## Cellular Motility



Howard Berg http://www.rowland.harvard.edu/labs/bacteria/movies/ecoli.php
Course 4: Mechanics 3 - Walking and Swimming
Thomas Lecuit
chaire: Dynamiques du vivant


COLLE GE DE FRANCE
$1530-$

## Summary <br> 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 |  |
|  |  | Bodor et al. and E. Paluch. Developmental Cell. 52: 550-562 (2020) |



Actin retrograde flow:
$v<0.25 \mu \mathrm{~m} / \mathrm{s}$
Cell: $\quad v \approx 0.15 \mu \mathrm{~m} / \mathrm{s}$


YJ. Liu et al, Cell 160, 659-672 (2015)
$v<12 \mu \mathrm{~m} / \mathrm{min} \approx 0.2 \mu \mathrm{~m} / \mathrm{s}$
$v<10 \mu \mathrm{~m} / \mathrm{min}$

## Summary

2D and 3D cell motility

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| Force transmission | Focal adhesion | Friction, protrusion intercalations, etc. |
| 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 | $2 D$ surfaces and 3D environments | $3 D$ confinement |
| Migration speed ${ }^{\text {a }}$ | $\sim 0.1-1 \mu \mathrm{~m} / \mathrm{min}$ | $\sim 1-10 \mu \mathrm{~m} / \mathrm{min}$ |
| Stresses exerted on substrate ${ }^{\text {b }}$ | $\sim 10^{2}-10^{5} \mathrm{~Pa}$ | $<1 \mathrm{~Pa}$ |
| Actin flow profile | Mainly in lamellipodium | At the cortex all along the cell body, <br> 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 <br> 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

Adhesive:


Frictional:


## Can cells walk? - What is the gait of walking cells?

Land animals can:


## Studying animal movement

zoopraxography: movement of walking/running animals


Eadweard Muybridge (I830-I904)


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

## The walk of single cells: Euplotes

## Cirri consists of bundles of cilia



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

A. Fleury Eur. J. Protistol. 27, 99-114 (1991)


## Euplotes within Ciliates

Ciliates (ciliophora): 8000 species


- Recently defined or established, not present in Lymn 2008 or Adf et al. 2012

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 I DOI:10.1371/journal.pone. 0165442


## The gaits of euplotes

## Quantitative analysis

## - Walking state:

Encoded as a l4-bit binary vector
0 : cirri in contact and stationary
I : not in contact and moving
No stereotypical pattern
Stochastic processes
What is the underlying structure?


## The gaits of Euplotes

Velocity does not correlate with the number of active cirri
But correlates with small-moderate change in number of active cirri


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 gait arises from biased, non-equilibrium-like (unbalanced) transitions, occurring at relatively high frequency from a small subset of states.
>> Stochastic gait cycle



## Mechanics of Euplotes' gaits

## Interconnected microtubule fibers mechanically couple cirri in gait coordination

- 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


## 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.



## Mechanical analogy

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

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, ${ }^{1}$<br>Dominick A. Motto, Margie A. Mathewson, ${ }^{3}$ Wiktor G. Stopka, ${ }^{3}$ Daria C. Zelasko, ${ }^{3}$ Joshua D. Shrout, ${ }^{4}$ Gerard C. L. Wong ${ }^{1,3}$

Pseudomonas aeruginosa

- walking: vertical
diffusive

- crawling: horizontal

superdiffusive or subdiffusive


persistence length

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)

## Animal

Squalus

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

Etienne -Jules Marey (1830-1904) Prof. at Collège de France (1869-1904) Histoire naturelle des corps organisés

## Swimming at low Reynolds number

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

$$
\operatorname{Re}=\frac{U L \rho}{\eta}^{\text {viscosity }}
$$



For a Bacterium: $I \mu \mathrm{~m}$ and $10 \mu \mathrm{~m} / \mathrm{s} \quad \operatorname{Re}=10^{-5}$

- Beating of flexible filament (e.g. cilia)

The flexible oar



- 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



## 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
E.coli



Sinorhizobium meliloti

- single flagellum rotates in single direction
- motor stops and flagellum relaxes and coils
- CW rotation of motor/flagellum in bundle
- slow rotation causes flagella to separate


## Bacteria swim, propelled by flagella

- Rotation of flagellum at angular velocity $\omega$ with respect to cell body, which rotates CCW at velocity $\Omega$. $\omega>\Omega$
- 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


- 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 $F \Omega$ and $F_{v}$
- $F \Omega$ and $F^{\prime} \Omega$ contribute to the Torque
- $\boldsymbol{F}_{v}$ and $\boldsymbol{F}^{\prime}{ }_{v}$ contribute to the Thrust


## Structural organisation of Flagellar motor

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

- Each flagellum is 25 nm wide, up to $50 \mu \mathrm{~m}$ long
- Rotates at 100 Hz in E. coli, 300 Hz in Salmonella and up to 1700 Hz in Vibrio
- Without the filament per se, $>175$ subunits, 6.3 MDa

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


## Structural organisation of Flagellar motor

- >175 subunits, 6.3 MDa
- 3 main parts:
— basal body: reversible motor
— hook: universal joint
- flexible filament
- Different rings: C -ring, $M S$ 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


## Rotation of Flagellar motor

## 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 mot $B$ transgene
- Cells are tethered to coverslip via a single flagellum
- Following induction (8-25 min), rotation of cells was rescued from $<\mathrm{IHz}$ to $>8 \mathrm{~Hz}$
- 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 II torque generating units using I $\mu \mathrm{m}$ fluorescent beads attached to tip of flagella
S. Reid et al. And J Armitage and R. Berry PNAS. 103: 8066-8071 (2006)


4 cells.Variation reflects difference in rotational drag

## Rotation of Flagellar motor

## Successive incorporation of force-generating units

- At low Reynolds, linear proportionality between torque and angular velocity, with proportionality constant being viscous drag: $M=b \eta \Omega$, where $b$ depends on cell geometry (sphere: $M=8 \pi \pi a^{3} \Omega$ )
- Estimate increments in torque associated with each force-generating unit: 2.7 dyn. $\mathrm{cm}=270 \mathrm{pN} . \mathrm{nm}$

(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 $(\mathbf{N})$ :
$2 \pi M=\varepsilon N e A p$.

| motor |
| :--- |
| efficiency (1) |

proton motive force $(162 \mathrm{mV})$

- There are n force generating units per motor: $n$ up to $16 \quad N=n m$.
- For each force generating unit: $M>=270 \mathrm{pN} . \mathrm{nm}$ so $m \approx 65$ electrons per revolution
- So for each motor: $N=16 \times 65=1040$ electrons per motor revolution.
- HC Berg gave similar estimate in 1974 based on tight coupling and zero dissipation:
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 machanisn in wheh the moverunat of one monentr? domm an elenmmentis] Eradiont (through the membrane) anses


[^0]
## Rotation of Flagellar motor

## Stoechiometry of stator component MotB in motor

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

- Photobleaching curves indicate stepwise decay of fluorescence with unique step of around 5400 counts consistent with single GFP molecule.
- Fluorophore counting indicates 22 (+/-6) GFP-MotB molecules per motor
- This is consistent with II stators/motor and 2 MotB per stator.

- FLIP and FRAP experiments indicate dynamic exchange with membrane pool of 200 GFP-MotB diffusing at $\sim 0.008 \mu^{2} \mathrm{~s}^{-1}$.


## Rotation of Flagellar motor

Rotation is driven by energy harnessed from $\mathrm{H}^{+}$or $\mathrm{Na}+$ gradient

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


## Mechanical adaptation of the flagellar motor

## Tuning the stator stoechiometry

- Each stator unit is an ion $\left(\mathrm{H}^{+}\right.$or $\mathrm{Na}+$ ) 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



## Mechanical adaptation of the flagellar motor

- 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



[^1]
## Mechanical adaptation of the flagellar motor

- Increased viscosity of the environment changes rotation speed -Short-term mechanical adaptation
-Rotation of flagellum decreases in more viscous environment


HC Berg Nature 278:349-351 (1979)
—As flagellum grows (up to $50 \mu \mathrm{~m}$ 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?

## Mechanical adaptation of the flagellar motor

## The stator is a dynamic mechanosensor

- Viscous drag on flagellum is increased by attachment of $I \mu \mathrm{~m}$ 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 300 Hz : torque is $\sim 10 \mathrm{pN} . \mathrm{nm}$


- $b$ : at higher load, the same stator slows down instantly $(6-8 \mathrm{~Hz})$ and driving torque increases to $100-200 \mathrm{pN} . \mathrm{nm}$. $-b-c$ : 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



## Mechanical adaptation of the flagellar motor

Mechanism of motor mechanosensitivity: catch-bond model

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


- Magnetic tweezer to stall and release motor
A. Nord et al, R. Berry and F. Pedaci. PNAS. 114:12952-12957 (2017)

Rotating electric field



- Electrorotation to vary applied torque
N. Wadhwa, R. Phillips and HC. Berg. PNAS. 116:11764-11769 (2019)


## Mechanical adaptation of the flagellar motor

- The applied torque due to electrorotation lowers the load on motor and torque/stator ( $\mathrm{I} \rightarrow 3$ )
- 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 $(300 \mathrm{~Hz}$ )

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



## Mechanical adaptation of the flagellar motor

- Model: kinetics of the torque-dependent stator assembly:
$-n$ stator bound to motor at time $t$ $k_{+}$and $k_{-}$are on and off rates

$$
\begin{align*}
\frac{\mathrm{d} p(n, t)}{\mathrm{d} t}= & (n+1) k_{-} p(n+1, t)+(N-n+1) k_{+} p(n-1, t) \quad \text { master equation }  \tag{1}\\
& -n k_{-} p(n, t)-(N-n) k_{+} p(n, t),
\end{align*}
$$

$$
\begin{equation*}
\frac{\mathrm{d}\langle n\rangle}{d t}=k_{+}(N-\langle n\rangle)-k_{-}\langle n\rangle \tag{D}
\end{equation*}
$$

$$
r=\frac{\langle n\rangle_{\mathrm{ss}}}{N}=\frac{1}{1+\frac{k_{-}}{k_{+}}}
$$

average occupancy at steady state

$$
\text { solution: } \quad\langle n\rangle(t)=\langle n\rangle_{\mathrm{ss}}+\left(n_{0}-\langle n\rangle_{\mathrm{ss}}\right) e^{-\left(k_{+}+k_{-}\right) t}
$$

$$
\text { relaxation time: } \quad \tau=\frac{1}{k_{-}+k_{+}}
$$

- 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)



Load ( $\mathrm{pN} \mathrm{nm} \mathrm{s)}$


## Mechanical adaptation of the flagellar motor

- 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 $k_{0}$ probability of assembly once contact occurred: $p_{\text {s }}$
$p_{\mathrm{s}}$ depends on contact time $t_{\mathrm{c}}$ and assembly rate $\kappa$
probability that stator unit contacting rotor at time 0 successfully assembles at time $t_{\mathrm{c}}$ is: $p_{\mathrm{s}}=1-e^{-\kappa t_{\mathrm{c}}}$
Therefore: $\quad k_{+}=k_{0}\left(1-e^{-\kappa t_{\mathrm{c}}}\right)$
Since the time of contact is inversely proportional to the rotation speed $F$

$$
k_{+}=k_{0}\left(1-e^{-\frac{\kappa}{F}}\right)
$$



- Torque dependent stator assembly

Equilibrium model: binding of stator to rotor changes its free energy by: Hypothesis: applied torque lowers the free energy change by: $\epsilon_{T}$

$$
\text { Therefore: } \quad r=\frac{\langle n\rangle_{\mathrm{ss}}}{N}=\frac{1}{1+e^{\beta\left(\epsilon_{\mathrm{b}}-\mu-\epsilon_{\mathrm{T}}\right)}}, \quad \text { Or } \quad \epsilon_{\mathrm{T}}=-\frac{1}{\beta} \log \left(\frac{\frac{1}{r}-1}{\frac{1}{r_{0}}-1}\right)
$$

$$
\begin{aligned}
& \text { average occupancy } \beta=\frac{1}{k_{\mathrm{B}} T} \\
& \text { at steady state }
\end{aligned}
$$

$$
k_{-}=k_{0} e^{\beta\left(\epsilon_{\mathrm{b}}-\mu-\epsilon_{\mathrm{T}}\right)}\left(1-e^{-\frac{\kappa}{F}}\right)
$$

so $\epsilon_{\mathrm{T}}$ is calculated for different torques:


## How the stator exerts torque on rotor

Structural insight: direct contact between MotB and C ring FligM


## Torque transmission in motor



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



## 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 ( $5-10 \mathrm{~s}$ for $>10 \mu \mathrm{~m}$ 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)


## Eukaryotic cilia and flagella bending and beating

## - Ultrastructure


cilium


H Ishikawa and WF Marshall Nature Reviews Mol Cell Biol 12: 222-234 (2011)

## Eukaryotic cilia and flagella bending

## - Bending models

## SJUDIDS ON EIGA

II. Exatuination of 1.10 Disklal Region of the Ciliary Shatt :sud the Role of the lilaments in Alotility

PFTFE ShTIR

Tie Jolrnale or Cell Bholocy - Volume 26, 1965


- Sliding model

- Contraction model Filaments shorten on one side to bend cilium


## Eukaryotic cilia and flagella bending

## - 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 $\sim 10 \mathrm{nN}$ to build up between neighbouring doublets.


## 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 ( $2 x$ 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


## Ciliary synchronization



## multicellular problem (next year)

ciliary bands produce vortices associated with motion and feeding


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).

## Cyanobacteria swim without flagella

## On the Mysterious Propulsion of Synechococcus <br> Kurt Ehlers ${ }^{\mathbf{1 , 2}}$, George Oster ${ }^{\mathbf{3} *}$ <br> Nathematics Department, Truckee Meadows Community College, Reno, Nevada, United States of America, 2 Department of Atmospheric Sciences, Desert Research  Berkeley, California, United States of America <br> Ehlers K, Oster G. PLoS ONE 7(5): e36081. doi:10.1371/journal.pone. 0036081 (2012)

Synechococcus swims at $25 \mu \mathrm{~m} / \mathrm{s}$


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

## How can a cyanobacteria swim without flagella?

## Model: Surface traveling wave (oscillations)

Small amplitude, high frequency waves: Swimming speeds of order $25 \mu \mathrm{~m} / \mathrm{s}$ are expected for a spherical cell propagating longitudinal waves of $0.2 \mu \mathrm{~m}$ length, $0.02 \mu \mathrm{~m}$ amplitude, and $160 \mu \mathrm{~m} / \mathrm{s}$ 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


## How can a cyanobacteria swim without flagella?

## Model: Surface traveling wave (oscillations)




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

## How can a cyanobacteria swim without flagella?

## Model: Surface traveling wave (helicoidal track)

- Cargo causes local deformation of surface layer and forms surface ridges.
- Synechococcus utilizes a continuous loop helical rotor
-Rotating helix model: motors anchored to the peptidoglycan layer drive rotation of the rotor creating helical waves along the cell surface
-Traveling cargo model: 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



## How can a cyanobacteria swim without flagella?

## 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


McCarren J, Heuser J, et al. J. Bacteriology, 187: 224-230. (2005)



[^0]:    
    
    
     dell through one ryele.

[^1]:    L. McCarter et al. Cell 54: 345-351 (1988)

