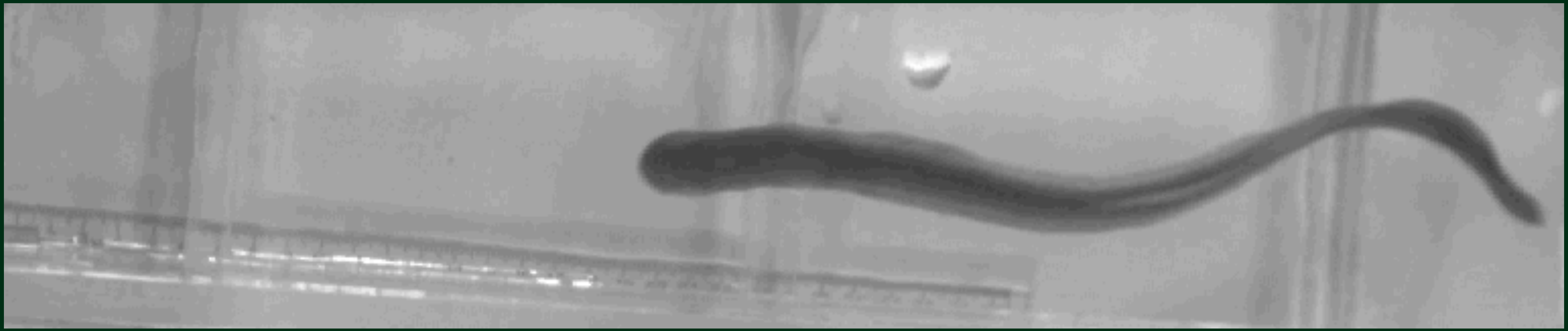
Computational modeling of a swimming lamprey driven by a central pattern generator with sensory feedback



Christina Hamlet[1], Eric Tytell[2], Kathleen Hoffman[3], Lisa Fauci[1]

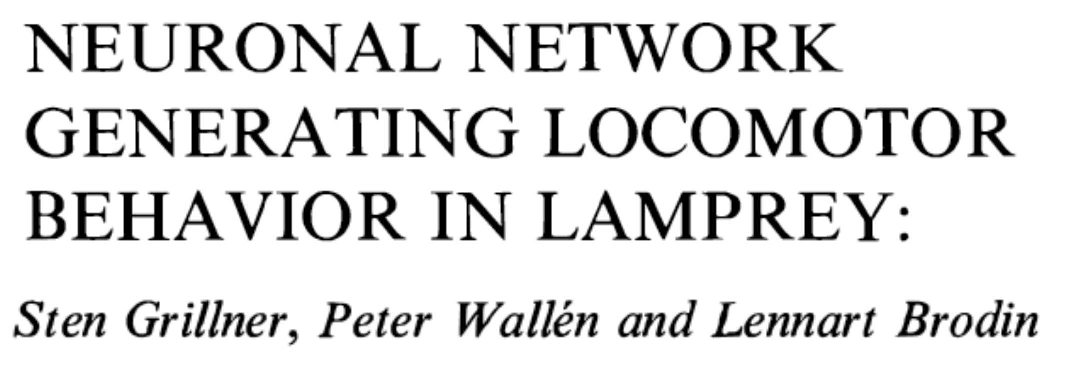
[1]Tulane University,[2]Tufts University,[3]UMBC

Outline

- Why study lampreys?
- Goals of the lamprey project
- Construction of an integrative, multi-scale model
- Neural activation
- Sensory feedback
- Results
- Current and future directions

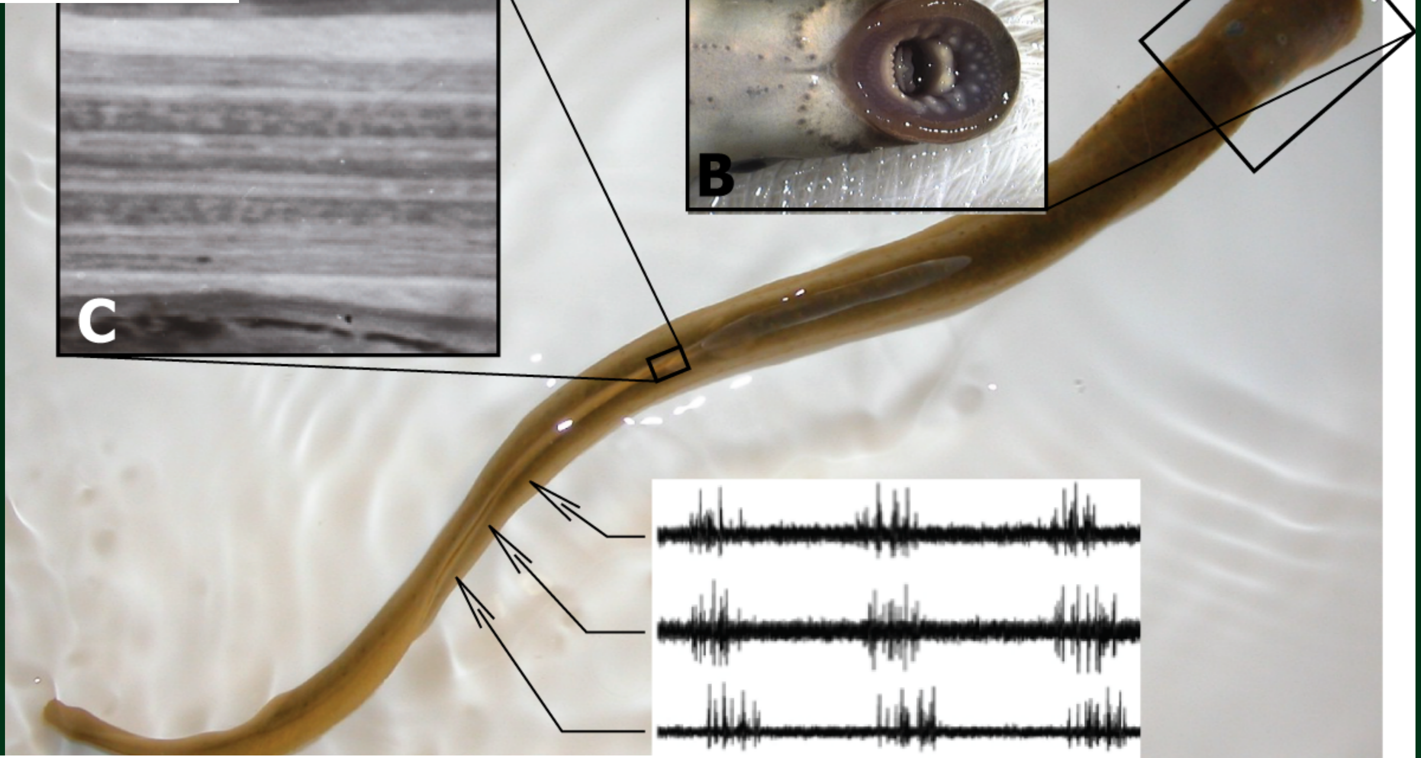
Image: www.redorbit.com

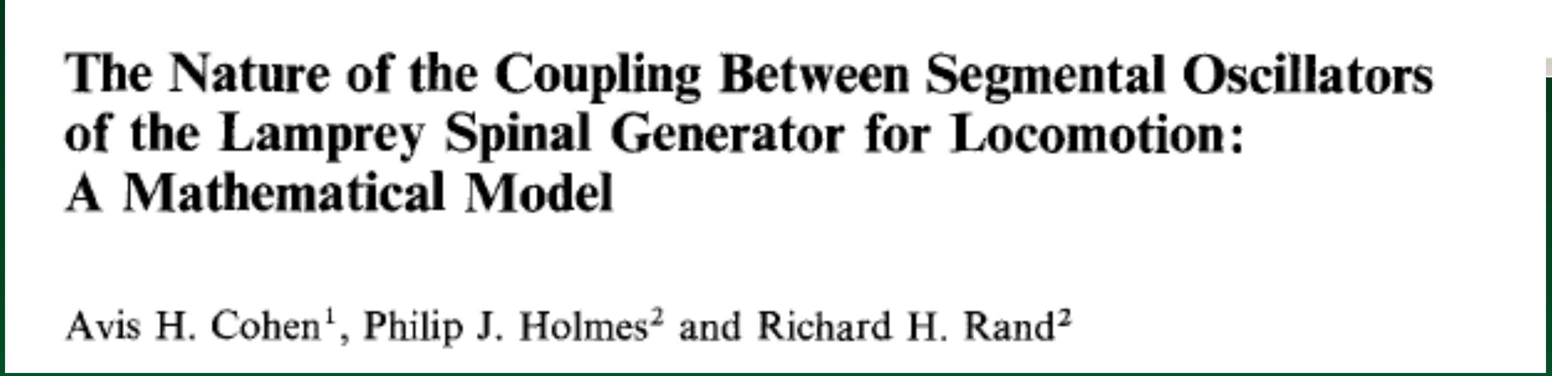
Lampreys are model organisms for swimming and neurophysiology



NEURONAL NETWORK GENERATING LOCOMOTOR BEHAVIOR IN LAMPREY:

Sten Grillner, Peter Wallén and Lennart Brodin



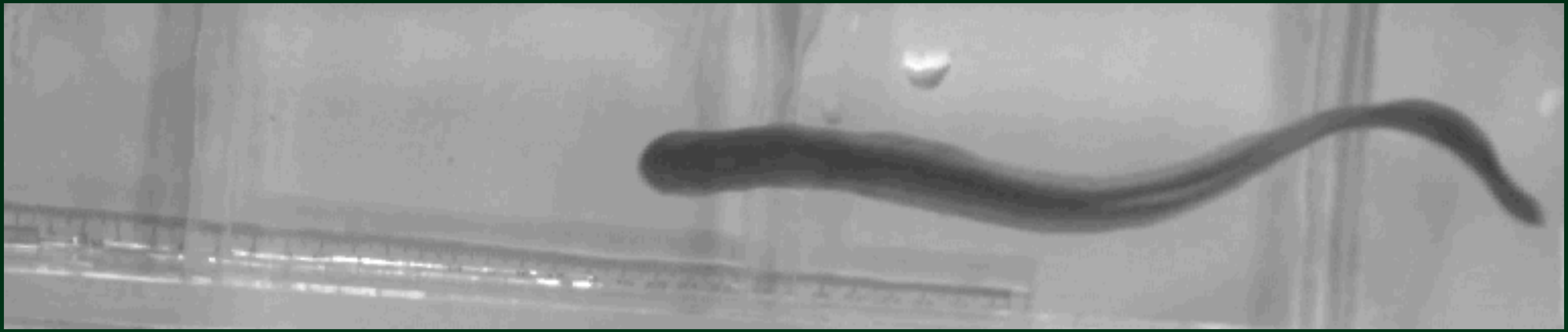


The Nature of the Coupling Between Segmental Oscillators of the Lamprey Spinal Generator for Locomotion: A Mathematical Model

Avis H. Cohen[1], Philip J. Holmes[2] and Richard H. Rand[2]

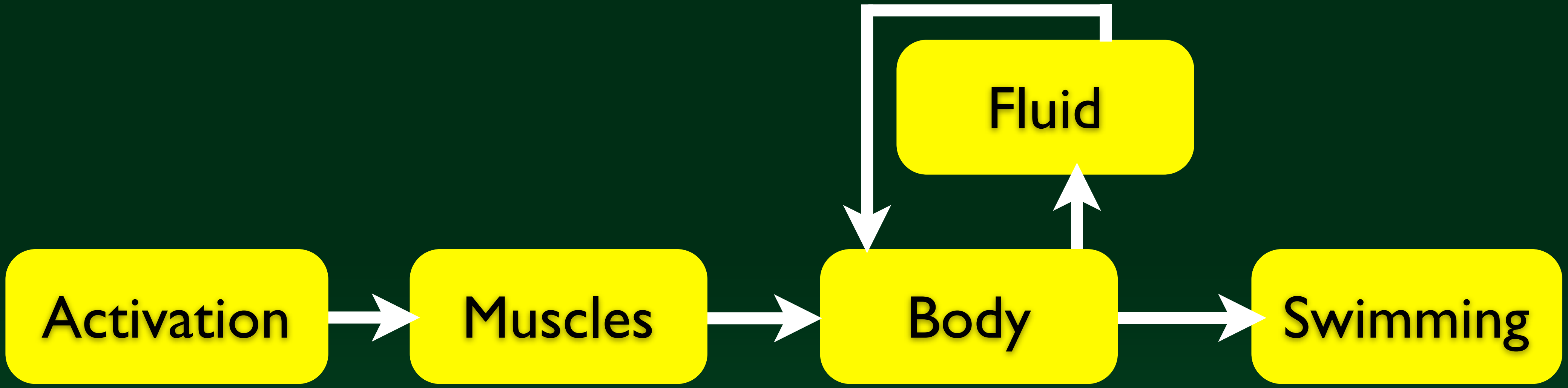
Lamprey swimming mode is a traveling wave

- Anguilliform (eel-like) swimming
- Passes waves of activation down the body to contract muscles and produce traveling curvature wave



Courtesy: E. Tytell (Tufts) and M. Leftwich (GWU)

Swimming behavior emergent from interacting systems



Fluid

Activation

Muscles

Body

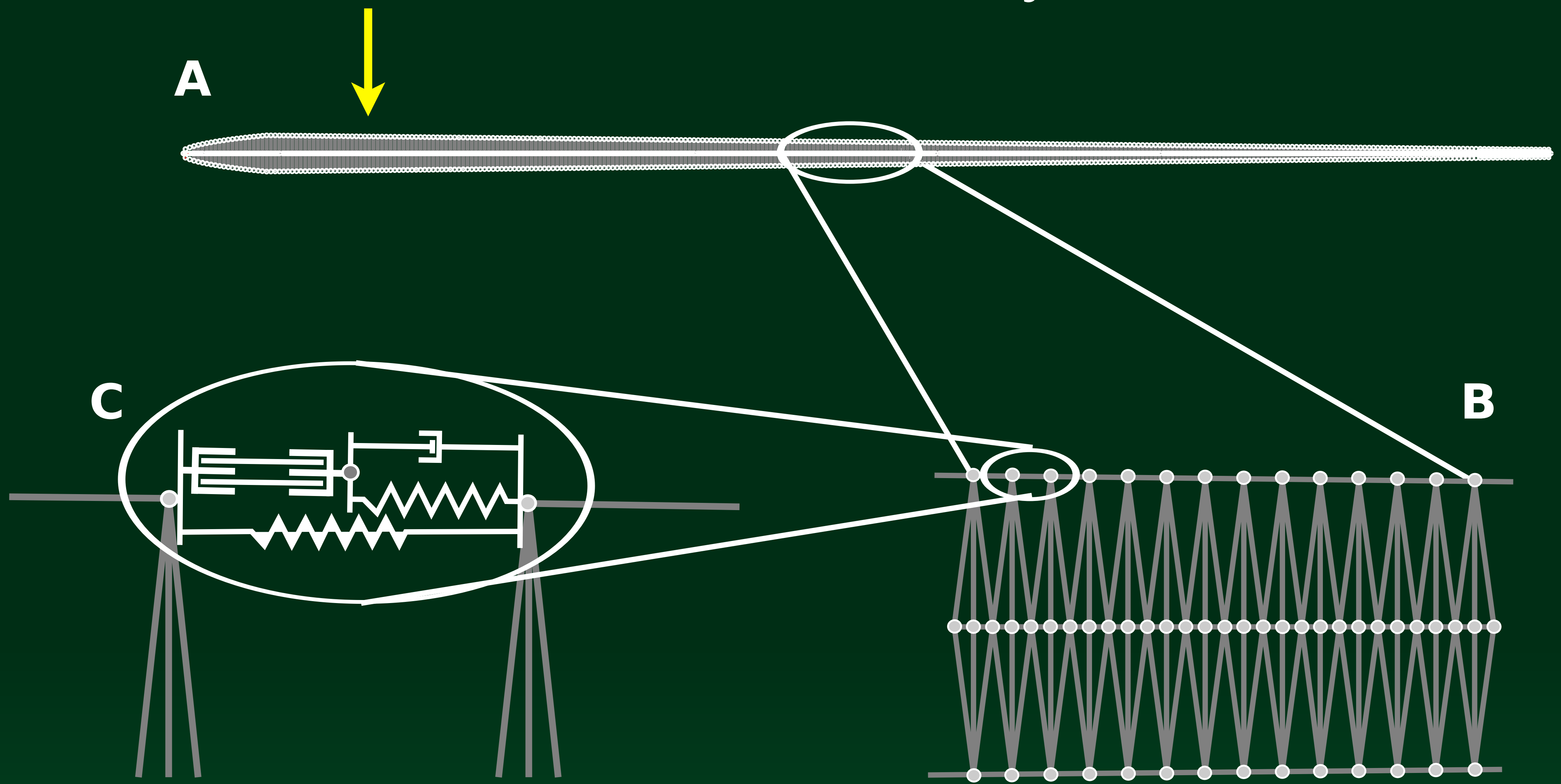
Swimming

Collaborators

Avis Cohen	University of Maryland, Biology
Eric Tytell	Tufts University, Biology
Chia-yu Hsu	National Taiwan University
Boyce Griffith	UNC Chapel Hill, CCIAM
Lisa Fauci	Tulane University, Center for Computational Science
Kathleen Hoffman	University of Maryland, B.C., Mathematics
Tim Kiemel	University of Maryland, Kinesiology
Thelma Williams	St. George’s Univ. of London, Basic Medical Sciences
Phillip Holmes	Princeton University, Mathematics
Lex Smits	Princeton University, Mechanical Engr.
Megan Leftwich	George Washington University, Mechanical Engr.

Computational body

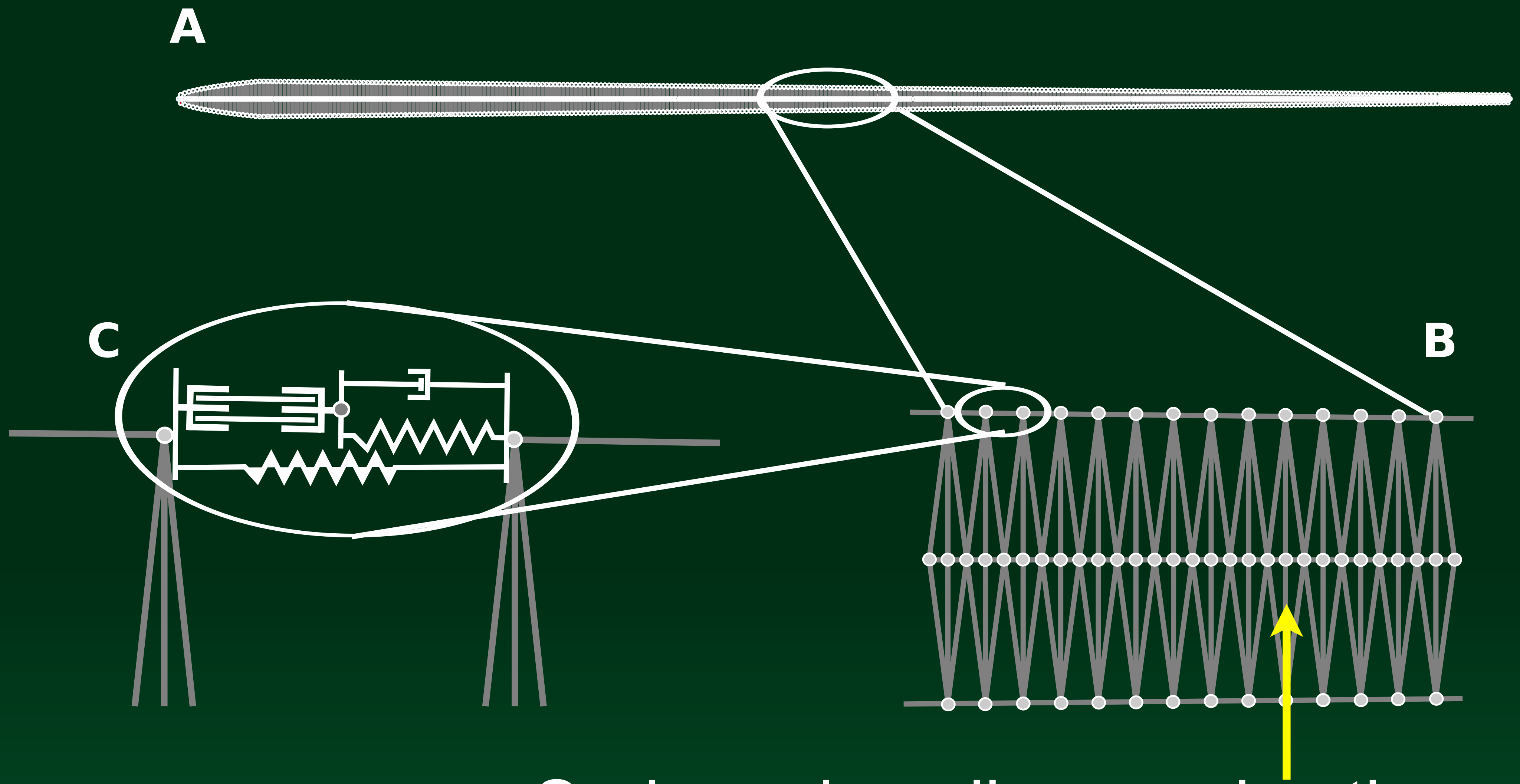
Points describe body



Hamlet, Fauci, Tytell, J.Theo. Bio 2015

Tytell, Hsu, William, Cohen, Fauci, PNAS 2011

Computational body

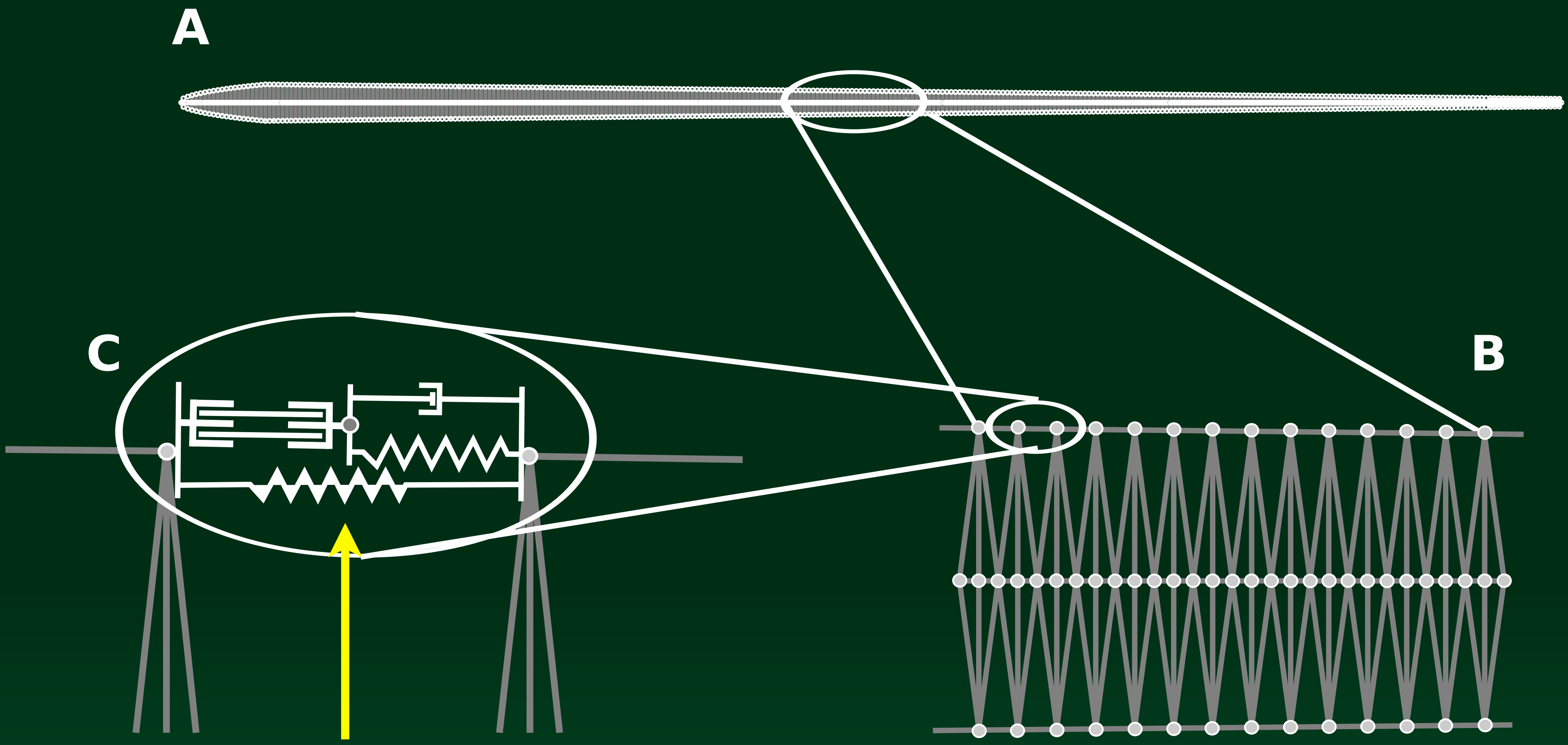


Springs describe passive tissues

Hamlet, Fauci, Tytell, J.Theo. Bio 2015

Tytell, Hsu, William, Cohen, Fauci, PNAS 2011

Computational body



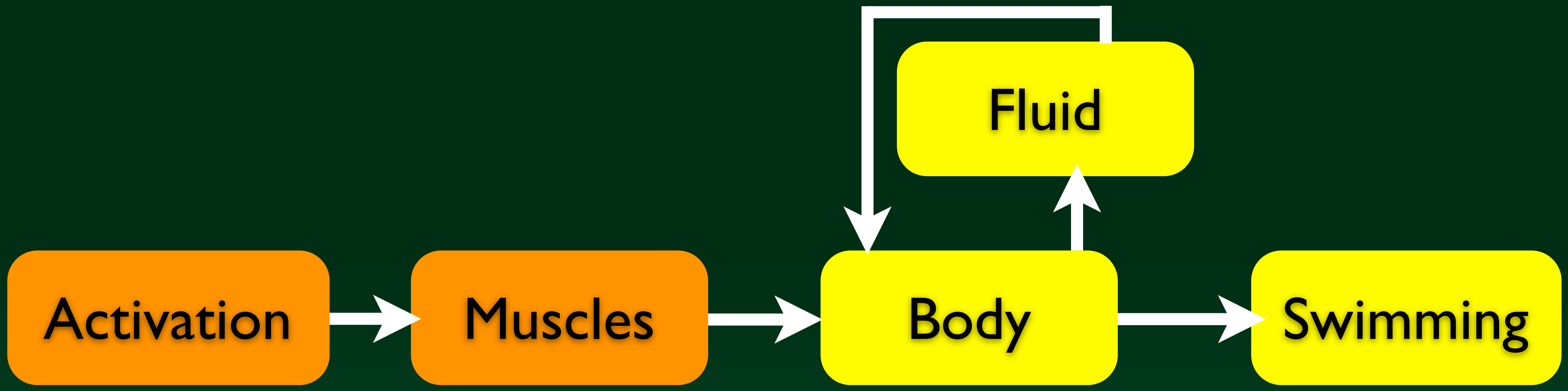
Muscle model inserted on lateral sides

Hamlet, Fauci, Tytell, J.Theo. Bio 2015

Tytell, Hsu, William, Cohen, Fauci, PNAS 2011

Connect signal to muscles

- Activation generates a signal to induce muscle contractions
  - Activation in the original model was a prescribed signal


Activation

Muscles

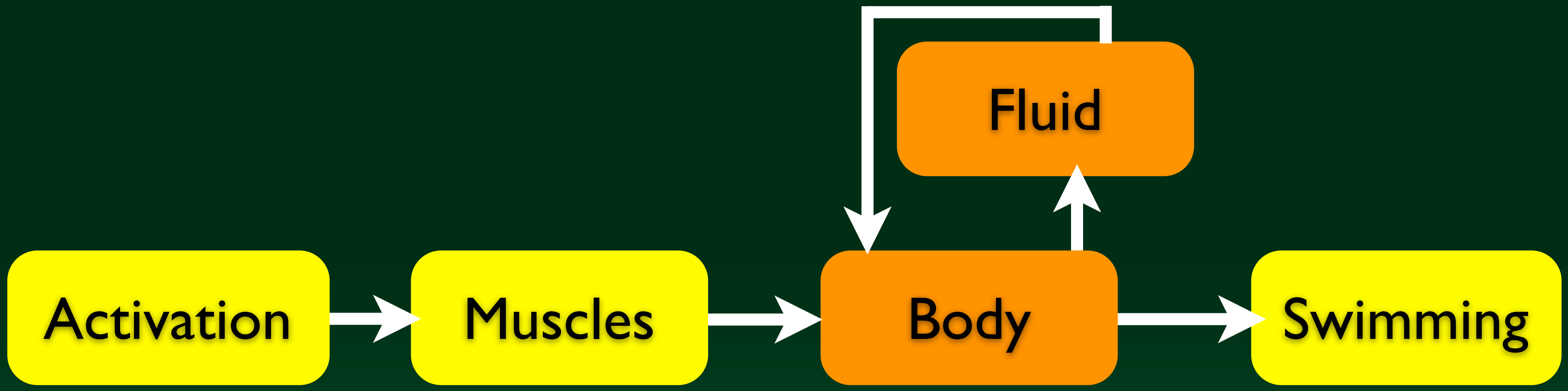
Body

Fluid

Swimming

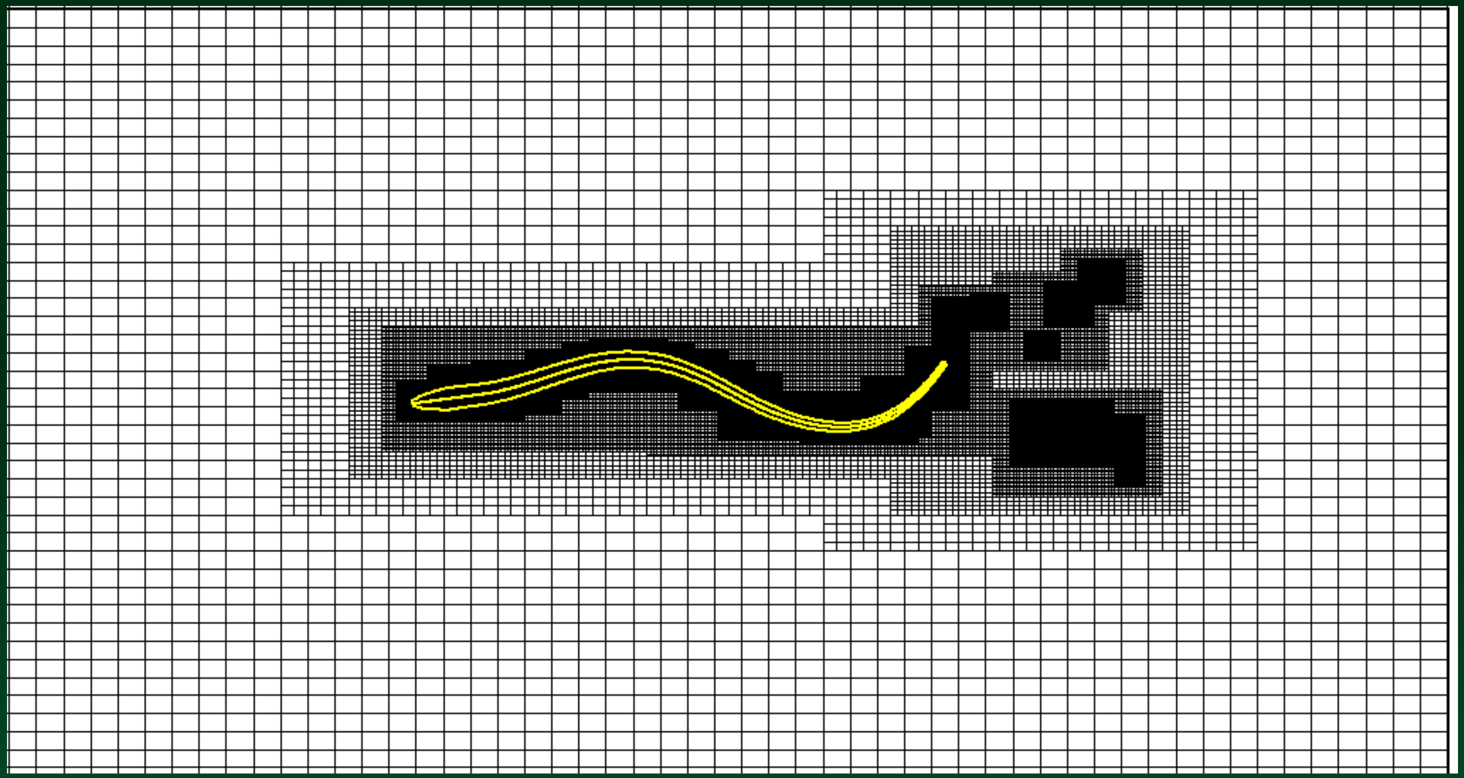
Numerically solve fluid structure interaction problem with immersed boundary method

- Couples structure to a full Navier-Stokes fluid model



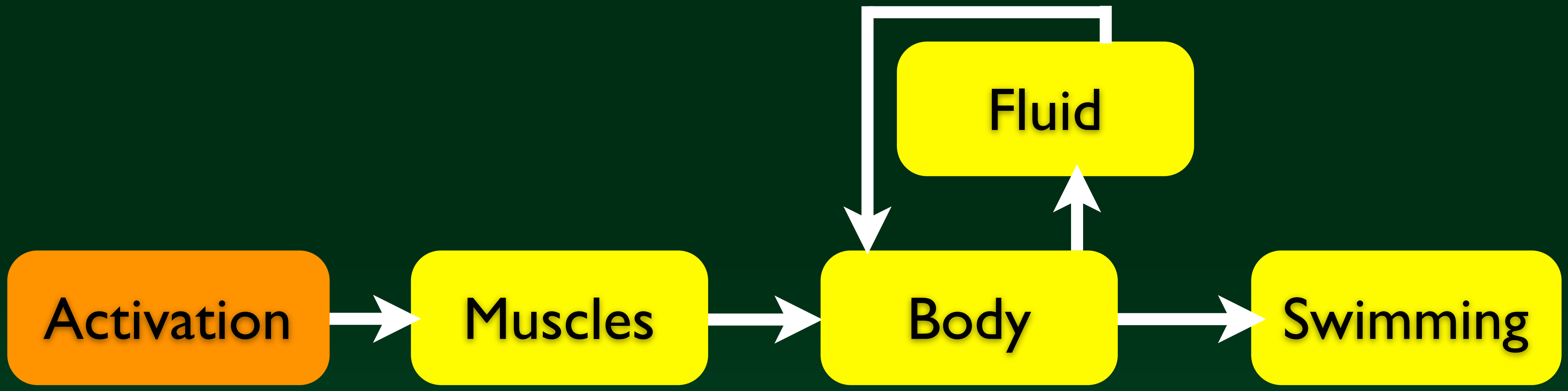
IBAMR

- Computationally intensive model, interface with IBAMR (Boyce Griffith, UNC)
- Adaptive mesh refinement - coarse grid most of the domain, finer grids near immersed points and higher vorticity regions



Activation wave drives system

- Generates a neural signal using a central pattern generators (CPG)



Fluid

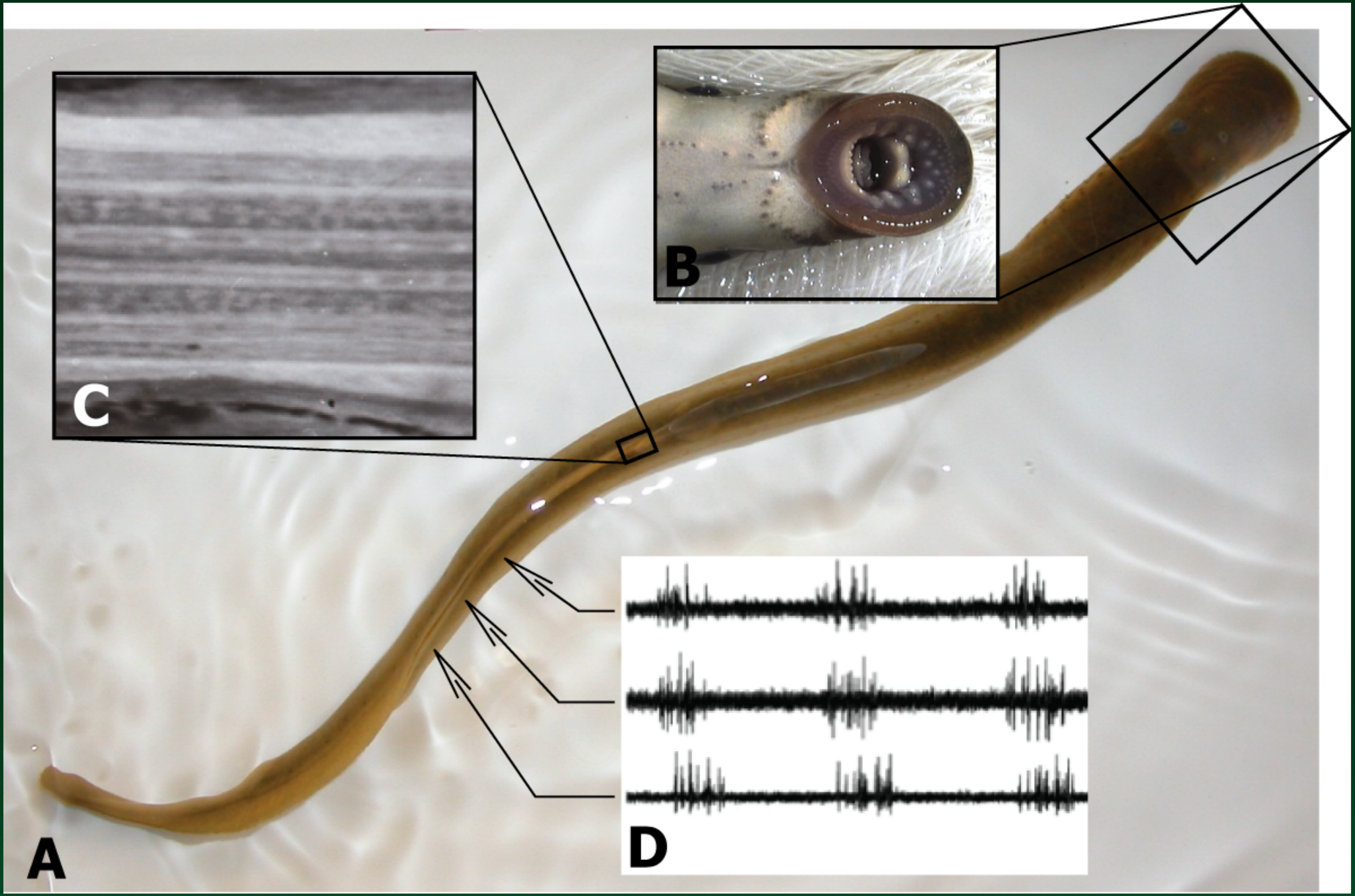
Activation

Muscles

Body

Swimming

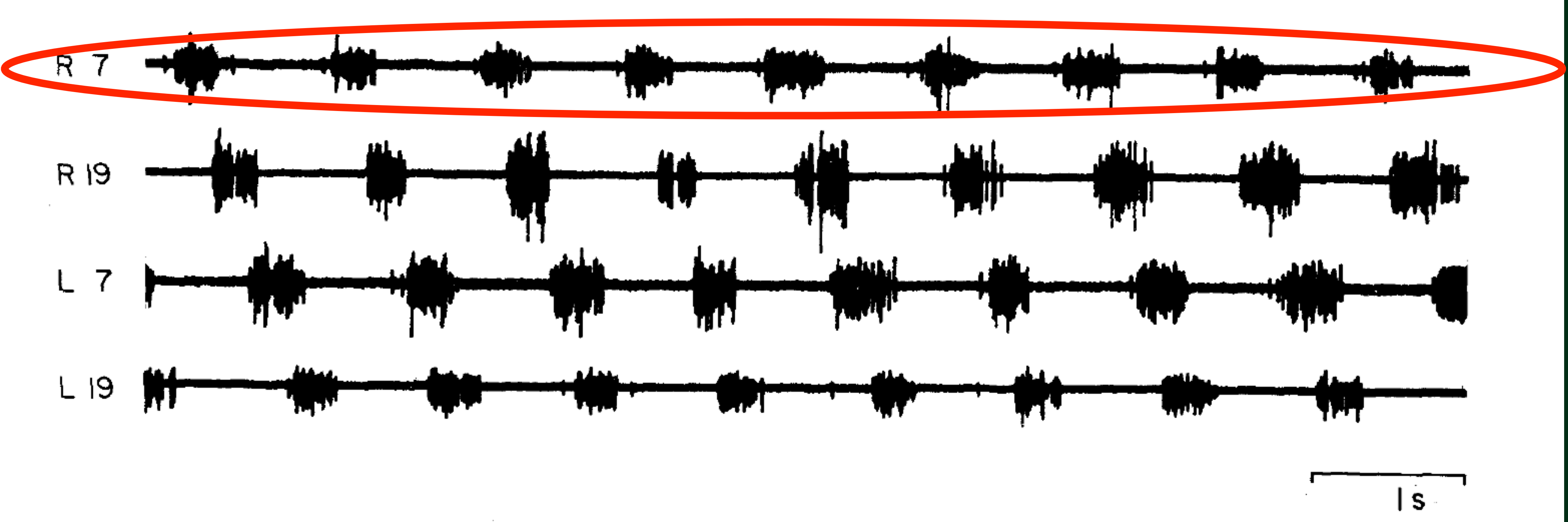
CPGs - neural networks produce rhythmic signal patterns along the body without sensory input



Neural signals at different segments on each side

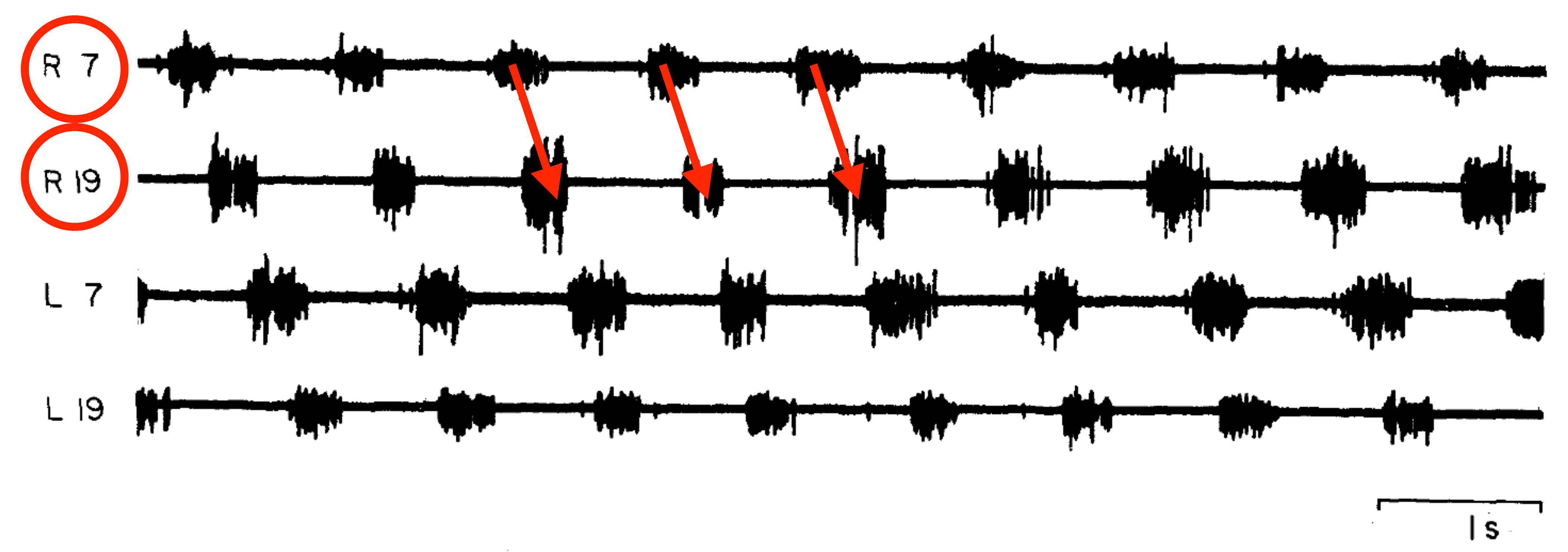
Cohen, Holmes, Rand, J. Math Biol. 1982

Each segment has a periodic bursting pattern



Cohen, Holmes, Rand, J. Math Biol. 1982

Phase lag from head to tail on each side

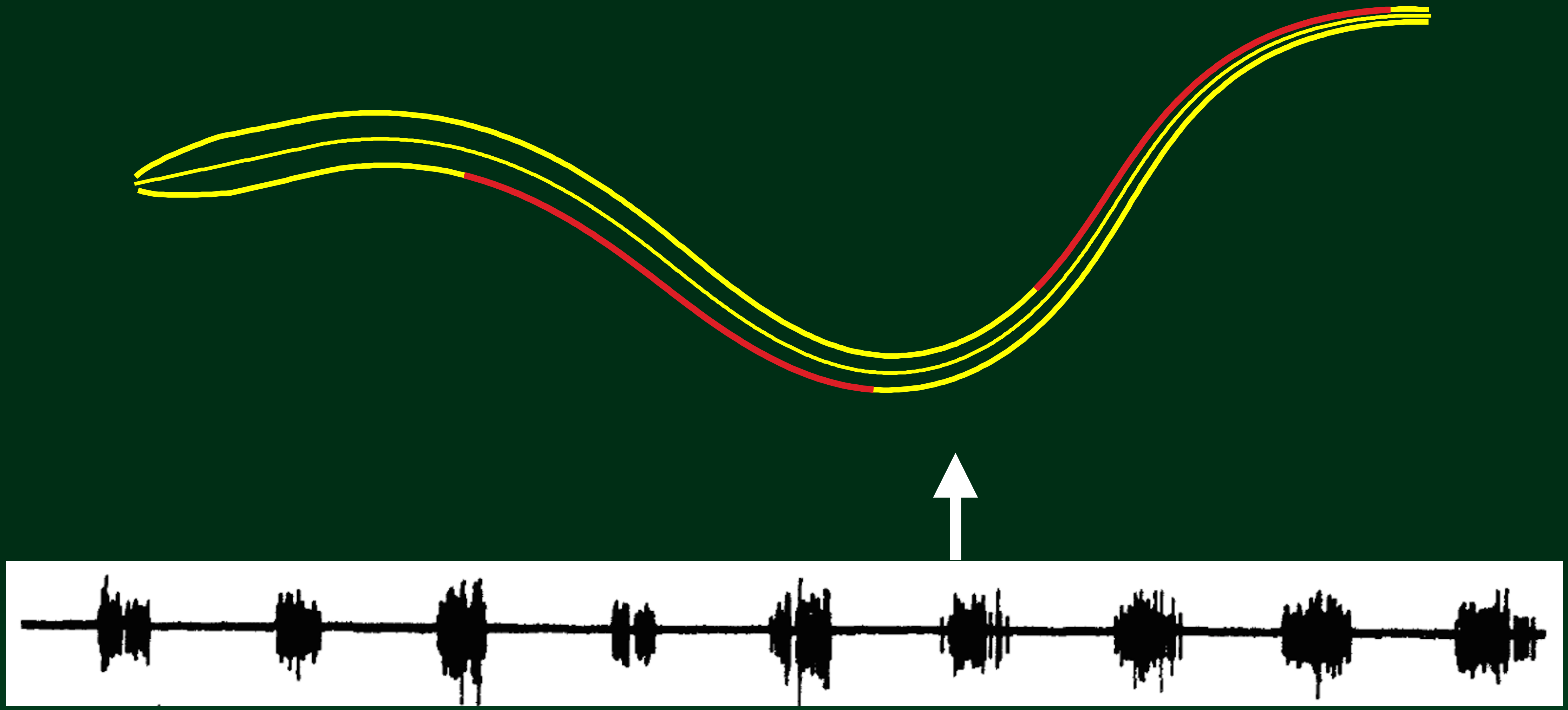


Cohen, Holmes, Rand, J. Math Biol. 1982

Signal on each side of a given segment in antiphase

Cohen, Holmes, Rand, J. Math Biol. 1982

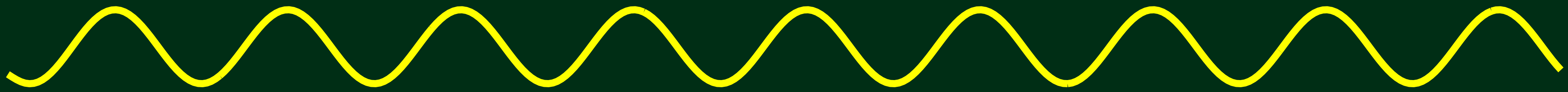
Modeling a CPG using oscillators



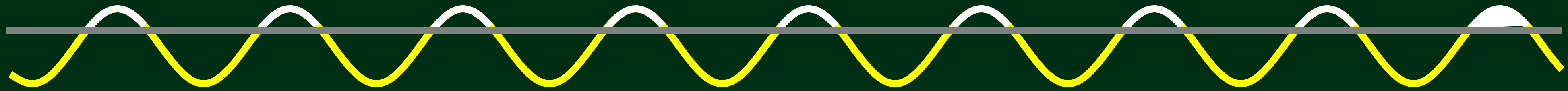
Cohen, Holmes, Rand, J. Math Biol. 1982

Periodic nature of CPG motivates modeling by an oscillator

Sample signal

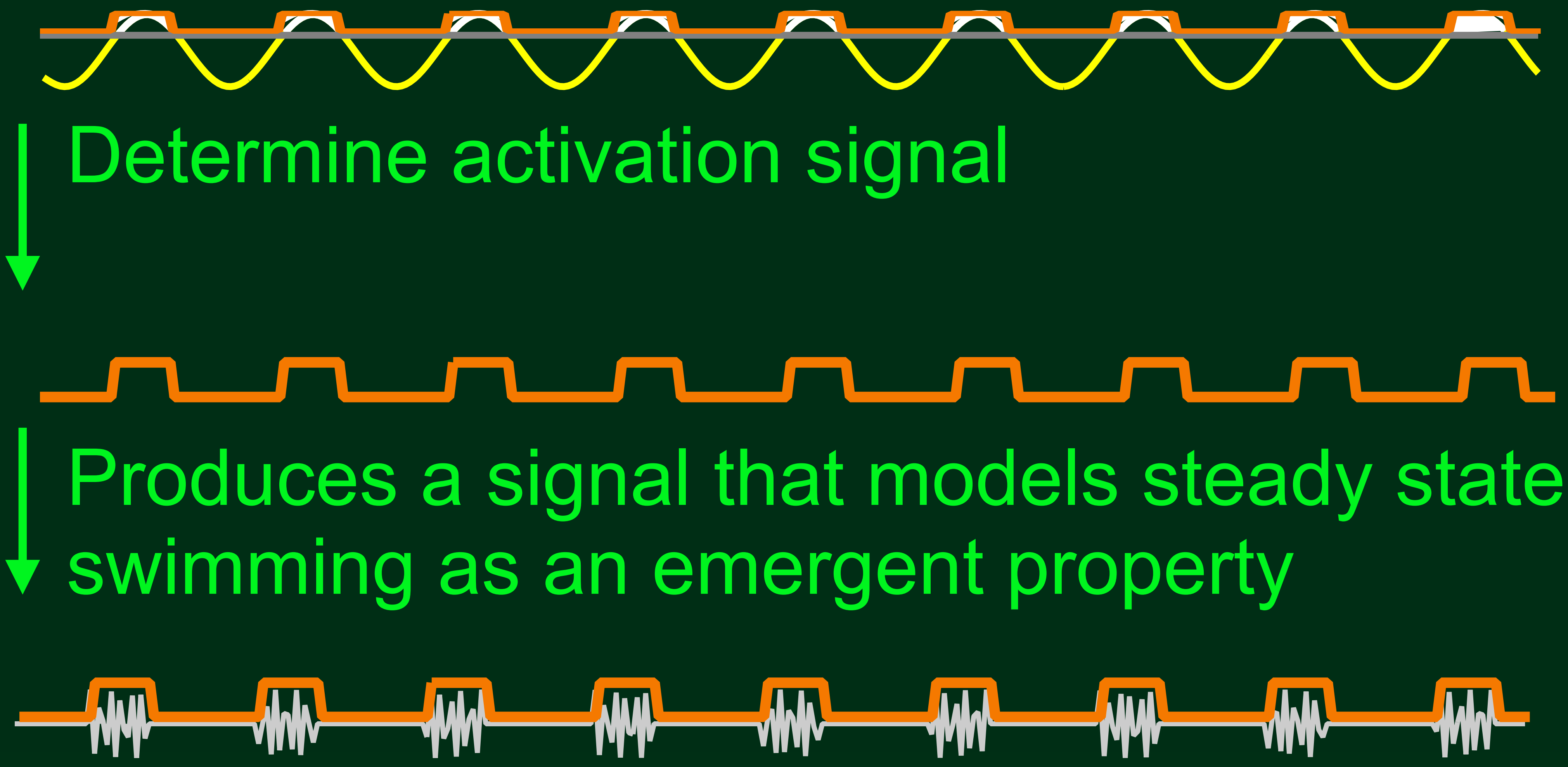


Oscillator generates a signal at a given frequency



Choose threshold based on steady swimming duration and frequency from experiments

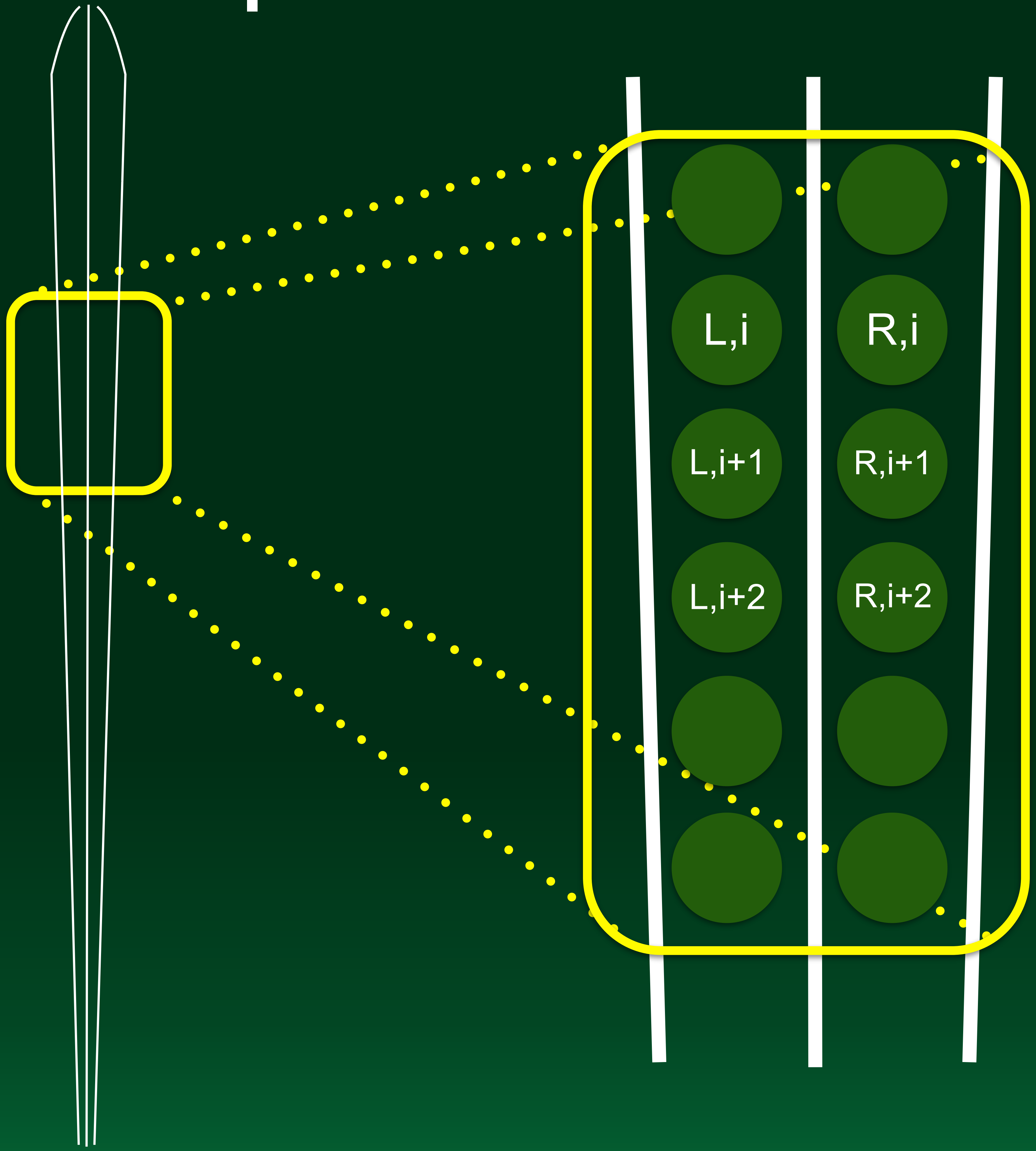
Oscillators generate a signal



Determine activation signal

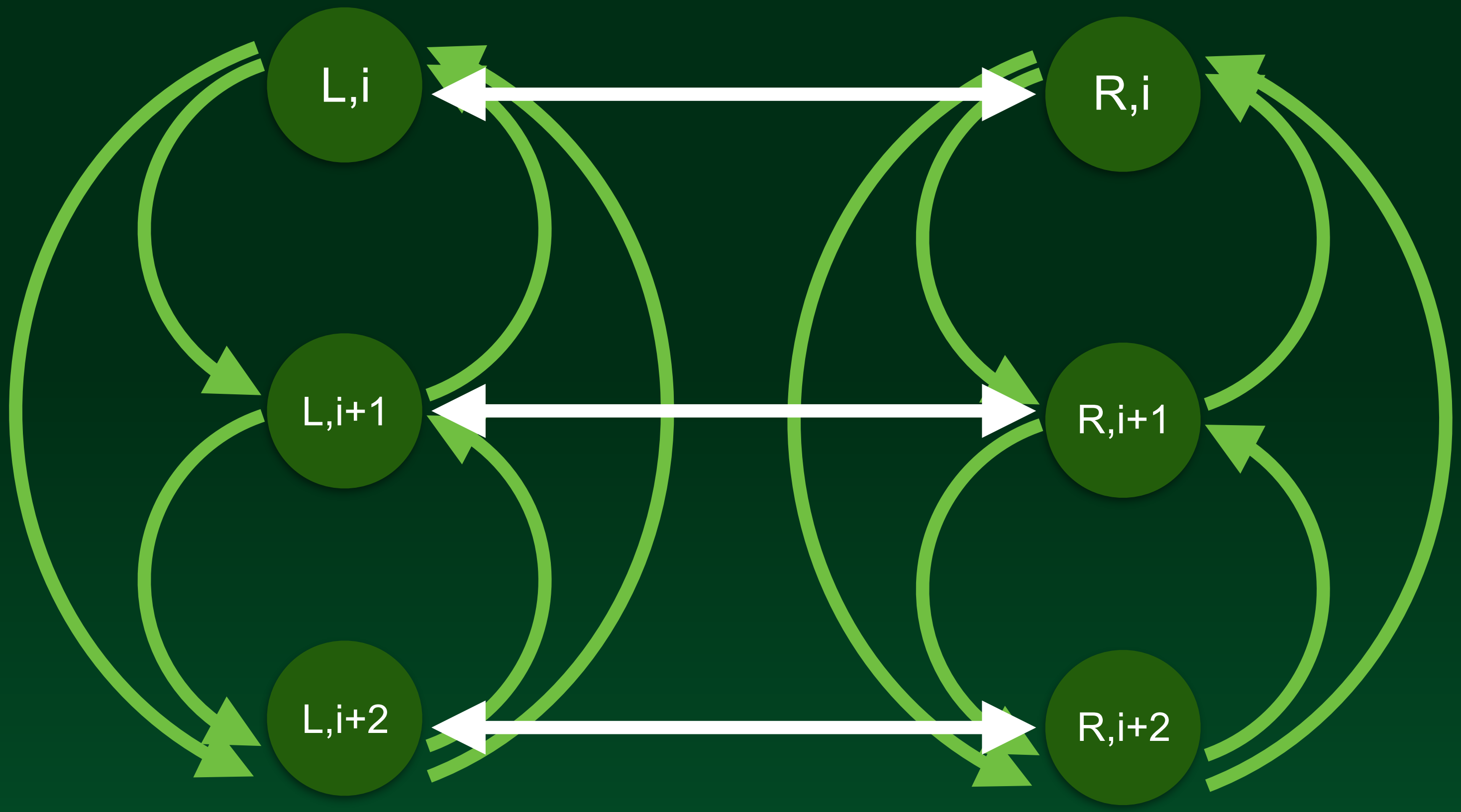
Produces a signal that models steady state swimming as an emergent property

Couple oscillators to muscle segments



ODE model of coupled oscillators

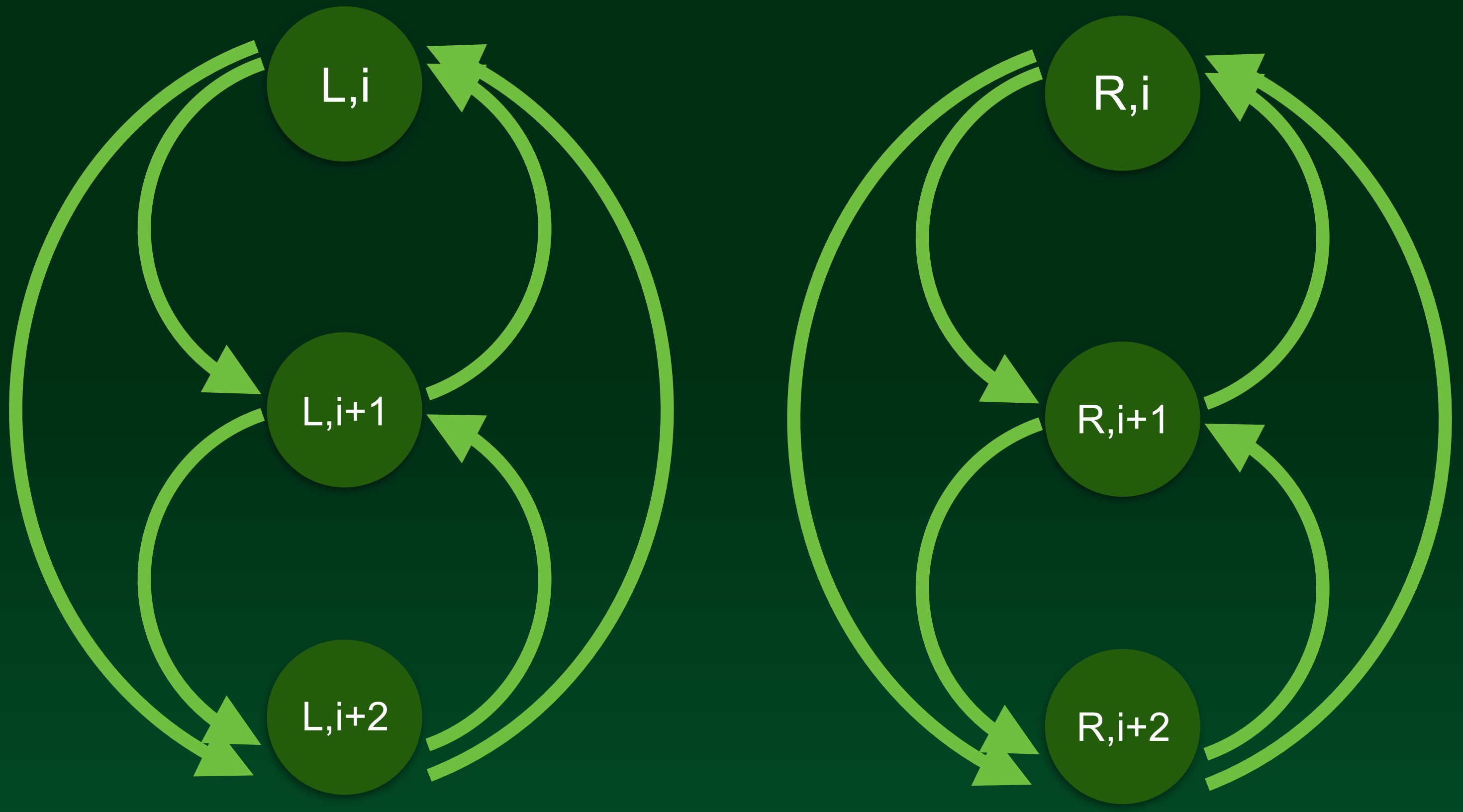
$$\dot{\theta}_{k,i} = \omega + \alpha_c \sin\left(2\pi\left(\theta_{k*,i} - \theta_{k,i} + \varphi_s\right)\right) + \sum_{j=1}^{n} \alpha_{i-j} \sin\left(2\pi\left(\theta_{k,j} - \theta_{k,i} - \psi_{i-j}\right)\right)$$



θ = phase

ODE model of coupled oscillators

$$\dot{\theta}_{k,i} = \omega + \alpha_c \sin\left(2\pi\left(\theta_{k*,i} - \theta_{k,i} + \varphi_s\right)\right) + \boxed{\sum_{j=1}^{n} \alpha_{i-j} \sin\left(2\pi\left(\theta_{k,j} - \theta_{k,i} - \psi_{i-j}\right)\right)}$$



Intersegmental connections

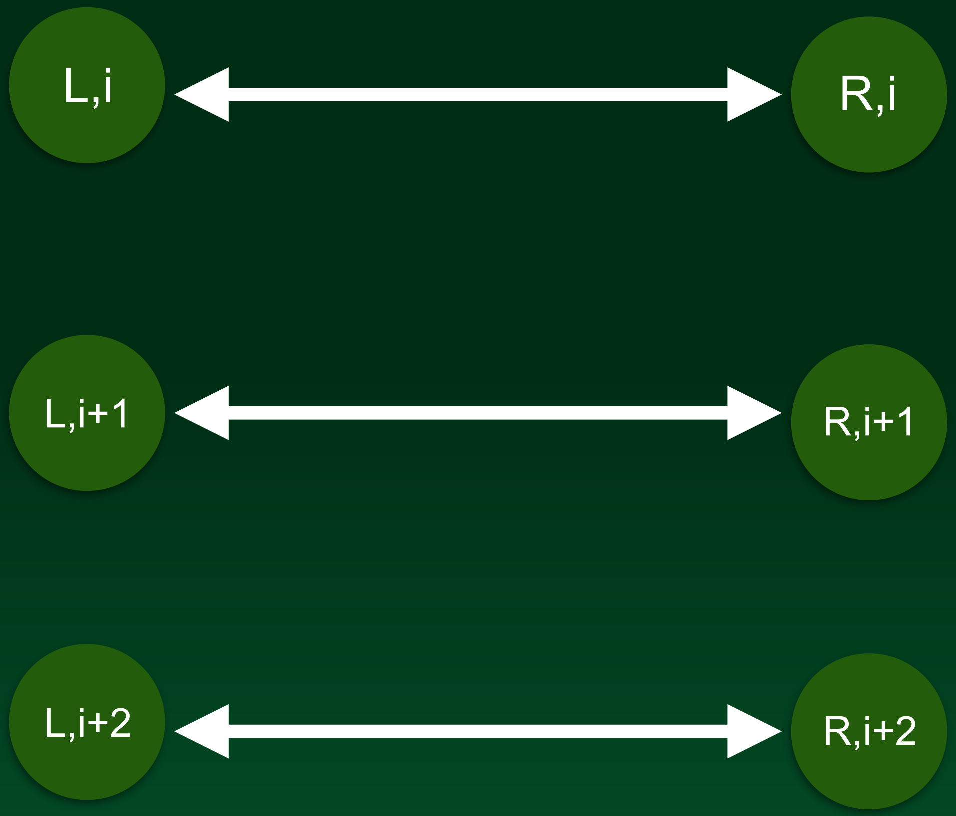
θ = phase

ψ_{i-j} = phase lag

ODE model of coupled oscillators

$$\dot{\theta}_{k,i} = \omega + \boxed{\alpha_c \sin\left(2\pi\left(\theta_{k*,i} - \theta_{k,i} + \varphi_s\right)\right)} \\ + \sum_{j=1}^{n} \alpha_{i-j} \sin\left(2\pi\left(\theta_{k,j} - \theta_{k,i} - \psi_{i-j}\right)\right)$$

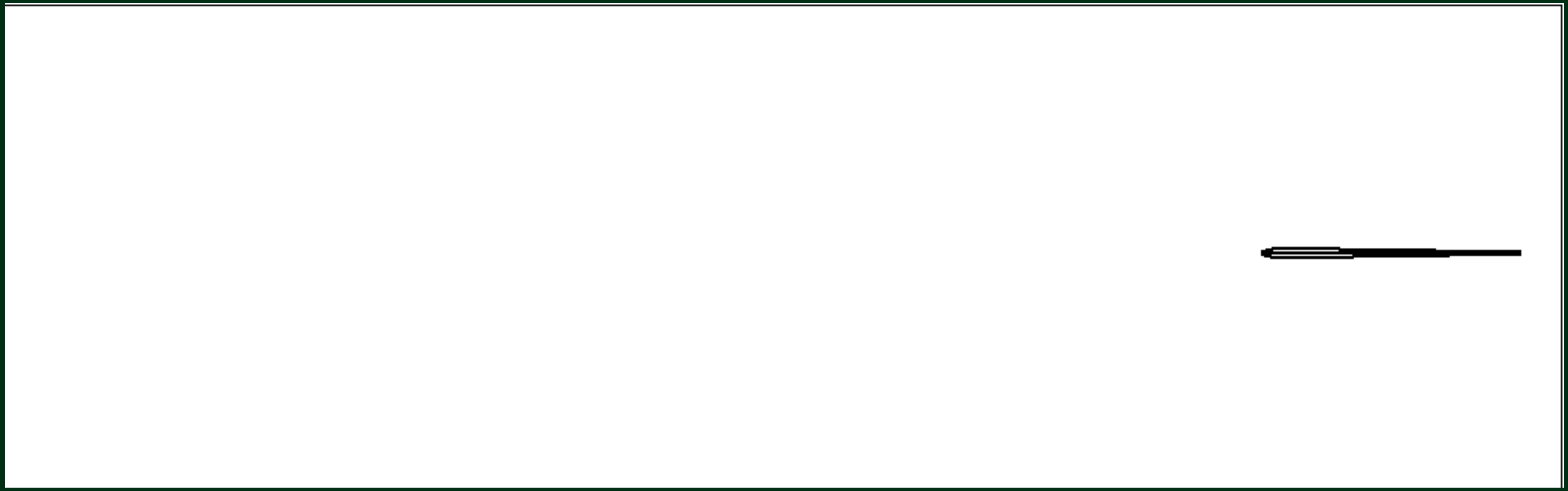
Cross connections



$\theta =$ phase

$\varphi_s =$ phase lag

Immersed boundary simulations of a swimmer in an incompressible viscous fluid



Lamprey (black) immersed in a fluid (white region)

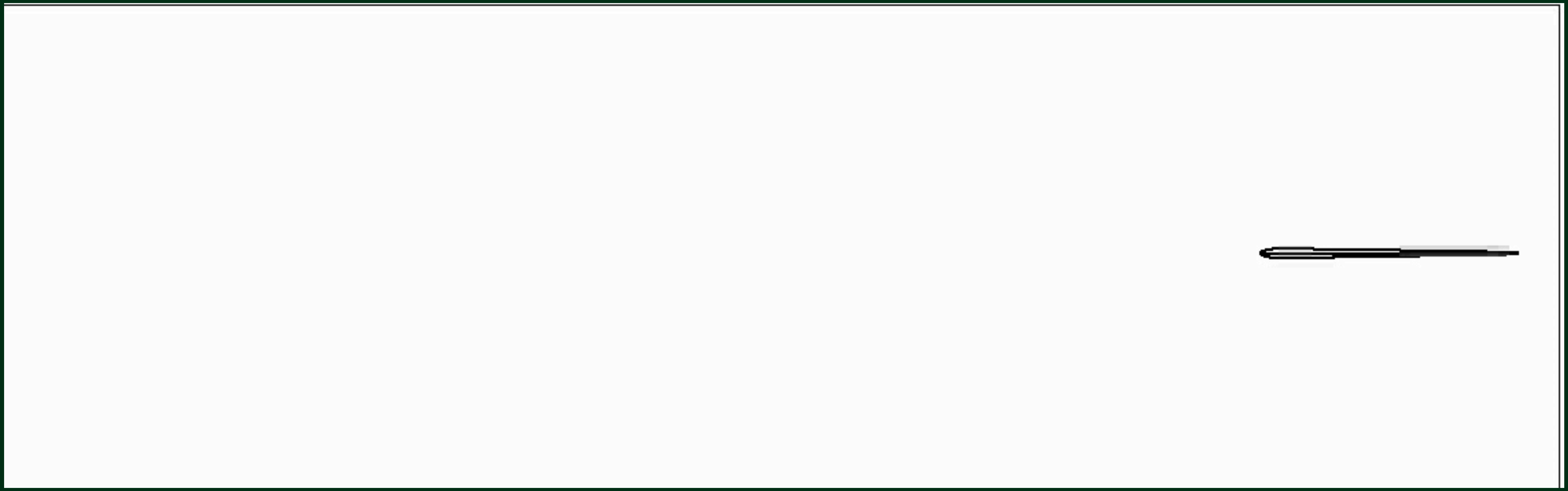
Oscillators given initial conditions

Evolved in time in immersed boundary simulation

Muscle segments generate forces

Hamlet, Fauci, Tytell, J.Theo. Bio 2015

Simulations show emergent swimming behavior



Vorticity plots, lamprey model immersed in fluid

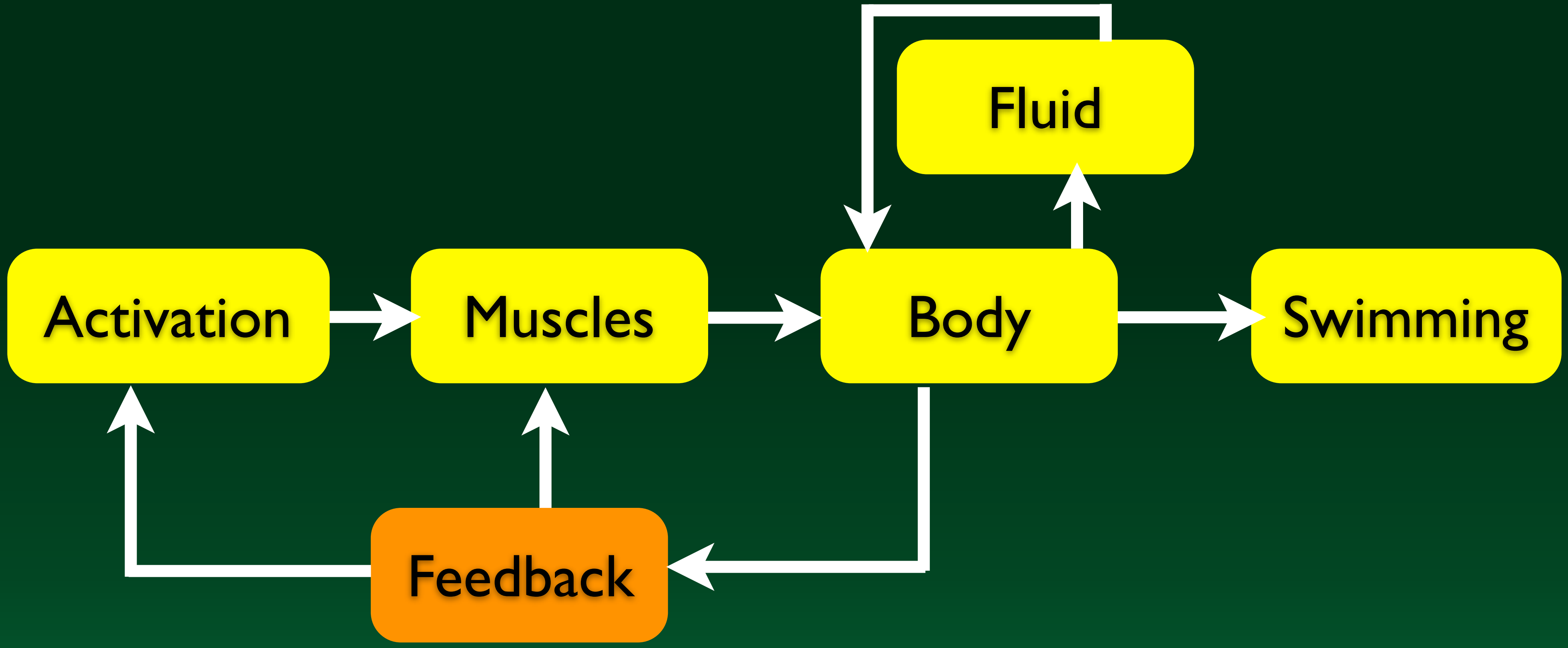
Red = counterclockwise vorticity

Blue = clockwise vorticity

Hamlet, Fauci, Tytell, J.Theo. Bio 2015

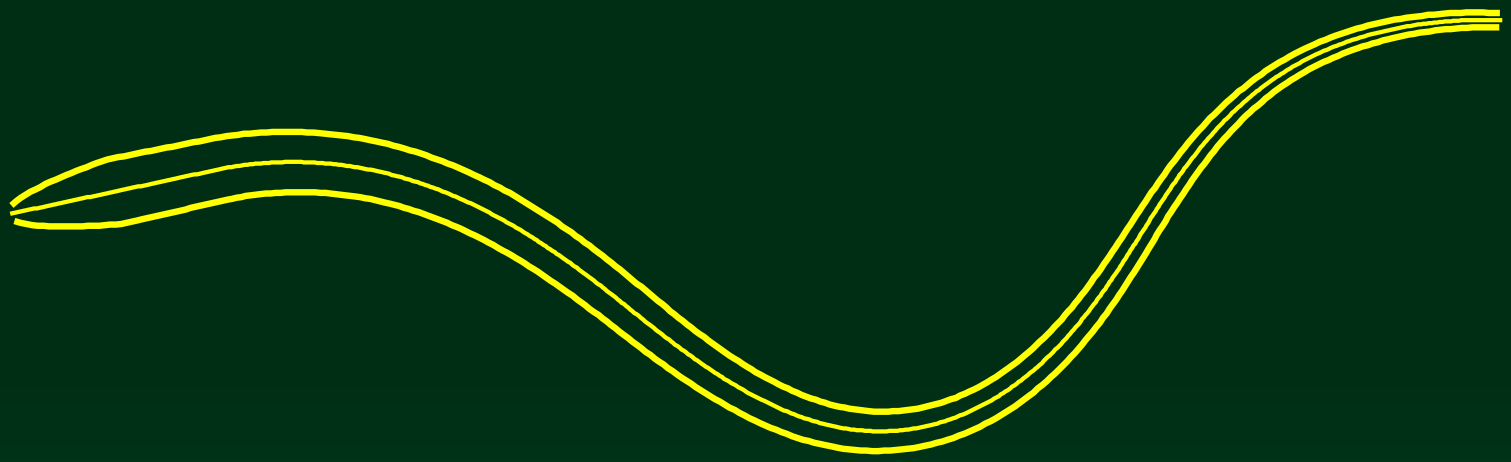
Sensory feedback closes the loop

- Proprioceptive (body-sensing) feedback affects activation
- Uses stretch receptors called edge cells

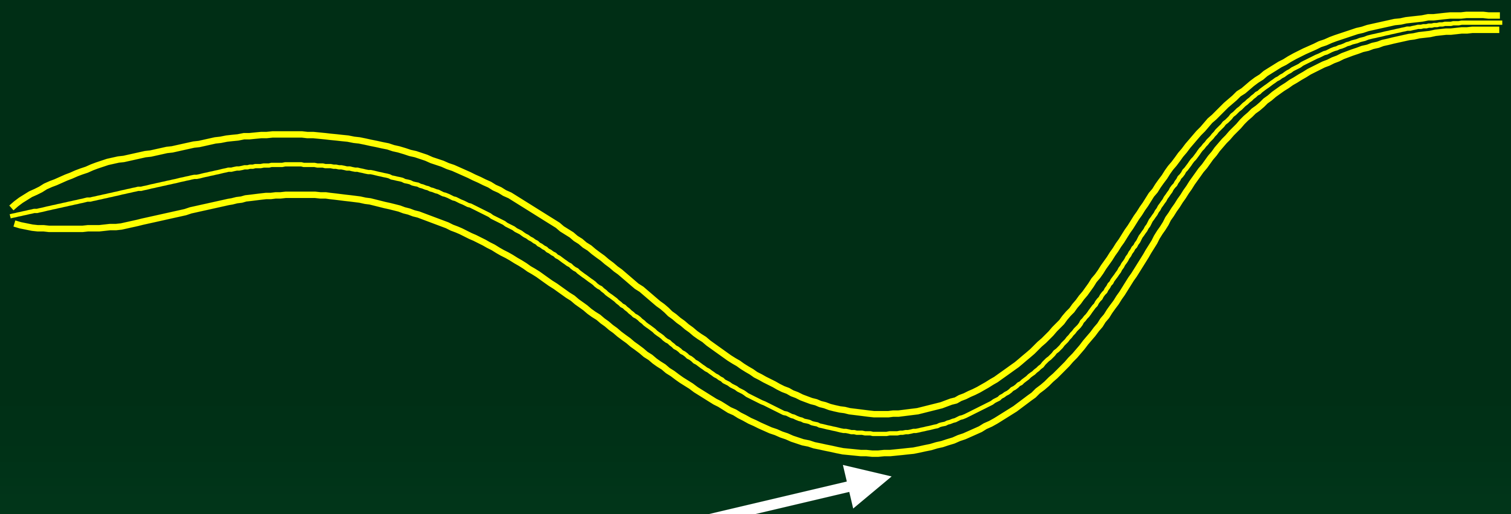


Edge cells and sensory feedback

- Edge cells give inhibitory and excitatory signals along the body

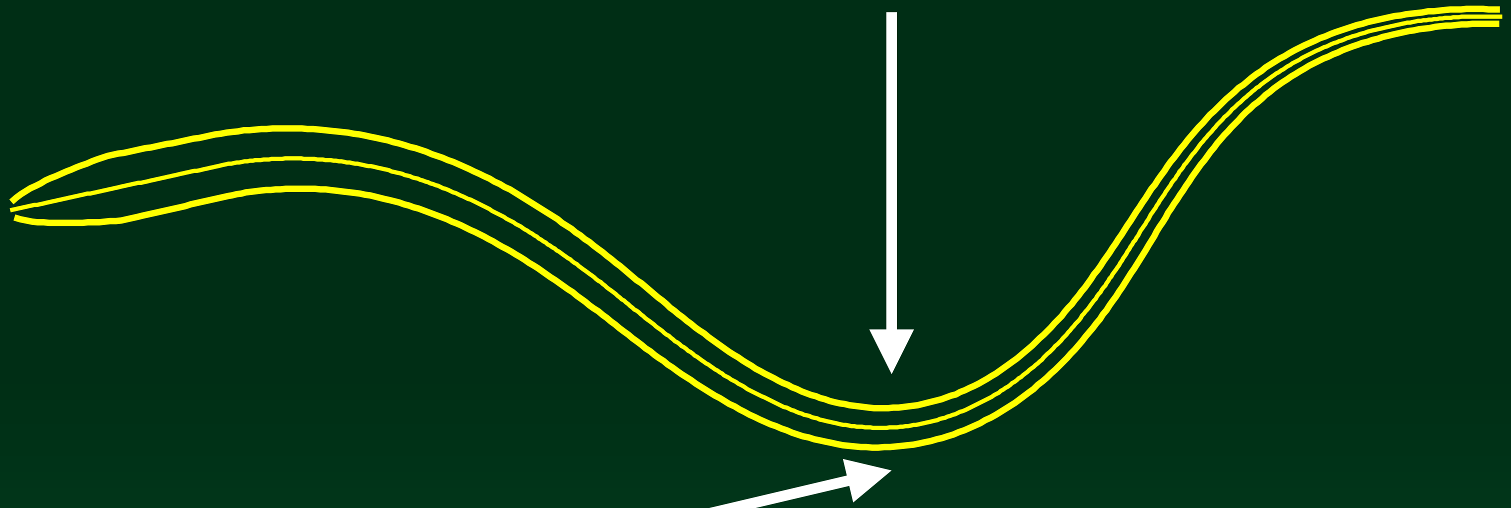


Edge cells and sensory feedback



If this side is
stretched…..

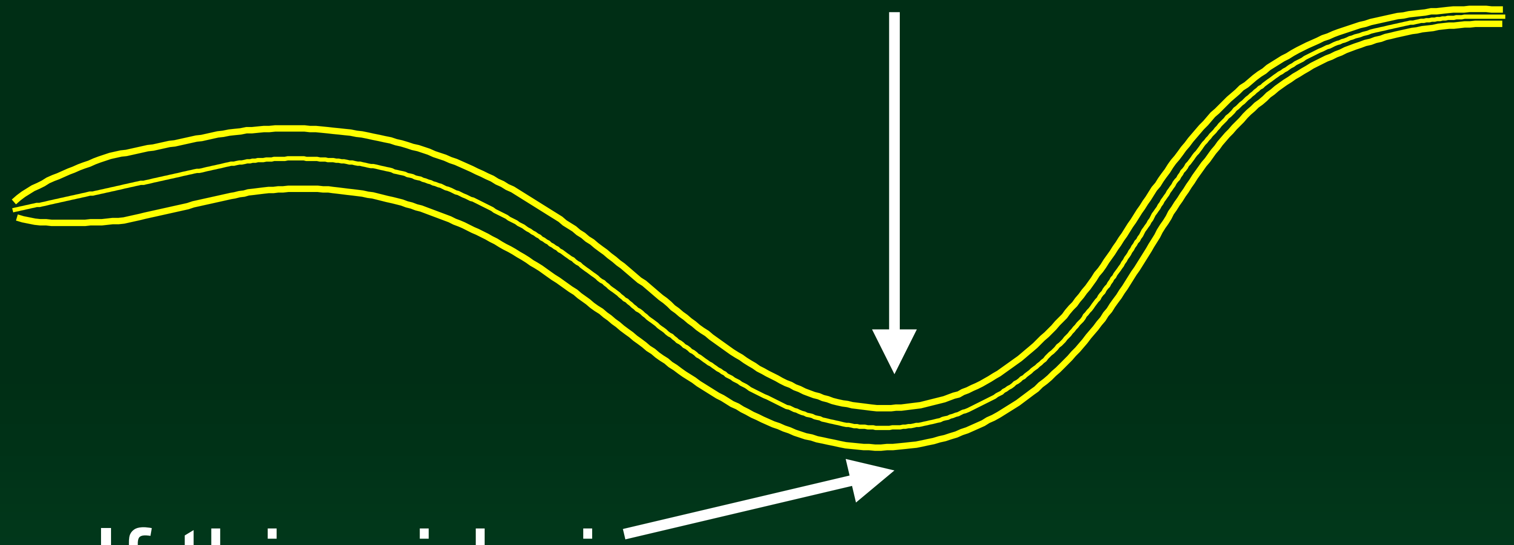
Edge cells and sensory feedback



…this side gets
an inhibitory
signal…

If this side is
stretched…..

Edge cells and sensory feedback



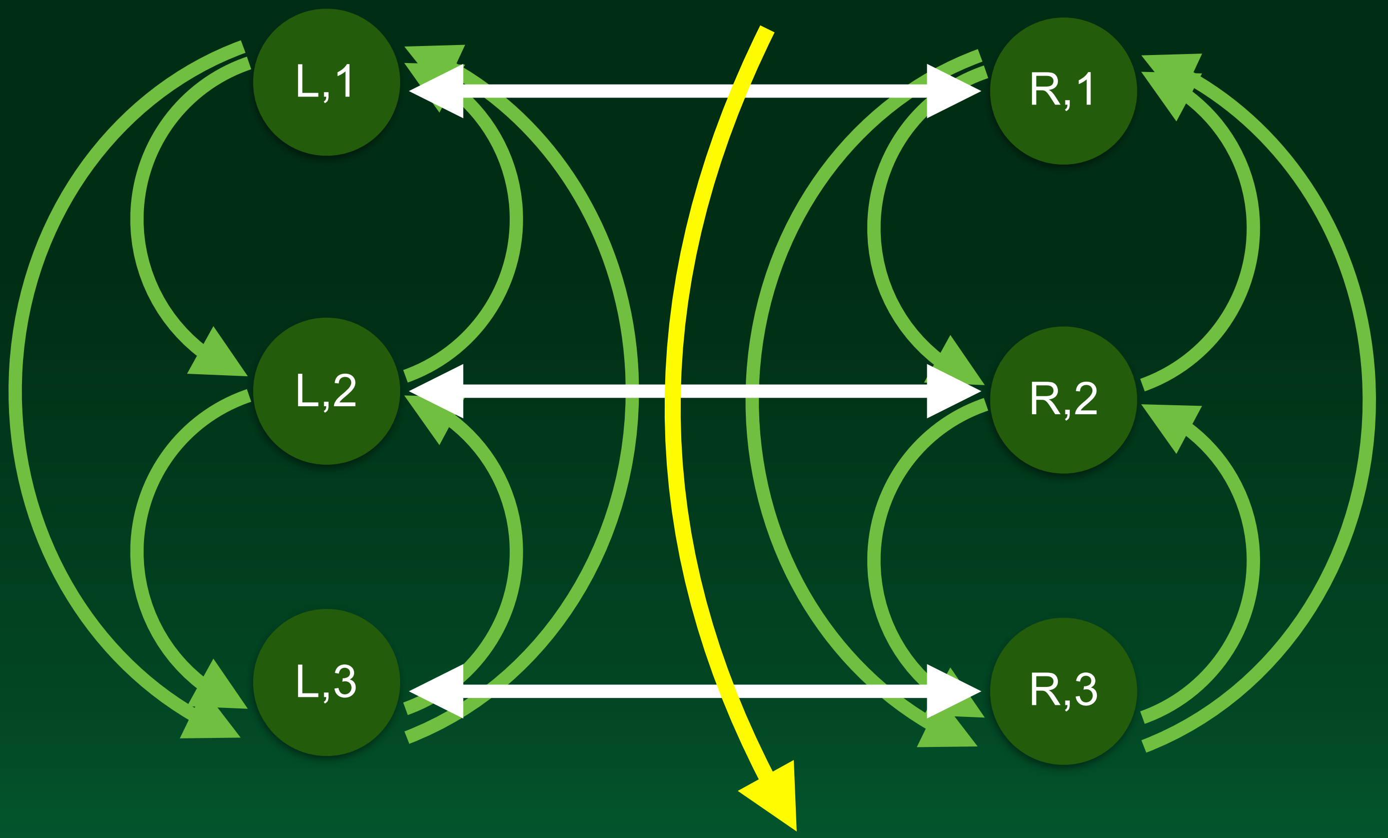
…this side gets
an inhibitory
signal…

If this side is
stretched…..

…and this side
gets an excitatory
signal

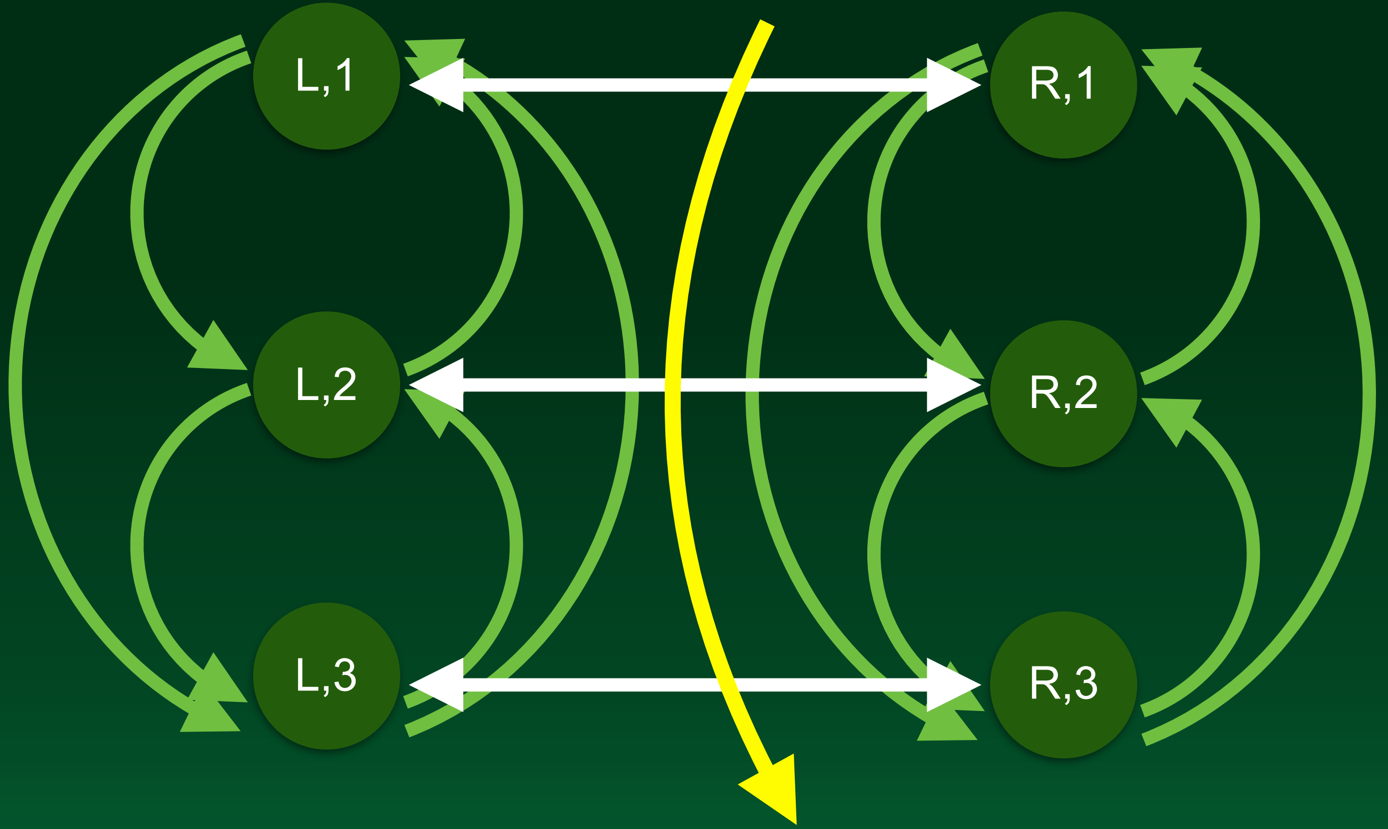
Connect sensory feedback to oscillators

$$\begin{aligned}\dot{\theta}_{k,i} &= \omega + \alpha_c \sin\left(2\pi\left(\theta_{k*,i} - \theta_{k,i} + \varphi_s\right)\right) \\ &\quad + \sum_{j=1}^{n} \alpha_{i-j} \sin\left(2\pi\left(\theta_{k,j} - \theta_{k,i} - \psi_{i-j}\right)\right) \\ &\quad + \boxed{\eta_{k,i}\left(\kappa\right)}\end{aligned}$$



Connect sensory feedback to oscillators

$$\begin{aligned}\dot{\theta}_{k,i} = {} & \omega + \alpha_c \sin\left(2\pi\left(\theta_{k*,i} - \theta_{k,i} + \varphi_s\right)\right) \\ & + \sum_{j=1}^{n} \alpha_{i-j} \sin\left(2\pi\left(\theta_{k,j} - \theta_{k,i} - \psi_{i-j}\right)\right) \\ & + \boxed{\eta_{k,i}\left(\kappa\right)} \longleftarrow \eta_{k,i} = g\left|\bar{\kappa}\right|\end{aligned}$$



Swimmer with negative gain slows down

Grey — No feedback

Black — Feedback

$$\eta_{k,i} = (-0.05)\,|\kappa|$$

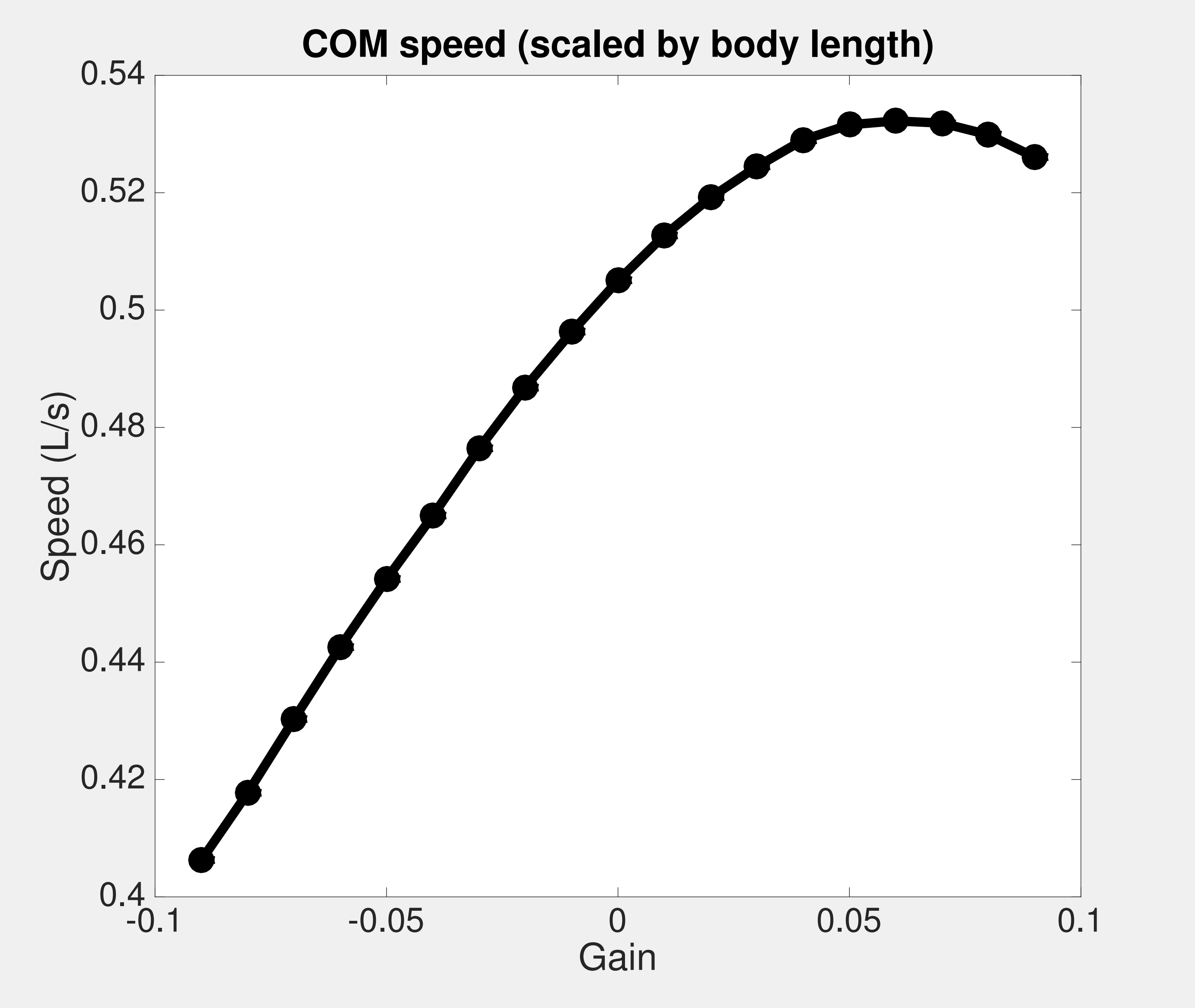
Swimmer with positive gain speeds up

Grey — No feedback

Black — Feedback

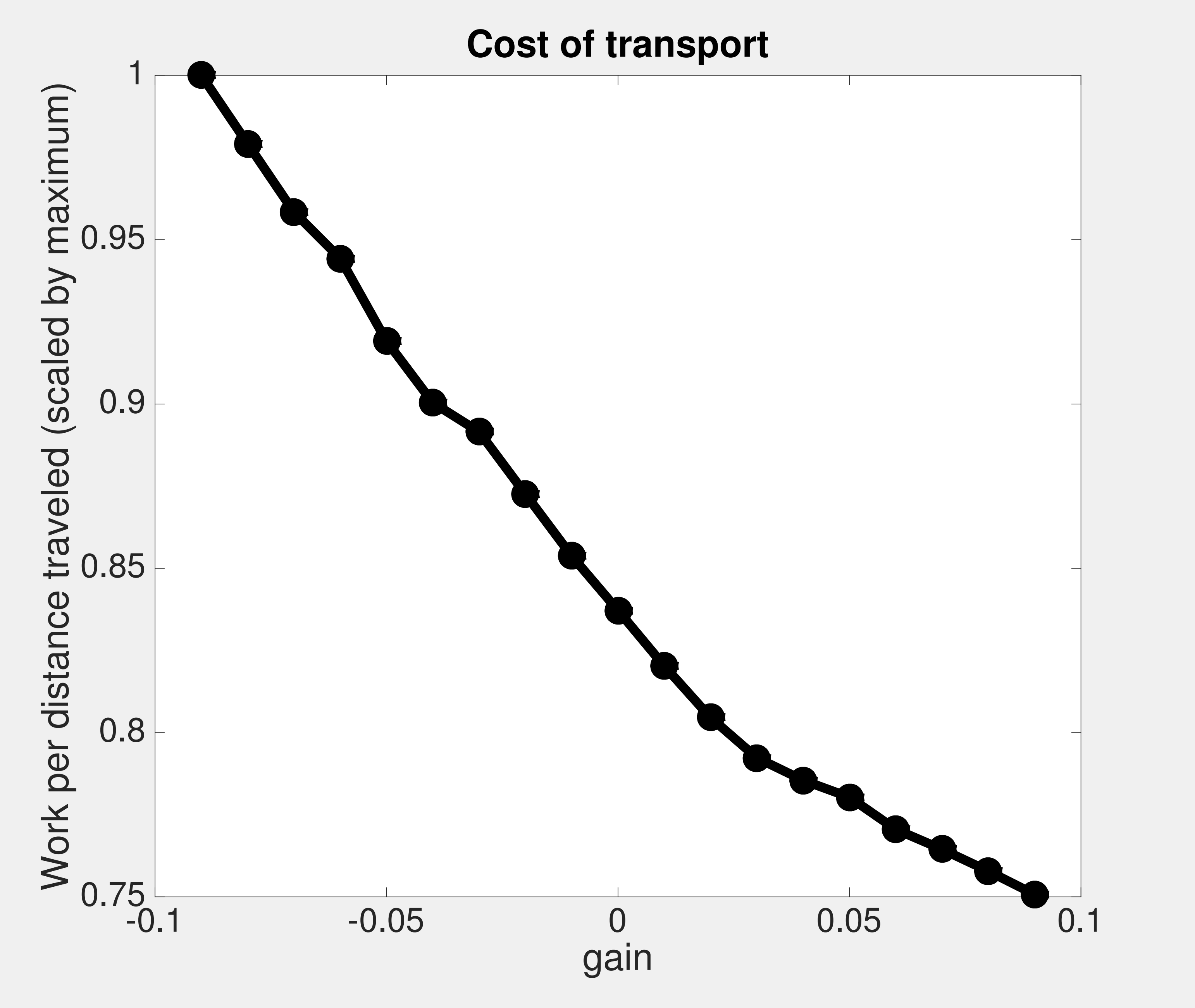
$$\eta_{k,i} = (0.05)\,|\kappa|$$

Center of mass speed increases to a point then starts to drop off



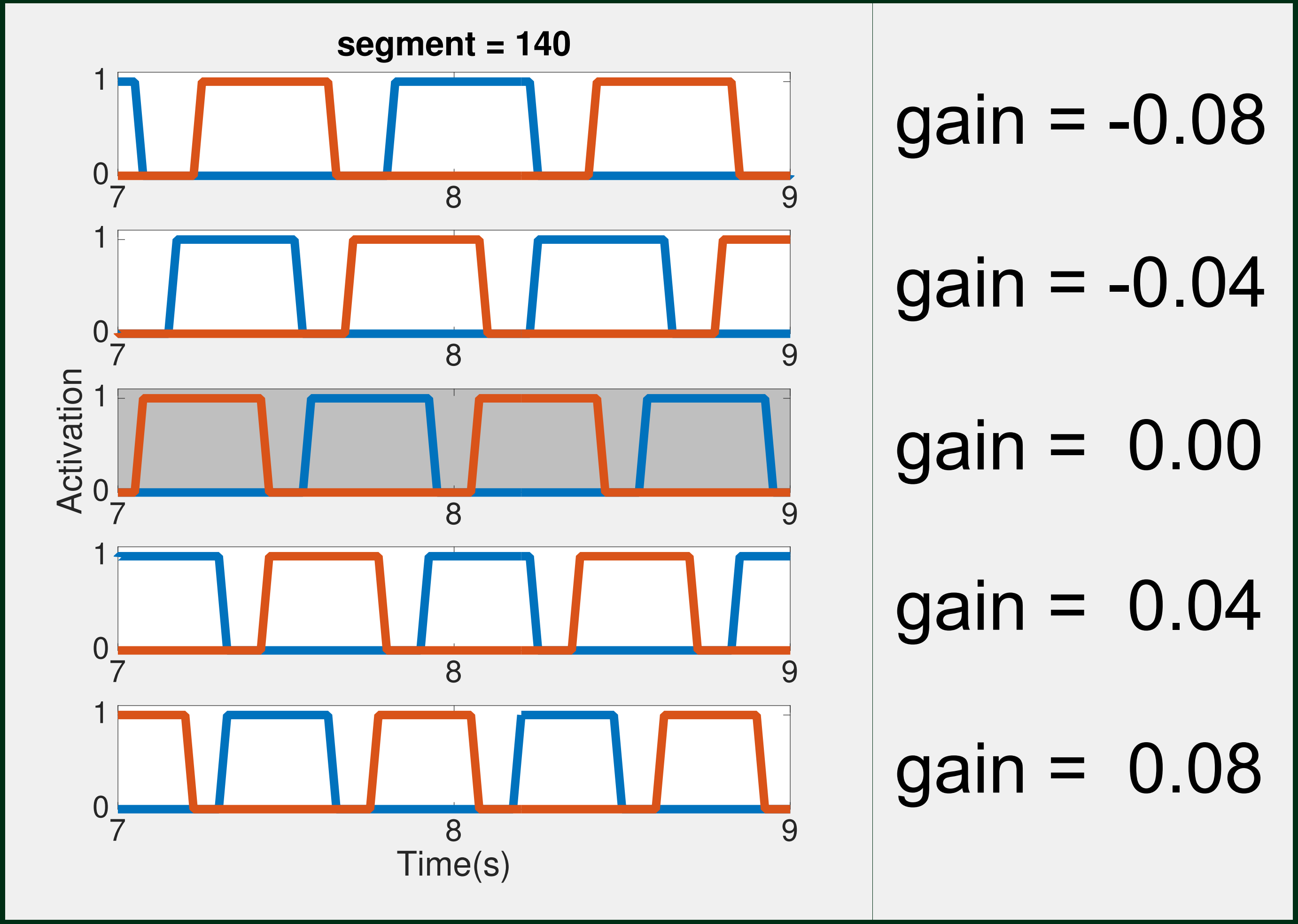
Steady swimming speed measured at center mass

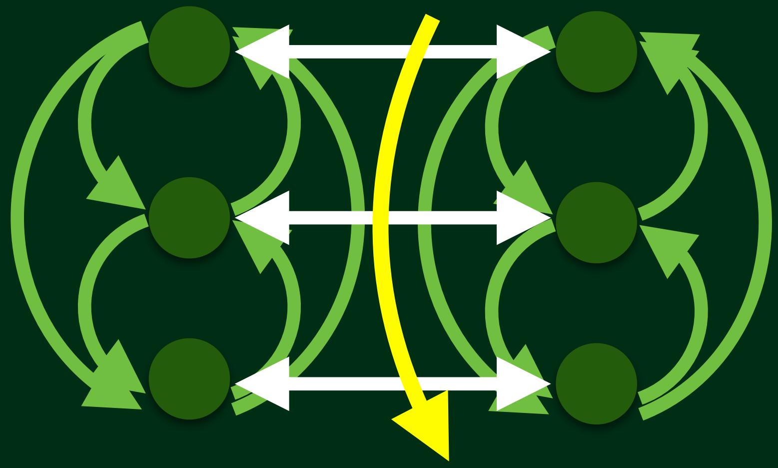
Metabolic cost to swim decreases as gain increases



Work to swim unit distance at steady swimming

Frequency increases as gain increases

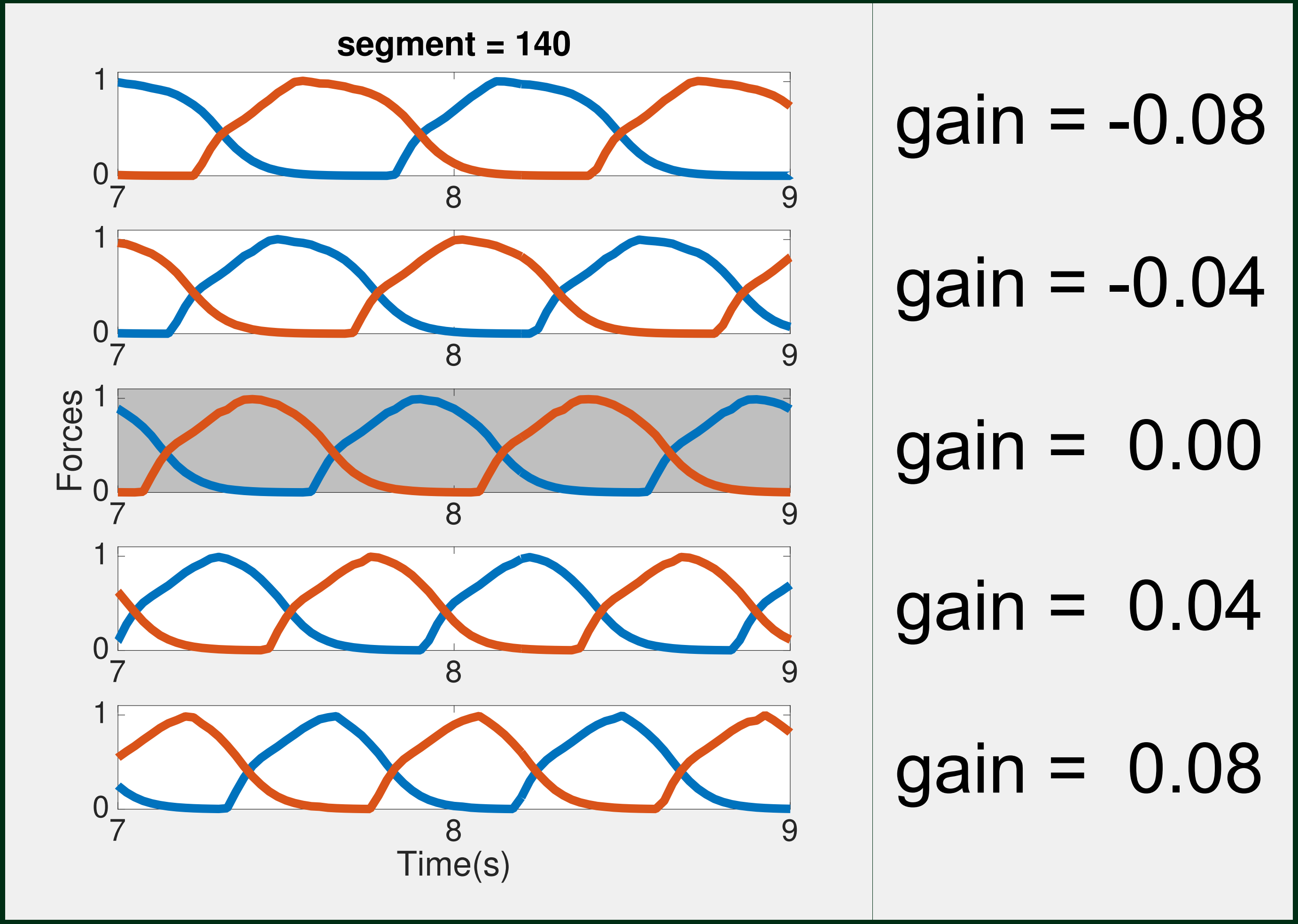




No. of activation cycles in 2 seconds

Blue = left side
Red = right side
Grey = no feedback (gain = 0)

Increasing frequency reduces force development period



Forces developed during each cycle

Blue = left side
Red = right side
Grey = no feedback (gain = 0)

Summary

- CPG produces swimming behavior without sensory input in the computational swimmer
- Adding curvature feedback closes the physiological loop in the organism
- Examine the interacting systems and physiological effects of coordination
- Explore effects of different functional forms of feedback based on experimental studies

Future work

- Add perturbations to test ability of sensory feedback to stabilize swimming
- Add in time derivatives of curvature (rate of bending)
- Construct different functional forms of curvature driven feedback

Funding

- Army Research Office (W911NF-13-1-0289)
- National Science Foundation (NSF DMS-1312987 and NSF DBI-RCN-1062052)