

Distribution of particle displacements in biomixing

JEAN-LUC THIFFEAULT

The experiments of Leptos *et al.* [1] show that the displacements of small particles affected by swimming microorganisms achieve a non-Gaussian distribution, which nevertheless scales diffusively. We use a simple model where the particles undergo repeated ‘kicks’ due to the swimmers to explain the shape of the distribution.

Leptos *et al.* study the microscopic algae *Chlamydomonas reinhardtii*. They measure experimentally the probability density function (PDF) of tracer displacements, $\rho_{X_t}(x)$. Thus, $\rho_{X_t}(x) dx$ is the probability of observing a particle displacement $X_t \in [x, x + dx]$ after waiting a time t . The range of t is chosen small enough that the swimmers are ‘ballistic,’ so their velocity is roughly constant.

At zero volume fraction ($\phi = 0$), the distribution $\rho_{X_t}(x)$ is Gaussian, due solely to molecular diffusivity. For higher number densities, exponential tails appear and the Gaussian core broadens. Leptos *et al.* fit their the distribution to the sum of a Gaussian and an exponential:

$$(1) \quad \rho_{X_t}(x) = \frac{1-f}{\sqrt{2\pi\delta_g^2}} e^{-x^2/2\delta_g^2} + \frac{f}{2\delta_e} e^{-|x|/\delta_e}.$$

They observe the scalings $\delta_g \sim A_g t^{1/2}$ and $\delta_e \sim A_e t^{1/2}$, where A_g and A_e depend on ϕ . They call this a *diffusive scaling*, since $x \sim t^{1/2}$. Their point is that this is surprising, since the distribution is not Gaussian.

Our goal is to derive the PDF of displacements $\rho_{X_t}(x)$ from a simple model. We use the model described by Thiffeault & Childress [2] and improved by Lin *et al.* [3], which in spite of its simplicity captures the important features observed in experiments.

We assume there are N swimmers in a volume V , so the number density of swimmers is $n = N/V$. Initially, each swimmer travels at a speed U in a uniform random direction. They keep moving along a straight path for a time τ , so that each traces out a segment of length $\lambda = U\tau$. After this a new direction is chosen randomly and uniformly, and the process repeats — each swimmer again moves along a straight path of length λ . Though far from realistic, this model captures many essential features of the system, as found in [2, 3].

We wish to follow the displacement of an arbitrary ‘target fluid particle.’ The swimmers are all simultaneously affecting this fluid particle, but in practice only the closest swimmers significantly displace it. It is thus convenient to introduce an imaginary ‘interaction sphere’ of radius R centered on the target fluid particle, and count the number M_t of ‘interactions,’ that is the number of times a swimmer enters this sphere. (Our treatment applies to two-dimensional systems simply by changing ‘sphere’ to ‘disk’ and ‘volume’ to ‘area.’) Figure 1 illustrates the situation. When Nt/τ is large and R is not too large, the distribution of M_t is well approximated by a Poisson distribution:

$$(2) \quad \mathbb{P}\{M_t = m\} \simeq \frac{1}{m!} \langle M_t \rangle^m e^{-\langle M_t \rangle},$$

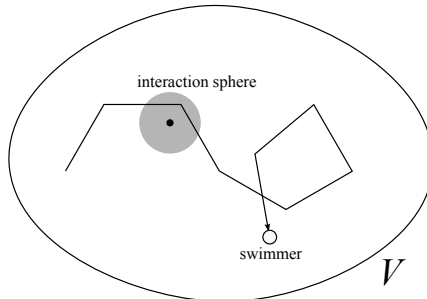


FIGURE 1. A swimmer moving inside a volume V along a series of straight paths, each of length λ and in a uniform random direction.

where the mean is given by the volume swept by the interaction sphere in time t :

$$(3) \quad \langle M_t \rangle \simeq n\pi R^2 \lambda (t/\tau).$$

Let us now consider these probabilities within the context of the Leptos *et al.* [1] experiments. The velocity of the swimmers is peaked at around $U \sim 100 \mu\text{m/s}$. Their volume fraction is less than 2.2%. Assuming spherical organisms of radius $5 \mu\text{m}$, this gives a number density $n \simeq 4.2 \times 10^{-5} \mu\text{m}^{-3}$. The maximum observation time is about $t \sim 0.3\text{s}$, so that a typical swimmer moves by a distance $\lambda \sim 30 \mu\text{m}$. From (3), we find

$$(4) \quad \langle M_t \rangle \simeq .004 \times (R/1 \mu\text{m})^2.$$

Hence, for $R = 20 \mu\text{m}$ (an interaction disk with a radius four times the swimmer's), we have $\langle M_t \rangle \simeq 1.58$. This is at the highest densities used in the experiments. We conclude that a typical fluid particle is only strongly affected by about one swimmer. The only displacements that a particle feels 'often' are the very small ones due to all the faraway 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. This is what is observed, and we will spend the remainder of the talk making this more precise.

Now that we've examined how often swimmers interact with a sphere of radius R centered around a target particle, we will look at how the particle gets displaced. Following Lin *et al.* [3], we start from a distribution of displacements $\Delta_\lambda \geq 0$ induced by a single swimmer. Each time a swimmer enters the interaction sphere we have an 'encounter,' which causes a displacement of the target particle in a random direction ψ_k ; thus, after m encounters, the displacement in some fixed direction is

$$(5) \quad X_m = \sum_{k=1}^m \Delta_\lambda \cos \psi_k$$

where each encounter has random i.i.d. values of the displacement Δ_λ .

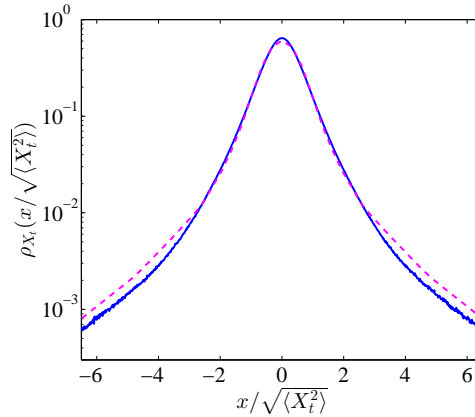


FIGURE 2. The PDF of particle displacements obtained from Eq. (6) by sampling from single-swimmer displacements. The data from Leptos *et al.* [1] is the dashed line.

The probability density of X_m is related to that of X_t , the displacement after a time t , by

$$(6) \quad \rho_{X_t}(x) = \sum_{m=0}^{\infty} \rho_{X_m}(x) \mathbb{P}\{M_t = m\},$$

where $\mathbb{P}\{M_t = m\}$ is given by Eq. (2). Figure 6 shows the PDF $\rho_{X_t}(x)$, normalized to unit standard deviation. The PDF was obtained by sampling from the single-swimmer displacements Δ_λ for a squirmer-type swimmer [3]. The fit to the data is good, though the tails are a bit depressed. This may be due to the use of a swimmer model that entrains particles slightly less far than the actual organism. Eckhardt & Zammert [4] have obtained better fit by invoking an anomalous diffusion model. In a future publication we will investigate whether our model can account for more details of the Leptos *et al.* experiment.

REFERENCES

- [1] K. C. Leptos, J. S. Guasto, J. P. Gollub, A. I. Pesci, and R. E. Goldstein, “Dynamics of enhanced tracer diffusion in suspensions of swimming eukaryotic microorganisms,” *Phys. Rev. Lett.* **103**, 198103 (2009).
- [2] J.-L. Thiffeault and S. Childress, “Stirring by swimming bodies,” *Phys. Lett. A* **374**, 3487 (2010).
- [3] Z. Lin, J.-L. Thiffeault, and S. Childress, “Stirring by squirmers,” *J. Fluid Mech.* **669**, 167 (2011).
- [4] B. Eckhardt and S. Zammert, “Non-normal tracer diffusion from stirring by swimming microorganisms,” *Eur. Phys. J. E* **35**, 96 (2012).