26 June 2024

Non-reciprocity in Microswimming

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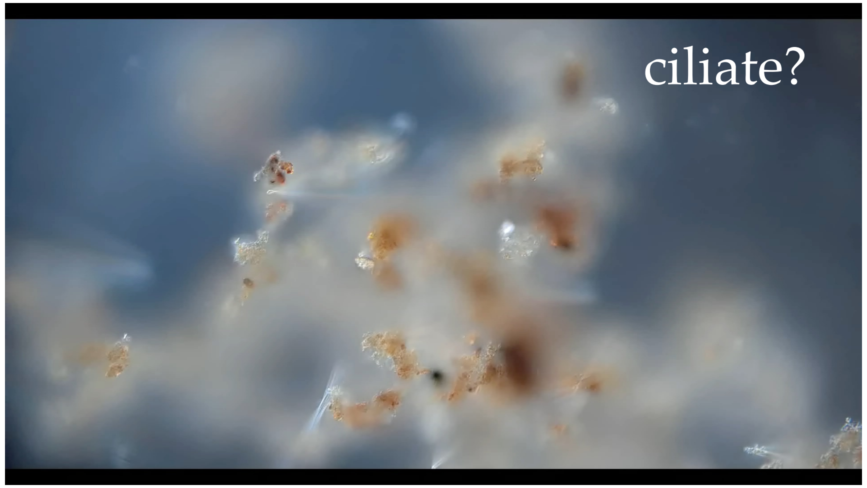
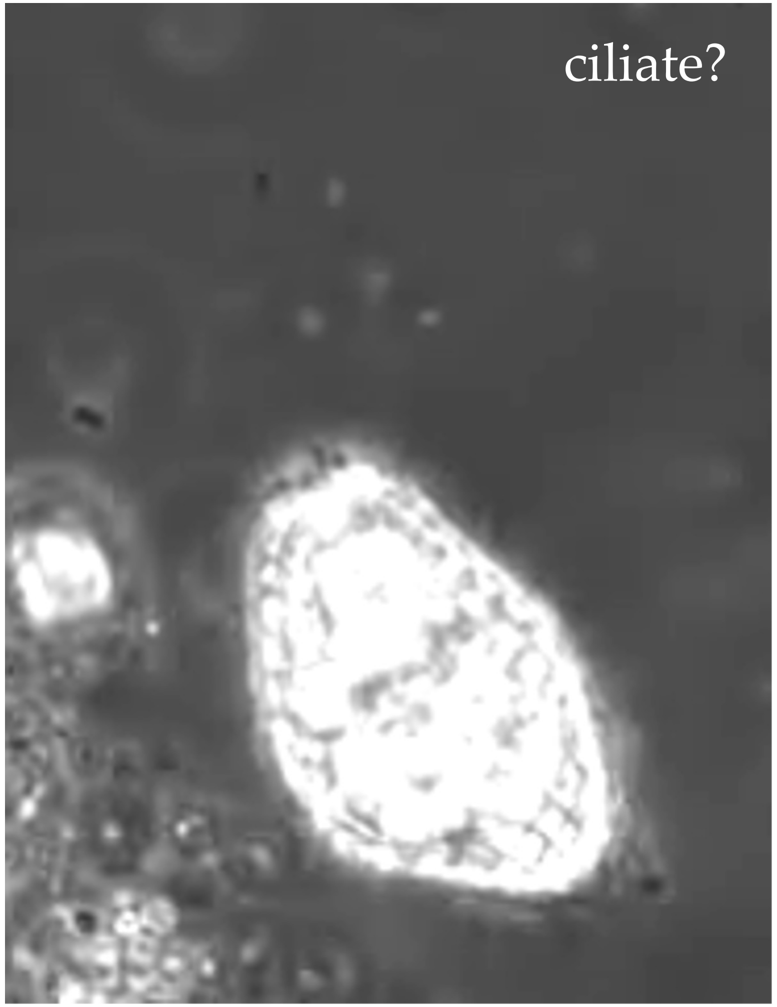
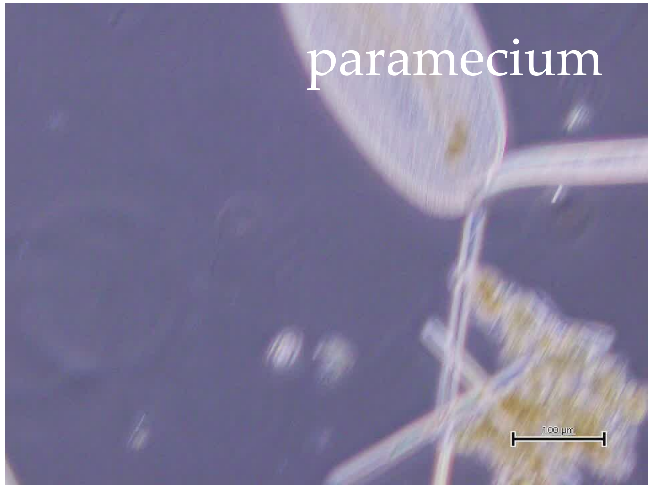
Swimming cell as living material





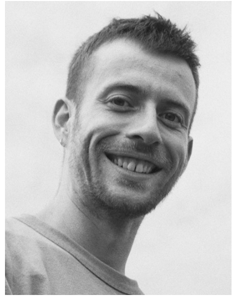


Outline

1. Introduction

- kinematic problem vs elastohydrodynamics

Kento Yasuda
(RIMS, Kyoto)



Clément Moreau
(CNRS/ LS2N)

Johann Herault
(IMT Atlantique)

2. Non-reciprocity & odd elasticity

- motivation & simple models
- applications in biological swimmers
- physical interpretations

[Ishimoto, Moreau & Yasuda, Phys Rev E (2022); PRX Life (2023)]

3. Emergence of non-reciprocity by mechanosensation

- elastohydrodynamics & coupled-oscillators

[Ishimoto, Moreau & Herault, arXiv: 2405.01802]

Microswimmers

Zero Reynolds number limit:

$$Re = \frac{\rho U L}{\mu} \ll 1$$

Stokes + force/torque free

$$\begin{cases} \mu \nabla^2 \boldsymbol{u} = \nabla p \\ \nabla \cdot \boldsymbol{u} = 0 \end{cases}, \quad \boldsymbol{F} = \boldsymbol{M} = \boldsymbol{0}$$

no-slip boundary conditions: $\boldsymbol{u} = \boldsymbol{u}_{\text{surface}}$

$$\boldsymbol{u}_{\text{surface}} = \boldsymbol{U} + \boldsymbol{\Omega} \times \boldsymbol{x} + \boldsymbol{u}'$$

deformation velocity (→ $\boldsymbol{u}'$)

Kinematic problems

- solve the swimming dynamics with a given shape gait
- no information needed for the material

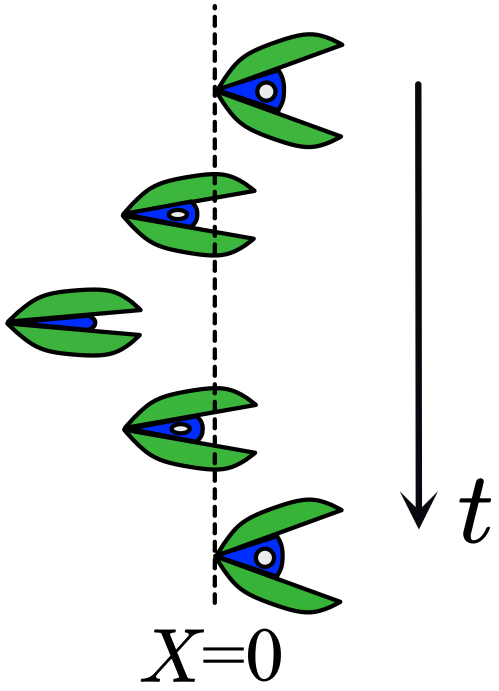
Elastohydrodynamics

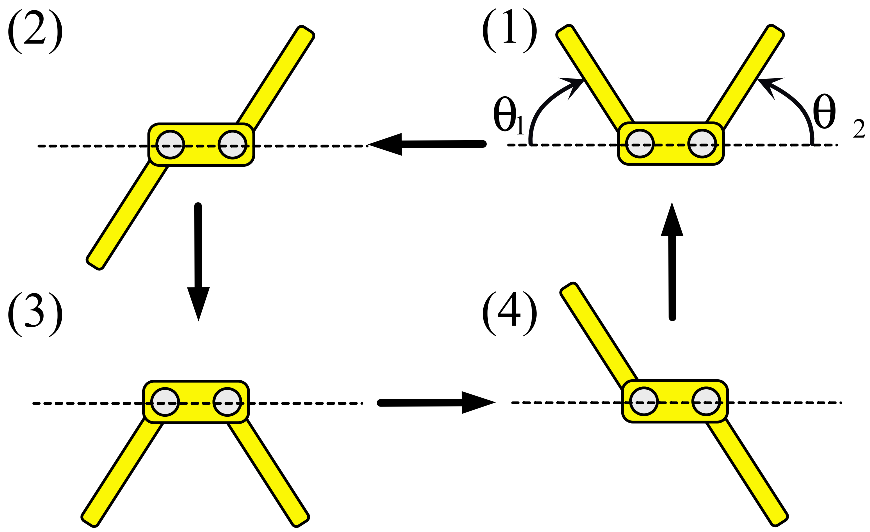
- solve the swimming dynamics together with the shape gait (shape gait is unknown)
- to specify the shape gait, we need constitutive relation for material response

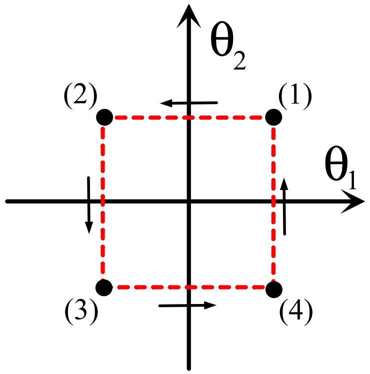
Non-reciprocity in microswimming

Purcell's scallop theorem [Purcell, Am J Phys (1977); Ishimoto & Yamada, SIAM J Appl Math (2012)]

- Microswimming requires **non-reciprocal deformation** **(non-time-reversal)**
- a simple model for non-reciprocal swimmer with two-hinges is called the Purcell swimmer







Kinematic microswimming formula

Gauge field theory for microswimming

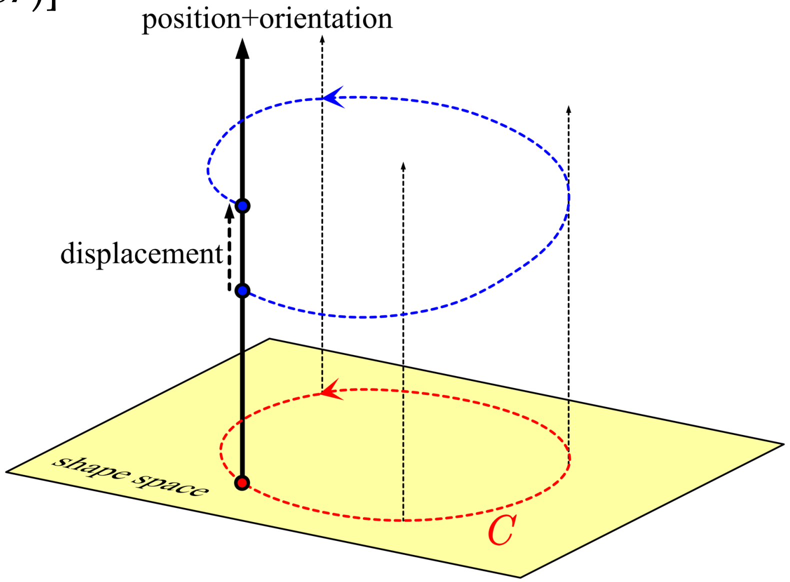
- analogy with particle field theory [Shapere & Wilczek, J Fluid Mech (1987)]
- periodic swimming beat is given by a loop in shape space

position + orientation

$$\mathbf{R} = \begin{pmatrix} \mathbf{R}_n & \boldsymbol{x} \\ \mathbf{0} & 1 \end{pmatrix} \qquad \dot{\mathbf{R}} = \mathbf{R}\mathbf{A}, \quad \mathbf{A} = \mathbf{A}_\alpha \alpha_\alpha$$

for 2D swimming

$$\mathbf{A} = \begin{pmatrix} 0 & -\dot{\theta} & \dot{x}_0 \\ \dot{\theta} & 0 & \dot{y}_0 \\ 0 & 0 & 0 \end{pmatrix}$$



$$\mathbf{R}(t) = \mathbf{R}(0)\overline{\mathrm{P}}\exp\left[\int_0^t \mathbf{A}(t')dt'\right]$$

$$= \mathbf{R}(0)\overline{\mathrm{P}}\exp\left[\int_{\boldsymbol{\alpha}(0)}^{\boldsymbol{\alpha}(t)} \mathbf{A}_\alpha(\boldsymbol{\alpha})d\alpha_\alpha\right]$$

= line integral in shape space

averaged velocity for a small-amplitude swimmer

$$\bar{\mathbf{A}} = \frac{1}{2}\mathbf{F}_{\alpha\beta}\alpha_\alpha\dot{\alpha}_\beta$$

$\mathbf{A}_\alpha$: gauge potential

$\mathbf{F}_{\alpha\beta}$: curvature of gauge field (field strength)

Elastohydrodynamic miroswimming

- flagellum as an actuated elastic rod
- Kirchhoff rod + Stokes equation

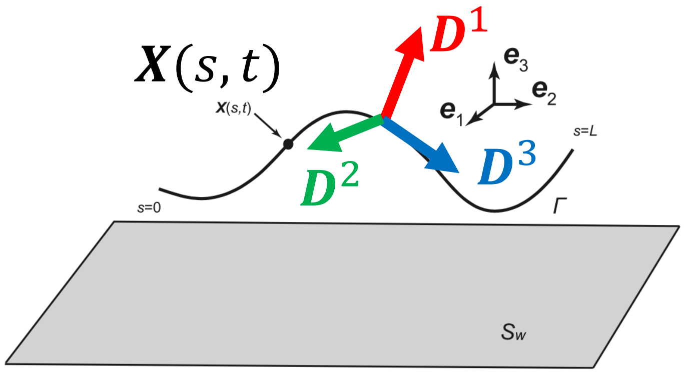
$$\boldsymbol{f}^{\mathrm{hyd}} + \frac{\partial \boldsymbol{F}}{\partial s} = \boldsymbol{0}$$

$$\boldsymbol{m}^{\mathrm{hyd}} + \frac{\partial \boldsymbol{M}}{\partial s} + \frac{\partial \boldsymbol{X}}{\partial s} \times \boldsymbol{F} = \boldsymbol{m}^{\mathrm{int}}$$

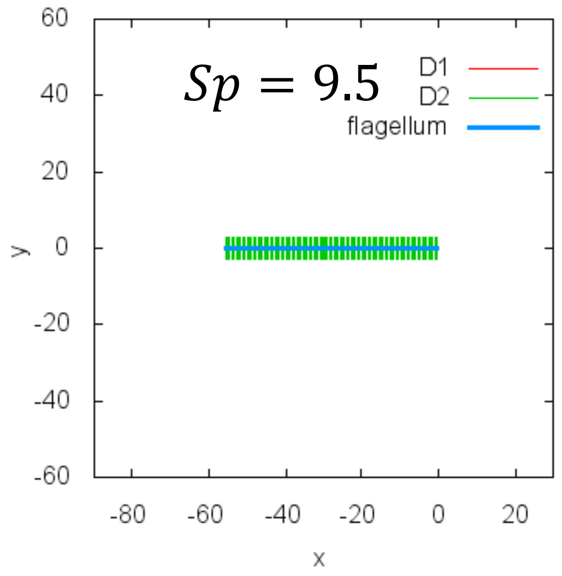
$$\boldsymbol{m}^{\mathrm{int}}(s,t) = A_1 \sin(kx - \omega t)\, \boldsymbol{D}^1 + A_2 \cos(kx - \omega t)\, \boldsymbol{D}^2$$

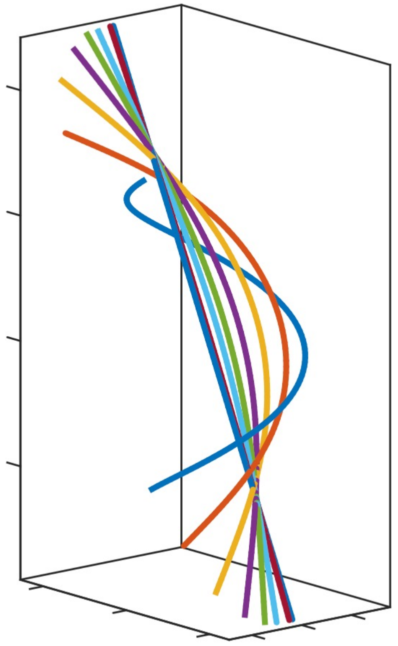
driving force is needed for propulsion

[Ishimoto & Gaffney, IAM J Appl Math (2018)]
[Walker, Ishimoto, Gadêlha & Gaffney, J Fluid Mech (2019)]
[Walker, Ishimoto & Gaffney, Phys Rev Fluids (2020)]



$$Sp = \left(\frac{\xi L^4}{T a_1}\right)^{1/4} \approx \frac{\text{viscous drag time}}{\text{elastic bending time}}$$





General descriptions of active soft matter?

Beyond the kinematic problem

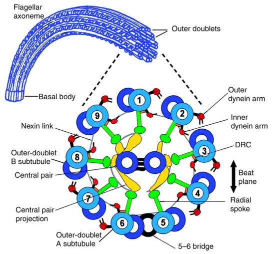
- Shape is determined by fluid-structure interaction
- material constitutive relation is needed

- general constitutive relation?
- material response w/o energy conservation?

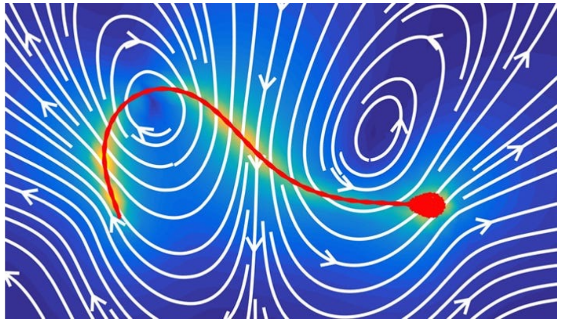
Swimming = Fluid+ Elasticity + Internal actuation

unified description?

- **Swimming cell as a non-equilibrium state of matter?**



energy injection
from molecular scales



energy dissipation
in the viscous fluid

swimming (deformation + motility)

Odd elasticity

Linear elasticity: collection of springs

- simple but canonical model of soft matter
- elastic matrix should be symmetric from the energy conservation

$$f_\alpha = K_{\alpha\beta} x_\beta \quad \alpha, \beta = 1,2,\cdots, N$$

$$K_{\alpha\beta} = K_{\beta\alpha}$$

Credit: Corentin Coulais

General description of active soft material

- **odd elasticity**: non-symmetric elastic matrix for non-energy conserving material
- self-sustained wave generated = non-reciprocal material response
- interpreted as a non-conservational force

$$K_{\alpha\beta} \neq K_{\beta\alpha}$$

[Scheibner et al. Nat Phys (2020)]
[Fruchart, Scheibner & Vitteli, Annu Rev Cond Matt (2023)]

Swimming with odd elasticity?

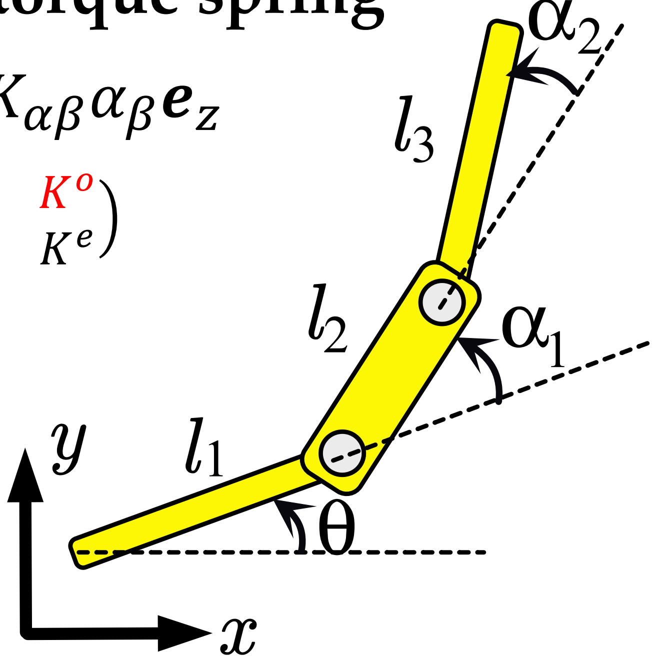
The simplest microswimmer with rotation

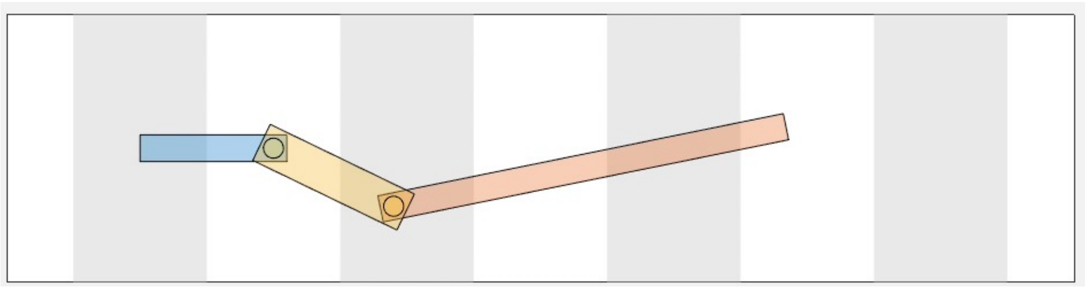
- Purcell's three-link swimmer can generate a stable locomotion as a limit cycle

odd-elastic torque spring

$$\boldsymbol{T}_\alpha = -K_{\alpha\beta}\alpha_\beta \boldsymbol{e}_z$$

$$\mathbf{K} = \begin{pmatrix} K^e & K^o \\ -K^o & K^e \end{pmatrix}$$





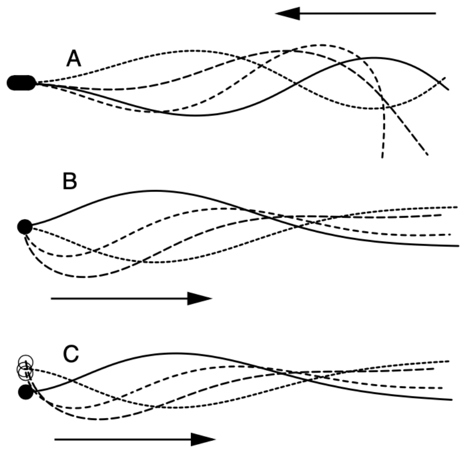
- self-organised swimming for pushers
- no driving-force, no control
- stable limit cycle via geometric nonlinearity

[Ishimoto, Moreau & Yasuda, Phys Rev E (2022)]

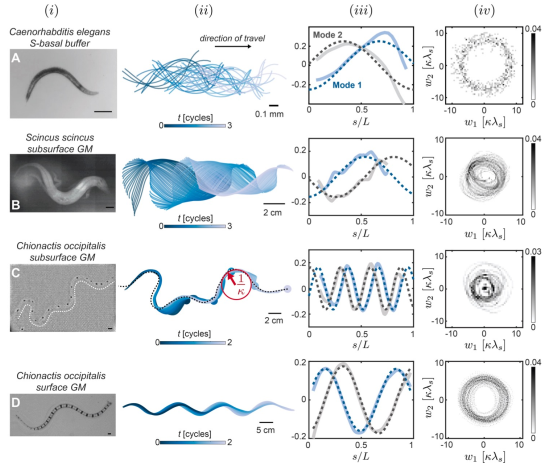
Swimming cell as an odd matter?

Periodic deformation = limit cycle in shape space

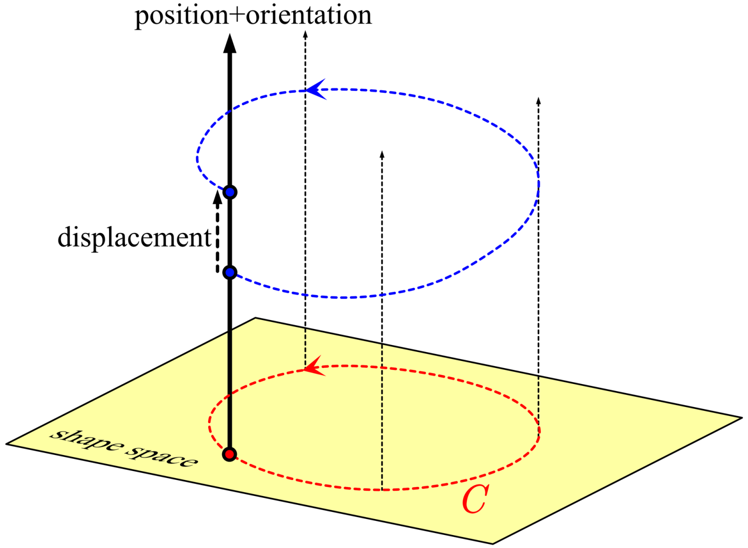
- Hopf bifurcation as a generic form of flagellar swimming
- Experimental observation in sperm and Chlamydomonas



[Camalet and Jülicher, New J Phys (2000)]



[Rieser et al. arXiv (2019)]

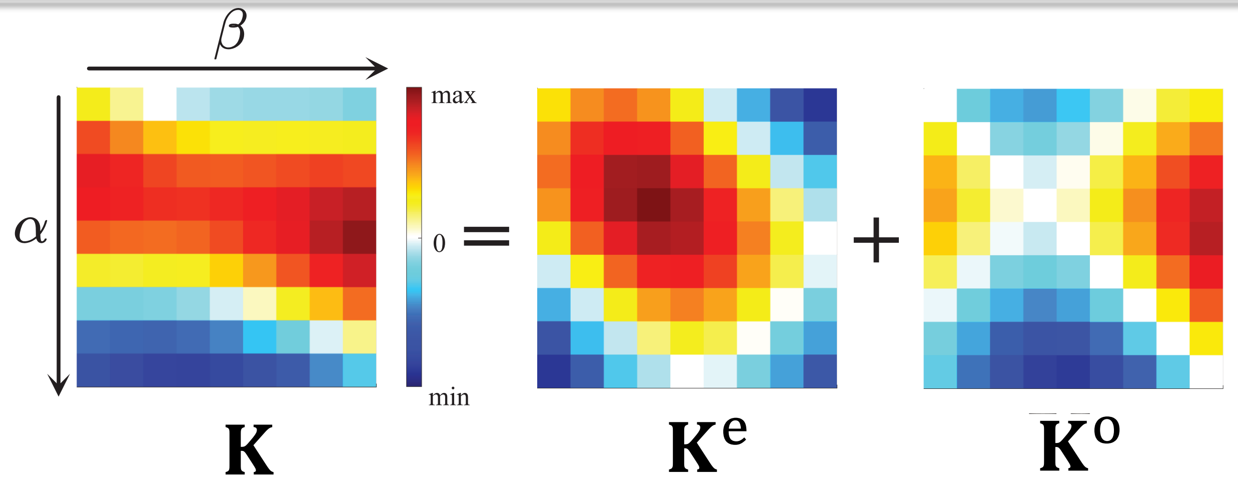


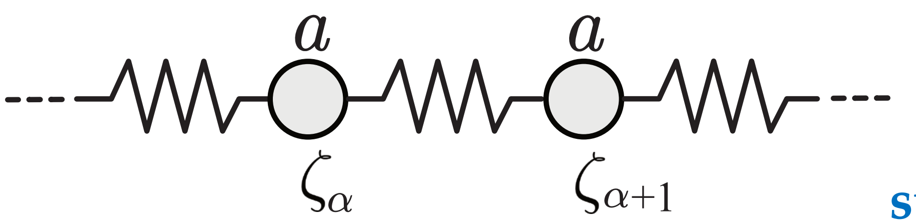
Q. Can we calculate the odd elastic matrix of a swimming cell?

N-dim elastic matrix?

$$\mathbf{K} = \begin{pmatrix} K^e & K^o \\ -K^o & K^e \end{pmatrix} \Rightarrow K_{\alpha\beta}$$

$$\alpha, \beta = 1, 2, \cdots, N$$





$$s_\alpha = (\alpha - 1)L/N$$

sphere-spring system with **mass** m and fluid viscous **drag** γ with neighbouring interaction of **spring constant** k

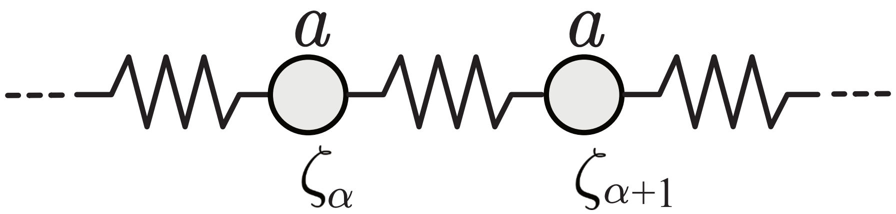
$$m\ddot{\zeta}_\alpha = -\gamma\dot{\zeta}_\alpha - K_{\alpha\beta}\zeta_\beta \qquad K_{\alpha\beta} = k\delta_{\alpha+1,\beta} - 2k\delta_{\alpha\beta} + k\delta_{\alpha-1,\beta}$$

⇝ **Wave equation**

Find the matrix $K_{\alpha\beta}$ that generates a sinusoidal wave with a single wavenumber ν_0: $\zeta(s_\alpha, t) = A\sin(\nu_0 s_\alpha - \omega t)$

Non-local, non-reciprocal interactions

Find the matrix $K_{\alpha\beta}$ that propagates a sinusoidal wave with a single wavenumber ν: $\zeta(s_\alpha, t) = A\sin(\nu_0 s_\alpha - \omega t)$



$s_\alpha = (\alpha - 1)L/N$

$\gamma = 0$ **(inertial limit)**

$$m\ddot{\zeta}_\alpha = -K_{\alpha\beta}\zeta_\beta$$

$$K_{\alpha\beta} = m\omega^2\cos(\nu_0(s_\alpha - s_\beta))$$

$$K_{\alpha\beta} = K_{\beta\alpha}$$

even elasticity

$m = 0$ **(zero-inertia limit)**

$$\gamma\dot{\zeta}_\alpha = -K_{\alpha\beta}\zeta_\beta$$

$$K_{\alpha\beta} = \gamma\omega\sin(\nu_0(s_\alpha - s_\beta))$$

$$K_{\alpha\beta} = -K_{\beta\alpha}$$

odd elasticity

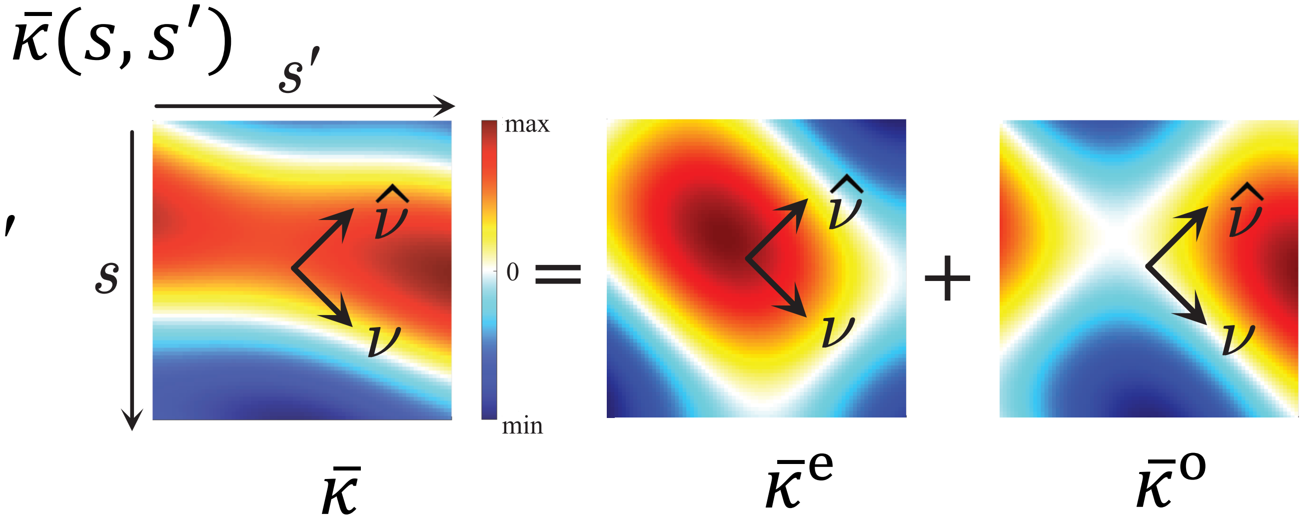
A quantity that characterises odd elasticity

odd-elastic modulus

$$\tilde{\kappa}(\hat{\nu}) = \iint \bar{\kappa}(s,s')e^{-i\hat{\nu}(s-s')}\mathrm{d}s\mathrm{d}s'$$

non-reciprocity : $\kappa(s,s') \neq \kappa(s',s)$

$$\mathrm{Im}[\tilde{\kappa}(\hat{\nu})] \neq 0$$

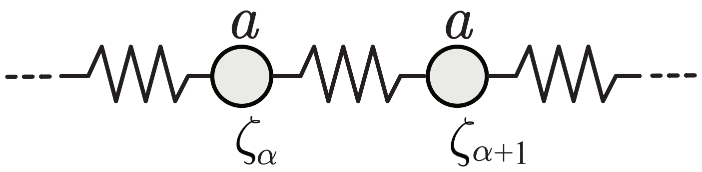


$\gamma = 0$ **(inertial limit)** $m = 0$ **(zero-inertia limit)**

$$\zeta(s,t) = A\sin(\nu_0 s - \omega t) \qquad \tilde{\kappa}(\hat{\nu}) = \frac{\bar{m}\omega^2}{2}[\delta(\hat{\nu}-\nu_0) + \delta(\hat{\nu}+\nu_0)] \qquad \tilde{\kappa}(\hat{\nu}) = \mathrm{i}\frac{\bar{\gamma}\omega}{2}[\delta(\hat{\nu}-\nu_0) - \delta(\hat{\nu}+\nu_0)]$$

real and even function **imaginary and odd function**

Active matter as autonomous system



$$\zeta(s,t) = A\sin(\nu_0 s - \omega t)$$

Non-autonomous (control system) → **Autonomous** (non-equilibrium state of matter)

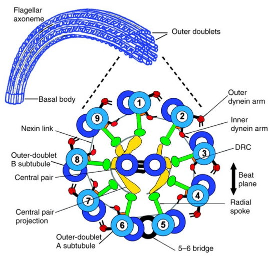
$$\gamma\dot{\zeta}_\alpha = -K_{\alpha\beta}\zeta_\beta + F_\alpha(t)$$

$$K_{\alpha\beta} = K_{\beta\alpha}$$

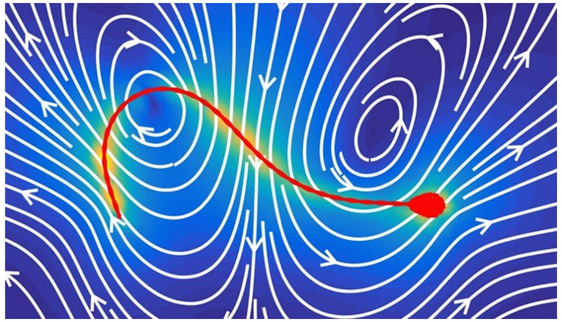
$$\gamma\dot{\zeta}_\alpha = -K_{\alpha\beta}\zeta_\beta \qquad \partial_t\zeta(s) = \int \bar{\kappa}(s,s')\zeta(s')\mathrm{d}s'$$

$$K_{\alpha\beta} \neq K_{\beta\alpha} \qquad \bar{\kappa}(s,s') \neq \bar{\kappa}(s',s)$$

- **Swimming cell as a non-equilibrium state of matter**



energy injection from molecular scales



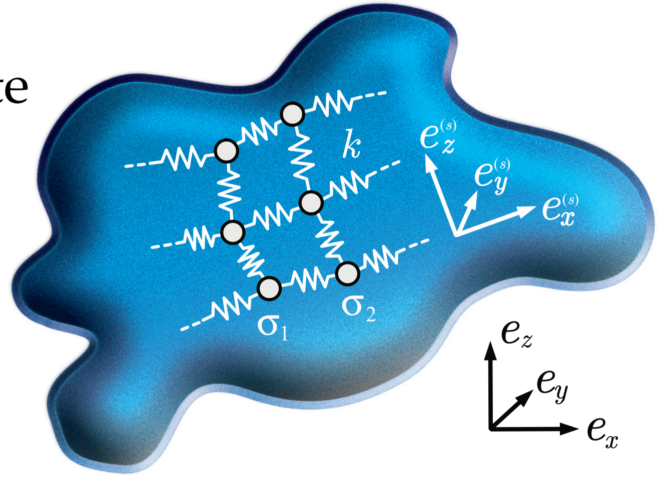
energy dissipation in the viscous fluid

swimming (deformation + motility)

Odd-elastohydrodynamics

Fluid-strucutre interactions

- general swimming in $\mathbb{R}^n$ $(n = 1,2,3,\dots)$ with shape space of $\mathbb{R}^N$
- generalized grand resistive tensor $\mathbf{M}$ is symmetric and positive-definite
- force- and torque-free conditions in the body-fixed coordinates



hydrodynamic drag (odd) elastic force

$$-\mathbf{M}(\sigma_1, \sigma_2, \cdots, \sigma_N)\dot{\boldsymbol{X}} = \begin{pmatrix} \mathbf{O} & 0 \\ 0 & \mathbf{K} \end{pmatrix} \boldsymbol{X}$$

state: $\boldsymbol{X} = (x_1, x_2, \cdots, x_n, \theta_1, \theta_2 \cdots, \sigma_1, \sigma_2, \cdots, \sigma_N)^{\mathrm{T}}$

position + orientation + shape (in the body-fixed coordinates)

Shape dynamics and swimming dynamics

$$\begin{cases} \boldsymbol{\sigma} = (\sigma_1, \sigma_2 \cdots, \sigma_N)^{\mathrm{T}} \\ \boldsymbol{z} = (x_1, x_2, \cdots, x_n, \theta_1, \theta_2, \cdots)^{\mathrm{T}} \\ \mathbf{N} = \mathbf{M}^{-1} = \begin{pmatrix} * & \mathbf{P} \\ * & \mathbf{Q} \end{pmatrix} \end{cases}$$

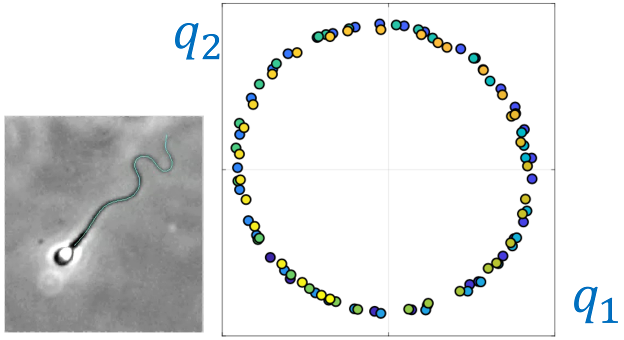
$$\begin{cases} \dot{\boldsymbol{\sigma}} = -\mathbf{Q}(\boldsymbol{\sigma})\mathbf{K}\boldsymbol{\sigma} \\ \dot{\boldsymbol{z}} = -\mathbf{P}(\boldsymbol{\sigma})\mathbf{K}\boldsymbol{\sigma} \end{cases}$$

or $\dot{\boldsymbol{z}} = -\mathbf{P}(\boldsymbol{\sigma})\mathbf{Q}^{-1}(\boldsymbol{\sigma})\boldsymbol{\sigma}$

Kinematic problem, if the shape gait is given

Intrinsic and apparent shape spaces

human sperm data in PCA shape space



[Ishimoto et al. J Theor Biol (2018)]

intrinsic shape space $\boldsymbol{\sigma}$
& **intrinsic** elasticity $\mathbf{K}(\boldsymbol{\sigma})$

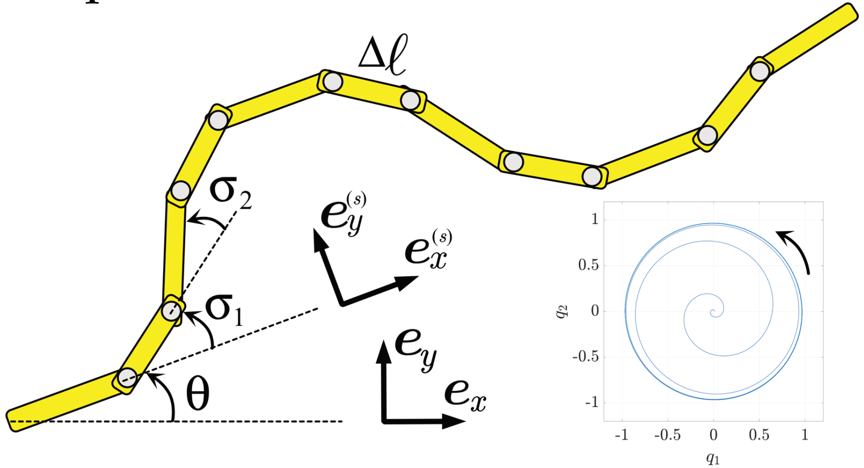
$$\dot{\boldsymbol{\sigma}} = -\mathbf{Q}(\boldsymbol{\sigma})\mathbf{K}(\boldsymbol{\sigma})\boldsymbol{\sigma}$$

$$\boldsymbol{\sigma} = \mathbf{W}\boldsymbol{q}$$

apparent shape space $\boldsymbol{q}$
& **apparent** elasticity $\widehat{\mathbf{K}}$

$$\dot{\boldsymbol{q}} = -\widehat{\mathbf{K}}\boldsymbol{q}$$

- estimate $\mathbf{K}(\boldsymbol{\sigma})$ from flagellar model and experimental data



- normal form of the Hopf bifurcation

$$\widehat{\mathbf{K}} = \begin{pmatrix} \widehat{\mathbf{K}}_{\mathrm{LC}} & 0 \\ 0 & \widehat{\mathbf{K}}_{\mathrm{d}} \end{pmatrix} \quad \widehat{\mathbf{K}}_{\mathrm{LC}} = \begin{pmatrix} k_e & k_o \\ -k_o & k_e \end{pmatrix} + \begin{pmatrix} k_n & k_{no} \\ -k_{no} & k_n \end{pmatrix} |\boldsymbol{q}|^2$$

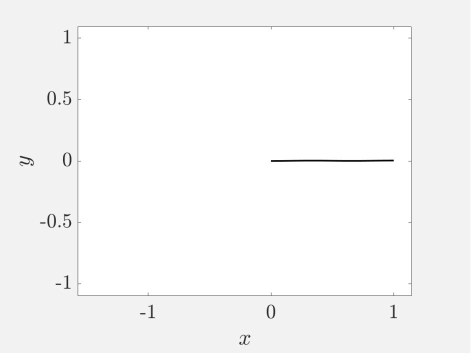
- N-link coarse-graining formulation with resistive force theory

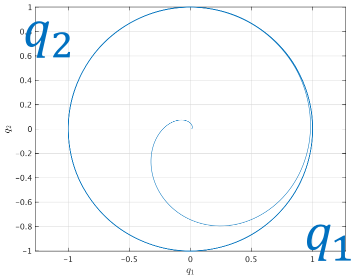
Odd bending modulus of simple swimmers

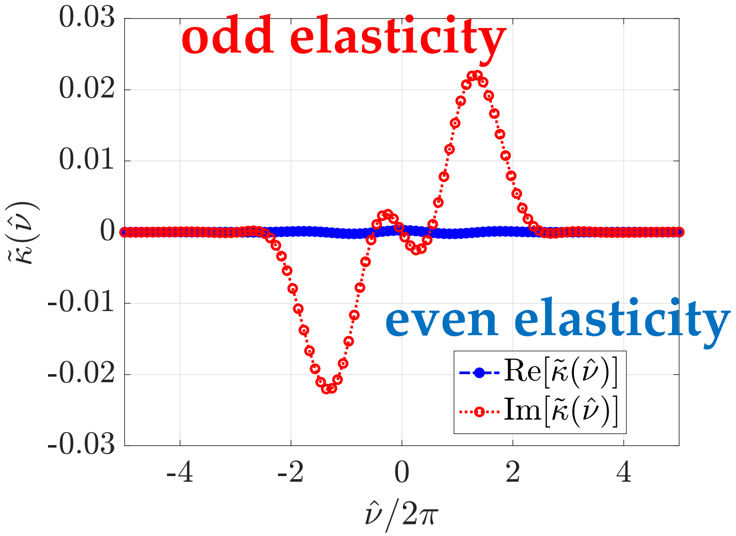
sinusoidal flagellum
[Gong et al.,R Phil Trans B (2018)]

$\sigma(s,t) = C_1 \sin(ks - \omega t)$

$k/2\pi = 1.5$

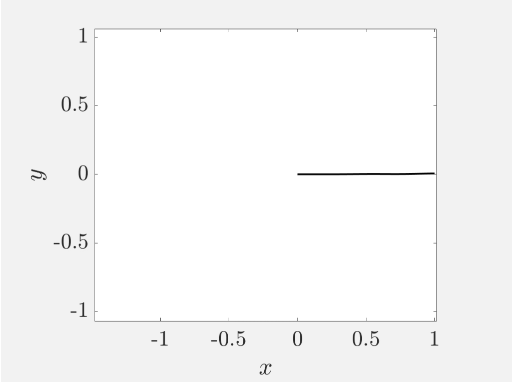


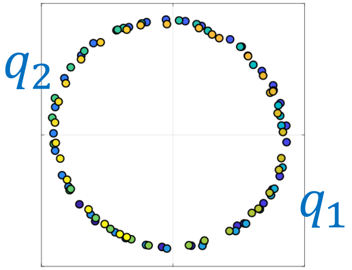


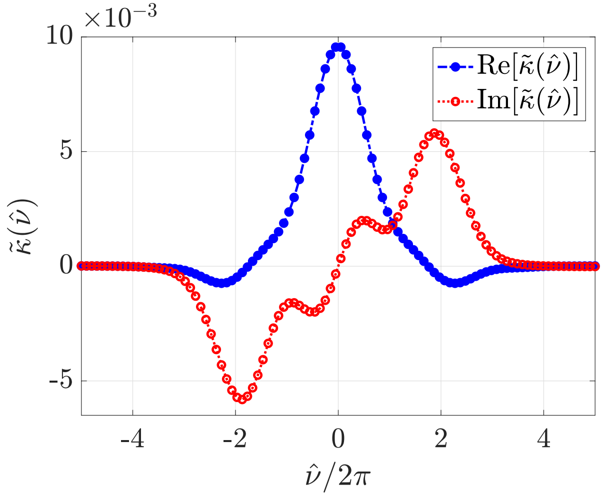


- purely odd-elastic material on the limit cycle

human sperm data
[Ishimoto et al. J Theor Biol (2018)]

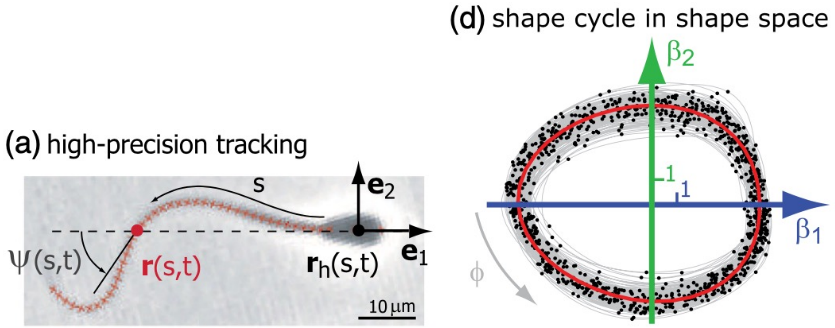






- negative even elasticity (pattern formation)
- existence of odd elasticity (phase velocity)

Swimming cell as a noisy limit cycle



[Ma et al. Phys Rev Lett (2014)]

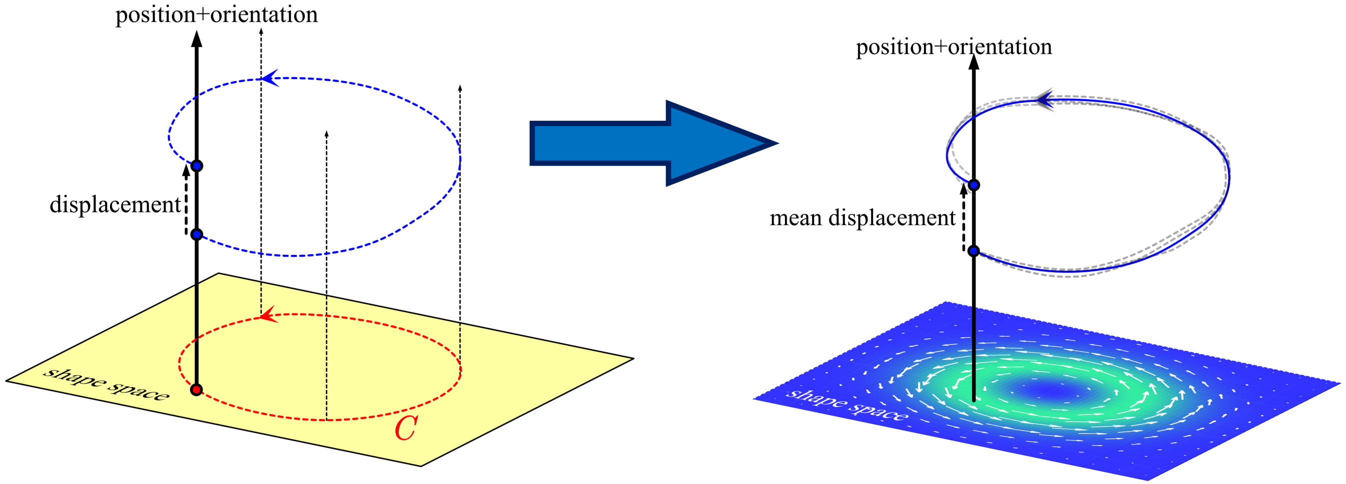
- **Normal form of Hopf bifurcation**

$$\boldsymbol{q} = Ae^{i\varphi}$$

$$\begin{cases} \dot{A} = -k_e A - k_n A^3 + A\zeta_A \\ \dot{\varphi} = k_0 + k_{no} A^2 + \zeta_\varphi \end{cases}$$

Stochastic swimming formula

$$\langle \mathcal{A} \rangle = \frac{1}{2} \mathbf{F}_{\alpha\beta} \langle q_\alpha \dot{q}_\beta \rangle = \mathrm{Tr}(\mathcal{F}\mathbf{J}) \quad J_{\alpha\beta} = \left\langle \oint q_\alpha dq_\beta \right\rangle$$



$$\langle \zeta_A(t) \zeta_A(t') \rangle = 2D_A \delta(t - t')$$

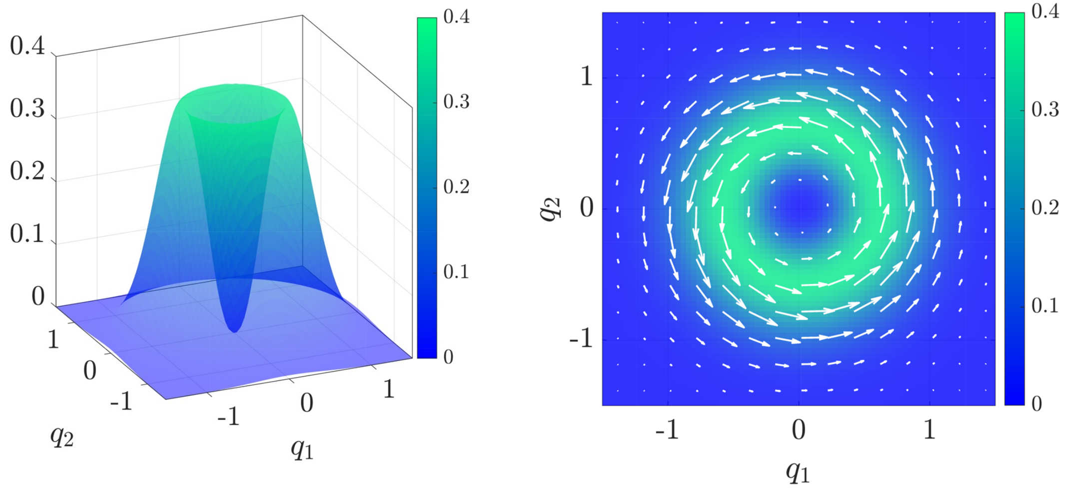
$$\langle \zeta_\varphi(t) \zeta_\varphi(t') \rangle = 2D_\varphi \delta(t - t')$$

Stochastic swimming formula

$$\langle \mathcal{A} \rangle = \frac{1}{2}\mathbf{F}_{\alpha\beta}\langle q_\alpha \dot{q}_\beta \rangle = \mathrm{Tr}(\mathcal{F}\mathbf{J}) \qquad J_{\alpha\beta} = \left\langle \oint q_\alpha dq_\beta \right\rangle$$

$$P_{st} \sim r^{\frac{|k_e|}{D_r}} e^{-\frac{k_{ne}}{2D_r}r^2}$$

$$J_{12} = -\frac{k_o}{2}\frac{|k_e|}{k_n} + \frac{k_{no}}{2}\frac{|k_e|}{k_n}\left[\frac{k_e}{k_n} + \frac{2D_A}{k_n}\right]$$



Averaged entropy production $\dot{e}_p = \dot{S} - \frac{\dot{Q}}{T}$

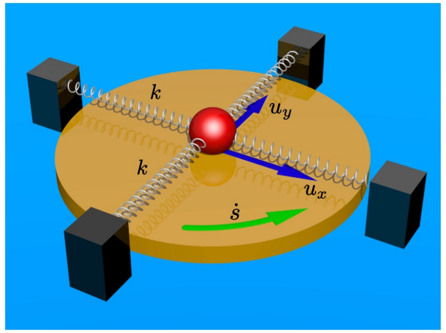
Work done by odd elasticity $\dot{W} = -\oint \hat{K}_{\alpha\beta} q_\beta dq_\alpha$

$$\rightsquigarrow \begin{cases} k_B T \dot{e}_p = \dot{W} \\ D_\varphi = k_B T \end{cases}$$

Emergence of odd elasticity

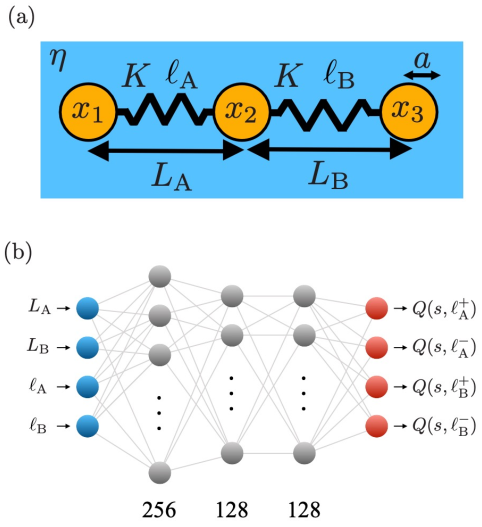
by eliminating internal/external degrees of freedom

[Lin et al., J Phys Soc Jpn (2023)]



by learning how to swim

[Lin, Yasuda, Ishimoto, Komura, Phys Rev Research (2024)]



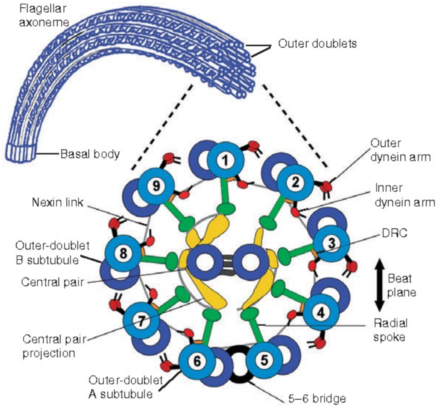
by local mechanosensory regulation

[Ishimoto, Moreau, Herault, arXiv: 2405.01802]

Mechanosory regulations?

Flagellar dynein regulation?

- many existing hypothesis on regulation mechanisms (mechanical clutch, curvature control…)
- **mechano-chemical oscillator**



[Lindemann et al. (2010)]

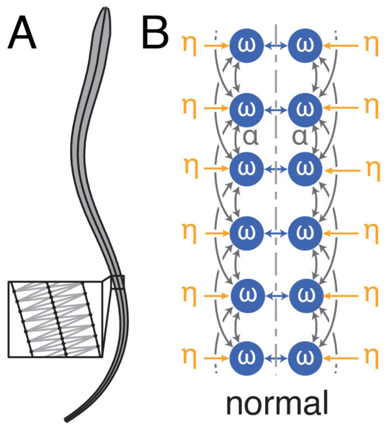
Flow exteroception?

- **intrinsic neural oscillator (CPG)**
- generator of rhythmic muscle contraction

⇝ **coupled oscillator model**

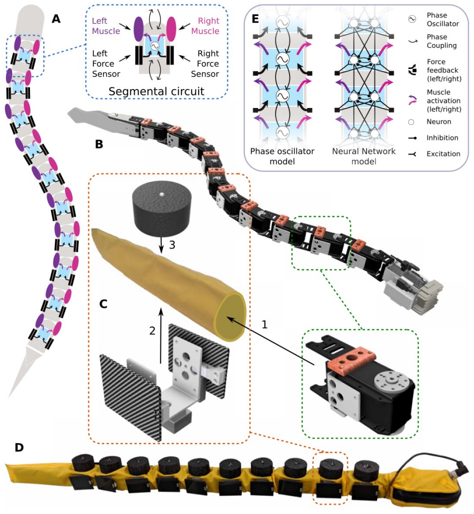
Fish undulatory swimming

2D Navier-Stokes



[Hamlet et al. PNAS (2023)]

Fish Robot



[Thandiackal et al. Sci Robot (2021)]

Our model

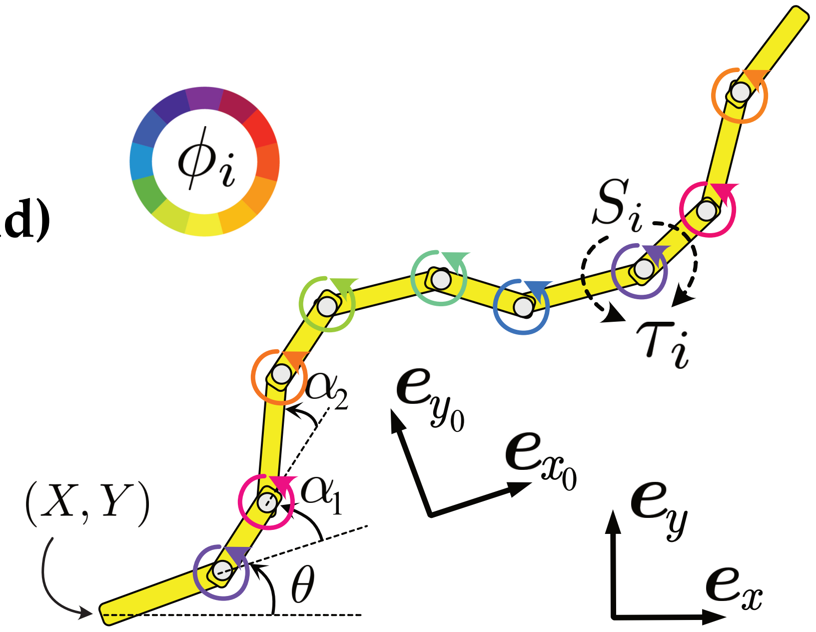
$M_i^{(j)}$ (hydrodynamic) torque on i-th link around j-th hinge

Force & torque balance

$$\begin{cases} \dot{\boldsymbol{\alpha}} = -\mathbf{Q}(\boldsymbol{\alpha})\boldsymbol{\tau} \\ \dot{\boldsymbol{z}} = -\mathbf{P}(\boldsymbol{\alpha})\boldsymbol{\tau} \end{cases}$$

$\mathbf{P}, \mathbf{Q}$: hydrodynamic coupling

$$\dot{\boldsymbol{z}} = (\dot{X}_0, \dot{Y}_0, , \dot{\theta})^{\mathrm{T}}$$



Actuation + elasticity

$$\tau_i = \tau \cos \phi_i - \kappa \alpha_i$$

Sensory signal (local torque load)

$$S_i(t) = M_i^{(i)} + M_{i+1}^{(i)}$$

Phase-coupled oscillators

$$\dot{\phi}_i = \omega_0 + C \sum_{k=\pm 1} \sin(\phi_{i+k} - \phi_i) + \underbrace{\sigma \cdot \cos \phi_i \cdot S_i}_{\text{phase response}}$$

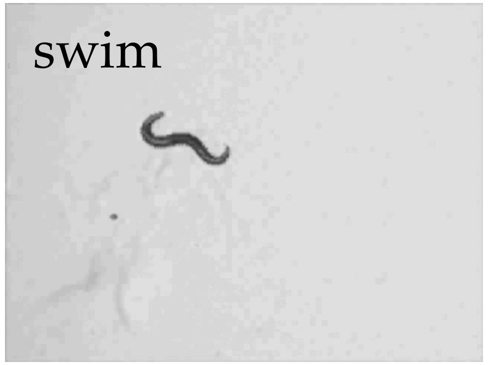
sensory signal $S_i(t)$

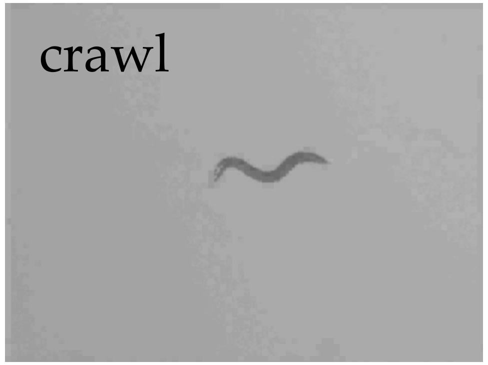
Inner state $\phi_i(t)$ → actuation τ_i → Body state $X, Y, \theta, \alpha_i(t)$ ⇄ Environment (resistive force theory)

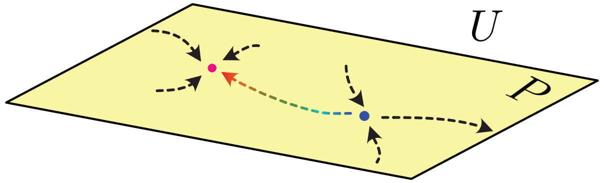
Robust undulatory swimming

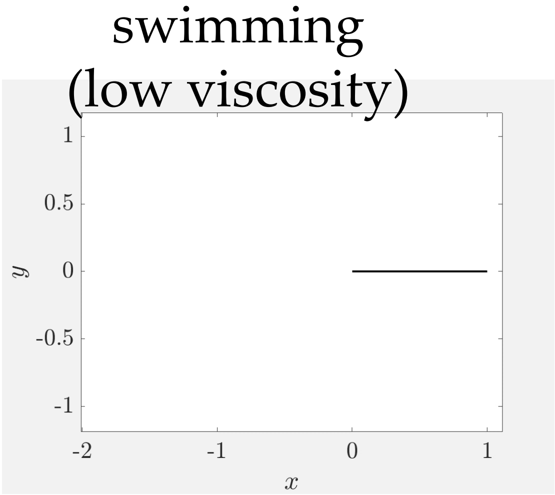
C. elegans locomotion

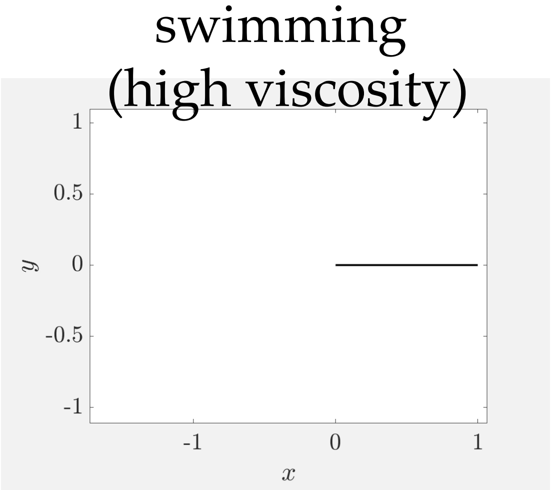
[Pierce-Shimomura et al. (2008)]

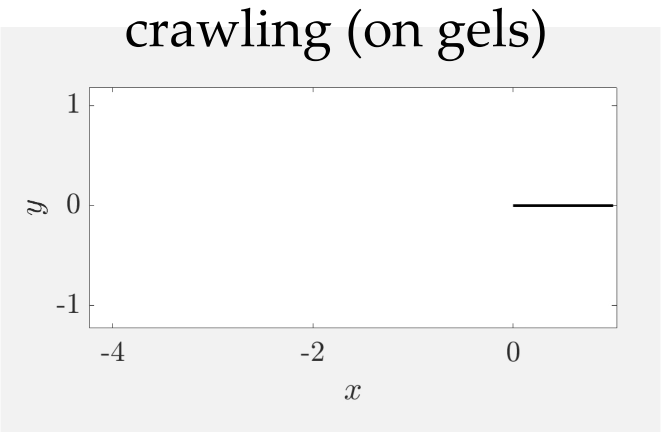


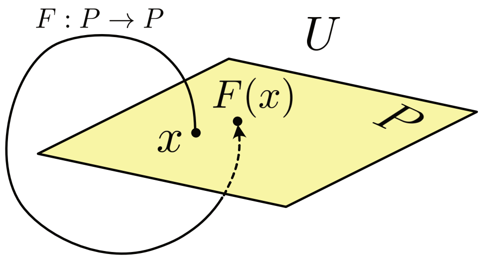












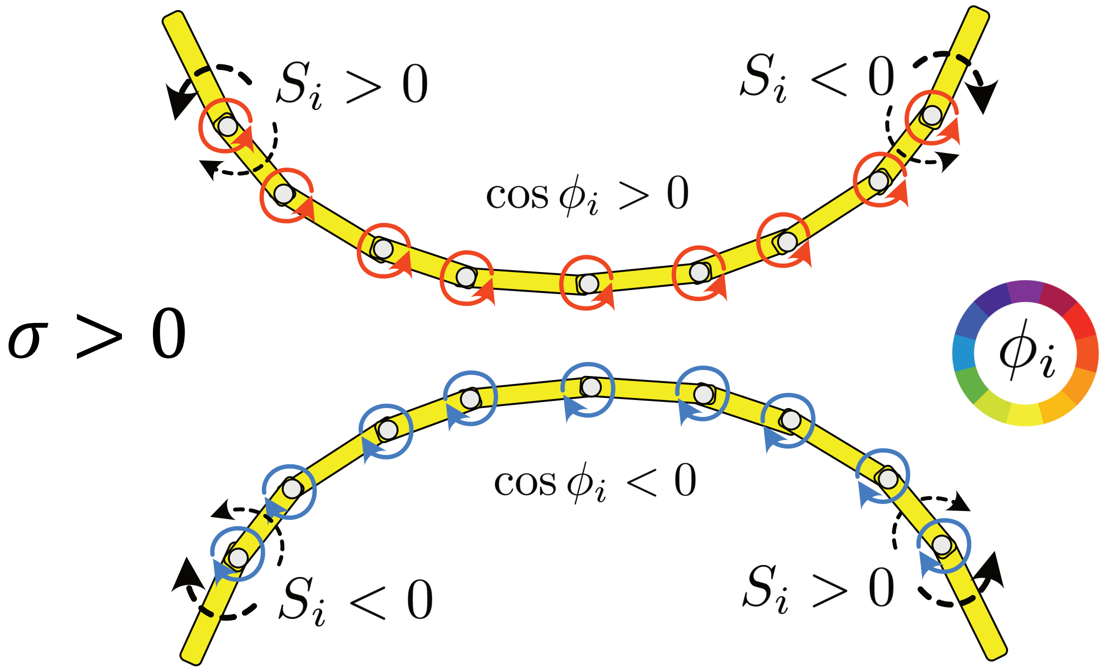
※ stable limit cycle emerges by local mechanosensory regulation

Emergence of non-reciprocity

Sensory signal (local torque load)

$S_i(t) = M_i^{(i)} + M_{i+1}^{(i)}$

$M_i^{(j)}$: torque on i-th link around j-th hinge



Symmetry breaking through geometrical non-locality

$\cos \phi_i \cdot S_i > 0$

phase accelerated

$\cos \phi_i \cdot S_i < 0$

phase deaccelerated

Summary

Conclusions

- ➢ Microswimming as a non-equilibrium state of matter
- ➢ Odd-elasticity characterises the non-reciprocity/activity in shape space
- ➢ Non-reciprocity can robustly emerge through local mechanosensory regulation

Collaborators

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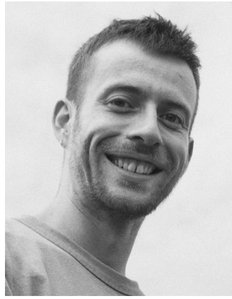

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