Persistence of strain in motor-filament assemblies

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Crosslinked semi-flexible and flexible filaments that are actively deformed by molecular motors occur in various natural settings, such as the ordered eukaryotic flagellum, and the disordered cytoskeleton. The deformation of these composite systems is driven by active motor forces and resisted by passive filament elasticity, and structural constraints due to permanent cross-links. Using a mean field theory for a one-dimensional ordered system, we show that the combination of motor activity and finite filament extensibility yields a characteristic persistence length scale over which active strain decays. This decay length is set by the ability of motors to respond to combination of the weak extensional elasticity, passive shear resistance and the viscoelastic properties of the motor assembly, and generalizes the notion of persistence in purely thermal filaments to active systems.

Semi-flexible and flexible filaments interacting with active molecular motors arise naturally in the cell as well as in in-vitro motor assays \cite{7}. The overall coordinated macroscopic mechanical response of such a composite assembly depends on the coupling between the active motors and the passive properties of the aggregate composite. A structurally ordered example of such a system is the eukaryotic flagellum comprised of relatively stiff filaments (microtubules), motors (dynein) and passive elastic elements (nexins) which together oscillate with well defined wavelengths and frequencies \cite{8,9,10}. To understand how coordinated motion can arise in such a system, a variety of models of varying degree of complexity \cite{9,10} have been proposed; those show that the wavelength of active beating is correlated with increasing flagellum length. However, experimental evidence strongly indicates that this relationship is altered for very long lengths \cite{11,12} and that the wavelengths attained in nature are self-limiting \cite{8,9} even as the flagella themselves range from tens of microns to nearly a centimeter. This strongly suggests that over large lengths, mechanical information transmission degrades substantially.

Indeed, in a passive context \cite{11}, it has been demonstrated that when bundles of filaments are forced to bend, the shearing forces between them are mediated by extensibility, leading to a characteristic scale over which mechanical information is transmitted. In an active system such as an array of soft filaments interacting with each other via motors, degradation of mechanical signal transmission occurs because the weak passive extensibility of the filaments limits the range over which motor-co-ordination can occur, while restrictions on the kinetics of motor activity set by ATP hydrolysis rates couple back to weak extensibility and alter the interaction between motor groups significantly. We illustrate this in Fig. 1(a) showing two distinct motor patches labeled I and II that cross-link a pair of thin filaments that may bend and shear. For inextensible filaments, mechanical activity by group (I) leads to shear (sliding) in this patch which is transmitted by attached motors in (II) over arbitrarily large inter-aggregate distances. For extensible filaments, there is an interplay between shear/slide and filament elongation along its contour and this leads to a decrease in the ability of group (I) to mechanically link with group (II). In this letter, we propose a minimal, mean-field theory to study the decay of deformations generated by localized steady or oscillatory strains in active, weakly noisy motor-filament assemblies. For simplicity we focus on purely extensional systems ignoring bending modes of deformation and restrict ourselves to a one dimensional setting.

The model system we analyze is illustrated in Fig. 1(b). A weakly extensible filament of length $\ell$, thickness $w \ll \ell$, Young’s modulus $E$ and lateral extent $b$ is animated by active motor proteins that are spaced uniformly with fixed areal density $\rho_m$. These motors are attached to an underlying rigid, straight substrate. Passive permanent cross-linkers connect the filament to the substrate maintaining a gap of size $D (w \leq D \ll \ell)$ between the filament and the substrate. These cross-links, spaced uniformly with areal density $\rho_N$, also act as linear elastic springs of stiffness $k_N$. Active motors are modeled as linear elastic springs of stiffness $k_m$, that attach and detach from the elastic filament. The inter-link spacing and the inter-motor spacing is assumed to be much smaller.

![Fig. 1](image-url)
than the filament length so that a continuum model is appropriate. Thus when $b \gg \max(w, l)$, the assembly acts as an effective one dimensional extensible composite filament, with the passive permanent cross-linkers that connect the filament to the substrate providing shear resistance. The effective shear modulus resulting from these passive springs is obtained by considering the relative displacement between the top sheet and bottom sheets due to a shearing stress acting on an area $bf$; this yields $G^* \sim DkN\rho_s$ and $G^* w/D \sim w kN\rho_s/2$ - consistent with analysis of a passive cross-linked railway track model [10].

Due to the motors, the filament is displaced horizontally as it is stretches. Let the displacement of a material point on the filament relative to its initial position in the undeformed state be $U(s, t)$, $s$ being the material/reference coordinate, and $t$ time. For an inertialess filament, the sum of forces on the filament arising from filament extensibility, springs and motors must vanish. If $F_m$ is the effective active force density per attached motor and $\rho_m$ the (total) motor density, local stress balance then yields

$$\partial_s (K_{pas} \partial_s U) - G_{pas} U + \rho_m F_m = 0.$$  \hspace{1cm} (1)

Here $K_{pas} \sim Ew$ and $G_{pas} \sim \rho_N k_N$ are the passive stretching and passive shear moduli (per unit width) for the composite filament. In the absence of activity, $F_m = 0$ so that the solution to (1) yields an exponential profile for the displacement with a relaxation length scale $\ell_E \equiv (K_{pas}/G_{pas})^2 = (Ew/\rho_N k_N)^2$, so that as the passive shear resistance $\rho_N k_N$ increases, the persistence length decreases.

When motors are present, $F_m \neq 0$. At the level of a single motor, we assume that motors attach to the elastic filament with an initial extension $d_m$ (that may vanish) and are then stretched due to two effects - a sliding velocity relative to the filament as well as the displacement of the filament due to the cumulative effect of other motors. Both of these lead to an increasing motor extension $y$ shown in Fig. 1(b). Assuming a simple linear relation for the force-velocity relation for an individual motor, we may then write $\partial_t y = \partial_t U + v_o (1 - k_m y/F_s)$ where the first term is the velocity of the filament and the second term is the velocity of the head relative to the track. Here the stall force $F_s$ and the load-free velocity $v_o$ are motor dependent parameters.

With this given motor-filament interaction, the average number of attached motors relates attached and detached probability densities to their corresponding fluxes via microscopic transition rates. In the mean-field limit, the density of motors $\rho_m$ is large enough that fluctuations in the time average of the density of attached motors $\rho_a = \rho_m N(t)$, where $N(t)$ is the fraction of attached motors are small compared to the mean value. Ensemble averaging the terms in the population balance equation over $y$ (see SI-§I) yields

$$\partial_t N = \omega_{on}^0 (1 - N) - \omega_{off} N,$$  \hspace{1cm} (2)

where the mean attachment rate $\omega_{on}^0$ is assumed to be constant, and the mean detachment rate $\omega_{off} = \omega_{on}^0 F(E, Y)$ is modified by motor extension, since the characteristic energy scale for detachment is $E \equiv k_m d_m^2/k_B T$ and depends on a typical length scale $\delta_m$ characterizing the extension at which motors detach. Consistent with previous studies [12, 13], we use two forms: $F(E, Y) = \exp(E Y)$ and $F(E, Y) = \cosh(E Y)$. The evolution of the mean motor extension $Y \equiv \langle y \rangle/\delta_m$ is obtained by write down the microscopic description for $\partial_t y$ for a single motor and then average over $y$. Relating the average stretching rate ($\partial_t y$) to $\partial_t \langle y \rangle$ yields

$$\partial_t Y = \frac{\partial_t U}{\delta_m} + A_1 \omega_{off}^0 (A_2 - Y) + \omega_{on}^0 (A_3 - Y) \left( 1 - N \right)$$  \hspace{1cm} (3)

The first term on the right is the passive convection of the motor head as the filament stretches [12] and second term arises as the motor head walks relative to the moving filament. The last term on the right corresponds to the rate at which the mean strain changes due to the kinetics of motor attachment and arises from the difference in extension of attaching and detaching motors. The parameters $A_1 \equiv v_o k_m/\omega_{off}^0 F_s$, $A_2 \equiv F_s/(k_m \delta_m)$ and $A_3 \equiv d_m/\delta_m$ relate the microscopic motor parameters to the population level dynamics. Finally, given the fraction of attached motors $N$ and their mean extension $Y$, the effective active force per motor in (1) is given by

$$F_m = k_m \delta_m N Y.$$  \hspace{1cm} (4)

Equations (1)-(4) specify the evolution of the filament displacement $U(s, t)$, the motor density $N(s, t)$ and the motor stretch $Y(s, t)$ in terms of the dimensionless parameters $A_1, A_2, A_3$ and $\Psi \equiv \omega_{off}^0/\omega_{on}^0$. While $\Psi$ is related to the duty ratio of the motors, $A_1$ and $A_3$ determine the mechanism that yields the average extension of attached motors. Specifically, when $A_3 \ll 1$, the role of the pre-strain $d_m$ is negligible [13] while when $A_1 \ll 1$, pre-strain dominates [12]. Our model complements and differs from previous attempts in a few important ways. Firstly, the detachment rate $\omega_{off}^0$ depends on the motor extension [12, 13] and not the rate of extension [18], consistent with experiments that show that bond failure is more naturally dependent on the extension and only weakly on the rate of extension [19]. Secondly, the non-linear coupling between passive and active deformations in [3] distinguishes our model from previous studies of motor mediated bending of filaments [18]. Finally, we assume that the filament is (weakly) extensible, bolstered by experimental evidence in passive systems [9] [11], and unlike all previous studies of active ordered filaments.

To understand the solutions of (1)-(4) and their stability, we expand the motor displacement $Y$, the filament extension $U$, and motor number density $N$ in pow-
ers of $\epsilon \ll 1$, the deviation from steady state, using the ansatz $(U, Y, N) = (U_0, Y_0, N_0) + \epsilon \text{Rea}l[e^{\sigma t}(U, Y, N)]$, with the first term corresponding to the steady, static state (that arises due to motor activity) while the second corresponds to the time dependent perturbations from the steady state - these could be due to intrinsic or imposed perturbations. Here $\epsilon U_{imp}/U_0(\ell) \ll 1$ and $\sigma$ is a complex growth rate. In the absence of external forcing, this growth rate determines the stability of the base state $(U_0, Y_0, N_0)$. Substituting in (1)-(3) we find at $O(\epsilon^2)$ that $U_0, N_0, Y_0$ satisfy

$$K_{pas} \partial_u U_0 - G_{pas} U_0 + G_{act} C = 0, \quad (5)$$

$$N_0 = (1 + \Psi F_0)^{-1}, \quad (6)$$

$$Y_0 = (A_1 A_2 + A_3 F_0)(A_1 + F_0)^{-1} \tag{7}$$

where $G_{act} = \rho_m k_m$, the active analogue of passive shear modulus and $C = \delta m N_0 Y_0 = \frac{1}{2} \frac{A_1 A_2 + A_3 F_0}{A_1 A_2 + A_3 F_0}$. Here, $N_0$ and $Y_0$ are independent of position, s. The steady extension at the free end $U_0(\ell)$ results purely from steady motor activity when $\epsilon = 0$ and is therefore obtained by imposing the constraint $\partial_u U_0(\ell) = 0$. Equations (5)-(7) determine the extensional (strain) field resulting due to activity. At $O(\epsilon)$, we find

$$K_{pas} \partial_u U - G_{pas} U + G_{act} \delta_m (N_0 Y + \dot{Y} \dot{N}) = 0, \quad (8)$$

$$- \dot{N} (\sigma + \omega_{on}^2 (1 + \Psi F_0) + \omega_{off}^2 \Psi N_0 F_0^2 \dot{Y} = 0, \quad (9)$$

$$\dot{Y} \left( \frac{\omega_{on}^2}{\omega_{on}^2 + \Psi (A_3 F_0)} + (A_3 - Y_0) \frac{N}{N_0} \right) = \frac{\sigma U}{\delta m \omega_{on}} = 0. \quad (10)$$

Equations (8)-(10) may be interpreted in two ways. In the absence of imposed oscillations, they determine the linear stability of the equations (5)-(7) to small perturbations. Alternately (8)-(10) can be interpreted as the linearised response to a small amplitude, externally imposed oscillation in which case in the limit $t \to \infty$ limit (provided $\text{Rea}l [\sigma] < 0$), $(\bar{U}, \bar{N}, \bar{Y})$ is slaved to the forcing frequency.

Before we approach the question of persistence of activity in an active filament, we ask if spontaneous strain fields can be generated by a small, localized patch of motors of length $\ell_s \ll (K_{pas}/G_{pas})^{1/2}$. The dynamics of this patch may be mapped to that of a rigid segment working against an effective spring with as well as active components - here, we lump these contributions together using an effective spring constant $K_s \sim G_{pas}$ (SI-§IIa). The displacement of this fragment follows

$$- K_s U + G_{act} \delta_m N Y = 0. \quad (11)$$

When $K_s > 0$ (for the degenerate case $K_s = 0$, see SI-§IIb) and global filament translation is prevented, equations (2), (3) and (11) admit two classes of solutions - a constant extension of the rigid filament with $\partial_u U = 0$, or a time-periodic, oscillatory extension. In the first case, the steady density and motor strain are given by equations (6) and (7) with the steady extension $G_{act} C/K_s$ where $C = \delta m N_0 Y_0$. This static state is however linearly unstable to oscillatory states and the onset of these oscillatory states can be readily obtained from (9), (10) and the linearised version of (11). Analyzing the conditions under which $\text{Rea}l [\sigma] = 0$ yields the neutral stability curve that demarcates the static state from stable, oscillatory states, emanating via supercritical Hopf-Poincare bifurcations; the necessary criterion for this being $\partial F/\partial Y(0) = F'_0 > 0$. The mechanism behind the oscillations is the coupling in (11) between the filament motion and attached motors that yields an effective compliance comprised of both in-phase and an out-of-phase term; the oscillatory solutions obtained are a result of positive feedback, when either or both of these terms turn negative, similar to that seen in flagellar $\text{IN}$ and spindle oscillations $\text{I2}$. In Fig.3 (a), we show neutral stability curves (SI-§IIIC) separating oscillatory from non-oscillatory steady regimes. For fixed motors density (fixed motor number) $\rho_m$, there is a range of $\Psi$ over which oscillations can be sustained. For fixed $\Psi$ there exists a critical motor density, related to $K_s/(\rho_m k_m)$ (units m$^{-2}$), above which the oscillations appear. When stably oscillating, the power due to activity balances dissipation due to motor friction - this yields an effective viscosity $\eta_{act} \sim \rho_m N_0 k_m (\partial y/\partial U)_{U=0} \equiv (\partial y/\partial U_{U=0})_{U=0}$ where $\rho_m N_0$ is the total number of attached motors. As $\Psi$ increases, both $\partial y/\partial U_{U=0}$ and $N_0$ typically decrease leading to an increase in the emergent frequency $\omega_c$ - c.f. Fig. 3(b) - here, $U_t = \eta_{act}$. Having identified the two stable localized dynamical states that can exist for a short fragment, we next combine this local analysis with a global description of the filament extension to obtain decay lengths for active assemblies. We first address decay lengths of steady extensions. For boundary conditions, we assume that $U(0, t) = 0$ and $U(\ell, t) = U_0(\ell) + \epsilon \text{Rea}l [e^{\sigma t} u_0]$, i.e. one end is fixed while the other is forced harmonically with amplitude

![FIG. 2. Oscillatory solutions for $A_s = 0$, $K_s > 0$ and $K_{pas} = 0$ obtained by analysis of (1)-(3). (a) Neutral stability curves $\Psi = \omega_{off}/\omega_{on}$ vs. number of motors (proportional to motor density) are shown for $\mathcal{E} = 4.944, Y_0 = 5 \times 10^{-1}$ and $\omega_{on} = 0.25$ s$^{-1}$. Curves are - (1) $\mathcal{F} = \cosh(\mathcal{EF}Y)$ and (2) $\mathcal{F} = \exp(\mathcal{EF}Y)$. For fixed $\Psi$, there is a critical number of motors required for oscillations to manifest (as illustrated for $\Psi = 0.6$). There is a critical value of $K_s/k_m$ for fixed motor density below which oscillations will not be seen. (b) Scaled frequency of oscillations, $\omega_c/\omega_{on}$, as a function of $\Psi$. The solid line is the exact result while the dashed line is the adiabatic approximation $Y_t \approx \Psi \mathcal{F}$. (Inset) The model spring-filament-motor homogeneous system.
\(\chi\) and not the strain. An elastically compliant inter-motor compliance because active motors sense only strain rates for \(k\) extensions depends only on the passive elastic properties such as stall force \(F_s\), free velocity \(v_0\) and the duty ratio via \(\Psi\). When activity is weak, \(\beta \ll 1\), an expansion of equation (14) in powers of \(\beta\) yields \(\lambda_E \approx \ell_E (1 - \frac{1}{2} \beta R - \frac{1}{8} \beta^2 (\lambda^2 - 3 R^2)) + O(\beta^3)\). For \(R > 0\), at \(O(\beta^2)\) the motor activity decreases \(\lambda_E\) with shear stiffening driving the stretching of the filament. The \(O(\beta^2)\) term can either enhance this effect or lessen it depending on the sign of the term \((\lambda^2 - 3 R^2)\). For strong activity, when \(\beta \gg 1\), we get \(\lambda_E \approx \sqrt{2 K_{\text{pas}} / G_{\text{act}}} (R + |\chi|)^{-\frac{1}{2}}\) with actively driven shear stiffening dominating.

The role of motor dynamics can be probed by examining the low and high frequency limits of (14). In the low frequency limit, motors undergo multiple mechanochemical cycles before they feel the imposed oscillation. In the high frequency limit, attached motors encounter several cycles of imposed oscillations before detaching. Activity will then increase the persistence length from the lower bound of a tightly coupled system. These trends are transparent when we examine the limit \(A_3 = 0\). In the low frequency limit, \(I \sim (\omega / \omega_{\text{off}}) (1 - \gamma + \gamma \tau) \) and \(R \sim (\omega / \omega_{\text{off}})^2 (1 - \gamma + \gamma \tau^2)\) with \(\gamma = A_0 \Psi F'_0\) and \(\tau = \omega_{\text{off}} / (\omega_{\text{off}} + \omega_{\text{on}})\) both dependent on \(Y_0\) but not on \(s\). Substituting these in (14), yields \(\lambda_E \approx \ell_E (1 - \frac{1}{2} (\omega / \omega_{\text{off}}) \{3 \beta^2 (1 - \gamma + \gamma \tau^2 + 4 \beta (1 - \gamma + \gamma \tau^2))\})\), which clearly indicates that activity, through \(\beta\), decreases the persistence length. In the limit of high \(\omega\), we find \(R \sim 1 - (\omega / \omega_{\text{off}})^2 (1 - \gamma + \gamma \tau^2)\), and \(I \sim (\omega / \omega_{\text{off}}) (1 - \gamma + \gamma / \tau)\) providing \(\lambda_E \approx (\ell_E / \sqrt{1 + \beta}) (1 + \frac{1}{2} (\omega / \omega_{\text{off}})^2 \{4 \beta (1 - \gamma + \gamma / \tau^2) - \frac{\beta^2}{1 + \beta} (1 - \gamma + \gamma / \tau)^2\})\). In the limit \(\omega \to \infty\), \(\lambda_E \to \ell_E / \sqrt{1 + \beta} = \sqrt{K_{\text{pas}} / (G_{\text{pas}} + G_{\text{act}})}\).

For fixed motor properties, the decay length sets a finite range of correlated activity that might be relevant for naturally ordered active matter such as eukaryotic flagella [20]. Modeling the flagellum as a composite filament driven by uniformly spaced dynein motors, we take \(w\), \(D\) and \(E\) as the radius, spacing and Young’s modulus of microtubules and \(K_N\) and \(\rho_0\) as the nexin stiffness (per length) and nexin density. From the existing literature, we find \(w \approx 20\) nm, \(D \approx 40\) nm [21], \(E \approx 1.2\) GPa [9, 21], \(K_N \approx 16 - 100\) pN \(\mu m^{-1}\), \(k_N = 10^{-10}\) N/m [22], \(\rho_m \approx 10^8\) m\(^{-1}\) and \(\rho_{\text{off}} \approx 10^5 - 10^7\) m\(^{-1}\) [17, 22]. We find that the frequency dependent decay length \(\ell_E \in [10 - 500]\) \(\mu m\). From the lower limit corresponds to all dyneins and nexins attached, and the upper bound corresponds to only nexins being attached - in the range of physically relevant length scales. For segments of the flagella separated by distances less than the decay length, one could have frequency entrainment with multiple oscillatory regions eventually synchronising.

Our theory accounts for extensional deformations in a model ordered active composite consisting of elastic elements that can be stretched and sheared by dynamically attaching motors. Extensibility, even if negligible locally, affects the scale over which deformations persist owing to the competition between extensibility and shear. For strain dependent motor kinetics, the decay of steady extensions is controlled by shear stiffening due to passive linkers. Localized oscillatory strains lead to global deformations that decay over longer length scales that involve passive and frequency dependent active properties of the assembly. Given that it is now possible to create partially ordered mixtures of motors and cytoskeletal
SI: Persistence of strain in motor-filament assemblies

I. COARSE-GRAINING YIELDS MEAN FIELD MODEL

Of the total motors per area at position $s$ along the filament let a fraction $N(t)$ be attached so that the density of detached motors is $\rho_d(s,t) = \rho_m(1 - N(s,t))$. Each motor experiences an internal spring extension $y$ which may be considered the distance between the head and the base or as an intrinsic coordinate of the underlying mechanochemical cycle. We choose $y = 0$ as our base state corresponding to an unstrained motor.

In the mean-field limit, the number of motors (and the density) is large (high) enough that fluctuations in the time average of the density of attached motors $\rho_a(s,t) = \rho_m N(s,t)$ are small compared to the mean value. The motor kinetics may be described by a set of population balances relating the attached and detached probability densities $\mathcal{P}_a(s,y,t)$ and $\mathcal{P}_d(s,y,t)$ to attachment and detachment fluxes $J_a$ and $J_d$ via the transition rates $\nu_{on}(y)$ and $\nu_{off}(y)$,

$$\begin{align*}
\frac{\partial_t \mathcal{P}_a}{\partial t} + \frac{\partial_y J_a}{\partial y} &= \nu_{on} \mathcal{P}_d - \nu_{off} \mathcal{P}_a, \\
\frac{\partial_t \mathcal{P}_d}{\partial t} + \frac{\partial_y J_d}{\partial y} &= \nu_{off} \mathcal{P}_a - \nu_{on} \mathcal{P}_d
\end{align*}$$

(15)

consistent with previous studies (see [6, 12] and references therein). For simplicity, the attachment frequency $\nu_{on}$ is chosen to be constant while the detachment rate is allowed to vary with the motor extension. Thus we write $\nu_{off} = \nu_{off}(y, \delta_m)$, $\delta_m$ being a measure of the motor extension at which the detachment rate becomes significant. Focusing on the noise-less limit, we make the assumption that thermal noise as described by Brownian effects of the motor diffusion of both the motor base (this is assumed to be attached permanently) and the motor head, is negligible. Where, in the absence of motor diffusion, $J_a = (d_y \mathcal{P}_a)$.

Consider now the flux of attached and detached motors. One scenario is that the detached motors could rapidly relax to their equilibrium internal state with a viscous relaxation time. Alternately the detached motors could relax to a delta function $\mathcal{P}_d = \rho_d(t) \delta(y)$ with the change occurring instantaneously. When the distribution in extension of attached motors is sharply peaked about the typical (average) length, transients to this distribution occur over times very small compared to the averaged macroscopic time scale, $t$ we can write $\mathcal{P}_a = \rho_a(t) \delta(y - \langle y \rangle)$. Averaged equations (moments) may be obtained from (SI-1) and (SI-2) by using the definition $\int X \mathcal{P}_a dy \equiv \langle X \rangle N \rho_m$.

Integrating either (SI-1) or (SI-2) over all configurations $y$ yields

$$\begin{align*}
\frac{\partial_t \rho_a}{\partial t} &= \omega_{on}^c \rho_m - \rho_a (\omega_{on}^c + \langle \nu_{off} \rangle).
\end{align*}$$

(17)

In deriving these equations, we have used the fact that averaging the transition rates yield the mean-field (effective) attachment rate $\omega_{on}^c$ (chosen to be a constant), and detachment rate, $\langle \nu_{off} \rangle = \omega_{off}$ that is modified by the mean motor extension.
The extension of attached motors $y$ for a location $s$ is peaked about the mean value $\langle y \rangle(s, t)$ with small deviations from this mean. Ignoring these deviations as done in previous studies \cite{6,12}, we choose $\nu_{\text{off}}(y)$ to depend only on the scaled mean motor extension $Y \equiv \langle y / \delta_m \rangle$ so that $\omega_{\text{off}}$ is just dependent on $(Y, \delta_m, \kappa_m)$. Thus we may write,

$$\langle \nu_{\text{off}} y \rangle \approx \nu_{\text{off}} \langle y \rangle \approx \omega_{\text{off}} Y \delta_m$$

and thus $\omega_{\text{off}} \equiv \omega_{\text{on}}^0 F(Y, \mathcal{E})$ where $\mathcal{E} \equiv k_m \delta_m^2 / k_B T$ is a measure of the energy needed to stretch the motors to their maximal extent. For subsequent analysis, we define

$$\mathcal{F}_0 \equiv \mathcal{F}(Y_0), \quad \mathcal{F}_0' \equiv \frac{d\mathcal{F}}{dY}(Y = Y_0).$$

Note that since $\rho_s(s, t) = \rho_m N(s, t)$, equation (SI-3) can be recast as

$$\partial_t N = \omega_{\text{on}}^0 - N(\omega_{\text{on}}^0 + \omega_{\text{off}}).$$

The final equation is for the evolution for the mean strain, $\langle y \rangle \equiv Y \delta_m$. This ensemble averaged quantity changes due to three effects - the pre-strain (pre-extension) value of attaching motors, the fact that motors detach at finite strain and the evolution of the strain whilst the motor is attached. The evolution of extension in attached motors is related to the correspondence between the change of the mean stretch, $\partial_t \langle y \rangle$, to the mean rate of stretch, $\langle \partial_t y \rangle$ and necessitates consideration of the local interaction between the motor heads and the filament tracks on which they move exemplified by an active velocity-force relationship and a passive force that is a measure of the elasticity of a fixed cross-bridge under conditions of rigor.

We consider a simple physical picture for how motors interact with the filament. We assume motors attach in a pre-strained state with initial extension at attachment $d_m$, and then once attached walk relative to the filament with velocity $v_m$ as they interact with the tilted potential that characterises the filament-head interaction. At the same time since the base is fixed, the increasing spring extension $y$ causes a force that ultimately at some point detaches the motor.

As the motor head moves relative to the potential field generated by the filament, it obeys a velocity-force relationship prescribed by microscopic details of the motor head-track interaction. One may then think of the velocity relative to the track as being caused by the hopping of the head from one potential local energy well (binding site) to another without detaching from the track. The simplest specification for the velocity of the motor head relative to the track after it is attached is given by a linear force-velocity relationship

$$v_m = \partial_t y = \partial_t U + v_o \left(1 - \frac{k_m \delta_m y}{F_s} \right)$$

where the first term $\partial_t U$ is the velocity of the filament (that convects the attached motor). The second term is the velocity of the head relative to the track and in this term $F_s$ is the stall force at which motion stops, $v_o$ is the velocity at zero force and $k_m \delta_m Y$ is the spring force. Taking the ensemble average of (SI-7) yields

$$\langle \partial_t y \rangle = \partial_t U + v_o \left(1 - \frac{k_m Y^{(i)}}{F_s} \right).$$

Finally, we put together these aspects of the motor extension. Multiplying (SI-2) by $y$ and then integrating over $y$, we can write

$$\partial_t \langle y \rangle = -\langle \nu_{\text{off}} y \rangle + \partial_t U + v_o \left(1 - \frac{k_m Y^{(i)}}{F_s} \right) + \langle \nu_{\text{off}} \rangle \langle y \rangle + \omega_{\text{on}}^0 (d_m - \langle y \rangle) \left(1 - \frac{N}{N} \right).$$

Since $\langle \nu_{\text{off}} y \rangle \approx \omega_{\text{off}} Y \delta_m$, we get the dimensional version

$$\partial_t \langle y \rangle = \partial_t U - \omega_{\text{on}}^0 \langle y \rangle \left(1 - \frac{N}{N} \right) + \omega_{\text{on}}^0 \left[v_o \frac{\omega_{\text{off}}}{\omega_{\text{off}}^0} \left(1 - \frac{k_m \langle y \rangle}{F_s} \right) + d_m \left(1 - \frac{N}{N} \right) \right].$$

Note that when $d_m = 0$, we recover the model proposed by Grill et. al. \cite{12} wherein motors attach at zero extension and then walk along the filament with a strain-dependent speed. When $v_o = 0$, we recover a different model \cite{6} wherein motors follow a two-state cross-bridge scheme and attach in a forward leaning position with an motor extension $d_m$. Equation (SI-10) is an approximation which allows one to interpolate between these two limiting cases.
FIG. 3. Stationary branches and stability of steadily translating solutions of a fragment of the filament when $K_s = 0$ and $A_1 = 0$. Here, $(u_0 \omega_0^s / \delta_m) \equiv Z$ is the continuation parameter. Parameters values are, scaled motor extension $d_m / \delta_m = 1$, ratio of kinetic, $\omega_0^s / \omega_{off}^s = 1$. The function $\mathcal{F} = \exp(|\mathcal{E}|)$ - solutions are shown for (a) $\mathcal{E} = 1$ and (b) $\mathcal{E} = 2$. Circles are limit points where stability changes from stable (solid line) to unstable (dashed line) regimes. Increasing the value of $\mathcal{E}$ opens up the unstable part of the branch.

Now using $Y \equiv \langle y \rangle / \delta_m$, and defining

$$A_1 \equiv v_o k_m (\omega_{off}^s F_s)^{-1}, \quad A_2 \equiv F_s (k_m \delta_m)^{-1}, \quad A_3 \equiv d_m / \delta_m$$

we can write (SI-10) as

$$\partial_t Y = \frac{\partial_t U}{\delta_m} - \omega_0^s Y \left( \frac{1 - N}{N} \right) + \omega_0^s \left[ A_1 \Psi (A_2 - Y) + A_3 \left( \frac{1 - N}{N} \right) \right].$$

To find steady homogeneous solutions, we set $\partial_t U = \partial_t Y = \partial_t N = 0$ in (SI-6) and (SI-12). This gives us

$$N_0 = \frac{1}{1 + \Psi \mathcal{F}_0}$$

and the implicit, non-linear equation

$$Y_0 = \frac{A_1 A_2 + A_3 \mathcal{F}_0}{A_1 + \mathcal{F}_0}.$$ \hspace{1cm} (28)

Note that when $A = 0$, then $Y_0 = A_3$. For later purposes we define a constant $C \equiv \delta_m N_0 Y_0$, so that

$$C = \delta_m \frac{1}{1 + \Psi \mathcal{F}_0} \frac{A_1 A_2 + A_3 \mathcal{F}_0}{A_1 + \mathcal{F}_0}.$$ \hspace{1cm} (29)
II. DYNAMICS OF A SMALL FRAGMENT

A. Mapping to an effective resisting spring

The dynamics of a fragment of the filament of length \( \ell_s \ll (K_{\text{pas}}/G_{\text{pas}})^{1/2} \) (the strip has lateral extent \( b \)) animated by the activity of motors may be mapped on to that of a rigid segment working against an effective spring that has both passive and active components - here we combine these contributions together in terms of an effective spring constant \( K_s \). The passive elasticity of this spring comes from both \( G_{\text{pas}} \) and \( K_{\text{pas}} \) while the active contribution comes from attached motors in neighbouring segments. If \( \rho_N = 0 \) then the passive part of \( K_s \propto K_{\text{pas}}/(\ell_s b) \), while a contribution solely due to passive linkers would suggest \( K_s \propto G_{\text{pas}} \). Since, active contributions merely rescale \( K_s \), we treat this as a external parameter.

B. Degenerate case of free fragment

When there is no restraining spring, \( K_s = 0 \), and equation (11) of the main text is irrelevant. We are left with equations (2) and (3) of the main text that describe an untethered, stiff filament forced by motors to move at velocity \( \partial_t U = V \). Treating \( \left( V/\delta_m\omega_{\text{on}}^o \right) \equiv Z \) as a continuation parameter and restricting ourselves to constant \( Z \), we numerically obtain solutions defined by the set \( N(Z) \) and \( Y(Z) \). Fig. 1 illustrates the dynamical characteristics of these solution branches when \( A_1 = 0 \) and \( F = \exp (E|Y|) \). The fraction of attached motors, \( N \) and \( Y \) selects the constant speed \( Z \). The stability of the translating solution is controlled by the form of the detachment rate and characteristic energies for motors to detach \( \mathcal{E} \). The range over which a stable, steadily translating velocity (solid curve) can exist is controlled by \( \mathcal{E} \). These results are relevant to microtubule-motor assays in which small rigid segments are moved about by the motor activity.

C. Dynamics of the tethered fragment - Linear stability and emergent oscillations

1. Limiting case: \( A_3 = 0 \)

The non-linear equations are

\[
\begin{align*}
\partial_t N &= \omega_{\text{on}}^o - N(\omega_{\text{on}}^o + \omega_{\text{off}}), \\
\partial_t Y &= \frac{\partial_t U}{\delta_m} - \omega_{\text{on}}^o Y \left( \frac{1 - N}{N} \right) + \omega_{\text{on}}^o A_1 \Psi (A_2 - Y).
\end{align*}
\]

The stationary solution is this limit is

\[
(N_0, Y_0) = \left( \frac{1}{1 + \Psi F_0}, \frac{A_1 A_2}{A_1 + F_0} \right).
\]

The equations governing disturbances \((N^*, Y^*, Z^*)\) about this stationary state are (for ease of notation, we denote time derivatives by dots)

\[
\begin{align*}
\dot{N}^* &= -(1 + \Psi F_o) N^* - N_o \Psi Y^* F_o', \\
\dot{Y}^* &= \dot{Z}^* - \Psi A_1 Y^* - Y^*(\frac{1 - N_o}{N_o}) + Y_o A_2 N^* + Y_o N^*-1, \\
Z^* &= \frac{G_{\text{act}}}{K_s} (N_o Y^* + Y_o N^*).
\end{align*}
\]

where we have scaled \( U \) by \( \delta_m \) and time by \((\omega_{\text{on}}^o)^{-1}\). Redefining

\[
\beta_o \equiv (1 + \Psi F_o), \quad A \equiv \Psi A_1 + \Psi F_o, \quad B \equiv Y_o \Psi F_o' N_o^{-1} \quad \text{and} \quad B \equiv \frac{G_{\text{act}}}{K_s}
\]
we find three growth rates of the linearized equations of the form $-s_1$ (real, negative growth rate - the dissipative effect), $-s_2$ and its complex conjugate, $-\bar{s}_2$. The critical frequency at onset $\omega_c \equiv \omega_c/\omega_{\text{on}}$ and the neutral stability curve are

$$\omega_c = \left( \frac{\mathcal{A} \beta_o + \mathcal{B}}{1 + \mathcal{B} N_o} \right)^{\frac{1}{2}}$$

and

$$\mathcal{B} Y_o \Psi F_o N_o = \Psi A_1 + (1 + 2 \Psi F_o) + \mathcal{B} N_o (1 + \Psi F_o).$$

Invoking various quasi-static assumptions - thus yielding approximations where the motor displacement is slaved to the density field - does not yield qualitative differences.

The physical mechanism for oscillations is an effective negative spring constant and negative friction co-efficient due to the interplay between the motor dynamics and the spring resistance of the rod leading to a positive feedback in the dynamics of the system. To formally see this we set $u = \Delta_1 \dot{U} \exp(i\omega t) + c.c., Y = Y_o + \Delta_1 \dot{Y} \exp(i\omega t) + c.c$ and $N = N_o + \Delta_1 \dot{N} \exp(i\omega t)$ and find the find the frequency dependent response of the active force term $F_o = \rho_m k_m \delta_m Y N$ which in frequency space writes as $\rho_m k_m \delta_m \chi(\omega)$. The frequency dependence of $\chi$ indicates that under certain conditions the elastic in-phase $\mathcal{R}(\chi)$ - and/or viscous out of phase $\mathcal{I}(\chi)$ - parts turn negative suggesting a positive feedback thus yielding eventually stable oscillations. For large values of $\Psi$, the number of attached motors is insufficient to supply the energy for oscillations thus yielding an upper bound. For small $\Psi$ too many attached motors increase the net elastic resistance and friction coefficients, causing a strong damping of oscillations. These trends are qualitatively consistent with related observations on mitotic spindle oscillations even though the governing equation differs due the exact averaging procedure [12]. In the stable oscillating state, the active energy input by motor attachment must balance the dissipation due to motor friction. Unfortunately, the equation for the emergent frequency is too algebraically complicated to be interpreted directly. It is however possible to estimate the effective active viscosity and anticipate how this affects emergent frequency. When motors adiabatically couple to the dynamics of the rod, as in [12] for instance, so that $\dot{Y} \approx \Psi Y \mathcal{F}$ and mean motor extension is slaved to the velocity of the rod and the mean time for which the motor stays attached, we find

$$\omega_c^2 \sim \frac{K_s (\omega_{\text{on}}^2 + \omega_{\text{off}}^2) F_o}{\rho_m k_m N_o (d(y)/dZ)_{Z=0}}$$

yielding an estimate of the effective motor friction

$$\eta_{\text{active}} \sim \rho_m k_m N_o (d(y)/dZ)_{Z=0}$$

As $\Psi$ increases with everything else held constant, $(d(y)/dZ)_{Z=0}$ typically decreases, as does $N_o$, resulting in an effective increase in $\omega_c$.

D. Limiting case: $A_1 = 0$

The ensemble averaged equations for the fraction of attached motors $N$ and the mean motor stretch $Y$ are

$$N_t = \omega_{\text{on}}^2 - N (\omega_{\text{on}}^2 + \omega_{\text{off}}^2)$$

$$Y_t = \frac{\partial U}{\partial m} + \omega_{\text{on}}^2 (A_3 - Y) \left( \frac{1 - N}{N} \right).$$

The stability of the stationary base state against small perturbations $Z^*, Y^*$ and $N^*$ is now governed by the evolution of the dimensionless set

$$Z^* = \frac{G_{\text{net}}}{K_s} (N_o Y^* + Y_o N^*)$$

$$\dot{Y}^* = \dot{Z}^* - Y^* \left( \frac{1 - N_o}{N_o} \right)$$

$$\dot{N}^* = -(1 + \Psi F_o) N^* - \Psi N_o F_o Y^*.$$
Seeking possible periodic solutions, we again find that the resulting equations admit either decaying solutions or oscillatory solutions. The neutral stability curve is given by

\[ 0 = (1 + 2\Psi F_\alpha) - BY_\gamma \Psi N_\alpha F'_\alpha + B N_\alpha (1 + \Psi F_\alpha). \]

and the frequency at onset is

\[ \tilde{\omega}_c = \left( \frac{\Psi F_\alpha (1 + \Psi F_\alpha)}{(1 + B N_\alpha)} \right)^{\frac{1}{2}}. \]

Again, further simplifications can be made in the various adiabatic limits discussed earlier with motor dynamics slaved to the dynamics of the rod. One such physically relevant limit is \( \Psi F_\alpha \gg 1 \) which is obtained when the detachment rate at the equilibrium point is much larger than the strain-independent attachment rate. An alternate approximation which may be treated as a variation of the mean field theory is \( \dot{Y} = \Psi Y F \). As \( \Psi \) increases with everything else held constant, \( N_\alpha \) decreases, resulting in an effective increase in \( \omega_c \).

### III. DECAY LENGTH CALCULATIONS

#### A. Decay length formula

Trying out complex solutions of the form \( U = U_s e^{s/\lambda} \) we get the solvability condition

\[ (G_{\text{pas}} + G_{\text{act}} R - K_{\text{pas}} \lambda^{-2})^2 + (G_{\text{act}} I)^2 = 0 \]

Thus \( \lambda \) is in general complex and satisfies

\[ \lambda^{-1} = \left[ \left( \frac{G_{\text{pas}}}{K_{\text{pas}}} + \frac{G_{\text{act}}}{K_{\text{pas}}} R \right) + i \left( \frac{G_{\text{act}}}{K_{\text{pas}}} I \right) \right]^{\frac{1}{2}} \]

where without loss of generality we have chosen the positive sign for the imaginary part. If

\[ \varphi_1 = \frac{G_{\text{pas}}}{K_{\text{pas}}} + \frac{G_{\text{act}}}{K_{\text{pas}}} R(\omega), \quad \text{and} \quad \varphi_2 = \frac{G_{\text{act}}}{K_{\text{pas}}} I(\omega), \]

we get the real and imaginary parts

\[ \text{Re}[\lambda_{\pm}^{-1}] = \pm \left( \frac{\varphi_1^2 + \varphi_2^2 + \varphi_1}{2} \right)^{\frac{1}{2}} \quad \text{and} \quad \text{Im}[\lambda_{\pm}^{-1}] = \pm \text{sgn}(I) \left( \frac{\sqrt{\varphi_1^2 + \varphi_2^2} - \varphi_1}{2} \right)^{\frac{1}{2}} \]

When the motor aggregates are in rigor, there is no intrinsic motor dynamics as they are stuck in fixed configurations (either attached or detached) and therefore \( \omega_{\text{on}} = 0, \omega_{\text{off}} = 0 \) and \( v_0 = 0 \). In this limit, the motors are bound permanently to the filament track and can actually sense the instantaneous displacement of the attachment point (where the head is) rather than just the rate of displacement. The number of attached motors \( N \) cannot change and equals \( N_0 \), the preexisting attached fraction. As a result, the \( \dot{Y} \) responds passively to the change in the attachment point, and satisfies \( \delta_m Y_t = -U_t \). Integrating this once yields \( \delta_m (Y(t) - Y_0) = -(U(t) - U_0) \). Writing \( U(t) - U_0 = \delta U \) we get \( E w(\delta U)_{ss} - \rho_N k_N (\delta U) - k_m \rho_m N_0 (\delta U) = 0 \). Thus the decay length of the strain is given by

\[ \ell_E = \left( \frac{E w}{k_m \rho_m N_0 + \rho_N k_N} \right)^{\frac{1}{2}} = \left( \frac{K_{\text{pas}}}{G_{\text{act}} N_0 + G_{\text{pas}}} \right)^{\frac{1}{2}}. \]

The effective shear modulus due to the links, \( G_{\text{eff}} \) is obtained by equating the force needed to shear the passive springs to the induced extension, \( \langle y \rangle \). That is \( \langle N_0 \rho_m k_m + \rho_N k_N \rangle (ds b) \langle y \rangle = F_s = G_{\text{eff}} \langle (y)/D \rangle ds b \), thus yielding the estimate \( G_{\text{eff}} \sim (N_0 \rho_m k_m + \rho_N k_N) D \).
B. Expression for $\chi$ when $A_3 \to 0$

Recall that $A_1 \equiv v_0 k_m (\omega_{\text{off}} F_s)^{-1}$ and $A_2 \equiv F_s (k_m \delta_m)^{-1}$. The constant $C$ is then

$$ C = \frac{A_1 A_2}{A_1 + F_0} \left( \frac{\delta_m}{1 + \Psi F_0} \right). \quad (51) $$

The (dimensionless) complex susceptibility in this limit is

$$ \chi(\omega) = -\delta_m (Y_0 T_2 + N_0 T_1) \quad (52) $$

where

$$ T_1 \equiv -\left( \frac{i \omega}{\delta_m} \right) (i \omega + \omega_{\text{on}} \Psi F_0 + \omega_{\text{off}} A_1) - \left( \frac{i \omega}{\delta_m} \right) \left( \frac{Y_0}{N_0} \left( \frac{i \omega + \omega_{\text{on}} + \omega_{\text{off}} F_0}{\omega_{\text{off}} F_0 N_0} \right) \right)^{-1} \quad (53) $$

and

$$ T_2 \equiv -\left( \frac{i \omega + \omega_{\text{on}} + \omega_{\text{off}} F_0}{\omega_{\text{off}} F_0 N_0} \right) T_1. \quad (54) $$

C. Expression for $\chi$ when $A_1 \to 0$

Recall that $A_3 \equiv d_m / \delta_m$. The constant $C$ in this limit is evaluated to be

$$ C = \delta_m A_3 \left( \frac{1}{1 + \Psi F_0} \right). \quad (55) $$

We find the complex susceptibility is $\chi(\omega) = (R + iI)$ with

$$ R(\omega) = \frac{(1 - A_3 \Psi F_0) \omega^2}{(\omega_{\text{off}} F_0)^2 + \omega^2} + \frac{A_3 \Psi F_0^2 \omega^2}{(\omega_{\text{on}} (1 + \Psi F_0))^2 + \omega^2} \quad (56) $$

and

$$ I(\omega) = \frac{\omega (1 - A_3 \Psi F_0) \omega_{\text{off}} F_0}{(\omega_{\text{off}} F_0)^2 + \omega^2} + \frac{A_3 \Psi F_0^2 \omega \omega_{\text{on}} (1 + \Psi F_0)}{(\omega_{\text{on}} (1 + \Psi F_0))^2 + \omega^2}. \quad (57) $$

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