Particle displacements by swimming organisms

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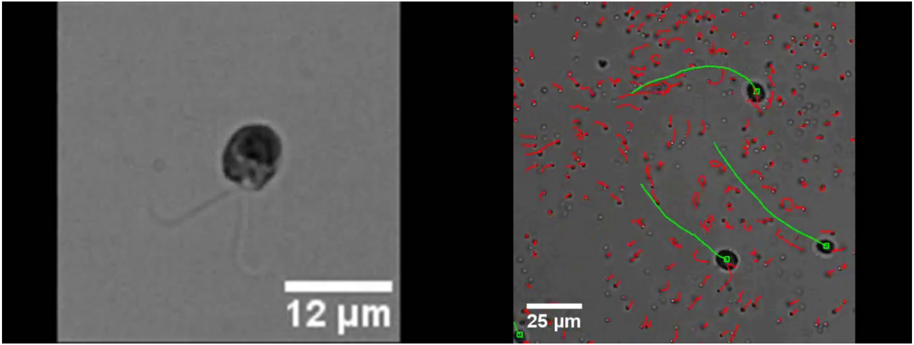
Mathematics Seminar, University of Exeter
20 April 2015

Supported by NSF grant DMS-1109315

Chlamydomonas reinhardtii



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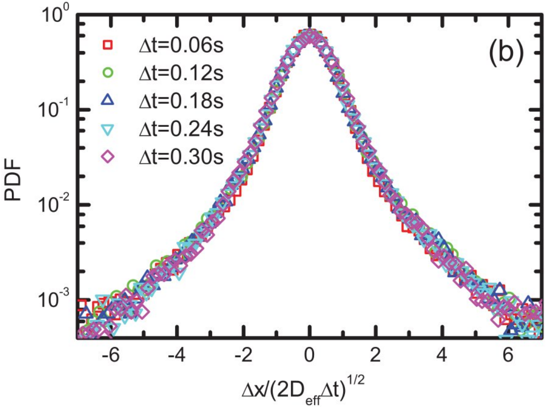
[Guasto, J. S., Johnson, K. A., & Gollub, J. P. (2010). *Phys. Rev. Lett.* **105**, 168102]

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

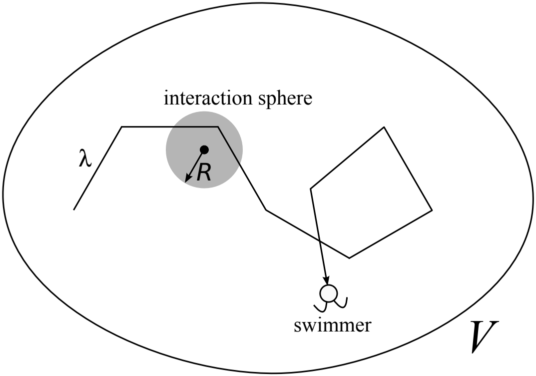
$$\mathbb{P}\{X_t \in [x, x + \mathrm{d}x]\} = \frac{1-f}{\sqrt{2\pi\delta_{\mathrm{g}}^2}}\,\mathrm{e}^{-x^2/2\delta_{\mathrm{g}}^2} + \frac{f}{2\delta_{\mathrm{e}}}\,\mathrm{e}^{-|x|/\delta_{\mathrm{e}}}.$$

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 unusual, 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 distance λ:

$$(\text{number density}) \times (\text{volume carved out by swimmer}) = n\,\lambda\,\pi R^2$$

n is the number density of swimmers.

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 $\lambda = Ut \sim 30\,\mu\mathrm{m}$.

Close encounters of the first kind

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

$$\boxed{n\lambda\,\pi R^2 \lesssim 0.4}$$

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 density of displacements for a swimmer

Finite-path drift function $\boldsymbol{\Delta}_\lambda(\boldsymbol{\eta})$ for a fluid particle, initially at $\mathbf{x} = \boldsymbol{\eta}$, affected by a single swimmer:

$$\boldsymbol{\Delta}_\lambda(\boldsymbol{\eta}) = \int_0^{\lambda/U} \mathbf{u}(\mathbf{x}(s) - \mathbf{U}s)\,\mathrm{d}s, \qquad \dot{\mathbf{x}} = \mathbf{u}(\mathbf{x} - \mathbf{U}t), \quad \mathbf{x}(0) = \boldsymbol{\eta}\,.$$

Assuming homogeneity and isotropy, we obtain the probability density of displacements,

$$p_{\mathbf{R}_\lambda^1}(\mathbf{r}) = \frac{1}{\Omega\, r^{d-1}} \int_V \delta(r - \Delta_\lambda(\boldsymbol{\eta}))\,\frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}$$

where $\Omega = \Omega(d)$ is the area of the unit sphere in d dimensions.

Here $\mathbf{R}_\lambda^1$ is a random variable that gives the displacement of the particle from its initial position after being affected by a single swimmer with path length λ.

Variance

The second moment (variance) of $\mathbf{R}_\lambda^1$ is

$$\langle (R_\lambda^1)^2 \rangle = \int_V r^2 \, p_{\mathbf{R}_\lambda^1}(\mathbf{r}) \, \mathrm{d}V_{\mathbf{r}} = \int_V \Delta_\lambda^2(\boldsymbol{\eta}) \, \frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}.$$

Let $\mathbf{R}_\lambda^N$ be the random particle displacement due to N swimmers;

$$\langle (R_\lambda^N)^2 \rangle = N \langle (R_\lambda^1)^2 \rangle = n \int_V \Delta_\lambda^2(\boldsymbol{\eta}) \, \mathrm{d}V_{\boldsymbol{\eta}}$$

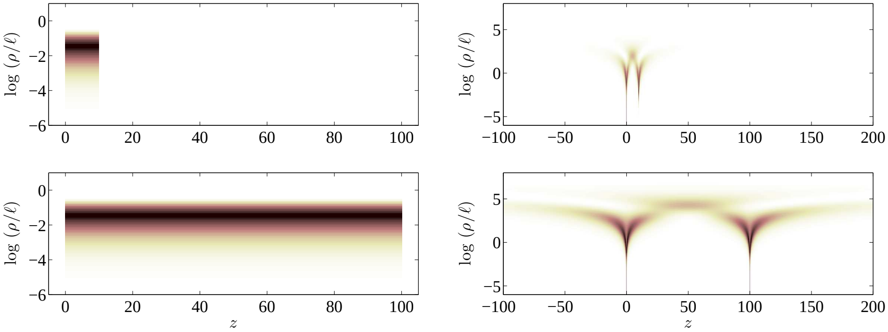
with $n = N/V$ the number density of swimmers.

Crucial point:

If the integral grows linearly in λ, then the particle motion is diffusive.

Two ways to get diffusive behavior

Plot of the integrand:



Left: support grows linearly with λ (typical of near-field). [Thiffeault & Childress (2010)]

Right: 'uncanny scaling' $\Delta_\lambda(\boldsymbol{\eta}) = \lambda^{-1} D(\boldsymbol{\eta}/\lambda)$ (typical of far-field stresslet). [Lin *et al.* (2011); Pushkin & Yeomans (2013)]

Probability density for x displacement

We integrate over y and z to get the pdf for one coordinate x only:

$$p_{X_\lambda^1}(x) = \tfrac{1}{2} \int_V \frac{1}{\Delta_\lambda(\boldsymbol{\eta})} \left[\Delta_\lambda(\boldsymbol{\eta}) > |x|\right] \frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}$$

where $[A]$ is an indicator function: it is 1 if A is satisfied, 0 otherwise.

Now we want $p_{X_\lambda^N}(x)$, the pdf for N swimmers. The road to this is through the characteristic function:

$$\langle \mathrm{e}^{\mathrm{i}kX_\lambda^1} \rangle = \int_{-\infty}^{\infty} p_{X_\lambda^1}(x)\, \mathrm{e}^{\mathrm{i}kx}\, \mathrm{d}x = \int_V \operatorname{sinc}\left(k\Delta_\lambda(\boldsymbol{\eta})\right) \frac{\mathrm{d}V_{\boldsymbol{\eta}}}{V}$$

where $\operatorname{sinc} x := x^{-1} \sin x$.

(In 2D, replace sinc by Bessel function $J_0(x)$.)

Characteristic function

To help integrals converge nicely later, it is better to work with

$$\gamma(x) := 1 - \operatorname{sinc} x.$$

Then,

$$\langle \mathrm{e}^{\mathrm{i}kX_\lambda^1} \rangle = 1 - (v_\lambda / V)\, \Gamma_\lambda(k)$$

where

$$\boxed{\Gamma_\lambda(k) := \frac{1}{v_\lambda} \int_V \gamma(k\Delta_\lambda(\boldsymbol{\eta}))\, \mathrm{d}V_{\boldsymbol{\eta}}}$$

Here v_λ is the volume 'carved out' by a swimmer moving a distance λ:

$$v_\lambda = \lambda\sigma$$

with σ the cross-sectional area of the swimmer in the direction of motion.

Many swimmers

The sum of many displacements has distribution given by a convolution of individual distributions.

The characteristic function for N swimmers is thus $\langle \mathrm{e}^{\mathrm{i}kX_\lambda^N} \rangle = \langle \mathrm{e}^{\mathrm{i}kX_\lambda^1} \rangle^N$:

$$\begin{aligned}\langle \mathrm{e}^{\mathrm{i}kX_\lambda^1} \rangle^N &= \left(1 - v_\lambda \Gamma_\lambda(k)/V\right)^{nV} \\ &\sim \exp\left(-n v_\lambda \Gamma_\lambda(k)\right), \quad V \to \infty.\end{aligned}$$

where we used $N = nV$.

Define the number of head-on collisions for path length λ:

$$\nu_\lambda := n v_\lambda$$

We take the inverse Fourier transform of $\langle \mathrm{e}^{\mathrm{i}kX_\lambda^1} \rangle^N$ to finally obtain

$$\boxed{p_{X_\lambda}(x) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \exp\left(-\nu_\lambda \Gamma_\lambda(k)\right) \mathrm{e}^{-\mathrm{i}kx} \, \mathrm{d}k}$$

A model swimmer

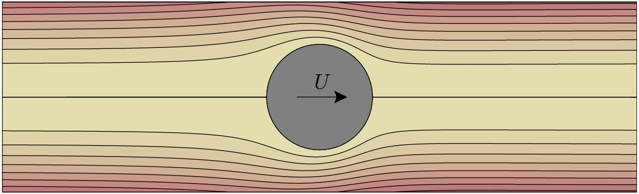
This is as far as we can go without introducing a model swimmer.

We take a squirmer, with axisymmetric streamfunction:

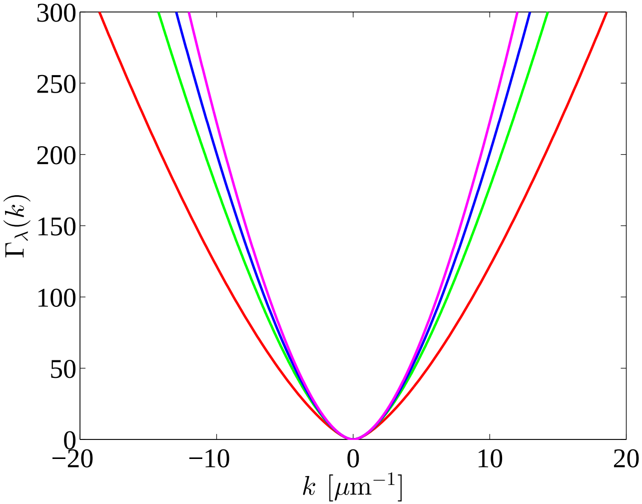
$$\Psi_{\mathrm{sf}}(\rho, z) = \tfrac{1}{2}\rho^2\, U \left\{ -1 + \frac{\ell^3}{(\rho^2 + z^2)^{3/2}} + \tfrac{3}{2}\,\frac{\beta \ell^2 z}{(\rho^2 + z^2)^{3/2}} \left(\frac{\ell^2}{\rho^2 + z^2} - 1 \right) \right\}$$

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

We use the stresslet strength $\beta = 0.5$, which is close to a treadmiller:



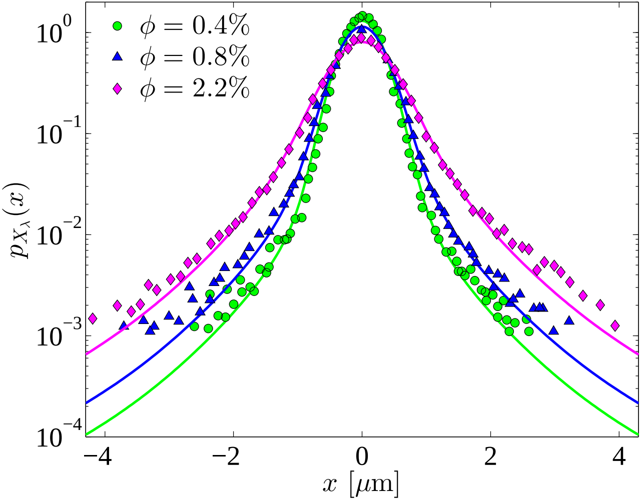
The function $\Gamma_\lambda(k)$ for the squirmer



From broadest to narrowest:

$$\lambda = 12\,\mu\mathrm{m},\ 36\,\mu\mathrm{m},\ 60\,\mu\mathrm{m},\ \text{and } 96\,\mu\mathrm{m}.$$

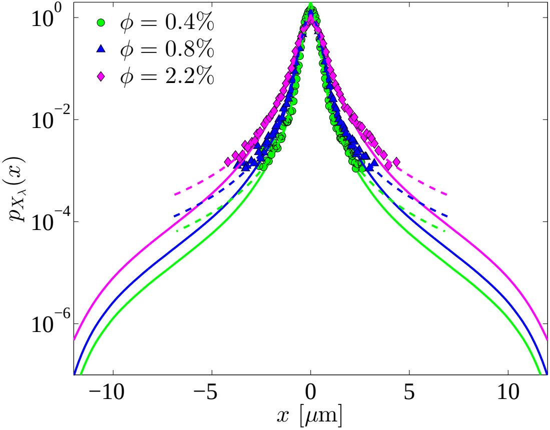
Comparing to Leptos *et al.*



The only fitted parameter is the stresslet strength $\beta = 0.5$.

Comparing to Eckhardt & Zammert

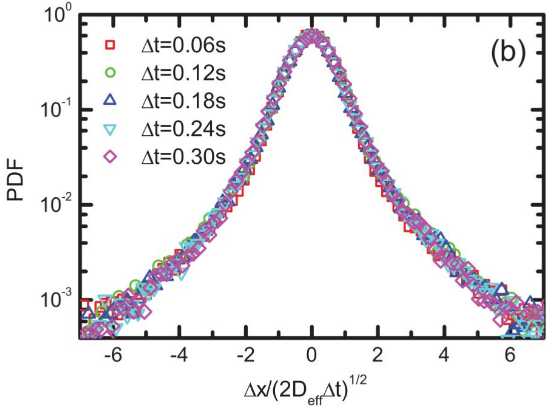
Eckhardt & Zammert (2012) have a beautiful fit to the data based on a phenomenological continuous-time random walk model (dashed):



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

The diffusive scaling from Leptos *et al.* (2009)

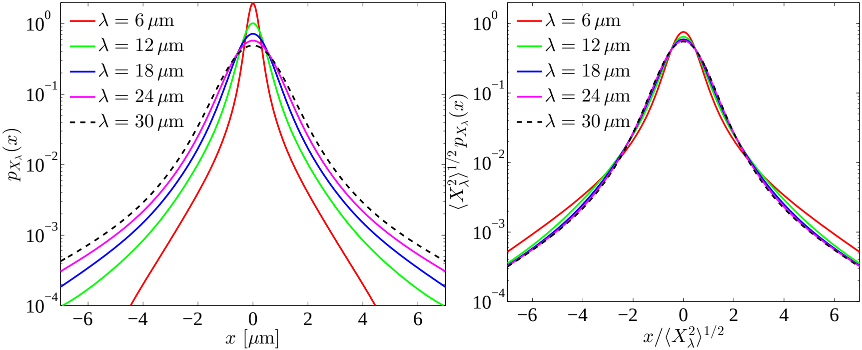
What about the 'diffusive scaling' mentioned at the start?



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

The diffusive scaling: model

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

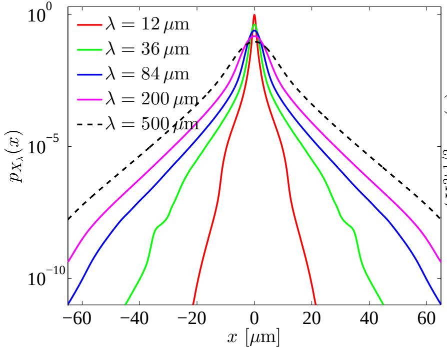


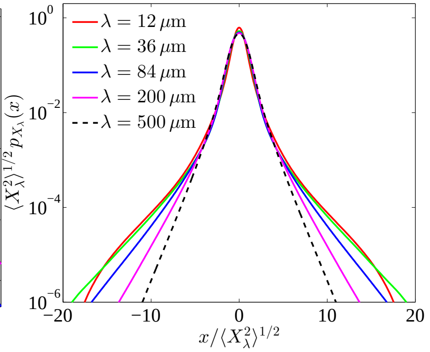
(Scaling a bit worse at early times, but this is consistent with experiment.)

The diffusive scaling: longer path lengths

The numerics are relatively easy: we can go for much longer path lengths than in the experiments. (No real sampling issues, since this is a direct calculation.)

Scaling gets worse for longer λ, particularly in the tails:





The diffusive scaling: origin

A straightforward argument shows that for the diffusive scaling to be approximately satisfied, the Taylor expansion

$$\nu_\lambda \Gamma_\lambda(\tilde{k}/\sqrt{\lambda})/n = \tfrac{1}{6}\,\tilde{k}^2\lambda^{-1}\int_V \Delta_\lambda^2(\boldsymbol{\eta})\,\mathrm{d}V_{\boldsymbol{\eta}} + \tfrac{1}{120}\,\tilde{k}^4\lambda^{-2}\int_V \Delta_\lambda^4(\boldsymbol{\eta})\,\mathrm{d}V_{\boldsymbol{\eta}} + \dots$$

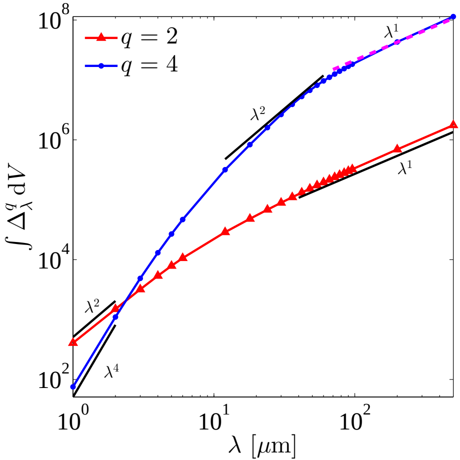
must be independent of λ. (The first term recovers the Gaussian approximation — the Central Limit Theorem.)

Hence, we need

$$\int_V \Delta_\lambda^2(\boldsymbol{\eta})\,\mathrm{d}V_{\boldsymbol{\eta}} \sim \lambda, \qquad \int_V \Delta_\lambda^4(\boldsymbol{\eta})\,\mathrm{d}V_{\boldsymbol{\eta}} \sim \lambda^2, \qquad \dots$$

For the diffusive scaling to persist forever, we would need moment $2q$ to scale as q.

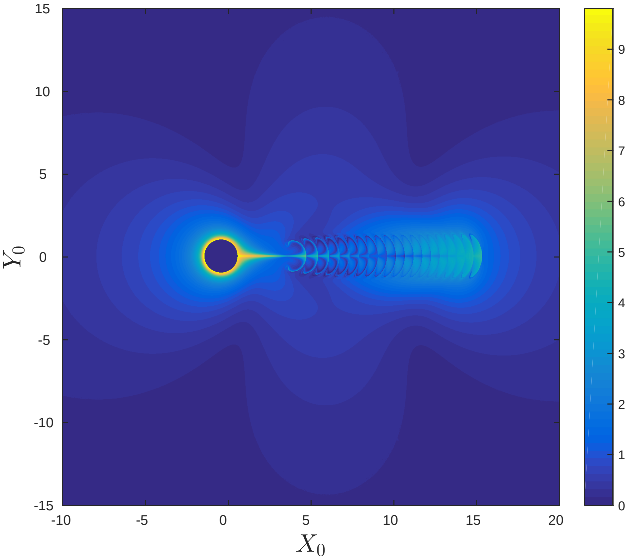
The diffusive scaling is transient



- Early times: moments are ballistic ($\int \Delta^q \sim \lambda^q$);
- Late times: moments are linear ($\int \Delta^q \sim \lambda^1$);

The slow crossover of $\int \Delta_\lambda^4$ is the origin of the 'diffusive scaling' of Leptos *et al.*, since in their narrow range of λ the curve is tangent to λ^2.

Time-dependent swimmer



Sphere-flagellum time-dependent swimmer [Peter Mueller]

play movie

Conclusions

- Leptos *et al.* (2009) find non-Gaussian distribution of displacements, with a diffusive scaling.
- 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.
- The Gaussian core arises because of the net effect of the distant swimmers, far from the test particle.
- The 'exact' distribution due to uncorrelated swimmers matches the data very well, with only one fitted parameter.
- The diffusive scaling is a transient due to slow crossover of the fourth moment between two regimes.
- Preprint (older version, ask for newer): `http://arxiv.org/abs/1408.4781`.

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