PHYSICAL REVIEW E **72**, 060901(R) (2005)

Nematic and polar order in active filament solutions

A. Ahmadi,[1] T. B. Liverpool,[2] and M. C. Marchetti[1]
[1]*Department of Physics, Syracuse University, Syracuse, New York 13244, USA*
[2]*Department of Applied Mathematics, University of Leeds, Woodhouse Lane, Leeds LS2 9JT, United Kingdom*
(Received 26 July 2005; revised manuscript received 30 September 2005; published 12 December 2005)

Using a microscopic model of interacting polar biofilaments and motor proteins, we characterize the phase diagram of both homogeneous and inhomogeneous states in terms of experimental parameters. The *polarity* of motor clusters is key in determining the organization of the filaments in homogeneous isotropic, polarized, and nematic states, while motor-induced bundling yields spatially inhomogeneous structures.

DOI: 10.1103/PhysRevE.72.060901 PACS number(s): 87.16.−b, 05.65.+b, 47.54.+r

Soft active systems are exciting examples of a 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 that the cell accesses as part of its cycle [3–5].

Recent theoretical studies of the dynamics of solutions of active filaments include numerical simulations [4,5], mesoscopic mean-field kinetic equations [6–9], and hydrodynamic equations where the system is described in terms of a few coarse-grained fields whose dynamics is inferred from symmetry considerations [10–13]. Previous work has focused on how motor activity renders homogeneous states unstable to the formation of spatial structures, such as bundles, vortices, or asters. In this paper we show that motor activity also controls the possible *homogeneous* states of the system [14]. In particular we find that the formation of a nonequilibrium polarized phase at low densities can be driven by motor *polarity* without filament polymerization [10,13]. The spatial structures observed in experiments are composed of the topological defects of a bulk *polarized* state (*XY* model) [4]. In order to describe them one must then understand how such a state can be generated in a system with length-stabilized filaments. A macroscopic polarized phase was not obtained in our earlier work and changes qualitatively the phase diagram of active solutions as compared to what is presented in Ref. [9].

We describe the system by a concentration of polar filaments $f(\mathbf{r},\hat{\mathbf{n}},t)$ in two dimensions ($d=2$), modeled as hard rods of *fixed* length ℓ and diameter b ($\ell \gg b$) at position $\mathbf{r}$ with filament polarity characterized by a unit vector $\hat{\mathbf{n}}$, and a density of motor clusters $m(\mathbf{r},t)$. The filament and motor concentrations satisfy the equations

$$\partial_t f = -\nabla\cdot\mathbf{J}_f - \boldsymbol{\mathcal{R}}\cdot\mathcal{J}, \quad (1)$$

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

where $\boldsymbol{\mathcal{R}}=\hat{\mathbf{n}}\times\partial_{\hat{\mathbf{n}}}$ and the translational $(\mathbf{J}_f,\mathbf{J}_m)$ and rotational $(\mathcal{J})$ currents have diffusive, excluded volume and active contributions. The rotational current is $\mathcal{J}=\mathcal{J}^D+\mathcal{J}^X+\mathcal{J}^A$, with a diffusive current $\mathcal{J}^D(\mathbf{r},\hat{\mathbf{n}},t)=-D_r\boldsymbol{\mathcal{R}}f(\mathbf{r},\hat{\mathbf{n}},t)$ and a contribution from excluded volume, $\mathcal{J}^X(\mathbf{r},\hat{\mathbf{n}},t)=-(D_r/k_BT)f(\mathbf{r},\hat{\mathbf{n}},t)\boldsymbol{\mathcal{R}}V_X(\mathbf{r},\hat{\mathbf{n}},t)$, with

$$V_X(\mathbf{r},\hat{\mathbf{n}}_1,t)=k_BT\int_{s_1}\int_{s_2}\int_{\hat{\mathbf{n}}_2}|\hat{\mathbf{n}}_1\times\hat{\mathbf{n}}_2|f(\mathbf{r}+\boldsymbol{\xi},\hat{\mathbf{n}}_2,t), \quad (3)$$

where $\boldsymbol{\xi}=\hat{\mathbf{n}}_1 s_1-\hat{\mathbf{n}}_2 s_2$ is the separation of the centers of mass of the two filaments and $\int_s\ldots=\int_{-\ell/2}^{+\ell/2}ds\ldots$ denotes an integration along the length of the filament, parametrized by s. The active contribution to the rotational current (low density approximation) is

$$\mathcal{J}^A(\mathbf{r},\hat{\mathbf{n}}_1,t)=b^2\int_{s_1}\int_{s_2}\int_{\hat{\mathbf{n}}_2}\boldsymbol{\omega}^A(\hat{\mathbf{n}}_1,\hat{\mathbf{n}}_2)m(\mathbf{r}+s_1\hat{\mathbf{n}}_1,t)\times f(\mathbf{r},\hat{\mathbf{n}}_1,t)f(\mathbf{r}+\boldsymbol{\xi},\hat{\mathbf{n}}_2,t), \quad (4)$$

where the motor-induced angular velocity is written as

$$\boldsymbol{\omega}^A=2(\gamma_0+\gamma_1\hat{\mathbf{n}}_1\cdot\hat{\mathbf{n}}_2)(\hat{\mathbf{n}}_1\times\hat{\mathbf{n}}_2). \quad (5)$$

It consists of two parts, corresponding to two classes of motor clusters (see Fig. 1): polar clusters that tend to bind to filaments with similar polarity ($\gamma_0/\gamma_1 \gg 1$) [4,5], and nonpolar clusters that bind to filament pairs of any orientation ($\gamma_0/\gamma_1 \ll 1$) [15]. Polar clusters ($\gamma_0\neq 0$) were not considered in our earlier paper [9], but are crucial for the formation of a polarized phase [16] (see also Ref. [14]). Both γ_0 and γ_1 increase with the increasing binding rate of the clusters to the filament. A passive polar crosslink will also have this effect

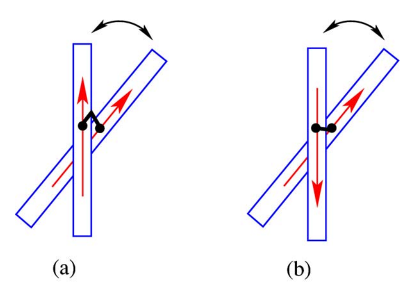

FIG. 1. (Color online) Polar and nonpolar clusters interacting with polar filaments. Assuming that clusters always bind to the smallest angle, polar clusters ($g\to\infty$) bind only to filaments in configuration (a) while nonpolar clusters ($g=0$) bind to both configurations equally.

[17], but with a different dependence on Adenosin Triphosphate (ATP) consumption.

The translational currents are $\mathbf{J}_f=\mathbf{J}^D+\mathbf{J}^X+\mathbf{J}^A$ and

$$\mathbf{J}_m = - D_m \boldsymbol{\nabla} m + \chi \int_s \int_{\hat{\mathbf{n}}} \hat{\mathbf{n}} f(\mathbf{r},\hat{\mathbf{n}},t) m(\mathbf{r}+\hat{\mathbf{n}}s,t), \tag{6}$$

where χ depends on the speed and processivity of the motors. The filament diffusive current, $J_i^D=-D_{ij}\partial_j f$, is expressed in terms of a diffusion tensor $D_{ij}=(D_\parallel+D_\perp)\delta_{ij}/2+(D_\parallel-D_\perp)\hat{Q}_{ij}$ with $\hat{Q}_{ij}=\hat{n}_i\hat{n}_j-\frac{1}{2}\delta_{ij}$. The excluded volume contribution is $J_i^X=-(D_{ij}/k_BT)f\partial_j V_X$. The active contribution to the translational current is

$$J_i^A(\mathbf{r},\hat{\mathbf{n}}_1,t) = b^2 \int_{s_1} \int_{s_2} \int_{\hat{\mathbf{n}}_2} v_i^A(\hat{\mathbf{n}}_1,\hat{\mathbf{n}}_2,\boldsymbol{\xi}) m(\mathbf{r}+\hat{\mathbf{n}}_1 s_1,t) \times f(\mathbf{r},\hat{\mathbf{n}}_1,t) f(\mathbf{r}+\boldsymbol{\xi},\hat{\mathbf{n}}_2,t), \tag{7}$$

with $\mathbf{v}^A$ the motor-induced velocity, taken of the form

$$\mathbf{v}^A = \frac{\beta}{2}(\hat{\mathbf{n}}_2-\hat{\mathbf{n}}_1) + \frac{\alpha}{2}\frac{\boldsymbol{\xi}}{2\ell} - \lambda(\hat{\mathbf{n}}_1+\hat{\mathbf{n}}_2). \tag{8}$$

The parameters α, β, and λ have dimensions of velocity and depend on the angle between the filaments. The term proportional to β drives the separation of filaments of opposite polarity, while the λ contribution arises from the net velocity of the filament pair [18]. The negative sign reflects the fact that filament mean motion due to motor activity is opposite to their polarity. The contribution proportional to α arises from spatial variations in motor activity along the filament, such as motors stalling before detaching at the polar end. It drives bundling of filaments of the same polarity. These parameters where estimated in Ref. [19] via a microscopic model of motor-induced filament dynamics as $\beta \sim \lambda \sim u_0$, $\alpha \sim u_0(l_m/l) \ll u_0$, with u_0 the mean motor stepping rate and l_m the length scale (of order of the motor cluster size) for spatial variations in motor activity. As seen below, this term is crucial for developing inhomogeneities and pattern formation.

To study the macroscopic properties of the solution, we truncate the exact moment expansion of $f(\mathbf{r},\hat{\mathbf{n}},t)$ as

$$f(\mathbf{r},\hat{\mathbf{n}},t) = \frac{\rho(\mathbf{r},t)}{2\pi}\{1+2\mathbf{p}(\mathbf{r},t)\cdot\hat{\mathbf{n}}+4S_{ij}(\mathbf{r},t)\hat{Q}_{ij}\}, \tag{9}$$

keeping only the first three moments,

$$\int d\hat{\mathbf{n}} f(\mathbf{r},\hat{\mathbf{n}},t) = \rho(\mathbf{r},t) \quad \text{(density)},$$

$$\int d\hat{\mathbf{n}}\hat{\mathbf{n}} f(\mathbf{r},\hat{\mathbf{n}},t) = \rho(\mathbf{r},t)\mathbf{p}(\mathbf{r},t) \quad \text{(polarization)},$$

$$\int d\hat{\mathbf{n}}\hat{Q}_{ij} f(\mathbf{r},\hat{\mathbf{n}},t) = \rho(\mathbf{r},t)S_{ij}(\mathbf{r},t) \quad \text{(nematic order)}. \tag{10}$$

Homogeneous bulk steady states. We first consider the dynamical equations for a spatially homogeneous solution. In this case the only contributions to the equation of motion of the filament density come from rotational currents. The motor density has a constant mean value (we let $m_0=mb^2$) and the filament density, $f(\mathbf{r},\hat{\mathbf{n}},t)$, and its moments can be expressed in terms of their spatial averages, i.e., $(1/A)\int d\mathbf{r} S_{ij}(\mathbf{r},t)=S_{ij}(t)$, $(1/A)\int d\mathbf{r}\mathbf{p}(\mathbf{r},t)=\mathbf{p}(t)$, with A the area of the system. In the following, all lengths are measured in units of the filament length, ℓ. Averaging over the orientation $\hat{\mathbf{n}}$ using Eq. (9), we find that in a homogeneous system $\rho=\rho_0=$constant and

$$\partial_t p_i = -(D_r - m_0\rho_0\gamma_0)p_i + \left[\frac{8D_r}{3\pi} - m_0(2\gamma_0-\gamma_1)\right]\rho_0 S_{ij} p_j, \tag{11}$$

$$\partial_t S_{ij} = -\left[4D_r - \frac{8D_r\rho_0}{3\pi} - m_0\rho_0\gamma_1\right]S_{ij} + 2m_0\rho_0\gamma_0\left(p_i p_j - \frac{1}{2}\delta_{ij}p^2\right). \tag{12}$$

In a passive system ($\gamma_0=\gamma_1=0$) there is a transition from an isotropic state to a nematic state. A mean-field description of such a transition, which is continuous in two dimensions ($2d$) (but first order in $3d$), requires cubic terms in the nematic order parameter in the equation of motion. The transition here is identified with the change in sign of the decay rate of S_{ij}, which signals an instability of the isotropic homogeneous state. This occurs when excluded volume effects dominate at a density $\rho_N=3\pi/2$. The homogeneous state is isotropic for $\rho_0<\rho_N$ and nematic for $\rho_0>\rho_N$. No homogeneous polarized state with a nonzero mean value of $\mathbf{p}$ is obtained in a passive solution.

We now turn to an active system. We introduce a dimensionless filament density, $\tilde{\rho}=\rho_0/\rho_N$, a dimensionless motor cluster activity, $\mu=\rho_N m_0\gamma_1/D_r$, and a parameter measuring the polarity of motor clusters, $g=\gamma_0/\gamma_1$ with $g=0$ corresponding to nonpolar clusters. Time is measured in units of D_r^{-1}. The steady states of Eqs. (11) and (12) are the stable solutions of

$$0 = -a_1 p_i + b_1\tilde{\rho}S_{ij}p_j, \tag{13}$$

$$0 = -a_2 S_{ij} + b_2\tilde{\rho}\left(p_i p_j - \frac{1}{2}\delta_{ij}p^2\right), \tag{14}$$

where

$$a_1 = 1 - \tilde{\rho}g\mu, \tag{15}$$

$$a_2 = 4[1-\tilde{\rho}(1+\mu/4)], \tag{16}$$

and $b_1=4+\mu(1-2g)$, $b_2=2g\mu$. At low density the only solution is $p_i=0$ and $S_{ij}=0$ and the system is isotropic (I). The homogeneous isotropic state can become unstable in two ways. As in the passive case, a change in sign of the coefficient a_2 signals the transition to a nematic (N) state. Motor activity lowers the density for the I-N transition that occurs at $\rho_{IN}(\mu)=1/(1+\mu/4)$. At $\tilde{\rho}>\rho_{IN}(\mu)$ the solution acquires nematic order, with $S_{ij}^0=S_0(n_i n_j-\delta_{ij}/2)$, where the unit vector

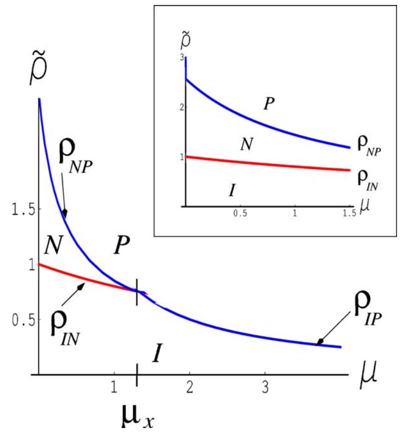

FIG. 2. (Color online) The homogeneous phase diagram for $g > 1/4$ (the figure is for $g=1$ and $c_2=50$). For $\mu > \mu_x$, where ρ_{IN} and ρ_{IP} intersect, no N state exists and the system goes directly from the I to the P state. The phase diagram for $g<1/4$ is shown in the inset ($g=1/10$, $c_2=50$).

$\mathbf{n}$ denotes the direction of broken symmetry. We obtain an expression for the amount of nematic order (S_0) by adding a cubic term $-c_2\tilde{\rho}^2 S_{kl}S_{kl}S_{ij}$ to Eq. (14) giving $S_0 = (1/\tilde{\rho})\sqrt{-2a_2/c_2}$. The isotropic state can also become linearly unstable via the growth of polarization fluctuations in any arbitrary direction. This occurs above a second critical filament density, $\rho_{IP}(\mu)=1/(g\mu)$, defined by the change in sign of the coefficient a_1 controlling the decay of polarization fluctuations. For $\tilde{\rho} > \rho_{IP}(\mu)$ the homogeneous state is polarized (P), with $p_i \neq 0$. The alignment tensor also has a nonzero mean value in the polarized state as it is slaved to the polarization. One can identify two scenarios depending on the value of g.

(i) For $g<1/4$, the density ρ_{IP} is always larger than ρ_{IN} and a region of nematic phase exists for all values of μ. At sufficiently high filament and motor densities, the nematic state also becomes unstable. Fluctuations in the alignment tensor are uniformly stable for $a_2<0$, but polarization fluctuations along the direction of broken symmetry become unstable for $a_1 \leqslant \tilde{\rho} b_1 S_0/2$, i.e., above a critical density

$$\rho_{NP} = \frac{1}{g\mu}\left[1 + \frac{b_1^2}{c_2 R}\left(1 - \sqrt{1 + \frac{2c_2R(1-R)}{b_1^2}}\right)\right], \quad (17)$$

where $R=\rho_{IN}/\rho_{IP}$. The polarized state at $\tilde{\rho} > \rho_{NP}$ has $p_i^0 = p_0 n_i$ and $S_{ij}^0 = S_P(n_i n_j - \delta_{ij}/2)$, where

$$p_0^2 = \frac{2a_1a_2}{\tilde{\rho}^2 b_1 b_2}\left[1 - \left(\frac{2a_1}{b_1\tilde{\rho}S_0}\right)^2\right],$$

$$S_P = S_0\sqrt{1 - \frac{\tilde{\rho}^2 b_1 b_2}{2a_1a_2}p_0^2} = 2\left|\frac{a_1}{\tilde{\rho}b_1}\right|.$$

The "phase diagram" is shown in the inset of Fig. 2.

(ii) When $g>1/4$, the boundaries for the I-N and the N-P transitions cross at $\mu_x = 1/(g-1/4)$ where $\rho_{IN}=\rho_{IP}=\rho_{NP}$ and the phase diagram has the topology shown in Fig. 2. For $\mu>\mu_x$ the system goes directly from the I to the P state at ρ_{IP}, without an intervening N state. At the onset of the polarized state the alignment tensor is again slaved to the polarization field, $S_{ij} = (b_2\tilde{\rho}/a_2)(p_i p_j - \frac{1}{2}\delta_{ij}p^2)$, and $p_i = p_0 n_i$ and p_0 are determined by cubic terms in Eq. (11).

If $\gamma_1=0$, with $\gamma_0 \neq 0$, the I-N transition is independent of motor density and always occurs at $\rho_0=\rho_N$.

Spatially inhomogeneous states. In vitro experiments have shown that uniform states are often unstable to the formation of complex spatial structures. The instability arises from the growth of spatial fluctuations in the hydrodynamic fields. In particular, the rate of motor-induced filament bundling can exceed that of filament diffusion yielding the unstable growth of density inhomogeneities [6–9]. States with spatially varying orientational order, where the filaments spontaneously arrange in vortex and aster structures, are also possible [10,13,14]. To understand the different nature of the instability from each homogeneous state, we have obtained coupled equations for the first three moments of the filament concentration defined in Eq. (9) by an expansion in spatial gradients described elsewhere [9,19]. With these equations we then study the dynamics of spatially varying fluctuations in the hydrodynamic fields. These are the fields whose characteristic decay times exceed any microscopic relaxation time and become infinitely long lived at long wavelengths. We find that the low frequency hydrodynamic modes of this active system are determined by fluctuations in the conserved densities and in variables associated with broken symmetries. A change in sign in the decay rate of these modes signals an instability of the macroscopic state of interest. For simplicity we only discuss here the case of constant motor density.

Isotropic state. This was studied in Ref. [9]. The only hydrodynamic variable is the filament density, ρ. The decay rate of Fourier components of $\delta\rho=\rho-\rho_0$ at wave vector k is controlled by the interplay of diffusion and motor-induced bundling described by α. The homogeneous I state is unstable at large length scales for $\rho_0>\rho_B$, with $\rho_B \sim D_\parallel/(m_0\alpha) \sim \gamma_1/(\alpha\mu)$. The homogeneous state is stabilized at short scales by excluded volume effects and higher order terms in the density gradients.

Polarized state. The hydrodynamic modes in the P state are those associated with fluctuations in the filament density and in the director field, $\mathbf{n}(\mathbf{r},t)$, defined by $\mathbf{p}(\mathbf{r},t) = p(\mathbf{r},t)\mathbf{n}(\mathbf{r},t)$, with $|\mathbf{n}|=1$. The coupled hydrodynamic modes describing the decay of Fourier components of density, $\delta\rho$ and director fluctuations, $\delta\mathbf{n}=\mathbf{n}-\hat{\mathbf{y}}=\hat{\mathbf{x}}\delta n_x$ of wave vector $\mathbf{k}$ are always propagating, with velocity whose magnitude and direction are controlled by *both* the activity parameters β and λ. For $\mathbf{k}$ along the broken symmetry direction, the modes decouple (i.e., $\delta\rho \sim e^{z_\rho(k)t}, \delta n_x \sim e^{z_n(k)t}$) and are given by

$$z_\rho = ikc_1\tilde{\rho}\mu\tilde{\beta} - \frac{k^2}{8}\left[1 - \frac{g\mu}{6} - 20\tilde{\rho}\mu\tilde{\alpha}\right], \quad (18)$$

$$z_n = -ikc_2\tilde{\rho}\mu\tilde{\beta} - \frac{5k^2}{48}\left[1 + \frac{2}{5}\tilde{\rho}\mu(g - 6\tilde{\alpha})\right], \quad (19)$$

where $\tilde{\beta}=\beta/\gamma_1$, $\tilde{\alpha}=\alpha/\gamma_1$, and c_1 and c_2 are numbers of order 1. We have used $D_\parallel = \ell^2 D_r/6$ and $\lambda \sim \beta$. Like the I state, the homogeneous P state is linearly unstable for $\rho_0 > \rho_B$. The nature of the instability changes, however, from diffusive in the I state to oscillatory in the P state, suggesting that spatially inhomogeneous oscillatory structures, such as vortices, may be stable at high filament or motor densities. The rotational effects described by $\mu \sim \gamma_1$ stabilize director fluctuations, but destabilize the density.

Nematic state. The hydrodynamic variables in the N state are again the filament density and a director field $\mathbf{n}(\mathbf{r},t)$, defined in terms of the alignment tensor as $S_{ij}=S_0\left(n_i n_j - \frac{1}{2}\delta_{ij}\right)$. The decay of density and director fluctuations is controlled by coupled diffusive hydrodynamic modes. The modes decouple for $\mathbf{k}$ along the broken symmetry direction, with

$$z_\rho = -k^2\left[\frac{1}{6} - 2\tilde{\rho}\mu\tilde{\alpha}\right], \tag{20}$$

$$z_n = -\frac{k^2}{8}\left[1 + \frac{19}{36}\tilde{\rho}\mu\right], \tag{21}$$

and the homogeneous N state is destabilized by the growth of density fluctuations for $\rho_0 > \rho_B$. For the arbitrary direction of $\mathbf{k}$ relative to the direction of broken symmetry, director fluctuations also become unstable at high density, but the fastest growing mode is always associated with the buildup of density inhomogeneities. In contrast to the P state, the instability is always diffusive.

We have studied the phase behavior of polar filaments interacting with polar clusters. In addition to the *isotropic* phase, both homogeneous *polarized* and *nematic* states can be obtained as a function of filament density and motor activity and polarity. Each of these homogeneous states is unstable at high filament and motor densities where it is replaced by complex spatial structures. The instability occurs

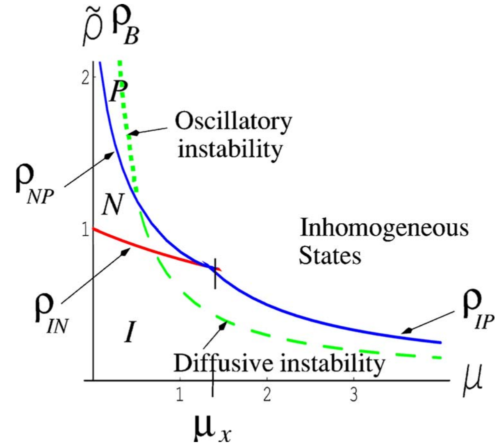

FIG. 3. (Color online) Bundling renders homogeneous states unstable for $\rho_0 > \rho_B$, where they are replaced by inhomogeneous solutions. The ρ_B line may lie above the $\rho_{NP}-\rho_{IP}$ line or cross through the N and I states, as shown in the figure ($g=1$, $c_2=50$, $\gamma_1/\alpha=0.6$), depending on the value of γ_1/α. The instability of the I and N states is diffusive (dashed line), while the instability of the P state is oscillatory (dotted line).

for $\rho_0 > \rho_B \sim \gamma_1/(\alpha\mu)$ and is controlled by the bundling rate α, which destabilizes all homogeneous states, albeit through different (diffusive versus oscillatory) mechanisms. The location of the instability line in the phase diagram depends on γ_1/α. If $\gamma_1/\alpha > 1/g = \gamma_1/\gamma_0$, then $\rho_B > \rho_P$ and the homogeneous nematic state is always stable, when it exists. If $\gamma_1/\alpha < 1/g = \gamma_1/\gamma_0$, then $\rho_B < \rho_P$ (Fig. 3) and all homogeneous states become unstable.

T.B.L. acknowledges the support of the Royal Society. M.C.M. acknowledges support from the National Science Foundation, Grants No. DMR-0305407 and DMR-0219292.

[1] B. Alberts *et al.*, *Molecular Biology of the Cell* (Garland, New York, 2002).
[2] J. Howard, *Mechanics of Motor Proteins and the Cytoskeleton* (Sinauer, New York, 2000).
[3] K. Takiguchi, J. Biochem. (Tokyo) **109**, 520 (1991); R. Urrutia *et al.*, Proc. Natl. Acad. Sci. U.S.A. **88**, 6701 (1991).
[4] F. J. Nédélec *et al.*, Nature (London) **389**, 305 (1997).
[5] T. Surrey *et al.*, Science **292**, 1167 (2001).
[6] H. Nakazawa and K. Sekimoto, J. Phys. Soc. Jpn. **65**, 2404 (1996).
[7] K. Kruse and F. Jülicher, Phys. Rev. Lett. **85**, 1778 (2000); Phys. Rev. E **67**, 051913 (2003).
[8] K. Kruse, S. Camalet, and F. Jülicher, Phys. Rev. Lett. **87**, 138101 (2001).
[9] T. B. Liverpool and M. C. Marchetti, Phys. Rev. Lett. **90**, 138102 (2003); **93**, 159802 (2004); F. Ziebert and W. Zimmermann, *ibid.* **93**, 159801 (2004).
[10] H. Y. Lee and M. Kardar, Phys. Rev. E **64**, 056113 (2001).
[11] R. A. Simha and S. Ramaswamy, Phys. Rev. Lett. **89**, 058101 (2002).
[12] K. Kruse *et al.*, Phys. Rev. Lett. **92**, 078101 (2004).
[13] S. Sankararaman *et al.*, Phys. Rev. E **70**, 031905 (2004).
[14] I. S. Aranson and L. S. Tsimring, Phys. Rev. E **71**, 050901(R) (2005).
[15] D. Humphrey *et al.*, Nature (London) **416**, 412 (2002).
[16] A model of the cluster as a torsional spring of constant κ gives $\gamma_0 \sim D_r\kappa/k_BT$.
[17] M. Tempel, G. Isenberg, and E. Sackmann, Phys. Rev. E **54**, 1802 (1996).
[18] Due to the anisotropy of the diffusion tensor, the motor cluster can induce a net velocity of the filament pair even without external forces [19].
[19] T. B. Liverpool and M. C. Marchetti, Europhys. Lett. **69**, 846 (2005).