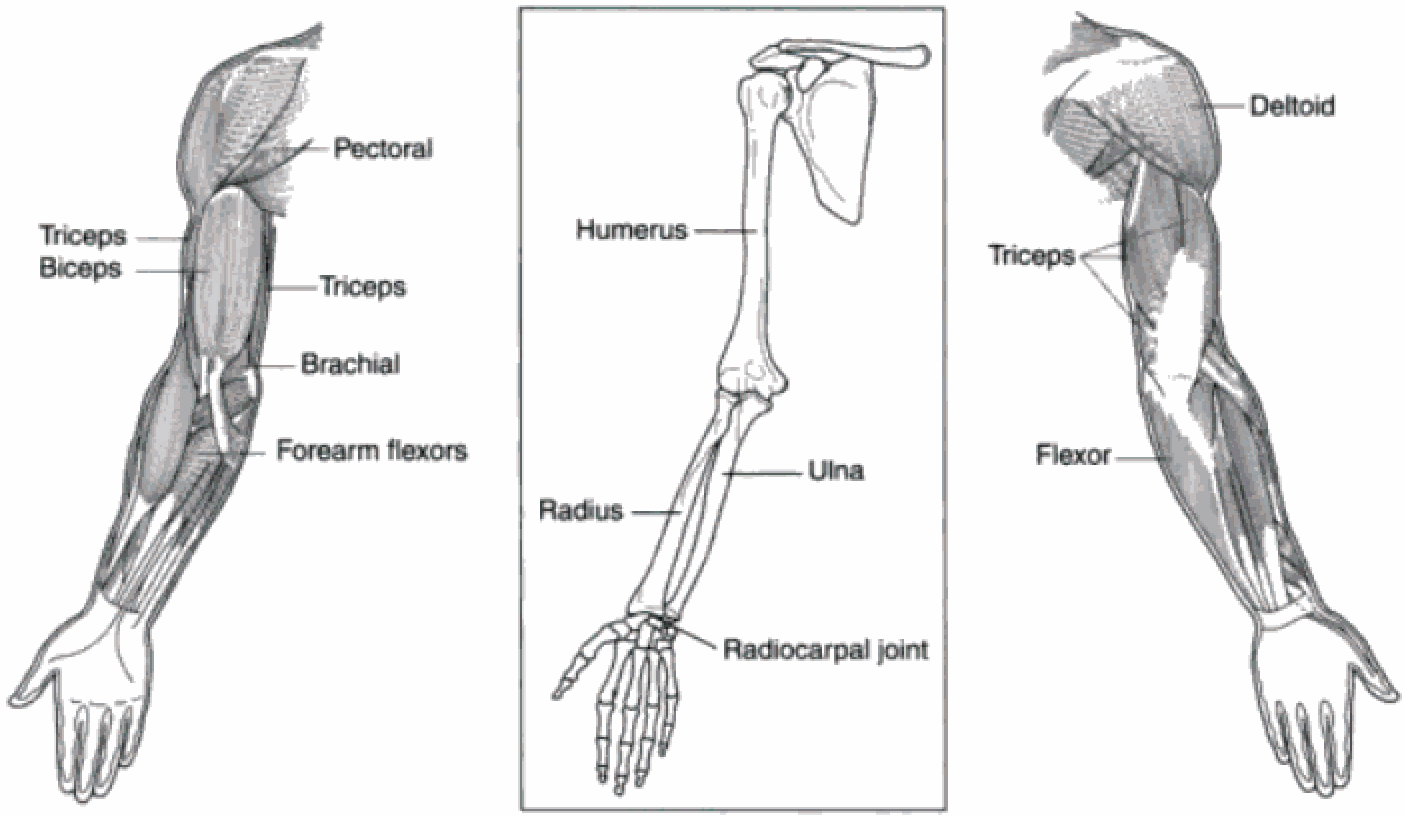


Figure 3.1
Selected forelimb muscles. (Drawn by George Nichols.)

From: Shadmehr R., Wise S.P. "The computational neurobiology of reaching and pointing", MIT press

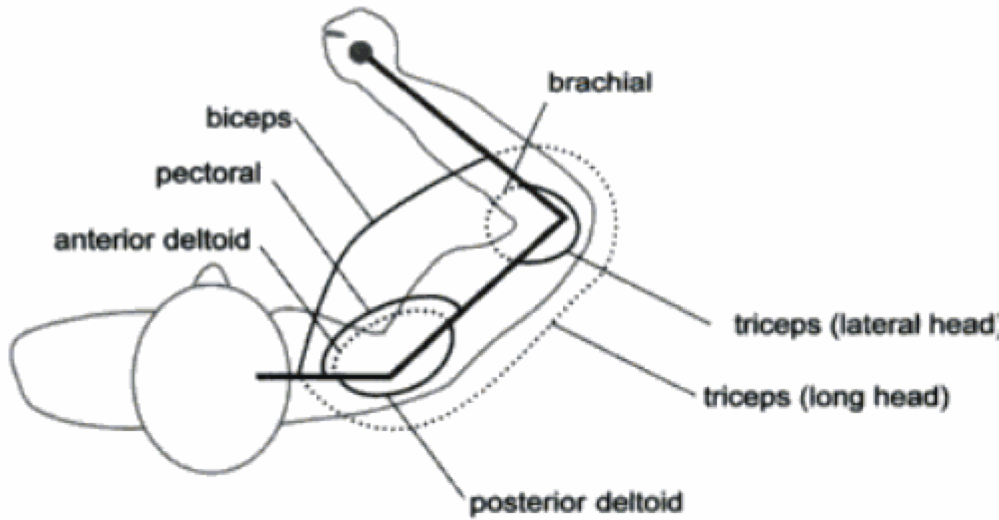


Figure 3.2
The actions of selected forelimb muscles on a two-joint arm.

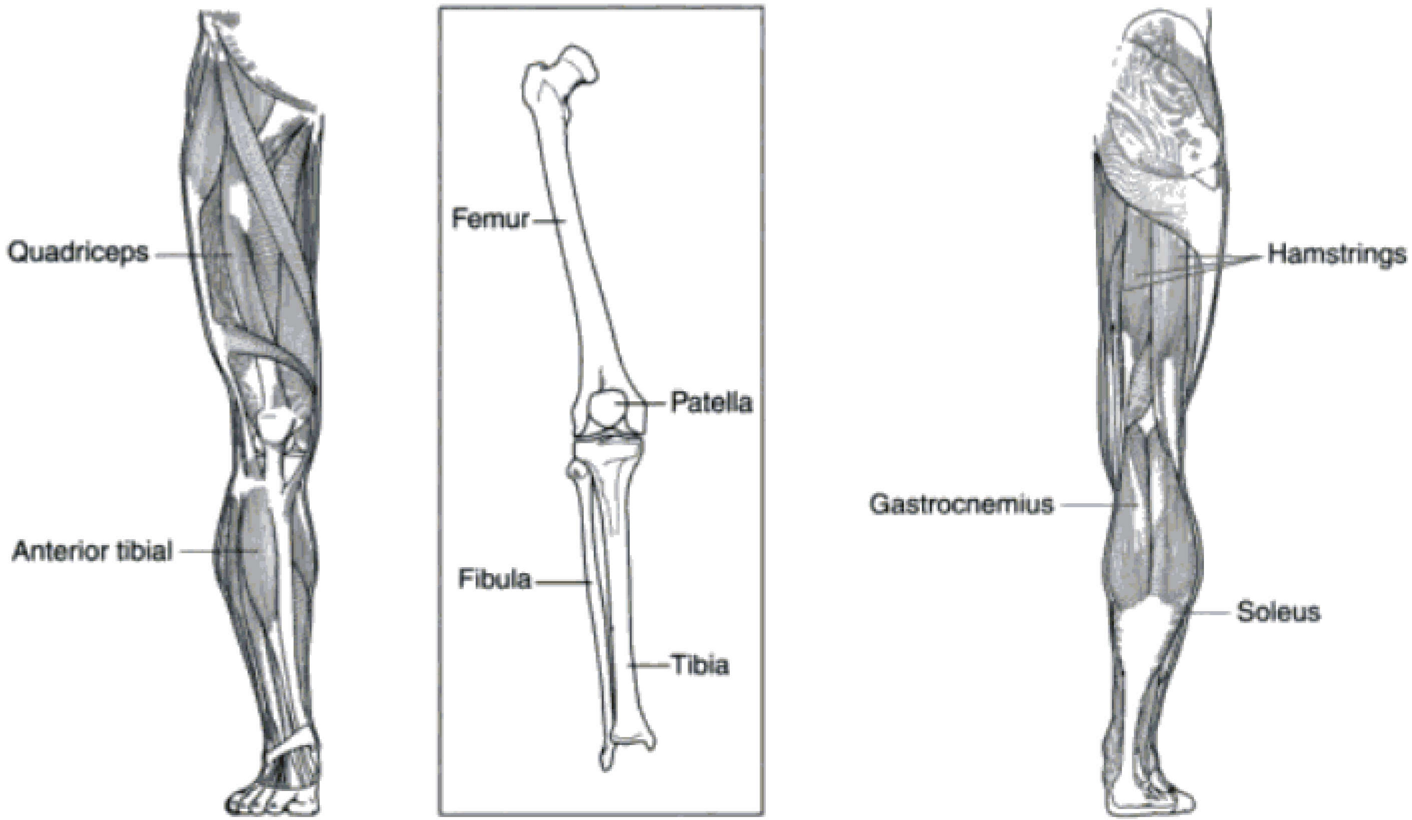
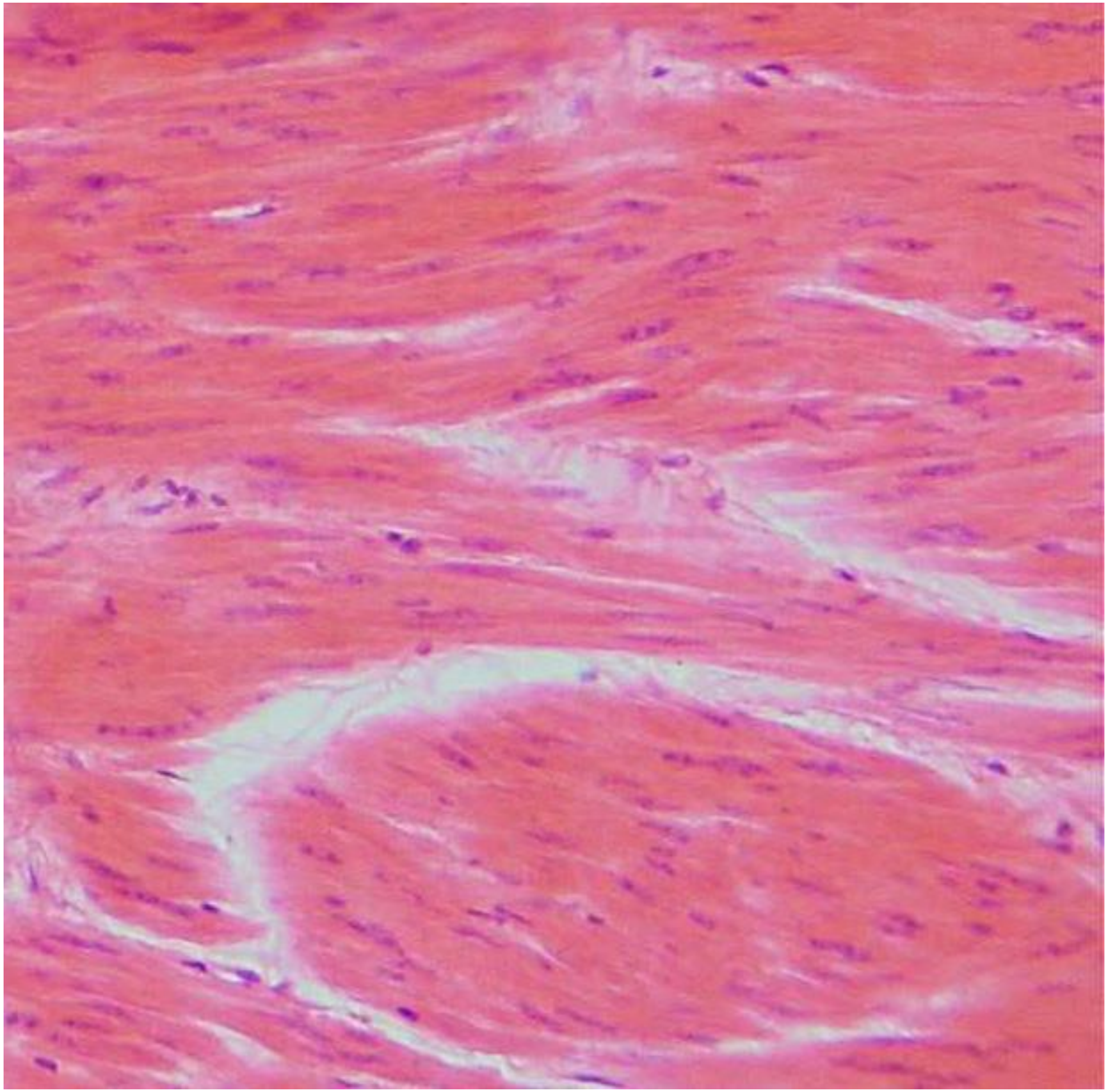
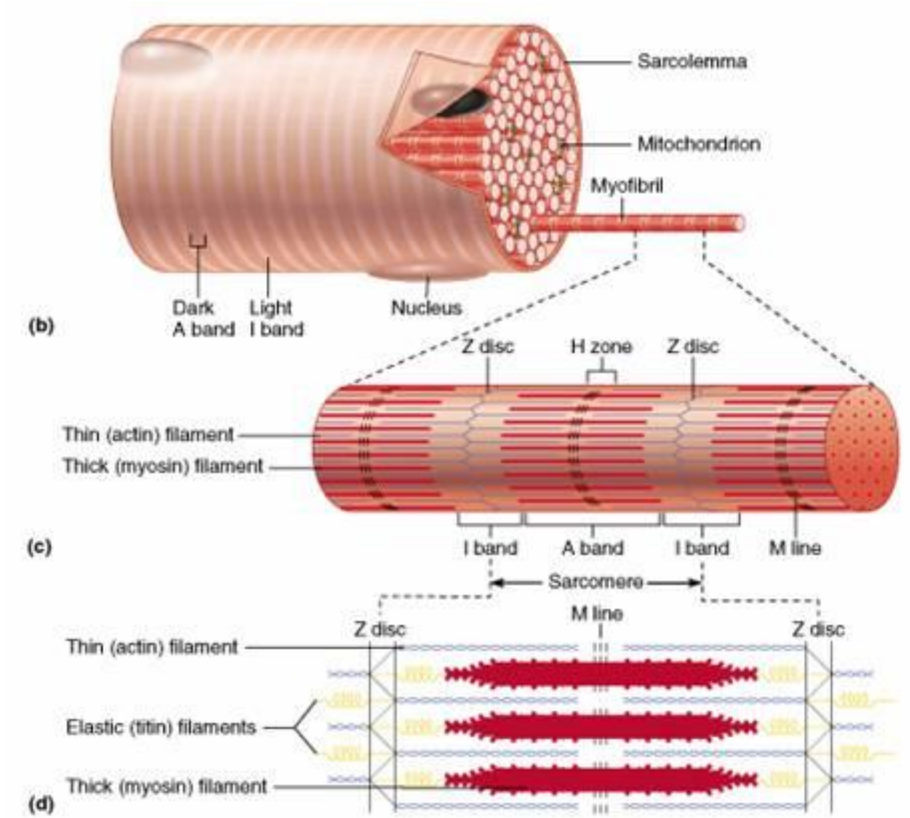


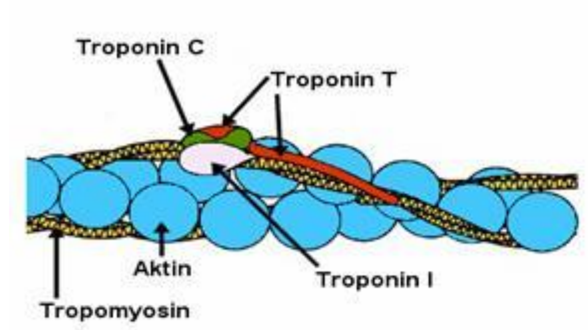
Figure 3.3
Selected hindlimb muscles. (Drawn by George Nichols.)

What generates force and feedback

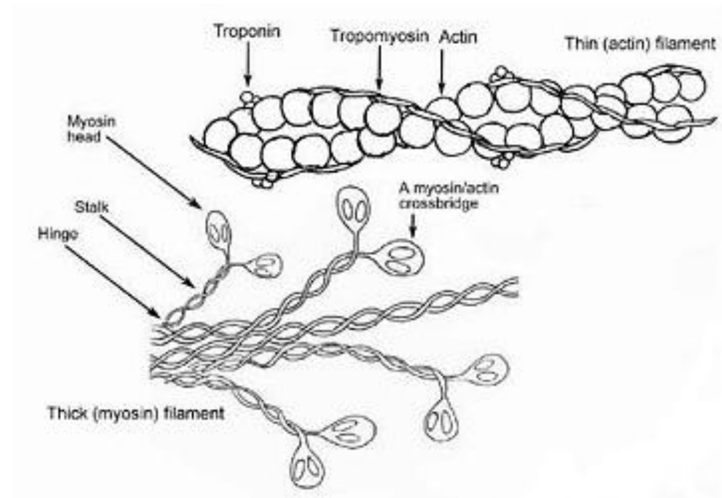
- Motors vs. muscles
  - Motor torque somewhat independent of the configuration (it depends on speed) vs. muscle force is a function of length (and thus of joint angles)
  - Muscle activation: 30ms (in the cat) ~ slow
  - Muscle can only pull (obviously), motors are bi-directional
  - Axonal conduction time (~speed of sound), in wires (~speed of light)







Thin filament



Thick filament

Three levels:

- Muscle-fiber level (cells)
- Myofibrils level
- Filament level

- Force generation depends on two molecules:
  - Actin (thin filaments) & Myosin (thick filaments)
  - Myosin has a head that can move (~60deg, 5-12nm)
- How?
  - Energy to change the Myosin head configuration provided by ATP hydrolysis
  - Command provided by action potentials and variations in the sodium-calcium concentration (depolarization) which eventually lead to the exposure of the actin sites that can bind the myosin heads
  - Therefore the myosin attaches to the acting and the head rotates
- This is what we need for now…

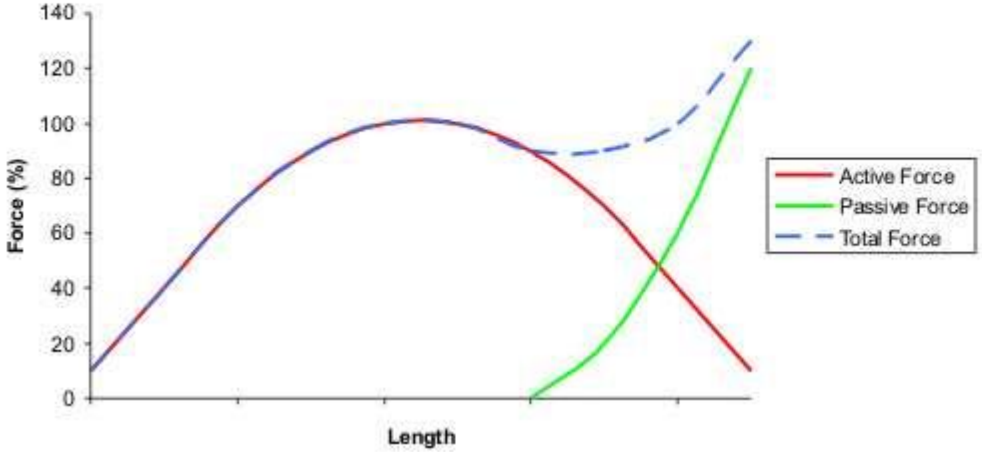
Length-tension properties

- Passive component: spring-like
  - Sarcomeres are somewhat constant in size/specs
  - but they can be stacked in parallel (thicker muscle, more force) or series (longer muscle, more speed)
  - Force is in the range of 1-8kg/cm^2 (for vertebrates)

- Active component: see next slide

Length-tension properties

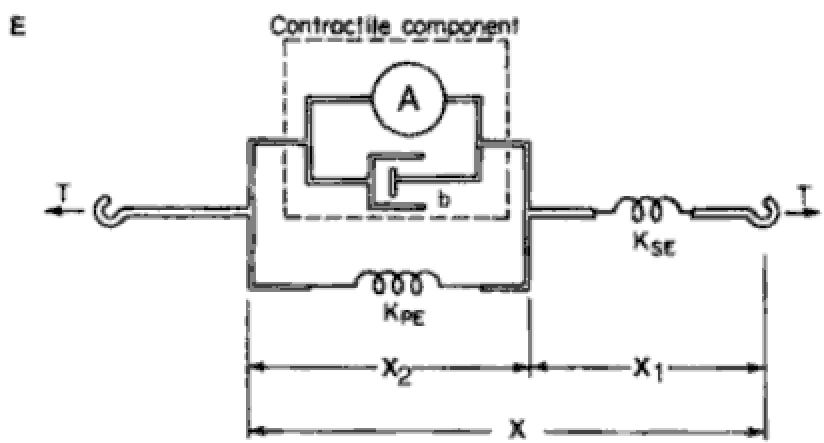
- Motor neurons are segregated in pools
  - Each innervate a particular muscle, each fiber receives only one “input” from a motor neuron
  - Innervation ratio: number of motor neurons vs. the number of muscle fibers
- Control of muscle:
  - Alpha motor neurons: extrafusal fibers (later for definitions)
  - Gamma motor neurons: intrafusal fibers



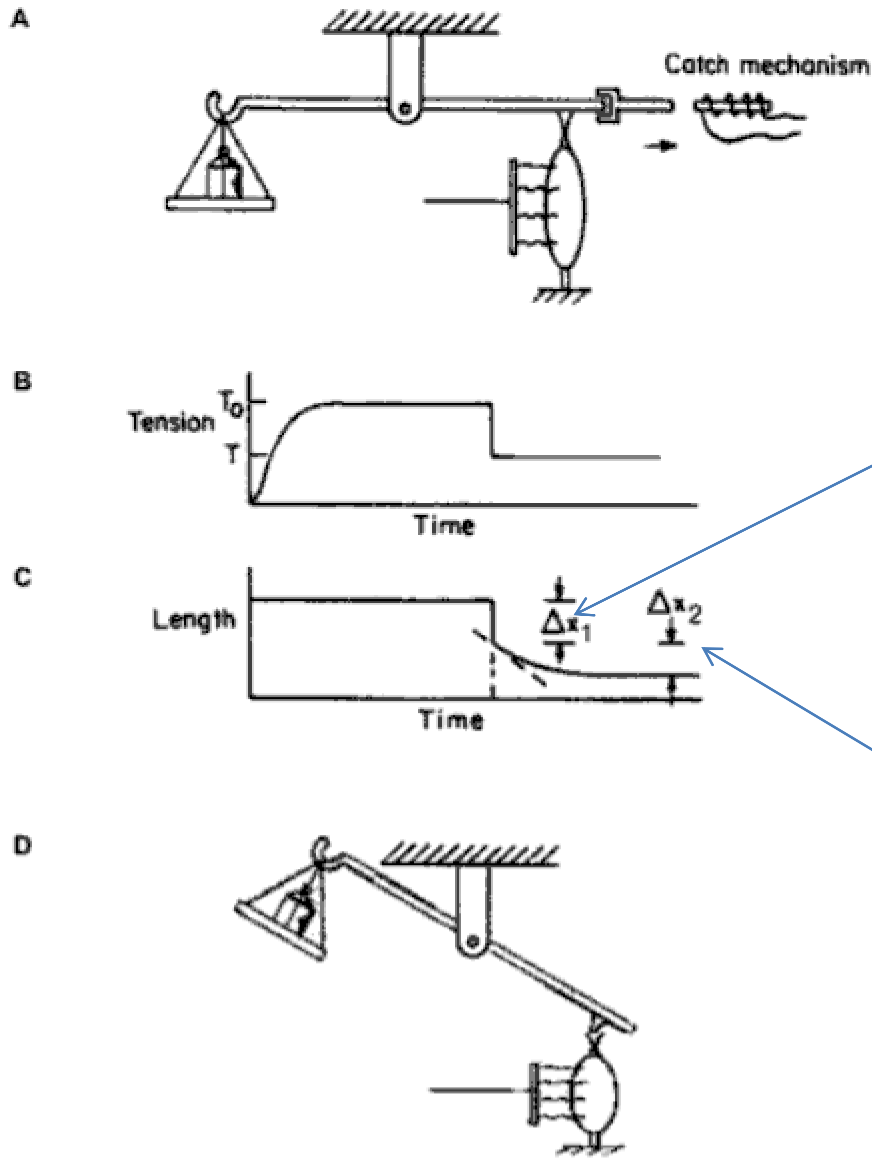
140
120
100
80
60
40
20
0
Force (%)
Length
Active Force
Passive Force
Total Force

Muscle model (Hill)

- Hill noted viscous effects in the muscle behavior
- … and did some experiments

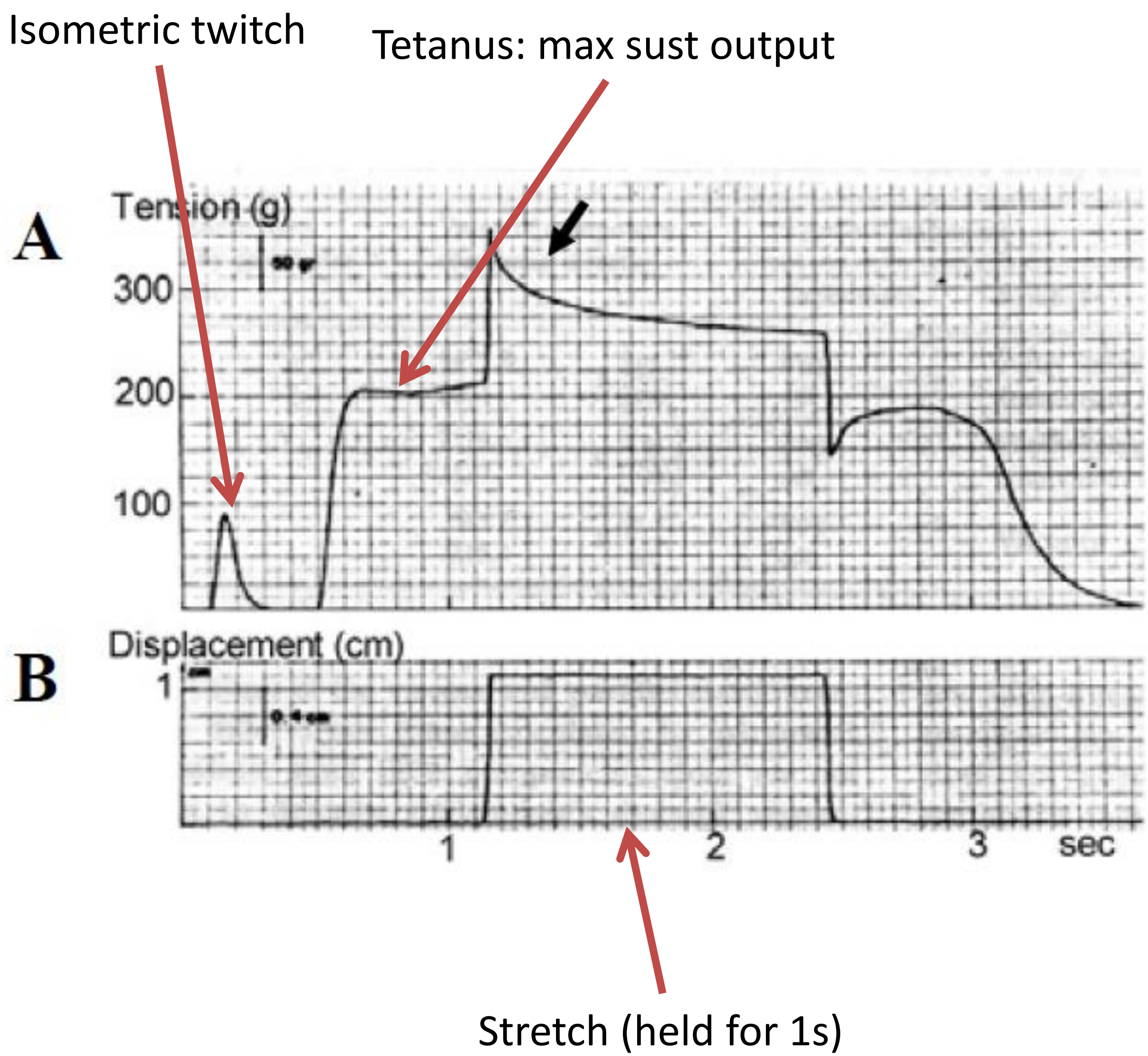


This is the result

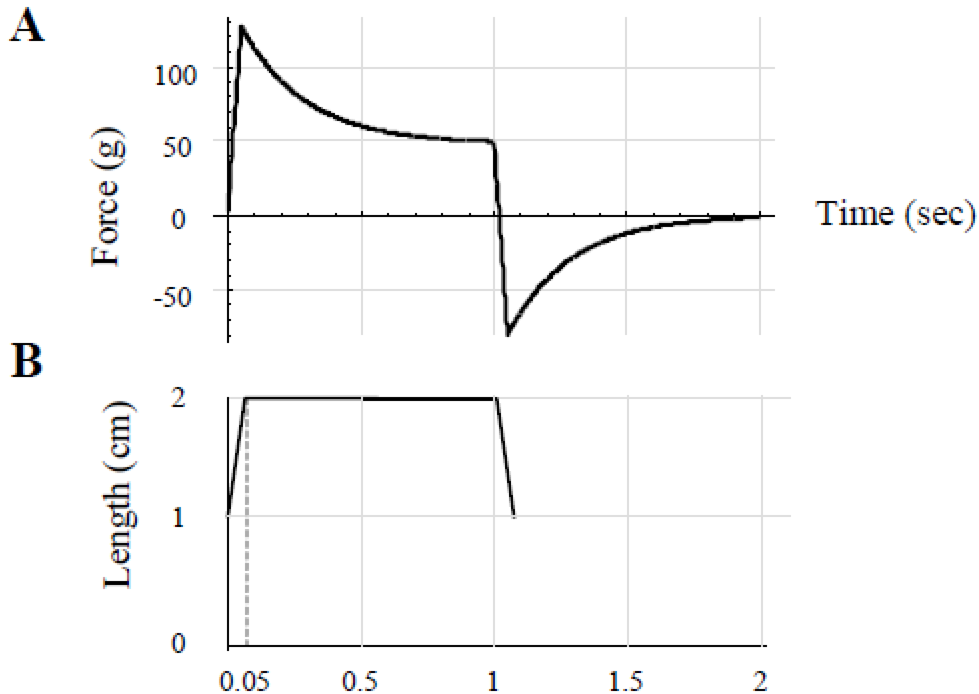


This is the series

Parallel + damping


Isometric twitch
Tetanus: max sust output
A
Tension (g)
300
200
100
B
Displacement (cm)
1
1
2
3
sec
Stretch (held for 1s)

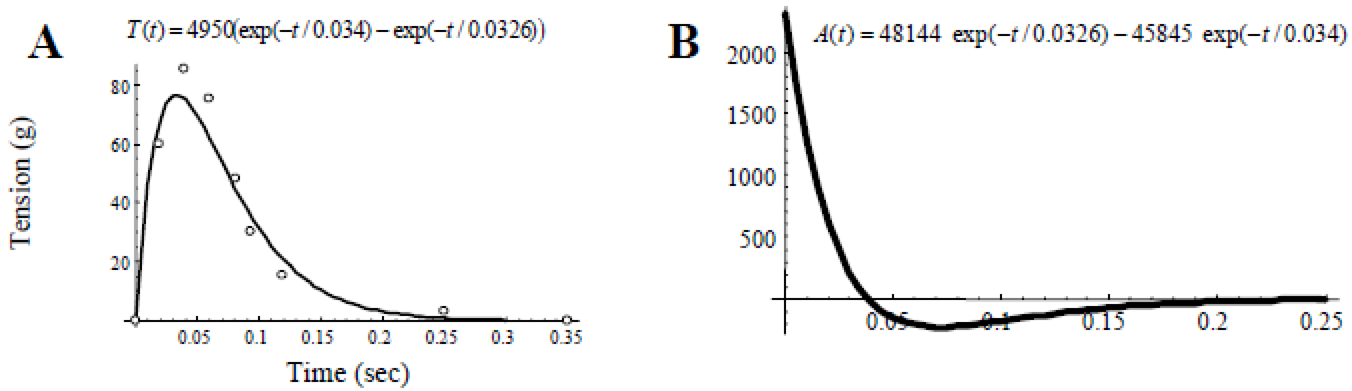
Simulation of passive properties



Notes

- Damping promotes stability (as for control systems)
- Intrinsic damping is good because the controller is slow (takes time for sensory signals to get to the “controller” and back to change the muscle state)

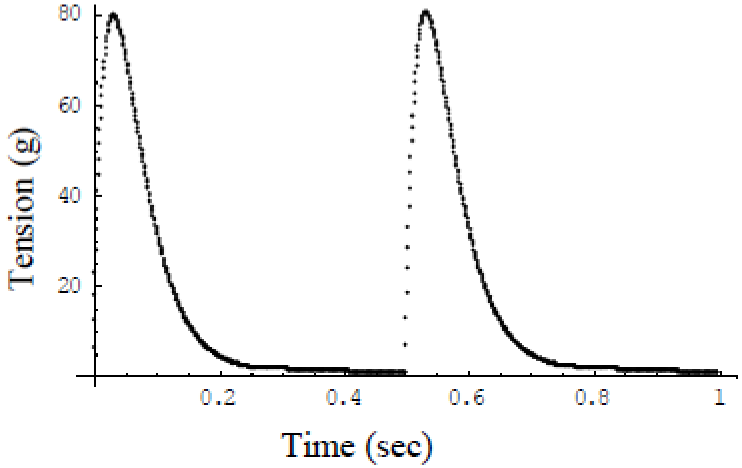
Simulation of active properties



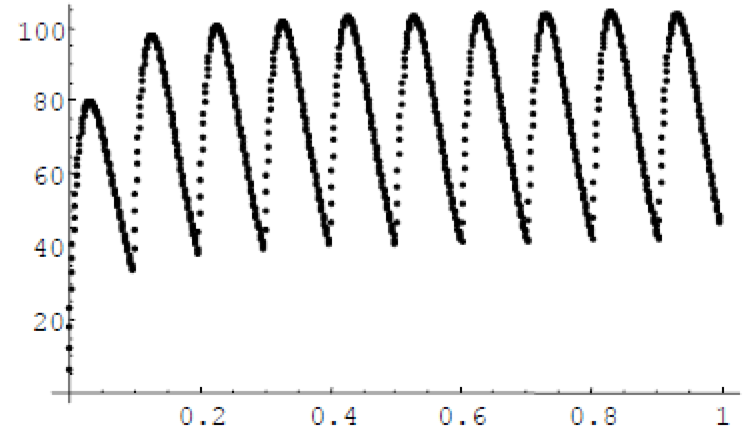
$$h(t) = 48144\exp(-t/0.0326) - 45845\exp(-t/0.034)$$

Impulse response (estimated)

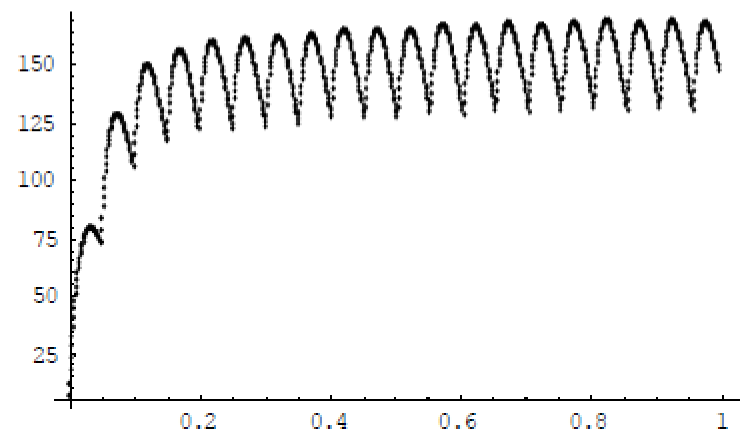
2 Hz stimulation

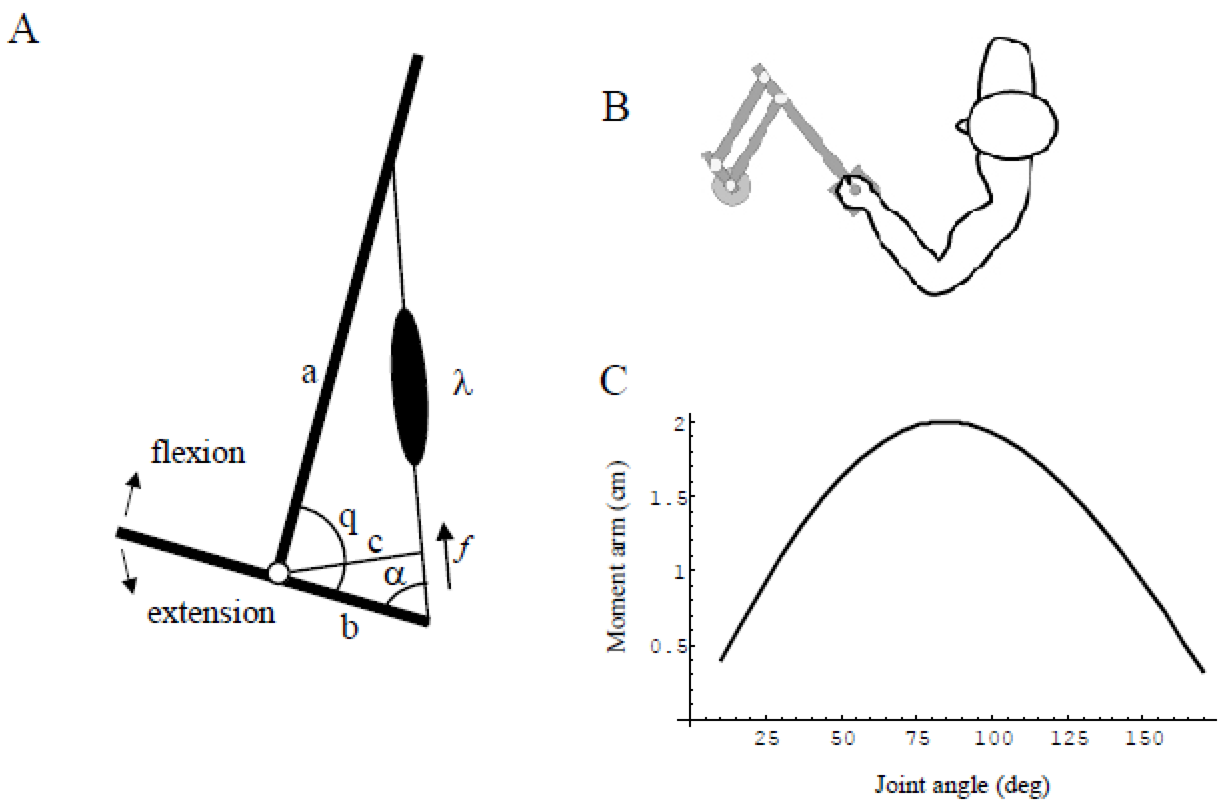


10 Hz stimulation

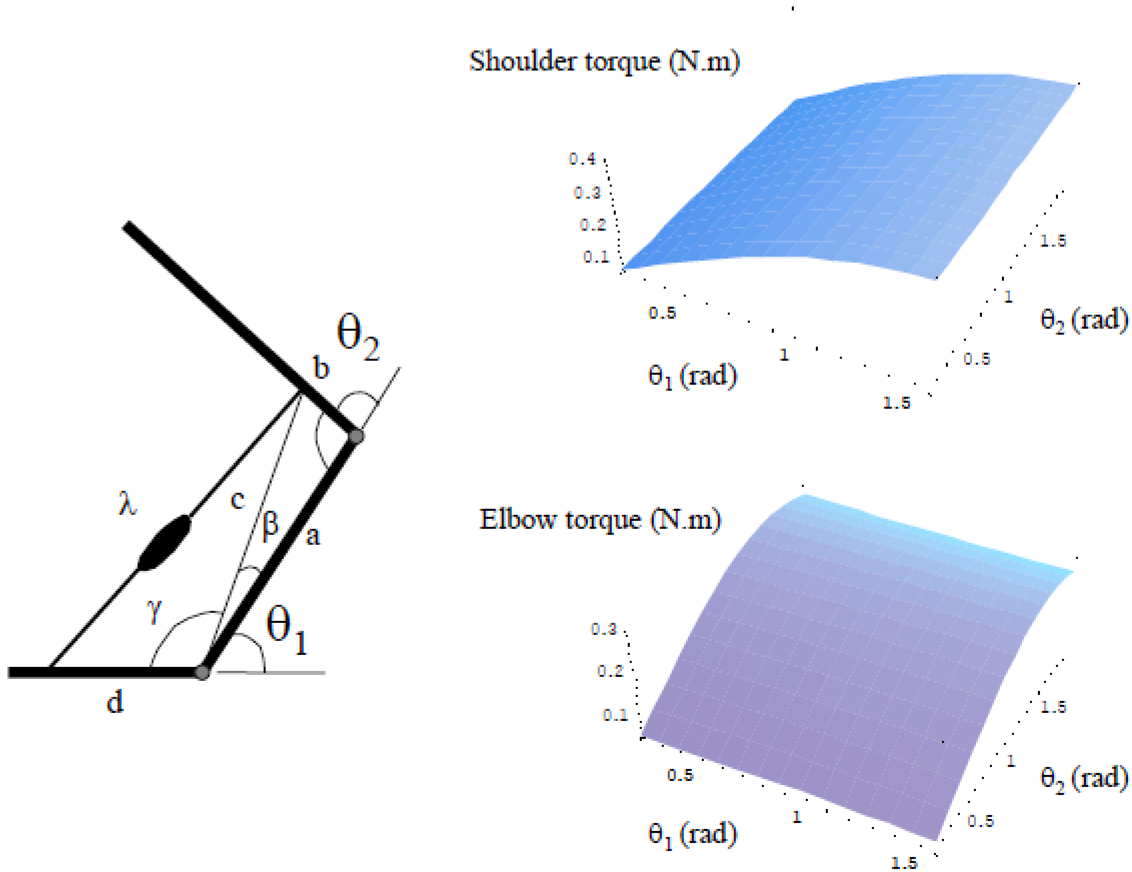


20 Hz stimulation

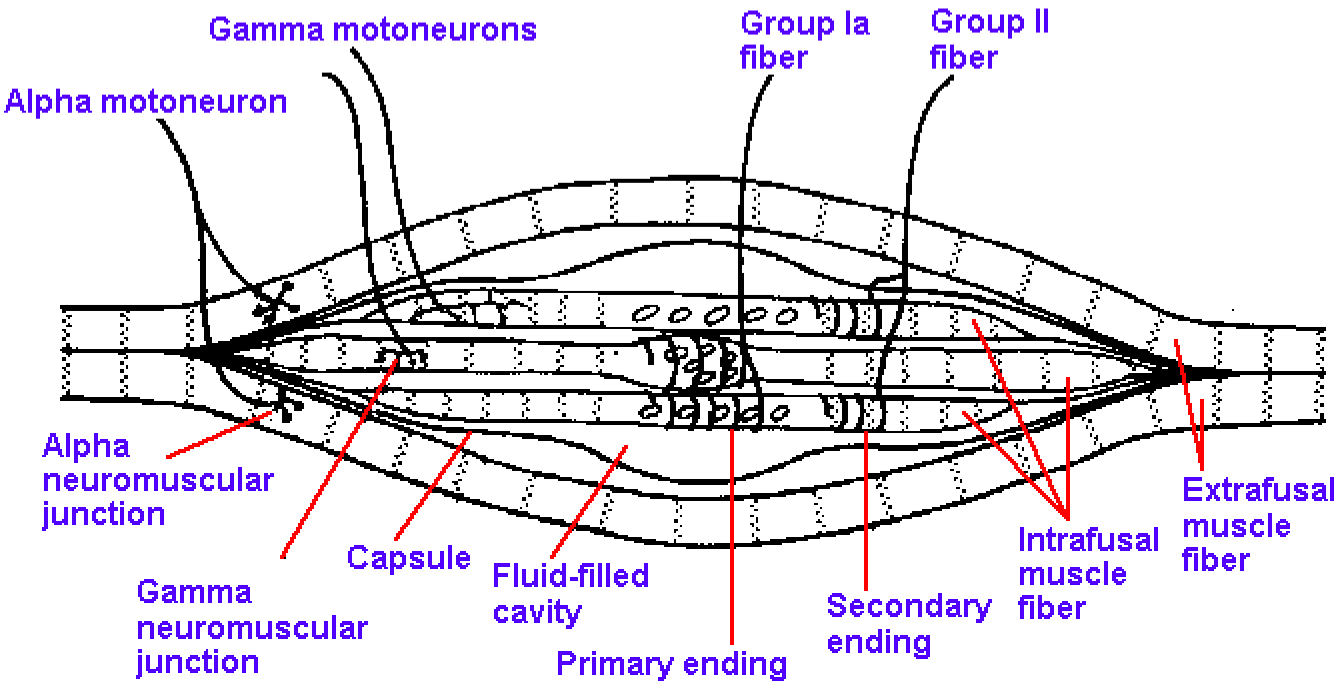


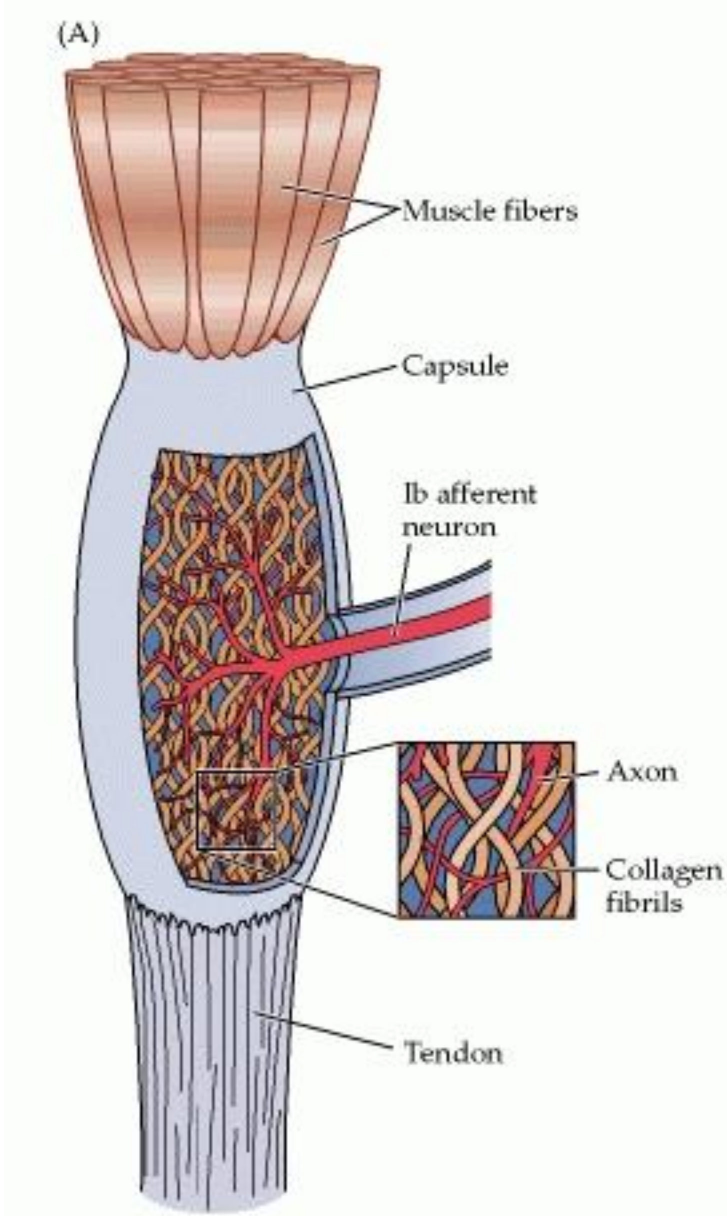


A
a
λ
flexion
q
c
f
α
extension
b
B
C
2
1.5
1
0.5
Moment arm (cm)
25
50
75
100
125
150
Joint angle (deg)


θ2
b
λ
c
β
a
γ
θ1
d
Shoulder torque (N.m)
0.4
0.3
0.2
0.1
0.5
1
1.5
θ1 (rad)
0.5
1
1.5
θ2 (rad)
Elbow torque (N.m)
0.3
0.2
0.1
0.5
1
1.5
θ1 (rad)
0.5
1
1.5
θ2 (rad)

Muscle afferents



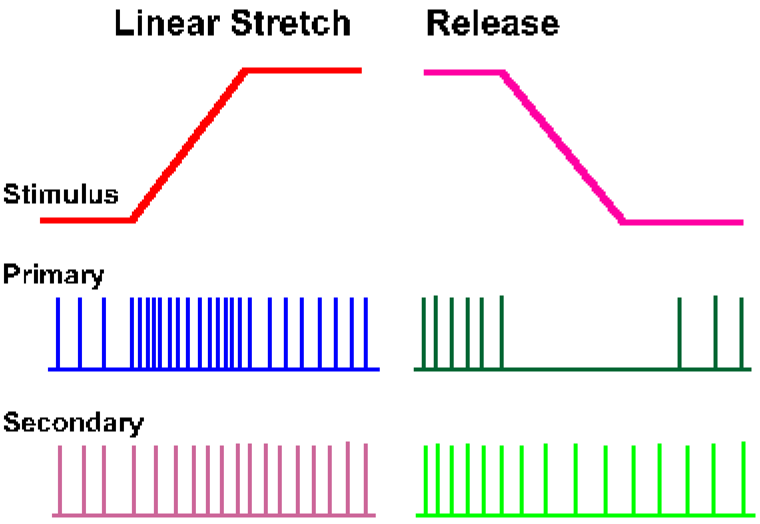

(A)
Muscle fibers
Capsule
Ib afferent neuron
Axon
Collagen fibrils
Tendon

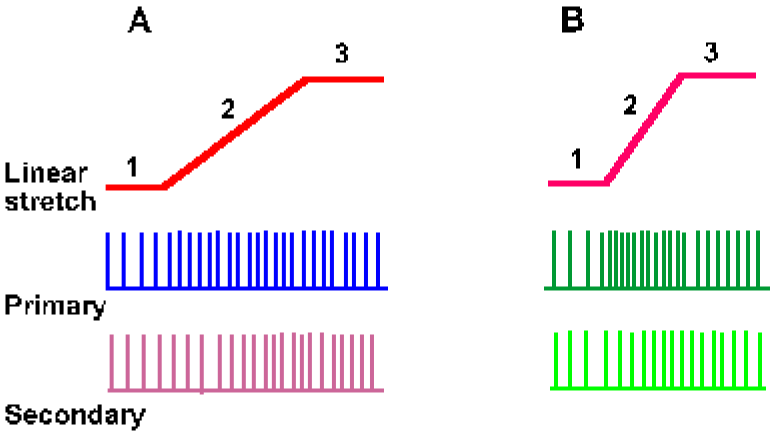
Summary

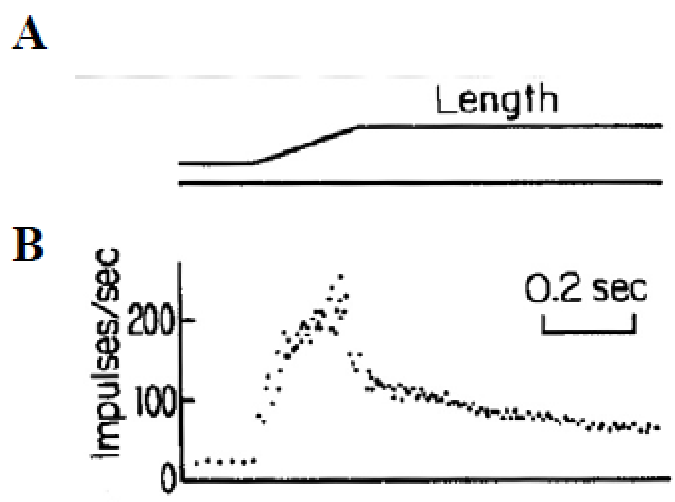
- Muscle spindles
  - Group Ia (primary, velocity) and IIa (secondary, length) muscle-spindle afferents
  - Primary & secondary refers to the diameter of the axons (different transmission rates), the larger the faster
  - Primary afferent connect to the fuse, secondary to the poles of the intrafusal fibers
- Golgi tendon organs
  - Group Ib afferents

Further

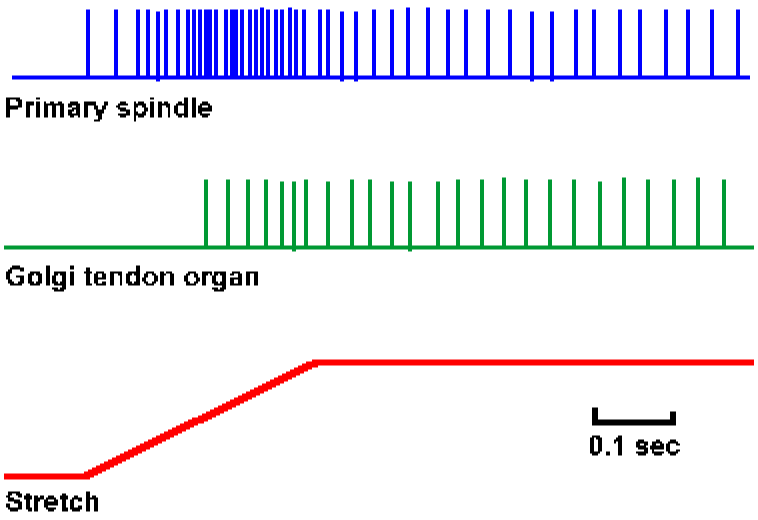
- Alpha motor neurons: innervate the extrafusal fibers, those generating forces
- Gamma motor neurons: innervate the intrafusal (spindles) fibers, calibrating the sensor


Linear Stretch
Release
Stimulus
Primary
Secondary

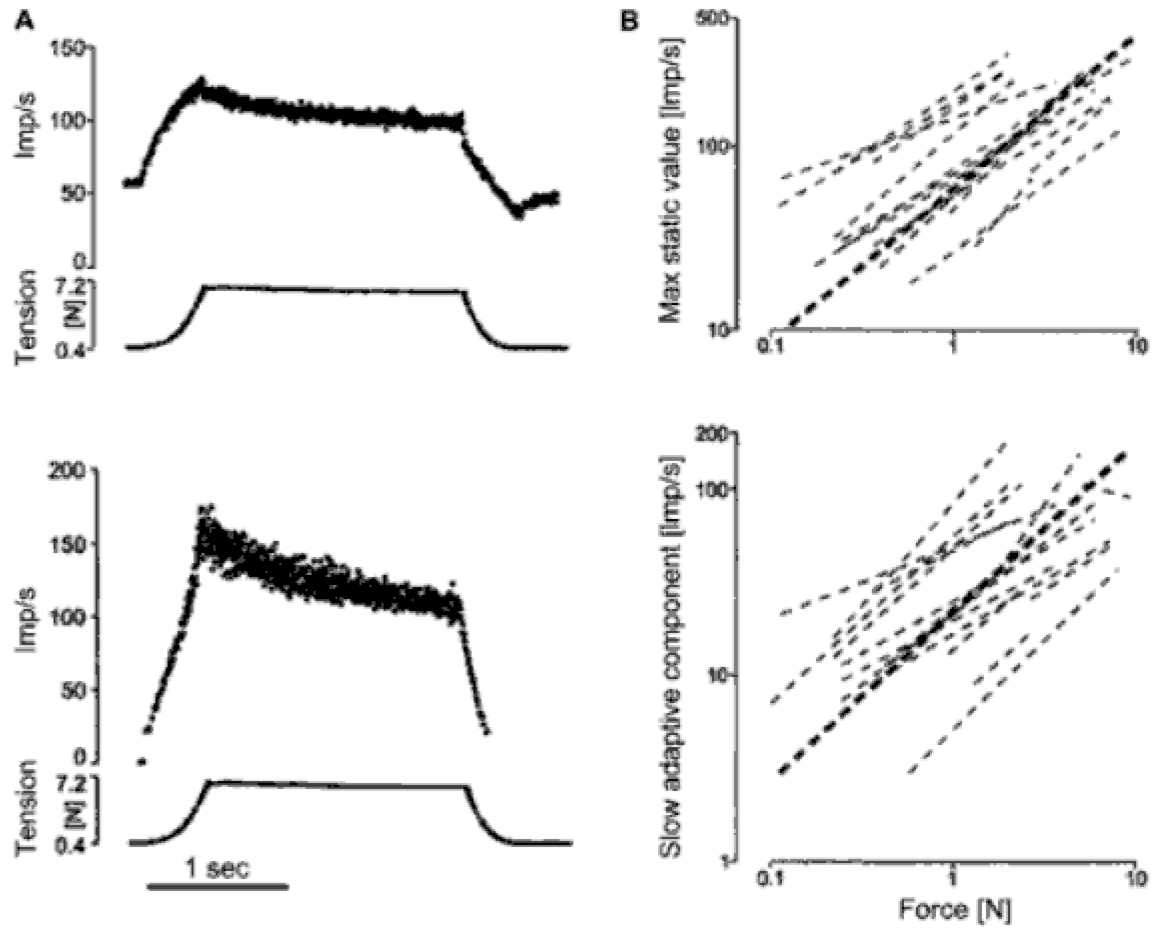

A
B
3
2
1
Linear
stretch
Primary
Secondary
3
2
1



This behavior can be explained by the parallel & series spring-like behavior of the fibers



Primary spindle
Golgi tendon organ
0.1 sec
Stretch



A
Imp/s
150
100
50
0
Tension
7.2
[N]
0.4
200
150
100
50
0
1 sec
B
Max static value [Imp/s]
500
100
10
0.1
1
10
Slow adaptive component [Imp/s]
200
100
10
1
Force [N]

Property	Primary Ending	Secondary Ending	Golgi Tendon Organ
1. Location	Mid-equatorial region of bag and chain fibers in spindles	Juxta-equatorial region of chain fibers in spindles	Muscle-tendon junction
2. Afferent fiber	Large, group Ia	Small, group II	Large, group Ib
3. Efferent control	Both static and dynamic fusimotor	Static fusimotor	None known
4. Response to ramp stretch with plateau	Dynamic and static (signals length)	Static (signals length)	Dynamic and static (signals tension)
5. Response to release of stretch	Abrupt silence	Progressive decrease	Abrupt silence
6. Response to tendon tap	Low threshold, vigorous	High threshold, little	High threshold, vigorous if threshold is exceeded
7. Sensitivity to small stretches	High, especially if rapid	Low	Low
8. Response to twitch contractions	Abrupt silence	Abrupt silence	Vigorous discharge
9. Signals	Muscle length and rate of change of length	Muscle length	Muscle tension and rate of change of tension