Computing the distribution of displacements
due to swimming microorganisms

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We examine the distribution of particle displacements for relatively short times, when the
swimmers can be assumed to move along straight paths. For this we need the partial-path
drift function for a fluid particle, initially at \( \mathbf{r} = \mathbf{r}_0 \), affected by a single swimmer:

\[
\Delta(\mathbf{r}_0, t) = U \int_0^t \mathbf{u}(\mathbf{r}(s) - U s) \, ds,
\quad \dot{\mathbf{r}} = \mathbf{u}(\mathbf{r} - U t), \quad \mathbf{r}(0) = \mathbf{r}_0.
\]  

(1)

Here \( Ut \) is the swimmer’s position, with \( U \) assumed constant. To obtain \( \Delta(\mathbf{r}_0, t) \) we must
solve the differential equation for each initial condition \( \mathbf{r}_0 \). After using homogeneity and
isotropy, we obtain the probability density of displacements, \( p_1(\mathbf{r}, t) = \frac{1}{\alpha_d^{d-1}} \int_V \delta(\mathbf{r} - \Delta(\mathbf{\eta}, t)) \frac{dV_{\eta}}{V} \)

(2)

where \( \alpha_d \) is the area of the unit sphere in \( d \) dimensions: \( \alpha_2 = 2\pi, \alpha_3 = 4\pi \). Here \( \mathbf{r} \) gives
the displacement of the particle from its initial position after a time \( t \), and \( p_1(\mathbf{r}, t) \) is the
probability density function of \( \mathbf{r} \) for one swimmer.

The second moment of \( \mathbf{r} \) for a single swimmer is

\[
\langle r^2 \rangle_1 = \int_V r^2 p_1(\mathbf{r}, t) \, dV_r = \int_V \Delta^2(\mathbf{\eta}, t) \, \frac{dV_{\eta}}{V}.
\]  

(3)

This goes to zero as \( V \to \infty \), since a single swimmer in an infinite volume shouldn’t give
any fluctuations. If we have \( N \) swimmers, the second moment is

\[
\langle r^2 \rangle_N = N \langle r^2 \rangle_1 = n \int_V \Delta^2(\mathbf{\eta}, t) \, dV_{\eta}
\]  

(4)

with \( n = N/V \) the number density of swimmers. This is nonzero (and might diverge) in
the limit \( V \to \infty \), reflecting the cumulative effect of multiple swimmers. Note that this
expression is exact, within the problem assumptions: it doesn’t even require \( N \) to be large.
It is not at all clear that \([1]\) leads to diffusive behavior, but it does \([2,4]\): the “support” of
the drift function \( \Delta(\mathbf{\eta}, t) \) typically grows in time: that is, the longer we wait, the larger the
number of particles displaced by the swimmer.

The rate of convergence to Gaussian can be estimated from

\[
\langle r^4 \rangle_N = N \langle r^4 \rangle_1 = n \int_V \Delta^4(\mathbf{\eta}, t) \, dV_{\eta}
\]  

(5)
and the ratio
\[ \frac{\langle r^4 \rangle_N}{\langle r^2 \rangle_N^2} = \frac{1}{n} \frac{\int_V \Delta^4(\eta, t) \, dV_n}{\left( \int_V \Delta^2(\eta, t) \, dV_n \right)^2} \sim (\ell/\lambda) \, \phi^{-1}. \tag{6} \]

Thus small \( \phi \) leads to slower convergence to Gaussian, but large \( \lambda \) compensates for this by making interactions more frequent.

From [2] with \( d = 2 \) we can compute \( p_1(x, t) \), the marginal distribution for one coordinate:
\[ p_1(x, t) = \int_{-\infty}^{\infty} p_1(r, t) \, dy = \int_{-\infty}^{\infty} \frac{1}{2\pi r} \delta(r - \Delta(\eta, t)) \, dy \frac{dV_n}{V}. \tag{7} \]

Since \( r^2 = x^2 + y^2 \), the \( \delta \)-function will capture two values of \( y \), and with the Jacobian included we obtain
\[ p_1(x, t) = \frac{1}{\pi} \int_{V} \frac{1}{\sqrt{\Delta^2(\eta, t) - x^2}} \, [\Delta(\eta, t) > |x|] \, \frac{dV_n}{V}, \tag{8} \]

where \([A]\) is an indicator function: it is 1 if \( A \) is true, 0 otherwise.

The marginal distribution in the three-dimensional case proceeds the same way from (2) with \( d = 3 \):
\[ p_1(x, t) = \frac{1}{2} \int_{V} \frac{1}{\Delta(\eta, t)} \, [\Delta(\eta, t) > |x|] \, \frac{dV_n}{V}. \tag{9} \]

For summing the displacements due to multiple swimmers, we need the characteristic function of \( p_1(x, t) \), defined by the Fourier transform
\[ \langle e^{ikx} \rangle_1 = \int_{-\infty}^{\infty} p_1(x, t) \, e^{ikx} \, dx. \tag{10} \]

For the three-dimensional pdf (9), the characteristic function is
\[ \langle e^{ikx} \rangle_1 = \frac{1}{2} \int_{V} \frac{1}{\Delta(\eta, t)} \int_{-\infty}^{\infty} \, [\Delta(\eta, t) > |x|] \, e^{ikx} \, dx \, \frac{dV_n}{V} \]
\[ = \frac{1}{2} \int_{V} \frac{1}{\Delta(\eta, t)} \int_{-\Delta}^{\Delta} e^{ikx} \, dx \, \frac{dV_n}{V} \]
\[ = \int_{V} \text{sinc} \left( k\Delta(\eta, t) \right) \, \frac{dV_n}{V} \]

where \( \text{sinc} \, x := x^{-1} \sin x \) for \( x \neq 0 \), and \( \text{sinc} \, 0 := 1 \). For the two-dimensional pdf (8), we have
\[ \langle e^{ikx} \rangle_1 = \int_{V} J_0(k\Delta(\eta, t)) \, \frac{dV_n}{V} \tag{11} \]
where \( J_0(x) \) is a Bessel function of the first kind.

We define (see Fig. 1)
\[ \gamma_d(x) := \begin{cases} 1 - J_0(x), & d = 2; \\ 1 - \text{sinc} \, x, & d = 3, \end{cases} \tag{12} \]
and write the two cases for the characteristic function together as
\[ \langle e^{ikx} \rangle_1 = 1 - \Gamma_d(k, t)/V. \tag{13} \]
where
\[ \Gamma_d(k, t) := \int_V \gamma_d(k \Delta(\eta, t)) \, dV. \] (14)

We have \( \gamma_d(0) = \gamma'_d(0) = 0 \), \( \gamma''_d(0) = 1/d \), so \( \gamma_d(\xi) \sim (1/2d) \xi^2 + O(\xi^4) \) as \( \xi \to 0 \). For large argument, \( \gamma_d(\xi) \to 1 \) as \( \xi \to \infty \).

We will need the following simple result:

**Proposition 1.** Let \( y(\varepsilon) \sim o(\varepsilon^{-M/(M+1)}) \) as \( \varepsilon \to 0 \) for an integer \( M \geq 1 \); then
\[
(1 - \varepsilon y(\varepsilon))^{1/\varepsilon} = \exp\left(- \sum_{m=1}^{M} \frac{\varepsilon^{m-1} y^m(\varepsilon)}{m}\right) (1 + o(\varepsilon^0)), \quad \varepsilon \to 0.
\] (15)

**Proof.** Observe that \( \varepsilon y(\varepsilon) \sim o(\varepsilon^{1/(M+1)}) \to 0 \) as \( \varepsilon \to 0 \). Writing \( (1 - \varepsilon y)^{1/\varepsilon} = e^{\varepsilon^{-1} \log(1-\varepsilon y)} \), we expand the exponent as a convergent Taylor series:
\[
(1 - \varepsilon y)^{1/\varepsilon} = \exp\left(- \varepsilon^{-1} \sum_{m=1}^{\infty} \frac{(\varepsilon y)^m}{m}\right) \text{ (converges since } \varepsilon y \sim o(\varepsilon^{1/(M+1)})\text{)}
\]
\[
= \exp\left(- \varepsilon^{-1} \left( \sum_{m=1}^{M} \frac{(\varepsilon y)^m}{m} + O((\varepsilon y)^{M+1}) \right) \right)
\]
\[
= \exp\left(- \varepsilon^{-1} \sum_{m=1}^{M} \frac{(\varepsilon y)^m}{m} \right) \exp\left(O(\varepsilon y^{M+1}) \right)
\]
\[
= \exp\left(- \varepsilon^{-1} \sum_{m=1}^{M} \frac{(\varepsilon y)^m}{m} \right) \left(1 + o(\varepsilon^0)\right). \]

Since we are summing their independent displacements, the characteristic function for \( N \) swimmers is \( e^{ikx}_N = e^{ikx}_1^N \). From [13],
\[
e^{ikx}_1^N = (1 - \Gamma_d(k, t)/V)^{n_V}, \tag{16}
\]
where we used $N = nV$, with $n$ the number density of swimmers. Let’s examine the assumption of Proposition 1 for $M = 1$ applied to (16), with $\varepsilon = 1/V$ and $y = \Gamma_d(k,t)$. For $M = 1$, the assumption of Proposition 1 requires

$$\Gamma_d(k,t) \sim o(V^{1/2}), \quad V \to \infty. \quad (17)$$

A stronger divergence with $V$ means using a larger $M$ in Proposition 1, but we shall not need to consider this here. Note that it is not possible for $\Gamma_d(k,t)$ to diverge faster than $O(V)$, since $\gamma_d(x)$ is bounded. In order for $\Gamma_d(k,t)$ to diverge that fast, the displacement must be bounded away from zero as $V \to \infty$, an unlikely situation which can be ruled out.

Assuming that (17) is satisfied, we use Proposition 1 with $M = 1$ to make the large-volume approximation

$$\langle e^{ikx} \rangle_N^1 = (1 - \Gamma_d(k,t)/V)^nV \sim \exp \left( -n \Gamma_d(k,t) \right), \quad V \to \infty. \quad (18)$$

If the integral $\Gamma_d(k,t)$ is convergent as $V \to \infty$ we have achieved a volume-independent form for the characteristic function, and hence for the distribution of $x$ for a fixed swimmer density.

A comment is in order about evaluating (14) numerically: if we take $|k|$ to $\infty$, then $\gamma_d(k\Delta) \to 1$, and thus $\Gamma_d \to V$, which then leads to $e^{-N}$ in (18). This is negligible as long as the number of swimmers $N$ is moderately large. In practice, this means that $|k|$ only needs to be large enough that the argument of the decaying exponential in (18) is of order one, that is

$$n \Gamma_d(k_{\text{max}}, t) \sim O(1). \quad (19)$$

Wavenumbers $|k| > k_{\text{max}}$ do not contribute to (18). (We are assuming monotonicity of $\Gamma_d(k,t)$ for $k > 0$, which will hold for our case.) Note that (19) implies that we need larger wavenumbers for smaller densities $n$: a typical fluid particle then encounters very few swimmers, and the distribution should be far from Gaussian.

We finally recover the pdf of $x$ as the inverse Fourier transform

$$p_N(x,t) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \exp \left( -n \Gamma_d(k,t) \right) e^{-ikx} \, dk. \quad (20)$$

Consider the case special when $\Delta(\mathbf{r},t)$ vanishes outside a specified ‘swept volume’ $V_{\text{swept}}$. Then

$$\Gamma_d(k,t) = \int_{V_{\text{swept}}} \gamma_d(k\Delta(\mathbf{\eta},t)) \, dV_\eta$$

$$= V_{\text{swept}} - \int_{V_{\text{swept}}} (1 - \gamma_d(k\Delta(\mathbf{\eta},t))) \, dV_\eta$$

$$= V_{\text{swept}} (1 - W_d(k,t))$$

where

$$W_d(k,t) = \frac{1}{V_{\text{swept}}} \int_{V_{\text{swept}}} (1 - \gamma_d(k\Delta(\mathbf{\eta},t))) \, dV_\eta. \quad (21)$$

Define $\phi_{\text{swept}} := nV_{\text{swept}}$; then we can Taylor expand the exponential in (20) to obtain

$$p_N(x,t) = \sum_{m=0}^{\infty} \frac{\phi_{\text{swept}}^m}{m!} e^{-\phi_{\text{swept}}} \frac{1}{2\pi} \int_{-\infty}^{\infty} W_d^m(k,t) e^{-ikx} \, dk. \quad (22)$$
FIG. 2. Contour lines for the axisymmetric streamfunction of a squirmer of the form (23), with $\beta = 0.5$. This swimmer is of the puller type, as for C. reinhardtii.

\[
\Psi_{sf}(\rho, z) = \frac{1}{2} \rho^2 U \left\{ -1 + \frac{\ell^3}{(\rho^2 + z^2)^{3/2}} + \frac{3}{2} \frac{\beta \ell z}{(\rho^2 + z^2)^{3/2}} \left( \frac{\ell^2}{\rho^2 + z^2} - 1 \right) \right\}
\]  

(23)

FIG. 3. (a) The pdf of particle displacements after a time $t = 0.12$ s, for several values of the volume fraction $\phi$. The data is from Leptos et al. [6], and the figure should be compared to their Fig. 2(a). (b) Same as (a) but on a wider scale, also showing the form suggested by Eckhardt and Zammert [7] (dashed lines).

The factor $\phi^m_{\text{swept}} e^{-\phi_{\text{swept}}/m!}$ is a Poisson distribution for the number of ‘interactions’ $m$, in exact agreement with [5]. Equation (20) is thus a more general formula that doesn’t require an ‘interaction sphere’ as used in [5].

We now compare the theory to the experiments of Leptos et al. We use a model swimmer of the squirmer type [8–12], with axisymmetric streamfunction (3)

in a frame moving at speed $U$. Here $z$ is the swimming direction and $\rho$ is the distance from the $z$ axis. To mimic C. reinhardtii, we use $\ell = 5 \mu m$ and $U = 100 \mu m/s$. We take also $\beta = 0.5$ for the relative stresslet strength, which gives a swimmer of the puller type, just like C. reinhardtii. The contour lines of the axisymmetric streamfunction (23) are depicted in Fig. 2. The parameter $\beta$ is the only one that was fitted to give good agreement.

The numerical results are plotted into Fig. 3(a) and compared to the data of Fig. 2(a) of
The agreement is excellent: we adjusted only one parameter, $\beta = 0.5$. All the other physical quantities were gleaned from Leptos et al. What is most remarkable about the agreement in Fig. 3(a) is that it was obtained using a model swimmer, the spherical squirmer, which is not expected to be such a good model for C. reinhardtii. The real organisms are strongly time-dependent, for instance, and do not move in a perfect straight line. Nevertheless the model captures very well the pdf of displacements.

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