

Nonmonotonic Diffusion in Sheared Active Suspensions of Squirmers

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We investigate how shear influences the dynamics of active particles in dilute to concentrated suspensions. Using apolar active suspensions of squirmers as model systems, we show how their longtime diffusive dynamics can surprisingly slow down and vary nonmonotonically with the shear rate arising from an interplay between the activity-induced persistent motion and shear-induced reorientation and diffusion. Further simulations of self-propelled particles with tunable persistence exhibit richer dynamics and confirm the observed coupling, suggesting that nonmonotonic diffusion may be a general feature of fluids endowed with an underlying microstructure and large persistence. Our results reveal a nonlinear effect of shear on diffusion in active suspensions, elucidate how internal and external forcing interact, and provide new possibilities to modulate transport in active fluids.

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Suspending particles able to inject energy in a fluid provides a means to drive the fluid out of equilibrium internally. Such *active suspensions*, or active fluids, have been the subject of intense study in recent decades, showing rich phenomena unseen in their passive, equilibrium counterparts [1,2]. As a typical example, bacterial suspensions have been found to display enhanced diffusion [3–8] and turbulentlike chaotic motion [9–13] in the absence of any external flow as well as upstream swimming [14–16] and superfluidlike rheology [17–19] under pressure- or shear-driven flows. Understanding how various internal and external driving mechanisms interact across spatial and temporal scales is important for predicting and controlling the dynamics and mechanics of active fluids in complex conditions, yet detailed knowledge of the interplay has not been established.

One of the simplest ways to drive a fluid externally is to *shear* it at a steady, homogeneous shear rate, $\dot{\gamma}$. When sheared, passive noncolloidal suspensions undergo *shear-induced diffusion* (SID) in the plane perpendicular to the mean flow [20–23]. SID arises from fluid-mediated

interparticle collisions, and dimensional analysis suggests that the resulting diffusion coefficient, D_s , scales as $\dot{\gamma}a^2f(\phi)$, where a is the particle radius and $f(\phi)$ is a function of the particle volume fraction, ϕ [24]. The precise form of $f(\phi)$ depends on the physical regime as well as the shape and surface properties of the particles [25–29]. However, regardless of the details, one expects D_s to increase with $\dot{\gamma}$ because particles collide more frequently at higher $\dot{\gamma}$.

In this Letter, we investigate the interplay between shear and activity and examine whether increasing the shear rate enhances diffusion in active fluids. To this end, we use a recently modified fast Stokesian dynamics (FSD) method [30,31] to perform large-scale hydrodynamic simulations of dilute to concentrated active suspensions ($\phi \in [10\%, 40\%]$). Specifically, we first consider a simple model—*apolar* active suspensions of “shakers,” particles that are active but not self-propelling and that collectively display *activity-induced hydrodynamic diffusion* [31]. The dynamics can be characterized by a diffusion coefficient, D_0 , allowing for a Péclet number, $Pe \equiv \dot{\gamma}a^2/D_0$, to be defined to measure the relative effect of shear versus activity. Extensive simulations of thousands of shakers at different Pe and ϕ show that such suspensions always reach diffusive dynamics at long times; however, surprisingly, the effective diffusion coefficient, D , can *drop below* D_0 for a range of Pe when ϕ is small. For example, $D/D_0 \approx 0.4$ when $Pe \approx 100$ and $\phi = 10\%$. As Pe increases further, D/D_0 rises again, with shear eventually dominating, resulting in *nonmonotonic* diffusion. We analyze this behavior in detail and trace its physical origin to an activity-induced persistent motion and a shear-induced

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negative velocity autocorrelation, both of which are more pronounced at lower volume fractions. To confirm and generalize our understanding, we then consider self-propelled particles with *tunable* persistence, which display nonmonotonic diffusion even in *concentrated* suspensions, provided that the persistence is large enough. Overall, our results demonstrate a nonlinear effect of shear on diffusion in active suspensions, elucidate how interactions between internal and external forcing influence these complex fluids, and suggest new ways to control mixing and mass transport in active fluids.

Models and methods—We model active particles as “squirmers,” spheres with a prescribed axisymmetric slip velocity [32–34]. The surface slip at position $\mathbf{r}$ from the sphere’s center may be expressed as

$$\mathbf{u}_s = -\mathbf{U}_s - \boldsymbol{\Omega}_s \times \mathbf{r} + \mathbf{E}_s \cdot \mathbf{r} + \dots, \quad (1)$$

where $\mathbf{U}_s$ is the self-propulsion velocity, $\boldsymbol{\Omega}_s$ is the self spin, $\mathbf{E}_s$ is the self strain rate, and dots denote terms involving higher-order irreducible tensors of $\mathbf{r}$ [35]. Specifically,

$$\mathbf{U}_s = \frac{2}{3}B_1\mathbf{p}, \quad \boldsymbol{\Omega}_s = \frac{C_1}{a^3}\mathbf{p}, \quad \mathbf{E}_s = -\frac{3B_2}{5a}\left(\mathbf{p}\mathbf{p} - \frac{1}{3}\mathbf{I}\right), \quad (2)$$

where B_1 and B_2 are the leading-order squirming modes, C_1 is a coefficient associated with azimuthal slip, $\mathbf{p}$ is the particle director, and $\mathbf{I}$ is an identity tensor [35]. Setting $B_1 = 0$ yields an immotile squirmer known as a shaker.

Although shakers are individually immotile, they swim collectively due to *hydrodynamic interactions* (HIs). To leading order, the HIs arise from $\mathbf{E}_s$ if $B_2 \neq 0$: $B_2 > 0$ corresponds to *pullers* and $B_2 < 0$ to *pushers*. Therefore, the ratio $\beta \equiv B_2/B_1$ indicates the type of swimmer and the relative importance of HIs and self-propulsion. In this

Letter, we first take $\beta \rightarrow \pm\infty$ to amplify the effect of HIs, and then consider neutral squirmers with $\beta = 0$ and additional rotational diffusion of $\mathbf{p}$ on each particle, effectively modeling *active Brownian particles* (ABPs). Higher-order squirming modes and the azimuthal slip (C_1) are neglected, as is common in the literature [36–38].

The dynamics of a suspension of squirmers is described by the active Stokesian dynamics framework [35]. For athermal particles, the governing equations can be written compactly as

$$\mathbf{U} = \mathbf{U}_\infty + \mathbf{U}_s + \mathcal{R}_{\text{FU}}^{-1} \cdot (\mathcal{R}_{\text{FE}} : (\mathbf{E}_\infty - \mathbf{E}_s) + \mathbf{F}_{\text{ext}}), \quad (3)$$

where the velocities ($\mathbf{U}, \mathbf{U}_\infty, \mathbf{U}_s$), strain rates ($\mathbf{E}_\infty, \mathbf{E}_s$), and force ($\mathbf{F}_{\text{ext}}$) are all N -tuples with elements defined at the particle centers, e.g., $\mathbf{U} \equiv (U_1 U_2 \dots U_N)^T$, and $\mathcal{R}_{\text{FU}}$ and $\mathcal{R}_{\text{FE}}$ are the resistance tensors coupling the force and velocity moments of all N particles. Note how individual particle activities couple to the large-scale flows through HIs. As illustrated in Fig. 1(a), we apply a shear in the x direction, $\mathbf{U}_\infty(x, y, z) = (\dot{\gamma}y, 0, 0)$, and impose a short-range repulsive force $\mathbf{F}_{\text{ext}}$ between the particles to model excluded-volume interactions; see the Supplemental Material (SM) [39] for further details. Equation (3) is then solved using FSD [30] for $N = 1024$ at different Pe and ϕ .

Shakers—Recently, we showed that apolar active suspensions of shakers, pulling or pushing, could undergo activity-induced diffusion without any external flow [31]. The effective diffusion coefficient was found to be $D_0 = (a^2/\tau_a)g(\phi)$, where $\tau_a \equiv a/|B_2|$ is the activity time scale, and $g(\phi) \sim \phi^{1/5}$ for $\phi \lesssim 10\%$ and reduces sharply with ϕ beyond. Furthermore, the short-time dynamics was ballistic and could last over tens of τ_a ; see the Pe = 0 case in Fig. 1(b). This *persistent* motion, therein due to HIs

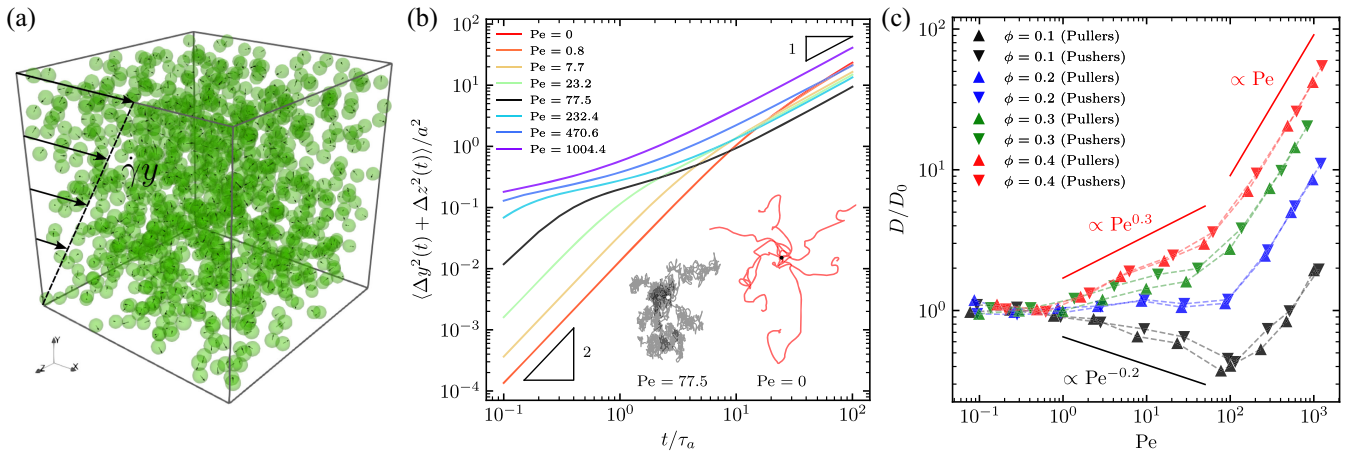


FIG. 1. Nonmonotonic diffusion in sheared active suspensions. (a) Illustration of 1024 particles at 10% volume fraction (ϕ) under shear. (b) Mean square displacements in the yz plane for pulling shakers ($\phi = 10\%$) at different Péclet numbers, Pe. The inset shows a few sample trajectories at Pe = 0 and 77.5. (c) Relative diffusion coefficient, D/D_0 , against Pe for pulling or pushing shakers at different ϕ . Slopes are theoretical estimates (see text).

between the active particles, is the main reason that active fluids display an enhanced diffusion [3,6,31].

Under shear, the particle dynamics is anisotropic and not diffusive in the flow direction (x); thus, we analyze the mean square displacement (MSD) in the yz plane, $\langle \Delta y^2(t) + \Delta z^2(t) \rangle$, where $\langle \cdot \rangle$ averages over all particles and time. Figure 1(b) shows the MSDs for pulling shakers under different Pe at $\phi = 10\%$ (see SM for results of pushers and at other ϕ [39]). We observe that the short-time MSD increases with Pe , similar to the behavior of passive suspensions [23]; however, surprisingly, the longtime dynamics can be *suppressed* by shear, with sustained *subdiffusive* motion, resulting in smaller MSDs at larger Pe . The reduced diffusion is also evident from direct visualization of individual particle trajectories. As shown in the inset in Fig. 1(b), increasing Pe could lead to more compact and less smooth trajectories at long times.

We extract the diffusion coefficient, D , by fitting the longtime MSD according to $\langle \Delta y^2(t) + \Delta z^2(t) \rangle = 4D(t - t_0)$, where t_0 is generally nonzero due to non-diffusive dynamics at short times. Figure 1(c) shows the relative diffusivity, D/D_0 , across four decades of Pe . Clearly, D/D_0 is nonmonotonic at $\phi = 10\%$, with a minimum of about 0.4 reached at $Pe \approx 100$, consistent with the observation in Fig. 1(b). At higher concentrations, the nonmonotonic behavior gradually disappears, and the scaling between D/D_0 and Pe depends on ϕ (see analysis later). However, in all cases, we observe $D/D_0 \approx 1$ for $Pe \lesssim 1$ and $D/D_0 \propto Pe$ for $Pe \gtrsim 100$. The same scalings apply to both pullers and pushers, as does the ϕ dependence of D_0 without shear (cf. Fig. 4) [31], implying similar but still irreversible macroscopic dynamics under time reversal.

To explain the nonmonotonic diffusion, we examine the short-time dynamics characterized by the *instantaneous* particle velocities projected onto the yz plane as in the MSD calculation. Figure 2(a) shows the root-mean-square

particle speeds under shear, U_{rms} , normalized by their values without shear, $U_{rms,0}$, for pullers and pushers at different ϕ . Remarkably, all data collapse onto a single curve, showing universal scalings with $U_{rms}/U_{rms,0} \approx 1$ for $Pe \lesssim 1$ and $U_{rms}/U_{rms,0} \propto Pe$ for $Pe \gtrsim 10$. The absence of any ϕ dependence suggests that the relative change in the short-time dynamics is controlled by shear alone, despite the underlying activity-induced dynamics, $U_{rms,0}$ and D_0 , depending nonmonotonically on ϕ [31].

The instantaneous velocities decorrelate over time and can be quantified by a velocity autocorrelation function, $\Phi_v(t) \equiv \langle \mathbf{U}(\tau) \cdot \mathbf{U}(\tau + t) \rangle / U_{rms}^2$, where $\langle \cdot \rangle$ averages over all particles and time. Figure 2(b) shows $\Phi_v(t)$ for pulling shakers under different Pe at $\phi = 10\%$ and passive particles ($Pe \rightarrow \infty$ as activity is turned off) at different ϕ . We observe faster decorrelation as Pe or ϕ increases and even a negative $\Phi_v(t)$ at sufficiently high Pe . Such *anticorrelation* has been noted in earlier simulations [23,26] and results from either hydrodynamic or excluded-volume interactions. Under shear, pairwise HIs render transient particle displacements that necessarily become zero at equal time after the encounter [47]; thus, the velocities change sign and $\Phi_v(t) < 0$. This effect is weakened at higher ϕ due to many-body HIs and more frequent collisions; however, particles tend to oscillate as they collide (see the videos in SM [39]), again making $\Phi_v(t) < 0$. The timescale of these shear-induced interactions is proportional to $\dot{\gamma}^{-1}$ and reduces with ϕ , cf. Fig. 2(b). The negative velocity autocorrelation is the reason for the subdiffusive motion observed in Fig. 1(b).

We now explain the observed diffusion. Figure 2(c) shows the phase diagram of all shaker simulations controlled by two parameters, ϕ and $\dot{\gamma}\tau_a = g(\phi)Pe$. As discussed, there are three diffusive regimes separated by $Pe \approx 1$ and 100, with different scalings between D/D_0 and Pe in each. Specifically, $Pe < 1$ corresponds to

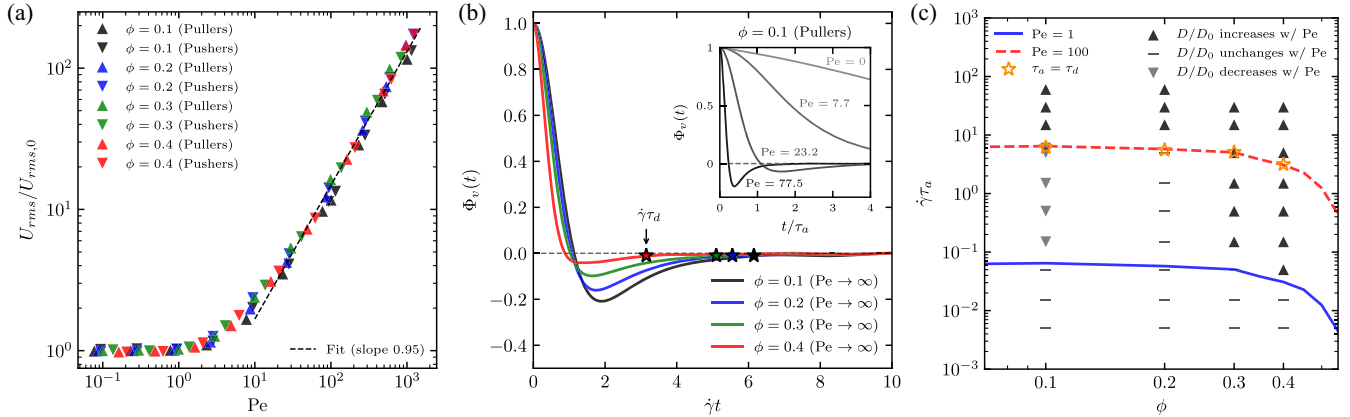


FIG. 2. Short-time dynamics and phase diagram. (a) Root-mean-square particle speeds under shear normalized by their values without shear at all Pe and ϕ . (b) Normalized velocity autocorrelation for passive particles at different ϕ [markers denote $\Phi_v(\dot{\gamma}\tau_a) = -10^{-2}$] and for pulling shakers under different Pe at $\phi = 10\%$ (inset). (c) Phase diagram of all simulation results for shakers, divided by $Pe = 1$ and 100 into three diffusive regimes with different scalings.

$a^2/D_0 < \dot{\gamma}^{-1}$, i.e., the activity-induced diffusion occurs faster than the shear-induced; thus, we observe the former, $D = D_0$. When $Pe > 1$, both activity and shear are at play, resulting in ϕ -dependent scalings, including a reduced diffusion at low ϕ due to the shear-induced velocity anticorrelation. However, at sufficiently large Pe , the dynamics must be controlled by shear, $D = D_s \propto \dot{\gamma} a^2$, leading to $D/D_0 \propto Pe$. Here, the threshold Pe corresponds to $\tau_d = \tau_a$, where $\dot{\gamma}\tau_d$ is a ϕ -dependent velocity decorrelation time, i.e., the time $\Phi_v(t)$ returns to zero from below, cf. Fig. 2(b). When $\tau_d < \tau_a$, diffusion occurs due to shear because even the shortest activity timescale (τ_a) is longer than the diffusive time of shear (τ_d). Indeed, Fig. 2(c) shows that $\tau_a = \tau_d$ approximates $Pe = 100$. Furthermore, we can also estimate the scaling between D/D_0 and Pe in the intermediate Pe range. Suppose $D/D_0 \sim Pe^\nu$, and let $D = D_0$ (or D_s) at $Pe = Pe_0$ (or Pe_s); then, $\nu = \log(D_s/D_0)/\log(Pe_s/Pe_0)$. Using $Pe_0 = 1$, $Pe_s = 100$, and $D_s/D_0 = 0.4$ (or 4.0), we obtain $\nu = -0.2$ (or 0.3) at $\phi = 0.1$ (or 0.4). Figure 1(c) verifies our estimates.

ABPs—One may wonder whether the nonmonotonic diffusion observed here is a general feature of fluids with persistent internal motion. After all, if it is observable in apolar active suspensions, the effect may be stronger for polar particles with a larger persistence. To test this hypothesis, we perform additional simulations of ABPs, a widely studied model [48] for *self-propelled* particles, e.g., self-phoretic colloids [49]. Specifically, we simulate neutral squirmers with $B_1 > 0$ and $B_2 = 0$ and impose a uniform rotational diffusion, d_r , to effect angular noise in the particle dynamics, $\langle \mathbf{\Omega}_s(t) \cdot \mathbf{\Omega}_s(t') \rangle = 2d_r \delta(t - t')$, where $\delta(t)$ is the Dirac delta. Translational noise is neglected, as is done typically [50]. Without shear, our ABPs self-propel with a constant speed, $U_s = \frac{2}{3}B_1$, unless they collide. Over time, collision and orientation relaxation render the motion diffusive, with $D_{0,ABPs} \rightarrow \frac{1}{3}U_s^2\tau_r$ as $\phi \rightarrow 0$, where $\tau_r \equiv \frac{1}{2}d_r^{-1}$. The persistence length, $\ell_p \equiv 3D_{0,ABPs}/U_{rms}$, is tunable and capped at $\ell_{p,0} \equiv U_s\tau_r$ as $\phi \rightarrow 0$ [39].

Figure 3 shows the separate diffusivities in y and z directions, D_{yy} and D_{zz} , relative to $D_{0,ABPs}$ for different $\ell_p \approx \ell_{p,0}$ [39] at $\phi = 10\%$ under shear. The diffusivities are extracted in the same way as for shakers. For D_{yy} , we observe the expected effect of ℓ_p , i.e., a larger persistence leads to a larger drop in diffusivity, which can be more than 90% if $\ell_p/a > 3$ [as a reference, $\ell_p/a \sim O(1)$ for shakers at $\phi = 10\%$ [31]]. Conversely, the nonmonotonic effect disappears when $\ell_p/a \ll 1$, and we have verified that the diffusivity of passive colloids ($\ell_p = 0$) strictly increases with shear [39]. The Pe at which motility ceases (or shear begins) to dominate, Pe_0 (or Pe_s), can be estimated similarly as in the case of shakers: motility dominates when $\max(a^2/D_{0,ABPs}, \ell_p^2/D_{0,ABPs}) < \dot{\gamma}^{-1}$, or $Pe < \min[1, (a/\ell_p)^2] \equiv Pe_0$, while shear dominates when

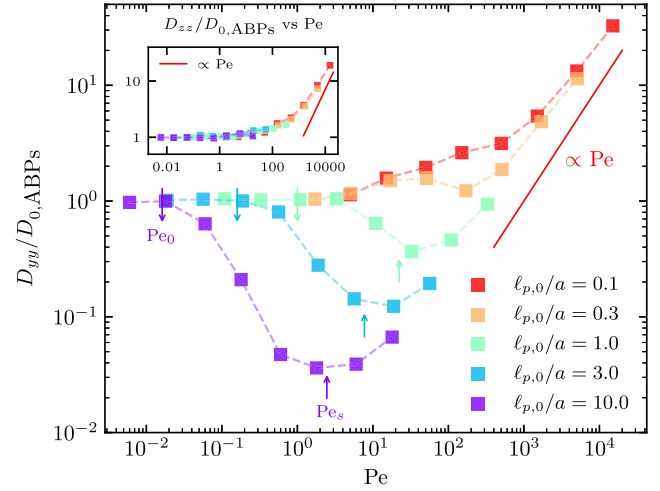


FIG. 3. Diffusivity of ABPs with different persistence lengths (ℓ_p) at $\phi = 10\%$. The main plot shows the relative diffusivity in the y direction; the inset in z . The down arrows denote $Pe_0 \equiv \min[1, (a/\ell_p)^2]$; the up arrows $Pe_s \equiv \dot{\gamma} a^2 / D_{0,ABPs}$, where $\dot{\gamma}_s \equiv \dot{\gamma} \tau_d / \min(\tau_s, \tau_r)$.

$\tau_d < \min(\tau_s, \tau_r)$, or $Pe > \dot{\gamma} a^2 / D_{0,ABPs} \equiv Pe_s$, where $\tau_s \equiv a/U_s$ and $\dot{\gamma}_s \equiv \dot{\gamma} \tau_d / \min(\tau_s, \tau_r)$. Here, a major difference between ABPs and shakers is that $D_{zz}/D_{0,ABPs}$ always increases with Pe , and the data at different ℓ_p collapse, scaling as SID. The reason for the contrasting behaviors is that ABPs hardly interact. As shear rotates all particles around the z -axis with a constant speed $\Omega_\infty = \dot{\gamma}/2$, ABPs oscillate in the xy plane but remain persistent along z (manifest in the MSDs [39]). Consequently, $D_{zz}/D_{0,ABPs}$ can decouple from $D_{yy}/D_{0,ABPs}$ over a large range of Pe , leading to highly anisotropic diffusion.

Discussion—The results of our simulations depict a general physical picture of the interplay between shear and activity. When shearing a fluid with an underlying persistence, arising from either activity-induced HIs (as in the case of shakers), self-propulsion (ABPs), or a combination of the two (squirmers in general), the rotational effect of shear reduces the persistent motion in the shear plane. For a single ABP without any SID (as $\phi \rightarrow 0$), this leads to a monotonically reducing $D_{yy}/D_{0,ABPs}$ with $\dot{\gamma}\tau_r$ [51,52]. At finite ϕ , both shear-induced rotation and collision are at play, and the dynamics depends on the competition of the intrinsic diffusion and SID. If $D_s(\dot{\gamma}_s, \phi) < D_0(\tau_a, \phi)$, where $\dot{\gamma}_s(\phi)$ is the shear rate above which SID dominates, we would expect a reduced diffusion as Pe increases from Pe_0 to Pe_s . Conversely, if $D_s(\dot{\gamma}_s, \phi) > D_0(\tau_a, \phi)$, an enhanced diffusion is expected. Figure 4 shows that D_0 of both pulling and pushing shakers cross D_s at $\phi \approx 20\%$, which is why D/D_0 is nearly independent of Pe up to Pe_s at $\phi = 20\%$; cf. Fig. 1(c). Furthermore, the inset in Fig. 4 suggests that diffusion could be suppressed even in concentrated suspensions, since $D_s(\dot{\gamma}_s, \phi) < D_{0,ABPs}(\tau_s, \tau_r, \phi)$ at sufficiently large ℓ_p ,

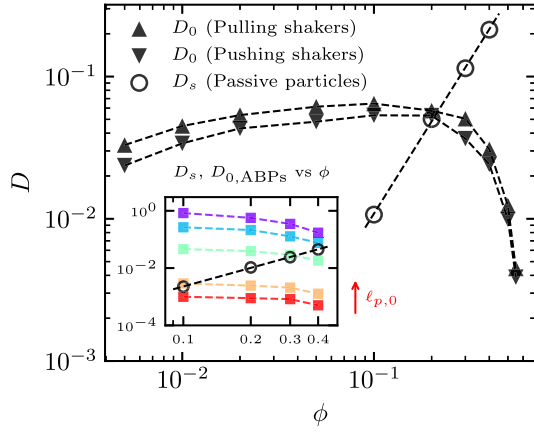


FIG. 4. Comparison of the different intrinsic and shear-induced diffusivities (in the same unit, a^2/τ_a). The main plot compares the D_0 for pulling or pushing shakers with D_s for passive particles at $\dot{\gamma}_s(\phi = 0.2)$. The inset compares $D_{0,ABPs}$ at different $\ell_{p,0}$ (same color legend as in Fig. 3) with D_s at $\dot{\gamma}_s(\phi = 0.4, \ell_{p,0}/a = 10)$.

which we indeed observe at $\phi = 40\%$ and $\ell_{p,0}/a = 10$ [39]. Therefore, we expect nonmonotonic diffusion to be a general feature when shearing fluids endowed with an underlying microstructure and large internal persistence. Finally, there is currently a growing interest in the relation of the dynamics, structure, and rheology of active fluids, which has great practical implications but is still not well understood [52–57]. Our study may shed some light on this problem.

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Data availability—The data that support the findings of this article are openly available [58].

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- [58] The source code to generate all data reported in this article is publicly available at <https://github.com/GeZhouyang/FSD>.