How swimming microorganisms displace fluid particles

Jean-Luc Thiffeault

Department of Mathematics
University of Wisconsin – Madison

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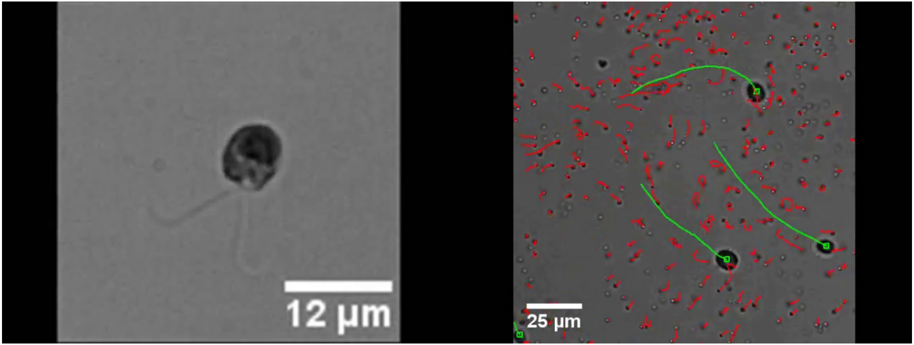
Chlamydomonas reinhardtii

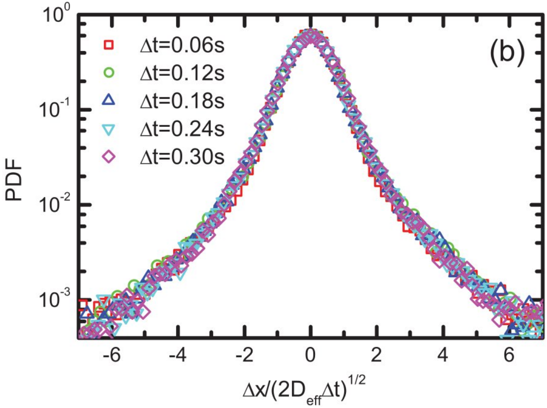


play movie

[Guasto, J. S., Johnson, K. A., & Gollub, J. P. (2010). *Phys. Rev. Lett.* **105**, 168102]

Probability density of displacements

Non-Gaussian PDF with 'exponential' tails:



[Leptos, K. C., Guasto, J. S., Gollub, J. P., Pesci, A. I., & Goldstein, R. E. (2009). *Phys. Rev. Lett.* **103**, 198103]

Probability density of displacements

Leptos *et al.* (2009) get a reasonable fit of their PDF with the form

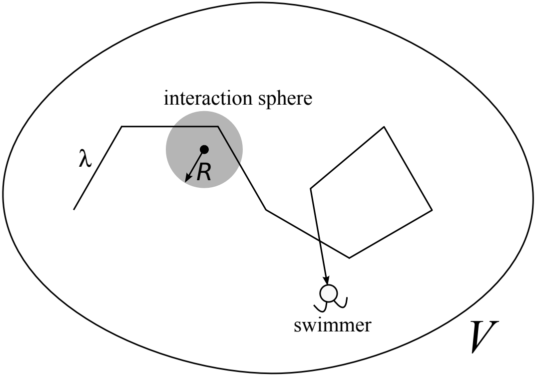
$$\mathbb{P}\{X_t \in [x, x + \mathrm{d}x]\} = \frac{1-f}{\sqrt{2\pi\delta_{\mathrm{g}}^2}}\,\mathrm{e}^{-x^2/2\delta_{\mathrm{g}}^2} + \frac{f}{2\delta_{\mathrm{e}}}\,\mathrm{e}^{-|x|/\delta_{\mathrm{e}}}.$$

They observe the scalings $\delta_{\mathrm{g}} \approx A_{\mathrm{g}} t^{1/2}$ and $\delta_{\mathrm{e}} \approx A_{\mathrm{e}} t^{1/2}$, where A_{g} and A_{e} depend on the volume fraction ϕ.

They call this a diffusive scaling, since $X_t/t^{1/2}$ is a scaling variable. Their point is that this is strange, since the distribution is not Gaussian.

Commonly observed in diffusive processes that are a combination of trapped and hopping dynamics (Wang *et al.*, 2012).

Modeling: the interaction sphere



Model for effective diffusivity:

[Thiffeault, J.-L. & Childress, S. (2010). *Phys. Lett. A*, **374**, 3487–3490]

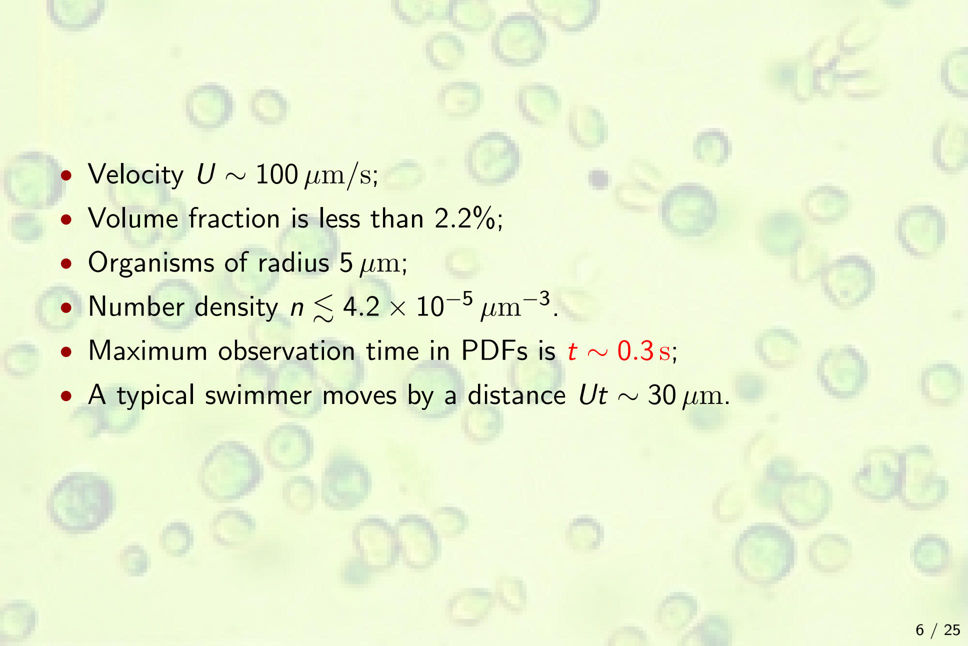
[Lin, Z., Thiffeault, J.-L., & Childress, S. (2011). *J. Fluid Mech.* **669**, 167–177]

Expected number of 'dings' (close interactions) after time t:

$$\langle M_t \rangle = n \left\{ V_{\text{swept}}(R,\lambda)\,(t/\tau) + V_{\text{sph}}(R) \right\}$$

n is the number density of swimmers, V_{swept} is the volume swept by the sphere of radius R moving a distance λ, and τ is the time between turns.

Parameters in the Leptos *et al.* experiment



- Velocity $U \sim 100\,\mu\mathrm{m/s}$;
- Volume fraction is less than 2.2%;
- Organisms of radius $5\,\mu\mathrm{m}$;
- Number density $n \lesssim 4.2 \times 10^{-5}\,\mu\mathrm{m}^{-3}$.
- Maximum observation time in PDFs is $t \sim 0.3\,\mathrm{s}$;
- A typical swimmer moves by a distance $Ut \sim 30\,\mu\mathrm{m}$.

Close encounters of the first kind

Combining this, we find the expected number of ‘dings’ after time t in the Leptos *et al.* experiment:

$$\boxed{\langle M_t \rangle \lesssim 0.6}$$

for the longest observation time, and interaction sphere $R = 10\,\mu\mathrm{m}$.

Conclude: a typical fluid particle is only strongly affected by about one swimmer during the experiment.

The only displacements that a particle feels ‘often’ are the very small ones due to all the distant swimmers.

We thus expect the displacement PDF to have a central Gaussian core (since the central limit theorem will apply for the small displacements), but strongly non-Gaussian tails.

Probability of displacements

- X_t is the displacement of a particle after a time t;
- X_m is the displacement of a particle after m encounters;
- But the number of encounters is a random variable M_t.
- How do we relate the two?

$$\begin{aligned}
\mathbb{P}\{X_t \in [x, x + \mathrm{d}x]\} &= \sum_{m=0}^{\infty} \mathbb{P}\{X_t \in [x, x + \mathrm{d}x]\,,\, M_t = m\} \\
&= \sum_{m=0}^{\infty} \mathbb{P}\{X_t \in [x, x + \mathrm{d}x] \,|\, M_t = m\}\, \mathbb{P}\{M_t = m\} \\
&= \sum_{m=0}^{\infty} \mathbb{P}\{X_m \in [x, x + \mathrm{d}x]\}\, \mathbb{P}\{M_t = m\}
\end{aligned}$$

Probability of encounters

When the volume is large, the number of interactions obeys a Poisson distribution:

$$\mathbb{P}\{M_t = m\} \simeq \frac{1}{m!} \langle M_t \rangle^m \, \mathrm{e}^{-\langle M_t \rangle}$$

We define the probability densities:

$$\rho_{X_m}(x) \, \mathrm{d}x := \mathbb{P}\{X_m \in [x, x + dx]\}$$

$$\rho_{X_t}(x) \, \mathrm{d}x := \mathbb{P}\{X_t \in [x, x + dx]\}$$

From previous slide:

$$\rho_{X_t}(x) = \sum_{m=0}^{\infty} \rho_{X_m}(x) \, \mathbb{P}\{M_t = m\}$$

Small number of interactions

Normally we would now go to the large m limit and use large-deviation theory. But this doesn't hold here. Instead, keep only $m \leq 1$,

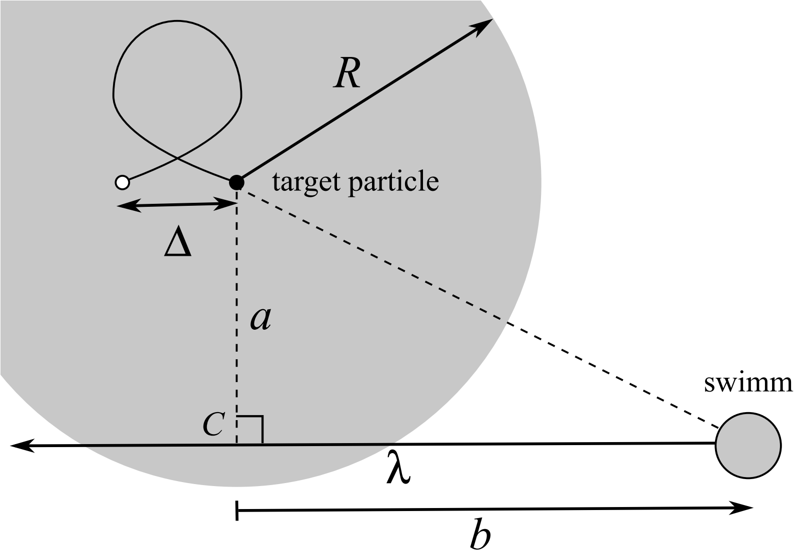
$$\begin{aligned}\rho_{X_t}(x) &= \sum_{m=0}^{\infty} \rho_{X_m}(x)\,\mathbb{P}\{M_t = m\} \\ &\simeq \mathbb{P}\{M_t = 0\}\,\rho_{X_0}(x) + \mathbb{P}\{M_t = 1\}\,\rho_{X_1}(x) + \dots\end{aligned}$$

i.e., most fluid particles feel only a few close encounters with swimmers.

$\rho_{X_0}(x)$ is due to thermal noise (or the combined effect of distant swimmers), so is Gaussian.

$\rho_{X_1}(x)$ is the displacement probability after one close interaction with a swimmer, which has strongly non-Gaussian tails.

Geometry of an encounter



The single-encounter probability $\rho_{X_1}(x)$

We can show that (Thiffeault, 2014)

$$\rho_{X_1}(x) = \tfrac{1}{2} \int_{\Omega_{ab}} \frac{\rho_{AB}(a,b)}{\Delta_\lambda(a,b)}\, \chi_{\{\Delta_\lambda > |x|\}}(a,b)\,\mathrm{d}a\,\mathrm{d}b,$$

where

- a and b are the impact parameters that describe the geometry of an encounter;
- Δ_λ is the drift function;
- χ is an indicator function (i.e., 0 or 1);
- $\rho_{AB}(a,b) = 2\pi a / V_{\text{swept}}(R,\lambda)$ is the probability density of the random impact parameters A and B.

The drift function is computed (laboriously) by integrating over fluid trajectories.

[Thiffeault, J.-L. (2014). arXiv:1408.4781]

More encounters

What about the density function for two encounters, $\rho_{X_2}(x)$?

Since X_2 is the sum of two i.i.d. random variables X_1, its PDF is just the convolution of $\rho_{X_1}(x)$ with itself:

$$\rho_{X_2}(x) = \int_{-\infty}^{\infty} \rho_{X_1}(x-y)\,\rho_{X_1}(y)\,\mathrm{d}y =: (\rho_{X_1} * \rho_{X_1})(x).$$

For m steps we have $\rho_{X_m}(x) = (\rho_{X_1} * \cdots * \rho_{X_1})(x)$.

[The central limit theorem / large deviation theory give estimates of this convolution for large m.]

A model swimmer

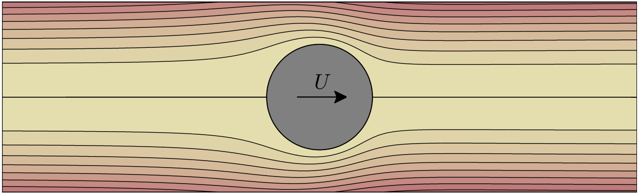
This is as far as we can go without introducing a model swimmer.

We take a squirmer, with axisymmetric streamfunction:

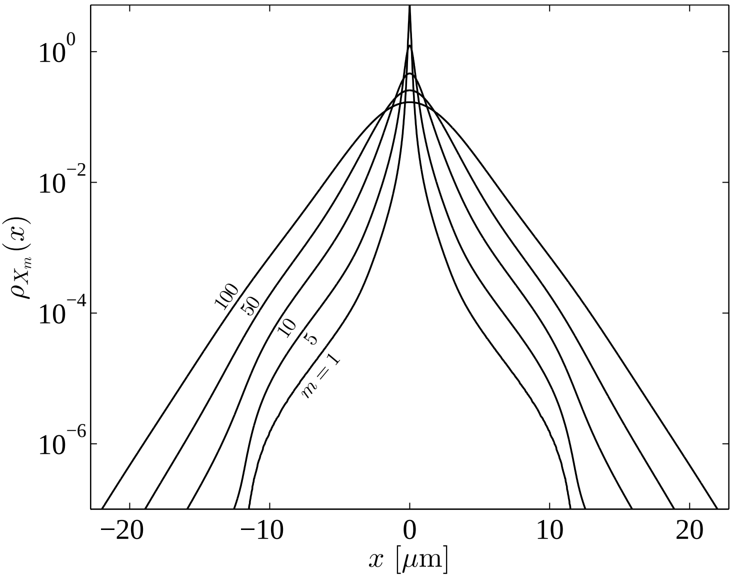
$$\Psi_{\mathsf{sf}}(\rho, z) = \tfrac{1}{2}\rho^2\, U \left\{ -1 + \frac{\ell^3}{(\rho^2 + z^2)^{3/2}} + \tfrac{3}{2}\frac{\beta\ell^2 z}{(\rho^2 + z^2)^{3/2}} \left(\frac{\ell^2}{\rho^2 + z^2} - 1 \right) \right\}$$

[See for example Lighthill (1952); Blake (1971); Ishikawa *et al.* (2006); Ishikawa & Pedley (2007b); Drescher *et al.* (2009)]

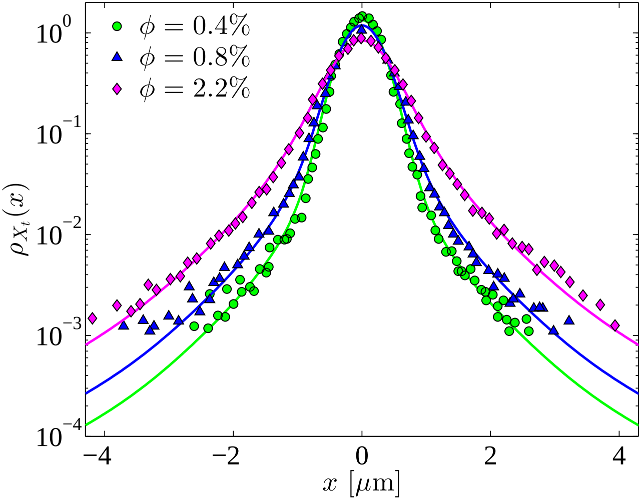
We use the stresslet strength $\beta = 0.6$, which is close to a treadmiller:



$\rho_{X_m}(x)$ for the squirmer



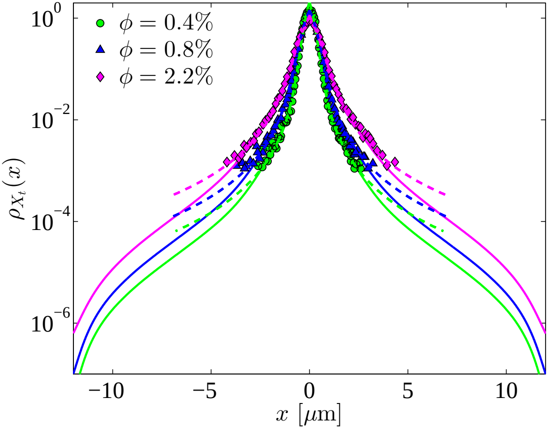
Comparing to Leptos *et al.*



The only fitted parameter is the stresslet strength $\beta = 0.6$.

Comparing to Eckhardt & Zammert

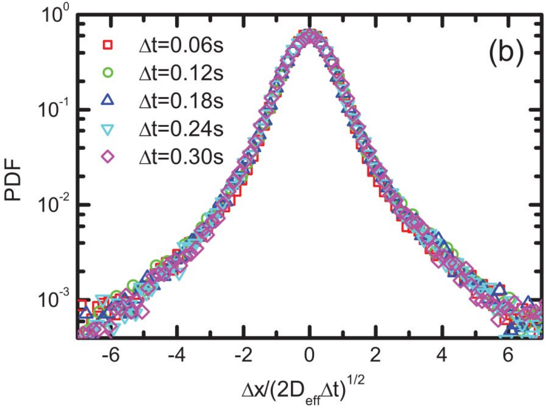
Eckhardt & Zammert (2012) have a beautiful fit to the data based on a phenomenological continuous-time random walk model (dashed):



Our models disagree in the tails, but there is no data there.

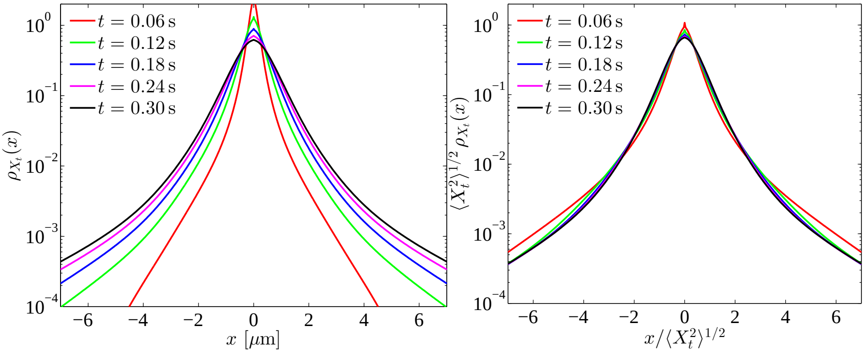
The diffusive scaling

What about the ‘diffusive scaling’ mentioned at the start?



The diffusive scaling: model

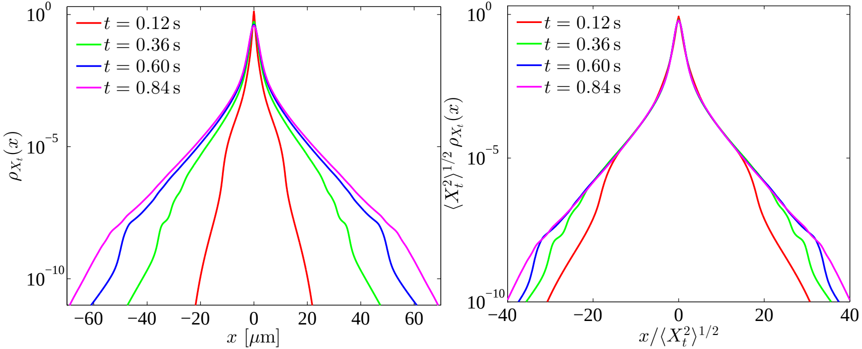
It’s present in our model as well:



(Earlier times are a bit worse.)

The diffusive scaling: tails

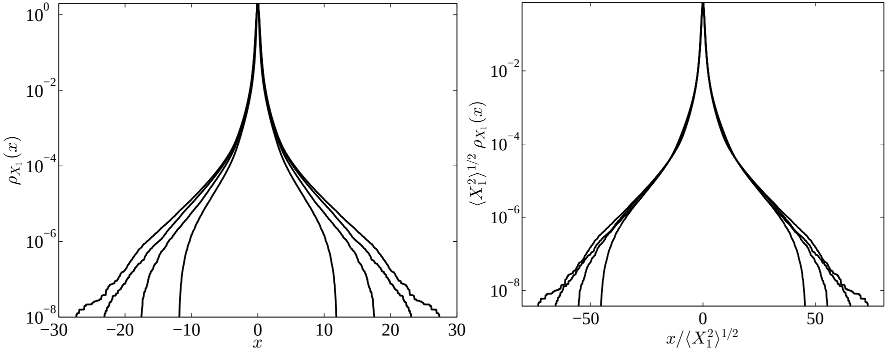
It persists (except for cut-off) further in the tails:



Note that the times are still short enough that the organisms don't have time to turn.

The diffusive scaling: single encounter

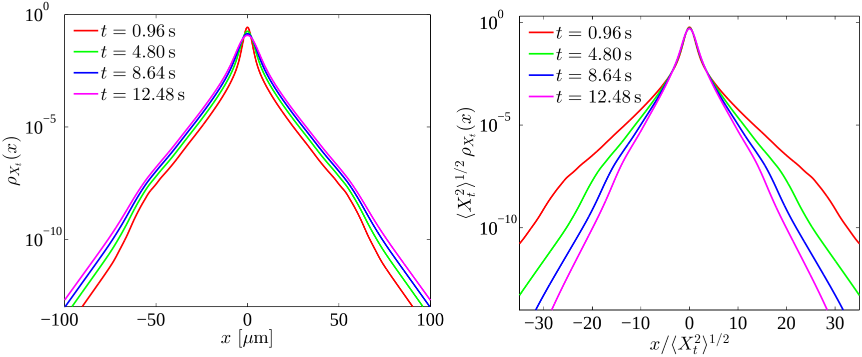
Appears to hold for a single encounter, for $\rho_{X_1}(x)$:



This means the scaling is not really statistical in nature: it's a property of the drift function Δ_λ itself for this type of swimmer.

The diffusive scaling: reorientation

If we go further in time and allow the organisms to reorient, the scaling seems to disappear completely:



Conclusions

- Times in Leptos *et al.* (2009) are so short that the tails are not determined by asymptotic laws, such as the central limit theorem or large-deviation theory.
- Retaining only 0 and 1 close interactions gives a linear combination of a Gaussian and a distribution with non-Gaussian tails, as observed by Leptos *et al.* (2009).
- The Gaussian core arises because of the net effect of the distant swimmers, far from the test particle.
- Preprint: `http://arxiv.org/abs/1408.4781`.

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