

# COLLECTIVE HYDRODYNAMICS OF SWIMMING MICROORGANISMS

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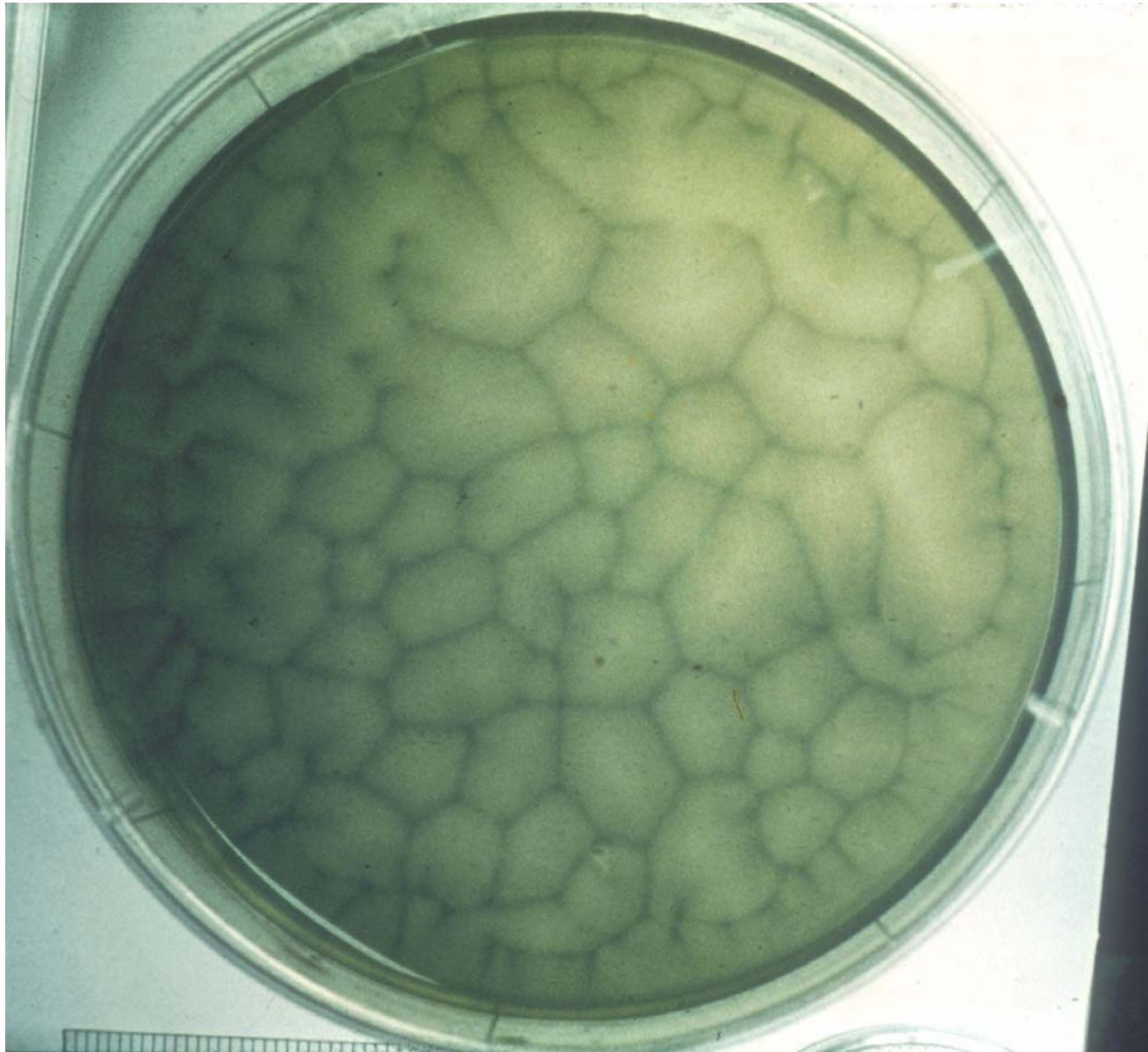
# OUTLINE

## 1 Bioconvection

- Mechanisms
- Model
- Instability of a uniform suspension
- Predictions for algae, bacteria, spermatozoa

## 2 Concentrated suspensions

- Coherent structures
- Simulations
- Pairwise interactions of squirmers
- Diffusion or aggregation?



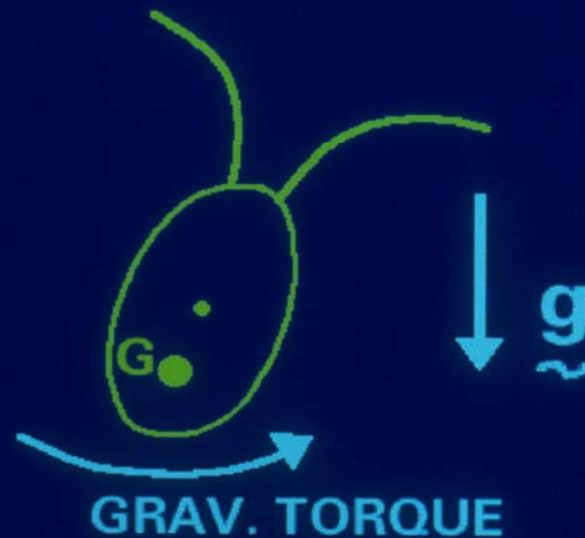


## MECHANISM I

**Shallow layer: upswimming of cells that are slightly denser than water generates an unstable density stratification which leads to overturning (cf. Rayleigh – Bénard)**

## MECHANISM II

Certain algae (at least) swim upwards because they are **bottom-heavy**





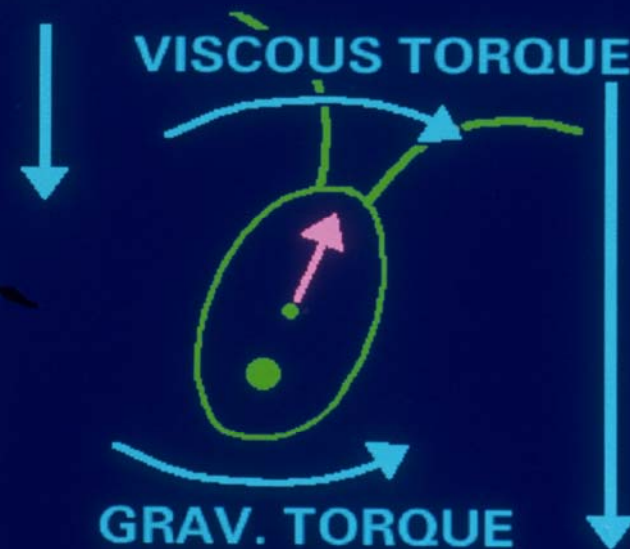
## MECHANISM II

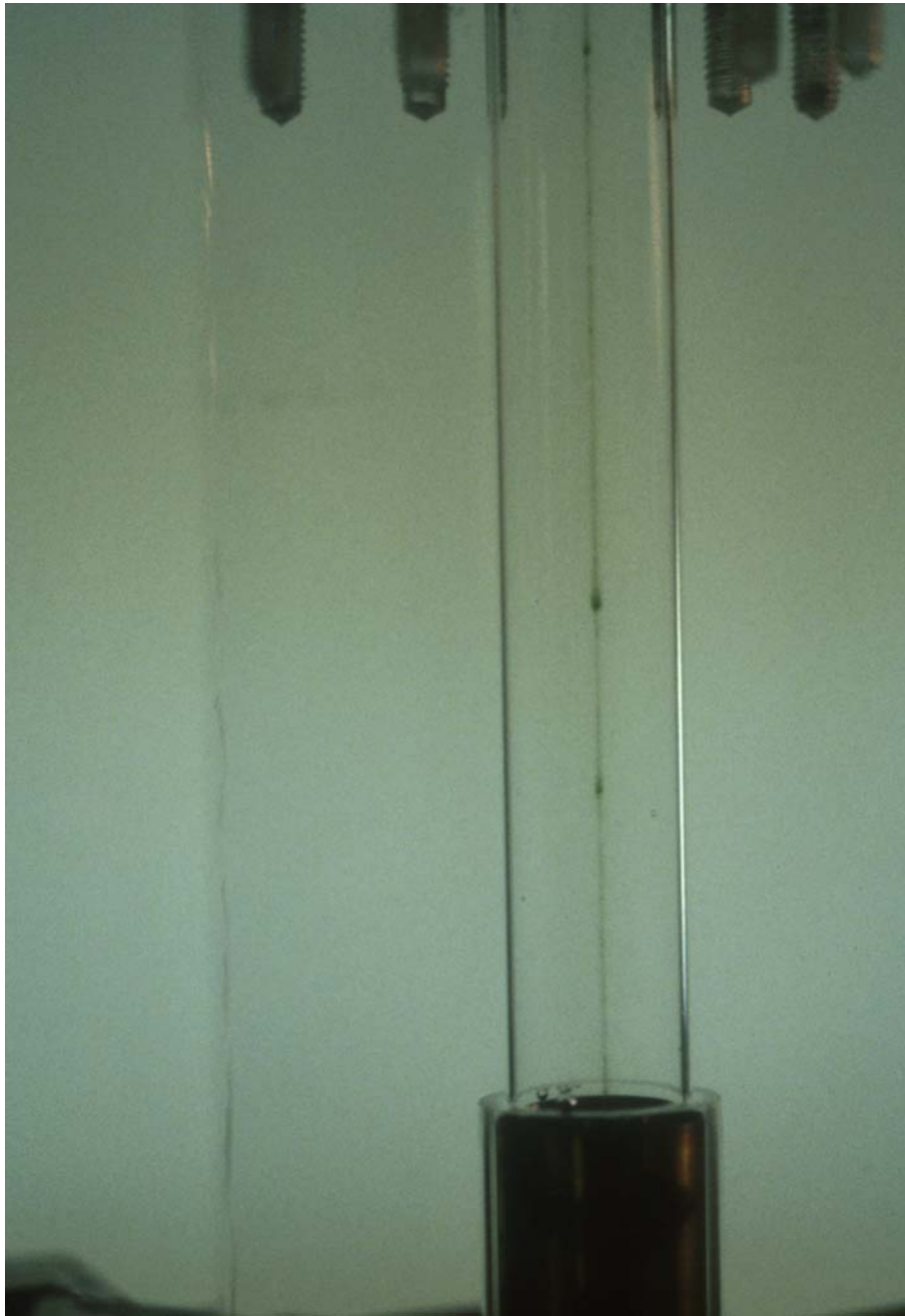
### CONSEQUENCE

When placed in a vertical shear flow the balance between viscous and gravitational torques means that such cells will swim (on average) at an angle to the vertical

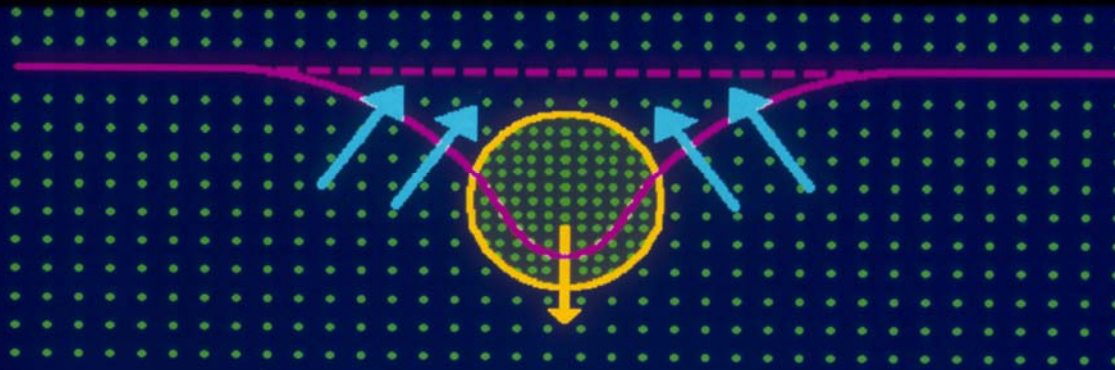
- GYROTAXIS
- FOCUSSING (in pipe flow)

It follows that a uniform suspension is unstable, which leads to bottom standing plumes





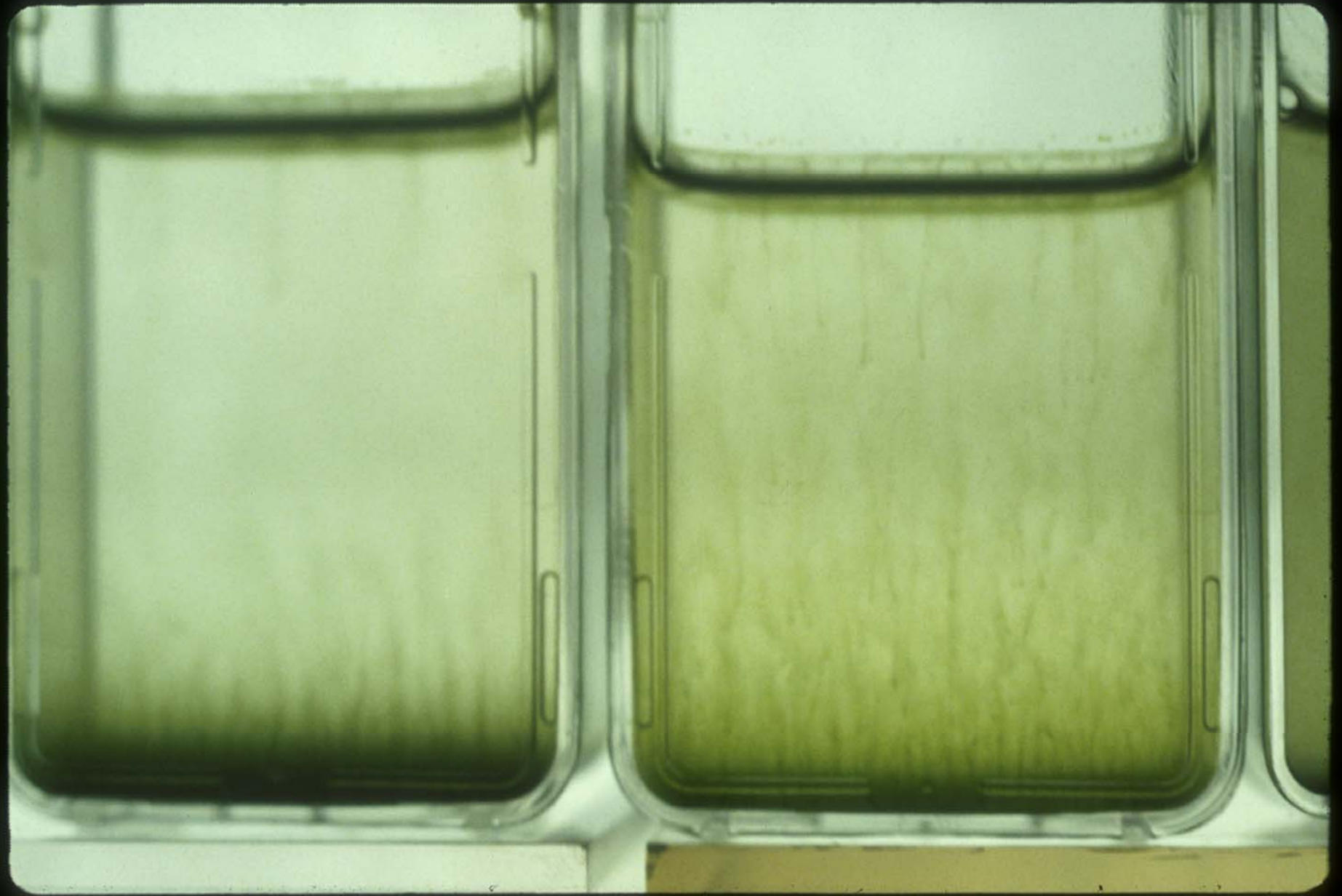




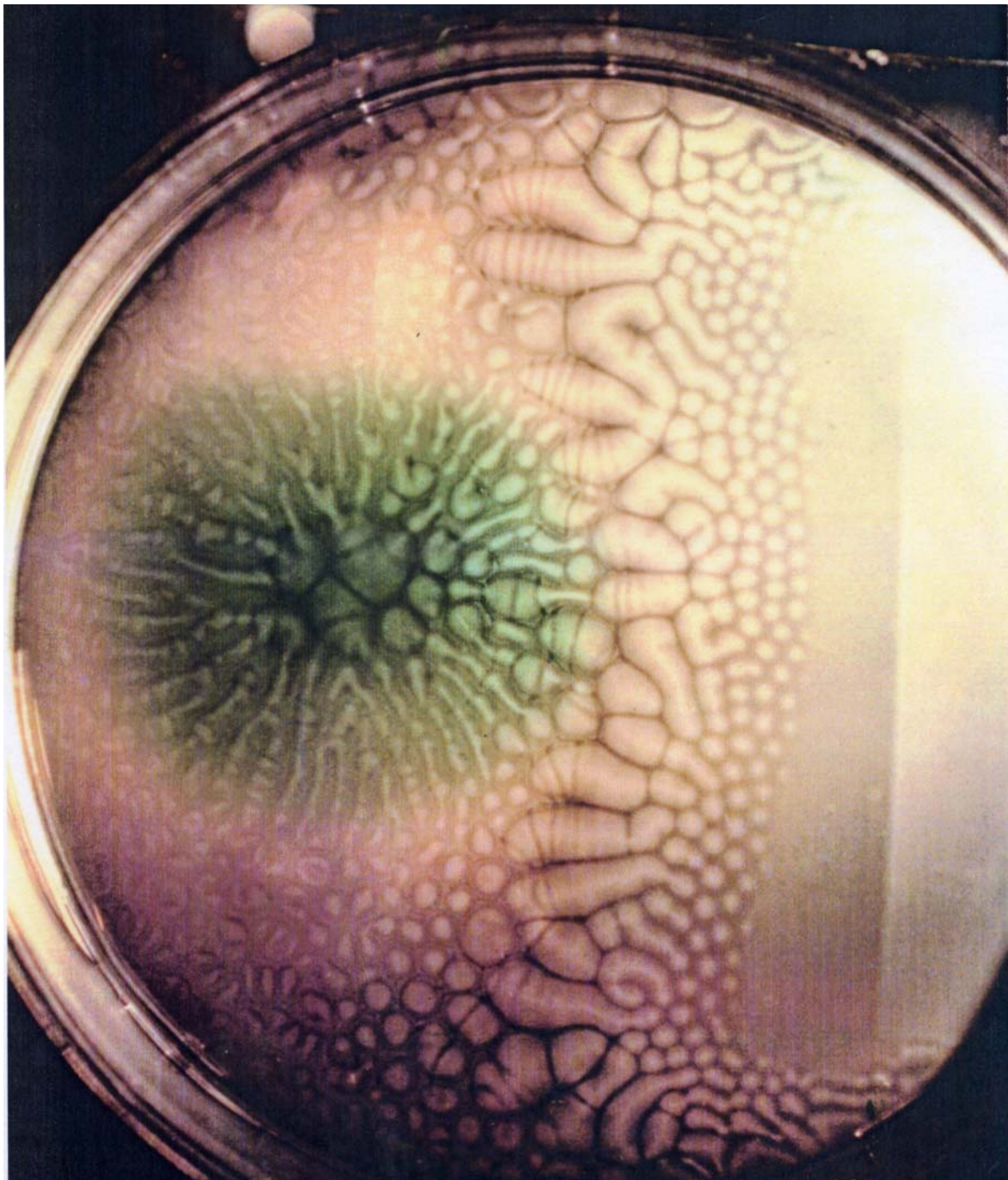
Suppose a natural fluctuation causes a **blob** of fluid to have a larger **cell concentration** than its surroundings. This **blob**, being denser, will fall, generating a velocity profile with shear.

Gyrotaxis will then cause more cells to be focussed into the wake of the blob.

### Gyrotactic Instability





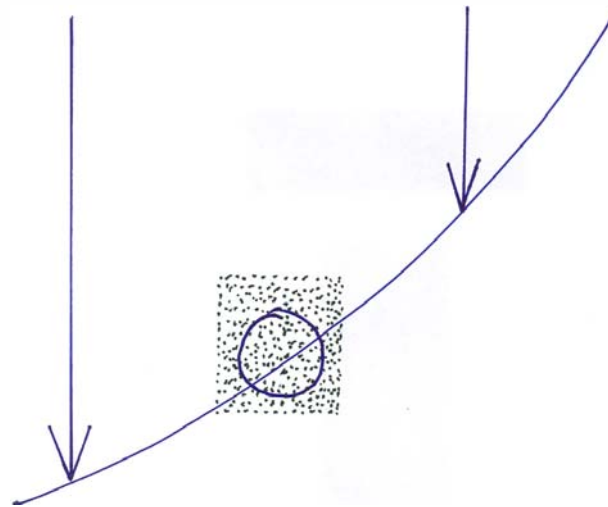


## CONTINUUM MODEL for the suspension as a whole

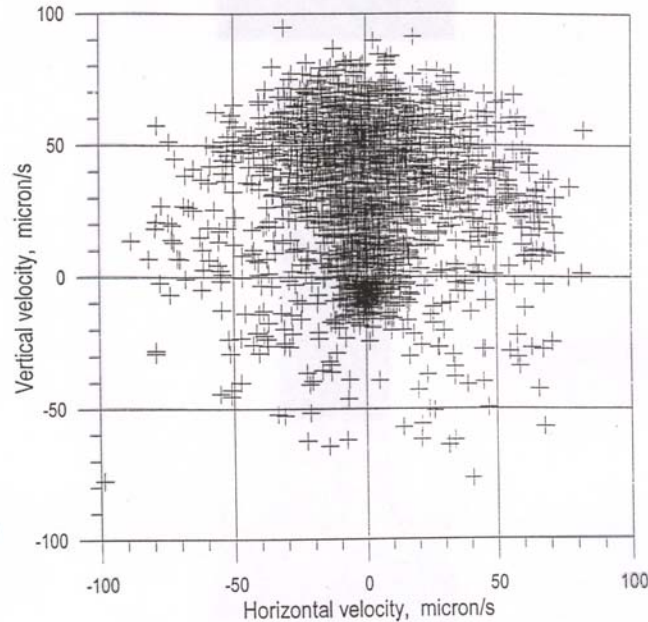
Assumes every volume element, small compared with the scale of the flow, contains very many cells.

Thus variables can be represented by their averages over the volume element.

Averaging not necessarily easy because cells swim in random directions.



# Particle Tracking (projection)



The result of measuring the velocities. Each cross corresponds to velocity detected. Number of tracks analysed is 359, number of points displayed is 2168. Dense cloud below the origin corresponds to sedimenting particles.

[Vladimirov, V.A. et al \(2000\) Marine & Freshwater Res. 51: 589-600.](#)

# Cell Conservation

$$\frac{Dn}{Dt} = -\nabla \cdot (nV_c + J_r)$$

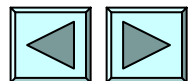
[+ birth, death, etc]

where

$V_c$  = mean cell swimming velocity,

$J_r$  = flux due to random cell swimming (chemokinesis) [=  $-D \cdot \nabla n$  ?]

Both consequences of cell swimming, directed and random respectively





# Cell Conservation Equation

$$\frac{\partial n}{\partial t} = -\nabla \cdot \left[ \underbrace{n(\mathbf{u} + \mathbf{V}_c)}_{\text{Swimming}} - \underbrace{\mathbf{D} \cdot \nabla n}_{\text{diffusion}} \right]$$

The random swimming behaviour can be quantified in terms of a probability density function  $f(\mathbf{p})$  for the cell swimming direction  $\mathbf{p}$  [and, in principle, another one for swimming speed  $V_s$ ]. Then ensemble averages are defined by

$$\langle \dots \rangle = \int \int \dots f(\mathbf{p}) d^2 \mathbf{p}$$

where the integral is taken over the unit sphere in  $\mathbf{p}$ -space.

Thus  $\mathbf{V}_c = \langle V_s \mathbf{p} \rangle = \bar{V}_s \langle \mathbf{p} \rangle$

But what is  $f(\mathbf{p})$  ?

And how do we calculate  $\mathbf{D}$  ?

# Rational model (?)

P&K (JFM, 212, 155-182, 1990)

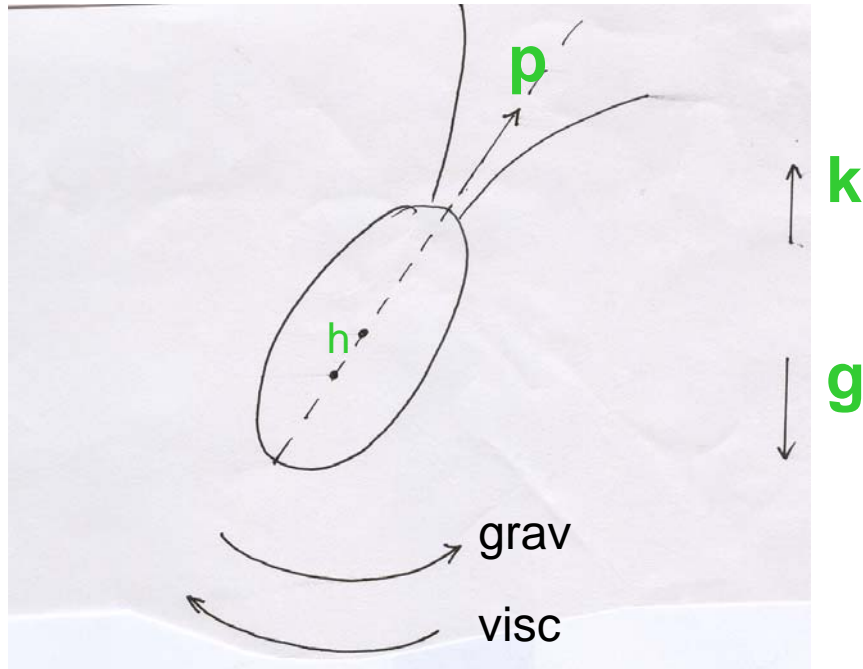
Intrinsic randomizing influences are balanced by the tendency to return to  $\hat{P}$ ;  $f(\mathbf{p})$  satisfies a Fokker-Planck equation:

$$\left( \frac{\partial f}{\partial t} + \right) \nabla_{\mathbf{p}} \cdot (\dot{\mathbf{p}} f) = D_r \nabla_{\mathbf{p}}^2 f$$

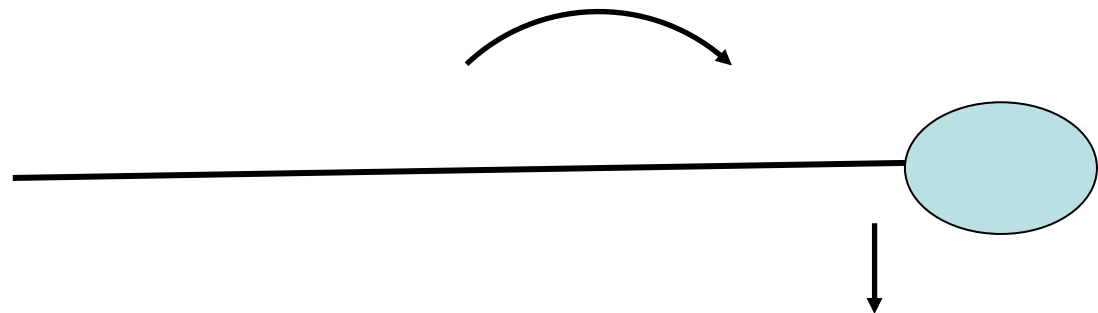
(probability conservation in  $\mathbf{p}$  - space)

(treats the suspension as analogous to a colloidal suspension subject to **Brownian rotation**)

Bottom heavy algae will rotate as a result of the torque balance



But note that sedimenting cells with uniform density but asymmetric shape will also rotate (e.g. spermatozoa)



(Katz & Pedrotti 1977; Roberts & Deacon 2002)

## Torque balance for algae

$$\dot{\mathbf{p}} + [(\mathbf{u} + \mathbf{v}) \cdot \nabla] \mathbf{p} = \beta [\mathbf{k} - (\mathbf{k} \cdot \mathbf{p}) \mathbf{p}] + \frac{1}{2} \boldsymbol{\omega} \wedge \mathbf{p} \\ + \alpha_o \mathbf{p} \cdot \mathbf{E} \cdot (\mathbf{I} - \mathbf{p} \mathbf{p}) - 2D_R \mathbf{p}$$

where  $\mathbf{u}$  = fluid velocity  
 $\mathbf{v}$  = sedimentation velocity  
 $\boldsymbol{\omega}$  = vorticity  
 $\mathbf{E}$  = strain-rate  
 $D_R$  = rotational diffusivity  
 $\alpha_o$  = 0 for spheres, 1 for rods  
 $\alpha_{\perp}$  = 6 for spheres  
 $\beta$  =  $\frac{\rho_c g h}{\alpha_{\perp} \mu_F}$  ;

$\beta$  is the angular velocity the cell would have if released from horizontal.

## GRAVITAXIS IN A STILL FLUID

Solving the Fokker-Planck equation gives

$$f(\mathbf{p}) = \mu e^{\lambda \mathbf{k} \cdot \mathbf{p}}$$

where

$$\lambda = 1/BD_r$$

and  $\mu$  is determined from  $\int f(\mathbf{p}) d^2\mathbf{p} = 1$

(Fisher distribution)

Compare with experiment





## Bioconvection Governing Equations (Dilute Suspension)

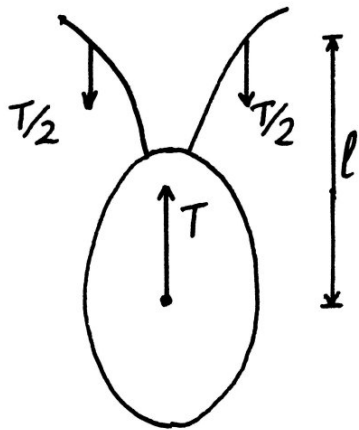
Navier-Stokes (Boussinesq)

$$\rho \frac{D\mathbf{u}}{Dt} = -\nabla P - n \rho \bar{g} \hat{\mathbf{k}} + \nabla \cdot \Sigma; \quad \nabla \cdot \mathbf{u} = 0$$

Where  $\mathbf{u}$  = bulk velocity,  $P$  = excess pressure,  $\Sigma$  =

deviatoric stress tensor,  $-g' \hat{\mathbf{k}}$  = reduced gravity,  $n$  = number density of cells.

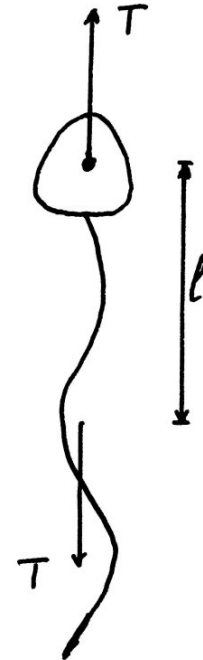
Stress includes Newtonian term plus term from intrinsic stresslets of the swimmers.



Algal cell

"Puller"

$$S = + Tl$$



Sperm



Bacterium

"Pushers"

$$S = - Tl$$

Contribution to bulk stress tensor :  $\Sigma = nS(\mathbf{pp} - \frac{1}{3} \mathbf{I})$

[Note that pushers tend to be head-heavy, not bottom-heavy]

## INSTABILITY OF A UNIFORM SUSPENSION

Assume dilute, spherical cells, isotropic cell diffusivity  $D$ .

Basic state:  $n = n_0$ ,  $\mathbf{u} = 0$ ,  $\mathbf{p} = \hat{\mathbf{k}}$ ,  $\Sigma^p = n_0 S(\hat{\mathbf{k}}\hat{\mathbf{k}} - \frac{1}{3}\mathbf{I})$

Linearised perturbation equations (primes for  $n, \mathbf{p}$  perturbations):

$$(1) \nabla \cdot \mathbf{u} = 0$$

$$(2) \partial_t \mathbf{u} = -\frac{1}{\rho} \nabla P - n' \bar{g} \hat{\mathbf{k}} + \nu \nabla^2 \mathbf{u} + \frac{S}{\rho} \left[ n' (\hat{\mathbf{k}}\hat{\mathbf{k}} - \frac{1}{3}\mathbf{I}) + n_0 (\hat{\mathbf{k}}\mathbf{p}' + \mathbf{p}'\hat{\mathbf{k}}) \right]$$

$$(3) \partial_t n' = -\nabla \cdot \left[ n_0 (\mathbf{u} + V_0 \mathbf{p}') + n' V_0 \hat{\mathbf{k}} - D \nabla n' \right]$$

$$(4) \partial_t \mathbf{p}' + V_0 (\hat{\mathbf{k}} \cdot \nabla) \mathbf{p}' = -\beta \mathbf{p}' + \frac{1}{2} \boldsymbol{\omega} \wedge \hat{\mathbf{k}} - 2 D_R \mathbf{p}'$$

( $\boldsymbol{\omega}$  = vorticity)

7 equations for 7 unknowns :  $u, v, w, P, n', p'_1, p'_2$ .

Uniform basic state means constant coefficients.

Set unknowns proportional to

$$\exp(\sigma t + i\kappa \cdot \mathbf{x}), \quad \kappa = (k, l, m).$$

Two types of mode can be found:

- (i) **Twist** Take curl of (2) and (4) and get, in dimensionless form,

$$(\sigma + \bar{\beta} + 2\bar{D}_R + i\kappa\mu)(\sigma + \kappa^2\bar{\nu}) + \bar{S}\kappa^2\mu^2 = 0$$

where  $\mu = m/\kappa = \cos\theta$ , length-scale is  $D/V_c$ , time-scale is  $D/V_c^2$

$$\text{and } \bar{\beta} = \frac{\beta D}{V_c^2}, \quad \bar{\nu} = \frac{\nu}{D}, \quad \bar{D}_R = \frac{D_R D}{V_c^2}, \quad \bar{S} = \frac{n_0 S}{2V_c^2 \rho}$$

(ii) **Splay** Take div of (2) and (4):

$$\begin{aligned} & (\sigma + \bar{\beta} + 2D_R + i\kappa\mu) (\sigma + \kappa^2 + i\kappa\mu)(\sigma + \bar{\nu}\kappa^2) \\ & - (\sigma + \kappa^2 + i\kappa\mu) \kappa^2 \bar{S} (1 - 2\mu^2) - (\hat{g} - i\bar{S}\kappa\mu) \kappa^2 (1 - \mu^2) = 0 \end{aligned}$$

where  $\hat{g} = \frac{n_0 \bar{g} D}{2V_c^3}$ .

# PARAMETER VALUES

	C nivalis	B subtilis (upswimming)	B subtilis (sedimenting)	Spermatozoa (sedimenting)
$\bar{\beta}$	0.2	$5 \times 10^{-3}$ ?	$-1.4 \times 10^{-3}$	-0.02
$\bar{S}$	1.4	-3400	-3400	$-1.2 \times 10^{-5} n_0$
$\bar{g}$	11	20	-37	$-6.9 \times 10^{-7} n_0$
$\bar{v}$	250	2750	2750	1200

Note:  $\bar{v} \gg 1$

Also 
$$\bar{D}_R = \frac{D_R D}{V_C^2} = 1/6$$

Hence  $\bar{\beta} + 2\bar{D}_R > 0$  in all cases



$$\bar{\nu} \gg 1 \Rightarrow \text{(i) } \sigma \approx -(\bar{\beta} + 2\bar{D}_R + \frac{\bar{S}}{\bar{\nu}}\mu^2 + i\kappa\mu)$$

$$\kappa = 0(1)$$

STABLE for  $\bar{\beta} > 0, \bar{S} > 0$ , i.e. for *C.nivalis*

(so not important that this mode was ignored by Pedley, Hill and Kessler (1988): PHK)

but UNSTABLE if  $\bar{\beta} + 2\bar{D}_R \leq 0$  or  $\bar{S}$  is sufficiently negative (pushers like *B.subtilis*)

$$\text{i.e. } \frac{\bar{S}}{\bar{\nu}} < -\frac{1}{3}$$

That instability was first noted by Simha & Ramaswamy (2002): SR

(ii)  $\bar{\nu} \gg 1$  gives a quadratic equation for  $\sigma$ .

$$(\sigma + \kappa^2 + i\kappa\mu) \left[ \sigma + \bar{\beta} + 2\bar{D}_R + i\kappa\mu - \frac{\bar{S}}{\bar{\nu}}(1 - 2\mu^2) \right] - \left( \frac{\hat{g}}{\bar{\nu}} - i\frac{\bar{S}}{\bar{\nu}}\kappa\mu \right) (1 - \mu^2) = 0$$

Consider small  $\kappa$  (but not so small that  $\bar{\nu}\kappa^2$  is not much larger than  $\sigma$ ):

$$\sigma^2 + \sigma \left[ \bar{\beta} - \frac{\bar{S}}{\bar{\nu}}(1 - 2\mu^2) \right] - \frac{\hat{g}}{\bar{\nu}}(1 - \mu^2) = 0$$

where  $\bar{\beta} = \bar{\beta} + 2\bar{D}_R$

(a)  $\bar{S} = 0$  (no particle stress)

$$\text{Then } 2\sigma = -\bar{\beta} \pm \sqrt{\bar{\beta}^2 + \frac{4\hat{g}}{\bar{\nu}}(1 - \mu^2)}$$

One root is positive if  $\hat{g} > 0$  ;  
this is the gyrotactic instability found by PHK

(b)  $\bar{S} \neq 0, \hat{g} = 0$  (no buoyancy)

$$\text{Then } \sigma = -\bar{\beta} + \frac{\bar{S}}{\nu}(1 - 2\mu^2)$$

which is negative (stability) for all  $\mu$  if  $\bar{\beta} > \frac{\bar{S}}{\nu}$ , so gyrotaxis wins over particle stresses (e.g. *C.nivalis*). However, if  $\bar{\beta} \leq 0$ , then there exist values of  $\mu$  for which  $\sigma < 0$  whatever the sign of  $\bar{S}$ . This follows from the factor  $(1 - 2\mu^2)$  and was the main result of SR.

In general, if  $0 < \bar{\beta} < \frac{|\bar{S}|}{\nu}$ , then instability will be found.

[Note: if  $\bar{\beta} = 0$ , there needs to be some other reason for cells to swim in the same direction in the basic state].

But, if we do not ignore the  $i\kappa\mu$  term the equation for  $\sigma$  becomes

$$\sigma^2 + \sigma \left[ \bar{\beta} - \frac{\bar{S}}{\bar{\nu}} (1 - 2\mu^2) \right] - \frac{\hat{g}}{\bar{\nu}} (1 - \mu^2) + i\bar{S}\kappa\mu (1 - \mu^2) = 0$$

The last, imaginary, term means that there is a (weak) instability whatever the sign of the coefficient of  $\sigma$ .

More detailed analysis shows that the unstable mode is rather different for pullers and pushers, the former giving greater growth rate.

This new instability arises from the fact that the particle stress is non-zero in the basic state.

Predictions for downswimming bacteria or spermatozoa

A uniform suspension will be unstable if

$$\frac{\bar{S}}{\bar{v}} > \bar{\beta} \quad \text{and} \quad \mu^2 > 1/2$$

which requires a sufficiently large cell concentration.

For *B subtilis* this would be about  
 $10^9$  cells per ml



## Collective behaviour:

Bioconvection - bottom-heavy algae  
(*Chlamydomonas nivalis*)

Bioconvection - oxytactic bacteria  
(*Bacillus subtilis*)

“Whirls and jets” - bacteria, in 3D or 2D configurations

[\(Ray Goldstein's movie\)](#)

Question - can the observed behaviour of the bacteria be explained in terms of hydrodynamic interactions alone, not chemical or other 'sensory' signals?



## Recent modelling of collective behaviour of small swimmers:

J-P Hernandez-Ortiz, C G Stoltz & M D Graham

Transport and collective dynamics in suspensions of confined swimming particles (PRL 95, 204501, 2005)

\* D Saintillan & M Shelley

Orientalional order and instabilities in suspensions of self-locomoting rods (PRL 99, 058102, 2007)

T Ishikawa, M P Simmonds & T J Pedley

Hydrodynamic interaction of two swimming model micro-organisms (J Fluid Mech, 568:119-160, 2006)

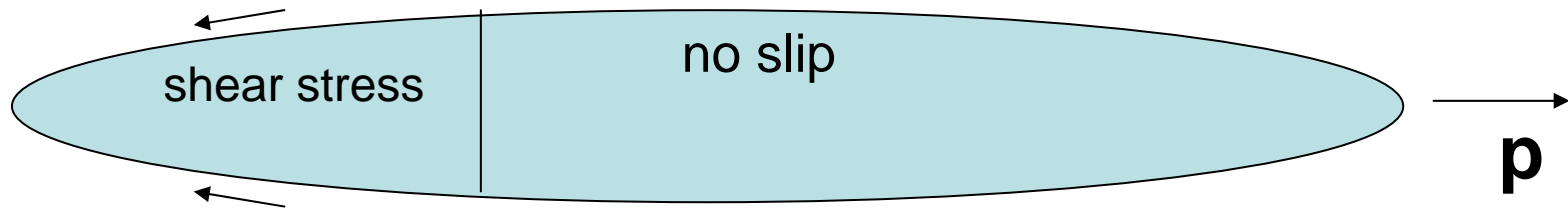
T Ishikawa & T J Pedley

- The rheology of a semi-dilute suspension of swimming model micro-organisms (J Fluid Mech, 2007)

- Diffusion of swimming model micro-organisms in a dilute suspension (J Fluid Mech, 2007)

# Saintillan & Shelley

Model the organism as a long prolate spheroid, with a given tangential shear stress over part of the surface, the rear for a pusher, the front for a puller. An “elongated squirmer”.



They use resistive force theory, which ignores near-field hydrodynamic interactions, and simulate a 3D (fairly shallow) suspension with periodic boundary conditions. (They state that putting in the near-field interactions makes little difference.)

Also, pushers tend to align with neighbours; pullers don't.

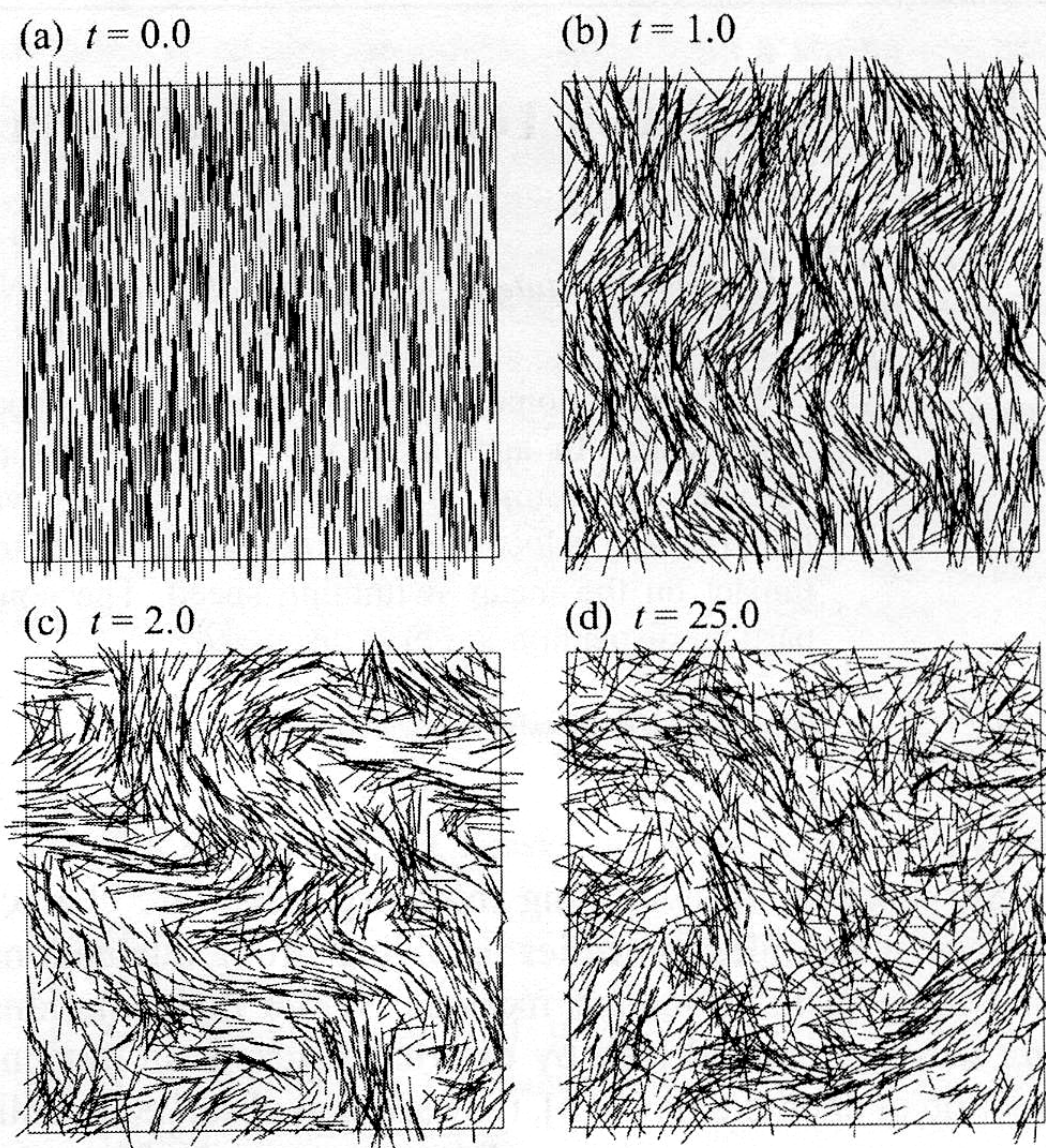


FIG. 1. Orientational instability in a polar nematic suspension of pushers, at an effective volume fraction of  $n(L/2)^3 = 1.0$ . The figure shows a region of dimensions  $10 \times 10 \times 3$  (in units of particle length) containing 2500 particles at different stages of the instability (a)–(d).

**Fluid dynamical interaction of two  
swimming model micro-organisms**

T. Ishikawa<sup>\*1</sup> and T. J. Pedley<sup>\*2</sup>

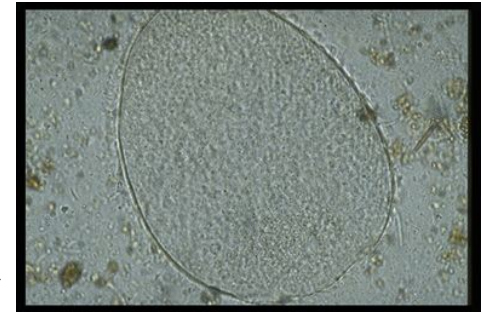
<sup>\*1</sup> Tohoku University, Sendai, Japan

<sup>\*2</sup> University of Cambridge, UK

## 2. Modelling a micro-organism

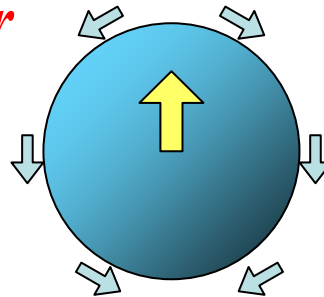
### Envelope model

Ciliate



The model micro-organism will be assumed to propel itself by generating tangential velocities on its surface.

*squirmers*



a micro-organism is modeled as a rigid sphere with squirming surface velocity

by J.R.Blake (1971)

$$u_s^\theta = \frac{B_1}{3} V_1 (\cos \theta) + B_2 V_2 (\cos \theta)$$

$$V_n = \frac{2 \sin \theta}{n(n+1)} P_n'$$

$P_n$  : Legendre polynomial of order  $n$

$B_n$  : coefficient of mode  $n$

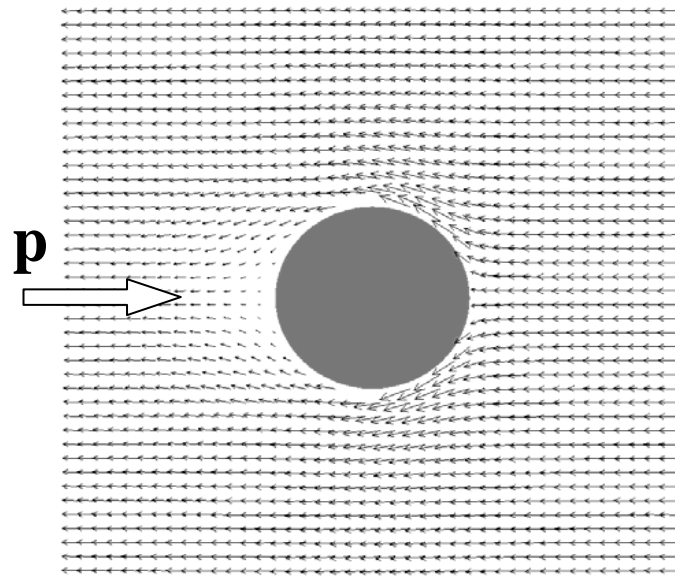
$$\beta = B2/B1$$

B1 ~ swimming speed

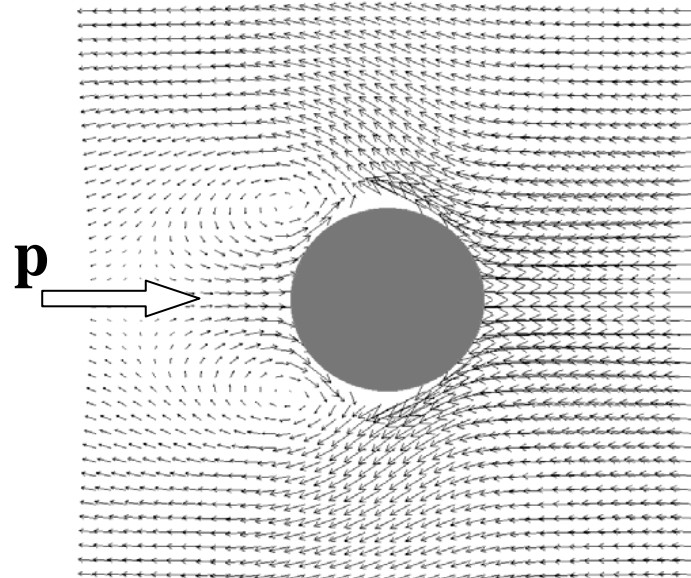
B2 ~ stresslet strength

$\beta > 1$  : puller

$\beta < 1$  : pusher



(a)  $\beta = 1$



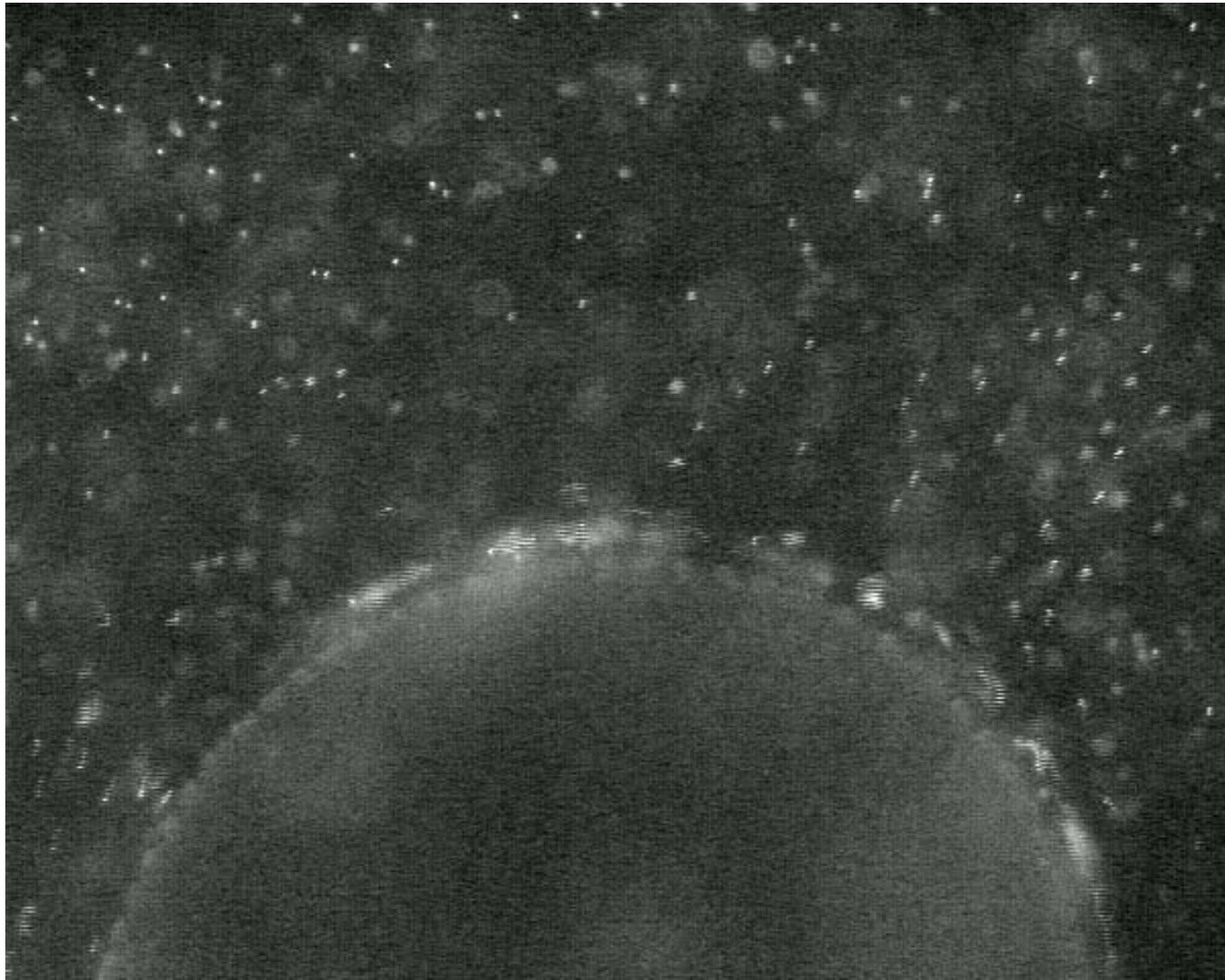
(b)  $\beta = 5$

Figure 1. Velocity vectors relative to the translational velocity vector of a squirmer. Uniform flow of speed 1.0, in dimension-free form, coming from far right. The scales of vectors in (a) and (b) are the same.

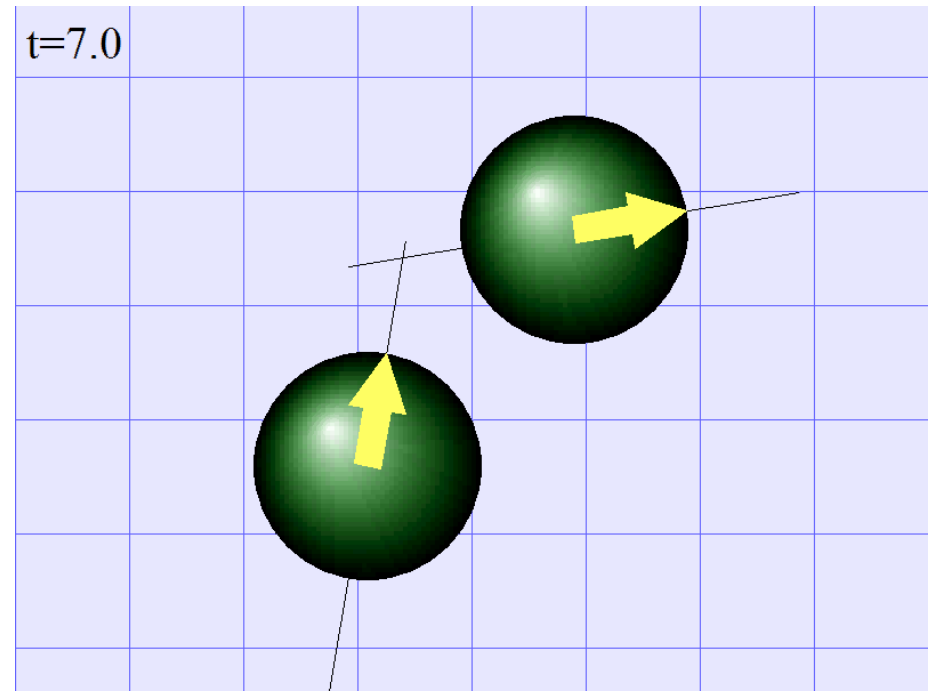


# A Closer View

Fluorescence



050504EIGHT.AVIvv

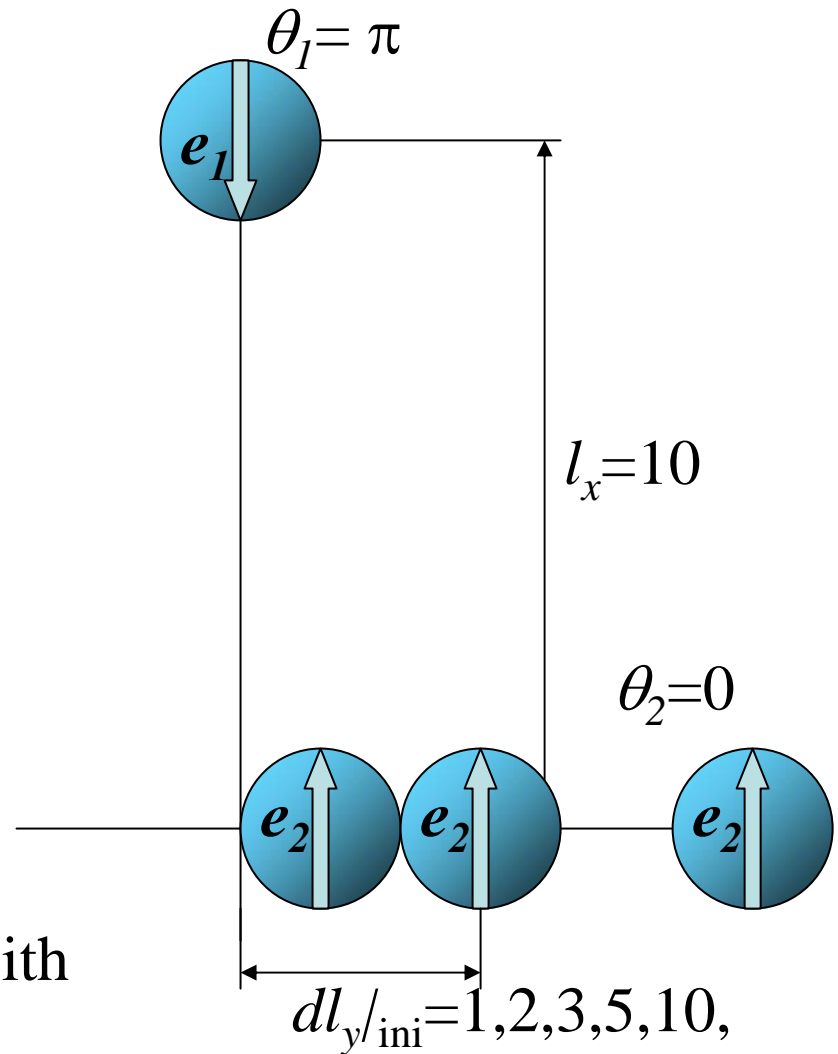


1. Interaction between two squirmers (Simulation)



Case1:  $\theta_1 = \pi$

Two squirmers are facing each other.



Sample movie with  $dl_y = 1$  and  $\beta = 5$ .

Case2:  $\theta_1 = \pi/2$

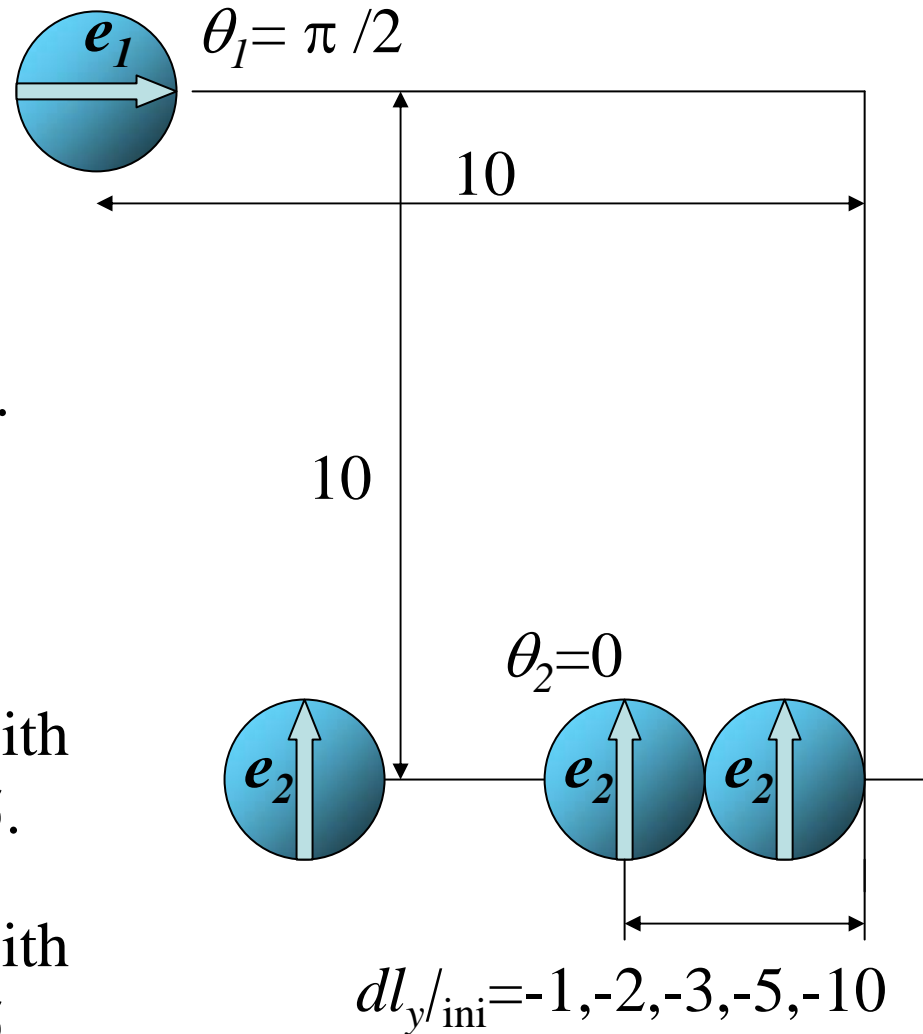
Two squirmers are crossing in a right angle.



Sample movie with  $dl_y = -1$  and  $\beta = 5$ .



Sample movie with  $dl_y = -5$  and  $\beta = 5$ .



# Numerical Results : Effect of 3D orientation

When  $\theta_1 = \pi/4$  and  $\beta = 5$ , there is a stable condition if we restrict their motion in 2D.

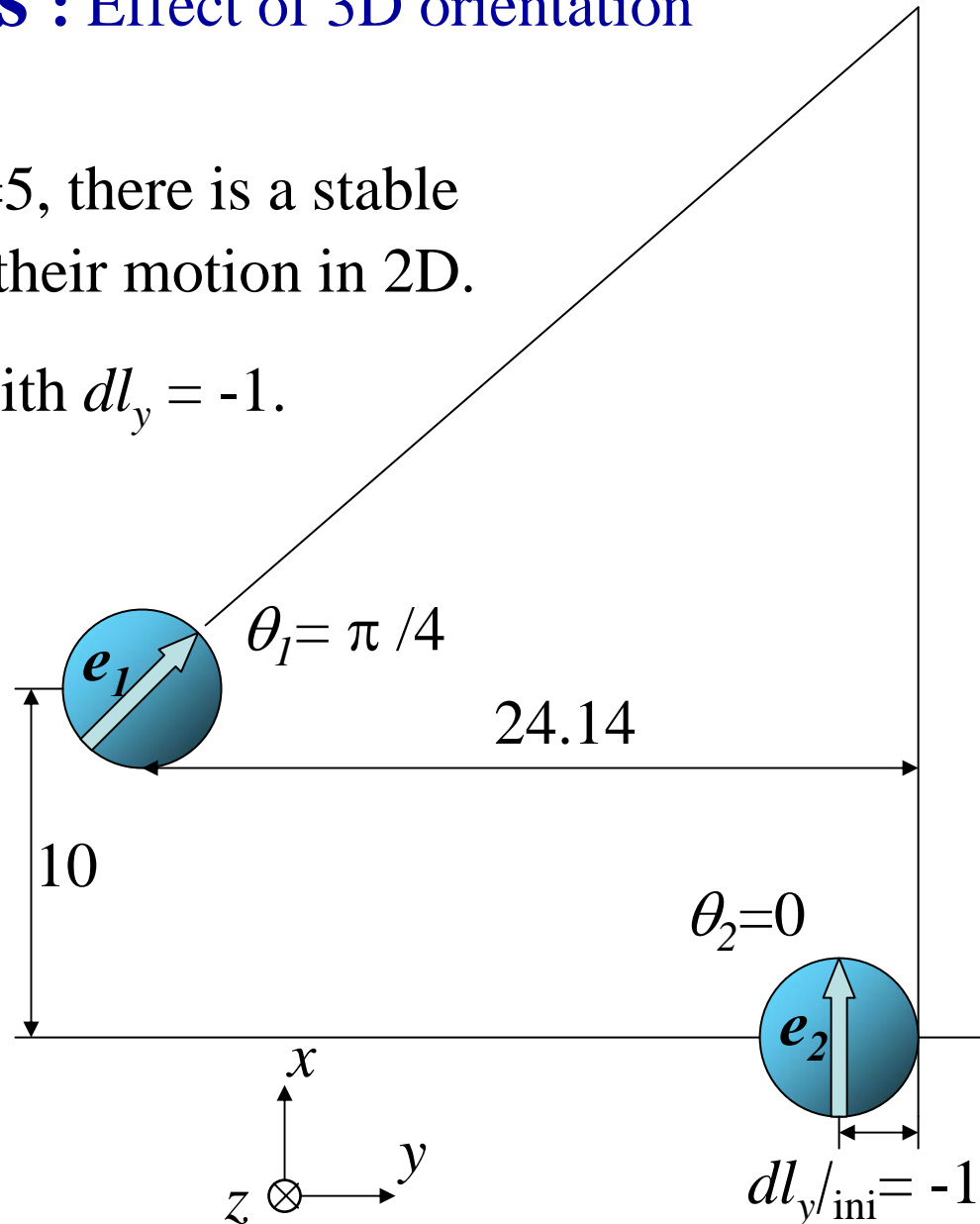


Sample movie with  $dl_y = -1$ .

In case with a gap in  $z$  direction, there is **no stable condition.**



Sample movie with  $dl_y = -1$  and  $dl_z/ini = -0.1$



- 1 Compute the motion of many interacting squirmers, using the database of pairwise interactions
- 2 Use full Stokesian Dynamics

Simulation shows aggregation in 2D, not in 3D

2D-c01

2D-c05

3D-c01

3D-c04

Bottom-heavy

2D-bh-c01

2D-bh-c05

3D-bh-c01

2D – aggregation or alignment

3D - diffusive spreading?

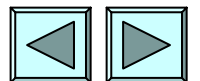
- some aggregation as well  
(see paper by J T Locsei)?

## Diffusion tensor, $\mathbf{D}$

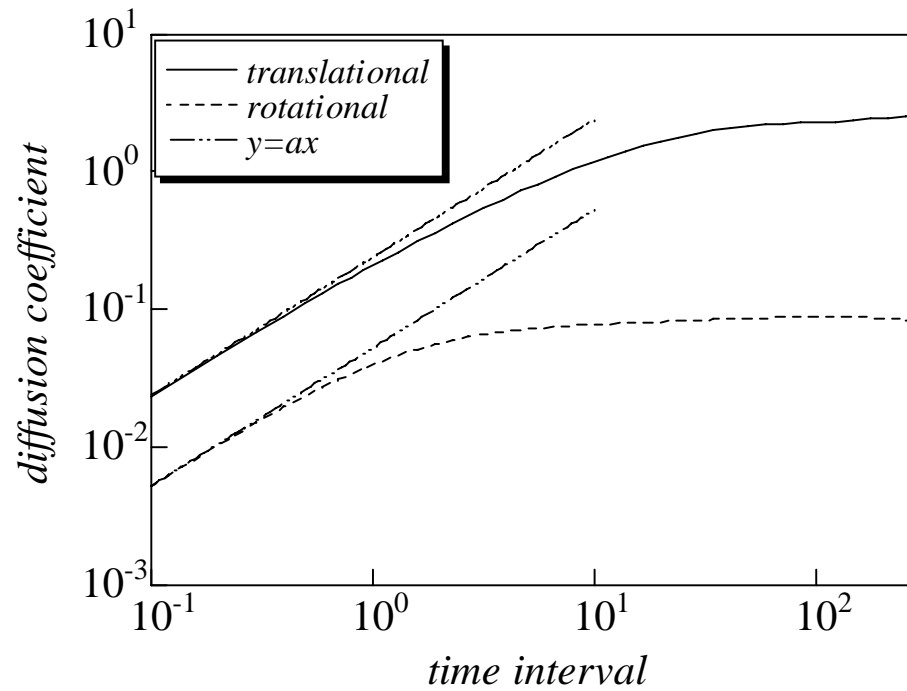
$$\begin{aligned} \mathbf{D}^T &= \int_0^\infty \langle \mathbf{V}(t)\mathbf{V}(t-t') \rangle dt' = \lim_{t \rightarrow \infty} \frac{\langle [\mathbf{r}(t+t_0) - \mathbf{r}(t_0)] [\mathbf{r}(t+t_0) - \mathbf{r}(t_0)] \rangle}{2t} \\ &\cong \frac{1}{MN} \sum_{k=1}^M \sum_{i=1}^N \frac{[\mathbf{r}_i(t+t_k) - \mathbf{r}_i(t_k)] [\mathbf{r}_i(t+t_k) - \mathbf{r}_i(t_k)]}{2t} \\ \mathbf{D}^R &= \int_0^\infty \langle \boldsymbol{\Omega}(t)\boldsymbol{\Omega}(t-t') \rangle dt' = \lim_{t \rightarrow \infty} \frac{\langle [\boldsymbol{\omega}(t+t_0) - \boldsymbol{\omega}(t_0)] [\boldsymbol{\omega}(t+t_0) - \boldsymbol{\omega}(t_0)] \rangle}{2t} \\ \boldsymbol{\omega} &= \int \boldsymbol{\Omega} dt \end{aligned}$$

In case of non-BH squirmers, their orientation is isotropic. Therefore, the diffusion tensor is also isotropic. Hence we discuss only the following quantities:

$$D^T = \frac{D_{xx}^T + D_{yy}^T + D_{zz}^T}{3}, \quad D^R = \frac{D_{xx}^R + D_{yy}^R + D_{zz}^R}{3}$$



# Diffusion tensor, $\mathbf{D}$





# SCALING

A squirmer's velocity changes in **direction**, not (much) in magnitude, due to interactions with others.

In a semi-dilute suspension such interactions can be considered as pairwise collisions, interspersed with more-or-less straight runs.

Hence model the system as molecules in a gas (kinetic theory): a random walk of runs separated by near collisions.

Speed of squirmer  $\sim U$  (constant)

Distance travelled between collisions  $\sim L_{\text{mfp}}$

Time between collisions  $\sim t_{\text{mfp}} = L_{\text{mfp}}/U$

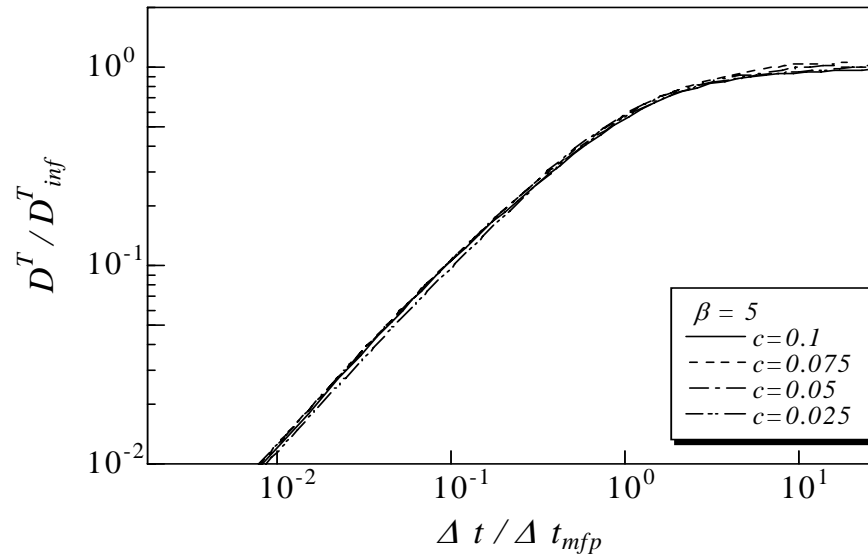
Volume swept out in this time  $V = \pi a^2 U t_{\text{mfp}}$

This will contain one other squirmer if

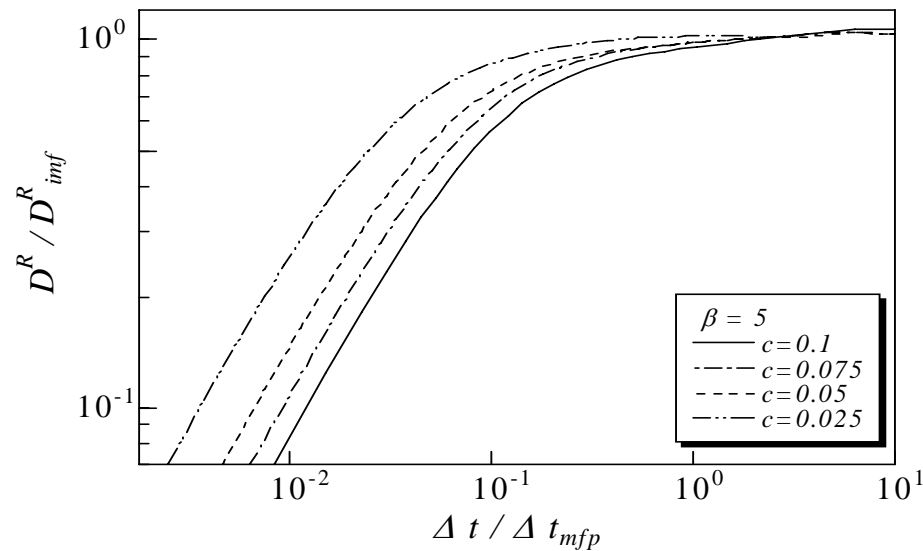
$$\text{volume fraction } c = 4 \pi a^3 / 3V$$

i.e.  $t_{\text{mfp}} = 4a/(3Uc) = 4/(3c)$  in dimensionless terms

But the time required for a significant change of **orientation**  
Will be the effective **duration** of a collision, independent of  
the number of collisions.

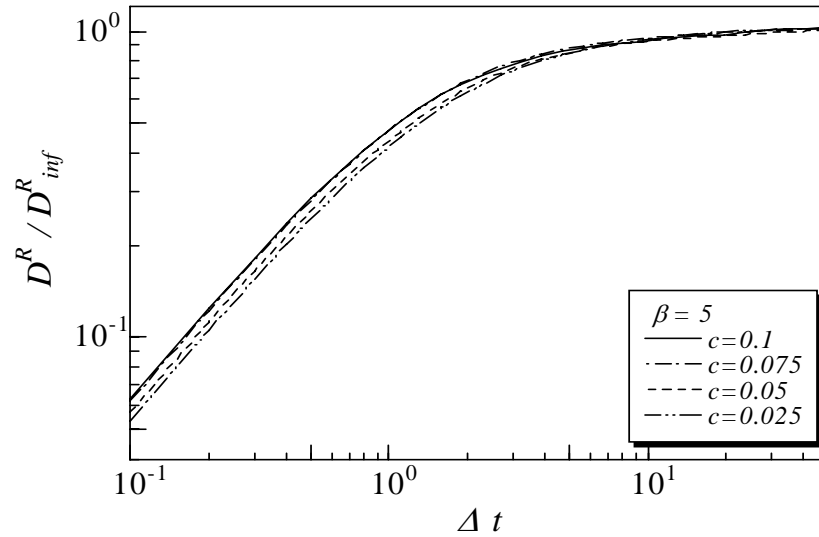


(a) translational diffusivity replotted against  $\Delta t / \Delta t_{mfp}$



(b) rotational diffusivity replotted against  $\Delta t / \Delta t_{mfp}$

Figure 9. The results of figure 6 are replotted by using different characteristic time  $\Delta t_{mfp}$  and  $\Delta t_{mps}$ . The vertical axis is normalized by  $D_{inf}$ .



(c) rotational diffusivity replotted against normal  $\Delta t$

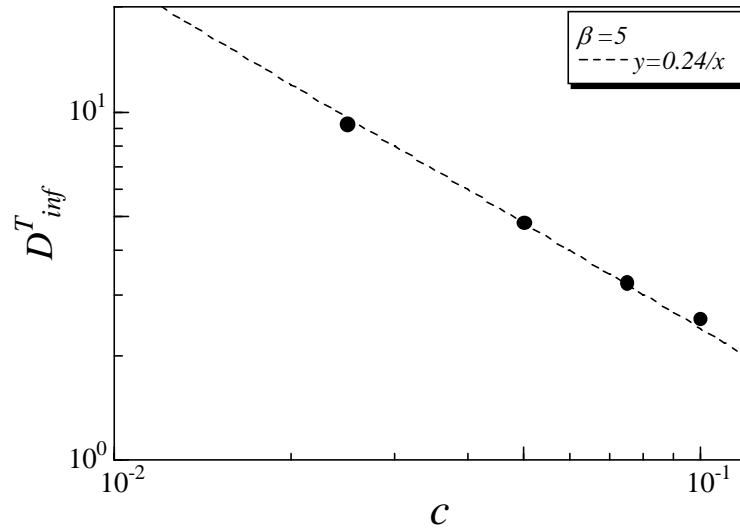
Figure 9. The results of figure 6 are replotted by using different characteristic time  $\Delta t_{mf}$ . The vertical axis is normalized by  $D_{inf}$ .

# Magnitudes?

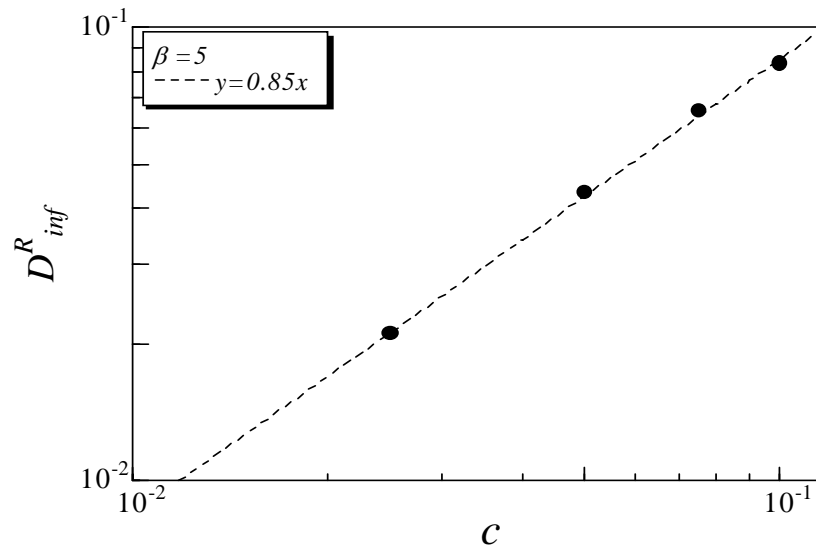
Random walk model:

$$D_{\text{Tinf}} = U L_{\text{mfp}} / 3 \sim t_{\text{mfp}} / 3 = 4/(9c)$$

$$D_{\text{Rinf}} = \frac{\langle \Delta \omega^2 \rangle}{6 t_{\text{mfp}}} \sim t_{\text{mfp}}^{-1} \sim c$$



(a) translational diffusivity



(b) rotational diffusivity

Figure 10. Correlation between  $D_{inf}$  and  $c$  ( $\beta = 5$ ).  $D_{inf}$  is the converged diffusivity after a sufficiently long time.

## Bottom-heavy squirmers ?

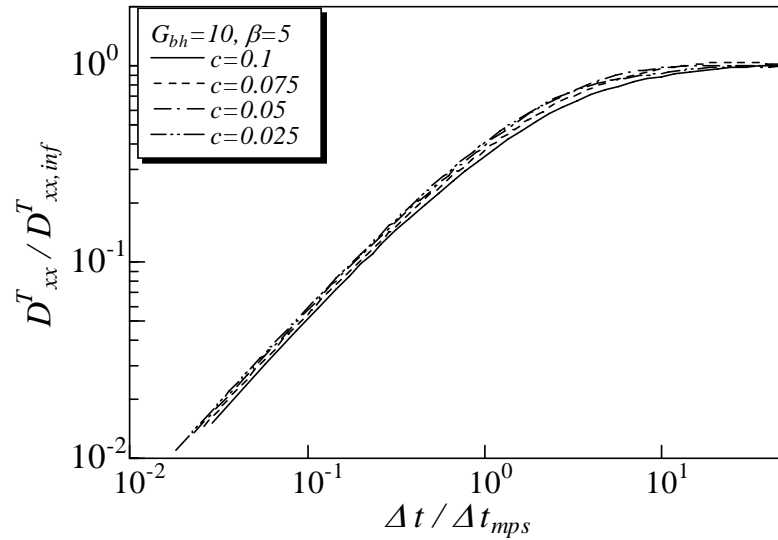
They all have a preferred swimming direction – upwards

Mean free path not significant – squirmer interaction dominated by configuration of surrounding squirmers, which changes on a length scale proportional to the particle spacing:

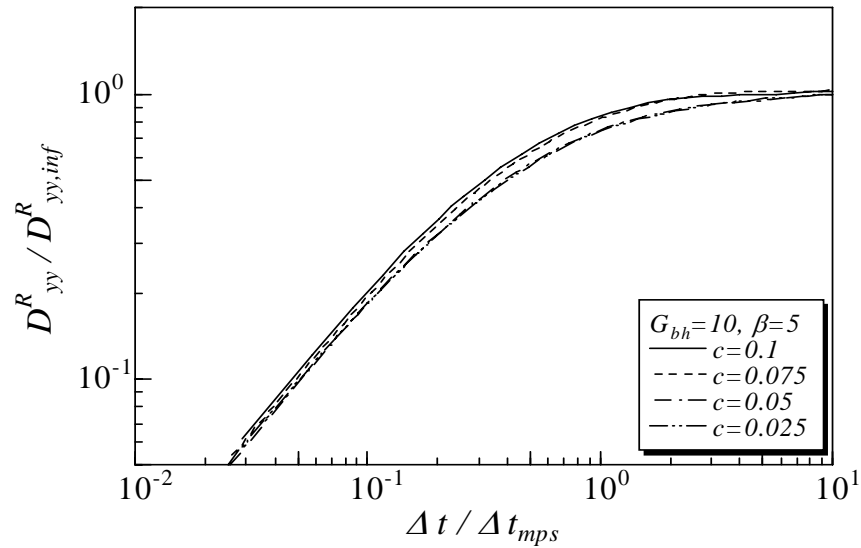
$$L_{\text{mps}} = \left( \frac{4\pi a^3}{3c} \right)^{1/3}$$

$$t_{\text{mps}} \sim (4\pi/3c)^{1/3}$$



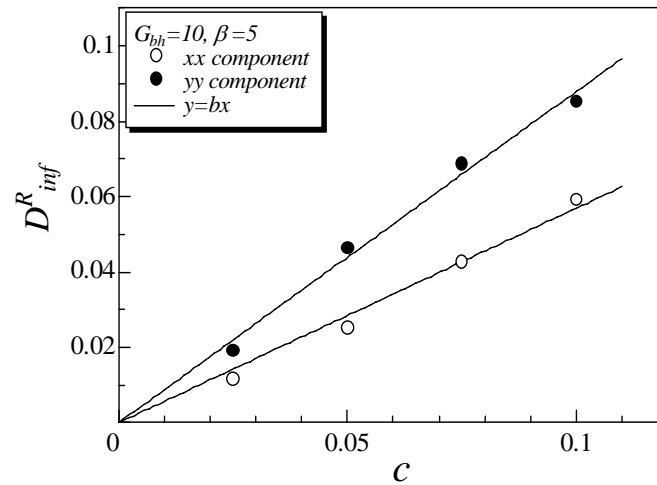


(a) translational diffusivity  $D_{xx}^T$



(b) rotational diffusivity  $D_{yy}^R$

Figure 18. The diffusivities are plotted in terms of  $\Delta t / \Delta t_{mps}$ . The vertical axis is normalized by  $D_{inf}$ .



(b) bottom-heavy squirmers ( $G_{bh} = 100$ )

Figure 21. Correlation between  $D_{inf}^R$  and  $c$  ( $G_{bh} = 100, \beta = 5$ ).  $D_{inf}^R$  is the converged rotational diffusivity after a sufficiently long time.

2D – aggregation or alignment

3D - diffusive spreading?

- some aggregation as well  
(see paper by J T Locsei)?