Coupling of transverse and longitudinal response in stiff polymers

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The time-dependent transverse response of stiff inextensible polymers is well understood on the linear level, where transverse and longitudinal displacements evolve independently. We show that for times beyond a characteristic time $t_\text{c}$, longitudinal friction considerably weakens the response compared to the widely used linear response predictions. The corresponding feedback mechanism is explained by scaling arguments and quantified by a systematic theory. Our scaling laws and exact solutions for the transverse response apply to cytoskeletal filaments as well as DNA under tension.

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In tracing back the viscoelasticity of the cell to properties of its constituents, a detailed understanding of the mechanical response of single cytoskeletal filaments is indispensable. Due to their large bending stiffness, these filaments exhibit highly anisotropic static \cite{1} and dynamic \cite{2,3,4} features, such as the anomalous $t^{3/4}$-growth of fluctuation amplitudes in the transverse direction \cite{2,4}, i.e., perpendicular to the local tangent. The related response to a localized transverse driving force has so far been examined only by neglecting longitudinal degrees of freedom \cite{5,6}, although these polymers are virtually inextensible, and transverse and longitudinal contour deformations therefore coupled. In this Letter we show that longitudinal motion strongly affects the transverse response even for weakly-bending filaments and leads to relevant nonlinearities beyond a characteristic time $t_\text{c}$.

The physical key factors controlling the transverse response may be understood from Fig. 1 which shows a weakly-bending polymer (bending undulations are exaggerated for visualization) shortly after a transverse driving force $f_\perp$ has been applied in the bulk. In response to this force, the contour develops a bulge. Due to the backbone inextensibility, this bulge can continue growing only by pulling in contour length from the filament’s tails. This effectively reduces the thermal roughness of the contour \cite{7,8,9}, at a rate substantially limited by longitudinal solvent friction. The resulting coupling to the longitudinal response tends to slow down the bulge growth. In order to describe this feedback mechanism, we start with a scaling analysis and treat the simpler athermal case first. To connect to the biologically important situations of prestressed actin networks \cite{10} and prestretched DNA \cite{11}, we then extend a recent theory of tension dynamics \cite{12} to calculate the nonlinear response for unstretched and prestretched initial conditions.

Consider the overdamped dynamics of an initially straight stiff rod of total length $L$. Suddenly applying a transverse pulling force $f_\perp$, for simplicity in the center of the rod, leads to the growth of a bulge deformation. The generated friction in the transverse and longitudinal direction needs to be balanced by corresponding driving forces. Viscous solvent friction is modeled via anisotropic friction coefficients \cite{(per length)} $\zeta_\perp$ and $\zeta_\parallel = \zeta_\perp$ with $\zeta \approx \frac{1}{2} \frac{\sqrt{\nu}}{L}$ for transverse and longitudinal motion, respectively. After a time $t$, the resulting bulge has some characteristic height $\Delta \perp(t)$ and width $\ell \perp(t)$. The transverse force $f_\perp$ balances the drag force $\zeta_\perp \ell \perp \Delta \perp(t)/t$ acting on a polymer section of length $\ell \perp(t)$ moving transversely with velocity $\Delta \perp(t)/t$ through the solvent; hence, $\Delta \perp \approx f_\perp t/(\zeta_\perp \ell \perp)$. Naturally, the contour length along the deformed rod section is larger than its longitudinal extent $\ell \parallel$. Assuming a simple “triangle” geometry as in the blow-up in Fig. 1 the difference is roughly given by $\Delta^2 \ell \perp / \ell \parallel$. In order to provide this stored (or excess) length, the filament’s tails are pulled in by a longitudinal force $f_\parallel$. The latter has to balance the longitudinal friction that acts on the filament’s tails of length $L$ moving longitudinally with a velocity given by the tempo-

\begin{figure}[h]
\centering
\includegraphics[width=0.5\textwidth]{fig1}
\caption{(Color online) A transverse point force $f_\perp$ applied to the contour $r(s)$ (dark) translates, through the formation of a bulge of height $\Delta \perp$ and width $\ell \perp$, into a longitudinal pulling force $f_\parallel$ acting on the polymer’s tails. This force induces backbone tension $f(s)$ (light) that penetrates the contour within a region of size $\ell \parallel$ where thermal undulations are straightened.}
\end{figure}
TABLE I: Summary of crossover scaling laws for an initially unstretched filament. The crossover time \( t_t \) is explicitly defined through \( f_j = f_j^{-2}(t_t) \), \( f_j(t) \) is the induced longitudinal force, \( \Delta_\perp \) is the transverse response and \( \ell_\perp \) is the transverse/longitudinal correlation length [5,13]. (a) Athermal case. \( f_j \) pulls in the filament’s tails of length \( L_t = (\gamma_0 f_j)^{-2} \) with \( \gamma_0 = (\zeta L)^{3/2} f_j^{1/3} \). (b) Thermal case. The filament’s tails have effective length \( \ell_\perp \ll L \), \( t_t = (\gamma f_j)^{-2} \) with \( \gamma = (\zeta \rho)^{3/2} f_j^{1/3} \).

\[
\begin{array}{|c|c|c|c|}
\hline
& \ell_\parallel(t) & f_j(t) & \Delta_\perp(t) \\
\hline
\hline
(a) & \ell_\parallel(t) & t^{1/4} & (\zeta L)^{3/4} f_j^{1/4} \ell_\parallel^{-1/4} \approx (\zeta L)^{-1/4} (f_j(t))^{3/5} \\
& t \ll t_t & t^{1/4} & (\ell_\parallel(t))^{1/2} \\
& t \gg t_t & t^{1/4} & (\ell_\parallel(t))^{1/2} f_j^{1/4} \ell_\parallel^{-1/4} \\
\hline
\hline
(b) & \ell_\parallel(t) & t^{1/4} & (\zeta \rho / \zeta L)^{3/2} f_j^{1/4} \ell_\parallel^{-1/4} \\
& t \ll t_t & t^{1/4} & (\ell_\parallel(t))^{1/2} f_j^{1/4} \ell_\parallel^{-1/4} \approx (\zeta \rho f_j)^{3/2} f_j^{1/4} \\
& t \gg t_t & t^{1/4} & (\ell_\parallel(t))^{1/2} f_j^{1/4} \ell_\parallel^{-1/4} \approx (\zeta \rho f_j)^{3/2} f_j^{1/4} \\
\hline
\end{array}
\]

The essential difference for nonzero temperatures is the presence of thermal contour undulations, see Fig. 1, decrease.

derate change of the excess contour length contained in the bulge. Estimating \( f_j \approx \zeta L \Delta_\perp^2 / (\ell_\perp t) \), we plug in \( \Delta_\perp \) from above and get \( f_j \approx \zeta L \ell_\perp^2 / (\zeta L^2 \ell_\perp^4) \).

The yet unknown time-dependent width \( \ell_\perp(t) \) of the bulge is controlled by the relaxation spectrum of bending deformations. In the weakly-bending limit, the transverse displacement field \( \mathbf{r}_\perp(s, t) \) of an overdamped inextensible rod with bending stiffness \( \kappa \) obeys

\[
\zeta_\perp \partial_t \mathbf{r}_\perp = -\kappa \mathbf{r}_\perp''' + f_j(t) \mathbf{r}_\perp''',
\]

in the presence of a longitudinal pulling force \( f_j(t) \). Primes denote derivatives with respect to the arclength coordinate \( s \in [-\frac{L}{2}, \frac{L}{2}] \). In the following, we set \( \kappa \) and \( \zeta_\perp \) to unity, such that then a length \( L \) and force a length \( -L \). From a simple scaling analysis of Eq. 11, \( \mathbf{r}_\perp / t \approx \mathbf{r}_\perp / (f_j \ell_\perp^2) \), we deduce the growing size \( \ell_\perp(t) \) of a bending deformation (assuming \( \ell_\perp \ll L \)). Inserting appropriate formulas [13] for \( \ell_\perp(t) \) into the relations for \( \Delta_\perp \) and \( f_j \) derived before finally yields the selfconsistent scaling laws for \( f_j(t) \) and the nonlinear response \( \Delta_\perp(t) \) summarized in Table II(a). For short times the coupling effect is irrelevant and \( \Delta_\perp \) is linear in \( f_j \). However, this requires the small force \( f_j \) to pull in more and more contour length from the tails and increases the longitudinal friction to be balanced by \( f_j \). At the crossover time \( t_t \), this force becomes large enough (typically, \( f_j \approx \gamma f_\perp \gtrsim f_\perp \)) to feed back onto the transverse dynamics, which is manifest in nonlinear dependencies [13] on \( f_\perp \). In particular, it considerably slows down the bulge growth, which in turn requires \( f_\perp \) to pull in contour length at a slower rate and eventually makes it decrease.

The essential difference for nonzero temperatures is the presence of thermal contour undulations, see Fig. 1, which are correlated over the persistence length \( \ell_p = (k_BT)^{-1} \), and straightened out by the longitudinal force \( f_\perp \). Still counteracted by longitudinal friction, this happens first only within a small but growing region of size \( \ell_\perp(t) \) (see Refs. [5,13]). Correspondingly, the force \( f_j(t) \) from above has to be generalized to a tension field \( \mathbf{f}(s, t) \), which decays over the length scale \( \ell_\parallel(t) \).

Crossover scaling laws for \( \ell_\parallel(t) \), shown in Table II(b), were derived for constant external force in Ref. [12] and can be generalized to (weakly) time-dependent “external” forces such as \( f_j(t) \). The thermal problem is essentially analogous to the athermal case for late times \( t > t_L \) where \( t_L \parallel \) is defined via \( \ell_\parallel(t_L) = L \). However, if the region \( \ell_\parallel(t) \), where the contour straightens, does not yet extend to the filament’s ends (\( \ell_\parallel \ll L \), or \( t < t_L \), the “thermal” rod only has an effective time-dependent length of \( \ell_\parallel(t) \). Hence, scaling laws for the nonlinear response are then obtained simply by replacing \( L \to \ell_\parallel \) in Table II(a), which gives the results summarized in Table II(b). These apply to initially unstretched filaments while the general case of prestretched initial conditions is discussed below and summarized in Fig. 8. Naturally, the replacement \( L \to \ell_\parallel \) affects only the long-time scaling of the nonlinear response \( \Delta_\perp(t) \) - on short times \( t < t_t \), the transverse dynamics evolves undisturbed by the longitudinal one. We expect the anomalously slow long-time response to be observable in many biological situations. In aqueous solution, we roughly estimate a crossover time \( t_t \approx 10^{-2} s/f_j([\text{pN}])^{1/5} \) for typical microtubules with \( L \approx 10 \mu m [13] \) (representing the athermal case). Under thermal conditions, where the “interesting” time window is between \( t_t \) and \( t_L \), we get \( t_t \approx 10^{-3} s/f_j([\text{pN}])^{1/5} \) and \( t_L \parallel \approx 0.2 s/f_j([\text{pN}]) \) for (unstretched) actin filaments of about 20 \( \mu m \) length [4], which implies that the actin response to myosin motors becomes nonlinear on time scales comparable to the duration of a single power stroke [15]. Filaments in actin networks (mesh size \( \xi \approx \frac{1}{m} L \approx 0.5 \mu m \)) under stresses of about 1 Pa [11] are usually so short that \( t_t \gg t_L \approx 10^{-4} s \), but the coupling nonlinearity should be observable in the viscoelastic response [5]. Finally, \( t_t \approx 10^{-5} s/f_j([\text{pN}])^{1/5} \) and \( t_L \parallel \approx 0.05 s/f_j([\text{pN}]/f_{pre}[\text{pN}])^{1/3} \) for DNA (\( L \approx 20 \mu m [12] \)) prestretched with \( f_{pre} \ll f_j \).

In order to support and quantify the scaling picture developed above, we proceed with a systematic approach similar to Ref. [13] based on the length scale separation \( \ell_\parallel(t) \gg \ell_\perp(t) \). As long as the dynamics induced by the transverse force is not influenced by end effects (\( \ell_\parallel \ll L \)), we consider a semi-infinite arclength interval, \( s \in [0, \infty) \), and represent the transverse force as a boundary condition at \( s = 0 \). In the wormlike chain Hamiltonian, \( \mathcal{H} = \frac{1}{2} \int ds \left[ \mathbf{r}''^2 + g \mathbf{r}^2 \right] \), the tension \( f(s, t) \) enforces the local inextensibility constraint \( \mathbf{r}'^2(s, t) = 1 \). Parametrizing the contour \( \mathbf{r}(s, t) = (r_\perp, r_\parallel)^T \) by its transverse and longitudinal displacements from a straight line (see Fig. 4), the weakly-bending limit of small contour gra-
dients \( \epsilon^2 \approx \mathcal{O}(\epsilon) \) is realized for very stiff polymers (\( \epsilon \equiv \ell_{f}/\ell_p \)), alternatively for semiflexible filaments strongly prestretched with a force \( f_{\text{pre}}(\epsilon \equiv f^{-1/2}_{\text{pre}}/\ell_p) \).

The conformational dynamics in solution follows from a balance of elastic and tensile forces \(-\partial H/\partial r\), thermal noise \( \xi \), and anisotropic friction \( |r^TR^2(1-r^TR)|\partial r \) \[2\]. Within the weakly-bending limit, transverse and longitudinal fluctuations have strongly different correlation lengths: \( \ell_{\perp}/\ell_p \approx \mathcal{O}(\epsilon^{1/2}) \); cf. Table II(b). An adiabatic approximation (justified via a multiple scale analysis) exploits this scale separation. The resulting equations of motion \[13\] are written in terms of formally independent rapidly and slowly varying arclength parameters \( s \) and \( \overline{s} \approx \epsilon^{1/2} \), respectively:

\[
\frac{\partial \bar{r}}{\partial t} = -\frac{\partial}{\partial \bar{s}} f + f_t \frac{\partial}{\partial \bar{s}} \bar{r} + \underline{\bar{\xi}} + \overline{f(s,t)\Theta(t)}; \tag{2a}
\]

\[
\frac{\partial}{\partial \bar{s}} f = -\bar{\zeta} (\partial \bar{s}/\partial \bar{r}). \tag{2b}
\]

Eq. (2a) gives the small-scale dynamics of the transverse displacements \( \bar{r}(s,t) \) for locally constant tension \( f = \bar{f}(\bar{s},t) \), cf. Eq. (1). Using a Cosine transform with respect to \( s \), it is readily solved by the response function

\[
\chi_{\perp}(q; t, t'; \bar{s}, \bar{t}) = e^{-q^2[(\bar{s}-\bar{t})^2] + f_t \bar{\zeta} \bar{f}(\bar{s},\bar{t})} \Theta(\bar{t} - \bar{t}'). \tag{3}
\]

Eq. (2b) describes the coarse-grained tension variations on the large scale \( \bar{s} \approx \epsilon^{1/2} \): it relates curvature in the tension to (average) changes in stored length density \( \overline{\Theta}(\bar{s},t) = \langle \frac{1}{2} r^2 \rangle / \langle \bar{s}, \bar{t} \rangle \). Averaged both thermally and spatially (on the small scale \( s \)), \( \overline{\Theta} \) inherits its remaining \( \bar{s} \)-dependence from the tension \( \bar{f} \) in Eq. (3):

\[
\langle \overline{\Theta} \rangle = \left\langle \frac{1}{2} \left[ \int_0^\infty \frac{q}{\pi} \int_0^t dt' q \chi_{\perp}(q; t, t') \xi_{\perp}(q, t') \right]^2 \right\rangle. \tag{4}
\]

Reintroducing a single unique arclength variable, \( \bar{s} \equiv s \), Eqs. (2b) and (4) result in a nonlinear partial integro-differential equation (PIDE) for \( \bar{f}(s,t) \), that was analyzed in Ref. 13 for explicitly prescribed boundary conditions. In the present case, however, the boundary condition at \( s = 0 \) has to be determined implicitly. The polymer’s inextensibility requires that the bulge be created using stored length from the tails. To formalize this condition, we demand at any time a vanishing average longitudinal velocity \( \langle \partial_s r \rangle \) at the origin where the force is applied, and also at infinity. Inextensibility \( \langle r'' \rangle = \frac{1}{\bar{s}} \frac{\partial}{\partial \bar{s}} r'' + \mathcal{O}(\epsilon^2) \approx \bar{q} \) gives 0 = \( \int_0^\infty ds \left( \partial_s r'' \right) = \int_0^\infty ds \left( \partial_s \bar{q} \right) \). With \( \partial_s \bar{f} |_{s \rightarrow \infty} = 0 \) and Eq. (2b), this constraint implies

\[
\partial_s \bar{f} |_{s = 0} = -\bar{\zeta} \int_0^\infty ds \partial_t \langle \bar{q} - \overline{\Theta} \rangle. \tag{5}
\]

The difference \( \langle \bar{q} - \overline{\Theta} \rangle \) represents the excess length stored in the bulge on the small length scale \( \ell_{\perp} \). Consequently, it did not contribute to Eq. (4), which was spatially coarse-grained on intermediate scales \( \ell_{\perp} \ll \ell_{\parallel} \). It can be obtained, though, from the right hand side of Eq. (1) upon replacing \( \xi_{\perp} \rightarrow -\bar{f} \sin \Theta(t) \). Evaluating the \( s \)-integral in Eq. (5) to leading order yields our central analytical result: a boundary condition for the tension that quantifies the feedback between “bulge” and “tail” dynamics:

\[
\partial_s \bar{f} |_{s = 0} = -\bar{\zeta} \int_0^\infty \frac{d\bar{q}}{\pi} \int_0^t dt' q \chi_{\perp}(q; t, t') |_{s = 0}^2. \tag{6}
\]

In terms of the response function \( \chi_{\perp}(q; t, t') \) of Eq. (3), the average displacement \( \Delta_{\perp}(t) \) induced by the transverse force (i.e., the nonlinear response) reads

\[
\Delta_{\perp}(t) = f_{\perp} \int_0^\infty \frac{d\bar{q}}{\pi} \int_0^t dt' \chi_{\perp}(q; t, t') |_{s = 0}, \tag{7}
\]

which is evaluated at \( s = 0 \) after the tension profiles \( \bar{f}(s,t) \) are computed from Eqs. (2b) and (4). To this end, we introduce two-variable scaling forms \[13\] that remove any parameter dependence: \( f(s,t) = \gamma f_{\perp} \varphi(s/s_t, t/t_t) \), with the crossover scales \( t_t \) and \( s_t \) and \( \gamma \) as in Fig. 2. Numerical solutions are obtained by mapping the PIDE onto a system of nonlinear equations \[16\]. Selected tension profiles are displayed in Fig. 2 and describe one half of the filament with \( f_{\perp} \) being applied at the origin. Our analytical approach is based on reducing the scaling forms \( \varphi(s/s_t, t/t_t) \) to one-variable scaling functions \( \varphi \sim (t/t_t)^{\alpha} \varphi(s/\ell_{\parallel}(t)) \) with \( \ell_{\parallel}(t) = s_t (t/t_t)^{\gamma} \) in the asymptotic limits of short and long times. In the latter limit \( t \gg t_t \), we recover either the taut-string approximation of Ref. 8 and may neglect bending and thermal forces, or the quasi-static approximation of Ref. 10, which lets us treat the tension as locally equilibrated. Which approximation is valid depends quite strongly on
the prestretching force \( f_{\text{pre}} \) through the ratio \( f_{\text{pre}}/(\gamma f_{\perp}) \), similar to the related scenario of longitudinal stretching forces applied to prestretched filaments \[16\]. The resulting intermediate asymptotic scaling laws for \( \Delta(t) \) (boxed formulas) are summarized in Fig. 3 including analytical prefactors. For a given ratio \( f_{\text{pre}}/(\gamma f_{\perp}) \), the evolution of \( \Delta(t) \) corresponds to a vertical path through Fig. 3. The exact solutions quickly converge to these asymptotes, as shown in the inset of Fig. 2 for the limiting case \( f_{\text{pre}} = 0 \).

In summary, we argue that the coupling between transverse and longitudinal response affects not only single polymers, but also single crosslinks, crosslinked networks, and tensegrity structures \[3, 9, 11, 17\]. For completeness, we note that our self-consistent approach both for the heuristic “bulge” idea as well as for the systematic derivation of Eq. \[2\] applies only to the nonlinear response on sufficiently small times \( t \ll t_{1}^{\perp} \), \( t_{c} \). At \( t_{1}^{\perp} \), end effects become important, and at \( t_{c} \), the weakly-bending assumption breaks down: the contour gradients become large when \( \Delta_{\perp} \ll \ell_{\perp} \). We find that \( t_{c} \gtrsim t_{1}^{\perp} \) for initially weakly-bending filaments (as those in the above discussed situations) \[14\]. Our analysis of the generic coupling mechanism is not constrained by the details of the relaxation regime \( t \gg t_{1}^{\perp} \) (which is similar to the athermal case).

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FIG. 3: (Color online) Regimes of intermediate asymptotics (separated by thick black lines) for the nonlinear response \( \Delta(t) \) (boxed formulas): time \( t/(\gamma f_{\perp})^{-2} \) vs. force ratio \( f_{\text{pre}}/(\gamma f_{\perp}) \) (log-log scale). The universal initial regime \[3\] (light shaded) is followed by a quasi-static regime (white) with different force scaling for asymptotically small (\( < \)) \[8\] force ratio: in these limits, the respective prefactors are \( b_{<} \sim (8\sqrt{2}/\pi^{3/2})^{1/4} \) and \( b_{>} \sim \pi^{-3/2} \). An intermediate taut-string regime (dark shaded) emerges for very small force ratio. The prefactor is \( a = [3(2 + \sqrt{2})/2\pi]^{2/3} \) if \( f_{\text{pre}} = 0 \).

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[18] Since the weakly-bending assumption still holds at \( t = t_{c} \), longitudinal friction is the only relevant nonlinearity and higher-order terms \( r_{\perp}^{2} \) in Eq. \[2a\] are negligible.
[19] \( t_{c} \sim ((\gamma f_{\perp}/L) t_{L}^{\perp}) \) if \( f_{\perp} \gg t_{p}^{2} \) and \( f_{\text{pre}} \lesssim t_{p}^{2} \); otherwise \( t_{c} \gg t_{L}^{\perp} \). For \( f_{\perp} \gtrsim \ell_{p}^{2}/L^{2} \) (\( f_{\text{pre}} \gtrsim \ell_{p}^{2}/L^{4} \)), \( t_{L}^{\perp} \) falls into the taut-string (quasi-static) regime (cf. Fig. 3).