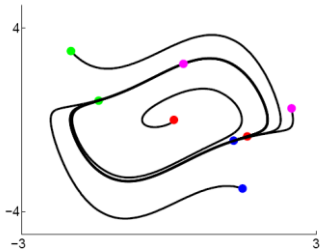
Computational Motor Control

Lecture 6:

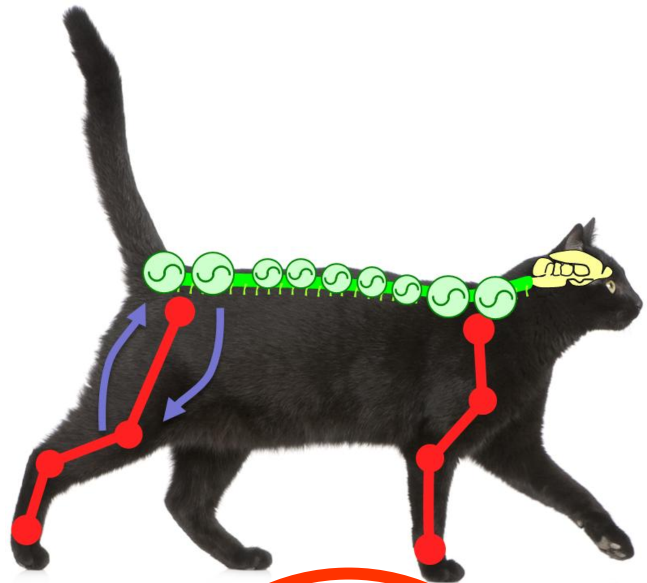
Locomotion control and models of lamprey swimming circuits

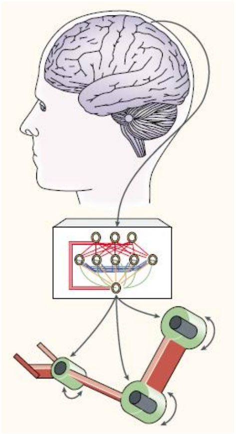
Auke Jan Ijspeert

Contents of lectures

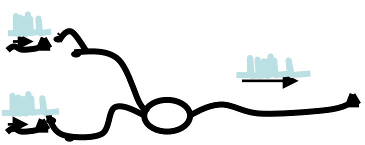


Dynamical systems

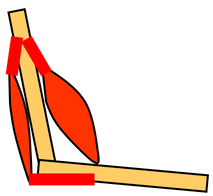




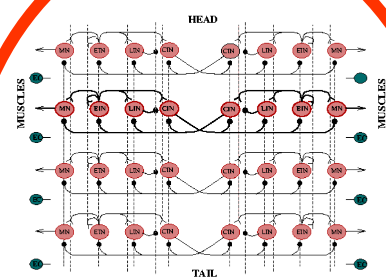
Neuroprosthetics



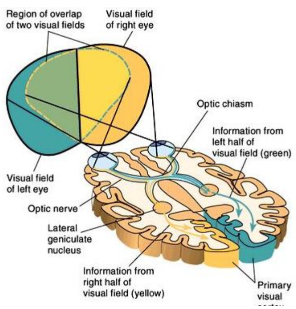
Neuron models



Muscle and Biomech. models



Motor system models



Visual system models

Today

Topics:

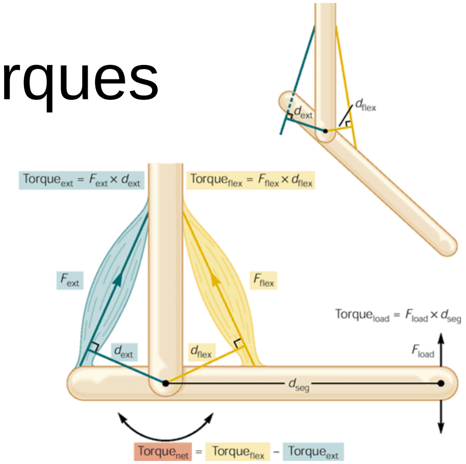
- Biomechanics of animal locomotion
- Locomotion control in animals
- Locomotion of the lamprey
- Modeling the lamprey locomotor system

Biomechanics of animal Locomotion

General principles:

1. To **rhythmically apply forces** to the environment,

2. Use of **antagonist muscles ➔** creation of torques + modification of the stiffness of a joint



3. **Storage of mechanical energy** (spring properties of muscles and tendons)

4. **Multiple degrees of freedom**

G.E. Loeb, C. Ghez (2000) The Motor Unit and Muscle Action. In: *Principles of Neural Science*. 4th edition. Edited by E.R. Kandel, J.H. Schwartz and T.M. Jessell. Appleton & Lange, New York. pp. 675-694.

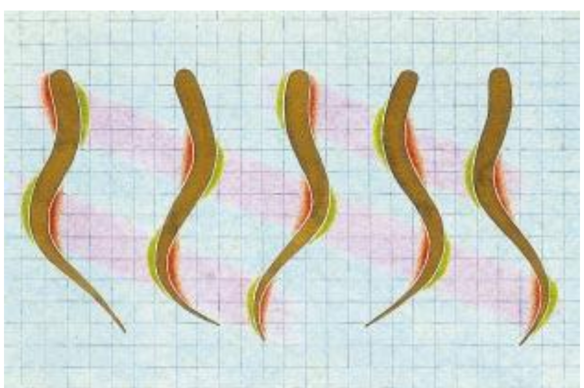
Biomechanics of animal Locomotion

Generation of forces:

5. Animals use the **principles of action-reaction**

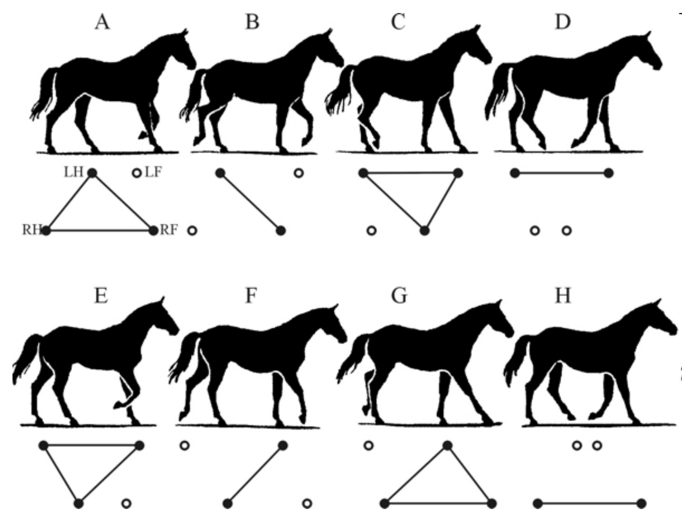
6. Key feature: **creation of asymmetries in the external forces due to the environment** (little resistance in the direction of locomotion compared to the other directions)

- Examples: elongated form of the body, scales on snake skin, legs (transition between swing and stance)



Asymmetric drag

Scales:
Asymmetric friction



Swing-stance alternation

Biomechanics of animal Locomotion

Large diversity of different types of locomotion in **different media**: swimming, crawling, walking, hoping, burrowing, flying,… but **all use the same principles**.

Multiple redundancies, Berstein problem

Control of locomotion is a difficult and « ill-posed » problem:

Requires good **coordination** (right frequencies, phases, signal shapes,…) of multiple degrees of freedom,

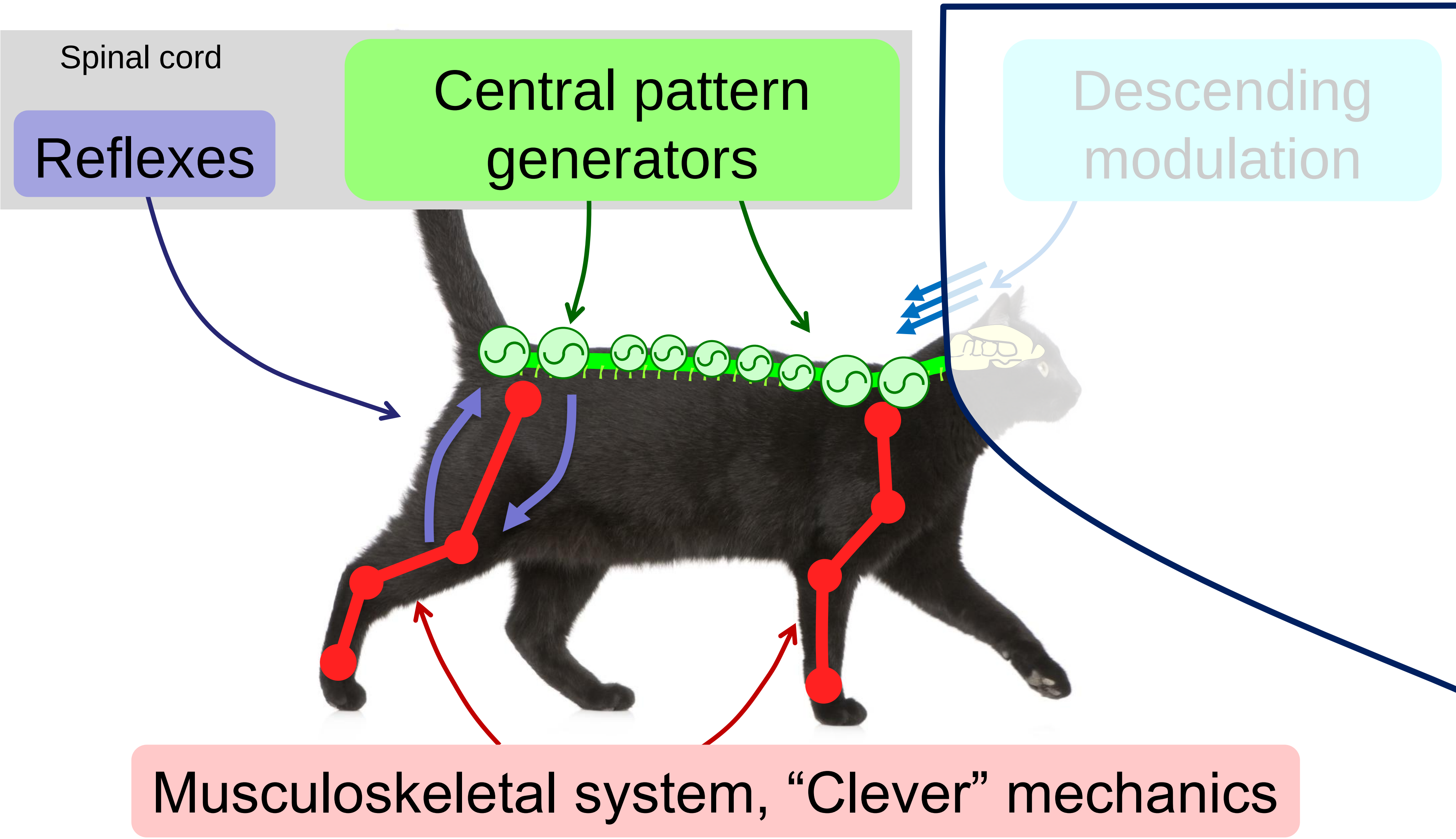
despite the multiple **redundancies**:

- Many possible **end-point trajectories**
- Many possible **postures** for a given end-point
- Many possible **muscle activations** for a given posture
- Many possible **motor unit** activations for a given muscle activation

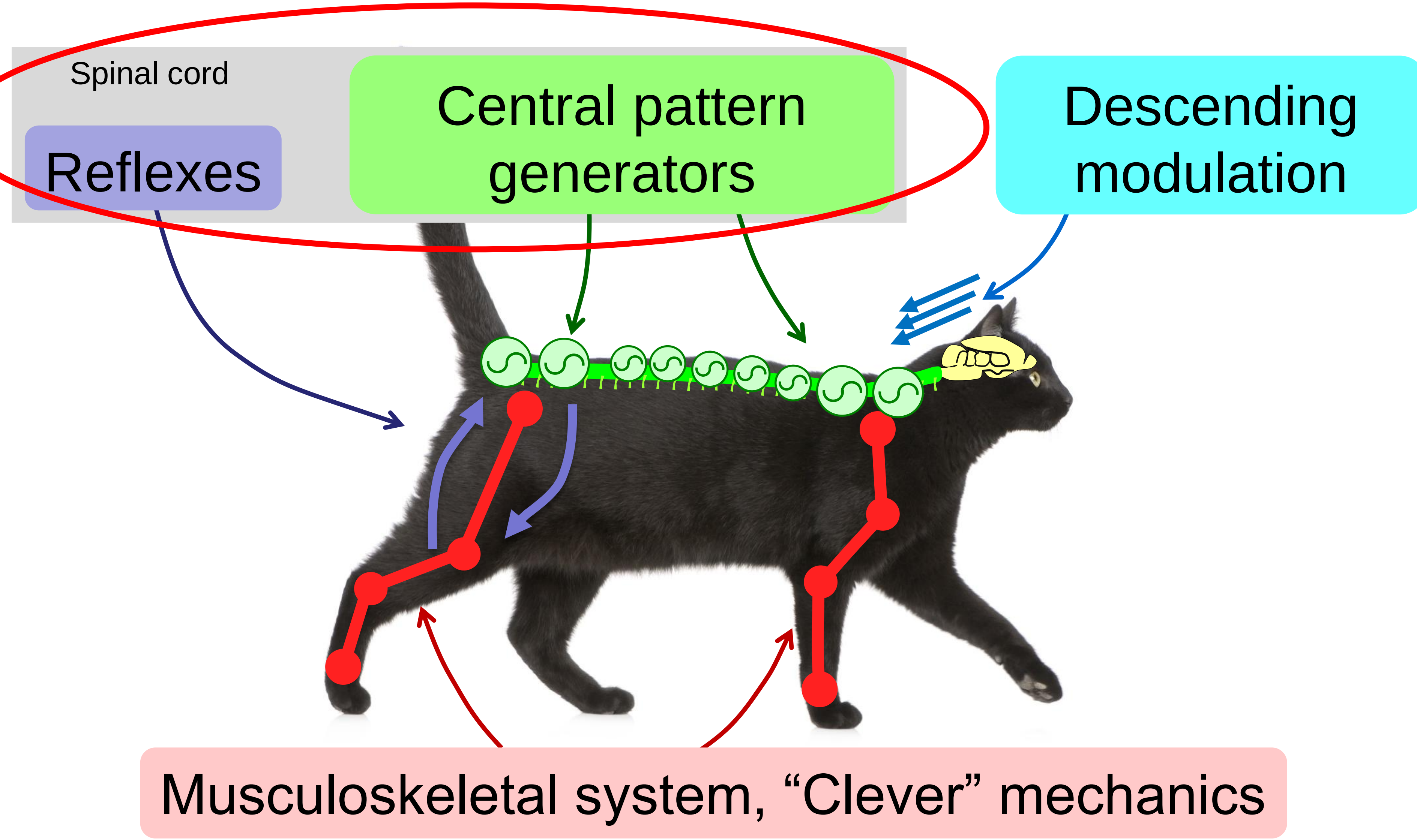
The problem of tackling these redundancies is sometimes called the "Bernstein problem". We will see that most of these redundancy problems are **solved by the spinal cord**.

https://en.wikipedia.org/wiki/Degrees_of_freedom_problem

Four essential ingredients in animal motor control



Four essential ingredients in animal motor control



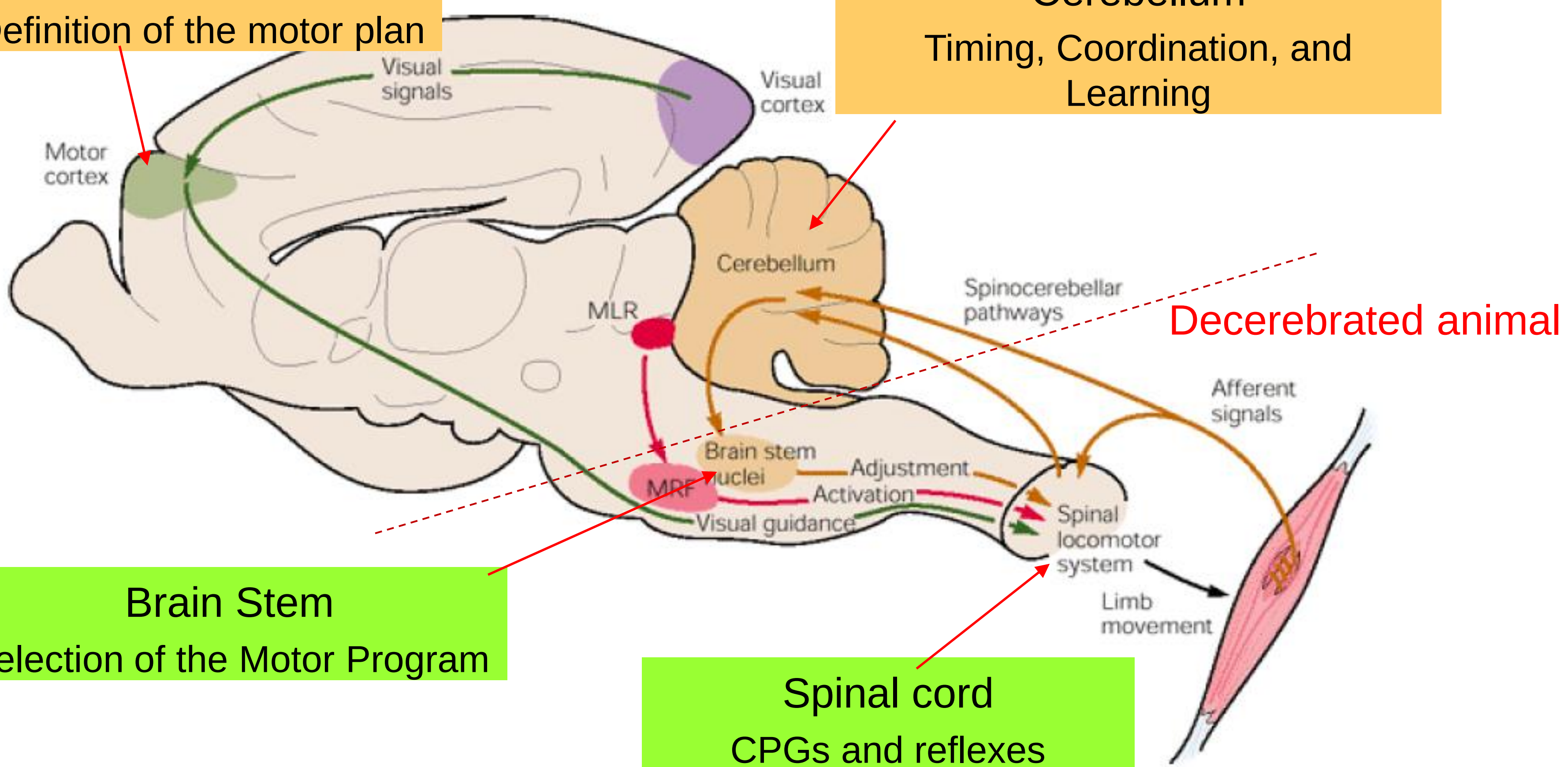
Vocabulary

- *Fictive locomotion*: neuronal patterns produced by the CPG when it is disconnected from sensory feedback, e.g. when the spinal cord is completely isolated in a petri dish or when dorsal roots are cut
- *Decerebrated animal*: disconnection above the brainstem (isolates the high brain regions from the brainstem + spinal cord)
- *Segment*: spinal circuits within one vertebra
- *Rostral*: towards the head
- *Caudal*: towards the tail
- *Projection*: length of an axon (e.g. a neuron can "project" up to *N* segments caudally)
- *Ipsilateral*: on the same side
- *Contralateral*: on the other side
- *Commissural neuron*: neuron that projects contralaterally within a segment (to the other side)
- *Afferent*: transmission that goes towards the central nervous system (CNS)
- *Efferent*: transmission that goes from the CNS towards the periphery
- *Descending pathways/tracts*: pathways/tracts that go from higher brain regions towards the spinal cord (therefore a type of efferent pathway)
- *Burst*: group of spikes (action potentials). Locomotion involves rhythmic burst generation in motoneurons that leads to periodic muscle activation.
- *Gray matter:* gray matter is made of neural cell bodies, axon terminals, and dendrites.
- *White matter:* white matter is composed of bundles of axons.
- *Sensory neuron:* neuron that processes sensory information (e.g. stretch receptors)
- *Motoneuron (or motor neuron):* neuron that project to muscle fibers. Sometimes they project back to interneurons.
- *Interneuron:* neuron that is in-between sensory and motoneurons. Typically a CPG is made of a network of interneurons.
- *Reflex arc*: circuit that implements a reflex (a rapid response) from sensory neurons to interneurons to motoneurons. A *short-latency* reflex has a single synapse in the circuit (directly connecting sensory neurons to motoneurons), a *long-latency* reflex involves more synapses (and therefore more neurons). Reflexes can be modulated by descending signals.

Brain centers involved in vertebrate motor control

Cerebral cortex
Definition of the motor plan

Cerebellum
Timing, Coordination, and Learning

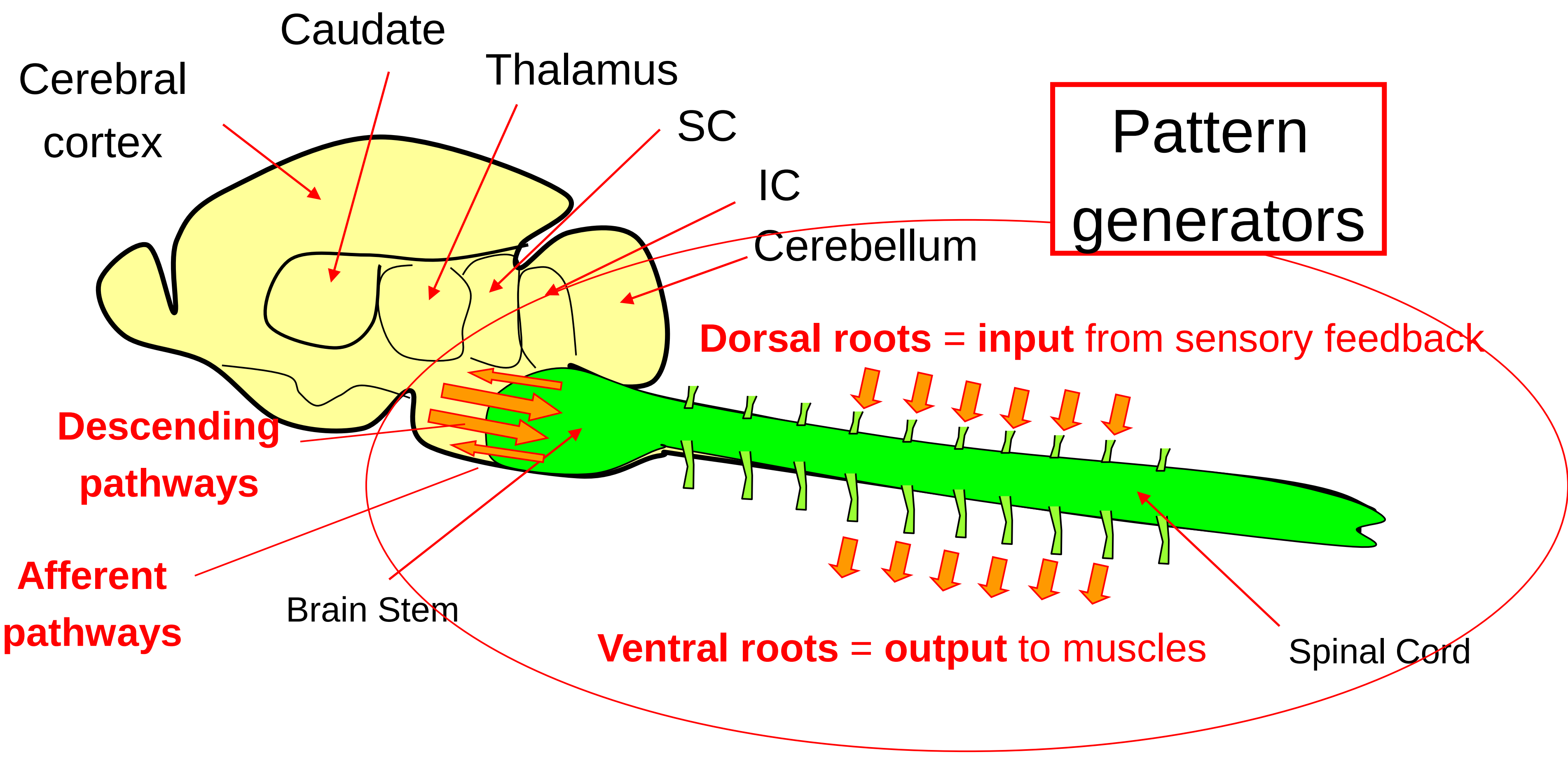


Brain Stem
Selection of the Motor Program

Spinal cord
CPGs and reflexes
Spatiotemporal Sequences
Activation of muscles

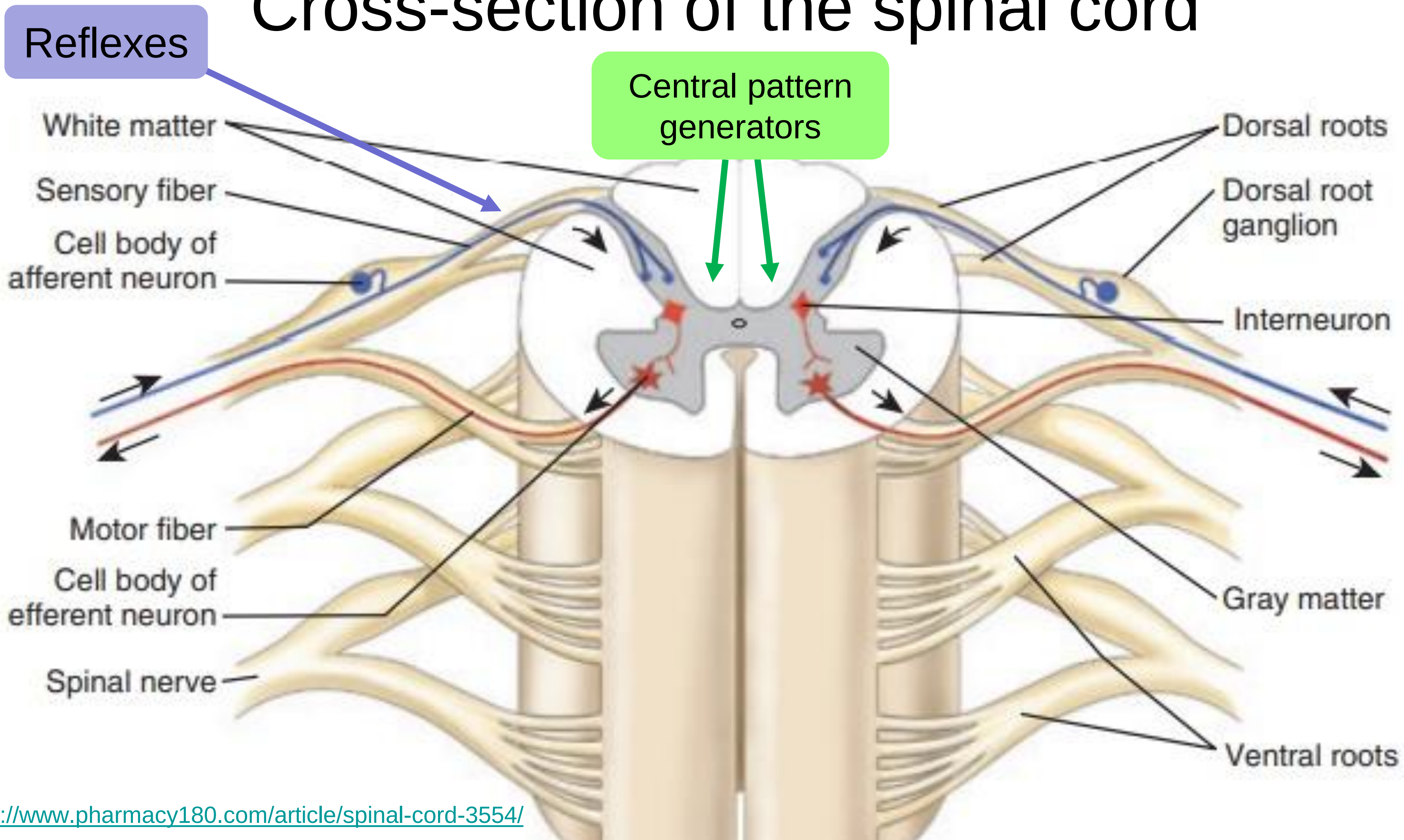
From: *Principles of Neural Science*. 4th edition. Edited by E.R. Kandel, J.H. Schwartz and T.M. Jessell. Appleton & Lange, New York.

Building bricks for motor control: **pattern generators**



Simple inputs ➔ complex outputs. E.g gait transition by electrical stimulation of the brain stem (Shik and Orlosky 1966)

Cross-section of the spinal cord



http://www.pharmacy180.com/article/spinal-cord-3554/

Important: the spinal cord is not just a relay station.

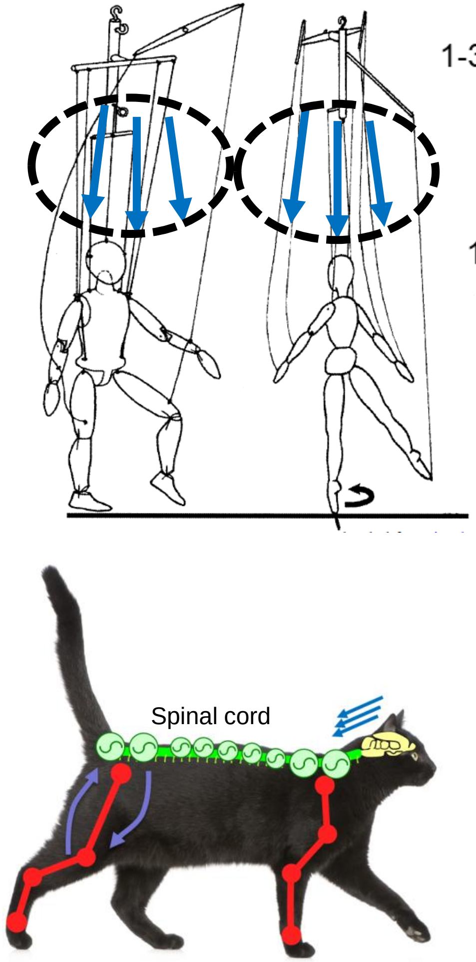
It has multiple **sophisticated circuits for motor control**

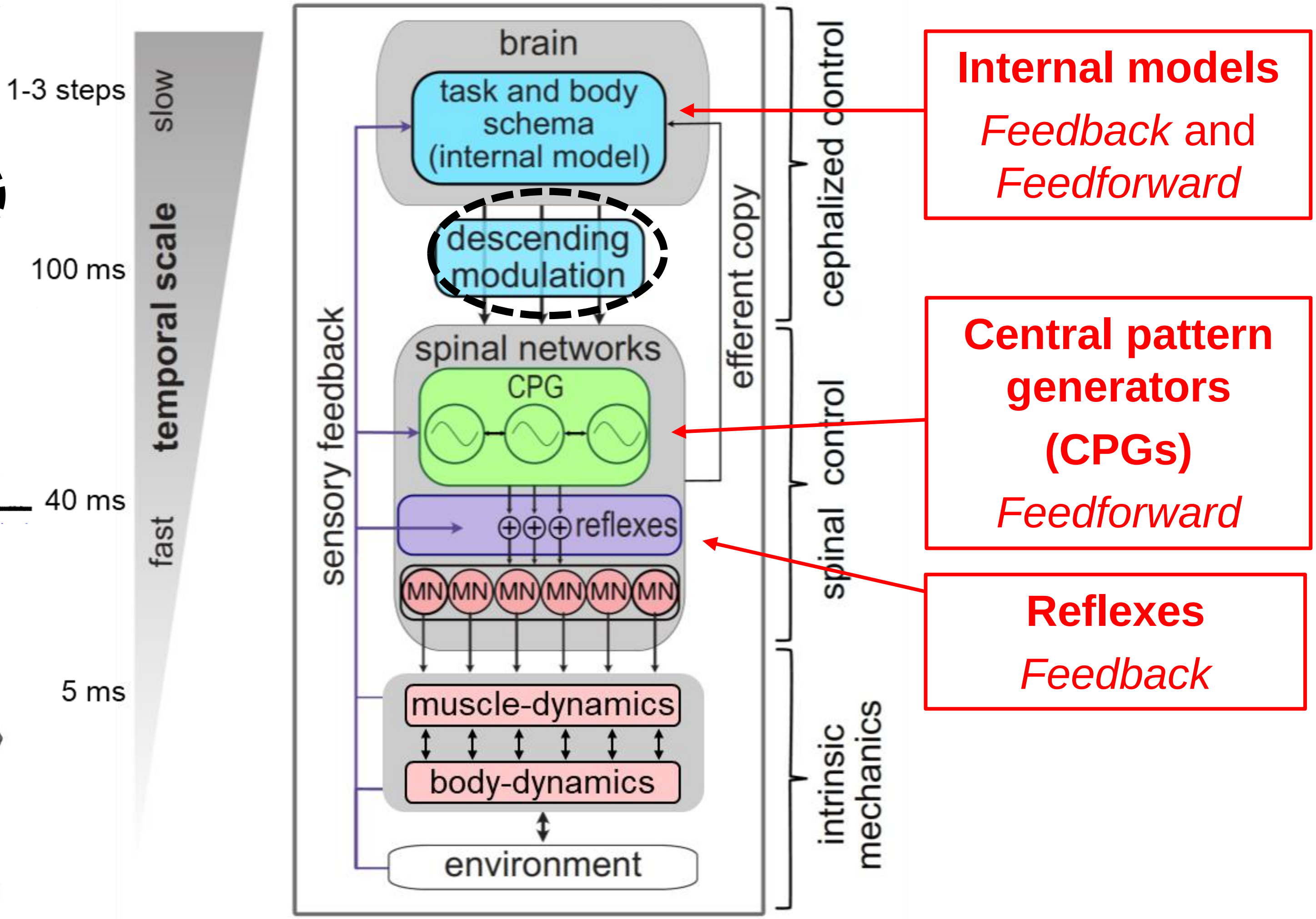
Text book figures like the one above often give the impression of (too) simple circuits in the spinal cord, which is not the case

A multi-layered control architecture

Because neurons are rather slow, animal motor control has multiple layers, and combines feedforward and feedback control.

Jerry Loeb's Puppet analogy

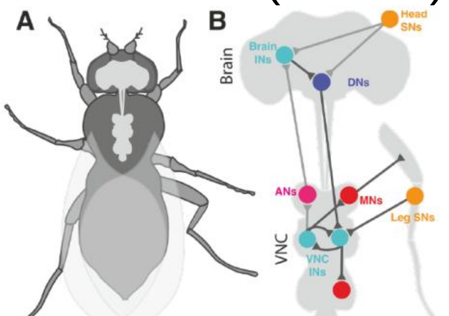




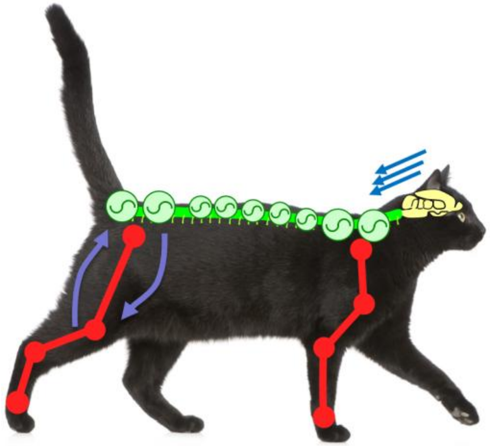
Ijspeert and Daley, JEB 2023

The neural organization is surprisingly conserved

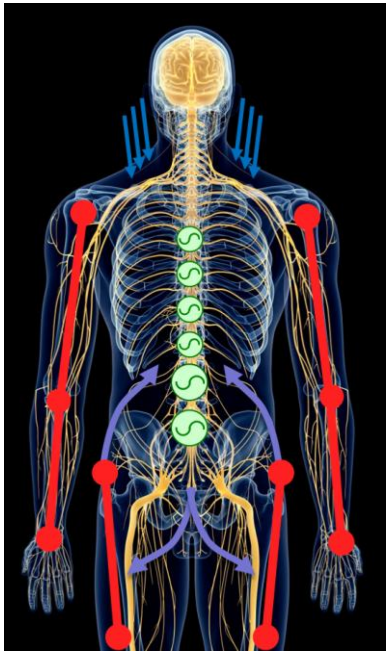
Also in invertebrates (insects)



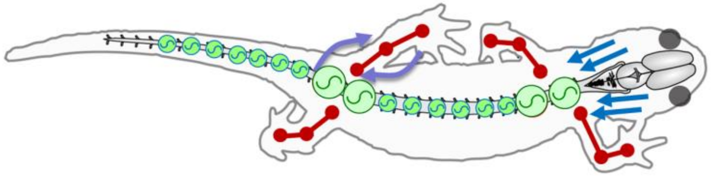
Büschges and Ache, *Physiological Reviews*, in print



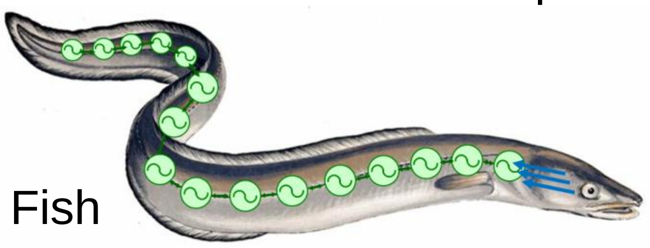
Mammals



Humans



Amphibians/reptiles



Fish

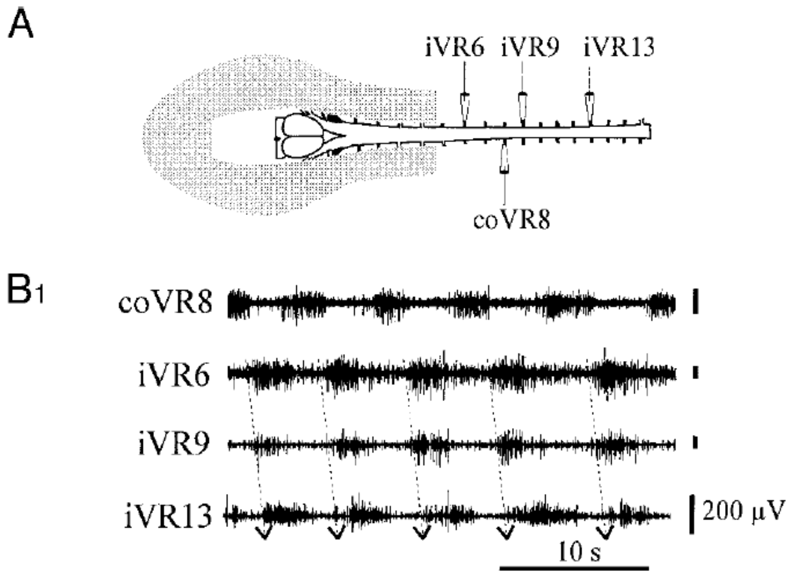
Much more than the morphology

Central pattern generators: observation 1

(1) CPGs can produce *fictive locomotion*: even completely isolated spinal cords can produced coordinated patterns of activity that closely resemble intact locomotion

Example:

Fictive swimming in salamander when the spinal cord is placed in an excitatory (NMDA) bath

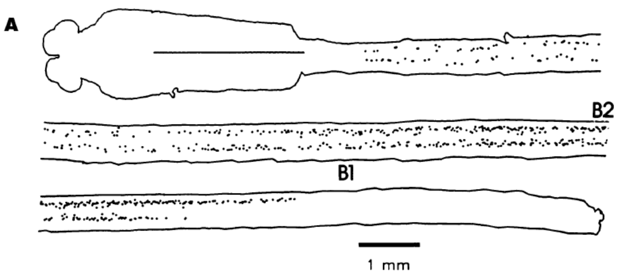


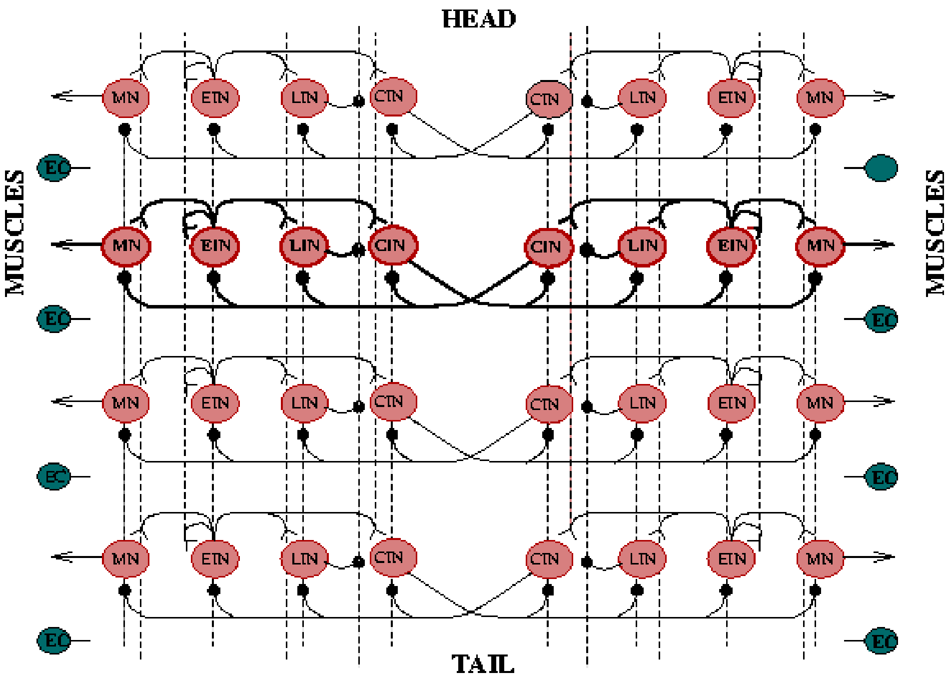
Delvolvé et al, J. Neurophysiology, 82, 1999:

Central pattern generators: observation 2

(2) Central pattern generators are **distributed and composed of multiple neuronal oscillators**

- Example the lamprey CPG is a double chain of neural oscillators distributed within 100 segments:





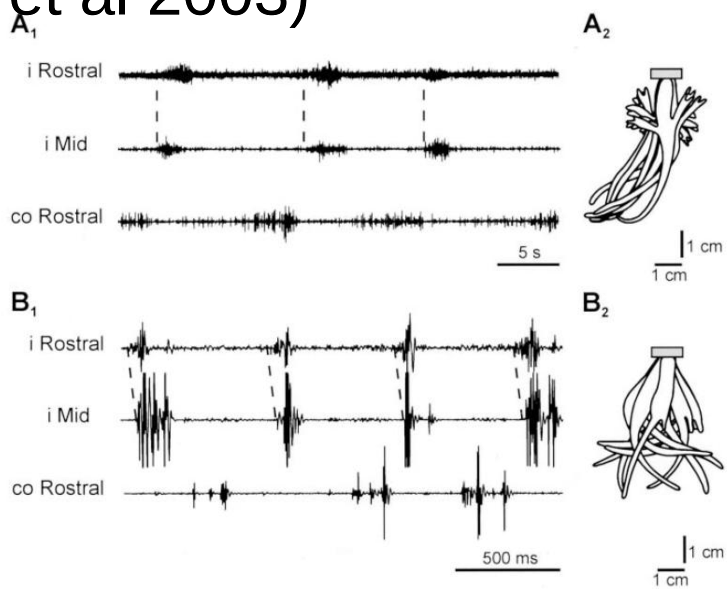
Central pattern generators: observation 3 and 4

(3) Central pattern generators can be **activated by simple electrical signals**,

(4) CPGs + sensory feedback **can produce different types of gaits**

Examples: induction and changes of gait by electrical stimulation in cat (Shik and Orlovsky 1966)

Induction and changes of gait by electrical stimulation in salamander (Cabelguen et al 2003)

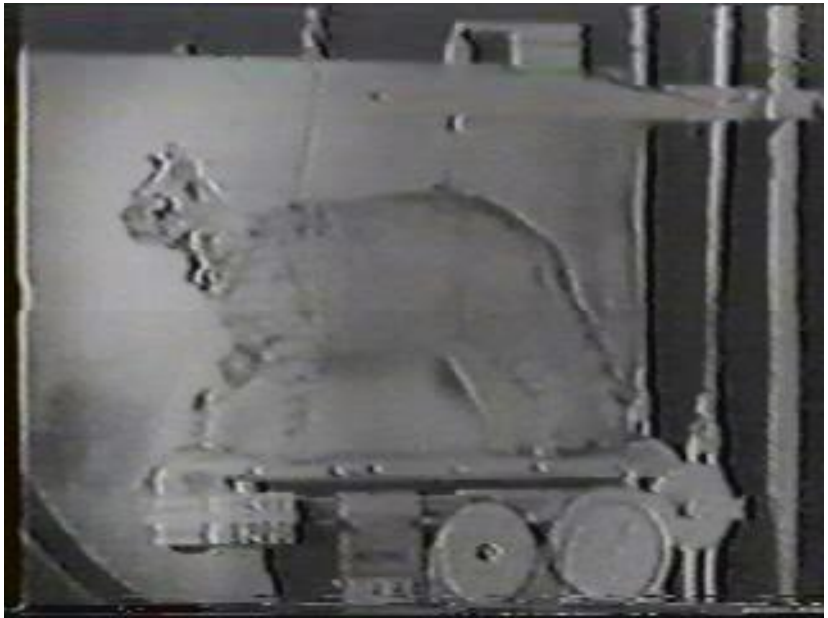


Central pattern generators: observation 5

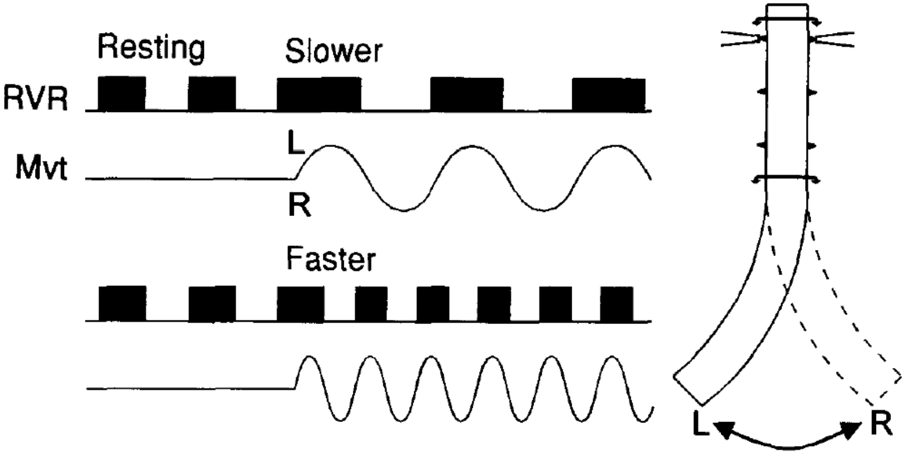
(5) Central pattern generators can be activated and entrained by sensory signals

Examples:

Induction of locomotion and changes of gait in a decerebrated cat with a **motorized treadmill** (Brown 1972)



Mechanical entrainment of the lamprey CPG (Grillner 1995)



Debate about CPGs in humans

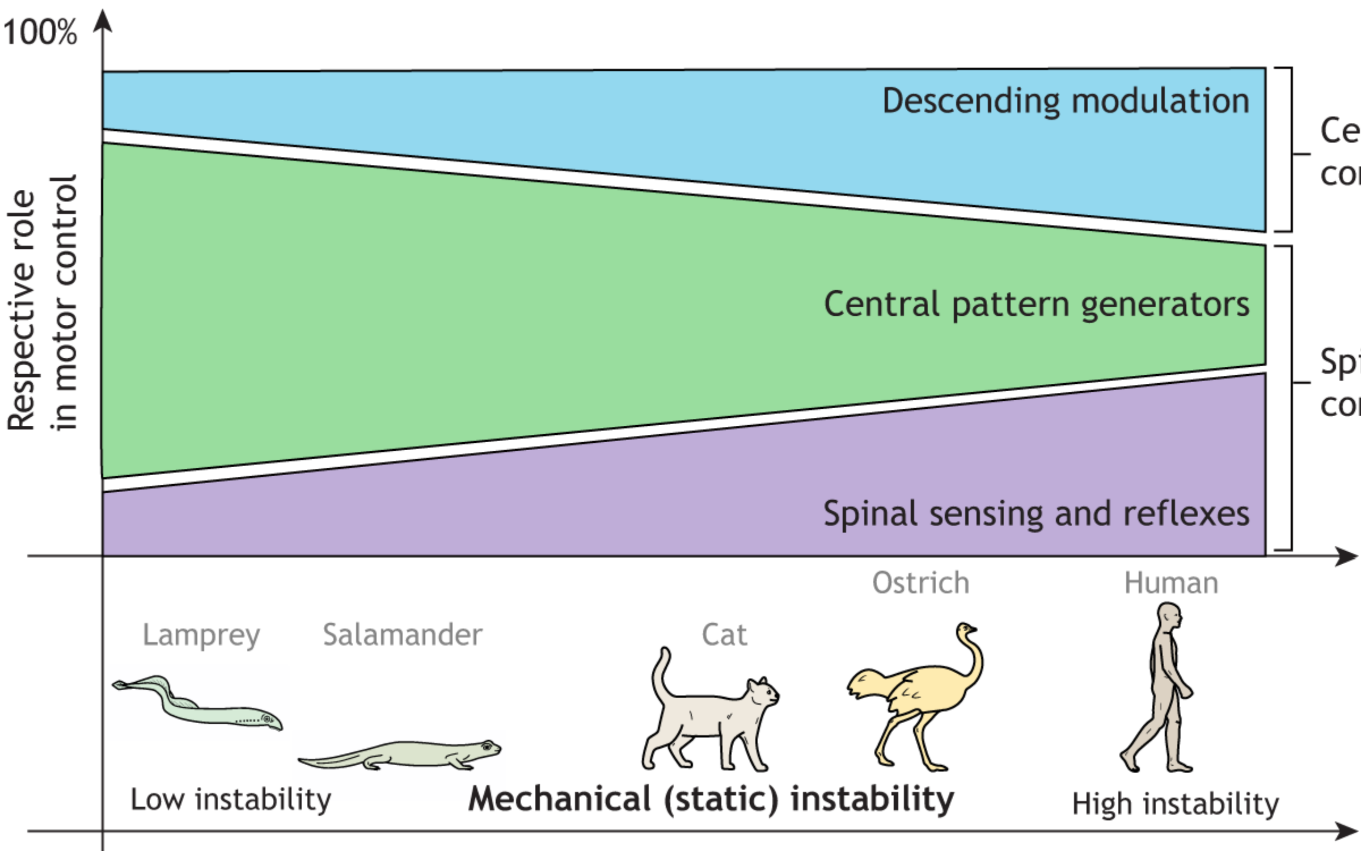
- It looks like CPGs are fundamental in lower vertebrates, possibly less so in higher vertebrates
- Still a debate of existence and role of CPGs in human locomotion

- **Ongoing debate:** some/most people believe human locomotion uses CPGs (like other vertebrates); others believe that it is based on other types of circuits without spinal oscillators that combine sensory feedback and more important role for higher centers (e.g. motor cortex and cerebellum).
- Review of (indirect) evidence of CPGs in humans:
- The Human Central Pattern Generator for Locomotion: Does It Exist and Contribute to Walking? Karen Minassian, Ursula S. Hofstoetter, Florin Dzeladini, Pierre A. Guertin, and Auke Ijspeert. The Neuroscientist, 1-15, 2017

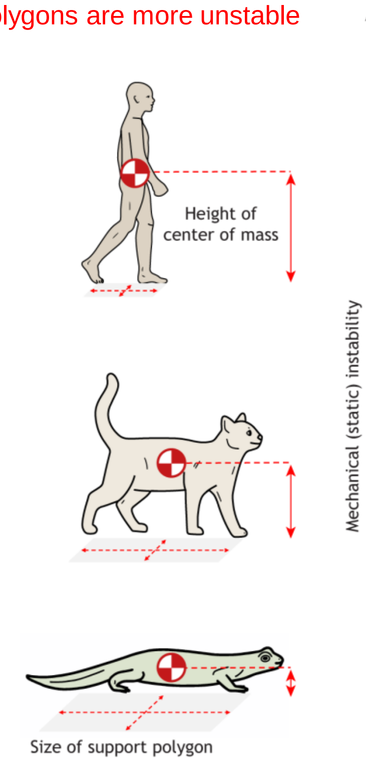
CPGs- feedback-descending modulation

It looks like CPGs are fundamental in lower vertebrates, possibly less so in higher vertebrates.

Locomotion that is **mechanically instable** requires **more sensing** and **more sophisticated descending modulation** for posture control and feet placement



Animals with high center of mass and small support polygons are more unstable

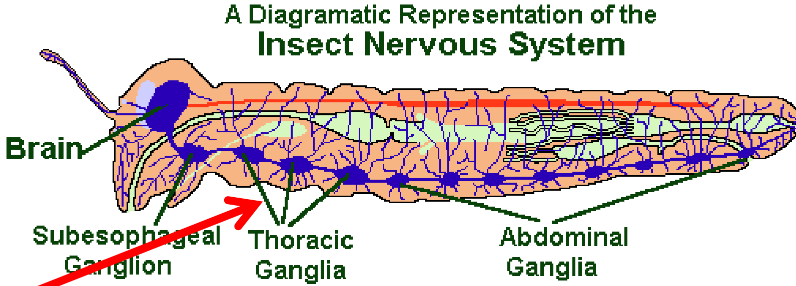


Support polygon: polygon connecting the points of contact with the ground

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

Invertebrate vs vertebrate nervous systems

- The overview we have made so far was for vertebrate animals.
- The nervous systems of invertebrates varies quite a bit depending on the species (e.g. from jelly fish, worms, insects, octopus,…)
- The insect nervous system is organized in a distributed fashion with several *ganglia*



http://www.earthlife.net/insects/anatomy.html

- **CPGs are located in the thoracic ganglia**
- Some insects (e.g. the cockroach) walk for ever when the brain is removed

Today

Topics:

- Biomechanics of animal locomotion
- Locomotion control in animals
- **Locomotion of the lamprey**
- Modeling the lamprey locomotor system

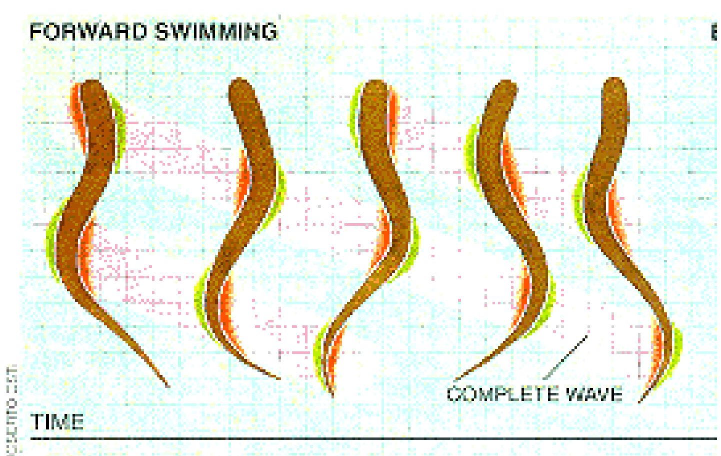
Why the lamprey?

Lamprey: one of the most primitive vertebrates

(relatively) simple anguiliform swimming

Movie by J.T. Buchanan

Has been studied in detail by neurobiologists



Good source of inspiration for a swimming robot

A lamprey robot

A. Crespi

A. Guignard

9.5 cm

Power board

Controller

Crespi A. *et al*, Robotics and Autonomous Systems, 2004.

Crespi A. *et al*, ICRA2005, Ijspeert and Crespi, ICRA 2007

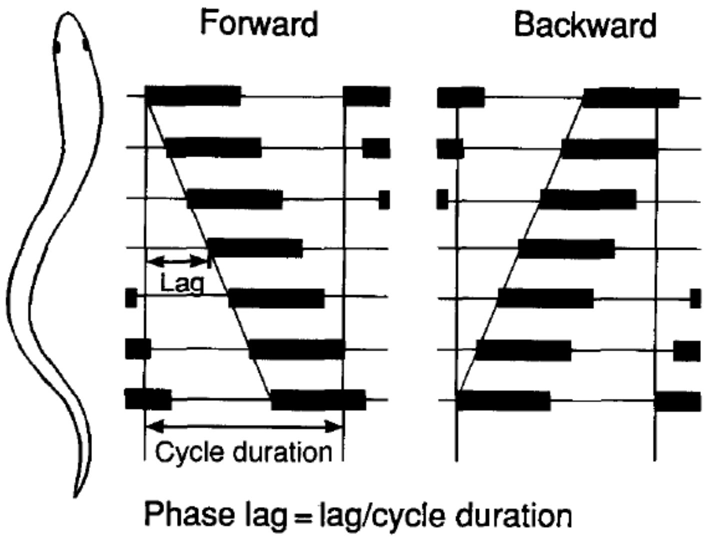
Characteristics of lamprey locomotion

- Traveling wave, with a **constant phase lag along the spinal cord**

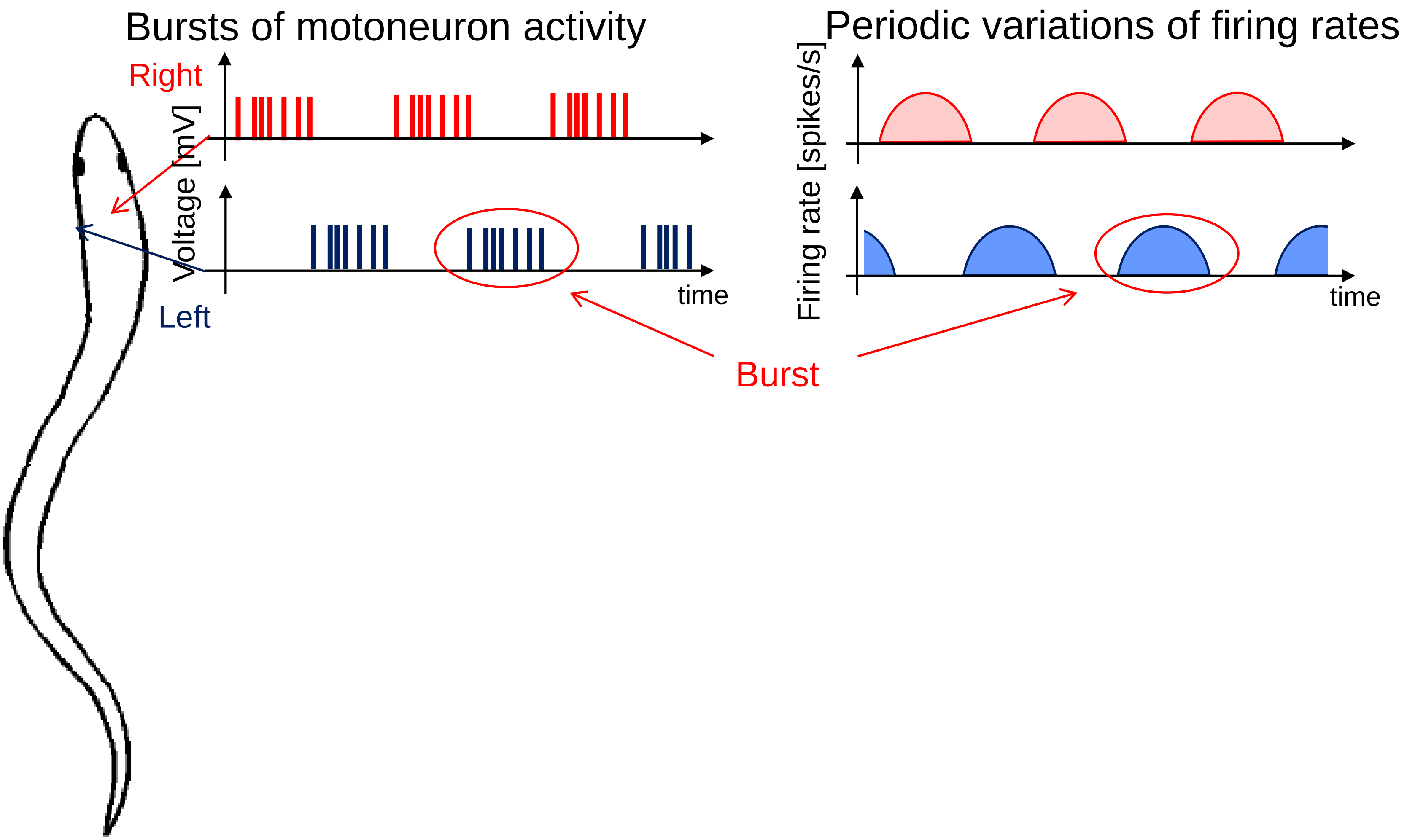
- The **relative phase lag between head and tail is usually 100%** for any frequency. In other words, the body always makes one complete « S » shaped undulation

- **Large frequency range** from 0.25 to 10.0 Hz

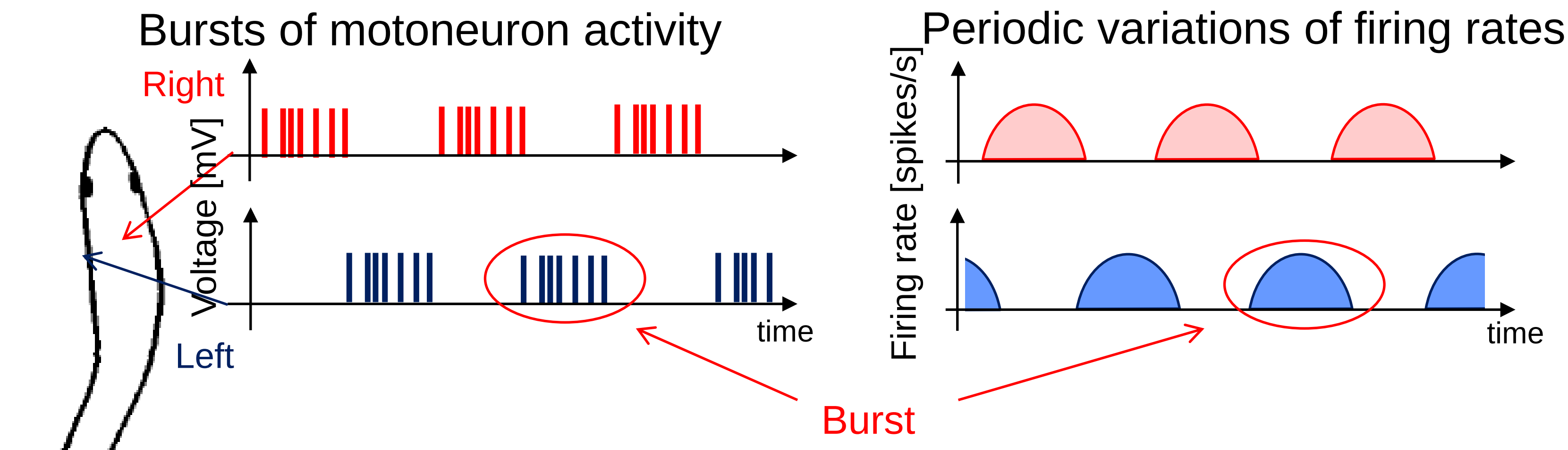
- The lamprey can swim backward by sending the traveling wave from tail to head



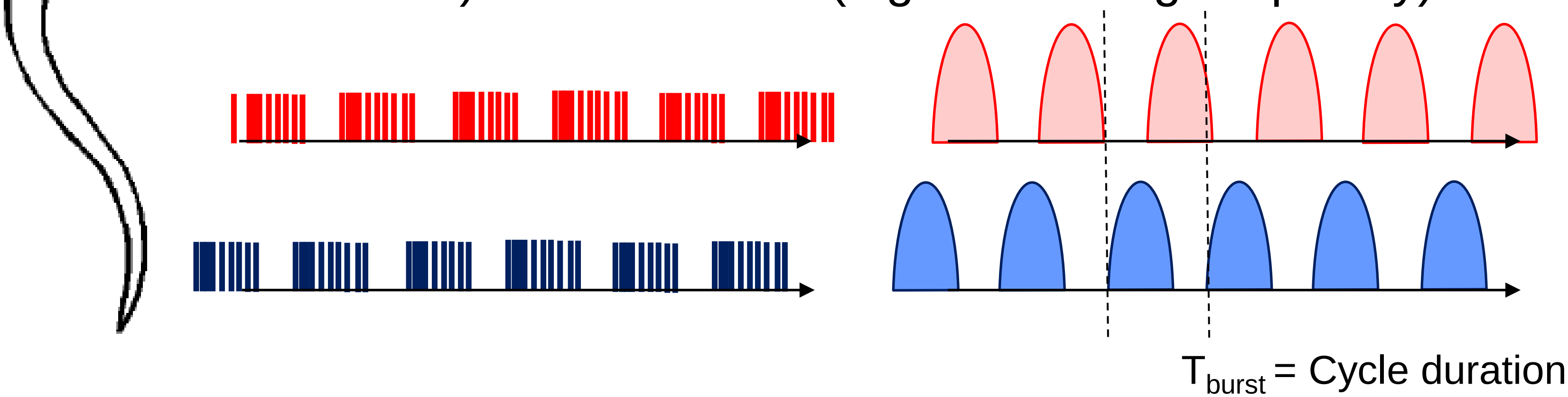
Antiphase left-right bursts



Antiphase left-right bursts



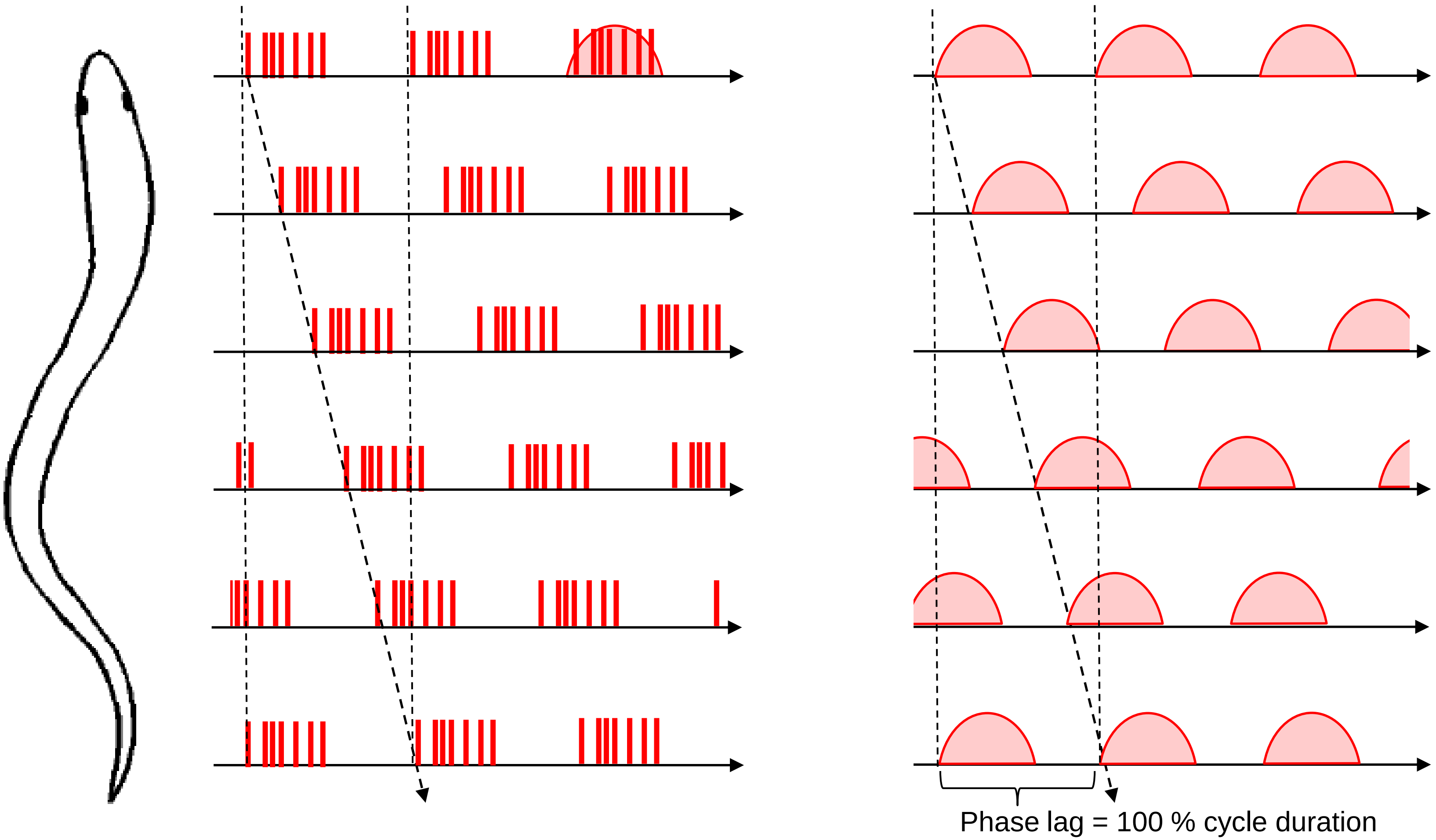
Faster swimming: **bursts have higher amplitude** (higher firing rates) and **are faster** (higher bursting frequency)



The **burst frequency** is the swimming frequency (1/cycle duration)

Traveling waves

Bursts of motoneuron activity | Periodic variations of firing rates

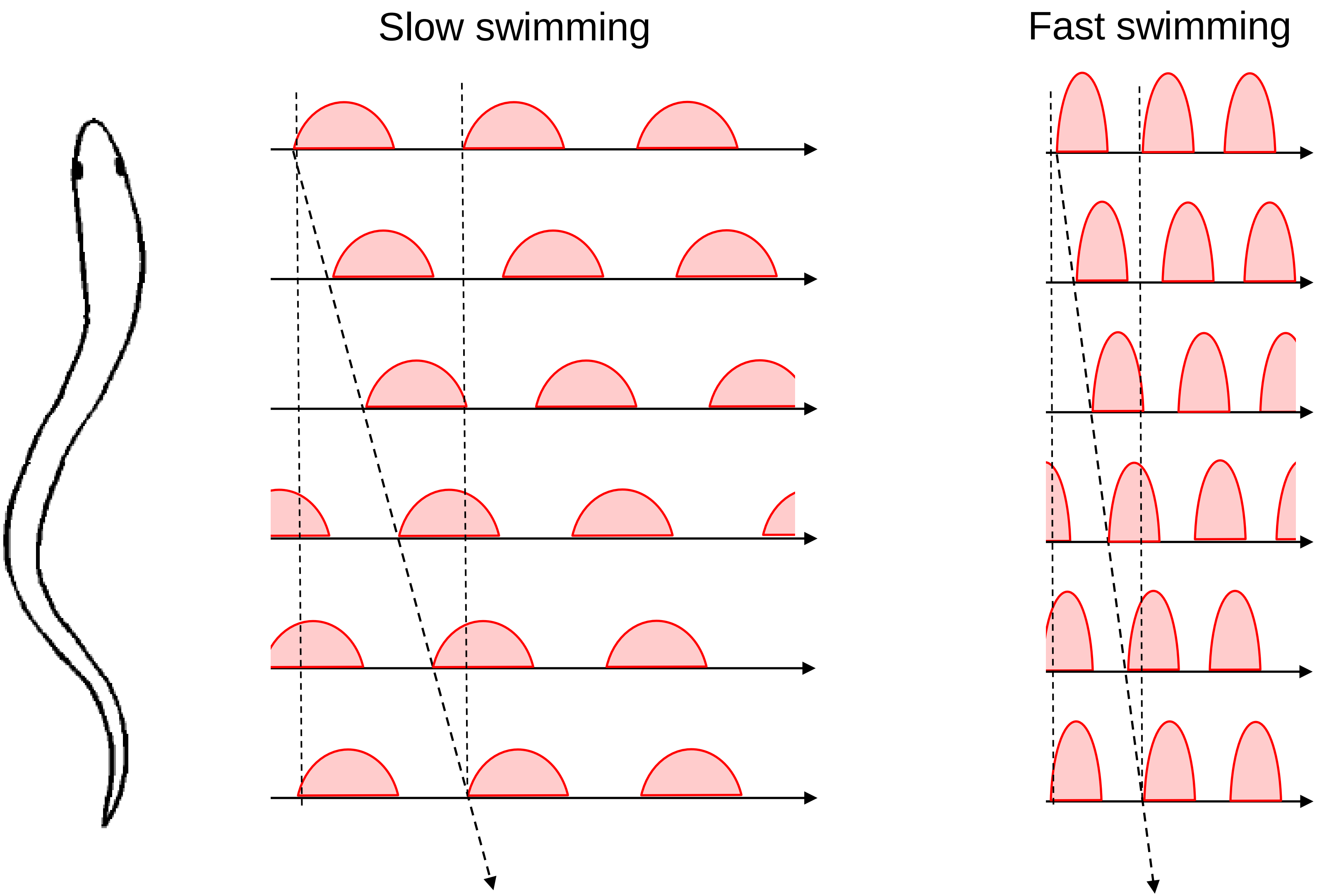


Approx. constant 1% relative phase lag between neighbor segments

100% relative phase lag from head to tail

wavelength = one body length

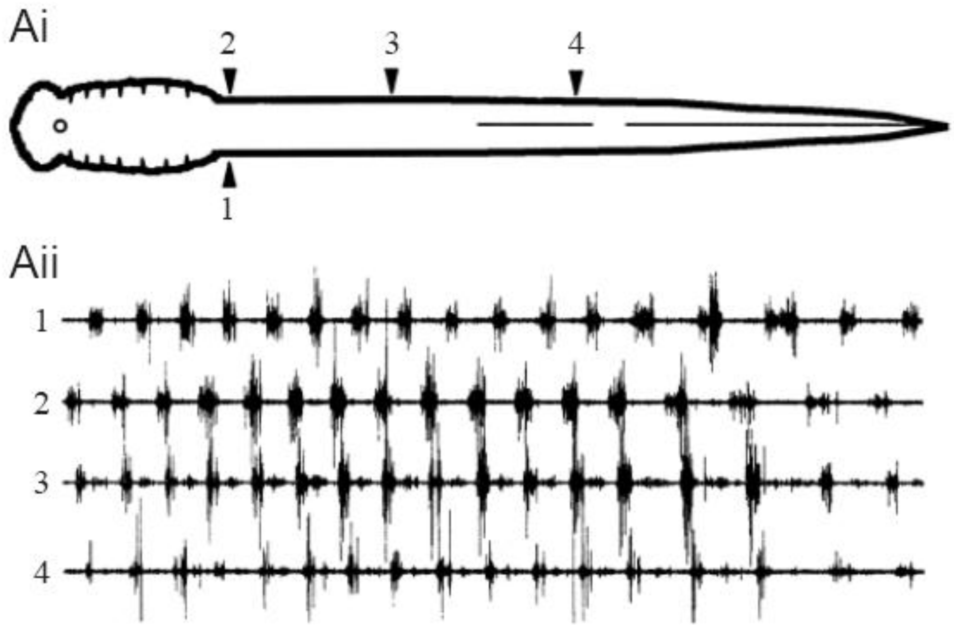
Traveling waves



The frequency changes, but the **relative phase lag** (and hence the wavelength) **is constant**

Characteristics of lamprey locomotion

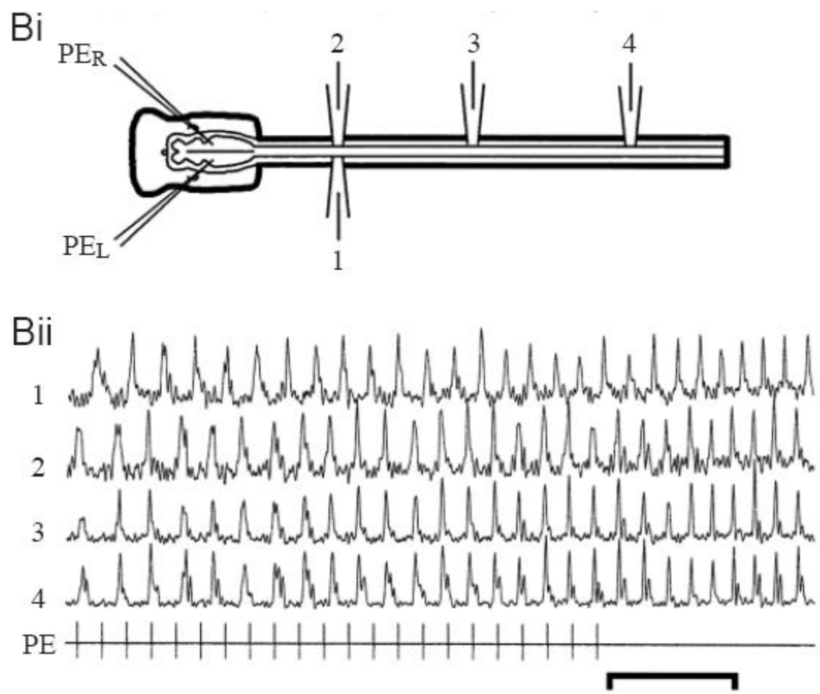
- The traveling wave can be recorded with **electromyographs (EMGs), i.e. recordings of muscle activity**



Boyd and McClellan, the Journal of Experimental Biology 2002

Characteristics of lamprey locomotion

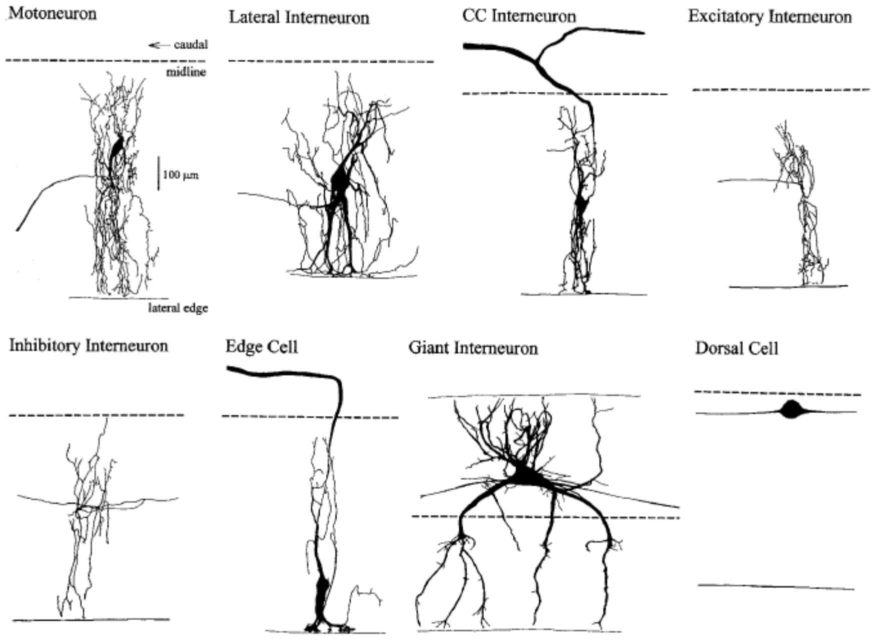
- The isolated spinal cord of the lamprey can be maintained in vitro for several days
- **Fictive swimming**: the CPG can be activated with chemicals (NMDA)
- Neural activity of the CPG can be measured at the ventral roots



Boyd and McClellan, the Journal of Experimental Biology 2002

Characteristics of lamprey locomotion

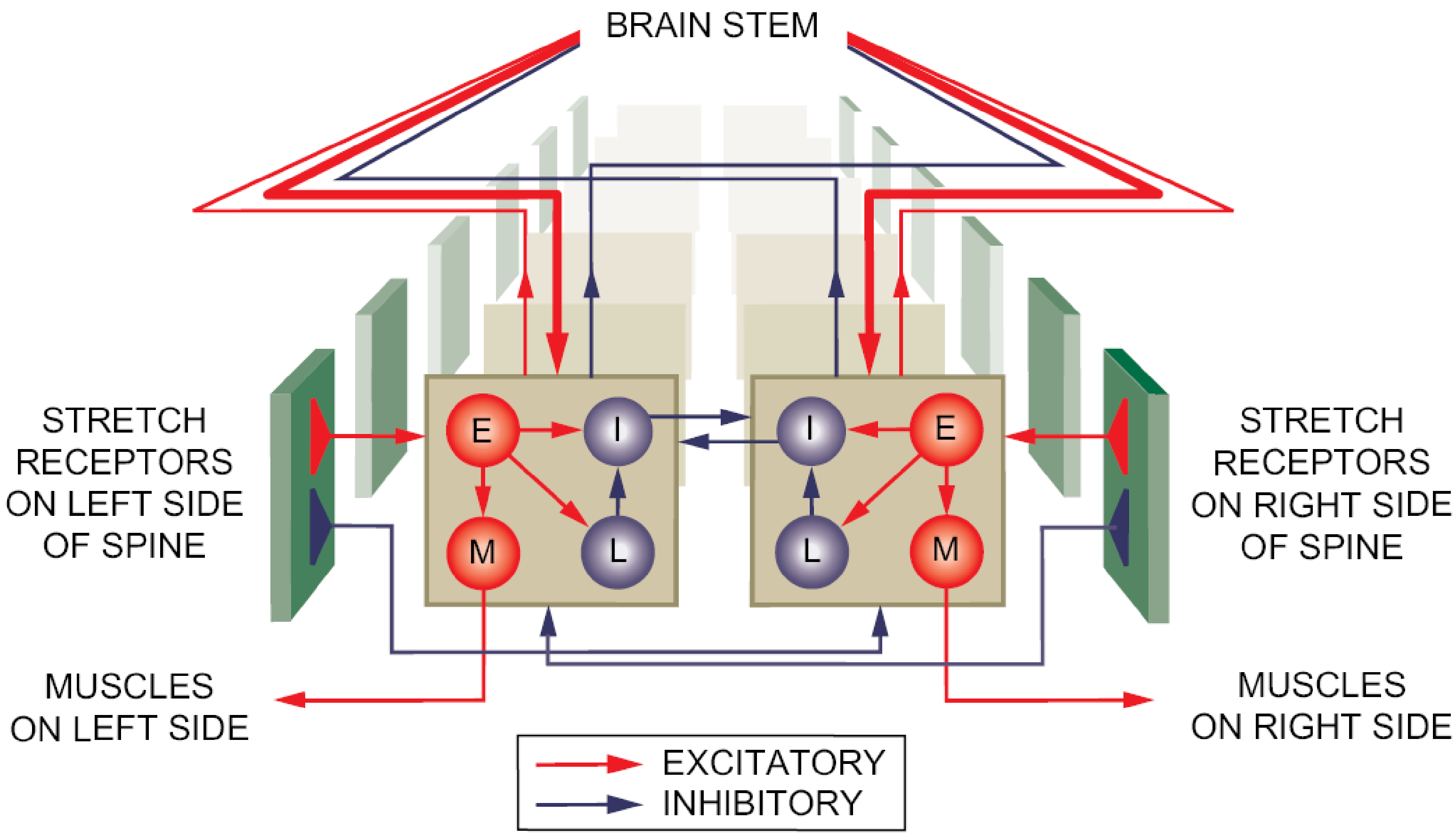
- The spinal cord is composed of approximately 100 segments
- Any isolated part (up to a single segment) can be made to oscillate
  ➔ the **generation of oscillation is distributed**
- Anatomical and intracellular recordings have given insights about the neuronal basis of rhythm generation



Buchanan, Prog. Neurobiology, 2001

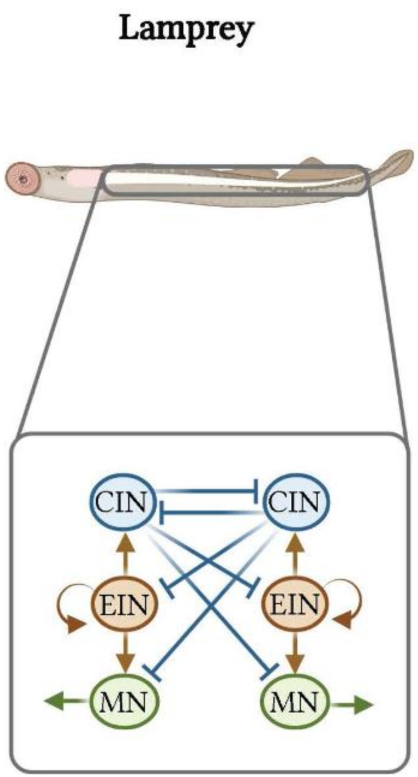
The lamprey swimming network

Conceptual model by Sten Grillner (Grillner et al, Sci. Am. 1996)



Lamprey and Zebrafish - Similarities

The segmental organization is quite similar
(distributed rhythm generation)



Segmental organization

100 segments | 32 segments

Both have **ipsilateral recurrent excitation**

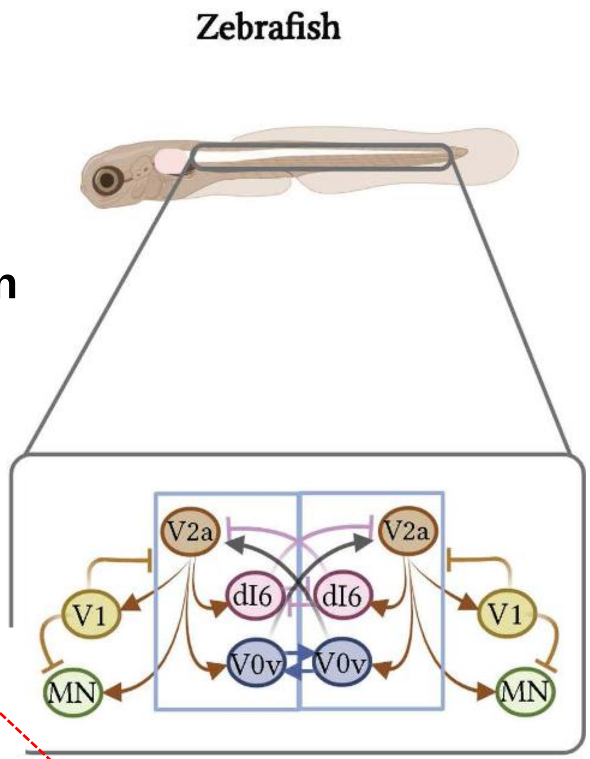
EIN = V2a

Both have **commissural inhibition**

CIN = dI6 (V0d)

Both have **direct (spinal) stretch feedback to the CPG**

Edge Cells = ILP Neurons



Note: compared to the previous slide, LIN interneurons are not shown here

Different names for the same types of neurons

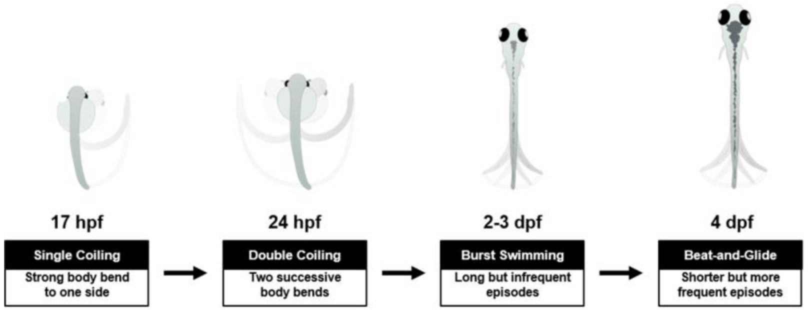
1. S. Grillner and A. El Manira, "Current Principles of Motor Control, with Special Reference to Vertebrate Locomotion," *Physiological Reviews*, vol. 100, no. 1, pp. 271–320, Jan. 2020
2. A. C. Wilson and L. B. Sweeney, "Spinal cords: Symphonies of interneurons across species," *Front. Neural Circuits*, vol. 17, p. 1146449, Apr. 2023.
3. Grillner, Sten, Thelma Williams, and Per-Åke Lagerbäck. "The edge cell, a possible intraspinal mechanoreceptor." *Science* 223.4635 (1984): 500-503.
4. L. D. Picton *et al.*, "A spinal organ of proprioception for integrated motor action feedback," *Neuron*, vol. 109, no. 7, pp. 1188-1201.e7, Apr. 2021

Lamprey and Zebrafish - Differences

The **zebrafish network** undergoes a **developmental switch**[1] (and not the lamprey).

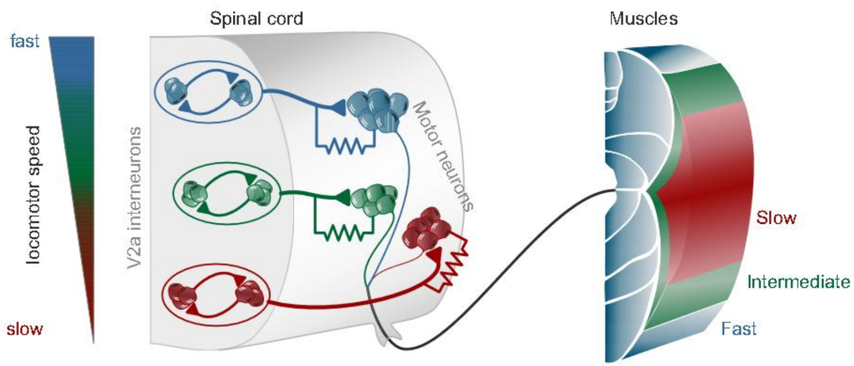
Different network architectures between larval and adult stages

Different locomotion patterns: first coiling, then **beat-and-glide** during larval stage, then **continuous swimming** as an adult



The **(adult) zebrafish network** presents a modular architecture with **different sub-networks for different speeds** (slow, intermediate and fast)[2] .

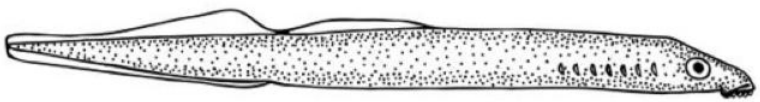
The lamprey has not, with only one sub-network than can cover a large range of frequencies.

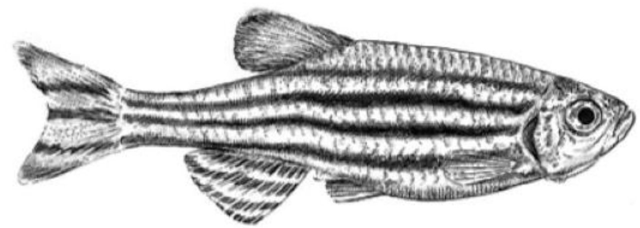


There is **modularity** in types of **muscles, motor neurons, and CPG interneurons in the zebrafish**

1. Y. Roussel, S. F. Gaudreau, E. R. Kacer, M. Sengupta, and T. V. Bui, “Modeling spinal locomotor circuits for movements in developing zebrafish,” p. 35, 2021.
2. S. Grillner and A. El Manira, “Current Principles of Motor Control, with Special Reference to Vertebrate Locomotion,” *Physiological Reviews*, vol. 100, no. 1, pp. 271–320, Jan. 2020

Lamprey and Zebrafish - Differences



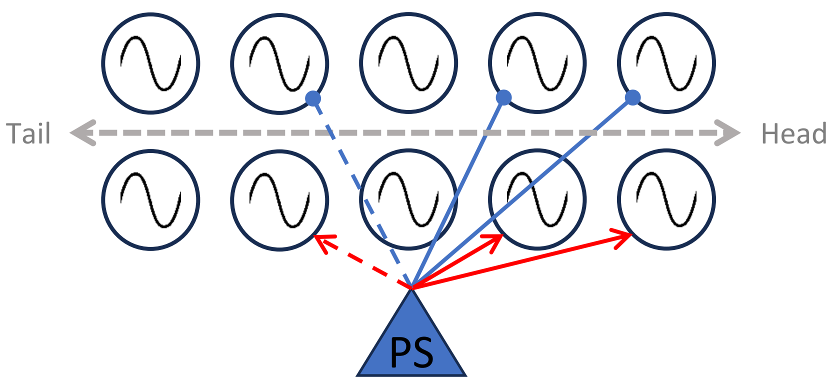


Different proprioceptive (stretch) sensory feedback connections[1,2,3,4]

Inhibition

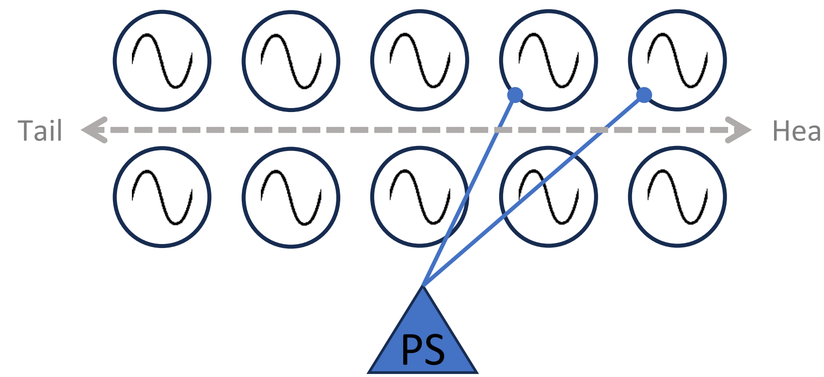
Excitation

The connectivity from the stretch sensors is more complicated in the lamprey



Commissural, Inhibitory[1,2] + Ipsilateral, Excitatory[1,2]

Ascending (mostly)[2,3] + Descending[2]



Commissural, Inhibitory[4]

Ascending (only)[4]

1. G. Viana Di Prisco *et al.*, “Synaptic effects of intraspinal stretch receptor neurons mediating movement-related feedback during locomotion,” *Brain Research*, vol. 530, no. 1, pp. 161–166, Oct. 1990
2. Grillner, Sten, Thelma Williams, and Per-Åke Lagerbäck. "The edge cell, a possible intraspinal mechanoreceptor." *Science* 223.4635 (1984): 500-503.
3. Rovainen, CARL M. "Effects of groups of propriospinal interneurons on fictive swimming in the isolated spinal cord of the lamprey." *Journal of neurophysiology* 54.4 (1985): 959-977.
4. L. D. Picton *et al.*, “A spinal organ of proprioception for integrated motor action feedback,” *Neuron*, vol. 109, no. 7, pp. 1188-1201.e7, Apr. 2021

Today

Topics:

- Locomotion control in animals
- Locomotion of the lamprey
- **Modeling the lamprey locomotor system**

Four levels of modeling

Analytical models of oscillators

Numerical models of nonlinear oscillators

Connectionist neural network models

Biophysical neural network models

abstract

detailed

Oscillator models

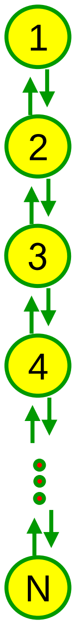
- Oscillator models have been useful to get a better understanding of:
  - How **traveling waves** are generated along the spinal cord
  - How they can be modulated to **go backwards**
  - How **sensory feedback** can entrain the CPG oscillations

- Important players: P.Holmes, R.Rand, N. Kopell, B. Ermentrout, T. Williams,…

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:

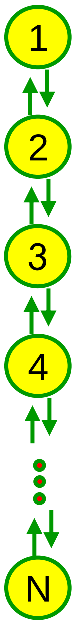
1. **Conduction delays** in the couplings
2. **Differences in intrinsic frequencies**
3. **Asymmetries in the coupling** between segments along the chain
4. **Sensory feedback loops** (effects of the biomechanics of swimming).



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

Hypothesis 1: traveling waves are due to conduction delays in the couplings

- This explanation is unlikely because **conduction delays are relatively constant** in axons, while the **time lags between segments vary significantly** to maintain the same phase lag at different frequencies



Time lag

Frequency,

Ranges from 0.25 to 10Hz

$$\Delta\phi_{ij} = \frac{\Delta t_{ij}}{T} = \Delta t_{ij}\,\omega$$

Period

Phase lag

(stays constant, approx at 1%)

- The other hypotheses will be tested with coupled phase oscillator models

Modeling steps

1. **Questions to be addressed**:

   How are traveling waves generated in the spinal cord?

   How is a constant phase lag maintained along the body?

2. **Important quantities**:

   Bursting frequency, phase lags between segments

3. **Level of abstraction**:

   Phase oscillators

4. **Assumptions**:

   See next

5. **Test the model**: see next

6. **Validation**: generation of traveling waves, but no constant phase lag (see next)

7. **Suggestion of new biological experiments**:

   Changing intrinsic frequencies, mechanical manipulation, …

Analytical analysis of chain of oscillators

- **Phase oscillator model by R. Rand, A. Cohen, and P. Holmes (Cohen, Holmes, Rand 1982, J. Math Biol. 13, 345-369)**

- **Phase oscillator**: abstract oscillator model in which effects of radius are ignored (e.g. Hopf oscillator without taking radius into account):

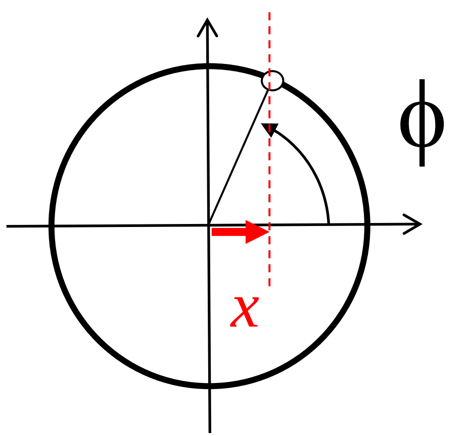
$$\frac{d\phi_i}{dt} = \omega_i + h(\phi_{i-1}, \phi_i, \phi_{i+1})$$

ϕ_i : (upper case Phi) Phase of oscillator i

ω_i : Intrinsic frequency of oscillator i

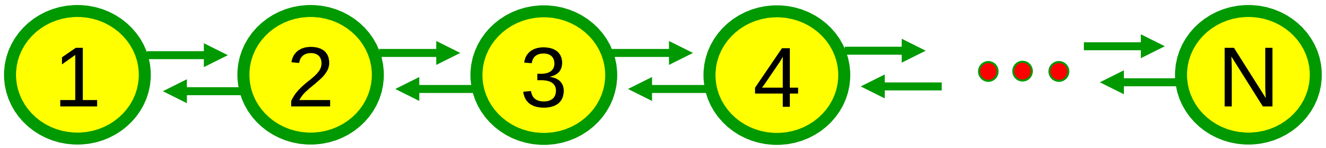
$h(\phi_{i-1}, \phi_i, \phi_{i+1})$: Coupling function

$x_i = A_i \cos(\phi_i)$: Oscillating output



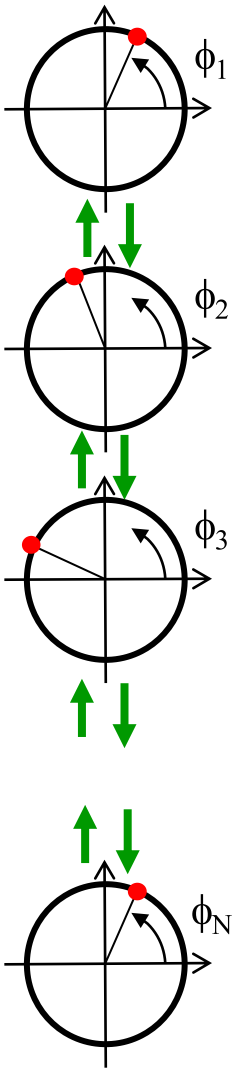
Analytical analysis of chain of oscillators

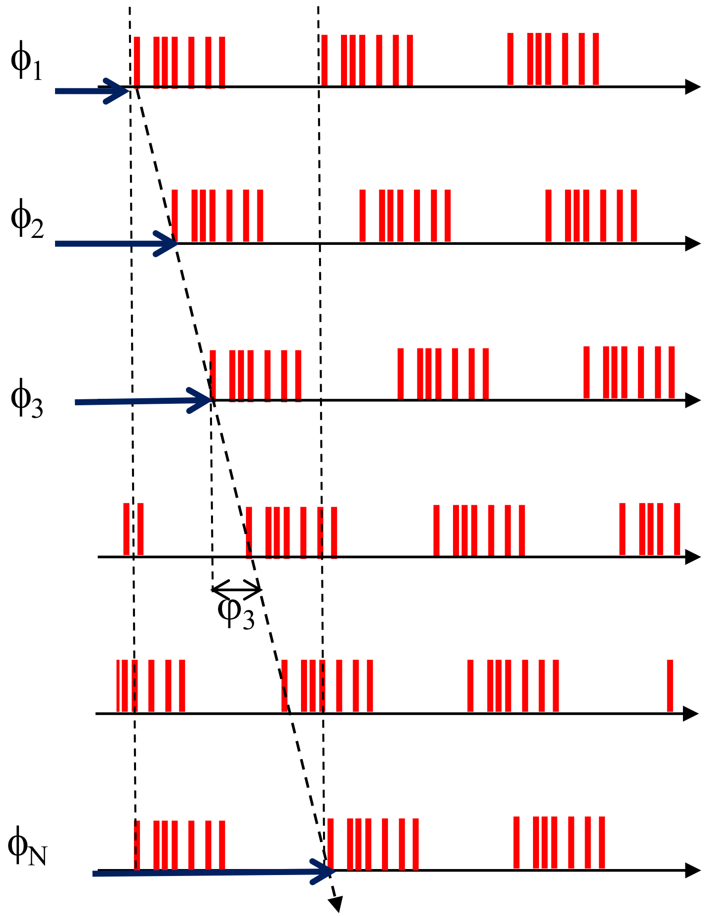
- Lamprey CPG modeled as a **chain with nearest neighbor coupling**:



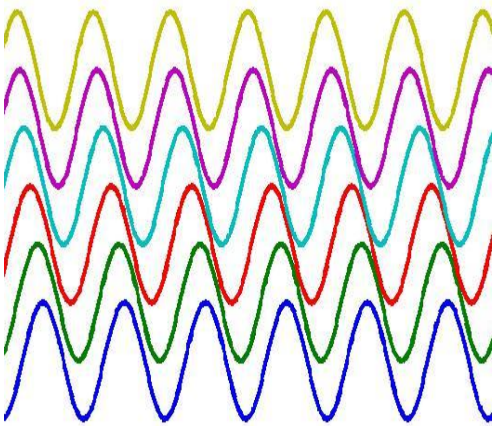
- **Assumptions/idealizations** compared to the real animal:
  - Single oscillator represents the activity of a whole oscillatory center (> 10'000 neurons)
  - Single chain instead of a (left-right) double chain
  - Only nearest neighbor coupling
  - All oscillators are identical from head to tail

Analytical analysis of chain of oscillators





$$x_i = A_i \cos(\phi_i)$$



We are interested in the **phase differences**:

$$\varphi_i = \phi_i - \phi_{i+1}$$

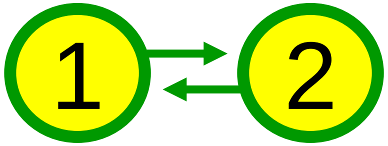
φ : (Lower case Phi)

Do they converge to a **constant value over time**? (synchronization)

Are they **constant between neighbors**? (lamprey-like swimming)

Analytical analysis of chain of oscillators

- Predicting the phase difference between two oscillators

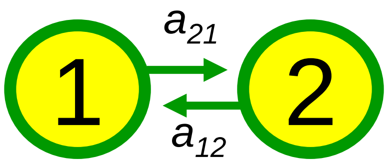


- First example: Let's assume a coupling that (1) depends only on the difference of phase between the oscillators, (2) has no effect if the two oscillators are in phase, and (3) is periodic. For instance

$$h(\phi_{i-1}, \phi_i, \phi_{i+1}) = a_{i,i+1} \sin(\phi_{i+1} - \phi_i)$$

Analytical analysis of chain of oscillators

- Predicting the phase difference between two oscillators



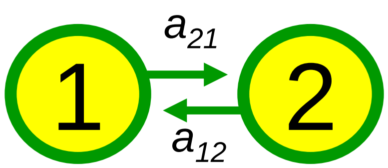
$$h(\phi_{i-1}, \phi_i, \phi_{i+1}) = a_{i,i+1} \sin(\phi_{i+1} - \phi_i)$$

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

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

Analytical analysis of chain of oscillators

- Predicting the phase difference between two oscillators



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

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

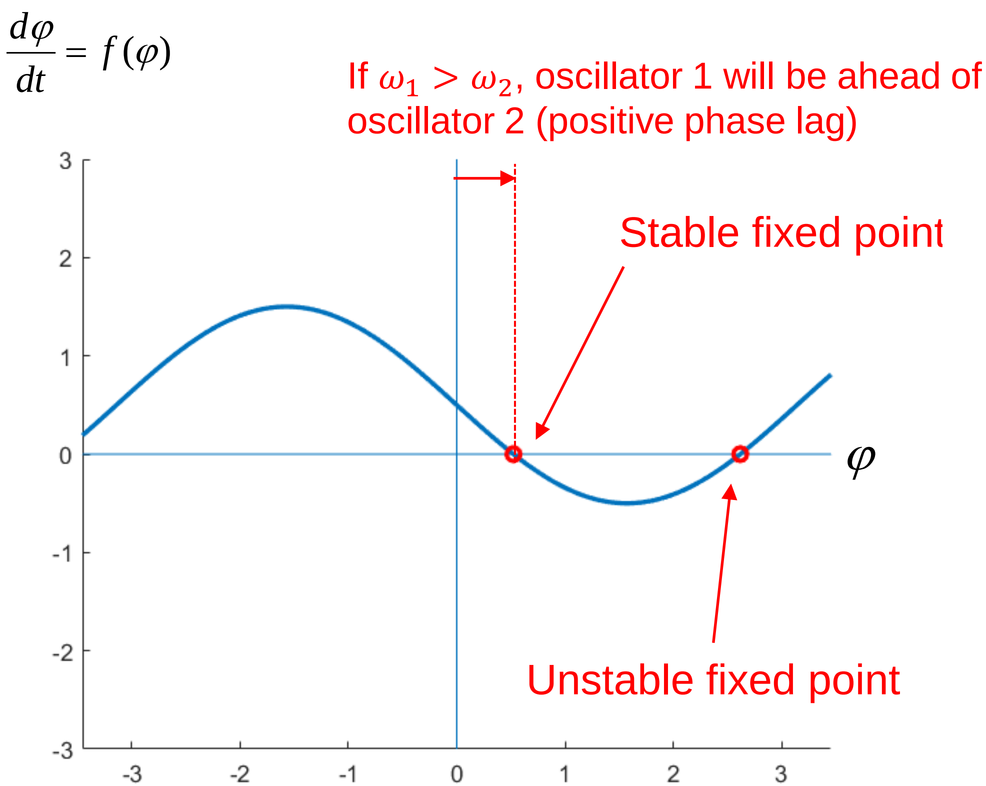
$$\frac{d\varphi}{dt} = (\omega_1 - \omega_2) - (a_{12} + a_{21})\sin(\varphi)$$

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

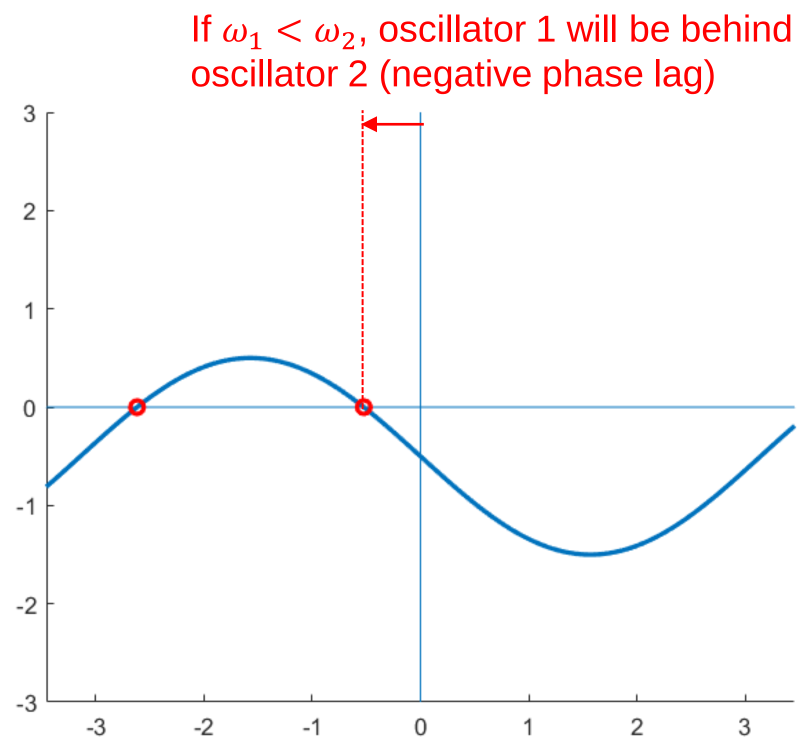
Analytical analysis of chain of oscillators

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

Depending on the parameter values, this function can have several fixed points:



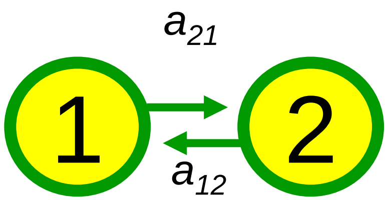
$\omega_1 = 1.5$
$\omega_2 = 1.0$
$a_{12} = a_{21} = 0.5$



$\omega_1 = 0.5$
$\omega_2 = 1.0$
$a_{12} = a_{21} = 0.5$

Analytical analysis of chain of oscillators

Finding the fixed points



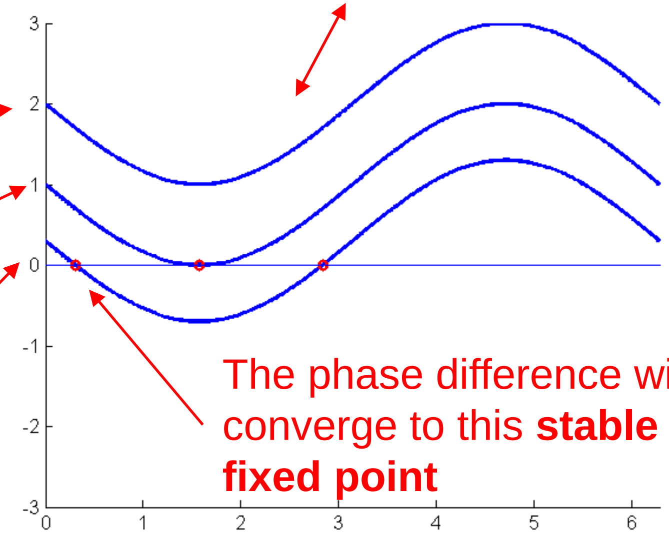
$$\frac{d\varphi}{dt} = 0 \quad \Rightarrow \quad \tilde{\varphi} = \arcsin\left(\frac{\omega_1 - \omega_2}{a_{12} + a_{21}}\right)$$

no fixed point if $\left|\frac{\omega_1 - \omega_2}{a_{12} + a_{21}}\right| > 1$

one fixed point if $\left|\frac{\omega_1 - \omega_2}{a_{12} + a_{21}}\right| = 1$

two fixed points if $\left|\frac{\omega_1 - \omega_2}{a_{12} + a_{21}}\right| < 1$

The phase difference increases all the time. The oscillators are said to ***drift***.



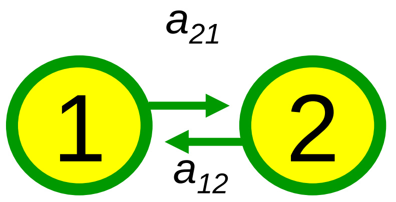
The phase difference will converge to this **stable fixed point**

Matlab example:
coupled_phase_oscillators

What is the resulting frequency?

- When the two oscillators are phase-locked they evolve with the same rate, i.e. have a common ***resulting frequency*** $\boldsymbol{\omega_R}$:

$$\frac{d\phi_1}{dt} = \frac{d\phi_2}{dt} = \omega_R$$



- The **resulting frequency** (the common rate) is the average of the different frequencies weighted by the coupling strengths

At the fixed point (once converged):

$$\frac{d\phi_2}{dt} = \omega_2 + a_{21}\sin(\tilde{\varphi}) = \omega_2 + a_{21}\frac{\omega_1 - \omega_2}{a_{12} + a_{21}} = \omega_R$$

$$\Rightarrow \quad \omega_R = \frac{a_{21}\omega_1 + a_{12}\omega_2}{a_{21} + a_{12}}$$

Important: once synchronized, the oscillators oscillate at a **resulting frequency** ω_R (the common rate), that can be different from their **intrinsic frequency** ω_i

General observations

- There is **no phase locking if the intrinsic frequencies are too different** for a given coupling strength (phases will increase at different rates, and drift compared to each other),

- The **resulting frequency** of a phase-locked system is the **average frequency of the oscillators weighted by the coupling strengths**

- The **oscillator with highest frequency tends to lead** (be in advance of) the others with positive couplings,

- This gives the **possibility to reverse a traveling wave simply by changing which oscillator has the highest intrinsic freq**.

- **Couplings can induce specific phase differences** (in this simple case with the sine coupling only 0 or π if intrinsic frequencies are identical)

Analytical analysis of chain of oscillators

Note:

These observations are **true for many systems of coupled oscillators**!

That makes these **simple models very useful** to characterize much more complex systems (e.g. complex neural networks)

Interesting reading: http://www.scholarpedia.org/article/Synchronization

Difference of intrinsic frequencies

Testing of hypothesis 2 (gradient of intrinsic frequencies) in a chain with symmetric coupling.

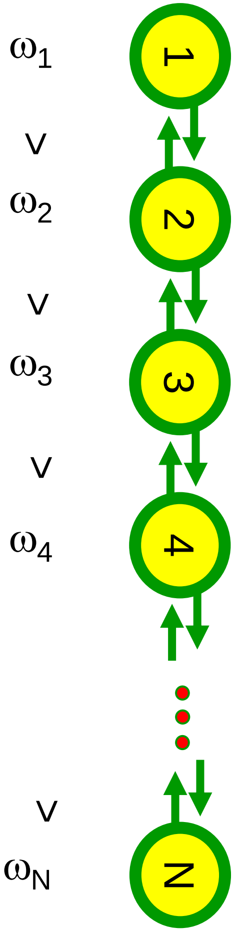
Questions:

- Can a gradient of intrinsic frequencies generate **stable traveling waves**? (yes!)

$$\omega_1-\omega_2=\omega_2-\omega_3=\ldots=e$$

- Are the phase lags between neighboring segments **constant along the spinal cord**? (no!)

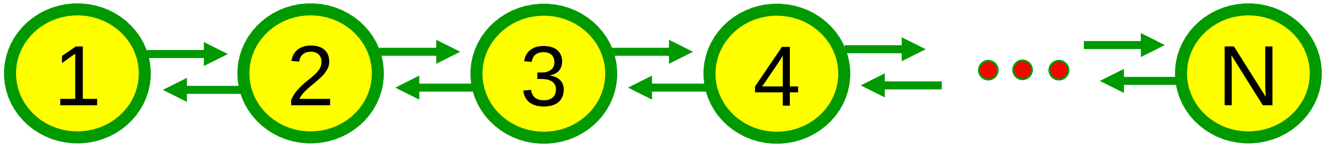
Higher intrinsic frequency in head segment



Lower intrinsic frequency in tail segment

Analytical analysis of chain of oscillators

- Extension of the analysis to a chain of N oscillators



- Assumptions: nearest neighbor coupling, same coupling constants *a*, symmetric coupling

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

$$\frac{d\phi_i}{dt} = \omega_i + a\sin(\phi_{i+1} - \phi_i) + a\sin(\phi_{i-1} - \phi_i)$$

$$\frac{d\phi_N}{dt} = \omega_N + a\sin(\phi_{N-1} - \phi_N)$$

Analytical analysis of chain of oscillators

Introducing the phase differences $\varphi_i = \phi_i - \phi_{i+1}$

This can be expressed in matrix form:

$$\frac{d\vec{\varphi}}{dt} = \vec{\Omega} + \mathbf{A}\vec{S}$$

$$\vec{\varphi} = \begin{bmatrix} \varphi_1 \\ \dots \\ \varphi_{N-1} \end{bmatrix}, \quad \vec{S} = \begin{bmatrix} \sin\varphi_1 \\ \dots \\ \sin\varphi_{N-1} \end{bmatrix}, \quad \vec{\Omega} = \begin{bmatrix} \omega_1 - \omega_2 \\ \dots \\ \omega_{N-1} - \omega_N \end{bmatrix}, \quad A = a\begin{bmatrix} -2 & 1 & & & \\ 1 & -2 & 1 & & \\ & \ddots & \ddots & \ddots & \\ & & 1 & -2 & 1 \\ & & & 1 & -2 \end{bmatrix}$$

Analytical analysis of chain of oscillators

Does the chain phase-lock? We look at $\frac{d\vec{\varphi}}{dt} = \vec{\Omega} + \mathbf{A}\vec{S} = 0$

Solution:

$$\tilde{\vec{\varphi}} \quad \text{such that} \quad \vec{S} = -\mathbf{A}^{-1}\vec{\Omega}$$

No solution exists if any of the components of $\mathbf{A}^{-1}\vec{\Omega}$ are larger than unity in absolute value (i.e. the system would drift).

Good news: the matrix A can be inverted in close form.

Analytical analysis of chain of oscillators

Example with 6 oscillators, and **constant frequency difference**,

$\omega_1 - \omega_2 = \omega_2 - \omega_3 = \ldots = e$:

e: difference of int. freq.

a: coupling strength

$$A^{-1} = -\frac{1}{6a}\begin{bmatrix} 5 & 4 & 3 & 2 & 1 \\ 4 & 8 & 6 & 4 & 2 \\ 3 & 6 & 9 & 6 & 3 \\ 2 & 4 & 6 & 8 & 4 \\ 1 & 2 & 3 & 4 & 5 \end{bmatrix}$$

$$\vec{\Omega} = \begin{bmatrix} e \\ \ldots \\ e \end{bmatrix}$$

Therefore:

$$\begin{bmatrix} \sin\varphi_1 \\ \sin\varphi_2 \\ \sin\varphi_3 \\ \sin\varphi_4 \\ \sin\varphi_5 \end{bmatrix} = \frac{e}{2a}\begin{bmatrix} 5 \\ 8 \\ 9 \\ 8 \\ 5 \end{bmatrix}$$

This system will **phase lock** if:

$$\left|\frac{e}{a}\right| \leq \frac{2}{9}$$

Generalization to N oscillators:

$$\left|\frac{e}{a}\right| \leq \frac{8}{N^2}$$ N even

$$\left|\frac{e}{a}\right| \leq \frac{8}{N^2 - 1}$$ N odd

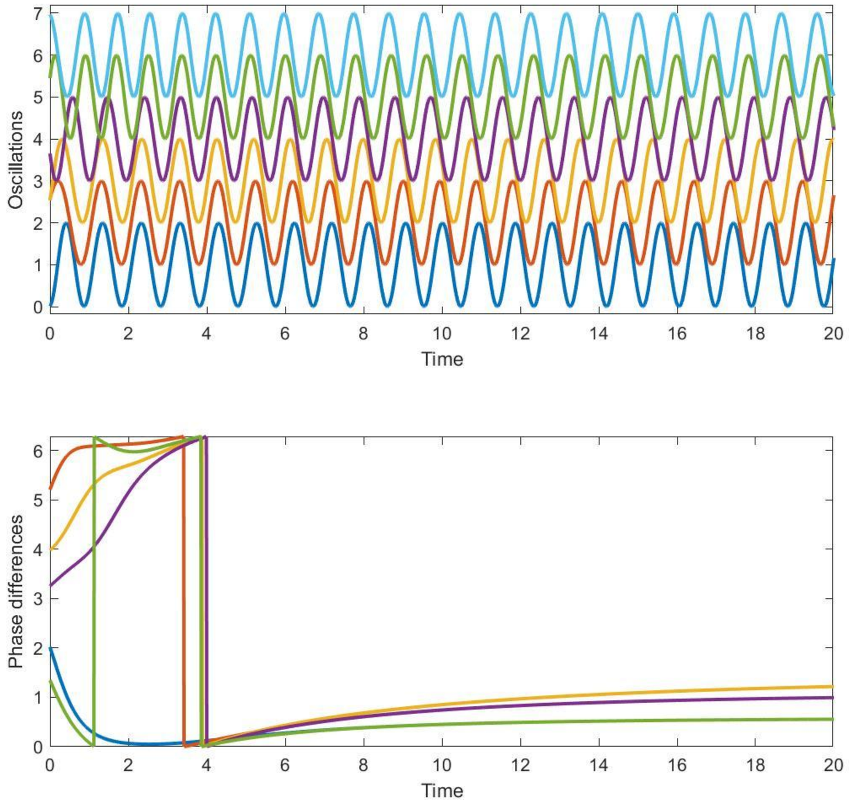
Note: oscillators close to the extremities synchronize “more easily” than in the middle

Analytical analysis of chain of oscillators

Example with 6 oscillators

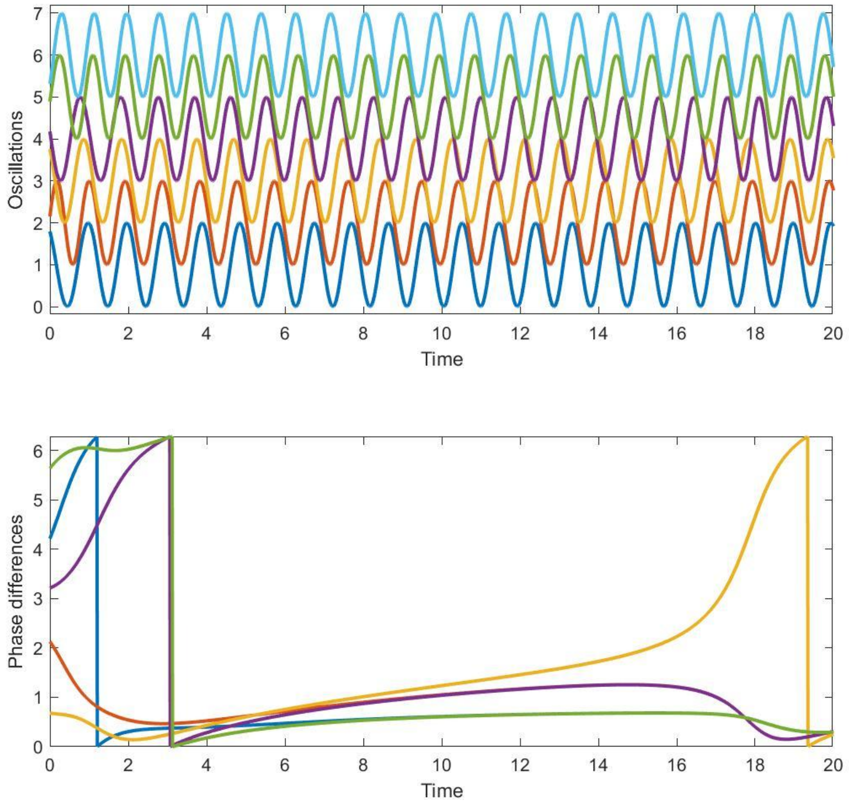
a=1.0,

➔ nice **synchronization**



a=0.7, coupling is too weak.

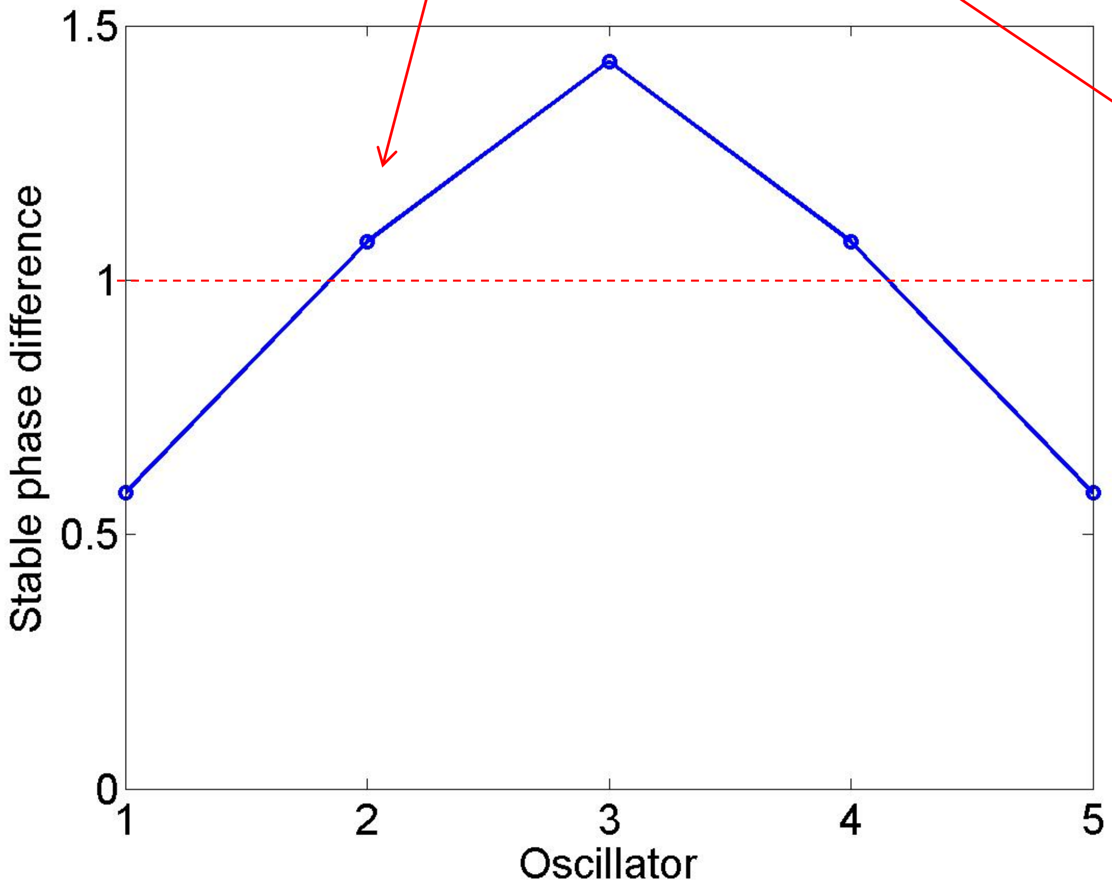
➔ no synchronization, and **drift**



Analytical analysis of chain of oscillators

Example with 6 oscillators e=0.22, a=1.0:

Note: the phase difference is **not constant along the spinal cord** (not the same value everywhere)



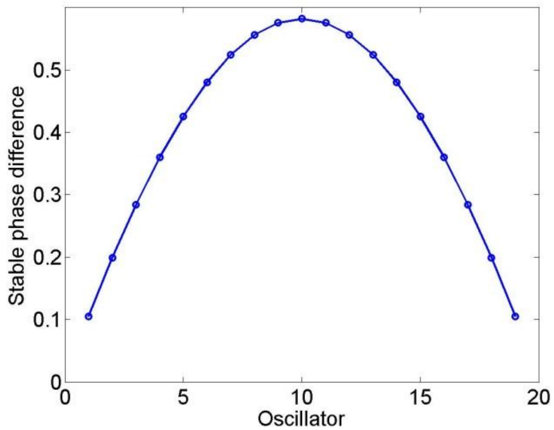
$$\begin{bmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \\ \varphi_4 \\ \varphi_5 \end{bmatrix} = \begin{bmatrix} \arcsin(5e/2a) \\ \arcsin(8e/2a) \\ \arcsin(9e/2a) \\ \arcsin(8e/2a) \\ \arcsin(5e/2a) \end{bmatrix}$$

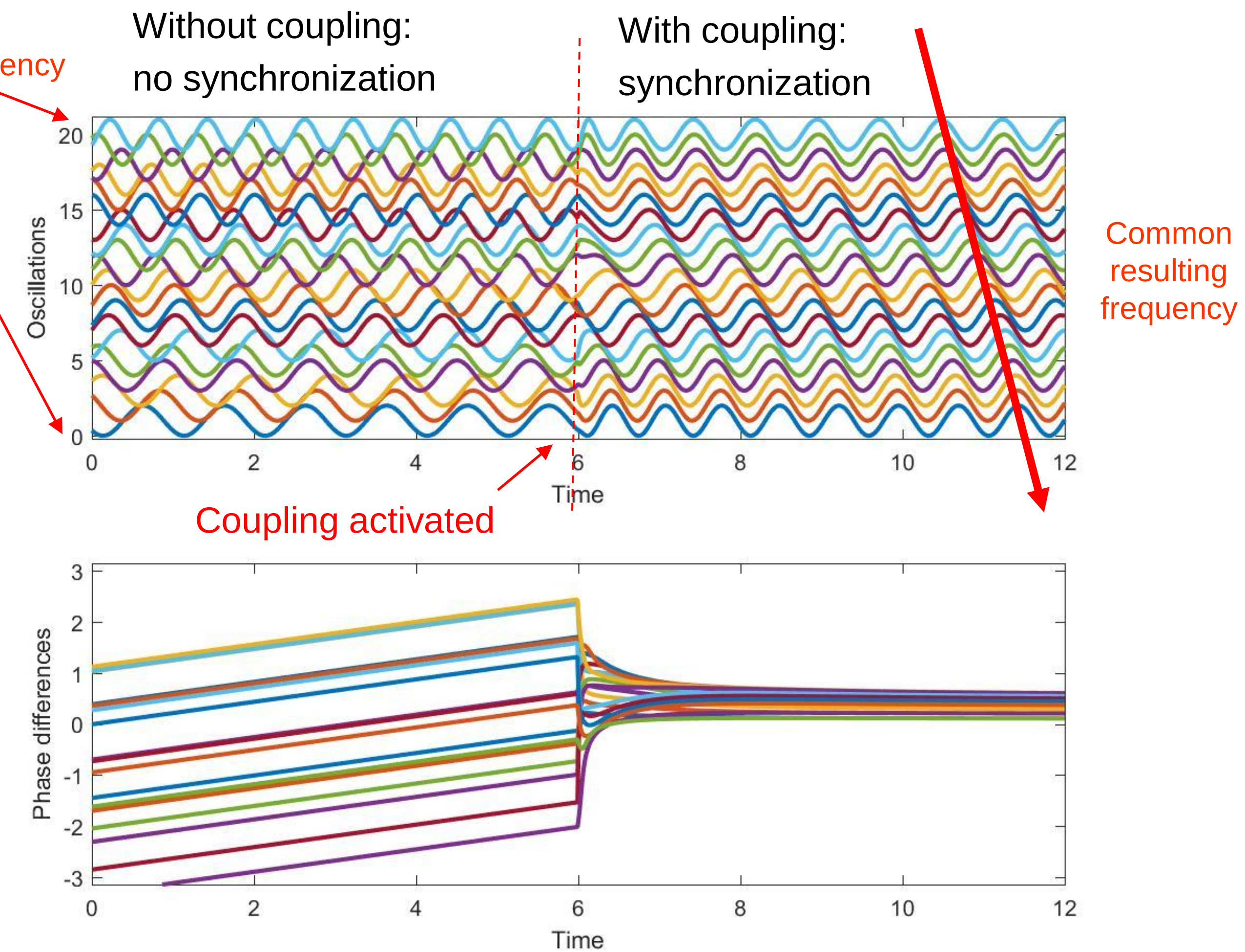
Matlab example:
chain_phase_oscil

Analytical analysis of chain of oscillators

Example with 20 oscillators

Nice traveling wave, but phase lags are not exactly constant along the spinal cord





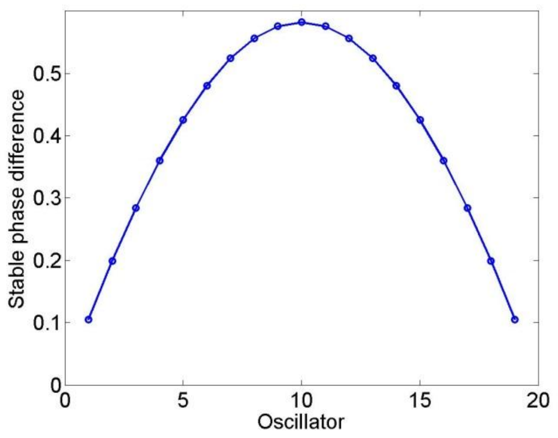
Phase differences increase all the time = **drift**

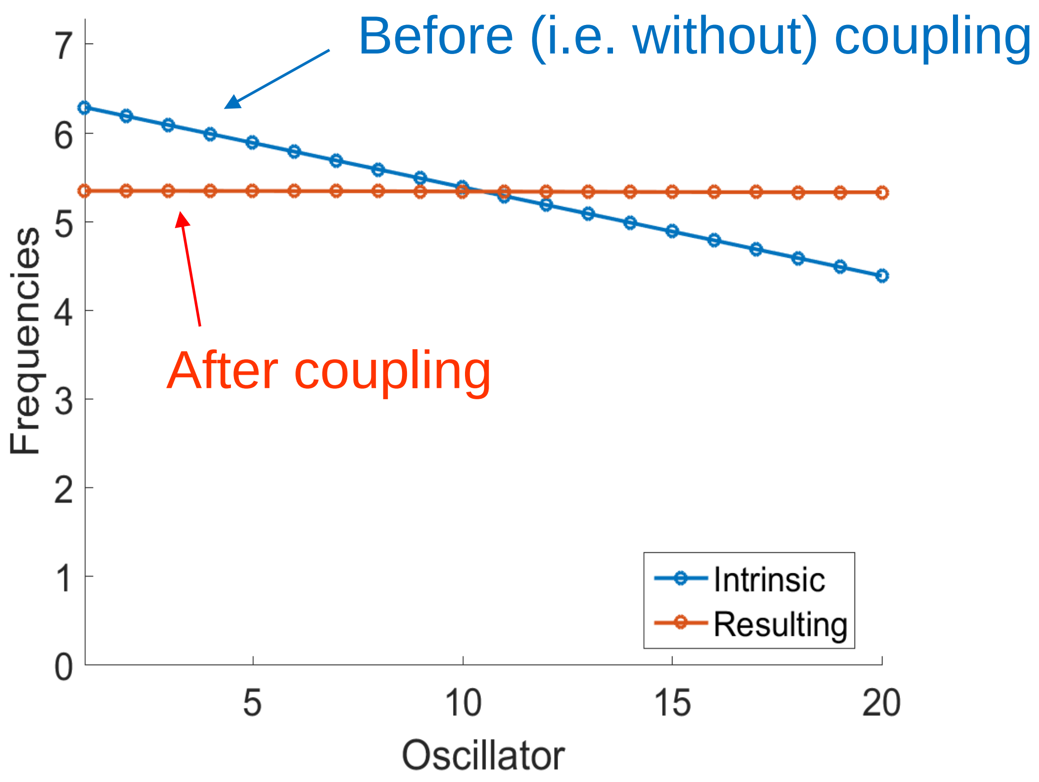
Phase differences reach constants = **synchonisation**

Analytical analysis of chain of oscillators

Example with 20 oscillators

Nice synchronization. Even if all oscillators have different intrinsic frequencies. They converge to the **same resulting frequency**.





Synchronization region, Arnold tongue

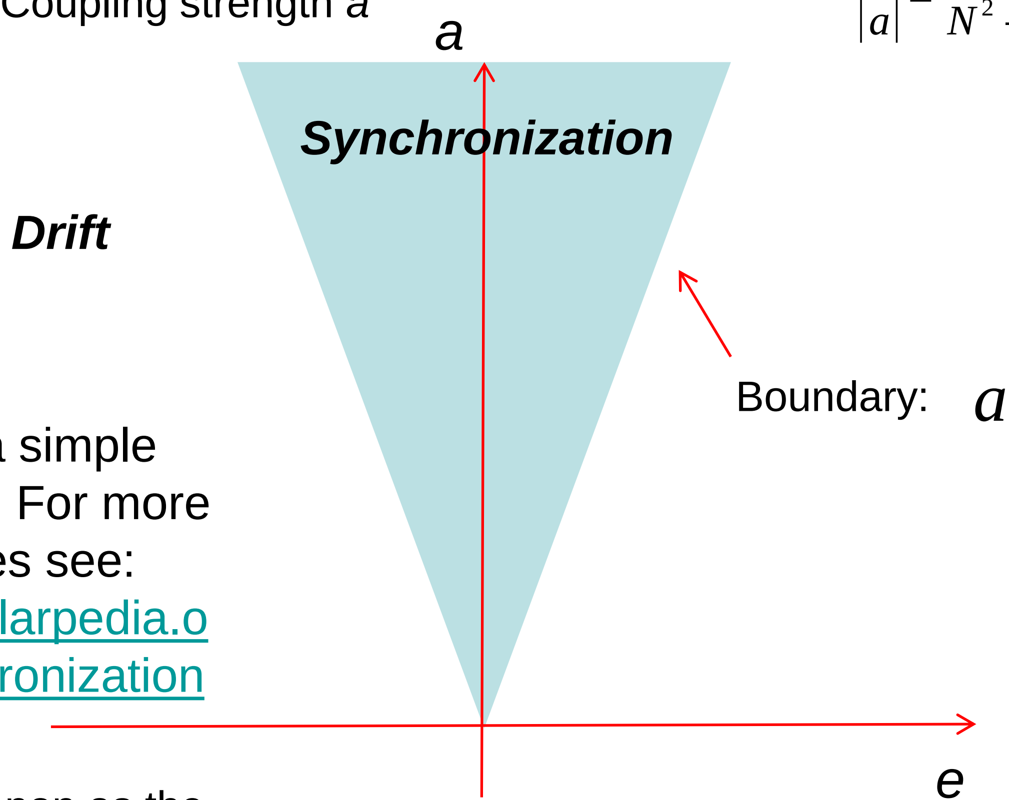
The system will synchronize (phase lock) if the following inequality is satisfied:

Generalization to N oscillators:

$$\left|\frac{e}{a}\right| \leq \frac{8}{N^2} \qquad \text{N even}$$

$$\left|\frac{e}{a}\right| \leq \frac{8}{N^2-1} \qquad \text{N odd}$$

Coupling strength *a*



Boundary: $$a = \frac{N^2}{8} e \qquad \text{N even}$$

Intrinsic frequency difference *e*

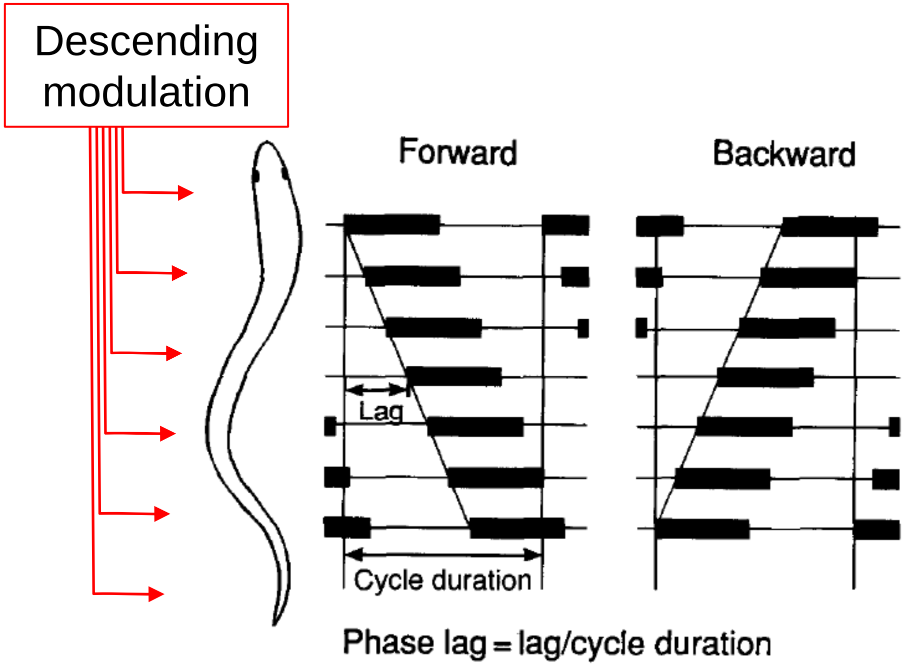
Note: this is a simple **Arnold tongue**. For more complex ones see: http://www.scholarpedia.org/article/Synchronization

Same phenomenon as the **synchronizing metronomes** we have seen in previous lectures

Analytical analysis of chain of oscillators

Note: The model shows that **changing the intrinsic frequency** of some oscillators leads to **changes in the phase lags**.

This can be the **mechanism for backward swimming**. By stimulating more the oscillators at the tail (i.e. by increasing their intrinsic frequency), this could possibly lead to a **reversal of the traveling wave**.



Analytical analysis of chain of oscillators

Conclusion: while this model allows one to explore important questions about the effect of variations of intrinsic frequencies and of coupling, **it is too simple compared to lamprey data:**

1. It **does not produce phase lags that are constant** over the spinal cord
2. And, more importantly, **no systematic variations of intrinsic frequencies have been identified in the lamprey spinal cord.**

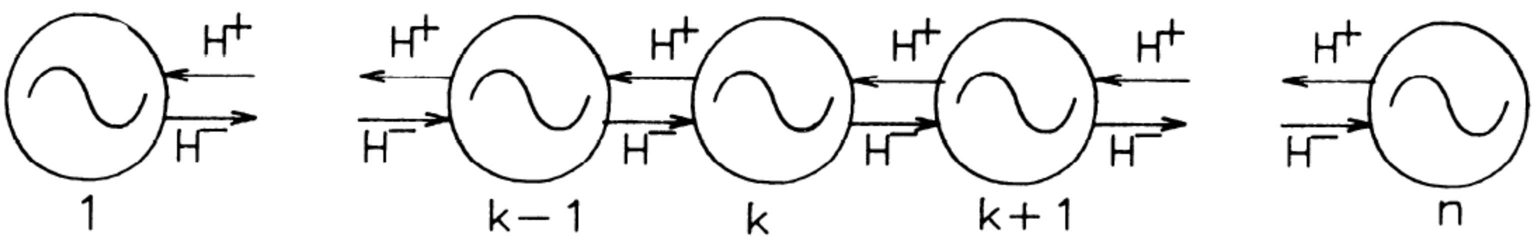
The traveling waves are most likely due to more complex interoscillator couplings (i.e. Hyp. 3), rather than differences of intrinsic frequencies. See next models.

Models by Williams, Sigvardt, Kopell and Ermentrout

Similar to the previous model, except that they use equal intrinsic frequencies for all oscillators and explore **more complex interoscillator couplings**

ascending — descending coupling

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



(Williams et al 1990) Forcing of Coupled Nonlinear Oscillators: Studies of Intersegmental Coordination in the Lamprey Locomotor Central Pattern Generator, J. of Neurophysiology, Vol. 64, No. 3, September 1990.

(Sigvardt and Kopell 1996) Effects of Local Oscillator Frequency on Intersegmental Coordination in the Lamprey Locomotor CPG: Theory and Experiment, J. of Neurophysiology, Vol. 76. No. 6. December 1996.

More complex oscillator models

The papers below present a very nice series of experiments whose results are partly predicted by theory. For instance related to how:

(1) **Mechanical forcing** can lead to entrainment of spinal cord circuits of different lengths

(2) **Influencing the intrinsic frequencies of local oscillators pharmacologically** affects the phase lags in the whole spinal cord

(Williams et al 1990) Forcing of Coupled Nonlinear Oscillators: Studies of Intersegmental Coordination in the Lamprey Locomotor Central Pattern Generator, J. of Neurophysiology, Vol. 64, No. 3, September 1990.

(Sigvardt and Kopell 1996) Effects of Local Oscillator Frequency on Intersegmental Coordination in the Lamprey Locomotor CPG: Theory and Experiment, J. of Neurophysiology, Vol. 76. No. 6. December 1996.

Possible exam questions

- Which general principles underlie the **biomechanics of animal locomotion**?
- What problems does the CNS need to solve for locomotion control? In particular which different types of **redundancies** does it have to handle?
- What is a **central pattern generator**? Which 5 key observations have been made about them?
- What are **useful features of CPGs** in term of locomotion control?

Possible exam questions

- What are the characteristics of **lamprey locomotion**?
- What are similarities and differences between the **lamprey and zebrafish circuits**?
- What are **different possible options to explain a traveling wave** of neural activity in the spinal cord as seen in the lamprey?
- Why can the traveling wave of lamprey swimming **not be explained by conduction delays** in action potentials from head to tail?
- Analyze the **conditions for synchronization** between two phase oscillators
- Compute the **resulting frequency** after synchronization between phase oscillators with different intrinsic frequencies

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

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

- Explain the steps needed to analyze **synchronization in a chain of phase oscillators**
- Discuss **what can and cannot be explained** about lamprey swimming in a chain of oscillators with a **gradient of intrinsic frequencies**.

Your feedback

Teaching activity :	Computational motor control
Teaching given in :	English
Teacher's name :	Ijspeert Auke
Academic year :	2024-2025
Period :	Master semester 2 ; Master semester 4 ; Spring semester
Number of registered students :	96
Number of answers :	15
Teaching activity offered to section(s) :	Robotics ; Computational and Quantitative Biology (edoc) ; Computational biology minor ; Neuro-X ; Robotics, Control and Intelligent Systems (edoc) ; Neuro-X minor ; Life Sciences Engineering ; Microengineering ; Mechanical Engineering
Teaching activity involving many teachers :	No

The running of the course enables my learning and an appropriate class climate [Single option]

Possible answers :	*Nb. answers :*	*In % :*
Strongly agree	10	67
Agree	5	33
Disagree	0	0
Strongly disagree	0	0
No opinion	0	0

Your feedback

Good professor, passionate about his work which make the class pleasant to attend to. Content is very interesting and well presented. **TP on the other hand are long and sometimes a bit too broad**. We often don't know what is asked in the questions. **Lots of work for a 4 credits** due to TPs.
Hope the **beamer** will be back in the next classes
make a break between the two hours
The code from the **labs can sometimes be difficult to use since already so much is coded**. I find it hard sometimes to grasp how some functions are working
The course is interesting and the professor teaches it well ! The **theory we see is not the most useful** thing but not that big of an issue ! :)
Very good lecture. The slides are very well structured and one is able to understand what is going on. Nevertheless, I am not a big fan of the exercises. It **is often unclear what the given code does and where we have to change things**. Additionally, the start of the project is very rough. The given **requirements.txt was wrong and the given code was impossible to run** until one of the students found a solution and posted this solution on the forum. Please fix that for future projects.

End of Lecture

Note: fewer teaching assistants this afternoon and next week because many lab members are at a conference in Canada (Cosyne).

Sorry about this. Please be indulgent/patient!

Thanks!