

Flow Due to the Motion of Cilia

Theodore A. Wilson

Department of Aerospace Engineering
and Mechanics, University of Minnesota

and

Kristian E. Schreiner

Department of Mathematics, University
of Oslo

A model, in which the exposed surface of the cilia covering a cell are assumed to form a moving boundary, is analyzed to determine the relation between the fluid motion and the wave motion in the wall. The results show that the direction of the mean fluid motion far from the wall may either be the same or opposite to the direction of wave propagation, depending on whether the wave is predominantly a transverse or longitudinal wave. Similarities between the two patterns of wave motion which are observed in cilia and the two optimum waves for the model are pointed out. The results of the analysis of the forces acting on the wall supports Schreiner's hypothesis that the "effective stroke" of the cilium is a passive motion and the "recovery stroke" is the working stroke.

Motility of single cells and fluid transport in larger organisms are often accomplished by the motion of cilia or flagella. For example, mammalian sperm, as shown in figure 1, are propelled by the motion of a tail. Thrust is developed by a transverse wave moving down the tail. The drag coefficient for flow in a direction normal to a cylinder axis is larger than the drag coefficient for flow along the cylinder axis (Hancock 1953), so the direction of the force acting on a cylinder will lie closer to the normal to the cylinder than the direction of the relative velocity between the fluid and the cylinder. A transverse wave passing along a flagellum will produce a net force on the body in the direction opposite to the direction of propagation of the wave, and rotation of a helical flagellum will produce a net force along the axis.

In other cases, the surface of the cell is covered with cilia and the motion of the cilia are metachronally coordinated to form waves, which propagate over the surface. In these cases, the mechanism which produces the motion of the cell is not clearly established. Examples of the two patterns of ciliary motion are shown in figure 2. The beat of an individual cilium is described as follows. In the first phase of the motion, called the effective stroke, the cilium remains straight, or nearly so, except near the base and rotates like a rigid rod around a hinge at the base. In the second phase, the recovery stroke, a bend moves outward from the base to the tip leaving the cilium straight for the beginning of the next effective stroke. The relation between

the ciliary beat and the metachronal wave may be such that the direction of the effective stroke is opposite to the direction of wave propagation, as in figure 2a, or the same, as in figure 2b. These two relations are called antiplectic metachronism and symplectic metachronism respectively. There are also cases where the ciliary beat takes place in a plane normal to the direction of wave propagation but this only seems to occur when the cilia do not cover a plane but are found along a narrow band on the cell surface.

Most biologists working in this field seem to believe that the mechanism by which the motion of the cilia produces a fluid motion is similar to the mechanism described above for propulsion by the motion of a flagellum. That is, the force on the cilium is greater during the effective stroke than during the recovery stroke because the cilium moves normal to its axis during this stroke and more nearly along its axis in the recovery stroke. For example Sleight (1969) says that "a cilium produces movement by a swing which has analogies with the stroke of an oar" and, in another place (1962), "cilia probably use more energy in the effective stroke than in the recovery stroke". It is, in fact, observed that for both symplectic and antiplectic metachronism, the cell motion is in the direction opposite to the direction of the effective stroke. However, from this view of the mechanics there is no functional reason for the ciliary beats being organized into waves and no particular relation between the direction of the wave motion and the direction of the cell

motion would be expected.

In an earlier report, Schreiner (1971), by considering the internal mechanics of the cilium, has argued that it is much more reasonable that the "recovery stroke" is in fact the active stroke and that the "effective stroke" may be a passive motion of the cilium. If work is being done during the effective stroke, a large moment must be developed at the base which acts over a large deformation and, at the same time, a particular distribution of moments is required in the rest of the cilium to keep that part of the cilium straight. The structure of the cilium appears to be uniform along its length and there is no evidence that it is adapted to providing the moments which would be required to produce the observed motion during the effective stroke. On the other hand, it is easy to imagine a flow which could produce this motion by dragging the cilium with it. Schreiner has suggested a simple mechanism for producing the wave of bending which propagates along the cilium during the recovery stroke. A distinctive feature of the structure of cilia is the nine longitudinal filaments evenly distributed around a cylinder parallel to the ciliary axis. Studies on cilia in different stages of bending show that these filaments are inextensible while the transverse dimension of the filament pattern seems to be constant during bending. If bonds are formed between the filaments and the matrix of the cilium, the cilium would be rigid and Schreiner suggests that a wave of bond formation or a wave of straightening moves out along the cilium during

the recovery stroke pushing the bend ahead of it. Certainly it is unlikely that the motion of the cilium during the recovery stroke could be produced as a passive response to the flow.

Taylor (1951) has analyzed the viscous flow due to a transverse wave propagating along a sheet and has shown that the sheet moves in a direction opposite to the direction of wave propagation. This was intended to be a model for the action of a flagellum, but, in a later paper (1952), he analyzes the flow past a cylinder and applies these results to the flagellum. His earlier work seems to be more useful as a model for propulsion by the motion of cilia. Reynolds (1965) and Drummond (1966) have extended Taylor's work but the case for which the longitudinal displacements of the wall are as large as the transverse displacements has not been treated. In this paper, Taylor's analysis is used with a model of the boundary condition imposed on the flow by the motion of the cilia. The object is to show that the organization of the ciliary motion into waves is important for producing a fluid motion and, by calculating the forces which act on the boundary, to provide information on the question of the mechanics of the ciliary beat.

Analysis of the flow.

Model. It would be difficult to formulate a model for the flow in the region in which the cilia lie. Perhaps the cilia could be represented as a moving porous medium, but it may not be reasonable to neglect the fact that the properties of the medium are not uniform, steady,

or isotropic. For example, during the recovery stroke, the cilia form a dense mat on the outer surface of this region.

In order to analyze the flow outside the region of the cilia, a model for the boundary condition at the surface separating the two regions is required. It is assumed that this surface is a wall made up of the locus of the exposed surfaces of the cilia and if the motion of the cilia is assumed to be given, the analysis of the outside flow is uncoupled from the description of the flow through the cilia. The points on the surface are assumed to move sinusoidally in the x and y direction so that the position (X,Y) of a point on the wall with mean position $(x,0)$ is given by

$$\begin{aligned} X &= a \sin(\omega t - kx) \\ Y &= b \sin(\omega t - kx + \phi) \end{aligned} \tag{1}$$

In this model, which is illustrated in figure 3, the motion of the tips of the cilia which make up the wall is organized into a sinusoidal wave in which the amplitude of the longitudinal motion is a , the amplitude of the transverse motion is b and the transverse motion leads the longitudinal motion by the phase angle ϕ .

Solution. It is assumed that the stream function is expanded in a power series in the parameters (ak) and (bk) . The stream function which satisfies the equation for viscous flow, $\nabla^4 \Psi = 0$, and satisfies the boundary condition to second order is given by

$$\begin{aligned} \frac{k^2}{\omega} \Psi = & -\alpha\eta e^{-\eta} \cos z - \beta(1+\eta)e^{-\eta} \sin(z+\phi) \\ & + \left[-\frac{1}{2}\alpha^2 \cos 2z + \frac{1}{2}\beta^2 \cos(2z+2\phi) - \alpha\beta \sin(2z+\phi) \right] \eta e^{-2\eta} \\ & + \left[\frac{1}{2}\alpha^2 - \frac{1}{2}\beta^2 - \alpha\beta \sin\phi \right] \eta \end{aligned} \quad (2)$$

In equation (2), $\alpha = ka$, $\beta = kb$, $\eta = ky$ and $z = (\omega t - kx)$. The fluid velocity components, u and v , are given by equation (3) and (4).

$$\begin{aligned} \frac{k}{\omega} u = & -\frac{k}{\omega} \frac{\partial \Psi}{\partial y} = \alpha(1-\eta)e^{-\eta} \cos z - \beta\eta e^{-\eta} \sin(z+\phi) \\ & + \left[\frac{1}{2}\alpha^2 \cos 2z - \frac{1}{2}\beta^2 \cos(2z+2\phi) + \alpha\beta \sin(2z+\phi) \right] (1-2\eta)e^{-2\eta} \\ & + \left[-\frac{1}{2}\alpha^2 + \frac{1}{2}\beta^2 + \alpha\beta \sin\phi \right] \end{aligned} \quad (3)$$

$$\begin{aligned} \frac{k}{\omega} v = & \frac{k}{\omega} \frac{\partial \Psi}{\partial x} = \alpha\eta e^{-\eta} \sin z + \beta(1+\eta)e^{-\eta} \cos(z+\phi) \\ & + \left[-\alpha^2 \sin 2z + \beta^2 \sin(2z+2\phi) + 2\alpha\beta \cos(2z+\phi) \right] \eta e^{-2\eta} \end{aligned} \quad (4)$$

It can be shown that this solution satisfies the boundary conditions on u and v to second order in α and β . That is, $u(x+X, Y) = a\omega \cos(\omega t - kx)$ and $v(x+X, Y) = b\omega \cos(\omega t - kx + \phi)$.

Discussion. There is, therefore, a steady flow of second order in α and β far from the body. Relative to the fluid far from the body, the body moves in the x -direction with speed U given by equation (5)

$$U = \frac{\omega}{k} \left(\frac{1}{2}\alpha^2 - \frac{1}{2}\beta^2 - \alpha\beta \sin\phi \right) \quad (5)$$

For a purely transverse wave, $\alpha = 0$, the body moves in the direction opposite to the wave, the result obtained by Taylor. For a purely longitudinal wave, $\beta = 0$, however, the body moves in the direction of the wave. The rate of energy dissipation per unit surface area, to lowest order, is $\frac{\mu\omega^2}{k} (\alpha^2 + \beta^2)$ where μ is the coefficient of viscosity. There are therefore two waves for which the distance the body moves per unit energy loss is optimized. These are the wave for which $\phi = -90^\circ$ and $\alpha/\beta = 2.4$ and the wave with $\phi = +90^\circ$, $\beta/\alpha = 2.4$. The first is predominantly a longitudinal wave, the wall particles move in a counterclockwise direction around an ellipse with the long axis horizontal and the body moves in the direction of the wave. The second optimum wave is predominantly a transverse wave, the wall particles move in a clockwise direction around an ellipse with the long axis vertical and the body moves in a direction opposite to the wave.

These two optimal waves can be compared with the patterns of ciliary motion shown in figure 2. In the antiplectic wave, the forward and backward horizontal excursions of the tip of the cilium relative to the base are nearly equal so that the ratio of the horizontal to the vertical amplitude of the motion is large. The effective stroke and the recovery stroke are combined, with the proper direction of the effective stroke, so that the y displacement of the tip lags behind the x displacement by 90° . The tip of the cilium moves in a counterclockwise direction around an elliptic path with the long axis horizontal and the body moves in the same direction as the wave. In the symplectic metachronal wave, the tip of the cilium lies

on the same side of the base during the entire beat. In this way, the transverse motion of the tip has a larger amplitude than the longitudinal motion. The tip lies to the right of the base and the effective stroke is in the direction of the wave motion so the tip follows an elliptic path in a clockwise direction and the body moves in the direction opposite to the wave. This motion does not correspond as closely to the second optimum wall motion as the antiplectic wave corresponds to the first optimum. The phase angle ϕ is greater than 90° and the ratio β/α is only a little larger than one.

The forces acting on the wall can be calculated from the velocity field. The shear stress acting on the wall, $\tau_{xy}(x,Y)$ is given by equation (6).

$$\begin{aligned} \frac{1}{\mu\omega} \tau_{xy}(x,Y) = & - 2\alpha \cos z + \beta^2 + 2\alpha\beta \sin\phi \\ & - 2\alpha^2 \cos 2z + \beta^2 \cos(2z+2\phi) - 2\alpha\beta \sin(2z+\phi) \end{aligned} \quad (6)$$

The first order term in the shear stress is 180° out of phase with the horizontal component of the wall velocity. This term represents a force which opposes the wall motion throughout the beat. For the first optimal wave, $\phi = -90^\circ$. At $z = 0$ and $z = 180^\circ$, the middle of the recovery stroke and effective stroke, respectively, the value of the second order term is $-2\alpha^2$. The second order terms therefore increase the force opposing the wall motion during the recovery stroke, but decreases the magnitude of the force opposing the motion in the effective stroke so that more work is done during the

recovery stroke. For the motion shown in figure 2a, the value of α is greater than one. It may be that the force on the wall is, in fact, in the direction of motion during the effective stroke, but this can not be predicted on the basis of the expansion technique used in this analysis. The evaluation of the forces acting on the wall in the middle of the effective stroke and recovery stroke of the symplectic wave is more complicated. The result of this computation does not show that the force opposing the motion is less during the effective stroke than during the recovery stroke. However, the cilium is not quite straight during the effective stroke of the beat shown in figure 2b. A bend which is smaller and opposite in direction from the bend in the recovery stroke, moves out along the cilium during this stroke. Sleight (1968) points out that "this organelle could be described as a short flagellum with a slightly asymmetric undulation".

Conclusion. The analysis of this model shows that the swimming of cells which are covered by moving cilia may depend on the organization of the ciliary beats into waves. The anti-plectic and symplectic waves which are observed appear to be representations of the two optimum wave motions of the model. From this view of the swimming mechanism, there is a functional reason for the observed relations between the ciliary beat and the metachronical wave.

The analysis also supports Schreiner's contention that it is unlikely that the cilium exerts a large force on the fluid when it is rotating rigidly around its base. The force acting

on the wall in the model for the antiplectic wave is less during the phase representing the effective stroke than in the phase representing the recovery stroke. The effective stroke may, in fact, be a passive motion of the cilium. It appears from the analysis of the model, however, that the effective stroke in the symplectic wave is not a passive motion and the swimming of cells in which the ciliary beats are organized into symplectic waves may be due to both the effect of the wave and the effect of the cilia acting as flagella.

An analysis of a more realistic model for the flow around the cilia is required in order to substantiate these last conclusions.

This work was supported by grants from the USPHS and The Norwegian Council for Scientific and Industrial Research. Figure 2 is reproduced from Sleigh (1962) by permissions of author and publisher.

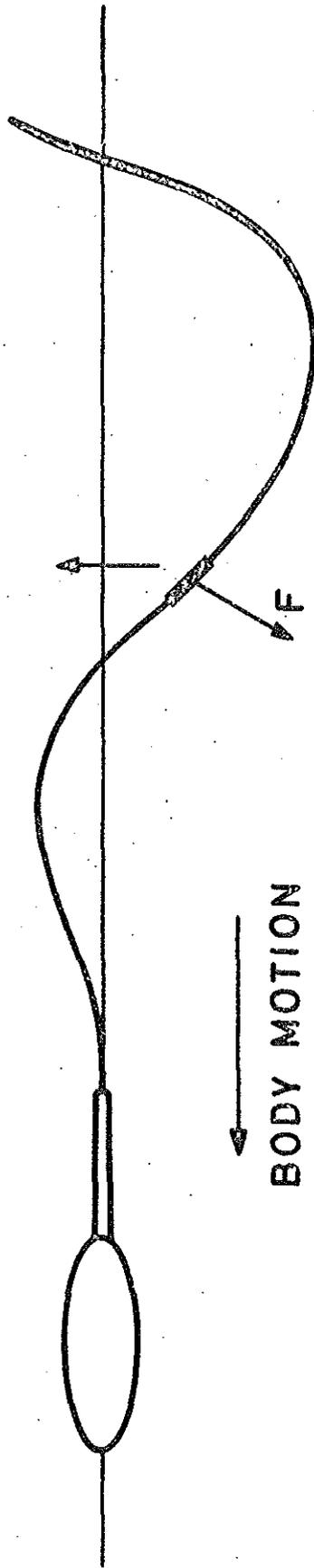
References

- Drummond, J.E. 1966, J.Fluid Mech. 25, 787
- Hancock, G.J. 1953, Proc. Roy. Soc. A.217, 96
- Reynolds, A.J. 1965 J.Fluid Mech. 23, 241
- Schreiner, K.E. 1971, Preprint nr. 1, Inst.Math.Univ.Oslo
- Sleigh, M.A. 1962, The Biology of Cilia and Flagella.
Oxford: Pergamon Press.
- Sleigh, M.A. 1968, Aspects of Cell Motility.
Cambridge: University Press.
- Sleigh, M.A. 1969, Handbook of Molecular Cytology. (ed. by
A. Lima-de-Faria) Amsterdam: North Holland Publishing Company.
- Taylor, G.I. 1951, Proc. Roy. Soc. A.209, 447
- Taylor, G.I. 1952, Proc. Roy. Soc. A.211, 225

Figure Captions

- Figure 1 Diagram of the forces acting on a sperm propelled by a transverse wave propagating down the tail.
- Figure 2 Diagram of the ciliary beat in a diaplectic metachronal wave (a) and a symplectic metachronal wave (b). (From Sleight 1962).
- Figure 3 Diagram of the model for the wall motion. The dashed ellipse is the locus of positions of a wall particle.

WAVE MOTION



BODY MOTION



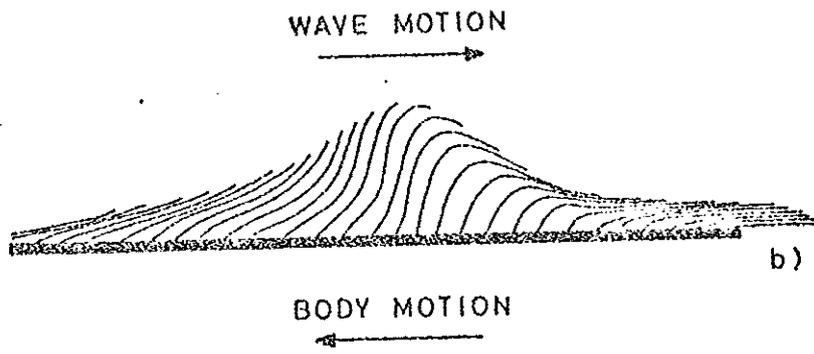
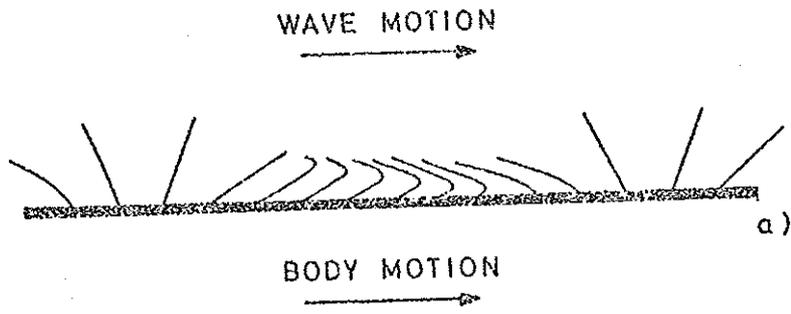
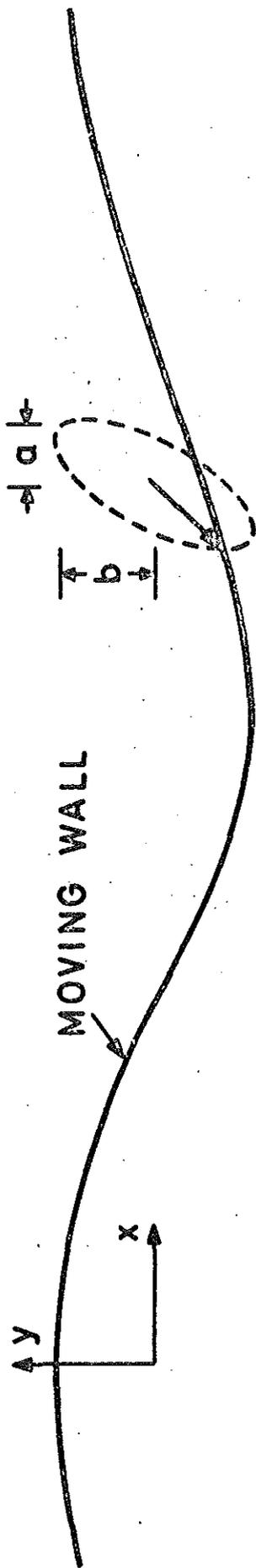


Fig 2

OUTSIDE REGION



REGION OF CILIA



Fig 3