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Hydrodynamics and rheology of active polar filaments

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Summary. The cytoskeleton provides eukaryotic cells with mechanical support and helps them perform their biological functions. It is a network of semiflexible polar protein filaments and many accessory proteins that bind to these filaments, regulate their assembly, link them to organelles and continuously remodel the network. Here we review recent theoretical work that aims to describe the cytoskeleton as a polar continuum driven out of equilibrium by internal chemical reactions. This work uses methods from soft condensed matter physics and has led to the formulation of a general framework for the description of the structure and rheology of active suspension of polar filaments and molecular motors.

1 Introduction

Cells are living soft matter. They are composed of a variety of soft materials, such as lipid membranes, polymers and colloidal aggregates, often constrained to a reduced spatial dimensionality and geometry. It is then reasonable to expect that the dynamics and interactions of these constituents that control cell function takes place on the same time and energy scales as those of synthetic soft materials. Life adds, however, a new feature not found in traditional soft matter: the constant flow of energy and information required to keep living organisms alive. This new feature makes cells of particular interest to physicists as understanding the behavior of *active* living matter requires the development of new theoretical concepts and experimental techniques.

The eukaryotic cell cytoskeleton is a perfect example of this novel type of *active material*. The cytoskeleton allows the cell to carry out coordinated and directed movements such as cell crawling, muscle contraction, and all the changes in cell shape in the developing embryo [1]. The cytoskeleton also supports intra-cellular movements such as the transport of organelles in the cytoplasm and segregation of chromosomes during cell division [2]. It is highly inhomogeneous, with a large variety of different dynamical *supramolecular* structures. Examples are contractile elements like stress fibres, or the contractile ring in mitosis, or astral objects like the mitotic spindle which forms during cell division [1, 2].

Self-assembled filamentous protein aggregates play an important role in the mechanics and self-organization of the cytoskeleton. In addition, a number of other proteins interact with them and modulate their structure and dynamics. Cross-linking proteins bind to two or more filaments together to form a dynamical gel. Molecular motor proteins bind to filaments and hydrolyze nucleotide Adenosine triphosphate (ATP). This process, coupled to a corresponding conformational change of the protein, turns stored chemical energy into mechanical work. Capping proteins modulate the polymerization and depolymerization of the filaments at their ends.

A key question is how the elements of the cytoskeleton cooperate to achieve its function. To what extent is there a 'cellular' brain and how closely does it control cellular mechanisms? How much of a role does spontaneous self-organization driven by general physical principles play?

Much of the recent progress in the understanding of the complex structures and processes that control the behavior and function of the cytoskeleton has been linked to the development of new biophysical probes allowing an unprecedented view of sub-cellular processes at work. Mechanical probes such as optical and magnetic tweezers [3], atomic force microscopes [4] and micropipettes probe the response of the elements of the cytoskeleton to locally applied forces. Visualization techniques using fluorescence microscopy, e.g. fluorescence imaging with one-nanometer accuracy [5] or single-molecule high-resolution co-localization [6] based on organic dyes allow one to follow the dynamics of single molecules inside living cells, (*in-vivo*) giving insights into the microscopic processes underlying cellular dynamics. Many of these experimental developments are reviewed in this book.

Because of the large number of unknown components, it is also of interest to study simplified systems consisting of a smaller number of well characterized elements, *in-vitro*. This has led to a number of experimental biophysical studies of purified solutions of cytoskeletal filaments and associated molecular motors that have established that motor-induced activity drives the formation of a variety of spatially inhomogeneous patterns, such as bundles, asters and vortices [7, 8, 9, 10, 11, 12, 13, 14]. These are reminiscent of some of the supramolecular structures present in the cytoskeleton [15, 16]. The mechanical properties of filament-motor systems has also been studied showing qualitative differences from passive filament suspension. Because of the controlled nature of their preparation and the detailed knowledge of their constituents, *in vitro* studies are particularly amenable to a quantitative description using techniques from theoretical physics. In this review we will be mostly concerned with describing the behavior of such simplified systems on large time scales (times \geq microsecond) where the atomistic details are not important and a coarse-grained phenomenological description may suffice.

The reductionist viewpoint typified by this approach also has its drawbacks. A simplified system necessarily can provide only a subset of the phenomena observed in living cells since only a small fraction of the components are present. A choice must also be made of *which* simplified system to study as different combinations of components may give different or similar behavior. This choice must of course be heavily influenced by previous experiments [7, 8]. A living cell is a highly optimized complex *system* of interacting agents with the ability to modulate its response to complex changes in its environment. This complexity will be missing from simple mechanical models described here. There is some hope, however, that this complexity can eventually be combined with the physical picture emerging from the approach we present here to give a more complete "biophysical" picture of motility in cells in

which the laws of physics provide important constraints on the possible "system" dynamics. Finally, even within our limited frame of reference, we will also make a number of simplifying assumptions in developing the models. Some of the important physical phenomena ignored here, such as active polymerization, treadmilling [19, 20] and filament flexibility [21, 22, 23, 24, 25, 26, 27], will be incorporated in future work.

We first review some recent theoretical approaches to describe active filament suspensions. We then describe some of our current work and give perspectives for the future.

2 Theoretical modeling of active systems

There have been a number of recent theoretical studies of the collective dynamics of mixtures of rigid filaments and motor clusters. First and most microscopic, numerical simulations with detailed modeling of the filament-motor coupling have yielded patterns similar to those found in experiments [11, 13], including vortices and asters. These simulations modeled the filaments as elastic rods with motor clusters being parameterized by three binding parameters, the on and off rates and the off-rate at the plus end of the filament. It was found that the rate of motor unbinding at the polar end of the filaments plays a crucial role in controlling the vortex to aster transitions at high motor densities [12].

A second interesting development has been the proposal of 'mesoscopic' mean-field kinetic equations first studied in one dimension [28, 29], where the effect of motors is incorporated via a motor-induced relative velocity of pairs of filaments, with the form of such a velocity inferred from general symmetry considerations. Kruse and collaborators [30, 31, 32] proposed a one dimensional model of filament dynamics and showed the existence of instabilities from the homogeneous state to contractile states [30] and traveling wave solutions [32]. We generalized the kinetic model to higher dimensions [33, 34] and used it to classify the nature of the homogeneous states and their stability [35, 36]. Related kinetic models have also been discussed by other authors [37, 38, 39, 40].

Finally, phenomenological continuum theories have been proposed where the mixture is described in terms of a few coarse-grained fields whose dynamics is inferred from symmetry considerations [41, 43, 42, 44, 45, 46, 47, 48, 49, 50, 51].

Lee and Kardar [43] proposed a simple hydrodynamic model for the coupled dynamics of a coarse-grained filament orientation and the motor concentration, ignoring fluctuations in the filament density. These authors argued that filament growth by polymerization provides a mechanism for an instability of the system from an isotropic to an oriented state [43, 42], with large-scale aster and vortex structures. They obtained a phase diagram for the system showing a transition from vortices to asters. This model was subsequently generalized by Sankararaman et al. [44] to include varying populations of bound and free motors, as well as an additional coupling of filament orientation to motor gradients. The effects of boundary conditions on the steady states of the system was also studied numerically.

A phenomenological hydrodynamic description for polar gels and suspensions including momentum conservation has been discussed by several authors [45, 46, 47, 48]. These equations generally consider incompressible suspensions and incorporate momentum conservation in the Stokes approximation, by assuming the form

of constitutive equation for the suspension's stress tensor on the basis of symmetry consideration. The coupling of flow and polar order is described via an equation for the local polarization of the suspension. This model has been used to identify the non-equilibrium defect structures that can occur in the polar state [45, 46] and to analyze the behavior of an active polar suspension in specific geometries [52, 47]. In particular, it was shown that the interplay between order and activity can yield a spontaneous flowing state for a solution near a wall [47]. Closely related hydrodynamic models have been used to describe generically the collective dynamics of self-propelled particles in solution, such as swimming bacterial colonies, in both nematic and polar states [49, 50, 51]. This work builds on earlier work by Toner and Tu on hydrodynamic models of flocking, where it was shown that the nonequilibrium nature of internally driven systems allows for novel symmetry breaking phase transitions that are forbidden in equilibrium systems with continuous symmetry in one and two dimensions [53, 54, 55].

The main objective of our work has been to establish the connection between microscopic single-polymer dynamics and the phenomenological hydrodynamic models by deriving the hydrodynamic equations from a mean-field kinetic equation of filament dynamics. In the phenomenological approach the system is described in terms of a few coarse-grained fields (conserved densities and broken symmetry variables) whose dynamics is inferred from symmetry considerations. The strength of this method is its generality. Its drawback is that for systems that are far from thermal equilibrium and therefore lack constraints such as those provided by the fluctuation-dissipation theorem or the Onsager relations, all the parameters in the equations are undetermined. We have bridged the gap between microscopic models and continuum theories by deriving the hydrodynamic equations through a systematic coarse-graining of the microscopic dynamics. This derivation provides an estimate of the various parameters in the equations in terms of experimentally accessible quantities. We start with a Smoluchowski equation for filaments in solution, where motor proteins are described as active cross-linkers capable of exchanging forces and torques between filaments. The active currents arising from such motor-mediated exchange of forces and torques are obtained by considering the kinematics of two filaments crosslinked by a single active protein cluster that can rotate and translate at prescribed rates as a rigid object relative to the filaments. The hydrodynamic equations are then obtained by suitable coarse-graining of the Smoluchowski equation. This method yields a general form of the hydrodynamic equations which incorporates all terms allowed by symmetry, yet it provides a connection between the coarse-grained and the microscopic dynamics. In a series of earlier publications we have described in details the derivation of the hydrodynamic equations for filaments in a quiescent solvent [33, 34, 56, 35, 36]. Here we generalize this work by incorporating the flow of the solvent. This is essential for describing the rheological properties of the solution. A brief account of some of the results presented here have been given elsewhere [57].

3 Hydrodynamics of a solution of polar filaments

We consider a collection of rigid polar filaments in a viscous solvent. The solution forms a quasi-two dimensional film, of thickness much smaller than the length of the filaments. Our goal is to study the interplay of order and flow in controlling the

phases and the rheology of the system. The filaments diffuse in the solution and can be crosslinked by both active and stationary protein clusters. Active crosslinkers are small clusters of motor proteins that use chemical fuel as an energy source to generate forces and torques on the filaments, sliding and rotating filaments relative to each other [2, 12]. In addition, other small proteins, such as α -actinins act as stationary crosslinkers and induce filament alignment [1].

As in passive solutions of rigid filaments, the large scale dynamics can be described in terms of a set of hydrodynamic equations for continuum fields that relax on time scales much longer than microscopic ones. These include the conserved variables of the systems, as well as any field associated with broken symmetries. Various forms of these equations have been written down phenomenologically by other authors. What distinguishes our work from these phenomenological approaches is that we derive the hydrodynamic equations from a mesoscopic model of coupled motor-filament dynamics. This allows us to estimate the various parameters in the hydrodynamic equations (which are undetermined in the phenomenological approach) and relate them to quantities that can be controlled in experiments. To make contact with the existing literature, we first present the equations and then discuss their derivation via coarse-graining of a Smoluchowski equation for rigid rods in a viscous solvent.

The conserved densities in a suspension of interacting filaments (rods) in a solvent are the mass densities of filaments (rods) $\rho_r(\mathbf{r}, t) = \mathbf{m}c(\mathbf{r}, t)$ and solvent $\rho_s(\mathbf{r}, t)$, and the total momentum density $\mathbf{g}(\mathbf{r}, t) = \rho(\mathbf{r}, t)\mathbf{v}(\mathbf{r}, t)$ of the solution (rods+solvent), with $\mathbf{v}(\mathbf{r}, t)$ the flow velocity and $\rho(\mathbf{r}, t) = \rho_s + \rho_r$ the total density. Here $c(\mathbf{r}, t)$ is the *number* density of rods and \mathbf{m} the mass of a rod. The conserved densities satisfy conservation laws, given by

$$\partial_t \rho = -\nabla \cdot \mathbf{g} , \quad (1)$$

$$\partial_t c = -\nabla \cdot \mathbf{J} , \quad (2)$$

$$\partial_t g_i + \partial_j (g_i g_j / \rho) = \partial_j \sigma_{ij} + \rho F_i^{ext} , \quad (3)$$

where $\mathbf{J}(\mathbf{r}, t)$ is the current density of rods and \mathbf{F}^{ext} the external force on the suspension. The stress tensor σ_{ij} is the i -th component of the force exerted by the surrounding fluid on a unit area perpendicular to the j -th direction of a volume element of solution. It includes all forces on a volume of suspension exerted by the surrounding fluid. It can be written as the sum of solvent and filament contributions as

$$\sigma_{ij} = \sigma_{ij}^s + \sigma_{ij}^r . \quad (4)$$

The solvent contribution has the usual form appropriate for a viscous fluid,

$$\sigma_{ij}^s = 2\eta_0 u_{ij} + (\eta_b - \eta_0) \delta_{ij} u_{kk} - \delta_{ij} \Pi_s(\rho) , \quad (5)$$

where η_0 and η_b are the shear and bulk viscosity of the solvent, $\Pi_s(\rho)$ is the pressure of the solvent, and u_{ij} is the symmetrized rate of strain tensor,

$$u_{ij} = \frac{1}{2} (\partial_i v_j + \partial_j v_i) . \quad (6)$$

In the low Reynolds number limit we can ignore the inertial terms on the left hand side of the solvent momentum equation, Eq. (3).

In a solution of long filaments states with liquid crystalline order are possible. Polar rods can form polarized and nematic states, both characterized by orientational order, but with different symmetries for the order parameters. Polar order in a fluid of N rods is characterized by a vector order parameter or polarization, $\mathbf{P}(\mathbf{r}, t)$, defined by

$$\mathbf{P}(\mathbf{r}, t) = \frac{1}{c(\mathbf{r}, t)} \left\langle \sum_{\alpha=1}^N \hat{\mathbf{u}}_{\alpha}(t) \delta(\mathbf{r} - \mathbf{r}_{\alpha}(t)) \right\rangle, \quad (7)$$

where \mathbf{r}_{α} is the position of the center of mass of the α -th rod and $\hat{\mathbf{u}}_{\alpha}$ is a unit vector directed along the polar direction. The angular bracket denote an ensemble average. The polarization vector \mathbf{P} can be written as

$$\mathbf{P}(\mathbf{r}, t) = P(\mathbf{r}, t) \mathbf{p}(\mathbf{r}, t), \quad (8)$$

where the magnitude of the polarization $P(\mathbf{r}, t)$ is the scalar order parameter and the unit vector $\mathbf{p}(\mathbf{r}, t)$ identifies the direction of broken symmetry in the ordered state.

Nematic order is described by the conventional nematic order parameter or alignment tensor, defined as

$$Q_{ij}(\mathbf{r}, t) = \frac{1}{c(\mathbf{r}, t)} \left\langle \sum_{\alpha=1}^N \left(u_{\alpha i}(t) u_{\alpha j}(t) - \frac{1}{d} \delta_{ij} \right) \delta(\mathbf{r} - \mathbf{r}_{\alpha}(t)) \right\rangle. \quad (9)$$

The subtracted part ensures that the order parameter vanishes in the isotropic state in d dimensions. The alignment tensor Q_{ij} is thus a traceless and symmetric second-order tensor field, with two independent degrees of freedom in $d = 2$. For uniaxial nematics the alignment tensor takes the form

$$Q_{ij} = S(\mathbf{r}, t) \left[n_i(\mathbf{r}, t) n_j(\mathbf{r}, t) - \frac{1}{d} \delta_{ij} \right], \quad (10)$$

where $S(\mathbf{r}, t)$ is the scalar nematic amplitude and $\mathbf{n}(\mathbf{r}, t)$ is the familiar nematic director. The nematic state has orientational order ($S \neq 0$) and it is invariant under inversion of the director, i.e., for $\mathbf{n} \rightarrow -\mathbf{n}$. The polarized state, in contrast, is not invariant for $\mathbf{p} \rightarrow -\mathbf{p}$. In a polarized state the alignment tensor Q_{ij} is slaved to the polarization and acquires a nonzero value, with $\mathbf{n} = \mathbf{p}$.

The dynamical equations for polarization and alignment tensor have the form (for simplicity we give the form for $d = 2$ only)

$$D_t(cP_i) = cF_i(\boldsymbol{\kappa}, \mathbf{P}) - \partial_j J_{ij} - R_i, \quad (11)$$

$$D_t(cQ_{ij}) = cF_{ij}(\boldsymbol{\kappa}, \mathbf{Q}) - \partial_k J_{ijk} - R_{ij}, \quad (12)$$

where $D_t = \partial_t + \mathbf{v} \cdot \nabla$, $\boldsymbol{\kappa}$ is the rate of strain tensor, $\kappa_{ij} = \partial_j v_i$, and

$$\begin{aligned} F_i(\boldsymbol{\kappa}, \mathbf{P}) &= -\omega_{ij} P_j + \lambda_P u_{ij} P_j - \frac{5}{4} u_{kk} P_i, \quad \text{or} \\ \mathbf{F}(\boldsymbol{\kappa}, \mathbf{P}) &= \frac{1}{2} (\nabla \times \mathbf{v}) \times \mathbf{P} + \lambda_P [\nabla \mathbf{v} + (\nabla \mathbf{v})^T] \cdot \mathbf{P} - \frac{5}{4} (\nabla \cdot \mathbf{v}) \mathbf{P}, \end{aligned} \quad (13)$$

$$\begin{aligned}
F_{ij}(\boldsymbol{\kappa}, \mathbf{Q}) = & -(\omega_{ik}Q_{kj} + \omega_{jk}Q_{ki}) + \frac{1}{3}\left(u_{ik}Q_{kj} + u_{jk}Q_{ki} - \delta_{ij}u_{kl}Q_{kl}\right) \\
& - \frac{4}{3}u_{kk}Q_{ij} + \lambda\left(u_{ij} - \frac{1}{2}\delta_{ij}u_{kk}\right). \tag{14}
\end{aligned}$$

Here λ_P and λ are the flow alignment parameters in the polarized and nematic states, respectively, and

$$\omega_{ij} = \frac{1}{2}(\partial_i v_j - \partial_j v_i). \tag{15}$$

The low density derivation based on the Smoluchowski equation described below gives $\lambda_P = 1/2$ and $\lambda = 1/(2S_0)$, with S_0 the magnitude of the nematic order parameter. Since typically in the nematic state even quite far from the I-N transition, $S_0 \ll 1$, we expect $\lambda > 1$, as required for flow alignment. In addition it is well known that deep in the nematic phase, higher order correlations can further increase the value of λ . In the following we will treat both λ_P and λ as unknown parameters. The first terms on the right hand side of Eqs. (11) and (12) generalize the convective derivative on the left hand side of the equation to the case of long, thin rods. These are standard terms in nematohydrodynamics that have been derived from a microscopic model before [58]. Different values for some of the numerical coefficients are reported in the literature, depending on the closure scheme used in evaluating various angular averages. The second and third terms on the right hand side of Eqs. (11) and (12) represent translational and rotational currents, including contributions from diffusion, excluded volume, and both stationary and active cross-linkers. The relaxation of the order parameters is controlled by the rotational currents and is non-hydrodynamic. In contrast, the relaxation of the broken symmetry variables \mathbf{p} and \mathbf{n} is controlled by hydrodynamic Goldstone modes, as appropriate in ordered states.

The long wavelength description of the solution is then given by the five equations (1-3) and (11-12). To close the hydrodynamic equations we must derive the constitutive equations for the fluxes (\mathbf{J} , J_{ij} , J_{ijk}), the rotational currents (R_i and R_{ij}), and the filament contribution to the stress tensor, σ_{ij}^r , as functions of the system's properties (density, filament concentration and order parameters) and of the driving forces (applied mechanical stresses and activity, as measured by the ATP consumption rate). This derivation is carried out below by adapting methods from polymer physics appropriate for a dilute solution of rigid rods. Although the specific expressions obtained by this method for the parameters in the hydrodynamic equations only apply at low concentration of filaments, the structure of the equations is general and remains the same at high density.

4 Derivation of hydrodynamic constitutive equations

Our goal is to derive the constitutive equations for the various hydrodynamic currents and stresses starting from a semi-microscopic model of the dynamics of single filaments coupled pairwise by active and stationary crosslinkers. The filaments are modeled as rigid rods of fixed length l and diameter $b \ll l$ immersed in a viscous solvent. They diffuse independently in the solvent and interact via excluded volume. In addition, filaments can be coupled pairwise by both stationary and active crosslinkers that generate additional active currents. Active crosslinkers are described as rigid

links that can walk along the filaments towards the polar end at a prescribed rate $u(s)$ proportional to the rate of ATP consumption. Generally $u(s)$ varies with the point s of attachment along the filament ($0 \leq s \leq l$). Both active and stationary cross-links also mediate the exchange of torques between the filaments by acting as torsional springs of prescribed stiffness, κ . Our goal is to obtain a coarse-grained description of the system where all the parameters in the hydrodynamic equations are characterized in terms of $u(s)$, κ , and the density of crosslinkers. Collective effects arising from multiple crosslinkers are neglected and the density of crosslinkers is assumed constant for simplicity. We also neglect the dynamics of crosslinkers binding and unbinding which occurs on faster time scales than those of interest here, so that we can treat a constant fraction of them as bound. The dynamics of crosslinkers binding and unbinding was considered for instance in Ref. [44] and it was found that varying the rates of motor binding and unbinding did not affect the nonequilibrium steady states of the active solution. The derivation of the active contributions to the various fluxes has been presented elsewhere [36] and will be summarized here for completeness. We also present novel results on the evaluation of the filament contribution to the stress tensor up to terms of first order in gradients of the hydrodynamic fields.

To proceed, we also make a series of simplifying assumptions on the dynamics of the solution. First, we assume that the friction between filaments and solvent is large and the filaments move at the flow velocity $\mathbf{v} = \mathbf{g}/\rho$ of the solution. In many fluid mixtures internal friction mechanisms are so strong that the flow velocities of the two components relax on microscopic time scales to the common value \mathbf{v} . There are situations, however, where the relaxation time of the relative momenta of the two species is slow enough to have a significant influence even on hydrodynamic time scales. In this case a two-fluid description is appropriate and useful. Such a "two-fluid model" of the system (rods and fluid background) will be described elsewhere, where we will show under which conditions one approaches the one-fluid model (which is always the true hydrodynamic limit).

We also limit ourselves to the case of incompressible solutions, with $\rho = \rho_s + \rho_r =$ constant, which requires

$$\nabla \cdot \mathbf{v} = 0 . \quad (16)$$

Finally, we neglect fluid inertial effect compared to the frictional forces between the colloidal rods and the solvent. In this limit the momentum equation (3) reduces to the Stokes equation

$$\partial_j \sigma_{ij} = -\rho F_i^{\text{ext}} , \quad (17)$$

or, in the absence of external forces,

$$\eta_0 \nabla^2 v_i - \partial_i \Pi_s = -\partial_j \sigma_{ij}^r . \quad (18)$$

Equation (18) shows that the flow velocity of the solution is determined by the stress introduced by the filaments. In turn, the forces that the filaments exert on each other and on the solvent depend on the flow of the suspension in which they are immersed and the problem must be solved self-consistently.

The dynamics of a dilute suspension of rods in the presence of a macroscopic flow field $\mathbf{v}(\mathbf{r})$ can be described by the Smoluchowski equation for the probability distribution $\hat{c}(\mathbf{r}, \hat{\mathbf{u}}, t)$ of rods with center of mass at \mathbf{r} and orientation $\hat{\mathbf{u}}$ at time t . The Smoluchowski equation describes the mean-field Brownian dynamics of extended colloidal particles at low Reynolds number, under the assumption that the particles

velocities have equilibrated on microscopic time scales to a local Maxwell-Boltzmann distribution at a temperature T_a [59, 60]. The effective temperature T_a incorporates nonthermal noise sources as may arise from fluctuations in motor concentration and ATP consumption rate. The Smoluchowski equation is given by

$$\partial_t \hat{c} + \nabla \cdot \mathbf{J}_c + \mathcal{R} \cdot \mathcal{J}_c = 0, \quad (19)$$

where $\mathbf{R} = \hat{\mathbf{u}} \times \partial_{\hat{\mathbf{u}}}$ is the rotation operator. The *translational* probability current, \mathbf{J}_c , and the *rotational* probability current, \mathcal{J}_c , are given by

$$J_{ci} = \hat{c}v_i - D_{ij}\nabla_j\hat{c} - \frac{D_{ij}}{k_B T_a}\hat{c}\nabla_j U_{\text{ex}} + J_{ci}^A, \quad (20)$$

$$\mathcal{J}_{ci} = \hat{c}\omega_i - D_r\mathcal{R}_i\hat{c} - \frac{D_r}{k_B T_a}\hat{c}\mathcal{R}_i U_{\text{ex}} + \mathcal{J}_{ci}^A, \quad (21)$$

where $\omega_i = \epsilon_{ijk}\hat{u}_j\hat{u}_l\partial_l v_k$. Also $D_{ij} = D_{\parallel}\hat{u}_i\hat{u}_j + D_{\perp}(\delta_{ij} - \hat{u}_i\hat{u}_j)$ is the translational diffusion tensor and D_r is the rotational diffusion rate. For a low-density solution of long, thin rods $D_{\perp} = D_{\parallel}/2 \equiv D/2$, where $D = k_B T_a \ln(l/b)/(2\pi\eta_0 l)$, and $D_r = 6D/l^2$. The potential U_{ex} incorporates excluded volume effects which give rise to the nematic transition in a solution of hard rods. It can be written by generalizing the Onsager interaction to inhomogeneous systems as $k_B T_a$ times the probability of finding another rod within the interaction area of a given rod. In two dimensions this gives

$$U_{\text{ex}}(\mathbf{r}_1, \hat{\mathbf{u}}_1) = k_B T_a \int d\hat{\mathbf{u}}_2 \int_{s_1 s_2} |\hat{\mathbf{u}}_1 \times \hat{\mathbf{u}}_2| \hat{c}(\mathbf{r}_1 + \boldsymbol{\xi}, \hat{\mathbf{u}}_2, t), \quad (22)$$

where s_i , with $-l/2 \leq s_i \leq l/2$, parameterizes the position along the length of the i -th filament, for $i = 1, 2$, and $\int_{s_i} \dots \equiv \int_{-l/2}^{l/2} ds_i \dots \equiv \langle \dots \rangle_{s_i}$. The filaments are constrained to be within each other's interaction volume, i.e., in the thin rod limit $b \ll l$ considered here, have a point of contact. The factor $|\hat{\mathbf{u}}_1 \times \hat{\mathbf{u}}_2|$ represents the excluded area of two thin filaments of orientation $\hat{\mathbf{u}}_1$ and $\hat{\mathbf{u}}_2$ touching at one point [61]. Finally, $\boldsymbol{\xi} = \mathbf{r}_2 - \mathbf{r}_1 \simeq \hat{\mathbf{u}}_1 s_1 - \hat{\mathbf{u}}_2 s_2$, is the separation of the centers of mass of the two rods. The translational and rotational active current of filaments with center of mass at \mathbf{r}_1 and orientation along $\hat{\mathbf{u}}_1$ are written as

$$\mathbf{J}_c^A(\mathbf{r}_1, \hat{\mathbf{u}}_1) = \hat{c}(\mathbf{r}_1, \hat{\mathbf{u}}_1, t) b^2 m \int_{\hat{\mathbf{u}}_2} \int_{s_1 s_2} \mathbf{v}_a(1; 2) \hat{c}(\mathbf{r}_1 + \boldsymbol{\xi}, \hat{\mathbf{u}}_2, t), \quad (23)$$

$$\mathcal{J}_c^A(\mathbf{r}_1, \hat{\mathbf{u}}_1) = \hat{c}(\mathbf{r}_1, \hat{\mathbf{u}}_1, t) b^2 m \int_{\hat{\mathbf{u}}_2} \int_{s_1 s_2} \boldsymbol{\omega}_a(1; 2) \hat{c}(\mathbf{r}_1 + \boldsymbol{\xi}, \hat{\mathbf{u}}_2, t), \quad (24)$$

where m is the density of bound crosslinkers and $(1; 2) = (s_1, \hat{\mathbf{u}}_1; s_2, \hat{\mathbf{u}}_2)$. Finally, $\mathbf{v}_a(1; 2)$ and $\boldsymbol{\omega}_a(1; 2)$ are the translational and rotational velocities, respectively, that filament 1 acquires due to the crosslinker-mediated interaction with filament 2, when the centers of mass of the two filaments are separated by $\boldsymbol{\xi}$ (see Fig. 1).

The derivation of the form of the active velocities in terms of motor parameters (the stepping rate $u(s)$ and the torsional stiffness κ) has been discussed in detail elsewhere [56, 36]. The angular velocity is

$$\boldsymbol{\omega}_a = 2[\gamma_P + \gamma_{NP}(\hat{\mathbf{u}}_1 \cdot \hat{\mathbf{u}}_2)](\hat{\mathbf{u}}_1 \times \hat{\mathbf{u}}_2), \quad (25)$$

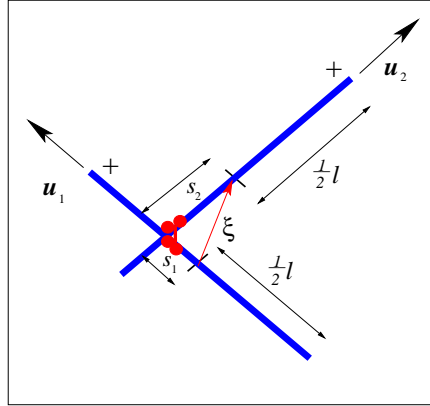


Fig. 1. The geometry of overlap between two interacting filaments of length l cross-linked by an active cluster. The cross-link is a distance s_1 , (s_2) from the center of mass of filament 1(2). The distance between centers is $\xi = \mathbf{r}_2 - \mathbf{r}_1 = s_1 \hat{\mathbf{n}}_1 - s_2 \hat{\mathbf{n}}_2$.

with γ_P and γ_{NP} motor-induced rotation rates due to polar and nonpolar crosslinkers, respectively (see Fig. 2). The motor-induced translational velocity has the form $\mathbf{v}_a(1; 2) = \frac{1}{2} \mathbf{v}_r + \mathbf{V}_m$, with [36]

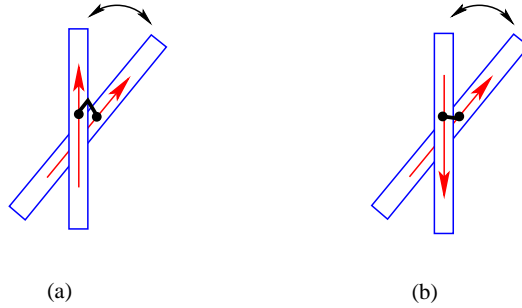


Fig. 2. Polar and nonpolar clusters interacting with polar filaments. Assuming that clusters always bind to the smallest angle, polar clusters bind only to filaments in configuration (a) while non-polar clusters bind to both configurations equally.

$$\mathbf{v}_r = \frac{\tilde{\beta}}{2} (\hat{\mathbf{u}}_2 - \hat{\mathbf{u}}_1) + \frac{\tilde{\alpha}}{2l} \xi ,$$

$$\mathbf{V}_m = A (\hat{\mathbf{u}}_2 + \hat{\mathbf{u}}_1) + B (\hat{\mathbf{u}}_2 - \hat{\mathbf{u}}_1) ,$$

where $\tilde{\alpha} = \alpha(1 + \hat{\mathbf{u}}_1 \cdot \hat{\mathbf{u}}_2)$ and $\tilde{\beta} = \beta(1 + \hat{\mathbf{u}}_1 \cdot \hat{\mathbf{u}}_2)$. The expressions for A and B have been obtained in [36] using momentum conservation. For long thin rods with $\zeta_{\perp} = 2\zeta_{\parallel} \equiv 2\zeta$, to leading order in $\hat{\mathbf{u}}_1 \cdot \hat{\mathbf{u}}_2$, we find $A = -[\beta - \alpha(s_1 + s_2)/2]/12$ and $B = \alpha(s_1 - s_2)/24$.

The rotational rates, γ_P and γ_{NP} , and the active velocities α and β can be related to the torsional stiffness κ of the crosslinkers and to the rate $u(s)$ at which a motor cluster attached at position s steps along a filament towards the polar end. This rate will in general depend on the point of attachment s , due for instance to crowding or stalling of motors near the polar end. The mean (averaged along the filament) stepping rate $u_0 = \langle u(s) \rangle / l$ is simply proportional to the mean rate R_{ATP} of ATP consumption via a the characteristic step length, which we take of order of the thickness b of the filaments, $u_0 \sim bR_{ATP}$. We emphasize, however, that in general the stepping rate $u(s)$ (and other active parameters) may be a *non-linear* and possibly even non-monotonic function of the rate of ATP consumption, R_{ATP} .

In our model there are three coupled mechanisms for crosslinker-induced filament dynamics, described by the parameters α , β and the rotational rates, γ_P and γ_{NP} . The first is the bundling of filament of similar polarity at a rate α given by [56]

$$\alpha = \int_{-l/2}^{l/2} \frac{ds}{l} \frac{s}{l} u(s) \approx u_0(b/l), \quad (26)$$

where the last approximate equality applies in situations where $u(s)$ exhibits strong spatial variations on length scales of order b , as may arise for instance from motor stalling at the polar end [56]. It is apparent from Eq. (26) that $\alpha = 0$ if $u(s)$ is constant. Bundling is driven by the contractile nature of motor clusters and in our mean field model requires spatial inhomogeneities in the rate at which motors step along the filaments. As we will see below, it tends to build up density inhomogeneities and is the main pattern-forming mechanism. The second mechanism of motor-induced dynamics will be referred to as "polarization sorting", although in general it involves coupled filament rotation and spatial separation of filaments of different polarity. It occurs at the rate

$$\beta = \int_{-l/2}^{l/2} \frac{ds}{l} u(s) = u_0, \quad (27)$$

and vanishes for aligned filaments. This mechanisms is especially important in the polar state where it allows for terms in the hydrodynamic equations corresponding to convection of filaments along the direction of mean polarization and it provides the mechanism for the transition to a state with spontaneous flow [47]. Finally, motor-induced filament rotations occur at rates γ_P and γ_{NP} for crosslinkers that preferentially bind to filaments of the same orientation (γ_P) or regardless of their orientation (γ_{NP}). As discussed in Ref. [36], we estimate

$$\gamma_P \sim \gamma_{NP} \sim \frac{\kappa}{\zeta_r}, \quad (28)$$

with $\zeta_r = k_B T_a / D_r$ a rotational friction. In general both active and stationary crosslinkers may induce rotation and be either polar or apolar in nature. In the following we will restrict ourselves for simplicity to the case where all polar crosslinkers are active motor clusters (of density m_a), while all apolar crosslinkers are stationary (of density m_s). In practice we do expect this to be often the case. The rotational rate γ_P will then depend on ATP consumption, with $\gamma_P \sim R_{ATP}$, while we expect γ_{NP} to be essentially independent of it. As mentioned above, the various active parameters may be non-linear and even non-monotonic functions of R_{ATP} . However, these effects will not be considered here.

From the Smoluchowski equation, Eq. (19), we obtain the hydrodynamic equations for filament concentration, polarization and alignment tensor by truncating the exact moment expansion of $\hat{c}(\mathbf{r}, \hat{\mathbf{u}}, t)$ as

$$\hat{c}(\mathbf{r}, \hat{\mathbf{u}}, t) = \frac{c(\mathbf{r}, t)}{2\pi} \left\{ 1 + 2\mathbf{P}(\mathbf{r}, t) \cdot \hat{\mathbf{u}} + 4Q_{ij}(\mathbf{r}, t)\hat{Q}_{ij}(\hat{\mathbf{u}}) + \dots \right\}, \quad (29)$$

with $\hat{Q}_{ij}(\hat{\mathbf{u}}) = \hat{u}_i\hat{u}_j - \frac{1}{2}\delta_{ij}$ and keeping only the first three moments,

$$\begin{aligned} \int d\hat{\mathbf{u}} \hat{c}(\mathbf{r}, \hat{\mathbf{u}}, t) &= c(\mathbf{r}, t) \quad (\text{density}), \\ \int d\hat{\mathbf{u}} \hat{\mathbf{u}} \hat{c}(\mathbf{r}, \hat{\mathbf{u}}, t) &= c(\mathbf{r}, t)\mathbf{P}(\mathbf{r}, t) \quad (\text{polarization}), \\ \int d\hat{\mathbf{u}} \hat{Q}_{ij}(\hat{\mathbf{u}}) \hat{c}(\mathbf{r}, \hat{\mathbf{u}}, t) &= c(\mathbf{r}, t)Q_{ij}(\mathbf{r}, t) \quad (\text{nematic order}). \end{aligned} \quad (30)$$

The details of the calculation, which involves using a small gradient expansion for the filament probability distribution and evaluating angular averages, are given in [36], where the full expression for the various fluxes and rotational currents are also displayed. The resulting hydrodynamic equations in the isotropic and ordered phases will be given below.

5 Stress tensor of an active solution

In this section we derive the constitutive equation for the filament contribution to the stress tensor of an active suspension of polar filaments. An important difference as compared to passive solutions is that in active systems stresses can be induced not just by externally applied mechanical deformations (yielding $\kappa_{ij} \neq 0$), but also by motor activity which maintains the system out of equilibrium by supplying energy at a rate R_{ATP} .

In the limit where inertial effects may be ignored (low Reynolds number) and in the absence of external forces, momentum conservation is described by Eq. (18), with $\nabla \cdot \mathbf{v} = 0$. Using standard methods from polymer physics, the filament contribution to the divergence of the stress tensor of a dilute suspension of hard, thin rods can be written as

$$\nabla \cdot \boldsymbol{\sigma}^r = - \int_{\boldsymbol{\xi}} \int_{\hat{\mathbf{u}}} \hat{c}(\mathbf{r} - \boldsymbol{\xi}, \hat{\mathbf{u}}, t) \left\langle \delta(\boldsymbol{\xi} - s\hat{\mathbf{u}}) \mathcal{F}^h(s) \right\rangle_s, \quad (31)$$

where $\mathcal{F}^h(s)$ is the hydrodynamic force per unit length exerted by the suspension on a rod at position s along the rod. It arises from interactions with other filaments and proteins and with solvent molecules. It depends implicitly upon direct interactions between the rods, as well as on hydrodynamic interactions mediated by the solvent.

The hydrodynamic force density on a rigid rod suspended in a viscous solvent can be expressed in terms of the force and torque at its center of mass. A sketch of the derivation is given in Appendix A. Further details of similar calculations can be found in [61, 62]. We find that the stress due to the filaments can be written in the form (to $\mathcal{O}(\nabla^2)$)

$$\begin{aligned} \nabla \cdot \boldsymbol{\sigma}^r(\mathbf{r}, t) &= \int_{\hat{\mathbf{u}}} \hat{c}(\mathbf{r}, \hat{\mathbf{u}}, t) \mathbf{F}^h(\mathbf{r}, \hat{\mathbf{u}}, t) \\ &\quad - \int_{\hat{\mathbf{u}}} \left\langle \left(\frac{s}{l} \right)^2 \left(\frac{\hat{\mathbf{u}} \cdot \nabla}{l} \right) \hat{c}(\mathbf{r}, \hat{\mathbf{u}}, t) \boldsymbol{\tau}^h(\mathbf{r}, \hat{\mathbf{u}}, t) \right\rangle_s . \end{aligned} \quad (32)$$

In the absence of inertial effects, the *total* hydrodynamic force, $\mathbf{F}^h(\mathbf{r}, \hat{\mathbf{u}}, t)$, exerted by the suspension *on the center of mass* of a rod can be found from the condition that all forces acting on the rod must balance. The solvent flow field on a given segment of a rod is calculated using a decoupling approximation where the hydrodynamic coupling to other segments of the same rod are treated explicitly within the Oseen approximation, while the hydrodynamic effects of other rods enter in the determination of a self-consistent value for the flow velocity of the solvent, yielding,

$$\mathbf{F}^h(\mathbf{r}, \hat{\mathbf{u}}, t) = k_B T_a \nabla \ln \hat{c} + \nabla U_{\text{ex}} - \mathbf{F}_a , \quad (33)$$

where $-k_B T_a \nabla \ln \hat{c}$ is the Brownian force, $-\nabla U_{\text{ex}}$ is the force due to the direct interaction of the rod with other rods (in this case, via excluded volume) and \mathbf{F}_a is the active force that can be written as

$$F_{ai} = \zeta_{ij}(\hat{\mathbf{u}}) J_{ci}^A / \hat{c} . \quad (34)$$

The rod friction tensor $\zeta_{ij}(\hat{\mathbf{u}})$ is proportional to the inverse of the rod diffusion tensor $D_{ij}(\hat{\mathbf{u}})$, with

$$\begin{aligned} \zeta_{ij}(\hat{\mathbf{u}}) &= k_B T_a [\mathbf{D}^{-1}(\hat{\mathbf{u}})]_{ij} \\ &= \zeta_{\parallel} \hat{u}_i \hat{u}_j + \zeta_{\perp} (\delta_{ij} - \hat{u}_i \hat{u}_j) , \end{aligned} \quad (35)$$

with $\zeta_{\parallel} = 2\pi\eta_0 l / \ln(l/b)$ and $\zeta_{\perp} = 2\zeta_{\parallel}$. Similarly the total hydrodynamic torque is given by

$$\begin{aligned} \boldsymbol{\tau}^h(\mathbf{r}, \hat{\mathbf{u}}, t) &= [k_B T_a \mathcal{R} \ln c + \mathcal{R} U_x - \boldsymbol{\tau}_a] \times \hat{\mathbf{u}} \\ &\quad - \frac{\zeta_{\perp}}{2} \hat{\mathbf{u}} \hat{\mathbf{u}} (\hat{\mathbf{u}} \cdot \nabla) \cdot \mathbf{v}(\mathbf{r}) , \end{aligned} \quad (36)$$

with $\boldsymbol{\tau}_a = \zeta_r \mathcal{J}_c^A / \hat{c}$ the active torque. The last term on the right hand side of Eq. (36) is a viscous contribution to the stress proportional to the velocity gradient.

The rod contribution to the stress tensor can now be evaluated explicitly using the truncated moment expansion for $\hat{c}(\mathbf{r}, \hat{\mathbf{u}}, t)$ given in Eq. (29). When evaluating the active contributions to the stress tensor, only terms up to first order in $\hat{\mathbf{u}}_1 \cdot \hat{\mathbf{u}}_2$ are retained in the active force $\boldsymbol{\zeta}(\hat{\mathbf{u}}_1) \cdot \mathbf{v}_a(1;2)$ exerted by a motor cluster on the filament. This approximation only affects the numerical values of the coefficients in the stress tensor, not its general form.

For simplicity, we consider solutions in the presence of a constant velocity gradient, κ_{ij} , and with a uniform mean rate of ATP consumption. We allow for spatial inhomogeneities in the filament concentration and orientational order parameters and evaluate the stress tensor up to first order in gradients of these hydrodynamic fields. The deviatoric part $\tilde{\sigma}_{ij} = \sigma_{ij} - (1/2)\delta_{ij}\sigma_{kk}$ of the stress tensor of the filaments is

$$\tilde{\sigma}_{ij}^r(\mathbf{r}, t) = \tilde{\sigma}_{ij}^A(\mathbf{r}, t) + \tilde{\sigma}_{ij}^v(\mathbf{r}, t) , \quad (37)$$

with

$$\begin{aligned}
\bar{\sigma}_{ij}^A &= 2k_B T_a c \left(1 - \frac{c}{c_{IN}}\right) Q_{ij} - k_B T_a \frac{c^2}{c_{IP}} \left(P_i P_j - \frac{1}{2} \delta_{ij} P^2\right) \\
&+ m_a b^2 \alpha \frac{k_B T_a l^3}{72D} c^2 \left(\frac{4}{3} Q_{ij} + P_i P_j - \frac{1}{2} \delta_{ij} P^2\right) \\
&+ m_a b^2 \beta \frac{k_B T_a l^4}{216D} c^2 \left[\partial_j P_i - \frac{1}{2} \delta_{ij} \nabla \cdot \mathbf{P} - \frac{1}{4} (\partial_i P_j - \partial_j P_i)\right], \quad (38)
\end{aligned}$$

where $c_{IP} = D_r / (m_a b^2 \gamma_P l^2)$, and $c_{IN} = c_N / [1 + c_N l^2 m_s b^2 \gamma_{NP} / (4D_r)]$ are the densities for the isotropic-polarized (IP) and isotropic-nematic (IN) transition, respectively, at finite density of active polar motor clusters (m_a) and stationary nonpolar crosslinkers (m_s) [36]. Finally, $c_N = 3\pi / (2l^2)$ is the density of the IN transition in passive systems. There are three types of contributions to the active part of the stress tensor. The first consists of the first two terms on the right hand side of Eq. (38). These are equilibrium-like terms, in the sense that they have the same structure one would obtain in a nematic and polar passive fluid, respectively, with the transition densities replaced by their active values. In particular, the first term on the right hand side of Eq. (38) should be compared to the corresponding contribution for isotropic ($c < c_N$) passive solutions, $\bar{\sigma}_{ij}^P = 2k_B T c \left(1 - \frac{c}{c_N}\right) Q_{ij}$. The third term is a homogeneous nonequilibrium contribution that remains nonzero even for $\kappa_{ij} = 0$. This "spontaneous stress" arises from activity and is proportional to the ATP consumption rate that acts as an additional driving force and can build up stresses even in the absence of mechanical deformations. This term is generated by motor-induced filament bundling and it is proportional to the bundling rate, α . It would therefore vanish in the absence of spatial inhomogeneities in the motor stepping rate. Finally, the fourth term contains active contributions proportional to gradients of the polarization (we have omitted here terms of linear order in the gradients containing both polarization and alignment tensor. The full expression for the stress tensor can be found in Appendix A). These stresses are generated by motor-induced filament sorting and are proportional to β . They are important only in the polarized phase, where we expect they will play an important role in enhancing the relaxation of longitudinal fluctuations of the filaments and the corresponding relaxation of shear via reptation.

Finally, the viscous contribution to the stress is

$$\begin{aligned}
\bar{\sigma}_{ij}^v &= \frac{l c \zeta_{\perp}}{48} \left[\frac{1}{2} (u_{ij} - \frac{1}{2} \kappa_{kk} \delta_{ij}) + \frac{1}{3} (Q_{ij} \kappa_{kk} - \delta_{ij} \kappa_{kq} Q_{qk}) \right. \\
&\quad \left. + \frac{2}{3} (u_{ik} Q_{kj} + u_{jk} Q_{ki}) \right], \quad (39)
\end{aligned}$$

6 Homogeneous states of a quiescent solution

We first examine the case of a quiescent suspension, with $\mathbf{v} = 0$. We consider a system with a concentration m_a of active, polar motor clusters and a concentration m_s of stationary nonpolar crosslinkers. For convenience we define a dimensionless parameter μ_a measuring activity as

$$\mu_a = m_a b^2 \frac{\gamma_P}{D_r} \sim m_a R_{ATP}, \quad (40)$$

where D_r is the rods' rotational diffusion constant and we have assumed that $\gamma_P \sim R_{ATP}$. We also introduce a dimensionless parameter μ_s measuring the effect of stationary crosslinkers as

$$\mu_s = m_s b^2 \frac{\gamma_{NP}}{D_r}, \quad (41)$$

and assume that μ_s is essentially independent of the ATP consumption rate. The bulk states of the system are determined by the solution of the homogeneous hydrodynamic equations containing only those terms that are of zeroth order in the gradients. This is the most coarse-grained description of the system. More detailed descriptions that incorporate slowly varying spatial variations can then be developed by including gradient terms in the hydrodynamics. The possible homogeneous states of the system are obtained as the stationary solution of the homogeneous hydrodynamic equations for filament concentration, polarization and alignment tensor, setting all gradient terms equal to zero. In this case the filament concentration is constant, $c = c_0$, and only contributions from rotational currents survive in equation for the polarization and the alignment tensor, which are given by

$$\partial_t P_i = -D_r [1 - \mu_a c_0] P_i + D_r [4c_0/c_N + (\mu_s - 2\mu_a)c_0] Q_{ij} P_j, \quad (42)$$

$$\partial_t Q_{ij} = -D_r [4(1 - c_0/c_N) - \mu_s c_0] Q_{ij} + 2D_r \mu_a c_0 \left(P_i P_j - \frac{1}{2} \delta_{ij} P^2 \right), \quad (43)$$

where all filament densities are measured in units of l^2 , and $c_N = 3\pi/2$.

There are three possible homogeneous stationary states for the system, obtained by solving Eqs. (42) and (43) with $\partial_t P_i = 0$ and $\partial_t Q_{ij} = 0$. These are:

$$\begin{aligned} \text{isotropic state (I):} & \quad P_i = 0 \quad Q_{ij} = 0, \\ \text{nematic state (N):} & \quad P_i = 0 \quad Q_{ij} \neq 0, \\ \text{polarized state (P):} & \quad P_i \neq 0 \quad Q_{ij} \neq 0. \end{aligned}$$

At low density the only solution is $P_i = 0$ and $Q_{ij} = 0$ and the system is isotropic (I). The homogeneous isotropic state can become unstable at high filament and/or motor density, as described below.

To discuss the instabilities it is convenient to measure time in units of D_r^{-1} and rewrite Eqs. (42) and (43) in a more compact form as

$$\partial_t P_i = -a_1 P_i + b_1 c_0 Q_{ij} P_j, \quad (44)$$

$$\partial_t Q_{ij} = -a_2 Q_{ij} + b_2 c_0 \left(P_i P_j - \frac{1}{2} \delta_{ij} P^2 \right). \quad (45)$$

The coefficients a_1 , b_1 , a_2 , and b_2 are given by

$$a_1 = 1 - \mu_a c_0, \quad (46)$$

$$a_2 = 4 [1 - c_0/c_N - \mu_s c_0/4], \quad (47)$$

$$b_1 = 4/c_N + \mu_s - 2\mu_a, \quad (48)$$

$$b_2 = 2\mu_a. \quad (49)$$

In the absence of crosslinkers ($\mu_s = \mu_a = 0$), no homogeneous polarized state with a nonzero mean value of \mathbf{P} is obtained. There is, however, a transition at the

density $c_N = 3\pi/2$ from an isotropic state with $Q_{ij} = 0$ for $c_0 < c_N$ to a nematic state with $Q_{ij} = S_0(n_i n_j - \frac{1}{2}\delta_{ij})$, with \mathbf{n} a unit vector along the direction of broken symmetry, for $c_0 > c_N$. The transition is identified with the change in sign of the coefficient a_2 of Q_{ij} on the right hand side of Eq. (45). A negative value of a_2 that controls the decay rate of Q_{ij} signals an instability of the isotropic homogeneous state. A mean-field description of such a transition, which is continuous in 2d (but first order in 3d), requires that one incorporates cubic terms in Q_{ij} in the equation for the alignment tensor. Adding a term $-a_4 c_0^2 Q_{kl} Q_{kl} Q_{ij}$ to Eq. (45) we obtain $S_0 = \frac{1}{c_0} \sqrt{-2a_2/a_4} = \frac{1}{c_0} \sqrt{-8(1 - c_0/c_N)/a_4}$.

If $\mu_a = 0$, but $\mu_s \neq 0$, there is again no stable polarized state. The presence of a concentration of nonpolar crosslinkers does, however, renormalize the isotropic-nematic (IN) transition, which occurs at a lower filament density given by

$$c_{IN} = \frac{c_N}{1 + \mu_s c_N/4}. \quad (50)$$

The presence on nonpolar crosslinks favors filament alignment and shifts c_{IN} downward. It should be noted that this occurs even with a higher effective temperature T_a . A qualitatively similar result has been obtained in numerical simulation of a two-dimensional system of rigid filaments interacting with motor proteins grafted to a substrate [64]. The amount of nematic order S_0 is also enhanced by the crosslinkers, with $S_0 = \sqrt{-2a_2/a_4 c_0^2} = \sqrt{\frac{8}{a_4 c_0^2} (c_0/c_{IN} - 1)}$.

If μ_a is finite, the system can order in both polarized and nematic homogeneous states. The homogeneous isotropic state can become unstable in two ways. As in the case $\mu_a = 0$, a change in sign of the coefficient a_2 signals the transition to a nematic (N) state at the density c_{IN} given in Eq. (50). In addition, the isotropic state can become linearly unstable via the growth of polarization fluctuations in any arbitrary direction. This occurs above a second critical filament density,

$$c_{IP} = \frac{1}{\mu_a}, \quad (51)$$

defined by the change in sign of the coefficient a_1 controlling the decay of polarization fluctuations in Eq. (44). For $c_0 > c_{IP}$ the homogeneous state is polarized (P), with $\mathbf{P} \neq 0$. The alignment tensor also has a nonzero mean value in the polarized state as it is slaved to the polarization. The location of the boundaries between the various homogeneous states is controlled by the relative strength and concentration of active polar motor clusters to stationary nonpolar crosslinkers. In order to simplify the discussion we fix the value of μ_s that determined the density of the nematic-isotropic transition to $\mu_s = 0$, so that the isotropic-nematic transition takes place at the density c_N of a suspension of rods with no crosslinkers. One can identify two regimes.

I) If $c_{IP} > c_N$, which corresponds to $\mu_a < 1/c_N$, a region of nematic phase exists between the isotropic and the polar state. At sufficiently high filament and motor densities, the nematic state becomes unstable. To see this, we linearize Eqs. (44) and (45) by letting $Q_{ij} = Q_{ij}^0 + \delta Q_{ij}$ and $\delta P_i = P_i$. Fluctuations in the alignment tensor are uniformly stable for $a_2 < 0$, but polarization fluctuations along the direction of broken symmetry become unstable for $a_1 \leq c_0 b_1 S_0/2$, i.e., above a critical density

$$c_{NIP} = \frac{1}{\mu_a} \left[1 + \frac{b_1^2}{a_4 R} \left(1 - \sqrt{1 + \frac{2a_4 R(1-R)}{b_1^2}} \right) \right] \quad (52)$$

where $R = c_N/c_{IP}$. The polarized state at $c_0 > c_{NP}$ has

$$P_i^0 = P_0 p_i, \quad (53)$$

$$Q_{ij}^0 = S_P(p_i p_j - \delta_{ij}/2), \quad (54)$$

with \mathbf{p} a unit vector in the direction of broken symmetry and

$$P_0^2 = \frac{2a_1 a_2}{c_0^2 b_1 b_2} \left[1 - \left(\frac{2a_1}{b_1 c_0 S_0} \right)^2 \right], \quad (55)$$

$$S_P = S_0 \sqrt{1 - \frac{c_0^2 b_1 b_2}{2a_1 a_2} P_0^2} = 2 \left| \frac{a_1}{c_0 b_1} \right|. \quad (56)$$

II) For $\mu_a > 1/c_N$, $c_{IP} > c_N$ and the polarity of motor clusters renders the nematic state unstable at all densities and the system goes directly from the I to the P state at c_{IP} , without an intervening N state. The phase diagram has the topology shown in Fig. 3. At the onset of the polarized state the alignment tensor is again slaved to the polarization field, $Q_{ij} = \frac{b_2}{a_2} c_0 (P_i P_j - \frac{1}{2} \delta_{ij} P^2)$, and $\mathbf{P} = P_0 \mathbf{p}$. The value of P_0 is determined by cubic terms in Eq. (44) not included here.

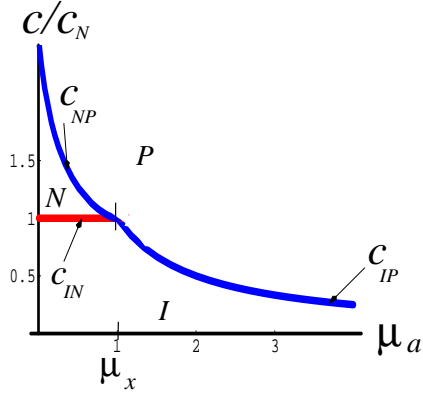


Fig. 3. (color online) The phase diagram for $\mu_s = 0$. For $\mu_a > 1/c_N$, where c_{IN} and c_{IP} intersect, no N state exists and the system goes directly from the I to the P state ($\gamma_P/D_r = 1$ and $a_4 = 50$).

For a fixed, but nonzero value of μ_s , the phase diagram has the same topology as shown in Fig. 3, but with c_N replaced by c_{IN} given in Eq. (50). The value of μ_a where the three phases coexist is shifted to a larger value, given by $\mu_a = (1 + \mu_s c_N/4)/c_N$.

Estimates of the various parameters can be obtained using a microscopic model of the motor-filament interaction of the type described in Appendix A. Using parameter values appropriate for kinesin ($\kappa \sim 10^{-22}$ nm/rad [65]) we estimate $\gamma_P \sim \gamma_{NP} \sim \kappa/\zeta_r = \kappa D_r/(k_B T_a) \sim 10^{-1}$ sec $^{-1}$, where we used the value $D_r \sim 10^{-2}$ sec $^{-1}$ appropriate for long thin rods in an aqueous solution [66] and $T_a \sim 300$ K. Using $m_a = m_s \equiv m$, $\gamma_P = \gamma_{NP}$, $l \sim 10 \mu\text{m}$, $b \sim 10$ nm, the value of m above which no nematic state exist is found to correspond to a three-dimensional crosslinker density

of about $0.5 - 1\mu\text{M}$ and a sample thickness of order $1\mu\text{m}$. This value is of order of the motor densities used in experiments on purified microtubule-kinesin mixtures such as those of Ref. [17], suggesting that the filament solution in this experiments is always in the region where the present mean field model predicts a uniform polarized state.

On the other hand, *in vitro* experiments generally fail to observe states with uniform polarization and report the formation of complex spatial structures. This can be understood in the context of the hydrodynamic theory described here by examining the dynamics of spatially varying fluctuations of the hydrodynamic fields from their uniform value in each state. It has been shown elsewhere that such fluctuations become unstable in a wide range of parameters. In both isotropic and ordered states the instability arises from filament bundling (controlled by the rate α) that tends to build up density inhomogeneities, eventually overtaking diffusion and driving the formation of spatially inhomogeneous structures. This instability is described in the next section for the isotropic state. The instability of the nematic and polarized state is driven by the same physical mechanisms, although the details are more subtle as in this case one must consider the coupled dynamics of fluctuations in the concentration and in the orientational order parameter. A complete description can be found in Ref. [36].

7 Hydrodynamics of flowing active suspensions

In this section we display the explicit form of the hydrodynamic equations for a suspension of active rods obtained by coarse-graining the Smoluchowski equation, as outlined in Sections 4 and 5. Phenomenological forms of these equations have already been used by other authors to study the interplay of order and flow in active systems in specific geometries [47, 52, 51]. Our work provides a derivation of the continuum theory starting from the dynamics of single filaments coupled by active crosslinkers and an estimate of the various parameters in the equations in terms of experimentally accessible quantities. As discussed in Section 4, we limit ourselves to the case of an incompressible suspension and neglect inertial fluid effects. In this case the flow velocity \mathbf{v} of the suspension is determined from the solution of Stokes' equation,

$$\eta_0 \nabla^2 \mathbf{v} - \nabla \Pi(c, \mathbf{P}, \mathbf{Q}; \boldsymbol{\kappa}, \mu) = -\nabla \cdot \tilde{\boldsymbol{\sigma}}^r(c, \mathbf{P}, \mathbf{Q}; \boldsymbol{\kappa}, \mu);, \quad (57)$$

with the incompressibility condition

$$\nabla \cdot \mathbf{v} = 0. \quad (58)$$

The pressure Π is the sum of solvent and filament contributions, $\Pi = \Pi_s(\rho) + \Pi_r$, and we have introduced the deviatoric stress tensor defined by subtracting out the hydrostatic pressure, $\Pi_r = (1/d)\sigma_{kk}^r$, as

$$\tilde{\sigma}_{ij}^r = \sigma_{ij}^r - \delta_{ij} \Pi_r. \quad (59)$$

Both isotropic and ordered (polarized and nematic) suspensions will be considered. The orientational order of the suspension affects the flow through the dependence of the pressure Π and the rods' contributions to the stress tensor $\tilde{\boldsymbol{\sigma}}^r$ on polarization and alignment tensor. The derivation of the constitutive equations for these quantities was described in Section 5.

7.1 Isotropic state

In an isotropic suspension the only hydrodynamic variable describing the filaments is the concentration, c . Its dynamics is governed by a nonlinear convection-diffusion equation

$$\partial_t c + \nabla \cdot (\mathbf{v}c) = \nabla \cdot \mathcal{D}(c)\nabla c, \quad (60)$$

where $\mathcal{D}(c)$ is an effective (concentration-dependent) diffusion coefficient, softened by active processes. It is given by

$$\mathcal{D}(c) = \frac{3D}{4}(1 + v_0c) - \alpha\tilde{m}_a c, \quad (61)$$

with $\tilde{m}_a = m_a b^2$. The first term on the right hand side of Eq. (61) is the diffusion coefficient of long thin rods, with $D = D_{\parallel} = 2D_{\perp}$, including excluded volume corrections, with $v_0 = 2l^2/\pi$. The second term on the right hand side of Eq. (61) arises from filament bundling driven at the rate α given in Eq. (26) and promotes density inhomogeneities. Equation (60) for the concentration couples to the Stokes equation, Eq. (57), with

$$\Pi_r^I(c, \mu) = k_B T_a c \left(1 + \frac{2c}{\pi}\right) + \tilde{m}_a \alpha \frac{5k_B T_a}{432D} c^2, \quad (62)$$

and

$$\tilde{\sigma}_{ij}^{r,I} = \left(2\eta_0 + \frac{k_B T_a}{96D} c\right) u_{ij}. \quad (63)$$

In an isotropic active suspension there are no active contributions to the deviatoric part of the stress tensor, which has the form usual for passive rods [61]. There is, however, an active contribution to the pressure corresponding to the second term on the right hand side of Eq. (62). The first term on the right hand side of Eq. (62) is standard for passive rods.

The homogeneous isotropic state in a quiescent suspension is characterized by $\mathbf{v} = 0$ and $c = c_0$. As discussed in the literature [30, 33, 36], the homogeneous state becomes unstable at high filament and motor concentration due to contractile effects generated by motor-induced filament bundling. Bundling is the main mechanism responsible for the instability of both isotropic and ordered homogeneous states in quiescent suspensions. It is therefore instructive to display explicitly the details of this instability for the simple isotropic case. To examine the dynamics of fluctuations in the isotropic state we let $c = c_0 + \delta c$ and $\mathbf{v} = \delta \mathbf{v}$ in Eq. (60) and only keep terms of first order in the fluctuations. Incompressibility requires $\nabla \cdot \delta \mathbf{v} = 0$ and the linearized equation for δc is simply

$$\partial_t \delta c = \mathcal{D}(c_0)\nabla^2 \delta c. \quad (64)$$

Expanding δc in Fourier components, $\delta c(\mathbf{r}, t) = \sum_{\mathbf{k}} c_{\mathbf{k}}(t)e^{i\mathbf{k}\cdot\mathbf{r}}$, one finds immediately that the relaxation of the Fourier amplitudes, $c_{\mathbf{k}}(t) = c_{\mathbf{k}}e^{-z_c(k)t}$, is controlled by a diffusive mode

$$z_c(k) = \mathcal{D}(c_0)k^2. \quad (65)$$

Density fluctuations become unstable when $z_c(k) < 0$, corresponding to $\mathcal{D}(c_0) < 0$ or $c > c_B$, where

$$c_B = \frac{3D}{4\tilde{m}\alpha - 3Dv_0} \sim \frac{3D}{4\tilde{m}\alpha} \quad (66)$$

is the concentration above which bundling overtakes diffusion. Using $\alpha \sim (b/l)u_0$, we can express the density c_B in terms of the activity parameter μ_a defined in Eq. (40) as $c_B = \frac{9}{2\mu_a}(l\gamma_P/\alpha)$, where we have used $D_r = D/(6l^2)$. A possible location of this instability line in the phase diagram is shown in Fig. 4.

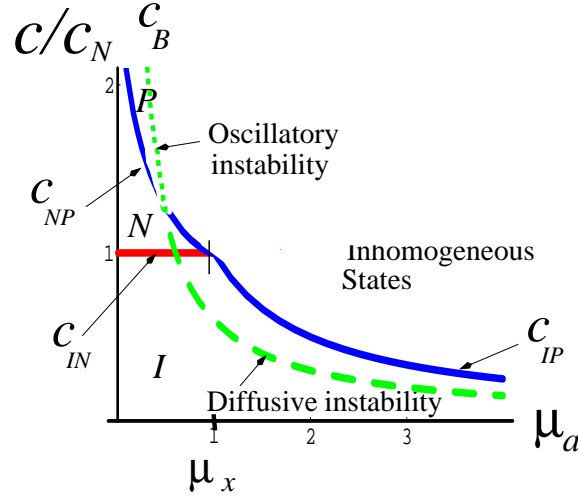


Fig. 4. (color online) The phase diagram of homogeneous states for $\mu_s = 0$ in the plane of filament density, c_0 , and motor activity μ_a , as defined in Eq. (40), showing the location of the bundling instability at $c_0 = c_B$. The horizontal line at $c_0 = c_N$ for the isotropic-nematic transition crosses c_{IP} at $\mu_a \mu_x = 1/c_N$. The c_B line may lie above the $c_{NP} - c_{IP}$ line or cross through the N and I states, as shown in the figure ($l\gamma_P/\alpha = 0.1$, $a_4 = 50$), depending on the value of $l\gamma_P/\alpha$, a numerical parameter to leading order independent of ATP consumption rate. The instability of the I and N states is diffusive (dashed line), while the instability of the P state is oscillatory (dotted line).

7.2 Nematic State

The continuum variables describing the large-scale dynamics of an active nematic solution are the density and flow velocity of the solution and the concentration and alignment tensor of the filaments. For simplicity we consider only the case where there are no stationary apolar cross-linkers, i.e., $m_s = 0$. In this case the transition from the isotropic to the nematic state occurs at the value c_N of passive suspensions. A finite fraction of stationary apolar crosslinkers lowers the value of the transition

density, as discussed in Section 6. In addition, it tends to stiffen all the liquid crystal elastic constants [36]. In the absence of external forces, the equations for filament concentration and alignment tensor are given by

$$\left(\partial_t + \mathbf{v} \cdot \nabla\right)c = \partial_i \mathcal{D}_{ij} \partial_j c + \partial_i \mathcal{D}^Q \partial_j (c Q_{ij}), \quad (67)$$

$$\left(\partial_t + \mathbf{v} \cdot \nabla\right)(c Q_{ij}) = c F_{ij}(\boldsymbol{\kappa}, \mathbf{Q}) + H_{ij}(c, \mathbf{Q}). \quad (68)$$

The tensor F_{ij} describes anisotropic convective and flow alignment effects and has the familiar form for passive nematic liquid crystals, as given in Eq. (14). At low density with the closure approximation described in Ref. [36] the alignment parameter has the value $\lambda = 1/(2S_0)$, with S_0 the nematic order parameter defined in Eq. (10). The tensor H_{ij} plays the role of the equilibrium molecular field for passive nematic liquid crystals, but it contains various active corrections. It is given by

$$\begin{aligned} H_{ij}(c, \mathbf{Q}) \simeq & K \nabla^2 (c Q_{ij}) + K' \left[\partial_i \partial_k (c Q_{jk}) + \partial_j \partial_k (c Q_{ik}) - \delta_{ij} \partial_k \partial_l (c Q_{kl}) \right] \\ & + \partial_k \left(K_{ijkl} \partial_l c \right) - 4D_r \left(1 - \frac{c}{c_N} \right) c Q_{ij} - D_r a_4 c^3 Q_{kl} Q_{kl} Q_{ij}, \end{aligned} \quad (69)$$

where

$$\begin{aligned} \mathcal{D}_{ij}(c, \mathbf{Q}) = & \frac{3D}{4} \left[1 + \left(1 - \frac{2}{3} S^2 \right) \frac{3c}{c_N} - \frac{4\alpha \tilde{m}_a c}{3D} \right] \delta_{ij} \\ & + \left(\frac{Dv_0}{2} - \frac{4}{3} \alpha \tilde{m}_a \right) c Q_{ij}, \end{aligned} \quad (70)$$

$$\mathcal{D}^Q(c) = \frac{D}{2} \left(1 - \frac{c}{c_N} \right) - \frac{2\alpha \tilde{m}_a c}{3}, \quad (71)$$

$$K_{ijkl}(c) = \left[\frac{D}{16} (1 + v_0 c) - \frac{2}{3} \alpha \tilde{m}_a c \right] (\delta_{ik} \delta_{jl} + \delta_{jk} \delta_{il} - \delta_{ij} \delta_{kl}), \quad (72)$$

$$K(c) = \frac{7D}{12} \left(1 - \frac{c}{c_N} \right), \quad (73)$$

$$K'(c) = \frac{D}{6} \left(1 - \frac{c}{c_N} \right) - \frac{\alpha \tilde{m}_a c}{18}. \quad (74)$$

The last term on the right hand side of Eq. (69), with $a_4 > 0$ has been introduced by hand. It arises from a quartic terms in the free energy of an equilibrium nematic and determines the magnitude of orientational order in passive rod solutions. It is apparent from the form of the various elastic constants in Eqs. (70-74) that bundling (described by the parameter α of Eq. (26)) always decreases the elastic constants of the nematic and therefore ultimately renders the uniform ordered state unstable.

The flow velocity of the suspension is again obtained from Stokes' equation, Eq. (57), with a rods' contribution to the pressure given by

$$\begin{aligned} \Pi_r^N(c, \mu) = & k_B T_a c \left[1 + \frac{3c}{2c_N} \left(1 - \frac{2}{3} S^2 \right) \right] + k_B T_a \frac{c}{36D} u_{kl} Q_{kl} \\ & + \tilde{m}_a \alpha \frac{k_B T_a}{432D} c^2 (5 - S^2), \end{aligned} \quad (75)$$

where the last term is new and arises from activity. The filament contribution to the deviatoric stress tensor is given by

$$\begin{aligned} \tilde{\sigma}_{ij}^{r,N} = & 2k_B T_a c \left(1 - \frac{c}{c_N}\right) Q_{ij} + \tilde{m}_a \alpha \frac{8k_B T_a}{432D} c^2 Q_{ij} \\ & + k_B T_a \frac{c}{24D} \left[\frac{1}{2} u_{ij} + \frac{2}{3} \left(u_{ik} Q_{kj} + u_{jk} Q_{ki} - \delta_{ij} u_{kl} Q_{kl} \right) \right]. \end{aligned} \quad (76)$$

Activity modifies the stress tensor of a nematic in two ways. The first term on the right hand side of Eq. (76) is equilibrium-like, in the sense that it can be obtained from the corresponding term in the stress tensor of passive rods, $\tilde{\sigma}_{ij}^{r,\text{passive}} = 2k_B T \left(1 - \frac{c}{c_N}\right) Q_{ij}$ by letting $T \rightarrow T_a$ (and replacing the transition density c_N by c_{IN} , when $m_s \neq 0$). The second term on the right hand side of Eq. (76) is a truly nonequilibrium contribution. It was first proposed phenomenologically by Hatwalne and collaborators [50] who argued that an active element in solution behaves like a force dipole. Correlations among the axis of each dipole build up orientational order and yield active contributions to the stress tensor proportional to the orientational order parameter, Q_{ij} . Our microscopic derivation [57] yields an estimate for the coefficient of this term (undetermined, even in sign, in the phenomenological theory) and shows that the active cross-linkers yield contractile stresses ($\alpha > 0$). Finally, the third term on the right hand side of Eq. (76) is the viscous contribution which has the standard form for a solution of rod-like filaments. Finally we note that active contributions proportional to the parameter β given in Eq. (27) do not appear in the hydrodynamics of the nematic phase. This is expected as terms proportional to β break the inversion symmetry of the ordered state and can only appear in a system with polar order.

7.3 Polarized State

The coarse-grained variables describing the dynamics of an active polarized suspension are the density and flow velocity of the solution and the concentration and polarization of the filaments. As shown in Section 6, in a polarized state the alignment tensor is slaved to the polarization field and it is not an independent continuum field. On the other hand, since our theory only considers terms that are quadratic in the fields, a nonzero value for $|\mathbf{P}|$ is only obtained by considering the coupled equations for \mathbf{P} to Q_{ij} and eliminating Q_{ij} in favor of \mathbf{P} in the polarization equation to generate a term of order $(\mathbf{P})^3$. To see, consider a filament density well into the polarized state, with $c > c_{IN}$ and $c > c_{IP}$, so that both coefficients $a_1 = 1 - c/c_{IP}$ and $a_2 = 1 - c/c_{IN}$ in Eqs. (44) and (45) satisfy $a_1 < 0$ and $a_2 < 0$. Setting the left hand side of Eqs. (44) and (45) to zero, we solve Eq. (45) for Q_{ij} to obtain

$$Q_{ij} = \frac{b_2 c}{a_2} \left(P_i P_j - \frac{1}{2} \delta_{ij} P^2 \right). \quad (77)$$

This solution, substituted in Eq. (44), yields a term $\sim P^2 P_i$ on the right hand side of Eq. (44) which has solution $P^2 = (2a_1 a_2)/(b_1 b_2 c^2)$.

The continuum equations for the polarized state are obtained by assuming that the alignment tensor relaxes on microscopic time scales to the form given by Eq. (77), which is then used to eliminate Q_{ij} in favor of \mathbf{P} . With the exception of homogeneous terms, such as the $\mathcal{O}((\mathbf{P})^3)$ term just described, this leads to a high density renormalization of the various coefficients in the continuum equations, but does not generate any new terms. For the sake of simplicity in the following we neglect this

renormalization and only keep those terms in the polarization equation generated by the coupling to the alignment tensor that have a qualitatively new structure. We also neglect all excluded volume corrections. The equation for filament concentration is given by

$$\begin{aligned} \partial_t c = & -\nabla \cdot c(\mathbf{v} - \frac{7}{36}\tilde{m}_a\beta c\mathbf{P}) + \partial_i(\mathcal{D}_{ij}^p(c)\partial_j c) \\ & - \frac{1}{2}\alpha\tilde{m}_a\partial_i[c^2\partial_j(P_i P_j)], \end{aligned} \quad (78)$$

with

$$\mathcal{D}_{ij}^p(c, \mathbf{P}) = \left(\frac{3D}{4} - \alpha\tilde{m}_a c\right)\delta_{ij} - \alpha\tilde{m}_a c\left(P_i P_j + \frac{1}{2}\delta_{ij}P^2\right). \quad (79)$$

The equation for the polarization vector has the form

$$\begin{aligned} (\partial_t + \mathbf{v} \cdot \nabla)(c\mathbf{P}) = & \frac{1}{2}(\nabla \times \mathbf{v}) \times (c\mathbf{P}) + \frac{\lambda_P}{2}[\nabla \mathbf{v} + (\nabla \mathbf{v})^T] \cdot c\mathbf{P} \\ & + \mathbf{H}(c, \mathbf{P}). \end{aligned} \quad (80)$$

where $\mathbf{H}(c, \mathbf{P})$ generalizes the molecular field of equilibrium polar fluids [63] by including active contributions. It is given by

$$\begin{aligned} H_i(c, \mathbf{P}) \simeq & -[D_r - \gamma_P\tilde{m}_a c + a_3 P^2]cP_i + \frac{2}{9}\tilde{m}_a\beta c\partial_i c - \frac{1}{36}\tilde{m}_a\beta\partial_j[c^2(P_i P_j - \frac{5}{2}\delta_{ij}P^2)] \\ & + [\partial_j K_p\partial_i(cP_j) + \partial_i K_p\partial_j(cP_j)] + \partial_j K_p\partial_j(cP_i) \\ & - \partial_j \mathcal{D}_{ijk}^p(c, \mathbf{P})\partial_k c + \gamma_P\frac{\tilde{m}_a c}{24}\nabla^2(cP_i), \end{aligned} \quad (81)$$

where

$$K_p(c) = \frac{D}{8} - \frac{\alpha\tilde{m}_a}{4}c, \quad (82)$$

$$K'_p(c) = \frac{5D}{8} - \frac{\alpha\tilde{m}_a}{4}c, \quad (83)$$

$$\mathcal{D}_{ijk}^p(c, \mathbf{P}) = c\left[\left(\frac{Dv_0}{8} + \frac{\alpha\tilde{m}_a}{3}\right)(P_i\delta_{jk} + \delta_{ij}P_k) + \left(\frac{17Dv_0}{8} + \frac{2\alpha\tilde{m}_a}{3}\right)P_j\delta_{ik}\right]. \quad (84)$$

The parameter a_3 determines the value P_0 of the magnitude of the polarization in a quiescent (active) suspension, with $P_0^2 = a_3/[D_r(c/c_{IP} - 1)]$.

In contrast to the case of the nematic, all three active mechanisms of motor-induced filament dynamics controlled by α , β and γ_P appear in the hydrodynamic equations of polarized active suspension. Polarization sorting at a rate $\beta \sim u_0$ yields novel convective contributions in the first term on the right hand side of the equation for the filament concentration, Eq. (78). In an equilibrium suspensions the filament concentration is convected with the suspension flow velocity, \mathbf{v} . In an active polar suspension, in contrast, the filament concentration is convected with the effective velocity $\sim \mathbf{v} + \tilde{m}_a\beta\mathbf{P}$. The terms linear in the gradients proportional to β in the polarization equation are of similar origin. These terms were also incorporated in the continuum description of self-propelled particles proposed by Simha and Ramaswamy. Bundling effects controlled by the rate α soften both the diffusion constant $\mathcal{D}_{ij}^p(c, \mathbf{P})$ in the concentration equation and the effective bend and splay

elastic constants K_p and K'_p of the polar fluid. Finally, the rotation rate γ_P builds up polar order and controls the very existence of a polar state.

For an incompressible suspension, the flow field \mathbf{v} is obtained again from the Stokes equation, Eq. (57). The filament contribution to the pressure is given by

$$\Pi_r^P = k_B T_a c \left(1 + \frac{c}{\pi}\right) + \tilde{m}_a \alpha \frac{k_B T_a}{144D} c^2 \left(\frac{5}{3} + 2P^2\right). \quad (85)$$

The filament contribution to the deviatoric stress tensor of a polarized suspension is

$$\begin{aligned} \tilde{\sigma}_{ij}^{r,P} = & \tilde{m}_a \alpha \frac{k_B T_a}{72D} c^2 \left(P_i P_j - \frac{1}{2} \delta_{ij} P^2\right) + \frac{k_B T_a}{48D} c u_{ij} \\ & + \frac{k_B T_a}{36D} \frac{c^2 b_2}{a_2} \left[u_{ik} P_k P_j + u_{jk} P_k P_i - \delta_{ij} P_k u_{kl} P_l - u_{ij} P^2\right] \\ & + \tilde{m}_a \beta \frac{k_B T_a}{432D} c^2 \left[\partial_j P_i - \frac{1}{2} \delta_{ij} \nabla \cdot \mathbf{P} - \frac{1}{4} (\partial_i P_j - \partial_j P_i)\right]. \end{aligned} \quad (86)$$

The first term on the right hand side of Eq. (86) is the active contribution to the stress tensor first discussed by Hatwalne and collaborators for a nematic suspension [50]. The second and third term arise from the viscous coupling of filaments to the solvent. Finally the last term contains active contributions proportional to gradients of the polarization. These are controlled by the polarization sorting rate $\beta \sim u_0$. Terms of these type are unique to the polarized state and vanish in a nematic suspension. They are expected to play an important role in renormalizing the rate of stress relaxation via reptation.

Continuum equations for a polarized active suspension have been written down phenomenologically by several authors [49, 48, 51]. It is useful to make contact with this work. The phenomenological description can be recovered from our model by making a few simplifying approximations. An equation for the concentration of filaments of the form given in Eq. (78) was proposed by Ramaswamy and collaborators [49, 51], although these authors neglected the diffusion terms, which play a crucial role in controlling the bundling instability of quiescent suspensions. The equation for the polarization vector \mathbf{P} reduces to the form used by Voituriez et al. [48] and by Simha et al. [49, 51], if all terms containing higher order gradients of the concentration ($P_i \nabla^2 c$, $P_i (\nabla c)^2$, $\mathbf{P} \cdot \nabla \partial_i c$, $(\mathbf{P} \cdot \nabla c)(\partial_i c)$), as well as terms containing both gradients of concentration and of polarization ($(\nabla \cdot \mathbf{P})(\partial_i c)$, $(\partial_j c)(\partial_j P_i)$, $(\partial_j c)(\partial_i P_j)$) are neglected. With this approximation Eq. (80) becomes

$$\begin{aligned} (\partial_t + \mathbf{v} \cdot \nabla) P_i = & \Gamma \left(1 - \frac{|\mathbf{P}|^2}{P_0^2}\right) P_i + \frac{1 + \lambda_P}{2} (\partial_j v_i) P_j - \frac{1 - \lambda_P}{2} (\partial_i v_j) P_j \\ & - w_1 c (\mathbf{P} \cdot \nabla) P_i - w_2 c P_i (\nabla \cdot \mathbf{P}) + w_3 c \partial_i |\mathbf{P}|^2 \\ & + \left[(w_4 + w_5 P^2) \delta_{ij} - w_6 P_i P_j \right] \partial_j c \\ & + (K_1 - K_3) \partial_i \nabla \cdot \mathbf{P} + K_3 \nabla^2 P_i, \end{aligned} \quad (87)$$

where $\Gamma = \gamma_P \tilde{m}_a c - D_r > 0$ and $P_0^2 = \Gamma/a_3$. Here the coefficients w_i have the form $w_i = c_i \tilde{m}_a \beta$, with c_i numerical coefficients of order one. Note, however, that the terms proportional to w_i other than w_1 are equilibrium-like, in the sense that they could also be obtained from a polar contribution to the free energy of the form

$\delta F_p = \int_{\mathbf{r}} \left[B_1 \delta c (\nabla \cdot \mathbf{P}) + B_2 c |\mathbf{P}|^2 (\nabla \cdot \mathbf{P}) + B_3 |\mathbf{P}|^2 \mathbf{P} \cdot \nabla c + \dots \right]$. The w_1 term, in contrast, is a true nonequilibrium contribution induced by activity and cannot be obtained from a free energy. All the remainder w_i 's contain in general both equilibrium-like contributions determined by the B_i and nonequilibrium ones proportional to $\beta \sim R_{ATP}$. Finally, K_1 and K_3 are the splay and bend elastic moduli, respectively, with

$$K_1(c) = \frac{7D}{8} - \frac{3\tilde{m}_a \alpha c}{4} + \frac{\tilde{m}_a \gamma_P c}{24}, \quad (88)$$

$$K_3(c) = \frac{5D}{8} - \frac{\tilde{m}_a \alpha c}{4} + \frac{\tilde{m}_a \gamma_P c}{24}. \quad (89)$$

The first term on the right hand side of Eq. (87) guarantees the formation of a uniformly polarized state with $|\mathbf{P}| = P_0$. The next two terms are conventional couplings of liquid crystalline order and flow, with λ_P the flow alignment parameter. Our low density calculation yields $\lambda_P = 1/2$. The three terms on the second line are nonequilibrium terms analogous to those first written down by Toner and Tu in models of flocking [53, 54, 55]. The third line describes nonequilibrium changes in polarization driven by concentration gradients. Only the first of these terms ($\sim w_4$) is generally included in phenomenological theories. Equations (88) and (89) show that motor-induced filament bundling ($\sim \alpha$) softens both the splay and bend elastic constants, while polar crosslinkers ($\sim \gamma_P$) tend to stiffen them. Such effects, i.e. the dependence of elastic constants on the active elements are clearly beyond the scope of phenomenological theories with arbitrary elastic constants. In addition, the microscopic derivation also provides contributions to the stress tensor which are higher order in gradients without the need for new unknown parameters, e.g. the expression for the stress tensor given in Eq. (86) contains novel contributions proportional to gradients of polarization that were not considered by other authors [49, 50, 46, 47] but whose microscopic origin is the same as those of lower order in the gradients.

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A Appendix: Derivation of the rods' stress tensor

We model very long, thin rods as rigid strings of spherical beads of diameter $b \ll l$ suspended in a fluid of viscosity η_0 . We assume each rod consists of an odd number $l/b = 2M + 1$ of such beads, a sketched in Fig. 5. The beads on the α -th rod are indexed by an integer m that runs from $-M$ to $+M$ and the center of the m -th bead is at $\mathbf{r}_\alpha(m) = \mathbf{r}_\alpha + mb\hat{\mathbf{u}}_\alpha$, with $\mathbf{r}_\alpha = \sum_m \mathbf{r}_\alpha(m)$ the center of mass of the rod. Momentum conservation at low Reynolds number is described by the Stokes equation

$$\eta_0 \nabla^2 \mathbf{v}(\mathbf{r}) - \nabla \Pi - \sum_\alpha \sum_{m=-M}^M \delta(\mathbf{r} - \mathbf{r}_\alpha(m)) \mathbf{f}_\alpha^h(m) = 0, \quad (90)$$

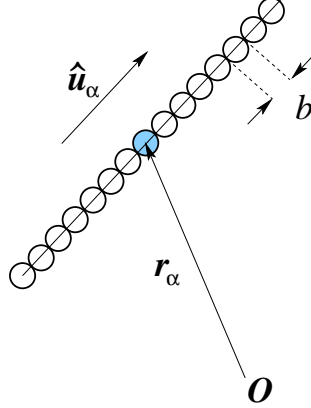


Fig. 5. (color online) The bead model of a rigid filament.

where we have modeled each bead as a point-force on the fluid at the position of its center of mass. Faxén's theorem for the hydrodynamic force on a sphere in an inhomogeneous flow relates the force $\mathbf{f}_\alpha^h(m)$ exerted by the fluid on a bead to the flow velocity field $\mathbf{v}_0(\mathbf{r})$ at the bead's position in the absence of that bead, according to

$$\mathbf{f}_\alpha^h(m) = -\zeta_b [\mathbf{v}_\alpha(m) - \mathbf{v}_0(\mathbf{r}_\alpha(m))], \quad (91)$$

where $\mathbf{v}_\alpha(m) = \mathbf{v}_\alpha + m\mathbf{b}\boldsymbol{\omega}_\alpha \times \hat{\mathbf{u}}_\alpha$ is the velocity of the bead, with \mathbf{v}_α and $\boldsymbol{\omega}_\alpha$ the center of mass and angular velocity of the rod, and $\zeta_b = 3\pi\eta_0 b$ is the Stokes friction coefficient of a sphere of diameter b in an unbounded fluid of viscosity η_0 . Using the linearity of the Stokes equation and the principle of superposition, the velocity of fluid at the position of the bead is given by

$$\mathbf{v}_0(\mathbf{r}_\alpha(m)) = \mathbf{v}(\mathbf{r}_\alpha(m)) - \sum_{n \neq m} \mathbf{H}(\mathbf{r}_\alpha(m) - \mathbf{r}_\alpha(n)) \cdot \mathbf{f}_\alpha^h(n), \quad (92)$$

where $\mathbf{v}(\mathbf{r})$ is the velocity of the fluid taking account of the presence of other rods and $H_{ij}(\mathbf{r}) = \frac{1}{8\pi\eta_0 r} (\delta_{ij} + \hat{r}_i \hat{r}_j)$ is the Oseen tensor. Here the hydrodynamic interactions between beads on the same rod have been included explicitly, while the hydrodynamic coupling to other rods is implicitly taken into account in determining the flow velocity $\mathbf{v}(\mathbf{r})$. The force on bead m on the α -th rod is therefore given by

$$\mathbf{f}_\alpha^h(m) = -\zeta_b [\mathbf{v}_\alpha(m) - \mathbf{v}(\mathbf{r}_\alpha(m))] - \frac{3}{8} \sum_{n \neq m} \frac{1}{|n-m|} (\boldsymbol{\delta} + \hat{\mathbf{u}}_\alpha \hat{\mathbf{u}}_\alpha) \cdot \mathbf{f}_\alpha^h(n). \quad (93)$$

Now we take the limit $l \gg b$ and introduce the continuous variable $s = bm$, where $-l/2 \leq s \leq l/2$, so that $\mathbf{r}_\alpha(s) = \mathbf{r}_\alpha + s\hat{\mathbf{u}}_\alpha$. The hydrodynamic force per unit length, $\mathcal{F}_\alpha^h(s)$, satisfies the equation

$$\mathcal{F}_\alpha^h(s) = -\zeta_s (\mathbf{v}_\alpha(s) - \mathbf{v}(\mathbf{r}_\alpha(s))) - \frac{3}{8} \int_{|s-s'| \geq b} \frac{ds'}{|s-s'|} (\boldsymbol{\delta} + \hat{\mathbf{u}}_\alpha \hat{\mathbf{u}}_\alpha) \cdot \mathcal{F}_\alpha^h(s'), \quad (94)$$

where $\zeta_s = 3\pi\eta_0 = \zeta_b/b$. Approximating

$$\frac{1}{|s-s'|} \approx \left\langle \frac{1}{|s-s'|} \right\rangle' \delta(s-s'), \quad (95)$$

where

$$\left\langle \frac{1}{|s-s'|} \right\rangle' = \frac{1}{l^2} \int_s \int_{s'} \Theta(|s-s'| - b) \frac{1}{|s-s'|} = 2 \ln(l/2b), \quad (96)$$

with $\Theta(x)$ the Heaviside function, we obtain

$$\frac{3 \ln(l/2b)}{4} (\boldsymbol{\delta} + \hat{\mathbf{u}}_\alpha \hat{\mathbf{u}}_\alpha) \cdot \mathcal{F}_\alpha^h(s) \simeq -\zeta_s [\mathbf{v}_\alpha(s) - \mathbf{v}(\mathbf{r}_\alpha(s))]. \quad (97)$$

Since $\mathbf{v}_\alpha(s) = \mathbf{v}_\alpha + s\boldsymbol{\omega}_\alpha \times \hat{\mathbf{u}}_\alpha$, then integrating equation (97) over s , we can obtain expressions for the hydrodynamic force, $\mathbf{F}_\alpha^h = \langle \mathcal{F}_\alpha^h(s) \rangle_s$ and torque $\boldsymbol{\tau}_\alpha^h = \langle \hat{\mathbf{u}}_\alpha s \times \mathcal{F}_\alpha^h(s) \rangle_s$ at the center of mass of a rod, with $\langle \dots \rangle_s = \int_{-l/2}^{l/2} ds \dots$ as

$$-\zeta^{-1}(\hat{\mathbf{u}}_\alpha) \cdot \mathbf{F}_\alpha^h = \mathbf{v}_\alpha - \frac{1}{l} \langle \mathbf{v}(\mathbf{r}_\alpha(s)) \rangle_s, \quad (98)$$

$$-\frac{1}{\zeta_r} \boldsymbol{\tau}_\alpha^h = \boldsymbol{\omega}_\alpha - I^{-1} \frac{1}{l} \langle \hat{\mathbf{u}}_\alpha \times s \mathbf{v}(\mathbf{r}_\alpha(s)) \rangle_s, \quad (99)$$

where $\zeta_{ij}(\hat{\mathbf{u}}) = \zeta_\perp (\delta_{ij} - \hat{u}_i \hat{u}_j) + \zeta_\parallel \hat{u}_i \hat{u}_j$, $\zeta_\perp = 2\zeta_\parallel = \frac{4\pi\eta_0 l}{\ln(l/2b)}$, $\zeta_r = \frac{\pi l^3 \eta_0}{3 \ln(l/2b)}$ and $I = l^2/12$. Performing a Taylor expansion of the fluid velocity about the center of mass, we obtain to lowest order in gradients

$$-\zeta^{-1}(\hat{\mathbf{u}}_\alpha) \cdot \mathbf{F}_\alpha^h = \mathbf{v}_\alpha - \mathbf{v}(\mathbf{r}_\alpha) - \frac{I}{2} (\hat{\mathbf{u}}_\alpha \cdot \nabla)^2 \mathbf{v}(\mathbf{r}_\alpha) + O(\nabla^4), \quad (100)$$

$$-\frac{1}{\zeta_r} \boldsymbol{\tau}_\alpha^h = \boldsymbol{\omega}_\alpha - \hat{\mathbf{u}}_\alpha \times (\hat{\mathbf{u}}_\alpha \cdot \nabla) \mathbf{v}(\mathbf{r}_\alpha) + O(\nabla^3). \quad (101)$$

Finally, we require that the hydrodynamic forces and torques be balanced by all other forces and torques on the rod. This gives

$$\mathbf{F}_\alpha^h = \nabla_\alpha U_{ex} + k_B T_a \nabla \ln \hat{c} - \mathbf{f}_\alpha^a, \quad (102)$$

$$\boldsymbol{\tau}_\alpha^h = \mathcal{R}_\alpha U_{ex} + k_B T_a \mathcal{R}_\alpha \ln \hat{c} - \boldsymbol{\tau}_\alpha^a, \quad (103)$$

where we have included contributions from fluctuations (non-equilibrium osmotic pressure), excluded volume interactions and active driving by the motors. Using Eqs. (97) and (100), we can calculate the hydrodynamic force per unit length on the rod as

$$\begin{aligned} \mathcal{F}_{\alpha i}^h(s) &= \zeta_{ij}(\hat{\mathbf{u}}_\alpha) [v_{\alpha j} - v_j(\mathbf{r}_\alpha) + s((\boldsymbol{\omega}_\alpha \times \hat{\mathbf{u}}_\alpha)_j - (\hat{\mathbf{u}} \cdot \nabla_\alpha) v_j(\mathbf{r}_\alpha))] \\ &\quad - \frac{s^2}{2} (\hat{\mathbf{u}} \cdot \nabla_\alpha)^2 v_j(\mathbf{r}_\alpha). \end{aligned} \quad (104)$$

from which we obtain Eq. (32). Furthermore, defining the translational and rotational currents as

$$\mathbf{J}_c(\mathbf{r}, t) = \left\langle \sum_\alpha \mathbf{v}_\alpha \delta(\mathbf{r} - \mathbf{r}_\alpha(t)) \right\rangle \quad (105)$$

$$\mathcal{J}_c(\mathbf{r}, t) = \left\langle \sum_\alpha \boldsymbol{\omega}_\alpha \delta(\mathbf{r} - \mathbf{r}_\alpha(t)) \right\rangle, \quad (106)$$

the Smoluchowski equation (19) for the dynamics of $\hat{c}(\mathbf{r}, \hat{\mathbf{u}}, t)$ follows.

From equation (32), we perform the coarse-graining procedure to obtain the stress tensor. Retaining all terms of first order in gradients of the hydrodynamic fields, the pressure is

$$\Pi_r^P = k_B T_a c \left(1 + \frac{c}{\pi}\right) + \tilde{m}_a \alpha \frac{k_B T_a}{144D} c^2 \left(\frac{5}{3} + 2P^2\right), \quad (107)$$

and the deviatoric stress tensor is given by

$$\begin{aligned} \tilde{\sigma}_{ij}^A = & 2k_B T_a c \left(1 - \frac{c}{c_{IN}}\right) Q_{ij} - k_B T_a \frac{c^2}{c_{IP}} \left(P_i P_j - \frac{1}{2} \delta_{ij} P^2\right) \\ & + \tilde{m}_a \alpha \frac{k_B T_a}{72D} c^2 \left(\frac{4}{3} Q_{ij} + P_i P_j - \frac{1}{2} \delta_{ij} P^2\right) \\ & + \tilde{m}_a \beta \frac{2k_B T_a}{432D} c^2 \left[\partial_j P_i - \frac{1}{2} \delta_{ij} \nabla \cdot \mathbf{P} - \frac{1}{4} (\partial_i P_j - \partial_j P_i)\right. \\ & + \frac{5}{3} (Q_{jk} \partial_k P_i - P_i \partial_k Q_{jk} - Q_{ik} (\partial_j P_k + \partial_k P_j) + (P_k \partial_j + P_j \partial_k) Q_{ik} \\ & \left. - Q_{ij} \nabla \cdot \mathbf{P} + \mathbf{P} \cdot \nabla Q_{ij}) + \frac{2}{3} (Q_{jk} (\partial_k P_i + \partial_i P_k) - (P_i \partial_k + P_k \partial_i) Q_{jk})\right. \\ & \left. + \frac{5}{6} \delta_{ij} (Q_{kl} \partial_k P_l - P_l \partial_k Q_{kl})\right]. \quad (108) \end{aligned}$$

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