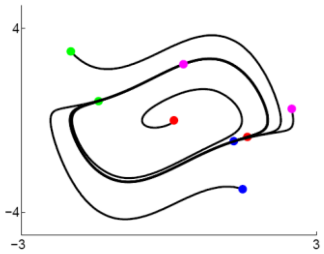
Computational Motor Control

Lecture 10:

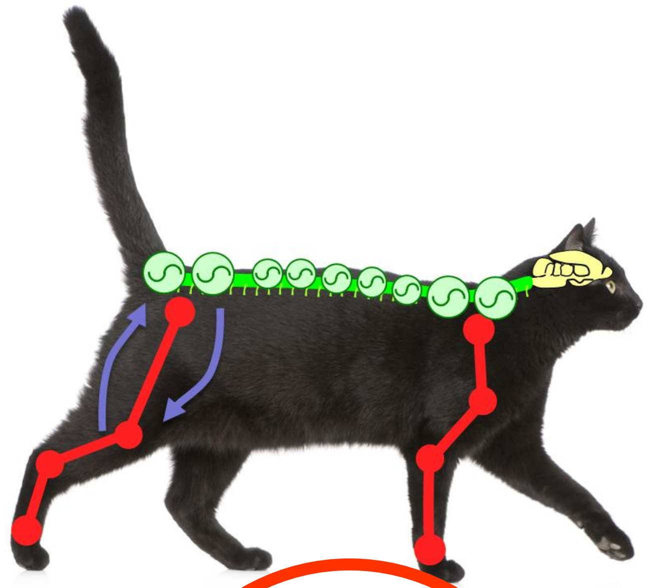
Models of arm movements

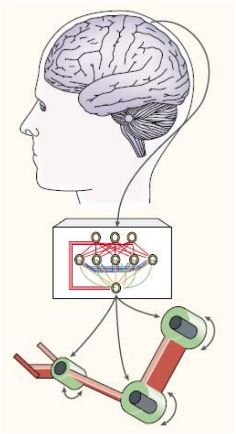
Auke Jan Ijspeert

Contents of lectures

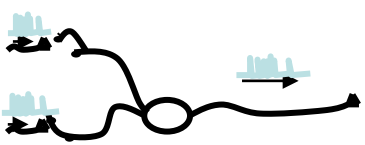


Dynamical systems

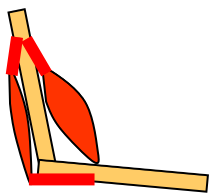




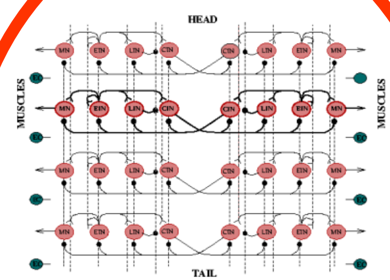
Neuroprosthetics



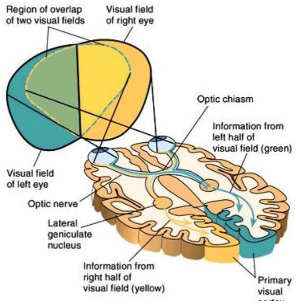
Neuron models



Muscle and Biomech. models



Motor system models



Visual system models

Lecture:
Models of arm movements

Topics:

- Invariants of arm movements

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

- Population coding

Invariants of arm 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

Note: these properties are **only valid for stereotypical movements** (e.g. movements done without thinking). When needed, **the brain can override those and perform almost arbitrary movements**.

Bell-shaped velocity profile

The **velocity profile** for reaching movements is **approximately bell-shaped** and the trajectory of the hand in free space is close to **a straight line**.

Morasso, P. Spatial control of arm movements. Exp. Brain Research, 42, pp. 223-227, 1981.

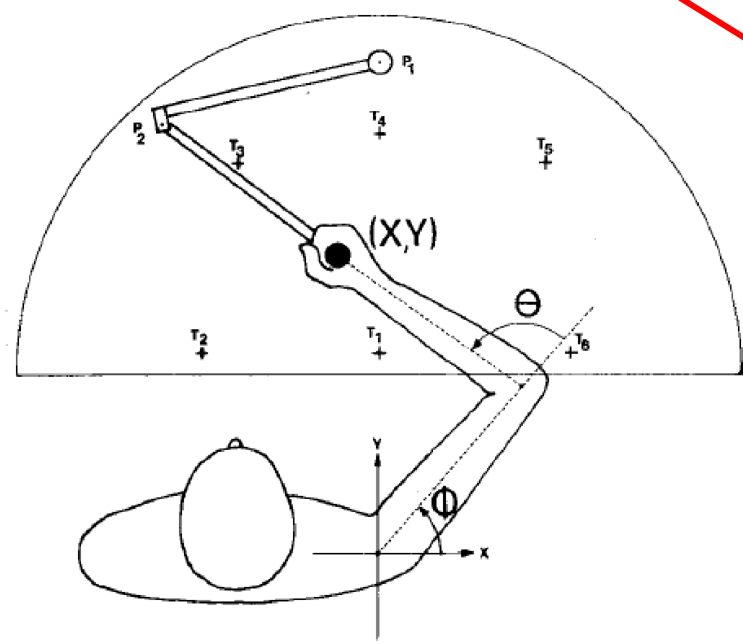
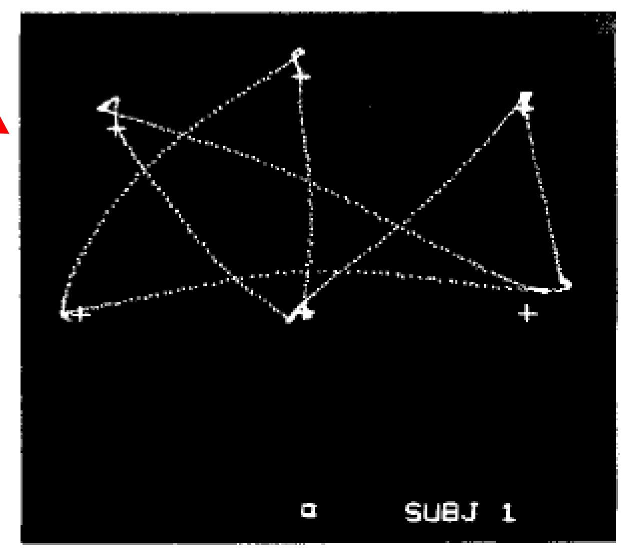


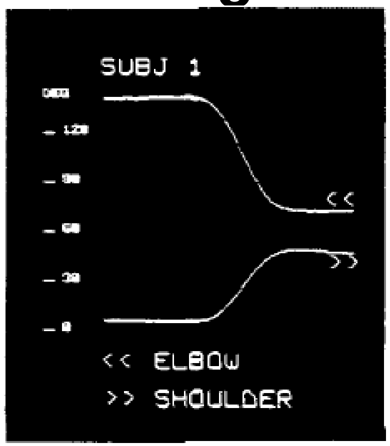
Fig. 1. Experimental setup for the study of reaching movements in the horizontal plane. Recorded variables: (X, Y) Cartesian Coordinates of the Hand, (Φ, θ) Angular Coordinates of the Joints (wrist movements were not allowed). Visual targets: $T_1, \ldots T_6$.



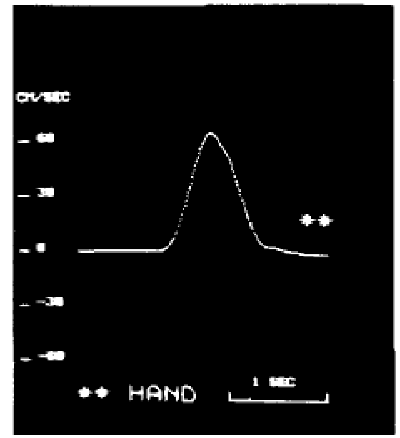
Bell-shaped velocity profile

The **velocity profile** for a reaching movements is **approximately bell-shaped** and the trajectory of the hand in free space is close to **a straight line**.

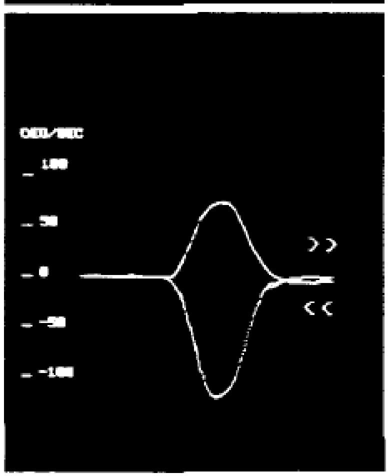
Joint angles:



hand velocity:



Joint angle velocities:

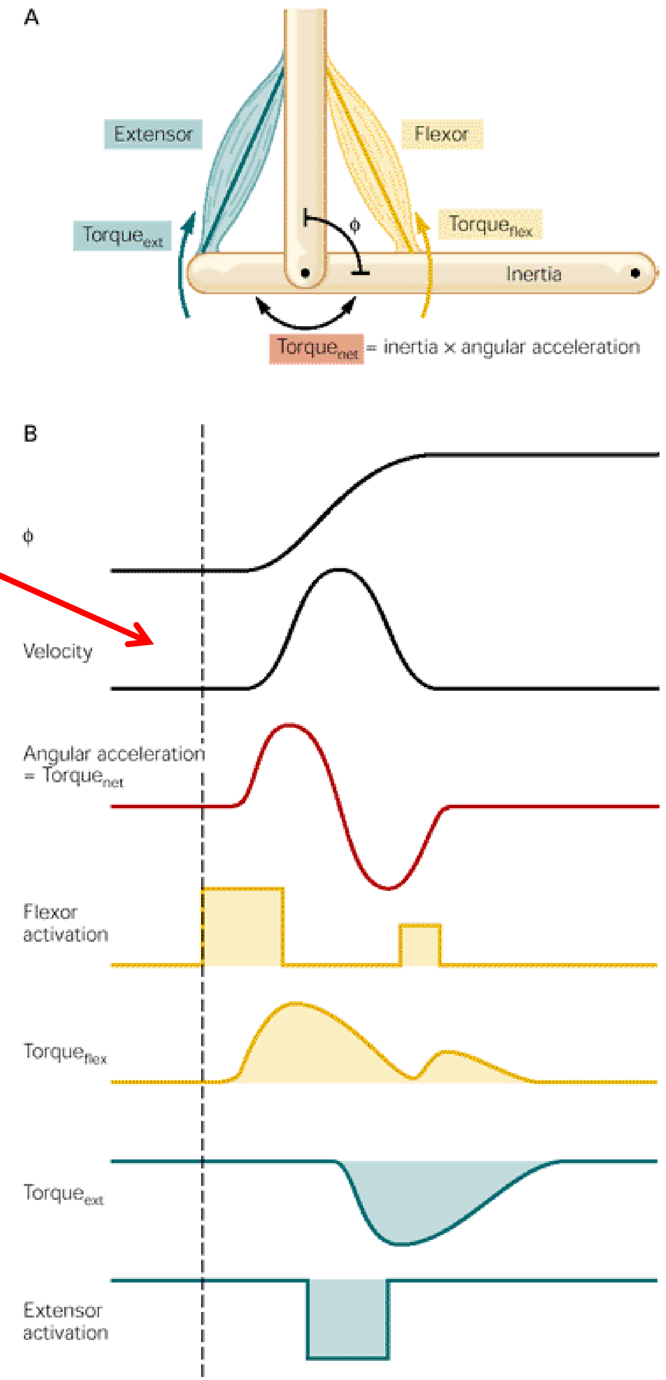


Bell-shaped profiles

Morasso, P. Spatial control of arm movements. Exp. Brain Research, 42, pp. 223-227, 1981.

Previous lecture: Muscles

Note: we had seen this type of <u>bell-shaped velocity profile</u> in the lecture on muscle models.

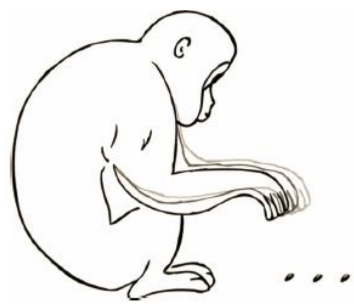


Isochrony principle in reaching mvts

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



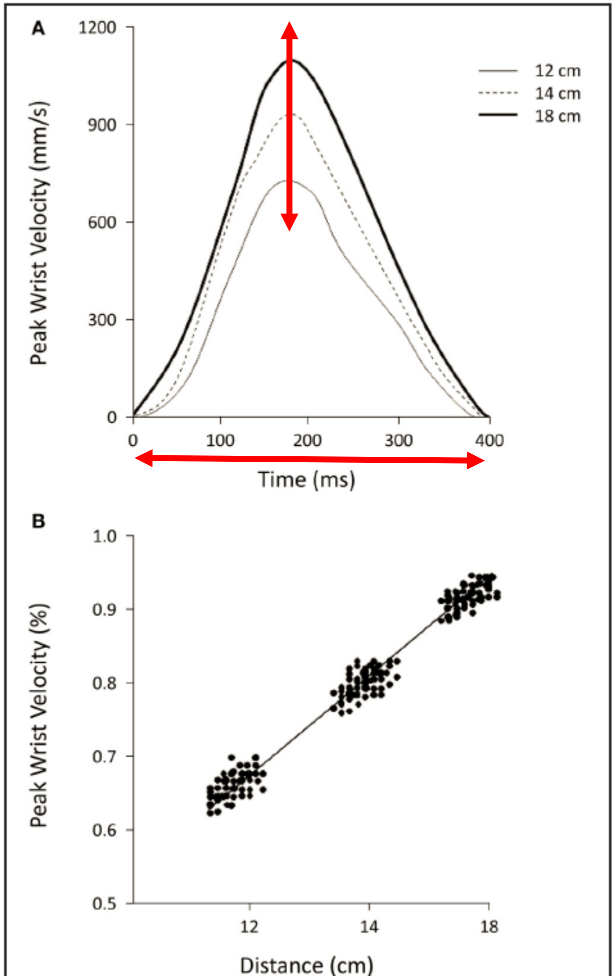


FIGURE 2 | (A) Shows the average peak wrist velocity for objects located at different distances. **(B)** Shows the relationship between mean peak wrist velocity and distance from the target. Values of peak velocity were normalized to the highest value for each subject. A linear regression very accurately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

Sartori et al 2013

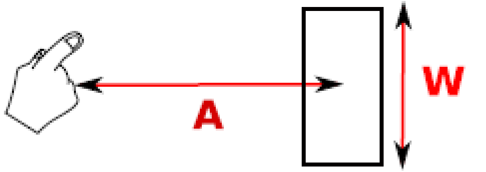
Viviani, P., and McCollum, G. (1983). The relation between linear extent and velocity in drawing movements.
Sartori, L., Camperio-Ciani, A., Bulgheroni, M., & Castiello, U. (2013). Reach-to-grasp movements in Macaca fascicularis monkeys: the Isochrony Principle at work. *Frontiers in psychology*, *4*.

Fitts' law

Fitts' Law: this law reflects the relationship between the difficulty to reach the target and the duration of the movement. It corresponds to a **speed/accuracy trade-off**. **Movements that require higher accuracy are performed slower.**

The duration of a fast motion to a target can be approximated by:

$$T = a + b \log_2 \left(\frac{A}{W} + 1 \right)$$



where A is the amplitude of the movement, W the width of the target and a, b are constants determined in an empirical way. The term $\frac{A}{W} + 1$ is called the **index of difficulty**.

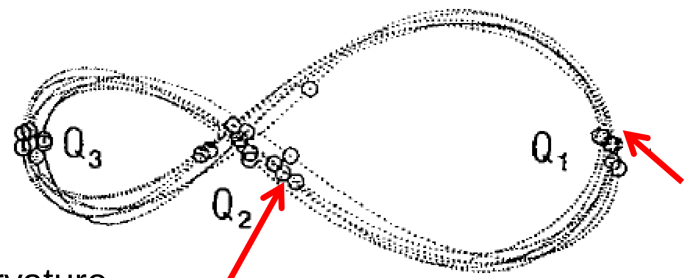
Note: the isochrony principle (previous slide) is therefore valid for movements with the same index of difficulty.

Fitts, P.M. The information capacity of the human motor system in controlling the amplitude of movement, Journal of Experimental Psychology, 47(6), pp. 381-391, 1954.

R.W. Soukoreff, I.S. MacKenzie / Int. J. Human-Computer Studies 61 (2004) 751–789

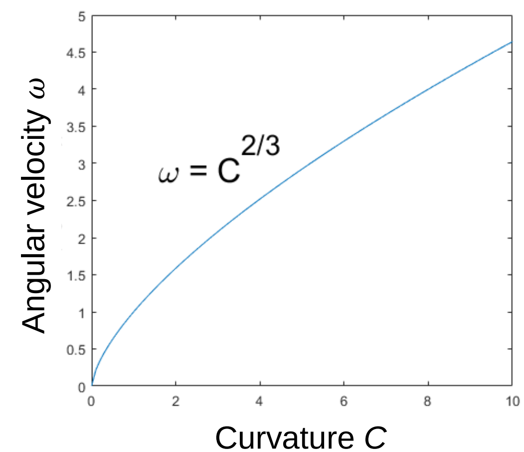
Two-Third Power Law

Two-Third Power Law: When drawing movements in the air on on paper, there is a **constant relationship between the kinematics** of elliptical motion **and the geometrical properties** of the trajectory.



High curvature
High angular velocity
Low instantaneous speed

Low curvature
Low angular velocity
High instantaneous speed



Two versions:

Angular velocity: $\omega(t) = kC(t)^{2/3}$

Instantaneous speed: $v(t) = kC(t)^{-1/3}$

Where k is a constant,
C(t) is the curvature of the hand trajectory,
C=1/R, where R is the radius

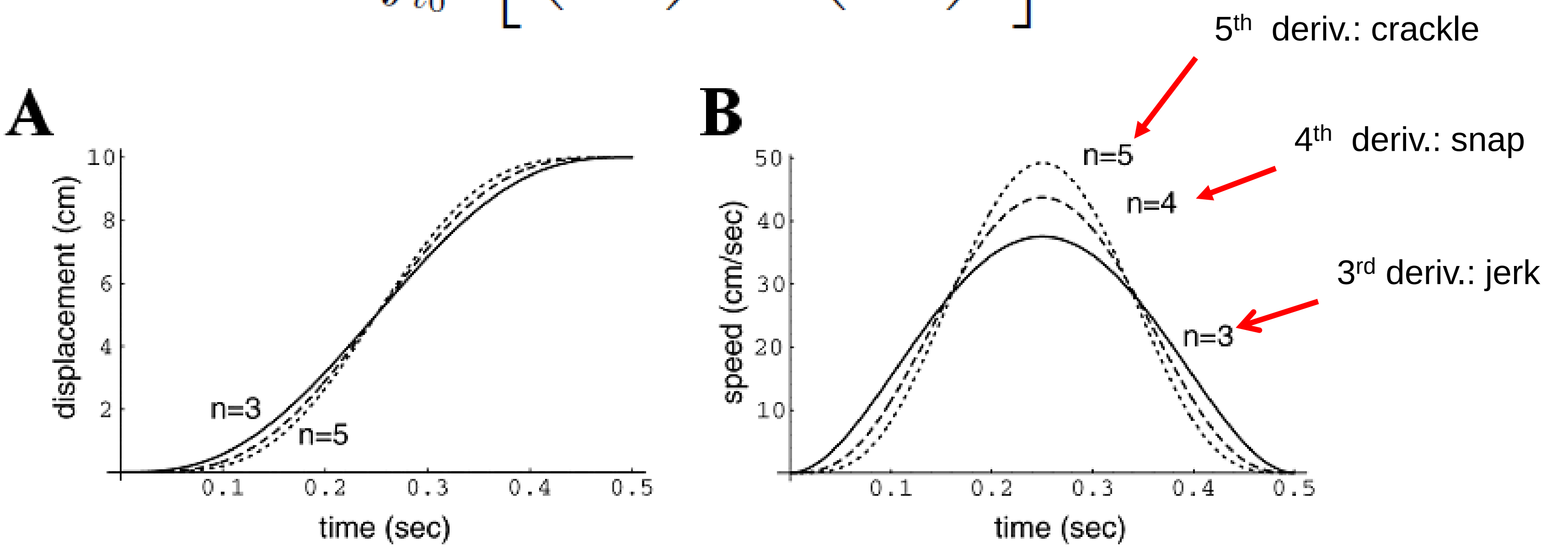
Note: $v = R\omega = \frac{\omega}{C}$
hence the $2/3$ vs $-1/3$ power laws

Lacquaniti. F.. Terzuolo. C.A. and Viviani, P. (1983) The law relating kinematic and figural aspects of drawing movements Acta Psycho. 54,115-130

Minimum Jerk

Human arm motions are **smooth.** They appear to **minimize jerk**, i.e. the **derivative of acceleration**.

Cost function: $$C = \int_{t_0}^{t_1} \left[\left(\frac{d^3x}{dt^3} \right)^2 + \left(\frac{d^3y}{dt^3} \right)^2 \right] dt$$



Flash, T., & Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *The journal of Neuroscience*, *5*(7), 1688-1703.

Shadmehr and Wise (2005), Computational Neurobiology of Reaching and Pointing: A Foundation for Motor Learning, MIT Press, Cambridge.

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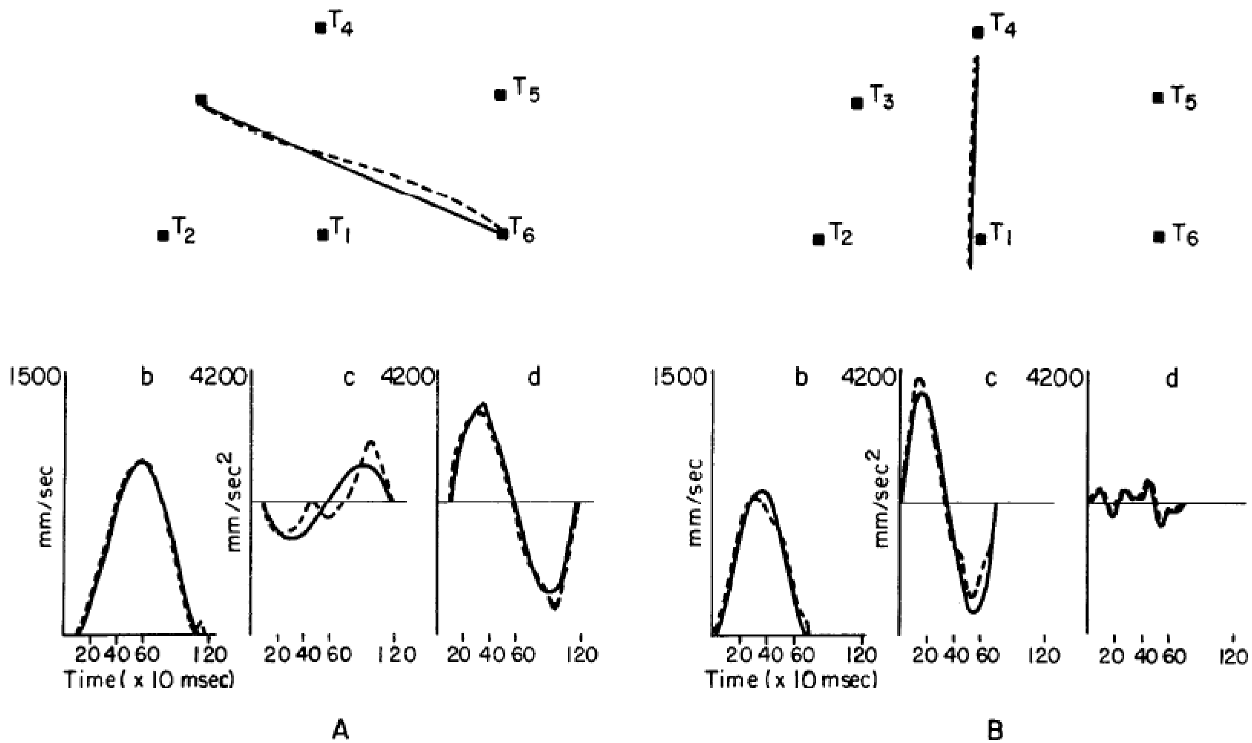

Figure 3. Overlapped predicted (*solid lines*) and measured (*dashed lines*) hand paths (*a*), speeds (*b*), and acceleration components along the *y*-axis (*c*), and along the *x*-axis (*d*) for two unconstrained point-to-point movements. *A*, A movement between targets 3 and 6. *B*, A movement between targets 1 and 4.

Good match between experimental data, and trajectories that minimize jerk

Flash, T., & Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *The journal of Neuroscience*, *5*(7), 1688-1703.

Minimum Jerk

Also good prediction of **via-point** experiments, i.e. reaching a target, while passing through a specific via point

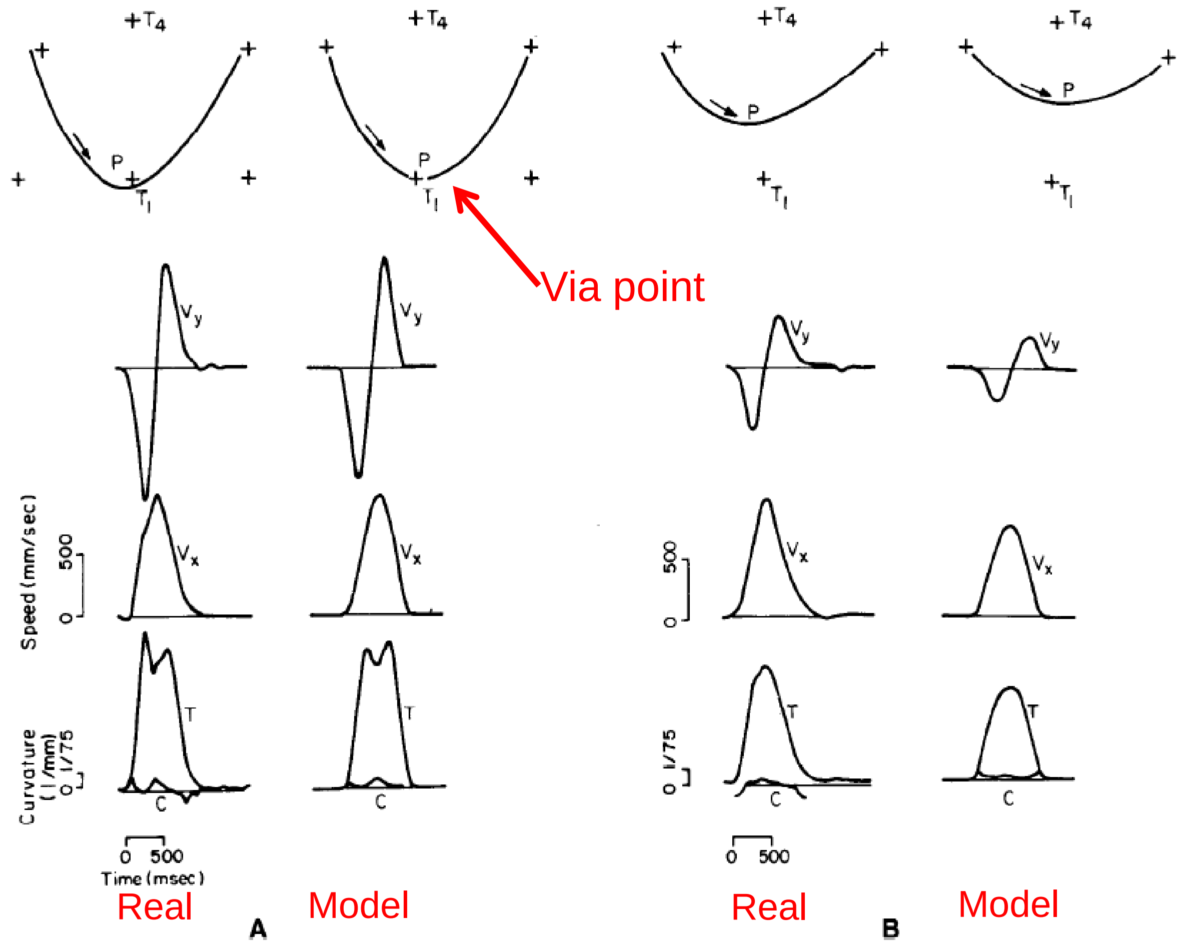

Figure 5. Representative examples of comparison between measured (*Real, left columns*) and predicted (*Model, right columns*) trajectories from a "via-point" experiment. Displayed are the hand paths, *P*, and plots of hand speed, *T*, curvature, *C*, and velocity components, V_x and V_y, versus time. The movement reversed its direction along the *y*-axis. *A*, The intermediate target was located at equal distances from the initial and final targets. *B*, The intermediate target was at equal distances from the movement end-points but closer to the line connecting them.

Flash, T., & Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *The journal of Neuroscience*, *5*(7), 1688-1703.

Relationship between invariants

One can find **links between these relationships**, e.g. between minimum jerk, 2/3 power law, and the isochrony principle, cf

Viviani, P., & Flash, T. (1995). Minimum-jerk, two-thirds power law, and isochrony: converging approaches to movement planning. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(1), 32.

Richardson, M. J., & Flash, T. (2002). Comparing smooth arm movements with the two-thirds power law and the related segmented-control hypothesis. *The Journal of neuroscience*, *22*(18), 8201-8211.

Huh, D., & Sejnowski, T. J. (2015). Spectrum of power laws for curved hand movements. *Proceedings of the National Academy of Sciences*, *112*(29), E3950–E3958. https://doi.org/10.1073/pnas.1510208112

Lecture:
Models of arm movements

Topics:

- Invariants of movements

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

- Population coding

Different schools of thoughts

There are different school of thoughts to explain the control of discrete (point-to-point) movements in humans:

The **internal model** based approach (IM) postulates that the CNS can plan kinematic trajectories and then reproduce them accurately thanks to internal models (both direct and inverse models).

The **equilibrium point hypothesis** approach (EPH) postulates that the CNS specifies a series of equilibrium positions of muscles, and relies on reflex loops and the spring-like properties of muscles to move the limb.

The **muscle synergies** approach postulates that the CNS and especially the spinal cord implements discrete pattern generators that reduce the dimensionality of control and that can serve as motor primitives for more complex movements.

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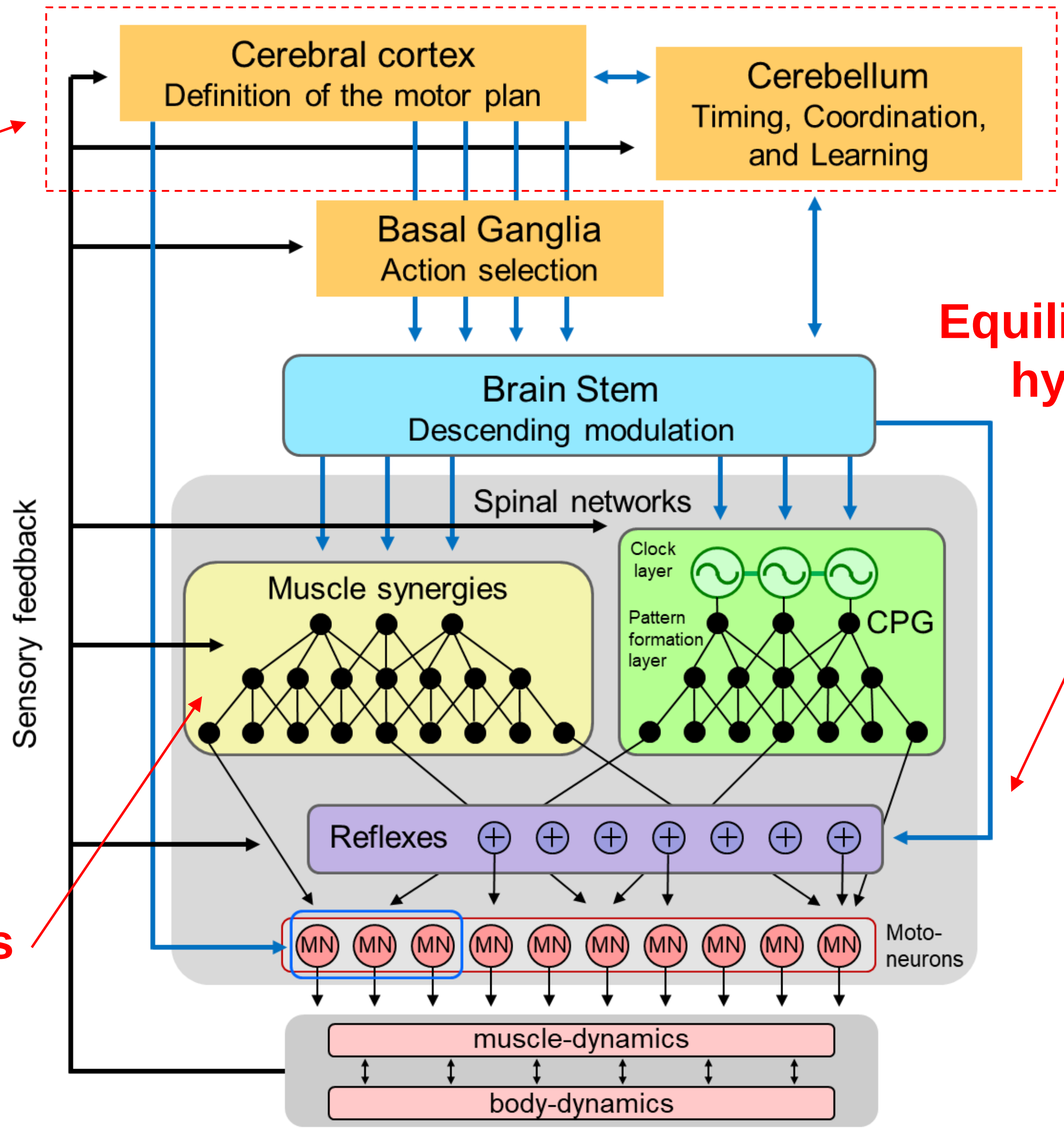
Different schools of thoughts

Internal model based approach

Equilibrium point hypothesis

Muscle synergies



Internal models

The **internal model** based approach (IM) postulates that the CNS can plan kinematic trajectories and then reproduce them accurately thanks to internal models.

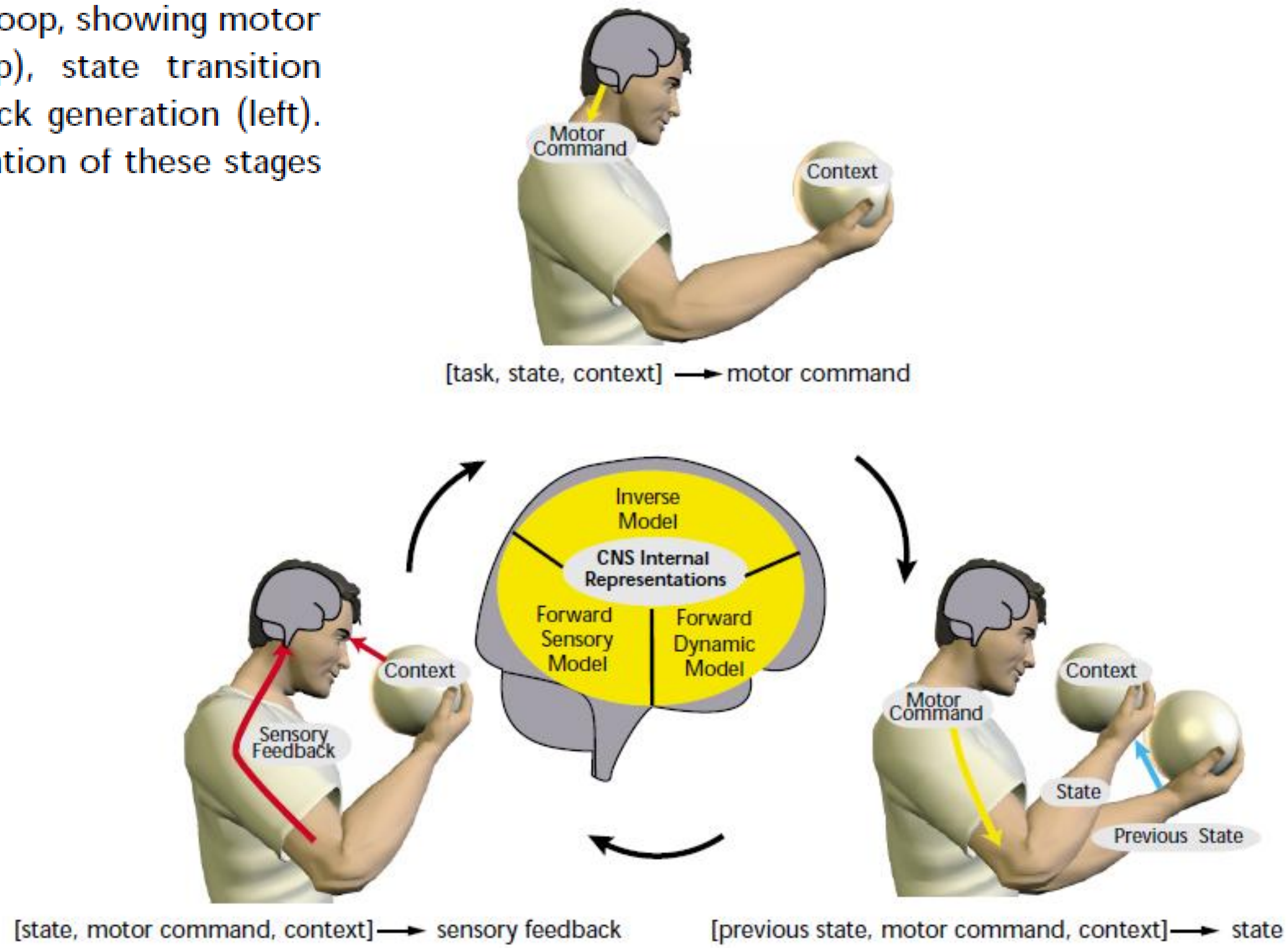
An **internal model** is **a neural structure emulating the physical processes** involved into

- the transformation of neural command into actual limb movements (**direct model**)
- the prediction of the neural command needed to perform a limb movement (**inverse model**)

Among other things, internal models allow the central nervous system to imagine the effect of movements without performing them.

Internal models

Fig. 1. The sensorimotor loop, showing motor command generation (top), state transition (right) and sensory feedback generation (left). Center, internal representation of these stages within the CNS.



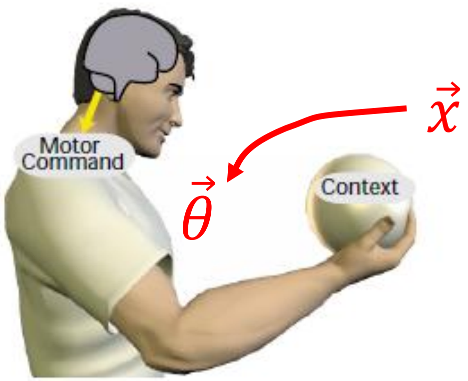
Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *nature neuroscience*, *3*, 1212-1217.

Example of internal models

Inverse kinematics model: maps a desired position $\vec{x}$ of the hand to (multiple) joint angles $\vec{\theta}$ in the arm

Forward kinematics: $\vec{x} = f(\vec{\theta})$

Inverse kinematics: $\overrightarrow{\theta} = f^{-1}(\vec{x})$



This is an **ill-posed problem for redundant systems** like arms, i.e. with more degrees of freedom (e.g. 7) than those needed to determine the hand position (3)

Redundancy can be solved by trying to stay close to preferred postures.

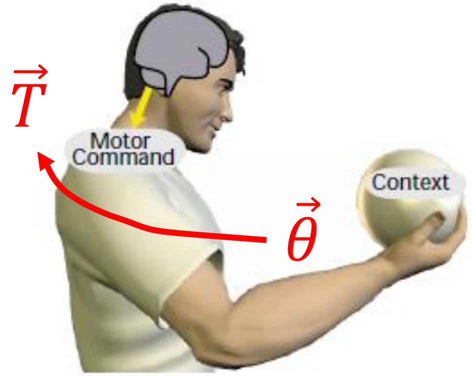
This is a **geometrical problem**.

Example of internal models

Inverse dynamics model: maps a desired posture of the arm in terms of joint angles $\vec{\theta}$ (and possibly joint angle velocities, and accelerations) to the necessary torques $\vec{T}$ (or muscle activations).

Forward dynamics: $[\vec{\theta}, \dot{\vec{\theta}}, \ddot{\vec{\theta}}] = g(\vec{T})$

Inverse dynamics: $\vec{T} = g^{-1}(\vec{\theta}, \dot{\vec{\theta}}, \ddot{\vec{\theta}})$

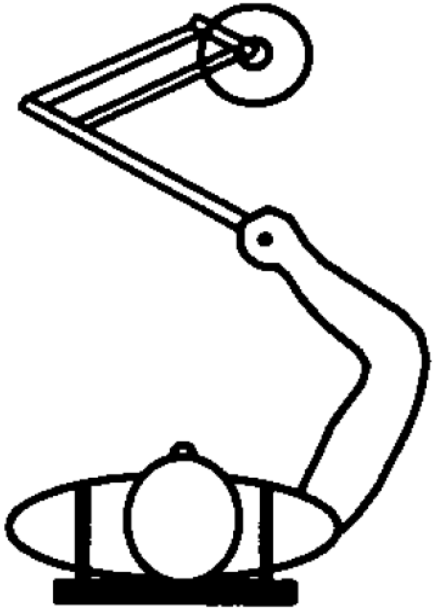


This is a complex high-dimensional and nonlinear problem since it **depends on the physics of the arm** (load, gravity, inertia, etc.). It is a problem involving **dynamics**.

Experiments to investigate internal models

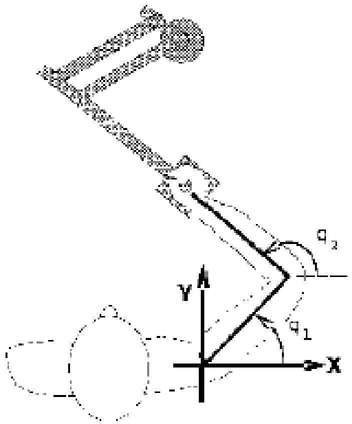
Researchers have designed several experiments to investigate whether the central nervous system can learn internal models.

For instance: inverse dynamics models using **manipulandum experiments,** i.e. experiments that record human movements in 2D (typically the horizontal plane)

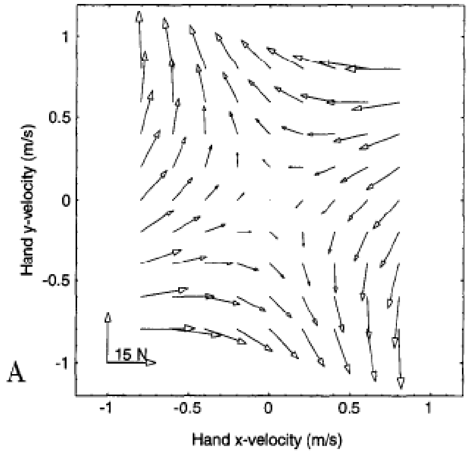


Conditt, M. A., & Mussa-Ivaldi, F. A. (1999). Central representation of time during motor learning. *Proceedings of the National Academy of Sciences*, *96*(20), 11625–11630. https://doi.org/10.1073/pnas.96.20.11625

Internal model of inverse dynamics?



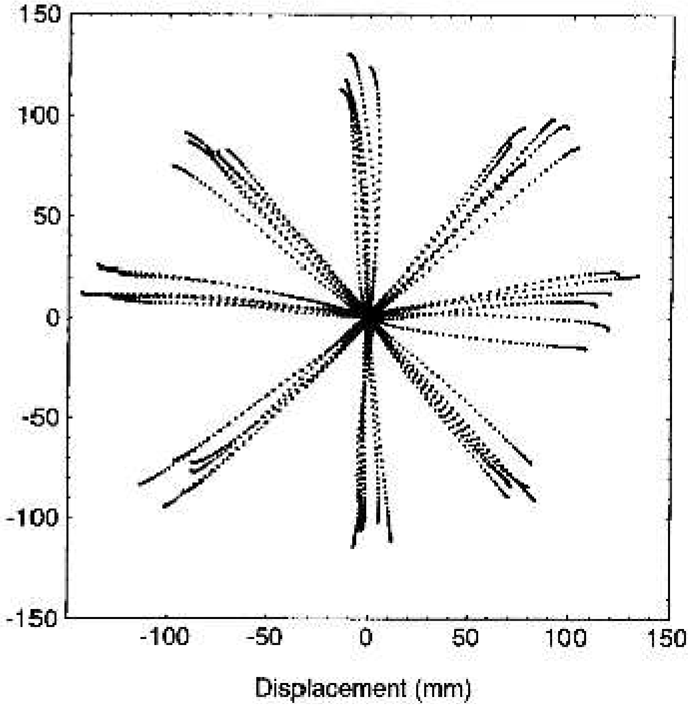
A user has to **move the handle of a manipulandum to a given target position**. The target and the position of the handle is shown on a monitor, but **the user does not see his/her own arm**.

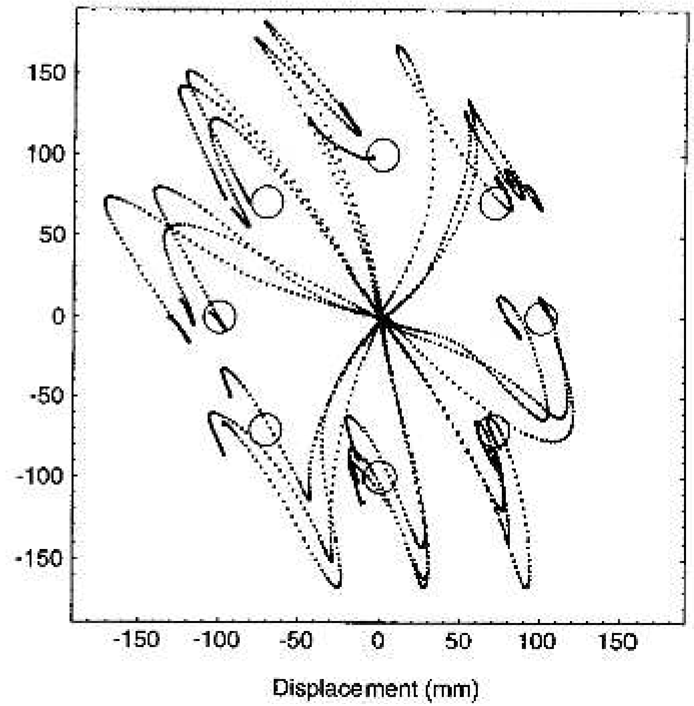


The manipulandum has two actuators at its basis to produce desired torque; a torque is applied so to produce **a force field depending on the velocity of the hand** (as depicted in the fig below).

Shadmehr and Mussa-Ivaldi (1994),**Adaptive representation of dynamics during learning of a motor task**, Journ. of Neuroscience.

Internal model
of inverse dynamics?

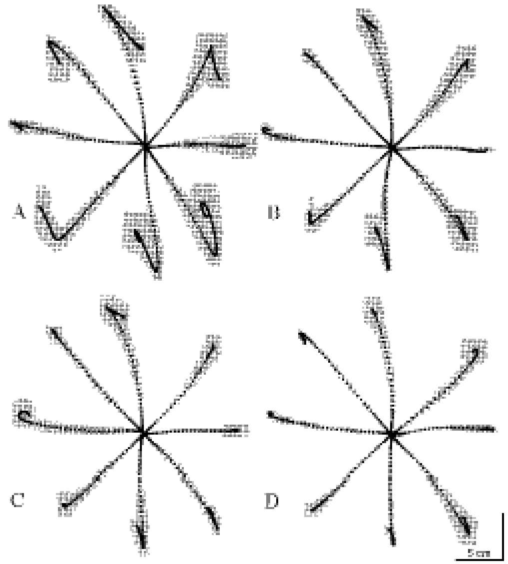




When no force field is applied, the user achieves to reach the target. The trajectory is straight.

When the force field is applied, the user makes error and needs make corrections to reach the target.

Internal model
of inverse dynamics?



Error has almost disappeared in the final trial

The error decreases as the number of trial increases (here first, second, third and final, 250th, trial).

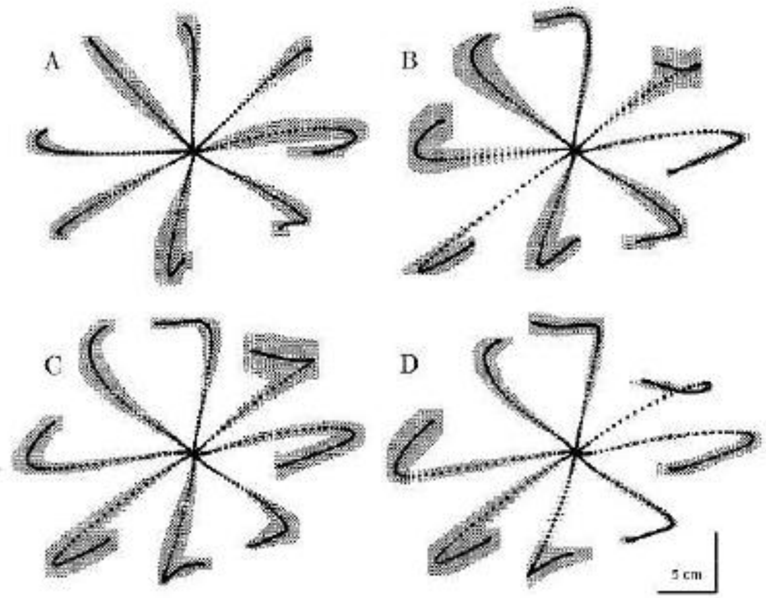
The trajectories suggest the existence of a **kinematic plan** (i.e. subjects want to perform straight lines).

Two possible explanations:

(1) The subject **learns a model of the force field**

(2) The subject ~~**increases the stiffness**~~ of the arm by cocontracting muscles

Internal model of inverse dynamics?



Strong after effects after 250 sessions of learning

When the force field is removed, the errors are approximatively **the mirror images** of the previous ones. This phenoma is called **after effects**.

- After effects would not appear if the correction was made by increasing the stiffness.
- This means that **the newly learned model of the dynamics is still used by CNS**.

Internal model of inverse dynamics?

The perturbation experiment designed by Shadmehr and Mussa-Ivaldi tends to support the idea of internal models.

And it looks like a **majority of researchers now favor the idea of kinematic plans and internal models**.

However some people think the experiment can also be explained by the EPH, see Gribble, P. L., & Ostry, D. J. (2000), in a few slides.

Learning inverse models

Direct and inverse models can be learned by *motor babbling*.

Motor babbling: more or less random movements like those performed by a baby.

By observing the results of actions both direct and inverse models can be learned.

E.g. **learning an inverse kinematics model**, that maps a desired position of the hand to (multiple) joint angles in the arm.

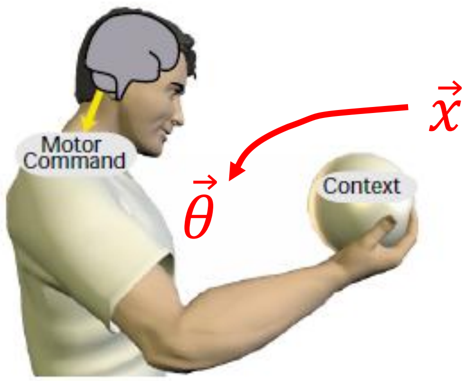
Example: D'Souza, A., Vijayakumar, S., & Schaal, S. (2001). Learning inverse kinematics. In *Intelligent Robots and Systems, 2001. Proceedings. 2001 IEEE/RSJ International Conference on* (Vol. 1, pp. 298-303). IEEE.

Learning inverse models

D'Souza, A., Vijayakumar, S., & Schaal, S. (2001). Learning inverse kinematics. In *Intelligent Robots and Systems, 2001. Proceedings. 2001 IEEE/RSJ International Conference on* (Vol. 1, pp. 298-303). IEEE.

Forward kinematics: $\vec{x} = f(\vec{\theta})$

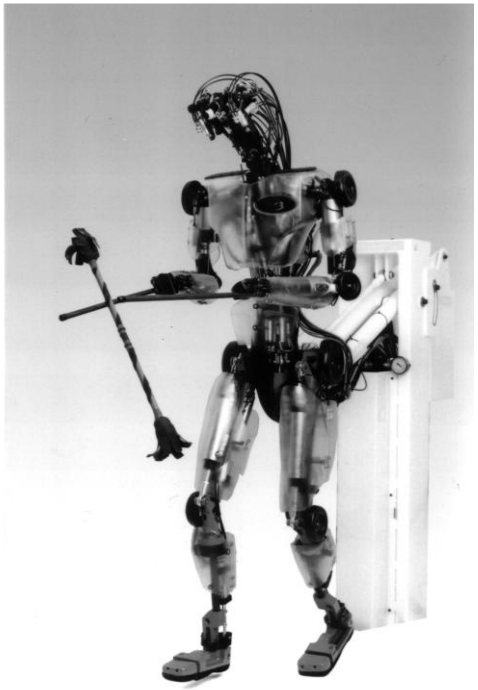
Inverse kinematics: $\vec{\theta} = f^{-1}(\vec{x})$



An ill-posed problem for redundant systems like arms, i.e. with more degrees of freedom (e.g. 7) than hand position (3)

They **solved this on a humanoid robot, using statistical learning methods**

Learning inverse models



DB, Humanoid robot at ATR

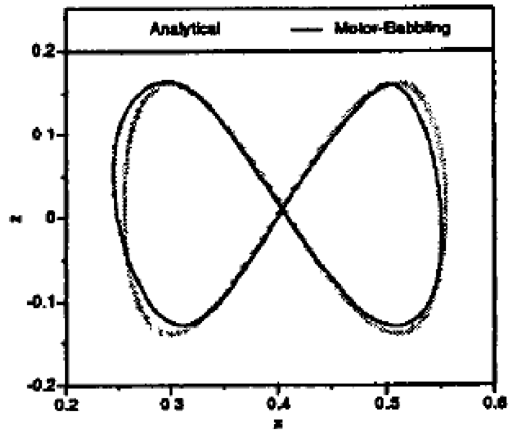


Figure 2: System performance after being trained on data collected from motor babbling.

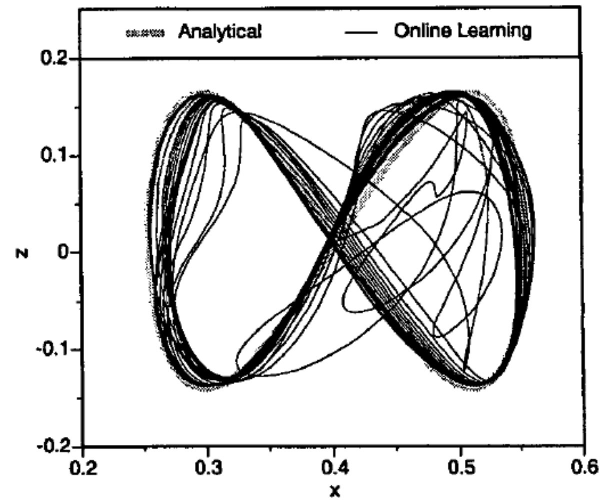


Figure 4: Trajectory followed in the first 3 minutes when learning the inverse kinematics from scratch while attempting to perform the figure-eight task.

They showed that **inverse kinematics learning** could be done on a humanoid robot after a motor babbling phase. It can also be done continuously, while performing movements.

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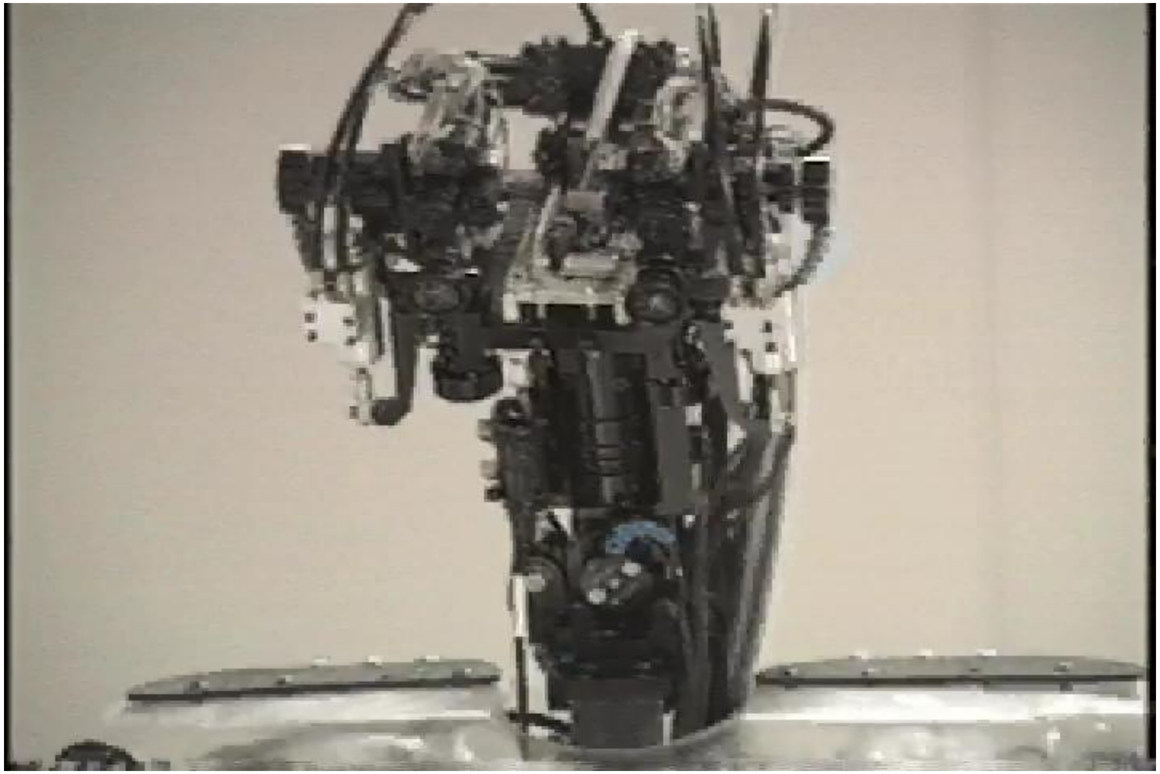
Learning inverse dynamics model

A similar approach to learn an **inverse dynamics model**, i.e. the mapping from a desired posture, to the torques necessary to get there.



By doing online learning, the inverse dynamics model is updated to take into account an additional load.

Sethu Vijayakumar, Aaron D'Souza, Tomohiro Shibata, Jorg Conradt and Stefan Schaal, Statistical Learning for Humanoid Robots, Autonomous Robot , Vol. 12, No.1, pp. 55-69 (2002).

Learning inverse models

Nice article:

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature neuroscience*, *3*, 1212-1217.

They claim: (1) **internal models are fundamental** for understanding a range of processes such as state estimation, prediction, context estimation, control and learning.

(2) **optimality** underlies many theories of movement planning, control and estimation and can account for a wide range of experimental findings.

(3) the motor system has to **cope with uncertainty about the world and noise** in its sensory inputs and motor commands, and the **Bayesian approach** provides a powerful framework for optimal estimation in the face of such uncertainty.

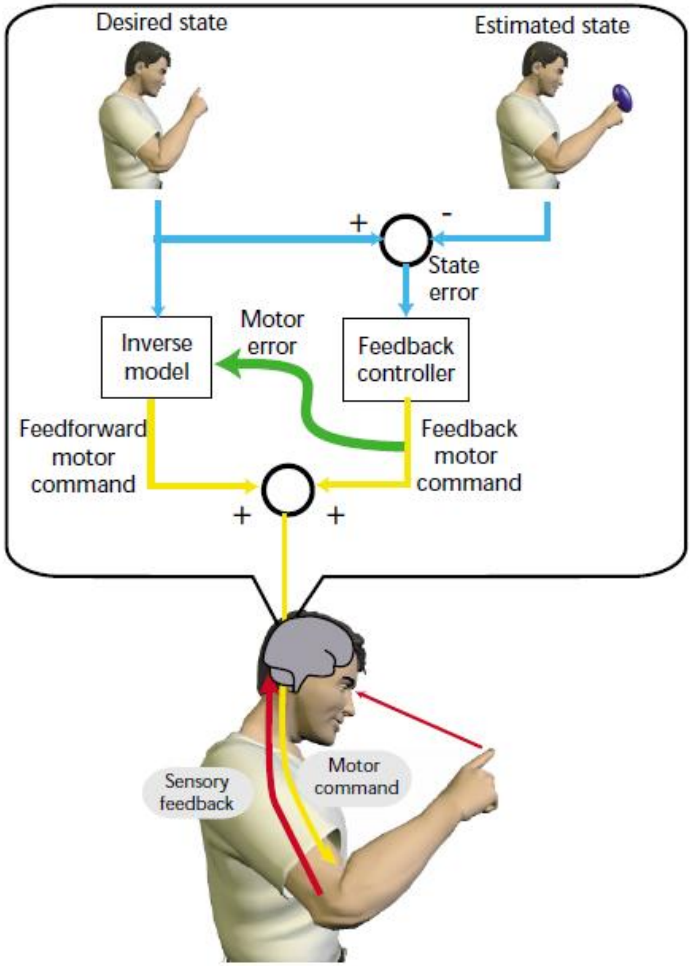


Fig. 5. A schematic of feedback-error learning. The aim is to learn an inverse model that can generate motor commands given a series of desired states. A hard-wired and low-gain feedback controller is used to correct for errors between desired and estimated states. This generates a feedback motor command that is added to the feedforward motor command generated by the inverse model. If the feedback motor command goes to zero, then the state error, in general, will also be zero. Therefore the feedback motor command is a measure of the error of the inverse model and is used as the error signal to train it.

Learning inverse models

Interesting hypothesis: rather than minimizing jerk, the **CNS minimizes the uncertainty**

This model assumes that there is **noise in the motor command** and that the amount of **noise scales with the motor command's magnitude**.

This **model accurately predicts the trajectories of both saccadic eye movements and arm movements**.

Very nice TED talk:

https://www.ted.com/talks/daniel_wolpert_the_real_reason_for_brains?language=en

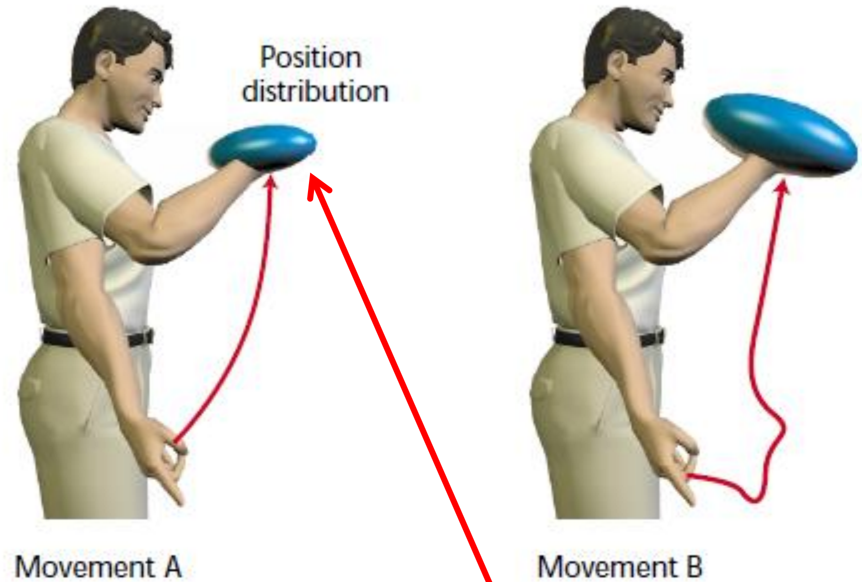


Fig. 2. Task optimization in the presence of signal-dependent noise (TOPS) model of Harris and Wolpert[9]. Average paths and expected final position distributions for two different motor sequences. Although the sequences bring the hand on average to the same final position, they have different final distributions because of noise in the motor commands. Movement A has smaller spread than B and therefore has lower cost than B. In general, the task determines the desired statistics of the movement, and the trajectory that optimizes the statistics is selected.

Movements that **maximize accuracy** (i.e. minimize uncertainty) are preferred.

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature neuroscience*, *3*, 1212-1217.

Lecture:
Models of arm movements

Topics:

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

Equilibrium point hypothesis

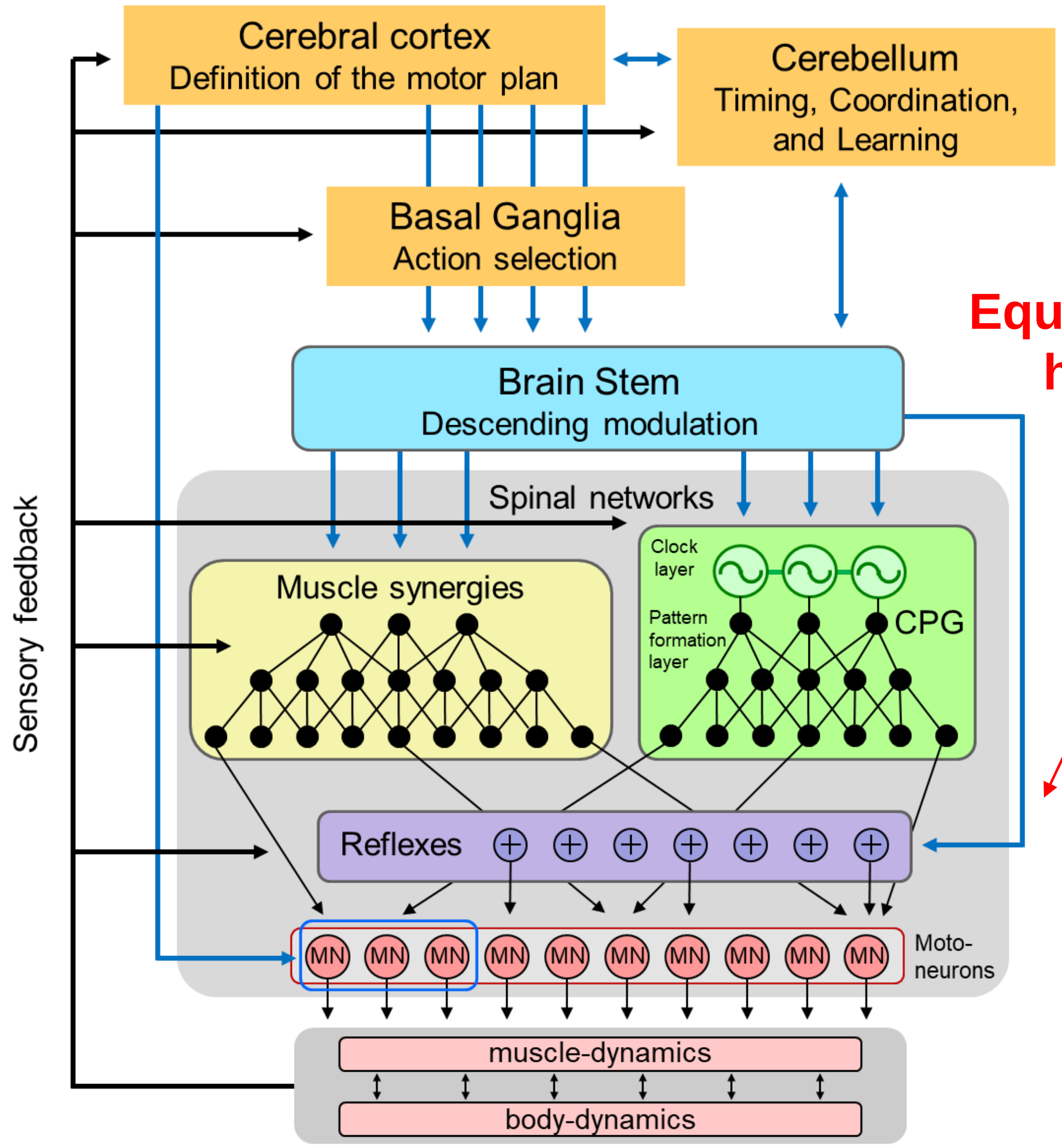
The **equilibrium point hypothesis** approach (EPH) postulates that the CNS specifies a series of equilibrium positions of muscles, and relies on reflex loops and the spring-like properties of muscles to move the limb.

No need for inverse models nor detailed kinematic plans

Was first proposed by Anatol Feldman

Key idea: **muscle reflexes** should not be viewed as hardwired stereotypical responses to stimuli, but rather as **tunable mechanisms** that form the basis of motor behavior.

Different schools of thoughts



Equilibrium point hypothesis

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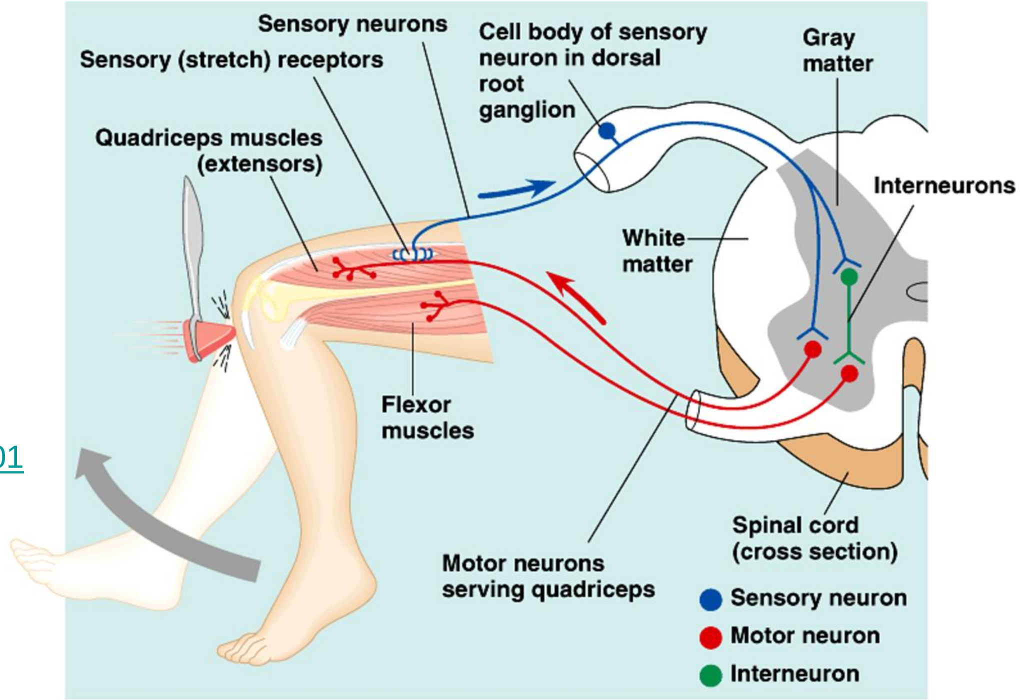
Tonic Stretch reflex

Wikipedia: The **stretch reflex** (myotatic reflex) is a muscle contraction in response to stretching within the muscle. It is a monosynaptic reflex which provides automatic regulation of skeletal muscle length.

https://www.youtube.com/watch?v=HfuhVWK8C0U

http://humanphysiology.academy/Neurosciences%202015/Chapter%202/P.2.2%20Spinal%20Reflexes.html

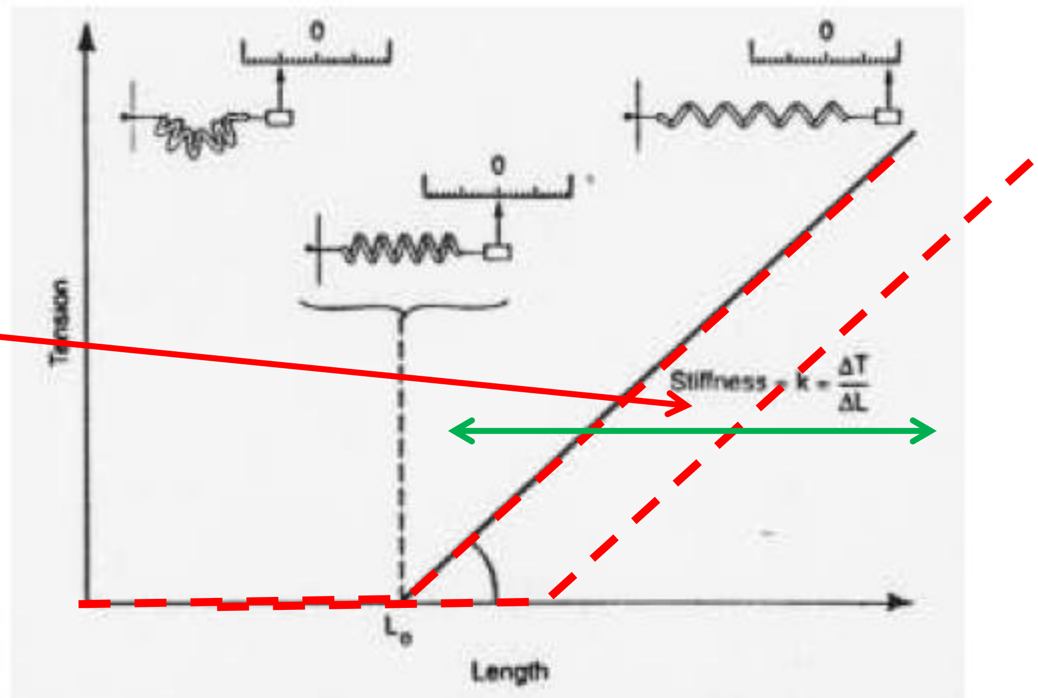


When a muscle lengthens, the muscle spindle is stretched and its nerve activity increases. This increases alpha motor neuron activity, causing the muscle fibers to contract and thus resist the stretching. A secondary set of neurons also causes the opposing muscle to relax. **The reflex functions to maintain the muscle at a constant length.** This is important e.g. to maintain a given posture.

Equilibrium point hypothesis

Based on the **spring like-behavior** of the muscles!

Descending signals (central command) can tune the tonic stretch reflex, and shift the force-length relationship



In cats, **constant descending signal** correspond to **a given force-length relationship**(stiffness) (Mathews, 1959)

Matthews P.B.C. (1959) The dependence of tension upon extension in the stretch reflex of the soleus of the decerebrate cat. Journal of Physiology 47: 521-546

Equilibrium point hypothesis

By changing the descending signals and tuning the tonic stretch reflex, <u>active movements can be generated towards new equilibrium points (i.e. new end postures)</u>

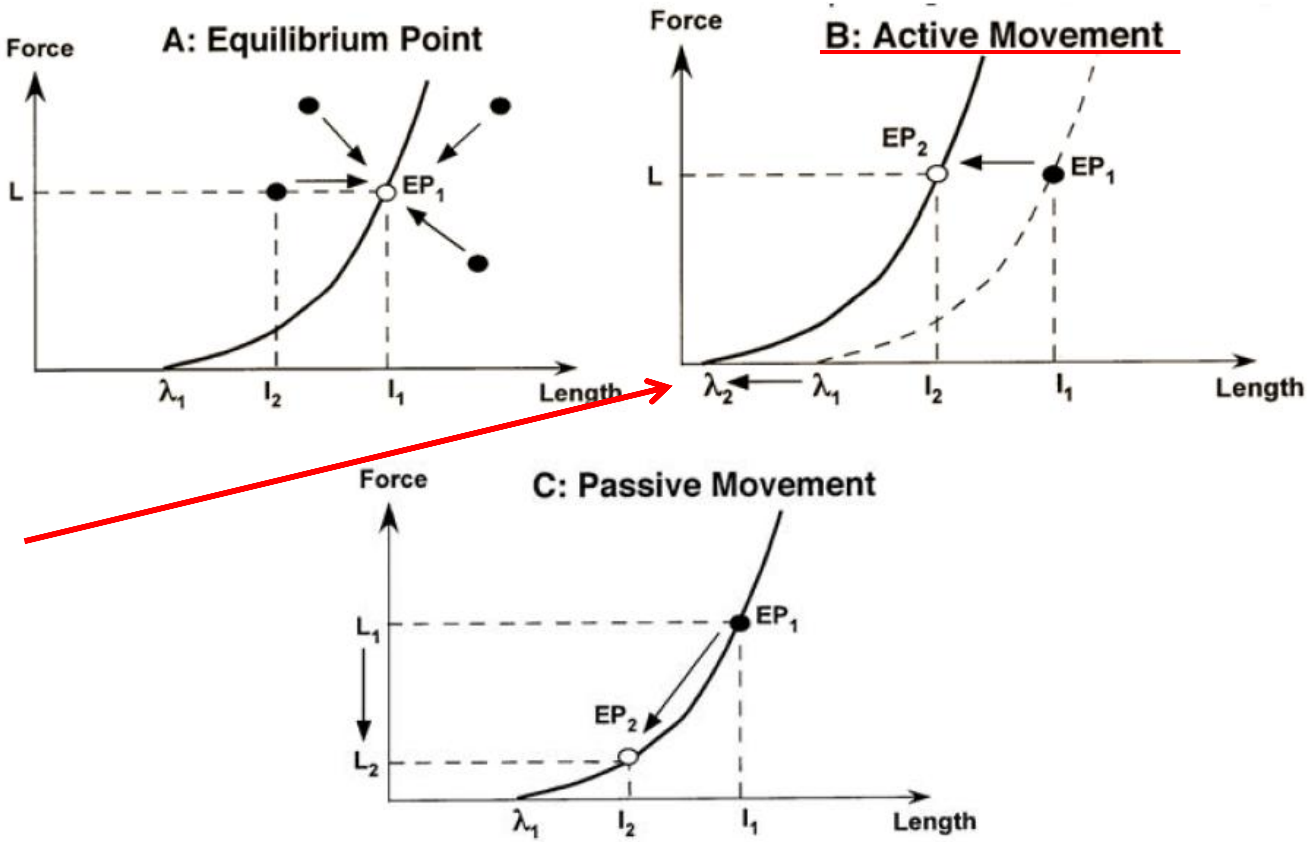


Fig. 1

An illustration of single-muscle control within the EP-hypothesis.
A: A central command (λ) defines a force-length characteristic. Given an external load (L), only one equilibrium point is possible (EP$_1$). Any deviations (filled points) from EP$_1$ will result in motion back to EP$_1$.
B: To perform an active movement, a change in λ is required (λ$_1$ to λ$_2$). As a result, a new equilibrium point (EP$_2$) is established, and a motion to EP$_2$ happens.
C: Movements can occur passively, as a result of a change in the load (L$_1$ to L$_2$).

Latash, M. L. (2008). Evolution of motor control: from reflexes and motor programs to the equilibrium-point hypothesis. *Journal of human kinetics*, *19*(1), 3-24.

Equilibrium point hypothesis

Adapted from Wikipedia:

- *In the Equilibrium Point hypothesis, all movements are generated by the nervous system through <u>a gradual transition of equilibrium points along a desired trajectory</u>.*

- *"Equilibrium point" in this sense is taken to mean a state where a field has zero force, meaning opposing muscles are in a state of balance with each other, like two rubber bands pulling the joint to a stable position.*

- *Equilibrium point control is also called "threshold control" because <u>signals sent from the CNS to the periphery are thought to modulate the threshold length of each muscle</u>. In this theory, motor neurons send commands to muscles, which changes the force–length relation within a muscle, resulting in a shift of the system's equilibrium point.*

- *As opposed to internal models, the <u>nervous system would not need to directly estimate limb dynamics, but rather muscles and spinal reflexes would provide all the necessary information about the system</u>.*

Equilibrium point hypothesis

Feldman thus postulated that:

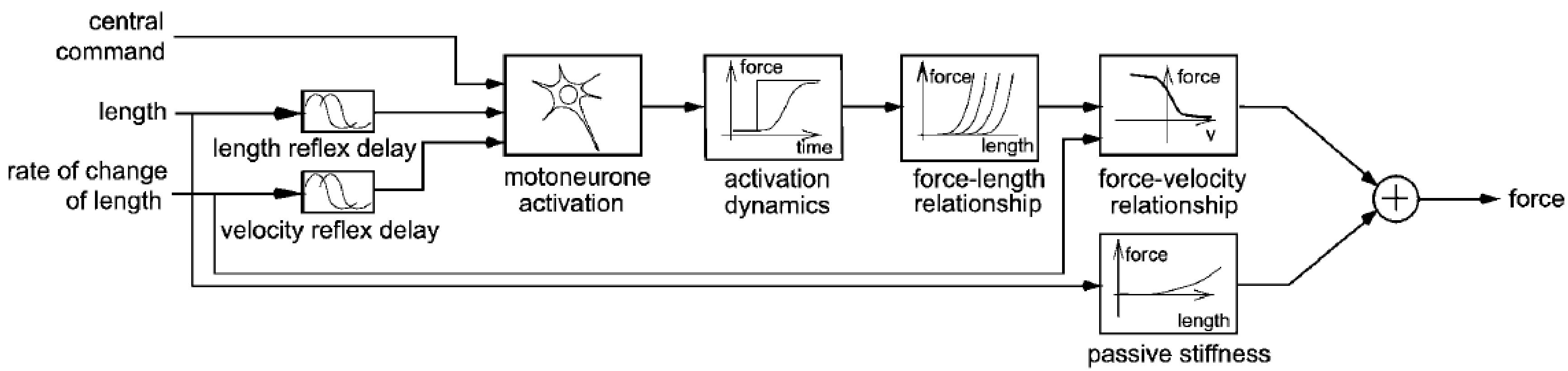
- H1 Muscles tend to have a given length λ at rest (i.e. an equilibrium point)
- H2: The CNS can modify the rest length of muscles
- H3: Movements are generated as a time sequences of the rest lengths by **changing reflex thresholds**

H1 and H2 are commonly accepted by neuroscientists. H3 is more controversial.

Feldman, A. G. (1986). Once more on the equilibrium-point hypothesis (λ model) for motor control. *Journal of motor behavior*, *18*(1), 17-54.

EPH and perturbation exp,

Gribble and Ostry tried to explain the results seen before with the **EPH** and **without an inverse dynamics model**.
The same perturbations than in Shadmehr et Mussa-Ivaldi (1994) are applied to a **dynamic model** of an arm.



It is assumed that the NS knows

- the **control signal** that has been sent
- the **desired trajectory**
- the **actual trajectory**

Gribble, P. L., & Ostry, D. J. (2000). Compensation for loads during arm movements using equilibrium-point control. *Experimental Brain Research*, *135*(4), 474-482.

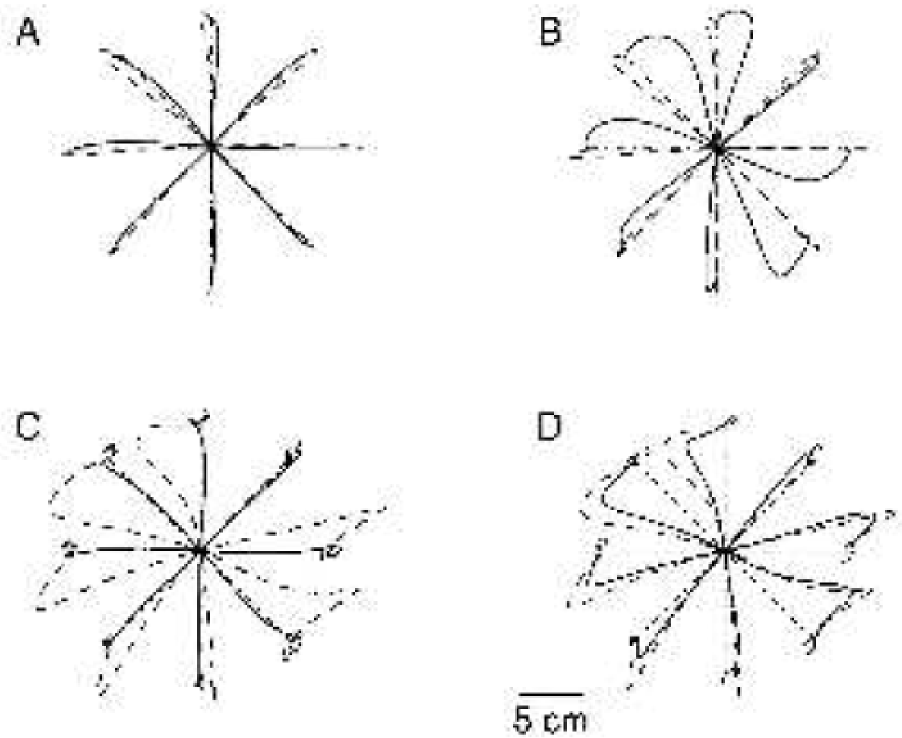
EPH and perturbation exp,

The following algorithm is used:

1. **Initial command** R for a **desired movement** M_{des}:
   $R(t) = M_{des}(t + d)$
2. Simulation of the movement $\rightarrow M_{obs}(t)$
3. **Computation of the error**: $M_{err}(t) = M_{obs}(t) - M_{des}(t)$
4. M_{err} is added to the initial control R: $R'(t) = R(t) + M_{err}(t + d)$
5. return in 1 with R' instead of R

Gribble, P. L., & Ostry, D. J. (2000). Compensation for loads during arm movements using equilibrium-point control. *Experimental Brain Research*, *135*(4), 474-482.

EPH and perturbation exp,



The following trajectories are obtained

- A null field
- B commands of A in a force field (no adapation)
- C force field and adaptation
- D command of C and null field

Qualitatively similar results are obtained

Gribble, P. L., & Ostry, D. J. (2000). Compensation for loads during arm movements using equilibrium-point control. *Experimental Brain Research*, *135*(4), 474-482.

Lecture:
Models of arm movements

Topics:

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

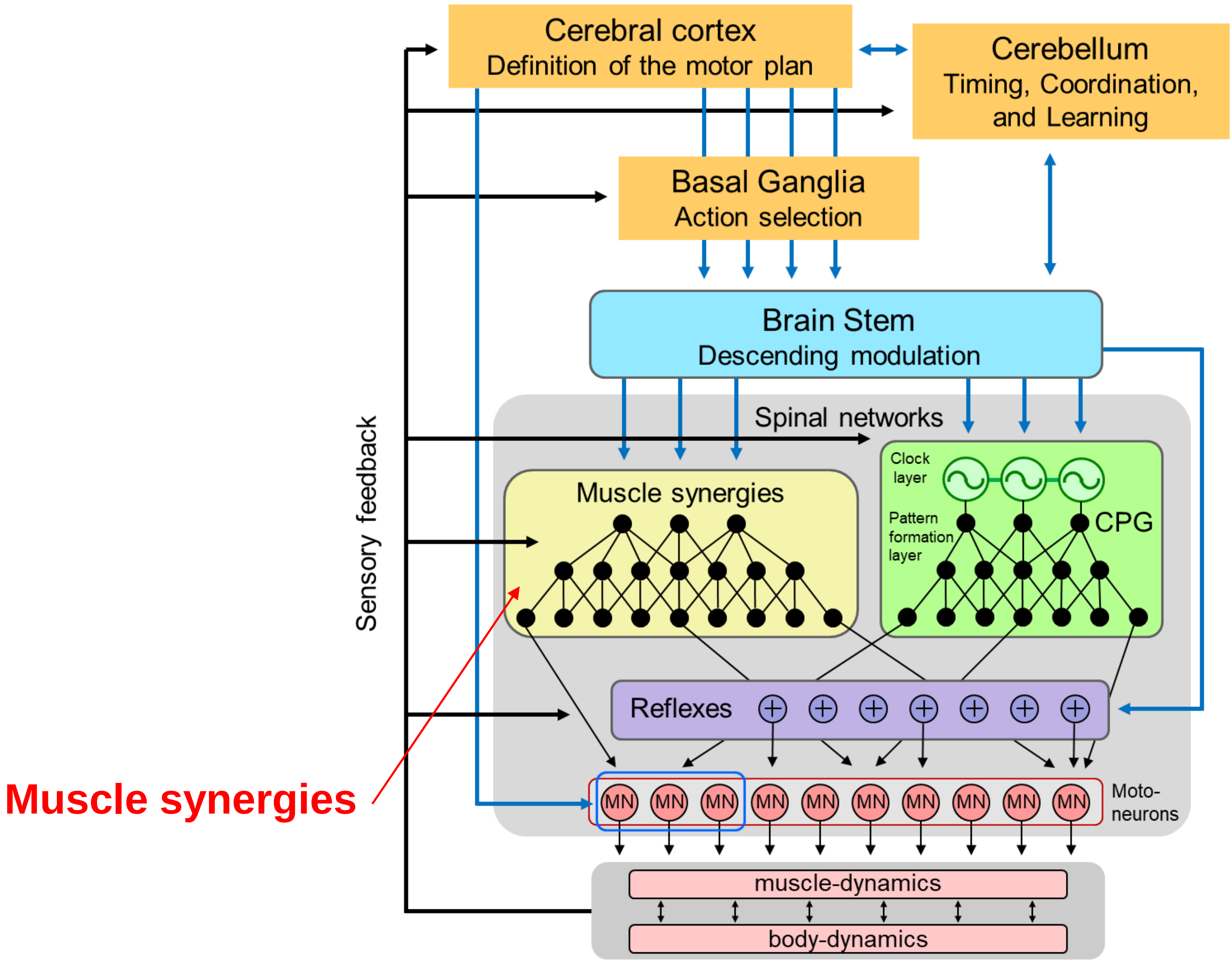
Muscle synergies

- ***Muscle synergies*** = observed coherent activations, in space or time, of a group of muscles, that have been proposed as building blocks that could simplify the construction of motor behaviors.

- Closely related topics: ***force fields***, or ***discrete pattern generators***: coordinated movements of a whole limb towards a target under the control of simple inputs

- Similarities to EPH —both are mainly **spinal cord mechanisms**— but without the focus on reflex tuning

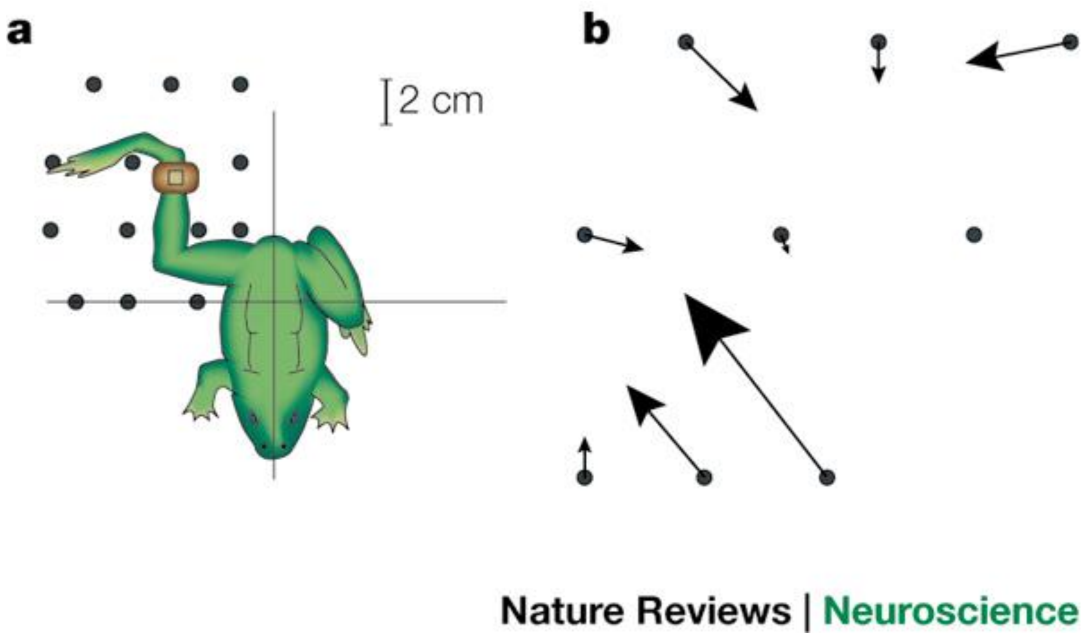
Different schools of thoughts



Force fields: pattern generators for discrete movements

Concepts of **force fields** (Mussa-Ivaldi, Bizzi et al):

- Stimulation of the spinal cord ➔ movement towards an equilibrium posture (from any initial conditions)



Force field:
Forces produced by the limb when a particular point in the spinal cord is stimulated

- Stimulation of different sites in the spinal cord
  ➔ different force fields, and different equilibrium postures

Force fields: pattern generators for <u>discrete</u> movements

- Stimulation of two sites ➔ linear superposition of the two force fields

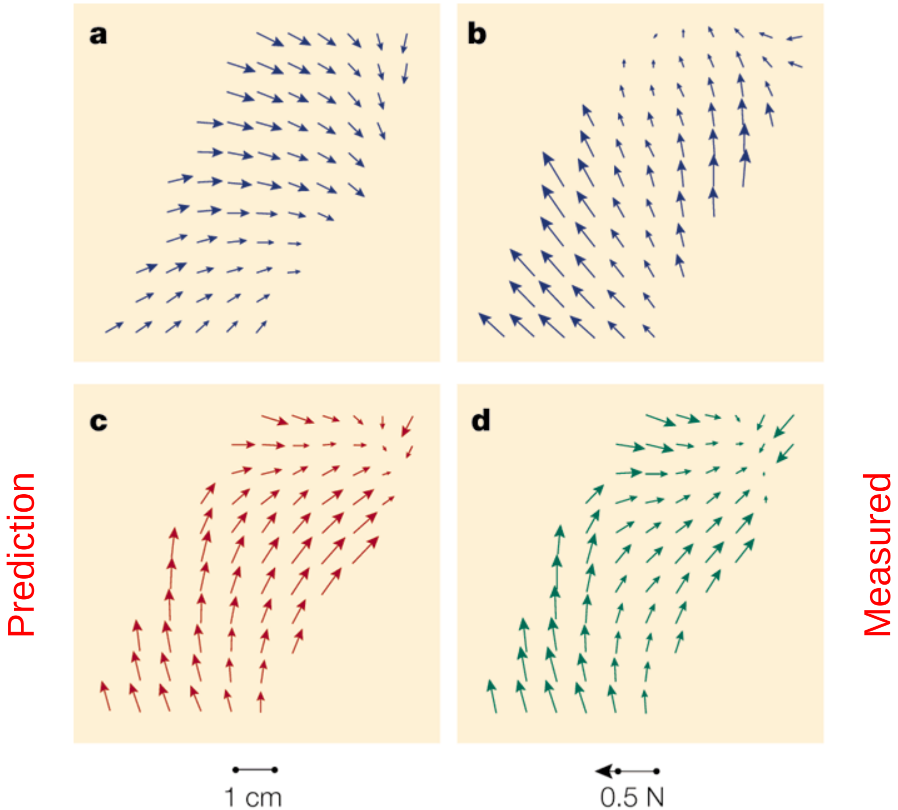


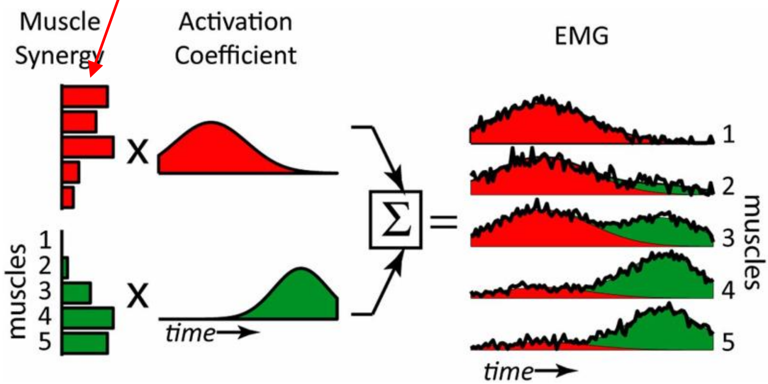
Figure 4 | **Summation of force fields by co-stimulation of sites in the frog spinal cord. a** and **b** | Two examples of force fields, evoked by stimulation of different sites in the spinal cord of a frog. **c** | Force field predicted by a simple summation of the force vectors measured at each position in the separate force fields shown in **a** and **b**. **d** | Force field actually produced by co-stimulation of the two spinal sites illustrated in **a** and **b**. The force field produced by co-stimulation of two sites in the spinal cord was very similar to the force field predicted by a simple summation of each separate force field (compare **c** and **d**). (Adapted from REF. 54.)

- This property is very useful for control
- S. Grillner now proposes to use the term CPGs for both rhythmic and discrete movements

Muscle synergies

Here a “static” muscle synergy

- The work on force fields motivated researchers to analyze EMG data underlying a large variety of movements.
- High-dimensional EMG data from many muscles can be explained by lower dimensional activation of ***muscle synergies***.
- Multiple types of movements might use a small set of synergies
- Muscle synergies are found by performing **Principle Component Analysis** or with optimization algorithms (when there are time-shifts)



A schematic illustrating how muscle synergies are linearly combined to generate muscle patterns recorded as electromyographic signals (EMGs). Each of the two muscle synergies shown (red and green bars) is represented as an activation balance profile across muscles (muscles 1–5) and activated, through multiplication, by a time-dependent coefficient. The EMG waveforms resulting from the activations of individual synergies are then summed together to reconstruct the recorded EMGs (black lines). In the schematic, each color in the EMG reconstruction reflects how the waveforms from the synergy coded by the same color contribute to the reconstruction.

http://www.pnas.org/content/109/36/14652

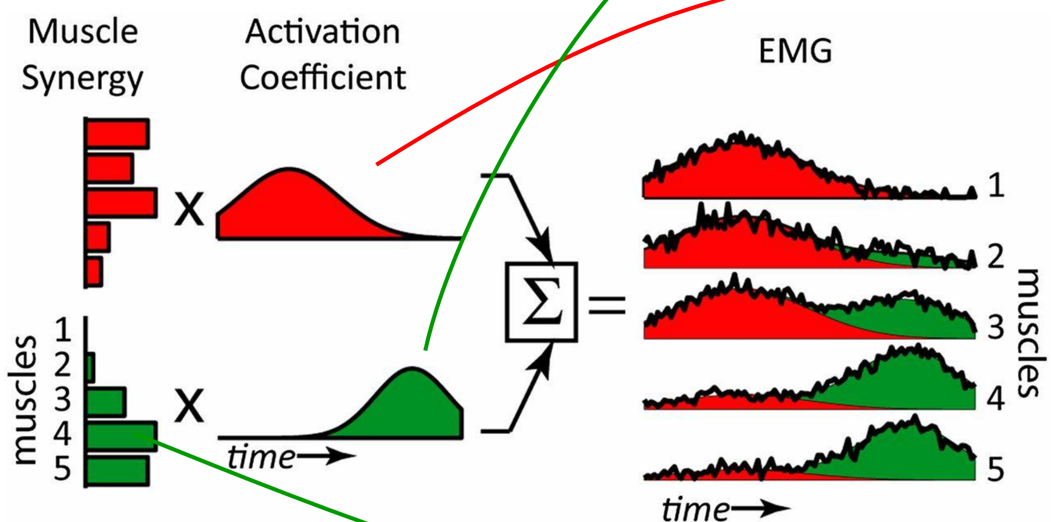
Muscle synergies as feedforward neural networks

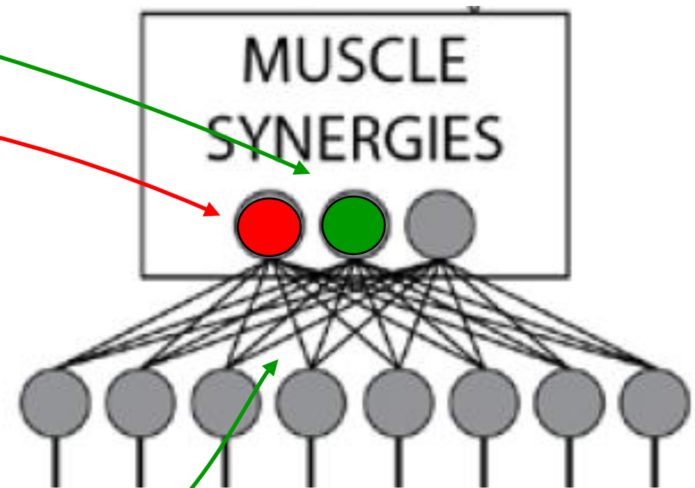
$$\vec{D}(t) = \sum_{i=1}^{N} c_i(t)\vec{w}_i + \vec{\varepsilon},$$

where $\vec{D}(t)$ is the vector of EMG activities collected at time t, N is the number of muscle synergies extracted, $\vec{w}_i$ is a time-invariant nonnegative vector in muscle space denoting the ith muscle synergy, $c_i(t)$ is the nonnegative activation coefficient for the ith synergy, and $\vec{\varepsilon}$ is any residual activities unexplained by the linear combination.

Activation

Here an example with 2 synergies (red + green):





motoneurons

Synaptic weights

Safavynia SA, Torres-Oviedo G, Ting LH.
Muscle Synergies: Implications for Clinical Evaluation and Rehabilitation of Movement.
Top Spinal Cord Inj Rehabil. 2011 Summer;17(1):16-24.

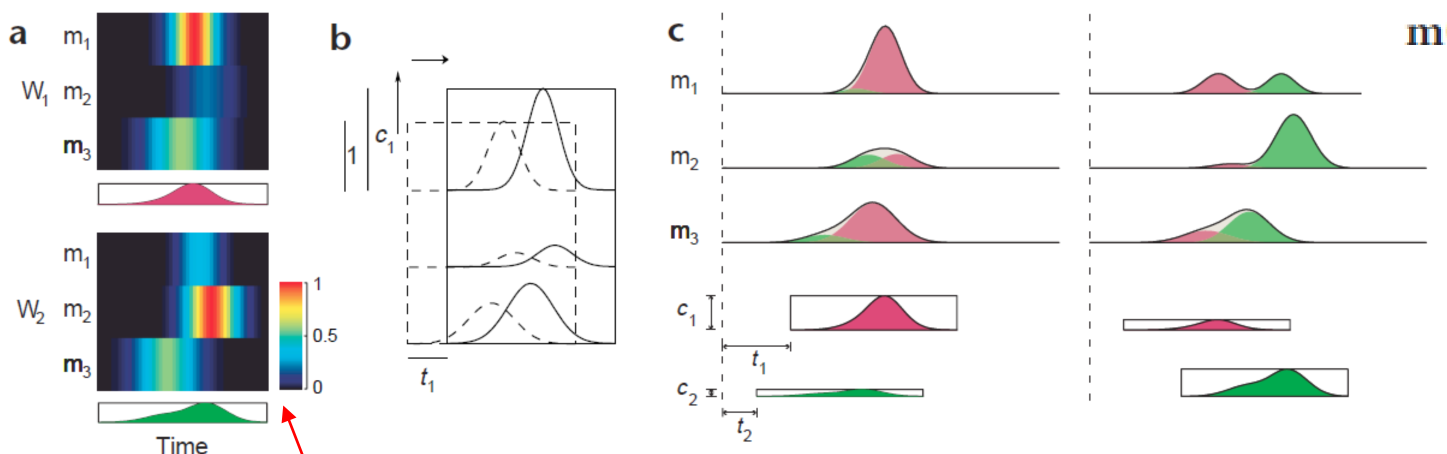
http://www.pnas.org/content/109/36/14652

Muscle synergies

Example: Combinations of three **time-varying muscle synergies** underlie the variety of muscle patterns required for the frog to kick in different directions. d'Avella, Saltiel, and Bizzi. "Combinations of muscle synergies in the construction of a natural motor behavior." *Nature neuroscience* 6.3 (2003): 300-308.

By modifying c_i and t_i for each synergy, different movements can be created

$$\mathbf{m}(t) = \sum_{i=1}^{N} c_i \mathbf{w}_i (t - t_i)$$



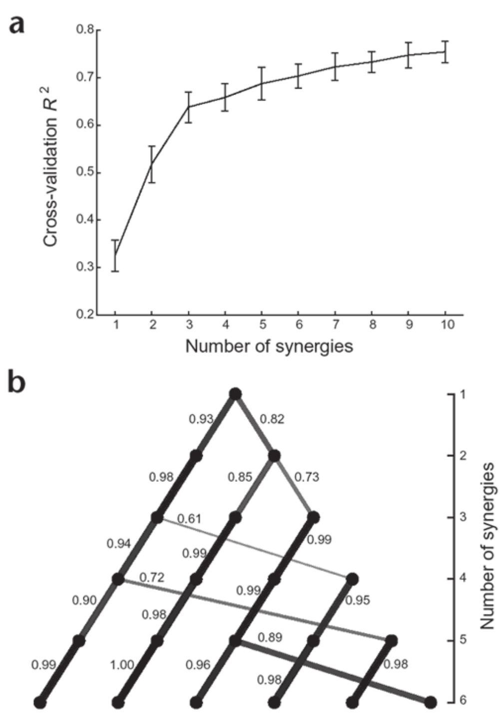
This study was particular as it also considered time shifts

Fig. 1. Time-varying synergies model. In this simulated example, two time-varying synergies (**a**) are scaled in amplitude and shifted in time (**b**), and then combined to construct two different patterns (**c**). (**a**) The rows in each synergy (W_1 and W_2) represent the activation time courses of the three muscles (m_1 to m_3), with the amplitude, shown in color code, normalized within each synergy to the value of the maximum sample. The profile in the box below each synergy represents the time course of the synergy averaged across muscles. (**b**) To generate a specific muscle pattern, every muscle in each synergy is first scaled in amplitude by a non-negative coefficient (c_1 in the illustration representing the time course of the three muscles of W_1) and shifted in time by an onset delay (t_1). The three curves in a box represent W_1 before (dashed traces) and after (solid traces) scaling and shifting. (**c**) The elements of the first synergy (magenta shaded area) are then summed together with corresponding elements of the second synergy (green shaded area) to generate the complete pattern (solid line). In this illustration, the amplitude coefficients (c_1 and c_2) are represented as the height of the rectangles below the muscle patterns, and the onset delays (t_1 and t_2) are represented by the horizontal position of the left edge of the rectangle.

Here the muscle synergy is time-varying (temporal pattern)

Muscle synergies

- Cross-validation procedure for finding the number of synergies needed for explaining most of the data
- The synergies extracted from each individual frog are generally very similar to each other (tests with 4 frogs)
- Significant **similarities among the synergies extracted from kicking and from different natural behaviors** (jumps, swimming and walking)



(**a**) Cross-validation procedure. For each number of synergies, the extraction is performed on a randomly selected 80% of the data, and the reconstruction tested on the remaining 20% of the data. Mean and standard deviation of the fraction of total variation (R^2) of five disjoint test sets explained by the synergies extracted from the remaining data is shown. The slope of the curve changes sharply at three, indicating that four or more synergies capture only a small additional fraction of the total variation in the data explained by three synergies. (**b**) Similarities between sets with different numbers of synergies. The nodes on each row of the pyramid represent the synergies extracted from sets with a number of elements ranging from 1 to 6. The links between the nodes in two adjacent rows connect synergies that are similar (similarity value above 0.6, with the value computed as the maximum of the normalized scalar product at different delays; Methods). The degree of similarity is indicated by the thickness and darkness of the link and the value shown close to each link.

Muscle synergies

Muscle synergies are a **way to reduce the dimensionality of the control problem**, and allow sharing of neural circuitry across many tasks. Key idea: **representing all useful muscle patterns as combinations of a small number of generators**

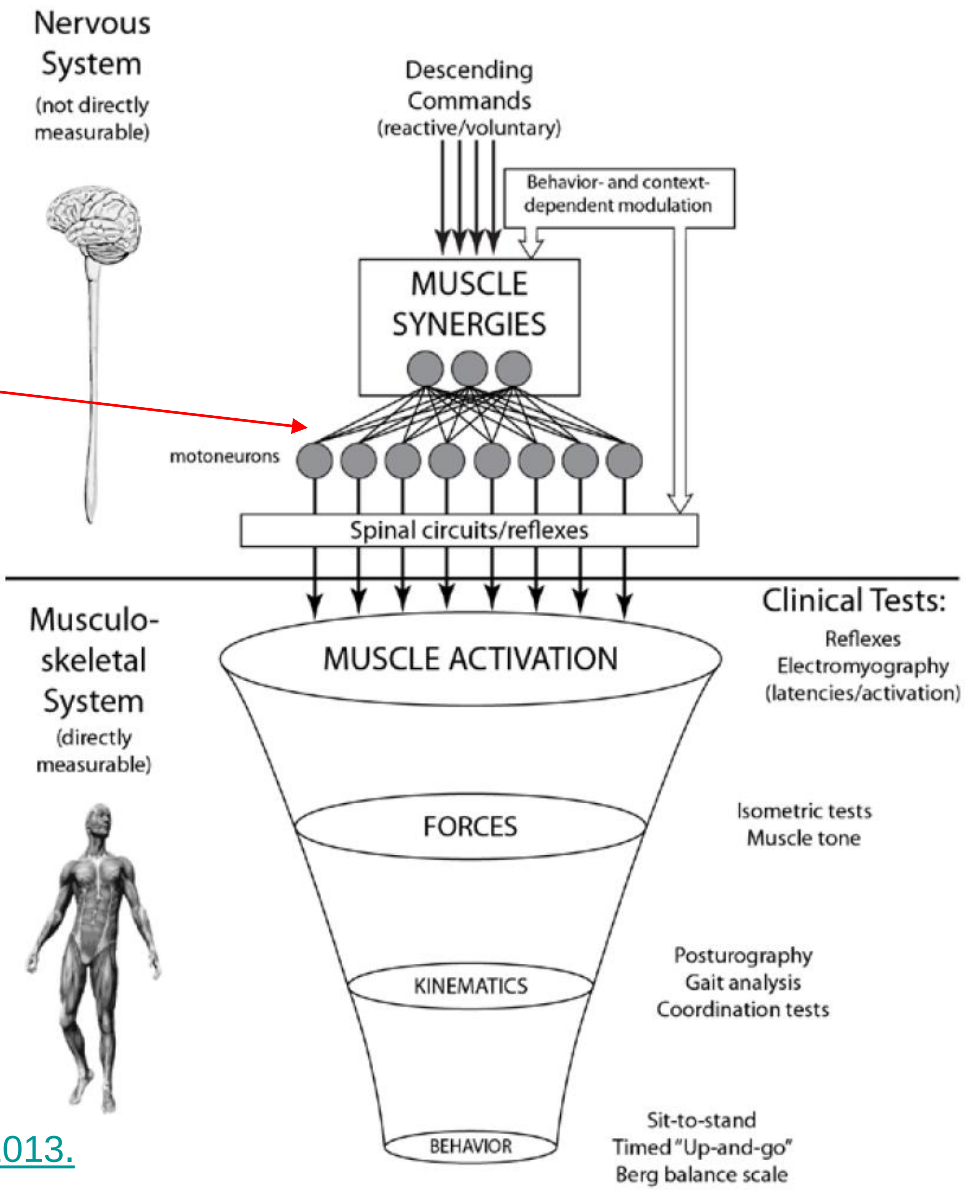
Muscle synergies appear to exist in humans e.g. for posture control, walking, arm movements, etc.

Note: while the regularities have been observed, the underlying neural circuits are still to be decoded. They could be implemented with **feedforward neural networks in the spinal cord**.

Could be compatible with control based on inverse models and optimal control.
Similarity to EPH (also spinal cord mech.) but without the focus on reflex tuning.

Muscle synergies

Muscle synergies could be implemented by **feedforward neural networks** in the spinal cord.



Safavynia SA, Torres-Oviedo G, Ting LH. Muscle Synergies: Implications for Clinical Evaluation and Rehabilitation of Movement. Top Spinal Cord Inj Rehabil. 2011 Summer;17(1):16-24.

See also http://journal.frontiersin.org/article/10.3389/fncom.2013.00051/full

Summary IM vs EPH

IM approach

- Focus on the plan of the trajectory
- Mainly feedforward
- Control of the final trajectory
- Complete knowledge of the system, need for direct and inverse models
- Big responsibilities for higher brain regions (motor cortex, cerebellum, etc.)

EPH approach

- Focus on the muscle dynamics from which the trajectory emerges
- Mainly feedback
- Only partial control of the trajectory
- Incomplete knowledge of the system, relies on reflexes, no inverse dynamics model
- Big responsibilites for spinal cord circuits

Summary muscle synergies

- The idea of muscle synergies is quite close to EPH (both are essentially spinal cord mechanisms) but is also compatible with IM as a way to reduce dimensions.

- **Personal opinion:** the nervous system is super redundant, it could use **several control principles at the same time**, and possibly **switch depending on tasks.**

- E.g. **muscle synergies/EPH for simple stereotyped movements**, and **internal models for more complex movements**

- Computational models will certainly help understanding this!

Lecture:
Models of arm movements

Topics:

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

Population Code

- For motor planning (e.g. imagining a hand trajectory in advance) and motor control (e.g. for verifying that a desired trajectory is followed), movements are encoded in the motor cortex based on a **population code**, and **direction-sensitive neurons**.
- Almost universal principle in the brain: an individual neuron is tuned to specific stimuli. Thus, a **<u>population</u> of neurons with different preferred stimuli can represent all possible stimuli**.
- Multiple examples of population code:
  - **Visual information** processing in the visual cortex (cf previous lecture)
  - **Tactile information** in the somatosensory cortex
  - Encoding of **plans for arm movements** in the motor cortex
  - **Place cells for navigation** in the hippocampus
  - …

Mean response and population coding

- Mean response exhibits a ***tuning curve***, typically well approximated by a Gaussian or cosine function.

Orientation tuning in the visual cortex:

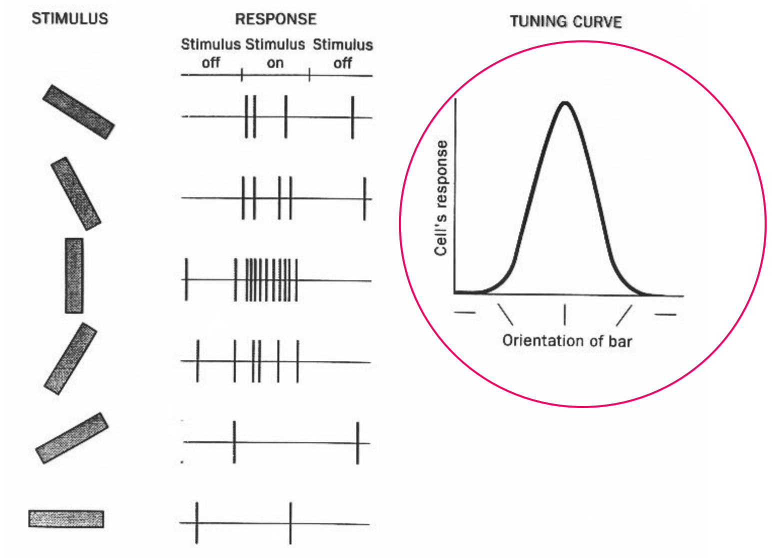
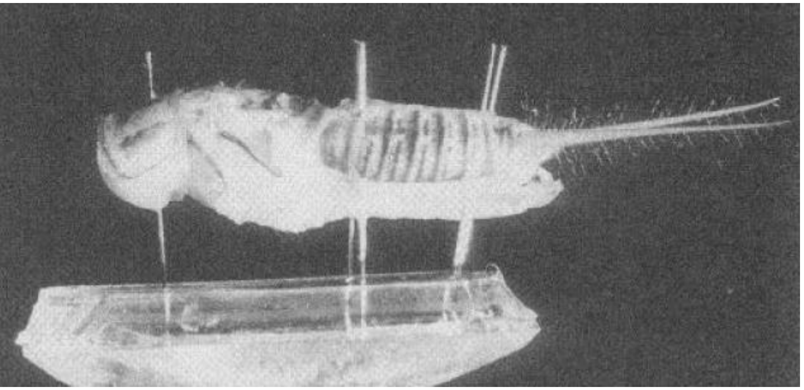


FIGURE 4.8 Response of a single cortical cell to bars presented at various orientations.

- The **curves are usually quite large**. Therefore the activity of a single neuron is not sufficient to identify the stimulus properly. ***The information is coded across the <u>whole population.</u>***
- *Cf the large receptive fields in the salamander optic tectum.*

How to extract information using a population code?

- Example: neurons detecting wind direction in the cricket (Miller et al 1991, Theunissen and Miller 1991, Salinas and Abbott 1994)



Miller et al 1991

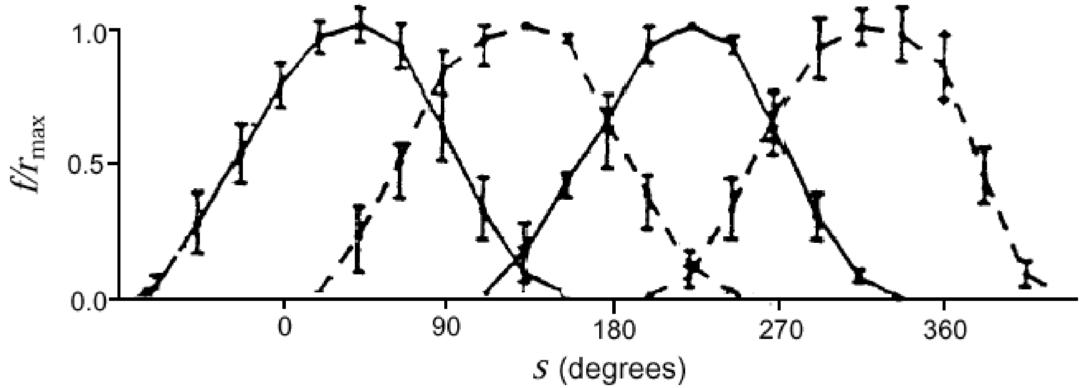
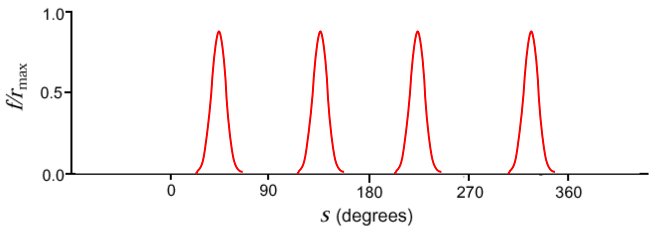


Figure 3.4: Tuning curves for the four low-velocity interneurons of the cricket cercal system plotted as a function of the wind direction s. Each neuron responds with a firing rate that closely approximated by a half-wave rectified cosine function. The preferred directions of the neurons are located 90° from each other, and r_{max} values are typically around 40 Hz. Error bars show standard deviations. (Adapted from Theunissen and Miller, 1991.)

Having large tuning curves is a good thing!
Too thin curves would "leave gaps"



Population Vector

Only small error

Represent each preferred stimulus by vector in stimulus space.

Population vector: weighted sum of preferred vectors (weighted by response)

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

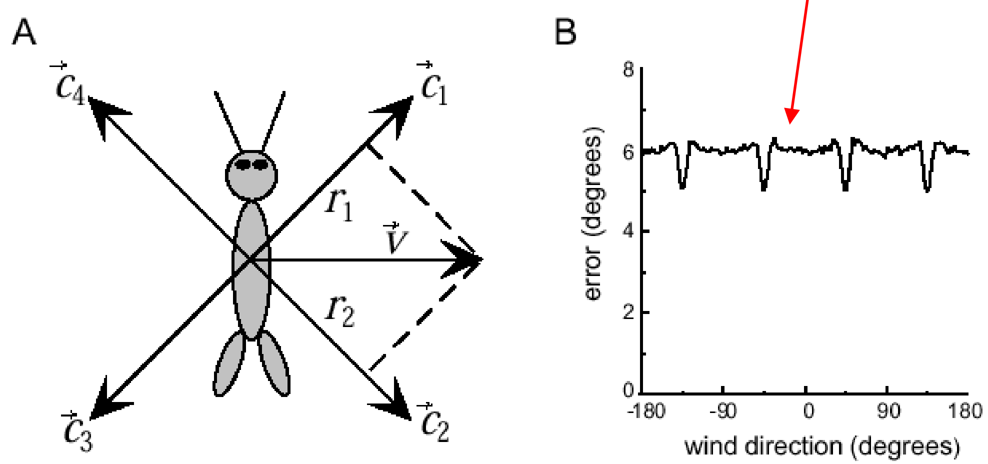
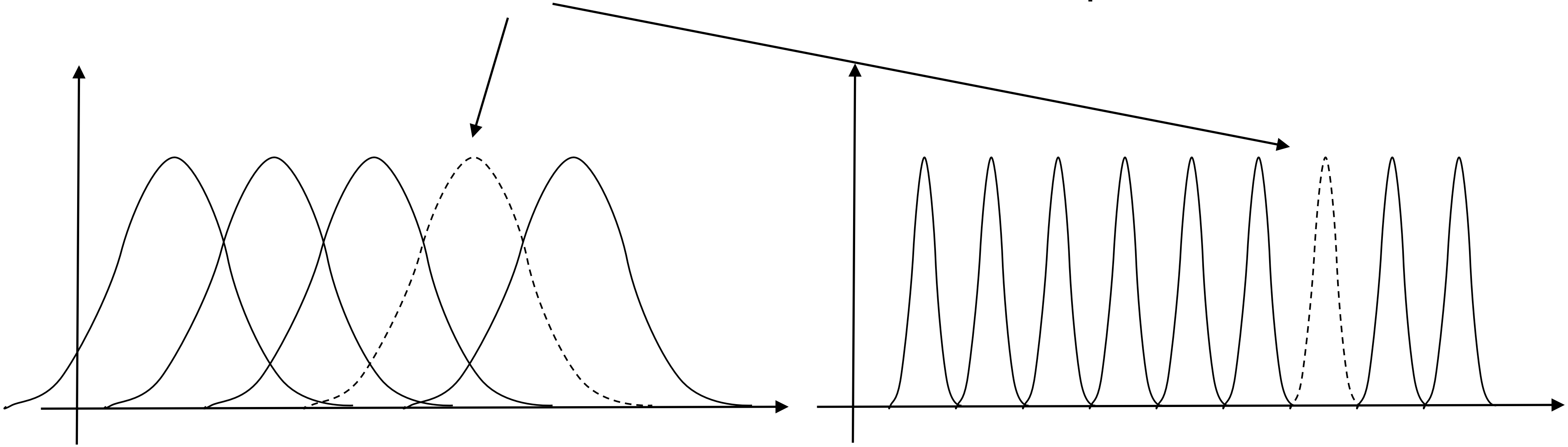


Figure 3.5: A) Preferred directions of four cercal interneurons in relation to the cricket's body. The firing rate of each neuron for a fixed wind speed is proportional to the projection of the wind velocity vector $\vec{v}$ onto the preferred direction axis of the neuron. The projection directions $\vec{c}_1, \vec{c}_2, \vec{c}_3$ and $\vec{c}_4$ for the four neurons are separated by 90°, and they collectively form a Cartesian coordinate system. B) The root-mean-square error in the wind direction determined by vector decoding of the firing rates of four cercal interneurons. These results were obtained through simulation by randomly generating interneuron responses to a variety of wind directions, with the average values and trial-to-trial variability of the firing rates matched to the experimental data. The generated rates were then decoded using equation 3.21 and compared to the wind direction used to generate them. (B adapted from Salinas and Abbott, 1994.)

Population Vector

Similarly to the coarse coding we have seen in the salamander optic tectum it is **beneficial that the tuning curves are rather large and overlapping**:

- Fewer neurons are sufficient to cover a large input space
- Less risk of “gaps” in the input space
- The loss of one neuron does not create a “blind” spot



Large tuning curves

Thin tuning curves

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

Motor cortex, arm movements

This can be used in neuroprosthetics to guide robotic arms.

Works very well in many cases!

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

The **direction of motion** can be predicted from the population vector

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

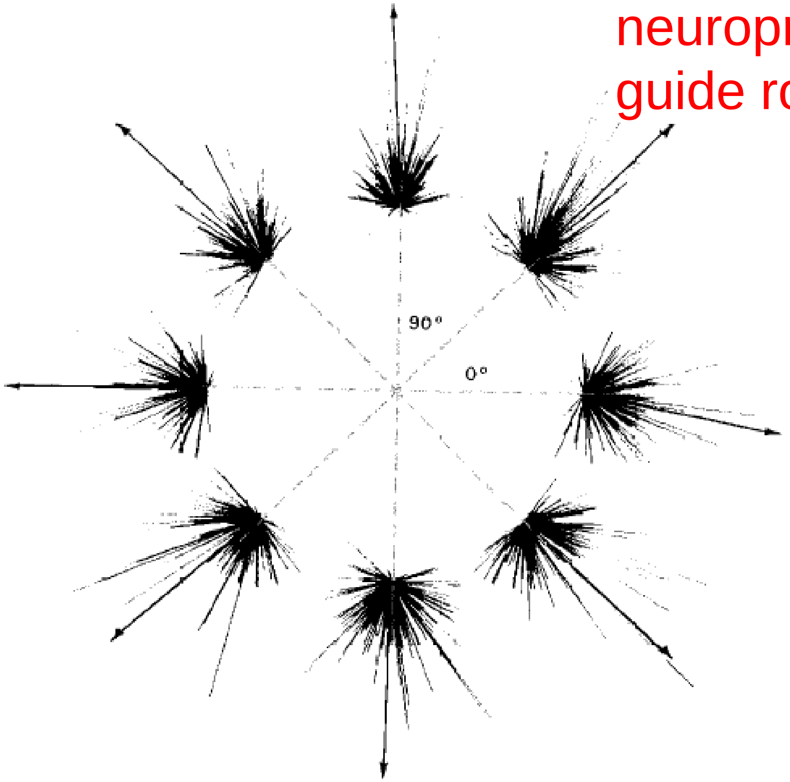
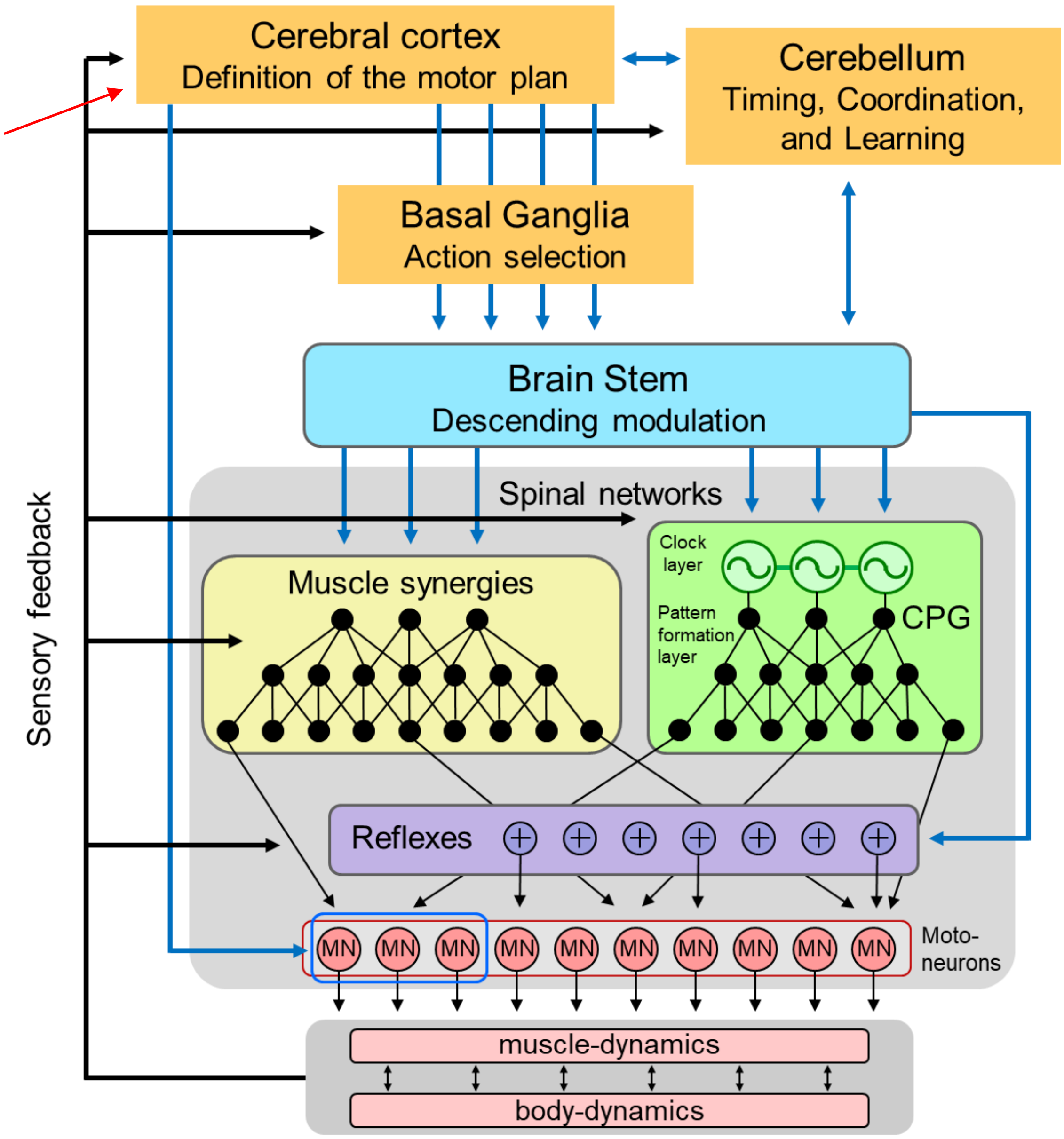


Figure 3.6: Comparison of population vectors with actual arm movement directions. Results are shown for eight different movement directions. Actual arm movement directions are radially outward at angles that are multiples of 45°. The groups of lines without arrows show the preferred direction vectors 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.)

Planning movements in the motor cortex

Population coding of the planned movement



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Extracting the motor plan from the motor cortex

More about this in the next neuroprosthetics lecture.

Andrew Schwarz and colleagues, U. of Pittsburgh

Meel Velliste, et al, *Cortical control of a prosthetic arm for self-feeding*, Nature, Vol 453, pp 1098-1101, 2008

Different types of possible estimators in population coding

- Pouget, et al 2000, Information processing with population codes, Nature reviews Neuroscience,

- Population coding with large tuning curves has many good properties:
  - Robustness against neural lesions
  - Robustness against noise
  - Can support short-term memory
  - Can implement complex nonlinear functions

- There are different types of estimators that can be used to extract information: **Voting methods** (like the population vector estimator of the cricket example) or **Probabilistic methods** (like maximum likelihood or maximum a-posteriori)

Interesting papers on population coding

- Pouget, et al 2000, Information processing with population codes, Nature Reviews Neuroscience, 2000 Nov;1(2):125-32.
- Salinas, E. & Abbot, L. Vector reconstruction from firing rate. *J. Comput. Neurosci.* 1, 89–108 (1994).
- Georgopoulos, A., Kalaska, J. & Caminiti, R. On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J. Neurosci.* 2, 1527–1537 (1982).
- Miller JP, Jacobs GA, Theunissen F (1991) Representation of sensory information in the cricket cercal sensory system. I. Response properties of the primary interneurons. J. Neurophysiol. 66:1680-1689
- Theunissen F, Miller JP (1991) Representation of sensory information in the cricket cercal sensory system. II. Information theoretic calculation of system accuracy and optimal tuning curve widths of four primary interneurons. J. Neurophysiol. 66:1690-1703.

Possible exam questions

- Describe **3 invariants** that have been observed in human arm movements (choose out of Bell-Shaped Velocity Profile, Isochrony principle, Fitts's Law, Two Third Power Law, Minimum Jerk hypothesis)

- Explain the **different school of thoughts to explain the control of discrete (point-to-point) movements** in humans: the internal model based approach, the equilibrium point hypothesis, and the muscle synergies. Explain the differences.

- Explain what an **internal model** is, give examples, and explain why they are useful for controlling the movements of an arm.

- Explain what a **population vector** is. Discuss how the width of a tuning curve affects computation with a population vector (e.g. what happens if the tuning curve is too thin or too large).

Written exam

- Exam will take place on **May 15, 10:15-12:15,** on the campus, in rooms AAC231 and SG 0211(info about room allocation will be given through the Moodle forum)
- **Closed book**, just bring your favorite pen (snacks and drinks)

- Questions close to the examples shown at the end of each lectures + to the exercises/practicals

- Some “**mathematical questions**”, e.g. about dynamical systems, limit cycles, and synchronization. To be solved analytically and geometrically. See also the practicals.

- Some **“knowledge” questions**

- Some **“discussion” questions**

End of Lecture

No lecture next week! (May 8)
Only the practicals in the afternoon