

Mechanism of phototaxis in marine zooplankton: Description of the model

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1 Mathematical Model

We describe here a model of a swimming *Platynereis* larva. The larva is self-propelled by ciliated cells located near the equator of its body, and the forces produced are modulated by the amount of light received by the eyes (see Fig. 1). The animal is not subject to any external forces. We first describe the equations of motion, examine the eye's activities and postulate how swimming strokes are affected by these activities. To complete the equations, we last derive the total force and torque from the cell positions and the forces generated by ventral and dorsal cells.

The resulting mathematical equations were integrated in a simulation which can be downloaded from www.cytosim.org/platynereis. The numerical trajectories show that the simple control operated by the eyes over the motor cells are sufficient to effectively steer the body towards light.

1.1 Equations of Motion

A swimming larva is characterized by the position x of its center and by its orientation, which is represented by a unit quaternion q . Using a unit quaternion is equivalent to using Euler angles or a rotation matrix (for an introduction on quaternion, see for example <http://en.wikipedia.org/wiki/Quaternion>). We denote Q the usual rotation associated to q , *i.e.* for any vector v we have $q \{0, v\} q^{-1} = \{0, Qv\}$, where $\{0, v\}$ is the pure imaginary quaternion built from v .

The equations governing x and q are of order 1, because inertia of the body can be neglected due to the microscopic scale:

$$\begin{aligned}\xi^T dx &= Q f(x, q) dt \\ \xi^R dq &= q \left\{ 0, \frac{1}{2} \mathcal{M}(x, q) \right\} dt,\end{aligned}\tag{1}$$

where $f(x, q)$ is the sum of all forces generated by the cilia on the spherical body, and $\mathcal{M}(x, q)$ is the associated total torque at the body center of mass. Furthermore, both $f(x, q)$ and $\mathcal{M}(x, q)$ are stated here in the moving reference frame associated with the swimmer. They are rotated appropriately by multiplying by Q and q in (1). These equations describe the dynamics of a sphere in a viscous fluid at low Reynolds number (*i.e.* when inertia is negligible). In particular, the equation on q that includes a multiplication on the right by the

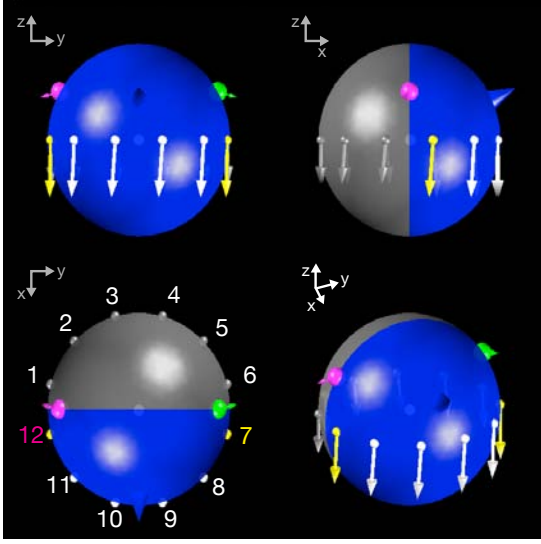


Figure 1: **Simulated body.** A larva is represented by a sphere with 12 ciliated cells on the equator (numbered 1 to 12) producing forces on the fluid (arrows). These forces are tangent to the sphere as expected since the fluid flow must be tangent. They are directed towards the bottom and propel the body upwards. Two eyes (left eye is green, right eye is red) on the top of the body receive light from the directions indicated by the arrows, and affect the forces produced by two adjacent cells (the left eye controls cell 7, and the right eye controls cell 12).

imaginary quaternion $\left\{0, \frac{1}{2} \mathcal{M}(x, q)\right\}$ leads to the usual rotation induced by a torque. The translational and rotational mobility factors ξ^T and ξ^R are obtained using Stokes' law, since the body is spherical and surrounded by a large amount of fluid: $\xi^T = 6\pi\eta R$ and $\xi^R = 8\pi\eta R^3$ where η is the viscosity of the fluid and R the body radius.

1.2 Light and Eye's Activities

Ambient light is represented by a normalized vector E , which is the direction of light propagation. To represent a distant source, E is constant of norm 1. The left and right eyes are characterized by d_L and d_R respectively, two normalized vectors which define the direction in which each eye is able to see in the body reference frame. We have used $d_L = \{-0.23, +0.93, -0.27\}$ and $d_R = \{-0.23, -0.93, -0.27\}$ as measured experimentally. The actual direction \tilde{d}_L and \tilde{d}_R in which an eye is looking to is also determined by the orientation of the body in space. Since we have noted Q the rotation associated with q , we have $\tilde{d}_L = Q d_L$ and a similar equation for the right eye. The activity $e \in [0, 1]$ of an eye looking in direction \tilde{d} is then obtained from the scalar-product $\tilde{d} \cdot E$:

$$e = \left\{ \begin{array}{ll} -\tilde{d} \cdot E & \text{if } -\tilde{d} \cdot E > 0 \quad (\text{looking towards light source}) \\ 0 & \text{if } -\tilde{d} \cdot E < 0 \quad (\text{looking away from light source}) \end{array} \right\} \quad (2)$$

In other words, an eye is able to receive light coming from a hemisphere, and its response is gradual within this hemisphere. The position of the eyes in the body is not considered here, because the body is transparent, and the light source is far away compared to the body size R .

The factors e_L and e_R for the left and right eye modulate the swimming forces of cell 7 and cell 12, respectively. Forces are modulated at time t by a factor $[1 - e(t - \tau)]$ (see details below). The regulation is negative as measured experimentally and includes a delay $\tau = 80$ ms between the time at which light is detected, and the time at which forces are affected. It is expected that delays which are comparable to the rotation time should have strong effects. We found on the contrary that a delay of 100 ms or below does not significantly affect the results (data not shown). For the measured delay of 80 ms, one may rightfully consider the simpler case $\tau = 0$.

1.3 Forces

12 ciliated cells on the equator of the body propel the larva. Their beating cilia exert forces on the fluid which are tangent to the sphere, as expected since the fluid cannot enter the body. The cells are regularly placed on the equator and numbered clockwise (Fig. 1). Cell $n \in [1, 12]$ is lying with angle $a_n = -\pi/2 - (2n-1)\pi/12$ on the equator, at position $R c_n$ with $c_n = \{\cos a_n, \sin a_n, 0\}$. We define α the magnitude of the force produced by one cell. In the moving reference frame (u_x, u_y, u_z) associated with the body:

- Dorsal cell n ($n = 1$ to 6) exert a force $f_n/\alpha = u_z + \mathbf{S} u_z \times c_n$,
- Ventral cell n ($n = 8$ to 11) exert a force $f_n/\alpha = \mathbf{L} u_z + \mathbf{S} u_z \times c_n$,
- Cell 7 exerts force $f_7/\alpha = (1 - e_L) \mathbf{L} u_z + \mathbf{S} u_z \times c_7$,
- Cell 12 exerts force $f_{12}/\alpha = (1 - e_R) \mathbf{L} u_z + \mathbf{S} u_z \times c_{12}$,

We have introduced two dimensionless parameters: the spin \mathbf{S} and the loop \mathbf{L} . They characterize the forces generated by the body and are easily interpretable. The operator \times is the vector cross-product, and thus if $\mathbf{S} > 0$ the larva spins on itself in a right-handed manner. The loop \mathbf{L} is the ratio between ventral and dorsal forces. If $\mathbf{L} > 1$ the larva loops with its ventral side facing outward.

The total force and torque on the body reads:

$$\begin{aligned} f(x, q) &= \alpha \sum_{n=1}^{12} f_n \\ \mathcal{M}(x, q) &= \alpha R \sum_{n=1}^{12} c_n \times f_n, \end{aligned} \tag{3}$$

which simplifies further to:

$$\begin{aligned} f(x, q)/\alpha &= [6 + (6 - e_L - e_R)\mathbf{L}] u_z \\ \mathcal{M}(x, q)/\alpha R &= (1 - \mathbf{L})(\sqrt{6} + \sqrt{2}) u_y + 12 \mathbf{S} u_z + \dots \\ &\quad \mathbf{L} \left[(e_L + e_R) \sin \frac{\pi}{12} u_y + (e_R - e_L) \cos \frac{\pi}{12} u_x \right] \end{aligned} \tag{4}$$

1.4 Parameters

Equations 1, 2 and 4 describe the system. They were solved numerically using the mid-point method with a time-step of 10 milli-seconds. To study the efficiency of swimming for a given amount of work produced by the animal, we derive the force coefficient α from a given speed \bar{v} . Indeed, the dorsal cells produce forces of magnitude $\alpha\sqrt{\mathbf{S}^2 + 1}$, while ventral cells produce approximately $\alpha\sqrt{\mathbf{S}^2 + \mathbf{L}^2}$. Thus by using $\alpha = \xi^T \bar{v} / (\sqrt{6\mathbf{S}^2 + 1} + 6\sqrt{\mathbf{S}^2 + \mathbf{L}^2})$, we remove the trivial effects that increasing \mathbf{L} or \mathbf{S} have on the speed of the animal. Once it is set, the parameter \bar{v} set the maximum speed, and the difference with the mean speed characterizes the efficiency of the trajectory, which is a combination of speed and precision. In practice, from the values of R and \bar{v} , we derived α/ξ^T and α/ξ^R , which is sufficient to solve the equations. The parameters of the simulation are by default:

Parameter	Symbol	Value
Body radius	R	90 μm
Swimming speed	\bar{v}	2000 $\mu\text{m/s}$
Loop (ratio ventral/dorsal force)	\mathbf{L}	1.6
Spin (axial rotation)	\mathbf{S}	0.3
Left eye direction	d_L	$\{-0.23, +0.93, -0.27\}$
Right eye direction	d_R	$\{-0.23, -0.93, -0.27\}$
Delay in eye response	τ	80 ms
Light vector	E	$\{1, 0, 0\}$

2 Relation to previous work

Previous authors have described the 3D trajectories using the Frenet-Serret formulae (1–3), and have assumed that the curvature and the pitch of the trajectory are controlled linearly by the steering mechanism. We used here a vector for the position and a quaternion for the orientation of the body, and postulated the direction and the magnitudes of the forces generated by ciliated cells on the surface of the body. Mathematically, our approach is equivalent (from the forces, one can calculate the effects on the trajectory), but it makes use of our measurements of fluid motion around the immobilized larvae (Fig. 4a,b). In addition, because the responses of the eyes are independent of the position, one can reduce the model to a problem of quaternion dynamics. Indeed, one can derive from equations 1, 2 and 4 a single first-order equation on q .

We have assumed as in (2) a linear response for the rotation speed as a function of the stimulus (cf. equations (2) and (4) below, and equation (16) in (2)), and confirmed the previous simulations (2) that demonstrated alignment of the trajectory to the stimulus. We found as well that the animal could be trapped in a superhelical trajectory in a plane perpendicular to the stimulus. In a thorough exploration of the parameter space (Fig. 4f), we define the regions

where alignment occurs (in blue) or fails (in red). The analytical treatment of chemotaxis (3) is not directly applicable to our model because the equations are different. Our system of equations is however amenable to such a perturbation analysis, which would give rigorous results in the limiting case of weak gradients.

3 Helical trajectories

The trajectory is a straight helix if the torque and forces are constant in the reference frame of the body. This happens either in the absence of light, or after the larva has aligned with the light vector. In such a situation, we can estimate the pitch and the period of the helix as follows. First, the axis of symmetry a of the trajectory must be parallel to the rotational vector \mathcal{M} of the larva. From this we deduce $a = \mathcal{M}/\|\mathcal{M}\|$. The speed along the axis and the speed of the revolution in the transverse plane can be derived from the translation speed $v = f/\xi^T$:

$$v_{\text{axial}} = a \cdot v \tag{5}$$

$$v_{\text{perp}} = v - v_{\text{axial}} a \tag{6}$$

The period of the rotation (the duration of one turn) is $T = 2\pi/\xi^R \|\mathcal{M}\|$, and from this we get the characteristics of the helical trajectory:

- The wave-length is $\lambda = T v_{\text{axial}}$
- The diameter of the helix is $d = \pi^{-1} T \|v_{\text{perp}}\|$

These formulae can be useful to relate to previous analysis of similar problems.

References

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