

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

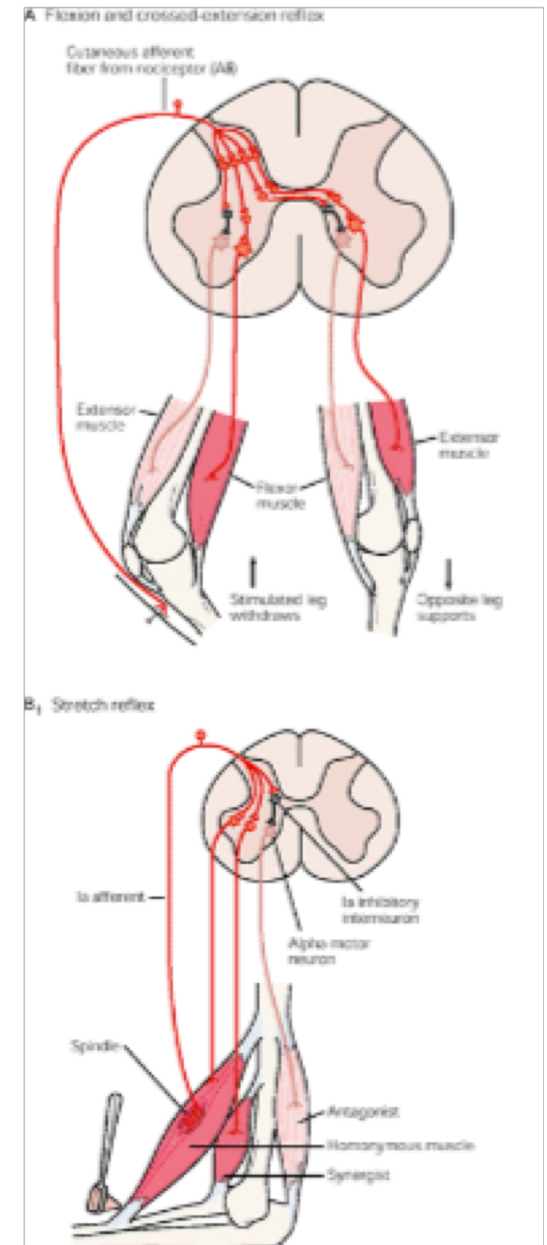
Three main types of movements

- 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

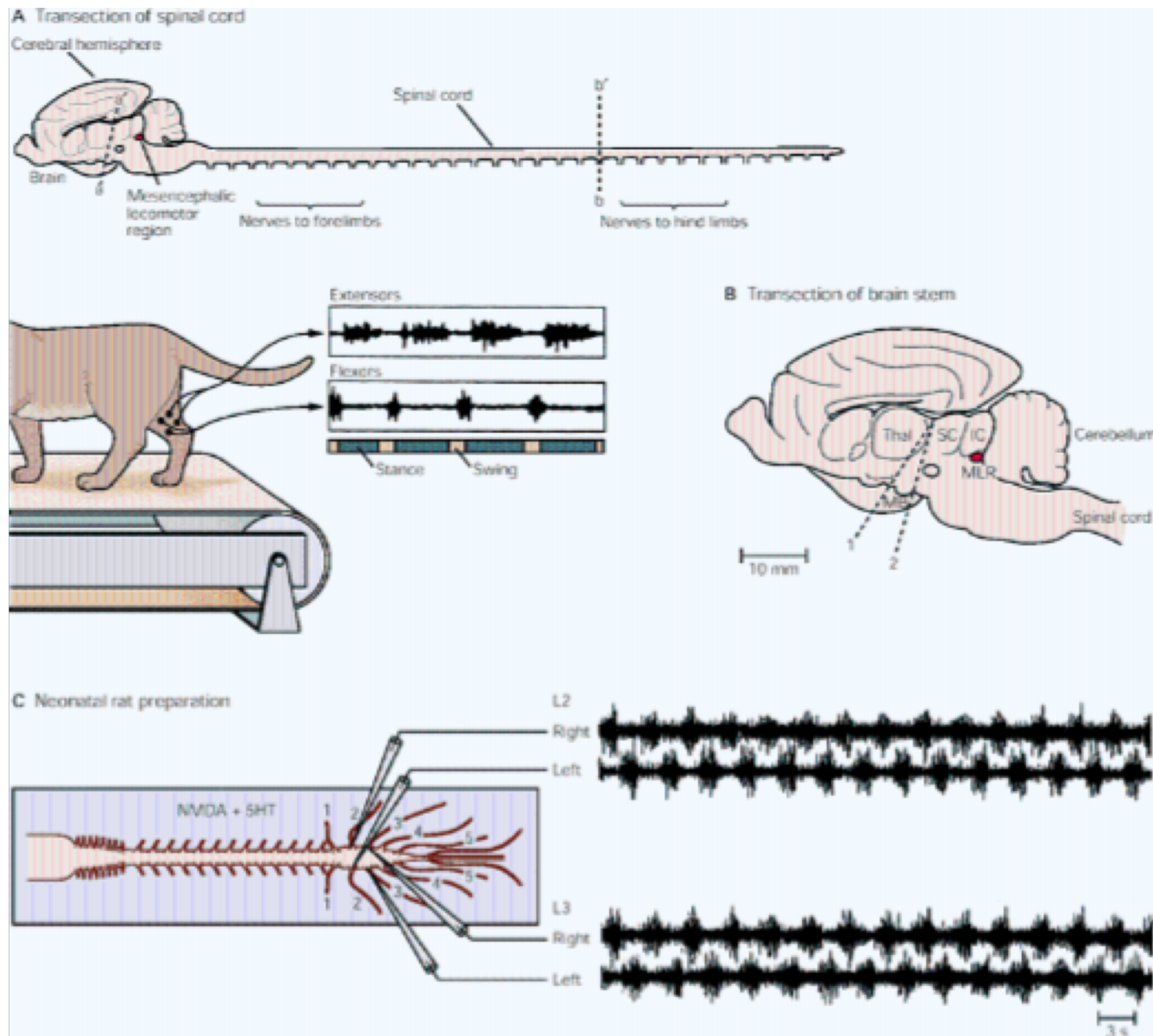
Stretch reflex: contraction of same and synergist and relaxation of antagonist



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

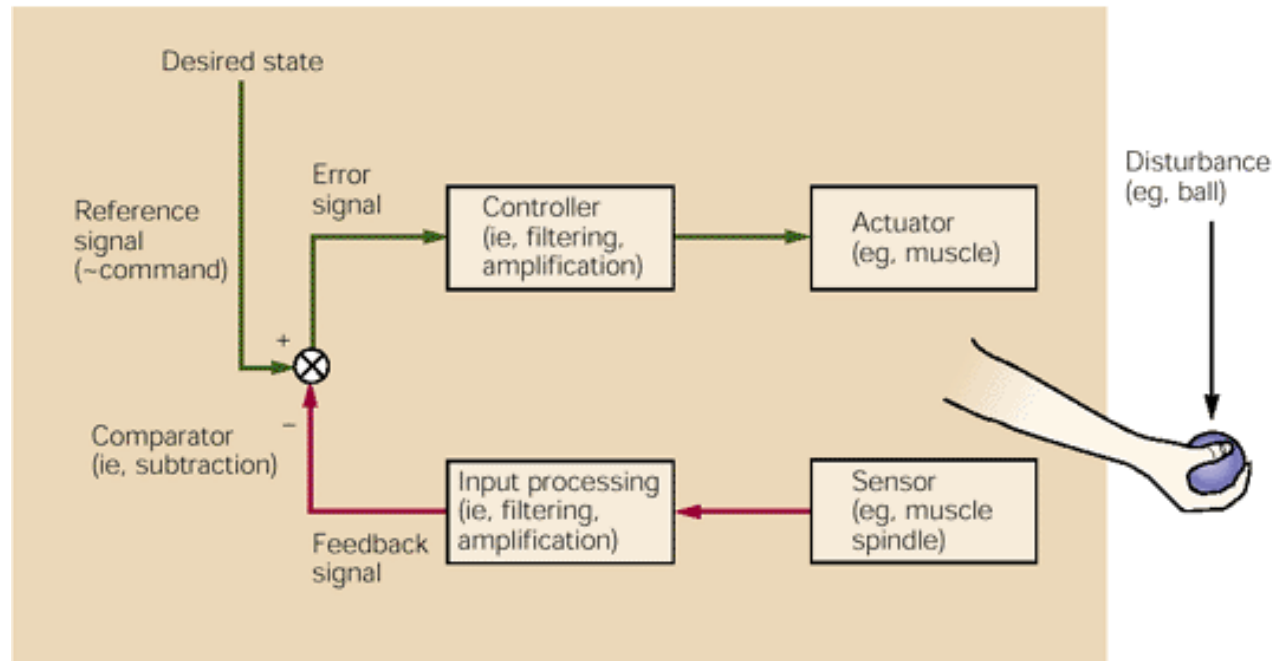
Goal directed

Reaching (~120 ms)



Feedback control (error correction)

A Feedback control: command specifies desired state



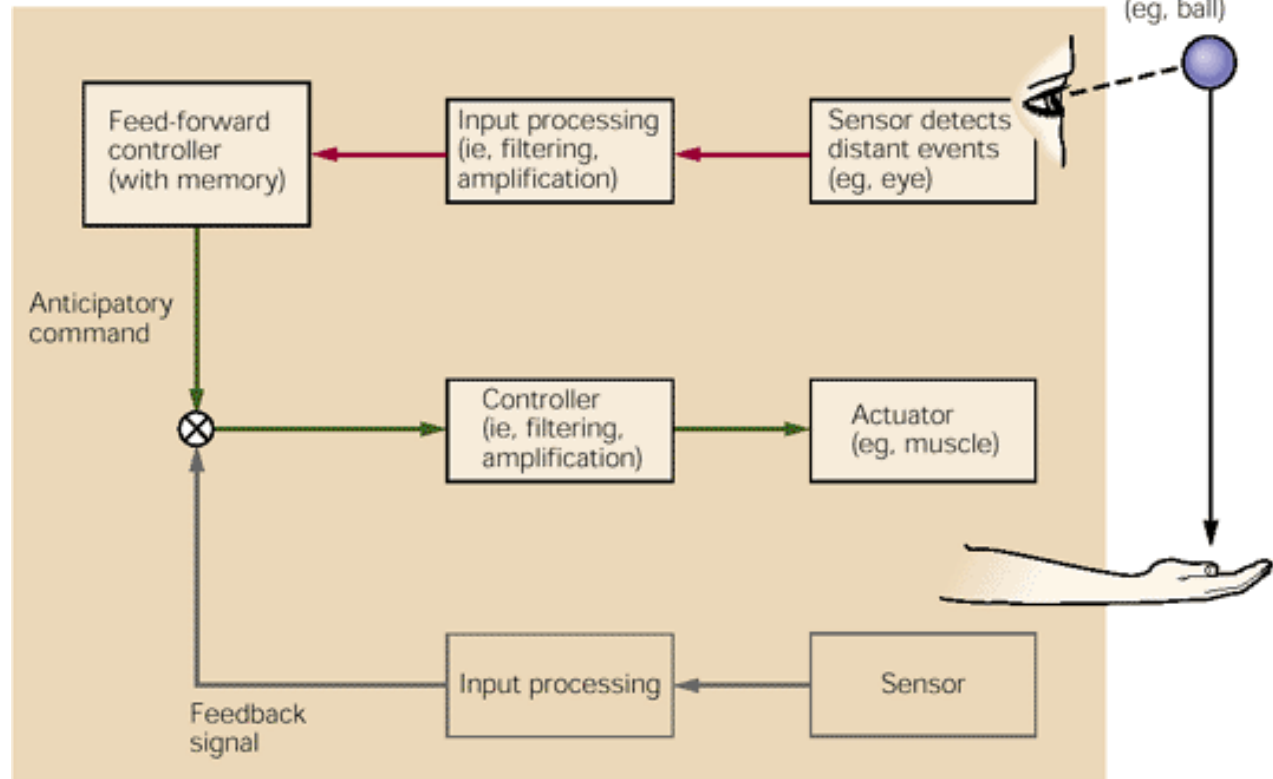
Vision
Proprioception

1. Gain

2. Delay (phase lag)

Feed-forward (open loop)

B Feed-forward control: command specifies response

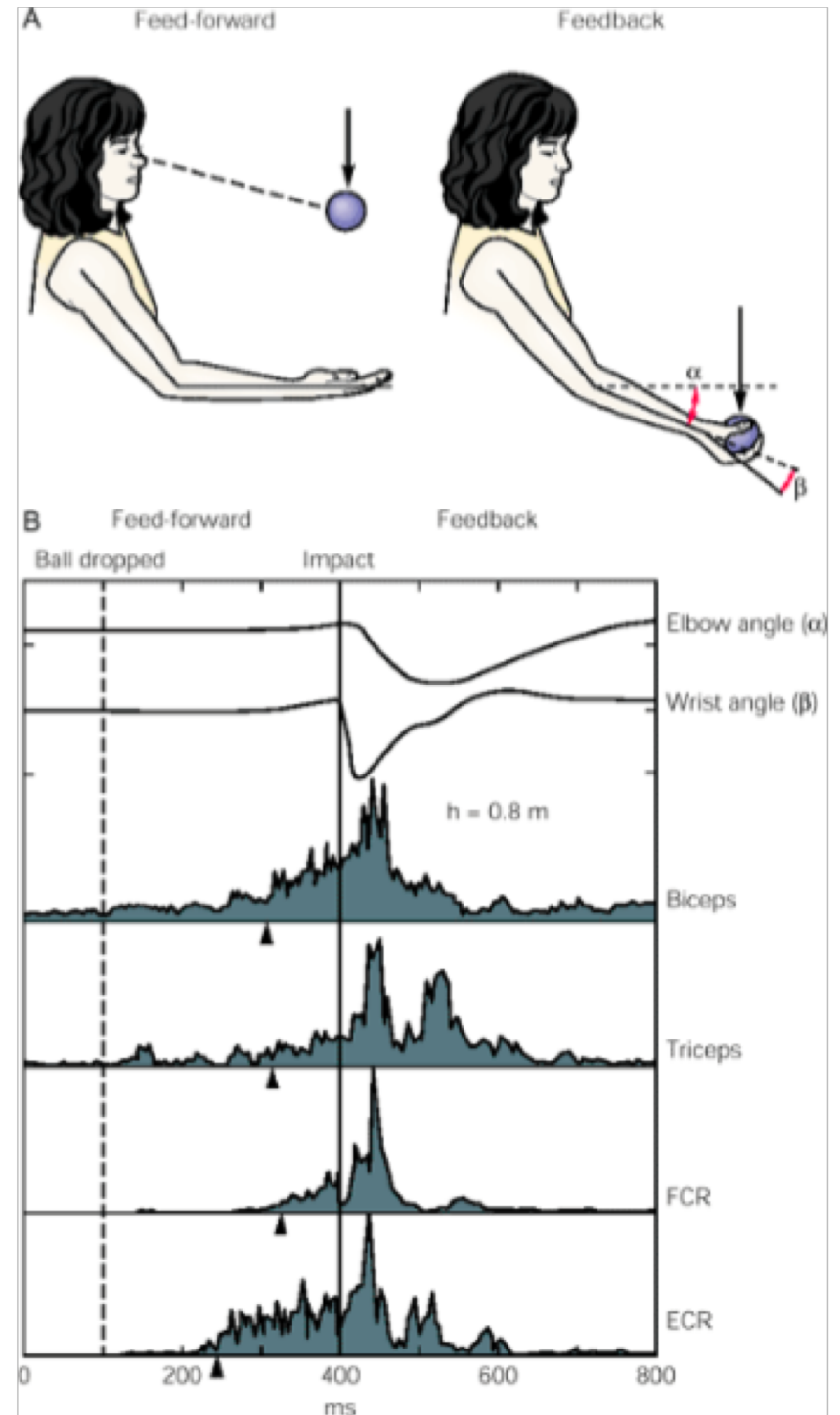


1. Very hard computationally

Feedback control (error correction)

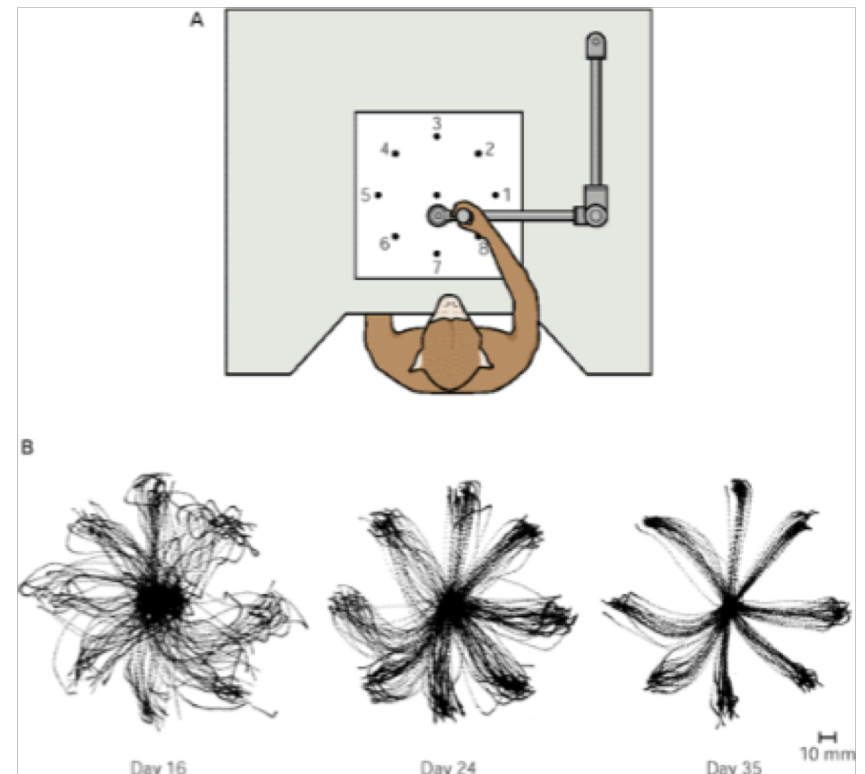
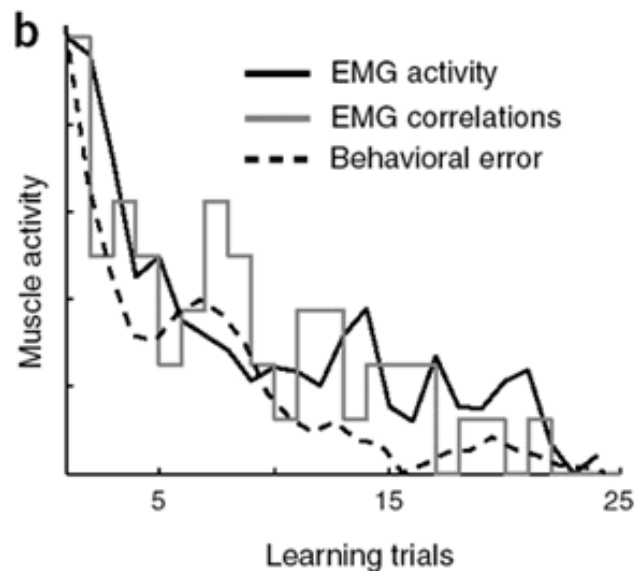
Feedforward (open loop)

Notice onset of muscles



Improve with practice

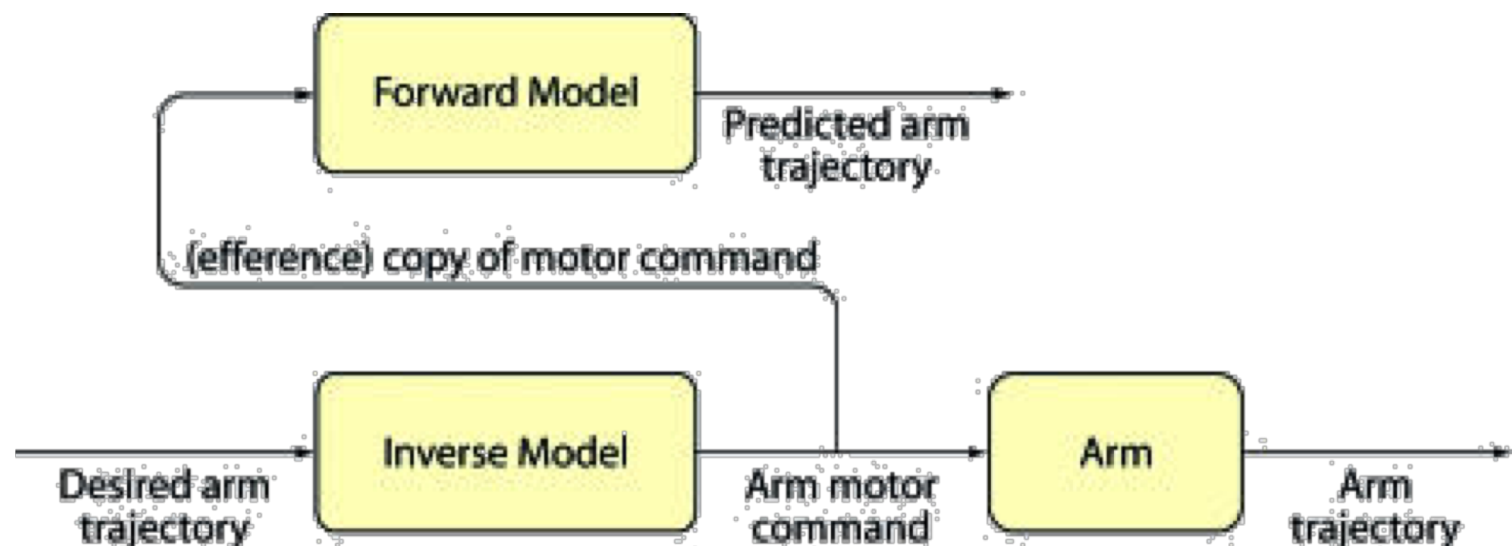
- Co-contraction of muscles
- **Internal models:** a neural representation of the relationship between the hand and the environment (how the arm would respond to the neural command).



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)

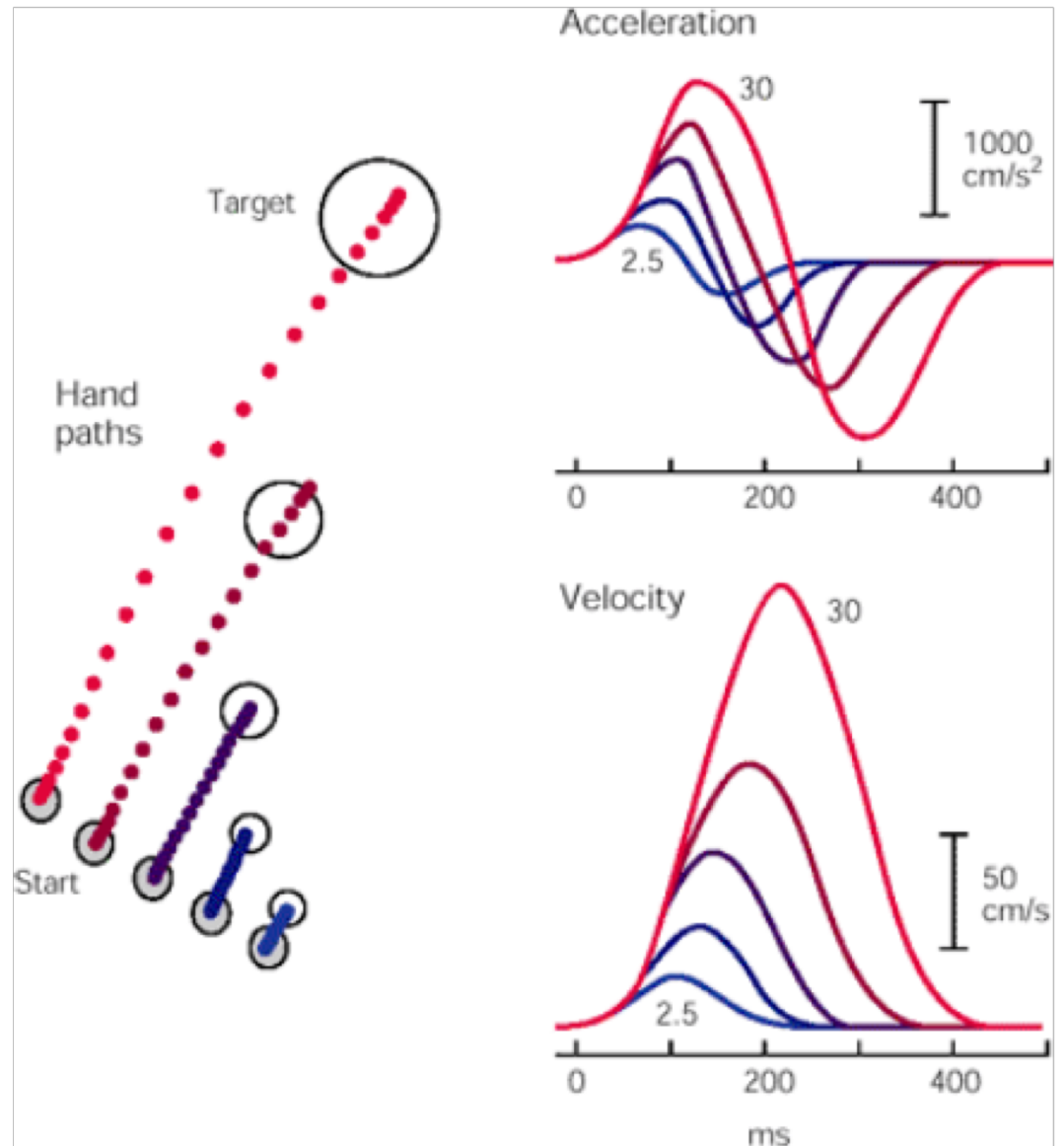


A Able was I ere I saw Elba
B Able was I ere I saw Elba
C Able was I ere I saw Elba
D Able was I ere I saw Elba
E Able was I ere I saw Elba

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;

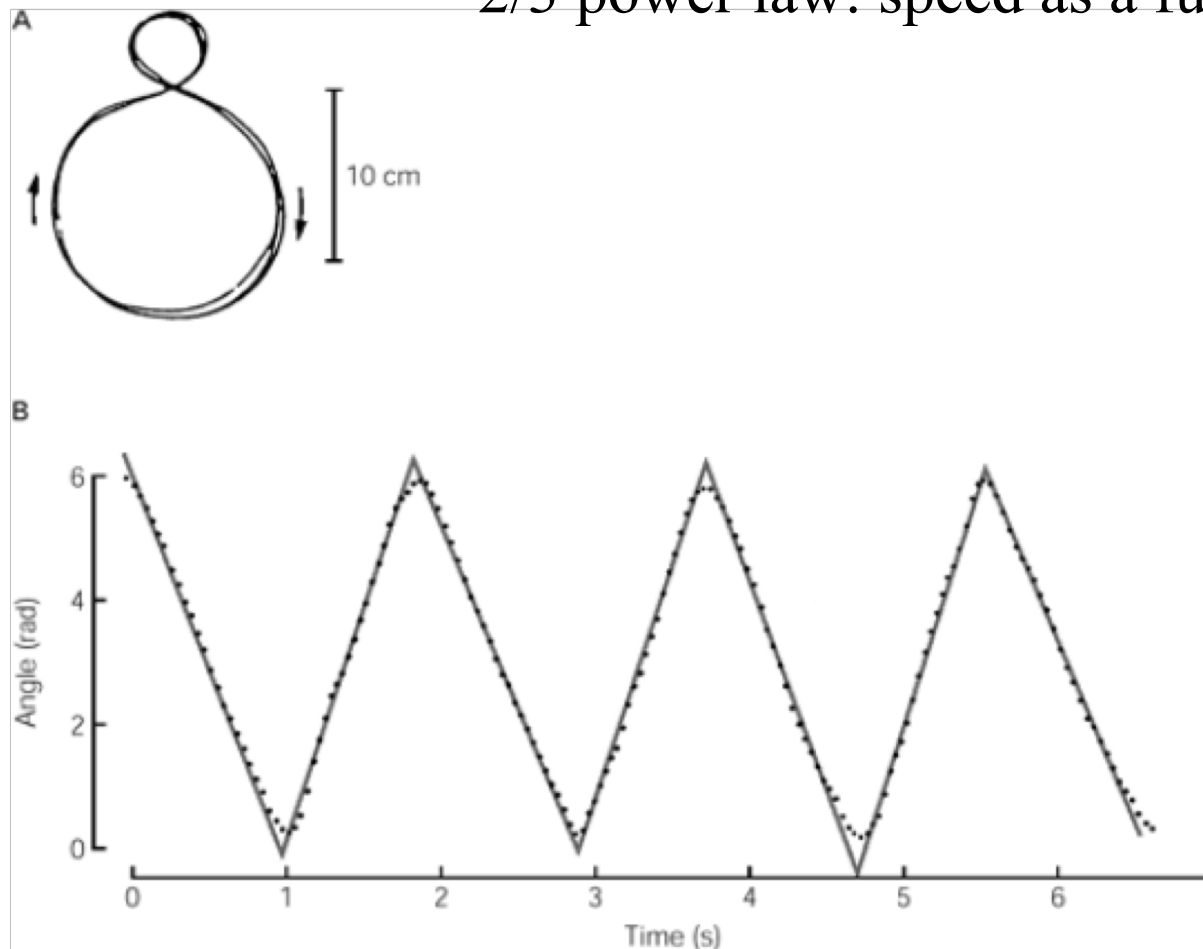
Dynamic transformation: relate motor commands to the motion of the system; in the reaching task here considered, the forces applied changed the system without changing the kinematics.

Building blocks – segmentation - primitives

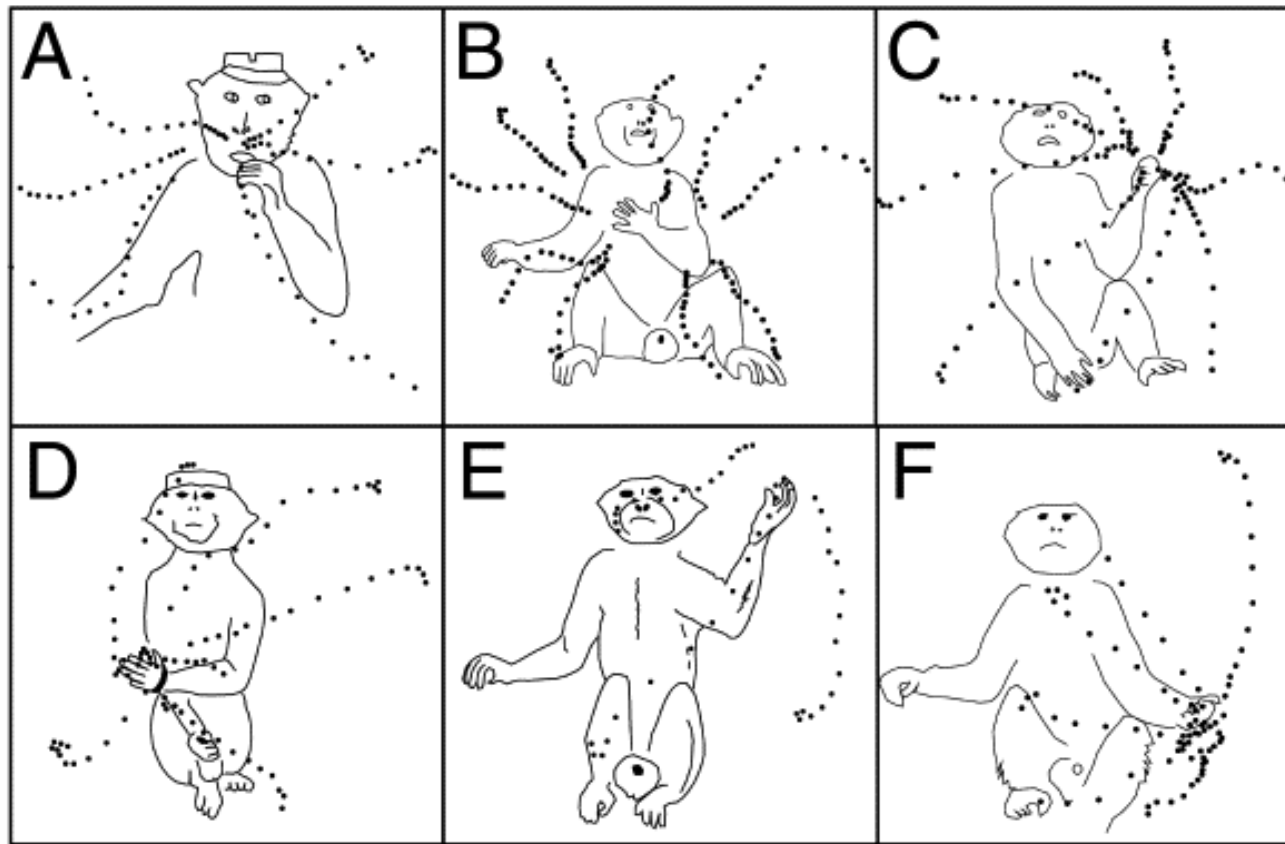
Isogony (equal angles)

Isochrony (duration independent of length)

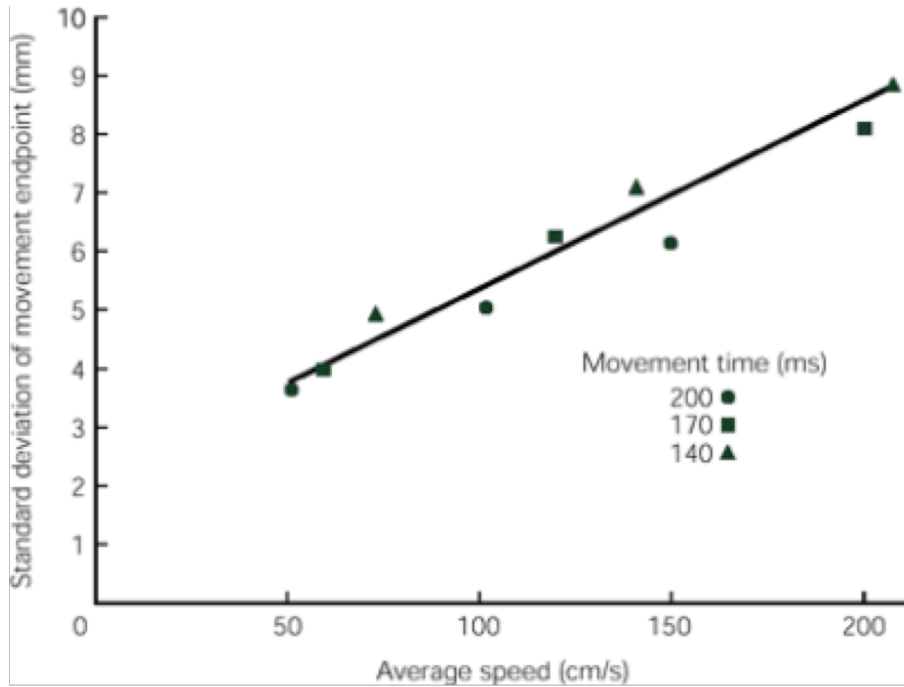
$2/3$ power law: speed as a function of curvature



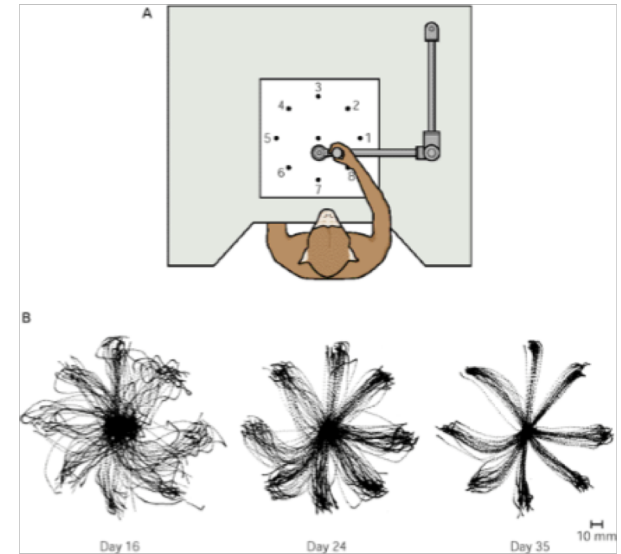
Stable behavioral gestures



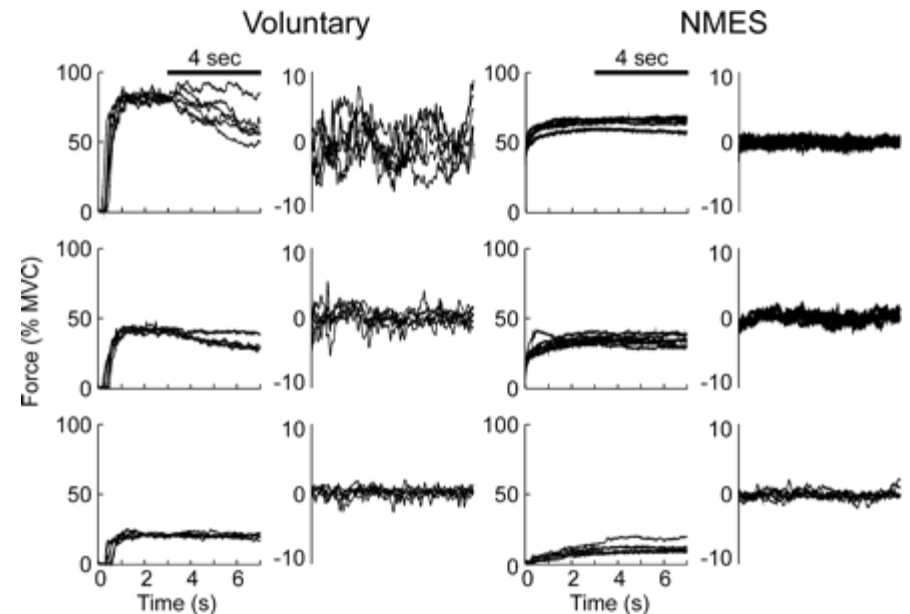
Speed – accuracy tradeoff (Woodsworth, 1890)



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



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

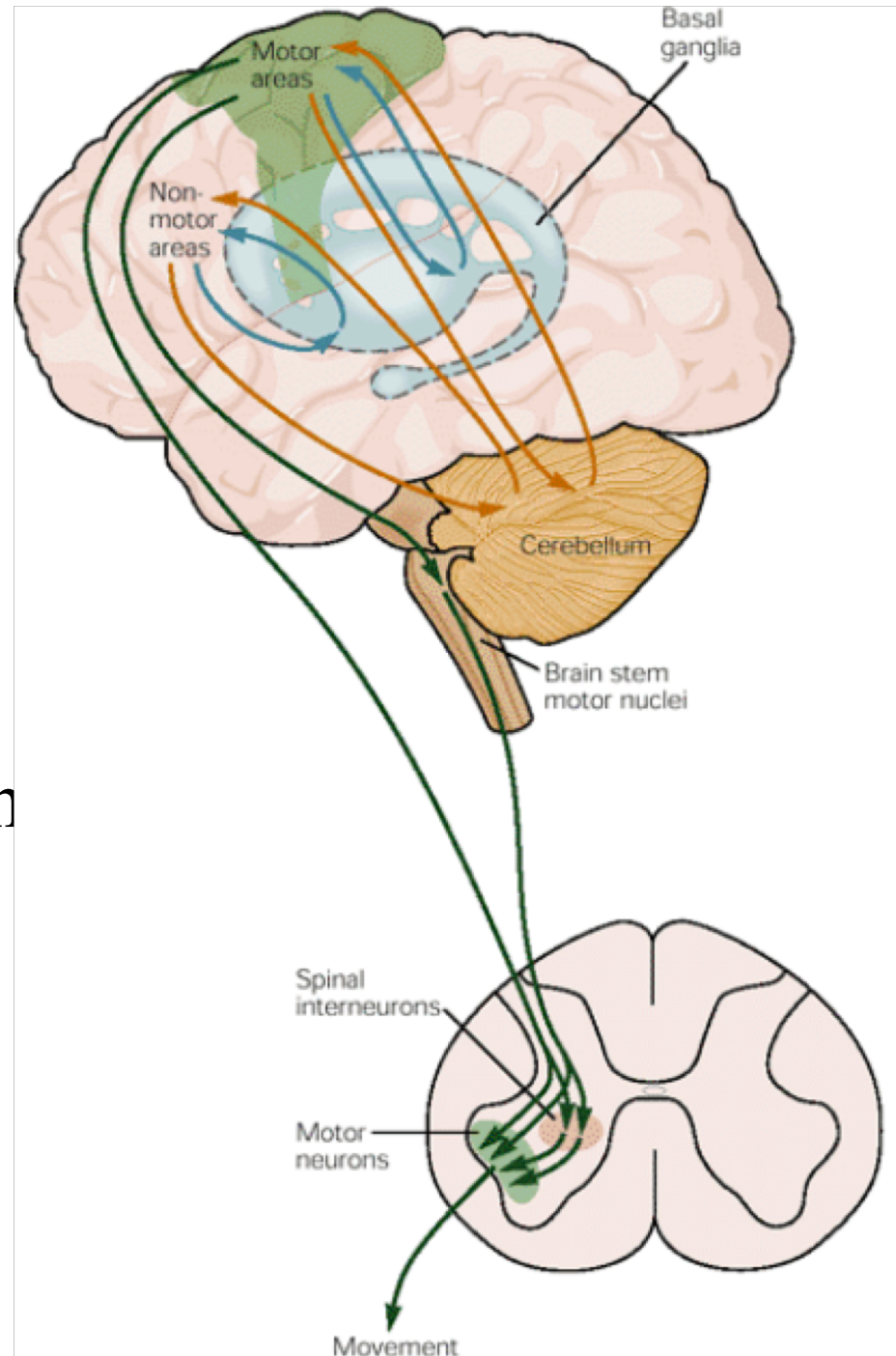


Overcoming noise: optimization principles

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

Hierarchical organization

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

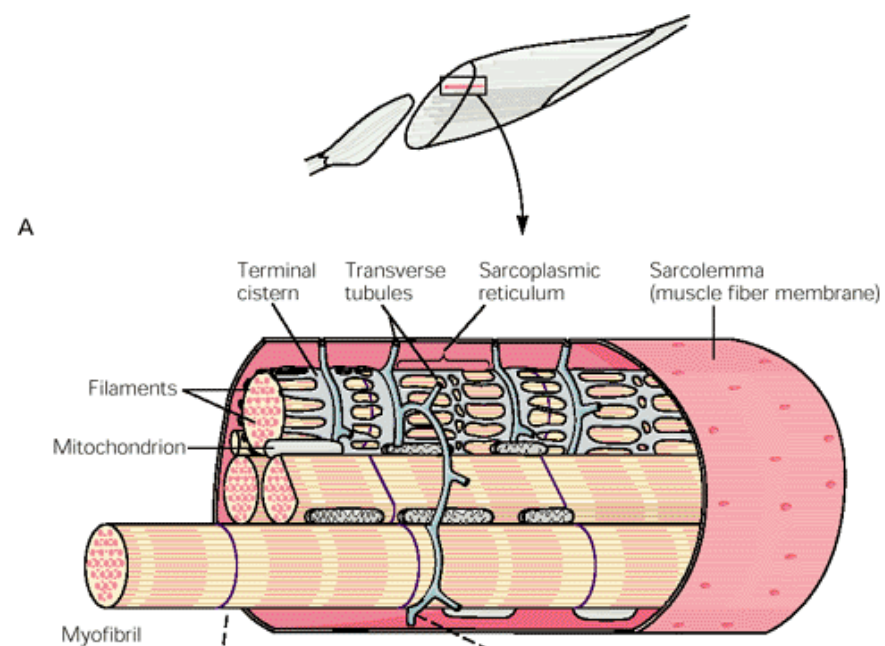


Muscles

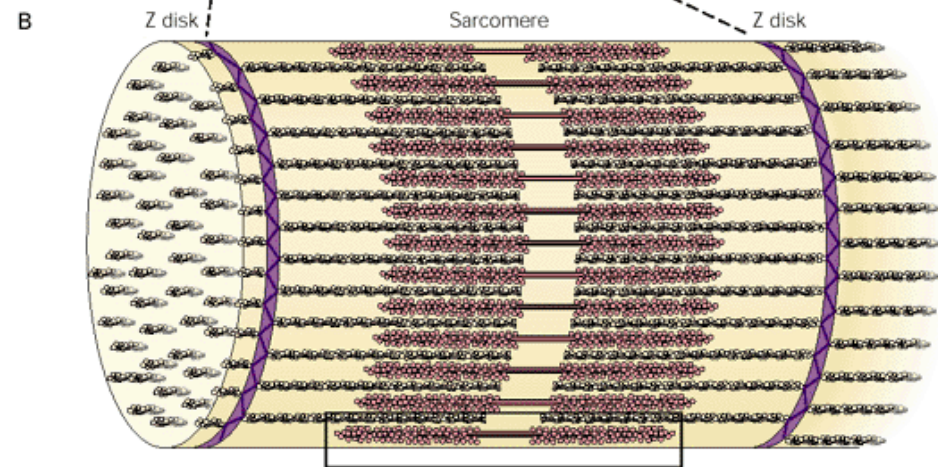
1. smooth muscles
2. cardiac muscles
3. **skeletal muscles**

Structure

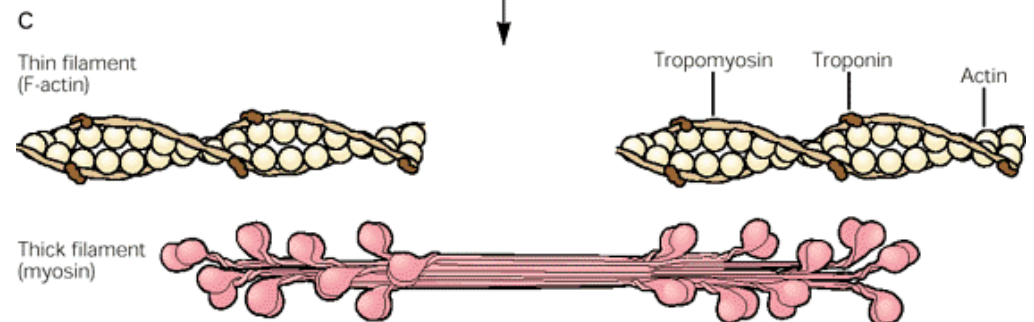
Muscle fiber



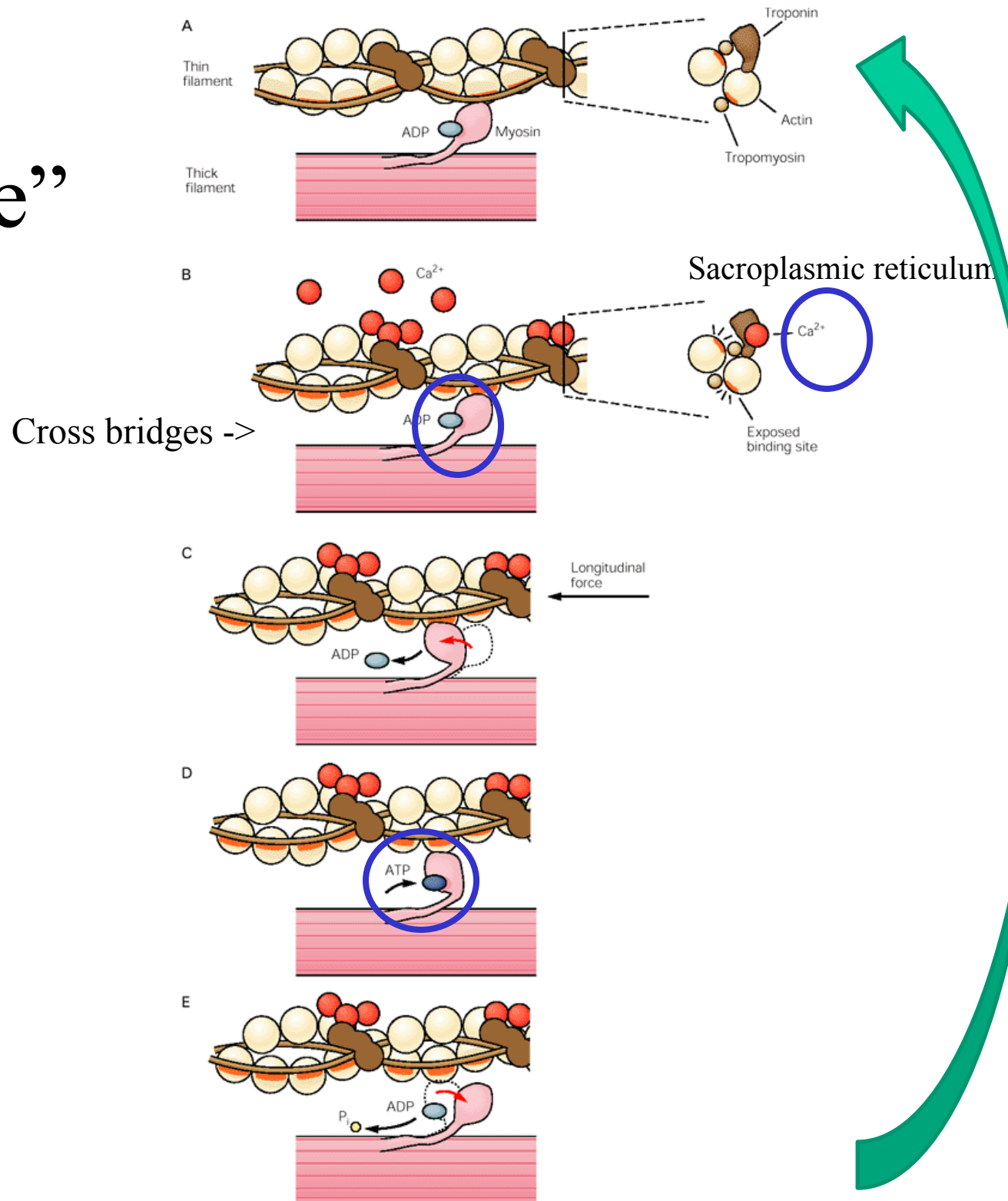
myofibril



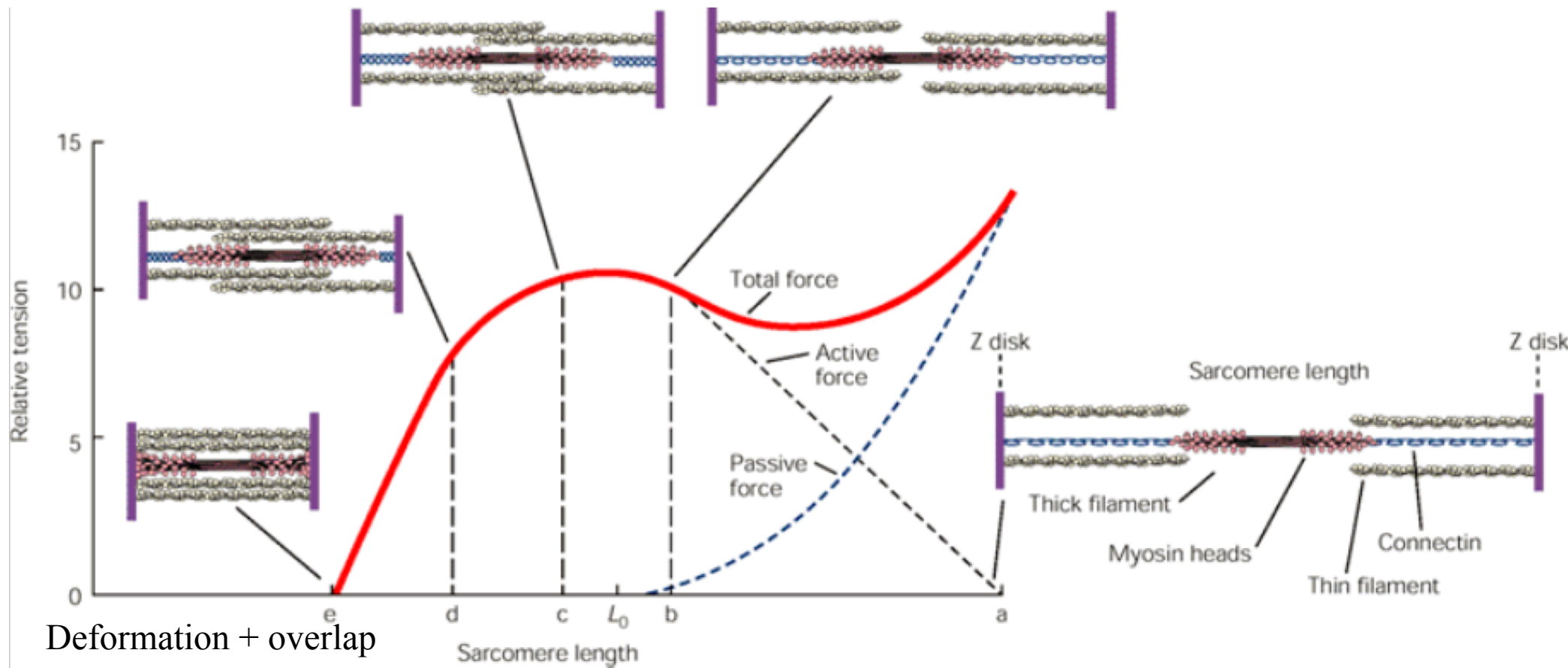
Sarcomere: functional unit



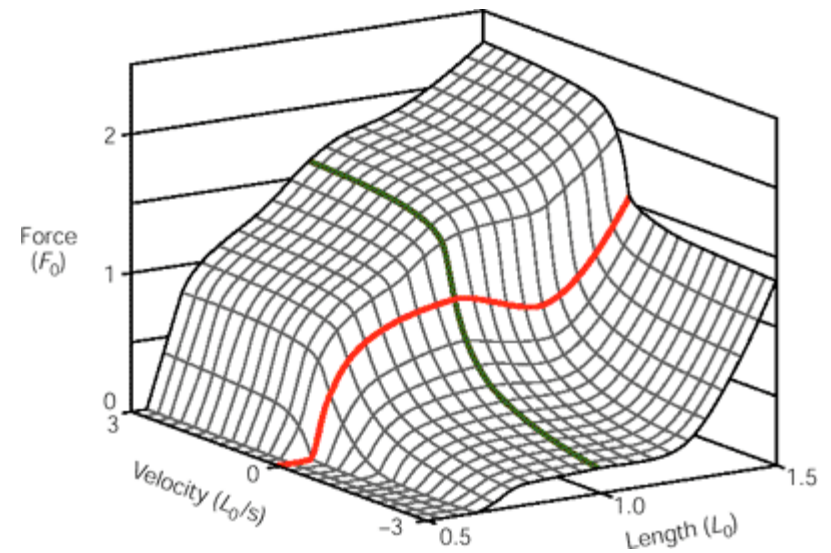
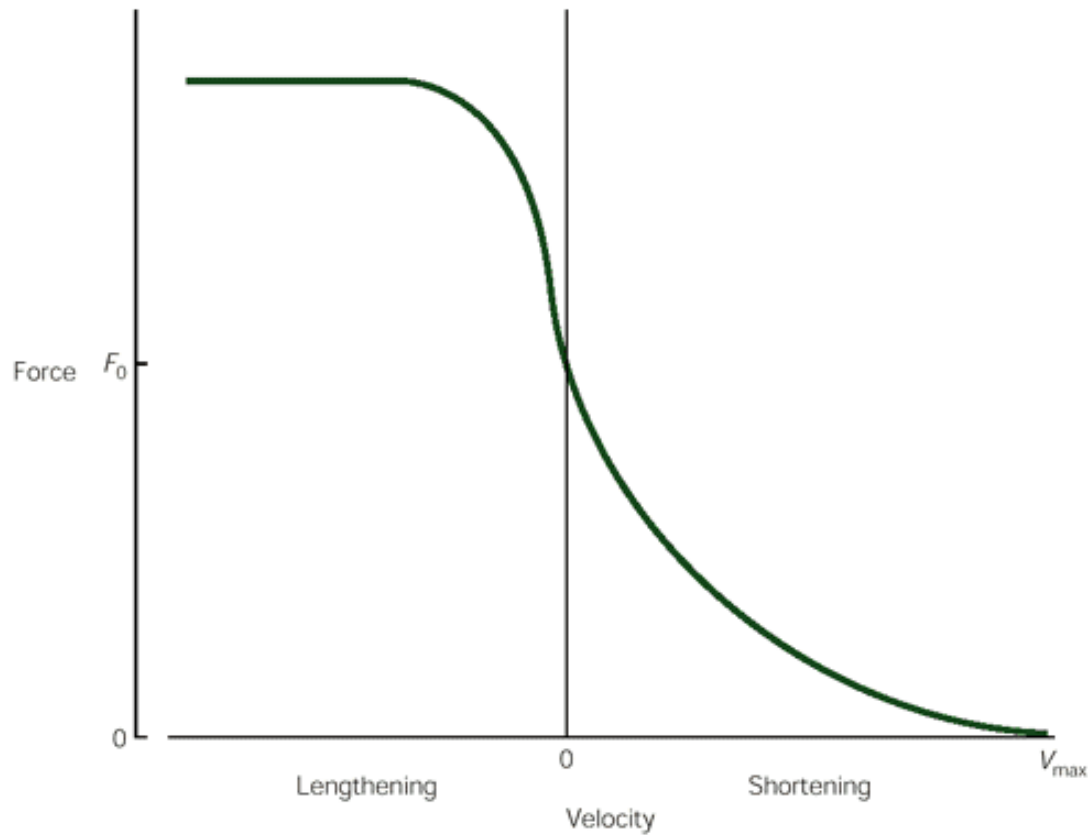
The “engine”



Force depends on length

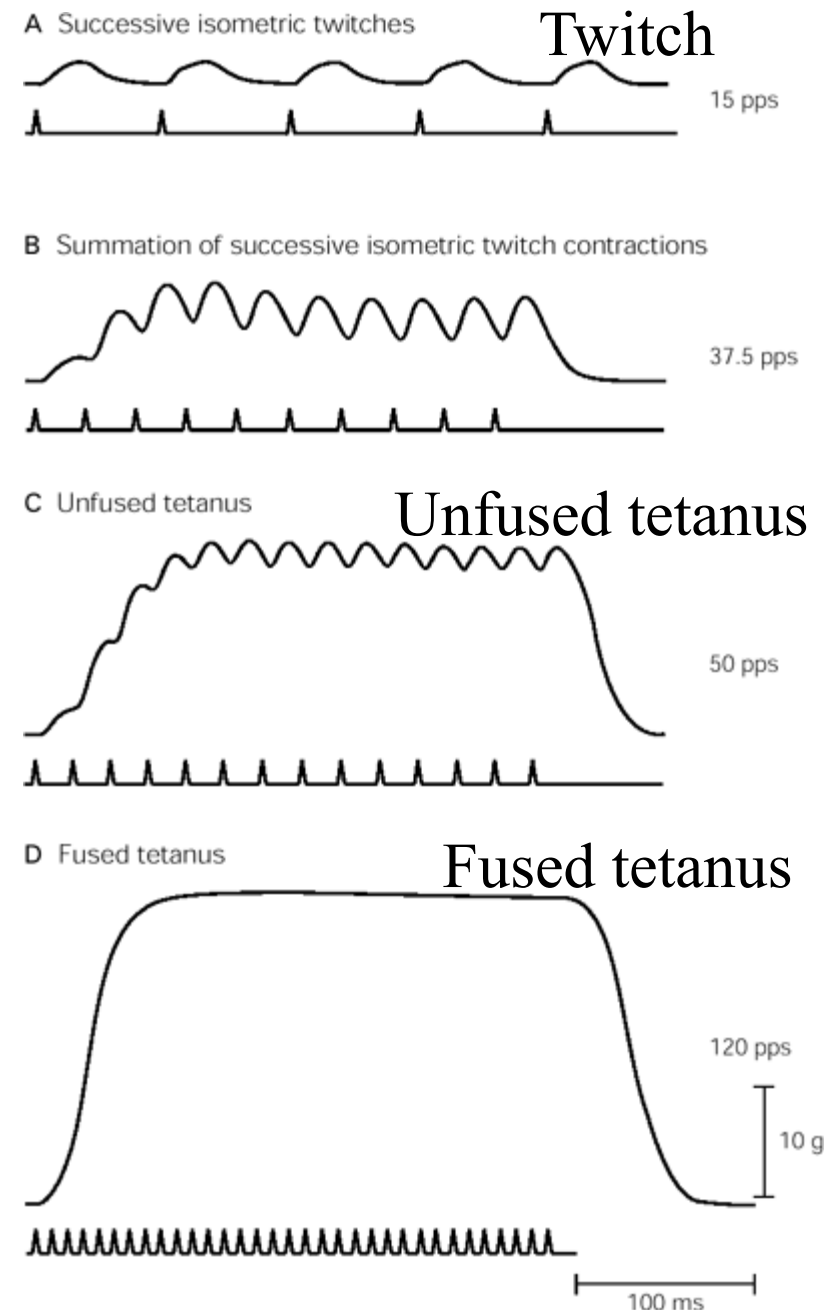


Force depends also on velocity

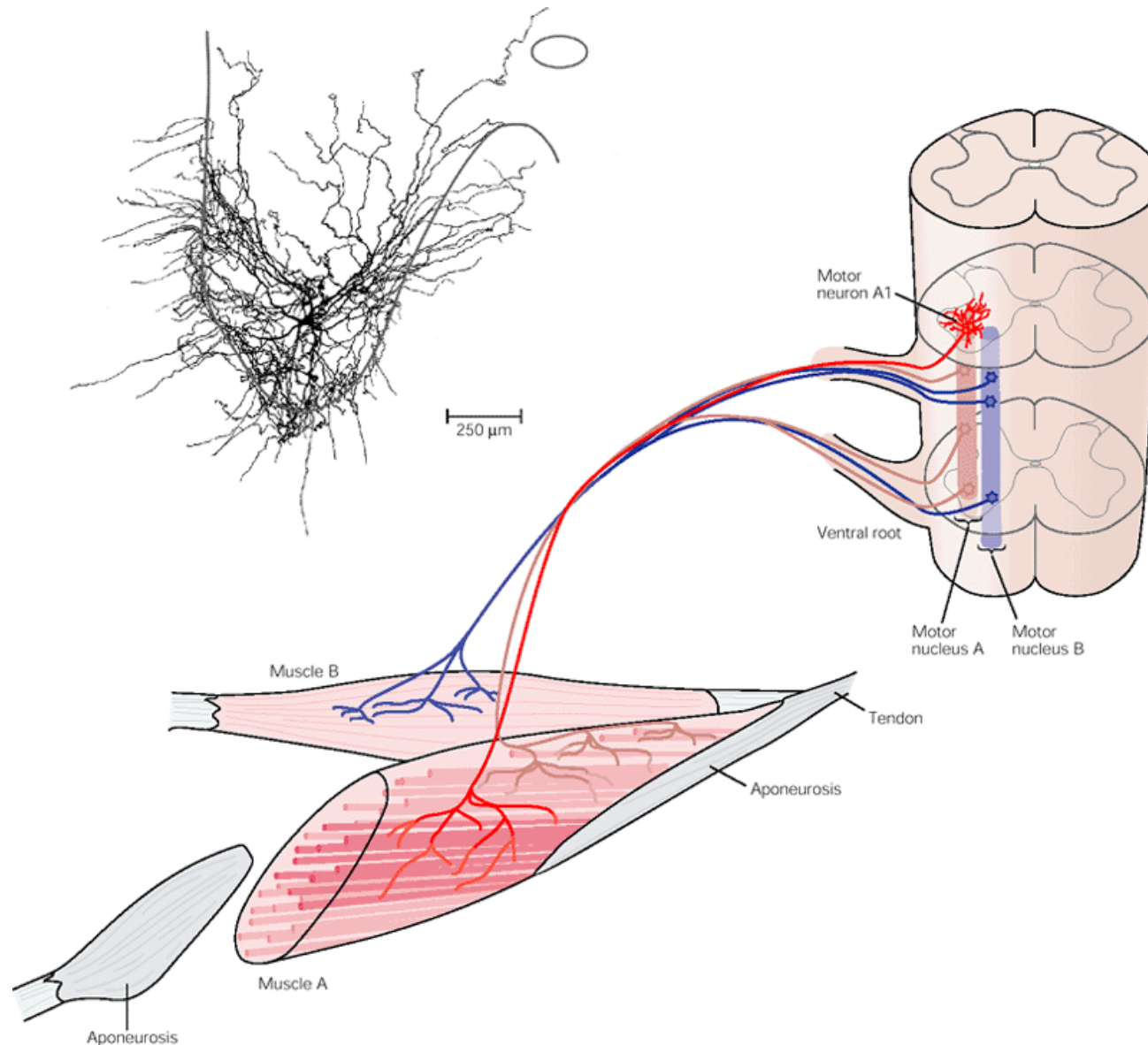


The force of a single muscle fiber is a function of

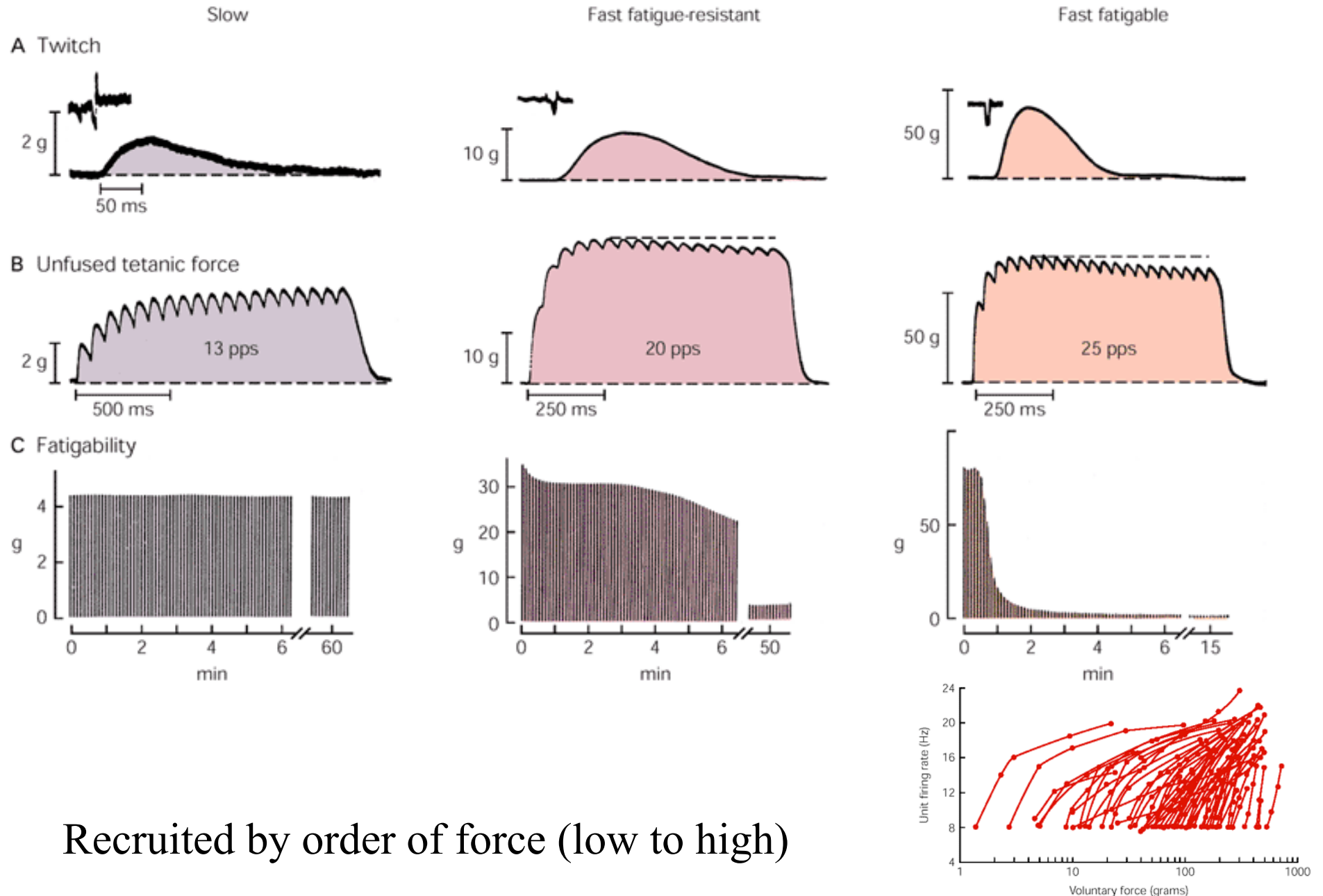
- Stimulation rate
- Stimulation pattern
- The muscle length
- The velocity of contraction
- The fiber type
- The fiber organization
- The duration of exercise - fatigue



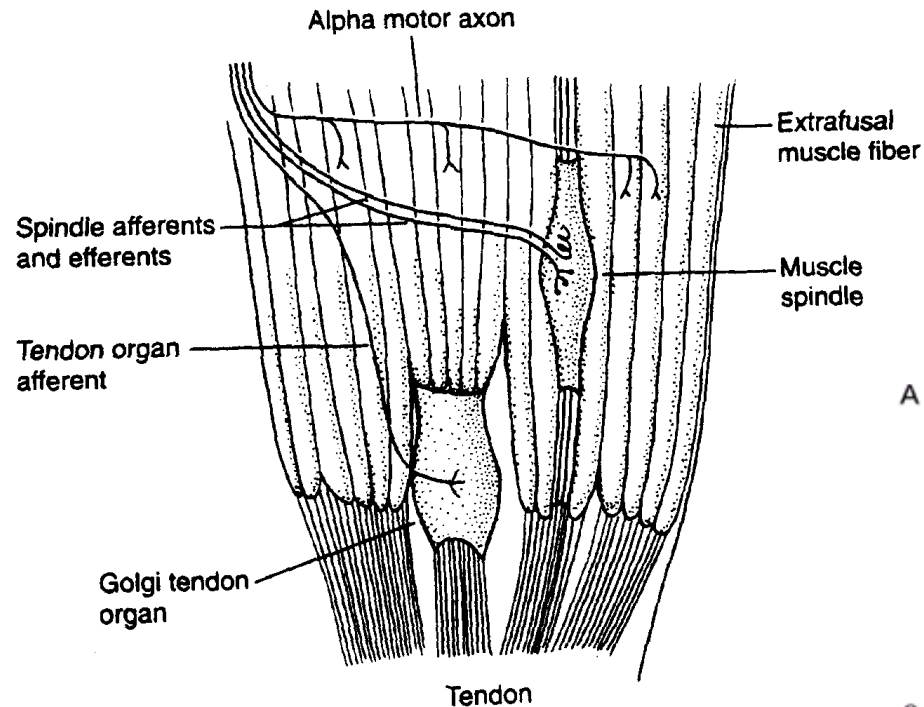
Motor unit:
motor neuron and the muscle fibers it innervates
(one to many)



3 types of motor unit:

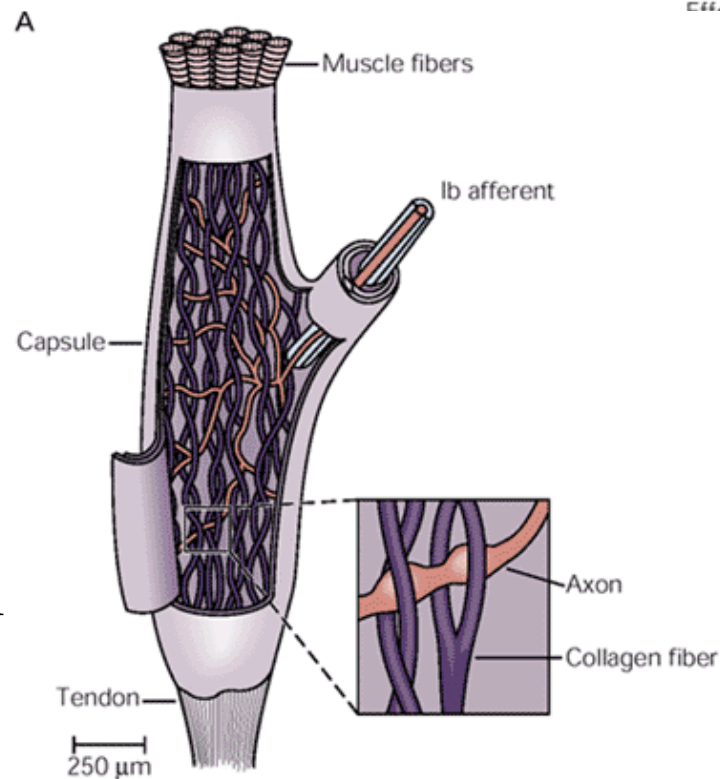


Muscle proprioceptive organs

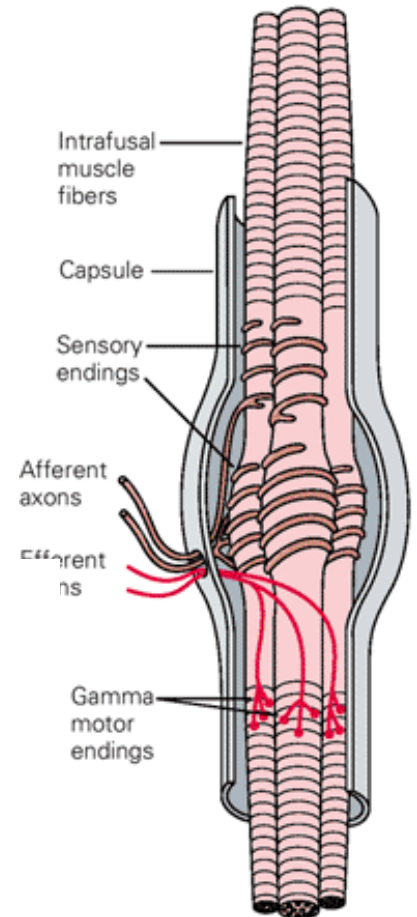


Golgi tendon: tension
Serial

Spindle: length
Parallel

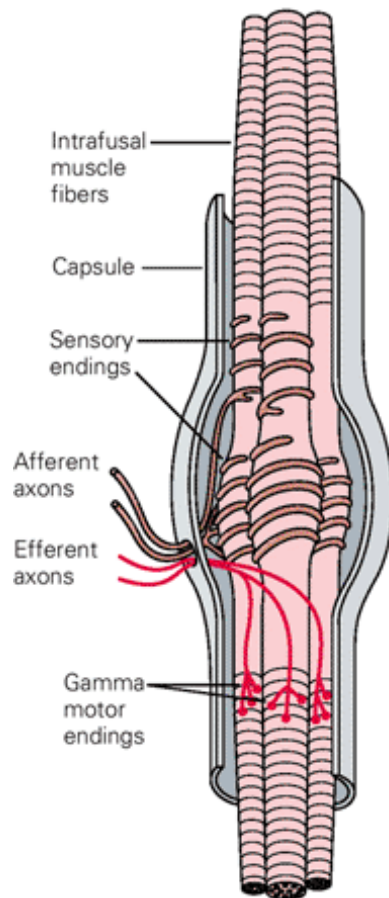


A Muscle spindle

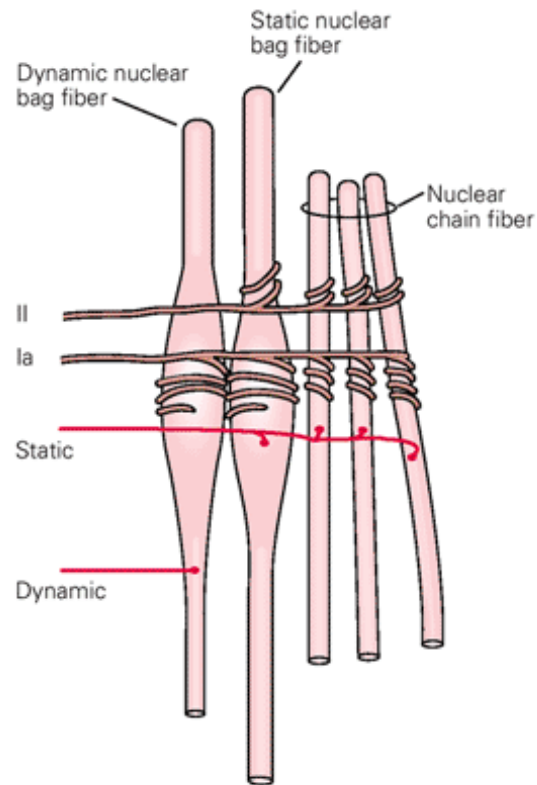


The muscle spindles are sensitive to changes in length

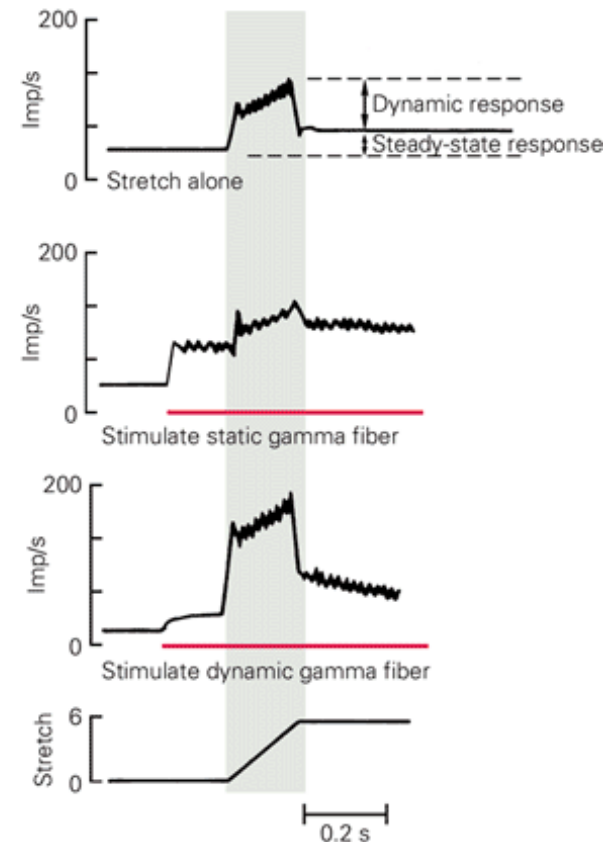
A Muscle spindle



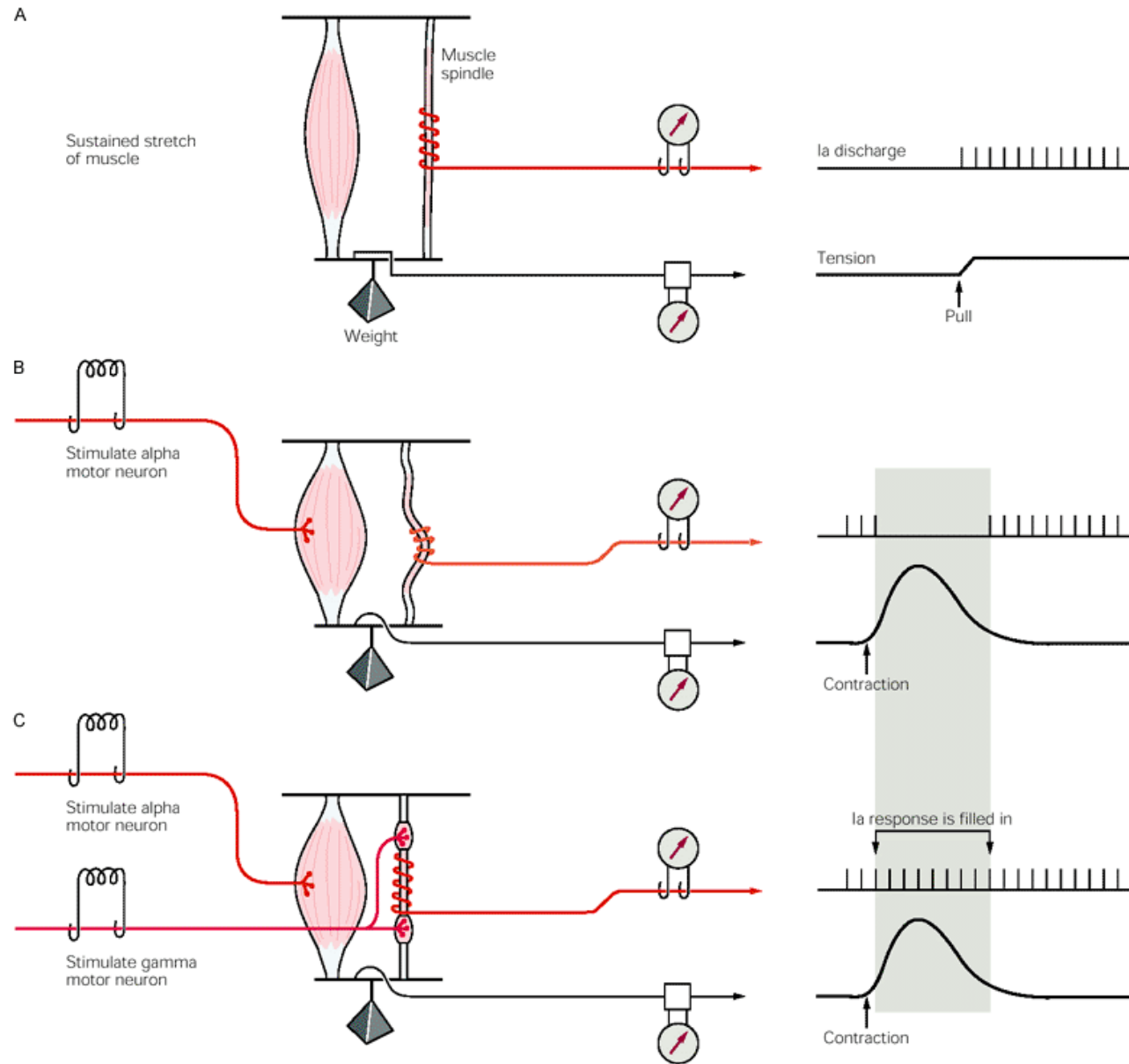
B Intrafusal fibers of the muscle spindle



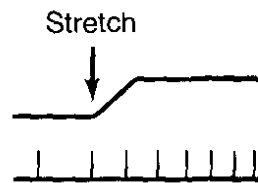
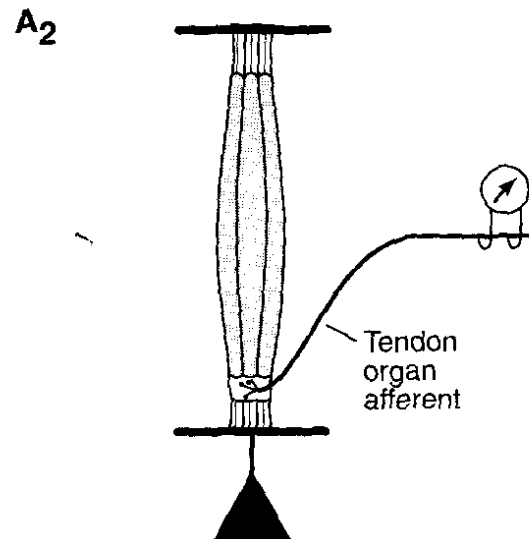
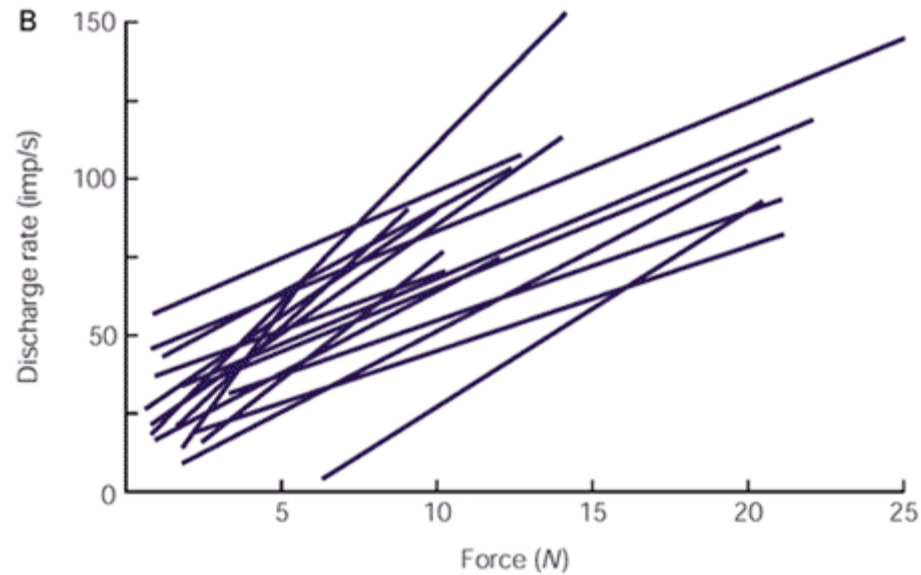
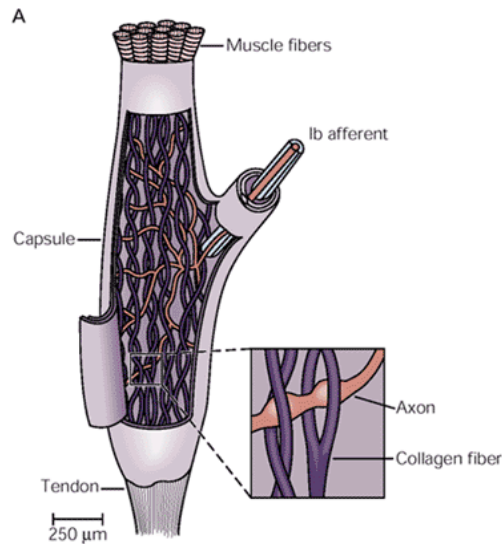
C Response of Ia sensory fiber to selective activation of motor neurons



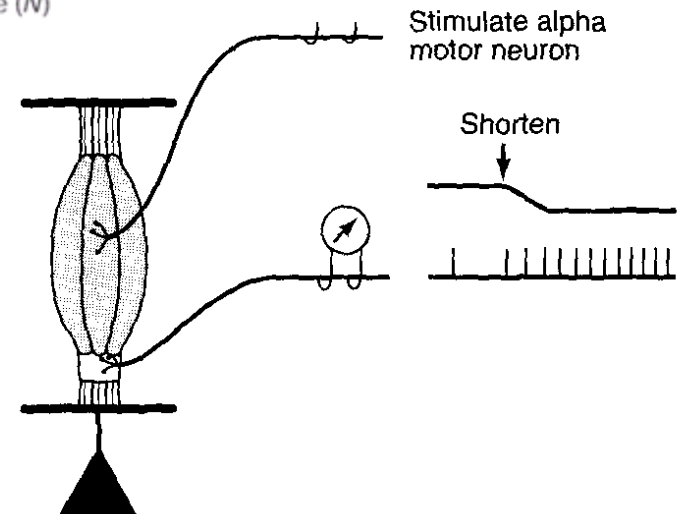
Active range can be dynamically modulated



Golgi tendon organs are sensitive to the tension



B₂



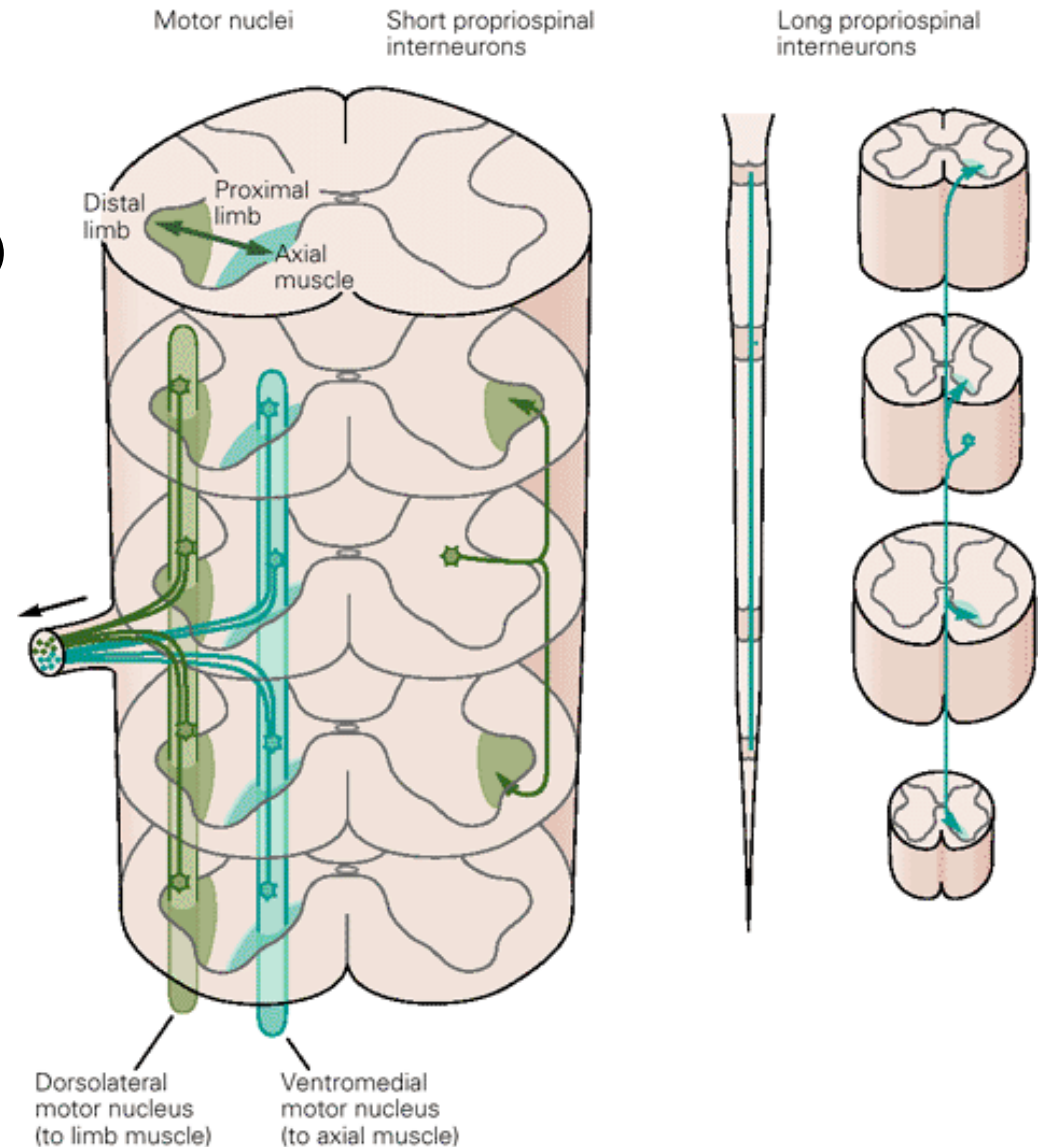
Spinal cord, Brain stem and spinal tracts

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

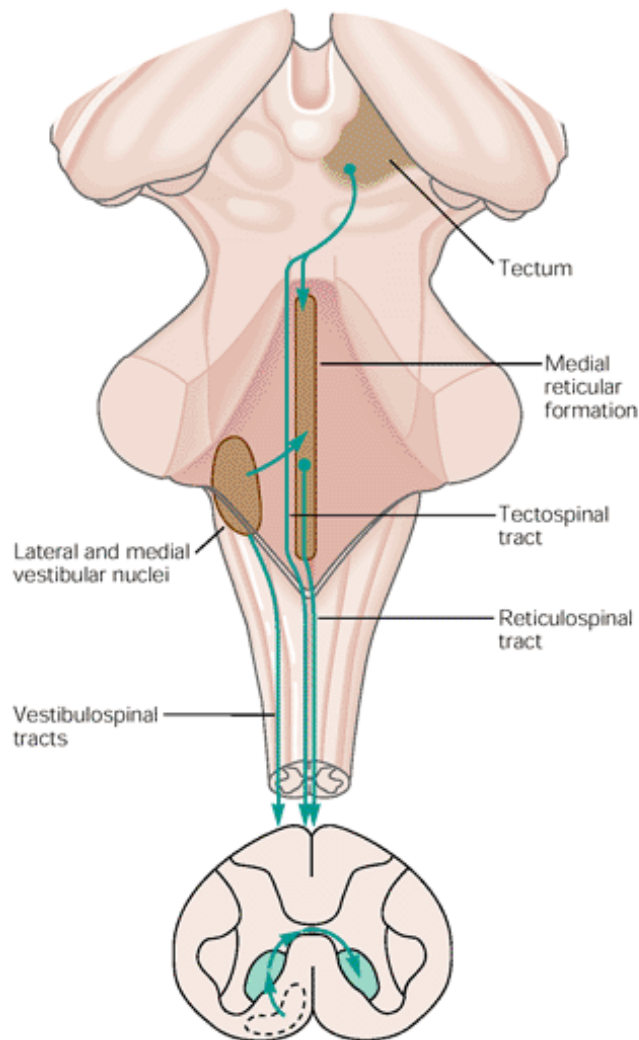


Brain stem pathways

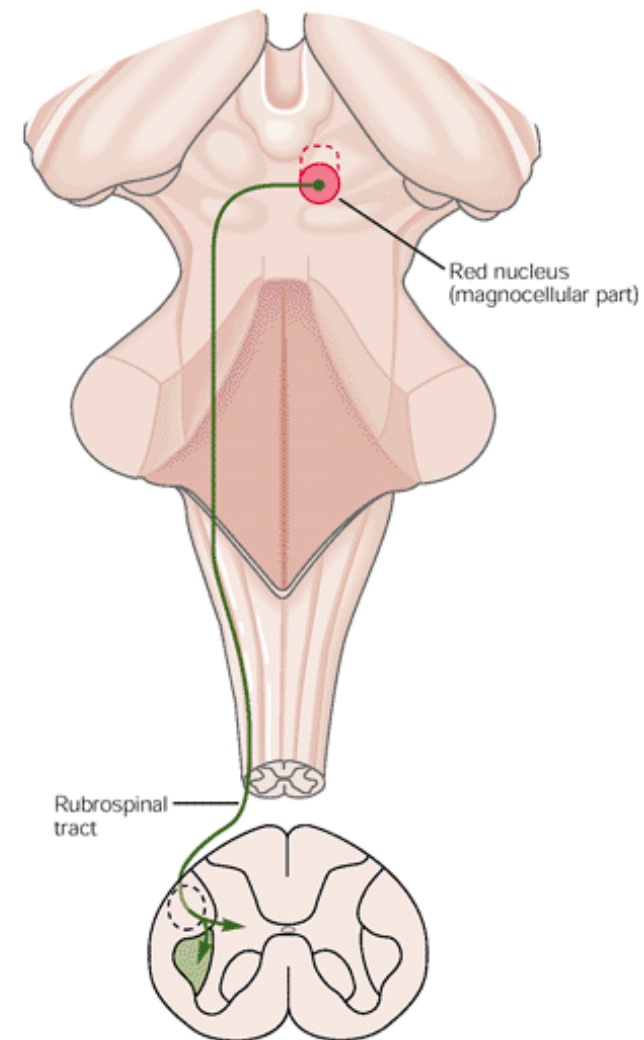
Medial pathways (vestibulospinal, reticulospinal, tectospinal), terminates in ventromedial (axial) for postural control.

Lateral pathways (rubrospinal) terminates in dorsolateral.

A Medial brain stem pathways

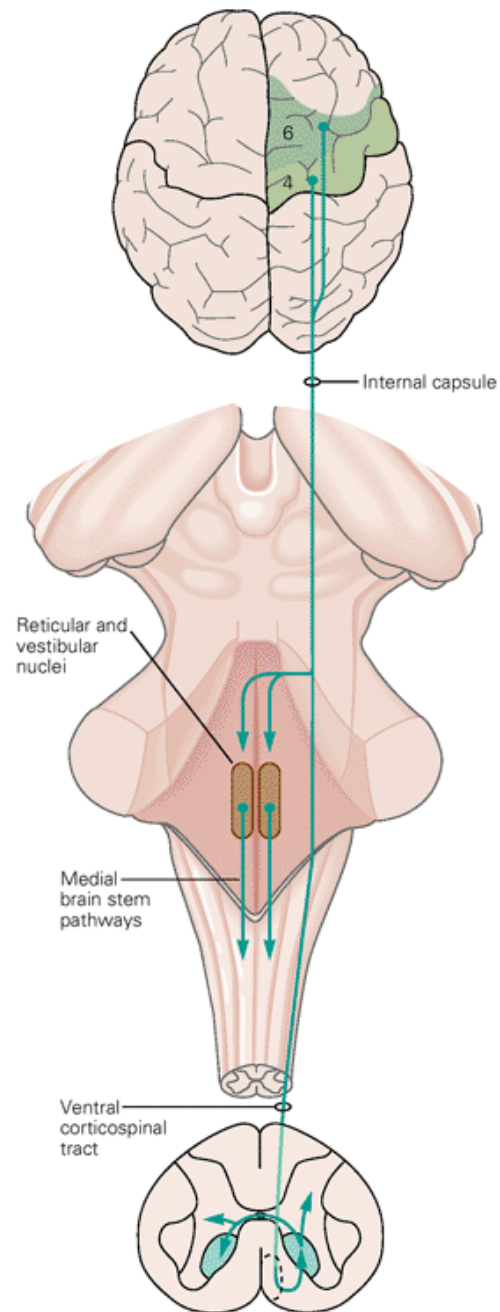


B Lateral brain stem pathways

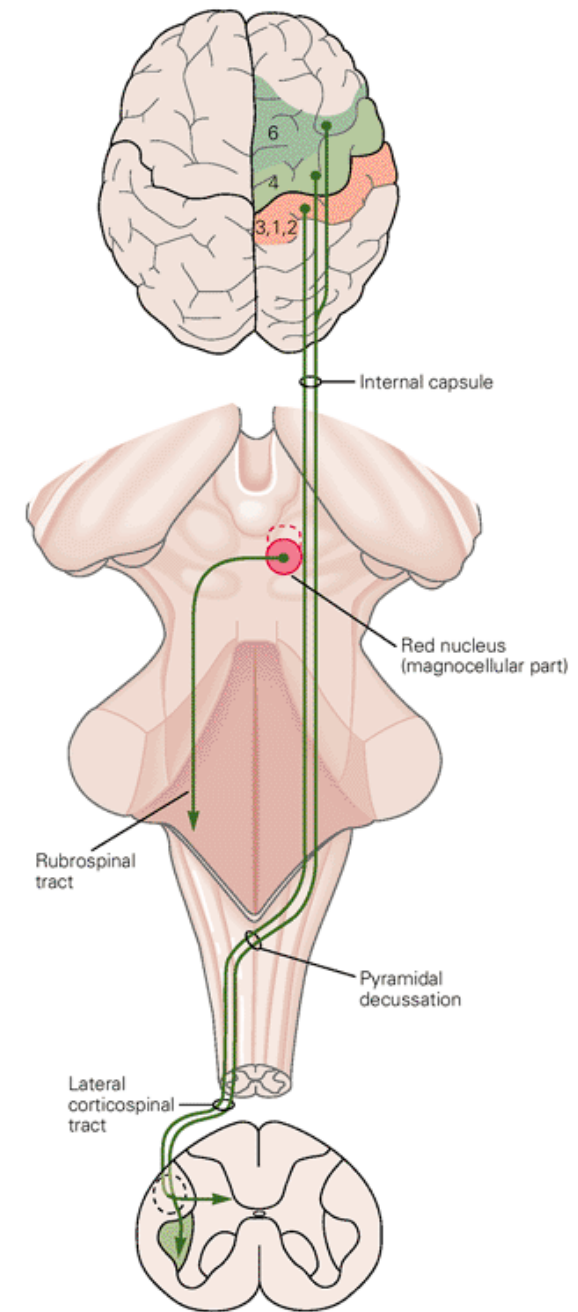


The corticospinal tract

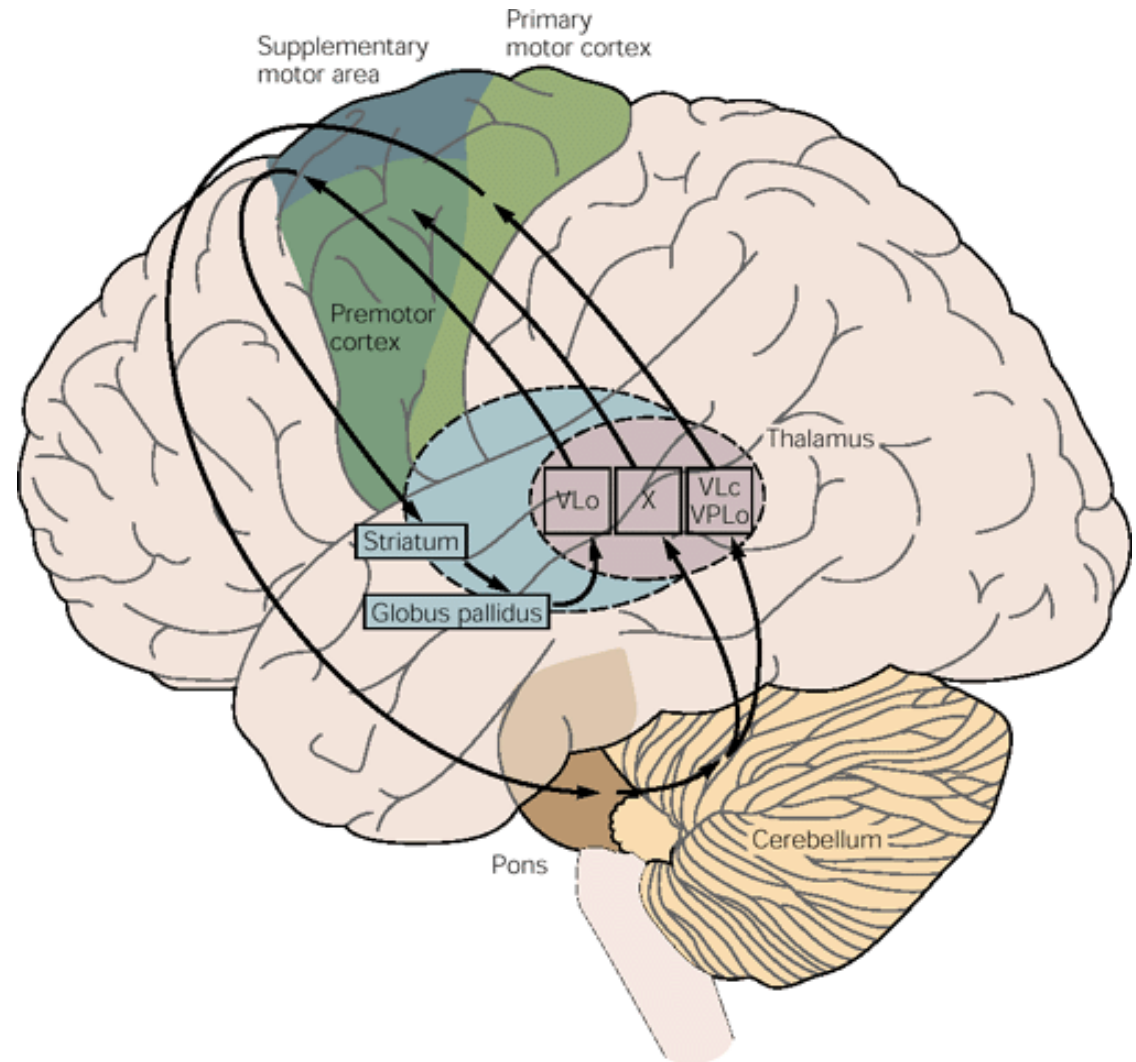
A Ventral corticospinal tract



B Lateral corticospinal tract



Cortex and control of voluntary movement



A Macaque monkey

Supplementary motor area
Primary motor cortex
Central sulcus
Leg
Arm
Face
6
4
3,1,2
5
7

Corpus callosum
Premotor cortex

Human

Supplementary motor area
Primary motor cortex
Primary somatic sensory cortex
Premotor cortex
Prefrontal cortex
Posterior parietal cortex
Leg
Arm
Face
6
4
3,1,2
5
7
8

B

C

SGm pre-SMA
SMA
M1
Leg
Arm
Leg
PMd
SPcS
Arm
Leg
M1
Arm
Fundus
Central sulcus
ArSs
PS
ArSi
PMv
Arm
Leg
5 mm

A Macaque monkey

Supplementary motor area
Primary motor cortex
Central sulcus
Leg
Arm
Face
6
4
3,1,2
5
7

Corpus callosum
Premotor cortex

Human

Supplementary motor area
Primary motor cortex
Primary somatic sensory cortex
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Leg
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B

C

SGm pre-SMA
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SPcS
Arm
Leg
M1
Leg
M1
Arm
Fundus
Central sulcus
ArSs
PS
ArSi
PMv
Arm
Leg
5 mm

Stimulation in M1

Electrical and magnetic stimulation

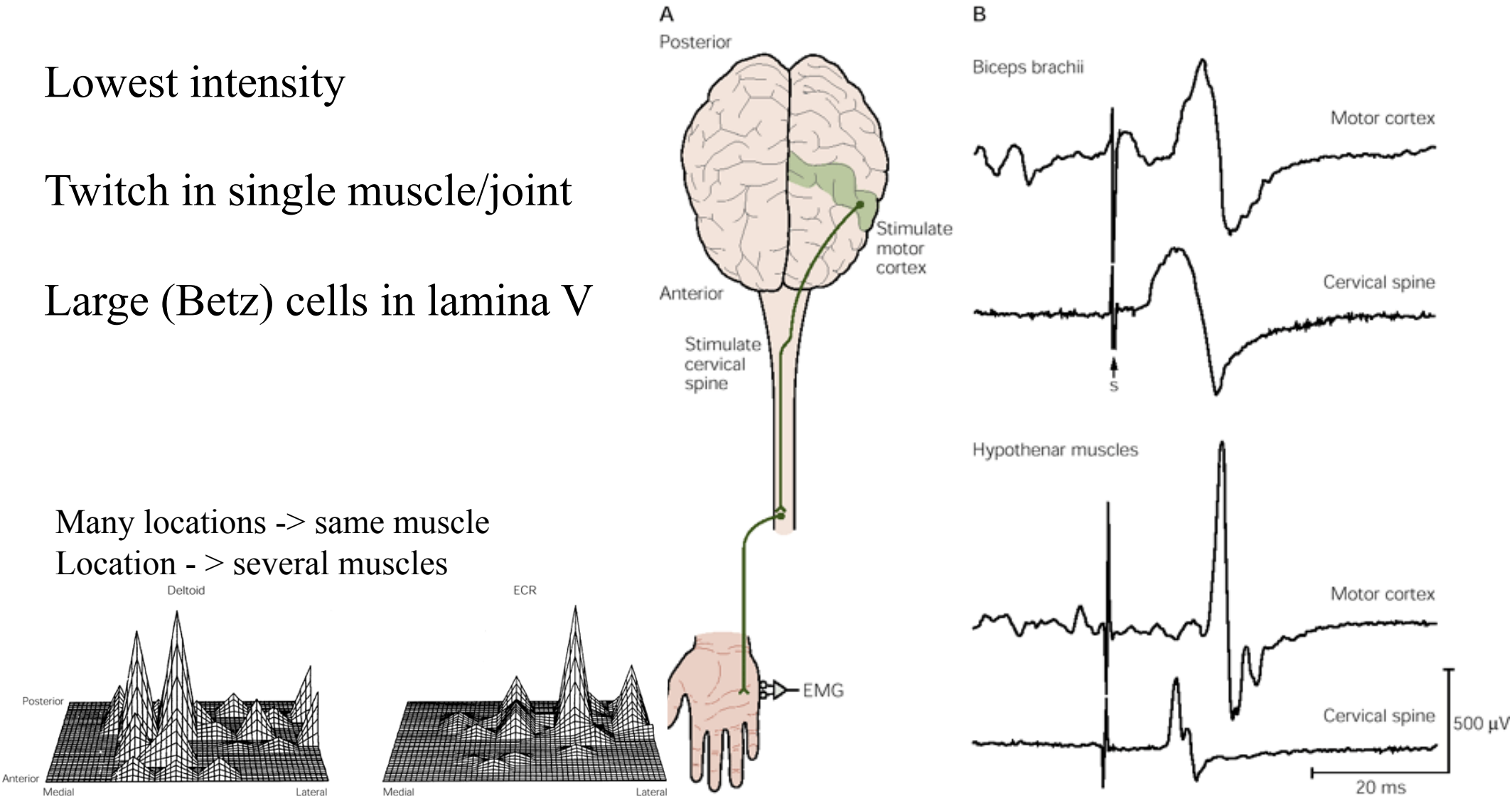
Lowest intensity

Twitch in single muscle/joint

Large (Betz) cells in lamina V

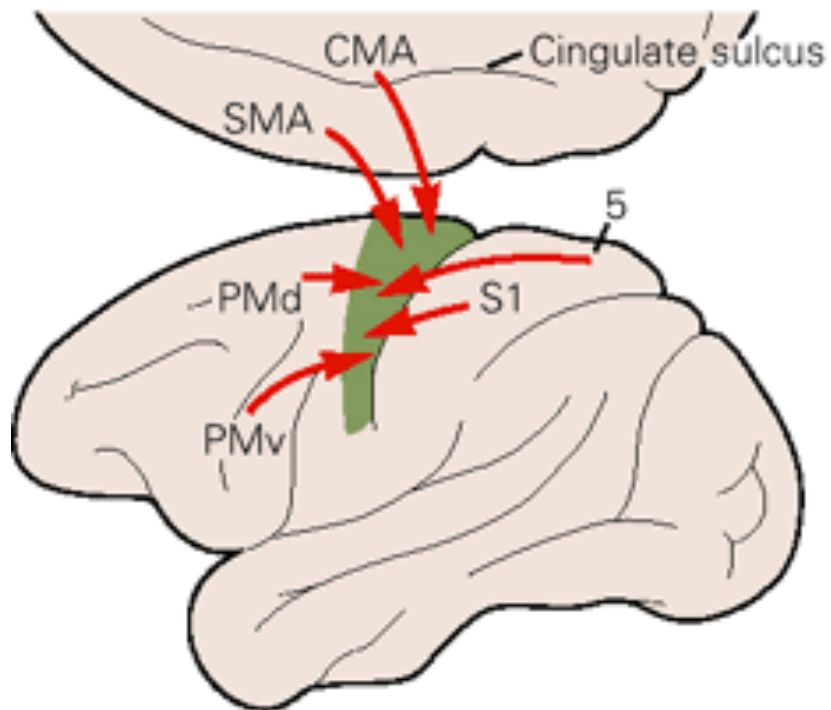
Many locations -> same muscle

Location - > several muscles

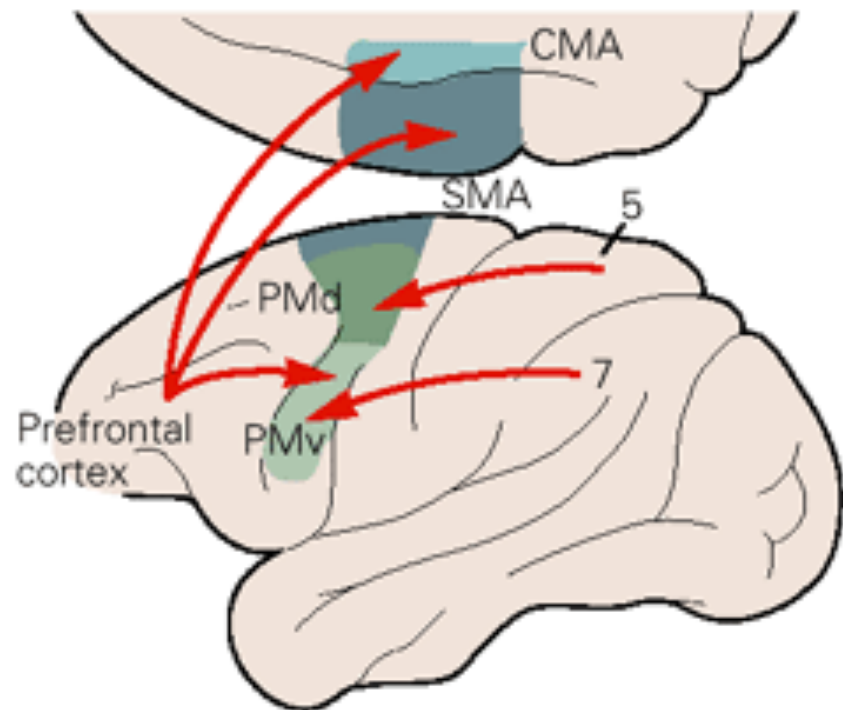


Cortical inputs

A Inputs to primary motor cortex



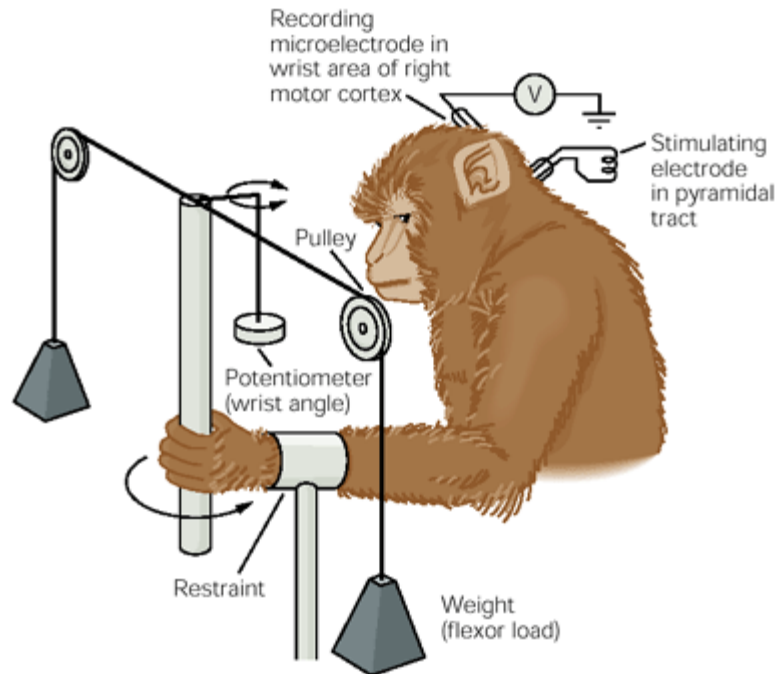
B Inputs to premotor areas



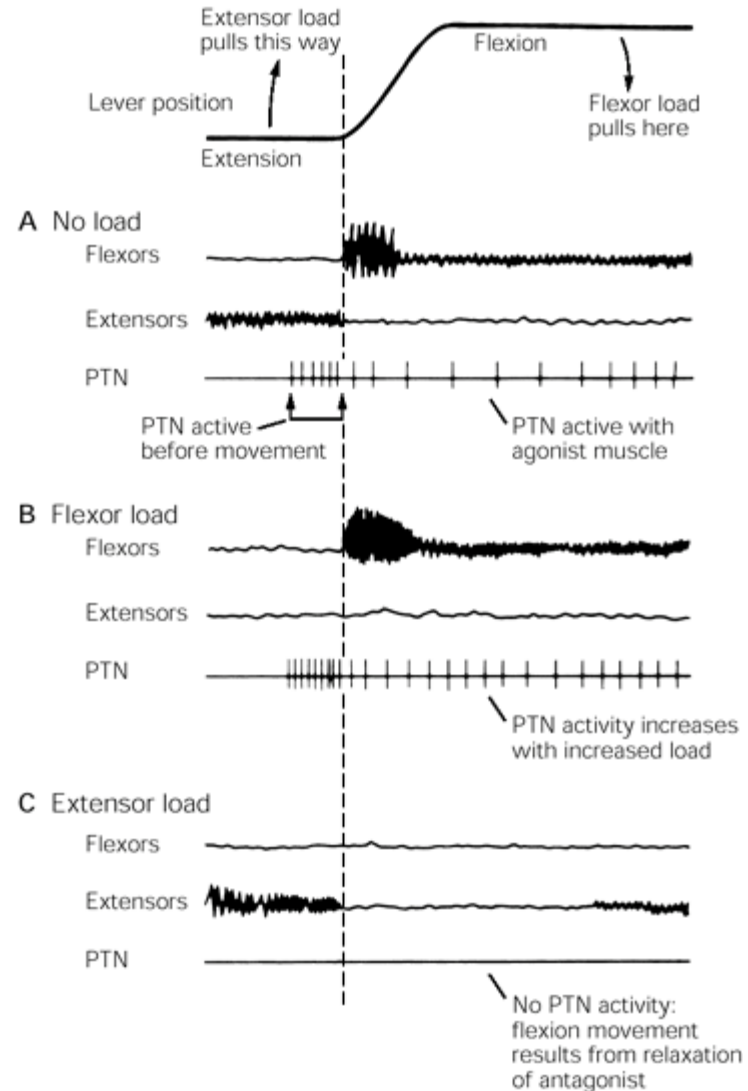
Coding of force in M1

Evarts, 68

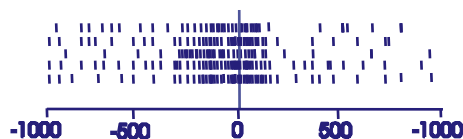
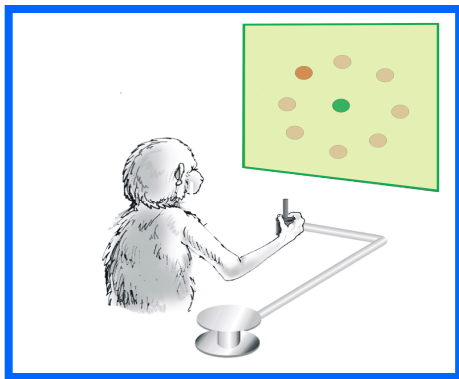
Experimental setup



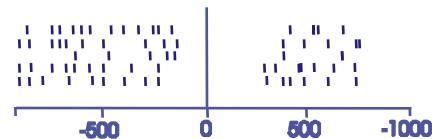
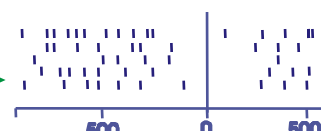
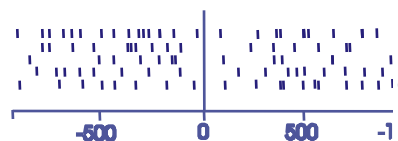
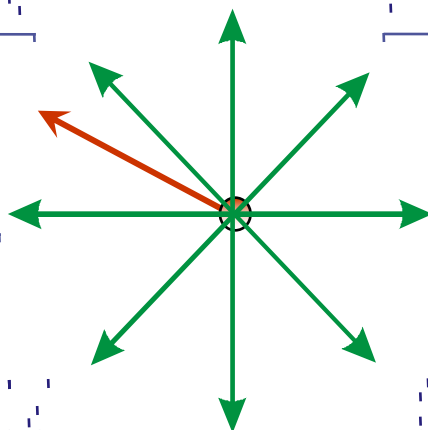
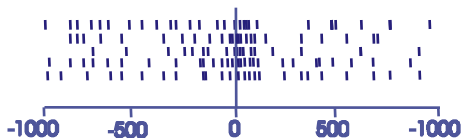
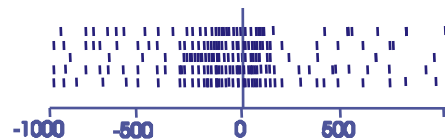
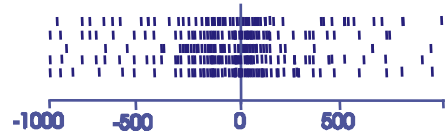
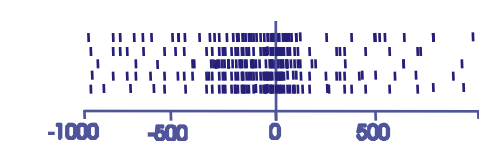
Records of behavior and cell activity



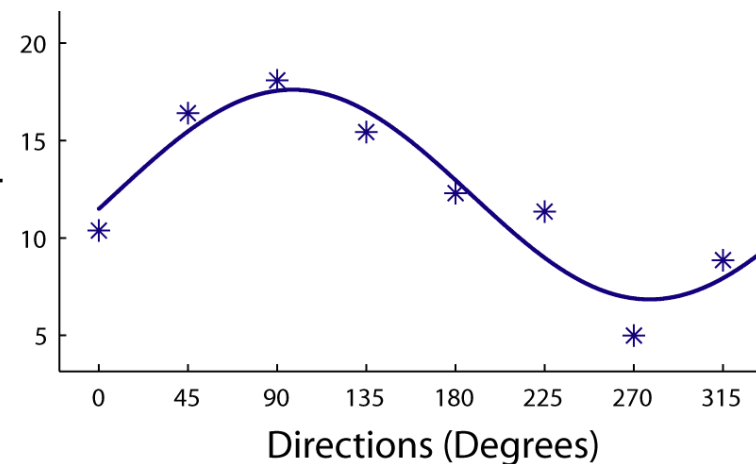
Coding of external direction



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



Rate (spikes/sec)



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.

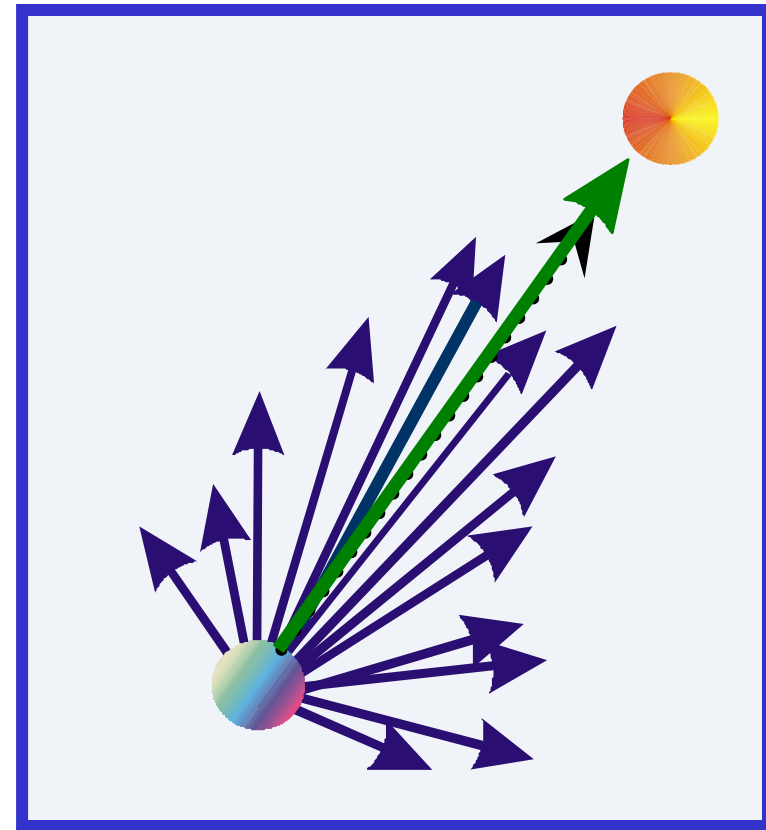
The population vector

If:

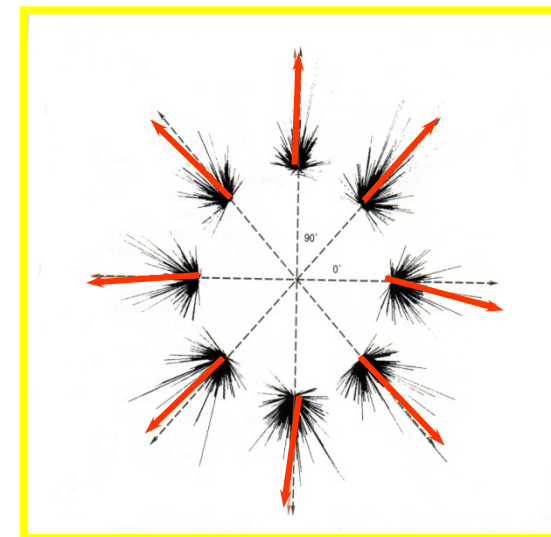
- Many cells “care” about direction of movement
- Cells are tuned “cosine like” with a preferred direction
- Preferred directions are uniformly distributed

Then:

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

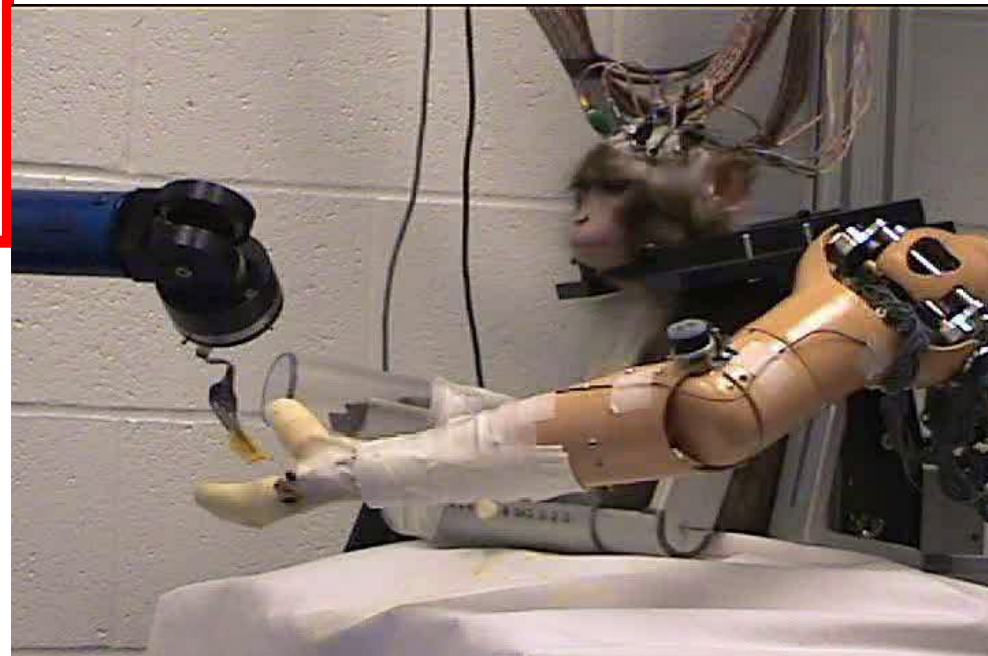
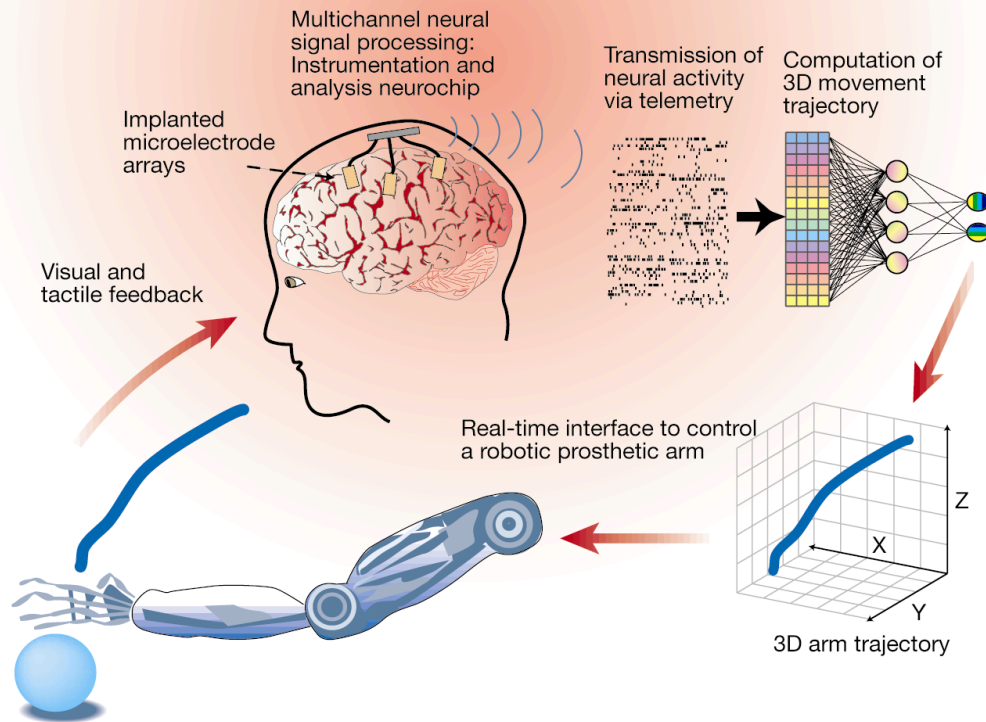


$$\overline{MD} \approx PV = \sum_{i=1}^N w_i \overline{C}_i$$



What can we do with it? Neural prostheses

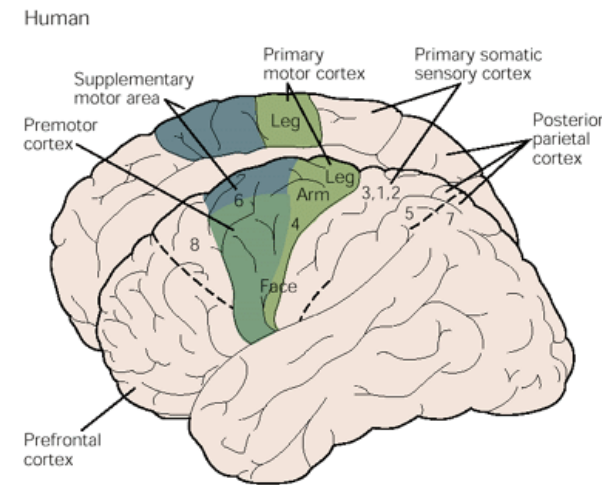
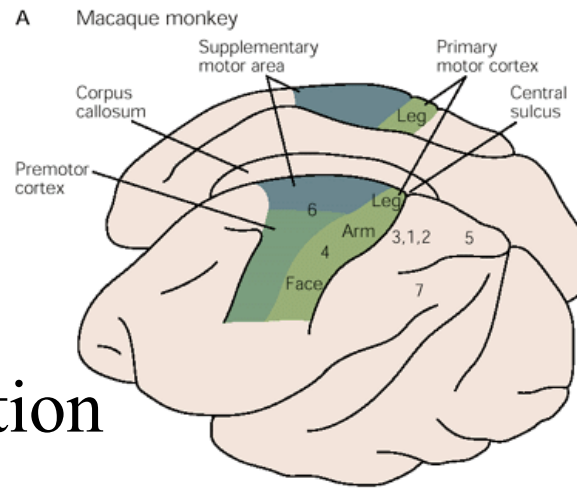
b



Schwartz AB

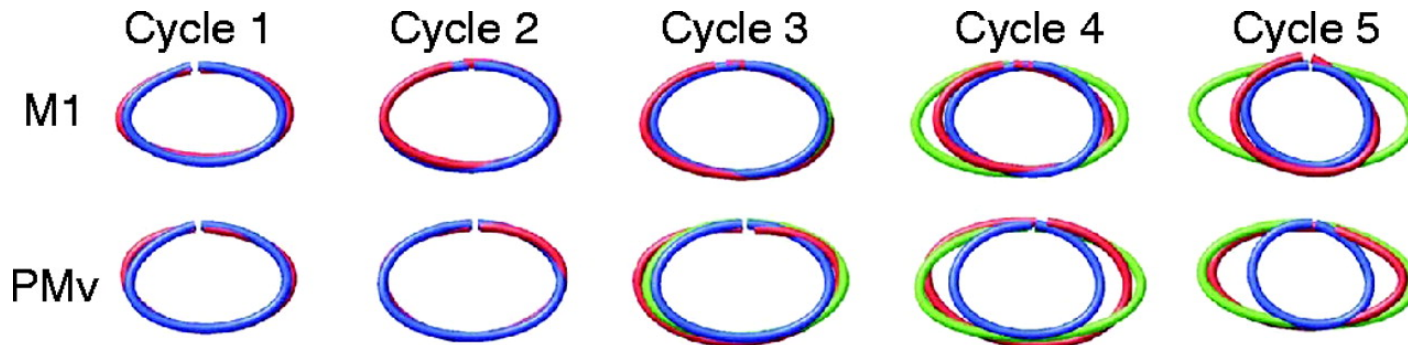
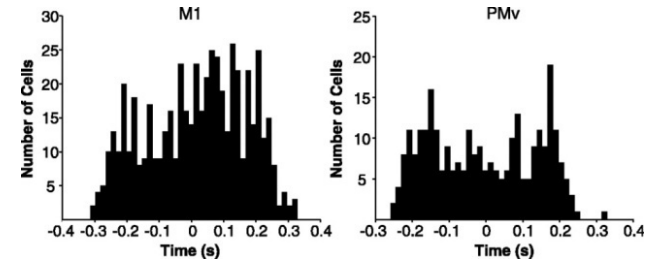
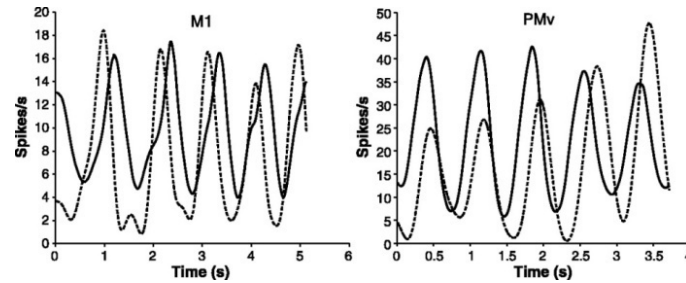
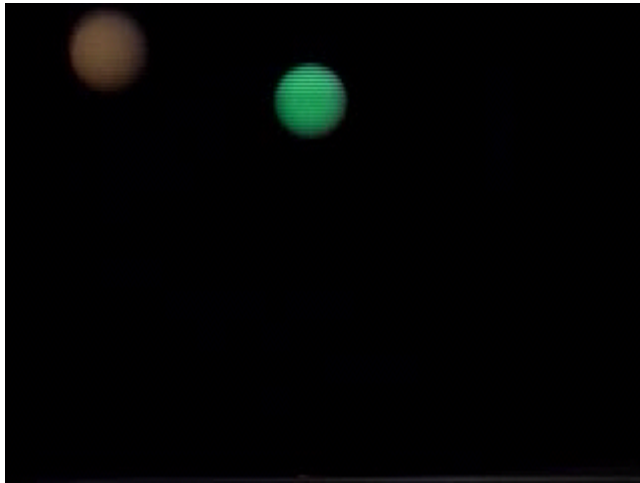
Premotor areas

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

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

The basal Ganglia

