The transport of active swimmers in shear flows

Helical swimmers in shear
Trapping of slender chemotactic bacteria in high shear

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Many plankton swim in helical paths.
Gyrotaxis: interaction of gravity and shear

At low Reynolds number, torques balance.
For moderate shear, there is an equilibrium stable state with $\Omega=0$ (zero angular velocity).

Kessler Nature 1985

Durham et al. Science 2009
Torque balance on spherical helical gyrotactic swimmer

Gravitational & viscous torques

$$L_0 \mathbf{p} \wedge \mathbf{k} + 8\pi \mu a^3 \left( \frac{1}{2} \omega - \Omega \right)$$

NEW for helical swimmers: ‘intrinsic’ torque

$$T \mathbf{n}$$

Solve Torque=0 to obtain angular velocity

$$\Omega = \frac{1}{2B} \mathbf{p} \wedge \mathbf{k} + R \mathbf{n} + \frac{1}{2} \omega$$

$$\frac{1}{2B} = \frac{L_0}{8\pi \mu a^3}, \quad R = \frac{T}{8\pi \mu a^3}$$

Bearon, J Math Biol 2013
Governing equations

Non-dimensionalise time on $2B$

Assume $\omega = \omega j$

$$\dot{x} = V + v p$$
$$\dot{p} = \Omega \wedge p, \quad \dot{n} = \Omega \wedge n$$

$$\Omega = p \wedge k + \Theta n + \Psi j$$

Key non-dimensional parameters

$$\Psi = B \omega, \quad \text{shear}$$
$$\Theta = 2RB, \quad \text{intrinsic rotation}$$
$$\cos \gamma = p \cdot n, \quad \text{angle between propulsive force and torque}$$

$x$ position
$V$ fluid velocity
$p$ swimming orientation
$v$ swimming speed
$\Omega$ angular velocity of cell
Example simulation in the absence of shear ($\Psi = 0$)

Equilibrium solution for orientation

$$\cos \theta_p = \cos \theta^e_p \quad \phi_p(t) = \Theta \frac{\cos \gamma}{\cos \theta^e_p} t + \phi_p(0)$$

where $0 < \theta^e_p < \frac{\pi}{2}$ and $x = (\cos \theta^e_p)^2$ satisfies

$$x^2 + (\Theta^2 - 1)x - \Theta^2 \cos^2 \gamma = 0$$
Equilibrium, zero angular velocity

\[ p_x^e = \Psi - \Theta \sqrt{1 - \left( \frac{\cos \gamma}{\Psi} \right)^2}, \quad p_y^e = -\frac{\Theta}{\Psi} \cos \gamma, \]

\[ \gamma = \pi/4 \]

Blue: feasible, \( px < 0 \); swim towards upwards flow

Red: feasible, \( px > 0 \); swim towards downwards flow

Equilibrium feasibility region

\[ \frac{\cos \gamma}{\Psi} \leq 1 \]

\[ \Psi \sqrt{1 - \frac{\cos^2 \gamma}{\Psi^2}} - \sin \gamma \leq \Theta \leq \Psi \sqrt{1 - \frac{\cos^2 \gamma}{\Psi^2}} + \sin \gamma \]
Helical swimmers in channel flow

Poiseuille flow

\[ \mathbf{V} = \Psi_{\text{max}} (x^2 - 1) \mathbf{k} \]
\[ \Psi = -\Psi_{\text{max}} x \]

Note: Shear varies with space

Recap Governing equations

\[ \dot{x} = \mathbf{V} + \nu \mathbf{p} \]
\[ \dot{\mathbf{p}} = \mathbf{\Omega} \wedge \mathbf{p}, \quad \dot{\mathbf{n}} = \mathbf{\Omega} \wedge \mathbf{n} \]

\[ \mathbf{\Omega} = \mathbf{p} \wedge \mathbf{k} + \Theta \mathbf{n} + \Psi \mathbf{j} \]
Gyrotactic focussing

(a) $\Theta = 0$, (b) $\Theta = 1$, $\gamma = \frac{\pi}{4}$, (c) $\Theta = 1$, $\gamma = \frac{7\pi}{16}$, (d) $\Theta = 1.05$, $\gamma = \frac{\pi}{3}$. 
Histogram of position & corresponding equilibrium swimming orientation

\( \Theta = 1, \gamma = \frac{\pi}{4} \)

\( \Theta = 1, \gamma = \frac{7\pi}{16} \)

\( \Theta = 1.05, \gamma = \frac{\pi}{3} \)
Linking individuals to populations

The Individual

E.g. Swimming speed, random reorientation, fluid rotation & advection

\( \psi(x, p, t) \): Probability of cell having position \( x \), orientation \( p \) at time \( t \)

\[
\frac{\partial \psi}{\partial t} + \nabla_x \cdot (\dot{x} \psi) + \nabla_p \cdot (\dot{p} \psi) = 0
\]

\[
\dot{x} = u + V_s p - D \nabla_x \ln \psi
\]

\( u \): swimming velocity, \( V_s \): fluid velocity, \( D \): translational Brownian diffusion

\[
\dot{p} = \beta p \cdot E \cdot (I - pp) + \frac{1}{2} \omega \wedge p - d_r \nabla_p \ln \psi
\]

\( E \): rate-of-strain tensor, \( \omega \): vorticity vector, \( \beta \): shape factor, \( d_r \): rotational diffusion of magnitude
Linking individuals to populations

Concentration of cells, \( n(x, t) = \int_\Omega \psi(x, p, t) \, dp \),

(sometimes) satisfies advection-diffusion equation

\[
\frac{\partial n}{\partial t} + \nabla_x \cdot \left[ (u + \mathbf{V}_s q) n - D \cdot \nabla_x n \right] = 0,
\]

Generalized Taylor dispersion
E.g. Hill & Bees 2002;
Manela & Frankel 2003
Bearon 2003
(Restrictions on types of flow)
Comparing population-level spatial distribution with individual-based simulation


Formation of thin layer in region of high shear
But sometimes drift-diffusion model fails...
Rusconi et al 2014
Spatial distribution cannot be captured by drift-diffusion physical space model. Return to physical/orientation space model:

\[
\frac{\partial \psi}{\partial t} + \nabla_x \cdot (\dot{x}\psi) + \nabla_p \cdot (\dot{p}\psi) \\
+ \lambda(x, p, t)\psi - \int_{\Omega} \lambda(x, p', t)K(p, p')\psi(x, p', t)dp' = 0
\]

\[
\begin{align*}
\lambda(x, p, t) & \quad \text{Tumble rate} \\
K(p, p') & \quad \text{Turning kernel} \\
\lambda(p) &= \lambda_0(1 - \zeta V_s p \cdot \nabla s) \quad \text{Chemotaxis}
\end{align*}
\]

Howard Berg’s *E. coli* tracks

Steady solution for 2D channel flow

\[ u = U(1 - y^2) \mathbf{i} \]

\[
\epsilon \frac{\partial}{\partial y} (\sin \theta \psi) - \epsilon^2 y \frac{\partial^2 \psi}{\partial y^2} + \frac{\partial}{\partial \theta} \left( yPe(1 - \beta \cos 2\theta) \psi - \frac{\partial \psi}{\partial \theta} \right) \\
+ (\sigma - \epsilon \chi \sin \theta) \psi - \frac{1}{2\pi} \int_0^{2\pi} (\sigma - \epsilon \chi \sin \theta') \psi(y, \theta') \, d\theta' = 0,
\]

\[ \mathbf{p} = \cos \theta \mathbf{i} + \sin \theta \mathbf{j} \]

Swimming direction

Isotropic tumbles

\[
K(\theta, \theta') = \frac{1}{2\pi},
\]

\[ \epsilon = 2V_s/W d_r \]

\[ Pe = 2U/W d_r \]

\[ d = Dd_r/V_s^2 \]

\[ \sigma = \lambda_0/d_r \]

\[ \chi = \lambda_0 \zeta \frac{ds}{dy} \]
No flux boundary conditions

Consider the cell concentration

\[ n(x, t) = \int_\Omega \psi(x, p, t) dp \]

Integrating governing equation gives conservation equation for \( n \) and defines cell flux, \( J \)

\[ \frac{\partial n}{\partial t} + \nabla_x \cdot J = 0, \]

\[ J = \int_\Omega \left( (u + V_s p)\psi - D\nabla_x \psi \right) dp. \]

For 2D flow, no flux condition at \( y=\pm 1 \)

\[ \int_0^{2\pi} \left( \sin \theta \psi - \epsilon d \frac{\partial \psi}{\partial y} \right) d\theta \bigg|_{y=\pm 1} = 0. \]

Numerical solution not unique, so instead impose

\[ \sin \theta \psi - \epsilon d \frac{\partial \psi}{\partial y} = 0 \]
Depletion of cells in central (low shear) region; no chemical gradient

Stars: Experiments
Black/grey lines: numerical simulation
Red line: asymptotic approximation

\[ Pe = [0, 1.25, 2.5, 5, 10, 25] \]
Effect of shape

Pe = 5

Pe = 25

Asymptotic approximation

Full numerical solution
Variable shear modifies distribution of chemotactic cells

\[ Pe = [0, 1.25, 2.5, 5, 10, 25] \]

Stars, experiments; Black, numerical simulation; Red asymptotic approximation
Take $d=0$ and consider approximation

$$
\psi = n(y)f^{(0)}(\theta; y) + \epsilon \psi^{(1)}(y, \theta)
$$

$f^{(0)}(\theta; y)$ leading order equilibrium orientation distribution at a given position

$$
\frac{\partial}{\partial \theta} \left( yPe(1 - \beta \cos 2\theta) f^{(0)} - \frac{\partial f^{(0)}}{\partial \theta} \right) + \sigma (f^{(0)} - \frac{1}{2\pi}) = 0,
$$

Leading order solution

$$
n(y) \propto \frac{e^{\chi y}}{V_{MS}}
$$

mean squared vertical swimming speed

$$
V_{MS}(y) = \int_{0}^{2\pi} \sin^2 \theta f(\theta; y)d\theta
$$
Leading order solution

\[ n(y) \propto \frac{e^{xy}}{V_{MS}} \]

\[ V_{MS}(y) = \int_0^{2\pi} \sin^2 \theta f(\theta; y) d\theta \]

\[ \mathbf{p} = \cos \theta \mathbf{i} + \sin \theta \mathbf{j} \]

Mechanism for trapping in high shear:
- Peak in orientation distribution in streamwise (x) direction
- Reduction in cross-channel (y) swimming
- Cell accumulation
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Estimating parameters from experimental data

- Mean speed ($v$)
- Mean orientation ($\cos \theta$)
- Period of oscillation

Solve pair of non-linear equations to estimate $\gamma$ and $\omega$

3D track reconstruction, Gurarie et al (2011)
Comparison of model solution with experimental data

Parameter estimates:

\[ v = 0.1 \text{mm s}^{-1} \]
\[ \Theta = 16.4 \]
\[ \cos \gamma = 0.55 \]
\[ B = 5 \text{s (assumed)} \]
\[ R = 1.64 \text{s} \]
Experimental parameters, increasing shear

\( \Theta = 16.4, \ \psi_{\text{max}} = 2, \ \cos \gamma = 0.55 \)

\( \Theta = 16.4, \ \psi_{\text{max}} = 10, \ \cos \gamma = 0.55 \)

\( \Theta = 16.4, \ \psi_{\text{max}} = 30, \ \cos \gamma = 0.55 \)

\( \Theta = 0, \ \psi_{\text{max}} = 2 \)

\( \Theta = 0, \ \psi_{\text{max}} = 10 \)

\( \Theta = 0, \ \psi_{\text{max}} = 30 \)
<table>
<thead>
<tr>
<th>Property</th>
<th>Symbol</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Swimming speed</td>
<td>$V_s$</td>
<td>50 $\mu$m s$^{-1}$</td>
</tr>
<tr>
<td>Rotational diffusion</td>
<td>$d_r$</td>
<td>1 s$^{-1}$</td>
</tr>
<tr>
<td>Tumble rate</td>
<td>$\lambda_0$</td>
<td>2 s$^{-1}$</td>
</tr>
<tr>
<td>Channel width</td>
<td>$W$</td>
<td>425 $\mu$m</td>
</tr>
<tr>
<td>Brownian translation diffusion$^a$</td>
<td>$D$</td>
<td>$2 \times 10^{-9}$ cm$^2$ s$^{-1}$</td>
</tr>
<tr>
<td>Cell shape factor</td>
<td>$\beta$</td>
<td>0.99</td>
</tr>
<tr>
<td>Chemotactic strength</td>
<td>$\chi$</td>
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<tr>
<td>Flow Péclet number</td>
<td>$Pe = 2U/Wd_r$</td>
<td>0–50</td>
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<tr>
<td>Swimming Péclet number</td>
<td>$\epsilon = 2V_s/Wd_r$</td>
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<tr>
<td>Relative tumble rate</td>
<td>$\sigma = \lambda_0/d_r$</td>
<td>2</td>
</tr>
<tr>
<td>Relative translation diffusion</td>
<td>$d = Dd_r/V_s^2$</td>
<td>$10^{-4}$</td>
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