

Anomalous behavior of the diffusion coefficient in thin active films

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Abstract. Inspired by recent experiments in cell biology, we elucidate the visco-elastic properties of an active gel by studying the dynamics of a small tracer particle inside it. In a stochastic hydrodynamic approach for an active gel of finite thickness L , we calculate the mean square displacement of a particle. These particle displacements are governed by fluctuations in the velocity field. We characterize the short-time behavior when the gel is a solid as well as the limit of long times when the gel becomes a fluid and the particle shows simple diffusion. Active stresses together with local polar order give rise to velocity fluctuations that lead to characteristic behaviors of the diffusion coefficient that differ fundamentally from those found in a passive system: the diffusion coefficient can depend on system size and diverges as L approaches an instability threshold. Furthermore, the diffusion coefficient becomes independent of the particle size in this case.

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1. Introduction

The rheological properties of a complex fluid are often measured by using ‘passive’ micro-rheology. In this approach, the visco-elastic moduli are calculated from the generalized Stokes–Einstein relation [1] by measuring the fluctuations of a tracer particle of micron size [2] embedded in the complex fluid. This experimental technique is, however, restricted to thermal equilibrium systems for which the fluctuation–dissipation theorem is valid, the generalized Stokes–Einstein relation being a specific case of this theorem. In a non-equilibrium system such as the actin cytoskeleton of a eukaryotic cell, measurements of the local rheology using ‘active micro-rheology’ and those of the fluctuations using ‘passive micro-rheology’ give different information. This is well illustrated by recent *in vitro* experiments where the fluctuation–dissipation theorem is shown to be violated at frequencies smaller than a few hertz [3] in an acto-myosin gel. The non-equilibrium character of the acto-myosin gel here is due to the consumption of adenosine-tri-phosphate (ATP), which is constantly hydrolysed into adenosine-di-phosphate (ADP) and inorganic phosphate.

Still, in a cell, passive rheological measurements following the motion of tracer particles are of considerable interest, as they yield information about the underlying small-scale dynamics and interactions [4] and therefore give insight into the nature of motions and transport of biological materials inside the cell. An example is given by recent experiments on the motion of secretory vesicles that are transported through the actin cortical layer in human carcinoid BON cells [5]. The mean square displacement $g(t) = \langle [\mathbf{x}(t) - \mathbf{x}(0)]^2 \rangle$ of a vesicle of instantaneous position $\mathbf{x}(t)$, attached to the cytoskeleton, is measured. The broad picture emerging from these experimental results is complex and interesting: one finds directed motion at short times and diffusive motion at long times but also phases of quasi-arrested motion and complex crossovers [4, 5].

The aim of this paper is to study the diffusion of a probe particle in a thin film of an active material, see figure 1. Surprisingly, we find that the diffusion coefficient has a component that is independent of the particle radius. In addition, this component diverges near an instability called the Frederiks transition and thus generically dominates any Stokes-like contribution.

We obtain these results from a stochastically driven coarse-grained hydrodynamic description of viscoelastic active gels [6, 7]. We calculate the motion of a small bead of size a inside a thin active gel film, with polar order, described by a polarization field p_α , $\alpha = x, y, z$. The film is infinite along the x, y plane, but has a finite thickness L in the z -direction. A typical example that we have in mind is the cortical actin layer in a cell where the orientation of the actin filaments can have a component parallel to the cell membrane. It has recently been shown that a liquid active gel film of thickness L with polarization either parallel or perpendicular

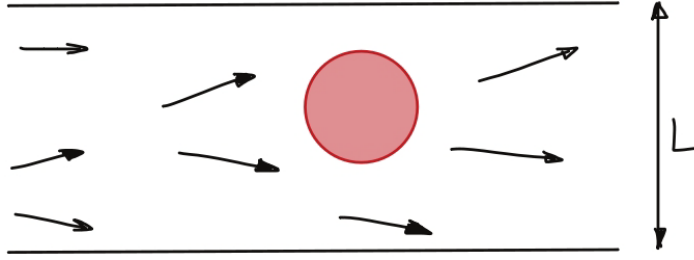


Figure 1. Schematic representation of a bead (red) diffusing in a thin active film of thickness L . The arrows show fluctuations of the polarity field.

to its surface has a spontaneous flow transition above a critical activity threshold, which has been called a Frederiks transition [8–10]. The transition is driven by the coupling between the polarization orientation and the active stress. The new anomalous contribution to the diffusion coefficient diverges near this transition; however, our results are more general and also apply to situations before the transition is reached. It is not yet clear whether the Frederiks transition plays a role in cellular systems such as cortical actin or the lamellipodia of moving cells.

2. Diffusion in an active thin film

We consider an incompressible viscoelastic film with a viscoelastic relaxation time τ . At short times, smaller than τ , the film behaves as a solid with a shear modulus E , and the mean squared displacement of a bead of size a remains bounded: $g(t) \simeq \frac{kT}{\pi E a}$. At long times $t \gg \tau$, the film is a liquid and the motion of the particle is diffusive. As the film is anisotropic, one must define a diffusion tensor $D_{\alpha\beta}$. For a particle at the origin at $t = 0$, it is defined by $g_{\alpha\beta}(t) = \langle x_\alpha(t)x_\beta(t) \rangle = 2D_{\alpha\beta}t$ for large t . If the particle follows the velocity field, $v_\alpha(\mathbf{x}, \mathbf{t})$, of the surrounding active fluid, the diffusion tensor can be written as

$$D_{\alpha\beta} = \frac{1}{V} \int_0^\infty dt \int \frac{d^3k}{(2\pi)^3} \langle e^{i\mathbf{k}[\mathbf{x}(t)-\mathbf{x}(0)]} \tilde{v}_\alpha(\mathbf{k}, 0) \tilde{v}_\beta(-\mathbf{k}, t) \rangle, \quad (1)$$

where $\tilde{v}_\alpha(\mathbf{k}, \mathbf{t})$ is the spatial Fourier transform of the velocity field and V denotes the system volume. In the following, we discuss both the diffusion tensor and the effective elastic modulus viewed by the bead at short times.

The force balance in an incompressible active gel can be expressed as $\partial_\beta(\tilde{\sigma}_{\alpha\beta} + \sigma_{\alpha\beta}^a - P\delta_{\alpha\beta} + \sigma_{\alpha\beta}^e) = 0$, where $\tilde{\sigma}_{\alpha\beta}$ denotes the traceless part of the symmetric deviatoric stress and the antisymmetric deviatoric stress is given by

$$\sigma_{\alpha\beta}^a = \frac{1}{2}(p_\alpha h_\beta - p_\beta h_\alpha). \quad (2)$$

Here $h_\alpha = -\delta F/\delta p_\alpha$ is the orientational field conjugate to the polarization p_α , where $F = \int d^3r f$ denotes the polarization free energy with free energy density f . The pressure P plays the role of a Lagrange multiplier to impose the incompressibility constraint $\partial_\alpha v_\alpha = 0$. Note that in a polar system the equilibrium stress can have anisotropies described by the Ericksen stress

$$\sigma_{\alpha\beta}^e = -\frac{\partial f}{\partial(\partial_\beta p_\gamma)} \partial_\alpha p_\gamma. \quad (3)$$

In the following, we consider the simple case when the polarity field has constant magnitude $p_\gamma p_\gamma = 1$ and we ignore stress contributions due to the Ericksen stress, i.e. we approximate $\sigma_{\alpha\beta}^e \simeq 0$. The constitutive equations of the active gel then read [7]

$$\left(1 + \tau \frac{D}{Dt}\right) \left\{ \tilde{\sigma}_{\alpha\beta} + \zeta \Delta \mu q_{\alpha\beta} + \frac{v_1}{2} \left(p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3} p_\gamma h_\gamma \delta_{\alpha\beta} \right) \right\} = 2\eta v_{\alpha\beta} + \xi_{\alpha\beta}^\sigma, \quad (4)$$

$$\frac{D}{Dt} p_\alpha = \left(1 + \tau \frac{D}{Dt}\right) \frac{1}{\gamma_1} h_\alpha - v_1 p_\beta \tilde{v}_{\alpha\beta} + \xi_{\perp\alpha}. \quad (5)$$

Here

$$q_{\alpha\beta} = \left(p_\alpha p_\beta - \frac{1}{3} \delta_{\alpha\beta} \right) \quad (6)$$

is the nematic tensor. The traceless part of the symmetric velocity gradient tensor is denoted by $\tilde{v}_{\alpha\beta}$. The shear viscosity at long times is denoted by η , γ_1 is the rotational viscosity and v_1 is the flow alignment parameter, which is a number of the order of 1. The viscoelastic properties of the gel are described by a Maxwell model with a relaxation time τ of elastic stresses. The noise correlations are given by

$$\langle \xi_{\alpha\beta}^\sigma(t, \mathbf{x}) \xi_{\gamma\delta}^\sigma(t', \mathbf{x}') \rangle = 2kT\eta \left[\delta_{\alpha\gamma} \delta_{\beta\delta} + \delta_{\alpha\delta} \delta_{\beta\gamma} - \frac{2}{3} \delta_{\alpha\beta} \delta_{\gamma\delta} \right] \delta(t - t') \delta(\mathbf{x} - \mathbf{x}'), \quad (7)$$

$$\langle \xi_{\perp\alpha}(t, \mathbf{x}) \xi_{\perp\beta}(t', \mathbf{x}') \rangle = 2 \frac{kT}{\gamma_1} [\delta_{\alpha\beta} - p_\alpha p_\beta] \delta(t - t') \delta(\mathbf{x} - \mathbf{x}'), \quad (8)$$

where k is the Boltzmann constant and T denotes temperature.

We now consider a film in a non-flowing stable steady state with a polarization unit vector p_α perpendicular to the surface of the film (similar results are obtained for a polarization parallel to the film). We consider a small perturbation to this non-flowing steady state where the polarization is tilted and where the active gel flows. From the velocity–velocity correlation functions, we determine the root mean square displacement tensor at long and short times. We discuss the bead fluctuations in both the viscous and the elastic limit of the viscoelastic active gel.

As the calculations are rather tedious, we first give scaling-like arguments which result from a simplified analysis of the problem. We then give the results of the full fluctuating hydrodynamic equations. For simplicity, we describe the tilt of the polarity with respect to the z -axis normal to the film surface by a single small angle θ . The rate of variation of the angle θ in the viscous limit ($\tau = 0$) is due to the elastic nematic torque with a Frank elastic constant K and according to equation (5) to a coupling to the strain rate u ,

$$\frac{\partial \theta}{\partial t} = \frac{K}{\gamma_1} \nabla^2 \theta - v_1 u + \xi_{\perp}(\mathbf{x}, t). \quad (9)$$

We have added in this equation the thermal noise of the polarization fluctuations $\xi_{\perp}(\mathbf{r}, t)$, which has zero mean and correlations given by $\langle \xi_{\perp}(\mathbf{x}, t) \xi_{\perp}(\mathbf{x}', t') \rangle = 2(kT/\gamma_1) \delta(t - t') \delta(\mathbf{x} - \mathbf{x}')$. We ignore here the tensorial character of the strain rate and consider u as one of its typical components.

If the polarization angle θ does not vanish, the active stress is finite and is compensated for by the viscous stress in the film

$$\eta u \simeq \zeta \Delta \mu \theta, \quad (10)$$

where we have for simplicity ignored the noise in the stress. Including this noise does not change qualitatively the final result. The two equations, (9) and (10), can be solved by Fourier expansion both in space and in time, writing the polarization angle as $\theta(\mathbf{x}, t) = \sum_n \sin(n\pi z/L) \int d\omega \int \frac{d\mathbf{q}}{(2\pi)^2} \exp i(\mathbf{q}\mathbf{r} - \omega t) \tilde{\theta}(n, \omega, \mathbf{q})$. Here, the position vector is $\mathbf{x} = (\mathbf{r}, z)$ with \mathbf{r} denoting the position in the plane parallel to the film, and the wavevector is $\mathbf{k} = (\mathbf{q}, n\pi/L)$ with \mathbf{q} denoting the wavevector parallel to the plane, while n describes the Fourier mode perpendicular. In the following, we focus only on the unstable mode $n = 1$. The Fourier transform of the polarization angle satisfies the equation

$$-i\omega\tilde{\theta} = \frac{1}{\tau_q}\tilde{\theta} + \tilde{\xi}_\perp(\omega), \quad (11)$$

where the relaxation time is given by $\tau_q^{-1} = -\frac{v_1}{\eta}[(|\zeta\Delta\mu| - \zeta\Delta\mu_c) - \frac{\eta K q^2}{v_1\gamma_1}]$. We have defined here the activity threshold for the flow instability of the thin active film $\zeta\Delta\mu_c = \frac{\eta K}{v_1\gamma_1 L^2}$. If the active stress $|\zeta\Delta\mu|$ is larger than this threshold, the non-flowing steady state is unstable and the film spontaneously flows. In this paper, we focus on the vicinity of the Frederiks transition. The polarization angle and the velocity correlation functions can be directly calculated from equation (11) leading to

$$\langle \tilde{v}(q, \omega) \tilde{v}(q', \omega') \rangle = \frac{kT\gamma_1(\zeta\Delta\mu)^2}{K^2 L \eta^2 (q^2 + 1/L^2)} \frac{1}{(\gamma_1\omega/K)^2 + (q^2 + q_c^2)^2} (2\pi)^3 \delta(\mathbf{q} + \mathbf{q}') \delta(\omega + \omega'), \quad (12)$$

where we have defined the wavevector q_c such that $q_c^2 = (\gamma_1 v_1/\eta)(\zeta\Delta\mu_c - |\zeta\Delta\mu|)/K$. In order to calculate the diffusion constant, we first approximate equation (1), assuming that the fluctuations of position and velocity are uncorrelated. We thus write the diffusion constant as

$$D \simeq \frac{1}{3V} \int_0^\infty dt \int \frac{d^3k}{(2\pi)^3} \langle e^{i\mathbf{k}[\mathbf{r}(t) - \mathbf{r}(0)]} \rangle \langle \tilde{v}(\mathbf{k}, 0) \tilde{v}(-\mathbf{k}, t) \rangle. \quad (13)$$

At long times, the motion is diffusive and $\langle e^{i\mathbf{k}[\mathbf{r}(t) - \mathbf{r}(0)]} \rangle = \exp(-Dk^2t)$ where D is the diffusion constant for particle motion parallel to the surface. The time-correlation function of the velocity is obtained by inverse Fourier transformation of equation (12)

$$\langle \tilde{v}(\mathbf{q}, 0) \tilde{v}(\mathbf{q}', t) \rangle = \frac{kT(\zeta\Delta\mu)^2 L}{\gamma_1 \eta^2} \tau_q \exp(-t/\tau_q) (2\pi)^2 \delta(\mathbf{q} + \mathbf{q}'), \quad (14)$$

where the velocity relaxation time τ_q for a wavevector \mathbf{q} obeys $\tau_q^{-1} = \frac{K}{\gamma_1}(q_c^2 + q^2)$. After calculation of the integral over the wavevectors, equation (13) gives an implicit equation for the diffusion constant

$$D \simeq \frac{kTL(\zeta\Delta\mu)^2}{DK\eta^2 q_c^2} \log\left(1 + \frac{\gamma_1 D}{K}\right). \quad (15)$$

In the vicinity of the Frederiks transition where $q_c \rightarrow 0$, the diffusion constant reads

$$D \simeq 2^{-1/2} \frac{K}{\gamma_1 v_1} \left(\frac{kT(\zeta\Delta\mu)^2}{LK\zeta\Delta\mu_c(\zeta\Delta\mu_c - |\zeta\Delta\mu|)} \right)^{1/2} \times \log^{1/2} \left(\frac{kT(\zeta\Delta\mu)^2}{v_1^2 LK\zeta\Delta\mu_c(\zeta\Delta\mu_c - |\zeta\Delta\mu|)} \right). \quad (16)$$

This is the main result of this paper. In a liquid active nematic film, the diffusion constant of a tracer particle diverges at the Frederiks transition as the inverse square root of the distance to the

transition threshold. This is consistent with the fact that above the transition, the film flows and the tracer no longer has a diffusive motion but it is convected by the flow at constant velocity. Another important result is that the diffusion constant does not depend on the size of the tracer particle but only on the thickness of the film.

This result can be understood by the following argument. Close to the Frederiks transition, the relaxation rate of the velocity fluctuations τ_q is long compared to the diffusion time ($1/Dq^2$) and the diffusion proceeds in a frozen fluctuating velocity field. The velocity thus fluctuates in space and the diffusing particle follows these velocity fluctuations. The correlation length of the velocity fluctuation is $1/q_c$ so that the diffusing particle makes at short times ballistic steps of the order of $1/q_c$ ⁶. The velocity during these ballistic steps is the instantaneous velocity of the particles that can be obtained by integrating the velocity correlation function given by equation (14) over the wavevectors $\langle \mathbf{v}^2 \rangle \simeq \frac{kTK}{L^3\gamma_1^2} |\log q_c a|$, which diverges logarithmically at the Frederiks transition. The diffusion constant is then $D \sim \langle \mathbf{v}^2 \rangle^{1/2}/q_c$ in agreement with equation (16). These scaling results are confirmed by a complete calculation using the full hydrodynamic equations of [7], which we give in the appendix. The actual calculation which treats correctly the tensorial character of the strain rate tensor and includes all sources of noise only leads to different prefactors in the scaling law.

At times shorter than the viscous relaxation time of the nematic active gel, the film has a solid-like behavior. In the elastic regime, the shear modulus is given by $E = \eta/\tau$ and the rotational modulus by $G = \gamma_1/\tau$. We introduce the local deformation δ such that the shear rate is $u = \frac{\partial \delta}{\partial t}$ and write the equations of motion (4) and (5) for the deformation δ and for the polarization angle θ directly in Fourier space,

$$\begin{aligned} -i\omega\eta\tilde{\delta} &= (1 - i\omega\tau)\zeta\Delta\mu\tilde{\theta} + \tilde{\xi}^\sigma, \\ -i\omega\tilde{\theta} &= -\frac{K(q^2 + 1/L^2)}{\gamma_1}(1 - i\omega\tau) + \nu_1 i\omega\tilde{\delta} + \tilde{\xi}_\perp. \end{aligned} \quad (17)$$

We have added there thermal noise in both equations. For simplicity, in a scaling-like argument, we ignore the noise associated with polarization. The correlation of the noise in the mechanical stress is $\langle \tilde{\xi}^\sigma(\mathbf{q}, \omega)\tilde{\xi}^{\sigma*}(\mathbf{q}', \omega') \rangle = 2kT\eta(2\pi)^3\delta(\omega + \omega')\delta(\mathbf{q} + \mathbf{q}')$. Looking at the limit where $\omega\tau$ is very large, we find the instability threshold for the Frederiks transition where polarization becomes tilted,

$$\nu_1\zeta\Delta\mu_c = E \left[1 + \frac{K}{GL^2} \right]. \quad (18)$$

This threshold is different from the threshold for the Frederiks transition of a liquid film described above.

From equation (17), we obtain the fluctuations in the deformation δ and thus the fluctuations in the tracer particle displacement δR^2 in the elastic regime by integration over frequency ω and wavevector \mathbf{q} :

$$\langle \delta R^2 \rangle \simeq \frac{kTLG}{EK} \left(1 + \frac{K}{GL^2} \right)^2 |\log q_c a| + \frac{kTK}{GEL}. \quad (19)$$

Note that in the solid regime, the mean square particle displacement does not increase with time as is also the case in chemical gels at long times. Here, we have defined the characteristic

⁶ Since we work with the generalized Stokes equation for the velocity field, the origin of this ballistic regime is *not* the inertia of the gel, but due to the (active and Onsager) stresses created by the polarization field \mathbf{p} .

wavevector q_c that vanishes at the transition by $q_c^2 = v_1(\zeta \Delta\mu_c - |\zeta \Delta\mu|) \frac{G}{EK}$. The root mean square displacement of the tracer particle therefore diverges logarithmically at the Frederiks transition. It also has a short-distance contribution which explicitly depends on the size of the particle and which increases upon decreasing the sizes. As above, this calculation ignores the tensorial character and thermal fluctuations of the polarization angle. However, detailed calculation given in the [appendix](#) predicts the same scaling behavior in the vicinity of the Frederiks transition.

Until now we have considered only the effects of the thermal noise. However, in an active gel the stochasticity is not entirely of thermal origin; there are non-thermal noises as well. In active polar gels, active stresses are generated, for example, by motor proteins which are driven by hydrolysis of ATP. The resulting chemical energy available per ATP molecule under physiological conditions is roughly $\Delta\mu \simeq 20kT$. Since this is significantly higher than kT , noises of non-thermal origin, and hence violation of the fluctuation dissipation theorem, are likely to be of relevance in a realistic description of cells. In the simplest case of an isotropic gel, such active stress fluctuations may be described by a zero-mean Gaussian noise with a variance (suppressing Cartesian indices) $\langle \xi^\sigma(\mathbf{x}, t) \xi^\sigma(\mathbf{x}', t') \rangle \simeq p(1-p)c_m f_0^2 a^2 \exp(-|t-t'|/\tau_m) \cos(\omega_0|t-t'|) \delta(\mathbf{x}-\mathbf{x}')$. This noise enters the constitutive equation for the stress (4). Here, a is the mesh size of the gel, c_m is the concentration of the independently acting force generators, which could be independent motors or small clusters and f_0 is the stall force of such force generators. Force generation is associated with a characteristic time scale τ_m . The probability for a force generator to be active and generate a force is p . The average active stress can be expressed in these quantities as $\zeta \Delta\mu \simeq c_m a f_0 p$. In general, groups of motors can generate noisy oscillations of frequency ω_0 [11]. For $\omega_0 = 0$, the noise fluctuations can be approximated on long time scales by variances $\langle \xi_\sigma(\mathbf{x}, t) \xi_\sigma(\mathbf{x}', t') \rangle \simeq p(1-p)c_m f_0^2 \delta(t-t') \delta(\mathbf{x})$. By comparing these noise strengths to the thermal noise, we can define the effective temperature of the active shear noise

$$kT_{\text{eff}} \simeq p(1-p) \frac{c_m f_0^2 a^2 \tau_m}{2\eta}. \quad (20)$$

3. Discussion and outlook

To summarize, we have studied the motion of a small bead inside a polar active gel slab of finite thickness L . The results obtained by the simplified scaling arguments discussed above can be confirmed by more detailed calculations taking the tensorial structure of the shear rates into account. This calculation is presented in the [appendix](#). We demonstrate that the active stress contributions to the diffusion and elastic coefficients diverge for constant thickness L at a critical value of the active stress $\zeta \Delta\mu_c$, or for constant active stress $\zeta \Delta\mu$ at a critical thickness L_c . The precise value of critical stress or critical length depends on other parameters characterizing the active fluid as well as on boundary conditions.

For times smaller than a characteristic relaxation time of polarization fluctuations $\tau_p = \gamma_1/(Kq_c^2)$ but still in the viscous regime ($\tau \ll t \ll \tau_p$), particle motion is ballistic and the velocity diverges as $v \sim \ln^{1/2}|\delta L/a|$ for small $\delta L = L_c - L$. In the long-time limit $t \gg \tau_p \gg \tau$, we recover a usual diffusive motion; however, the diffusion coefficient depends on the system size L and diverges as $D \sim \delta L^{-1} \ln^{1/2} \delta L$ for small δL . For small times, in the elastic limit ($t \ll \tau$), effective elastic constants depend on the system size L , in contrast with equilibrium elastic solids.

The overall picture that emerges is that the diffusion constants of tracer particles in viscoelastic thin active films and their rheological behaviors have activity-dependent contributions which depend on the system size L and diverge for small δL at the Frederiks transition. This is a general result for any active films, which is not limited to the vicinity of the transition. The dependences on L are suggestive of long-range correlations in the system, all of which are of active origin. In this work, we have looked at fluctuations around the reference state $\mathbf{p} = \hat{e}_z$ to obtain the linearized equations of motion. If the polarization $\langle \mathbf{p} \rangle$ is along the XY -plane in the reference state, all qualitative features including the scaling of the active stress contributions to the elasticity and diffusivity with the system size remain unchanged, although numerical coefficients would change. Our linearized theories do not yield superdiffusive motions as reported in [12]. Nonlinear effects may be important for understanding this feature. In fact, the divergence that we predict signals the long-range convective order and superdiffusive behavior which are expected to obey the Toner and Tu predictions for active stresses larger than the critical value [13].

There are several possible *in vivo* biological examples to which our results should apply. For example, Caspi *et al* [4] found in *in vivo* micro-rheology experiments inside a living cell that the MSD of an engulfed micro-sphere scales as $t^{3/2}$ at short times and crosses over to subdiffusive or ordinary diffusion scaling at large t . More recently, Huet *et al* [5] characterized the dynamics of secretory vesicles in experiments on the subplasmalemmal region of human carcinoid BON cells, and found the existence of different classes of motion, including constrained, directed and diffusive. These are reminiscent of our results on the temporal behavior of the bead MSD for different values of time. These experiments are not yet quantitative and cannot be used to provide a test of our theory. However, our work shows that novel physical mechanisms exist that are related to activity that might be important for understanding these experiments. In principle, one would like to develop new model experiments on active fluids and gels that are well controlled and quantitative. So far, such systems are only beginning to emerge. Note that the results presented here are very general and apply to a broad range of active thin films. In particular, we predict that in such systems, in addition to a Stokes-like contribution to the diffusion coefficient, there is also an activity-dependent contribution independent of the particle size but depending on film thickness.

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Appendix

Here, we discuss the full calculation of the velocity fluctuations of a particle of size a embedded in an active gel in the viscous and elastic regimes separately. We start from relations (2)–(5) and determine the conjugate field to the polarity vector h_α from a Frank free energy that describes the energies of splay, bend and twist deformations by parameters K_1 , K_2 and K_3 . For simplicity, we consider here the limit $K_1 \rightarrow \infty$ (i.e. the splay modes are suppressed, $\nabla \cdot \mathbf{p} = 0$). We furthermore introduce the constraints $\mathbf{p}^2 = 1$ and $\nabla \cdot \mathbf{v} = 0$, i.e. we ignore fluctuations in the

magnitude of \mathbf{p} and treat the fluid as incompressible. The two constraints $\nabla \cdot \mathbf{p} = 0$ and $p^2 = 1$ are imposed by the two Lagrange multipliers h_{\parallel} and ϕ in the free energy functional

$$F = \frac{1}{2} \int d^3x [K_2(\nabla \times \mathbf{p})^2 + K_3(\partial_z \mathbf{p})^2 - h_{\parallel} p^2 + 2\phi \nabla \cdot \mathbf{p}], \quad (\text{A.1})$$

where we have assumed that \mathbf{p} exhibits small fluctuations around a reference state $\mathbf{p}_0 = \hat{\mathbf{e}}_z$, the unit vector along the z -axis. The incompressibility constraint is imposed via the pressure P as the Lagrange multiplier.

The gel is confined between two surfaces at $z = 0$ and $z = L$. We impose the following boundary conditions: no flow across the boundary surfaces $v_z(z = 0) = 0$ and $v_z(z = L) = 0$ and vanishing surface shear stress at the boundaries: $\partial v_{\alpha}/\partial z = 0$, at $z = 0$ and $z = L$ for $\alpha = x, y$. In addition, we impose $\mathbf{p}(z = 0) = \hat{\mathbf{e}}_z$ and $\mathbf{p}(z = L) = \hat{\mathbf{e}}_z$. These boundary conditions are satisfied by the Fourier mode expansions

$$v_{\alpha}(\mathbf{x}, t) = \int \frac{d^2q}{(2\pi)^2} \frac{d\omega}{2\pi} \sum_n \tilde{v}_{\alpha}^n(\mathbf{q}, \omega) \exp[-i\omega t + i\mathbf{r} \cdot \mathbf{q}] \cos\left(\frac{n\pi z}{L}\right), \quad (\text{A.2})$$

$$v_z(\mathbf{x}, t) = \int \frac{d^2q}{(2\pi)^2} \frac{d\omega}{2\pi} \sum_n \tilde{v}_z^n(\mathbf{q}, \omega) \exp[-i\omega t + i\mathbf{r} \cdot \mathbf{q}] \sin\left(\frac{n\pi z}{L}\right), \quad (\text{A.3})$$

$$p_{\alpha}(\mathbf{x}, t) = \int \frac{d^2q}{(2\pi)^2} \frac{d\omega}{2\pi} \sum_n \tilde{p}_{\alpha}^n(\mathbf{q}, \omega) \exp[-i\omega t + i\mathbf{r} \cdot \mathbf{q}] \sin\left(\frac{n\pi z}{L}\right), \quad (\text{A.4})$$

where $\alpha = x, y$. Here, \mathbf{r} is a vector in the x - y plane and the corresponding wavevector is denoted as \mathbf{q} .

We linearize the state of the system around a reference state with $v_{\alpha} = 0$, $v_z = 0$ and $\mathbf{p} = \hat{\mathbf{e}}_z$. The force balance equation together with the incompressibility condition and the constitutive equation, (4), for $\tau = 0$ lead to equations for the flow field

$$\begin{aligned} -\eta \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \tilde{v}_z^n(\mathbf{q}, t) &= \zeta \Delta \mu P_{z\beta} \frac{n\pi}{L} \tilde{p}_{\beta}^n + i \zeta \Delta \mu P_{zz} q_{\beta} \tilde{p}_{\beta}^n - \frac{\nu_1}{2} P_{zz} \left(i q_{\beta} \tilde{h}_{\beta}^n - \frac{n\pi}{L} \tilde{h}_z^n \right) \\ &\quad - \frac{\nu_1 n\pi}{2L} (P_{z\beta} \tilde{h}_{\beta}^n - P_{zz} \tilde{h}_z^n) - \frac{1}{2} \left(i q_{\beta} \tilde{h}_{\beta}^n - \frac{n\pi}{L} \tilde{h}_z^n \right) + P_{z\beta} \tilde{\xi}_{\beta}^{\sigma,n} + P_{zz} \tilde{\xi}_z^{\sigma,n}, \\ -\eta \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \tilde{v}_{\alpha}^n(\mathbf{q}, t) &= \zeta \Delta \mu P_{\alpha\beta} \frac{n\pi}{L} \tilde{p}_{\beta}^n + i \zeta \Delta \mu P_{\alpha z} q_{\beta} \tilde{p}_{\beta}^n - \frac{\nu_1}{2} \left(P_{\alpha\beta} \frac{n\pi}{L} \tilde{h}_{\beta}^n - P_{\alpha z} \frac{n\pi}{L} \tilde{h}_z^n \right) \\ &\quad - \frac{\nu_1}{2} P_{\alpha z} \left(i q_{\beta} \tilde{h}_{\beta}^n - \frac{n\pi}{L} \tilde{h}_z^n \right) + \frac{1}{2} \frac{n\pi}{L} \tilde{h}_{\alpha}^n + P_{\alpha\beta} \tilde{\xi}_{\beta}^{\sigma,n} + P_{\alpha z} \tilde{\xi}_z^{\sigma,n}, \end{aligned} \quad (\text{A.5})$$

where $\alpha, \beta = x$ or y . Here, we have introduced the projection operators $P_{zz} = q^2/(q^2 + n^2\pi^2/L^2)$, $P_{\alpha\beta} = \delta_{\alpha\beta} - q_{\alpha}q_{\beta}/(q^2 + n^2\pi^2/L^2) = P_{\beta\alpha}$ and $P_{\alpha z} = -i q_{\alpha}(n\pi/L)/(q^2 + n^2\pi^2/L^2) = P_{z\alpha}$ and the pressure P has already been eliminated. The noise terms $\tilde{\xi}_{\alpha}^{\sigma,n}$ have zero mean with variance

$$\langle \tilde{\xi}_{\alpha}^{\sigma,n}(\mathbf{q}, \omega) \tilde{\xi}_{\beta}^{\sigma,m}(\mathbf{q}', \omega') \rangle = 2\eta k_B T \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) (2\pi)^3 \delta(\mathbf{q} + \mathbf{q}') \delta(\omega + \omega') \delta_{\alpha\beta} \delta_{nm}, \quad (\text{A.6})$$

where α and $\beta = x, y, z$.

The dynamic equation for the polarization field reads

$$-i\omega\tilde{p}_\alpha^n = -\tilde{\omega}_{\alpha z}^n - \frac{K}{\gamma_1} \left(q^2 + \frac{n^2\pi^2}{L^2} \right) \tilde{p}_\alpha^n - \frac{1}{\gamma_1} (h_\parallel \tilde{p}_\alpha^n - i q_\alpha \tilde{\phi}^n) - \nu_1 \tilde{u}_{\alpha z}^n + \tilde{\xi}_{\perp,\alpha}^n \quad (\text{A.7})$$

with $\tilde{u}_{\alpha z}^n = (-\frac{n\pi}{L} \tilde{v}_\alpha^n + i q_\alpha \tilde{v}_z^n) / 2$, $\tilde{\omega}_{\alpha z}^n = -(\frac{n\pi}{L} \tilde{v}_\alpha^n + i q_\alpha \tilde{v}_z^n)$ and noise correlations

$$\langle \tilde{\xi}_{\perp,\alpha}^n(\mathbf{q}, \omega) \tilde{\xi}_{\perp,\beta}^m(\mathbf{q}', \omega') \rangle = \frac{2kT}{\gamma_1} (2\pi)^3 \delta(\mathbf{q} + \mathbf{q}') \delta(\omega + \omega') \delta_{\alpha\beta} \delta_{nm}. \quad (\text{A.8})$$

Further, with $K_2 = K_3 = K$ we have $h_\alpha = -\frac{\delta F}{\delta p_\alpha} = K \nabla^2 p_\alpha + h_\parallel p_\alpha + \nabla_\alpha \phi$ in the real space. The constraints $\nabla \cdot \mathbf{p} = 0$ and $\mathbf{p}^2 = 1$ (which to the lowest order is the same as imposing $p_z = 1$) give rise to two equations for Lagrange multipliers h_\parallel and ϕ :

$$\left(q^2 + \frac{n^2\pi^2}{L^2} \right) \phi^n(\mathbf{q}) = -\frac{n\pi}{L} h_\parallel^n + \gamma_1 \frac{\nu_1 + 1}{2} \left(q^2 + \frac{n^2\pi^2}{L^2} \right) v_z^n - i q_\beta \xi_{\perp,\beta}^n + \frac{n\pi}{L} \xi_{\perp,z}^n, \quad (\text{A.9})$$

$$h_\parallel^n = -\nu_1 \gamma_1 \tilde{u}_{zz}^n + \frac{n\pi}{L} \phi^n + \gamma_1 \xi_{\perp,z}^n. \quad (\text{A.10})$$

Inserting solutions for the Lagrange multipliers ϕ and h_\parallel into equations (A.5)–(A.7) leads to

$$-\eta \left(q^2 + \frac{n^2\pi^2}{L^2} \right) \tilde{v}_z^n = P_{zz} \xi_z^{\sigma,n} + P_{z\beta} f_\beta^{\sigma,n}, \quad (\text{A.11})$$

$$-\eta \left(q^2 + \frac{n^2\pi^2}{L^2} \right) \tilde{v}_\alpha^n = \zeta \Delta \mu \frac{n\pi}{L} \tilde{p}_\alpha^n + \frac{\nu_1 - 1}{2} \frac{n\pi}{L} K \left(q^2 + \frac{n^2\pi^2}{L^2} \right) \tilde{p}_\alpha^n + P_{\alpha\beta} \tilde{\xi}_\beta^{\sigma,n} + P_{\alpha z} \tilde{\xi}_z^{\sigma,n}, \quad (\text{A.12})$$

$$\frac{\partial \tilde{p}_\alpha^n}{\partial t} = -\frac{K}{\gamma_1} \left(q^2 + \frac{n^2\pi^2}{L^2} \right) \tilde{p}_\alpha^n + \frac{\nu_1 - 1}{2} \frac{n\pi}{L} \tilde{v}_\alpha^n + P_{\alpha\beta} \tilde{\xi}_{\perp,\beta}^n + P_{\alpha z} \tilde{\xi}_{\perp,z}^n. \quad (\text{A.13})$$

Note that \tilde{v}_z^n decouples from \tilde{p}_α^n . Combining equations (A.12) and (A.13), we find expressions for the fluctuations of \tilde{p}_α^n :

$$\left(\frac{\partial}{\partial t} + \frac{1}{\tilde{\tau}_q} \right) \tilde{p}_\alpha^n = -\frac{n\pi}{L} \frac{\nu_1 - 1}{2} \frac{P_{\alpha\beta} \tilde{\xi}_\beta^{\sigma,n} + P_{\alpha z} \tilde{\xi}_z^{\sigma,n}}{\eta \left(q^2 + \frac{n^2\pi^2}{L^2} \right)} + P_{\alpha\beta} \tilde{\xi}_{\perp,\beta}^n + P_{\alpha z} \tilde{\xi}_{\perp,z}^n, \quad (\text{A.14})$$

where we have identified an effective relaxation time $\tilde{\tau}_q$ of the polarization fluctuations \tilde{p}_α^n :

$$\tilde{\tau}_q = \left[\frac{K}{\gamma_1} \left(q^2 + \frac{n^2\pi^2}{L^2} \right) + \frac{\nu_1 - 1}{2} \left(\zeta \Delta \mu + \frac{\nu_1 - 1}{2} K \left(q^2 + \frac{n^2\pi^2}{L^2} \right) \right) \frac{n^2\pi^2}{L^2} \frac{1}{\eta \left(q^2 + \frac{n^2\pi^2}{L^2} \right)} \right]^{-1}. \quad (\text{A.15})$$

The reference state of constant polarity is stable only if $\tilde{\tau}_q > 0$. Time scale $\tilde{\tau}_q$ is the analogue of the time scale τ_q that we extract from equation (11). We can Fourier transform equation (A.14)

in time to obtain a closed equation for \tilde{v}_α^n :

$$-\eta \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \tilde{v}_\alpha^n(\mathbf{q}, t) = \left[\xi \Delta \mu + \frac{\nu_1 - 1}{2} K \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \right] \frac{\frac{\nu_1 - 1}{2} \frac{n^2 \pi^2}{L^2} \tilde{v}_\alpha^n}{-i \omega + \frac{K}{\gamma_1} \left(q^2 + \frac{n^2 \pi^2}{L^2} \right)} + \frac{n \pi}{L} \frac{P_{\alpha\beta} \tilde{\xi}_{\perp,\beta}^n + P_{\alpha z} \tilde{\xi}_{\perp,z}^n}{-i \omega + \frac{K}{\gamma_1} \left(q^2 + \frac{n^2 \pi^2}{L^2} \right)} + P_{\alpha\beta} \tilde{\xi}_\alpha^{\sigma,n} + P_{\alpha z} \tilde{\xi}_z^{\sigma,n}. \quad (\text{A.16})$$

The correlation function $C_{\alpha\beta}^n(\mathbf{q}, \omega)$ of the velocity field $\tilde{v}_\alpha^n(\mathbf{q}, \omega)$ is defined by

$$\langle \tilde{v}_\alpha^n(\mathbf{q}, \omega) \tilde{v}_\beta^n(\mathbf{q}', \omega') \rangle = C_{\alpha\beta}^n(\mathbf{q}, \omega) (2\pi)^3 \delta(\mathbf{q} + \mathbf{q}') \delta(\omega + \omega'). \quad (\text{A.17})$$

Due to the rotational symmetry in the XY -plane, the time-dependent diffusion coefficient for a particle of radius a is (using that $\langle \tilde{v}_x^n(\mathbf{q}, t) \tilde{v}_x^n(-\mathbf{q}, 0) \rangle = \langle \tilde{v}_y^n(\mathbf{q}, t) \tilde{v}_y^n(-\mathbf{q}, 0) \rangle$)

$$D_{xx}(t) = D_{yy}(t) = D(t) = \frac{\pi}{V} \sum_n \int_{q^2 \leq (\pi/a)^2} \frac{d^2 q}{(2\pi)^2} \int_0^t dt' \exp[-2D(t')(q^2 + n^2 \pi^2 / L^2) t'] \times \langle v_x^n(\mathbf{q}, t') v_x^n(-\mathbf{q}, 0) \rangle, \quad (\text{A.18})$$

where $j = x$ or y . In the long-time limit $t \rightarrow \infty$, the diffusion coefficient D is given by

$$D = kT \sum_n \int_{q^2 \leq (\pi/a)^2} \frac{d^2 q}{(2\pi)^2} \left[\frac{\pi}{L} \frac{1}{(2D + \Delta_n) \Delta_n} \times \left[\eta(2 - P_{zz}) \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) + \frac{1}{\gamma_1} \frac{n^2 \pi^2}{L^2} \frac{\left[\xi \Delta \mu + \frac{K}{2} (\nu_1 - 1) \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \right]^2}{(K/\gamma_1)^2 (q^2 + n^2 \pi^2 / L^2)^2} \right] \right] \quad (\text{A.19})$$

with

$$\Delta_n = \eta \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) + (\nu_1 - 1) \frac{n^2 \pi^2}{L^2} \frac{\gamma_1}{2K} \frac{\xi \Delta \mu + \frac{K}{2} (\nu_1 - 1) \left(q^2 + \frac{n^2 \pi^2}{L^2} \right)}{\left(q^2 + \frac{n^2 \pi^2}{L^2} \right)}. \quad (\text{A.20})$$

The anomalous diffusion behaviors of a particle in an active gel are captured by equation (A.19). A divergence of D occurs if $\Delta_n = 0$ when $q^2 = 0$. This divergence corresponds to a Frederiks transition for $n = 1$ which occurs for a critical active stress

$$\zeta \Delta \mu_c = -\frac{\pi^2}{L^2} \Gamma \quad (\text{A.21})$$

with

$$\Gamma = -\left[\frac{K}{\gamma_1} + \frac{K(\nu_1 - 1)^2}{4\eta} \right] \frac{2\eta}{\nu_1 - 1}. \quad (\text{A.22})$$

Equation (A.21) is the analogue of the estimation of $\zeta \Delta \mu_c$ given below equation (11). Alternatively, we can introduce for a given $\zeta \Delta \mu$ the critical system size L_c for which the instability occurs: $L_c^2 = -\pi^2 \Gamma / (\zeta \Delta \mu)$. Note that at this threshold the effective relaxation

time scale $\tilde{\tau}_p$ diverges. In the following, we discuss the behavior of D in the limit of small $\delta L = L_c - L$. Keeping only the divergent contributions in the limit $\delta L \rightarrow 0$, we obtain

$$D \simeq \sqrt{\frac{kT}{\gamma_1 \eta}} \left[\frac{\pi^4}{L_c^4} (\zeta \Delta \mu)^2 + 2 \frac{\pi^2}{L_c^2} \zeta \Delta \mu \frac{v_1 - 1}{2} \right]^{1/2} \sqrt{\log \left(\frac{\eta D}{\Gamma} \right) \frac{1}{K^{1/2}} \frac{1}{\delta L^{1/2}}}. \quad (\text{A.23})$$

We thus find that D diverges as $\delta L^{-1/2}$ for small δL . Note that because v_z is independent of p_α , the diffusion coefficient D_{zz} is given by its thermal equilibrium value for an isotropic fluid: $D_{zz} = 2k_B T / (\eta a)$.

From the defining relation (A.18), we see that for times $t \ll [D(t)(q^2 + \frac{n^2 \pi^2}{L^2}) + \Delta_n(q)]^{-1}$ (but still in the viscous regime) we encounter a different behavior. We again consider the case $K_1 \rightarrow \infty$ and $K = K_2 = K_3$ and use equations (A.16) to calculate the displacement correlations. We show only the contribution that diverges at the transition for $L = L_c$. We obtain

$$\begin{aligned} \langle \delta R_x^2(t) \rangle &= \int_0^t dt_1 \int_0^t dt_2 \int_{-\infty}^{\infty} \frac{d\omega}{2\pi} \int \frac{d^2 q}{2\pi^2} \sum_n \frac{\pi}{L} \frac{2kT}{\gamma_1} \left| -i\omega \eta \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \right. \\ &\quad \left. + \eta \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \frac{1}{\tilde{\tau}_q} \right|^{-2} (\zeta \Delta \mu)^2 \frac{n^2 \pi^2}{L^2}. \end{aligned} \quad (\text{A.24})$$

Thus $\langle \delta R_x(t)^2 \rangle$ again has an activity-dependent part that diverges when τ_p diverges, i.e. at $L = L_c$. Evaluating in the limit $L \rightarrow L_c$, we find that in this short-time regime

$$\langle \delta R_x(t)^2 \rangle \simeq -kT \frac{(\zeta \Delta \mu)^2}{LK \gamma_1 [\eta/4 + \gamma_1 (v_1 - 1)^2]} t^2 \ln |\delta L/a|, \quad (\text{A.25})$$

which corresponds to ballistic motion with a velocity obeying $v_s^2 = \langle \delta R_x(t)^2 \rangle t^{-2}$.

Finally, we consider the elastic limit of the dynamics. We begin with the viscoelastic version of equations (A.12) and (A.13):

$$-\eta \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \tilde{v}_\alpha^n = \left(1 + \tau \frac{\partial}{\partial t} \right) \left[\zeta \Delta \mu + \frac{v_1 - 1}{2} K \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \right] \frac{n\pi}{L} \tilde{p}_\alpha^n + P_{im} \tilde{\chi}_\beta^{\sigma,n} + P_{\alpha z} \tilde{\chi}_z^{\sigma,n} \quad (\text{A.26})$$

$$\frac{\partial \tilde{p}_\alpha^n}{\partial t} = - \left(1 + \tau \frac{\partial}{\partial t} \right) \frac{K}{\gamma_1} \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \tilde{p}_\alpha^n + \frac{v_1 - 1}{2} \frac{n\pi}{L} \tilde{v}_\alpha^n + P_{\alpha\beta} \tilde{\chi}_{\perp,\beta}^n + P_{\alpha z} \tilde{\chi}_{\perp,z}^n. \quad (\text{A.27})$$

Equations (A.26) and (A.27) may be obtained from the constitutive relations (4) and (5) with a finite τ by following the derivations of (A.12) and (A.13). Fourier transforming in time t and defining local displacement field \tilde{u}_α^n through the relation $\tilde{v}_\alpha^n(\mathbf{q}, \omega) = -i\omega \tilde{u}_\alpha^n(\mathbf{q}, \omega)$, we obtain

$$\begin{aligned} \eta \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) i\omega \tilde{u}_\alpha^n &= (1 - i\omega\tau) \left[\zeta \Delta \mu + \frac{v_1 - 1}{2} K \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \right] \frac{n\pi}{L} \tilde{p}_\alpha^n + P_{\alpha\beta} \tilde{\chi}_\beta^{\sigma,n} + P_{\alpha z} \tilde{\chi}_z^{\sigma,n} \\ &\quad \times \left[-i\omega \left(1 + \frac{K}{G} \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \right) + \frac{K}{\gamma_1} \left(q^2 + \frac{n^2 \pi^2}{L^2} \right) \right] \tilde{p}_\alpha^n \\ &= -\frac{v_1 - 1}{2} \frac{n\pi}{L} i\omega \tilde{u}_\alpha^n + P_{\alpha\beta} \tilde{\chi}_{\perp,\beta}^n + P_{\alpha z} \tilde{\chi}_{\perp,z}^n. \end{aligned}$$

Looking at the limit $\omega\tau \gg 1$ and eliminating \tilde{u}_α^n , we obtain

$$\left[-i\omega\Delta_e + \frac{K}{\gamma_1} \left(q^2 + \frac{n^2\pi^2}{L^2} \right) \right] \tilde{p}_\alpha^n = -\frac{\nu_1 - 1}{2\eta \left(q^2 + \frac{n^2\pi^2}{L^2} \right)} \frac{n\pi}{L} (P_{\alpha\beta}\chi_\beta^{\sigma,n} + P_{\alpha z}\chi_z^{\sigma,n}) + P_{\alpha\beta}\chi_{\perp,\beta}^n + P_{\alpha z}\chi_{\perp,z}^n, \quad (\text{A.28})$$

where

$$\Delta_e = 1 + \frac{K}{G} \left(q^2 + \frac{n^2\pi^2}{L^2} \right) + \frac{\nu_1 - 1}{2E \left(q^2 + \frac{n^2\pi^2}{L^2} \right)} \left[\zeta \Delta\mu + \frac{\nu_1 - 1}{2} \left(q^2 + \frac{n^2\pi^2}{L^2} \right) K \right] \frac{n^2\pi^2}{L^2}, \quad (\text{A.29})$$

where $E = \eta/\tau$ and $G = \gamma_1/\tau$. Thus the instability threshold corresponding to equation (18) obeys

$$2E \left[1 + \frac{K\pi^2}{GL^2} \right] + \frac{(\nu_1 - 1)^2 \pi^2}{4L^2} K = -\zeta \Delta\mu_c \frac{\nu_1 - 1}{2}, \quad (\text{A.30})$$

allowing us to define a critical wavevector $q_c^2 = \zeta \Delta\mu - \zeta \Delta\mu_c$. Equating the instantaneous position vector $\delta\mathbf{R}$ of the bead with the local displacement vector field \mathbf{u} at the location of the bead, we find that

$$\langle \delta\mathbf{R} \cdot \delta\mathbf{R} \rangle \simeq - \left(\frac{\zeta \Delta\mu}{E} \right)^2 \frac{kT}{K} \left(1 + \frac{\gamma_1}{4\eta} \right) \frac{L}{1 + \frac{K\pi^2}{GL^2}} \log q_c a, \quad (\text{A.31})$$

where we have shown only the diverging part depending on activity. When the instability threshold is approached, q_c vanishes and $\langle \delta\mathbf{R} \cdot \delta\mathbf{R} \rangle$ diverges logarithmically. Noting that near the threshold $\zeta \Delta\mu$ may be replaced by $\zeta \Delta\mu_c$ and using the relation between $\zeta \Delta\mu_c$ and E (see the text above equation (19)), equation (A.31) reduces to equation (19) up to numerical factors.

References

- [1] Forster D 1995 *Hydrodynamic Fluctuations, Broken Symmetry and Correlation Functions (Advanced Book Classics)* (New York: Westview Press)
- [2] Squires T and Mason T 2010 *Annu. Rev. Fluid Mech.* **42** 413–38
- [3] Mizuno D *et al* 2007 *Science* **315** 370
- [4] Caspi A, Granek R and Elbaum M 2002 *Phys. Rev. E* **66** 011916
- [5] Huet S *et al* 2006 *Biophys. J.* **91** 3542
- [6] Kruse K, Joanny J F, Jülicher F, Prost J and Sekimoto K 2004 *Phys. Rev. Lett.* **92** 078101
- [7] Basu A, Joanny J F, Jülicher F and Prost J 2008 *Eur. Phys. J. E* **27** 149
- [8] Voituriez R, Joanny J F and Prost J 2005 *Eurphys. Lett.* **70** 404
- [9] Sankararaman S and Ramaswamy S 2009 *Phys. Rev. Lett.* **102** 118107
- [10] deGennes P G and Prost J 1993 *The Physics of Liquid Crystals* (Oxford: Oxford University Press)
- [11] Jülicher F, Ajdari A and Prost J 1997 *Rev. Mod. Phys.* **69** 1269
- [12] Lau A W C and Lubensky T 2009 *Phys. Rev. E* **80** 011917
- [13] Toner J and Tu Y 1998 *Phys. Rev. E* **58** 4828