# Steering Chiral Swimmers

Frank Jülicher

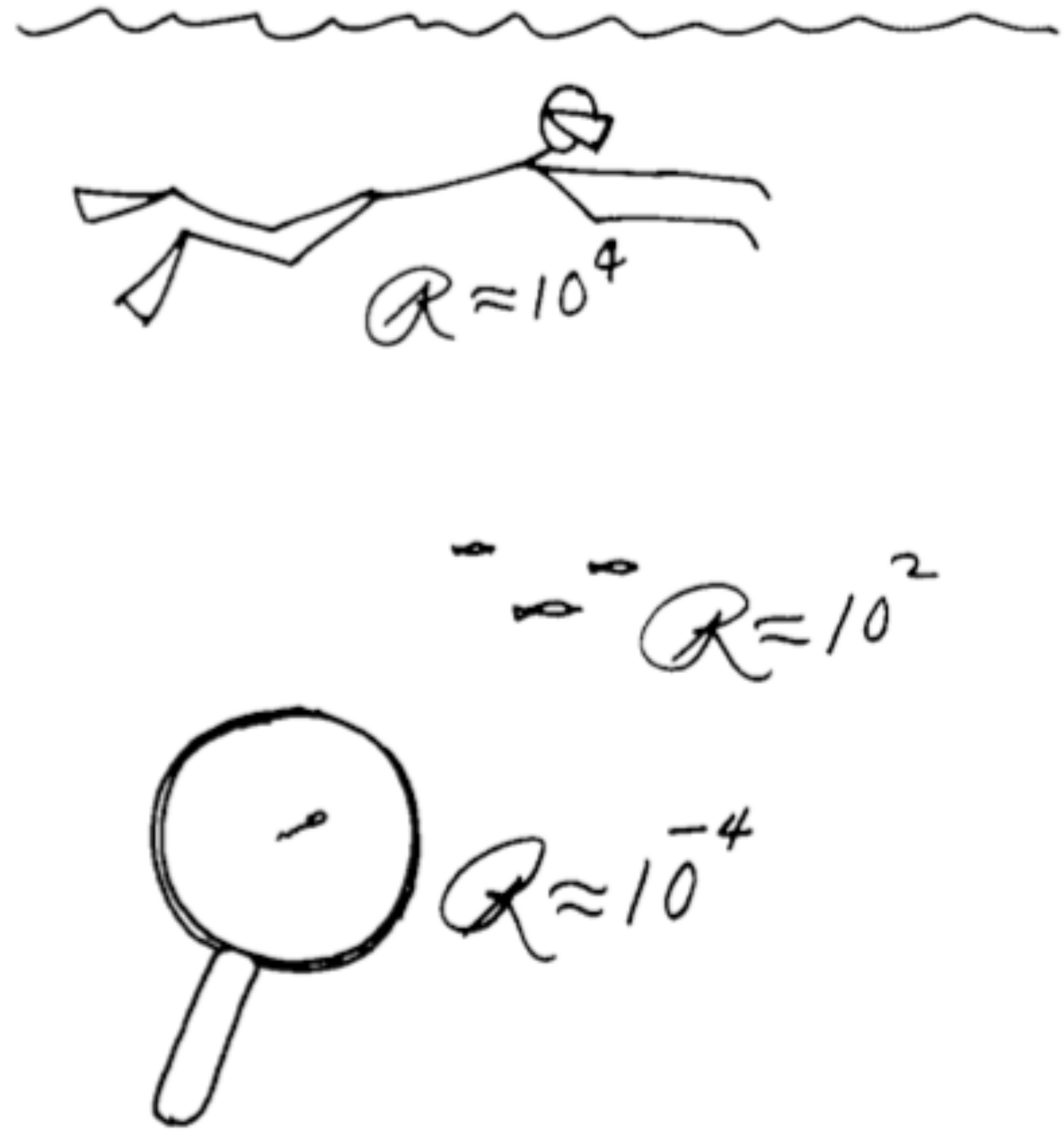
Max Planck Institute
for the Physics of Complex Systems
Dresden, Germany

# Edward Mills Purcell

**Life at low Reynolds number**

E. M. Purcell
*Lyman Laboratory, Harvard University, Cambridge, Massachusetts 02138*
(Received 12 June 1976)

Am. J. Phys. 45 (1977)



## Max Planck Institute for the Physics of Complex Systems

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Andreas Hilfinger
Benjamin Friedrich

S. Grill

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J. Howard
I. Riedel-Kruse
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U.B. Kaupp (Bonn)

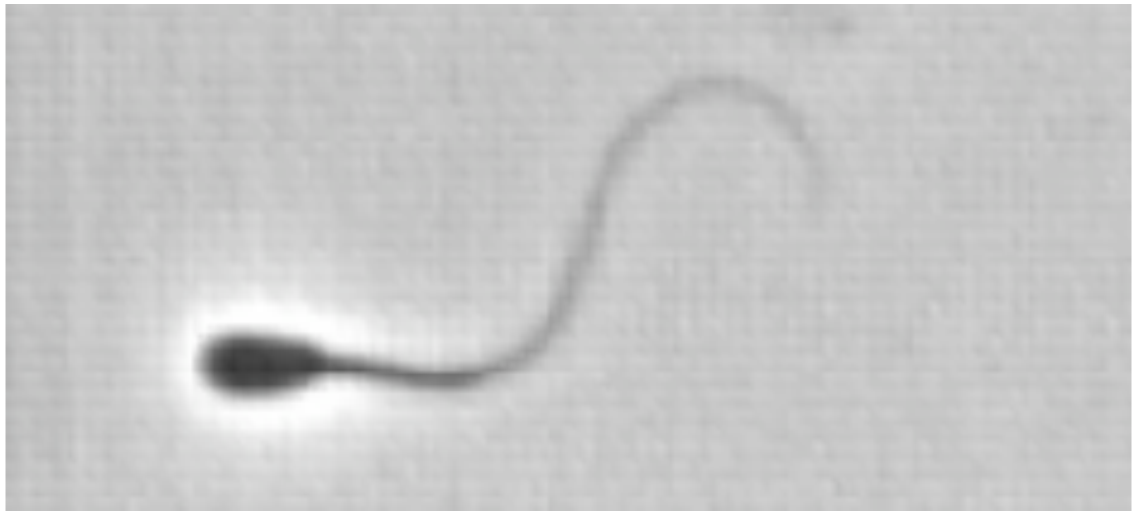
J. Prost (Paris)
J.-F. Joanny (Paris)

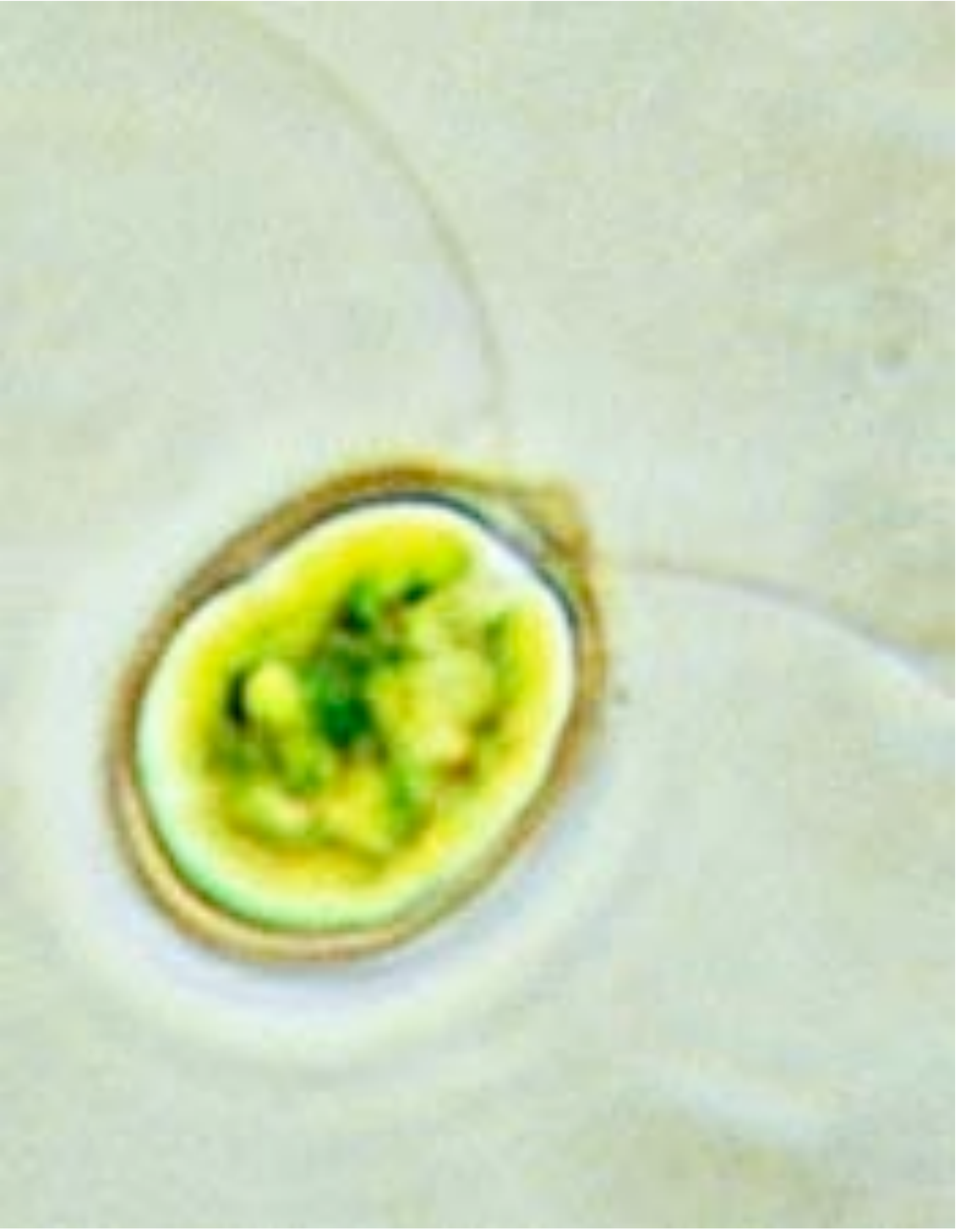
A. Vilfan (Lubljana)

# Ciliar motility

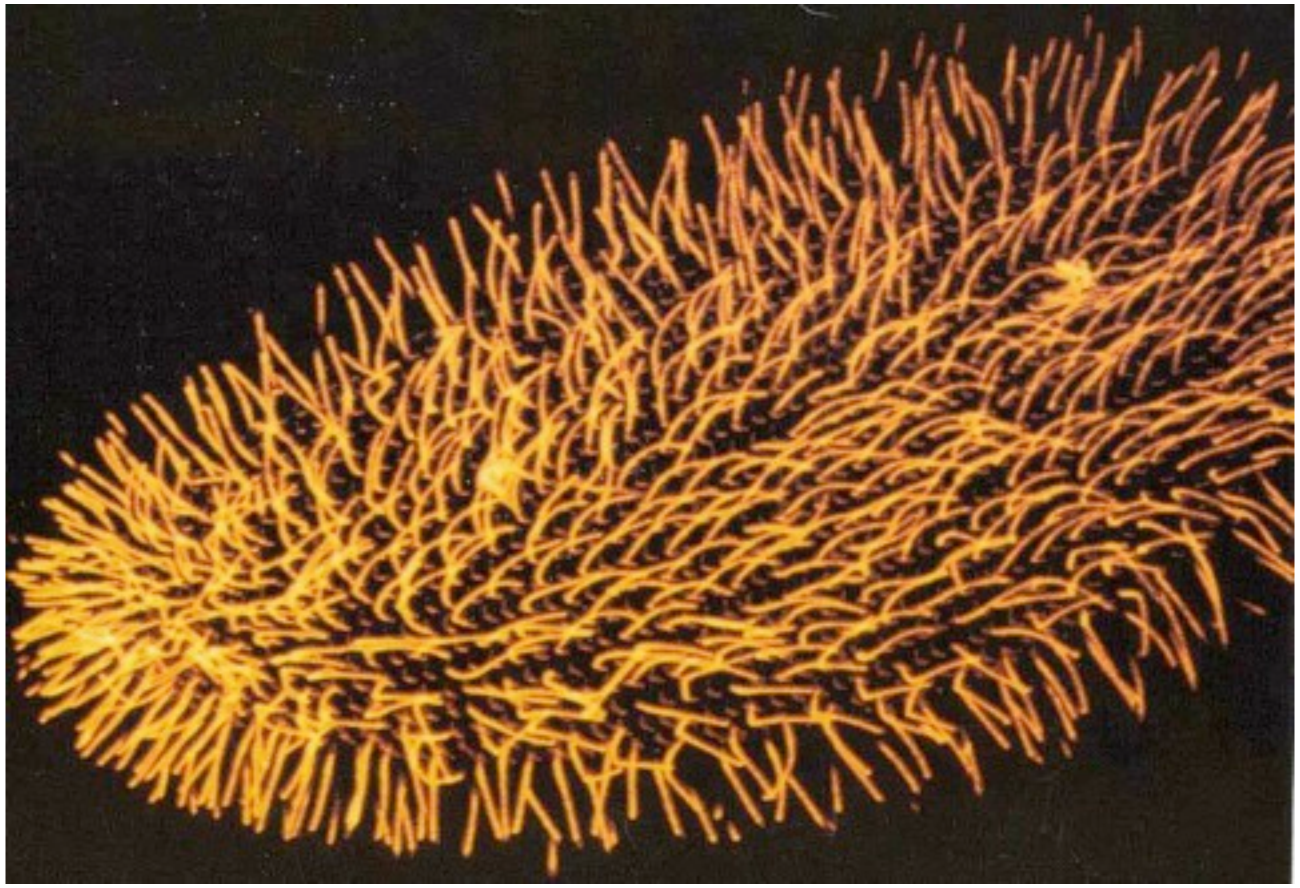
Swimming of cells

Sperm





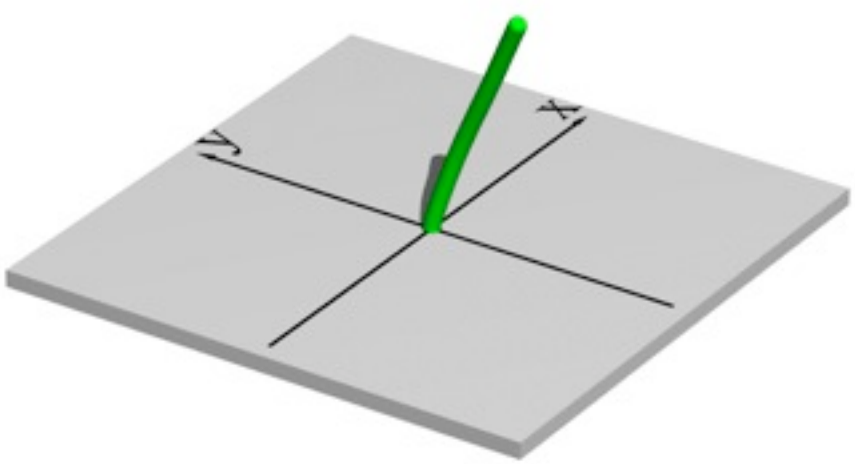
Chlamydomonas



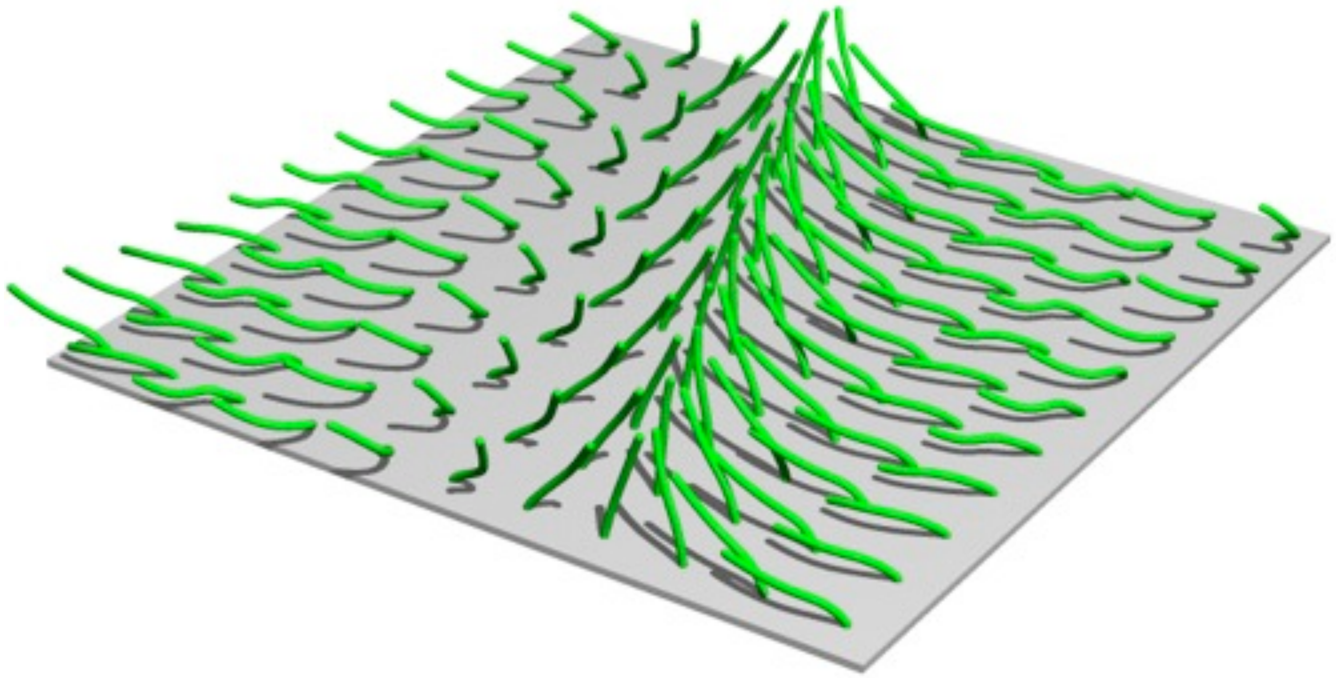
Paramecium

# Ciliar motility

Stirring fluids

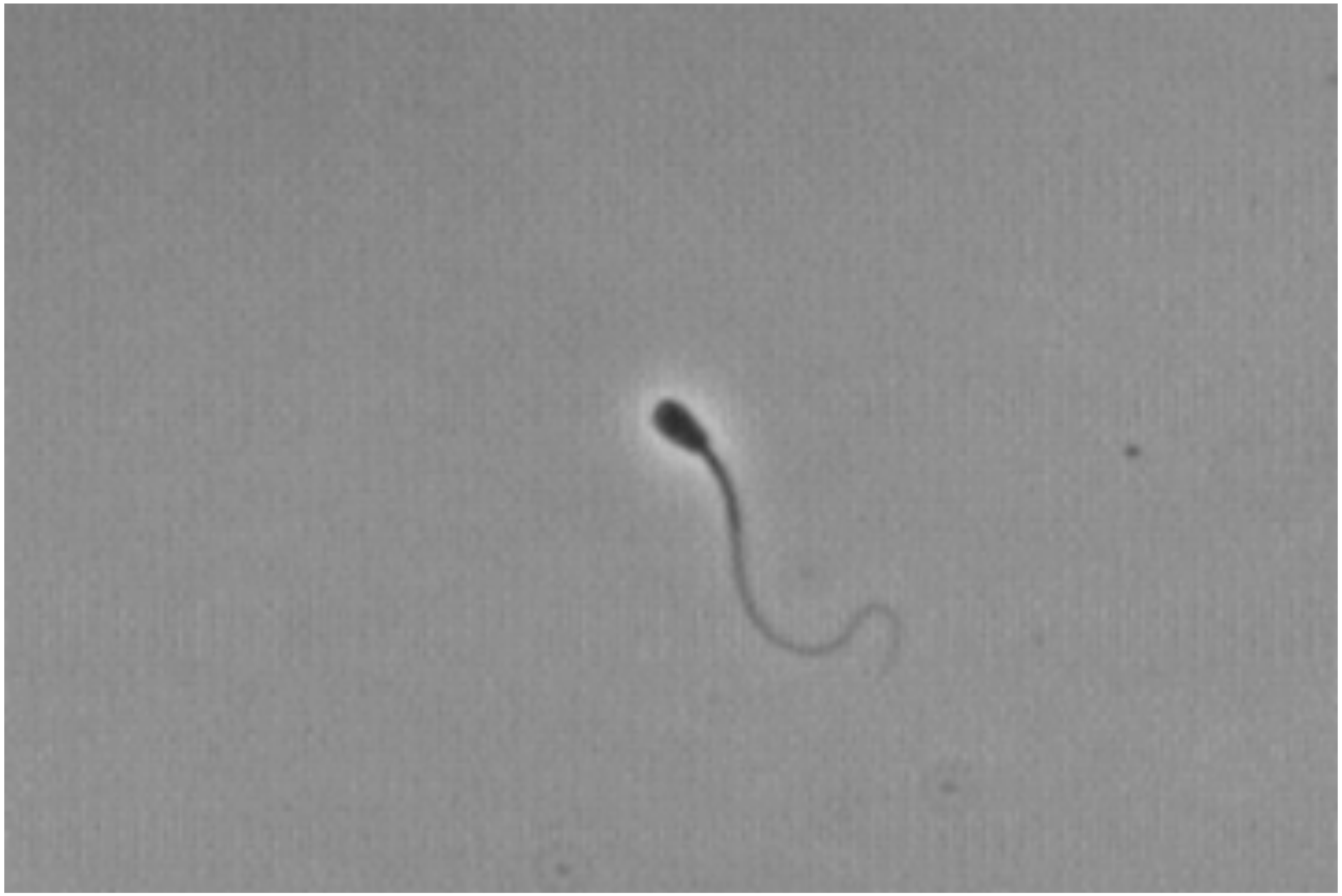



Ciliar stroke



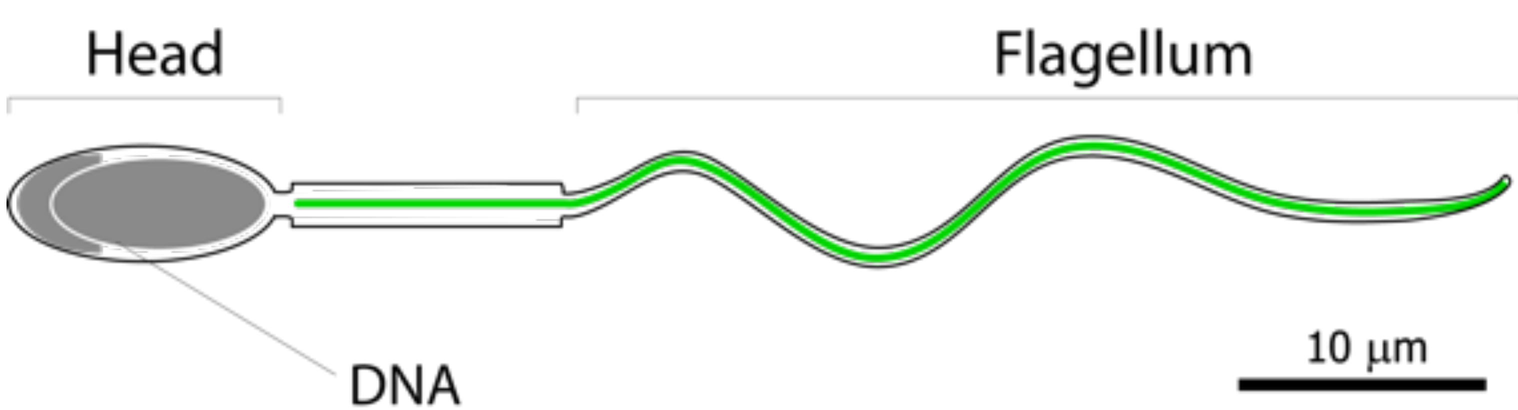
Metachronal waves

# Swimming



Bull sperm

$20\mathrm{Hz}$




Ingmar Riedel-Kruse
Jonathon Howard

# Cilia as sensory elements

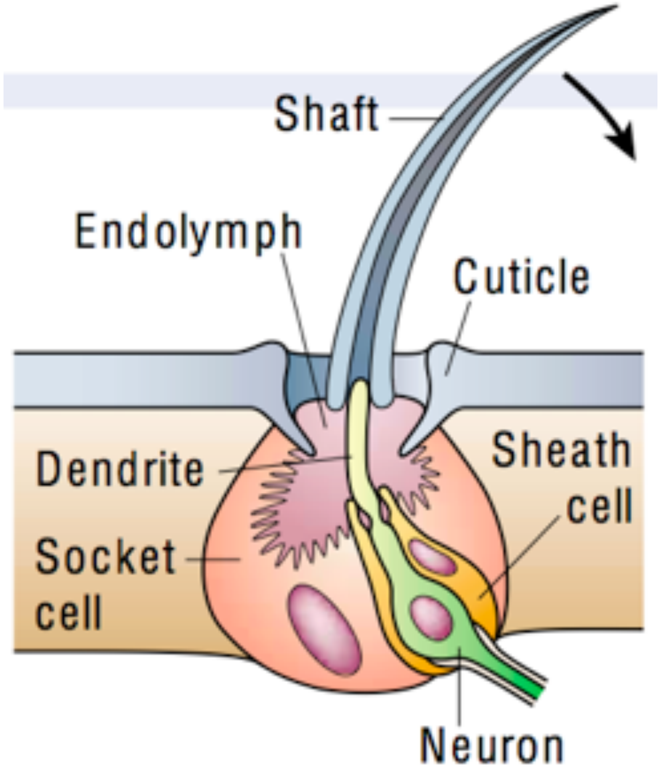
## Mechanosensors

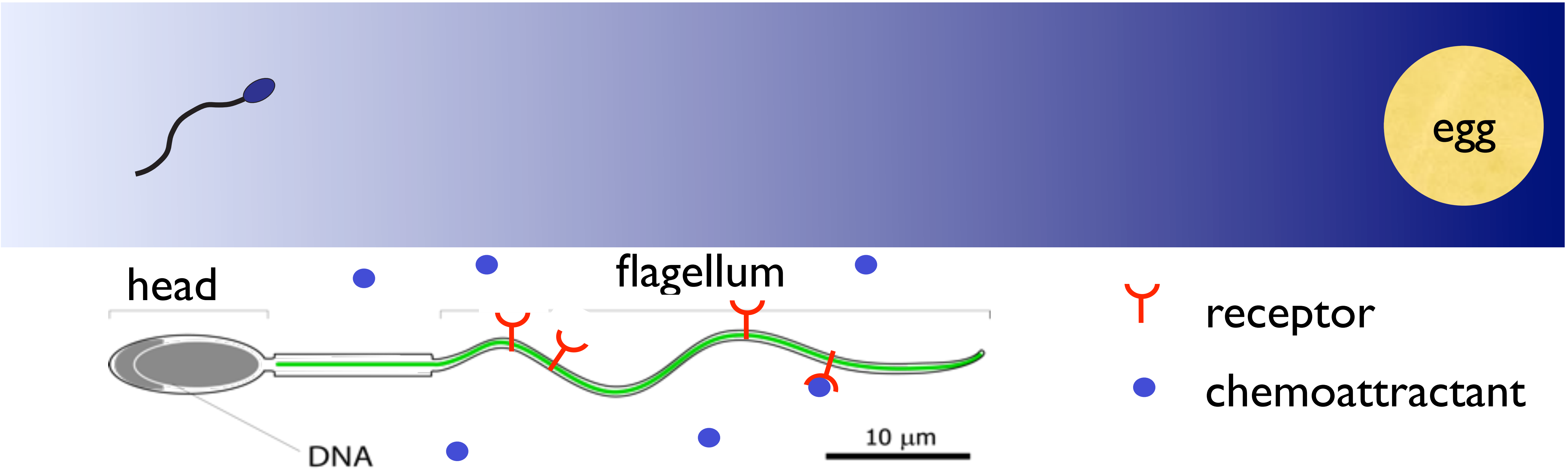
Insect mechanosensors

## Chemosensors

Olfactory neurons

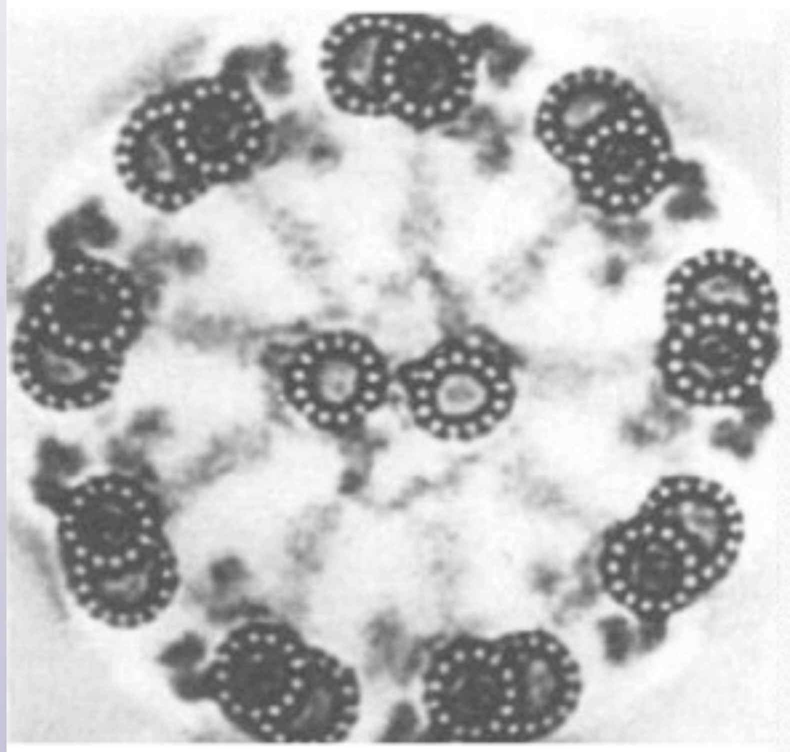
Sperm chemotaxis

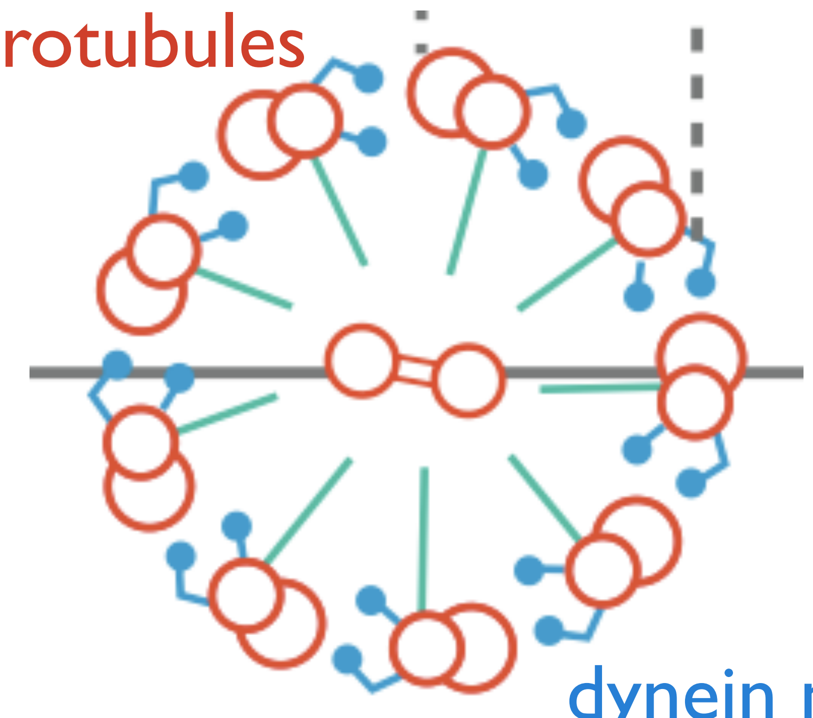


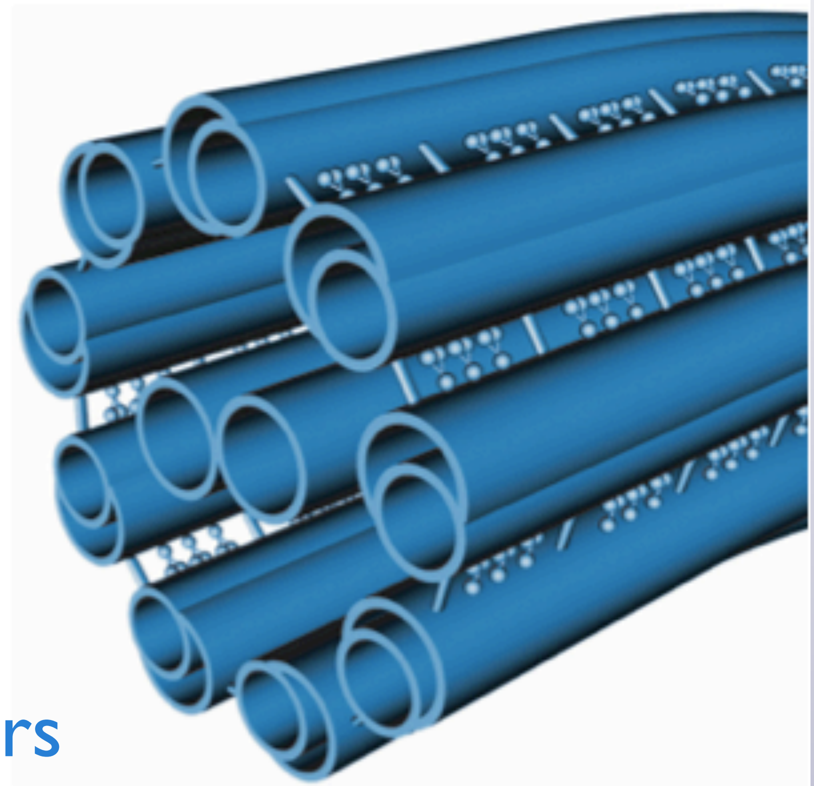



# Ciliar structure: the axomene

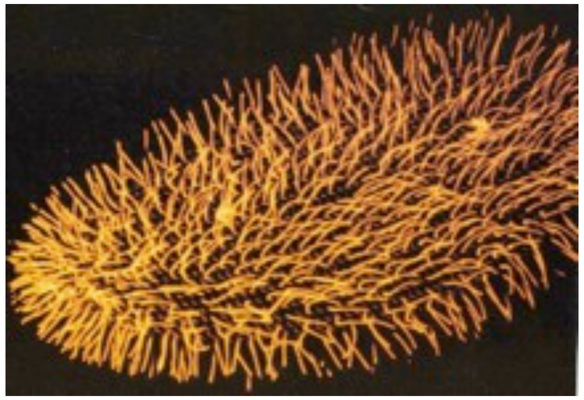
9+2 Axoneme



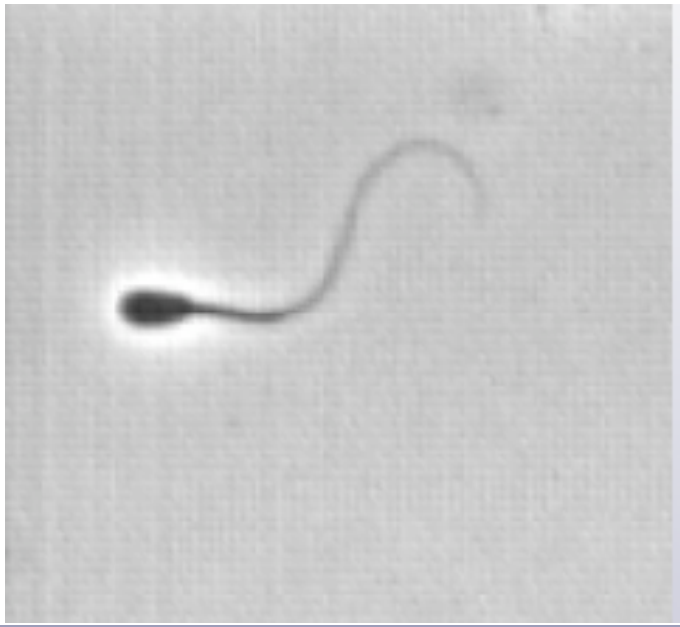


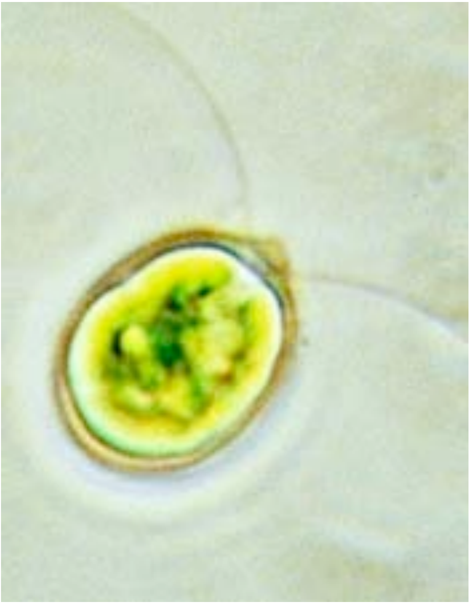
Paramecium



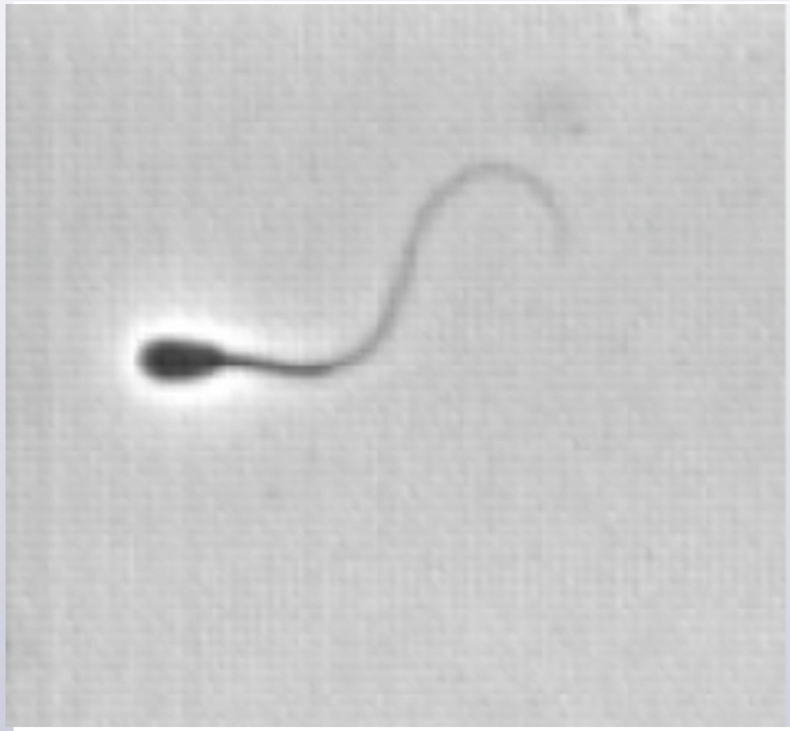
Sperm

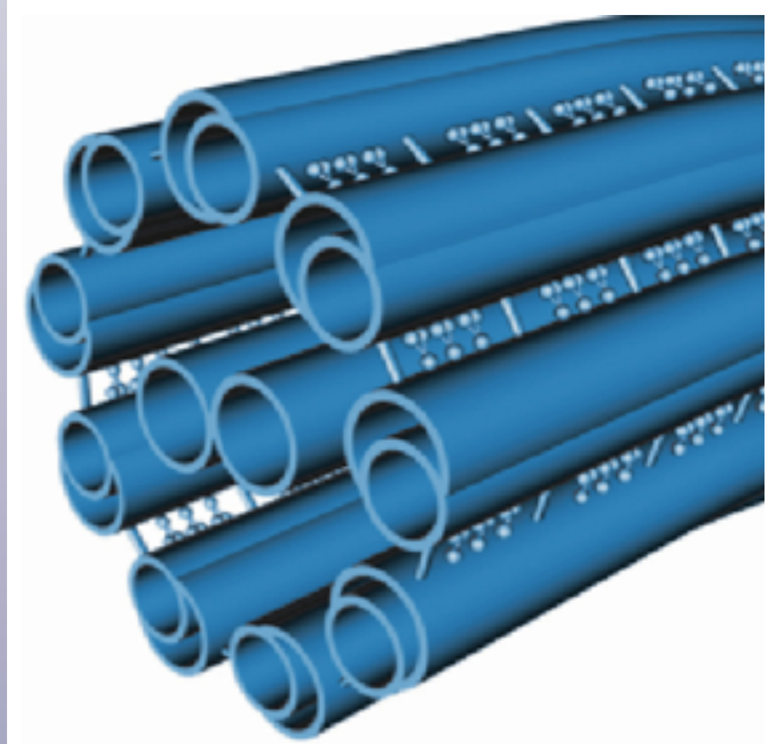


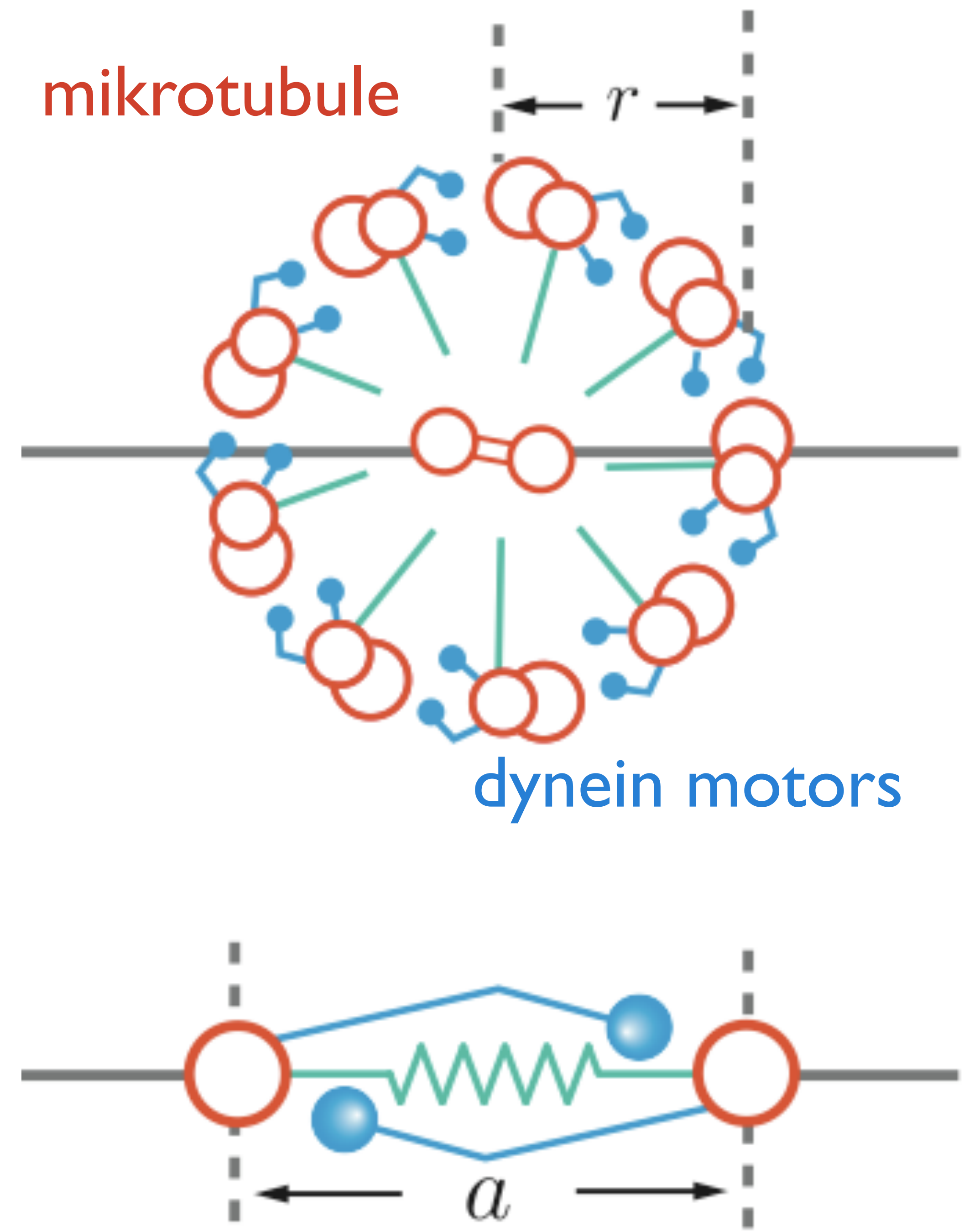
Chlamydomonas



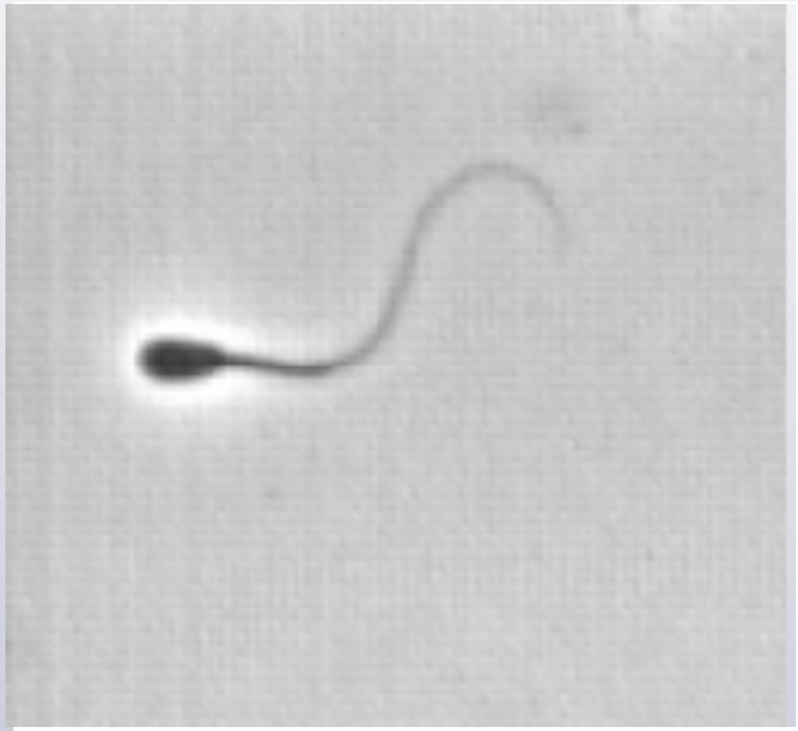
# Planar ciliar beat

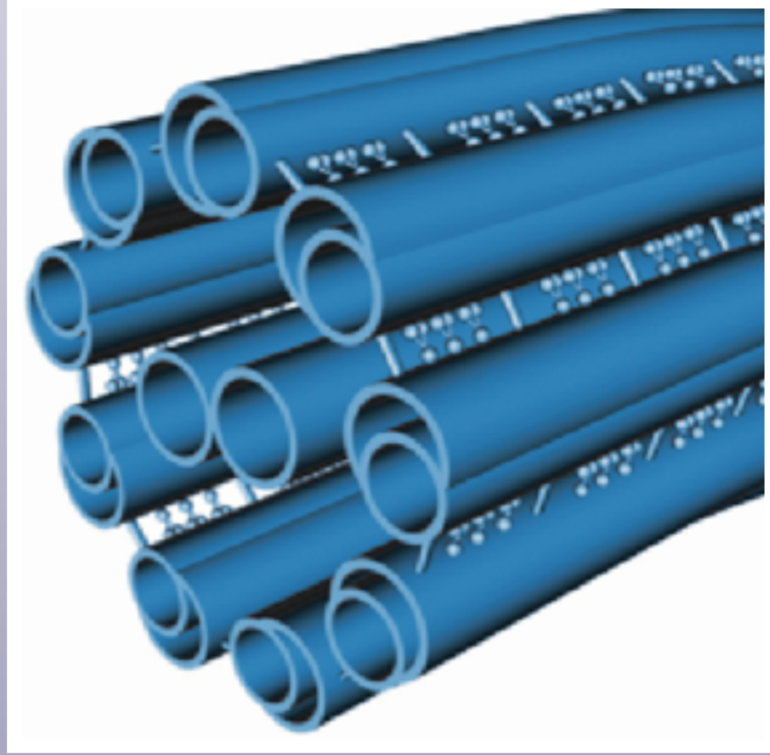


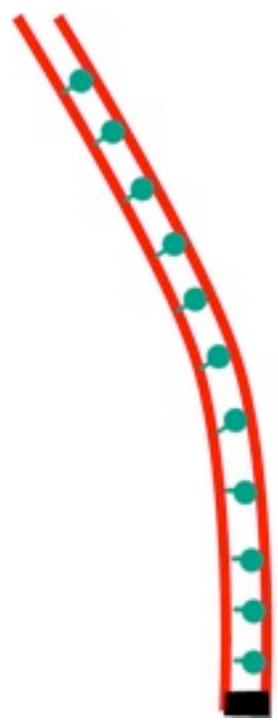


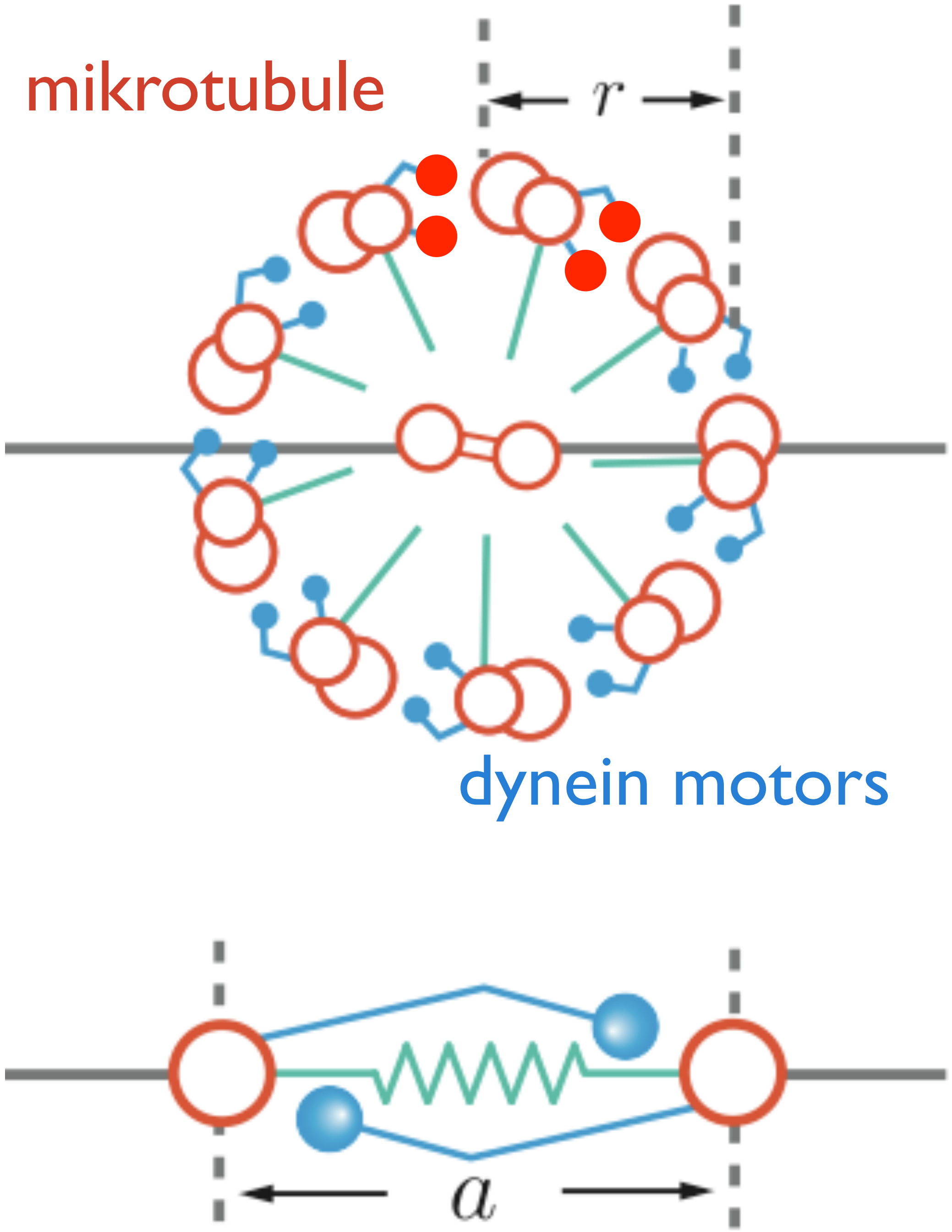


# Planar ciliar beat









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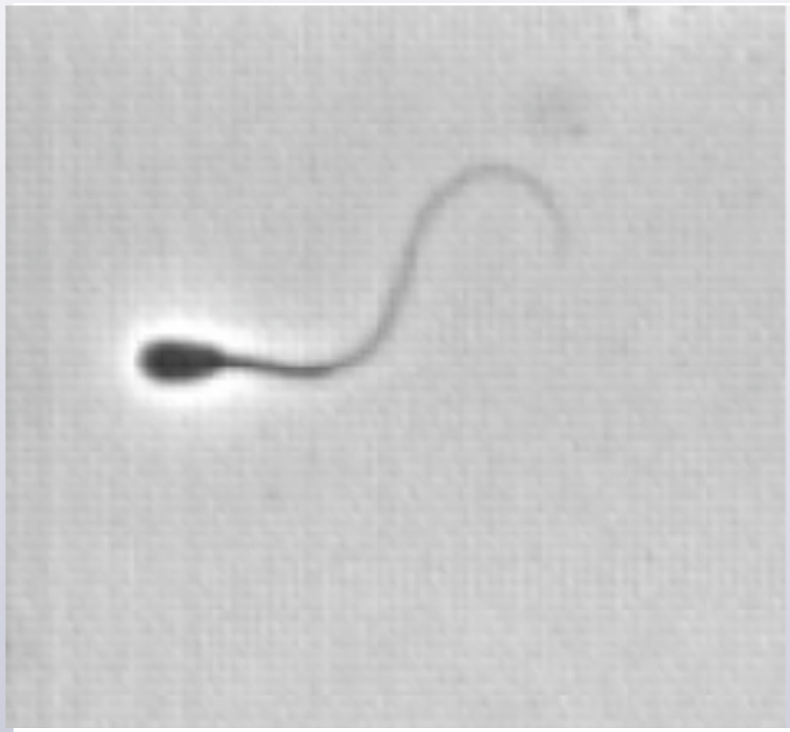
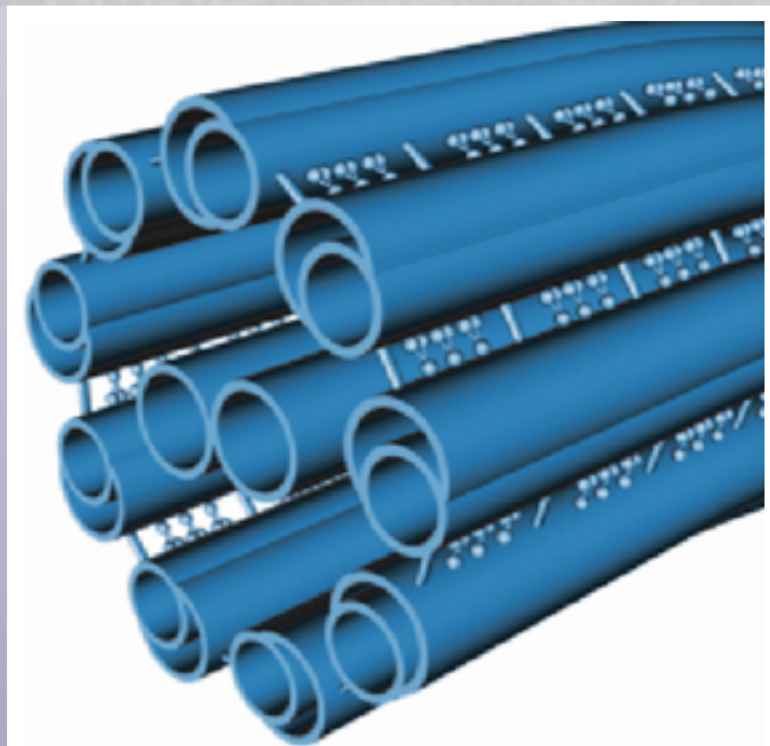
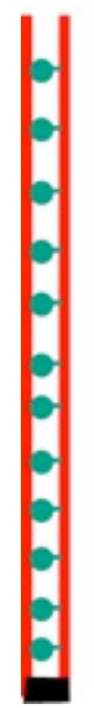
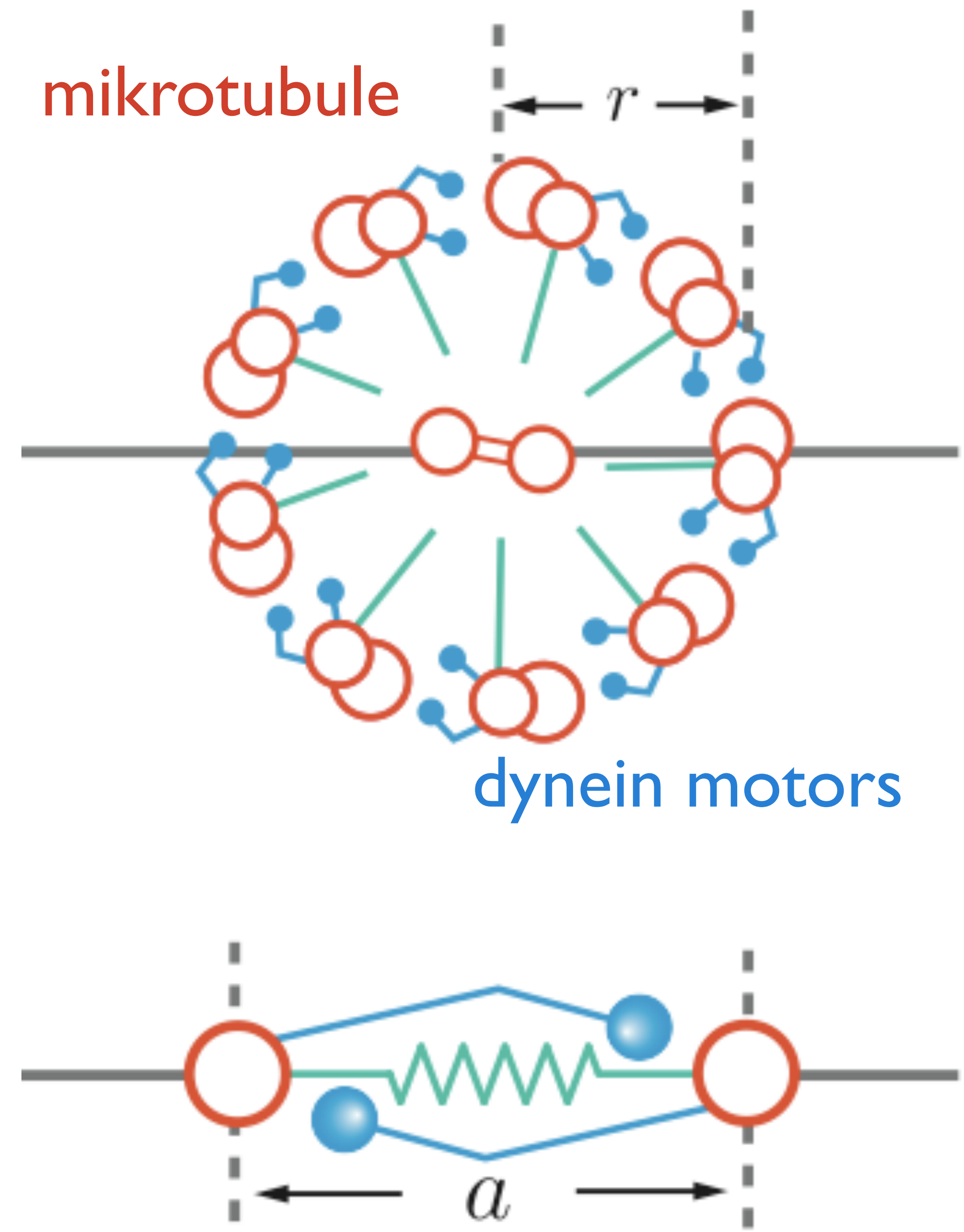
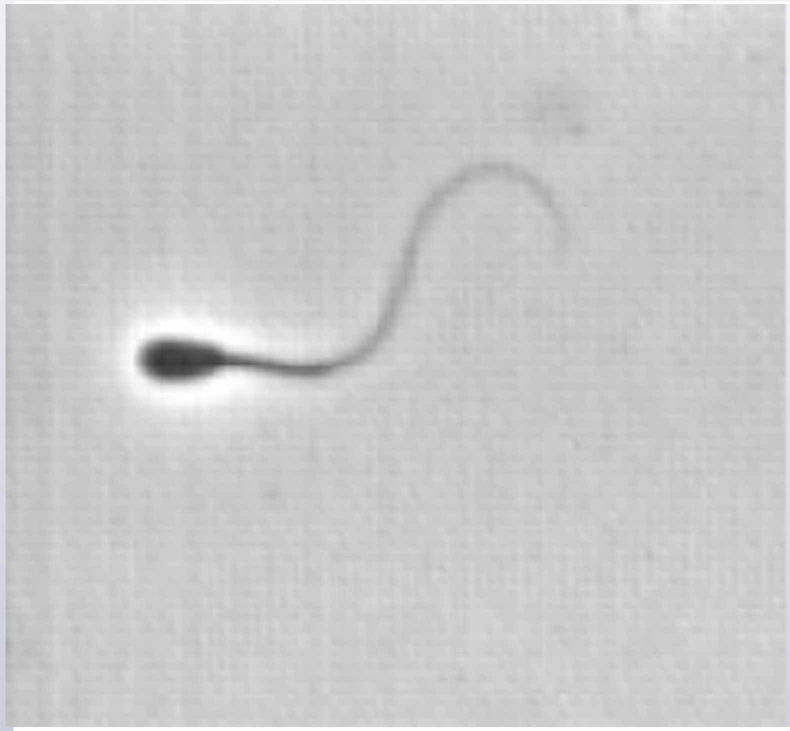


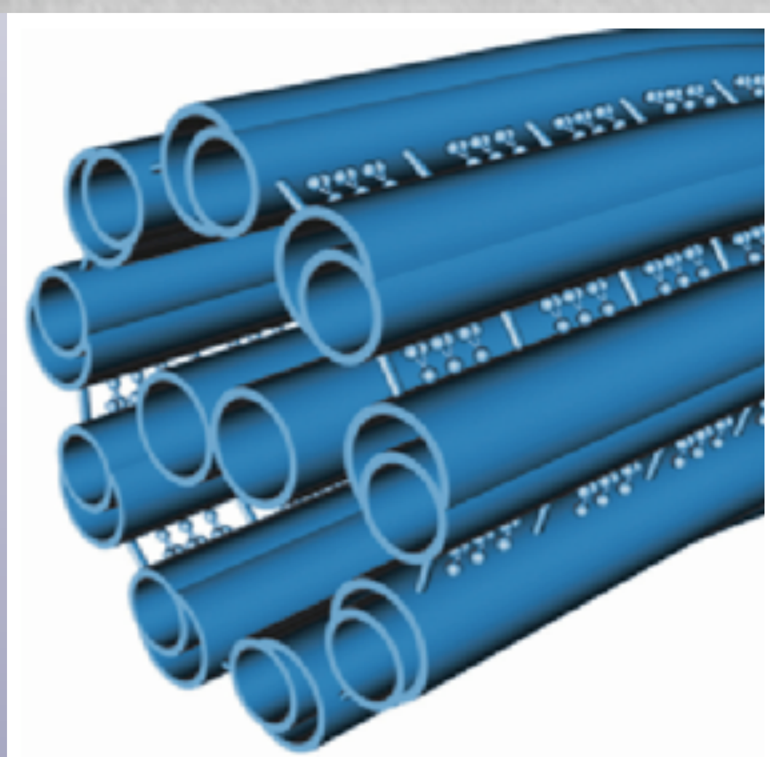


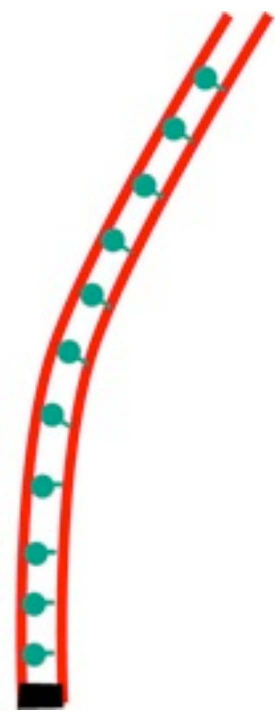


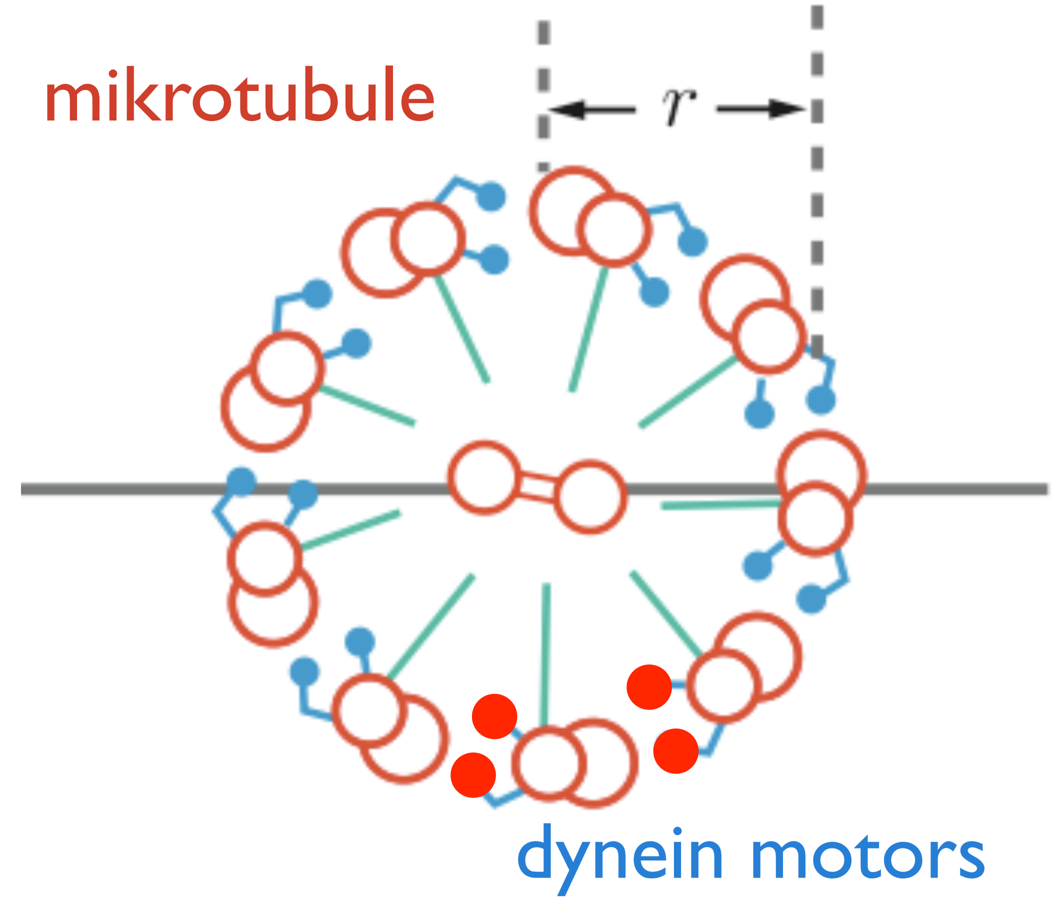


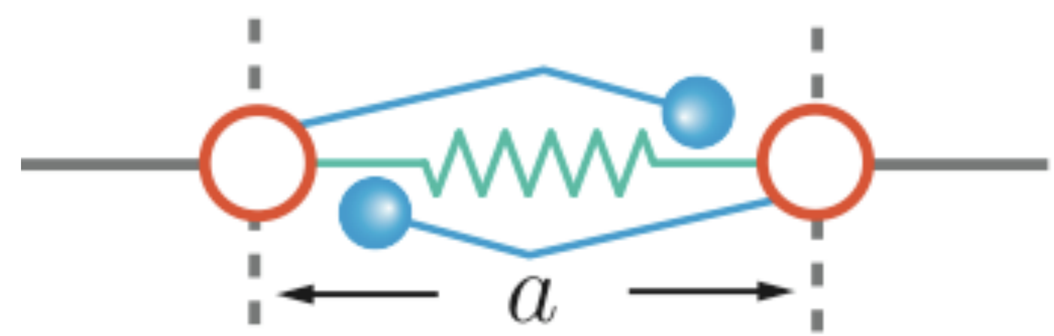
# Planar ciliar beat









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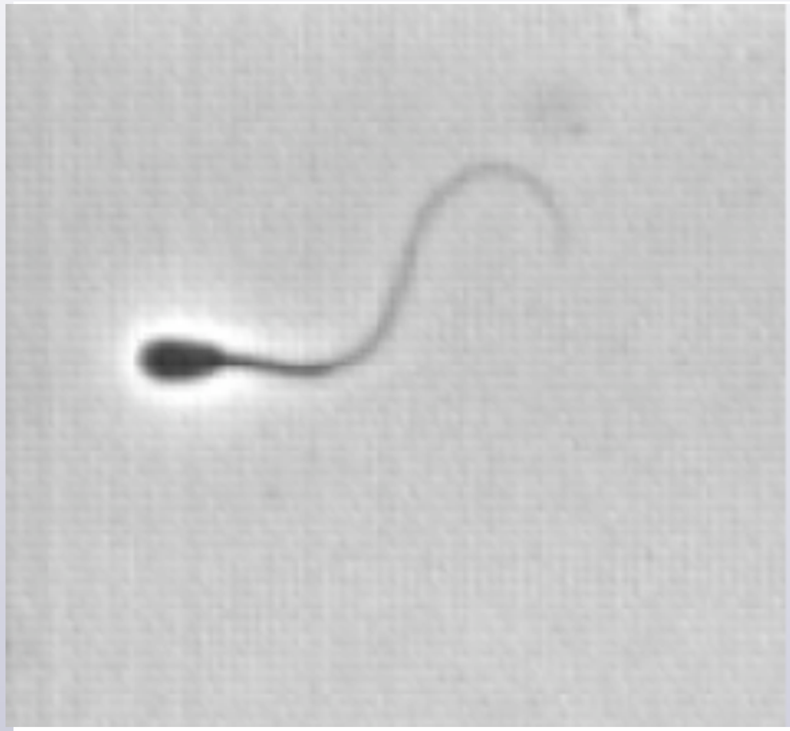
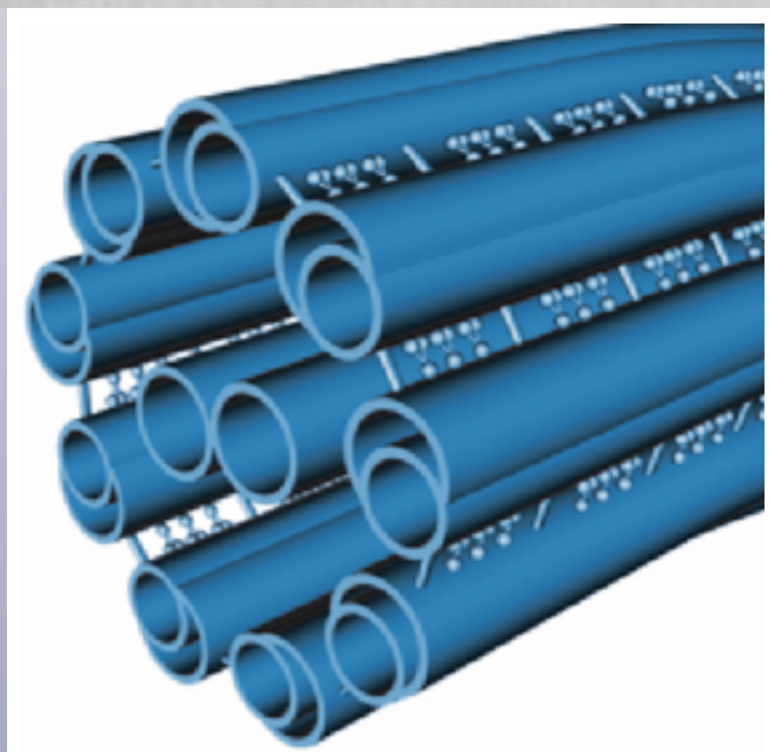
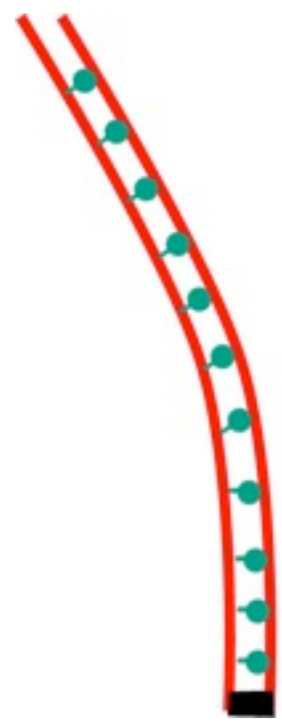
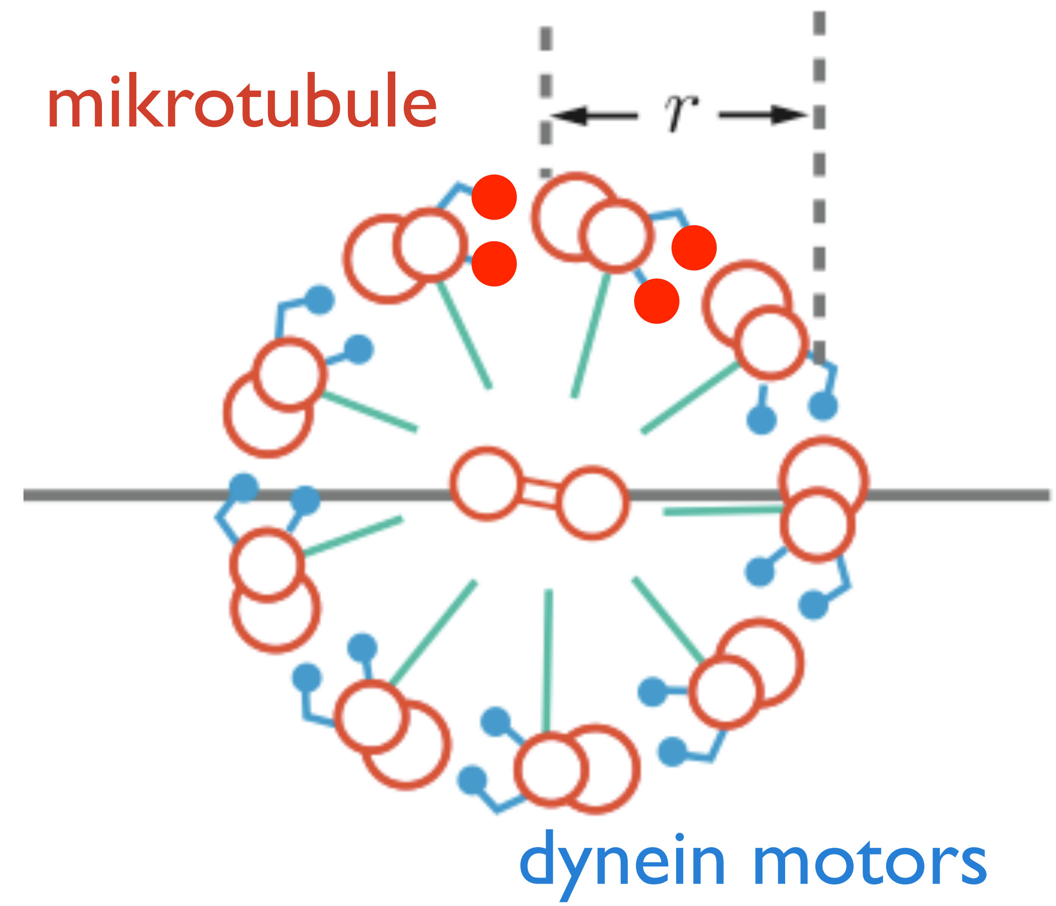
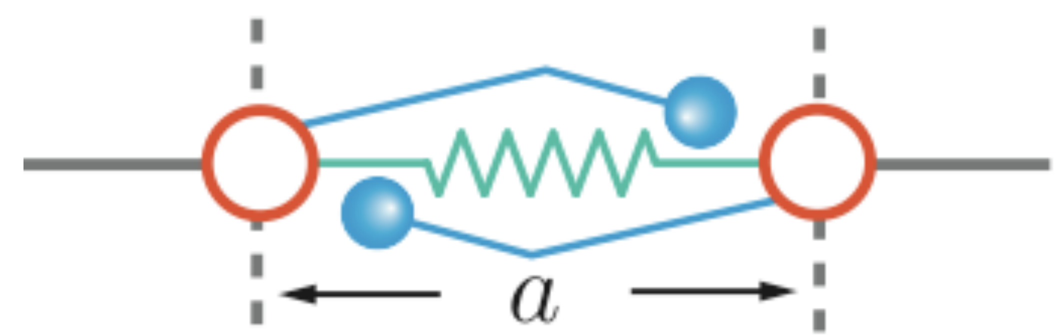






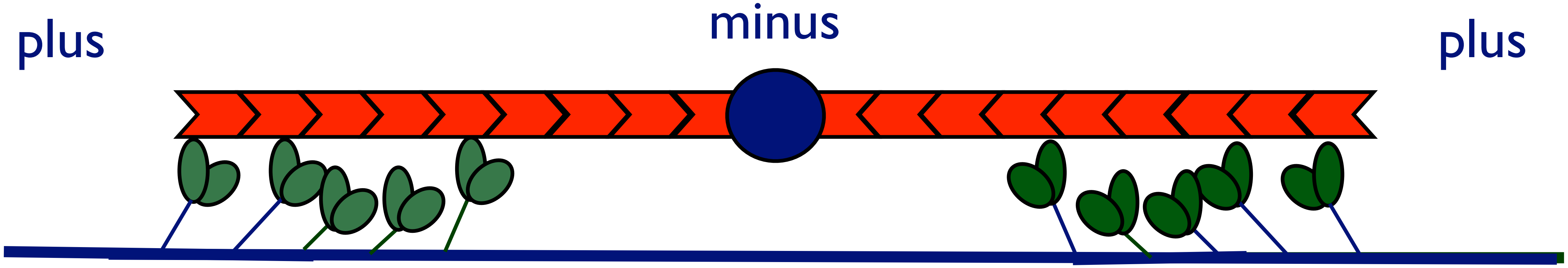


# Antagonistic motors

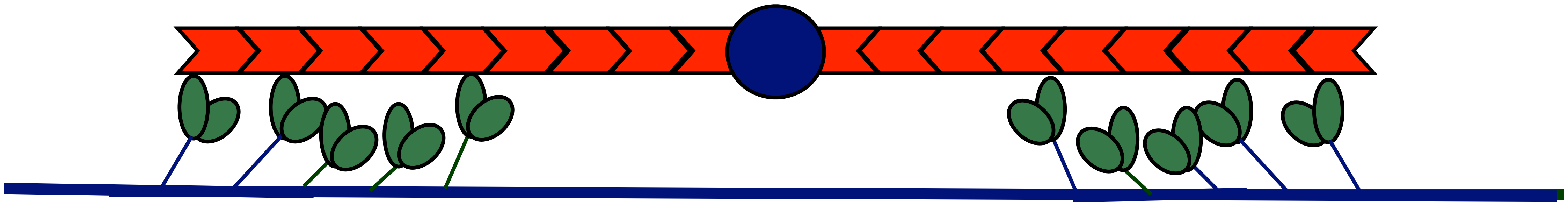
Two groups of motors that act in opposition

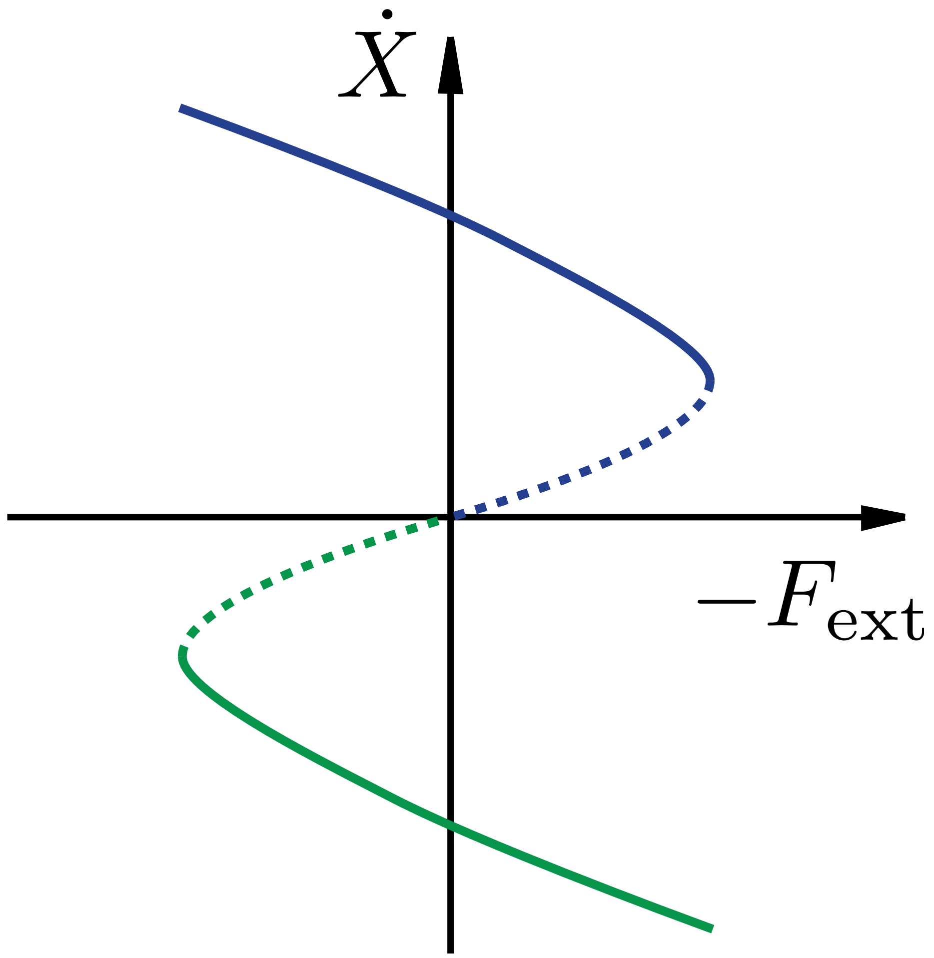
"Tug of war"




Enhanced collective effects and instabilities

# Instability and bistability

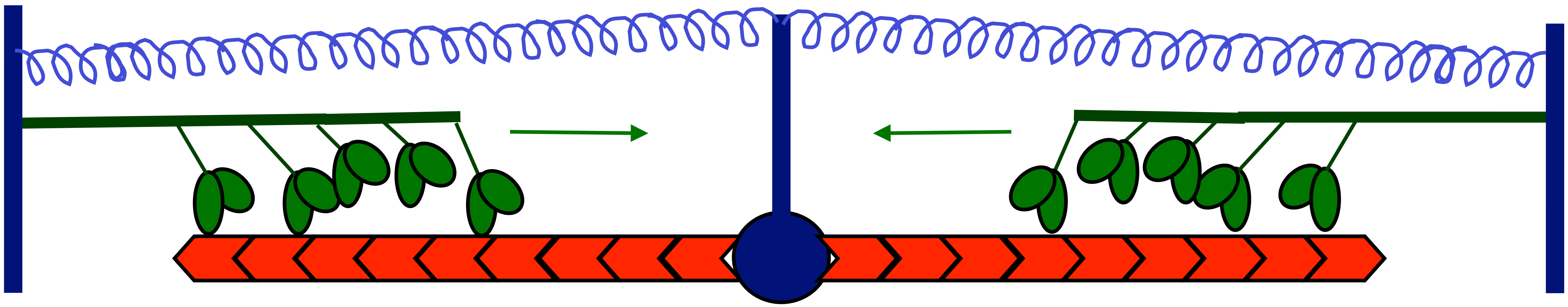





bistability

negative friction

# Nonlinear oscillator




Effective dynamics

$$m_{\text{eff}}\ddot{x} + (\xi - \Gamma)\dot{x} + Kx + B\dot{x}^3 = 0$$

delays due to on- and off-rates

negative friction

centering stiffness

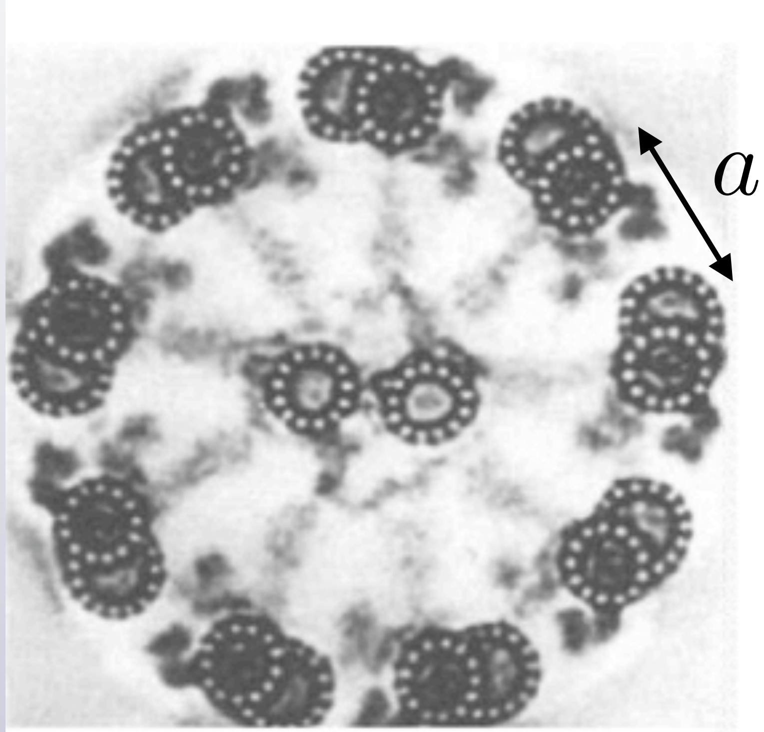
nonlinear effects

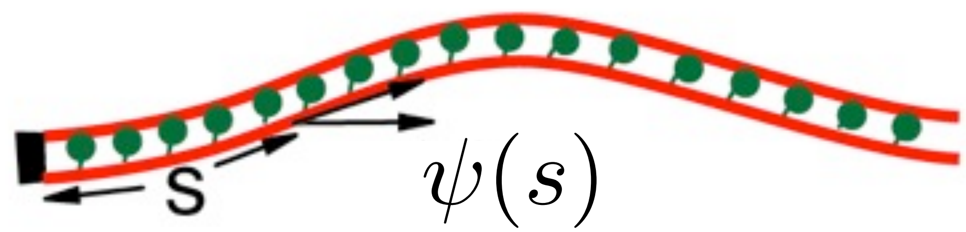
Jülicher and Prost, PRL (1997)

Grill, Kruse, Jülicher PRL (2005)

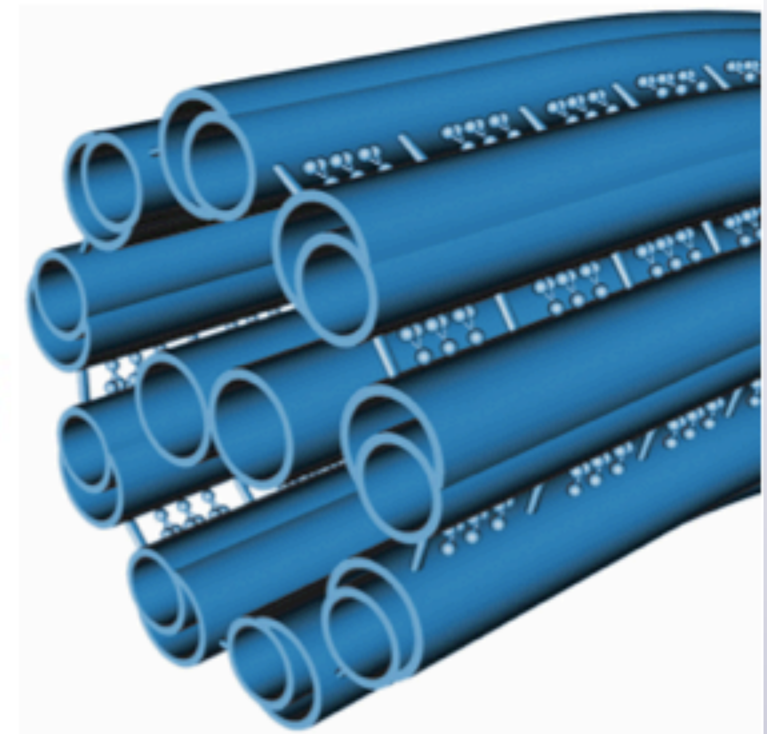
Pecreaux et. al., Current Biology (2006)

# Planar ciliar beat




$$\psi(0) = 0$$



$$G = \int_0^L ds(\frac{\kappa}{2}\dot{\psi}^2 + f(s)x(s))$$

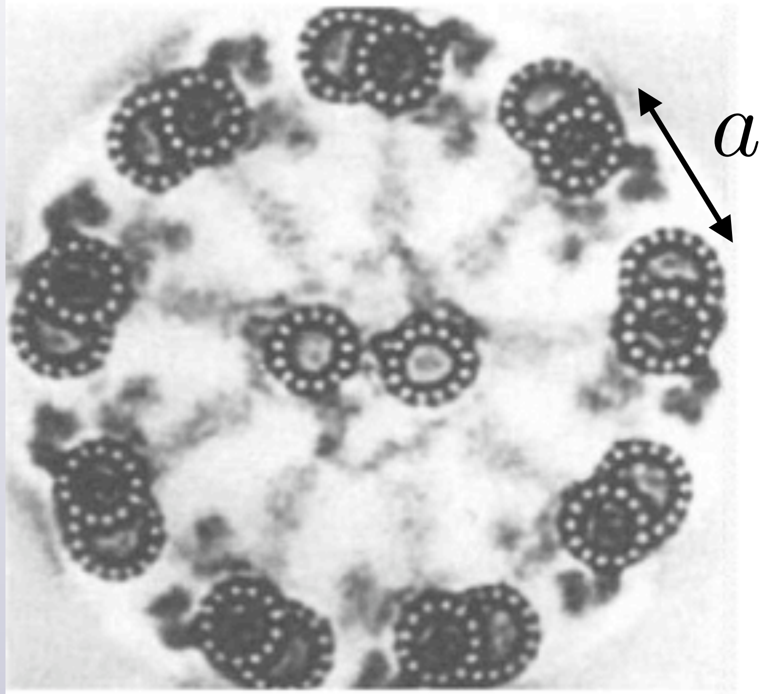
Bending energy + work term

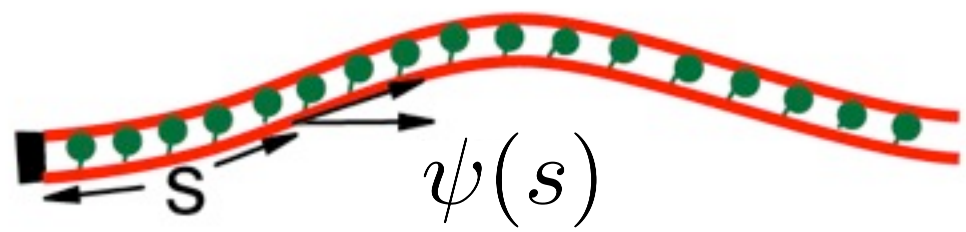
$$x(s) = x_0 + a\psi(s)$$

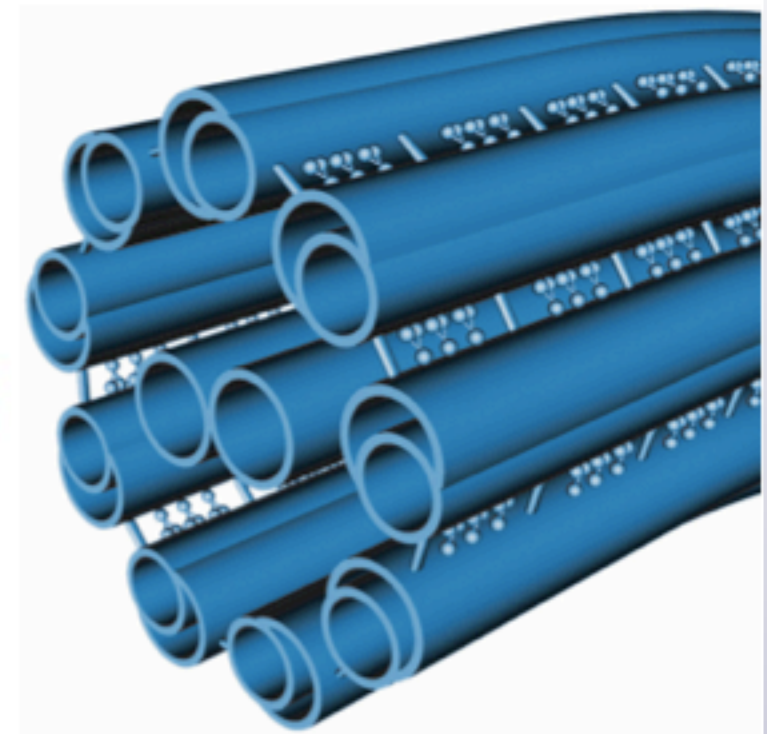
$x(s)$ motor displacement

$f(s)$ motor force density

# Planar ciliar beat

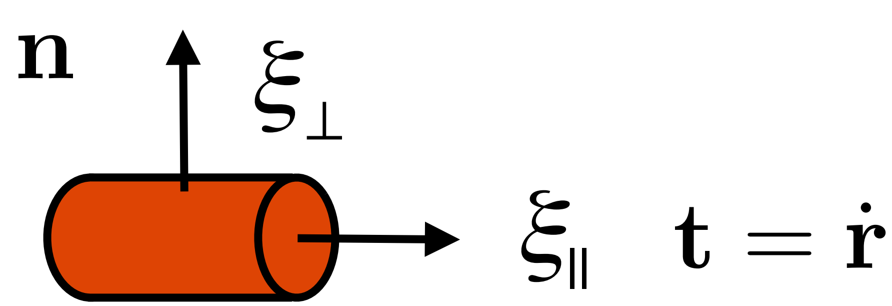


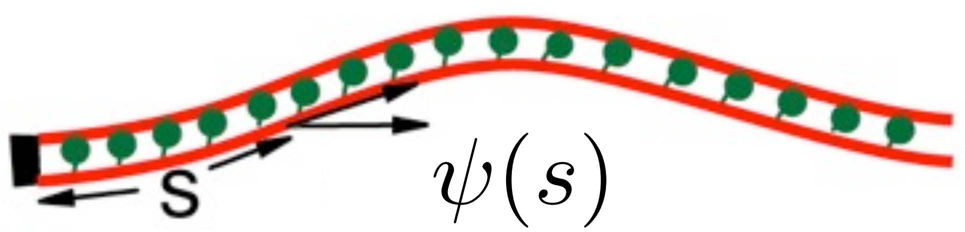



Dynamic equations

$$\partial_t \mathbf{r} = -\left( \frac{1}{\xi_\perp} \mathbf{n}\mathbf{n} + \frac{1}{\xi_{||}} \mathbf{t}\mathbf{t} \right) \frac{\delta G}{\delta \mathbf{r}}$$



# Linearized dynamics




force density of dynein motors $f(s,t)$

local angle of cilium $\psi(s,t)$

Shape equation for the flagellar beat

$$\xi_\perp \partial_t \psi \simeq -\kappa \partial_s^4 \psi + a \partial_s^2 f$$

friction

bending elasticity

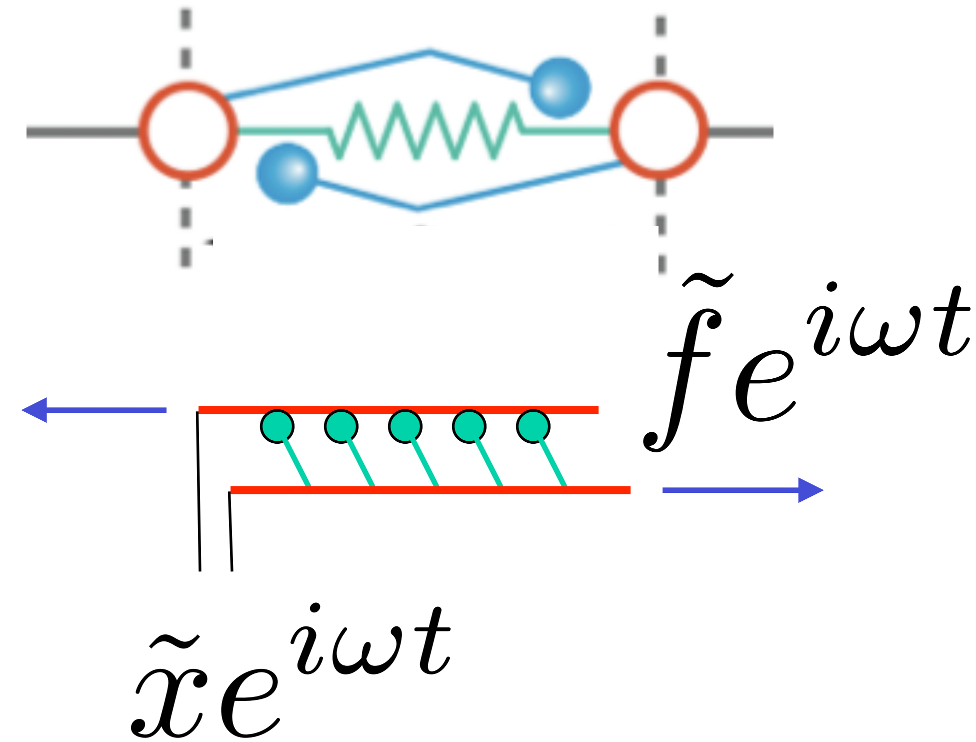
motor forces

# Sliding control of motors

Active material

Linear response

$$\tilde{f} \simeq \chi(\omega)\tilde{x}$$



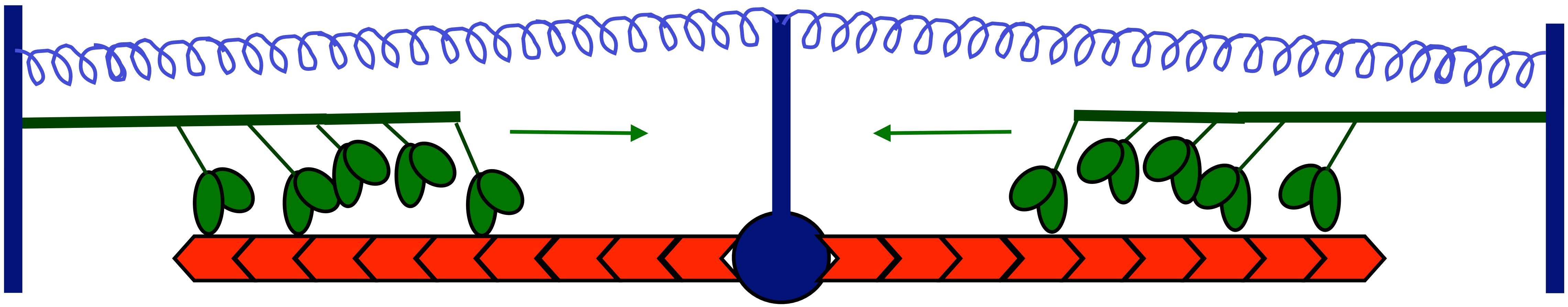

Frequency dependent susceptibility

$$\chi = k + i\lambda\omega$$

$$x(s) = x_0 + a\psi(s)$$

Camalet and Jülicher, NJP 2 (2000)

# Nonlinear oscillator




Effective dynamics

$$m_{\text{eff}}\ddot{x} + (\xi - \Gamma)\dot{x} + Kx + B\dot{x}^3 = 0$$

delays due to on- and off-rates

negative friction

centering stiffness

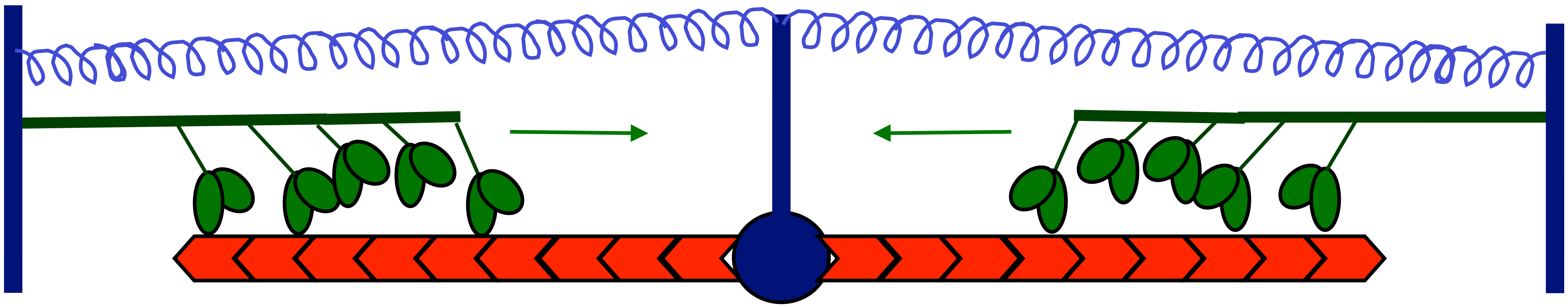
nonlinear effects

Jülicher and Prost, PRL (1997)

Pecreaux et. al., Current Biology (2006)

Riedel, Hilfinger, Howard, Jülicher, HFSP J. (2007)

# Motor response function




linear motor response

$$\chi(\omega) = -m_{\mathrm{eff}}\omega^2 + i(\xi - \Gamma)\omega + K$$

delays due to on- and off-rates

negative friction

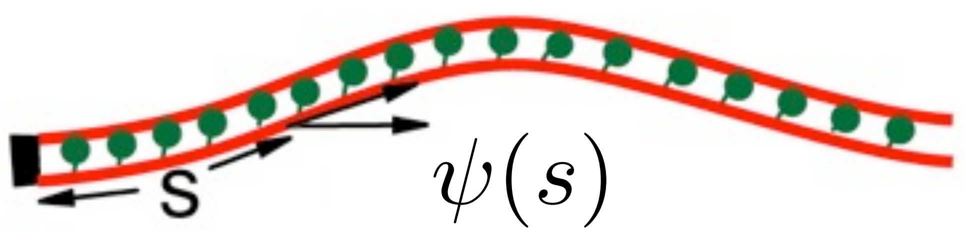
centering stiffness

Jülicher and Prost, PRL (1997)

Pecreaux et. al., Current Biology (2006)

Riedel, Hilfinger, Howard, Jülicher, HFSP J. (2007)

# Linear wave equation

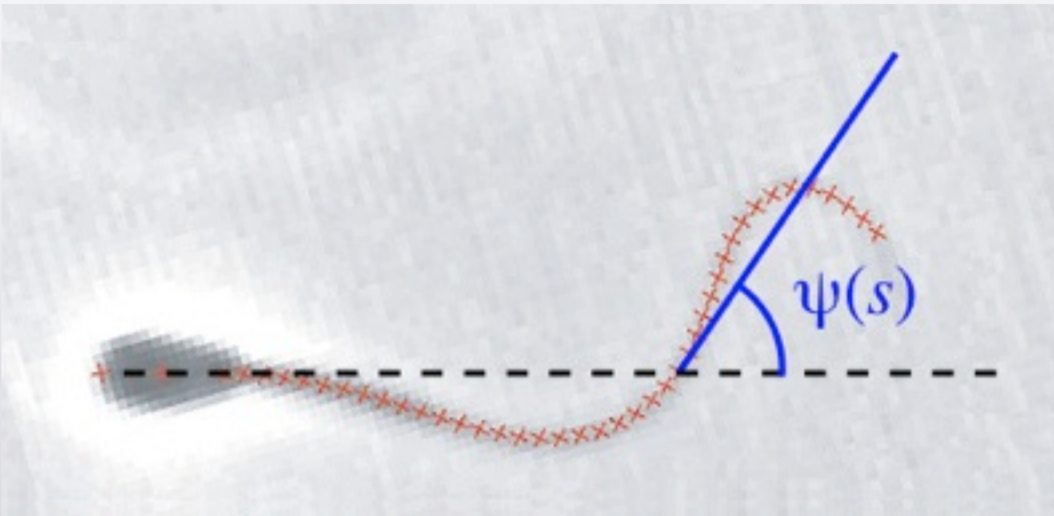



sliding control $\tilde{f} \simeq \chi(\omega)\tilde{x}$

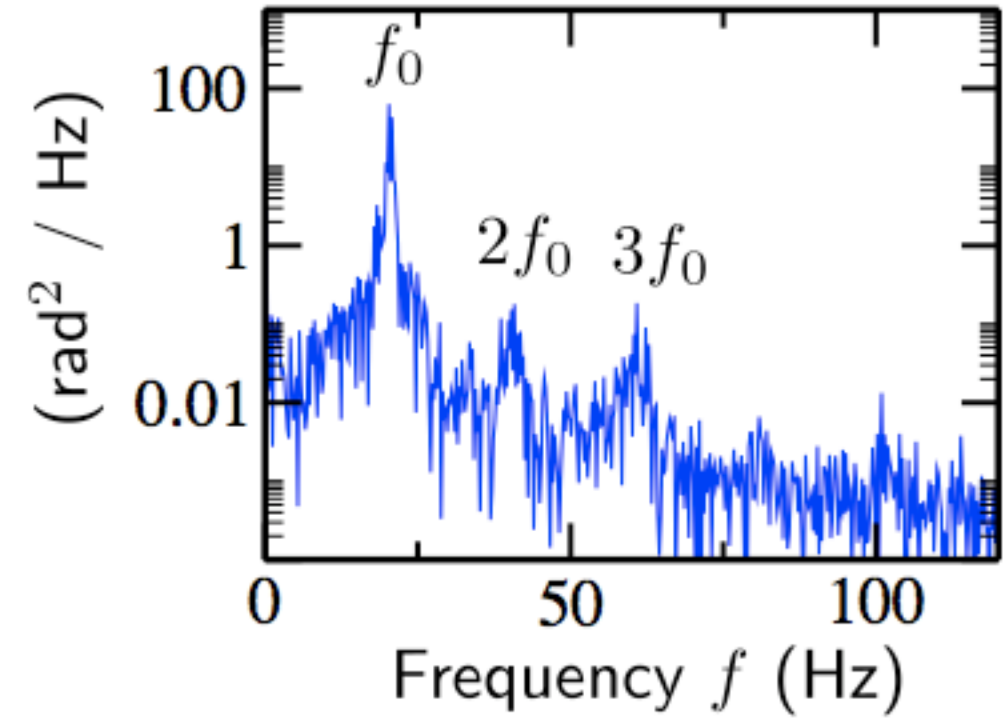
local angle of cilium $\psi(s,t)$

$$\underbrace{i\omega\xi_\perp\tilde{\psi}}_{\text{friction}} \simeq \underbrace{-\kappa\partial_s^4\tilde{\psi}}_{\text{bending elasticity}} + \underbrace{a^2\chi\partial_s^2\tilde{\psi}}_{\text{motor forces}}$$

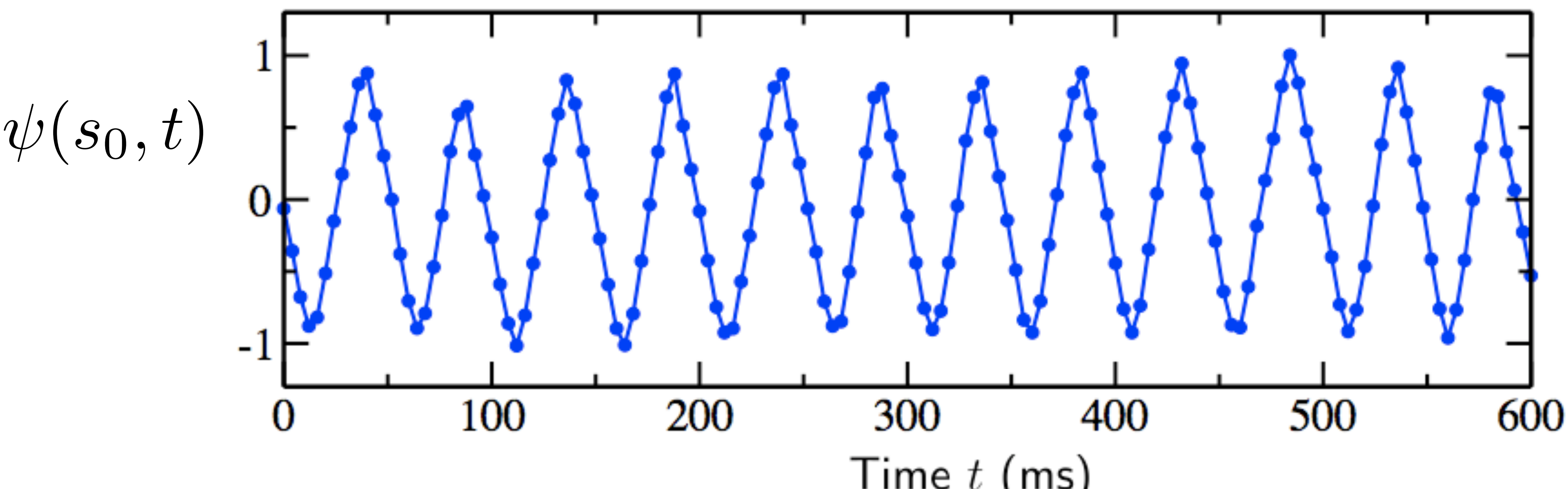
# Experimental results




Spectral density

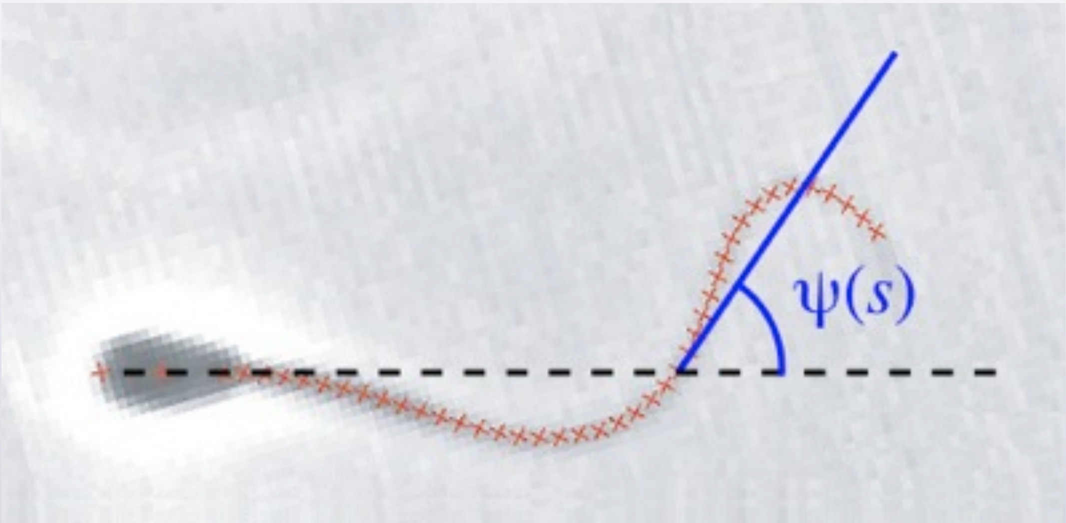



Angle as a function of time at fixed place



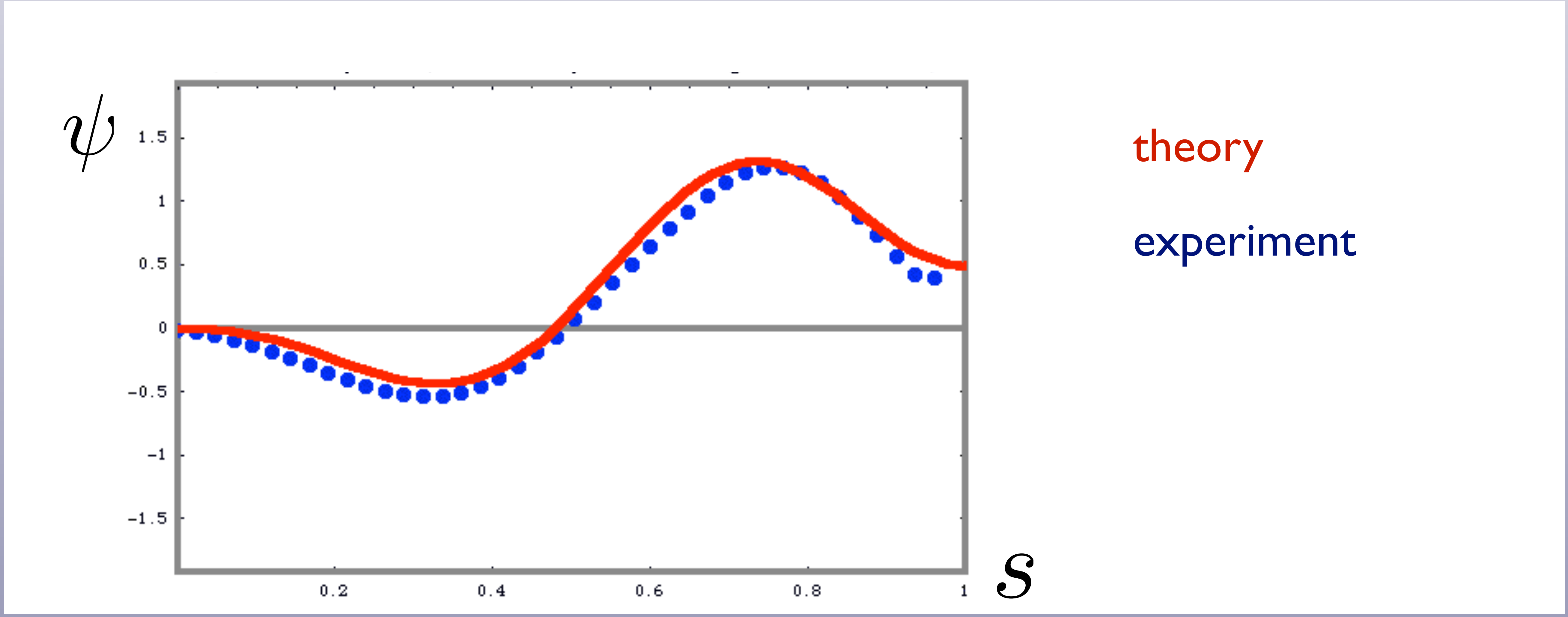

I. Riedel-Kruse, A. Hilfinger, J. Howard, F. Jülicher, HFSP Journal 3 (2007)

# Theory-Experiment

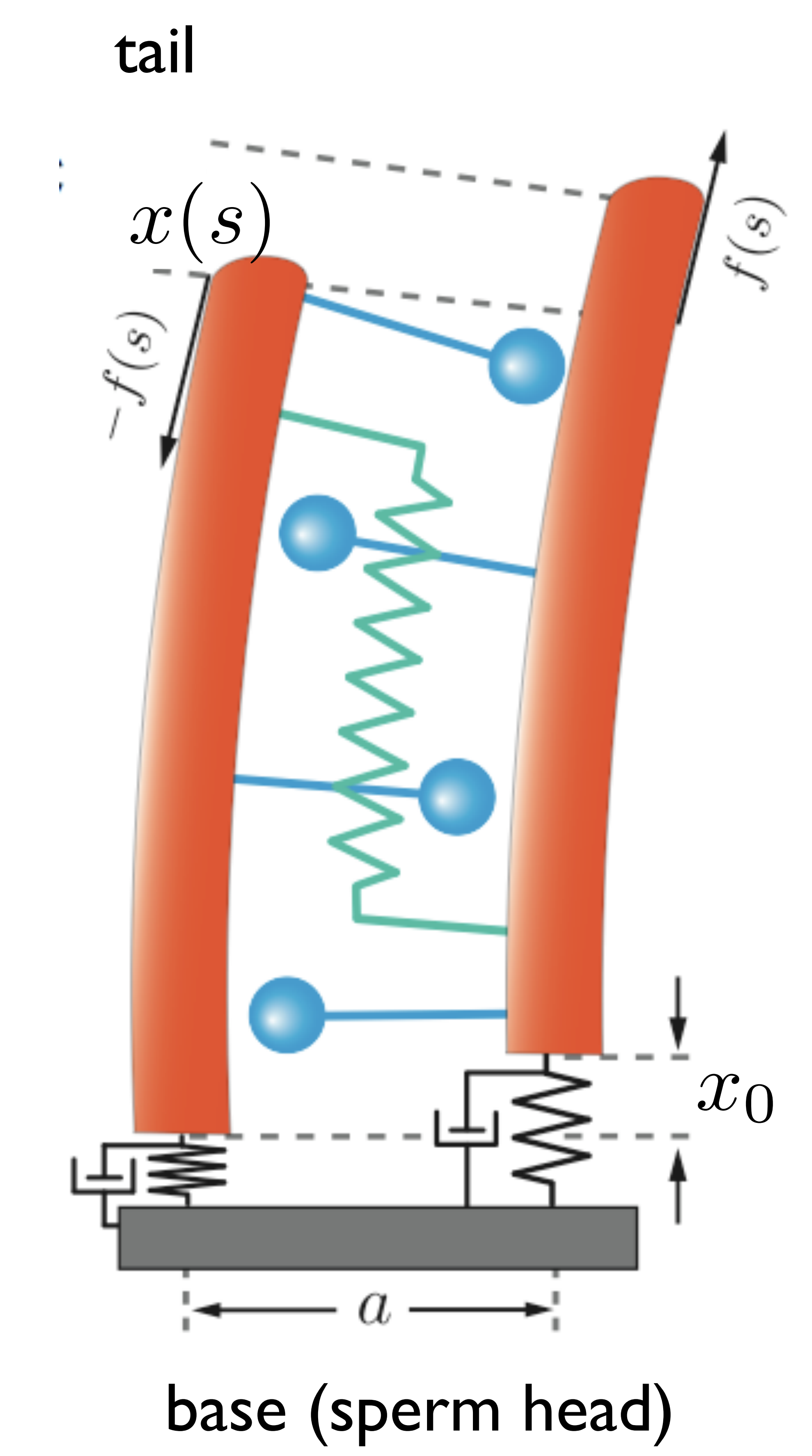



Sliding control

$$\psi(s,t) = \tilde{\psi}(s)e^{i\omega t}$$



# Basal sliding




Basal sliding

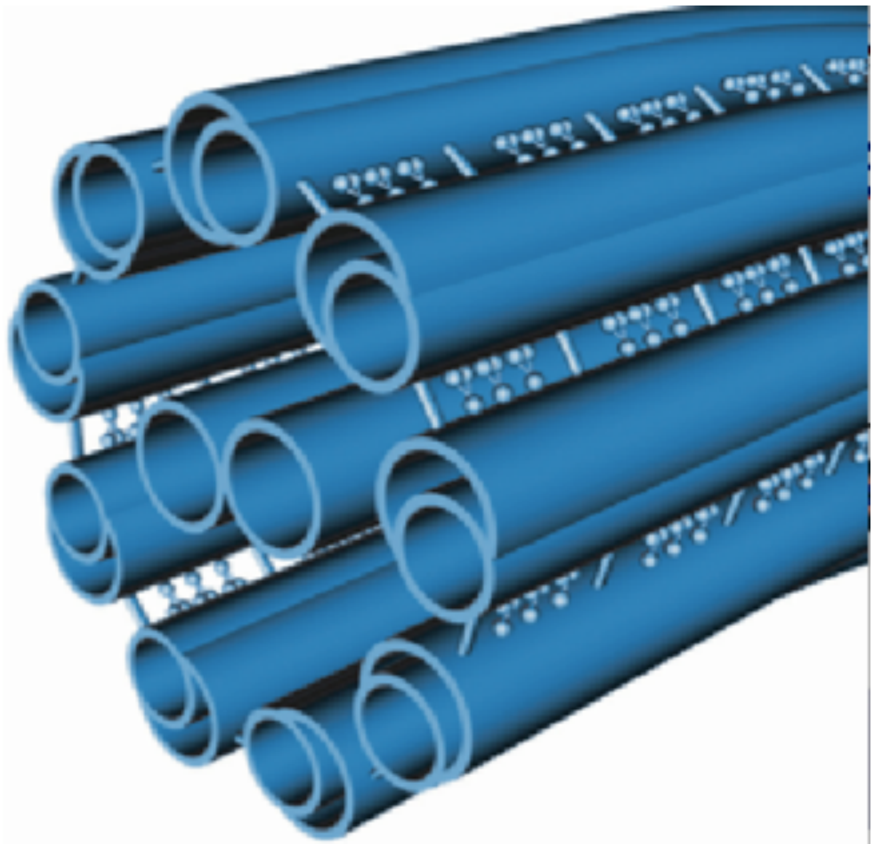
$$x(s) = x_0 + a\psi(s)$$

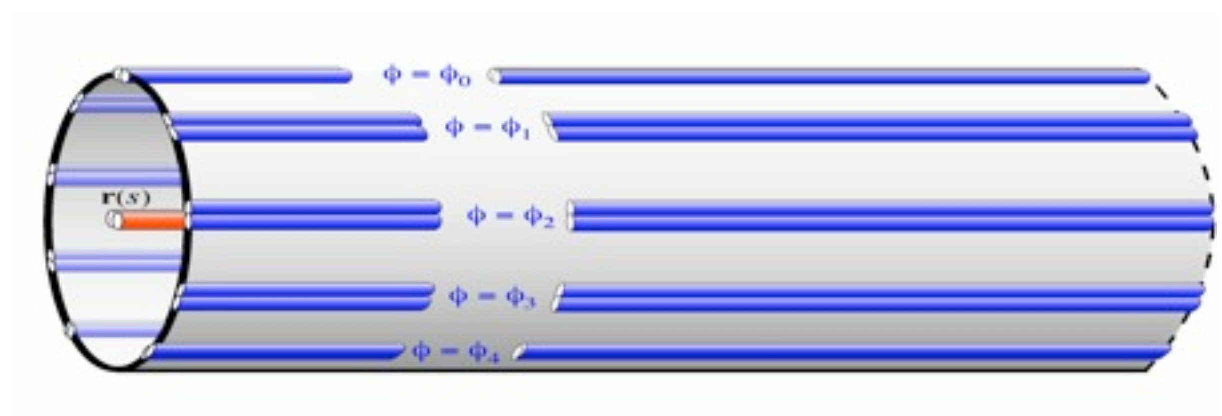
basal sliding $\quad x_0(t)$

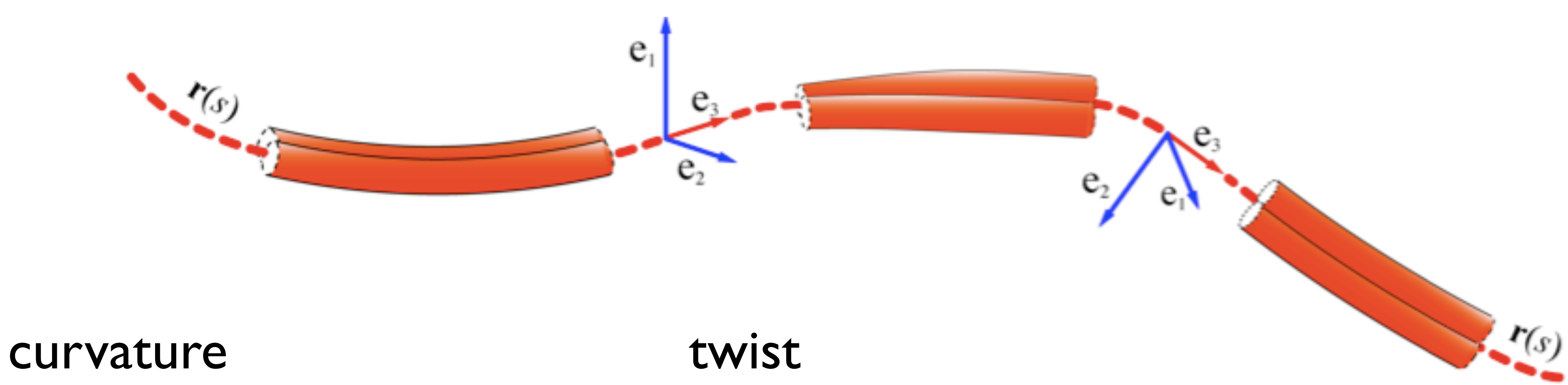
$$|\tilde{x}_0| \simeq 160\text{nm}$$

basal compliance

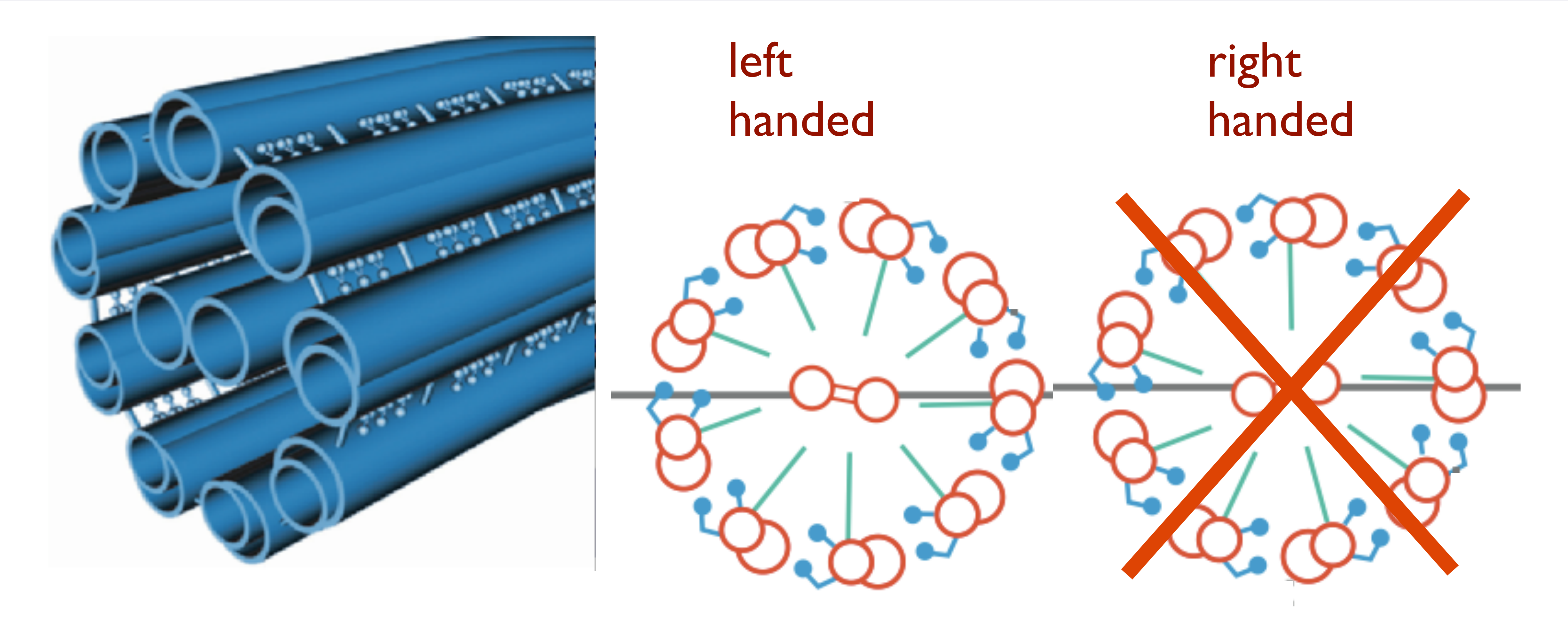
# Ciliar beat in three dimensions

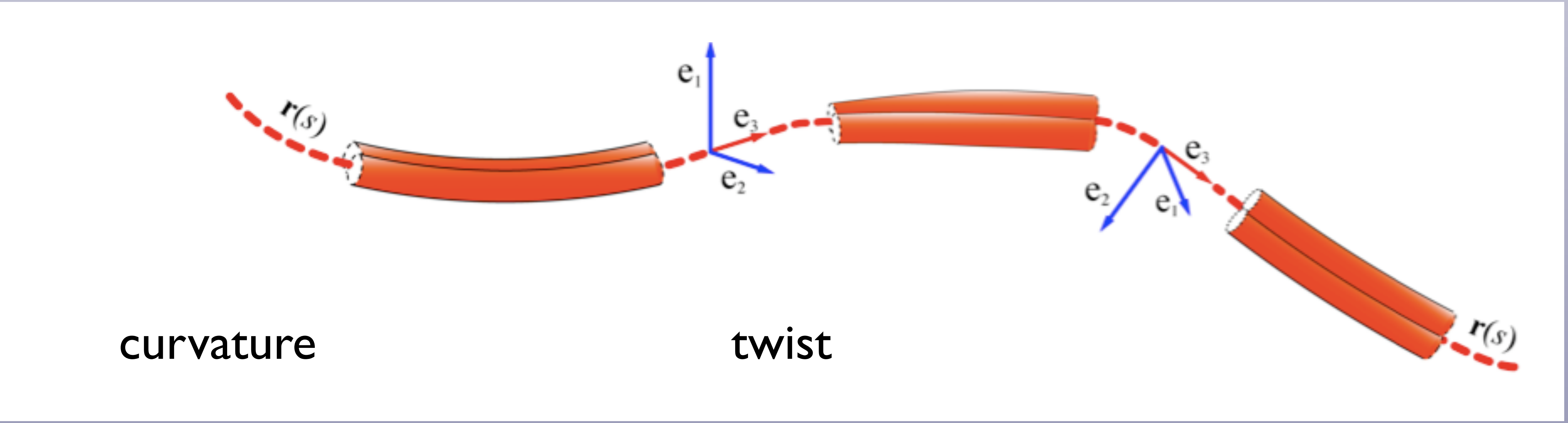




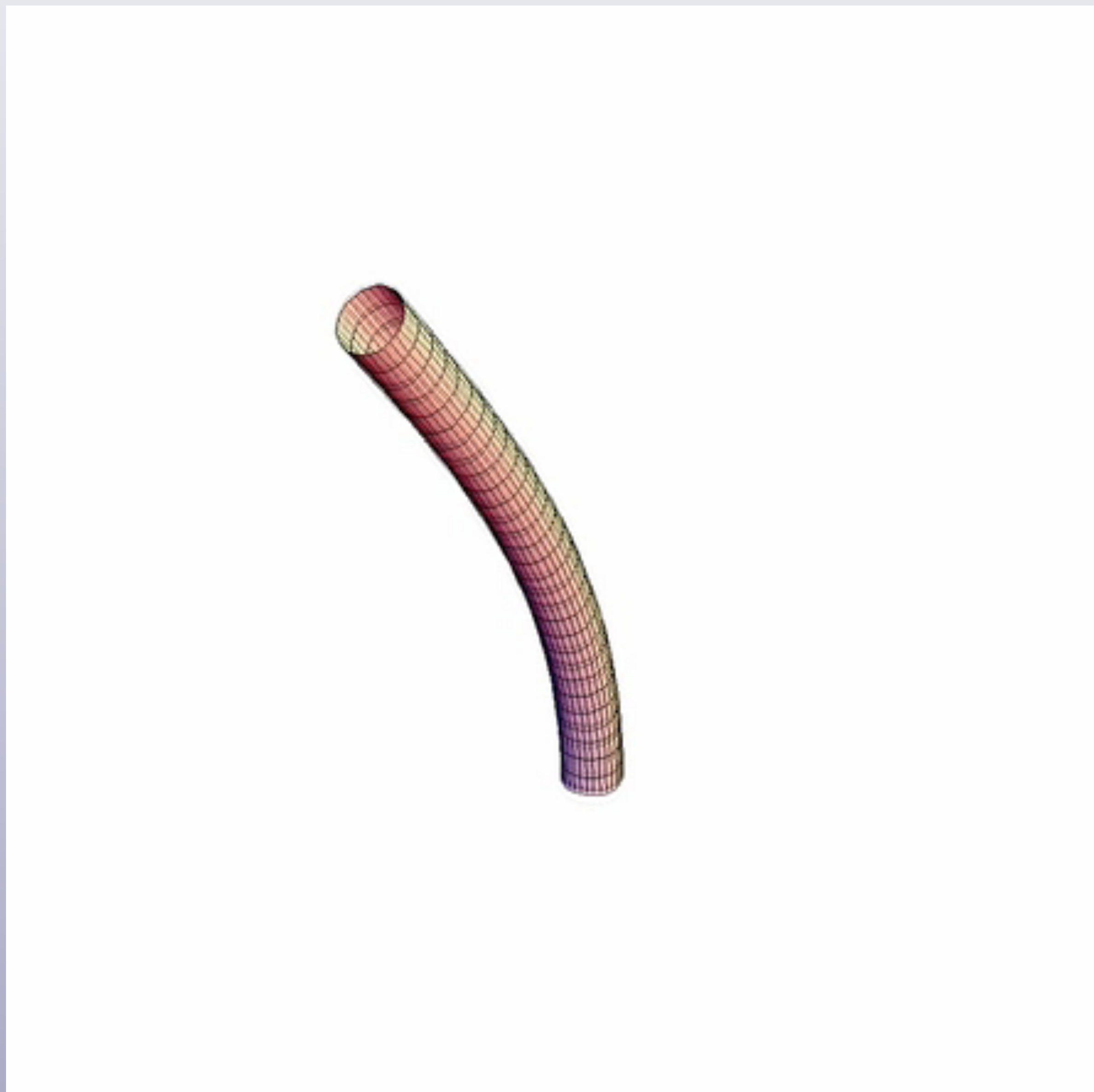



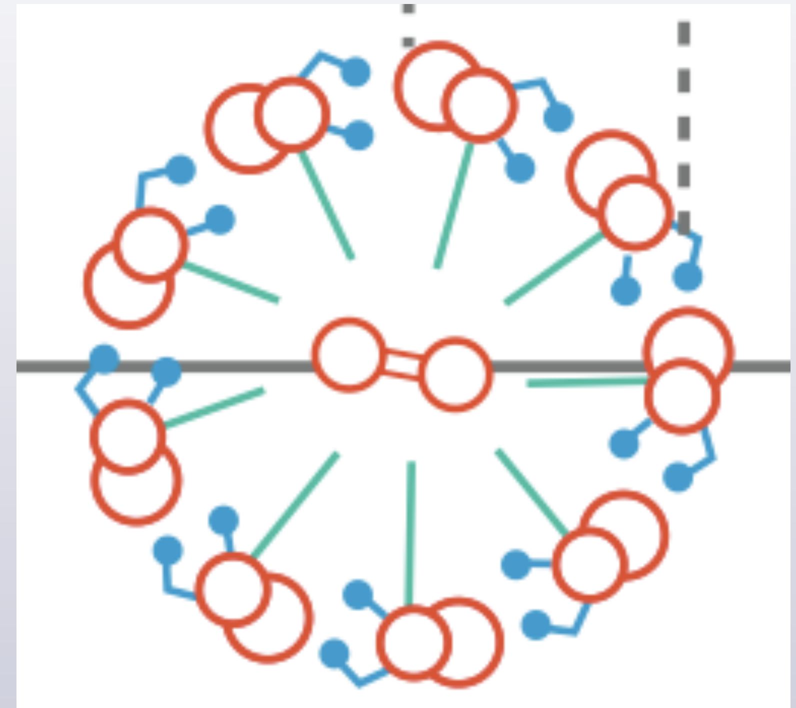
# Chirality


left
handed
right
handed

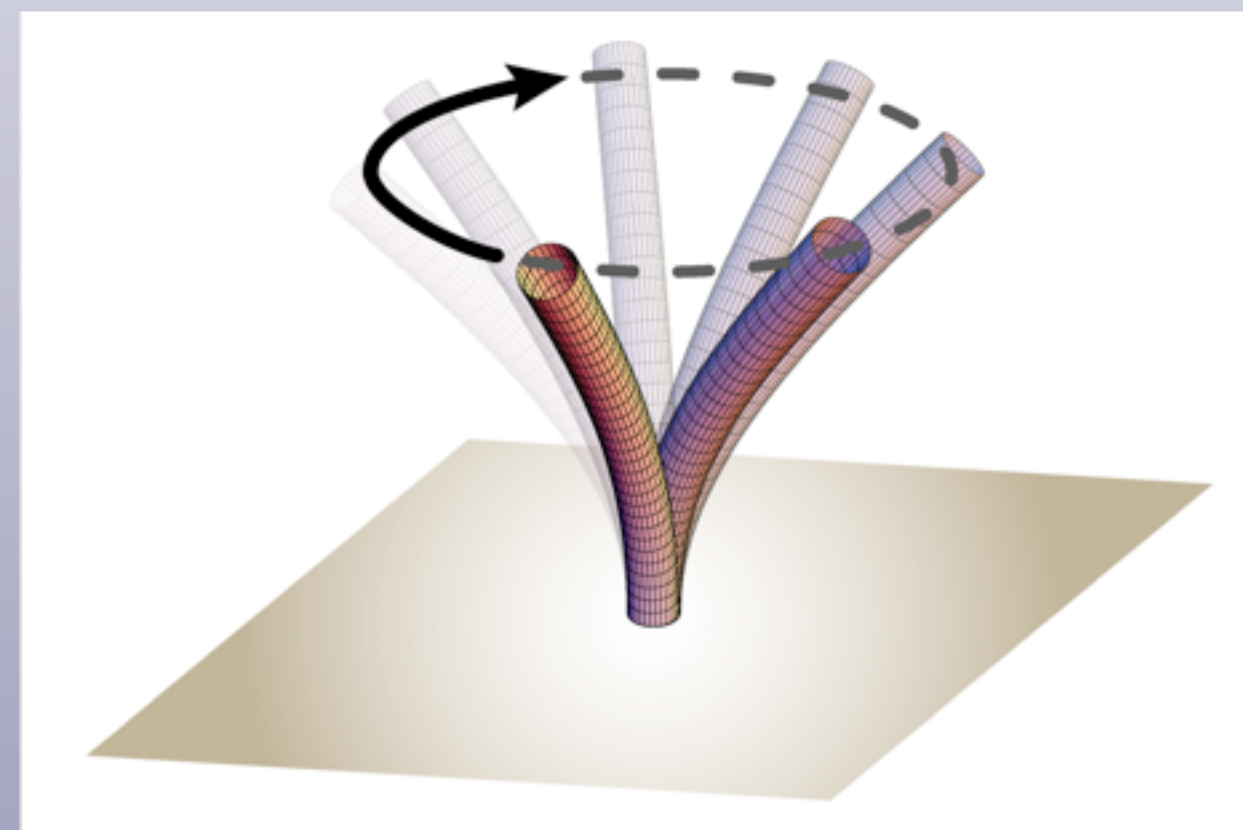

r(s)
e1
e3
e2
e3
e2
e1
r(s)
curvature
twist

# Rotating waves



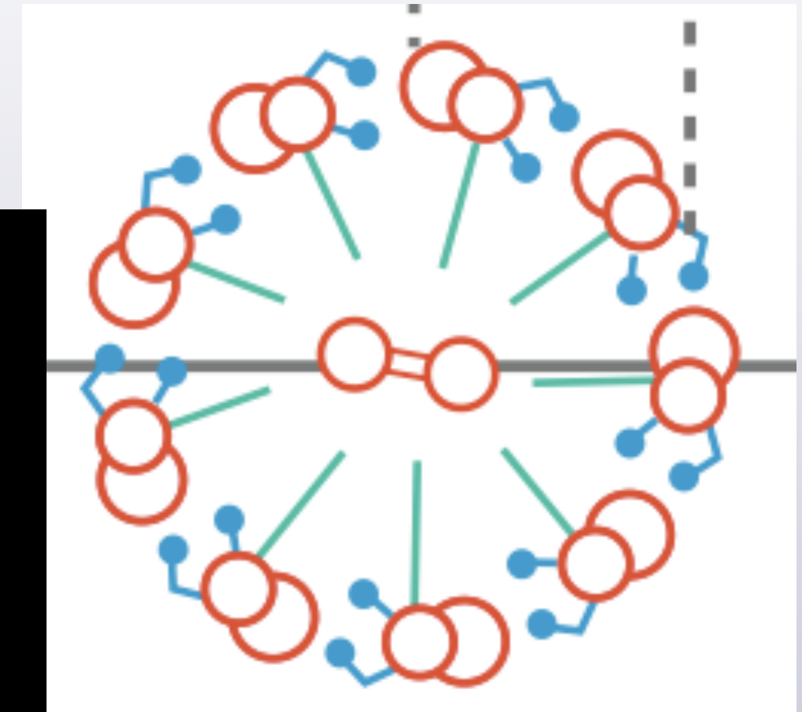


chiral cilium

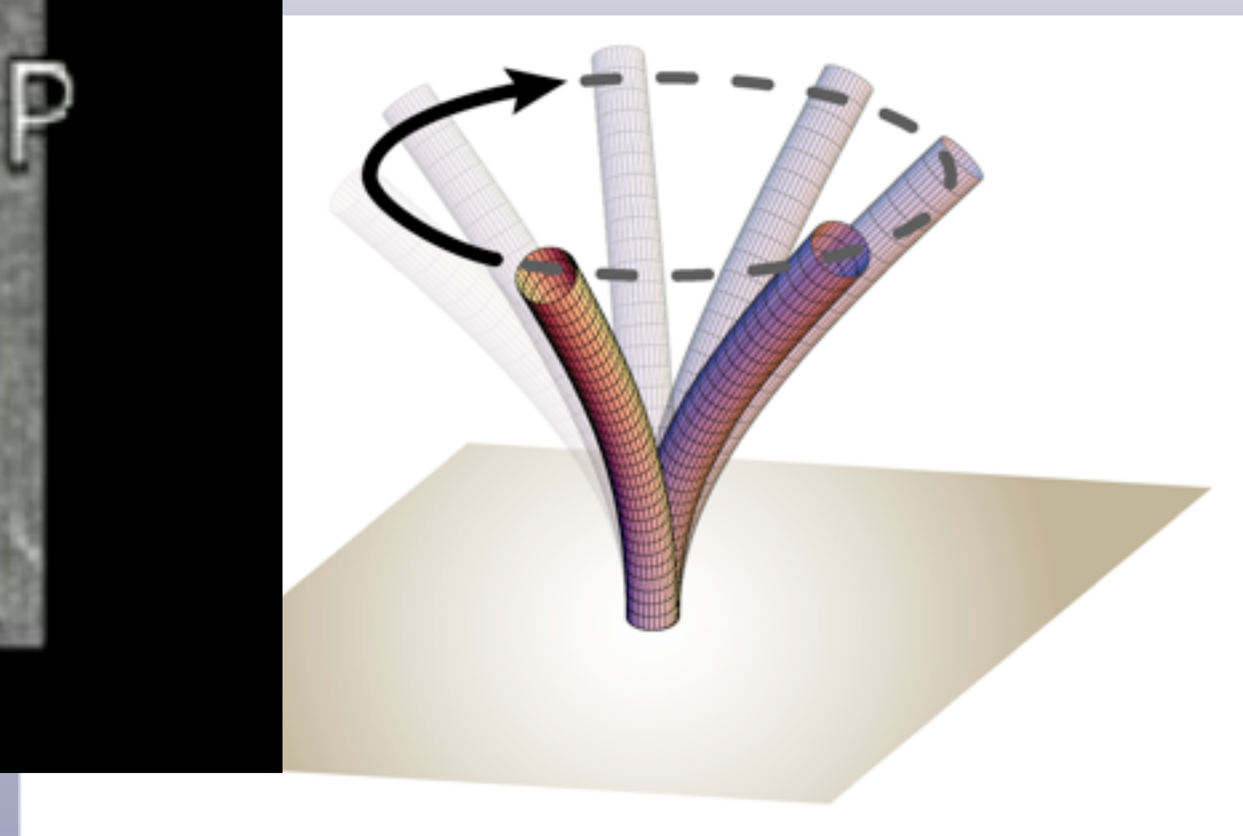


A. Hilfinger and F. Jülicher, Physical Biology 5 (2008)

# Rotating waves

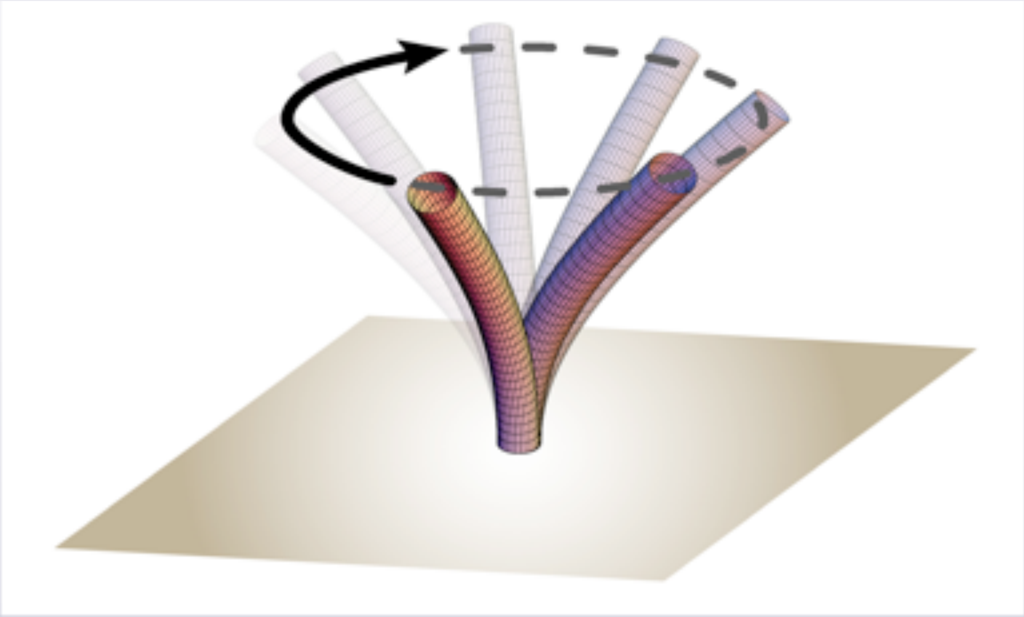



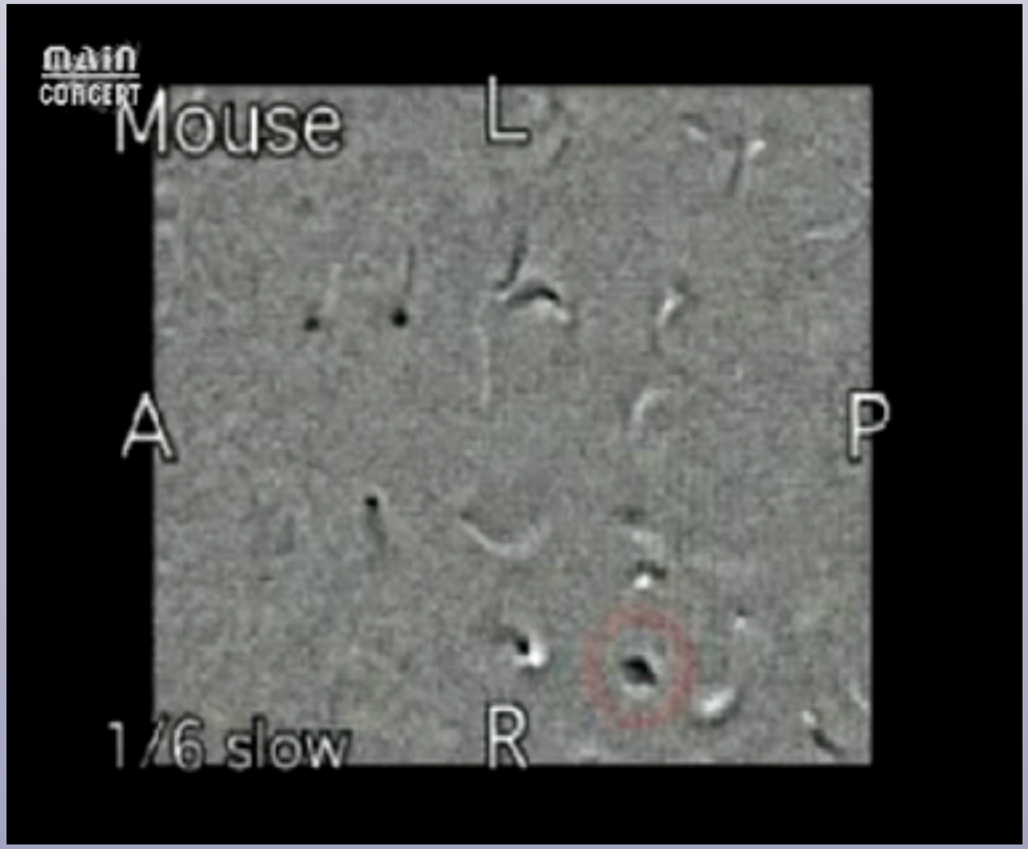
chiral
cilium

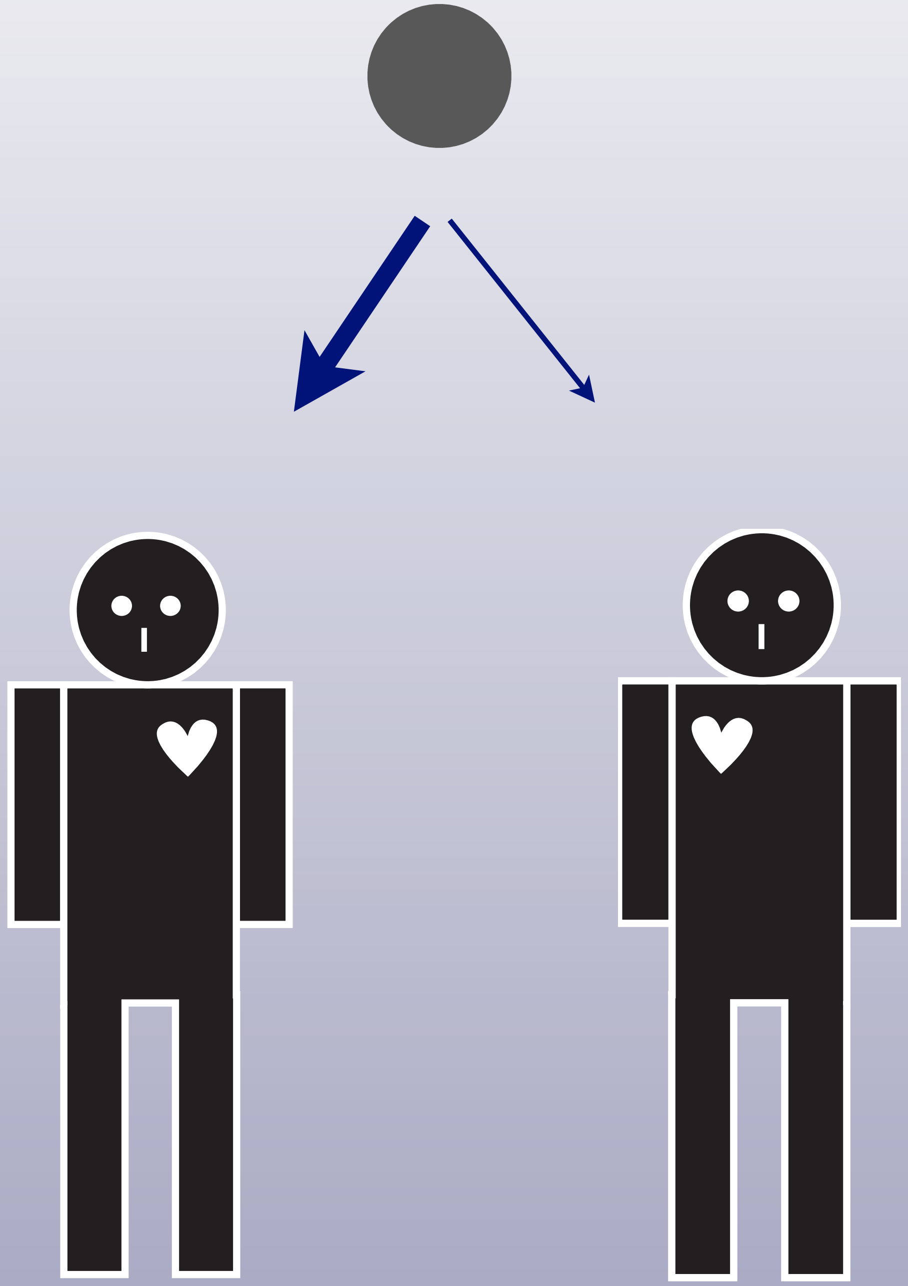


Y. Okada et al. Cell, 121(4): 633 (2005); S. Nonaka et al. Cell, 95 (6): 829 (1998)

# left-right asymmetry

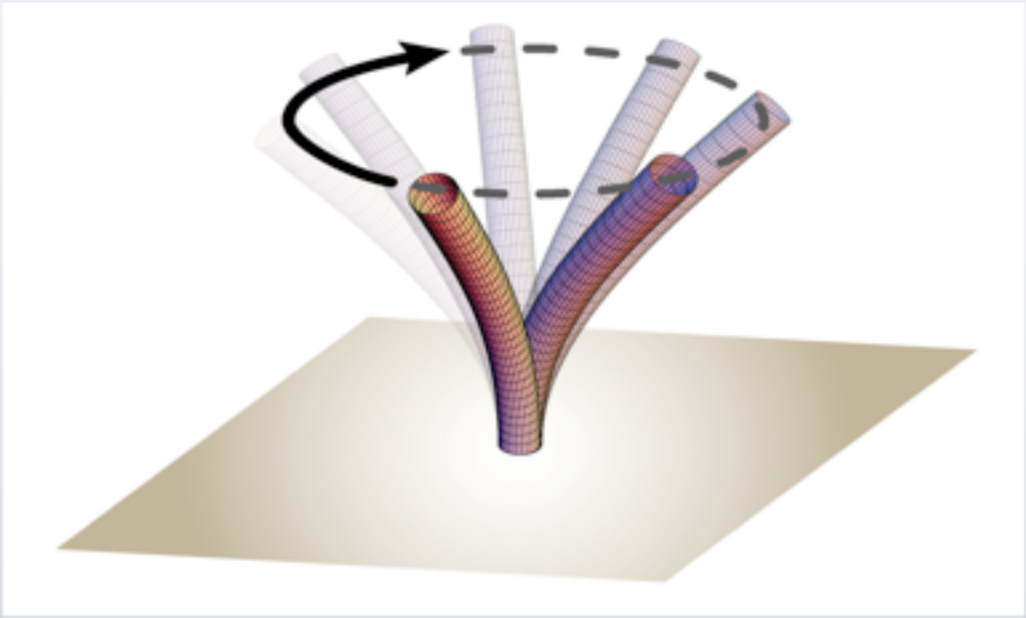


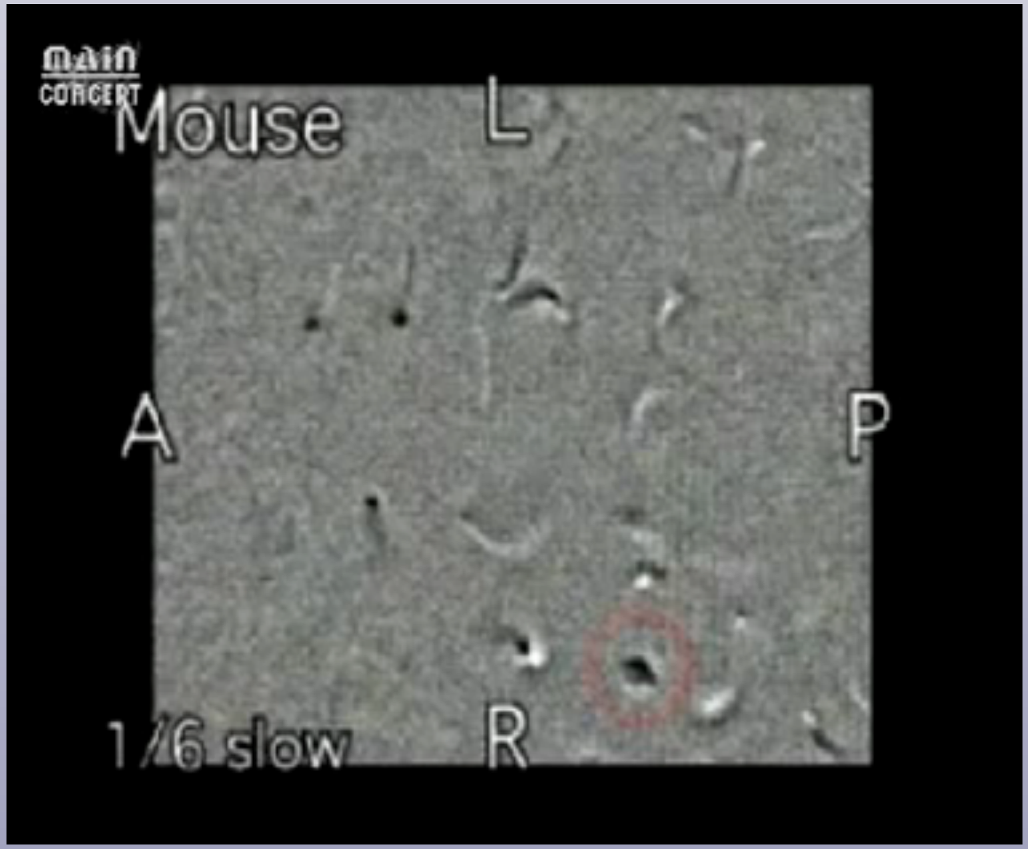


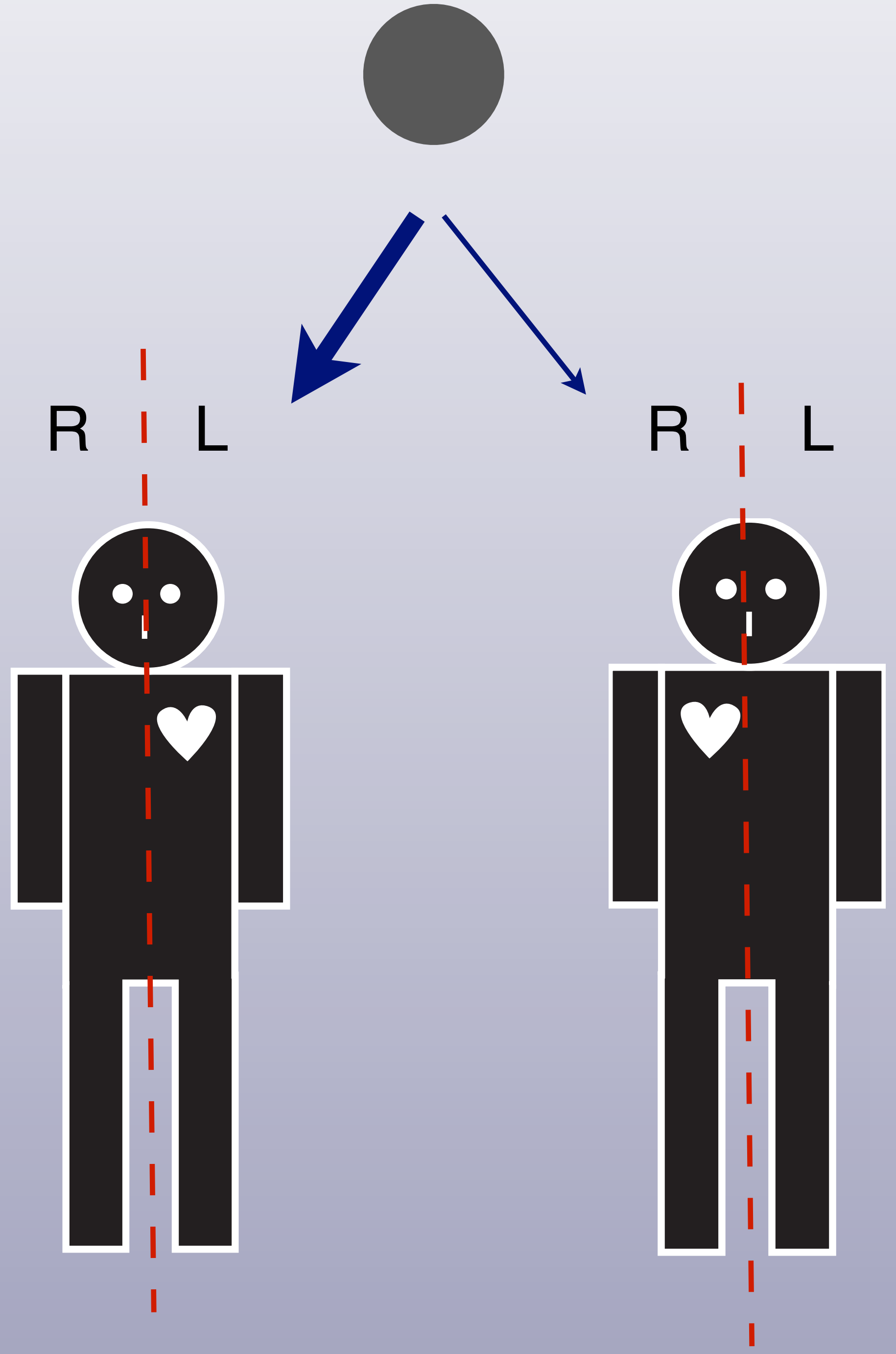



Y. Okada et al. Cell, 121(4): 633 (2005); S. Nonaka et al. Cell, 95 (6): 829 (1998)

# left-right asymmetry



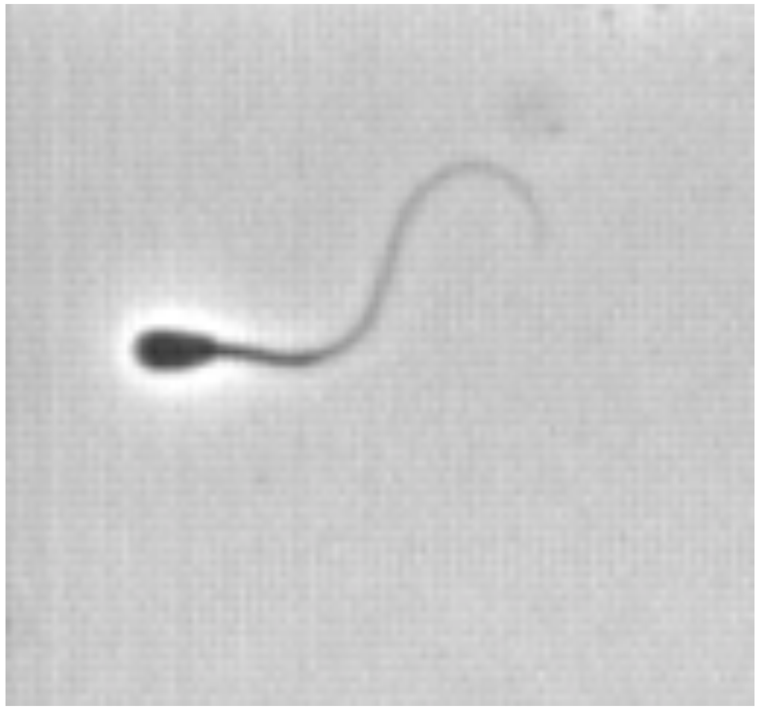



Y. Okada et al. Cell, 121(4): 633 (2005); S. Nonaka et al. Cell, 95 (6): 829 (1998)

# Flagellar beat and swimming


free swimming

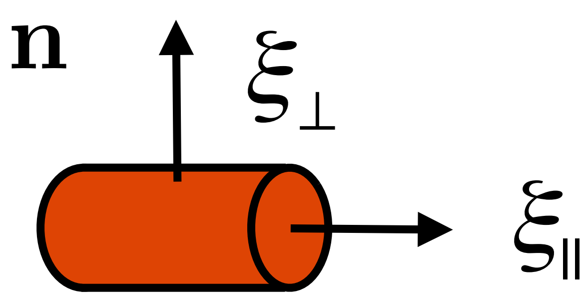


Bull sperm
20 Hz slow motion

no net force    no net torque

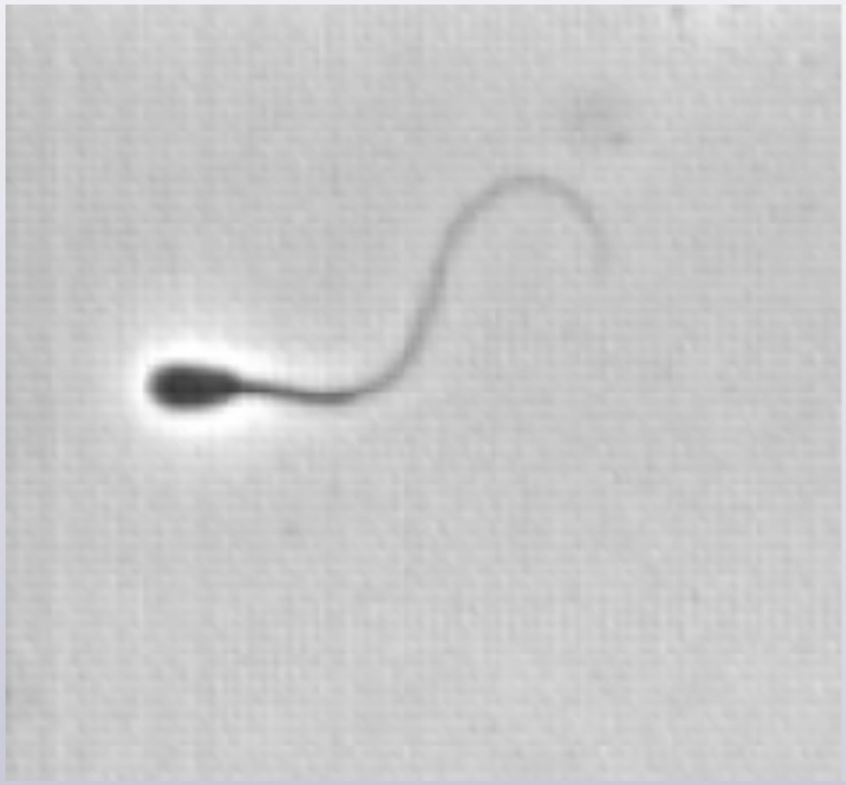
translation velocity $\mathbf{V}$

rotation rate $\mathbf{\Omega}$

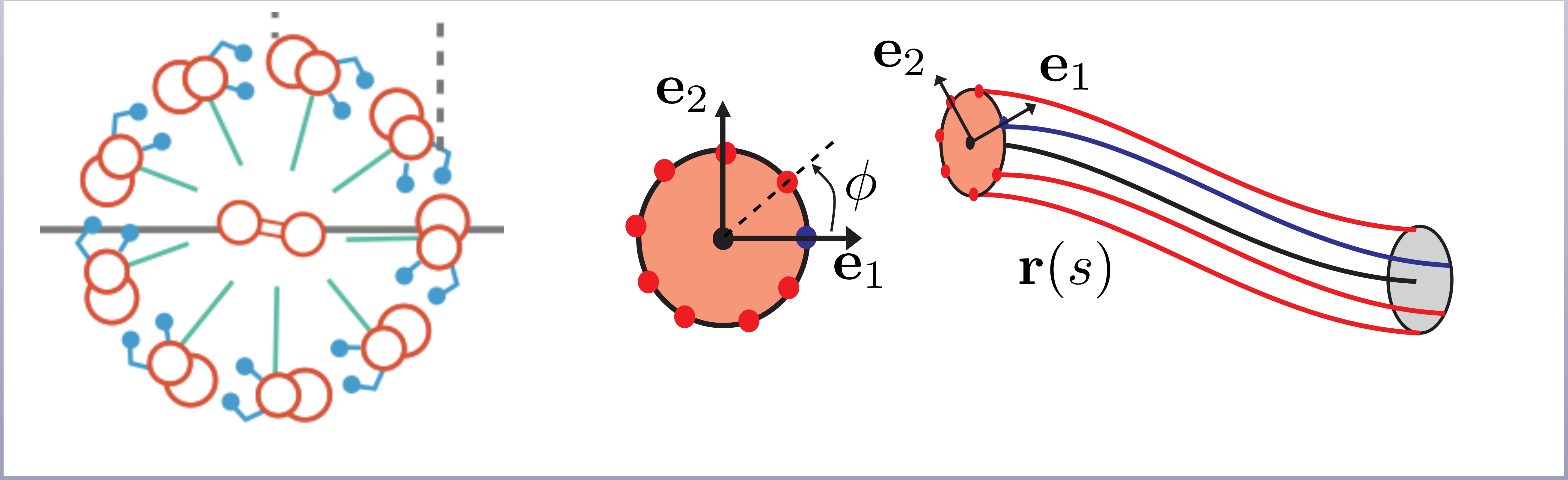



G.I. Taylor Proc. Roy Soc. A (1951)    Gray and Hancock, J. Exp. Biol. (1955)

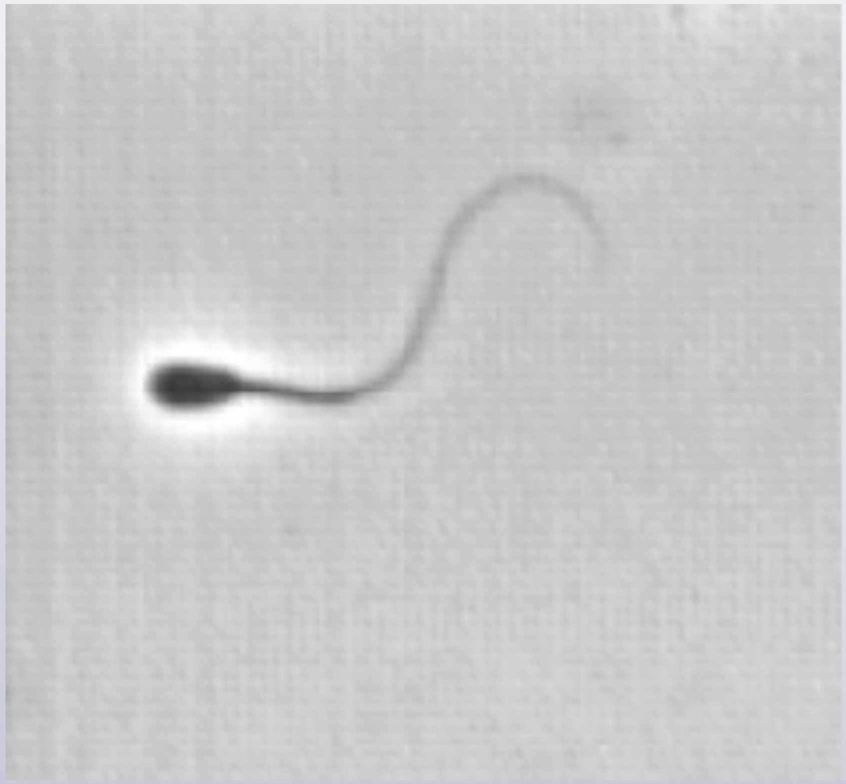
# Chiral swimmers

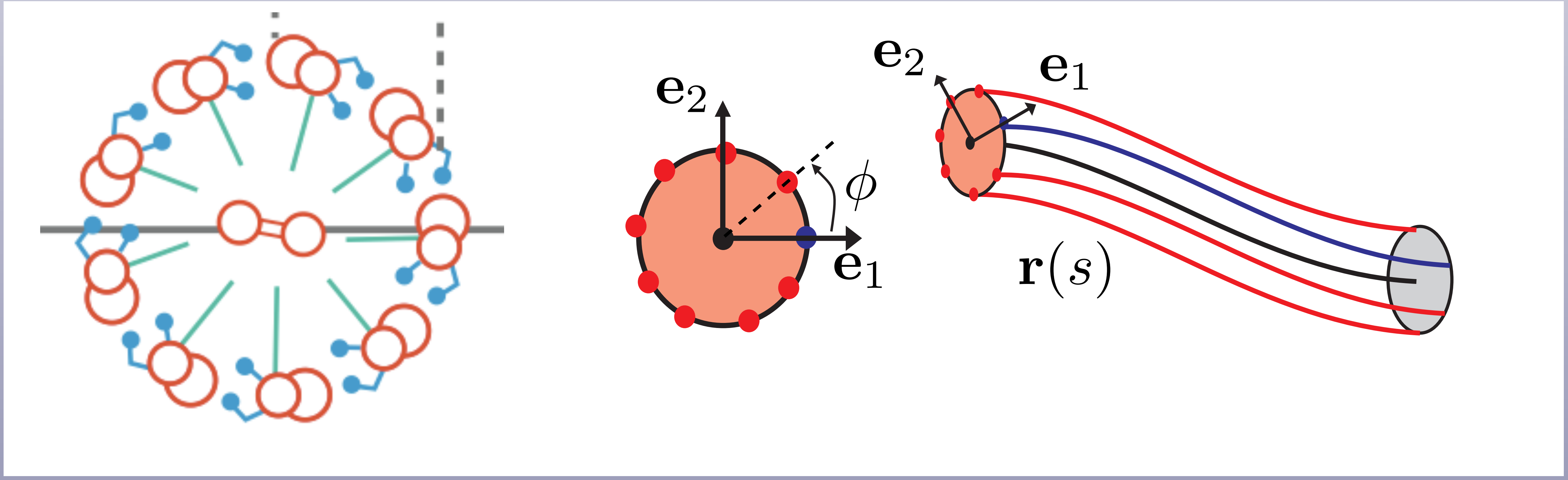


Plane of flagellar beat

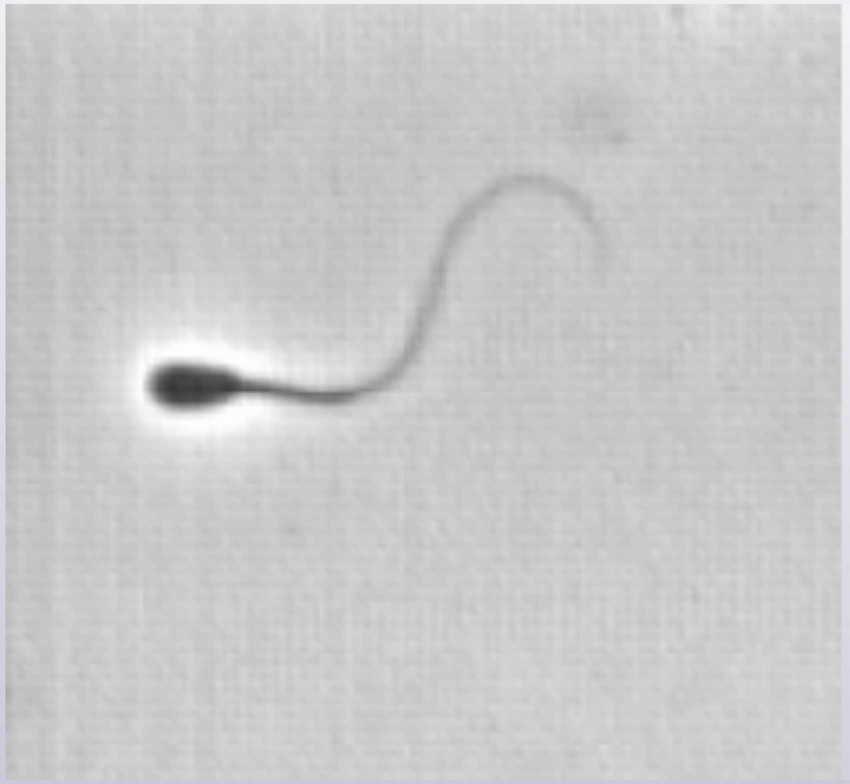


# Chiral swimmers



# Chiral swimmers




Translation $\mathbf{v} = v_0 \mathbf{t}$

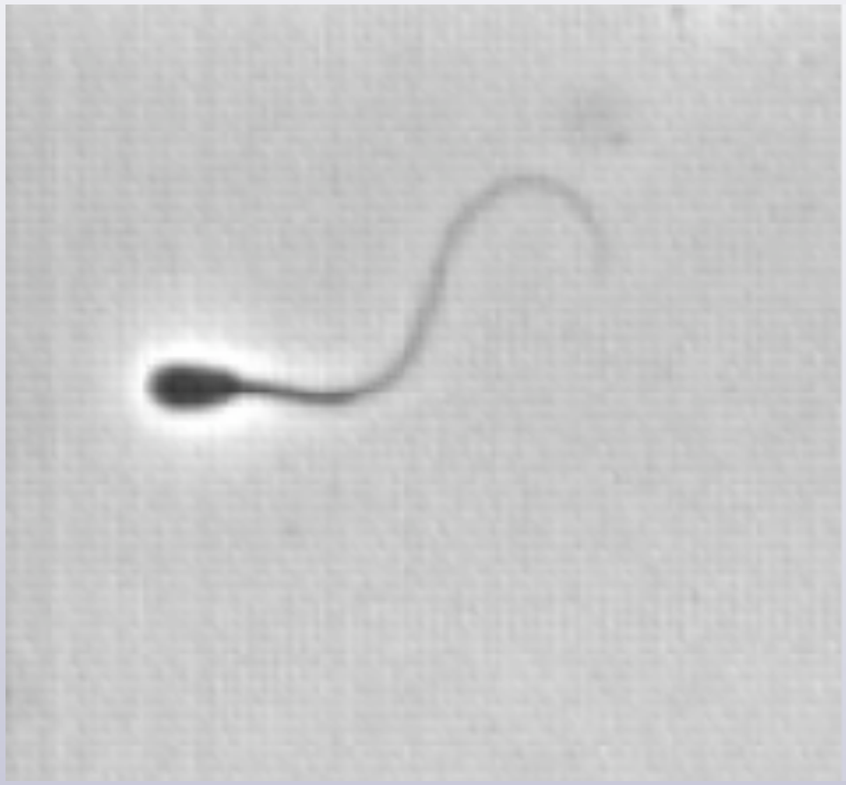
Rotation $\boldsymbol{\Omega} = \omega_{\|} \mathbf{t} + \omega_{\perp} \mathbf{b}$

generated by flagellar beat

Curvature $\kappa = \omega_{\perp} / v_0$

Torsion $\tau = \omega_{\|} / v_0$

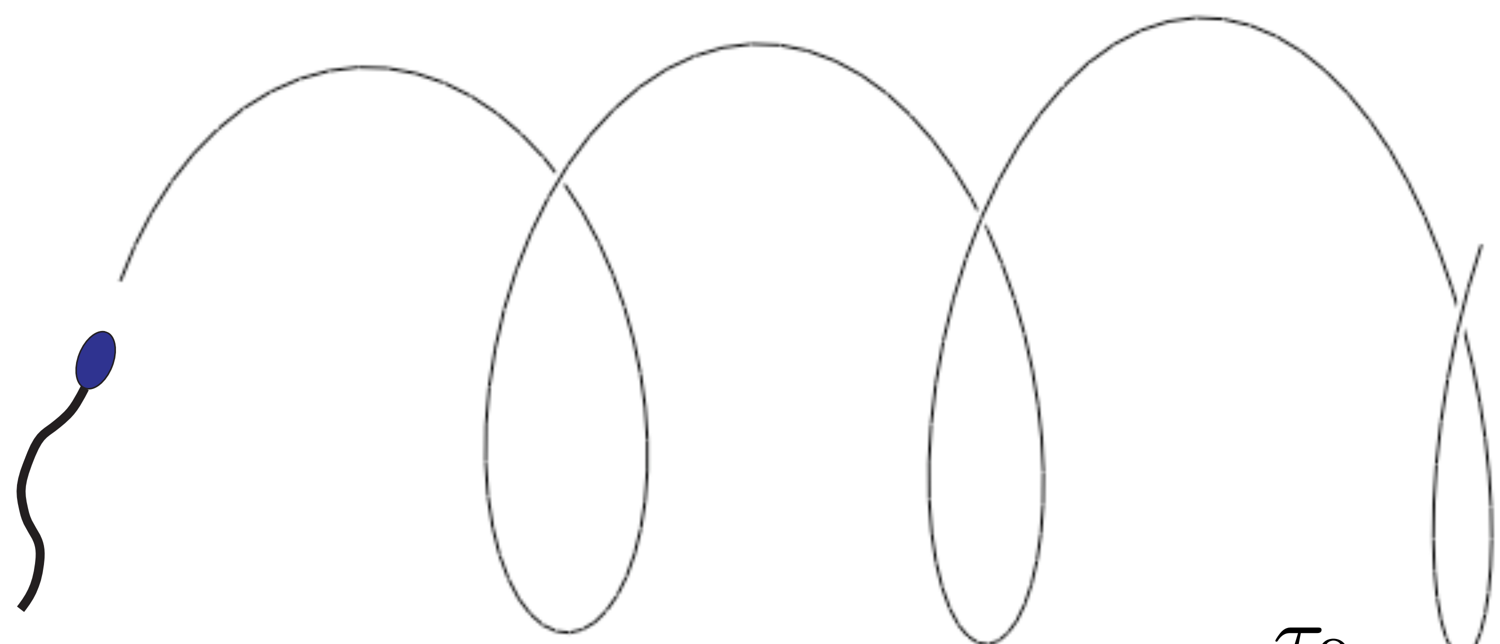
# Chiral swimmers



weakly twisted


Plane of flagellar beat

helical
swimming path



curvature $\kappa_0$

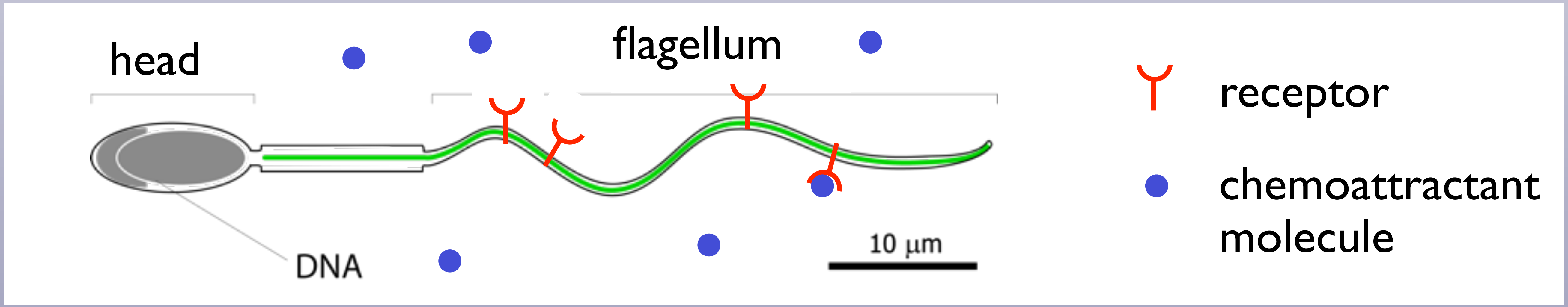
torsion $\tau_0$

radius $r_0 = 1/\kappa_0$ pitch $h_0 = \dfrac{\tau_0}{\kappa_0^2 + \tau_0^2}$

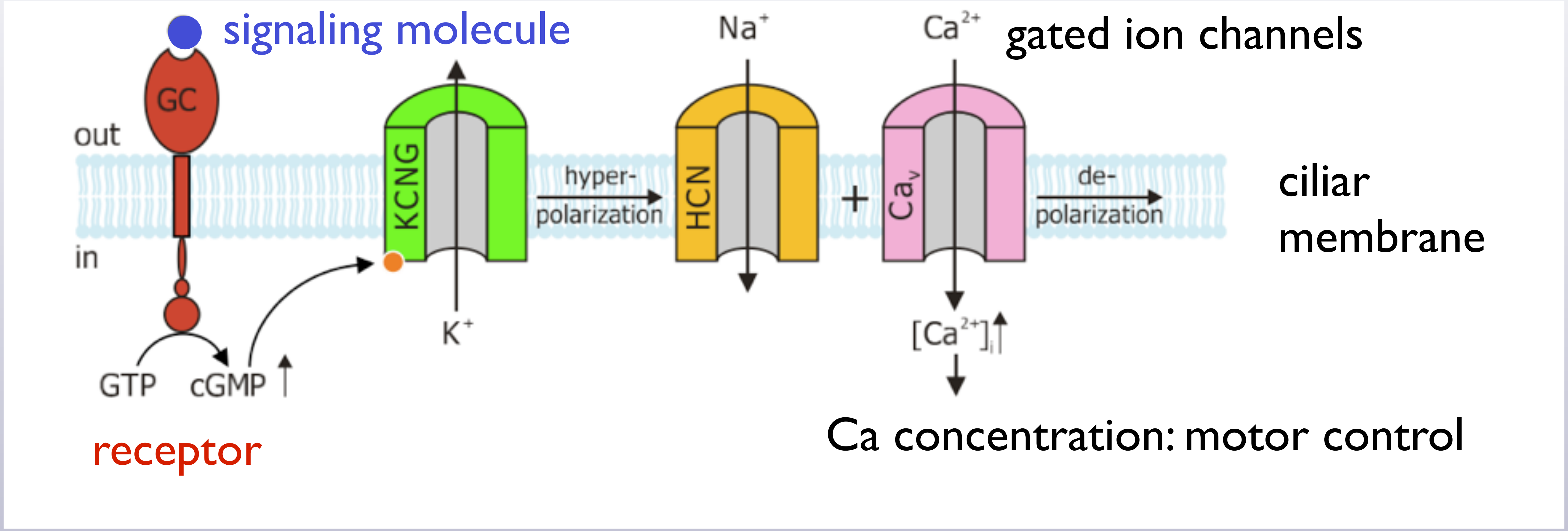
# Cilium as sensory antennae

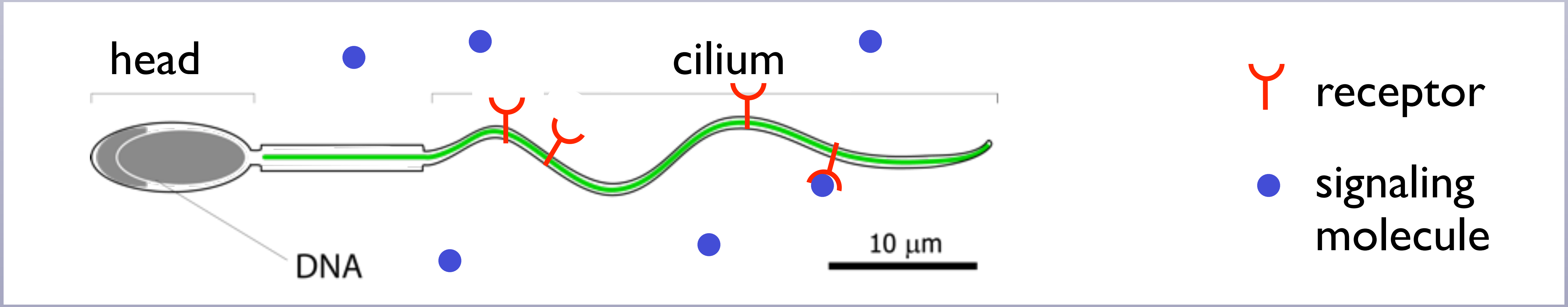
Chemical gradient guides sperm to the egg


Motility controlled by chemical signals



# Signaling system




T. Strünker et al. Nature Cell Biology 8 (2006)

# Steering towards a chemical signal

Experiments: optical uncaging of chemoattractant

Sea urchin sperm

Sperm swim towards high concentration of chemoattractant

Single molecule detection

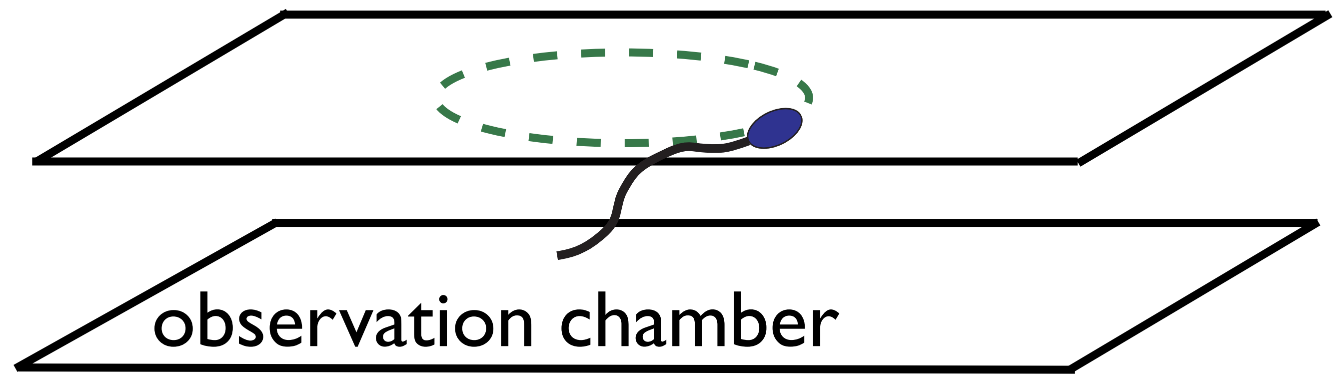
L. Dai, L. Alvarez, U.B. Kaupp, caesar research center, Bonn

Böhmer et al. EMBO J. (2005)

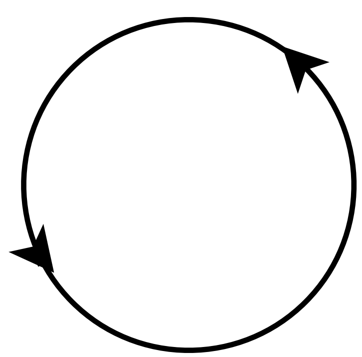
# Confinement: planar geometry

Swimming on circular paths

$$\kappa_0 = 1/r_0$$

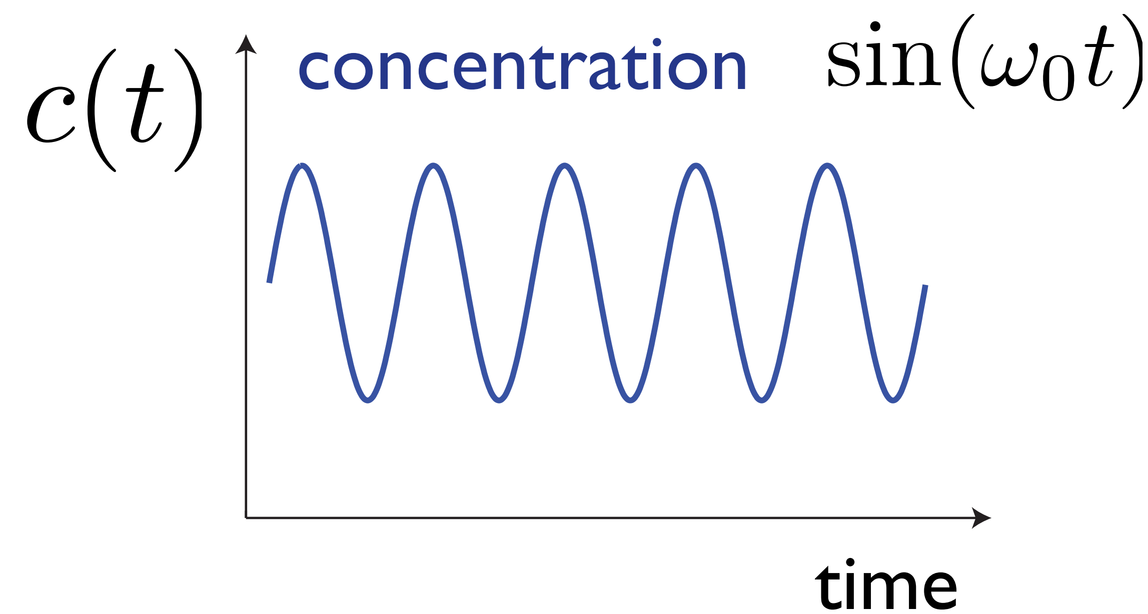



$$\mathbf{r}(t)$$



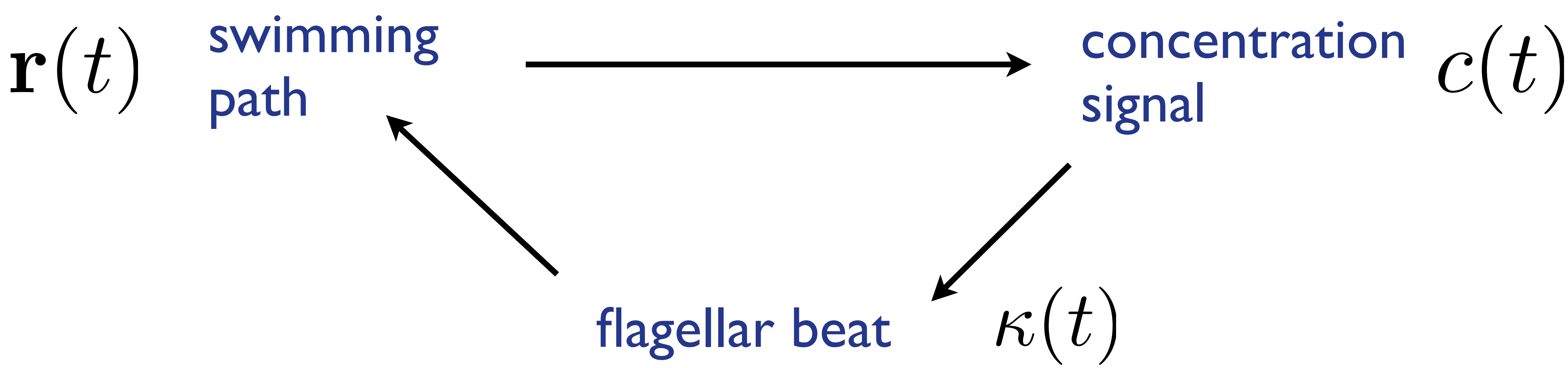
constant curvature

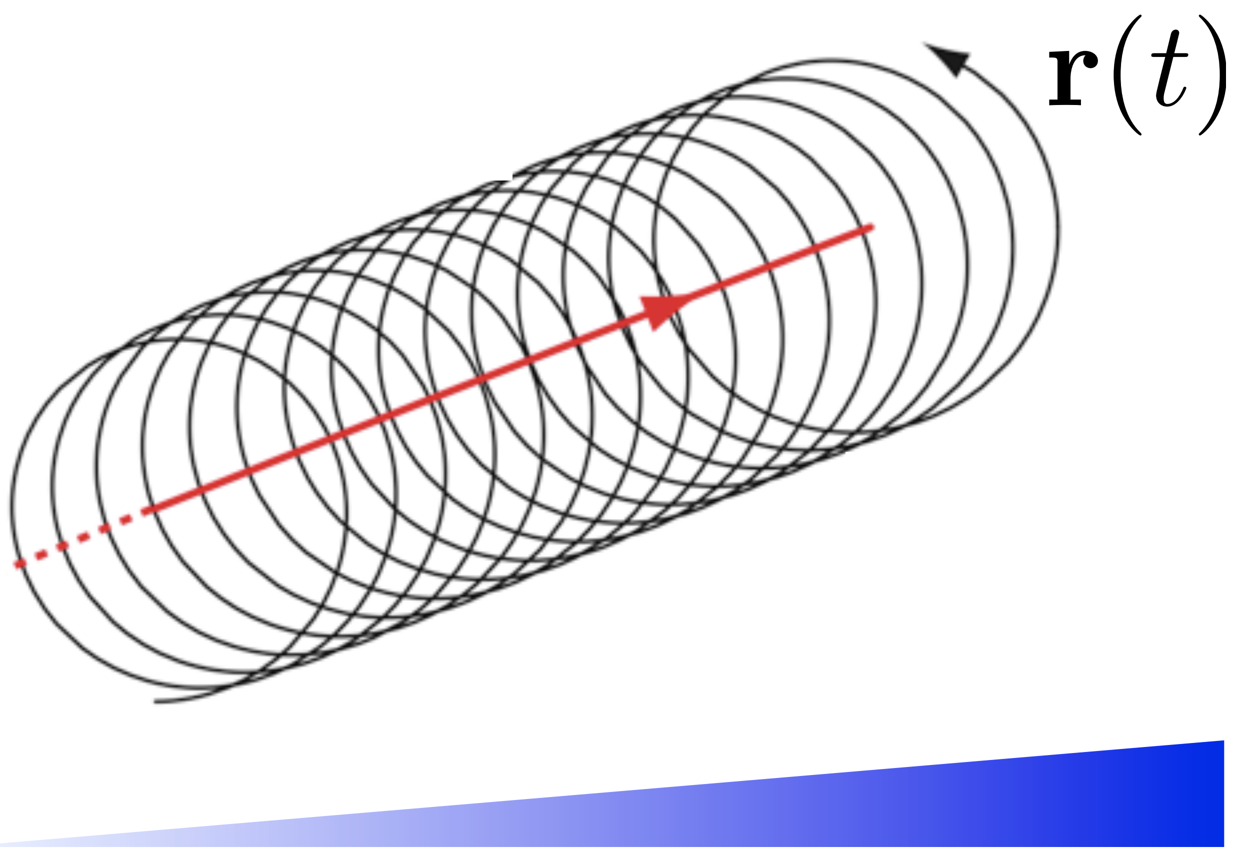
$$\omega_0 = v_0 \kappa_0$$

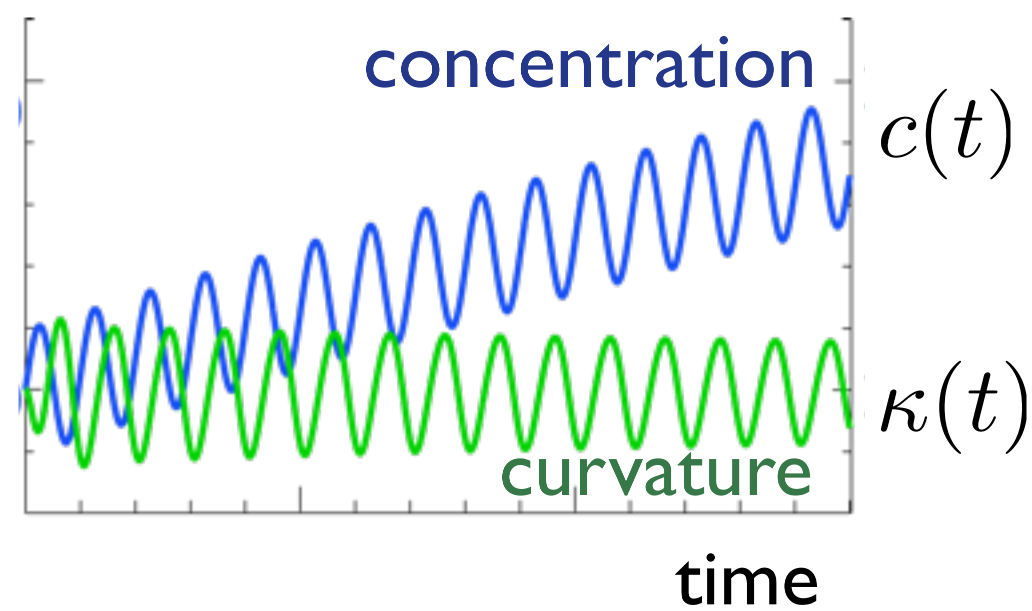



concentration gradient

# Steering in the plane

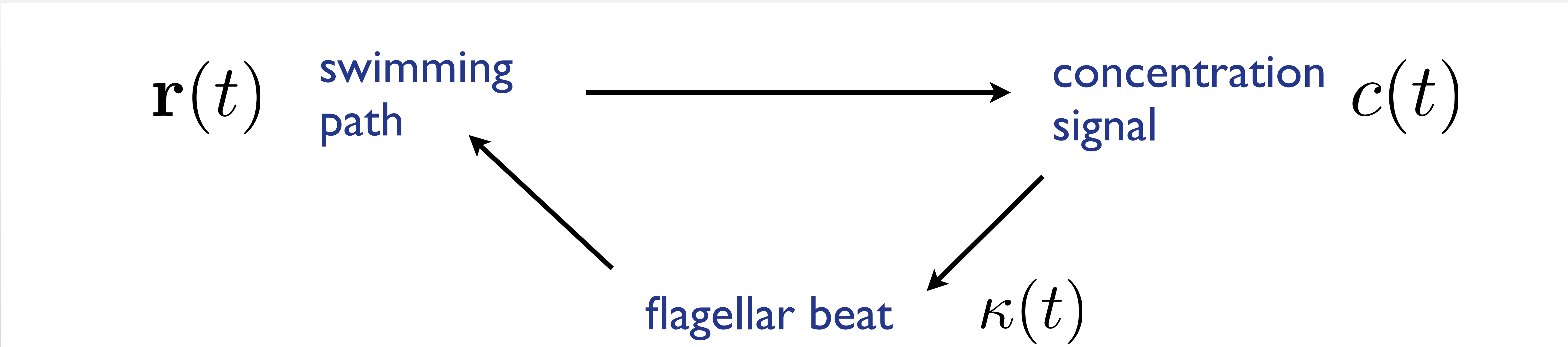


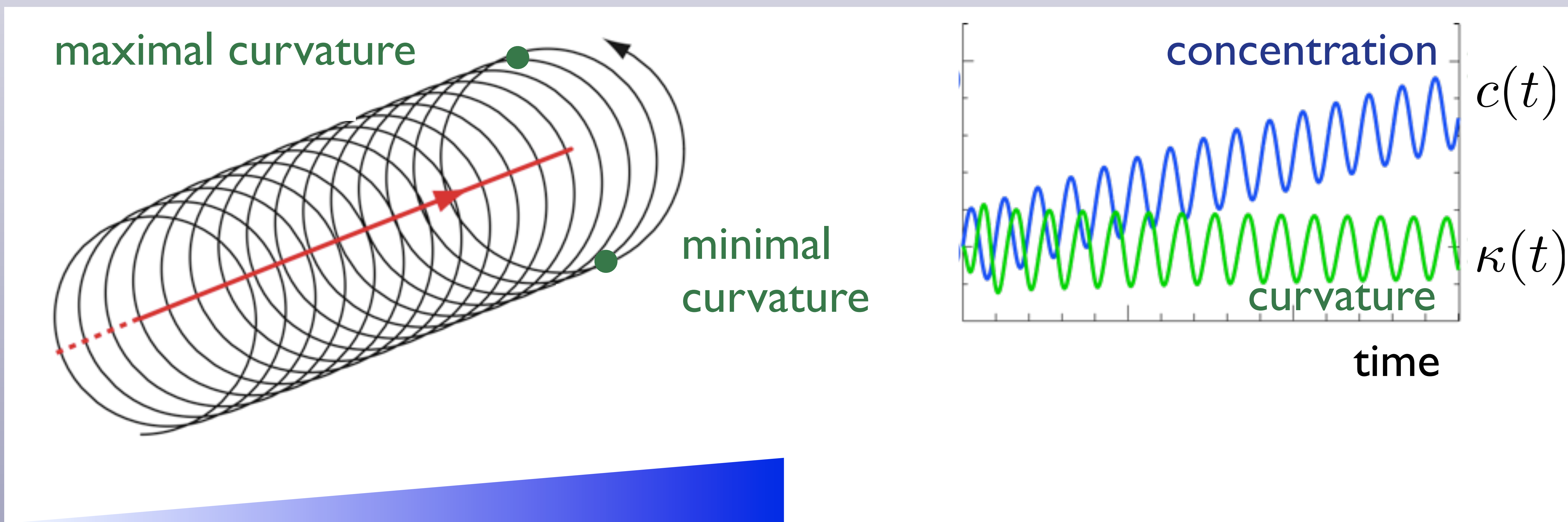




B.M. Friedrich, F. Jülicher, PNAS 104, 13256 (2007)

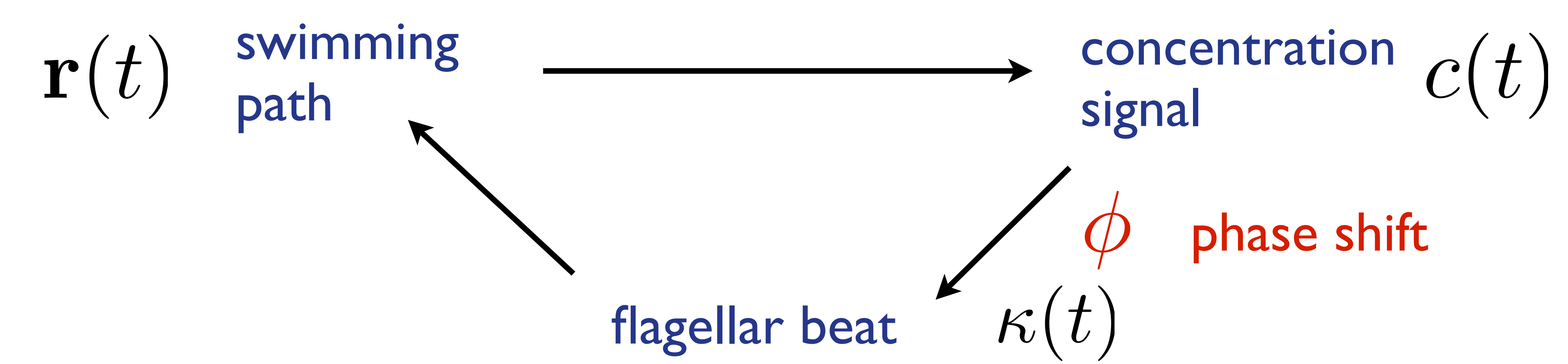
# Steering in the plane

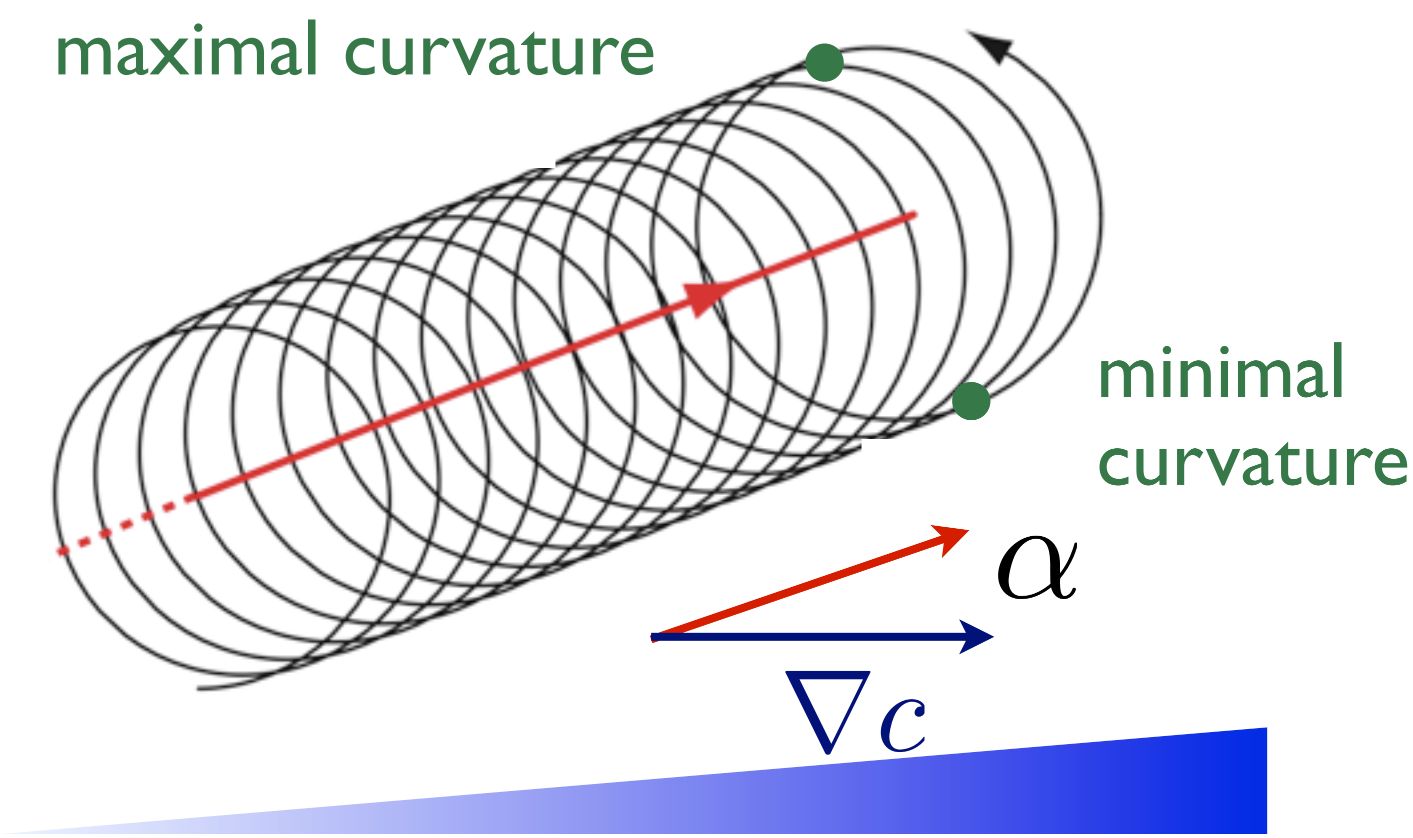


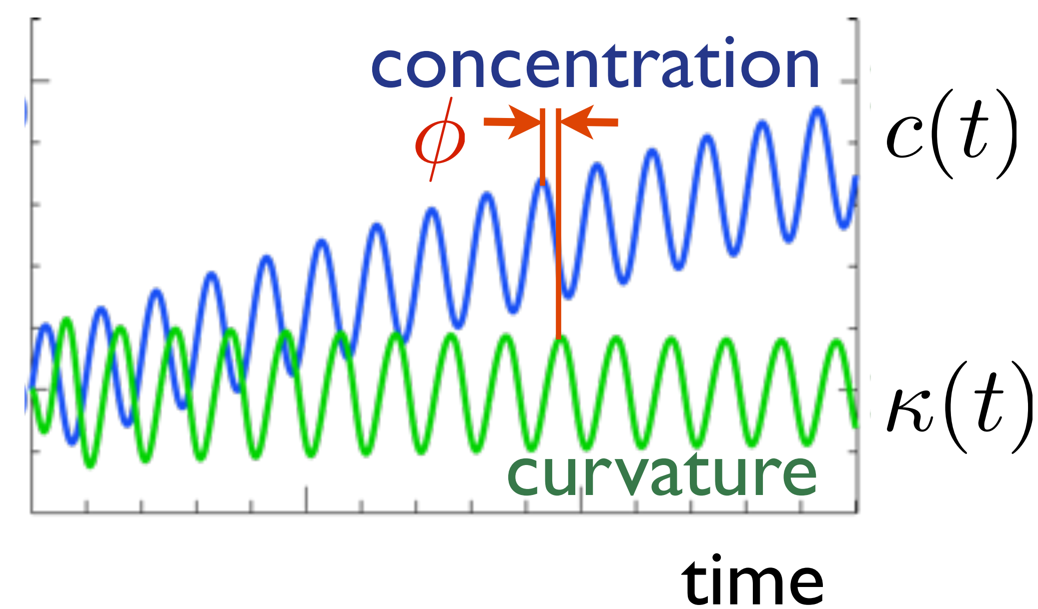




B.M. Friedrich, F. Jülicher, PNAS 104, 13256 (2007)

# Steering in the plane



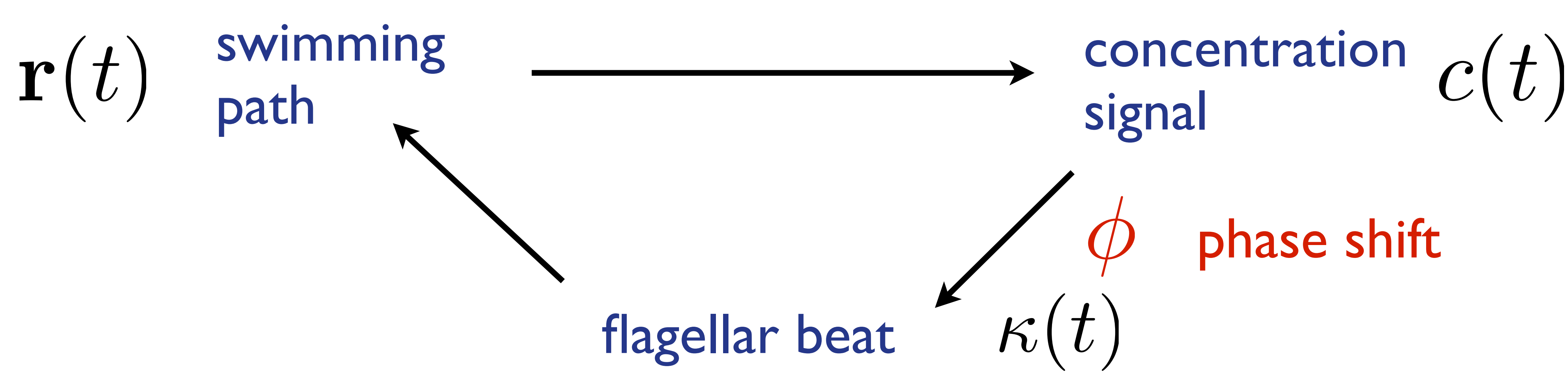




$$\alpha = \frac{3\pi}{2} - \phi$$

B.M. Friedrich, F. Jülicher, PNAS 104, 13256 (2007)

# Signaling in linear response




linear response function

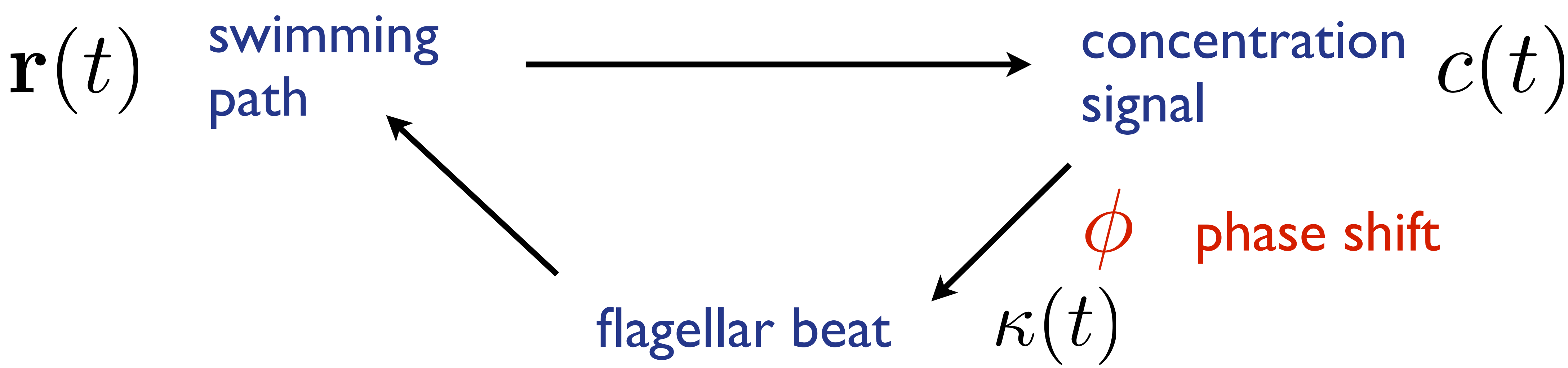
adaptation $\Delta c/c$

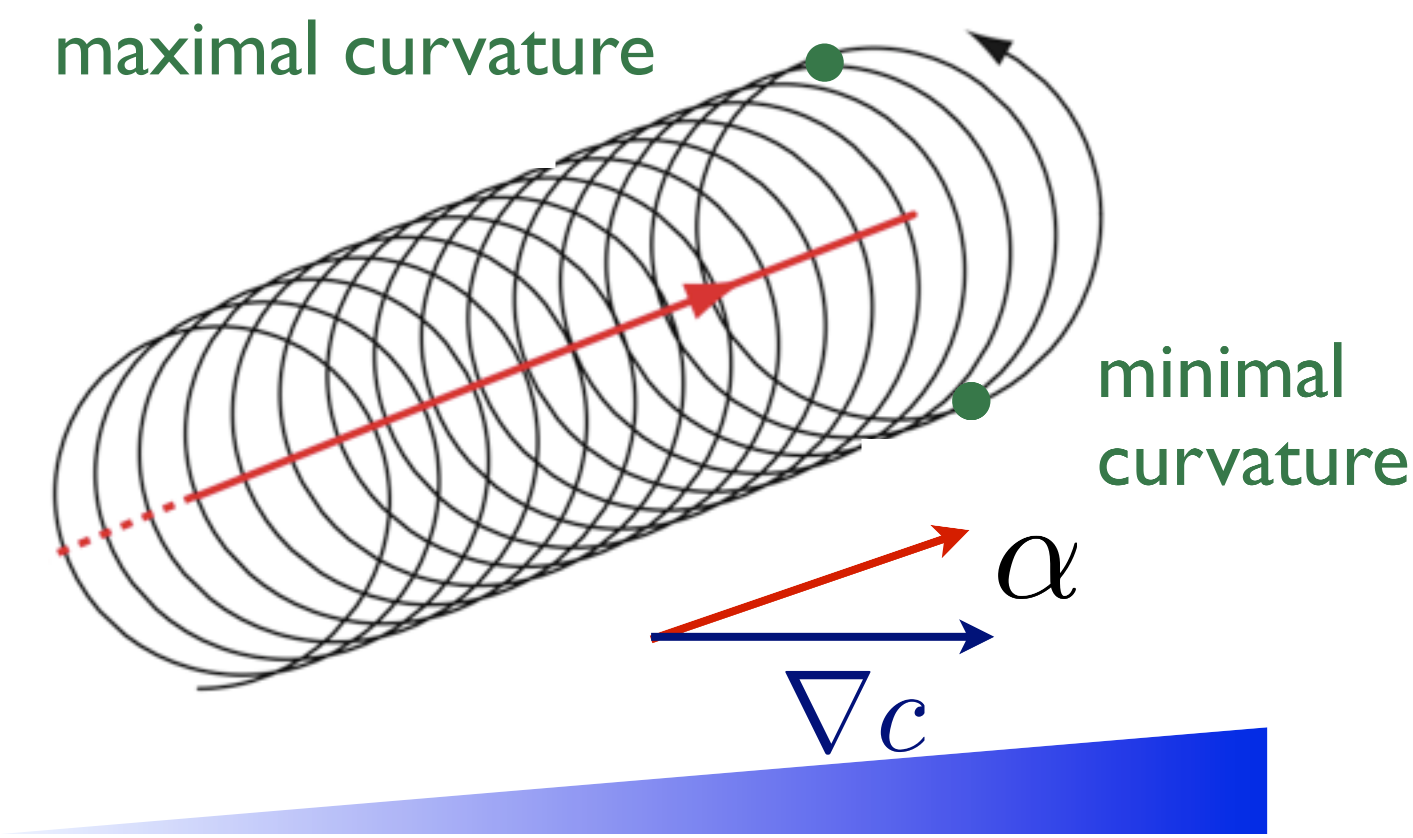
$$\tilde{\kappa}(\omega) = \chi_\kappa(\omega)\tilde{c}(\omega)$$

$$\chi_\kappa = \rho e^{i\phi}$$

$$\rho \sim 1/c$$

# Steering in the plane




$$\chi_\kappa(\omega_0) = \rho e^{i\phi}$$

$$v_d \simeq \frac{1}{2} v_0 r_0^2 \rho |\nabla c|$$

$$\alpha = \frac{3\pi}{2} - \phi$$

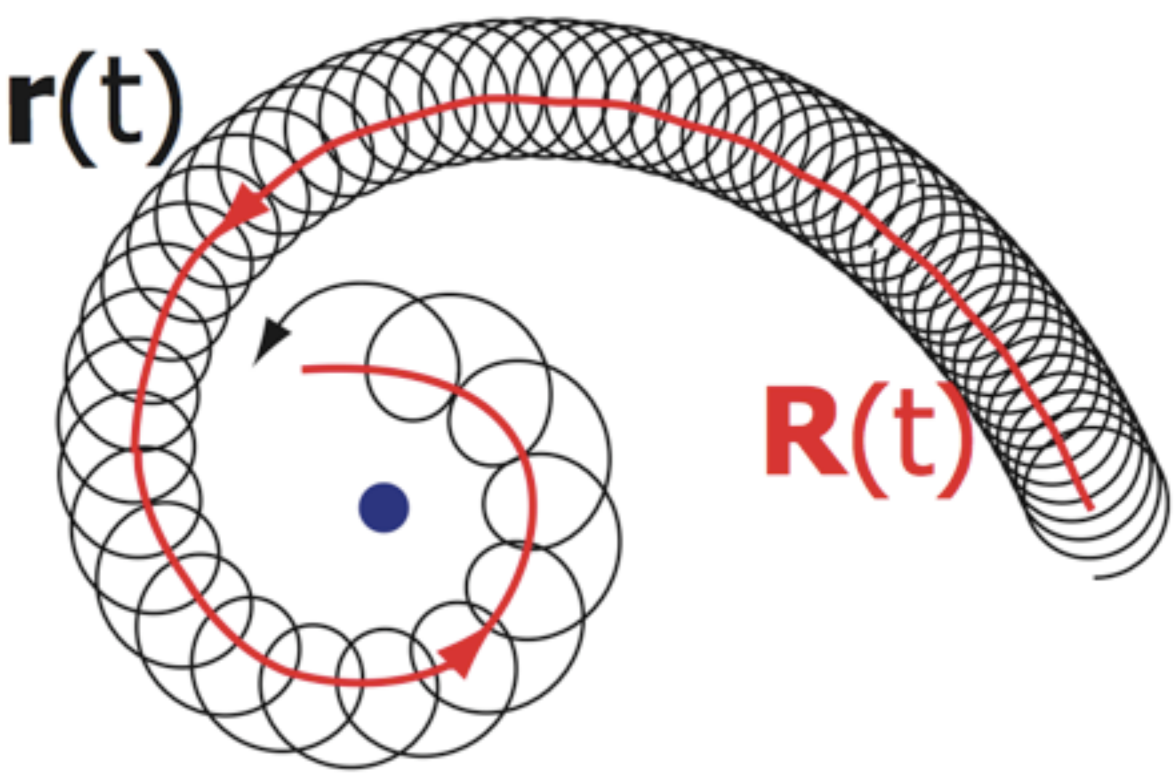
chemotaxis: $-\frac{\pi}{2} < \alpha < \frac{\pi}{2}$ $\qquad \chi'_\kappa < 0$

# Steering in the plane

$\mathbf{r}(t)$ swimming path

concentration signal $c(t)$

flagellar beat $\kappa(t)$




radial concentration field

spiralling motion to the center

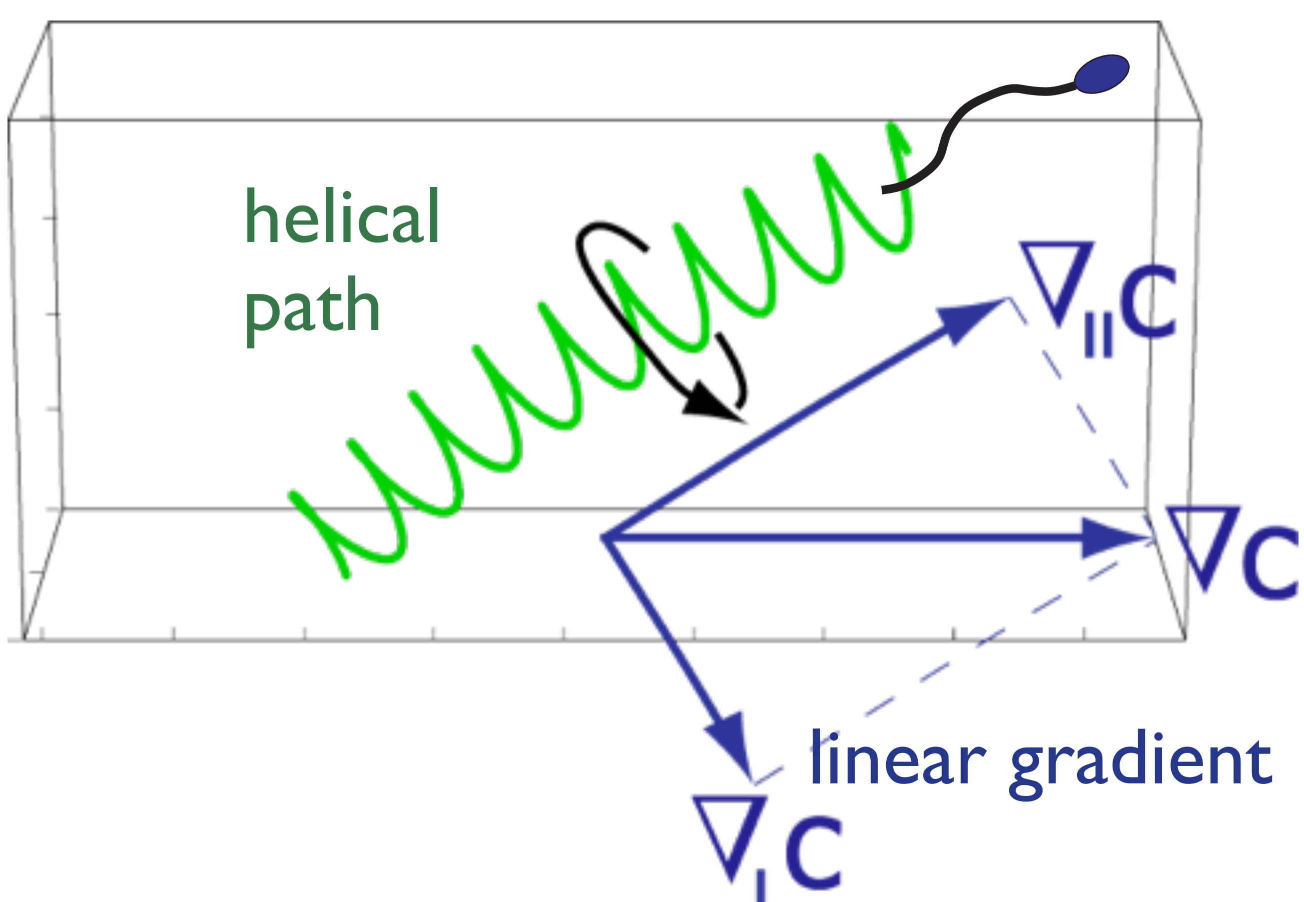
$$\alpha = \frac{3\pi}{2} - \phi$$

chemotaxis: $-\frac{\pi}{2} < \alpha < \frac{\pi}{2}$ $\chi'_\kappa < 0$

# Motion in 3-d space

$\mathbf{r}(t)$ swimming path $\longrightarrow$ concentration signal $c(t)$

flagellar beat $\kappa(t)\,\tau(t)$




periodic concentration signal

$$c(t) \simeq R\nabla_{\perp}c\;\sin(\omega t)$$

periodic modulation of $\kappa$
$\tau$

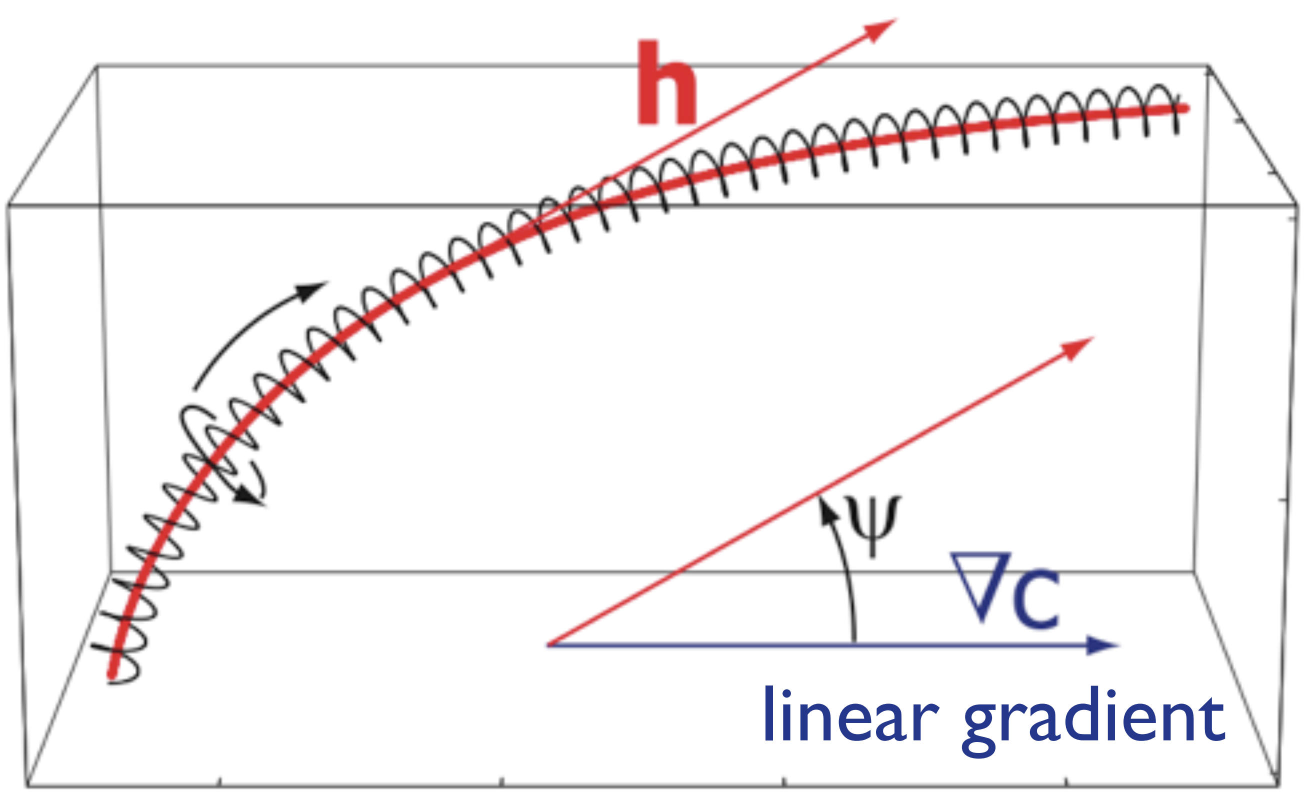
$\chi_{\kappa}(\omega)\quad \chi_{\tau}(\omega)$

# Motion in 3-d space

$\mathbf{r}(t)$ swimming path → concentration signal $c(t)$

concentration signal → flagellar beat $\kappa(t)\,\tau(t)$

flagellar beat → swimming path




Helix bending

$$\dot{\psi} = -\beta \sin \psi$$

$$\beta = (\epsilon_\tau \chi'_\tau - \epsilon_\kappa \chi'_\kappa)|\nabla c|$$

$$\epsilon_\kappa = \omega_0 r_0 h_0/2 \qquad \epsilon_\tau = \omega_0 r_0^2/2$$

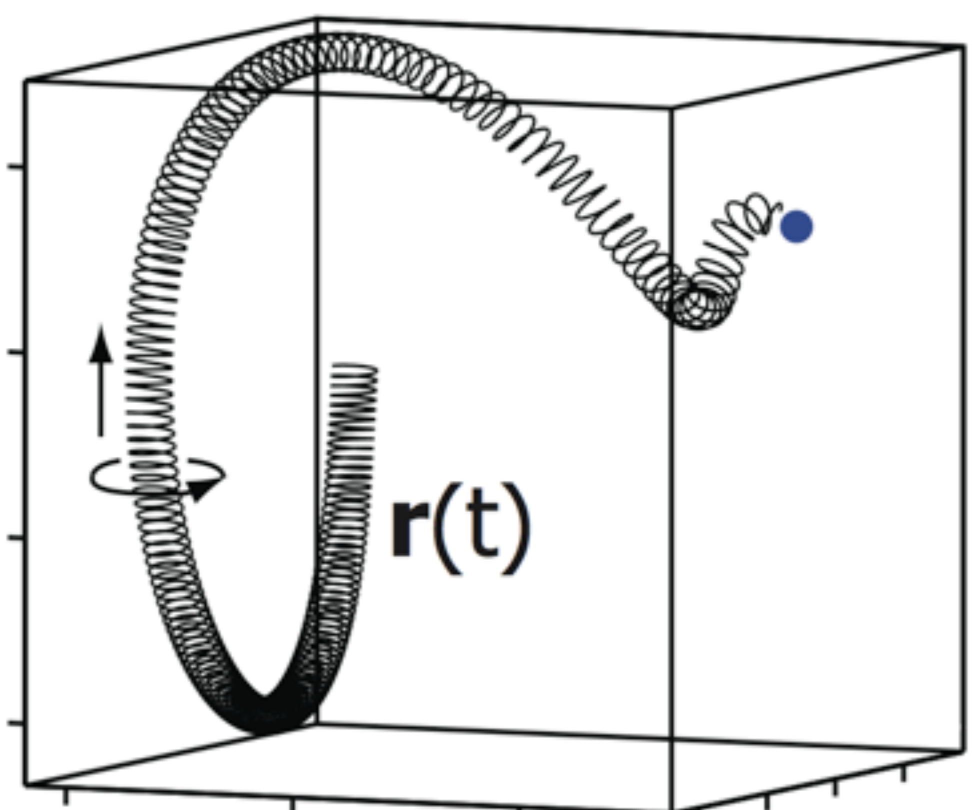
B.M. Friedrich, F. Jülicher, PNAS 104, 13256 (2007)

# Radial concentration in 3-d

$\mathbf{r}(t)$ swimming path → concentration signal $c(t)$

concentration signal → flagellar beat $\kappa(t)\,\tau(t)$

flagellar beat → swimming path




Nonlinear dynamics on superhelical swimming paths

$$\dot{R} = -\omega h \cos\psi - \gamma \sin^2\psi$$

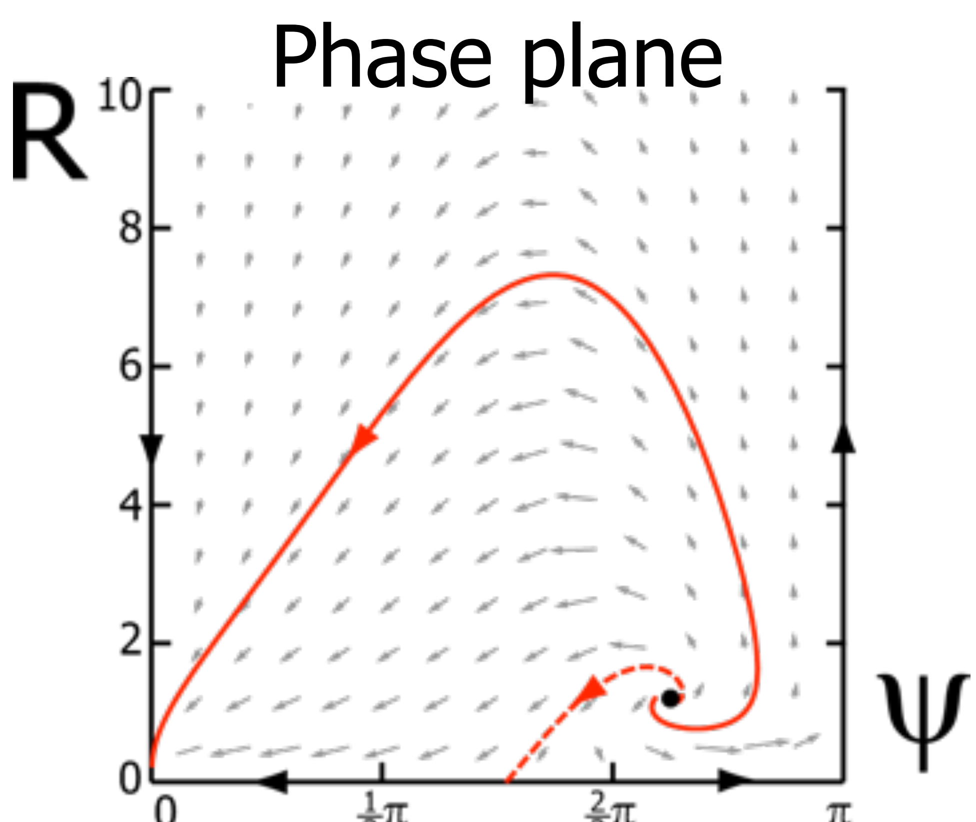
$$\dot{\psi} = -\sin\psi\left(\beta - \frac{1}{R}(\omega h - \gamma\cos\psi\right)$$

B.M. Friedrich, F. Jülicher, PNAS 104, 13256 (2007)

# Radial concentration in 3-d

$\mathbf{r}(t)$ swimming path $\longrightarrow$ concentration signal $c(t)$

flagellar beat $\kappa(t)\,\tau(t)$



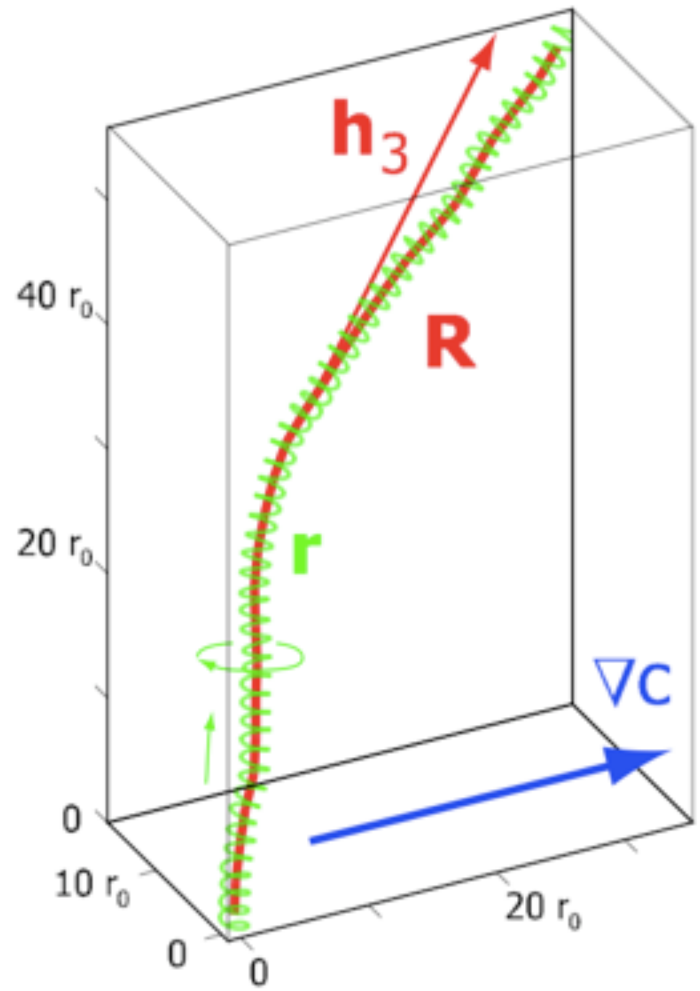

$\beta > 0 \quad \gamma > 0$

Nonlinear dynamics on superhelical swimming paths

$$\dot{R} = -\omega h \cos\psi - \gamma \sin^2\psi$$

$$\dot{\psi} = -\sin\psi\left(\beta - \frac{1}{R}(\omega h - \gamma\cos\psi\right)$$

# Shot noise

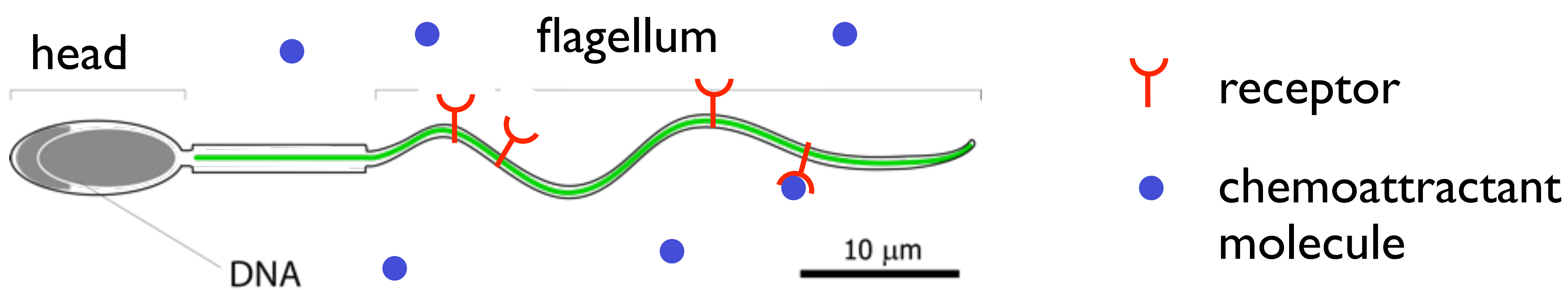



Single molecule detection

$$c(t) = \sum_n \delta(t - t_n)$$

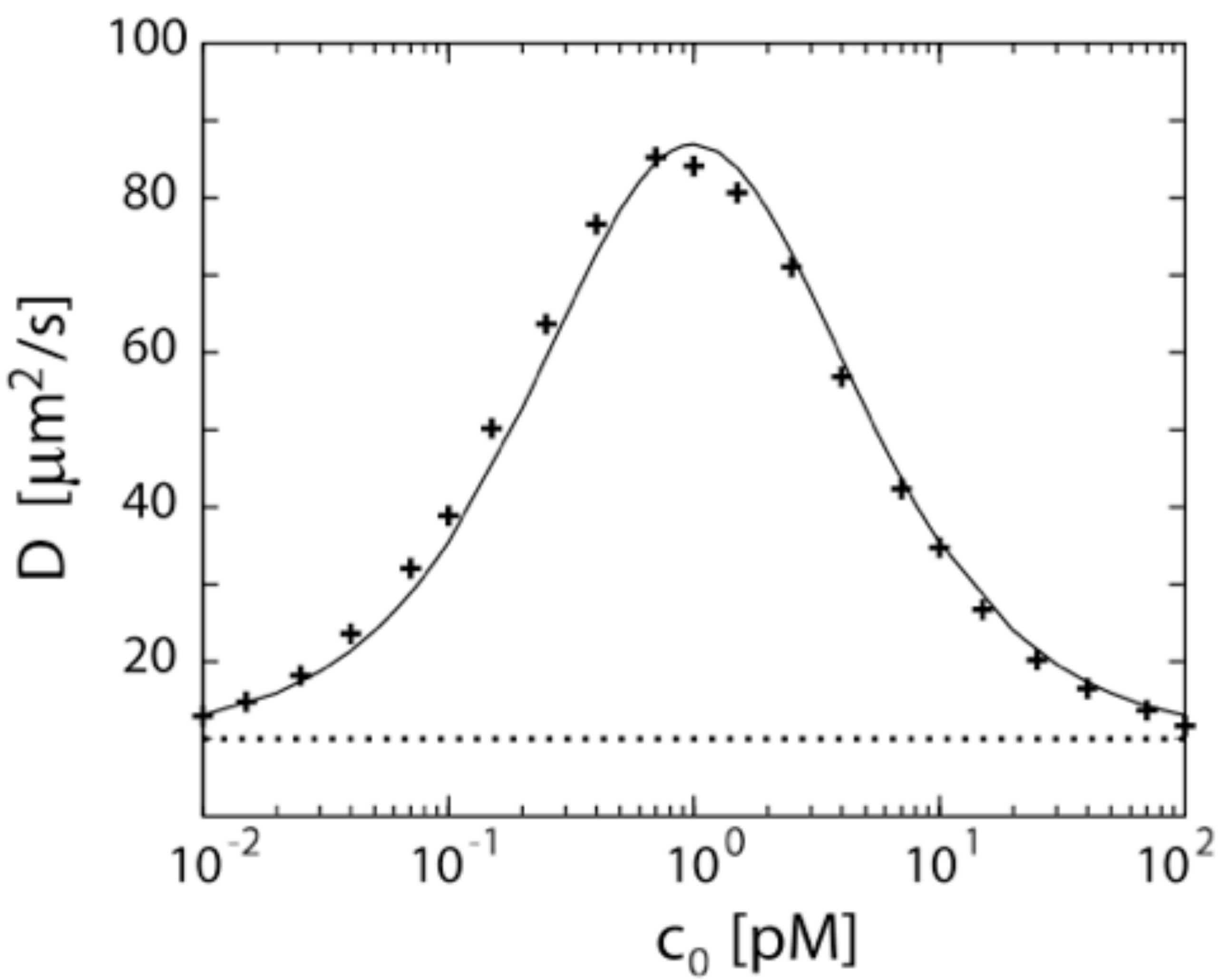
Stochastic differential geometry

Robust steering: drift + diffusion

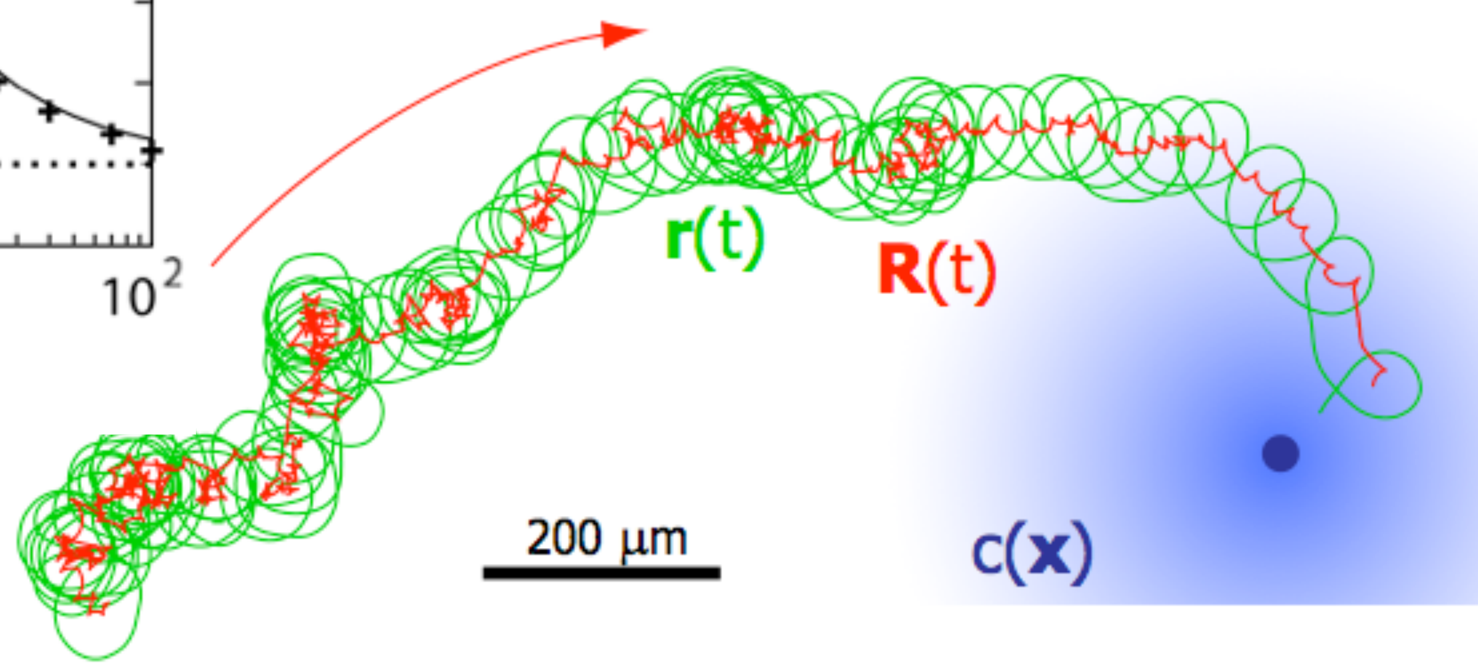


# Shot noise

Stochastic simulations of chemotaxis




$$D = r_0^2 v_0^2 \tilde{S}_\kappa(\omega_0)/4$$



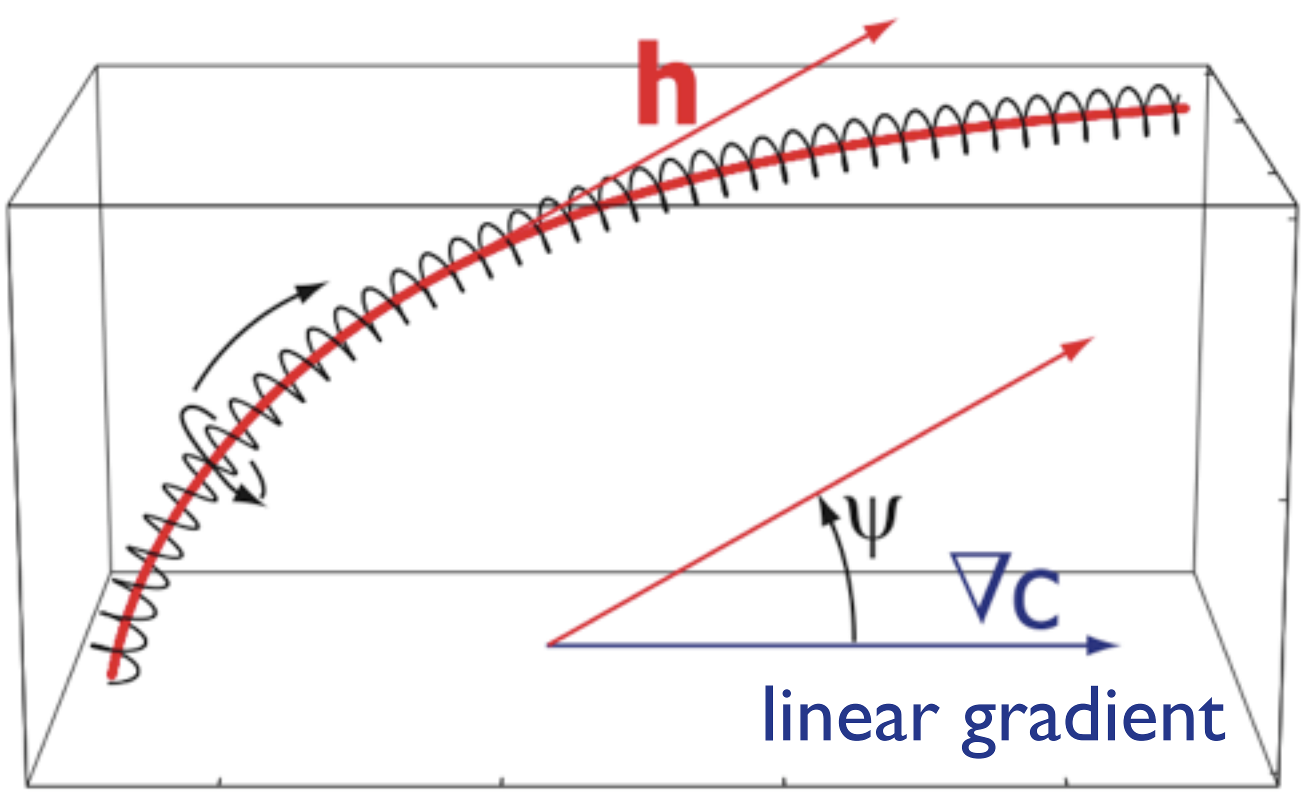

B. Friedrich F. Jülicher, NJP 10 (2008)

# Chemotaxis with noise

$\mathbf{r}(t)$ swimming path → concentration signal $c(t)$

concentration signal → flagellar beat $\kappa(t)\,\tau(t)$

flagellar beat → swimming path




Helix bending

$$\dot{\psi} = -\beta \sin\psi + D\cot\psi + \xi$$

noise-induced drift ($D\cot\psi$)

noise ($\xi$)

B.M. Friedrich, F. Jülicher, Phys. Rev. Lett. (2009)

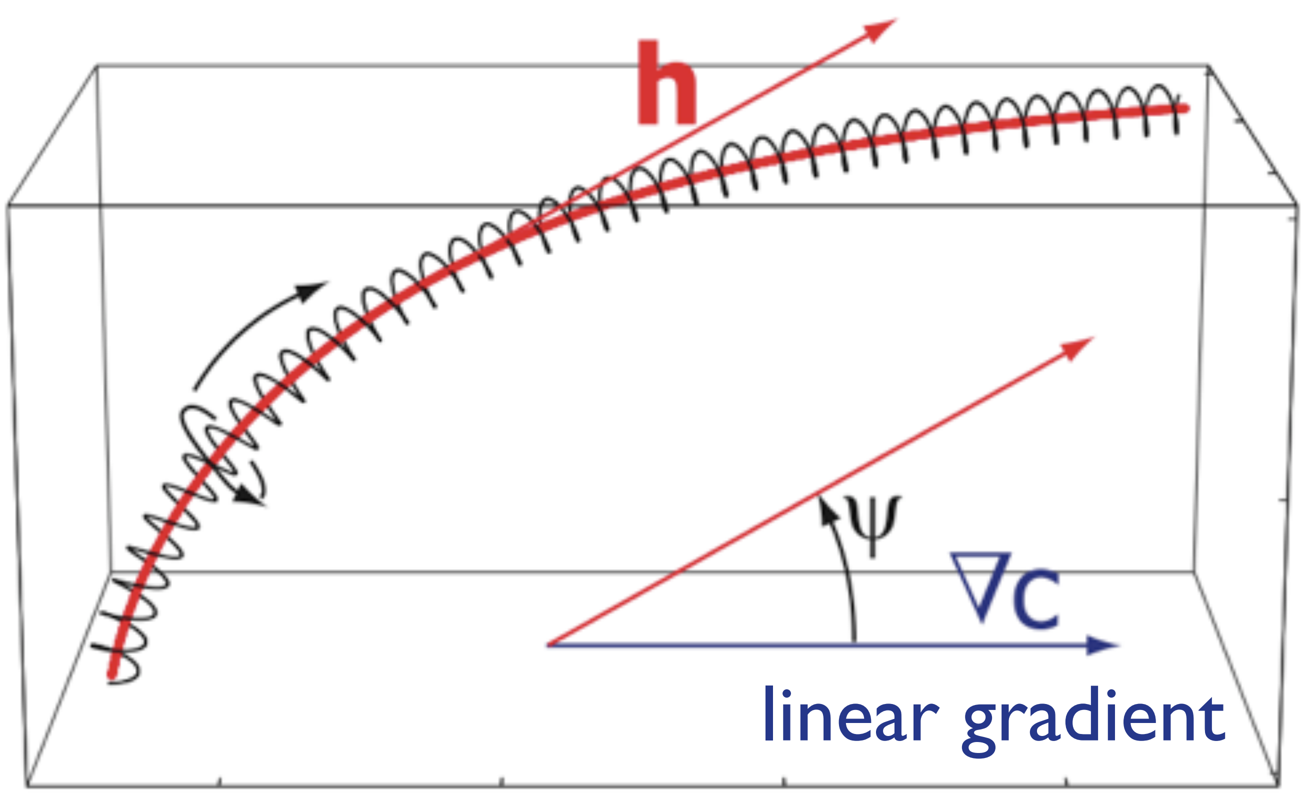
# Chemotaxis with noise

Noise strength

$$D = \omega_0^2 (h_0^2 \tilde{S}_\kappa(\omega_0) + r_0^2 \tilde{S}_\tau(\omega_0) - 2 r_0 h_0 \tilde{S}_{\kappa,\tau}(\omega_0))/2$$

Persistence time

$$t_P = (2D)^{-1}$$




Helix bending

$$\dot{\psi} = -\beta \sin\psi$$

$$+D \cot\psi + \xi$$

noise-induced drift

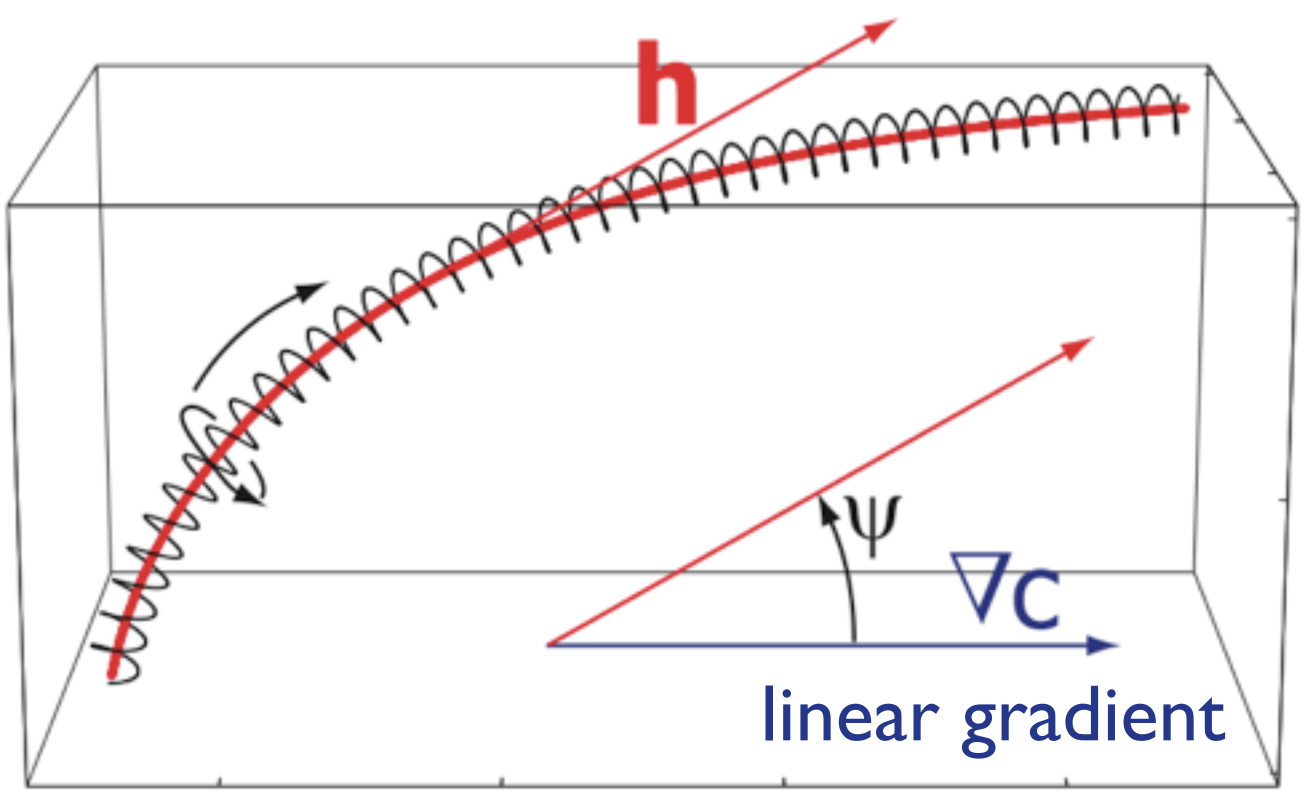
noise

B.M. Friedrich, F. Jülicher, Phys. Rev. Lett. (2009)

# Chemotaxis with noise

$$P_0(\cos\psi) \sim \exp(\cos\psi\beta/D)$$

$$\langle\cos\psi\rangle = \coth(\frac{\beta}{D}) + \frac{D}{\beta}$$




Helix bending

$$\dot{\psi} = -\beta\sin\psi$$
$$+D\cot\psi + \xi$$

noise-induced drift

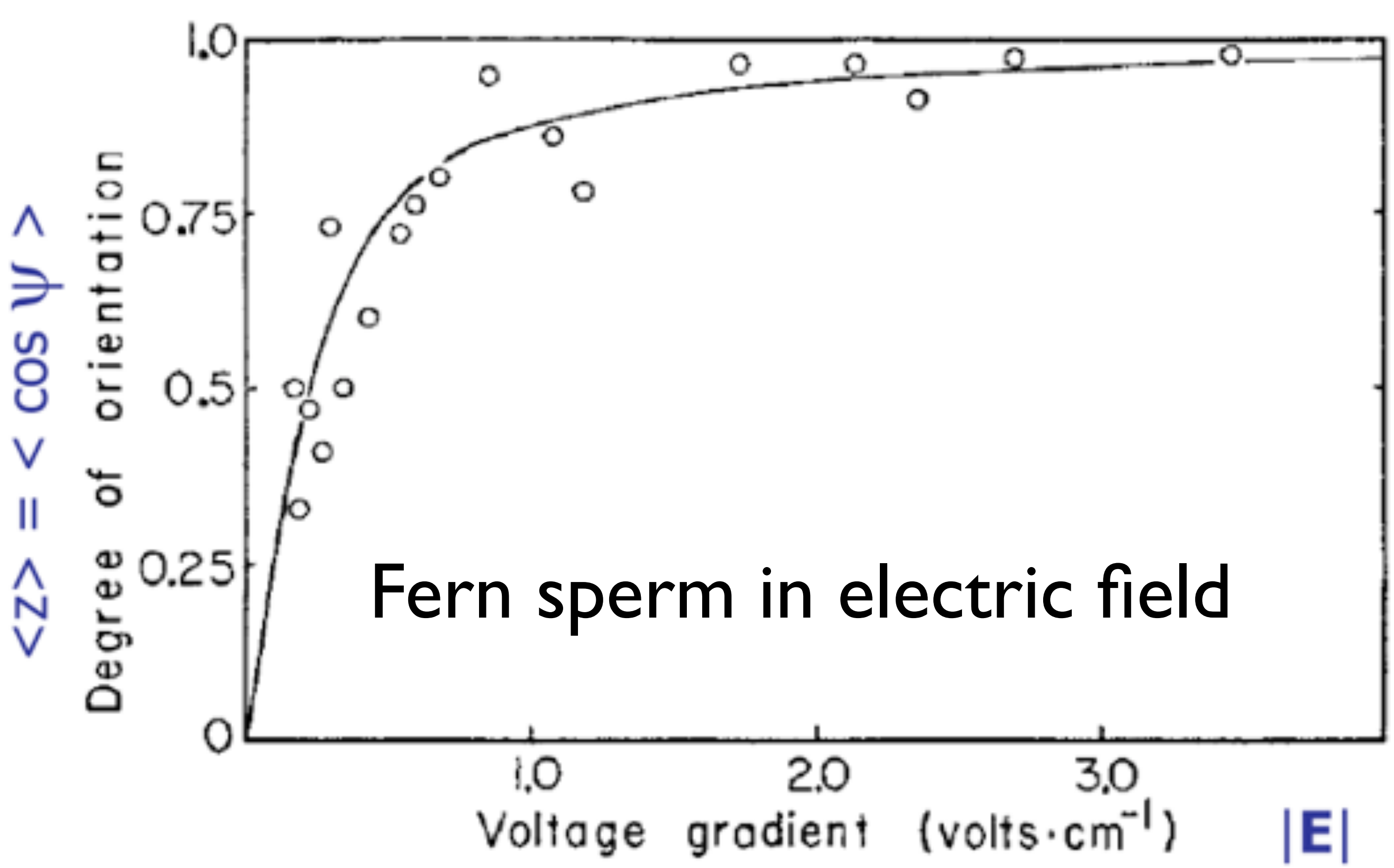
noise

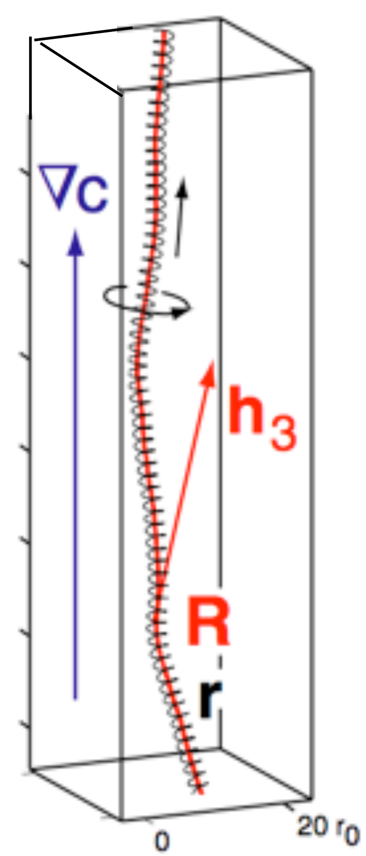
B.M. Friedrich, F. Jülicher, Phys. Rev. Lett. (2009)

# Chemotaxis with noise

$$P_0(\cos\psi) \sim \exp(\cos\psi\,\beta/D)$$

$$\langle \cos\psi \rangle = \coth(\frac{\beta}{D}) + \frac{D}{\beta}$$



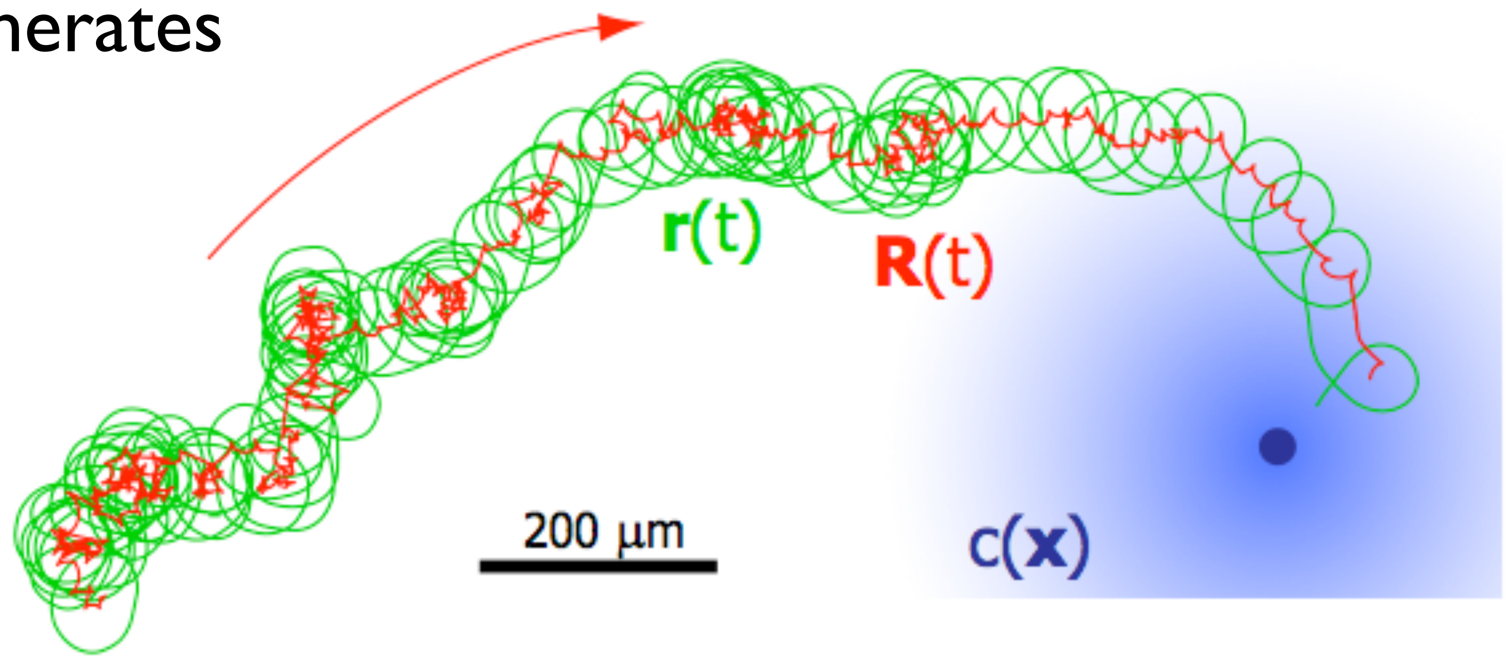

$$\beta/D \sim |E|$$

$$\beta/(D|E|) \simeq 8 \cdot 10^{-2} m/V$$

C. Brokaw, J. Exp. Biol. 35 (1958)

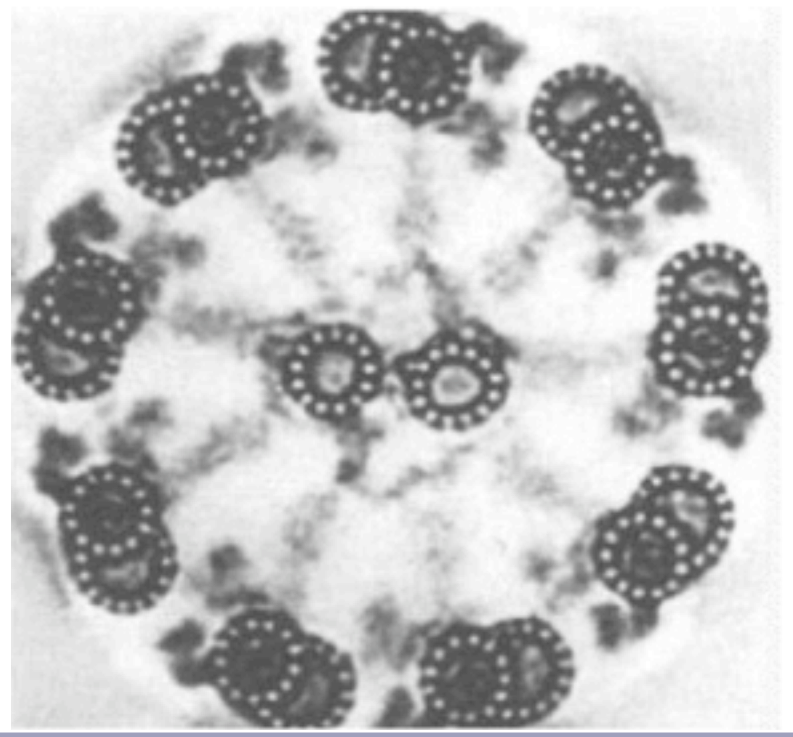
# Summary Outlook

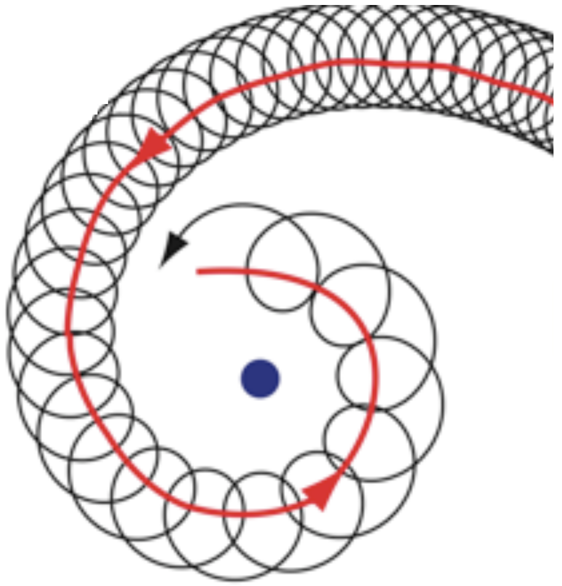
- Self-organization of motors generates chiral sperm beat
- Chiral swimming provides a mechanism for steering
- Robust under noisy conditions




- Chiral swimming:
  general principle for target search

  chemotaxis
  phototaxis
  ...





## Max Planck Institute for the Physics of Complex Systems

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