# WAVE PROPAGATION ALONG FLAGELLA

By K. E. MACHIN

*Department of Zoology, University of Cambridge*

The nature of the mechanism which initiates and propagates transverse bending waves along the length of a flagellum has been the subject of discussion for many years. Two possible mechanisms have been advocated: (i) that the flagellum is a passive elastic filament set in motion by an active process located at its proximal end, the propagation of the wave along the filament being the result of its elastic properties; (ii) that actively contractile elements exist along the length of the flagellum. The latter view has received the greatest support, but no definite proof appears to have been established.

In this paper the problem is approached theoretically by considering the types of wave propagation which can occur along an elastic filament immersed in a viscous medium.

To simplify the analysis the following assumptions have been made: (i) the flagellum is circular in cross-section; (ii) the waves are propagated in a plane; (iii) inertial forces are negligible; (iv) the amplitude of the waves is sufficiently small* that only the forces normal to the axis need be considered.

Assumptions (i) and (ii) are not inconsistent with the biological evidence (Gray, 1955).

At the very low Reynolds number appropriate to flagellar motion (of the order of $10^{-3}$–$10^{-5}$) assumption (iii) is certainly valid. Although assumption (iv) is not true for observed flagellar motion, results derived using it are not likely to be greatly in error even when applied to large-amplitude waves.

## THE MODES OF WAVE PROPAGATION ALONG A FLAGELLUM

Two sets of forces govern the motion of a flagellum and hence determine the form and rate of propagation of waves along it: (i) elastic forces which tend to straighten the flagellum; (ii) viscous forces which oppose the motion of each element through the water.

Consider the forces acting on an element $dx$ of the flagellum (Fig. 1).

The elastic force $dF_E$ is given by equation (1), which occurs in the theory of vibrating beams (Morse, 1948):

$$dF_E = -QSK^2 \frac{\partial^4 y}{\partial x^4} dx, \tag{1}$$

where $Q$ is Young's modulus, $S$ is the area of cross-section and $K$ is the radius of gyration of the section.

* For clarity, wave amplitudes in all diagrams have been shown large.

The viscous force $dF_V$ can be calculated from the formula for the drag of a cylinder at low Reynolds numbers (Lamb, 1932):

$$dF_V = \frac{4\pi\mu}{2\cdot0 - \log R} \frac{\partial y}{\partial t} dx, \tag{2}$$

where $\mu$ is the viscosity and $R$ is the Reynolds number.

Strictly this relation is non-linear, since $R$ is a function of $\partial y/\partial t$. At these very low Reynolds numbers, however, the coefficient in (2) varies only slowly with $R$, and may, without serious error, be considered constant over most of the cycle of oscillatory movement. Only as the velocity approaches zero does this approxima-tion break down, but here both $dF_E$ and $dF_V$ are approaching zero, so little error will result.
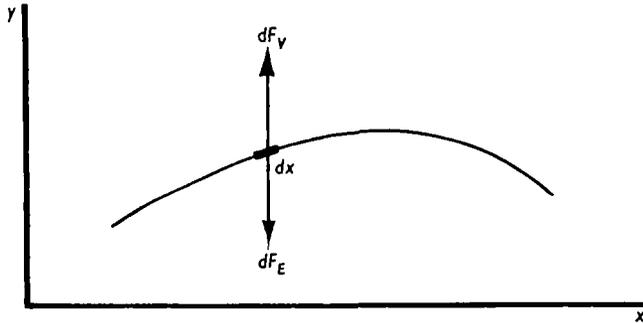


Fig. 1. Forces acting on an element of a flagellum.

Since $dF_E$ must equal $dF_V$,

$$-QSK^2 \frac{\partial^4 y}{\partial x^4} dx = \frac{4\pi\mu}{2\cdot0 - \log R} \frac{\partial y}{\partial t} dx, \tag{3}$$

or

$$\frac{\partial^4 y}{\partial x^4} = -\frac{1}{QSK^2} \frac{4\pi\mu}{2\cdot0 - \log R} \frac{\partial y}{\partial t}. \tag{4}$$

The steady-state solution of this differential equation can be shown to be

$$y = e^{i2\pi ft}(A e^{r_1 x/l_0} + B e^{r_2 x/l_0} + C e^{r_3 x/l_0} + D e^{r_4 x/l_0}), \tag{5}$$

where $f$ is the frequency of oscillation, $r_1, r_2, r_3, r_4$ are the four values of $\sqrt[4]{-i}$; $A, B, C, D$ are complex constants depending on the conditions at the two ends of the flagellum and $l_0$ is the 'scale length' given by

$$l_0 = \sqrt[4]{\left( \frac{QSK^2}{2\pi f} \cdot \frac{2\cdot0 - \log R}{4\pi\mu} \right)}. \tag{6}$$

Each of the four terms of equation (5) represents one of the four types of wave (or 'modes') which can propagate along the elastic filament (Fig. 2). The relative amplitude and phase of the modes depend on the conditions at the ends of the

filament. The characteristics of the four modes are given in Table 1, where the 'damping distance' is the distance the wave travels before its amplitude falls to $1/e$ of its original value.

On an infinite unconstrained flagellum only the principal mode will exist. This wave carries the flux of energy distally along the flagellum, the continuous loss of energy along the length manifesting itself as a decrease in amplitude. Any lateral constraint (e.g. a rigid hinge) at the proximal end will initiate the secondary mode. If, in addition, the flagellum is of finite length, both principal and secondary modes are reflected at the distal end to give modes III and IV.
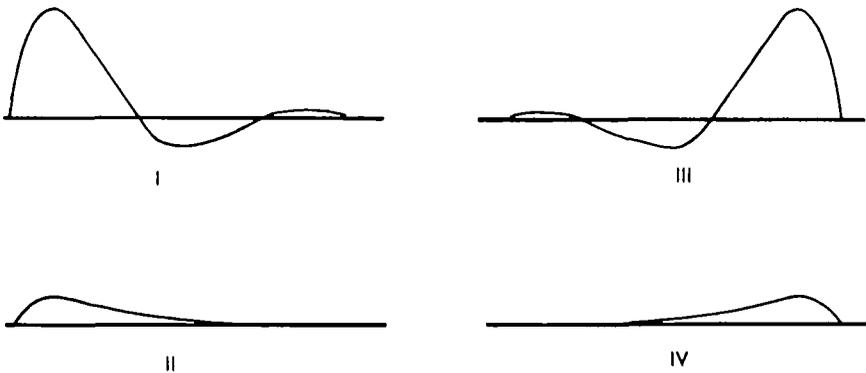


Fig. 2. Modes of wave propagation along a flagellum.

It is important to note that all wavelengths and damping distances are proportional to $l_0$, the scale length. This length depends on the frequency of oscillation, the mechanical properties of the flagellum and the nature of the medium; it is the only term in which these parameters enter into the wave equation. It thus follows that the *form* of the waves propagated along a flagellum is independent of all these parameters. Variation of stiffness, frequency, viscosity, etc., only affect the *scale* of the waves.

Table 1

| Designation of mode | Direction of propagation | Direction in which amplitude decreases | Wave-length | Damping distance |
|---|---|---|---|---|
| I. Principal | Increasing $x$ | Increasing $x$ | $6 \cdot 8 l_0$ | $2 \cdot 6 l_0$ |
| II. Secondary | Decreasing $x$ | Increasing $x$ | $16 \cdot 5 l_0$ | $1 \cdot 1 l_0$ |
| III. Reflected principal | Decreasing $x$ | Decreasing $x$ | $6 \cdot 8 l_0$ | $2 \cdot 6 l_0$ |
| IV. Reflected secondary | Increasing $x$ | Decreasing $x$ | $16 \cdot 5 l_0$ | $1 \cdot 1 l_0$ |

As mentioned earlier, the relative amplitudes of each of the four modes are determined by end conditions. In the next section one specific set of proximal end conditions will be imposed and the resultant wave-patterns computed.

## THE FLAGELLUM DRIVEN BY ANGULAR OSCILLATION
## OF THE PROXIMAL END

If the proximal end of a filament is constrained to move about a rigid hinge, and the energy is fed in by angular displacement of the constrained end, the system approximates to a flagellum attached to a stationary head. The boundary conditions are then:

$$y = 0 \quad \text{at} \quad x = 0 \quad \text{for all } t, \tag{7}$$

$$\frac{\partial y}{\partial x} = G e^{i 2\pi f t} \quad \text{at} \quad x = 0. \tag{8}$$

Here $G$ determines the amplitude of the motion.

At the distal end, both bending moment and shearing force vanish:

$$\frac{\partial^2 y}{\partial x^2} = 0, \tag{9}$$

$$\frac{\partial^3 y}{\partial x^3} = 0. \tag{10}$$

If the total length of the flagellum is $L$, equations (5) and (7)–(10) give

$$y = G l_0 e^{i(2\pi f t + \pi/4)} \left\{ \frac{1}{2 + 2\cos\phi \cosh\phi} \right\} \times \{ \sin\theta + \sinh\theta + \sin\phi \cosh(\phi - \theta)$$
$$- \cos\phi \sinh(\phi - \theta) - \cosh\phi \sin(\phi - \theta) + \sinh\phi \cos(\phi - \theta) \}, \tag{11}$$

where
$$\theta = \frac{x}{l_0}(0 \cdot 92 - 0 \cdot 38i) \tag{12}$$

and
$$\phi = \frac{L}{l_0}(0 \cdot 92 - 0 \cdot 38i) \tag{13}$$

Wave-patterns have been computed from equation (11) for various values of $L$; the results are shown in Fig. 3. Since distances are expressed in terms of $l_0$, these patterns will represent the motion of any passive flagellum, whatever the values of the physical parameters. In Fig. 3 the shape of the flagellum at successive intervals of one-eighth of a complete cycle is displayed; the dotted line represents the envelope of the motion.

## DISCUSSION OF THE CALCULATED FLAGELLAR MOTIONS

The motion of the infinite flagellum constrained at its proximal end will be considered first. Under such conditions the maximum amplitude occurs at about $1 \cdot 2 \, l_0$ from the proximal end (Fig. 3 H). From this point onwards the principal wave predominates; its amplitude decays exponentially, and is virtually zero at $10 \, l_0$. Irrespective of its length, the flagellum can exhibit only about $1\frac{1}{2}$ visible wavelengths.

When the flagellum is of finite length the reflected waves affect the resulting wave-pattern, the amplitude of the distal end increasing with progressive shortening of the length. When $L = 3 l_0$ the amplitude of the free distal end is greater than that of any other part of the flagellum; the envelope acquires a characteristic fish-like form
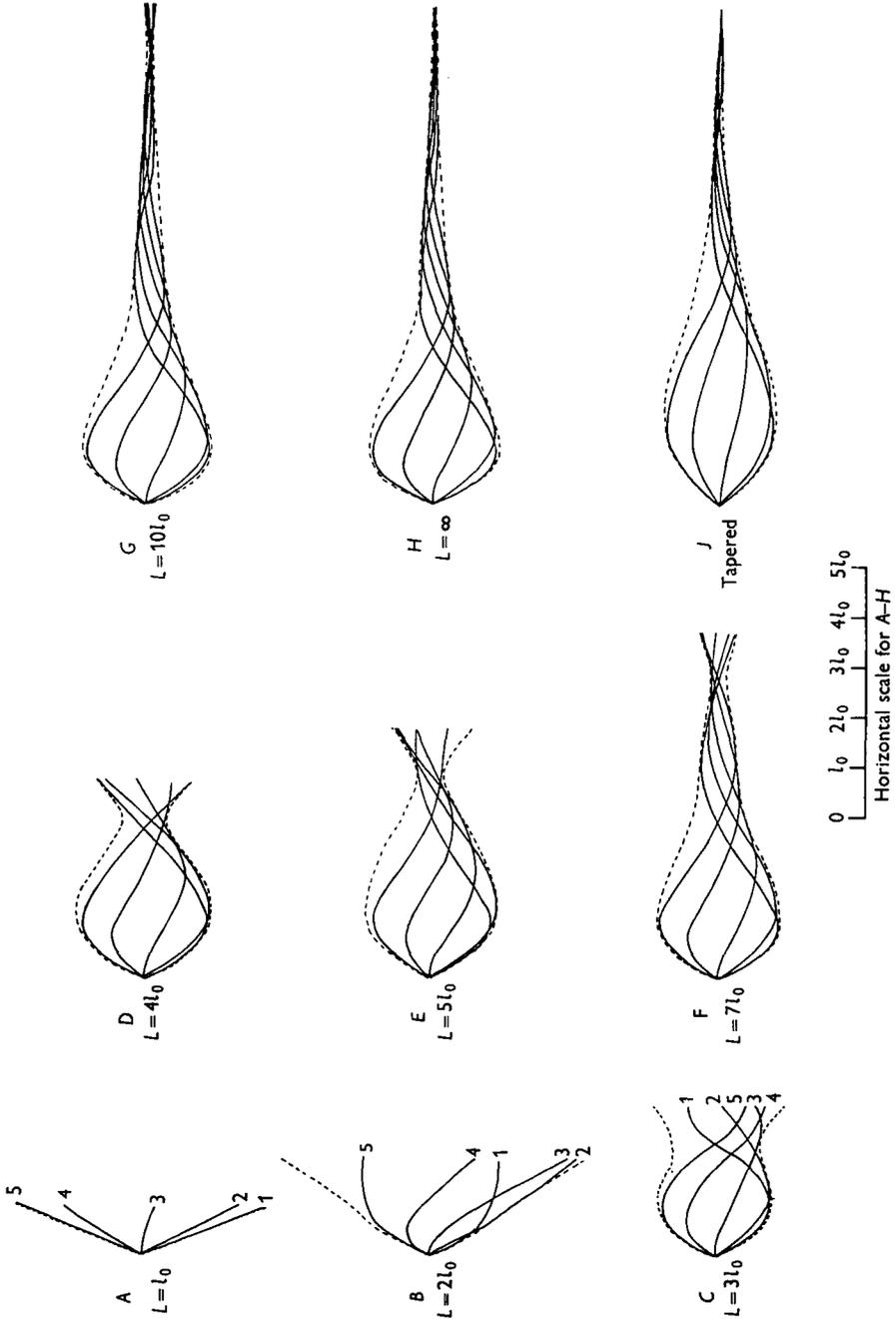
Fig. 3. Calculated wave-patterns on a flagellum. Vertical amplitudes have been exaggerated for clarity.

but contains less than one wavelength. When $L < 2l_0$ the motion approximates to that of a relatively rigid cilium.

Two of the arguments purporting to show that distributed contractile elements must exist along flagella are: (i) Since in observed flagellar motions the point of maximum amplitude occurs some way from the proximal end, energy is being fed in near this point; (ii) inertial forces are necessary to maintain a progressive wave system. The results of Fig. 3, derived for a weightless passive flagellum, show that these arguments are not valid.

However, it is clear from Fig. 3 that a passive elastic flagellum of uniform cross-section driven from one end cannot exhibit more than $1\frac{1}{2}$ wavelengths along its length. Further, the amplitude of the wave decreases exponentially. If a flagellum exhibits more than $1\frac{1}{2}$ wavelengths, or has a sustained amplitude along its length, the propagation of the waves cannot be due to a passive mechanism. This conclusion is unaffected by the nature of the drive at the proximal end, since the secondary wave becomes negligible beyond $3l_0$.

So far only uniform flagella have been considered. The behaviour of a flagellum whose size or mechanical properties vary along its length can readily be described, provided that the variation is slow compared with the wavelength. Under these conditions the value of $l_0$, the scale length, will vary along the flagellum, giving a non-linear 'stretch' to the wave-patterns of Fig. 3. The result of this is shown in Fig. 3J drawn for a flagellum whose distal end is one-third of the diameter of the proximal end. Again waves of sustained amplitude appear impossible.

So far as is known, the only instance in which the envelope of an actual flagellum has the form of any of the curves of Fig. 3 is in the case of 'ageing' spermatozoa described by Gray (1955). On the other hand, passive models described by Gray (1955) have envelopes very similar to those of Fig. 3.

It appears, then, that under certain abnormal circumstances sperm tails behave as though they were passive, but that to explain their normal motion an active mechanism is essential.

### BENDING MOMENTS IN AN ACTIVE FLAGELLUM

As it seems clear that the waves exhibited by a passive elastic filament cannot resemble those observed on a normal flagellum, it is of interest to consider the alternative hypothesis of actively bending elements distributed along the length of the filament.

If a distribution $B(x)$ of active bending moment along the flagellum is postulated, equation (1) becomes

$$dF_E = -QSK^2 \frac{\partial^4 y}{\partial x^4} \, dx - \frac{\partial^2 B}{\partial x^2} \, dx, \tag{14}$$

and (3) becomes

$$-QSK^2 \frac{\partial^4 y}{\partial x^4} \, dx - \frac{\partial^2 B}{\partial x^2} \, dx = \frac{4\pi\mu}{2\cdot0 - \log R} \frac{\partial y}{\partial t} \, dx; \tag{15}$$

therefore

$$\frac{\partial^2 B}{\partial x^2} = -QSK^2 \frac{\partial^4 y}{\partial x^4} - \frac{4\pi\mu}{2\cdot0 - \log R} \frac{\partial y}{\partial t}. \tag{16}$$

This equation gives implicitly the form of $B(x)$ corresponding to any specified motion.

As an example the form of $B(x)$ will be calculated for the case of a sine wave of constant amplitude $b$ and wavelength $\lambda$ propagating along the flagellum.

Putting

$$y = b e^{i2\pi(ft - x/\lambda)}, \tag{17}$$

$$QSK^2 = \alpha \tag{18}$$

and

$$\frac{4\pi\mu}{2 \cdot 0 - \log R} = \beta, \tag{19}$$

equation (16) gives

$$-\frac{1}{b}\frac{\partial^2 B}{\partial x^2} = \alpha\left(\frac{2\pi}{\lambda}\right)^4 e^{i2\pi(ft-x/\lambda)} + i2\pi f\beta e^{i2\pi(ft-x/\lambda)}, \tag{20}$$

or

$$B = b e^{i2\pi(ft-x/\lambda)}\left\{\alpha\left(\frac{2\pi}{\lambda}\right)^2 + i2\pi f\beta\left(\frac{\lambda}{2\pi}\right)^2\right\}. \tag{21}$$

This represents a progressive wave of bending moment with a wavelength, velocity and direction of propagation similar to the wave of displacement; there is, however, a phase difference between the waves.
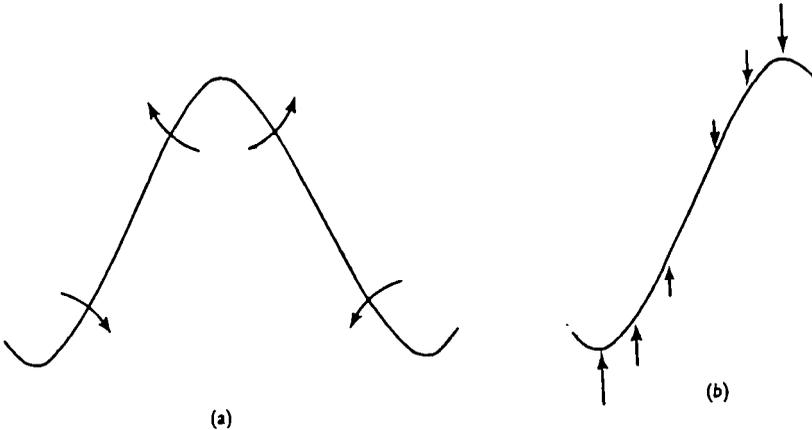


Fig. 4. Forces on a flagellum.

Equation (21) comprises two components, corresponding to the two terms within the brackets. The first component is a progressive wave in phase with the wave of displacement and represents the bending moment necessary to produce the sinusoidal elastic deformation of the filament. The second component is a progressive wave in quadrature with the wave of displacement, being the bending moment required to equalize the viscous forces on the filament. The origin of these two components is illustrated in Fig. 4. In (a) the elastic forces tending to straighten the filament are shown; it is clear that the maximum bending moment occurs at the point of maximum displacement. The viscous forces shown in (b) produce a maximum moment at the point where the displacement is zero.

The resultant total bending moment is the sum of the two components; if elastic forces predominate, the resultant is nearly in phase with the displacement, while if viscous forces predominate, the resultant approaches quadrature with the displacement.

## ENERGY CONSIDERATIONS FOR AN ACTIVE FLAGELLUM

Some of the energy fed into each element of the flagellum will be used to overcome viscous forces; the remainder is absorbed in elastic deformation of the element. Unless a reversible mechanism exists to convert this elastic energy back into chemical energy, it is irrecoverable and will degrade into heat in the elastic or contractile components. While there is some evidence for reversibility in vertebrate muscle under special circumstances (Abbott, Aubert & Hill, 1951) it seems unlikely that in the present case any appreciable fraction of the elastic energy will be recovered.

On this assumption, the power expended in the flagellum can be shown to be

$$P = b^2 L \left\{ \frac{\beta}{2} (2\pi f)^2 + \alpha f \left( \frac{2\pi}{\lambda} \right)^4 \right\}. \tag{22}$$

In this equation the first term represents the power used in overcoming viscous forces, and the second the power required for the elastic deformation.

Taylor (1952) and Hancock (1953) have shown that for a small undulating organism carrying waves of small amplitude the forward velocity $v$ is given by

$$v = \frac{2\pi^2 b^2 f}{\lambda}. \tag{23}$$

From (22) and (23)

$$v = \frac{P/L}{(2\pi/\lambda)^3 \alpha/\pi + \beta(2\pi f)(\lambda/2\pi)}. \tag{24}$$

For a given power $P$ and frequency $f$, equation (24) gives a maximum value of $v$ when

$$\left( \frac{\lambda}{2\pi} \right)^4 = \frac{3\alpha}{2\pi^2 f \beta}. \tag{25}$$

Substituting from equations (6), (18) and (19)

$$\lambda = 6.3 l_0.$$

Comparison of this value with those given in Table 1 shows that for an active flagellum the maximum propulsive efficiency (i.e. maximum forward speed for a given power) is attained when the wavelength of the actively generated wave is very nearly the same as that of the principal wave on a passive flagellum.

At the condition for maximum efficiency it can be shown from equation (22) that one-quarter of the power is used for elastic deformation, the remainder being dissipated by viscous forces. Furthermore, from equation (21) it can be shown that the real and imaginary components of the wave of bending moment are very nearly

equal. This indicates that the progressive wave of bending moment leads the wave of displacement by about one-eighth of a complete cycle.

For a wavelength other than the optimum, the phase difference between the waves of bending moment and displacement will lie between 0 and $\frac{1}{4}\pi$.

## THE ACTIVATION OF CONTRACTILE ELEMENTS

A flagellum can be idealized into an elastic filament surrounded by or enclosing a series of bilaterally arranged contractile elements, differential contraction of elements on the two sides producing localized bending moments (Fig. 5). The relation between the tension and length of the elements and the displacement and bending moment of the flagellum is given in Table 2, where $A$ and $B$ refer to the elements on the opposite sides (Fig. 5).
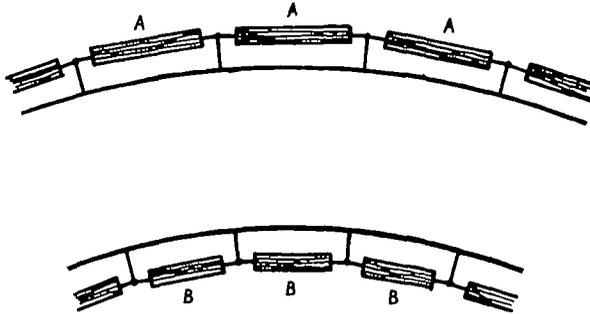


Fig. 5. Contractile elements surrounding an elastic filament.

Table 2

| A | | B | |
|---|---|---|---|
| Tension | Bending moment | Tension | Bending moment |
| High | Negative | High | Positive |
| Low | Positive | Low | Negative |
| Length | Displacement | Length | Displacement |
| Long | Positive | Long | Negative |
| Short | Negative | Short | Positive |

It was shown earlier that for maximum propulsive efficiency the wave of active bending moment leads the wave of displacement by about $\frac{1}{4}\pi$. From Table 2 it will be seen that for both elements $A$ and $B$ this implies that the tension should lag on the length by about $\frac{3}{4}\pi$. The phase relations for the two elements are shown in Fig. 6.

Pringle (1957) has suggested that the rhythmic activity of a spermatazoon might arise from a myogenic mechanism; this suggestion will now be examined in the light of the present results. In studies of insect fibrillar muscle, Boettiger, Machin & Pringle (1958) have shown that these muscles behave like a combination of two components: (i) an ordinary visco-elastic element and (ii) an elastic element in

which the force due to a change of length only appears after a time delay of the order of a few milliseconds. In the muscles studied, the ordinary elasticity was rather larger than the 'delayed elasticity'; for sinusoidal movements a phase lag of only about $\frac{1}{4}\pi$ between length and force could occur. It is of course somewhat speculative to relate this result to the minute contractile elements of a flagellum. It seems, however, not unreasonable to postulate that such a delayed elastic effect could predominate in these contractile elements; a phase lag of $\frac{3}{4}\pi$ between force and length might then be sustained.
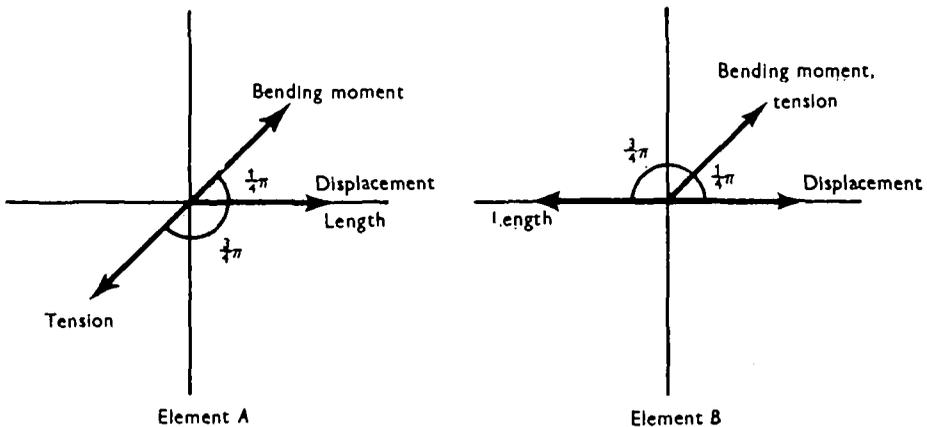


Fig. 6. Phase relationships for contractile elements.

In this way actively induced bending at the proximal end of a flagellum could give rise to a propagated wave whose amplitude was sustained by energy arising in the more distal elements. These elements would be activated when deformed by a passively propagated wave of bending from the immediately proximal region. No mechanism for the transmission of control information to the contractile elements would be necessary.

Such a system could account for the following observed phenomena: (i) a flagellum is motionless when separated from the middle piece of the spermatazoon or from the basal granule (Gray, 1955); (ii) a small obstruction causes the more distal region of the flagellum to become motionless (Gray, 1955)—further experiments on this effect would be valuable; (iii) while fresh spermatazoa show sustained amplitude along all their length, ageing sperms have an envelope similar to those drawn in Fig. 3 for passive filaments (Gray, 1955). It is postulated that as the sperms age the contractile elements in the tail become inactive, although the oscillatory bending at the proximal end continues.

## QUANTITATIVE COMPARISON WITH OBSERVATION

As already shown, for maximum propulsive efficiency the wavelength on an active flagellum must be of the order of $6l_0$. The value of $l_0$, the scale length, is given by equation (6). Using the parameters given by Gray (1955) and Gray & Hancock (1955)

for the spermatozoa of *Psammechinus miliaris* the value of $l_0$ is $1 \cdot 8\,\mu$, corresponding to a wavelength for maximum efficiency of $12\,\mu$; the observed value is $24\,\mu$. In view of the approximate nature of the theory and of the value of Young's modulus employed, the prediction of the wavelength to within a factor of two is satisfactory.

## SUMMARY

1. The types of bending waves which can propagate along a thin elastic filament immersed in a viscous medium are derived.

2. It is not possible to account for the form of the waves observed on actual flagella if the flagellum is regarded merely as a passive elastic filament driven from its proximal end.

3. The observed wave forms can be explained by assuming active contractile elements distributed along the length of the flagellum. These elements could be activated by local bending.

## REFERENCES

ABBOTT, B. C., AUBERT, X. M. & HILL, A. V. (1951). The absorption of work by a muscle stretched during a single twitch or tetanus. *Proc. Roy. Soc.* B, **139**, 86–104.

BOETTIGER, E. J., MACHIN, K. E. & PRINGLE, J. W. S. (1958). Fibrillar muscle. *Proc. XV Int. Conf. Zool.* (in the Press).

GRAY, J. (1955). The movement of sea-urchin spermatozoa. *J. Exp. Biol.* **32**, 775–801.

GRAY, J. & HANCOCK, G. J. (1955). The propulsion of sea-urchin spermatozoa. *J. Exp. Biol.* **32**, 802–14.

HANCOCK, G. J. (1955). The self-propulsion of microscopic organisms through liquids. *Proc. Roy. Soc.* A, **217**, 96–121.

LAMB, H. (1932). *Hydrodynamics*, p. 616. Cambridge University Press.

MORSE, P. M. (1948). *Vibration and Sound*, p. 154. New York: McGraw Hill.

PRINGLE, J. W. S. (1957). Myogenic Rhythms. In *Recent Advances in Invertebrate Physiology*, pp. 99–115. Oregon: University of Oregon Publications.

TAYLOR, G. I. (1952). The action of waving cylindrical tails in propelling microscopic organisms. *Proc. Roy. Soc.* A, **211**, 225–39.