

The motor system: An overview of its functions and computations

Vincent C. K. Cheung

School of Biomedical Sciences, Gerald Choa Neuroscience Institute

The Chinese University of Hong Kong

vckc@cuhk.edu.hk

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Why the motor system is interesting

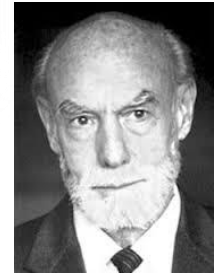
- Principal function of the nervous system

Understand the primary business of the brain continues to be the governing, directly or indirectly, of overt behavior.

Overt behavior, upon analysis, we find to be constituted almost entirely of patterns of muscular contraction. It follows that the principal function of the nervous system is the coordinated innervation of the musculature. Its fundamental anatomical plan and working principles are understandable only on these terms.

Further support for this point of view may be found in the study of brain architecture. One searches the cerebrum in vain for any structures that seem to be designed for the purpose of coordinating movement.

- Roger Sperry, 1952



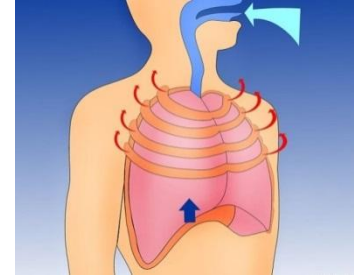
- Diseases of the motor system:
Stroke, Parkinson's Disease, Huntington's Disease, spinal cord injury, traumatic brain injury etc.
- Movement as a hallmark of life

Different types of movement

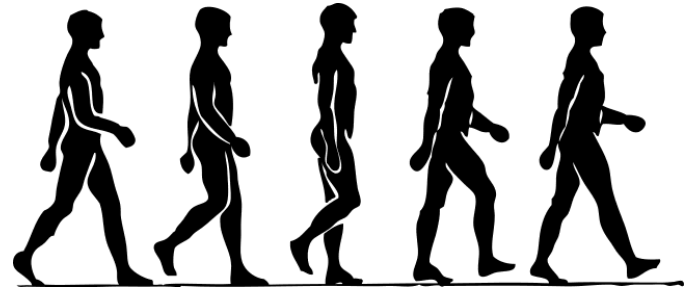
1. Voluntary movement



2. Breathing



4. Locomotion & posture



3. Speech production

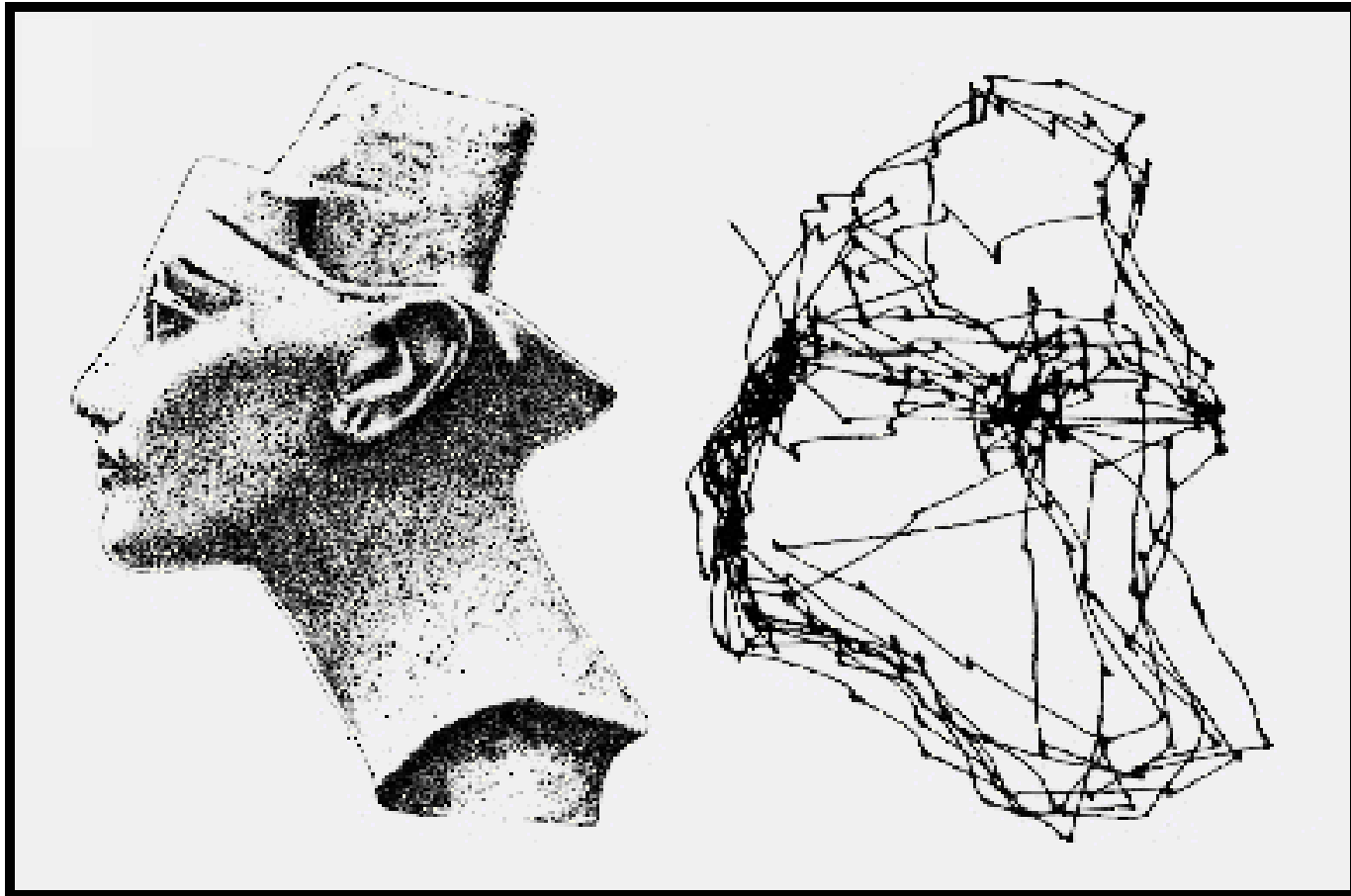


5. Reflexes



Different types of movement

6. Eye movement: saccades; smooth pursuit

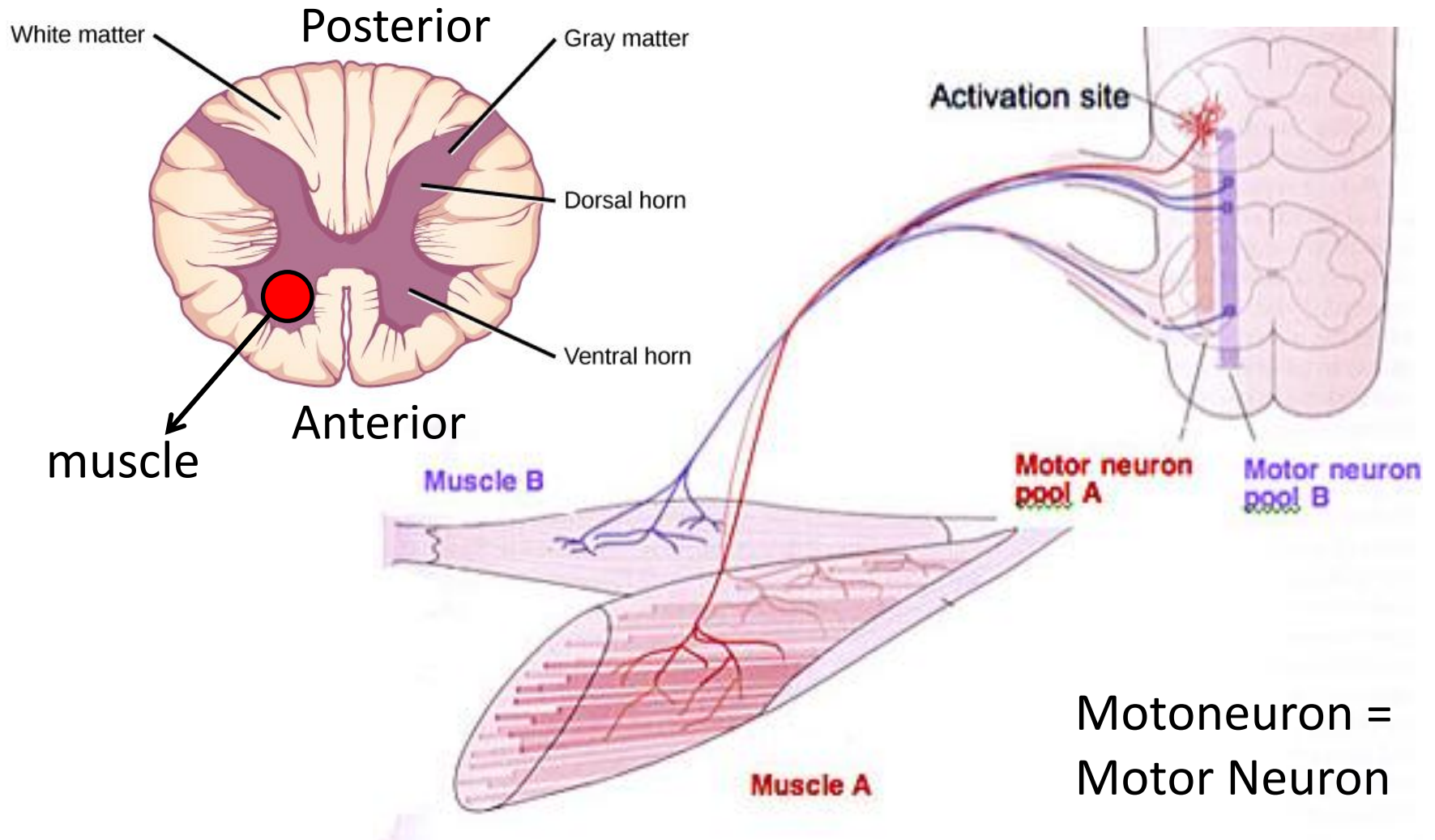


Saccadic eye movement of a subject over the “Bust of Nefertiti”

Plan for this lecture

1. A **general overview** of the motor system
2. The **primary motor cortex (M1)**: Past and recent ideas on how M1 activities may be understood
3. The **spinal cord**: How spinal interneuronal activities and connectivity may be understood through the concept of **neuromotor modularity**

Skeletal muscles are innervated by motoneurons in the ventral horn of the spinal cord.



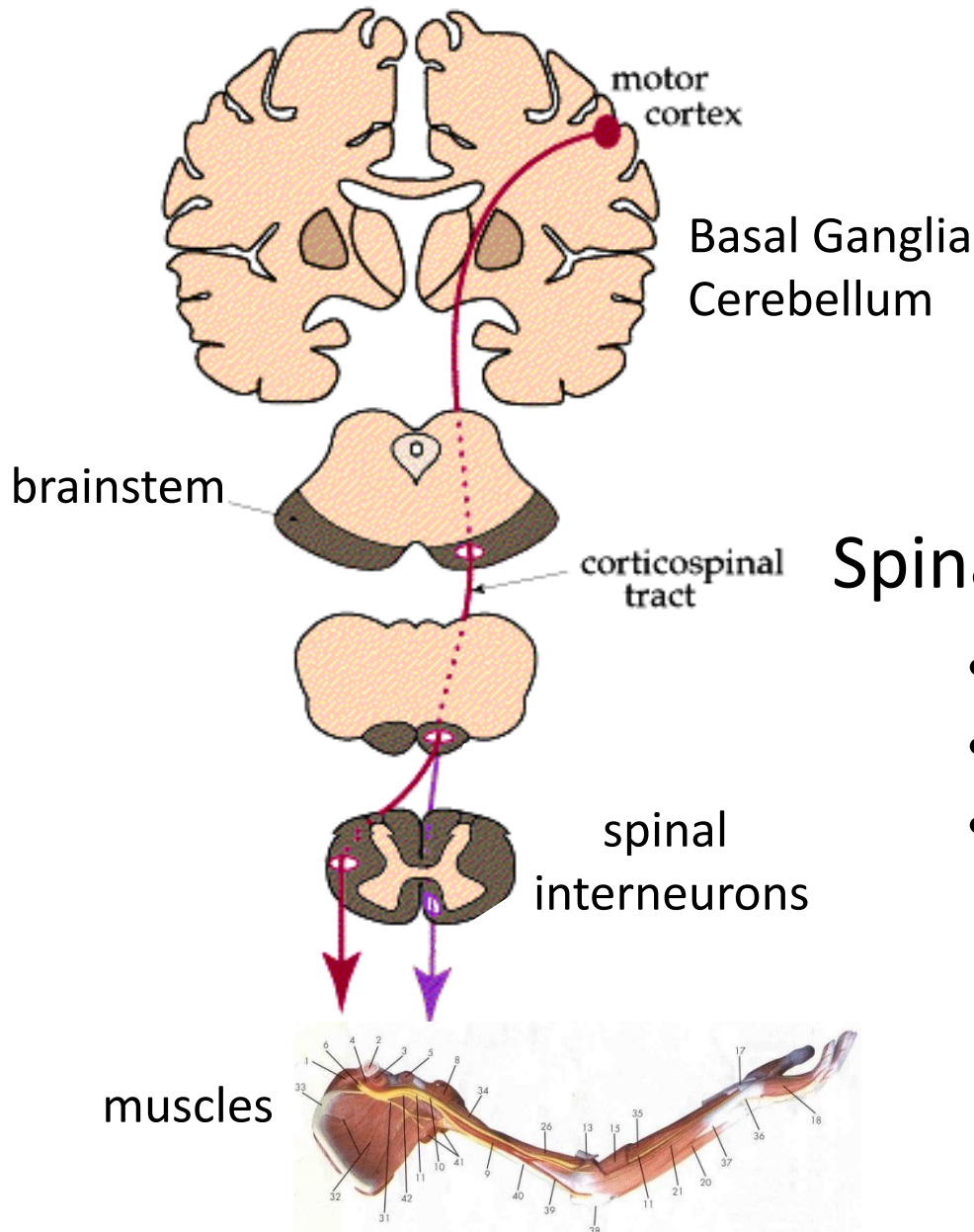
Motor control is achieved by many regions in CNS.

Motor cortical areas

- Voluntary actions (and others)

Spinal cord and brain stem

- Voluntary actions
- Locomotion
- Stereotypical motor patterns elicited by sensory stimuli (reflexes)



Functions of reflexes: 1. Stereotypical motor responses

Examples

- Withdrawal reflex
- Righting reflex



Functions of reflexes: 2. Limb stability

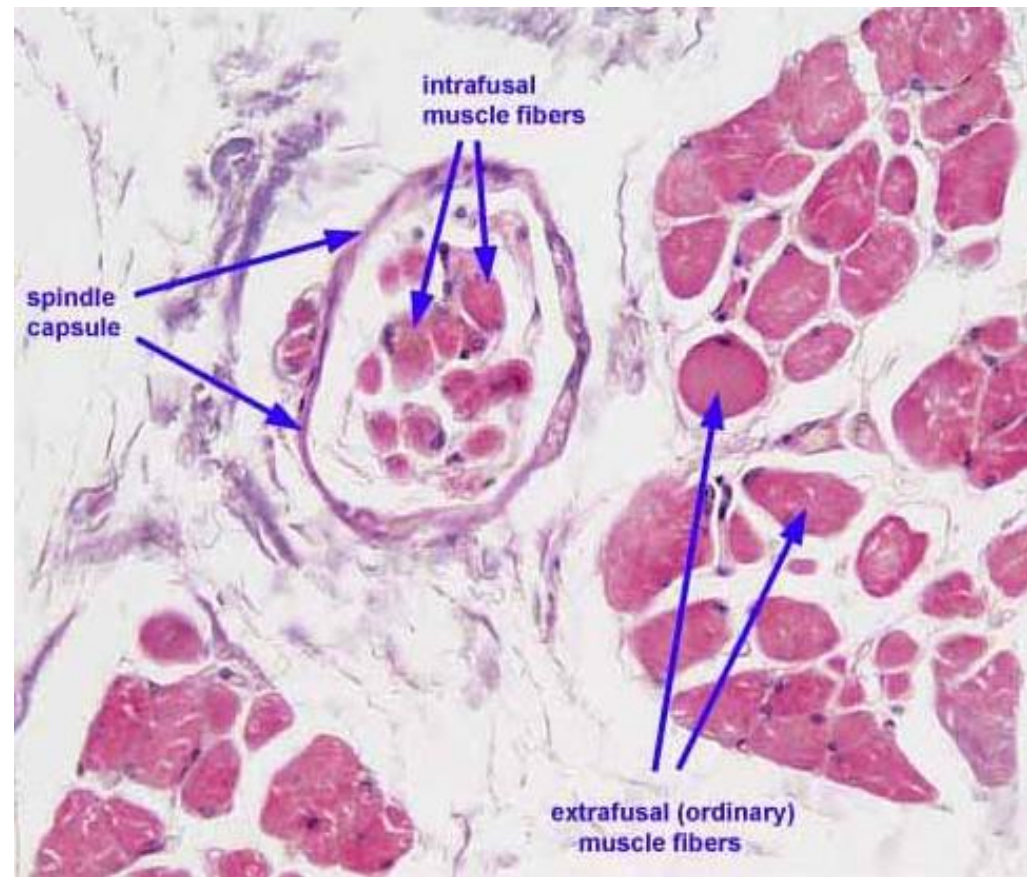
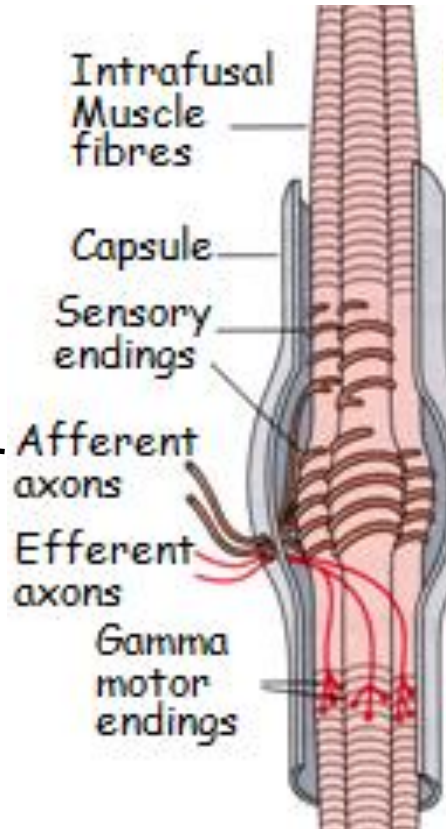
Monosynaptic stretch reflex:

Muscle contraction elicited by stretching of the muscle. A reflexive response that resists change in muscle length.

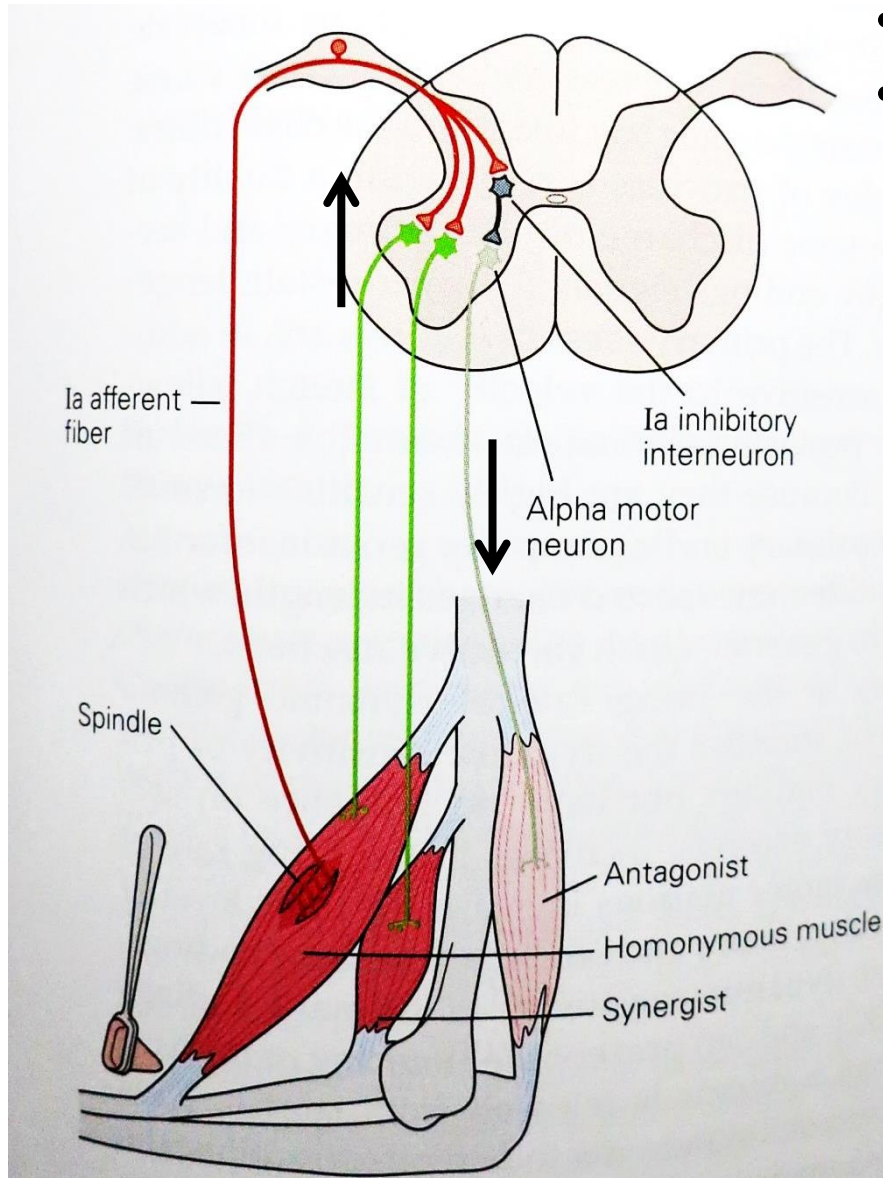
Sensor: Muscle spindles

- Muscle length
- Change in muscle length
- Speed of muscle-length change

conveying

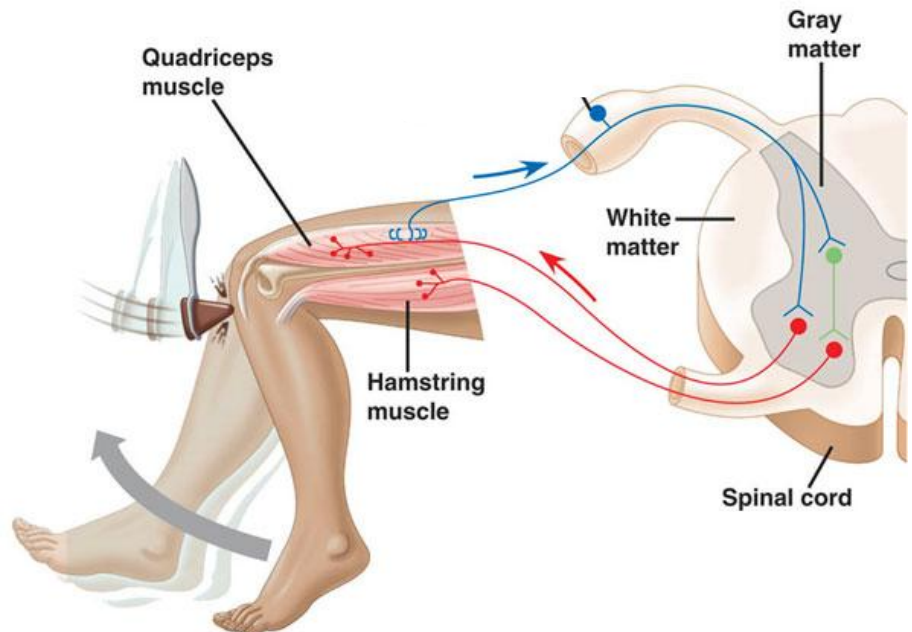


Monosynaptic stretch reflex pathway



- Agonist activation
- Inhibition of antagonist through “Ia Inhibitory Interneuron”

Knee jerk reflex: an example of stretch reflex

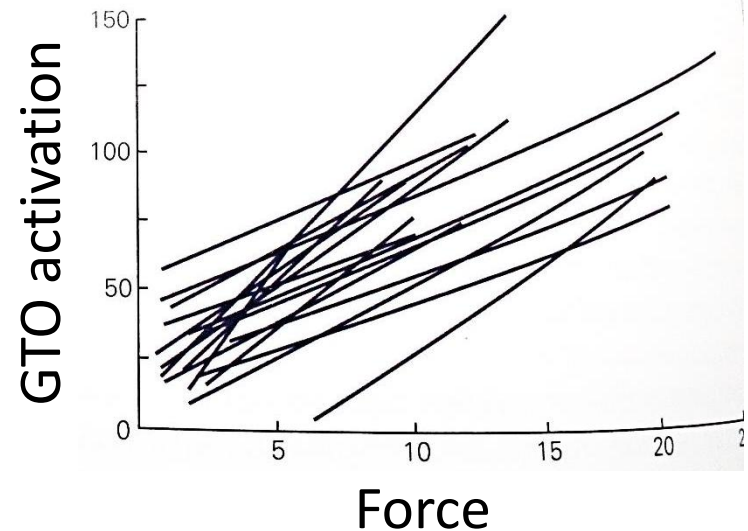
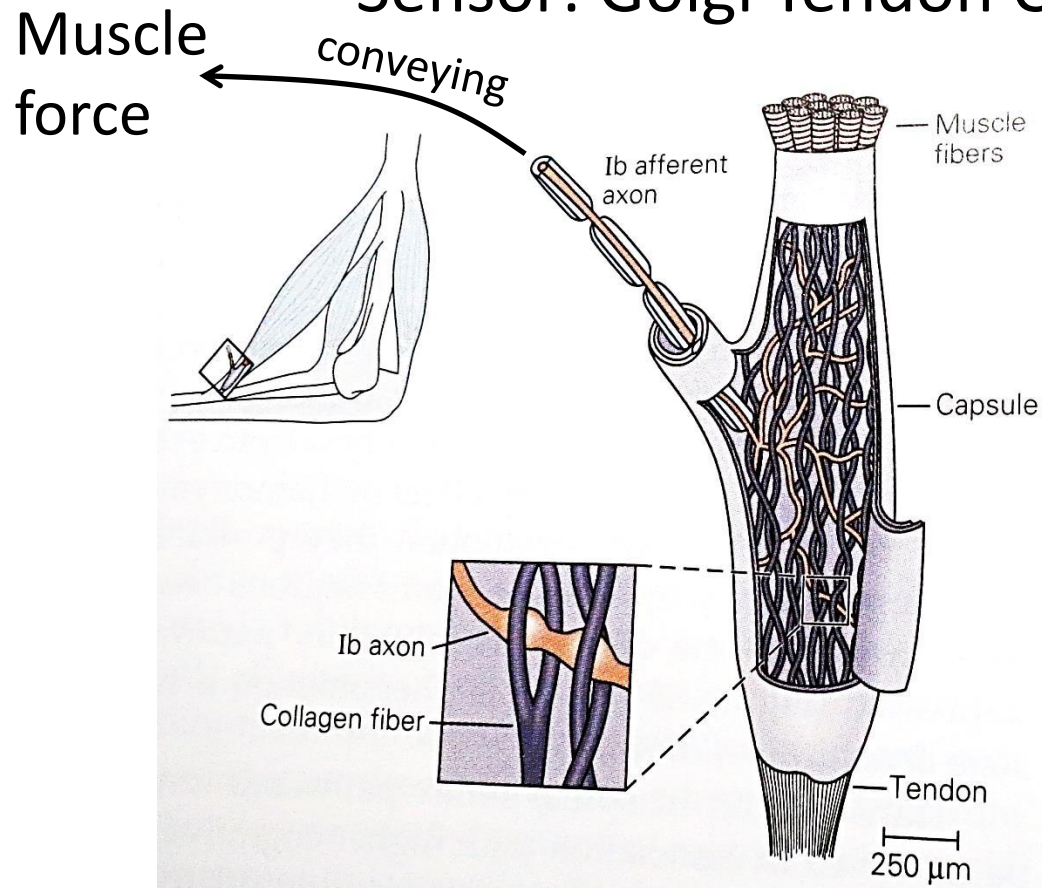


Functions of reflexes: 3. Prevent muscle damage from high muscle tension

Example: Autogenic inhibition reflex (polysynaptic)

- Reflexive relaxation of muscle (i.e., inhibition of activation) when muscle tension is high

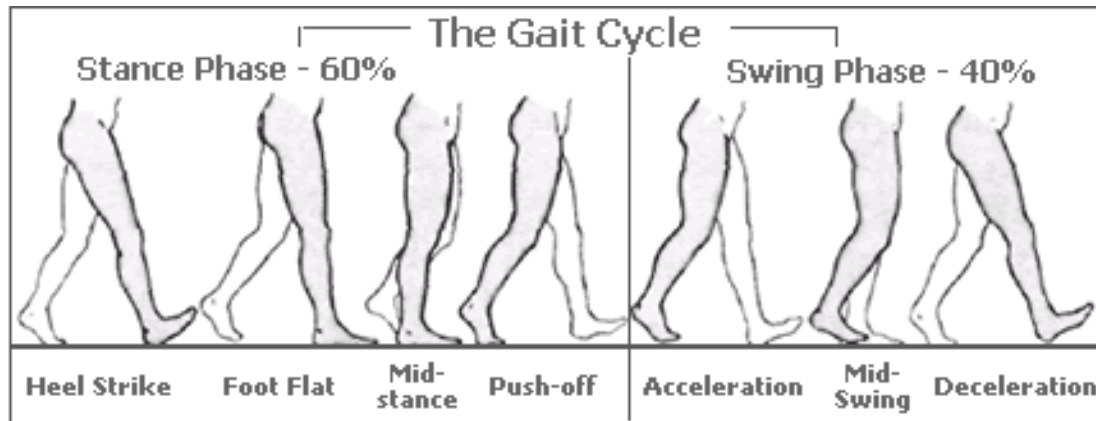
Sensor: Golgi Tendon Organ (GTO)



Locomotor behaviours include movement achieved by rhythmical, cyclical motion cycles

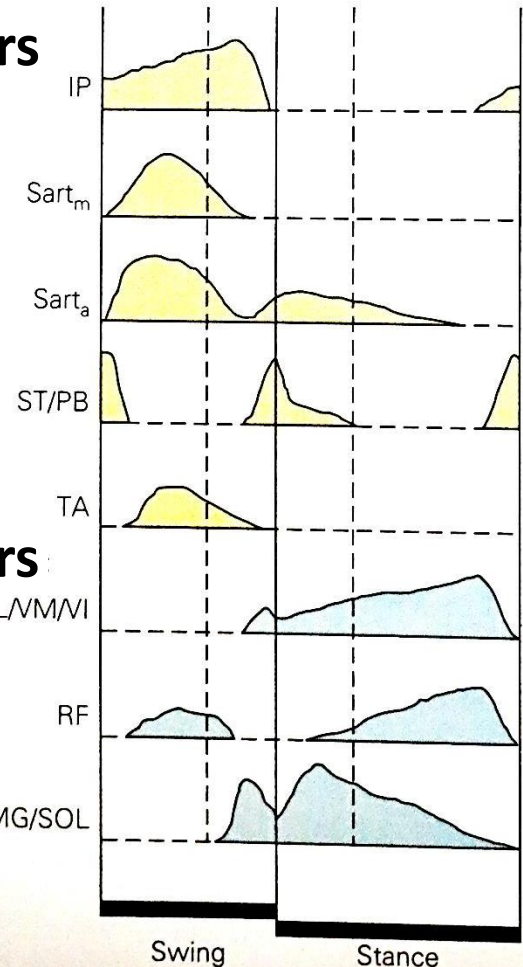
- Walking
- Running
- Crawling
- Flying
- Swimming

For walking, each gait cycle can be divided into stance and swing phases.

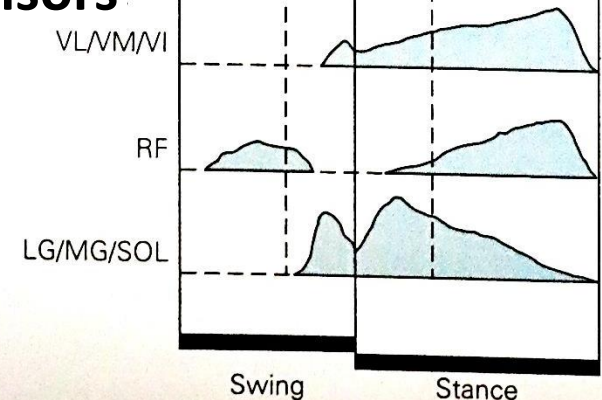


Complex muscle activation patterns from the walking cat

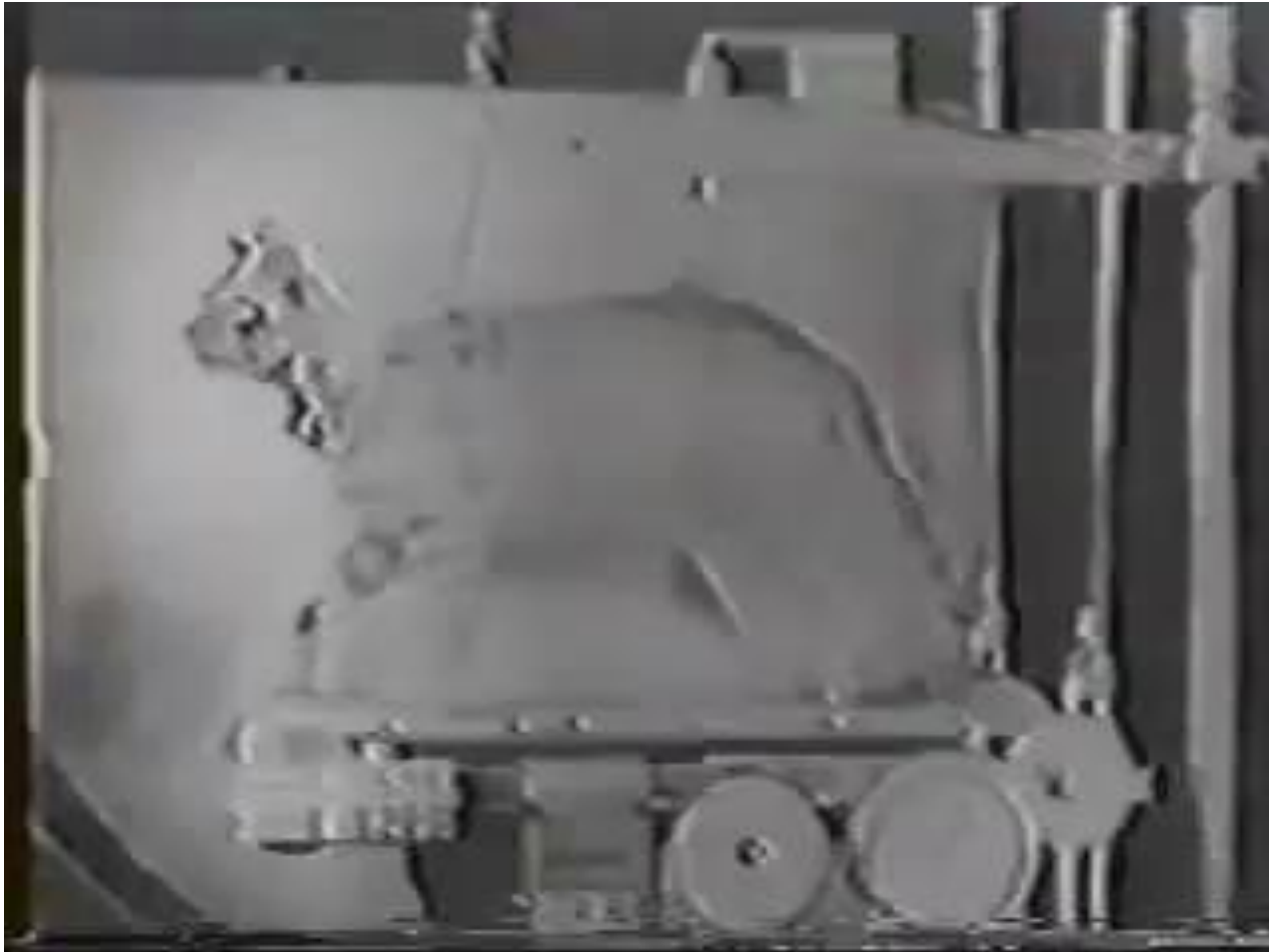
Flexors



Extensors

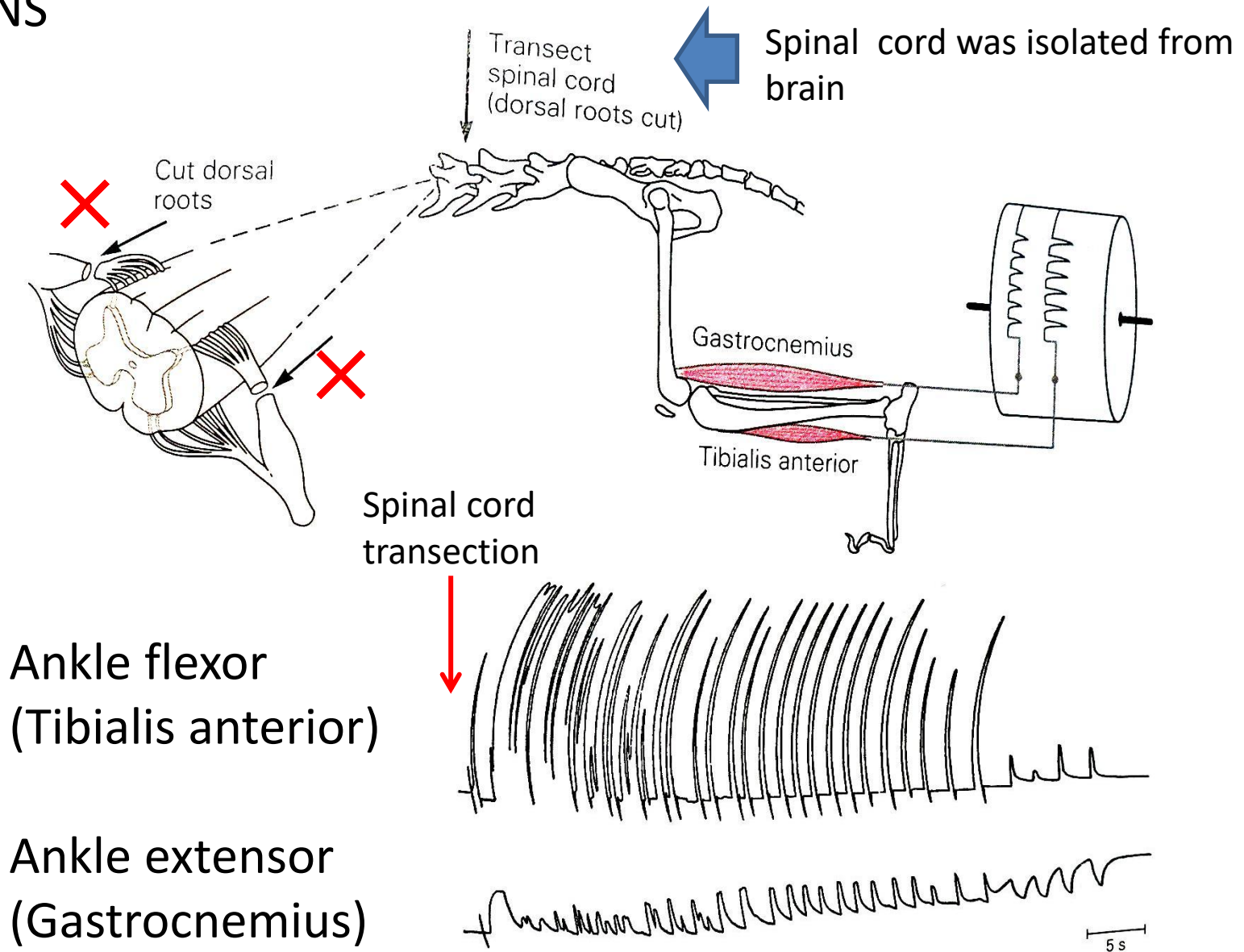


Sufficiency of the spinal cord for generating locomotor patterns in the cat



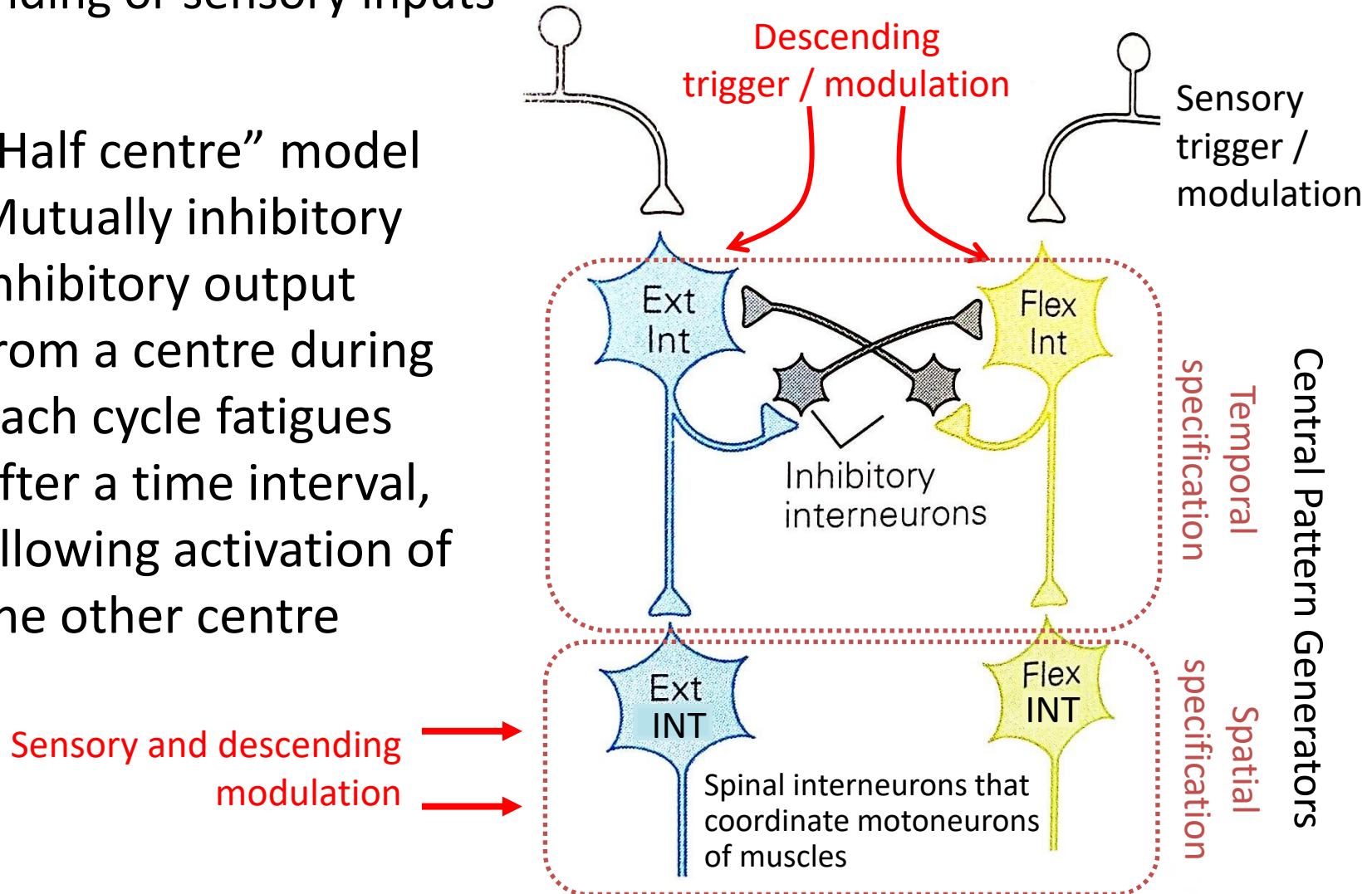
Decerebrate cat (Forebrain severed from brainstem)

Graham Brown's 1911 "Deafferentation" Experiment: locomotor rhythmic activities can be generated without sensory inflow to the CNS

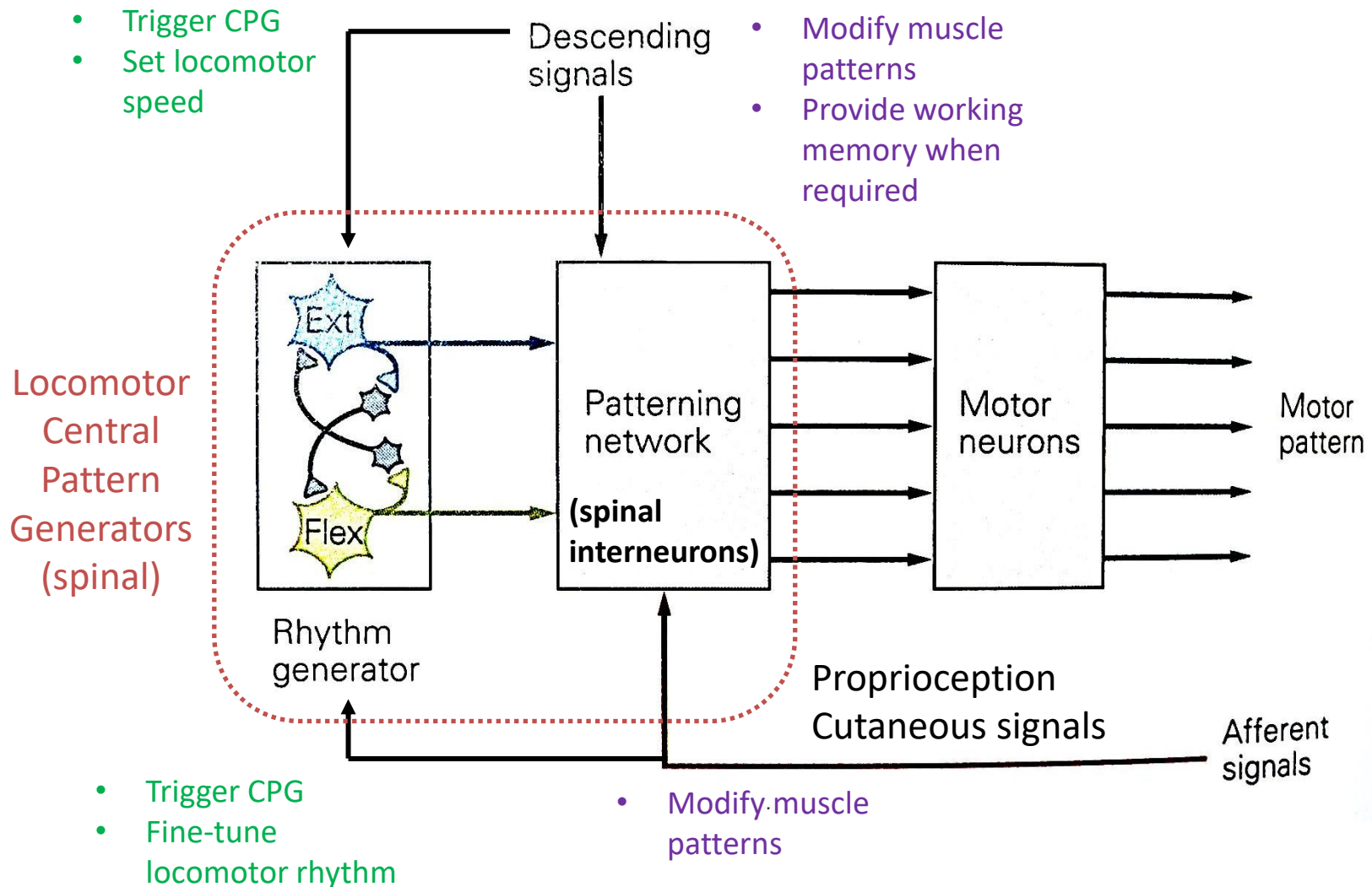


Central pattern generators (CPG): Neuronal networks within the CNS capable of generating rhythmic motor activity pattern without requiring sensory inputs for the maintenance of the rhythmic outputs, *once the temporal component of the networks are triggered to start by descending or sensory inputs*

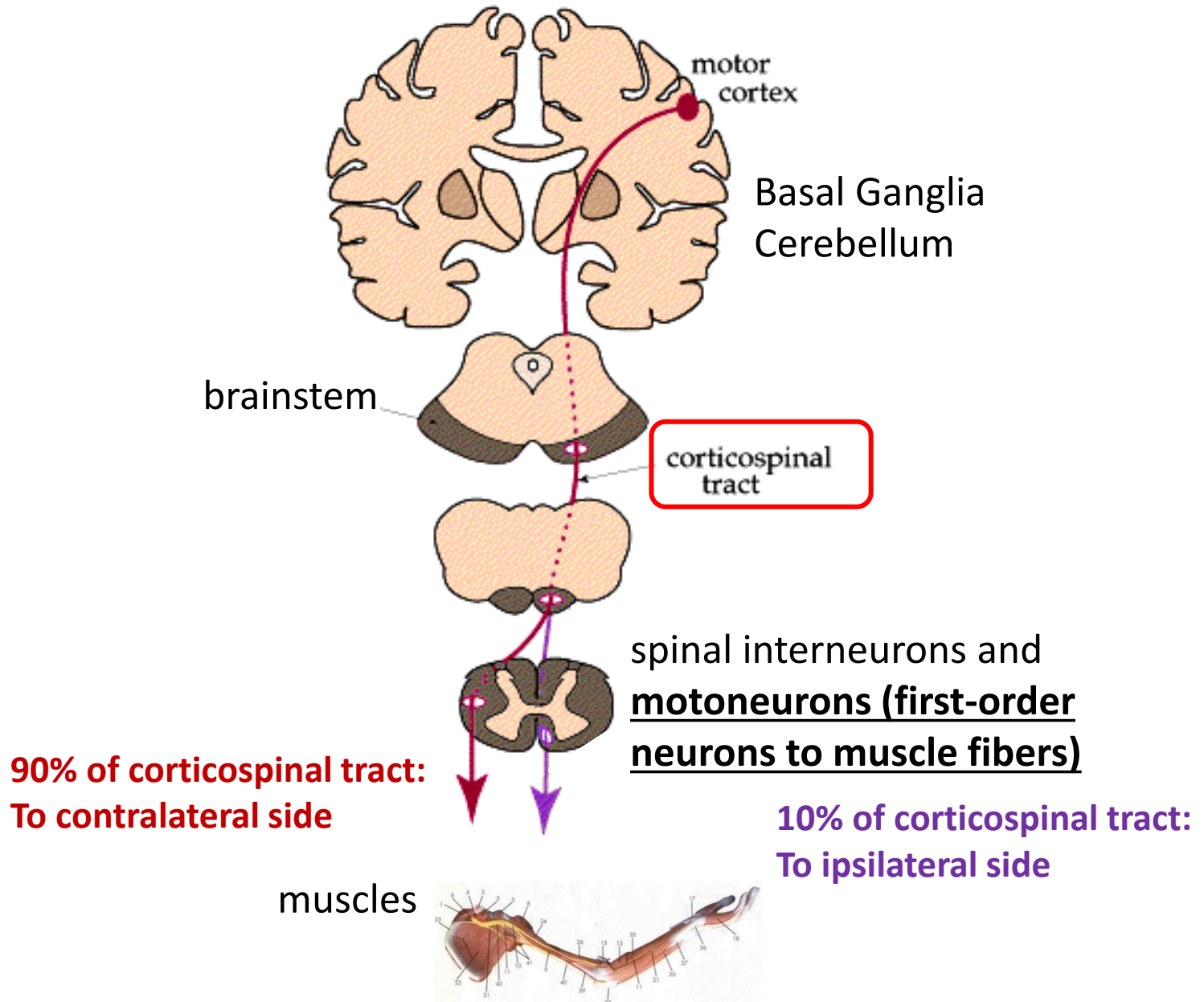
- “Half centre” model
- Mutually inhibitory
- Inhibitory output from a centre during each cycle fatigues after a time interval, allowing activation of the other centre



Take-home message: spinal locomotor patterns are never rigid. CPG temporal rhythm & spatial patterning networks are under constant sensory and descending regulations.



In humans, generation of **voluntary movement** requires inputs from the motor cortex.



Stages of movement generation

Task goal

Trajectory
(of the hand)

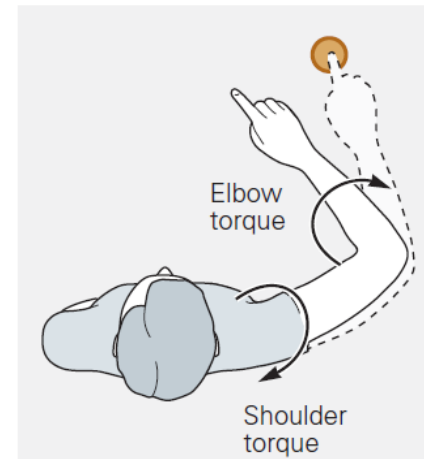
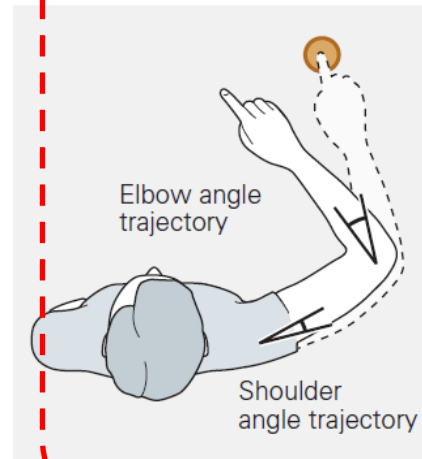
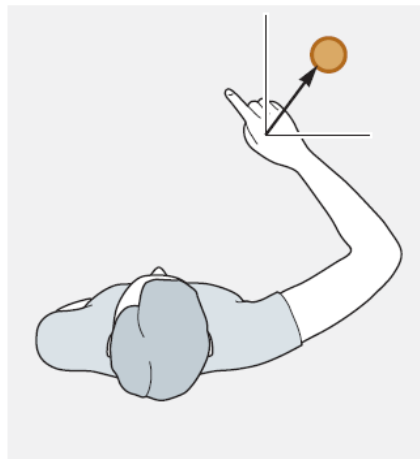
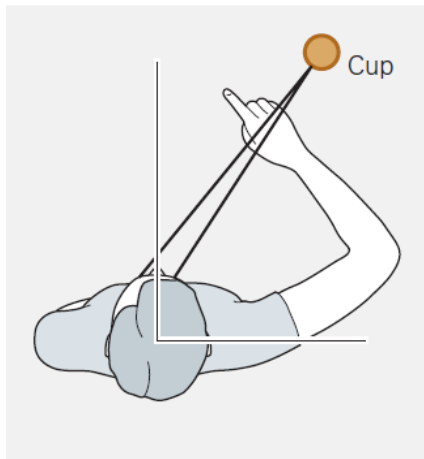
Joint angle
pattern for
the hand
trajectory

Joint torques and
muscle activations
for the joint angle
profile

*Movement
planning*

*Inverse
kinematics*

*Inverse
dynamics*

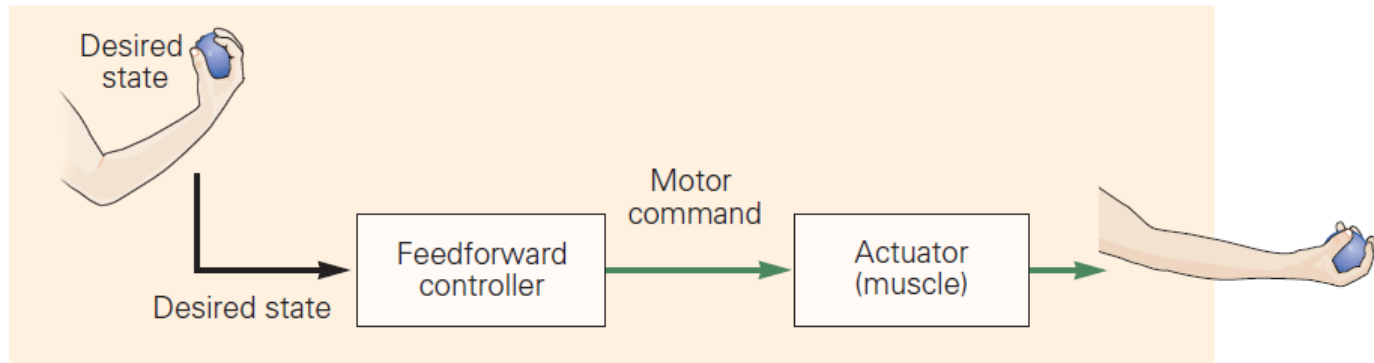


Motor execution

Joint angle => torque => muscle pattern => motion

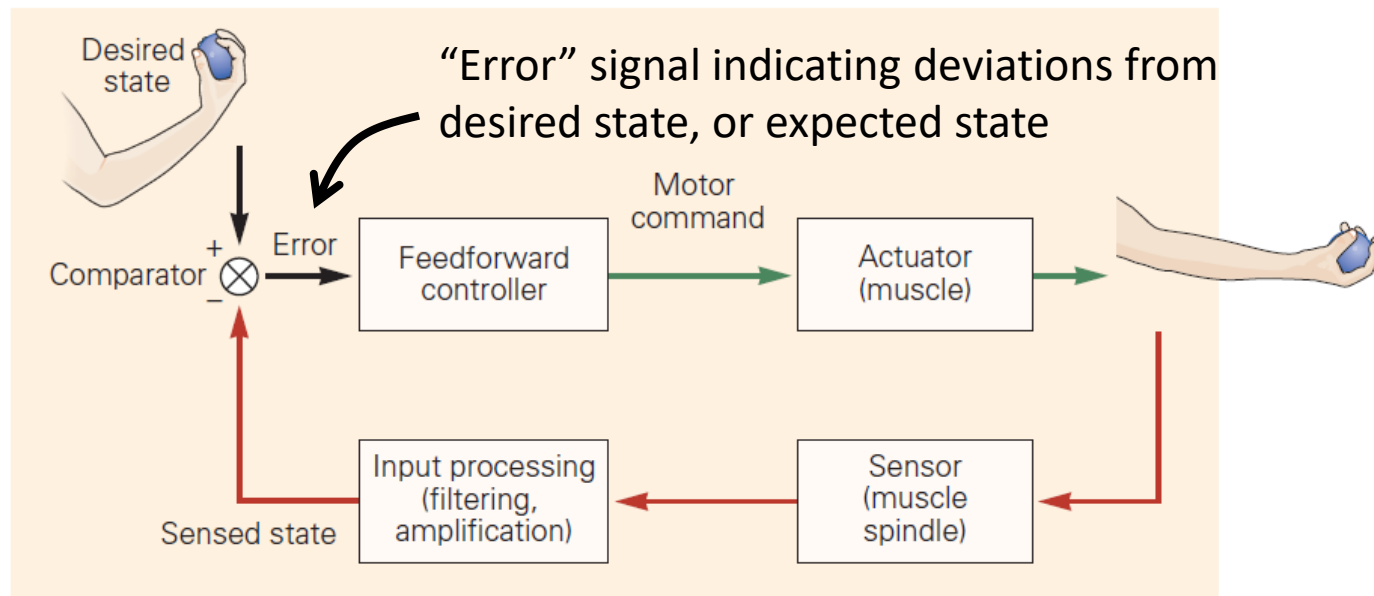
Two general strategies of motor execution

Feedforward Motor Control



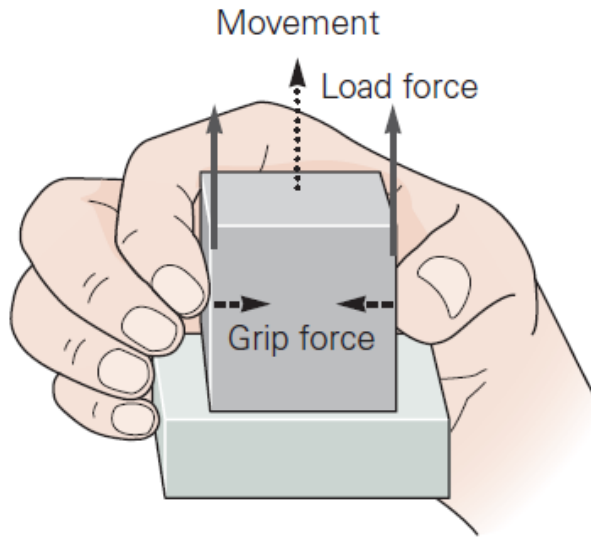
- Centrally generated commands without regard to consequence

Feedback Motor Control



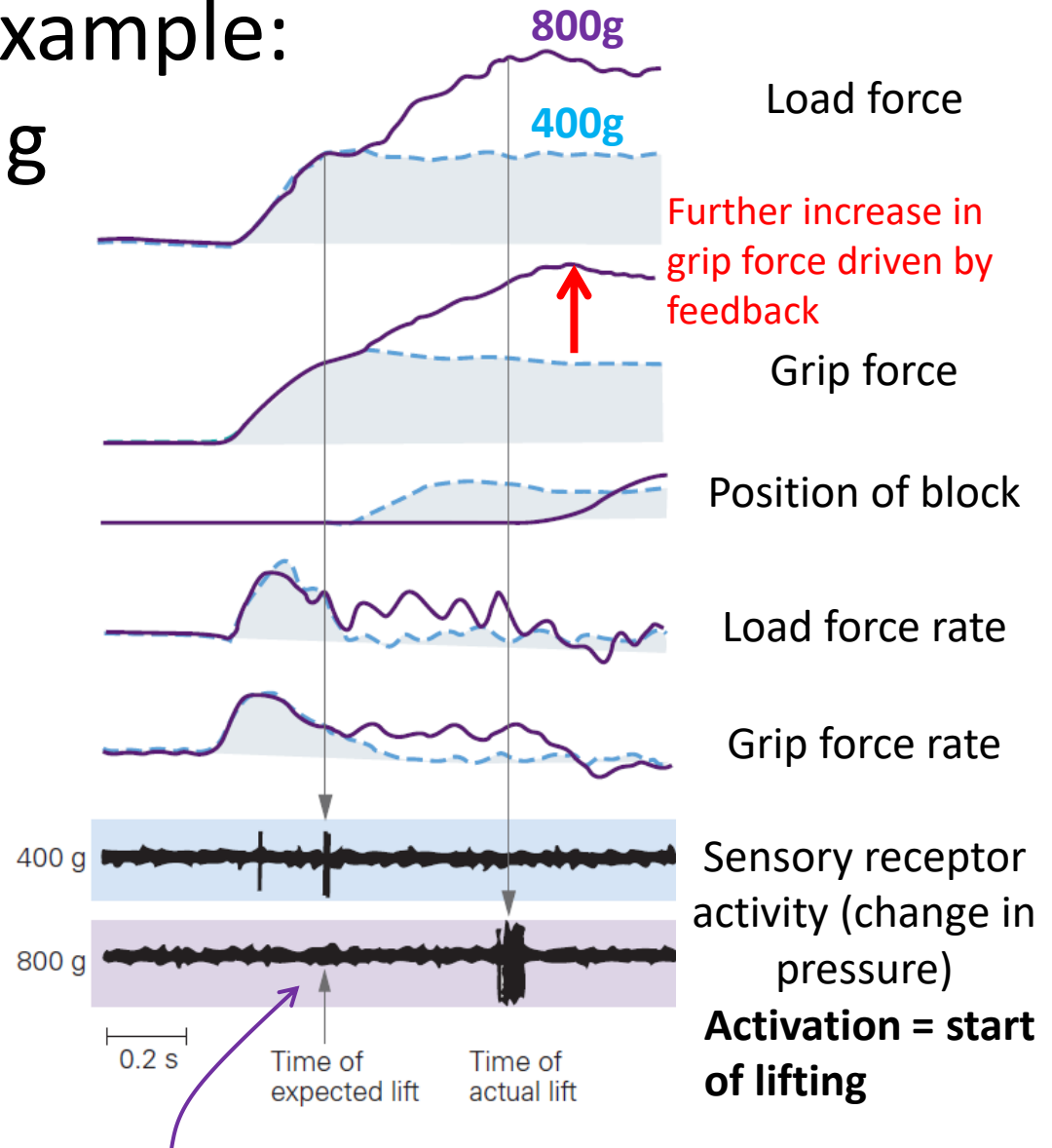
- Motor commands for correcting movement error specified by comparing the desired state and the actual state (according to sensory information)

Feedback control example: Precise object lifting



Task

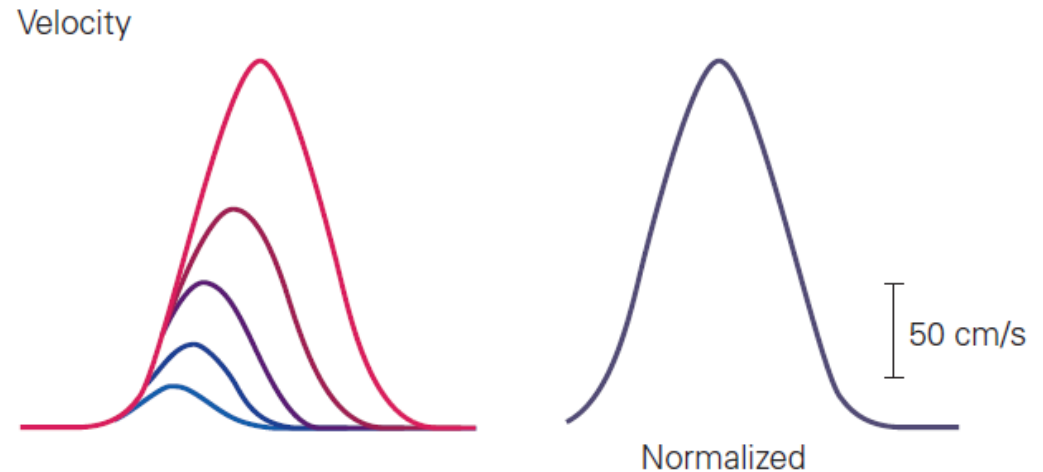
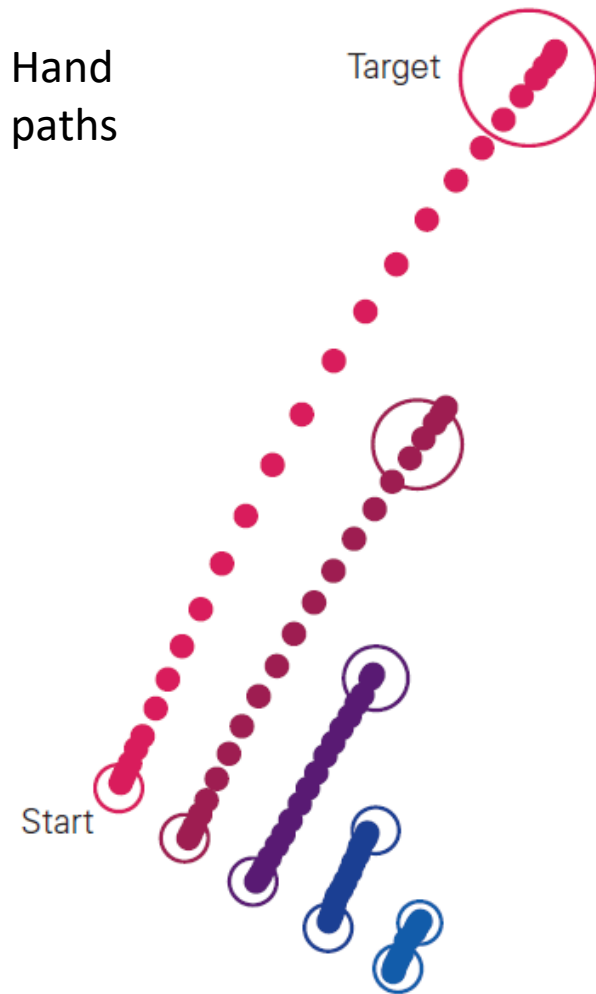
- lifting an object from a table
- Several trials with 400g object
- Followed by 800g object (surprise)



800g: Absence of activities at expected time of lift due to slippage represents an “error signal” (i.e., actual signal deviates from the expected signal), which triggers an increase in force production

Feedforward control examples:

- The beginning portions of almost all movements
- Fast (“ballistic”) upper-limb reaching



- Single velocity peak: indicative of pre-specified motor commands
- If feedback control: first peak would be identical across targets; secondary peaks from feedback adjustment should be observed

Feedforward VS Feedback control

Feedforward control advantages:

- Fast generation; no need to wait for sensory signals
- Precise commands can be shaped through learning

Feedforward control disadvantages:

- Movement error (from imprecise planning or execution or unexpected perturbations) cannot be corrected
- CNS needs good knowledge of the limb biomechanical properties
- Needs not-too-noisy neural system

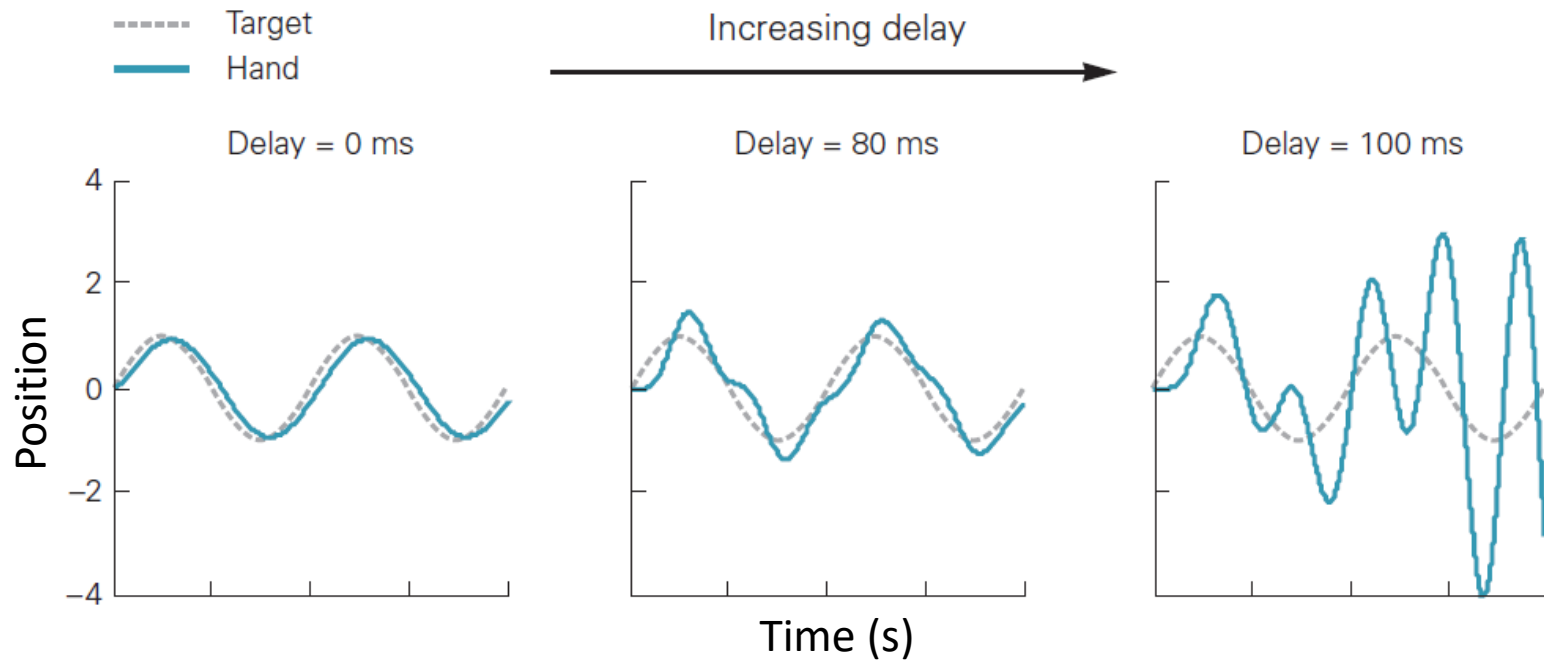
Feedforward VS Feedback control

Feedback control advantages:

- Precise movement possible with feedback-driven correction

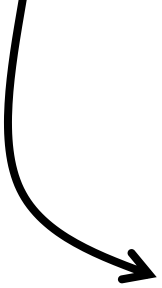
Feedback control disadvantages:

- Delayed arrival of sensory information can cause **movement instability** (sensory information at time T arrives at $T+\text{delay}$, and compared with desired state at $T+\text{delay}$ due to delayed arrival)



Some key concerns of motor neuroscience:

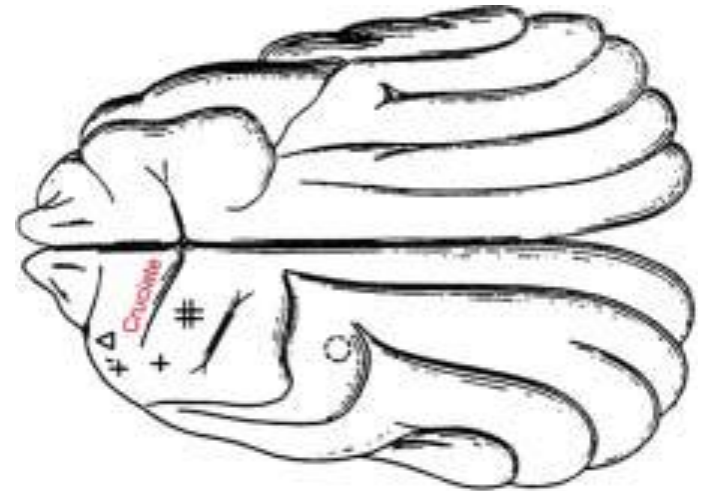
- How is an intention to move translated into a motor plan by the nervous system?
- How are motor commands for the muscles computed by the motor system to result into the desired movement trajectory (while accounting for limb biomechanics)?



What **movement parameters** (if any) are “encoded” or represented by the activities of motor cortical neurons?

Assumption: Movement parameters are encoded in the primary motor cortex (M1)

Why the obsession with the primary motor cortex (M1)?

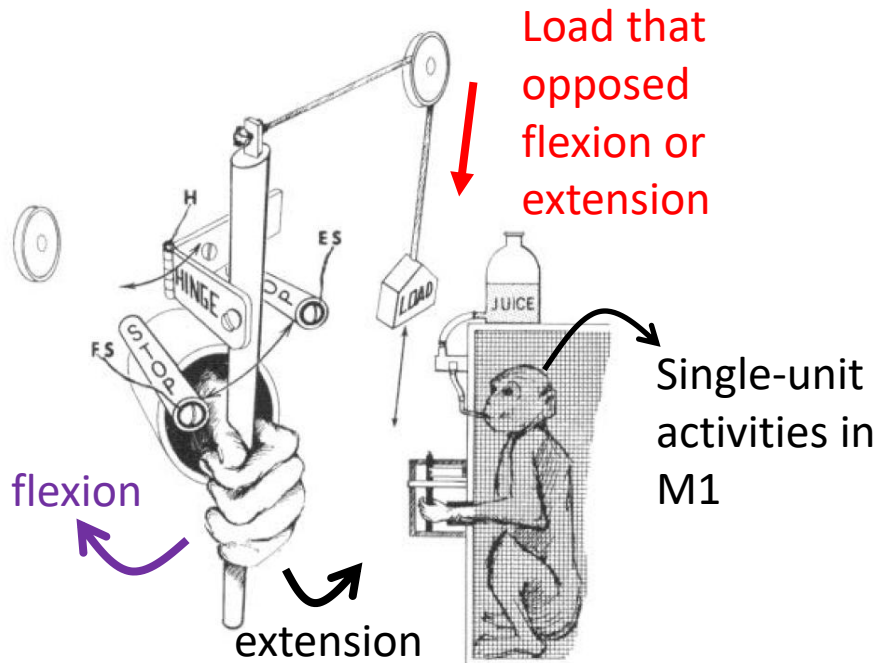


Dog cortex

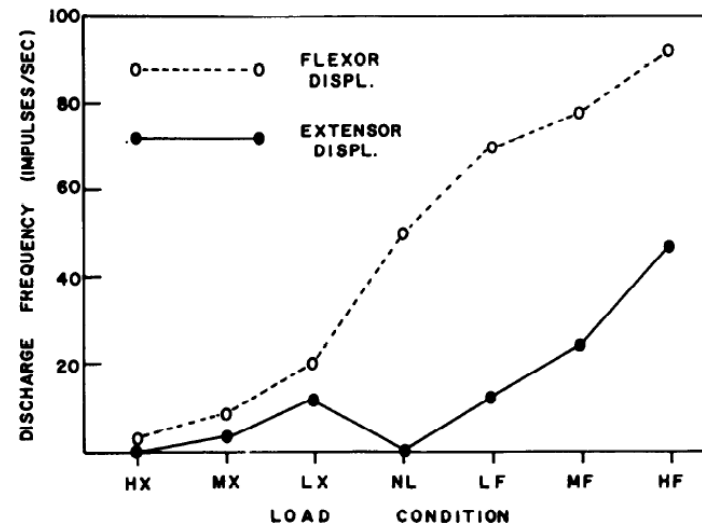
Fig. 1. Gustav Fritsch (left) and Eduard Hitzig.

- First cortical brain mapping with electrical currents
- Evoking contralateral muscle twitches from stimulations of M1 but not other areas

Classic results from Evarts argue that **the force demanded by the task**, rather than joint displacement, is represented in motor cortex



Neuron active during heavy flexion load, in both extension- or flexion-displacement trials

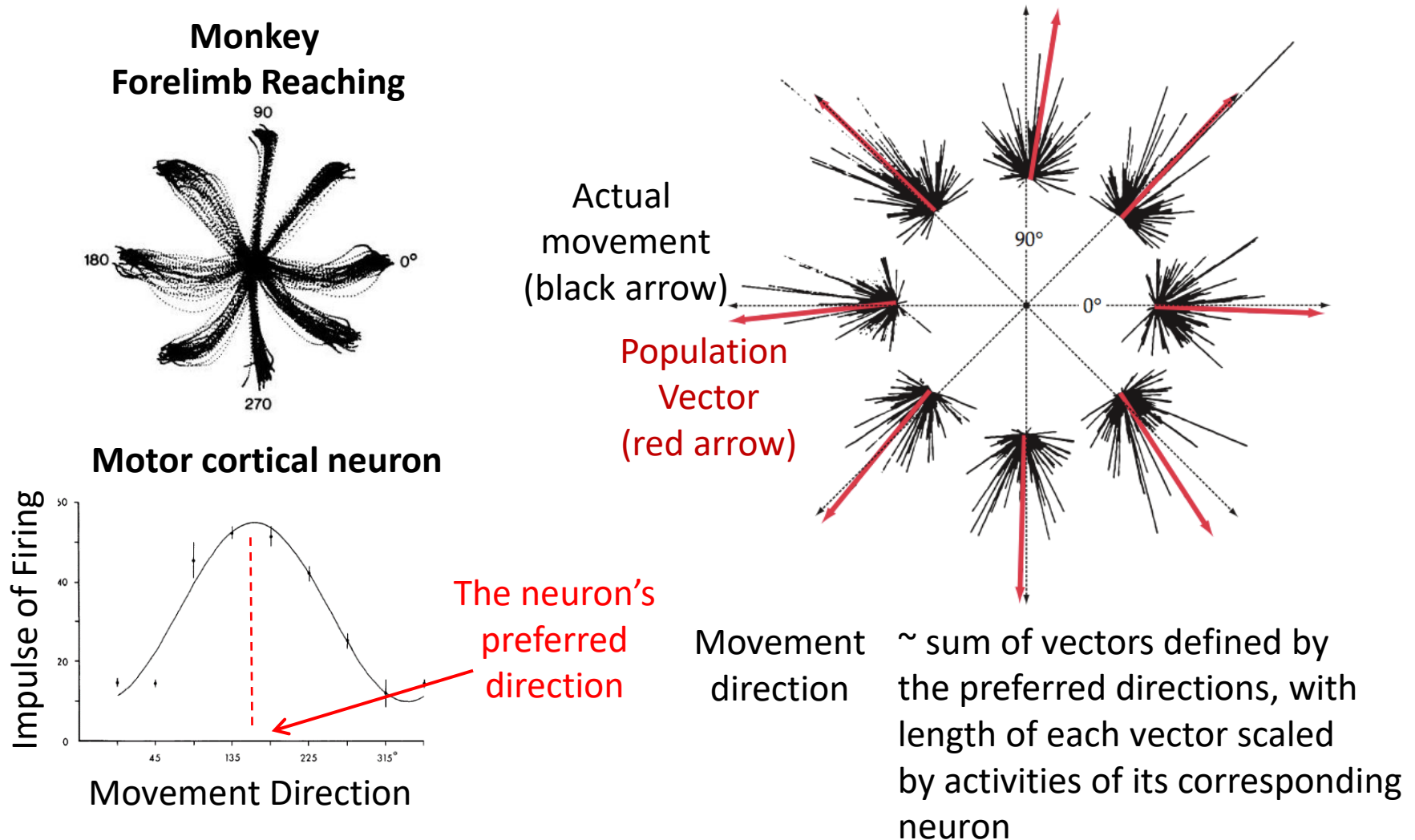


Heavy load Extension direction ← No load → Heavy load Flexion direction

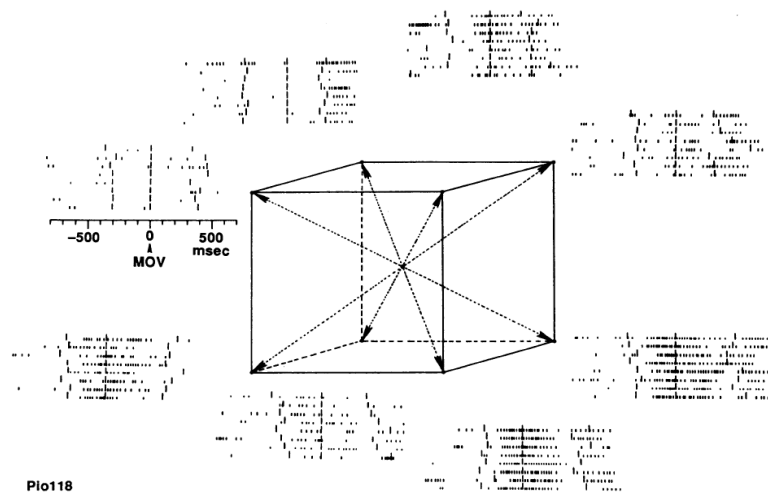
- *Dissociation* between force and displacement: different loads applied during flexion and extension trials
- Monkey had to complete trial against load within a fixed duration for reward

- 26 of 31 neurons showed primary modulation with load instead of displacement

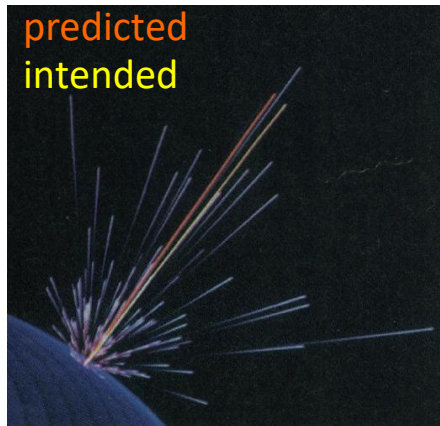
Subsequently, Georgopoulos *et al.* argued, using monkey M1 data from reaching, that M1 activities encode **upper-limb reaching direction**



Georgopoulos *et al.* posited that movement direction can be *decoded* from ensemble M1 activities using the “population vector” derived by summing the neurons’ “preferred direction”, weighted by each neuron’s instantaneous firing rate



Plot118



Recorded activity Intended direction Difference in angle between intended and preferred directions

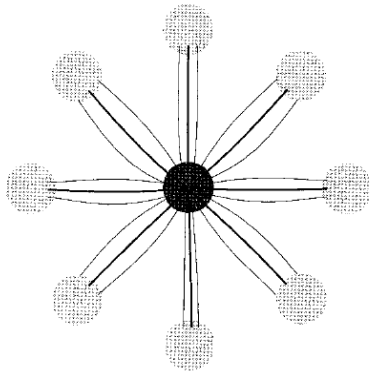
$$d(\vec{M}) = b + k \cos(\theta_{CM})$$

$$\vec{M} \approx P(\vec{M}) = \sum_{i=1}^N (d_i(\vec{M}) - BL_i) * \vec{C}_i$$

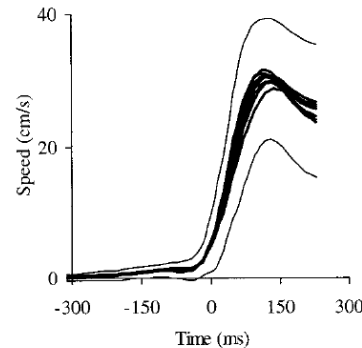
Predicted direction Baseline activity Preferred direction

Moran and Schwartz (1999, *J Neurophysiol*) further demonstrated that motor cortical firing rates could be related to **speed and movement direction**

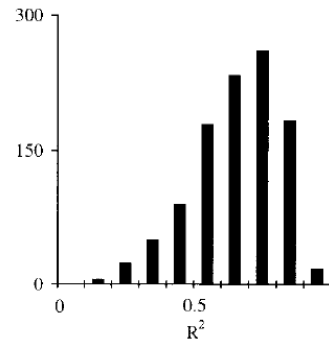
Planar reaching



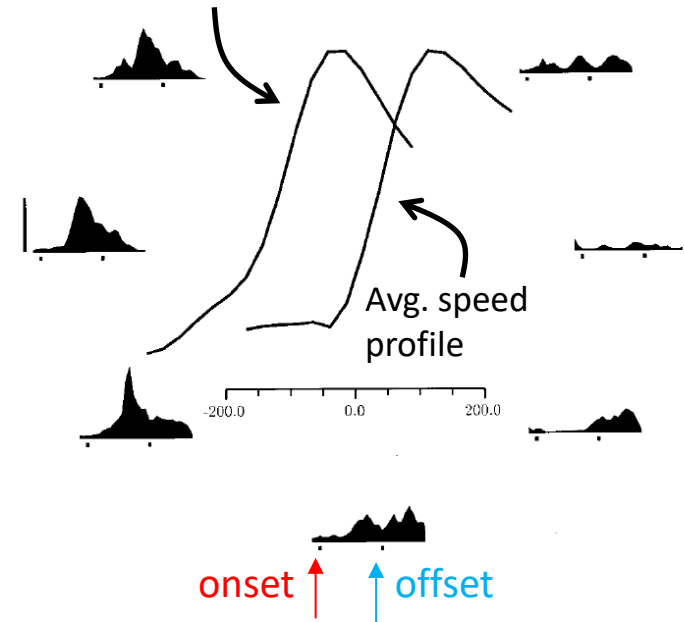
Speed profile



Distribution of R^2 :
Regression of
activities to model
(N=1039)



Avg. activity
across targets



Firing rate $\rightarrow$ $D(t - \tau) - b_0 = \|\vec{V}(t)\| (b_n + b_y \sin [\theta(t)] + b_x \cos [\theta(t)])$

time delay $\rightarrow$ τ

Movement direction $\rightarrow$ $\theta(t)$

Velocity $\rightarrow$ $\vec{V}(t)$

Correlations between M1 neuronal activities and other combinations of movement-related parameters have since then been identified. Many neurons also appeared to show **mix selectivity** to many parameters.

Fu, Flament, Coltz, Ebner (1995) *J Neurophysiol*

- Movement direction, distance to target, target position

Kakei, Hoffman, Strick (1999) *Science*

- Muscle activity, hand movement direction in space, wrist rotation direction

Paninski, Hatsopoulos, Donoghue (2004) *J Neurosci*

- Hand position, velocity, acceleration, **and** firing of neighboring cells

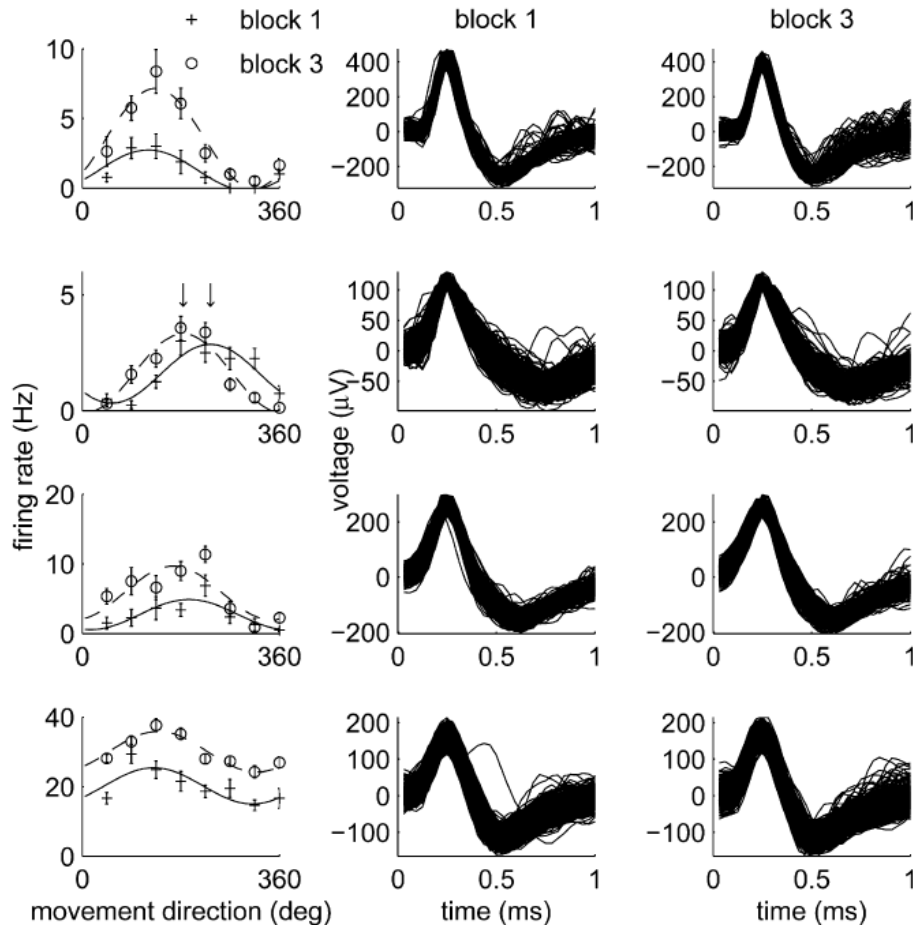
... and other combinations of the
parameters listed above

To further complicate the picture, the representation of some of the parameters appear to undergo (random?) changes over time

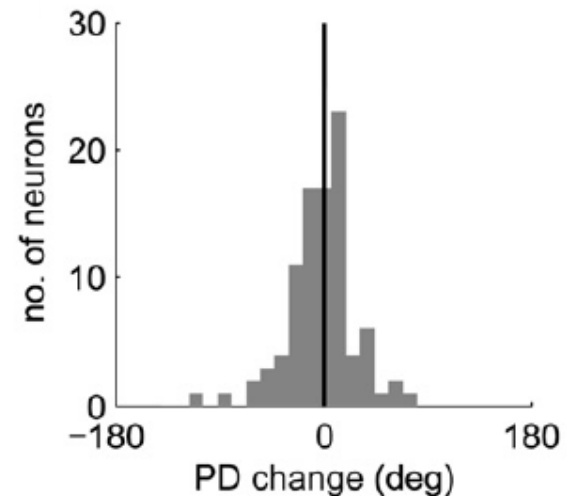
Examining consistency of preferred direction across within-session blocks

Similar waveforms:

Same neurons



Distribution of changes of preferred direction of M1 neurons from block 1 to block 3



Rokni *et al.* (2007) *Neuron*

Perhaps to progress in our understanding in motor cortical functions, a paradigm shift is necessary (Scott, 2008, *J Physiol*)

J Physiol 586.5 (2008) pp 1217–1224

SYMPOSIUM REPORT

Inconvenient Truths about neural processing in primary motor cortex

Stephen H. Scott

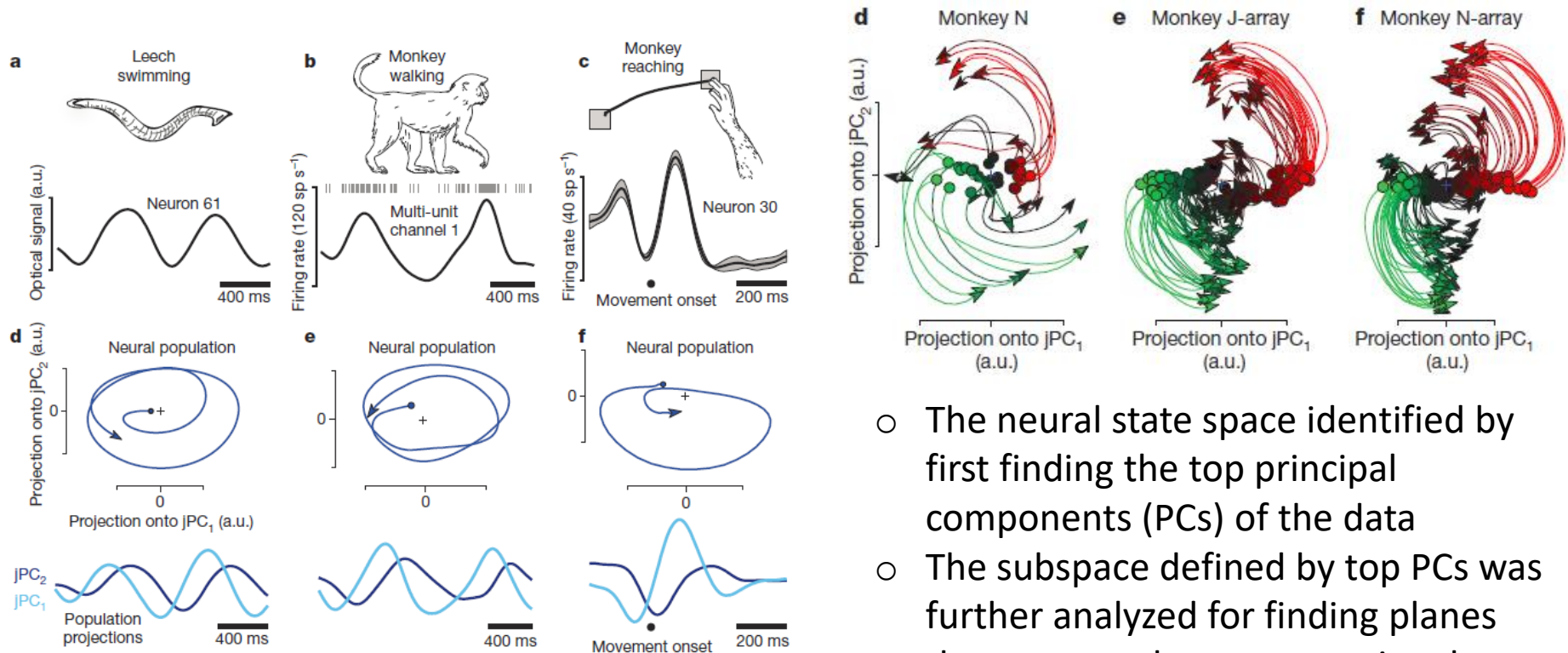
Centre for Neuroscience Studies, Departments of Anatomy & Cell Biology and Medicine, Queen's University, Kingston, ON K7L 2W2 Canada

“Studies have shown that M1 activity correlates with ***a broad range of parameters*** of motor performance from spatial target location, hand or joint motion, joint torque and muscle activation patterns. Further these representations ***can change across behaviors***, such as from posture to movement. What do heterogeneous, labile neural representations mean and how do they help us understand how M1 is involved in volitional motor control?”

One proposed alternative view of M1 concerns modeling M1 neuronal activities as reflecting the state-space dynamics in dynamical system

$$\dot{\mathbf{r}} = f(\mathbf{r}(t)) + \mathbf{u}(t)$$

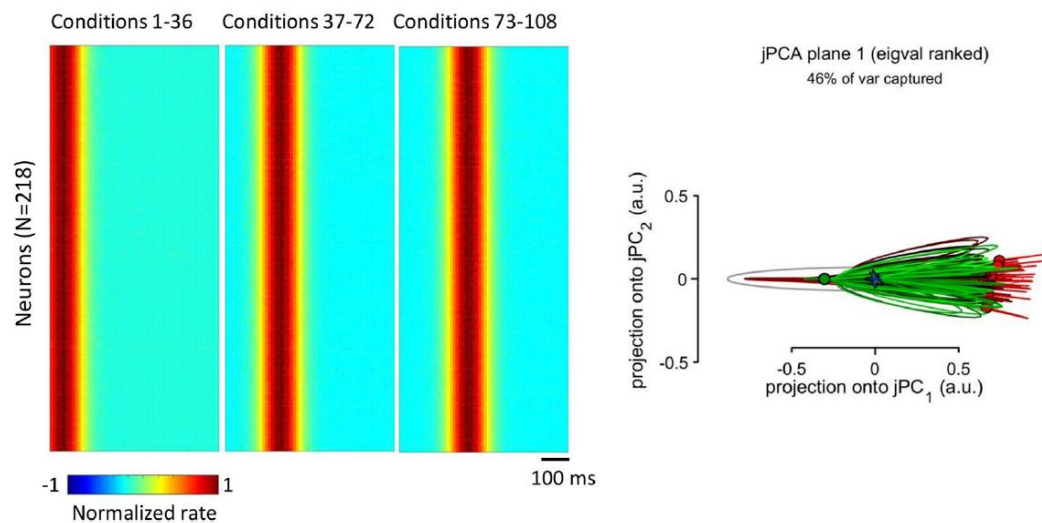
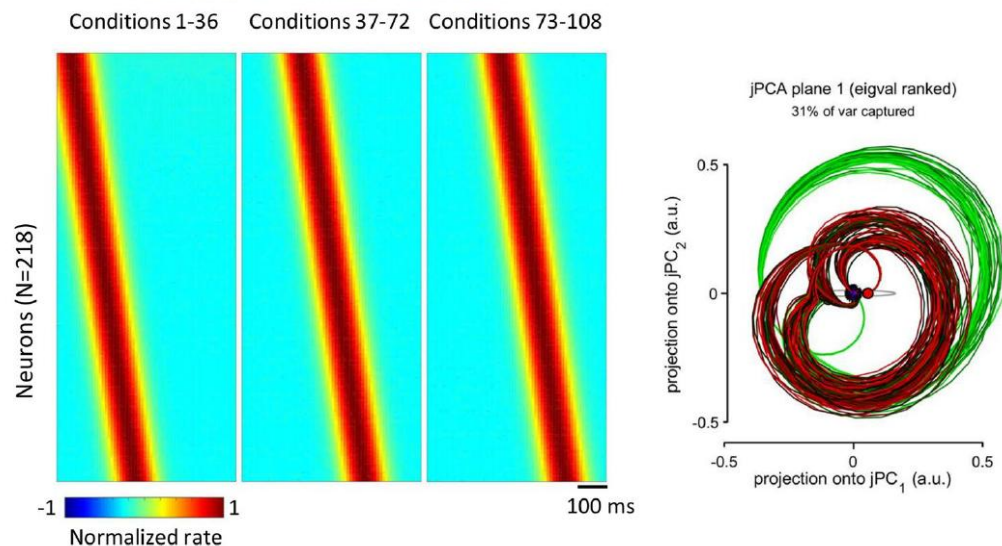
↑
Ensemble firing rate
←
External control signal



- The neural state space identified by first finding the top principal components (PCs) of the data
- The subspace defined by top PCs was further analyzed for finding planes that capture the most rotational structures (using **jPCA**)

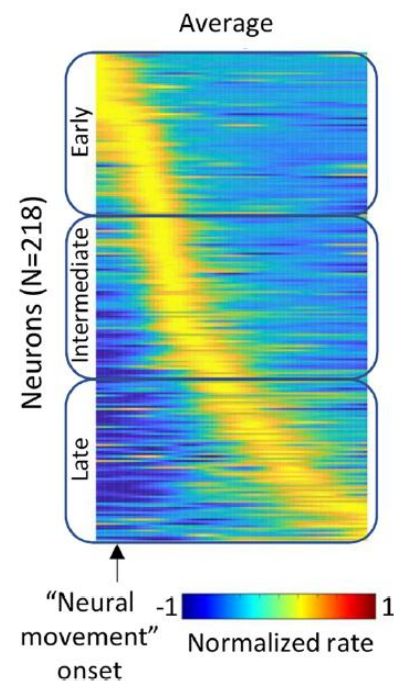
Functional significance of rotational dynamics?

Simulated neurons

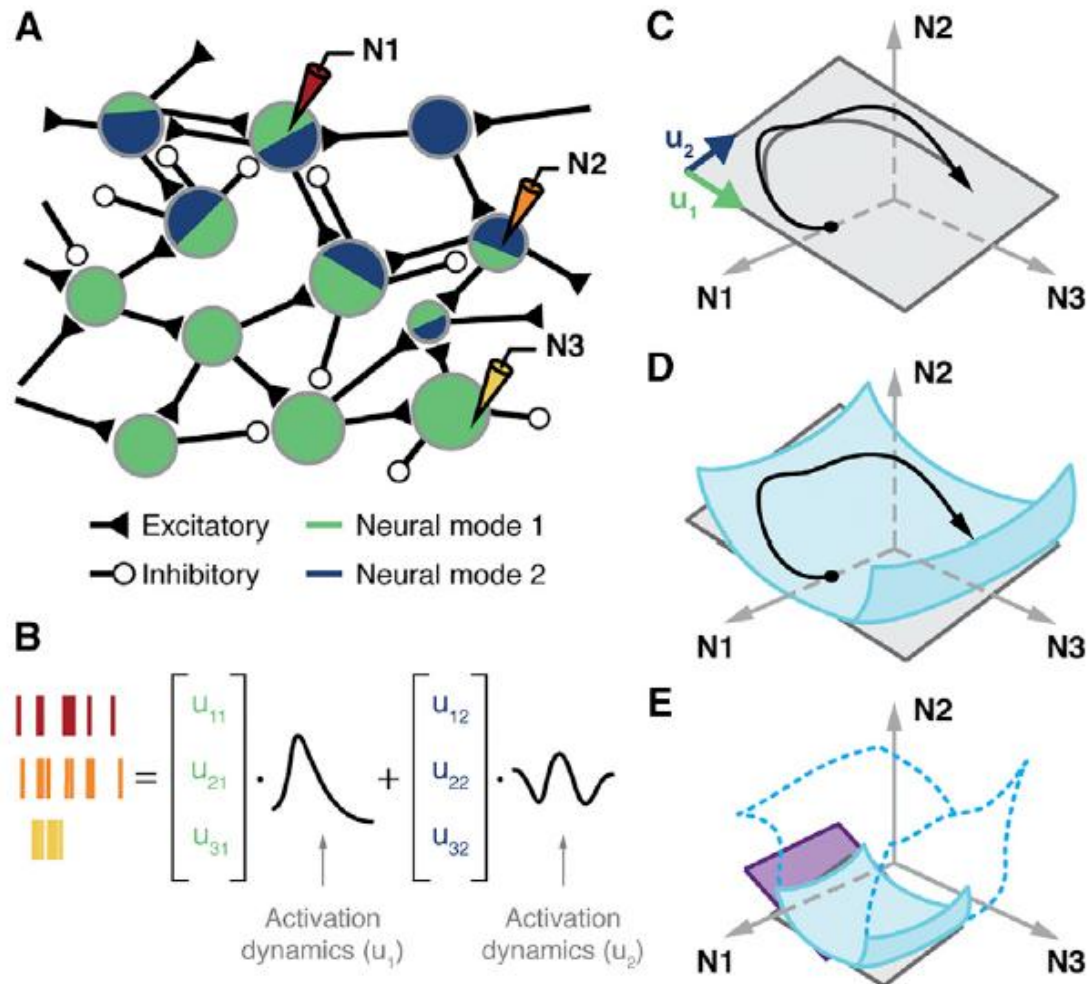


- Rotational dynamics after $jPCA$ can arise trivially without any explicit modeling of M1 response properties
- Two conditions: (1) temporal order of peak firing across neurons; (2) same order in all conditions

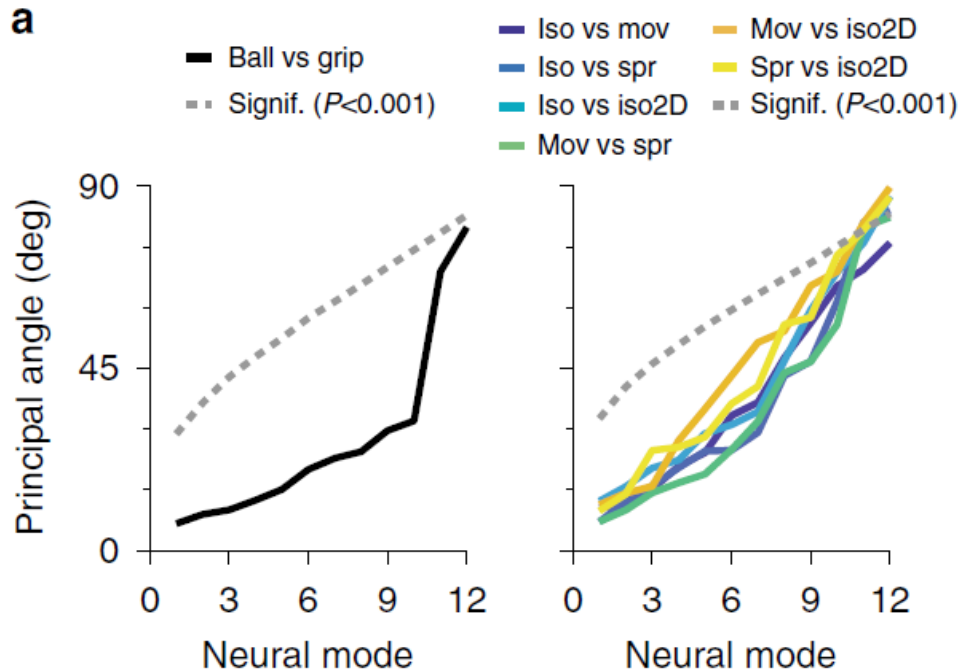
Churchland's data



Variability of neuronal responses and their relationship with movement may be better understood from neuronal dynamics within neural manifolds

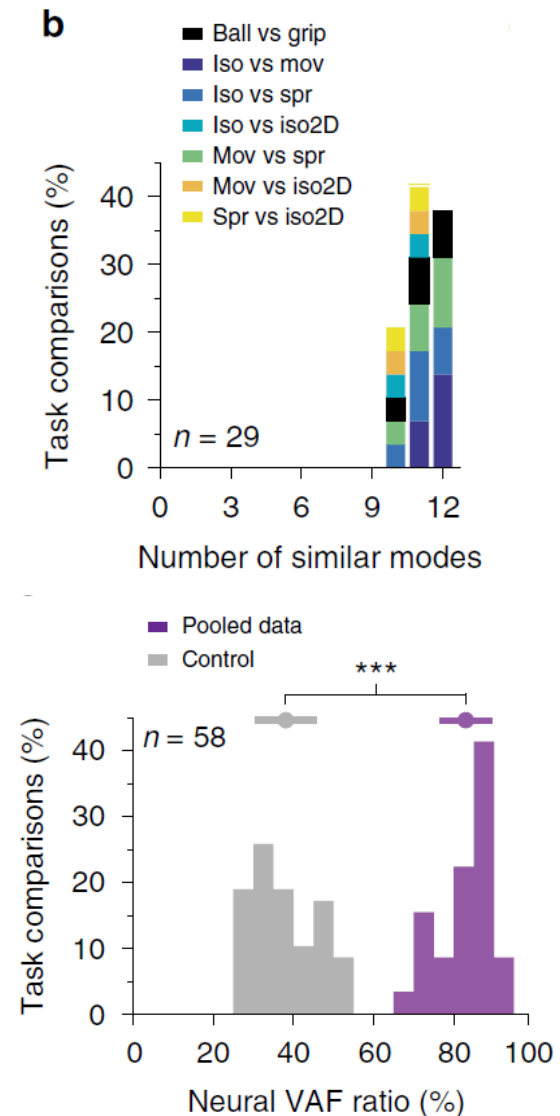


M1 neural manifolds from PCA appears to be preserved across multiple motor tasks



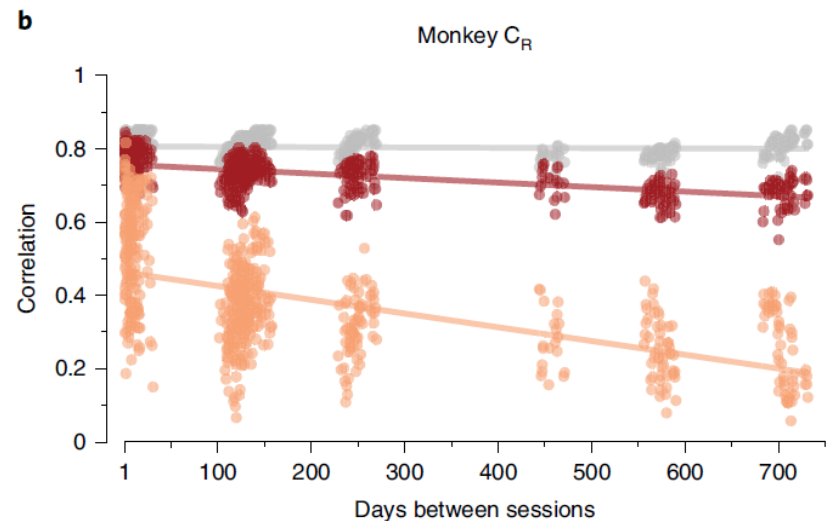
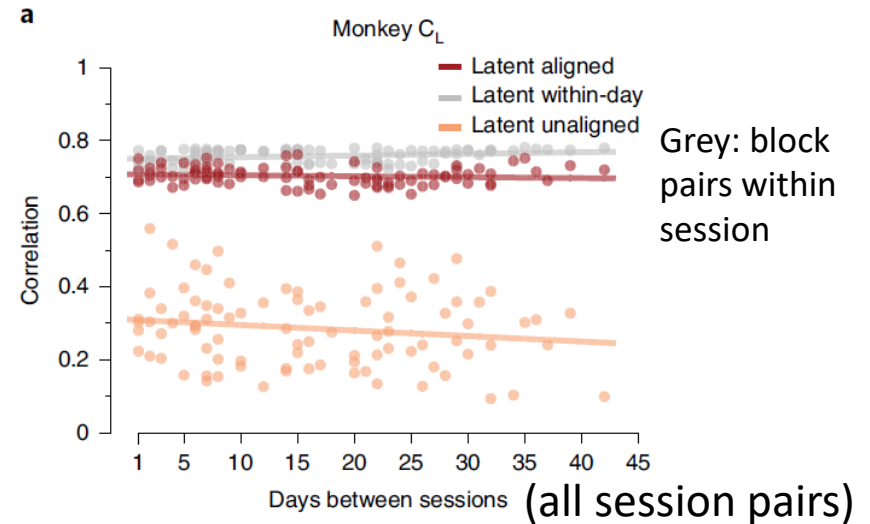
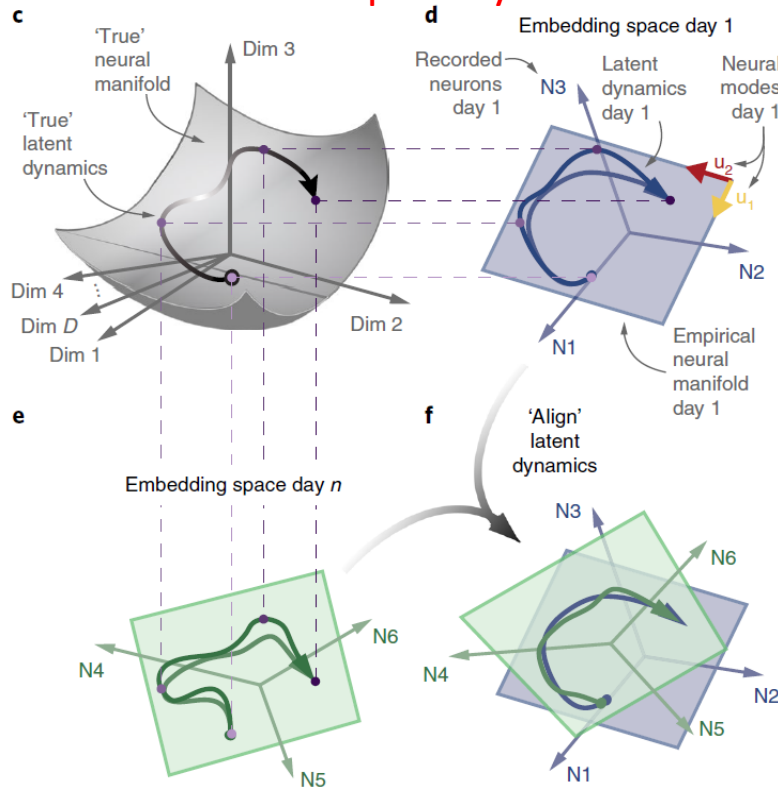
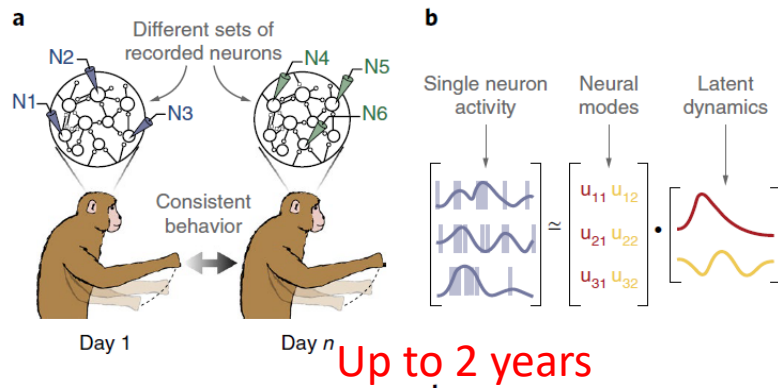
reach-and-grasp (ball), power grip (grip),
isometric wrist (iso), wrist motion (mov),
elastic load (spr), isometric centre-out (iso2D)

Gallego, Miller *et al.* (2018) *Nat Comm*



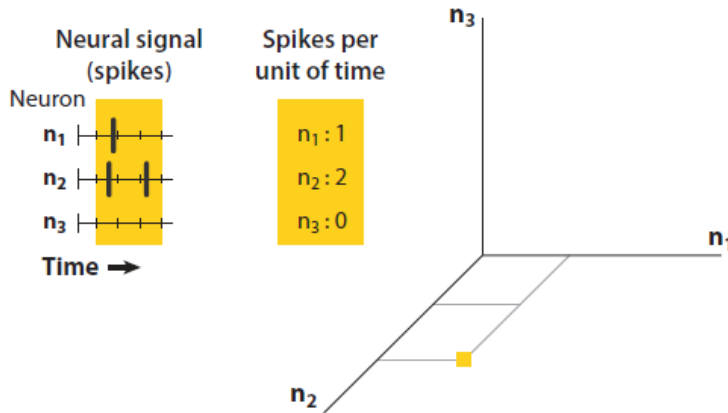
VAF project to mnf different task to
VAF project to mnf same task

Linear neural manifolds identified by dimensionality reduction appear robust across time despite neuron turnover

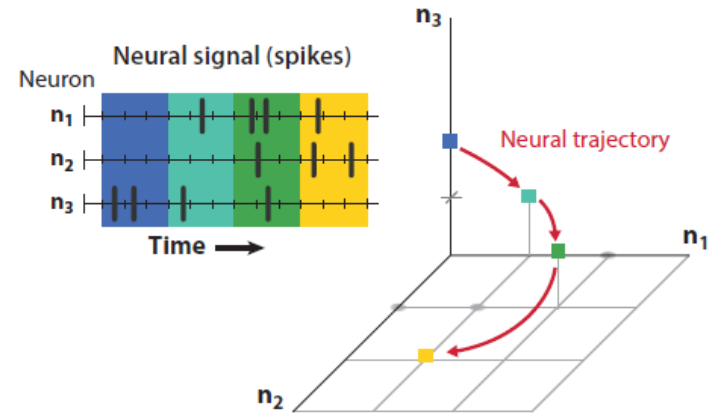


The structure of neural population activities may be best characterized by task-specific neural trajectories in neural state space

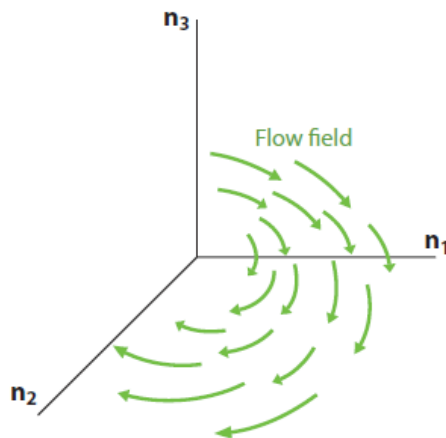
a Defining neural state



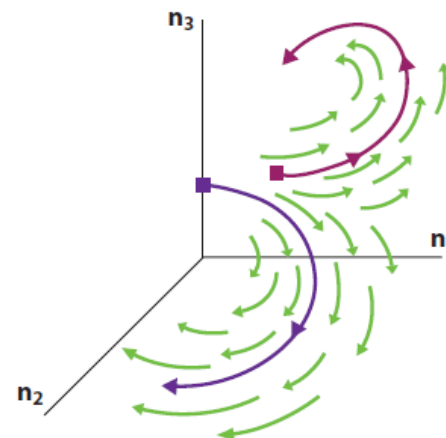
b Neural trajectory



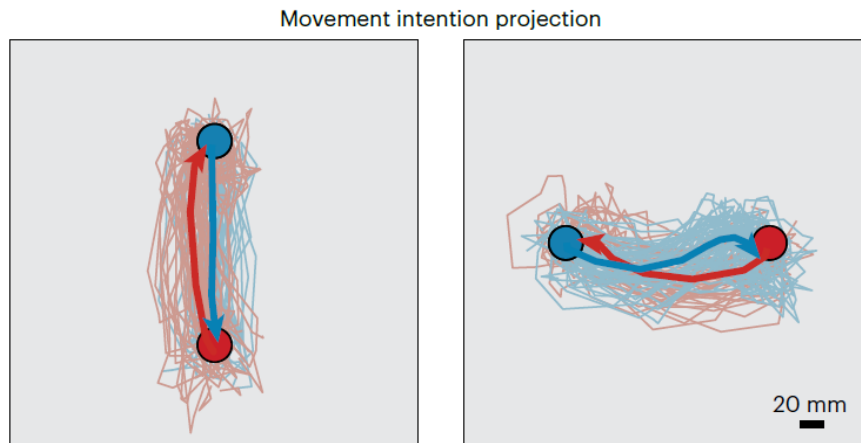
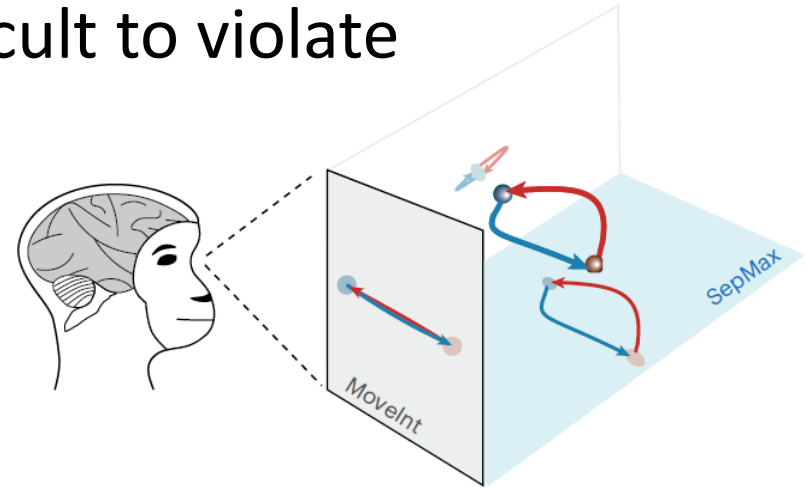
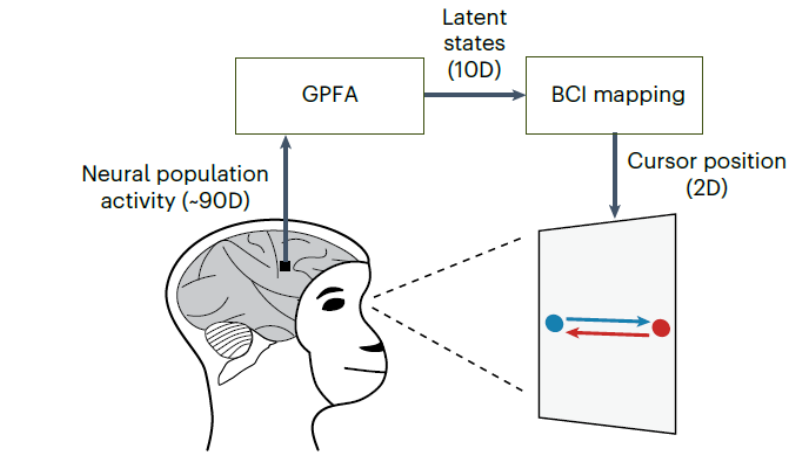
c Neural flow field



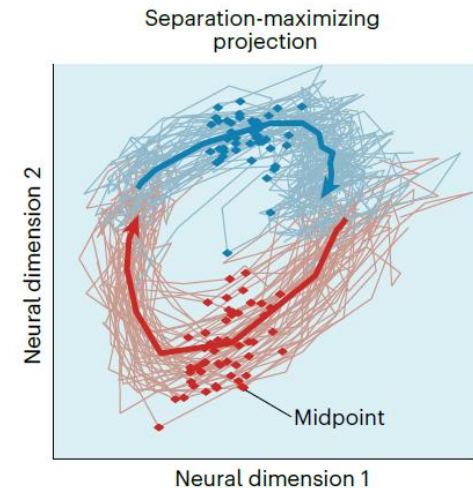
d Initial conditions influence neural trajectory



The geometry of the neural trajectories, once acquired, appears to be robust and difficult to violate

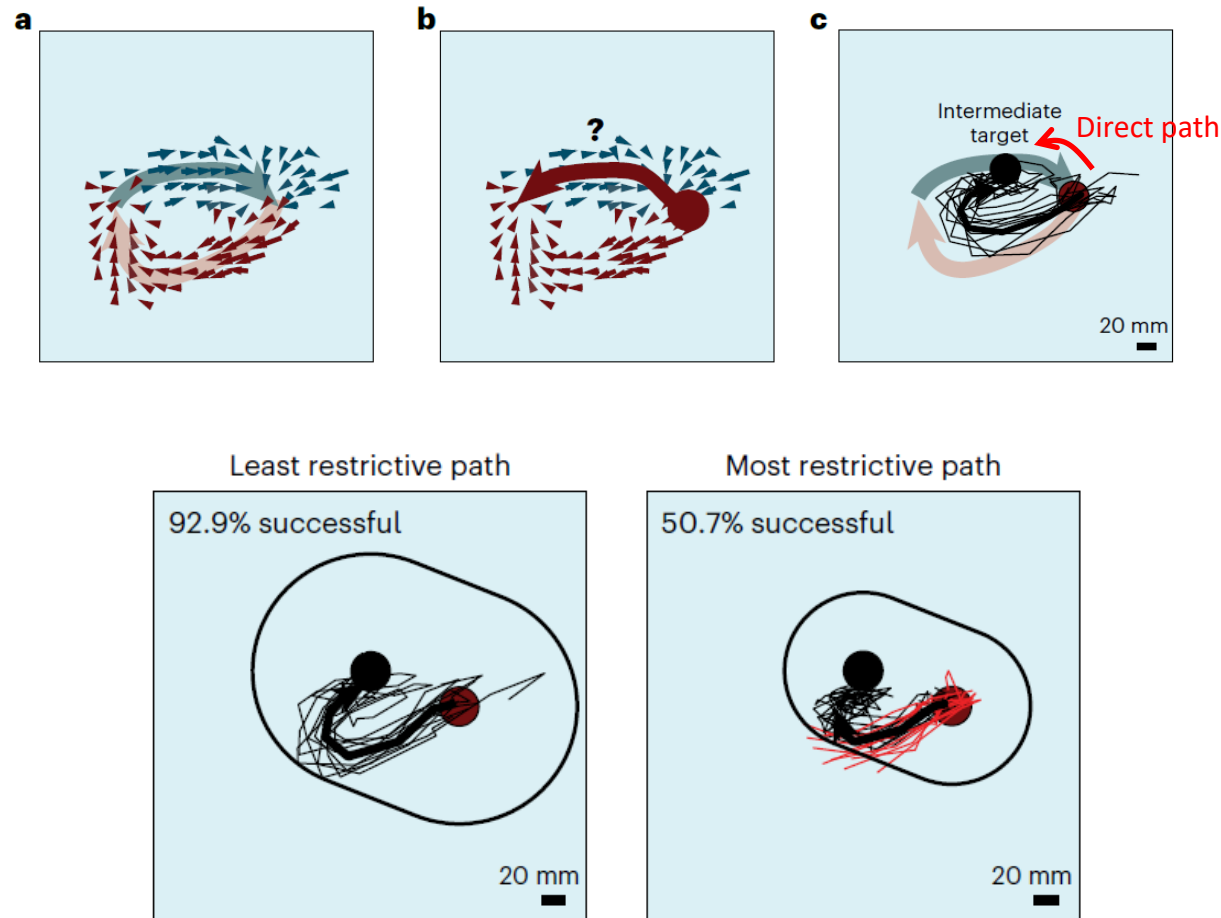
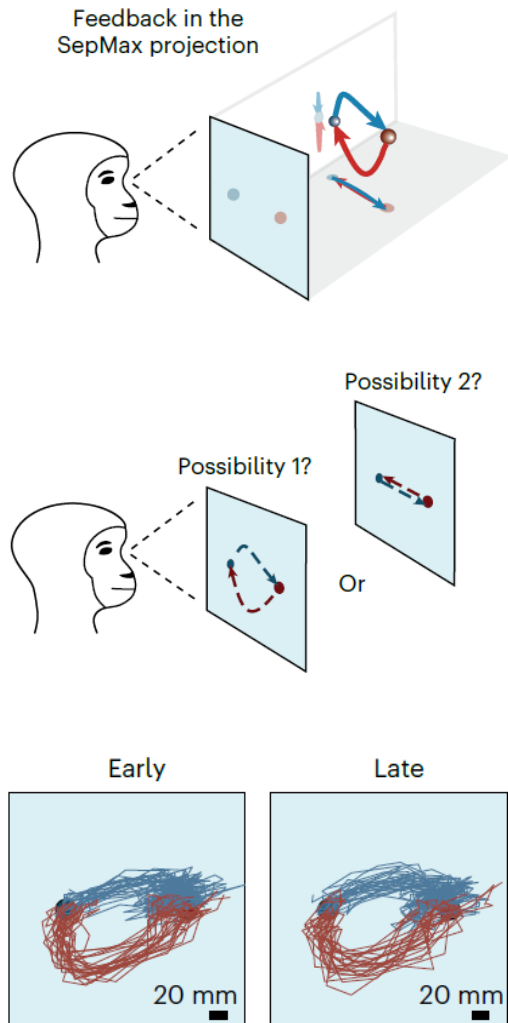


- Neural trajectory projections that align with monkey's movement intention, shown as visual feedback to monkey

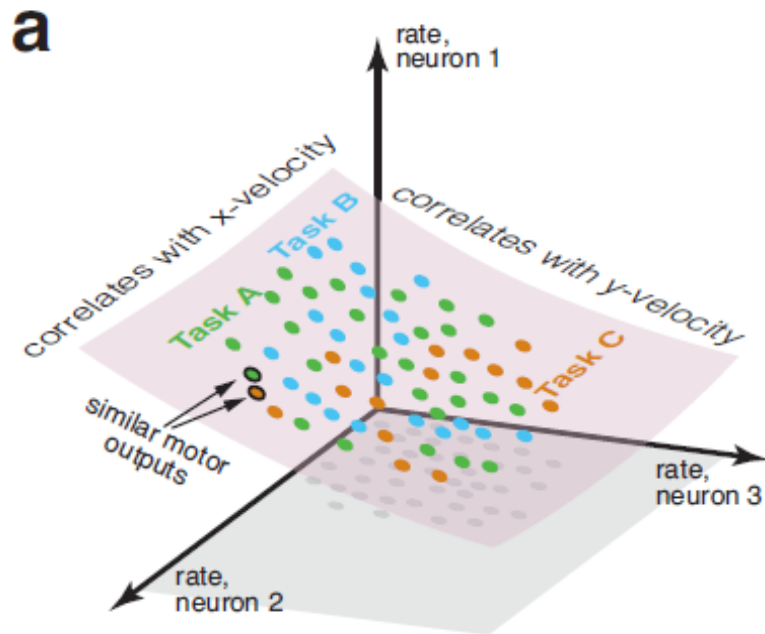


- Projections of neural trajectory with max. separation between the two paths, shown to monkey

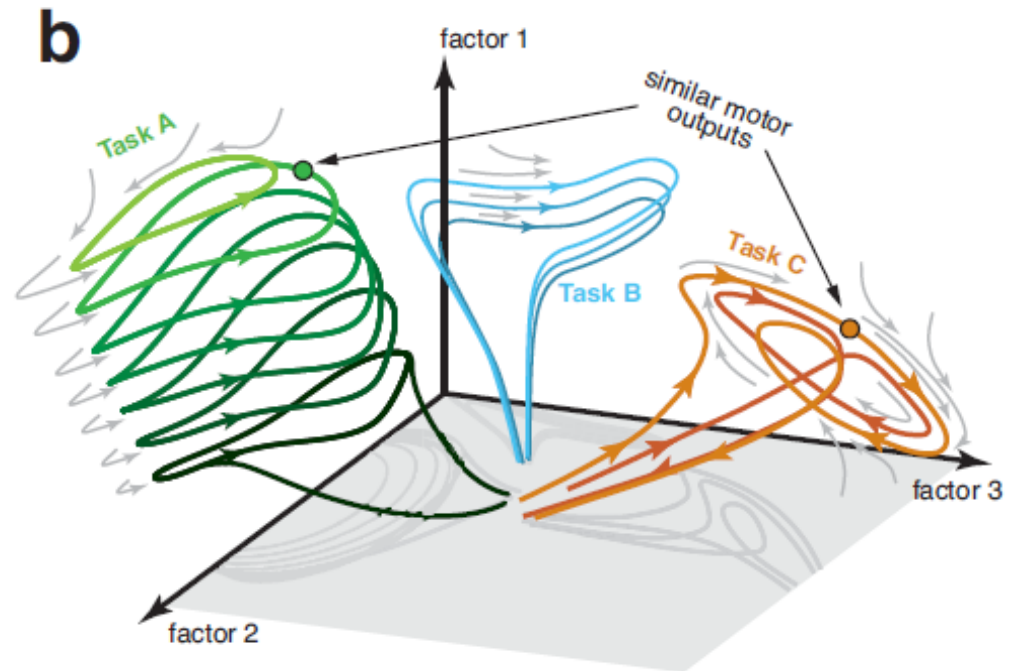
The flow direction of the neural trajectory for a learned motor task appears difficult to violate



It may be most useful to approximate behaviorally relevant neural manifold with collection of neural trajectories rather than linear subspaces derived from dimensionality reduction

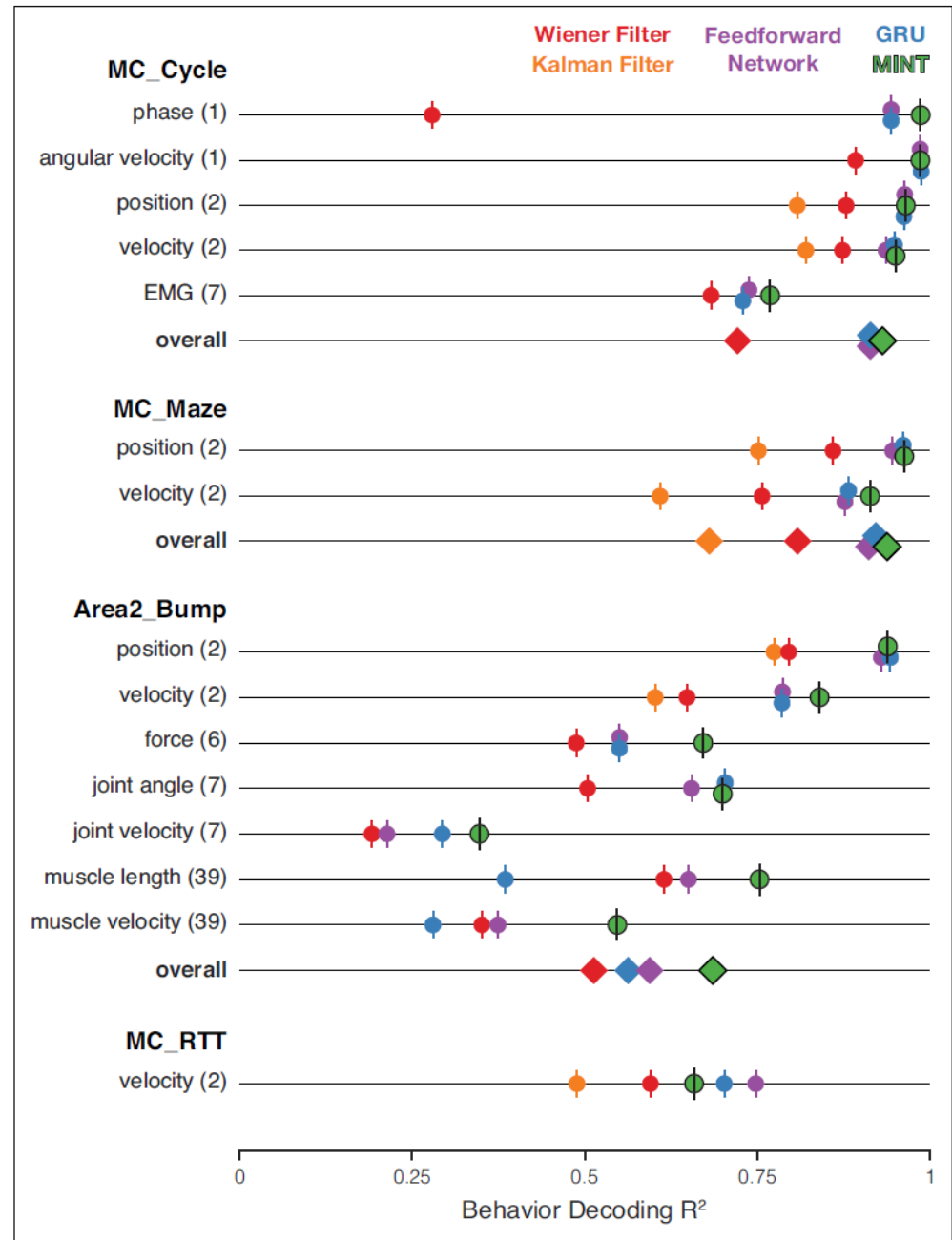


- Dimensions within manifold may correlate with movement variables
- Similar points in manifold lead to similar motor outputs



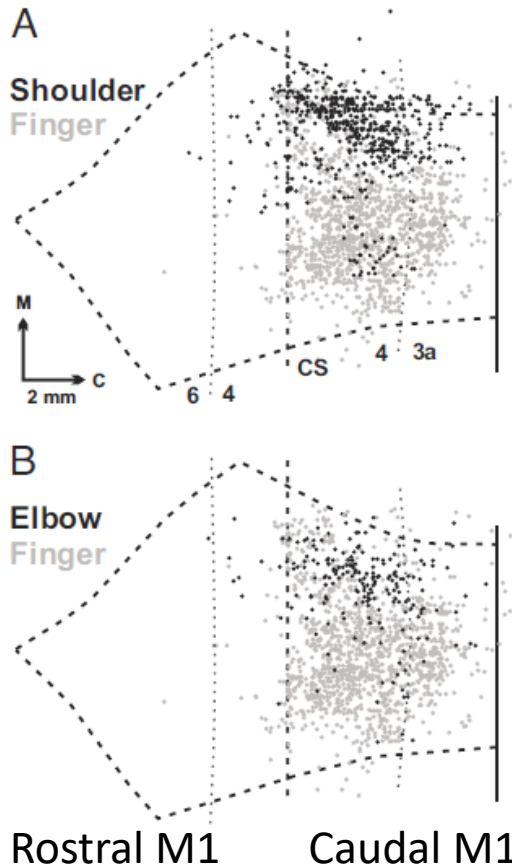
- Primary constraint is not the subspace, but a sparse manifold in which activities flow according to a flow field (dynamic constraint)
- Neural activity time courses reflect network connectivity

Consistent with the neural geometry view, an M1 decoder based on dynamic neural trajectories outperformed most other decoders

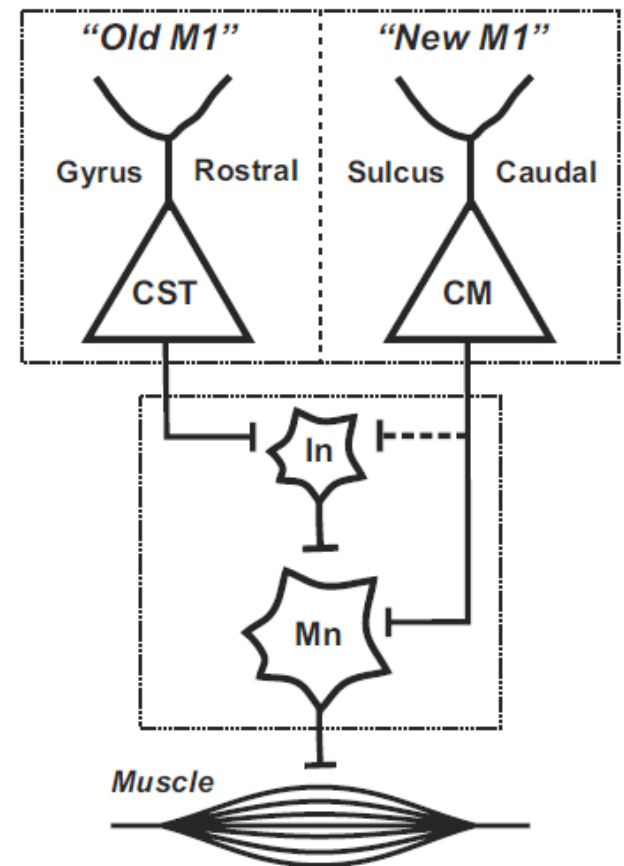
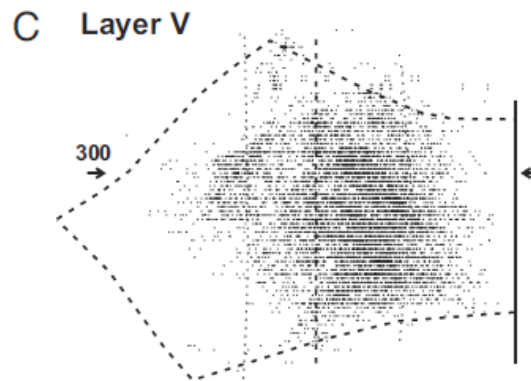


Can better insights into motor control be gained by considering the neuronal layer closer to the muscles themselves – the **spinal interneuronal network**?

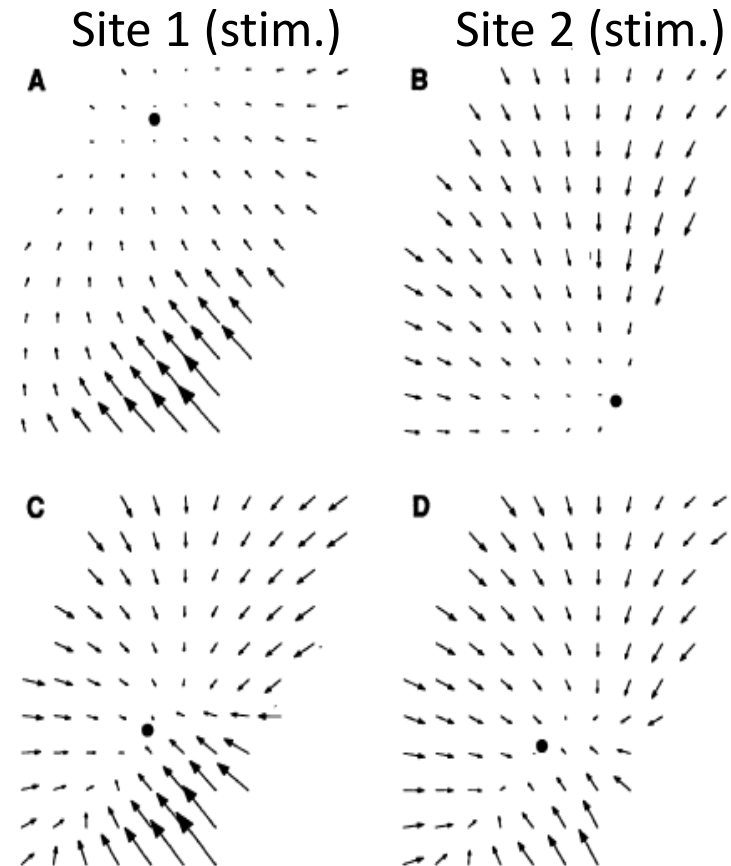
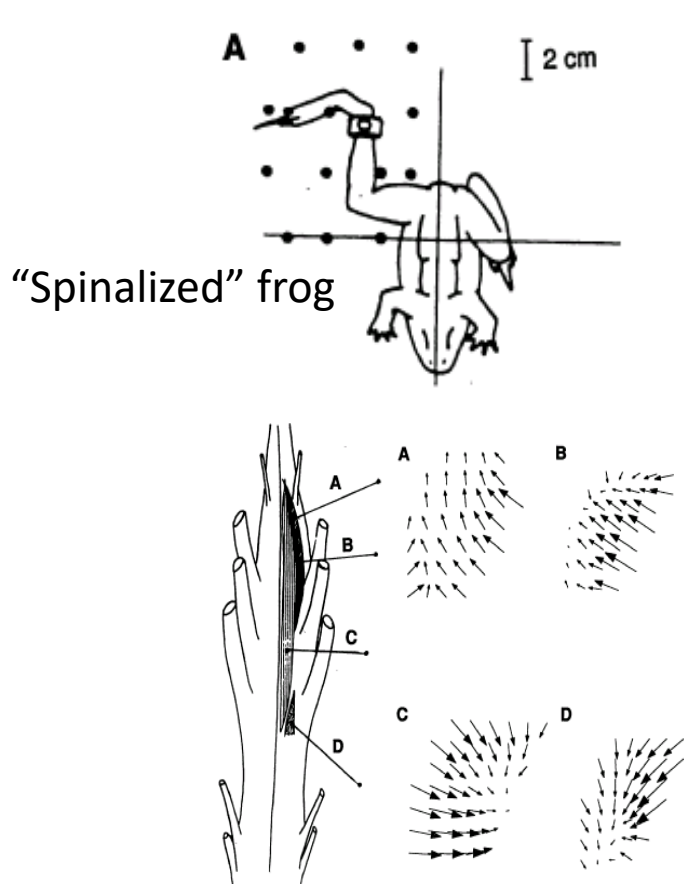
Labeling 2nd order neurons from muscles



Labeling 3rd order neurons from muscles



The spinal cord may encode discrete motor primitives that can be linearly combined to generate diverse patterns of motor behaviors

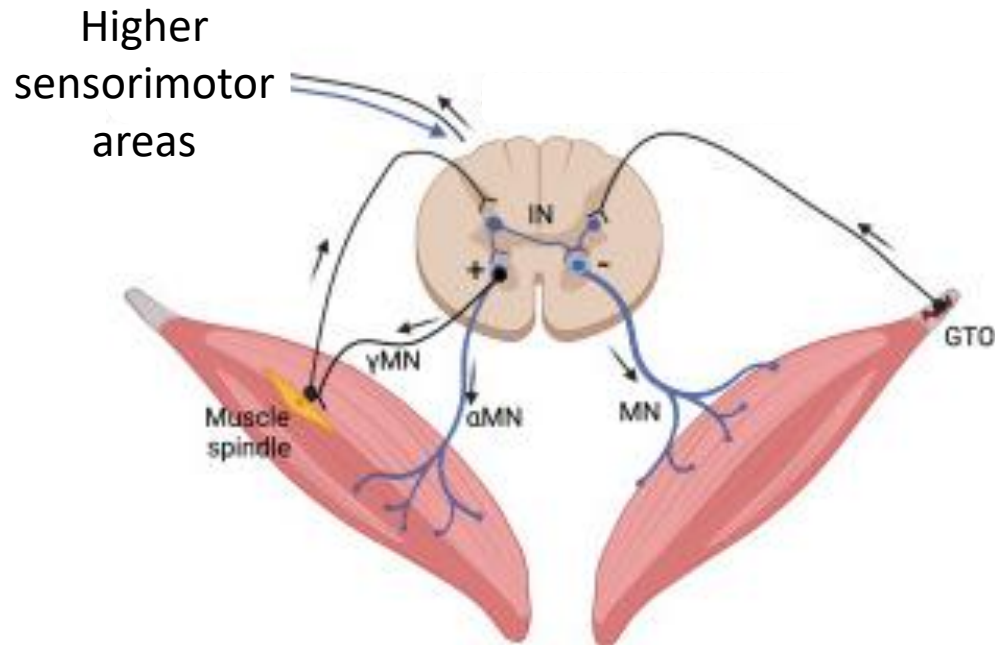


Vector sum of
fields 1 & 2

Simultaneous
stimulation of
sites 1 & 2

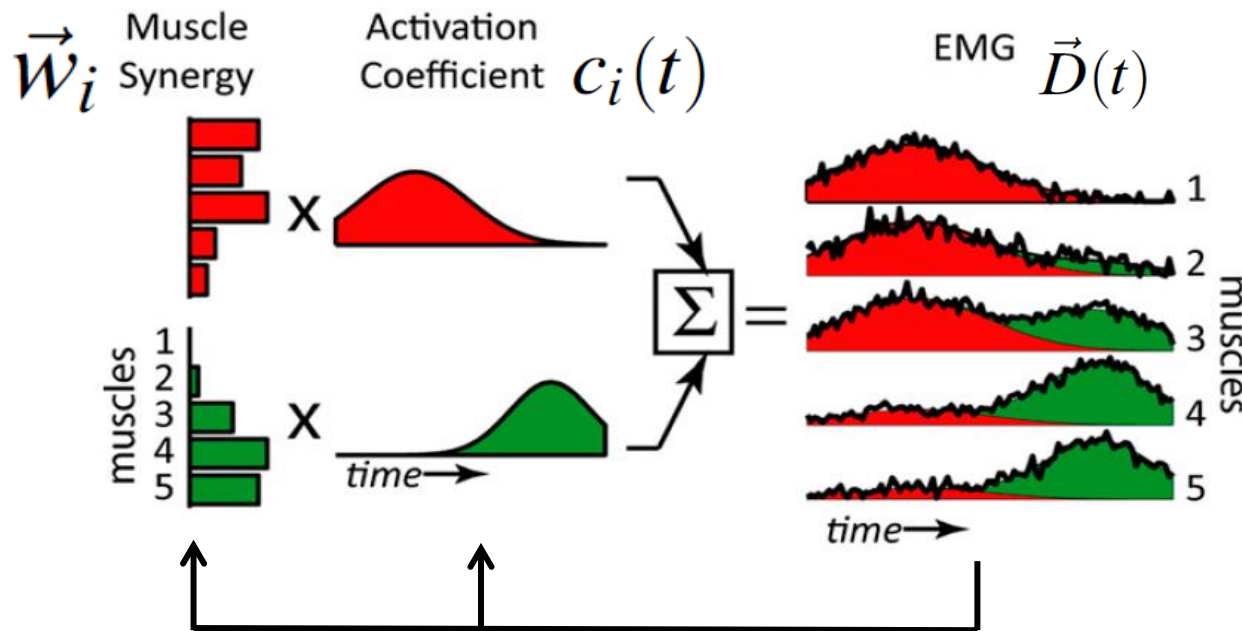
Are there **statistical regularities** in **multi-muscle activities** that reflect the motor control computations implemented by the activities and dynamics of neuronal networks in the **spinal cord** and **motor cortices**?

Do these muscle-activity regularities implement specific **limb biomechanical functions**?



Muscle synergy: Linear representations of statistical regularities of multi-muscle activities

- Muscle synergy as **neuromotor control module** that implements limb biomechanical functions for motor behavior generation
- This model permits **identification** of modules from experimental EMG data as synergies



$$\vec{D}(t) = \sum_{i=1}^N c_i(t) \vec{W}_i + \vec{\epsilon}$$

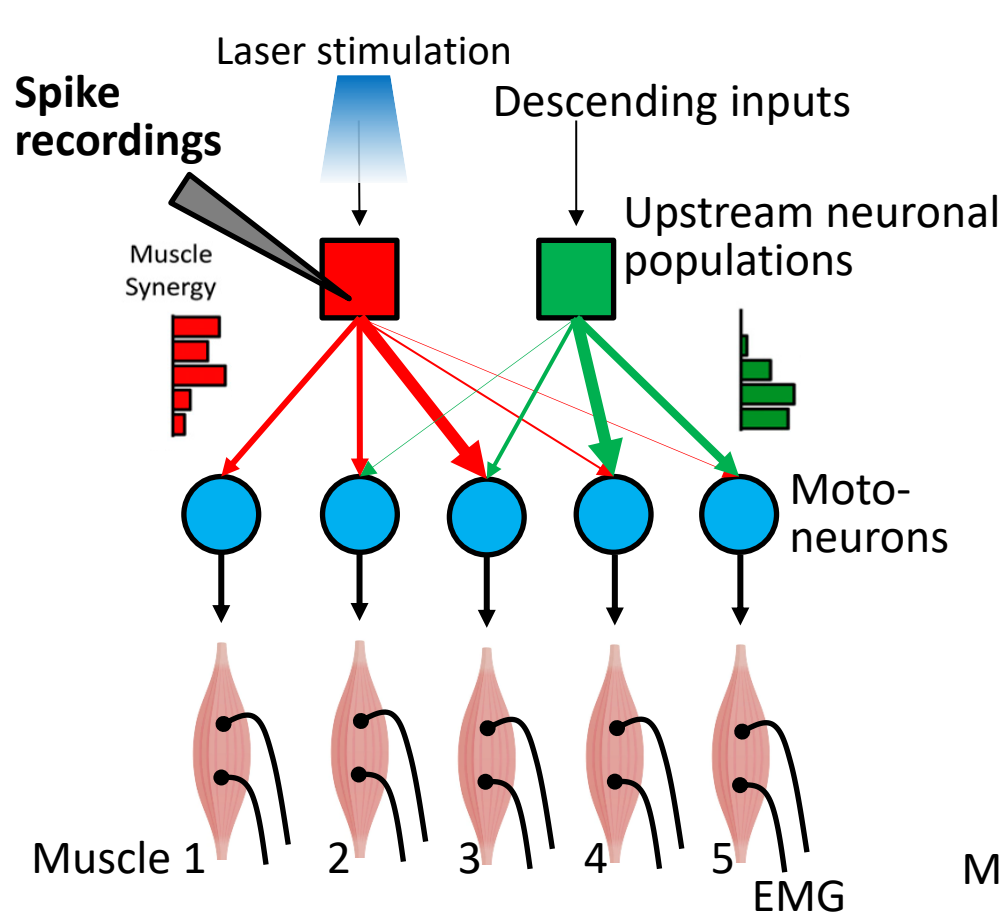
Lee and Seung (1999) *Nature*
Tresch, d'Avella, Cheung (2006) *J Neurophysiol*
Devarajan and Cheung (2014) *Neural Comput*
Devarajan and Cheung (2016) *Neural Comput*

Non-negative matrix factorization (NMF)
Other machine learning methods

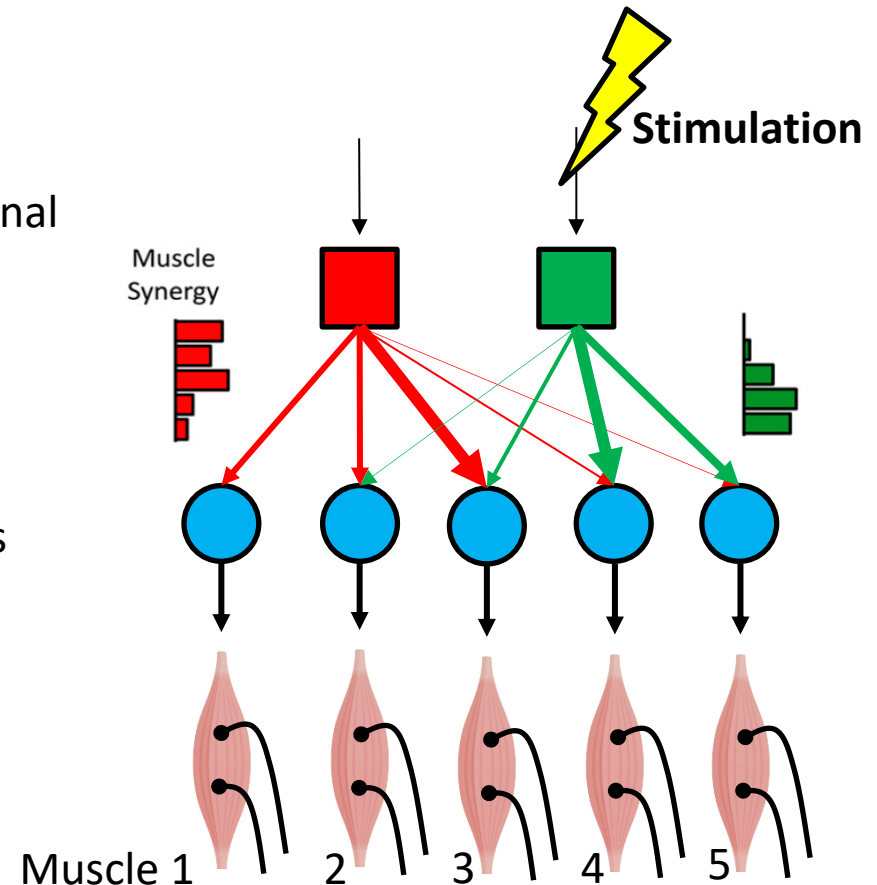
Scientific Questions

1. Are the muscle synergies conveniently identified from EMGs **neurophysiological entities** used by CNS for movement generation?
 - Decoding synergies from **neuronal recordings** (mice)
 - Eliciting synergies by **CNS stimulations** (humans)
2. Can muscle synergies can guide **neuro-rehabilitation** for movement disorders?
 - **Targets** of personalized FES interventions for stroke survivors

Neural basis of synergies: Validating the neural origin of muscle synergies by **neuronal recordings** and **stimulation**



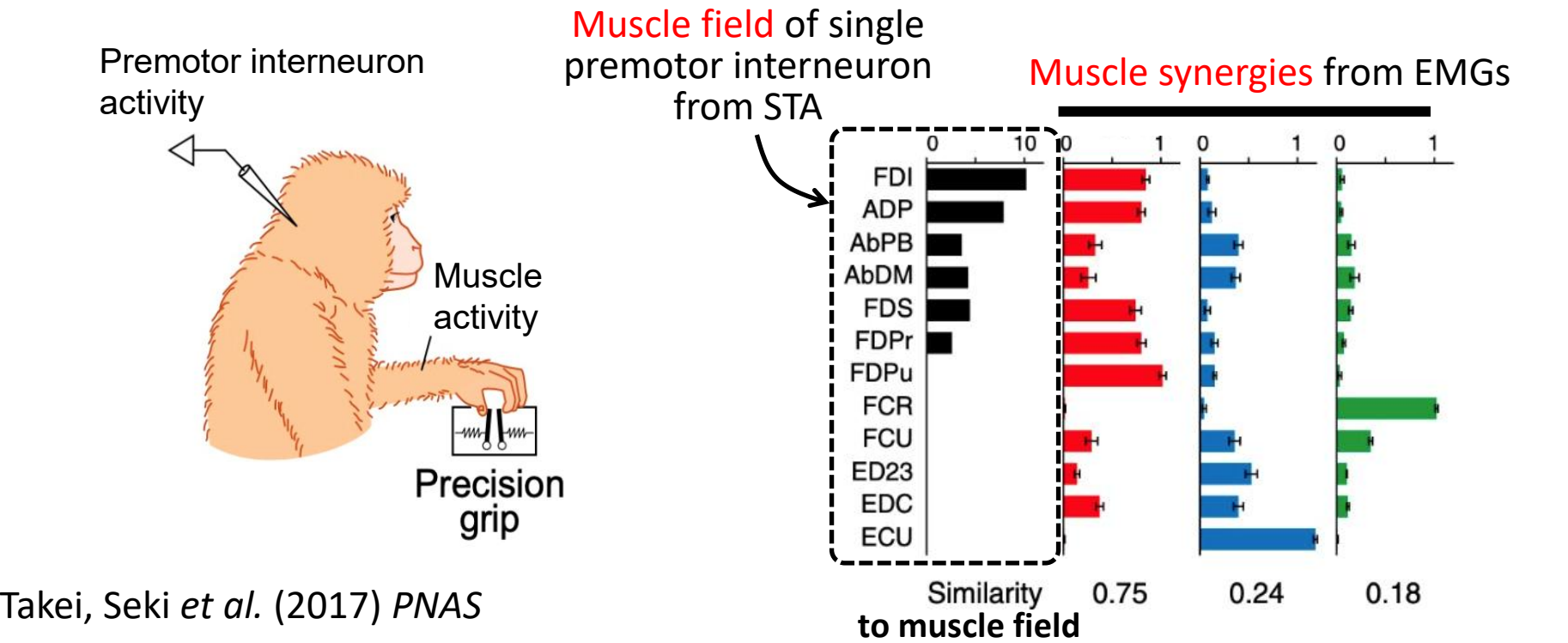
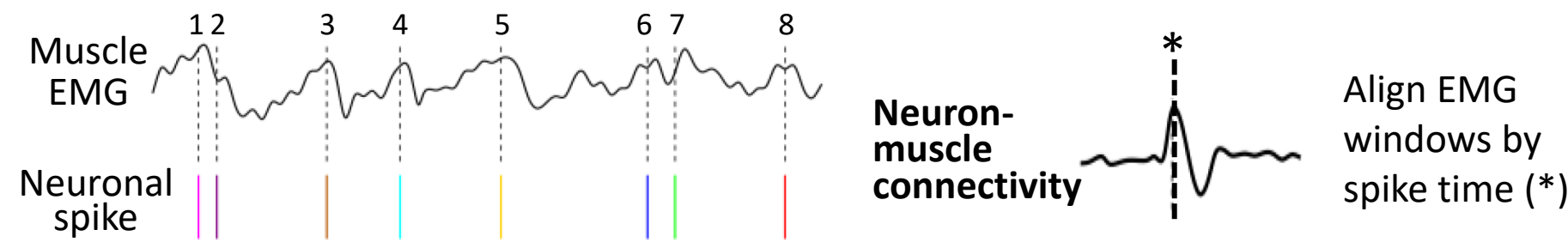
Does the connectivity pattern between the recorded neuronal population and motoneurons of the muscles match the EMG-derived muscle synergies?



Do the muscle synergies recruited by stimulation match the behavioral muscle synergies?

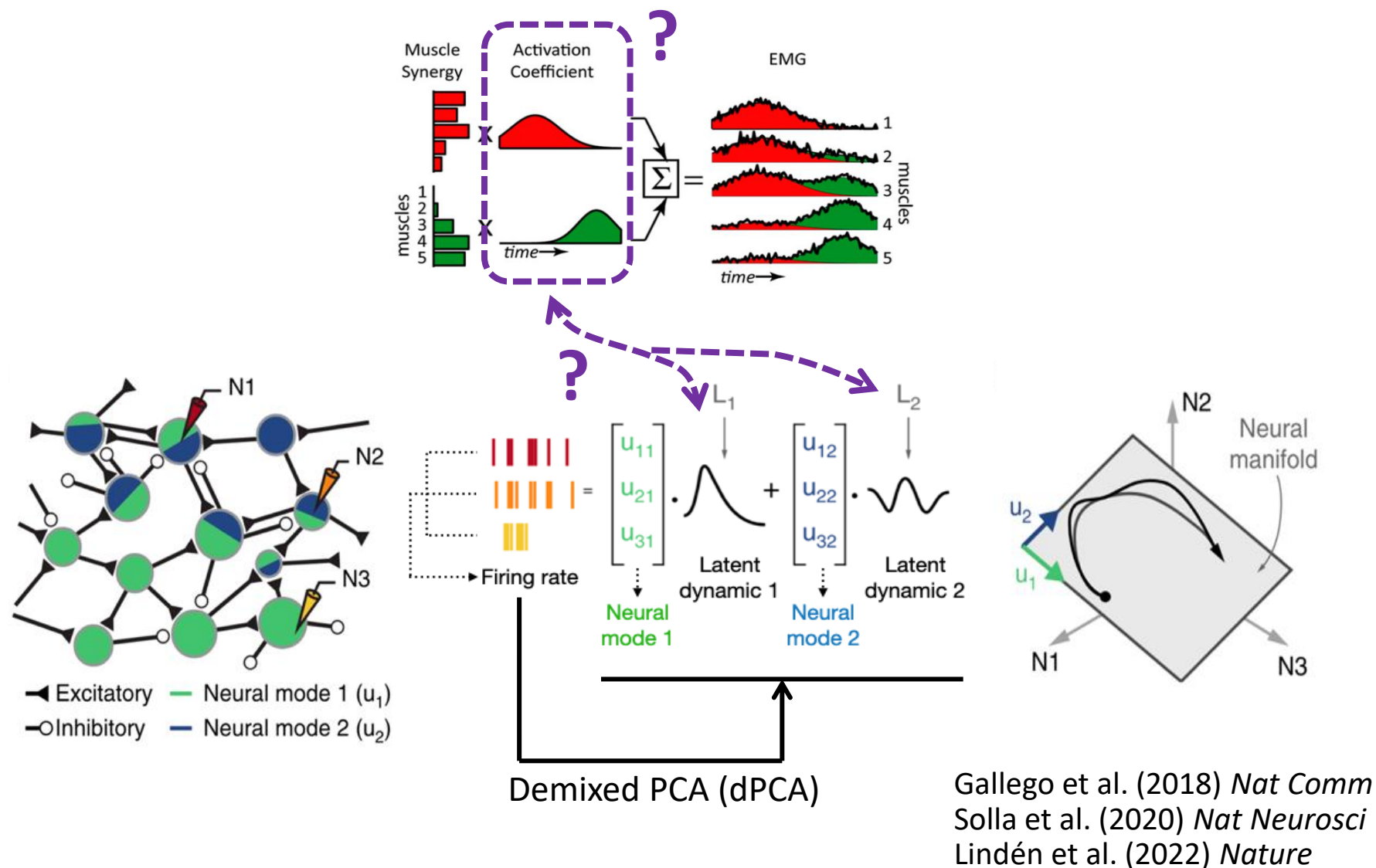
Neural basis of synergies by recordings

Connectivity between **individual neurons** and muscles can be represented as **muscle fields**, revealed by **spike-triggered averages (STA)** of EMG

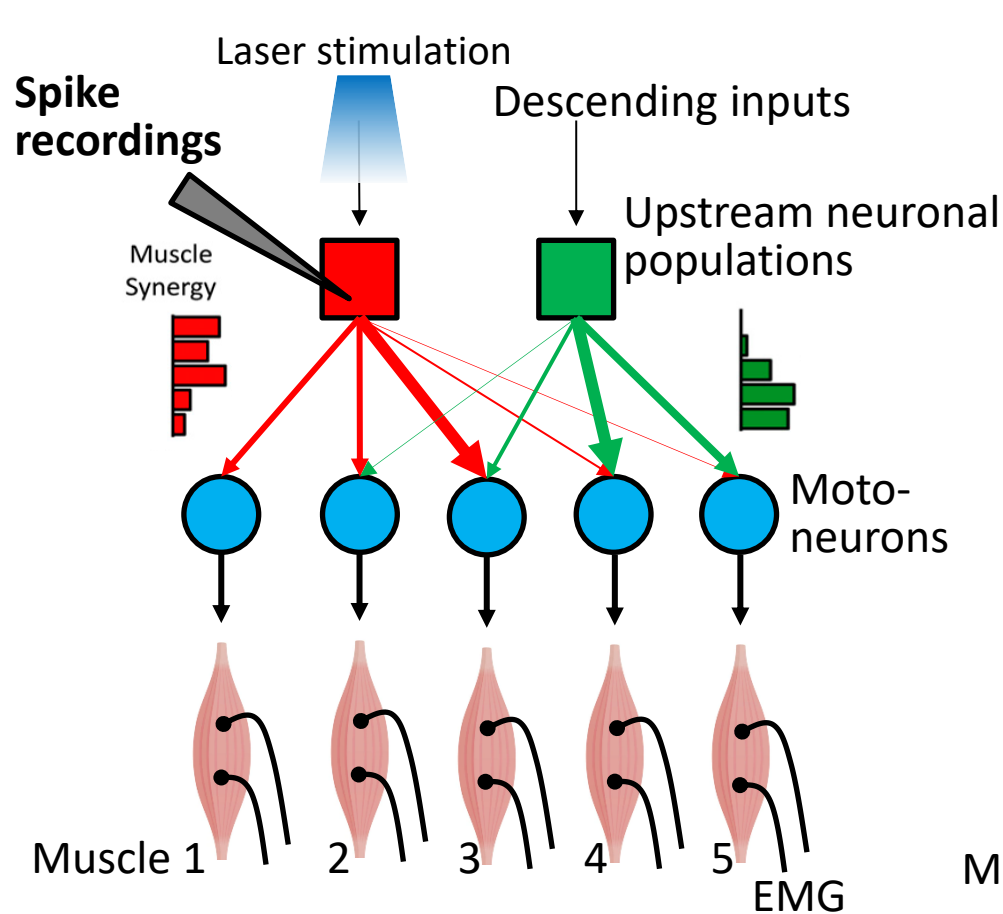


Neural basis of synergies by recordings

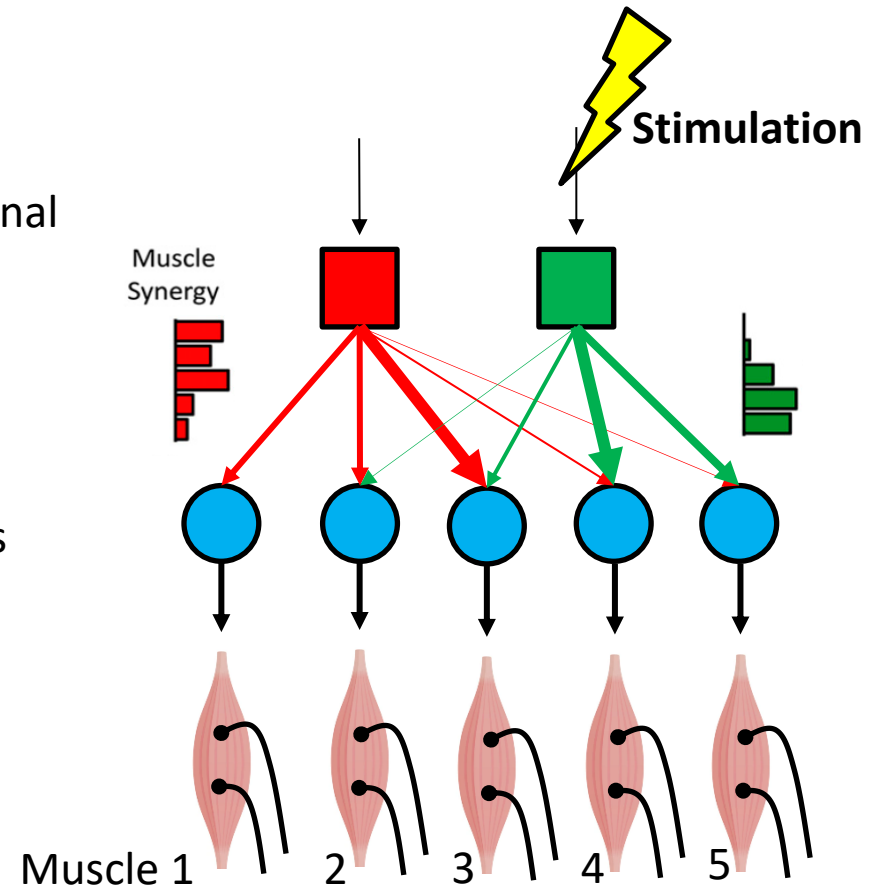
Can the muscle synergies' temporal activities be accounted for by the latent dynamics of spinal interneuronal populations?



Neural basis of synergies: Validating the neural origin of muscle synergies by **neuronal recordings** and **stimulation**

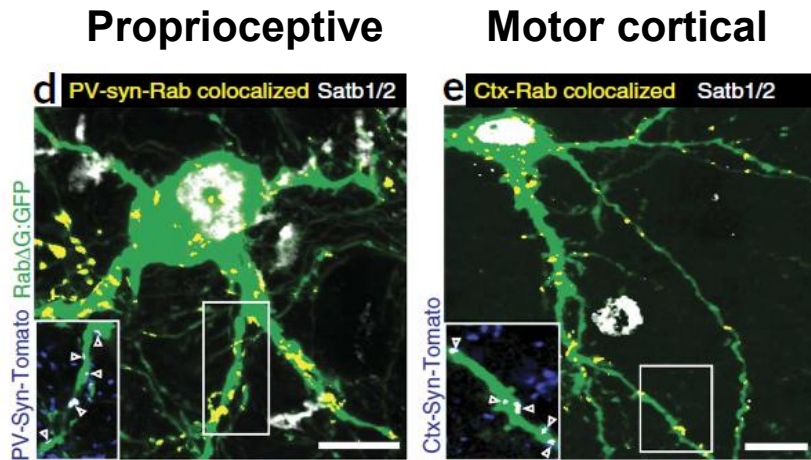


Does the connectivity pattern between the recorded neuronal population and motoneurons of the muscles match the EMG-derived muscle synergies?



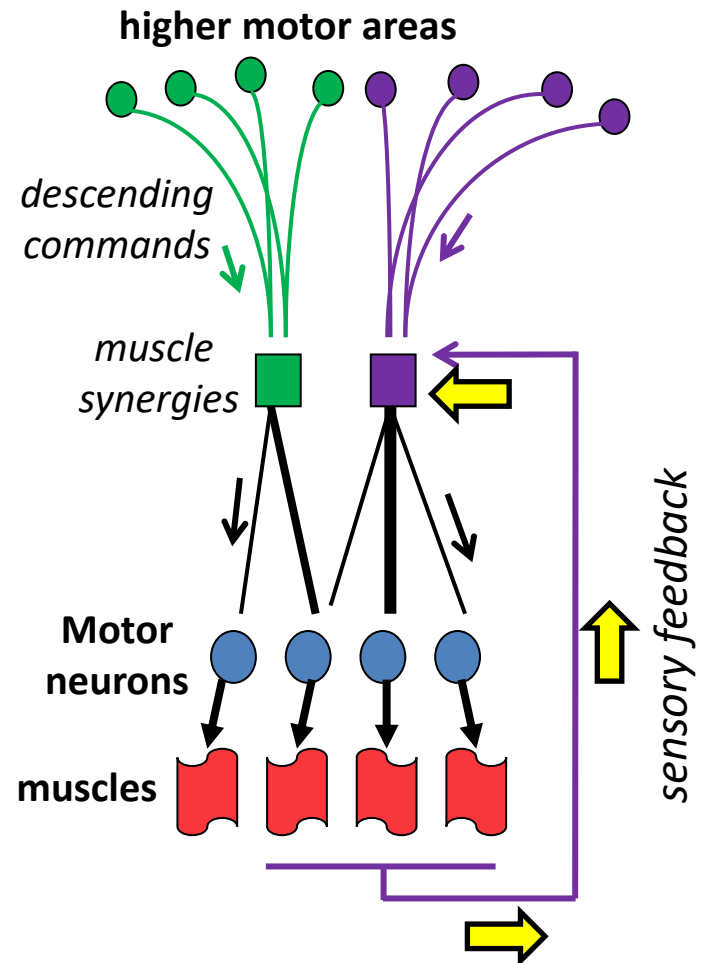
Do the muscle synergies recruited by stimulation match the behavioral muscle synergies?

EMG-derived muscle synergies are neurophysiological entities encoded by spinal interneurons, and driven by motor cortical commands



Levine et al. (2014) *Nature Neurosci*

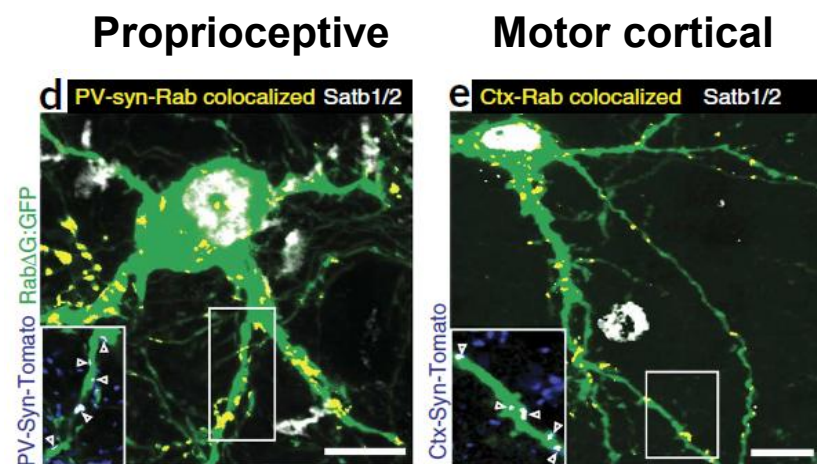
Proprioceptive drives from the muscles in a muscle synergy can **reinforce** the same synergy's activation



Cheung, Niu, Lan et al. (2019) *IEEE Rev BME*
Cheung, Seki (2021) *J Neurophysiol*

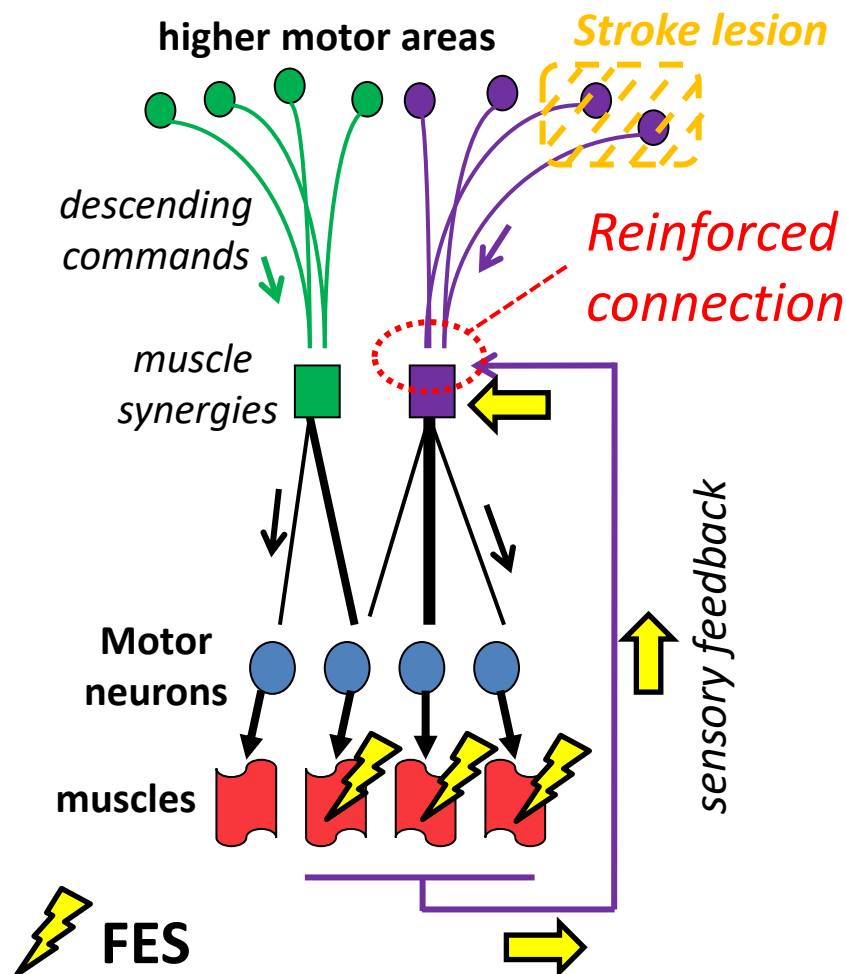
Synergies as targets of intervention

Can muscle synergies be specific targets of rehabilitation for movement disorders such as stroke?



Levine *et al.* (2014) *Nature Neurosci*

Sensory drives from FES applied to muscles in a synergy can **reinforce** the synergy's activation **during active task execution**



Cheung, Niu, Lan *et al.* (2019) *IEEE Rev BME*

Scientific Questions

1. Are the muscle synergies conveniently identified from EMGs **neurophysiological entities** used by CNS for movement generation?
 - Decoding synergies from neuronal recordings (mice)
 - Eliciting synergies by CNS stimulations (humans)
2. Can muscle synergies can guide **neuro-rehabilitation** for movement disorders?
 - **Targets** of personalized FES interventions for stroke survivors

Summary

- Statistical regularities within multi-muscle EMGs may be identified as muscle synergies by EMG factorization. Muscle synergies are control modules that reflect the connectivity between spinal interneurons and the motoneuronal pools.
- Muscle synergies encoded by spinal interneurons can be accessed by motor cortical neurons.
- Synergy-based personalized functional electrical stimulation can be a viable neuro-rehabilitation strategy for restoring gait in chronic stroke survivors.

Major unsolved questions and opportunities in motor neuroscience

- Cross-level models that offer insights on how descending commands, multi-level feedback, and pattern generators in cortex, basal ganglia, cerebellum, brainstem, and spinal cord are integrated
- Models that incorporate both neuronal networks and musculoskeletal biomechanics
- Models of motor development, learning, and recovery from injury (at multiple time-scale) while also accounting for stability of learned motor behaviors

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