Rheology of Active Filament Solutions

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We study the viscoelasticity of an active solution of polar biofilaments and motor proteins. Using a molecular model, we derive the constitutive equations for the stress tensor in the isotropic phase and in phases with liquid crystalline order. The stress relaxation in the various phases is discussed. Contractile activity is responsible for a spectacular difference in the viscoelastic properties on opposite sides of the order-disorder transition.

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Soft active systems are exciting examples of a new type of condensed matter where stored energy is continuously transformed into mechanical work at microscopic length scales. A realization of this are polar filaments interacting with associated molecular motors in the cell cytoskeleton [1,2]. These systems are characterized by a variety of dynamic and stationary states which the cell accesses as part of its cycle [3–5]. Recent experimental and theoretical studies of the dynamics of solutions of active filaments have focused on the formation of both homogeneous and inhomogeneous states with spatial structures, such as bundles, vortices, or asters [4–14].

In this Letter, we study the effect of motor activity on the rheological properties of active solutions under an externally imposed stress. Understanding the viscoelasticity of cells, and cellular extracts *in vitro*, is a very important problem currently receiving a lot of experimental attention [15–20]. From a theoretical point of view, describing the mechanics of the cytoskeleton in its full complexity remains very challenging. As a first step in this direction, we focus on using methods from polymer physics to understand the effect of motor activity on the viscoelasticity of a dilute solution of long stiff biopolymers. A phenomenological description of the rheology of isotropic suspensions of active particles near the isotropic-nematic transition was proposed recently by Hatwalne *et al.* [21]. The present work provides a microscopic basis for their results, it yields a general framework for analyzing the viscoelastic behavior of active solutions in *both* isotropic and ordered states [10,20,21], and it presents new results for the normal stresses in the nematic phase.

Our model makes several predictions. First, as suggested in Ref. [21], activity yields a contribution to the viscosity of an isotropic solution that diverges at the isotropic-nematic transition (see Fig. 1) [22]. This behavior is reminiscent of an equilibrium liquid-solid transition, rather than a liquid-liquid transition, and is a direct consequence of contractile bundling. The divergence is localized at the transition and the viscosity is finite in the nematic regime. A second signature of activity is found in the nematic phase, where our microscopic calculation shows that the stress tensor acquires a nonequilibrium contribution proportional to the ATP (adenosine triphosphate) consumption rate that remains finite for a zero deformation rate [10,20,21]. In other words, an active nematic solution is driven into a state with a nonzero macroscopic stress by the energy input from ATP hydrolysis, even in the absence of an external mechanical deformation [23].

We consider a suspension of polar filaments in a thin film of constant thickness comparable to the length of the filaments (quasi-two dimensions) and a constant density m of motor clusters. A concentration $\rho(\mathbf{r}, t)$ of filaments is suspended in an incompressible solvent of viscosity η_0 characterized by a fluid velocity $\mathbf{v}(\mathbf{r}, t)$, with $\boldsymbol{\nabla} \cdot \mathbf{v} = 0$. Momentum conservation yields

$$\rho_s(\partial_t \mathbf{v} + \mathbf{v} \cdot \boldsymbol{\nabla}\mathbf{v}) = \boldsymbol{\nabla} \cdot \boldsymbol{\sigma}^s + \boldsymbol{\nabla} \cdot \boldsymbol{\sigma}^f, \tag{1}$$

with ρ_s the (constant) density of the solution. The solvent contribution to the stress tensor is

$$\boldsymbol{\nabla} \cdot \boldsymbol{\sigma}^s = \eta_0 \nabla^2 \mathbf{v} - \nabla p,$$

with p the pressure. The filament contribution $\boldsymbol{\sigma}^f$ must be determined in terms of the driving forces (velocity gradients $\kappa_{ij} = \partial_j v_i$ and motor activity $\mu \sim$ ATP consumption rate) and the conserved and order parameter fields

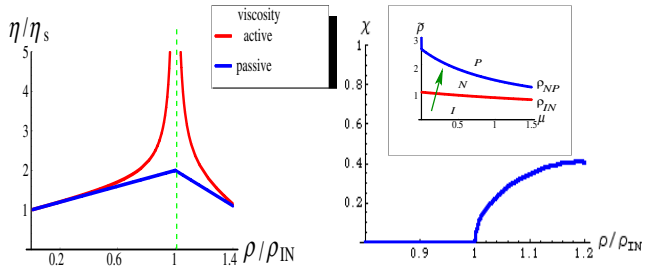

FIG. 1 (color online). (a) The steady-state shear viscosity on both sides of the IN transition for passive and active nematics. (b) The "motility" parameter χ [see Eq. (17)] relating the magnitude of the active component of shear stress to the "activity" μ (∼ATP consumption). Inset: Phase diagram showing the IN transition.

describing the filaments

$$\boldsymbol{\sigma}^f = \boldsymbol{\sigma}^f(\rho, \mathbf{p}, S_{ij}; \boldsymbol{\kappa}, \mu), \tag{2}$$

where $\mathbf{p}$ and S_{ij} are the local polarization and nematic alignment tensor, respectively, that describe the orientational order of the filaments. The derivation of this constitutive equation from a model of filament dynamics is one of the central outcomes of this work.

The filaments are modeled as hard rods of *fixed* length l and diameter a ($l \gg a$) at position $\mathbf{r}$ with filament polarity characterized by a unit vector $\hat{\mathbf{u}}$. The filament contribution to the stress tensor is [24]

$$\boldsymbol{\nabla} \cdot \boldsymbol{\sigma}^f = -\int_{\mathbf{r}_1}\int_{\hat{u}_1} c(\mathbf{r}_1, \hat{\mathbf{u}}_1, t)\langle \delta(\mathbf{r} - \mathbf{r}_1 - s\hat{\mathbf{u}}_1)\boldsymbol{\mathcal{F}}(s)\rangle_s,$$

where $\boldsymbol{\mathcal{F}}(s)$ is the hydrodynamic force per unit length on a rod at position s along the rod, $\langle \ldots \rangle_s \equiv \int_{-l/2}^{l/2} ds \ldots$, and $c(\mathbf{r}, \hat{\mathbf{u}}, t)$ is the concentration of polar filaments with position and orientation $\{\mathbf{r}, \hat{\mathbf{u}}\}$. The force on the rod is specified by its interaction with the solvent, other rods, and the motor clusters. For low Reynolds numbers $\mathrm{Re} \ll 1$, viscous effects dominate inertia and we can set the left-hand side of Eq. (1) to zero.

We calculate the force per unit length $\boldsymbol{\mathcal{F}}(s)$ by decomposing a rod into a sequence of beads of diameter a and solving self-consistently for the flow field around the rod [24] on scales much bigger than a. The stress due to the filaments is given by [to $\mathcal{O}(\nabla^2)$]

$$\nabla \cdot \boldsymbol{\sigma}^f(\mathbf{r}, t) = \int_{\hat{\mathbf{u}}} \mathbf{f}(\mathbf{r}, \hat{\mathbf{u}}, t) - \int_{\hat{\mathbf{u}}} \left\langle \left(\frac{s}{l}\right)^2 \left(\frac{\hat{\mathbf{u}} \cdot \nabla}{l}\right) \boldsymbol{\tau}(\mathbf{r}, \hat{\mathbf{u}}, t) \right\rangle_s, \tag{3}$$

where [25]

$$\begin{aligned} \mathbf{f}(\mathbf{r}, \hat{\mathbf{u}}, t) &= c[k_B T_a \boldsymbol{\nabla} \ln c + \boldsymbol{\nabla} U_x - \mathbf{F}_a(\mathbf{r}, \hat{\mathbf{u}}, t)], \\ \boldsymbol{\tau}(\mathbf{r}, \hat{\mathbf{u}}, t) &= \mathbf{T} \times \hat{\mathbf{u}} - c\frac{\zeta_\perp}{2} \hat{\mathbf{u}}\,\hat{\mathbf{u}}(\hat{\mathbf{u}} \cdot \nabla) \cdot \mathbf{v}(\mathbf{r}), \\ \mathbf{T} &= c[k_B T_a \mathcal{R} \ln c + \mathcal{R} U_x - \mathbf{T}_a], \end{aligned} \tag{4}$$

with $\mathcal{R} = \hat{\mathbf{u}} \times \frac{\partial}{\partial \hat{\mathbf{u}}}$ and $U_x(\mathbf{r}, \hat{\mathbf{u}}_1) = k_B T \int_{\hat{\mathbf{u}}'} \int_{\boldsymbol{\xi}} c(\mathbf{r} + \boldsymbol{\xi}, \hat{\mathbf{u}}')$ the excluded volume potential, with $\boldsymbol{\xi} = \hat{\mathbf{u}}_1 s_1 - \hat{\mathbf{u}}_2 s_2$. The expressions (4) for the force density $\mathbf{f}$ and torque density $\mathbf{T}$ can be inferred from the local conservation law for the concentration $c(\mathbf{r}, \hat{\mathbf{u}}, t)$ of polar filaments given in Ref. [25],

$$\partial_t c + \boldsymbol{\nabla} \cdot (\mathbf{v}c) + \mathcal{R} \cdot (\boldsymbol{\omega} c) + \boldsymbol{\nabla} \cdot \mathbf{J} + \mathcal{R} \cdot \mathcal{J} = 0, \tag{5}$$

with $\boldsymbol{\omega} = \hat{\mathbf{u}} \times \boldsymbol{\kappa} \cdot \hat{\mathbf{u}}$ and translational and rotational currents $\mathbf{J} = -\boldsymbol{\zeta}^{-1}(\hat{\mathbf{u}}) \cdot \mathbf{f}(\mathbf{r}, \hat{\mathbf{u}})$ and $\mathcal{J} = -\zeta_r^{-1}\mathbf{T}(\mathbf{r}, \hat{\mathbf{u}})$, respectively. The force density has contributions from fluctuations or diffusion (both thermal and nonthermal—hence the *active temperature* $T_a \neq T$), excluded volume, and motor activity. There is also a viscous contribution to the stress proportional to the velocity gradient [$\zeta_\perp = 4\pi\eta_0 l/\ln(l/a)$]. Finally, the active force and torque in Eqs. (4) have been given in Ref. [25]:

$$\begin{aligned} \mathbf{F}_a(\mathbf{r}, \hat{\mathbf{u}}_1) &= -m_0 \int_{\hat{\mathbf{u}}_2} \langle \boldsymbol{\zeta}(\hat{\mathbf{u}}_1) \cdot \mathbf{v}_a(1;2) c(\mathbf{r} + \boldsymbol{\xi}, \hat{\mathbf{u}}_2)\rangle_{s_1, s_2}, \\ \mathbf{T}_a(\mathbf{r}, \hat{\mathbf{u}}_1) &= -m_0 \int_{\hat{\mathbf{u}}_2} \langle \zeta_r \boldsymbol{\omega}_a(1;2) c(\mathbf{r} + \boldsymbol{\xi}, \hat{\mathbf{u}}_2)\rangle_{s_1, s_2}, \end{aligned} \tag{6}$$

where $m_0 = ma^2$, $(1;2) \equiv (s_1, \hat{\mathbf{u}}_1; s_2, \hat{\mathbf{u}}_2)$, and $\boldsymbol{\zeta}(\hat{\mathbf{u}}) = \zeta_\perp(\boldsymbol{\delta} - \hat{\mathbf{u}}\,\hat{\mathbf{u}}) + \zeta_\parallel \hat{\mathbf{u}}\,\hat{\mathbf{u}}$, with $\zeta_\perp$, $\zeta_\parallel$, and ζ_r friction coefficients. The angular velocity is taken as $\boldsymbol{\omega}_a = 2[\gamma_0 + (\hat{\mathbf{u}}_1 \cdot \hat{\mathbf{u}}_2)\gamma_1](\hat{\mathbf{u}}_1 \times \hat{\mathbf{u}}_2)$, with γ_0 and γ_1 motor-induced rotation rates proportional to ATP consumption, and tends to align filaments [26]. The motor-induced translational velocity has been derived from a model of motors walking along the filaments at a mean rate β. It has the form $\mathbf{v}_a(1;2) = \frac{1}{2}\mathbf{v}_r + \mathbf{V}_m$, with [25,27]

$$\begin{aligned} \mathbf{v}_r &= \frac{\tilde{\beta}}{2}(\hat{\mathbf{u}}_2 - \hat{\mathbf{u}}_1) + \frac{\tilde{\alpha}}{2l}\boldsymbol{\xi}, \\ \mathbf{V}_m &= A(\hat{\mathbf{u}}_2 + \hat{\mathbf{u}}_1) + B(\hat{\mathbf{u}}_2 - \hat{\mathbf{u}}_1), \end{aligned}$$

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 parameter $\alpha \sim \beta(a/l)$ is controlled by spatial inhomogeneities in the motor stepping rate [25,27]. Momentum conservation yields expressions for A and B. 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 $B = \alpha(s_1 - s_2)/24$. When evaluating the contribution 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 in the first of Eqs. (6). This approximation affects only the numerical values of the coefficients in the stress tensor, not its general form.

The conserved and broken symmetry fields are the density $\rho(\mathbf{r}, t)$, polarization $\mathbf{p}(\mathbf{r}, t)$, and nematic order $S_{ij}(\mathbf{r}, t)$, defined as moments of the probability distribution, $\int_{\hat{\mathbf{u}}} c(\mathbf{r}, \hat{\mathbf{u}}, t) = \rho(\mathbf{r}, t)$, $\int_{\hat{\mathbf{u}}} \hat{\mathbf{u}} c(\mathbf{r}, \hat{\mathbf{u}}, t) = \rho(\mathbf{r}, t)\mathbf{p}(\mathbf{r}, t)$, $\int_{\hat{\mathbf{u}}} \hat{Q}_{ij} c(\mathbf{r}, \hat{\mathbf{u}}, t) = \rho(\mathbf{r}, t) S_{ij}(\mathbf{r}, t)$, where $\hat{Q}_{ij} = \hat{u}_i \hat{u}_j - \frac{1}{2}\delta_{ij}$. Continuum equations for these fields are obtained from Eq. (5) by the coarse-graining procedure described in Ref. [25].

The constitutive equation for the stress tensor $\boldsymbol{\sigma}^f$ is obtained by evaluating the right-hand side of Eq. (3). For simplicity, we consider spatially homogeneous solutions in the presence of a constant velocity gradient κ_{ij}. To lowest order in gradients, the deviatoric part $\tilde{\sigma}_{ij} = \sigma_{ij} - (1/2)\delta_{ij}\sigma_{kk}$ of the stress tensor of the filaments is

$$\tilde{\sigma}^f_{ij}(\mathbf{r}, t) = \tilde{\sigma}^A_{ij}(\mathbf{r}, t) + \tilde{\sigma}^v_{ij}(\mathbf{r}, t), \tag{7}$$

with

$$\begin{aligned} \tilde{\sigma}^A_{ij} = 2k_B T_a \rho\left(1 - \frac{\rho}{\rho_{\mathrm{IN}}}\right) S_{ij} - k_B T_a \frac{\rho^2}{\rho_{\mathrm{IP}}}\left(p_i p_j - \frac{1}{2}p^2 \delta_{ij}\right) \\ + \frac{2}{3}\mu k_B T_a \rho^2 \left(\frac{4}{3}S_{ij} + p_i p_j - \frac{1}{2}p^2 \delta_{ij}\right), \end{aligned} \tag{8}$$

where $\mu = m_0 \alpha l^3/48D$, $\rho_{\mathrm{IP}} = D_r/(m_0\gamma_0 l^2)$, and $\rho_{\mathrm{IN}} = \rho_N/[1 + \rho_N l^2 m_0 \gamma_1/(4D_r)]$ are the densities for the isotropic-polarized (IP) and isotropic-nematic (IN) transi-

tion at finite motor density [25], with $\rho_N = 3\pi/(2l^2)$ the density of the IN transition in passive systems. Equation (8) should be compared to the corresponding contribution for passive solutions, $\tilde{\sigma}^P_{ij} = 2k_BT\rho[1 - (\rho/\rho_N)]S_{ij}$. Finally, the viscous contribution to the stress is

$$\tilde{\sigma}^v_{ij} = \frac{l\rho\zeta_\perp}{48}\Big[\frac{1}{2}\Big(\kappa^s_{ij} - \frac{1}{2}\kappa_{kk}\delta_{ij}\Big) + \frac{1}{3}S_{ij}\kappa_{kk} + \frac{2}{3}(\kappa^s_{ik}S_{kj} + \kappa^s_{jk}S_{ki} - \delta_{ij}\kappa_{kq}S_{qk})\Big], \quad (9)$$

with $\kappa^s_{ij} = (\kappa_{ij} + \kappa_{ji})/2$.

In agreement with Ref. [21], we find that active units generate force dipoles in the fluid yielding contributions to the stress which are equilibriumlike, i.e., have the same form as those appearing in an equilibrium solution, but with new contractile stresses ($\alpha > 0$) which have no analogue in their equilibrium counterparts.

For a homogeneous solution $\rho =$ constant, and the equations for the polarization and nematic order parameter are obtained by averaging Eq. (5) over $\hat{\mathbf{u}}$,

$$\partial_t p_i = -\Omega_i - D_r\Big(1 - \frac{\rho}{\rho_{\rm IP}}\Big)p_i + 2D_r\Big(\frac{2\rho}{\rho_{\rm IN}} - \frac{\rho}{\rho_{\rm IP}}\Big)S_{ij}p_j, \quad (10)$$

$$\partial_t S_{ij} = -\Omega_{ij} - 4D_r\Big(1 - \frac{\rho}{\rho_{\rm IN}}\Big)S_{ij} + \frac{2D_r\rho}{\rho_{\rm IP}}\Big(p_ip_j - \frac{1}{2}\delta_{ij}p^2\Big), \quad (11)$$

with $\rho\Omega_i = \int d\hat{\mathbf{u}}\hat{u}_i\boldsymbol{R}\cdot(\boldsymbol{\omega}f)$ and $\rho\Omega_{ij} = \int d\hat{\mathbf{u}}\hat{Q}_{ij}\boldsymbol{R}\cdot(\boldsymbol{\omega}f)$. We find

$$\Omega_i = -\kappa_{ij}p_j + \tfrac{1}{2}[\kappa^s_{ij}p_j + \tfrac{1}{2}\kappa_{kk}p_i], \quad (12)$$

$$\Omega_{ij} = -\tfrac{1}{2}[\kappa^s_{ij} - \tfrac{1}{2}\delta_{ij}\kappa_{kk}] - (\kappa_{ik}S_{kj} + \kappa_{jk}S_{ki}) + \tfrac{1}{3}[S_{ij}\kappa_{kk} + \delta_{ij}S_{kl}\kappa_{kl} + 2(S_{ik}\kappa^s_{kj} + S_{jk}\kappa^s_{ki})]. \quad (13)$$

The homogeneous (bulk) steady states are obtained by setting the right-hand side of Eqs. (10) and (11) to zero. We find isotropic ($\mathbf{p} = 0$, $S_{ij} = 0$), nematic ($\mathbf{p} = 0$, $S_{ij} \neq 0$), and polarized ($\mathbf{p} \neq 0$, $S_{ij} \neq 0$) phases. It can be shown that in a *stationary* bulk fluid the passive contribution to the stress tensor is identically zero in each phase, while the active contribution is nonzero. In the following, we consider the geometry of pure shear flow with $\kappa_{ij} = \dot{\epsilon}\delta_{ix}\delta_{jy}$ and discuss the *linear* viscoelastic response of the active solution in the isotropic (I), polarized (P), and nematic (N) phases.

Isotropic phase.—In the isotropic phase close to the IN transition, a shear flow builds up nematic order, yielding a nonzero value for S_{ij} to $\mathcal{O}(\dot{\epsilon})$. The shear stress is linear in the strain rate, $\sigma_{xy} = \mathcal{O}(\dot{\epsilon})$, while the normal stress is quadratic, $\sigma_{xx} - \sigma_{yy} = \mathcal{O}(\dot{\epsilon}^2)$. To linear order, we obtain $(\partial_t + 1/\tau_A)S_{xy} = \dot{\epsilon}/4$, with $\tau_A = (\tau_0/4)(1 - \rho/\rho_{\rm IN})^{-1}$, where $\tau_0 = 1/D_r$ and $D_r = k_BT_a/\zeta_r$ is the rotational diffusion constant. The time scale τ_A diverges as we approach the active IN transition. In a sheared sample, the total stress (filaments + solution) is

$$\sigma_{xy} = \tilde{\eta}\,\dot{\epsilon} + 2k_BT_a\rho\Big(1 - \frac{\rho}{\rho_{\rm IN}} + \frac{4}{9}\mu\rho\Big)S_{xy}, \quad (14)$$

where $\tilde{\eta} = \eta_0[1 + (\pi l^2\rho/24)]$. The first contribution in Eq. (14) is from the solvent and the viscous stress; the second is from passive and active stresses.

For an oscillatory applied shear, we define the frequency-dependent shear viscosity $\sigma_{xy}(\omega) = \eta_A(\omega)\dot{\epsilon}$, with low frequency limit

$$\eta_A = \tilde{\eta} + \frac{k_BT\rho}{8D_r}\Big(1 + \frac{16}{9}\tau_AD_r\mu\Big), \quad (15)$$

which *diverges* as we approach the IN transition (see Fig. 1). This behavior should be contrasted to that of a passive solution of rods at the *equilibrium* IN transition. In this case, the stress relaxation time $\tau_P = D_r^{-1}/(1 - \rho/\rho_N)$ also diverges at ρ_N, but the zero-frequency viscosity $\eta = \tilde{\eta} + k_BT\rho/(8D_r)$ remains *finite*, as required by the fluctuation-dissipation theorem.

Nematic phase.—In the nematic phase, there is the possibility of alignment of the nematic director by the shear flow. The director $\mathbf{n}$ and the magnitude S of the nematic order parameter are defined by $S_{ij} = S(\hat{n}_i\hat{n}_j - \delta_{ij}/2)$. The equation of motion for the director in a steady shear flow is obtained from Eq. (11), as $\partial_t\hat{n}_i = (\delta_{ij} - \hat{n}_i\hat{n}_j)\hat{n}_k\partial_tS_{jk}/S$. Defining $\hat{\mathbf{n}} = (\cos\theta, \sin\theta)$, we obtain a steady-state solution for the director given by $\cos2\theta = 2S$. For $S > 1/2$, there are no steady-state solutions, possibly pointing to the existence of periodic or chaotic solutions characterized by "wagging" or "kayaking" of the nematic director [28].

The steady-state stress tensor in the active nematic state is obtained from Eq. (8) as

$$\sigma_{ij} = -\frac{k_BT\rho}{2D_r}\Big(\frac{\Omega_{ij}}{\rho}\Big) + \sigma^A_{ij} + \sigma^v_{ij}, \quad (16)$$

from which the 6 Leslie coefficients of the active nematic can be obtained using Eqs. (8), (9), and (13) [24,29].

The novel nature of the constitutive equation is best illustrated by the simple case of an active nematic in the *flow-aligning* regime ($S < 1/2$), where the steady-state shear stress is given by

$$\sigma_{xy} = \eta\dot{\epsilon} + \chi\mu, \quad (17)$$

where $\eta = \tilde{\eta} + (k_BT/2D_r)\rho(\frac{1}{4} - S^2)(1 + \frac{16}{9}D_r\tau'_A\mu)$ and $\chi = \frac{8}{9}k_BT\rho^2S\sqrt{(1/4) - S^2}$, with $1/\tau'_A = 8D_r(\rho/\rho_{\rm IN} - 1)$. The magnitude of nematic order S relaxes on a time scale τ'_A, while the director relaxes on the shear time scale $\dot{\epsilon}$, leading to nonmonotonic stress relaxation [29].

The signature of this constitutive equation is a shear stress that does not vanish for zero deformation rate. This is because the active solution is driven out of equilibrium

by two sources of energy. One is external, due to the shear, and the other is internal, due to the activity of the motors (see Fig. 1) which can maintain the system in a marginally rigid state. The viscosity diverges as the IN transition is approached, but it decreases dramatically as one goes deeper into the nematic phase (see Fig. 1). This is a direct consequence of flow alignment as S increases with density. All corrections to η vanish at $S = 1/2$, where the flow-aligned regime ceases to exist.

Another novel signature of an active nematic is an anomalous constitutive equation for the first normal stress difference with a nonzero value at zero shear rate

$$\sigma_{yy} - \sigma_{xx} = \eta_N \dot{\epsilon} + \chi_N \mu, \tag{18}$$

where $\eta_N = (k_B T/2D_r)\rho S\sqrt{(1/4) - S^2}$ and $\chi_N = \frac{8}{9} k_B T \rho^2 2S^2$.

Both anomalous stresses (shear and normal) should be observable via linear rheological experiments at varying shear rates, although a precise comparison with experiments will require a careful treatment of the boundary conditions at the rheometer's plates.

Polarized phase.—In a polarized state, with $\mathbf{p} = p_0\hat{\mathbf{p}}$, a uniform density, and a constant velocity gradient, the unit vector $\hat{\mathbf{p}}$ satisfies the dynamical equation

$$\partial_t \hat{p}_i + \omega_{ij}\hat{p}_j = \lambda \delta^T_{ij} \kappa^s_{jk} \hat{p}_k, \tag{19}$$

where $\lambda = 1/2$, $\omega_{ij} = (\kappa_{ji} - \kappa_{ij})/2$, and $\delta^T_{ij} = (\delta_{ij} - \hat{p}_i\hat{p}_j)$. Voituriez *et al.* [14] have recently suggested that a spontaneously flowing state (with finite velocity gradients and flow alignment) can be obtained in active polar films. Flow alignment, however, requires $\lambda > 1$, while the present (low density) calculation yields $\lambda = 1/2$. Corrections to λ can be obtained by coupling to the alignment tensor which is slaved to the polarization. However, an analysis of such corrections shows that they fail to increase λ to values larger than 1, suggesting that no steady uniformly flowing polarized state exists for a thin film at low density. An interesting alternative is the possibility of periodic or chaotic states [30].

In summary, we have used a molecular model to study the macroscopic mechanical response of active filament solutions in both isotropic and ordered states. Motor activity leads to a novel coupling of mechanical properties to order and to anomalous constitutive equations in the liquid crystalline state. The theoretical framework developed here can be generalized to consider stress inhomogeneities. This is relevant for understanding the microrheology of active filament systems where new behavior is expected even in the isotropic regime [29].

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