Reduction of Viscosity in Suspensions of Swimming Bacteria
Experiment and Theory

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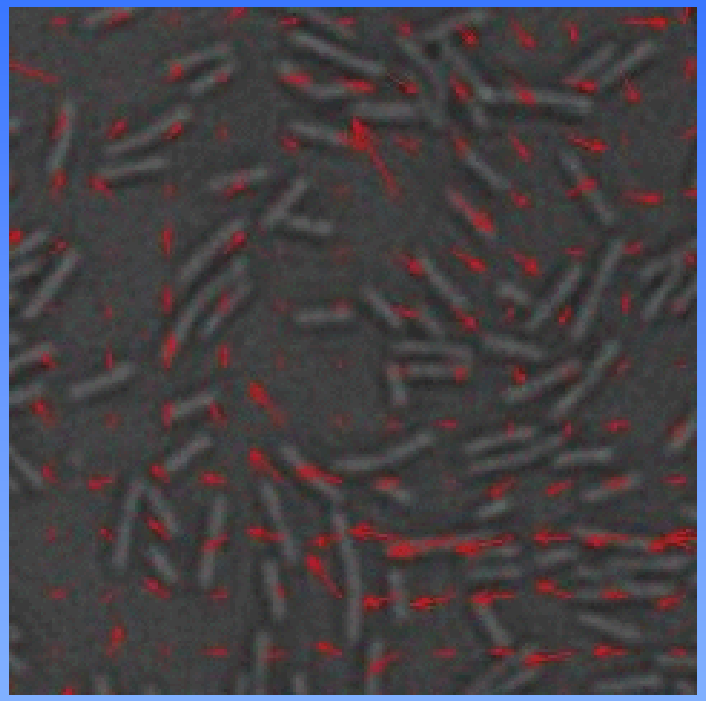

Experiment:
Andrey Sokolov, *ANL (now in Princeton)*

Theory:
Brian Haines and Shawn Rayn, *PennState*
Dmitrii Karpeev, *ANL*
Leonid Berlyand, *PennState*

Supported by US Department of Energy

Sokolov, I.A, PRL (2009), Haines et al PRE (2009), Sokolov et al, PNAS 2009

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Outline

- Experiments
  - Collective Behavior
  - Viscosity Measurements

- Theory

-Dilute Suspensions

-Simulations

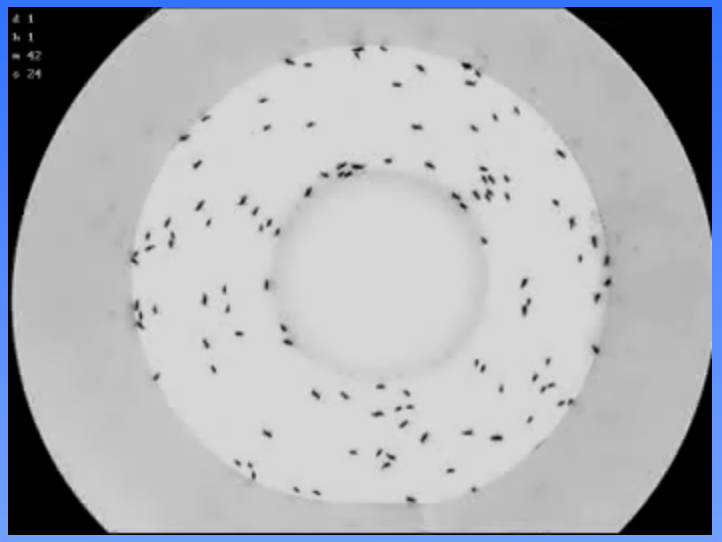
-Hydrodynamic Interactions

- Conclusions

Emergent Large-Scale Motion in Nature (or Science)

Moutons (French Sheep), 100 m

Meso-scale (marching locusts I. Couizin group), 1 m



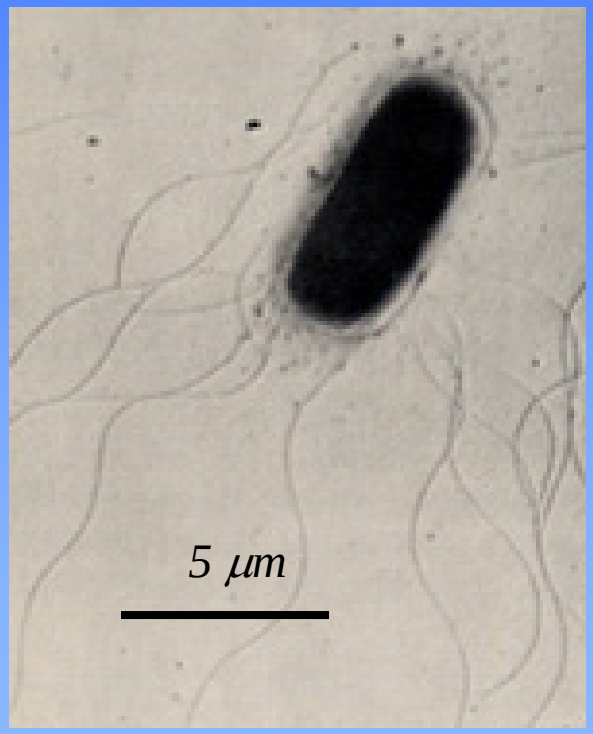
Cytoskeleton (Nedelec at al) 20 microns

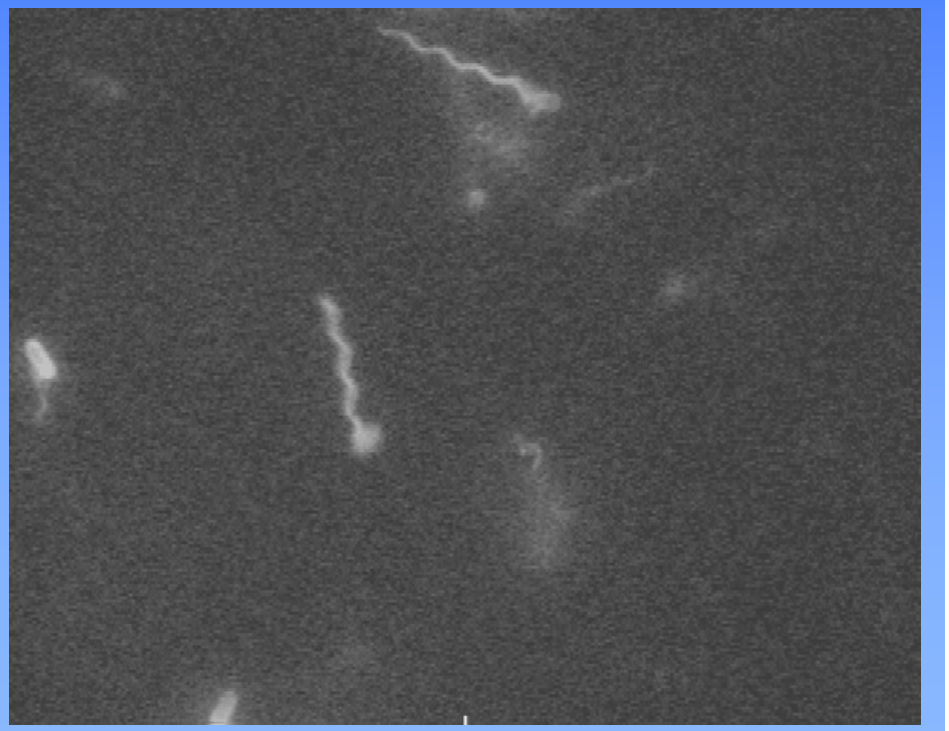
Fundamental Questions ("Non-Biologist" point of view)

- Nature of the transition to collective motion with the increase of concentration
- Role of long-range interactions (e.g. hydrodynamic) vs short-range
- Effects of activity on the rheology/materials properties

Self-Propelled BioParticles

- swimming aerobic bacteria *Bacillus Subtilis*
- length 5 μm, speed 20 μm/sec, Re=10^{-4}
- collective flows up to 100 μm/sec
- need Oxygen (oxygentaxis)
- Called pushers



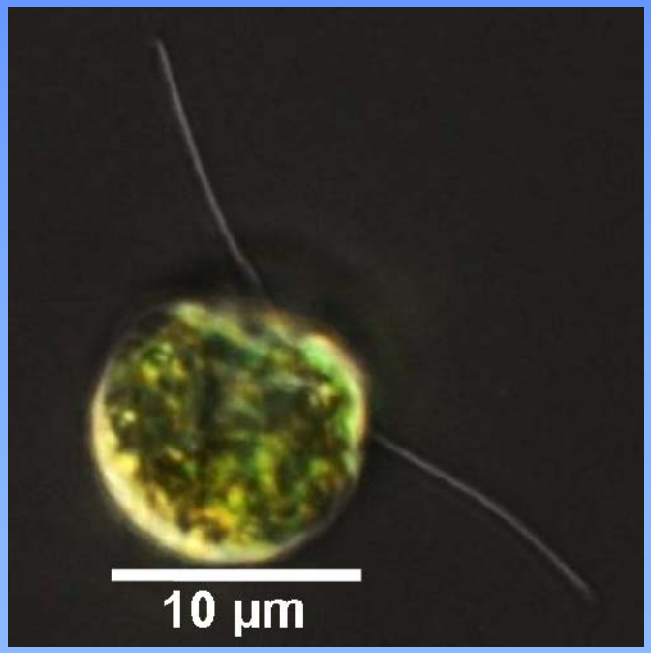


Turner, Ryu, and Berg (E. coli)

Swimming Algae

- Eukaryotic *Clamydomonas reinhardtii*
- Size: 10 μm, two flagella ~10 μm
- Swimming speed: 50-100 μm/sec
- Highly asocial animals
- Called pullers

Single Alga

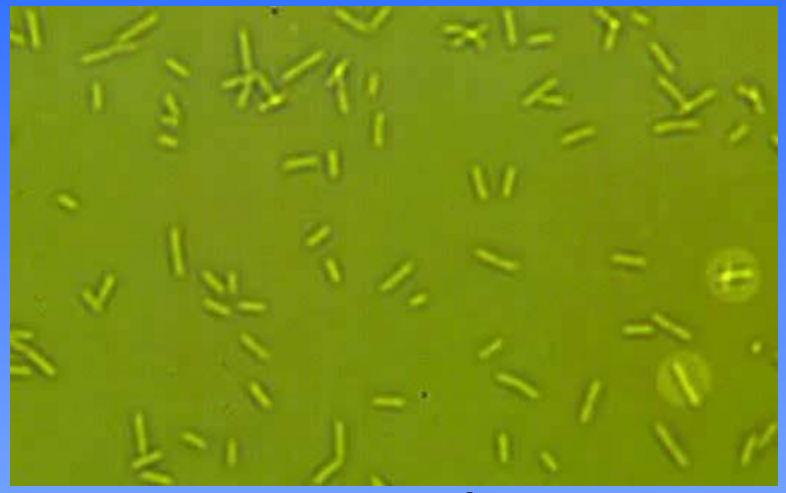


Algae Suspension

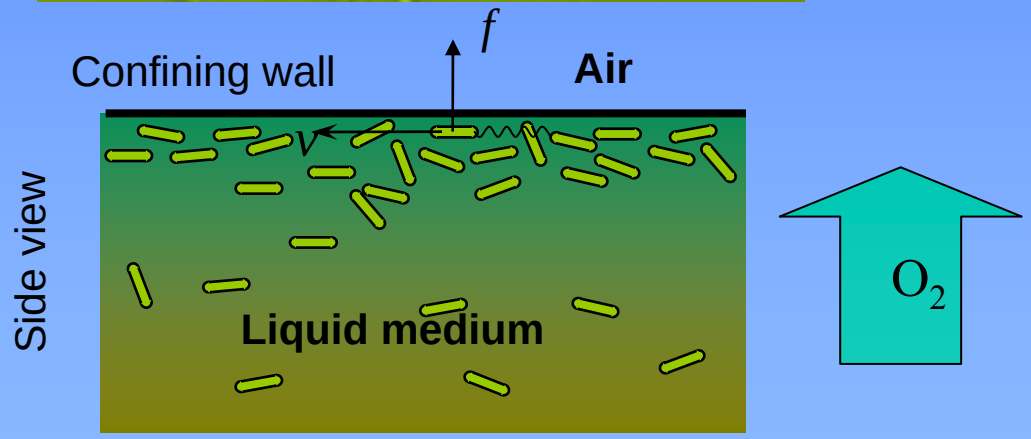
Bacillus subtilis primary behaviors

Collision of two bacteria in thin films

Top view

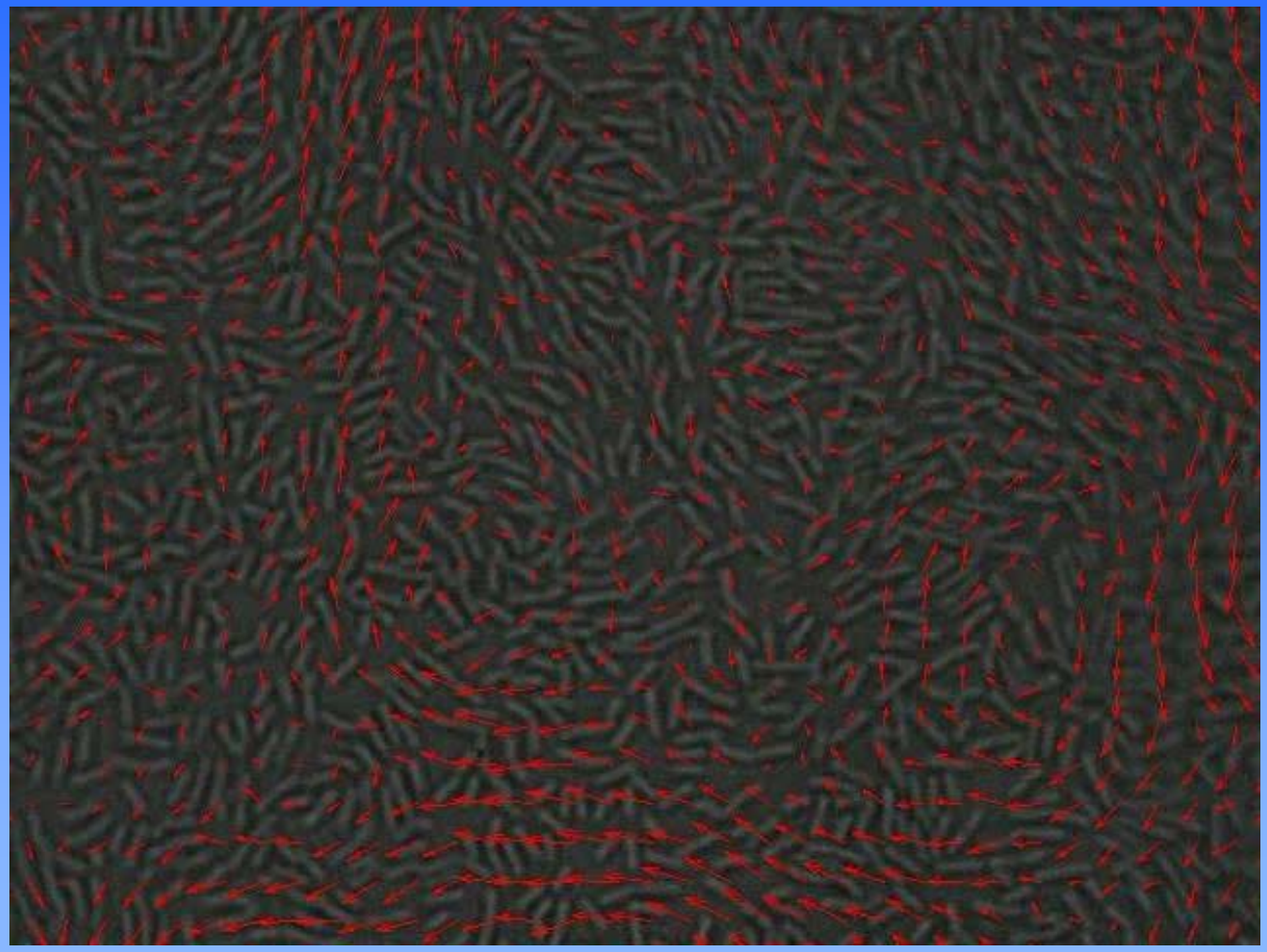


- *Excellent swimmers*
- *No tumbling*



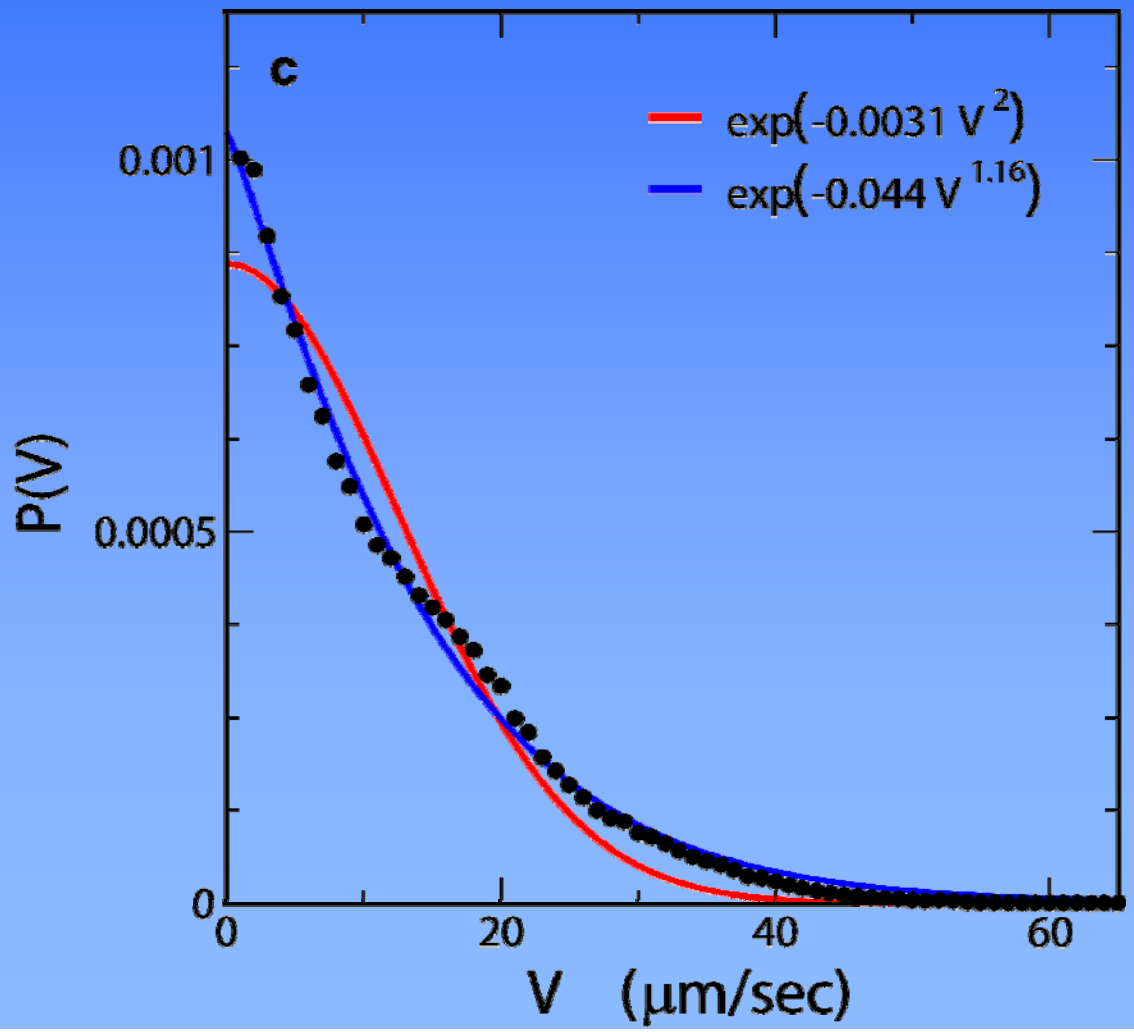
Concentration of bacteria near the surface due to gradient of dissolved Oxygen

Bacterial Turbulence



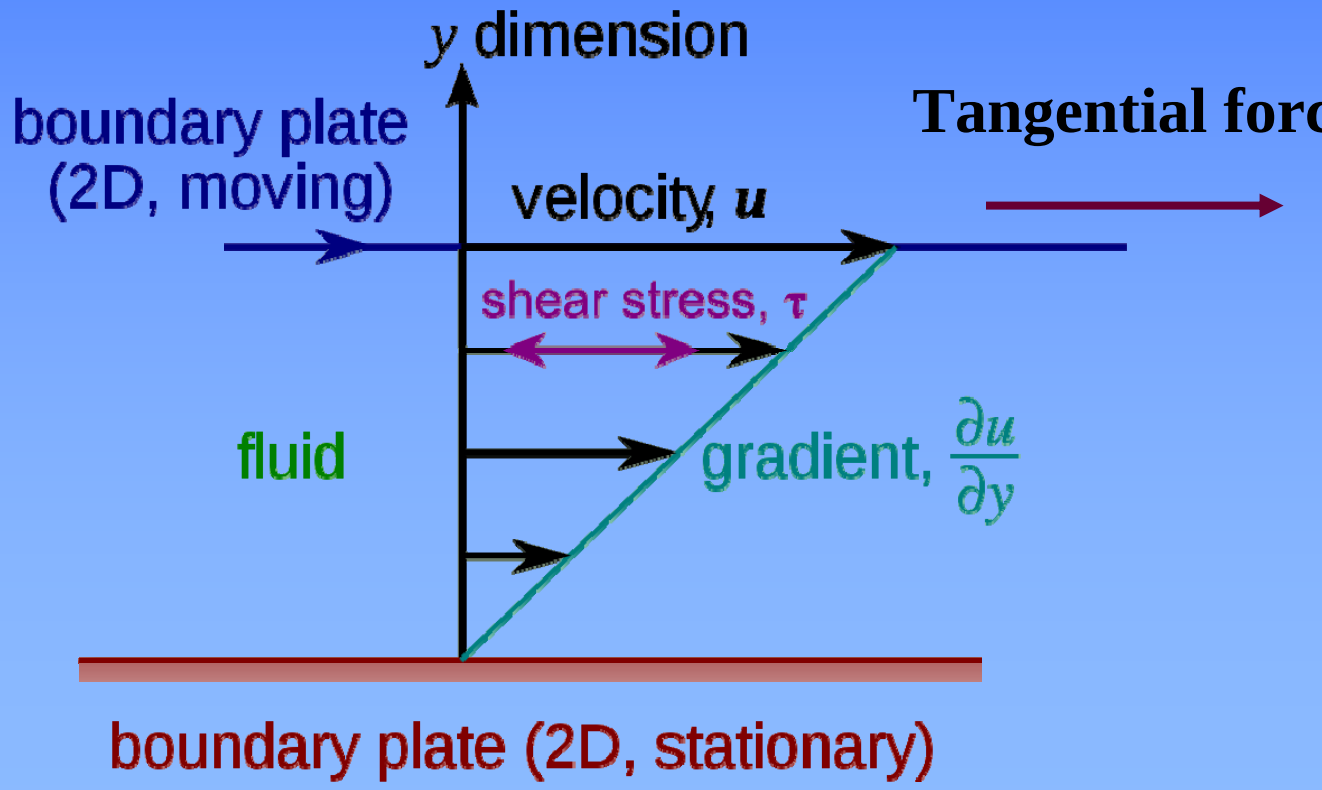
Sokolov, Goldstein, Kessler, I.A., PRL 2007

Bacteria velocities distribution in collective swimming regime: fat tails



Apparent viscosity: not very practical

$$\text{viscosity} = \frac{\text{shear stress}}{\text{strain rate} = \partial u_x / \partial y} = \frac{\text{tangential force}}{\text{plate's velocity}}$$



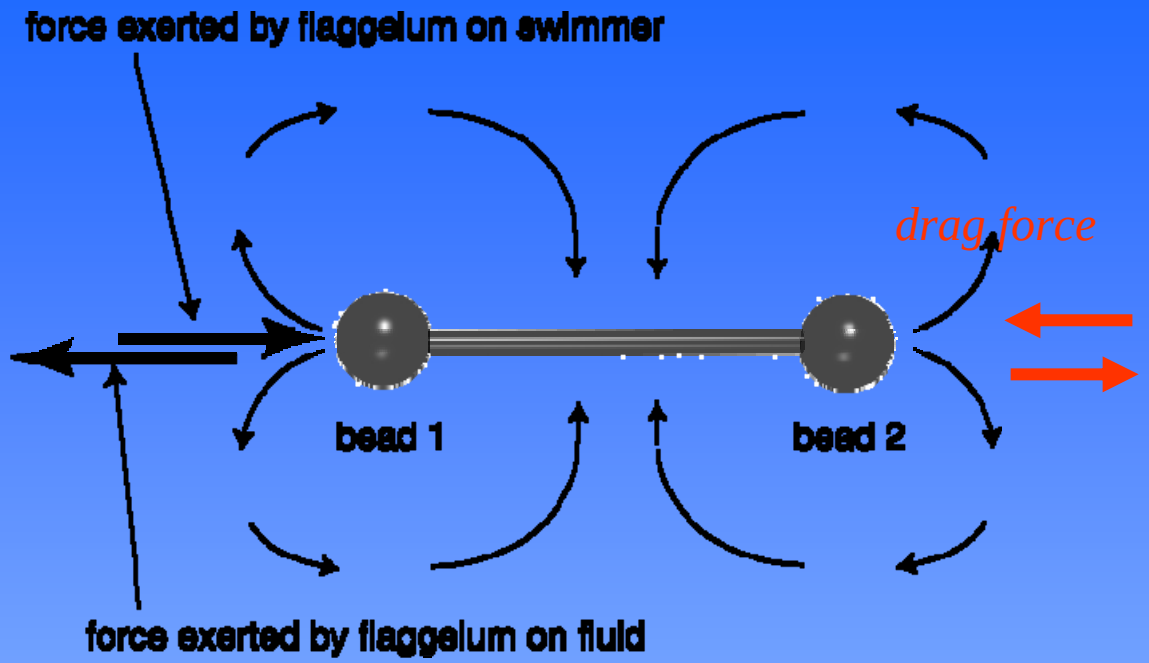
Viscosity of Passive Suspensions: (Albert) Einstein theory

- Dilute suspensions of impenetrable spheres, zero Reynolds number (Stokes limit)

$$\eta = \eta_0 \left(1 + \frac{5}{2}\phi + O(\phi^2) \right)$$

- η_0 – viscosity of the background fluid,
- ϕ – volume fraction of spheres

Bacteria are force dipoles



- **Bacteria are low Reynolds number creatures: Re=V L/n~10^{-4}**
- **Bacteria motion is overdamped: no acceleration, zero net force**
- **Bacterium acts as a force dipole: force of self-propulsion and force opposing drag act on water in opposite directions**

Michael Graham et al, PRL 2005

Self-propulsion and Viscosity?

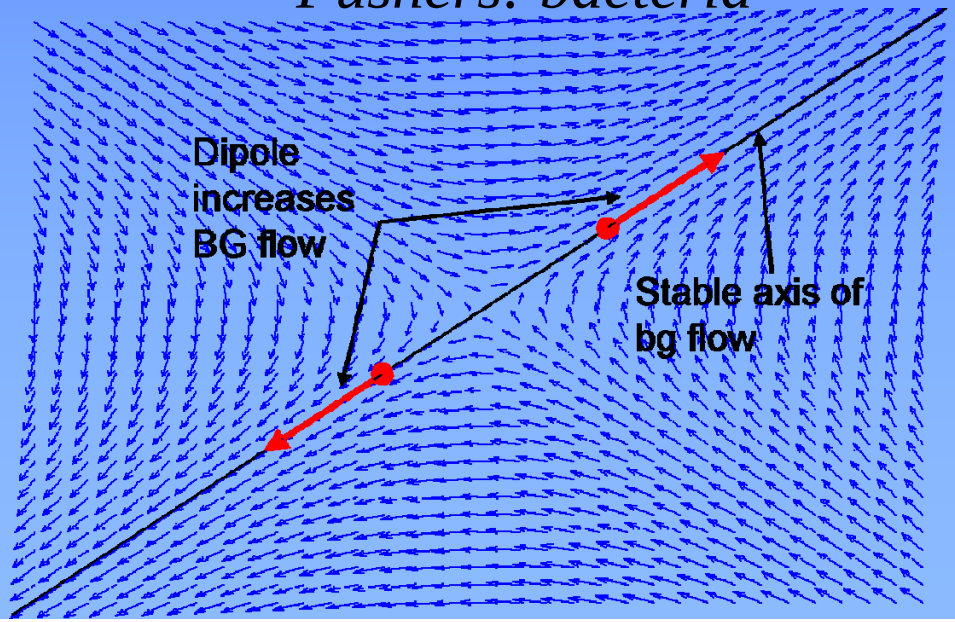
- **When dipole is aligned with flow, dipole increases rate of strain without changing forces at the boundary**

- **Non-spherical particles tend to align with stable axis of flow**

- **Increase of background (bg) flow, decrease of viscosity**

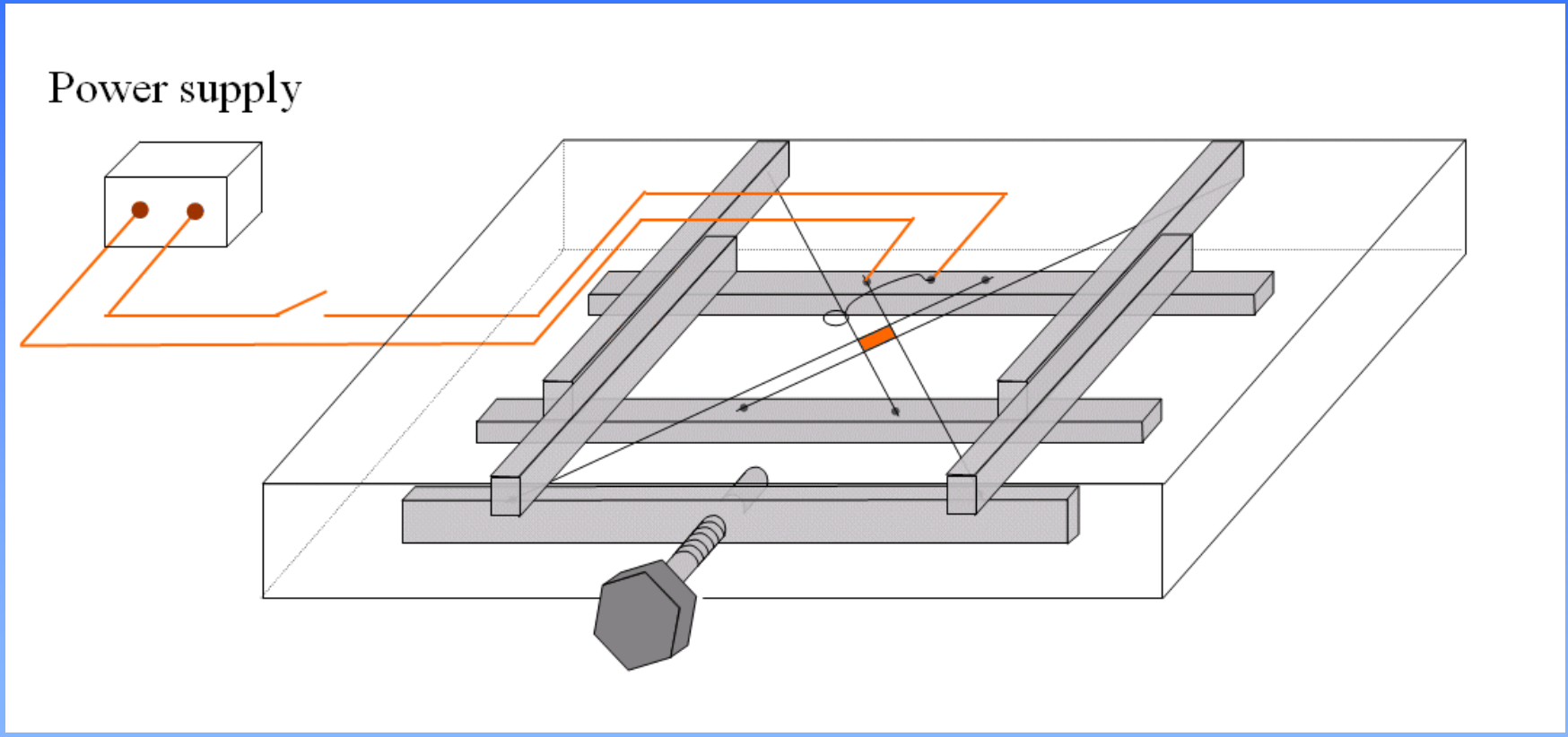
- **For passive suspensions and pullers , viscosity increases with concentration of inclusions**

Pushers: bacteria



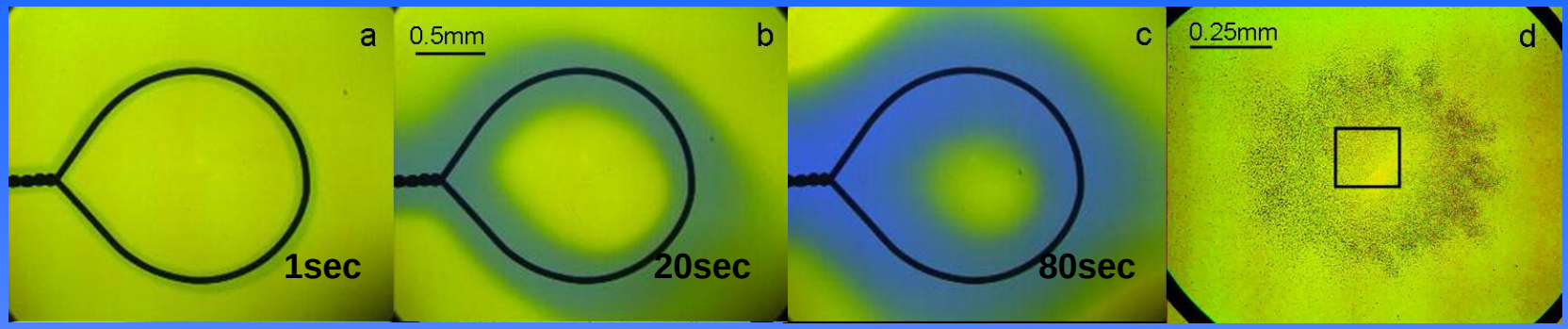
Schematics of Experimental Setup

Concept: Andrey Sokolov and I.A , ANL Invention



Thin free-standing film concept
Adjustable thickness
Adjustable concentration of bacteria

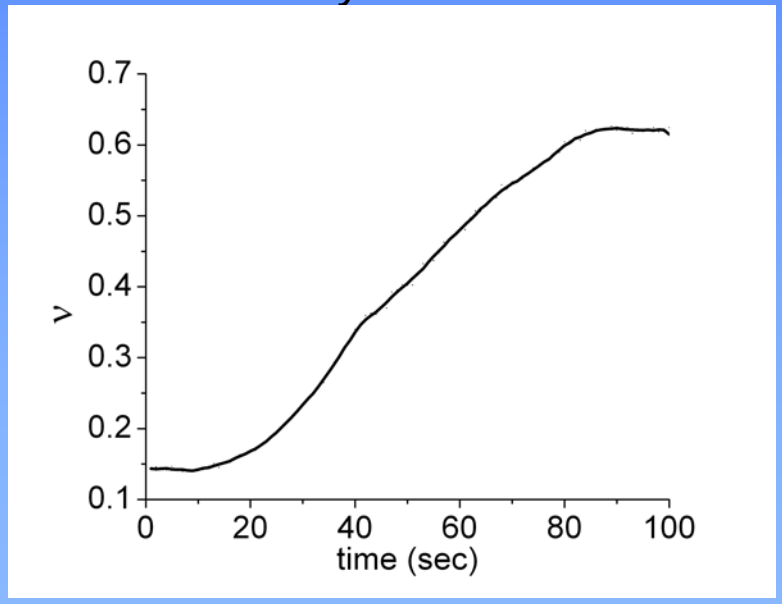
pH-Taxis & concentration of cells



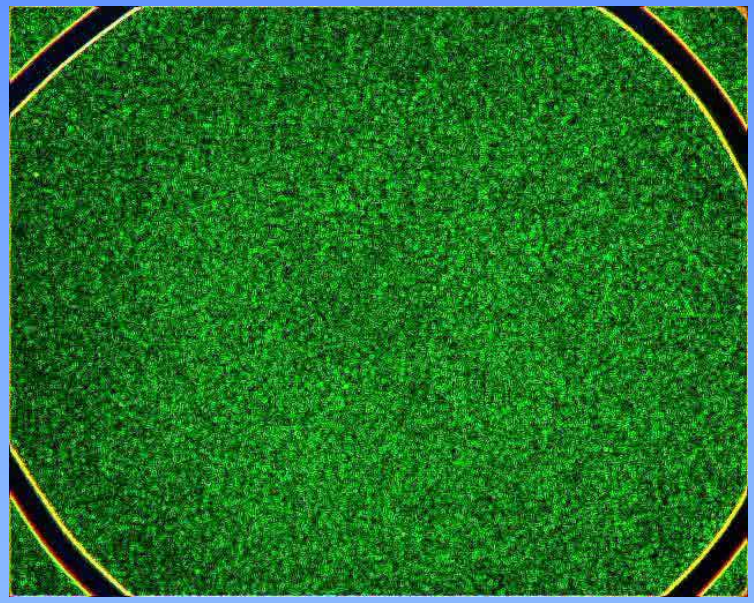
pH indicator (bromothynol blue) was added

field of view

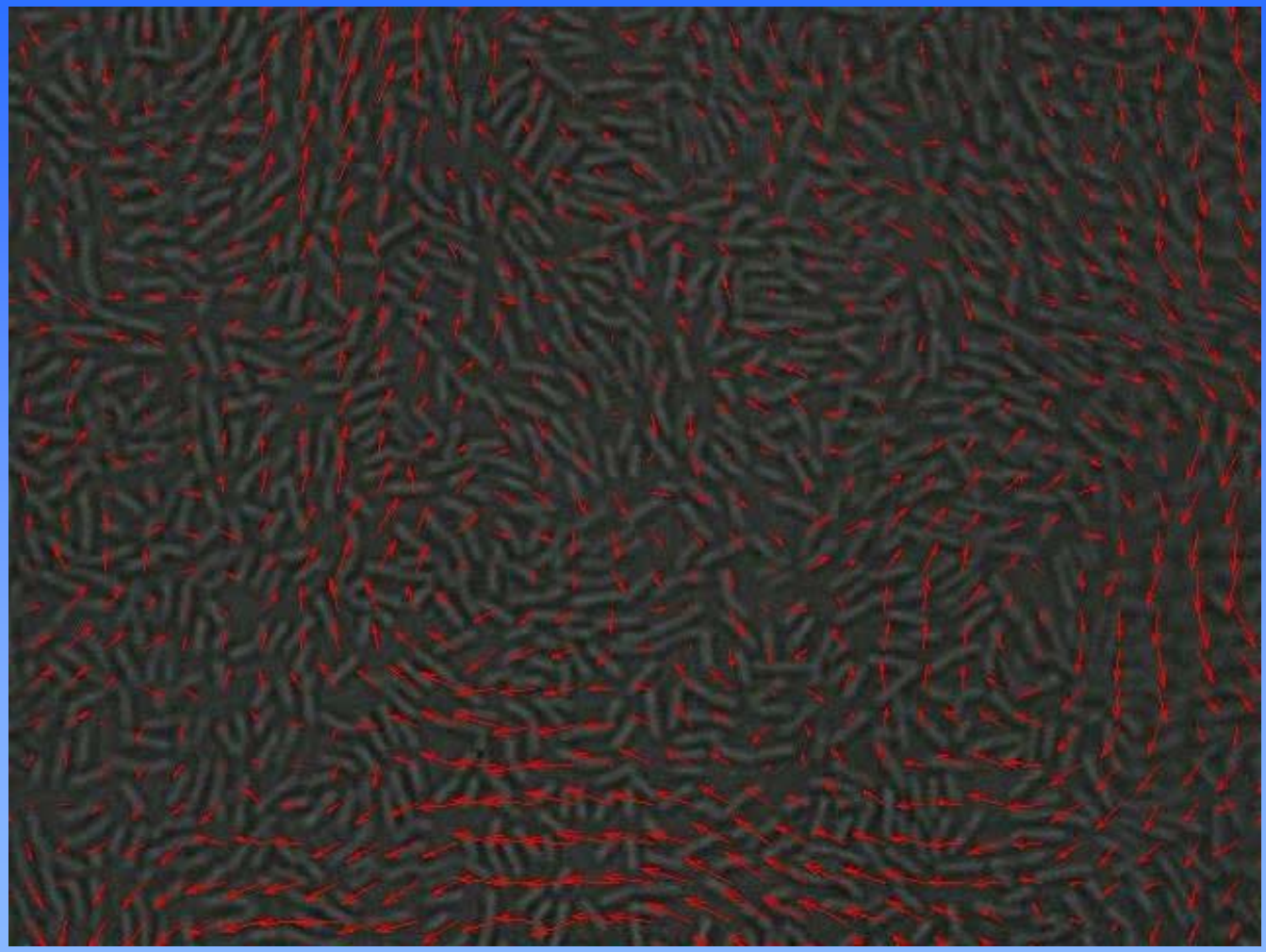
density vs. time



Bacteria crowd control

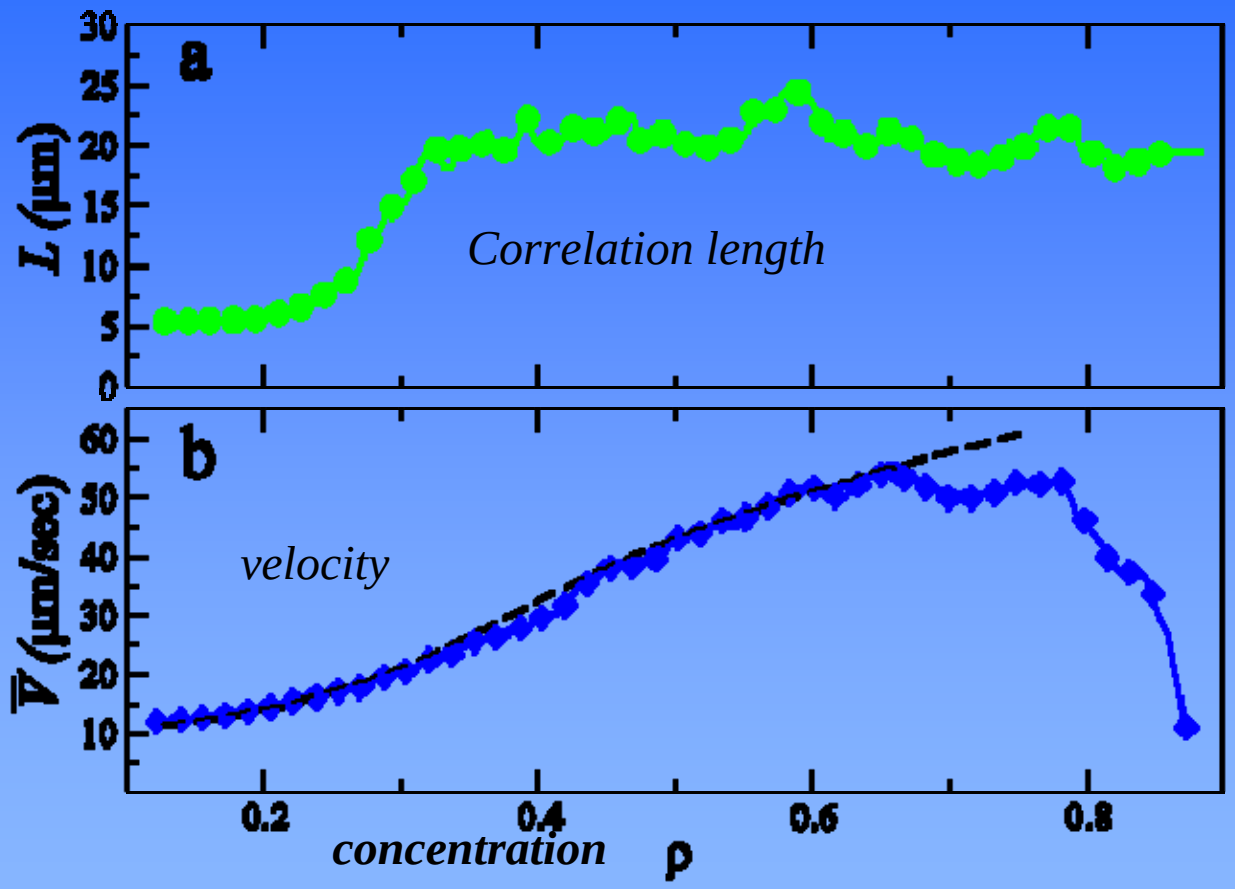


Bacterial turbulence



Sokolov, Goldstein, Kessler, I.A PRL (2007)

Transition to Collective Swimming



ρ-density

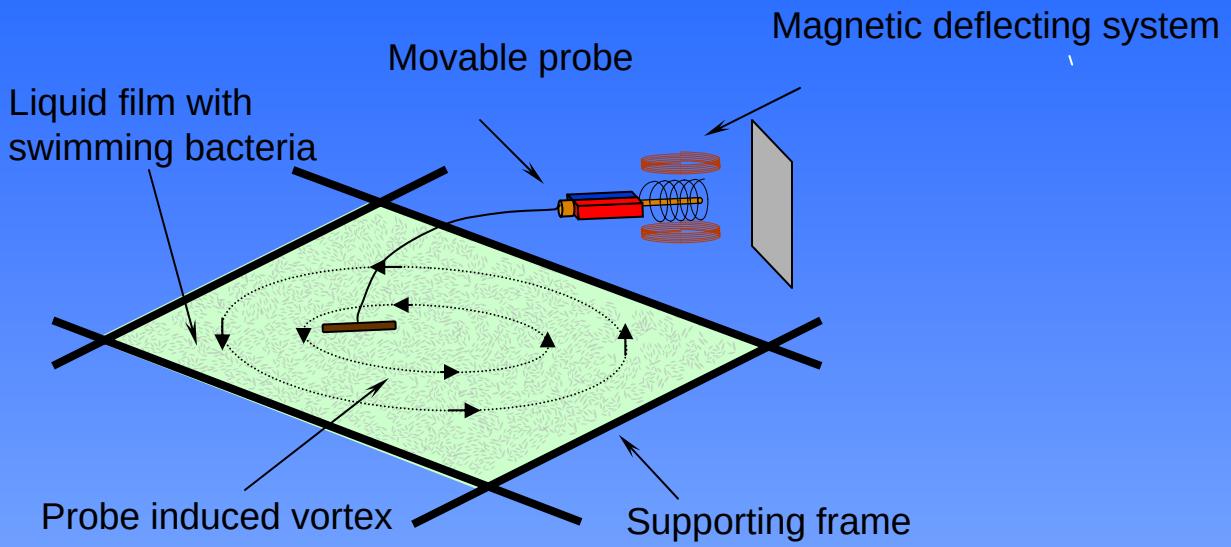
$\bar{V}$-rms velocity

L-correlation length

Fit : $\frac{\partial V}{\partial t} = (\rho - \rho_c)V - V^3 + \eta(t)$

Boids model: first order transition, Gregoire and Chate

Probing Micro-Rheology of Active Suspensions Experiment #1



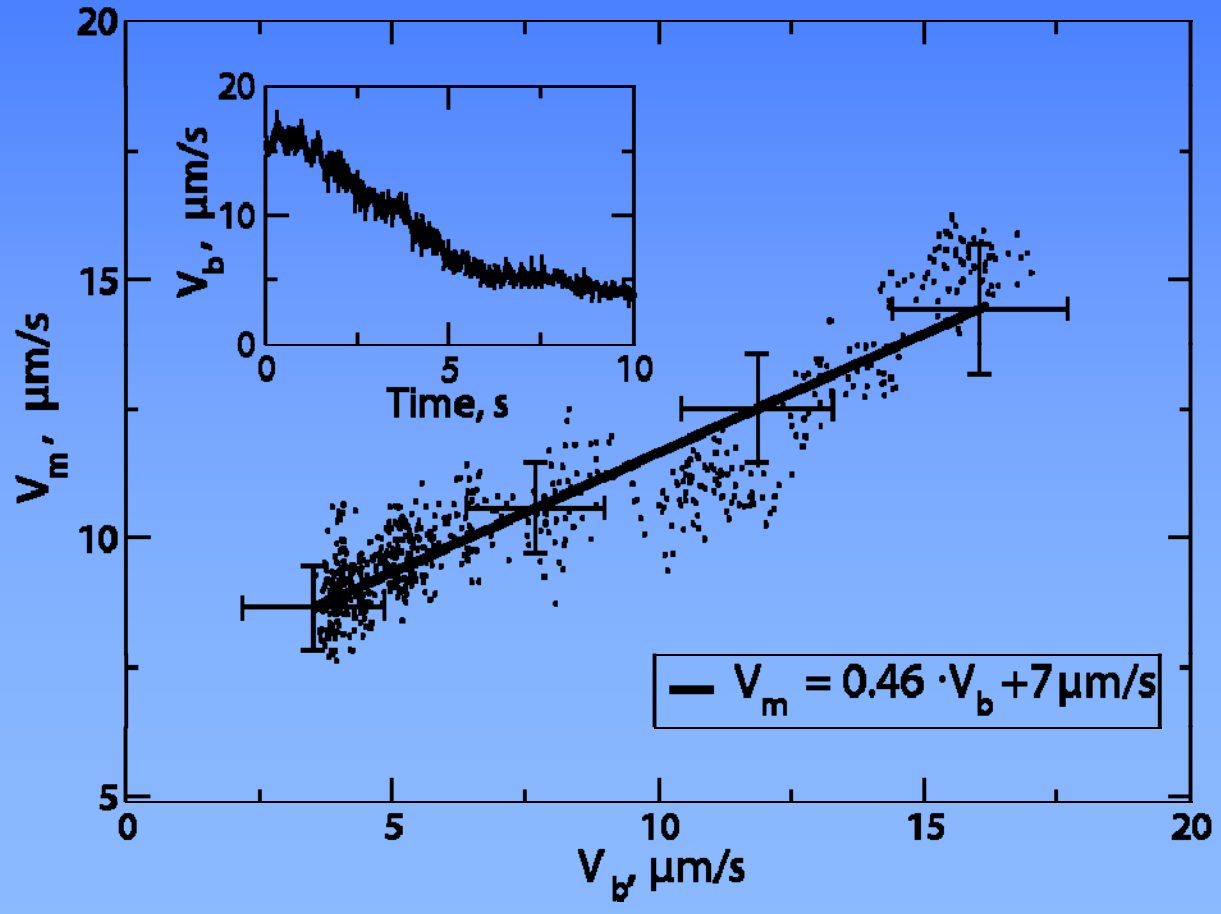
- Microrheology is studied in thin free-standing film geometry
- Experiment performed in closed chamber in air and in Nitrogen
- Control of activity: $N_2 \rightarrow$no swimming, $O_2 \rightarrow$swimming
- Viscosity is extracted from decay time (T) of a large vortex (L)

Sokolov & Aranson, PRL 2009 and also Physics World

Controlling the Speed: Filling Chamber with Nitrogen

V_b – speed of bacteria

V_m – speed of 2.5 μm fluorescent tracers

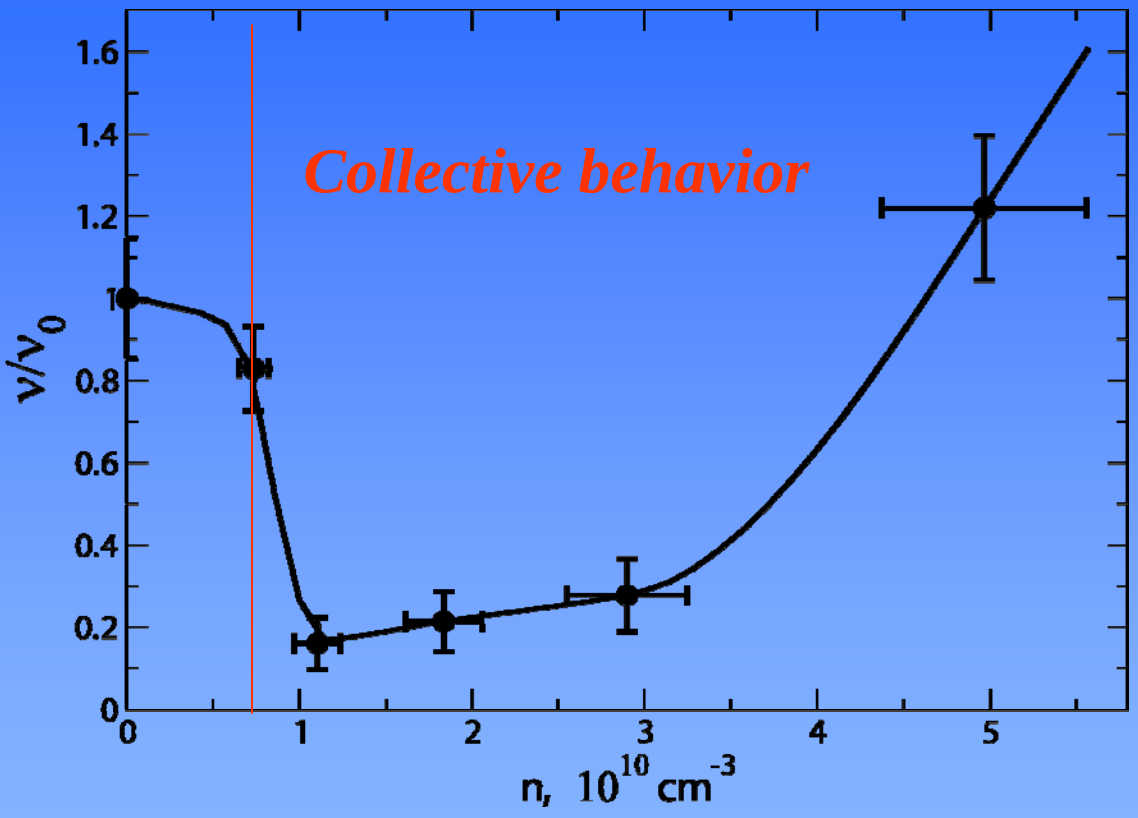


Relaxation of vortex

live bacteria

dead bacteria

Viscosity vs. Concentration
Reduction of viscosity - bacteria



Assuming that the viscosity is spatially independent

$$V(t) = V_0 \exp\left(-\frac{a_0}{L^2} \int_0^t \nu(\dot{\gamma}(\tau)) d\tau \right)$$

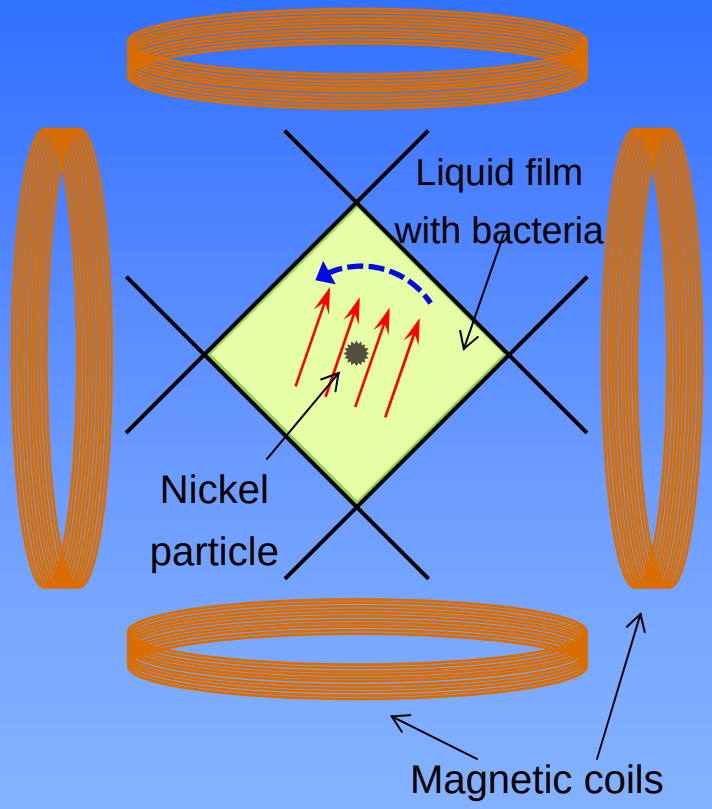
Assuming that the viscosity is time-independent

$$V(t) = V_0 \exp\left(-\frac{a_0}{L^2} \nu t \right)$$

viscosity: $$\nu = -\frac{L^2}{a_0} \frac{d[\ln(V(t))]}{dt}$$

Concentration: ***10-20 times stationary growth conditions***

Rotation of microparticle Experiment#2



Earth's magnetic field is compensated

Amplitude of magnetic field: $H = 3\,G$

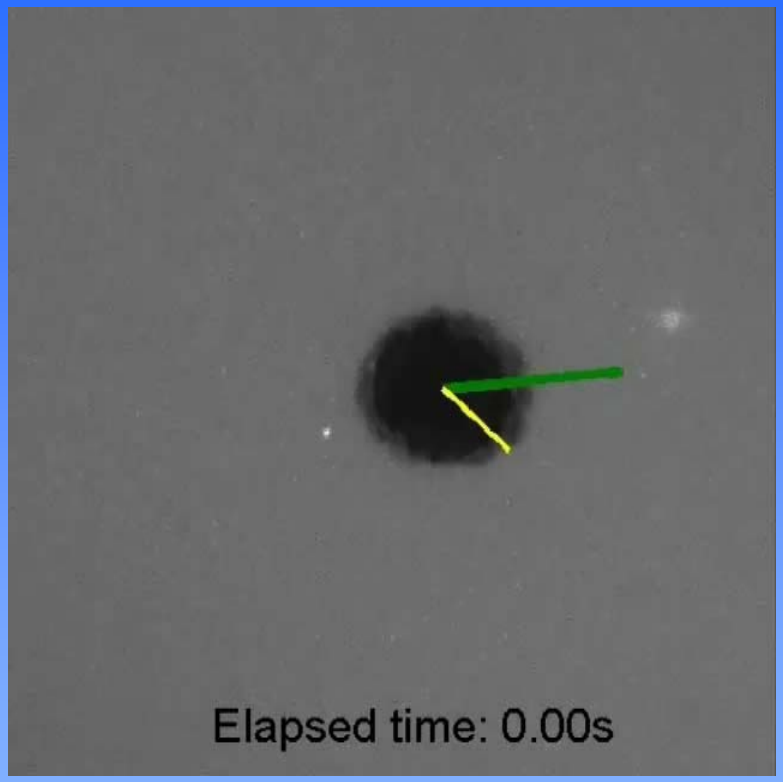
Frequency of rotation: $2\ Hz$

Viscous drag: $T_\nu \propto \nu \dfrac{\partial \alpha}{\partial t} = \nu \Omega$

Magnetic torque: $T_m \propto \mu_0 H \sin \phi_m$

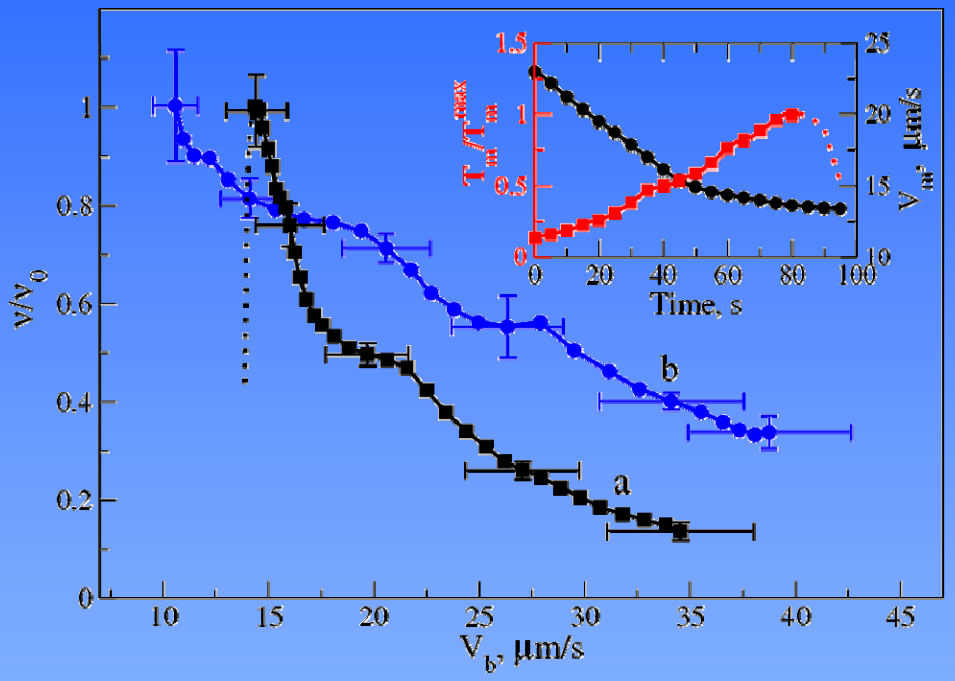
Viscosity: $\nu \propto \mu_0 H \sin \phi_m / \Omega$

Viscosity vs Swimming Speed



Yellow – internal magnetic moment

Green – external magnetic field



a) $n=1.8\cdot10^{10}$ cm^{-3}

b) $n=10^{10}$ cm^{-3}

Summary of Experimental Part

- viscosity of bacterial suspension strongly depends on the concentration and swimming speed of bacteria

- viscosity of bacterial suspension can be seven times lower than the viscosity of the same liquid without bacteria or with dead bacteria

Viscosity of Active Suspensions: Earlier Studies

- Hathwalne and Ramaswamy, Phenomenological coarse-grained model for active suspension, swimmers→ point dipoles; suggested dependence of viscosity on activity

- Ishikawa and Pedley; bacteria→ spheres with prescribed velocity, Observed numerically increase of viscosity

- Effects of shape of bacteria, background flow, way of propulsion, tumbling and interactions?

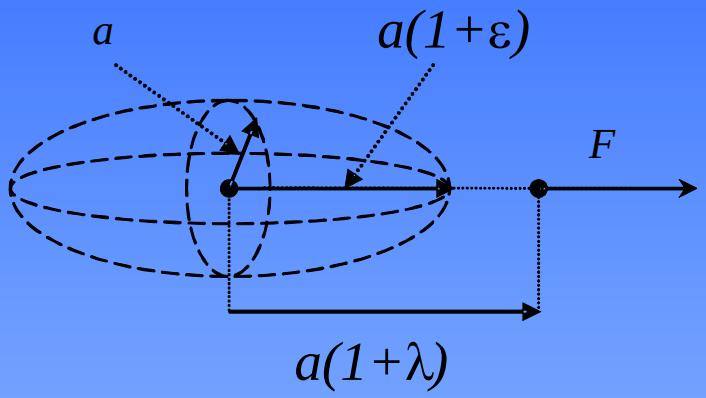
- Statistical properties, such as orientation distribution functions, etc ?

Extension of Einstein Theory for Dilute Suspensions

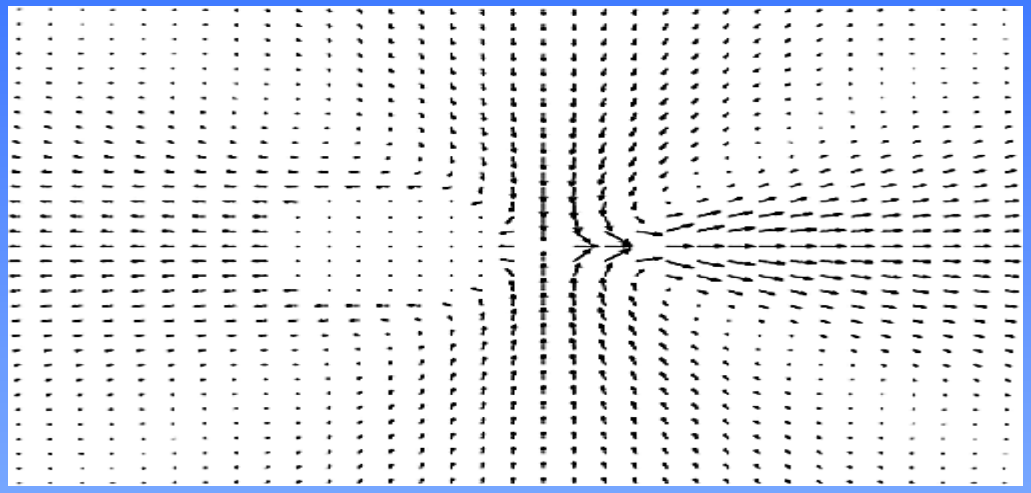
- Dilute limit in 3D geometry
- Impenetrable prolate ellipsoids
- Point propulsion force – flagella
- Pure shear and planar shear background flows
- Stokes limit – Re=0
- Bacteria experience random fluctuations (tumbling)
- Viscosity calculated via dissipation rate

Haines et al, Phys Biology 2008, PRE 2009.
For the case of point dipoles: David Saintillan, 2010

Model

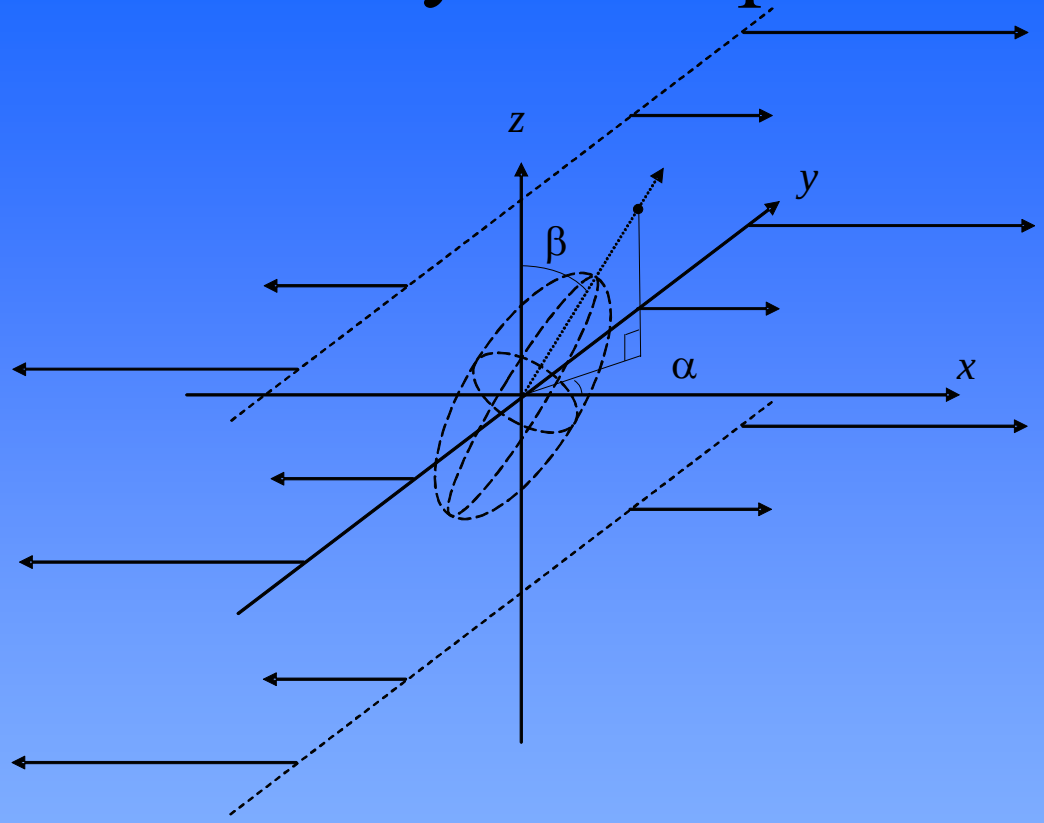


Velocity field



- Elongated impenetrable body (leads to alignment)
- Point force, makes bacteria force dipole
- Velocity (quadruple) decays away from bacterium as $1/R^2$
- Random tumbling, makes unique probability distribution of bacteria orientations

Geometry of the problem



- **Planar shear flow: v=(*0*,γy,*0*) , γ strain rate, or pure shear**
- **α,β – polar angles**
- **$\varepsilon<<1$ – aspect ratio parameter: sphere ε=0, ε=1 needle**

Particles rotation: Jeffrey orbits

$$\dot{\alpha} = \Omega + E\varepsilon\cos(2\alpha) + \xi_\alpha$$

$$\dot{\beta} = E\varepsilon\sin(2\alpha)\sin(2\beta) + \xi_\beta$$

- Ω and E – vorticity and rate of strain of background flow
- $\xi_{\alpha,\beta}$ fluctuations (tumbling) with the strength D

$\alpha=\Omega t$ for $\varepsilon<<1$ – pure rotation

$\varepsilon\sim(b^2-a^2)/(a^2+b^2)$, a,b - semiaxis

Linear Fokker-Planck Equation

$$\frac{\partial P}{dt} = -\nabla \cdot (\kappa P) + D\nabla^2 P$$

- $P(\alpha,\beta)$ – probability distribution function for bacteria orientations
- κ – angular velocity vector

Calculating effective viscosity

$$\hat{\eta} := \frac{\text{bulk deviatoric stress}}{2 \times \text{bulk rate of strain}}$$

The bulk deviatoric stress (as a random variable) is defined by

$$\Sigma_{ij} := \frac{1}{|V|} \int_V \left(\sigma_{ij} - \frac{1}{3} \delta_{ij} \sigma_{kk} \right) dx.$$

(we expect $\Sigma_{ij} = 2\hat{\eta} E_{ij}$; $E_{kk} = 0$, $\Sigma_{kk} = 0$)

In dilute limit, we approximate this by sum of bulk stresses due to single bacterium and take the expectation value:

$$\Sigma_{ij} \approx \frac{1}{|V|} \sum_{l=1}^{N} \int_{S^2} \int_V \left(\sigma_{ij}(\alpha^l, \beta^l) - \frac{1}{3} \delta_{ij} \sigma_{kk}(\alpha^l, \beta^l) \right) P^\infty(\alpha^l, \beta^l) dx dS$$

Bacterial orientations all realizations of i.i.d. random variables and hence $P^\infty(\alpha^m, \beta^m) = P^\infty(\alpha^n, \beta^n) = \forall m, n$, thus

$$\Sigma_{ij} = \frac{N}{|V|} \int_{S^2} \int_V \left(\sigma_{ij}(\alpha, \beta) - \frac{1}{3} \delta_{ij} \sigma_{kk}(\alpha, \beta) \right) P^\infty(\alpha, \beta) dx dS$$

Take $E = \frac{1}{2} \begin{pmatrix} 0 & \gamma & 0 \\ \gamma & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$ in (SBP) (p. 20), then $\frac{1}{|V|} \int_V e dx = E$ and $\hat{\eta} = \hat{\eta}_{1212} = \frac{\Sigma_{12}}{\gamma}$

Bulk Stress

- Contribution due to passive spheroid (Kim & Karilla, 1991)
- Contribution due to tumbling (noise) (Leal & Hinch, 1971)
- Contribution due to self-propulsion (Haines et al, 2009)
- K, Y^H – resistance functions (depend on aspect ratio and position of flagella)

$$\Sigma_{ij} = 2\eta E_{ij} + \frac{5b}{a}\phi\eta \int_{S^2} \Lambda_{ijkl} P^{\infty} dS E_{kl}$$
$$+ 3\eta\phi Y^H \frac{b}{a} \int_{S^2} (\epsilon_{ikl} d_j + \epsilon_{jkl} d_i) d_l (\Omega_k - \omega_k^D - \omega^R) P^{\infty} dS$$
$$+ \frac{1}{16\pi b^2} \phi K \int_{S^2} (\delta_{ij} - 3 d_i d_j) P^{\infty} dS + \mathcal{O}(\phi^2),$$

Effective Viscosity in 3D (almost spheres)

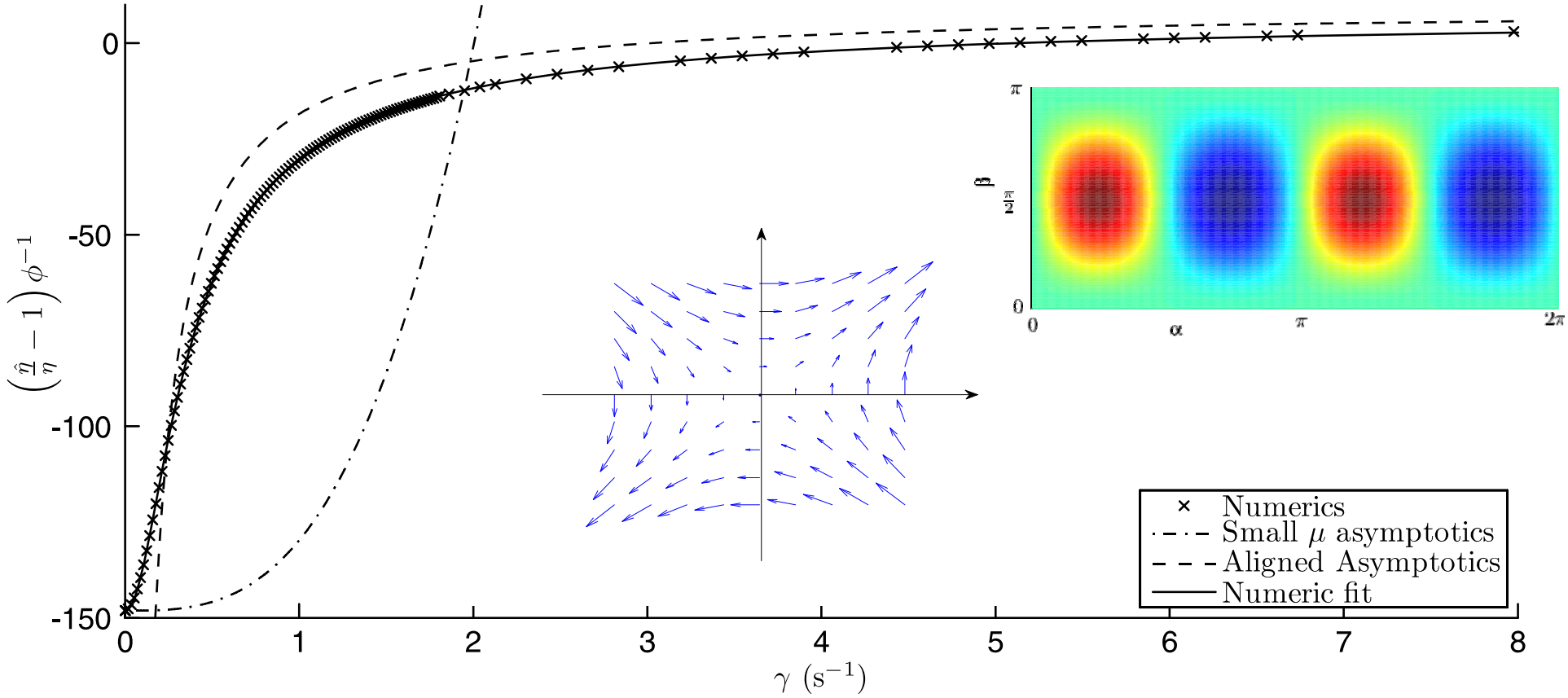
$$\eta_{eff} = \eta\left(1+\frac{5}{2}\phi\right) - \varepsilon\phi\frac{9DF}{20\pi a^2(36D^2+\gamma^2)}\frac{5\lambda^2+2+10\lambda}{(1+\lambda)^4} + O(\varepsilon^2)$$

$$\eta_{eff} = \eta\left(1+\frac{5}{2}\phi - \varepsilon\phi V_0\frac{27D}{10a(36D^2+\gamma^2)}\frac{5\lambda^2+2+10\lambda}{(1+\lambda)^4}\right)$$

- V_0 – swimming speed, F -propulsion force
- small fluctuations limit ($D \ll \gamma$) is singular
- Decrease of viscosity due to swimming (for pushers, $\lambda>0$)
- Also strain rate $\gamma \to 0$ limit is singular limit

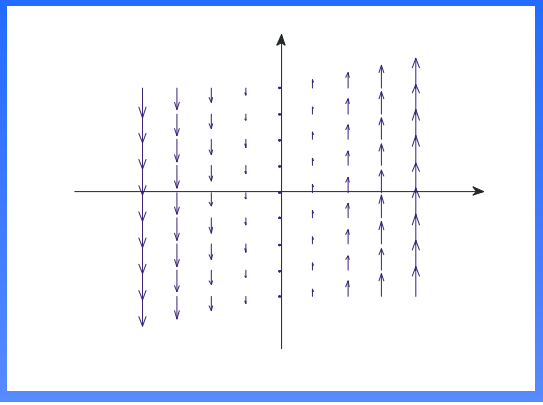
Flow without Vorticity

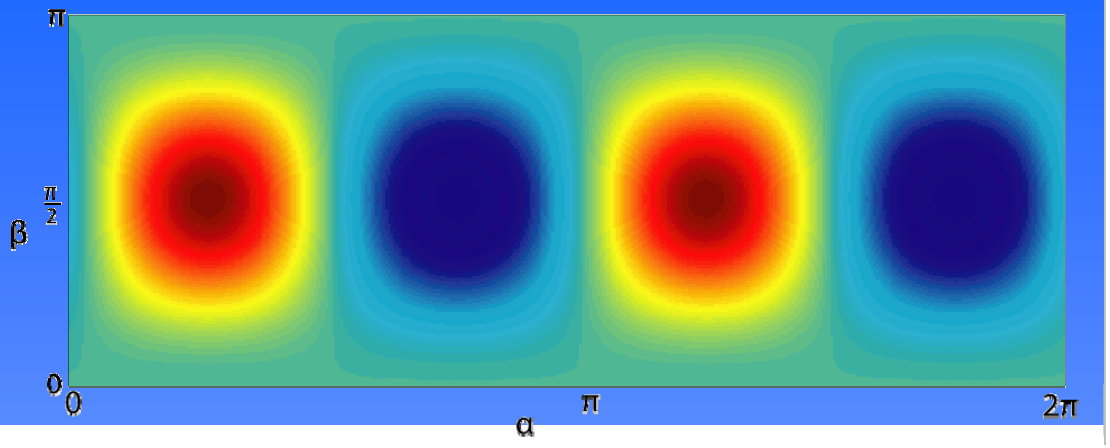
Negative contribution to viscosity for small stain rates

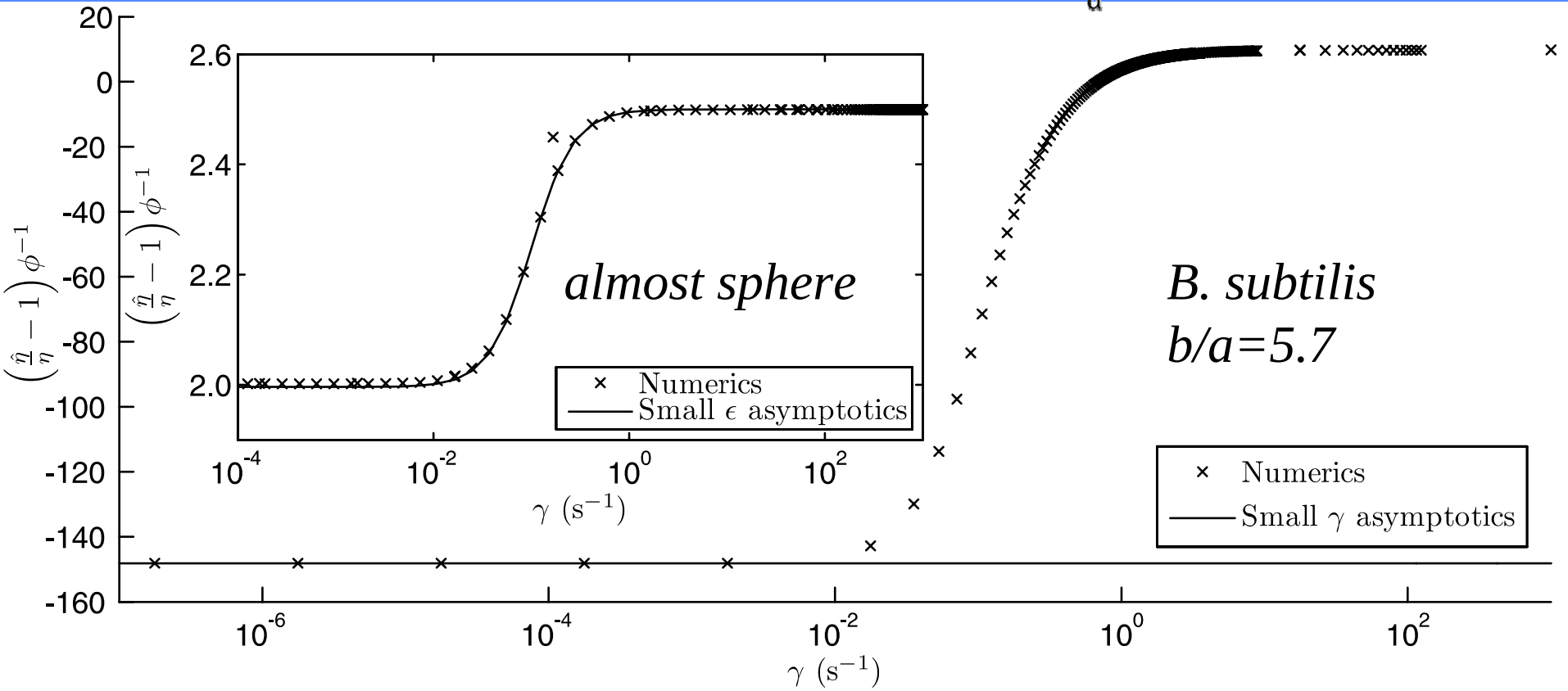


$\mu \sim \varepsilon\gamma/D << 1$ – weak tendency to align; $\mu >> 1$ – strong alignment

Planar Shear Flow







Simulations

- Bacteria are modeled by swimming point dipoles
- No tumbling
- Short-range repulsion to account for finite particle size
- 3D simulation domain
- Lee-Edwards boundary conditions in the case of the shear
- >100,000 particles
- Simulations are implemented on GPU

Shawn Ryan, Penn State Univ, 2010

Equations

$$\frac{d\mathbf{r}_i}{dt} = \mathbf{V}_{bg} + V_0\mathbf{d}_i + \sum_{i\neq j}\mathbf{U}_{ij} + \sum_{i\neq j} L_{ij}$$

$$\frac{d\mathbf{d}_i}{dt} = \Omega_{bg} + \mathbf{E}_{bg} + \sum_{i\neq j}\left(\mathbf{c}_{ij} + \mathbf{E}_{ij}\right)$$

$\mathbf{V}_{bg} = (0, \dot{\gamma}x, 0), \dot{\gamma}$ – strain rate of background (bg) flow

$\Omega_{bg}, \mathbf{E}_{bg}$ - vorticity and rate of strain of bg flow

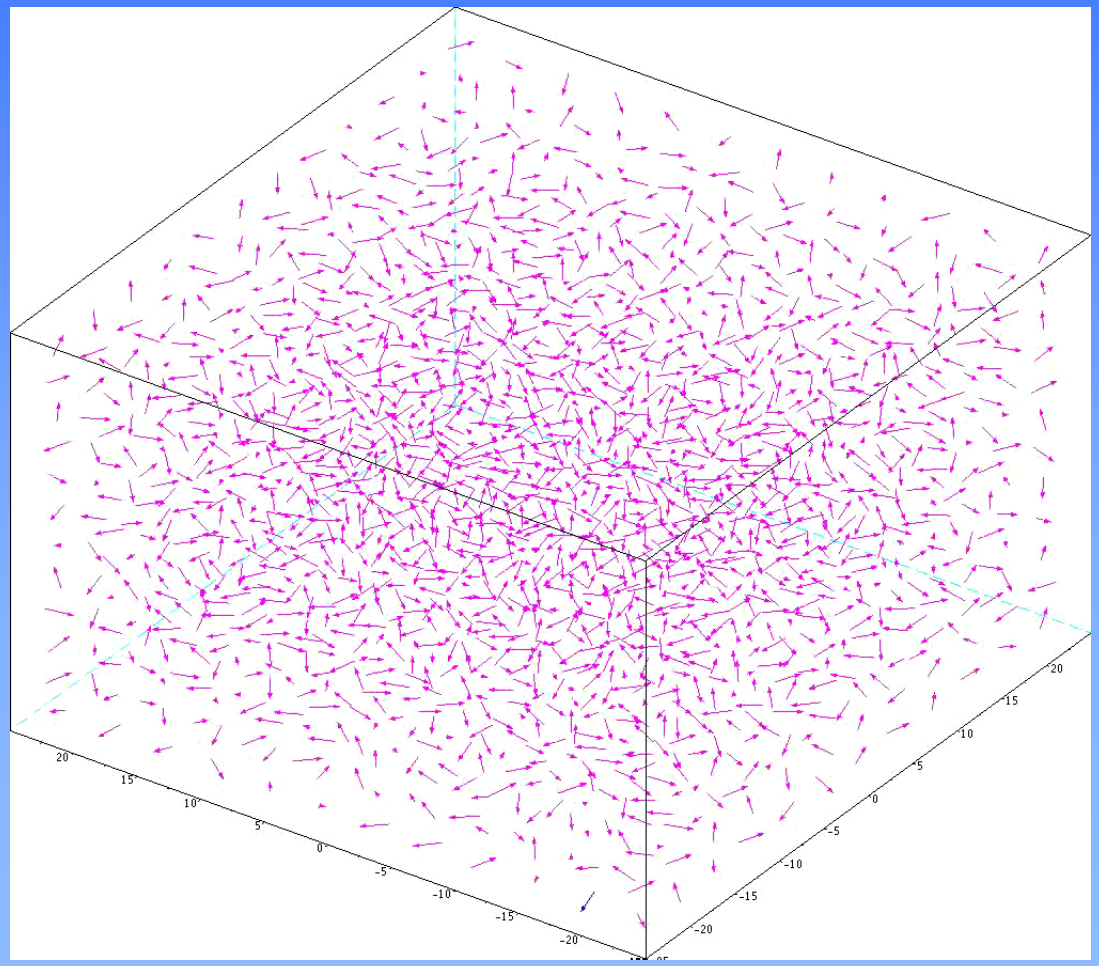
V_0 – swimming speed

$\mathbf{U}_{ij}, \mathbf{c}_{ij}, \mathbf{E}_{ij}$ – velocity, voticity and rate of strain of j-bacteia

L_{ij} – short-range repulsion force (Lennar-Jones type)

Typical simulation

- Full 3D, up to 48^3 particles
- Fermi GTX480 GPU, 2-3 hours
- Range of velocities, concentrations, strains



Stress Tensor

$$\Sigma = \Sigma_{dipoles} + \Sigma_{forces}$$

$$\Sigma_{dipoles} = -\frac{U_0}{volume}\sum_{j,k}\left(d_j d_k - \frac{1}{3}\delta_{ij} \right) - \text{from point dipoles}$$

U_0 – dipole strength (*stresslet*)

$$\Sigma_{forces} = \frac{1}{volume}\sum_{j,k}\mathbf{r}_{jk}\mathbf{F}_{ij}$$

$\mathbf{r}_{jk}, \mathbf{F}_{ij}$ – interparticles distance and forces

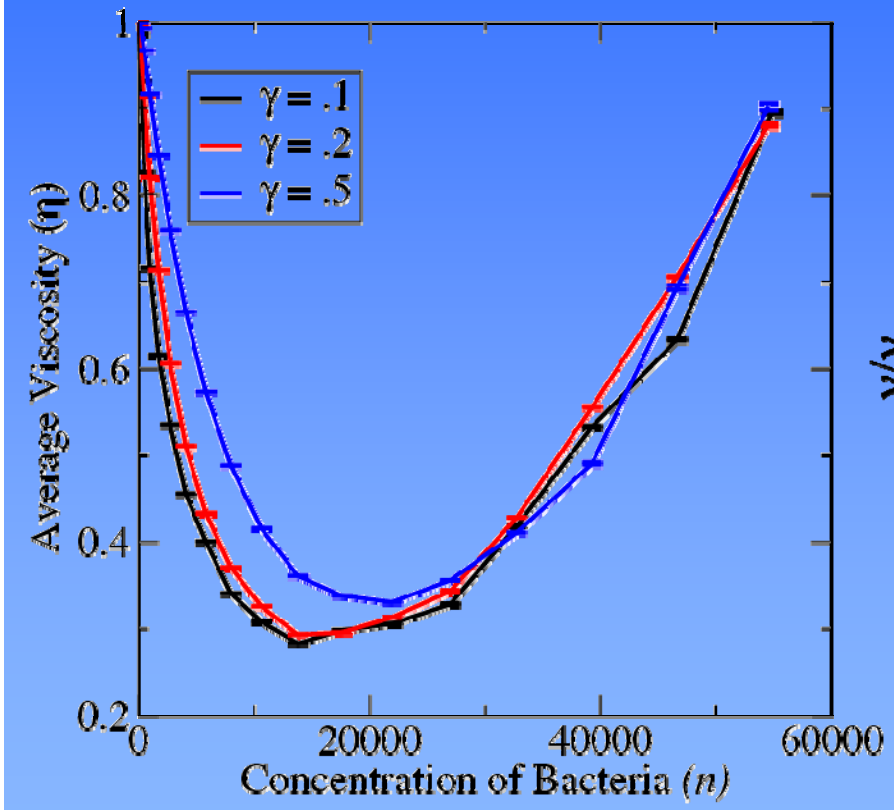
Effective Viscosity

$$\eta = \frac{E_{bg}\Sigma}{E_{bg}E_{bg}} - \text{viscosity}$$

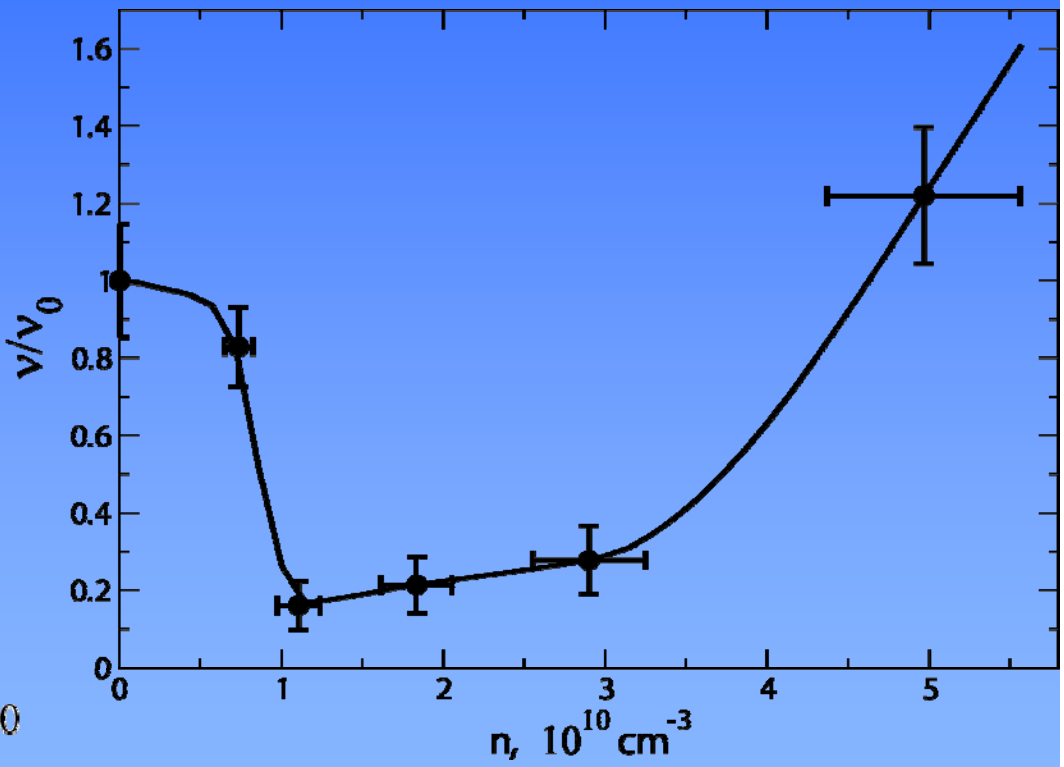
$$E_{bg} = \dot{\gamma}\begin{pmatrix} 0 & \frac{1}{2} & 0 \\ \frac{1}{2} & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} - BG \text{ rate of strain tensor}$$

Viscosity vs Concentration

Simulations

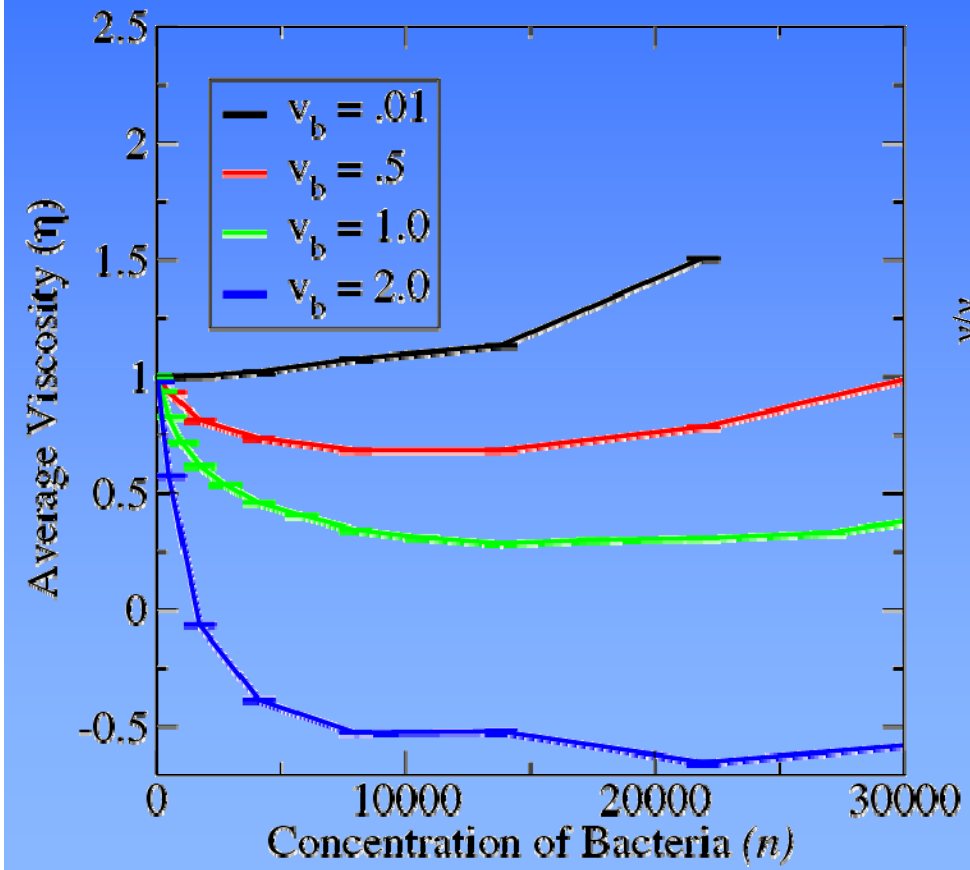


Experiment

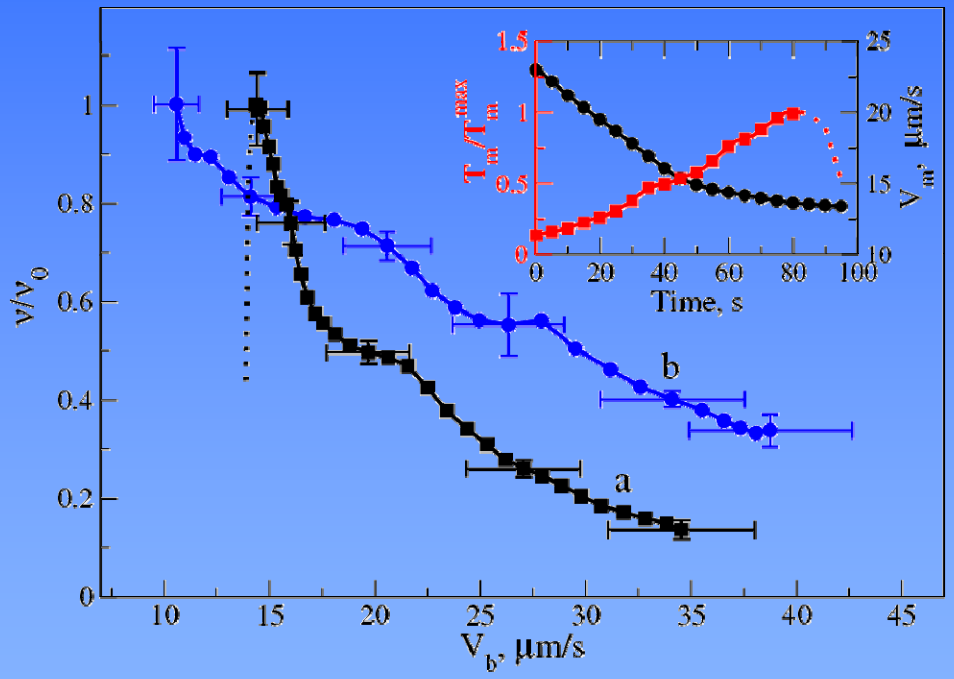


Viscosity vs Swimming Speed

Simulations



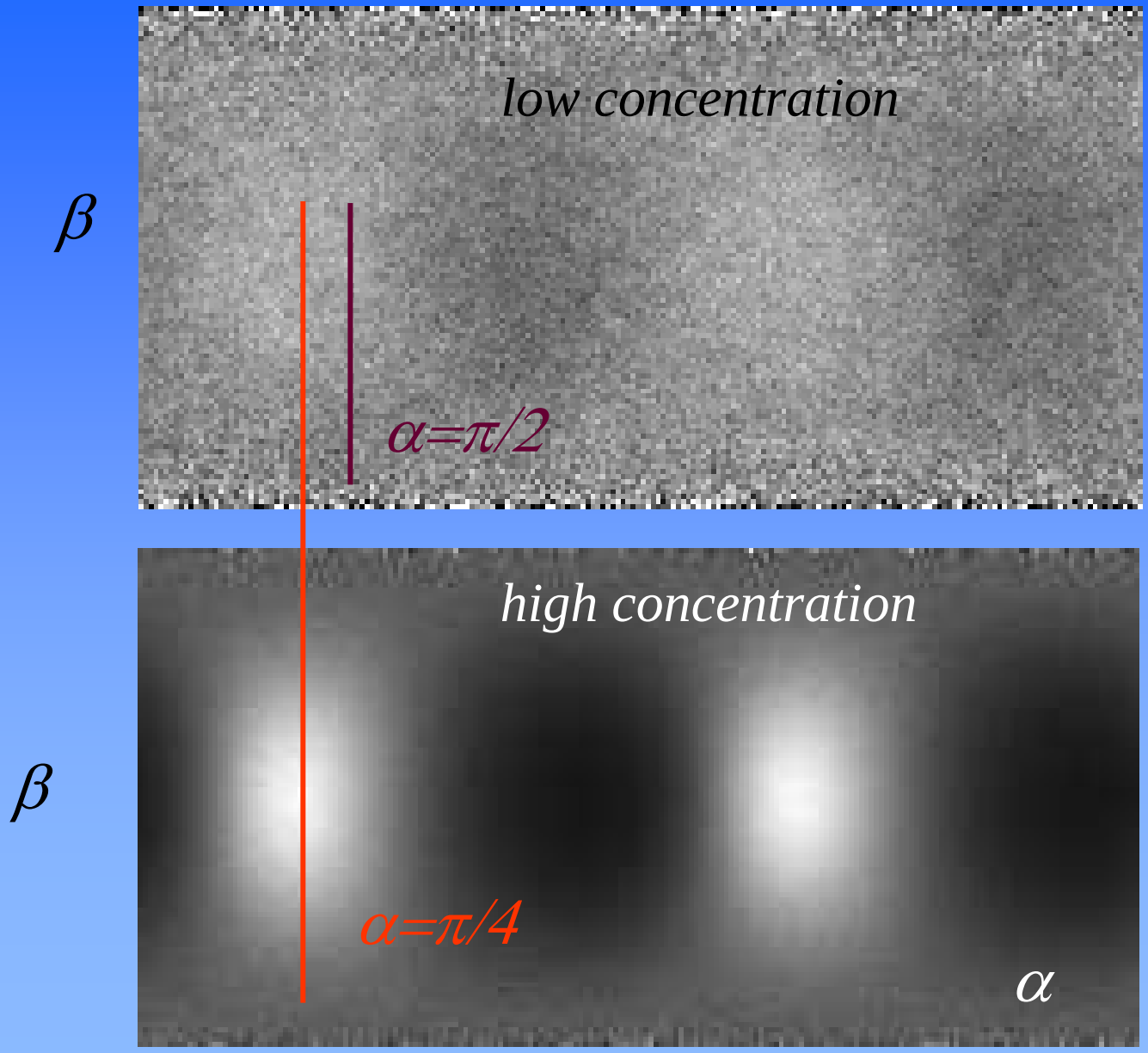
Experiment



a) $n=1.8\cdot10^{10}$ cm^{-3}

b) $n=10^{10}$ cm^{-3}

Orientation Distribution Functions P(α,β)



Analytical Results

$$\text{Continuum limit}: \sum_j \to \frac{1}{V}\int P(\mathbf{r}',\mathbf{d}')d\mathbf{r}'d\mathbf{d}'$$

$$\text{Kinethic equation}: \partial_t P(\mathbf{r},\mathbf{d}) = -\nabla_{\mathbf{r},\mathbf{d}}\left(J(P(\mathbf{r}',\mathbf{d}'))P(\mathbf{r},\mathbf{d})\right)$$

$$\text{Viscosity for } B\to 0: \eta \sim \frac{BU_0}{\langle\rho\rangle\left(\dot{\gamma}^2+\varepsilon^2\right)}\left\langle\rho^2-\langle\rho\rangle^2\right\rangle$$

ρ – local density

Starting point similar to D Saitillan & M Shelley's works, 2008/2009

Conclusions

- Extension of previous analytical results for passive suspensions on the case of self-propelled particles
- Additional terms due to self-propulsion are obtained, explicit dependence on parameters of bacteria
- Model is in agreement with experiment
- Semi-dilute case and role of interactions