BioFluids Lecture 5:   Swimming of a flapping sheet or array of cilia.

Many organisms employ large numbers of flagella (which we now call cilia) to generate forward motion. The essence of ciliar swimming is that rather than have each flagellum perform a travelling wave, a wave may be generated by suitable time lapses between cilia undergoing a simple, identical motion. We will assume each cilium moves periodically. Typically, this motion consists of a wide sweep at some distance from the boundary, which we call the swimming stroke, followed by a recovery stroke with the cilium close to the boundary. This may be likened to the technique of a child on a swing, although the mechanical processes are very different. If the swimming stroke is in the same direction as the travelling wave the motion is called *simplectic*, whereas if it is in the opposite direction it is called *antiplectic*.

Each cilium might swim by itself if its motion is irreversible (remember the scallop theorem.) However, the essence of ciliar swimming is that a large number of these motions are superposed in a travelling wave-like manner. This kind of ciliar motion is also used inside the body to transport mucus linings, for example in the lungs; there the fluid may well be non-Newtonian, however.

We consider an organism with a planar surface $y = 0$ which is coated with an array of cilia. We shall assume the cilia undergo a z-independent, sinusoidal travelling wave motion in the x-direction. Thus as they wave around, the tip of the cilium tethered at $(x_0, 0)$ is at (x_s, y_s) where

$$x_s = x_0 + a\cos(\xi - \phi), \qquad y_s = y_0 + b\sin\xi \qquad \text{where} \quad \xi = kx_0 - \omega t. \qquad (5.1)$$

Here x_0 is a variable essentially labelling the cilia, whereas y_0 is an average extension which we will take to be the same for each cilium. We could easily extend the theory to include z-dependence, but that would increase the algebra. Note that we may take a and b to be positive without loss of generality.

We will assume $k > 0$ and $\omega > 0$, so that the wave travels to the right with phase speed k/ω. We have included a phase factor ϕ to allow for various swimming modes. When the cilium is fully extended ($\xi = \frac{1}{2}\pi$) the x-component of its tip velocity is $\partial x_s/\partial t = a\omega\cos\phi$, so that the motion is *simplectic* for $|\phi| < \frac{1}{2}\pi$.

Eliminating t from(5.1), we find that the orbit of the cilium at position x_0 is

$$\left[b(x_s - x_0) - a\sin\phi(y_s - y_0)\right]^2 + a^2\cos^2\phi(y_s - y_0)^2 = a^2b^2\cos^2\phi \qquad (5.2)$$

so that the tip of each cilium (x_s, y_s) describes an ellipse.

Now the fluid is constrained to have the cilium velocity at each point (x_s, y_s). So if the density of cilia is high enough we expect it will be reasonable to model the array of cilia as a rigid sheet with shape (x_s, y_s). This sheet is in some sense the **envelope** of the ciliar motion. At each time instant t, the sheet shape is given parametrically in terms of x_0. Note that the sheet so defined will not in general be inextensible as we ensured for the

single flagellum. However, there is no reason why it should be, as it models a discrete set of cilia.

We therefore consider the Stokes flow above the boundary given by (5.1). On this boundary, the velocity must be given by

$$\mathbf{u} = \left(\frac{\partial x_s}{\partial t}, \frac{\partial y_s}{\partial t}, 0 \right) = (a\omega \sin(\xi - \phi), -b\omega \cos \xi, 0) \qquad \text{on } x = x_s, \ y = y_s. \tag{5.3}$$

Note that x appears implicitly in this equation through ξ. Combining (5.1) and (5.3) will generate terms like $\sin n\xi$ for all integers n.

We seek the solution to the Stokes equations in $y > y_s$ satisfying (5.3). As we have a two-dimensional geometry, we can use a streamfunction ψ with

$$\mathbf{u} = \nabla \wedge (0,\, 0,\, \psi) = (\psi_y,\, -\psi_x,\, 0) \tag{5.4}$$

so that the Stokes equations reduce to the biharmonic equation for ψ

$$\nabla p = \mu \nabla^2 \mathbf{u} \implies \nabla^2(\nabla^2 \psi) = 0. \tag{5.5}$$

We replace x and y with the scaled variables,

$$\xi = kx - \omega t, \qquad \eta = ky, \implies \psi_{\eta\eta\eta\eta} + 2\psi_{\eta\eta\xi\xi} + \psi_{\xi\xi\xi\xi} = 0. \tag{5.6}$$

We shall assume the amplitudes a and b of the wave motion are small (and of similar order) compared to the wavelength, and seek a power series solution in ka, kb. We will also need a boundary condition as $y \to \infty$. As we are using a frame fixed in the body, if the organism swims the fluid at infinity will appear to move in the opposite direction, so we expect

$$k\frac{\partial \psi}{\partial \eta} \equiv \frac{\partial \psi}{\partial y} \to U, \qquad \frac{\partial \psi}{\partial \xi} \equiv \frac{\partial \psi}{\partial x} \to 0 \qquad \text{as } y, \eta \to \infty, \tag{5.7}$$

where positive U indicates the organism swims in the negative x-direction.

If we Fourier analyse in the x-direction, an appropriate set of separable solutions to the biharmonic equation $\nabla^4 \psi = 0$ are

$$\psi = \sum_{n=0}^{\infty} V_n \equiv \sum_{n=0}^{\infty} \left[(A_n + B_n \eta) \sin n\xi + (C_n + D_n \eta) \cos n\xi \right] e^{-n\eta}, \tag{5.8}$$

We now move the boundary conditions from the point $(x_s,\, y_s)$ to $(x,\, y_0)$ using Taylor series:

$$\psi_x(x_s,\, y_s) = \psi_x + (x_s - x)\psi_{xx} + (y_s - y_0)\psi_{xy} + \tfrac{1}{2}(x_s - x)^2 \psi_{xxx} +$$
$$(x_s - x)(y_s - y_0)\psi_{xxy} + \tfrac{1}{2}(y_s - y_0)^2 \psi_{xyy} + \dots \tag{5.9}$$

where all derivatives on the RHS are evaluated at (x, y_0). In terms of ξ and η, using (5.1), (5.4) and (5.3), this becomes (dropping the zero suffix on (ξ)

$$\frac{\omega b}{k} \cos \xi = \psi_\xi(\xi_s,\, \eta_s) = \psi_\xi + ka \cos(\xi - \phi)\psi_{\xi\xi} + kb \sin \xi \psi_{\xi\eta}$$
$$+ \tfrac{1}{2}k^2 \left[\psi_{\xi\xi\xi} a^2 \cos^2(\xi - \phi) + \psi_{\xi\xi\eta} 2ab \cos(\xi - \phi) \sin \xi + (b^2 \sin^2 \xi)\psi_{\xi\eta\eta} \right] + O(k^3) \tag{5.10}$$

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where the RHS is evaluated at $\eta = 0$. A similar expansion for ψ_y leads to the other boundary condition

$$
\begin{aligned}
\frac{a\omega}{k}\sin(\xi - \phi) &= \psi_\eta(\xi_s, \eta_s) = \psi_\eta + ka\cos(\xi - \phi)\psi_{\eta\xi} + kb\sin\xi\psi_{\eta\eta} \\
&+ \tfrac{1}{2}k^2\left[\psi_{\eta\xi\xi}\,a^2\cos^2(\xi - \phi) + \psi_{\eta\xi\eta}\,2ab\cos(\xi - \phi)\sin\xi + b^2(\sin^2\xi)\psi_{\eta\eta\eta}\right] + O(k^3)
\end{aligned}
\tag{5.11}
$$

We now expand ψ as a power series in k

$$
\psi = \frac{\omega}{k}\psi_1(\xi,\,\eta) + \omega\psi_2(\xi,\,\eta) + \ldots
\tag{5.12}
$$

We can choose suitable coefficients A_1, B_1, C_1, D_1 in (5.7) so that

$$
\psi_{1\xi}(\xi,\,0) = b\cos\xi, \qquad \psi_{1\eta} = a\sin(\xi - \phi),
\tag{5.13}
$$

and we find the leading order solution

$$
\psi_1 = (b + b\eta)e^{-\eta}\sin\xi - a\eta\sin(\xi - \phi)e^{-\eta}.
\tag{5.14}
$$

As $\eta \to \infty$, we get $\psi_\eta \to 0$ and we get no swimming. At the next order though, we hope to get terms in $\cos^2\xi$ and $\sin^2\xi$ which have a non-zero mean.

At $O(k^2)$, (5.11) and (5.12) require that on $\eta = 0$,

$$
\psi_{2\xi} = -a\cos(\xi - \phi)\psi_{1\xi\eta} - b\sin\xi\psi_{1\xi\eta}, \quad \psi_{2\eta} = -a\cos(\xi - \phi)\psi_{1\eta\xi} - b\sin\xi\psi_{1\eta\eta}, \quad (5.15)
$$

We can now substitute in from (5.14) and we find that

$$
\psi_{2\xi} = 0, \qquad \psi_{2\eta} = -a^2\cos^2(\xi - \eta) + b^2\sin^2\xi + 2ab\sin\xi\sin(\xi - \phi).
\tag{5.16}
$$

We can once more choose solutions of the form (5.11) and arrange for suitable constants to satisfy (5.16). The swimming speed will depend on the '$n = 0$' term, which we can find directly from (5.16) by taking the average over ξ. After some algebra we obtain

$$
\psi_2 = U\eta - \tfrac{1}{2}\eta e^{-2\eta}\left[2\gamma(b + \beta)\sin 2\xi + (b + \beta + \gamma)(b + \beta - \gamma)\cos(2\xi)\right].
\tag{5.17}
$$

where we have written $\beta = a\cos\phi$, $\gamma = a\sin\phi$ and at this order we get a swim speed

$$
U = \tfrac{1}{2}\omega k(b^2 + 2ab\cos\phi - a^2).
\tag{5.18}
$$

This can be positive or negative according to the values of the stroke parameters a, b and ϕ, in a non-obvious manner. If $a \ll b$, so that the motion is mainly up and down, we would expect the collection of cilia to behave a bit like a single wave-carrying flagellum, and hence swim in the opposite direction to the wave; this is confirmed. Conversely, however, if $a \gg b$ the cilial motion is predominantly lateral, and the swimming is in the opposite direction to the wave.

We could continue to next order in k, which, while straightforward, is a little messy compared to the elegant formula (5.18). At the very least, we can first seek the values of a, b and ϕ which lead to efficient swimming, and predict in which direction the organism will move.

Bacterial Power – Rate of working of the ciliar sheet

It is a simple matter to derive the pressure field associated with the flow using the x-component of Stokes equations and (5.14),

$$\frac{\partial p}{\partial x} = \mu \nabla^2 \left(\frac{\partial \psi}{\partial y} \right) \quad \Longrightarrow \quad p = -2\mu\omega k e^{-\eta}[b\cos\xi + a\cos(\xi - \phi)] + O(k^2). \qquad (5.19)$$

We can then calculate the total force on the cilia-sheet, $\mathbf{F}$, and the rate of working (per unit area) of the organism, W, by integrating over the sheet $\sigma_{ij}n_j$ and $u_i\sigma_{ij}n_j$ respectively, where the stress tensor

$$\sigma_{ij} = \begin{pmatrix} -p + 2\mu\psi_{xy} & \mu(\psi_{yy} - \psi_{xx}) \\ \mu(\psi_{yy} - \psi_{xx}) & -p - 2\mu\psi_{xy} \end{pmatrix}_{ij}, \qquad (5.20)$$

and averaging over a time-period. This gives the result

$$W = \mu\omega^2 k(a^2 + b^2) + O(k^2). \qquad (5.21)$$

Optimal Stokes Strokes: Swimming Efficiency

We can now pose a simple optimization problem: What values of the stroke parameters a, b and ϕ given a maximum swim speed $|U|$ for given effort W? If we write $a = r\cos\theta$, $b = r\sin\theta$ then keeping r fixed ensures constant W. Then

$$U \propto [\sin^2\theta + 2\sin\theta\cos\theta\cos\phi - \cos^2\theta] \propto [-\cos 2\theta + \cos\phi\sin 2\theta]. \qquad (5.22)$$

Setting the partial derivatives of U with respect to θ and ϕ to zero, we have

$$\sin\phi\sin 2\theta = 0, \qquad \sin 2\theta + \cos\phi\cos 2\theta = 0 \qquad (5.23)$$

so that either (1) $\sin 2\theta = 0$ and $\cos\phi = 0$, or (2) $\phi = 0$ and $\tan 2\theta = -1$, or (3) $\phi = \pi$ and $\tan 2\theta = +1$. This translates into the cases

(1) $a = 0$ or $b = 0$ and $U = \pm\frac{1}{2}k\omega r^2$ (normal or lateral motion only, either swim direction)

(2) $\phi = 0$ and $a = b(\sqrt{2} - 1)$ so that $U = \frac{1}{\sqrt{2}}k\omega r^2$ (simplectic, opposite to wave).

(3) $\phi = \pi$ and $b = a(\sqrt{2} - 1)$ and $U = -\frac{1}{\sqrt{2}}k\omega r^2$ (antiplectic, same direction as wave.)

We see that combining lateral and normal cilial displacements can increase the swimming speed by a factor of $\sqrt{2}$ (or alternatively reduce the power required to travel at a given speed by that factor.) The simplectic and antiplectic modes have the same efficiency; indeed, the organisms *Opalina* and *Paramecium* arguably and approximately use the simplectic and antiplectic cases (2) and (3) respectively.

BioFluids Lecture 6:   Swimming at higher Reynolds number

We have shown that an organism covered in a sheet of cilia, undulating about $y = 0$, can swim at low Reynolds number $R \ll 1$ by adopting the travelling wave shape

$$x_s = x + a\cos(\xi - \phi), \qquad y_s = y_0 + b\sin\xi \qquad \text{where} \quad \xi = kx - \omega t. \qquad (6.1)$$

assuming $ka \ll 1$, $kb \ll 1$. We show now that in this long wave limit, we can also include inertia in the theory, provided also $a\omega, b\omega \ll \nu k$ where ν is the kinematic viscosity. Non-dimensionalising space, time and the streamfunction ψ with respect to k^{-1}, ω^{-1} and ω/k^2, the two-dimensional vorticity equation is

$$R(\Omega_t + \mathbf{u} \cdot \nabla\Omega) = \nabla^2\Omega \qquad \text{where} \quad \Omega = -\nabla^2\psi, \qquad (6.2)$$

where we have defined a suitable Reynolds number

$$R = \frac{\omega}{\nu k^2}. \qquad (6.3)$$

If we seek solutions depending only on $\xi = kx - \omega t$ and $\eta = ky$, we have

$$R\left[-\frac{\partial}{\partial\xi} + \psi_\eta\frac{\partial}{\partial\xi} - \psi_\xi\frac{\partial}{\partial\eta}\right]\nabla^2\psi = \nabla^4\psi. \qquad (6.4)$$

We now expand, as before (note ψ_1 and ψ_2 have dimensions length and (length)^2,)

$$\psi = k\psi_1(\xi, \eta) + k^2\psi_2(\xi, \eta). \qquad (6.5)$$

At leading order, inertia only enters in the time derivative and not the nonlinearity,

$$L\psi_1 \equiv \nabla^4\psi_1 + R\frac{\partial}{\partial\xi}\nabla^2\psi_1 = 0, \qquad (6.6)$$

which is to be solved subject to the boundary conditions (see 5.10)

$$\psi_{1\xi}(\xi, 0) = b\cos\xi, \qquad \psi_{1\eta} = a\sin(\xi - \phi), \qquad (6.7)$$

If we seek a solution $\propto e^{i\xi}$, so that $\psi_1'''' + (iR - 2)\psi_1'' + (1 - iR)\psi_1 = 0$, we find

$$\psi_1 = \Re e\left[\left(Ae^{-\eta} + Be^{-\lambda\eta}\right)e^{i\xi}\right], \qquad (6.8)$$

where $\Re e$ denotes the real part and

$$\lambda = \sqrt{1 - iR}, \qquad A = \frac{(\lambda + 1)}{R}(\lambda b + ae^{-i\phi}), \qquad B = -\frac{(\lambda + 1)}{R}(b + ae^{-i\phi}). \qquad (6.9)$$

We note that the boundary layer behaviour we associate with high R already manifests itself in one of the exponentials in (6.8).

At next order, we begin to get quadratic interactions,

$$L\psi_2 = R\left[\psi_{1\eta}\frac{\partial}{\partial\xi}\nabla^2\psi_1 - \psi_{1\xi}\frac{\partial}{\partial\eta}\nabla^2\psi_1\right].\tag{6.10}$$

The boundary conditions on $\eta = 0$ are given by (6.8) substituted into (5.12).

However, as we are mainly interested in the mean swimming speed, it is easier to average the equations over time (or equivalently over ξ) before solution. We use the fact that if $p = \Re(Pe^{i\omega t})$ and $q = \Re(Qe^{i\omega t})$ then the time average of pq is $\frac{1}{2}\Re(PQ^*)$, where the $*$ denotes a complex conjugate. We take the average of (6.10) with (6.8) to obtain

$$\overline{\psi}_{\eta\eta\eta\eta} = -\tfrac{1}{2}R^2\,\Re\left[AB^*(1+\lambda^*)e^{-(1+\lambda^*)\eta} + |B|^2(\lambda+\lambda^*)e^{-(\lambda+\lambda^*)\eta}\right],\tag{6.11}$$

where $\overline{\psi}(\eta)$ is the mean of $\psi_2(\xi,\eta)$ over a wave period. Equation (6.11) can be integrated four times. At infinity we impose $\overline{\psi} \sim U\eta$ where U is to be found. The boundary condition on the plate come from averaging (6.8) substituted into (5.12).

$$\overline{\psi}_\eta(0) = \tfrac{1}{2}\Re\left[\lambda b^2 + (\lambda+1)abe^{-i\phi} - a^2\right].\tag{6.12}$$

We arrive with the result that

$$\overline{\psi}(\eta) = U\eta - \tfrac{1}{2}R^2\,\Re\left[AB^*(1+\lambda^*)^{-3}e^{-(1+\lambda^*)\eta} + |B|^2(\lambda+\lambda^*)^{-3}e^{-(\lambda+\lambda^*)\eta}\right]\tag{6.13}$$

where the swim speed U is given by

$$U = \tfrac{1}{2}\Re\left[b^2\lambda + (\lambda+1)abe^{-i\phi} - a^2 - R^2\left(AB^*(1+\lambda^*)^{-2} + (\lambda+\lambda^*)^{-2}|B|^2\right)\right].\tag{6.14}$$

Setting $R = 0$, we recover the low Reynolds number swim speed we found earlier. We can now investigate the effect on U of varying R as well as the gait parameters a, b and ϕ. The first correction to U for small R is $\frac{1}{4}Rab\sin\phi$. We look at some special cases. See figure.

If we set $a = 0$, then after some algebra we find

$$U = \tfrac{1}{4}b^2\left[1 + \frac{1}{F(R)}\right]\qquad\text{where}\quad F(R) = \left[\frac{1+\sqrt{(1+R^2)}}{2}\right]^{1/2}.\tag{6.15}$$

The function $1/F(R)$ decreases from 1 to 0 as the Reynolds number increases. The corresponding dimensional swim speed U_{dim} decreases from $\frac{1}{2}b^2k\omega$ to $\frac{1}{4}b^2k\omega$.

We can also evaluate the swim speed easily when $b = 0$. We then find that the dimensional swim speed is

$$U_{dim} = -\tfrac{1}{2}a^2k\omega\left(\frac{3}{2} - \frac{1}{2F(R)}\right).\tag{6.16}$$

This time, the speed increases as R increases from $\frac{1}{2}a^2k\omega$ to $\frac{3}{4}a^2k\omega$ (in the opposite direction). We can also work out the rate of working in this case, generalising (5.18). We find that when either $a = 0$ or $b = 0$,

$$W = \tfrac{1}{2}\omega^2k^2(a^2+b^2)(1+F(R)).\tag{6.17}$$

This increases as $\sqrt{R}$ for moderately large R, so that in some sense it gets harder to swim by this mechanism as the Reynolds number increases.

It is rare to be able to find a flow for all values of R; of course we have only done so in the limit $kR \to 0$. We now begin a more general discussion of swimming at high R.