was considered for active liquid-crystalline suspensions by Simha and Ramaswamy (2002a). The two other terms can be derived from a free energy and have both active and passive contributions. Within the Onsager linear hydrodynamics scheme, other polar terms in the equations show up only at nonlinear order or at sub-leading order in a gradient expansion. Active stresses proportional to $\Delta \mu (p_{\alpha} p_{\beta} + p_{\beta} p_{\alpha})$ unique to polar fluids are obtained from the microscopic theory (Marchetti and Lioerpool, 2007), but are considered nonlinear in the driving forces in the context of the Onsager approach. The effect of these polar terms has been studied in detail by Giomi and collaborators (Giomi et al., 2008). In general these polar terms are important when describing an active suspension as opposed to the one-component system considered here. In this case these terms yield spatial inhomogeneities in the concentration of active particles (Giomi and Marchetti, 2012), Tjhung et al., 2011) that are not obtained in active suspensions with nematic symmetry (Giomi et al., 2011, 2012).

The effect of noise in active polar gels can be studied by
introducing random Langevin forces in the constitutive equations. For treatments including thermal and active non-thermal noise sources in a systematic way, see [Basu et al., 2008; Chen et al., 2007; Hatwalne et al., 2004; Lau et al., 2003; Lau and Lubensky, 2009; and Sarkar and Basu, 2011]. The precise description of the statistics of active noise requires a microscopic description of the gel which is not generic and goes beyond the scope of this review [Basu et al., 2008]. Hatwalne et al. [2004] introduce the active noise in the isotropic phase of an active gel through the fluctuating active stress in the Navier-Stokes equation, and use scaling arguments to estimate the apparent temperature it would generate in a tracer diffusion measurement.

Most active systems described in the earlier sections of this review are multicomponent systems containing a solvent and active objects. In many instances these systems can be described by an effective one-component theory as described here. However, in particular when considering viscoelastic effects the one-component theory ignores the permeation of the solvent through the active gel. A detailed two component theory of active gels that takes into account properly permeation effects is given by Callan-Jones and Julicher [2011].

D. Active Defects

Ordered phases of active matter, like their counterparts at thermal equilibrium, should exhibit topological defect configurations, generated either through specific boundary conditions or spontaneously in the bulk. As in equilibrium systems, the nature of these defects should depend on whether the system has polar or apolar symmetry (de Gennes and Prost, 1993; Kung et al., 2006; Palffy-Muhoray et al., 1998). The selection criterion for the defect strength in active systems is not obvious, as one cannot a priori invoke free-energy minimization as in equilibrium systems. However, it does appear that experiments see strength +1 and strength +1/2 defects, respectively, in polar (Nédélec et al., 1997) and apolar (Narayan et al., 2007) active systems. Activity confers a particularly interesting property on defects, namely rotational (Kruse et al., 2006a; Nédélec et al., 1997) or translational (Dogic, 2012; Narayan et al., 2007) movement, with sense or direction determined by the chirality or polarity associated with the defect.

The first quantitative experiments which explicitly demonstrated how active mixtures of long rods (microtubules) and motors (kinesin) could spontaneously form defects such as asters and spirals were reported in Nédélec et al. [1997] and Surrey et al. [2001]: see Fig. 2. These patterns showed a remarkable resemblance to the microtubule-based spindle patterns in the cell, thus suggesting that the gross features of spindle patterning could be understood as arising from a self-organization of simple elements. Several qualitative features of these experiments including the defect patterns could be simply understood using continuum models describing the polar orientation of the rigid filaments and the density of processive motors (Lee and Kardar, 2001; Sankararaman et al., 2004).

A detailed study of the nature of defects and their phase transitions within the framework of the active gel theory was done by Kruse et al. [2004, 2006a] who showed that flows arising from active stresses leads to systematic rotation of chiral defects. We summarize here the calculation, working as in Kruse et al. [2004] with the ordered state described by a vectorial order parameter \( p \) in two dimensions. Polarity enters nowhere in the analysis, except as justification for working with a strength +1 defect. We parametrize a two-dimensional defect configuration of the polarization field \( p \) (of unit magnitude) with topological charge \( \pm 1 \) using polar coordinates \((r, \theta)\). Thus charge +1 defects such as asters, vortices and spirals, may be represented by an angle \( \psi \), with \( p_r = \cos \psi \) and \( p_\theta = \sin \psi \), such that \( \psi = 0 \) (or \( \pi \)) is an aster, \( \psi = \pm \pi/2 \) a vortex and \( \psi = \psi_0 \) (any other constant) a spiral. At equilibrium, a situation corresponding to defect configurations in a ferroelectric nematic liquid crystal, the optimal value of \( \psi \) is obtained by minimizing the Frank free-energy functional \( F \) with \( K_2 = 0 \) (no twist as we are working in two dimensions). With appropriate boundary conditions, it easy to see that the stable defect configurations are (i) asters when \( K_1 < K_3 \), so that splay is favored, (ii) vortices when \( K_1 > K_3 \), i.e., bend is favored, and (iii) spirals when \( K_1 = K_3 \). In an active system, however, the stability of defect configurations is obtained by solving the dynamical equations for the polarization \( p \) together with the conditions of force balance and overall incompressibility, as in section III.B.

Suppose \( K_1 < K_3 \), so that the aster is stable in the absence of activity, \( \Delta \mu = 0 \). Now introduce activity. Linear stability analysis shows that at sufficiently large contractile active stresses \( \zeta \Delta \mu < 0 \), the aster gets destabilized giving rise to a spiral with an angle \( \psi_0 \) set by the flow alignment parameter \( \nu_1 \) (assuming stable flow alignment). An entirely similar analysis, starting from a stable vortex for \( K_1 > K_3 \), with \( \Delta \mu = 0 \), shows again an instability for large enough \( \Delta \mu \). The reason this happens here and does not happen for systems without activity is that the active stresses associated with the perturbed director configuration give rise to flows whose effect on the director is to reinforce the perturbation. Figs. 19 and 20 illustrate the flow associated with the spiral instability and the stability domains of the defects, respectively. The active spiral has a sense of direction and will therefore rotate. The angular speed can be obtained by solving the steady state equations for \( \psi \) and \( \nu_\theta \), leading to

\[
\nu_\theta(r) = \omega_0 \log \left( \frac{r}{r_0} \right),
\]

(50)
where, as is inevitable on dimensional grounds, $\omega_0$ scales as the ratio of the active stress to a viscosity, with a detailed form that includes a dependence on the director kinetic coefficient and the flow-alignment parameter. In a finite system of size $R$, imposing a vanishing velocity at the outer boundary due to the presence of a wall, we can set the length scale $r_0 = R$.

In the above analysis we ignored the dynamics of the concentration field $\rho$. This is probably acceptable when the active units are long and rigid or when their concentration is so high that excluded volume considerations do not permit significant density inhomogeneities. We can include $\rho$ through an extra term $v_1 \int d^3r \rho \nabla \cdot \mathbf{p}$ in the free energy, with the form of a spontaneous splay that depends on the local concentration, and restore the concentration equation, $\partial_t \rho = -\nabla \cdot \mathbf{J}$, where the filament current $\mathbf{J} = v_0 \rho \mathbf{p} - D \nabla \rho$, has an active advective and a diffusive contribution. Now for large enough $A$, the defect configurations are generated by the internal dynamics (and insensitive to the boundary for large systems) and so have finite size. When advection is negligible, the defect size is set by the ratio of the spontaneous splay coupling strength $A$ to a Frank modulus, $K$, as it would be in an equilibrium polar liquid crystal. On the other hand, when advection is appreciable so as to have density clumping in regions where $\rho$ points inwards towards a common center, the defect size is set by the ratio of diffusion to active advection, $D/v_0$. Since defects now have a finite size, it is possible to have an array of defects which interact with each other. Such studies have shown that under certain conditions, one obtains a stable lattice of asters accompanied by a variety of phase transitions (Gowrishankar and Rao, 2012; Voituriez et al., 2006; Ziebert and Zimmermann, 2005). A detailed study of defect-defect interactions and the dynamics of defects and their merger in this active context are open problems for the future.

So far we have discussed charge 1 defects generated in polar active media. Apolar active media, described by a local orientational tensor $\mathbf{Q}$, exhibit $\pm 1/2$ strength disclinations, topologically identical to those obtained in equilibrium nematic liquid crystals (Fig. 7). The orientation field around a defect of strength $+1/2$ has a 3-fold symmetric appearance. On general grounds, the $+1/2$ defect should move spontaneously whereas the $-1/2$ defect should show no such tendency. Precisely this behavior seems to be observed in the active nematic phase in a vibrated granular-rod monolayer (Narayan et al., 2007).

### E. Current status on active gels

The nonequilibrium thermodynamic description of active systems is a systematic approach based on symmetries and in particular on invariance against time inversion. It is however based on a linear expansion of fluxes in terms of forces and can in principle only describe systems close to equilibrium where $\Delta \mu$ tends to zero. One of the main application though is to biological systems that are mostly far from equilibrium systems. There is no systematic extension of the theory to systems far from equilibrium. One must rely either on a microscopic description that generates non-linear contributions by coarse-graining to large length scales and long time scales or on
experimental results that emphasize specific non-linear aspects, which can then be introduced in the theory. Microscopic or mesoscopic descriptions of molecular motors are a good example of the first case and lead to motor forces or velocities that are not linear in $\Delta \mu$ (Julicher and Prost 1997, Liverpool et al. 2009). Several experiments suggest that the treadmilling associated to the polymerization and depolymerization of actin in a cell depends on the force applied on the filaments or the local stress in a non-linear way (Mogilner and Oster 1999, Prost et al. 2007). The force-dependent treadmilling is essential for many cellular processes such as cell migration or cell adhesion and a full description including these effects in the active gel theory has not been proposed yet (Keren et al. 2008).

Another intrinsic limitation of the current active gel theory is the assumption of linear rheology and the use of the Maxwell model with a single relaxation time. A large body of experimental work shows that for many types of cells as well as for actomyosin gels there is a broad distribution of relaxation times leading to a complex modulus that does not depend on the size of the particle but only on the thickness of the film. We believe that the treadmilling associated to the polymerization and depolymerization of actin in a cell depends on the force applied on the filaments or the local stress in a non-linear way (Mogilner and Oster 1999, Prost et al. 2007). The force-dependent treadmilling is essential for many cellular processes such as cell migration or cell adhesion and a full description including these effects in the active gel theory has not been proposed yet (Keren et al. 2008).

The hydrodynamic description of active polar or nematic gels is very close to that of nematic liquid crystals. Nevertheless the existence of an active stress leads to several non-intuitive and spectacular phenomena. The most spectacular is the flow instability described below that leads to spontaneously flowing states. Other spectacular effects are associated with active noise in these systems. In all active systems the noise has a thermal and a non thermal active component. The properties of the active noise cannot be inferred from the macroscopic hydrodynamic theory and must be derived in each case from a specific microscopic theory. The study of tracer diffusion in a thin active film for example (Basu et al. 2011) leads to an anomalous form of the diffusion constant that does not depend on the size of the particle but only on the thickness of the film. We believe that there are still many unusual properties of active gels to be discovered and that in many cases, this will require detailed numerical studies of the active gel hydrodynamic equations such as the one performed in Marenduzzo et al. (2007).

Active gel models have also been used to describe cross-linked motor-filament systems that behave as soft solids at large scales (Banerjee and Marchetti 2011, Levine and MacKintosh 2009, MacKintosh and Levine 2008, Yoshinaga et al. 2010) and also to understand the origin of sarcomeric oscillations, both from microscopic as well as from a continuum viewpoint (Banerjee and Marchetti 2011, Günther and Kruse 2007). Further, active gel models have been shown to successfully account for the experimentally observed traction stresses exerted by cells and cell sheets on compliant substrates (Banerjee and Marchetti 2011, Edwards and Schwarz 2011, Mertz et al. 2012).

Finally, a large part of the theoretical activity on active gels aims at a quantitative description of biological phenomena at the scale of the cell and of cellular processes involving the cytoskeleton. Some success has already been obtained in discussing lamellipodium motion (Kruse et al. 2006a) or the formation of contractile rings during cell division (Salbreux et al. 2009). An important step is the connection of the parameters of the hydrodynamic theory with the more microscopic parameters that can be monitored experimentally which requires an explicit coarse graining of the microscopic theories as discussed in section IV. At larger scale one can build a hydrodynamic theory of tissues that shares many features with the active gel theory described here (Ranft et al. 2010).

IV. HYDRODYNAMIC CONSEQUENCES OF ACTIVITY

In this section we describe a number of remarkable hydrodynamic phenomena induced by activity. Most of the section is devoted to the description of materials properties of active gels, such as thin film instabilities and rheology. In section IV.D we also highlight some of the remarkable successes of the hydrodynamic theory of active gels in describing phenomena observed in living cells. A more complete review of these latter class of phenomena can be found in Joanny and Prost (2010).

A. Instabilities of thin liquid active films

1. Spontaneous flow of active liquid films

One generic property of active orientable liquids, whether polar or apolar, is the instability of any homogeneous non-flowing steady state toward an inhomogeneous spontaneously flowing state, as shown by Simha and Ramaswamy (2002a). We illustrate this instability in the simple geometry of a thin active nematic liquid film (Voituriez et al. 2005).

We study a thin film of thickness $h$ supported by a solid substrate. For simplicity we only consider the two-dimensional geometry sketched in Fig. 21 where the sub-
strate is along \( x \) and the normal of the film is along \( y \). We choose anchoring conditions parallel to the film surface so that for \( y = 0, h \) the polarization is along \( x \), \( p_x = 1, p_y = 0 \). An obvious solution for the equations of motion of an active liquid is a non flowing state \( \mathbf{v} = 0 \) with a constant polarization parallel to \( x \). We now discuss the stability of this steady state. We look for a state of the system which is invariant by translation along \( x \) so that all derivatives with respect to \( x \) vanish and with a polarization that is not parallel to the film surfaces \( p_x = \cos \theta(y), p_y = \sin \theta(y) \). The velocity is along the \( x \) direction and the shear rate tensor only has one non vanishing component \( v_{xy} \equiv w = \frac{1}{2} \partial_y v_x \).

The total stress can be written as \( \sigma^t_{\alpha \beta} = -P \delta_{\alpha \beta} + \sigma^A_{\alpha \beta} + \sigma^\perp_{\alpha \beta} \) where the last term is the deviatoric stress given by the constitutive equations (49) and the previous term is the antisymmetric component of the stress. Force balance in the film is written as \( \partial_y \sigma^t_{yx} = 0 \). Taking into account the fact that on the free surface the shear stress vanishes, we obtain \( \sigma^t_{yx} = 0 \). Using the constitutive equation, this leads to

\[
-h_{\perp} = 4 \eta w - \zeta \Delta \mu \sin 2\theta + \nu_1 (h_{||} \sin 2\theta + h_{\perp} \cos 2\theta) , \tag{51}
\]

where we have introduced the parallel and perpendicular components of the orientational field \( h_{||} = h_x \cos \theta + h_y \sin \theta \) and \( h_{\perp} = h_y \cos \theta - h_x \sin \theta \).

The constitutive equations for the polarization of Eq. (49) give

\[
-w \sin \theta = \frac{h_x}{\gamma_1} - \nu_1 w \sin \theta ,
\]

\[
w \cos \theta = \frac{h_y}{\gamma_1} - \nu_1 w \cos \theta . \tag{52}
\]

Combining Eqs. (51) and (52), we obtain the perpendicular field and the velocity gradient

\[
h_{\perp} = \frac{\zeta \Delta \mu \sin 2\theta (1 + \nu_1 \cos 2\theta)}{\frac{4 \eta}{\gamma_1} + 1 + \nu_1^2 + 2 \nu_1 \cos 2\theta} ,
\]

\[
w = \frac{\zeta \Delta \mu \sin 2\theta}{\frac{4 \eta}{\gamma_1} + 1 + \nu_1^2 + 2 \nu_1 \cos 2\theta} . \tag{53}
\]

In the approximation where the Frank constants are equal, the perpendicular molecular field is \( h_{\perp} = -\frac{\delta \mathbf{F}}{\partial \theta} = K \partial^2 \theta / \partial y^2 \). If the angle \( \theta \) is small, an expansion of Eq. (53) for the perpendicular field to lowest order in \( \theta \) gives

\[
\nabla^2 \theta + \frac{\alpha}{\gamma_1} = 0 \]

where the characteristic length \( L \) is defined by

\[
\frac{1}{L^2} = \frac{-2 \zeta \Delta \mu (1 + \nu_1)}{K [\frac{4 \eta}{\gamma_1} + (1 + \nu_1)^2]} . \tag{54}
\]

Assuming \( 1 + \nu_1 > 0 \), if the activity coefficient \( \zeta \) is negative corresponding to a contractile stress, \( L^2 > 0 \) and the length \( L \) is indeed real. The polarization angle varies then as \( \theta = \theta_0 \sin (\frac{\pi w}{L}) \). This satisfies the anchoring condition on the solid surface \( y = 0 \) but the anchoring condition on the free surface \( y = h \) can only be satisfied if \( h = \pi L \). If the film is thin \( h \leq \pi L = L_c \) there is no solution with a finite \( \theta \) and the non-flowing steady state is stable. For a film thicker than the critical value \( h \approx \pi L \) a solution with a finite value of the polarization angle \( \theta \) exists and the non-flowing steady state is unstable. If \( h > L_c \) there is spontaneous symmetry breaking and two possible solutions with amplitudes \( \pm \theta_0 \). The amplitude \( \theta_0 \) can be obtained by expansion at higher order of Eq. (53) and vanishes if \( h = \pi L \). In this case the second of Eq. (53) gives a finite velocity gradient and the film spontaneously flows with a finite flux. Note that in general the onset of spontaneous flow is controlled by the sign of the combination \( \zeta (1 + \nu_1) \). The flow coupling coefficient (also known as flow alignment parameter) \( \nu_1 \) can in general have both positive and negative values (de Gennes and Prost 1993). It is controlled by the shape of the active units and the degree of nematic order. Deep in the nematic state, \( \nu_1 < -1 \) corresponds to elongated rod-like particles, while \( \nu_1 > 1 \) corresponds to disk-like particles. The onset of spontaneous flow is therefore controlled by the interplay of the contractile/tensile nature of the active forces and the shape of the active particles. A detailed description of this can be found in Edwards and Yeomans (2009) and Giomi et al. (2008).

This transition is very similar to the Frederiks transition of nematic liquid crystals in an external electric or magnetic field (de Gennes and Prost 1993). The active stress \( \zeta \Delta \mu \) plays here the role of the external field. If the thickness is larger than the critical value \( L_c \), a distortion of the polarization appears. Any distortion of the polarization creates a gradient of active stress that must be balanced by a viscous stress which implies the appearance of a finite flow.

The Frederiks transition could also be considered at a constant film thickness varying the active stress \( \zeta \Delta \mu \). The film spontaneously flows if the active stress is large enough (in absolute value).

Finally, to properly describe the spontaneous flow transition for polar active films one needs to consider a two-fluid model that allows for variations in the concentra-
tion of active particles. In this case spontaneous flow is accompanied by spatial inhomogeneities in the concentration or “banding” not seen in active nematics (Giomi et al. 2008). In addition for stronger values of activity in polar films steady spontaneous flow is replaced by oscillatory flow that becomes increasingly complicated and even chaotic for strong polarity.

2. Instabilities of thin films

The Fredericks active film instability discussed in section [V.A.1] occurs in situations where the geometry of the film is fixed and its surface cannot deform, whereas many beautiful phenomena in thin film flow (Oron et al. 1997; Sarkar and Sharma 2010) involve distortions of the free surface. In the context of cell biology, a study of a film of active fluid with a dynamic free surface is the natural starting point for a complete description of a moving lamellipodium, which is a thin, flat, fluid projection, full of oriented actin, that forms the leading edge of a crawling cell (Small et al. 2002; Verkhovsky et al. 1999). The spreading of bacterial suspensions (Bees et al. 2000; 2002) is another biological instance in which the processes discussed in this section could intervene. However we discuss here simpler situations where mechanisms such as cell division in the bacterial case and actin treadmilling in the lamellipodium case are not included and that in a first step could only be compared to model biomimetic experiments. Despite these limitations, the problems of an active drop or an active film are interesting as novel variants of classic fluid mechanics problems and as settings for phenomena of relevance to biology.

We review in this section the hydrodynamics of thin films of fluid containing orientable degrees of freedom and endowed with locally uniaxial active stresses, bounded on one side by a solid surface, and on the other side by a surface free to undulate in response to flows in the film. We present in some detail the case of an unbounded film (Sankararaman and Ramaswamy 2009), to highlight the exotic physical effects that arise from polar orientational order in an active system. In this example, we consider an active system comprising a solvent fluid and dissolved active particles. In the language of the previous section, we thus consider a multicomponent active fluid. We assume that the polar material velocity with respect to the background fluid (related to the relative current between the two components) is strictly slaved to the polar order and equals \( v_0 \). This assumption is meaningful in the case of bacterial colonies but would have to be reconsidered in the discussion of a cell lamellipodium. We also sketch results for the case of a finite, partially wetting drop with small equilibrium contact angle and apolar orientational order (Joanny and Ramaswamy 2012), where topological defects play a role. In both cases, we consider only planar alignment (de Gennes and Prost 1993) where the local orientation field is anchored parallel to the free surface and the rigid base, and free to point in any direction in the plane of anchoring. Our focus is of course on the effects specifically due to the active stresses and currents.

Following Sankararaman and Ramaswamy (2009), we consider a fluid film (Fig. 22) containing active particles with number density \( \rho(r,t) \) and orientation field \( p(r,t) \) as a function of time \( t \) and three-dimensional position \( r = (r_x, r_y, r_z) \), where \( z \) denotes the coordinate normal to the horizontal coordinates \( r_\perp = (x, y) \), and the solid surface lies at \( z = 0 \). In the case of the drop, where we consider only apolar order, we identify the vector \( p \) with the nematic director field, with \( p \rightarrow -p \) symmetry. The free surface is located at \( z = h(r_\perp, t) \). The flow of the film is characterized by the 3-dimensional incompressible velocity field \( \mathbf{v}(r,t) \). We focus on the case where the film or drop has macroscopic order, i.e., the mean \( \langle p \rangle \) is nonzero, which means that variations in the direction, not the magnitude, of \( p \) plays the central role. Our aim is to obtain an effective equation of motion for the thickness \( h \) and the \( z \)-averaged density and polarization. This requires solving the Stokes equation in the presence of stresses generated by the active particles. At the end of the section, we offer a qualitative physical explanation as well.

The dynamics of the height \( h \) is related to the velocity through the kinematic condition \( h = v_z - v_\perp \cdot \nabla h \) (Stone 2005). The incompressibility of the suspension implies volume conservation, so that the height dynamics becomes a local conservation law (Stone 2005)

\[
\partial_t h + \nabla_\perp \cdot (h \nabla_\perp) = 0
\]

in the \( \perp \) plane, where \( \nabla_\perp \) is the in-plane velocity field averaged over the thickness of the film. With our assumptions, the flux of active particles in the laboratory reference frame is \( \mathbf{j} = \rho (\mathbf{v} + v_0 \mathbf{p}) \) so that the concentration \( \rho \) obeys the continuity equation

\[
\partial_t \rho = -\nabla \cdot [\rho (\mathbf{v} + v_0 \mathbf{p})],
\]

which simply generalizes (2a) to the case where the particles are moving not through an inert background but through a suspension with velocity field \( \mathbf{v} \). The velocity field \( \mathbf{v} \) obeys the Stokes equation

\[
\eta \nabla^2 \mathbf{v} = \nabla P - \nabla \cdot (\sigma^a + \sigma^p),
\]

with viscosity \( \eta \), pressure \( P \), and stresses \( \sigma^a = -\zeta \Delta \mu p \mathbf{p} \) and \( \sigma^p \) arising from activity with strength...
\(\zeta \Delta \mu\) and nematic elasticity \cite{deGennes1993}, respectively, as given in Eqs. (45b) and (45a). Note that we have imposed here an explicit linear dependence of the active stress \(\sigma^a\) on the local concentration \(\rho\) of active particles as expected in a bacterial suspension whereas for filament-motor systems the active stress increases faster than linear with the filament density. The polar order parameter \(p\) obeys (adapting Simha and Ramaswamy \cite{Simha2002} to the case where \(p\) is coupled to the free-surface tilt)

\[
\frac{Dp_\perp}{Dt} + \nu_1 \alpha_\beta p_\perp + \lambda_1 (p \cdot \nabla)p_\perp = -\frac{\delta F_p}{\delta p_\perp} + C \frac{\partial a}{\partial h} + f_\perp
\]

where \(\frac{D}{Dt}\) is the time-derivative in a frame comoving and corotating with the fluid, defined in Eq. (36), \(\nu_1\) is the flow alignment parameter introduced in Eq. (41b), and \(\lambda_1\) is the coefficient of the advective nonlinearity in Eq. (2b), and \(\alpha_\beta\) is the strain rate tensor defined in Eq. (45a). This is the liquid limit (\(\tau = 0\)) of Eq. (49), where the polar active term proportional to \(\lambda_1\) has been included. Finally, \(F_p\) is the free-energy functional for \(p\) and \(\rho\) given in Eq. (4), whose content will be discussed further below. Equation (58) generalizes Eq. (5) to the case where a fluid medium is present.

It has been argued in Sankararaman and Ramaswamy \cite{Sankararaman2009} that in a geometry of finite thickness in the \(z\) direction, symmetry could not rule out a term of the form \((C/h) \nabla \cdot h\), in the \(z\)-averaged equation of motion for \(p\). Such a term arises through the interaction of \(p\) with the free surface, and the coefficient \(C\) encodes the preference of \(p\) to point uphill or downhill with respect to a tilt of the free surface. Possible microscopic mechanisms and estimates of magnitudes for such a term are discussed in Sankararaman and Ramaswamy \cite{Sankararaman2009}. A key additional remark needs to be made: such an effect, while allowed by symmetry, must explicitly involve properties of the free surface and the base; it cannot emerge simply from a \(z\)-averaging of the bulk 3d hydrodynamics. We therefore add such a term to (58).

We now proceed to solve the Stokes equation (57) for the velocity in terms of \(\rho\), \(p\), and \(h\), restricting ourselves to the lubrication approximation \cite{Batchelor2000} and Oron et al. \cite{Oron1997} \(\nabla \cdot v \gg |\nabla \cdot v|\).

We study perturbations about a reference configuration of the film with uniform concentration \(\rho_0\) and height \(h_0\), spontaneously ordered into a state with nonzero mean polarization \((\hat{p}) = p_0 \hat{x}\). As we have chosen the active-particle current relative to the medium in (50) to be entirely along \(p\), with no explicit diffusive contribution, and as the particles cannot escape the fluid film, the normal components of \(p\) must vanish at the bounding surfaces at \(z = 0\) and \(z = h\) in agreement with the planar alignment condition that we impose. In a perturbed state with a non-uniform film thickness, this means that \(p_\perp(z = h) \simeq \partial_z h\) to linear order in \(\nabla h\). The \(z\) direction being the smallest dimension in the problem, it is consistent to assume that the variation of \(p\) with respect to \(z\) is at mechanical equilibrium via nematic elasticity. The instantaneous value of \(p_\perp\) is then related to the thickness profile by \(p_\perp = (z/h)\partial_z h\). In the \(z\)-averaged description that we are aiming for, \(p_\perp = (1/2)\partial_z h\) and \(\partial_z p_\perp \simeq h^{-1}\partial_z h\).

Let us represent the perturbed state as \(p_\perp = \hat{x} + \theta \hat{y}\), \(\theta \ll 1\) The divergence of the active stress has components \(\partial_\alpha \sigma^a_{\alpha\beta} = \zeta \Delta \mu(\partial_\beta \theta + \partial_\alpha \rho/h^{-1} \partial_z h), \partial_\alpha \sigma^a_{\alpha\beta} = \zeta \Delta \mu \partial_\beta \theta\) and \(\partial_\alpha \sigma^a_{\alpha\beta} = \zeta \Delta \mu \partial_\beta h/2\) to linear order. We apply the thin film approximations of Oron et al. \cite{Oron1997} \cite{Stone2005} to first calculate the pressure and then obtain the linearized expression of the averaged in-plane velocity

\[
\nabla h(z) = \frac{h z - z^2/2}{\eta} \left( \gamma \nabla^2 h - \frac{1}{2} \zeta \Delta \mu h \partial_\beta \nabla \nabla_a h - f_\perp \right),
\]

where \(f_\perp = \zeta \Delta \mu \left( \partial_\beta h + \partial_\beta \rho/h^{-1} \partial_z h \right) \hat{x} + \partial_\beta \theta \hat{y}\) contains the dominant contributions of activity. Inserting this result in the incompressibility condition (55) and linearizing \(h = h_0 + \delta h\), \(\rho = \rho_0 + \delta \rho\), leads to the dynamical equations

\[
\partial_t \delta h_{\mathbf{q}} = - \frac{\zeta \Delta \mu h_0^2}{3 \eta} \left[ 2 h_0 q_x q_y \theta_\mathbf{q} + h_0 q_x^2 \frac{\delta \rho_0}{\rho_0} \right] + \left( 1 - \frac{1}{2} h_0^2 q_y^2 \right) \delta h_{\mathbf{q}} - \frac{\gamma h_0^3}{3 \mu} q_y^2 \delta h_{\mathbf{q}}
\]

for the in-plane spatial Fourier transforms \(\delta h_{\mathbf{q}}(t), \delta \rho_{\mathbf{q}}(t), \theta_{\mathbf{q}}(t)\) of the perturbations in height, concentration and orientation. The group of terms multiplied by \(\zeta \Delta \mu\) on the right-hand side of (60) displays four consequences of activity, viz., from right to left: (i) pumping by curvature (see Fig. 23); (ii) anisotropic osmotic flow, through the interplay of a uniform orientation field and a concentration inhomogeneity; (iii) splay-induced flow from tilting the free surface (the spontaneous flow instability discussed in the previous section, but adapted to the case of a deformable surface) and (iv) an active anisotropic contribution to the effective tension. Following these active terms is conventional surface tension. Terms (iii) and (iv) are, respectively, destabilizing and stabilizing for contractile stresses, and the other way around for extensile stresses; the reader will see that this is physically reasonable. We now turn to the equation of motion for the polar orientation \(p\). After linearizing (58), and averaging over \(z\), in the hydrodynamic limit, we obtain

\[
\partial_t \theta_{\mathbf{q}} = + \frac{i C}{h_0} q_y \delta h_{\mathbf{q}} - (D + q_z^2 + D - q_z^2 + i \lambda_1 q_x) \theta_{\mathbf{q}} - (i \zeta q_y - \Phi q_x q_y) \delta \rho_{\mathbf{q}},
\]

where \(D = D - (\lambda_1 \pm 1) h_0^2 \zeta \Delta \mu / 4 \eta\), \(D = K / \eta\) being a director diffusivity with \(K\) the Frank constant (assuming that the Frank constants are all equal), and \(\Phi = (\nu_1 - 1) h_0^2 \zeta \Delta \mu / 4 \rho_0 \eta\).
Linearizing the active particle conservation law \( \delta \rho \) about the ordered uniform state gives to leading order in wavenumber:

\[
\partial_t \delta \rho_q = -i \rho_0 v_0 \theta_q \delta \rho_q - iv_0 q_x \delta \rho_q + O(q_x^2 \delta \rho_q, q_x^2 \delta h_q). \tag{62}
\]

The most accessible and interesting instability, arising from the combination of activity and the tilt coupling \( C \), can be understood by ignoring the concentration and motility \( (v_0 = 0) \), but retaining contractile or extensile active stresses \( (\zeta \Delta \mu \neq 0) \). The dispersion relation has the complex form:

\[
\omega = \pm \sqrt{2} \frac{i \text{sgn}(q_x C \zeta \Delta \mu) \left( \frac{h_0^3}{3 \eta} \right)^{1/2} |C \zeta \Delta \mu q_x|^{1/2} |q_y|}{|C \zeta \Delta \mu q_x|^1} \tag{63}
\]

The relative signs of \( \zeta \Delta \mu \) and \( C \) determine the direction \( \pm \hat{x} \) of propagation of the unstable mode. Fig. 23 attempts to explain the mechanism of this intriguing instability. The effects of concentration fluctuations, and the suppression of the instability as the motility \( v_0 \) is increased, are discussed in Sankararaman and Ramaswamy (2009).

So far we have assumed an unbounded film, i.e., no component normal to free surface or base. The geometry of the drop forces a topological defect in the interior that itself induces a deformation of the drop. The simplest case to consider is a defect consisting of two “boojums” with orientation pattern as in Fig. 25 (left), with the assumption that the drops spreads uniaxially in the \( x \) direction. Two possible defect structures are two “boojums” with orientation pattern as in Fig. 25 (left) and an aster as in Fig. 25 (right). The active stress amounts to a peculiar kind of disjoining pressure \( P_{\text{act}} = \zeta \Delta \mu \ln(h/h_0) \), which can be rationalized on dimensional grounds by noting that the activity strength itself has units of stress so that the dependence on thickness has to be logarithmic. The resulting static shape of a drop depends on the sign of the active stress: the drop is flat if the active stress is extensile, and elevated, if it is contractile. For a linear structure like Fig. 25 (left), if we assume spreading only along the long axis at fixed width \( w \) the result, for a fixed volume \( \Omega \) and viscosity \( \eta \), is a drop of linear dimension

\[
R(t) \sim \left( \frac{\zeta \Delta \mu \Omega^2 t}{w^2 \eta} \right)^{1/4}. \tag{64}
\]

A drop of volume \( \Omega \) with an aster defect as in Fig. 25 (right) spreads isotropically with

\[
R(t) \sim \left( \frac{\zeta \Delta \mu \Omega^2 t}{\eta} \right)^{1/6}. \tag{65}
\]

Further details including the behavior of other defect configurations are discussed in Joanny and Ramaswamy (2012).

B. Polar active suspensions with inertia

In section III we summarized the continuum flocking model of Toner and Tu (1995, 1998) for polar self-propelling particles moving on a frictional substrate. Deep in the ordered phase, the theory predicted novel propagating sound-like waves, coupling orientation
and density fluctuations, with direction-dependent wave speeds and giant density fluctuations. The discussion thereafter, when the ambient fluid medium was introduced, focused on destabilizing effects arising from the interplay of activity and the hydrodynamic interaction for bulk suspensions in the Stokesian regime where viscosity dominates. However, we claimed in section III that our hydrodynamic approach applied to flocks from sub-cellular to oceanic scales. Bacterial suspensions, cell aggregates, and the cytoskeleton or its extracts (see section III) are well approximated in the Stokesian limit where inertia is altogether ignored. For collections of large swimmers, such as fish, where inertial effects are important and the role of viscosity can be ignored an alternative emphasis is appropriate. Simha and Ramaswamy (2002a) originally formulated their general theory of ordered states and fluctuations for active particles suspended in a fluid with a view to describing both viscosity- and inertia-dominated flows. Let us briefly review the discussion of Simha and Ramaswamy (2002a) in the case where inertia is taken into account through the acceleration term in the momentum equation. We ignore the advective nonlinearity $\mathbf{v} \cdot \nabla \mathbf{v}$, so the treatment amounts to the unsteady Stokes equation, but this is precisely the level of description in which the propagating modes of translationally ordered crystalline or liquid-crystalline phases are discussed by Martin et al. (1972).

The slow variables in a polar active suspension are the number density, the broken symmetry variable $\mathbf{p}$ for polar order (defined in section I A. ) and the momentum density of the suspension $\mathbf{g}$ coming from momentum conservation. We proceed initially as in section III A.2, through the momentum equation (31) \[ \partial_t g_\alpha = -\partial_\beta \Pi_{\alpha\beta}, \] with the stress tensor $\Pi_{\alpha\beta} = -\sigma_{\alpha\beta} + m p v_{\alpha} v_\beta$, where $\sigma_{\alpha\beta}$ contains the various contributions listed in Eqs. (38), (41a), (41b) and (44), including the crucial active stress. In systems where inertia is important, it is essential to retain the acceleration $\partial_t \mathbf{g}$ even while ignoring the inertial contributions $m p v_{\alpha} v_\beta$ to the stress which are non-linear in $\mathbf{g}$. The equation for the vector order parameter $\mathbf{p}$ is as in section III. The number density is governed by Eq. (56).

The hydrodynamic modes implied by these equations of motion are obtained by linearizing and Fourier transforming in space and time (Simha and Ramaswamy 2002a). Imposing overall incompressibility with the condition $\nabla \cdot \mathbf{g} = 0$, the number of modes is five. We briefly state here the main results of this analysis (Simha and Ramaswamy 2002a). First, when viscosity is ignored and acceleration is included, polar ordered suspensions are not in general linearly unstable, that is, a parameter range of nonzero measure exists for which stable behavior is found. The dynamic response displays a whole new range of propagating waves as a result of the interplay of hydrodynamic flow with fluctuations in orientation and concentration: a pair of bend-twist waves and three waves, generalizations of those in Toner and Tu (1998), coupling splay, concentration and drift each with exceedingly complicated direction-speed wave relations (Simha and Ramaswamy 2002a). The bend/twist waves result from the interplay of $\nabla \times p_\perp$ and $\nabla \times v_\perp$, which provides a qualitative difference with respect to dry flocks. These propagating modes can be observed on length scales where it is reasonable to ignore their damping – due to viscosity for the total momentum and velocity fluctuations, and diffusion for concentration fluctuations. This gives a large range of length scales for large fast swimmers like fish. Possibly experiments like those of Makris et al. (2006), which do speak of fish density waves, could test the existence of these modes in detail. Secondly, within this linearized treatment, quasilinear density correlations of the density show the same features in the ordered phase as we already saw for dry systems in section II.A3.c with the number variance, scaled by the mean $N$, predicted to diverge as $N^{1/2+1/d}$ in $d$ dimensions as in Eq. (20). Presumably nonlinearities, which power-counting readily shows to be relevant below 4 dimensions, but which are even more painful to analyze here than in dry flocks, will change the exponents but not the essential fact of supernormal fluctuations. It is not clear that the power-law static structure factor seen by Makris et al. (2006) in shoals is evidence for these giant fluctuations; a fair test of flocking theories requires a school rather than a shoal.

C. Rheology

The active hydrodynamic framework of section III not only allows us to predict spontaneous-flow instabilities as in sections IV.A.1 and IV.A.2 but also the response of an active fluid to an imposed flow, i.e., the rheology of active soft matter (Gioni et al. 2010; Haines et al. 2009; Hatwalne et al. 2004; Liverpool and Marchetti 2006; Saintillan 2010).

For concreteness, we associate the purely coarse-grained description of section III with a microscopic picture of a suspension containing active particles of linear size $\ell$, at concentration $\rho$, each particle carrying a force dipole of strength $f \ell$, where $f$ is the propulsive thrust, with the activity of an individual particle correlated over a time $\tau_0$, and collective fluctuations in the activity correlated over length scales $\xi$ and timescales $\tau$.

We apply the approach here to the isotropic phase of active particles in a fluid, to extract linear rheological properties (Hatwalne et al. 2004; Liverpool and Marchetti 2006) and the autocorrelation of spontaneous stress fluctuations (Chen et al. 2007; Hatwalne et al. 2004) when noise is included.

We consider an apolar system described by orientation order in terms of the tensor $\mathbf{Q}$, defined in Eq. (21). We obtain predictions for the rheology of active suspensions
through the coupled dynamics of \(Q\) and the hydrodynamic velocity field \(v = \mathbf{g}/\rho_{\text{tot}}\), where \(\mathbf{g}\) and \(\rho_{\text{tot}}\) are the total densities of momentum and mass of the suspension. Neglecting inertial contribution to the stress tensor, conservation of total momentum of particles + fluid is expressed by \(\partial_t \mathbf{g} = \nabla \cdot \sigma^t\), where the stress tensor \(\sigma^t\) is as in section III.B.1. In addition, we must allow for noise sources of thermal and non-thermal origin. The former, though mandated in the equilibrium limit by the fluctuation-dissipation relation connecting them to the solvent viscosity in \((38)\), are quantitatively negligible in comparison to effects arising from activity. Such active fluctuating stresses can further arise in two ways: directly, as additive white-noise contributions to the stress in \((38)-(44)\), which we shall ignore as they add no new physics, or indirectly, via the stochastic dynamics of the orientational field, which is the case of interest.

Consistent with Section III we write the active stress in terms of the alignment tensor in the form

\[
\sigma_{\alpha\beta}^a = -\zeta \Delta \mu Q_{\alpha\beta}.
\]

We note for later reference that we will eventually consider the concentration dependence of active stresses, \(\zeta \propto \rho\), which is physically reasonable and also follows from an explicit realization in terms of dipolar force densities associated with the active particles \(Baskaran and Marswamy 2009; H"{a}twalne et al. 2004; Simha and Ramaswamy 2002a\). We remind the reader that we are dealing with force-free, neutrally buoyant, self-propelling particles. Thus there are no external forces on the system, so that the simplest active particle, on long timescales, is a permanent force dipole \(Brennen and Winet 1977; Pedley and Kessler 1992\). Although we have already discussed the magnitude and sign of \(\zeta \Delta \mu\) in section III it is useful to note here that for a system with concentration \(\rho\) the quantity \(\zeta \Delta \mu/\rho \sim \ell f\) characterizes the strength of the elementary force dipoles associated with, for example, individual swimming organisms. Negative and positive \(\zeta \Delta \mu\) refer respectively to contractile swimmers, or “pullers”, and extensile swimmers, or “pushers”, whose distinct rheological behavior we outline below.

The rheology is to be obtained from the momentum equation together with the equations of motion for the order parameter field and particle concentration. We begin with a description of the linear rheology of active matter in the isotropic and orientationally ordered phases, and follow it up with a brief survey of the nonlinear rheology of active matter.

1. Linear rheology of active isotropic matter

To appreciate what is unique about active matter rheology, it is useful to recall the linear rheology of passive nematogens. The stresses arising from distortions of the orientational order parameter \(Q\) and concentration \(\rho\) are derived from a free-energy functional \(F_Q(Q,\rho)\) (Eq. \((23)\)), giving rise to a passive deviatoric order-parameter stress \(\sigma_{op}\) \((67)\), where \(H \equiv -\delta F_Q/\delta Q + (1/3) Tr \delta F_Q/\delta Q\) is the nematic molecular field. The mean deviatoric passive stress \((67)\) is zero in the isotropic phase at equilibrium (and in the nematic phase as well). In addition, fluctuations of the deviatoric stress are small as one nears the transition to the nematic phase, as can be seen by making small perturbations \(\delta Q\) in the isotropic phase, leading to a change in the free energy \(F_Q \propto (\alpha_Q/2) \int Tr (\delta Q)^2\), which in turn gives rise to stress fluctuations \(\sim \alpha_Q \delta Q\) with a coefficient \(\alpha_Q\) that decreases on approaching the isotropic-nematic (IN) transition to the ordered phase. Thus even though fluctuations of \(Q\) are large as one approaches the IN transition, their contribution to rheology is small, resulting simply in a renormalisation of \(\tau\), the order parameter relaxation time. As shown below, this pretransitional feature is fundamentally different in active isotropic systems. In the following we take a purely coarse-grained approach and follow closely the work of Giomi et al. \((2010)\); Hatwalne et al. \((2004)\); and Liverpool and Marchetti \((2006)\); for a more microscopic treatment see Haines et al. \((2009)\) and Saintillan \((2010)\).

For the active system, the deviatoric reactive stress has to be obtained from the equations of motion for the order parameter and concentration, rather than simply from the free energy functional. The linearized equations for \(Q\) in the isotropic phase, are of the form,

\[
\frac{\partial Q_{\alpha\beta}}{\partial t} = -\frac{1}{\tau} Q_{\alpha\beta} + D \nabla^2 Q_{\alpha\beta} + \nu_1 v_{\alpha\beta} + \ldots + f_{\alpha\beta},
\]

\[\text{(68)}\]
where Eq. (68) can be regarded as the modification of Eq. (22) to include the effect of shear flow to linear order. Here $\tau$ is the orientational relaxation time, which could for example be the run time in a collection of run-and-tumble bacteria, or the rotational diffusion time, perhaps modified by collective and/or active effects in an actomyosin extract, $D$ is a diffusivity ($\sim \ell^2/\tau_0$) related to the ratio of a Frank constant to a viscosity, $\nu_1$ is a “reversible” kinetic coefficient or flow coupling parameter, taken for simplicity to be of the same order in the one entering the equation for the polarization $p$ (Forster 1974), $f_{\alpha\beta}$ is a traceless, symmetric, spatiotemporally white tensor noise representing active fluctuations, and the dots include the coupling of orientation to flow. Note that this form of the linearized equation is valid for the passive system too, with the time scale $\tau$ given by the order parameter relaxation time proportional to $1/\alpha_Q$, which gets larger as one approaches the IN transition.

One can now proceed to calculate the linear viscoelastic properties of the active suspension. In addition to the active deviatoric stress (66), we include the contribution from the viscous dissipative stress $\sigma^{d}_{\alpha\beta}$ given in Eqs. (68), and applying them to spatially uniform ($q=0$) oscillatory shear flow at frequency $\omega$ in the $xy$ plane one obtains, to linear order in the fields,

$$\sigma_{xy}(\omega) = \left[ \eta + \left( \alpha_Q - \zeta \Delta \mu \right) \nu_1 \right] \epsilon_{xy}(\omega).$$

The rheological response is defined by the complex modulus $G(\omega) = \sigma_{xy}(\omega)/\epsilon_{xy}(\omega)$, with $\epsilon_{xy}(\omega) = v_{xy}(\omega)/(-i\omega)$ the strain. The corresponding storage (in-phase) and loss (out-of-phase) moduli $G'(\omega)$ and $G''(\omega)$, defined by $G(\omega) = G'(\omega) + iG''(\omega)$, characterize the elastic and viscous response of the system to an oscillatory shear flow. These moduli can be read out from Eq. (69).

The active isotropic system is rheologically a Maxwell fluid to linear order. This is best highlighted by the behavior of the apparent shear viscosity $\eta_{app} = \lim_{t\to0} G'(\omega)/(t \omega)$, which shows an active excess viscosity $\eta_{act} \propto -\zeta \Delta \mu \rho$, corresponding to either an enhancement or reduction, depending on the sign of $\zeta$. This active thickening (thinning) can be understood as follows (Fig. 20); in an imposed flow, in the absence of activity, discs (rods) tend to align their symmetry axis along the compression (extension) axis of the flow (Forster 1974).

When activity is switched on, the flow induced by the intrinsic force dipoles clearly opposes the imposed flow in Fig. 20 (a) and (b), and enhances it in (c) and (d). Activity thus enhances viscosity in Fig. 20 (a) and (b), since $\zeta \Delta \mu < 0$, and reduces it in (c) and (d) ($\zeta \Delta \mu > 0$). For $\zeta \Delta \mu < 0$ (69) shows that the viscosity grows substantially as the system approaches a transition to orientational order as $\tau$ is increased, and in fact should diverge if $\tau$ could grow without bound. Even more strikingly, a system of pushers, i.e., extensile swimmers, should show a prodigious reduction in viscosity as $\tau$ grows; indeed, nothing rules out a negative viscosity, that is, spontaneous flow in an initially quiescent isotropic system. Experiments by Sokolov and coworkers (Sokolov and Aranson 2009) have indeed shown that the extensile activity of Bacillus subtilis, a “pusher” swimmer, can substantially lower the viscosity of a suspension. By contrast, in a passive, i.e., thermal equilibrium, system approaching a continuous or weak first-order transition to a nematic phase, the excess viscosity $\sim \alpha Q \tau$ is roughly constant since $\tau \propto 1/\alpha_Q$, as required by the constraints of thermal equilibrium.

The active excess viscosity obtained within the linear theory should be compared to the well-known result of Einstein (1906, 1911) that the fractional excess viscosity due to the addition of passive particles to a fluid is proportional to the particle volume fraction $\phi = \pi \rho \ell^3/6$, to lowest order in $\phi$, with a coefficient 5/2 for spheres. For this purpose it is convenient to take the active coupling proportional to the concentration $\rho$ and define an active stress per particle $W$ as

$$\zeta \Delta \mu = f \ell \rho \equiv W \phi,$$

where $W = f/\ell^2$. Then

$$\eta_{act} = -W \tau \phi.$$

Equation (71) can be viewed as an additive correction to the 5/2, proportional to $W \tau$, which of course can be of either sign. Behavior consistent with these predictions is seen in recent experiments measuring the activity-induced thickening in a system of Chlamydomonas algae (pullers, $W < 0$), as shown in Fig. IV.C.1 (Rafaì et al. 2010).
and extreme thinning in a system of *Bacillus subtilis* bacteria (pushers, $W > 0$) \cite{Sokolov2009}. In the case of chlamydomonas, there is some question as to the direct applicability of the mechanism discussed above, as recent experiments have shown that the flow field generated by these microorganisms, although contractile, is more complex than dipolar \cite{Drescher2010, Guasto2010}. In general the linear rheology is controlled by the interplay of the nature of the active stresses, determined by $\zeta$, and the flow alignment coefficient $\nu_1$. A remarkable duality has been identified that shows that tensile ($\zeta > 0$) rod-shaped flow-aligning particles ($|\nu_1| > 1$) are rheologically equivalent (to linear order in the strain rate) to contractile ($\zeta < 0$) discotic flow-tumbling particles ($|\nu_1| > 1$) \cite{Giomi2010}.

Equation (69) also predicts strong viscoelasticity as $\tau$ increases. For passive systems, $\zeta|\Delta\mu| = 0$ and $\alpha_0 \propto \tau^{-1}$, and so $G'(\omega \tau \gg 1)$ decreases as $\nu_1 \eta / \tau$, suggesting as earlier, that there is little viscoelasticity near an equilibrium IN transition. For active contractile ($\zeta|\Delta\mu| < 0$) systems, by contrast, the active contribution is of $O(1)$ and independent of $\tau$ even close to the IN transition. Thus, as $\tau$ grows,

$$G'(\omega \tau \gg 1) \approx -\zeta \Delta\mu$$

(72) independent of $\tau$!

In addition to this enhanced elasticity, the dynamic range over which elastic behavior is seen increases. This is quite a dramatic rheological manifestation of activity, since at equilibrium, one would expect such strong viscoelastic behavior from a fluid or suspension near translational freezing, as at a glass transition, not near orientational ordering. Put more radically, the orientationally ordered phase of contractile active particles is a peculiar yield-stress material, with nonzero shear and normal stresses in the limit of zero shear rate \cite{Giomi2010, Hatwalne2004, Liverpool2006, Marchetti2006, Marenduzzo2007} as discussed in section IV.C.3.

Another observable manifestation of activity is an enhanced noise temperature as inferred for example from tracer diffusion measurements in bacterial suspensions \cite{Wu2000}, and frequency-dependent shear viscosity arising from fluctuations in stress and concentration \cite{Chen2007, Hatwalne2004}. Activity is the transduction of chemical energy, say in the form of ATP hydrolysis equal to about $20k_BT$ per ATP molecule. This suggests that fluctuations from this thermal noise would be significant. Following \cite{Hatwalne2004}, we may estimate the strength of nonequilibrium stress fluctuations that result from fluctuations of the force generation of active particles, through the variance of the active stress at zero wavenumber and frequency.

The divergence of the active stress $\sigma^a = -\zeta|\Delta\mu|Q$ appears as a forcing term in the momentum equation. Assuming the active objects, whether biofilaments or bacteria, are collectively in a spatially isotropic state, this forcing can be viewed as a noise on scales large compared to the correlation length and time $\xi$ and $\tau$ defined at the start of this section. Recall that in fluctuating hydrodynamics \cite{Landau1998}, for a thermal equilibrium fluid with shear viscosity $\eta$ and temperature $T$, the variance of the random stresses at zero frequency is $\eta T$. For an active fluid, then, the apparent temperature as probed by the motion of a tracer particle can be estimated by the zero-frequency, zero-wavenumber variance of the active stress $\eta_{eff} \sim (\zeta|\Delta\mu|)^2 \int d^3 r dt \langle Q(0,0) Q(r,t) \rangle$. The simplest dimensional argument would then give $\eta_{eff} \sim (\zeta|\Delta\mu|)^2 \xi^2 \tau / \eta$. An Ornstein-Zernike form $(k_B T) \exp(-r/\xi)$ for the equal-time correlations of $Q$, which requires the introduction of a microscopic length which we take to be the active-particle size $l$. gives instead $\eta_{eff} \sim (\zeta|\Delta\mu|)^2 \xi^2 l / \eta$. From (70), using rough estimates for the bacterial system of Wu and Libchaber \cite{Wu2000}, $f \sim \nu/l$ with $\eta \approx 10^{-2}$ Poise, $l \sim 1 \mu m$, $\phi \sim 0.1$, $\xi \approx 20 \mu m$ corresponding to a “run” for a time $\tau = 1 s$ and speed $v \approx 20 \mu m/s$ yields $\eta_{eff}$ about 400 times room temperature, consistent with the measurements in \cite{Wu2000}. Note that this enhancement is independent of the sign of $\zeta|\Delta\mu|$, i.e., the diffusivity increases regardless of whether the viscosity decreases or increases, a tell-tale sign of the nonequilibrium nature of the system. A further interesting consequence \cite{Hatwalne2004} of this excess noise is a huge enhancement of the amplitude of the well-known $t^{-d/2}$ long-time tails in the autocorrelation of tagged-particle velocities. We know of no experiment that has probed this last feature.

More extended analyses of fluctuations in active systems, demarcating the dynamical regimes lying within and beyond the conventional fluctuation-dissipation theorem include work by Kikuchi et al. \cite{Kikuchi2009} and Mizuno et al. \cite{Mizuno2007}.

We now turn to nonlinear fluctuation effects \cite{Chen2007, Hatwalne2004}. From (66), the fluctuations in the deviatoric stress gets contributions from fluctuations bilinear in the orientation $Q$ and the concentration $\rho$. The stress autocorrelation is therefore a convolution of $Q$ and $\rho$ correlations. The former is evaluated from (65), while the latter can be calculated from the the linearized equations for the concentration, $\delta \dot{\rho} = -\nabla \cdot J$, where the current $J_\alpha = -D \delta_\alpha \dot{\rho} - W' \rho_0 \delta_\beta Q_{\beta\alpha} + f'_{\alpha}$, where $D$ is the diffusion constant, $\rho_0$ the mean concentration, $f'_{\alpha}$ a random noise, and $W'$ is an activity parameter. The resulting key findings of \cite{Chen2007} and Lau and Lubensky \cite{Lau2009} are an excess fluctuation $\phi \omega^{-3/2}$ in the stress fluctuations, and no excess response, i.e., viscosity, in the range studied, again a sign of nonequilibrium behaviour. Hatwalne et al. \cite{Hatwalne2004} consider stress contributions nonlinear in $Q$ and show they should lead to excess viscosity as well of similar form, but the effect is presumably below detectable levels in the Chen et al.
In extending the study of rheology to active oriented matter, we immediately encounter a problem. As remarked in Section V.A.1, long-range uniaxial orientational order, whether polar or apolar, in active Stokesian suspensions of polar particles is always hydrodynamically unstable to the growth of long wavelength splay or bend fluctuations, depending on the sign of $\zeta \Delta \mu$. This instability has no threshold in a spatially unbounded system (Simha and Ramaswamy, 2002a), and the growth rate is highest at wavenumber $q = 0$. Frank elasticity with stiffness $K$ stabilizes modes with $q$ greater than

$$q_0 \propto \sqrt{|\zeta \Delta \mu|/K},$$

so that there is a band of unstable modes from 0 to $q_0$. Note that $q_0$ is simply an approximate form of the length scale defined by Eq. (54). In any case, in the limit of infinite system size there is no stable reference state, no ideal active nematic or polar liquid crystal whose rheology one can study as a geometry-independent material property. We must therefore ask what suppresses this generic instability (Ramaswamy and Rao, 2007). A mechanism for suppression of the instability is confinement by boundary walls. The existence of a crossover wavenumber $q_0$ implies that the instability exists only if the sample’s narrowest dimension $h > \sqrt{K/|\zeta \Delta \mu|}$; equivalently, for fixed $h$ the activity must cross a threshold $\sim K/h^2$. This is the essential content of the treatment of Voituriez et al. (2005) discussed in section V.A.1. Confinement along $y$, with the director spontaneously aligned along $x$ and free to turn in an unbounded $x$-$z$ plane, shows (Ramaswamy and Rao, 2007) a similar threshold but with a $q^2$ dependence of the growth rate at small in-plane $q$. In either case, it is clear that confinement can produce a stable active liquid crystal whose linear rheology one can study. Alternatively, the instability can be suppressed by imposing an external shear flow or by the presence of partial translational order, either columnar or lamellar. Orientational stabilization can also be achieved in flow aligning systems ($|\nu_1| > 1$) by imposing a uniform shear flow with shear rate $\dot{\gamma}$. This stabilizes those wavevectors whose growth rate is smaller than the shear rate $\dot{\gamma}$. As $\dot{\gamma}$ is increased more and more modes are stabilized, until at a threshold $\dot{\gamma}_c$, the oriented phase is completely stabilized by the shear flow, yielding a stability diagram controlled by two variables, the flow alignment parameter $\nu_1$ and the ratio of the shear to active stress (Giomi et al., 2010; Muhuri et al., 2007). Translational order, both partial as in smectic or columnar liquid crystal, or full as in three-dimensional crystalline systems can also yield a stable active system, whose properties have been the subject of recent studies (Adhikapak et al., 2012).

Stabilizing the orientational phase of active matter now sets the stage for a study of its unusual rheology (Giomi et al., 2010; Hatwalne et al., 2004; Liverpool and Marchetti, 2006). We have already seen that on approaching the orientationally ordered state from the isotropic fluid, a suspension of active contractile elements ($W < 0$) exhibits solid-like behaviour without translational arrest. In the orientationally ordered phase, the orientational order parameter $\langle Q \rangle \neq 0$, which by (66) immediately leads to a nonzero steady-state average of the deviatoric stress, in the absence of any external deformation. This prestress is a truly nonequilibrium effect, and has no analogue in a passive equilibrium nematic fluid which has a purely isotropic mean stress, i.e., a pressure, despite its orientational order. This prestress implies that in a flow experiment, the shear stress will not vanish at zero deformation rate. The same features of being first order in shear rate and having a nonzero value at zero shear rate are exhibited by the normal stresses $\sigma_{yy} - \sigma_{xx}$. We emphasize that this strange kind of yield stress is a manifestation of the rheology of an active oriented fluid without any form of translational arrest.

We end this section on the rheological properties of active oriented matter by drawing the attention of readers to an interesting analogy between active stress of contractile filaments with macroscopic orientational order and fragile jammed granular matter, as discussed by Ramaswamy and Rao (2007).

### 3. Nonlinear rheology of active nematics

We now turn to the rheological properties of orientationally ordered active fluids beyond the linear regime. As detailed in the previous section, the generic instability of orientationally ordered active suspensions (Simha and Ramaswamy, 2002a) can be suppressed by confinement or by imposing an external shear (Marenduzzo et al., 2007; Muhuri et al., 2007). It is therefore meaningful to explore the dynamics and rheology of these phases in confined geometries. Extensive numerical studies of active nematic and polar films (Cates et al., 2008; Fielding et al., 2011; Giomi et al., 2010; Marenduzzo et al., 2007) under shear reveal a rich variety of phenomena influenced by boundary conditions and geometry. This complex behavior results again from the interplay between local stresses generated by activity (quantified by the parameter $\zeta$), the flow-aligning property of these particles (characterized by the parameter $\nu_1$) and the typical self-propulsion velocity $v_0$ in polar active fluids. A complete understanding of their response to shear necessitates exploring the space spanned by these parameters under various boundary conditions.

We present only a summary of the main results obtained in the literature. While detailed theoretical and numerical studies of linear active rheology including the
effect of polarity can be found in [Giomi et al., 2010], the nonlinear rheology has so far been studied mainly for apolar systems. For contractile active fluids in an orientationally ordered state, numerical studies of the hydrodynamic equations [Cates et al., 2008] when only one-dimensional variation is allowed show the onset of solid-like behavior of [Hatwalne et al., 2004] and the existence of a yield shear stress as in [Liverpool and Marchetti, 2006] [Ramaswamy and Rao, 2007]. Studies of extensile fluids, allowing variation in one (Cates et al., 2008) and two (Fielding et al., 2011) spatial directions display the onset of spontaneous flowing states, with complex flow states including bands in 1d and rolls and turbulence in 2d. Related experimental findings include large scale chaotic flows in bacterial systems [Aranson et al., 2007] [Dombrowski et al., 2004], as remarked earlier. An important general feature [Cates et al., 2008; Fielding et al., 2011] is that dimensionality matters: imposed restrictions to 1d spatial variation lead to significantly different rheology from that seen when 2d variation is allowed, for example. Active stresses generally appear to stabilize shear bands, but have the opposite effect close to the isotropic-nematic transition. In systems with free boundary conditions, the approach to the isotropic-nematic contractile transition shows [Cates et al., 2008] an active enhancement of viscosity. As claimed in [Hatwalne et al., 2004], orientational ordering in active systems indeed resembles translational arrest in equilibrium systems.

The relation between the rheology of active fluids in external shear and the onset of spontaneous flow in absence of shear is discussed in [Giomi et al., 2010]. This work has also analyzed in detail the nonlinear rheology of active fluids, revealing strongly non-monotonic stress vs strain-rate curves beyond a threshold value of activity, as suggested in [Hatwalne et al., 2004], with macroscopic yield-stress behavior, and hysteresis. Finally, at even higher activity, the theoretical stress-strain curve has a discontinuous jump at zero strain rate, corresponding to a finite “spontaneous stress” in the absence of applied shear.

Given the complexity and richness of the nonlinear rheology of active fluids, we refer the reader to the literature for further details.

D. Applying the hydrodynamic theory to phenomena in living cells

To demonstrate that the hydrodynamic theory of active gels described in the previous sections indeed provides generic tools for addressing questions relevant to living cells, we briefly summarize here a few examples of concrete successes of the theory. A more complete review can be found in [Grill, 2011] and [Joanny and Prost, 2010].

The first example is directly relevant to cell motility, in particular to the migration of fish keratocytes, eukaryotic cells extracted from fish scales that are among the fastest moving cells, migrating on a substrate at a steady speed of about 10 $\mu$m/min. This cells have a characteristic fan shape, with a large flat region extending in front of the nuclei, towards the direction of forward motion, known as the lamellipodium. This region is filled with a cross-linked actin gel, where myosin motor complexes use the energy from ATP hydrolysis to grab on neighboring actin filaments and exert stress. Actin polymerization takes place at the leading edge of the lamellipodium, while the filaments disassemble in the rear region, in a process that plays a crucial role in driving the motility. Using active gel theory to model the lamellipodium, Kruse and collaborators [Kruse et al., 2006b] were able to evaluate quantitatively the profile of the retrograde actin flow that accompanies the forward motion of the lamellipodium. Such a retrograde flow has been seen in experiments, as shown in Fig. 28 [Vallotton et al., 2005].

A second example is that of shape oscillations, observed ubiquitously in many cells. An example is shown in Fig. 29. This phenomenon has been described successfully by the active gel theory, augmented by assuming a coupling to calcium channels in the cell membrane that in turn are gated by the deformations in the actin cortical layer. Calcium concentration couples to local myosin activity that in turn controls the stretching and compression of the actin layer, in a feedback loop that results in sustained oscillations [Salbreux et al., 2007].

The active gel theory has also been used recently to model cortical flow in the C. elegans zygote [Mayer et al., 2010], as shown in Fig. 30. The theory supported experiments in successfully identifying two prerequisites for large-scale cortical flow necessary to initiate the anteroposterior cell polarization which directs the asymmetry of the first mitotic division: a gradient in actomyosin contractility to drive flow, and a sufficiently large viscosity of the cortex to allow flow to be long-ranged.

Another recent success of active hydrodynamics has
FIG. 29 Shape oscillations of non-adhering fibroblasts. The second frame shows the periodic oscillation of the projected area of the cell and the associated Fourier spectrum. The period of the oscillation of these cells is very well defined and of the order of 30 s. The oscillation period is found to decrease when myosin activity increases. The latter can in turn be modulated by the addition of various drugs. Adapted with permission from Salbreux et al. (2007).

FIG. 30 (color online) This figure displays the imaging of tension in the cortex of a C. elegans zygote obtained before and after cortical laser ablation (COLA) performed on the actomyosin meshwork. The left image shows a schematic of COLA performed with a pulsed ultraviolet laser along a 6 µm line (light blue in both images) along the anterior-posterior (AP) axis, in the posterior of the cell. The center frames show the pre- (top) and post-cut image (bottom) of posterior COLA. The image to the right shows the tension measurement in the zygote’s actomyosin cortex upon laser ablation along the blue line. The black arrows are the displacements between pre-cut (purple) and post-cut images (green). The average speed of this initial recoil measured in a direction orthogonal to the cut line is proportional to the normal component of the 2D tension tensor. The white bar is 4 µm. Adapted with permission from Mayer et al. (2010).

FIG. 31 (color online) The top images (A) show a circular actin wave in the lamellipodium in a Drosophila cell fixed to a substrate and treated to enhance polarization of actin filaments. The wave travels along the cell’s periphery, with the arrow marking the region of maximum actin density at various times. (B) Phase contrast microscopy picture of a control Drosophila cell fixed to a substrate with a typical circular shape. (C) In the theoretical model, the cell perimeter is represented by a circle of radius R. (D) The calculated concentration of active filaments as a function of the polar angle φ and time. Adapted with permission from Asano et al. (2009).

come from its application to the organization and dynamics of molecules on the surface of living metazoan cells (Gowrishankar and Rao, 2012). The lateral compositional heterogeneity of the plasma membrane at sub-micron scales, termed “lipid rafts”, has been the subject of intense research (Lingwood and Simons, 2010). Most attempts to understand this heterogeneity are based on equilibrium thermodynamics. Using a variety of fluorescence microscopy techniques, and confirmed by other methods, it has been shown that the dynamics, spatial distribution and statistics of clustering of a key ‘raft’ component, viz., GPI-anchored proteins, is regulated by the active dynamics of cortical actin filaments (Goswami et al., 2008). Following this, Gowrishankar and collaborators (Gowrishankar and Rao, 2012) have developed a model for an active composite cell membrane based on active hydrodynamics, which shows how the dynamics of transient aster-like regions formed by active polar filaments (actin) can drive passive advective scalars (molecules such as GPI-anchored proteins) to form dynamic clusters. In addition to successfully explaining the many striking features of the dynamics and statistics of clustering of GPI-anchored proteins on the cell surface, this model makes several predictions, including the existence of giant number fluctuations which have been verified using fluorescence microscopy (Gowrishankar and Rao, 2012). These studies suggest that rafts are actively constructed and that the active mechanics of the cortical cytoskeleton regulates local composition at the cell surface via active currents and stresses.

Finally, Fig. 31 shows polarized actin waves propagating around the periphery of a Drosophila cell that has been fixed to a substrate, preventing it from moving, under condition of enhanced actin polymerization (Asano et al. 2009). In this case the hydrodynamic theory of a polar active gel successfully reproduces the existence of a critical value of polarity above which the polarization waves will occur, as observed in experiments.
V. MICROSCOPIC DESCRIPTIONS OF ACTIVE MATTER

A. Review of microscopic models

While the macroscopic equations of motion of active matter can be obtained from general considerations of symmetry, determination of the magnitude and often even the sign of the coefficients requires additional physical assumptions. Unlike for systems near equilibrium, the assumptions are not easily identified. Furthermore the relaxation of the constraints required by equilibrium allows the possibility of a much larger number of terms. Physical insight can be provided by using the tools and methods of nonequilibrium statistical mechanics (Zwanzig, 2001) to derive the continuum equations via systematic coarse-graining of simplified microscopic models of the active processes driving the system (Aran- son and Tsimring, 2005; Baskaran and Marchetti, 2008a; Bertin et al., 2006, 2009; Kraikivski et al., 2006; Kruse et al., 2001; Kruse and Jülicher, 2000; Liverpool, 2003; Liverpool et al., 2001). One approach is to start from stochastic equations for the microscopic dynamics and then systematically project the microscopic degrees of freedom on to macroscopic variables, such as the density \( \rho(\mathbf{r}, t) \) and polarization \( \mathbf{p}(\mathbf{r}, t) \), defined in Eq.(1a,1b). This procedure yields hydrodynamic equations for the macroscopic variables on length scales long compared to the size \( \ell \) of the individual active elements. For simplicity, we restrict ourselves here to overdamped systems, where the medium through which the active particles may move (fluid or substrate) is inert and only provides friction. In this case the momentum of the active particles is not conserved and the microscopic degrees of freedom are the positions \( \nu_n(t) \) and orientations \( \nu_\alpha(t) \) of the active elements, plus (possibly) other microscopic degrees of freedom describing internal active processes. Of course medium-mediated hydrodynamic interactions can play a crucial role in controlling the dynamics of collections of swimmers. To incorporate such effects one needs to consider a two-component system and explicitly describe the exchange of momentum between particles and solvent. Both the translational and rotational velocities of each particle must be incorporated in the microscopic model, as well as the solvent degrees of freedom. This more general case is outlined briefly in section V.B.4.

In general approximations are required both to identify a tractable microscopic model and to carry out the coarse-graining procedure to derive equations for the macroscopic variables. The form of the resulting equations is general, as it is dictated by symmetry, and the microscopic description allows a calculation of the phenomenological parameters and transport coefficients involved in the hydrodynamic equations. This is important for example for biological systems because it allows to predict the variation of the transport coefficients with the biological parameters that can be changed in the experiments.

The purpose of this section is to review a number of such derivations and summarize their similarities and differences. In equilibrium statistical mechanics there is a long tradition of simplified microscopic models which have eventually led to a number of paradigmatic minimal models (Ising, XY, Heisenberg) that capture the essentials of the behavior of variety of equilibrium systems. Similarly here we describe some minimal microscopic descriptions of active matter that have provided insight into the complex physics of these systems. An interesting aspect of these microscopic realizations is that they allow one to identify the common behavior of different experimental systems. Two examples which we will focus on are (1) mixtures of cross-linking motor constructs and protein filaments (Nédélec, 1998; Nédélec et al., 1997; Surrey et al., 2001) and (2) collections of self-propelled particles. Experimental realizations of the latter may be actin filaments in motility assays (Butt et al., 2010; Kron and Spudich, 1986; Schaller et al., 2010) or suspensions of swimming micro-organisms (Dombrowski et al., 2004; Zhang et al., 2010).

1. Self-propelled particles

A microscopic realization of active systems is provided by interacting self-propelled particles (SPP). While these can be thought of as simplified agent based models of flocks of birds or shoals of fish (Vicsek et al., 1995), they can also act as realistic models for less complex systems, such as polar protein filaments (e.g. F-actin) in gliding motility assays on surfaces decorated with molecular motors (e.g. myosin) (Kron and Spudich, 1986; Schaller et al., 2010), suspensions of swimming micro-organisms (Dombrowski et al., 2004; Zhang et al., 2010), or even layers of vibrated granular rods (Narayan et al., 2007). It should be stressed, however, that there have been suggestions that hydrodynamic interactions may be important in motility assays at high filament density (Schaller et al., 2011b).

Each self propelled particle has a position and an orientation. It also has an individual self-propulsion velocity of magnitude \( v_0 \) and direction specified by the particle’s orientation. SPP interact with neighboring particles either via a local rule (Vicsek et al., 1995) or via physical steric or other interactions (Baskaran and Marchetti, 2008a,b, 2009; Leoni and Liverpool, 2010). Mean field models for the stochastic dynamics of the particles can be expressed in terms of the one particle density, \( c(\mathbf{r}, \mathbf{v}, t) \). This measures the probability of finding a self-propelled particle with position \( \mathbf{r} \) and orientation \( \mathbf{v} \) at time \( t \). The equation of motion for \( c(\mathbf{r}, \mathbf{v}, t) \) takes into account the interplay of fluctuations (diffusion), interactions and self-propulsion. These mean-field models are valid in the regime of weak interactions, low density and...
weak density correlations. The kinetic equation for the one-particle density can then be solved directly either analytically or numerically for specific geometries and initial condition (Santillan 2012). Alternatively, to describe macroscopic behavior, the kinetic theory can also be further coarse-grained by projecting on to macroscopic fields such as $\rho(\mathbf{r},t)$ and $\mathbf{p}(\mathbf{r},t)$ to obtain the equivalent of Eq. 5, where the parameters $\alpha, \beta, K, v_1, \lambda_{1,2,3}$ are expressed in terms of the microscopic parameters of the system (Baskaran and Marchetti 2008a, 2010, Bertin et al. 2009, Ihle 2011). A concrete example of this procedure is given in section V.B.3 below.

2. Motors and filaments

Another microscopic realization of active matter is provided by suspensions of polar protein filaments cross-linked by active cross-links consisting of clusters of molecular motors (Backouche et al. 2006, Mizuno et al. 2007, Nedelec 1998, Nedelec et al. 1997, Surrey et al. 2001). The motivation for this in vitro work is to provide an understanding of the mechanics of the eukaryotic cell cytoskeleton from the bottom up. Molecular motors are proteins that are able to convert stored chemical energy into mechanical work by hydrolyzing ATP molecules. The mechanical work is done by the motors moving in a uni-directional manner along the polar filaments. Particular motor proteins are associated with specific polar filaments, e.g. kinesins ‘walk’ on microtubules while myosins ‘walk’ on filamentous actin. Since the filaments are ‘polar’, they can be characterized by a position and an orientation. Some authors (Ahmadi et al. 2006, Kruse and Jülicher 2000, 2003, Liverpool 2003, Liverpool and Marchetti 2005) have modeled the motor clusters as active cross linkers (see schematic in Fig. 32) capable of walking along the filaments and exchange forces and torques among filament pairs, hence yielding additional (active) contributions to the translational and rotational velocities of filaments. Another model has been proposed by Aranson and coworkers (Aranson and Tsimring 2005, 2006) who have described the filament dynamics via a stochastic master equations for polar rigid rods interacting via instantaneous inelastic “collisions”. Both models express the stochastic dynamics of the active system in terms of the one particle density of filaments: $c(\mathbf{r}, \mathbf{v}, t)$. The kinetic equation for $c(\mathbf{r}, \mathbf{v}, t)$ takes account of the interplay of diffusion and active contributions induced by the cross linking motor clusters or the inelastic collisions. The kinetic equations can again be further coarse-grained by projecting on the continuum fields, such as $\rho(\mathbf{r},t)$ and $\mathbf{p}(\mathbf{r},t)$ to obtain the equivalent of Eq. 5, where the parameters $\alpha, \beta, K, v_1, \lambda_{1,2,3}$ can again be related to microscopic parameters characterizing the filaments and motor clusters. Although the parameter values depend on the microscopic model, the continuum equations obtained by these two approaches have the same structure. The work by (Aranson and Tsimring 2005, 2006) incorporates, however, terms of higher order in the gradients of the continuum fields neglected in (Ahmadi et al. 2006, Kruse and Jülicher 2000, 2003, Liverpool 2003). These models give rise to contracted states and propagating density/polarization waves in both one (Kruse et al. 2001, Kruse and Jülicher 2000) and higher dimensions (Liverpool 2003, Liverpool and Marchetti 2005), as well as aster and spiral patterns (Aranson and Tsimring 2005, 2006). Finally, a number of other mean-field implementations of the dynamics of motor filament suspensions, some including explicitly motor dynamics or additional passive cross linkers, have been used by other authors to understand pattern formation in these systems (Lee and Kardar 2001, Sankararaman et al. 2004, Ziebert et al. 2007, Ziebert and Zimmermann 2004, 2005).

In the next sections we briefly outline one procedure for going from the fluctuating microscopic dynamics to the macroscopic equations of motion. We restrict our discussion to dry systems. For wet systems we refer the reader to published work (Baskaran and Marchetti 2009, Leoni and Liverpool 2010, Liverpool and Marchetti 2006, Marchetti and Liverpool 2007).

B. From stochastic dynamics to macroscopic equations

We consider a collection of $N$ identical (a simplification) anisotropic particles, each described by a position $\mathbf{r}_n(t)$ and orientation $\mathbf{v}_n(t)$ for particle $n$. The microscopic stochastic equations of motion for the positions and orientations are given by

$$\partial_t \mathbf{r}_n = \mathbf{v}_n(\mathbf{r}_n, \mathbf{v}_n(t)) + \xi_n(t), \quad (74a)$$
$$\partial_t \mathbf{v}_n = \omega_n(\mathbf{r}_n, \mathbf{v}_n(t)) \times \mathbf{v}_n + \Theta_n(t). \quad (74b)$$

The first terms on the rhs are the deterministic contributions to the motion arising from both passive interactions (e.g., steric repulsion, attractive interactions, etc.) and active velocities. Their specific form depends on the particular model system considered. The second terms on the rhs of Eqs. (74) are stochastic forces arising from a variety of noise sources, including but not limited to thermal noise. They are assumed to be Gaussian and white, with zero mean and correlations

$$\langle \xi_{n\alpha}(t) \xi_{m\beta}(t') \rangle = 2\Delta_{\alpha\beta}(\mathbf{v}_n) \delta_n m \delta(t - t'), \quad (75a)$$
$$\langle \Theta_{n\alpha}(t) \Theta_{m\beta}(t') \rangle = 2\Delta_R \delta_n m \delta_{\alpha\beta} \delta(t - t'). \quad (75b)$$

The translational noise correlation tensor is of the form $\Delta(\mathbf{v}) = \Delta \mathbf{v} \mathbf{v} + \Delta_\perp (\mathbf{v} - \mathbf{v})$. In a thermal system $\Delta = D_\parallel$ and $\Delta_\perp = D_\perp$, with $D_\parallel$ and $D_\perp$ describing Brownian diffusion along the long direction of the particle and normal to it, respectively. Also in this case $\Delta_R = D_R$, with $D_R$ is the rotational diffusion rate. In
an active system the noise strengths are in general an independent quantities.

For particles with fixed self-propulsion speed $v_0$ along their long axis the deterministic part of the velocities in Eqs. (74) has the form

$$v_n(r_n, \dot{r}_n) = v_0 \dot{r}_n + \left[\zeta(\dot{r}_n)\right]^{-1} \sum_m f(r_n, r_m; \dot{r}_n, \dot{r}_m),$$

(76a)

$$\omega_n(r_n, \dot{r}_n) = \zeta^R \sum_m \tau(r_n, r_m; \dot{r}_n, \dot{r}_m),$$

(76b)

with $\zeta(\dot{r}) = \zeta_\parallel \dot{r} + \zeta_\perp (\delta - \dot{r})$ a friction tensor and $\zeta^R$ a rotational friction coefficient. Again, in a Brownian system in thermal equilibrium at temperature $T$ friction and diffusion (which in this case is also the strength of the noise) are related by the Stokes-Einstein relation, $D_{\alpha\beta} = k_B T \left[\zeta^{-1}\right]_{\alpha\beta}$ and $D_R = k_B T / \zeta_R$. In active systems these relations do not in general hold and noise and friction should be treated as independent.

The pairwise forces and torques in Eqs. (76) can be expressed in terms of the total passive and active interactions in the system. The case of particles propelled by internal torques has also been considered in the literature, but will not be discussed here (Fily et al. 2012).

1. Smoluchowski dynamics

For simplicity we again restrict ourselves to the case of particles with overdamped dynamics. Starting from the Langevin equations (74) for the individual filaments, standard techniques can be used to derive an equation for the one-particle probability distribution function $f(r_n, \dot{r}_n, t)$ of a Brownian particle in thermal equilibrium. The traditional method is to write the 2-particle distribution function as a product of two 1-particle densities (Aranson and Tsimring 2005; Bertin et al. 2009; Kruse and Jülicher 2000; Liverpool 2003), as in the familiar molecular chaos approximation used to obtain the Boltzmann equation.

This procedure gives a nonlinear equation for the 1-particle density, $c(r, \dot{r}, t) = \sum_n (\delta(r - r_n)\delta(\dot{r} - \dot{r}_n))$, where the bracket denotes a trace over all other degrees of freedom and an average over the noise, in the form of a conservation law, given by

$$\partial_t c + \nabla \cdot J_c + R \cdot J_c = 0,$$

(77)

where $R = \nabla \times \partial_\nu$ is the rotation operator. The translational probability current, $J_c(r, \dot{r}, t)$, and the rotational probability current, $\mathcal{J}_c(r, \dot{r}, t)$, are given by (Doi and Edwards 1986)

$$J_c = v - \Delta \cdot \nabla c, \quad \mathcal{J}_c = \omega - \Delta R \mathcal{R} c,$$

where $v$ and $\omega$ are given in Eqs. (76) and $\Delta$ and $\Delta_R$ are respectively the translational and rotational noise strengths introduced in Eqs. (75).

It should be stressed that this closure scheme may yield different physical approximations for different classes of microscopic dynamics (Bialké et al. 2012; Fily and Marchetti 2012). An illustrative example can be found in Baskaran and Marchetti (2010) which systematically derives a kinetic equation for self-propelled hard rods starting with a microscopic Langevin dynamics that includes inertia by first obtaining a Fokker-Planck equation for the joint probability distribution of both position/orientation and velocities, and finally derive the Smoluchowski limit where friction is large relative to inertia at the level of the kinetic equation by making a non-thermal assumption on the local distribution of velocities. This procedure yields a different Smoluchowski equation from that obtained by simply taking the overdamped limit at the level of the Langevin equation. While the structure of the hydrodynamic equations obtained by coarse-graining the one-particle kinetic equation is the same in both cases (as it is dictated by symmetry considerations), the values of the parameters in the continuum equations and particularly their dependence on $v_0$ and noise strength depend on whether the overdamped limit is taken right at the outset, i.e., at the level of the microscopic dynamics, or at the level of the kinetic equation. Much work remains to be done to understand this subtle point and therefore we will not discuss it further in this review. A further interesting open question is how to systematically obtain a stochastic equation for the 1-particle density which prop-

FIG. 32 (color online) The figure shows a schematic of a pair of filaments of length $\ell$ with mid-point positions and orientations $r_1, \dot{r}_1$ and $r_2, \dot{r}_2$ driven by an active cross-link.
positions and orientations $r_1, \ell_1$ and $r_2, \ell_2$ driven by motors tethered to a plane.

erly includes the noisy dynamics of the density fluctuations for active systems (Dean, 1996).

We leave some of these very interesting open questions for the reader and discuss below how to use the Smoluchowski dynamics as described by Eqs. (77) in the derivation of hydrodynamic equations.

2. From Smoluchowski to hydrodynamics

One approach, explored extensively by Saintillan, Shelley and collaborators (Saintillan and Shelley, 2007, 2008a,b), is to solve directly the Smoluchowski equations, either analytically or numerically. This work has been used to investigate the stability of both aligned and isotropic suspensions of active particles with hydrodynamic interactions (see also below) and has revealed a rich dynamics with strong density fluctuations. This approach will not be discussed further here. A recent review can be found in Saintillan (2012).

Here we focus instead on obtaining the description of the dynamics of the system in terms of a few macroscopic fields introduced phenomenologically in the first part of this review. A crucial assumption in deriving this continuum or hydrodynamic theory is the choice of the continuum fields as those whose fluctuations are long lived on large length scales. They include fields associated with conserved quantities and possible broken symmetries of the system. In a collection of active particles with no momentum conservation, the only conserved quantity is the number of particles and hence the density, defined in Eq. (1a) is a slow variable. In addition, to allow for the possibility of broken orientational order, with either polar or nematic symmetry, we consider the dynamics of a polarization field (Eq. (1b)) and an alignment tensor (Eq. (21)). The fields are defined as moments of the one particle distribution function as.

$$
\rho(r, t) = \int d\nu \ c(r, \hat{\nu}, t), \\
\rho(r, t)p(r, t) = \int d\nu \ \nu \cdot c(r, \hat{\nu}, t), \\
\rho(r, t)Q(r, t) = \int d\nu \ \hat{Q}(\hat{\nu}) \ c(r, \hat{\nu}, t).
$$

with $\hat{Q}(\hat{\nu}) = \nu \hat{\nu} - \frac{1}{2}1$ and $d$ the system’s dimensionality. In general one could write an exact expansion of $c(r, \hat{\nu}, t)$ in terms of all its moments and transform the Smoluchowski equation into an infinite hierarchy of equations for the moments. The hydrodynamic description is obtained by assuming that higher order moments relax quickly on the time scales of interest and by truncating this expansion to include only conserved quantities and order parameter fields. Equivalently, considering for simplicity the case of $d = 2$, one can simply write

$$
c(r, \hat{\nu}, t) = \frac{\rho(r, t)}{2\pi} \left\{ 1 + 2p(r, t) \cdot \hat{\nu} + 4Q(r, t) : \hat{Q}(\hat{\nu}) \right\},
$$

insert this ansatz into the Smoluchowski equation, Eq. (77), and obtain the hydrodynamic equations for filament concentration, polarization and alignment tensor. For the details of the calculation, which also involves using a small gradient expansion for the filament probability distribution and evaluating angular averages, we refer the reader to the literature (Ahmadi et al., 2006; Baskaran and Marchetti, 2008a; Bertin et al., 2009; Ihle, 2011; Liverpool, 2003). The result is a set of coupled equations for the hydrodynamic variables, $\rho(r, t), p(r, t), Q(r, t)$ that has the form given in section II with parameter values that are calculated explicitly in terms of microscopic properties of the system.

In particular, one finds that the continuum equations governing the dynamics of motor-filament systems and collections of self-propelled particles have the same structure, but important qualitative differences arise in the hydrodynamic parameters. In models of SPP the activating internal processes drive each individual unit (as for instance in bacterial suspensions or actin filaments in motility assays, where the filaments are driven by the action of a carpet of myosins tethered to a plane) and active contributions to the dynamics arise even at the single-particle level. In cell extracts of cytoskeletal filaments and associated motor proteins activity arises from interactions among the filaments mediated by motor clusters that act as active crosslinkers, exchanging forces among the filaments. As a result, the various active parameters in the hydrodynamic equations are proportional to the square of the density of filaments, resulting in different behavior at large scales. For this reason motor-filament suspensions have also been referred to as systems of “mutually propelled particles” (MPP) (Giomi et al., 2012), to distinguish them from SPPs.
3. An example: derivation of continuum equations for aligning Vicsek-type particles

To illustrate the method, we show in this section the derivation of the continuum equations for a simple model of self-propelled point particles on a substrate in two dimensions with a polar angular interaction that tends to align particles as in the Vicsek model. We consider \( N \) particles with polarity defined by an axis \( \nu_n = (\cos \theta_n, \sin \theta_n) \). The dynamics is governed by Eqs. (74) that now take the explicit form

\[
\partial_t \mathbf{r}_n = v_0 \nu_n - \zeta^{-1} \sum_m \frac{\partial V}{\partial r_n} + \xi_n(t),
\]

\[
\partial_t \theta_n = \zeta^{-1} \sum_m \frac{\partial V}{\partial \theta_n} + \Theta_n(t),
\]

where \( \xi_n(t) \) and \( \Theta_n(t) \) are Gaussian white noise processes with zero mean.

To obtain hydrodynamic equations, we now proceed as outlined in section V.B.2 and transform the kinetic equation into a hierarchy of equations for the angular moments of the one-particle probability density, \( c \). In two dimensions the moments are most simply written by introducing an angular Fourier transform \( f_k(r,t) = \int_0^{2\pi} c(r,\theta,t)e^{ik\theta} d\theta \). By comparing with Eqs. (78) it is easy to see that \( f_0 = \rho \), \( f_1 = w_x + iw_y \), with \( \rho = \mathbf{p} \cdot \mathbf{r} \) the polarization density, and the real and imaginary parts of \( f_2 \) are proportional to the two independent components of the alignment tensor, \( \mathbf{Q} \). Using \( 2\pi c(r,\theta,t) = \sum_k f_k e^{-ik\theta} \) and retaining for simplicity only terms up to linear order in the gradients, we obtain a hierarchy of equations

\[
\partial_t \mathbf{r} + v_0 \mathbf{r} - \zeta^{-1} \sum_m \frac{\partial V}{\partial \mathbf{r}} + \mathbf{r} \nabla \mathbf{V} = 0,
\]

\[
\partial_t \mathbf{p} + v_0 \mathbf{p} \cdot \nabla \mathbf{p} = \frac{1}{2} \gamma (\mathbf{p} - \mathbf{Q} \mathbf{r}) \nabla \mathbf{p} - \frac{\gamma^2}{8\Delta_R} \mathbf{w}^2 \mathbf{w} - \frac{v_0}{2} \mathbf{p} \cdot \nabla \mathbf{p} + \frac{5v_0 \gamma}{32\Delta_R} \mathbf{w}^2 \nabla \mathbf{w} - \frac{5v_0 \gamma}{16\Delta_R} \mathbf{w} \cdot \nabla \mathbf{w} + \mathcal{O}(\nabla^2)
\]

where \( \mathbf{w} = \mathbf{r} \cdot \mathbf{p} \) rather than an equation for the polarization density \( \mathbf{w} = \mathbf{r} \cdot \mathbf{p} \) as given in Eq. (5). Of course it is straightforward to use the density equation to transform the equation for \( \mathbf{w} \) into an equation for \( \mathbf{p} \).
with the result,
\[
\partial_t \rho + (p \cdot \nabla) \rho = - \left[ a(\rho) + \beta |p|^2 \right] p - v_1 \cdot \nabla \rho
\]
\[
+ \frac{\lambda_3}{2} \nabla |p|^2 + \lambda_2 p (\nabla \cdot p) + O(\nabla^2), \tag{84}
\]
with
\[
a(\rho) = \Delta R - \frac{1}{2} \gamma \rho, \tag{85a}
\]
\[
\beta = \frac{\gamma^2 R^2}{8 \Delta R}, \tag{85b}
\]
\[
\lambda_1 = \frac{3 v_0 \gamma \rho}{16 \Delta R}, \tag{85c}
\]
\[
\lambda_2 = -\lambda_3 = \frac{5 v_0 \gamma \rho}{16 \Delta R}, \tag{85d}
\]
\[
v_1 = \frac{v_0}{2 \rho} \left( 1 - \frac{5 \gamma \rho}{8 \Delta R} \right) \delta - \frac{v_0}{\rho} \left( 1 - \frac{\gamma \rho}{2 \Delta R} \right) pp. \tag{85e}
\]

Eq. (84) has the same structure as Eq. (5), although noise has been neglected here. The various coefficients are expressed in terms of microscopic parameters and are in general found to depend on density and order parameter. In particular, the coefficient \( v_1 \) of the \( \nabla \rho \) term is now a tensor, describing anisotropic pressure gradients that can play a role in the ordered state. These effects were neglected for simplicity in the phenomenological model. We also stress that there is an important difference between the parameter values obtained in the present model and those obtained by Baskaran and Marchetti (2008a) and Bertin et al. (2009) as in both the latter models the effective interaction strength (here \( \gamma \)) depends linearly on \( v_0 \). As a result, both Baskaran and Marchetti (2008a) and Bertin et al. (2009) find that \( \lambda_i \sim v_0^2 \), while here \( \lambda_i \sim v_0 \). This difference arises because in Baskaran and Marchetti (2008a) and Bertin et al. (2009) the authors systematically describe binary collisions, yielding an instantaneous change of direction with probability one in a small time interval, while the model of Farrell et al. (2012) presented here (and chosen for illustrative purpose because of its simplicity) considers a continuous evolution of the position due to the application of a force in the Langevin equation. These differences may of course be important for large values of \( v_0 \).

This example shows how the derivation of hydrodynamics from a microscopic model yields explicit values for the various parameters in the continuum equations in terms of microscopic parameters. Of course, as stressed above, these values are model dependent. In addition, there is a price to be paid in that in the derivation one has made two important assumptions. The first is the assumption of low density, that allows us to replace the two-particle probability distribution by the product of two one-particle distribution functions in the kinetic equation. The second is effectively an assumption of weak interaction that enters in the moment closure approximation. The two assumptions are not independent and essentially amount to the so-called assumption of “molecular chaos” used for instance in the derivation of the familiar Boltzmann equation.

4. Hydrodynamic interactions

The examples presented above ignore the momentum exchange between the active particles and the solvent that one would have for instance in suspensions of swimming organisms. This physical effect is important for understanding the properties of a wide variety of experiments and should be included for a complete microscopic description of active matter.

The coupling to the solvent has been treated in the literature in at least two ways.

One approach is to include an additional equation for the solvent velocity field \( \mathbf{v}(\mathbf{r}, t) \) which is coupled to the microscopic equations of motion (Liverpool and Marchetti 2006; Marchetti and Liverpool 2007) or to the corresponding Smoluchowski equation (Pahlavan and Saintillan 2011; Saintillan and Shelley 2008a). The active particles are convected and rotated by the local fluid flow while also imparting additional forces (stresses) onto the fluid. This gives rise to a coupled equation of motion for the concentration of filaments \( c(\mathbf{r}, \mathbf{v}, t) \) and the velocity field \( \mathbf{v}(\mathbf{r}, t) \) which can be solved directly (Pahlavan and Saintillan 2011; Saintillan and Shelley 2008a) or coarse-grained as described above to give coupled equations for \( \rho(\mathbf{r}, t), \mathbf{p}(\mathbf{r}, t), \mathbf{Q}(\mathbf{r}, t), \mathbf{v}(\mathbf{r}, t) \). For the case where the suspension is incompressible (\( \rho = \) constant), the momentum (\( \mathbf{v} \)) equation has the form \( \rho (\partial_t + \mathbf{v} \cdot \nabla) \mathbf{v} = \nabla \cdot \sigma \). This equation may also be often treated in the Stokes approximation, \( \nabla \cdot \sigma = 0 \), appropriate for systems at low Reynolds number. The active forces due to the swimmers are incorporated as an additional (active) contribution to the stress tensor, so that \( \sigma_{\alpha \beta} = \sigma^p_{\alpha \beta} + \sigma^{a}_{\alpha \beta} \), where the passive contribution \( \sigma^p_{\alpha \beta} \) has the form obtained in equilibrium liquid crystals (de Gennes and Prost 1993). The active contribution \( \sigma^{a}_{\alpha \beta} \) is evaluated by noting that in the absence of external body forces, the force distribution exerted by the active particles on the fluid can be written as a multipole expansion with lowest order non vanishing term being a dipole. The active stress \( \sigma^{a}_{\alpha \beta} \) can then be identified with the active reactive fluxes proportional to \( \zeta \Delta \mu \) (see Eq. 11). To leading order in a gradient expansion it contains two additive contributions. The first, \( \sigma^{a1}_{\alpha \beta} \propto \zeta \Delta \mu q_{\alpha \beta} \), has nematic symmetry and is present in both polar and nematic systems, where it is written as \( \sigma^{a1}_{ij} \propto \zeta \Delta \mu q_{ij} \). In addition, for polar systems only, the active stress also contains terms \( \sigma^{a2}_{\alpha \beta} \propto \zeta \Delta \mu \partial_{\alpha} p_{\beta} + \zeta' \Delta \mu \partial_{\beta} p_{\alpha} \) (Liverpool and Marchetti 2006; Marchetti and Liverpool 2007). When the hydrodynamic equations are written on the basis of the entropy production formulation discussed in section III.B this term is discarded as one of higher order in the driv-
ing forces. It is also of higher order in the gradients as compared to $\sigma_{ij}^{\alpha\beta}$, although only of first order, rather than quadratic, in the polarization field. Finally, it is the leading non-vanishing contribution to the active stress that has polar (as opposed to nematic) symmetry and it does play a role in controlling the onset of oscillatory states in these systems (Giomi and Marchetti, 2012; Giomi et al., 2008). This shows that a microscopic derivation is needed to go beyond linear hydrodynamics.

Alternatively, one may integrate out the solvent velocity field to generate effective hydrodynamic interactions at the two-body level which give rise to additional long-range pair-wise contribution to the deterministic velocities and angular velocities $v_n, \omega_n$ in Eqs. (74) (Baskaran and Marchetti, 2009; Leoni and Liverpool, 2010). These interactions arise from the forces generated on the fluid by the active particles. The local force distribution due to the active elements can be expanded in a multipole expansion. The lowest non vanishing term in this expansion is a dipole, which also gives the longest range interactions. The simplest static models of swimming organisms then are force dipoles which can be characterized as contractile or extensile depending on the direction of the forces making up the dipole. Coarse-graining the equations leads to a set of coupled integral equations for $\rho(r,t), p(r,t), Q(r,t)$ which in extended (large) domains can be used to obtain generalized linear hydrodynamic modes whose behavior is identical to that obtained when keeping an explicit velocity field. Hydrodynamic equations for collections of static force dipoles have been obtained (Baskaran and Marchetti 2009) which show all the phenomenology described before. Swimming objects however are dynamic, undergoing an internal cyclical motion that leads to self-propulsion. The collective behavior of simplified dynamic models of swimmers with such internal cycles has also been studied and used to generate effective hydrodynamic equations (Leoni and Liverpool 2010). Averaged over an internal cycle such dynamic models have an average force distribution that also has a multipolar expansion whose lowest term is generically a force dipole. The hydrodynamic equations obtained are then similar to those obtained for static dipoles. However by tuning internal parameters one can also study self-propelled swimmers whose averaged force distribution starts at quadrupolar order. Here the symmetry broken between contractile and extensile objects is restored and only nematic phases are possible (Leoni and Liverpool 2010 2012).

C. Current Status of Microscopic Theories of Active Matter

Perhaps the most important open question in deriving active theories from microscopic or mesoscopic models concerns understanding the nature of the noise. Thermal noise is often negligible in active systems at low frequency, but noise is nonetheless ubiquitous and plays a crucial role in controlling the large scale behavior, as it can both act to destroy large scale coherence or drive synchronization, depending on the specific situation. So far practically all work on active systems has either neglected noise or modeled it as a Gaussian, white random force, akin to thermal noise, but of unknown strength. In general one expects the noise to depend on activity. Multiplicative or non-Markovian random forces could also be at play in active systems. For instance, the multiplicative character of the noise introduces (Mishra et al., 2012) singular features into the fluctuation-driven phase-separation (Mishra and Ramaswamy 2006) that characterizes a stable active nematic. Microscopic models are needed that attempt to take into account the stochastic nature of active forces and to derive a coarse-grained model where the effective noise amplitude is expressed in terms of local nonequilibrium processes that may lead to temporal or spatial correlations at large scales. An example is the work of Lacoste and Lau (2005) that couples the shot noise associated with the on/off switching of energy-dissipating pumps in active membranes to the membrane curvature and demonstrates that pump stochasticity plays a crucial role in controlling super diffusive behavior in the membrane.

Of great interest is also the detailed understanding of hydrodynamic interactions in bacterial suspensions and their role in controlling the large-scale behavior. Recent experiments have probed for the first time the flow fields induced by swimming unicellular organisms. Measurements on Chlamydomonas have revealed qualitative differences as compared to the puller stresslet configuration that had been used in the literature (Drescher et al., 2010) and have further shown complex time-dependent oscillatory patterns. In contrast it was found that the flow field of E.coli is well described by a pusher stresslet, but its strength is very small and it is washed out by rotational diffusion of the swimming direction (Drescher et al. 2011). These results have important implications for the behavior of microorganisms near surfaces and open the way to new quantitative investigations of the role of hydrodynamic interactions.

Finally, an area that is receiving increasing attention is the study of active matter at high density, where active glassy or solid states may emerge. As mentioned in section II.C the collective dynamics of confluent layers of epithelial cells has been likened to that of glassy and supercooled systems. Mesoscopic models of interacting cell layers and tissues are beginning to emerge (Henkes et al., 2011), although much more work remains to be done to understand the complex interplay of contractile stresses and substrate adhesion in controlling the build up of cellular stresses in collective cell migration.
VI. CONCLUSIONS, OUTLOOK AND FUTURE DIRECTIONS

In this review we have discussed two dimensional and three dimensional active systems, that are maintained out of equilibrium by a permanent energy consumption that takes place locally in each active unit. In these systems local polarity, when present, yields spontaneous motion of the polar entities with respect to the center of mass motion. Typically, models of active matter describe the collective behavior of systems like fish shoals, birds flock or animals herds as well as vibrated granular matter, bacterial colonies or the cellular cytoskeleton. From a spatial symmetry point of view these systems are not different from ferroelectric and nematic liquid crystals. The fundamental difference stems from the fact that active systems consume and dissipate energy at all times. This feature has a number of profound consequences which we have addressed in this review:

- Polar flocks on a substrate, e.g., animal herds, keratoctyes on a glass slide, display long-range order in two dimensions. This behavior is fundamentally different form that of equilibrium systems that are bound to obey the Mermin-Wagner theorem and can at best exhibit quasi-long range order;
- nematic as well as polar ordered phases systems on a substrate exhibit giant density fluctuations, breaking the familiar $\sqrt{N}$ equilibrium scaling of number fluctuations in subregions with $N$ particles on average;
- the uniform ordered state of bulk momentum-conserving systems of polar and nematic symmetry is generically unstable in the Stokesian regime;
- the end result of this instability for the typical active suspension appears to be turbulence at low Reynolds number (Dombrowski et al. 2004, Wolgemuth 2008) driven by the competition between forcing by active stress and relaxation by orientational diffusion.
- all these systems can support a new type of sound-like propagating waves that can have different propagation laws in opposite directions due to polarity.

We have described how macroscopic hydrodynamic equations for active systems can be obtained either from symmetry arguments, from generalized thermodynamics close to equilibrium, or from microscopic models. In each case we have presented the simplest description that highlights the generic features uniquely associated with activity. Our analysis is restricted to two and three dimensions and we have deliberately left aside one-dimensional and quasi one-dimensional systems, which have already been investigated extensively (Helbing 2001, Reichenbach et al. 2006). We note, however, that the mechanisms leading to the onset of traffic jams are probably related to the giant density fluctuations predicted in active systems in two dimensions [see also (Fily et al., 2012, Yang et al., 2010)].

The rewarding feature is that all these unusual features have either been observed experimentally or confirmed in careful numerical simulations. It is very difficult to establish the existence of long range order experimentally, but simulations with a large number of active particles show unambiguously its existence. This is an important result that the statistical physics community was not inclined to believe. Giant density fluctuations have now been observed in simulations (Chaté et al., 2008a), experimentally in vibrated granular media (Narayan et al., 2007) and in bacterial suspensions (Zhang et al., 2010). These observations have confirmed the theoretically predicted scaling. We note, however, that this scaling has recently been questioned by (Toner 2012). These large fluctuations are also present in the cellular cytoskeleton and their role is starting to be recognized (Gowrishankar and Rao 2012) and their potential physiological relevance is beginning to be explored (Chaudhuri et al., 2011, Goswami et al., 2008, Gowrishankar et al., 2012).

The long wavelength instability of momentum conserving systems is confirmed by numerical simulation and in fact can give rise to "low Reynolds number turbulence" in some instances (Dombrowski et al., 2004). It is a good paradigm for explaining bacterial swirls but also the rotating microtubule spindles observed both in vivo and in vitro (Nédélec 1998, Nedelec et al. 1997). Furthermore, the existence of "low Reynolds number" waves have also been predicted in crystals moving without inertia through a dissipative medium, such as sedimenting colloids (Lahiri and Ramaswamy 1997) or drifting Abrikosov lattices (Balents et al., 1998, Ling et al., 1998, Simha and Ramaswamy 1999), and also observed and understood in microfluidic drifting drop arrays (Beatus et al., 2007, 2006). Such waves propagating in only one direction have been observed in cell lamellipodia, as expected from active gel theory (Giannoni et al., 2004).

Eventually, one may be able to discuss with order of magnitude accuracy phenomena such as cell wound healing (Petitjean et al., 2010), cell division (Salbreux et al., 2009), and cell oscillations (Salbreux et al., 2007). One can thus say that we currently have a good qualitative understanding of active systems. What do we need to get to the next stage, that is to get to real quantitative understanding? One ingredient which we have omitted on purpose up to now is signaling: biochemical signaling for cell biology or bacterial colonies external factors like food, smell or sun in flocks, shoals and herds. Such factors have been discussed in bacterial colonies and shown to give rise to beautifully ordered structures (Cates et al., 2010). A direction that looks particularly promising, is coupling of active gel physics and chemical reactions in the context...
of cells and tissues, resulting for instance, in increasing considerably the range of existence of Turing structures \cite{Bois2011,Giomietal2010,Giomietal2012}, and in the spatiotemporal control and enhancement of chemical reaction rates in signaling and sorting \cite{Chaudhuri2011}. A complete understanding of cell biology will obviously require including detailed biochemical signaling networks. However this cannot be achieved without an extensive experimental input. Symmetry considerations and conservation laws are no longer sufficient and this task requires the cooperation of several disciplines. It is worth the effort though, since it could be extended to tissue dynamics and developmental biology.

Another natural extension in the case of herds, flocks and shoal is the investigation of a putative leader role \cite{Couzin2011,Leonard2012}. Up to now, completely “democratic” rules have been assumed. Within this approach, a leader could appear like a delta function, and its role involve the response function of the collection of individuals. In another promising direction, \cite{Guttal2010} treat the parameters in a Vicsek-style model of flocking and migration as heritable, selectable attributes, and study their dynamics on evolutionary timescales, finding a remarkable range of evolutionarily stable strategies including coexistence of distinct behaviors in a herd.

Another frontier concerns active quantum systems. A beautiful classical mimic has been introduced recently \cite{Alicea2005} and some Al-Ga-Se heterostructures give rise to zero resistivity behavior described by equations very similar to those of Toner-Tu \cite{Adhyapak2012}. A general investigation of the type we present here would be very useful.

Eventually working with real systems is necessary and important, but it is often difficult. Artificial systems such as provided by layers of vibrated granular matter \cite{Deseigne2010,Kudrolli2008,Kumar2011,Narayan2007}, noisy walkers \cite{Kumar2008}, artificial swimmers \cite{Bartolo2007}, and colloids propelled by catalytic reactions \cite{Gibbs2011,Golestanian2009,Golestanian2005,Howse2007,Palacci2010,Paxton2004} are very useful but are often restricted to two dimensions (granular layers) or have been studied only at relatively low density (artificial self-propelled particles). It would be nice to have three dimensional active systems driven by light or chemical reactions \cite{Buttinoni2011}. Attempts have been made \cite{Prost2010} to raise interest among chemists, but so far progress towards realizing artificial active gels has been limited. Such systems would allow one to vary parameters over a wide range and in a controlled manner and would therefore provide extremely valuable artificial realizations of active matter.

**ACKNOWLEDGMENTS**

We would like to thank many colleagues for invaluable discussions and suggestions, and colleagues of the work summarized here, including: Aparna Baskaran, Shiladitya Banerjee, Andrew Callan-Jones, Yaonuen Fiy, K. Gowrishankar, Yashodhan Hatwalne, Silke Henkes, Karsten Kruse, Frank Jülicher, Norio Kikuchi, Gautam Menon, Satyajit Major, Narayan Menon, Shradha Mishra, Vijay Narayan, Guillaume Salbreux, Sumithra Sankararaman, Ken Sekimoto, John Toner and Rafael Voituriez. MCM was support by the National Science Foundation on grants DMR-0806511 and DMR-1004789. JFJ, JP, SR and MR acknowledge support from grant 3504-2 of CEFIPRA, the Indo-French Centre for the Promotion of Advanced Research. TBL acknowledges the support of the EPSRC under grant EP/G026440/1.

**REFERENCES**

Adhyapak, T. C., S. Ramaswamy, and J. Toner (2012), “Hydrodynamics of an active smectic (arxiv:1204.2708).”

Ahmadi, A., M. C. Marchetti, and T. B. Liverpool (2005), Phys. Rev. E 72, 060901(R) (4 pages).

Ahmadi, A., M. C. Marchetti, and T. B. Liverpool (2006), Phys. Rev. E 74 (6), 061913.

Aldana, M., V. Dossetti, C. Husepe, V. M. Kenkre, and H. Larralde (2007), Phys. Rev. Lett. 98, 095702.

Alicea, J., L. Balents, M. Fisher, A. Paramekanti, and L. Radzihovsky (2005), Phys. Rev. B 71, 235322.

Angelani, L., R. DiLeonardo, and R. Giancarlo (2009), Phys. Rev. Lett. 102, 048104.

Angellini, T. E., E. Hannezo, X. Trepat, J. J. Fredberg, and D. A. Weitz (2010), Phys. Rev. Lett. 104 (16), 168104.

Angellini, T. E., E. Hannezo, X. Trepat, M. Marquez, J. J. Fredberg, and D. A. Weitz (2011), PNAS 108 (12), 4714.

Aranson, I. S., A. Snejzhko, J. S. Olafsen, and J. S. Urbach (2008), Science 320, 612.

Aranson, I. S., A. Sokolov, J. O. Kessler, and R. E. Goldstein (2007), Phys. Rev. E 75, 040901(R) (4 pages).

Aranson, I. S., and L. S. Tsimring (2005), Phys. Rev. E 71, 050901(R) (4 pages).

Aranson, I. S., and L. S. Tsimring (2006), Phys. Rev. E 74, 031915 (15 pages).

Asano, Y., A. Jiménez-Dalmaroni, T. Liverpool, M. Marchetti, L. Giomi, A. Kiger, T. Duke, and B. Baum (2009), HFSP J. 3, 194.

Backouche, F., L. Haviv, D. Groszwater, and A. Bernheim-Brechot (2009), Phys. Biol. 3, 264.

Baglietto, G., and E. V. Albano (2009), Phys. Rev. E 80, 050103(R).

Balents, L., M. Marchetti, and L. Radzihovsky (1998), Phys. Rev. E 57, 7705.

Ballest, M., N. D. R. At, D. Icard, S. Fereol, A. Asnacios, J. Browaeys, S. Henon, and F. Gallet (2006), Phys. Rev. E 72, 021911 (21 pages).

Ballé, M., N. Cabilio, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini, M. Viale, and V. Zdravkovic (2008), Proceedings of the National Academy of Sciences 105, 1232.
Gardel, M., J. Shin, F. MacKintosh, L. Mahadevan, P. Matsudaiera, and D. Weitz (2004), Science 304, 1301.
de Gennes, P. G., and J. Prost (1993), The Physics of Liquid Crystals (Clarendon Phys. Rev. Ess, Oxford).
Giannone, G., B. J. Dubin-Thaler, H. G. Döbereiner, N. Kieffer, A. R. Bresnick, and M. P. Sheetz (2004), Cell 116, 431.
Gibbs, J., and Y. Zhao (2011), Front. Mat. Sci. 5, 25.
Ginelli, F., and H. Chaté (2010), Phys. Rev. Lett. 104, 184502.
Gomi, L., T. B. Liverpool, and M. C. Marchetti (2010), Phys. Rev. E 81, 051908.
Gomi, L., L. Mahadevan, B. Chakraborty, and M. F. Hagan (2011), Phys. Rev. Lett. 106, 218101 [4 pages].
Gomi, L., L. Mahadevan, B. Chakraborty, and M. F. Hagan (2012), Nonlinearity 25, 2245.
Gomi, L., and M. C. Marchetti (2012), Soft Matter 8, 129.
Gomi, L., M. C. Marchetti, and T. Liverpool (2008), Phys. Rev. Lett. 101, 198101 (4 pages).
Golestanian, R. (2009), Phys. Rev. Lett. 102, 188305 (4 pages).
Golestanian, R., T. Liverpool, and A. Ajdari (2005), Phys. Rev. Lett. 94, 220801.
Gönczi, B., M. Nagy, and T. Vicsek (2008), Eur. Phys. J. Special Topics 157, 53.
Gopinath, A., M. F. Hagan, M. C. Marchetti, and A. Baskaran (2012), Phys. Rev. E 85, 061903 [8 pages].
Goswami, D., K. Gowrishankar, S. Bilgrami, S. Ghosh, R. Argupathy, R. Chadda, R. Vishwakarma, M. Rao, and S. Mayor (2012), Cell 135, 1085.
Gowrishankar, K., S. Ghosh, S. Saha, R. C., S. Mayor, and M. Rao (2012), Cell 149, 1353.
Gowrishankar, K., and M. Rao (2012), “Nonequilibrium phase transitions in active contractile polar filaments.”
Grégoire, G., and H. Chaté (2004), Phys. Rev. Lett. 92 (2), 025702.
Grill, S. W. (2011), Current Opinion in Genetics & Development 21, 647652.
de Groot, S. R., and P. Mazur (1984), Non-Equilibrium Thermodynamics (Dover, New York).
Grunder, H., U. Dewald, and M. Eberhardt (1999), Eur. Phys. J. B 11, 187.
Guasto, J. S., K. A. Johnson, and J. P. Gollub (2010), Phys. Rev. Lett. 105, 168102.
 Günther, S., and K. Kruse (2007), New J. Phys. 9, 417.
Guttal, V., and I. D. Couzin (2010), Proceedings of the National Academy of Sciences 107, 16172.
ten Hagen, B., S. van Teeffelen, and H. Löwen (2009), Condensed Matter Physics 12, 725738.
Haines, M., A. Sokolov, I. S. Aranson, L. Berlyand, and D. A. Karpeev (2009), Phys. Rev. E 80, 041922.
Hatwalne, Y., S. Ramaswamy, M. Rao, and R. A. Simha (2004), Phys. Rev. Lett. 92 (11), 118101.
Head, D. A., W. J. Briels, and G. Grömp ponder (2011), BMC Biophysics 4, 18.
Helbing, D. (2001), Rev. Mod. Phys. 73, 1067.
Henkes, S., Y. Fily, and M. C. Marchetti (2011), Phys. Rev. E 84, 040301(R).
Hohenberg, P. C. (1967), Phys. Rev. 158, 383.
Hoswe, J. R., R. A. L. Jones, A. J. Ryan, T. Gough, R. Vafabakhsh, and R. Golestanian (2007), Phys. Rev. Lett. 99, 048102.
Ihle, T. (2011), Phys. Rev. E 83, 030901.
Ishikawa, T. (2009), Journal of The Royal Society Interface 6, 815.
Joanny, J. F., F. Julicher, K. Kruse, and J. Prost (2007), New Journal of Physics 9, 422.
Joanny, J.-F., and J. Prost (2009), HFSP J. 3, 94.
Joanny, J.-F., and J. Prost (2010), in Poincaré Seminar 2009, edited by B. Duplantier and V. Rivasseau (Birkhauser).
Joanny, J.-F., and S. Ramaswamy (2012), “A drop of active matter.”
Julicher, F., K. Kruse, J. Prost, and J.-F. Joanny, Phys. Rep. 449, 3.
Julicher, F., and J. Prost (1997), Phys. Rev. Lett. 78, 4510.
Kareiva, M., and N. Shigesada (1983), Ecological 56, 234.
Kemkemer, R., D. Kling, D. Kaufmann, and H. Gruler (2000), Eur. Phys. J. E 1, 215.
Keren, K., Z. Pincus, G. Allen, E. Barnhart, A. Marriott, A. Mogilner, and J. Theriot (2008), Nature 453, 475.
Kikuchi, N., A. Ehrlicher, D. Koch, J. A. Käs, S. Ramaswamy, and M. Rao (2009), Proceedings of the National Academy of Sciences 106 (47), 19776.
Koch, D. L., and G. Subramanian (2011), Annual Review of Fluid Mechanics 43, 637.
Koenderink, G. H., Z. Dogic, F. Nakamura, P. M. Bendix, F. C. MacKintosh, J. H. Hartwig, T. F. Stossel, and D. A. Weitz (2009), PNAS 106, 15192.
Krait kovski, P., R. Lipowsky, and J. Kierfeld (2006), Phys. Rev. Lett. 96, 258103.
Kron, S. J., and J. Spudich (1986), Proc. Natl. Acad. Sci. USA 83, 6272.
Kruse, K., S. Camalet, and F. Jülicher (2001), Phys. Rev. Lett. 87, 138101.
Kruse, K., F. Joanny, F. Jülicher, J. Prost, and K. Sekimoto (2004), Phys. Rev. Lett. 92, 078101 (4 pages).
Kruse, K., F. Joanny, F. Jülicher, J. Prost, and K. Sekimoto (2006a), Eur. Phys. J. E 16, 5.
Kruse, K. J. F. Joanny, F. Jülicher, and J. Prost (2006b), Phys. Biol. 3, 130.
Kruse, K. F. Joanny, F. Jülicher, J. Prost, and K. Sekimoto (2005), Eur. Phys. J. E; Soft Matter and Biological Physics 16 (1), 5.
Kruse, K., and F. Jülicher (2000), Phys. Rev. Lett. 85, 1778.
Kruse, K., and F. Jülicher (2003), Phys. Rev. E 67, 051913.
Krus e, K., and F. J. Jülicher (2006), Eur. Phys. J. E 20, 459.
Kudrolli, A. (2010), Phys. Rev. Lett. 104, 088001.
Kudrolli, A., G. Lunay, D. Volson, and L. S. Tsimring (2009), Phys. Rev. Lett. 100, 058001.
Kumar, K. V., S. Ramaswamy, and M. Rao (2008), Phys. Rev. E 77, 020102.
Kumar, N., S. Ramaswamy, and A. K. Sood (2011), Phys. Rev. Lett. 106, 118001.
Kung, W., M. C. Marchetti, and K. Saunders (2006), Phys. Rev. E 73, 031708 (8 pages).
Lacoste, D., and A. W. C. Lau (2005), Europhys. Lett. 70, 418.
Lahir i, R., and S. Ramaswamy (1997), Phys. Rev. Lett. 79, 1150.
Landau, and Lifshitz (1998), Fluid Mechanics (Butterworth-Heinemann).
Larson, R. (1988), Equations for Polymer melts and Solutions (Butterworths).
Lau, A. W. C., B. D. Hoffman, A. Davies, J. C. Crocker, and T. C. Lubensky (2003), Phys. Rev. Lett. 91, 198101 (4 pages).
Lingwood, D., and K. Simons (2010), Science
Levine, A. J., and F. C. MacKintosh (2009), J. Phys. Chem.
Leoni, M., and T. B. Liverpool (2012), Phys. Rev. E
Ling, X. S., J. E. Berger, and D. E. Prober (1998), Phys.
Leoni, M., and T. B. Liverpool (2010), Phys. Rev. Lett.
Liverpool, T. B. (2003), Phys. Rev. E
Lee, H. Y., and M. Kardar (2001), Phys. Rev. E
Lee, H. Y., and M. Kardar (2001), Phys. Rev. E
Mizuno, D., C. Tardin, C. F. Schmidt, and F. C. MacKintosh (2007), Science 315, 370.
Mogilner, A., and G. Oster (1996), Biophys. J. 71, 3030.
Mogilner, A., and G. Oster (1999), Eur. Biophys. J. 28, 235.
Muhuri, S., M. Rao, and S. Ramaswamy (2007), EPL 78, 48002.
Murray, J. D. (2003), Mathematical Biology vol. II: Spatial Models and Biomedical Applications, 3rd edn. (New York: Springer).
Narayan, V., S. Ramaswamy, and N. Menon (2007), Science 317 (5834), 105.
Narayan, V., S. Ramaswamy, and d. N. Menon (2008), Science 320 (2008), Science 320, 612.
Nédélec, F. (1998), Auto-organisation d’un Melange de Micro-tubules et de Moteurs, Ph.D. thesis (Université Paris 11), http://www.cytosin.org/reprints/these/index.html.
Nédélec, F., T. Surrey, A. Maggs, and S. Leibler (1997), Nature 389, 305.
Onsager, L. (1949), Ann. N.Y. Acad. Sci. 51, 627.
Oron, A., S. H. Davis, and S. G. Bankoff (1997), Rev. Mod. Phys. 69, 931.
Pahlavan, A. A., and D. Saintillan (2011), Phys. Fluids 23, 011901.
Palacci, J., B. Abécasis, C. Cottin-Bizonne, C. Ybert, and L. Bocquent (2010), Phys. Rev. Lett. 104, 138302 [4 pages].
Palffy-Muhoray, F., M. A. Lee, and R. G. Petschek (1988), Phys. Rev. Lett. 60, 2030.
Parrish, J. K., and W. M. Hammer (1997), Three Dimensional Animals Groups (Cambridge University Phys. Rev. Ess., Cambridge, England).
Paxton, W. F., K. C. Kistler, C. C. Olmeda, A. Sen, S. K. S. Angelo, Y. Cao, T. E. Mallouk, P. E. Lammert, and V. H. Crespi (2004), J. Am. Chem. Soc. 126, 13424.
Pedley, T. J., and J. O. Kessler (1992), Annu. Rev. Fluid Mech. 24, 313.
Peruani, F., A. Deutsch, and M. Bär (2006), Phys. Rev. E 74, 030904 (4 pages).
Peruani, F., A. Deutsch, and M. Bär (2008), Eur. Phys. J. Special Topics 157, 111.
Peruani, F., J. Stuppa, V. Jakovljevic, L. Sogaard-Andersen, A. Deutsch, and M. Bär (2012), Phys. Rev. Lett. 108, 098102 [5 pages].
Petitjean, L., M. Reffay, E. Grasland-Mongrain, M. Poujade, B. Ladoux, A. Buguin, and P. Silberzan (2010), Biophys. J. 98 (9), 1790.
Pinot, M., F. Chesnel, J. Z. Kubiak, I. Arnal, F. J. Nedelec, and Z. Gueron (2009), Current Biology 19, 954960.
Poujade, M., E. Grasland-Mongrain, A. Hertzog, J. Jouanneau, P. Chavrier, B. Ladoux, A. Buguin, and P. Silberzan (2007), PNAS 104 (41), 15988.
Prevost, A., P. Melby, D. A. Egolf, and J. S. Urbach (2004), Phys. Rev. E 70, 050301(R).
Prost, J. (2010), From non-covalent assemblies to molecular machines, Vol. 21st Solvay Conference in Chemistry, edited by J. Sauvage and P. Gaspard (Wiley).
Prost, J., and R. Bruinsma (1996), Europhys. Lett. 33, 321.
Prost, J., J. Joanny, P. Lenz, and C. Sykes (2007), The Physics of Listeria propulsion in Cell motility, edited by P. Lenz (Springer Verlag (New York)).
Rafai, S., L. Jibuti, and P. Peyla (2010), Phys. Rev. Lett. 104, 098102.
Ramaswamy, S. (2010), Annu. Rev. Condens. Matter Phys. 1, 323.
Ramaswamy, S., and G. F. Mazenko (1982), Phys. Rev. A 26, 1735.
Ramaswamy, S., and M. Rao (2001), C. R. Acad. Sci. Paris, Série IV 2, 817.
Ramaswamy, S., and M. Rao (2007), New J. Phys. 9, 423.
