Enhanced velocity fluctuations in interacting swimmer suspensions

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A dilute non-interacting suspension of micro-swimmers exhibits a finite velocity variance and short-ranged correlations that decay over a swimmer length. For a suspension of interacting straight swimmers, however, pair-interactions leads to a non-decaying velocity covariance, and a variance that diverges logarithmically with system size. The divergence is arrested on inclusion of orientation decorrelation mechanisms. Results for suspensions of run-and-tumble particles (RTPs) are presented, where the underlying straight-swimmer divergence leads to a broad cross-over between the ballistic and diffusive regimes, of immersed passive tracers, in the limit of long run lengths. Our analysis explains long-standing experimental observations of a volume-fraction dependent crossover time for passive tracer dynamics.

Suspensions of rear-actuated swimming microorganisms (pushers), such as bacterium *E. coli* and *B. subtilis*, exhibit a state of large-scale coherent motion that arises, in part, due to long-ranged hydrodynamic interactions [3, 13]. Experiments [14, 15] and simulations [3, 12, 16] show that the transition to collective dynamics occurs beyond a threshold concentration, leading to ‘bacterial turbulence’ [16]. Collective motion has important consequences for both transport and rheology, with experiments and mean-field theories having shown a reduction in viscosity leading to apparent superfluidity and unexpected shear-banding behavior [17–24]. This transition has often been inferred from an anomalous enhancement in the diffusivities of passive tracer particles [3, 12, 25, 29].

A large body of theoretical work studying swimmer suspensions relies on phenomenological and mean-field models [1, 4, 6, 14, 20, 33]. For a dilute swimmer suspension, mean-field theory has shown that it is the long-ranged hydrodynamic interactions [3, 6] between pushers and the mutually reinforcing orientation and velocity fluctuations that are responsible for the said transition. In this letter, we go beyond this limiting mean-field assumption, and demonstrate the crucial role played by hydrodynamically induced swimmer-correlations. The interplay of swimming with long-ranged hydrodynamic interactions is shown, for the first time, to lead to diverging velocity fluctuations in a suspension of straight swimmers. This is consistent with recent simulations of pusher and puller suspensions (the swimming mechanism in this case being front-actuated as is typically the case for algae [3, 9, 12, 34, 35]), which have revealed a bifurcation of the fluid velocity variance beyond a threshold, with pusher suspensions exhibiting enhanced fluctuations [3, 10, 12, 29].

In a homogeneous Stokesian suspension of sedimenting particles with a random microstructure, the velocity variance is predicted to diverge linearly with system size [37–47]. The resolution of this divergence has been a long-standing theoretical challenge [38, 45, 46]. It arises due to the long-ranged $O(1/r)$ disturbance velocity fields of the individual particles acting as point-forces (monopoles), as shown in figure 11. The fluid velocity variance at a given point $x$ may be estimated as $(u(x) \cdot u(x)) \approx \int nU^2/s r^2 dr \sim (nL^3)U^2/L$. Here, $U$ is the mean sedimenting speed, $L$ the box size, and $nL^3$ is the hydrodynamic volume fraction, with $n$ being the particle number density, and $L$ a characteristic particle size. Unlike passive particles, microswimmers, both pushers and pullers, act as force-dipoles in the far-field, leading to a disturbance velocity field that decays more rapidly as $O(1/r^2)$. An argument along lines similar to that for the passive Stokesian suspension above gives $(u(x) \cdot u(x)) \sim (nL^3)U^2$, implying that the velocity variance remains finite in the limit $nL^3 \ll 1$ with correlations between swimmers being neglected at leading order [49]: the covariance $(u(x) \cdot u(x+r)) \sim (nL^3) \int U^2/(r^3) dr'$ at this order exhibits an $O(1/r)$ decay for $r \gg L$ [3, 10]. Introducing pair-level correlations in straight swimmer suspensions, as shown in figure 11, leads to a pair-orientation probability density that decays as $O(1/r^2)$ in the far-field. In this scenario, where a given swimmer interacts pair-wise with a cloud of swimmers surrounding it, one has the fluid velocity variance due to ‘each cloud’ scaling as $(u(x) \cdot u(x))_{cloud} \equiv nL^3 \int U^2 r^2 dr'/(r^3) \sim nL^3 U^2/r^3$, which when integrated over all such correlation clouds gives $(u(x) \cdot u(x)) \equiv (nL^3)^2 \ln(L_{box}/L)$: a logarithmically divergent variance. In sharp contrast to passive sedimenting suspensions [48], the fact that correlations act to yield a divergent variance in interacting straight swimmer suspensions, highlights the novel consequences of activity (swimming).

In what follows, we first establish the character of the velocity (co)variance in a suspension of straight swimmers that interact pairwise, showing the logarithmic system-size dependence highlighted in the aforementioned scaling arguments. Next, we consider run-and-tumble particles, in which case the fluid velocity variance scales as $O(\ln U\tau/L)$, the
FIG. 1: The window on the left shows the $O(1/r)$ contributions due to individual spheres contributing to the variance at $x$ in an (infinite) sedimenting suspension. The right window corresponds to a straight swimmer suspension with each swimmer surrounded by a pair-correlation cloud. The variance at $x$ is the sum of the contributions of these individual clouds, and is logarithmically divergent.

logarithmic divergence being cut off on scales of order the large but finite run length $U\tau$ ($\tau$ being the mean run time); the variance scales as $O(U\tau/L)$ for $U\tau/L \ll 1$ due to a more rapid, $O(1/r^3)$ decay of the pair-correlation function. Importantly, hydrodynamic interactions act to differentiate between pusher and puller suspensions, leading to the aforementioned bifurcation in the velocity variance and tracer diffusivities. The fluid velocity covariance is expressible as, $\langle u(x) \cdot u(x') \rangle = \langle \sum_{i,j=1}^{N} u_i(x) \cdot u_j(x') \rangle$, where $\langle \cdot \rangle$ represents an ensemble average over the $N$-swimmer probability density, $\Omega_N([x,p]^N_{i=1},t)$; here, $x_i$ and $p_i$ denote the position and orientation of the $i^{th}$ swimmer at time $t$. For straight swimmers, $\Omega_N$ satisfies the Liouville equation, and evolves due to swimming, and due to convection and rotation of each swimmer by the disturbance velocity fields due to the remaining swimmers. For a homogeneous isotropic swimmer one has $\Omega_1 = nL^3/(4\pi)$ [50]. In the dilute limit, integrating over the degrees of freedom of the remaining $N-2$ swimmers, while neglecting three-swimmer interactions, we obtain an equation for the pair probability density $\Omega_2$, at steady state, as:

$$\nabla_r \cdot \{[(U_p_2 + u_1) - (U_p_1 + u_2)]\Omega_2\} + \nabla_{p_1} \cdot (\dot{p}_{12}\Omega_2) + \nabla_{p_2} \cdot (\dot{p}_{21}\Omega_2) = 0.$$  

(1)

The terms within braces in (1) denote the convection of $\Omega_2$ by the relative velocity of the swimmer pair that includes contributions due to both swimming $(U_p_1, U_p_2)$ and the disturbance velocity fields $(u_2, u_1)$; $r = x_2 - x_1$ being the swimmer separation vector. The third and fourth terms denote rotation of the swimmer orientations due to the disturbance velocity fields, with $\dot{p}_{ij}$ denoting the rotation of swimmer $i$ from the disturbance velocity field generated by swimmer $j$.

Considering slender swimmers, with aspect ratio $\kappa \gg 1$, leads to logarithmically weak interactions on length scales of $O(L)$ (scales that contribute dominantly to the velocity variance), and this allows one to expand $\Omega_2$ as a series in $(\ln \kappa)^{-1}$: $\Omega_2 = \Omega_2^{(0)} + 1/(\ln \kappa)\Omega_2^{(1)} + \ldots$, where $\Omega_2^{(0)} = (nL^3)^2/(4\pi)^2$ represents the leading order uncorrelated state, and $\Omega_2^{(1)} \equiv \Omega_2^{(1)}(r,p_1,p_2)$ captures the first effects of the pair-correlations [51]. Neglecting the convection by the $O[(\ln \kappa)^{-1}]$ disturbance velocity fields in (1), pair-correlations develop along straight swimming trajectories, so that: $\Omega_2^{(1)} = -(nL^3)^2/((4\pi)^2U(p_2 - p_1))\int_{-\infty}^{\infty} dz' \langle \nabla_{p_1} \cdot \dot{p}_{12} + \nabla_{p_2} \cdot \dot{p}_{21} \rangle$; here $z$ is the coordinate along the relative swimming velocity. The $\dot{p}_{12}$ and $\dot{p}_{21}$ in this expression are defined by viscous slender body theory [52, 53]; for instance, $\dot{p}_{21} = 12/L^3 \int_{-L/2}^{L/2} s(p_2 \wedge u_1) \wedge p_2 \, ds$ [50], where $u_1$ is determined from the Stokes equations:

$$-\nabla P_1 + \eta \nabla^2 u_1 = \int_{-L/2}^{L/2} s f(s)p_1\delta(x_2 - x_1 - sp_1)ds,$$  

(2)

where $P_1$ is the pressure field, and the right side of (2) corresponds to a line distribution of forces along the swimmer axis $(s)$, consistent with the force-free constraint $(\int_{-L/2}^{L/2} f(s)ds = 0)$. Here, $f(s)$ denotes the $O(\eta L^2/\ln \kappa)$ linear force density, $\eta$ being the suspending fluid viscosity. We consider a piecewise constant force density such that $f(s) = \eta Us\mathrm{sgn}(s)$ implying a for–aft symmetric swimmer [4].

Incorporating (12) in the expression for the velocity covariance, and after some algebra the Fourier transformed velocity covariance is expressible as $\langle \dot{u}(k) \cdot \dot{u}(k') \rangle = \delta(k + k')F(k; nL^3)$. Here $\delta(k + k')$ signifies the translational invariance associated with statistical homogeneity, and $F(k; nL^3)$ [50] is given by:

$$F(k; nL^3) = \frac{1}{k^4} \left[ (nL^3)^2 \frac{1}{16\pi^2} \int dp \sin^4(\frac{\pi k \cdot p}{2}) \left( \frac{1}{(k \cdot p)^2} - \frac{1}{k^2} \right) + (nL^3)^2 \frac{1}{4\pi^6} \int dp dp' \sin^2(\frac{\pi k \cdot p}{2}) \sin^2(\frac{\pi k \cdot p'}{2}) \left( \frac{p \cdot p'}{(k \cdot p)(k \cdot p')} - \frac{1}{k^2} \right) \Omega_2^{(1)} \right].$$  

(3)

where $k$ is the wavenumber scaled by $L$. The first term in (3) is the $O(nL^3)$ contribution due to non-interacting swimmers, whose far-field form has been reported earlier [10]. The physical-space covariance, in the non-interacting limit, is shown in figure 2a. It starts from a (variance) plateau
of \(nL^3/\{96\pi(\ln \kappa)^2\}\), and transitions to the dipole-asymptote, \(nL^3/[120\pi(\ln \kappa)^2r]\), for \(r \gg L\) \[11, 50\].

The second term in \(3\) is the \(O(nL^3)^2\) pair-correlation contribution, with \(\Omega_2 = c \delta \{ \mathbf{r}_2 - \mathbf{r}_1 \} \cdot \langle \mathbf{p}_2 \cdot \mathbf{p}_1 \rangle\) being the Fourier transformed pair-probability density \[56\], here the constant \(c\) is determined from an initially uncorrelated system of infinitely separated pair of swimmers. The \(O(nL^3)^2\) integral in \[3\] is not well defined for any \(r\), and in particular, results in a logarithmically divergent variance on setting \(r = 0\). Figure 2b highlights the said divergence as a function of \(k_{\text{min}}\), with \(k_{\text{min}}^{-1}\) enforcing a long wavelength cutoff. This is consistent with earlier simulations \[10\] and scaling arguments above. The ill-posed Fourier integral above also leads to a non-decaying covariance, rendering the straight-swimmer limit a singular one.

In practice, the logarithmic divergence above will be cut off at an appropriate screening length \(L_{\text{screen}}\), so the variance takes the form \(c_1(nL^3)^2 \{ \Omega_2 \ln[L_{\text{screen}}/L] + c_3 \}\), the constants \(c_1\)’s being functions of swimmer aspect ratio. In box-size limited simulations, the largest admissible wavelength is set by the computational domain, so \(L_{\text{screen}} = L_{\text{box}}\). For real bacteria, intrinsic decorrelation mechanisms such as rotary diffusion or run-and-tumble dynamics, lead to \(L_{\text{screen}} = U/D_r\) or \(U\tau\), where \(D_r\) is the rotary diffusivity and \(\tau\) the mean run duration. Note that the rotary diffusion above could be entirely hydrodynamic in origin. For slender straight swimmer suspensions not limited by box size, one expects the logarithmic divergence to nevertheless be cut off at \(L_{\text{screen}} \sim O(U/D_r)\), \(D_r \sim O(nUL^2/\ln \kappa)\) being a hydrodynamic rotary diffusivity arising from slender-swimmer interactions, and has been calculated earlier \[3\].

For suspensions of run-and-tumble swimmers, in which case \(\Omega_2^{(1)}\) is governed by:

\[
\frac{U \tau}{L} \langle \mathbf{p}_2 - \mathbf{p}_1 \rangle \cdot \nabla_r \Omega_2^{(1)} + \left[ \Omega_2^{(1)} - \frac{1}{4\pi} \int \Omega_2^{(1)} dp_1 \right] + \left[ \Omega_2^{(1)} - \frac{1}{4\pi} \int \Omega_2^{(1)} dp_2 \right] + \frac{(nL^3)^2 U \tau}{(4\pi)^2 L} \left[ \nabla_{\mathbf{p}_1} \cdot \mathbf{P}_{12} + \nabla_{\mathbf{p}_2} \cdot \mathbf{P}_{21} \right] = 0. 
\]

where lengths and time have been scaled by \(L\) and \(U/\tau\), respectively. The second and third terms on the left side of \(4\) model a random tumbling process obeying Poisson’s statistics with a mean tumbling frequency \(1/\tau\) \[6, 29\]. To \(O(nL^3)^2\), the velocity covariance for arbitrary \(U/\tau/L\) \[56\] is now expressible as:

\[
\langle \mathbf{u}(\mathbf{x}) \cdot \mathbf{u}(\mathbf{x} + \mathbf{r}) \rangle = nL^3 \left\{ \frac{U^2}{4\pi^6 r} \int_0^1 \frac{1}{k} \sin(2\pi kr) dk \right\}^{1/2} \]

where \(j_0\) is the spherical Bessel’s function of the first kind \[57\]. The variance obtained from setting \(r = 0\) in \(3\) is plotted in figure \[8\]. In accordance with the earlier scaling arguments, \[5\] takes the form, \(c_1(nL^3)^2 \{ \Omega_2 \ln[U/\tau/L] + c_3 \}\) for large \(U/\tau/L\). In contrast, for \(U/\tau/L \ll 1\), \(\Omega_2^{(1)} \sim (\nabla_{\mathbf{p}} \cdot \mathbf{p} + \nabla_{\mathbf{p}'} \cdot \mathbf{p'}) \sim O(1/r^3)\), and this rapid decay leads to the variance scaling as, \(c_1(nL^3)^2 + c_2(U/\tau/L)(nL^3)^2\). Importantly, the correlated contribution to the variance is proportional to \(D^3\), with \(D \sim O(nUL^2)\) being the swimmer dipole strength, and unlike the \(O(nL^3)^3\) contribution, depends on the sign of \(D\) \((D < 0 \text{ for pushers and } D > 0 \text{ for pullers})\), and therefore, on the swimming mechanism. Consistent with recent simulations \[12, 29\], at \(O(nL^3)^2\), \[5\] predicts enhanced fluctuations in pusher suspensions.

The \(O(nL^3)^2\) contribution to the covariance for pusher suspensions is plotted in figure \[8\]. For \(U/\tau/L \ll 1\), the covariance directly transitions from the initial variance plateau to an \(O(1/r)\) decay for \(r \gg L\). In contrast, for \(U/\tau/L \gg 1\), there emerges an intermediate logarithmic regime, with the covariance being \(O(1/\ln[r/(U\tau)])\) for \(L \ll r \ll U\tau\). This delays the onset of the eventual \(O(1/r)\) decay, and as \(U\tau/L \rightarrow \infty\), one asymptotes to a non-decaying
the time scale $\tau\ U/L$

the decay of the velocity correlations, irrespective of

$a L/U$; being $O(\tau/L$) for

$U\gg U\tau/L$; the swimmer-tracer interaction time; being

$L/U$ the total for

$\tau\ U/L$ $O(\tau/L$). The small (dotted) and large (dash-dotted) $U\tau/L$
young for both pushers and pullers, along with the uncorrelated

correlation contribution (solid line).

collapse for

Fig 5 (inset) confirms these scalings. In the straight swimmer limit, the correlated contribution to the
diffusivity thus diverges linearly in $U\tau/L$. The

tracer diffusivity variation with volume fraction also

shows a pusher-puller bifurcation similar to the ve-
cocity variance (not shown).

From Fig 5 we also note that the time taken
to transition the ballistic to the diffusive regime,

for large $U\tau/L$, increases with increasing volume-

fraction. This surprising behavior can be explained

by noting the differing time scales for the decay of

the velocity correlations at $O(nL^3)$ (the time scale

being $O(U/L)$) and $O(nL^3)^2$ (the time scale being

$O(\tau)$). As a result, the transition time between the

ballistic and diffusive regimes diverges as $U\tau/L$. The

resulting broad cross-over gives the impression of an

$nL^3$-dependent anomalous exponent for intermediate
times ($L/U \ll t \ll \tau$) (see Fig 5). For rapid tumblers ($U\tau/L \ll 1$), the transition time is $O(\tau)$

regardless of $nL^3$, and there is no intermediate anom-

alous scaling.

Several experiments probing bacterial suspension
dynamics with passive tracers have reported an inter-

mediate super-diffusive regime and a volume frac-

tion dependent cross-over time $[25, 60–64]$. To the

best of our knowledge, this letter is the first theo-

retical explanation for these observations. Our

arguments also imply that when a passive tracer is

given by:

$$
\frac{nL^4U}{(\ln \kappa)^2} \left( d_1 + \frac{nL^3U\tau}{\ln \kappa L d_2} \right) \quad \text{for } U\tau/L \gg 1,
$$

and

$$
\frac{nL^3U^2\tau}{(\ln \kappa)^2} \left( d_3 + \frac{nL^3U\tau}{\ln \kappa L d_4} \right) \quad \text{for } U\tau/L \ll 1.
$$

Fig 5 (inset) confirms these scalings. In the straight swimmer limit, the correlated contribution to the
diffusivity thus diverges linearly in $U\tau/L$. The

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retical explanation for these observations. Our

arguments also imply that when a passive tracer is
confined by a harmonic potential with a radius of \( O(U\tau) \) immersed in a bacterial bath, the swimmer velocity correlations would not decay away, leading to a strongly non-Gaussian distribution as has indeed been observed in experiments \([6, 62, 63]\).

In this letter, we have shown that long-ranged pair-correlations lead to divergent velocity fluctuations and tracer diffusivities in straight-swimmer suspensions. For RTP’s, this divergence is replaced by a logarithmic increase of the velocity variance, and a linear increase of the tracer diffusivity, with the run length for \( U\tau/L \gg 1 \). Correlated fluctuations are also crucially dependent on the swimming mechanism pusher vis-a-vis pullers, being larger for pusher suspensions. Thus, in contrast to recent work emphasizing the role of anisotropic tracers \([62, 66]\), spherical tracers already discriminate between pusher and puller suspensions due to correlated fluctuations.

While the detailed analysis given is limited to slender swimmers, scaling arguments preceding the analysis only involve far-field hydrodynamics, and therefore have a universal character, being applicable to suspensions of general anisotropic swimmers \([67]\). Evidence of logarithmic scaling in simulations of regularized point dipoles \([10, 68]\) reinforces this assertion. The spherical squirmer model often used in studies may therefore represent an exceptional scenario and the results obtained need to be extrapolated with care \([65, 70]\).

We have focused on correlations due to direct pairwise hydrodynamic interactions between the swimmers, while not accounting for those induced by long-wavelength fluctuations in the suspension velocity and orientation fields. It is well-known that these fluctuations lead to an instability of the pusher suspension, in turn implying diverging contributions of the ‘collective effects’ to statistical correlations at the threshold \([6, 29, 71]\). This divergence is distinct from the one described here. Nevertheless, the framework needed for this calculation requires the pair-probability determined here as an input, for arbitrary \( U\tau/L \), and will be reported in future-work. Our work thus lays the foundation for understanding pairwise swimmer interactions in the state of bacterial turbulence \([16]\).

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[49] See the supplementary information for exact expressions in terms of the velocity correlation functions.

[50] Typical bacteria such as E. coli and B. subtilis are quiet slender $12, 72$, and this assumption reasonably reproduces experimentally-measured disturbance velocity fields to distances of $O(L)$ $22$ $()$.

[51] There is an O(1) change in the force density in a non-fore-aft symmetric swimmer, and thence the disturbance fluid velocity it generates. However, none of the principal conclusions change due to this swimmer asymmetry $()$.

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