Cellular Motility



Howard Berg http://www.rowland.harvard.edu/labs/bacteria/movies/ecoli.php

<u>Course 4:</u> Mechanics 3 – Walking and Swimming

Thomas Lecuit chaire: Dynamiques du vivant



Summary 2D and 3D cell motility

Migration Mode	Adhesive	Non-adhesive
Protrusion type	Usually lamellipodia	Usually blebs
Propelling force generation	Filament extension/actin flow	Cortex flow
Force transmission	Focal adhesion	Friction, protrusion intercalations, etc.
Substrate interaction	Specific	Non-specific

Bodor et al. and E. Paluch. Developmental Cell. 52: 550-562 (2020)



Actin retrograde flow:

- v < 0.25µm/s
- $\label{eq:cell:v} Cell: v \approx 0.15 \mu m/s$



YJ. Liu et al, Cell 160, 659-672 (2015)

- v <12 μ m/min \approx 0.2 μ m/s
- $v < 10 \mu m/min$



Summary 2D and 3D cell motility

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Propelling force generation	Filament extension/actin flow	Cortex flow
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Substrate interaction	Specific	Non-specific
Duration of cell-substrate interactions	Longer than dwell time	Shorter than dwell time
Speed-substrate interaction strength relationship	Bell curve	Plateau
Environment	2D surfaces and 3D environments	3D confinement
Migration speed ^a	\sim 0.1–1 μ m/min	\sim 1–10 μ m/min
Stresses exerted on substrate ^b	$\sim 10^{2} - 10^{5} \text{ Pa}$	<1Pa
Actin flow profile	Mainly in lamellipodium	At the cortex all along the cell body, max velocity in cell center
Force dipole	Contractile	Expansile

- In 2D, the strength and duration of molecular bonds must be strong enough to counteract Brownian motion (eg. catch bond for intern coupling to actin, and mechanical feedbacks)
- In 3D, confinement prolongs the contacts of weak molecular interactions and multiply them over the entire cell surface
- In non-adhesive motion, friction does not interfere with cell retraction. Increasing friction does not lead to a plateau of migration speed, and no slowing down is expected even at high friction.



Summary 2D and 3D cell motility

- Opposite force dipole in adhesion and adhesion independent motility
- Adhesion dependent: Negative force dipole of traction forces reflects combined effect of retrograde actin flow and cell contraction Contraction is used to de-adhere

• Adhesion free:

Positive force dipole reflects expansion due to contraction at the back and frictional resistance





Bergert M, et al and G. Salbreux and E. Paluch. *Nat. Cell Biol.* 17:524–29 (2015)

Can cells walk? – What is the gait of walking cells?

Land animals can:

crawl/creep







Studying animal movement

zoopraxography: movement of walking/running animals



Eadweard Muybridge (1830-1904)



Thomas Séon

Les Lois d'échelle

La physique du petit et du grand





Physical principles of movement swimming, walking, flying etc Dimensional analysis



The walk of single cells: Euplotes

Euplotes are ciliates that can swim or walk on a substrate

Euplotes eurystomus



https://www.youtube.com/watch?v=i9DUz9hOsaE

14 cirri on the ventral side cilia form the membranellar band



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Ben T. Larson, J. Garbus, J. B. Pollack, Wallace F. Marshall bioRxiv 2021.02.26.433123; doi: https://doi.org/10.1101/2021.02.26.433123 (2021)

The walk of single cells. Fundates





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R. Phillips, J. Kondev, J. Thériot & H. Garcia. Physical Biology of the Cell (Garland Science) 2012

Euplotes within Ciliates



Ciliates (ciliophora): 8000 species

Gao et al and Song. Eur. J. Prostistology. 261(Pt B):409-423. doi: 10.1016/j.ejop.2017.04.009. (2017)

MJ. Syberg-Olsen et al PlosOne | DOI:10.1371/journal.pone.0165442









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Ben T. Larson, J. Garbus, J. B. Pollack, Wallace F. Marshall bioRxiv 2021.02.26.433123; doi: https://doi.org/10.1101/2021.02.26.433123 (2021)

а h

Cirrus

30

The gaits of Euplotes



The transition between gait states is necessary to account for movement



The gaits of Euplotes

Transition dynamics between gaits show stereotypy and stochasticity

- Restricted transitions between gaits are observed
- A few number of gait transitions are unbalanced (asymmetric) reflecting out of equilibrium state Some give rise to cycles: $2 \rightarrow 3 \rightarrow 17 \rightarrow 2$
- Majority of transitions are balanced •

- The majority of cell movement occurs during infrequent, equilibrium-like (balanced) transitions.
- Temporal irreversibility or directedness in the ۲ gait arises from biased, non-equilibrium-like (unbalanced) transitions, occurring at relatively high frequency from a small subset of states.

>> Stochastic gait cycle









Unbalanced Transitions @

Ben T. Larson, J. Garbus, J. B. Pollack, Wallace F. Marshall bioRxiv 2021.02.26.433123; doi: https://doi.org/10.1101/2021.02.26.433123 (2021)

Balance

Mechanics of E

Interconnected microtubule fibers mech

- A fiber system connects cirri
- It was initially thought to be a rudimentary nervous system
- It consists instead of microtubule bundles (thick and thin) that mechanically couple individual cirri into a network
- The pattern of connectivity does not predict a simple covariation of activity of cirri
- However, cirri that are closer to one another and with fiber-cortex contacts in nearby regions of the cell tend to have higher mutual information

- Microtubule deploymerization reduces the size of fibers, reduces motility
- And modifies the transition states between gaits





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Ben T. Larson, J. Garbus, J. B. Pollack, Wallace F. Marshall bioRxiv 2021.02.26.433123; doi: https://doi.org/10.1101/2021.02.26.433123 (2021)

Walking Euplotes as a microtubule based finite state machine

Working Model:

- Broken detailed balance in gait transitions gives rise to:
 - -A combination of stereotypy and variability in gait transitions
 - -Cyclic activity

• Proposed mechanism:

— biased, actively controlled cyclic transitions serve to establish strain in fiber-cirri network, effectively storing stress in certain cirri.

— the spontaneous release of these cirri from the substrate, during a series of unbiased gait state transitions, allows the cell to move forward.

The ensemble of unbiased transitions associated with cellular movement is consistent with motility not depending on the precise order in which the strained cirri are released from the substrate.

---return to the cycle states then are necessary to establish this process anew by winding up the system for continued, proper cell movement.





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Ben T. Larson, J. Garbus, J. B. Pollack, Wallace F. Marshall bioRxiv 2021.02.26.433123; doi: https://doi.org/10.1101/2021.02.26.433123 (2021)

Mechanical analogy

Theo Jansen — Strandbeest (« beach animals ») Plastic skeletons get their energy from the wind. based on evolution by selection of functional (moving) forms



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https://www.strandbeest.com/

Walking choanoflagelates

S. rosetta alternate between colonial and solitary state In solitary state, they can swim, remain static or walk





Walking bacteria

Bacteria Use Type IV Pili to Walk Upright and Detach from Surfaces

Maxsim L. Gibiansky,¹* Jacinta C. Conrad,²* Fan Jin,¹ Vernita D. Gordon,¹ Dominick A. Motto,⁴ Margie A. Mathewson,³ Wiktor G. Stopka,³ Daria C. Zelasko,³ Joshua D. Shrout,⁴ Gerard C. L. Wong^{1,3}†



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M. Gibiansky et al. Science 330:197 (2010)

J. Conrad et al, Biophysical Journal 100:1608–1616 (2011)

Swimming

Cell

Sperm from Sea Urchin



Brokaw C. Science 243:1593–1596 (1989)

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Animal

Squalus





cited in : Thomas Séon – Les lois d'échelle . ed. Odile Jacob. 2018



https://www.youtube.com/watch?v=yMpXCODiU-4

Swimming at low Reynolds number

 Non-reciproqual movement leads to net forward movement at low Reynolds number



For a Bacterium: 1 μ m and 10 μ m/s Re= 10⁻⁵

- **Beating** of *flexible* filament (e.g. cilia)
- The flexible car





Backward (recovery) stroke

• Rotation of *helical* structure (e.g. flagellum)







Bacteria swim, propelled by flagella

- 6 flagella bundle when they rotate counterclockwise (CCW)
- Bundles rotate and propel *E. coli* along runs
- Runs are followed by tumbles due to CW rotation of flagella which are no longer bundled



Howard Berg http://www.rowland.harvard.edu/labs/bacteria/movies/ecoli.php





Howard Berg and Douglas Brown. 1972, Nature 239, 500-504

Bacteria swim, propelled by flagella

Variations on the theme of flagella rotation in different bacteria



Howard Berg http://www.rowland.harvard.edu/labs/bacteria/movies/ecoli.php

Rhodobacter sphaeroides

- single flagellum rotates in single direction
- motor stops and flagellum relaxes and coils



E.coli

Sinorhizobium meliloti

- CW rotation of motor/flagellum in bundle
- slow rotation causes flagella to separate



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J. Armitage and R. Schmidt Microbiology. 143, 3671-3682 (1997)

Bacteria swim, propelled by flagella

- Rotation of flagellum at angular velocity ω with respect to cell body, which rotates CCW at velocity Ω. ω>Ω
- Why does rotation of a flagellum generate thrust?
 - I. Low Reynolds number: movement is dominated by viscosity of fluid
 - 2. The viscous drag coefficient f on a thin rod/ filament (or ellipsoid) is about *twice* for lateral movement compared to longitudinal movement



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- For each segment along flagellum: its movement at velocity v, is decomposed into normal and parallel velocities v_p and v_n . The drag forces acting on each segment F_n and F_p are such that $F_n/F_p \approx 2 v_p/v_n$.
- F_n and F_p can be decomposed into forces normal and parallel to helical axis F_{Ω} and F_{ν}
 - F_{Ω} and F'_{Ω} contribute to the Torque
 - F_{ν} and F'_{ν} contribute to the Thrust

Structural organisation of Flagellar motor

Propeller: helical structure powered by a rotary motor anchored to cell periphery

- Each flagellum is 25nm wide, up to 50µm long
- Rotates at 100 Hz in *E. coli*, 300 Hz in *Salmonella* and up to 1700Hz in *Vibrio*
- Without the filament per se, >175 subunits , 6.3MDa





https://www.youtube.com/watch?v=cwDRZGj2nnY



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R. Phillips, J. Kondev, J. Thériot & H. Garcia. Physical Biology of the Cell (Garland Science) 2012

Structural organisation of Flagellar motor

- >175 subunits , 6.3MDa
- 3 main parts:
 - basal body: reversible motor
 - hook: universal joint
 - flexible filament
- Different rings: C-ring, MS ring, L and P rings



J. Tan et al. Cell 184, 2665–2679 (2021)



Basal body:

• Rotational elements: Rotor can rotate clockwise or anticlockwise

 Static elements:
 Stator is anchored in inner membrane and peptidoglycan layer
 LP ring supports rotation of rod



Reference perioe

Successive incorporation of force-generating units

- a motB mutant E. coli cell does not swim and cannot rotate its flagella. It is rescued by lac promoter induced expression of *motB* transgene
- Cells are tethered to coverslip via a single flagellum
- Following induction (8-25 min), rotation of cells was rescued from <|Hz| to >8Hz
- At low speed, rotation rate doubled in discontinuous steps.
- Rotation evolved in 7 steps of constant size.
- Up to 16 steps could be inferred
- Suggests that incorporation of individual units contribute increment of applied torque in each flagellum
- Confirmed to be at least 11 torque generating • units using 1 µm fluorescent beads attached to tip of flagella

S. Reid et al. And J Armitage and R. Berry PNAS. 103: 8066–8071 (2006)





Successive incorporation of force-generating units

- At low Reynolds, linear proportionality between torque and angular velocity, with proportionality constant being viscous drag: M = bηΩ, where b depends on cell geometry (sphere: M = 8πηa³Ω)
- Estimate increments in torque associated with each force-generating unit: 2.7 dyn.cm = 270 pN.nm (correspond to 10 pN per force generating unit at periphery of rotor (27 nm)



S. Block & HC Berg *Nature* 309:470-472 (1984)

• Calculate number of protons passing through motor in one revolution (N):

 $2\pi M = \epsilon N e \Delta p$, motor proton motive force (162mV)

- There are n force generating units per motor: n up to 16 N = nm.
- For each force generating unit: $M \ge 270 \text{ pN.nm so}$ $m \approx 65 \text{ electrons per revolution}$
- So for each motor: N = 16x65 = 1040 electrons per motor revolution.
- HC Berg gave similar estimate in 1974 based on tight coupling and zero dissipation:

How is the lorque generated? Larsen et dL^{13} have found that an intermediate in oxidative phosphorylation (but not ATP) is required for motility in E, coli. This suggests a mechanism in which the movement of one molecule down an electrochemical gradient (through the membrane) causes another molecule to event a force on the S ring Since the power dissipation for an *E. coli* spinning 10 r.p.s. is of order 10^{-9} erg s⁻¹ and the energy which can be gained from the transit of one molecule through the membrane is of order 10^{-13} erg, 10^{8} such events could drive the cell through one cycle.



Stoechiometry of stator component MotB in motor

Evanescent field

- Rescued of *motB* mutant with *GFP-MotB* transgene
- Track fluorescence intensity at single, functional flagellum (cell rotation), using TIRF



- Fluorophore counting indicates 22 (+/-6) GFP-MotB molecules per motor
- This is consistent with 11 stators/motor and 2 MotB per stator.
- FLIP and FRAP experiments indicate dynamic exchange with membrane pool of 200 GFP-MotB diffusing at $\sim 0.008 \,\mu m^2 \, s^{-1}$.





M. Leake et al R. Berrry and J. Armitage. Nature 443:355-358 (2006)

Rotation is driven by energy harnessed from H+ or Na+ gradient



https://m.youtube.com/watch?v=B7PMf7bBczQ





Tuning the stator stoechiometry

- Each stator unit is an ion (H+ or Na+) translocating unit anchored to the peptidoglycan layer and inner membrane
- It causes rotation of MS ring in rotor
- The number of stator units is tunable







A. Baker and G. O'Toole. J. Bacteriol. doi:10.1128/JB.00088-17 (2017)

- Increased viscosity of the environment is associated with a switch to swarm behavior
 - Long-term genetic adaptation

swarming: multicellular movement across surface powered by rotating flagella

-Induction of flagellar genes and increase in number of flagella per cell

Flagella cover the entire cell (peritrichous flagella)

Peritrichous flagella bundle together when they rotate to increase the effective flagellar stiffness and make force generation more efficient in viscous liquids



Kearns DB (2010) A field guide to bacterial swarming motility. Nat Rev Microbiol 8(9): 634-644. (2010)

----synthesis of new flagella (lateral flagella) in Vibrio parahaemolyticus: flagellar dynamometer



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L. McCarter et al. Cell 54: 345-351 (1988)



HC Berg Nature 278:349-351 (1979)

—As flagellum grows (up to $50\mu m$ in *E. coli*), the viscous drag increases, so rotation needs to adapt so rotation persists.

Moreover, adaptation ensures that the energy engaged in rotation is adjusted to the needs (see later)

Q: How do cells perceive increased viscous load as they swim?



The stator is a dynamic mechanosensor

- Viscous drag on flagellum is increased by attachment of 1µm bead to filament stub (using optical tweezer)
- This causes a sudden drop in rotation speed
- And is followed by a stepwise increase in CCW and CW rotation speed
- Torque adapts to viscous load:
 a: near zero load for a single stator element at 300Hz: torque is ~10 pN.nm

b: at higher load, the same stator slows down instantly (6-8Hz) and driving torque increases to 100-200 pN.nm.
 b-c: as stator units are recruited, torque increases

- Much higher viscous load when cell attached to substrate
- Rotation speed increases along with YFP-MotB recruitment to motor

Indicates that the number of stators driving the motor at a very low load is less than at a high load





Mechanism of motor mechanosensitivity: catch-bond

• The lifetime of stator unit in motor increases when higher force is applied





release N 350 load line Torque 250 200 Torque 150 of stators stall steady-state Ż -100 6 100 200 300 400 Speed Time (s)

• Magnetic tweezer to stall and release motor

A. Nord et al, R. Berry and F. Pedaci. PNAS. 114:12957 12957 (2017)



• Electrorotation to vary applied torque

N. Wadhwa, R. Phillips and HC. Berg. PNAS. 116:11764-11769 (2019)

- The applied torque due to electrorotation lowers the load on motor and torque/stator (1→3)
- When applied torque is released, motor rotation speed is lower (4)



• This reduction in rotation is enhanced as applied torque increases, up to zero torque (300Hz)



repeated cycles (8s ON, 1s OFF, recording)









 $+(N-n+1)k_{+}p(n-1,t) \text{ master equation}$ $-nk_{-}p(n,t) - (N-n)k_{+}p(n,t), \qquad [1]$ $\frac{\mathrm{d}\langle n \rangle}{\mathrm{d}t} = k_{+}(N-\langle n \rangle) - k_{-}\langle n \rangle, \qquad \qquad r = \frac{\langle n \rangle_{\mathrm{ss}}}{N} = \frac{1}{1+\frac{k_{-}}{k_{+}}}, \underline{K_{D}}$ average occupancy at steady state
solution: $\langle n \rangle(t) = \langle n \rangle_{\mathrm{ss}} + (n_{0} - \langle n \rangle_{\mathrm{ss}})e^{-(k_{+}+k_{-})t} \qquad \text{relaxation time: } \tau = \frac{1}{k_{-}+k_{+}}$

• **Data:** steady state number of stator units increases with load, so K_D decreases with load.

Only consistent with load-dependent off rate (catch-bond model)





A. Nord et al, R. Berry and F. Pedaci. *PNAS*. 114:12952-12957 (2017) N. Wadhwa, R. Phillips and HC. Berg. *PNAS*. 116:11764-11769 (2019)

• Model for speed dependent on rate k_+ to assemble a complex between stator unit and rotor (made of 26 FligG).

— contact between stator and rotor: diffusion limited $k_{\rm o}$ probability of assembly once contact occurred: $p_{\rm s}$

 $p_{
m s}$ depends on contact time $\, t_{
m c} \,$ and assembly rate $\, \kappa \,$

probability that stator unit contacting rotor at time 0 successfully assembles at time t_c is: $p_s = 1 - e^{-\kappa t_c}$

Therefore: $k_{+} = k_0 (1 - e^{-\kappa t_c})$

Since the time of contact is inversely proportional to the rotation speed F

$$k_+ = k_0 \left(1 - e^{-\frac{\kappa}{F}}\right)$$

free energy of bound stator at zero torque

chemical potential for taking stator out of membrane pool

• Torque dependent stator assembly

Equilibrium model: binding of stator to rotor changes its free energy by: $\epsilon_{\rm b}-\mu$

Hypothesis: applied torque lowers the free energy change by: ϵ_{T}



N. Wadhwa, R. Phillips and HC. Berg. PNAS. 116:11764-11769 (2019)

Structural insight: direct contact between MotB and C ring FligM







The LP ring applies electrostatic forces to support rotation of the rod



Run and Tumble require rotational switch



Mechanism of rotational switch









Mechanism of rotational switch





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Y. Chang et al and J. Liu. Nature Structural & Molecular Biology. 27:1041–1047 (2020)

Motor coordination at both poles : mechanical?

- A run in spirochetes requires opposite direction of rotation of flagella at both poles
- Cells are too long for chemical coordination at poles (5-10 s for >10µm length)





Eukaryotic cilia and flagella bending and beating



https://www.youtube.com/watch?v=4vsYNPwSZks

- Cilia swimming protists
 - Pharyngomonas kirbyi Protist, 162, 691–709 (2011)

Flagella — Sperm cell (sea Urchin)



Brokaw C. 1989. *Science* 243:1593–1596. doi: 10.1126/science.2928796 **20µm**



10µm



Eukaryotic cilia and flagella bending and beating



Chlamydomonas reinhardtii Green algae

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DE



Eukaryotic cilia and flagella bending

Bending models

STUDIES ON CILIA

II. Examination of the Distal Region of the Ciliary Shaft and the Role of the Filaments in Motility

PETER SATIR

From the Whitman Laboratory, University of Chicago, Chicago, Elipsia

THE JOURNAL OF CELL BIOLOGY - VOLUME 26, 1965



100 nm Axoneme



Sliding model



Contraction model • Filaments shorten on one side to bend cilium



Eukaryotic cilia and flagella bending

dynein arm radial spoke inner sheath central singlet nicrotubule plasma membrane inner dvnein arm (A) 100 nm A microtubule B microtubule outer doublet microtubule linking proteins +ATP bend isolated doublet normal flagellum microtubules due to crosslinks and (A) DYNEIN PRODUCES (B) **DYNEIN CAUSES** constraints at the base of MICROTUBULE SLIDING MICROTUBULE TO BEND axoneme

- Motor driven sliding forces bend cilia

- Cilia bend in response to collective effect of Dynein motor activity
- Dynein induce sliding forces at doublets interfaces

Dynein motors convert the chemical energy of $\sim 10^5$ ATP per beat into a relative sliding motion among the nine microtubule doublets of the axonemal sheath. This causes a tension of ~ 10 nN to build up between neighbouring doublets.



R. Phillips, J. Kondev, J. Thériot & H. Garcia. *Physical Biology of the Cell (Garland Science)* 2012

Eukaryotic cilia and flagella beating

– Beating models: Mechanical Feedbacks

- Bending and beating require spatial and temporal coordination of motor activity on both sides of axoneme
- Bending induces stresses that feedback on and regulate motor activity
- Dynein motor activity needs to alternate between the 2 sides of axoneme. If forces are equal, then they cancel each other and no bending occurs
- Motor switching is rapid (2x per cycle
 @ 100Hz in Chlamydomonas) :
- Mechanical feedback model





Eukaryotic cilia and flagella beating

– Beating models: Mechanical Feedbacks

- Bending and beating require spatial and temporal coordination of motor activity on both sides of axoneme
- Bending induces stresses that feedback on and regulate motor activity
- Model I: Sliding-forces and slip bond behavior of Dynein, when forces opposed to sliding. Build up of tension on one side induces detachment on other side
- Model 2: Curvature of doublets (opposite signe of curvature on both sides of the axoneme)
- Model 3: Normal forces



P. Sartori et al. F. Jülicher and J. Howard. eLife 2016;5:e13258. DOI: 10.7554/eLife.13258



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Gilpin, W., Prakash, V. & Prakash, M. Vortex arrays and ciliary tangles underlie the feeding-swimming trade-off in starfish larvae. Nature Phys 13, 380-386 (2017).



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Gilpin, W., Bull, M.S. & Prakash, M. The multiscale physics of cilia and flagella. *Nat Rev Phys* **2**, 74–88 (2020). https://doi.org/10.1038/s42254-019-0129-0

Cyanobacteria swim without flagella

On the Mysterious Propulsion of Synechococcus

Kurt Ehlers^{1,2}, George Oster³*

1 Mathematics Department, Truckee Meadows Community College, Reno, Nevada, United States of America, 2 Department of Atmospheric Sciences, Desert Research Institute, Nevada System of Higher Education, Reno, Nevada, United States of America, 3 Department of Molecular & Cell Biology, and ESPM, University of California, Berkeley, California, United States of America

Ehlers K, Oster G. PLoS ONE 7(5): e36081. doi:10.1371/journal.pone.0036081 (2012)

Synechococcus swims at 25µm/s



Waterbury, J.B. et al. A cyanobacterium capable of swimming motility. *Science* 230, 74-76 (1985).



http://www.rowland.harvard.edu/labs/bacteria/movies/synecho.php



Model: Surface traveling wave (oscillations)

Small amplitude, high frequency waves: Swimming speeds of order 25 μ m/s are expected for a spherical cell propagating longitudinal waves of 0.2 μ m length, 0.02 μ m amplitude, and 160 μ m/s speed



- water molecules are moved away (up) and closer (down) to the cell surface as the contraction waves pass
- the molecules are pushed farther to the right than to the left because the velocity decays away from surface
- the cell moves in same direction as the wave

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Ehlers, K.M., Samuel, A.D.T., Berg, H.C. and Montgomery, R. Do cyanobacteria swim using traveling surface waves? *Proc. Natl. Acad. Sci. USA* 93, 8340-8343 (1996).

Model: Surface traveling wave (oscillations)

Synechococcus

Spicules cover the entire surface





Model: an unidentified motor embedded in the cell membrane utilizes the spicules as oars to generate a traveling wave external to the surface layer

Cristalline arrangement of spicules



freeze-fracture EM



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S: surface layer

Samuel, A.D.T., Petersen, J.D. and Reese, T.S. BMC Microbiology 2001 1:4

Model: Surface traveling wave (helicoidal track)

- Cargo causes local deformation of surface layer and forms surface ridges.
- Synechococcus utilizes a continuous loop helical rotor

-<u>Rotating helix model:</u> motors anchored to the peptidoglycan layer drive rotation of the rotor creating helical waves along the cell surface

—<u>Traveling cargo model</u>: motor cargos move along the helical track creating deformations along the cell surface

- Motor drives helicoidal wave of surface indentation
- Surface travelling wave drives cell movement











Model: Surface traveling wave (helicoidal track)

- The surface layer presents tilted spicules
- The surface layer amplifies the distorsions induced by the cargo
- The intrinsic asymmetry of the S layer causes an asymmetry in the surface deformation
- and asymmetric fluid flow

—when cargo moves against tilt, this causes large transverse deformations and fluid flow in the direction of the wave

—when cargo moves in direction of tilt, this causes local expansion of the membrane and fluid flow in opposite direction of wave

—therefore, CW and CCW rotation of cargo causes fluid flow in the same direction, and the cell moves in the opposite direction of flow

• This in turn causes the unidirectionality of cell movement



