

BioFluids Lecture 13: Bioconvection with gyrotaxis.

We have shown that bioconvection can occur, assuming that all the organisms swim vertically upwards, relative to any fluid motion. Yet if they experience a viscous torque, they will surely lose their vertical orientation and might swim off in an unintended direction. A more accurate model should calculate the actual swimming direction, $\hat{\mathbf{p}}$, when the organism tries to swim in an upwards direction relative to fluid which is not at rest.

For simplicity we shall consider a spherical organism, whose centre of mass is displaced a distance h from the centre of the sphere in the opposite direction from which it wishes to swim. In the absence of fluid motion, the organism will swim upwards in a stable manner. If the fluid is in motion, however, it may feel a viscous torque, τ_v , which causes it to swim at an angle θ to the vertical. This will cause a gravitational torque

$$\tau_g = mgh \hat{\mathbf{z}} \wedge \hat{\mathbf{p}} \quad (13.1)$$

which has the magnitude $mgh \sin \theta$, attempting to reorientate the organism towards upwards swimming. At low Reynolds numbers, the total torque, $\tau_g + \tau_v$, must be zero. Now the viscous torque on a sphere can be written

$$\tau_v = 4\pi\mu a^3 (\nabla \wedge \mathbf{u} - 2\Omega) \quad (13.2)$$

where Ω is the angular velocity of the sphere. The straining part of the local motion does not contribute to the torque for spherical organisms (Batchelor 1970). However, it does have an effect for spheroidal (egg-shaped) organisms, and we will consider the modifications it induces below. For a sphere in equilibrium, when $\Omega = 0$, we therefore have

$$\sin \theta = B\omega \quad \text{where} \quad B = \frac{4\pi\mu a^3}{mgh}, \quad (13.3)$$

and ω is the horizontal vorticity component of the bulk flow in which the organism resides. Clearly, if $B|\omega| > 1$, no steady swim direction exists, and the cell rotates, or tumbles, as it swims. For non-spherical cells, the local strain rate e_{ij} also contributes to the gyrotaxis.

It is clear that gyrotactic effects are vital in understanding the behaviour of cells in an $O(1)$ flow. For example, if we place the cells in a vertical tube containing Poiseuille flow, they will tend to swim towards the centre of the tube if the flow is downwards, but towards the walls of the tube if the flow is upwards. This is an easy experiment to perform. We might also anticipate an instability mechanism for an upswimming configuration. If the cells start swimming towards the centre of the tube they will generate a local density increase, which could form a downwards plume. Such a plume will generate shear which could encourage the cells to swim towards it.

It comes as no surprise therefore that the stability analysis we performed above requires some modification. An $O(\varepsilon)$ flow leads to an $O(\varepsilon B)$ change in the swimming direction, which is the same order as terms we have included in the analysis.

We modify the governing equations (11.1)–(11.3) to include the new swimming direction

$$\left. \begin{aligned} \nabla \cdot \mathbf{u} &= 0 \\ \frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} &= -\nabla P + \alpha g c \hat{\mathbf{z}} + \nu \nabla^2 \mathbf{u} \\ \frac{\partial c}{\partial t} + \mathbf{u} \cdot \nabla c &= -\nabla \cdot (cV\hat{\mathbf{p}}) + D\nabla^2 c. \end{aligned} \right\} \quad (13.4)$$

Here $P = (p/\rho_0 + gz)$. Now the bioconvective instability we investigated before depended on the position and nature of the container boundaries. The modified model exhibits instabilities even for a uniform distribution in an infinite fluid. Thus we will assume that the swimming velocity is constant, $V = V_0$, and that the equilibrium state is $\mathbf{u} = 0$, $c = c_0$. We perturb the system in the form

$$c = c_0 + \varepsilon c_1, \quad \mathbf{u} = \varepsilon \mathbf{u}_1, \quad P = \alpha g c_0 z + \varepsilon P_1, \quad \hat{\mathbf{p}} = \hat{\mathbf{z}} + \varepsilon \hat{\mathbf{p}}_1 \quad (13.5)$$

to obtain

$$\left. \begin{aligned} \nabla \cdot \mathbf{u}_1 &= 0 \\ \frac{\partial \mathbf{u}_1}{\partial t} &= -\nabla P_1 + \alpha g c_1 \hat{\mathbf{z}} + \nu \nabla^2 \mathbf{u}_1 \\ \frac{\partial c_1}{\partial t} &= -V_0 \frac{\partial c_1}{\partial z} - V_0 c_0 \nabla \cdot \hat{\mathbf{p}}_1 + D\nabla^2 c_1. \end{aligned} \right\} \quad (13.6)$$

Now the local swim direction is determined by

$$\hat{\mathbf{p}} \wedge \hat{\mathbf{z}} = \varepsilon B \boldsymbol{\omega}_1 \quad \implies \quad \hat{\mathbf{p}}_1 = B \hat{\mathbf{z}} \wedge \boldsymbol{\omega}_1, \quad (13.7)$$

recalling that $\hat{\mathbf{p}}$ is a unit vector so that $\hat{\mathbf{p}}_1 \cdot \hat{\mathbf{z}} = 0$. Thus $\nabla \cdot \hat{\mathbf{p}}_1 = B \hat{\mathbf{z}} \cdot \nabla^2 \mathbf{u}_1$. Now unlike the model we considered above, all the coefficients in the PDEs are constants. As a result we can Fourier analyse in all three space directions, seeking solutions with c_1 and \mathbf{u}_1 both proportional to

$$\zeta \equiv \exp(ikx + ily + imz + st), \quad \text{and we write } \kappa^2 = k^2 + l^2 + m^2. \quad (13.8)$$

Once again we take two curls of the momentum equation, and then the z -component to eliminate the pressure and all velocity components other than $W_1 \equiv \hat{\mathbf{z}} \cdot \mathbf{u}_1$. We then obtain

$$(s + \nu \kappa^2) \kappa^2 W_1 = \alpha g (\kappa^2 - m^2) c_1, \quad (13.9)$$

as $\nabla^2 \rightarrow -\kappa^2$, while the cell equation gives

$$(s + imV_0 + D\kappa^2) c_1 = BV_0 c_0 \kappa^2 W_1. \quad (13.10)$$

Combining these two, we obtain the dispersion relation

$$(s + imV_0 + D\kappa^2)(s + \nu \kappa^2) = \alpha g V_0 c_0 B (\kappa^2 - m^2) \equiv \beta (\kappa^2 - m^2). \quad (13.11)$$

We want to know whether for given parameter values $\Re(s) > 0$, giving instability.

Clearly, without gyrotaxis ($B = 0$) both roots have negative real part, but when $B > 0$, instability may occur. Let us first consider z -independent modes ($m = 0$). Then the quadratic has roots

$$s = \frac{1}{2}\kappa^2 \left[-(D + \nu) \pm \sqrt{(D - \nu)^2 + 4\beta/\kappa^2} \right] \quad (13.12)$$

where β is given by (13.11). As $\beta > 0$, we see that we have instability for

$$\kappa < \kappa_c \equiv [\beta/(\nu D)]^{1/2}. \quad (13.13)$$

So sufficiently long waves are unstable. We can calculate the maximum growth rate by setting $ds/d(\kappa^2) = 0$. After a little algebra we find that the maximum is

$$s_{max} = \frac{\beta}{(\sqrt{\nu} + \sqrt{D})^2} \quad \text{at} \quad \kappa = \kappa_m = \frac{(\beta/\sqrt{\nu D})^{1/2}}{\sqrt{\nu} + \sqrt{D}}. \quad (13.14)$$

We now consider whether vertical variation ($m \neq 0$) has an effect, i.e. is either the critical wavenumber κ_c , or the maximum growth rate, s_{max} increased by non-zero m ? It is found that no major changes occur – although 3-D disturbances can be unstable, the 2-D ones are the most important. The analysis is simplified if we assume $mV_0 \ll \kappa^2(\nu + D)$.

Finite depths: We cannot strictly treat the case of a finite container depth H using the above theory, as we have assumed a z -independent cell flux. However, it is reasonable to assume the theory is valid away from the boundaries provided we restrict attention to sufficiently small vertical wavelengths, i.e. require $m \gg m_0 \equiv 2\pi/H$. We then find that for instability we must have H large enough. Defining a horizontal wave number $\kappa_h = (\kappa^2 - m^2)^{1/2}$, then with mV_0 small as above, we get instability in (13.11) if

$$\kappa_c^2 \kappa_h^2 > \kappa^4 \quad \implies \quad 1 - \left(1 - \frac{4m^2}{\kappa_c^2}\right)^{1/2} < \frac{2\kappa_h}{\kappa_c} < 1 + \left(1 - \frac{4m^2}{\kappa_c^2}\right)^{1/2}, \quad (13.15)$$

and $\kappa_c^2 > 4m^2$, so that for instability, $\kappa_c \gg 4\pi/H$ with κ_c given by (12.13).

Spheroidal shapes: We can repeat the above analysis for organisms with an elliptical profile. If we have a prolate spheroid with axes a and b , and define an eccentricity

$$\alpha_0 = \frac{a^2 - b^2}{a^2 + b^2}, \quad (13.16)$$

then it is not solely the vorticity which appears in (12.2). As shown by Pedley *et al* (1988), the RHS of (13.11) should then be modified to

$$\beta(\kappa^2 - m^2) [(1 - \alpha_0) + 2\alpha_0 m^2/\kappa^2]. \quad (13.17)$$

For z -independent perturbations, the new critical wave-number is

$$\kappa_c = [\beta/(\nu D)]^{1/2} (1 - \alpha_0)^{1/2}. \quad (13.18)$$

We can show that if $m \neq 0$, there are instabilities with $\kappa > \kappa_c$ as defined by (13.18) provided $\alpha_0 > 1/3$. Furthermore these can be the most unstable disturbances.