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Analysis of the swimming of microscopic organisms

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Large objects which propel themselves in air or water make use of inertia in the surrounding fluid. The propulsive organ pushes the fluid backwards, while the resistance of the body gives the fluid a forward momentum. The forward and backward momenta exactly balance, but the propulsive organ and the resistance can be thought about as acting separately. This conception cannot be transferred to problems of propulsion in microscopic bodies for which the stresses due to viscosity may be many thousands of times as great as those due to inertia. No case of self-propulsion in a viscous fluid due to purely viscous forces seems to have been discussed.

The motion of a fluid near a sheet down which waves of lateral displacement are propagated is described. It is found that the sheet moves forwards at a rate $2\pi^2b^2/\lambda^2$ times the velocity of propagation of the waves. Here b is the amplitude and λ the wave-length. This analysis seems to explain how a propulsive tail can move a body through a viscous fluid without relying on reaction due to inertia. The energy dissipation and stress in the tail are also calculated.

The work is extended to explore the reaction between the tails of two neighbouring small organisms with propulsive tails. It is found that if the waves down neighbouring tails are in phase very much less energy is dissipated in the fluid between them than when the waves are in opposite phase. It is also found that when the phase of the wave in one tail lags behind that in the other there is a strong reaction, due to the viscous stress in the fluid between them, which tends to force the two wave trains into phase. It is in fact observed that the tails of spermatozoa wave in unison when they are close to one another and pointing the same way.

Introduction

The manner in which a fish swims by causing a wave of lateral displacement to travel down its body from head to tail seems to be understood through the work of James Gray and his colleagues. This movement gives rise to circulations round the body which, in a fluid of small viscosity like water, are necessary to produce a forward force by dynamical reaction. In other words, the creature owes its ability to propel itself entirely to the inertia forces set up in the surrounding fluid by its muscular movements. Viscosity is important only in so far as it plays a part in the mechanics of the boundary layer, which in turn plays a part in determining the magnitude of the circulations with which the inertia reaction of the water is associated.

The propelling organs of some very small living bodies (spermatozoa for instance) bear a superficial resemblance to those of fish, in that propulsion is achieved by sending waves of lateral displacement down a thin tail or flagellum. The direction of movement of the organism is, like that of the fish, opposite to that of propagation of the waves of lateral displacement. The dynamics of a body as small as a spermatozoon—say 5×10^{-3} cm. long with a tail 10^{-5} cm. diameter—swimming in water must, however, be completely different from that of a fish. If L is some characteristic length defining the size of a body moving in water with velocity V, in a fluid of density ρ, and viscosity μ, the Reynolds number, $R = LV\rho/\mu$, expresses in numerical form the order of magnitude of the ratio

$$\frac{\text{stress in fluid due to inertia}}{\text{stress due to viscosity}}.$$

In most fishes R is of order many thousands, in a tadpole it is perhaps of order 10^2, and in bodies of the size of spermatozoa it is of order 10^{-3} or less. It will be seen, therefore, that the forces due to viscosity, which may legitimately be neglected in comparison with inertia forces, in studying the motions of fish, may be thousands of times as great as the inertia forces in the case of the smallest swimming bodies.

Reynolds number is usually defined in relation to a body moving steadily through a fluid with velocity V. In cases where the body is vibrating the inertia stresses arise from the reaction between the vibrating surface and the surrounding fluid. The number which corresponds with Reynolds number in describing the order of magnitude of the ratio

$$\frac{\text{stress due to inertia}}{\text{stress due to viscosity}} \text{ is } nL^2\rho/\mu,$$

where n is the frequency of vibration. In the case of a spermatozoon n is of order 100 c./sec., and μ for water is 10^{-2}. The length which is of importance in considering the stress in the fluid is the diameter of the tail rather than its length, so that L is of order 10^{-5} cm. and $nL^2\rho/\mu$ is of order 10^{-6}. In considering the motions of spermatozoa therefore it is necessary only to take account of viscous forces. Inertia forces may legitimately be neglected.

These considerations naturally give rise to the following question. How can a body propel itself when the inertia forces, which are the essential element in self-propulsion of all large living or mechanical bodies, are small compared with the forces due to viscosity?

An attempt will be made to answer this question by showing that self-propulsion is possible in a viscous fluid when bodies immersed in it execute movements which bear a strong resemblance to those which spermatozoa are known to make.

Self-propulsion in a viscous fluid

The only problems concerning the motion of solids in viscous fluids which have so far been solved relate to bodies which are moved by the application of an external force like gravity. The motion of spheres and ellipsoids in an infinitely extended fluid under external forces or couples has been analyzed. It has been found that such bodies tend to move along with them a very large volume of the surrounding fluid. Long cylindrical bodies move so much fluid that the whole volume, extending to infinity, moves with the body. The fact that a cylinder in steady motion gives rise to finite fluid velocity at an infinite distance was discussed by Stokes (1851) who also obtained the solution to the problem presented by an oscillating cylinder in which inertia stresses are comparable with those due to viscosity. He pointed out that as the frequency of oscillation decreases the volume of fluid which moves with the cylinder increases till, as the frequency approaches zero, the disturbance tends to extend to infinity.

When large bodies like ships or aeroplanes are propelled by some internal mechanism through a fluid, the mechanics of their motion is always analyzed by considering separately (a) a propelling mechanism like a paddle wheel or airscrew which develops a forward force by pushing fluid backwards, and (b) resistance which arises because the body entrains some of the surrounding fluid and thus gives it a forward momentum. When the self-propelled body is moving at a steady pace it is clear that the backward momentum considered under (*a*) exactly balances the forward momentum of (*b*).

When a body propels itself in a viscous fluid it is still true that the total rate of production of momentum is zero. In other words the resultant force which the fluid exerts on the body must be zero. On the other hand, it is clear that when inertia stresses are negligible compared with those due to viscosity it is no longer possible to use the conception of propulsion as being due to the separable effects of a propulsive unit and fluid resistance. The truth of this statement is at once obvious if the body considered is two-dimensional, in the form of an infinitely long cylinder, for the effect on the fluid of moving the cylinder—considered independently of the propulsive unit—would, as Stokes showed, be to move the whole fluid in which it was immersed. There is no reason to suppose that a self-propelling body would move a great volume of the fluid surrounding it, in fact in the particular problem the solution of which fills most of this paper, the influence of a self-propelling body extends only a very short distance from it.

Provided that no attempt is made to separate propulsion from resistance, but the motions of the whole fluid and the body are considered as inseparable, Stokes's difficulty disappears. Though microscopic swimming creatures are certainly three-dimensional, yet the great simplicity of two-dimensional, compared with three-dimensional analysis, makes it worth while to discuss the problem of self-propulsion in a viscous fluid in two dimensions.

The propelling organ of a spermatozoon is a thin tail down which the organism sends waves of lateral displacement. Whether this tail moves in two or three dimensions is not clear (Rothschild 1951). The analogous two-dimensional problem is that of a sheet down which waves of lateral displacement are propagated. This problem will be investigated with a view to finding out whether such waves can give rise to viscous stresses which drive the sheet forwards.

Waves of small amplitude in sheet immersed in a viscous fluid

Take axes which are fixed relative to the mean position of the particles of the sheet. The waving surface will be taken represented by

$$y_0 = b \sin(kx - \sigma t). \tag{1}$$

The velocity of the wave is σ/k and it moves in the direction x positive. The wave-length is $2\pi/k = \lambda t$ represents time. b, the amplitude, will be assumed small compared with λ. If the sheet is inextensible and the amplitude of the wave small, material particles will oscillate in a path which is nearly parallel to the axis of y, though, as will be seen later, their actual paths are narrow figures of 8. The components of velocity of a particle of the sheet are u_0, v_0 where

$$u_0 = 0, \quad v_0 = \frac{\partial y_0}{\partial t} = -b\sigma \cos(kx - \sigma t). \tag{2}$$

The problem is therefore to find a motion in a viscous fluid which satisfies (2) as a boundary condition on $y_0 = b \sin(kx - \sigma t)$. The field equation which viscous flow in two dimensions satisfies when inertia is neglected is

$$\nabla^4 \psi = 0, \tag{3}$$

where ψ is a stream function and the components of velocity are

$$u = -\frac{\partial \psi}{\partial y}, \quad v = \frac{\partial \psi}{\partial x}. \tag{4}$$

As a first approximation when bk is small assume for ψ

$$\psi = (A_1 y + B_1)\,\mathrm{e}^{-ky} \sin(kx - \sigma t) - Vy. \tag{5}$$

This function satisfies (3). The velocity of the fluid at infinity is V, so that if V has a finite value the particles of the waving surface will move relative to the main body of viscous fluid with velocity $-V$. The conditions to be satisfied at the surface $y_0 = b \sin(kx - \sigma t)$ are

$$\frac{\partial \psi}{\partial x} = v_0 = -b\sigma \cos(kx - \sigma t), \quad -\frac{\partial \psi}{\partial y} = u_0 = 0. \tag{6}$$

To the first order (when bk is small) the values of u and v at $y = 0$ will be the same as those at $y = b \sin(kx - \sigma t)$, so that the boundary conditions (6) are satisfied if

$$-V + (A_1 - B_1 k) \sin(kx - \sigma t) = -u_0 = 0 \tag{7}$$

and

$$B_1 k \cos(kx - \sigma t) = v_0 = -b\sigma \cos(kx - \sigma t). \tag{8}$$

(7) and (8) are satisfied if

$$V = 0, \quad A_1 = B_1 k = -b\sigma. \tag{9}$$

Inserting values of A_1 and B_1 in (5) it is found that

$$\psi = -\frac{b\sigma}{k}(1 + ky)\,\mathrm{e}^{-ky} \sin(kx - \sigma t), \tag{10}$$

and ψ represents the flow near a sheet down which waves of small amplitude are travelling. It will be noticed that since $V = 0$ the waves in the sheet do not propel it through the fluid. This conclusion, however, will be modified when the equations are treated, using a higher order of accuracy than that which led to (7) and (8).

The dissipation of energy can be found by calculating the work done per unit area of the sheet against viscous stress. Its mean value is

$$W = -\overline{\frac{dy_0}{dt} Y_y}, \tag{11}$$

where Y_y is the stress normal to the sheet and (Lamb 1932)

$$Y_y = -p + 2\mu \frac{\partial v}{\partial y}. \tag{12}$$

Here $-p$ is the mean value of the principal stress components. p is described as pressure. The pressure associated with the stream function (10) is

$$p = 2\sigma b k \mu\,\mathrm{e}^{-ky} \cos(kx - \sigma t), \tag{13}$$

and since at the surface $u = 0$, $\partial u/\partial x = 0$ so that $\partial v/\partial y = 0$. Hence

$$W = 2b^2\sigma^2 k\mu\,\overline{\cos^2(kx - \sigma t)} = b^2\sigma^2 k\mu. \tag{14}$$

Since the motion vanishes at infinity, it is clear from what has been said that the total force on the sheet must be zero. In fact the forward component of the force which the pressure exerts on the plate is

$$F_1 = \overline{p\frac{dy_0}{dx}} = -\mu\sigma b^2 k^2. \tag{15}$$

This is negative so that the pressure tends to drive the sheet in the direction $-x$. The force, due to the tangential component of stress at any point, is $\mu(\partial u/\partial y)$. To the first order of small quantities the mean value F_2 of the tangential stress on the sheet is zero, but it must be remembered that the tangential stress actually acts over the wavy surface $y_0 = b\sin(kx-\sigma t)$. Thus taking the variation in tangential stress due to this fact into account, the mean stress is the mean value of $\mu(\partial u/\partial y)$ over this surface is

$$F_2 = \mu\sigma bk\overline{(ky-1)\,\mathrm{e}^{-ky}\sin(kx-\sigma t)}; \tag{16}$$

putting $y = b\sin(kx-\sigma t)$ in (16), and remembering that $\overline{\sin^2(kx-\sigma t)} = \frac{1}{2}$,

$$F_2 = \mu\sigma b^2 k^2. \tag{17}$$

The total mean force per unit area exerted by the fluid on the surface is F_1+F_2. From (15) and (17) it is seen that $F_1+F_2 = 0$, a result which was anticipated on general principles.

Propulsive effect of waves which are not small

It has been shown that waves of small amplitude travelling down a sheet do not give rise to propulsive stresses in the surrounding viscous fluid. It is now proposed to discuss the effect of waves whose amplitude is not so small that terms containing b^2k^2 can be neglected. It does not seem to be possible to discuss by analytical methods waves whose amplitude is unlimited, but it is possible to consider the effect of waves of finite amplitude by expanding the various terms in the mathematical expressions representing the disturbance produced by the waving sheet in powers of bk. This expansion will be carried to include terms containing powers of bk as high as $(bk)^4$. To simplify the analysis the equations will be written in non-dimensional form by taking $k = 1$. If z is written for $x-\sigma t$ the appropriate form to assume for ψ is

$$\frac{1}{\sigma}\psi = \sum_{n\text{ odd}}^{\infty}(A_n y+B_n)\,\mathrm{e}^{-ny}\sin nz + \sum_{n\text{ even}}^{\infty}(C_n y+D_n)\,\mathrm{e}^{-ny}\cos nz - \frac{Vy}{\sigma}. \tag{18}$$

This satisfies $\nabla^4\psi = 0$, and the disturbance rapidly decreases with distance from the sheet.

The term Vy/σ is again inserted to allow for the possibility that the waving sheet may move relatively to the fluid far distant from it with velocity $-V$.

Boundary conditions

It will be assumed that the form of the sheet is

$$y_0 = b\sin z, \tag{19}$$

even when b is not small. The boundary condition which must be satisfied by the fluid in contact with the sheet is that there is no slip at its surface. The fact that the sheet is in the form $y_0 = b\sin z$ controls the component of velocity normal to its surface, but some further physical assumption must be made about the sheet before the component parallel to its surface can be expressed in mathematical form. This assumption will be that the sheet is *inextensible*.

Velocity of particles in an inextensible sheet disturbed by transverse waves

The velocity of the waves is σ. Their external shape can be reduced to rest by imparting to the whole fluid a velocity $-\sigma$. The velocity of particles of an inextensible sheet moving along the fixed curve $y = b\sin z$ is

$$Q = \sigma \times \left(\frac{\text{length of a curve in one wave-length}}{\text{one wave-length}}\right). \tag{20}$$

This ratio is
$$\frac{1}{2\pi}\int_0^{2\pi}(1+b^2\cos^2 z)^{\frac{1}{2}}\,dz. \tag{21}$$

Expanding (21) in powers of b up to b^4

$$\frac{Q}{\sigma} = 1+\tfrac{1}{4}b^2-\tfrac{3}{64}b^4. \tag{22}$$

The velocity components of particles in the sheet relative to axes which travel with the waves are
$$u_1 = -Q\cos\theta, \quad v_1 = -Q\sin\theta, \tag{23}$$

where
$$\tan\theta = \frac{dy_0}{dz} = b\cos z. \tag{24}$$

After some reduction it is found from (22), (23) and (24), retaining all terms up to those containing b^4, that

$$\frac{u_1}{\sigma}+1 = -\tfrac{1}{32}b^4+(\tfrac{1}{4}b^2-\tfrac{1}{8}b^4)\cos 2z-\tfrac{3}{64}b^4\cos 4z, \tag{25}$$

$$\frac{v_1}{\sigma} = -(b-\tfrac{1}{8}b^3)\cos z-(\tfrac{1}{8}b^3)\cos 3z. \tag{26}$$

Since $u_1+\sigma, v_1$ are the components of velocity of the particles of the sheet relative to the original axes the boundary conditions for ψ are

$$-\frac{1}{\sigma}\left[\frac{\partial\psi}{\partial y}\right]_{y=b\sin z} = -\tfrac{1}{32}b^4+(\tfrac{1}{4}b^2-\tfrac{1}{8}b^4)\cos 2z-\tfrac{3}{64}b^4\cos 4z, \tag{27}$$

$$\frac{1}{\sigma}\left[\frac{\partial\psi}{\partial z}\right]_{y=b\sin z} = -(b-\tfrac{1}{8}b^3)\cos z-\tfrac{1}{8}b^3\cos 3z. \tag{28}$$

It will be noticed that if only terms containing b are retained the particles oscillate in the lines parallel to the axis y. If terms containing b^2 and b are retained particles of the sheet traverse paths in the form of figures of 8.

It remains to find the values of $\partial\psi/\partial z$ and $\partial\psi/\partial y$ on the boundary. For this purpose it is convenient to expand ψ near $y = 0$ in powers of y. Thus

$$(A_n y+B_n)\,e^{-ny} = B_n+(A_n-nB_n)\,y+\left(-nA_n+\frac{n^2}{2!}\right)y^2+\left(\frac{n^2}{2!}A_n-\frac{n^3}{3!}B_n\right)y^3+\dots$$

and

$$\frac{d}{dy}(A_n y + B_n)\,\mathrm{e}^{-ny} = A_n - nB_n + 2\left(-nA_n + \frac{n^2}{2!}B_n\right)y + 3\left(\frac{n^2}{2!}A_n - \frac{n^3}{3!}B_n\right)y^2 + \dots .$$

At $y = y_0 = b\sin z$

$$\begin{aligned}\frac{1}{\sigma}\frac{\partial\psi}{\partial y} = {} & \{A_1 - B_1 + y_0(-2A_1 + B_1) + y_0^2(\tfrac{3}{2}A_1 - \tfrac{1}{2}B_1) + y_0^3(-\tfrac{2}{3}A_1 + \tfrac{1}{6}B_1)\}\sin z \\ & + \{C_2 - 2D_2 + y_0(-4C_2 + 4D_2) + y_0^2(6C_2 - 4D_2)\}\cos 2z \\ & + \{A_3 - 3B_3 + y_0(-6A_3 + 9B_3)\}\sin 3z \\ & + \{C_4 - 4D_4\}\cos 4z - V/\sigma,\end{aligned} \tag{29}$$

$$\begin{aligned}\frac{1}{\sigma}\frac{\partial\psi}{\partial z} = {} & [B_1 + y_0(A_1 - B_1) + y_0^2(-A_1 + \tfrac{1}{2}B_1) + y_0^3(\tfrac{1}{2}A_1 - \tfrac{1}{6}B_1)]\cos z \\ & + [D_2 + y_0(C_2 - 2D_2) + y_0^2(-2C_2 + 2D_2)](-2\sin 2z) \\ & + [B_3 + y_0(A_3 - 3B_3)](3\cos 3z) \\ & + D_4(-4\sin 4z).\end{aligned} \tag{30}$$

In order that the boundary conditions may be satisfied for all values of z it is necessary to express terms like $y_0^n\binom{\cos}{\sin}mz$ in (29) and (30) in the form $\Sigma A_l\binom{\cos}{\sin}lz$, l being an integer. The coefficients of $\binom{\cos}{\sin}lz$ in the expressions for the boundary conditions (27) and (28) may then be equated. The expressions necessary for developing the expansions up to terms containing b^4 are given in table 1. Using this table, the coefficients given in table 2 may be equated to zero.

Table 1. Relations necessary for expanding boundary conditions in powers of b up to b^4

$y_0 = b\sin z$		
$y_0\sin z = \tfrac{1}{2}b(1-\cos 2z)$	$y_0^2\sin z = \tfrac{1}{4}b^2(3\sin z - \sin 3z)$	$y_0^3\sin z = \tfrac{1}{8}b^3(3 - 4\cos 2z + \cos 4z)$
$y_0\cos z = \tfrac{1}{2}b\sin 2z$	$y_0^2\cos z = \tfrac{1}{4}b^2(\cos z - \cos 3z)$	$y_0^3\cos z = \tfrac{1}{8}b^3(2\sin 2z - \sin 4z)$
$y_0\sin 2z = \tfrac{1}{2}b(\cos z - \cos 3z)$	$y_0^2\sin 2z = \tfrac{1}{4}b^2(2\sin 2z - \sin 4z)$	
$y_0\cos 2z = \tfrac{1}{2}b(\sin 3z - \sin z)$	$y_0^2\cos 2z = \tfrac{1}{4}b^2(-1 + 2\cos 2z - \cos 4z)$	
$y_0\sin 3z = \tfrac{1}{2}b(\cos 2z - \cos 4z)$		
$y_0\cos 3z = \tfrac{1}{2}b(\sin 4z - \sin 2z)$		

Table 2. Coefficients to be equated to zero in the development of (27) and (28)

1	$(-2A_1 + B_1)\tfrac{1}{2}b + (-\tfrac{2}{3}A_1 + \tfrac{1}{6}B_1)\,\tfrac{3}{8}b^3 - \tfrac{1}{4}b^2(6C_2 - 4D_2) - \tfrac{1}{32}b^4 - \dfrac{V}{\sigma}$	(*a*)
$\sin z$	$(A_1 - B_1) + (\tfrac{3}{2}A_1 - \tfrac{1}{2}B_1)\,\tfrac{3}{4}b^2 - \tfrac{1}{2}b(-4C_2 + 4D_2)$	(*b*)
$\cos 2z$	$-(-2A_1 + B_1)\tfrac{1}{2}b - \tfrac{1}{2}b^3(-\tfrac{2}{3}A_1 + \tfrac{1}{6}B_1) + C_2 - 2D_2 + \tfrac{1}{2}b^2(6C_2 - 4D_2) + \tfrac{1}{2}b(-6A_3 + 9B_3) + \tfrac{1}{4}b^2 - \tfrac{1}{8}b^4$	(*c*)
$\sin 3z$	$-\tfrac{1}{4}b^2(\tfrac{3}{2}A_1 - \tfrac{1}{2}B_1) + (-4C_2 + 4D_2)\tfrac{1}{2}b + A_3 - 3B_3$	(*d*)
$\cos 4z$	$+\tfrac{1}{8}b^3(-\tfrac{2}{3}A_1 + \tfrac{1}{6}B_1) - \tfrac{1}{4}b^2(6C_2 - 4D_2) - \tfrac{1}{2}b(-6A_3 + 9B_3) + C_4 - 4D_4 - \tfrac{3}{64}b^4$	(*e*)
$\cos z$	$B_1 + \tfrac{1}{4}b^2(-A_1 + \tfrac{1}{2}B_1) - 2(C_2 - 2D_2)\,\tfrac{1}{2}b + b - \tfrac{1}{8}b^3$	(*f*)
$\sin 2z$	$\tfrac{1}{2}b(A_1 - B_1) + (\tfrac{1}{2}A_1 - \tfrac{1}{6}B_1)\,\tfrac{1}{4}b^3 - 2D_2 - b^2(-2C_2 + 2D_2) - \tfrac{3}{2}b(A_3 - 3B_3)$	(*g*)
$\cos 3z$	$-\tfrac{1}{4}b^2(-A_1 + \tfrac{1}{2}B_1) + b(C_2 - 2D_2) + 3B_3 + \tfrac{1}{8}b^3$	(*h*)
$\sin 4z$	$-\tfrac{1}{8}b^3(\tfrac{1}{2}A_1 - \tfrac{1}{6}B_1) + b^2(-C_2 + D_2) + \tfrac{3}{2}b(A_3 - 3B_3) - 4D_4$	(*i*)

It will be noticed that C_4 and D_4 occur only in (e) and (i). The constants A_1, B_1, C_2, D_2, A_3 and B_3 may be obtained by equating (b), (c), (d), (f), (g), (h) to zero. The equation (a) can then only be satisfied when V has a particular value. It will be noticed that in order that (b) and (f) may be satisfied it is necessary that A_1 and B_1 shall be of the form

$$A_1 = -b + \text{higher powers of } b$$

and

$$B_1 = -b + \text{higher powers of } b.$$

In fact, in order that the six equations may be satisfied for all values of b it is necessary that A_1, B_1, C_2, D_2, A_3 and B_3 shall be of the form

$$A_1 = -b(1+\alpha b^2), \quad B_1 = -b(1+\beta b^2), \quad C_2 = \gamma_1 b^2 + \gamma_2 b^4,$$
$$D_2 = \delta_1 b^2 + \delta_2 b^4, \quad A_3 = \epsilon b^3, \quad B_3 = \eta b^3.$$

It remains to determine $\alpha, \beta, \gamma_1, \gamma_2, \delta_1, \delta_2, \epsilon, \eta$ from the equations (b), (c), (d), (f), (g) and (h). It can be verified that the appropriate values are

$$\alpha = -\tfrac{1}{2}, \quad \beta = -\tfrac{1}{4}, \quad \gamma_1 = \tfrac{1}{4}, \quad \gamma_2 = -\tfrac{1}{6}, \quad \delta_1 = 0, \quad \delta_2 = \tfrac{1}{12}, \quad \epsilon = 0, \quad \eta = -\tfrac{1}{12}. \tag{31}$$

Inserting these in (e) and (i) it is found that

$$C_4 = \tfrac{29}{192} b^4, \quad D_4 = \tfrac{1}{24} b^4. \tag{32}$$

Propulsive effect of propagating transverse waves in a sheet

(a) may be written in the form

$$\frac{V}{\sigma} = \tfrac{1}{2} b^2 + (\alpha - \tfrac{1}{2}\beta + \tfrac{3}{16} - \tfrac{3}{2}\gamma_1 - \tfrac{1}{32})\, b^4. \tag{33}$$

Hence from (31)

$$\frac{V}{\sigma} = \tfrac{1}{2} b^2 (1 - \tfrac{19}{16} b^2).$$

In the non-dimensional units the velocity of the wave relative to the particles of the sheet is σ. When dimensional units are used (33) is written

$$\frac{Vk}{\sigma} = \tfrac{1}{2} b^2 k^2 (1 - \tfrac{19}{16} b^2 k^2),$$

or if the velocity of the waves of lateral displacement relative to the material of the sheet is V

$$\frac{V}{U} = \frac{2\pi^2 b^2}{\lambda^2}\left(1 - \frac{19}{4}\frac{\pi^2 b^2}{\lambda^2}\right). \tag{34}$$

V is the velocity of the fluid at infinity relative to the material of the sheet. Since V is positive the sheet moves with velocity $-V$ relative to the fluid at infinity when waves of lateral displacement travel with velocity $+U$ down the sheet.

Viscous fluid on both sides of the sheet

In the foregoing discussion the reaction of the viscous fluid on one side only of the waving sheet has been considered. In applying the results to the swimming of microscopic organisms it is necessary to suppose that the sheet is in contact with the fluid on both surfaces. In that case for a wave of given amplitude the sheet will move relative to the fluid at infinity at the same speed V that has been calculated when fluid on one side only was contemplated. On the other hand, the rate of dissipation of energy is $2W$ instead of W where W has the same meaning as in (14).

It has been proved therefore that when small but not infinitesimal waves travel down a sheet immersed in a viscous fluid they propel the sheet at a rate which is $2\pi^2 b^2/\lambda^2$ times the wave velocity and in the opposite direction to that of propagation of the waves. It would have been less laborious to calculate only the first term of the expression for V/U. The second term containing the factor b^4/λ^4 was calculated in order to form some idea of how large the amplitude might be before a serious error might be expected in the analysis. The outside limit at which the formula might be expected to give reasonably accurate results would be when the second term was, say, one-quarter, as big as the first. That is when

$$\frac{b}{\lambda} = \sqrt{\frac{1}{19\pi^2}} = 0{\cdot}073.$$

In that case $$V/U = \tfrac{3}{4}(\tfrac{2}{19}) = 0{\cdot}079.$$

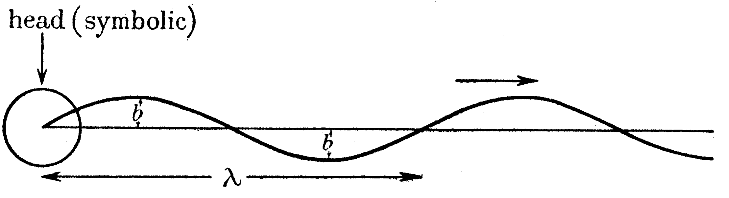

FIGURE 1. Symbolic representation of microscopic organism swimming. Shape of waving tail when $kh = 0{\cdot}25$, $b/\lambda = 0{\cdot}073$; $\rightarrow$, direction of propagation of waves in tail.

The shape of the tail in this case is shown in figure 1. A tail of the shape shown in figure 1 would have to oscillate $1/0{\cdot}079 = 12{\cdot}7$ times in order to progress 1 wavelength. It will be noticed that the wave shown in figure 1 is not very large. It may well be that waves of larger amplitude would propel the sheet more than $1/12{\cdot}7$ of a wave-length per oscillation, but the method of analysis here adopted could hardly be used in discussing such a case without great labour. The Southwell's relaxation technique might perhaps be employed.

Stress in the tail

The internal mechanism necessary to produce lateral motion can only be due to tensions and compressions acting across each normal section of the tail so as to produce a couple M. This couple varies along the tail. Its magnitude can be calculated when the distribution of pressure along the tail is known. In the case of a waving sheet which has fluid on both sides the equilibrium equation is

$$\frac{dM}{dx} = F, \quad \frac{dF}{dx} = -P, \tag{35}$$

where P is the difference of pressure on the two sides of the sheet. The pressure variations are equal in magnitude but of opposite signs on the two sides of the sheet. Equation (13) therefore gives

$$P = 4\sigma bk\mu \cos(kx - \sigma t)$$

so that (35) becomes $$\frac{d^2M}{dx^2} = -4\sigma bk\mu \cos(kx - \sigma t).$$

Hence $$M = \frac{4\sigma b\mu}{k}\cos(kx - \sigma t).$$

The maximum value of M is $$\frac{4\sigma b\mu}{k} \quad \text{or} \quad 4nb\mu\lambda,$$

where n is the frequency of vibration of the tail. The magnitude of the maximum stress can only be calculated if the thickness d of the tail is known. The minimum possible value of the maximum stress is then

$$\frac{4M}{d^2} \quad \text{or} \quad 16\mu bn\lambda/d^2.$$

Taking the case when $\lambda = 10^{-3}$ cm., $\mu = 10^{-2}$, $b = \frac{1}{4}\lambda$, $d = 10^{-5}$ cm., $n = 50$ c./sec., this stress is 2×10^4 or 20 g. weight/sq. cm.

Mechanical reaction between neighbouring waving tails

It has been observed that when two or more spermatozoa are close to one another there is a strong tendency for their tails to vibrate in unison. James Gray (1928) writes: 'Numerous authors have observed that when the heads of individual spermatozoa are in intimate contact their tails beat synchronously and a very striking example of the phenomenon can be observed in *Spirochaeta balbianii*.' Figure 2, which is reproduced from figure 78, p. 119 of James Gray's book *Ciliary movement* (1928), shows his idea of the way in which aggregates of these organisms which vibrate in unison are formed. Rothschild (1949) attributes certain comparatively large-scale motions in dense suspensions of bull or ram spermatozoa to 'periodic aggregation of spermatozoa the tails of which probably beat synchronously in the aggregations'.

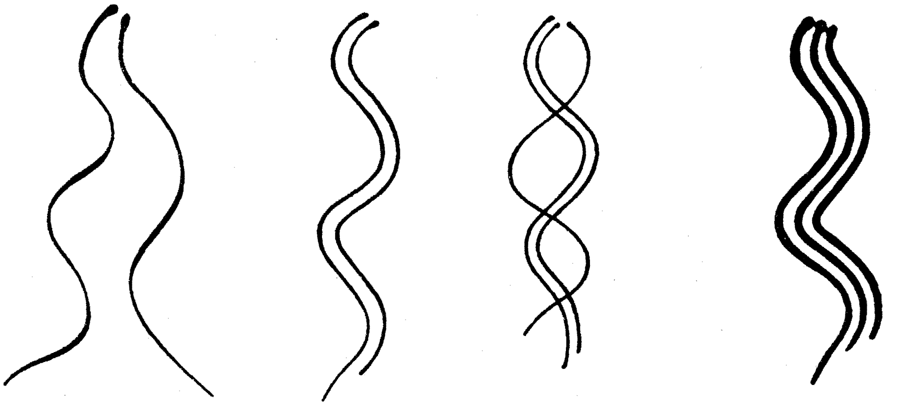

FIGURE 2. *Spirochaeta balbianii* forming aggregates, the individuals in which soon establish synchronous movements. (Reproduced from Gray's *Ciliary movement*.)

Among the various possible explanations of this phenomenon it might be supposed that the stresses set up in the viscous fluid between neighbouring tails may have a component which would tend to force their waves into phase. It is of interest therefore to analyze the field of flow between two waving sheets when their waves are not in phase in order to find out whether the viscous stresses are of such a nature as to tend to force them into phase.

Taking axes of co-ordinates midway between the two sheets which are at $y = \pm h$ it will be assumed that waves of the same amplitude, b, travel down each sheet with the same velocity σ/k. It will be assumed also that the phase of the sheet at $y = +h$ lags behind that of the sheet at $y = -h$ by an angle 2ϕ. All cases will be covered if ϕ is taken to lie in the range $0 < \phi < \frac{1}{2}\pi$.

The equations to the two sheets are then

$$\left.\begin{aligned} y &= h + y_1 = h + b\sin(z+\phi), \\ \text{and} \quad y &= -h + y_2 = -h + b\sin(z-\phi), \end{aligned}\right\} \tag{36}$$

where $$z = kx - \sigma t.$$

Figure 3*c* shows the sheets when $\phi = 45°$ so that y_1 lags $90°$ behind y_2.

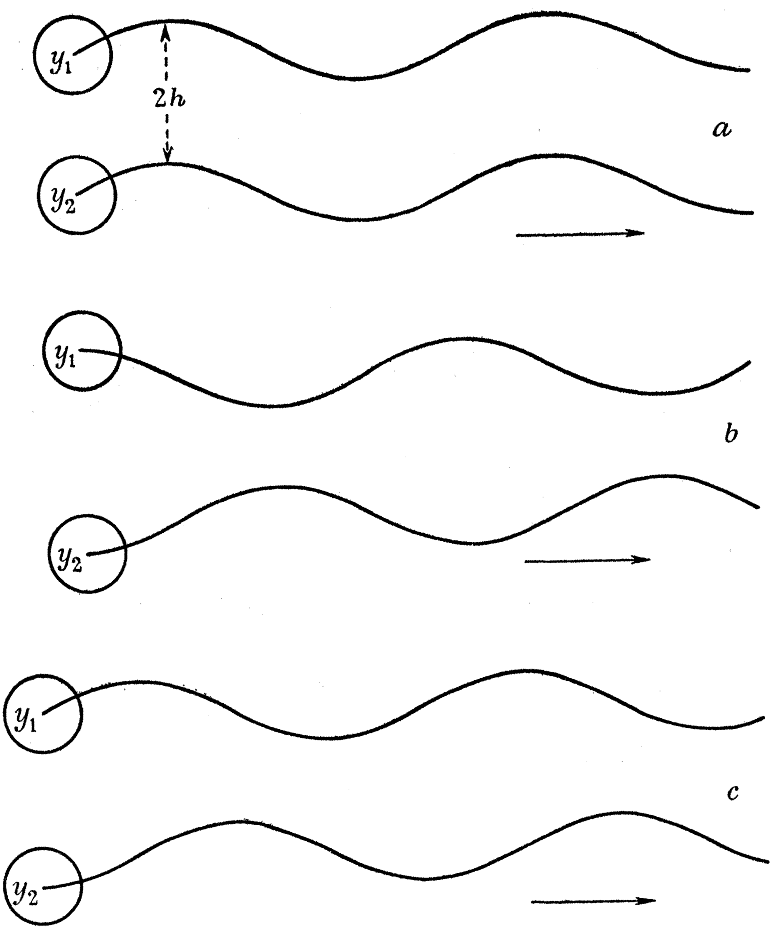

FIGURE 3. *a*, waves in phase, $\phi = 0$, $b/\lambda = 0{\cdot}073$, $2h/\lambda = \frac{3}{8}$. *b*, waves in opposite phase, $\phi = \frac{1}{2}\pi$, $b/\lambda = 0{\cdot}073$, $2h/\lambda = \frac{3}{8}$. *c*, wave y_1 lags behind y_2, $\phi = \frac{1}{4}\pi$. The arrows indicate the direction of wave propagation.

The stream function is assumed to be

$$\psi = (A_1 y \sinh ky + B_1 \cosh ky) \cos\phi \sin z + (A_2 y \cosh ky + B_2 \sinh ky) \sin\phi \cos z. \quad (37)$$

The condition $\partial\psi/\partial y = 0$ at $y = \pm h$ is satisfied provided

$$\frac{B_1 k}{A_1} = -(kh \coth kh + 1), \quad \frac{B_2 k}{A_2} = -(kh \tanh kh + 1); \quad (38)$$

the second condition to be satisfied at $y = +h$ is

$$\frac{\partial\psi}{\partial x} = \frac{\partial y_1}{\partial z}\frac{\partial z}{\delta t} = -\sigma\frac{\partial y_1}{\partial z},$$

and at $y = -h$ is

$$\frac{\partial\psi}{\partial x} = -\sigma\frac{\partial y_2}{\partial z}.$$

Both these are satisfied if

$$\left.\begin{aligned} A_1 h \sinh kh + B_1 \cosh kh &= -b\sigma/k, \\ A_2 h \cosh kh + B_2 \sinh kh &= -b\sigma/k. \end{aligned}\right\} \quad (39)$$

From (38) and (39)

$$\left.\begin{aligned} A_1 &= \frac{b\sigma \sinh kh}{\sinh kh \cosh kh + kh}, \quad B_1 = -\frac{b\sigma}{k}\left(\frac{kh \cosh kh + \sinh kh}{\sinh kh \cosh kh + kh}\right), \\ A_2 &= \frac{b\sigma \cosh kh}{\sinh kh \cosh kh - kh}, \quad B_2 = -\frac{b\sigma}{k}\left(\frac{kh \sinh kh + \cosh kh}{\sinh kh \cosh kh - kh}\right). \end{aligned}\right\} \quad (40)$$

It is now possible to calculate the stress which the viscous fluid exerts on the sheets. The component perpendicular to the sheet is as in (12)

$$Y_y = -p + 2\mu\frac{\partial v}{\partial y} = -p. \quad (41)$$

The pressure p corresponding with the stream function (37) is given by

$$\frac{p}{2\mu kb\sigma} = \frac{\sinh ky \sinh kh \cos\phi \cos z}{\sinh kh \cosh kh + kh} - \frac{\cosh ky \cosh kh \sin\phi \sin z}{\sinh kh \cosh kh - kh}. \quad (42)$$

At $y = h$ the pressure is p_1, where

$$\frac{p_1}{2\mu kb\sigma} = \alpha \cos\phi \cos z - \beta \sin\phi \sin z \quad (43)$$

and

$$\alpha = \frac{\sinh^2 kh}{\sinh kh \cosh kh + kh}, \quad \beta = \frac{\cosh^2 kh}{\sinh kh \cosh kh - kh}. \quad (44)$$

The mean rate of dissipation of energy between the two sheets is equal to the mean rate at which the sheets do work. The rate at which unit length of the sheet $y = h + y_1$ does work on the fluid is

$$-p_1\frac{\partial y_1}{\partial t} = (\alpha \cos\phi \cos z - \beta \sin\phi \sin z)(\cos\phi \cos z - \sin\phi \sin z)(z\mu kb^2\sigma^2). \quad (45)$$

Since $\overline{\cos^2 z} = \overline{\sin^2 z} = \frac{1}{2}$ and $\overline{\sin z \cos z} = 0$,

the mean rate of doing work is

$$\overline{E} = -\overline{p_1\frac{\partial y_1}{\partial t}} = \mu kb^2\sigma^2(\alpha \cos^2\phi + \beta \sin^2\phi). \quad (46)$$

Since α is less than β for all values of kh the rate of dissipation is least when $\phi = 0$, so that the waves are in phase as in figure 3*a*. $\bar{E}$ is greatest when $\phi = \frac{1}{2}\pi$ as in figure 3*b*. The ratio

$$\frac{\overline{E_1}}{\overline{E_2}} = \frac{\text{rate of dissipation when waves are in phase}}{\text{rate of dissipation when waves are in opposite phase}}$$

$$= \tanh^2 kh \left(\frac{\sinh kh \cosh kh - kh}{\sinh kh \cosh kh + kh}\right). \tag{47}$$

The way in which $\overline{E_1}/\overline{E_2}$ depends on kh is shown in figure 4. It will be seen that E_1 is much less than E_2 when kh is small. The point X in figure 4 refers to the sheets shown in figures 3*a* and *b*. In figure 3*a*, *b* and *c* the sheets are separated by a distance $\frac{3}{8}\lambda$. It will be seen that even at this distance there is a very large difference between $\overline{E_1}$ and $\overline{E_2}$. For $2h/\lambda = \frac{1}{10}$, which corresponds with the waves shown in Gray's drawing, figure 2, $\overline{E_1}/\overline{E_2} = 8 \times 10^{-4}$. The effort required to make the tails wave in unison is in this case only one-thousandth of that necessary to make them wave if out of phase.

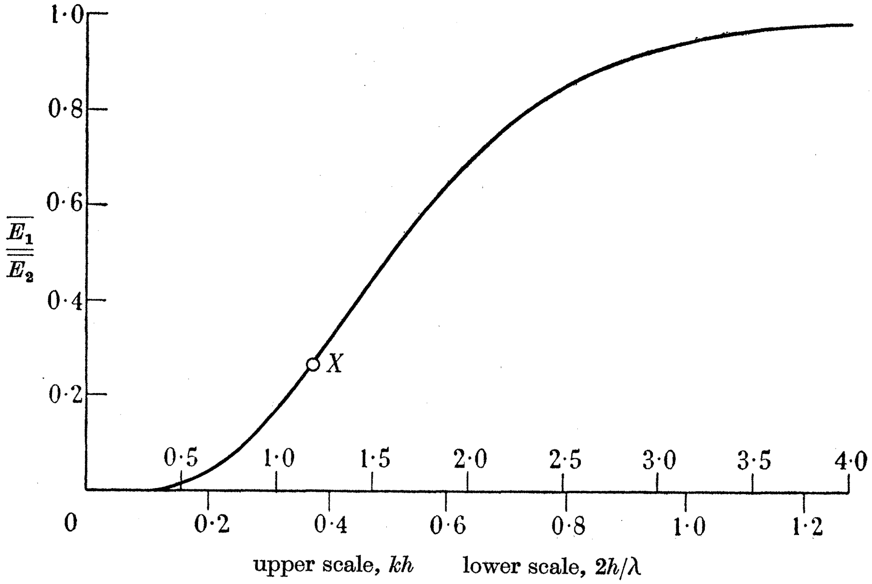

FIGURE 4

The reduction in the rate of dissipation of energy when the waves on the two sheets get into phase is very striking when kh is small, but without knowledge of the internal mechanism which moves the tail it is not possible to say with certainty that the tails will in fact get into the position where least energy is dissipated. On the other hand, it seems that whatever that mechanism may be, it is likely that a component of pressure which is in phase with the displacement of the sheet y_1 will tend to decrease the frequency of oscillation, while a component which is in the opposite phase will increase it. When the two sheets are so far away from one another that they do not influence one another the relationship between pressure and displacement of each sheet is that expressed by (1) and (13) so that the phases of p_1 and y_1, differ by

$\frac{1}{2}\pi$. The reaction of the fluid therefore does not exert any *direct* force tending to increase or decrease the frequency. This must not be taken to imply that it has no effect. The work done by the sheet may have a great indirect effect on the frequency which the internal mechanism of the tail of a living object may be able to excite.

When kh is not large the sheets influence one another through the medium of the fluid. Comparing (43) with (36) it will be seen that it is only when $\alpha = \beta$ that y_1 is exactly out of phase with p_1. To find whether the *direct* effect of pressure is to increase or decrease the frequency of the sheet y_1 it is necessary to find the sign of $\overline{y_1 p_1}$. The direct effect of the viscous stress would be to increase or decrease the frequency according as $\overline{y_1 p_1}$ is negative or positive.

Writing (43) in the form

$$\frac{p_1}{2\mu kb\sigma} = C\cos(z+\phi+\epsilon), \tag{48}$$

$$C^2 = \alpha^2+\beta^2 \quad \text{and} \quad \tan(\phi+\epsilon) = \frac{\beta}{\alpha}\tan\phi. \tag{49}$$

Since from (44) $\beta > \alpha$ and by definition $0 < \phi < \frac{1}{2}\pi$, (49) shows that ϵ is positive.

The mean value of $y_1 p_1$ is

$$\overline{y_1 p_1} = 2\mu kb^2\sigma C(-\tfrac{1}{2}\sin\epsilon),$$

so that $\overline{y_1 p_1}$ is negative. The direct effect of pressure is therefore to tend to increase the frequency of the sheet y_1. At the sheet $y = -h+y_2$, the condition that the direct effect of pressure shall be to increase frequency is that $\overline{y_2 p_2}$ shall be positive (a positive pressure presses y_1 in the positive direction and y_2 in the negative direction).

Using (42) the pressure p_2 at the sheet y_2 is

$$\begin{aligned}\frac{p_2}{2\mu kb\sigma} &= -\alpha\cos\phi\cos z-\beta\sin\phi\sin z\\ &= -C\cos(z-\phi-\epsilon),\end{aligned} \tag{50}$$

where α, β and c have the same meaning as before and

$$\tan(\phi+\epsilon) = \frac{\beta}{\alpha}\tan\phi,$$

so that ϵ also has the same meaning as before. From (36) and (50)

$$\frac{y_2 p_2}{2\mu kb^2\sigma} = -C\sin(z-\phi)\cos(z-\phi-\epsilon), \tag{51}$$

so that

$$\frac{\overline{y_2 p_2}}{2\mu kb^2\sigma} = -\tfrac{1}{2}C\sin\epsilon. \tag{52}$$

Since ϵ is positive, $\overline{y_2 p_2}$ is negative. Thus the *direct* effect of pressure on the sheet y_2 is to decrease its frequency. Since the phase of y_1 lags behind that of y_2, the direct effect of the reaction between the two sheets is to increase the velocity of the waves in sheet y_1 and decrease that of the waves in y_2. In other words, the *direct* effect of the reaction of one sheet on the other through the viscous medium is to make the waves get into phase as illustrated in figure 3*a*.

In conclusion, I should like to express my thanks to Professor James Gray and Lord Rothschild for calling my attention to this problem.

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Studies of nuclear collisions involving 8 MeV deuterons by the photographic method

I. The experimental method

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An improved apparatus for the study of disintegrations produced by high-energy particles accelerated in a cyclotron has been constructed. The instrument employs the photographic method of detecting charged particles, and allows the numbers and energy of the scattered and disintegration products to be determined—at any angle with respect to the primary beam, in the interval from 15 to 165°—as a result of a single exposure.

By means of a slit system, the spread in energy of the deuteron beam from the Liverpool cyclotron has been reduced to 60 keV, and the angular divergence of the beam to $\pm\frac{1}{3}°$. 'Targets' composed of gases or thin foils have been used. The Q-values of the resulting nuclear reactions which lead to the emission of protons and α-particles can, in the refined conditions provided by the instrument, be determined to within $\pm 0{\cdot}03$ MeV; separate proton groups with a difference of energy of 0·08 MeV can be resolved.

1. INTRODUCTION

Previous experiments

In 1940–1 experiments were made on the scattering by various light elements of 4·2 MeV protons and 6·3 MeV deuterons accelerated in the Liverpool cyclotron; a specially designed 'scattering camera' was used, and the photographic emulsion technique was employed for the detection of particles. The construction of the 'camera' and the details of the experimental method were described in a paper (Chadwick, May, Pickavance & Powell 1944), which will be referred to as A, and the results of the investigations were given in a series of papers published in 1947 (May & Powell 1947; Heitler, May & Powell 1947; Guggenheimer, Heitler & Powell 1947).

These early experiments proved the photographic technique to be a powerful and reliable method for studying nuclear processes, and especially for establishing the existence of nuclear energy levels and determining their characteristics. The early results were of value in the interpretation of nuclear phenomena; but they