

BioFluids Lecture 3: Flagellar swimming – resistive-force theory.

See the course Webpage: <http://www.ma.ic.ac.uk/~ajm8/BioFluids>

Today we analyse how motion of a long, thin flagellum can propel an organism such as *Chlamydomonas* (see Pictures file) at low Reynolds number.

Low Reynolds number flows have several nice properties: they are unique, stable, linear, time-reversible and establish themselves instantaneously. For example, the steady motion of a solid sphere of radius a with speed U gives rise to the flow in $r > a$

$$\mathbf{u} = \frac{1}{4}U \left[\left(\frac{6a}{r} - \frac{2a^3}{r^3} \right) \cos \theta, - \left(\frac{3a}{r} + \frac{a^3}{r^3} \right) \sin \theta, 0 \right], \quad p - p_\infty = \frac{3\mu U a \cos \theta}{2r^2} \quad (3.1)$$

in terms of spherical polar coordinates (r, θ, η) aligned with the swimming direction. The total drag acting on the sphere can be shown to be

$$F = 6\pi a \mu U. \quad (3.2)$$

We can interpret the motion in (3.1) as the sum of two flow fields, a potential flow scaling as r^{-3} and the **Stokeslet** which scales as r^{-1} . The former is a source/sink dipole, describing the fluid being pushed away from the front of the sphere and reappearing at the rear. The Stokeslet is the flow resulting from a point force in the flow direction of strength $F\delta(\mathbf{r})$ at the origin. From (3.2) and (3.1), the Stokeslet velocity is

$$\mathbf{u}_S = \frac{F}{8\pi\mu} \left[\frac{2 \cos \theta}{r}, -\frac{\sin \theta}{r}, 0 \right]. \quad (3.3)$$

We can attempt to describe the motion of a general body by distributions of dipole and Stokeslet singularities over its surface.

More useful when considering flagellum driven swimming is the motion of a long thin cylinder, of radius a . Physically, we might regard the effect of a thin cylinder moving through a fluid as the combined effect of a uniform distribution of point forces. Let us consider a uniform distribution of Stokeslets on the z -axis between $z = -b$ and $z = c$ each of strength $f = F/(b + c)$ moving with uniform velocity in the z -direction. Using the linearity, we can superpose the velocity fields from all of the Stokeslets. The z -component of velocity a distance a from the z axis at $z = 0$ is therefore

$$\frac{f}{8\pi\mu} \int_{-b}^c \left[\cos \theta \left(\frac{2 \cos \theta}{r} \right) + \sin \theta \left(\frac{\sin \theta}{r} \right) \right] dz = \frac{f}{8\pi\mu} \int_{-b}^c \frac{2z^2 + a^2}{(a^2 + z^2)^{3/2}} dz, \quad (3.4)$$

expressing r and θ in terms of z . Performing the integration, and evaluating it on the cylinder surface and assuming $a \ll b, c$ we obtain

$$\mathbf{u}_T = \frac{f_T}{8\pi\mu} \left(0, 0, -2 + 2 \log \frac{4bc}{a^2} \right). \quad (3.5)$$

where the suffix T denotes motion parallel to the cylinder axis. An inconvenient logarithm appears, which prevents us from considering an infinite cylinder, or one of zero radius. Moreover, we see that the velocity is not exactly constant. As we vary b and c keeping the length $(b + c)$ constant, \mathbf{u} varies slightly. However if a is very small, to leading order this represents a cylinder moving with constant speed parallel to its axis. We can therefore define a tangential resistance coefficient,

$$K_T = \frac{4\pi\mu}{-1 + \log \frac{4bc}{a^2}}, \quad (3.6)$$

so that $f_T = K_T U_T$ for motion with speed U parallel to the cylinder axis.

Similarly, let us try to model a cylinder moving normal to its axis. This time, we must also include some of the irrotational dipoles. A similar calculation then gives the flow

$$\mathbf{u}_N = \frac{f_N}{8\pi\mu} \left(0, 0, 1 + \log \frac{4bc}{a^2} \right), \quad (3.7)$$

where N denotes motion normal to the cylinder axis. Once more, as a is small, we deduce that a rigid cylinder moving normally to its axis can be approximately represented by a uniform distribution of Stokeslets and dipoles. Furthermore, we can define a normal resistance coefficient, $f_N = K_N U_N$ where

$$K_N = \frac{8\pi\mu}{1 + \log \frac{4bc}{a^2}}. \quad (3.8)$$

We note that the resistance to normal motion is approximately twice the resistance to tangential motion if a is small enough. Because of the linearity of the Stokes equations, motion in an oblique direction can be considered as a suitable sum of the normal and horizontal flows.

Resistive Force Theory

Let us now consider a thin flagellum, which undergoes prescribed motion. We would like to calculate the force exerted on the fluid; if this is non-zero on average, then the flagellum will have net movement, and will swim. Furthermore, if it is attached to an inert head, the entire organism will swim, but at a lower speed than would the flagellum by itself.

A useful approximation, known as **resistive force theory**, was introduced by Gray and Hancock. They argued that as the flagellum undulates, provided its radius of curvature is large compared to its diameter, the forces corresponding to the normal and tangential motion would be approximately given by the local flagellum velocity and the above coefficients K_N and K_T for straight cylinders. Thus approximately the force exerted by a flagellar segment is

$$\mathbf{F} \simeq K_N \mathbf{u}_N + K_T \mathbf{u}_T, \quad (3.9)$$

where \mathbf{u}_N is the normal velocity component and \mathbf{u}_T the tangential component. The total force can then be obtained by integrating over the flagellum.

BioFluids Lecture 4: Propulsion by travelling waves on a flagellum

Consider a flagellum with total length L . At time $t = 0$, we define its position by

$$\mathbf{r} = (X(s), Y(s), Z(s)), \quad 0 < s < L, \quad (3.10)$$

where s denotes arclength along the flagellum from one end. The unit tangent vector to this curve is then

$$\hat{\mathbf{T}} = \frac{d\mathbf{r}}{ds} = (X', Y', Z') \quad \text{where} \quad X'^2 + Y'^2 + Z'^2 = 1. \quad (3.11)$$

Observation shows that sending travelling waves down the flagellum is a popular way to swim. So we assume that the shape is periodic with period Λ down its length. We assume that the flagellum oscillates about the x -axis, and that swimming is in the x -direction. We have then

$$Y(s + \Lambda) = Y(s), \quad Z(s + \Lambda) = Z(s) \quad \text{and} \quad X(s + \Lambda) = X(s) + \lambda. \quad (3.12)$$

Here λ is a projection onto the x -axis of the wave-length; we write

$$\lambda = \alpha\Lambda \quad \text{where} \quad 0 < \alpha \leq 1, \quad (3.13)$$

so that α is the proportion by which the flagellum contracts as it wiggles around.

We further assume that the solid flagellum is inextensible and incompressible. This means that its tangential velocity must be a constant, say Q . With respect to a frame moving in the x -direction with the wave speed V , where for consistency we must have $V = \alpha Q$, the material particles in the flagellum appear to be at rest, so that

$$\mathbf{r} = (X(s - Qt), Y(s - Qt), Z(x - Qt)). \quad (3.14)$$

Now suppose the flagellum swims with velocity $(-U, 0, 0)$, in the opposite direction to the wave. Each part of the flagellum then moves relative to the fluid with velocity

$$\mathbf{u} = (V - U, 0, 0) - Q\hat{\mathbf{T}} = (V - U) \sin \theta \hat{\mathbf{N}} + [(V - U) \cos \theta - Q] \hat{\mathbf{T}} \quad (3.15)$$

where θ is the angle between the x -axis and the tangent, so that $\cos \theta = X'(s - Qt)$.

Now that we have the normal and tangential components we can use resistive force theory, claiming that the local resistance to the velocity $U_N \hat{\mathbf{N}} + U_T \hat{\mathbf{T}}$ is $K_N U_N \hat{\mathbf{N}} + K_T U_T \hat{\mathbf{T}}$. We then take the component in the x -direction and integrate along the body to obtain the total force on the fluid

$$P = \int_0^L (K_T [(V - U)X' - Q]X' + K_N (V - U)(1 - X'^2)) ds. \quad (3.16)$$

Now

$$\int_0^L X'(s - Qt) ds = \alpha L \quad \text{and we define} \quad \int_0^L (X')^2 ds = \beta L, \quad (3.17)$$

so that β is the mean square cosine of the body shape. Clearly $0 < \beta \leq 1$. In fact Schwarz' inequality states $\beta \geq \alpha^2$. Equation (3.16) can then be written

$$P = K_T L[(V - U)\beta - V] + K_N L(V - U)(1 - \beta). \quad (3.18)$$

Now if we have included everything in the problem, the flagellum should be in equilibrium, with no net force acting, i.e. $P = 0$. Alternatively, the force P may be used to propel an inert head with the swimming velocity U . We assume the drag force for the head motion is independent of the flagellar motion, and for convenience we write this drag as $K_N L U \delta$, so that

$$\delta = \frac{\text{resistance to forward motion of head}}{\text{resistance to sideways motion of entire flagellum}}. \quad (3.19)$$

Equating the head drag to the extra propulsive force P ,

$$P = K_N L U \delta,$$

and solving for the swimming speed U gives

$$\frac{U}{V} = \frac{(1 - \beta)(1 - \rho)}{1 - \beta(1 - \rho) + \delta} = 1 - \frac{\rho + \delta}{1 - \beta(1 - \rho) + \delta} \quad \text{where} \quad \rho = \frac{K_T}{K_N}. \quad (3.20)$$

Note no swimming occurs ($U = 0$) if $\rho = 1$, so the differential resistance is crucial to the swimming procedure.

If $\rho > 1$, $U < 0$ and the swimming is in the same sense as the wave, but for Stokes flow $\rho < 1$ and the swimming is in the opposite sense. Obviously $\beta = 1 = \alpha$ means the flagellum isn't moving at all. In (3.20) U increases as β decreases towards zero, so we can say

$$U < \frac{V(1 - \rho)}{1 + \delta}. \quad (3.21)$$

Of course if the flagellum swims at all, it can propel an arbitrarily large head at a slow speed (until its energy source runs out.)

Gray and Hancock obtained reasonable agreement with observations assuming a value $\rho = 0.5$. Unfortunately, the more realistic value of $\rho = 0.7$ gives worse results. Lighthill suggested that the proximity of the sperms in their experiment to a solid boundary, with resultant interactions with images, should arguably lead to a lower value of ρ .