

The motor system



To move things is all that mankind can do...
whether in whispering a syllable or in felling a forest
C. Sherrington 1920

- Principles
- Components: Muscles, Spinal cord and spinal tracts, Subcortical areas, Cortical fields.
- Learning and plasticity

Three main types of movements

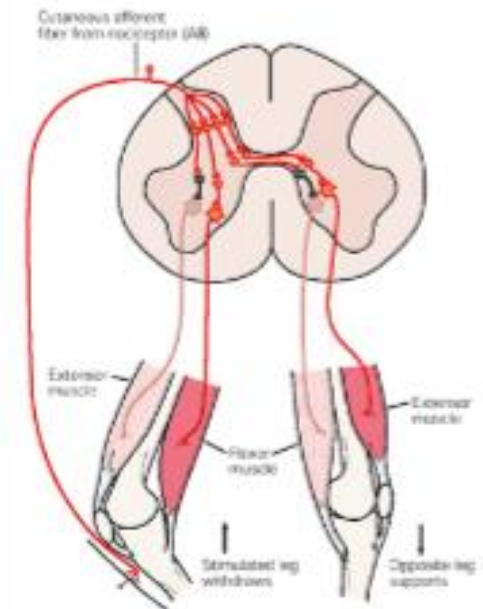
- Reflex
- Rhythmic
- Voluntary

- **Reflex:** *involuntary* coordinated patterns of muscle contraction and relaxation elicited by peripheral stimuli (~40ms)

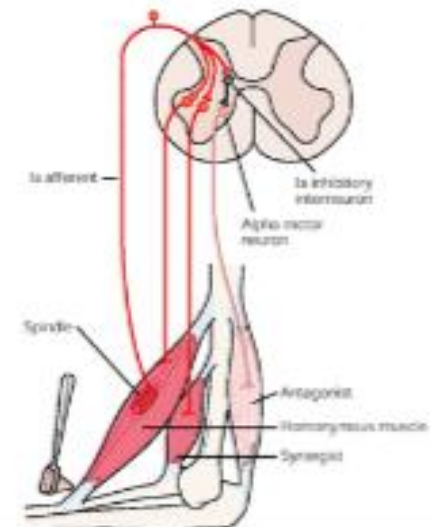
Noxious stimuli excites ipsilateral flexor, and excites contralateral extensor

Stretch reflex: contraction of same and synergist and relaxation of antagonist

A. Flexion and crossed-extension reflex



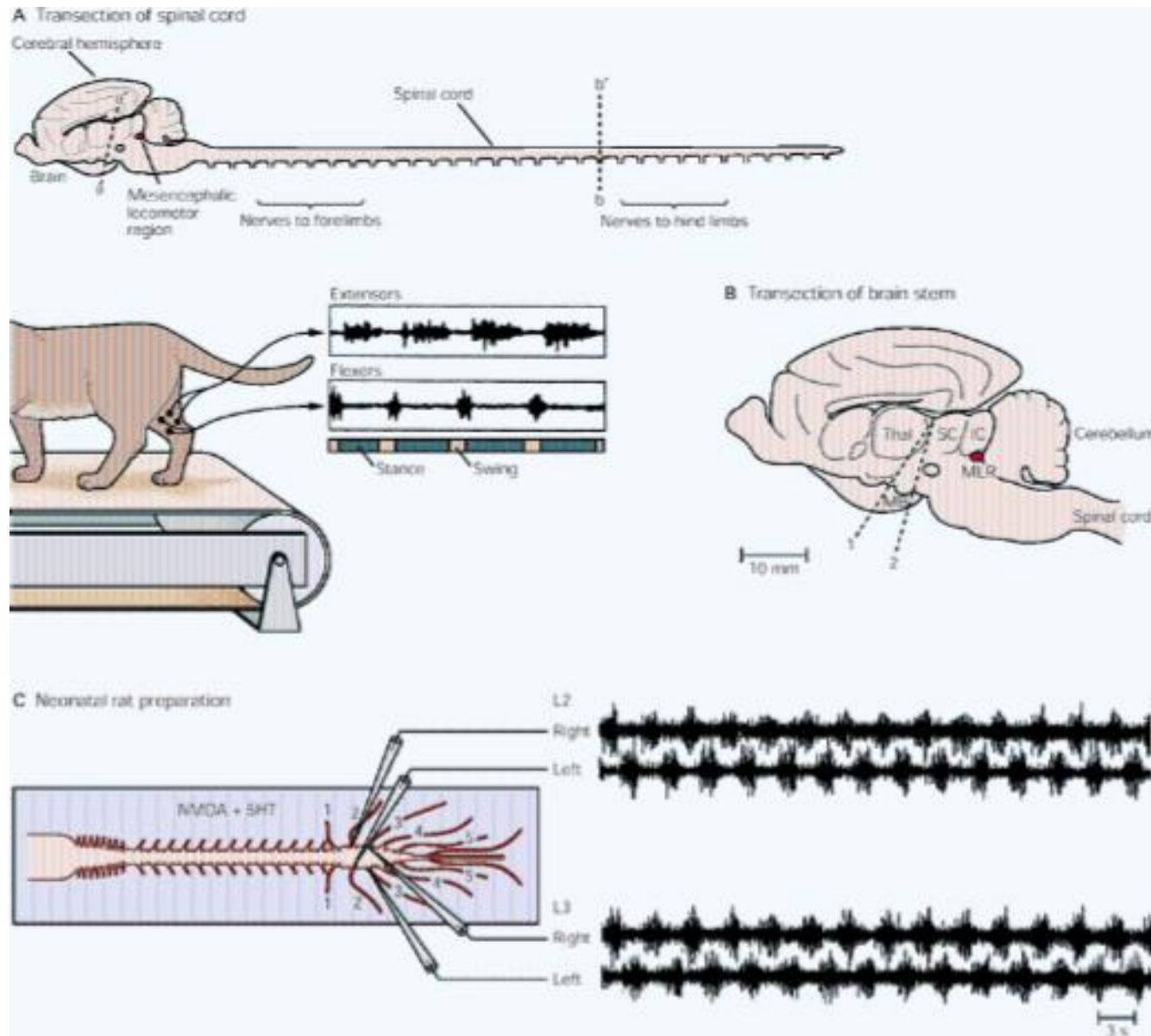
B. Stretch reflex



Rhythmic: Chewing, swallowing, and scratching, quadrupedal locomotion.

- The spinal cord and brain stem.
- Triggered by peripheral stimuli that activate the underlying circuits.

CPG: central pattern generators



Voluntary movements: principles

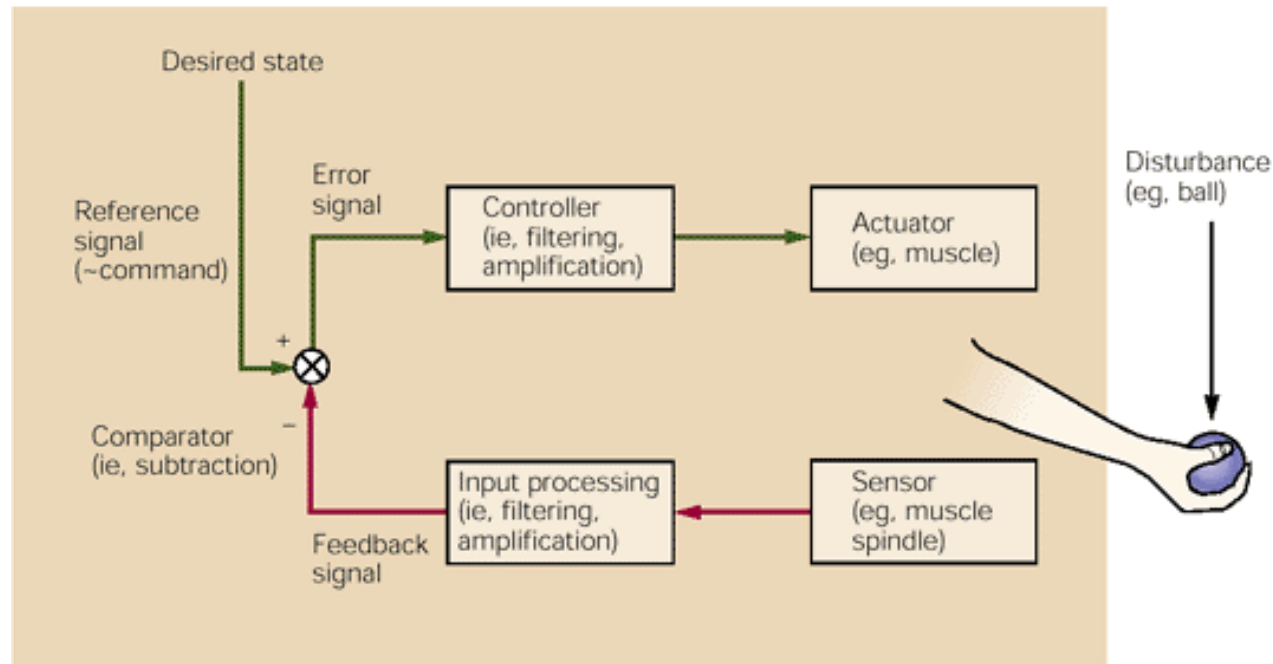
Goal directed

Reaching (~120 ms)



Feedback control (error correction)

A Feedback control: command specifies desired state



Vision

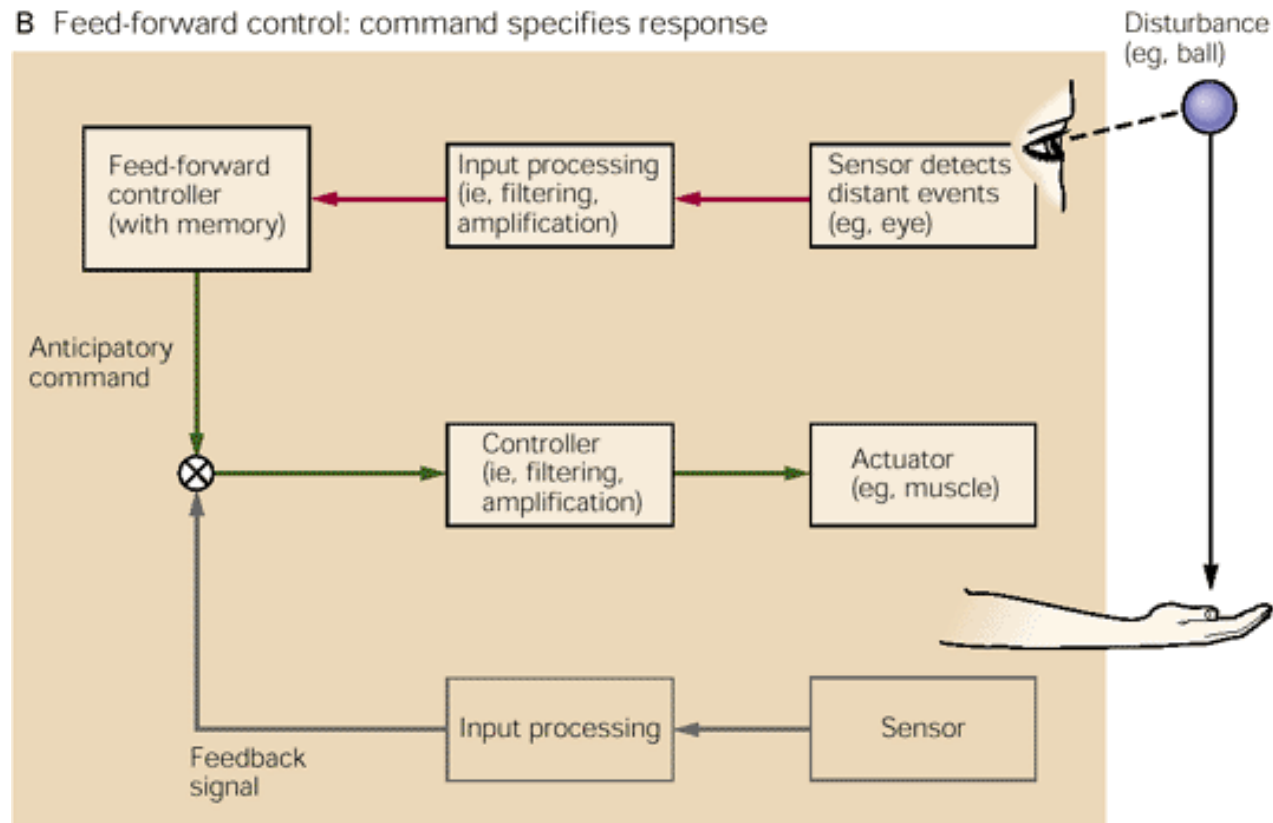
Proprioception

1. Gain

2. Delay (phase lag)

Feed-forward (open loop)

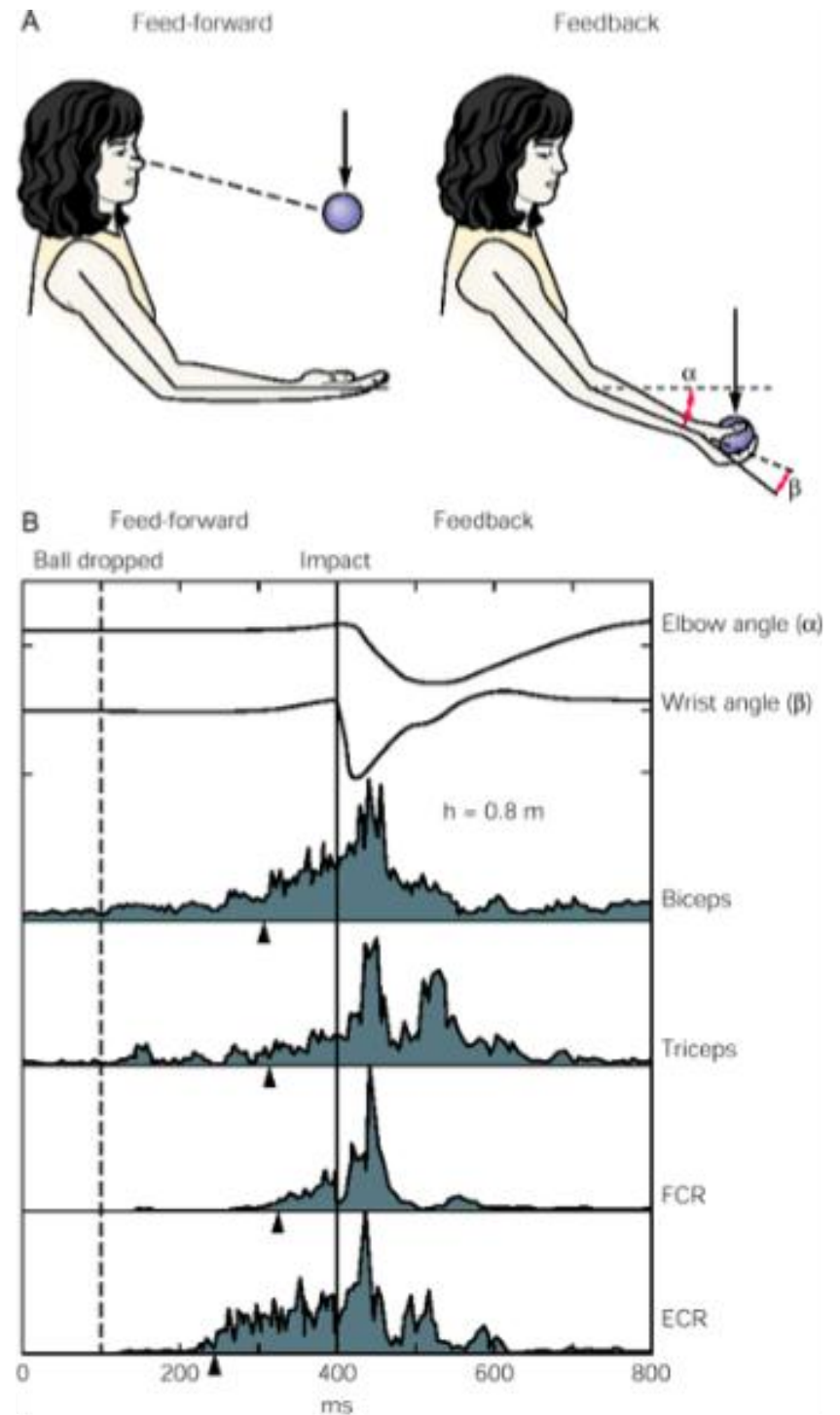
B Feed-forward control: command specifies response



1. Very hard computationally

Feedback control (error correction)

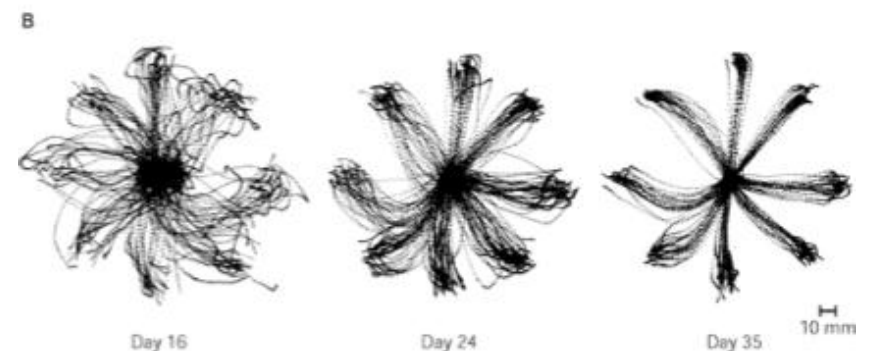
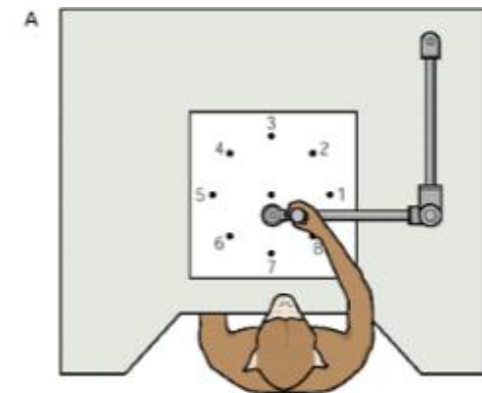
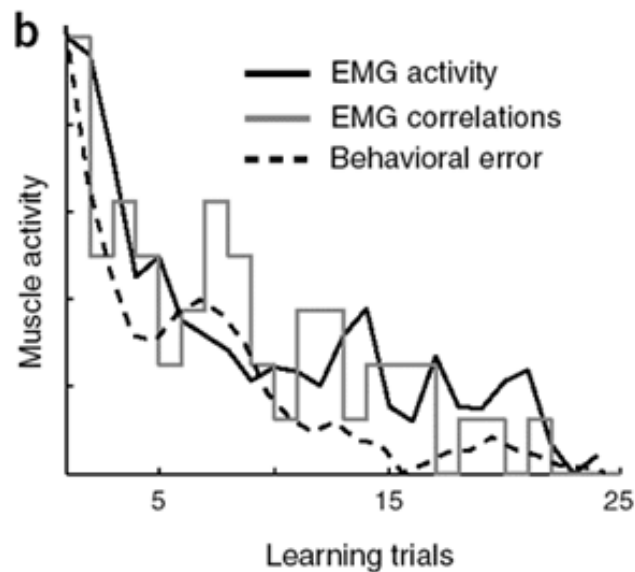
Feedforward (open loop)



Notice onset of muscles

Improve with practice

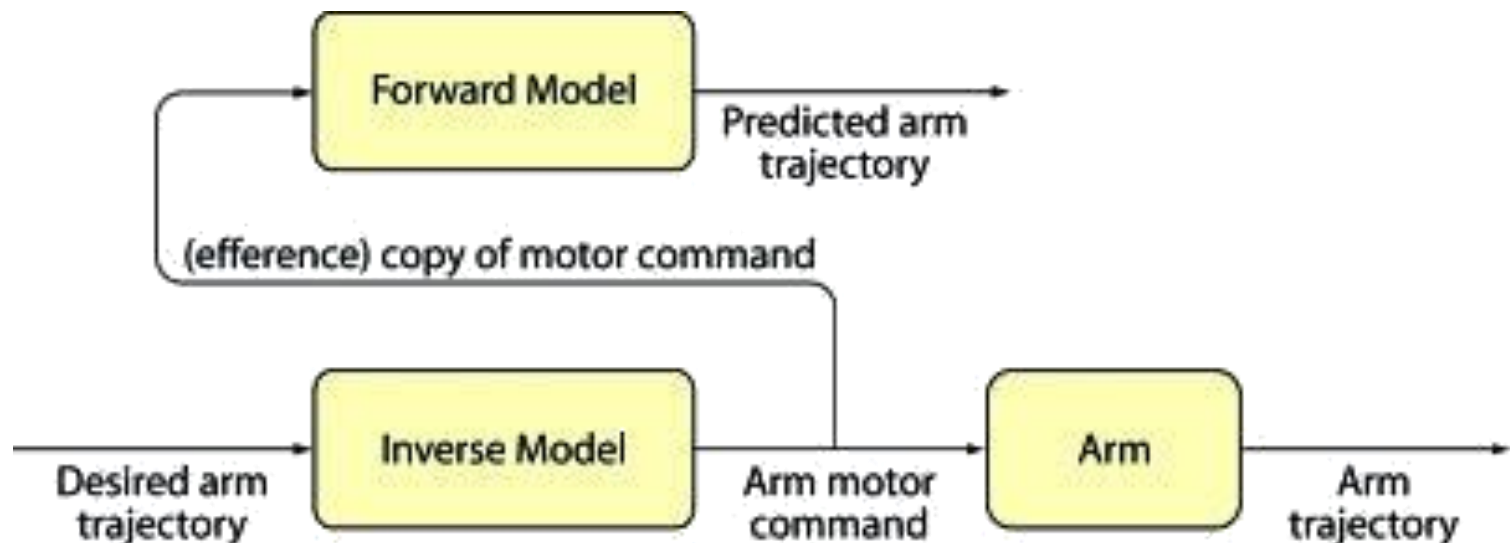
- Co-contraction of muscles
- **Internal models:** a neural representation of the relationship between the hand and the environment (how the arm would respond to the neural command).



Inverse and forward internal models

An **internal model** is used either:

- to predict the movement consequences of a motor commands (*forward model*).
- to determine the motor commands needed to achieve a desired movement trajectory (*inverse model*).



Motor programs and Invariants

Motor equivalence

(Donald Hebb, 1950)

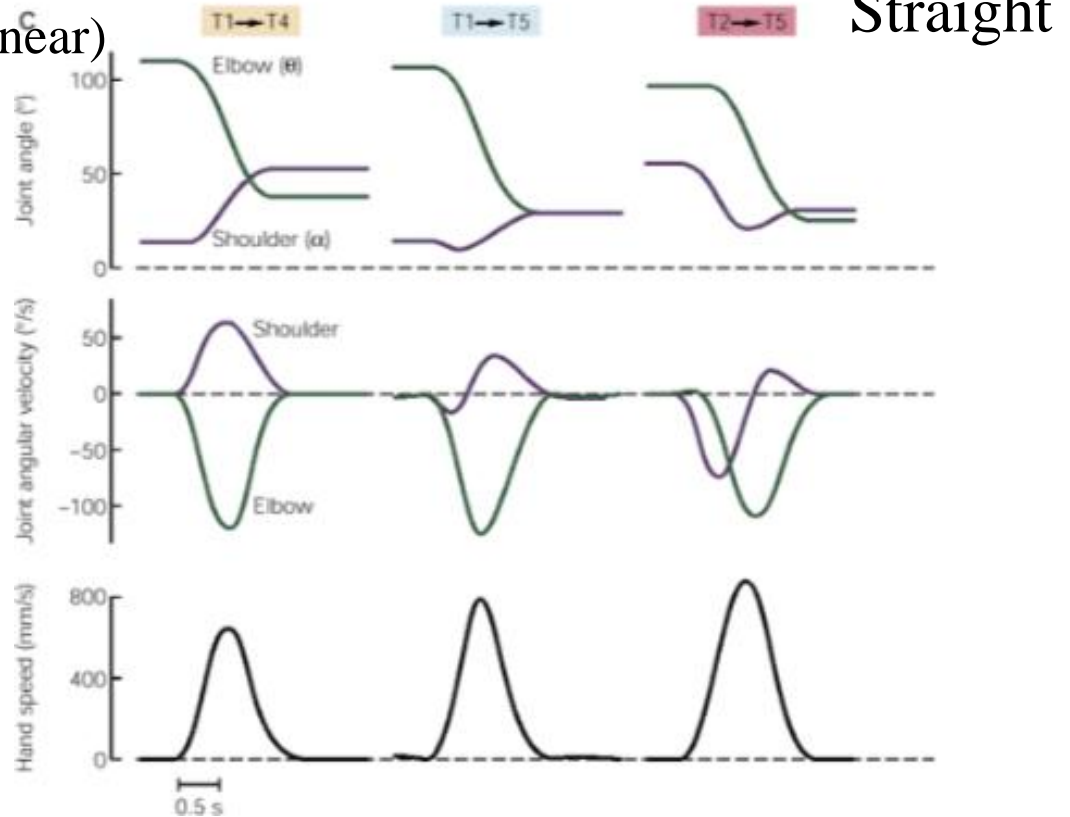
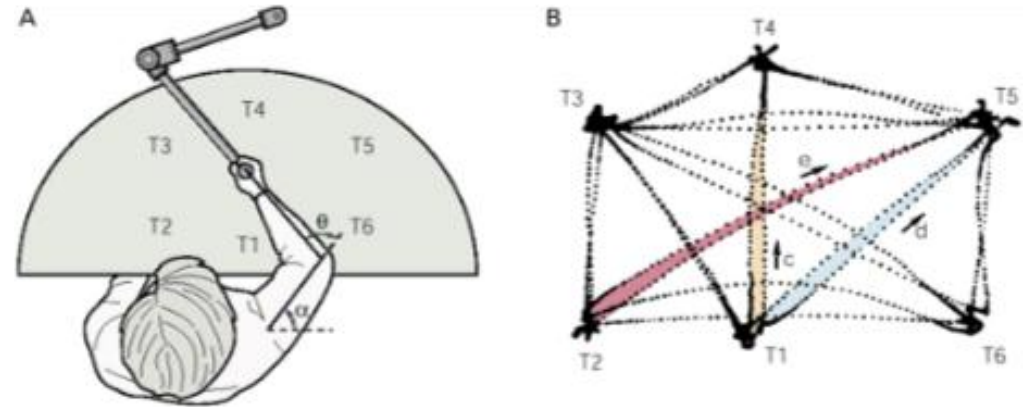


- A Able was I ere I saw Elba
- B Able was I ere I saw Elba
- C Able was I ere I saw Elba
- D Able was I ere I saw Elba
- E Able was I ere I saw Elba

The motor program- trajectories and kinematics

Suggests planning in reference to the hand

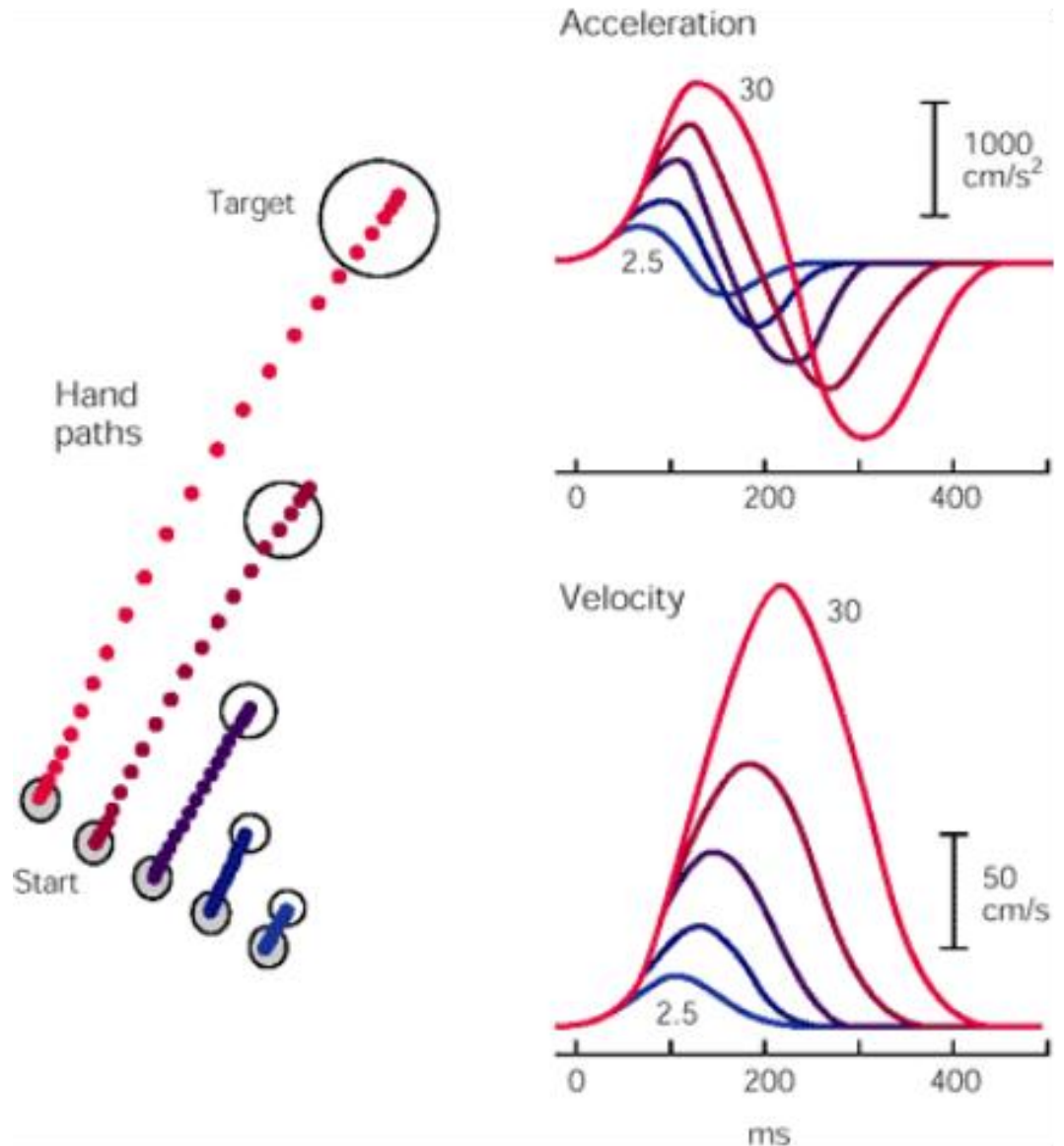
rather than joints and muscles (linear vs. nonlinear)



Pre-planning in vectors

Is there online visual feedback?
No - scaling of acceleration and speed

Invariant time (Isochrony)



Kinematic transformation: to transform a target position into a command to the skeletal system to move the hand i.e. to convert between coordinate systems;

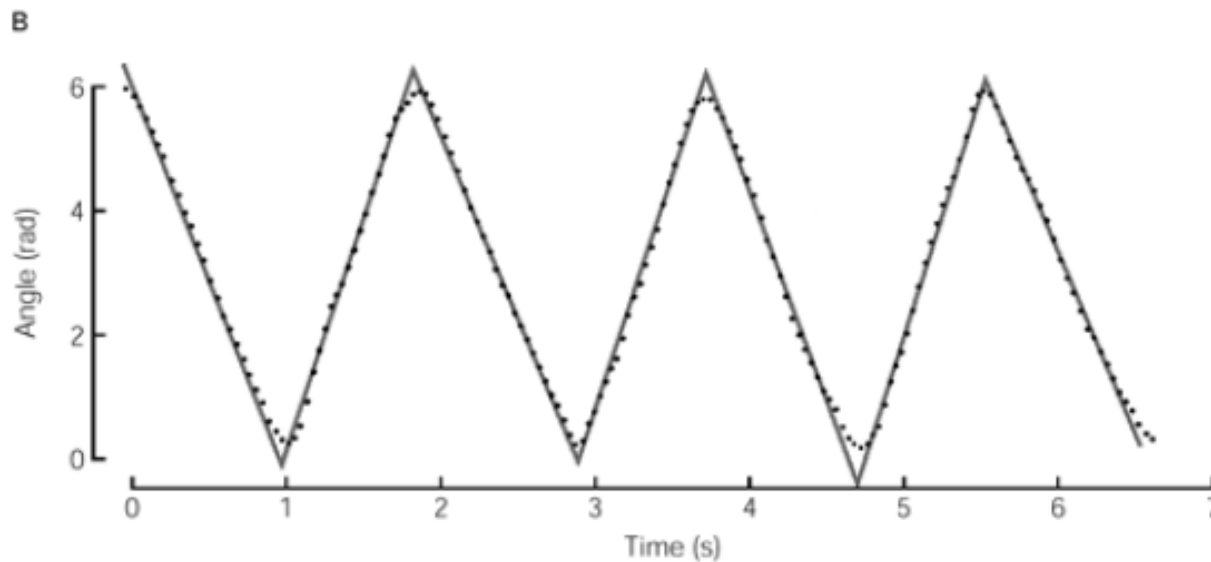
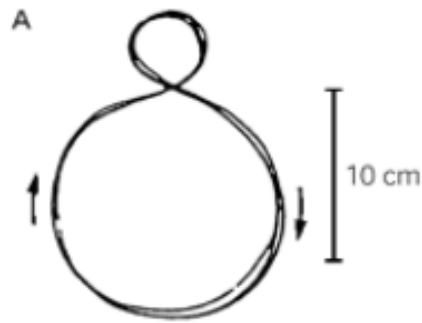
Dynamic transformation: relate motor commands to the motion of the system; in the reaching task here considered, the forces applied changed the system without changing the kinematics.

Building blocks – segmentation - primitives

Isogony (equal angles)

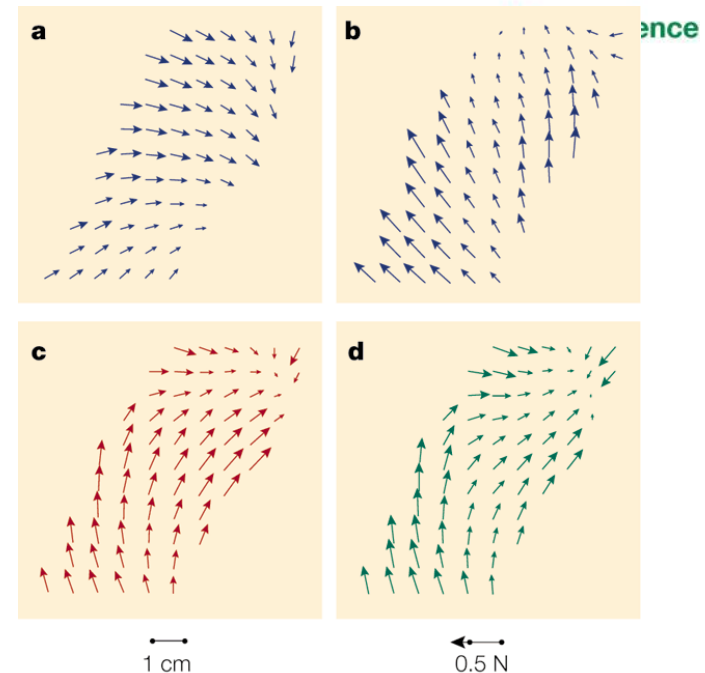
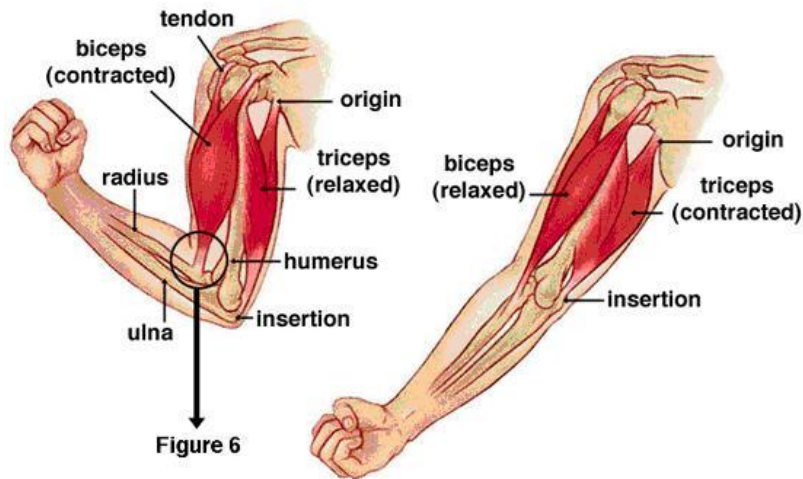
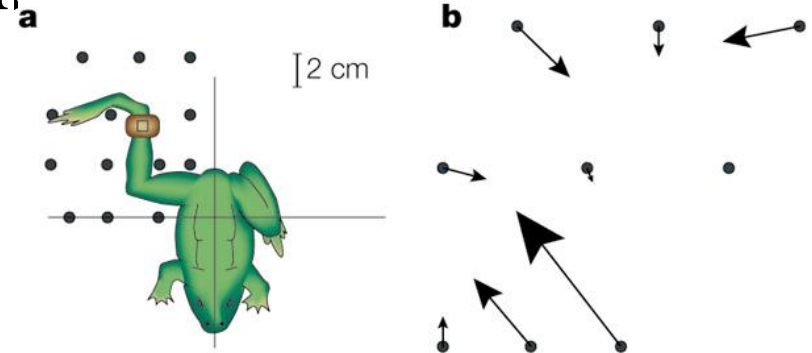
Isochrony (duration independent of length)

$2/3$ power law: speed as a function of curvature

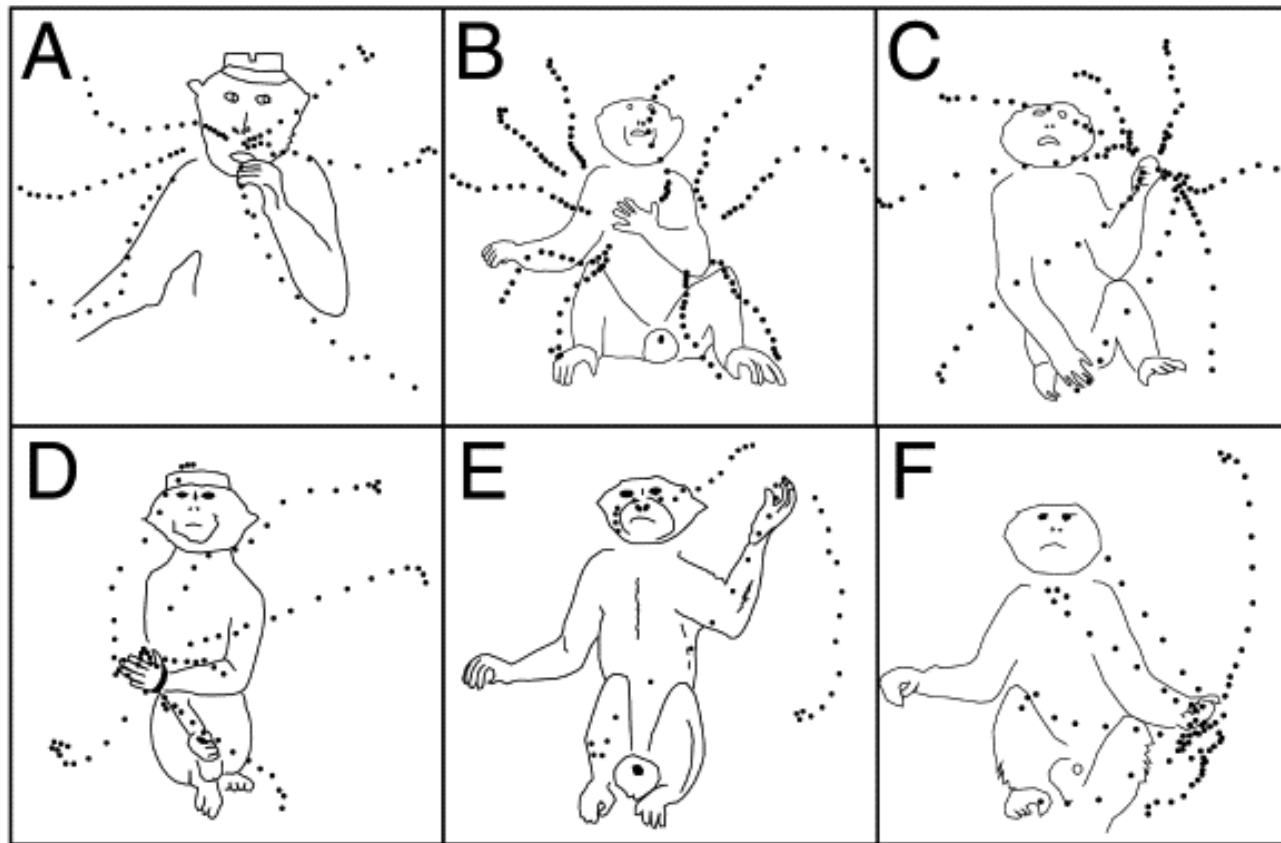


Designing a complex trajectory with limitations

- Antagonistic muscles
- Equilibrium point trajectory

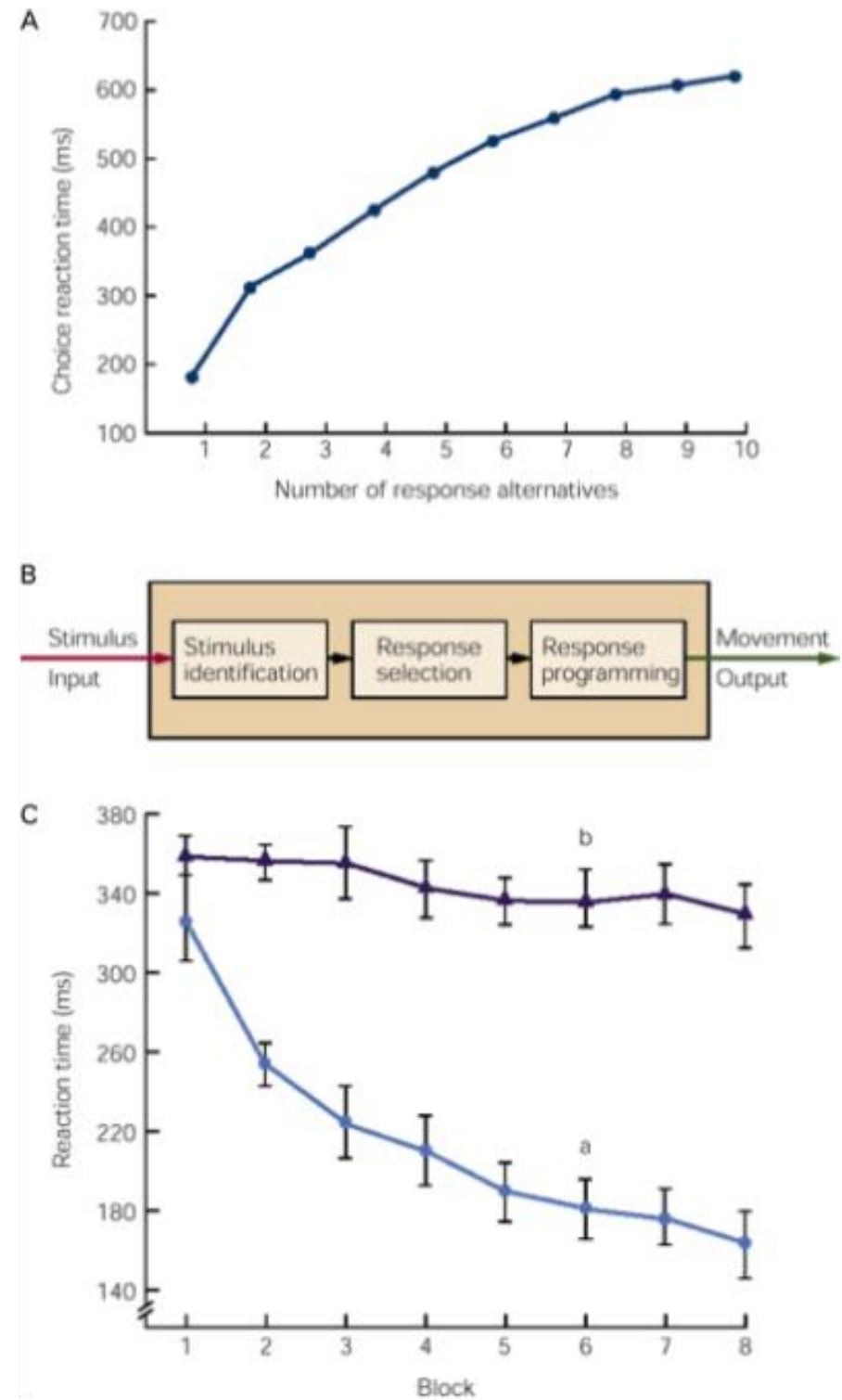


Stable behavioral gestures

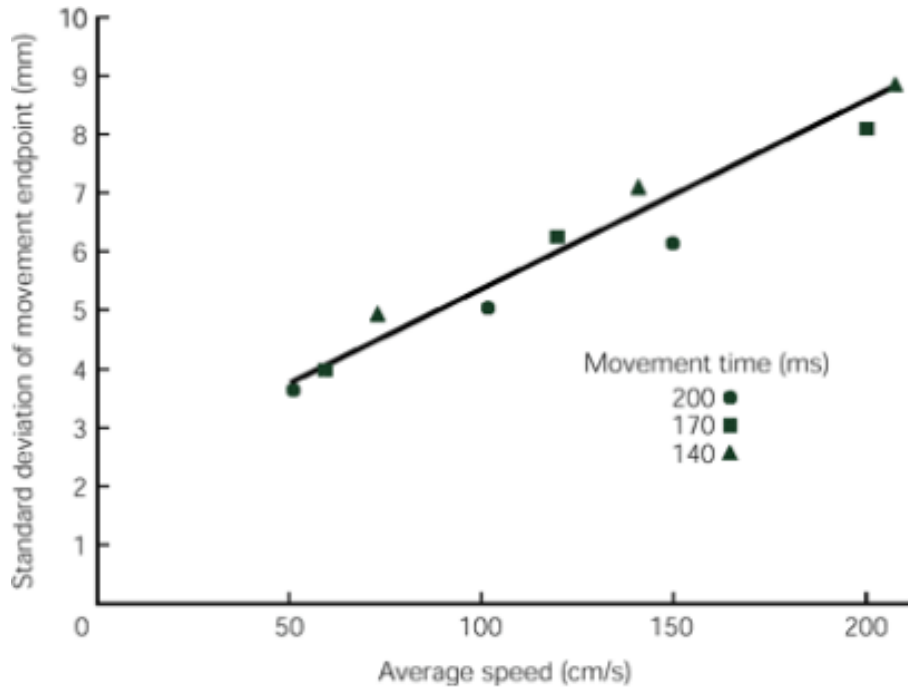


Reaction time and information

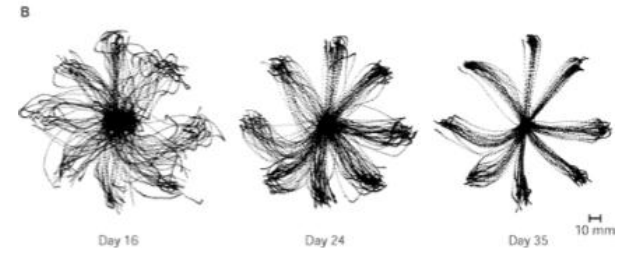
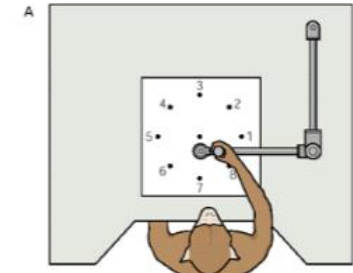
$\geq 40\text{ms}$ for reflex
 $\geq 120\text{ms}$ for voluntary
100ms for each bit of information



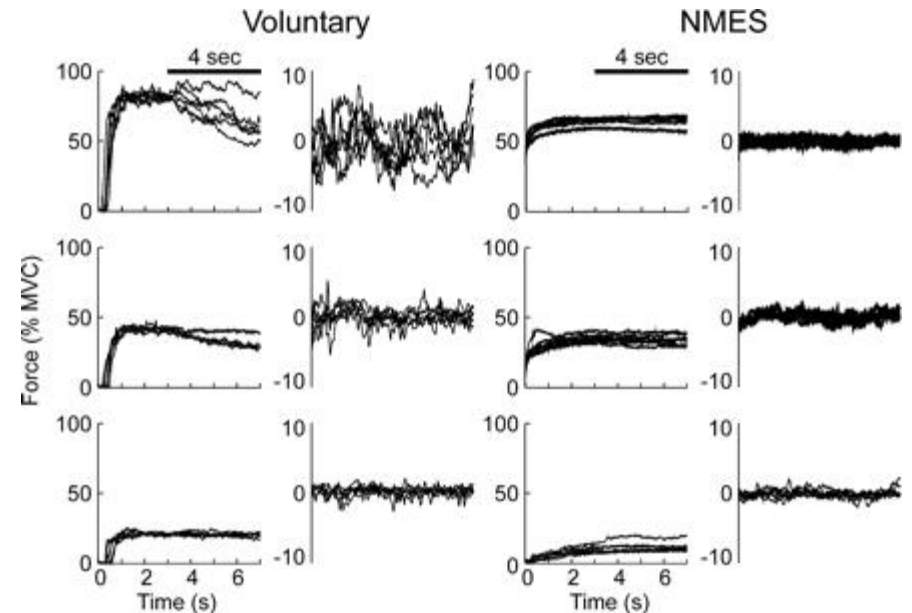
Speed – accuracy tradeoff (Woodworth, 1890)



Less time for feedback corrections?
No, even without sensory feedback



Variability/noise of the components
(neurons! much more than muscles)

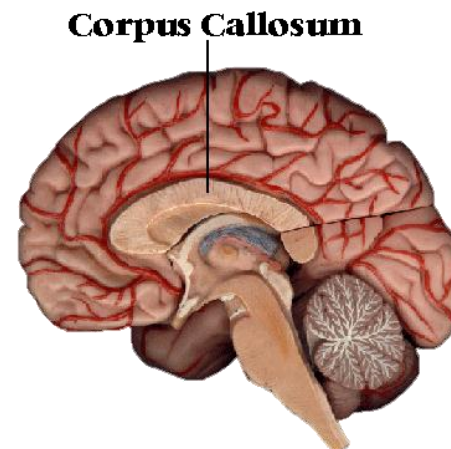
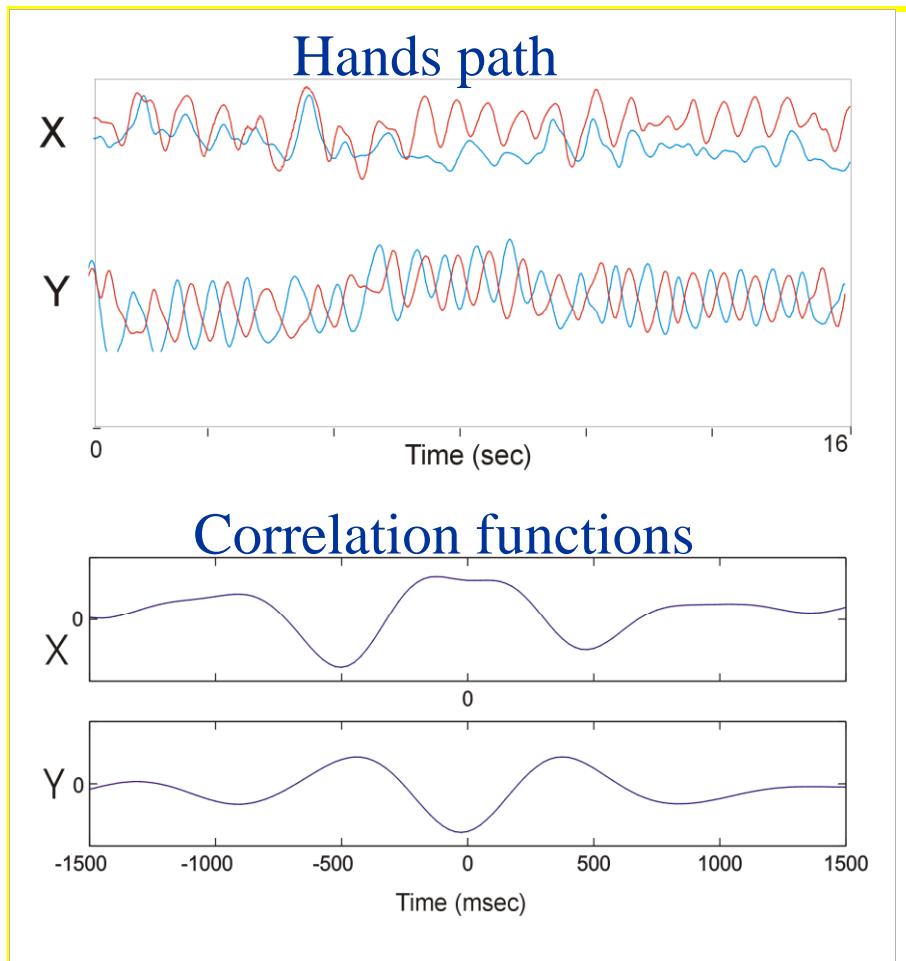


Overcoming noise: optimization principles

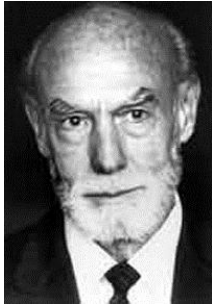
- Minimum jerk (smooth acceleration)
- Minimum signal-dependent noise
- Optimal control: minimize only what is relevant, and ignore other variables.

Lateralization

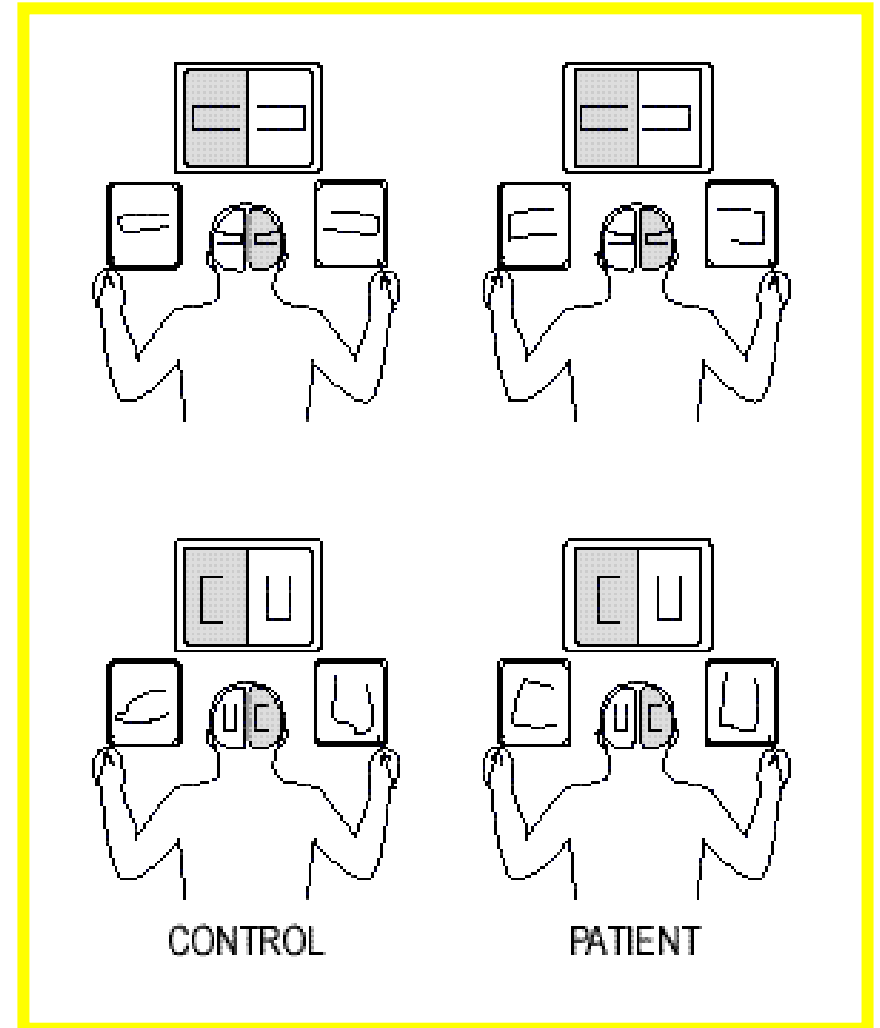
- Wilder G. Penfield together with Herbert Jasper, treated epileptic patients by destroying neurons.
- Before that, he applied stimulation to different brain areas to probe the epileptic loci.
- One main finding was that each hemisphere controls (efferent nerves) and gets sensory inputs (afferent nerves) from the *contralateral* side of the body.



Decoupling can help, sometimes

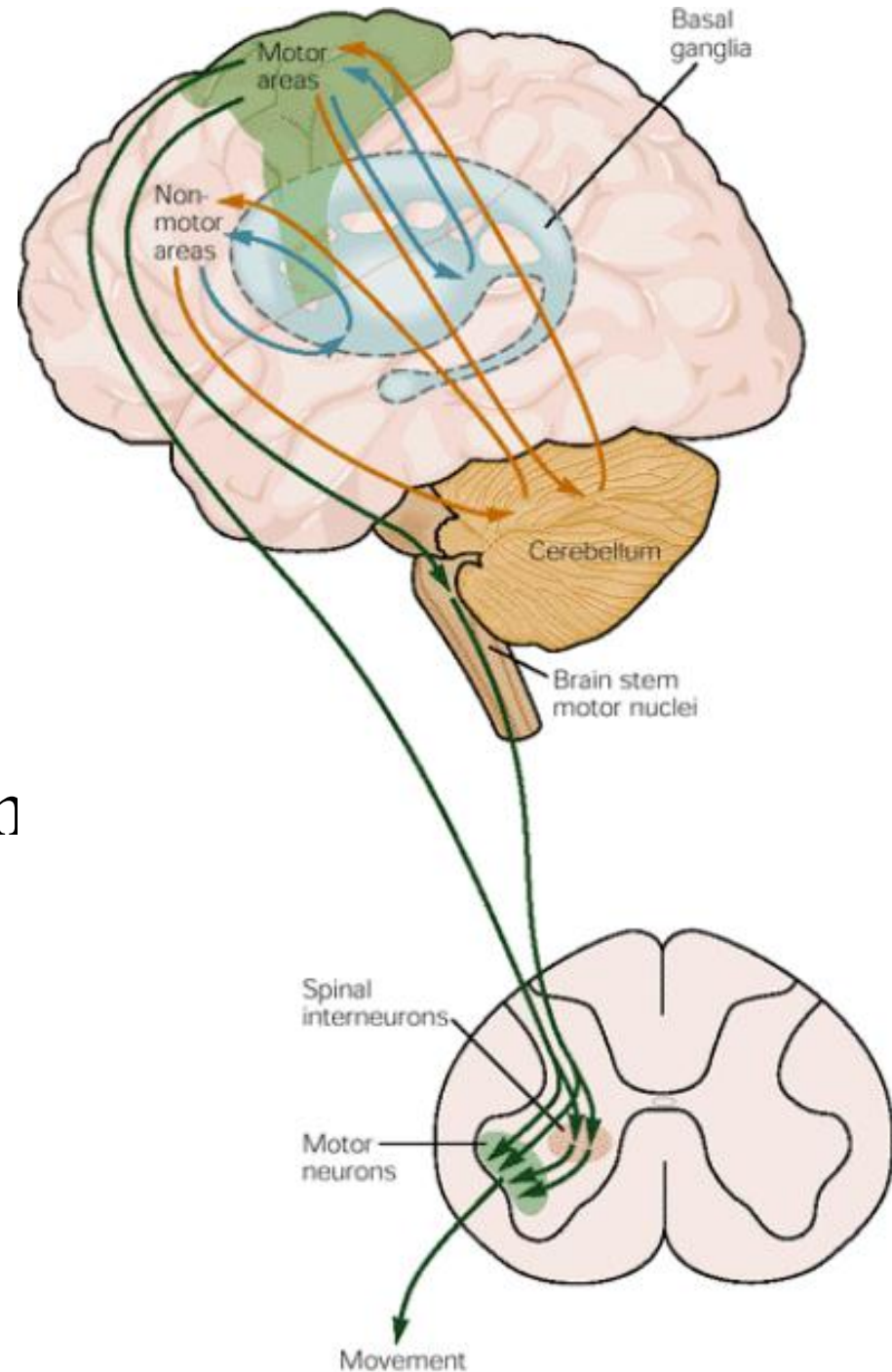


- Roger W. Sperry (1913-94, Nobel), **Athlete scholarship!!!**, died from Kuru.
- & Michael S. Gazzaniga
- Observed split-brain patients (removed corpus-callosum) and found that each hemisphere is a conscious system in its own right, even in conflicting mental processes.
- Object in the left visual field, will not be vocally named, but can be handled with the _____ hand



Hierarchical organization

- Cortex
- Basal-ganglia, cerebellum
- Brain stem
- Spinal tracts
- Spinal cord
- Muscles



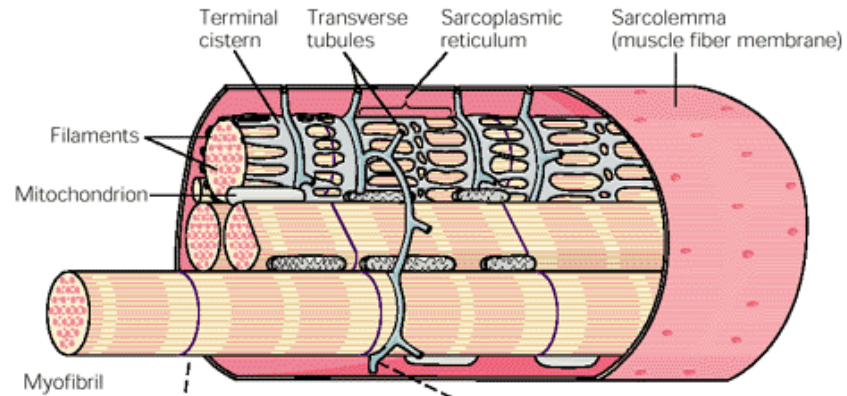
Muscles

1. smooth muscles
2. cardiac muscles
3. **skeletal muscles**

Structure

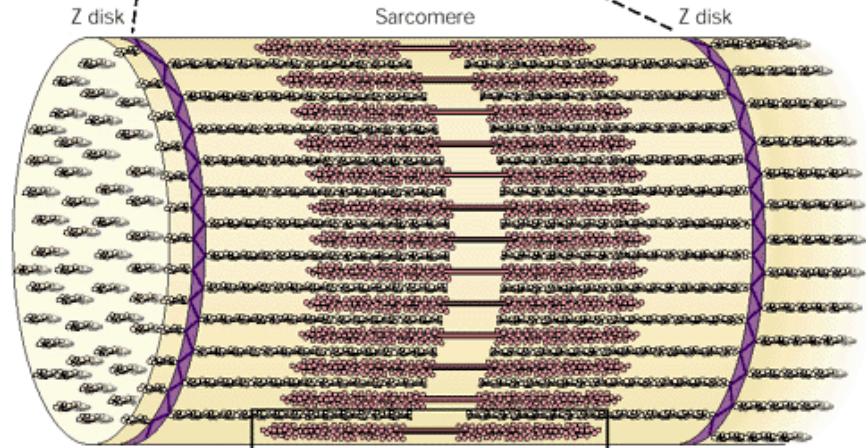
Muscle fiber

A



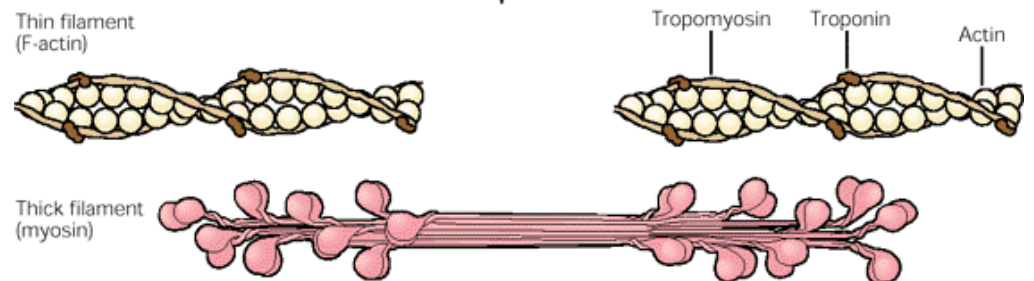
myofibril

B

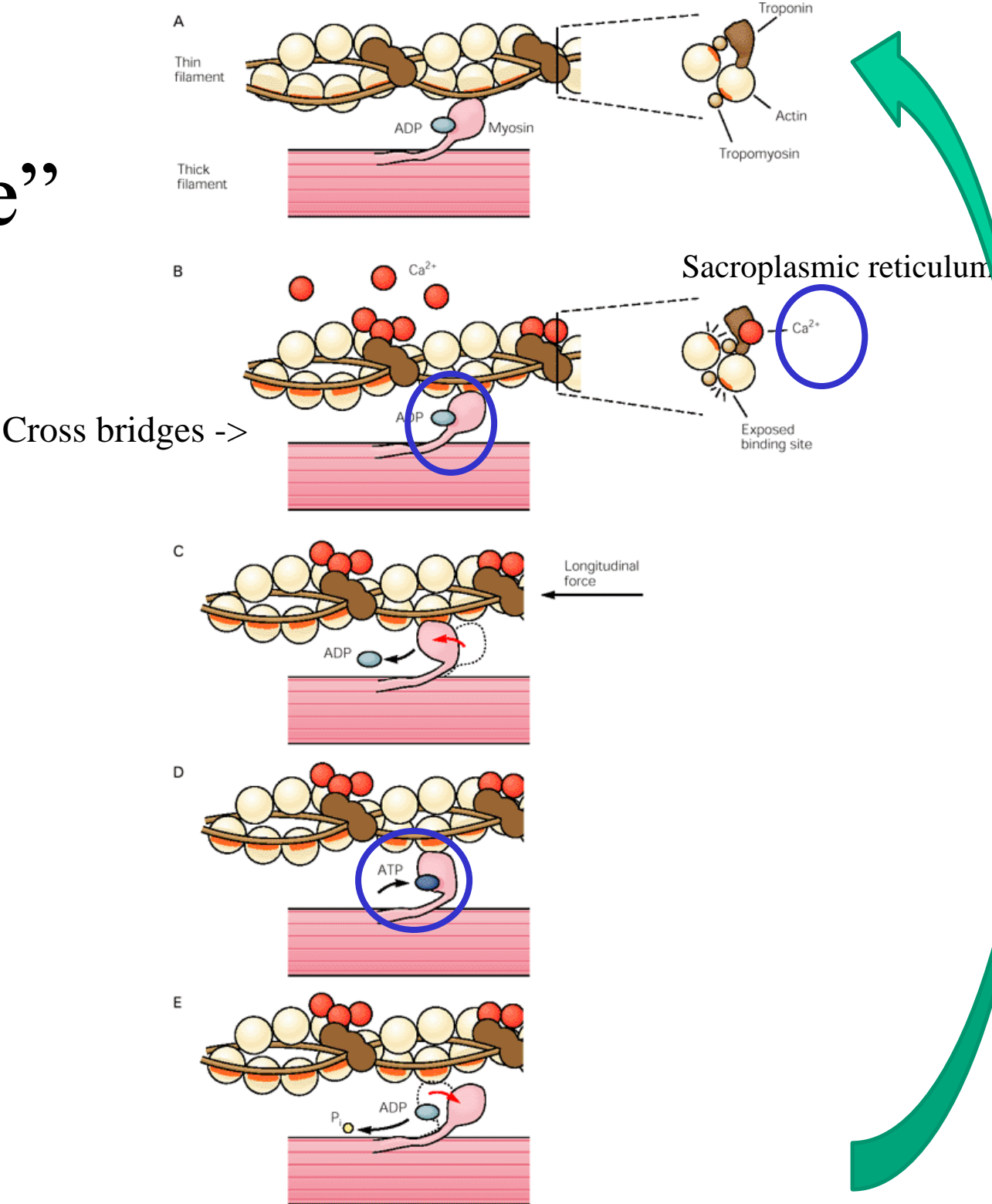


Sarcomere: functional unit

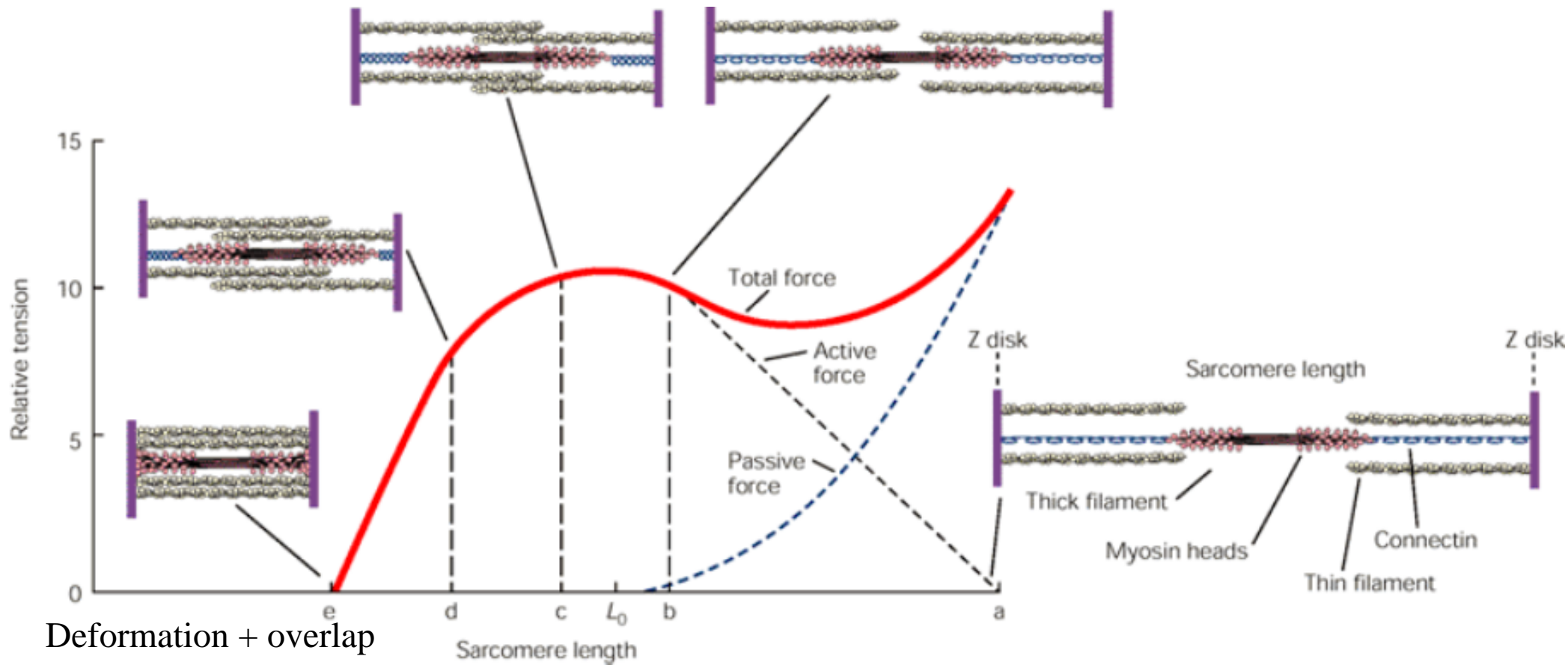
C



The "engine"



Force depends on length



Deformation + overlap

Sarcomere length

Total force

Active force

Passive force

Z disk

Sarcomere length

Thick filament

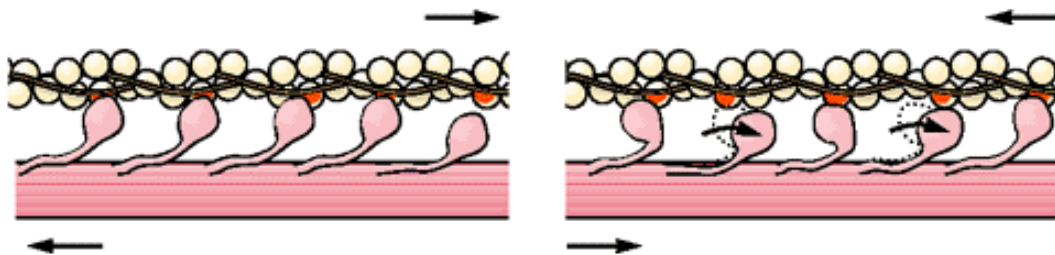
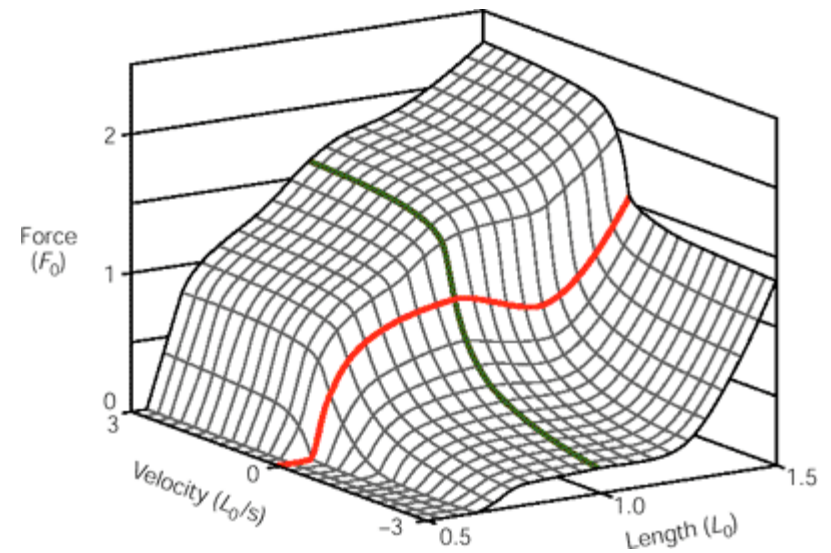
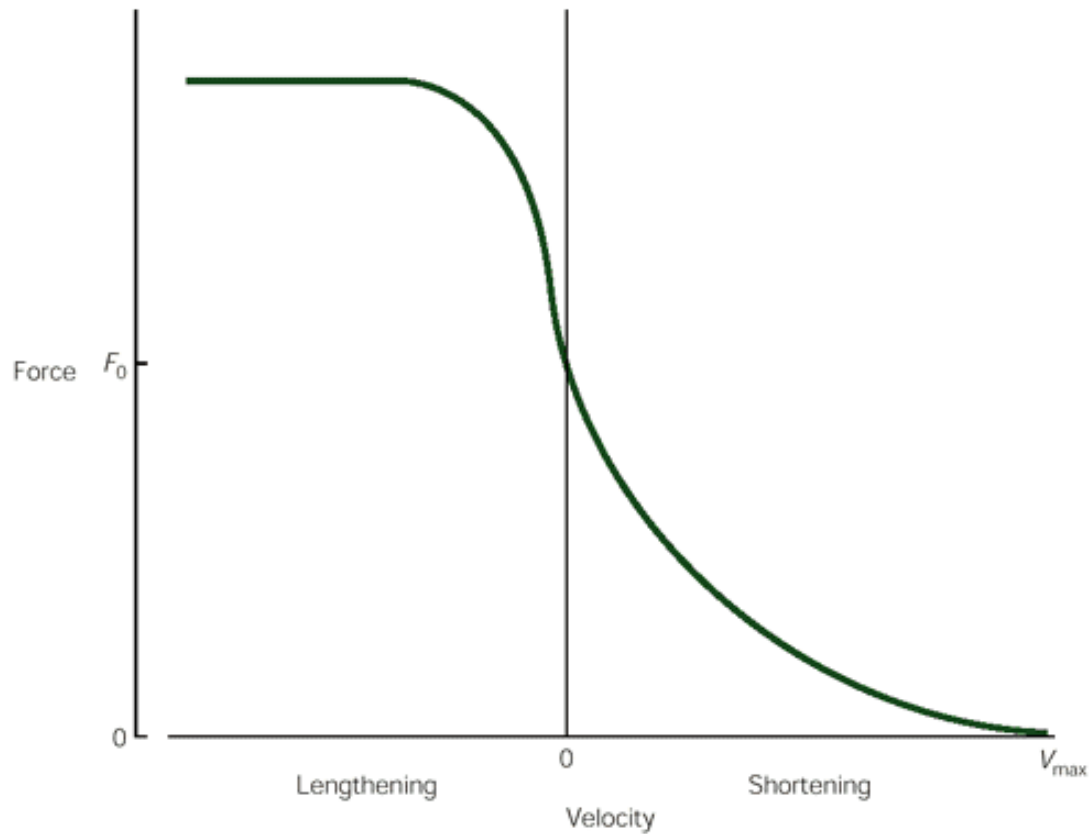
Myosin heads

Thin filament

Connectin

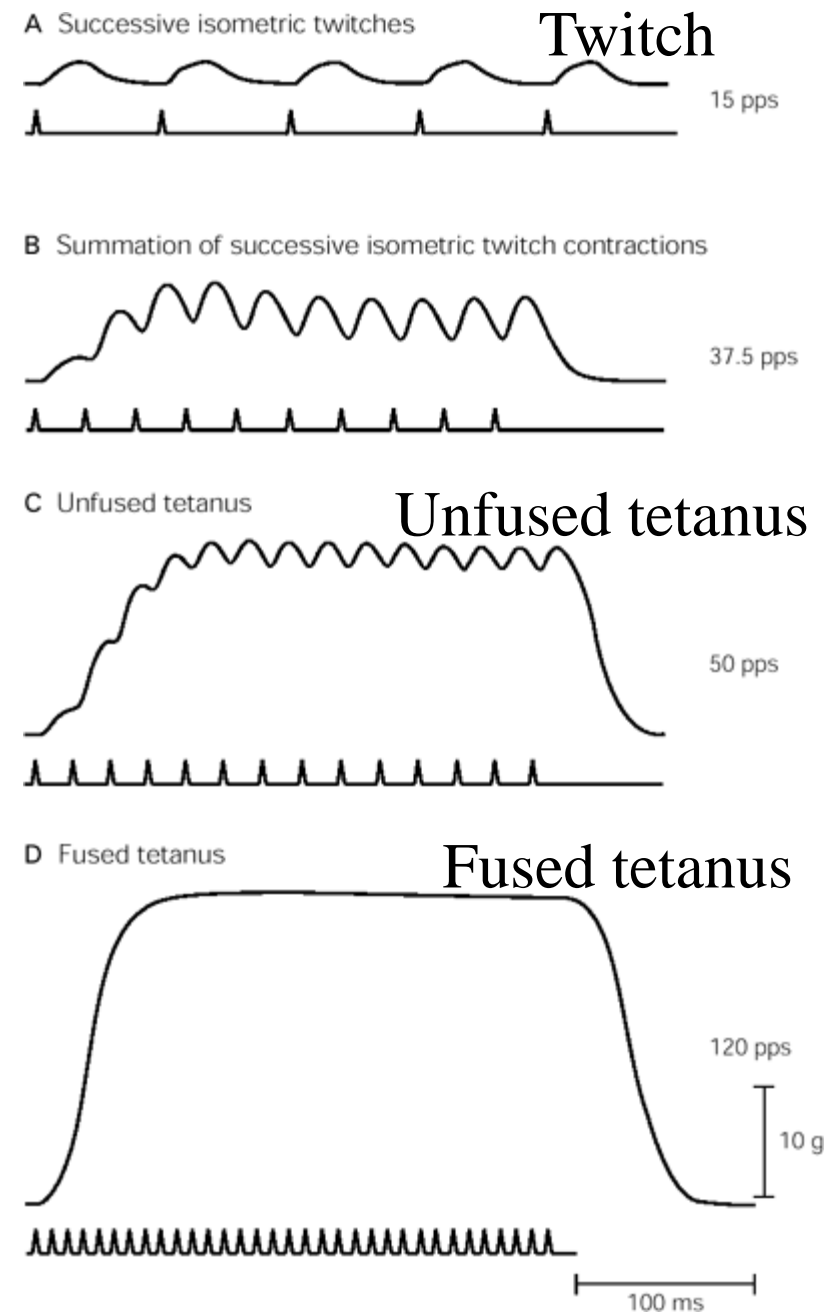
Z disk

Force depends also on velocity

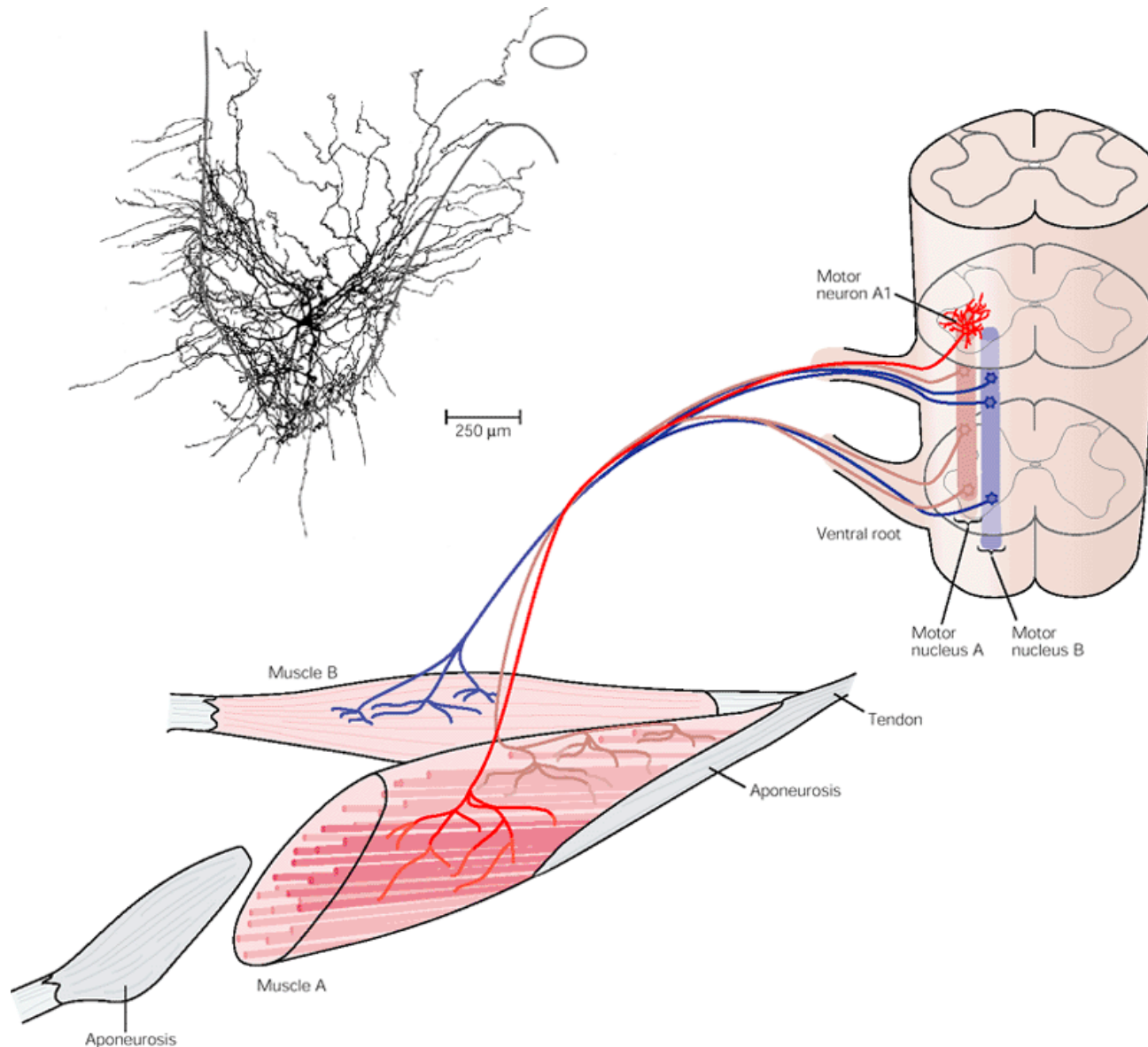


The force of a single muscle fiber is a function of

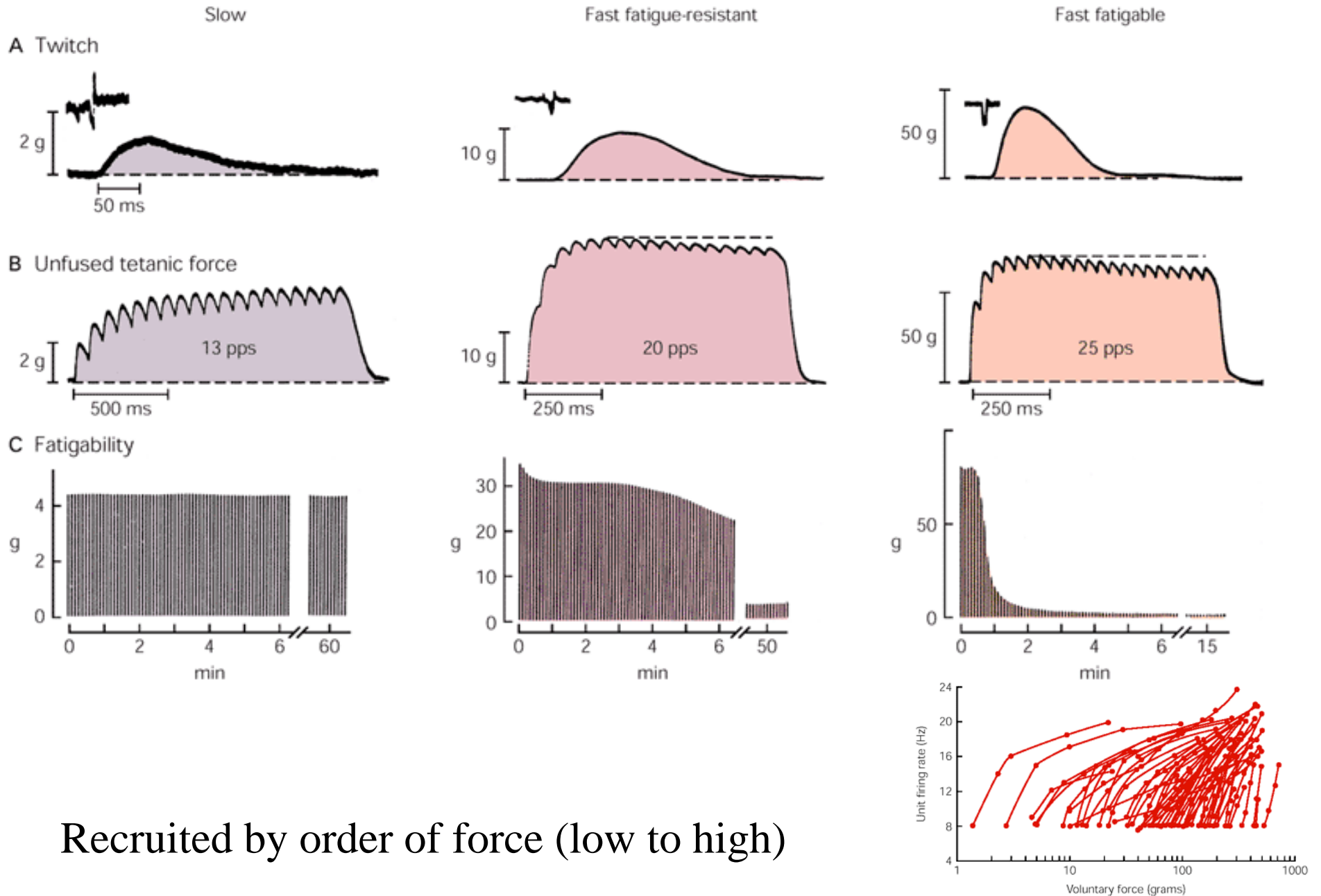
- Stimulation rate
- Stimulation pattern
- The muscle length
- The velocity of contraction
- The fiber type
- The fiber organization
- The duration of exercise - fatigue



Motor unit: motor neuron and the muscle fibers it innervates (one to many)

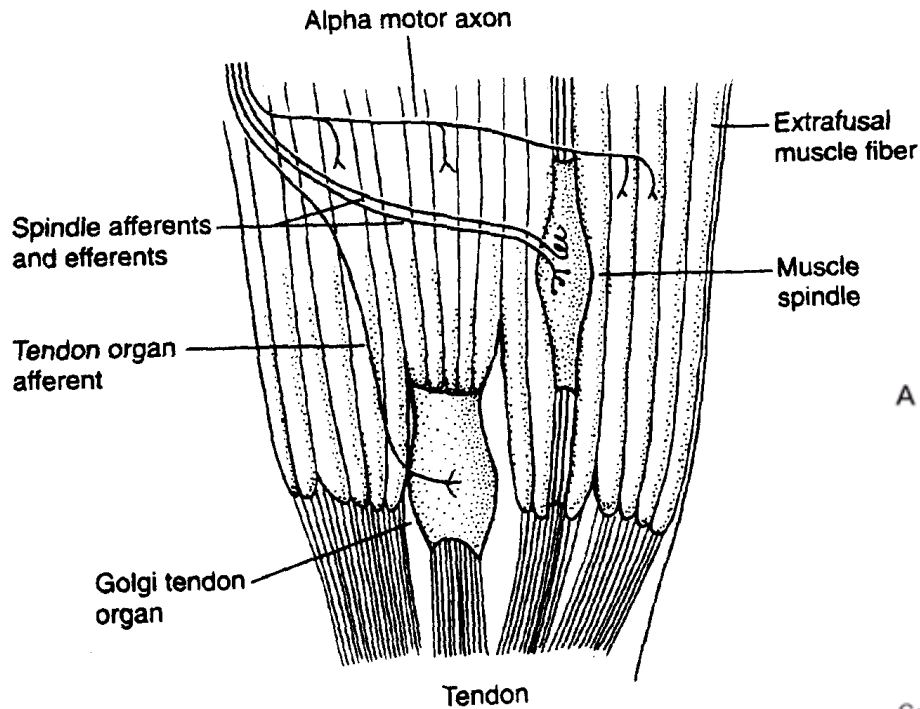


3 types of motor unit:



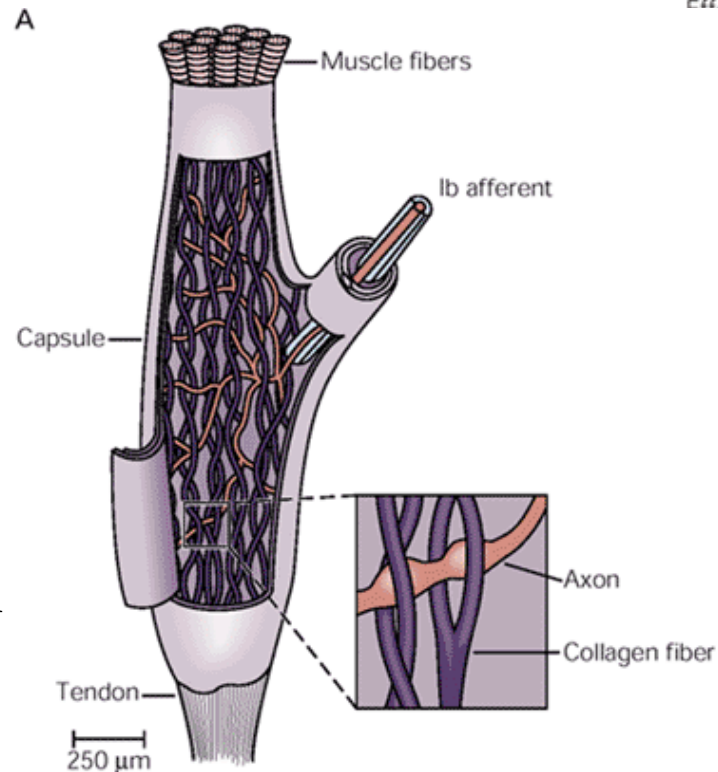
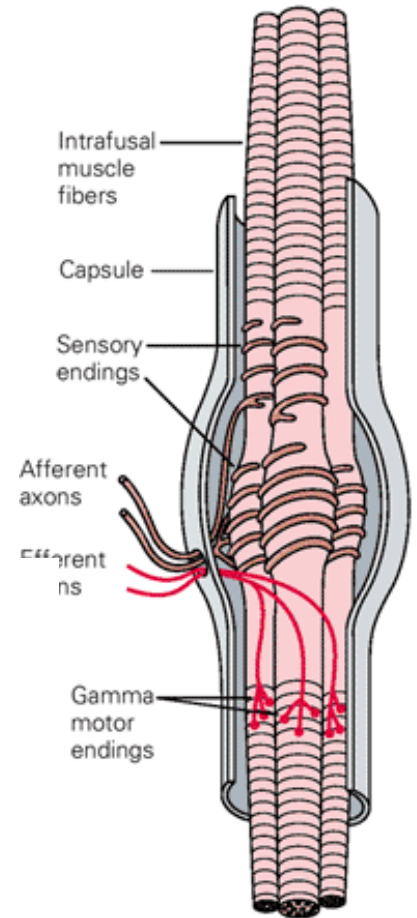
Recruited by order of force (low to high)

Muscle proprioceptive organs



Spindle: length
Parallel

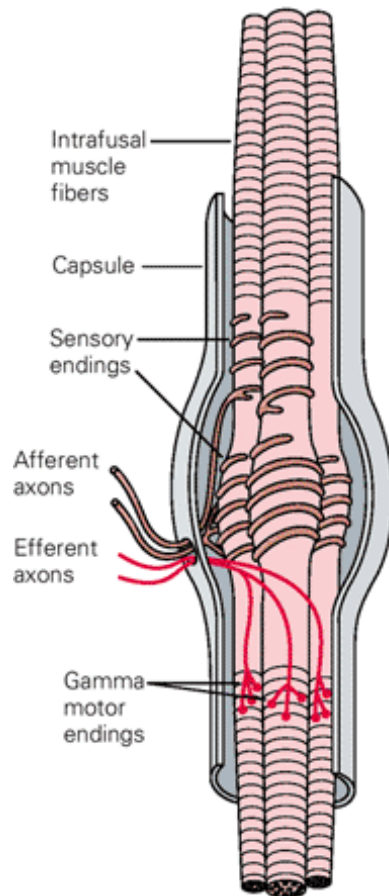
A Muscle spindle



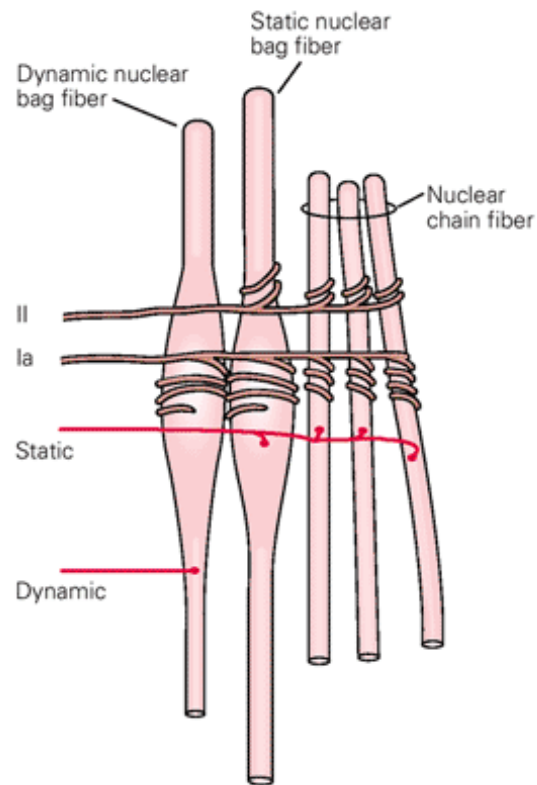
Golgi tendon: tension
Serial

The muscle spindles are sensitive to changes in length

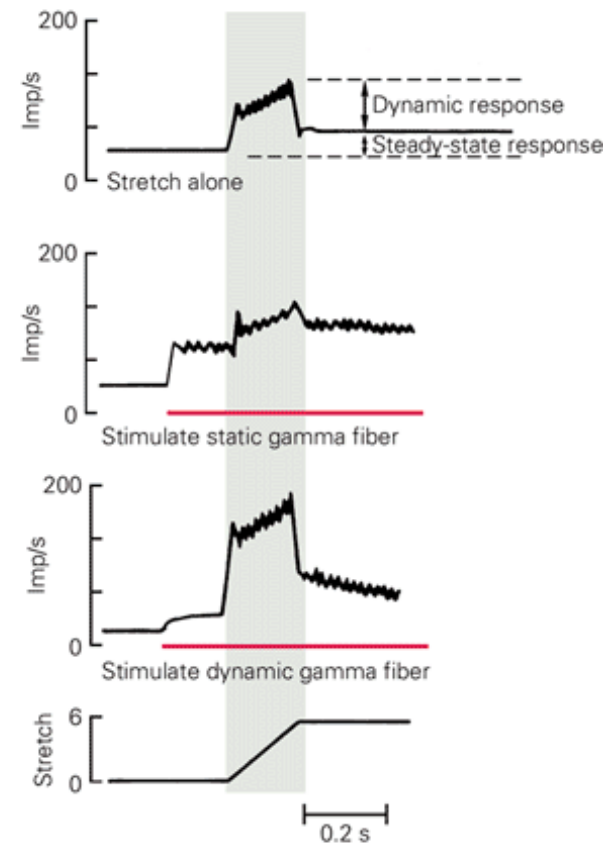
A Muscle spindle



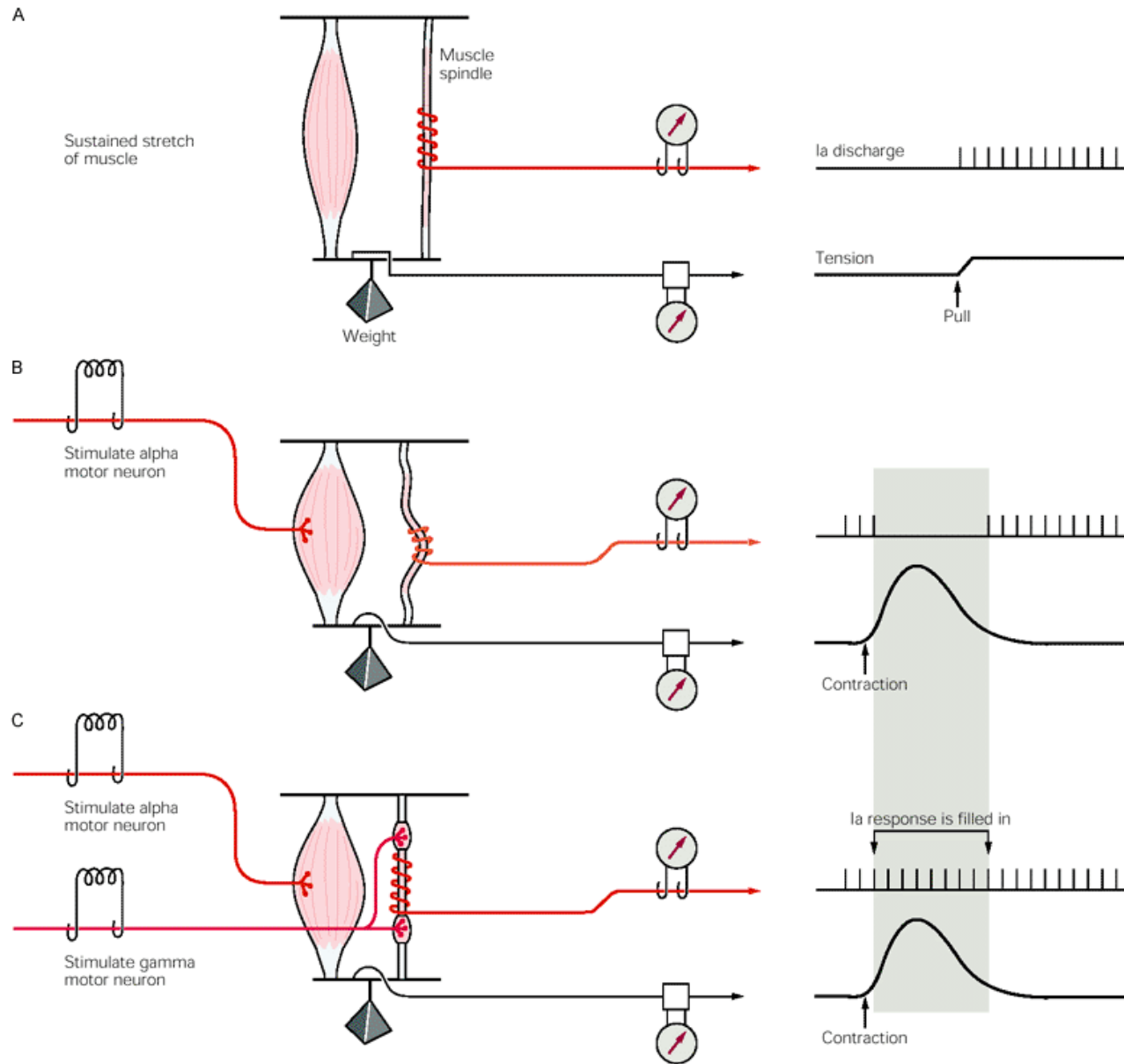
B Intrafusal fibers of the muscle spindle



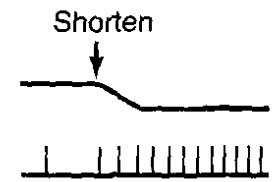
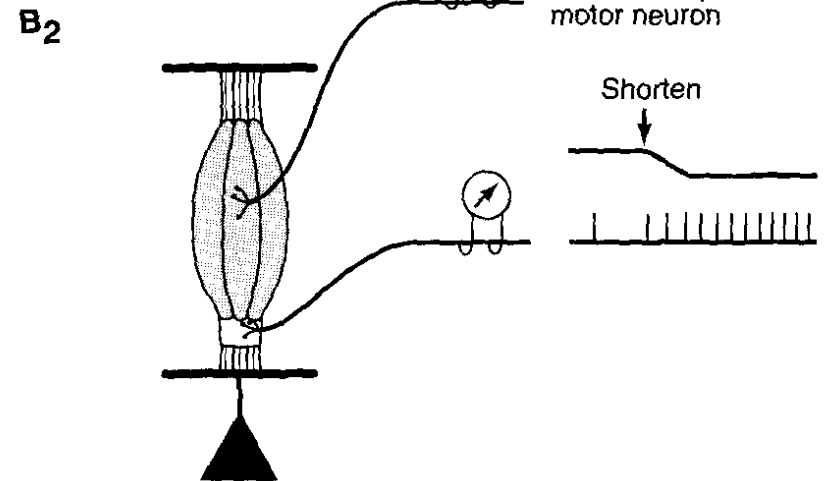
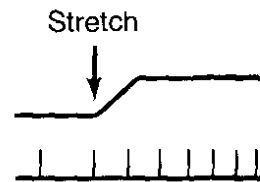
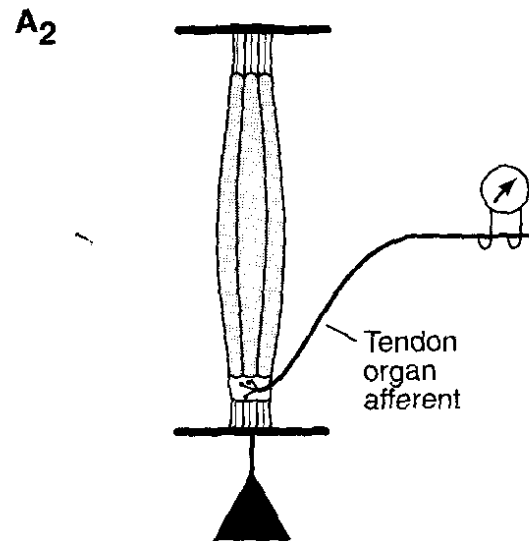
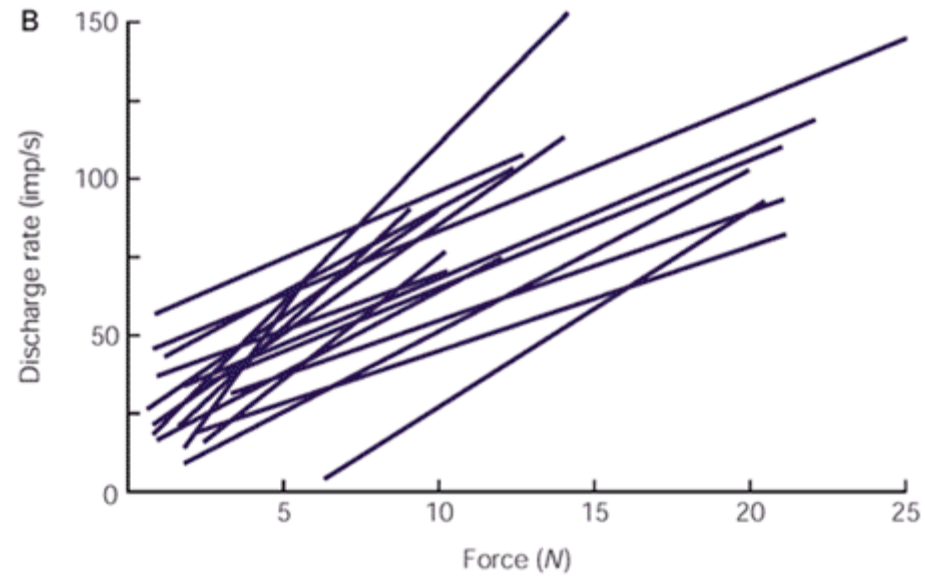
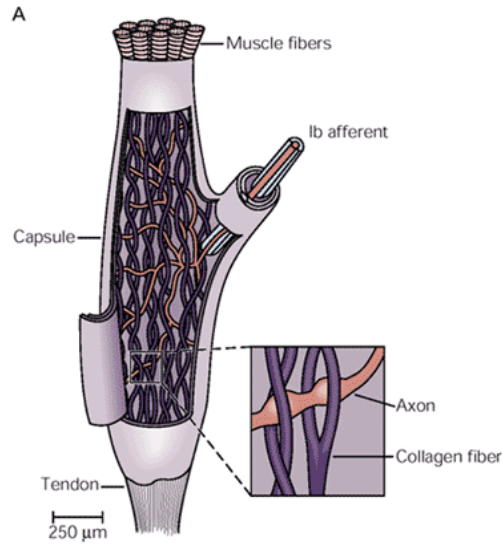
C Response of Ia sensory fiber to selective activation of motor neurons



Active range can be dynamically modulated

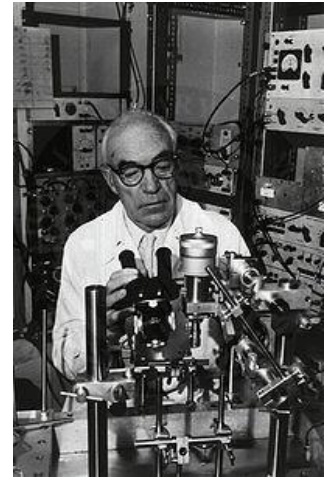


Golgi tendon organs are sensitive to the tension

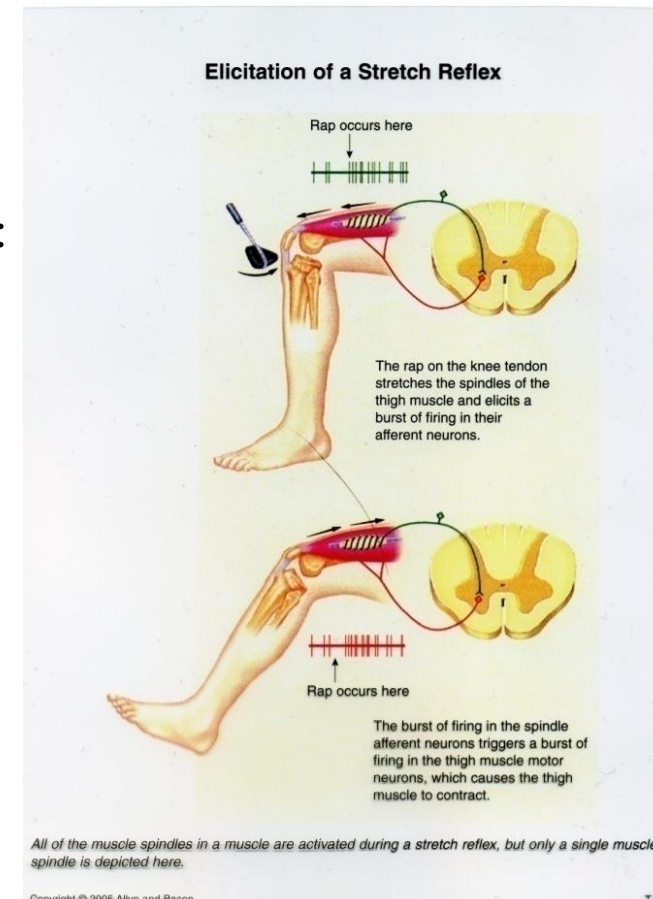




Reflexes and actions



- Charles S. Sherrington (1857-1952, Nobel, English Neurophysiologist)
- Together with John Langley, supported the “*localization of function*” theory for the brain.
- Mapped dorsal and ventral roots; opposing muscles, reciprocal innervations.
- “reflexes are the simplest expressions of the interactive action of the nervous system”
- John C. Eccles (1902-1997, Nobel, Australian Neurophysiologist): using the stretch reflex as a model, he studied synaptic excitation and inhibition.
- Consists of only two neurons: a sensory neuron (the muscle spindle fiber) and the motor neuron. The sensory neuron synapses onto the motor neuron in the spinal cord. When Eccles passed a current into the sensory neuron in the quadriceps, the motor neuron innervating the quadriceps produced a small excitatory postsynaptic potential (EPSP). When he passed the same current through the hamstring, the opposing muscle to the quadriceps, he saw an inhibitory postsynaptic potential (IPSP) in the quadriceps motor neuron.
- Bernard Katz (1911-2003, Nobel): neurotransmitter release in synapses is quantal (Ach in motor nerve -> muscles)



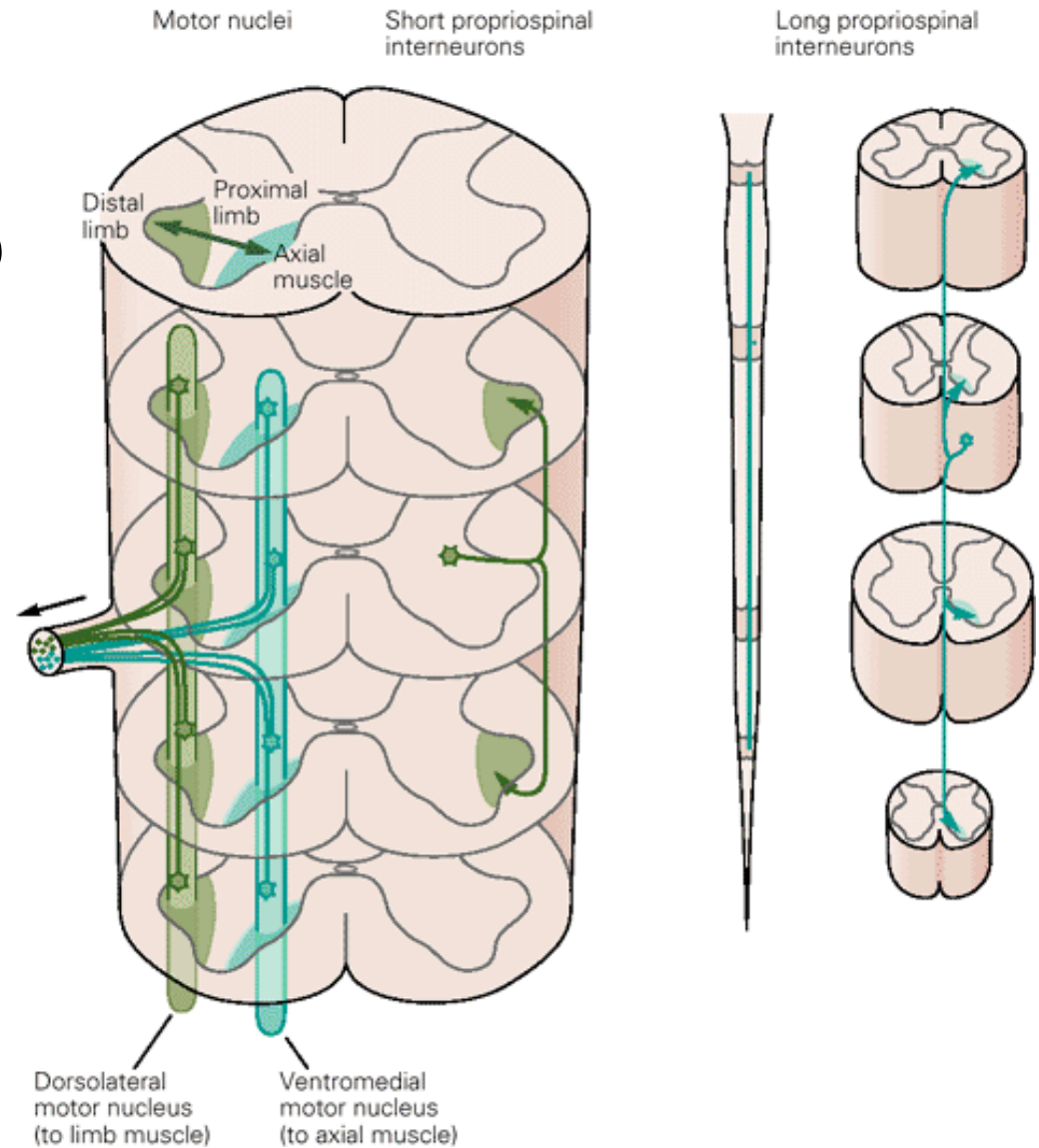
Spinal cord, Brain stem and spinal tracts

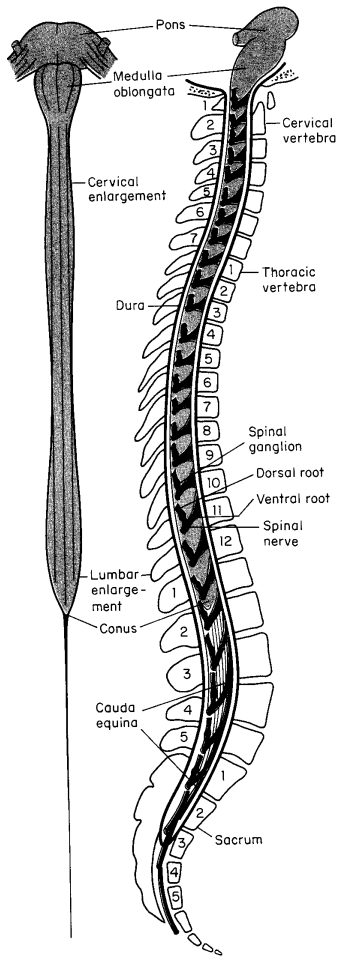
Spinal cord

1. Local interneurons
2. Propriospinal (across segments)
3. Projection (to upper centers)
4. Motor neurons

Motor nuclei: cell bodies of motor neurons that innervate a muscle.

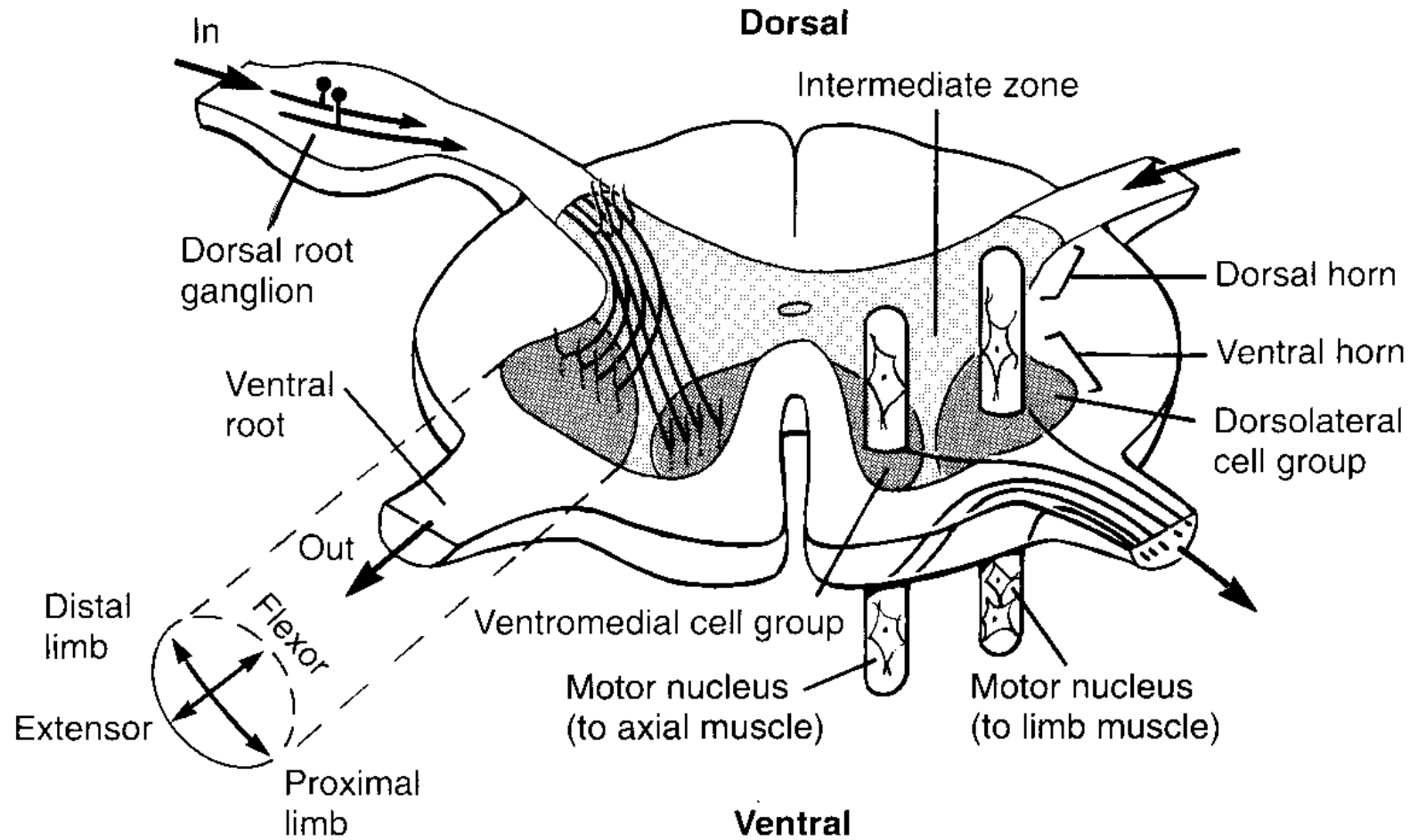
Medial nuclei are long across segments
Lateral are shorter





Course of afferent fibers

Location of motor nuclei

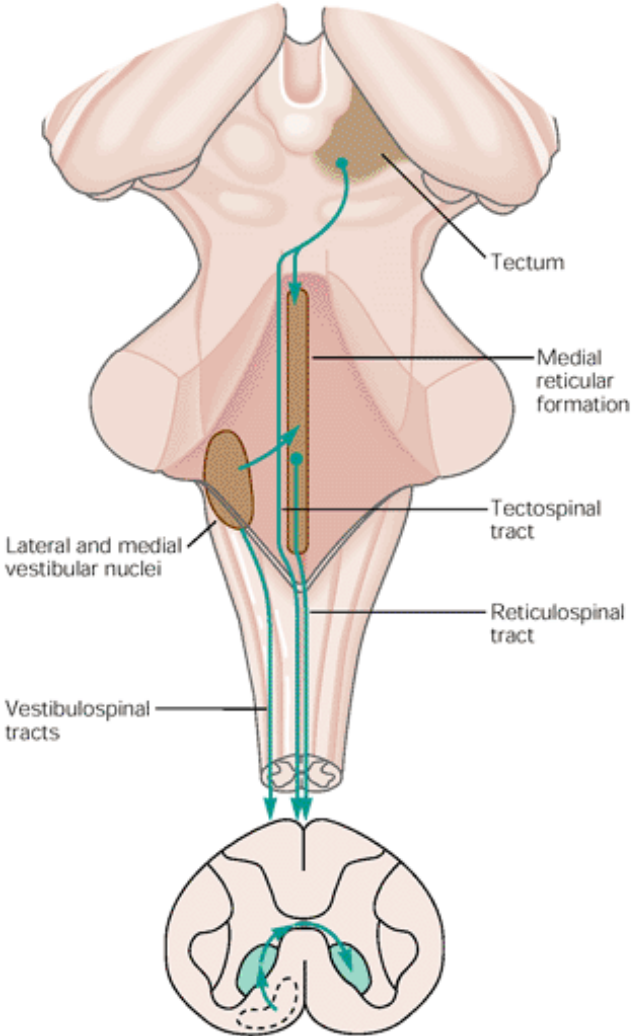


Brain stem pathways

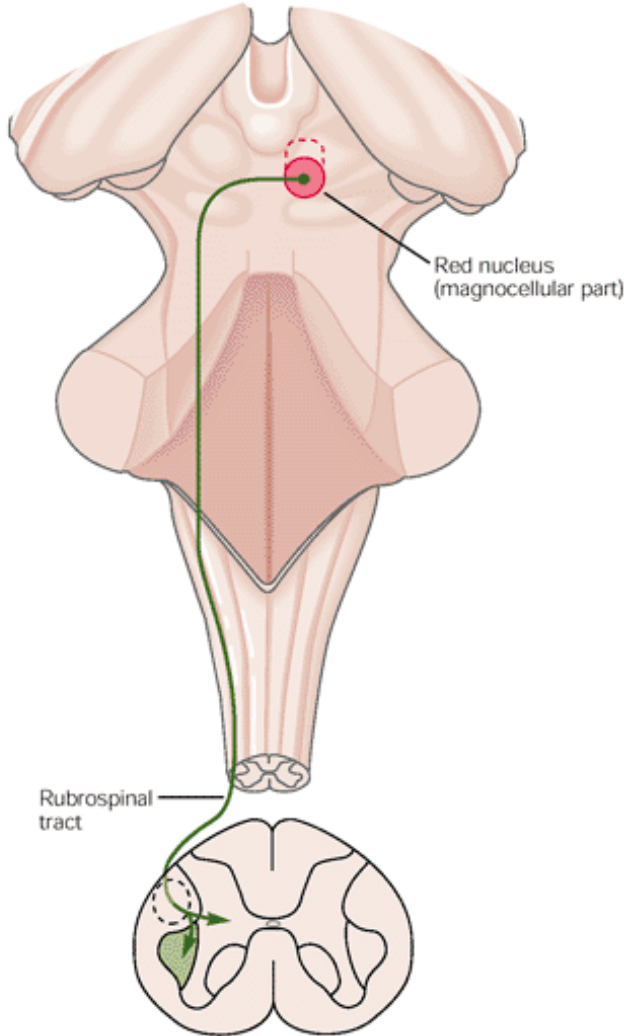
Medial pathways (vestibulospinal, reticulospinal, tectospinal), terminates in ventromedial (axial) for postural control.

Lateral pathways (rubrospinal) terminates in dorsolateral.

A Medial brain stem pathways

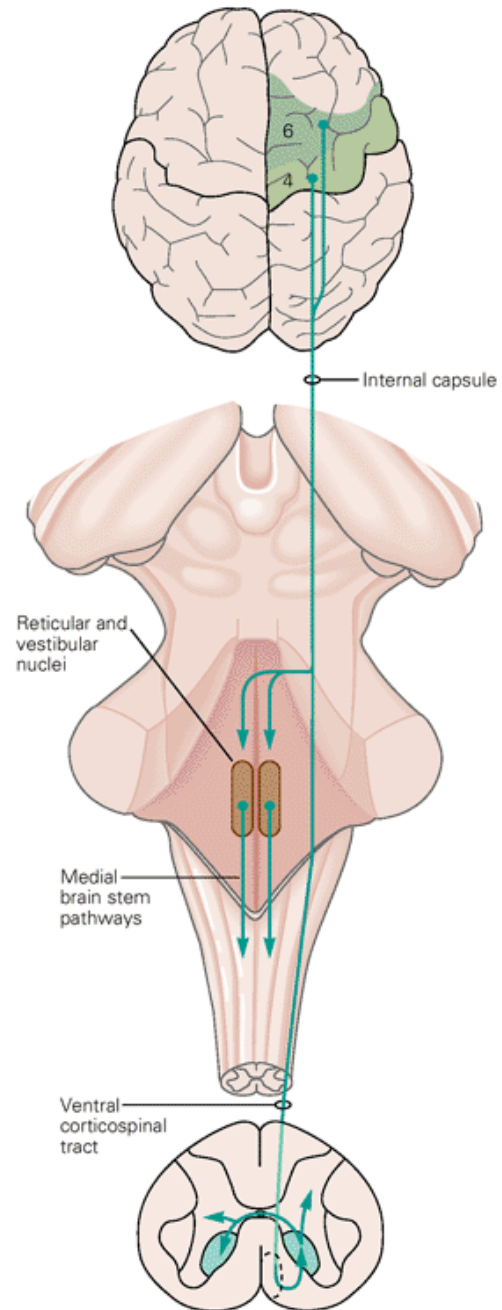


B Lateral brain stem pathways

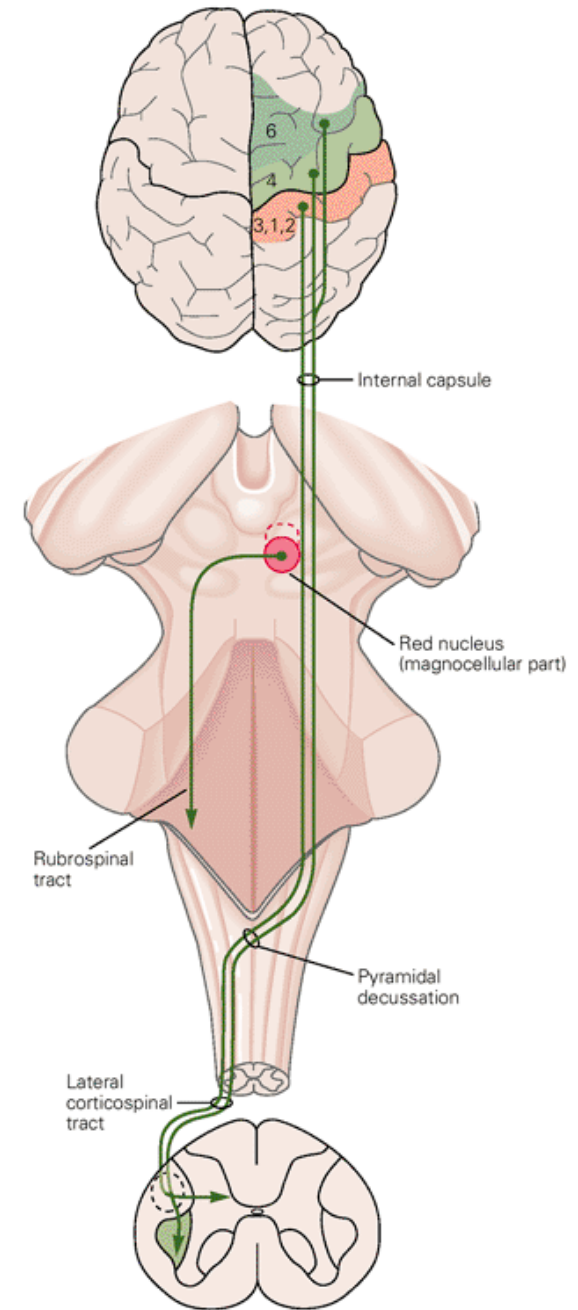


The corticospinal tract

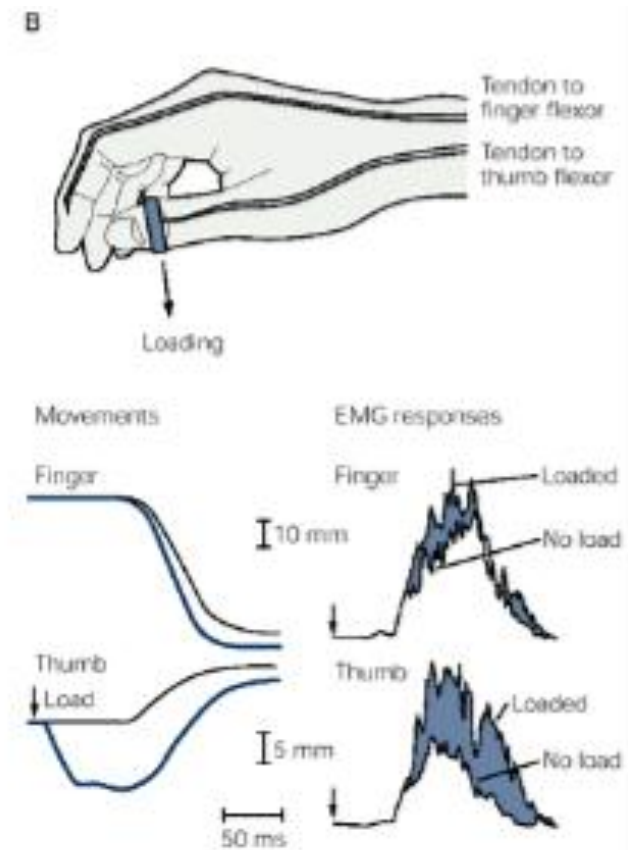
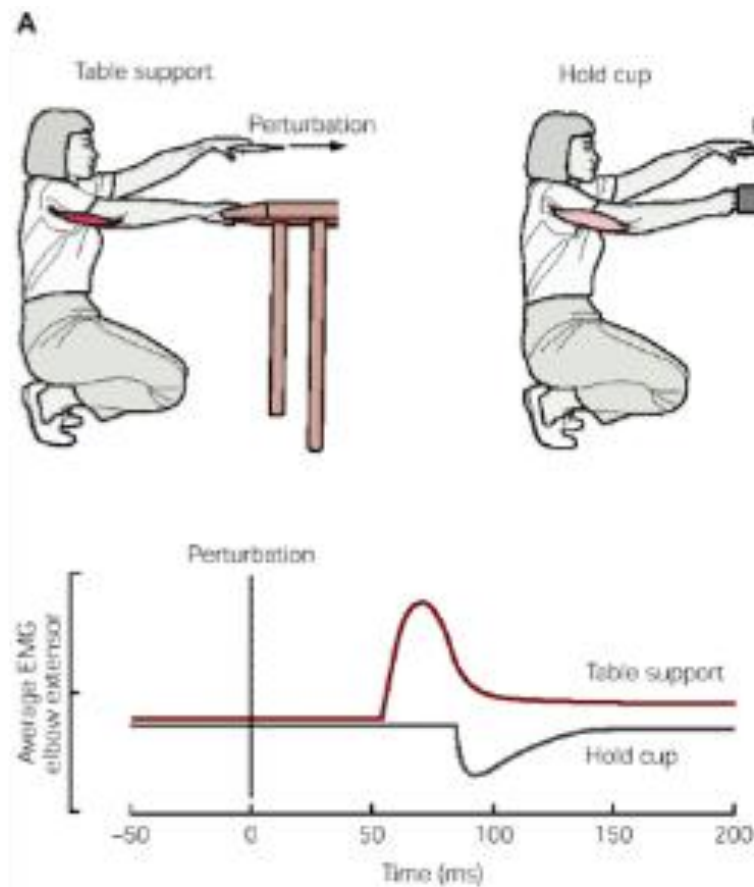
A Ventral corticospinal tract



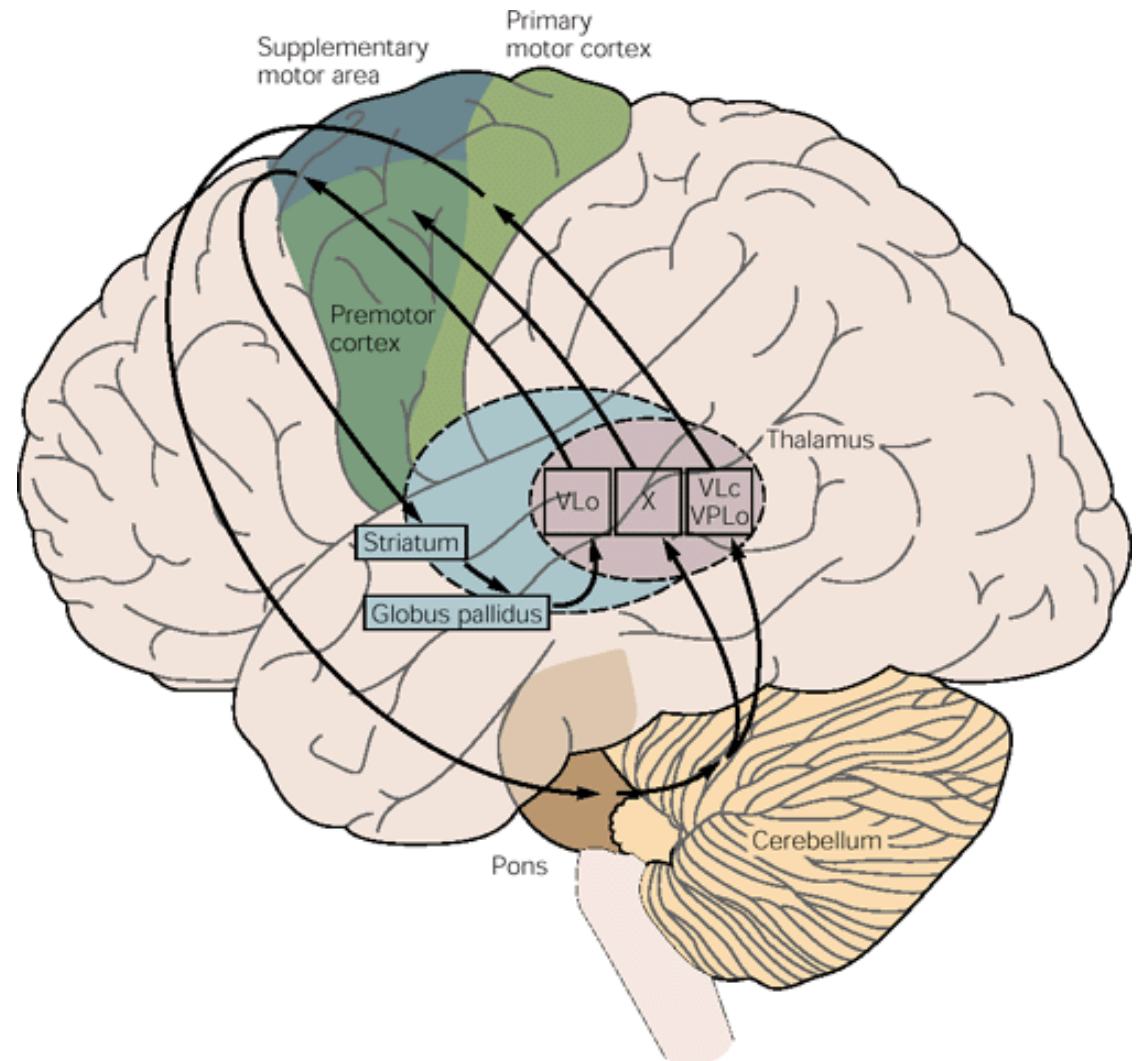
B Lateral corticospinal tract

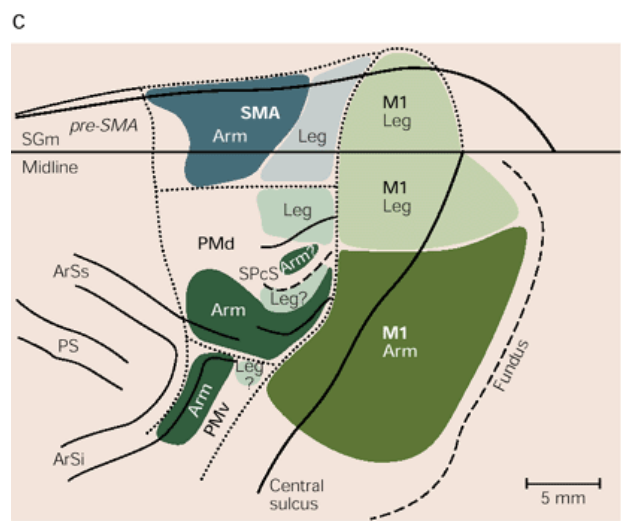
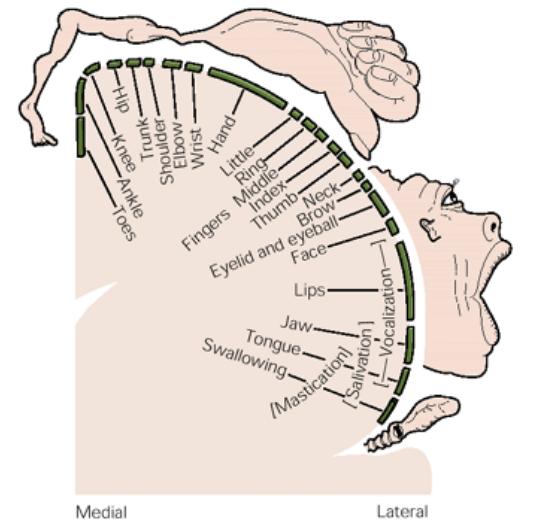
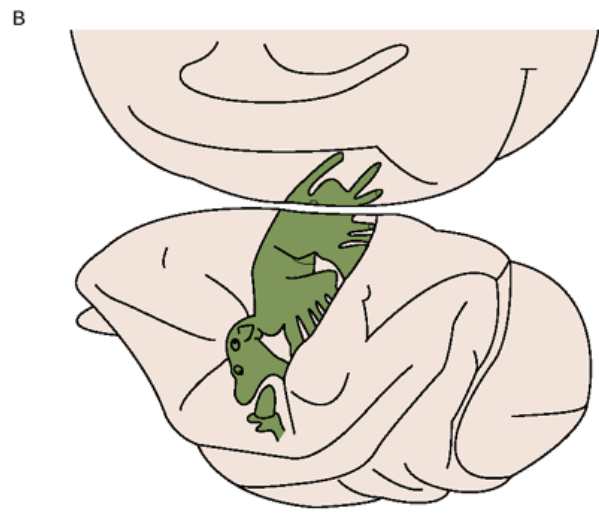
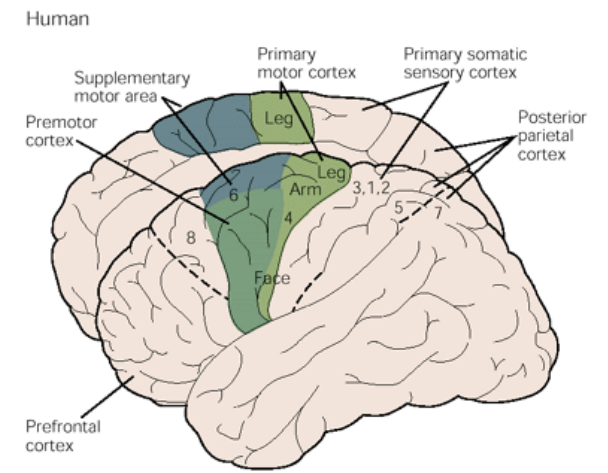
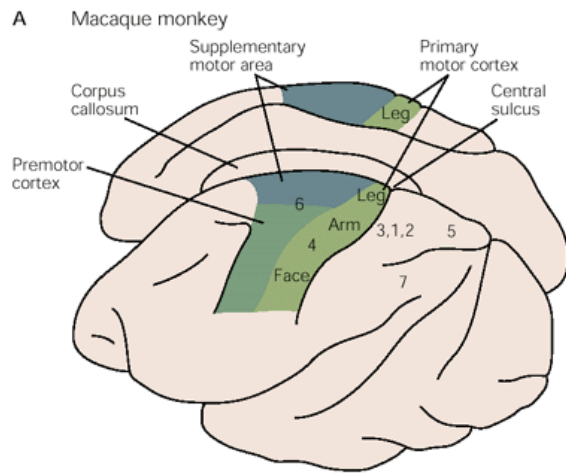


Modulation by task and descending pathways



Cortex and control of voluntary movement





Somato-topical organization

Stimulation in M1

Electrical and magnetic stimulation

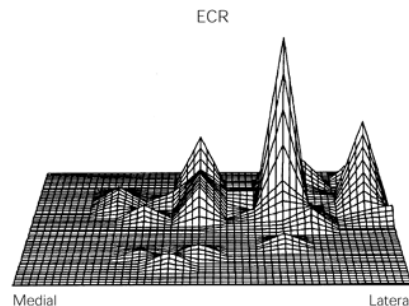
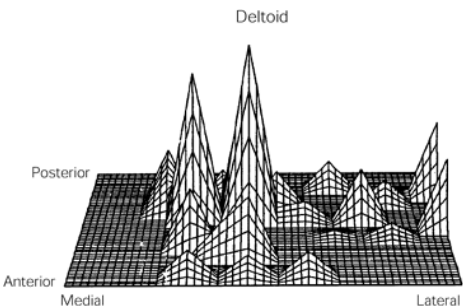
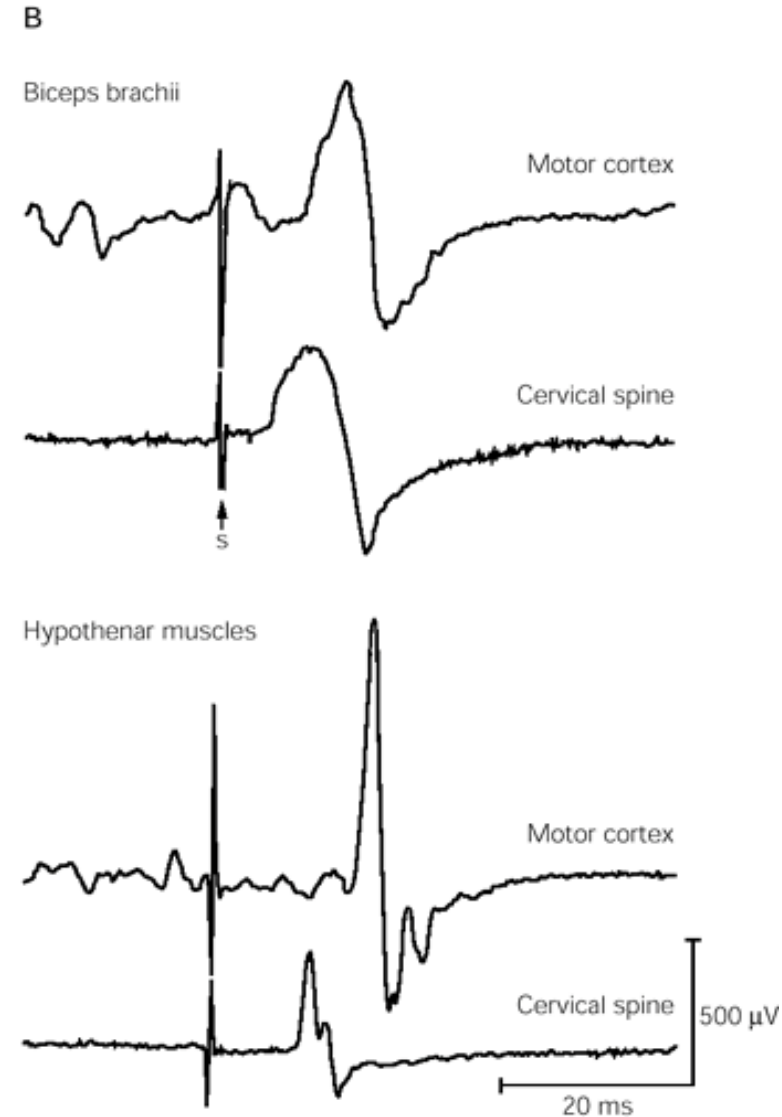
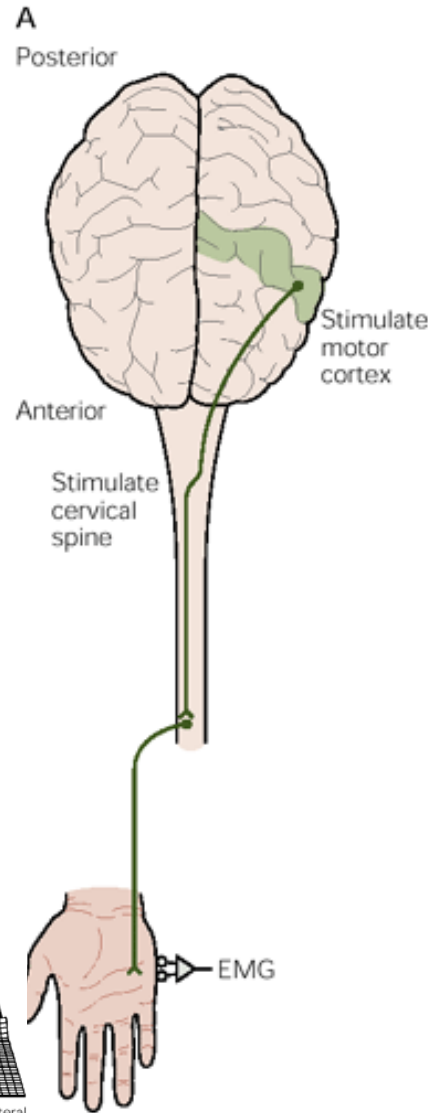
Lowest intensity

Twitch in single muscle/joint

Large (Betz) cells in lamina V

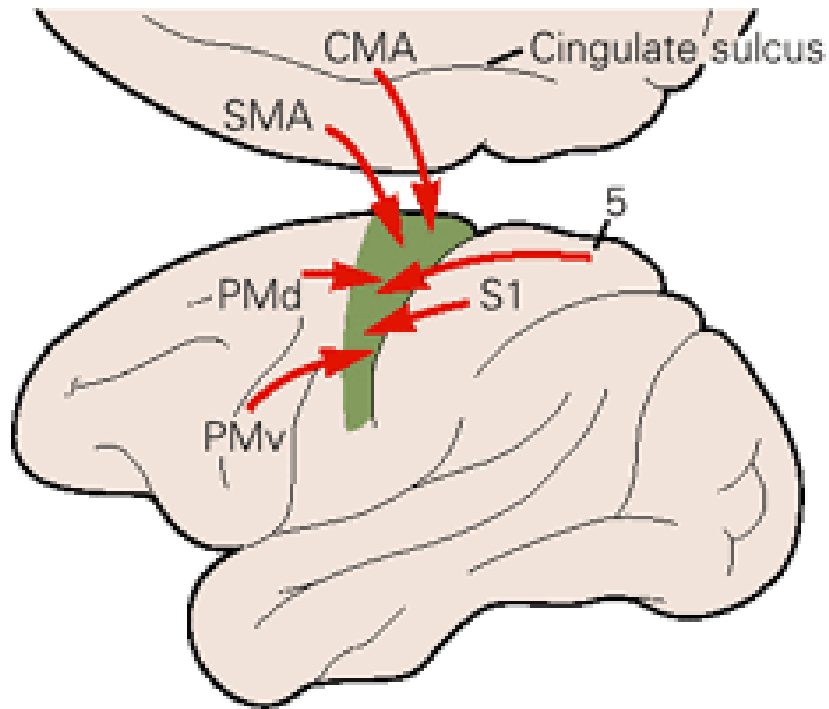
Many locations -> same muscle

Location -> several muscles

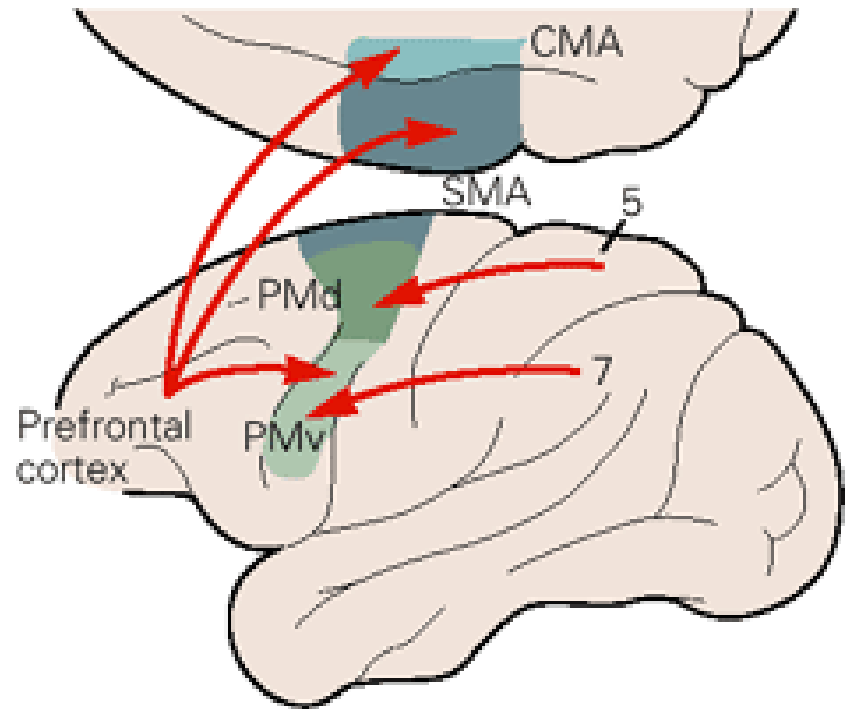


Cortical inputs

A Inputs to primary motor cortex



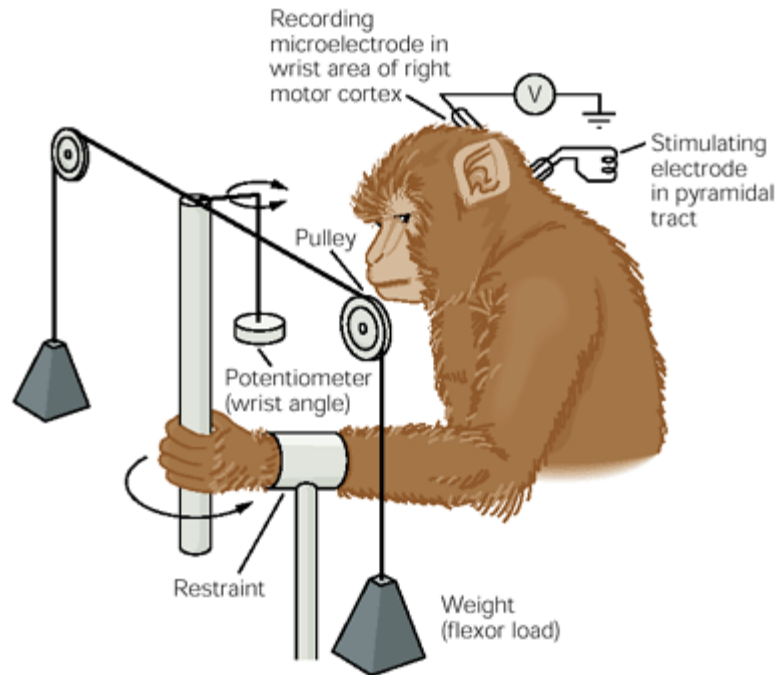
B Inputs to premotor areas



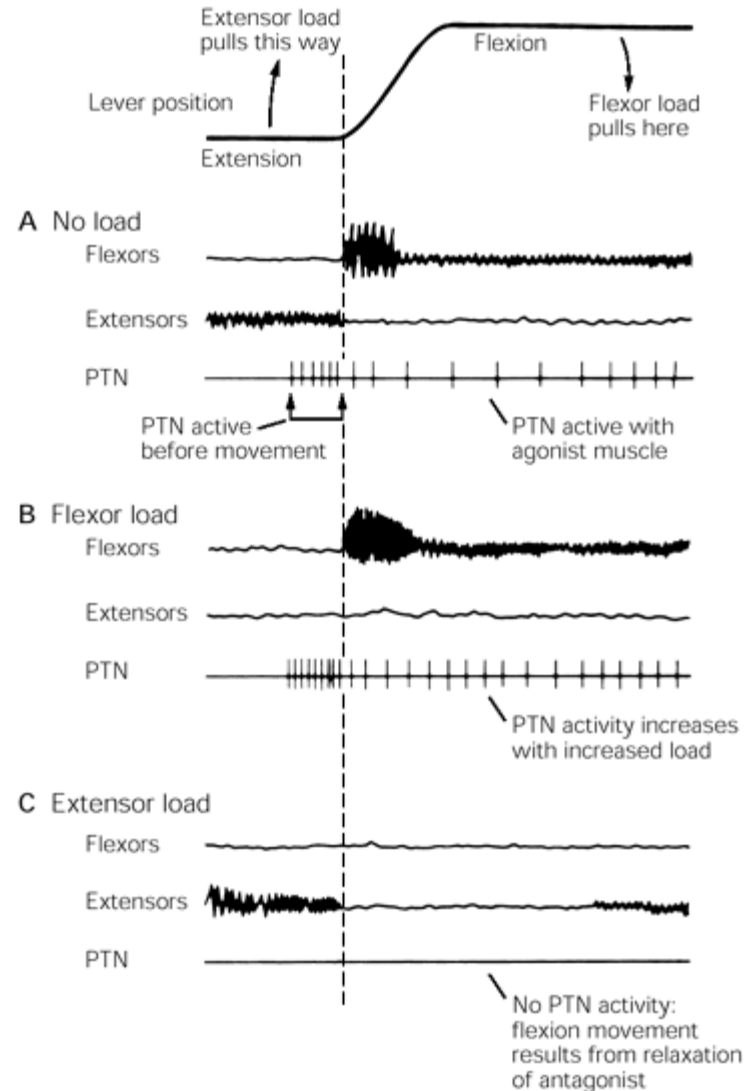
Coding of force in M1

Evarts, 68

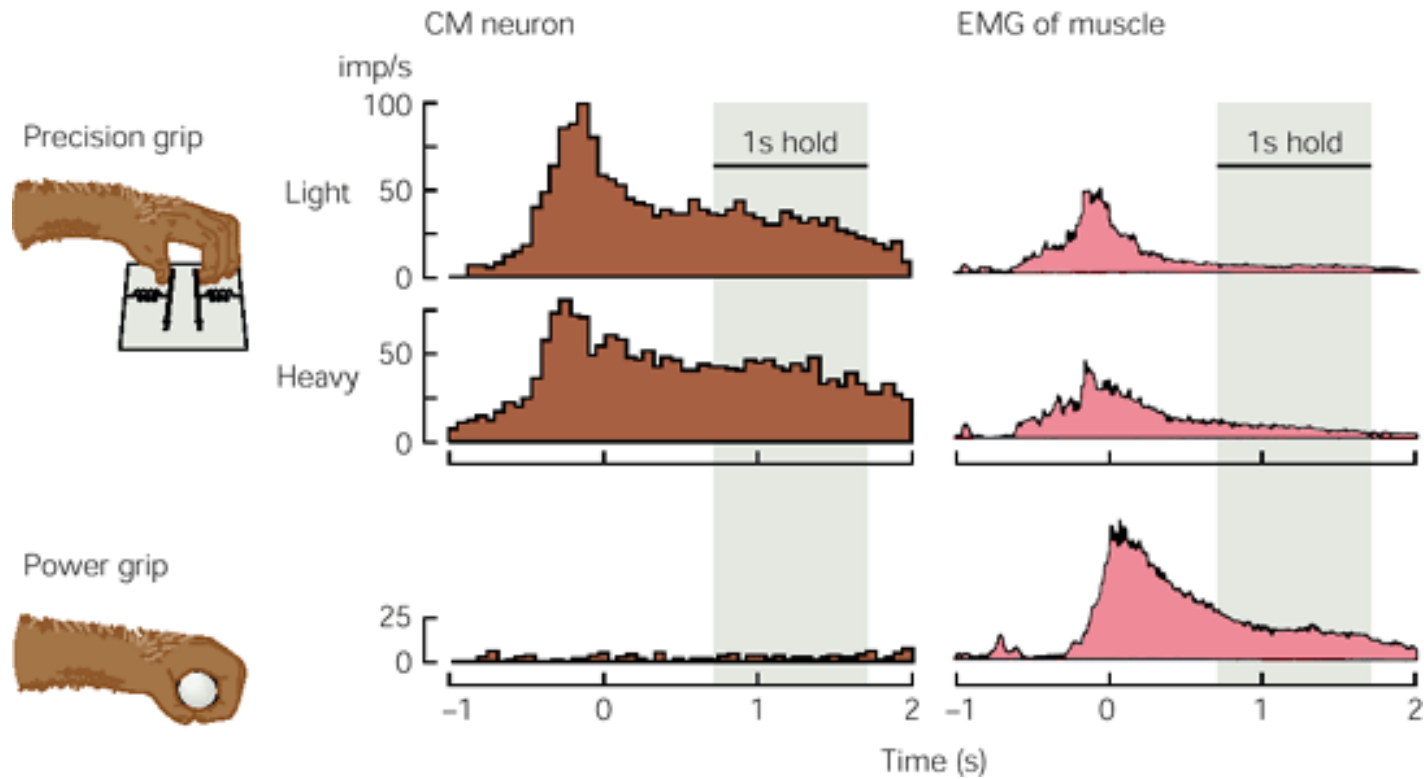
Experimental setup



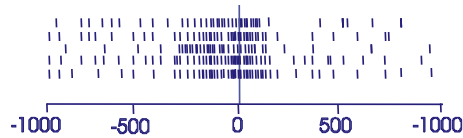
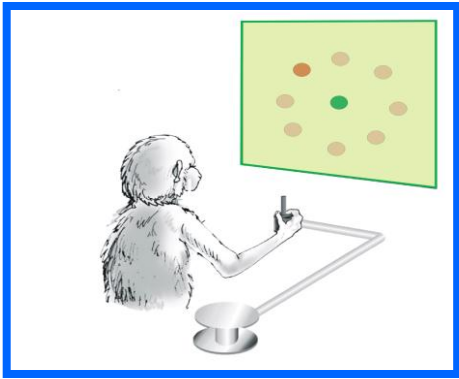
Records of behavior and cell activity



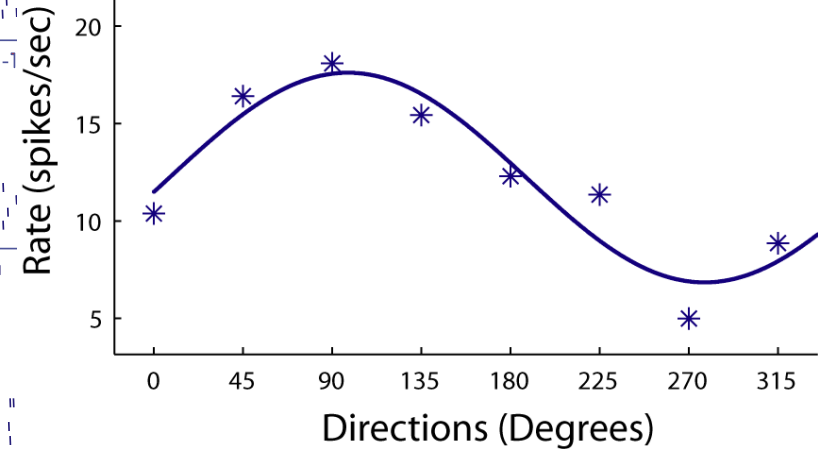
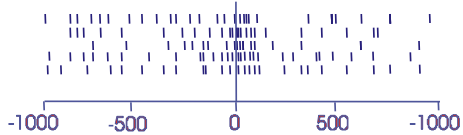
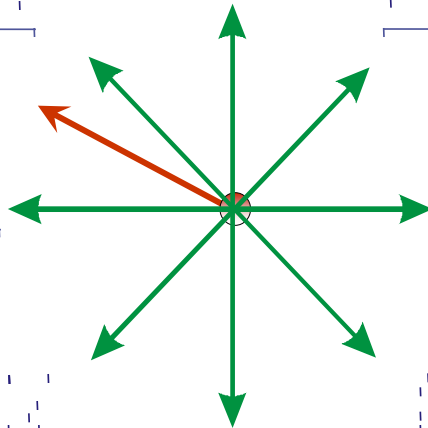
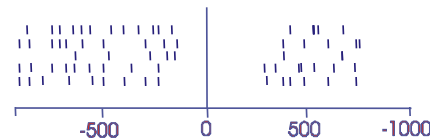
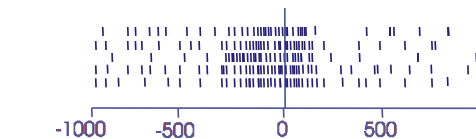
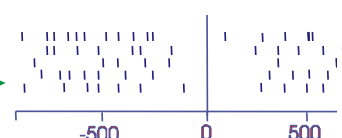
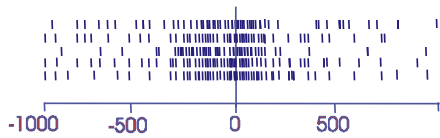
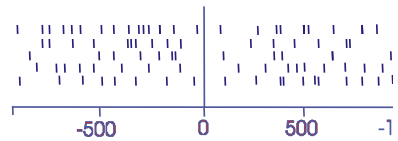
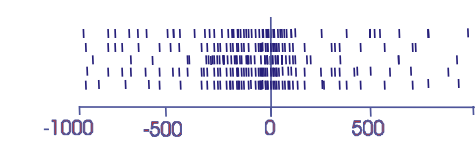
Neurons can be context-dependent



Coding of external direction



$$f r_i(\overline{MD}) \approx b_i + k_i \cos(\theta_i - \theta_{MD})$$



Georgopoulos 1982

Kinematics vs. dynamics

Extrinsic variables (end-point velocity/ position):

- Relative to torso

- Relative to eye

- Relative to shoulder

Intrinsic coordinates:

- Muscles shortening velocity

- Muscles tension

Joints' velocity, torque, power.

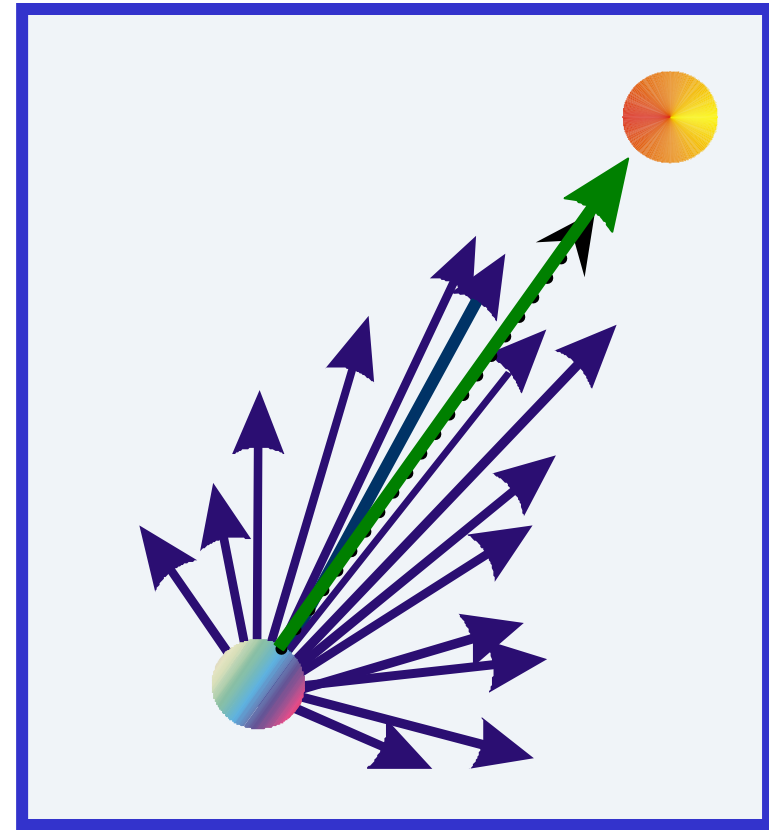
The population vector

If:

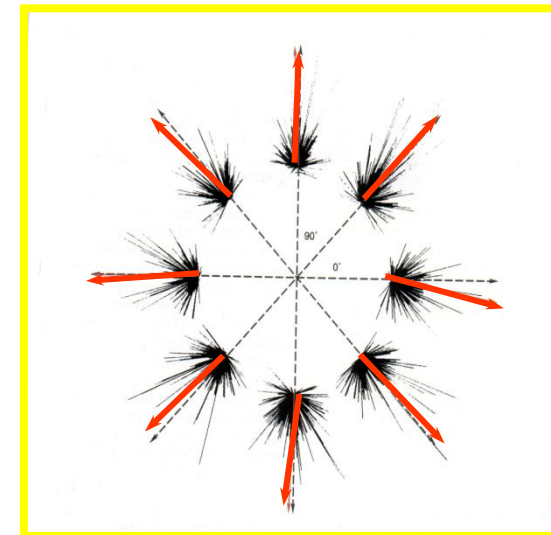
- Many cells “care” about direction of movement
- Cells are tuned “cosine like” with a preferred direction
- Preferred directions are uniformly distributed

Then:

The actual movement can be estimated in Cartesian coordinates by a linear combination of weighting the preferred directions with the actual firing rate

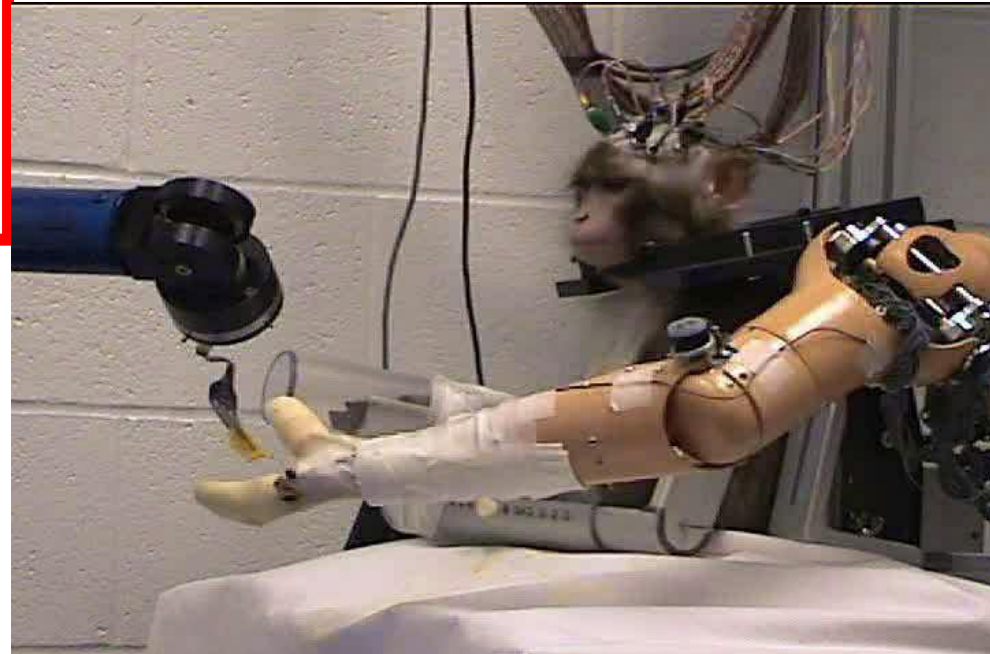
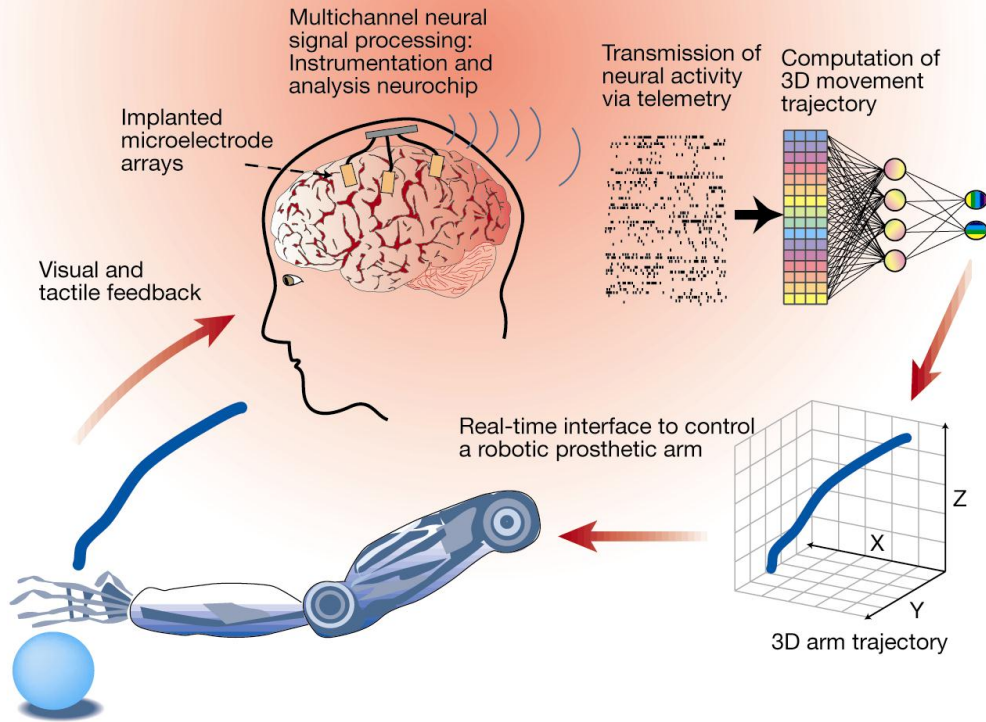


$$\overline{MD} \approx PV = \sum_{i=1}^N w_i \overline{C}_i$$



What can we do with it? Neural prostheses

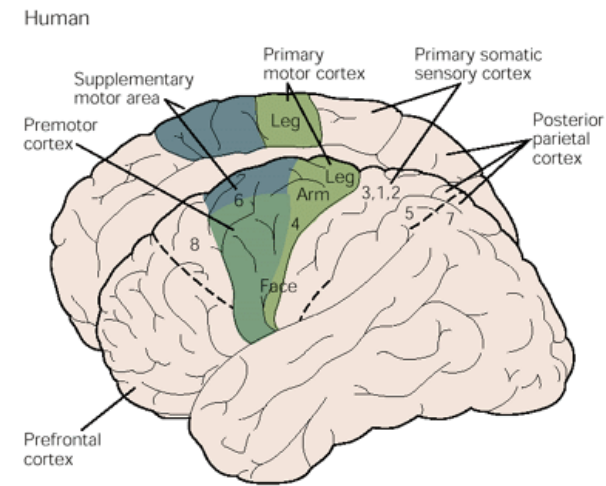
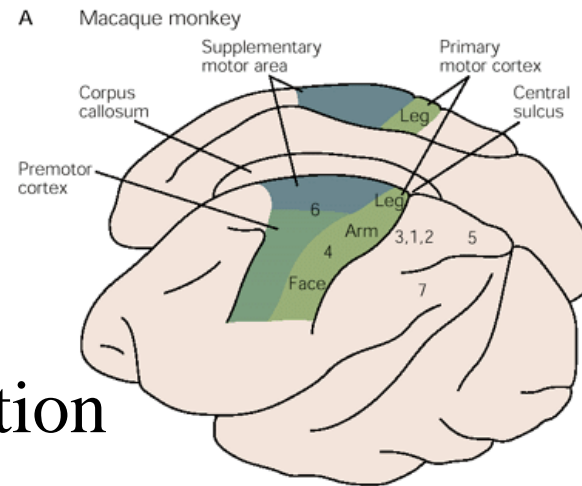
b



Schwartz AB

Premotor areas

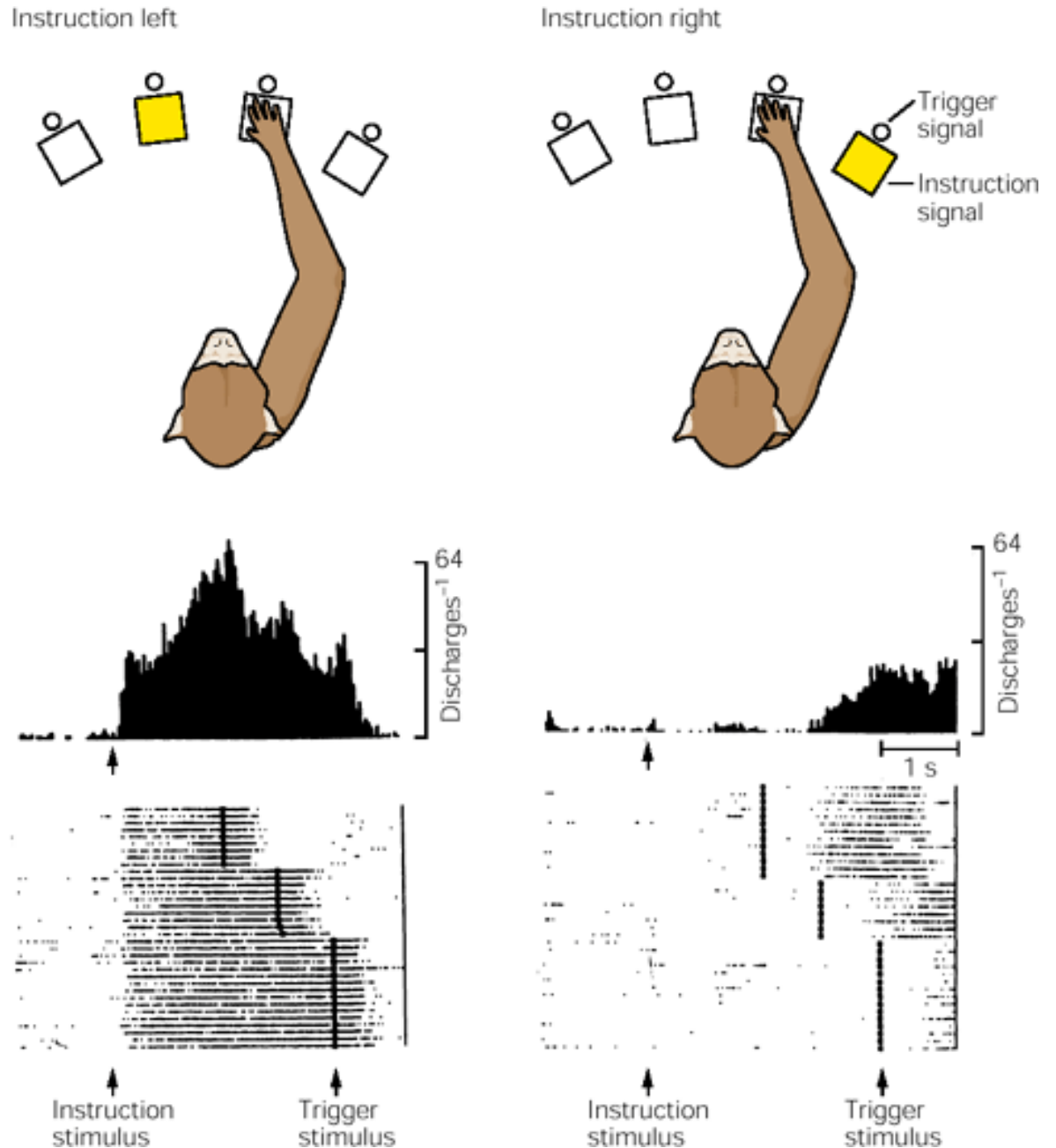
Premotor dorsal (PMd), premotor ventral (PMv), supplementary motor area (SMA), cingulate (CMA)



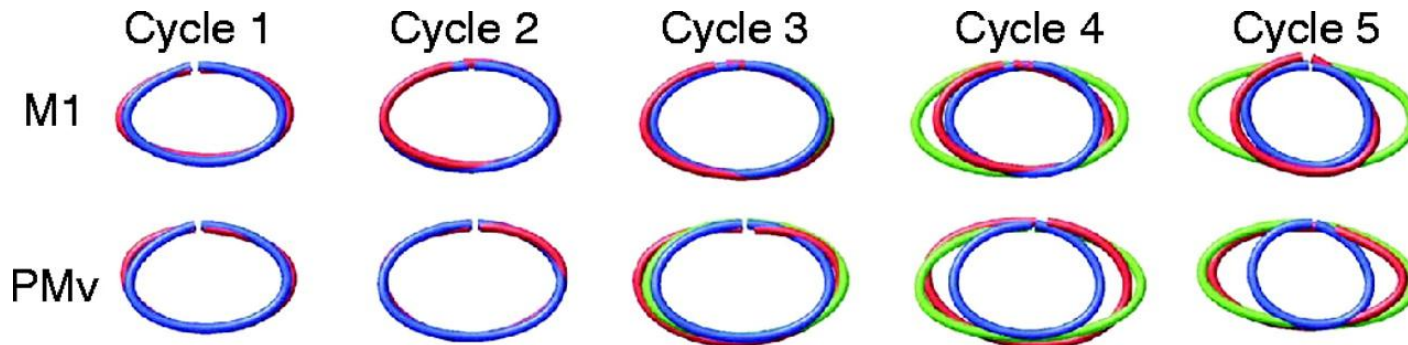
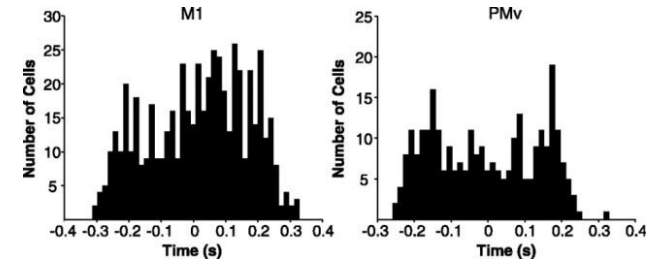
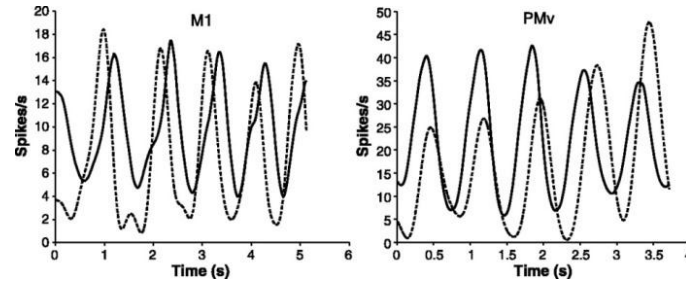
- Multi-joint representation
- Complex, meaningful
- Sensorimotor transformations
- Preparatory (set) activity
- Bimanual coordination (SMA)
- Sequence learning (SMA)
- Self-initiation (PMv, SMA) vs. cue-driven (PMd)
- Language, theory of mind

Preparatory (set)

neurons are active
before the movement

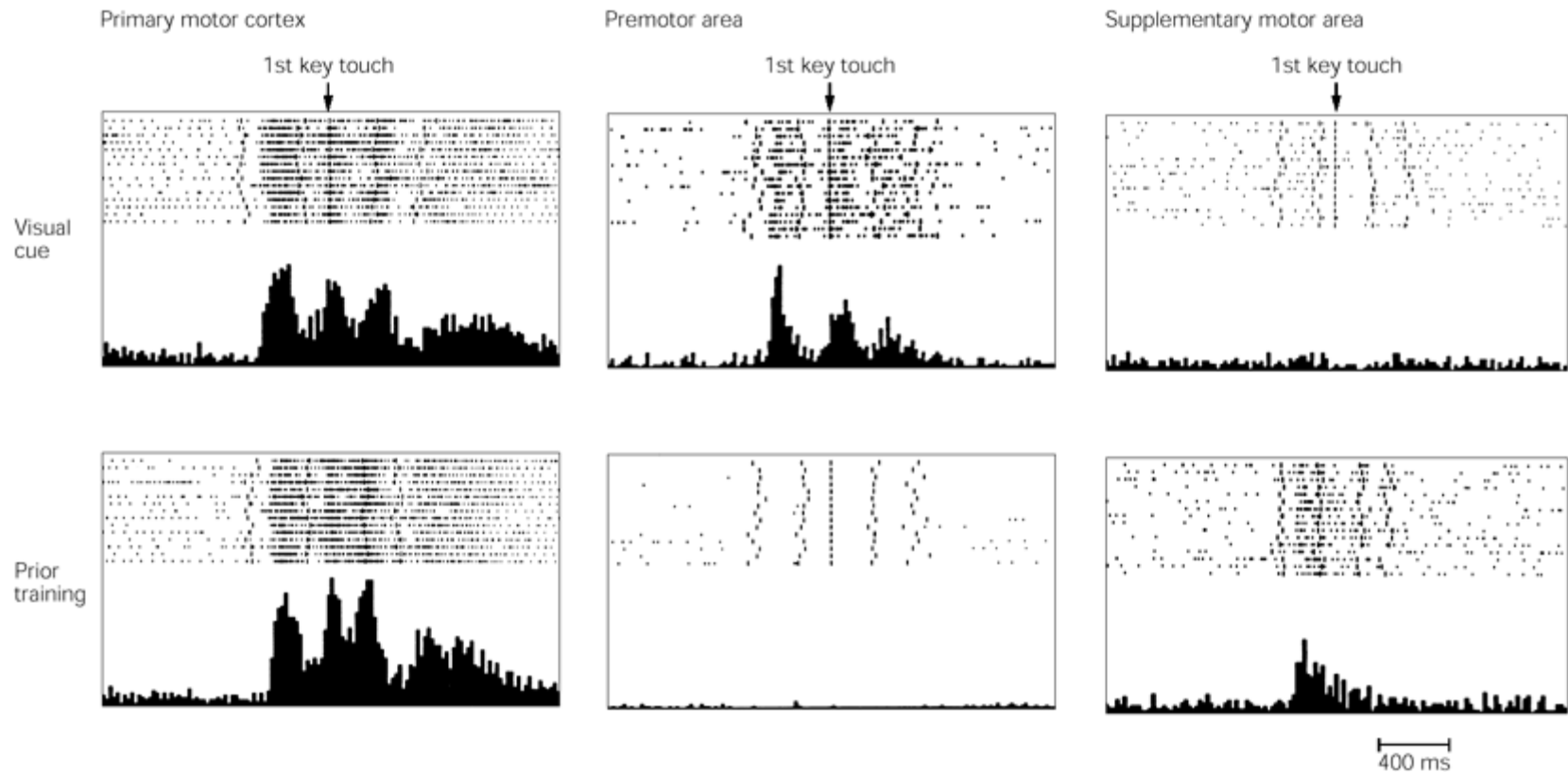


Representation of plan and execution

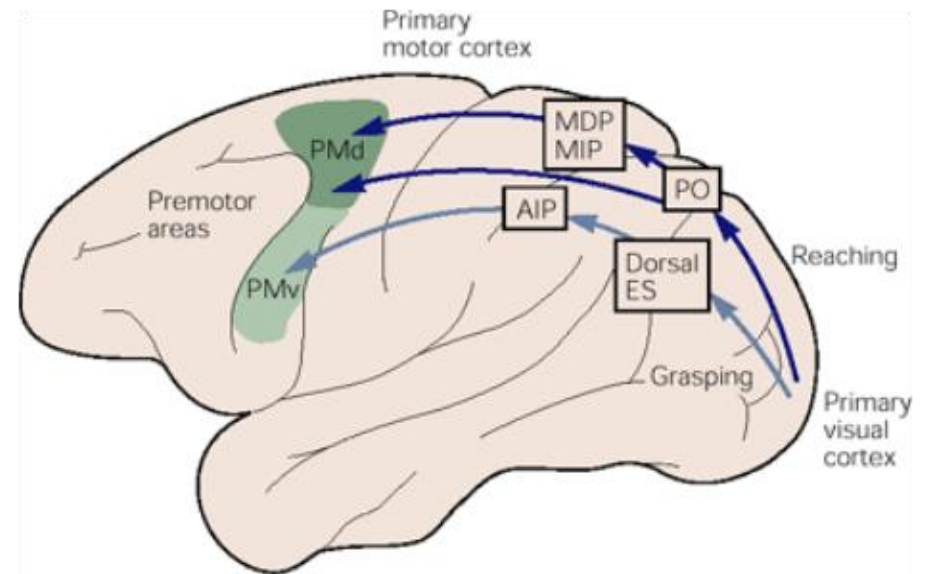
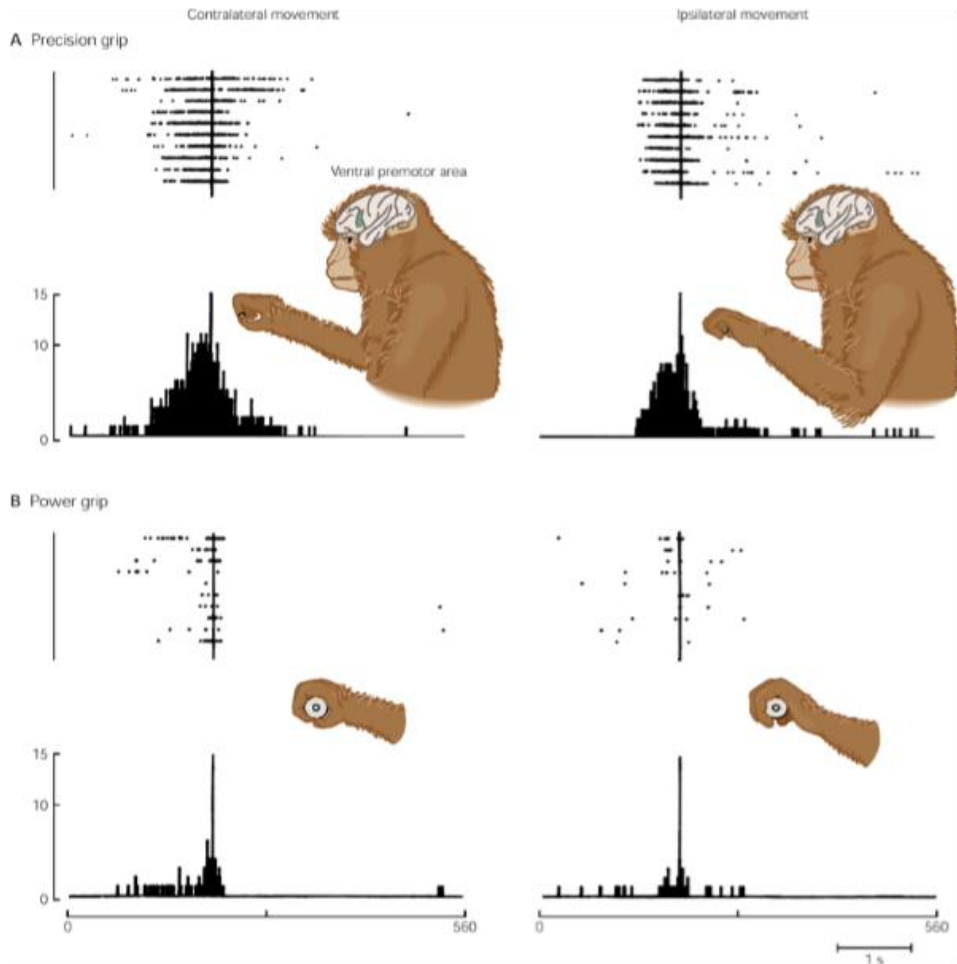


Illusion task trajectories. Top row is five cycles from M1 units. Bottom row is from the PMv. The hand trajectory is blue, cursor trajectory is green, and neural trajectory is red. Each displayed trajectory is the mean across five repetitions

Cue-driven vs. self-initiated

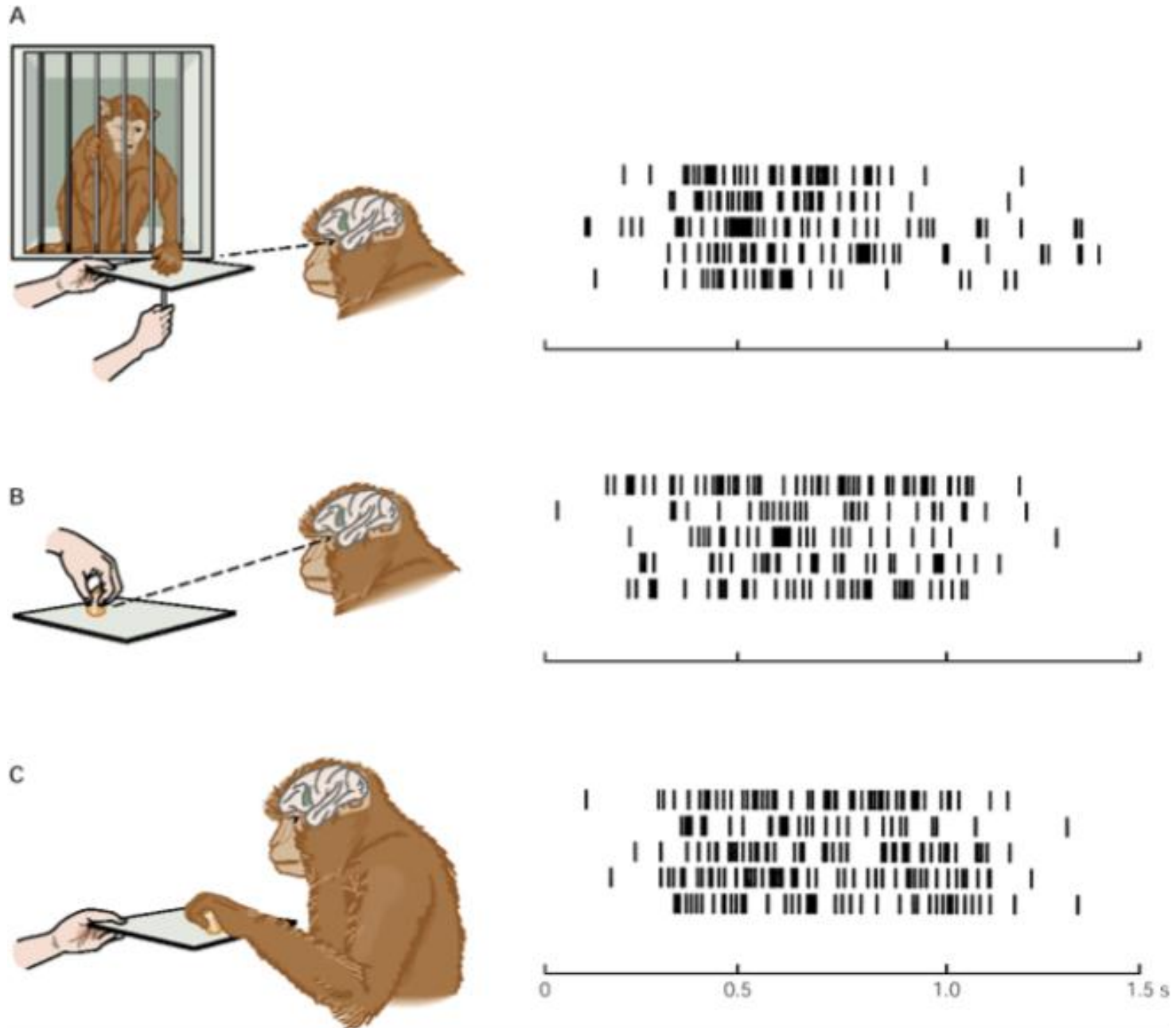


Prehension: reaching and grasping

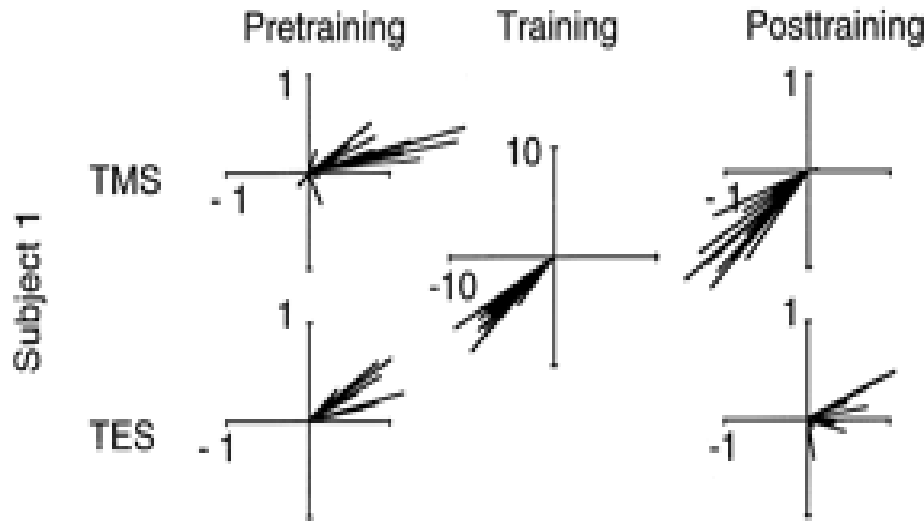
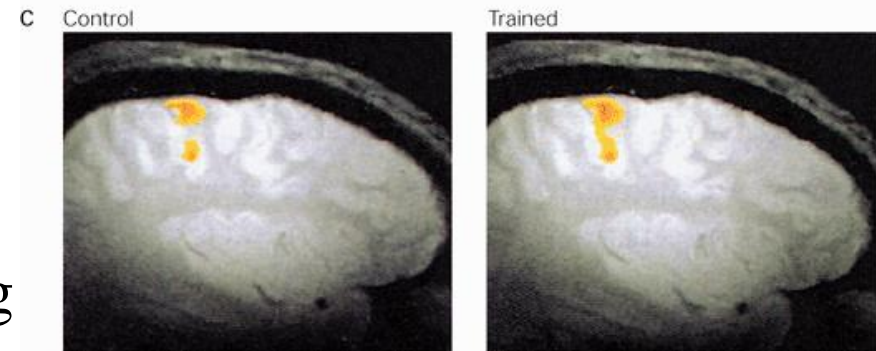
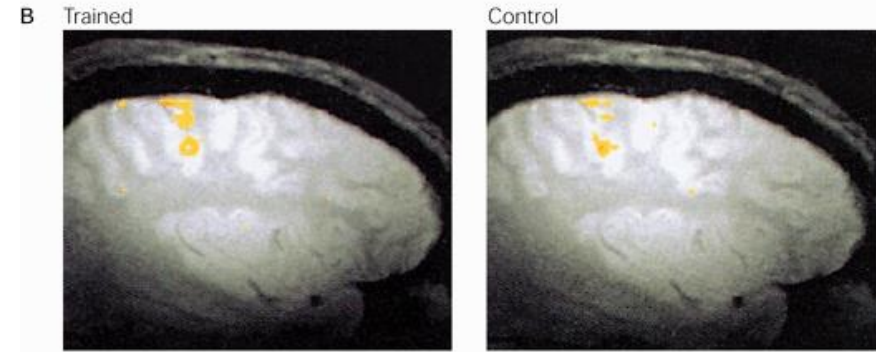
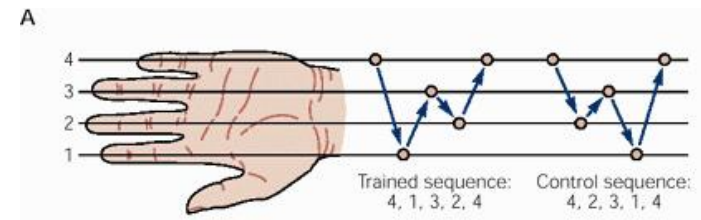


Neurons are context-specific (fire for a specific movement)

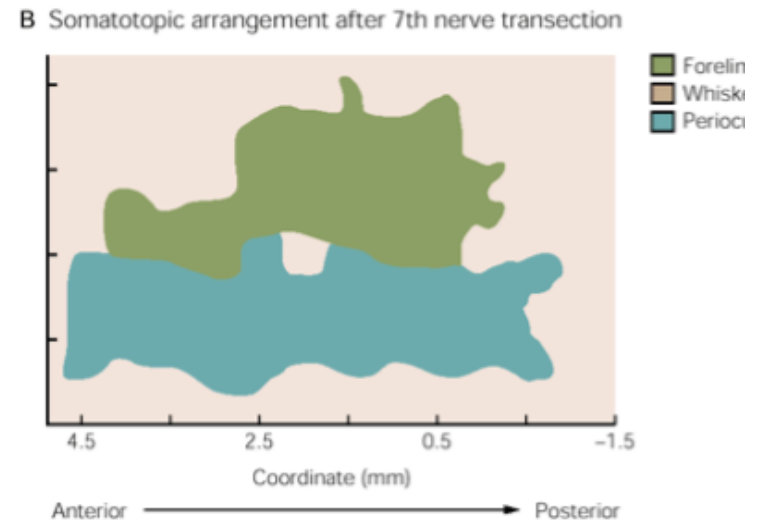
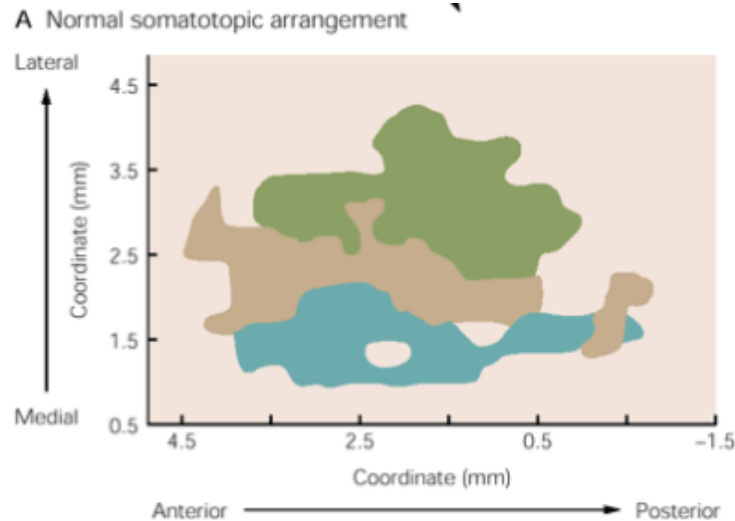
Mirror neurons



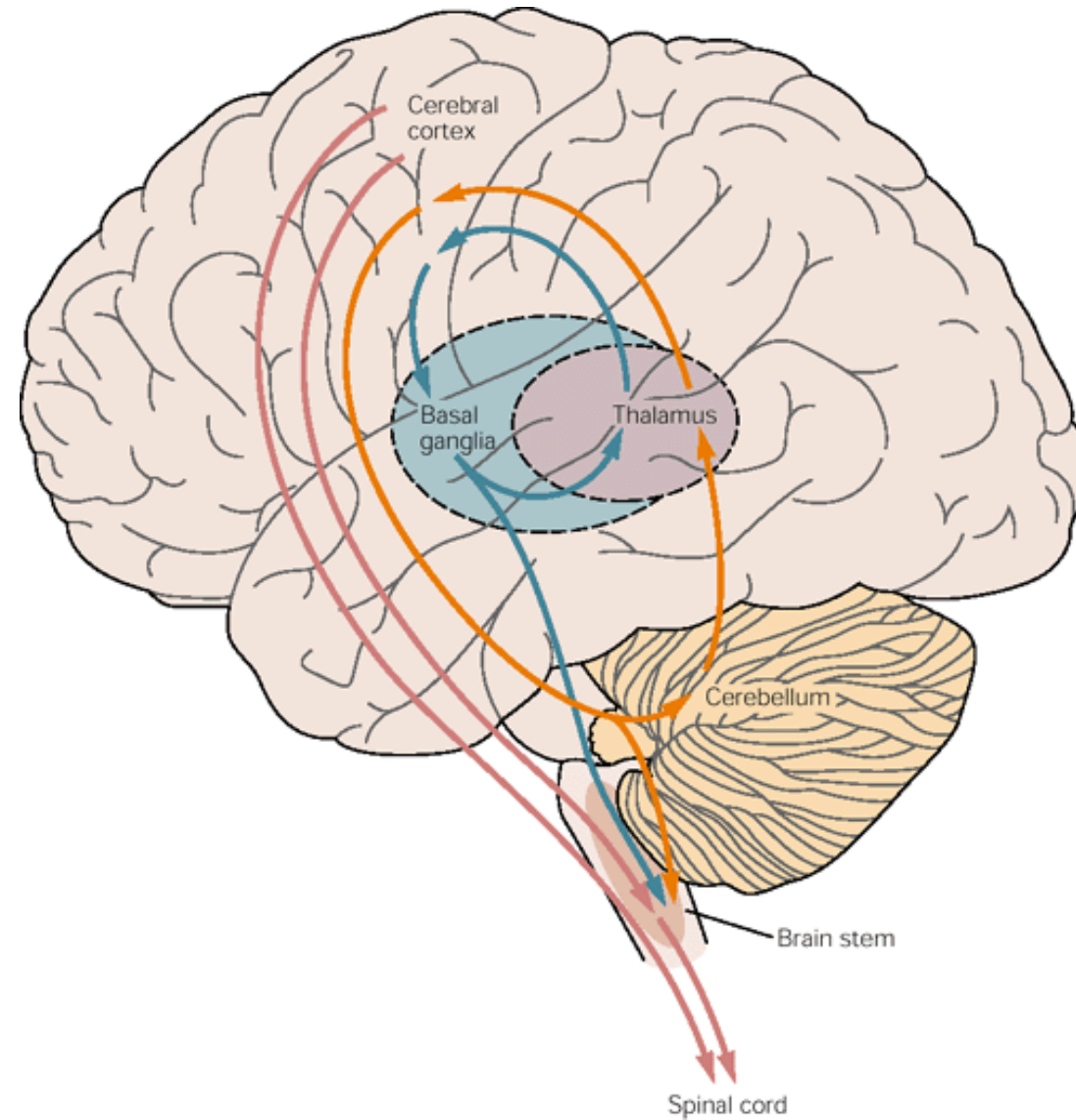
Learning and Plasticity

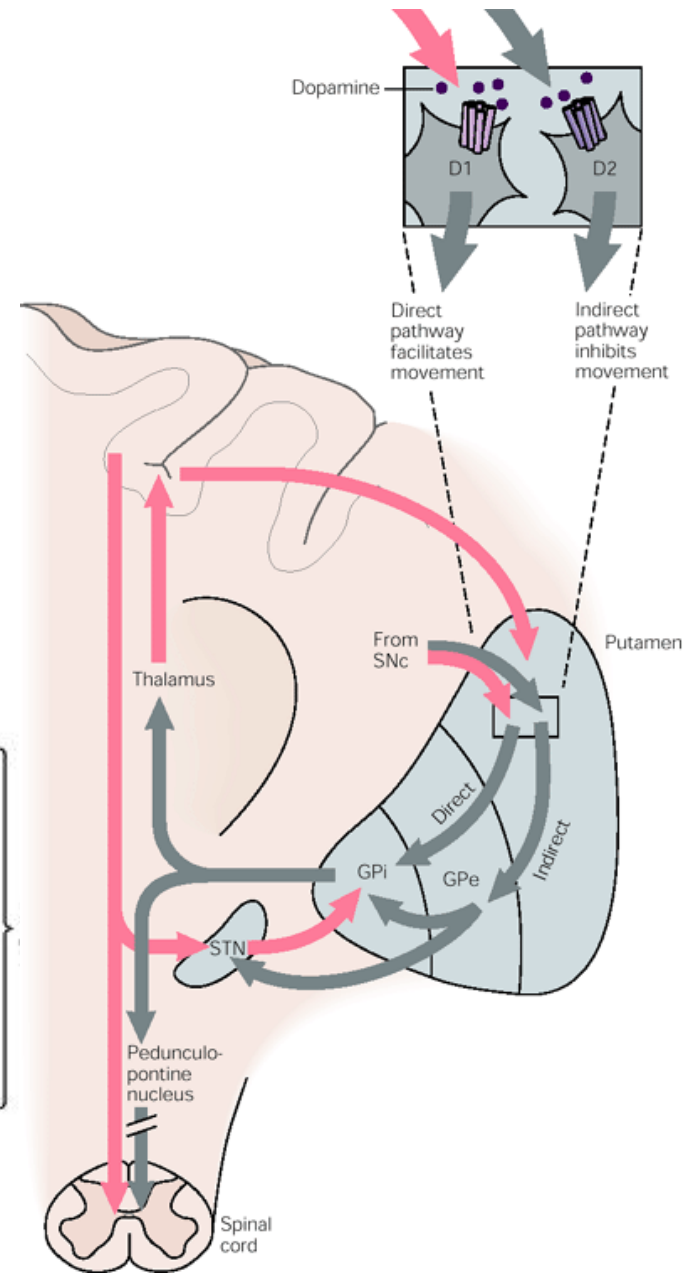
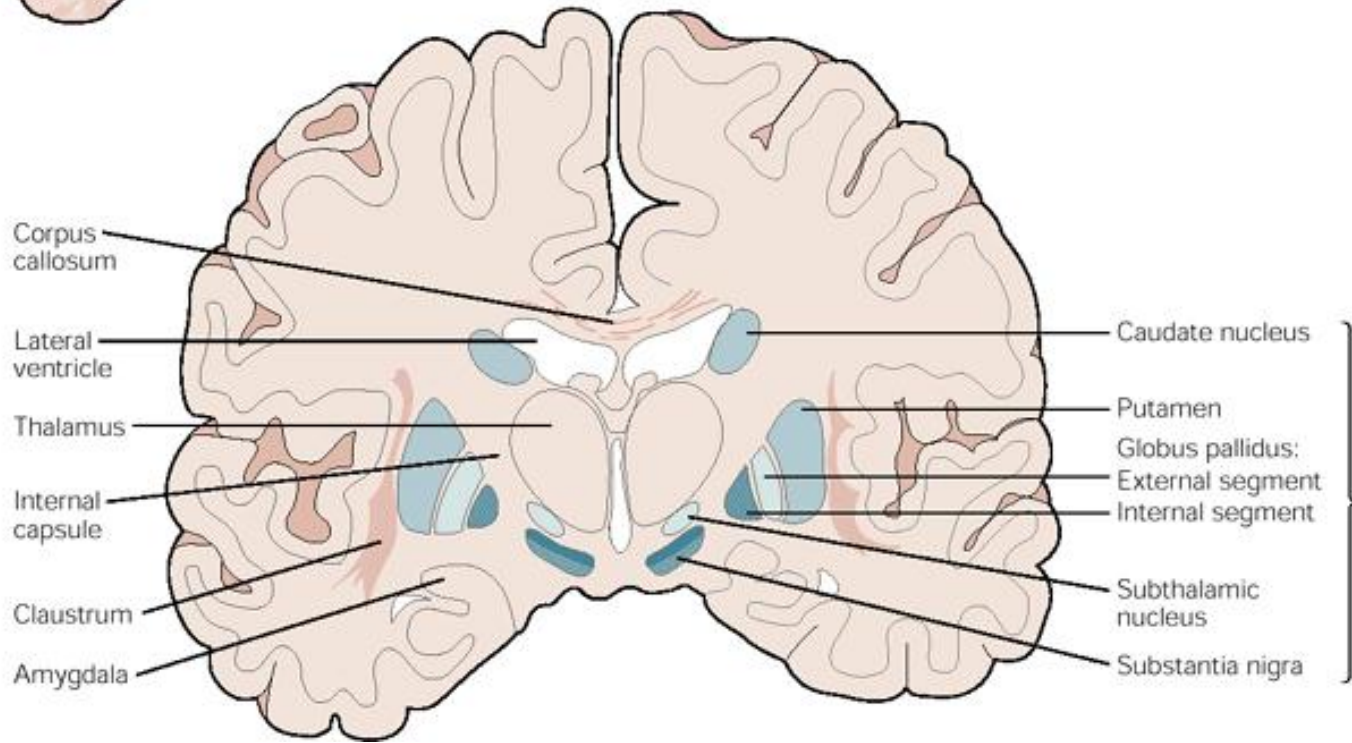
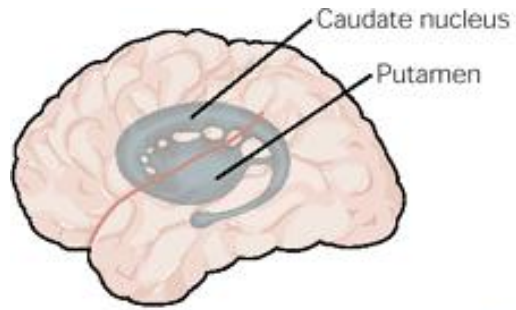


Maps: by lesions and skill learning

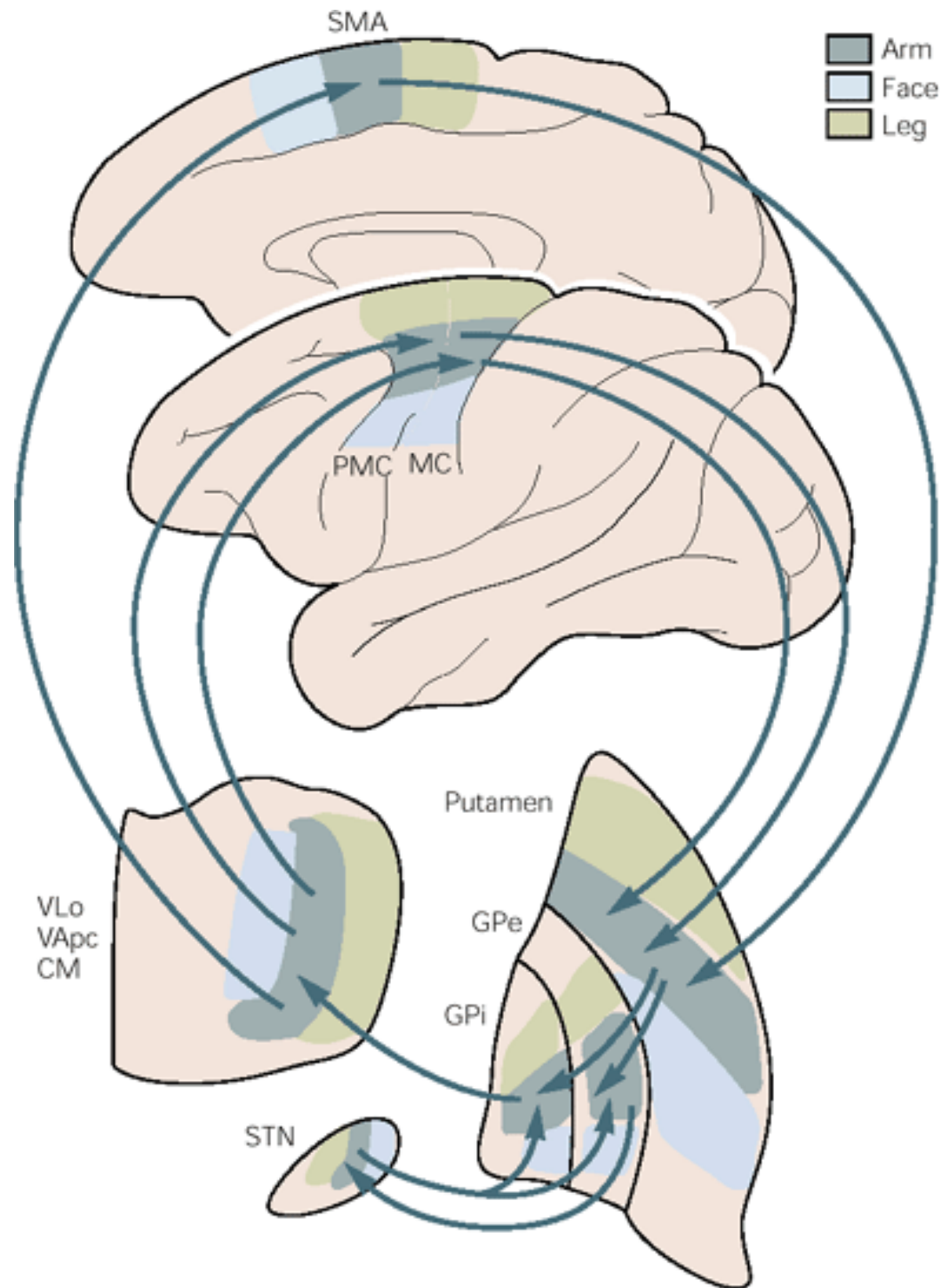


The basal Ganglia



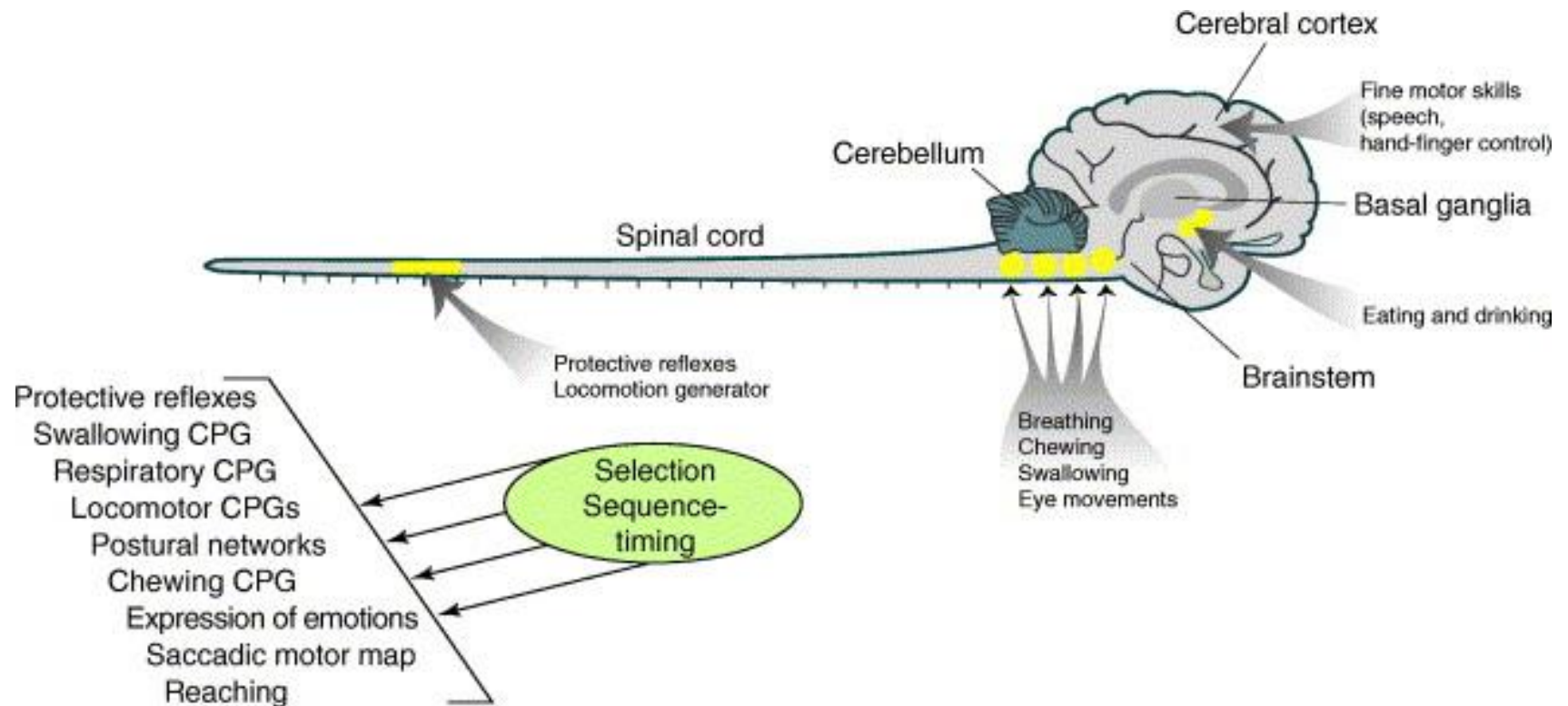


Cortico loops



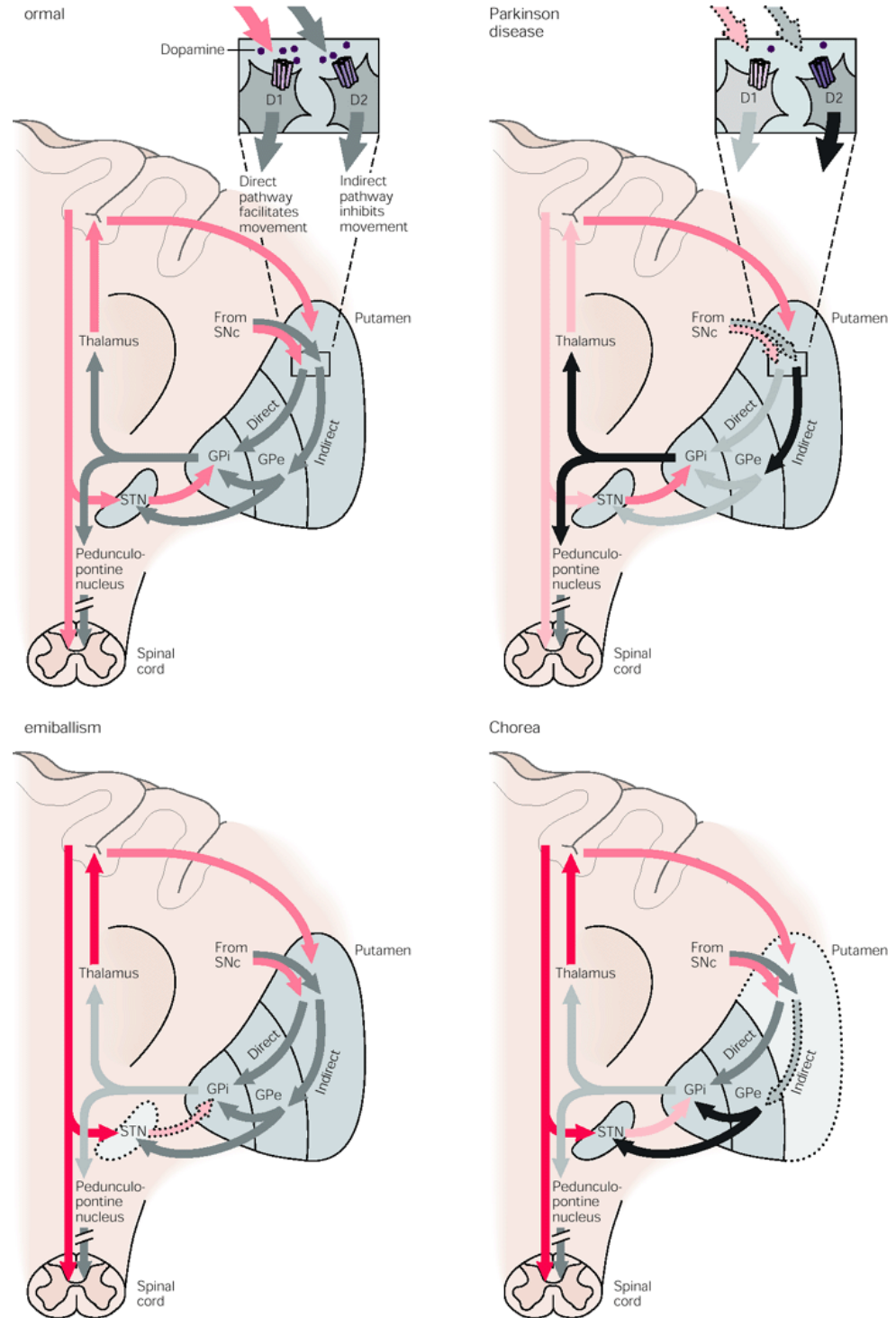
Action - Selection

Direct pathway: facilitates movement.
Indirect pathway: inhibits movement.



Parkinson and Dopamine

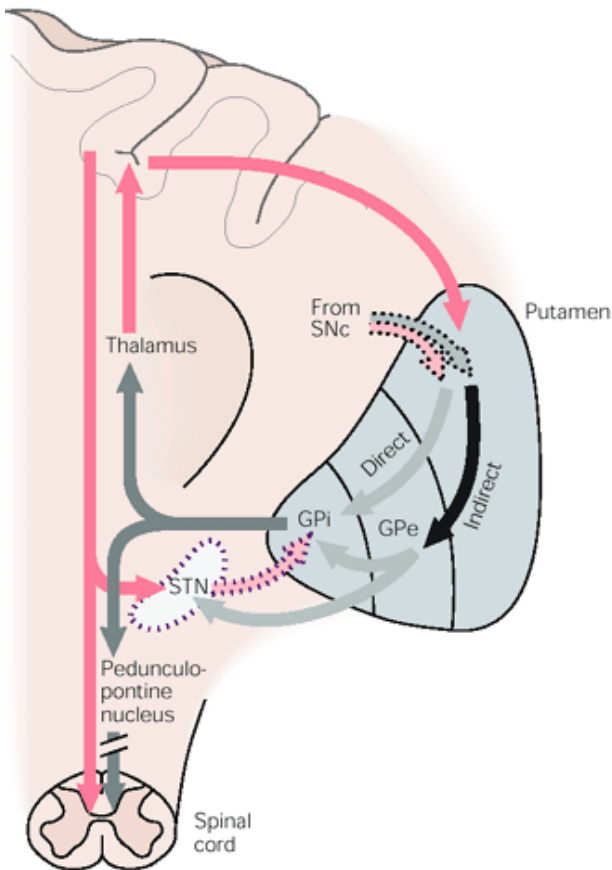
Loss of dopaminergic input leads to increase in the indirect and decrease in the direct pathway => increase GPI => inhibition =? Hypokinesia



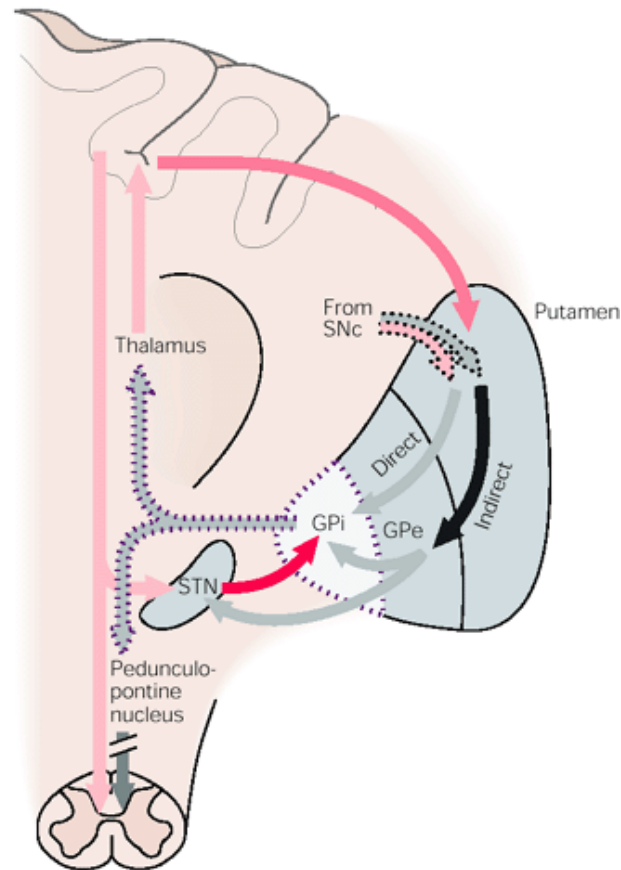
Treatment: pallidotomy or DBS

Parkinson disease + surgical therapies

TN lesion

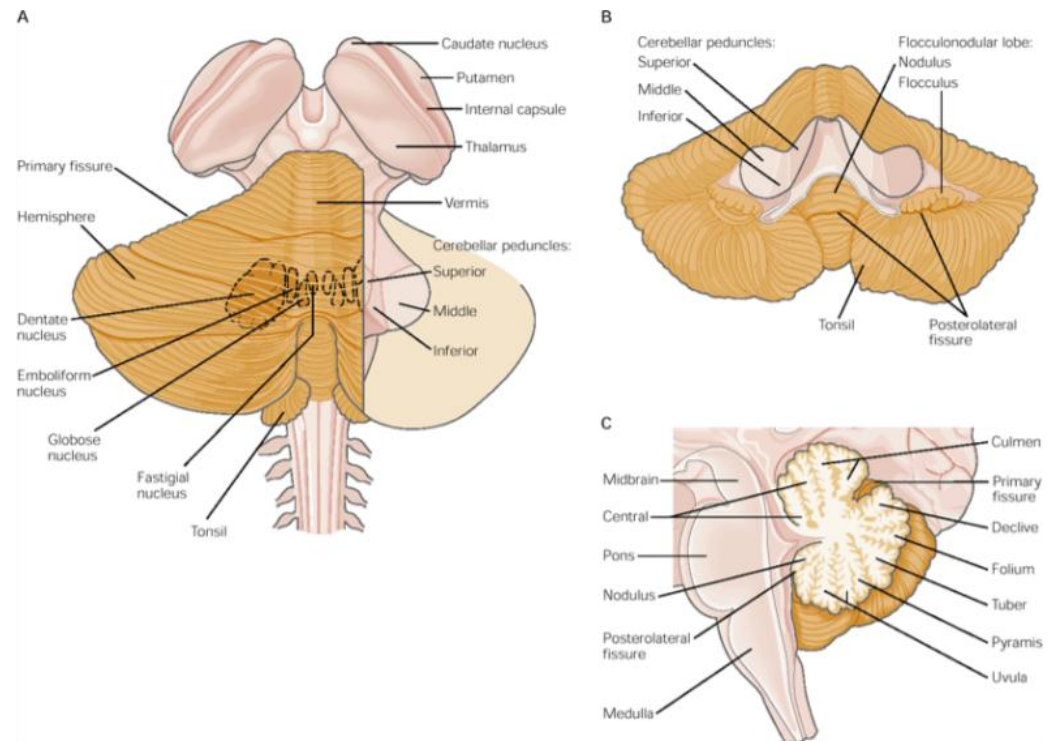


GPI lesion



The cerebellum

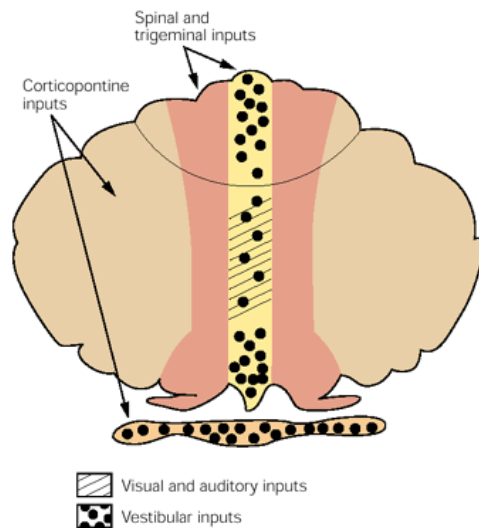
- 10% of volume, >50% of neurons
- High regularity – a basic circuit module, but with different inputs and outputs
- Lesions result in damage of spatial accuracy and temporal coordination of movement



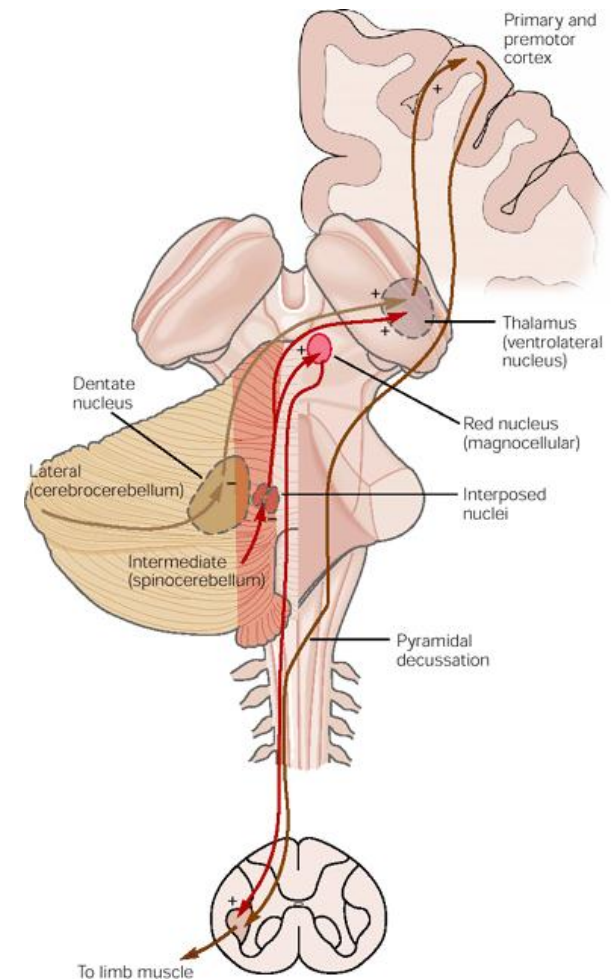
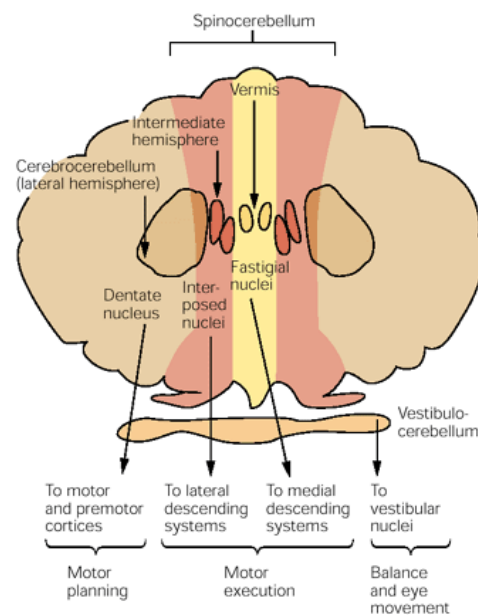
Error correction

- Evaluating disparities between action and intention (as perceived from sensory information).

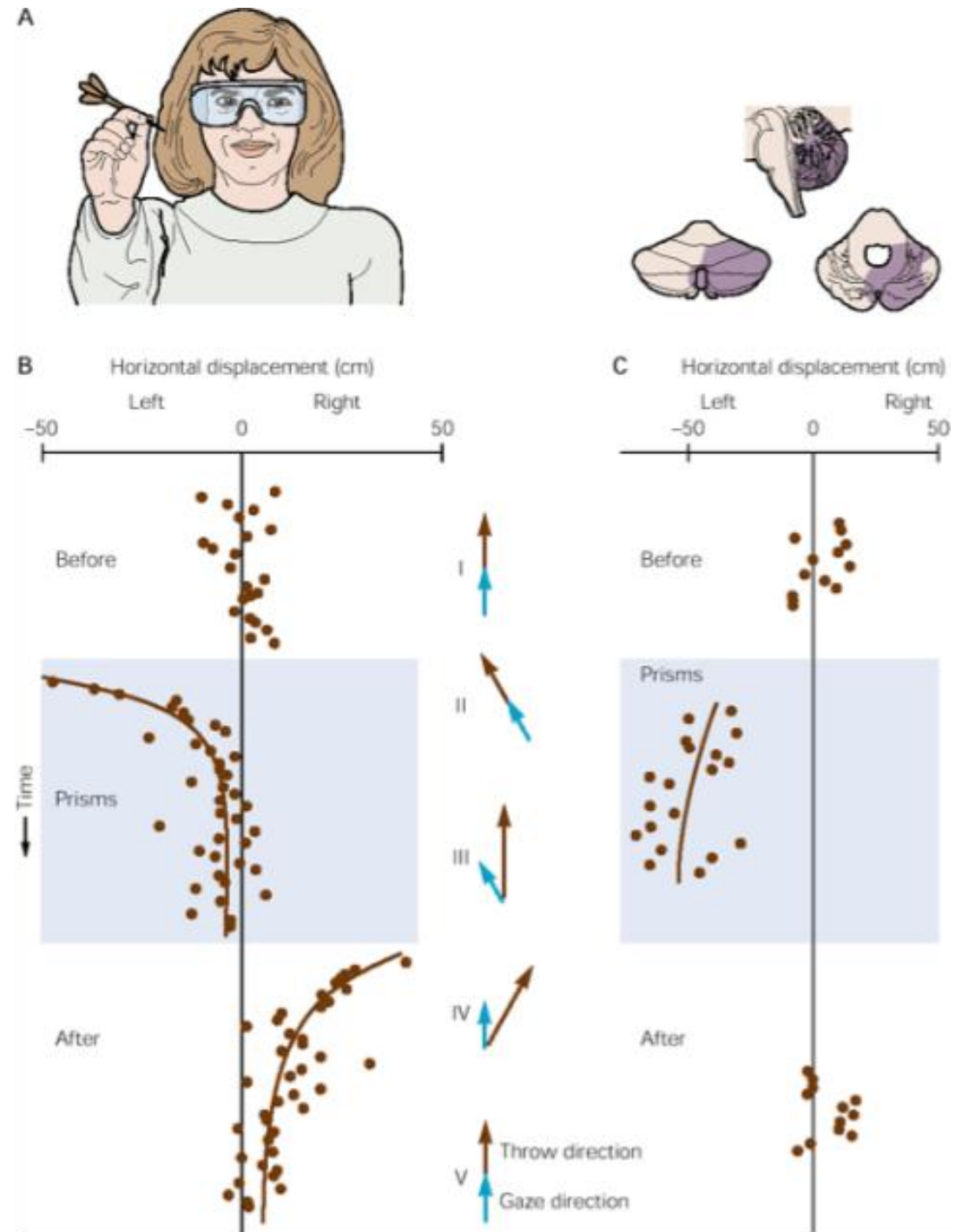
A Inputs



B Outputs



Adaptation and motor learning via sensory feedback



Coordination and timing

- **Timing:** the ability to produce consistent intervals between movements based on an internal representation of time.
- **Coordination:** motor commands to one effector depend on the predicted state of another effector.

Thanks

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<http://www.weizmann.ac.il/neurobiology/labs/rony/>