# Anomalous fluctuations of active polar filaments

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Using a simple model, we study the fluctuating dynamics of inextensible, semiflexible polar filaments interacting with active and directed force generating centers such as molecular motors. Taking into account the fact that the activity occurs on time scales comparable to the filament relaxation time, we obtain some unexpected differences between both the steady-state and dynamical behaviors of active as compared to passive filaments. For the statics, the filaments have a length-scale-dependent rigidity. Dynamically, we find strongly enhanced anomalous diffusion.

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## I. INTRODUCTION

Filamentous proteins are major components of the cell cytoskeleton [1]. Examples are actin filaments, microtubules, and intermediate filaments. Their mechanical properties are important for cell stability and support and have been well studied at thermodynamic equilibrium by *in vitro* experiments. However, the conditions in the living cell are very different from those in the laboratory. Protein filaments interact with other proteins such as molecular motors and cross linkers. This has led to a flurry of recent *in vitro* experiments of mixtures of filaments and their associated proteins in order to compare with their purified state [2–4]. From a theoretical point of view, the proteins are typically far from equilibrium and, therefore, even to understand their steady-state behavior, one has to study their dynamics. Nonequilibrium effects have also recently been studied in biological membranes [5,6].

In this paper, motivated by recent experiments on *F*-actin and myosin in the presence of adenosine triphosphate (ATP) [4], we study an example of the nonequilibrium behavior of biofilaments: the fluctuating dynamics of polar filaments with active centers. This is also a model system for the study of nontrivial aspects of semiflexible filament dynamics. A key point of our analysis is the fact that the activity of the proteins occurs over a time scale $\tau$ which may be comparable to the relaxation time of the filament. Unlike recent work on motile solutions [7], the active centers considered here are associated with single filaments (i.e., are not cross links) and cannot move one filament with respect to another. The viscosity of the solvent is given by $\eta$. We note that the typical energy scale of a biochemical reaction is of the order of a few $k_BT$ at physiological conditions.

The filament can be parametrized by a curve through its center, $\mathbf{R}(s)$ (see Fig. 1). The unit tangent vector is defined as $\mathbf{t}(s)=\partial\mathbf{R}/\partial s$. An easily measured quantity using, e.g., video microscopy is the steady-state tangent correlation function $C_{\mathbf{t}}(s)\equiv\langle\mathbf{t}(s)\cdot\mathbf{t}(0)\rangle$. For a semiflexible polymer in equilibrium, it decays exponentially, $C_{\mathbf{t}}(s)=\exp[-|s|/L_p]$, which defines the persistence length $L_p$.

## II. MAIN RESULTS

We calculate $C_{\mathbf{t}}(s)$ and find that due to activity on a time scale $\tau$, the filaments develop a *length-scale*-dependent bending rigidity. On short length scales, typical conformations have the bare persistence length while on longer length scales the filaments may be characterized by a lower ''renormalized'' persistence length. There is a *crossover* length between the two regimes, $\ell_c\sim(\tau k_BTL_p/2\pi\eta)^{1/4}$. Therefore an analysis of the filament conformations can give information about the timescale $\tau$ at which the activity occurs. We also obtain modified relaxational dynamics with anomalous diffusion, which we show has an effect on the high frequency

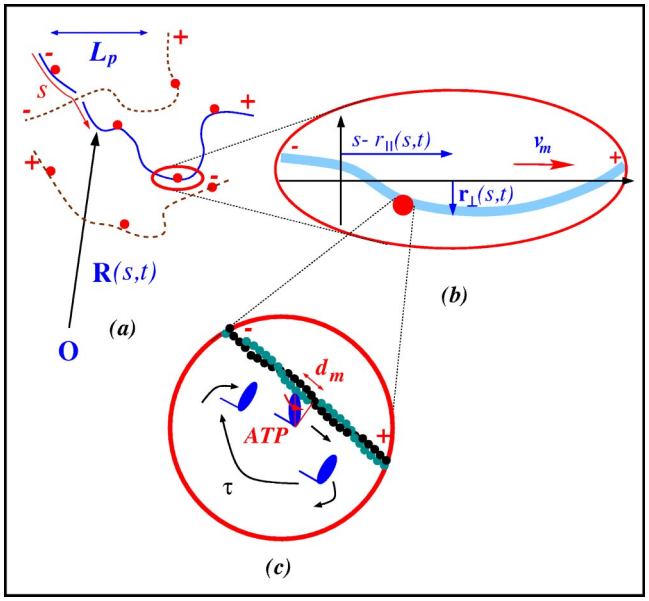


FIG. 1. (a) The fluctuating *polar* filaments of persistence length $L_p$ parametrized by $\mathbf{R}(s,t)$ decorated by active centers. Note that there is a + and a − end for each filament. (b) The filament on length scales below $L_p$ showing the transverse $\mathbf{r}_\perp(s,t)$ and longitudinal $r_\|(s,t)$ motion. (c) A schematic of the cycle of activity of a motor such as myosin with activity time $\tau$.

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viscoelasticity. The shear modulus of the active filament solution apparently has a frequency dependent effective temperature. There is a crossover from a shear modulus corresponding to the bare temperature at high frequencies to a modulus equivalent to the higher renormalized temperature at lower frequencies, both with a scaling of $\omega^{3/4}$. In the crossover regime, the modulus *appears* to have a stronger frequency dependence with a power law $G^*(\omega)\propto\omega^{\alpha}$, where $\alpha>3/4$. A simple consequence of filament polarity is a *small* ballistic component to the motion of the filament.

### III. EXPLICIT ANALYSIS

We model the filaments with the Kratky-Porod wormlike chain [8,9], which takes into account the *bending* energy cost of the chain. The wormlike chain Hamiltonian is $\mathcal{H}_{wlc}[\{\mathbf{R}(s)\}]=(\kappa/2)\int_{-L/2}^{L/2}ds(\partial^2\mathbf{R}/\partial s^2)^2$. The stretching energy of chain molecules is much higher than the bending energy and we may consider the chain as inextensible. The persistence length is defined as $L_p=\kappa/k_BT$.

The dynamics at finite $T$ may be expressed by the Langevin equation

$$\frac{\partial}{\partial t}\mathbf{R}(s,t)-\int ds'\mathbf{H}(s,s')\cdot\left[-\kappa\frac{\partial^4\mathbf{R}}{\partial s'^4}+\frac{\partial}{\partial s'}\left(\Lambda(s',t)\frac{\partial\mathbf{R}}{\partial s'}\right)\right]=\mathbf{f}(s,t)+\mathbf{f}^{(m)}(s,t), \tag{1}$$

where $\Lambda(s,t)$ (a Lagrange multiplier) is an *instantaneous*, fluctuating ''tension,'' which enforces the *local* inextensibility of the chain. The inextensibility constraint fixes the tension, $\Lambda(s,t)$, by $0=|\partial\mathbf{R}/\partial s|^2-1$. Because of this constraint, the dynamics of semiflexible filaments is nonlinear and generally insoluble. In addition to the thermal velocity $\mathbf{f}(s,t)$, there is an additional active velocities $\mathbf{f}^{(m)}(s,t)$ correlated over a time $\tau$. The polarity of the filament implies that the active forces have a mean direction along the contour of the filaments (see Fig. 1). Hydrodynamics is taken into account by the mobility tensor $\mathbf{H}(s,s')$. For completeness, we note that there are a number of terms omitted from the stochastic differential equation (1). These are related to the nonlocal nature of the hydrodynamic interactions, the nature of the discretization of time, and the implementation of the inextensibility constraint. These terms do not affect the linear analysis of this paper. In general, $\mathbf{f}(s,t)$ will also depend on $\mathbf{R}(s,t)$ [10]. We assume that the activity does not affect the thermal forces, i.e., the active proteins do not affect the collisions of the solvent molecules with the filament. Then the thermal velocities satisfy the fluctuation-dissipation theorem, and $\mathbf{f}(s,t)$ have zero mean and Gaussian fluctuations, given [10] by $\langle f_i(s,t)f_j(s',t')\rangle=2k_BTH_{ij}(s,s')\delta(t-t')$.

We consider rodlike segments and restrict the analysis to length scales $\ell$ below $L_p$, so that we can decompose the dynamics into transverse and longitudinal motion (see Fig. 1) and write the position of the filament as $\mathbf{R}(s,t)=[s-r_{\|}(s,t)]\hat{\mathbf{u}}(t)+\mathbf{r}_{\perp}(s,t)$, where $s\in\{-\ell/2,\ell/2\}$ and $\hat{\mathbf{u}}$ is a time-dependent unit vector giving the orientation. We can obtain results within a systematic small gradient expansion for $|\mathbf{r}_{\perp}(s,t)|,|r_{\|}(s,t)|\ll s$. The mobility tensor is given by $H_{ij}(s,s')=h(s-s')[(\delta_{ij}-\hat{u}_i\hat{u}_j)+2\hat{u}_i\hat{u}_j+O(|\partial_s\mathbf{r}_{\perp}|^2)]$ where in this and the following, for a function $A(x)$, $\partial_xA\equiv\partial A/\partial x$. We can thus decompose Eq. (1) into parallel and perpendicular components in an expansion to $O(|\partial_s\mathbf{r}_{\perp}|^2)$,

$$\partial_t\mathbf{r}_{\perp}(s,t)=\int ds'h(s-s')[-\kappa\partial_{s'}^4\mathbf{r}_{\perp}+\Lambda(s',t)\partial_{s'}^2\mathbf{r}_{\perp}+\partial_{s'}\Lambda\partial_{s'}\mathbf{r}_{\perp}]+\mathbf{f}_{\perp}(s,t)+\mathbf{f}_{\perp}^{(m)}(s,t), \tag{2}$$

$$\partial_tr_{\|}(s,t)=\int ds'2h(s-s')[-\kappa\partial_{s'}^4r_{\|}-\partial_{s'}\Lambda]+f_{\|}(s,t)+f_{\|}^{(m)}(s,t), \tag{3}$$

which are coupled by the constraint of inextensibility,

$$\partial_sr_{\|}=\tfrac{1}{2}(\partial_s\mathbf{r}_{\perp})^2+O(|\partial_s\mathbf{r}_{\perp}|^4). \tag{4}$$

For simplicity, in most of this paper we consider the Rouse model, which assumes local friction. We also focus on dilute solutions. Long range hydrodynamics and nonzero concentration of filaments will modify some of the results (see below). For the Rouse model $h(s-s')=\delta(s-s')/\zeta_{\perp}$, where $\zeta_{\perp}=4\pi\eta=2\zeta_{\|}$. We model the active velocities by a Gaussian noise with mean $\langle\mathbf{f}_{\perp}^{(m)}\rangle=0$ and $\langle f_{\|}^{(m)}\rangle=v_m$, a drift, reflecting the polar nature of the filament, and mean square fluctuations $\delta\mathbf{f}^{(m)}=\mathbf{f}^{(m)}-\langle\mathbf{f}^{(m)}\rangle$ given by

$$\langle\delta f_i^{(m)}(s,t)\delta f_j^{(m)}(s',t')\rangle=\sqrt{2}\,\frac{\alpha_i}{\zeta_i^2}\Theta\delta_{ij}\delta(s-s')\Phi(t-t'), \tag{5}$$

where $\Phi(t)=\exp\{-|t|/\tau\}$ and $\{i,j\}$ refer to $\perp,\|$. The level of *activity* is controlled by the parameter $\Theta$. Correlations of the active force decay over a time $\tau$, the typical activity period. The constants $\alpha_{i,j}$ measure the relative partitioning of the activity between transverse and longitudinal components and satisfy the relationship $\alpha_{||}^2+\alpha_{\perp}^2=1$. In general, the force applied by the motor protein on the filament will not be purely tangential, depending, for example, on its trajectory of approach of the filament and the conformation of the neck and chain region [1]. Averaging over orientations, *only* the longitudinal component will have a nonzero average, because of the filament polarity. In addition, the remainder of the energy of the actomyosin reaction that is not converted to directed work will be dissipated as heat contributing to the fluctuations on the same (reaction) timescale. It is difficult *a priori* to estimate $\alpha_{i,j}$ and we choose somewhat arbitrarily, $\alpha_{\perp}=\alpha_{||}=1/\sqrt{2}$. Between active events the ''motors'' diffuse freely in the solution, so it is reasonable to assume that there is no spatial correlation between active sites. We emphasize that unlike the thermal noise, the active noise correlations *do not* satisfy the fluctuation dissipation theorem.

Equations (2)–(4) are most easily studied by analyzing the motion of the bending modes of wave vector $q$ and frequency $\omega$. Defining $F(s,t)=\int(dq/2\pi)(d\omega/2\pi)\tilde{F}(q,\omega)\exp(i\omega t+qs)$ we only consider $q$ such that $\pi/a\gg q\gg\pi/\ell$. On length scales below $L_p$, $C_{\mathbf{t}}(s)$ can be

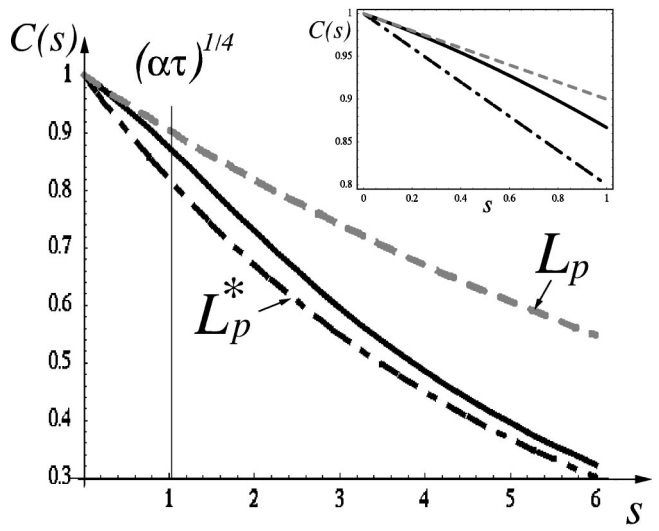


FIG. 2. The tangent correlation function for the active filament of *bare* persistence length $L_p=10$, compared with those simple wormlike chains of persistence length of $L_p=10$ and $L_p^*=5$ using units such that $\alpha\tau=1$. Inset: $C_{\mathbf{t}}(s)$ near $s=0$.

obtained from the transverse fluctuations. The transverse dynamics are approximately given by

$$\tilde{\mathbf{r}}_\perp(q,\omega)\simeq\frac{\tilde{\mathbf{f}}_\perp(q,\omega)+\tilde{\mathbf{f}}_\perp^{(m)}(q,\omega)}{i\omega+\alpha q^4}, \tag{6}$$

where $\alpha=\kappa/\zeta_\perp$. Corrections due to the tension $\Lambda(s,t)$ are of higher order in the gradient expansion. The transverse fluctuations at time $t$ are relaxed over a length scale $\ell_\perp(t)=(\alpha t)^{1/4}$. Because of inextensibility, in Eq. (4) there is an induced *time-independent* longitudinal motion $r_\parallel^{(0)}(s)$ due to the averaged transverse motion, $\partial_s r_\parallel^{(0)}(s)=\langle\frac{1}{2}(\partial_s\mathbf{r}_\perp)^2\rangle_\perp$.

The tangent correlation function is given by

$$C_{\mathbf{t}}(s)=\langle\mathbf{t}(s,t)\cdot\mathbf{t}(0,t)\rangle\simeq\langle 1-\partial_s r_\parallel^{(0)}(s,t)-\partial_s r_\parallel^{(0)}(0,t)+\partial_s\mathbf{r}_\perp(s,t)\cdot\partial_s\mathbf{r}_\perp(0,t)\rangle_\perp. \tag{7}$$

Using Eqs. (4), (6), and (7), the tangent correlation function has the form

$$C_{\mathbf{t}}(s)\simeq\exp\left\{-\frac{s}{L_p}-\frac{2\Theta}{\alpha^2}\int\frac{dq}{2\pi}\frac{1-\cos(qs)}{q^2[q^4+(\alpha\tau)^{-1}]}\right\}. \tag{8}$$

The correlation function is plotted in Fig. 2. For length scales less than $\ell_c\simeq\ell_\perp(\tau)=(\kappa\tau/\zeta_\perp)^{1/4}$, the effective persistence length is approximately equal to the bare persistence length $L_p$, whilst for length scales above $\ell_c$, the conformations can be well modeled by a wormlike chain with a lower renormalized persistence length given by $L_p^*=L_p(1+\Theta\tau\zeta_\perp/k_BT)^{-1}$. Dimensional analysis suggests a new *active* temperature scale given by $k_BT_a=\Theta\tau\zeta_\perp$.

## IV. DYNAMICS

The dynamics of inextensible filaments is anisotropic [11,12,14,15]: longitudinal motion has different relaxation dynamics from the transverse. Viscous dissipation due to longitudinal motion must be taken into account, giving a time scale over which ''tension'' propagates along the filament [11,12,14,15]. From Eq. (6), we can calculate the transverse dynamic fluctuations, $R_\perp^2(t)=\langle[\mathbf{r}_\perp(s,t)-\mathbf{r}_\perp(s,0)]^2\rangle_\perp$,

$$R_\perp^2(t)=\begin{cases}t^2\dfrac{\Theta}{\sqrt{2}}\kappa^{3/4}\zeta_\perp^{-3/4}\tau^{7/4}, & t\ll\tau\\ t^{3/4}\dfrac{8\Gamma(1/4)}{3\pi}\kappa^{1/4}\zeta_\perp^{-3/4}(k_BT+\Theta\zeta_\perp\tau), & t\gg\tau.\end{cases} \tag{9}$$

There is a crossover from ballistic motion at short times to subdiffusive behavior at long times. Note the thermal and active contributions to the subdiffusive regime.

We can solve for the longitudinal motion self-consistently as follows: we average over *only* the transverse fluctuations and use the inextensibility constraint [14,15] to give a relationship between the tension and the longitudinal motion, $iq[\tilde{r}_\parallel(q,\omega)-\tilde{r}_\parallel^{(0)}(q)]=K(\omega)\tilde{\Lambda}(q,\omega)$, defining a frequency dependent *extensional* compliance $K(\omega)=K_{eq}(\omega)+K_a(\omega)$, which has equilibrium and active contributions. The equilibrium compliance given by $K_{eq}(\omega)\simeq 2^{-3/4}k_BT\kappa^{-5/4}(i\zeta_\perp\omega)^{-3/4}$ is not new and has been obtained previously [12,13]. We find, in addition, an active contribution given by

$$K_a(\omega)=\frac{4\Theta\tau}{\kappa}\int_k\frac{[\alpha k^4\tau+f(\alpha k^4\tau)-i\omega\tau]}{f(\alpha k^4\tau)(2\alpha k^4-i\omega)[f(\alpha k^4\tau)-i\omega\tau]}, \tag{10}$$

where $f(x)=x+1$. In the limit $\omega\to 0$, it is given by $K_a(\omega)\simeq 2^{-3/4}\Theta\tau\zeta_\perp\kappa^{-5/4}[(i\omega\zeta_\perp)^{-3/4}-\frac{1}{4}(\zeta_\perp/2\tau)^{-3/4}]+O(\omega)$. The compliance $K(\omega)$ is then substituted into the longitudinal dynamics. This self-consistent approach corresponds to an infinite resummation of a set of diagrams of the perturbation expansion in $\Lambda$ [14]. We obtain the following equation for the longitudinal motion:

$$\tilde{r}_\parallel(q,\omega)-\tilde{r}_\parallel^{(0)}(q)\simeq\frac{\tilde{f}_\parallel(q,\omega)+\tilde{f}_\parallel^{(m)}(q,\omega)}{i\omega+q^2K^{-1}(\omega)/\zeta_\parallel}. \tag{11}$$

As defined above, $r_\parallel^{(0)}(s)$ is the time-independent motion in the longitudinal direction due to the averaged transverse motion. Given this, we calculate the longitudinal dynamical fluctuations $R_\parallel^2(t)=\langle[r_\parallel(s,t)-r_\parallel(s,0)]^2\rangle_\parallel$,

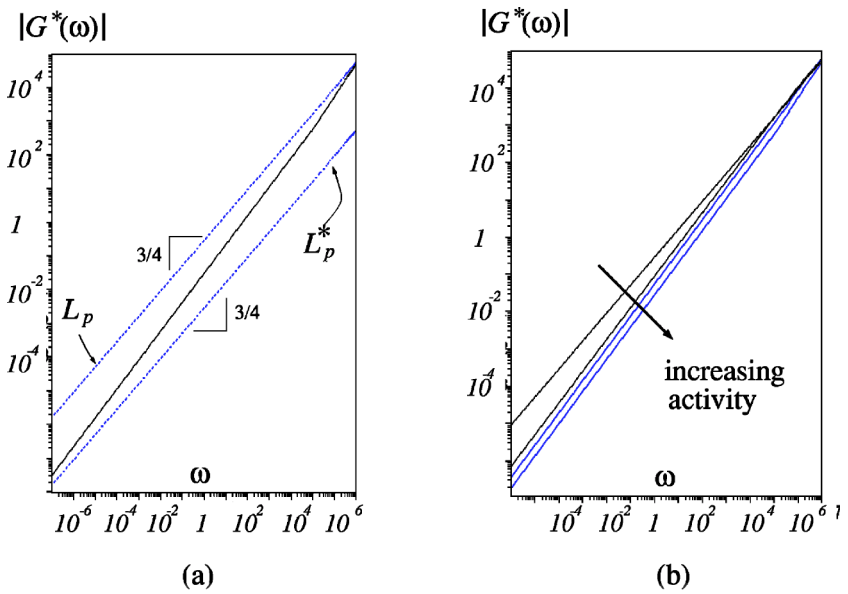


FIG. 3. The magnitude of the high frequency modulus for active filaments. We have chosen units of length and time such that $\alpha\tau=1$ and $k_BT/\zeta_\perp=1$. In these units, the bare persistence length of the filaments is $L_p=1$. (a) The crossover to a renormalized persistence length $L_p^*=1/101$. (b) Increasing activity corresponding to $\Theta\zeta_\perp\tau=k_BT_a=25,50,100$.

$$R_\parallel^2(t) = \begin{cases} t^2(v_m^2+\Theta\zeta_\parallel^{1/2}2^{-3/4}\kappa^{3/8}\zeta_\perp^{-3/8}\tau^{1/8}), & t\ll\tau \\ t^2v_m^2+t^{7/8}\dfrac{8\Gamma(1/8)}{7\pi}\dfrac{(2\kappa)^{5/8}(k_BT+\Theta\zeta_\perp\tau)^{3/8}}{\zeta_\parallel^{7/8}}, & t\gg\tau. \end{cases} \tag{12}$$

Because of the drift term (the directed motor-filament interaction), the longitudinal diffusion is ballistic for all time scales.

## V. HIGH FREQUENCY VISCOELASTICITY

The complex shear modulus of a solution of semiflexible filaments at high frequencies is dominated by the extensional compliance and $G^*(\omega)=\frac{2}{15}\rho K^{-1}(\omega)\simeq 0.133\rho/[K_{eq}(\omega)+K_a(\omega)]$ [7,12,13], which for a solution of passive filaments is given by $G^*(\omega)\propto\omega^{3/4}$. For the active filaments, using Eq. (10), we plot the absolute value of the complex high frequency modulus for varying activity in Fig. 3. We see a crossover from a modulus corresponding to the bare temperature $T$ at high frequencies to a modulus equivalent to the higher renormalized active temperature $T+T_a$ at high frequencies, *both* with a scaling of $\omega^{3/4}$. In the crossover regime, the modulus appears to have a stronger frequency dependence with a power law $G^*(\omega)\propto\omega^\alpha$, where $\alpha>3/4$. It is interesting to note that the crossover occurs over a very wide frequency range.

## VI. HYDRODYNAMICS

Within the (screened) Oseen approximation the mobility tensor is given by Ref. [8], $H_{ij}[\mathbf{r}]=(e^{-|\mathbf{r}|/\xi}/8\pi\eta|\mathbf{r}|)(\delta_{ij}+\hat{r}_i\hat{r}_j)$ for $|\mathbf{r}|>a$. The hydrodynamic screening length $\xi\to\infty$ for dilute solutions and is equal to the mesh size $\xi=(\rho_a a)^{-1/2}$ for semidilute solutions with actin concentration $\rho_a$ and filament diameter $a$. Therefore, $h(s-s')=e^{-|s-s'|/\xi}/8\pi\eta|s-s'|$ in Eqs. (2) and (3). For dilute solutions ($\xi\to\infty$), this gives logarithmic corrections to the Rouse model described above and implies a modification of the crossover length to $\ell_c\sim(\kappa\tau/\zeta_\perp\ln[(\kappa\tau/\zeta_\perp)^{1/4}/a])^{1/4}$. For concentrated solutions ($\xi$ finite), the friction coefficient crossover length is $\ell_c\sim(\kappa\tau/\zeta_\perp\ln[\xi/a])^{1/4}$.

## VII. ENTANGLED SOLUTIONS

For entangled solutions, the filament can be modeled as confined in its *tube*. Given a meshsize $\xi$, we can define a tube diameter $D_e\sim L_p(\xi/L_p)^{6/5}$ and entanglement length $L_e\sim L_p(\xi/L_p)^{4/5}$ [16]. The tube can be modeled as a confining potential for $\mathbf{r}_\perp$, which we can model as $V_{tube}=\frac{1}{2}k|\mathbf{r}_\perp|^2$ with $k\simeq\kappa/L_e^4$ chosen so as to give $\langle|\mathbf{r}_\perp(L_e)-\mathbf{r}_\perp(0)|^2\rangle^{1/2}=D_e$, the tube diameter. We obtain the tangent correlation function

$$C_{\mathbf{t}}(s)=1-\frac{s}{L_p}-\frac{2\Theta}{\alpha^2}\int\frac{dq}{2\pi}\frac{1-\cos(qs)}{q^2[q^4+(\alpha\tau)^{-1}+k/\kappa]}.$$

## VIII. DISCUSSION

Our results should be relevant for recent experiments on mixtures of *F*-actin and *S*1 myosin [4]. The molecular motor myosin interacts with *F*-actin in the presence of ATP, undergoing a conformational change in the process. Hydrophobic interactions between tails of a common variant, myosin II [17], lead to multiheaded clusters, which can act as active crosslinks [3,7] between two or more filaments. In contrast, *S*1 myosin is a single-headed version of myosin that is without a tail. Therefore, in general, *S*1 myosin (ATP) interacts with single *polar* actin filaments applying biased nonequilibrium forces. The *S*1 experiments found surprisingly different steady-state and dynamic behavior of the filaments as compared to the pure *F*-actin system [4].

We now estimate the values for the parameters of our model corresponding to the *S*1 experiment. For an actin monomer concentration $\rho_a$, the fraction of bound myosin $\phi$

can be estimated using the equilibrium constant [1], $k_{eq}=500$ nM for the passive reaction actin $+$myosin$\Leftrightarrow$actomyosin. The fraction of bound myosin is given by $\phi=\rho_a/(k_{eq}+\rho_a)$ leading a the typical separation of the active sites (motors) on the filament, $\ell_m \simeq(\phi\rho_m\xi^2)^{-1}=a(\rho_a/\phi\rho_m)$, where $\rho_m$ is the concentration of $S1$ myosin. Then we may divide the filament into regions of size $\ell_m$ in which the motors are expected to act independently. Therefore $\langle \mathbf{f}(s,t)\mathbf{f}(s',t')\rangle=\ell_m\delta(s-s')\langle \mathbf{f}_m(t)\mathbf{f}_m(t')\rangle$. We assume that motor attachment on the filaments is a Poisson process [18], i.e., that motors arrive at random times $t_n$ with a constant rate $\lambda$. The number of motors arriving during a period $\Delta t \gg 1/\lambda$ has a Poisson distribution. The forces applied by each motor are assumed to decay over a time scale $\tau$, so that the force at time $t$ is given by

$$\mathbf{F}_m(t)=\sum_{n=1}\frac{a}{\ell_m}\mathbf{f}_0 g(t-t_n), \tag{13}$$

where $g(t)=\exp(-t/\tau), t>0$ and $g(t)=0, t<0$ and $\mathbf{f}_0$ is the typical force applied by a motor to a filament of diameter $a$. After some standard manipulations [18] and averaging over orientations, the velocity correlations can be shown to be given by Eq. (5) above, with the activity parameter given by $\Theta\simeq\lambda\tau\ell_m^{-1}(f_0 a)^2$ and we set $\lambda=1/\tau$. Similarly, the drift can be estimated as $v_m\simeq(f_0/\zeta_\parallel)\ell_m^{-1}$. The typical force $f_0$ and active time scale $\tau$ can be obtained from biochemical data. The viscosity of water is $\eta\simeq 10^{-3}$ Pa s and F-actin has diameter $a\simeq 7$ nm and persistence length $L_p\simeq 15$ $\mu$m. The stall force of myosin is $\approx 5$ pN and the duration of the motor cycle is $\tau\simeq 5$ ms. The motor step size $d_m$ is $\simeq 10$ nm. For ATP saturation and 5 $\mu$M $S1$ and 14 $\mu$M $F$-actin concentrations, we find $\phi\approx 0.9$ and $\ell_m\approx 2a$. This leads to an estimate for $\Theta\zeta_\perp\tau\simeq k_BT$ at 310 K giving $L_p^*\simeq\frac{1}{2}L_p$ and $\ell_c\sim 0.1$ $\mu$m.

In conclusion, we have studied a simple model of active filaments and obtained different static and dynamical properties as compared to passive semiflexible polymers. These differences should be observable with video microscopy and in linear rheological experiments, and be relevant for experiments on actin-myosin systems.

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