

Particle fluctuations induced by microswimmers

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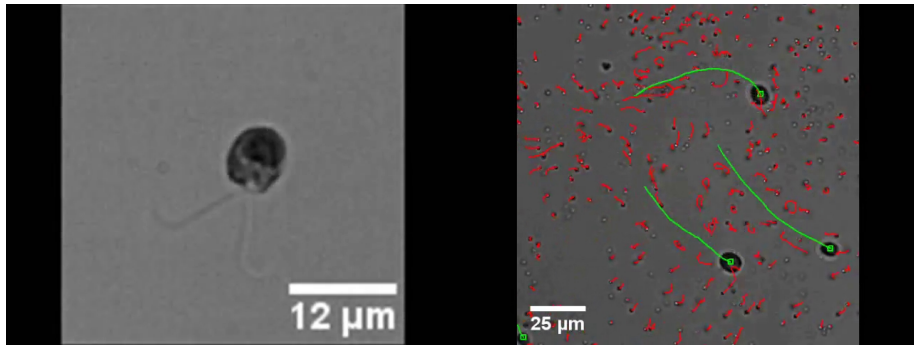
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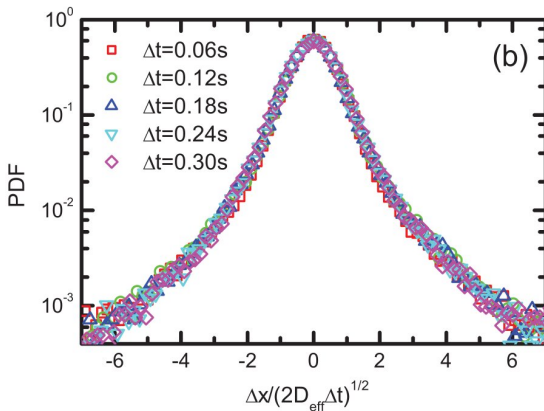
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[Guasto, J. S., Johnson, K. A., & Gollub, J. P. (2010). *Phys. Rev. Lett.* **105**, 168102]

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]

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

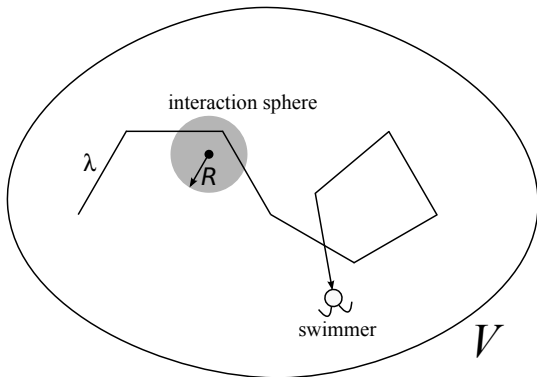
$$\mathbb{P}\{X_t \in [x, x + dx]\} = \frac{1-f}{\sqrt{2\pi\delta_g^2}} e^{-x^2/2\delta_g^2} + \frac{f}{2\delta_e} e^{-|x|/\delta_e}.$$

They observe the scalings $\delta_g \approx A_g t^{1/2}$ and $\delta_e \approx A_e t^{1/2}$, 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).

The paper by Leptos *et al.* has attracted considerable interest (**140 citations as of June 2015**), so it is worth trying to explain in detail.



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.



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

Close encounters of the first kind



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

$$n\lambda\pi R^2 \lesssim 0.4$$

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

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**.

Strategy for the probability density of displacements



- Find the **distribution of displacements** for a **single** swimmer.
- The sum of displacements for many swimmers is the **convolution** of single-swimmer displacements.
- In **Fourier space** (**characteristic function**), the convolution is a simple product, but we must then take an inverse transform.
- Usually this inverse transform is approximated using the **Central Limit Theorem**, but here we must evaluate it explicitly.
- Care must be taken when going to the **infinite-volume limit**.
- In the end, we must assume some **hydrodynamic model** to obtain the single-swimmer displacements.



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

$$\Delta_\lambda(\boldsymbol{\eta}) = \int_0^{\lambda/U} \mathbf{u}(\mathbf{x}(s) - \mathbf{U}s) ds, \quad \dot{\mathbf{x}} = \mathbf{u}(\mathbf{x} - \mathbf{U}t), \quad \mathbf{x}(0) = \boldsymbol{\eta}.$$

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

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

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

Here \mathbf{R}_λ^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 .

The **second moment** (**variance**) of \mathbf{R}_λ^1 is

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

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

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

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

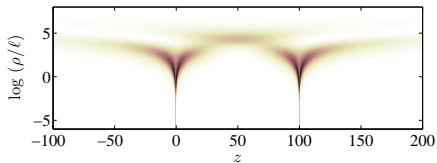
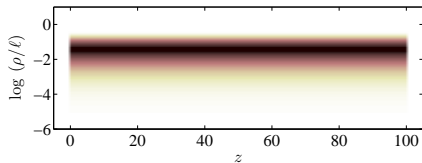
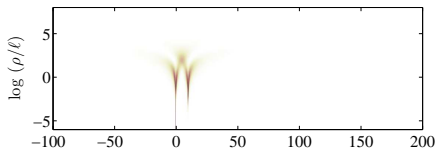
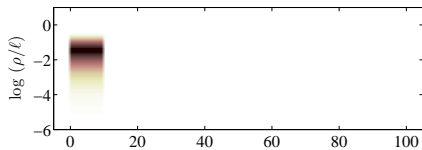
Crucial point:

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)]



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

$$p_{X_\lambda^1}(x) = \frac{1}{2} \int_V \frac{1}{\Delta_\lambda(\boldsymbol{\eta})} [\Delta_\lambda(\boldsymbol{\eta}) > |x|] \frac{dV_\boldsymbol{\eta}}{V}$$

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**:

$$\langle e^{ikX_\lambda^1} \rangle = \int_{-\infty}^{\infty} p_{X_\lambda^1}(x) e^{ikx} dx = \int_V \text{sinc}(k\Delta_\lambda(\boldsymbol{\eta})) \frac{dV_\boldsymbol{\eta}}{V}$$

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

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

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

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

Then,

$$\langle e^{ikX_\lambda^1} \rangle = 1 - (v_\lambda/V) \Gamma_\lambda(k)$$

where

$$\Gamma_\lambda(k) := \frac{1}{v_\lambda} \int_V \gamma(k\Delta_\lambda(\boldsymbol{\eta})) dV_\boldsymbol{\eta}$$

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.

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

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

$$\begin{aligned}\langle e^{ikX_\lambda^1} \rangle^N &= (1 - \nu_\lambda \Gamma_\lambda(k)/V)^{nV} \\ &\sim \exp(-n\nu_\lambda \Gamma_\lambda(k)), \quad V \rightarrow \infty.\end{aligned}$$

where we used $N = nV$.

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

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

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

$$p_{X_\lambda}(x) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \exp(-\nu_\lambda \Gamma_\lambda(k)) e^{-ikx} dk$$

A model swimmer



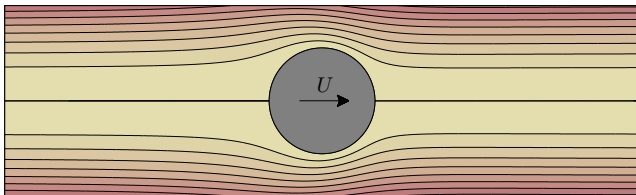
This is as far as we can go without introducing a model swimmer.

We take a **squirmers**, with axisymmetric streamfunction:

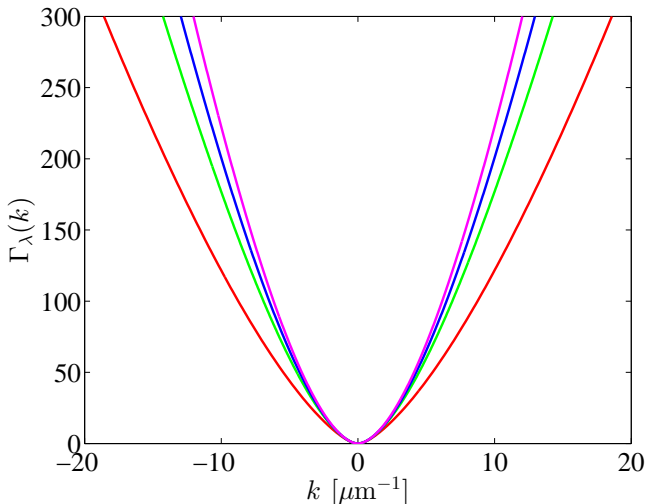
$$\Psi_{\text{sf}}(\rho, z) = \frac{1}{2}\rho^2 U \left\{ -1 + \frac{\ell^3}{(\rho^2 + z^2)^{3/2}} + \frac{3}{2} \frac{\beta \ell^2 z}{(\rho^2 + z^2)^{3/2}} \left(\frac{\ell^2}{\rho^2 + z^2} - 1 \right) \right\}$$

[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**:



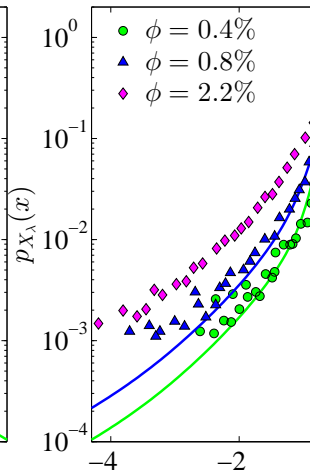
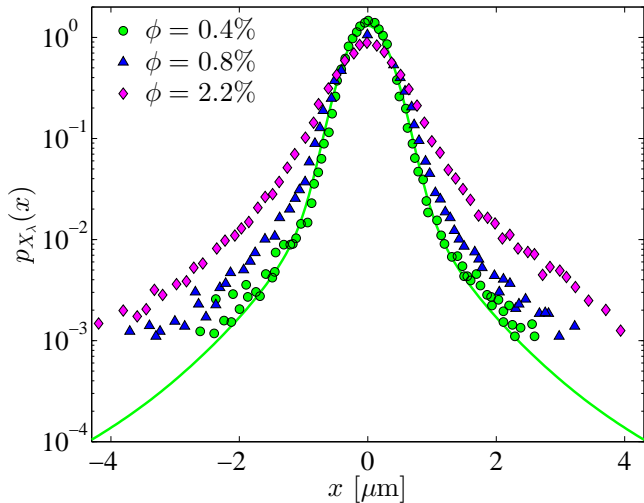
The function $\Gamma_\lambda(k)$ for the squirmer



From broadest to narrowest:

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

Comparing to Leptos *et al.*

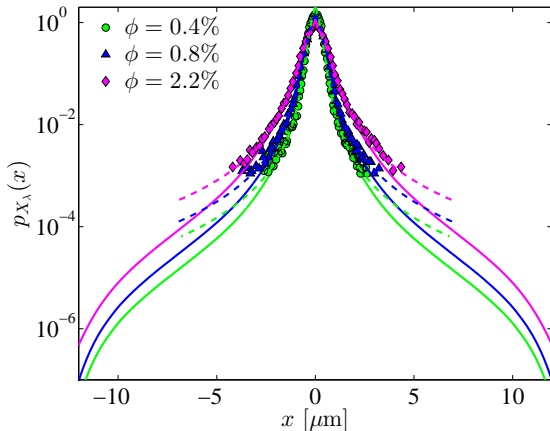


Fit the stresslet strength $\beta = 0.5$ to one curve. **The only fitted parameter is the stresslet strength $\beta = 0.5$.**

Comparing to Eckhardt & Zammert



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

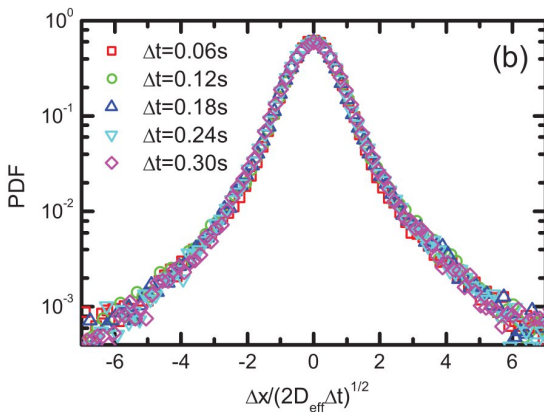


Our models disagree in the tails, but there is no data there.

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



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

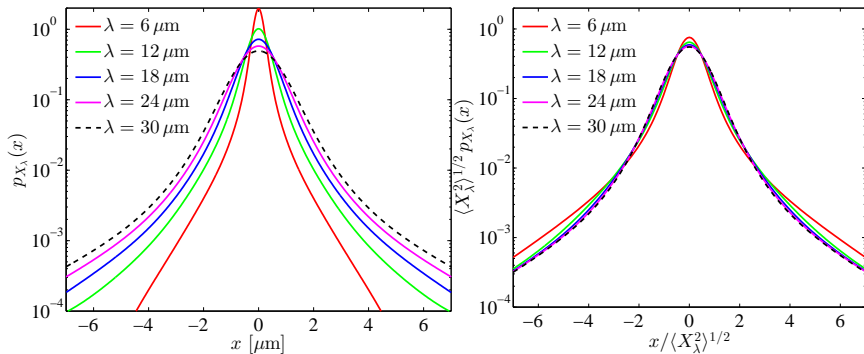


Note the **red squares** (early times) are on the inside center.

The diffusive scaling: model



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



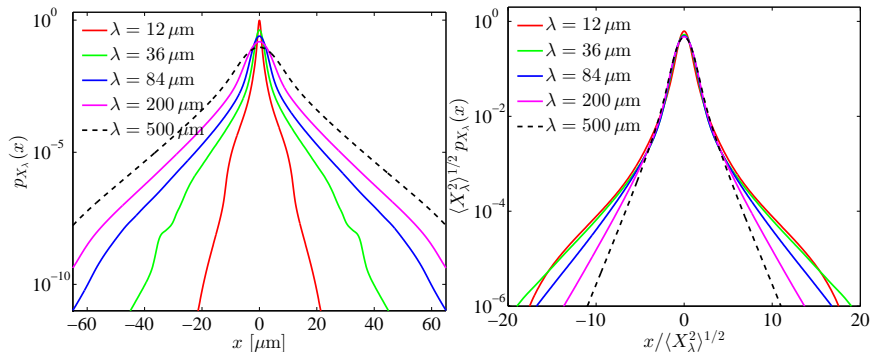
(Scaling a bit worse at early times, but this is consistent with experiment.)

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

$$\nu_\lambda \Gamma_\lambda(\tilde{k}/\sqrt{\lambda})/n = \frac{1}{6} \tilde{k}^2 \lambda^{-1} \int_{\mathcal{V}} \Delta_\lambda^2(\boldsymbol{\eta}) dV_\eta + \frac{1}{120} \tilde{k}^4 \lambda^{-2} \int_{\mathcal{V}} \Delta_\lambda^4(\boldsymbol{\eta}) dV_\eta + \dots$$

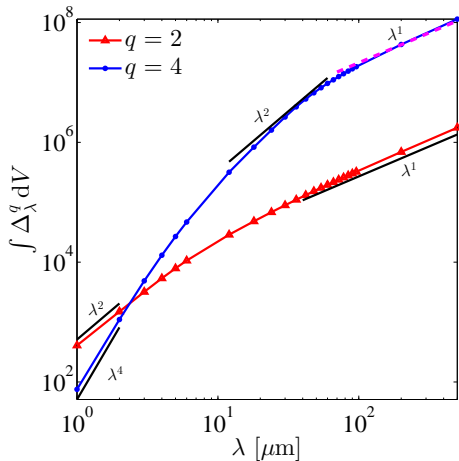
must be independent of λ . (The first term recovers the Gaussian approximation — the Central Limit Theorem.)

Hence, we need

$$\int_{\mathcal{V}} \Delta_\lambda^2(\boldsymbol{\eta}) dV_\eta \sim \lambda, \quad \int_{\mathcal{V}} \Delta_\lambda^4(\boldsymbol{\eta}) dV_\eta \sim \lambda^2, \quad \dots$$

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

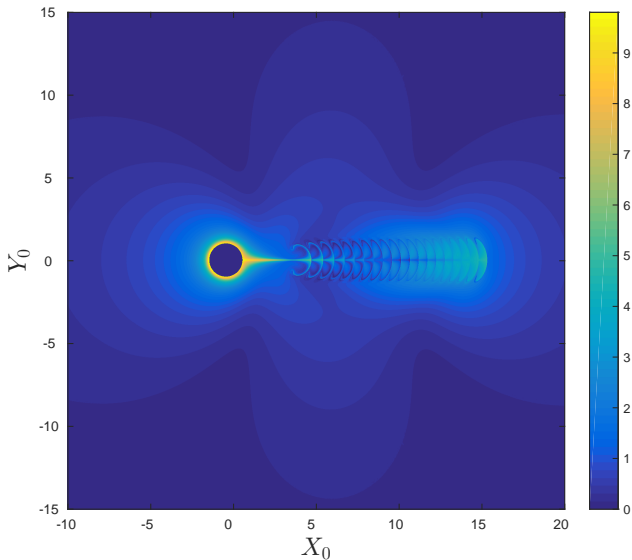
The diffusive scaling is transient



- 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]

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- 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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