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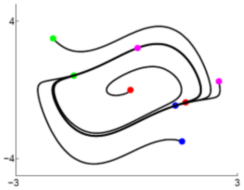
EPFL Biorobotics Laboratory

Computational Motor Control
Lecture 7:

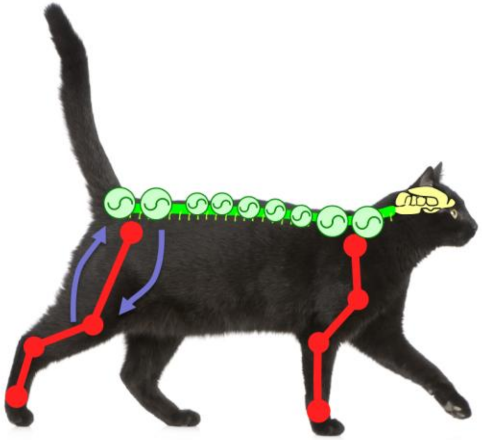
Lamprey and salamander locomotion

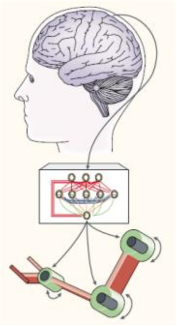
Auke Jan Ijspeert

Contents of lectures

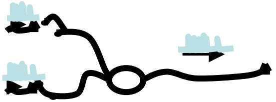


Dynamical systems

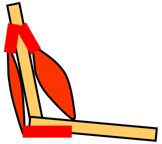




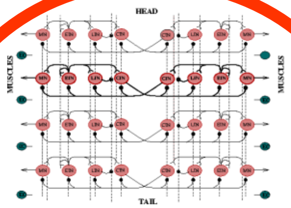
Neuroprosthetics



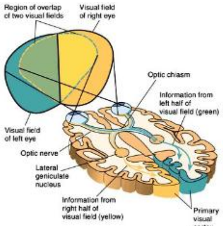
Neuron models



Muscle and Biomech. models



Motor system models



Visual system models

Today

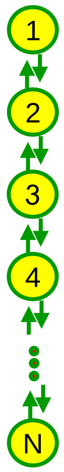
Topics:

- Modeling the lamprey locomotor system (Part 2)
- Modeling the salamander locomotor system

Possible explanations of the traveling wave generation

There are (at least) four potential explanations for the generation of traveling waves in a chain of coupled oscillators:

1. **Conduction delays in the couplings**
2. **Differences in intrinsic frequencies**
3. **Asymmetries in the coupling between segments along the chain**
4. **Sensory feedback loops (effects of the biomechanics of swimming).**



As we will see next, the third and fourth explanations are the most likely!

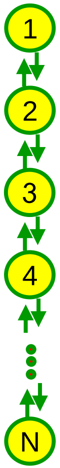
Hyp 3: Asymmetries in the coupling

Traveling waves can be generated **through asymmetries in the intersegmental coupling** without needing different intrinsic frequencies:

$$\dot{\phi}_i = \omega + \sum_{j=1}^{N} w_{ij} \sin(\phi_i - \phi_j - \psi_{ij})$$

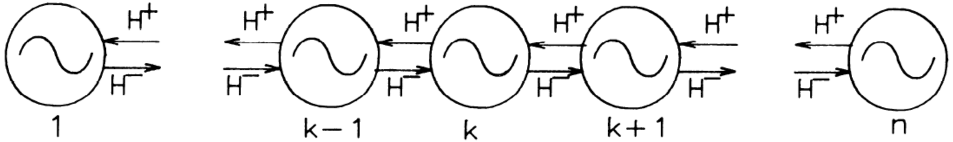
Here all oscillators have the same intrinsic frequency

New: phase bias ψ_{ij} (psi)



This is a particular implementation of the general model by Ermentrout and Kopell:

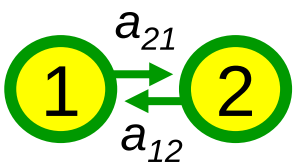
$$d\Theta_k/dt = \omega_k + H^+(\Theta_{k+1} - \Theta_k) + H^-(\Theta_{k-1} - \Theta_k)$$



Asymmetries in the coupling

Predicting the phase difference between two oscillators

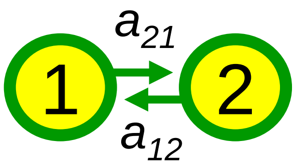
$$\dot{\phi}_i = \omega + \sum_{j=1}^{N} w_{ij} \sin(\phi_i - \phi_j - \psi_{ij})$$



$$\frac{d\phi_1}{dt} = \omega_1 + a_{12} \sin(\phi_2 - \phi_1 - \psi_{12})$$
$$\frac{d\phi_2}{dt} = \omega_2 + a_{21} \sin(\phi_1 - \phi_2 - \psi_{21})$$

Asymmetries in the coupling: two oscillators

Predicting the phase difference between two oscillators



We assume the phase biases of both coupling to be “in agreement”:

Phase difference: $\varphi = \phi_1 - \phi_2$

$$\psi_{21} = -\psi_{12}$$

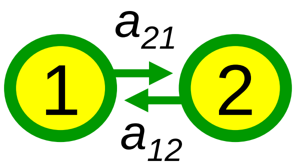
$$\frac{d\phi_1}{dt} = \omega_1 + a_{12}\sin(\phi_2 - \phi_1 - \psi_{12})$$

$$\frac{d\phi_2}{dt} = \omega_2 + a_{21}\sin(\phi_1 - \phi_2 - \psi_{21})$$

$$\frac{d\varphi}{dt} = (\omega_1 - \omega_2) - (a_{12} + a_{21})\sin(\varphi - \psi_{12})$$

Asymmetries in the coupling: two oscillators

$$\frac{d\varphi}{dt} = 0 \quad \Rightarrow \quad \tilde{\varphi} = \arcsin\left(\frac{\omega_1 - \omega_2}{a_{12} + a_{21}}\right) + \psi_{12}$$



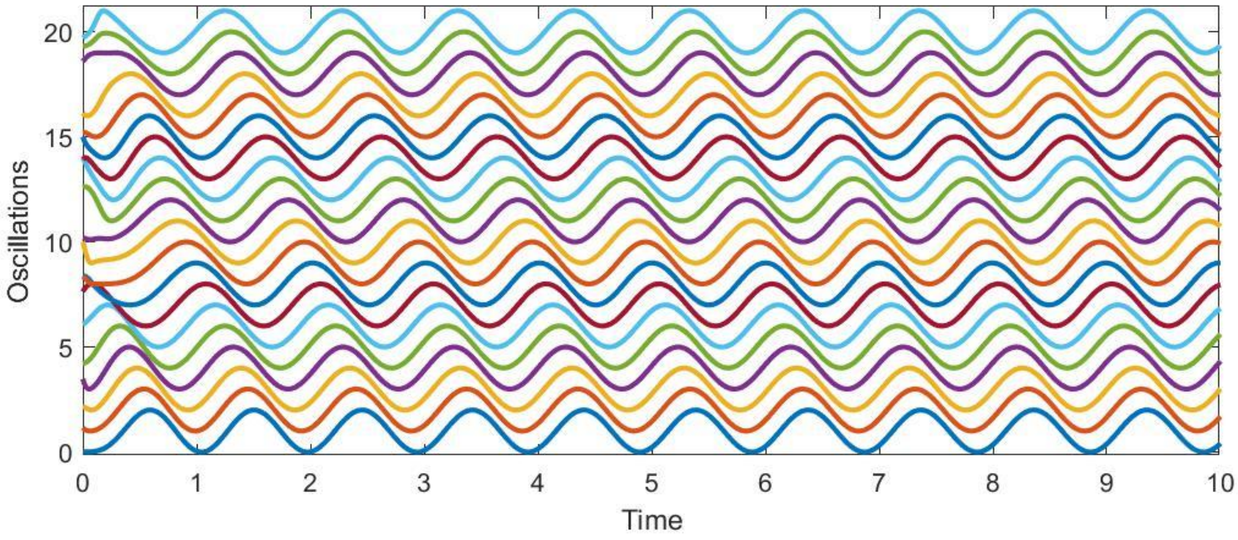
If **same intrinsic frequencies**:

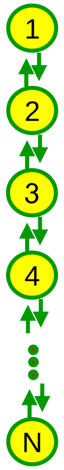
$$\omega_1 = \omega_2 \Rightarrow \quad \boxed{\tilde{\varphi} = \psi_{12}}$$

Here the phase difference always converges to the **phase bias ψ_{12}!**

Asymmetries in the coupling: chain of oscillators

$$\dot{\phi}_i = \omega + \sum_{j=1}^{N} w_{ij}\ \sin(\phi_i - \phi_j - \psi_{ij}) \qquad \psi_{ij} = -\psi_{ji} = \frac{2\pi}{N}$$

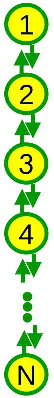




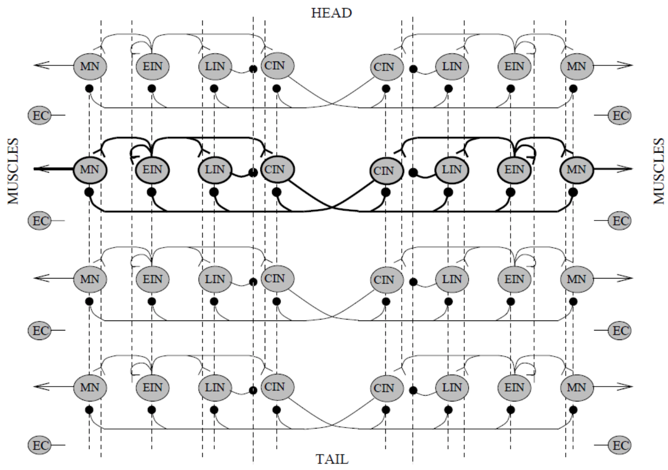
Hypothesis 3 is in good agreement with biological data: (1) **Traveling waves** in isolated spinal cord, (2) phase lag is **constant along the spinal cord**, (3) phase lag stays **constant at different frequencies**.

Asymmetries in the coupling, neural circuits

In a neural circuit, similar phase biases due to coupling can be implemented with **different strengths and different lengths of projections of neural connections**. Neurons tend to project further towards the tail than towards the head. These asymmetries explain why isolated spinal cords produce traveling waves.



Equivalent



$$\dot{\phi}_i = \omega + \sum_{j=1}^{N} w_{ij} \, \sin(\phi_i - \phi_j - \psi_{ij})$$

Ekeberg, Ö. (1993). A combined neuronal and mechanical model of fish swimming. *Biological Cybernetics*, *69*, 363–374.
Ijspeert, A. J., Hallam, J., & Willshaw, D. (1999). Evolving swimming controllers for a simulated lamprey with inspiration from neurobiology. Adaptive Behavior, 7(2), 151–172.

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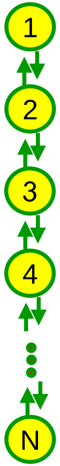
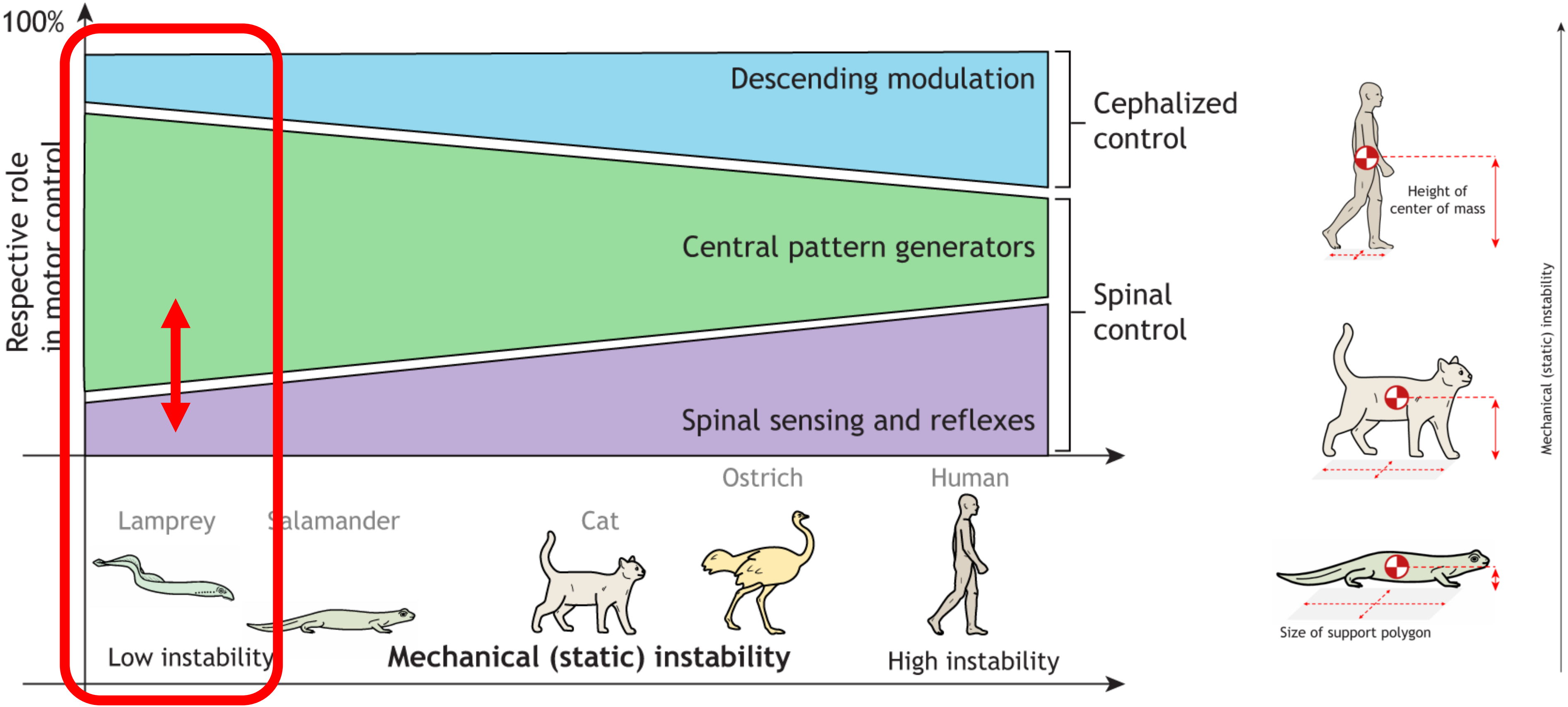


As we will see next, the third and fourth explanations are the most likely!



Ijspeert and Daley, J. of Exp. Biol., JEB 2023

Eels are amazingly robust

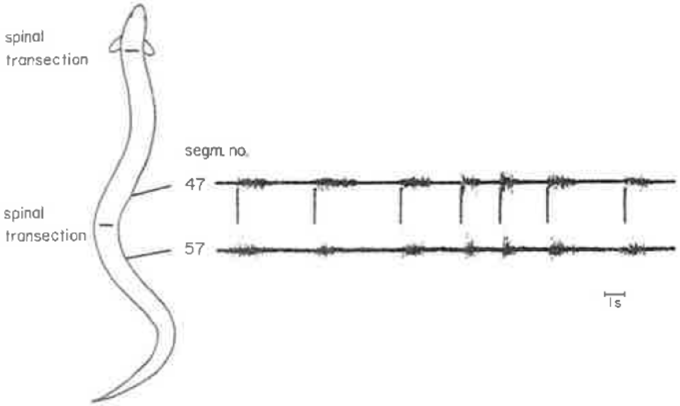
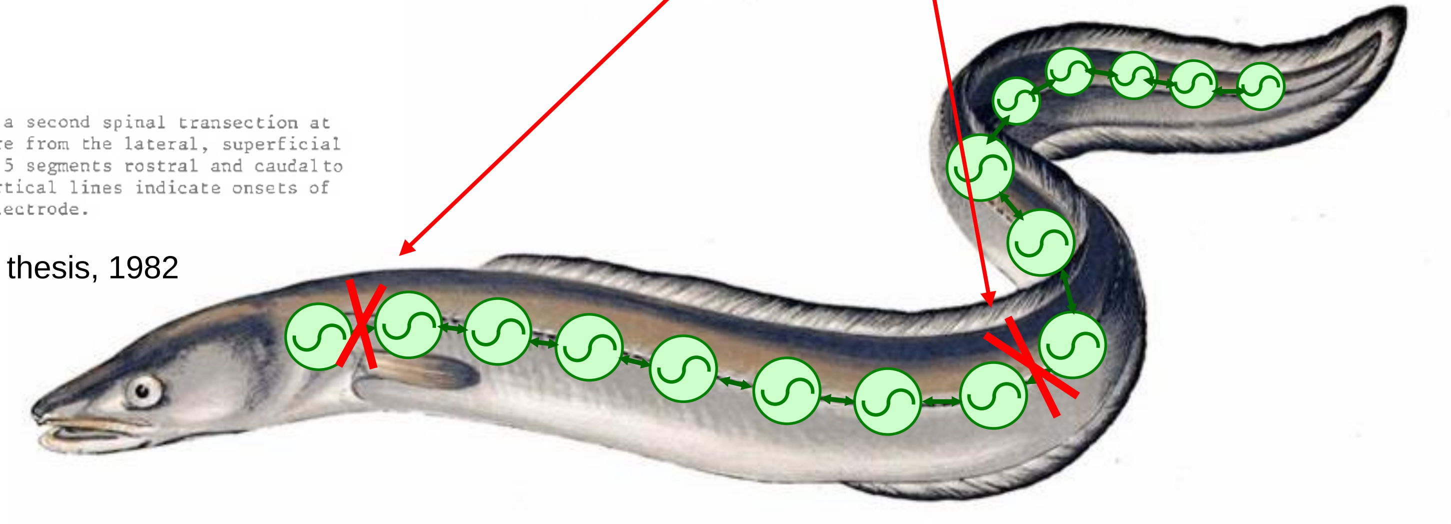


Fig. 3. Swimming spinal eel, with a second spinal transection at mid-body level. Electromyograms are from the lateral, superficial musculature at segments indicated, 5 segments rostral and caudal to the transection, respectively. Vertical lines indicate onsets of burst discharges at the rostral electrode.

Peter Wallen, PhD thesis, 1982

Coordinated swimming despite one or two **full spinal cord transections**

Likely explanation: important role for **stretch and pressure feedback**



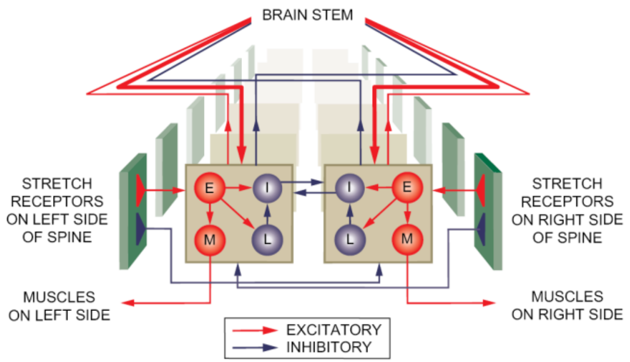
https://www.ttbook.org/interview/weird-world-eels

Stretch receptors in the lamprey

Stretch receptors within the spinal cord:

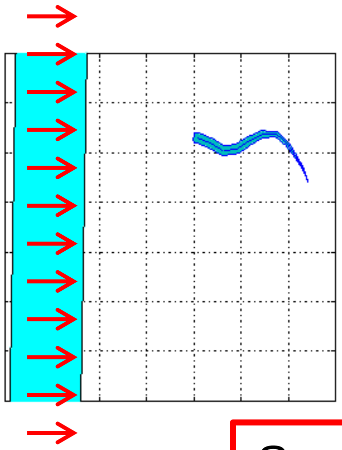
- Participate to **burst termination**.

- Help **handle perturbations**, e.g. a speed barrier.

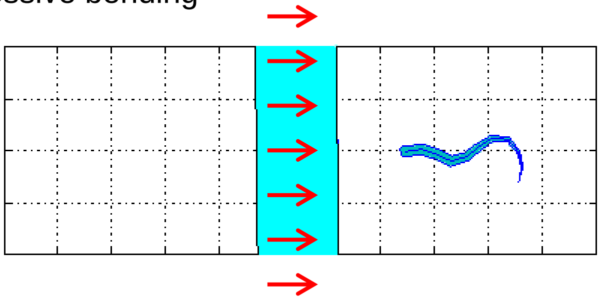


Grillner, Sci. Am. 1996

Swimming through a speed barrier
without sensory feedback (only CPG)



Swimming through a speed barrier ***with*** sensory feedback. The stretch feedback provides a **local stiffening mechanism** that prevents excessive bending



Sensory feedback helps handle perturbations

Synchronization through local pressure feedback

- CPG: Distributed phase oscillators
- **Local sensory <u>pressure</u> feedback**
- Sensors: dorsal cells (mechano-receptors)

Phase oscillator dynamics:

$$u_i = \cos(\phi_i)$$

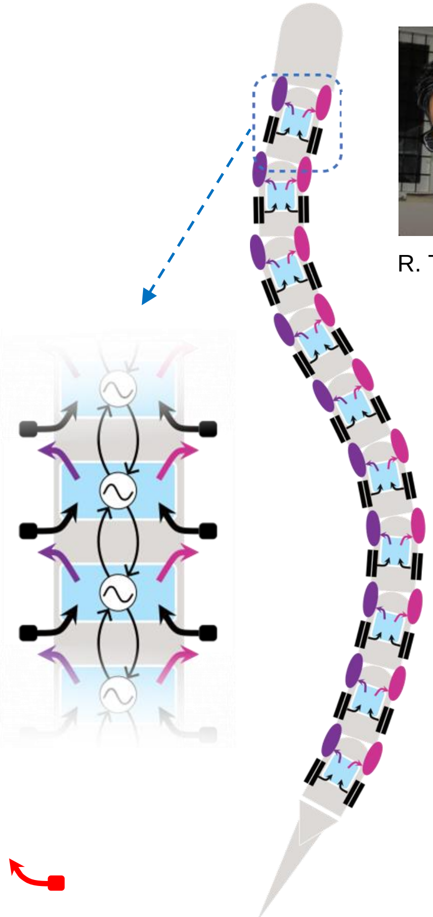
Muscle contraction signal

$$\dot{\phi}_i = \underbrace{\omega}_{\text{CPG oscillator}} + \underbrace{\sum_{j=1}^{N} w_{ij}\ \sin\left(\phi_i - \phi_j - \psi_{ij}\right)}_{\text{CPG coupling}} + \underbrace{b\ F_i \cos(\phi_i)}_{\text{Local feedback}}$$

CPG oscillator

CPG coupling

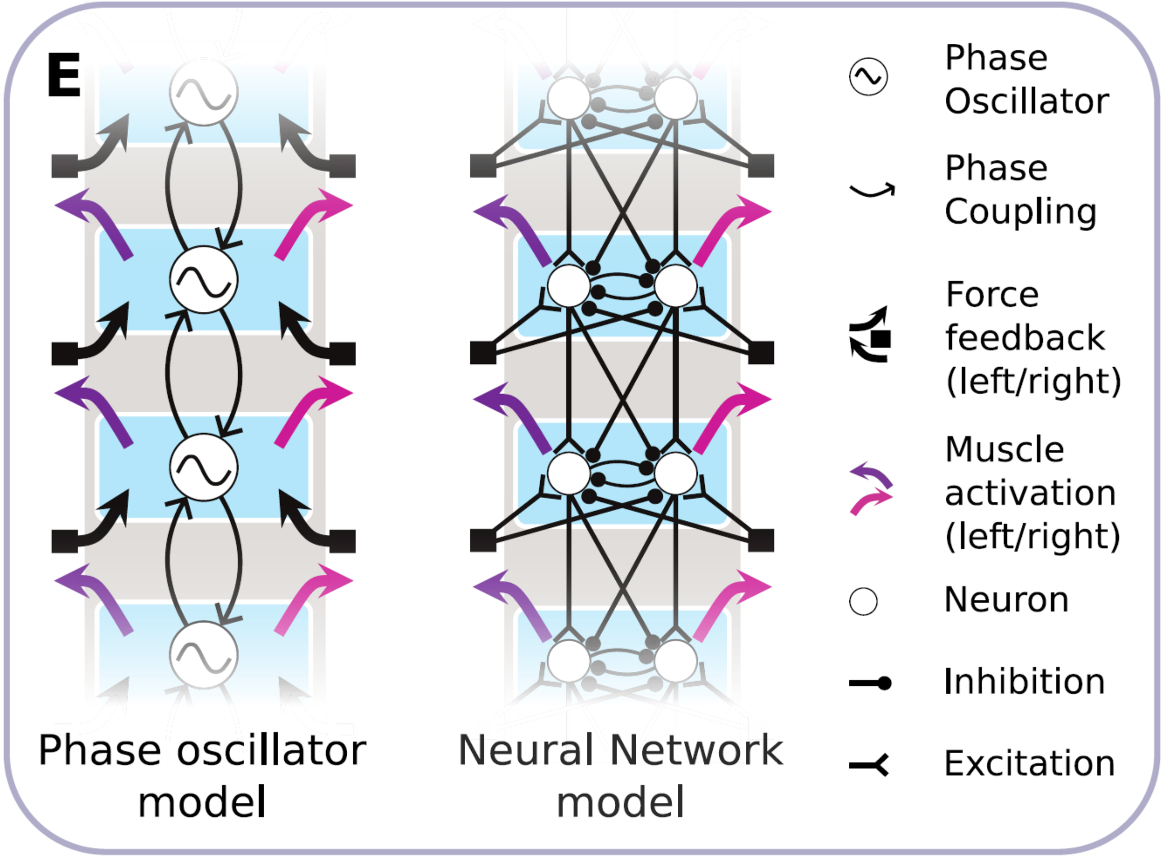
Local feedback

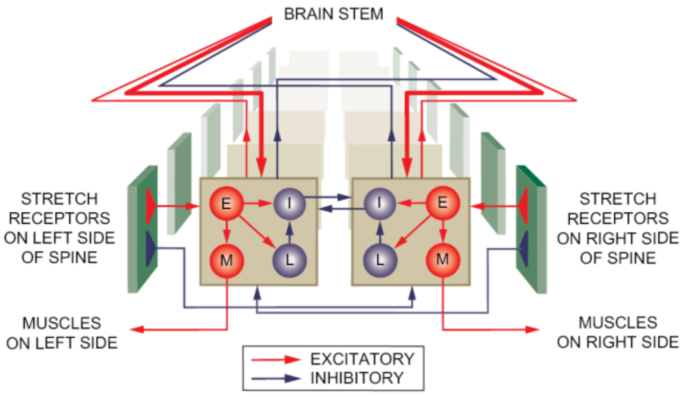


R. Thandiackal

Thandiackal *et al*, *Science Robotics*, 2021

Oscillator and neural network implementations





Grillner, Sci. Am. 1996

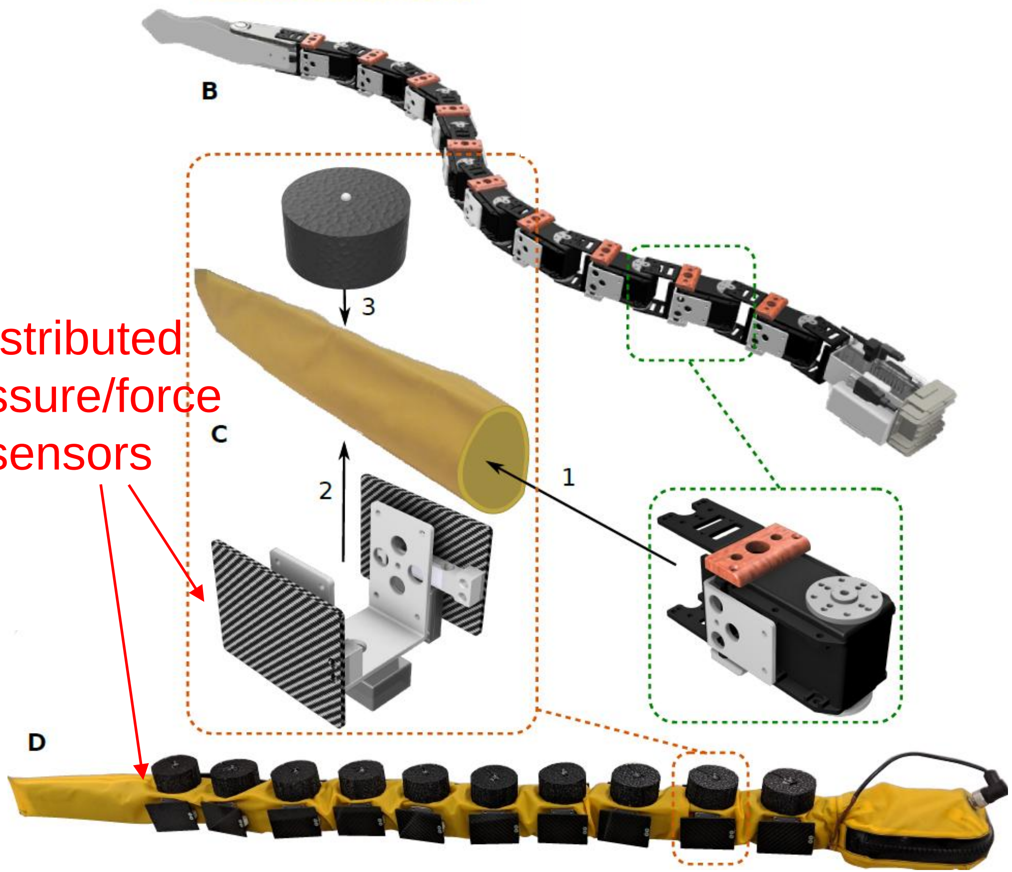
$u_i = \cos(\phi_i)$ Muscle contraction signal

$$\dot{\phi}_i = \omega + \sum_{j=1}^{N} w_{ij} \sin(\phi_i - \phi_j - \psi_{ij}) + b\, F_i \cos(\phi_i)$$

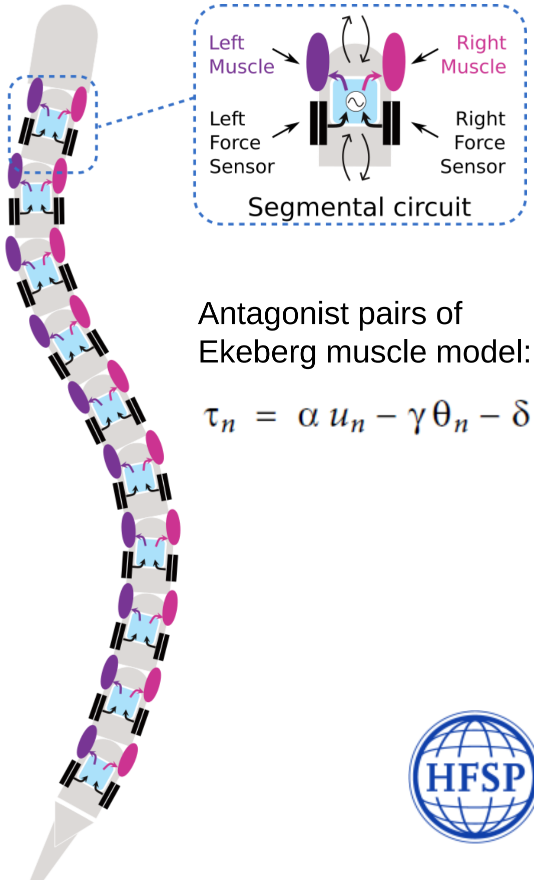
CPG oscillator — CPG coupling — Local feedback

Thandiackal *et al*, *Science Robotics*, 2021

Swimming coordinated by pressure feedback



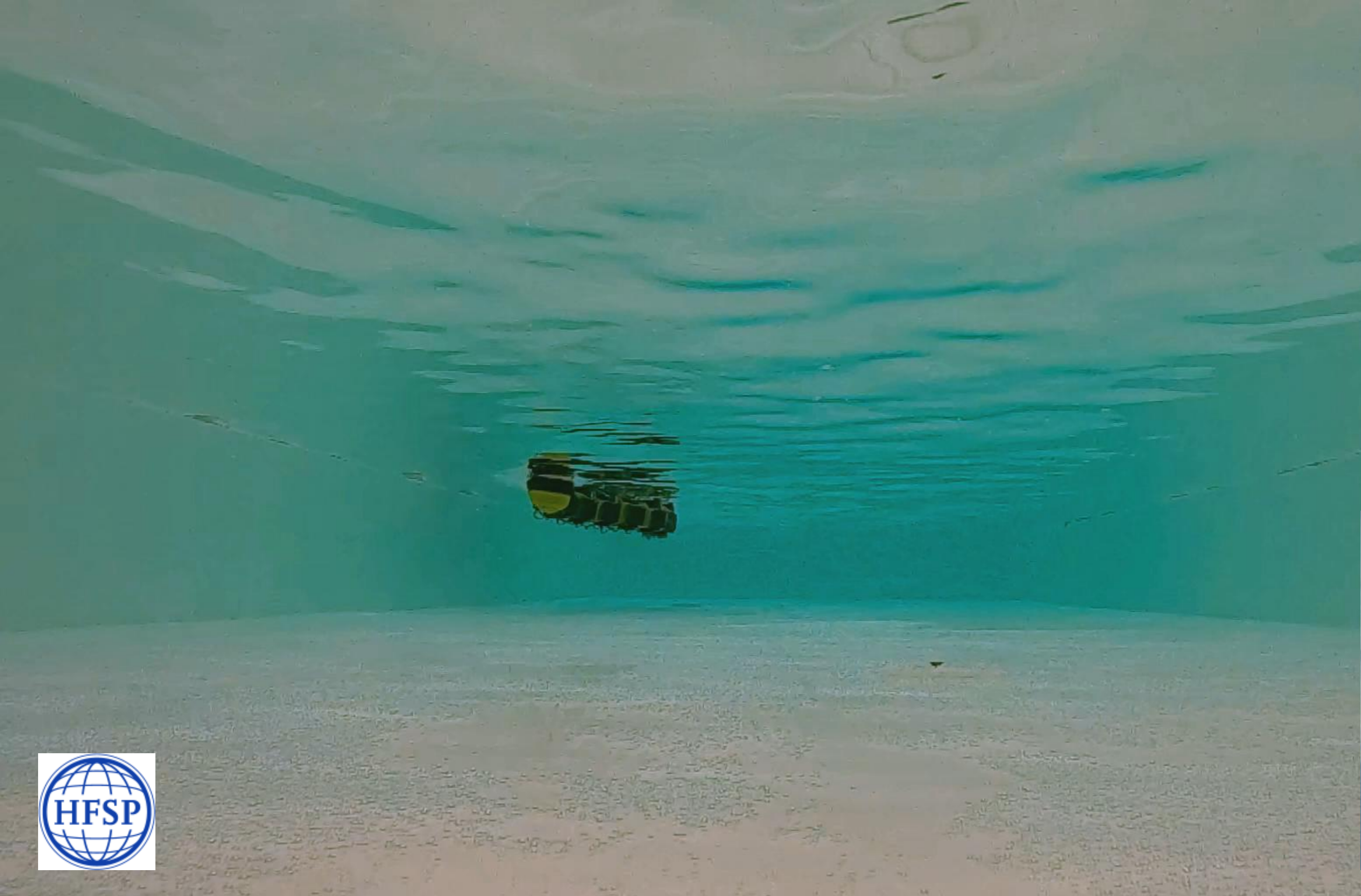
Distributed pressure/force sensors



Antagonist pairs of Ekeberg muscle model:

$$\tau_n = \alpha u_n - \gamma \theta_n - \delta \dot{\theta}_n$$

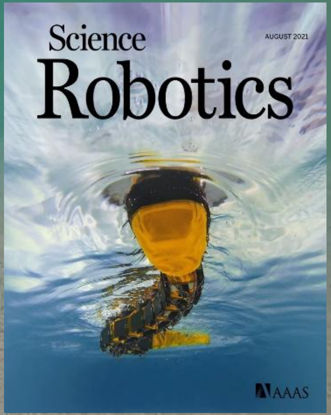
Thandiackal *et al*, *Science Robotics*, 2021



R. Thiandiackal

K. Melo

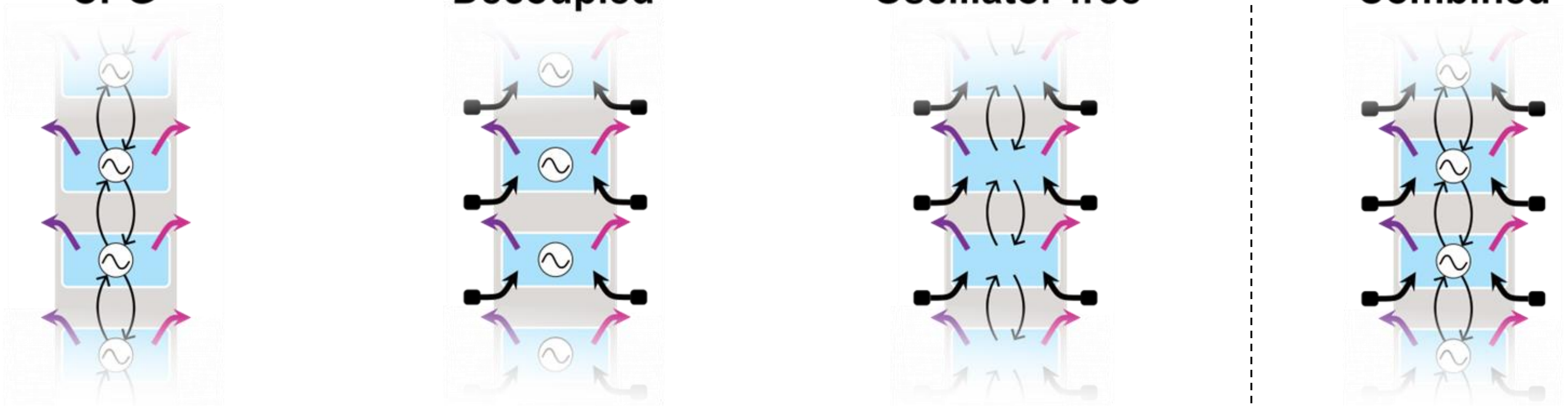
L. Paez



Thandiackal *et al*, *Science Robotics*, 2021

Test of different configurations

CPG | Decoupled | Oscillator-free | Combined



Central | Mainly peripheral | Combined

Muscle contraction signal

$$u_i = \cos(\phi_i)$$

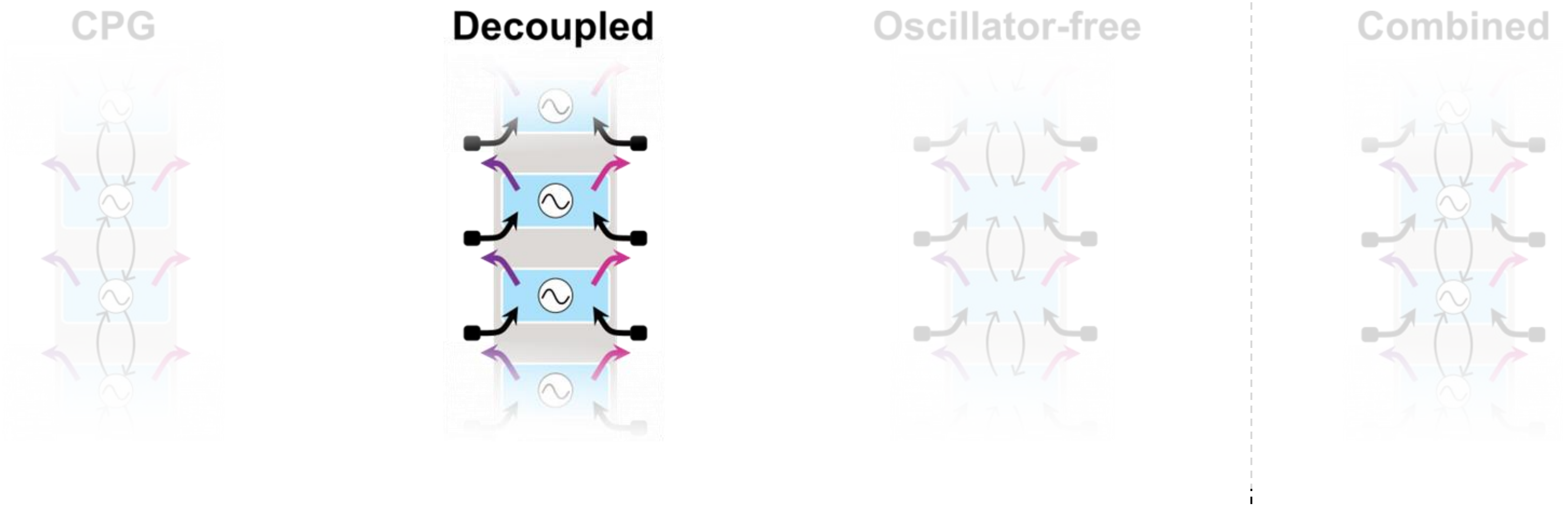
$$\dot{\phi}_i = \omega + \sum_{j=1}^{N} w_{ij} \sin(\phi_i - \phi_j - \psi_{ij}) + b\, F_i \cos(\phi_i)$$

CPG

CPG coupling

Local feedback

Test of different configurations



Muscle contraction signal

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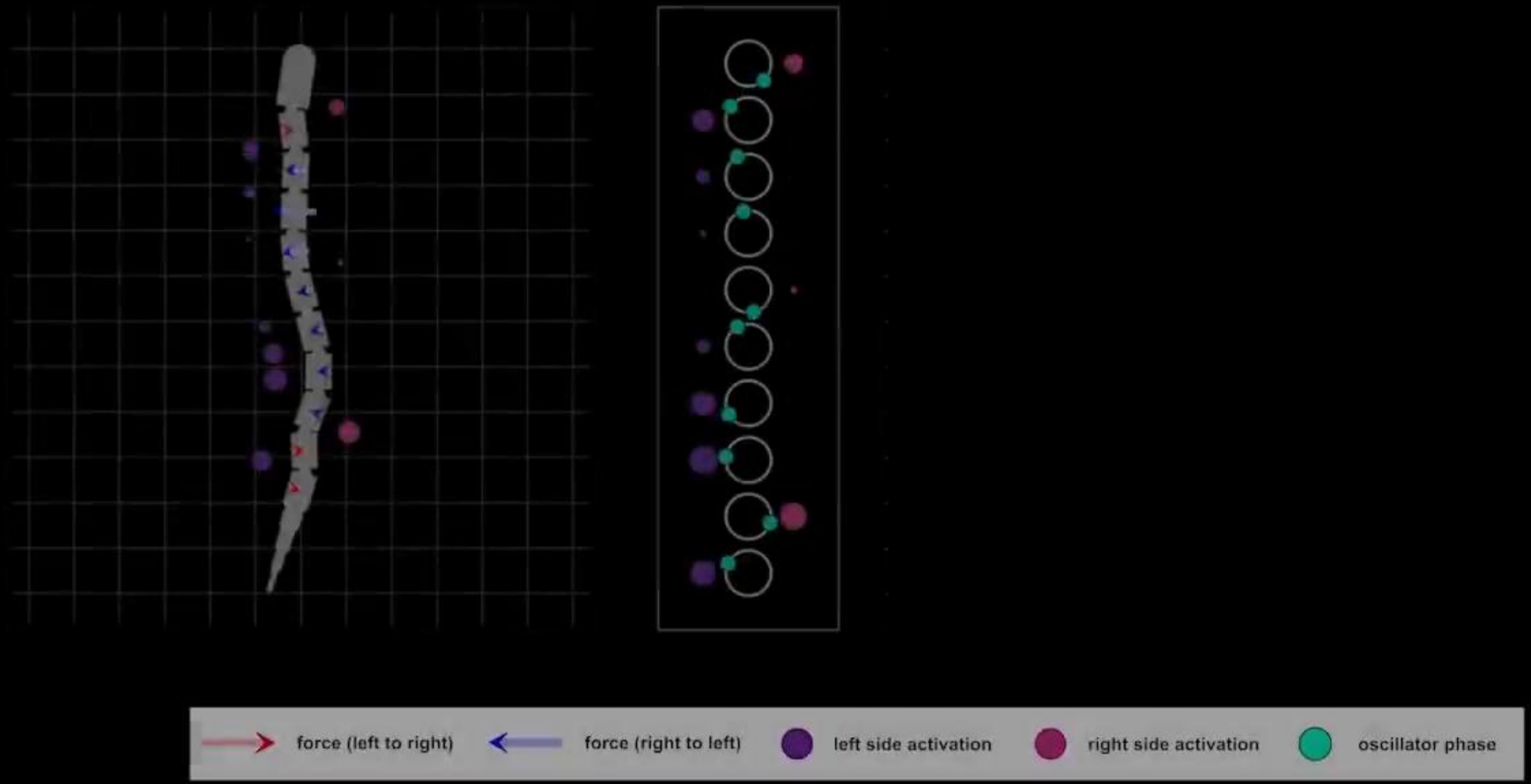
CPG

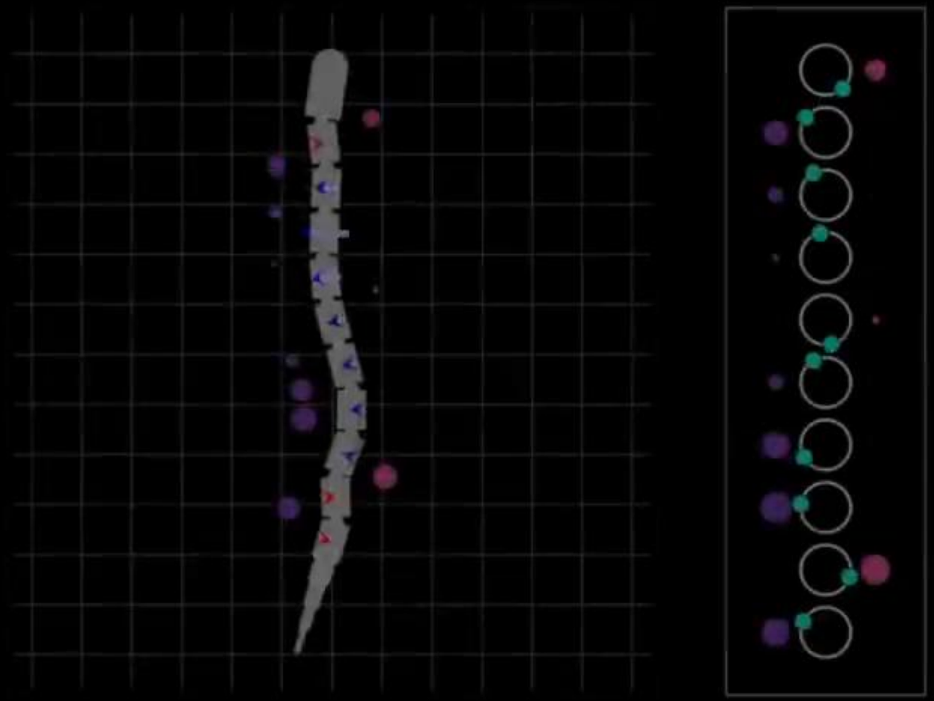
~~CPG coupling~~

Local feedback

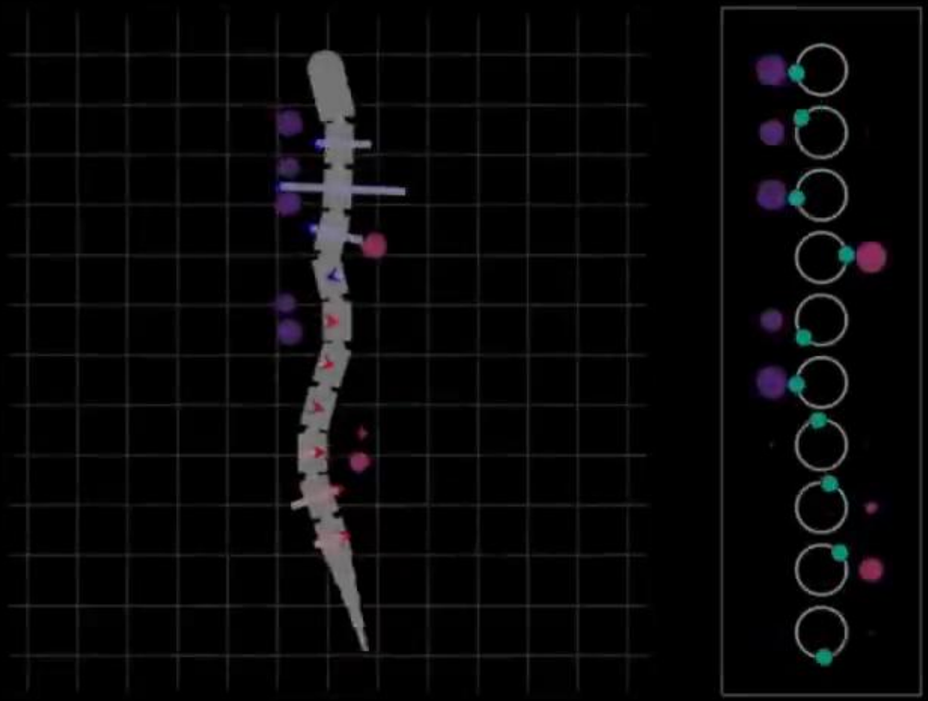
Decoupled Configuration Without Feedback



Decoupled Configuration Without Feedback



Decoupled Configuration With Feedback



Sensory feedback can **synchronize decoupled oscillators**

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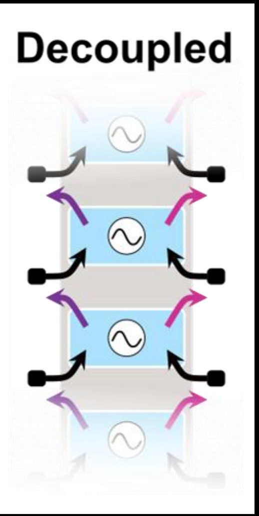
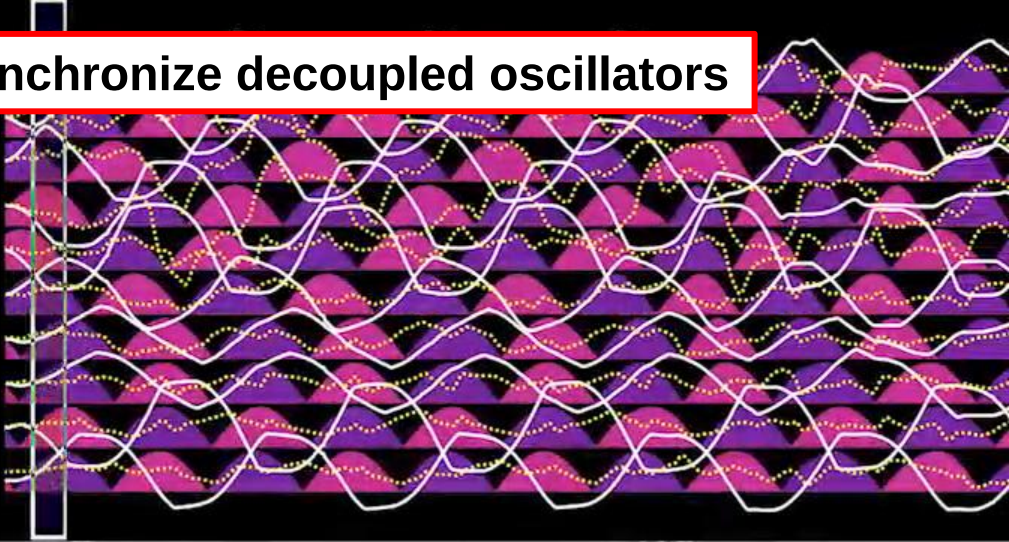
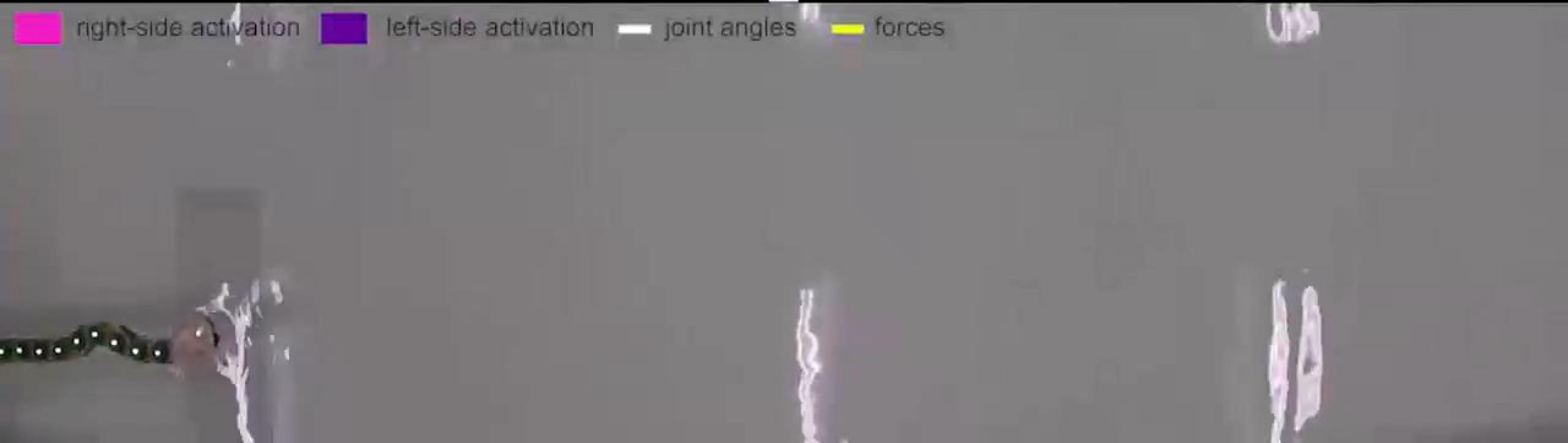






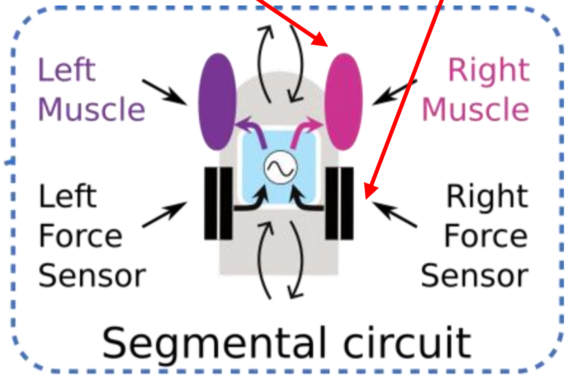
Why a caudo-rostal traveling wave?

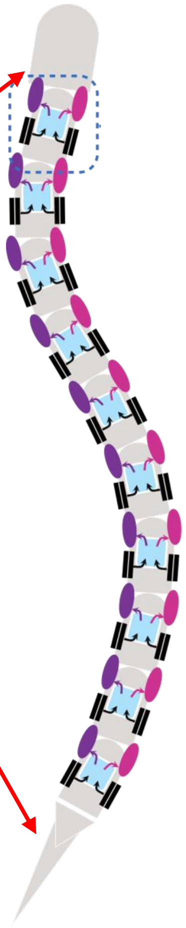
Why does the traveling wave travel from head to tail?

1. Asymmetry of the body (tail and head)

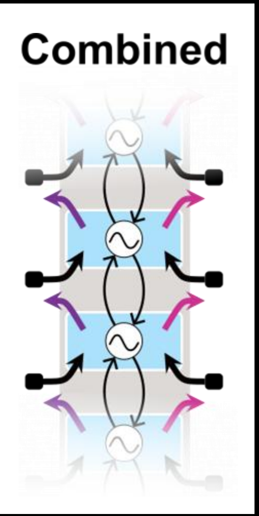
2. Spatial shift between actuation and perception

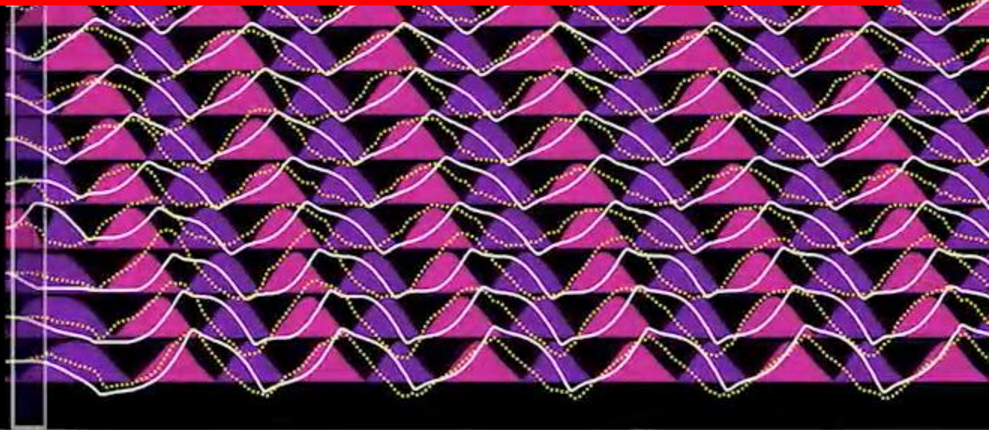
Pressure-sensitive dorsal cells in the lamprey tend to have receptive fields that are caudal (i.e. closer to the tail) to their position in the spinal cord

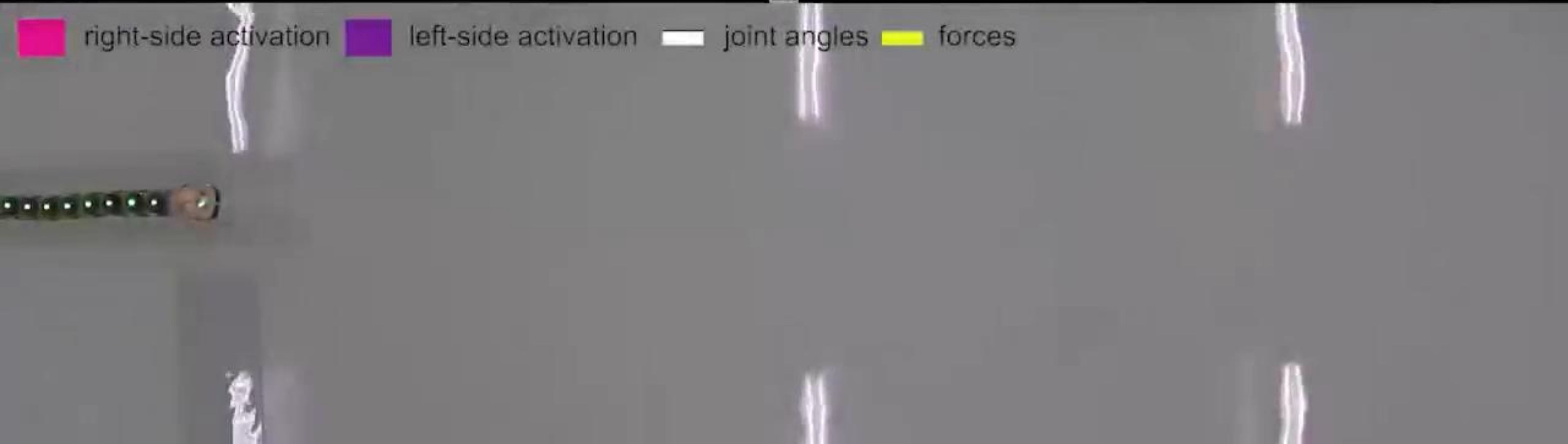




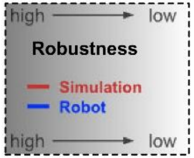
Best and most robust swimming with the **combined** configuration

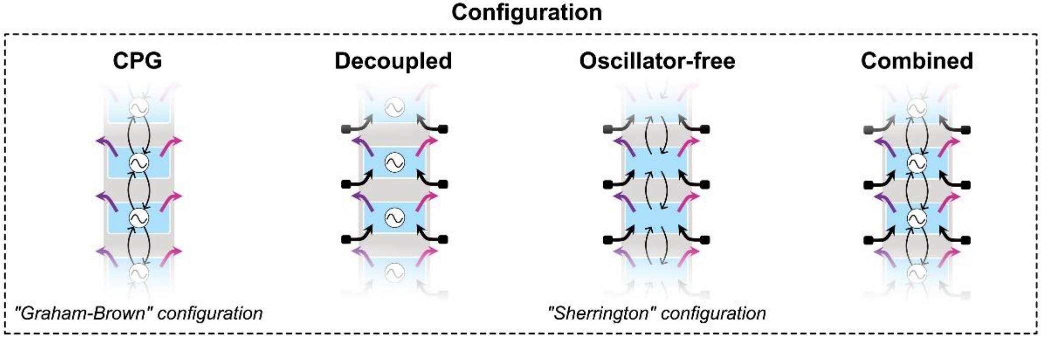




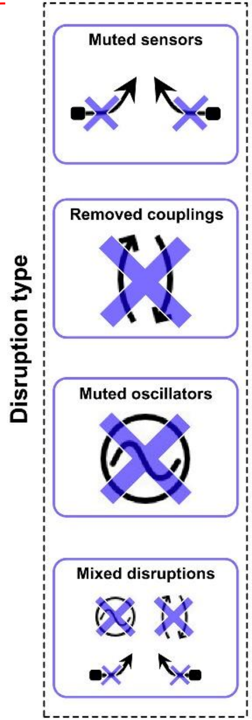


Robustness to neural disruptions



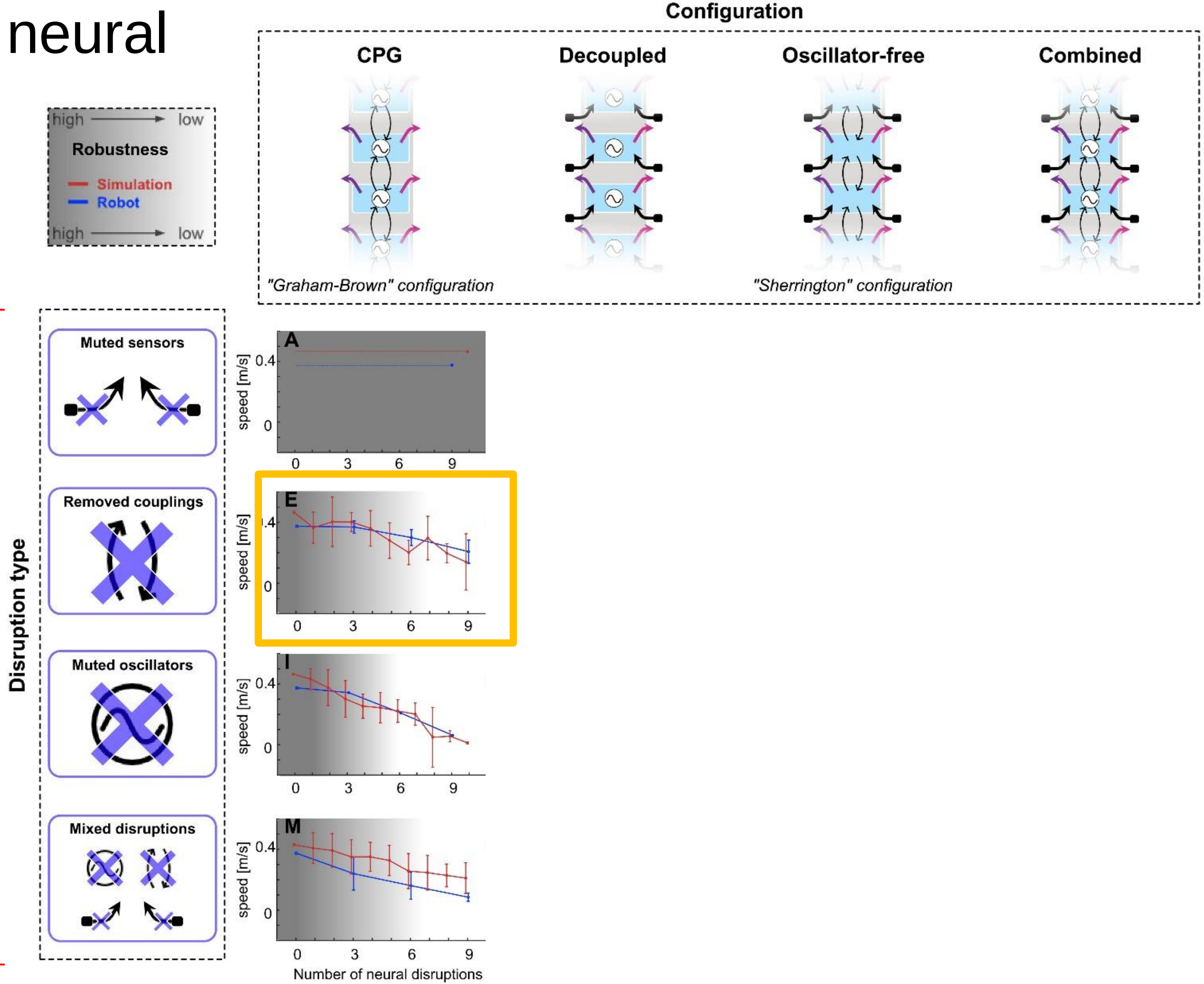


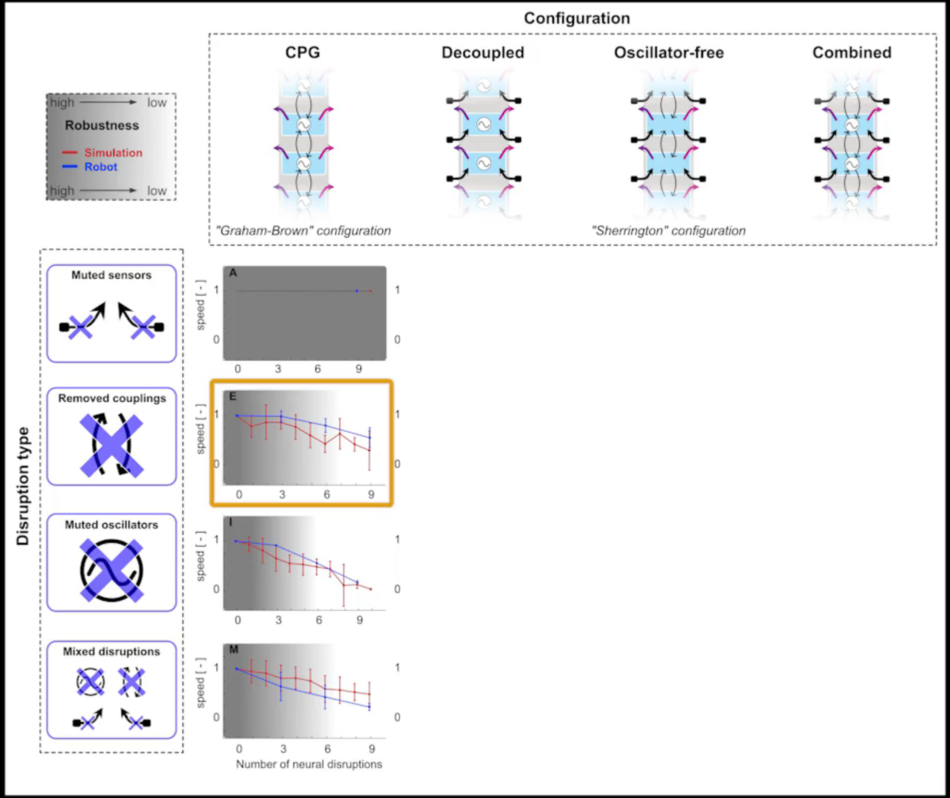
Different types of neural disruptions

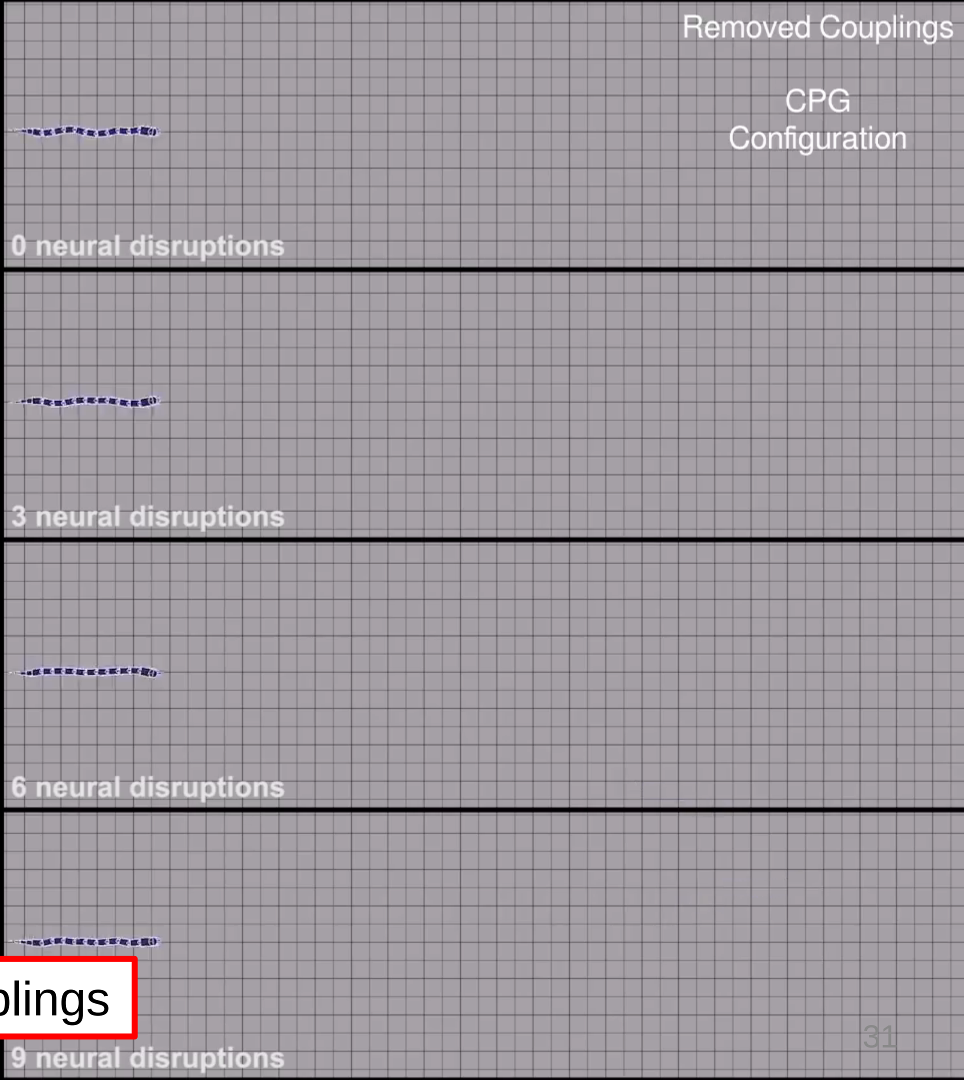


Robustness to neural disruptions

Different types of neural disruptions

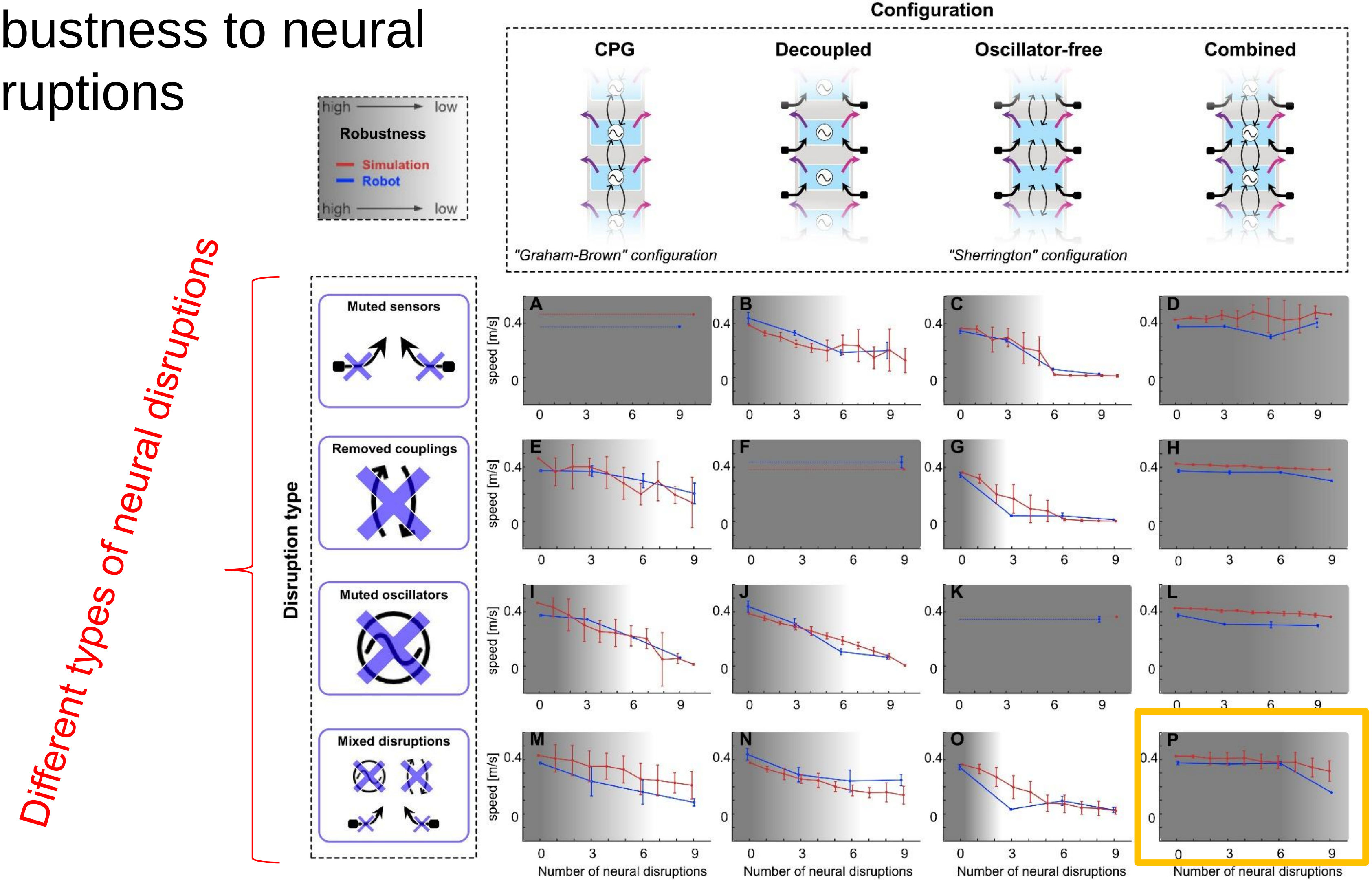


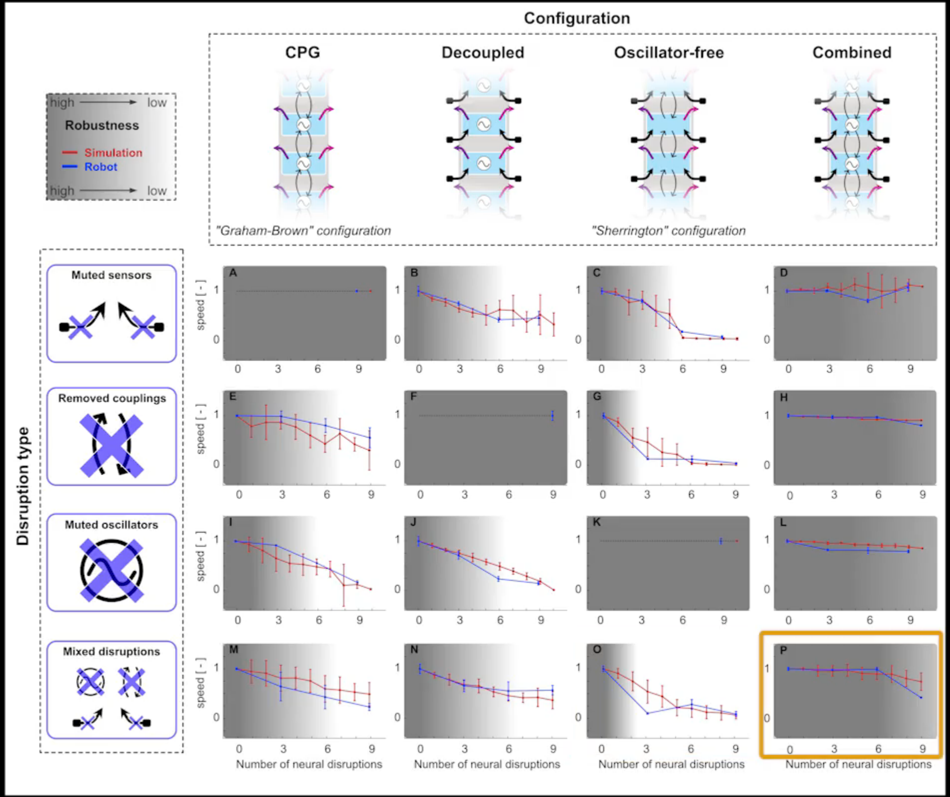


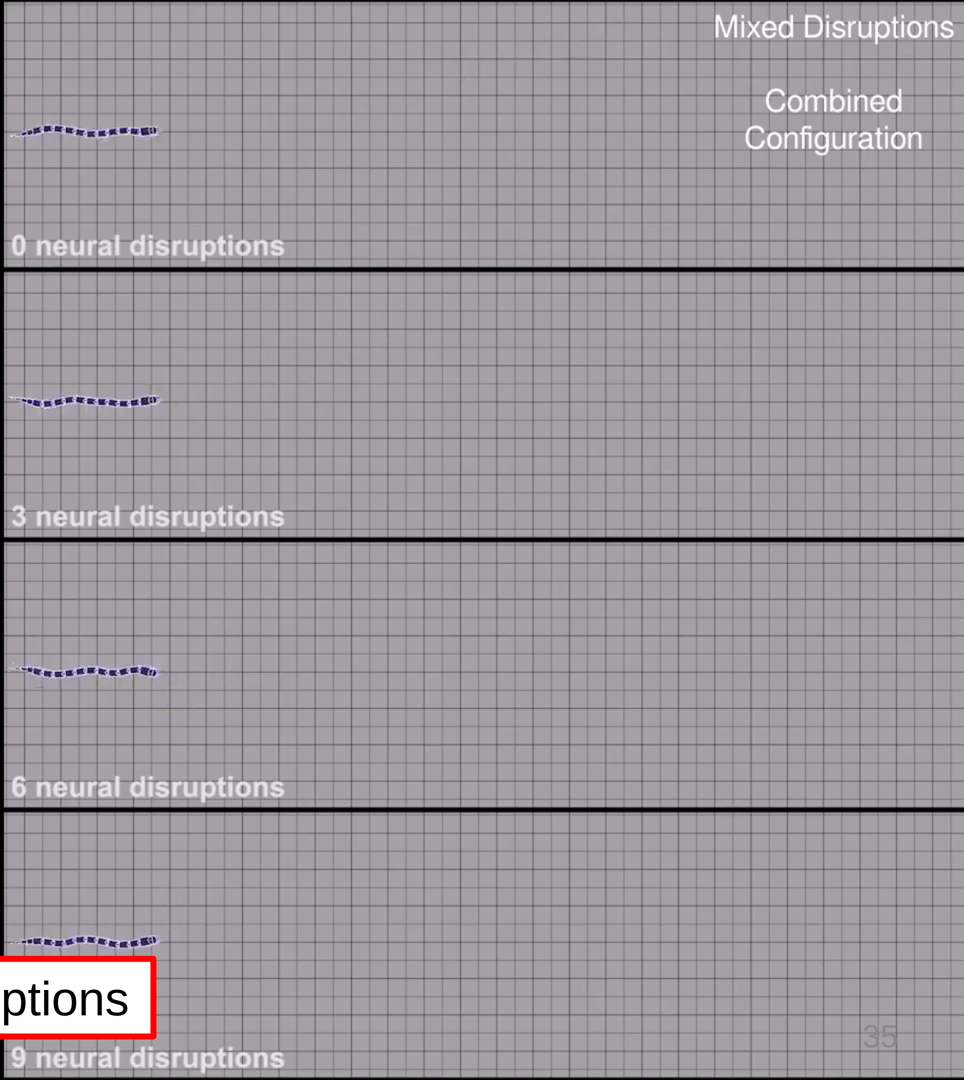


CPG circuit is **fragile** against removed couplings

Robustness to neural disruptions

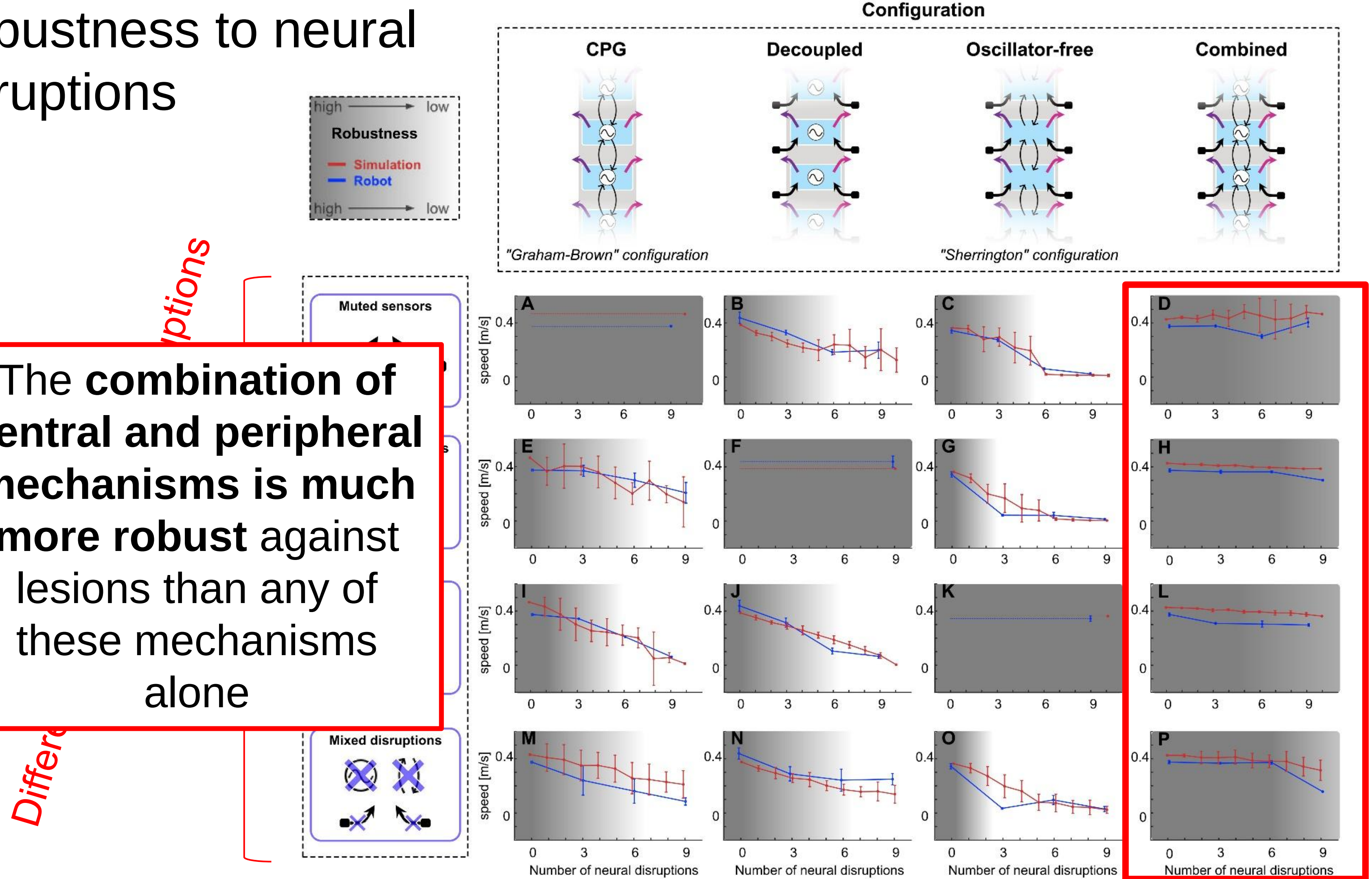






Combined circuit is **robust** against all disruptions

Robustness to neural disruptions



The **combination of central and peripheral mechanisms is much more robust** against lesions than any of these mechanisms alone

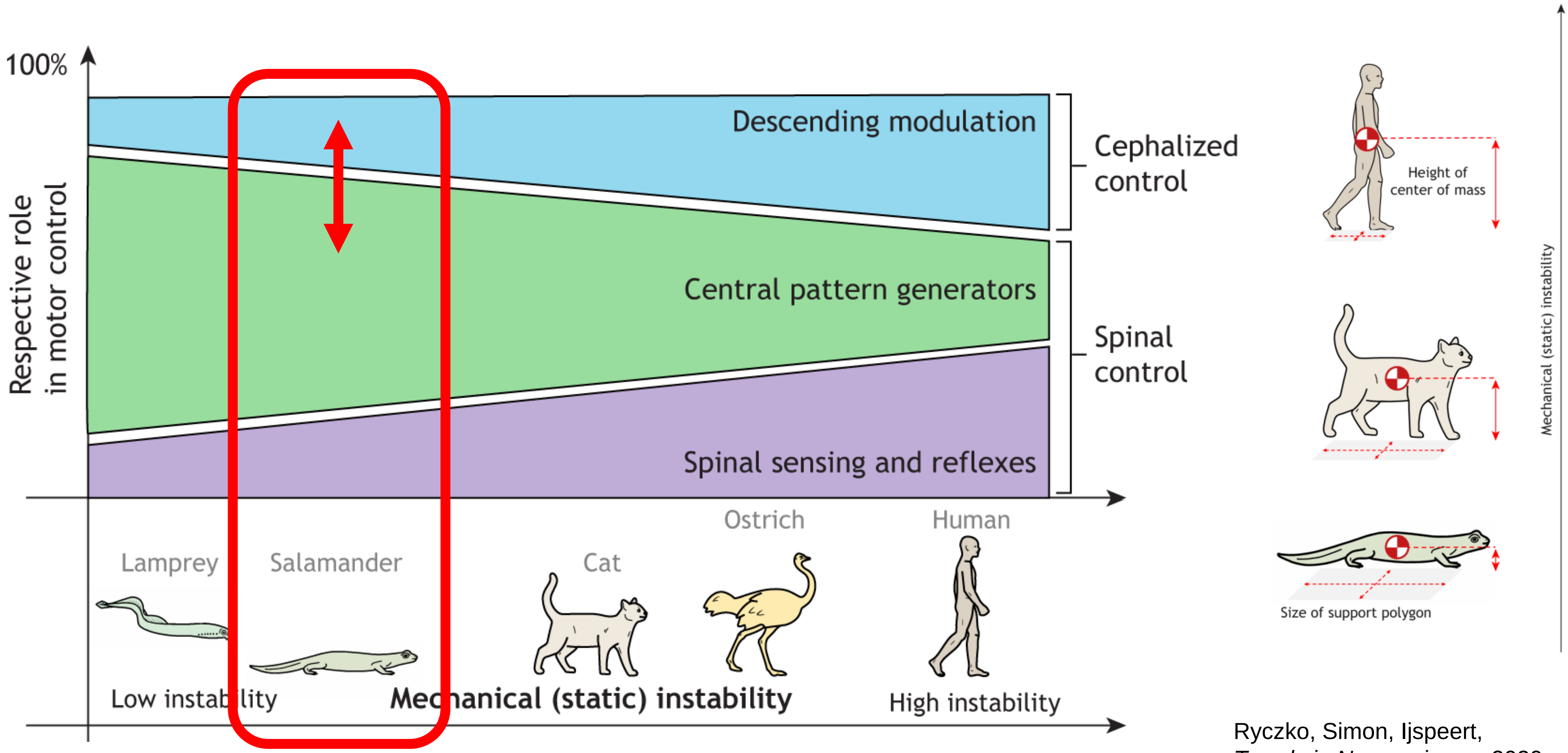
Lamprey summary

- Numerical models have played a key role in identifying the mechanisms of lamprey swimming.
- **Two mechanisms, one central and one peripheral, probably co-exist for traveling wave generation**: asymmetric couplings (hyp 3) and sensory feedback (hyp 4).

- Local sensory feedback (peripheral mechanism):
  - helps **handle perturbations**
  - Can also contribute to
    - **synchronize oscillators** (i.e. replace intersegmental coupling)
    - **generate rhythms** (i.e. replace oscillators)

- **Self-organized locomotion** (multiple mechanisms are contributing)
- **Strong robustness and redundancy**

- Work in progress: still many things to explore such as other sensor modalities, …



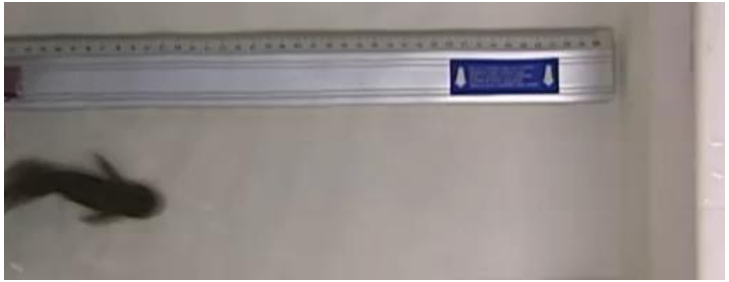
Ryczko, Simon, Ijspeert, *Trends in Neuroscience,* 2020

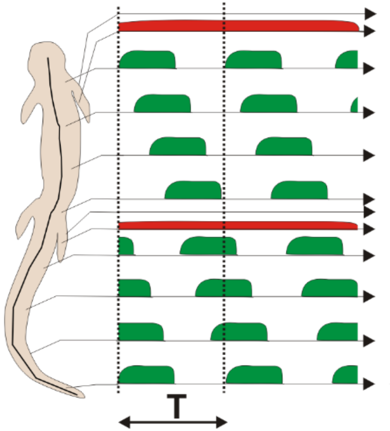
Ijspeert and Daley, J. of Exp. Biol., JEB 2023

- Relatively simple animal
- Interesting bimodal locomotion
- Its body plan has changed little over 150 million years (Gao & Shubin, Nature, 2002).
- Good link between lamprey and mammal research

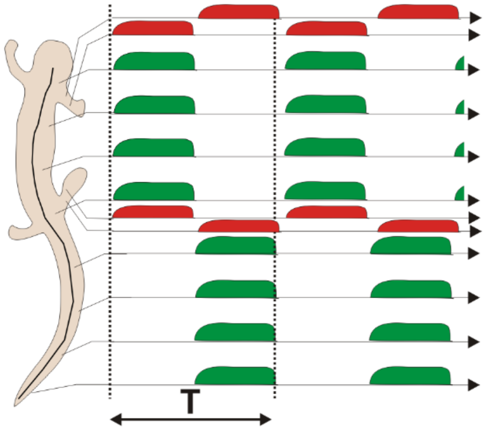
TSI, Swiss Italian Television

Bimodal locomotion (cartoon)



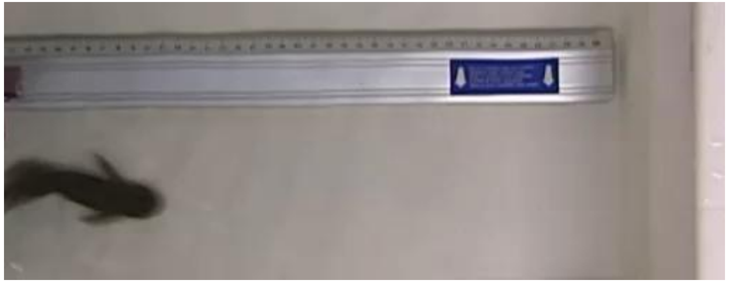


Swimming:
Traveling wave in axial muscles
Wavelength ≈ body length
Limb retractors are tonic
Short cycle durations



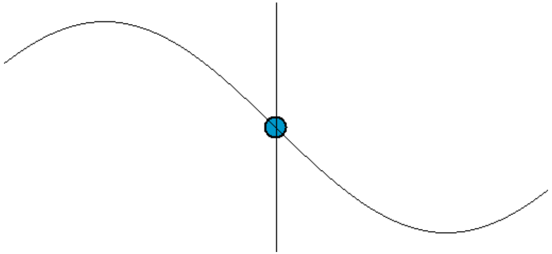
Walking:
Standing wave
Limb retractors/protactors are phasic
Longer cycle durations

Bimodal locomotion (cartoon)



Traveling wave

Standing wave



Traveling waves:

The nodes travel along the body

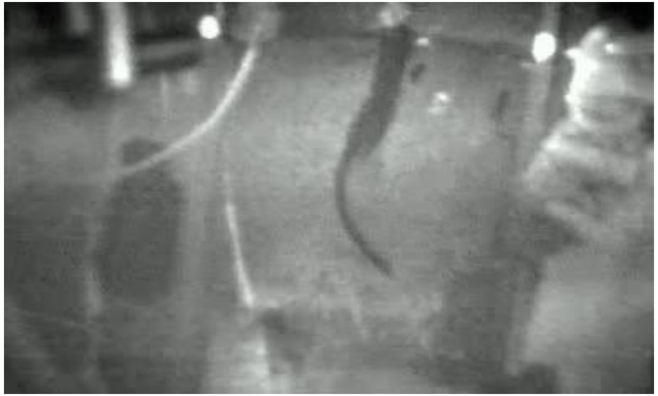
Standing waves:

The nodes stay at the same place.
In the salamander, the nodes are at the ***girdles***, the points where the limbs are attached

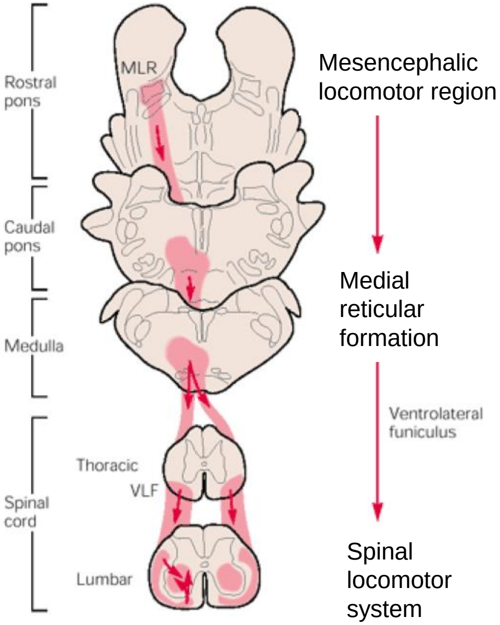
Stimulation of MLR can induce gait transition

MLR: Mesencephalic Locomotor Region
Cabelguen et al, Journal of Neuroscience, 23 (6), 2003

Low current stimulation:
(slow) stepping

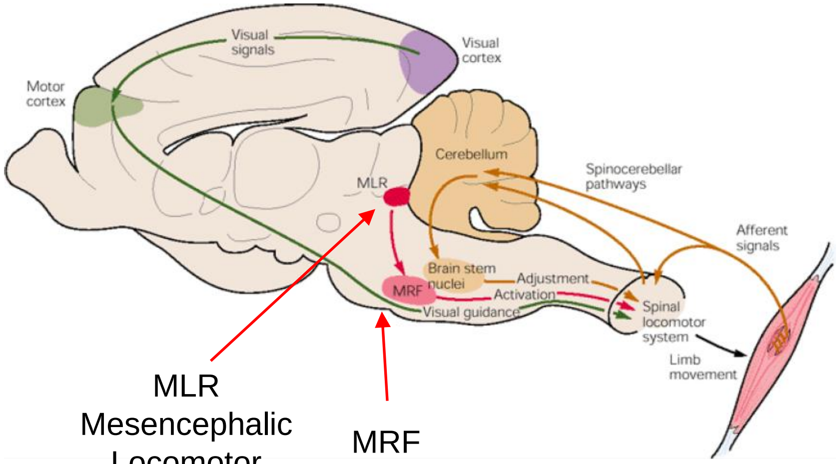


Larger current stimulation:
(fast) swimming



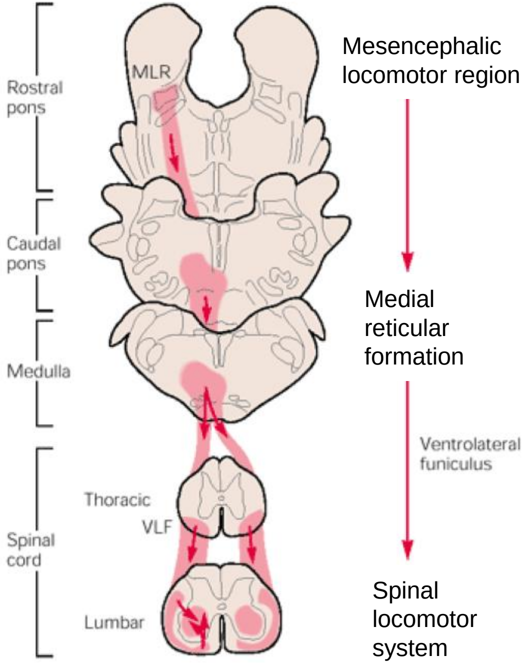
Gait transitions in vertebrates

Stimulation of the mesencephalic locomotor region (MLR) induces locomotion and gait transitions in vertebrate animals



MLR
Mesencephalic
Locomotor
region

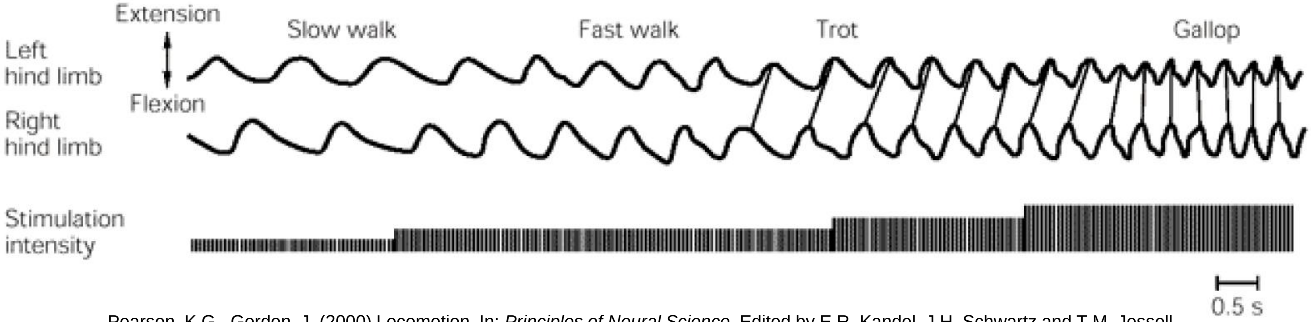
MRF
Medial
Reticular
formation



Pearson, K.G., Gordon, J. (2000) Locomotion. In: *Principles of Neural Science*.
Edited by E.R. Kandel, J.H. Schwartz and T.M. Jessell.

Gait transitions in vertebrates

From **walk to trot to gallop** in a decerebrated cat (Shik and Orlovksy 1966)



Pearson, K.G., Gordon, J. (2000) Locomotion. In: *Principles of Neural Science*. Edited by E.R. Kandel, J.H. Schwartz and T.M. Jessell.

From **walk to flight** in birds (Steeves et al 1987)

From **walking to swimming** in salamander (Cabelguen et al 2003)

Modeling the salamander locomotor circuits: different levels of abstraction

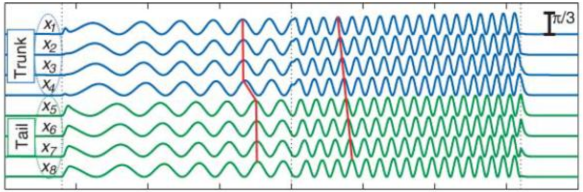
- Coupled oscillators

(**Ijspeert et al 2007, Knüsel et al 2020**, Suzuki et al 2021)

$$\dot{\theta}_i = 2\pi\nu_i + \sum_j r_j \, w_{ij} \, \sin(\theta_j - \theta_i - \phi_{ij})$$

$$\ddot{r}_i = a_i\left(\frac{a_i}{4}(R_i - r_i) - \dot{r}_i\right)$$

$$x_i = r_i(1 + \cos(\theta_i))$$

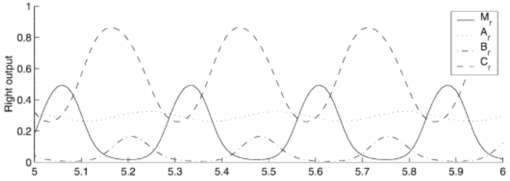


- Leaky-integrator neurons

(Ijspeert 2001)

$$\tau_i \frac{\mathrm{d}m_i}{\mathrm{d}t} = -m_i + \sum_j w_{i,j} x_j$$

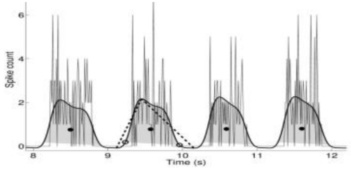
$$x_i = (1 + \mathrm{e}^{(m_i + b_i)})^{-1}$$



- Integrate-and-fire neurons

(Knuesel et al 2013, Pazzaglia et al 2025)

$$\tau \dot{u} = -g(u - E_{rest}) - \alpha_1\omega_1 - \alpha_2\omega_2 + RI + \sum w_{syn} g_{syn}(u - E_{revsyn})$$

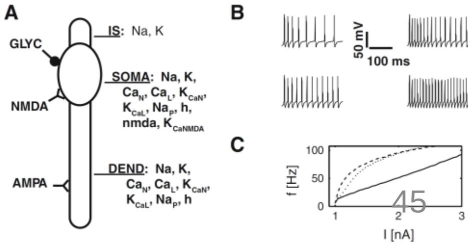


- Hodgkin-Huxley types of neurons

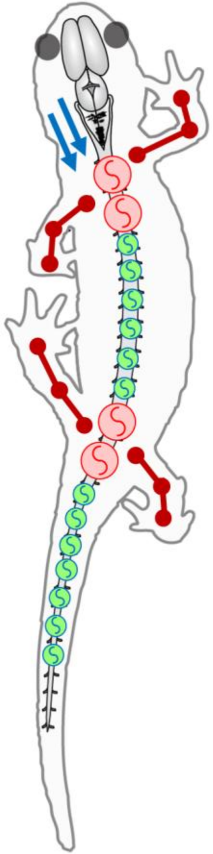
(Bicanski et al 2013)

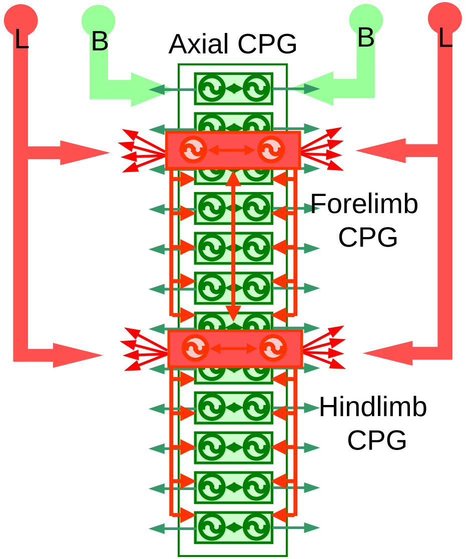
$$C\frac{\mathrm{d}U}{\mathrm{d}t} = \sum_i (U_i - U) g_{\text{core}} + \sum_j I_j + I_{\text{leak}},$$

$$I_j = g_j p^a q^b (U_i - E_{\text{rev}})$$

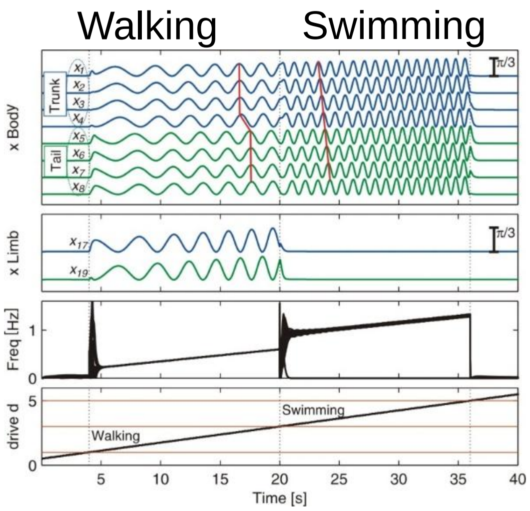


A mathematical model to study the transition from swimming to walking





System of coupled oscillators

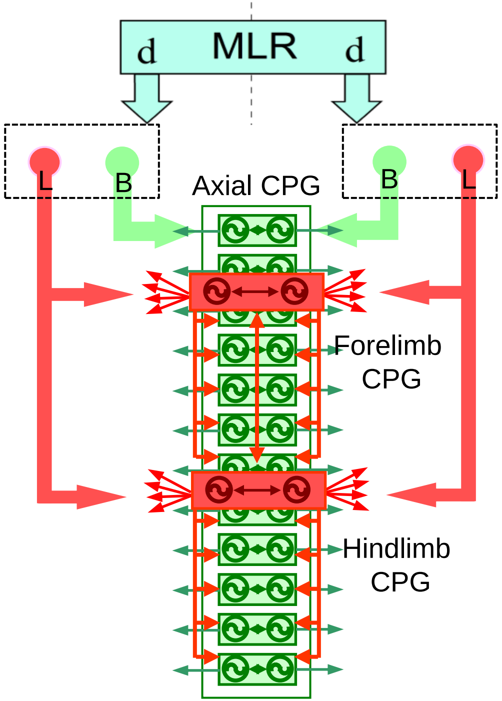


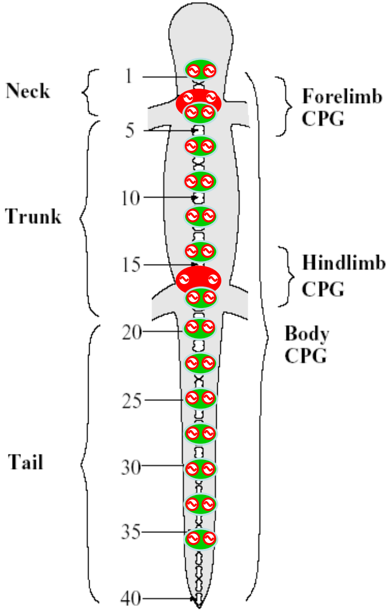
Gait transition due to an increase of the descending drive

Ijspeert *et al*, *Science*, March 2007

Hypotheses underlying the model

Hypothesis 1 (topology): The isolated **axial CPG is lamprey-like** and spontaneously produces traveling waves when activated with a tonic drive. The **limb CPG, when activated, forces the whole CPG into the walking mode**.





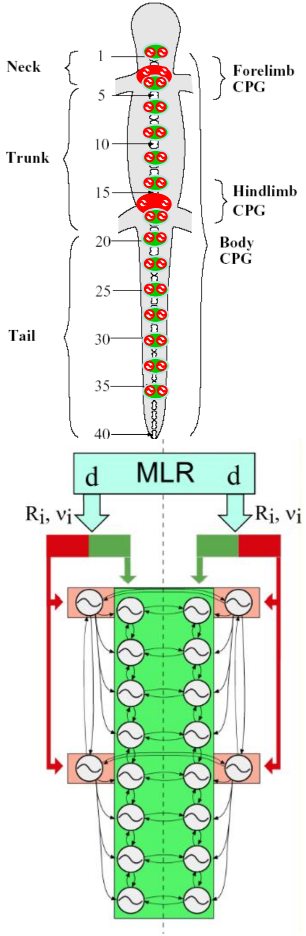
Hypotheses (continued)

Hypothesis 2 (topology): the strengths of the **couplings from limb to axial oscillators are stronger** than those from axial to axial oscillators and from axial to limb oscillators.

Hypothesis 3 (oscillators): **Limb oscillators can not oscillate at high frequencies**, that is, they saturate and stop oscillating at high levels of tonic drive.

~~Hypothesis 4 (oscillators): For the same tonic drive, **limb oscillators have lower intrinsic frequencies** than the axial oscillators.~~

Observation



[Ijspeert *et al*, *Science*, March 2007].

Modeling the CPG with coupled oscillators

A segmental oscillator is modeled as an amplitude-controlled phase oscillator as used in (Cohen, Holmes and Rand 1982, Kopell, Ermentrout, and Williams 1990) :

Phase:

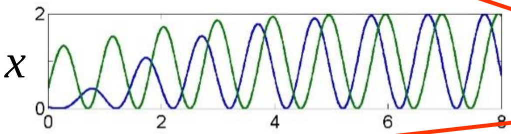
$$\dot{\theta}_i = 2\pi \nu_i + \sum_j r_j w_{ij} \sin(\theta_j - \theta_i - \phi_{ij})$$

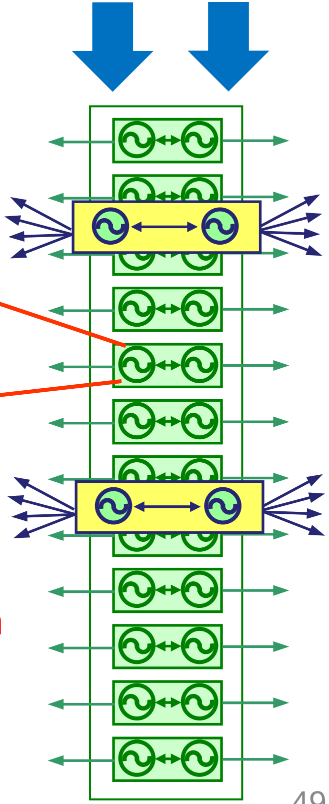
Amplitude:

$$\ddot{r}_i = a_i \left(\frac{a_i}{4} (R_i - r_i) - \dot{r}_i \right)$$

Output:

$$x_i = r_i (1 + \cos(\theta_i))$$





Setpoints:

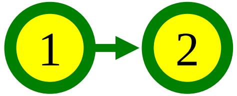
$$\varphi_i = x_i - x_{N+i} \quad \textit{for the axial motors}$$

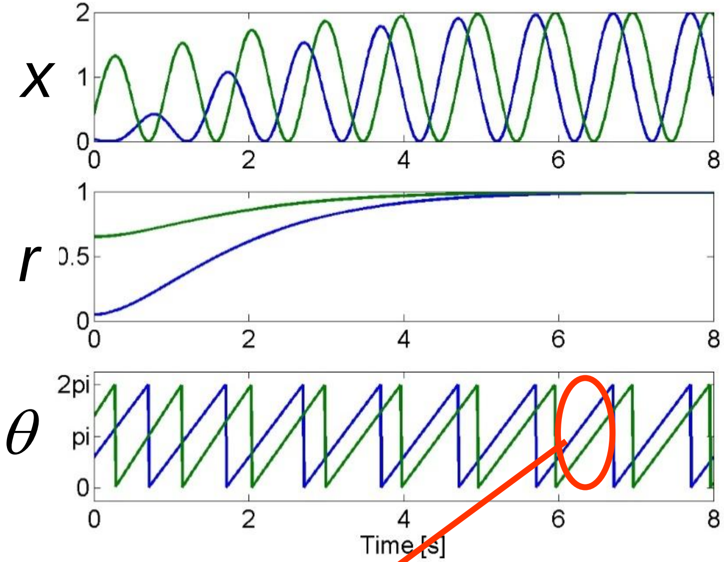
$$\varphi_i = f(\theta_i) \quad \textit{for the (rotational) limb motors}$$

!! Other notation than lamprey models

Ijspeert *et al*, *Science*, March 2007

Example with two oscillators





$$\dot{\theta}_i = 2\pi \nu_i + \sum_j \left(r_j w_{ij} \sin(\theta_j - \theta_i - \phi_{ij}) \right)$$

$$\ddot{r}_i = a_i \left(\frac{a_i}{4} (R_i - r_i) - \dot{r}_i \right)$$

$$x_i = r_i (1 + \cos(\theta_i))$$

The phase difference $\phi = \theta_1 - \theta_2$
between two oscillators converges to

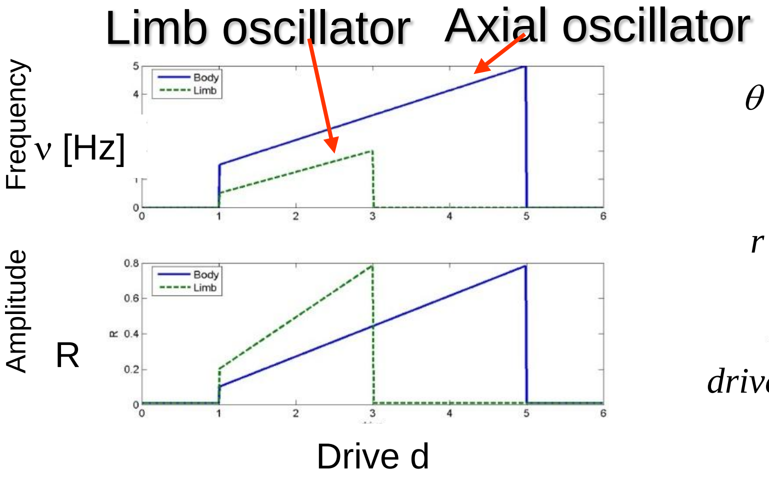
$$\phi_\infty = \arcsin\left(\frac{2\pi(\nu_1 - \nu_2)}{R_1 w_{21}} \right) - \phi_{21}$$

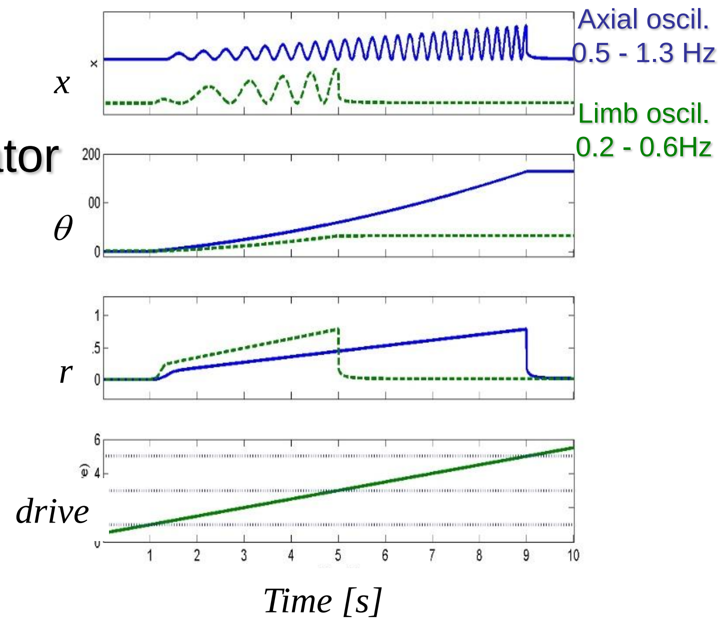
[Ijspeert *et al*, *Science*, March 2007].

Oscillator model: saturation function

Tonic drive *d* modulates the frequency and the amplitude of the oscillations between a lower and upper threshold.

Hypotheses 3 and 4:
limb oscillators are slower
and
saturate at a lower drive
than the axial oscillators





CPG couplings

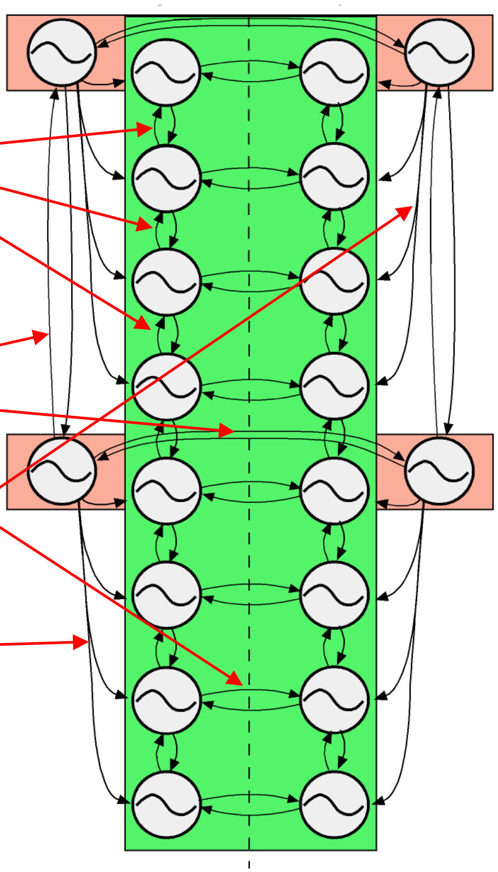
Hyp. 1: axial CPG makes traveling waves

Axial CPG: Traveling wave $\phi_{ij} = \pm\frac{2\pi}{8}, w_{ij} = 10$

Antiphase $\phi_{ij} = \pi, w_{ij} = 10$

In phase $\phi_{ij} = 0, w_{ij} = 30$

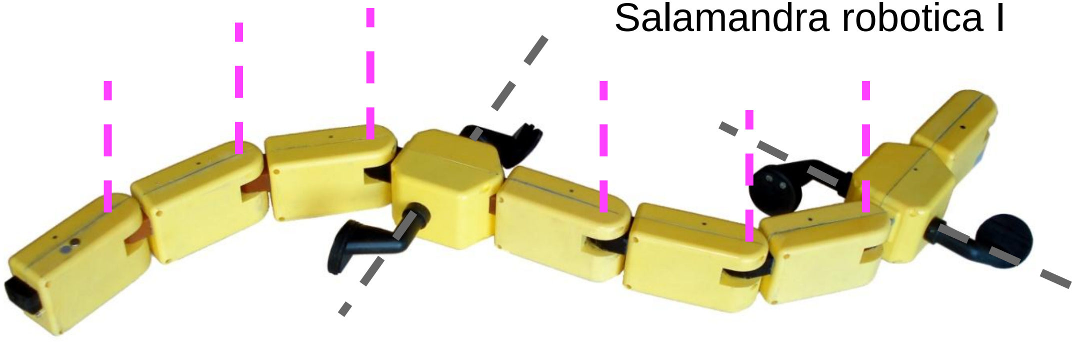
Hyp. 2: strong limb to body couplings



Note these long-range couplings from limb to axial oscillators do likely not exist

Salamandra robotica I and II

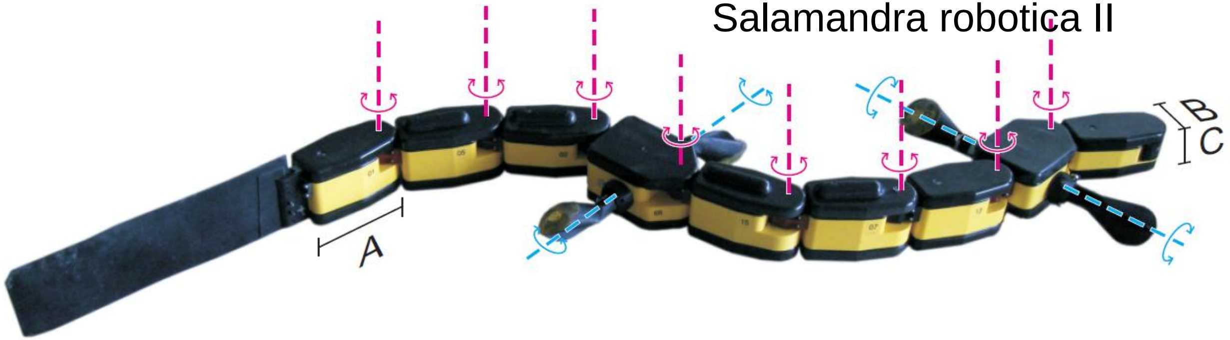
Salamandra robotica I



10 DOFs

Ijspeert *et al*, *Science*, 2007

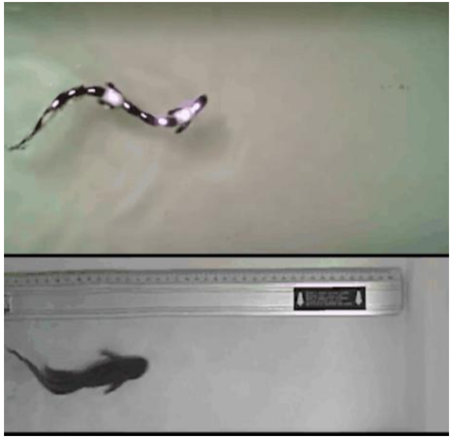
Salamandra robotica II

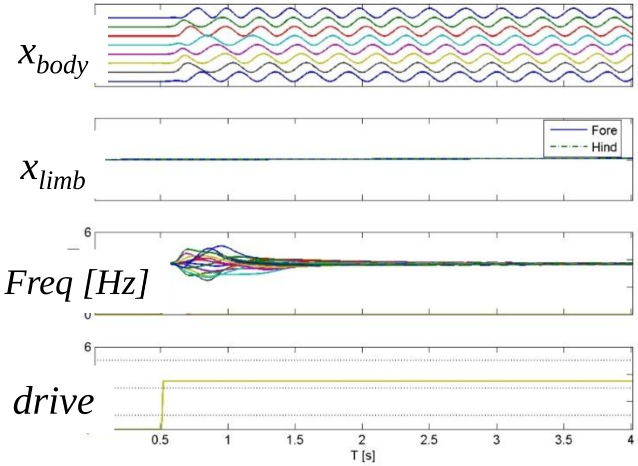


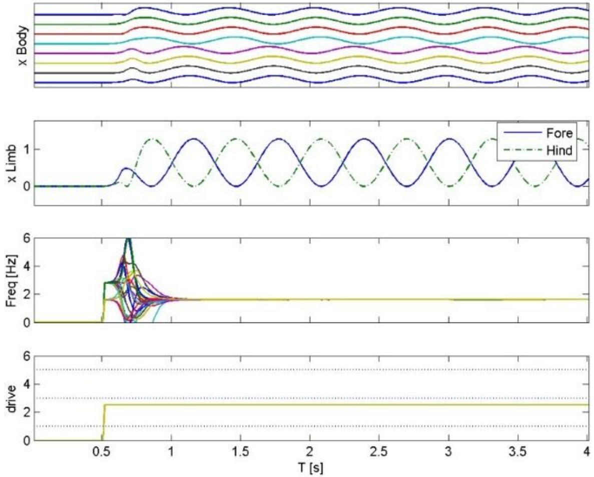
12 DOFs

Crespi et al, *IEEE TRO*, 2013

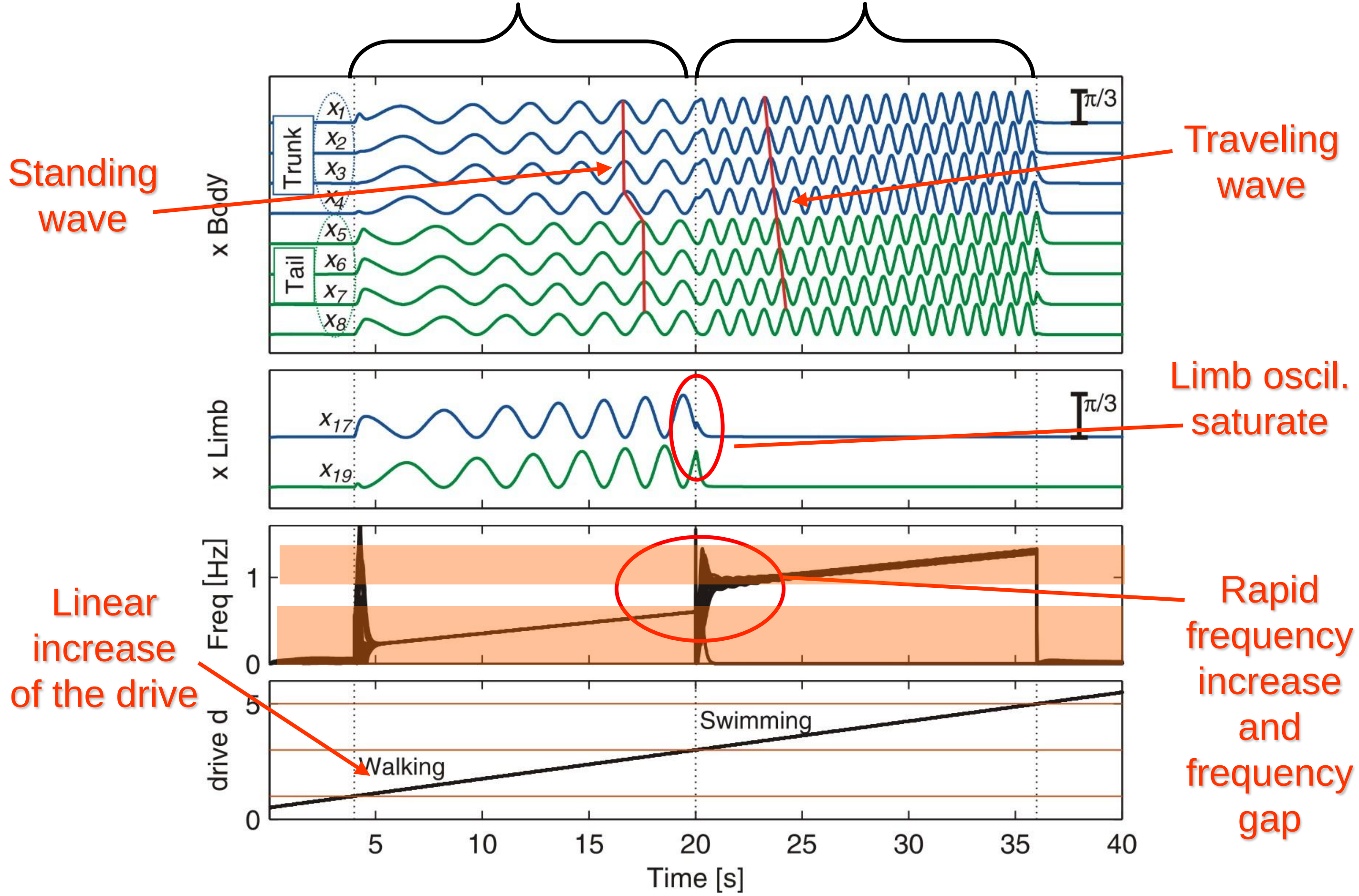
Swimming and Walking



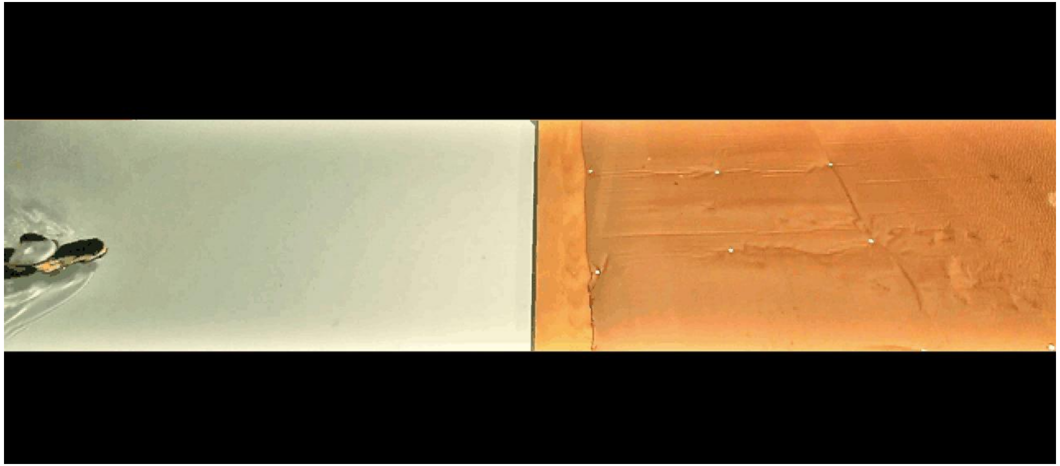




From walking to swimming

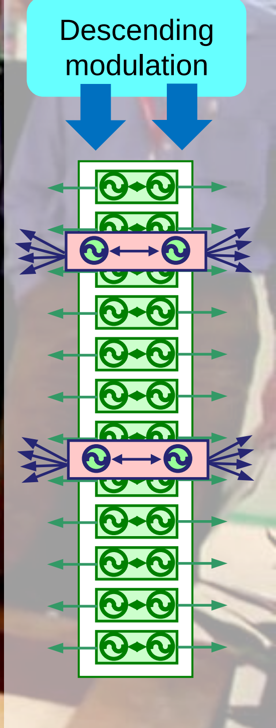


From swimming to walking



Salamander robot

Real salamander



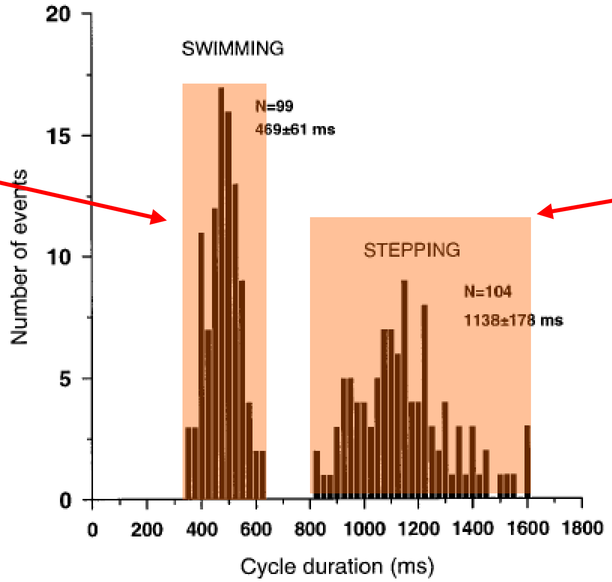
CPGs can modulate speed, heading, and type of gait under the modulation of a few drive signals

Ijspeert *et al*, *Science*, 2007, Crespi et al, *IEEE TRO*, 2013.

Kinematic and EMG studies

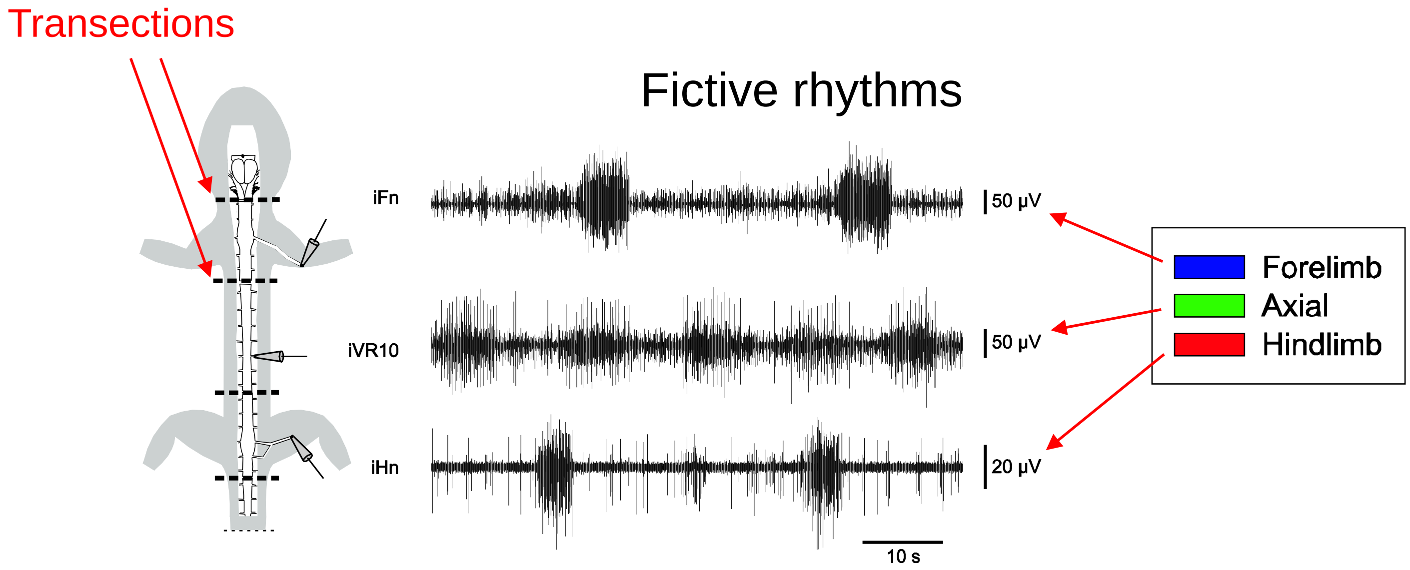
The frequencies of swimming are systematically higher than those of stepping in freely behaving animals

Swimming: 1.6-3.0 Hz



Stepping: 0.6-1.2 Hz

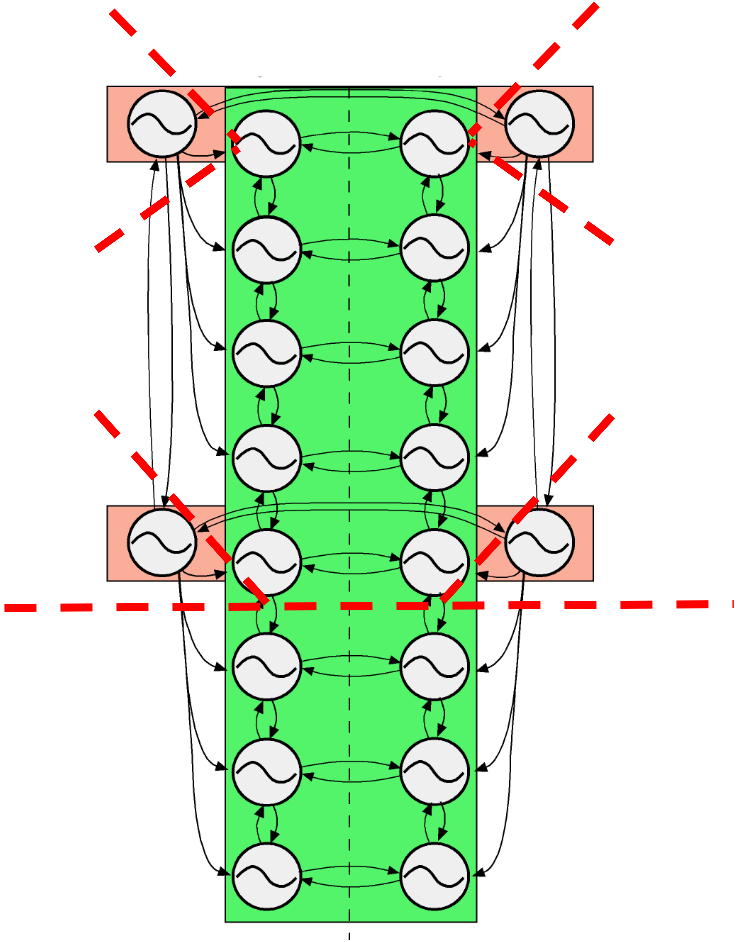
Experiment:
measuring frequencies of limb and body oscillators



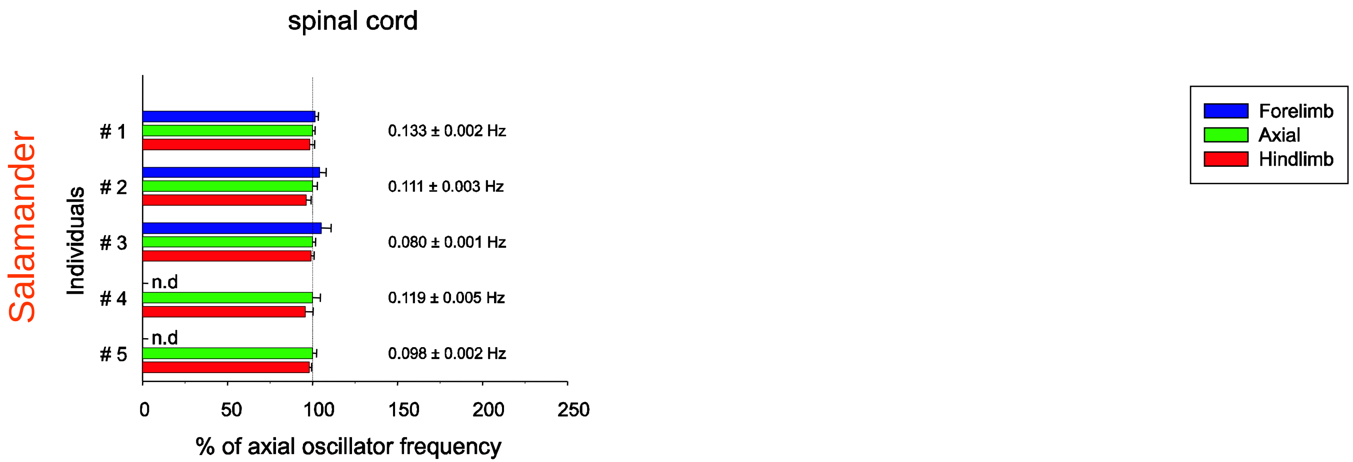
Rhythms are activated with pharmacological excitation (same concentration in the whole spinal cord)

They are measured before and after transections, to isolate the limb oscillators from the axial oscilaltors.

Corresponding transections in the model

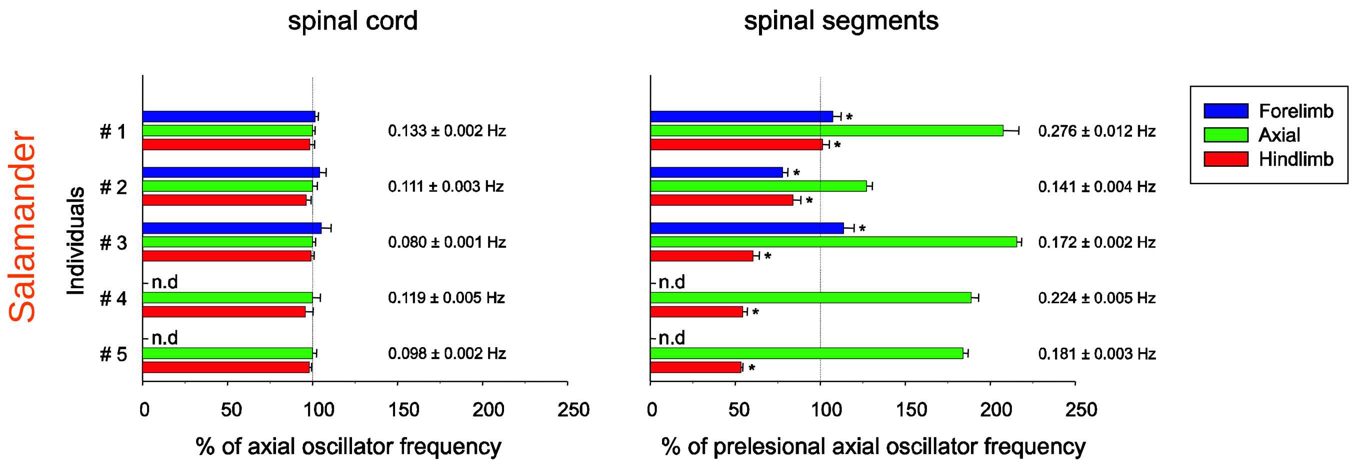


Limb oscillators are slower!



Before transection:
Common resulting frequency
Phase-locked regime

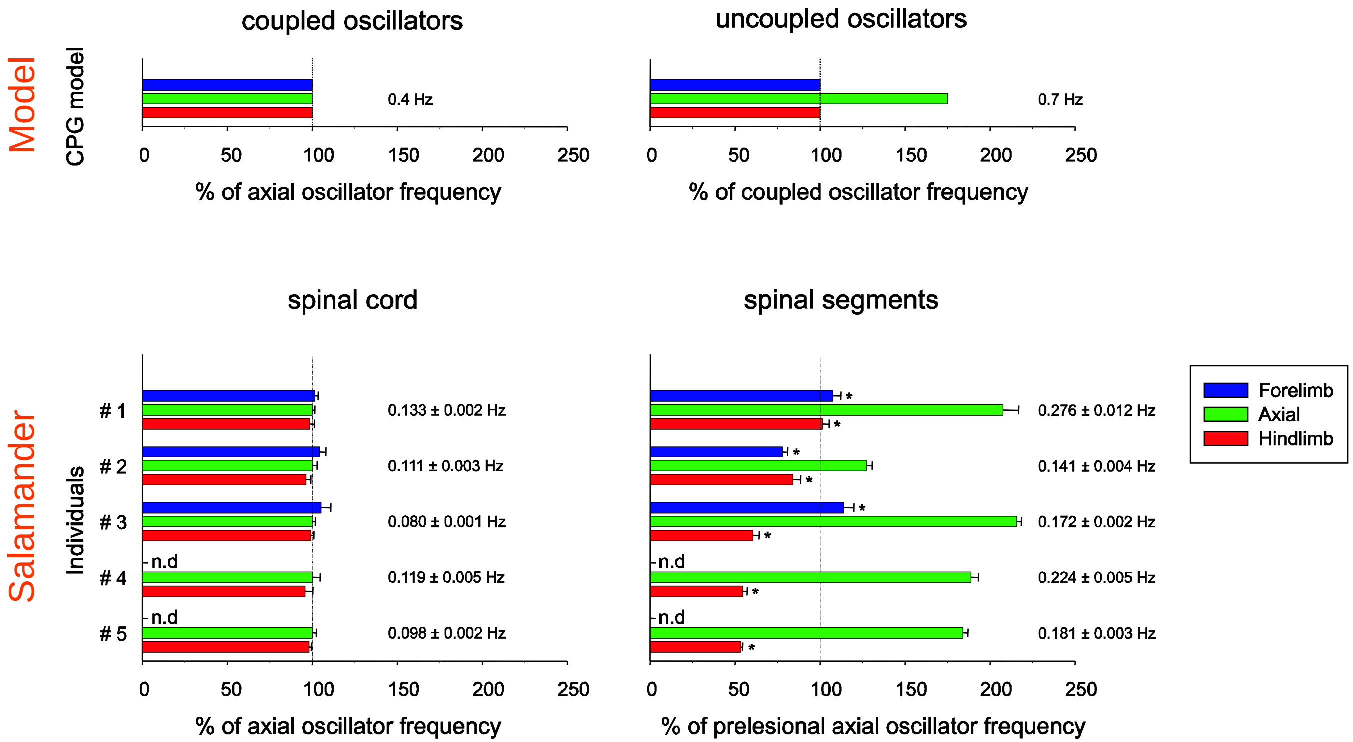
Limb oscillators are slower!



Before transection:
Common resulting frequency
Phase-locked regime

After transection:
Evidence of **different intrinsic frequencies**

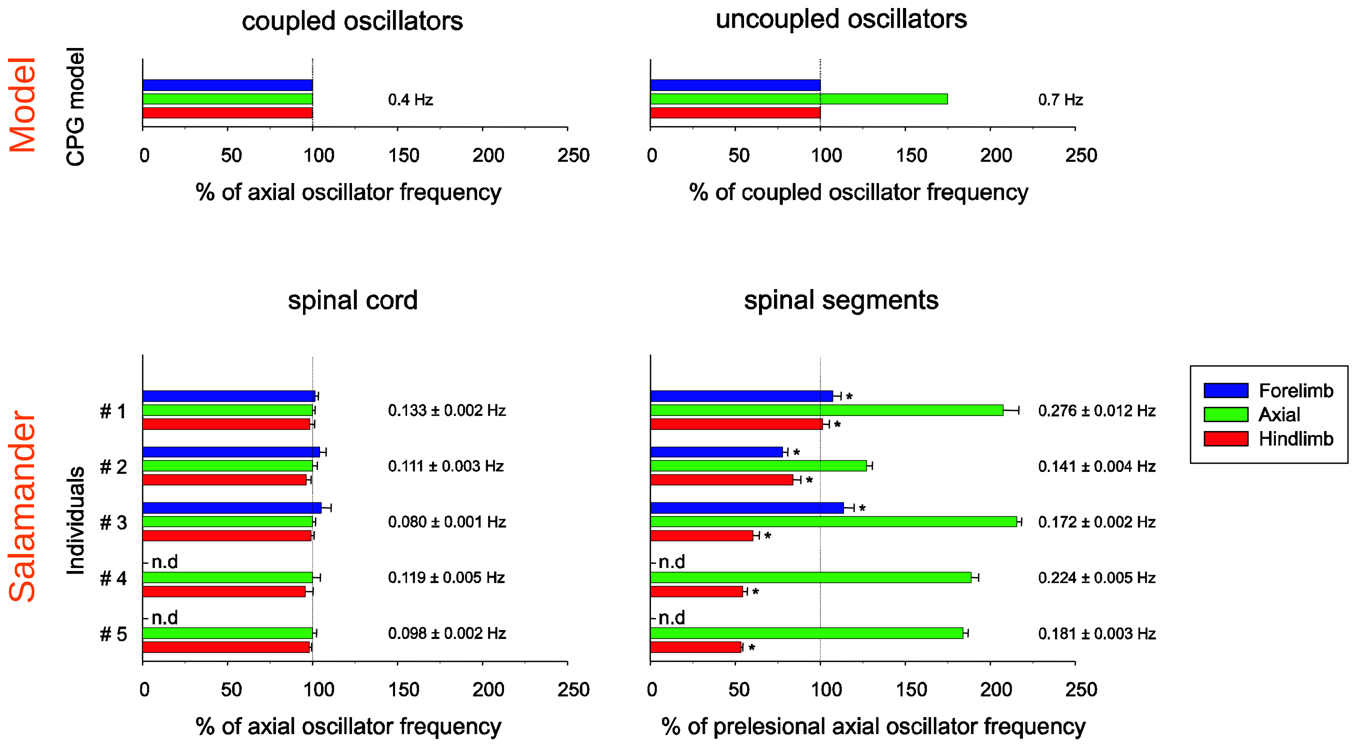
Limb oscillators are slower!



Before transection:
Common resulting frequency
Phase-locked regime

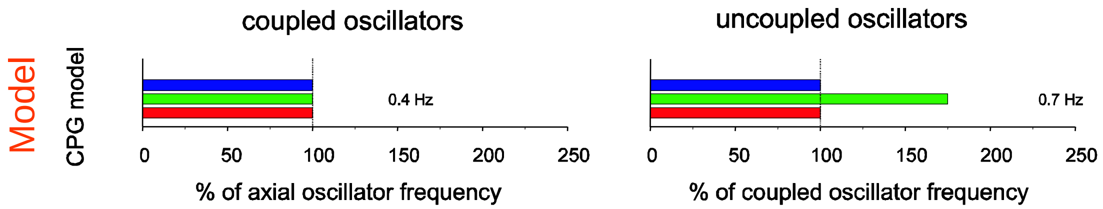
After transection:
Evidence of **different intrinsic frequencies**

Limb oscillators are slower!



Hypothesis 4 is confirmed

Limb oscillators are slower!



Note: this also supports Hyp 2, i.e. that **couplings from limb to axial oscillators are much stronger** than those from axial to limb oscillators

Remember the analysis of the resulting frequency of two coupled oscillators (lamprey model):

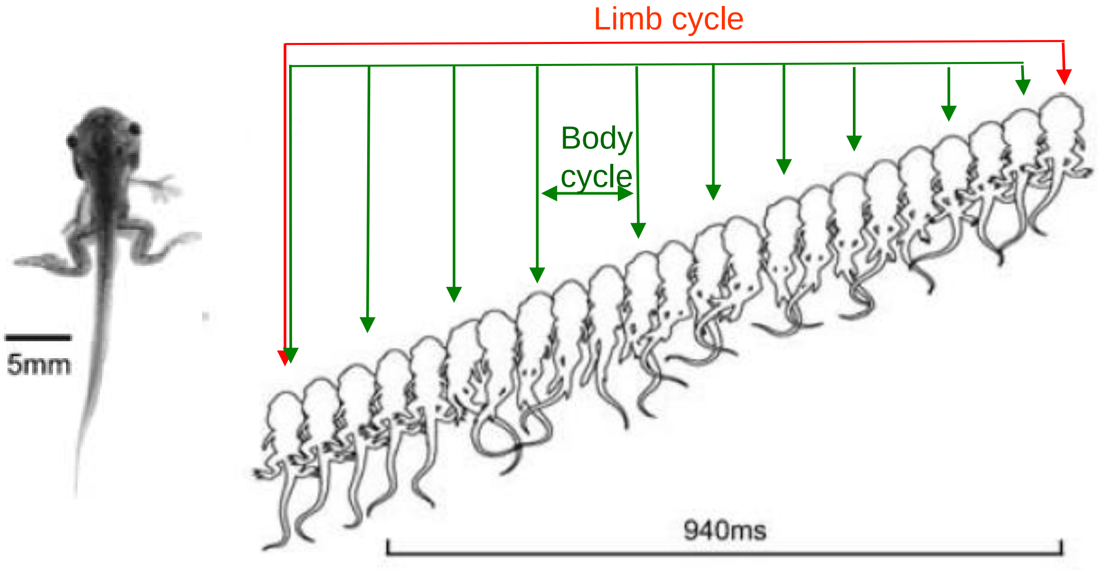
$$\Omega = \frac{a_{21}\omega_1 + a_{12}\omega_2}{a_{21} + a_{12}}$$

$$\Omega = \frac{a_{limb\_to\_axial}\omega_{limb} + a_{axial\_to\_limb}\omega_{axial}}{a_{limb\_to\_axial} + a_{axial\_to\_limb}}$$

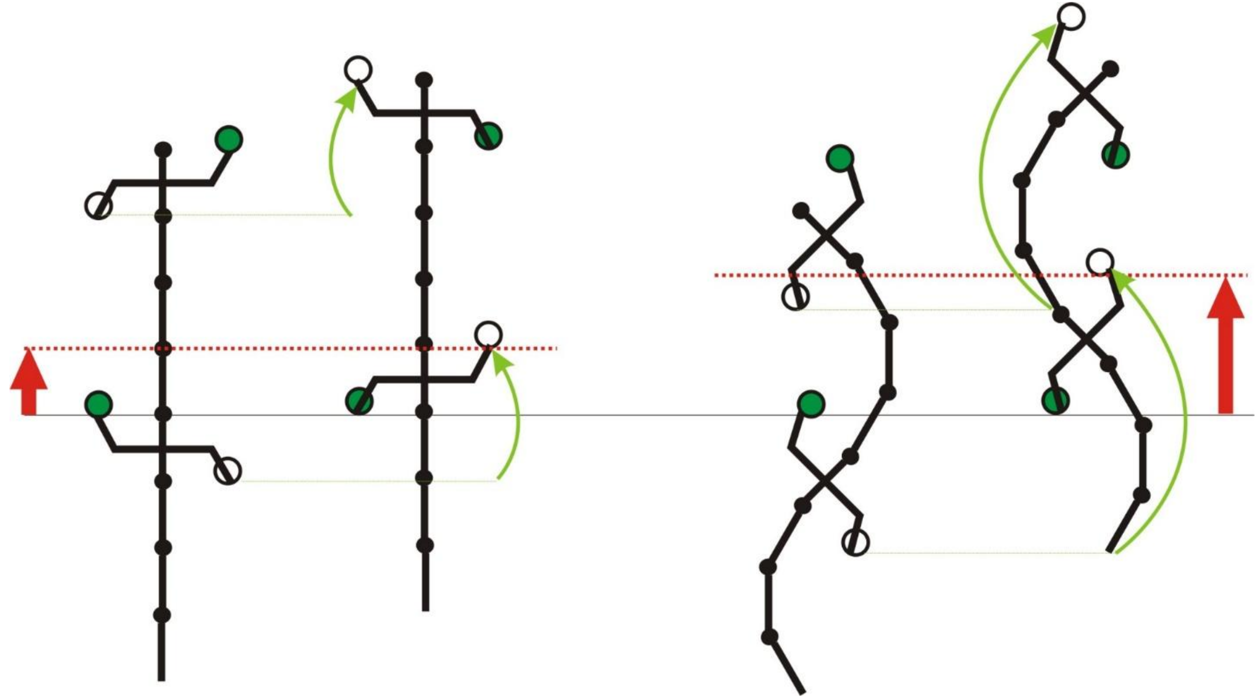
here $\Omega \approx \omega_{limb}$ which suggests that $a_{limb\_to\_axial} \gg a_{axial\_to\_limb}$

Limb oscillators appear to be slower also in metamorphosing tadpoles

D. Combes et al (J Physiol 559.1, 2004) observe that the **rhythm subserving the tail was faster** (mean period 0.56±0.05 s) and involved sequences of many consecutive cycles similar to those seen during fictive axial swimming in younger pre-metamorphic animals. In contrast, the **hindlimb motor rhythm was slower** (mean period 1.60±0.08 s) and more closely resembled the appendicular rhythm generated exclusively by older froglets after the tail circuitry has completely disappeared.



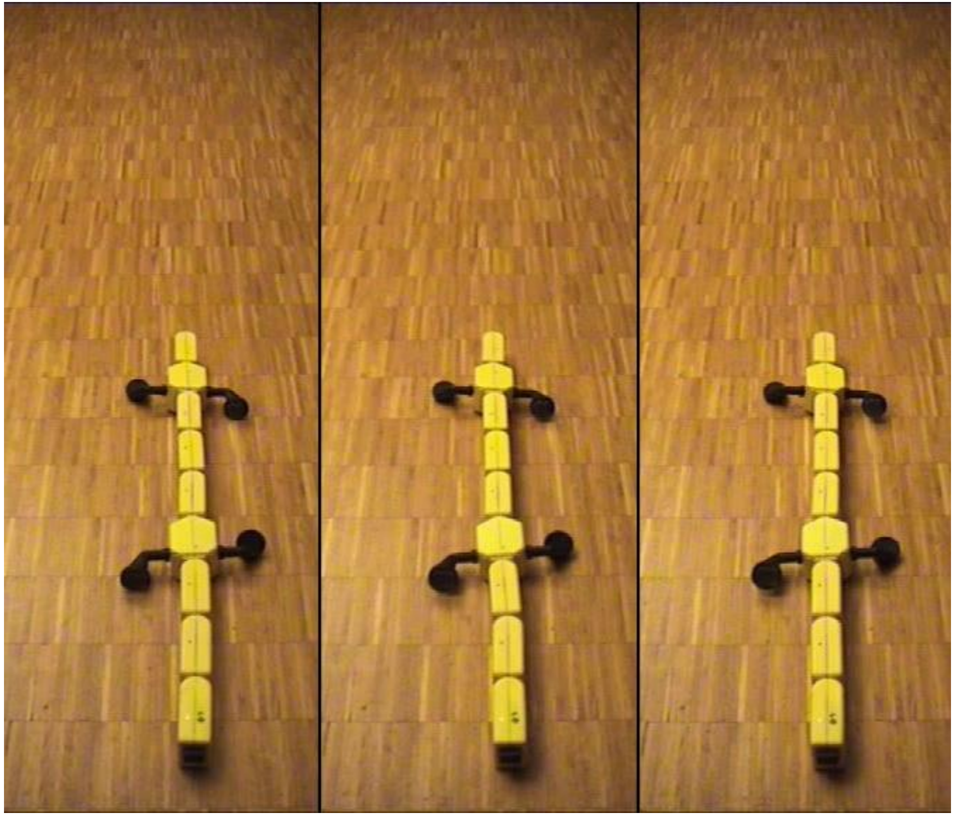
The body limb coordination optimizes speed

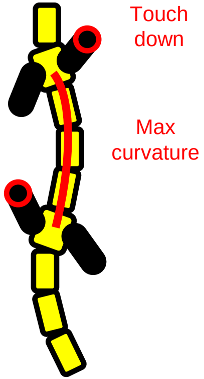


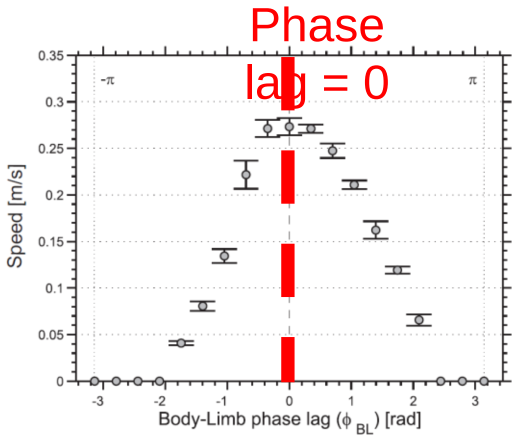
Straight spine

Spine undulating with
an S-shaped standing wave

The body limb coordination optimizes speed







Summary

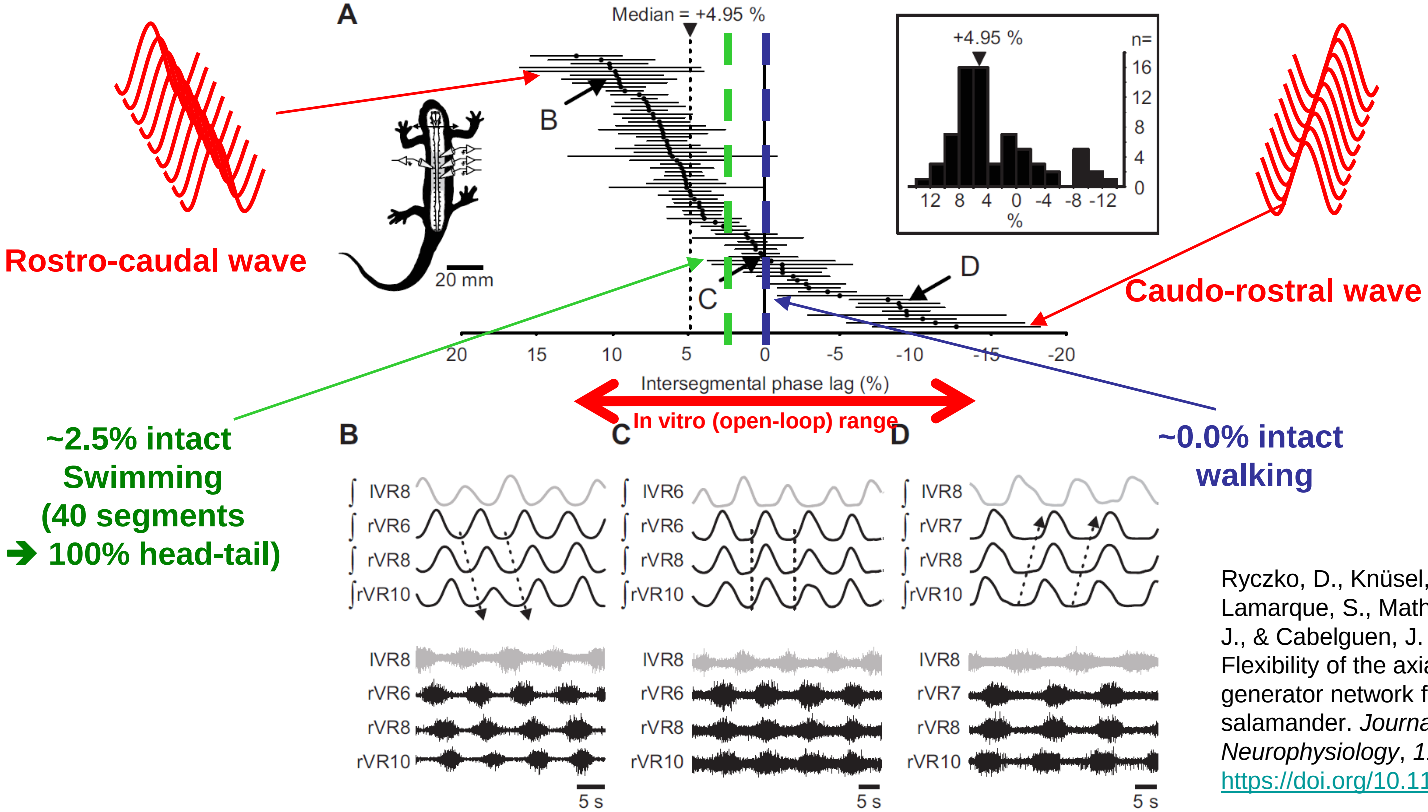
The CPG model provides an explanation for:

- The **automatic transition** from walking to swimming by simple electrical stimulation,
- The **rapid increase of frequency** at the gait transition
- The **lack of overlap between walking and swimming frequencies**
- the **control of speed and direction** by the modulation of a simple tonic drive.

Evolution: **addition of oscillatory centers with different intrinsic frequencies and saturation frequencies** to a lamprey CPG

But this is only part of the story, currently we look at the **role of sensory feedback**

New **in vitro** data from Ryczko et al 2015: **Large variability of intersegmental phase lags** in the axial CPG during fictive locomotion (NMDA, open loop)



Ryczko, D., Knüsel, J., Crespi, A., Lamarque, S., Mathou, A., Ijspeert, A. J., & Cabelguen, J. M. (2015). Flexibility of the axial central pattern generator network for locomotion in the salamander. *Journal of Neurophysiology*, *113*(6), 1921–1940. https://doi.org/10.1152/jn.00894.2014

Three new observations

1. **Isolated CPGs show a large range of phase lags** (much larger than intact animals)

2. **Oscillations** can be obtained in **hemi-segments**

3. **Axial CPGs can exhibit traveling waves even when limb CPGs are active.**

Ijspeert et al 2007

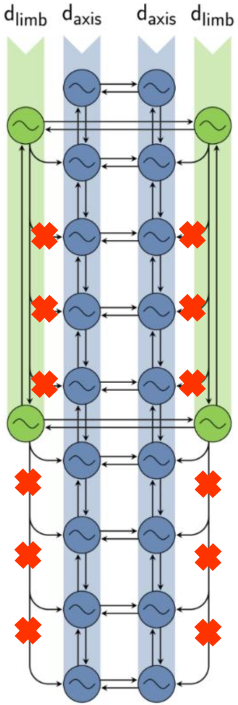
Correcting wrong phase patterns

- (open loop) **CPGs show a large range of phase lags**
- Many of these lead to bad/slow swimming

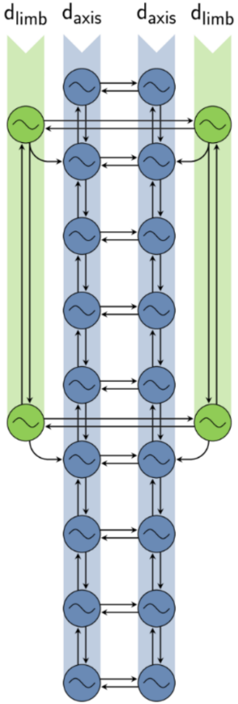
- **Intact animals** have phase lags in a much **narrower range**

- Two possible explanations:
  - Phase lags are **corrected by descending modulation**
  - Phase lags are **corrected by sensory feedback**

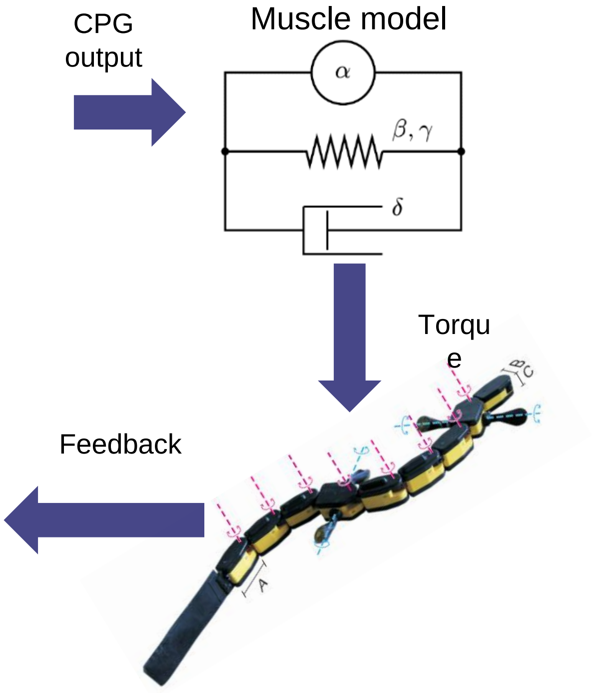
New model of Knuesel et al 2020



Old



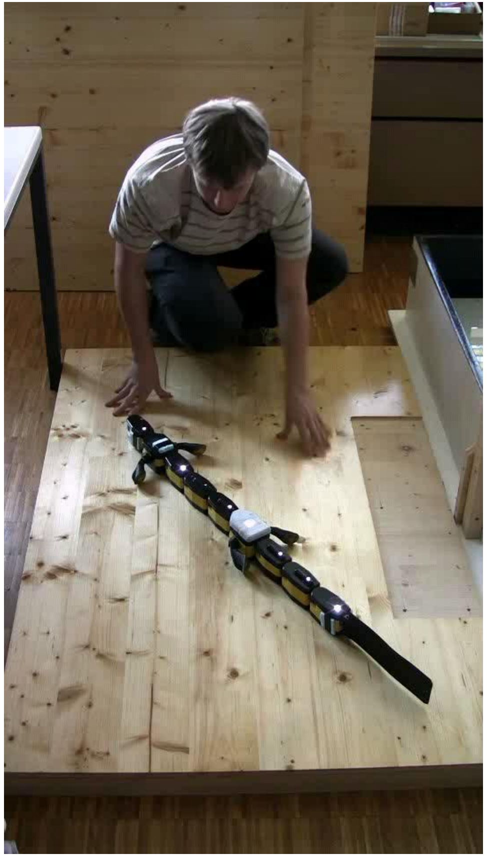
New

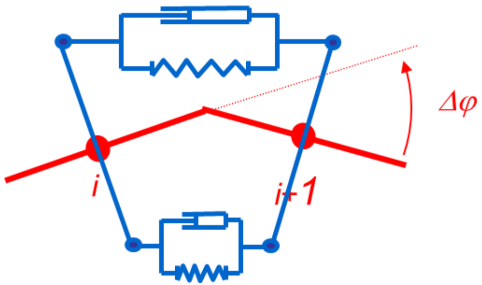


J. Knuesel

Knüsel, J., Crespi, A., Cabelguen, J.-M., Ijspeert, A. J., & Ryczko, D. (2020). Reproducing Five Motor Behaviors in a Salamander Robot With Virtual Muscles and a Distributed CPG Controller Regulated by Drive Signals and Proprioceptive Feedback. *Frontiers in Neurorobotics*, *14*. https://www.frontiersin.org/articles/10.3389/fnbot.2020.604426

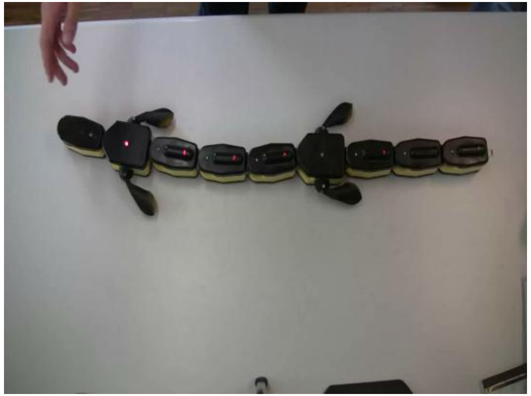
Simulated Ekeberg muscles





$$T = \alpha(M_f - M_e) + \beta(M_f + M_e + \gamma)\Delta\varphi + \delta\Delta\dot{\varphi}$$

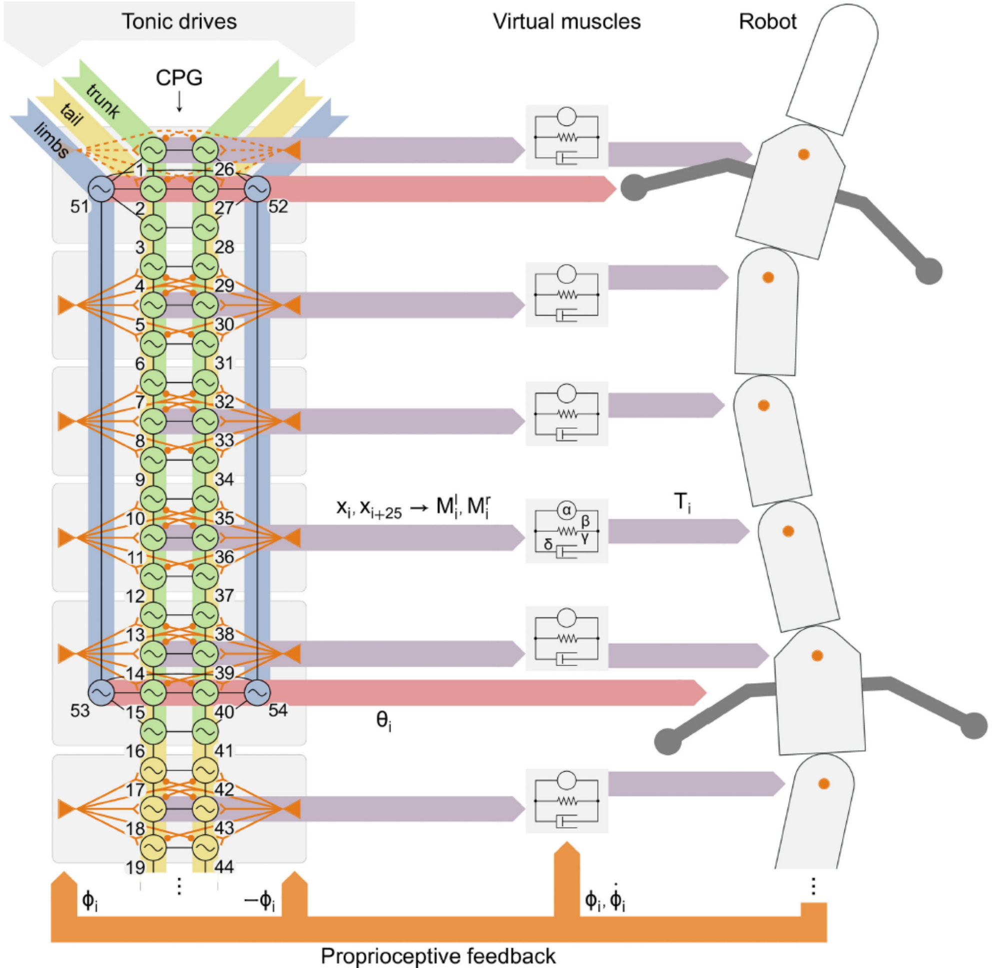
High tonic input to muscles



Low tonic input to muscles

Knuesel et al. *Frontiers in Neurorobotics*, 2020

Knuesel et al 2020

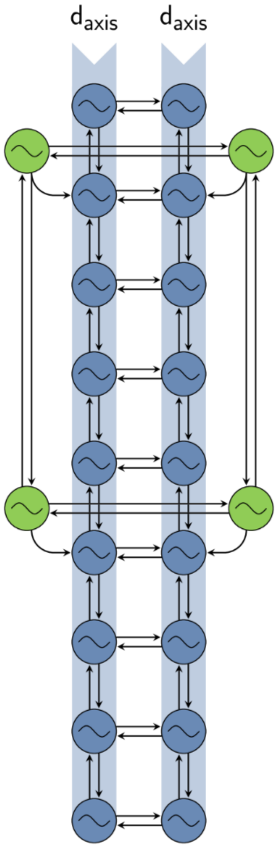


Novelty compared to Ijspeert et al 2007:

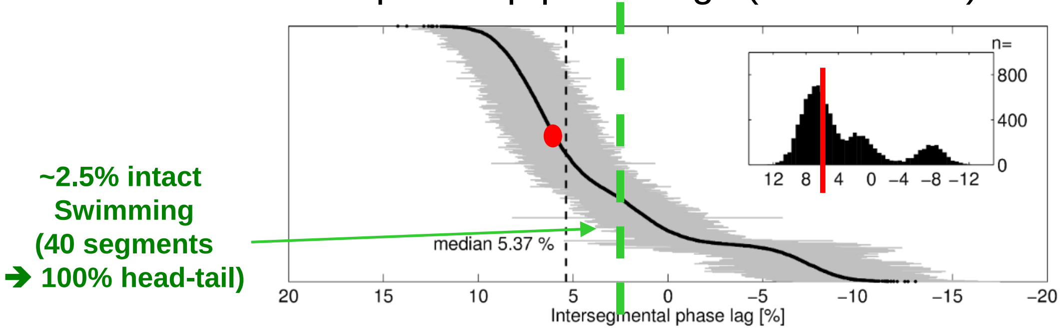
- Slightly different topology
- **No long-range coupling from limb CPGs to axial oscillators**
- Random setting of intrinsic frequencies
- **More descending pathways**
- **Sensory feedback** from **stretch receptors**
- Muscle model
- Distributed implementation on the robot

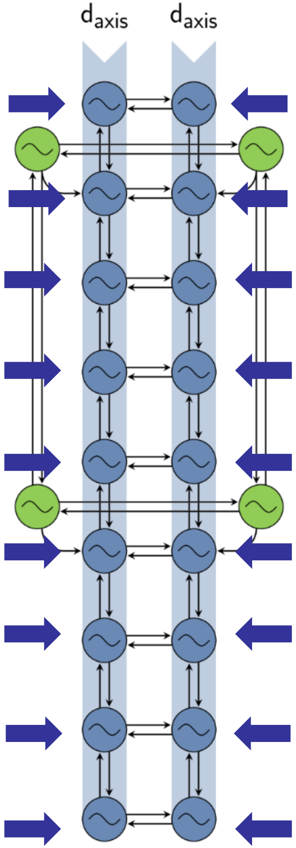
Bad open-loop swimming:

Example of too large "in vitro phase lag" inappropriate for swimming



Open loop phase lags (animal data):

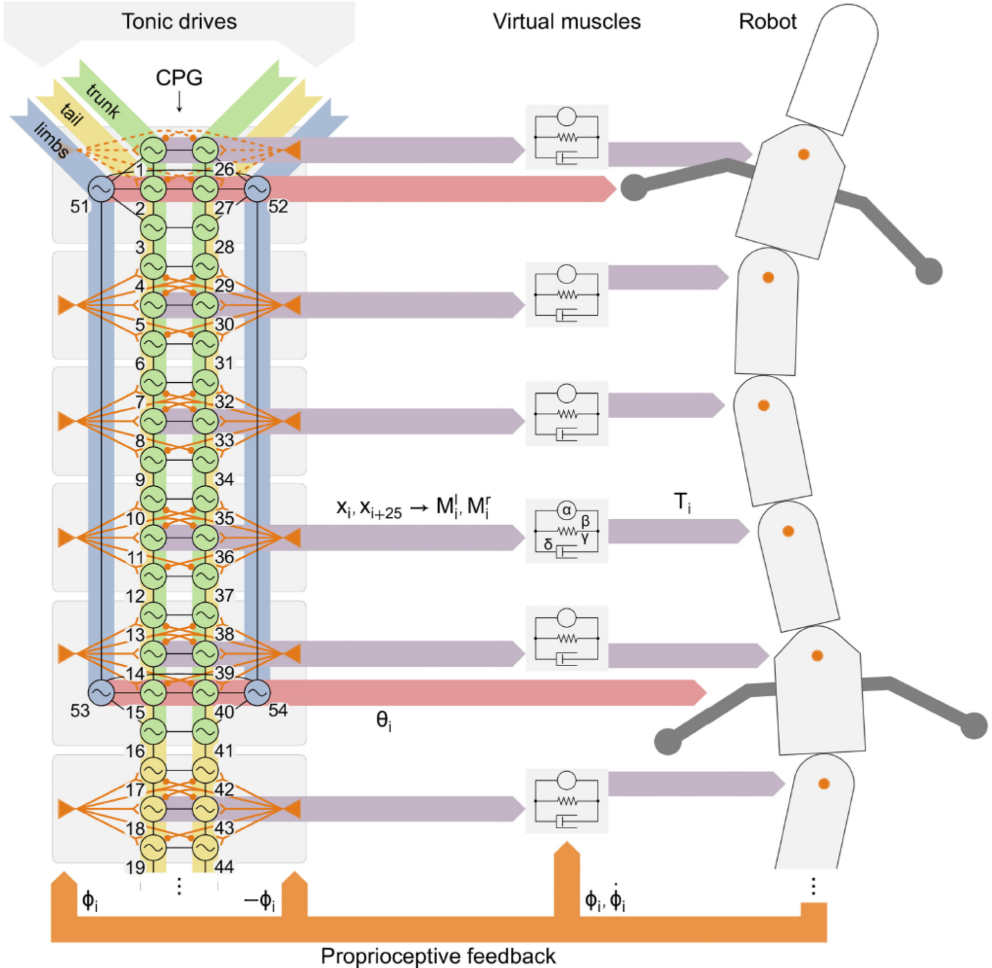




Good closed-loop swimming:
Phase lag can be **regulated by local proprioceptive sensory feedback**
(from stretch sensors)

15% frequency increase

Knuesel et al 2020



Main findings:

- **Different motor behaviors** can be explained by using the **same CPG circuit** + descending pathways + sensory feedback
- **Sensory feedback reduces variability** of isolated (open-loop) CPG
- Sensory feedback can **“correct” wrong open-loop CPG patterns**

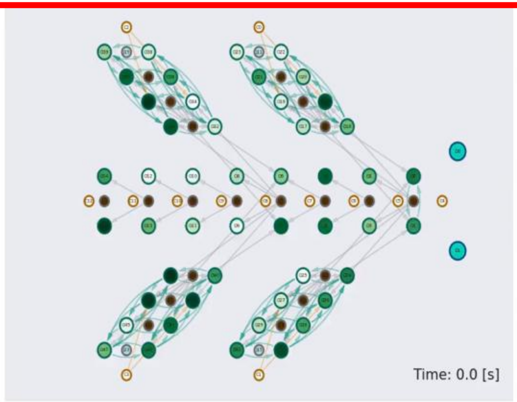
Distributed control

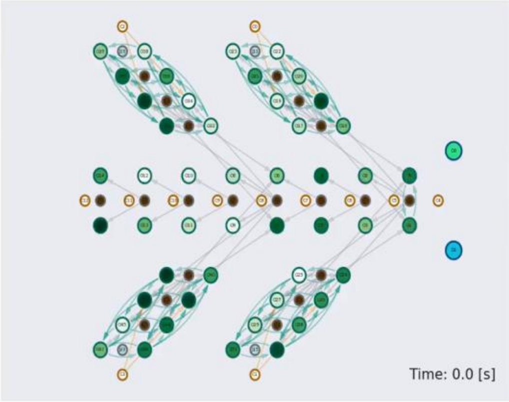
CPGs can be implemented in a distributed way, with robustness about changing morphology

Knuesel et al. *Frontiers in Neurorobotics*, 2020

Swimming and walking coordinated through sensory feedback

Quite good locomotion **coordinated by sensory feedback**





Jonathan Arreguit O'Neil

No axial coupling
No interlimb coupling
(but intralimb coupling)

Three types of feedback:

- Limb force
- Muscle stretch
- Muscle stretch velocity

Manuscript in preparation

It even works for **amphibious centipede locomotion!**

FARMS

MuJoCo

Manuscript in preparation

Salamander summary

CPGs are sophisticated control circuits that can produce and modulate complex movement patterns (modulation of speed, heading, and type of gait)

Salamander-like locomotion can be explained by **adding a limb CPG and new descending pathways to a lamprey-like swimming circuit**

Local **sensory feedback** (together with distributed oscillators):

- helps **handle perturbations**
- can **synchronize oscillators** (in addition to intersegmental coupling)
- can **reduce variability** and **correct wrong patterns of open-loop CPGs**
- could possibly explain **transitions between traveling waves** (swimming) and **standing waves** (walking)

Inter-oscillator coupling is probably not as strong as previously thought.
Work in progress: still many things to explore such as other sensor modalities, …

Further readings on salamander models

- Ijspeert, A. J. (2001). A connectionist central pattern generator for the aquatic and terrestrial gaits of a simulated salamander. *Biological Cybernetics*, *84*(5), 331–348. https://doi.org/10.1007/s004220000211
- Ijspeert, A. J., Crespi, A., Ryczko, D., & Cabelguen, J.-M. (2007). From swimming to walking with a salamander robot driven by a spinal cord model. *Science*, *315*(5817), 1416–1420. https://doi.org/10.1126/science.1138353
- Bicanski, A., Ryczko, D., Cabelguen, J.-M., & Ijspeert, A. J. (2013). From lamprey to salamander: An exploratory modeling study on the architecture of the spinal locomotor networks in the salamander. *Biological Cybernetics*, *107*(5), 565–587. https://doi.org/10.1007/s00422-012-0538-y
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- Karakasiliotis, K., Thandiackal, R., Melo, K., Horvat, T., Mahabadi, N. K., Tsitkov, S., Cabelguen, J. M., & Ijspeert, A. J. (2016). From cineradiography to biorobots: An approach for designing robots to emulate and study animal locomotion. *Journal of the Royal Society Interface*, *13*(119). https://doi.org/10.1098/rsif.2015.1089
- Knüsel, J., Crespi, A., Cabelguen, J.-M., Ijspeert, A. J., & Ryczko, D. (2020). Reproducing Five Motor Behaviors in a Salamander Robot With Virtual Muscles and a Distributed CPG Controller Regulated by Drive Signals and Proprioceptive Feedback. *Frontiers in Neurorobotics*, *14*. https://www.frontiersin.org/articles/10.3389/fnbot.2020.604426
- Suzuki, S., Kano, T., Ijspeert, A. J., & Ishiguro, A. (2021). Spontaneous Gait Transitions of Sprawling Quadruped Locomotion by Sensory-Driven Body–Limb Coordination Mechanisms. *Frontiers in Neurorobotics*, *15*, 92. https://doi.org/10.3389/fnbot.2021.645731
- Pazzaglia, Alessandro, Andrej Bicanski, Andrea Ferrario, Jonathan Arreguit, Dimitri Ryczko, and Auke Ijspeert. "Balancing Central Control and Sensory Feedback Produces Adaptable and Robust Locomotor Patterns in a Spiking, Neuromechanical Model of the Salamander Spinal Cord." *PLOS Computational Biology* 21, no. 1 (January 21, 2025): e1012101. https://doi.org/10.1371/journal.pcbi.1012101.

Possible exam questions

- Describe the different **hypotheses explaining traveling waves in lamprey**
- Which effects can **sensory feedback** have during swimming in the **lamprey model**?
- Describe the **characteristics of salamander swimming and walking**, discuss why it is an interesting animal to study.
- Describe the **4 hypotheses underlying the salamander model** presented in the lecture. Explain how they were implemented in the model of coupled oscillators.
- Explain the implications related to the **hypothesis that limb oscillators are slower than axial oscillators** (answer: axial oscillation frequencies are slowed down when limbs are active, and frequency gap between slow walking and fast swimming), and discuss which experiment was performed on the real animal to confirm that hypothesis.
- Why is the **axial body undulation** useful for the salamander? (on ground and in water)
- Discuss which roles **sensory feedback might play in the salamander**.

End of Lecture

Again: fewer TAs today, sorry. Do not hesitate to use the forum !