

A mechanical analysis of the ciliary beat

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The distribution of internal forces needed to balance the external forces and moments from the fluid resistance on the beating cilium is analysed. It is found that the "sliding filament" model is unable to explain the motion during the so-called effective stroke, and that energy may be transmitted to the liquid only in the so-called recovery stroke. A model based on the forming of new links between slightly displaced junctions is presented, to explain the motion during the latter stroke. This model also explains the motion of waves in undulating flagella.

Introduction.

Propulsion of one-celled organisms by ciliary motion is easily observed in the microscope, and it has therefore been studied in the hope that it may throw some light on the functions of the cell. These studies have been reviewed by Sleigh (1962, 1968, 1969).

The fluid mechanics of the propulsion of small objects at low velocities, where viscous forces rather than inertial forces dominate, pose difficult analytical problems, (Schreiner()). The mechanical analysis must therefore be based on simplifications and approximations. This approach has had some success in the case of flagellar propulsion, specially when the organism is propelled by one relatively long flagellum. The analysis of ciliary motion is more complicated, since the relative motion between cilium and liquid, and the resulting resistive forces, will be influenced by the presence of a wall and of other cilia. Actually, the motion of the fluid in the proximity of the micro-organism is not well known at all. The simplifications and approximations must therefore be substantial.

The present work is an attempt to correlate the internal forces in the cilium with the resistive forces from the surrounding liquid. The results do not support the traditional picture of the cilium acting as an oar. Neither do they give evidence to the sliding filament model of the source of ciliary movement. An alternative model focusing on the motion in the so-called recovery stroke is therefore suggested. In this model the motion takes

place because the length of the inner straight region of the cilium in the "recovery stroke" increases; in the "effective stroke" the cilium is thought to be passively following the motion of the liquid.

Observations on cilia.

The beating of non-solitary cilia may be coordinated in metachronal waves that move through the cilia like wind-waves in a cornfield. The beating of each cilium is asymmetric, and a direction of beating can therefore be defined. This direction is in some cases normal to the direction of metachronal wave propagation, in other cases parallel to it, and then the cilia may beat with the waves or against them. In some organisms the direction of propagation of the waves, and with that the direction of the beat, may be reversed.

Although there are variations and exceptions, a "typical" ciliary beat has a rigid rotation phase and a bending and returning phase. At the start of the rotation phase, phase 1, the cilium is straight and pointing at an angle from the wall of attachment. The cilium then rotates as a rigid body around the base through an angle in the order of 90° .

In the bending and returning phase, phase 2, a bend progresses outward from the base, leaving the inner region straight and more or less in the direction it has at the start of phase 1. The total angle of bending - the angle between the axial direction at the base and at the tip - may vary through phase 2, but it is commonly

found to be rather constant, as is the velocity of the bend, and its radius of curvature.

Electron micrographs of a transverse section of the cilium show a pattern of two central and nine peripheral filaments. The pattern is very stable, there is no obvious distortion in the bent cilium, and it takes some digestion to disrupt it. The filaments do not all terminate at the same distance from the tip, and there are special features at the base, but in between the $9 + 2$ pattern of filaments is constant. While there does not seem to be changes in the transverse pattern, the filaments are observed to slide relative to each other under bending, and the observed relative displacements are as predicted if the filaments are inextensible, as shown by Satir (1965, 1968). His observations also seem to indicate that the rest of the central structure - the matrix - deforms without relative displacements in longitudinal direction. Thus the filaments are displaced relative to the matrix in the bent cilium.

The central filaments seem to consist of single tubules, and the peripheral filaments of two parallel connected tubules with two arms protruding from one of them. Excluding the base and tip regions, each filament seems to be built with the same kind of building blocks through its length. The protein dynein, which probably plays a part in stimulation of internal forces, is found in the arms on the peripheral filaments (Gibbons (1963)).

It should be mentioned that the fact that the $9 + 2$ pattern shows up in electron micrographs, while the matrix does not, is due to the chemistry of the structures, not the physics.

As opposed to the filament structure, the outer membrane of the cilium has a baggy appearance in electron micrographs of both longitudinal and transverse sections.

External forces.

The forces on the cilium from liquid resistance are proportional to the relative velocity between the cilium and the liquid. If the velocity of an element dl of a cylinder relative to the surrounding liquid is $\vec{v}_T = v_T \vec{j}'$ in axial direction and $\vec{v}_N = v_N \vec{i}'$ along a normal to the axis, then the force $d\vec{F}$ on the element is

$$\begin{aligned} d\vec{F} &= \left[-c_N v_N \vec{i}' - c_T v_T \vec{j}' \right] dl \\ &= -c_N dl \left[v_N \vec{i}' + \gamma v_T \vec{i}' \right]. \end{aligned}$$

\vec{i}' and \vec{j}' are unit vectors in normal and axial directions respectively, see Figure 1, and c_N and $c_T = \gamma c_N$ are the quotients of proportionality. These quotients are known only for some special simple cases of cylinder motion, which does not include the present case. Both their absolute values and their variation through the stroke are unknown, but their values should be higher the closer the element is to the wall. Further, although we know that the cilia are propulsive organelles, we do not know how this propulsion is actually accomplished. Consequently, we do not know how the liquid moves in the close proximity of the organism. Thus even if the motion of the cilium relative to the body can be described, the relative velocity between cilium and

liquid remains unknown. In the expression for the force, c_N , c_T , v_N and v_T are therefore not known.

With so many unknowns, the following simple model of the ciliary cycle of motion may be warranted. In phase 1, Figure 1 a, the straight cilium of length L rotates from a position normal to the wall to a position parallel to the wall with a uniform angular velocity ω . In phase 2, Figure 1 b, a bend of constant radius of curvature R and constant angle of total bending $90^\circ = \frac{\pi}{2}$ moves with constant velocity U outward from the base, returning the cilium to the normal position. In this phase the outer part of the cilium remains parallel to the wall, while it moves outward with the velocity U , and its length decreases with the same velocity.

Let $[\vec{i}, \vec{j}, \vec{k}]$ be unit vectors on the wall, \vec{i} parallel to the cilium at the end of phase 1, \vec{j} parallel to the cilium at the start of phase 1, and \vec{k} normal to \vec{i} and \vec{j} in positive direction, and let $[\vec{i}', \vec{j}']$ be unit vectors in the cilium in normal and axial directions respectively, coinciding with $[\vec{i}, \vec{j}]$ at the start of phase 1. If α is the angle between the directions of \vec{j} and \vec{j}' at any element of the cilium, then the velocity relative to the wall of the element at distance l from the base is in phase 1

$$\vec{v}_1 = \omega l \vec{i}' = \omega l (\cos \alpha \vec{i} - \sin \alpha \vec{j}).$$

In phase 2 the velocity is given by

$$\begin{aligned} \vec{v}_2 &= U \vec{j} - U \vec{j}' = U(\vec{j} - \vec{j}') \\ &= -U(\sin \alpha \vec{i}' + (1 - \cos \alpha) \vec{j}') \\ &= -U(\sin \alpha \vec{i} - (1 - \cos \alpha) \vec{j}). \end{aligned}$$

Thus in the outer straight region where $\alpha = \frac{\pi}{2}$

$$\begin{aligned}\vec{v}_2 &= -U(\vec{i} - \vec{j}) \\ &= -U(\vec{i}' + \vec{j}') ,\end{aligned}$$

while in the inner straight region where $\alpha = 0$

$$\vec{v}_2 = 0 .$$

As mentioned, the flow of the liquid in the proximity of the body, and thereby the relative velocity of cilium and liquid, is not known. Actually, this implies that we do not know in which part of the beat cycle the cilium transmits energy to the liquid, and in which part it may follow the motion of the liquid.

Let us start with the assumption that energy is transmitted to the liquid during phase 1.

For the sake of argument, we then assume that the fluid does not move relative to the wall. Then the velocity of the cilium relative to the liquid is equal to its velocity relative to the wall. In phase 1 the force on an element a distance l from the base due to liquid resistance is then

$$d\vec{F} = -c_N \omega l \, dl \, \vec{i}' .$$

This means that the moment of the resistive forces on the outer region of the cilium around a section at l is

$$\begin{aligned}\vec{M}_1 &= \int_1^L \vec{r} \times d\vec{F} = \vec{k} \int_1^L (r - l) c_N \omega dr \\ &= \vec{k} \omega \int_1^L (r - l) c_N(r) dr ,\end{aligned}$$

where $c_N(r)$ is an unknown decreasing function of r , and $1 < r < L$. It is easily shown that $c_N(r)$ cannot be chosen so that \vec{M}_1 is independent of l . As an approximation we then put $c_N = \text{constant}$, which gives

$$\vec{M}_1 = \frac{1}{6} c_N \omega L^3 \vec{k} \left(1 - \frac{1}{L}\right)^2 \left(2 + \frac{1}{L}\right).$$

The function $M_1/(c_N \omega L^3)$ is diagrammed in Figure 2 as a function of $1/L$.

Alternatively, instead of the cilium acting on the fluid and transmitting energy to it during phase 1, it may just follow the motion of the liquid. The relative velocities between the cilium and the liquid would then be much less than in the former case, and so would consequently also the external forces and their moments.

On the other hand, it does not seem possible that the much more complicated motion of the cilium during phase 2 can be driven by the liquid flow.

Then the cilium must move through the liquid during phase 2. If again we assume that the liquid does not move relative to the wall, then the force on an element of the cilium is

$$\begin{aligned} d\vec{F} &= \left[c_N U \sin \alpha \vec{i}' + c_T U (1 - \cos \alpha) \vec{j}' \right] dl \\ &= c_N U dl \left[\sin \alpha \vec{i}' + \gamma (1 - \cos \alpha) \vec{j}' \right]. \end{aligned}$$

On the outer straight region where $\alpha = \frac{\pi}{2}$ each element of force has a component pointing towards the wall, and a component

pointing towards the tip. The external forces therefore tend to stretch the outer straight region, and to compress the inner straight region.

The moment of the external forces on the outer region around a section at curvelength l from the base is

$$\vec{M}_2 = \int_0^L \vec{r} \times d\vec{F}.$$

In this phase the distance to the wall is very nearly the same for all moving elements. At any moment c_N and $c_T = \gamma c_N$ are therefore practically independent of l or r . Therefore, if l is on the outer straight region,

$$\vec{M}_2 = - c_N U L^2 \vec{k} \cdot \frac{1}{2} \left(1 - \frac{l}{L}\right)^2,$$

if l is in the bend

$$\begin{aligned} \vec{M}_2 = & - c_N U L^2 \vec{k} \left\{ \left(1 - \frac{\pi}{2} \frac{R}{L} - \frac{p}{L}\right) \left[\frac{R}{L} (\cos \alpha + \gamma (1 - \sin \alpha)) \right. \right. \\ & + \left. \frac{1}{2} \left(1 - \frac{\pi}{2} \frac{R}{L} - \frac{p}{L}\right) \right] + \left(\frac{R}{L}\right)^2 \left[(\gamma + \frac{1}{2}(1 + \gamma) \cos \alpha) \left(\frac{\pi}{2} - \alpha\right) \right. \right. \\ & \left. \left. + \gamma (\sin \alpha - \cos \alpha - 1) \right] \right\}, \end{aligned}$$

where p is the length of the inner straight region, and $l = p + R\alpha$, and if l is on the inner straight region

$$\begin{aligned} \vec{M}_2 = & - c_N U L^2 \vec{k} \left\{ \left(1 - \frac{\pi}{2} \frac{R}{L} - \frac{p}{L}\right) \left[\frac{R}{L} (1 + \gamma) + \frac{1}{2} \left(1 - \frac{\pi}{2} \frac{R}{L} - \frac{p}{L}\right) \right. \right. \\ & \left. \left. + \gamma \left(\frac{p}{L} - \frac{1}{L}\right) \right] + \left(\frac{R}{L}\right)^2 \left[\left(\frac{1}{2} + \frac{3\gamma}{2}\right) \frac{\pi}{2} - 2\gamma \right] + \frac{1}{2} \frac{R}{L} (1 + \gamma) \left(\frac{p}{L} - \frac{1}{L}\right) \right\}. \end{aligned}$$

The function $-M_2/(c_N U L^2)$ of l/L from the expressions above is diagrammed in Figure 3, with the curvelength of the bend one fifth of the total length, $\frac{\pi R}{2L} = \frac{1}{5}$, and $\gamma = \frac{1}{2}$, which is the value for infinite cylinders in infinite liquid, for the three positions of the bend $p = 0$, $p = \frac{1}{2}(L - \frac{\pi}{2}R)$, and $p = L - \frac{\pi}{2}R$, corresponding to no inner straight region, two straight regions of equal length, and no outer straight region.

The important feature of Figures 2 and 3 is that the moment of the external forces on the region of the cilium outside l about the section at l varies with the position of l , from a maximum at the base to zero at the tip. This feature is independent of our special simplifications; it will always be present when the cilium acts on the liquid.

Internal forces.

Since it retains ^{its} shape during each phase, except for the shifting of the bend position in phase 2, the cilium is either rigid, or the moment of the external forces is exactly balanced by the moment of the stimulated internal forces at every section. It follows that in the latter case the internal moments must vary from section to section.

In the following "internal forces" is written for "stimulated internal forces".

Internal forces in phase 1.

The central system of the cilium seems to have two components, a longitudinal system of $9 + 2$ inextensible filaments, and a matrix whose lateral dimensions are constant under bending. If these two systems were bonded together in a region of the cilium, this region would be rigid.

But that can not be the case in phase 1, where the two systems move relative to each other. So in this phase either the matrix itself is rigid, or the external and internal moments balance in every section.

Taking the latter case first, the moment of the external forces is positive, and the moment of the internal forces must be negative. Internal forces must in all probability act along links either between the filaments, or between filament and matrix. Stimulated forces are contractile, and the links must tend to contract under their influence. So either permanent links are contracting towards an equilibrium length, or new links are formed everywhere all through phase 1.

If each link is contracting between the same junctions, the links must be long. For then the force in the link would act mainly in the longitudinal direction of the cilium, and there could also be room for the changing molecular bonds at a lower scale. Further, the junctions would then be able to undergo the large relative displacements even if the strain in the link stayed in the order of $\pm 50\%$, as it does in muscles. But there does not seem to be any evidence of such long permanent links in the cilium. And since the direction of the beat would be

determined by the relative junction displacements at the start of phase 1, the mechanism is unable to explain the beat reversals that are observed in cilia on several organisms.

If on the other hand new links are being formed between new junctions we would expect them to be short. For then the relative displacement that the junctions undergo during the existence of one link is small, and therefore the new gap to be bridged is only a little longer than the old bridge. No complicated mechanism would then be needed to guide the forming of the new bridge. This seems to indicate that the changing links would be the changing molecular bonds between two sets of junctions themselves. It also follows that one set of junctions should be found on the peripheral filaments, the other on the matrix.

With constant lateral dimensions along the cilium, the internal forces must vary proportionally to the external moment. In the simplified case this means that the internal force varies with l according to

$$\left(1 - \frac{1}{L}\right)^2 \left(2 + \frac{1}{L}\right) .$$

A variation of the internal force along the cilium might be accomplished by a similar variation either in the force in each link, or in the number of links per unit length. The length of the links between junctions on two structural members must be constant at any time through any straight region of the cilium. Were they not, the two sets of junctions would form an interference pattern, and the orderly formation of new links would be impossible. But at least on the molecular level forces along equal links of

equal length must be equal, so the first case above must be ruled out.

If the number of links per unit length shall vary, then either the number of available junctions must vary, or there must be a control system in the cilium that engages just enough links in each element to balance the external moments and keep the cilium straight. In the former case the sets of junctions would again form interference patterns, this time like the scales on a slide rule, and the number of available junctions would be very low at any time. The control system in the cilium is then the only possibility left. When it is recognized that both the absolute size of the external forces and their distribution along the cilium probably changes through the stroke of phase 1, it seems unlikely that the complicated control system needed could exist in a comparatively simple structure like the cilium.

Thus a moment balance by internal forces at all sections during phase 1 does not seem likely.

If the cilium is rigid during phase 1, the rigidity must be in the matrix. Further, this rigidity must be biased, since the cilium bends in phase 2, that is, the bend is rigid for positive moments, non-rigid for negative moments. If the cilium is rigid, the internal forces must balance the external moment at the base. At least in the simplified motion the external moment is maximum at the base, and this is probably the case even with more realistic relative motions. If the internal forces were acting anywhere along the cilium, their moment would then not be balanced by the local moment of the external forces, and

the cilium would bend over toward the wall. Since this is not observed, the internal forces would have to act at the base.

Internal forces in phase 2.

Since there is no relative motion between the different components in the cilium outside the bend, the straight regions are rigid if these components are locked together there. As discussed earlier, links of varying length may permanently connect two sets of junctions, in which case the links must be long, or short links may have been formed between adjacent junctions.

In the former case the contracted links would be found in the inner straight region, link contraction would go on in the bend, and in the outer straight region links would be extended to their maximum length. As already mentioned, however, there is no evidence of such long permanent connections in the cilium. And further, the external moments in the inner straight region would have to be balanced by the moment of the longitudinal components of forces that act along links that in this region are essentially transverse. Since the links would be long, the forces in them would then have to be uneconomically large.

Alternatively the structural components are connected by short links formed between adjacent junctions in the straight regions of the cilium. In the analysis of the internal forces in phase 1 we found that varying external moments can not be balanced by changing links in regions where filaments move relative to each other or relative to the matrix. In phase 2

the bend is such a region. But if there is an inherent limit to the curvature of the cilium, small moments would bend the cilium to this limit, while higher moments would not bend the cilium further. This would be similar to a rigidity in that the external moments need not be balanced by the internal forces locally. That such an inherent curvature limit exists is supported by Brokaw's (1965) observations on the shape of the wave in undulating flagella, which consists of straight regions between circular arcs of alternating curvature. (The bending of the cilium in phase 1 takes place at the base, which is morphologically different and where the curvature limit therefore need not exist.)

A process that made the inner straight region increase and the outer straight region decrease in length would then explain the motion of phase 2. The easiest way to accomplish this would be to form new links between matrix and filaments at the inner end of the bend, and have links released at the outer end of the bend. Independent of the total angle of bending of the cilium, the new links are then formed between junctions that are only slightly displaced, with distances of the order needed for molecular forces to act. As the freshly linked junctions are aligned, a new set of junctions are brought into the configuration needed for the next link forming, and the alignment progresses outward.

Instead of terminating, the organelle may have a bend in the opposite direction of the first, and another straight region, that is, it may be shaped like an undulating flagellum. The motion of the wave in such flagella is thus explained by the present mechanism,

with new links being formed at the outer end of each straight region and being released at the inner end.

Conclusions.

Internally, the basic difference between the motions in the two phases is that in phase 1 the matrix and the filaments move relative to each other along the whole cilium, while in phase 2 this relative motion takes place in a restricted region only. We have seen that the external forces and their moments can not be balanced by stimulated internal forces in regions where such relative motion goes on. Also, if the motion in phase 1 were set up by internal forces along the cilium, then these forces would act between structural components in relative motion, and thus work would be performed all along the cilium through the whole of phase 1, while simultaneously new links would have to be formed everywhere. In phase 2, on the other hand, with the presented model, the forces act between structural members that do not move relative to each other, except at one section, namely at the inner end of the bend where new links are formed between slightly displaced junctions. This is then the only place in the cilium where net work is performed, and thus work is done in any segment only once for a short part of the duration of each phase 2.

It has been shown that the motion in phase 1 could be generated by internal forces acting at the base of a cilium with biased rigidity. This mechanism can not produce the motion

observed in phase 2, however. It may not be impossible to have two completely different motile mechanisms in the cilium, but since the motion in phase 1 can be accounted for without any internal activity, the duplex motile mechanism may seem unlikely.

With only one motile system the liquid flow is generated by the motion of the cilium during phase 2. The component of this flow normal to the wall in one region must be compensated by the flow in other regions on the wall. And this latter flow can then drag the cilium along through phase 1 and return it to the starting position of phase 2.

The commonly used notations "effective stroke" for phase 1 and "recovery stroke" for phase 2 would then seem somewhat misleading.

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Figure legends.

- Fig. 1 Simplified motion of cilium in phase 1, a), where it rotates from normal to parallel position, and in phase 2, b), where the cilium is returned to the normal position.
- Fig. 2 Distribution of (non-dimensional) moment along the cilium during phase 1.
- Fig. 3 Distribution of (non-dimensional) moment along the cilium at three different stages in phase 2.

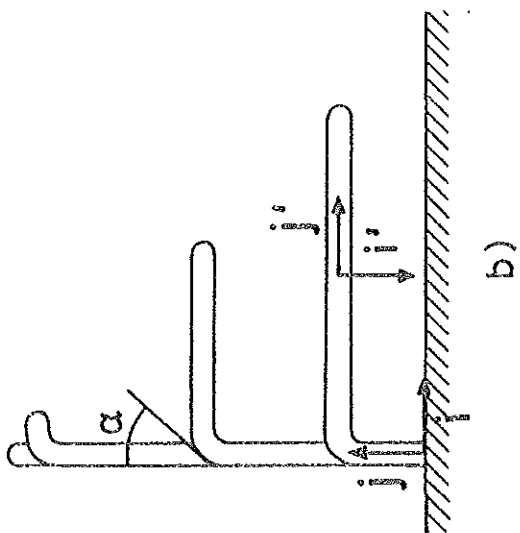
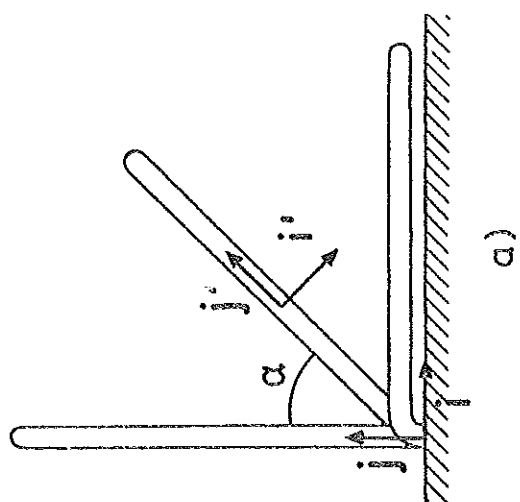


Fig. 1

