Effects of inertia on conformation and dynamics of active filaments

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Many macroscopic active systems such as snakes, birds, and fishes have flexible shapes and inertial effects on their motion, in contrast to their microscopic counterparts, cannot be ignored. Nonetheless, the consequences of interplay between inertia and flexibility on their shapes and dynamics remain unexplored. Here, we examine inertial effects on the most studied active flexible system, i.e., linear active filaments pertinent to worms, snakes, and filamentous robots. Performing Langevin dynamics simulations of active polymers with underdamped and overdamped dynamics for a wide range of contour lengths and activities, we uncover striking inertial effects on their conformation and dynamics. Inertial collisions increase the persistence length of active polymers and remarkably alter their scaling behavior. In stark contrast to passive polymers, inertia leaves its fingerprint at long times by an enhanced diffusion of the center of mass. We rationalize inertia-induced enhanced dynamics by analytical calculations of center of mass velocity correlations, revealing significant contributions from active force fluctuations convoluted by inertial relaxation.

Active matter systems, consisting of self-driven units, exhibit emergent properties which defy the laws of equilibrium statistical mechanics [1, 2]. The majority of studies in the last decades have focused on active particles moving in the realm of low Reynolds numbers, e.g., bacteria and active colloids whose motion is overdamped [2, 3]. However, a wide range of macroscopic organisms including birds, fish, worms, as well as synthesized agents such as microflyers [4–6] and shaken granulate chains [7], often having elongated flexible shapes, exhibit non-negligible inertial effects on their dynamics. Indeed, recent studies have revealed significant inertial effects on dynamics of individual and collectives of point-like and rigid active particles [4, 6, 8–17]. Notably, inertia enhances diffusive dynamics of active Brownian particles [4, 6, 16], unlike their passive counterparts which do not hold any memory of inertia at long times. These findings raise the interesting question whether inertia induces memory effects and enhanced dynamics for active macroscopic systems with flexible bodies like fishes and snakes. Presently, consequences of inertia on shape and dynamics of macroscopic active systems remain an open question.

To explore the role of inertia on flexible active particles, we consider the widely studied system of linear active filaments [18, 19] spanning a diverse range of biological systems such as biopolymers driven by molecular motors [20, 21], worms [22–24] and snakes [25]. Recently even filamentous robots [24–26] have been achieved, belonging to this class of active systems. Investigations of single overdamped active filaments [18, 19, 27–31] have revealed that interplay between activity and flexibility profoundly alters the chain conformation and dynamics. However, it is unknown under what conditions inertial effects become dominant and how they affect the active polymer structural and dynamical features. To address this, we model an active filament as a self-avoiding chain of active beads connected by springs, and study the inertial effects as a function of bead mass, contour length and activity strength using Langevin dynamics simulations. Worms, snakes, and filament-like robots are examples of active filaments with non-negligible inertia, which propel their bodies along their backbones. Hence, we take the orientation of active force on each bead parallel to the local tangent of the backbone as in the *tangentially-driven* active polymer model [27].

Our simulations reveal marked changes in conformation and dynamics of inertial active chains at activities where the timescale of advection by active force per bead becomes smaller than inertial timescale. At large activities, inertial collisions of active monomers with relative high velocities result in extended chain conformations, inducing an activity-dependent persistence length. We find that inertia enhances diffusive dynamics of the center of mass of inertial active polymers remarkably, in contrast to passive polymers for which inertial effects vanish at long timescales [32–34]. To understand the origin of enhanced dynamics, we put forward analytical calculations which derive the center of mass velocity autocorrelation function in the steady-state limit for an arbitrary active force distribution along a polymer backbone. These calculations elucidate that the enhanced long-time diffusion stems from fluctuations of total active force on a filament convoluted by an exponential relaxation with inertial timescale. For tangentially-driven polymers where the active force is coupled to the polymer conformation, we show that the long-time diffusion coefficient is proportional to the mean-squared end-to-end distance, illuminating the link between enhanced dynamics and extended polymer conformations.

To further elaborate our new insights, we start by out-
linning our Langevin dynamics simulations of tangentially-driven active polymers. The equation of motion for each monomer of an active chain of $N$ beads of mass $m$ in three dimensions is described by

$$m\ddot{{\mathbf{r}}}_i = -\gamma \dot{{\mathbf{r}}}_i - \sum_j \nabla_{\mathbf{r}_i} U(r_{ij}) + f_i^a + f_i^r,$$

in which $\mathbf{r}_i$ is the coordinate of bead $i$ with the dots denoting derivatives with respect to time, and $\gamma$ is the friction coefficient of the bead with the surrounding medium. $r_{ij}$ denotes the distance between beads $i$ and $j$. The potential energy $U(r_{ij})$ includes contributions from harmonic springs of equilibrium length $\ell$ and stiffness $k_s$ between adjacent monomers and interbead excluded volume interactions modelled by the WCA potential \[35\],

$$U_{\text{excel}}(r) = 4\epsilon \left[\left(\frac{r}{\sigma}\right)^{12} - \left(\frac{r}{\sigma}\right)^{6} + \frac{1}{4}\right]$$

for $r < r_c = 2^{1/6}\sigma$. $f_i^a$ and $f_i^r$ are the active and random forces acting on the bead $i$, respectively. The active force on each bead, except for end monomers, is given by:

$$f_i^a = \frac{\nu_m}{\tau_m} (\mathbf{r}_{i-1} - \mathbf{r}_i + \mathbf{r}_{i+1})$$

where $\mathbf{r}_{i+1} = \mathbf{r}_{i+1} - \mathbf{r}_i$ defines the bond vector connecting $(i+1)$-th and $i$-th monomers. The active forces on the end monomers are given by:

$$f_N^a = \frac{\nu_m}{\tau_m} \mathbf{r}_{1,2}$$

and

$$f_1^a = \frac{\nu_m}{\tau_m} \mathbf{r}_{N-1,N}.$$  

The spring constants are chosen stiff enough, $k_s \gg f^a/\ell$, to ensure that the mean bond-length and polymer contour length remain almost constant, see Supplemental Material (SM) \[36\] for details. The random force is chosen as a white noise of zero mean and correlation $(f_i^r(t) \cdot f_j^r(t')) = 6D_0\gamma^2\delta_{ij}\delta(t - t')$.

We choose $\nu = \sigma$, $E_u = \epsilon$, and $\tau_u = \gamma\sigma^2/\epsilon$, with $\gamma = 1$, as the units of length, energy and time, respectively, denoting reduced quantities with *' superscripts. We fix $\ell/\sigma = 1$ and dimensionless diffusion coefficient $D_0 = 0.1$. To elucidate the role of inertia, we compare the scaling behavior and overall dynamics of underdamped active polymers with $m^* = m\epsilon/(\gamma\sigma)^2 = 1$ and overdamped chains $m^* = 0$, varying chain length $50 \leq N \leq 1000$ and active force strength $f^a* = f^a/\epsilon$ in the range $0.01 \leq f^a* \leq 100$. More results when varying mass $0 \leq m^* \leq 5$ can be found in SM \[36\].

We use these simulations to first investigate inertial effects on the global conformation of polymers. Fig. 1(a) shows that chain conformation is significantly more extended for high active forces in the underdamped scenario. Thus, we plot the end-to-end distance (calculated as $R^*_e = \sqrt{\langle R^*_e^2 \rangle}$ of active polymers in their steady-state as a function of activity $f^a*$ for different chain lengths $N$ as presented in Fig. 1(b). For $f^a* \gg 1$, when active force per monomer exceeds damping force, we observe a striking contrast between conformations of inertial and overdamped active polymers. Chains with underdamped dynamics swell, whereas overdamped chains slightly shrink. The onset of departure from the overdamped limit is set by the ratio of the inertial timescale $\tau_m = m/\gamma$ to the time of advection by active force $\tau_{adv} = \sigma\gamma/f^a$. At large active forces when $\tau_m/\tau_{adv} > 1$, large velocities gained by inertial monomers promote collisions, resulting in chain unwinding. Conformations of inertial chains are more extended and anisotropic, resulting in a larger asphericity and broader distribution of end-to-end distance, see Figs. S2 and S3, and videos in SM \[36\].

![FIG. 1. (a) Snapshots of active polymers of size $N = 500$ with active forces $f^a* = 1$ (blue) and 100 (red) in the steady state obtained in the overdamped (left) and underdamped (right) regimes. (b) The end-to-end distance $R^*_e$ versus active force $f^a*$ for different chain lengths as given in the legend. (c,d) Scaling exponent $\nu$ of end-to-end distance and generalized Flory constant $C_\infty$, as a function of $f^a*$, assuming $R^*_e^2(N, f^a*) = C_\infty(f^a*)N^{2\nu}/(f^a*)^2$. The bold and empty symbols in panels (b)-(d) correspond to underdamped and overdamped chains, respectively. The lines are guides to the eyes.](image-url)
polymer backbone. Fig. 1(d) shows the extracted $C_\infty$ as a function of $f^a$ for active polymers with underdamped and overdamped dynamics. $C_\infty \sim 1$ up to $f^a = 1$, whereas for $f^a > 1$ it rises steeply suggesting an increased conformational rigidity for inertial polymers compatible with more straight conformations found for inertial active polymers, see the case of $f^a = 100$ in Fig. 1(a). A reduced $\nu$ combined with an increased $C_\infty(f^a)$ at large activities means that the average conformation of inertial active polymers resembles that of compact globule-like polymers with a large persistence length.

A growing $C_\infty$ implies an increasing persistence length with $f^a$. To verify this, we extract the persistence length from orientational bond-bond correlation function $\langle \cos(\theta(s)) \rangle$ against curvilinear distance $s$ along the polymer backbone, see Fig. S5 in [36]. We define the persistence length $\ell^*_p$ as the curvilinear distance at which $\langle \cos(\theta(\ell^*_p)) \rangle = 1/\epsilon$. Fig. 2 shows the extracted $\ell^*_p$’s for overdamped and inertial chains versus $f^a$ for different $N$. For overdamped polymers, $\ell^*_p$ remains unity up to $f^a \sim 1$ and increases weakly beyond it, whereas for inertial polymers $\ell^*_p$ increases steeply with $f^a$ when $\tau_m/\tau_o d\nu^a > 1$. The inertia-induced persistence length at large activities scales linearly with $f^a$ and it can be interpreted as the distance where an active monomer travels by speed $v^a = f^a/\gamma$ during inertial timescale $\tau_m$ giving rise to $\ell^*_p \sim f^a \tau_m/\gamma^2$. For $N = 50$ and 100, $\ell^*_p$ exhibits a decrease when the contour length becomes comparable to the persistence length $\ell^*_p \sim N$. We defer discussion of this new instability regime to elsewhere. Overall, we recognize a similar trend for $\ell^*_p$ and $C_\infty$ against active force corroborating the surmise of an inertia-induced bending rigidity in active polymers.

Having explored the inertial effects on structural features of active polymers, we examine signatures of inertia on the dynamics. We start by investigating the polymer orientational dynamics. To this end, we compute the time auto-correlation function (TACF) of the end-to-end vector normalized by its mean-squared value in the steady-state limit $\hat{C}_e(t) = \lim_{t' \to \infty} \langle \hat{R}_e(t + t') \cdot \hat{R}_e(t') \rangle$. As the total active force $F^a$ is proportional to the end-to-end vector, $F^a = \sum_{i=1}^N f^a_i = l^*_p \hat{R}_e$, the relaxation time of $\hat{C}_e$ is identical to persistence time of total active force. Fig. 3(a) shows $\hat{C}_e$ at different activities for inertial and overdamped chains of length $N = 500$. Although for large $f^a$, the $\hat{C}_e(t)$ of inertial chains exhibits a decay with oscillatory behavior, the overall relaxation timescales of $\hat{C}_e(t)$ of the two kinds of dynamics are very similar in contrast to huge difference in their chain conformations. This trend suggests that we have a universal persistence time $\tau_e(N, f^a)$, which depends only on the strength of active force and the chain length. We find that the initial decay of $\hat{C}_e(t)$ for both overdamped and underdamped polymers can be approximately described by an exponential function, see Fig. S7 in [36]. The extracted relaxation times $\tau^*_e$, shown in Fig. 3(b), follow

$$\tau^*_e(N, f^a) = 0.6N/f^a,$$

similar to the scaling behavior reported for overdamped active polymers [28].

We subsequently extract the long-time diffusion coef-
The dynamics of center of mass velocity vcm and the total active force \( \mathbf{F}^a \) in an earlier study of overdamped active polymers \[28\]. Our results clearly show that inertia significantly affects the long-time dynamics of active polymers and raise questions about origin of inertia-induced enhanced dynamics.

To rationalize the remarkable enhancement of dynamics, we put forward analytical calculations which illuminate the relationship between TACFs of the velocity and the total active force \( \mathbf{F}^a \) in the steady-state limit for any active polymer model. We compare theoretical predictions and simulation results for tangentially-driven polymers. The dynamics of center of mass velocity \( \mathbf{v}_{\text{cm}}(t) = \frac{1}{N} \sum_{i=1}^{N} \mathbf{v}_i \) is obtained by summing the equations of motions of all the beads given by Eq. (1). As contributions from the internal forces cancel out, the equation for \( \mathbf{v}_{\text{cm}}(t) \) simplifies to:

\[
m\mathbf{v}_{\text{cm}} = -\gamma \mathbf{v}_{\text{cm}} + \frac{1}{N}(\mathbf{F}^a + \mathbf{F}^r)
\]

in which \( \mathbf{F}^r = \sum_{i=1}^{N} \mathbf{f}_i^r \) is a sum of all the random forces with a zero mean and \( \langle \mathbf{F}^r(t) \cdot \mathbf{F}^r(t') \rangle = 6N\gamma^2\delta(t-t') \).

Integrating this first-order differential equation yields

\[
\mathbf{v}_{\text{cm}}(t) = \mathbf{v}_{\text{cm}}(t_0)e^{-\frac{\gamma}{N}(t-t_0)} + \frac{1}{Nm} \int_{t_0}^{t} d\tau \left[ \mathbf{F}^a(\tau) + \mathbf{F}^r(\tau) \right] e^{-\frac{\gamma}{N}(t-t_0-\tau)}
\]

Using this solution, we calculate the velocity TACF in the steady-state limit, defined as \( \bar{C}_v(t) = \lim_{t' \to \infty} \langle \mathbf{v}_{\text{cm}}(t + t') \cdot \mathbf{v}_{\text{cm}}(t') \rangle / \langle \mathbf{v}_{\text{cm}}^2(t') \rangle \), yielding

\[
\bar{C}_v(t) = \frac{3\gamma D_0}{Nm} \frac{-t}{e^{\gamma t/m}} + \frac{1}{2m\gamma N^2} \int_{0}^{+\infty} \left[ C_f(u-t) + C_f(u+t) \right] e^{-\gamma t/m} du,
\]

in which \( C_f(t) = \lim_{t' \to \infty} \langle \mathbf{F}^a(t + t') \cdot \mathbf{F}^a(t') \rangle \) is the TACF of the total active force. The first term in Eq. (5) represents the passive diffusive contribution from random forces which decays exponentially with the relaxation time \( \tau_m \) \[32\], whereas the second term entangles the correlation of the total active force with the inertial relaxation. This term reflects memory effects induced by active forces and accounts for the emergent inertial effects. For tangentially-driven polymers for which the total active force \( \mathbf{F}^a = f^a \mathbf{R}_e/\ell \) is directly coupled to the chain conformation and \( C_f(t) = (f^a^2(R_e^2)/\ell^2) \bar{C}_e(t) \).

As demonstrated in Fig. S9 of SM \[36\], prediction of Eq. (5) shows excellent agreement with velocity correlations computed from simulations.

For an active force TACF with exponential decay \( C_f = A_f e^{-t/\tau_f} \), Eq. (5) simplifies to

\[
\bar{C}_v(t) = \frac{3\gamma D_0}{Nm} \frac{-t}{e^{\gamma t/m}} + \frac{A_f^2}{(Nm)^2} \left( \frac{\tau_m^2 \tau_f}{\tau_f^2 - \tau_m^2} \right) \left[ e^{-t/\tau_f} - \tau_m e^{-t/\tau_m} \right],
\]

which consists of exponential decays at two timescales: the inertial time \( \tau_m \) and decay time of active force TACF \( \tau_f \). In this case, the center of mass velocity TACF of active polymers becomes identical to that of inertial active Ornstein–Uhlenbeck model \[11, 16\]. The approximation of exponential decay of active force TACF becomes exact in the case of an active Brownian polymer model \[38, 39\] with only translational inertia, see Sec. VI in SM \[36\]. As discussed earlier, \( \bar{C}_e(t) \) approximately follows an exponential decay. Thus, Eq. (7) also provides a good description of tangentially-driven active polymers provided that we consider an activity-dependent amplitude \( A_f \) which is coupled to polymer mean conformation.

The explicit form of the TACF of velocity given by Eq. (5), allows us to predict the long-time diffusion of center of mass by integrating it over time delay: \( D_L = \frac{1}{\bar{C}_v} \int_{0}^{+\infty} dt \bar{C}_v(t) \). For inertial tangentially-driven polymers,
this yields
\[ D_L = \frac{D_0}{N} + \frac{f a^2 \langle R_e^2 \rangle}{6m \gamma N^2 \ell^2} \int_0^{+\infty} dt \int_0^{+\infty} \left[ \tilde{C}_e(u-t) + \tilde{C}_e(u+t) \right] e^{-u/\tau_m} du. \] (7)

For the overdamped chains, in the limit of \( m \to 0 \), Eq. (7) simplifies to
\[ D_L = \frac{D_0}{N} + \frac{f a^2 \langle R_e^2 \rangle}{3 \gamma N^2 \ell^2} \int_0^{+\infty} dt \tilde{C}_e(t), \] (8)

compatible with results of reference [28]. Predictions of Eqs. (7) and (8) are shown in Fig. 4 by empty circles and triangles, respectively, demonstrating excellent agreement with simulation results. Using the exponential approximation for \( \tilde{C}_e(t) = e^{-t/\tau_e} \) and Eq. (2) for the relaxation time, Eqs. (7) and (8) yield an identical equation for inertial and overdamped systems:
\[ D_L \approx \frac{D_0}{N} + \frac{f a^2 \langle R_e^2 \rangle \tau_e}{3N^2 \gamma^2 \ell^2}. \] (9)

This equation shows that at sufficiently large activities the dominant contribution in \( D_L \) comes from activity, which weakly depends on \( N \) as \( D_L \sim N^{2\nu-1} \). Especially, it clarifies that the inertia-induced enhancement of \( D_L \) originates from extended chain conformations generating an overall larger \( \langle R_e^2 \rangle \). The predictions of this approximate equation are also included in Fig. 4, revealing good agreement with simulation results.

In conclusion, we have combined coarse-grained simulations and analytical theory to provide new insights into the fundamental interplay between inertia, activity and flexibility in active filaments. For tangentially-driven filaments, where active forces are coupled to polymer conformations, we demonstrate that inertia conspicuously affects both conformational and dynamical features. We find that when the inertial timescale of a monomer becomes longer than its advection time by active force, inertial effects become significant. Inertial collisions of high-speed monomers cause extended conformations, hence increasing the persistence length of polymers. The chain unwinding in turn results in enhanced mean velocity and diffusion of the center of mass, as elucidated by our theoretical analysis. The key quantity determining the enhanced dynamics in active polymers is the ratio of end-to-end distance to contour length. It is noteworthy that our theoretical predictions are valid for any active polymer model including semiflexible polymers although for simplicity we focused on active polymers with a persistence length comparable to the bead size. Our findings provide a guideline for design of active robotic worms, for which inertial effects are non-negligible. Moreover, they inspire investigation of a deeper link between memory effects and inertia in the collective dynamics of active filaments and more generally other active systems with internal degrees of freedom.

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