FLIP FLOPS IN BACTERIAL FLAGELLA

DAN COOMBS
RAY GOLDSTEIN } ARIZONA
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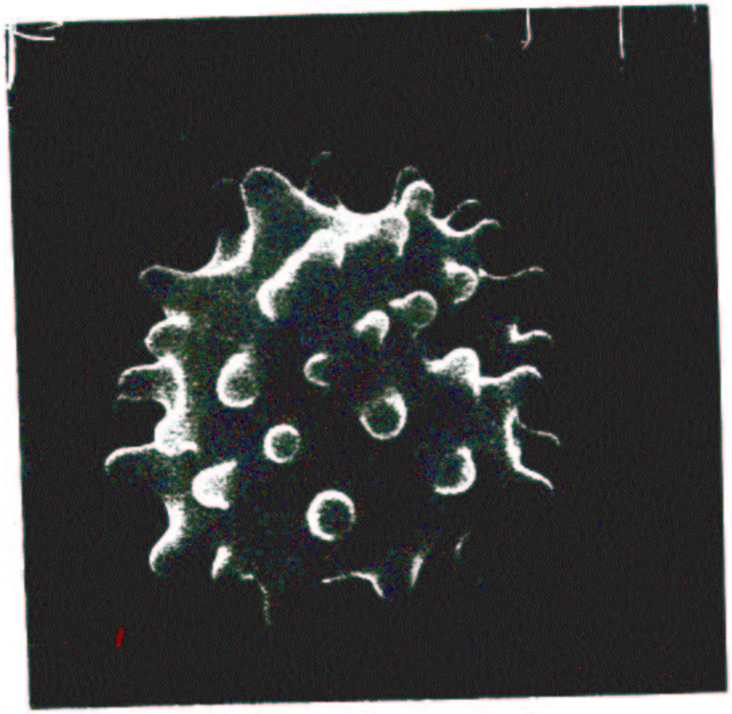
SPECIAL THX: ALAIN GORIELY
TOM POWERS
CH. WOLGEMUTH

SECRETS OF ALIEN TECHNOLOGY REVEALED !!!



HOW DO BACTERIA SWIM?

Salmonella

STOKES FLOW

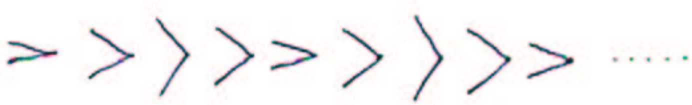
$$\vec{\nabla}\cdot\vec{u} = 0$$

$$\vec{\nabla}p = \mu\nabla^2\vec{u} + \vec{F}$$

RESULT FROM DROPPING INERTIAL TERMS FROM NAVIER-STOKES. VALID WHEN $Re = UL\rho/\mu \ll 1$.

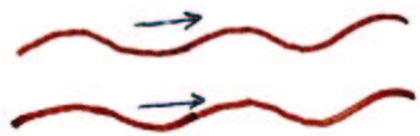
PROPERTIES: LINEAR, NO TIME! $\nabla\cdot(\text{EQ}) \to$ HARMONIC EQS.

BEAUTIFUL PROPERTIES: "SCALLOP THM." (PURCELL, 1977)



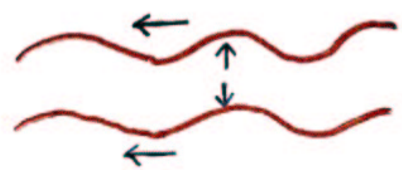
SYMMETRY ARGUMENTS

CONSIDER TWO INFINITE SHEETS WITH SINE-WAVES MOVING TO THE RIGHT



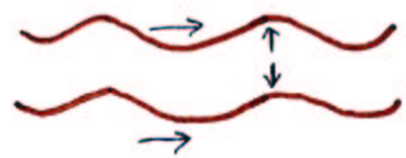
SUPPOSE THEY MOVE IN SYNCH AND MOVE CLOSER.

TIME REVERSE ⇓

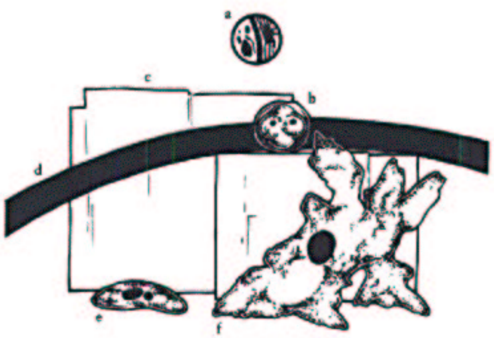


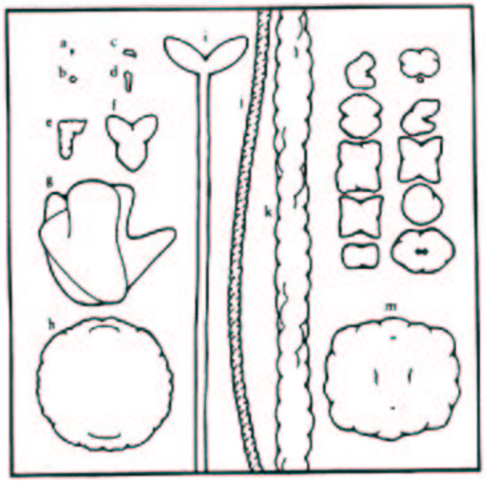
THEY ARE NOW LEFT-MOVING, AND MOVING APART.

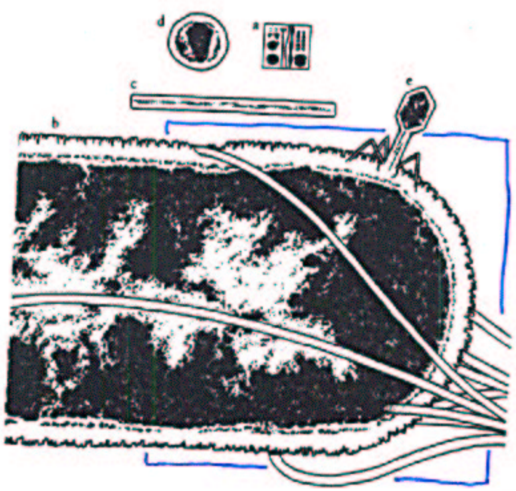
ROTATE BY 180° ↻



WAVES ARE NOW RIGHT-MOVING AND MOVING APART.

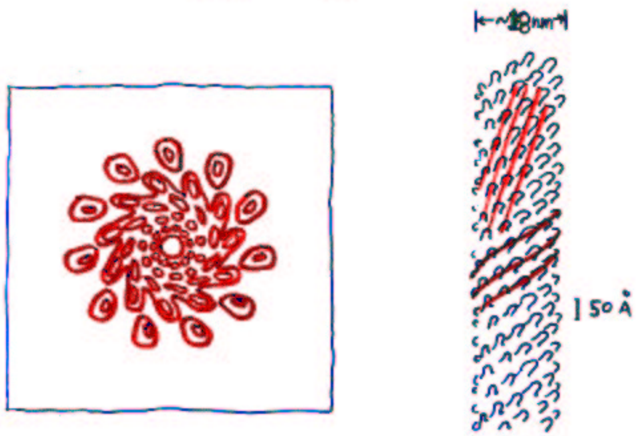






BACTERIA

FLAGELLAR FILAMENT FINE STRUCTURE
(e.g. E. coli)



DENSITY CONTOUR MAP

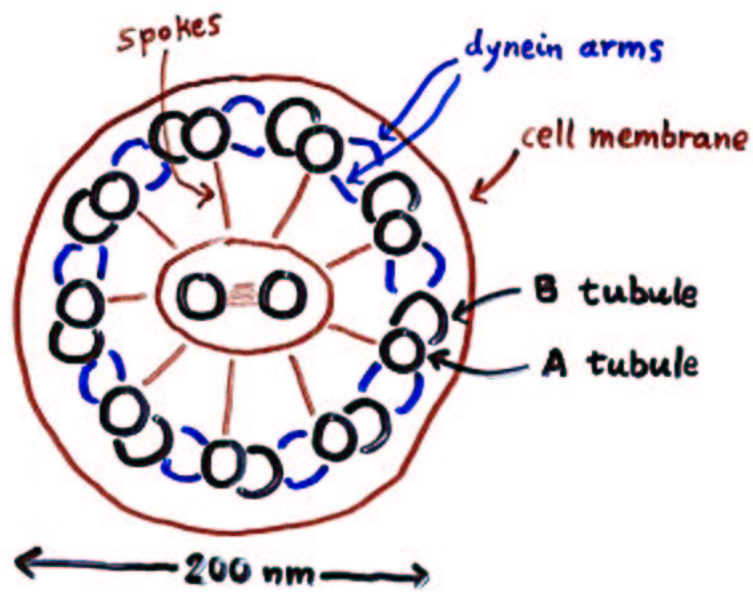
3-D RECONSTRUCTION

(FROM DEROSIER'S LAB)

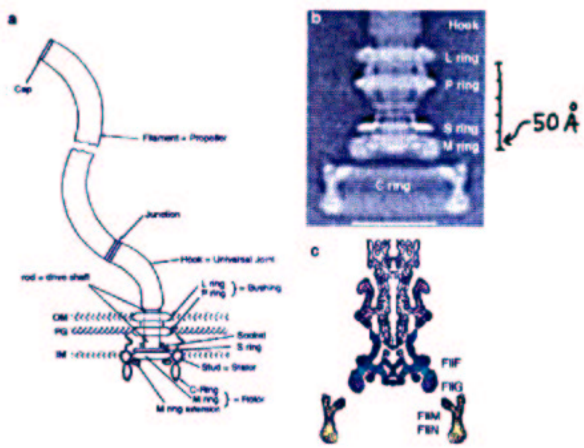
EUKARYOTES

(e.g. mammalian sperm)

FILAMENT FINE STRUCTURE



FLAGELLUM & MOTOR



from D.J. DeROSIER CELL 93 17 (1998).

N.R. FRANCIS et al. J. MOLEC. BIOL. 235 1261 (1994).

Bacterial Flagellar Motor Structure 1267

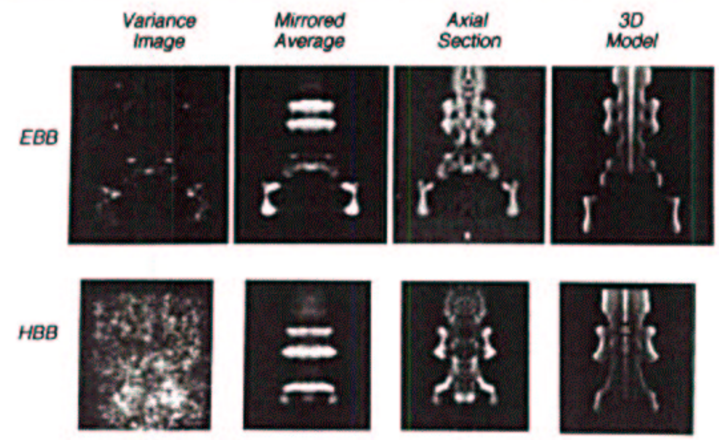
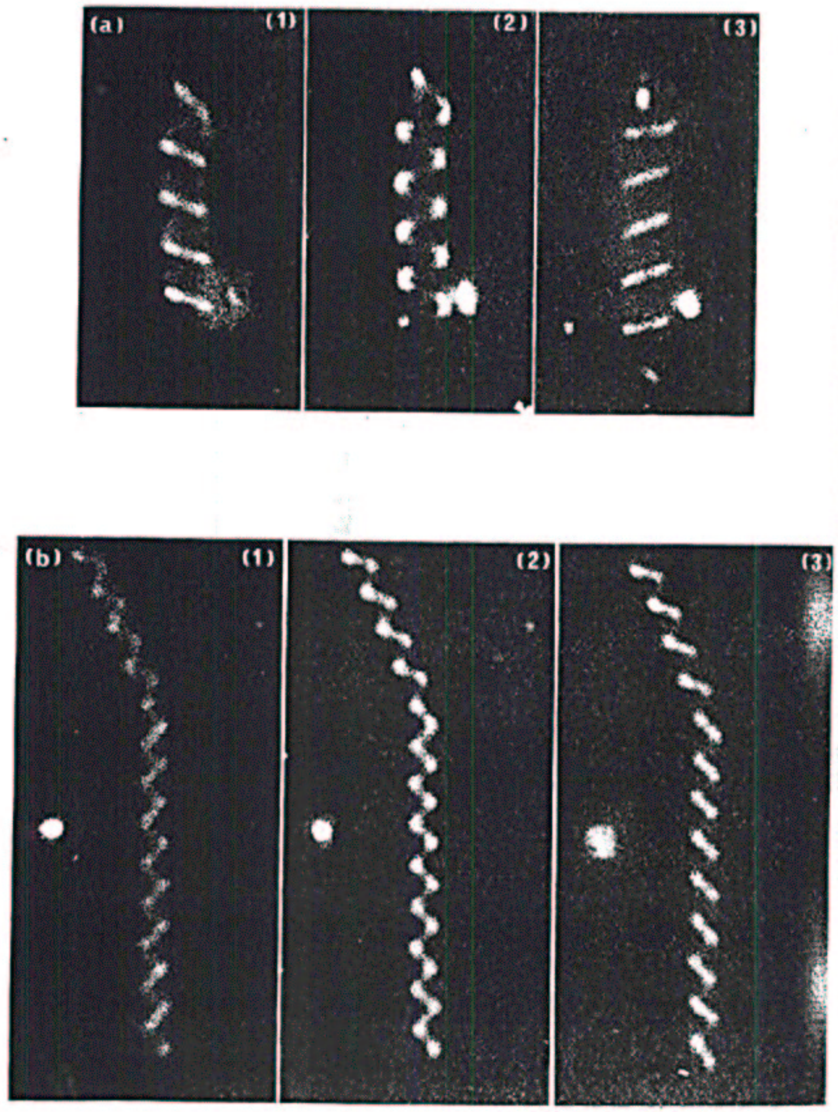
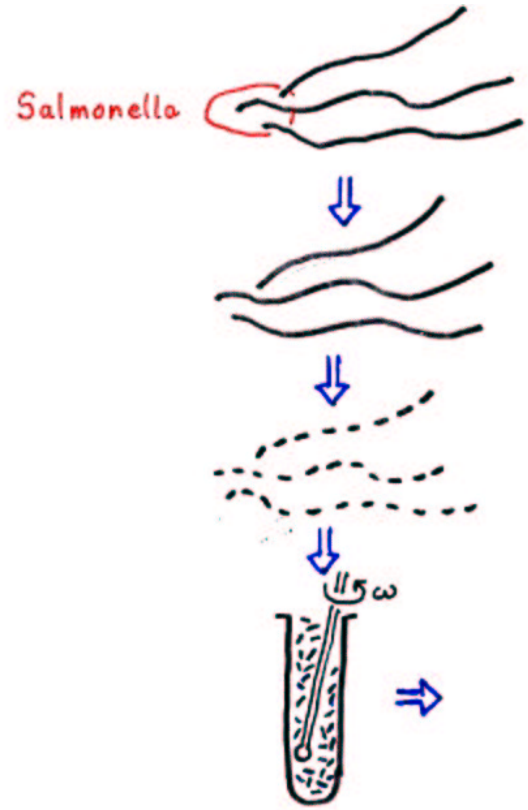
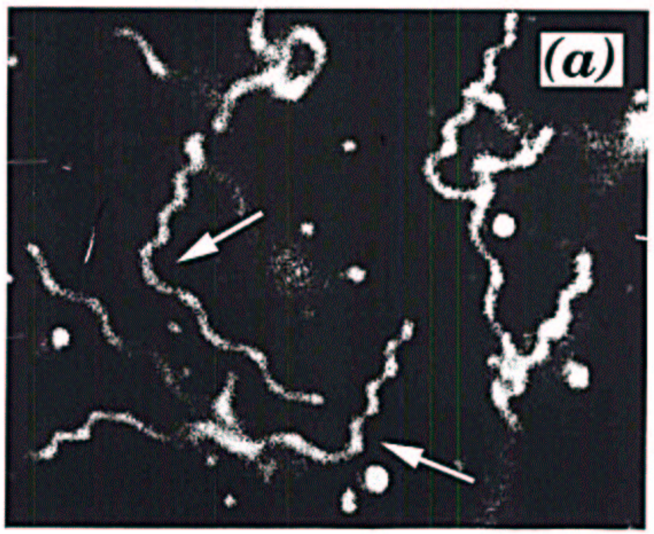


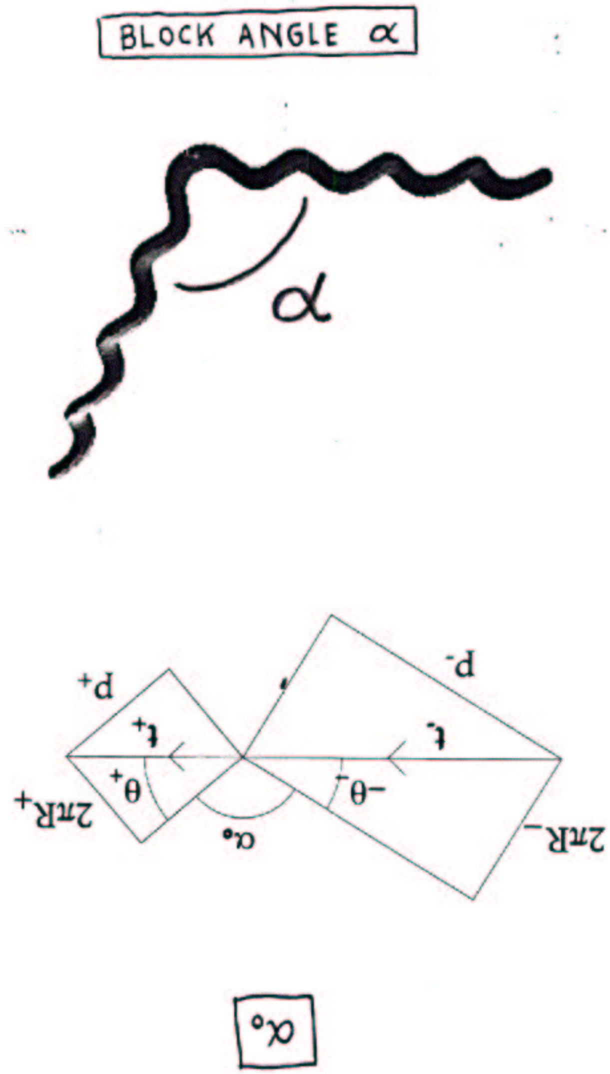
Figure 4. Image averages and 3-dimensional reconstruction of extended basal bodies and standard basal bodies. Variances, mirror-symmetrized averages, axial sections from the cylindrical reconstructions, and 3-dimensional models are shown for both the C ring complex containing basal body (EBB) (top panel) and basal bodies (HBB) prepared by the Aizawa *et al.* (1985) procedure (bottom panel); reprinted from Sosinsky *et al.* (1992*a*).



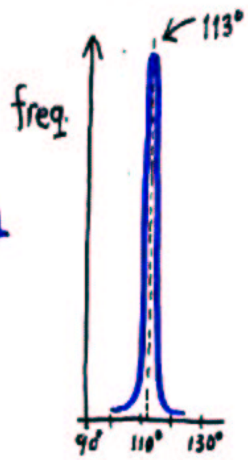
H. Hotani, J. Mol. Biol. 106 (1976) 151.




(a)


BLOCK ANGLE α
α

CURLY-NORMAL

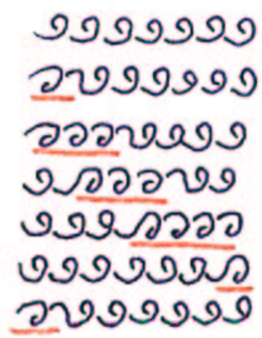


OTHER "BISTABLE" EXPERIMENTS

Bacterial flagella display "chirality inversions" under dynamical circumstances

(i) motor reversal (Macnab, Berg)

(ii) external flow (Hotani)



~ periodic traveling domains of flipped chirality

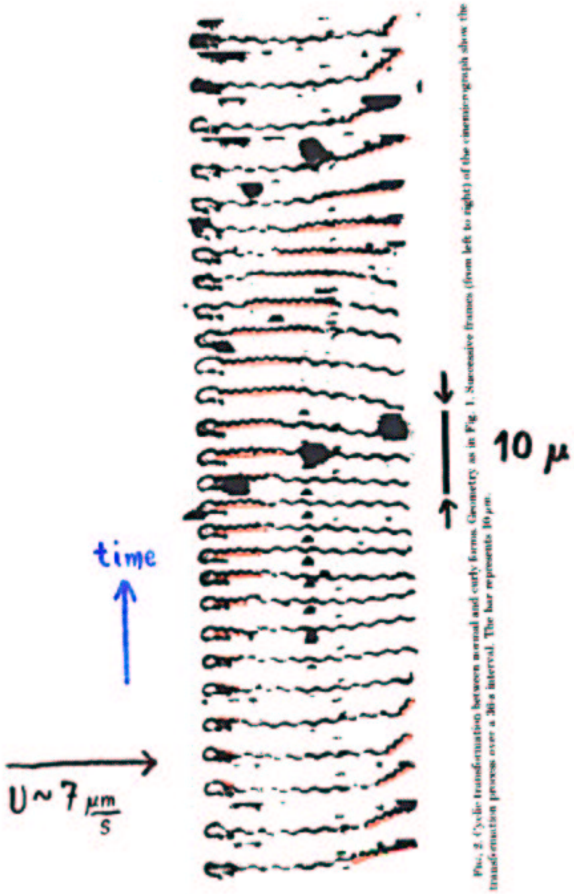
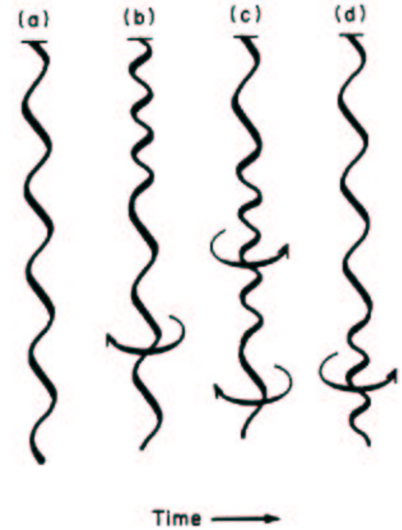


FIG. 2. Cyclic transformation between normal and curly forms. Geometry as in Fig. 1. Successive frames (from left to right) of the cinemicrograph show the transformation process over a 36-s interval. The bar represents 10 μm.



FIGURES

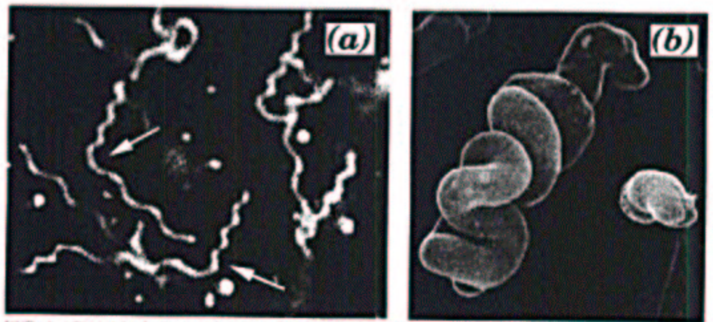
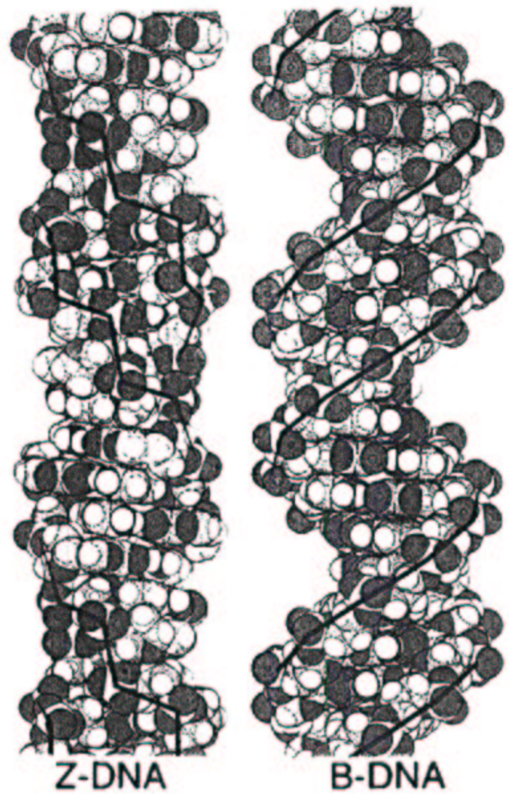
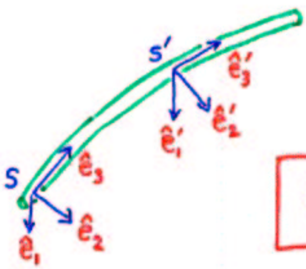


FIG. 1. Bistable helices. (a) Flagella of *Salmonella*, with coexisting left- and right-handed helices (arrows), courtes of H. Hotani. (b) Solenoidal form of *B. subtilis* fiber, with coexisting helices, courtesy of M. Tilby. Scale bars: 5 and 2 μm.



ELASTIC FILAMENT ENERGETICS



rotation of material frame

$$\boxed{\partial_s \hat{e}_i = \vec{\Omega}\times\hat{e}_i}$$

$$\boxed{\mathcal{E} = \int ds\left\{\underbrace{\tfrac{1}{2}A(\Omega_1^2+\Omega_2^2)}_{\text{bending}} + \underbrace{\tfrac{1}{2}C\Omega_3^2}_{\text{twisting}} - \Lambda\right\}}$$

Frenet-Serret frame

$$\partial_s \begin{pmatrix}\hat{t}\\ \hat{n}\\ \hat{b}\end{pmatrix} = \begin{pmatrix}0 & \kappa & 0\\ -\kappa & 0 & \tau\\ 0 & -\tau & 0\end{pmatrix}\begin{pmatrix}\hat{t}\\ \hat{n}\\ \hat{b}\end{pmatrix}$$

force/unit length

$$-\frac{1}{\sqrt{g}}\frac{\delta\mathcal{E}}{\delta\vec{r}} = \mathcal{F}_n\hat{n} + \mathcal{F}_b\hat{b} + \mathcal{F}_t\hat{t}$$

⇒ complicated, nonlinear, possibly singular results

Young-Laplace

$$\mathcal{F}_n = -A\left(\kappa_{ss} + \tfrac{1}{2}\kappa^3 - \kappa\tau^2\right) - C\Omega\kappa\tau - \Lambda\kappa$$

$$\mathcal{F}_b = -A(2\kappa_s\tau + \kappa\tau_s) + C(\Omega\kappa)_s$$

$$\mathcal{F}_t = -\Lambda_s$$

Marangoni

DYNAMICS

"ARISTOTELIAN" (force ∝ velocity)

$$\boxed{\zeta\,\vec{r}_t = -\frac{1}{\sqrt{g}}\frac{\delta\mathcal{E}}{\delta\vec{r}}}$$

translational drag coeff.

rotation angle

$$\boxed{\zeta_r\,\chi_t = C\,\Omega_s}$$

rotational drag coeff.

twisting moment density

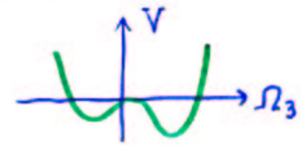
GENERALIZED ELASTICITY FOR BISTABILITY

- A helix is the ground state of energy with intrinsic curvature and intrinsic twist

$$\mathcal{E} = \frac{1}{2}\int_0^L ds\left\{A\left[(\Omega_1-\Omega_1^\circ)^2 + (\Omega_2-\Omega_2^\circ)^2\right] + C(\Omega_3-\Omega_3^\circ)^2\right\}$$

Now generalize this à la Landau:

$$\boxed{\mathcal{E}_\Omega = \int_0^L ds\left\{\tfrac{1}{2}\lambda^2\left(\frac{\partial\Omega_3}{\partial s}\right)^2 + V(\Omega_3)\right\}}$$



Twist dynamics

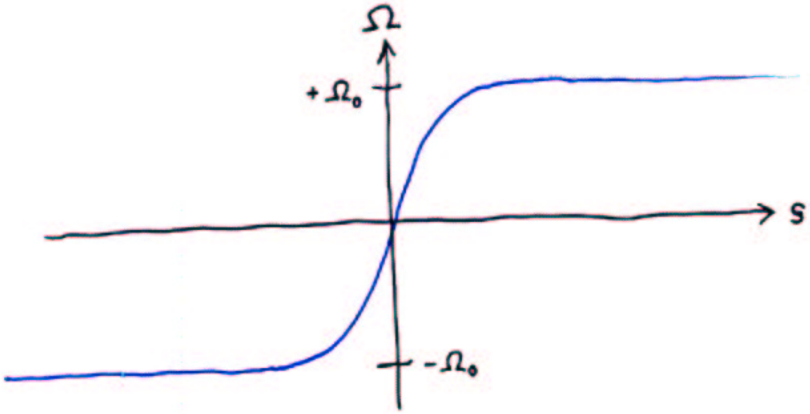
$$\boxed{\zeta_r(\Omega_3)_t = \partial_{ss}\left(\frac{\delta\mathcal{E}_\Omega}{\delta\Omega_3}\right) + \cdots}$$

~ Cahn-Hilliard eqn

Transverse force

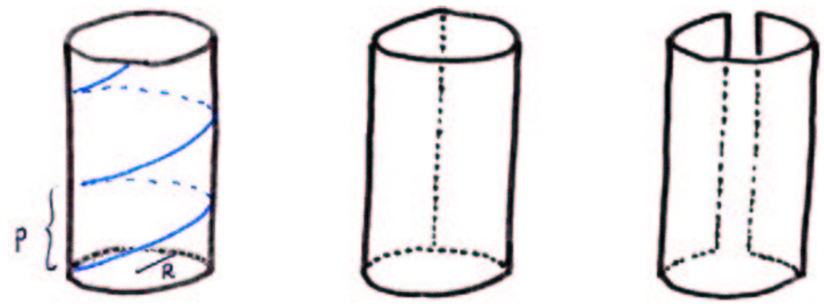
$$\boxed{\mathcal{F}_\perp = -A\left[\partial_{ss}(\psi-\psi_0) + \tfrac{1}{2}\left(|\psi|^2 - |\psi_0|^2\right)\psi\right] + i\left[\frac{\delta\mathcal{E}}{\delta\Omega_3}\psi\right]_s}$$

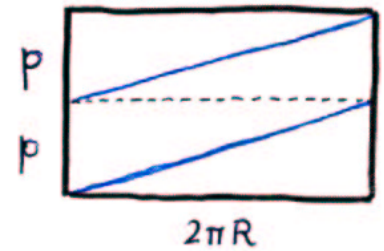
FRONT SOLUTIONS

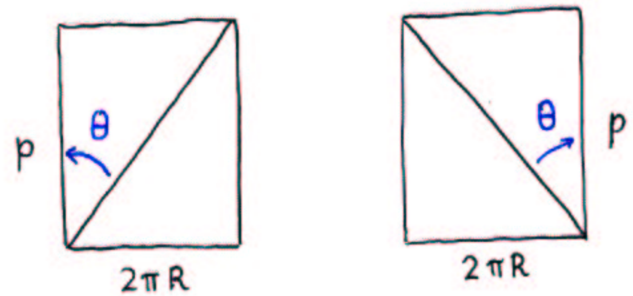


$$\Omega = \Omega_0 \tanh(s/2\xi)$$
$$\psi = \Omega_2^0 \exp(2i\xi\Omega_0 \log[\cosh(s/2\xi)])$$

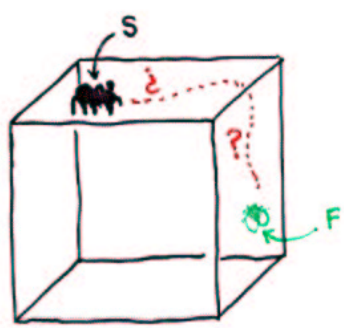
What is the filament shape ?

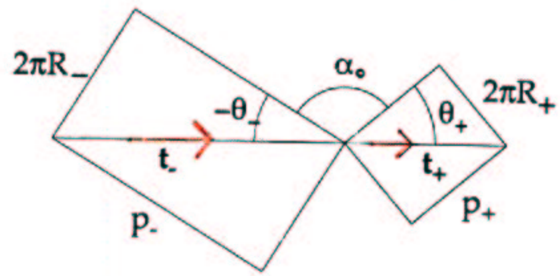






$$\boxed{\frac{2\pi R}{p} = \tan\theta}$$





$$\boxed{\theta_+ + \alpha_0 - \theta_- = \pi}$$

EXAMPLE

$$\begin{aligned}
\alpha_0 &= \pi - \{\theta_+ - \theta_-\} \\
&= 180^\circ - \{39.^\circ 6 - (-31.^\circ 6)\} \\
&= 180^\circ - \{71.^\circ 2\} = 108.^\circ 8
\end{aligned}$$

$$\boxed{\alpha}$$

$$\cos\alpha = \int_{-\infty}^{\infty} ds \, \frac{\kappa\,\Omega_s}{\kappa^2+\Omega^2} \left\{ \int_0^s ds' \sqrt{\kappa^2+\Omega^2} \right\}^2$$

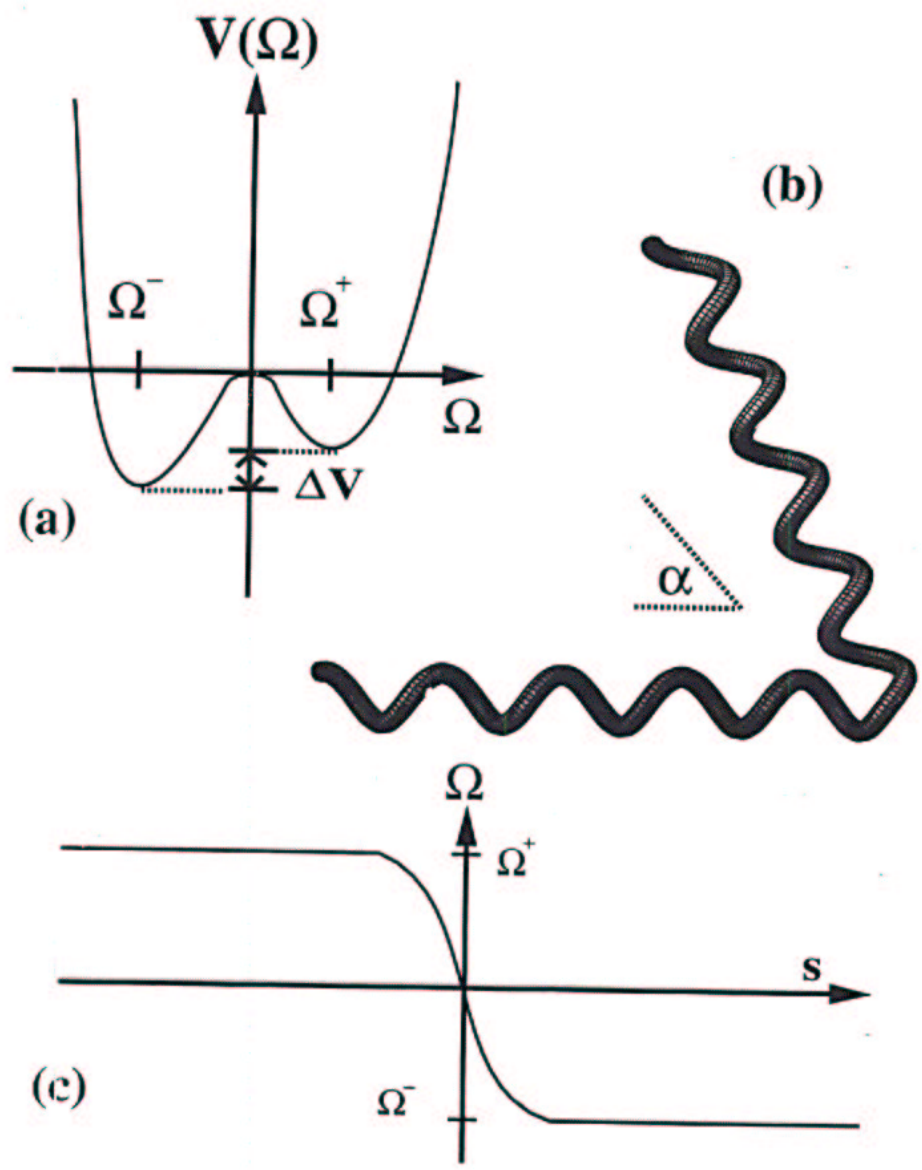
$(\Omega \equiv \Omega_3)$

$$\alpha = \alpha_0 + \underbrace{\mathcal{O}(\xi^2)}_{\pi(\kappa\Omega)\xi^2} \qquad ?$$

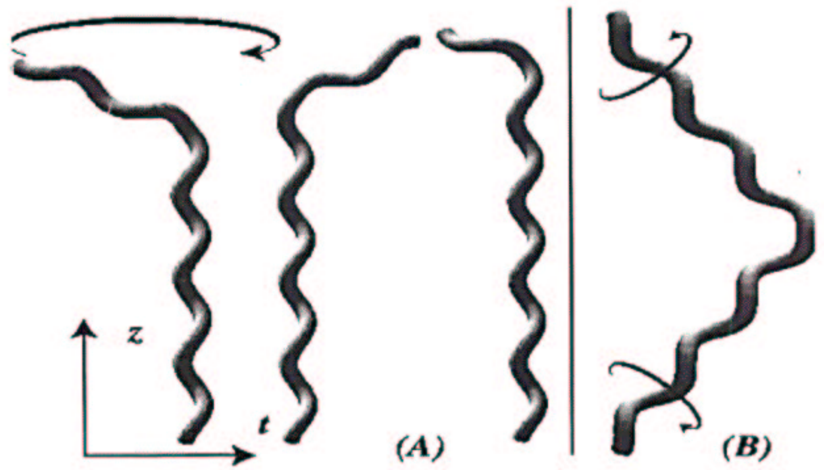
$$\xi_0 = (\kappa\Omega)^{-1/2}$$

$$\Downarrow$$

$$\xi \lesssim 80 \text{ nm}$$



Viscous Fronts of Bistable Helices



CRANKSHAFTING

$P_{cr} \sim \zeta_\perp \omega^2 L^3 \sin^2\alpha$

SPEEDOMETER CABLING

$P_{sp} \sim \zeta_\perp R^2 \omega^2 L$

$\boxed{\text{BOTEC of front speed}}$

$$\underbrace{\zeta_\perp R^2 \omega^2 L}_{\text{lost due to viscous rotation}} \sim \underbrace{\Delta V c}_{\text{generated by flip}}$$

use $\Delta V = \Delta T \cdot \Delta\Omega$

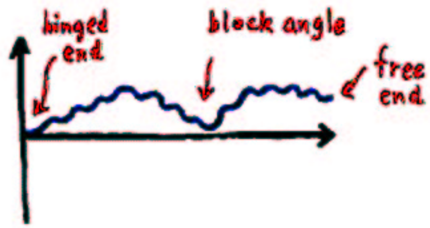
$\omega = \Delta\Omega\, c$

$$c \sim \Delta T / \zeta_\perp R^2 L \,\Delta\Omega$$

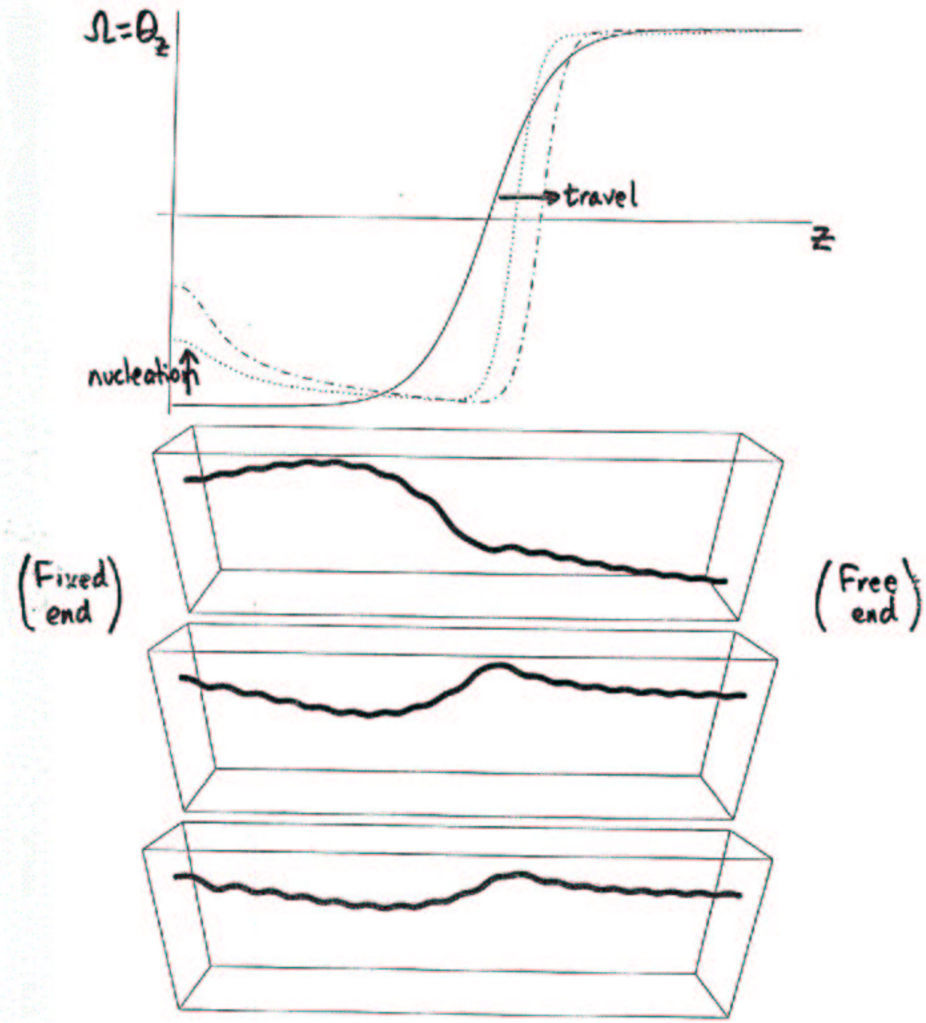
$\Downarrow$

$5 \cdot 10^{-4}$ cm s^{-1}

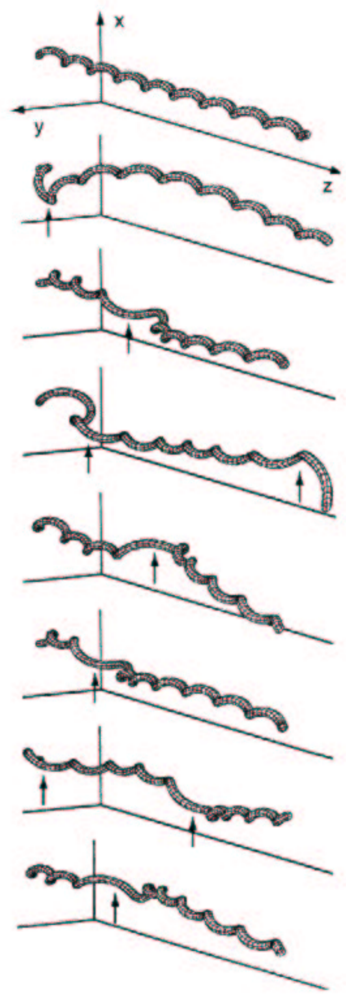
	(cgs)
ΔT	$5 \cdot 10^{-12}$
$\zeta_\perp$	0.5
R	$2 \cdot 10^{-5}$
L	10^{-3}
$\Delta\Omega$	$4 \cdot 10^{4}$

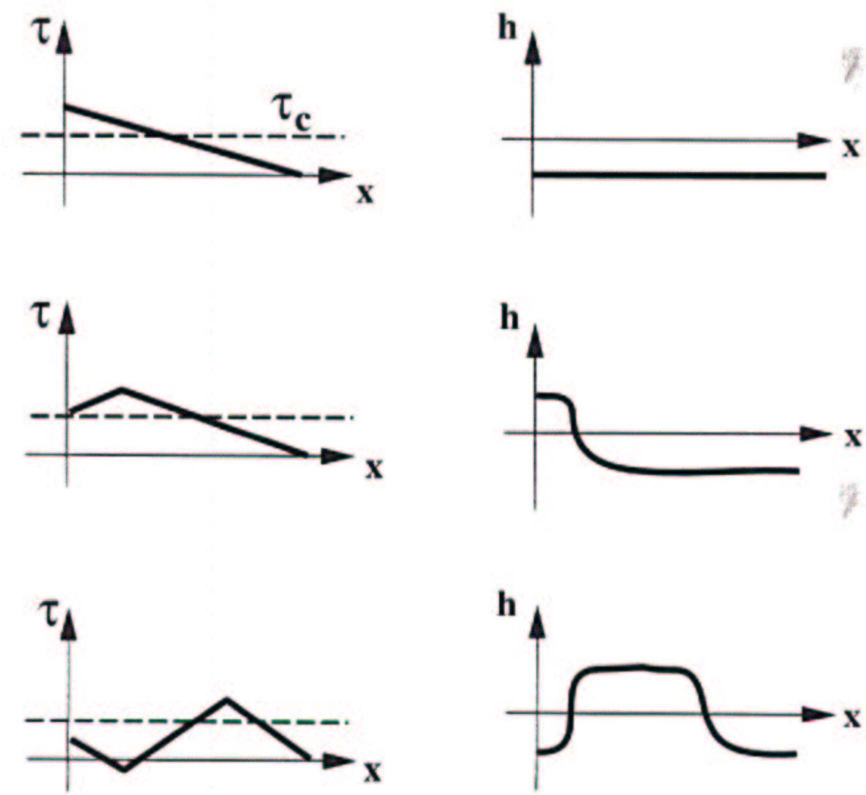


hinged end
block angle
free end



Ω=θ_z
travel
z
nucleation
(Fixed end)
(Free end)


x
y
z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