MOTILITY OF BASAL FRAGMENTS OF SEA URCHIN SPERM FLAGELLA

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SUMMARY

Both live and reactivated sea urchin sperm flagella were broken by passage through a pipette. Distal fragments stopped, but basal fragments continued to beat. Intact flagella were about 48 µm long; basal fragments were about 4–20 µm long.

Beat periods of tritonated fragments were 11% shorter than those of unbroken controls, possibly reflecting decreased viscous loading; beat periods of live fragments were 18% shorter than those of unbroken controls, possibly reflecting reduced rates of ATP consumption as well as decreased viscous loading.

The undulations of basal fragments were compared with those of the basal regions of unbroken flagella, using the patterns of development of the radii and angles of basal bends. Fragments closely resembled basal regions of unbroken flagella, except that bends tended to open as they approached the distal end of a fragment, so that their radii increased more rapidly than those of unbroken flagella.

Fragments about 4 µm long contained only one bend during part of the cycle, and appeared to be straight during part of the cycle. They flipped back and forth with fairly constant angular speeds and abrupt changes in direction, so that plots of angle between their distal end and base often resembled triangular waves, although the peaks of the waveforms were often rounded. This behaviour suggests a mechanism in which sliding switches between 2 modes. Both the speed of sliding and the maximum angles attained in one direction of bending were greater than those attained in the other direction, suggesting differences between the doublets on the 2 sides of the axoneme. Sliding of the doublets continued at fast speeds as the fragments straightened, in contrast to the characteristics of some curvature-sensitive models.

These flagellar fragments provide a simplified system for the study of flagellar oscillations.

INTRODUCTION

Beating has been reported for short regenerating flagella (Rosenbaum & Child, 1967), for flagella fragments resulting from random mechanical breakage (Brokaw & Goldstein, 1979; Gibbons, 1974, 1980; Gibbons & Gibbons, 1980), and for fragments of flagella that have been broken with microneedles (Terni, 1933; Holwill & McGregor, 1974; Lindemann & Rikmenspoel, 1972; Okuno & Hiramoto, 1976) or irradiated by a microbeam (Terni, 1933; Walker, 1961; Goldstein, 1969; Goldstein, Holwill & Silvester, 1970). Beating can continue in sections that contain the basal end. Beating does not continue in distal isolated pieces of echinoderm sperm flagella, although it can in some other types of flagella. The waveforms of short basal fragments have generally not been analysed in detail. In the study reported here, the flagella of sea urchin spermatozoa were broken by passage through a pipette and the beating
basal fragments were photographed. Their waveforms were analysed and compared with those of unbroken flagella.

Some of the results have been presented in abstract form (Goldstein, 1979a).

MATERIALS AND METHODS

The California sea urchin *Lytechinus pictus* and the Bermuda sea urchins *Tripneustes esculentus* and *Lytechinus variegatus* were spawned by injection of 0.6 M-KCl and the semen was collected, diluted with an approximately equal volume of artificial sea-water or isotonic NaCl, and stored on ice until used. Live spermatozoa were diluted as needed about 1:5000 in artificial sea-water containing 0.5 % (w/v) bovine serum albumin (Goldstein, 1977). Reactivated spermatozoa were prepared as described by Brokaw (1975), using a reactivating solution containing 10^-10 to 10^-8 M free Ca^2+ and usually containing 0.2 mM-ATP. Spermatozoa were broken by repeated rapid passage through a Pasteur pipette; for live spermatozoa the tip of the pipette had usually been drawn to a diameter of about 0.5 mm.

Stroboscopic microscope illumination was used and results were recorded with dark-field multiple-exposure photographs as described previously, with the film either stationary (Brokaw, 1970) or moving (Goldstein, 1976), at magnifications of 160-400 x. The photographs shown in the figures were taken with the film moving, and are negative prints made from intermediate positive transparencies. Measurements were made on prints as described previously (Goldstein, 1976). The beat periods (to the nearest 0.1 ms) of the photographed flagella were determined by adjusting the flash period of the stroboscope until the flagellum appeared not to be beating. Usually the beat periods of unbroken spermatozoa in the same field were recorded during the course of filming broken ones, to provide data on approximately equal numbers of broken and unbroken flagella (typically 5 to 10 of each per film) for statistical comparisons of beat frequencies. Observations were made at 21 °C for the Bermudian spermatozoa and 18 °C for the Californian ones. The basal ends of flagella could usually be seen in photographs of reactivated spermatozoa, but the basal ends of live flagella were obscured by the midpieces. Live flagellar fragments may therefore have been longer than measured, although discrepancies are probably less than 1 μm. The directions of flagellar bases of live spermatozoa were estimated from images in which a basal bend was just beginning to travel toward the tip and the proximal end of the bend had just become visible, since any basal curvature that was obscured by the base should have been minimal in these images. The basal direction was taken to be the direction of the most proximal visible portion of the flagellum, which usually coincided with the axis of the head. In very short fragments the basal direction was taken to be that of the fragment in images in which the fragment appeared to be straight. The angle between the axis of the head and the flagellar base was assumed to remain constant in live spermatozoa for estimation of basal direction in other images.

RESULTS

Unbroken flagella

An unbroken flagellum is shown in Fig. 1A. The variation in the angle (θ) between the flagellar base and a point on the flagellum 3 μm from the base is shown in Fig. 1B. The slope of this plot is proportional to the speed of sliding between the doublets at this point on the flagellum (Satir, 1965). This plot of θ resembles a triangular wave, with constant angular speeds and rapid transitions when the maximum angles are reached. This is not always the case: the peak angle of the flagellum in the direction of the reverse bend (θ^R_{max}) in this photograph is rounded when measured 5 μm from the base, and in photographs of some other spermatozoa both θ^R_{max} and the maximum angle of the flagellum in the direction of the principal bend (θ^P_{max}) are rounded when
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measured 3 μm from the base, indicating that changes in direction are not always as abrupt as they are in Fig. 1A. These angle plots were generally asymmetric for points within several μm of the base, with the maximum angle in one direction being larger than that in the other direction. This was true even in photographs of tritonated spermatozoa, in which the principal and reverse bends of the most symmetrically beating flagella could develop to equal angles (Goldstein, 1976). In those photographs in which the principal and reverse bends could be distinguished, $\theta_{\text{max}}^{\text{P}}$ was generally larger than $\theta_{\text{max}}^{\text{R}}$ at 3 μm from the base. The maximum angles attained in the directions of greater and lesser bending at points near the flagellar base are

![Image of sperm flagella](image)

Fig. 1. Unbroken reactivated spermatozoon of *L. pictus*. A. Attached to glass by head, with beat period of 81 ms in 0.2 mM-ATP. Period between exposures approx. 76 ms. First image on left. Arrowhead indicates point 3 μm from base. Bar 10 μm. B. Angle between base and point 3 μm from base. Each point is directly beneath the corresponding image in A.

therefore denoted $\theta_{\text{max}}^{\text{P}}$ and $\theta_{\text{max}}^{\text{R}}$ respectively. Data on points 3 μm from the base of 3 live and 4 tritonated unbroken flagella are shown in Fig. 2. Only angles subtended during relatively constant angular speeds were used, to produce least-squares regression lines for the maximum angular speeds. The point at which $\theta = 0$ in the direction of swing from $\theta_{\text{max}}^{\text{P}}$ toward $\theta_{\text{max}}^{\text{R}}$ is taken as $t = 0$. This was estimated by linear interpolation between the nearest exposure on either side of that point. The 'fraction of cycle' designated for a point is the time elapsed between $t = 0$ and that point, divided by the duration of a complete cycle. To allow the combining of data from a number of photographs, all angles between 0 and $\theta_{\text{max}}^{\text{P}}$ were normalized to $\theta_{\text{max}}^{\text{P}}$ of the photograph in which they appeared, and angles between 0 and $\theta_{\text{max}}^{\text{R}}$ were similarly normalized to $\theta_{\text{max}}^{\text{R}}$. The regression lines are (Mood & Graybill, 1963): 

I, $\theta = 1.50 (\pm 0.14) + 2.41 (\pm 0.33)t (n = 26)$; II, $\theta = 0.54 (\pm 0.033) - 4.34 (\pm 0.24)t$
(n = 15); III, $\theta = -0.163 \pm 0.06 \cdot 4.40 \pm 0.50$ (n = 14); IV, $\theta = -1.38 \pm 0.18 + 2.34 \pm 0.47$ (n = 19). I-IV represent phases of the beat cycle as noted in Fig. 2. There is no significant difference between the slopes (i.e. the normalized angular speeds) during phases I and IV, or between those during phases II and III, but the angular speeds are significantly higher during phases II and III than during phases I and IV. That is, the speeds of swing from $\theta_{\max}$ to $\theta_{\max}$ were greater than the speeds in the other direction.

In both broken and unbroken flagella a new bend starts at the base before the previous, developing, bend has completed its growth, so that the angles of the developing bend and the newly forming bend increase simultaneously (cf. Goldstein, 1976, 1977). The angle subtended by a developing bend was plotted as a function of the angle subtended by the following, newly forming, basal bend, as a way of characterizing bend development. A principal bend was used as the more fully developed bend where it was possible to distinguish between them. The results for 50 live spermatozoa are shown in Fig. 3. The regression line is: $y = 1.70 \pm 0.12 + 0.65 \pm 0.25x$ (n = 50; r = 0.35) (Mood & Graybill, 1963). The data for reactivated
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Fig. 3. Angle subtended by a developing bend on live flagella as a function of the angle subtended by the following bend beginning to form at the base. (O, ——) Unbroken flagella; (●, ----) broken flagella.

spermatozoa (not shown), which beat more symmetrically (Goldstein, 1976), yield the regression line: \( y = 1.43 \pm 0.13 + 1.00 \pm 0.23 \times x \). Because these lines are used for comparison with those for flagellar fragments, which did not usually develop large bend angles, only angles less than 0.8 rad have been used.

Broken flagella

Flagella appeared to break more or less at random along their length, and spermatozoa with lengths between about 4 and 20 \( \mu m \) were photographed. Both freely swimming flagella and those attached to the glass were used for measurements. Unbroken flagella were about 48 \( \mu m \) long.

Both live and tritonated short flagella beat asymmetrically and followed curved

Fig. 4. Broken live spermatozoon of *L. variegatus* swimming freely in a circular path of radius 12.5 \( \mu m \). Beat period, 15 ms; period between exposures, 73 ms. Bar 20 \( \mu m \).
paths when swimming next to a surface, as shown in Fig. 4. Broken spermatozoa that have attached to a cover-glass are shown in Figs. 5–7.

**Angles on broken flagella**

The angle between the flagellar base and the tip of the flagellum of Fig. 5A is shown in Fig. 5B. These plots are generally asymmetric, with $\theta_{\text{max}}^p$ larger than $\theta_{\text{max}}^d$, and the peaks are often more rounded than those of Fig. 5B. However, the angular speeds were usually fairly constant during much of the beat cycle between peaks. Angles between the tip and base of broken flagella, using data from 6 live and 5 tritonated spermatozoa, are shown in Fig. 8. Only angles subtended during relatively constant angular speeds were used, and angles were normalized as in Fig. 2. The
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Fig. 7. A. Broken reactivated spermatozoon of *L. pictus*, attached to glass by flagellum, with beat period of 800 ms in 10⁻⁹ m-ATP. Period between exposures, 50 ms. Bar 10 μm. B, C, D. Enlargements of exposures, indicated by the lines marked (B), (C), (D) in A, in which the flagellum appears to pass through a straight phase.

Regression lines are: I, \( \theta = 1.56 (\pm 0.12) + 2.62 (\pm 0.31)t \) (\( n = 33 \)); II, \( \theta = 0.073 (\pm 0.04) - 4.37 (\pm 0.35)t \) (\( n = 32 \)); III, \( \theta = -0.164 (\pm 0.06) - 3.56 (\pm 0.38)t \) (\( n = 32 \)); IV, \( \theta = -1.47 (\pm 0.13) + 2.70 (\pm 0.39)t \) (\( n = 30 \)).

Bends travelling along broken flagella 'open' as they approach the distal end, in contrast to bends on unbroken flagella, in which the radius does not increase appre-

Fig. 8. Angles between base and distal end of broken flagella, normalized to maximum angle in respective directions for each flagellum. Symbols same as in Fig. 2.
ciably as they travel off the tip, as reported by Brokaw (1965). The maximum angle attained by a bend increases with the length of a fragment, which must be about 20 to 30 \( \mu \text{m} \) long for bends to attain their normal angle (Gibbons, 1974). However, fragments that were at least 10–15 \( \mu \text{m} \) long usually sustained the development of a bend long enough for the following bend to begin to form at the base, so that the angle subtended by the developing bend could be plotted as a function of the angle subtended by the newly forming basal bend. Results for 35 live broken spermatozoa are shown in Fig. 3. The regression line is: 

\[
y = 1.74 \pm 0.07 + 0.79 \pm 0.16 \times (n = 38; r = 0.54).
\]

The data for tritonated broken spermatozoa (not shown) yield the regression line: 

\[
y = 1.56 \pm 0.14 + 0.76 \pm 0.30 \times (n = 24; r = 0.47).
\]

These values are not significantly different from those for unbroken flagella. There appeared to be little correlation between the length of a fragment and the angle subtended by a developing bend at the time the following bend could first be seen to form.

**Bend radii on broken flagella**

A bend typically began as a sharp curve near the base, which then increased in length and radius as it developed, in a manner similar to that seen in unbroken flagella (Goldstein, 1976, 1977). The only difference noted was the opening of bends as they approached the distal end, as noted above, so that the radii of developing bends on broken flagella increased more rapidly than those on unbroken ones. On fragments 10 to 20 \( \mu \text{m} \) long, the radius of curvature of a bend was 4 to 5 \( \mu \text{m} \) when the following bend began to develop. This is about 75 \% greater than that in unbroken flagella (Goldstein, 1977). On fragments less than 5 \( \mu \text{m} \) long, a bend had often opened completely by the time the following bend began to form, so that these flagella often appeared straight at one or two points in the beat cycle, as in Figs. 5–7. This straight form occurred during those phases of the beat cycle in which the angular speeds—and hence the relative sliding speeds between the doublets (Satir, 1965)—were greatest.

**Frequency of broken flagella**

The beat frequencies of broken flagella were greater than those of unbroken controls; the increase in frequency was more pronounced in live flagella than in tritonated ones.

For reasons of accuracy and convenience, beat periods were recorded instead of frequencies. To allow the beat periods of spermatozoa from a number of samples to be combined for analysis, the periods of all spermatozoa within a sample were normalized to the mean period of the unbroken controls within that sample. For live spermatozoa, unbroken flagella had normalized periods of 1.00 \( \pm 0.14 \) (\( n = 45 \)); mean period of all live unbroken flagella = 21.4 ms), while those of broken flagella were 0.82 \( \pm 0.19 \) (\( n = 68 \)). The difference between these means is 0.18 \( \pm 0.03 \) (Lindgren, 1975). For tritonated spermatozoa, unbroken flagella had normalized periods of 1.00 \( \pm 0.08 \) (\( n = 150 \)); mean period of all tritonated unbroken flagella = 73.6 ms), while those of broken flagella = 0.89 \( \pm 0.10 \) (\( n = 161 \)). The difference between these means is 0.11 \( \pm 0.03 \). Live broken flagella thus exhibited beat periods 18 \% shorter
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than those of unbroken controls, while tritonated broken ones exhibited beat periods 11% shorter than those of unbroken controls. Using the inverses of these values as mean frequencies, the live broken spermatozoa exhibited frequencies 22% greater than those of unbroken controls, while tritonated broken spermatozoa exhibited frequencies 12% greater than those of unbroken controls.

DISCUSSION

Short basal fragments of both live and tritonated sea urchin sperm flagella beat in a manner quite similar to that of the basal region of unbroken flagella, as judged by plots of angle versus time; sliding velocities of doublets during different phases of the beat cycle; and growth of the radii and angles of developing bends. This similarity indicates that the control of the initiation and development of new bends at the base is localized to this region, and that it is relatively insensitive to the presence of the rest of the flagellum. This finding is in agreement with the observation of motility in the basal region of sea urchin sperm flagella following laser microbeam irradiation (Goldstein, 1969), and with the observation that basal bends can develop in sperm flagella under conditions in which there is little or no associated sliding of doublets distal to them (Goldstein, 1976, 1979b). It is also in agreement with the observations that basal fragments of sea urchin spermatozoa exhibit calcium-sensitive asymmetry (Brokaw & Goldstein, 1979) and quiescence (Gibbons, 1980; Gibbons & Gibbons, 1980) similar to those seen in unbroken spermatozoa. Fragments of echinoderm sperm flagella that do not contain the base do not beat (Brokaw & Benedict, 1968; Goldstein, 1969), although isolated distal fragments of some other flagella are capable of beating (Terni, 1933; Holwill & McGregor, 1974; Goldstein et al. 1970) and distal regions of unbroken sea urchin spermatozoa supplied locally with ATP can produce bends or beat (Brokaw & Gibbons, 1973; Shingyoji, Murakami & Takahashi, 1977). It may be that echinoderm sperm flagella require a region of high shear resistance at the base to transform the microtubular sliding into propagated bends.

Both live and tritonated fragments beat with higher frequencies than those of unbroken controls. A similar increase has been reported for live spermatozoa of the tunicate, Ciona (Brokaw, 1966b), and for tritonated spermatozoa of the sea urchin, Tripneustes gratilla (Gibbons, 1974). The increase in beat frequencies of tritonated flagella suggests a sensitivity of frequency to external viscous loading, which should decrease appreciably upon breakage. Brokaw (1975) found that unbroken tritonated sea urchin sperm flagella exhibit a decrease in frequency with increasing viscosity, with frequency $\propto$ (viscosity)$^{-0.18}$ in 0-2 mM-ATP. The increase of 12% observed in the beat frequencies of broken tritonated flagella could be accounted for by a decrease in viscous loading of about 50% under these conditions. The development of bends in these tritonated flagella involves little associated distal microtubular sliding before breakage (Goldstein, 1976), so that a decrease in internal shear resistance resulting from breakage is probably not an important factor. The increase of frequency in live spermatozoa was appreciably larger than in tritonated ones; this may be partly the result of a higher intracellular concentration of ATP in the broken
ones: fragments consume less ATP per beat than unbroken flagella (Brokaw & Benedict, 1968; Brokaw & Simonick, 1977), and might therefore have a higher ATP concentration (Brokaw, 1966b), and beat frequency is approximately proportional to the concentration of ATP (Gibbons & Gibbons, 1972). On the other hand, Brokaw (personal communication) has found that the difference in beat frequencies of broken and unbroken flagella diminishes at low ATP concentrations, at which the viscous forces are reduced. Live flagella beat at higher frequencies than reactivated ones in the present study, so that the greater increase in beat frequencies seen in the live flagella may have been due at least in part to the larger viscous forces acting on them. The latter explanation is also suggested by the finding of Gibbons (1974) that re-activated spermatozoa of the sea urchin, *Tripneustes gratilla*, beating at a high frequency (28 Hz) exhibited an increase in beat frequency of about 18% when broken to lengths of 8 to 10 μm—which is similar to the results on live spermatozoa in the present study.

The distal ends of broken flagella and points near the base of unbroken ones exhibited asymmetric beating, both in the peak angles and in the maximum speeds of bending. Generally $\theta_{\text{max}}^{p}$ appeared to be in the direction of the principal bend, and may provide a useful marker in cases where the principal and reverse bends cannot be otherwise distinguished. Similarly, the larger angular speed appeared to occur in going from $\theta_{\text{max}}^{p}$ to $\theta_{\text{max}}^{r}$ in both broken and unbroken flagella, strengthening the suggestion that the $\theta_{\text{max}}^{p}$ and $\theta_{\text{max}}^{r}$ indicate the directions of the principal and reverse bends, respectively, before breakage. The asymmetry of bend angle near the base of tritonated flagella, in which the principal and reverse bends can develop to equal maximum angles (Goldstein, 1976), appeared to be associated with larger radii of curvature in developing reverse bends of unbroken flagella.

Phase I of Figs. 2 and 8 corresponds to the formation of a principal bend, and phase II corresponds to the start of propagation of that bend toward the tip; phase III corresponds to the formation of a reverse bend, and phase IV corresponds to the start of propagation of that bend toward the tip. The greater speed of angular change—and of sliding between neighbouring doublets—seen in phases II and III therefore occurs during the start of propagation of a principal bend toward the tip and the formation of a reverse bend. If the undirectional sliding seen by Sale & Satir (1977) in *Tetrahymena* cilia also occurs in sea urchin sperm flagella, then phases I and IV represent sliding produced by the doublets on one side of the axoneme and phases II and III represent sliding produced on the other side. There thus appears to be a difference in the maximum shear speeds developed by the doublets on the 2 sides of the axoneme during the beat cycle. The values shown in Figs. 2 and 8 have been normalized to the peak angles in the respective directions of movement. Since $\theta_{\text{max}}^{p}$ is greater than $\theta_{\text{max}}^{r}$, this implies that the angular speeds during phases I and II were greater than those during phases IV and III, respectively; that is, the angular speed appeared to change as a flagellum passed through the points in the cycle at which it subtended an angle of zero with respect to the bases.

The fact that plots of bend angles *versus* time were often triangular waves suggests the characterization of bend formation at the flagellar base as a 2-state system in
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which the direction of sliding of the doublets reverses when a critical value occurs; the relevant factor might be bend angle, curvature or relative displacement of the doublets (Brokaw, 1980a). The maintenance of constant speed until the peak angles are reached suggests that elastic resistance to bending caused by microtubular stiffness does not limit the speed of sliding of the doublets, since this resistance should increase gradually. This complements the finding of Gibbons & Gibbons (1973) that partial removal of the dynein arms does not significantly alter the flagellar waveform, suggesting that maximum curvature is not determined by a balance between active shear force and this elastic resistance to bending. Partial digestion of axonemes with elastin, however, which probably acts preferentially on the nexin links, causes an increase in bend angle and a decrease in frequency, with the sliding speeds remaining approximately constant (Brokaw, 1980b); this finding suggests that maximum curvature - but not sliding rate - is affected by the nexin links. It may be that the elasticity of the nexin links is quite non-linear, and that they offer little resistance until stretched to a critical length (Hines & Blum, 1978). The apparent insensitivity of flagellar bends to extrinsically imposed sliding of the doublets (Goldstein, 1977), however, suggests that bend parameters are not strongly affected by instantaneous displacements of the microtubules.

The detailed features of the patterns of beating reported here should, however, be considered to be merely suggested by the present data. This is especially true for the computations presented in Figs. 2, 3 and 8, in which the data have been compiled from a number of photographs, often with only one point from a given photograph; they may therefore reflect trends among flagella in addition to patterns within individuals. These features will be studied in more detail with photographs of higher temporal resolution.

Flagella less than about 5 μm long could beat with relatively simple waveforms, in which no more than one bend was present at any time, so that they flipped back and forth and appeared to be straight during part of the cycle. A simple curvature-dependent model, in which shear force is proportional to curvature (Brokaw, 1971), should slow down and stop as the flagellum straightens, rather than continuing with high angular speeds as the flagella did in the present study. These data, then, do not support that model. Similarly, basal bends do not appear to be well described by the model of Lubliner & Blum (1971). This model, which is based on the curvature-activation model proposed by Brokaw (1966a) and describes fully formed bends, characterizes a flagellar bend as one in which a constant radius is actively produced and maintained for a prescribed time when a critical level of passive bending is attained. In some photographs of very short fragments, little curvature is seen beyond about 1 or 2 μm from the base. This suggests that oscillatory sliding can be sustained in the absence of bending beyond the base. The phase delay that is required for control of active shear force by curvature in order to balance the elastic resistances of a flagellum (Brokaw, 1971, 1972; Hines & Blum, 1978) may be an important factor in explaining the oscillation of short flagella.

Hiramoto & Baba (1978) have taken careful measurements of angles on sequences of ciné films of live starfish spermatozoa, at 10-μm intervals from the apparent flagellar
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base. They concluded that their data are fit well by sine-generated curves, i.e. that plots of angle versus time at any point are sine waves. However, they did not report measurements taken in the vicinity of 3 \( \mu m \) from the base. Rikmenspoel (1978) has reported measurements of curvature and displacement from the swim path on points at 10-\( \mu m \) intervals along flagella of sea urchin spermatozoa, using images from ciné films. He was able to fit these data to sine-generated curves, although the resolution of his images was less than that obtained by Hiramoto & Baba, and he did not show plots in the vicinity of 3 \( \mu m \) from the base.

The plots of angles in the study reported here exhibited variability between photographs. Some of this variability may be an artifact, due to the fact that each image in a photograph records a separate beat cycle. However, it probably reflects the variations in waveform that are commonly observed among individual flagella. Because variations do exist between individual flagella, and because bends can propagate under conditions in which sliding is clearly non-sinusoidal (e.g. Goldstein, 1979b) it would probably be premature to conclude that any particular temporal pattern of sliding reflects an essential flagellar cycle.

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