Overview of Motor Systems and Motor Control

- Movement must be adaptive
- Movements must conform to body and its mechanical properties
- Movements must adapt to environmental conditions

Movement: what's involved?

- 1. Response to sensory input (rare)
  - Input >> integration >> simple coordinated output
    - Input: sensory receptor activation
    - Integration: spinal cord and brain
    - Output: motoneuron activation > muscle contraction > simple behavior
- 2. Ongoing behavior + input (predominant)
  - Input >> integration and accommodation >> adaptively altered output pattern
    - Input: sensory receptor activation
    - Integration: spinal cord and brain
    - Output: motoneuron activation > muscle contraction > complex behavior

Overview of Motor tutorial

- Muscle properties
- Motoneurons – the neurons that drive muscles
- Muscles and their properties
- Spinal cord and its organization
  - Muscle synergies: building in adaptive sequencing through interneurons
  - Muscle synergies: higher order movement primitives
    - Body centered movement control?
- Motor cortex – M1
  - Input/output relationships with muscles and body
    - World centered movement control?
    - Shoulder centered movement control?

Summary of control scheme: Details remain to be specified

- Cortex activation is to world or some body centered coordinates
- Spinal cord translates cortical signals to body centered coordinates
- Spinal interneurons activate synergistic movements adaptively controlled to final desired position relative to body at a given moment

Question:

- Remember that there are multiple limbs
- Each limb has multiple joints, each with multiple degrees of freedom
- Each joint has multiple muscles, each with multiple muscle fibers
- Each muscle fiber type produces a different pattern of contraction
- Each muscle fiber has multiple elements

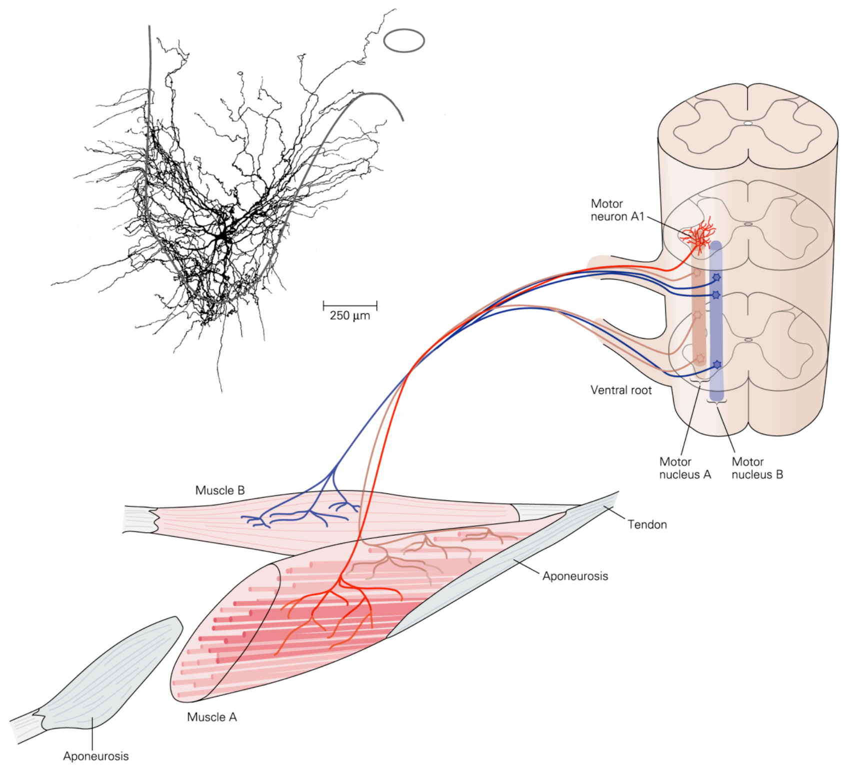
How are all these degrees of freedom controlled? Why don't we fall on our faces every time we try to kick a ball?

Question for robot construction:

- How do we solve the degrees of freedom problem as we add more joints and degrees of freedom for joints?
- If we use “adaptive reflexes” like Tekken, can a CPG chip give us enough for free?
- What about when we add more actuators? How do we provide subtle control of limbs?
- Sarcos and Asimo mimic us, but principles don’t exploit the biology fully.

Motoneurons and muscle units

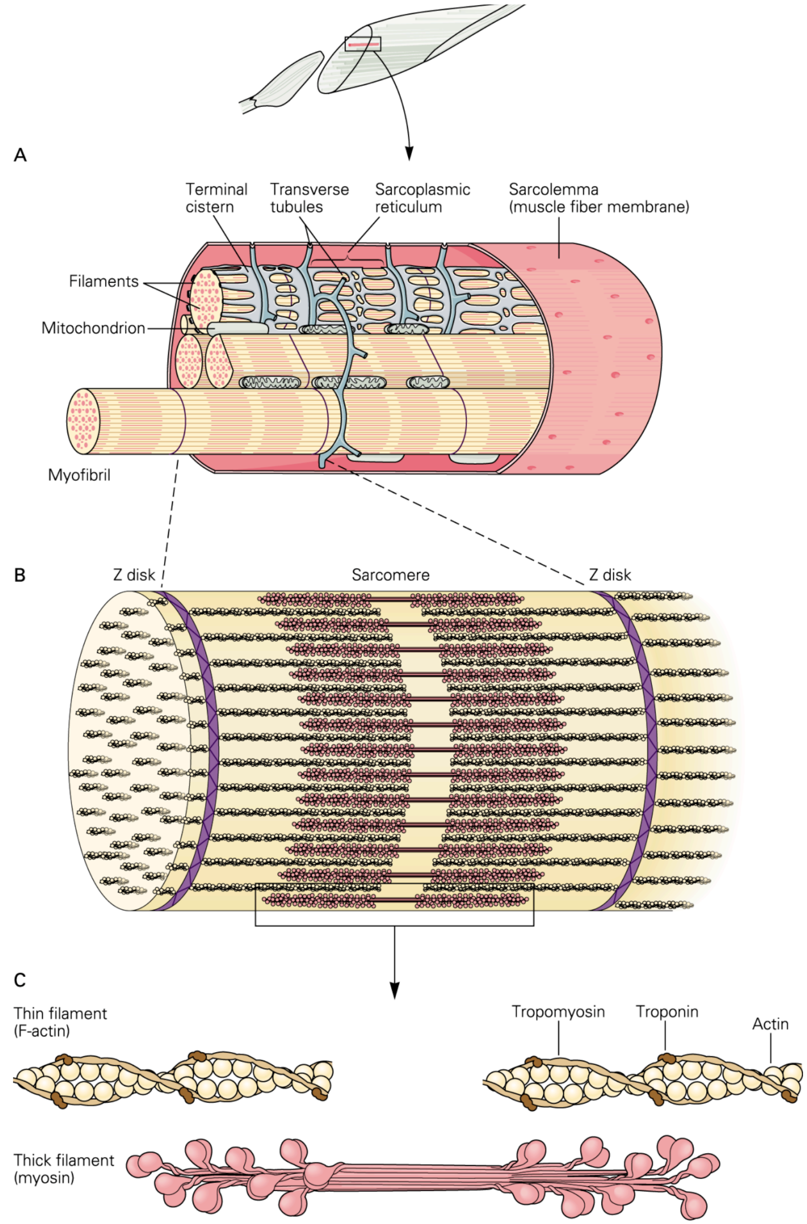
- Motoneuron in spinal cord – part of **motor nucleus** for a given muscle
- Innervates muscle fibers – to form **muscle unit**
- Muscle unit is distributed throughout a portion of the muscle



Distributed contraction provides smooth output

Muscles and their fibers

- Gross organization of muscle – **extrafusal** *fibers*
  - Myofilaments (thick and thin) >
  - Sarcomere >
  - Myofibril
  - Muscle fiber >
- Muscle fiber (diagrammatic)
  - separated by tubules of sarcoplasmic reticulum
  - Includes mitochondria



Relative proportions of sarcomeres determine strength and speed of contraction

Muscle composition

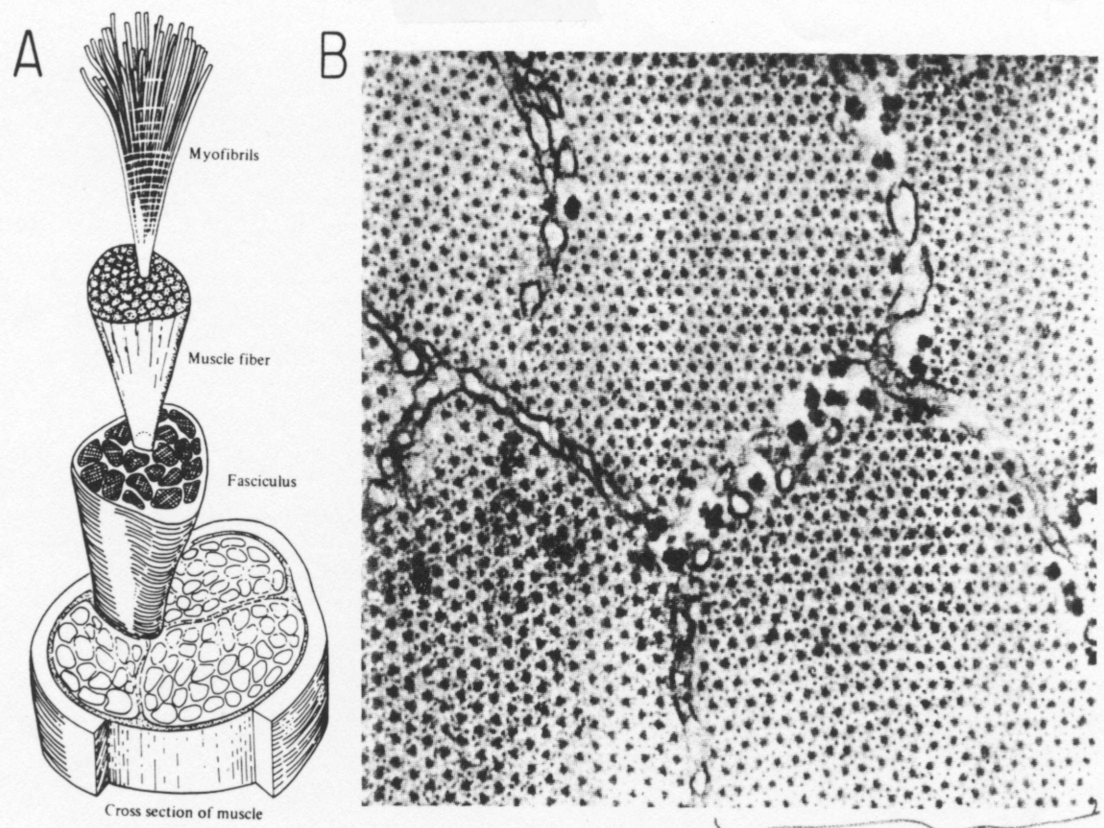
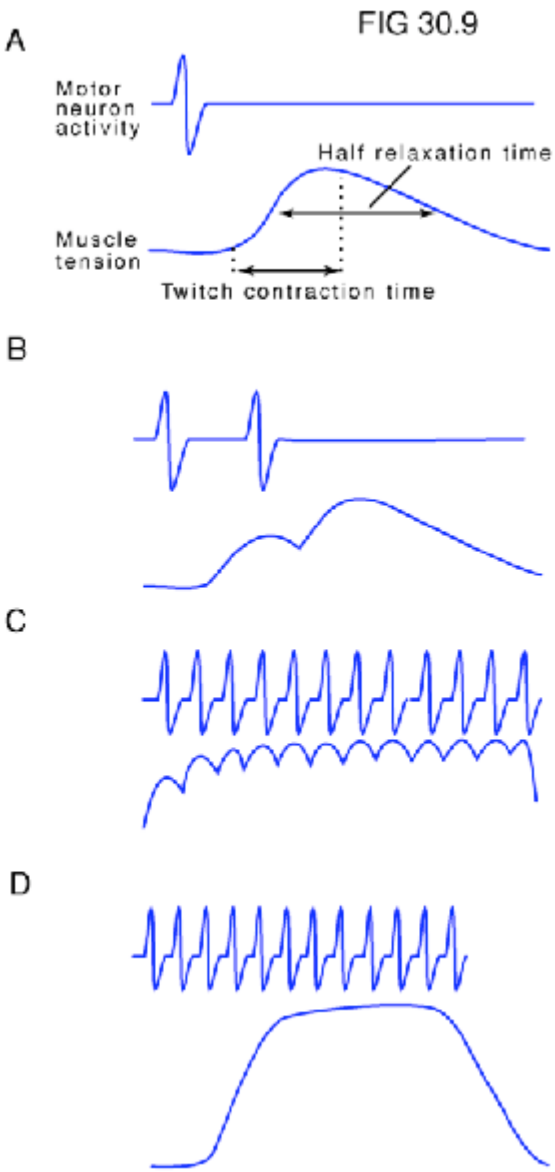


Fig. 8.1 (A) A diagram of a muscle cross section showing its gross organization and terminology. (B) An electron micrograph of several myofibrils each surrounded by tubules of the sarcoplasmic reticulum. Within each myofibril a hexagonal array of thick and thin filaments is seen. (From Dowben, 1969.)

- (A) Another view of muscle from myofibrils to whole muscle via fasciculus
- (B) EM cross section of muscle fibers – notice thick and thin filaments in arrays
  - separated by tubules of sarcoplasmic reticulum
  - Includes mitochondria also

Numbers of mitochondria and enzyme types determine speed and durability of contraction

Contraction characteristics

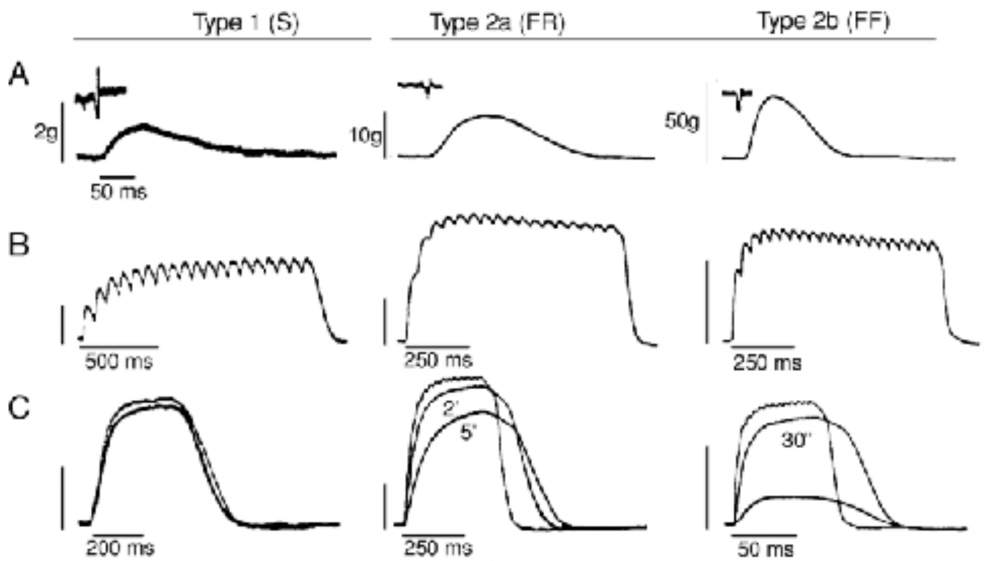


- (A) Action potential => Muscle contraction
- (B) Tension sums
- (C) Reaches maximum
- (D) Tetanic contraction – maximal force

- Motor unit = motor neuron + muscle fibers it innervates
- Muscle unit = muscle fibers innervated by one fiber

Motor unit properties

FIG 30.10



MUSCLE FIBER TYPES

S – slow, small force, less fusion, no fatigue

FR – faster, more force, more fusion, not much fatigue

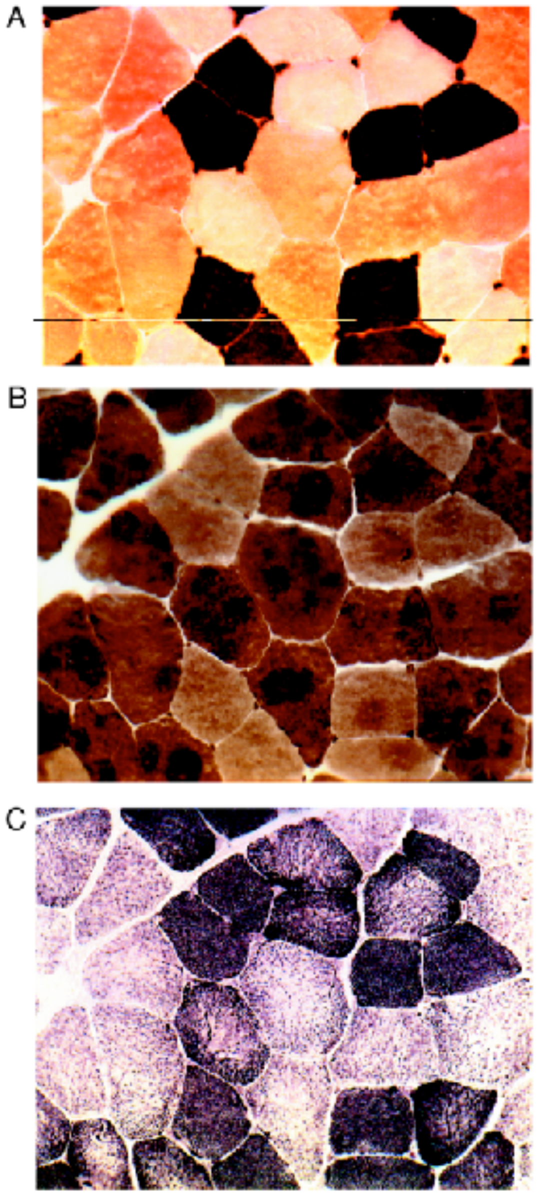
FF – fast, most force, rapidly fatigue

- (A) single contraction – note amplitude, speed of contraction is typical for fiber type
- (B) fusion of tension – degree and ease of fusion is typical of fiber type
- (C) maximal force production with tetanic contraction – amplitude and decay typical of fiber type

- NOTE: Scale differences on each graph!

Muscle types

FIG 30.7



Fibers of muscle and muscle unit sectioned and stained in different slices – stained are one unit

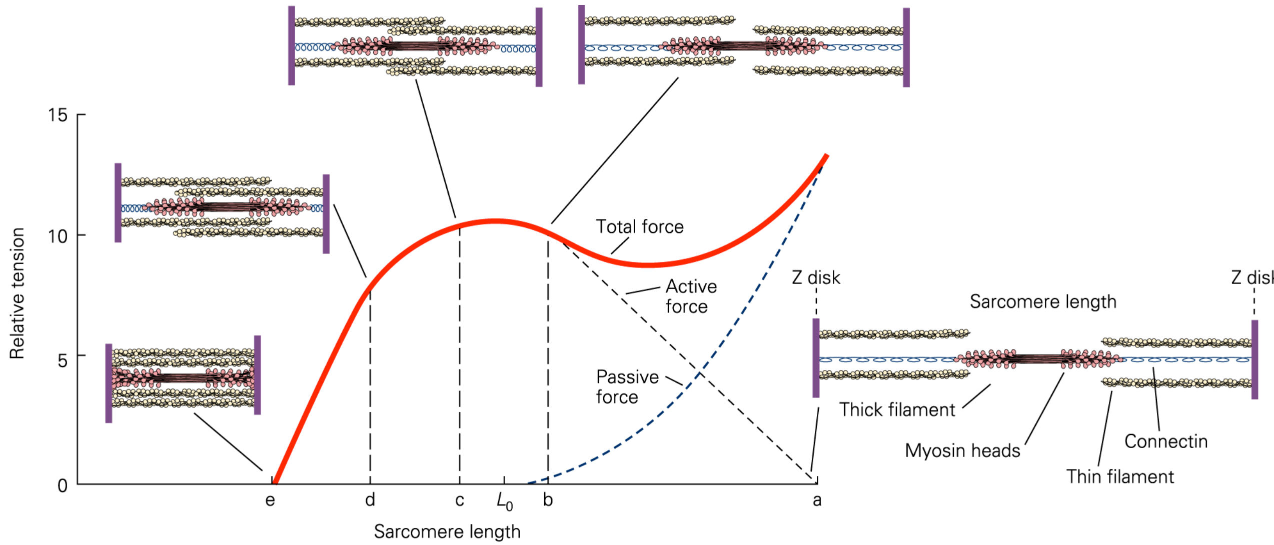
- Muscle fibers types
  - Oxidative = slow – S, type 1
  - Mixed = fast fatigue resistant – FR, type 2a
  - Glycolytic = fast fatiguable – FF, type 2b
- Specified by neuron innervating fibers – α *motor neuron*
- Neuron innervates many fibers – distributed around muscle fascicule

(A) Type 1 – oxidative

(B) Type 2b – glycolytic

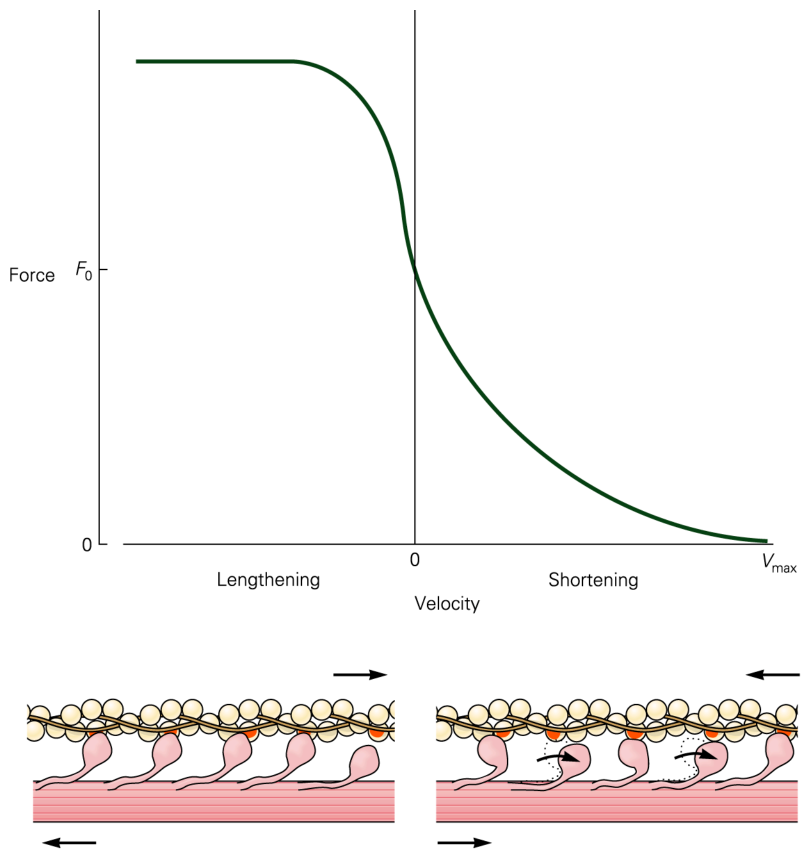
(C) Type 1 and 2a (lighter) – oxidative but 2a are faster than 1

Dynamics of muscle force production



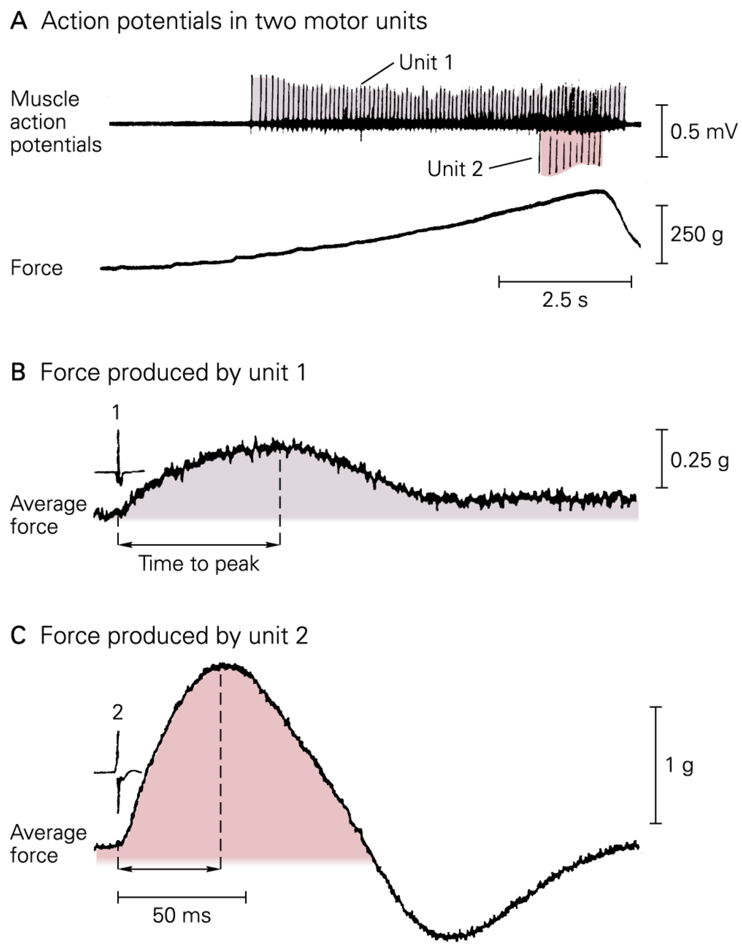
- (A) Because of formation and action of cross-bridges:
  - Optimal length = maximal overlap thick and thin filaments (optimal at c)
  - Less optimal = reduced overlap with too much stretch
  - Less optimal = too much overlap with too short stretch
- NB: even better is while pulling on muscle at optimal length – "lengthening contraction" is best!

Lengthening contraction



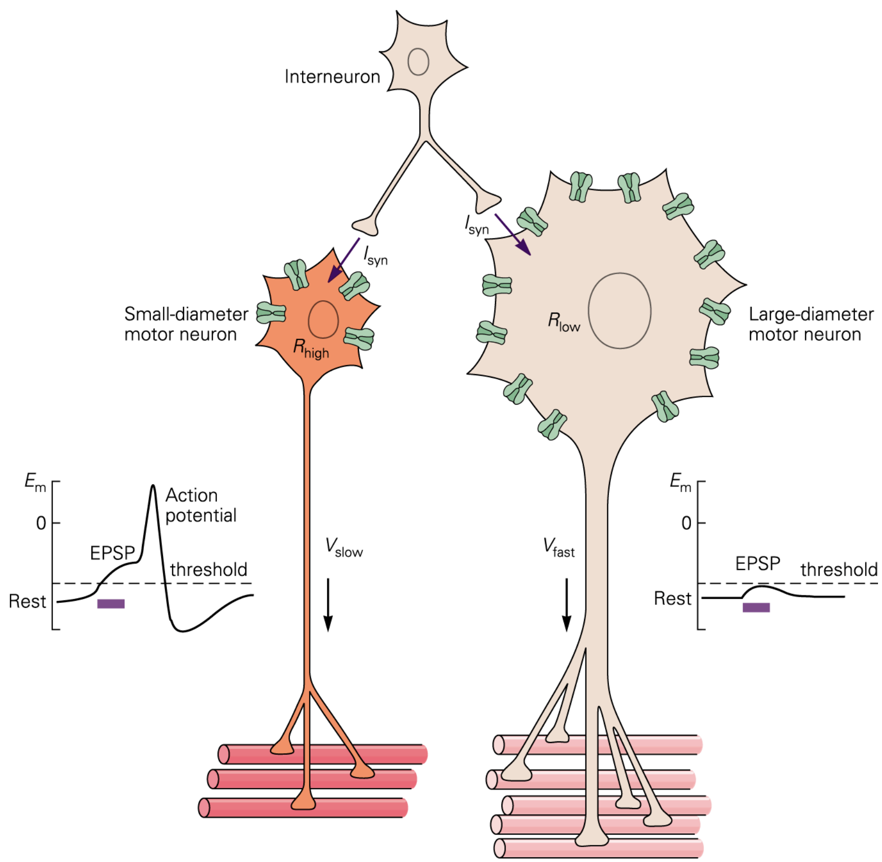
- Greatest force production when muscle is being stretched
- Far less force as muscle is being shortened

Muscle recruitment – by size



- Small units with slow fibers are recruited (turned on) first
- Larger units with more force production are recruited as more force is generated and required

Proposed mechanism for recruitment order



- Smaller motoneurons innervate slow fibers – higher input resistance >> fire more easily than larger motoneurons with lower input resistance

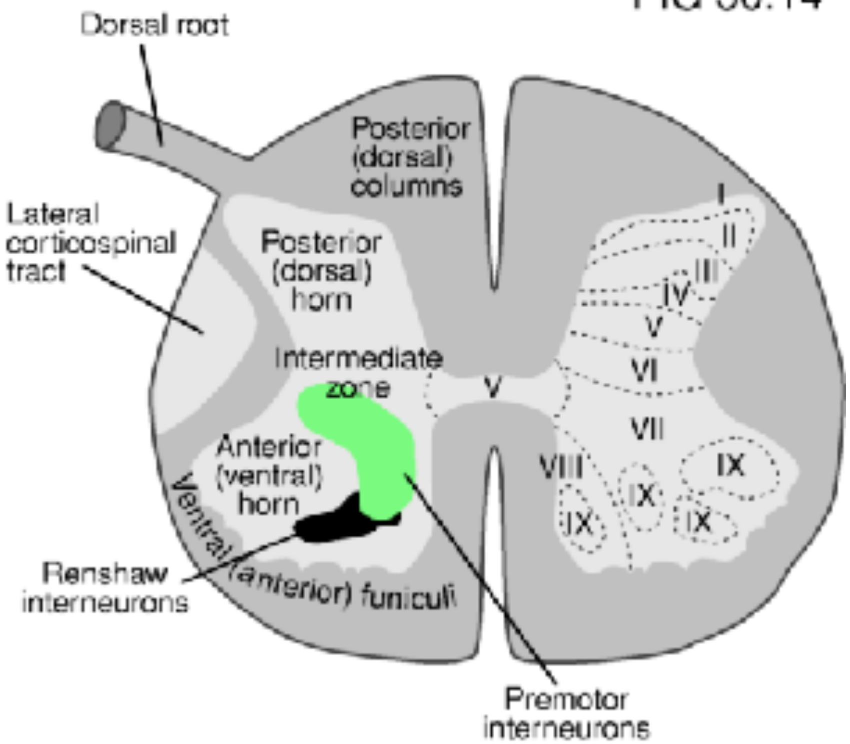
- Not entirely agreed upon mechanism

Statements & Questions (not to be answered now)

- Some characteristics of muscle fiber contractions are determined by the structure and composition of muscles.
- Some characteristics of whole muscle contraction are determined by the distribution of fibers and their recruitment order.
- Motoneuron "matches" fiber type to produce appropriate contraction for its type.

•How do the properties and structure develop to match each other?
•How do motoneurons find their appropriate fiber types? Or do they induce the appropriate fiber types?

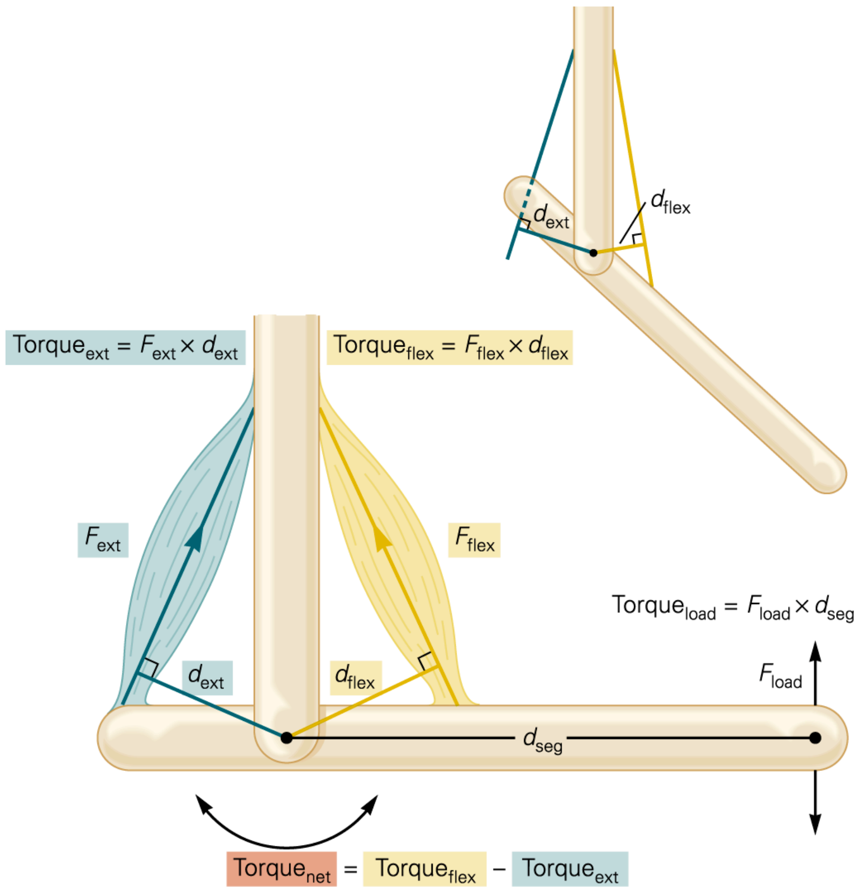
Spinal cord



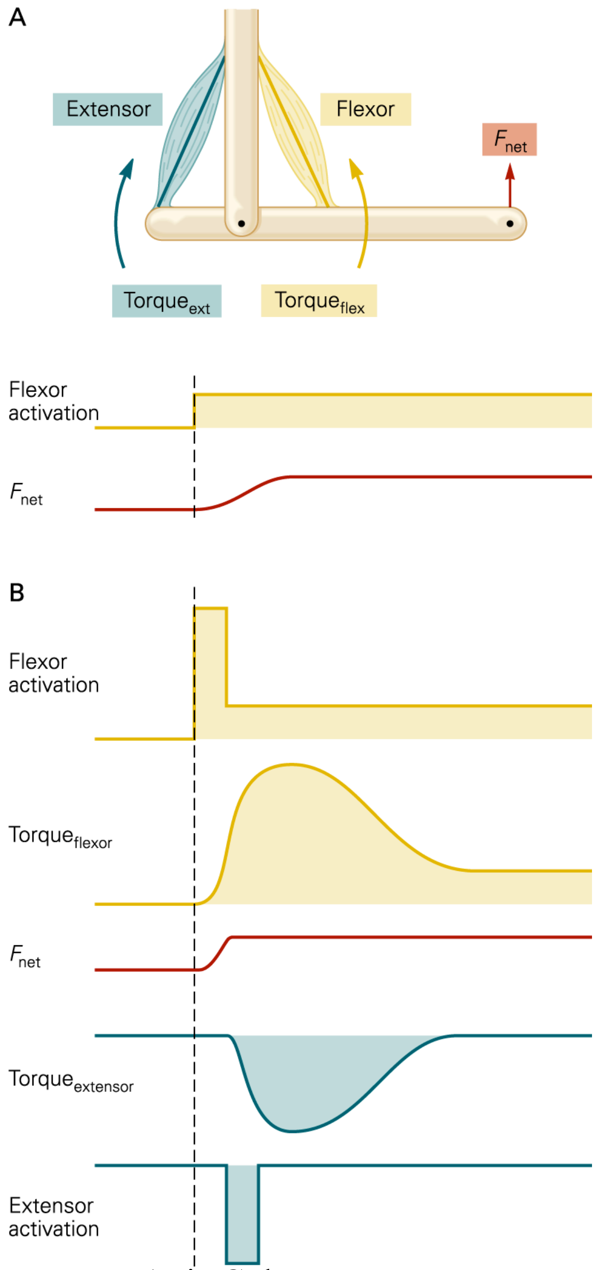
- Dorsal root and horn – sensory input
- Ventral root – output
- Interneurons in laminae
  - Renshaw interneurons: inhibitory, self-damping
  - Premotor interneurons, coordinate and drive
- Fiber tracts in white matter
  - Descending from brain
  - Propriospinal: Ascending and descending within spinal cord

Lamina I-V: sensory
Lamina VI,VII,VIII: motor integration
Lamina IX: motor neuron cell bodies
Motor pools: one for each muscle in columns longitudinally in spinal cord

Diagram of forces

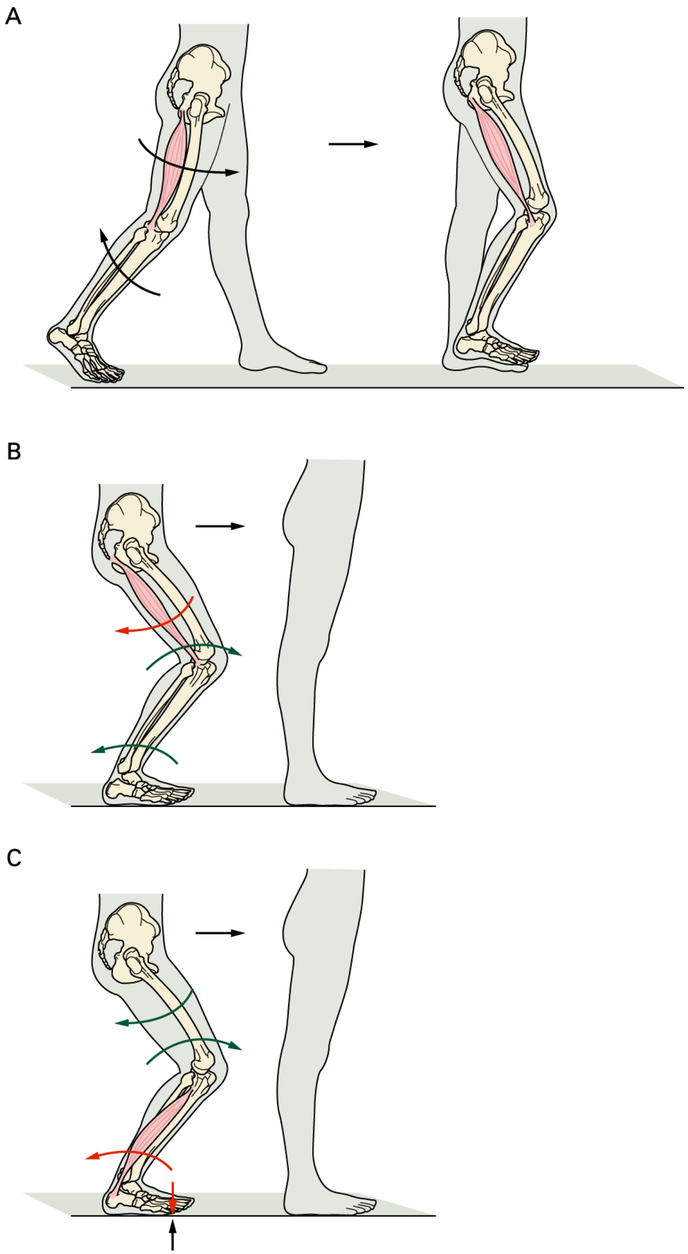


- Force generation is along the line of the tendon (not usually simple as shown)
- Torque is generated at joint as a function of moment arm and force (moment arm: the length of a perpendicular from the line of pull of the muscle to the center of rotation of the joint) – changes as muscle contracts…



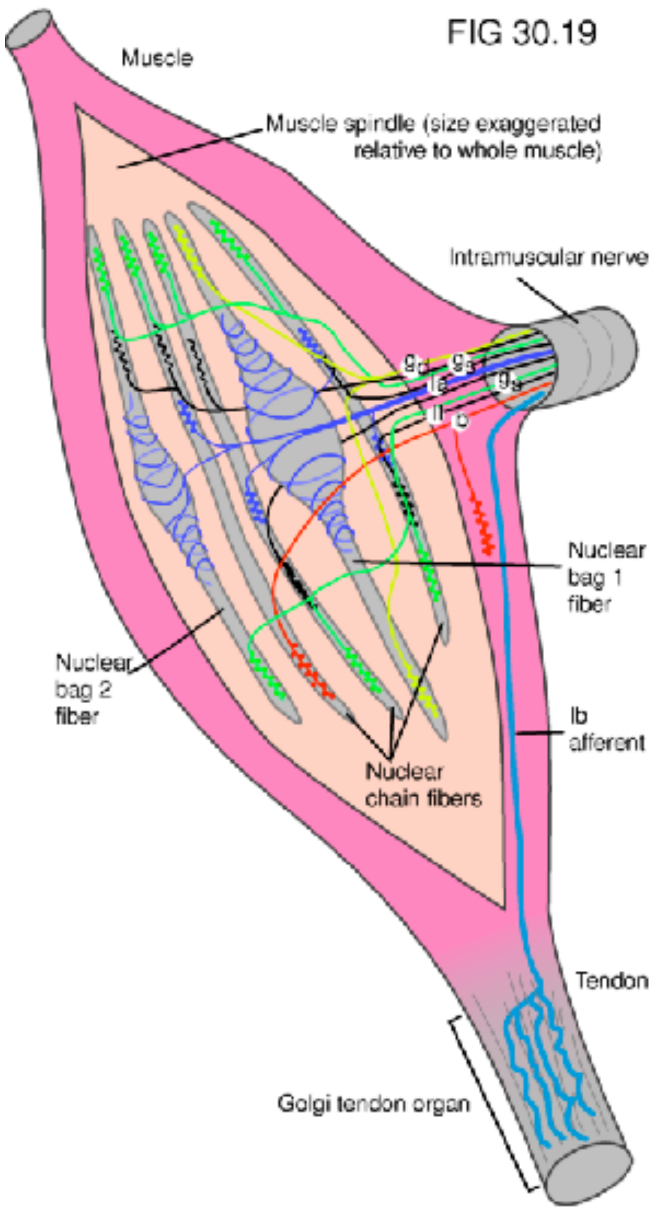
Actual force generation is slower than neural activation

- Neural activation occurs > activates contraction mechanism in muscle > slowly generates force (torque) at joint
- The amount of torque will depend on angle of joint and motion of joint when contraction builds
- Remember that length tension relationship will mean that larger joint angle and increasing angle will generate more force than reduced angle and decreasing angle



Biarticular muscles

- Hamstring muscle – hip extensor/knee flexor is made more efficient by lengthening of muscle during activation
  - Knee flexion shortens it
  - Hip flexion lengthens it >> swinging limb forward lengthens it producing increased force for extension of limb as it lands
- Generally, motion creates complex mechanics with the biarticular muscles



Spindle organ: stretch receptor and γ–motoneurons: servo-assist mechanism

- Muscle fibers contain spindle fibers – stretch elements
- Spindle fibers contain small muscle fibers at their ends – these γ-motoneuron fibers control the action of the spindle but generate no force during movement
- Action of spindle is determined more by the small muscle fibers than by the large force generating muscle

Motor control

(g) in figure = γ

Reflexes

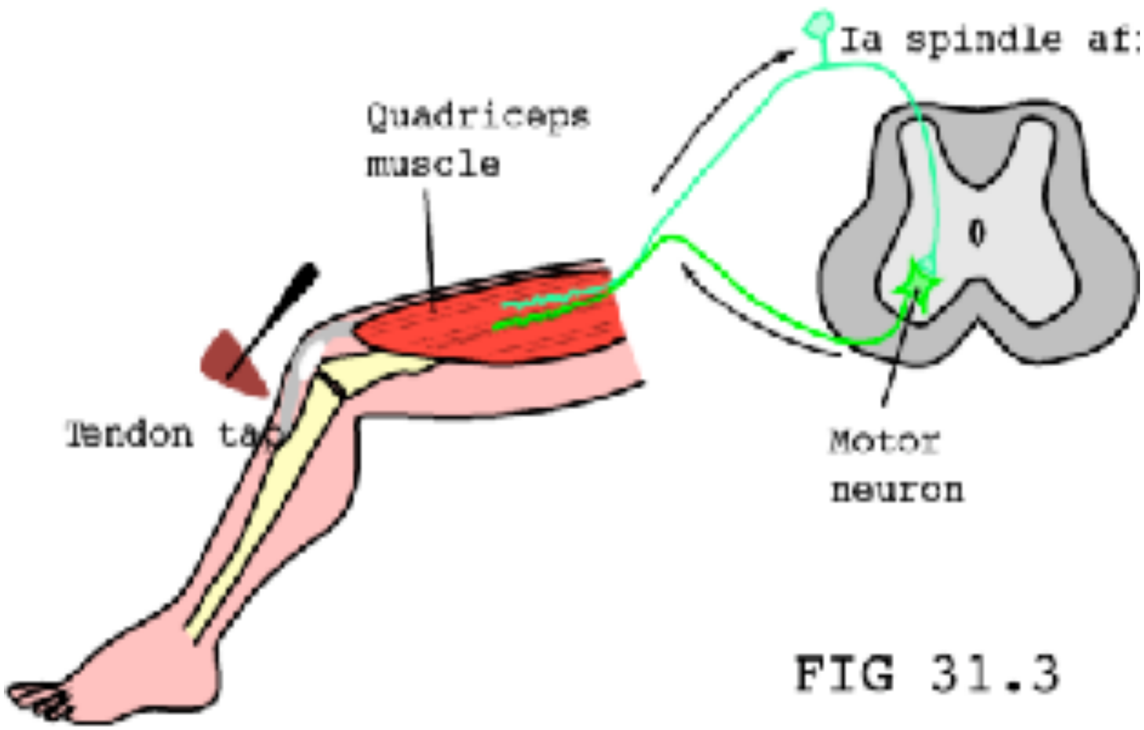
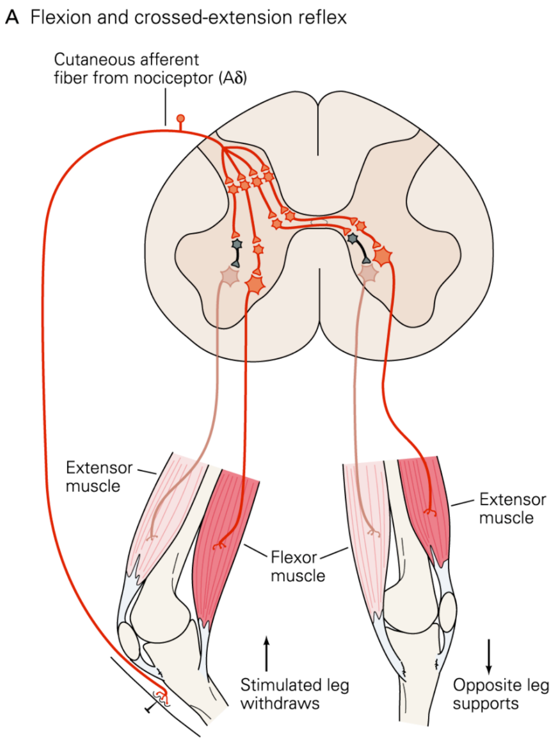
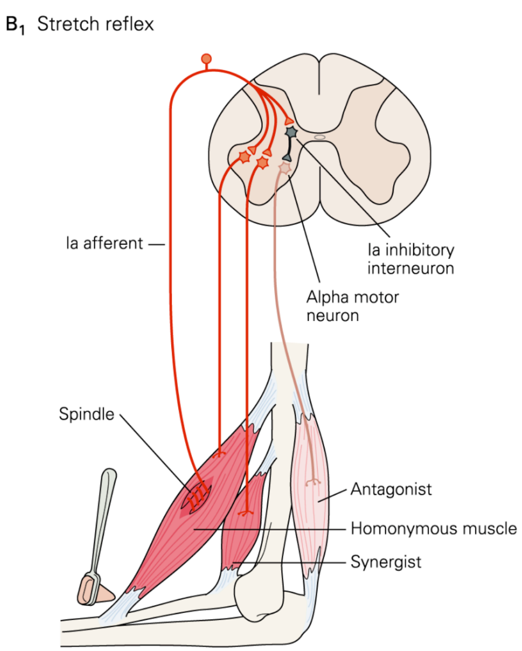


FIG 31.3

- Stretch reflex – action via Ia's of spindles
  - Simple monosynaptic reflex
  - Monosynaptic action is excitation of homonymous muscle
- Stretch > contraction





Coordinated reflexes

- Reflexes of extensors and flexors across a joint are coupled – as one is excited, the other is inhibited >> lengthens the correct one and shortens the antagonist – mediated by spindles and Ia's
- Reflexes across the girdle are also coordinated to give properly coordinated movement

Role of γ's in movement: intrafusal fibers – part of spindle

- Hypothesis: γ's drive α's with activation through Ia's
- Prediction: γ's fire just before α's

____||||||_________________ α's

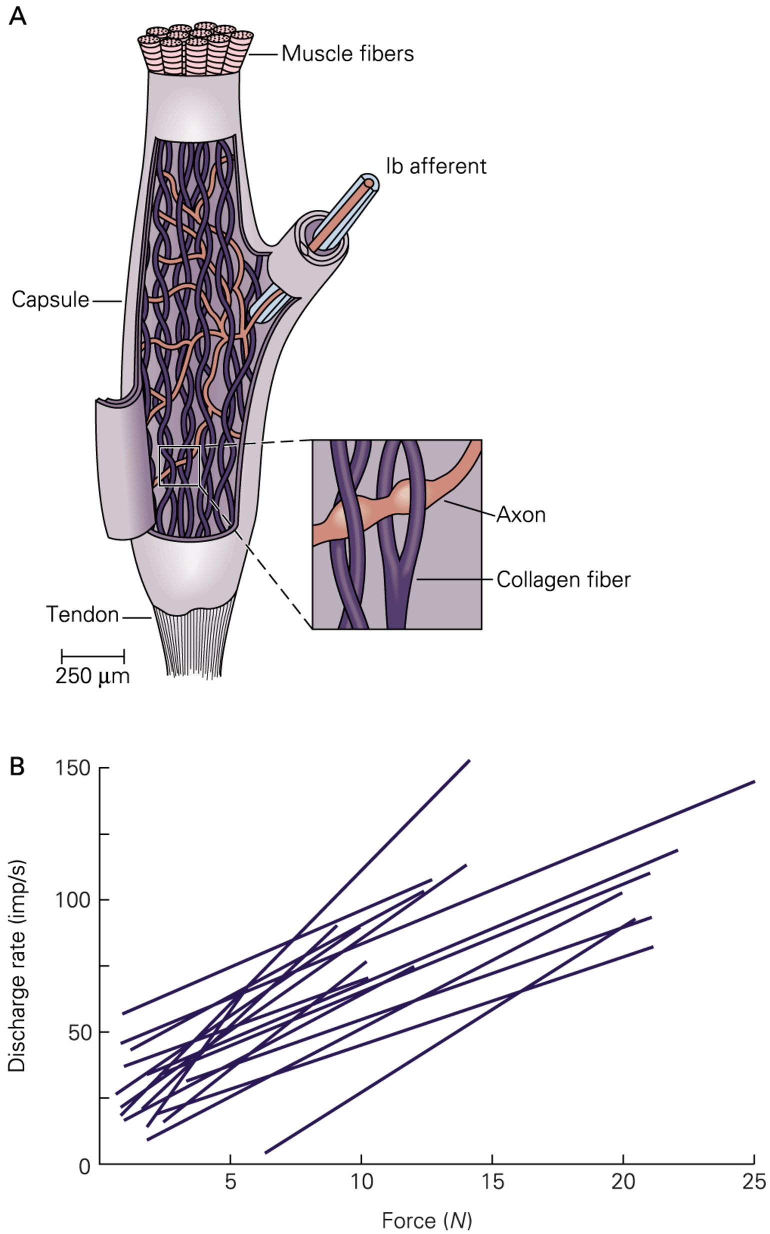
___|||||||_________________ γ's

- Seen in "reduced preparations" but not in natural movements >> False

- After pause γ's do fire and maintain stretch >> servo-assist after slackening from initial contraction

_____||||||||_________________ α's

_____|| ||||_________________ γ's



Golgi tendon organs: GTOs

- Mediate inhibitory reflexes from sensors to motoneurons – believed to prevent over forcing muscle, but used over the full range of motion

Add Interneurons to coordinate

- Ia Interneuron inhibitory
  - Input from Ia spindles (guarantees reciprocal action of muscles)

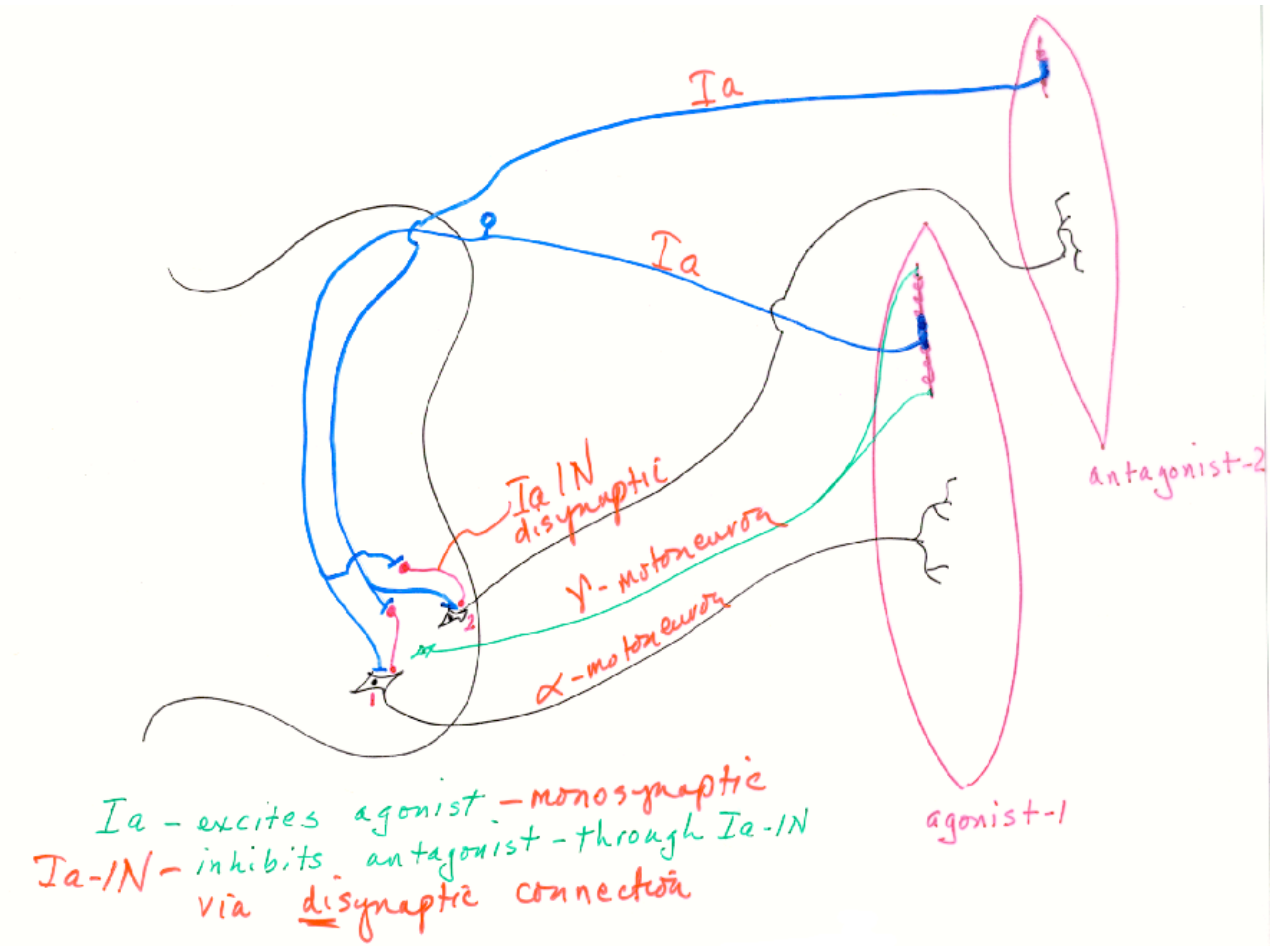
- Renshaw cell inhibitory
  - Input from motoneuron collatoral (provides self-damping?)

- Ib Interneuron inhibitory
  - Input from Golgi tendon organs (prevents over-stretching?)

- Ia presynaptic inhibitory
- Ia presynaptic excitatory
- Group II +/- ??
  - Input from group II spindles

Each goes to its own population of motor neurons

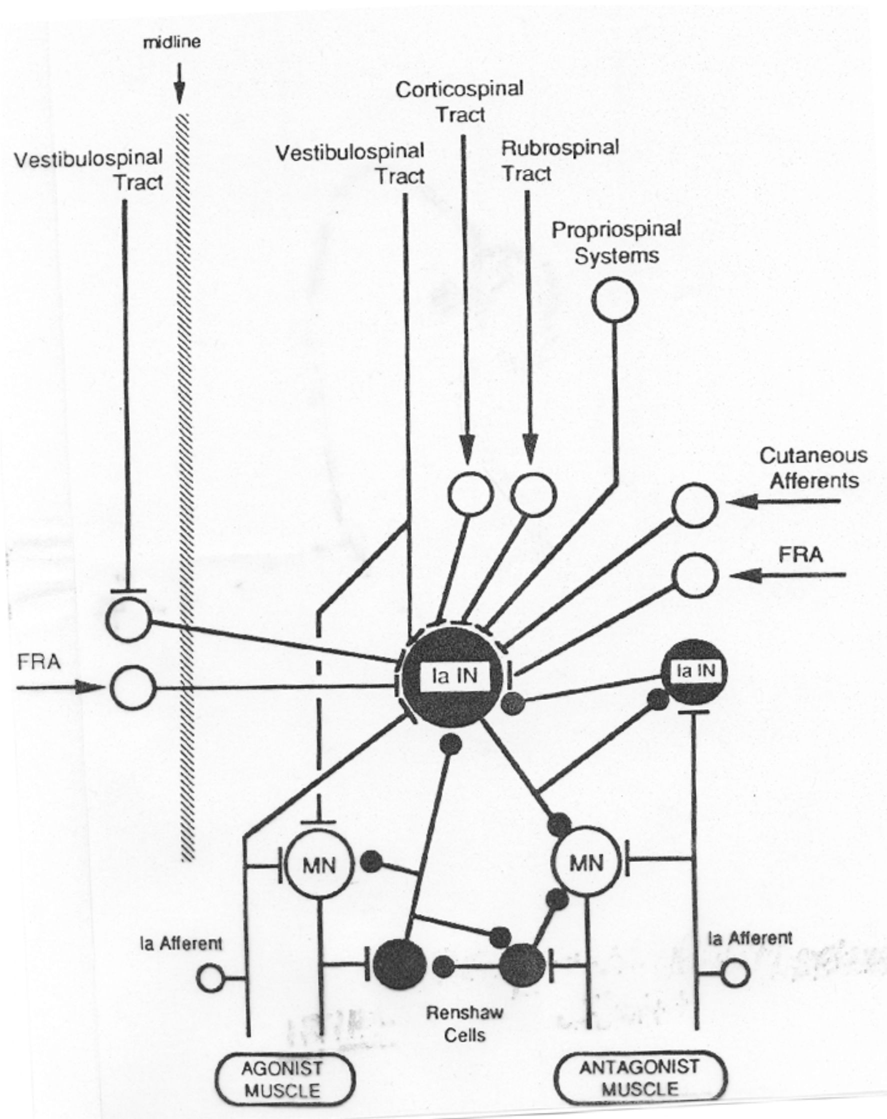
Reflex connection between antagonists



- Ia excites agonist – monosynaptic connection
- Ia-IN inhibits antagonist – di-synaptic connection
- Ib inhibits its own muscle – di-synaptic connection via Ib-IN
- **Question 2 again: How does this develop?**

Thus: sensory inputs can coordinate complex and organized movements

Jankowska: spinal cord circuitry



- Interneurons are part of a circuitry that coordinates muscles for movements.
- Interneurons serve multipurpose roles
  - Receive descending inputs
  - Receive sensory inputs
  - Project to motor neurons
  - Participate in voluntary movements
  - Participate in reflex movements

Example is IaIN, but principle holds for all INs

Spinal Organization: Answer to original question

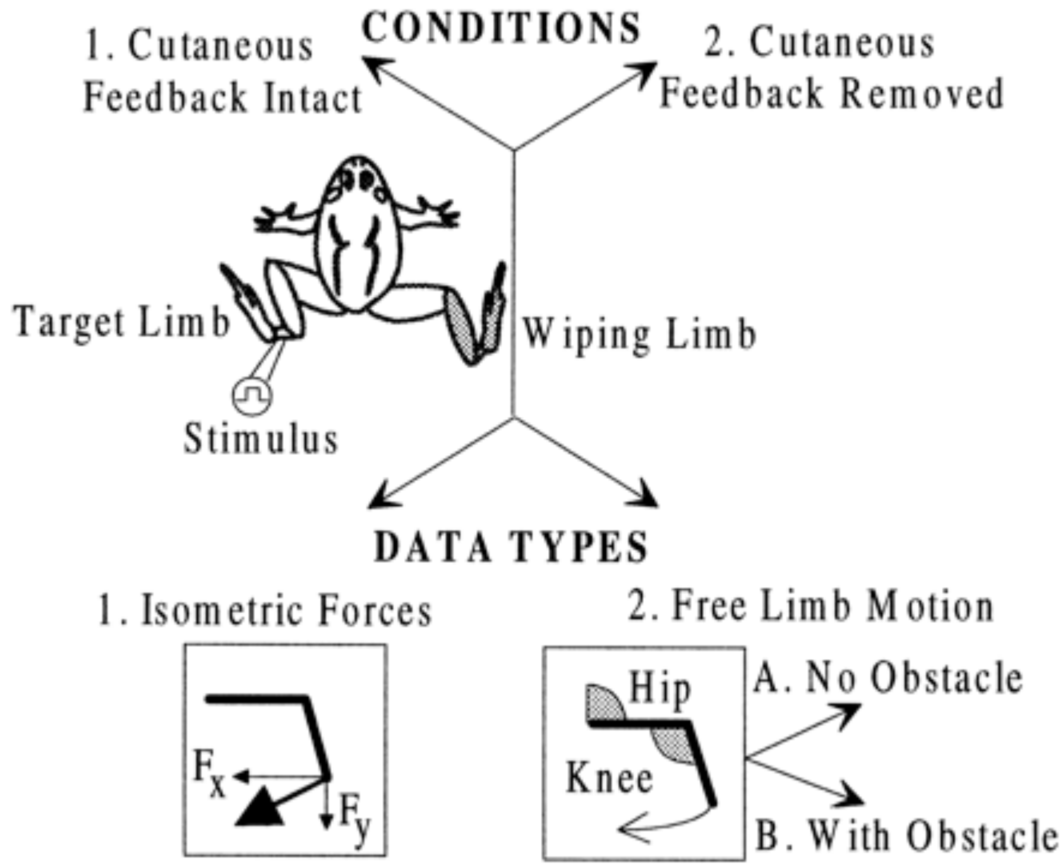
- The spinal cord is organized around synergies.
- Unless overridden by descending systems, the outputs will be coordinated sequences of muscle contractions –

  for free! Controls many degrees of freedom
- Descending activation will typically activate these same synergies.
- Sensory feedback is organized around the synergies.
- CPG is part of the synergistic organization – not a special structure
- Feedback from CPG to sensory control neurons shapes responses to environment

Spinal "Force Fields" – movement primitives

- Analysis of "force fields" – movement primitives or spinal control modules
- Frog is spinalized and decerebrated
- Force fields: movements that exhibit invariant force directions and magnitudes over time – only a few were found per animal when evoked by interneuron microstimulation and when movement was isometric
- Complex movements: summations of these primitives

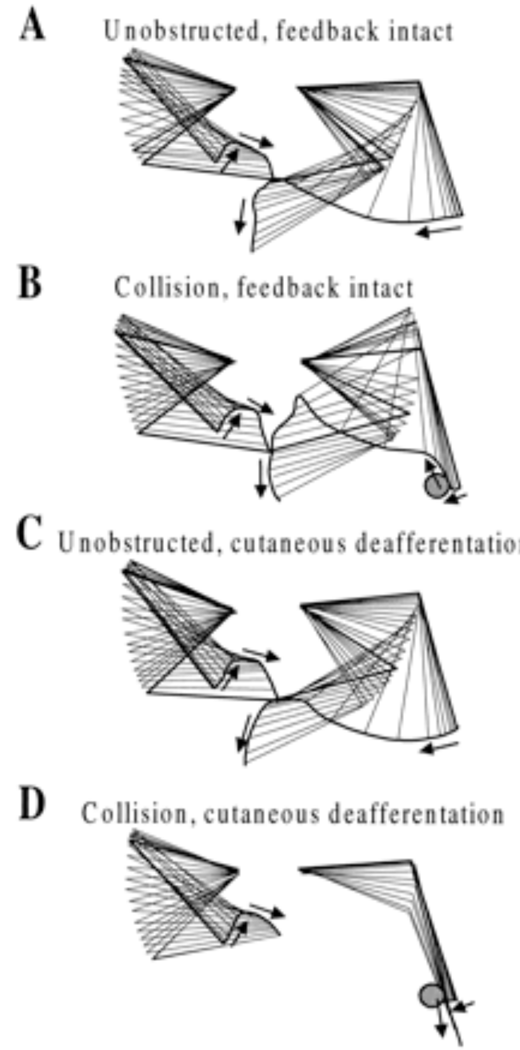
- Newer study: elicit movements with sensory stimulus and allow free movement



From Giszter

Movement Primitives

- Movements are elicited by sensory stimuli to hind leg
- Movement compensates for obstacles when sensory feedback is present
- Without sensory feedback, movement is still normal if unobstructed
- Without sensory feedback, obstacle cannot be avoided and movement is blocked in obstructed limb
- Remove obstacle, and limb continues its trajectory - reaches same point

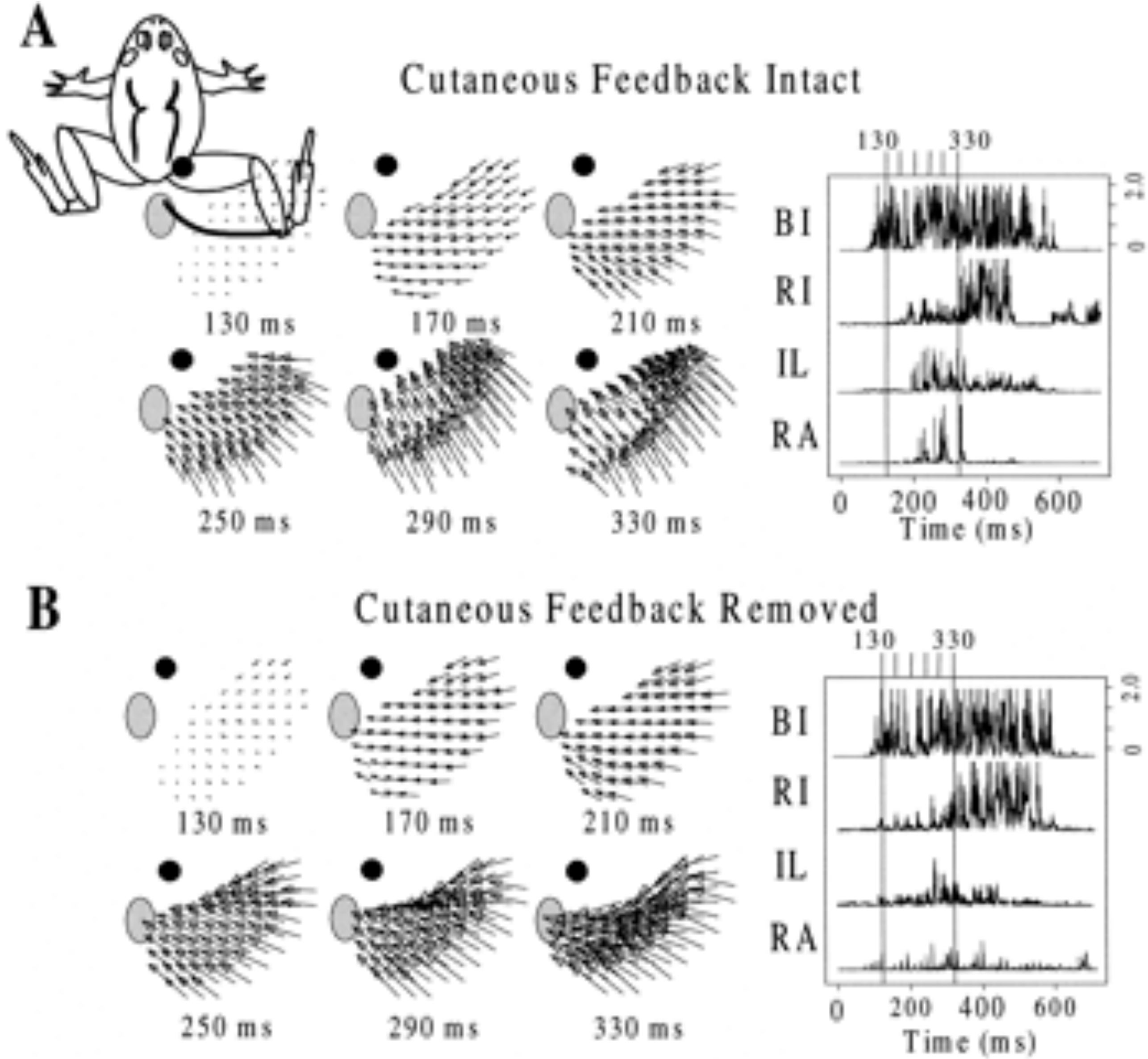


Partial mechanism for effect:

- Relative contraction forces of opposing muscles specifies a joint angle
- Dynamics of muscle - length-tension characteristics, and elastic properties produce passive portion of this effect - lead to joint angle
- Again: muscle properties take care of some degrees of freedom, and neural control specifies some others.

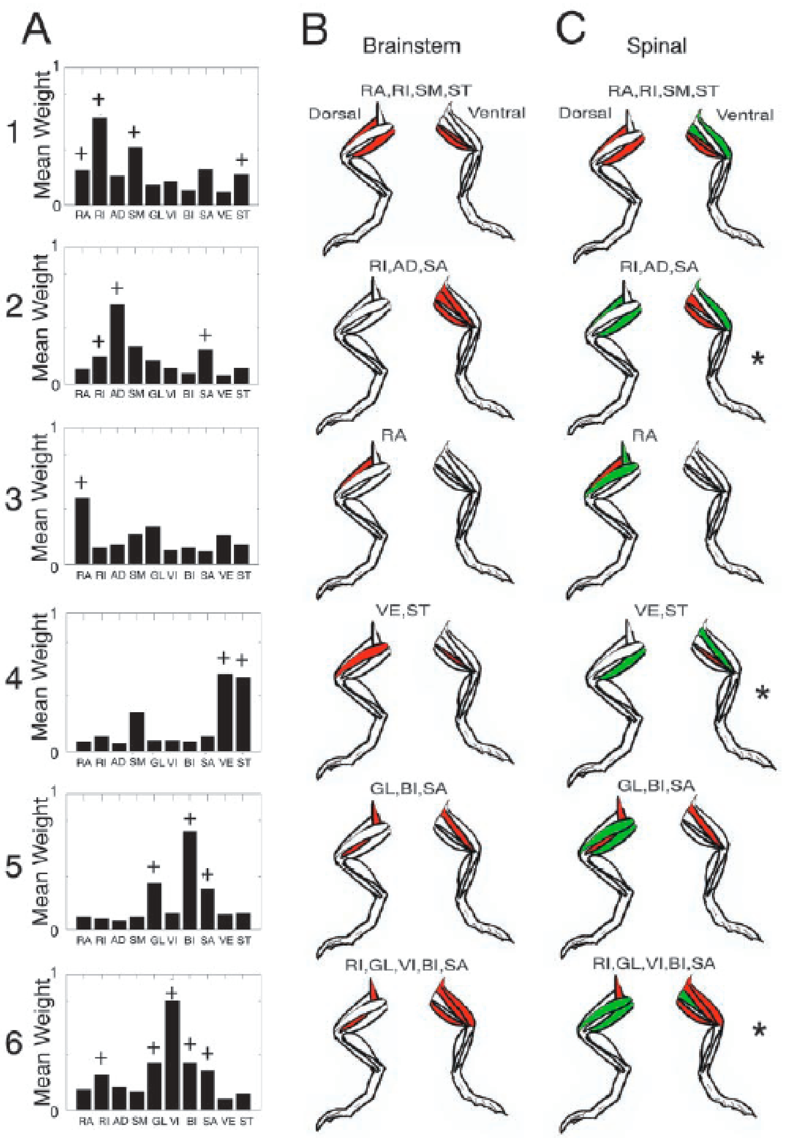
Summation of Movement Primitives

- Force vectors for movements begun at a variety of initial positions
- To see if movements are superpositions of primitives, they subtract vector fields of A-B to get correction responses…..



Avis Cohen
ISR/Biology: UMD

Latest iteration: Independent component analysis



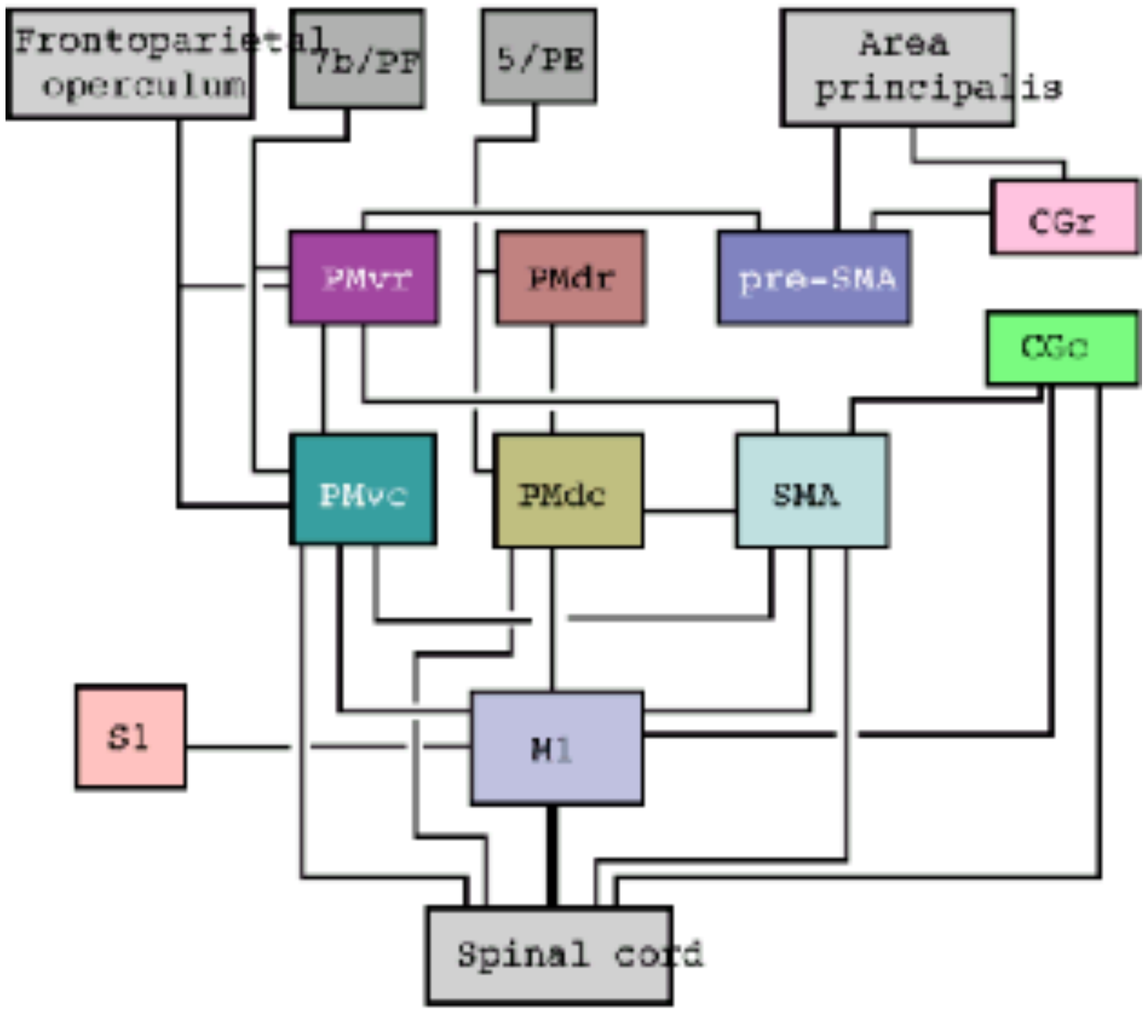
- ICA reveals 6 independent components from several behaviors
- Same mechanisms seem to be involved so far
- Synergists are linked during contractions to reduce the degrees of freedom

Onto Motor Cortex: M1

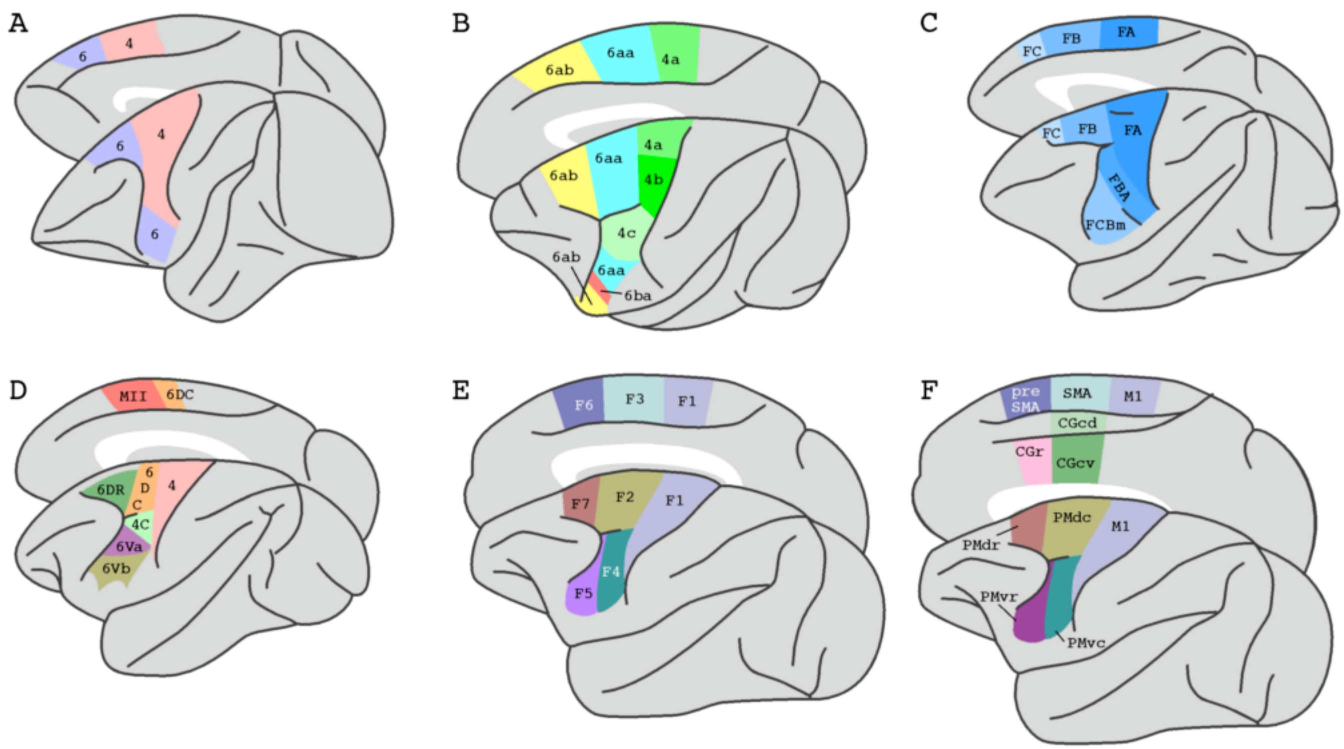
- One of last stops as motor signals exit brain and go to spinal cord

- Overlooks lots of other motor areas in which processing occurs:
  – Basal ganglia
  – Cerebellum (mixed sensory/motor)
  – Other cortical areas
    - prefrontal motor
    - Supplemental motor
    - Frontal eye fields
    - Etc.

Other motor cortical areas

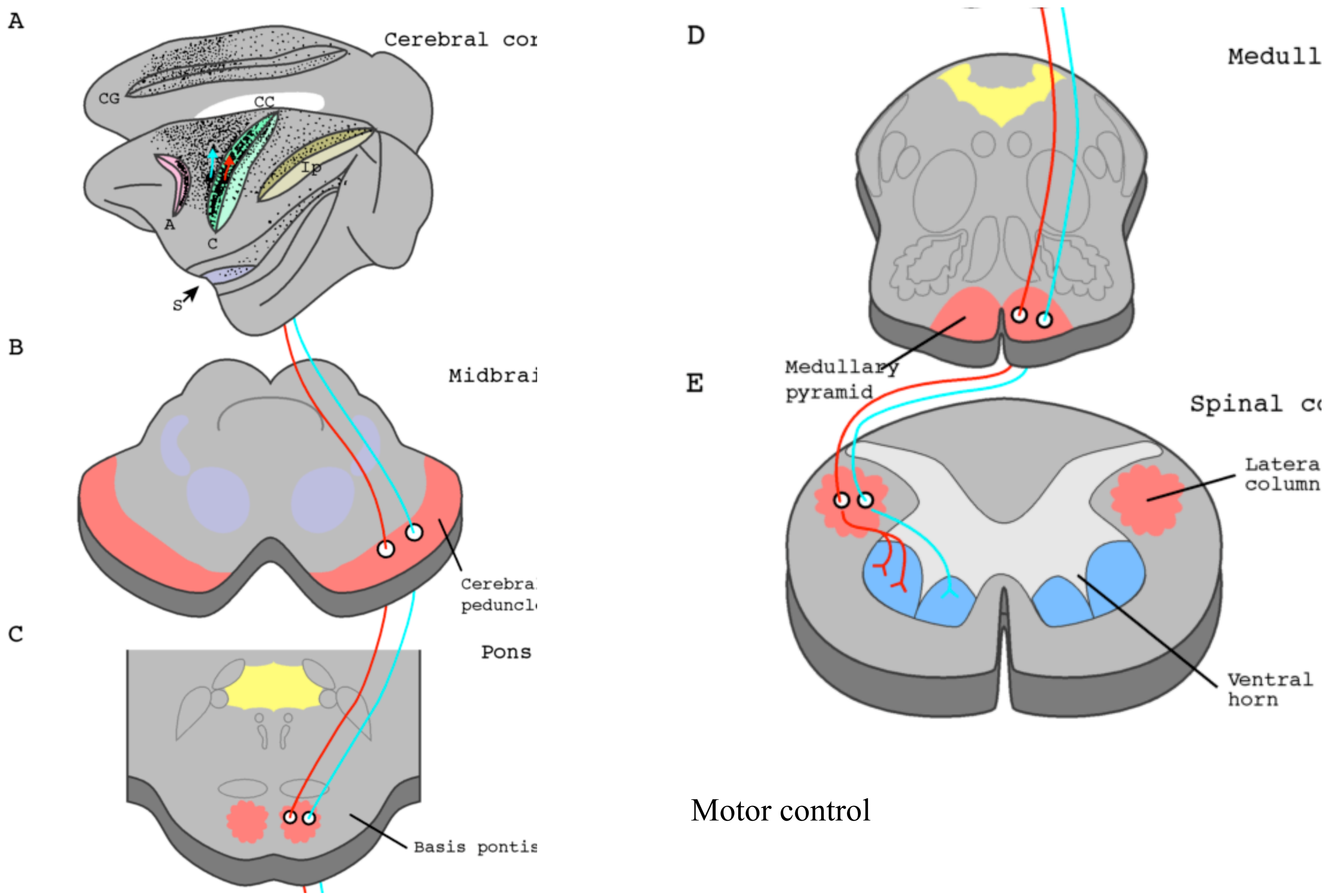


Motor cortical areas in macaque monkey as named by different people



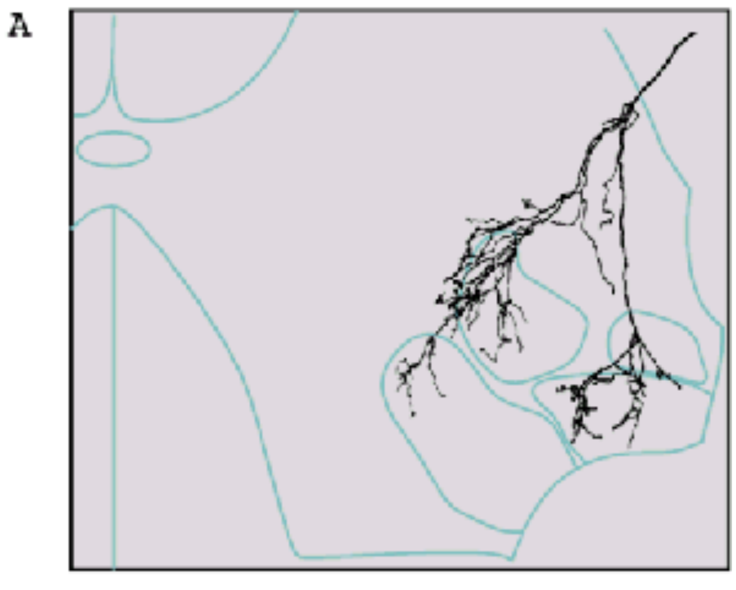
- Note area 4 (Brodmann)/M1(modern), just in front of big fissure - all are frontal lobe - in front of sensory areas

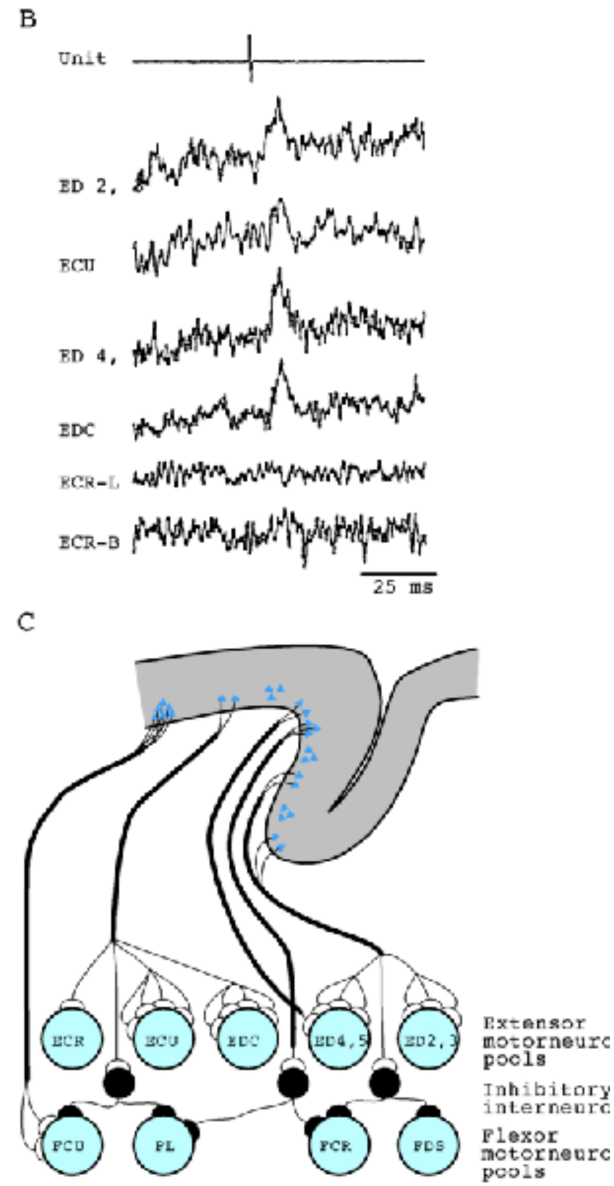
Pathway from M1 to Motoneurons



Motor control

M1 > Motoneurons
1:many





Avis Cohen
ISR/Biology: UMD

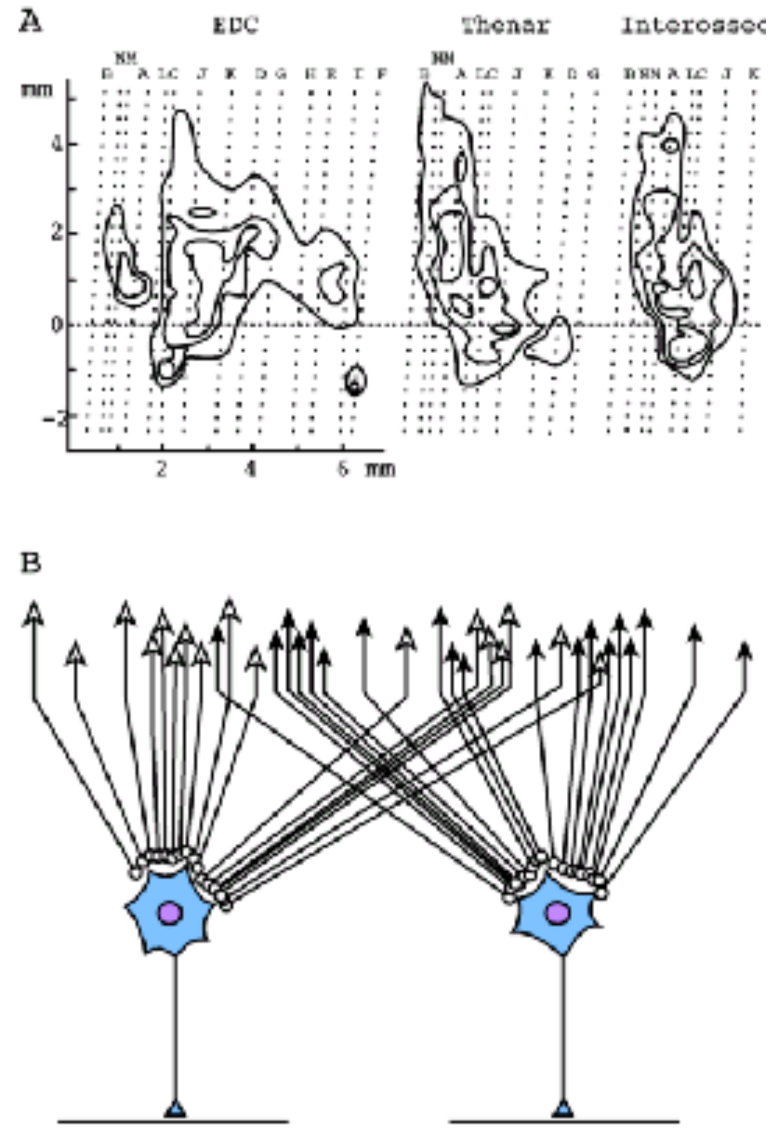
M1 > Motoneurons
Many:1

M1 to spinal cord is not simple signal >command

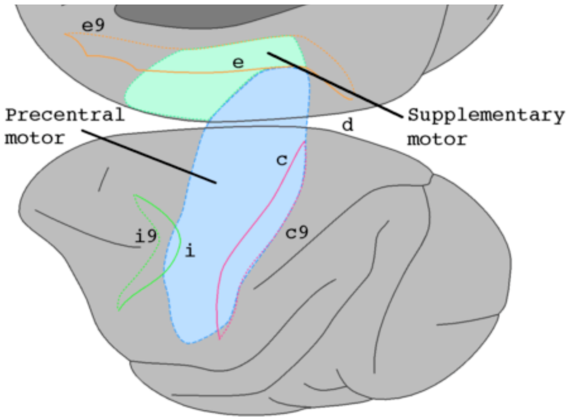
No little man giving orders

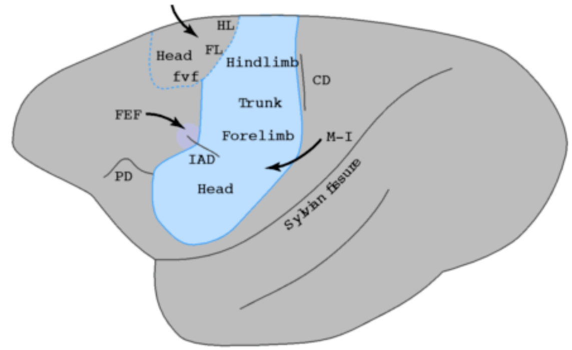
Distributed input to motoneurons and to interneurons

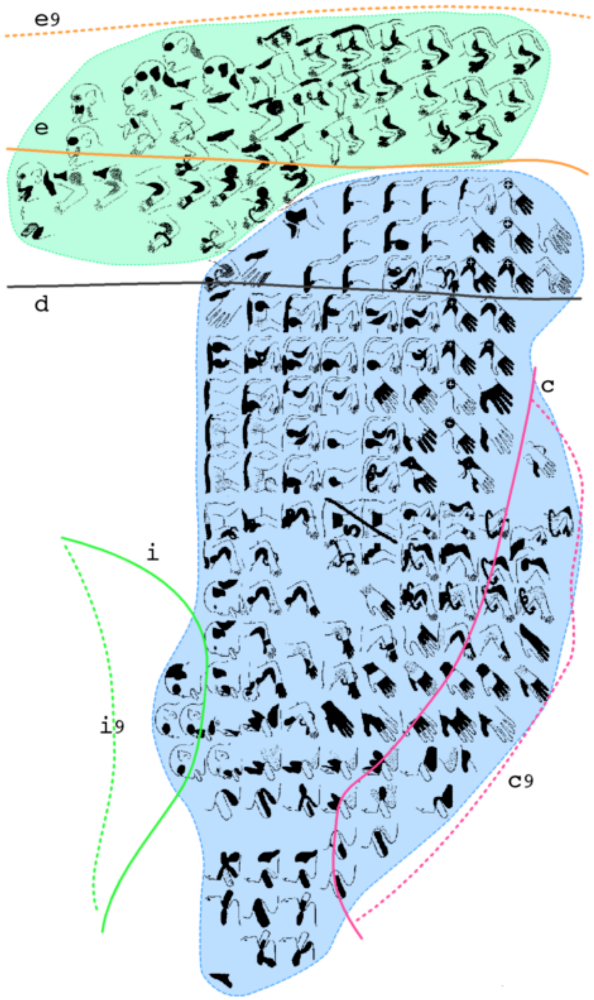
Inputs to organized spinal cord

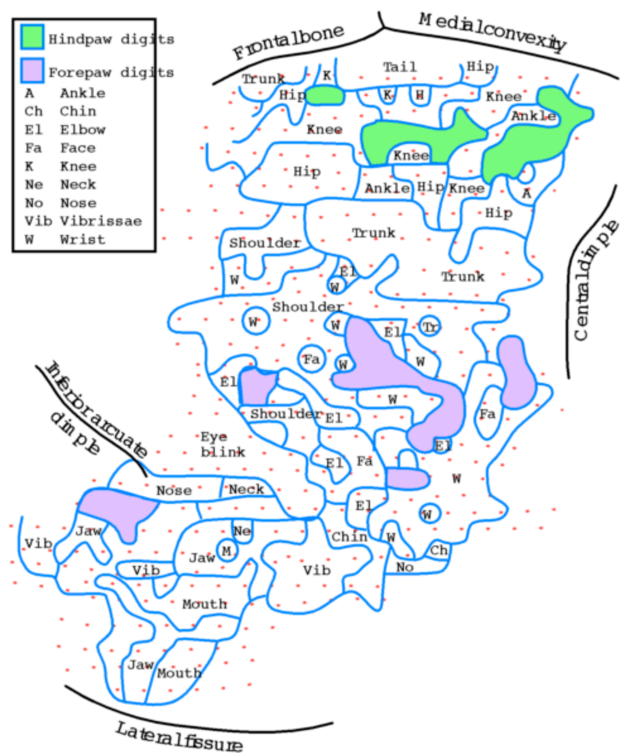


Current mapping of body to M1









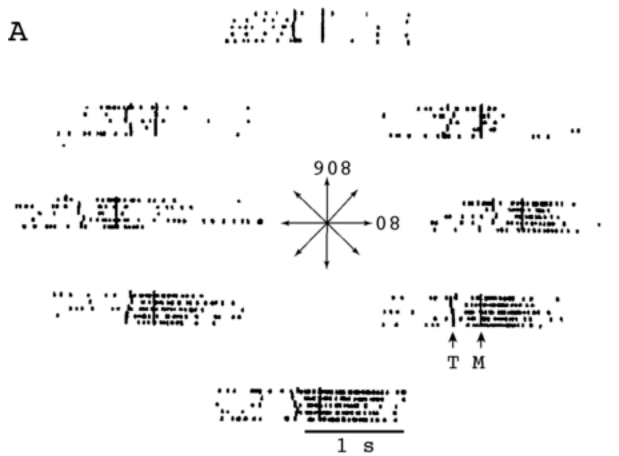
Good evidence now exists that functional mapping of M1 to motoneurons is not simple somatotopic map.

More complexity; more overlap of points; more scatter

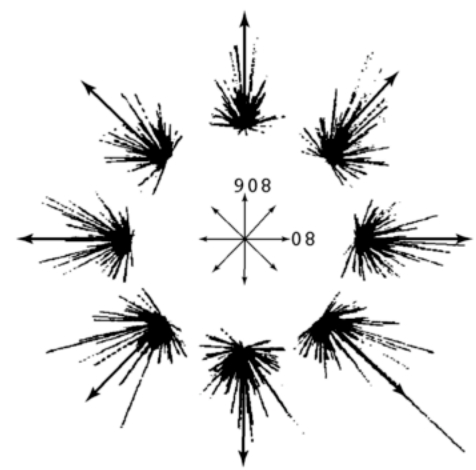
Distributed function in M1: Cartesian coordinate system

- Georgopoulos: recording in monkey M1
  - One neuron's responses to stimuli in different positions in space.
    - Note that the given neuron responds all around the workspace – with a preference for some areas over others (A)
    - Vector is constructed for that neuron's responses (B)
  - When the responses of all recorded neurons to one direction is vector summed, the vector sum is the "correct" response.
- Thus, the vector sums of all the neurons codes for the positions in absolute space. Each neuron contributes to the total vector.

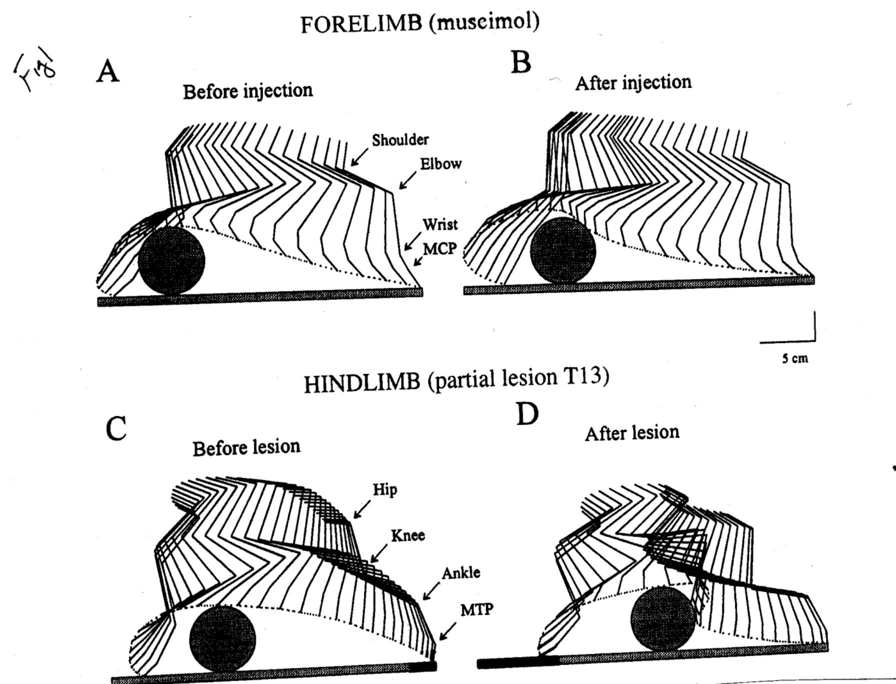
A

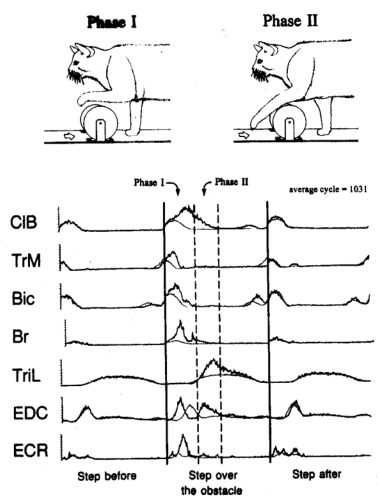


B



Interaction between CPG and cortex





rol

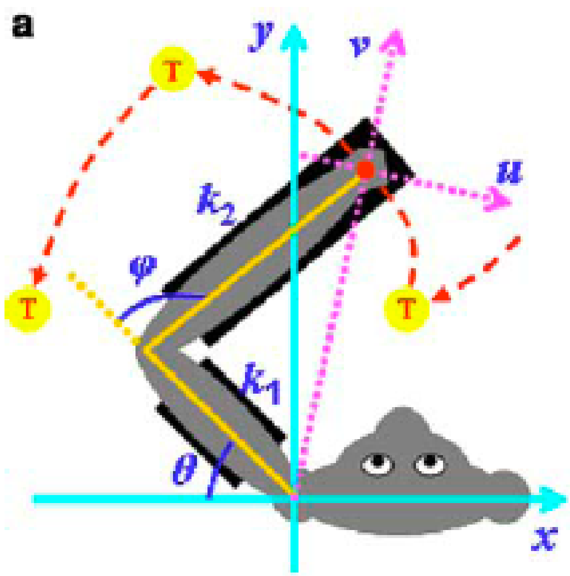
Georgopoulos: M1 control of muscles

- About 50% of M1 neurons specify positions in space
- Remainder specify other characteristics
  - Muscle
  - Force
  - Joint angle

- Control is distributed and functionally organized because it utilizes the spinal synergies

- Only fingers have 1:1 control from cortex, and that only in primates and raccoons

Hatsopoulos: New view of M1



- Using tetrodes (multielectrode recording system)
- Evidence AGAINST a single coordinate system
  - Adds Shoulder Centered
  - Joint based
- Adds them to Cartesian coordinates

Motor Cortical Control of Movement

- Georgopoulos: Activity of M1 is best correlated with
  - A vector representation of space – world centered (~45%)
  - Muscle activation
  - Muslce force

- NB: The cortex is partly sending signals to the spinal cord interneurons and motoneurons to move to a position in space.
- The spinal cord is sending signals to the motoneurons to move to a position relative to the body.

Input to spinal cord motoneurons: heavily from Premotor areas for hand

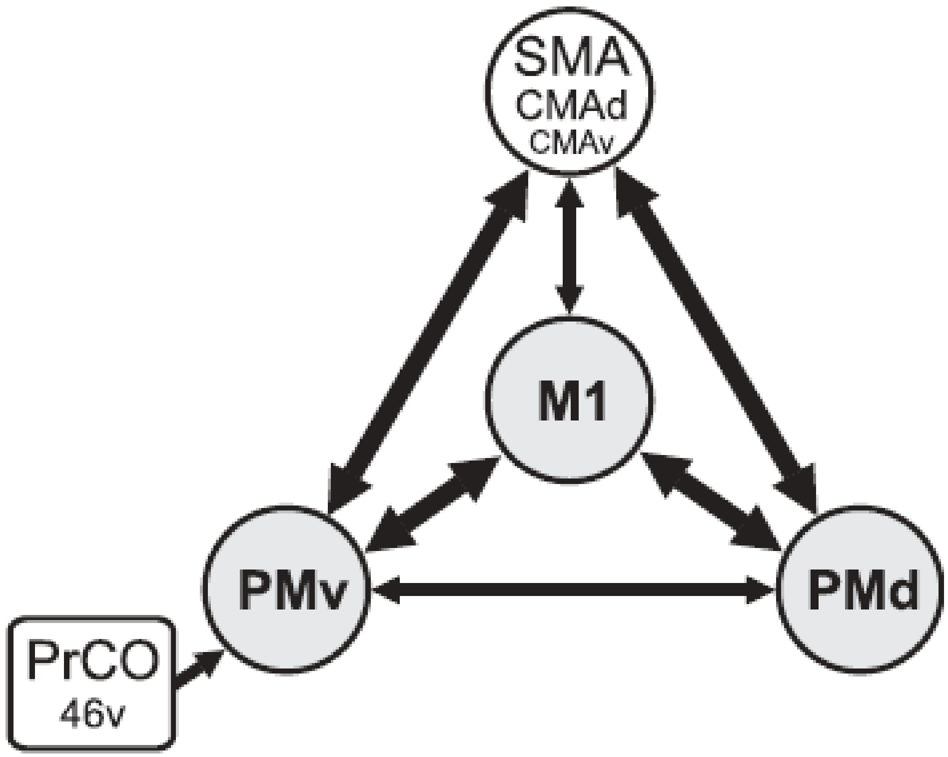


Figure 10. Frontal lobe network for hand movements. The size of the arrows indicates the relative strength of an input. Shaded circles indicate motor areas on the lateral surface. Unshaded circles are motor areas on the medial wall. The square indicates prefrontal areas of the cortex. Abbreviations are as in Figures 1 and 4.

- New anatomical evidence from Dum and Strick
- Needs to be validated in physiology, but very likely

Conclusion and Questions

- Thus:

- Cortex signals are to world centered coordinates
- Spinal cord translates to body centered coordinates
- Spinal interneurons activate synergistic movements adaptively controlled to final desired position

What is transformations between cortex and spinal cord and spinal cord and limbs?

Do areas sum, or does each have its own map?

How many synergies are there?

Does each map use its own, or are they shaped w/i one common one?