Computational motor control
Lecture 1

Auke Jan Ijspeert

Content of today's lecture

- Explanation of the **objectives and organization** of the course

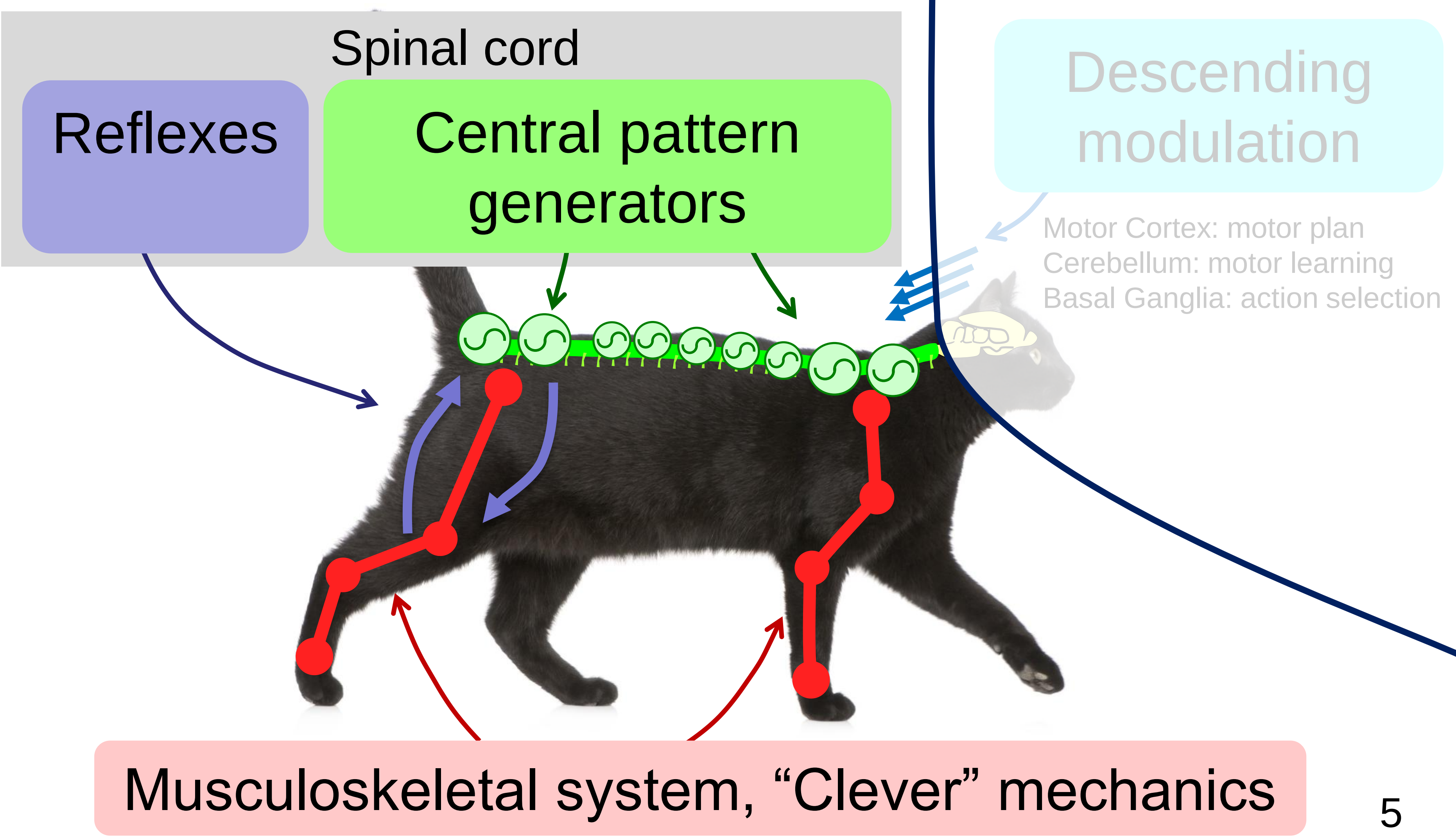
- Overview of the **numerical modeling approach**

- **Overview of the content** of all lectures

The beauty of animal locomotion

https://www.youtube.com/watch?v=CoL8Gtvxfl0

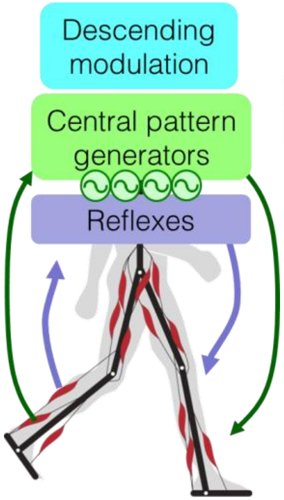
The beauty of animal locomotion

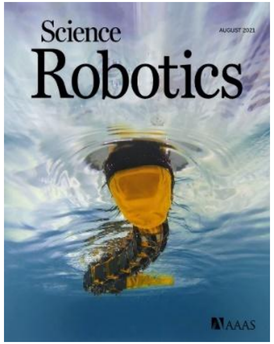

Spinal cord
Reflexes
Central pattern generators
Descending modulation
Motor Cortex: motor plan
Cerebellum: motor learning
Basal Ganglia: action selection
Musculoskeletal system, "Clever" mechanics

Biorobotics Laboratory (Ijspeert)

Robotics

Engineering locomotion





Biology

Healthcare

Understanding locomotion

Assisting locomotion

Goals of the course

- To explore how **numerical simulations can be used to explain *motor control* in biology** (note: *motor control* = control of movements in neuroscience)
- To learn **how to design good numerical models**, and **how to evaluate them**

- To present how inspiration from biology can bring useful contributions to the **new design and control principles for robotics**

- To apply concepts from the lectures to (1) **design and test simple models in Python**, and (2) **develop sensory-motor models applied to a simulated zebrafish**

Implementation

- Lectures every week: Thursday 10:15-12:00 AAC 231
- Support for modeling projects: 13:15-15:00, INF 2
- Video recordings will be made available as much as possible (but try to attend lectures)

- Handouts: copies of slides before each course + additional articles/documents

- Use of Moodle for all course materials, cf http://moodle.epfl.ch

Implementation (continued)

- Practical work:
  (1) Series of **modeling exercises in Python**
  (2) Sensory-motor models of a **zebrafish**

- Teams of three students

- One written report, with different subparts (exploration of swimming gaits, exploration of muscle properties, implementing a controller based on phase oscillators, exploring the role of sensory feedback).

- Final mark: **40% written exam, 60% reports**

- **Written exam** at the end of the semester, **on May 15 (TBC)**

Prerequisites

- Good background in mathematics (differential equations)
- At ease with programming (for the practical)
- Python (installation and tutorial today)

- Interest in
  - understanding biology,
  - using mathematical and numerical tools to do science (computational science),
  - using inspiration from biology to develop new algorithms and new robot controllers
- Be proactive, curious, willing to explore new territories

https://gitlab.com/farmsim

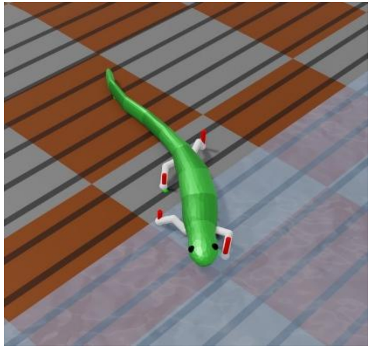
FARMS
Framework for animal and robot modeling and simulation

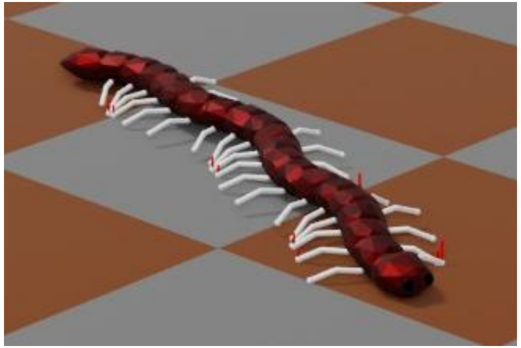

Jonathan Arreguit O'Neil

Shravan Ramalingasetty

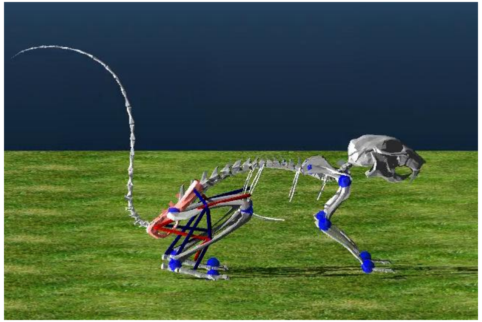
Pavan Ramdya

Lobato-Rios et al, Nature methods 2022

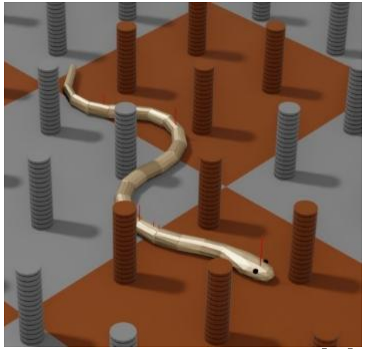




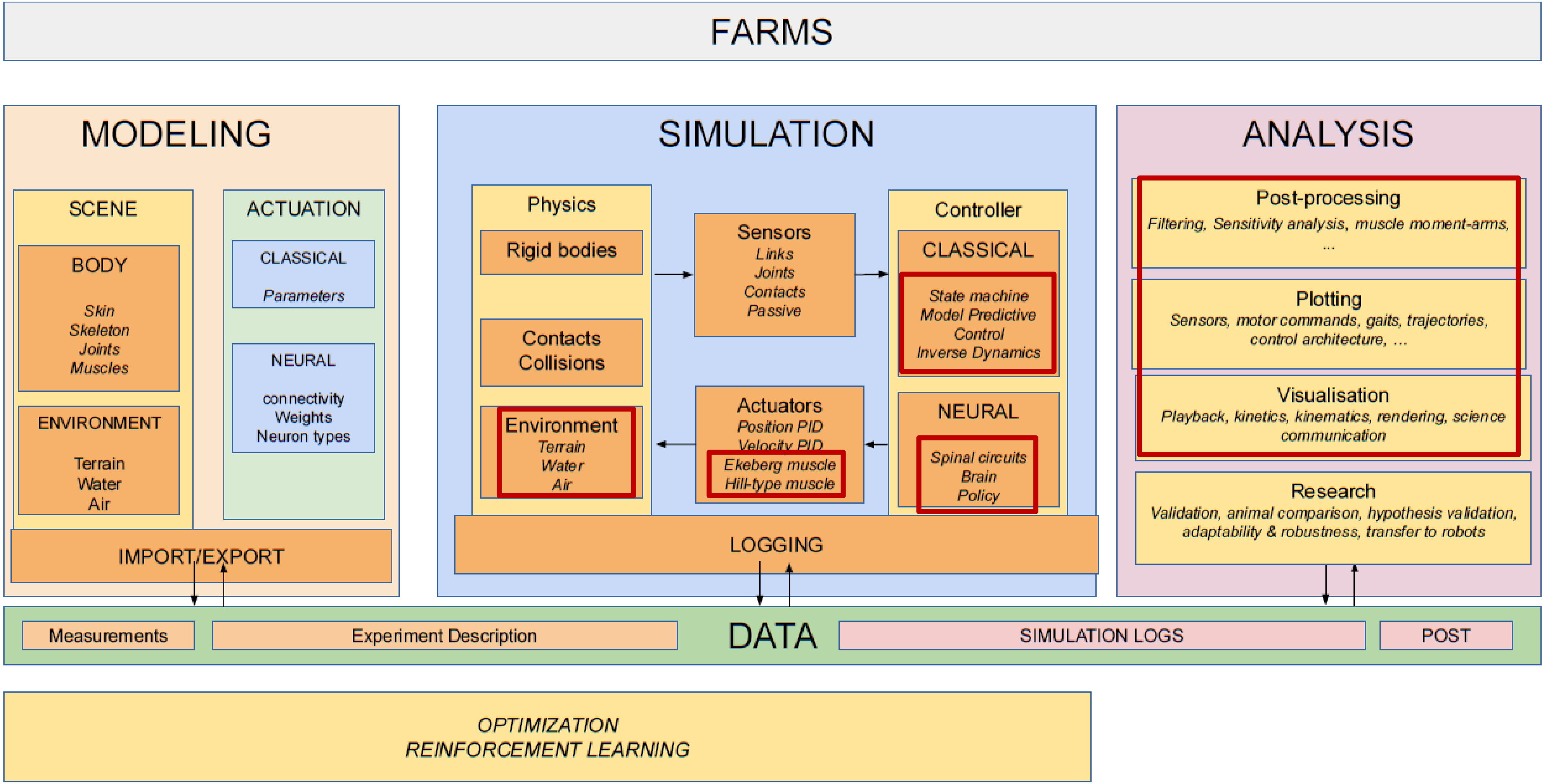
Simon Danner



Tata Ramalingasetty et al, IEEE Access 2021

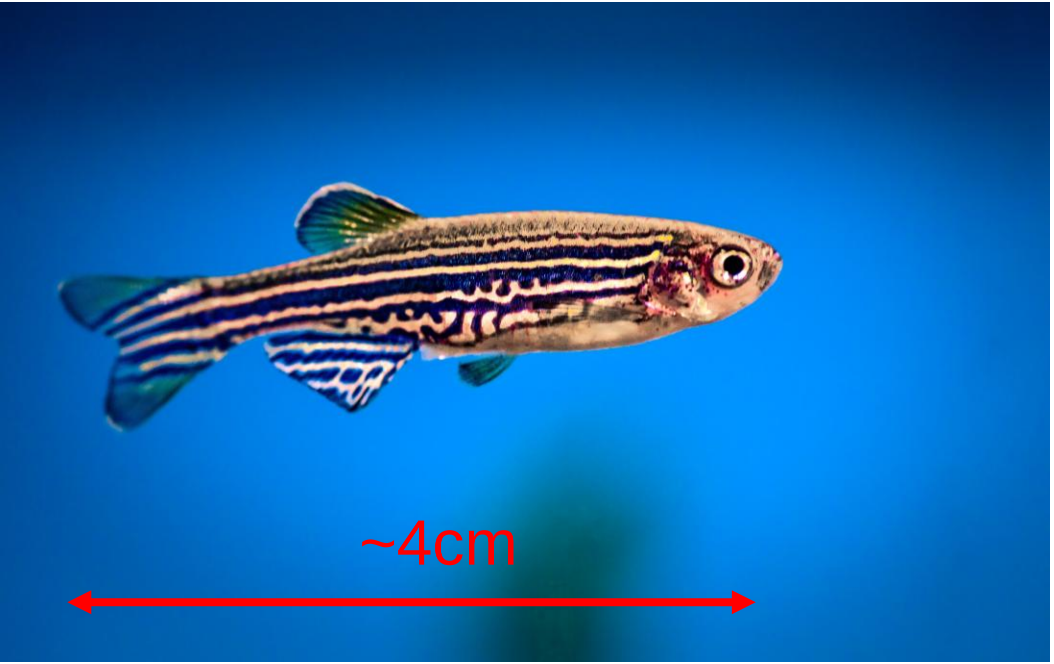


Arreguit, Tata Ramalingasetty, Ijspeert, BioRxiv, 2023


FARMS
MODELING
SCENE
BODY
Skin
Skeleton
Joints
Muscles
ENVIRONMENT
Terrain
Water
Air
ACTUATION
CLASSICAL
Parameters
NEURAL
connectivity
Weights
Neuron types
IMPORT/EXPORT
SIMULATION
Physics
Rigid bodies
Contacts
Collisions
Environment
Terrain
Water
Air
Sensors
Links
Joints
Contacts
Passive
Actuators
Position PID
Velocity PID
Ekeberg muscle
Hill-type muscle
Controller
CLASSICAL
State machine
Model Predictive Control
Inverse Dynamics
NEURAL
Spinal circuits
Brain
Policy
LOGGING
ANALYSIS
Post-processing
Filtering, Sensitivity analysis, muscle moment-arms, ...
Plotting
Sensors, motor commands, gaits, trajectories, control architecture, ...
Visualisation
Playback, kinetics, kinematics, rendering, science communication
Research
Validation, animal comparison, hypothesis validation, adaptability & robustness, transfer to robots
Measurements
Experiment Description
DATA
SIMULATION LOGS
POST
OPTIMIZATION
REINFORCEMENT LEARNING

Model for the practicals

Neuromechanical model of the Zebrafish



https://powersscientific.com/effects-of-lighting-on-zebrafish/

Why the zebrafish?

- **Key model animal** in biology and in neuroscience
- Many **transgenic lines**
- **Transparent** at the larval stage
- Ideal for **optogenetic experiments**
- Increasing number of papers studying its locomotion

Model for the practicals

Neuromechanical model of the Zebrafish

Slower than real time

- Exploration of **swimming gaits,**
- Exploration of **muscle properties**,
- Implementation of a **central pattern generator model made of phase oscillators**,
- Exploring the **role of sensory feedback**
- Open-ended question

Reports

- What is important: **good reports with a careful scientific evaluation of the model and the results**
- To get a good mark:
  - **Good scientific graphs**
  - Careful and **critical analysis of the results**
  - Relate the results to **biological observations**
  - Suggestions of **additional experiments**
  - Possibly: **make predictions**

- Note: this is research, i.e. solutions might not be known yet and there will be less guidance than usual lab projects

- **Warning: no plagiarism!! (also between teams)**
- **Tell us asap if work is not properly shared among team members.**

Content of today’s lecture

- Explanation of the objectives and organization of the course
- **Overview of the numerical modeling approach**
- Overview of the content of all lectures

What do we mean by model?

- A **mathematical description** or a **numerical simulation** of a biological system (i.e. systems of equations or algorithms)

- Should be **based on well-specified (explicit) assumptions and idealizations**

- Should **answer a clear question**

- Should **allow experimenting**, i.e. exploration of how changes of parameters affect the behavior of the model

- Should be **carefully evaluated and validated** against biological data

- Should **make predictions** and **suggest new biological experiments** for future validation

What are assumptions and idealizations?

- ***Assumptions*** are statements or premises that are taken as given within a particular scientific framework. They may or may not be strictly true, but they are accepted to enable the development of a theory or model.

- ***Idealizations***, on the other hand, are **deliberate distortions or simplifications** of reality that are introduced to make problems more tractable or to highlight key mechanisms. Unlike assumptions, idealizations are knowingly false but useful approximations.

	Assumptions	Idealizations
Truth value	May be true or false	Explicitly false
Purpose	Provide foundational premises	Simplify reality for modeling
Role in models	Set boundaries or define a system	Distort reality to highlight key mechanisms
Example	"The speed of light is constant" (empirical assumption)	"A pendulum swings without air resistance" (idealization)

Note: In this course, we will often treat them as having the same meaning

Why make numerical models?

Scientific Value:

- They force us to **conceptualize all the relevant components of a system and the mechanisms of interaction between them**
- They help **understanding the mechanisms of complex dynamical regimes**
- They allow us to **test hypotheses and validate them against biological data**
- They allow **recording and monitoring multiple quantities** (many of which might not be able to be recorded in animal experiments)
- They allow us **to make predictions, and suggest new experiments**

Why make numerical models?

Ethical value:

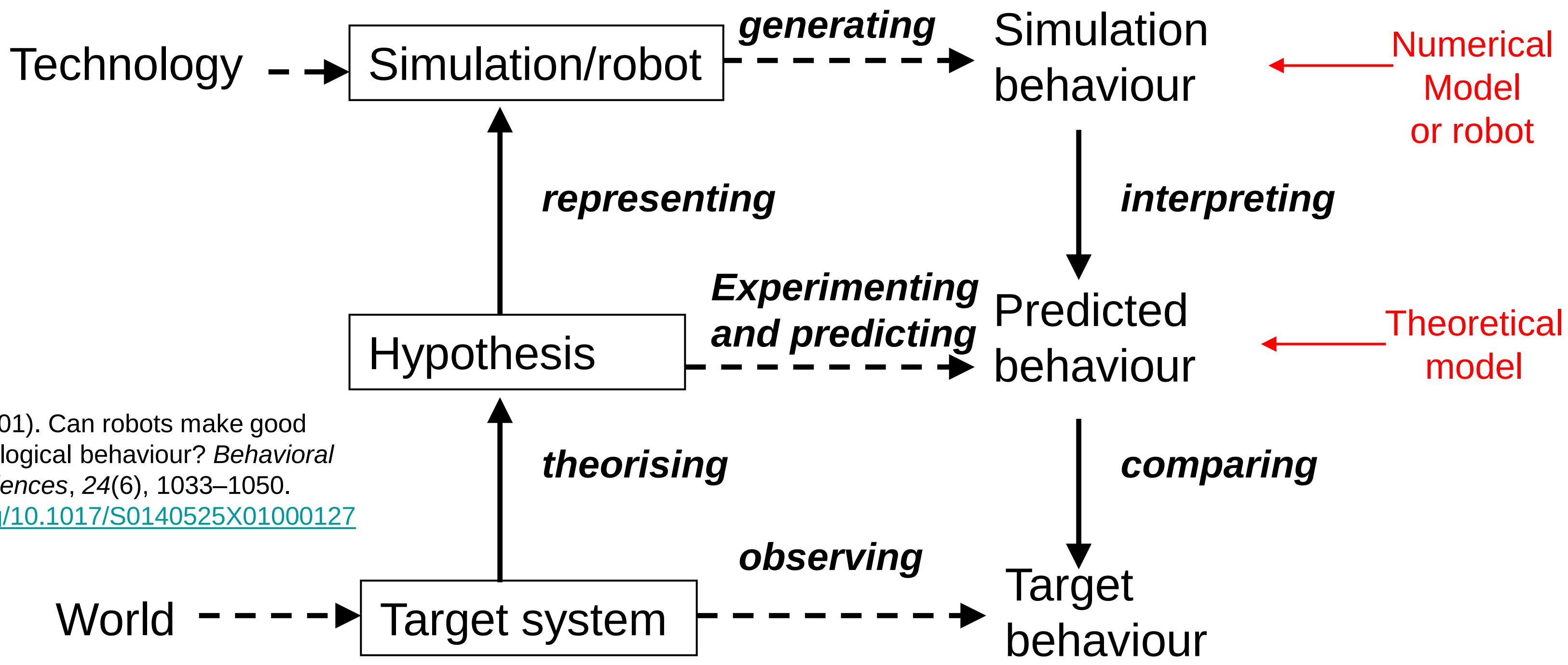
- Using numerical models can **reduce the number of animal experiments**

Economical value:

- Numerical experiments are **much cheaper to run than real animal experiments** (e.g. in terms of recording equipment + animal costs)
- Modeling can **serve as inspiration for new algorithms, devices or robots**
- Numerical models can be used for **optimization** (e.g. designing an optimal prosthesis, improving athletes, …)

Scientific methodology (from B.Webb 2001)

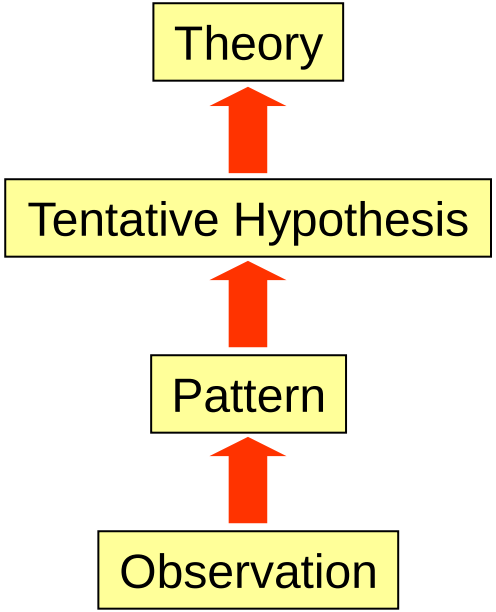
Models, and especially numerical simulations, are now an essential element of a scientific approach:



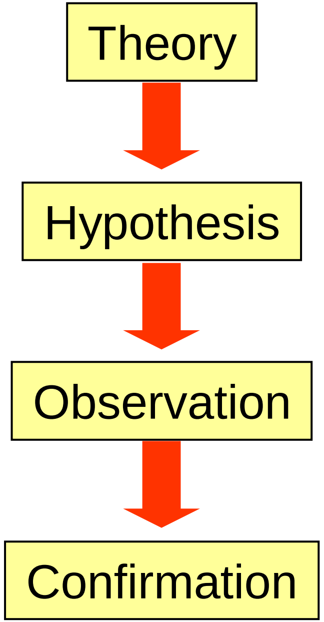
Webb, B. (2001). Can robots make good models of biological behaviour? *Behavioral and Brain Sciences*, *24*(6), 1033–1050. https://doi.org/10.1017/S0140525X01000127

Inductive vs deductive research

Inductive reasoning:
From the specific observations
to generalization



Deductive reasoning:
From the general to the specific



Modeling and numerical simulation

Some additional thoughts:

A model should be **as simple as possible**, but not more (Einstein?) (i.e. not much can be learned from a model that is as complex as the real thing)

A model should have **explanatory power** (i.e. not only descriptive, e.g. as a blackbox).

Like any scientific theory, you should be **ready to throw away models** when they do not correspond to new evidence from experiments.

But models that can not explain some biological data are still useful to indicate that more thinking is needed.

All models are wrong, some are useful… (George Box, statistician)

Interesting example of the modeling approach: the lamprey swimming network

Neural networks that co-ordinate locomotion and body orientation in lamprey, S. Grillner et al, Trends in Neuroscience, 18, pp 270-279, 1995

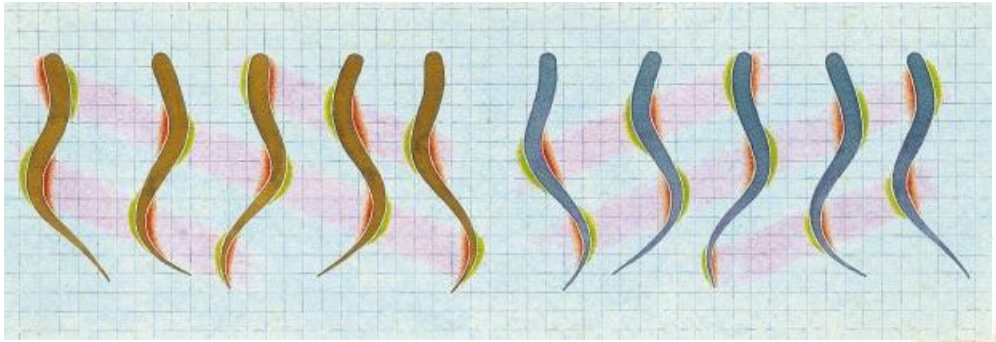
Neural networks for vertebrate locomotion. S. Grillner. Scientific American, 274(1), pp 64-69, 1996

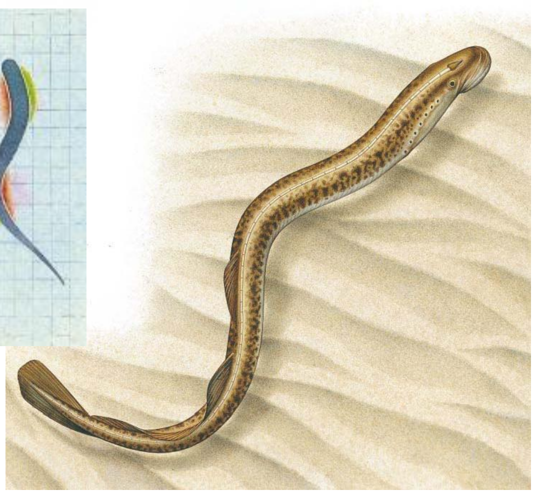
A combined neuronal and mechanical model of fish swimming. Ö. Ekeberg. Biological Cybernetics, 69:363-374, 1993.

The lamprey

- Lamprey: one of the most primitive vertebrate
- Anguilliform swimming
- Believed to be very similar to the ancestor of all vertebrates
- Has been studied in detail by neurobiologists
- Very nice example of fruitful interaction between neurobiology and computational neuroscience (i.e. modeling)

Movie by J.T. Buchanan





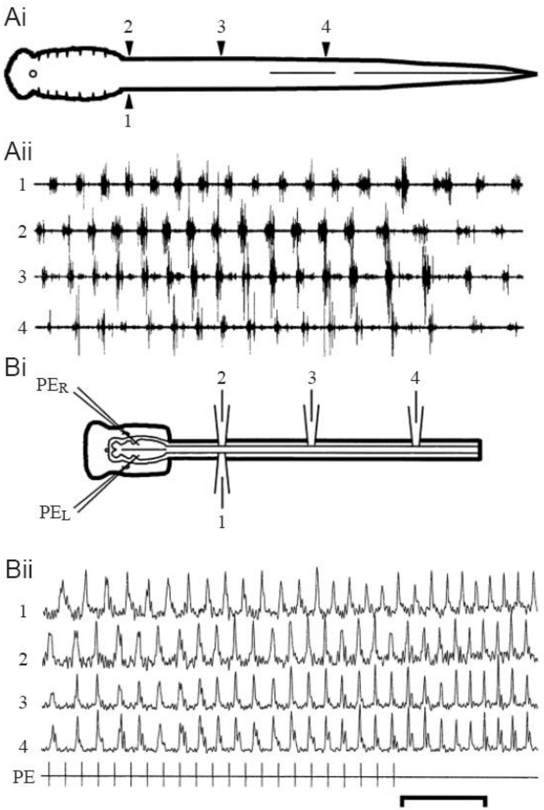
The lamprey

Example of recordings
(Boyd and McClelland 2002)

Electromyographs (EMGs)

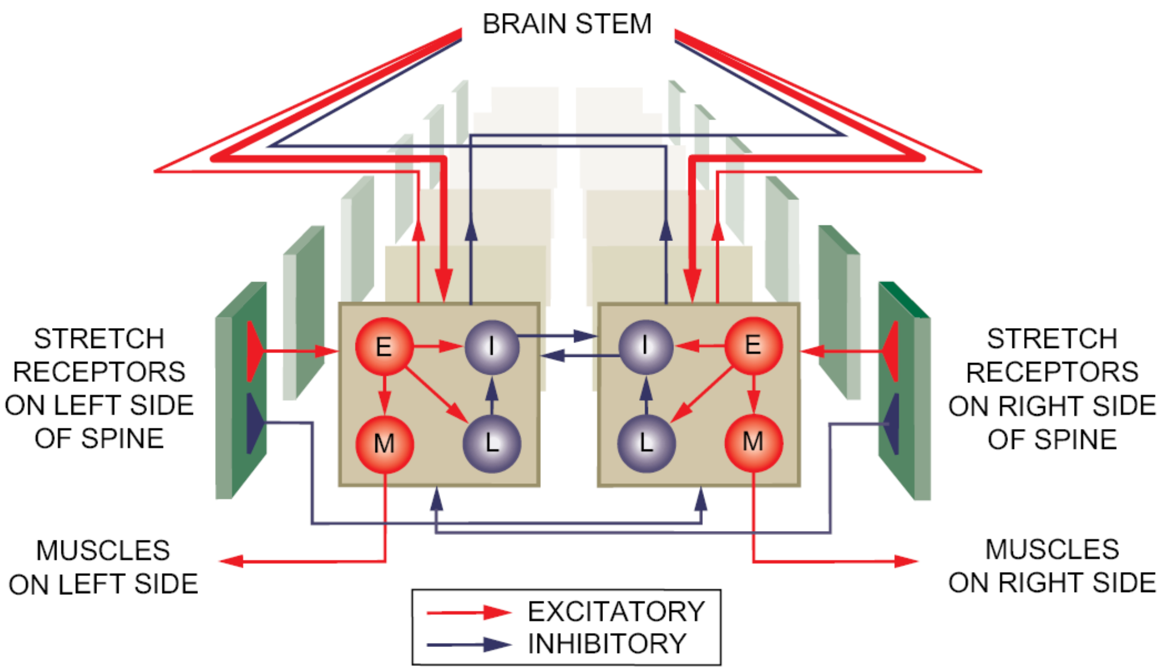
Fictive locomotion:
the spinal cord can produce
rhythmic patterns in a petri dish!
No muscles, no sensory feedback

Ventral root recordings
of an isolated spinal cord



The lamprey swimming network

Conceptual model (Grillner, Sci. Am. 1996)



Methodology of modeling

Important steps:

1. Identify the **questions to be addressed**,
2. Identify **important quantities** in the biological data,
3. Choose the **level of abstraction**,
4. Specify the **assumptions (idealizations)**,
5. Extensively **test the model**
6. **Validate the results** against biological data
7. **Suggest new biological experiments**

Lamprey models: four levels of abstraction

Analytical models of oscillators

abstract

Numerical models of nonlinear oscillators

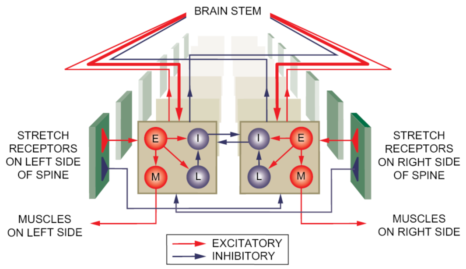
Connectionist neural network models

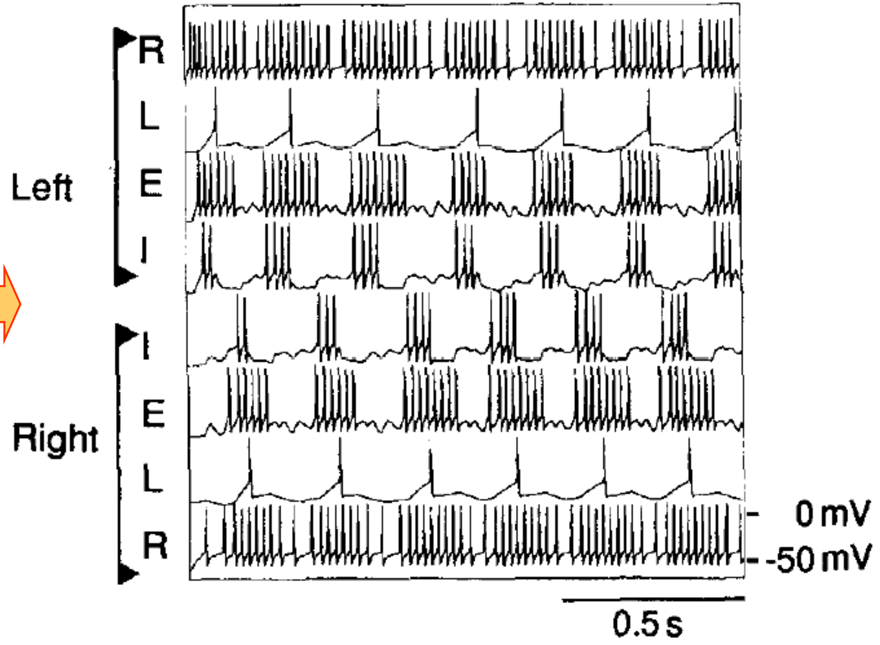
detailed

Biophysical neural network models

The lamprey: biophysical models

Biophysical models have helped **understanding the oscillating properties of the segmental network**





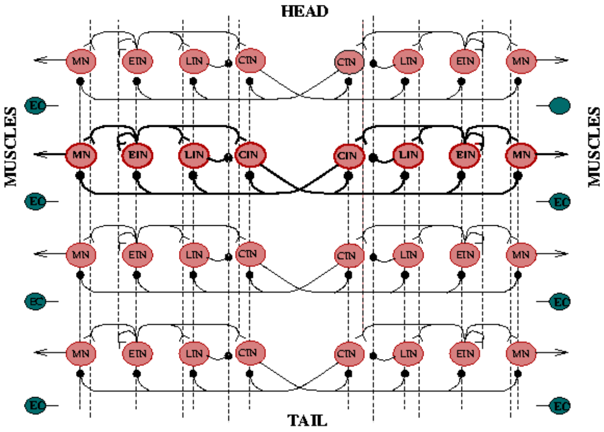
(Grillner et al 1995)

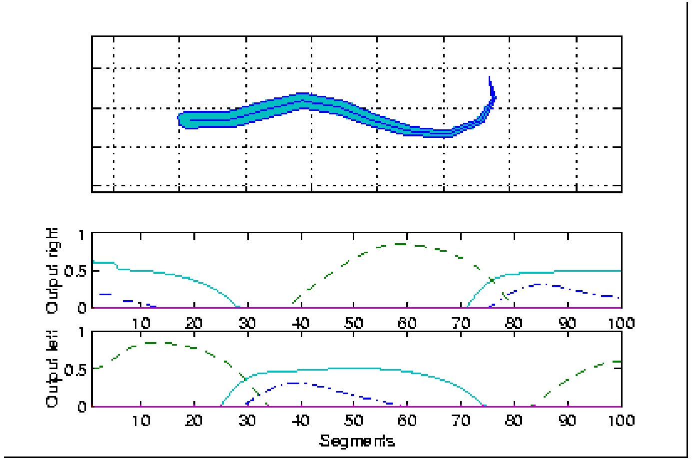
Biophysical models: steps

1. **Questions to be addressed**:
   How are oscillations generated in a segmental network?
2. **Important quantities**:
   Intracellular voltages, ion concentrations,…
3. **Level of abstraction**:
   Biophysical model: Hodgkin-Huxley like neuron model
4. **Assumptions**:
   Single cell represents a whole population of neurons,…
5. **Test the model**:
   See (Grillner et al 1995)
6. **Validation**
   Several mechanisms act together to produce oscillations. Production of oscillations over a large frequency range. See (Grillner et al 1995)
7. **Suggestion of new biological experiments**:
   Pharmacological manipulations, …

The lamprey: connectionist models

Leaky-integrator models have **helped understanding the intersegmental coupling mechanisms that generate traveling waves**





(Ekeberg 1993)

Connectionist models: steps

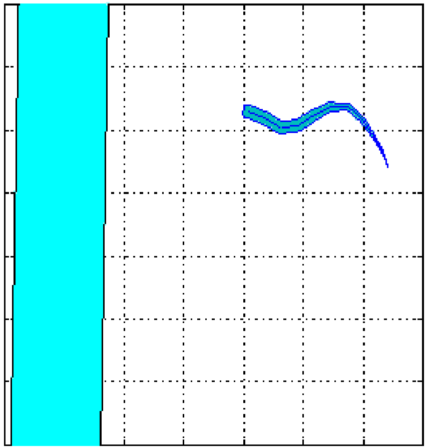
1. **Questions to be addressed**:
   How are traveling waves generate in the spinal cord?
   How is a wavelength of one body length maintained?
2. **Important quantities**:
   Average firing frequency, phase lags between segments,…
3. **Level of abstraction**:
   Connectionist model: leaky-integrator neuron model
4. **Assumptions**:
   Symmetries (left-right, along the spinal cord), …
5. **Test the model**: see (Ekeberg 1993)
6. **Validation**: Constant wavelength at different frequencies, see (Ekeberg 1993)
7. **Suggestion of new biological experiments**:
   Mechanical manip., changing the sensory feedback, …

Neuromechanical models

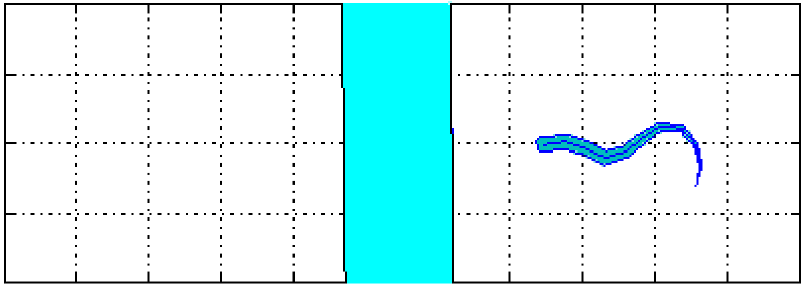
Neuromechanical models = models of neural circuits + of the biomechanics
They have helped understanding:

- **the role of sensory feedback** from stretch receptor cells in **burst termination**.

Swimming through a speed barrier ***without*** sensory feedback



Swimming through a speed barrier ***with*** sensory feedback



(Ekeberg et al 1995, Ijspeert et al 1999)

For more details about the usefulness of modeling see:

Webb, B. (2001). Can robots make good models of biological behaviour? *Behavioral and Brain Sciences*, *24*(6), 1033–1050. https://doi.org/10.1017/S0140525X01000127

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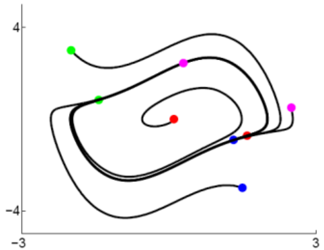
A combined neuronal and mechanical model of fish swimming. Ö. Ekeberg. Biological Cybernetics, 69:363-374, 1993.

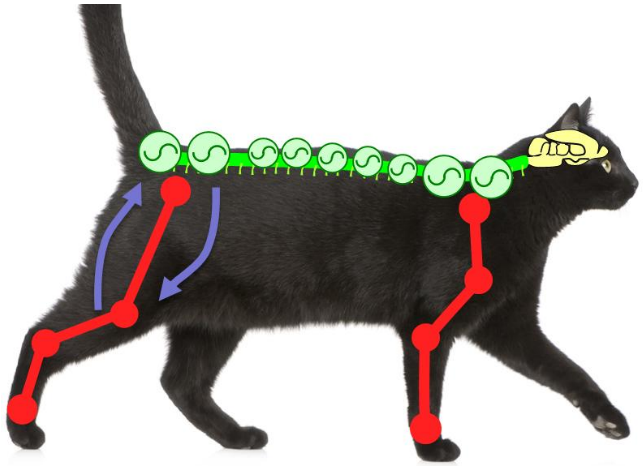
Cf Moodle folder

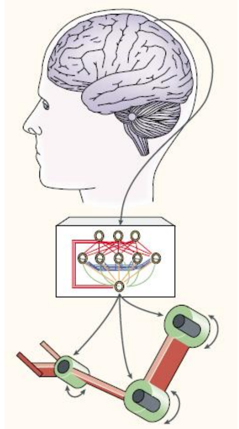
Overview of the content of the course

Contents of lectures

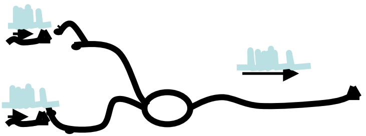


Dynamical systems

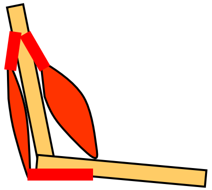




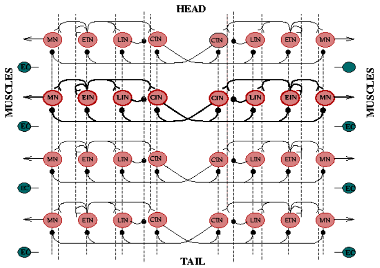
Neuroprosthetics



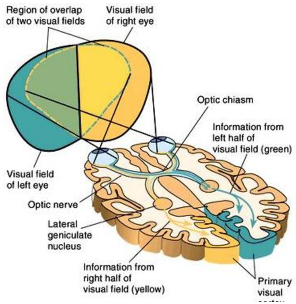
Neuron models



Muscle and Biomech. models



Motor system models



Visual system models

Introduction to nonlinear dynamical systems

Topics:

- Ordinary differential equations (ODEs)
- Methods for solving (ODEs)
- Geometrical interpretation, phase portrait
- Differences between linear and nonlinear systems
- Linear stability analysis

Introduction to nonlinear dynamical systems

Topics:

- Oscillators and limit cycles
- Different oscillator models
- Chains of oscillators
- Bifurcations and chaos

Ordinary differential equations

Most models presented in the course will be based on ordinary differential equations (ODEs):

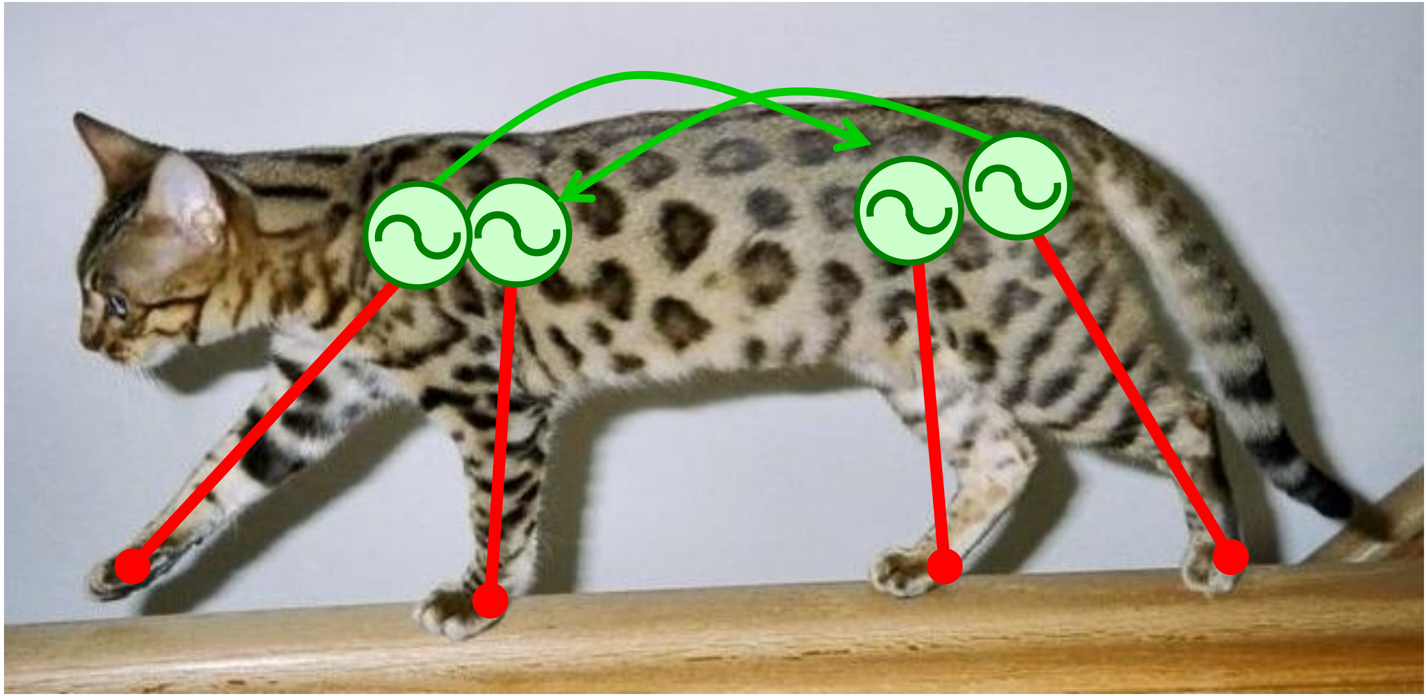
$$\frac{d}{dt}\vec{x} = f(\vec{x},\vec{\alpha},t)$$

These types of equations are used in many types of numerical models. They determine how the *state variables* $\vec{x}$ vary over time. The time derivative of the state variables $\vec{x}$ are described as a (usually nonlinear) function of the state variables, some *parameters* $\vec{\alpha}$ and (possibly) the time *t*.

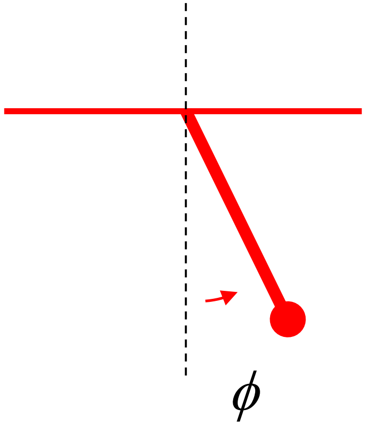
Autonomous ODEs: $\frac{d}{dt}\vec{x} = f(\vec{x},\vec{\alpha})$ no explicit dependence on time

Non-autonomous ODEs: $\frac{d}{dt}\vec{x} = f(\vec{x},\vec{\alpha},t)$ explicit time dependence, much harder to deal with

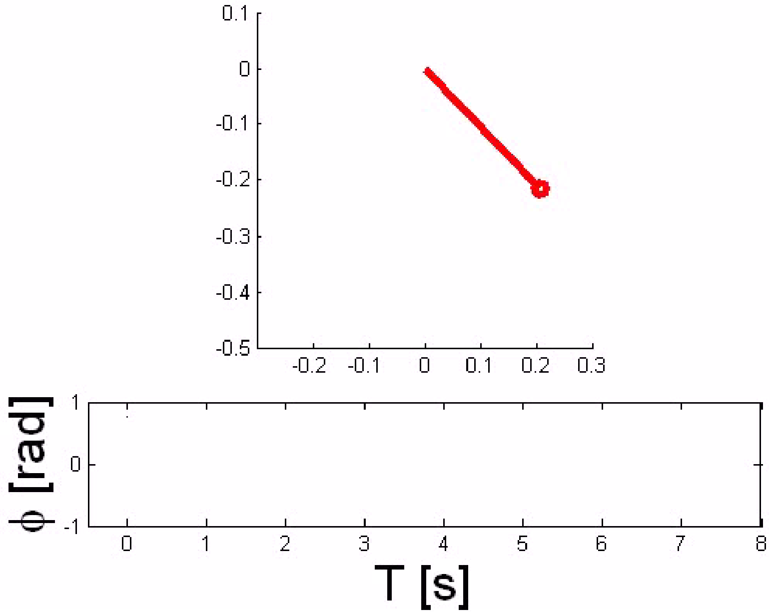
Numerical simulation of systems of coupled oscillators



A limb ≅ a damped pendulum



$$\ddot{\phi} = -d\,\dot{\phi} - \sin(\phi)\cdot\frac{g}{L}$$



ϕ: angle
d: damping
g: gravity
L: length

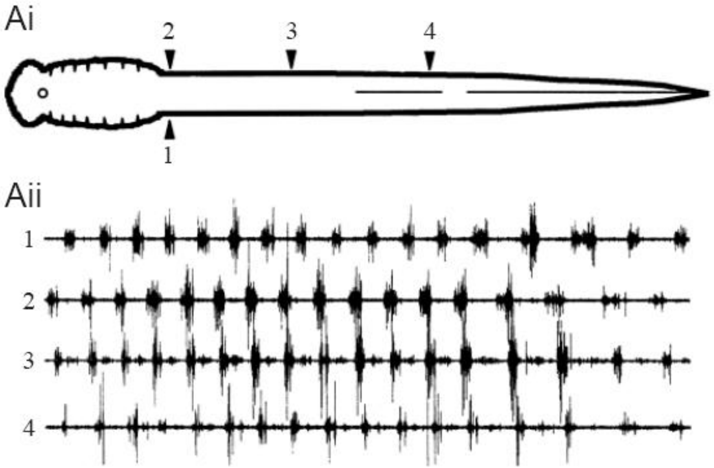
Frequency of oscillation: $\omega = \sqrt{\frac{g}{L}} = \sqrt{\frac{9.81}{0.3}} = 2\pi\cdot 0.9[Hz]$

A Hopf oscillator to model a neural oscillatory center

$$\dot{x} = \alpha(\mu - \sqrt{x^2 + y^2})\, x - \nu\, y$$

$$\dot{y} = \alpha(\mu - \sqrt{x^2 + y^2})\, y + \nu\, x$$

μ: amplitude
α: positive parameter
v: intrinsic frequency
w_i: couplings



Boyd and McClellan, the Journal of Experimental Biology 2002

Frequency of oscillation: ν

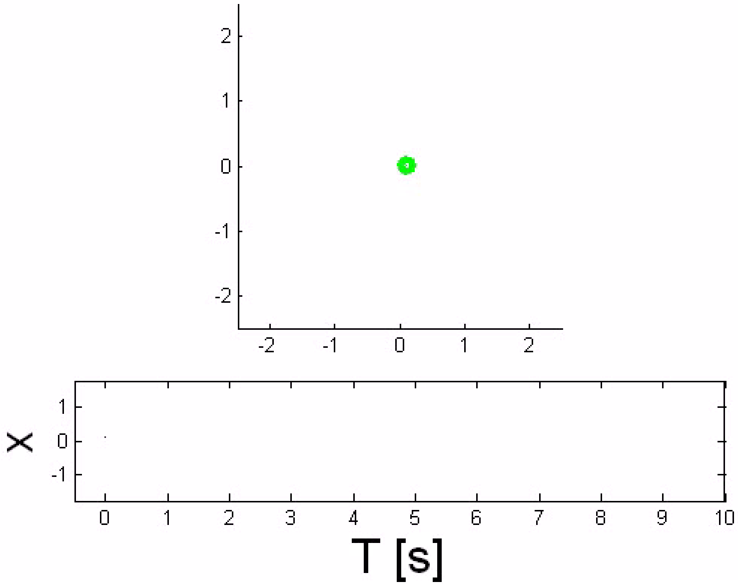
A Hopf oscillator to model a neural oscillatory center

Stable limit cycle:

$$\dot{x} = \alpha(\mu - \sqrt{x^2 + y^2})\,x - \nu\,y$$

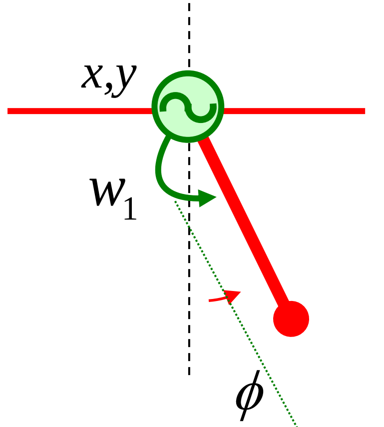
$$\dot{y} = \alpha(\mu - \sqrt{x^2 + y^2})\,y + \nu\,x$$

μ: amplitude
α: positive parameter
v: intrinsic frequency
w_i: couplings



Frequency of oscillation: ν

A pendulum coupled to an oscillator



$$\ddot{\phi} = -d\,\dot{\phi} - \sin(\phi)\cdot\frac{g}{L} + w_1\,x$$

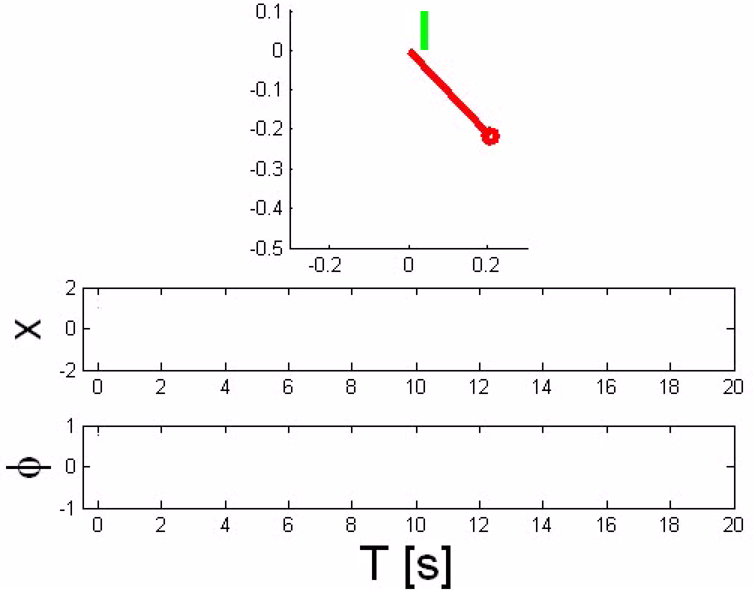
$$\dot{x} = (\mu - \sqrt{x^2 + y^2})\,x - \nu\,y$$

$$\dot{y} = (\mu - \sqrt{x^2 + y^2})\,y + \nu\,x$$

ϕ: angle
d: damping
g: gravity
L: length

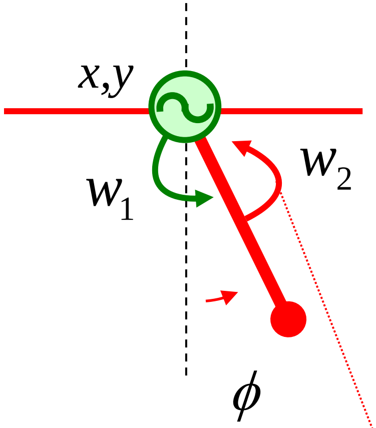
μ: amplitude
v: intrinsic frequency
w_i: couplings

Forced pendulum: complex dynamics



Raibert: **“the central nervous system does not *control* the body; it can only *make suggestions*”**.

A pendulum coupled to an oscillator



$$\ddot{\phi} = -d\,\dot{\phi} - \sin(\phi)\cdot\frac{g}{L} + w_1\, x$$

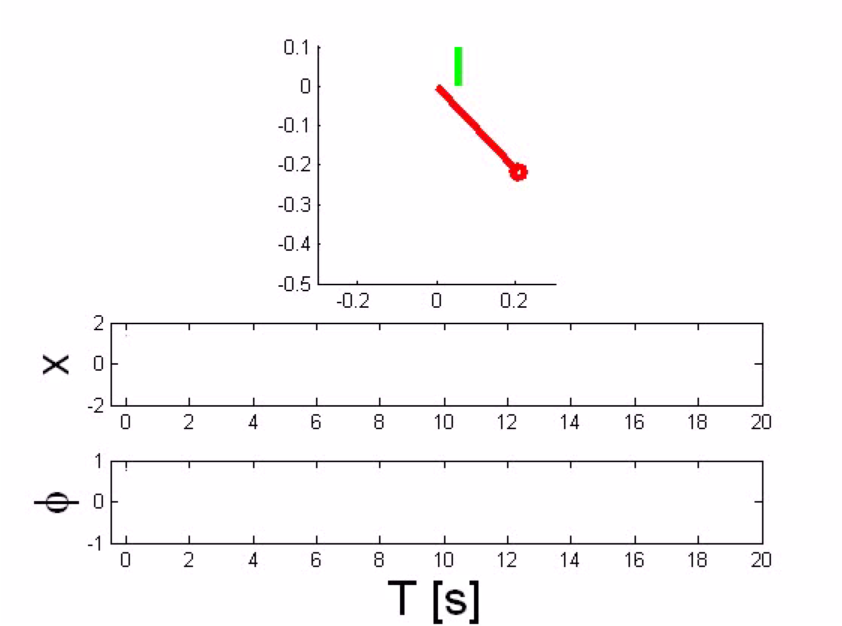
$$\dot{x} = (\mu - \sqrt{x^2 + y^2})\, x - \nu\, y + w_2\phi$$

$$\dot{y} = (\mu - \sqrt{x^2 + y^2})\, y + \nu\, x$$

Bidirectional coupling:

Entrainment!!

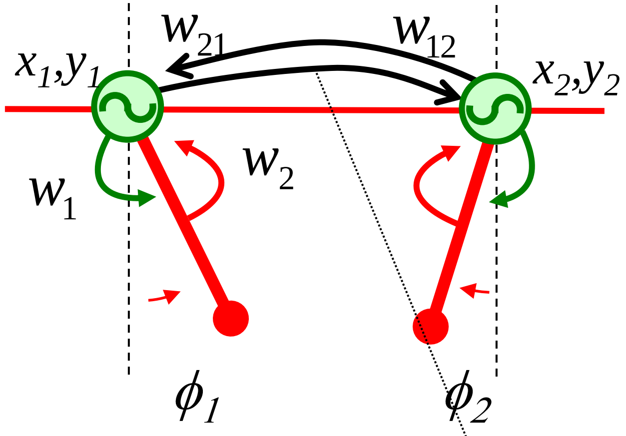
(different systems reaching a same resulting frequency)



ϕ: angle
d: damping
g: gravity
L: length

μ: amplitude
v: intrinsic frequency
w_i: couplings

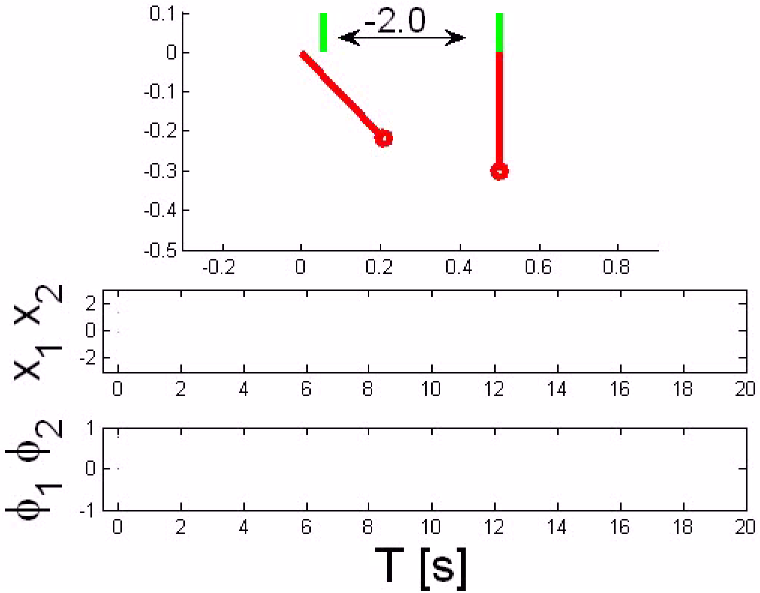
More legs !



$$\dot{x}_1 = (\mu - \sqrt{x_1^2 + y_1^2})\, x_1 - \nu\, y_1 + w_2\phi_1 + w_{21}x_2$$

$$\dot{y}_1 = (\mu - \sqrt{x_1^2 + y_1^2})\, y_1 + \nu\, x_1 + w_{21}y_2$$

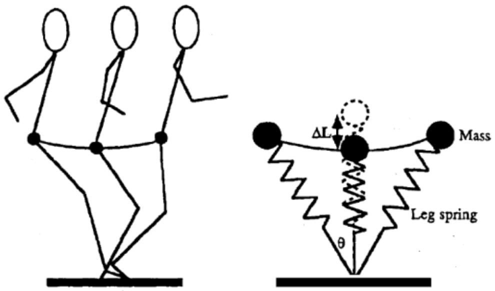
Interlimb coordination and gait transition !!



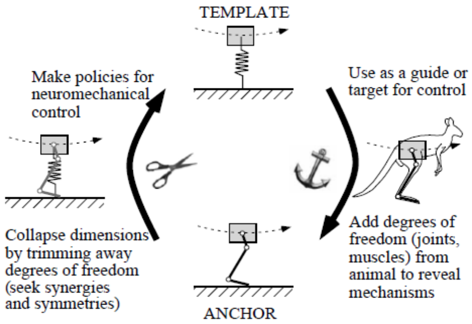
ϕ: angle
d: damping
g: gravity
L: length

μ: amplitude
v: intrinsic frequency
w_i: couplings

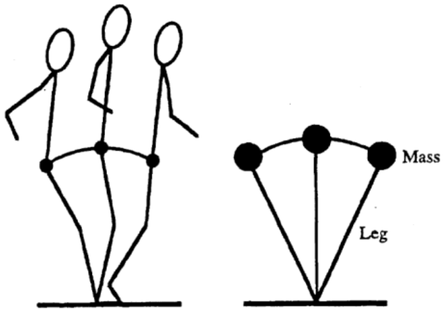
Mathematical models
are very useful to study locomotion



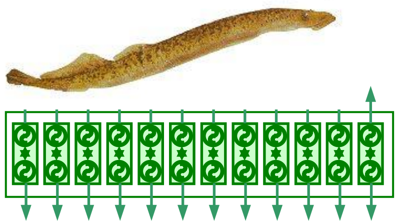
Spring-loaded inverted pendulum (SLIP) (Blickhan,



Templates and anchors (Koditchek and Full 1999)

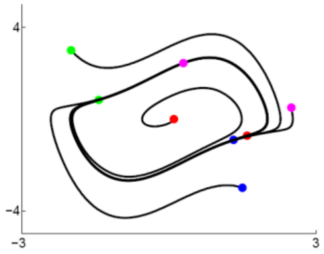


Inverted pendulums

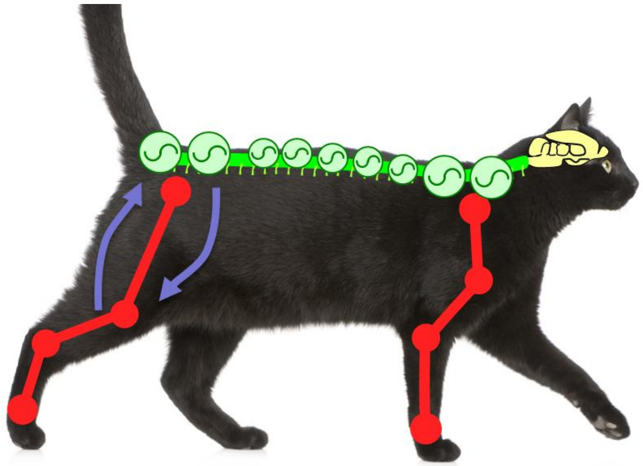


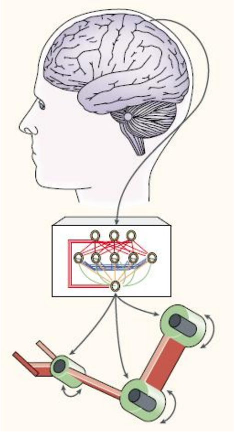
Systems of coupled oscillators, Kopell, Ermentrout, …

Contents of lectures

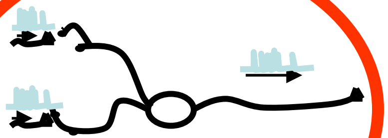


Dynamical systems

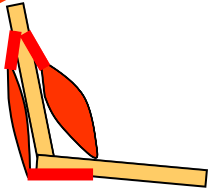




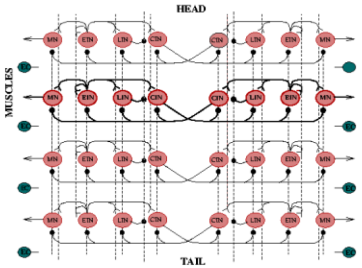
Neuroprosthetics



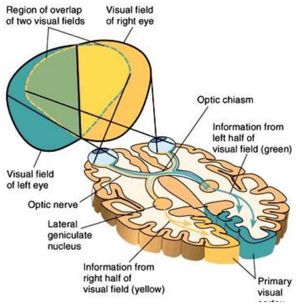
Neuron models



Muscle and Biomech. models

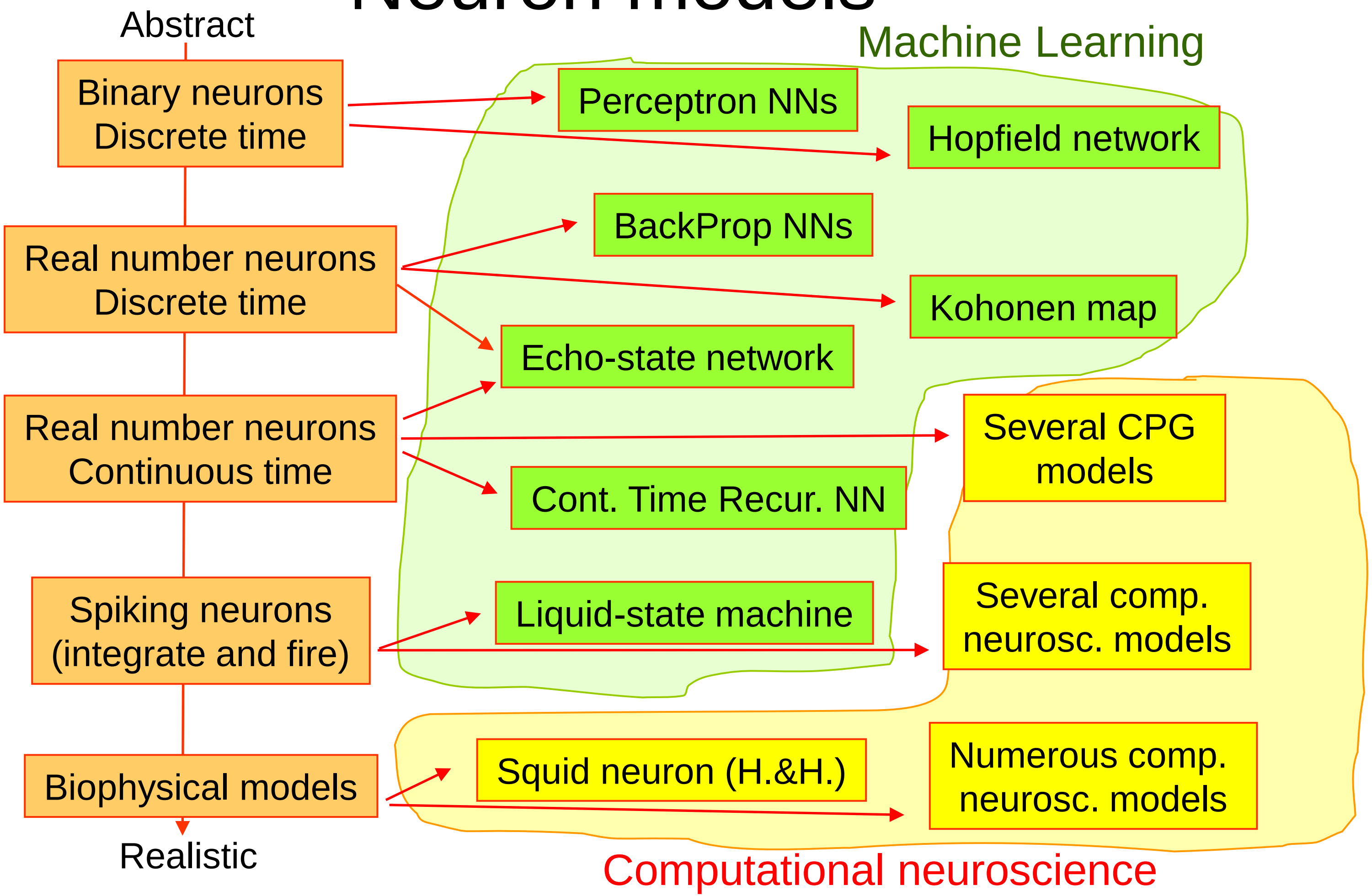


Motor system models

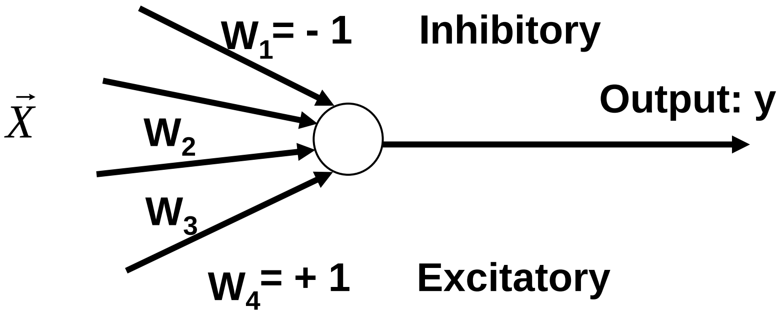


Visual system models

Neuron models



McCulloch-Pitts neuron



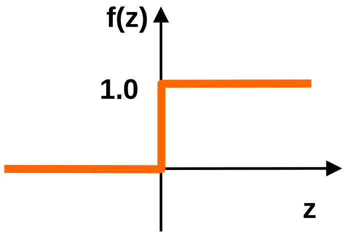
X: *Input vector* from all other neurons
w_i: the *strength/weight* of each synapse
y: neuron *output*
f(x): transfer function

$$y = f\left(\sum_i w_i \cdot x_i\right)$$

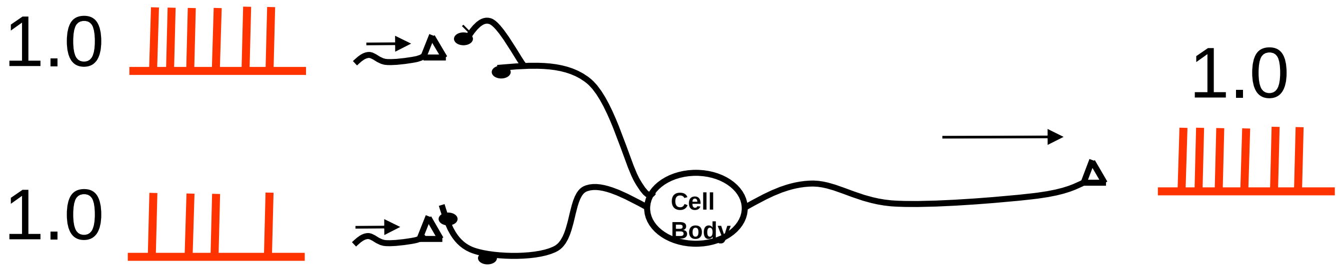
McCulloch-Pitts neuron (1943)

Transfer function = threshold function :

$$f(z) = \theta(z) = \begin{cases} 1 & \text{if } z \geq 0 \\ 0 & \text{if } z < 0 \end{cases} \Rightarrow y = \theta\left(\sum_i w_i \cdot x_i\right)$$



- This type of transfer function depends on **firing rates**, not individual spikes
- Binary neuron: a neuron is either in a high firing rate 1, or a low firing rate 0



McCulloch-Pitts neuron (1943)

Transfer function = threshold function :

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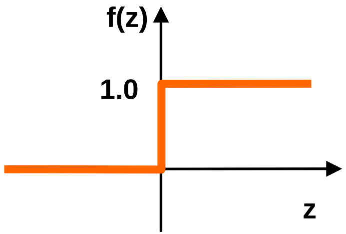
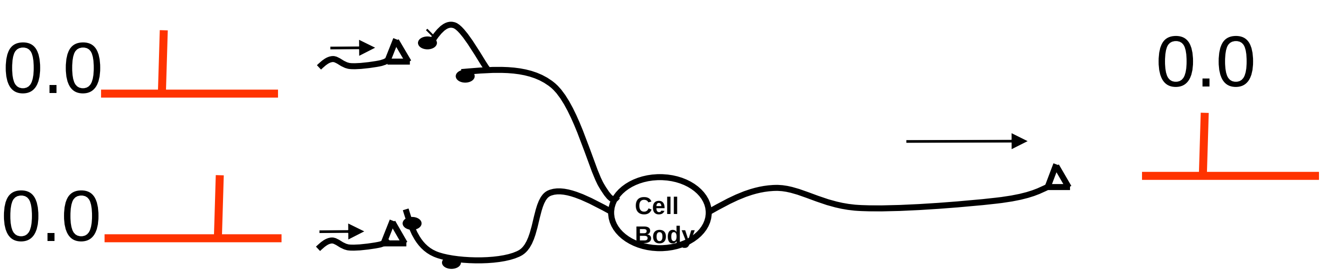


- This type of transfer function depends on **firing rates**, not individual spikes
- Binary neuron: a neuron is either in a high firing rate 1, or a low firing rate 0



Leaky integrator neuron model

Idea: add a state variable m_j (membrane potential) that is controlled by a differential equation

$$\tau_j \frac{dm_j}{dt} = -m_j + S$$

$$x_j = \frac{1}{1+e^{-D\cdot(m_j+b)}}$$

m_j : membrane potential

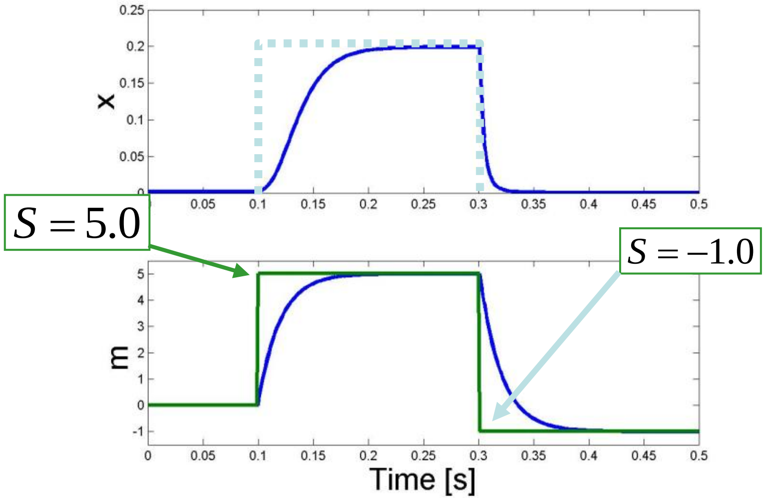
x_j : firing rate

τ_j : time constant

b : bias

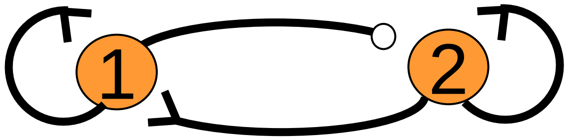
S : input (dendritic sum)

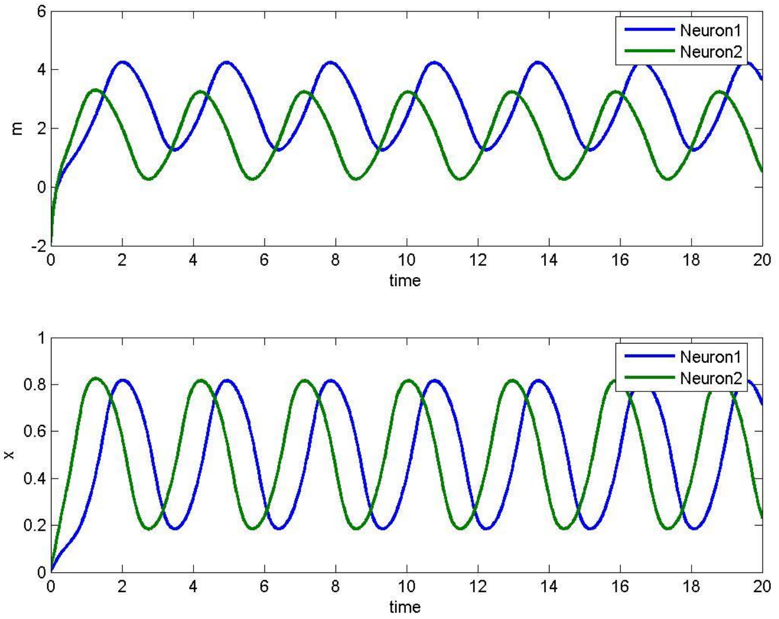
$$S = \sum_i w_{ij} \cdot x_i$$



m_j converges to S with a speed that depends on τ_j

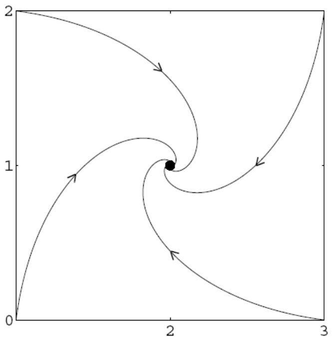
Two-neuron oscillator

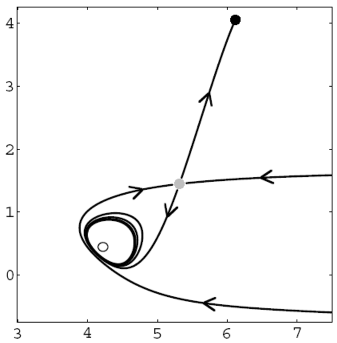




Two-neuron network: other possible behaviors

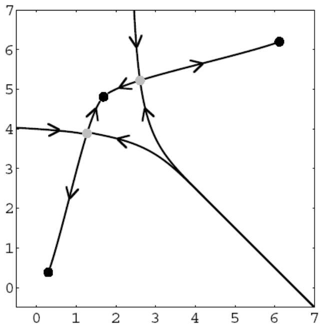
One stable point

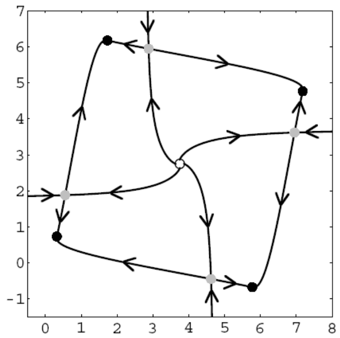




One stable point
One unstable
One saddle
One limit cycle

Three stable points
Two saddles





Four stable points
One unstable
Four saddles

See Beer (1995), Adaptive Behavior, Vol 3 No 4

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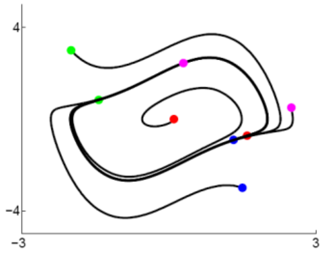
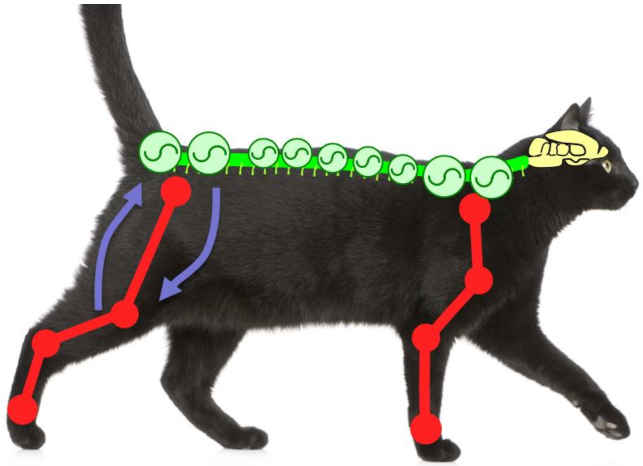
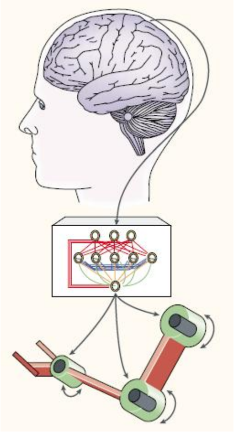
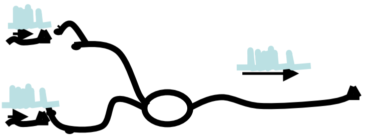


Dynamical systems

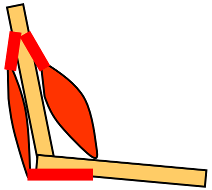




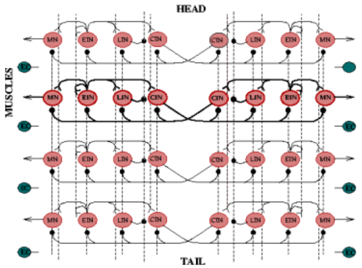
Neuroprosthetics



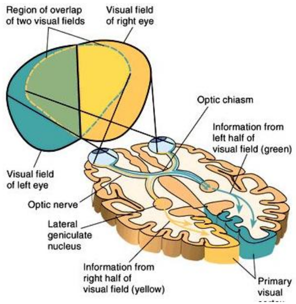
Neuron models



Muscle and Biomech. models



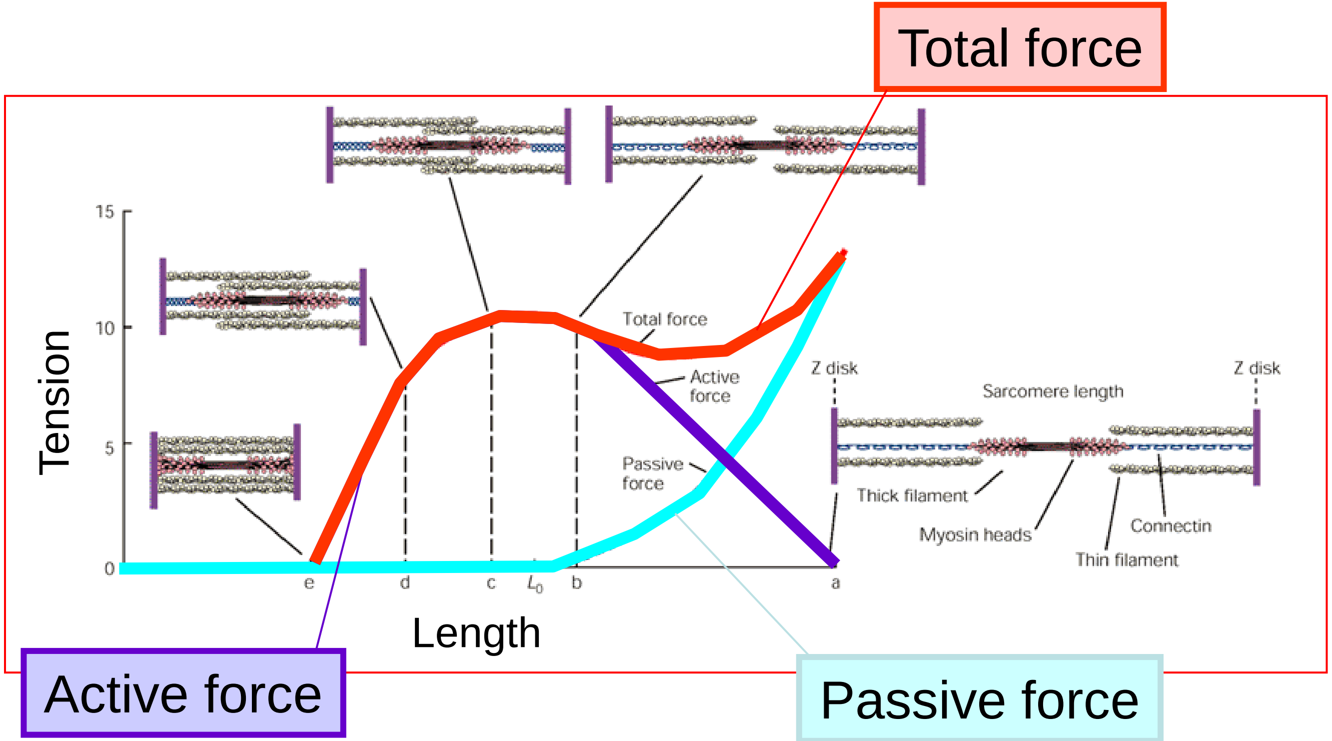
Motor system models



Visual system models

Muscle models

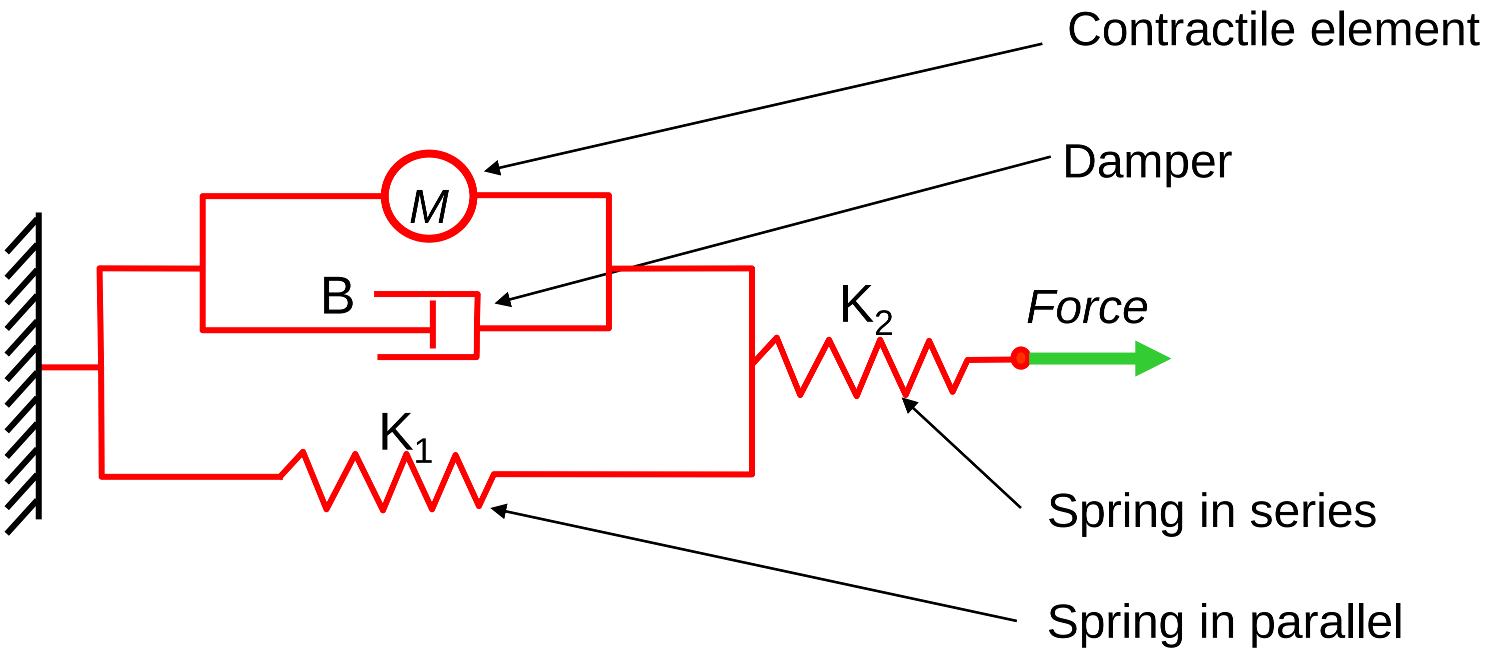
The amount of active contractile force developed during contraction depends on the degree of overlap of thick and thin filaments



Hill Muscle model

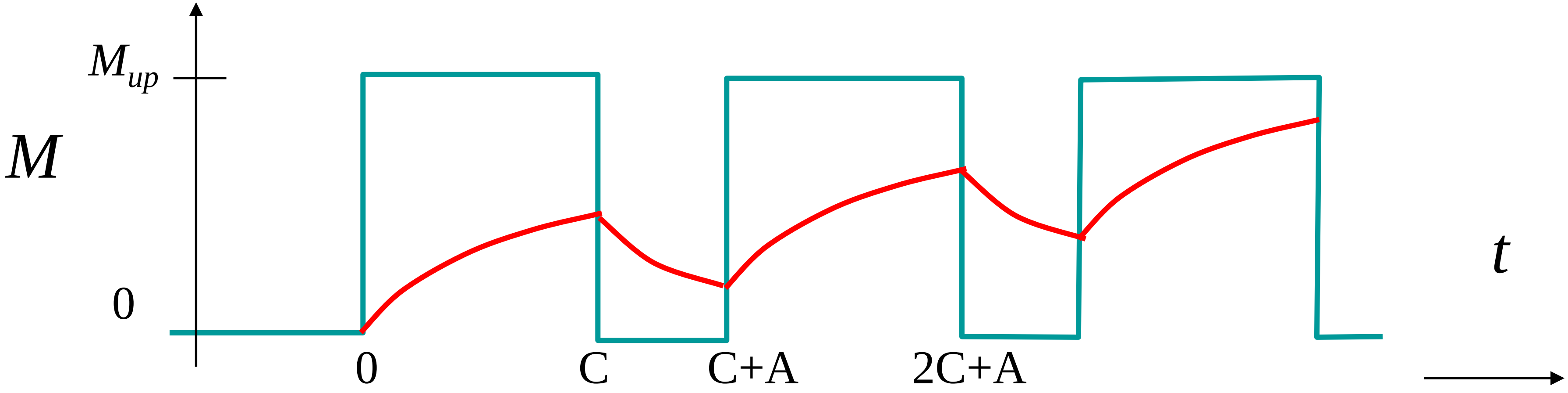
Very influential model made in the 1930’s, most modern models are variations of it.

It is made of 4 elements:



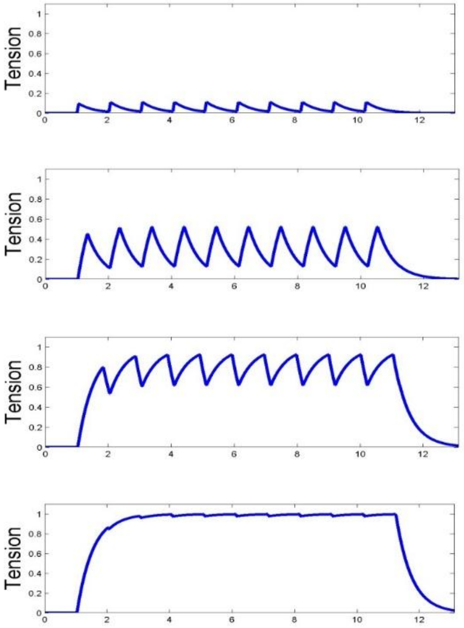
Hill model: isometric case with pulse stimulation

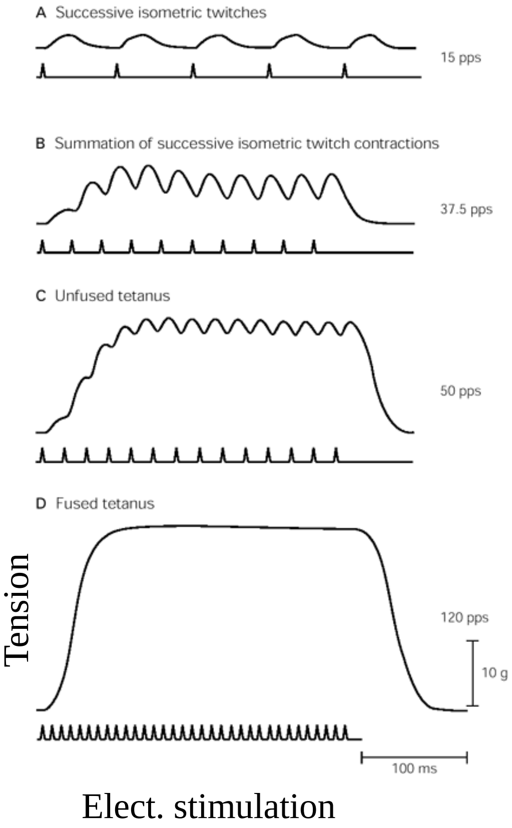
$$T(t) = (T_0 - M)\, e^{-\frac{K}{B}(t - t_0)} + M \quad where \quad M = \begin{cases} 0 \\ M_{up} \end{cases} depending\, on\, t_0$$



Hill model: isometric case with pulse stimulation

This is a good approximation of
how tension builds up in a muscle





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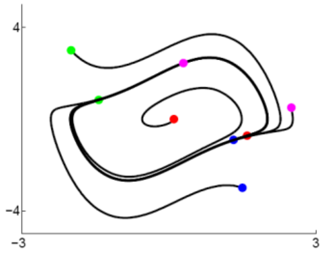
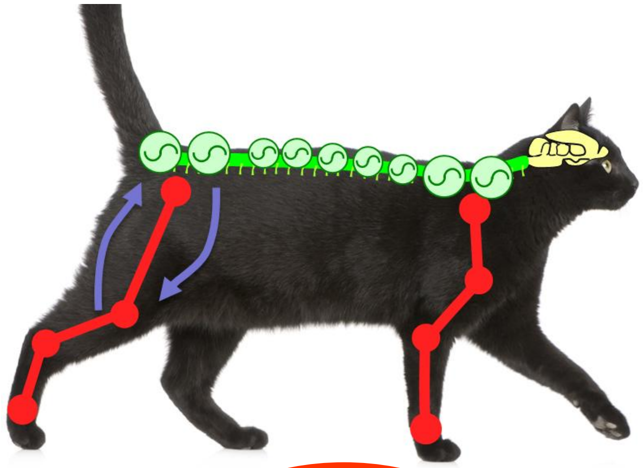
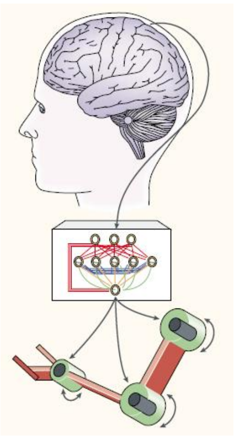
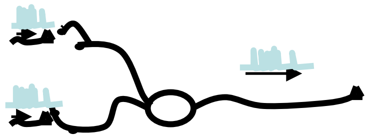


Dynamical systems

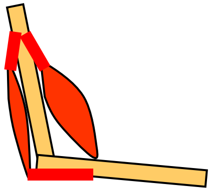




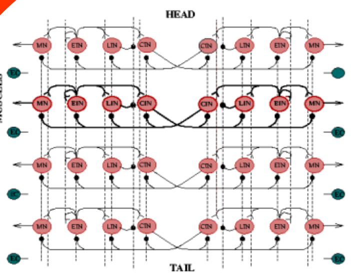
Neuroprosthetics



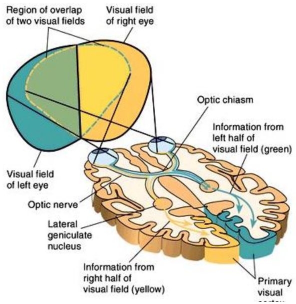
Neuron models



Muscle and Biomech. models



Motor system models



Visual system models

Models of locomotion control

Topics:

- Locomotion control in animals
- Locomotion of the lamprey
- Different models of the lamprey locomotor system
- Neuromechanical simulation of the salamander
- Applications to robotics

Biomechanics of animal Locomotion

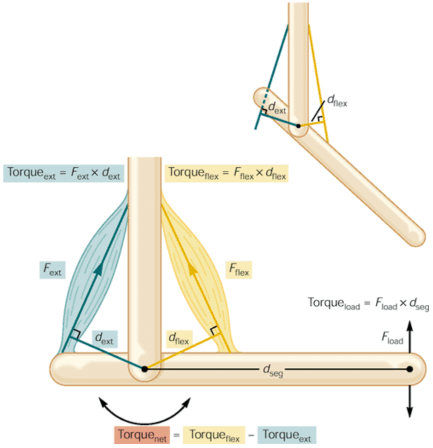
General principles:

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**



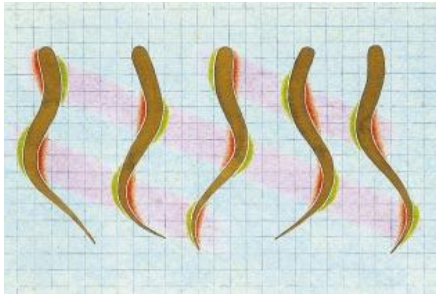
G.E. Loeb, C. Ghez (2000) The Motor Unit and Muscle Action. In: *Principles of Neural Science*. 4th edition. Edited by E.R. Kandel, J.H. Schwartz and T.M. Jessell. Appleton & Lange, New York. pp. 675-694.

Animal Locomotion (ct’d)

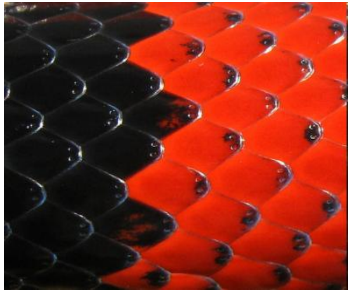
Generation of forces:

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

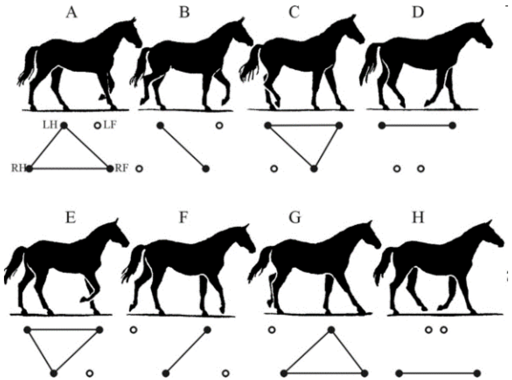
- Key feature: **creation of asymmetries in the external forces due to the environment** (little resistance in the direction of locomotion compared to the other directions)
- Examples: elongated form of the body, scales on snake skin, legs (transition between swing and stance)



Asymmetric drag



Scales:
Asymmetric friction

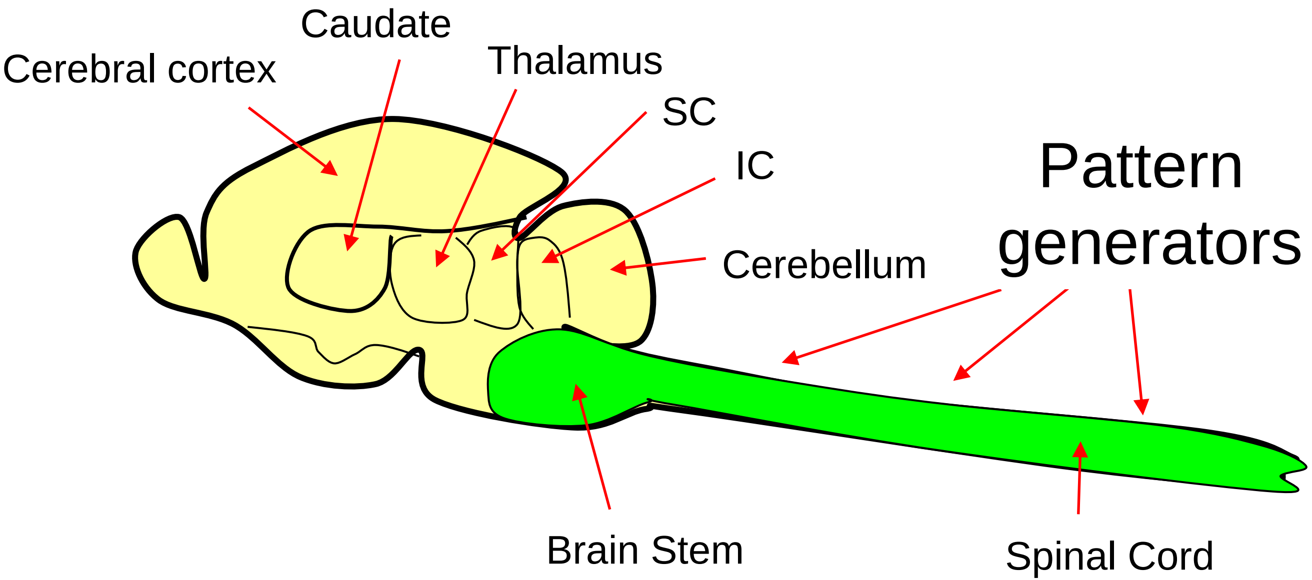


Swing-stance alternation

Animal locomotion

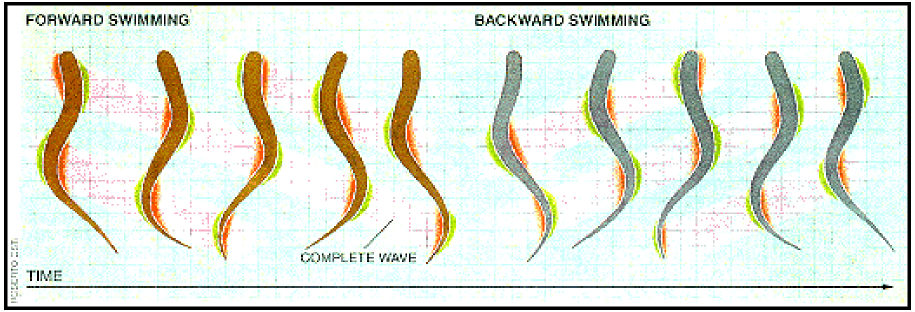
Large diversity of different types of locomotion:swimming, crawling, walking, hoping, burrowing, flying,… but **all use the same principles**.

Neural control of movement



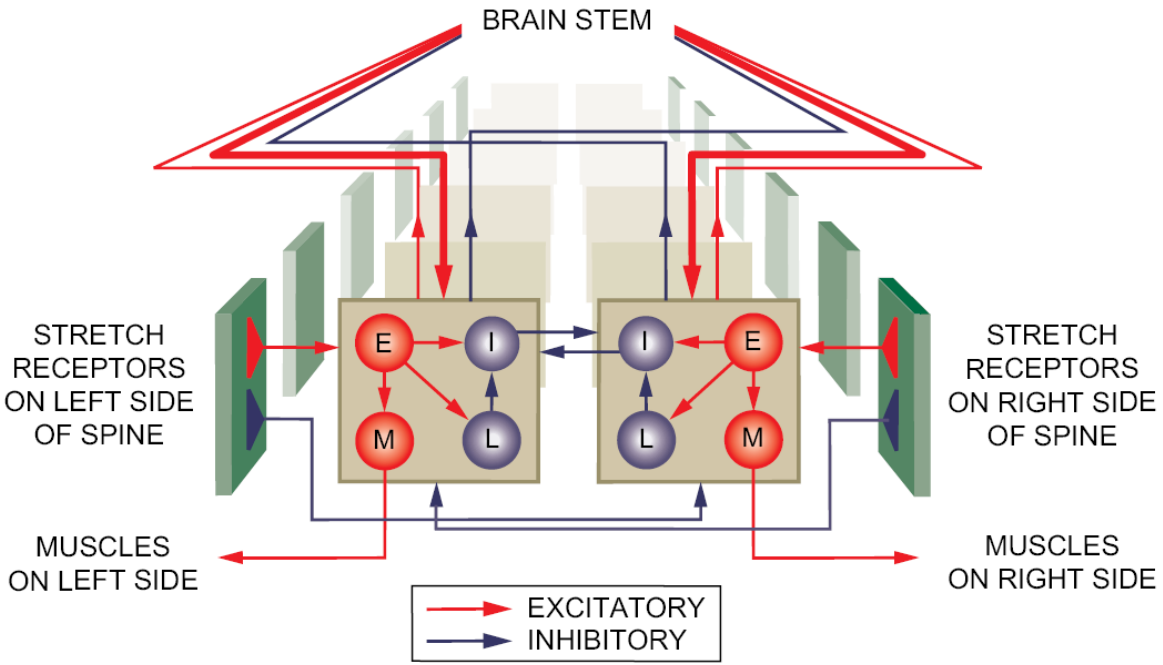
Locomotion of the lamprey

- Lamprey: one of the most primitive vertebrate
- Anguiliform swimming
- Has been studied in detail by neurobiologists
- Believed to be very similar to the ancestor of all vertebrates



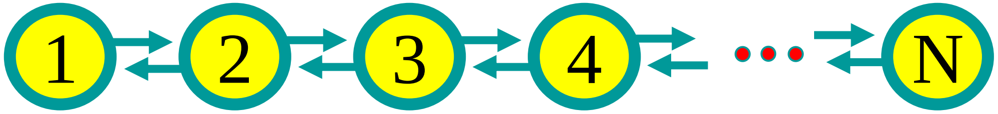
The lamprey swimming network

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

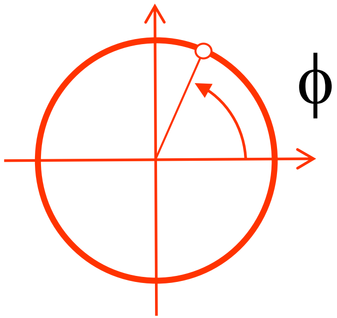


Lamprey: Analytical analysis of chain of oscillators

Lamprey CPG modeled as a chain of oscillators with nearest neighbor coupling:



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



ϕ_i : 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

Lamprey: Analytical analysis of chain of oscillators

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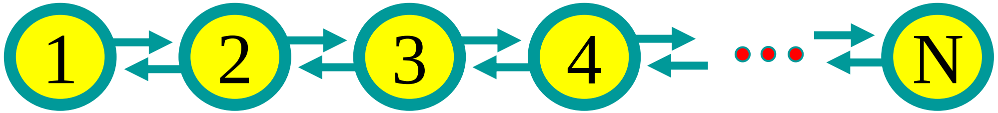


Assumptions: nearest neighbor coupling, same coupling constants *a*, symmetric coupling

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

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

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

Lamprey: Analytical analysis of chain of oscillators

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

This can be expressed in matrix form:

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

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

Lamprey: 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:

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

No solution exists if any of the component 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.

Lamprey: Analytical analysis of chain of oscillators

Example with 6 oscillators, and constant frequency difference,
$w_1 - w_2 = w_2 - w_3 = \ldots = e$:

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

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

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:

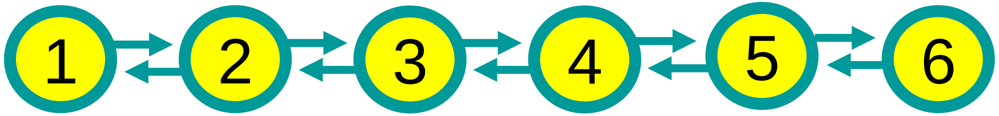
$$\left|\frac{e}{a}\right| \leq \frac{2}{9}$$

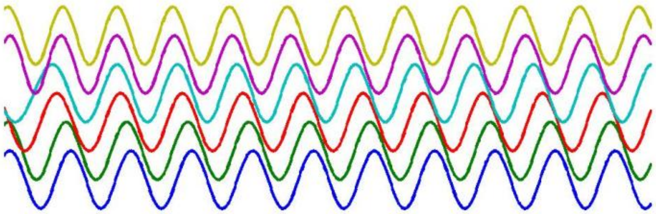
$$\left|\frac{e}{a}\right| \leq \frac{8}{N^2}$$ N even

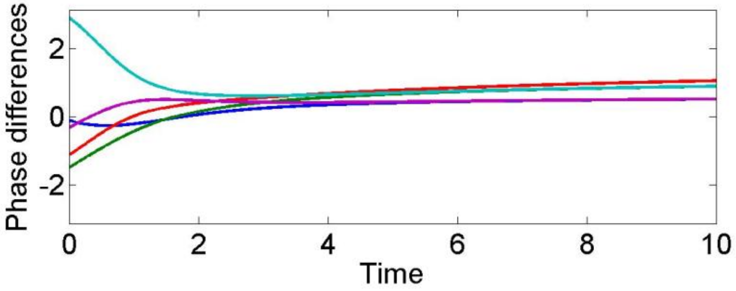
$$\left|\frac{e}{a}\right| \leq \frac{8}{N^2 - 1}$$ N odd

Lamprey: Analytical analysis of chain of oscillators

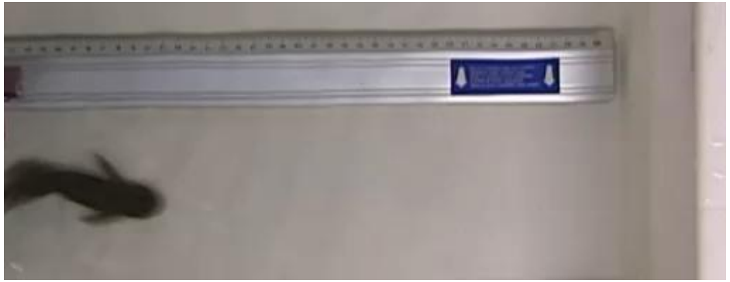
Example with 6 oscillators

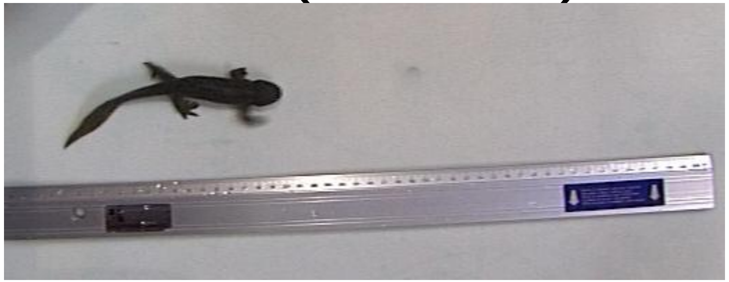


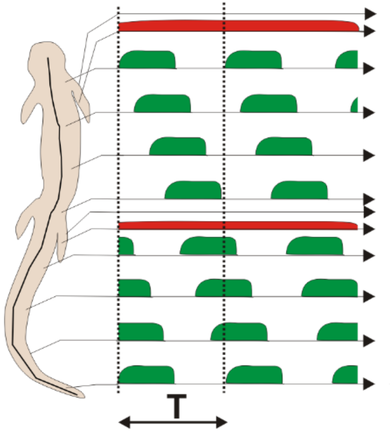




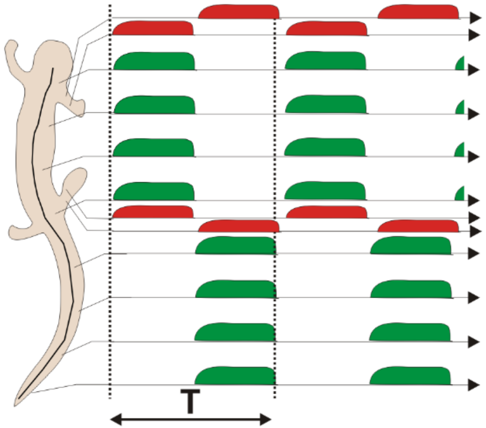
Bimodal locomotion of salamander (cartoon)





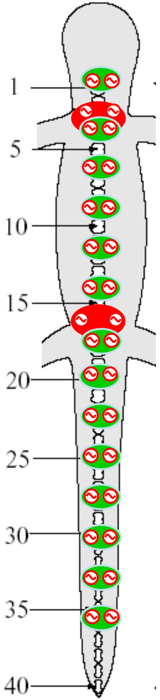


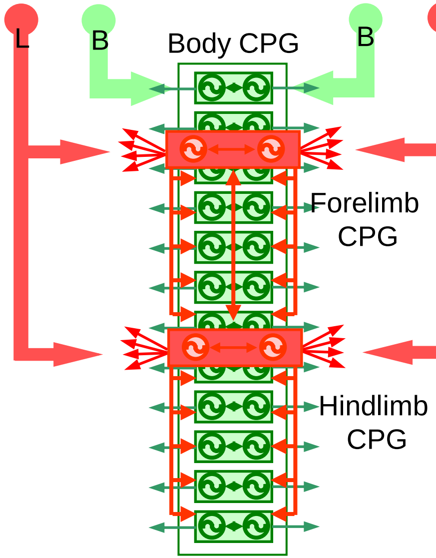
Swimming:
Traveling wave in axial muscles
Wavelength ≈ body length
Limb retractors are tonic
Short cycle durations



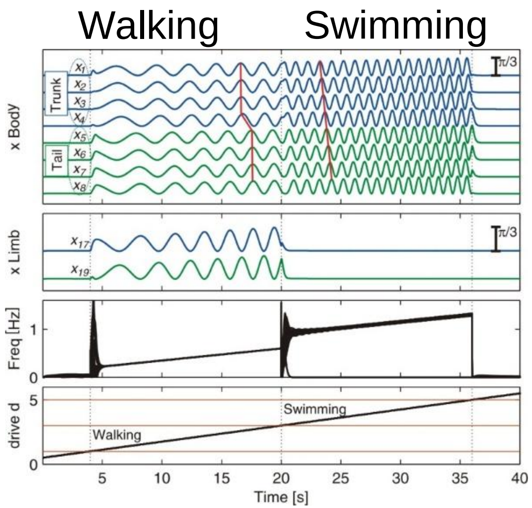
Walking:
Standing wave
Limb retractors/protactors are phasic
Longer cycle durations

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].

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:

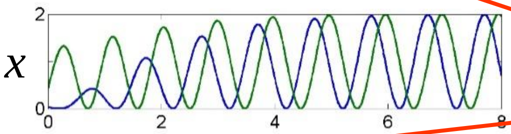
$$\dot{\theta}_i = 2\pi \nu_i + \sum_j r_j w_{ij} \sin(\theta_j - \theta_i - \phi_{ij})$$

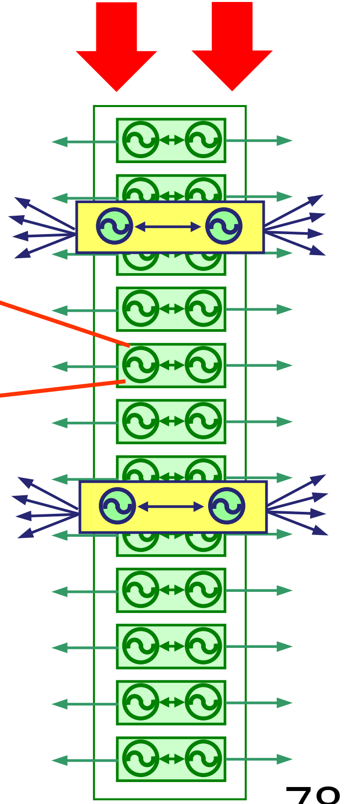
Amplitude:

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

Output:

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



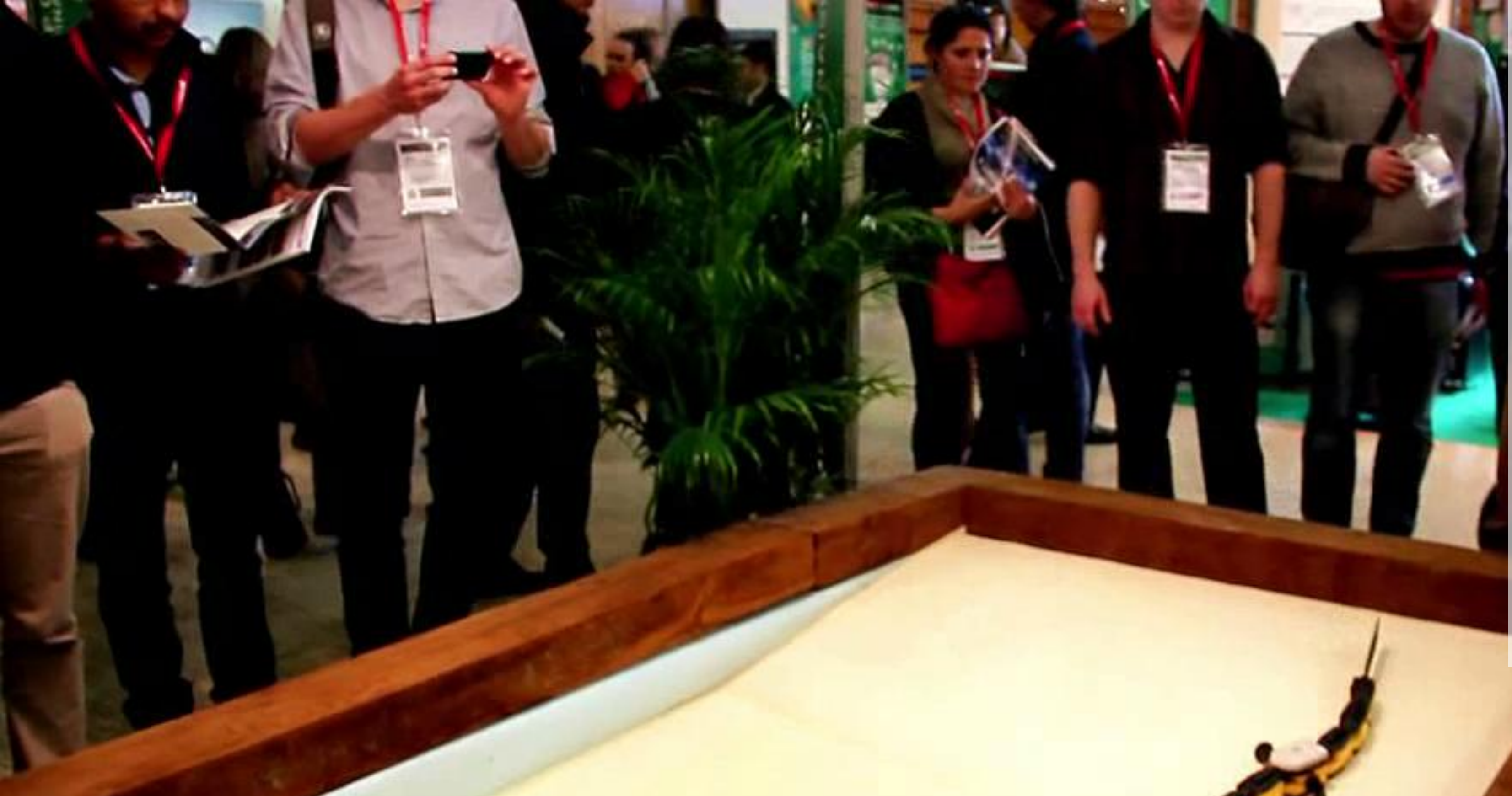


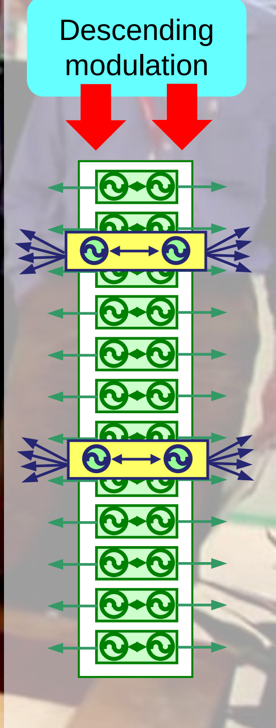
Setpoints:

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

$$\varphi_i = f(\theta_i) \qquad \text{for the (rotationd) limb motors}$$

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





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

Senses that affect locomotion

All sensing modalities affect locomotion:

- Tactile
- Proprioception
- Vestibular system (inner ear)
- Vision
- Audition
- Smell
- …

As we will see next, many of these interactions take place in the spinal cord, others involve higher parts of the brain.

Tight integration: **CPG and reflex pathways often share the same interneurons**. This explains why **reflexes are phase-dependent.**

Sensory information influencing locomotion in mammals

Spinal

- **Muscle spindles**: provide information about **length,** and changes of lengths of muscles
- **Golgi tendon organs**: provide information about (internal) **force** (i.e. tension) in muscle
- **Cutaneous receptors**: provide information about **contact forces**

Supraspinal

- **Vestibular system**: provides the sense of balance, rotational and linear **accelerations**
- **Visual system**: very rich information about visual scene, **optical flow**, colors, edges, patterns, etc.

Examples of sensory responses

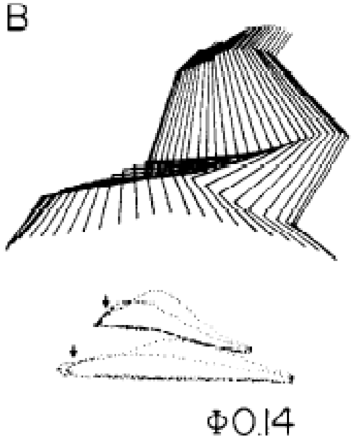
We will see next that these types of sensory information are used to implement multiple **sensory responses**, for instance:

- Stumbling correction reflex
- Leg extension reflex
- Withdrawal reflex (cross extensor reflex)
- Vestibular oculo reflex
- Posture control
- …

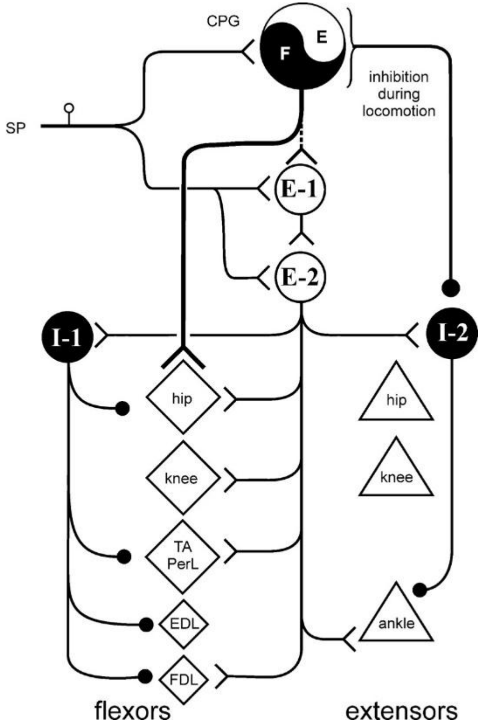
Stumbling correction reflex

Stumbling correction reflex:

- **Rapid lifting of leg when hitting something during swing**
- Useful to **avoid stumbling and falling**
- **Phase-dependent**: active only during swing, not during stance
- Note: many (most?) reflexes are phase-dependent. Reflexes share interneurons with CPG circuits. CPG activity can therefore gate/modulate reflexes



Stumbling corrective reaction: a phase-dependent compensatory reaction during locomotion. H. Forssberg. Journal of Neurophysiology Jul 1979, 42 (4) 936-953;



Jorge Quevedo et al. J Neurophysiol 2005;94:2053-2062

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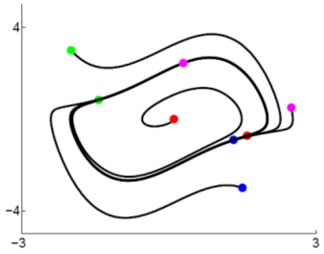
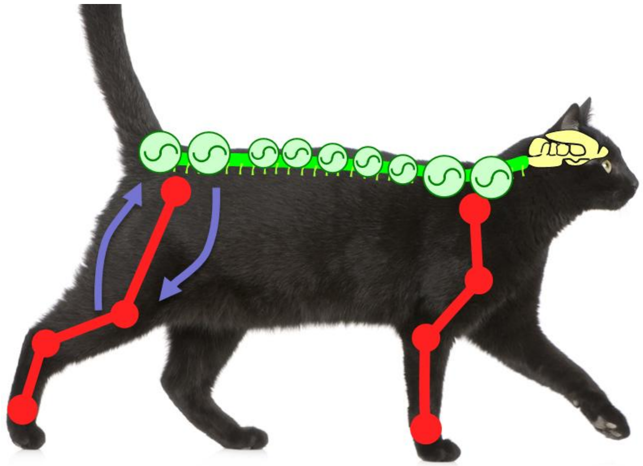
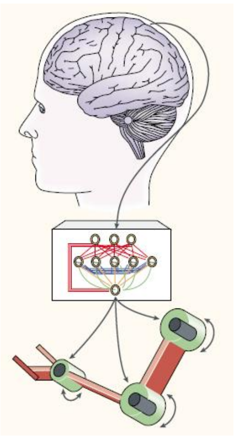
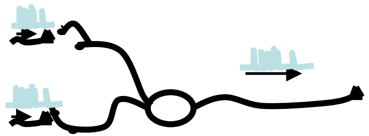


Dynamical systems

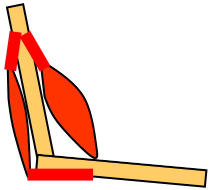




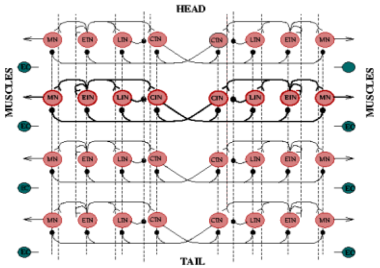
Neuroprosthetics



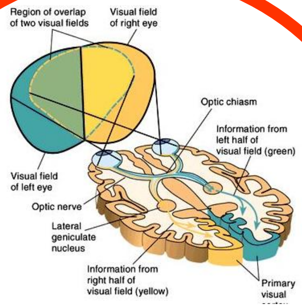
Neuron models



Muscle and Biomech. models



Motor system models



Visual system models

Feature detection in the retina:
Center-Surround response

In addition to their receptive fields, neurons are often **sensitive to special features**. E.g. the **center-surround response in retinal ganglion cells**

There are two types of ganglion cells:
On-center: maximally active with light on the center and dark on the surround
Off-center: opposite response

Stimulus: White circle

Maximal response

Minimal response

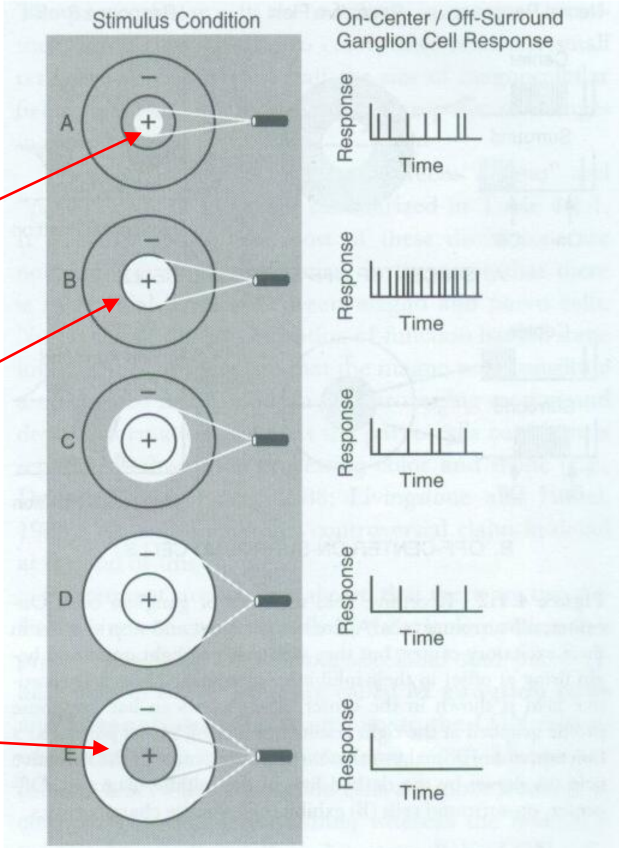


Figure 4.1.1 Responses of on-center, off-surround ganglion cells. As the size of a spot of light increases, the response of an on-center, off-surround ganglion cell first increases (A), reaching a maximum when it covers just the excitatory center (B), and then decreases as the spot falls on the inhibitory surround (C and D). Minimum response (E) occurs when light falls only on the inhibitory surround.

Center-surround

The center-surround response is generated within the retina by excitatory and inhibitory neurons.

This generates a response that corresponds to a ***mexican-hat* profile**, with **excitation in the center and inhibition on the surround**

The underlying network is a **feedforward network**

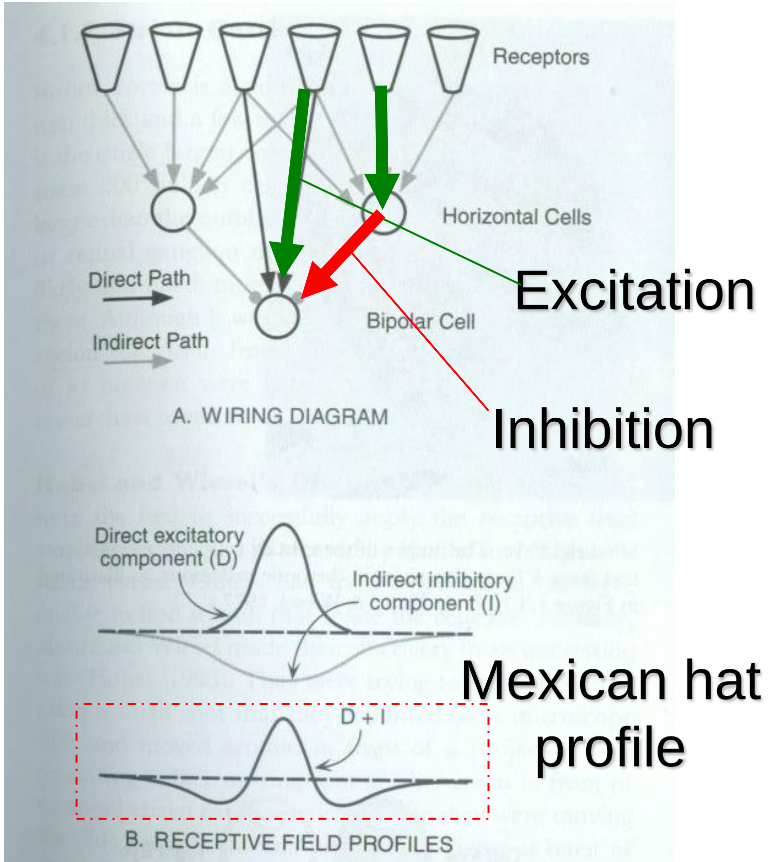
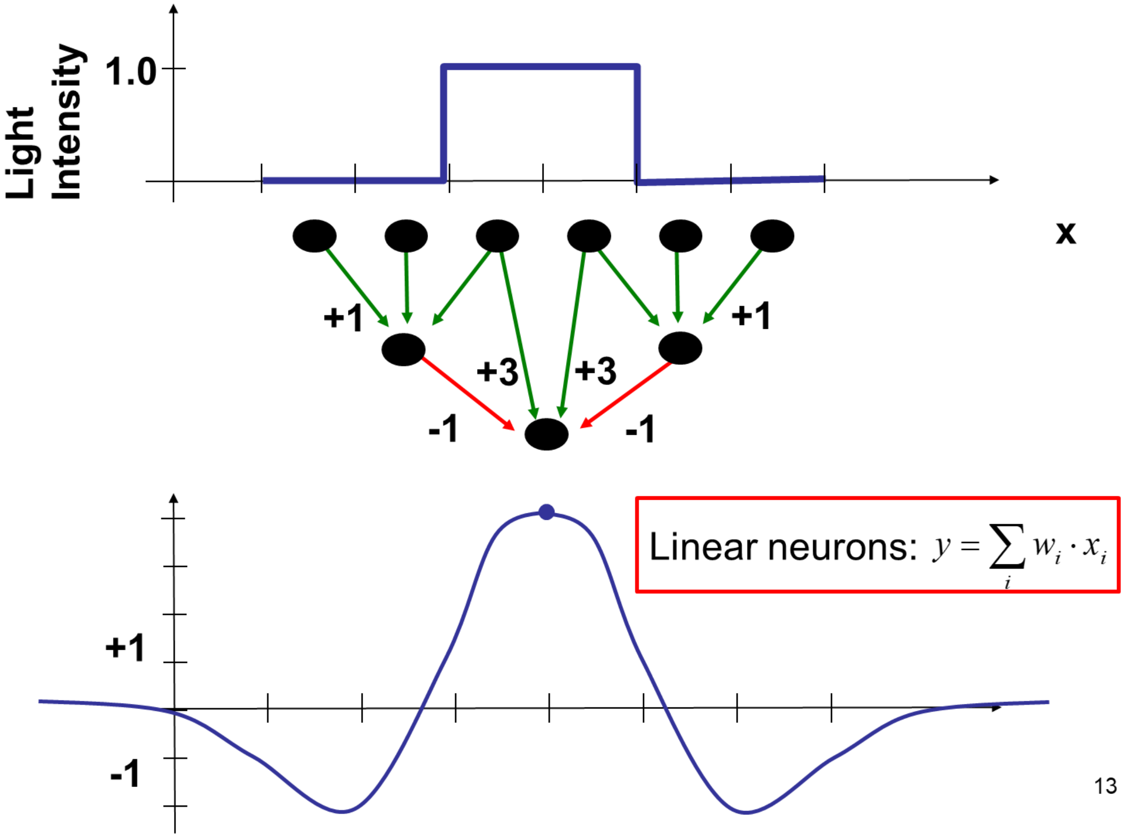


Figure 4.1.3 Neural inputs to an on-center, off-surround bipolar cell. The direct path (black connections) comes from receptors in the center of the receptive field. The indirect path of opposite polarity (gray connections) comes from receptors throughout the receptive field via horizontal cells.

Models of the center-surround response

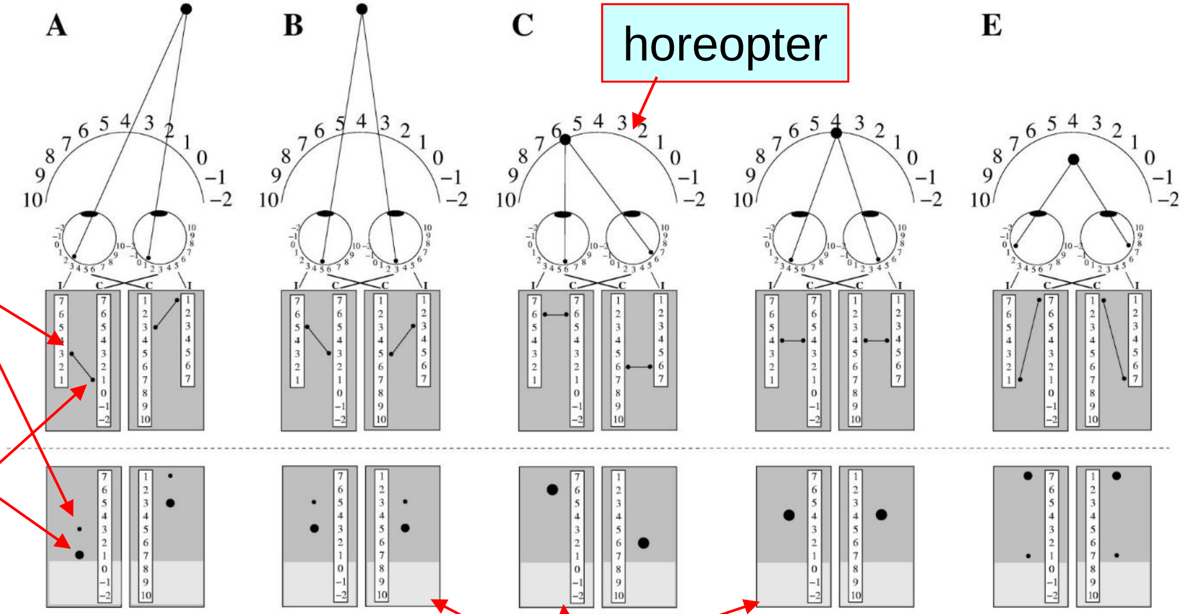


Models of salamander optic tectum

Comparisons between left and right maps in the tectum can be used to compute a target’s **angular position <u>and</u> distance**:

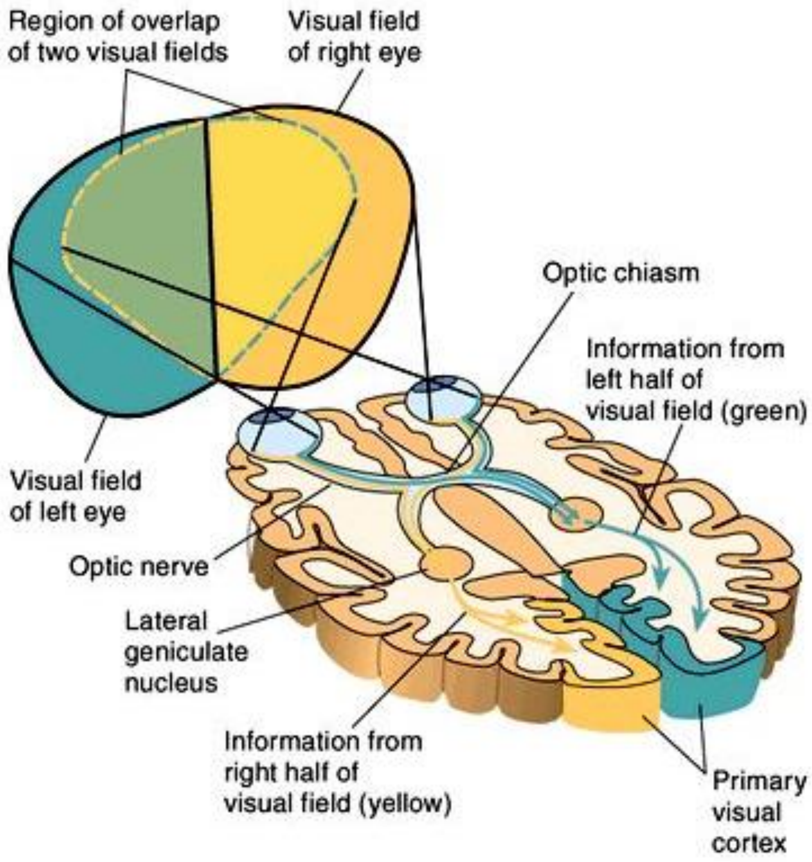
Activity due to ipsilateral connections

Activity due to contralateral connections



Recorded activity in the tectum

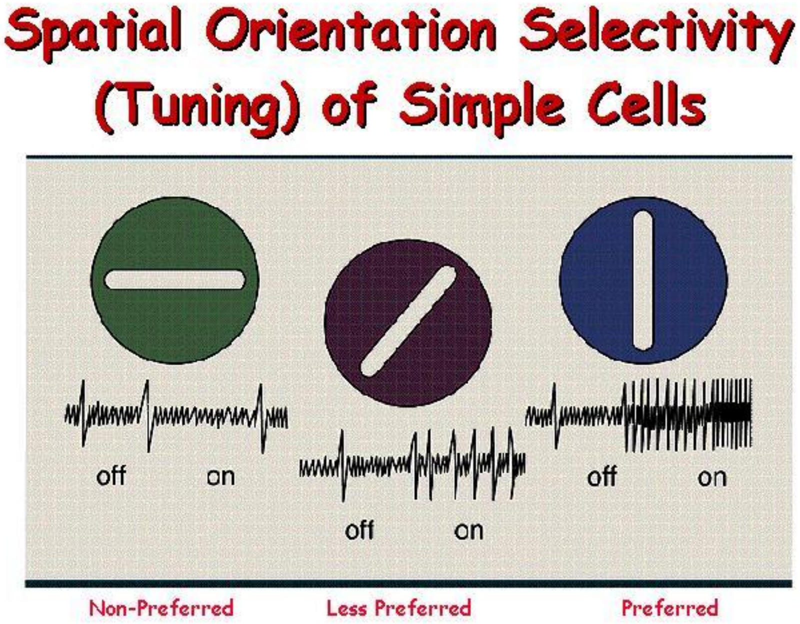
Primary Visual Pathway in primates



Visual cortex: Neuronal Tuning

In addition to responding only to stimuli in a circumscribed region of the visual space, **neurons in the visual cortex typically only respond to some specific classes of stimuli** (e.g., of given color, orientation, spatial frequency).

A neuron exhibits a ***tuning curve*** that describes the decrease of its response to stimuli increasingly different from the preferred stimulus.



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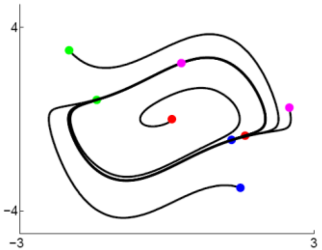
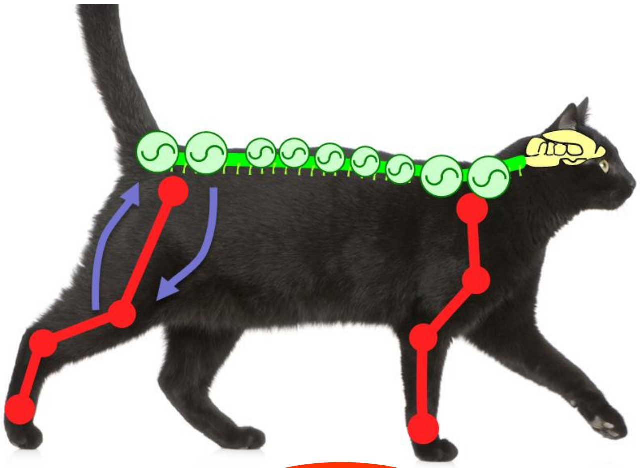
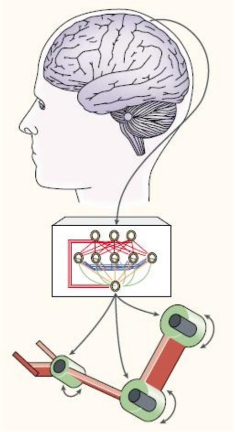
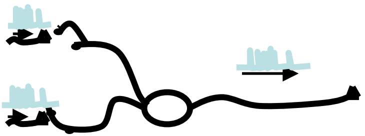


Dynamical systems

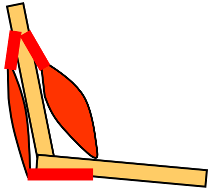




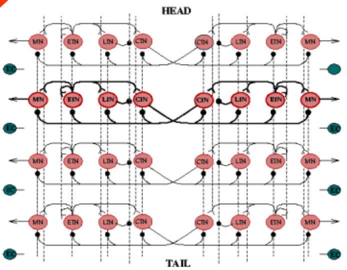
Neuroprosthetics



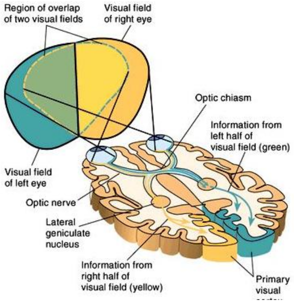
Neuron models



Muscle and Biomech. models



Motor system models



Visual system models

Models of arm movements

Topics:

- Invariants of movements
- Different school of thoughts:
  - Internal Models
  - Equilibrium Point Trajectory
  - Muscle synergies

Invariants of movements

Despite the large variety of movements that humans can make, most of our (typical) movements show several invariants.

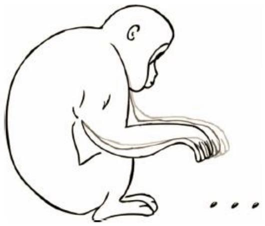
- Bell-Shaped Velocity Profile and Straight Trajectory
- Isochrony principle
- Fitts's Law
- Two Third Power Law
- Minimum Jerk hypothesis

Isochrony principle in reaching movements

Isochrony principle:

Spontaneous tendency to increase the velocity of movements depending on the distance in order to keep **execution time approximately constant**.

In other words: the velocity of voluntary movements increases proportionally with their linear extension



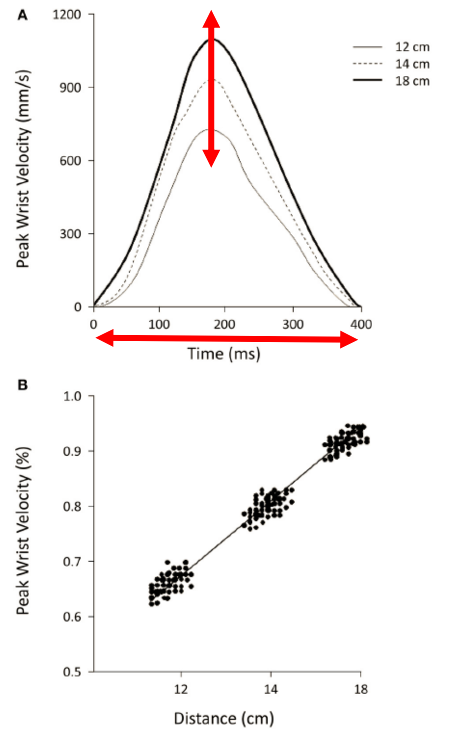
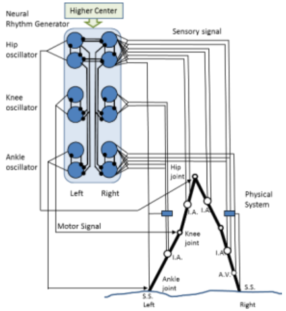


FIGURE 2 | (A) Shows the average peak wrist velocity for objects located at different distances. **(B)** Shows the relationship between mean peak wrist velocity and distance from the target. Values of peak velocity were normalized to the highest value for each subject. A linear regression very accurately fits the data points. The data outlined in the two panels are from one representative subject (*N* = 8).

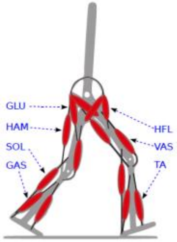
Sartori et al 2013

Viviani, P., and McCollum, G. (1983). The relation between linear extent and velocity in drawing movements.
Sartori, L., Camperio-Ciani, A., Bulgheroni, M., & Castiello, U. (2013). Reach-to-grasp movements in Macaca fascicularis monkeys: the Isochrony Principle at work. *Frontiers in psychology*, *4*.

Neuromechanical models of human locomotion

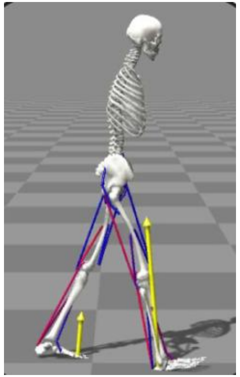


Taga 1991, 1995



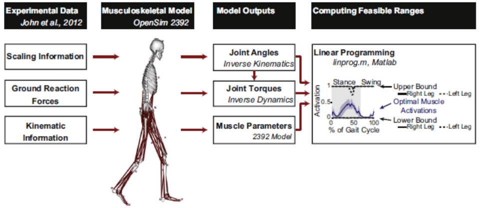
Geyer and Herr, 2010.
Song and Geyer 2015

Lee et al 2019



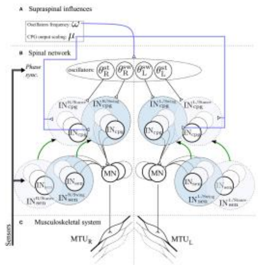
Ong et al 2019

Y. Nakamura lab
(Sreenivasa et al 2012)



L. Ting lab (Simpson et al 2015)

Falisse et al 2019



Dzeladini et al 2014

Geyer and Herr's sensory-driven model

Sensory-driven model

+

7 muscles per leg

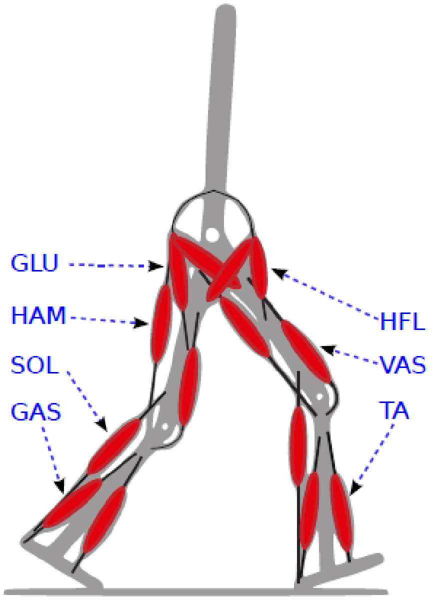
+

Different reflexes

(positive and negative force feedback, limits of overextension, …)

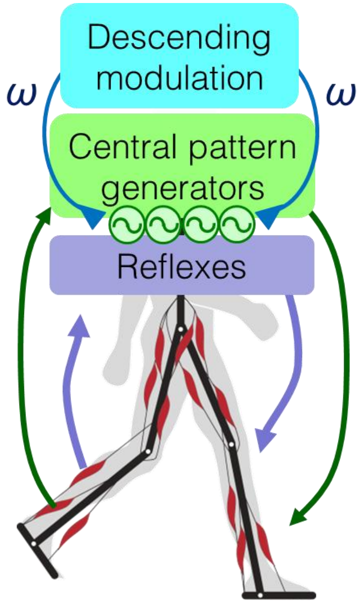
+

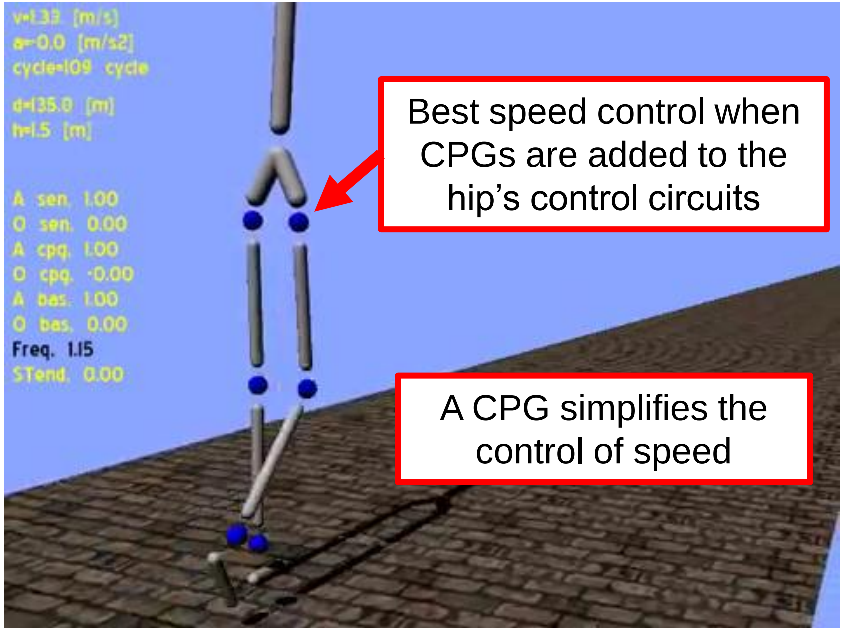
Posture control (torso angle)



H Geyer, HM Herr. A muscle-reflex model that encodes principles of legged mechanics produces human walking dynamics and muscle activities. **IEEE Trans Neural Syst Rehabil Eng** 18(3): 263-273, 2010.

Speed control





Dzeladini et al, The contribution of a central pattern generator in a reflex-based neuromuscular model, ***Frontiers in Human Neuroscience***, Vol 8, 371, 2014

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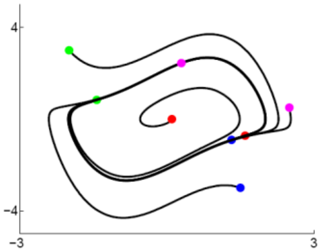
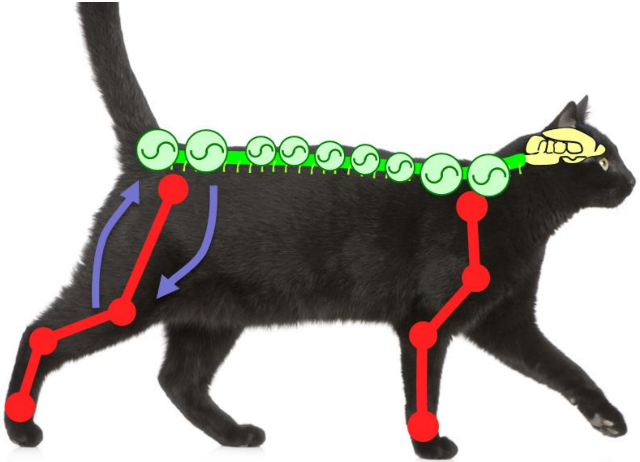
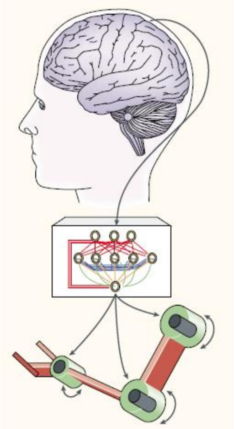
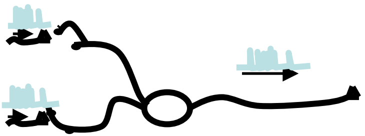


Dynamical systems

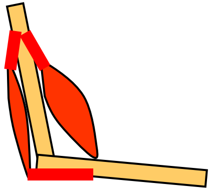




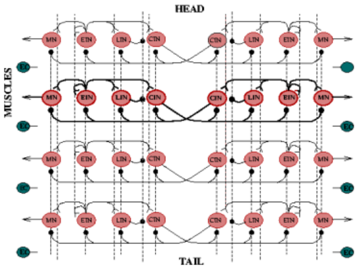
Neuroprosthetics



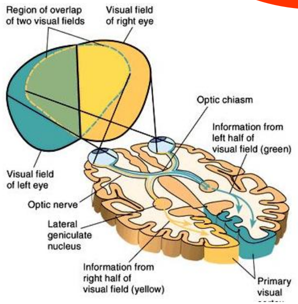
Neuron models



Muscle and Biomech. models

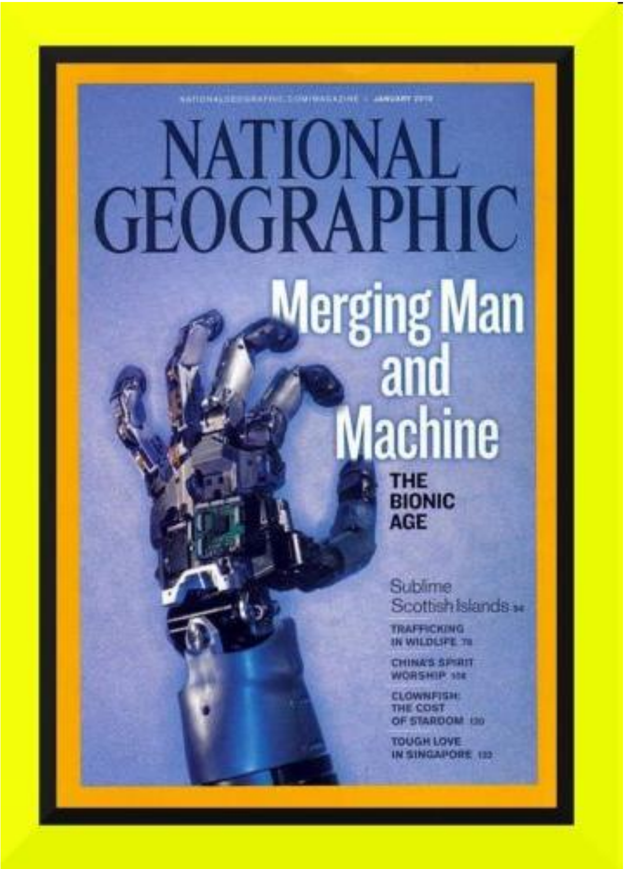


Motor system models



Visual system models

Neuroprosthetics



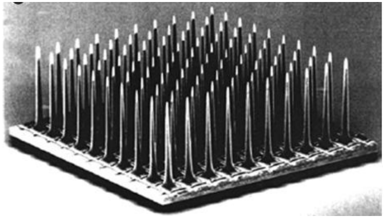
Neuroprosthetics

Topics:

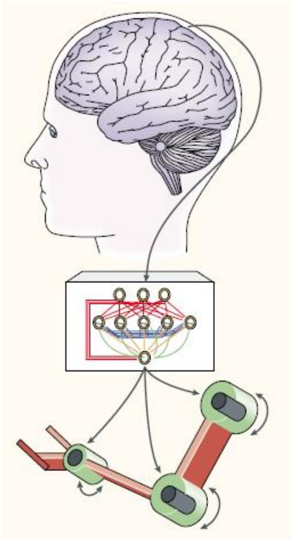
- Restoring mobility:
  - Prosthesis versus orthosis
  - Spinal cord stimulation
  - Functional Electromyographic stimulation
  - Control of lower limb orthosis

- Restoring upper limb movements:
  - Arm/hand replacement
  - Cortical implants and population coding

Cortical implants and population coding



Advances in **multi-array electrodes**



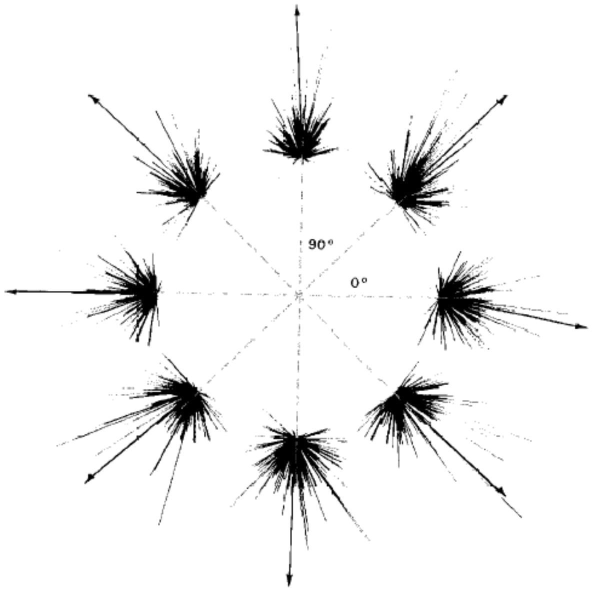
And in the **understanding of movement coding in the cortex**

have allowed the design of **cortical interfaces**

(Nicolelis 2003)

Population Vector

E.g. **encoding of arm movements in the motor cortex**



$$\vec{v}_{\text{pop}} = \sum_{a=1}^{4} \left(\frac{r}{r_{\text{max}}} \right)_a \vec{c}_a \, .$$

Figure 3.6: Comparison of population vectors with actual arm movement directions. Results are shown for eight different movement directions. Actual arm movement directions are radially outward at angles that are multiples of 45°. The groups of lines without arrows show the preferred direction vectors of the recorded neurons multiplied by their firing rates. Vector sums of these terms for each movement direction are indicated by the arrows. The fact that the arrows point approximately radially outward shows that the population vector reconstructs the actual movement direction fairly accurately. (Figure adapted from Kandel et al., 1991 based on data from Kalaska et al., 1983.)

Interfacing with a robot

Andrew Schwarz and colleagues, U. of Pittsburgh

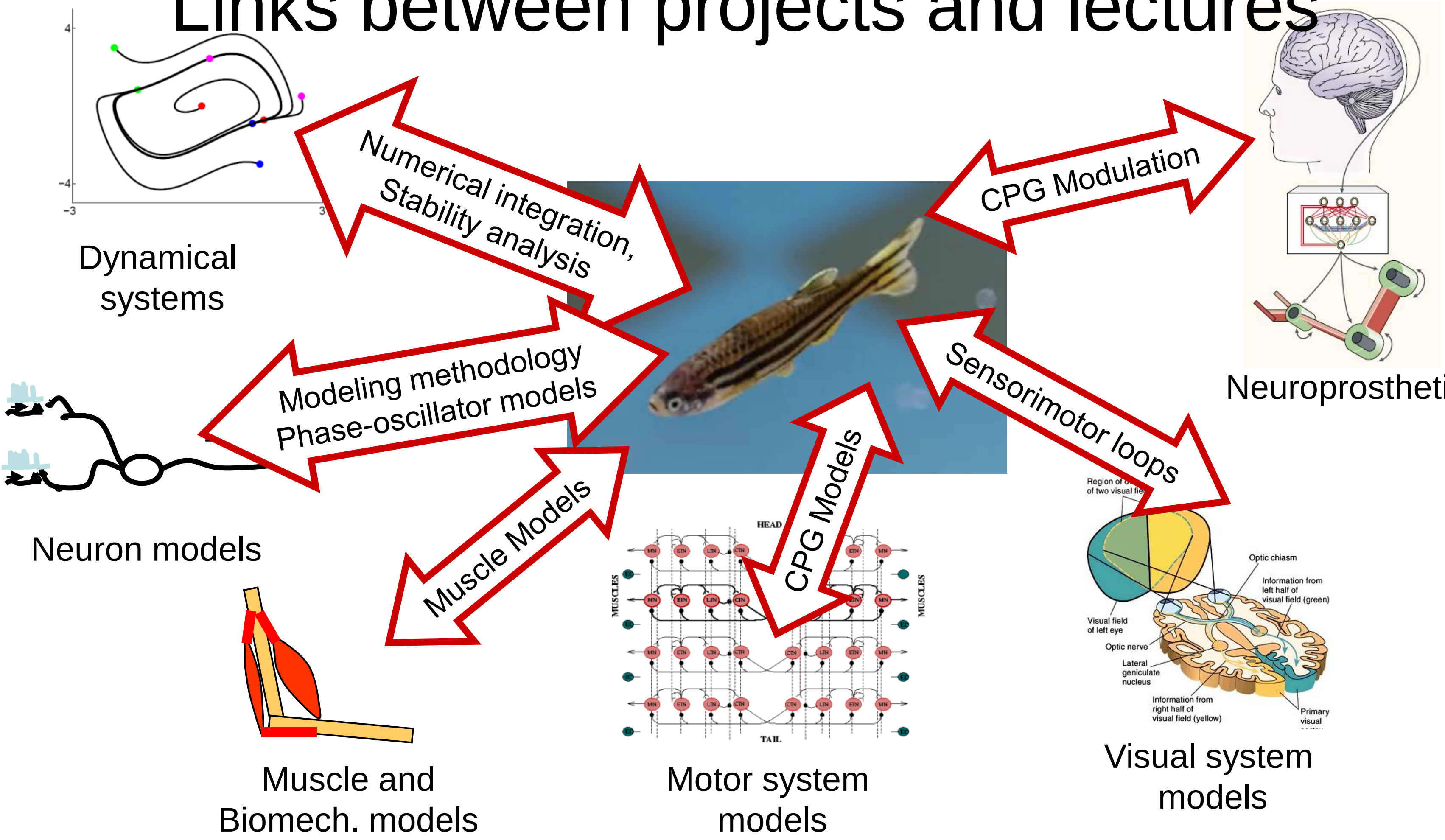
Expected outcomes of this course

You will (hopefully) get:

- An **overview of how numerical tools are used in biology**, as part of a scientific methodology
- A **mathematical background** for designing and analyzing models
- Illustrations of interesting **interactions between biology and robotics/computer science**

- **Practical experience of designing, programming, and testing your own models**
- Practical experience of **writing scientific reports**

Links between projects and lectures



Possible exam questions

- What is **a computational model** and why is it useful in biology?
- What is the **difference between inductive and deductive reasoning**? Which approach is typically used in computational motor control (answer: inductive reasoning)
- **Methodology of modeling**: What are the key steps in developing a computational model?
- **Discuss how models have been used to investigate the lamprey locomotor circuit.** Give two different examples of models at different levels of abstraction and how they were selected to answer specific scientific questions (see also next lectures).

End of Lecture 1:

Practicals start this afternoon at 13:15 in INF2