

# Internal Mechanics of the Helical Flagellum

by

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It is shown how the model of junction alignment suggested by Schreiner (1971) to explain the motion of cilia and undulating flagella also explains the motion of the rotating helical flagellum. It is found that whether the flagellum exhibits an undulating or a rotating motion only depends on how the motion is initiated. Geometrical considerations show that the maximum longitudinal displacement that can exist between linked junctions is 2 nm, and considerations on the rate of work by the organism in swimming show that the average force component from each link in the direction of the filament is at least  $5.5 \cdot 10^{-8}$  dyn.

## Introduction.

In a paper on the mechanics of the ciliary beat, Schreiner (1971) argues - in opposition to the commonly held view - that the cilium drives the surrounding liquid during the so-called recovery stroke, while it follows the motion of the liquid during the so-called effective stroke. This picture is supported by an analysis by Wilson & Schreiner (1971) of the flow due to the motion of cilia. On the basis of this alternative view of the ciliary beat, Schreiner (1971) suggests a model that will explain the observed motion of bends in cilia and undulating flagella.

The model is based on the assumption - supported by observations reported in the literature (Satir (1965, 1968)) - that the shaft of cilia and flagella has two main structural components, a longitudinally inextensible set of 9+2 filaments parallel to the axis, and a matrix whose transverse dimensions are retained under bending and where originally normal sections remain normal to the axis. Any region of the organelle where these two structural components are locked together will then be rigid. Further, the angle of bending between two locked regions is constant as long as both regions remain locked. If there is an inherent limit to the curvature of the organelle - more realistically the relation between bending moment and curvature could be non-linear - the outer locked region and a bend of constant shape will be pushed outward when the length of the inner locked region increases. The locking is perceived as links formed between sets of junctions in the matrix and a set of junctions on each peripheral filament, Figure 1. The length of a locked region will then

increase when new links are formed between pairs of slightly displaced junctions at one end of the region. The junction pairs will then be aligned by the contractile force in the new link. As the bend propagates along the organelle, links are broken at the front end of the bend, the junctions remain unlinked through the bend, and new links are formed at the rear end of the bend, but now with another pairing of the junctions.

Linking of matrix and filament junctions on the helical flagellum.

The above description applies to bends propagating in a plane. In the helical flagellum the bend is three-dimensional, and reaches from one end of the organelle to the other. Thus if matrix and filaments are locked together in regions, these regions must necessarily be in the bend.

The moment at a point on the helical axis of the external forces acting on the part of the rotating helix to the rear of this point has been determined by Schreiner (1970). If the expression for the moment is developed along the flagellum itself, the component along the axis of an element of the flagellum expresses the torsion on the element, and the component normal to the axis expresses the bending moment on the element. In this way the torsion and the bending moment along the single rotating helical flagellum of a microorganism plotted in Figure 2 were determined. The  $\vec{i}$ -component of the bending moment -  $[\vec{i}, \vec{j}, \vec{k}']$  are unit vectors along the helical radius, the axis of the element, and the positive normal to these, respectively - varies both in sign and size, while the  $\vec{k}'$ -component varies in size only. The  $\vec{k}'$ -component could

be balanced by an inherent limit to the curvature, but an additional mechanism is needed to balance the  $\vec{i}$ -component and maintain the shape of the helix. The protein dynein, which is generally assumed to be associated with the generation of forces in cilia and flagella, has been found on the peripheral filaments, but not on the central filaments (Gibbons (1963)). Within the frame of the model this indicates that the central filaments are permanently locked to the matrix. The  $\vec{i}$ -component of the bending moment would then be balanced if in addition a peripheral filament not on the  $\vec{i}$ -axis were locked to the matrix.

When the helix, Figure 3a, has a constant radius  $R$  and pitch angle  $\theta$ , its radius of curvature is  $R_c = R/\cos^2\theta$ . If the angle  $\nu$ , Figure 3b, is measured from the positive  $\vec{k}$ -direction the strain on the bent cylinder of radius  $r$  is

$$\epsilon = \frac{r}{R_c} \sin \nu = \frac{r}{R} \cos^2 \theta \sin \nu. \quad (1)$$

Since the junction sets in the matrix deforms with the matrix, while sets on the filaments are inextensible, (1) shows that the most favorable conditions for linking the two sets occur where  $\sin \nu = 0$ , that is where  $\nu = 0^\circ$  and  $\nu = 180^\circ$ . With nine peripheral filaments there can not always be a filament at either of these angles in every transverse section when the flagellum rotates like a speedometer wire. The linking must therefore be possible even with some distortion in the matrix. The central angle between neighbour filaments is on the average  $360^\circ/9 = 40^\circ$ , and there will therefore always be a filament in either of the diametrically opposite bands  $\nu \pm \beta_0$  and  $180^\circ + \nu \pm \beta_0$  when  $\beta_0 = 10^\circ$ . It follows that if linking of matrix and

peripheral filaments can be accomplished within the bands  $\nu_0 \pm \beta_0$  and  $180^\circ + \nu_0 \pm \beta_0$ , where as will be shown below  $0 < \nu_0 \leq \beta_0$ , then the  $\vec{i}$ -component of the bending moment can be balanced everywhere.

In his review of flagellar movement, Holwill (1966) reports that both the central and the peripheral filaments "appear to extend continuously along the flagellum without twisting and spiraling". On the helix the peripheral filaments then cut the lines  $\nu = \text{constant}$  at an angle  $\alpha$ , Figure 3a, given by

$$\text{tg}\alpha = \frac{2\pi r}{2\pi R/\cos\theta} = \frac{r}{R} \cos\theta, \quad (2)$$

where  $2\pi R/\cos\theta$  is the curvelength of one full turn of the helix. The length  $S$  of each region of a filament that is inside the band where junctions may be linked is then given by

$$S \text{ tg}\alpha = 2r\beta_0,$$

and by (2)

$$S = 2R\beta_0/\cos\theta,$$

where  $\beta_0$  is measured in radians.

On a helix of positive thread the filaments have a negative twist relative to the lines  $\nu = \text{constant}$ , Figure 3a, Figure 4. With the speedometer wire rotation corresponding to the positive threaded helix pushing the head - see Schreiner (1970) - new links between the stretched matrix and the filament are formed at A. The contractile forces in the stretched links force the flagellum to rotate, reducing the angle  $\nu$  of each link, and thereby also the length of each link. At B the matrix set is unstrained and the link length is at its minimum, from which it is eventually stretched until the links are

broken at C. Then another filament enters the diametrically opposite band at A'. New links are formed between the filament and the surrounding compressed matrix. These links then go through the same process, contracting between A' and B', stretching between B' and C'.

Only the balancing of the bending moment has so far been considered, but even the torsion will be balanced by the linking of matrix and filaments. For since the peripheral filaments are twisted relative to the lines  $v = \text{constant}$  and at intervals connected to the matrix, the situation is

equivalent with the one shown in Figure 5. There two non-deformable planes are connected by central and peripheral non-deformable filaments, and the structure is then rigid under torsion.

Thus both the bending moment and the torsion on the rotating helical flagellum can be balanced by the linking of matrix and filaments originally suggested to explain the motion of cilia.

In cilia and undulating flagella all peripheral filaments are connected to the matrix in the same regions, while in the helical flagellum only one filament is connected to the matrix in any region. This difference could be a consequence of differing organizations of the motile system, but it could also be a result solely of how the motion is initiated. The latter case would imply that a) the motion of the organelle is initiated in a restricted region and that b) the alignment of one newly linked junction pair leads to the linking of the next pair. When two junctions are too far apart their linking may be impossible. But when their distance is reduced to a certain level by contractions in the neighbouring

link, the junctions are automatically linked. Therefore any linked region will grow in the direction away from where it was initiated. An undulating wave moving down the tail will then be the result when the segment closest to the head is made to swing back and forth, and a helical wave results when the innermost segment is made to rotate on a cone.

We note that unlinked junctions probably also have a lateral displacement. For if not the passive motion of the cilium through its "effective" stroke might be impossible, since on first occasion all junctions along one filament would simultaneously be linked to the matrix junctions, the cilium would turn rigid, and further rotation would be impossible.

#### Displacements in the helix.

If sections in the matrix originally normal to the axis remain strictly normal, the relative displacement  $D(v^*)$  between the matrix and filament junction sets a distance  $\ell^*$  along the filament measured from B towards A - Figure 4b - will be given by

$$D(v^*) = \ell^* \frac{\epsilon}{2},$$

where  $\epsilon$  is the matrix strain expressed by (1), and the factor  $\frac{1}{2}$  enters because only one endpoint of  $\ell^*$  is displaced. As seen in (2)  $\alpha$  is a small angle when  $r \ll R$ , and therefore

$$\ell^* = rv^*/\sin \alpha \approx rv^*/\text{tg } \alpha = Rv^*/\cos \theta.$$

Introducing  $\epsilon$  from (1) we then get

$$D(v^*) = \frac{1}{2} r \cos \theta v^* \sin v^*, \quad (3)$$

where  $v^*$  is measured in radians. The new links are

formed at A, where  $v^* = v_0 + \beta_0$ , and where therefore the junction displacement is

$$D(v_0 + \beta_0) = \frac{1}{2}r \cos \theta (v_0 + \beta_0) \sin (v_0 + \beta_0).$$

According to Sleight (1962) the diameter  $2r$  of the peripheral filament pattern is  $\sim 1.6 \cdot 10^2$  nm. With  $\theta = 40^\circ$ ,  $\beta_0 = 10^\circ$  and  $v_0 \leq \beta_0$  the longitudinal junction displacement at which links may be formed is then

$$D_c < 2 \text{ nm.}$$

#### Forces in the helix.

Stimulated forces act on the deforming matrix only when it is connected to the filaments. The net work on any linked segment <sup>Figure 4,</sup> AC is then equal to the difference between the work done in link contraction on AB and in link stretching on BC. Figure 6 shows a sketch of the changing links between A and B. With constant lateral distance  $a$  between the two junction sets the changes in link length are due to the changes in the longitudinal displacement of the matrix set alone. If  $\Delta \vec{p}$  is the - unknown - contractile force in the link and  $\dot{\vec{D}}$  is the longitudinal velocity of the matrix junction  $J_1$  relative to the filament junction  $J_2$ , then the rate of work done in the link is

$$\Delta w_t = \Delta \vec{p} \cdot \dot{\vec{D}} = \delta \vec{p} \cdot \dot{\vec{D}}, \quad (4)$$

where  $\delta \vec{p}$  is the longitudinal component of the link force. The absolute size of  $\delta p = \Delta p \sin \beta$  depends on both the size of  $\Delta p$  and on the angle  $\beta = \arctg(D/a)$ , where  $a$  is unknown. If the distance between the junctions on the filament is  $b$



the number of links pr unit length is  $b^{-1}$ , and the longitudinal force pr unit length at  $\ell^*$  is

$$p(\ell^*) = \delta p(\ell^*)/b .$$

The longitudinal force in an element  $d\ell^*$  is then

$$d\vec{p} = p(\ell^*)d\ell^*(-\sin \alpha \vec{i}^* + \cos \alpha \vec{j}^*) , \quad (5)$$

where  $[\vec{i}^*, \vec{j}^*, \vec{k}^*]$  are unit vectors in the direction of the periphery, the axis and the normal to cylindrical flagellum respectively, at the point  $\ell^*$  of the element.

From (3) the longitudinal displacement vector is

$$\vec{D}(v^*) = \frac{1}{2}r \cos \theta v^* \sin v^* (\sin \alpha \vec{i}^* - \cos \alpha \vec{j}^*) .$$

During the speedometer wire rotation of the flagellum new junctions will continuously pass through the element at the angle  $v^* = \text{constant}$ , and the intersection B between the filament and the line  $v = 0^\circ$  or  $v = 180^\circ$  progresses along the flagellum. The rate of change in longitudinal displacement of junctions at  $v^*$  is then

$$\dot{\vec{D}}(v^*) = \frac{1}{2}r \cos \theta \dot{v}(\sin v^* + v^* \cos v^*)(\sin \alpha \vec{i}^* - \cos \alpha \vec{j}^*) ,$$

and the rate of work is then from (4)

$$dw_t = d\vec{p} \cdot \dot{\vec{D}} = -\frac{1}{2}r \cos \theta p(\ell^*)d\ell^*\dot{v}(\sin v^* + v^* \cos v^*) .$$

Since  $\ell^* = Rv^*/\cos \theta$ , the rate of work on the segment AC is

$$\begin{aligned} w_t &= -\frac{1}{2}r R \dot{v} \int_{v_0 - \beta_0}^{v_0 + \beta_0} p(\ell^*(v^*))(\sin v^* + v^* \cos v^*)dv^* \\ &= -\frac{1}{2}r R \dot{v} I(v_0) \end{aligned} \quad (6)$$

Since each filament is linked to the matrix twice on each full turn of the helix, the total available rate of work in a helix of  $k$  full turns is

$$W_t = 2 \cdot 9 \cdot k \cdot w_t = - 9krR \dot{v} I(v_0) , \quad (7)$$

which must be equal to the rate of external work. Expressions for this rate of external work and for  $\dot{v} = \omega_2$  are given by Schreiner (1970). If the radii of head and helix are both  $A$ , and the ratio between longitudinal and transverse friction on an element of the cylindrical flagellum is  $\gamma = \frac{1}{2}$  we get from Schreiner (1970)

$$W_t \sim 64 \cdot 6\pi\mu AU^2 \quad (8)$$

and

$$\omega_2 \sim - 15 \frac{U}{A} \quad (9)$$

respectively, where  $\mu$  is the viscosity of the surrounding liquid and  $U$  is the velocity of swimming. The value for  $\gamma$  taken above is probably too low, but its actual value is unknown. (With  $\gamma = 0.55$ ,  $w_t \sim 80 \cdot 6\pi\mu AU^2$ .) When the relations (8) and (9) are introduced in (7), we find that

$$I(v_0) \sim 2.8 \mu \frac{A^2}{krR} U . \quad (10)$$

As long as the distribution of longitudinal force pr unit length  $p(\ell^*(v^*))$  remains unknown the integral

$$I(v_0) = \int_{v_0 - \beta_0}^{v_0 + \beta_0} p(\ell^*(v^*)) (\sin v^* + v^* \cos v^*) dv^*$$

is unsolvable. If the force in the link is the same under contraction and extension,  $I(v_0)$  will be zero for  $v_0 = 0$  and reach its maximum for  $v_0 = \beta_0$ . Therefore we expect the value of  $v_0$  to lie between these extremes,  $0 < v_0 \leq \beta_0$ .

When  $v_0 = 0$  no motion is possible. If the average longitudinal force pr unit length is  $P_0$ , the integral will with  $v_0 = \beta_0 = 10^0$  be

$$I_0 = P_0 \int_0^{2\beta_0} (\sin v + v \cos v) dv = P_0 \cdot 2\beta_0 \sin 2\beta_0 = 0.12 P_0. \quad (11)$$

(10) and (11) then show that the average value of the longitudinal force pr unit length must at least be

$$P_0 > 23 \pi \mu \frac{A^2}{krR} U.$$

If a microorganism with a helix of two full turns  $k = 2$  and radius equal to the radius of the spherical head,  $R = A = 1 \mu\text{m}$ , say, and radius of the filament pattern  $r \sim 8 \cdot 10^{-2} \mu\text{m}$ , swims through water with a velocity  $U = 100 \mu\text{m/s}$ , then

$$P_0 > 4.5 \cdot 10^{-2} \text{ dyn/cm.}$$

Dynein is found (Gibbons (1963)) in the arms protruding from the peripheral filaments at regular intervals of 12-14 nm (Hopkins (1970)). If these arms are the connections between matrix and filaments, then the component of the force in these connections parallel to the filament is on the average at least

$$\delta p = P_0 b = 4.5 \cdot 10^{-2} \cdot 12 \cdot 10^{-7} = 5.5 \cdot 10^{-8} \text{ dyn.}$$

Since its relation to  $\delta p$  is

$$\Delta p = \delta p / \sin(\text{arc tg } \frac{D}{a}),$$

the average link force  $\Delta p$  still remains unknown, due to the unknown minimum link length  $a$ .

The idea of junction linking and alignment is just a model, and it is possible that this model has been stretched to arrive at the last numerical results. Much more has to be known about the details of flagellar structure before the internal forces can be fully described.

Literature.

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Figure Legends.

- Figure 1. The inextensible filament junction sets AA and BB and the deformable matrix sets A'A' and B'B' can be connected in the straight regions.
- Figure 2. Plots of the dimensionless torsion a) and bending moment b) along the helical flagellum.  $\Psi_0 = \ell \cos \theta / R$ , where  $\ell$  is distance along the flagellum from the tip,  $\theta$  is pitch angle and R is helical radius. (Parameter values  $\frac{R}{A} = 1$ ,  $\theta = 40^\circ$ ,  $\gamma = \frac{1}{2}$ ).
- Figure 3. a) Sketch of a part of the helix, with the notations used in the analysis. A filament AA cuts the line  $v = 0$ , RB, at an angle  $\alpha$ .  
b) Notations in a section normal to the flagellar axis.
- Figure 4. a) Segments ABC and A'B'C' of the filaments may be connected to the matrix.  
b) Notations on the segment ABC.
- Figure 5. A cylinder where non-deformable parallel sections are connected by central and peripheral filaments of unchanging length is rigid under torsion.
- Figure 6. Sketch of a contracting link between the matrix junction  $J_1$  and the filament junction  $J_2$ , with the notations used in the analysis of the force.

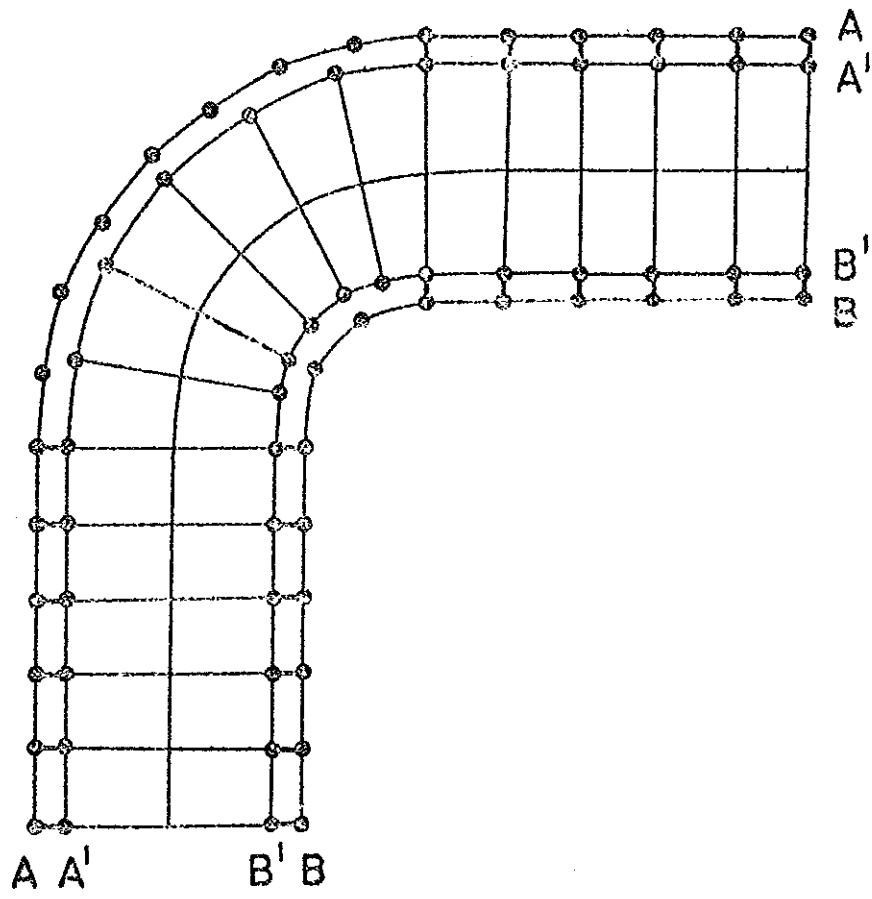


Fig.1

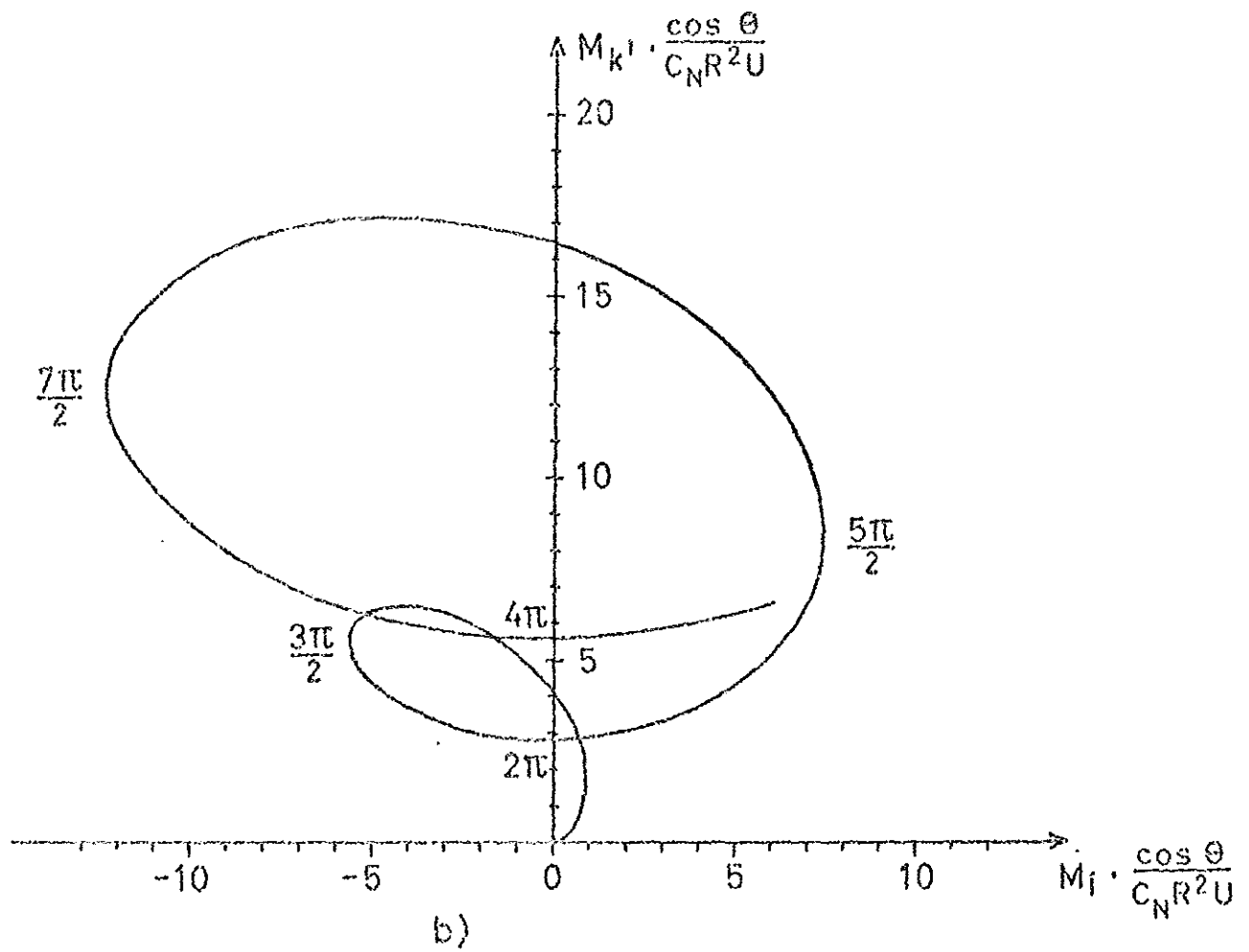
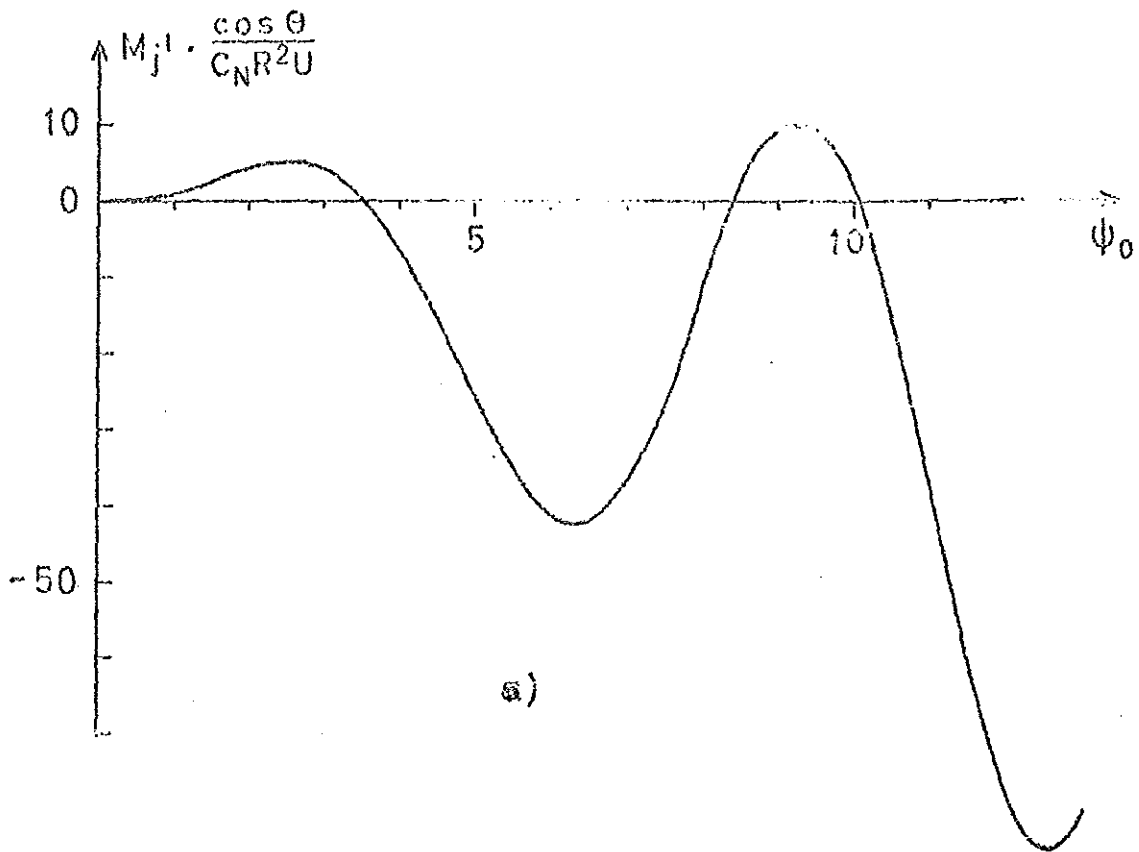


Fig. 1

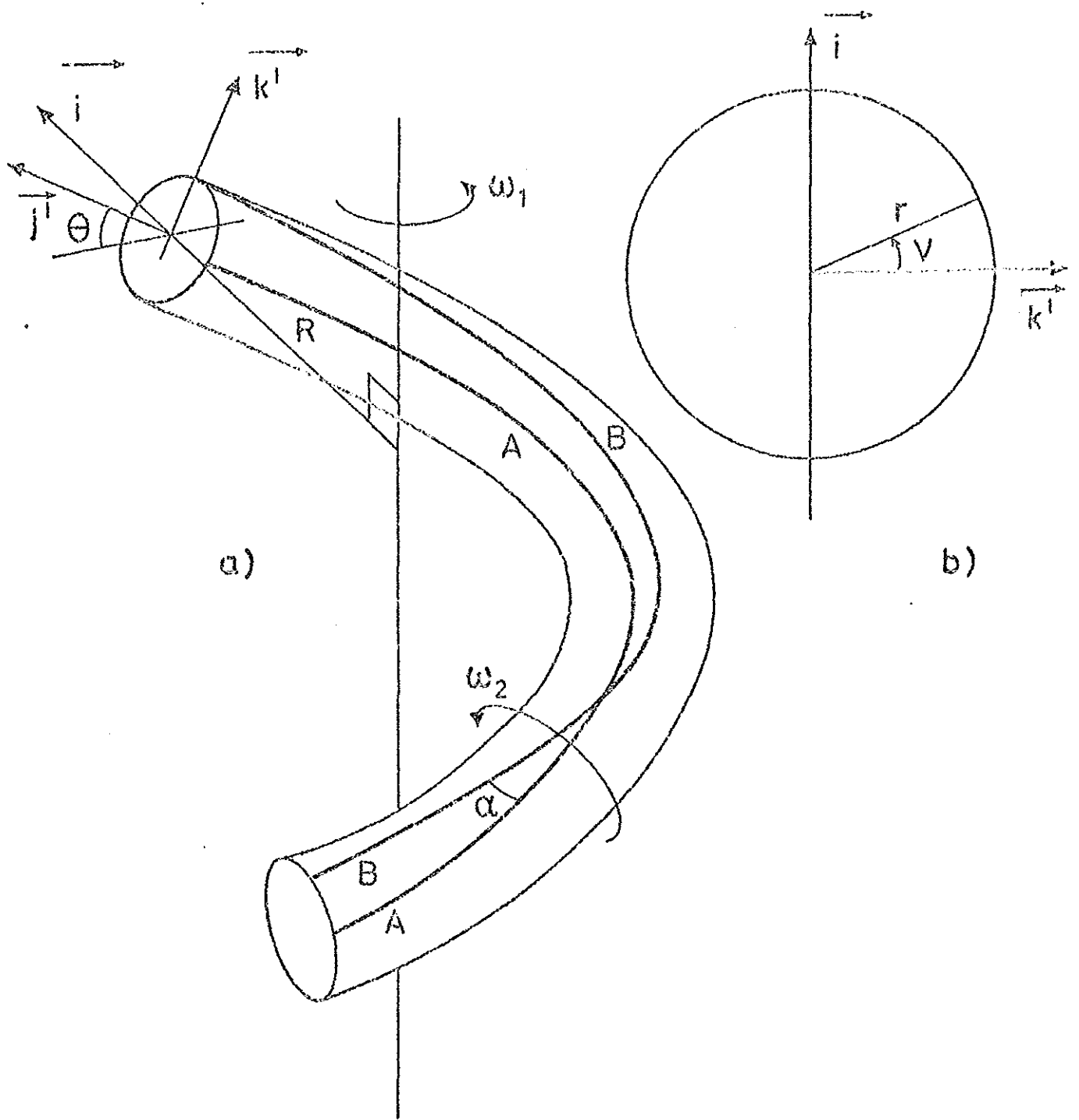
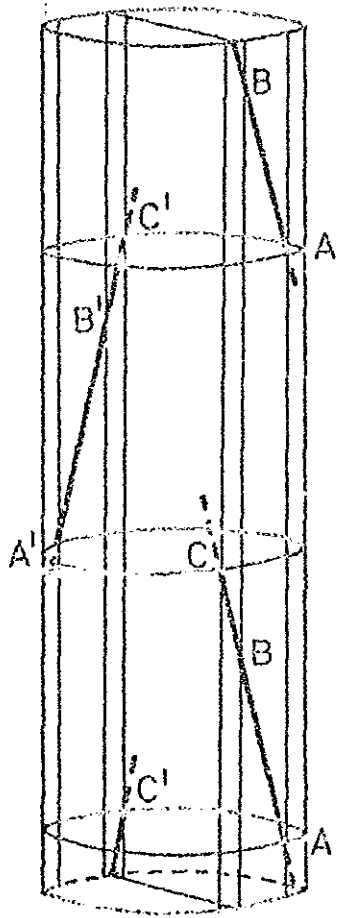
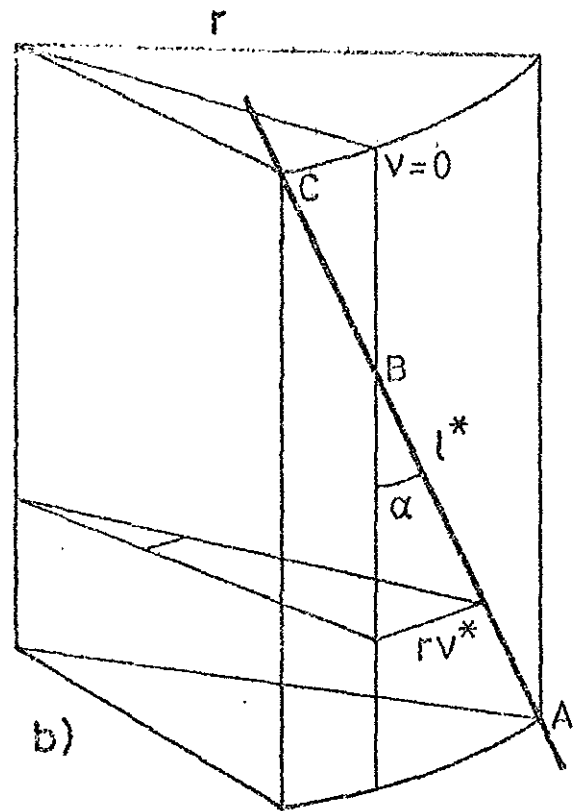


Fig. 3





a)



b)

Fig. 4

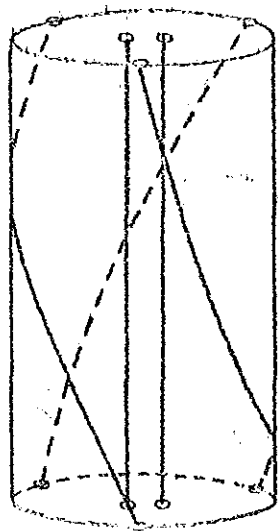


Fig. 5

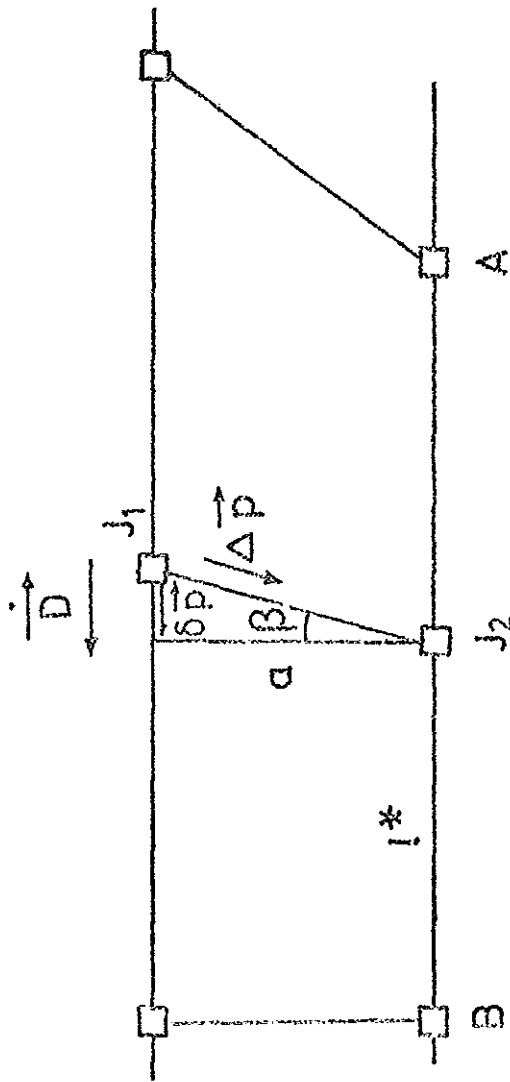


Fig. 6