Particle displacements by swimming organisms

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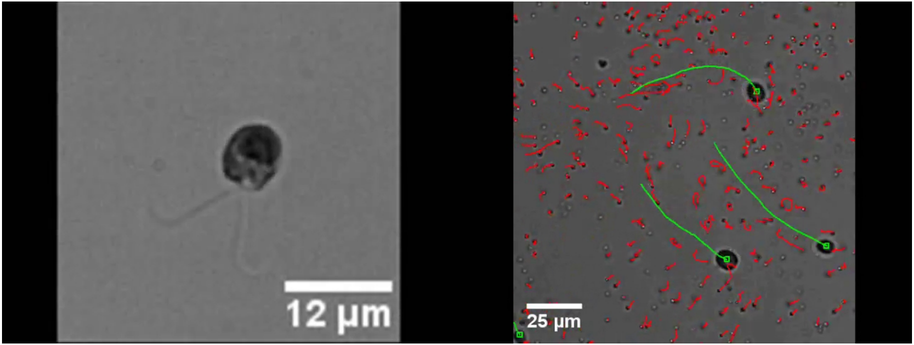
Chlamydomonas reinhardtii

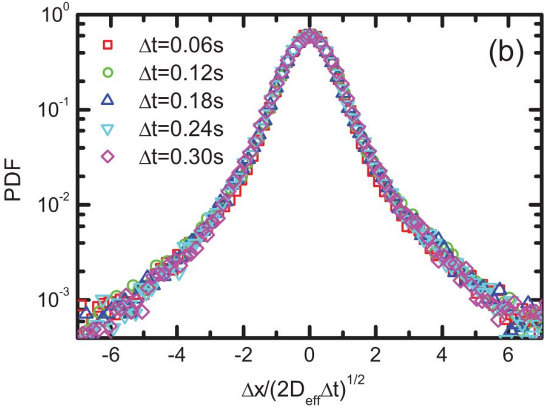


play movie

[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

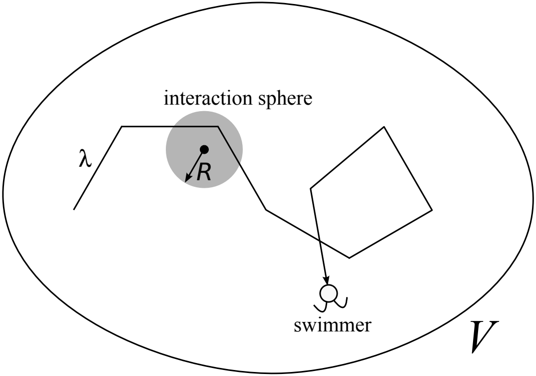
$$\mathbb{P}\{X_t \in [x, x + \mathrm{d}x]\} = \frac{1-f}{\sqrt{2\pi\delta_{\mathrm{g}}^2}}\,\mathrm{e}^{-x^2/2\delta_{\mathrm{g}}^2} + \frac{f}{2\delta_{\mathrm{e}}}\,\mathrm{e}^{-|x|/\delta_{\mathrm{e}}}.$$

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:

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

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 $m \leq 1$,

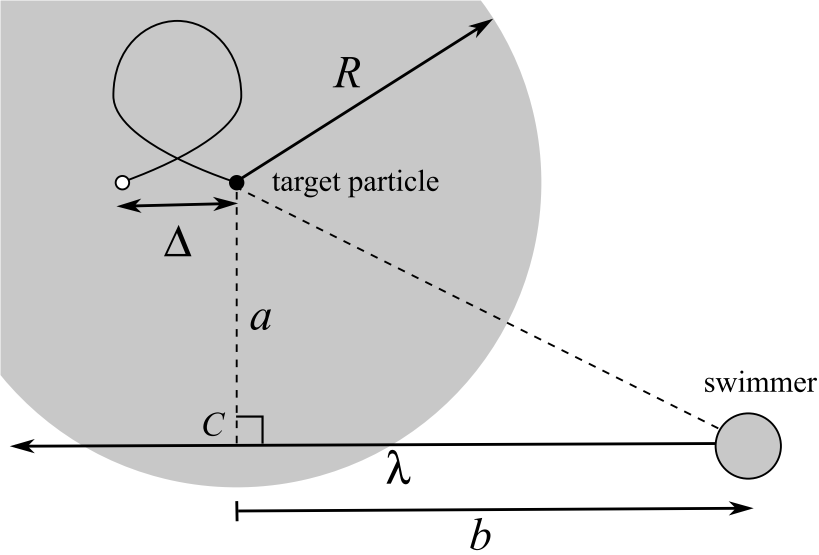
$$\rho_{X_t}(x) = \sum_{m=0}^{\infty} \rho_{X_m}(x)\, \mathbb{P}\{M_t = m\}$$
$$\simeq \mathbb{P}\{M_t = 0\}\, \rho_{X_0}(x) + \mathbb{P}\{M_t = 1\}\, \rho_{X_1}(x) + \dots$$

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

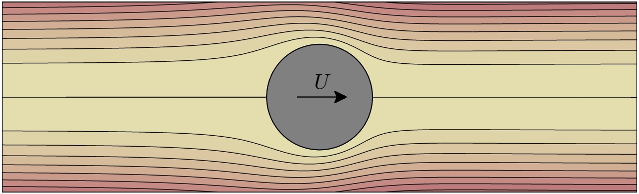
This is as far as we can go without introducing a model swimmer.

We take a squirmer, with axisymmetric streamfunction:

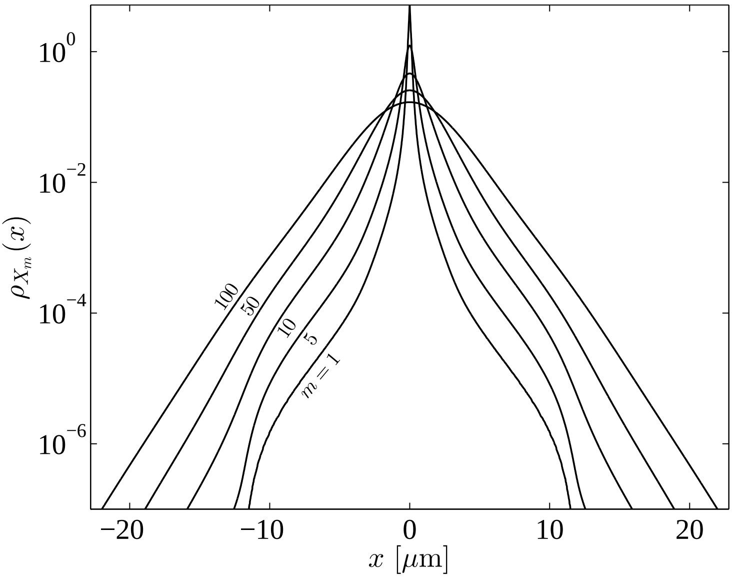
$$\Psi_{\mathrm{sf}}(\rho, z) = \tfrac{1}{2}\rho^2\, U \left\{ -1 + \frac{\ell^3}{(\rho^2+z^2)^{3/2}} + \tfrac{3}{2}\frac{\beta\ell^2 z}{(\rho^2+z^2)^{3/2}}\left(\frac{\ell^2}{\rho^2+z^2} - 1\right)\right\}$$

[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:

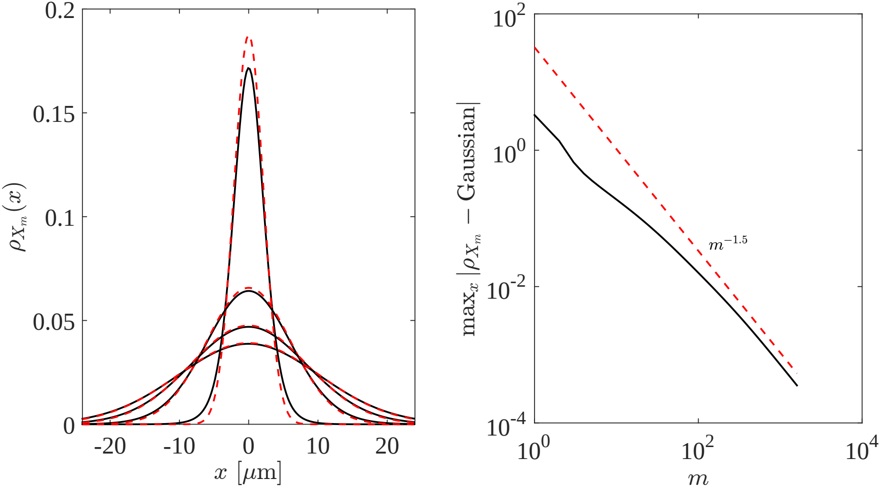


$\rho_{X_m}(x)$ for the squirmer



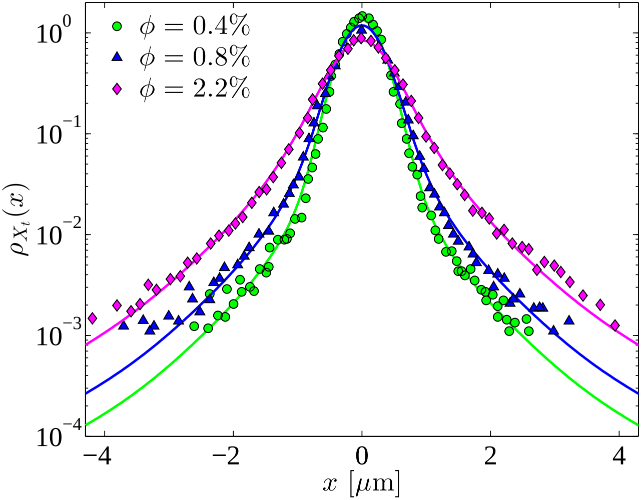
Convergence to Gaussian

The Central Limit Theorem is satisfied: the absolute error decays with m.



The tails may look non-Gaussian, but they barely contribute to the error.

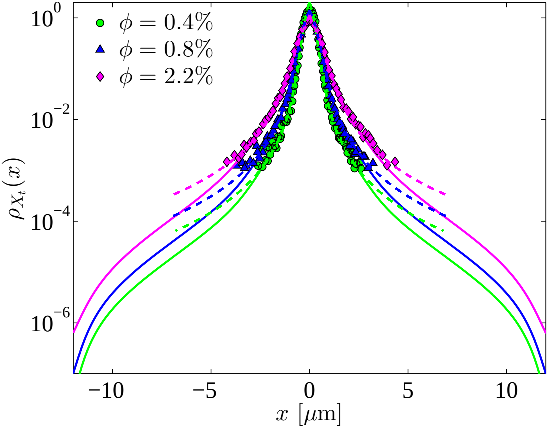
Comparing to Leptos *et al.*



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

Comparing to Eckhardt & Zammert

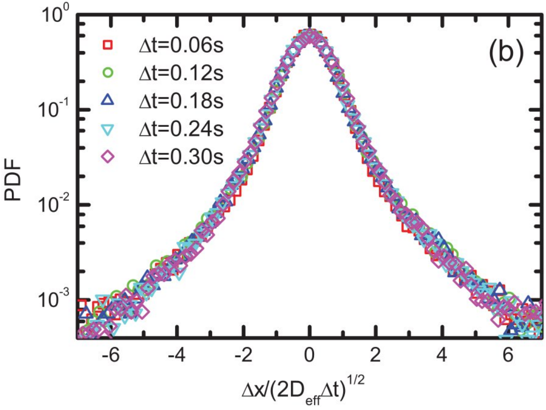
Eckhardt & Zammert (2012) have a beautiful fit to the data based on a phenomenological continuous-time random walk model (dashed):



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

The diffusive scaling

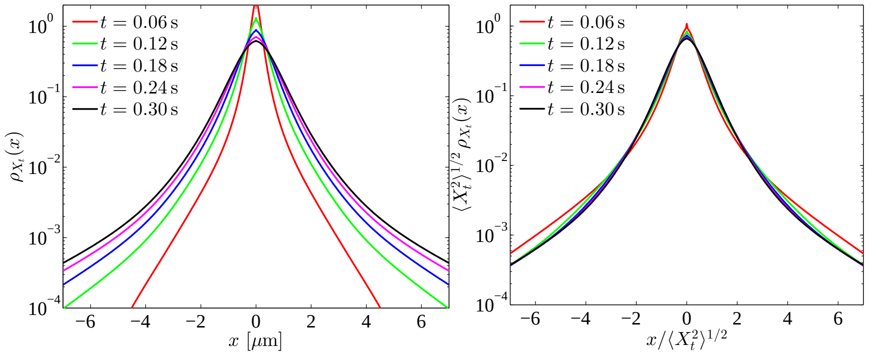
What about the 'diffusive scaling' mentioned at the start?



Note the red squares (early times) are on the inside center.

The diffusive scaling: model

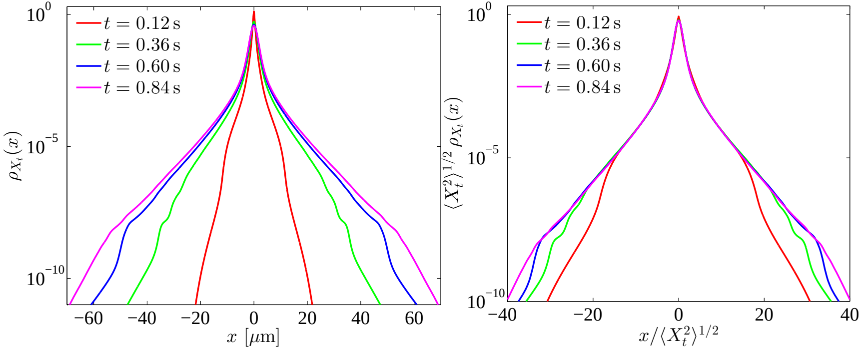
It's present in our model as well (no noise, so more peaked):



(Scaling a bit worse at early times, but this is consistent with experiment.)

The diffusive scaling: tails

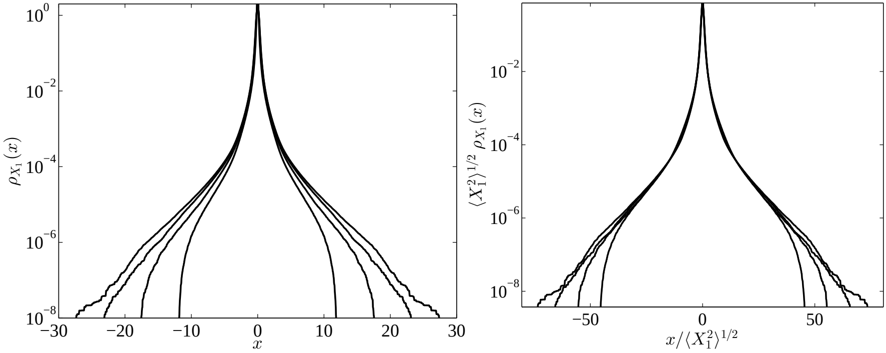
Scaling persists (except for cut-off) further in the tails:



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

The diffusive scaling: single encounter

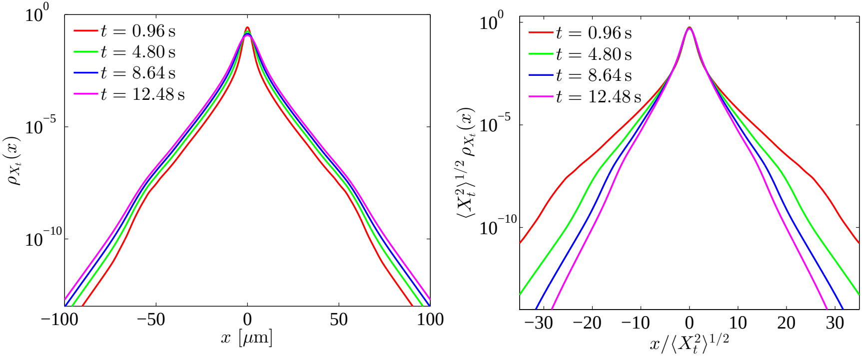
Appears to hold for a single encounter, for $\rho_{X_1}(x)$:



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 posited by Leptos *et al.* (2009).
- The Gaussian core arises because of the net effect of the distant swimmers, far from the test particle.
- With re-orientation (tumbling, etc.), the diffusive scaling seems to disappear. Longer experiments would be great...
- Preprint: `http://arxiv.org/abs/1408.4781`.

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