

## THE RELATIONS BETWEEN MEMBRANE POTENTIAL AND PARAMETERS OF CILIARY BEAT IN FREE-SWIMMING *PARAMECIUM CAUDATUM*

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### INTRODUCTION

It has been known for many years that electric currents flowing through a suspension of *Paramecium* modify the beating characteristics of the cilia in such a way that the organisms turn and move towards the cathode (Ludloff, 1895; Jennings, 1906). Jahn (1961) has accounted for this behaviour by supposing that current flows through the cell membrane and either enhances or reverses the normal ciliary beat, depending on the direction of the current. Naitoh & Kaneko (1972) have recently shown that the important parameter in controlling the direction of ciliary beat in models of *Paramecium* extracted with Triton X-100 is the internal calcium ion concentration, and Eckert (1972) has proposed a unifying theory of bioelectric control of ciliary activity in which the internal calcium concentration is governed by the cell-membrane potential. The response of *Paramecium* to electric fields can then be understood in terms of a variation in membrane potential causing local changes in the direction and frequency of ciliary beat.

This paper describes experiments on *Paramecium caudatum* in which the normal movement is perturbed by external electric fields. The underlying changes in the parameters of ciliary beat are then deduced and interpreted in terms of changes in membrane potential. This method obviates the need for micro-electrodes which would otherwise be necessary to perturb the membrane potential, and the results furnish a useful check on the reliability of the usual micro-electrode studies.

### APPARATUS AND METHOD

Specimens of *Paramecium caudatum*, reared in hay infusion, were washed in distilled water containing 1 mM  $\text{CaCl}_2$  and 4 mM KCl/l. Most of the observations were made in this medium. Organisms moving in a shallow glass dish were photographed from above with a Vinten Mk. 3 scientific cine camera coupled to a low-power Zeiss microscope. Horizontal illumination was provided by a projector lamp and condenser lens. Electric fields were applied between two long parallel stainless-steel electrodes placed a distance 40 mm apart in the dish. Organisms were kept away from the electrodes by filter paper barriers 10 mm away from each electrode.

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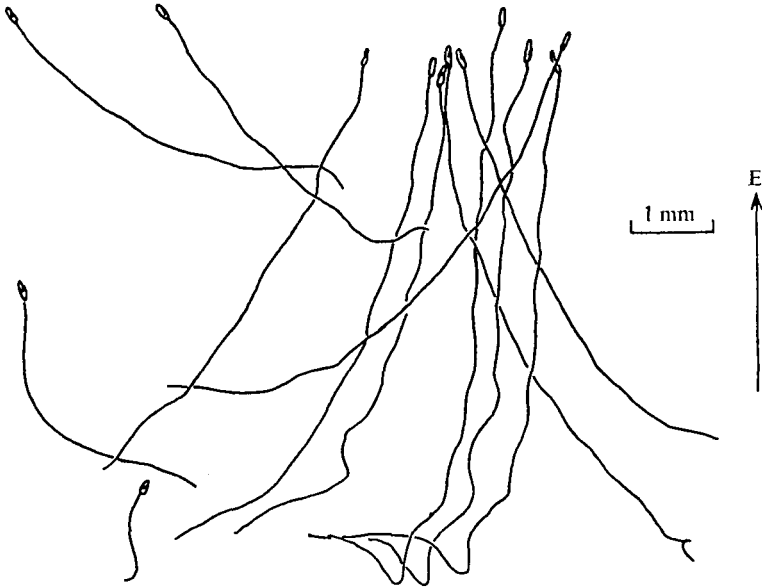


Fig. 1. *Paramecium* tracks recorded by cine photography in a field of  $100 \text{ V m}^{-1}$ . The curvatures of the tracks towards the cathode are consistent with the equation  $(d\theta/dt) = -\beta \sin \theta$  where  $\theta$  is the angle between the long axis of the organism and the electric field. Thus  $\beta$  is the maximum rate of turning which is obtained when  $\theta = 90^\circ$ . Values of  $\beta$  in this recording lie in the range  $0.2\text{--}0.6 \text{ rad s}^{-1}$ .

Field-tracing experiments showed that these barriers produced a less than 5% deviation from a uniform field over the central region of the dish.

Swimming velocity ( $u$ ), axial spin ( $W$ ) and orientation rate ( $\beta$ ) were inferred from the cine record. Tracks lying in the plane of the dish were selected to eliminate geometrical errors. The curvature of the trajectories could be measured directly in electric fields above  $100 \text{ V m}^{-1}$  (Fig. 1). At lower field strengths track curvatures were too small to be measured in this way, and instead the 'pile up' distribution adjacent to the cathodal barrier was measured from the film. Under these conditions the number density of organisms falls exponentially with increasing distance from the barrier, and if the scale length of the distribution is  $\delta$ , the mean orientation rate is given by

$$\beta = u/(2\delta)$$

(Roberts, 1970*a*). The parameters  $u$ ,  $W$  and  $\beta$  were measured for electric fields in the range  $0\text{--}200 \text{ V m}^{-1}$ .

## RESULTS

### (i) *Variation in swimming velocity with electric field*

When a field is applied there is an immediate increase in swimming velocity, the degree of the increase depending on the field strength. Fig. 2 shows the swimming velocity 10 s after applying the field. Above about  $37 \text{ V m}^{-1}$  the organisms move in straight lines towards the cathode, and begin to exhibit their characteristic anterior swinging motion above about  $70 \text{ V m}^{-1}$ . The velocity starts to fall off above  $100 \text{ V m}^{-1}$ , and this peaking appears to coincide with the onset of large-amplitude swinging.

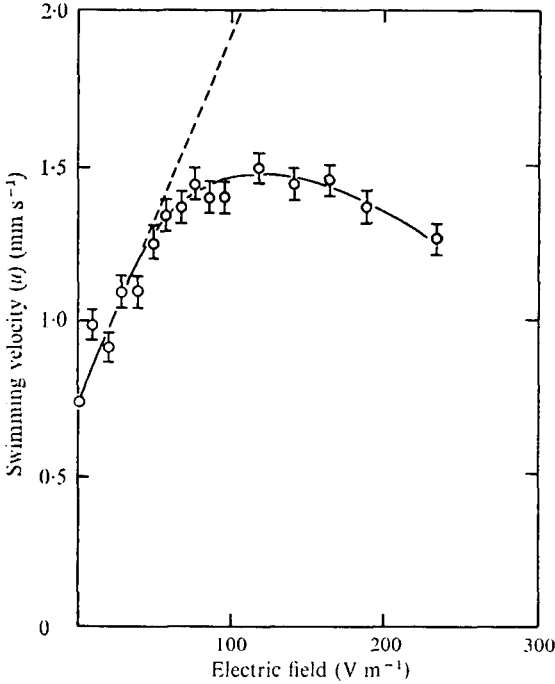


Fig. 2. The average swimming velocity in a suspension of *P. caudatum* as a function of applied electric field strength. Error bars indicate the standard error in the mean. Temperature 25 °C.

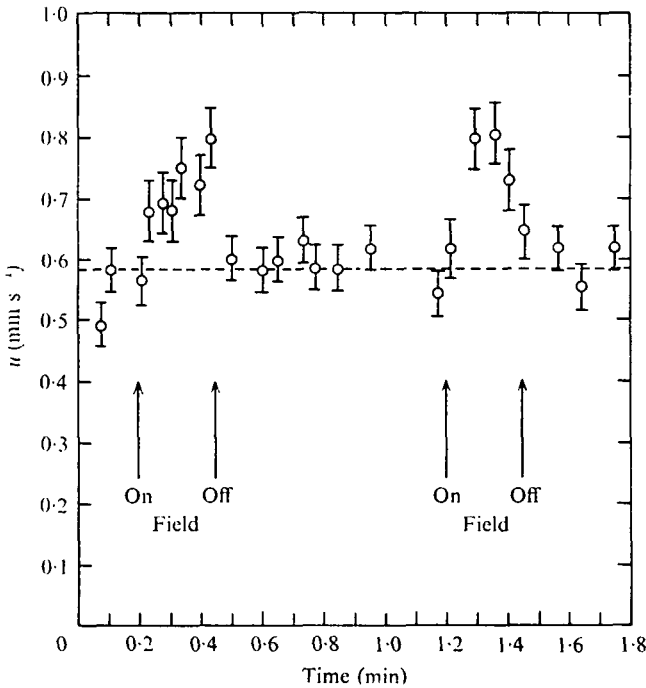


Fig. 3. Average swimming velocity as a function of time when pulses of electric field are applied ( $E_0 = 50 \text{ V m}^{-1}$ ; 25 °C). Accommodation to the field can be seen during the second application of the field. Electrodes were kept on open circuit in the absence of electric field to prevent backward current flow caused by ionic concentration gradients.

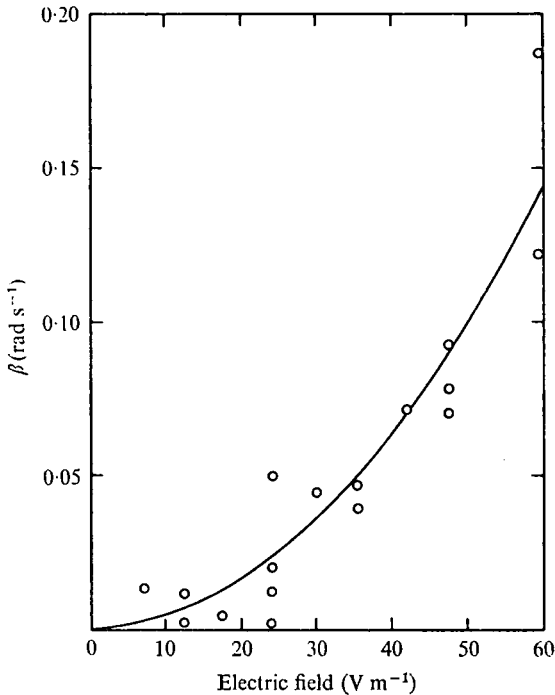


Fig. 4. The maximum orientation rate ( $\beta$ ) as a function of electric field strength. Temperature 25 °C.

Fig. 3 shows the swimming velocity as a function of time for  $E_0 = 50 \text{ V m}^{-1}$ . During the second pulse the swimming velocity is returning to its pre-field value, even in the presence of the field. Accommodation to the field takes longer, the stronger the field, but for all field strengths appears to be complete within 2 min.

(ii) *The rate of orientation in the electric field*

Fig. 4 shows the orientation rate  $\beta$  as a function of field strength for equilibrated specimens. Within the accuracy of the experiments all the points lie on the solid line indicated; no significant differences were noted as the concentrations of potassium and calcium ions were varied separately over a range limited by half and twice the standard concentrations. No evidence of accommodation of  $\beta$  was observed over periods of up to 15 min in field strengths below about  $100 \text{ V m}^{-1}$ .

ANALYSIS OF RESULTS

The forward swimming velocity  $u$  of a ciliate may be expected to be proportional to the force produced by each individual cilium. This is in turn related to the average frequency ( $\bar{\nu}$ ), the angular sweep ( $A$ ) and the angle ( $\Phi$ ) that the power stroke makes with the longitudinal axis of the organism by the equation

$$u = (\text{constant}) \times \bar{\nu} A \cos \Phi, \quad (1)$$

where the constant depends on the kinetics of the ciliary beat, the distribution of cilia, the geometry of the organism and the viscosity of the surrounding medium.

Kinosita, Dryl & Naitoh (1964) have shown that the swimming velocity in *P. caudatum* is approximately proportional to frequency in media containing adequate concentrations of calcium ions. The following analysis assumes the basic validity of equation 1.

(i) *The increase of swimming velocity in weak electric fields*

The marked increase in swimming velocity with  $E_0$  can only be interpreted in terms of equation 1 as an increase in frequency.  $\Phi$  is typically  $10\text{--}15^\circ$  in normal locomotion (Kinosita, 1954; Machemer, 1972) so that  $\cos \Phi$  cannot increase by more than 3%. Studies of beating cilia show that their amplitude is generally close to the geometrically permitted maximum (Sleigh, 1968). Thus, for example, if  $E_0 = 50 \text{ V m}^{-1}$  the velocity increases by 72% (Fig. 2), and equation 1 implies that the average frequency has also increased by this amount.

The change in membrane potential over the organism can readily be calculated (Appendix A). For an average *Paramecium* moving towards the cathode in a field of  $50 \text{ V m}^{-1}$  the maximum depolarization (at the cathodal end) is  $\sim 6 \text{ mV}$  and the maximum hyperpolarization (at the anodal end) is also  $\sim 6 \text{ mV}$ ; the membrane potential varies linearly along the length of the organism. If the frequency depends uniquely on the membrane potential then the frequency will be unchanged at the centre of the organism when the field is applied, and will exhibit maximal changes at cathodal and anodal extremities. The very fact that metachrony exists in ciliary arrays implies that the frequency is influenced by neighbouring cilia; this and the smooth co-ordinated motion at low field strengths suggests that in an electric field all the cilia beat at virtually the same frequency, which is itself a function of the perturbing field. If either depolarizing or hyperpolarizing perturbations of the membrane caused a decrease in frequency then to a first approximation no mechanism would exist for increasing swimming velocity, since the mean frequency would be unchanged. The present observations are therefore consistent with only one hypothesis, namely, that depolarizations and hyperpolarizations both produce increases in frequency. The magnitude of the increase in previously unexposed organisms is 10 s after application of the field is  $(23 \pm 3)\% \text{ mV}^{-1}$  (Fig. 2), although the magnitude of the increase is highly dependent upon the previous history of the organism (Fig. 3).

The changes in swimming velocity with higher field strengths are considered after the next section.

(ii) *Cathodal orientation in electric fields*

The most striking conclusion from Fig. 4 is that the orientation rate  $\beta$  is not linear in  $E_0$ . A semi-logarithmic plot of the data shows that the best fit is obtained to an  $E_0^2$  relationship of the form

$$\beta E_0^{-2} = (4 \pm 1) \cdot 10^{-5} \text{ rad s}^{-1} \text{ V}^{-2} \text{ m}^2.$$

In terms of equation 1 and the previous discussion it is clear that changes in frequency cannot account for the orientation observed in electric fields. If hyperpolarizations and depolarizations produce exactly the same increase in frequency then no mechanism for turning exists. Alignment towards the cathode could be obtained if depolarizations were less effective than hyperpolarizations in increasing the frequency, but there is no evidence to support this contention; furthermore, it is easy to show

that it would lead to  $\beta \propto E_0$  (Roberts, 1970*b*). A frequency-change hypothesis for orientation also makes the observed axial spin difficult to explain.

The only conclusion that can reasonably be drawn is that changes in  $\Phi$ , rather than in  $\bar{v}$ , are responsible for orientation. It is assumed here that  $\Phi$  is related to membrane perturbation  $\Delta V_m$  by a Taylor expansion of the form

$$\left. \begin{aligned} \Phi &= \Phi_0 + \gamma_1(\Delta V_m) + \gamma_2(\Delta V_m)^2 + \dots \text{ for a depolarization} \\ \text{and } \Phi &= \Phi_0 \qquad \qquad \qquad \qquad \qquad \qquad \text{for a hyperpolarization} \end{aligned} \right\} \quad (2)$$

As a first approximation  $\Phi$  is linear in  $\Delta V_m$  ( $\gamma_j = 0$  for  $j \geq 2$ ). The orientation rate  $\beta$  is calculated on the basis of a simple model in Appendix B, and it is noteworthy that the orientation does indeed depend upon the square of the field strength, as is observed. The value of  $\gamma_1$  required to fit the results of Fig. 4 is  $(160 \pm 20)$  rad  $V^{-1}$  or  $(9 \pm 1)$  degree  $mV^{-1}$ . This is an average figure in that during normal locomotion the organism spins about its long axis with a typical frequency of  $0.5-1.0$  Hz, thus subjecting each portion of the membrane to an alternating field to which it cannot accommodate. By extrapolation the depolarization required to produce full reversal ( $\Phi = 180^\circ$ ) is 20 mV, which is in fact some 2-5 mV less than that required for complete depolarization. Kinosita (1954) has found a good correlation using micro-electrodes between direction of beat and spontaneous membrane potential changes in *Opalina*, obtaining rates of change for different organisms in the range 4.5-10 degree  $mV^{-1}$ .

The present results therefore suggest that the angle of ciliary beating is strongly dependent on depolarizing deviations of the membrane potential from its resting value, that the relationship is probably quasi-linear, and that hyperpolarizations cause little or no change in the direction of beat. Micro-electrode studies (Kinosita, 1954) indicate that when the ionic constitution of the outside medium is changed both  $\Phi$  and  $V_m$  change simultaneously; whilst  $V_m$  reaches a new equilibrium level,  $\Phi$  soon returns to its original value. Both types of experiment therefore suggest that the angle of beat depends upon the perturbation in membrane potential rather than upon its absolute value.

### (iii) *The decrease in swimming velocity in strong electric fields*

If the above picture is correct some further consequences follow. As the field strength is increased the cilia on the anterior half of the organism will turn progressively backwards, and the swimming velocity will decrease accordingly. The expected decreases have been calculated for an organism spinning uniformly about its longitudinal axis (Appendix B) and are shown in Table 1. At low field strengths the swimming velocity increases with increasing field strength because the frequency increases. Assuming that the swimming velocity increases at the same rate at higher field strengths (the dotted line in Fig. 2) the percentage reductions in actual swimming speed can be calculated, and are shown in Table 1. The general agreement between the measured and predicted values suggests that changes in angle of beat can account for the variations in swimming velocity in electric fields.

Table 1. The predicted decrease in swimming velocity due to changes in the direction of ciliary beat (equation (B 2) with  $\Phi_0 = 10^\circ$ ) and the actual decreases (compared to the dotted line in Fig. 2) as a function of field strength

Electric field strength (V m <sup>-1</sup> )	Predicted reduction (%)	Observed reduction (%)
50	10	2 ± 1
75	19	11 ± 2
100	28	22 ± 2
150	47	40 ± 3
200	60	53 ± 4

(iv) *Axial spinning*

The theoretical model predicts the rate at which axial spinning should occur (Appendix B). If  $\Phi_0 \sim 10\text{--}15^\circ$  the predicted rate of spin is about 0.5–0.75 Hz, which is what is in fact observed. This clearly confirms the idea that the spiralling of *Paramecium* is due to transverse components of ciliary thrust (Machemer, 1972) and not to any asymmetry in body geometry.

As the electric field is applied, the rate of spinning should increase to a maximum of about 1.25 Hz at 150 V m<sup>-1</sup>, and decrease at higher field strengths. In real organisms, however, uniform spinning about one axis does not occur at fields above about 70 V m<sup>-1</sup>; instead, the anterior end traces out a cone, and the organism spirals forward in such a way that the same parts of the membrane tend to be on the outside of the spiral. This could be due to variations in electrical sensitivity along the surface of the organism, to asymmetries produced by the presence of the oral groove, or to a combination of both. The present experiment cannot distinguish between the two possibilities, however.

The gyration in the electric field can explain Dryl's (1963) observation that organisms near a boundary exhibit oblique orientation to the field direction in fields above 70 V m<sup>-1</sup>; the boundary prevents full gyration from occurring, and the organism moves along the boundary at an angle determined by the asymmetry of the ciliary forces.

(v) *Internal calcium levels*

The present results can be correlated with the observations of Naitoh & Kaneko (1972) on the changes in swimming velocity with internal calcium concentration. The angle of beat ( $\Phi$ ) changes almost linearly from zero to 90° (this follows from equation 1) as the internal calcium concentration is increased logarithmically from 0.1 to 1.0  $\mu\text{M l}^{-1}$ . The average rotation is thus 90° per calcium decade. Since the present results show that this rotation is also produced by a depolarization of 10 mV, the internal calcium ion concentration must vary with membrane depolarization at the rate of approximately one decade/10 mV. Thus the increase in calcium ion concentration at the ciliary apparatus is about 25% for a depolarization of 1 mV. The two principal problems now are to elucidate the mechanism by which the membrane potential governs the internal calcium concentration, and to determine how this governs the direction of ciliary beat.

## SUMMARY

1. A method of analysing the parameters of ciliary beat as a function of membrane potential in free-swimming organisms is presented. The method obviates artefacts which may be produced on impaling small organisms with micro-electrodes.

2. Changes in the membrane potential of *Paramecium caudatum* produce two effects: an increase in frequency of beat of up to  $(23 \pm 3) \% \text{ mV}^{-1}$  at  $25^\circ \text{C}$  for both depolarizations and hyperpolarizations which falls to zero within a few minutes, and a change in the direction of ciliary beat of  $(9 \pm 1)$  degree  $\text{mV}^{-1}$  for depolarizations only, which in a spiralling organism do not accommodate to the field.

3. The orientation of *P. caudatum* towards the cathode in an electric field is due principally to changes in the angle of ciliary beat on the cathodal side of the organism; changes in frequency seem to be relatively unimportant.

4. Axial spinning during normal locomotion in *P. caudatum* is satisfactorily accounted for by transverse components of ciliary thrust.

5. The oblique orientation of *P. caudatum* near boundaries is caused by an asymmetry (geometrical or electrical or both) over the surface of the organism.

6. Comparison with observations on extracted organisms indicates that a change in the direction of beat of  $9^\circ$  is associated with an increase in calcium concentration at the ciliary apparatus of about 25 %.

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APPENDIX A

*The modification of membrane potential by an external electric field*

Consider a spherical cell of radius  $a$  and resistivity  $\rho_1$ , bounded by a membrane of resistivity  $\rho_2$  and thickness  $\delta$ , immersed in a medium of resistivity  $\rho_3$ . When an electric field  $E_0$  is established in the medium the change in membrane potential,  $\Delta V_m$ , is found (solving Laplace's equation) to be

$$\Delta V_m = \frac{9\alpha\delta E_0 \cos \theta}{(2+\alpha)(2+\beta)+2(1-3\delta/a)(1-\alpha)(1-\beta)}, \quad (\text{A } 1)$$

where  $\alpha = \rho_2/\rho_1$ ,  $\beta = \rho_3/\rho_2$ , and  $\theta$  is the angle between the field direction and the line drawn from the centre of the cell to the point in question on the surface of the cell; this approximation is valid if powers of  $\delta/a$  ( $\sim 10^{-4}$  for *P. caudatum*) higher than the first are neglected. In practice  $\alpha \sim 10^8 \gg 1$  and  $\beta \sim 10^{-6} \ll 1$  and consequently, to a very good approximation ( $\pm 0.05\%$ ) equation (A 1) becomes

$$\Delta V_m = \frac{3}{2}E_0 a \cos \theta,$$

which is just the formula for the potential distribution over an insulated sphere in a conducting medium permeated by a uniform static electric field.

If the membrane capacitance  $C_m$  is explicitly included in  $\rho_2$  then the membrane resistivity becomes complex ( $\rho_2'$ ) such that

$$\frac{1}{\rho_2'} = \frac{1}{\rho_2} + S\delta C_m, \quad (\text{A } 2)$$

where  $S$  is the complex frequency.

If the electric field is turned on at time  $t = 0$  then it follows from equations (A 1) and (A 2) that

$$\Delta V_m = \frac{3}{2}E_0 a \cos \theta \{1 - \exp[-t/(a\rho_1 C_m)]\}. \quad (\text{A } 3)$$

If typical values of  $a$  ( $50 \mu\text{m}$ )  $\rho_1$  ( $2.0 \Omega\text{m}$ ) and  $C_m$  ( $2 \times 10^{-2} \text{ F m}^{-2}$ ) are used to evaluate the time constant ( $a\rho_1 C_m$ ) in equation (A 3) a value of  $\sim 2 \mu\text{s}$  is obtained. This time constant is very much less than the intrinsic membrane time constant of 40–50 ms for *P. caudatum*. Hence the applied field can be considered to act as a form of 'voltage clamp' with a response time very much less than the characteristic membrane time constant.

A typical *P. caudatum* is a prolate spheroid with a major semi-axis of length  $110 \mu\text{m}$  and minor semi-axes of length  $30 \mu\text{m}$ . It has been shown that it will be quite adequate, in practice, to compute the potential distribution over an insulated prolate spheroid immersed in a conducting medium in the presence of a static uniform electric field. The general solution involving Lamé's equation and ellipsoidal harmonics is ponderous, but solutions for special cases can be obtained in a straightforward manner. If  $E_0$  is parallel to the major semi-axis (in the  $x$ -direction) then

$$\Delta V_m = 1.08E_0 x \quad (\text{A } 4)$$

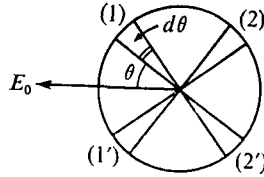


Fig. B 1.

Table 2. Summary of data used in the numerical model

$b$	diameter of model <i>Paramecium</i> ( $60 \mu\text{m}$ )
$f$	ciliary driving force per unit membrane area ( $3.1 \times 10^{-3} \text{ N m}^{-2}$ )*
$l$	length of model <i>Paramecium</i> ( $220 \mu\text{m}$ )
$R$	viscous resistance to turning about a transverse axis ( $9.1 \times 10^{-15} \text{ N m rad}^{-1} \text{ s}$ )†
$S$	viscous resistance to axial spinning ( $2.2 \times 10^{-15} \text{ N m rad}^{-1} \text{ s}$ )†
$\gamma$	first-order ciliary rotation constant (determined from the experimental results to be $(160 \pm 20)$ rad $\text{V}^{-1}$ )

\* Obtained by computing the viscous drag per unit surface area.

† Computed from the theoretical work of Jeffery (1923).

and if  $E_0$  is parallel to a minor semi-axis (in the  $y$  or  $z$  directions) then

$$\Delta V_m = 1.86 E_0 \begin{Bmatrix} y \\ z \end{Bmatrix}. \quad (\text{A } 5)$$

For arbitrary orientations it is necessary to resort to approximate solutions or tabulated values of the appropriate ellipsoidal harmonic functions.

The multiples of 1.08 and 1.86 in equations (A 4) and (A 5) are within 8% of 1.0 and 2.0, which are the appropriate values for a cylindrical body with length much greater than the diameter. This is the justification for using a cylindrical model for the electro-mechanical analysis presented in Appendix B.

## APPENDIX B

*The mechano-electric response of P. caudatum to an external electric field*

For the reason given in Appendix A a cylindrical model of *P. caudatum* is utilized here.

(i) *The rate of orientation in the electric field*

The maximum turning effect in electric fields arises when the organism is at right angles to the field direction. Cilia on the hyperpolarized (anodal) half beat as usual whilst on the depolarized (cathodal) half they beat at an angle  $\Phi$  determined by the membrane depolarization  $\Delta V_m$  (equation 2). Consider a transverse section (Fig. B 1) and the corresponding elements (1, 1') and (2, 2'). The propulsive force from (2, 2') is, for each,  $(\frac{1}{2}b)lf d\theta$  and for (1, 1') is  $(\frac{1}{2}b)lf \cos \Phi d\theta$  (symbols are defined in Table 2). The resultant torque  $dT$  due to these strips is then given by

$$dT = (\frac{1}{2}b^2)lf(1 - \cos \Phi) \cos \theta d\theta.$$

For small values of  $\Phi$  the total torque is given by

$$T = \int dT = \frac{1}{8} \gamma^2 b^4 lf E_0^2.$$

This torque is balanced by the viscous drag  $R\beta$ , where  $R$  is the viscous resistance to

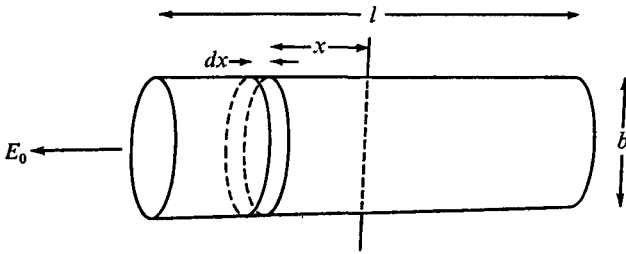


Fig. B 2.

turning per unit angular velocity about a transverse axis and  $\beta$  is the rate of turning. Thus

$$\beta = (b^4 \gamma^2 l f / (6R)) E_0^2 \tag{B 1}$$

and shows that  $\beta$  is proportional to  $E_0^2$ .

(ii) *The fall-off in swimming velocity with increasing electric field*

Consider a cylindrical organism moving towards the cathode (Fig. B 2). The propulsive force  $F_p$  from the posterior hyperpolarized half is  $(\frac{1}{2}\pi) b l f$  and the propulsive force  $dF_a$  from an anterior ring at a distance  $x$  from the centre of the organism is  $\pi b f \cos \Phi dx$  where  $\Phi = \Phi_0 + \gamma \Delta V_m$ . Assuming that  $\Delta V_m = E_0 x$  the total propulsive force  $F$  is

$$\begin{aligned} F &= F_a + F_p = \int_0^{\frac{1}{2}l} \pi b f \cos(\Phi_0 + \gamma \Delta V_m) dx + \frac{1}{2} \pi b l f \\ &= \pi b f \left[ \frac{\sin(\Phi_0 + \frac{1}{2} \gamma E_0 l) - \sin \Phi_0}{\gamma E_0} + \frac{l}{2} \right]. \end{aligned} \tag{B 2}$$

In steady motion the swimming velocity is proportional to  $F$ , and equation (B 2) gives the velocity variation with electric field.

(iii) *The rate of axial spinning for a smoothly swimming organism*

Consider a cylindrical organism swimming parallel to  $E_0$  (Fig. B 2). The ring at  $x$  will produce an axial torque given by

$$\frac{\pi b^2 f}{2} \int_0^{\frac{1}{2}l} \sin \Phi dx.$$

If  $S$  is the viscous resistance to axial rotation and  $\Phi = \Phi_0 + \gamma \Delta V_m$  the axial spinning rate due to the field is given by

$$W = \frac{\pi b^2 f l}{4S} \left[ \sin \Phi_0 + \frac{\cos \Phi_0 - \cos(\Phi_0 + \frac{1}{2} \gamma E_0 l)}{\frac{1}{2} \gamma E_0 l} \right]. \tag{B 3}$$

If  $E_0 = 0$  the organism then spins naturally about its long axis at a rate given by

$$W_0 = \frac{\pi b^2 f l}{2S} \sin \Phi_0. \tag{B 4}$$