

# Supporting Information: Chemotaxis of sperm cells

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## I. PERTURBATION CALCULATION OF SWIMMING PATHS IN TWO DIMENSIONS

We study the chemotactic feedback loop for two space dimensions (1), (2), (3) and (4) in the limit of weak chemoattractant gradients. For weak gradients, the dimensionless parameter  $\nu = \rho_\kappa r_0^2 |\nabla c|$ , which describes the strength of the perturbation of the swimming path by chemotactic signaling, is small. We determine the swimming path in a linear concentration field by a perturbation calculation in  $\nu$ . We anticipate that the swimming path  $\mathbf{r}(t) = (x(t), y(t))$  is perfect circle whose shape is perturbed to first order in  $\nu$

$$\mathbf{r}(t) = r_0(\cos \omega_0 t, \sin \omega_0 t) + \mathcal{O}(\nu) \quad . \quad (\text{S1})$$

The chemoattractant concentration field is linear with the the gradient chosen to point in  $x$ -direction for simplicity

$$c(x, y) = c_0 + c_1 x \quad . \quad (\text{S2})$$

A sperm moving along  $\mathbf{r}(t)$  samples according to equation (2) a time-dependent stimulus

$$s(t) = c_0 + r_0 c_1 \cos \omega_0 t + \mathcal{O}(\nu^2) \quad . \quad (\text{S3})$$

The stimulus contains a monotonically increasing or decreasing contribution  $\sim c_1 v_d \cos(\alpha) t$  which is of second order in  $\nu$ . The chemotactic signaling network responds with an output that to linear order in  $\nu$  evokes curvature oscillations

$$\kappa(t) = \kappa_0 + \rho_\kappa c_1 r_0 \cos(\omega_0 t + \phi_\kappa) + \mathcal{O}(\nu^2) \quad . \quad (\text{S4})$$

Integrating equation (1) with this time dependence of the curvature gives the swimming path

$$\mathbf{r}(t) = r_0 (\cos \theta(t), \sin \theta(t)) + v_d (\cos \alpha, \sin \alpha) t + \mathcal{O}(\nu^2) \quad , \quad (\text{S5})$$

with rotation rate  $\dot{\theta} = \Omega_3 = \omega_0 + v_d \kappa_0 \cos(\omega_0 t + \phi_\kappa)$  and drift velocity  $v_d = \delta_\kappa \rho_\kappa c_1 + \mathcal{O}(\nu^2)$  where  $\delta_\kappa = \frac{1}{2} v_0 r_0^2$ . For the angle with respect to the gradient we obtain

$$\alpha = 3\pi/2 - \phi_\kappa + \mathcal{O}(\nu) \quad , \quad (\text{S6})$$

where  $\phi_\kappa$  is the phase of the linear response coefficient  $\chi_\kappa$  at the angular frequency  $\omega_0$ .

## II. PERTURBATION CALCULATION OF SWIMMING PATHS IN THREE DIMENSIONS

As in the planar case, the chemotactic feedback loop for three space dimensions (2), (4), (6) and (7) can be studied in the limit of weak gradients by a perturbation calculation in the small parameter  $\nu = (\rho_\kappa/\kappa_0 + \rho_\tau/\tau_0)r_0|\nabla c|$ . Again we assume that the nonlinearities of the concentration field  $c(\mathbf{x})$  are small on the length-scale  $r_0$ ,  $|\nabla^2 c| \ll |\nabla c|/r_0$ , which implies that during a few helical turns of the swimming path we approximate the concentration field linearly. In the presence of a chemoattractant stimulus, the swimming path will be a deformed helix that winds around a centerline  $\mathbf{R}(t)$ . Recall that such a helical swimming path can be described as the trajectory of a point on the circumference of an imagined solid disk of radius  $r_0$  that rotates in its plane with rotation rate  $\Omega_3$  and whose center moves along the centerline  $\mathbf{R}(t)$ . The orientation of the disk is characterized by the unit vector  $\mathbf{h}$  normal to the disk, which we call the helix vector. Note, that  $\mathbf{h}$  is not necessarily parallel to  $\dot{\mathbf{R}}$ , see Fig. 5. We introduce the material frame of the imagined disk consisting of orthogonal unit vectors  $\mathbf{e}_1$  and  $\mathbf{e}_2$ , in the plane of the disk and  $\mathbf{h} = \mathbf{e}_3 = \mathbf{e}_1 \times \mathbf{e}_2$ . The deformed helical swimming path can now be written as

$$\mathbf{r}(t) = \mathbf{R}(t) + r \mathbf{e}_1(t) \quad , \quad (\text{S7})$$

where the radius  $r$  may change only on a slow time-scale. The time dependence of the frame  $\mathbf{e}_i$  is given by pure rotations  $\dot{\mathbf{e}}_i = \epsilon_{jik} \Omega_j \mathbf{e}_k$ , where  $\Omega_j$  denote rotation rates. In the absence of a chemotactic stimulus, the swimming path is a perfect helix with  $\dot{\mathbf{R}} = \omega_0 h_0 \mathbf{h}$ ,  $r = r_0$ ,  $\Omega_1 = \Omega_2 = 0$  and  $\Omega_3 = \omega_0$ . We also define the complex gradient vector

$$\mathbf{g} = \nabla_{\perp} c + i \mathbf{h} \times \nabla_{\perp} c \quad , \quad (\text{S8})$$

where  $\nabla_{\perp} c$  denotes the concentration gradient projected on the disk plane which is perpendicular to  $\mathbf{h}$ . The real and imaginary parts of  $\mathbf{g}$  form a basis for the plane of the disk.

These notions will allow us to present results in a concise form. For the calculation we use cartesian coordinates with  $\mathbf{R}(t=0) = (0, 0, 0)$ ,  $\mathbf{e}_1(t=0) = (1, 0, 0)$ ,  $\mathbf{e}_2(t=0) = (0, 1, 0)$ ,  $\mathbf{h}(t=0) = (0, 0, 1)$  and a concentration field with a gradient in the  $x$ - $z$  plane at  $(0, 0, 0)$ :

$$c(x, y, z) = c_0 + c_x x + c_z z \quad . \quad (\text{S9})$$

Here we have distinguished the components of the gradient perpendicular  $c_x = |(\nabla_{\perp} c)|_{t=0}$  and parallel  $c_z = |(\nabla_{\parallel} c)|_{t=0}$  to the helix axis at  $t=0$ . Thus, at time  $t=0$ ,  $\nabla_{\perp} c$  is parallel to  $\mathbf{e}_1$ . We anticipate that the swimming path  $\mathbf{r}(t)$  is a perfect helix whose shape is perturbed to first order in  $\nu$

$$\mathbf{r}(t) = (r \cos \theta(t), r \sin \theta(t), \omega h_0 t) + \mathcal{O}(\nu) \quad , \quad (\text{S10})$$

with an angular frequency  $\omega = \omega_0 + \mathcal{O}(\nu)$ , a radius  $r = r_0 + \mathcal{O}(\nu)$ , a pitch  $2\pi h = 2\pi h_0 + \mathcal{O}(\nu)$ , and a rotation rate  $\dot{\theta} = \Omega_3 = \omega + \mathcal{O}(\nu)$ . The swimming path  $\mathbf{r}(t)$  samples a temporal stimulus from the locally linear concentration field which to first order in  $\nu$  and for  $t \ll (\nu\omega_0)^{-1}$  reads

$$s(t) = c(\mathbf{r}(t)) = c_0 + \omega_0 h_0 c_z t + r_0 c_x \cos \omega_0 t + \mathcal{O}(\nu^2) \quad . \quad (\text{S11})$$

It combines a linear ramp and a periodic component. To first order in  $\nu$  the signaling network generates the output  $a(t) = 1 + a_1 + \rho r_0 c_x \cos(\omega t + \phi) + \mathcal{O}(\nu^2)$  where  $a_1 = \mu \omega_0 h_0 c_z / c_0^2$  and  $\chi = \rho \exp(i\phi)$  is the linear response coefficient of equation (4) at the helix frequency  $\omega_0$ . This output elicits curvature and torsion oscillations

$$\begin{aligned} \kappa(t) &= \kappa_0 + \kappa_1 a_1 + \rho_{\kappa} c_x r_0 \cos(\omega t + \phi_{\kappa}) + \mathcal{O}(\nu^2) \\ \tau(t) &= \tau_0 + \tau_1 a_1 + \rho_{\tau} c_x r_0 \cos(\omega t + \phi_{\tau}) + \mathcal{O}(\nu^2) \quad . \end{aligned}$$

Curvature  $\kappa(t)$  and torsion  $\tau(t)$  determine the swimming path by the Frenet-Serret equations (6). If we express the swimming path in the form of equation (S7), the centerline  $\mathbf{R}(t)$  and the vectors  $\mathbf{e}_i(t)$  have to change according to

$$\begin{aligned} \dot{\mathbf{R}} &= \omega h \mathbf{h} - \delta_{\kappa} \text{Im}(\chi_{\kappa} \mathbf{g}) + \delta_{\tau} \text{Im}(\chi_{\tau} \mathbf{g}) + \mathcal{O}(\nu^2) \\ \dot{\mathbf{h}} &= -\varepsilon_{\kappa} \text{Re}(\chi_{\kappa} \mathbf{g}) + \varepsilon_{\tau} \text{Re}(\chi_{\tau} \mathbf{g}) + \mathcal{O}(\nu^2) \\ \dot{\mathbf{e}}_1 &= \Omega_3 \mathbf{e}_2 - \dot{\mathbf{h}} \cdot \mathbf{e}_1 \\ \dot{\mathbf{e}}_2 &= -\Omega_3 \mathbf{e}_1 - \dot{\mathbf{h}} \cdot \mathbf{e}_2 \end{aligned} \quad (\text{S12})$$

for the time dependent curvature and torsion to satisfy equation (S12). Here the coefficients read  $\delta_{\kappa} = \omega_0 r_0 (2r_0^2 + 3h_0^2)/4$ ,  $\delta_{\tau} = \omega_0 r_0^2 h_0/4$ ,  $\varepsilon_{\kappa} = \omega_0 r_0 h_0/2$ , and  $\varepsilon_{\tau} = \omega_0 r_0^2/2$ . The helix

frequency  $\omega = \omega_0 + \omega_0(r_0\kappa_1 + h_0\tau_1)a_1 + \mathcal{O}(\nu^2)$ , the helix radius  $r = r_0 + ((h_0^2 - r_0^2)\kappa_1 - 2r_0h_0\tau_1)a_1 + \mathcal{O}(\nu^2)$ , and the helix pitch  $2\pi h = 2\pi h_0 + (-2r_0h_0\kappa_1 + (r_0^2 - h_0^2)\tau_1)a_1 + \mathcal{O}(\nu^2)$  are perturbed to first order in  $\nu$ . The rotation rate is given by the helix frequency  $\omega$  plus a periodic modulation  $\Omega_3 = \omega + \omega_0|\nabla_{\perp}c|/4[(2r_0^2 + h_0^2)\rho_{\kappa} \cos(\omega_0 t + \phi_{\kappa}) + r_0h_0\rho_{\tau} \cos(\omega_0 t + \phi_{\tau})] + \mathcal{O}(\nu^2)$ .

From equation (S12), we see that two fundamental perturbations of a perfect helix are important in the presence of a gradient. The helix can bend for  $\dot{\mathbf{h}} \neq 0$  or it can tilt if  $\dot{\mathbf{R}}$  and  $\mathbf{h}$  do not align. In the limit of  $\tau_0 = \tau_1 = 0$  with  $\delta_{\tau} = 0$ ,  $\varepsilon_{\kappa} = \varepsilon_{\tau} = 0$  and  $h_0 = 0$ , we recover chemotaxis in a plane as discussed above. Note that this calculation is general and applies to any signaling system which shows adaptation and is characterized by linear response coefficients  $\chi_{\kappa}$  and  $\chi_{\tau}$  for curvature and torsion.

### III. RADIAL CONCENTRATION FIELDS IN THREE DIMENSIONS

In a radial concentration field  $c(\mathbf{x}) = C(|\mathbf{x}|)$ , we can simplify equation (S12) by exploiting rotational symmetry. We can express the centerline position  $\mathbf{R}$  and the helix vector  $\mathbf{h}$  by five parameters, the distance to the origin  $R = |\mathbf{R}|$ , the angle  $\psi$  between the helix vector  $\mathbf{h}$  vector and the radial direction of the gradient  $\nabla c$ , as well as three Euler angles  $\theta, \xi, \eta$ , as

$$\begin{aligned}\mathbf{R} &= R \mathbf{e}_r \\ \mathbf{h} &= -\cos \psi \mathbf{e}_r - \sin \psi (\cos \eta \mathbf{e}_{\theta} + \sin \eta \mathbf{e}_{\xi})\end{aligned}\tag{S13}$$

where  $\mathbf{e}_r = (\cos \theta, \cos \xi \sin \theta, \sin \xi \sin \theta)$ ,  $\mathbf{e}_{\theta} = \frac{\partial}{\partial \theta} \mathbf{e}_r$ ,  $\mathbf{e}_{\xi} = \mathbf{e}_r \times \mathbf{e}_{\theta}$ . Inserting equation (S13) into equation (S12) yields

$$\begin{aligned}\dot{R} &= -\Lambda \cos \psi - \gamma \\ \dot{\psi} &= -\sin \psi \left( \beta - \frac{\Lambda}{R} \right) \\ \dot{\theta} &= -\frac{\sin \psi}{R} (\gamma' \sin \eta + \Lambda \cos \eta) \\ \dot{\xi} &= -\frac{\sin \psi}{R \sin \theta} (\gamma' \cos \eta - \Lambda \sin \eta) \\ \dot{\eta} &= -\beta' - \gamma' \frac{\cos \psi}{R} - \frac{\cot \theta \sin \psi}{R} (\gamma' \cos \eta - \Lambda \sin \eta)\end{aligned}\tag{S14}$$

where  $\Lambda = \omega h - \gamma \cos \psi$ ,  $\beta - i\beta' = |\nabla c|(\varepsilon_{\tau}\chi_{\tau} - \varepsilon_{\kappa}\chi_{\kappa})$ , and  $\gamma' + i\gamma = |\nabla c|(\delta_{\tau}\chi_{\tau} - \delta_{\kappa}\chi_{\kappa})$ . From this we obtain equation (12) with  $\dot{R}, \dot{\psi}$  independent of  $\theta, \xi, \eta$ .