

Behavior Hierarchy: Principles and Algorithms

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A prescient comment

Hierarchical organization, a candidate principle for ethology

Richard Dawkins

(1977)

If we look far into the future of our science, what will it mean to say we “understand” the mechanism of behaviour? The obvious answer is what may be called the neurophysiologist’s nirvana: **the complete wiring diagram of the nervous system of a species**, every synapse labelled as excitatory or inhibitory; presumably also a graph, for each axon, of nerve impulses as a function of time during the course of each behaviour pattern. ... and because we are still in the early stages, the ultimate conclusion does not worry us. **But it would not constitute understanding of how behaviour works in any real sense at all.** No man could hold such a mass of detail in his head. Real understanding will only come from distillation of general principles at a higher level, to parallel for example the great principles of genetics ...

Also see a Study of Instinct Tinbergen 1942

integration and, moreover, they are organized in a hierarchical system, like the staff organization of an army or of other human organizations. Fig. 89 illustrates the principle. The facts (1) that at each of the levels an external stimulus can have a specific releasing influence and (2) that each reaction has its own motor pattern, mean that there is a hierarchical system of IRMs and of motor centres. So far as we can judge at present, each IRM is able to collect sensory impulses according to the rule of heterogeneous summation, and each motor centre controls a configurational pattern of muscle contractions.

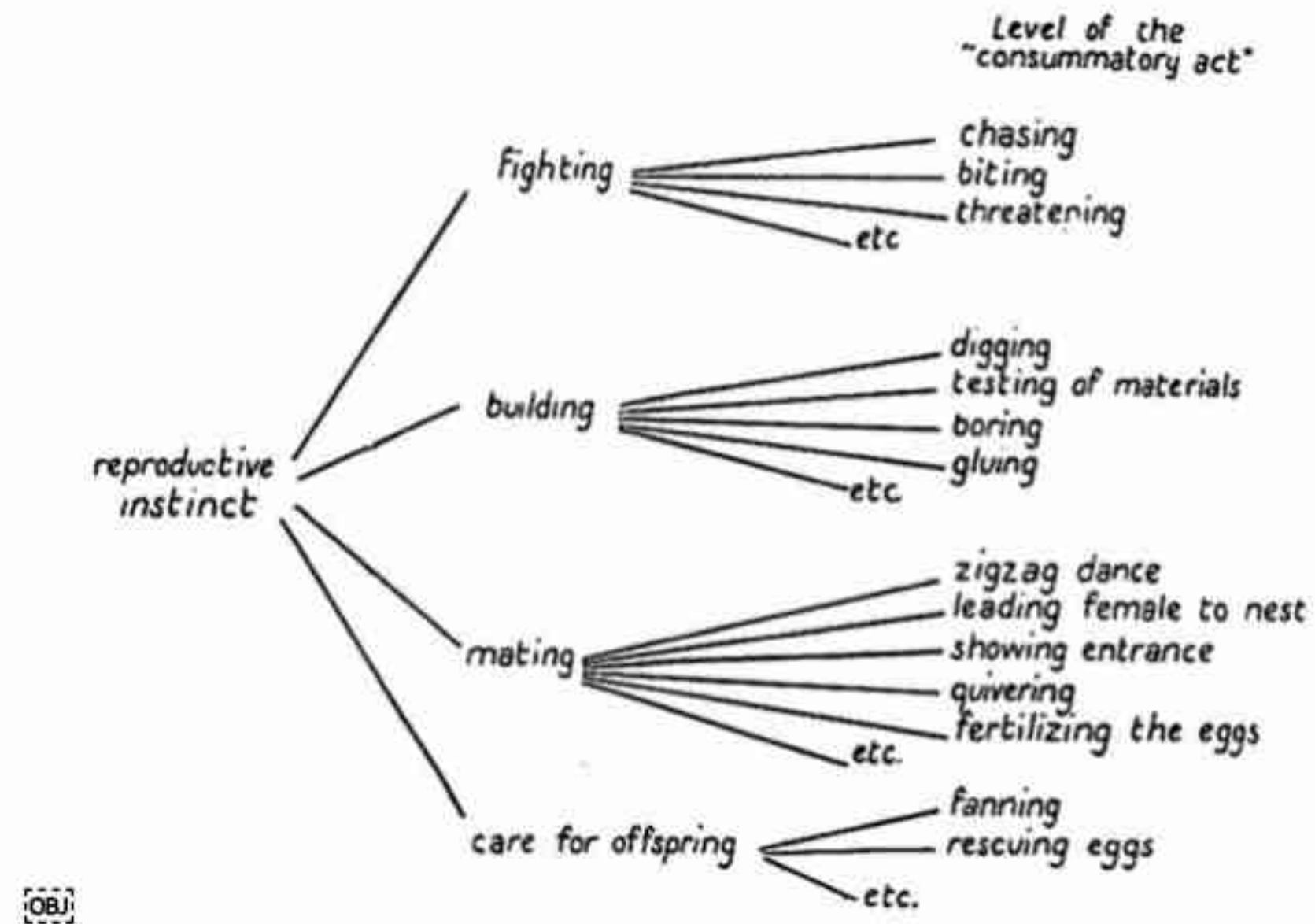


Fig. 89. The principle of hierarchical organization illustrated by the reproductive instinct of the male three-spined stickleback. After Tinbergen, 1942.

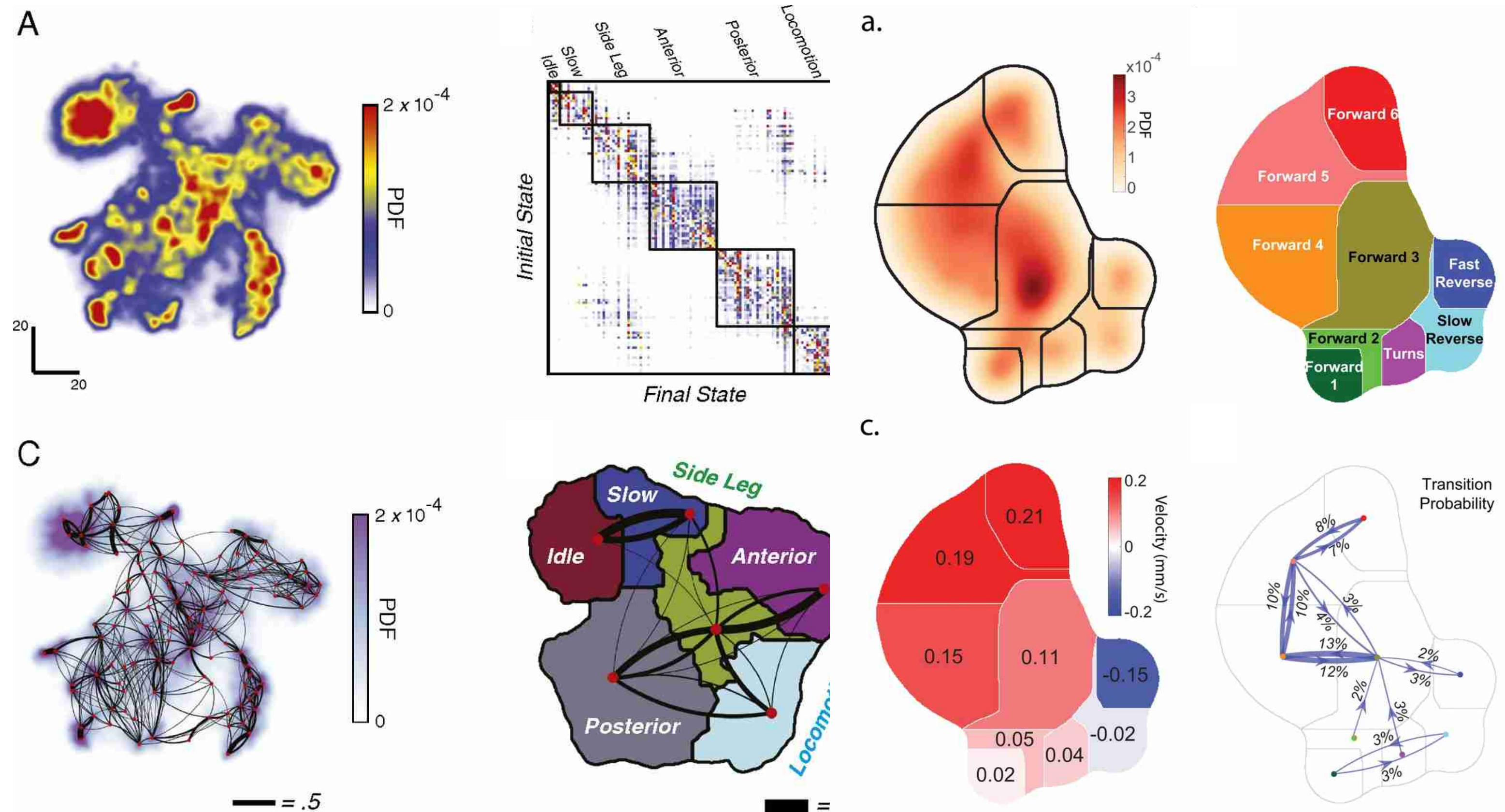
The principle of hierarchical organization has been tested in but three cases: the digger wasp *Ammophila campestris* (Baerends, 1941), the three-spined stickleback (Tinbergen, 1942), and the turkey (Räber, 1948), and although the principle is undoubtedly sound, nearly nothing is known in detail about the way it works out in the various drives and in different species of animals. Before a more detailed discussion can be attempted, a closer consideration of motor responses is necessary.

Also see a Study of Instinct Tinbergen 1942

APPETITIVE BEHAVIOUR AND CONSUMMATORY ACT

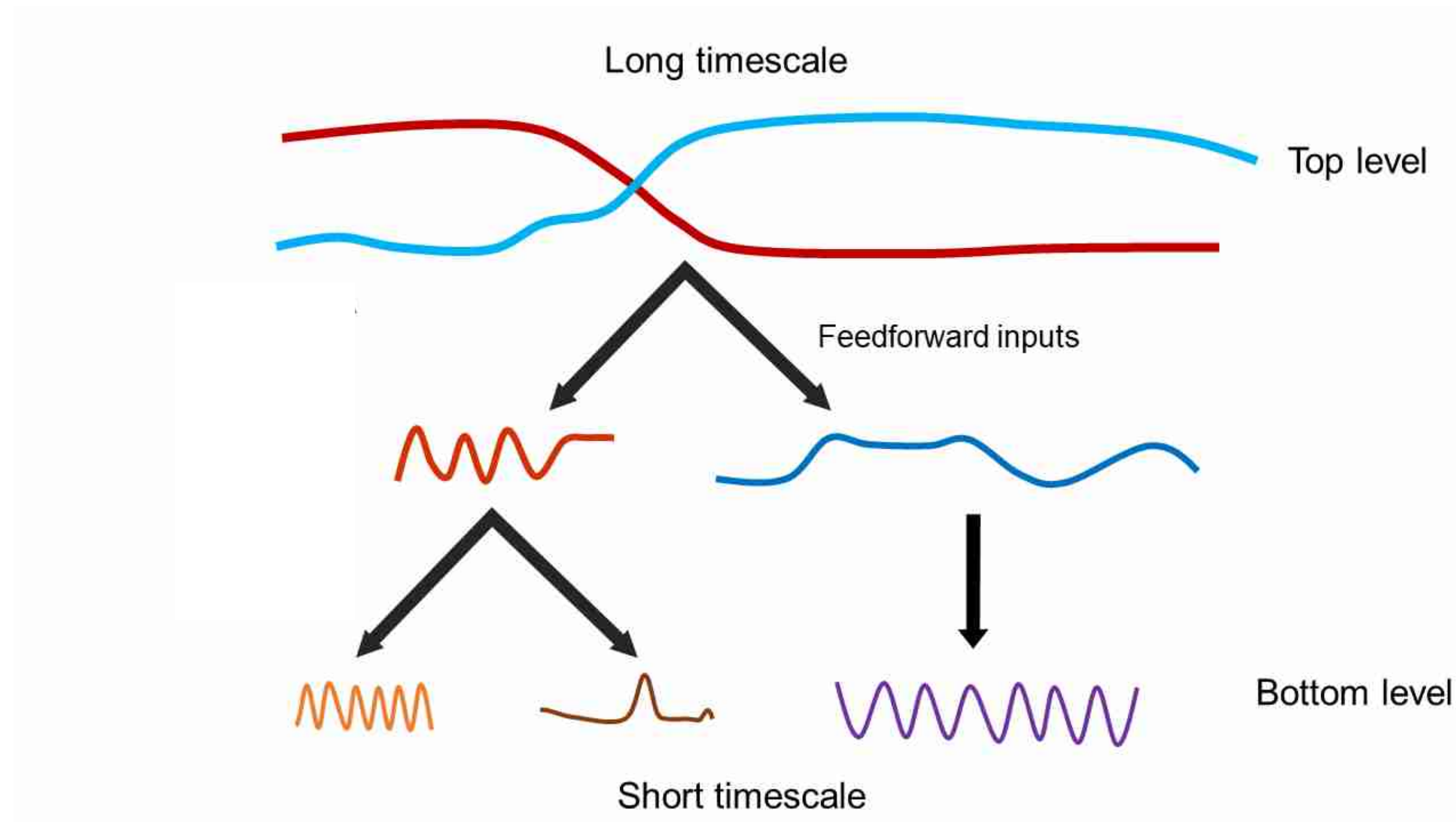
The activation of a centre of the lowest level usually, perhaps always, results in a relatively simple motor response: biting

The hierarchical behavior map



Berman, Bialek & Shaevitz 2016
Liu et. al., 2018

Hierarchical neural architecture for movement control

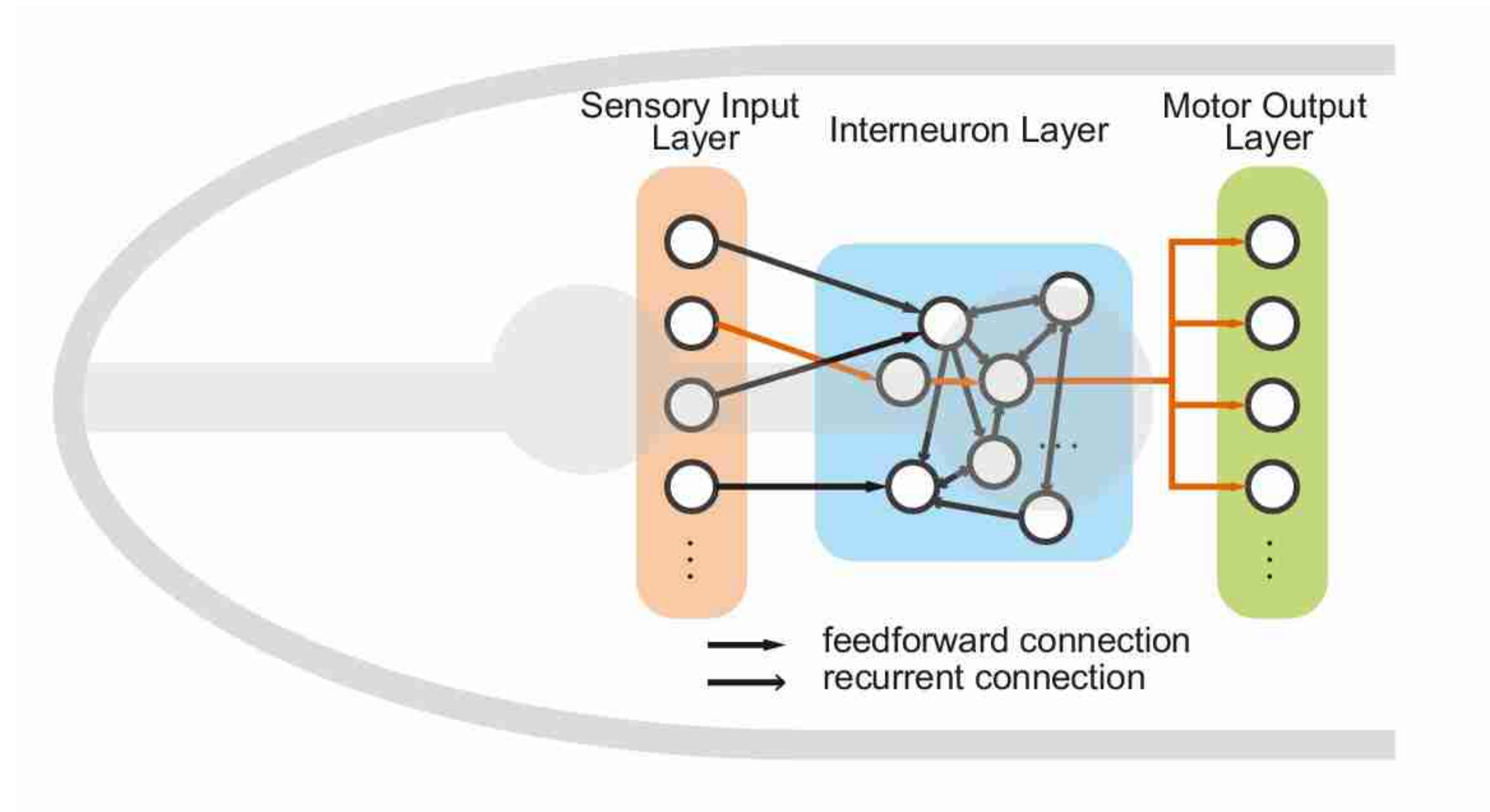


To understand how to build behavior dynamics across timescales



300 neurons

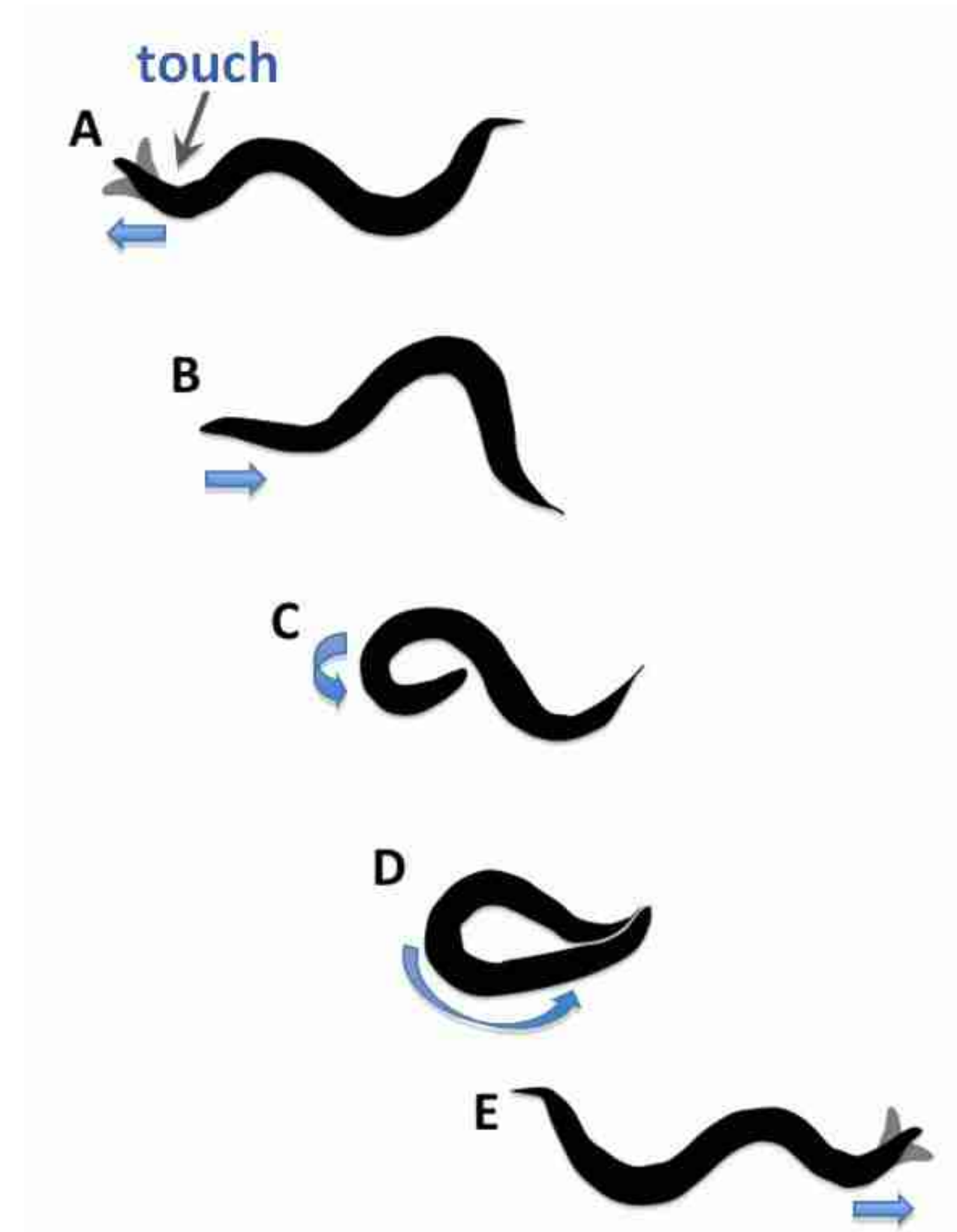
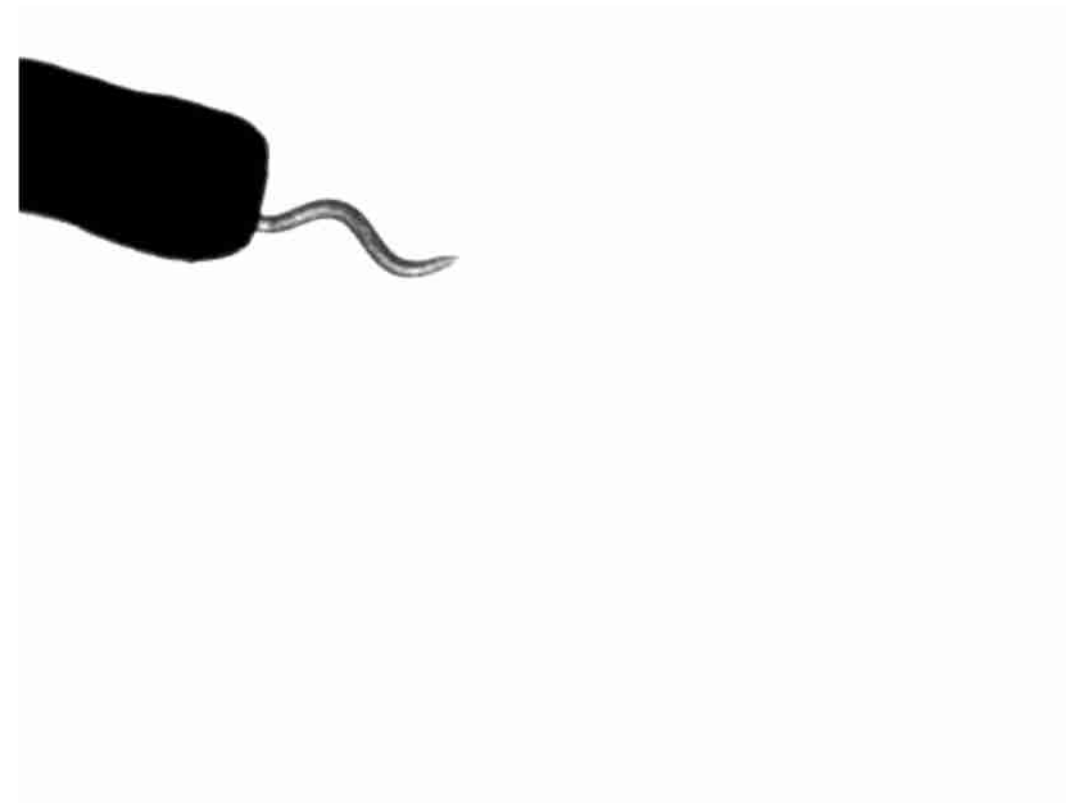
C. elegans nervous system can be viewed as a three-layer neural network



John White et. al., 1986

Motor sequence generation on a longer timescale

The escape response



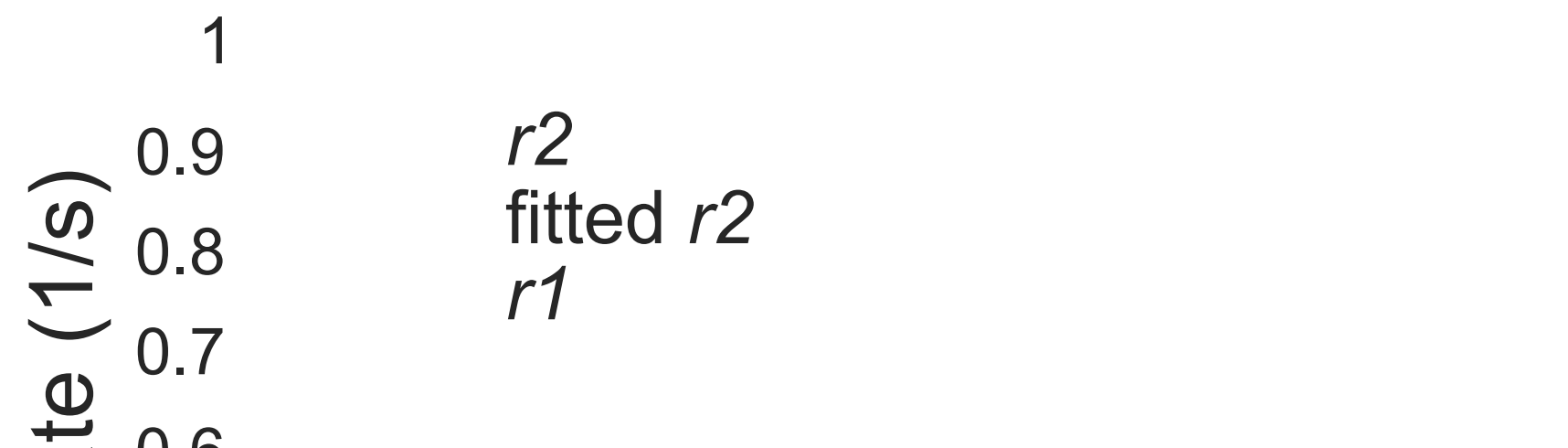
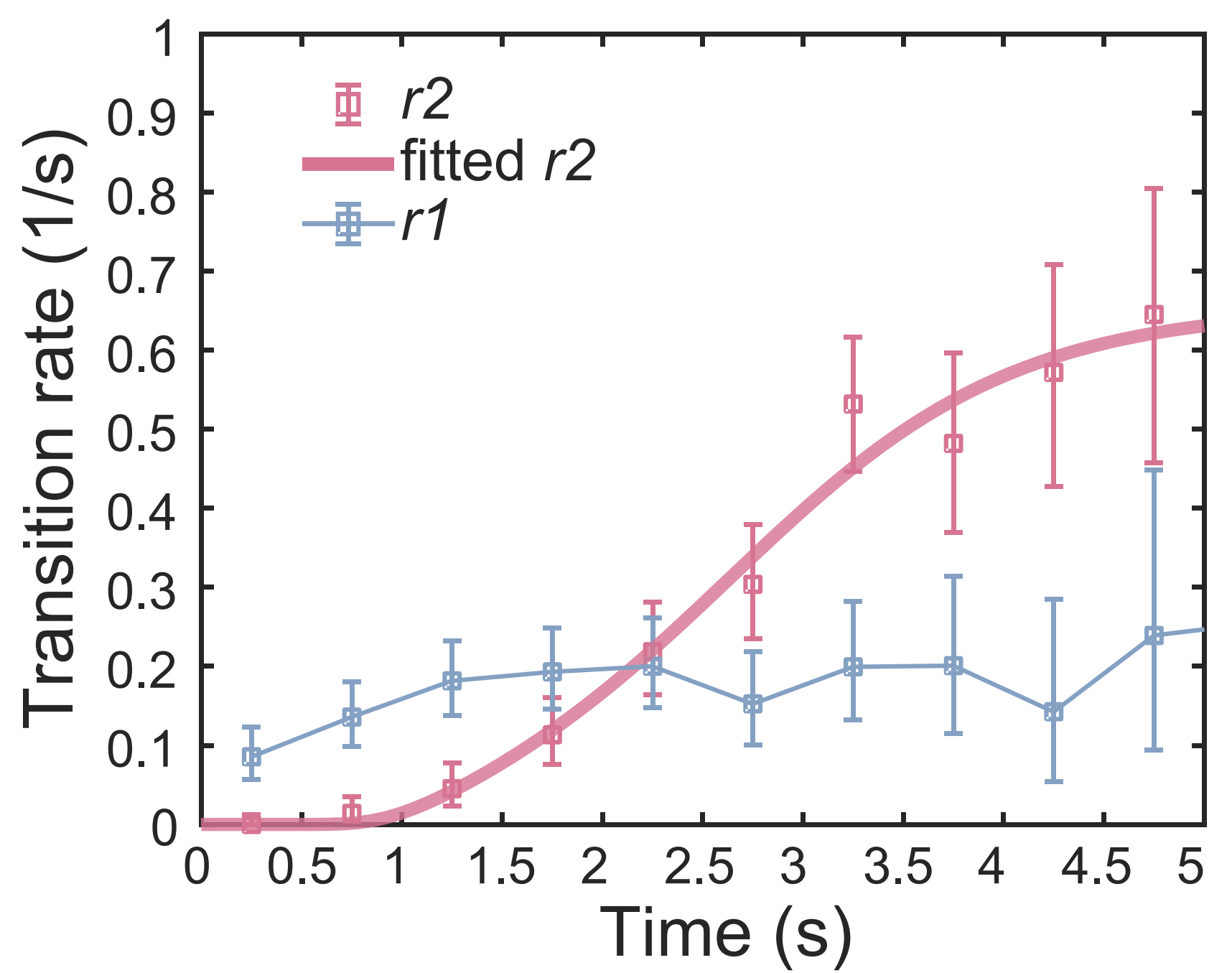
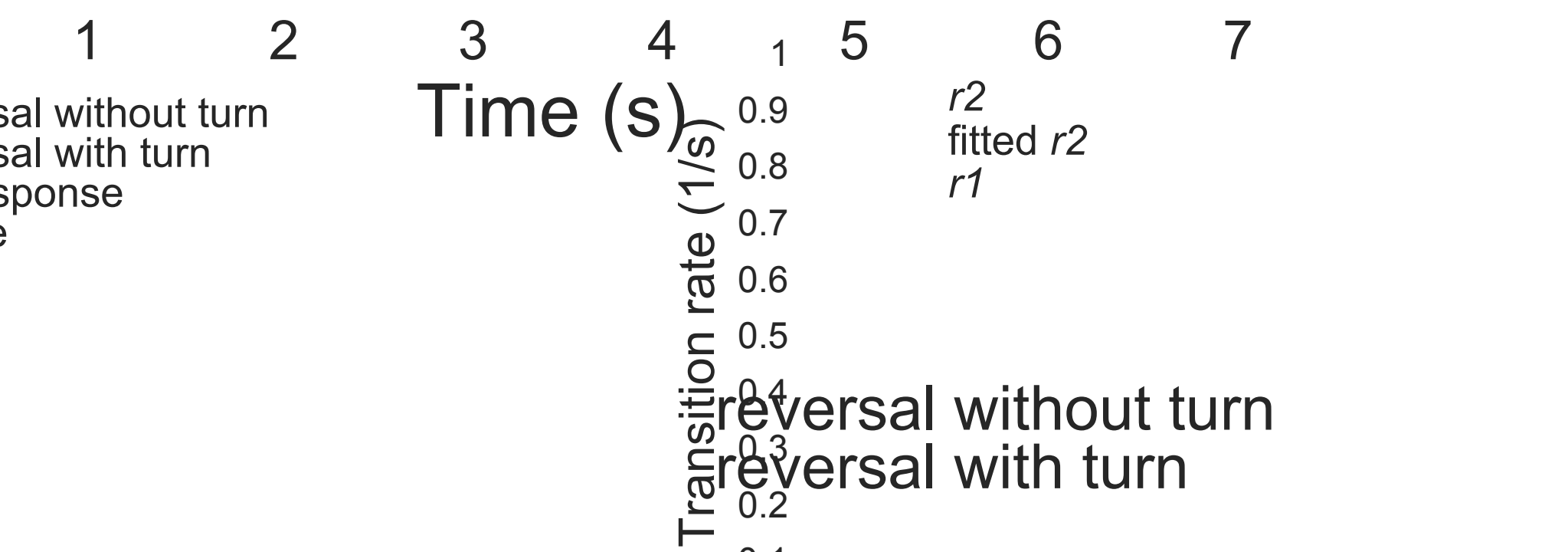
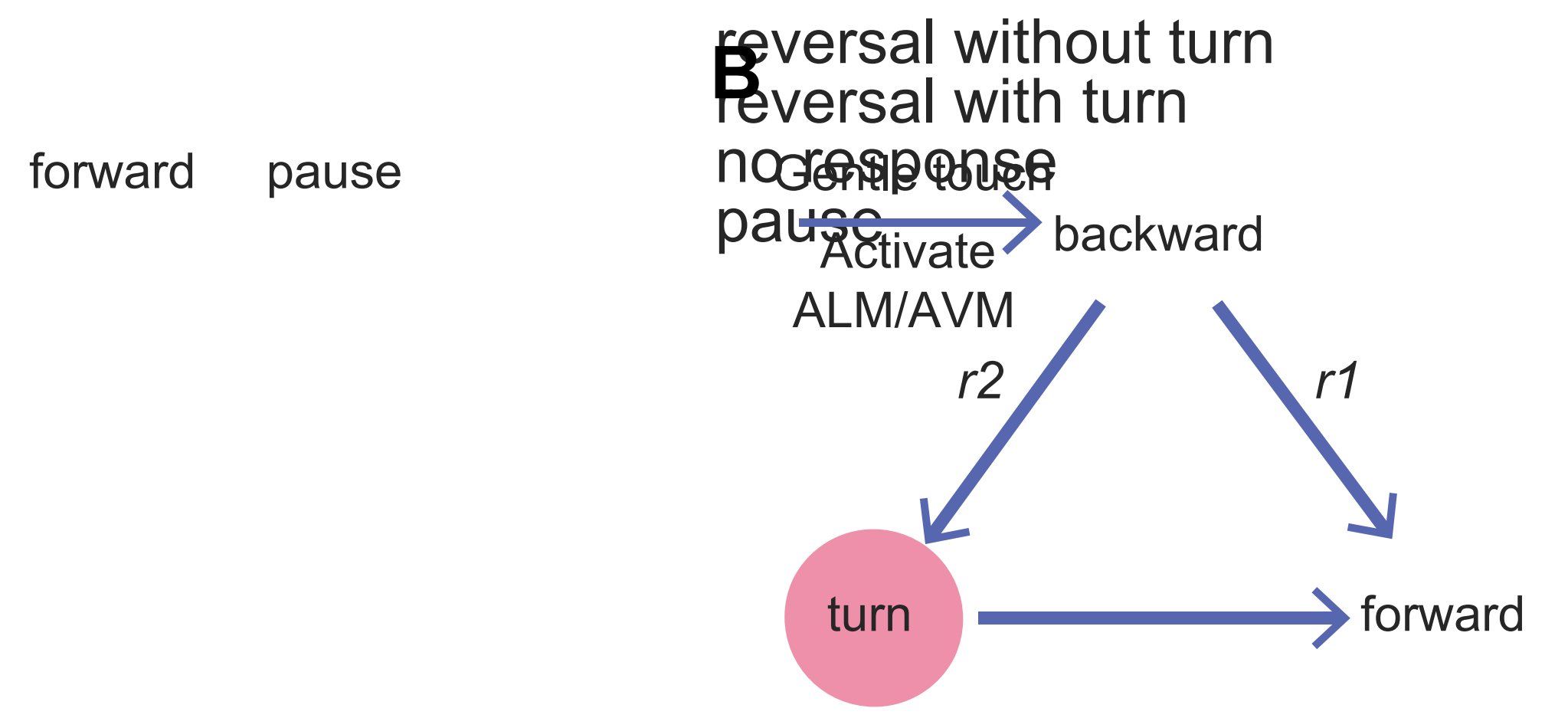
From Mark Alkema

...cting premotor interneurons ALM/AVD/AVE relay mechanosensory inputs to motor neurons
...reliably drive a backward movement (Chalfie et al., 1985; Pirri et al., 2009; Wicks et al.,
...). While *C. elegans* stays committed to its escape decision, the animal remains flexible in its
...back to complete the motor sequence. After the reversal, the animal may or may not reorient
...body via a deep omega (W) turn, before moving forward (Figure 1A). This allows the animal to
...me forward movement in either the original or a new direction. Notably, which action to select
...when to execute exhibit trial to trial variability, and they can be coupled. For example, a

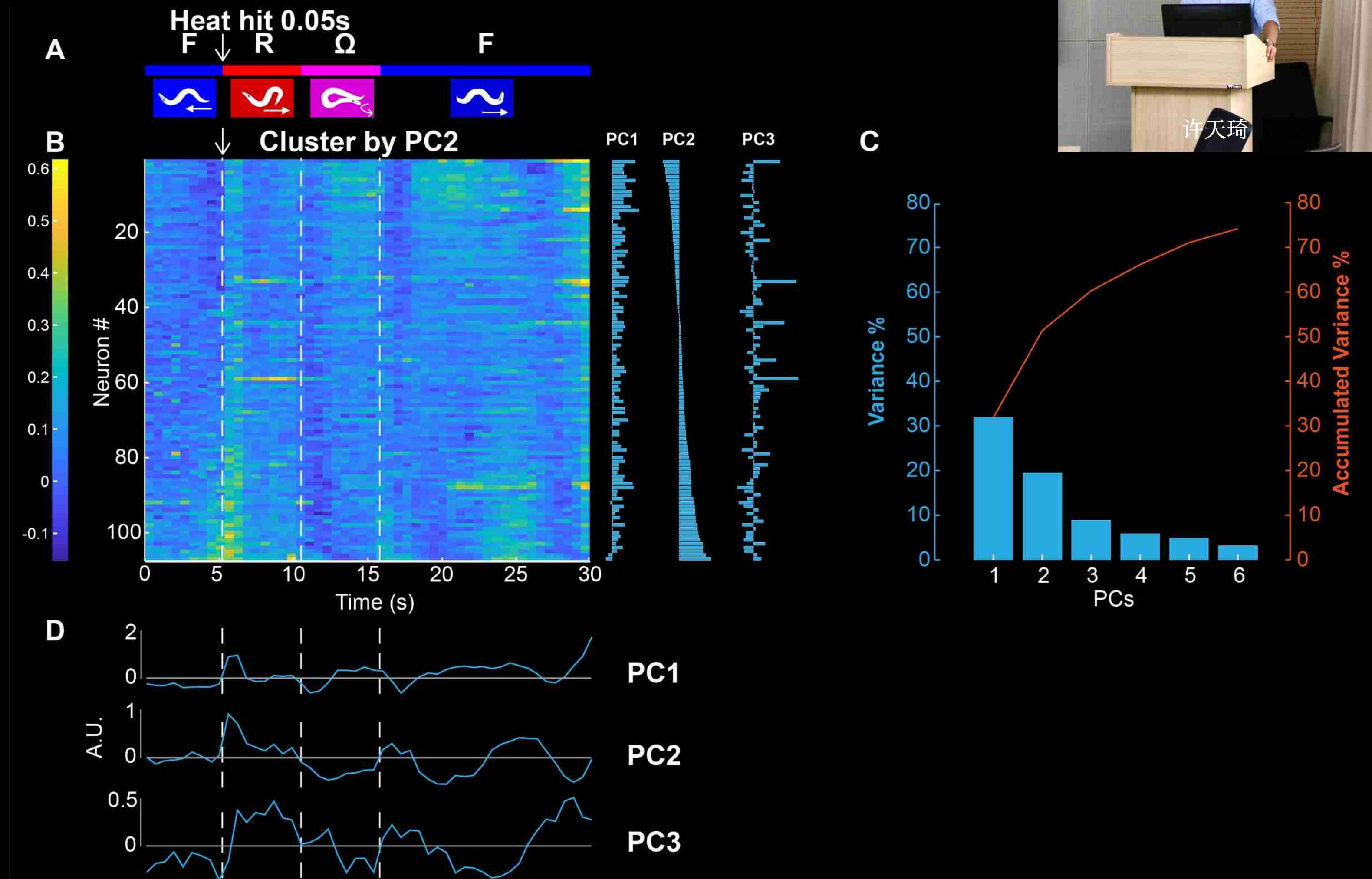
ALM/AVM
r2
turn

r1

The motor sequence transitions Markovian viewpoint



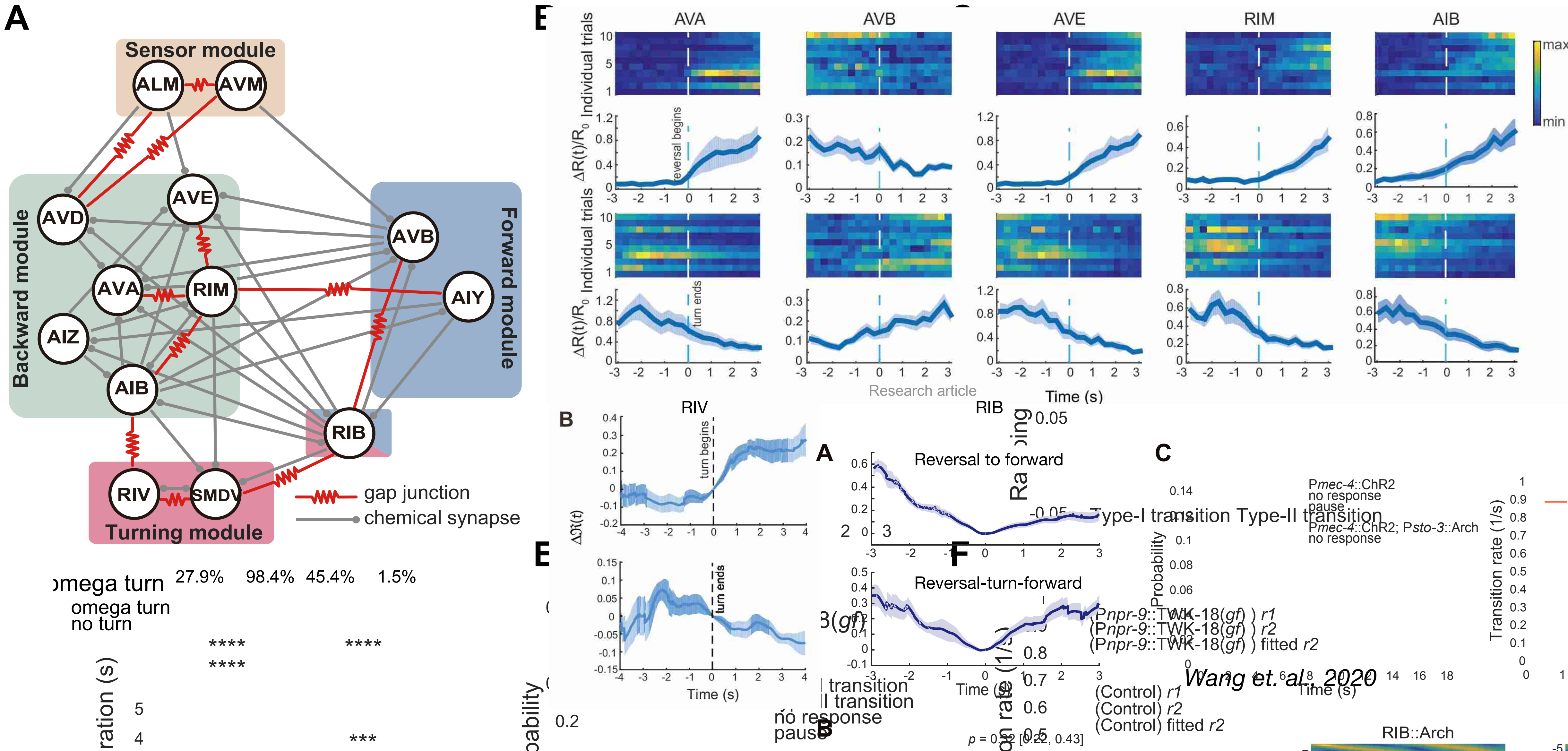
Whole brain imaging during escape responses



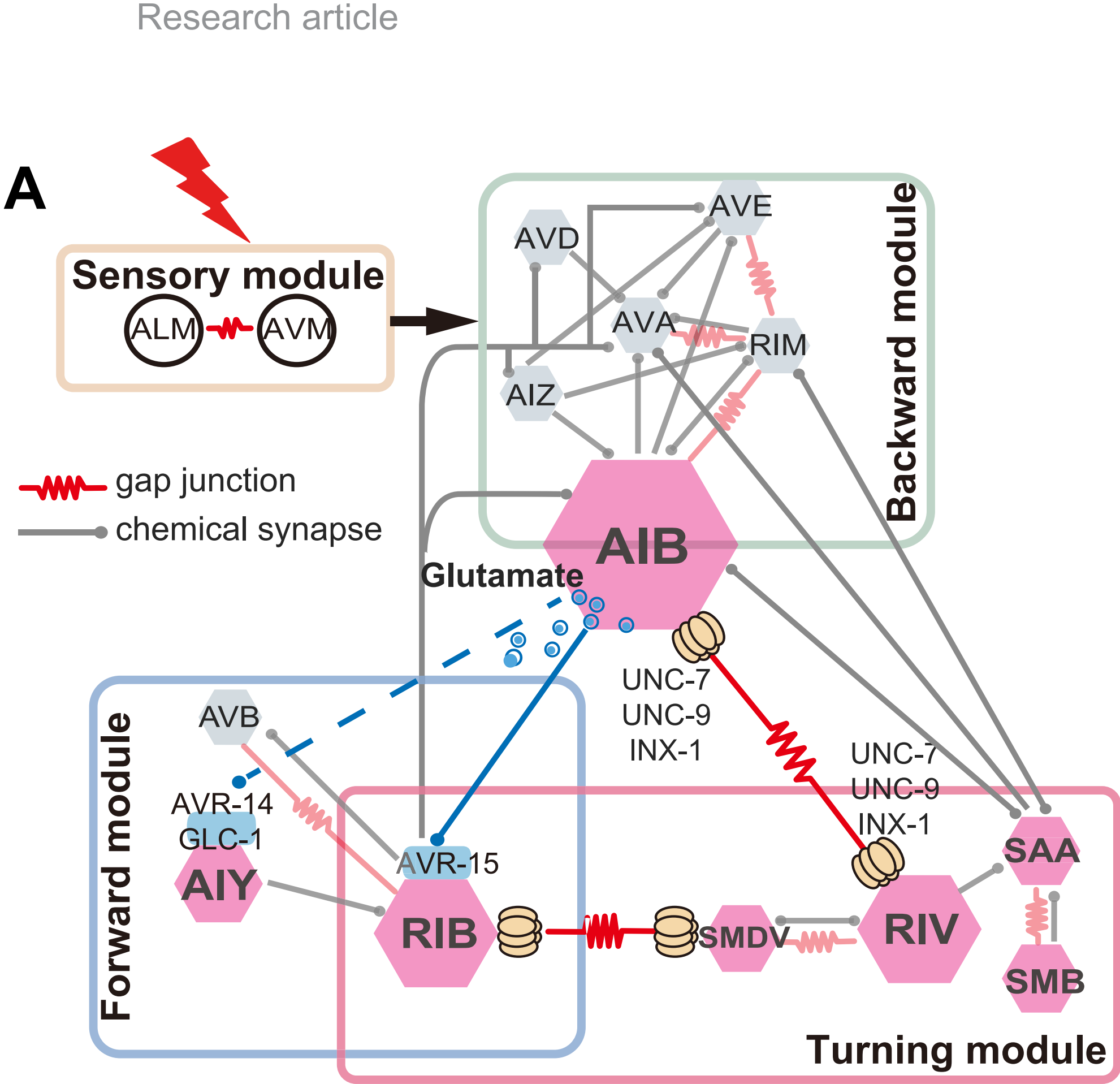
Research article

Rapid segregation from sensory to motor representation

Neuroscience

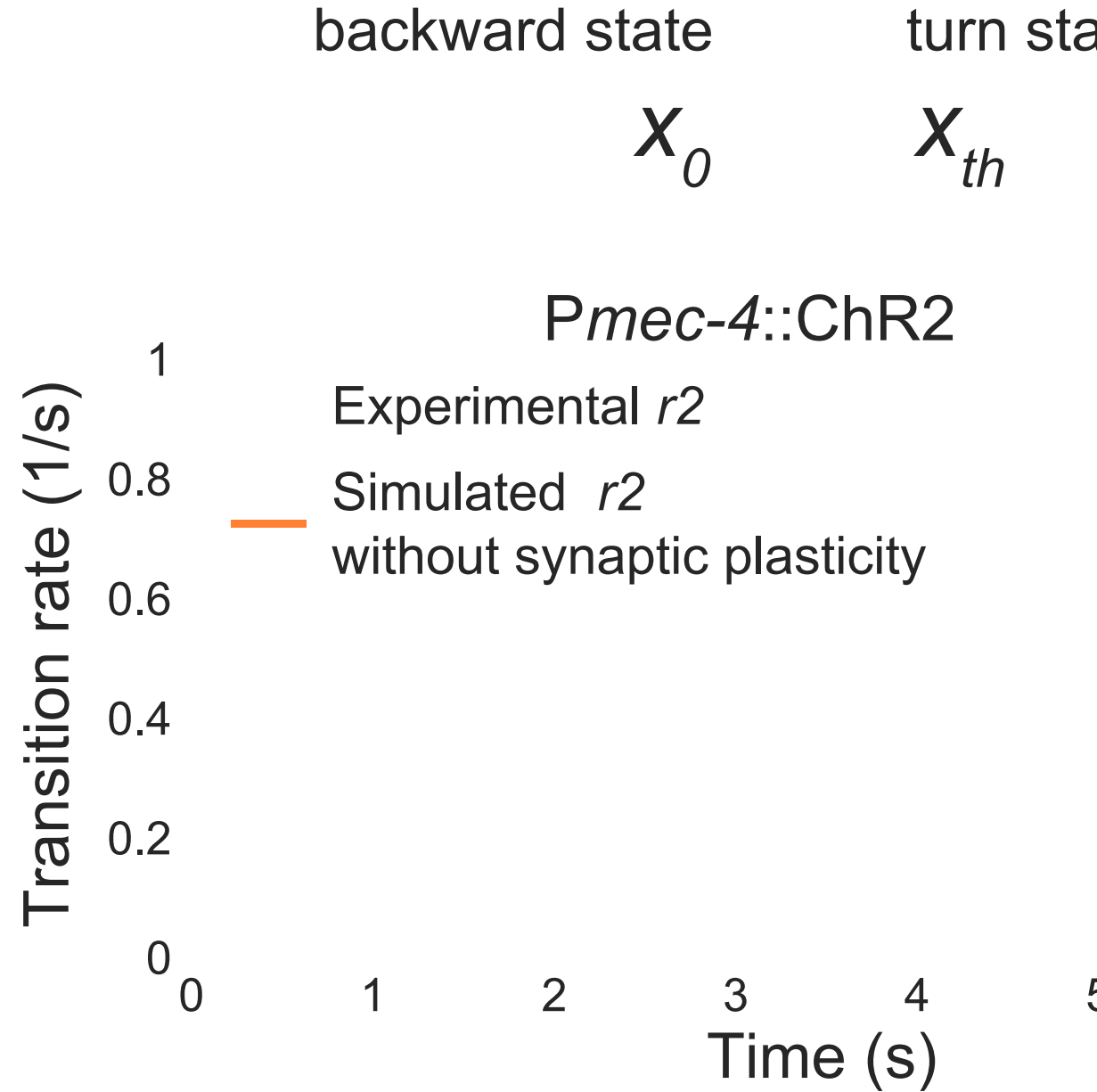


Flexible and robust motor state transition: the algorithms



B

C



D

self-excitation

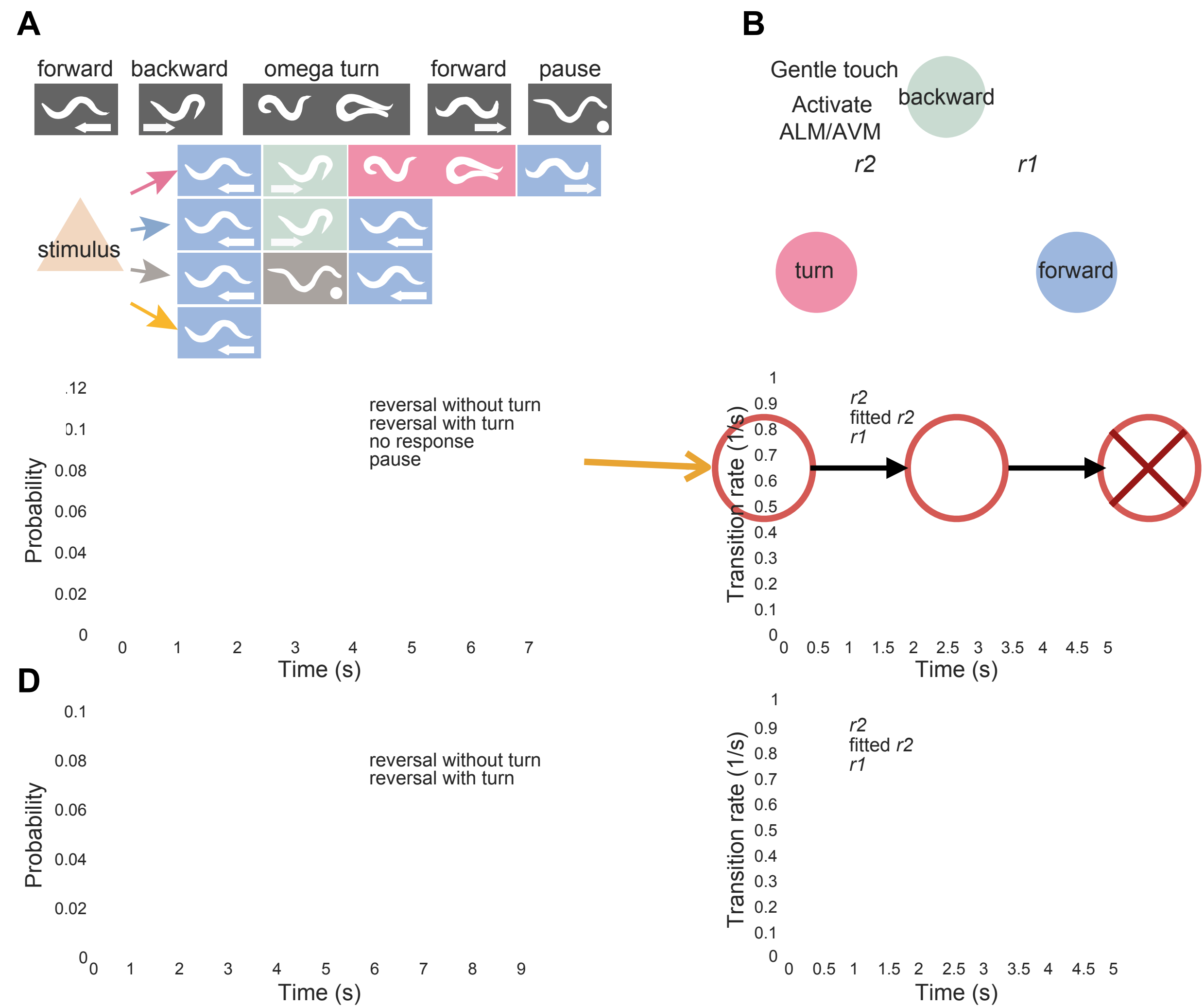
E

experimental r_2

Wang et. al., 2020

resume forward movement in either the original or a new direction. Notably, which action to select and when to execute exhibit trial to trial variability, and they can be coupled. For example, a

How is the activity in one module terminated?



*Abele M, 1991
Corticonics: Neural Circuit
of the Cerebral Cortex
Cambridge University Press*

Figure 1. Flexible motor sequence generation during *C. elegans* escape responses. (A) Optogenetic stimulation of mechanosensory neurons ALM/AVM (Pmec-4::ChR2) was carried out with blue light (473 nm, 4.63 mW/mm²) for 1.5 s during animal forward movement. Identical stimuli could induce four different behavioral outputs: reversal followed by an omega turn, reversal followed by forward movement, pause state or forward movement (no

Control

ALM/AVM::ChR2

1.5 sec activation

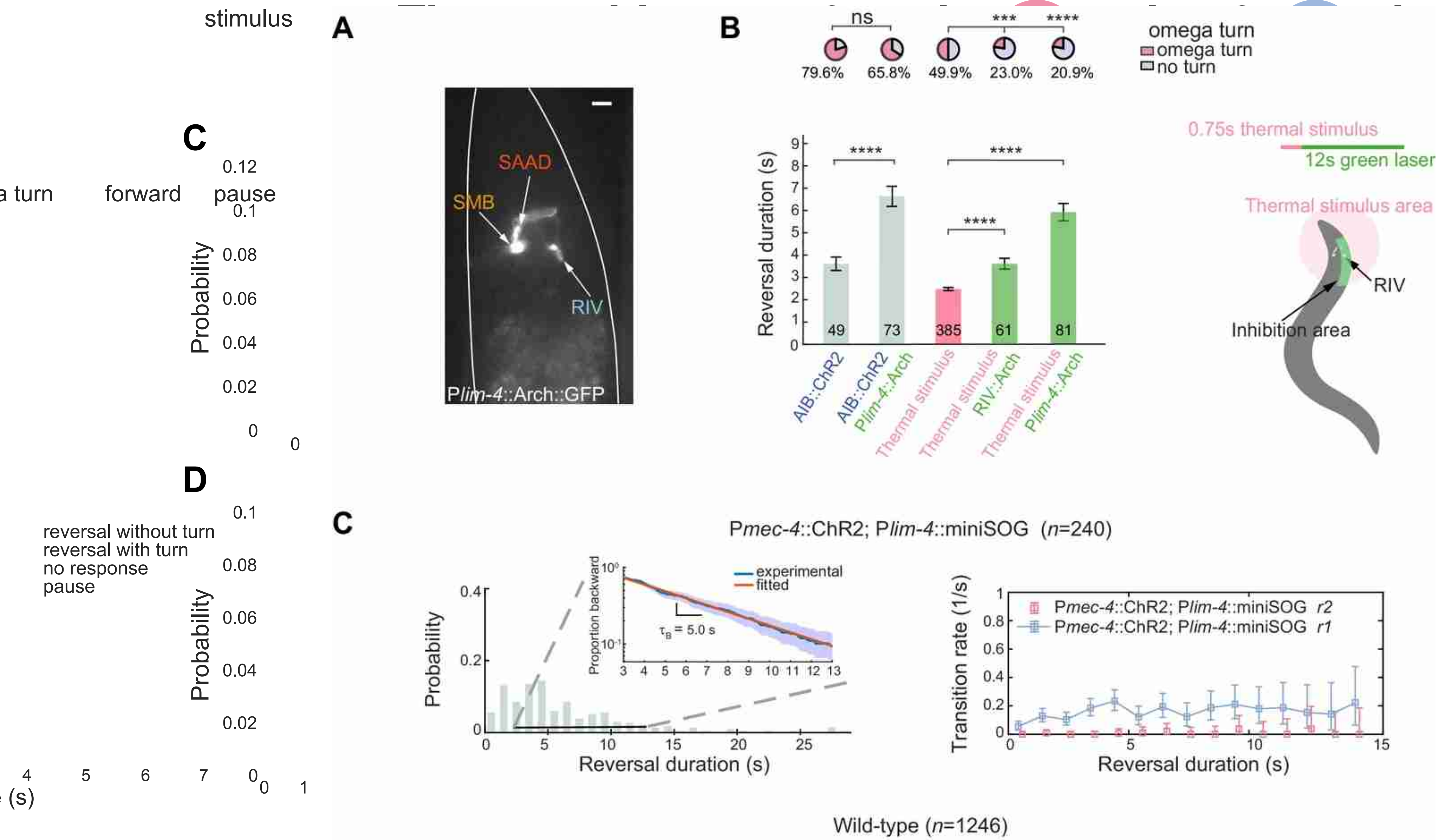
Ablating the turning module

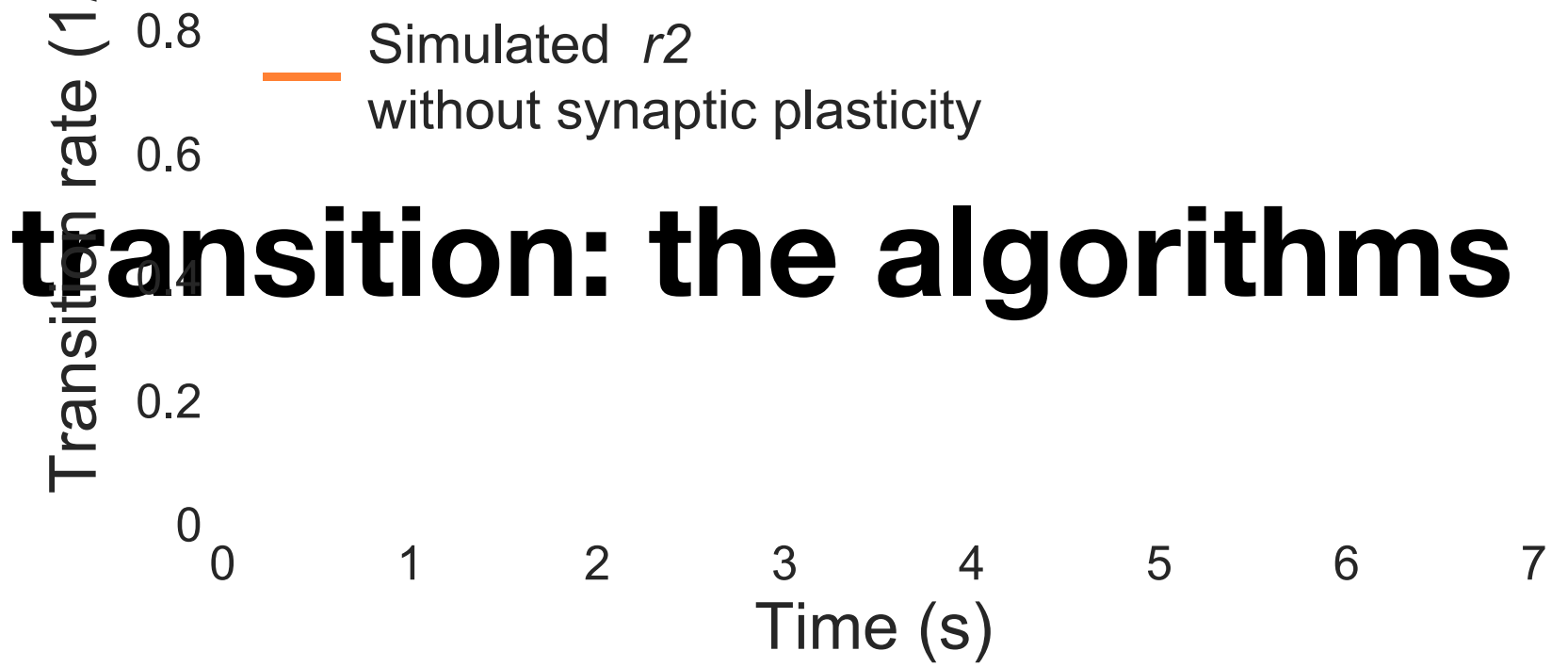
ALM/AVM::Cfr2
P_{lin-4}::miniSOG

1.5 sec activation

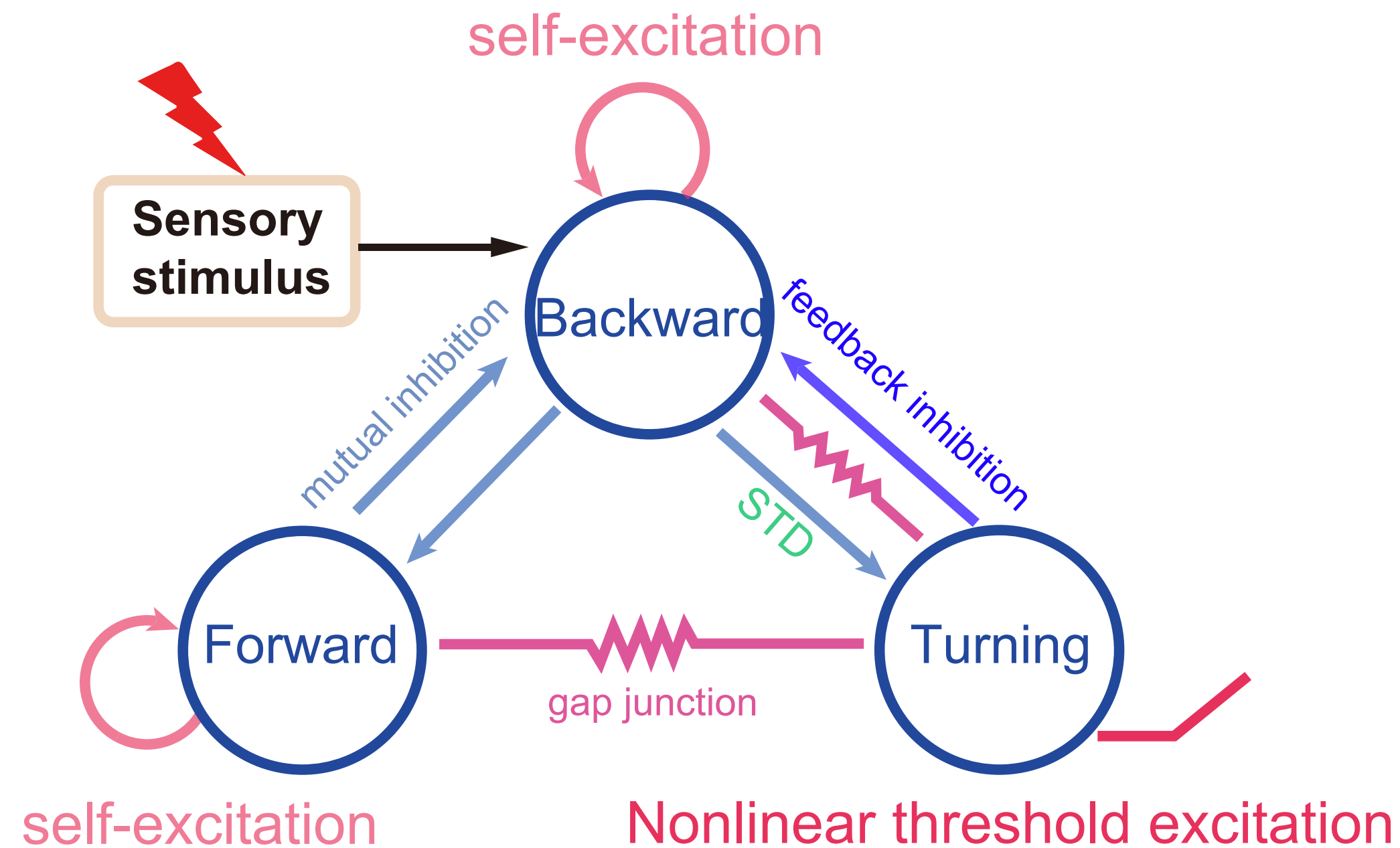
Wang et. al., 2020
Also see Kumar & Leifer 2023

its body via a deep omega (W) turn, before moving forward (Figure 1A). This allows the animal to resume forward movement in either the original or a new direction. Notably, which action to select and when to execute exhibit trial to trial variability, and they can be coupled. For example, a





D



E

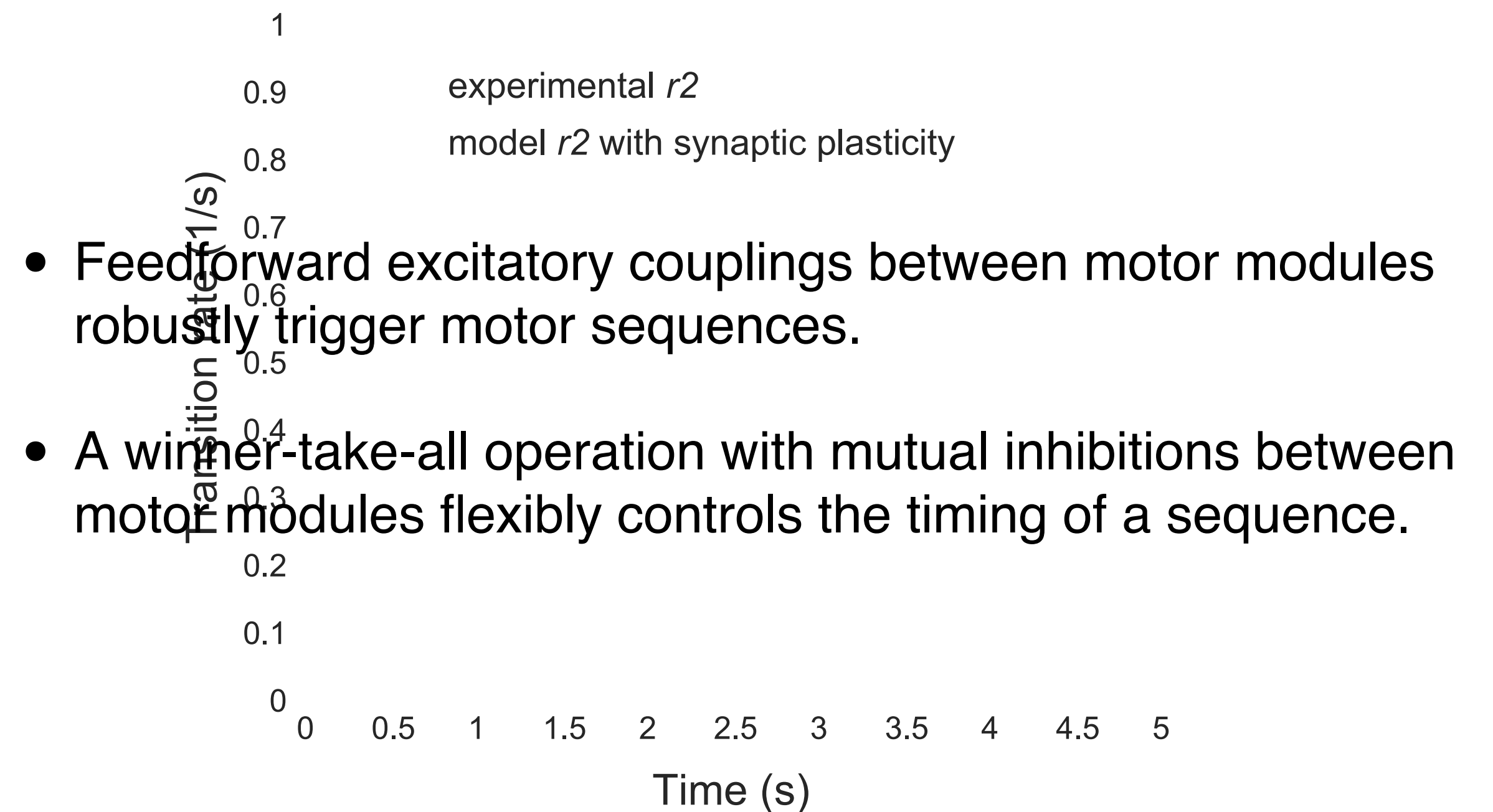


Figure 7. A model summary for motor sequence generation. (A) Schematics of neuronal circuit of *C. elegans* avoidance behavior. Feedforward excitation between local interneurons AIB and RIV triggers turning behavior. Glutamatergic inhibition between AIB and RIB flexibly controls the motor state transitions. Feedback inhibition from the turning module helps terminate backward behavior. (B) Illustration of the biophysical meaning of the Wang *et. al.*, 2020 type-II transition. The sub-threshold membrane potential of RIV fluctuates around the fixed point x_0 , just like a particle (red) in an energy well. When RIV membrane potential crosses the threshold x_{th} , RIV along with other neurons in the turning module become fully activated and a turn starts. (C) A simple stochastic model without short-term synaptic plasticity cannot account for the experimentally observed transition rate. (D) Schematics of a three-module

Neuron

Feedforward function within recurrent architecture

Goldman et. al., 2009

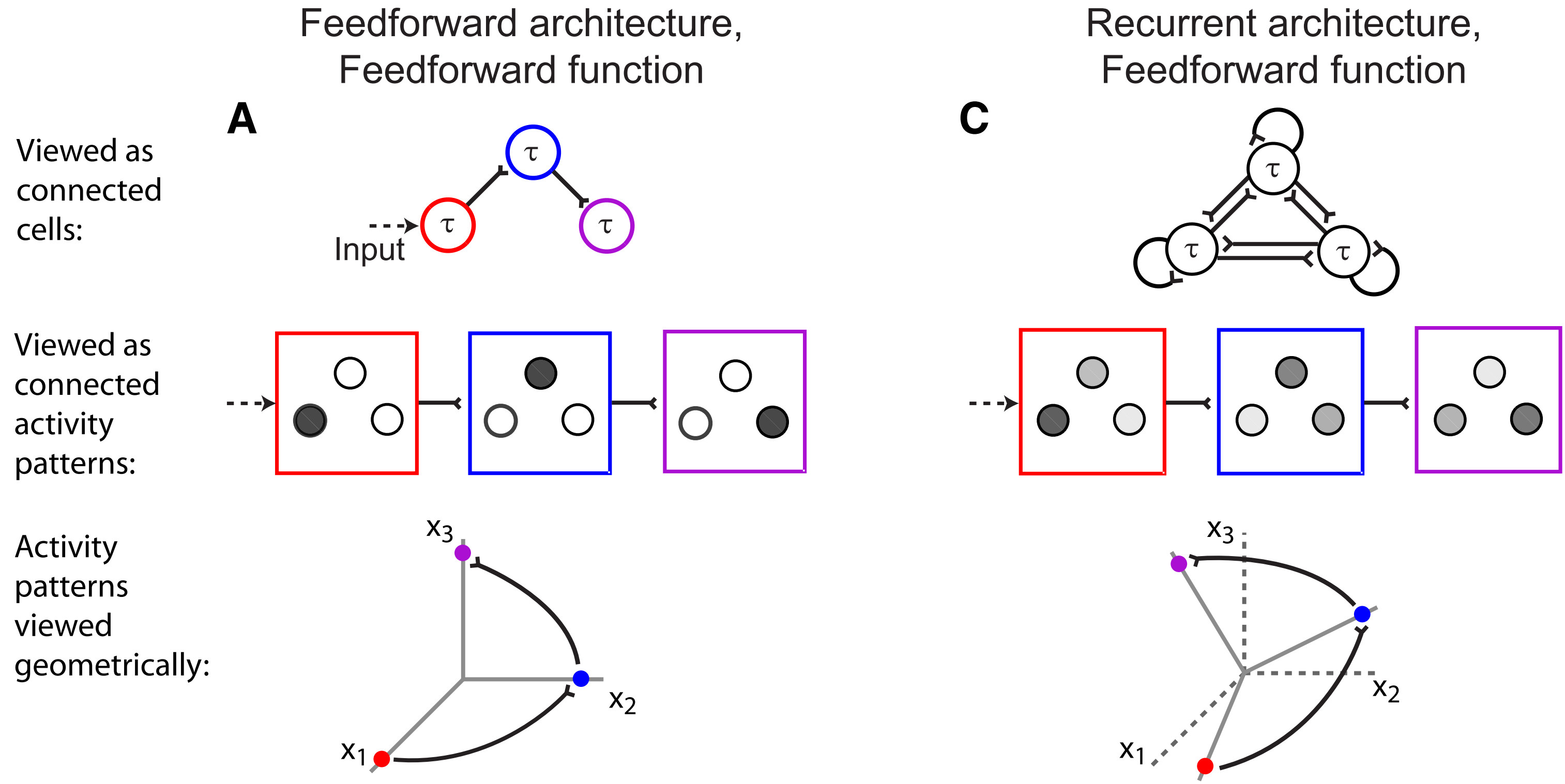


Figure 3. Feedforward Processing by a Recurrent Network

(A) Processing by an architecturally network (top). Firing of each individual neuron can be alternatively viewed as firing of a pattern in which this neuron is active and the others are silent (middle). In this view, the connections between neurons are replaced by connections between patterns so that earlier patterns trigger subsequent patterns of activity. Each activity pattern can be represented by a point in N -dimensional space (here) whose component along the i th axis represents the i th neuron's activity level in that pattern.

(B) Amount of activity in each pattern over time, when a pulse of input stimulates the first activity pattern. Because the activity patterns correspond to a single neuron being active, the graph reproduces the progression of activity of individual neurons.

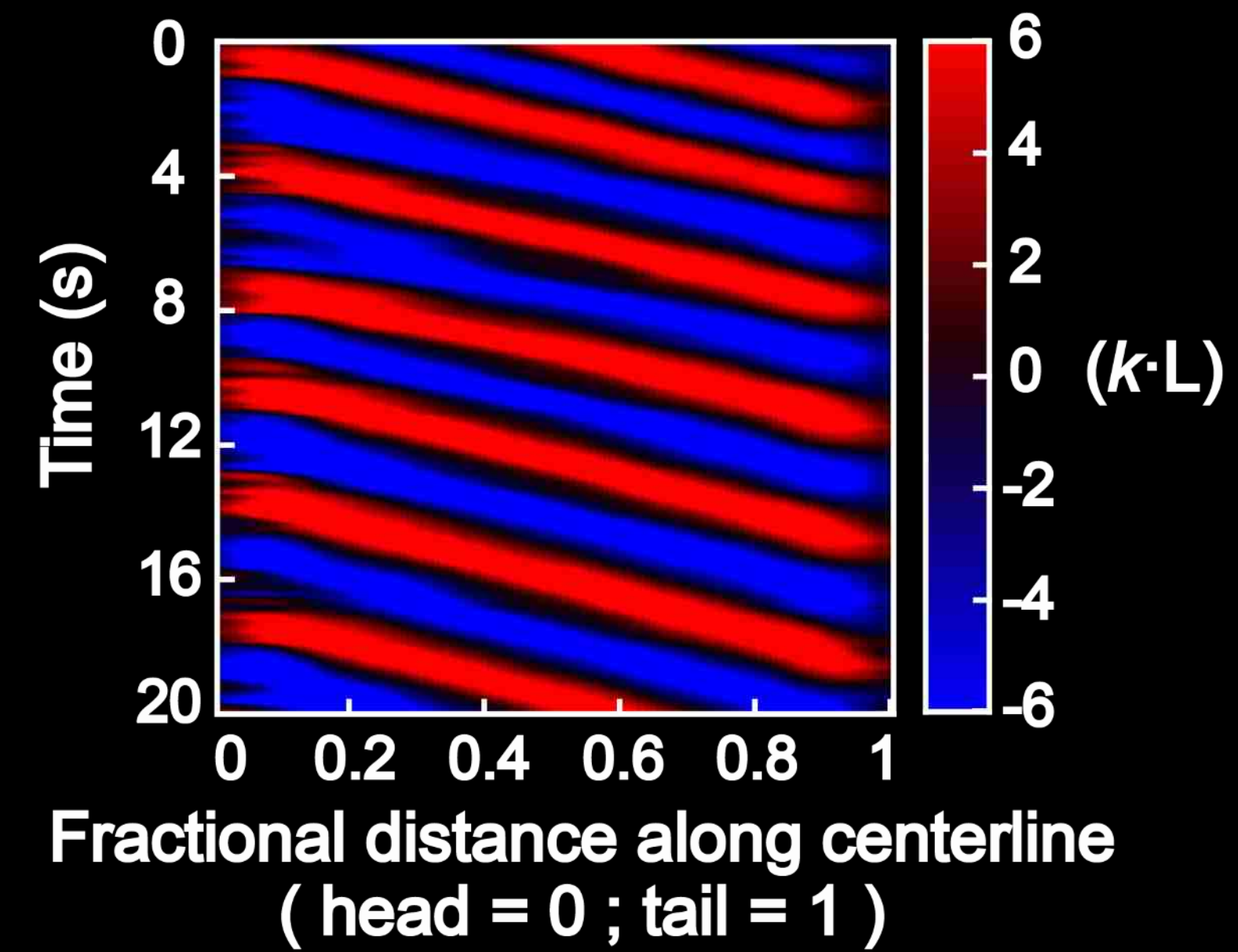
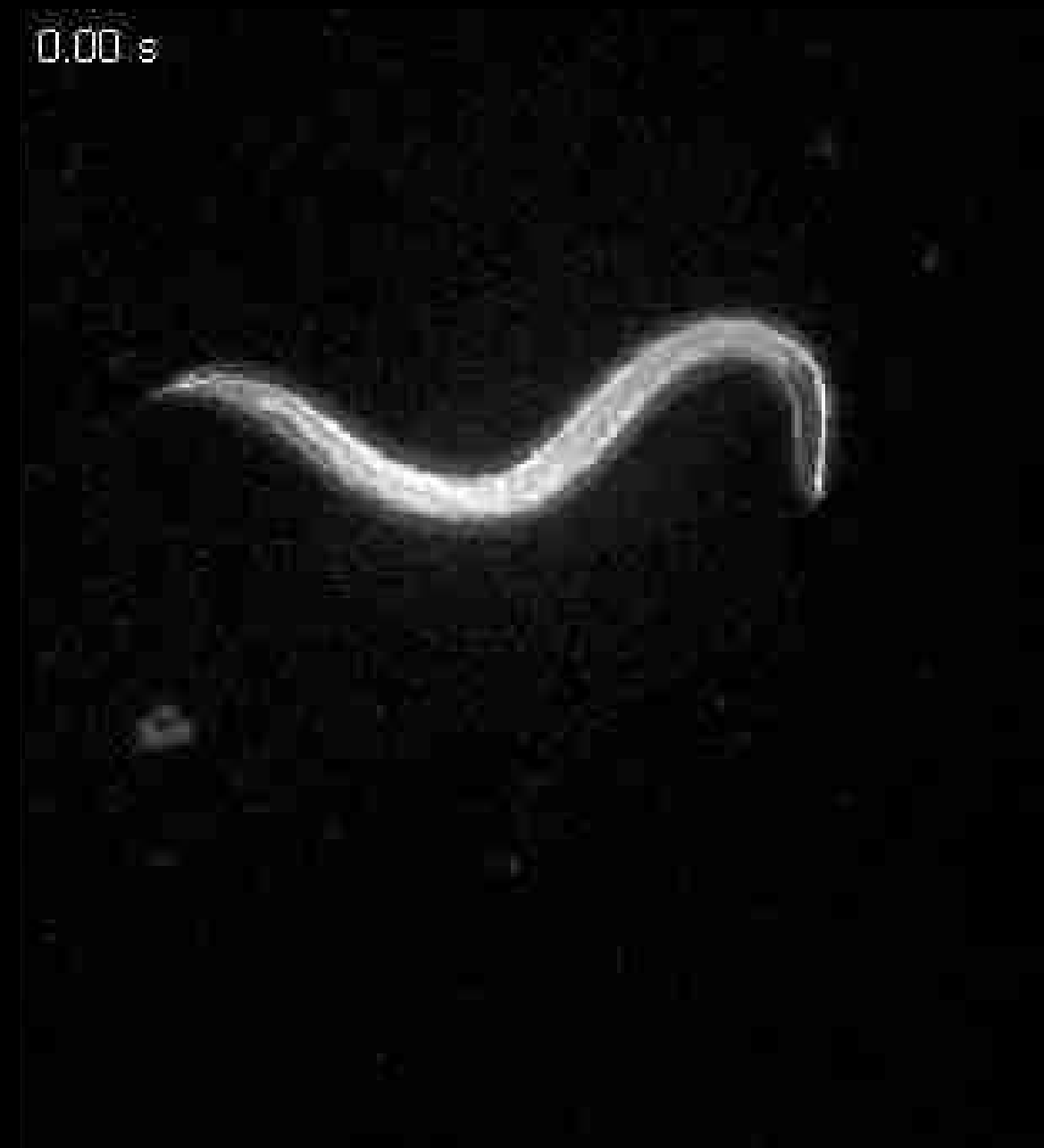
(C) Recurrent network that behaves like the feedforward network of panel (A). It propagates in a feedforward manner through orthogonal patterns (middle, bottom).

(D) When a pulse of input stimulates the first activity pattern, the network propagates the activity through the recurrent connections, reproducing the progression of activity of individual neurons.

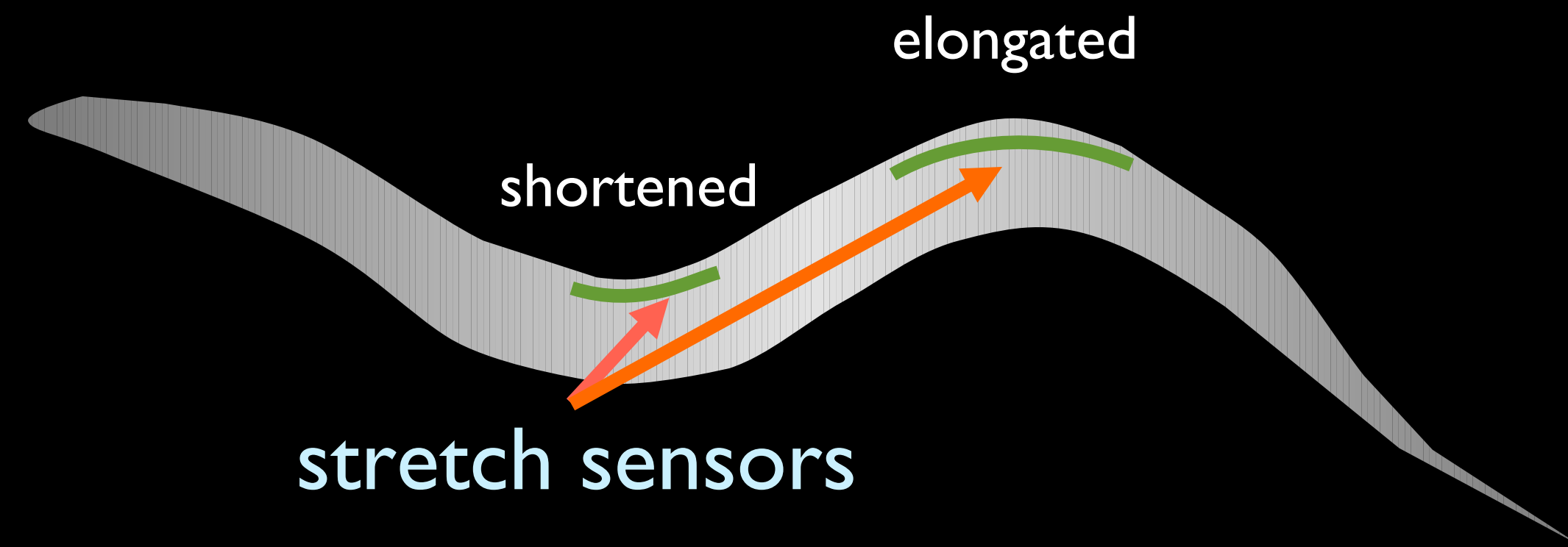
Discover feedforward modes within RNN using Shur decomposition

Motor sequence generation on a shorter timescale

Propagating bending waves across spacetime



Proprioception

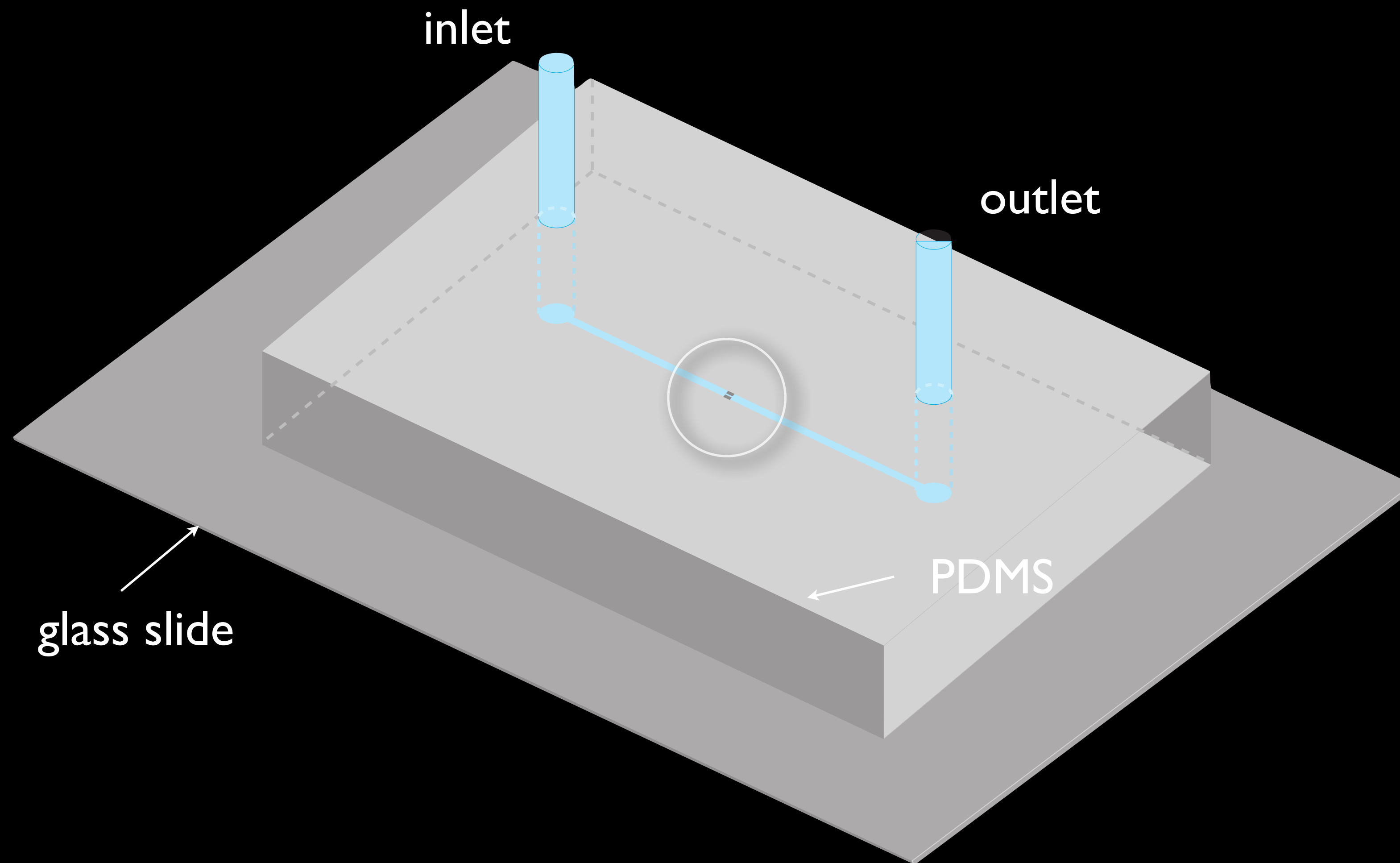


Richard L Russell 1970s

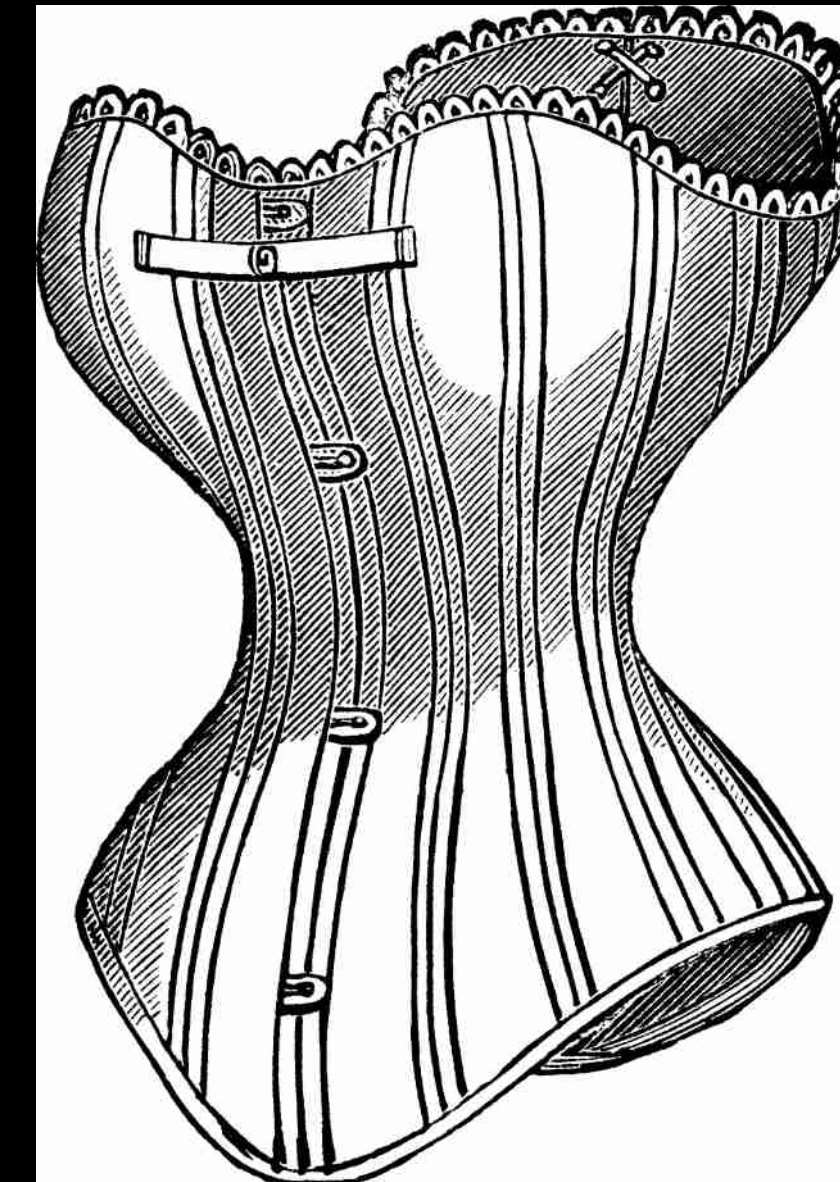
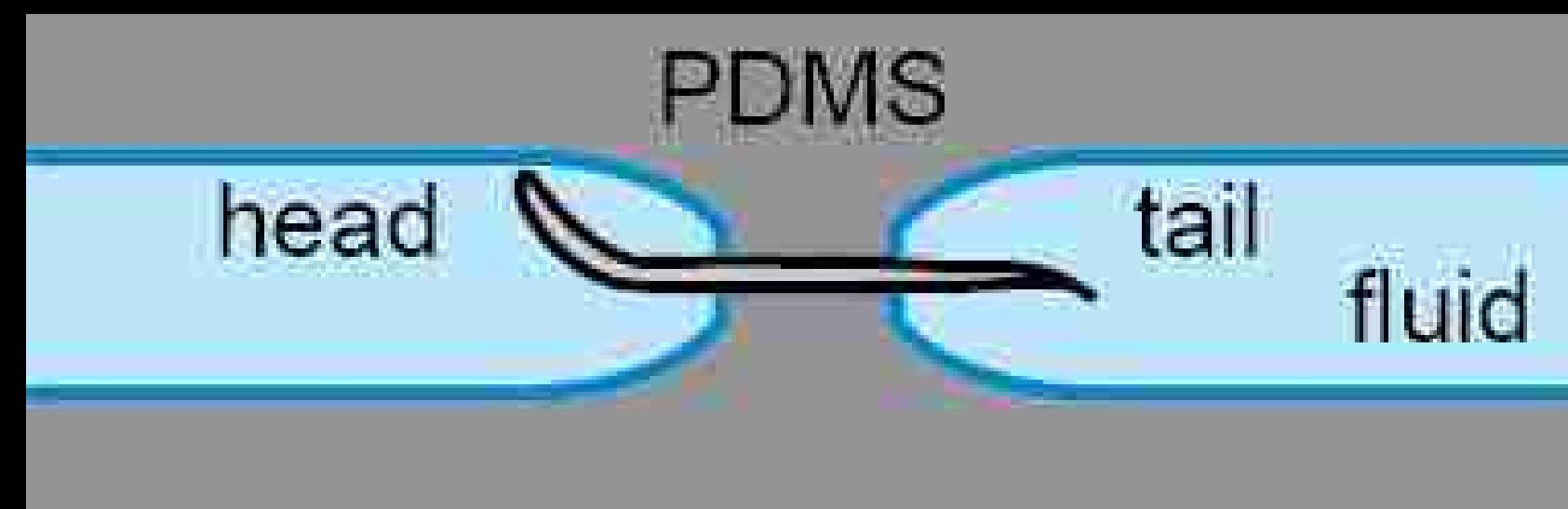
Wen et al, 2012

University of Texas

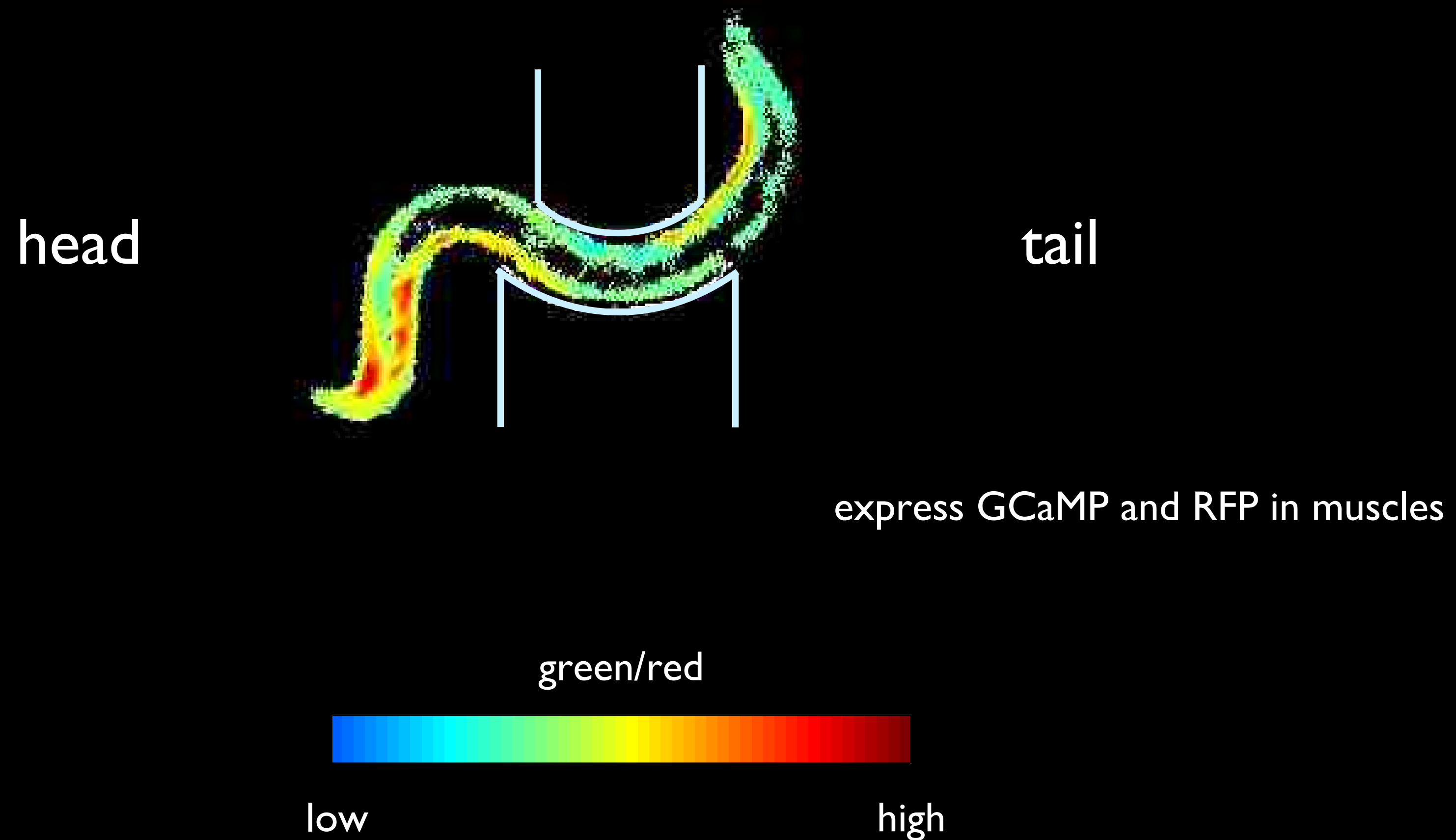
Microfluidics



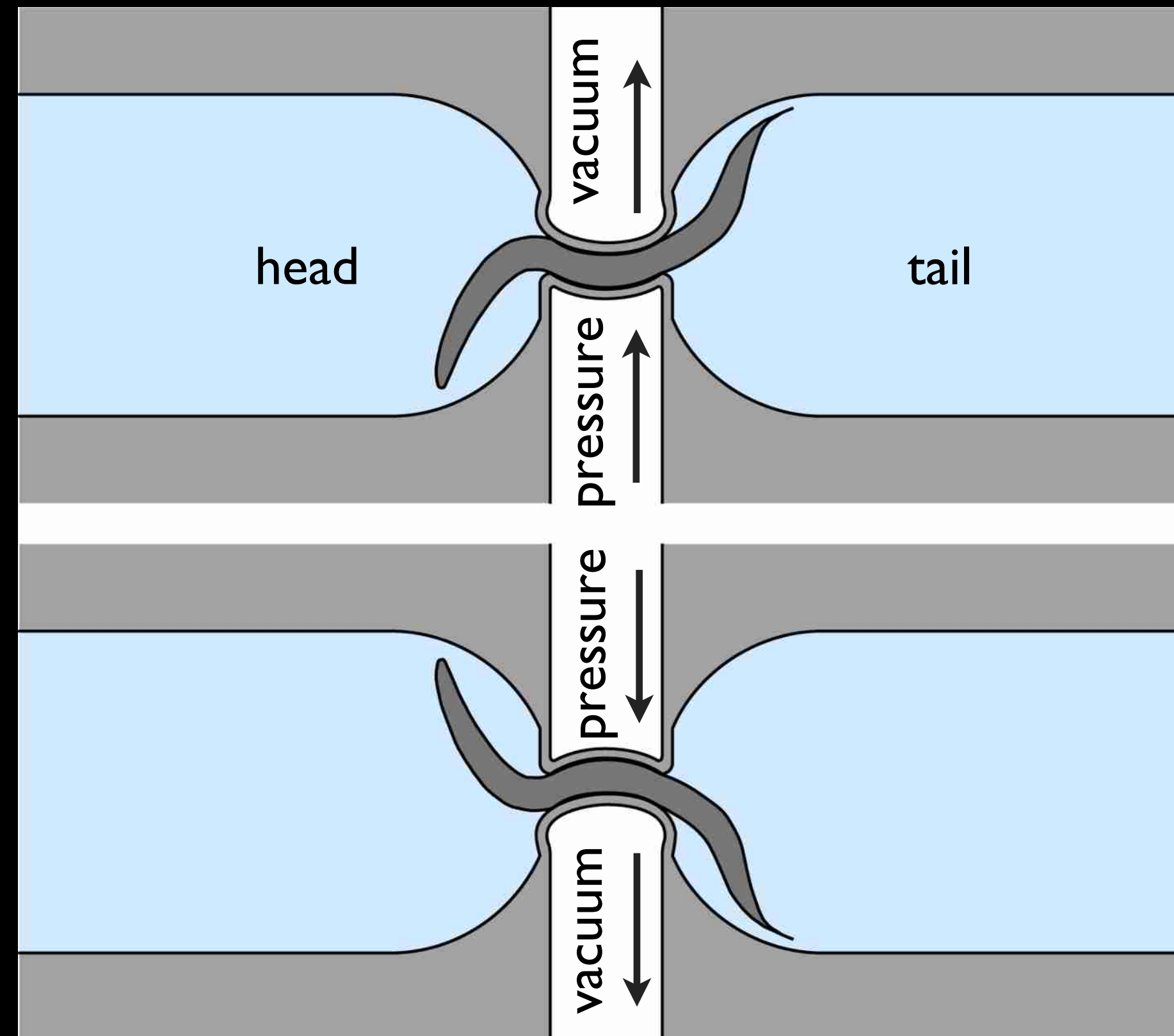
Microfluidic corset



Posterior body region is compelled to bend in the same direction as its anterior neighbor



Pneumatic microfluidic device

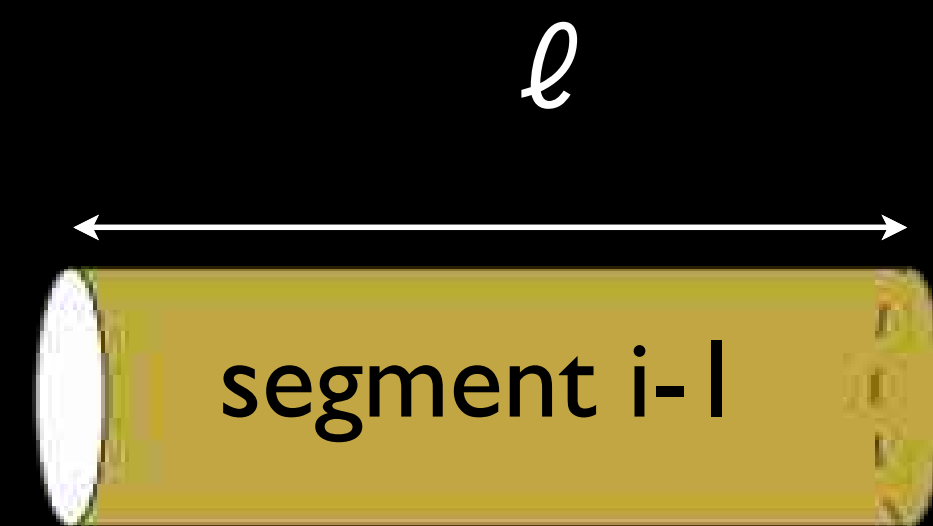


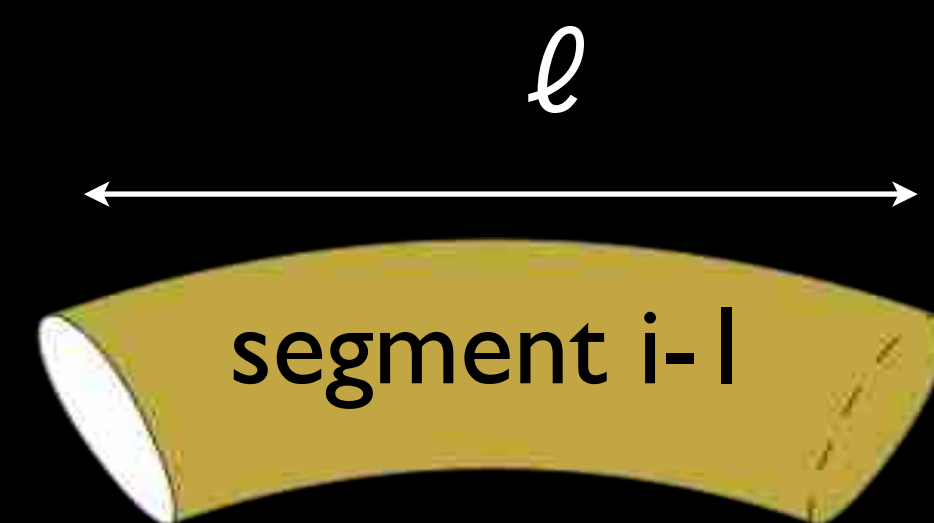
more viscous medium
medium: water

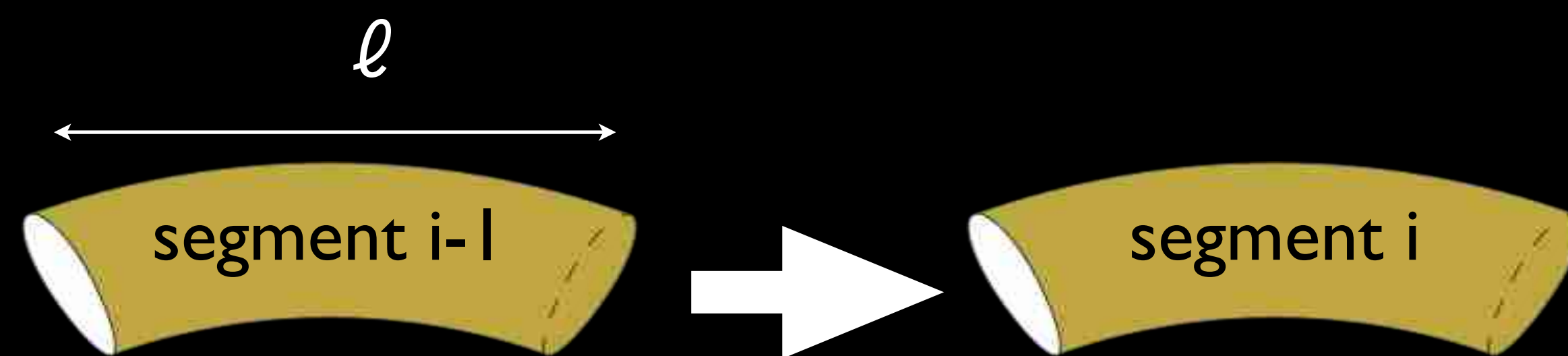
head



tail







A linear proprioceptive coupling model



$$\tau_c \frac{dv_i}{dt} = -v_i + cK_{i-1}$$

$$\tau_\eta \frac{dK_i}{dt} = -K_i + v_i \alpha_{max}/b$$

$$\tau_\eta \sim \eta \lambda^4 / b$$

K : segment curvature

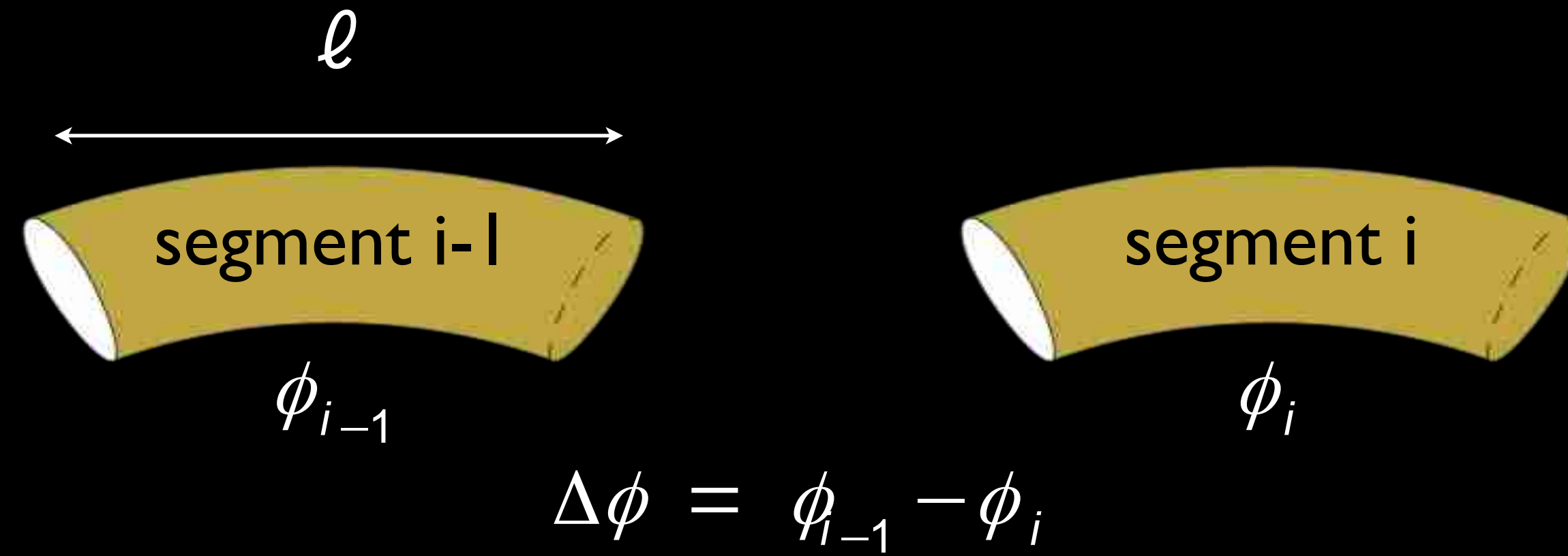
v : relative motor neuron activity

τ_c : internal coupling delay within the circuit
(say cell membrane time constant)

τ_η : delay between motor neuron activities and
local body curvature imposed by external load

η : viscosity of a medium (*given*)

b : bending modulus that reflects
the stiffness of a worm (*measured*)



$$\Delta\phi \approx \omega(\tau_c + \tau_\eta)$$

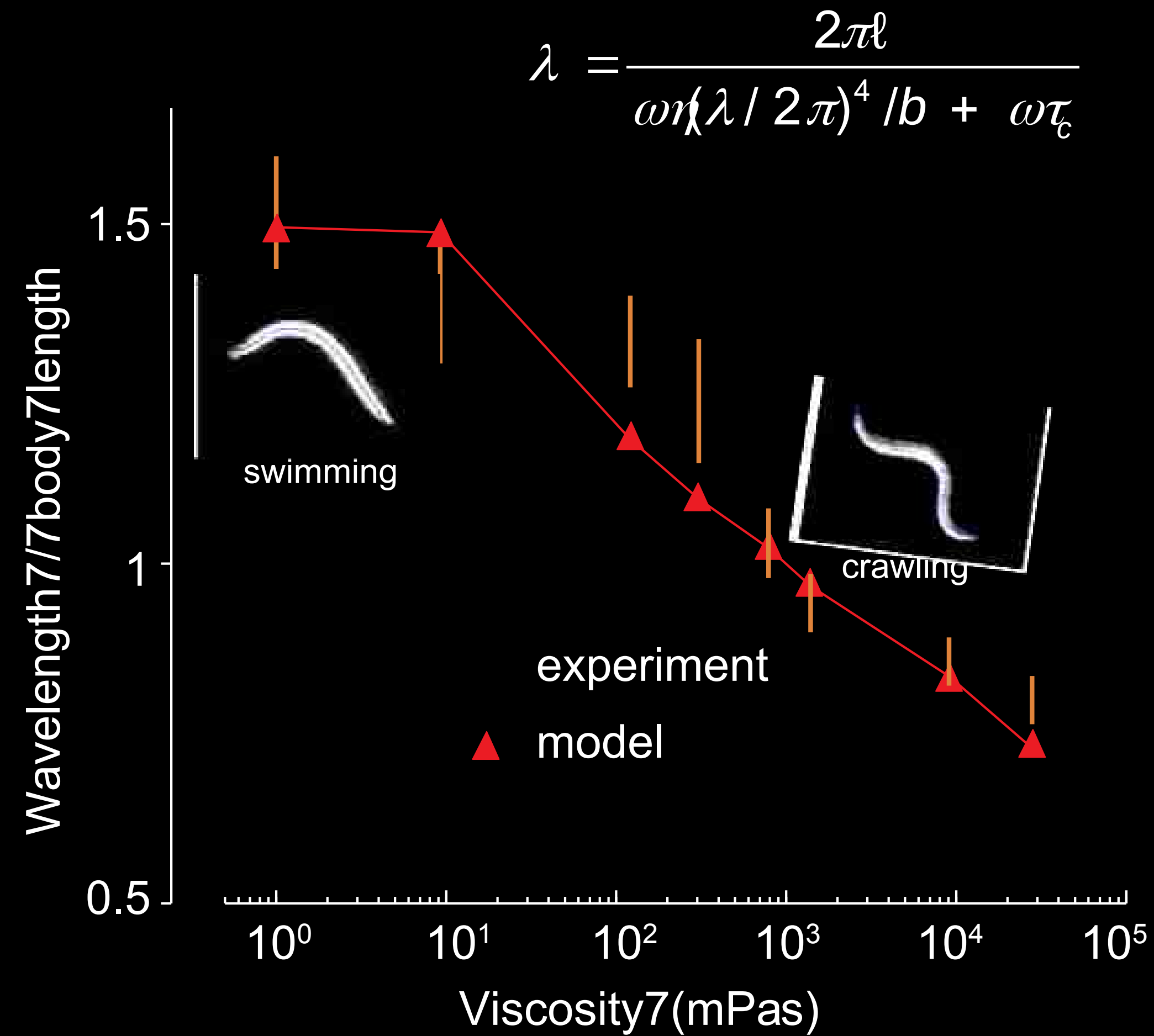
ω : angular undulation frequency

$$\lambda = \frac{2\pi}{\Delta\phi} \ell$$

λ : undulation wavelength
 ℓ : spatial length of proprioceptive coupling (*measured*)

$$\tau_\eta \gg \tau_c$$

Continuous gait adaptation



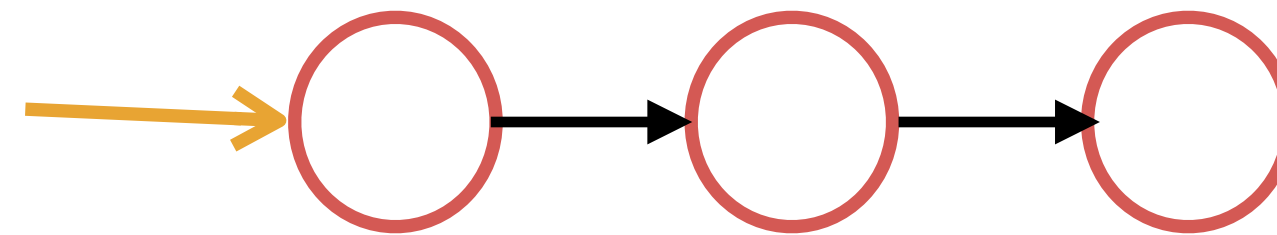
Fang-Yen et. al, 2009

Wen Q. et al, 2012

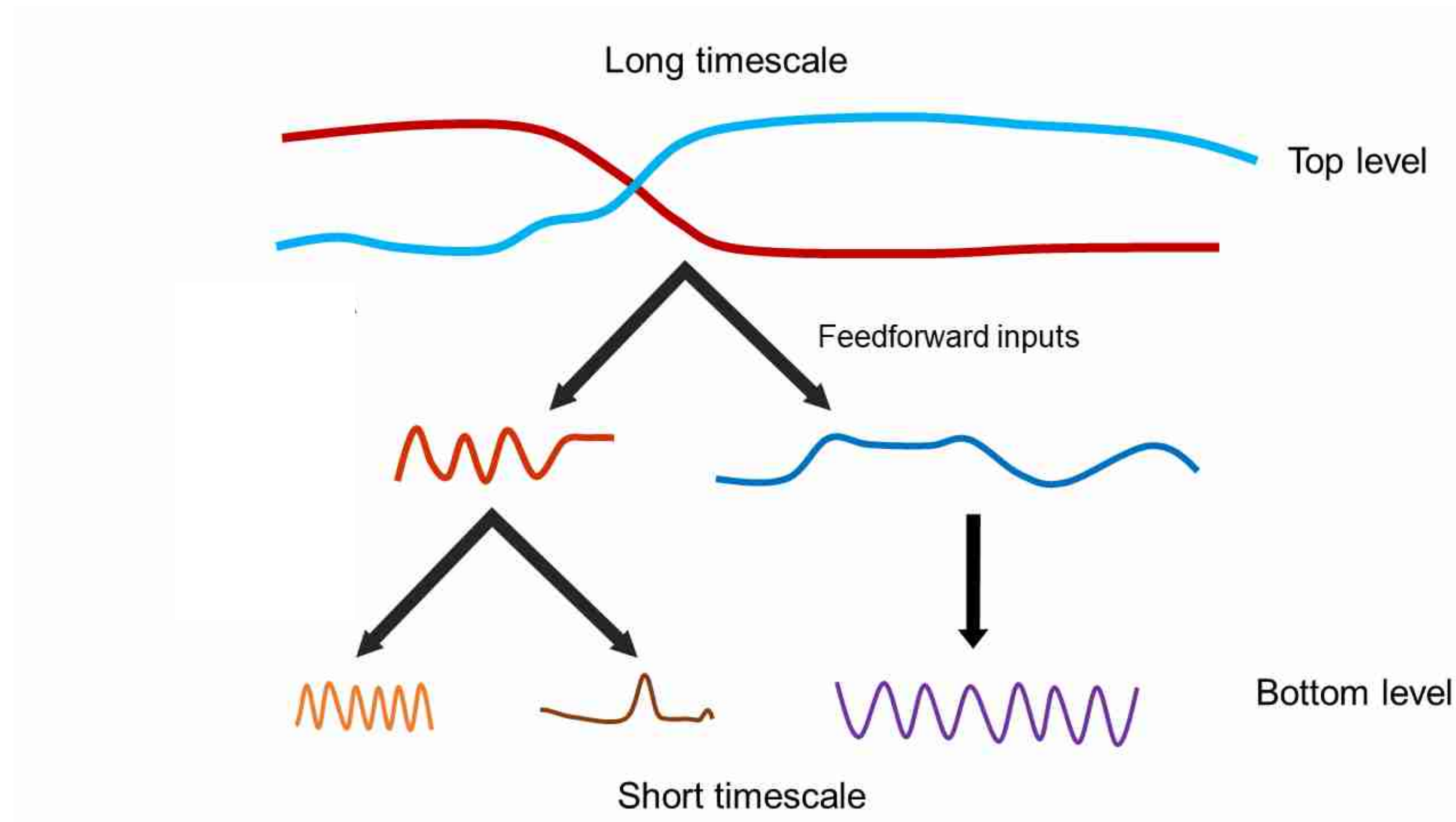
Wen Q. et al, 2012

The algorithm of faster motor sequence generation

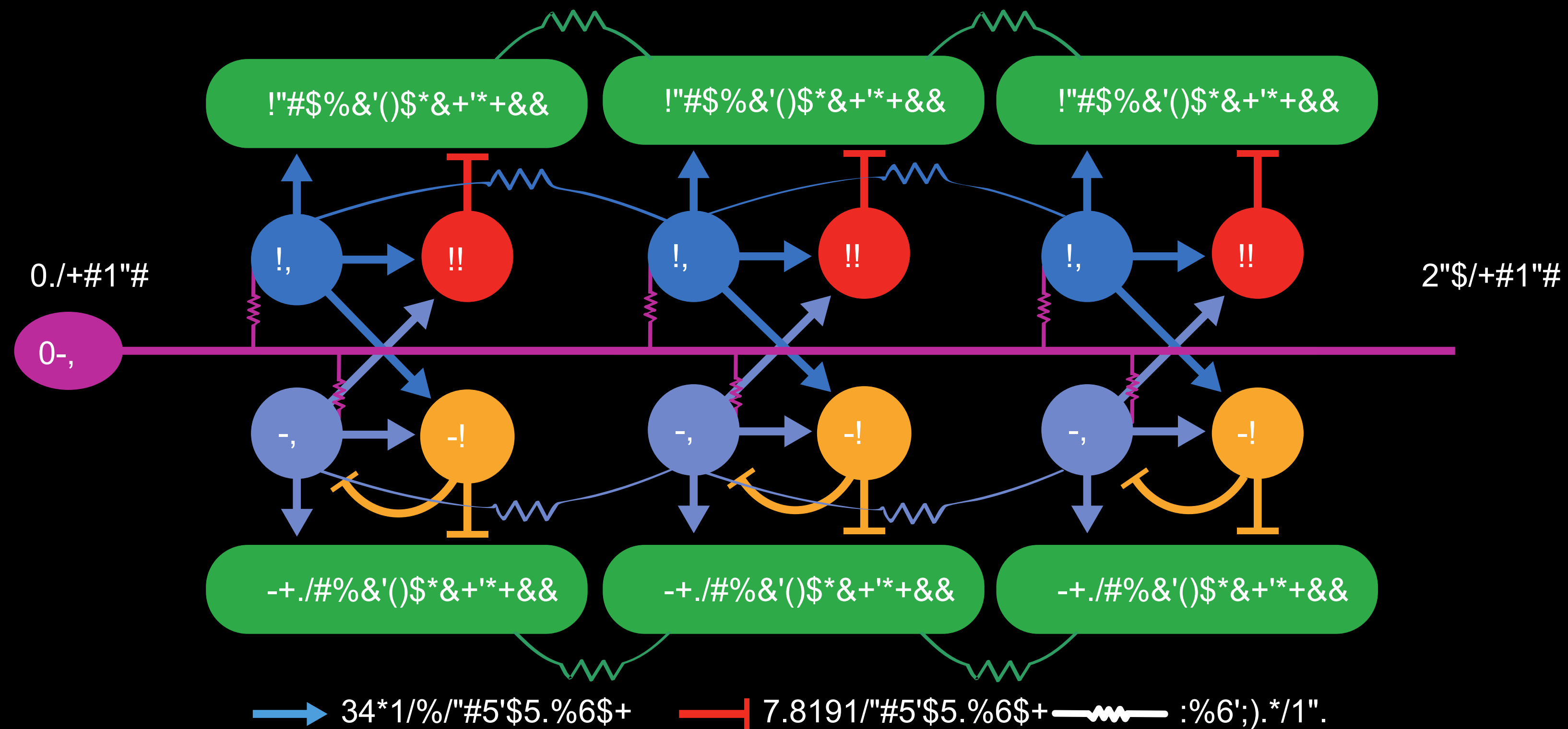
- Local proprioceptive coupling propagates the bending activity along the worm body, which can also be viewed as a feedforward chain model.



Hierarchical neural architecture for movement control



Gap junction *highway* and *byway* in forward motor circuit



AVB descending inputs provide command signals

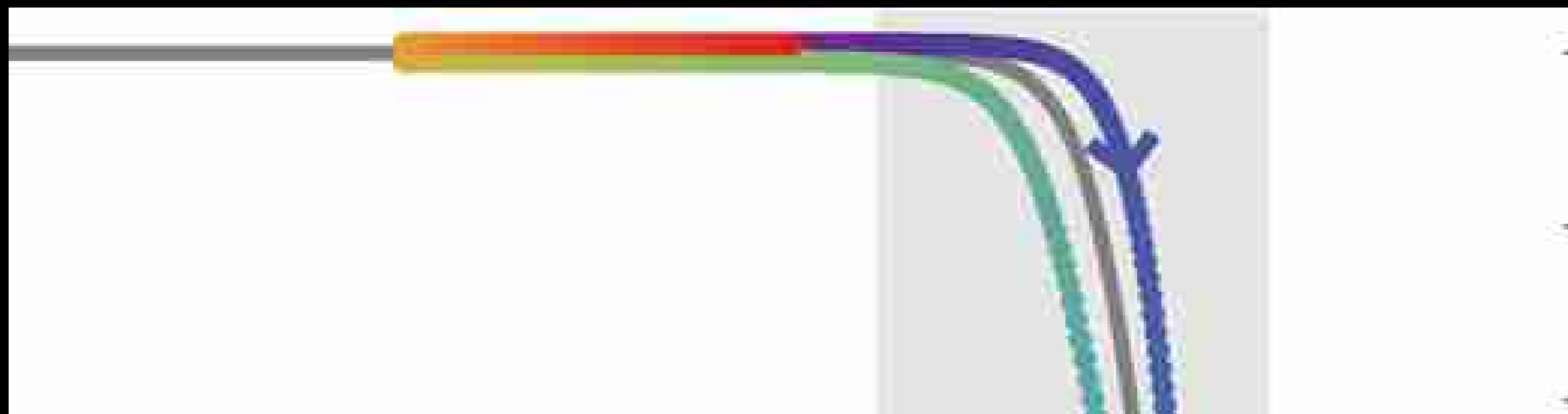
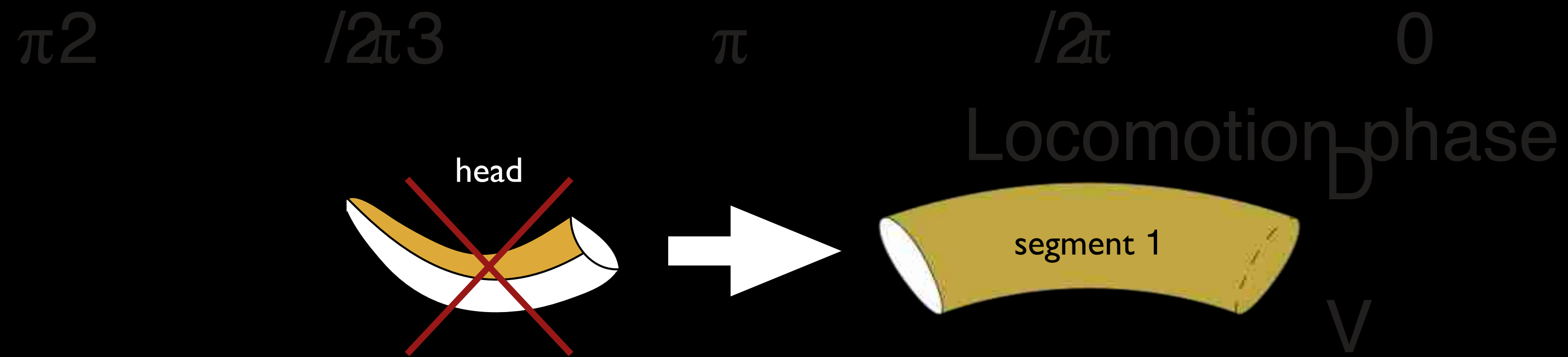


Activation

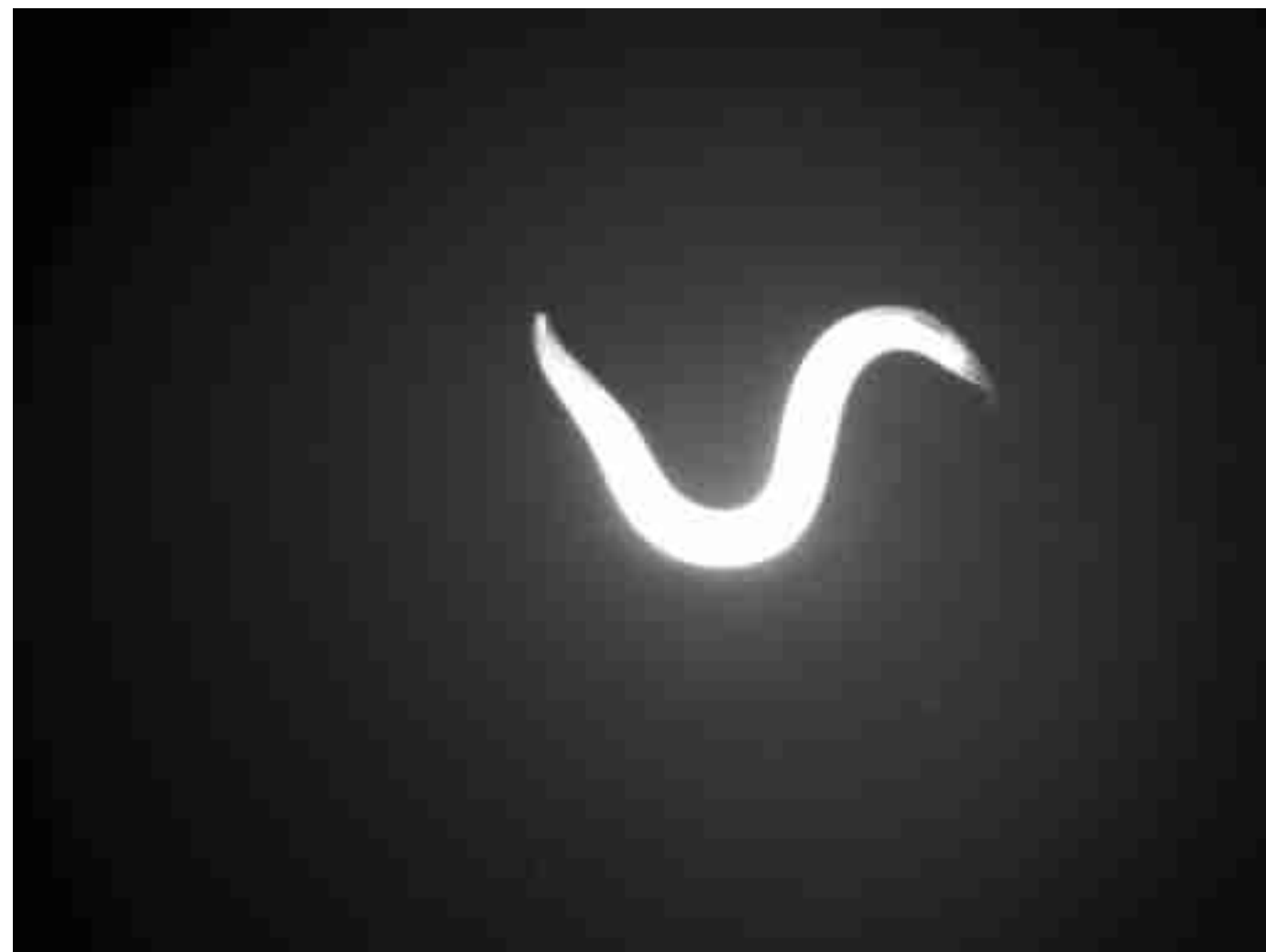


Inhibition

The segment 0



The segment 0



Neural ablation of all head cholinergic motor neurons

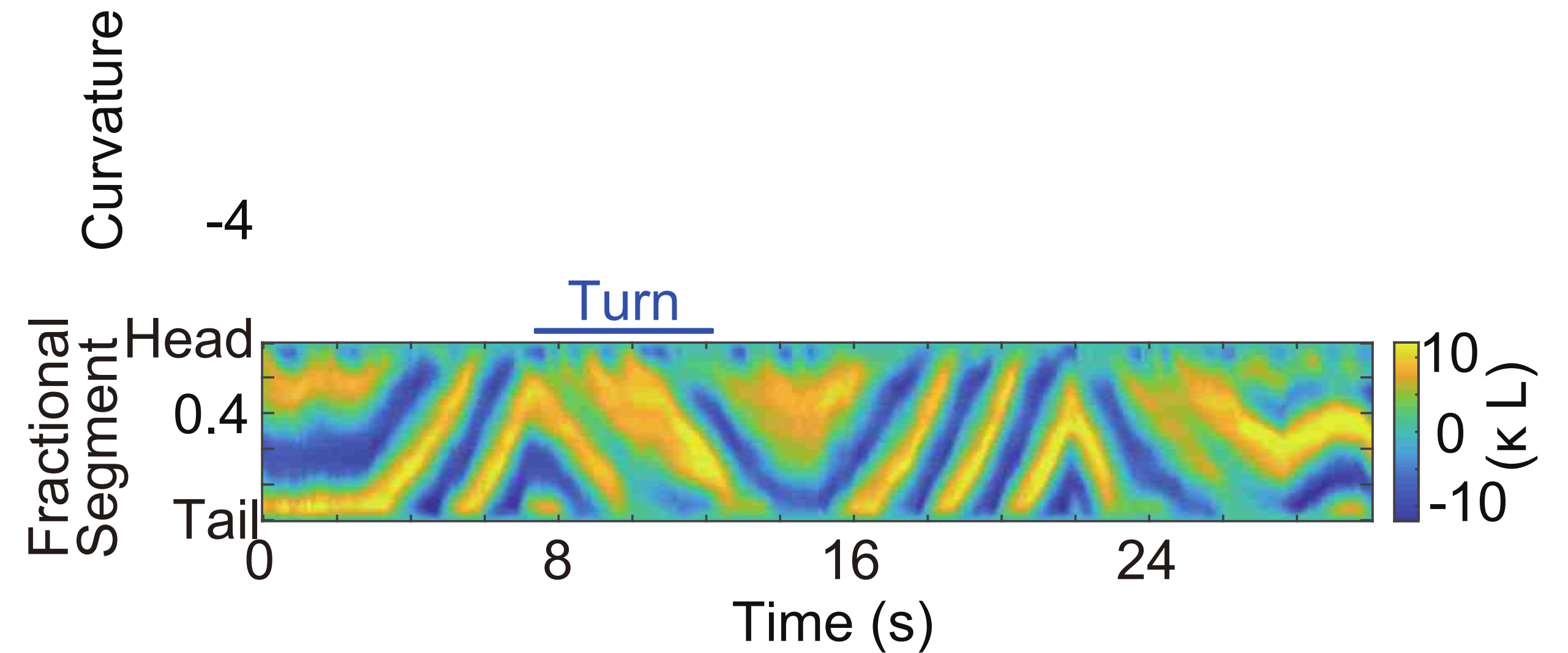
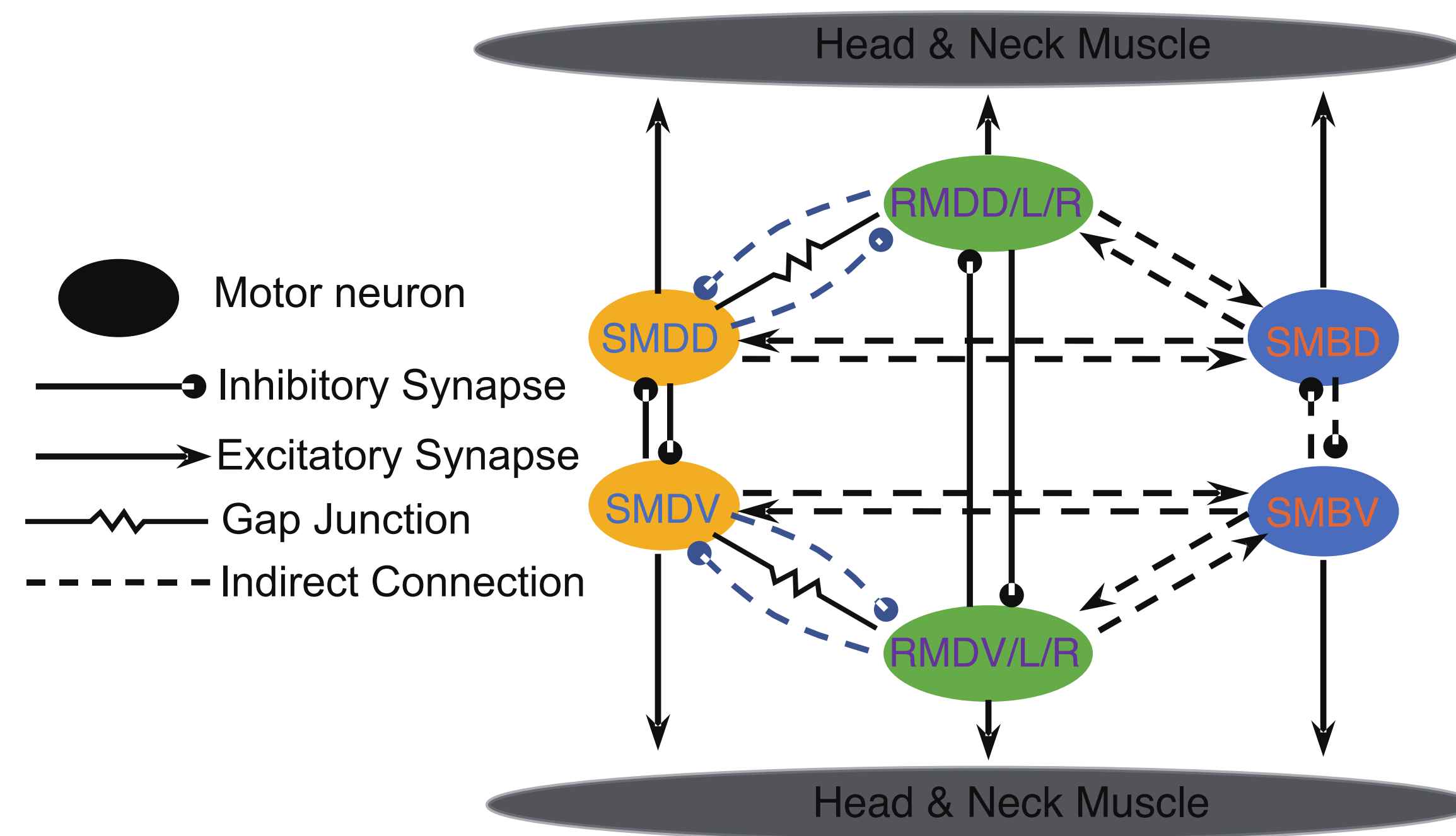


Figure 3. Ablation of different motor neuron types. **A.** Representative head curvature. **B.** Power ratio of fast dynamic mode and slow dynamic mode in N2 (n=108, 18 worms), SMD-ablated animals (n=101, 15 worms), and SMB-ablated animals (n=85, 21 worms) of forward movement. **C.** Head bending amplitude in N2 and motor neuron ablated animals of forward movements. The rate is defined as the number of head casts with a large

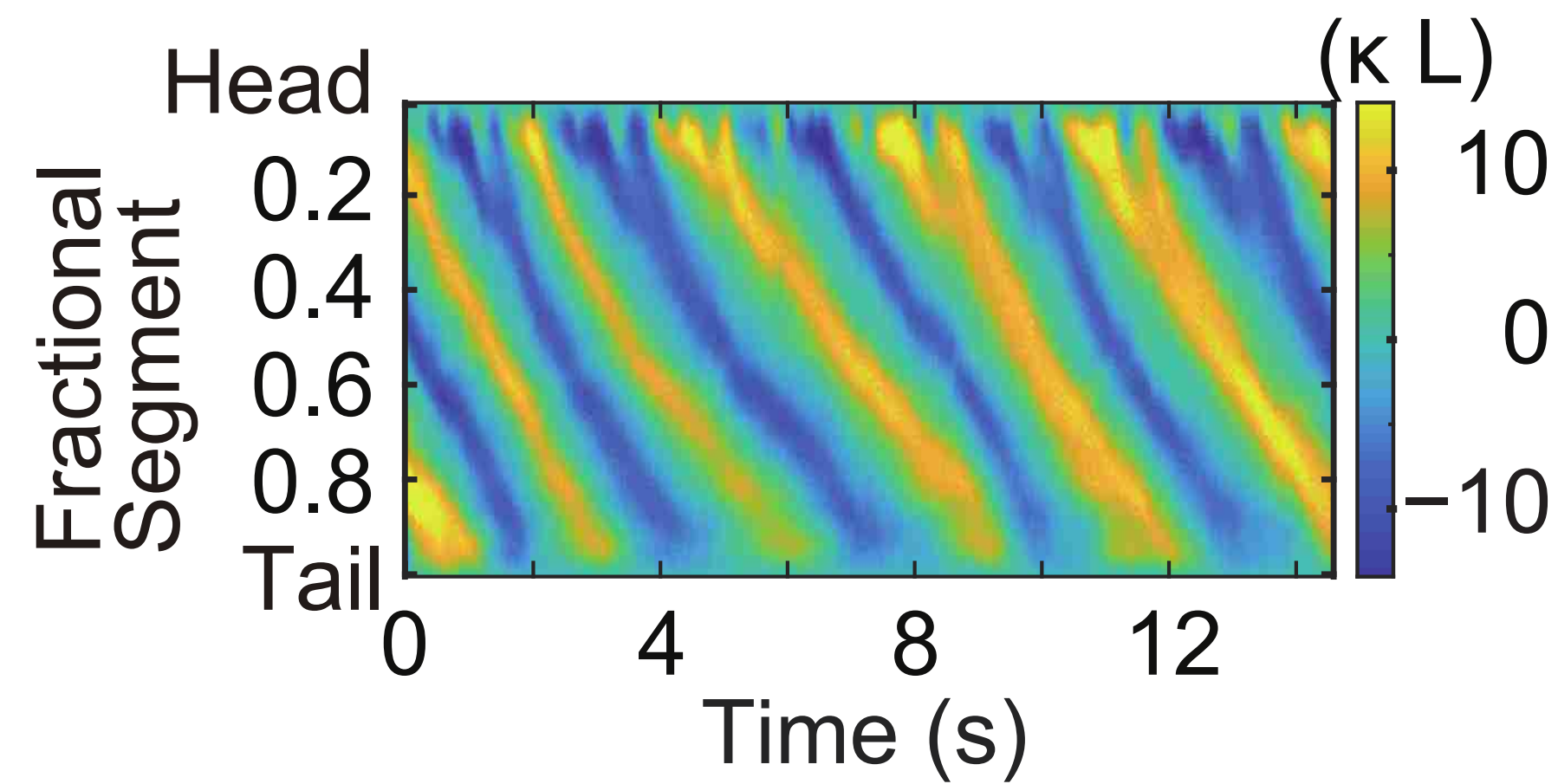
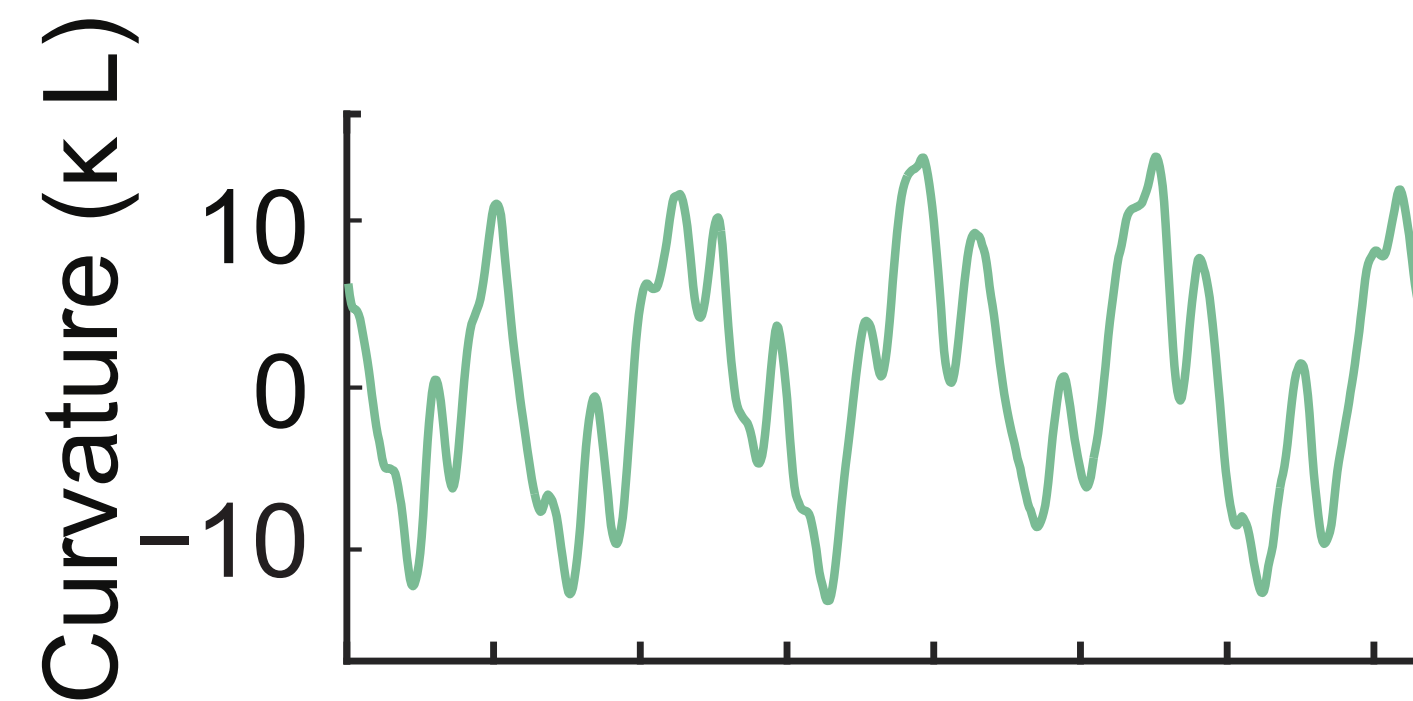
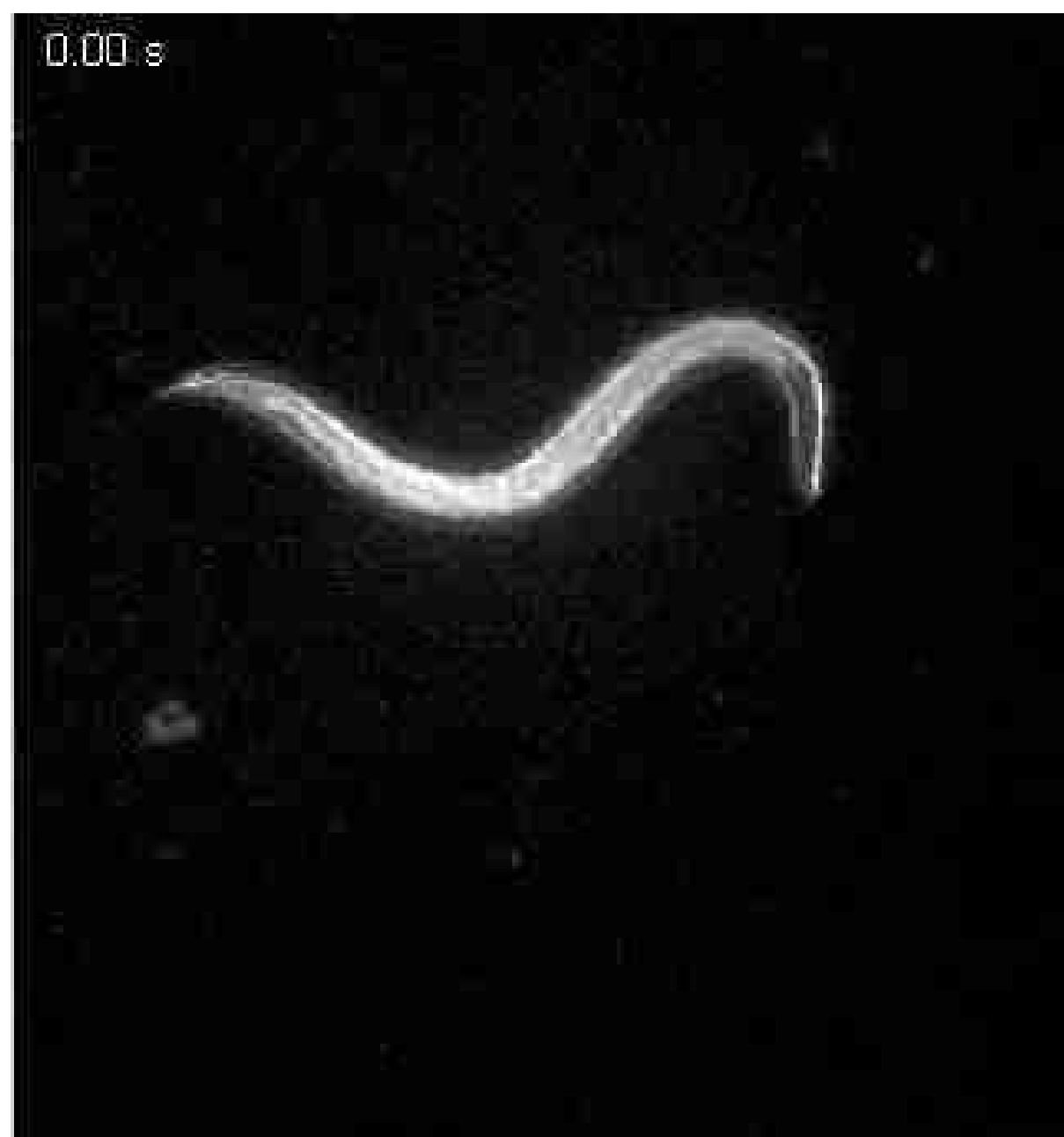
The head motor circuit

Why does the worm need so many different motor neuron types?

RMD, SMD, SMB, ...



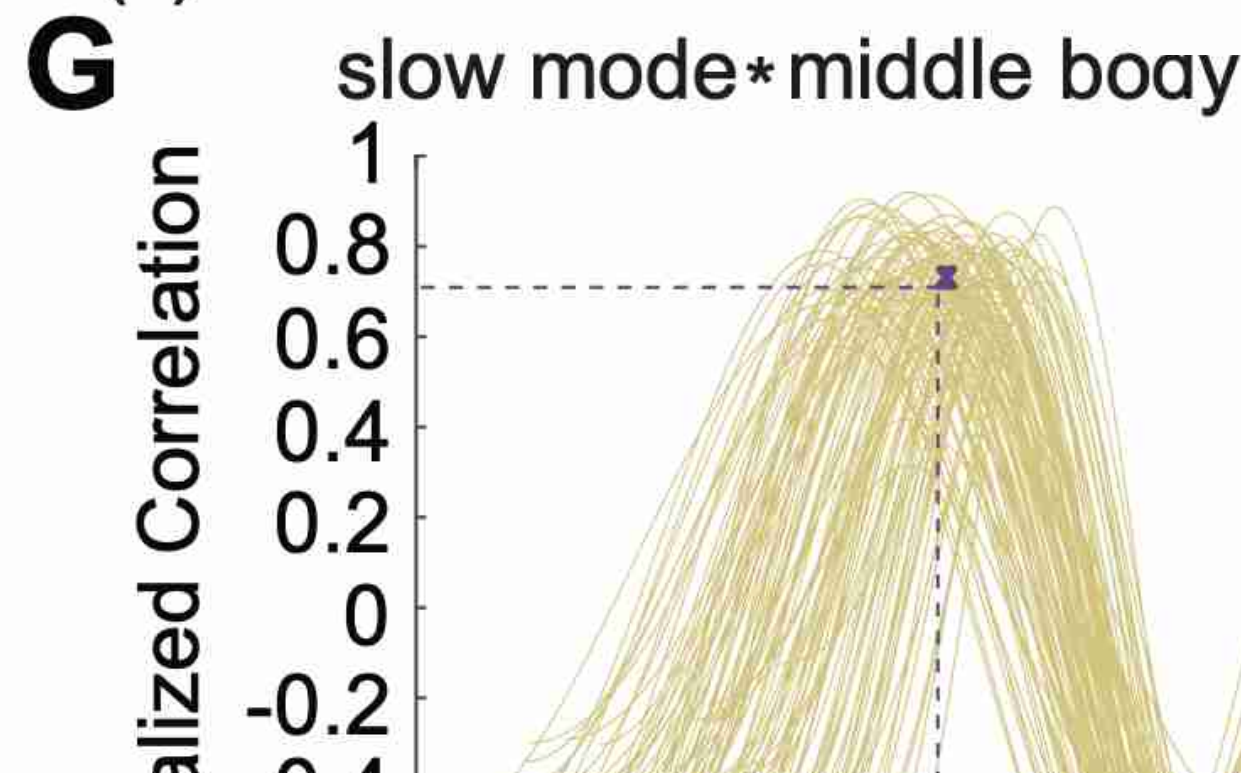
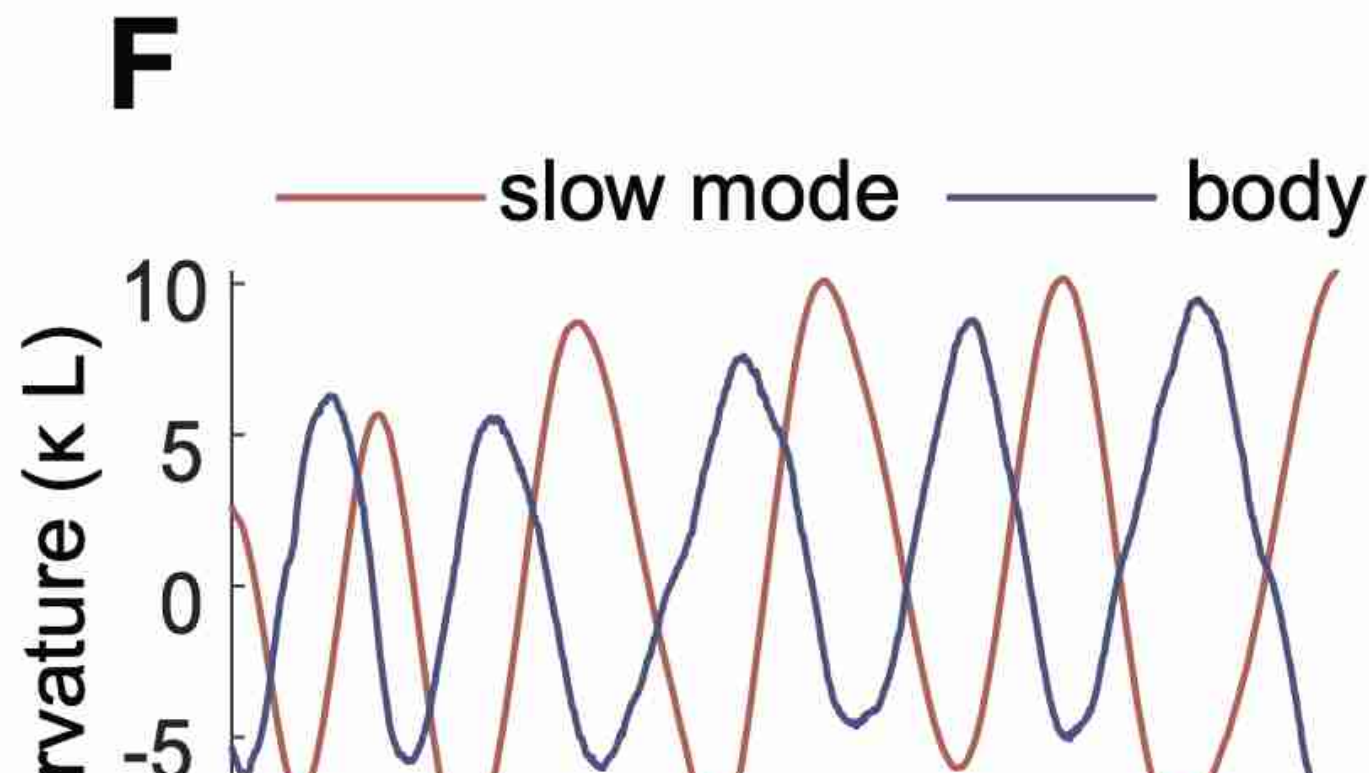
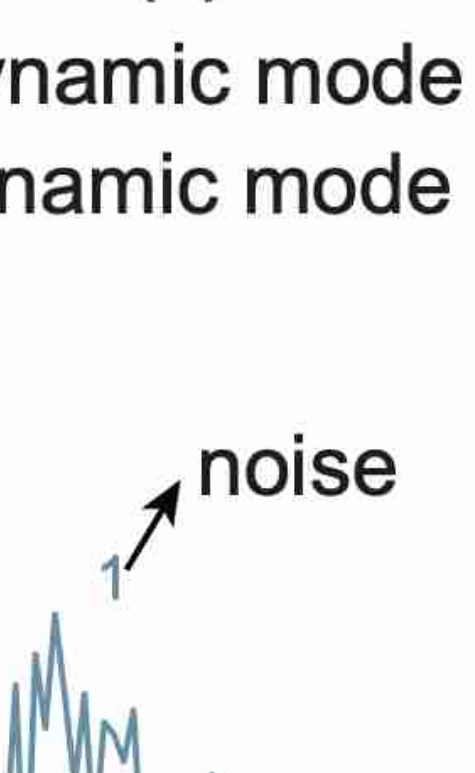
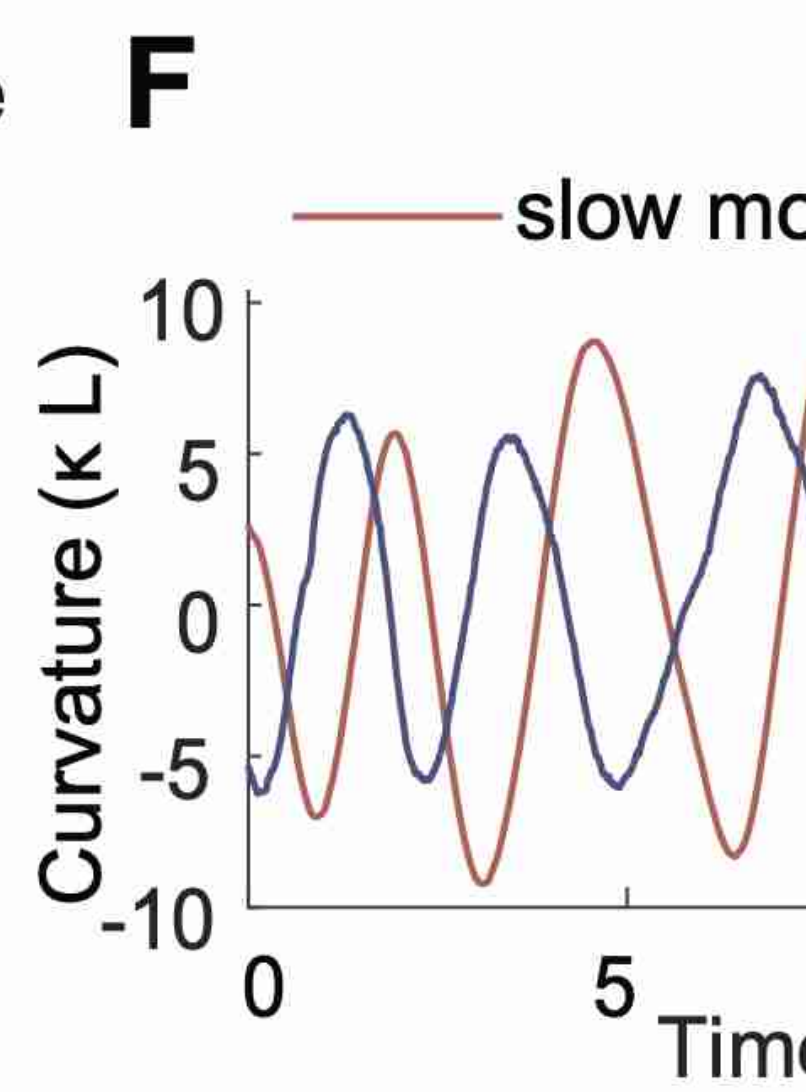
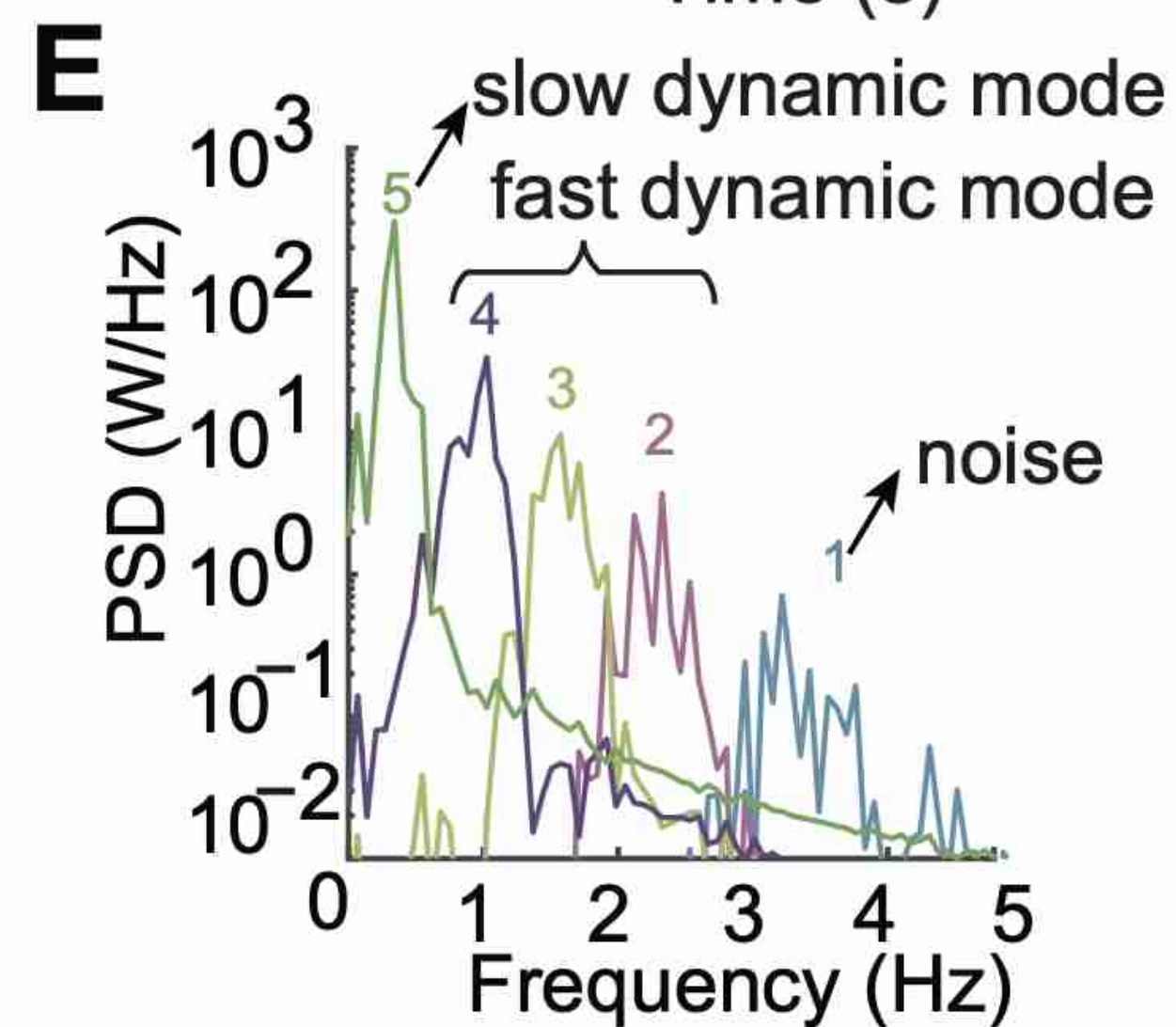
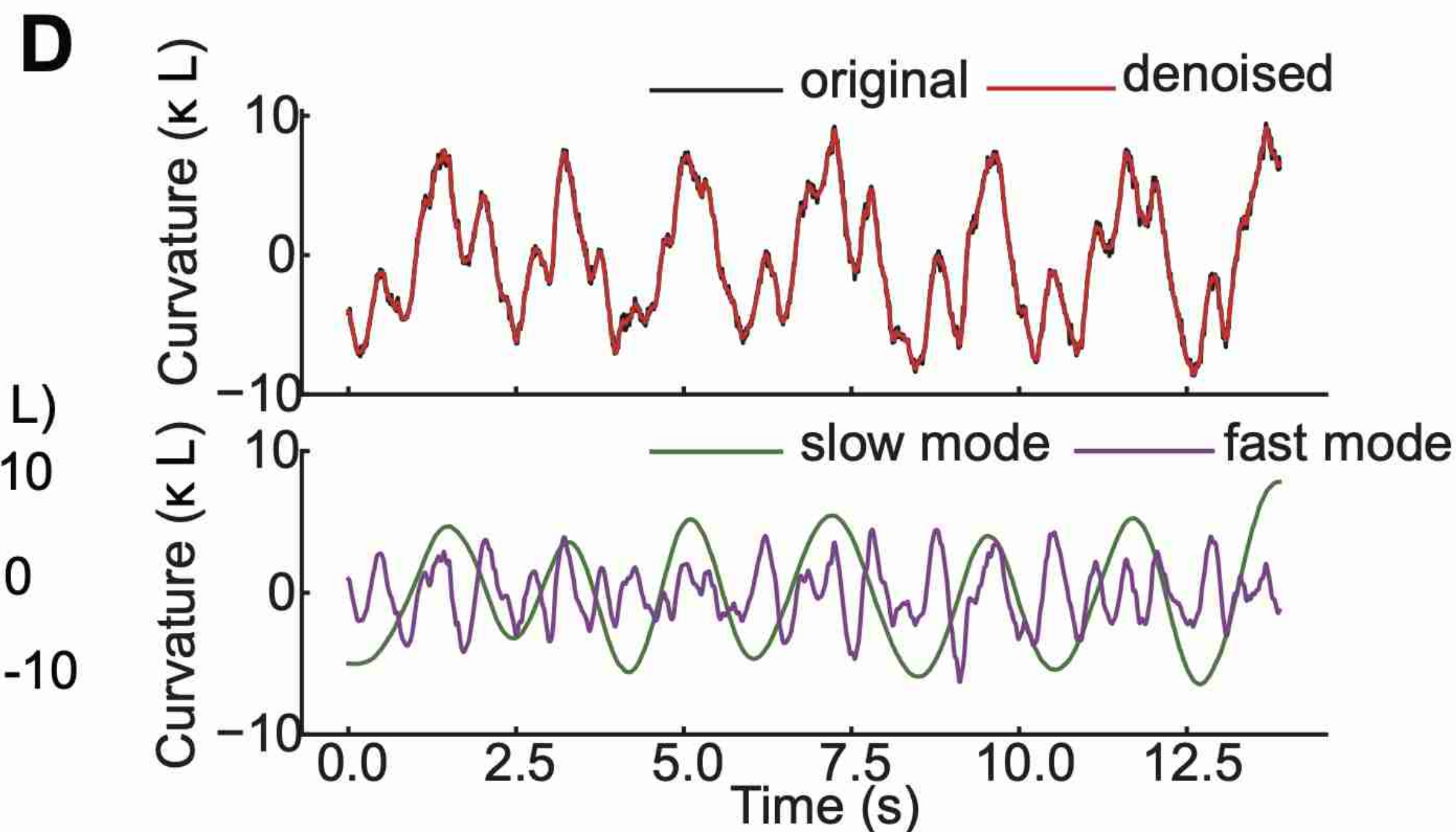
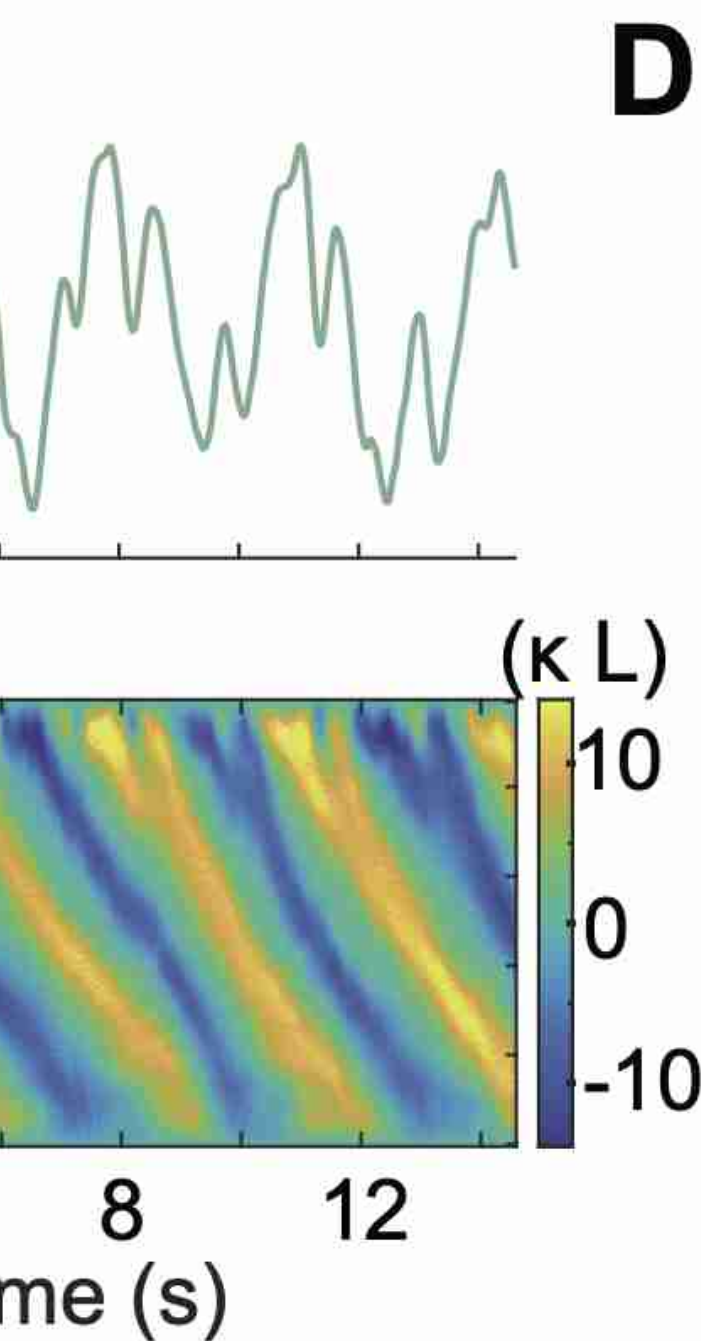
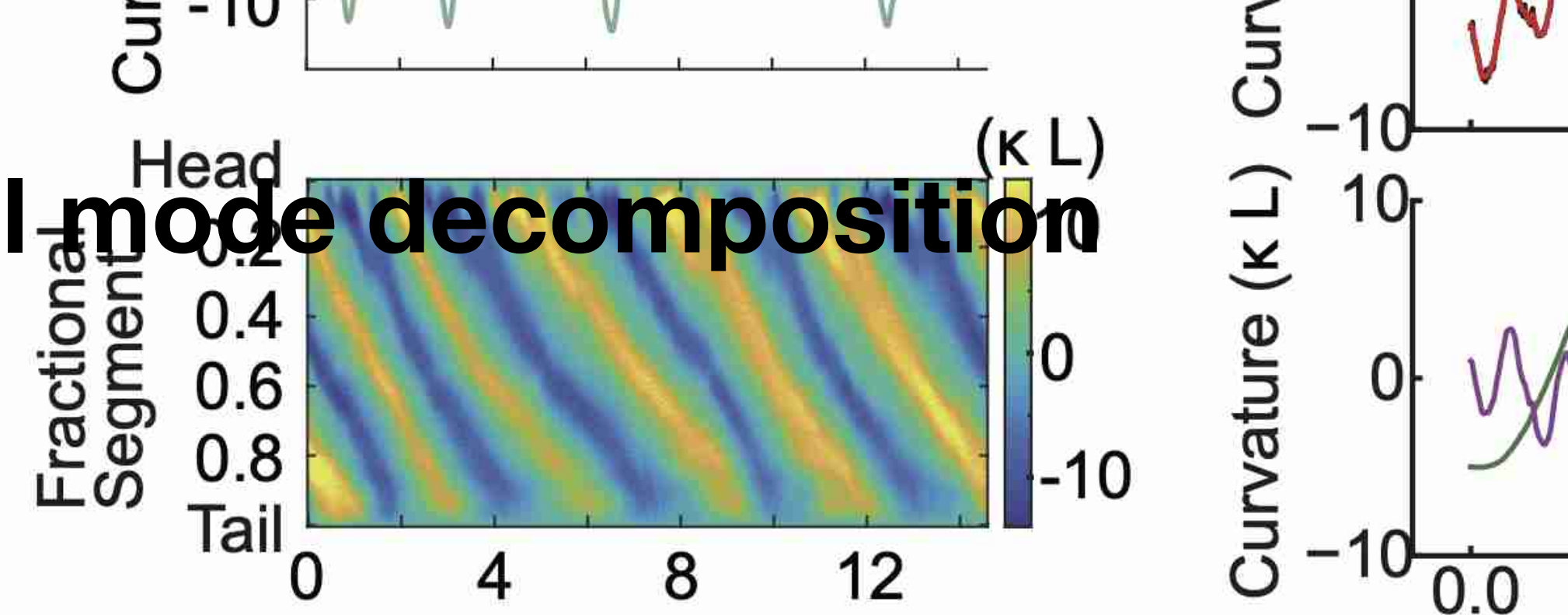
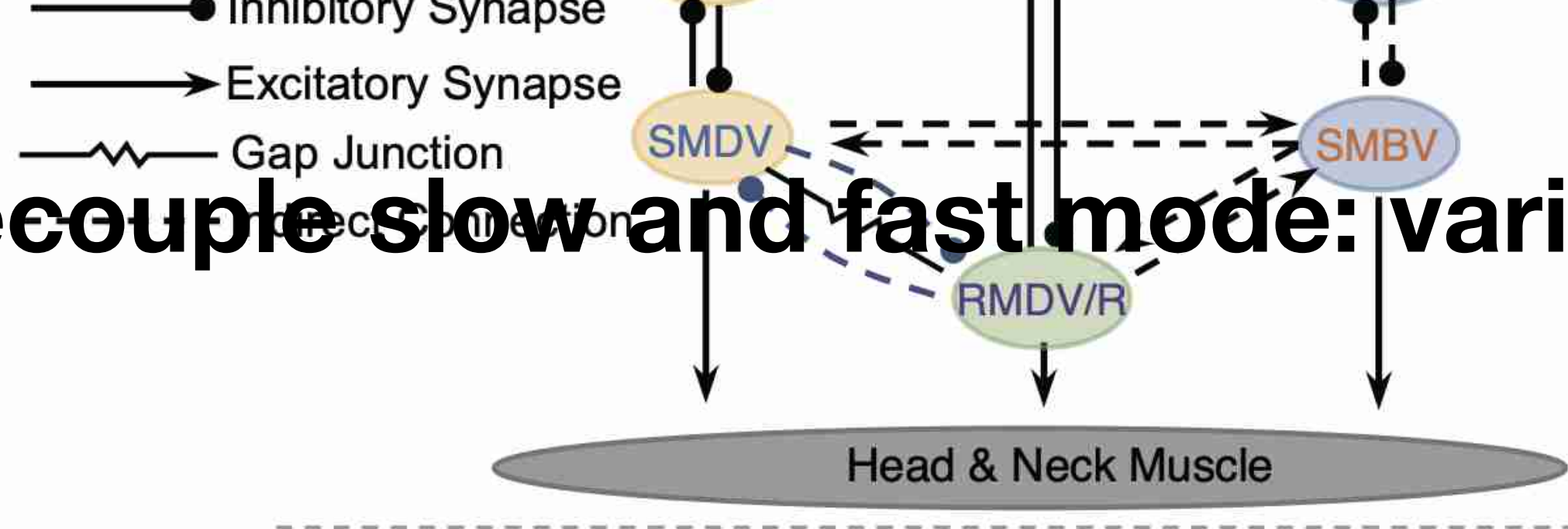
Motor sequence at the finest timescale: the head exploratory behavior

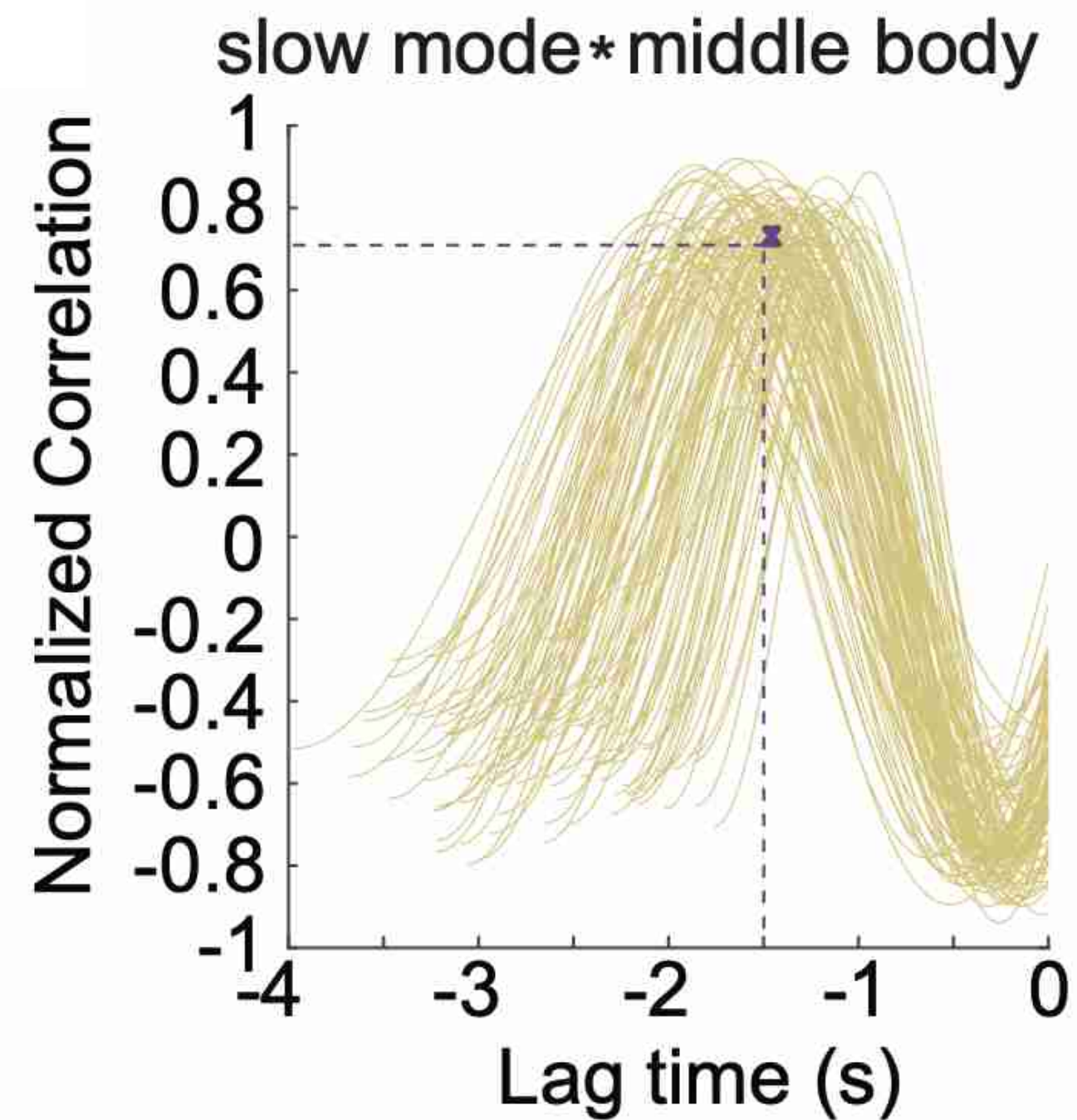
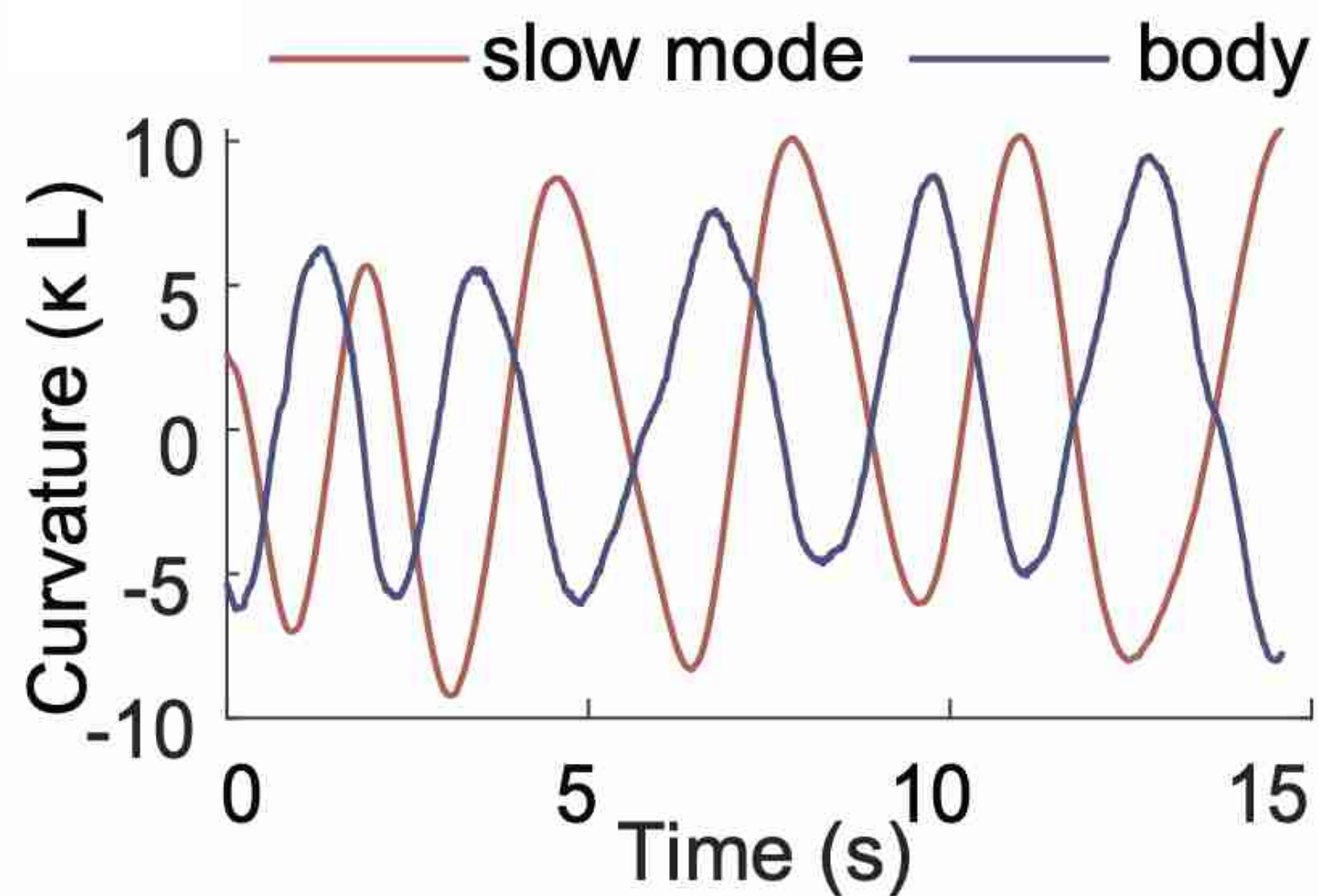
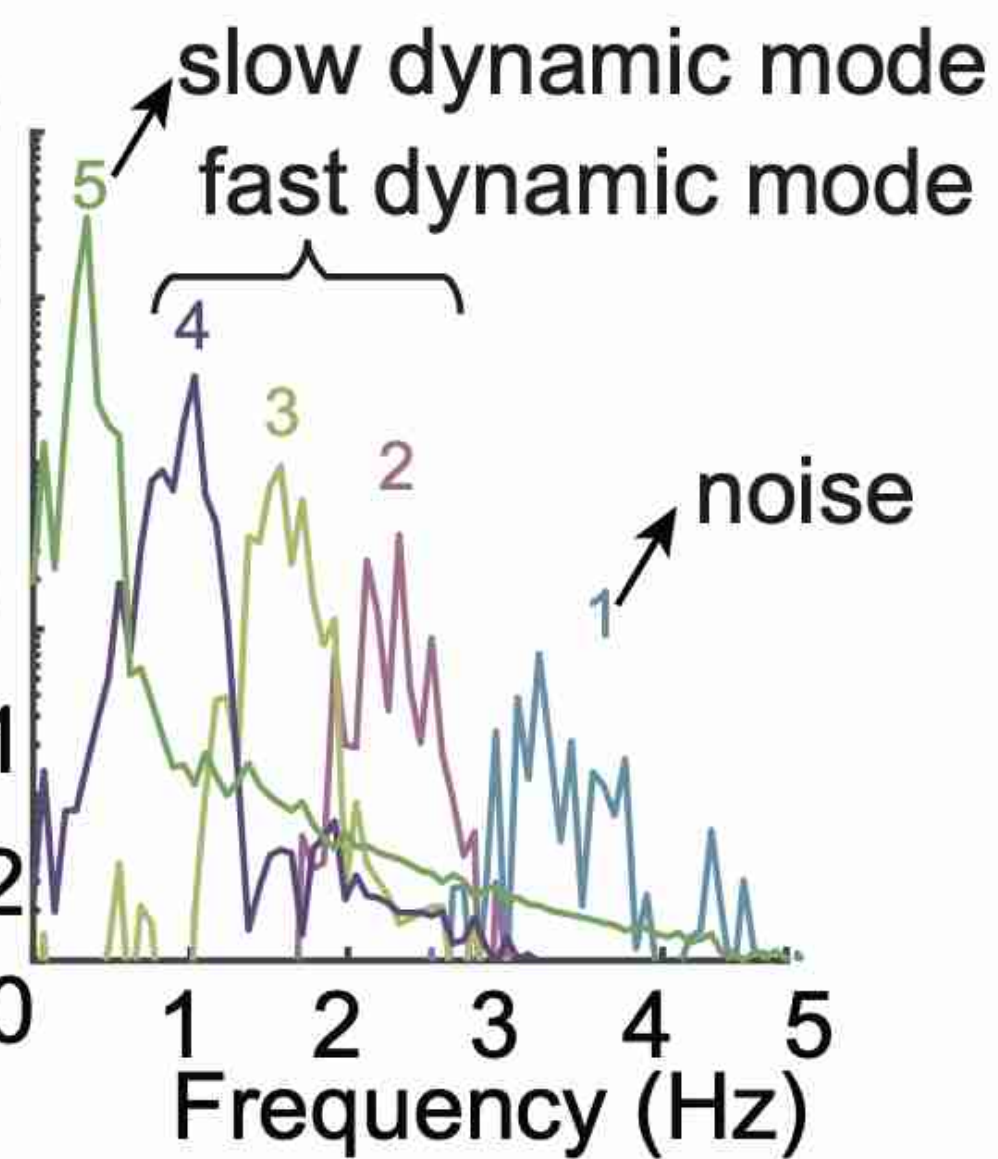
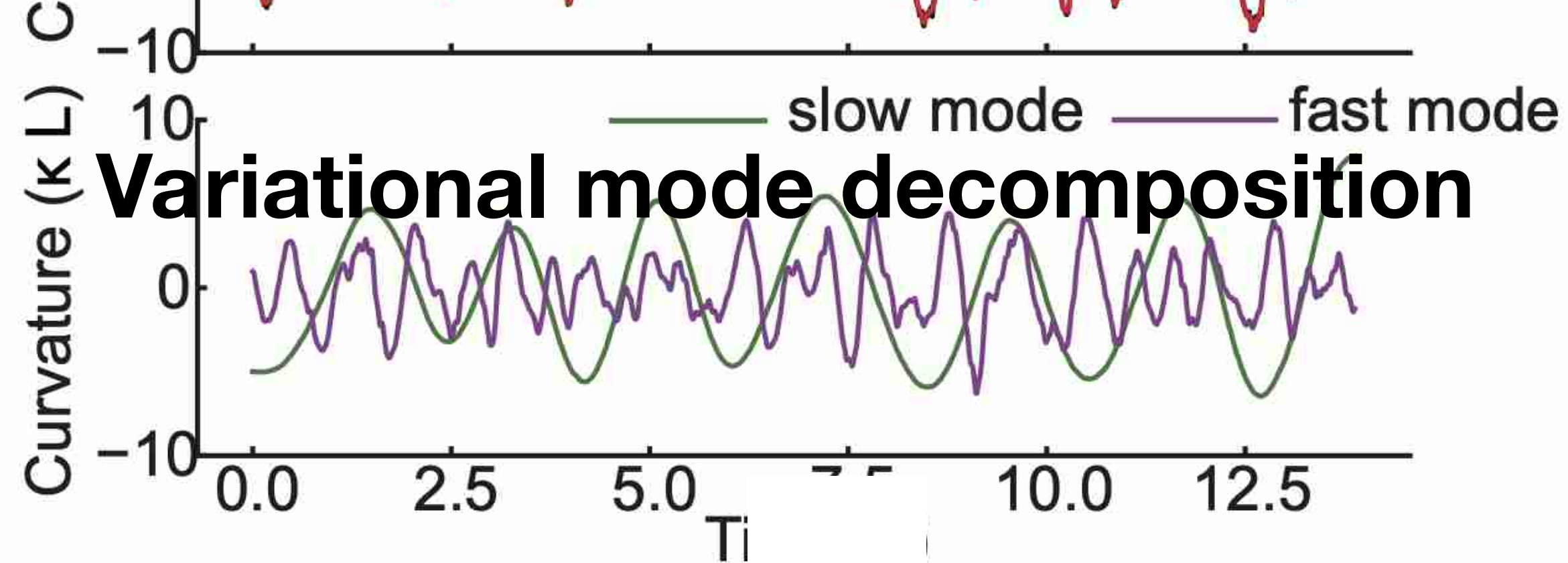
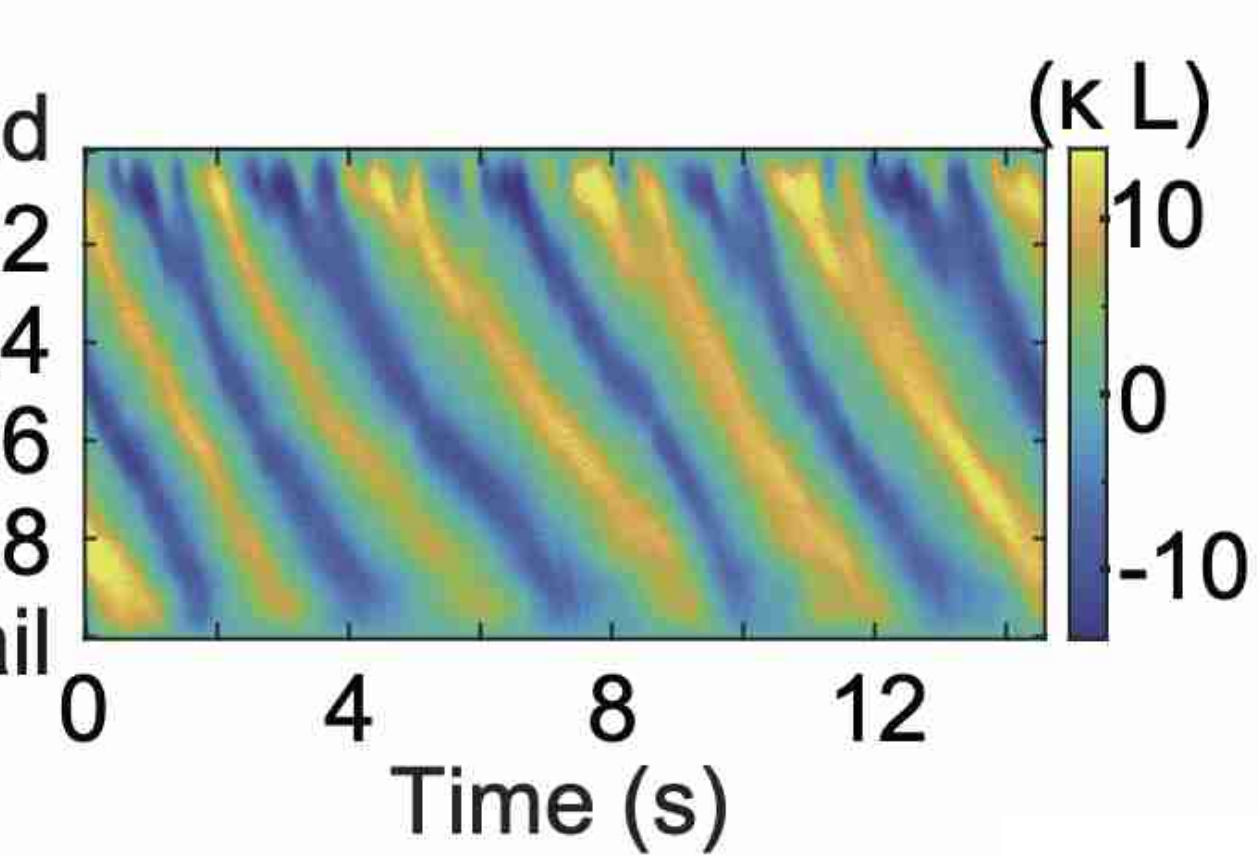


E

F

Decouple slow and fast mode: variational mode decomposition





a ventral-dorsal bias of head casting. This led us to hypothesize that this bias might translate into changes in running direction (see example trajectory in Fig. 2B). To empirically assess this idea, we introduced a head bias index, calculated as the area under the curve $\omega(t)$ over three undulation cycles. Our subsequent analysis confirmed that this bias index is significantly positively correlated with the change in movement orientation (Fig. 2E) as this bias can propagate along the body (Fig. S2 F). Together, our findings underscore the importance of fine head movements in guiding exploratory behavior.

Head cast in the fast mode

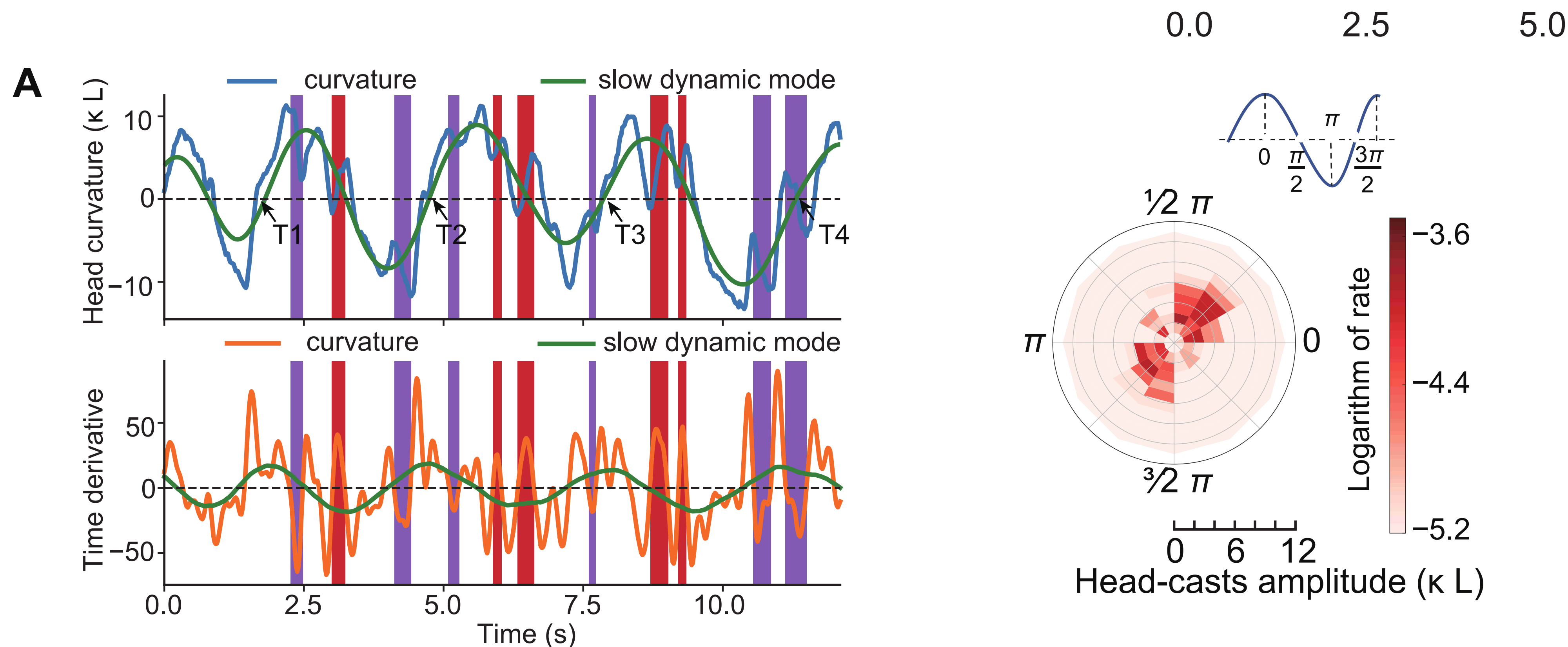
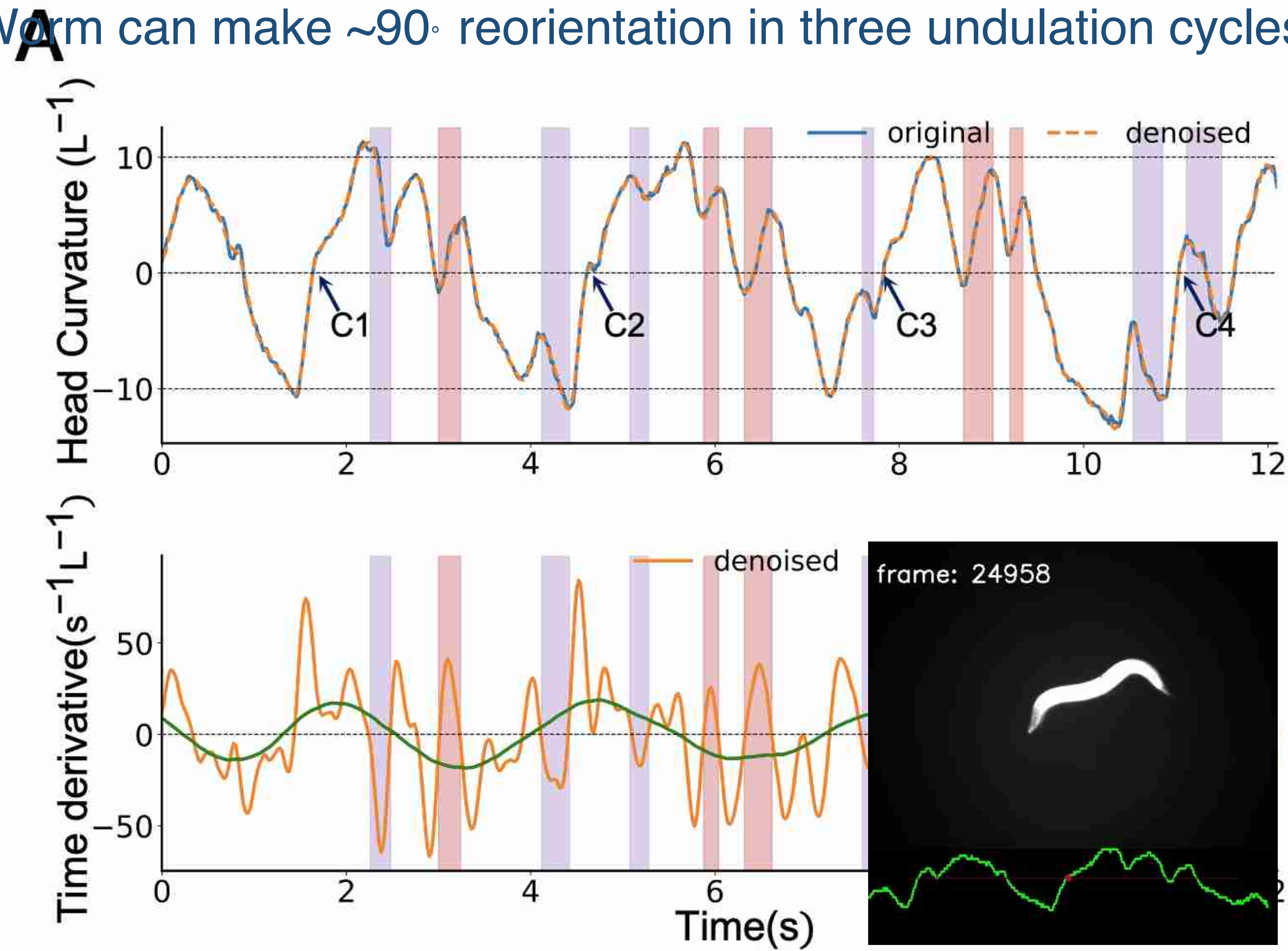


Figure 2. Illustration of head casts and their association with bending curvature and the corresponding slow dynamic mode. Top: Time derivative of head curvature and the corresponding slow dynamic mode. T1-T4: dorsal and ventral head casts, respectively. Bottom: Time derivative of head curvature. Sequential snapshots of the nematode's posture over three consecutive undulation cycles showing gradual directional changes and persistent dorsal head casting. C: dorsal head casting and phase $\pi/2$ where the phase is defined by the slow dynamic mode.

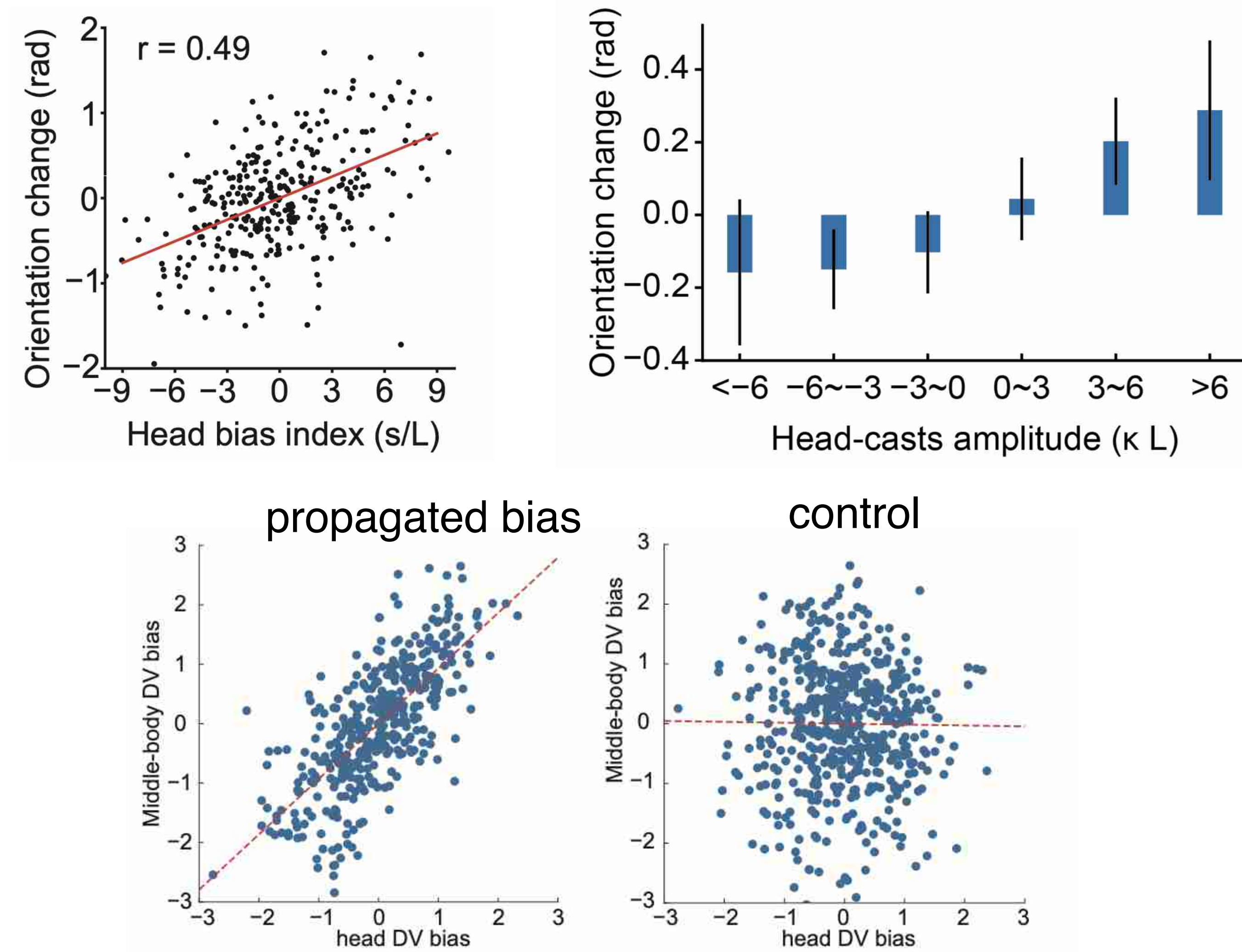
Phase-specific head casts cause shallow turns

Example: Worm can make $\sim 90^\circ$ reorientation in three undulation cycles



Biased dorsal-ventral head bending

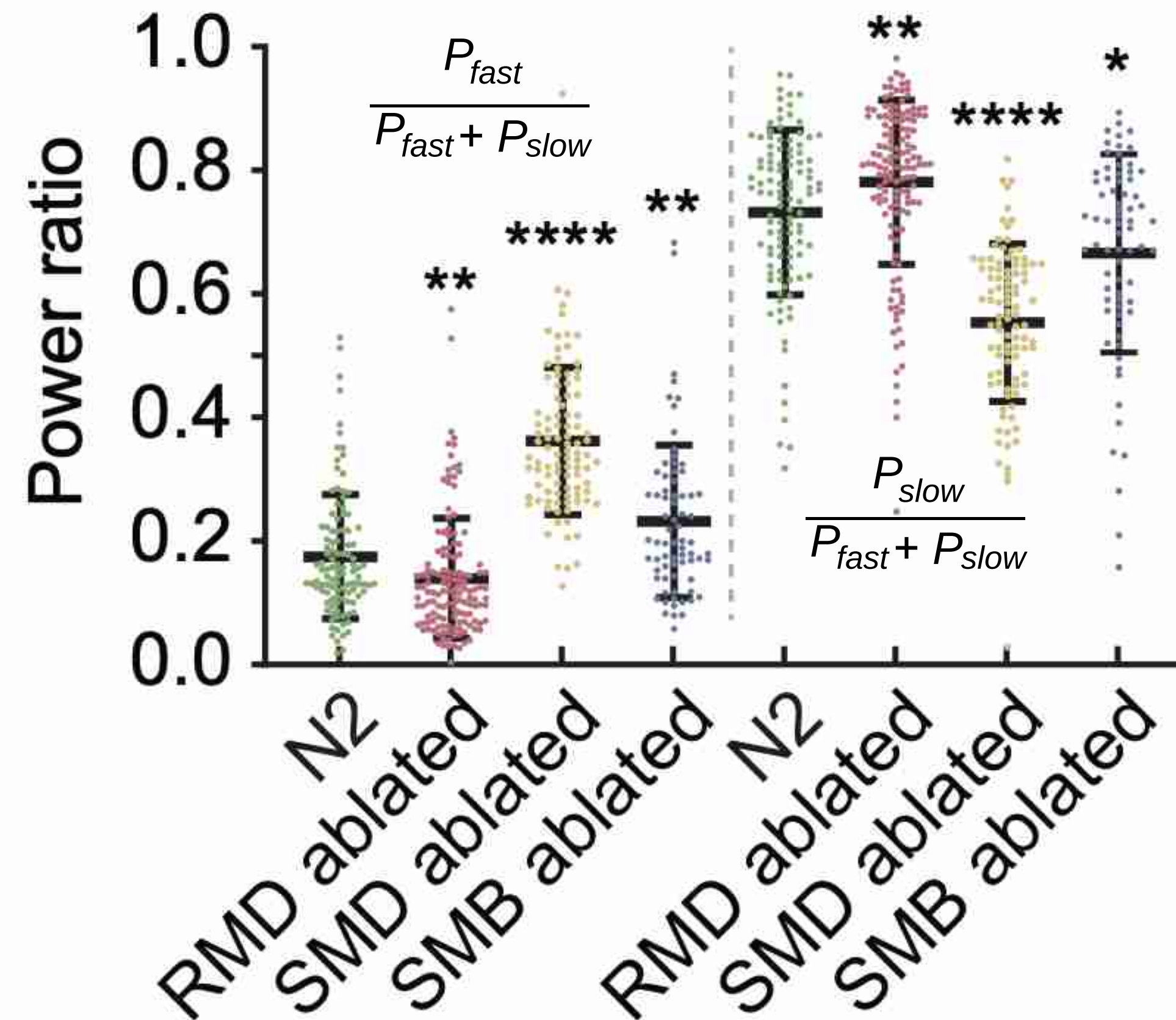
Phase-specific head casts cause shallow turns



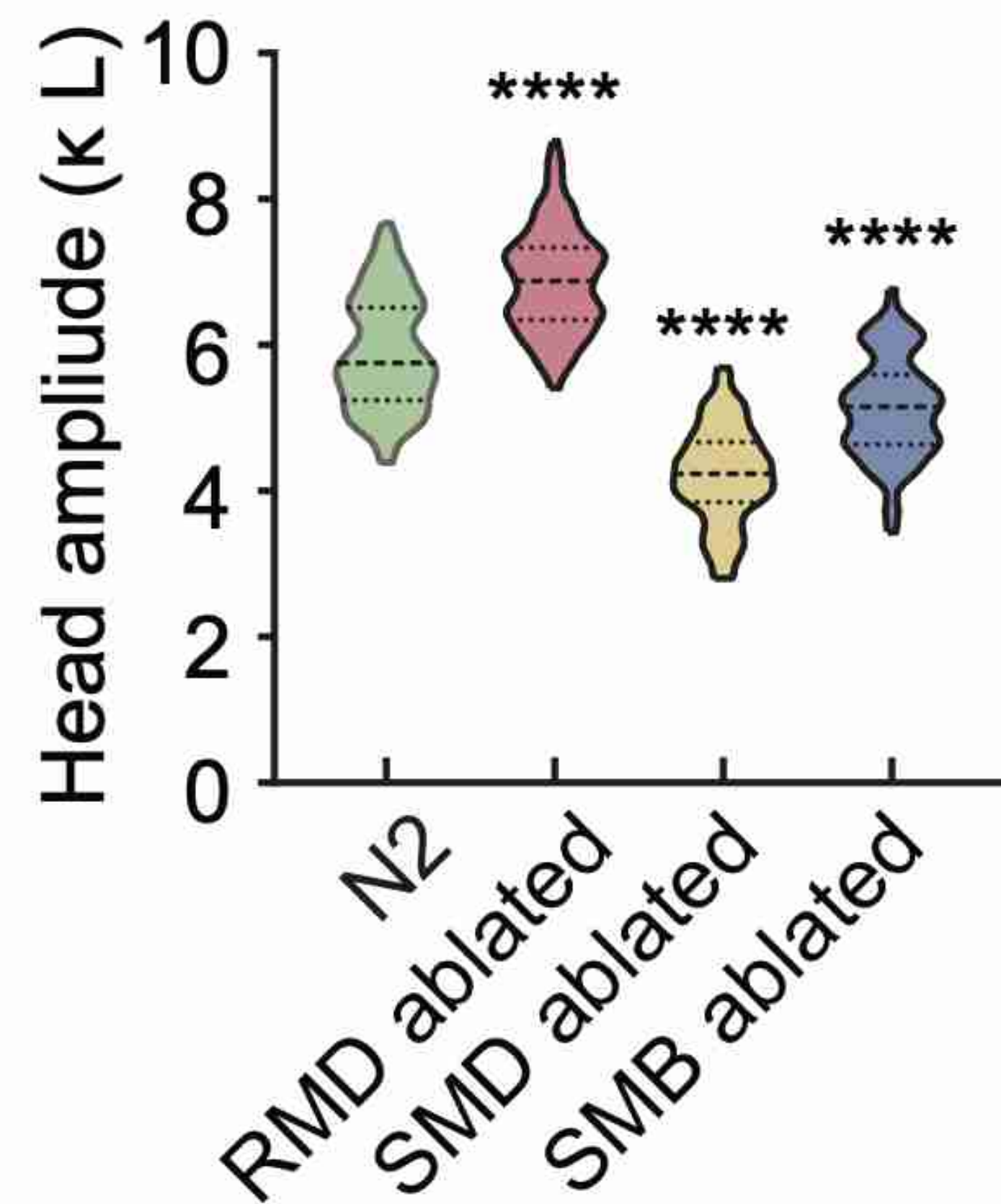
Head casts $\longrightarrow$ Dorsoventral bias $\longrightarrow$ Propagate $\longrightarrow$ Shallow turns

Single cholinergic motor neuron type ablation

B



C



E

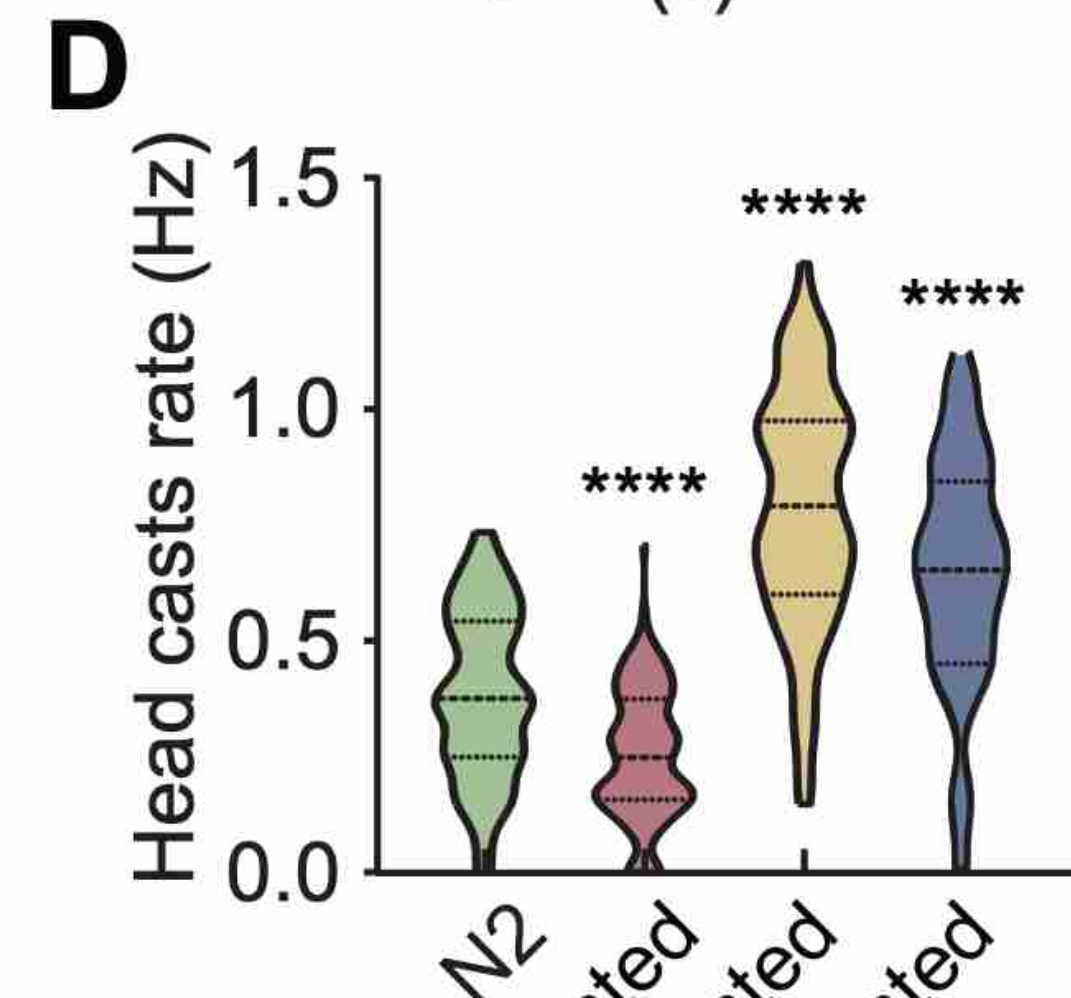
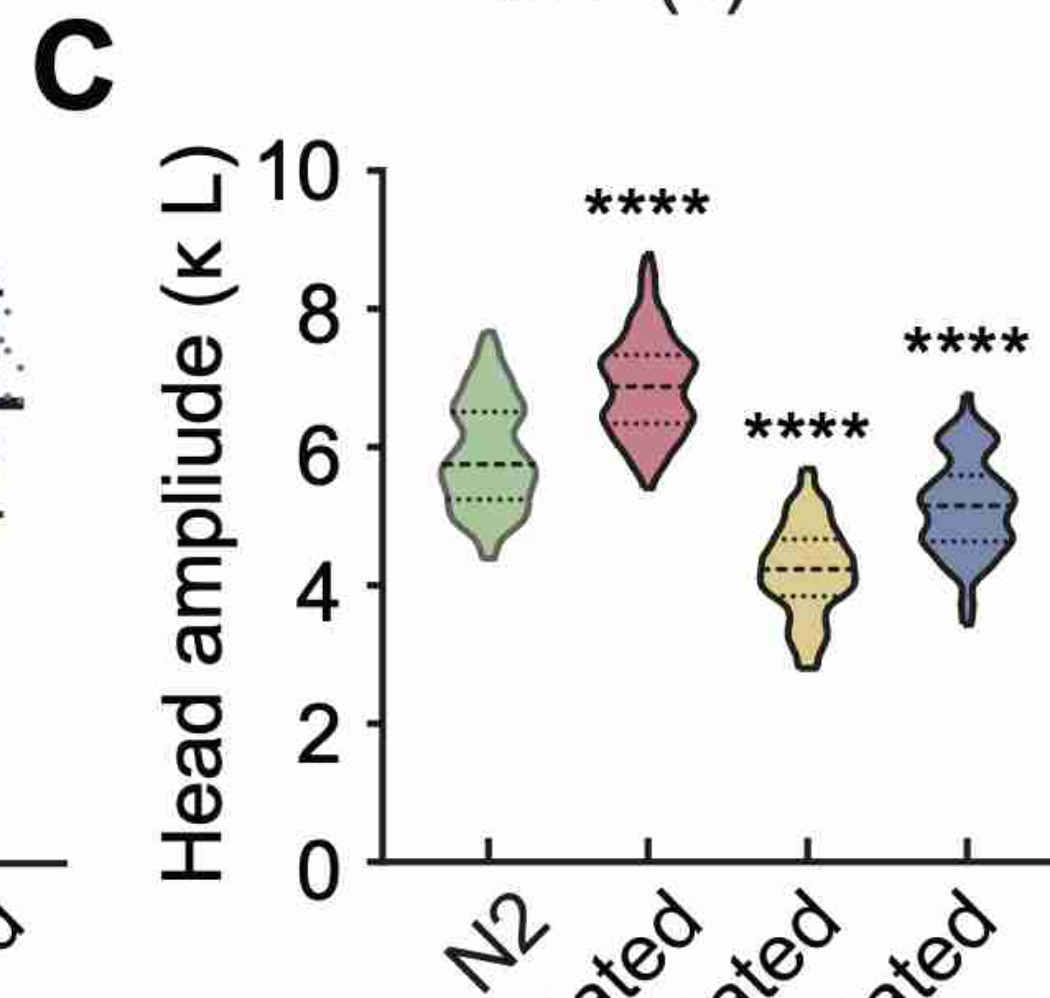
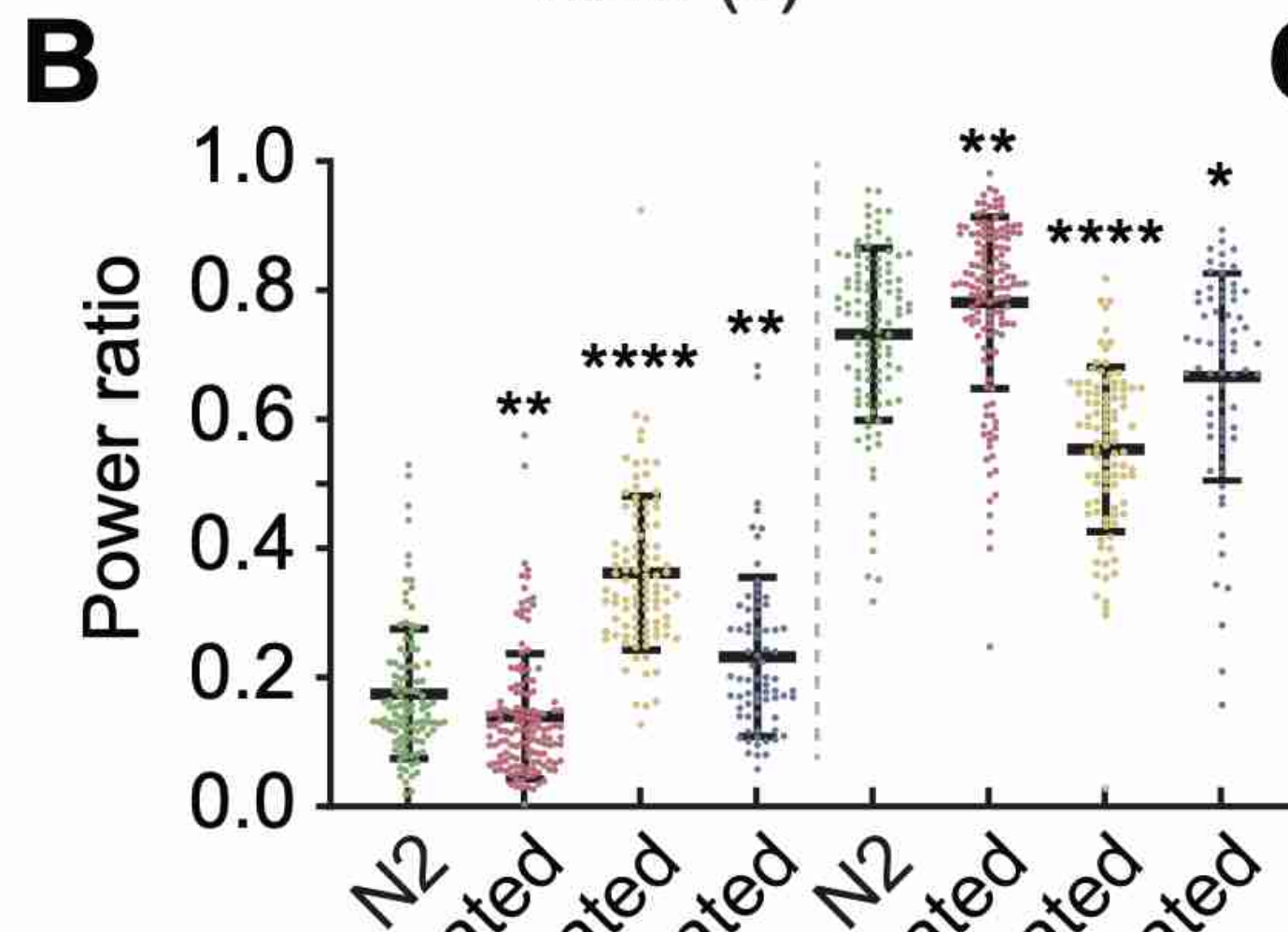
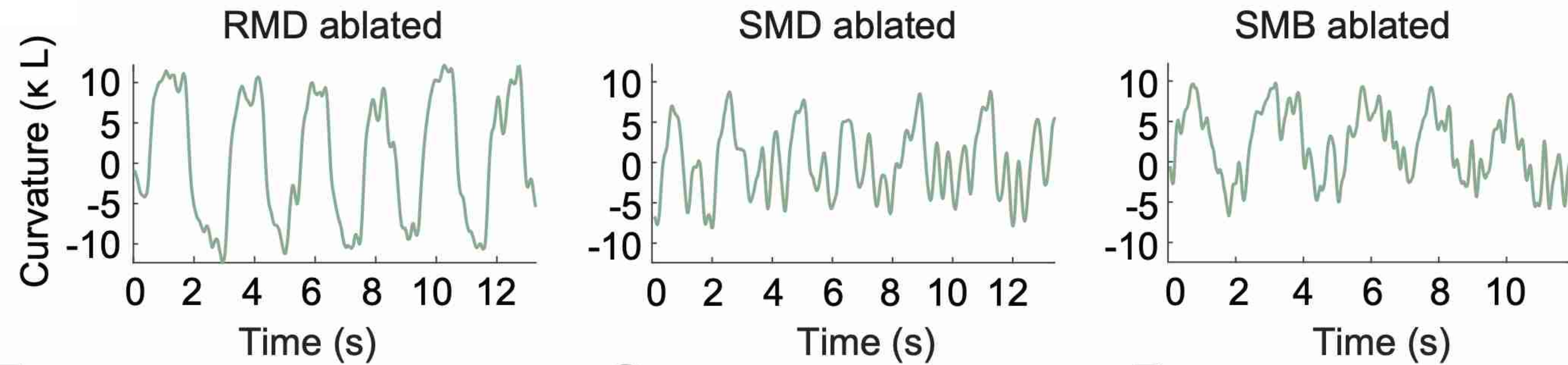
RMD ablated

$1/2 \pi$

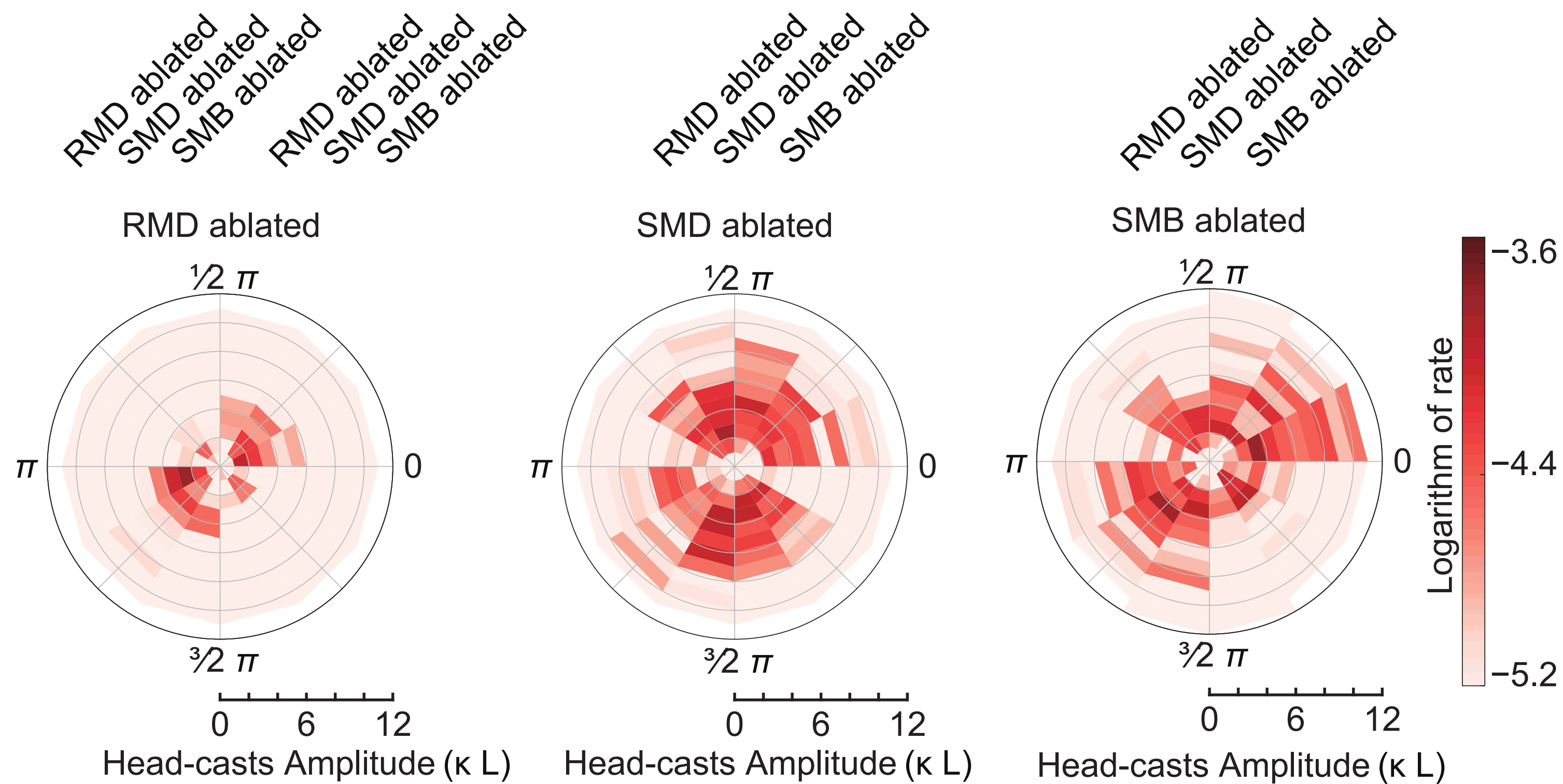
SMD ablated

$1/2 \pi$

Single cholinergic motor neuron type ablation



Head cast in the fast mode

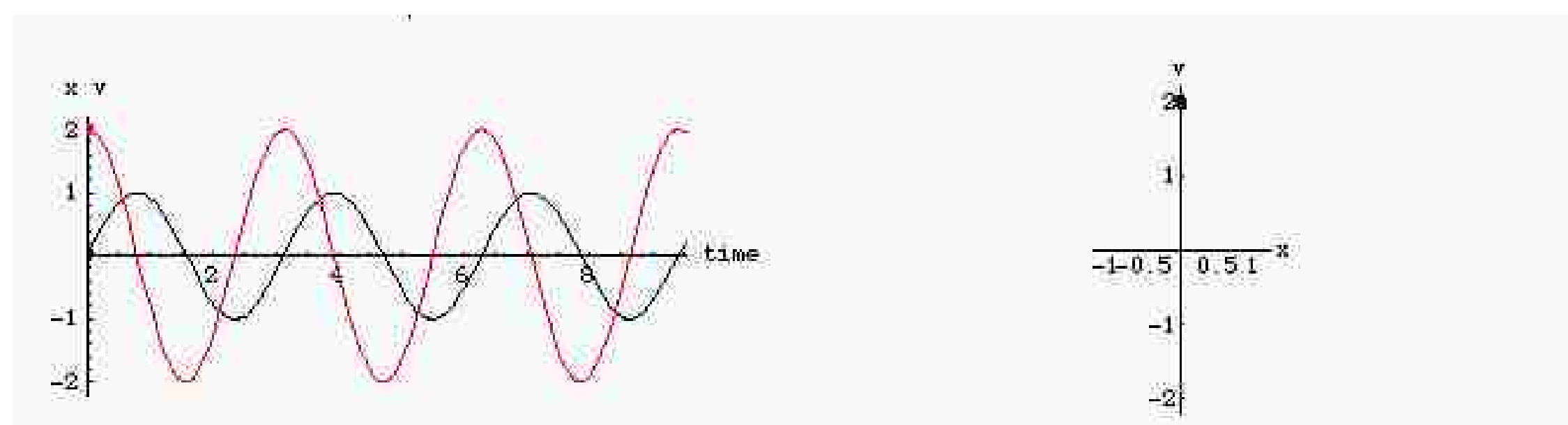


Phase space of a harmonic oscillator: connecting equations with geometry

$$\dot{x} = v$$

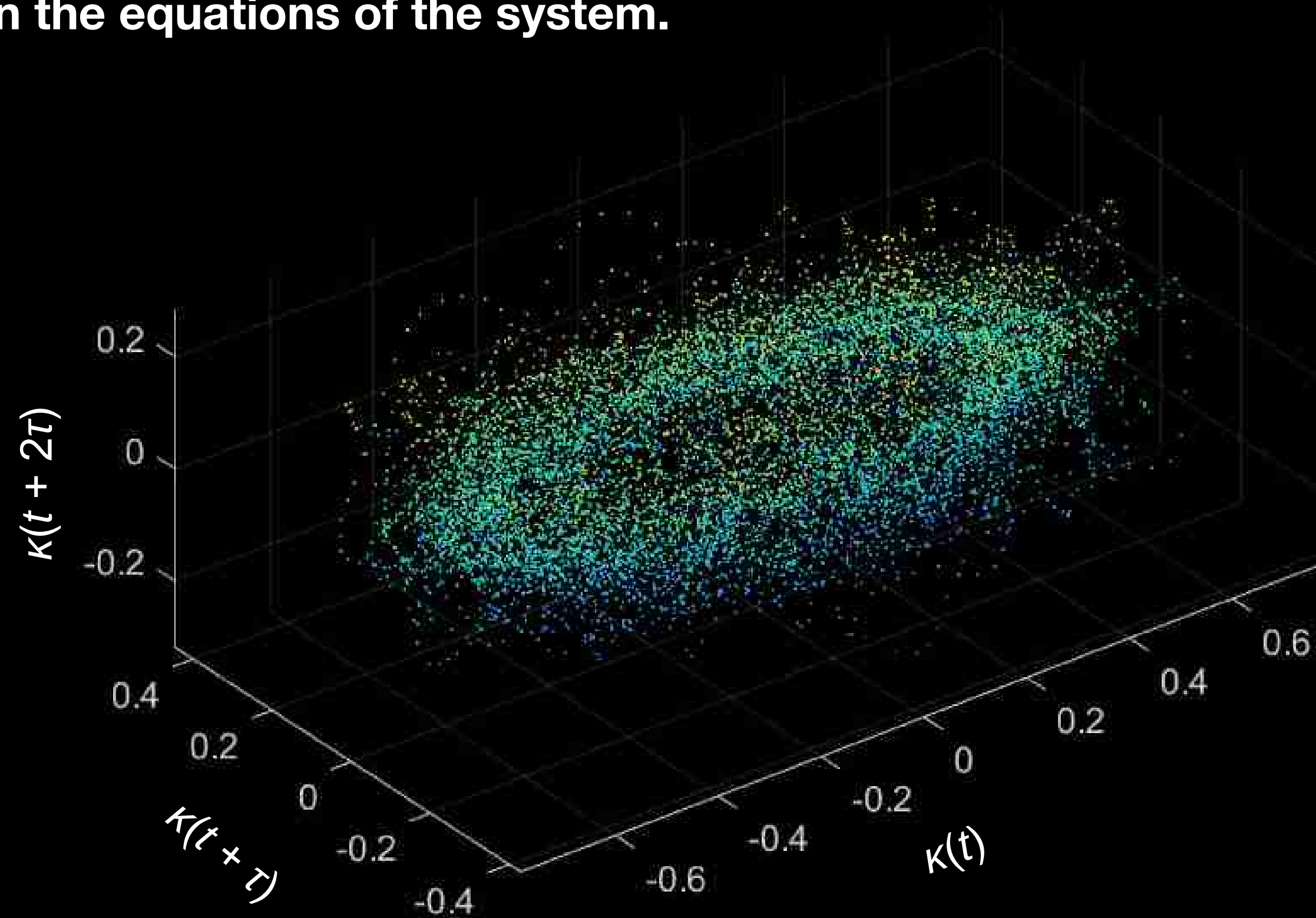
$$\dot{v} = -\omega^2 x$$

$$\omega = \sqrt{\frac{k}{m}}$$

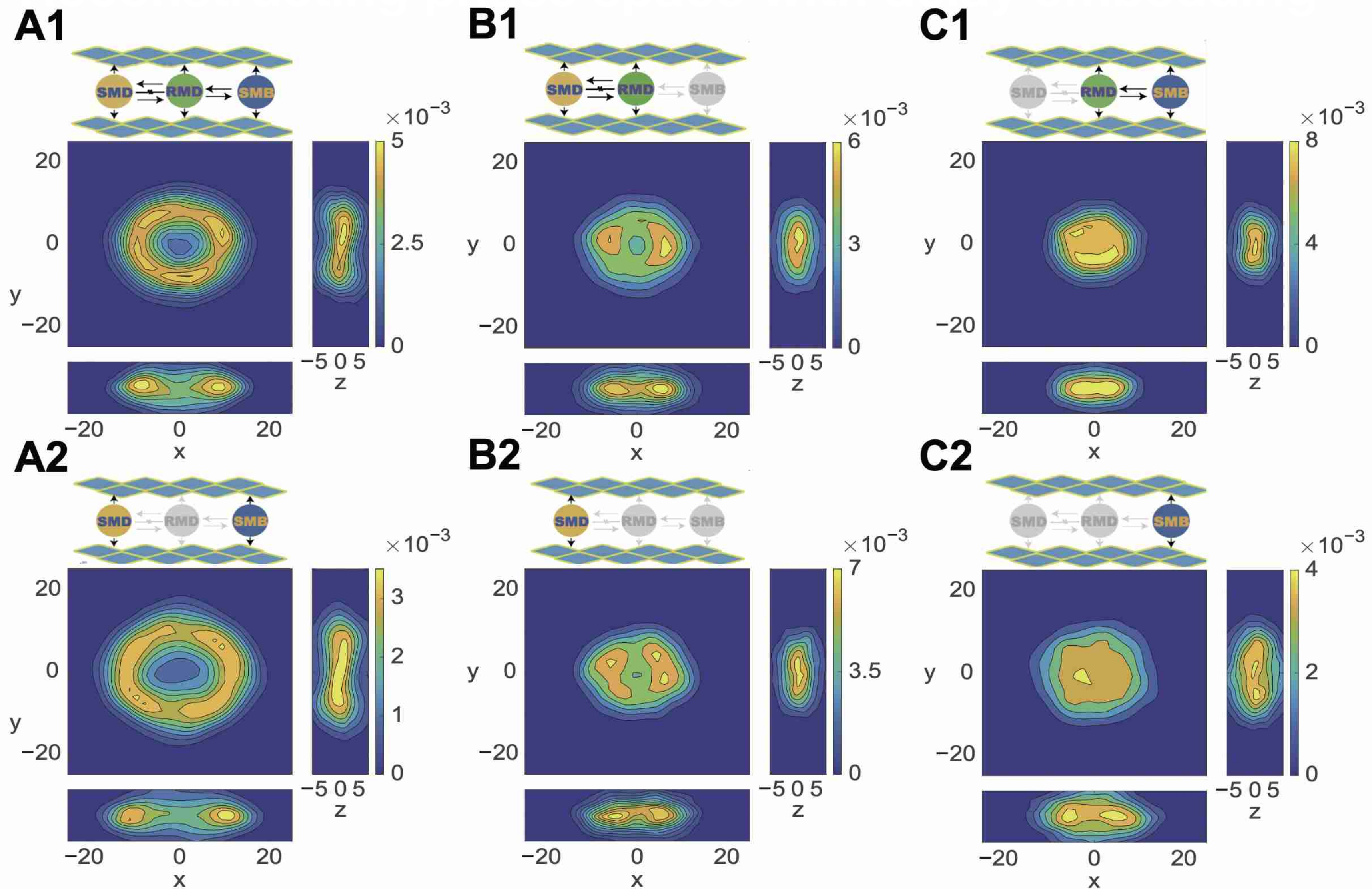


Reconstructing phase space with delay embedding

When τ and dimensions are properly chosen, *Takens Theorem* states that delay embedding can obtain a structure that is topologically equivalent to the attractor of the observed system, **despite the fact that we don't even know how to write down the equations of the system.**



Reconstructing phase space with delay embedding

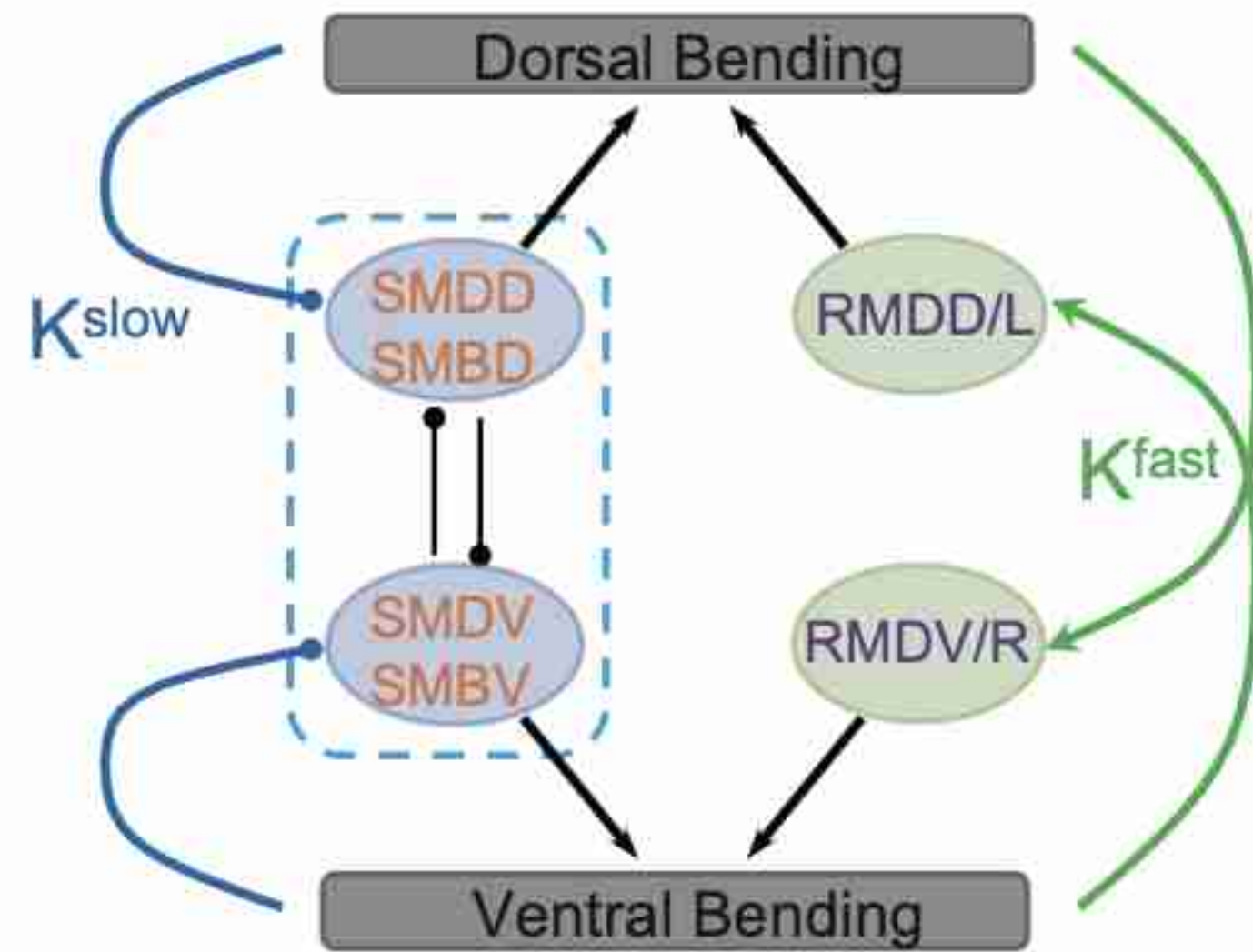


Intrinsic dynamics and structural composition emerge from low-level circuits

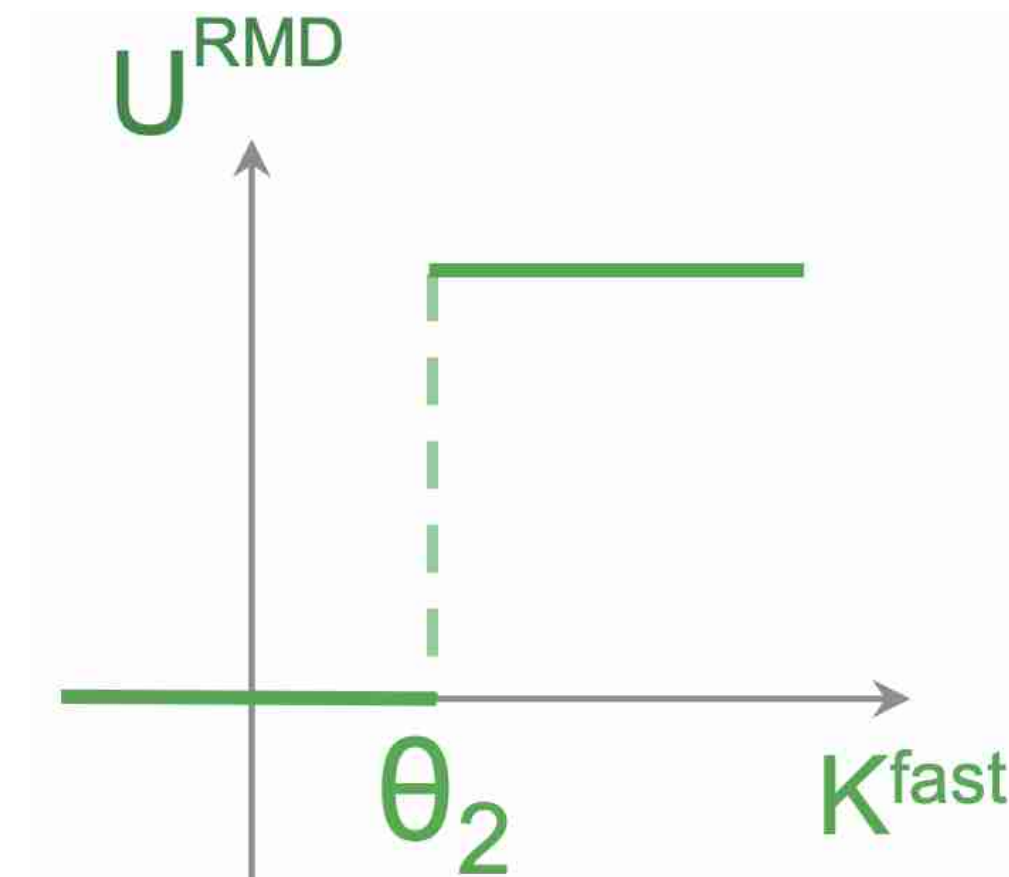
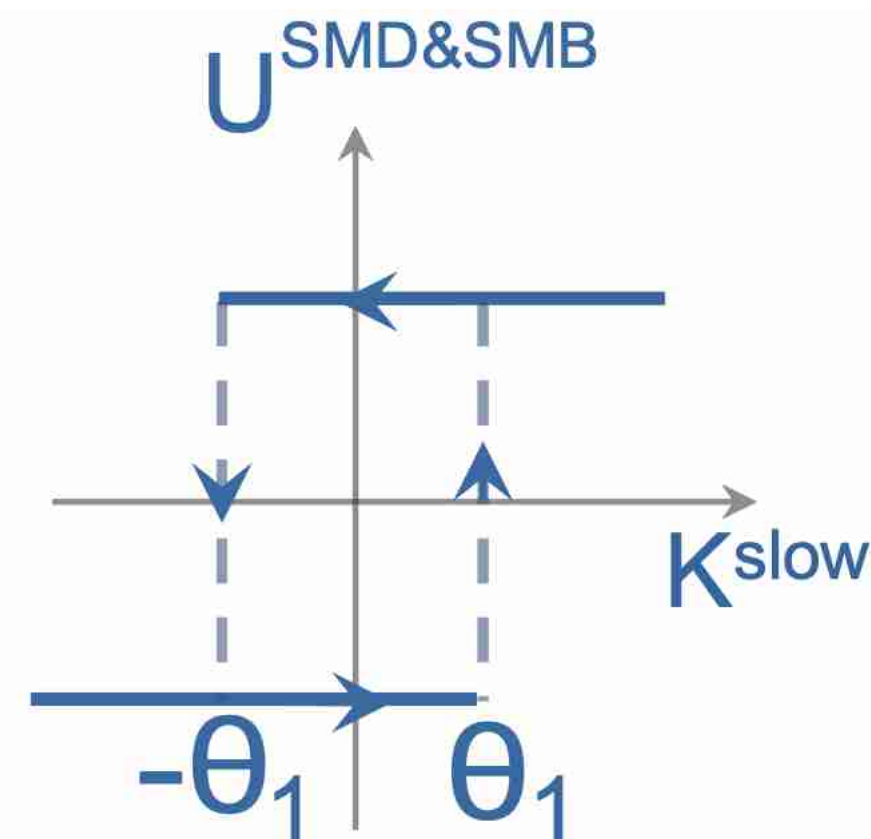
- RMD contribute to control fast head casts.
- SMD maintain dorsal/ventral slow bending states.
- SMB & SMD collaborate to facilitate low frequency rhythmic bending and head-body coupling.

A dual-timescale feedback model

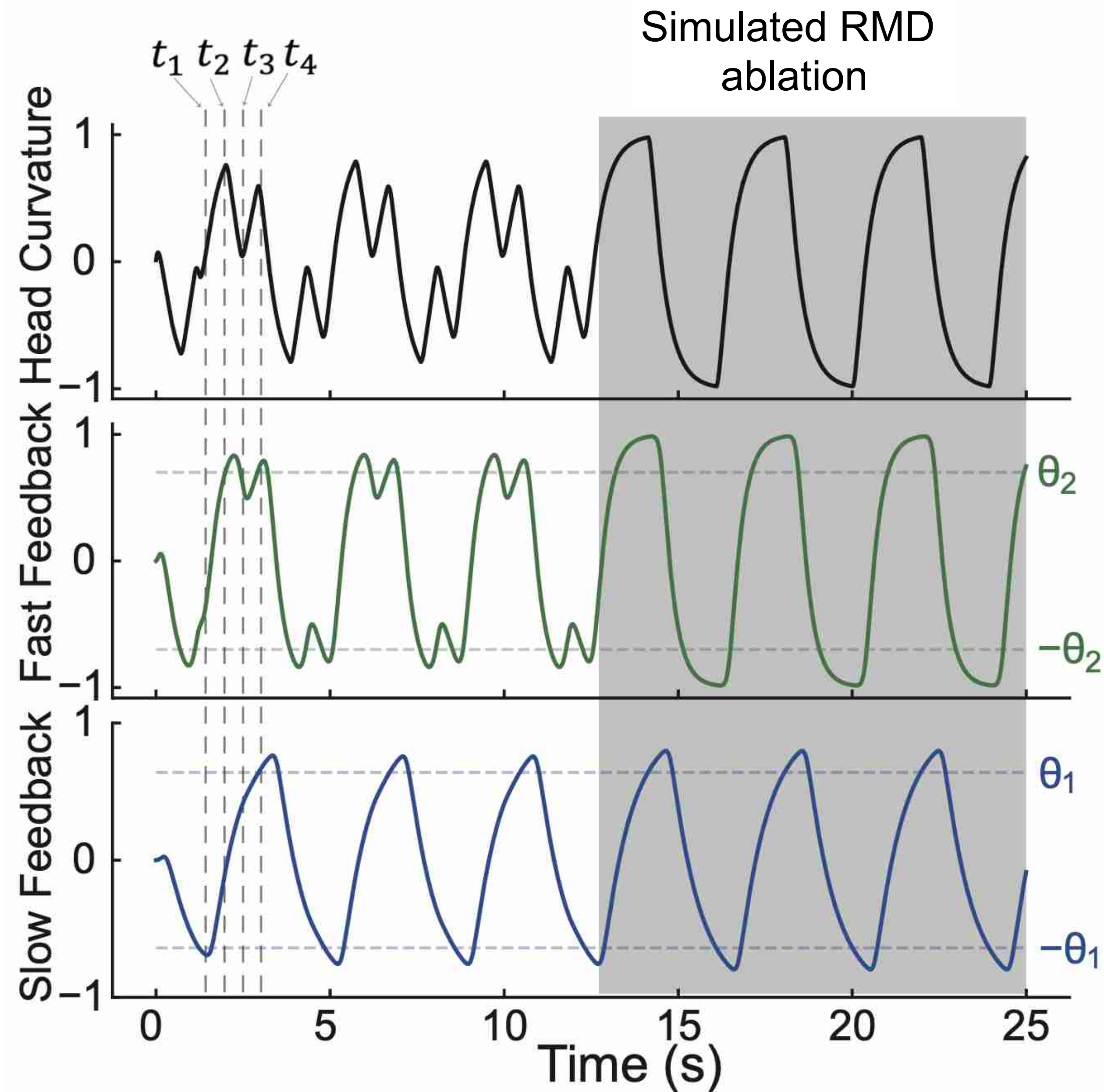
Model circuits:



$$\begin{aligned} \tau_f \frac{dK^{fast}}{dt} &= -K^{fast} + a^f \tanh(b^f * \kappa) && \text{(from mechanoreceptors)} \\ \tau_s \frac{dK^{slow}}{dt} &= -K^{slow} + a^s \tanh(b^s * \kappa) && \text{(from neck bending)} \\ \tau_M \frac{dM}{dt} &= -M + cU_t^{SMD/B}(-K^{slow}) + U_t^{RMDD}(-K^{fast}) - U_t^{RMDV}(K^{fast}) \\ \tau_\kappa \frac{d\kappa}{dt} &= -\kappa + M \end{aligned}$$

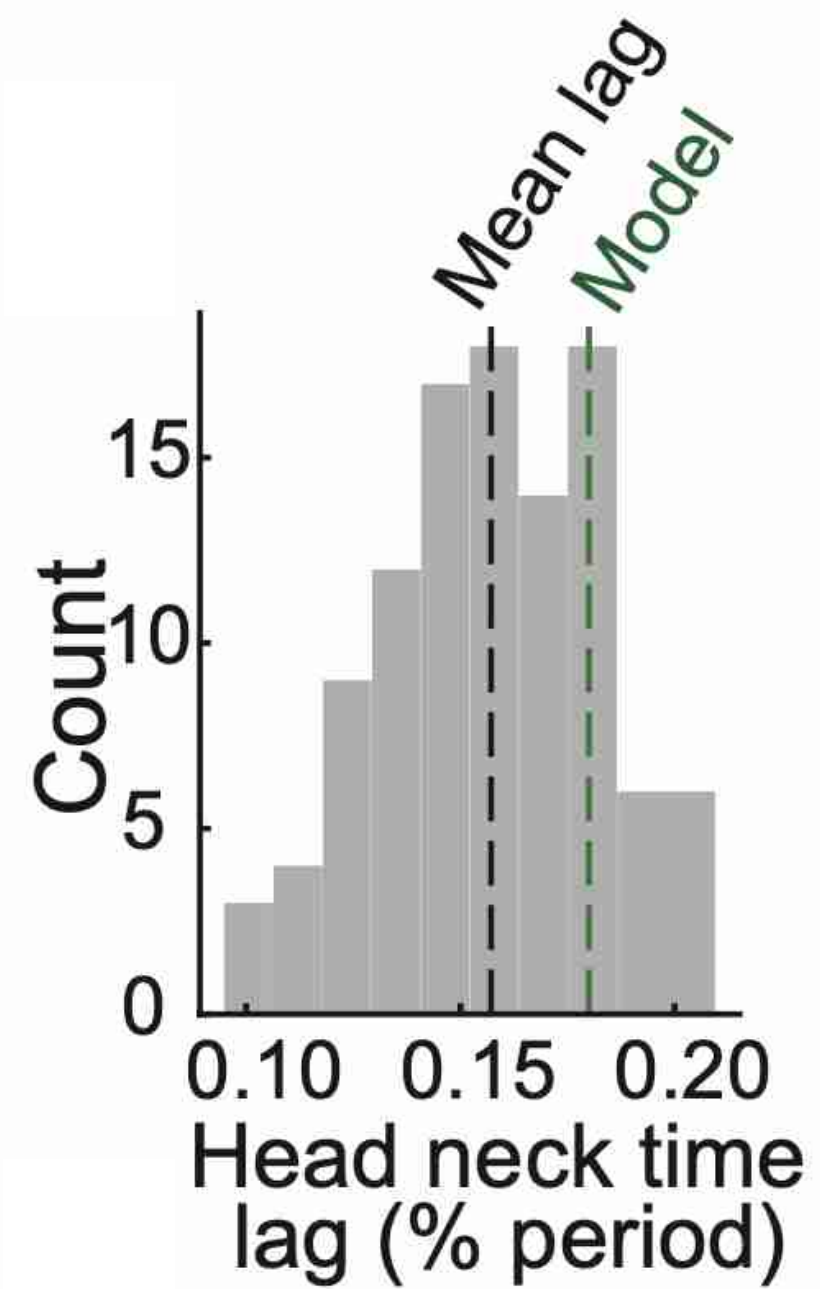
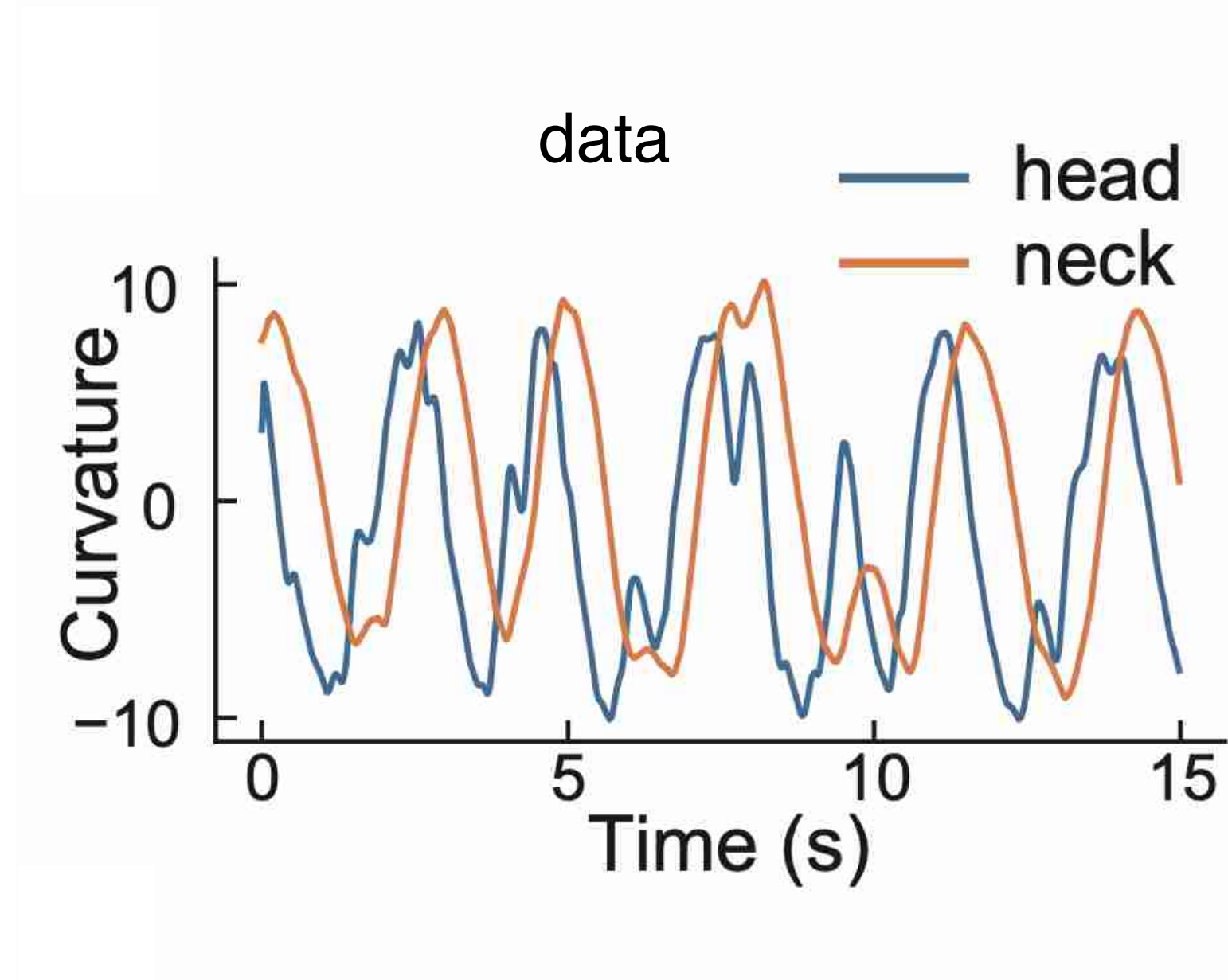


Model results

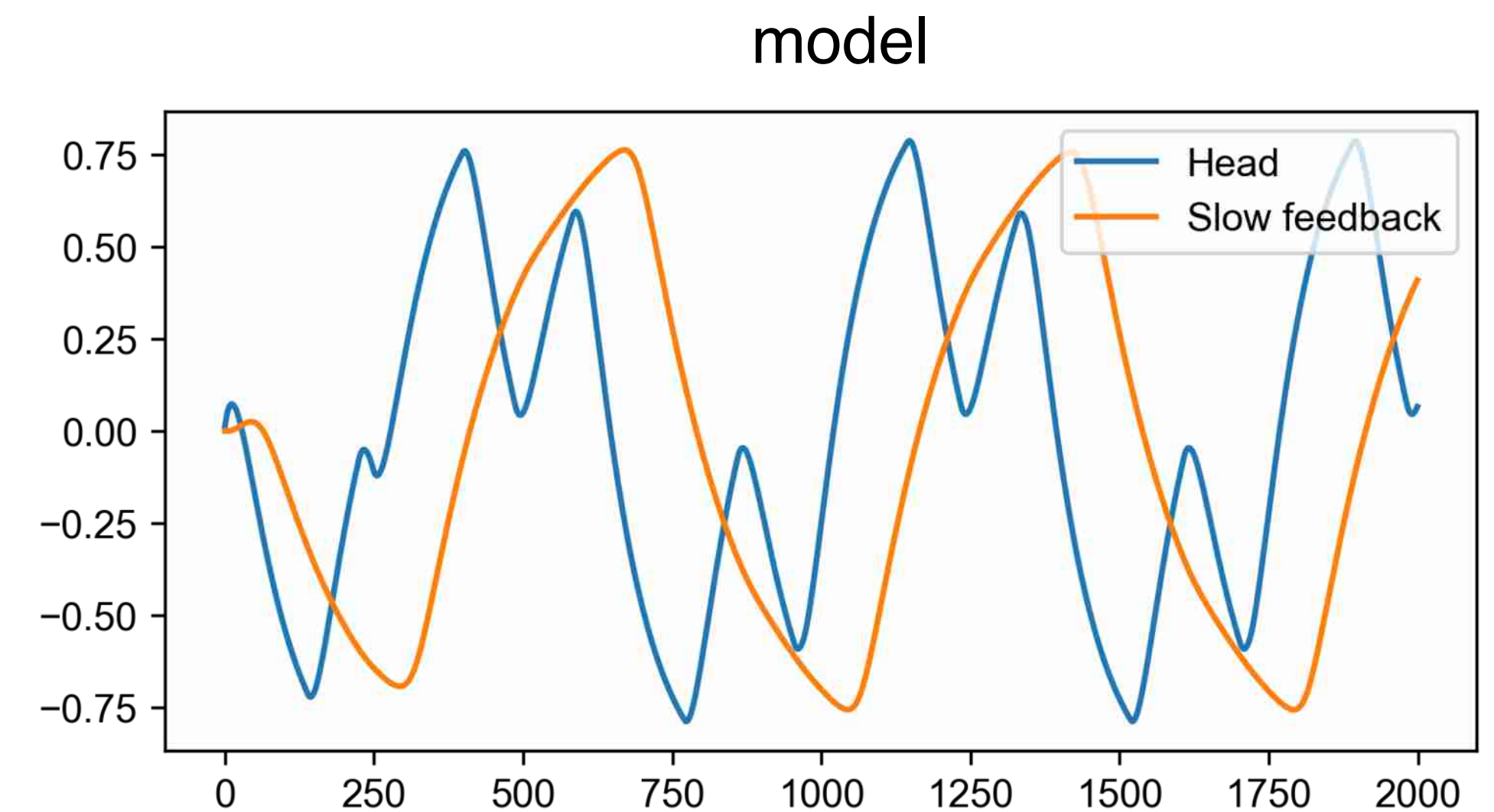


Hypothesis: slow feedback comes from the bending signal of the neck

Evidence 1: similar phase lag



The mean delay between the head and neck curvature is around **0.16 period**

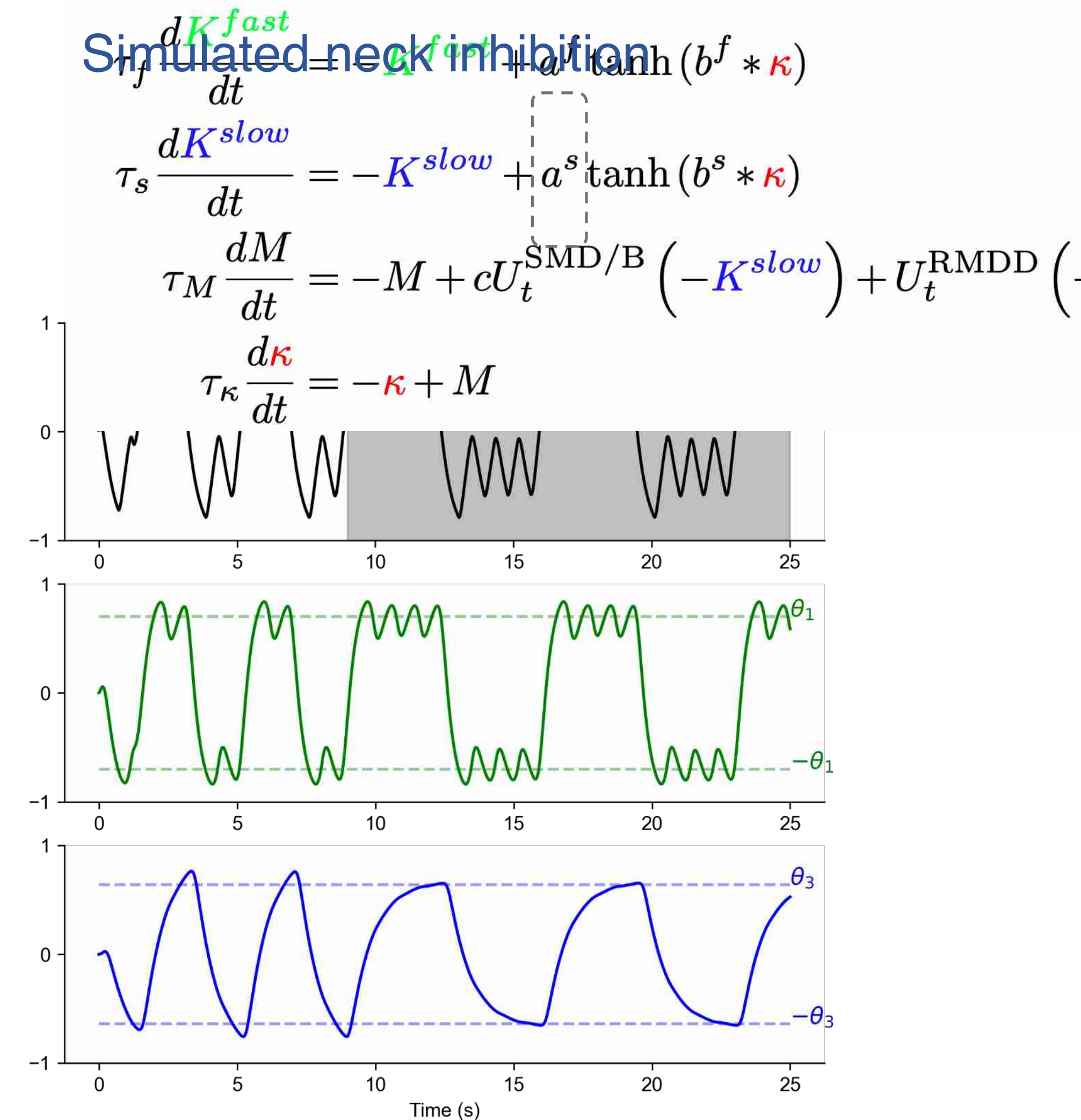
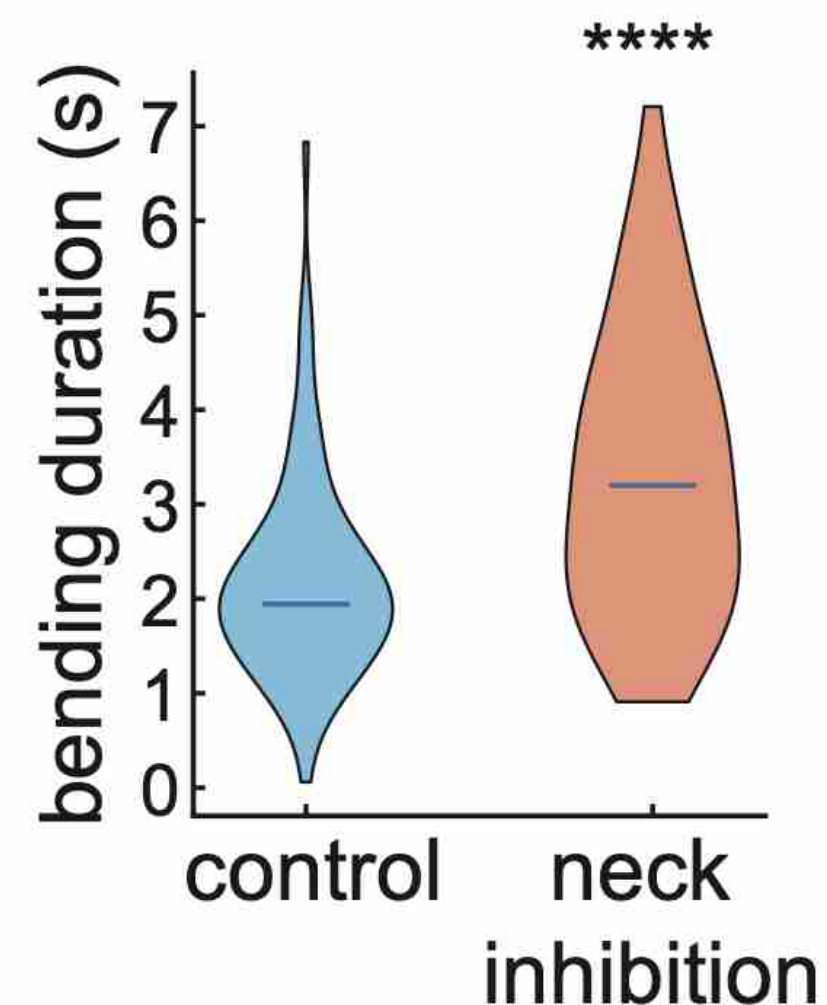
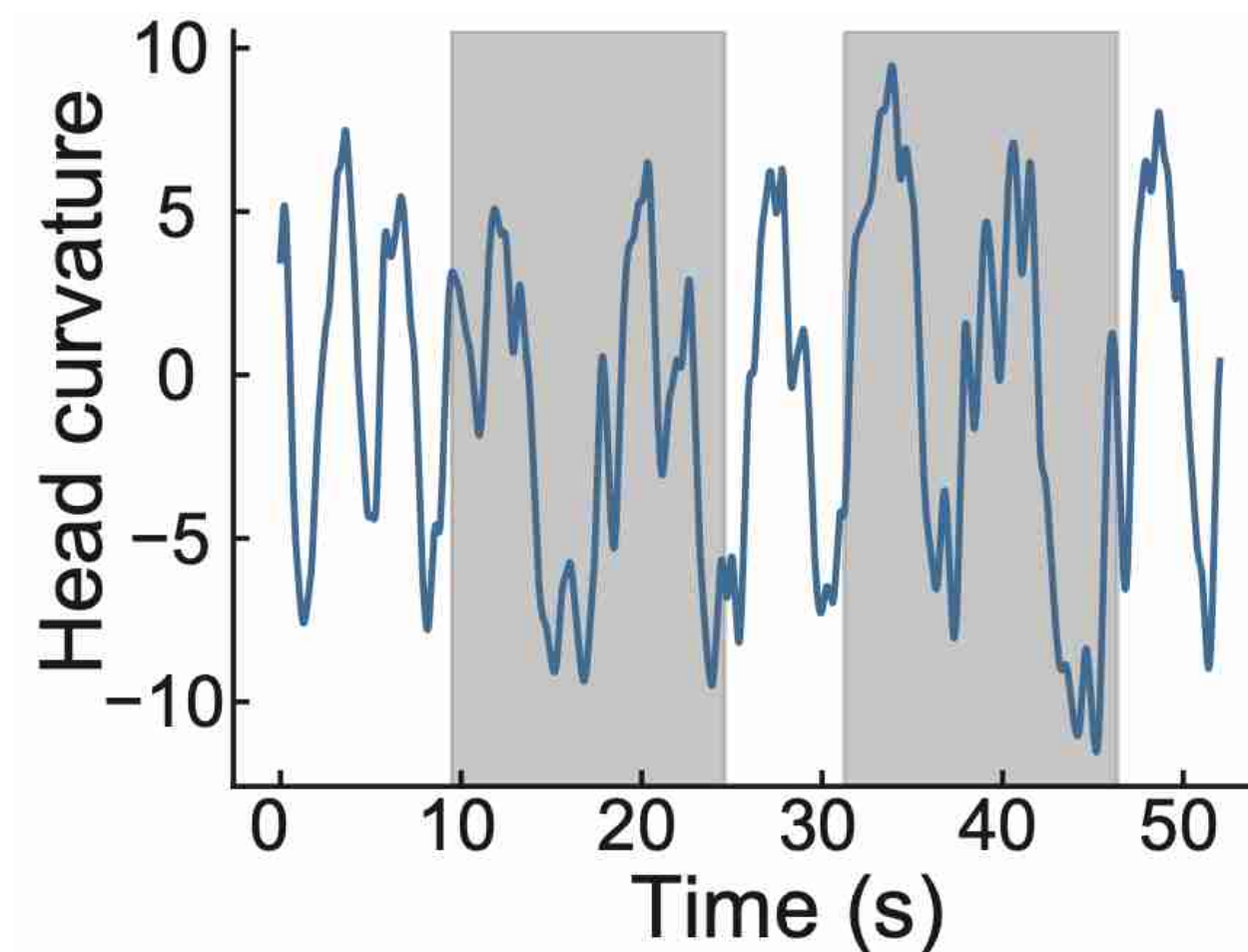


The delay between the head curvature and slow feedback is around **0.18 period**

Hypothesis: slow feedback comes from the bending signal of the neck

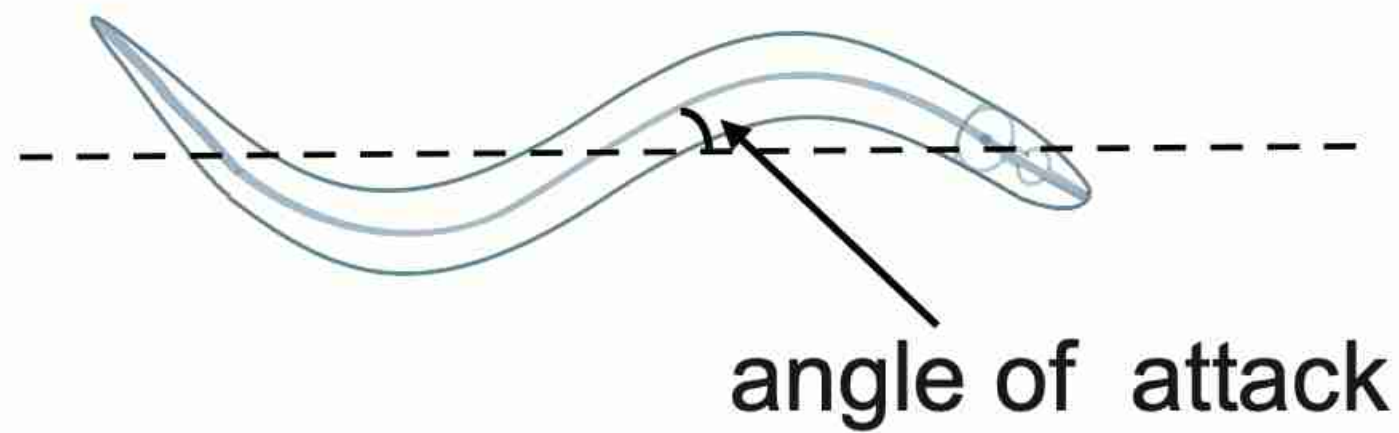
Evidence 2: Neck muscle-inhibited worm will exhibit an extended oscillation period and increased head casts

Optogenetic neck inhibition

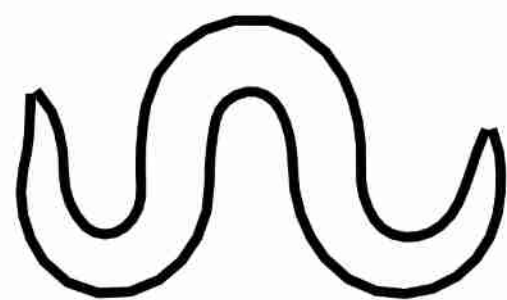


Head-casting strategy from the perspective of optimizing locomotion efficiency

Optimal bending angle for maximum velocity



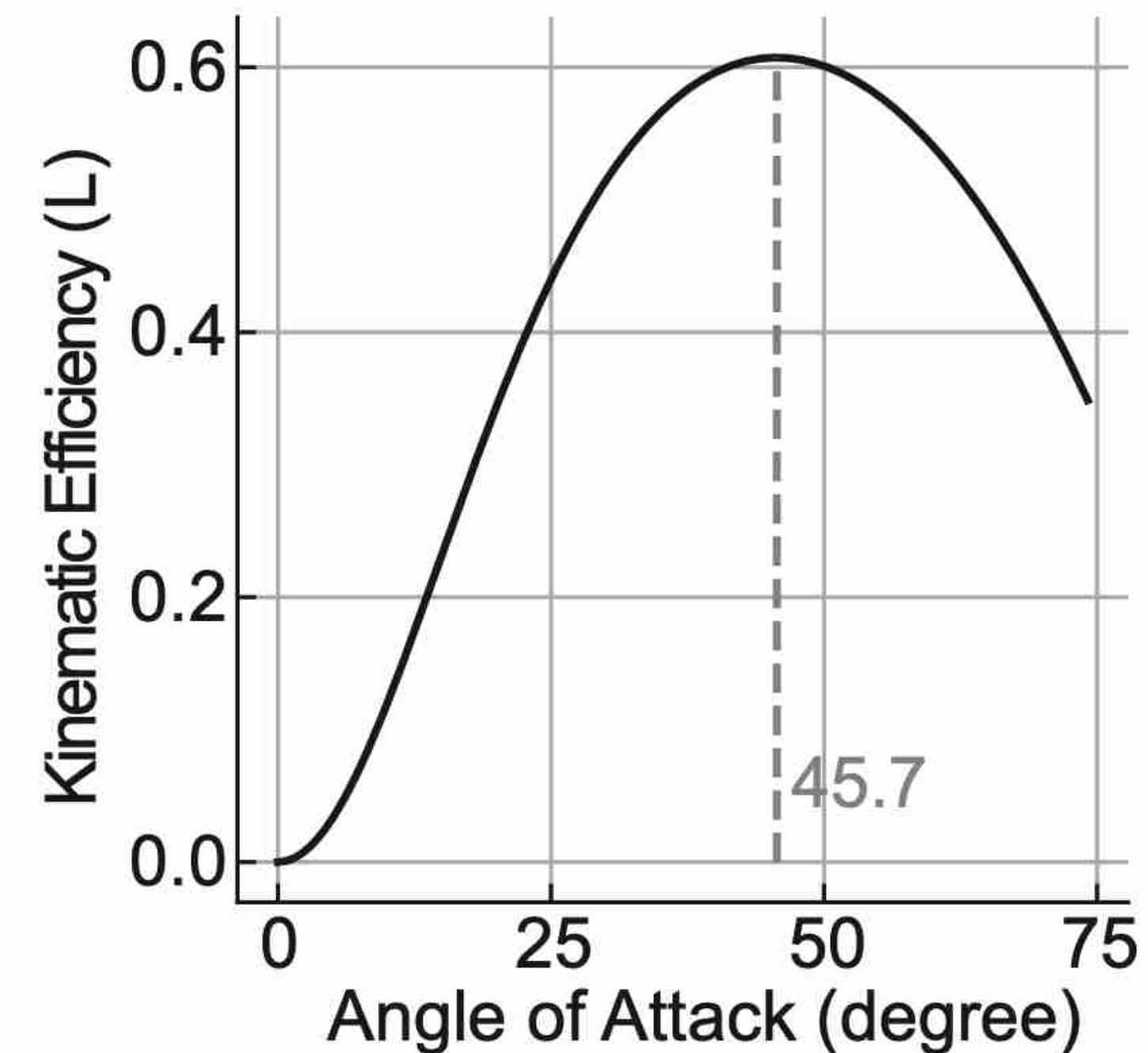
Small angle of attack
Small gain
Large wave speed



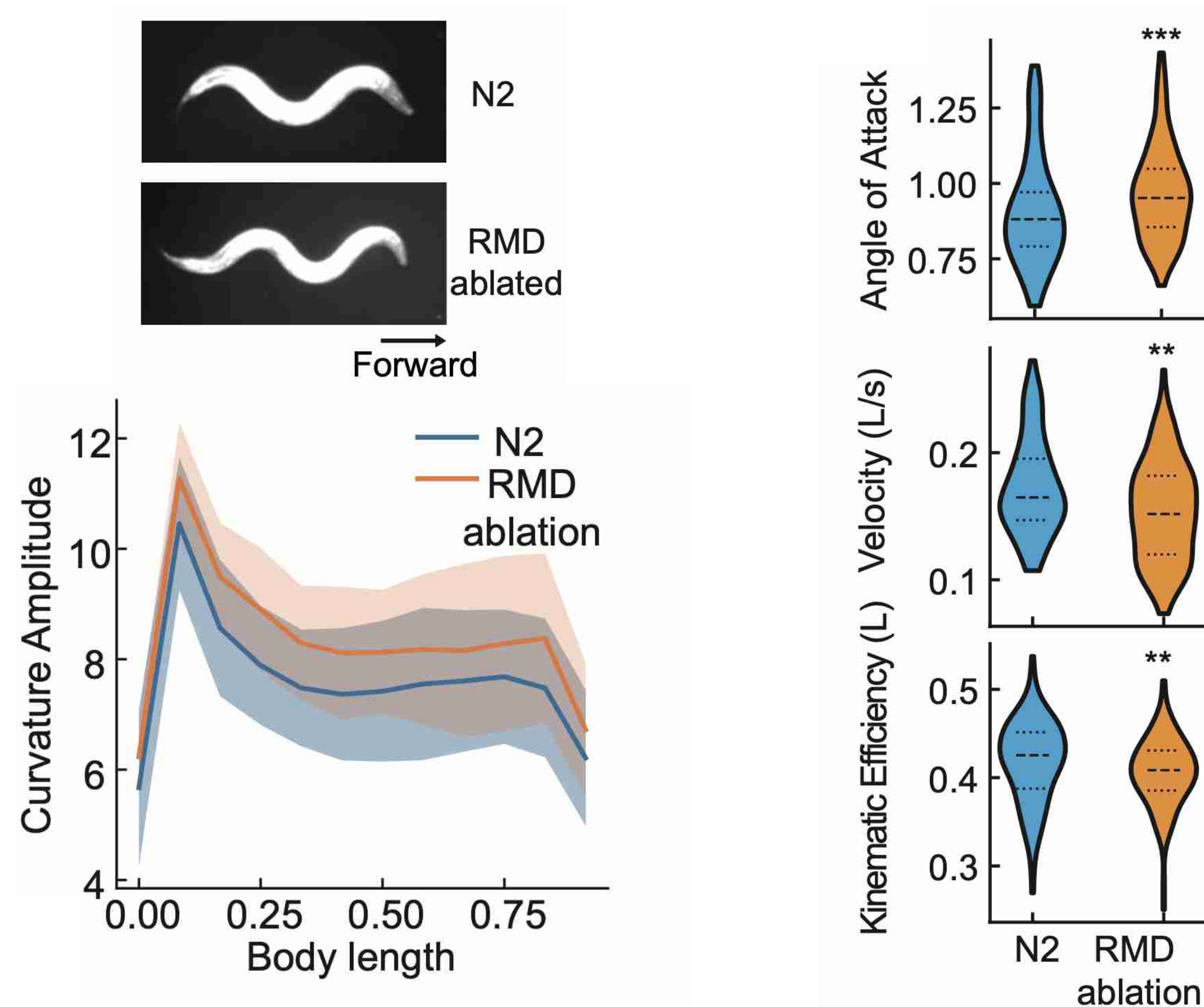
Large angle of attack
Large gain
Small wave speed

$$V = \underbrace{\frac{\frac{C_N}{C_L} - 1}{\frac{C_N}{C_L} + \frac{2}{\tan^2(A_a)}}}_{\text{gain}} \underbrace{f \lambda_x(b, k)}_{\text{wave speed}}$$

Kinematic efficiency V/f

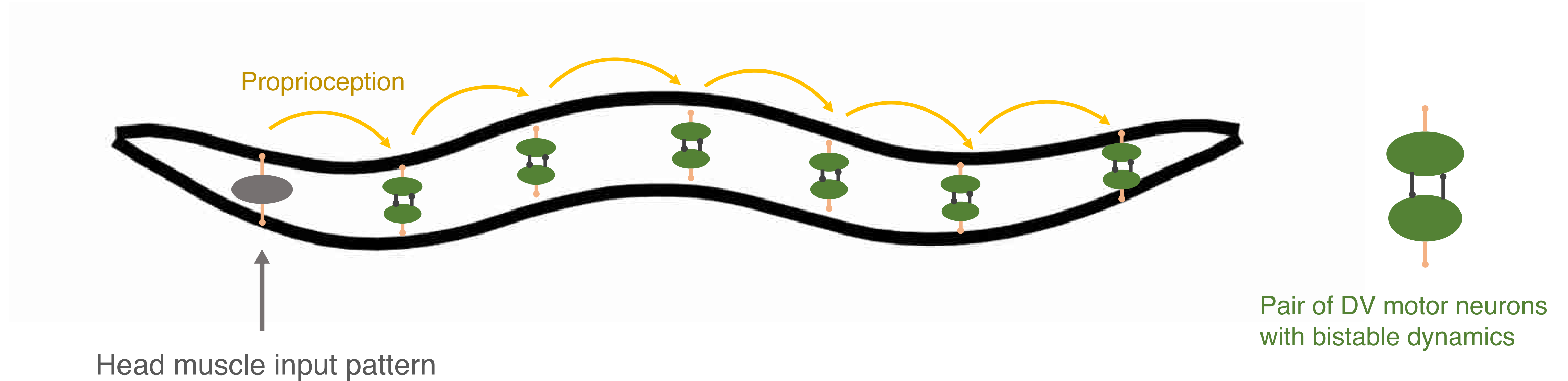


RMD-ablated worms exhibited excessive head bending, which compromised their crawling speed



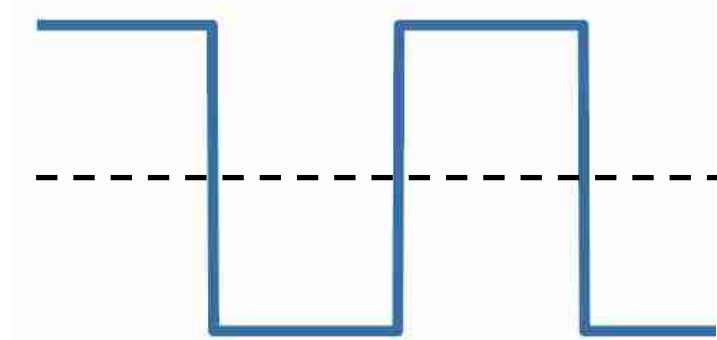
What head-bending pattern yields the highest speed?

A realistic neuro-mechanical model:



Simulation input and output:

Input temporal profile



Neuro-mechanical
model simulation

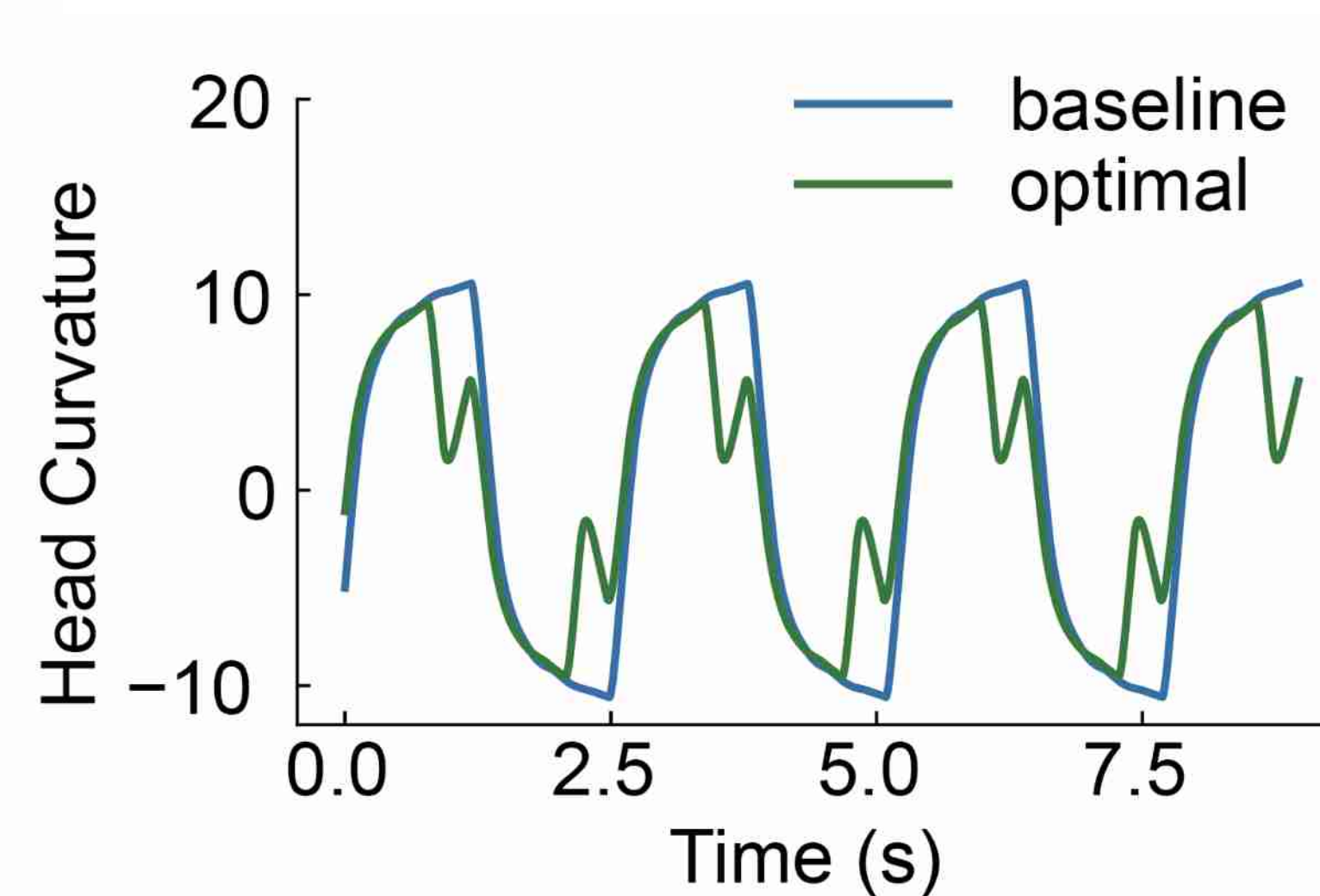
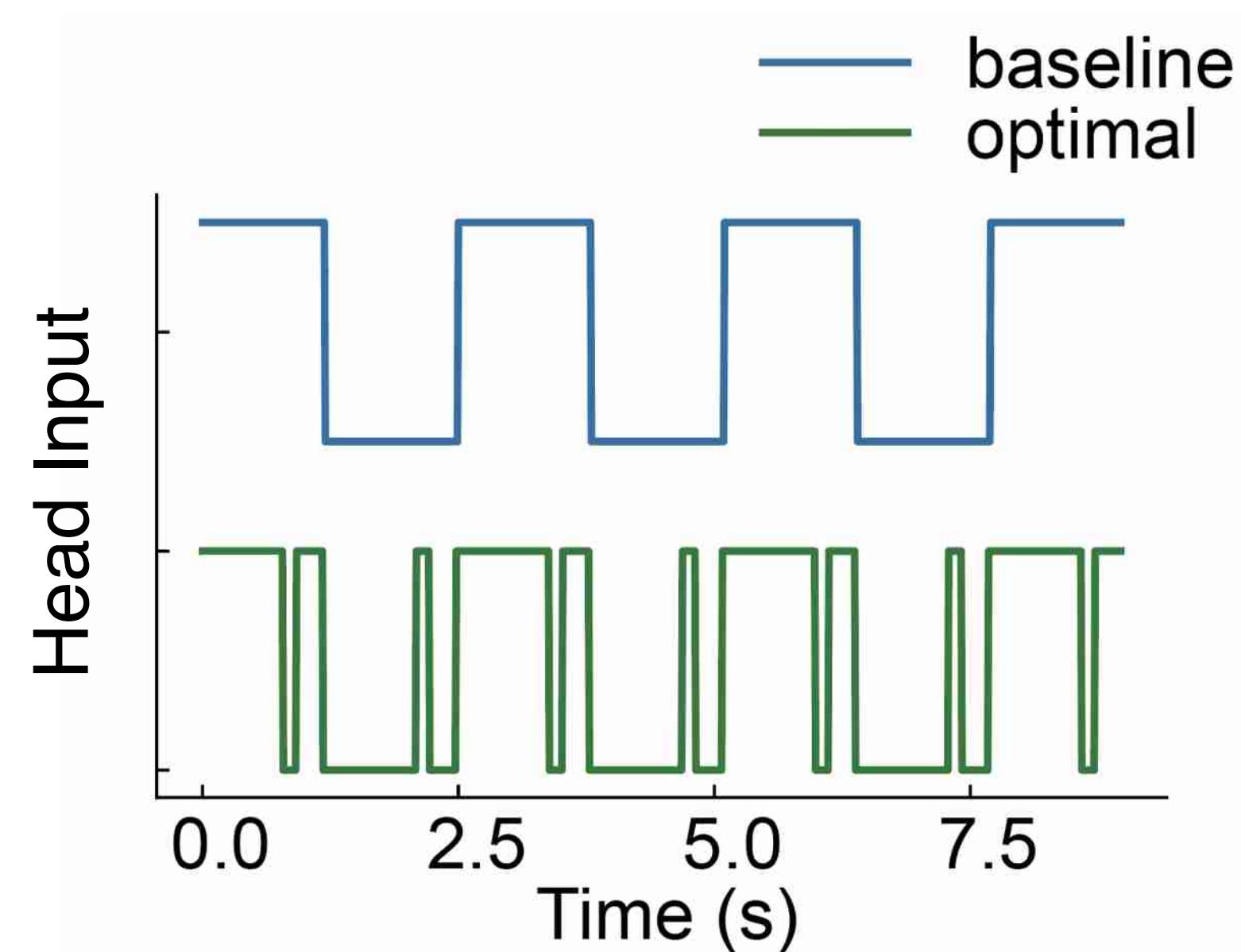


Forward speed

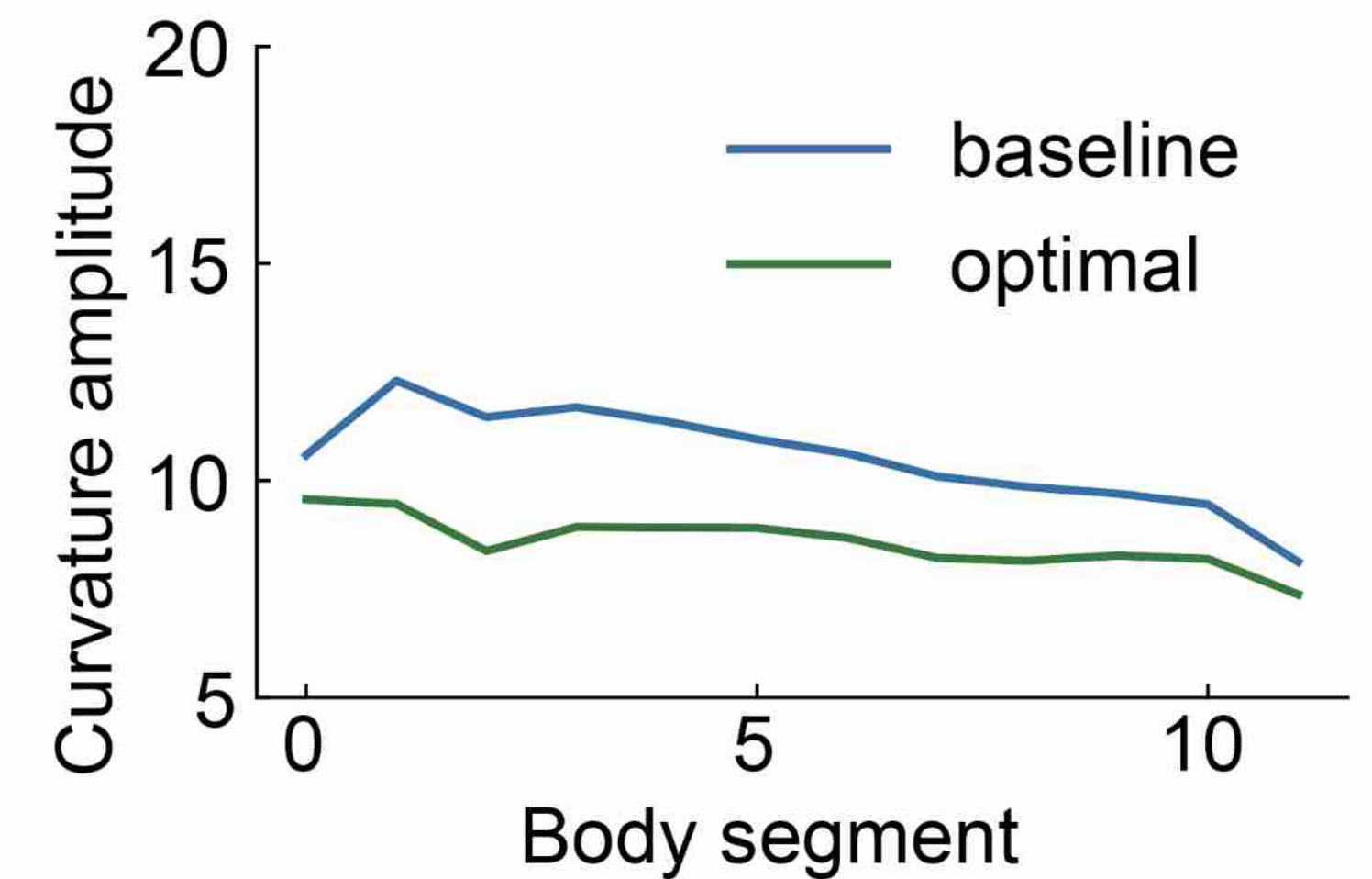
Head casts emerge from speed optimization

Head input function space:

1. Binary
2. Periodic
3. Symmetric for dorsal and ventral activation
4. Switch at most twice in half a period

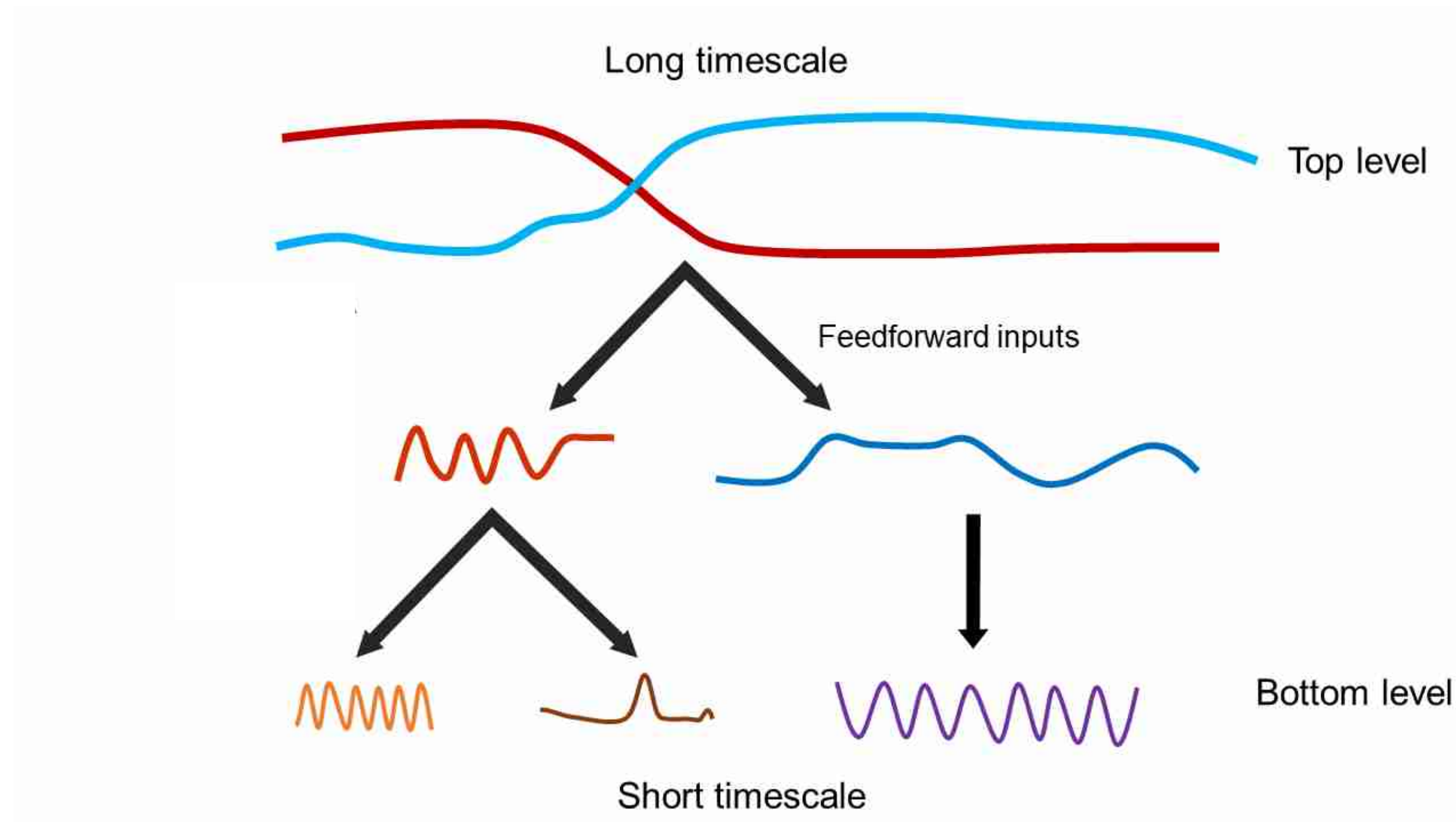


Speed increased 14%

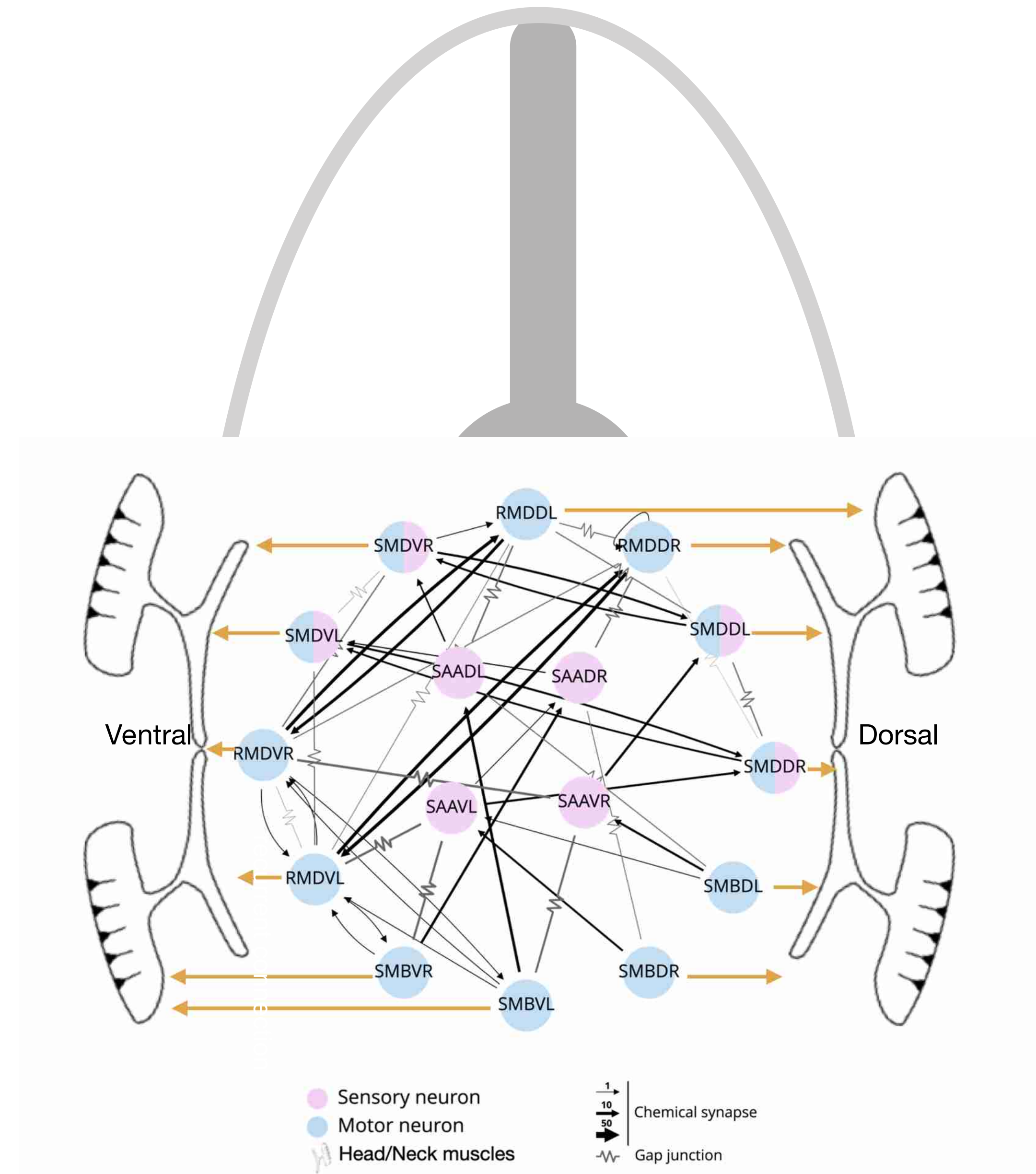


Li, Zhang et al bioRxiv 2024

Hierarchical neural architecture for movement control



Low-level head interneurons play a dual role in short and long timescales



SAA modulate fast locomotion gait



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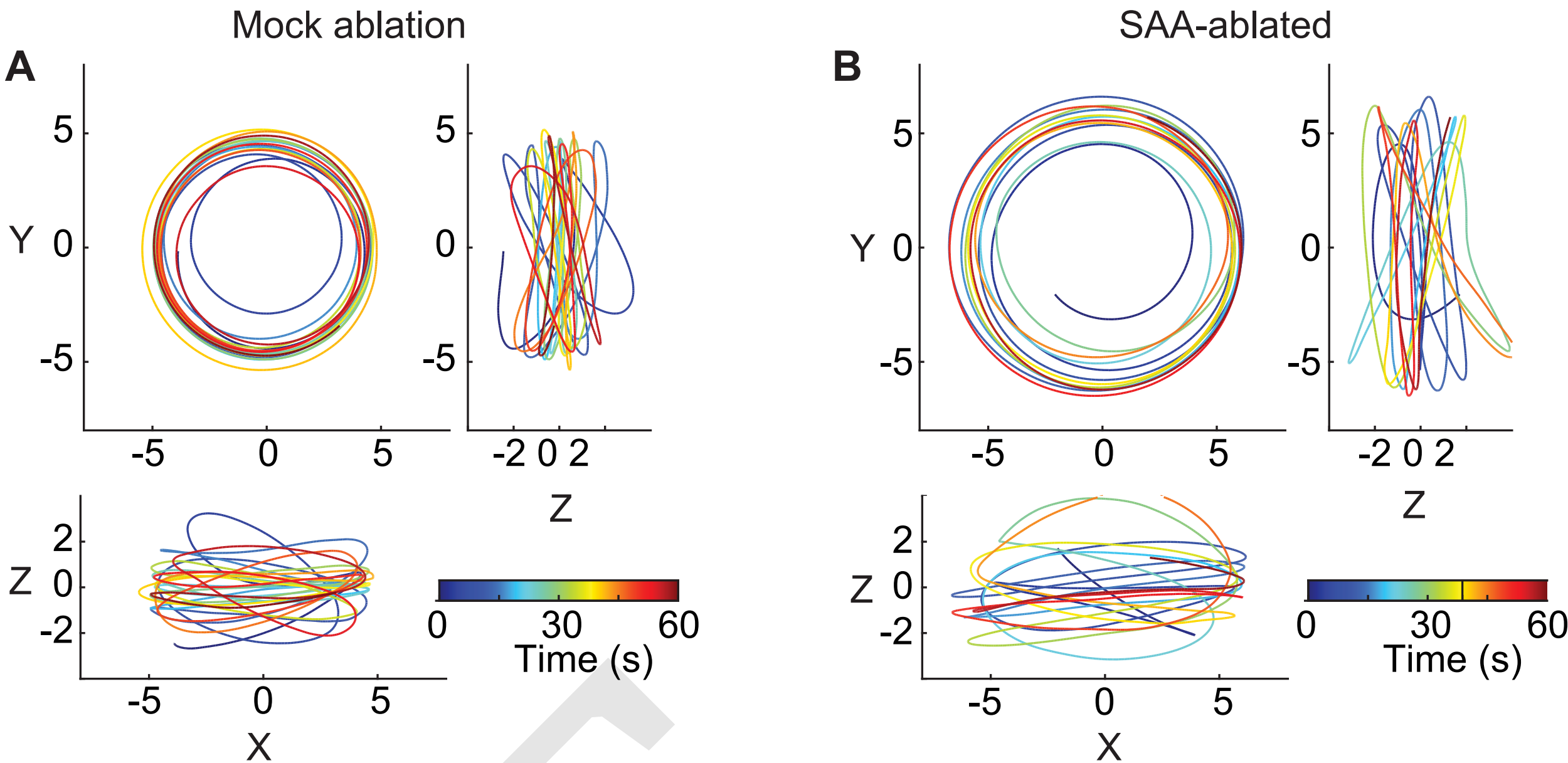
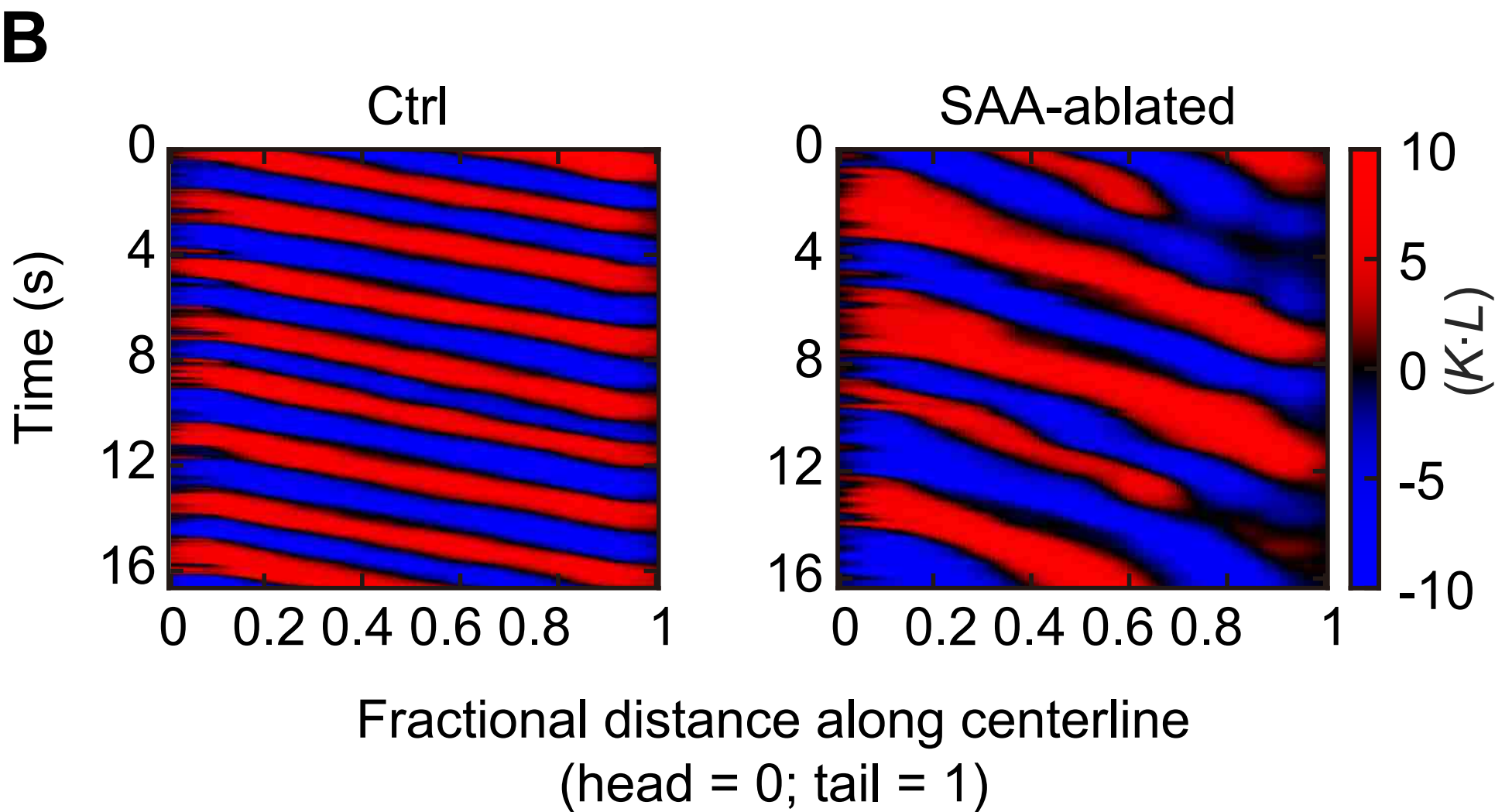
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SAA also contribute to motor state transitions

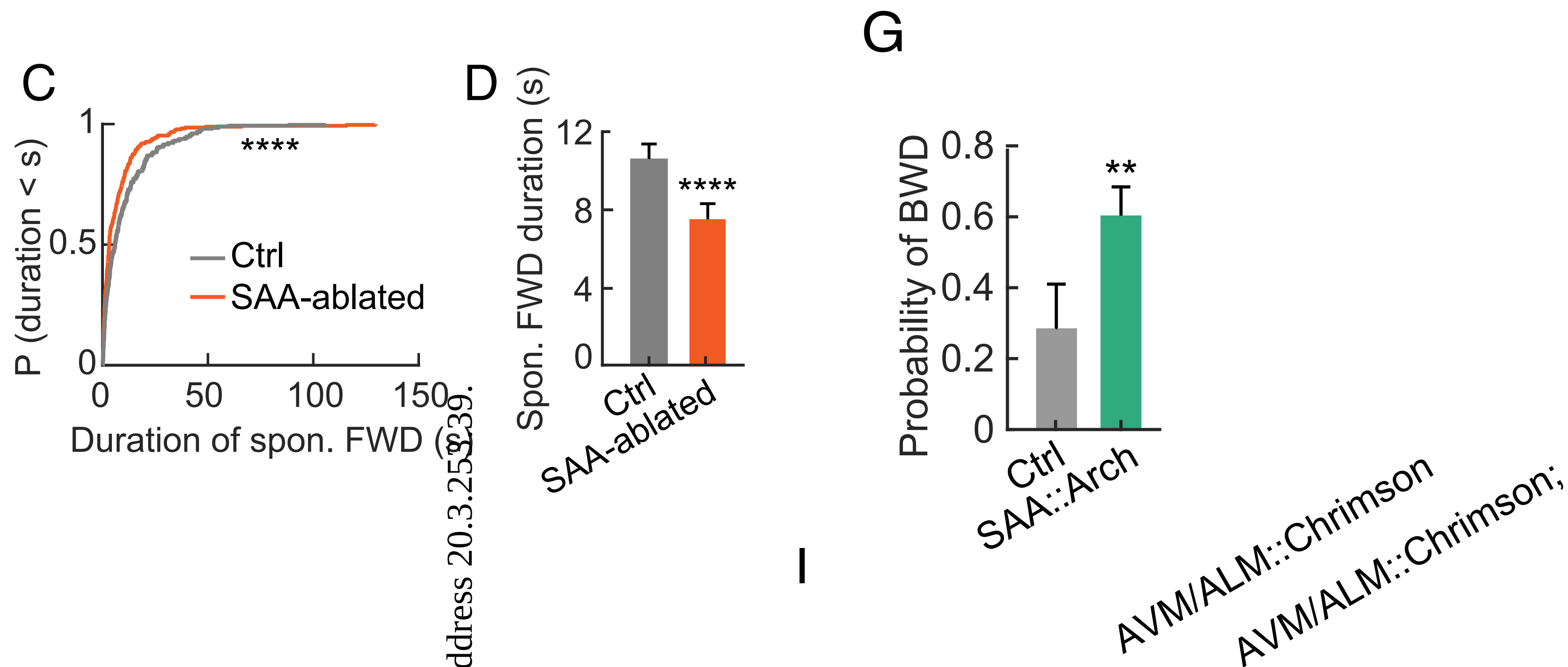


Fig. 4. Impact of SAA on the long timescale crawling behaviors. (A) Representative crawling states are color-coded, and arrows indicate the pause state. Each worm was recorded for about 10 minutes. (B) Fractional time spent in each state. **** $P < 0.0001$, χ^2 test was performed on fractional time spent in each state. (C) Cumulative distributions of the forward run length. Related to (B). * $P < 0.05$, χ^2 test was performed on fractional time spent in each state. n = 308, 8 animals; SAA-ablated: n = 273, 8 animals. (D) Mean duration of spontaneous forward runs. **** $P < 0.0001$, χ^2 test was performed on fractional time spent in each state. (E) Mean duration of spontaneous backward runs. ** $P < 0.01$, χ^2 test was performed on fractional time spent in each state. (F) Mean duration of spontaneous forward runs in AVM/ALM::Chrimson and AVM/ALM::Chrimson; worms. **** $P < 0.0001$, χ^2 test was performed on fractional time spent in each state.

SAA implement feedback inhibition during motor state transition

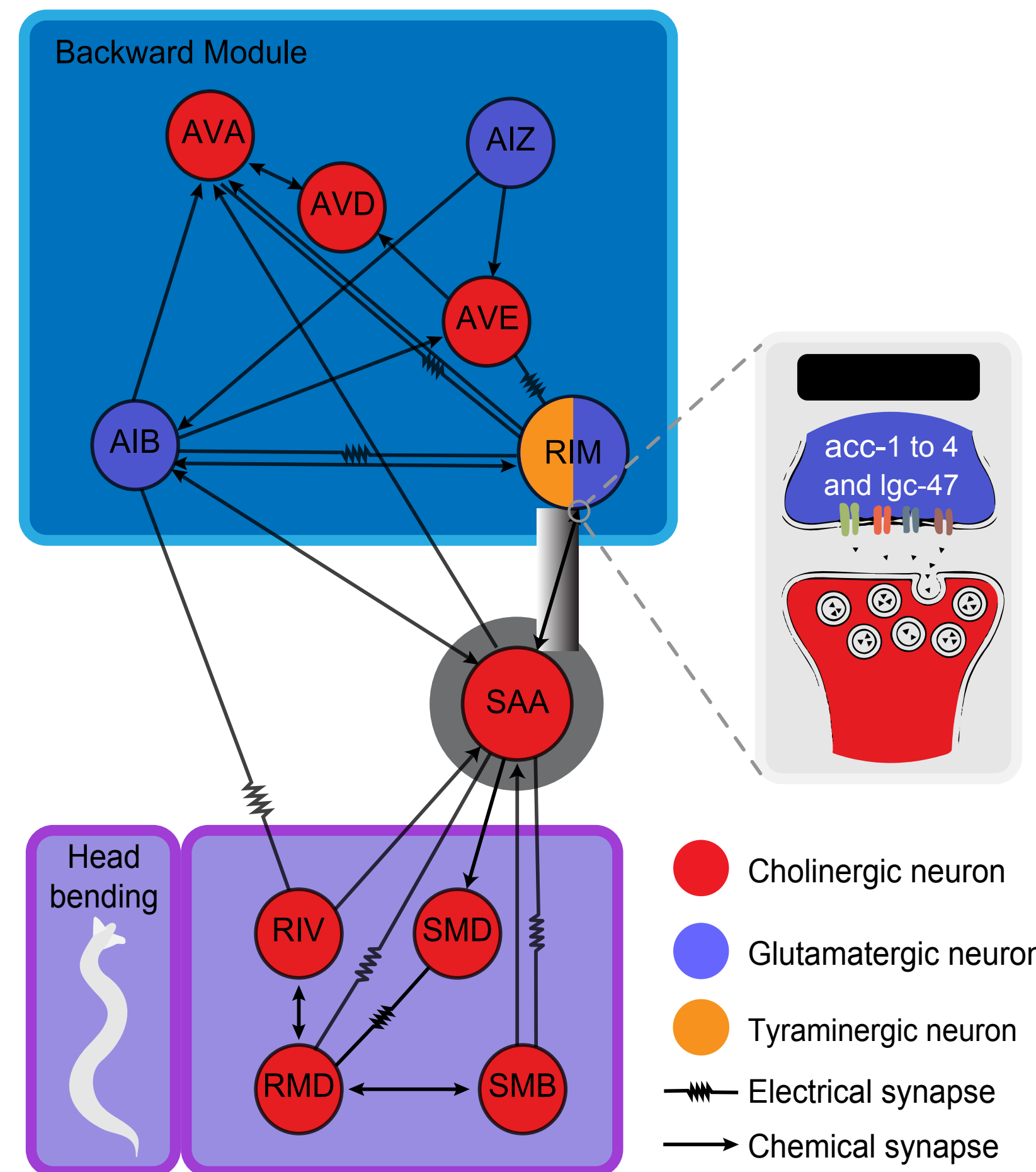


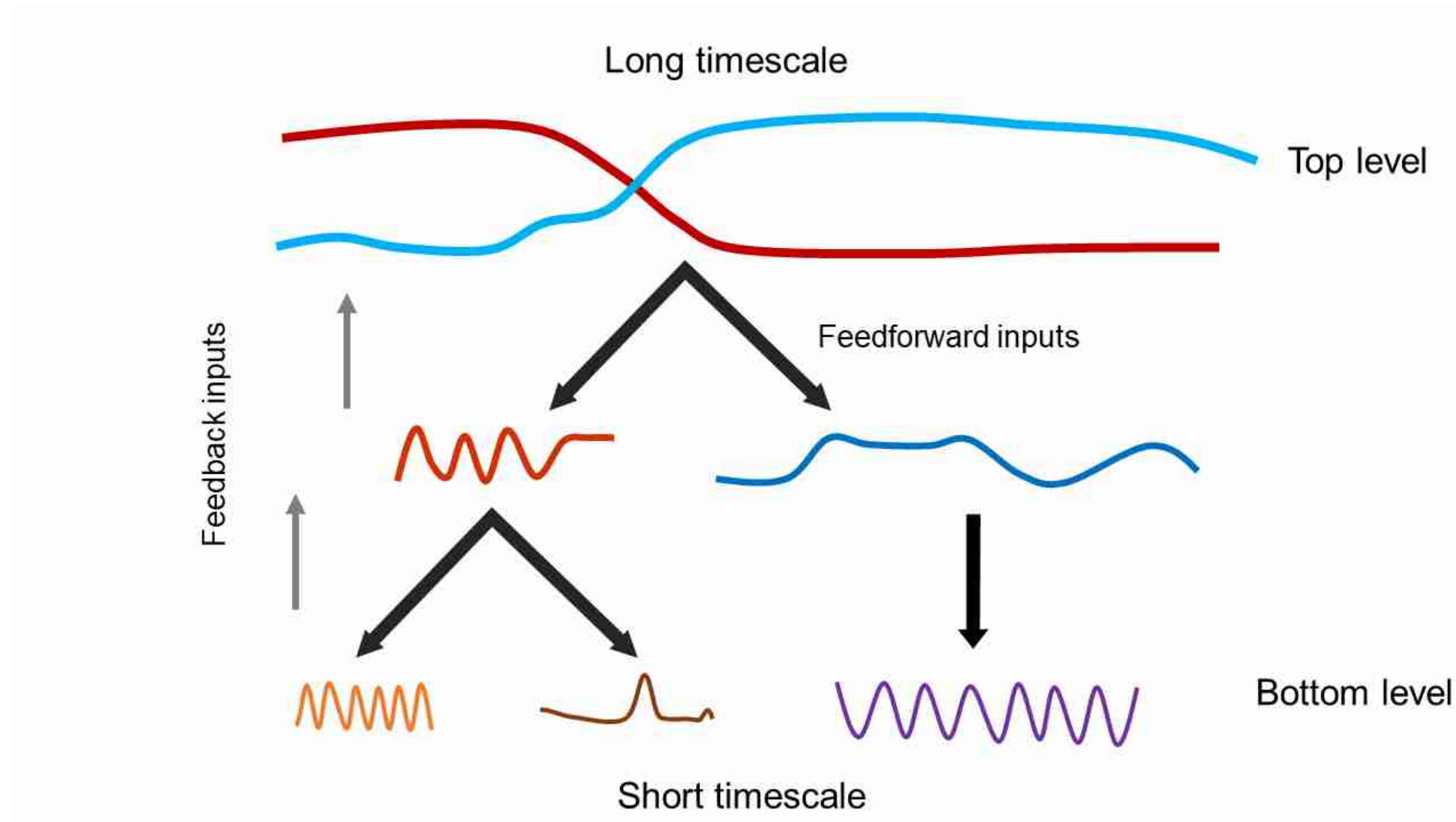
Fig. 7. SAA interneurons bridge circuit modules that control short and long timescale motor behaviors.

disruption of movement kinematics reduces locomotion speed

change in RIM activity can promote or suppress the reversal (36, 48). During stimulus-triggered escape responses, feedback inhibition is part of the winner-take-all strategy (35) that ensures a rapid and smooth transition from a reversal state to a turn/forward movement state, accompanied by increased calcium activity in SAAD (Fig. 5F). This inhibition is achieved by cholinergic synapses. Interestingly, we find that RIM expresses all four acetylcholine-gated chloride channel subunits, and our data suggest that different ACC channel subunits do not act redundantly (SI Appendix, Fig. S7). Here, we postulate that the spatial combination of ACC subunits in the RIM cell body or neurites may contribute to fine-tuning the RIM membrane potential and enable precise control of motor state transitions.

Functional Diversity of Interneurons. In *C. elegans*, interneurons situated between sensory and motor neurons play crucial roles in action selection and modulation of adaptive motor behavior. Interneurons such as AIY and AIB, which receive substantial sensory inputs, demonstrate a rapid transition from sensory to motor representation: Their Ca^{2+} activities encode distinct motor states over extended timescales. Disrupting these neurons alters the likelihood of transitions between motor states without affecting rapid fast motor kinetics, such as movement speed (SI Appendix, Fig. S10) (27, 35, 61). Descending the sensorimotor hierarchy, interneurons with extensive connections to motor neurons, such as AVB, AVA, and RIB, show a different function. Manipulation of these neurons through optogenetic stimulation or inhibition can initiate or stop movements, respectively (26, 30, 35, 37). Their removal or persistent inhibition of these neurons significantly reduces movement speed [SI Appendix, Fig. S10 and and the amplitude of undulation (30), indicating that sustained

Hierarchical neural architecture for movement control



An adaptation of the essay “Birds and Frogs”

*by Freeman Dyson
AMS Einstein Lecture 2008*

Birds fly high in the air and survey broad vistas of brain forest; frogs live in the mud below and they delight in neuronal trees and flowers that grown nearby. Neuroscience needs both birds and frogs: it is rich and beautiful because birds give it a panoramic view and frogs give it intricate details.

Acknowledgement



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