Lecture 4: Stirring by swimming organisms, part 2[a]

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In the previous lecture we found the expression for the pdf of displacements due to swimming organisms:

$$p_n(x,t) = \frac{1}{2\pi}\int_{-\infty}^{\infty} \exp\left(-n\,\Gamma_d(k,t)\right) \mathrm{e}^{-\mathrm{i}kx}\,\mathrm{d}k, \tag{1}$$

where

$$\Gamma_d(k,t) := \int_V \gamma_d(k\Delta(\boldsymbol{\eta},t))\,\mathrm{d}V_{\boldsymbol{\eta}}\,. \tag{2}$$

Consider the case special when $\Delta(\boldsymbol{r},t)$ vanishes outside a specified 'swept volume' $V_{\text{swept}}(t)$. Then

$$\begin{aligned}\Gamma_d(k,t) &= \int_{V_{\text{swept}}} \gamma_d(k\Delta(\boldsymbol{\eta},t))\,\mathrm{d}V_{\boldsymbol{\eta}} \\ &= V_{\text{swept}} - \int_{V_{\text{swept}}} \left(1-\gamma_d(k\Delta(\boldsymbol{\eta},t))\right)\mathrm{d}V_{\boldsymbol{\eta}} \\ &= V_{\text{swept}}\left(1-\mathcal{W}_d(k,t)\right)\end{aligned}$$

where

$$\mathcal{W}_d(k,t) := \frac{1}{V_{\text{swept}}}\int_{V_{\text{swept}}} \left(1-\gamma_d(k\Delta(\boldsymbol{\eta},t))\right)\mathrm{d}V_{\boldsymbol{\eta}}\,. \tag{3}$$

Define $\phi_{\text{swept}} := nV_{\text{swept}}$; then we can Taylor expand the exponential in (1) to obtain

$$p_n(x,t) = \sum_{m=0}^{\infty} \frac{\phi_{\text{swept}}^m}{m!}\,\mathrm{e}^{-\phi_{\text{swept}}}\,\frac{1}{2\pi}\int_{-\infty}^{\infty} \mathcal{W}_d^m(k,t)\,\mathrm{e}^{-\mathrm{i}kx}\,\mathrm{d}k. \tag{4}$$

The factor $\phi_{\text{swept}}^m\,\mathrm{e}^{-\phi_{\text{swept}}}/m!$ is a Poisson distribution for the number of 'interactions' m — the number of times a particle has been affected by a swimmer. The other factor in the sum is a probability density,

$$p_{(m)}(x) := \frac{1}{2\pi}\int_{-\infty}^{\infty} \mathcal{W}_d^m(k,t)\,\mathrm{e}^{-\mathrm{i}kx}\,\mathrm{d}k, \tag{5}$$

for the distribution of displacements given that a particle has interacted with a swimmer m times (see also [1]).

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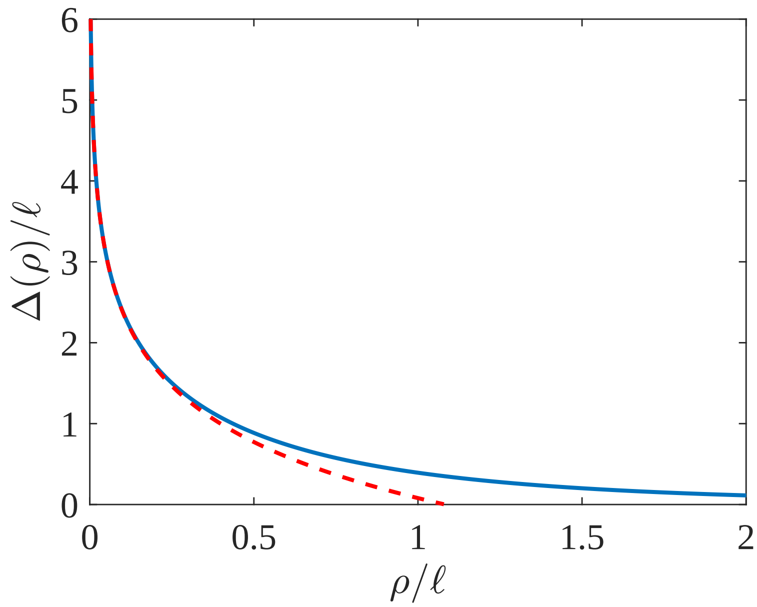

FIG. 1. The 'log model' for the displacement function of a cylinder of unit radius moving in an inviscid fluid. The solid line is the true displacement function, as computed by Maxwell [2] and Darwin [3]. The dashed line is the asymptotic form $C\,\log(\ell/\rho)$, with $\ell = 8/\mathrm{e}^2 \simeq 1.08268$. The simplified 'log model' consists of using only the logarithmic asymptotic form for $\rho < \ell$, and zero otherwise.

Let us apply (4) to a specific example. A model for cylinders and spheres of radius ℓ traveling along the z axis in an inviscid fluid [4, 5] is the *log model*,

$$\Delta(\rho, z, t) = \begin{cases} \Delta(\rho), & \text{if } 0 \le z \le Ut, \\ 0, & \text{otherwise,} \end{cases} \qquad \Delta(\rho) := C \log^{+}(\ell/\rho) \tag{6}$$

where ρ is the perpendicular distance to the swimming direction and $\log^{+} x := \ln\max(x, 1)$. The logarithmic form comes from the stagnation points on the surface of the swimmer, which dominate transport in this inviscid limit. The constant C is set by the linear structure of the stagnation points [4–6], and usually scales with the size of the organism (*not* with time t, for long enough times). For example, $C = 1$ for a cylinder of unit radius moving through inviscid fluid [4, 6]. For spheres in the same type of fluid, $C = \frac{4}{3}$ [4]. This model is also appropriate for a spherical 'treadmiller' swimmer in viscous flow. The function (6) is compared to the exact drift function for a cylinder in Fig. 1.

For a drift function of the form (6), the function $\Gamma_d(k, t)$ defined in (2) becomes

$$\begin{aligned} \Gamma_d(k, t) &= \int_V \gamma_d(k\Delta(\boldsymbol{\eta}, t))\,\mathrm{d}V_{\boldsymbol{\eta}} \\ &= \int_0^{Ut}\int_0^{\infty} \gamma_d(k\Delta(\rho))\,\alpha_d \rho^{d-2}\,\mathrm{d}\rho\,\mathrm{d}z \\ &= \alpha_d U t \int_0^{\infty} \gamma_d(k\Delta(\rho))\,\rho^{d-2}\,\mathrm{d}\rho\,. \end{aligned}$$

Assuming a monotonic relationship between ρ and $\Delta(\rho)$, with $\Delta(0) = \infty$ and $\Delta(\infty) = 0$, we change integration variable from ρ to Δ:

$$\Gamma_d(k,t) = \alpha_d U t \int_0^\infty \gamma_d(k\Delta)\, \rho^{d-2}(\Delta)\, |\rho'(\Delta)|\, \mathrm{d}\rho\,. \tag{7}$$

We can write $\rho = \ell\, \mathrm{e}^{-\Delta/C}$, with $|\rho'(\Delta)| = (\ell/C)\, \mathrm{e}^{-\Delta/C}$. Then

$$\mathcal{W}_d(k,t) = \frac{d-1}{C} \int_0^\infty (1 - \gamma_d(k\Delta))\, \mathrm{e}^{-(d-1)\Delta/C}\, \mathrm{d}\rho\,. \tag{8}$$

where we used $V_{\text{swept}} = \alpha_{d-1}\ell^{d-1}Ut$ and $\alpha_d/\alpha_{d-1} = d-1$. We can carry out the integrals explicitly to obtain

$$\mathcal{W}_d(k) = \begin{cases} (1 + (Ck)^2)^{-1/2}, & \text{(cylinders);} \\ (Ck/2)^{-1} \arctan(Ck/2), & \text{(spheres).} \end{cases} \tag{9}$$

This is independent of t, even for short times (though the model is not valid for short times).

Furthermore, for $d = 2$ we can also explicitly obtain the convolutions that arise in (5) to find

$$p_{(m)}(x) = \frac{1}{C\sqrt{\pi}\,\Gamma(m/2)} \left(|x|/2C\right)^{(m-1)/2} K_{(m-1)/2}(|x|/C), \tag{10}$$

the full distribution,

$$p_n(x,t) = \mathrm{e}^{-\phi_{\text{swept}}} \left(\delta(x) + \sum_{m=1}^{\infty} \frac{\phi_{\text{swept}}^m}{m!} \frac{1}{C\sqrt{\pi}\,\Gamma(m/2)} \left(|x|/2C\right)^{(m-1)/2} K_{(m-1)/2}(|x|/C) \right), \tag{11}$$

where $K_\alpha(x)$ are modified Bessel functions of the second kind, and $\Gamma(x)$ is the Gamma function (not to be confused with $\Gamma(k,t)$ above). Equation (11) is a very good approximation to the distribution of displacements due to inviscid cylinders. Unfortunately no exact form is known for spheres: we must numerically evaluate (1) given (9), or use asymptotic methods (see [7]).

The log model is more appropriate for swimmers in an inviscid fluid. To compare the theory to the experiments of Leptos *et al.* we need a swimmer in a viscous environment, as appropriate for microswimmers. We use a model swimmer of the squirmer type [10–14], with axisymmetric streamfunction [5]

$$\Psi_{\text{sf}}(\rho,z) = \tfrac{1}{2}\rho^2\, U \left\{ -1 + \frac{\ell^3}{(\rho^2+z^2)^{3/2}} + \tfrac{3}{2} \frac{\beta \ell^2 z}{(\rho^2+z^2)^{3/2}} \left(\frac{\ell^2}{\rho^2+z^2} - 1 \right) \right\} \tag{12}$$

in a frame moving at speed U. Here z is the swimming direction and ρ is the distance from the z axis. To mimic *C. reinhardtii*, we use $\ell = 5\,\mu$m and $U = 100\,\mu$m/s. We take also $\beta = 0.5$ for the relative stresslet strength, which gives a swimmer of the puller type, just like *C. reinhardtii*. The contour lines of the axisymmetric streamfunction (12) are depicted in Fig. 3. The parameter β is the only one that was fitted to give good agreement.

The numerical results are plotted into Fig. 4(a) and compared to the data of Fig. 2(a) of Leptos *et al.* [8]. The agreement is excellent: we adjusted only one parameter, $\beta = 0.5$. All the other physical quantities were gleaned from Leptos *et al.* What is most remarkable about the agreement in Fig. 4(a) is that it was obtained using a model swimmer, the spherical

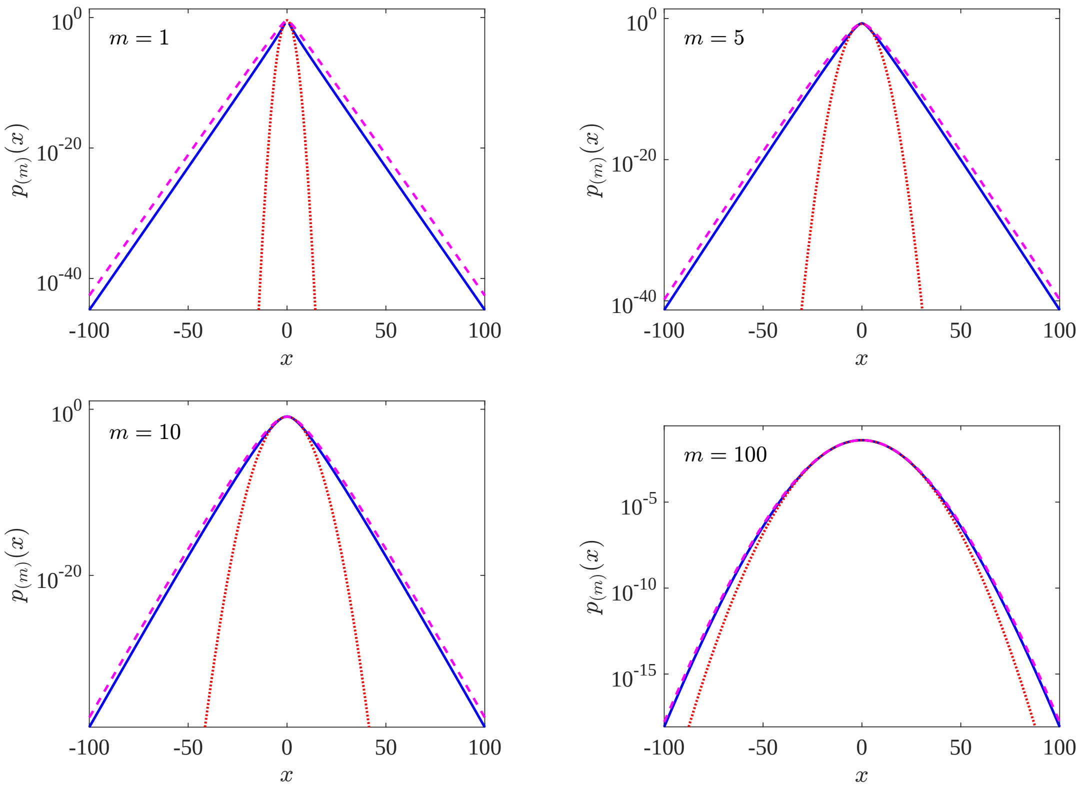

FIG. 2. For the log model: the exact pdf $p_{(m)}(x)$ from (10) for different values of m (solid line) and $C = 1$, as well as the large-deviation (dashed line) and Gaussian (dotted line) approximations.

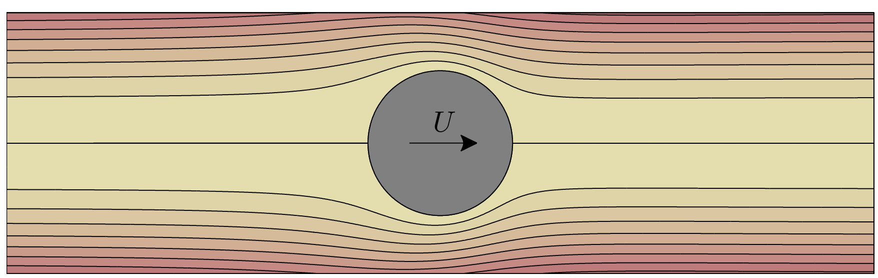

FIG. 3. Contour lines for the axisymmetric streamfunction of a squirmer of the form (12), with $\beta = 0.5$. This swimmer is of the puller type, as for *C. reinhardtii*.

squirmer, which is not expected to be such a good model for *C. reinhardtii*. The real organisms are strongly time-dependent, for instance, and do not move in a perfect straight line. Nevertheless the model captures very well the pdf of displacements. New work with my student Peter Mueller uses a more realistic model for *C. reinhardtii*, involving a no-slip sphere for the body and a point force for the flagellum. We observe a lifting of the tails

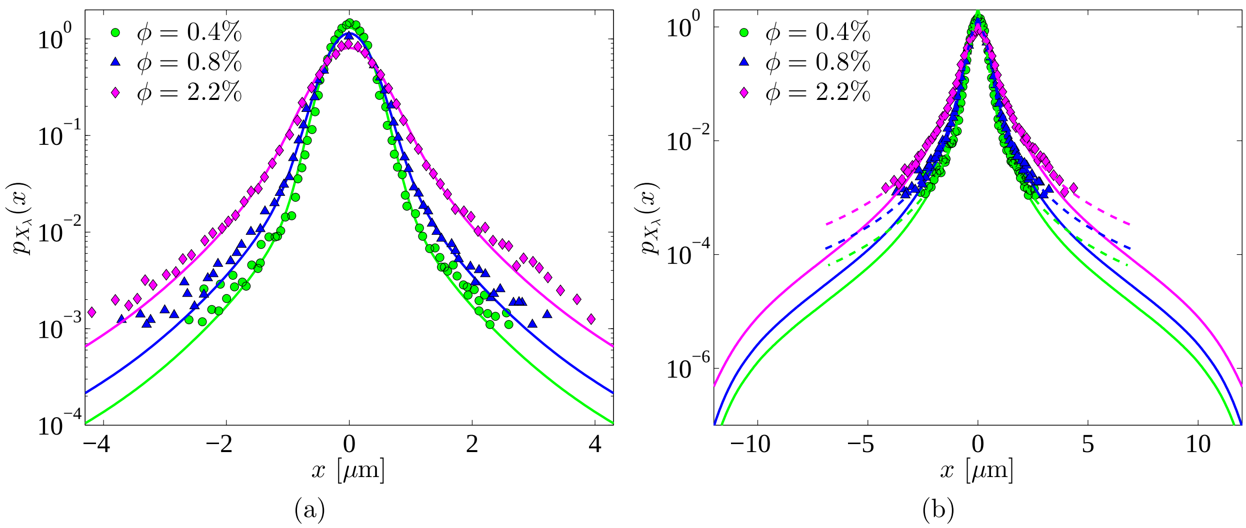

FIG. 4. (a) The pdf of particle displacements after a time $t = 0.12\,\text{s}$, for several values of the volume fraction ϕ. The data is from Leptos *et al.* [8], and the figure should be compared to their Fig. 2(a). (b) Same as (a) but on a wider scale, also showing the form suggested by Eckhardt and Zammert [9] (dashed lines).

which matches the data better.

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