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SLIDING FILAMENTS IN CILIA AND FLAGELLA

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Sliding filaments in cilia and flagella.

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Abstract.

The kinematics, rather than the dynamics, of idealized ciliary and flagellar motion is analysed, and it is shown how it correlates with the allowed discrete rates of motion in sliding filament mechanisms (Schreiner (1971 b)). A model for the organelle motion is proposed, according to which ATP is released in regions where active sliding and changes in orientation occur, while regions of constant orientation are in rigor, in the same way as in muscles, under ATP deficiency. The progression rates of bends in plane organelle motion would then be determined by the rate at which crosslinks are transformed from an active state to a state of permanent attachment and rigor at the rear end of the bend.

Introduction.

The motions of cilia and flagella pose questions that may have relevance^{to} motile organic elements in general. The asymmetric ciliary beat generates a fluid flow parallel to the surface of the underlying body, while the symmetric flagellar motion sets up a fluid flow normal to the surface of the body of attachment (Sleigh (1962)). The internal structure appears to be the same in the two kinds of organelles (Afzelius (1959), Gibbons & Grimstone (1960), Gibbons (1961)), however, and since the motion must be generated in the organelles (Gray (1955), Machin (1958)) a common motile mechanism might be expected.

The organelles work on the fluid, and the forces and moments due to the fluid resistance to motion must be balanced internally. Thus the internal mechanism in cilia and flagella must both generate the motion and supply the necessary forces and moments - the necessary stiffness - to support this motion.

Organelle motion. Cilia.

According to Sleigh (1962, 1968) the cilium is more or less straight and pointing at an angle from the wall of attachment at the start of the "effective" stroke, in which the cilium performs a rigid rotation around the base through an angle of 90° - 120° . In the "recovery" stroke a bend progresses outwards from the base, leaving the inner region straight and in position for another effective stroke. In some cases the region outside the bend seems to be straight and of constant orientation, but in other cases it looks as if a compliant outer region is pulled along by the progressing bend (Sleigh (1968)). Sleigh also indicates that

in several organisms the velocity of the bend is nearly constant, and according to Satir (1967) the curvature is constant through the bend, although it may change somewhat as the bend approaches the tip (Satir (1967), Sleigh (1968)).

Undulating flagella.

Brokaw & Wright (1963) and Brokaw (1965, 1966b) have found that the wave of undulating flagella is best fitted by circular bends of alternating curvature, separated by short straight regions. In the "typical" wave the orientation of each straight region is nearly constant. The same is the case with the velocity of wave propagation, while the curvature exhibits the small decrease towards the tip also observed in cilia. At significantly higher fluid viscosities Brokaw (1965,^{1966b}) observes the same general picture, but the curvature is then much larger. As is the case with ciliary motion, many variants to the "typical" motion are reported (Brokaw (1965), Goldstein (1969)).

Helical flagella.

Although plane waves are most common, three-dimensional waves are also frequently observed (Holwill (1966)). The typical three-dimensional wave is a helix, wound on a cylinder or on a cone, whose directrix may be circular or elliptic. Any cylindrical helix can be described as the sum of two orthogonal plane sine-waves of proper amplitude and phase difference, but not as the sum of two plane undulations of the type observed by Brokaw (1965,^{1966b}). Contrary to what is observed in that motion, on the helix there is one continuous bend from one end of the organelle to the other.

Schreiner (1971a) has shown that the axial moment on the single helical propeller must be balanced by the viscous moment

on the contra-rotating head. In the absence of rotational joints the flagellum itself must follow the rotation of the head. In "typical" helical motion the configuration then rotates as a helix with constant orientation of each element relative to the head and the helical axis, while each of these elements rotates about its own axis with an angular velocity numerically equal to the angular velocity of the head.

Organelle structure.

As already mentioned the internal structure of cilia and flagella appears similar (Afzelius (1958), Gibbons & Grimstone (1960), Gibbons (1961)). Electron micrographs of transverse sections show two single central tubules surrounded by a circular pattern of nine peripheral filaments consisting of two parallel tubules sharing a part of their wall. Satir (1965, 1968) has observed that in cilia the peripheral filaments slide relative to each other when the orientation changes, and that the observed relative displacements are as predicted if the filaments were inextensible. The filaments may thus be considered as laying in a cylindrical shell which deforms by the longitudinal displacement of the inextensible filaments. Electron micrographs of transverse sections of bent cilia (Satir(1963, 1965)) show the circular pattern of filaments to be little deformed, and this indicates that the matrix of the organelle, in which the filaments are embedded (Behnke & Forer (1967)), deforms as a solid cylinder, with stretching on the outside and compression on the inside of the bend. The filaments then slide both relative to each other and relative to the matrix when the organelle bends.

Geometric and kinematic relations in the bend.

Fibers on the outside of a bent cylinder are stretched and those on the inside are compressed, while the fibers in the neutral plane retain their length. In an element of the bend where the radius of curvature is R and through which the axial orientation changes by $d\varphi$, an element of a fiber at the distance ΔR from the neutral plane has been stretched from the original length $Rd\varphi$ to the length $(R + \Delta R)d\varphi$. The change in length in the element is thus $\Delta R d\varphi$, which is independent of R . Between two sections in the organelle where the difference in axial direction is φ the fiber stretching is then

$$\Delta l = \Delta R \cdot \varphi ,$$

while the displacement of an embedded inextensible filament relative to the surrounding matrix fibers is

$$\Delta s = - \Delta R \cdot \varphi . \quad (1)$$

If the filaments are twisted relative to the bend a factor depending on the winding number should be included in (1), a more general form of which is therefore

$$\Delta s \propto - \Delta R \cdot \varphi , \quad (1')$$

where ΔR is the distance of the filament from the neutral plane in an end section, say.

From (1) the relative displacement of two filaments at distances ΔR_1 and ΔR_2 from the neutral plane is

$$\Delta s_r = \Delta s_2 - \Delta s_1 = - (\Delta R_2 - \Delta R_1) \varphi . \quad (2)$$

If the radius of the filament pattern is r and ν is the

polar angle of a filament in a cross-section measured from the neutral plane, then

$$\Delta R = r \sin \nu .$$

The displacements may then be written

$$\Delta s = - r\varphi \sin \nu , \quad (3)$$

and

$$\begin{aligned} \Delta s_r &= - r\varphi(\sin \nu_2 - \sin \nu_1) \\ &= - 2r\varphi \sin \frac{\nu_0}{2} \cos \left(\nu_1 + \frac{\nu_0}{2} \right) , \end{aligned} \quad (4)$$

where $\nu_0 = 360^\circ/9$ is the central angle between neighbour filaments, and $\nu_2 = \nu_1 + \nu_0$.

The rate of displacement changes - the rate of sliding - between filament and matrix in the organelle is from (1) and (3)

$$\begin{aligned} v &= \frac{d}{dt} (\Delta s) = - \frac{d}{dt} (\Delta R)\varphi - \Delta R \frac{d\varphi}{dt} \\ &= - r\dot{\nu}\varphi \cos \nu - r\dot{\varphi} \sin \nu , \end{aligned} \quad (5)$$

and between adjacent filaments from (2) and (4)

$$\begin{aligned} v_r &= \frac{d}{dt} (\Delta s_2 - \Delta s_1) = - \frac{d}{dt} (\Delta R_2 - \Delta R_1)\varphi - (\Delta R_2 - \Delta R_1) \frac{d\varphi}{dt} \\ &= 2r\dot{\varphi} \sin \frac{\nu_0}{2} \sin \left(\nu_1 + \frac{\nu_0}{2} \right) - 2r\dot{\nu} \sin \frac{\nu_0}{2} \cos \left(\nu_1 + \frac{\nu_0}{2} \right) . \end{aligned} \quad (6)$$

The first term in each two-term expression in (5) and (6) represents the sliding rate due to changes in ΔR , that is to the rotation of the organelle, while the second term represents sliding rate due to changes in orientation.

From (3) and (5) it is noted that the largest filament to

matrix displacements and the largest sliding velocity due to orientational changes occur along the filaments farthest away from the neutral plane, while the sliding rate due to rotation is largest in the neutral plane. (4) and (6) show the opposite to be the case for filament to filament sliding.

In plane organelle motion where ΔR is constant for each filament

$$v = - \Delta R \frac{d\phi}{dt}$$

and

$$v_r = - (\Delta R_2 - \Delta R_1) \frac{d\phi}{dt} ,$$

respectively.

If the velocity of bend progression relative to the organelle is c , then

$$cdt = - R d\phi$$

and

$$\frac{d\phi}{dt} = - \frac{c}{R} ,$$

and then the sliding rates may be expressed by

$$v = \frac{c}{R} \Delta R \tag{7}$$

and

$$v_r = \frac{c}{R} (\Delta R_2 - \Delta R_1) . \tag{8}$$

Dynamics of organelle motion.

The external forces and moments acting on any organelle element must be balanced by the internal forces in the element; consequently the internal forces are known with the external forces. Several attempts have been made to determine these ex-

ternal forces on the organelle due to the fluid resistance to motion. Both the size and the velocity indicate that the fluid forces are viscid rather than inertial. The analytical problems of viscous flow are formidable, and the resistance to the translation of bodies must therefore be determined by indirect - usually phenomenological - methods. One feature of the viscous flow is that the fluid resistance depends strongly on the presence of other fluid boundaries. Thus for a cylinder "boundaries 500 diameters away will completely dominate the drag ..., and it is not until they are some 10.000 diameters away that their influence disappears" (Happel & Brenner (1965)). The presence of neighbour organelles and the wall of attachment will therefore modify the fluid forces on each organelle. On solitary flagellar propellers the distance to the head is nearly constant for each element during the motion, and for optimal values of the parameters even the variation of the friction along the organelle may not be too critical (Schreiner (1971 a)). Computations of forces and moments on flagella (Taylor (1952), Gray & Hancock (1955), Holwill & Burge (1963), Brokaw (1965, 1970), Schreiner (1971 a)) may therefore have some merit.

On cilia, however, the distance both to neighbour organelles and to the wall of attachment changes during the beat cycle. The friction on long ellipsoids in otherwise unbounded fluid was determined by Jeffery (1922) and Burgers (1938), but neither the magnitude nor the variation of the viscous friction on a finite cylinder moving in the proximity of a wall are known. The accuracy of computations (Harris (1961), Sleigh & Holwill (1969)) and experiments (Yoneda (1962)) that do not recognize the effect of the wall may therefore be questionable.

At the present stage of analysis of the motile system of cilia and flagella it may, however, be enough to note that the external moment varies along organelles that act on the fluid. That this is the case along cilia seems plausible, and it is certainly the case along freeswimming undulating flagella (Brokaw 1965, 1970)) and along helical propellers (Schreiner (1971 a)). On undulating flagella Brokaw found that the external moment oscillates between extremal values in the centre of each straight region, being zero in the middle of each bend. And on the helical flagellum Schreiner found an oscillating torsion and an oscillating bending moment that also varies in orientation in space.

Moment balance in the organelle.

Several attempts have been made to correlate the external moment - i.e. the bending moment - M_b , with the moment M_e of the internal elastic forces (Gray (1955), Machin (1958), Brokaw (1966 a), Rikmenspoel (1966, 1971), Sleight & Holwill (1969), Rikmenspoel & Sleight (1970)). The necessary moment balance would then be expressed by

$$M_b + M_e = 0 . \quad (9)$$

By Hooke's law the elastic forces under small strains from a stressfree equilibrium are proportional to the strains. In the works referred to above it is assumed that this stressfree equilibrium is represented by the straight organelle. When a straight rod is bent the moment of the elastic forces in any section is

$$M_e = - \frac{1}{R} E I , \quad (10)$$

where R is the local radius of curvature, E is Youngs modulus

of elasticity for the rod material, and I is the moment of inertia of the cross-section defined by its shape. When (10) is introduced in (9) the more familiar form

$$M_b = \frac{1}{R} EI \quad (11)$$

results. This shows that if the elastic moment balances the bending moment, the latter must everywhere be proportional to the curvature of the rod. This is neither the case in free-swimming undulating flagella (Brokaw (1965, 1970)) nor in helical propellers (Schreiner (1971 a)). An elastic moment due to deformations from the straight shape must by (10) be zero in every straight region and constant through each bend. Along the free-swimming flagellum the periodic elastic moment is then 90° out of phase with the oscillating external moment it supposedly helps balance.

Gray (1955) and Machin (1958) noticed that the elastic moment alone could not balance the bending moment, and Machin suggested that active forces in the organelle might supply the additional internal moment. This idea has been taken up by Brokaw (1971), Rikmenspoel & Sleigh (1970), and Rikmenspoel (1971). As indicated by Brokaw (1971) the active moment must be a result of energy-consuming processes in the deformed organelle. The moment balance can then be expressed by

$$M_b + M_e + M_a = 0 ,$$

where M_a is the active moment. Since it takes energy to generate active forces there must be energy loss when the elastic moment is balanced by the active moment, the loss being smaller the lesser the elastic moment. The minimum loss occurs when

$M_e = 0$, and

$$M_b + M_a = 0 \quad (12)$$

everywhere in the organelle.

The assumed existence of an elastic moment of deformation seems to be based on observations that resting organelles are straight and rigid. A possible explanation of straightness and rigidity in the resting organelle that does not imply elastic resistance to deformation during motion is presented in the discussion. If this explanation is correct the moment balance in the organelle may everywhere be expressed by (12), where M_a is generated in the motile mechanism of the organelle.

Sliding filament model of the motile mechanism.

Afzelius (1958), Satir (1967, 1968), Sleight (1968, 1969) and Brokaw (1968, 1971) have suggested that the displacement of the peripheral filaments might be the origin of organelle motion rather than a result of it. The sliding could result from configurational changes in crosslinks between structural members that exhibit relative displacement, that is between adjacent peripheral filaments, or between each filament and its surrounding matrix (Satir (1967)). The sidearms on the a-tubule of each peripheral doublet with their myosin-like protein dynein (Gibbons (1963)) have been mentioned as possible crosslinks (Satir (1967), Sleight (1968)).

Since the bending moment must be balanced everywhere by the moment of the internal forces, these forces must vary along the organelle. If filament sliding is a result of configurational changes in crosslinks, then crosslink

force may be constant while the number of attached crosslinks per unit length varies, or the number of attached crosslinks per unit length may be constant while the crosslink force varies.

H.E. Huxley (1971), discussing the sliding filaments of muscle myofibrils, has pointed out that the cross-bridges must move asynchronously for a steady force to be developed, and Schreiner (1971 b) has noted that if all cross-bridges are alike and go through the same configurational cycle, they can only move asynchronously when the repeat distances on the two filaments are different - as actually observed in muscles (Huxley (1967)). If the repeat distance is constant on each filament, and if the time spent in crossbridge recovery is independent of the time spent in the active part of each cycle, Schreiner (1971 b) finds that sliding can only occur at the rates given by

$$v = \frac{1}{t_b} (nd_a - d), \quad (13)$$

where t_b is the time needed for recovery, d_a is the repeat distance between attachment sites, d is filament displacement during the active part of the cycle, and n is an integer number. The only condition on n is that it must be larger than d/d_a . The discreteness of allowed sliding rates shown in (13) results from necessary conditions on the geometry of the mechanism, and it therefore should apply to all sliding filament systems.

If active sliding takes place in the plane bends of cilia and flagella, (13) may be introduced in (7) and (8) to give

$$R = ct_b \frac{\Delta R}{nd_a - d} \quad (14)$$

and

$$R = ct_b \frac{\Delta R_2 - \Delta R_1}{nd_a - d} \quad (15)$$

respectively. The progression rate c of the bend relative to the organelle may vary along the organelle, but at each station it seems to remain constant (Sleigh (1968)). Both (14) and (15) show that the radius of curvature can then only take distinct values defined by the integer number n , and by the distance ΔR , respectively ΔR_2 and ΔR_1 , from the neutral plane to the filament or filaments along which active sliding occur. Thus a jump in the radius of curvature may correspond to a jump in the sliding rate, or to a jump in active sliding from one filament or filament pair to another. However that is, that distinct constant values of curvature are observed in the organelles (Brokaw (1965,1966b)) may indeed indicate that organelle motion is generated by sliding filaments.

If one of the junction sets of the sliding filament system is in the matrix, the repeat distance of this set will change when the matrix deforms. The strain in the matrix is

$$\epsilon = \frac{\Delta R}{R}$$

anywhere, however, and if R is constant, so is the strain at the distance ΔR from the neutral plane. In plane organelle motion the repeat distance of the matrix set is therefore uniform along any one filament, and Schreiners (1971 b) results are applicable. In helical motion, on the other hand, where the neutral plane twists with the helix, while the peripheral filaments are without any twist or spiralling along the organelle (Holwill (1966)), ΔR is not constant for each filament, the repeat distance of each matrix set is not uniform, and Schreiners (1971 b) results may not be applicable.

Sliding filaments in plane organelle motion.

In plane organelle motion ΔR of each filament is constant while the orientation of each organelle element may change with time. Along any region that retains its shape the rate of internal changes - i.e. the sliding - must be constant. When the cilium swings over during the effective stroke the sliding is the same in all elements outside the stationary bend, in the straight regions of constant orientation in recovering cilia and undulating flagella no sliding takes place, and in progressing bends of constant curvature the sliding rate is constant along each filament.

The angle of bending between regions of no sliding is constant, and since the curvature of the bend is determined by the allowed sliding rates the shape of the bend is completely determined. As the bend arrives "permanent" attachment in front of the bend must be broken, the filaments are forced to slide as the bend passes, and thereupon new "permanent" attachment takes place.

The undulations of flagella can propel microorganisms, and they are no doubt "active" - work is done on the liquid in this motion. The similarity of the flagellar undulation to the ciliary recovery stroke may indicate that also the latter is an "active" motion. It has not been obvious how fluid flow is generated by ciliary motion, however. The notations "effective" and "recovery" strokes stem from an assumed analogy between the ciliary beat and the stroke of an oar, but ciliary motion is resisted by viscous forces and the oar blade by inertial forces, and the analogy is superficial. Lately Blake (1971 a, b, c) has shown that fluid motion may be generated by the metachronal waves moving through the typical non-solitary cilia. This finding is supported by the fact that the water flow through *Mytilus* gills may be up to four times as fast as the motion of the tips of the lateral cilia gene-

rating the flow, during their effective stroke (Barker Jørgensen (1971)). If the streamfunction given by Blake (1971 a) is used to compute the forces on the envelope formed by the ciliary tips, it is found that in antiplectic metachronism - which according to Sleight (1962) is the most common - most work is done on the liquid by the part of the surface representing the recovering cilia (Wilson & Schreiner (1971)). This evidence points to the conclusion that cilia act on the fluid through the motion of the metachronal wave, and that the recovery stroke, where the whole outer region of the cilium forms a part of the wave surface, is an active stroke. The role of the effective stroke is not as clear. The observations by Yoneda (1960, 1962) on the very atypical abfrontal cilia of *Mytilus* gills - solitary compound organelles consisting of up to 50 single cilia - show that motion is generated in the compound during the phase corresponding to the effective stroke in cilia. Sleight & Holwill (1969) have found, however, that even by this compound organelle more work is done on the fluid during the motion corresponding to the recovery stroke than during the effective stroke.

Sliding filaments in three-dimensional organelle motion.

During helical flagellar motion each element of the organelle rotates around its axis, while the orientation of each element relative to the base may remain constant. Then by (5) the filament/matrix sliding rate is

$$v = - r\dot{\varphi} \cos \nu ,$$

and by (6) the filament/filament sliding rate is

$$v_r = - 2r\dot{\varphi} \sin \frac{\nu_0}{2} \sin(\nu + \frac{\nu_0}{2}) .$$

\dot{v} , which is the same as ω_2 in Schreiners (1971 a) paper on helical propellers, is a rather complicated function of the velocity of translation of the helix, the rate of helical rotation, and the radius and pitch of the helix. The effect of the discreteness of sliding rates on the shape of the rotating flagellum is thus not readily accessible. In addition comes the possible difficulty of the non-uniform deformation of the matrix along each filament. Analysis of the rotational motion is therefore not presently pursued.

Discussion.

The relative number of attached crosslinks may be related to the kinematics rather than to the dynamics of filament motion (Schreiner (1971 b)), and this number should therefore be constant along any organelle region where the kinematics are constant. To supply the varying internal force along the organelle it is then necessary that the crosslink force varies. Thus the organelle motion may be controlled through the internal kinematics, while the crosslink force adjusts to the external force generated by the organelle motion.

The plane motion of cilia and flagella can then be explained if three different states exist between the sliding elements, a state of rigor when the elements are connected by "permanent" crosslinks, a state of compliancy when no crosslinks are established between the elements and therefore passive sliding may occur, and a state of activity when changing crosslinks are established. Since no motion occurs under rigor, this state would represent the lowest level of energy need, while active motion would represent the highest level of energy need. If no energy

is supplied in a region it would be in rigor, while active sliding might be induced when energy is supplied. Supply of energy would probably mean supply of ATP.

The inner region of the recovering cilium and the straight regions on the undulating flagellum where the bending moment is largest (Brokaw (1965, 1970)) would then be rigid without any cost of energy. If no new bend is initiated the whole organelle is left straight and in rigor as the last bend reaches the end, and in this state the organelle would be at rest. This rigor must be relieved before organelle motion and corresponding filament sliding can occur, whether this sliding be active or passive. The rigor of the resting organelle is then not representative of the state in the moving organelle.

In the recovering cilium and the undulating flagellum active sliding seems to take part only in the bend. It might then be perceived that the bend itself may act as the agent for pumping or releasing energy, that is ATP. With the distinct allowed sliding rates and bend curvatures no sophisticated mechanism is needed to control the bend shape, and the rate at which the cross-links are transferred from activity to permanent attachment at the rear end of the bend will determine its progression rate.

If in the relaxed organelle active sliding is initiated in a short region, and if at the proper end of this region the cross-links are allowed to drop into permanent attachment, a bending wave will be generated that will move in the direction of its "free" end. Since in the base the filaments are probably never allowed to slide, the seed for permanent attachment is always present there. The region just outside the base is then a likely

region of bend initiation. According to Holwill (1966) bends may also be initiated at the tip. Since the motion in the bend is asymmetric, it is possible that bends **may** be initiated only in similarly asymmetric regions. If active sliding is initiated in the outermost region, the tip might be left without the necessary supply of ATP, and therefore drop into rigor, whereupon the bend would have to move inwards.

It may be perceived how a signal from the base might start active sliding in the nearest region, but it is not clear how the whole organelle is relaxed from rigor, and how active sliding is initiated in the outermost region, or in the whole organelle for the active motion of the effective ciliary beat - if active sliding is needed for the latter motion.

The three proposed states in the sliding filament apparatus correspond to the three similar states known to exist in muscle myofibrils. It is therefore possible that the way these states are controlled in muscle may indicate how similar control is effectuated in cilia and flagella.

Within limits the crosslink force adjusts to the external load, and the variation of the force from crosslink to crosslink depends on the load distribution. In muscles, where the external loads act longitudinally on the endpoints of the filament system, the crosslinks act in parallel and the load is evenly distributed between them. In cilia and flagella the external load changes along the system, and the crosslink force is not uniform. If the load on a crosslink exceeds a critical limit, it is possible that the attachment breaks and that the motion is transformed to another mode where the crosslink force is lower, especially since the crosslink load is largest in the region at the base where

motion usually is generated. The distinct curvatures observed in undulating flagella at different fluid viscosities (Brokaw (1965, 1966 b)) may be examples of such modes.

It is quite possible that the crosslinks are elastically deformed under loading. As a result the radius of curvature may vary along the organelle, and the straight regions may not be quite straight. But while the elastic deformation may give a phase difference between the motions of the two crosslink end-points the elastic force can of course not enhance the force transmitted by the crosslink.

Grimstone & Klug (1966) report that the a- and b-tubules of each peripheral doublet are built of equal interconnected parallel fibers. It may then seem likely that repeat distances would be the same on both tubules, which would exclude the possibility of establishing changing crosslinks between neighbour filaments. Further, Gibbons (1967) finds that separated sidearm material reattach at proper positions on the a-tubule, while no material attaches to the b-tubule. And it is not easily perceived how crosslinks between filaments may be established through a matrix that moves relative both to the filaments and to the crosslinks during organelle motion. Although not conclusive these arguments seem to indicate that the crosslinks are established between the cylinder of filaments and the solid cylindrical matrix rather than within the filament shell alone.

Conclusions.

Compared to the dynamics both external and internal organelle kinematics are relatively simple under plane motion. These simple kinematics correlates well with the distinct values of possible displacement rates between sliding filaments. The main conclu-

sions of the analysis are

- 1) Ciliar and flagellar motion is generated by sliding filaments.
- 2) Organelle shape is defined by the distribution of regions of rigor, passive sliding, and active sliding, corresponding to similar states in muscles. Rigor is maintained without energy cost, while energy is needed for active sliding. In undulating flagella active sliding takes place in the bends, while the short straight regions are in rigor. In recovering cilia active sliding takes place in the bend, the inner region is in rigor, the outer region in rigor or in passive sliding. In the effective ciliary stroke sliding - active or passive - occurs along the whole cilium. The organelle is in rigor when it is resting, and it must be relaxed before motion can start.
- 3) The constant plane bend curvatures are determined by the discrete displacement velocities of sliding filaments and by the constant distance of each peripheral filament from the neutral plane of bending. The rate of wave progression may be determined by the rate at which crosslinks are transformed from an active state to a state of rigor at the rear end of each bend. Due to the discreteness of the kinematics of the mechanism no complicated system is needed to control and maintain the waves of bending, but signals for relaxation from rigor and for initiation of active sliding may be needed.
- 4) Crosslink force is not necessarily constant, but adjusts to the local external load.

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