■ **The point source dipole, also known as the potential dipole**

Hence

$$D_{ij} = \frac{\partial}{\partial x_{0,j}} \left(\frac{\hat{\mathbf{x}}}{r^3} \right) = -\frac{\delta_{ij}}{r^3} + 3\frac{\hat{x}_i \hat{x}_j}{r^5}$$

and (with summation)

$$u_i = D_{ij} q_j$$

is a solution of Stokes equations for any constant vector $\mathbf{q}$.

The solution for a translating sphere By linearity, any linear combination of the potential dipole and stokeslet also solves Stokes equations. We can combine them to find the solution to Stokes equations for a neutrally buoyant sphere of radius a translating at constant speed $\mathbf{U}$ in the absence of other boundaries:

$$-\nabla p + \mu \nabla^2 \mathbf{u} = \mathbf{0}, \quad \nabla \cdot \mathbf{u} = 0 \quad \text{for} \quad |\mathbf{x} - \mathbf{x}_0| > a \tag{12}$$

with

$$\mathbf{u} = \mathbf{U}, \quad \text{const}, \quad \text{for} \quad |\mathbf{x} - \mathbf{x}_0| = a$$

and $\mathbf{u} \to \mathbf{0}$ at spatial infinity, with the sphere centred at $\mathbf{x}_0$ at any given instant.

To find the flow field at the field point $\mathbf{x}$ external to, or on the sphere, consider

$$u_i = G_{ij} g_j + D_{ij} q_j.$$

By construction it is a solution of the Stokes equation and decays at spatial infinity. Imposing the no-slip condition on the sphere boundary $r = a$ we have

$$U_i = \frac{g_i}{a} - \frac{q_i}{a^3} + \hat{x}_i \hat{x}_j \left[\frac{1}{a^3} g_j + \frac{3}{a^5} q_j \right].$$

Comparing coefficients, we have

$$\mathbf{q} = -\frac{a^2}{3} \mathbf{g} \ \text{ and hence } \ \mathbf{g} = \frac{3}{4} a \mathbf{U} = \frac{1}{8\pi\mu} [6\pi a \mu \mathbf{U}],$$

giving the solution for the flow around a translating sphere.

This readily allows us to calculate the viscous drag exerted by the surrounding fluid on a translating sphere, which is known as Stokes drag. In particular the potential dipole does not contribute to the force (it is the limit of a linear combination of "equal but opposite" solutions, which thus do not exert a force prior to taking the limit, and hence do not exert a force after taking the limit).

Stokes Drag

Let $\sigma_{ij}^{Stk} = T_{ijp}^{Stk} m_p$ be the stress associated with Stokeslet solution 11. We thus have

$$\nabla_j \sigma_{ij}^{Stk} = m_p \nabla_j T_{ijp}^{Stk} = -m_i \delta(\mathbf{x} - \mathbf{x}_0).$$

The stress due to the Stokeslet contributions for the sphere solution is thus

$$\sigma_{ij}^{Sphere} = 8\pi\mu T_{ijp}^{Stk} g_p$$

and hence the total drag force, that is the force exerted by the fluid on the sphere, is

$$\begin{aligned} F_i &= \int_{Sphere} \sigma_{ij}^{Sphere} \cdot n_j \mathrm{d}S = \int_{Sphere} \nabla_j \sigma_{ij}^{Sphere} \mathrm{d}V \\ &= 8\pi\mu \int_{Sphere} g_p \nabla_j T_{ijk}^{Sphere} dV = -8\pi\mu \int_{Sphere} g_p \delta(\mathbf{x} - \mathbf{x}_0) dV = -8\pi\mu g_p. \end{aligned}$$

Hence the drag force is given by

$$\mathbf{F} = -6\pi\mu a \mathbf{U}. \tag{13}$$

2.4.2 Resistive force theory

Foundation of resistive force theory

Consider a small element of a very slender filament of circular cross section moving in a viscous fluid. To provide the foundation for resistive force theory, our objective is to relate the drag force per unit length, **f** to the velocity of the filament, analogous to the relationship between the drag **F** and velocity **U** of a sphere in equation 13.

By the linearity of Stokes equations and symmetry of the circular cross section, the relation between drag per unit length and velocity must be of the form

$$\mathbf{f} = -C_N(\mathbf{I} - \mathbf{e}_T\mathbf{e}_T)\mathbf{U} - C_T(\mathbf{e}_T \cdot \mathbf{U})\mathbf{e}_T, \tag{14}$$

with C_T denoting the resistance coefficient in the tangential direction, $\mathbf{e}_T$ and C_N denoting the resistance coefficient in the normal and binormal directions.
Thus our task reduces to finding $C_T,\ C_N$.

Resistive Force Theory

Definition. Any theory of swimming that considers the mechanics of a beating cilium or flagellum by using only the relationship between velocity and drag for isolated infinitesimal filament elements given by equation (14), is referred to as *resistive force theory.* Such theories neglect possible non-local hydrodynamic interactions between different parts of the filament, eg if it turns back on itself, or hydrodynamic interactions between a cilium/flagellum and the cell to which it is attached

To derive the relationship between drag and velocity for resistive force theory, consider a straight filament of length L and cross section radius a, with $a/L \ll 1$.

Suppose the filament is aligned along the x axis, between $x = 0$ and $x = L$, and is subject to a constant external force, uniformly distributed along its length, with force density per unit length $\mathbf{f}^{ext}$. We split the rod into $N = L/a \gg 1$ elements of equal length, a.

Initially all hydrodynamic interactions of an element with its neighbours is neglected; the force each element exerts on the fluid is then $(L/N)\mathbf{f}^{ext}$.

Invoking linearity of Stokes equations, the speed of the α^{th} element must be of the form

$$u_i^\alpha = \frac{L}{N} A_{ij}^\alpha f_j^{ext},$$

where the tensor $\mathbf{A}_{ij}^\alpha$ has $O(1)$ coefficients and, by the no slip boundary condition, this is also the speed of the fluid on the surface of the rod element. As all elements are equivalent the tensor A_{ij}^α in fact does not depend on α and we drop the superscript in the following.

To consider hydrodynamical interactions, at least approximately, we approximate each rod element by a Stokeslet, of strength $L\mathbf{f}^{ext}/N$, at locations $\mathbf{x}_0^\alpha = (L/[2N], 0, 0) + (L\alpha/N, 0, 0)$, for $\alpha \in \{1, ..., N\}$. This is equivalent to approximating each rod element as a sphere of radius $a = L/[2N]$; the far field of such an object is dominated by the Stokeslet which decays like the inverse of distance; the potential dipole decays like the inverse of the cubed distance. Even at a distance of $2a$, ie. the next element, this approximation induces a relative error of about $2/2^3$, i.e. 25%, with improvements in considering more distant elements. Given the level of accuracy of resistive force theory, this is a tolerable error.

The flow induced by the α^{th} stokeslet is

$$u_i^\alpha(\mathbf{x}) = \frac{1}{8\pi\mu} \frac{L}{N} G_{ij}(\mathbf{x}, \mathbf{x}_0^\alpha) f_j^{ext}.$$

Invoking linearity once more, the velocity at the β^{th} segment is thus the linear superposition of the flow induced by the β^{th} element and the flow induced by (our Stokeslet approximation of) all the other elements.

■ Foundation of resistive force theory

Hence, the flow at a point on the surface of the β^{th} element, $\mathbf{x}^\beta \in \partial\Omega^\beta$, is

$$\begin{aligned} u_i^\beta(\mathbf{x}^\beta) &= A_{ij} f_j^{ext} L/N + \sum_{\alpha;\ \alpha\neq\beta} \frac{L}{N} G_{ij}(\mathbf{x}^\beta, \mathbf{x}_0^\alpha) f_j^{ext} \\ &= A_{ij} f_j^{ext} L/N + \sum_{\alpha;\ \alpha\neq\beta} \frac{L}{8\pi\mu N} \left\{ \frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3} \right\} f_j^{ext} \end{aligned}$$

where $\mathbf{r} = \mathbf{x}^\beta - \mathbf{x}_0^\alpha$, $r = |\mathbf{r}|$.

Foundation of resistive force theory

For $N \gg 1$ we have the velocity at the centre of filament can be derived as follows.

We approximate the sum by an integral, excluding a region around $\mathbf{x}^\beta$. Thus, we have

$$\begin{aligned} u_i^\beta(\mathbf{x}^\beta) &= A_{ij} f_j^{ext} L/N + \frac{1}{8\pi\mu}\int_0^{s^\beta} ds \left\{\frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3}\right\} f_j^{ext} \\ &+ \frac{1}{8\pi\mu}\int_{s^\beta+2a}^{L} ds \left\{\frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3}\right\} f_j^{ext} + O(L/N) \end{aligned}$$

where $s^\beta = \beta L/N$ and $\mathbf{x}^\alpha \to s\mathbf{e}_x$ noting that $\mathbf{x}^\beta$ is still a fixed point on $\partial\Omega^\beta$. With the (crude!) approximation

$$\mathbf{r} \sim \left(s^\beta + \frac{L}{2N} - s\right)\mathbf{e}_x,$$

and using $L/[2N] = a$, we have

$$\begin{aligned} u_i^\beta &\sim A_{ij} f_j^{ext} L/N + \frac{1}{8\pi\mu}\left[\delta_{ij} + \delta_{i1}\delta_{j1}\right] f_j^{ext}\left[\int_0^{s^\beta}\frac{ds}{|s^\beta - s + a|} + \int_{2a+s^\beta}^{L}\frac{ds}{|s^\beta - s + a|}\right] \\ &\sim A_{ij} f_j^{ext} L/N \\ &+ \frac{1}{8\pi\mu}\left[\delta_{ij} + \delta_{i1}\delta_{j1}\right] f_j^{ext}\log\left(\frac{s^\beta(L-s^\beta)}{a^2}\right)\left(1 + O\left(\frac{a(L-2s^\beta)}{s^\beta(L-s^\beta)}\frac{1}{\log\left(\frac{s^\beta(L-s^\beta)}{a^2}\right)}\right)\right) \end{aligned}$$

Considering away from the ends of the rod, so that $s^\beta = \gamma L$, with γ not close to zero or unity, so that $|\log(\gamma(1-\gamma))| \sim O(1)$, we have

$$u_i^\beta \sim A_{ij} f_j^{ext} L/N + \frac{1}{4\pi\mu}\left[\delta_{ij} + \delta_{i1}\delta_{j1}\right] f_j^{ext}\log\left(\frac{L}{a}\right)\left(1 + \frac{1}{2}\frac{\log(\gamma(1-\gamma))}{\log\left(\frac{L}{a}\right)} + h.o.t.\right).$$

Hence

$$u_i^\beta \sim \frac{1}{4\pi\mu}\left[\delta_{ij} + \delta_{i1}\delta_{j1}\right] f_j^{ext}\log\left(\frac{L}{a}\right) \quad \text{as } \frac{1}{N}, \frac{a}{L} \to 0,$$

though extensive further work (eg matching into a prolate ellipsoid cap) is required to determine corrections at the ends.

A flagellum. Approximating a flagellum as a collection of slender straight elements, the velocity of the centre of each rod is related to the hydrodynamic force density exerted on the rod, at this level of approximation, by

$$u_i \sim \frac{1}{4\pi\mu}\left[\delta_{ij} + \delta_{i1}\delta_{j1}\right] f_j^{ext}\log\left(\frac{L}{a}\right).$$

Note this gives the velocity of a segment given the force per unit length applied on the fluid by the filament. We require the drag force per unit length, ie the force per unit length exerted on the filament by the fluid; this differs just by a minus sign (by Newton's third law).

Hence, the relationship between the hydrodynamic forces and velocities of elements of a flagellum are related by

$$f_T = -C_T u_T, \quad f_N = -C_N u_N, \quad \text{where } \; C_N = 2C_T = \frac{4\pi\mu}{\log\left(\frac{L}{a}\right)},$$

with f_T, u_T, C_T denoting the force density, velocity and resistance coefficient in the tangential direction and f_N, u_N, C_N denoting the analogous quantities in the normal and binormal directions.

The original, more rigorous but harder, analysis can be found in [4], where the flow field adjacent to a sinusoidally moving filament is determined invoking asymptotics in a/L. Differentiating these flow field yields the stress tensor, and hence the resistance coefficient can be explicitly determined, as first noted by [3]. You will immediately note the increase in complexity of the analysis if you read the original papers with further complexity if the careful asymptotics of [5] are explored; therefore a crude technique, rather than a rigorous one, is presented here.

2.4.3 Example. Predicting the speed of a swimming cell.

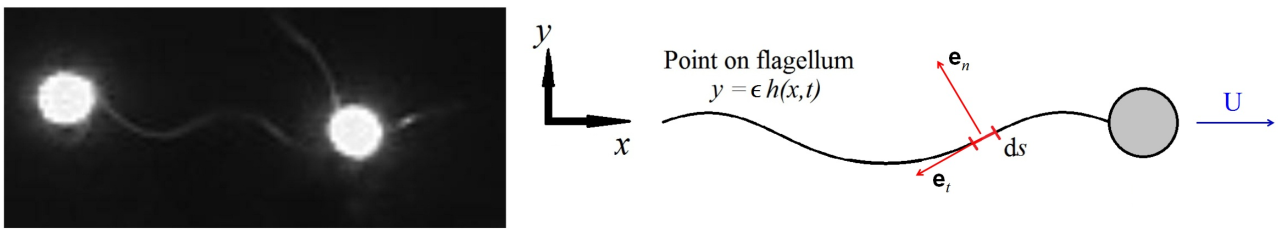

Figure 4: Left. An image of two carp spermatozoa highlighting the spherical cell body, courtesy of Galina Prokopchuk and Jacky Cosson, University of South Bohemia, Faculty of Fisheries and Protection of Waters, Research Institute of Fish Culture and Hydrobiology. The head radius is exaggerated in the image due to an optical effect as the microscopy is fine tuned to make the flagellum visible, which requires phase contrast microscopy, rather than standard microscopy, since the flagellar cross sectional radius is less than a wavelength of light. Right. The model; shallow planar waves of the form $y = \epsilon h(x,t)$ propagate down the flagellum, where the plane $y = 0$ is the mid-plane of the flagellum.

For simplicity, we consider a swimmer with a spherical cell body. These are not that common – instead there is an array of interesting cell shape geometries. Nonetheless, numerous fish spermatozoa, for instance carp and turbot, have spherical bodies.

Let $y = 0$ correspond to the midplane about which the flagellum beats, and let $y = \epsilon h(s,t)$ denote the location of the flagellum at time t and arclength s. We assume a small amplitude beat so that $\epsilon \ll 1$.

Finally, in most expositions, it is assumed that the spermatozoon body has negligible velocity in the y direction, i.e. that the cell body velocity is $(U, 0)$ and that it does not rotate. Below we make this assumption, but it is generally unjustified. See for example page 13 of the supplementary information, where the trajectory a cell head is the magenta curve. We consider when such assumptions are valid in more detail in the problems.

Our objective below is thus to find U, that is the swimming velocity, in terms of $h(x,t)$.

■ Total force balance on the flagellum

- The spherical cell body moves with speed $\mathbf{U}$. Hence it experiences a drag force of $-6\pi\mu a\mathbf{U}$ from the fluid.
- Considered in isolation there is no net force on the cell as the Stokes number R_S, is essentially zero.
- Thus

$$-6\pi\mu a\mathbf{U} + (\text{Drag force on flagellum}) = \mathbf{0}.$$

Hence

$$6\pi\mu a\mathbf{U} = (\text{Drag force on flagellum}). \tag{15}$$

We now use resistive force theory to determine the drag force on the flagellum in terms of $h(s,t)$. This gives us an equation for $\mathbf{U}$, and we takes its projection onto the x-axis to find U, the swimming speed in the x direction, working to the leading non-trivial order in $\epsilon \ll 1$.

■ Prediction for U via resistive force theory

We have $\mathbf{e}_t = (-1, \epsilon h_s)$, $\mathbf{e}_n = (\epsilon h_s, 1)$ and the velocity of the flagellum element is given by $\mathbf{U} = (U, \epsilon h_t)$ noting there is no cell body velocity in the y-direction. Hence the drag force per unit length on the element ds is given by

$$\mathbf{f} = -\left[C_N \mathbf{e}_n \cdot \mathbf{U}\mathbf{e}_n + C_T \mathbf{e}_t \cdot \mathbf{U}\mathbf{e}_t\right] = -\left[(C_N - C_T)\mathbf{e}_n \cdot \mathbf{U}\mathbf{e}_n + C_T\mathbf{U}\right]$$

and projecting this onto the x-direction we have

$$\begin{aligned} \mathbf{f}\cdot\mathbf{e}_x &= -\left[(C_N - C_T)\mathbf{e}_n \cdot \mathbf{U}\mathbf{e}_n \cdot \mathbf{e}_x + C_T U\right] \\ &= -\left[(C_N - C_T)(\epsilon^2 h_s^2 U) + (C_N - C_T)(\epsilon^2 h_s h_t) + C_T U\right] \end{aligned}$$

Hence, by equation (15)

$$6\pi a\mu U = -\int_0^L \left[(C_N - C_T)\epsilon^2 h_s^2 U + (C_N - C_T)(\epsilon^2 h_s h_t) + C_T U\right] \mathrm{d}s \tag{16}$$

Rearranging gives

$$\left[6\pi a\mu + (C_N - C_T)\epsilon^2 \int_0^L h_s^2 ds + C_T L\right] U = -(C_N - C_T)\epsilon^2 \int_0^L h_s h_t \mathrm{d}s.$$

Dropping the clearly subleading $O(\epsilon^2)$ term on the left-hand side immediately yields

$$U = \epsilon^2 \frac{C_T - C_N}{6\pi a\mu + C_T L} \int_0^L h_s h_t \mathrm{d}s.$$

We note that Friedrich et. al [2] have recently reported a very good agreement between resistive force theory predictions and spermatozoan trajectories.