Wet, active solids: Physics and Physiology

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Active Matter and Beyond, ICTS, Bangalore
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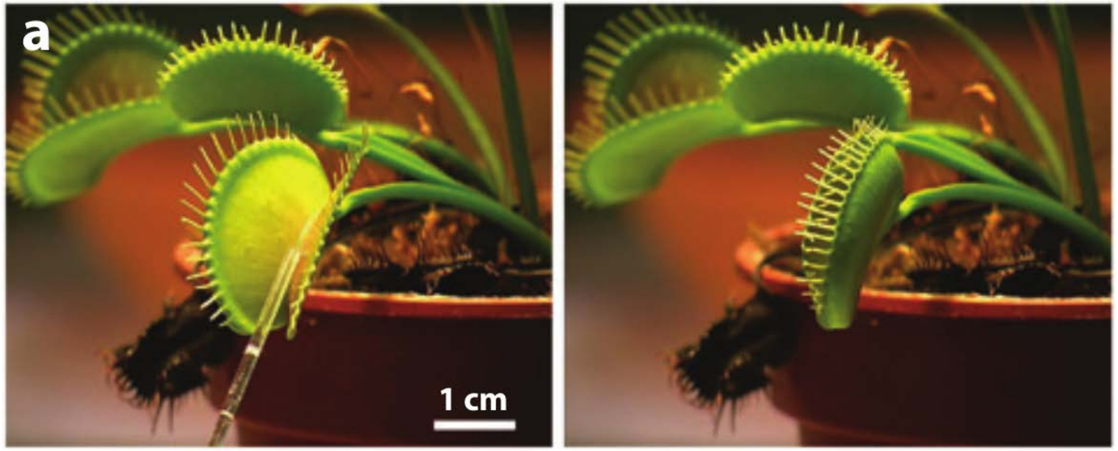
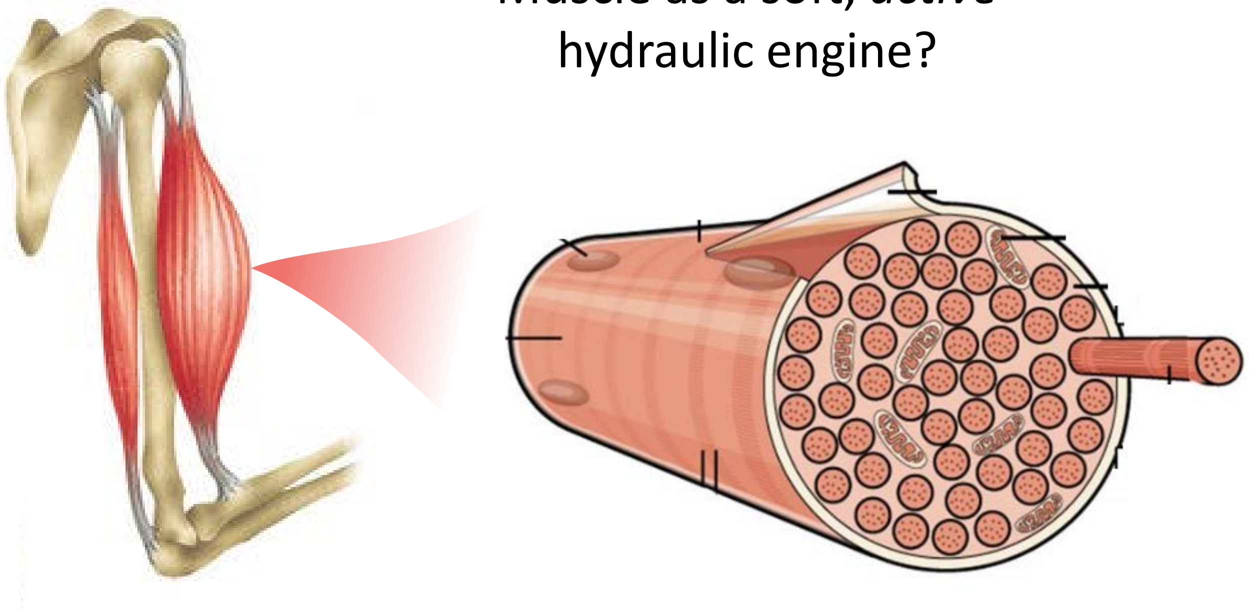
Plants are nature's hydraulic machines



Forterre et al., 2005

Muscle as a soft, *active* hydraulic engine?



Active muscular hydraulics, **SS**, Mahadevan, bioRxiv:2022.02.20.481216, 2022

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The slow, fast and furious

Eye movements
~10 Hz

Flight

~80-1000 Hz

Sound production
~50-500 Hz

Rome, Lindstedt, 1998;
Syme, Josephson, 2002

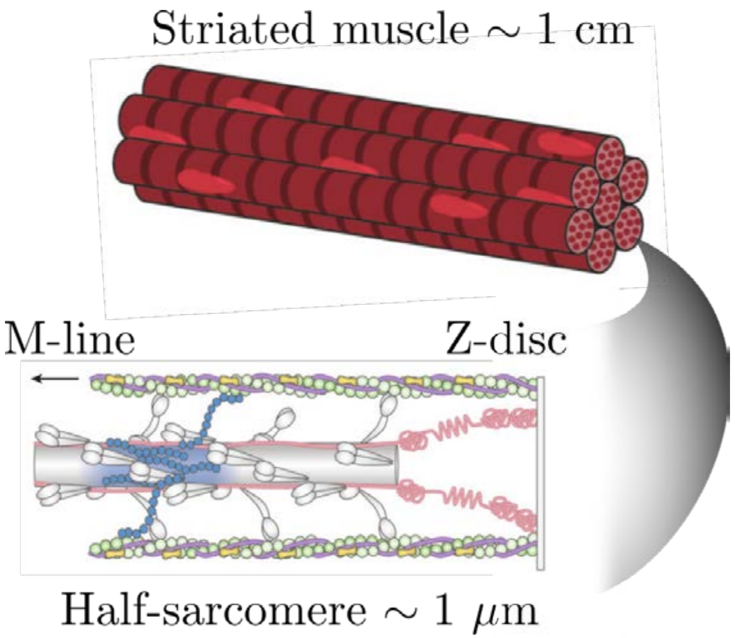
Questions

Biophysical determinants of the range and limits of muscular performance?

Go beyond molecules - mesoscale properties? Spatial effects?

Dynamic/energetic consequences for physiology?

A multiscale contractile engine



Powers et al., Ann. Rev. Biophys., 2021

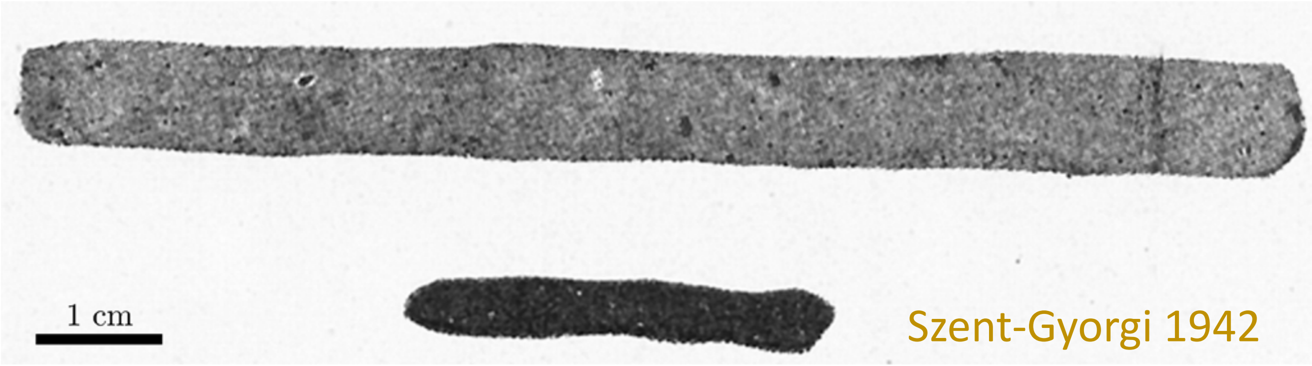
Muscle is a soft, active, anisotropic and wet solid

Active sponge!

Spatially heterogeneous strains?

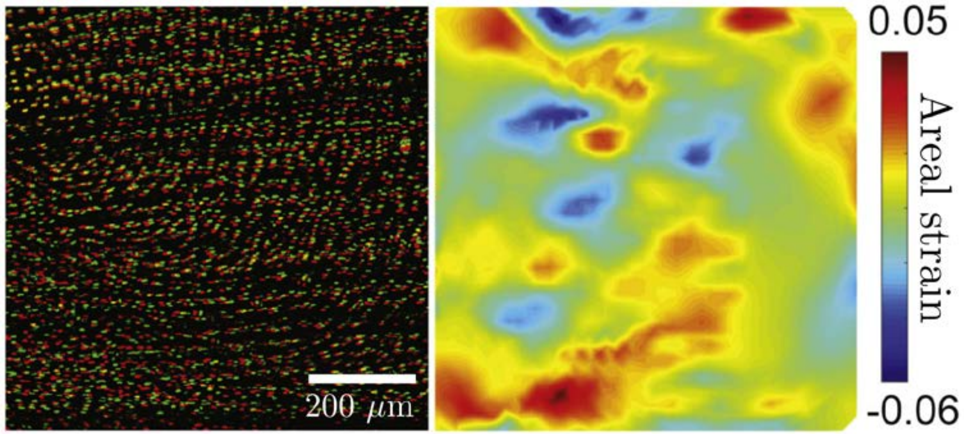
3D deformations? Fluid flow?

Actomyosin threads extracted from muscle



Szent-Gyorgi 1942

In-vivo



Ghosh et al., Cell reports 2019

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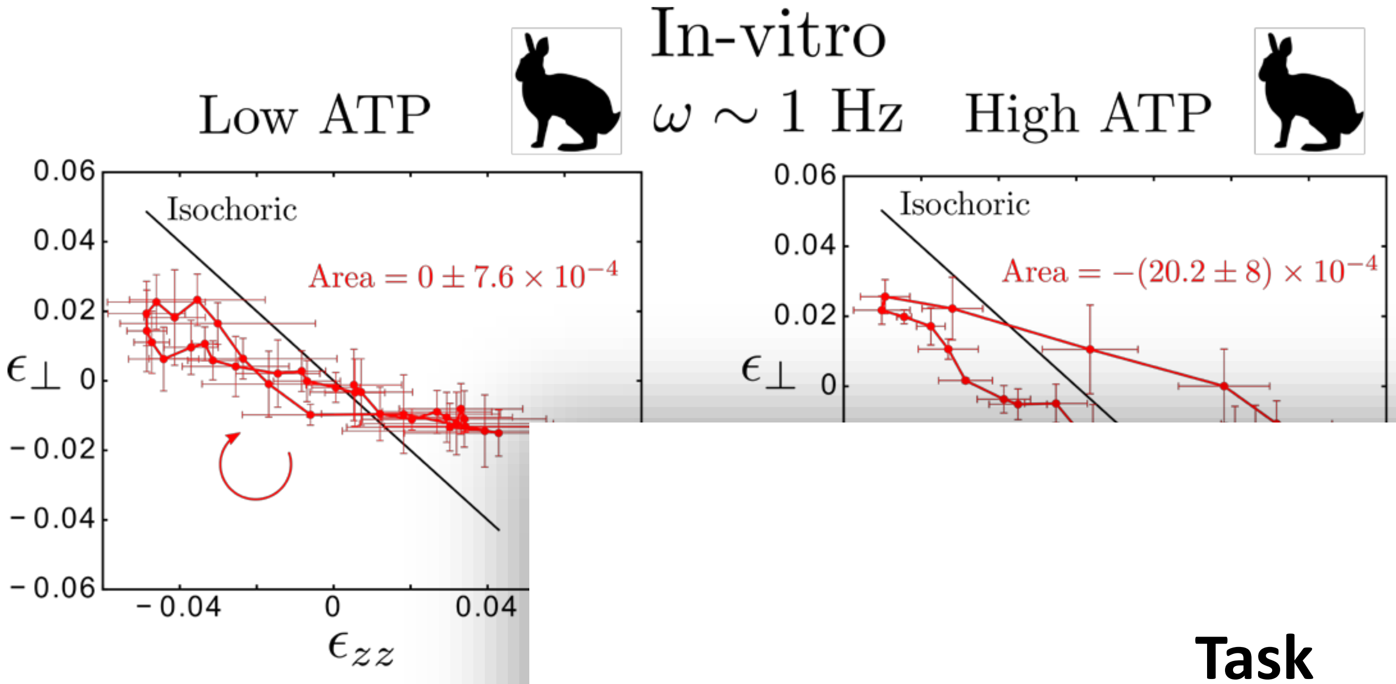
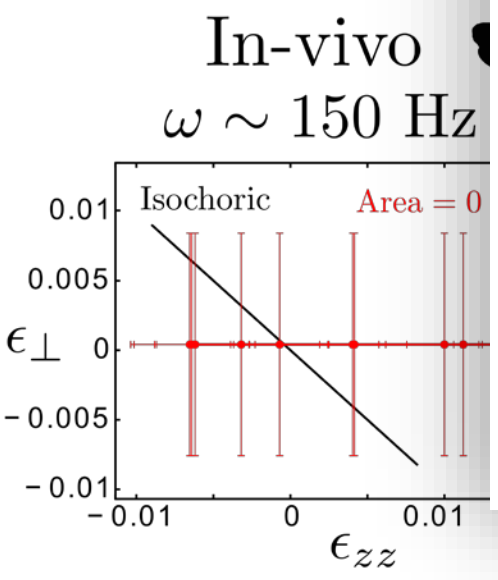
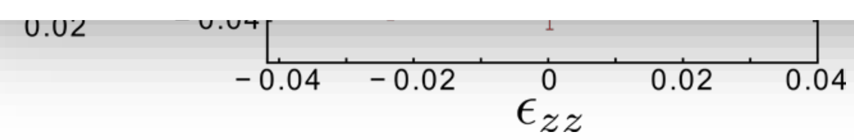
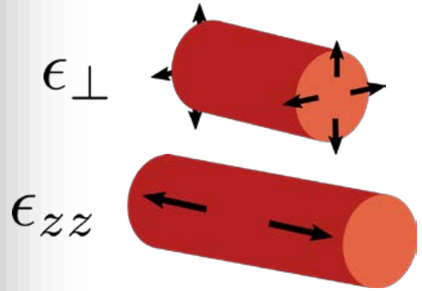
Quantitative evidence?

Spontaneous oscillations across muscle types and species









Task

Build a **multiscale spatial** model of muscle as an **active sponge**!

…t constant

…n form cycles

Data: Kono et al., 2020; Washio et al., 2019; Dickinson et al., 2005; Cass et al., 2021

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Fiber mechanics & hydraulics

Poroelastic model

cf Biot 1941

Force balance

$$\nabla \cdot \left[\phi(\boldsymbol{\sigma}^{el} \qquad) - (1-\phi)p\mathbf{1}\right] = \mathbf{0}$$

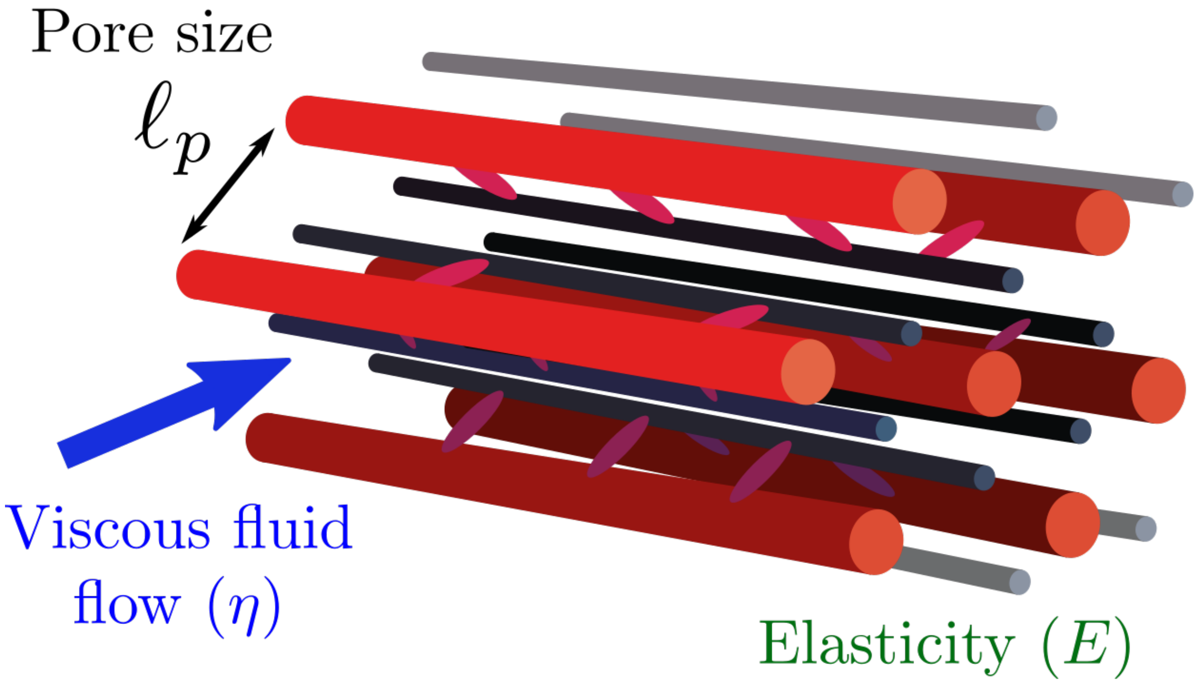
Fluid permeation

$$(1-\phi)(\mathbf{v} - \partial_t \mathbf{u}) = -\frac{\ell_p^2}{\eta}\mathbf{K} \cdot \nabla p$$

Incompressibility

$$\nabla \cdot [\phi \partial_t \mathbf{u} + (1-\phi)\mathbf{v}] = 0$$

Pressure diffuses! $\tau_p \sim \frac{\eta}{E}\left(L/\ell_p\right)^2$



Fiber mechanics & hydraulics

Active Poroelastic model

cf Biot 1941

Force balance

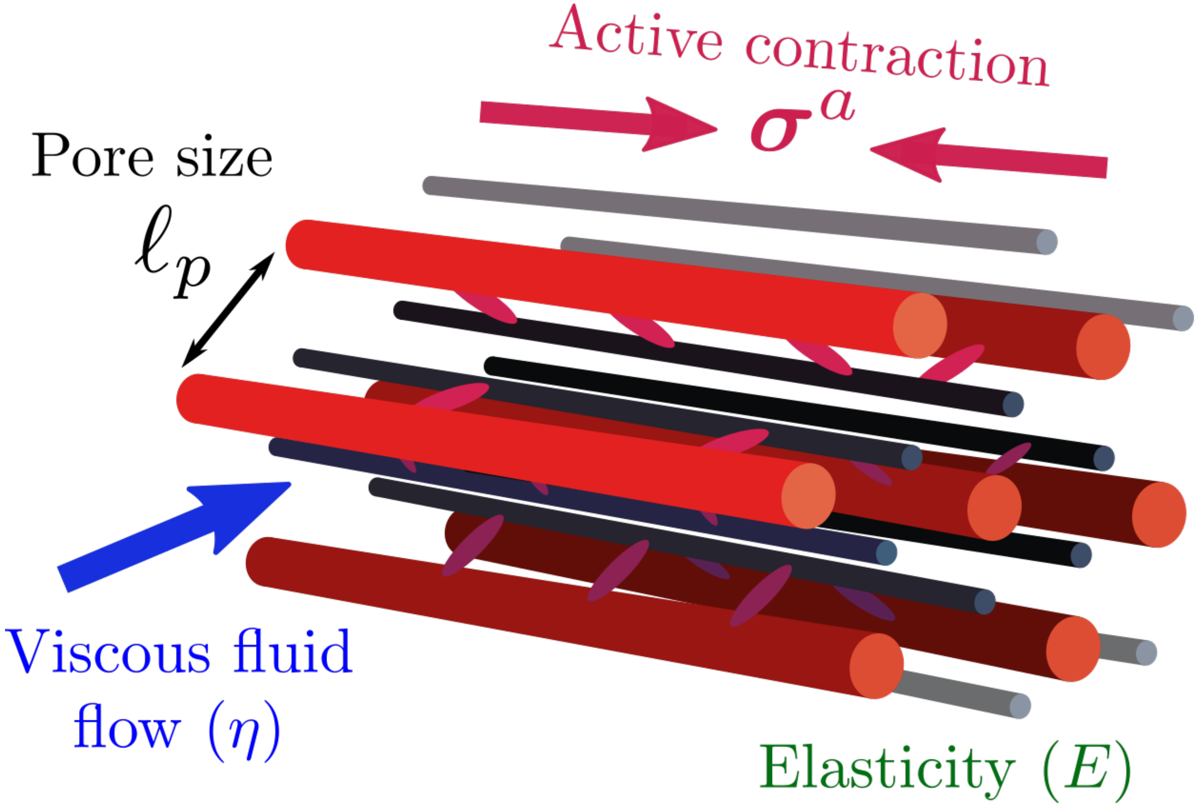
$$\boldsymbol{\nabla} \cdot \left[\phi(\boldsymbol{\sigma}^{el} + \boldsymbol{\sigma}^{a}) - (1-\phi)p\mathbf{1}\right] = \mathbf{0}$$

Fluid permeation

$$(1-\phi)(\mathbf{v} - \partial_t \mathbf{u}) = -\frac{\ell_p^2}{\eta}\mathbf{K} \cdot \boldsymbol{\nabla} p$$

Incompressibility

$$\boldsymbol{\nabla} \cdot [\phi \partial_t \mathbf{u} + (1-\phi)\mathbf{v}] = 0$$



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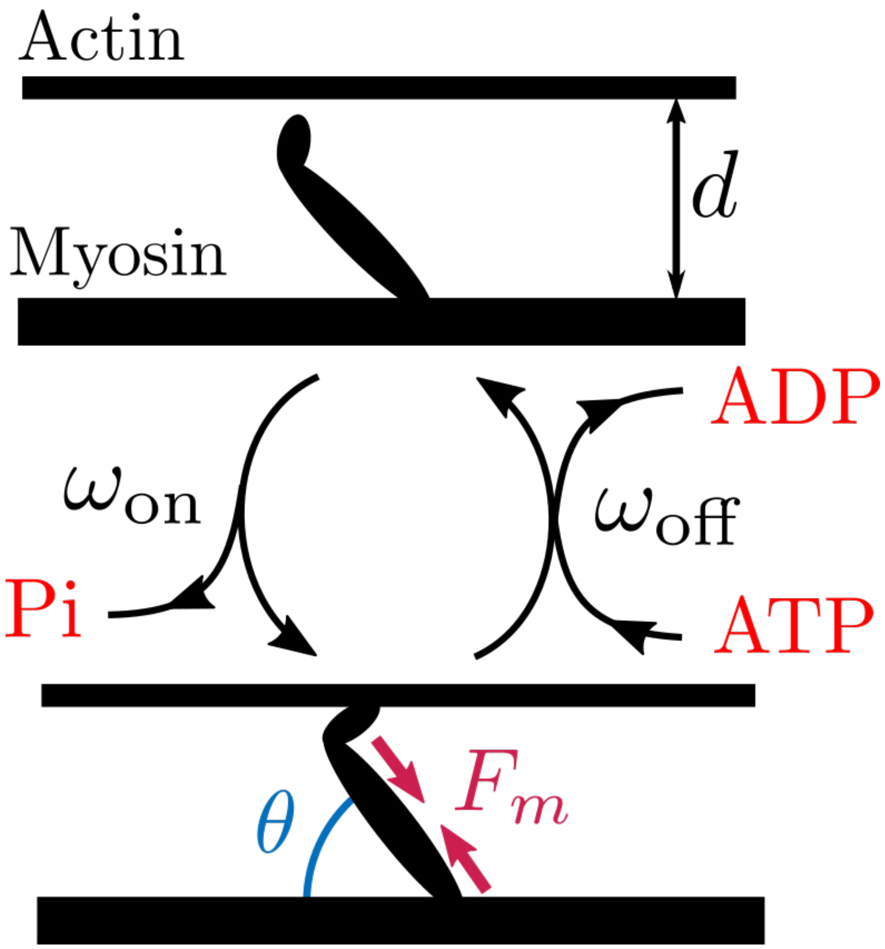
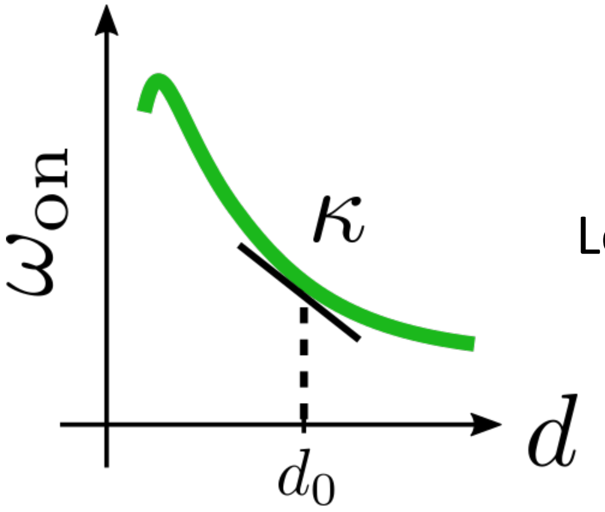
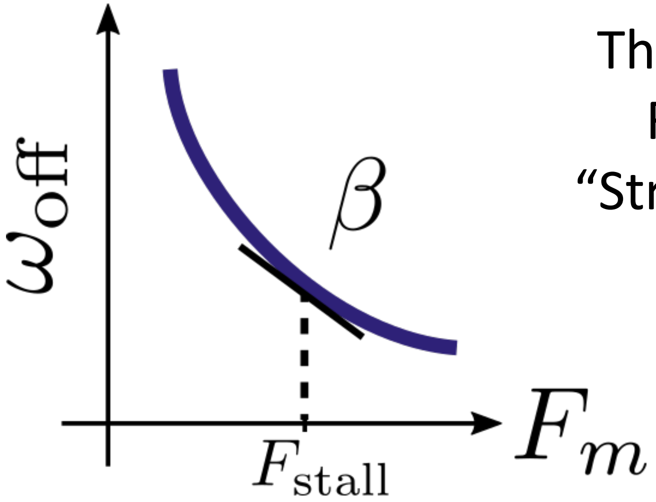
Molecular basis of contraction

Minimal model of actomyosin kinetics with biophysical feedback





Geometric -
Length/size sensing



Thermodynamic -
Force sensing
"Stretch activation"

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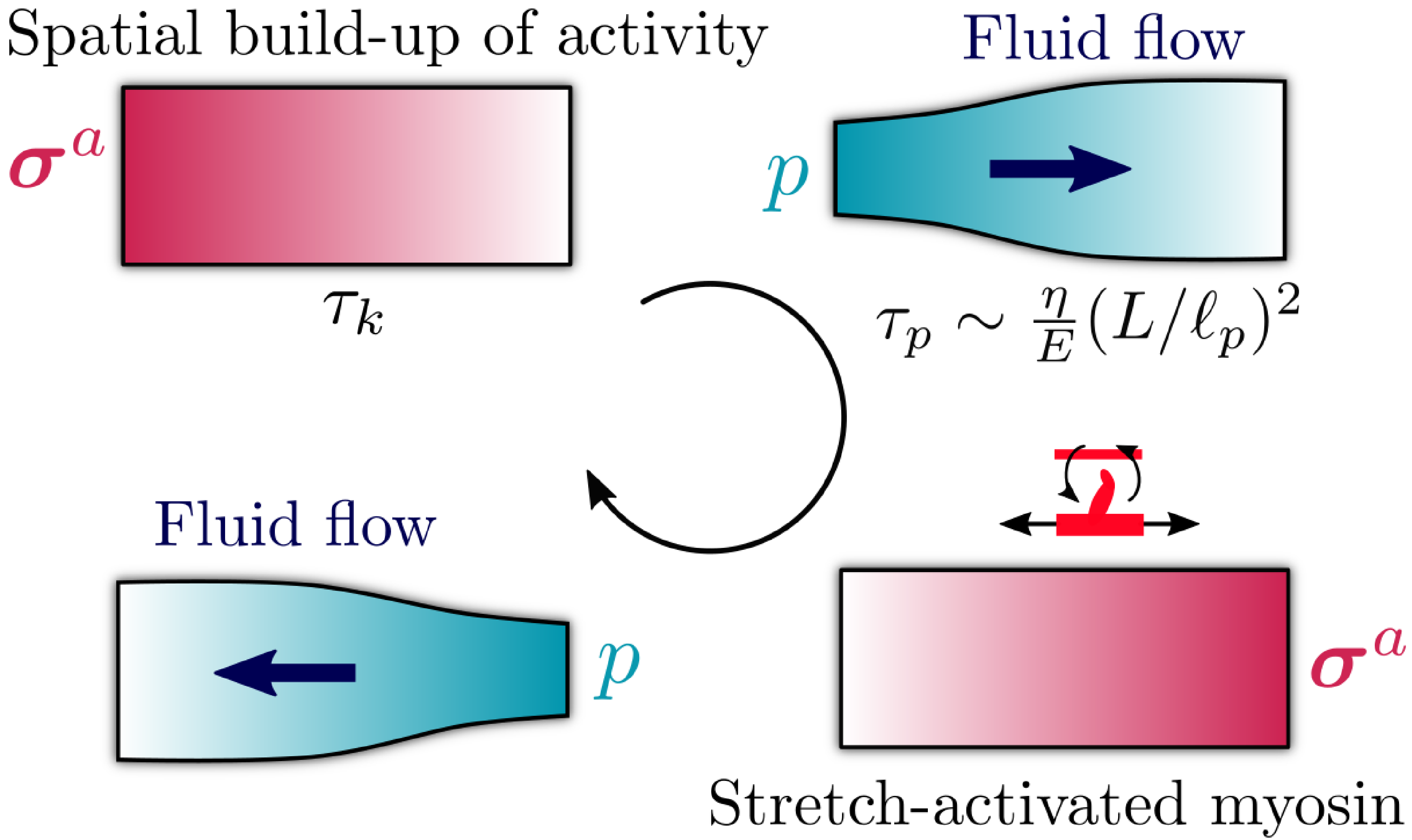
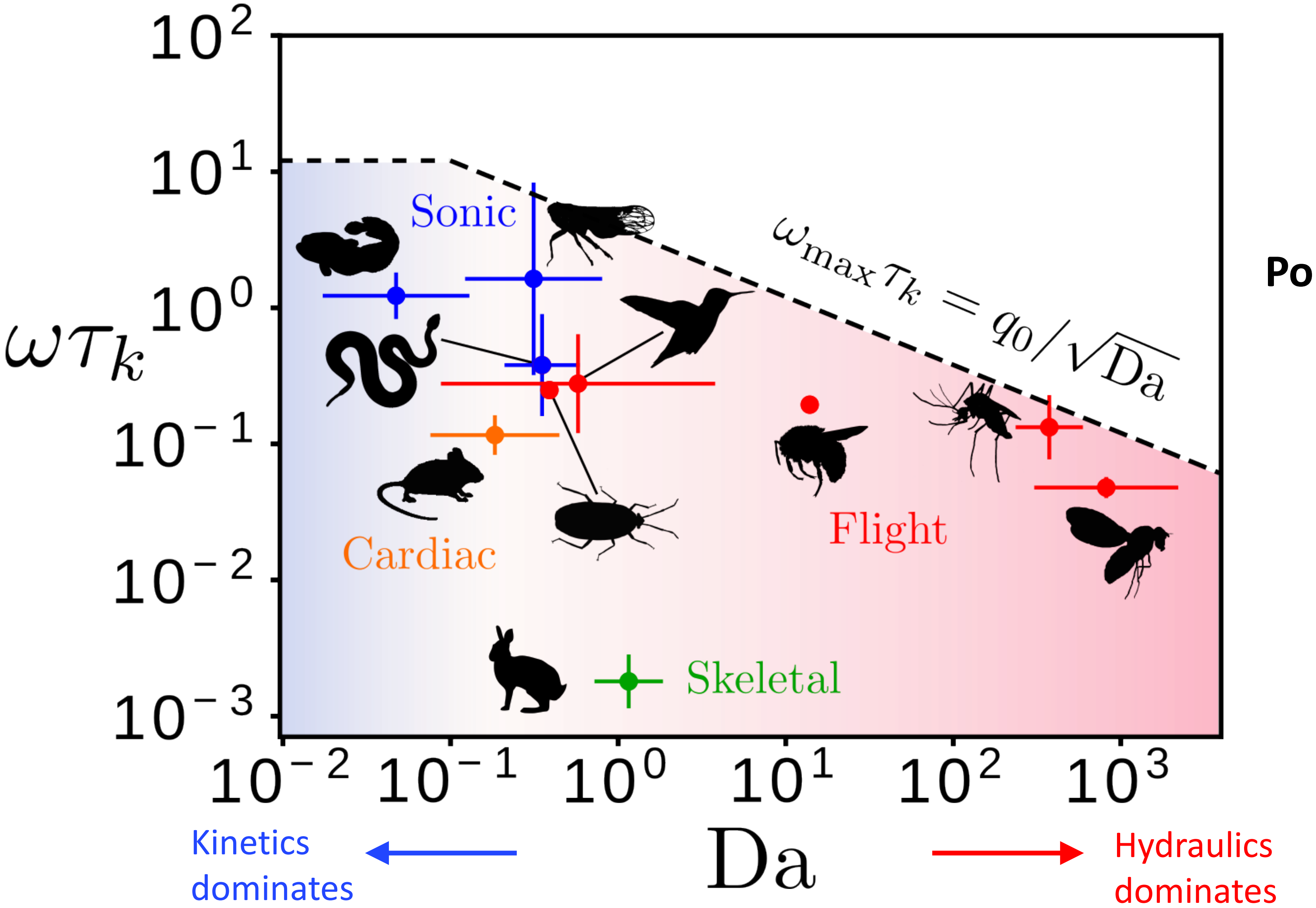
Dynamics: Active hydraulic oscillations



Oscillations compromise between the molecular and hydraulic time scales

$$\omega \sim \frac{1}{\sqrt{\tau_k \tau_p}}$$

Physiological relevance?



Poroelastic Damkohler number

$$Da = \frac{\tau_p}{\tau_k}$$

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Mechanics: Nonreciprocal active response

Linear elastic response

$$\sigma_{ij} = \mathcal{A}_{ijk\ell}\epsilon_{k\ell}$$

Maxwell-Betti reciprocity

Energy conservation: $$\mathcal{A}_{ijk\ell} = \mathcal{A}_{k\ell ij}$$

Biot 1939;
Truesdell 1963

Mechanics: Nonreciprocal active response

Linear ela

$\sigma_{ij} =$

Isotropic

Shear

Biot 1939;
Truesdell 1963

oner et al., 2020

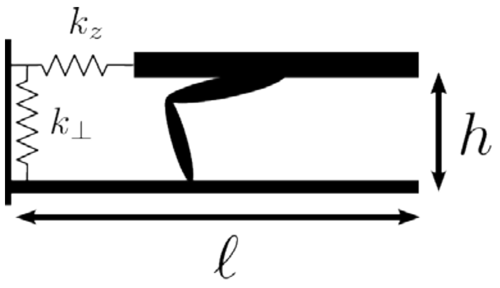
y present in
ds!

Zahalak 1996

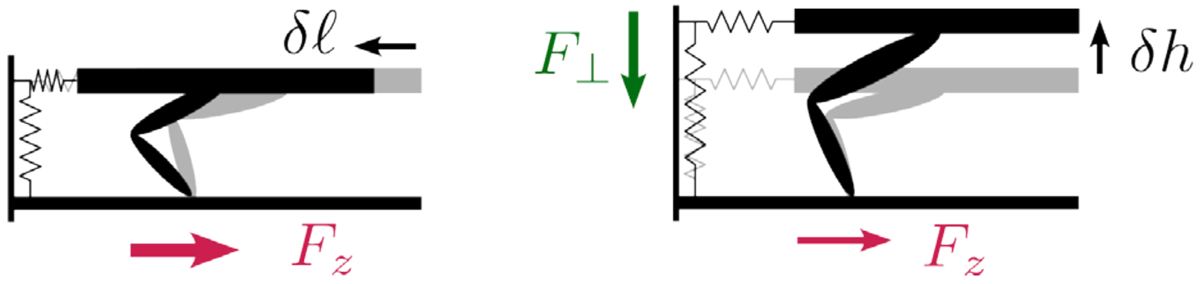
ss tensor does not
r elasticity theory:
$B_{ijpq} = B_{jipq}$, $B_{ijpq} = B_{ijqp}$, and $B_{ijpq} = B_{pqij}$.

Microscopic origin of odd elasticity?

Single crossbridge is nonreciprocal on average



$$\begin{pmatrix} F_z \\ F_\perp \end{pmatrix} = \begin{pmatrix} F_{\text{stall}} \\ 0 \end{pmatrix} + \begin{bmatrix} -k_z & -k_o \\ 0 & -k_\perp \end{bmatrix} \begin{pmatrix} \delta\ell \\ \delta h \end{pmatrix}$$



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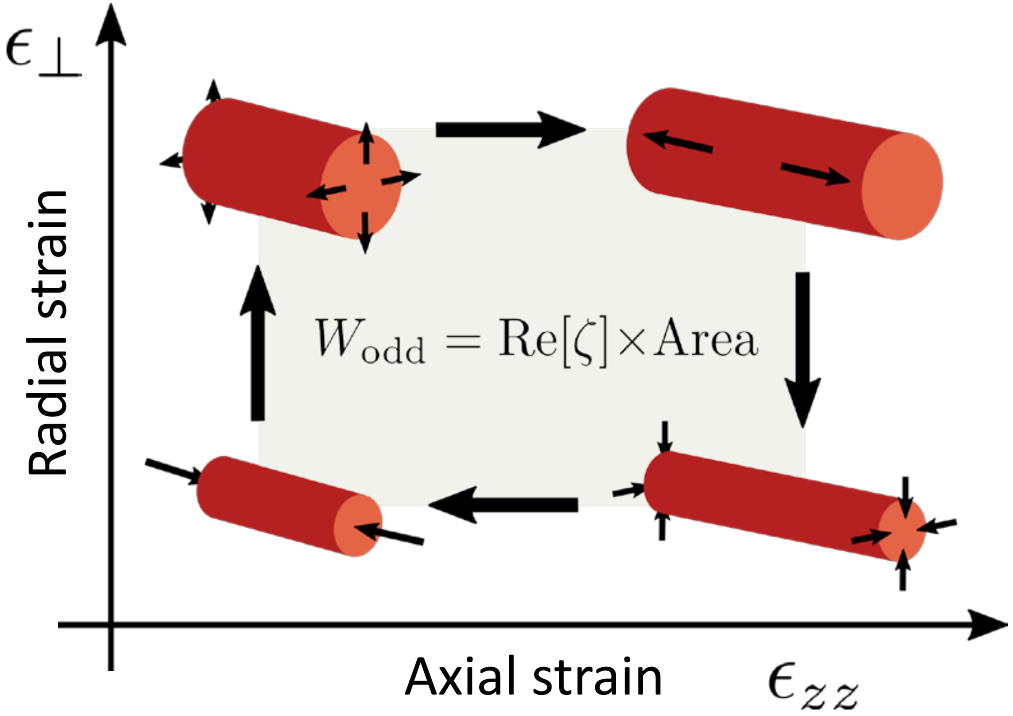
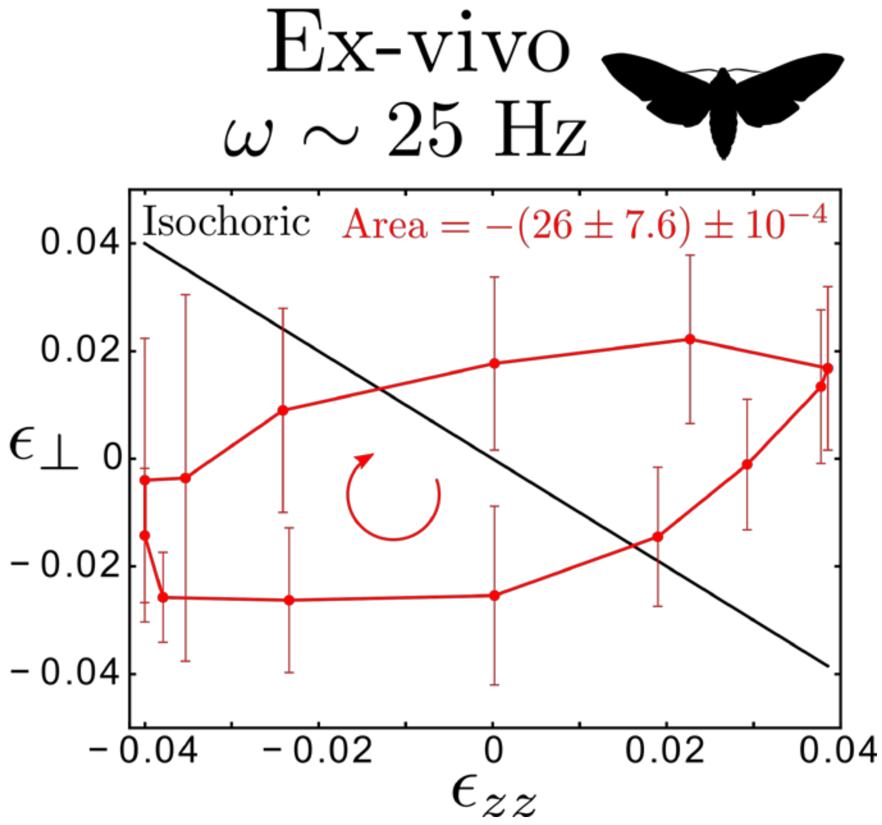
Energetics: Work from strain cycles

Nonreciprocal elasticity can generate work!



Cass et al., Biophys J. 2021



Physiologically relevant?

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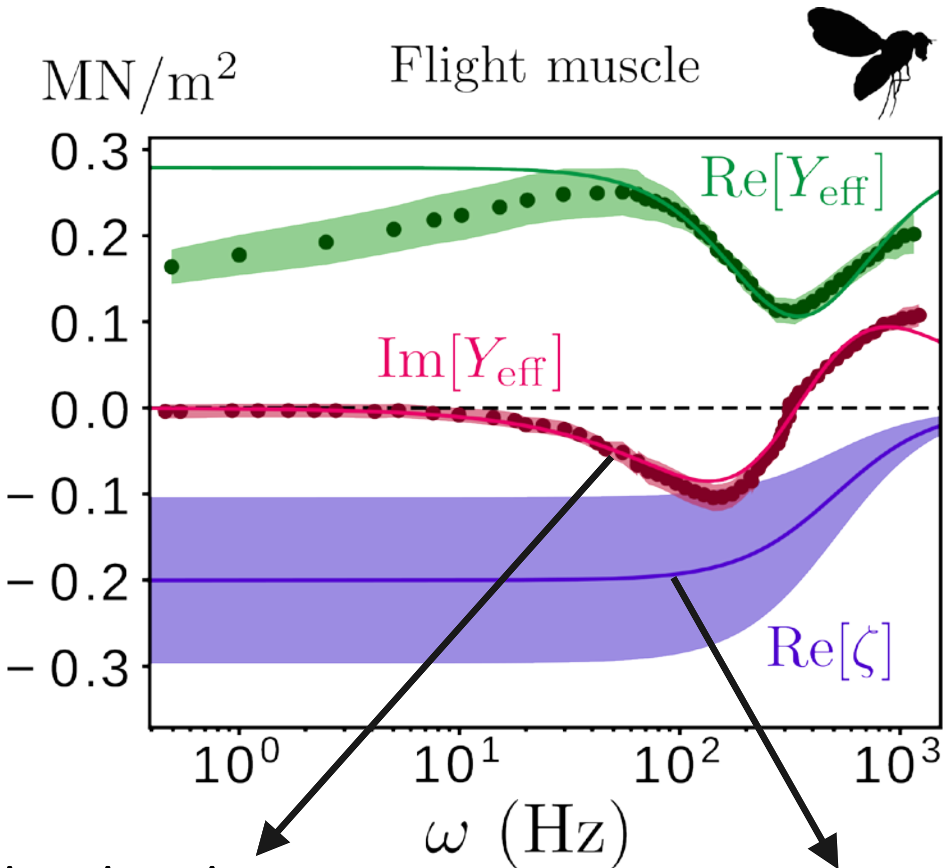
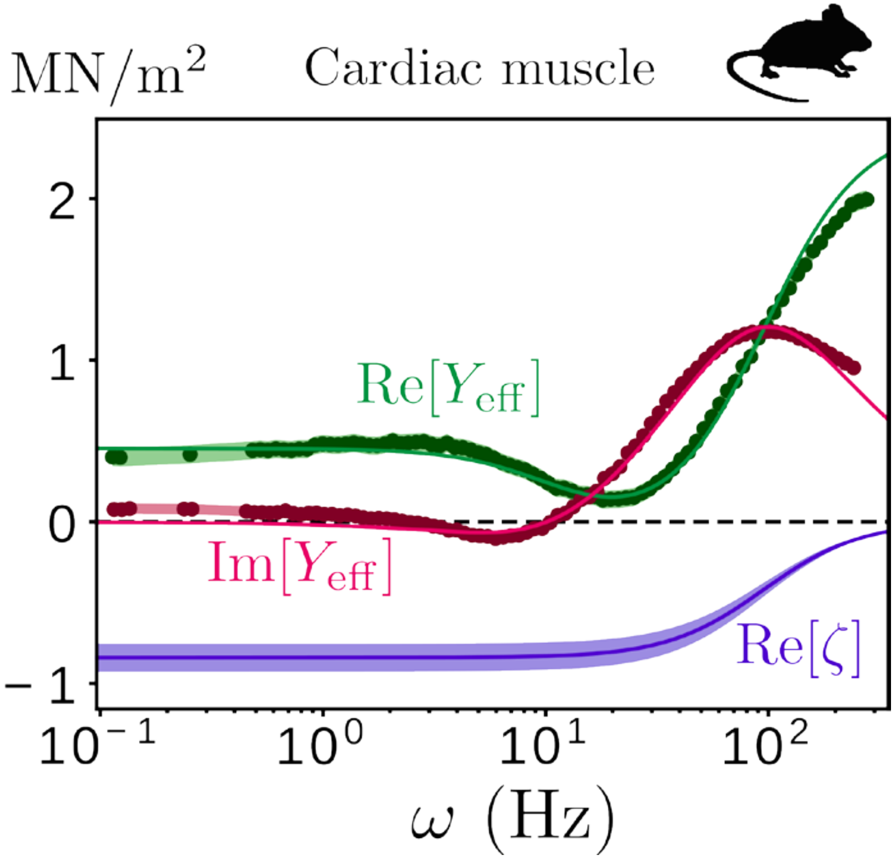
Muscular rheology in 1D

Oscillatory linear response of permeabilized muscle





Negative viscosity produces work from *strain rates*

Nonreciprocal **elasticity** produces work from *strain!*

Tanner et al., Biophys J. 2012; Palmer et al., Biophys J. 2007

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Machina carnis: more mush than machine

Active muscular hydraulics, **SS**, Mahadevan, bioRxiv:2022.02.20.481216, 2022

L. Mahadevan

- Muscle behaves as an active hydraulic engine with nonreciprocal mechanics - multiscale origins of soft hydraulic power are key to understand animal behavior/motion.
- Task/rate based trade-off between spatial and temporal modes of power generation?
- Evolutionary consequences across muscle types and phylogeny? Hydraulic limits to powering locomotion and behaviour?
- Similar effects in other soft, active tissues? Rapid movements in ciliates, sponges, other basal organisms etc.?
- Effects of external loading (environment) and neural signalling (control)?

Thank you!