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 $\boldsymbol{r} = \boldsymbol{r}_0$, affected by a single swimmer:

$$\boldsymbol{\Delta}(\boldsymbol{r}_0, t) = U \int_0^t \boldsymbol{u}(\boldsymbol{r}(s) - \boldsymbol{U}s)\,\mathrm{d}s, \qquad \dot{\boldsymbol{r}} = \boldsymbol{u}(\boldsymbol{r} - \boldsymbol{U}t), \quad \boldsymbol{r}(0) = \boldsymbol{r}_0\,. \tag{1}$$

Here $\boldsymbol{U}t$ is the swimmer's position, with $\boldsymbol{U}$ assumed constant. To obtain $\boldsymbol{\Delta}(\boldsymbol{r}_0, t)$ we must solve the differential equation for each initial condition $\boldsymbol{r}_0$. After using homogeneity and isotropy, we obtain the probability density of displacements, [1]

$$p_1(\boldsymbol{r}, t) = \frac{1}{\alpha_d\, r^{d-1}} \int_V \delta(r - \Delta(\boldsymbol{\eta}, t))\, \frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V} \tag{2}$$

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

The second moment of $\boldsymbol{r}$ for a single swimmer is

$$\langle r^2 \rangle_1 = \int_V r^2 p_1(\boldsymbol{r}, t)\,\mathrm{d}V_{\boldsymbol{r}} = \int_V \Delta^2(\boldsymbol{\eta}, t)\, \frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}. \tag{3}$$

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

$$\langle r^2 \rangle_N = N \langle r^2 \rangle_1 = n \int_V \Delta^2(\boldsymbol{\eta}, t)\,\mathrm{d}V_{\boldsymbol{\eta}} \tag{4}$$

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 (4) leads to diffusive behavior, but it does [2–4]: the "support" of the drift function $\Delta(\boldsymbol{\eta}, t)$ 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

$$\langle r^4 \rangle_N = N \langle r^4 \rangle_1 = n \int_V \Delta^4(\boldsymbol{\eta}, t)\,\mathrm{d}V_{\boldsymbol{\eta}} \tag{5}$$

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and the ratio

$$\frac{\langle r^4\rangle_N}{\langle r^2\rangle_N^2} = \frac{1}{n}\,\frac{\int_V \Delta^4(\boldsymbol{\eta},t)\,\mathrm{d}V_{\boldsymbol{\eta}}}{\left(\int_V \Delta^2(\boldsymbol{\eta},t)\,\mathrm{d}V_{\boldsymbol{\eta}}\right)^2} \sim (\ell/\lambda)\;\phi^{-1}. \tag{6}$$

Thus small ϕ leads to slower convergence to Gaussian, but large λ 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:

$$p_1(x,t) = \int_{-\infty}^{\infty} p_1(\boldsymbol{r},t)\,\mathrm{d}y = \int_V \int_{-\infty}^{\infty} \frac{1}{2\pi r}\,\delta(r - \Delta(\boldsymbol{\eta},t))\,\mathrm{d}y\,\frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}. \tag{7}$$

Since $r^2 = x^2 + y^2$, the δ-function will capture two values of y, and with the Jacobian included we obtain

$$p_1(x,t) = \frac{1}{\pi}\int_V \frac{1}{\sqrt{\Delta^2(\boldsymbol{\eta},t) - x^2}}\,[\Delta(\boldsymbol{\eta},t) > |x|]\,\frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}\,, \tag{8}$$

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 $d = 3$:

$$p_1(x,t) = \tfrac{1}{2}\int_V \frac{1}{\Delta(\boldsymbol{\eta},t)}\;[\Delta(\boldsymbol{\eta},t) > |x|]\;\frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}. \tag{9}$$

For summing the displacements due to multiple swimmers, we need the characteristic function of $p_1(x,t)$, defined by the Fourier transform

$$\langle \mathrm{e}^{\mathrm{i}kx}\rangle_1 = \int_{-\infty}^{\infty} p_1(x,t)\,\mathrm{e}^{\mathrm{i}kx}\,\mathrm{d}x. \tag{10}$$

For the three-dimensional pdf (9), the characteristic function is

$$\begin{aligned}
\langle \mathrm{e}^{\mathrm{i}kx}\rangle_1 &= \tfrac{1}{2}\int_V \frac{1}{\Delta(\boldsymbol{\eta},t)}\int_{-\infty}^{\infty}[\Delta(\boldsymbol{\eta},t) > |x|]\;\mathrm{e}^{\mathrm{i}kx}\,\mathrm{d}x\,\frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}\\
&= \tfrac{1}{2}\int_V \frac{1}{\Delta(\boldsymbol{\eta},t)}\int_{-\Delta}^{\Delta}\mathrm{e}^{\mathrm{i}kx}\,\mathrm{d}x\,\frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}\\
&= \int_V \operatorname{sinc}\left(k\Delta(\boldsymbol{\eta},t)\right)\frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}
\end{aligned}$$

where $\operatorname{sinc} x := x^{-1}\sin x$ for $x \neq 0$, and $\operatorname{sinc} 0 := 1$. For the two-dimensional pdf (8), we have

$$\langle \mathrm{e}^{\mathrm{i}kx}\rangle_1 = \int_V J_0(k\Delta(\boldsymbol{\eta},t))\,\frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V} \tag{11}$$

where $J_0(x)$ is a Bessel function of the first kind.

We define (see Fig. 1)

$$\gamma_d(x) := \begin{cases} 1 - J_0(x), & d = 2;\\ 1 - \operatorname{sinc} x, & d = 3, \end{cases} \tag{12}$$

and write the two cases for the characteristic function together as

$$\langle \mathrm{e}^{\mathrm{i}kx}\rangle_1 = 1 - \Gamma_d(k,t)/V. \tag{13}$$

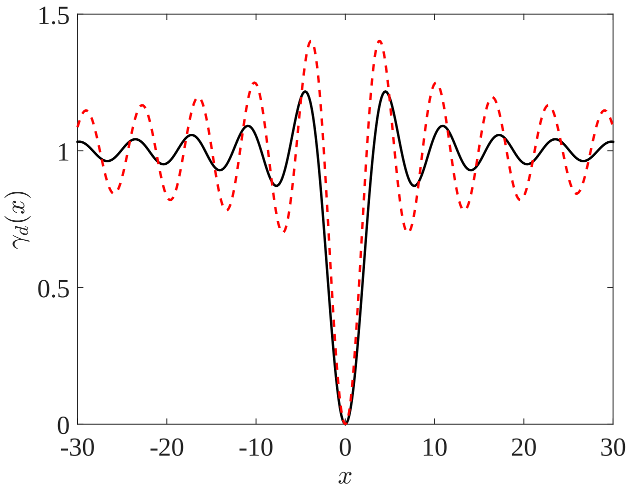

FIG. 1. The function $\gamma_d(x)$ defined by (12) for $d = 3$ (solid) and $d = 2$ (dashed).

where

$$\Gamma_d(k,t) := \int_V \gamma_d(k\Delta(\boldsymbol{\eta},t))\,\mathrm{d}V_{\boldsymbol{\eta}}\,. \tag{14}$$

We have $\gamma_d(0) = \gamma_d'(0) = 0$, $\gamma_d''(0) = 1/d$, so $\gamma_d(\xi) \sim (1/2d)\,\xi^2 + \mathrm{O}(\xi^4)$ 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 $y(\varepsilon) \sim \mathrm{o}(\varepsilon^{-M/(M+1)})$ as $\varepsilon \to 0$ for an integer $M \geq 1$; then*

$$(1 - \varepsilon y(\varepsilon))^{1/\varepsilon} = \exp\biggl(-\sum_{m=1}^{M} \frac{\varepsilon^{m-1} y^m(\varepsilon)}{m}\biggr)\left(1 + \mathrm{o}(\varepsilon^0)\right), \quad \varepsilon \to 0. \tag{15}$$

Proof. Observe that $\varepsilon y(\varepsilon) \sim \mathrm{o}(\varepsilon^{1/(M+1)}) \to 0$ as $\varepsilon \to 0$. Writing $(1 - \varepsilon y)^{1/\varepsilon} = \mathrm{e}^{\varepsilon^{-1}\log(1-\varepsilon y)}$, we expand the exponent as a convergent Taylor series:

$$\begin{aligned}
(1 - \varepsilon y)^{1/\varepsilon} &= \exp\biggl(-\varepsilon^{-1}\sum_{m=1}^{\infty}\frac{(\varepsilon y)^m}{m}\biggr) \quad (\text{converges since } \varepsilon y \sim \mathrm{o}(\varepsilon^{1/(M+1)}))\\
&= \exp\biggl(-\varepsilon^{-1}\biggl(\sum_{m=1}^{M}\frac{(\varepsilon y)^m}{m} + \mathrm{O}((\varepsilon y)^{M+1})\biggr)\biggr)\\
&= \exp\biggl(-\varepsilon^{-1}\sum_{m=1}^{M}\frac{(\varepsilon y)^m}{m}\biggr)\exp\left(\mathrm{O}(\varepsilon^M y^{M+1})\right)\\
&= \exp\biggl(-\varepsilon^{-1}\sum_{m=1}^{M}\frac{(\varepsilon y)^m}{m}\biggr)\left(1 + \mathrm{o}(\varepsilon^0)\right). \qquad \square
\end{aligned}$$

Since we are summing their independent displacements, the characteristic function for N swimmers is $\langle \mathrm{e}^{\mathrm{i}kx}\rangle_N = \langle \mathrm{e}^{\mathrm{i}kx}\rangle_1^N$. From (13),

$$\langle \mathrm{e}^{\mathrm{i}kx}\rangle_1^N = \left(1 - \Gamma_d(k,t)/V\right)^{nV}, \tag{16}$$

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

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

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 $\mathrm{O}(V)$, 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

$$\langle \mathrm{e}^{\mathrm{i}kx} \rangle_1^N = (1 - \Gamma_d(k,t)/V)^{nV} \sim \exp\left(-n\,\Gamma_d(k,t)\right), \quad V \to \infty. \tag{18}$$

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 ∞, 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

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

Wavenumbers $|k| > k_{\max}$ 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

$$p_N(x,t) = \frac{1}{2\pi}\int_{-\infty}^{\infty} \exp\left(-n\,\Gamma_d(k,t)\right) \mathrm{e}^{-\mathrm{i}kx}\,\mathrm{d}k. \tag{20}$$

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

$$\begin{aligned}\Gamma_d(k,t) &= \int_{V_{\text{swept}}} \gamma_d(k\Delta(\boldsymbol{\eta},t))\,\mathrm{d}V_{\boldsymbol{\eta}} \\ &= V_{\text{swept}} - \int_{V_{\text{swept}}} (1 - \gamma_d(k\Delta(\boldsymbol{\eta},t)))\,\mathrm{d}V_{\boldsymbol{\eta}} \\ &= V_{\text{swept}}\,(1 - \mathcal{W}_d(k,t))\end{aligned}$$

where

$$\mathcal{W}_d(k,t) = \frac{1}{V_{\text{swept}}}\int_{V_{\text{swept}}} (1 - \gamma_d(k\Delta(\boldsymbol{\eta},t)))\,\mathrm{d}V_{\boldsymbol{\eta}}\,. \tag{21}$$

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

$$p_N(x,t) = \sum_{m=0}^{\infty} \frac{\phi_{\text{swept}}^m}{m!}\,\mathrm{e}^{-\phi_{\text{swept}}}\,\frac{1}{2\pi}\int_{-\infty}^{\infty} \mathcal{W}_d^m(k,t)\,\mathrm{e}^{-\mathrm{i}kx}\,\mathrm{d}k. \tag{22}$$

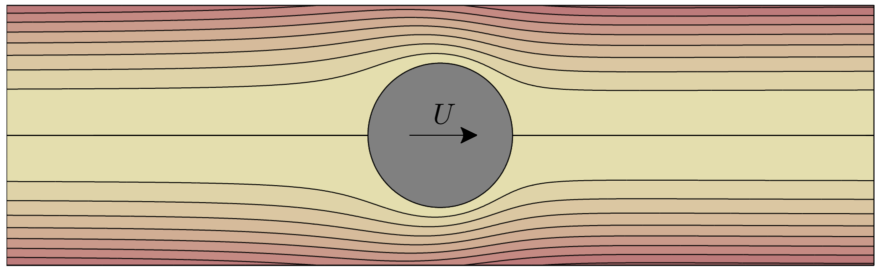

FIG. 2. Contour lines for the axisymmetric streamfunction of a squirmer of the form (23), with $\beta = 0.5$. This swimmer is of the puller type, as for *C. reinhardtii*.

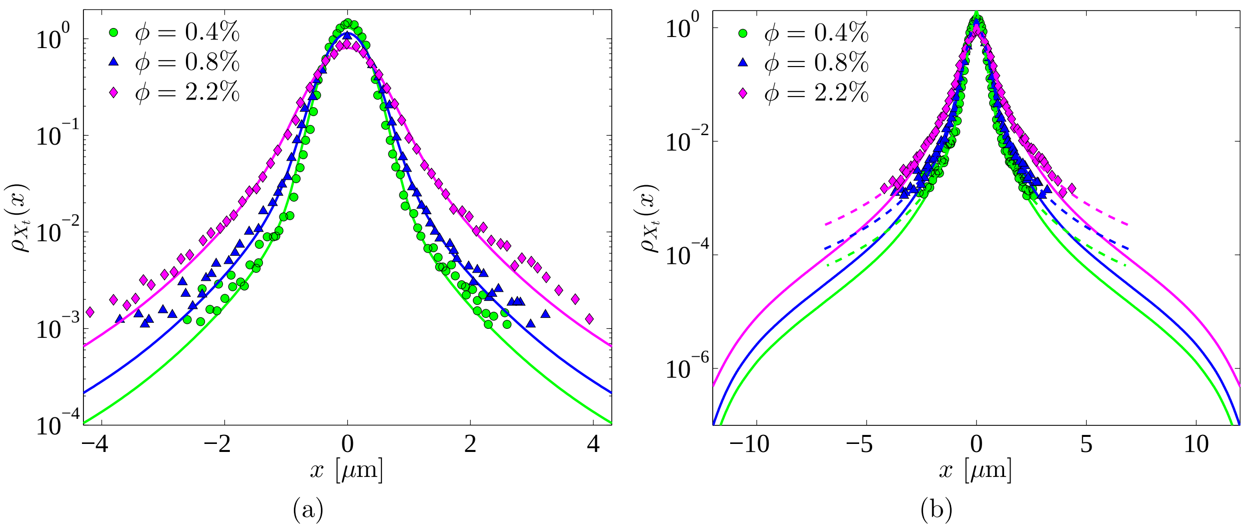

FIG. 3. (a) The pdf of particle displacements after a time $t = 0.12\,\mathrm{s}$, for several values of the volume fraction ϕ. The data is from Leptos *et al.* [6], and the figure should be compared to their Fig. 2(a). (b) Same as (a) but on a wider scale, also showing the form suggested by Eckhardt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

The factor $\phi_{\mathrm{swept}}^m\,\mathrm{e}^{-\phi_{\mathrm{swept}}}/m!$ 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]

$$\Psi_{\mathrm{sf}}(\rho, z) = \tfrac{1}{2}\rho^2\, U \left\{ -1 + \frac{\ell^3}{(\rho^2 + z^2)^{3/2}} + \tfrac{3}{2}\frac{\beta \ell^2 z}{(\rho^2 + z^2)^{3/2}} \left(\frac{\ell^2}{\rho^2 + z^2} - 1 \right) \right\} \tag{23}$$

in a frame moving at speed U. Here z is the swimming direction and ρ is the distance from the z axis. To mimic *C. reinhardtii*, we use $\ell = 5\,\mu\mathrm{m}$ and $U = 100\,\mu\mathrm{m/s}$. 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 β 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

Leptos *et al.* [6]. 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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