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Control Strategies for the Polarotactic Orientation of the Microorganism *Euglena gracilis*

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A simple mathematical model for the signal received by the dichroic photoreceptor molecules in the motile alga, *Euglena gracilis*, when irradiated by polarized light, is described and used to test hypotheses for the control strategies employed by the microorganism during negative phototaxis. The model is used to analyse and explain the experimental results of Häder (1987. *Arch. Microbiol.* **147,** 179–183).

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1. Introduction

Euglena gracilis is a unicellular organism with a single long emergent flagellum located at its anterior end and, in the absence of external stimuli, the organism changes direction in an apparently random manner every 3–6 s (Kuźnicki *et al.*, 1990). *Euglena gracilis*, like many other motile microorganisms, responds to a variety of external physical and chemical stimuli to find a suitable orientation within its environment. The main responses are those to gravity and light, with cells swimming towards the light (positive phototaxis) at low fluence rates ($< 1.4\ \mathrm{W\ m^{-2}}$) and away from the light (negative phototaxis) at higher fluence rates ($> 12.65\ \mathrm{W\,m^{-2}}$), with extreme precision for fluence rates $> 126.5\ \mathrm{W\,m^{-2}}$ (Häder & Reinecke, 1991 and references cited therein).

The photoreceptor is thought to be a flavoprotein arranged in a paracrystalline array in an organelle called the paraflagellar body (PFB), a swelling at the base of the emergent flagellum (Häder & Reinecke, 1991 and references cited therein). It has been reported that the cell's orientation depends on both the light intensity and polarization of the light, with cells orienting perpendicular to the plane of polarization at low intensities and parallel at higher intensities (Häder & Reinecke, 1991), with an intermediate orientation of about 30° clockwise of the polarization plane for intermediate light intensities (Häder, 1987). It has been suggested (Häder & Reinecke, 1991) that these results could be explained by the existence of two different photoreceptor systems or that the two polarotactic reactions are caused by two different absorbing vectors within the receptor molecules (Johansson *et al.*, 1979).

In this paper, we analyse a straightforward mathematical model and propose simple control strategies to explain the directed motion with respect to the polarization of light as reported by Häder (1987) for negative phototaxis. From these experiments, the three-dimensional orientation of the absorbing vectors of the photoreceptor pigments within the PFB was calculated with respect to two axes fixed in the cell. The vector of maximal absorption of the dichroic array

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deviates 25° clockwise from the cell's long axis and, seen from above, 60° counterclockwise from the flagellar plane. We use a mathematical model to try to verify this hypothesis and propose an alternative mechanism and different dichroic orientation of the photoreceptor molecules for the cells. The control strategies are simple but they are not easily understood without the use of a mathematical model. We do not consider, however, how the cells implement a control strategy. The model we propose is an extension of the model suggested by Hill & Vincent (1993) with the addition of dichroic molecules within the photoreceptor. Häder (1993) also modelled polarotaxis in *Euglena* but there appears to be an error in the equation describing the absorption of polarized light by the dichroic molecules in the photoreceptor (Häder, 1999, pers. comm.). We only address negative phototaxis because no suitable quantitative experiments, that would allow us to determine orientation of the dichroic molecules that control positive phototaxis, have been carried out.

2. The Mathematical Model

Most swimming microorganisms rotate as they move forwards allowing their photoreceptor to scan its environment. The mathematical model simulates the periodic shading of the photoreceptor by the stigma in a typical algal cell, such as *Euglena*. The model consists of a sphere, which rotates about an axis defined by the unit vector $\hat{\mathbf{p}}$, fixed in the sphere, and a small photoreceptor positioned at its surface. The photoreceptor contains a dichroic array of molecules, with the molecules' long axis lying in the direction of the unit vector $\hat{\mathbf{d}}$. $\hat{\mathbf{n}}$ is the unit vector normal to the sphere's surface at the receptor and makes an angle θ to the cell's axis of rotation. The spherical body of the model microorganism shades the photoreceptor which can only receive light when it faces the source.

The key concepts in this model are that the photoreceptor is shaded from one side and that it rotates about the cell's swimming direction. It does not matter that the receptor lies in the surface of a spherical body. The receptor of a real cell may well be an organelle that is inside the cell and shaded by a stigma but the significance of this model is that it retains the fundamental features of the cell's light-detecting apparatus while being simple enough for the principles of the model to be easily comprehended.

To specify the orientation of $\hat{\mathbf{p}}$ and $\hat{\mathbf{n}}$ we define two sets of rectangular Cartesian axes, the laboratory frame of reference OXYZ and the cell's frame of reference Oxyz, where O is the centre of the sphere and the directions of the X, Y, Z axes are fixed relative to the laboratory (see Fig. 1). The cell's frame of reference is defined such that its rotation axis $\hat{\mathbf{p}}$ lies along Oz and makes an angle α with OZ ($0° \leqslant \alpha \leqslant 180°$). O$y$ is

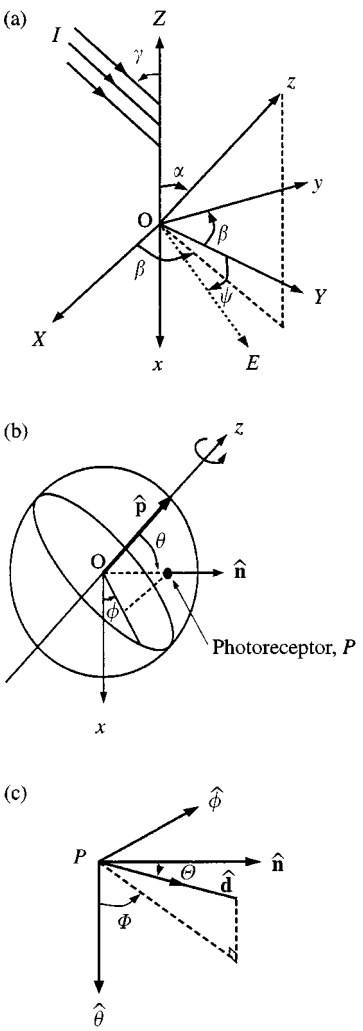

FIG. 1. The geometry used to describe the orientation of the cell and the beam of light. (a) The orientation of the OXYZ and Oxyz coordinate axes and the direction $\mathbf{I}$ of the light. (b) The position of the cell's photoreceptor with respect to the axis of rotation. (c) The angles defining the dichroic array, $\hat{\mathbf{d}}$, within the receptor where the projection of $\hat{\mathbf{d}}$ lies in the $\hat{\theta}$, $\hat{\phi}$ plane through P.

perpendicular to Oz and lies in the XY-plane and the angle between OY and Oy is β ($0^\circ \leqslant \beta \leqslant 360^\circ$). Note therefore that α, measured from OZ, and β, measured from OX, give the cell's swimming direction. Thus, relative to OXYZ, the orientation of the cell is

$$\hat{\mathbf{p}}_{lab} = \begin{pmatrix} \sin\alpha\cos\beta \\ \sin\alpha\sin\beta \\ \cos\alpha \end{pmatrix}. \tag{1}$$

For convenience, we note that the transformation or rotation matrix from OXYZ to Oxyz is

$$\mathbf{R} = \begin{pmatrix} \cos\alpha\cos\beta & \cos\alpha\sin\beta & -\sin\alpha \\ -\sin\beta & \cos\beta & 0 \\ \sin\alpha\cos\beta & \sin\alpha\sin\beta & \cos\alpha \end{pmatrix}. \tag{2}$$

The normal relative to the cell's frame of reference Oxyz is defined by the Euler angles, θ and ϕ, so that

$$\hat{\mathbf{n}}_{cell} = \begin{pmatrix} \sin\theta\cos\phi \\ \sin\theta\sin\phi \\ \cos\theta \end{pmatrix}. \tag{3}$$

The direction of a parallel beam of light which shines upon the cell is given relative to the laboratory frame OXYZ by the vector

$$\mathbf{I}_{lab} = \begin{pmatrix} -\sin\gamma \\ 0 \\ -\cos\gamma \end{pmatrix}, \quad 0^\circ \leqslant \gamma \leqslant 180^\circ. \tag{4}$$

Without loss of generality, $\mathbf{I}$ lies in the XZ-plane and γ is the angle between the light beam and the Z-axis. The equations given so far are the same as those used by Hill & Vincent (1993). We now refine the model by allowing for the effects of the polarization of the light. The beam of light is polarized and the electric field vector $\mathbf{E}$ is perpendicular to $\mathbf{I}$. Note that $\mathbf{E}$ does not lie in the XY-plane unless $\gamma = 0^\circ$ and ψ is the angle $\mathbf{E}$ makes with the Y-axis ($0^\circ \leqslant \psi \leqslant 180^\circ$), so that in the laboratory frame OXYZ

$$\mathbf{E}_{lab} = \begin{pmatrix} \sin\psi\cos\gamma \\ \cos\psi \\ -\sin\psi\sin\gamma \end{pmatrix}. \tag{5}$$

Note that if $\gamma = 0^\circ$ then

$$\mathbf{E}_{lab} = \begin{pmatrix} \sin\psi \\ \cos\psi \\ 0 \end{pmatrix}. \tag{6}$$

To define the directionality, $\hat{\mathbf{d}}$, of the dichroic molecules in the photoreceptor, we use the spherical polar angles Θ and Φ measured relative to the unit vectors $\hat{\mathbf{n}}$, $\hat{\boldsymbol{\theta}}$, $\hat{\boldsymbol{\phi}}$ at the receptor (see Fig. 1) so that

$$\hat{\mathbf{d}} = \hat{\mathbf{n}}\cos\Theta + \hat{\boldsymbol{\theta}}\cos\Phi\sin\Theta + \hat{\boldsymbol{\phi}}\sin\Phi\sin\Theta \tag{7}$$

and in the cell's reference frame, $Oxyz$,

$$\hat{\mathbf{d}}_{cell} = \begin{pmatrix} \cos\Theta\sin\theta\cos\phi + \cos\Phi\sin\Theta\cos\theta\cos\phi - \sin\Phi\sin\Theta\sin\phi \\ \cos\Theta\sin\theta\cos\phi + \cos\Phi\sin\Theta\cos\theta\sin\phi + \sin\Phi\sin\Theta\sin\phi \\ \cos\Theta\cos\theta - \cos\Phi\sin\Theta\sin\theta \end{pmatrix}. \tag{8}$$

Now the cell can only perceive a signal when the photoreceptor is pointing towards the light. The intensity of the light reaching the photoreceptor is proportional to the cosine of the angle between the light vector, $\mathbf{I}$, and the receptor, $\hat{\mathbf{n}}$. Some of this light may be absorbed by the dichroic array. The absorption is proportional to the cosine squared of the angle between the electric field vector, $\mathbf{E}$, and the direction of the dichroic molecules' long axis, $\hat{\mathbf{d}}$ (Bennett, 1995; Hecht

& Zajac, 1974). Thus the signal, S, received by the cell is given by

$$S = \max\{0, (-\mathbf{I}\cdot\hat{\mathbf{n}})(\hat{\mathbf{d}}\cdot\mathbf{E})^2\}. \quad (9)$$

(The minus sign in the expression $-\mathbf{I}\cdot\hat{\mathbf{n}}$ occurs because $\mathbf{I}$ and $\hat{\mathbf{n}}$ are in opposite directions when light falls upon the face of the receptor.)

To calculate $\mathbf{I}\cdot\hat{\mathbf{n}}$ and $\hat{\mathbf{d}}\cdot\mathbf{E}$, all the vectors must be written down relative to the same reference frame, so we convert $\mathbf{I}$ and $\mathbf{E}$ to the cell's frame, using the rotation matrix, as follows:

$$\mathbf{I}_{cell} = \mathbf{R}\cdot\mathbf{I}_{lab} = \begin{pmatrix} \sin\alpha\cos\gamma - \cos\alpha\cos\beta\sin\gamma \\ \sin\beta\sin\gamma \\ -\sin\alpha\cos\beta\sin\gamma - \cos\alpha\cos\gamma \end{pmatrix} \quad (10)$$

and

$$\mathbf{E}_{cell} = \mathbf{R}\cdot\mathbf{E}_{lab} = \begin{pmatrix} \cos\alpha\cos\beta\sin\psi\cos\gamma + \cos\alpha\sin\beta\cos\psi + \sin\alpha\sin\psi\sin\gamma \\ -\sin\beta\sin\psi\cos\gamma + \cos\beta\cos\psi \\ \sin\alpha\cos\beta\sin\psi\cos\gamma + \sin\alpha\sin\beta\cos\psi - \cos\alpha\sin\psi\sin\gamma \end{pmatrix}. \quad (11)$$

There is evidence that *E. gracilis* swims in such a way that its photoreceptor is effectively at an angle slightly greater than 90° to its axis of rotation (Jennings, 1906; Colombetti & Marangoni, 1991), so for the purposes of this model θ is set equal to 100°.

3. Häder's (1987) Experiments

The model described in the previous section is now used to test possible hypotheses for the orientation mechanism employed by *E. gracilis*. In 1987, Häder studied the swimming directions of *E. gracilis* in thin horizontal and vertical cuvettes, irradiated by polarized light from above or from the side. From these experiments, he suggested values for the dichroic orientation of the photoreceptor molecules. Three experiments using polarized light were carried out and the following results were found:

1. When a population of cells in a thin, flat, horizontal cuvette—which allows only horizontal movements—is irradiated from above with polarized light, the cells preferred to move in two opposite directions, as shown in Fig. 4 of Häder (1987). The figure shows the distribution of directions to be bimodal and quite broad. The mean direction appears to lie between 20° and 60° clockwise of the **E**-vector as seen from above, and is reported to be close to 30°. However, neither a Rayleigh test nor any other statistical analysis was carried out.

2. In a narrow, flat, vertical cuvette with polarized light shining from the side onto the face of the cuvette, the cells swam upwards with a high degree of orientation at almost all polarization angles, with a reported Rayleigh statistic $\bar{r} = 0.73$. However, when the plane of polarization was turned by about 25° clockwise to the vertical, the degree of orientation decreased drastically ($\bar{r} = 0.29$), and the organisms swam predominantly clockwise to the vertical at a mean angle, which we estimate from Fig. 6 of Häder (1987) to be 45°.

3. In a narrow, flat, vertical cuvette irradiated from above with polarized light, the plane of polarization was rotated around the vertical axis. At most polarization angles with respect to the cuvette, the organisms moved downwards guided by negative phototaxis caused by the strong actinic light. However, at angles between about 20° and 55°, the mean swimming direction was upwards although the distributions are again very broad. The greatest degree of upwards orientation ($\bar{r} \approx 0.28$) was found when the plane of polarization was offset by about 30° from the plane of the cuvette. In a wider cuvette—where the orientation is not constrained—the cells swam downwards, away from the light, at all polarization angles.

From these experiments and based on the hypothesis that cells change their orientation when they detect a sharp peak in light intensity, he concluded that the electric dipole transition moments can be defined with respect to two axes in the cell. In experiment 3, he suggested that the cells are mechanically prevented from turning downwards when the flagellar axis is perpendicular to the cuvette axis, and that, if during negative phototaxis the cells try to minimize the fluence rate perceived by the photoreceptor, the attempted flagellar reorientation occurs during maximal absorption. Thus, the absorption transition moments are 60° counterclockwise from the flagellar plane. Following the same line of reasoning for experiment 2, he concluded that the absorption transition moments are 25° clockwise from the cells' long axis. Häder also suggested that, since the cells had been reported to be swimming perpendicular to the polarization plane at light intensities that induce positive phototaxis (Creutz & Diehn, 1976) whereas in experiment 1 they orient 30° clockwise of the polarization plane, the two responses are either mediated by two different sets of photoreceptor pigments or by different molecular transition moments of the same molecules. There is further evidence of different responses to the plane of polarization depending on light intensity given by Häder & Reinecke (1991).

4. Results

Using the model, we firstly consider Häder's suggestion that the cells reorient when they receive a peak in the signal as they rotate, so that they choose an orientation for which the signal is constant as the cell rotates. Häder does not include the effects of shading in his conclusions, while shading of the photoreceptor by the stigma and cell body is included in our model. His explanation does not work when shading is incorporated into the model. This is illustrated in Fig. 2, where the **E**-vector of 30° clockwise from the swimming direction as in experiment 1 and the angles used are those suggested by Häder. The signal received by the cell is clearly not flat and it would attempt to turn away from this orientation. Furthermore, we examined the orientation of the dichroic array by considering 30° increments over the full range of each of the angles Θ and Φ and showed that no other angles are consistent with the experimental results.

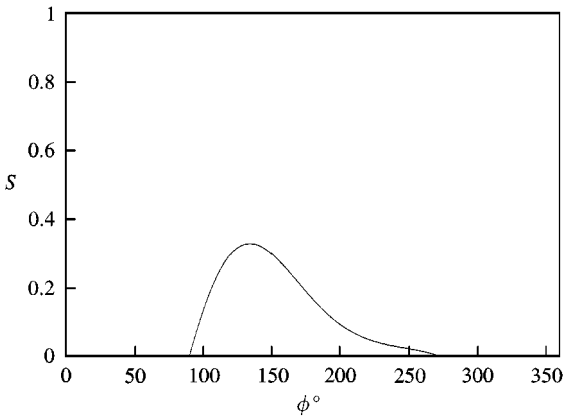

FIG. 2. The signal, S, received by a cell as it rotates in a thin flat horizontal cuvette, as in experiment 1, if $\Theta = 60°$ and $\Phi = 155°$. The cells are swimming at 30° clockwise to the **E**-vector.

Secondly, we consider the hypothesis proposed by Hill & Vincent (1993), that the cells orient with respect to the total integrated signal received per revolution. In their model, the cells orient to minimize the integrated signal that they receive at a light intensity that induces positive phototaxis. At the intensity we are considering in this paper, the cells are negatively phototactic, and so we propose that the cells orient so as to maximize the total *integrated* signal, S^*, received per revolution, and we search for pairs of angles (Θ, Φ) that are consistent with Häder's (1987) experiments. The complete range of possible angles for the dichroic orientation of the photoreceptor molecules, in 30° increments, was analysed to determine the angles best fitting the experimental results. Only two pairs, (Θ, Φ), of angles are compatible with the experimental results; because of the symmetry these two pairs of angles are diagonally opposite to each other, one pair corresponding to $\hat{\mathbf{d}}$ going into the cell and the other to $\hat{\mathbf{d}}$ pointing out of the cell. Without loss of generality, we choose the angles $\Theta = 120°$, $\Phi = 50°$ with $\hat{\mathbf{d}}$ directed into the cell and demonstrate below that this hypothesis is sufficient to explain the results of Häder's (1987) experiments. For each experiment, we define the laboratory axes so that the light enters along the Z-axis and so $\gamma = 0°$.

In experiment 1, the cuvette is horizontal and irradiated from above (see Fig. 3) so that $\alpha = 90°$.

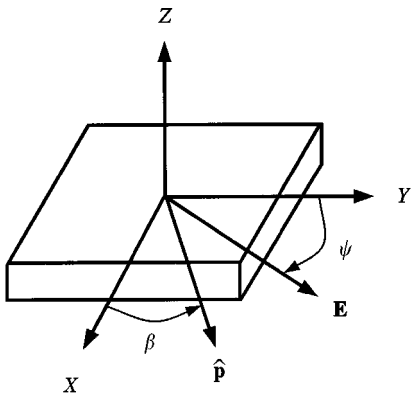

FIG. 3. The laboratory axes for experiment 1.

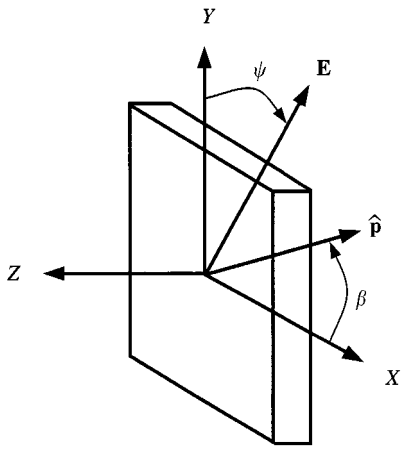

FIG. 5. The laboratory axes for experiment 2.

Note that β is measured anticlockwise from the X-axis, and ψ is measured clockwise from the Y-axis. Without loss of generality, we choose the **E**-vector to lie along the Y-axis so that $\psi = 0^\circ$. From Fig. 4, we can see that the maximum value of the integrated signal and the cells' preferred orientation occurs when $\beta = 35^\circ$, so the cell is swimming at 55° clockwise of the **E**-vector. This is a difference of 25° from the experimental result of 30° observed by Häder (1987) and is discussed further in Section 5.

For experiment 2, the cuvette is vertical and irradiated from the side (see Fig. 5) so that $\alpha = 90^\circ$. As β represents the swimming direction measured from the X-axis and the cells swim upwards at most polarization angles, using the laboratory axes as shown in Fig. 5, we take $\beta = 90^\circ$ and rotate the plane of polarization by varying ψ. Note that the polarization plane is measured from the vertical. In this experiment, we hypothesize that the cells' natural tendency to swim upwards is moderated by a negative phototactic response which causes the cells to seek to maximize the integrated signal. Consequently, the cells avoid swimming in directions that minimize the integrated signal. From Fig. 6, we see that the cells receive a minimum signal when the **E**-vector is 35° from the vertical and hence with the **E**-vector at this angle the cells tend to swim away from the vertical. This is a difference of 10° from Häder's result and is discussed further in Section 5.

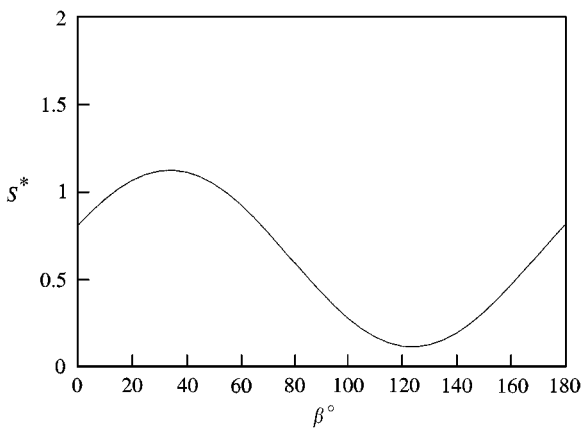

FIG. 4. The integrated signal, S^*, received by the cell when swimming in a thin, flat, horizontal cuvette as in experiment 1 when $\psi = 0^\circ$, showing a preferred orientation 55° clockwise of the **E**-vector.

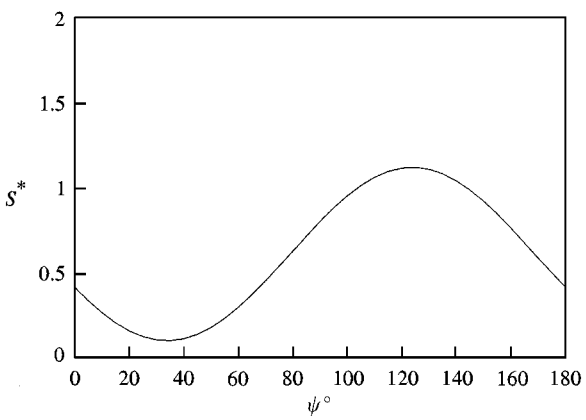

FIG. 6. The integrated signal, S^*, received by the cell when swimming in a narrow flat cuvette as in experiment 2, showing that the cell receives a minimum signal when the **E**-vector is 35° from the vertical.

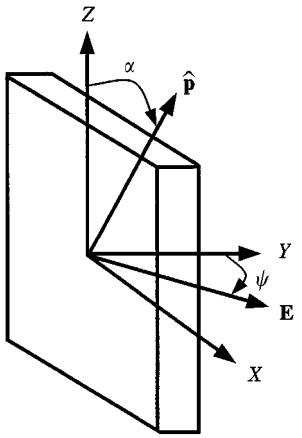

FIG. 7. The laboratory axes for experiment 3.

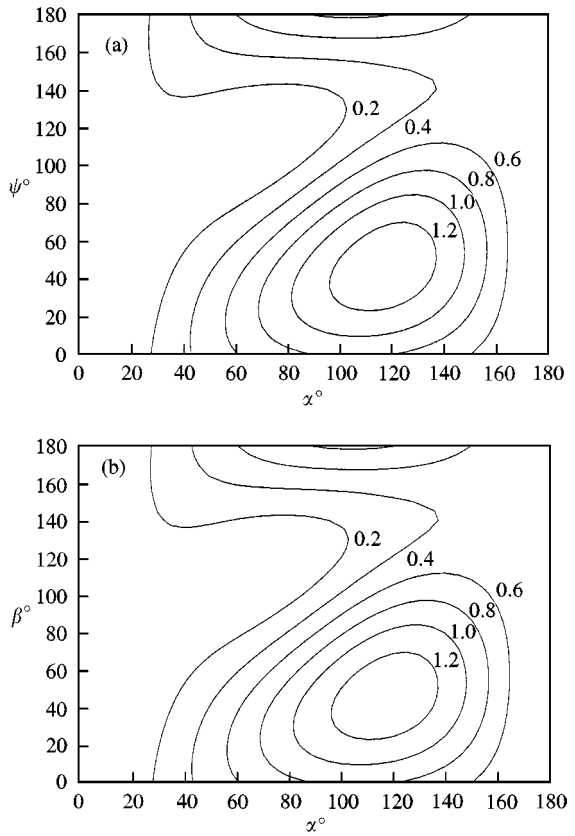

FIG. 8. Two-dimensional contour plot of the integrated signal, S^*, received by a cell during one revolution in experiment 3: (a) $\beta = 0^\circ$ and (b) $\psi = 0^\circ$. In (b), because of symmetry, $S^*(\alpha, \beta) = S^*(\alpha, \beta + 180^\circ)$ so we only show the plot for $0^\circ \leqslant \beta \leqslant 180^\circ$.

For the first part of experiment 3, the cells are restricted to swimming in the plane of a thin, vertical cuvette irradiated from above (see Fig. 7), and β is the angle that the swimming direction vector, $\hat{\mathbf{p}}$, makes with the X-axis which is horizontal and lies in the plane of the cuvette. We can take $\beta = 0^\circ$ or 180° because the cuvette is thin. The angle between $\hat{\mathbf{p}}$ and the vertical Z-axis is α. As in experiment 2, we hypothesize that the cells tend to swim upward ($\alpha = 0^\circ$) unless there is a variation in the *integrated* light signal, S^*, sufficient to cause them to orient so as to maximize S^*. Note that, when the polarization is 30° from the X-axis, $\psi = 120^\circ$, as ψ is measured clockwise from the Y-axis (see Figs. 1 and 7). The contour plot in Fig. 8(a) shows the integrated signal plotted as a function of α and ψ, for $\beta = 0^\circ$. When $\psi = 120^\circ$, we can see that the signal that the cells receive is almost independent of α. There is only a weak maximum in the signal that the cells detect as α varies, which we interpret as being insufficient to cause the cells to swim downwards, and hence the cells orient with respect to gravity. In contrast, in a wider cuvette as used in the second part of experiment 3, the cells are unrestricted and β can take any value between 0° and 360°. Individual cells change swimming directions at random even though there are preferred orientations. S^* depends on α, and on the angle between the polarization vector $\mathbf{E}$, and the projection of $\hat{\mathbf{p}}$ onto the horizontal XY-plane, not on ψ and β independently. Without loss of generality, we can choose the Y-axis to be parallel to $\mathbf{E}$ so that $\psi = 0^\circ$. Then as α and β vary, the cells search the whole of the contour diagram shown in Fig. 8(b), in which S^* is plotted as a function of α and β. Since the cells are unconstrained, they orient to maximize S^* and so swim at an angle $\alpha = 120^\circ$ to the vertical, with a significant downward component. This is consistent with Häder's observation that the cells swim downwards.

5. Discussion

A simple mathematical model for the signal detected by a small dichroic photoreceptor of the swimming microorganism *E. gracilis* has been described and used to analyse experiments in which cells are constrained to two-dimensional motion, with polarized light incident upon them.

We considered the angles suggested by Häder, which were calculated without taking into account the effects of shading, and all other possible angles for the dichroic orientation of the photoreceptor molecules. Including the effects of shading and using the hypothesis that cells reorient when they receive a peak in the signal, we were unable to explain the experimental results.

Alternatively, the hypothesis that the cells orient with respect to the integrated signal received per revolution (Hill & Vincent, 1993) leads to values for the orientation of the dichroic molecules in the photoreceptor that give results which agree with the experiments, to within the experimental accuracy. For self-consistency, we would expect that the angle between the maximum and minimum absorptions of a dichroic array would be 90°, but Häder's experiments imply a difference of only 55°. This is because, if the cells are orienting to maximize the integrated signal they receive, the cells receive the maximum signal when swimming 30° clockwise from the **E**-vector (experiment 1), and the minimum signal when swimming 25° counterclockwise of the **E**-vector (experiment 2), a difference of 55°. Again, the discrepancy of 35° (i.e. between 55° and 90°) lies within the experimental error because of the breadth of the distributions (see Section 3 above).

In experiment 3, when the cells are trying to maximize the integrated signal per revolution, we can see from Fig. 8(a) that if the cells are in a thin cuvette the signal is almost flat, although slightly stronger in the downward swimming direction, so we propose that there is a cut-off value here, below which the cells do not reorient away from the light, as the signal that they receive is not strong enough to overcome the upward swimming due to negative gravitaxis.

There is literature on phototaxis in *E. gracilis* that are dark-bleached (i.e. with only traces of chlorophylls) and/or stigmaless cells [after treatment with streptomycin (Bound & Tollin, 1967; Checcucci *et al.*, 1975; Häder, 1993; Häder & Reinecke, 1991)]. This provides some evidence that cells can still orient, albeit in a modified way, with respect to polarized light. However, there is no experimental work on negative phototaxis (the subject of this paper) with which we can make any direct comparisons. Nevertheless, it is of interest to remove all shading, either by the stigma or the cell's body in our model to see what behaviour is predicted. This was done mathematically by replacing eqn (9) for the signal, S, received by the cell with

$$S = (\hat{\mathbf{d}} \cdot \mathbf{E})^2 \tag{12}$$

and re-running experiments 1 and 3.

Figure 9 shows the integrated signal received by the cell as a function of β (cf. Fig. 4). Assuming, as before, that the cells orient to maximize the signal, we predict that the cells would swim 90° clockwise of the **E**-vector. The results for experiment 3 are shown in Fig. 10 [cf. Fig. 8(a)]. We conclude that when $\psi = 0°$ (rather than 120°), the signal received by the cell is almost independent of α so that the cells would orient with respect to gravity and swim upwards. $\psi = 0°$ corresponds to the plane of polarization being perpendicular to the plane of the thin cuvette shown in Fig. 7. In the wide cuvette used in experiment 3, the cells would orient to maximize the integrated signal, S^*, and would tend to swim horizontally since the maximum lies at about $\alpha = 90°$.

Unlike our idealized model, the shading of the photoreceptor by the cell's body is not uniform and depends on the stigma and the position of organelles such as the chloroplasts and nucleus. This is undoubtedly a source of error in the

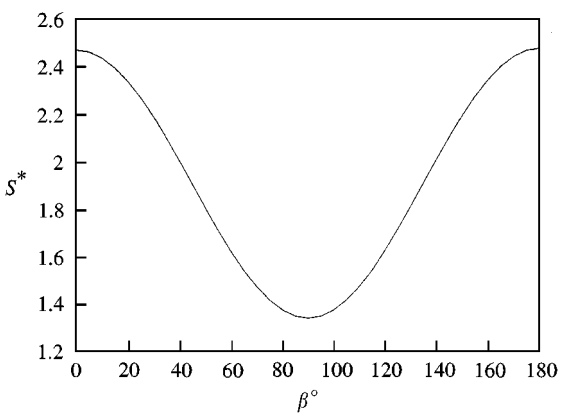

FIG. 9. The integrated signal, S^*, received by the cell when swimming in a thin, flat, horizontal cuvette as in experiment 1 when $\psi = 0°$, showing a preferred orientation 90° clockwise of the **E**-vector.

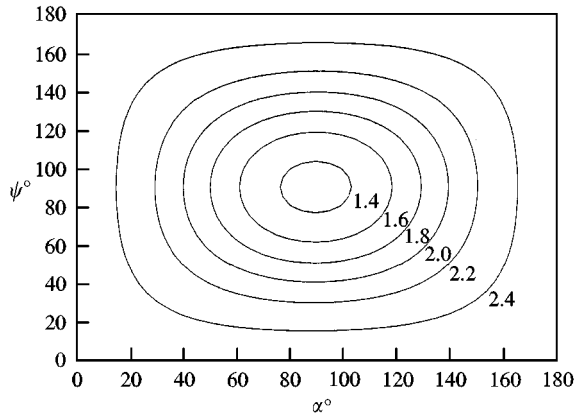

FIG. 10. Two-dimensional contour plot of the integrated signal, S^*, received by bleached, stigmaless cells during one revolution in experiment 3 when $\beta = 0°$.

model. Nevertheless, it seems to be a conceptually useful tool in analysing the responses of polarotactic microorganisms.

The model and control strategies presented in this paper should be effective for other microorganisms that orient with respect to polarized light. To validate the model further, we would need more experiments performed systematically at high, intermediate and low light intensities. In addition, experiments using two beams of polarized light, perpendicular to each other, with parallel and perpendicular polarizations at the same three light intensities would give further information about the dichroic orientation of the receptor molecules.

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