Self-Diffusiophoresis and biological motility

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Informal Seminar, University of Oxford, 8th June 2011

ACTIN BASED PROPULSION

Listeria monocytogenes



Courtesy of Julie Theriot http://cmgm.stanford.edu/theriot/movies.htm



ACTIN AND LISTERIA MOTILITY



POLLARD ET AL Ann. Rev. Biophys. Biomol. Struct. 29, 545–576 (2000)



IN-VITRO REALISATIONS

Courtesy of Julie Theriot http://cmgm.stanford.edu/ theriot/movies.htm

 $\times 60$

sphere

"All" you need is

- Actin and buffer w/ATP
- Arp2/3 makes new growing ends
- Capping protein kills them off
- ADF/cofilin severs filaments
- Profilin converts ADP-G-actin to ATP-G-actin
- Bead coated with ActA, VCA, activates Arp2/3



CAMERON ET AL Curr. Biol. 11, 130 (2001)

how does self-assembly of actin into a branched structure lead to motility?



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CAMERON ET AL Curr. Biol. 11, 130 (2001)

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BROWNIAN DYNAMICS SIMULATIONS





- Polymerisation at + end (K_+)
- Depolymerisation at end (K_{-})
- Branching (K_a)
- Debranching (K_d)
- Capping



BROWNIAN DYNAMICS SIMULATIONS

- 2D projection of 3D simulation
- Motion allowed in $\pm z$ direction only



BROWNIAN DYNAMICS SIMULATIONS



- 2D projection of 3D simulation
- Motion allowed in $\pm z$ direction only



ACTIN CONCENTRATION GRADIENT



- Disk activates Arp2/3, which recruits F-actin
- Concentration of F-actin is high behind the disk compared to average
- If the disk repels actin then it will move forwards to avoid F-actin
- In real systems the concentration gradient is even bigger; mechanism should still apply



ASYMMETRIC CELL DIVISION

Most cells divide symmetrically

Caulobacter crescentus and Vibrio cholerae divide asymmetrically





• What is the mechanism for chromosomal motility?





DISASSEMBLY DRIVEN MOTILITY

• How does the chromosome move across the cell during chromosomal segregation in certain asymmetric bacteria?

Caulobacter crescentus



DISASSEMBLY DRIVEN MOTILITY

• How does the chromosome move across the cell during chromosomal segregation in certain asymmetric bacteria?





Courtesy of C. W. Shebelut, J. M. Guberman and Z. Gitai

CHROMOSOMAL SEGREGATION IN C. CRESCENTUS AND V. CHOLERAE



Courtesy of C. W. Shebelut, J. M. Guberman and Z. Gitai

VIBRIO CHOLERAE



FOGEL & WALDOR Genes & Dev. 20, 3269–3282 (2006)



A CLOSER LOOK AT THE PROCESS



FOGEL & WALDOR Genes & Dev. 20, 3269–3282 (2006)



ParA disassembles and origin moves

Origin and terminus switch places

• Origin is decorated with ParB which binds to and hydrolyses ParA



ParA filament structure depolymerises and drags ParB along

CONCENTRATION GRADIENT DRIVES MOTION



 System uses depolymerisation to create a steady-state concentration gradient to move up



BANIGAN ET AL submitted (2011)

BIOLOGICAL MOTILITY

• Two examples of motion involving the assembly or disassembly of filaments

Courtesy of J. Theriot





FOGEL & WALDOR Genes & Dev. 20, 3269–3282 (2006)





 Simulations replicate interaction with filaments - suggests motion in a filament concentration gradient

but without fluid flow





Particle interacts with the concentration field and moves





Particle interacts with the concentration field and moves down the gradient if it is repelled





Particle interacts with the concentration field and moves up the gradient if it is attracted





Particle interacts with the concentration field and moves up the gradient if it is attracted

In self-diffusiophoresis the particle itself generates the concentration gradient





HOWSE ET AL Phys. Rev. Lett. 99, 048102 (2007)



A PARED DOWN MODEL



Rest frame of the particle

- Spherical particle
- Axisymmetry, steady state
- Single solute species
- Purely radial potential with compact support
- Zero Reynolds number



GOLESTANIAN, LIVERPOOL & AJDARI Phys. Rev. Lett. 94, 220801 (2005) GOLESTANIAN, LIVERPOOL & AJDARI New J. Phys. 9, 126 (2007)

Motion involves a balance between diffusion and advection

 $Pe = \frac{advection}{diffusion} = \frac{Ua}{D}$

Diffusion dominated



HOWSE ET AL Phys. Rev. Lett. 99, 048102 (2007)

Advection dominated



Courtesy of Julie Theriot http://cmgm.stanford.edu/theriot/movies.htm



BOUNDARY LAYER ANALYSIS



The interaction occurs close to the surface in a boundary layer of thickness δ

Solve Stokes in the upper half space

$$\mathbf{0} = -\nabla p + \mu \nabla^2 \mathbf{u} - c \,\nabla V \qquad \mathbf{0} = \nabla \cdot \mathbf{u}$$



ANDERSON Ann. Rev. Fluid Mech. 21, 61–99 (1989) JÜLICHER, PROST Eur. Phys. J. E 29, 27–36 (2009)

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Tangential slip velocity

$$\mathbf{u}^{\mathrm{slip}} = m^D \nabla_{\parallel} c \big|_{z=1}$$

diffusiophoretic mobility (Derjaguin)

$$m^{D} = \frac{k_{B}T}{\mu} \delta^{2} \int_{0}^{1} \mathrm{d}z \, z \left[1 - \mathrm{e}^{-V/k_{B}T} \right]$$

ANDERSON Ann. Rev. Fluid Mech. 21, 61–99 (1989) JÜLICHER, PROST Eur. Phys. J. E 29, 27–36 (2009)



SQUIRMERS



Slip velocity provides an inner boundary condition for the exterior flow

General solution provided by Lighthill's squirmer model

$$u_r = U \left[1 - \left(\frac{a}{r}\right)^3 \right] \cos(\theta) + \sum_{l=2}^{\infty} B_l \left[\left(\frac{a}{r}\right)^l - \left(\frac{a}{r}\right)^{l+2} \right] P_l \left(\cos(\theta)\right)$$
$$u_\theta = -U \sin(\theta) + \sum_{l=2}^{\infty} B_l \left[\frac{l-2}{2} \left(\frac{a}{r}\right)^l - \frac{l}{2} \left(\frac{a}{r}\right)^{l+2} \right] V_l \left(\cos(\theta)\right)$$

Matching the boundary condition gives the speed

$$U = \frac{2m^{D}}{3a} c_{1}$$

first Legendre coefficient
 $c|_{r=a+\delta} = \sum_{l=0}^{\infty} c_{l} P_{l}(\cos(\theta))$

BLAKE J. Fluid Mech 46, 199–208 (1971) LIGHTHILL Commun. Pure Appl. Math. 5, 109–118 (1952)



SOLUTE PROFILE

 $u_{ heta}^{ ext{slip}}$

V(r

a

Outside the boundary layer the solute is conserved

 $\partial_t c + \mathbf{u} \cdot \nabla c - D\nabla^2 c = 0$

Rate of transport across the boundary layer equals rate of production

$$\int_{r=a+\delta} \left(u_r^{\rm slip} c - D\partial_r c \right) = \int_{r=a} \alpha$$



ANDERSON Ann. Rev. Fluid Mech. **21**, 61–99 (1989) GOLESTANIAN, LIVERPOOL & AJDARI Phys. Rev. Lett. **94**, 220801 (2005) GOLESTANIAN, LIVERPOOL & AJDARI New J. Phys. **9**, 126 (2007)

SOLUTE PROFILE

 $u_{ heta}^{ ext{slip}}$

V(r

a

Outside the boundary layer the solute is conserved



Rate of transport across the boundary layer equals rate of production

$$\int_{r=a+\delta} (u \wedge c - D\partial_r c) = \int_{r=a} \alpha$$
solve pointwise

$$c(r,\theta) = \sum_{l=0}^{\infty} \frac{a+\delta}{(l+1)D} \alpha_l \left(\frac{a+\delta}{r}\right)^{l+1} P_l(\cos(\theta))$$

ANDERSON Ann. Rev. Fluid Mech. **21**, 61–99 (1989) GOLESTANIAN, LIVERPOOL & AJDARI Phys. Rev. Lett. **94**, 220801 (2005) GOLESTANIAN, LIVERPOOL & AJDARI New J. Phys. **9**, 126 (2007)





Boundary layer analysis neglects

fluid continuity; radial slip

$$\frac{1}{r^2}\partial_r \left(r^2 u_r\right) + \frac{1}{r\sin(\theta)}\partial_\theta \left(\sin(\theta)u_\theta\right) = 0$$

not constant





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not constant







- fluid continuity; radial slip
- topology of the sphere







boundary

layer

U

a

 $u_{ heta}^{ ext{slip}}$

I(r



Boundary layer analysis neglects

- fluid continuity; radial slip
- topology of the sphere



Neglecting the radial slip is not a good approximation near $\theta = 0, \pi$

consequence of topology rather than axisymmetry (Poincaré-Hopf)



Boundary layer analysis neglects

- fluid continuity; radial slip $u_r^{\text{slip}} \sim \frac{\delta}{a} u_{\theta}^{\text{slip}}$
- topology of the sphere Poincaré-Hopf

Such a simple problem can be solved exactly

$$\mathbf{0} = -\nabla p + \mu \nabla^2 \mathbf{u} - \mathbf{e}_r \, c(r,\theta) \,\partial_r V \qquad \mathbf{0} = \nabla \cdot \mathbf{u}$$

- Spherical particle
- Axisymmetry, steady state
- Single solute species
- Purely radial potential
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E.g., the speed is

$$U = \frac{2}{3a} \frac{k_B T}{\mu} c_1 \delta^2 \int_0^1 \mathrm{d}z \, z \left(1 - \frac{\delta}{6a} \frac{3z + 2\delta z^2/a}{(1 + \delta z/a)^2} \right) \left[1 - \mathrm{e}^{-V/k_B T} \right]$$





Boundary layer analysis neglects

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scaling $U \sim \frac{k_B T \alpha_1}{\mu D} \, \delta^2 \left(1 + \frac{\delta}{a} \right)$

SABASS, SEIFERT Phys. Rev. Lett. **105**, 218103 (2010) Alexander & Idema in preparation (2011)



BOUNDARY LAYER FLOW





ALEXANDER & IDEMA in preparation (2011)

BOUNDARY LAYER FLOW





ALEXANDER & IDEMA in preparation (2011)

WHAT CHANGES IF THE PÉCLET NUMBER IS LARGE?



 concentration gradients drive tangential flow in a thin boundary layer

postulate $\mathbf{u}^{\text{slip}} = m^A \nabla_{\parallel} c$



U



WHAT CHANGES IF THE PÉCLET NUMBER IS LARGE?



Basic mechanism remains unchanged

 concentration gradients drive tangential flow in a thin boundary layer

postulate $\mathbf{u}^{\text{slip}} = m^A \nabla_{\parallel} c$

But ...

- if the solute does not diffuse then it will only be found where it is produced
- tangential slip only generated within the active patch
- radial influx at the boundary and outflux from the interior



SOLUTE TRANSPORT

Outside the boundary layer the solute is conserved

$$\partial_t c + \mathbf{u} \cdot \nabla c - D\nabla^2 c = 0$$

Rate of transport across the boundary layer equals rate of production

$$\int_{r=a+\delta} \left(u_r^{\text{slip}} c - D\partial_r c \right) = \int_{r=a} \alpha$$



U



SOLUTE TRANSPORT

Outside the boundary layer the solute is conserved

$$\partial_t c + \mathbf{u} \cdot \nabla c - D \mathbf{x}^2 c = 0 \quad \text{Pe} \gg 1$$

Rate of transport across the boundary layer equals rate of production

$$\int_{r=a+\delta} \left(u_r^{\text{slip}}c - D\sigma_r c \right) = \int_{r=a} \alpha$$

radial slip is important



U

a

u^{slip}

 $u_{ heta}^{ ext{slip}}$

(z)

 $u_r^{
m slip}$

RADIAL SLIP



U

Radial outflux

$$2\pi(a+\delta)^2 \int_0^{\theta_q} \mathrm{d}\theta \,\sin(\theta) \, u_r^{\mathrm{slip}}$$

Tangential influx



$$U \sim \frac{m^D \bar{\alpha}}{D} \, \sin^2(\theta_p)$$



$$U \sim \left(\frac{m^A \bar{\alpha}}{\delta \ln\left(\frac{a}{\delta}\right)}\right)^{1/2} \sin^3\left(\frac{1}{2}\theta_p\right)$$





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$$V$$
 $Pe \gg 1$

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Transport balance $\int_{r=a+\delta} \left(u_r^{\text{slip}}c - D\partial_r c \right) = \int_{r=a} \alpha$ $\propto |u_{\theta}^{\text{slip}}|$







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Transport balance $\int_{r=a+\delta} (u_r^{\text{slip}}c - D\partial_r c) = \int_{r=a} \alpha$ $\propto |\sin(\theta)u_{\theta}^{\text{slip}}| \qquad \propto |u_{\theta}^{\text{slip}}|$ $\text{by fluid continuity} \qquad \text{by postulate}$





$$U \sim \frac{m^D \bar{\alpha}}{D} \sin^2(\theta_p)$$



$$U \sim \left(\frac{m^A \bar{\alpha}}{\delta \ln\left(\frac{a}{\delta}\right)}\right)^{1/2} \sin^3\left(\frac{1}{2}\theta_p\right)$$





$$U \sim \frac{m^D \bar{\alpha}}{D} \sin^2(\theta_p)$$

$$U \sim \alpha_1 \sim \int_{\cos(\theta_p)}^1 \mathrm{d}s \, s\bar{\alpha}$$
$$\sim \sin^2(\theta_p)$$

first Legendre coefficient of activity



$$U \sim \left(\frac{m^A \bar{\alpha}}{\delta \ln\left(\frac{a}{\delta}\right)}\right)^{1/2} \sin^3\left(\frac{1}{2}\theta_p\right)$$

 $U \sim \int_0^{\theta_p} \mathrm{d}\theta \, \sin^2(\theta) u_{\theta}^{\mathrm{slip}}$ $\sim \sin^2\left(\frac{1}{2}\theta_p\right)$

by, e.g., Stone & Samuel

tangential flux is conserved



STONE & SAMUEL Phys. Rev. Lett. 77, 4102–4104 (1996)



$$U \sim \frac{m^D \bar{\alpha}}{D} \sin^2(\theta_p)$$



$$U \sim \left(\frac{m^A \bar{\alpha}}{\delta \ln\left(\frac{a}{\delta}\right)}\right)^{1/2} \sin^3\left(\frac{1}{2}\theta_p\right)$$

does not vanish for total coverage $\theta_p \to \pi$





$$U \sim \frac{m^D \bar{\alpha}}{D} \sin^2(\theta_p)$$





$$U \sim \left(\frac{m^A \bar{\alpha}}{\delta \ln\left(\frac{a}{\delta}\right)}\right)^{1/2} \sin^3\left(\frac{1}{2}\theta_p\right)$$

does not vanish for total coverage $\theta_p \to \pi$

is state of total coverage unstable?
if so, what is the critical Péclet number for the instability?

Penn

CAMERON ET AL Proc. Natl. Acad. Sci. USA 96, 4908-4913 (1999)

DIFFERENT SCENARIOS





$$U \sim \frac{m^D \bar{\alpha}}{D} \, \sin^2(\theta_p)$$



FOUR SCENARIOS

repulsive producer attractive producer

 $V > 0, \ \alpha > 0$ $V < 0, \ \alpha > 0$

repulsive consumer $V > 0, \ \alpha < 0$ $V < 0, \ \alpha < 0$

attractive consumer



DIFFERENT SCENARIOS



$$U \sim \frac{m^D \bar{\alpha}}{D} \, \sin^2(\theta_p)$$



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FOUR SCENARIOS

repulsive producer attractive producer

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- Droplets containing a catalyst dispersed in a bulk fuel
- Fuel hydrolysed at the surface
- Waste product accumulates on the surface and is released at the rear
- Self-maintained surface tension gradients drive Marangoni flows



TOYOTA ET AL J. Am. Chem. Soc. 131, 5012–5013 (2009)



Rest frame of the particle

- Spherical particle
- Axisymmetry, steady state
- Single solute species
- Purely radial potential with compact support
- Zero Reynolds number
- Zero Péclet number



LEVICH, KRYLOV Ann. Rev. Fluid Mech. 1, 293–316 (1969) LEVICH, KUZNETSOV Dokl. Akad. SSSR 146, 145–147 (1962) REDNIKOV, RYAZANTSEV, VERLARDE Phys. Fluids 6, 452–468 (1994)



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Stress balance at the interface



LEVICH, KRYLOV Ann. Rev. Fluid Mech. 1, 293–316 (1969) LEVICH, KUZNETSOV Dokl. Akad. SSSR 146, 145–147 (1962) REDNIKOV, RYAZANTSEV, VERLARDE Phys. Fluids 6, 452–468 (1994)



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Spherical particle

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Solve as before; e.g., the speed is

$$U = \frac{k_B T}{3\mu} \frac{\mu + \tilde{\mu}}{\mu + \frac{3}{2}\tilde{\mu}} \frac{c_1 \delta^2}{a} \int_0^1 dz \left(\left(2 + \frac{\tilde{\mu}}{\mu + \tilde{\mu}} \right) z + \frac{\mu}{\mu + \tilde{\mu}} \frac{a}{\delta} - \frac{\delta}{2a} \frac{\tilde{\mu}}{\mu + \tilde{\mu}} \frac{3z^2 + 2\delta z^3/a}{(1 + \delta z/a)^2} \right) \left[1 - e^{-V/k_B T} \right]$$





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 $\begin{array}{ll} \mbox{limit} \ \frac{\mu}{\tilde{\mu}} \to 0\\ \mbox{(solid particle)} \end{array}$

$$U \sim \frac{k_B T \alpha_1}{\mu D} \, \delta^2$$

independent of particle size

$$U \sim \frac{k_B T \alpha_1}{\mu D} \, a\delta$$

limit $\frac{\tilde{\mu}}{\mu} \to 0$ (gas bubble)

proportional to particle radius



ACTIVITY ON THE INSIDE



Rest frame of the particle

- No need for a favourable environment
 -- take everything you need with you!
- "Clean" system; everything is internal
- Only interaction between droplets is hydrodynamic



ACTIVITY ON THE INSIDE



Rest frame of the particle

- No need for a favourable environment
 -- take everything you need with you!
- "Clean" system; everything is internal
- Only interaction between droplets is hydrodynamic

Solve as before; e.g., the speed is

$$U = \frac{k_B T}{3\mu} \frac{\mu}{\mu + \frac{3}{2}\tilde{\mu}} \tilde{c}_1 \tilde{\delta} \int_0^1 \mathrm{d}z \left(1 - 5\frac{\tilde{\delta}}{a}z + 6\left(\frac{\tilde{\delta}}{a}\right)^2 z^2 - 2\left(\frac{\tilde{\delta}}{a}\right)^3 z^3\right) \left[1 - \mathrm{e}^{-\tilde{V}/k_B T}\right]$$

Scaling

$$U \sim \frac{k_B T \alpha_1}{\mu D} \frac{\mu}{\mu + \frac{3}{2}\tilde{\mu}} a\tilde{\delta}$$

same as the "gas bubble"



SURFACE TENSION GRADIENTS



Rest frame of the particle

- Activity due to a surface active catalyst
- Surface adsorbed species lower the surface tension
- Chemical reaction near surface produces local heating; lowers surface tension
- Non-uniform surface tension drives Marangoni flows

Stress balance at the interface





PEARSON J. Fluid Mech. 4, 489–500 (1958) STERNLING, SCRIVEN AICHE J. 5, 514–523 (1959) LEVICH, KRYLOV Ann. Rev. Fluid Mech. 1, 293–316 (1969)

SURFACE TENSION GRADIENTS



Rest frame of the particle

- Activity due to a surface active catalyst
- Surface adsorbed species lower the surface tension
- Chemical reaction near surface produces local heating; lowers surface tension
- Non-uniform surface tension drives Marangoni flows

Additional contribution to the speed

$$\frac{\mu + \tilde{\mu}}{3\mu\left(\mu + \frac{3}{2}\tilde{\mu}\right)}\gamma_1$$

typically surface tension is **lowered** so that γ_1 is **negative** Marangoni flows then **oppose** self-diffusiophoresis



SURFACE TENSION GRADIENTS



Rest frame of the particle

rat

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Additional contribution to the speed

$$\frac{\mu + \tilde{\mu}}{3\mu\left(\mu + \frac{3}{2}\tilde{\mu}\right)}\gamma_1$$

io
$$\frac{\text{Marangoni}}{\text{diffusiophoresis}} \sim \frac{\mu + \tilde{\mu}}{\mu} \frac{D\gamma_1}{k_B T \alpha_1 a \delta}$$

can this be made small?



DROPLET DEFORMATION



Rest frame of the particle

- Particle is a fluid droplet -- no reason why it won't deform
- Normal stress balance is really an equation for the drop shape

droplet remains approximately spherical provided



Stress balance at the interface



Penn

TAYLOR Proc. Roy. Soc. Lond. A 146, 501-523 (1934)
TAYLOR, ACRIVOS J. Fluid Mech. 18, 466-476 (1964)
STONE, LEAL J. Fluid Mech. 220, 161-186 (1990)

THANKS!

ANDREA LIU, TIMON IDEMA



- High Péclet number relevant to biological motility
- Different scaling with activity, dependence on coverage and successful strategies



- Fluid drops can move due to internal motor
- "Clean" system
- Faster than a solid particle

Acknowledgements

We are grateful to Ed Banigan and Kun-Chun Lee for beneficial discussions and to Randy Kamien for his support and encouragement

FUNDING



NSF DMR05-47230 UPENN-MRSEC DMR05-20020

