Muscle

Structure and Force Generation

Modeling of
Human Movement

MCEN 4228/5228

Fall 2021

Muscle

- Skeletal muscle
  - Unit cell structure
  - Muscle mechanics
    - Force-length relation
    - Force velocity relation
  - Activation
    - Rate encoding
    - Motor unit recruitment
    - Electromyography
    - Modeling muscle activation
  - Force-length-velocity-activation relationship

Skeletal Muscle

- Striated and voluntary
  - Cardiac muscle is striated and involuntary
  - Smooth muscle is unstriated and involuntary

- Attaches to skeleton via tendons
- Most abundant tissue in the body
  - 45-75% of body weight

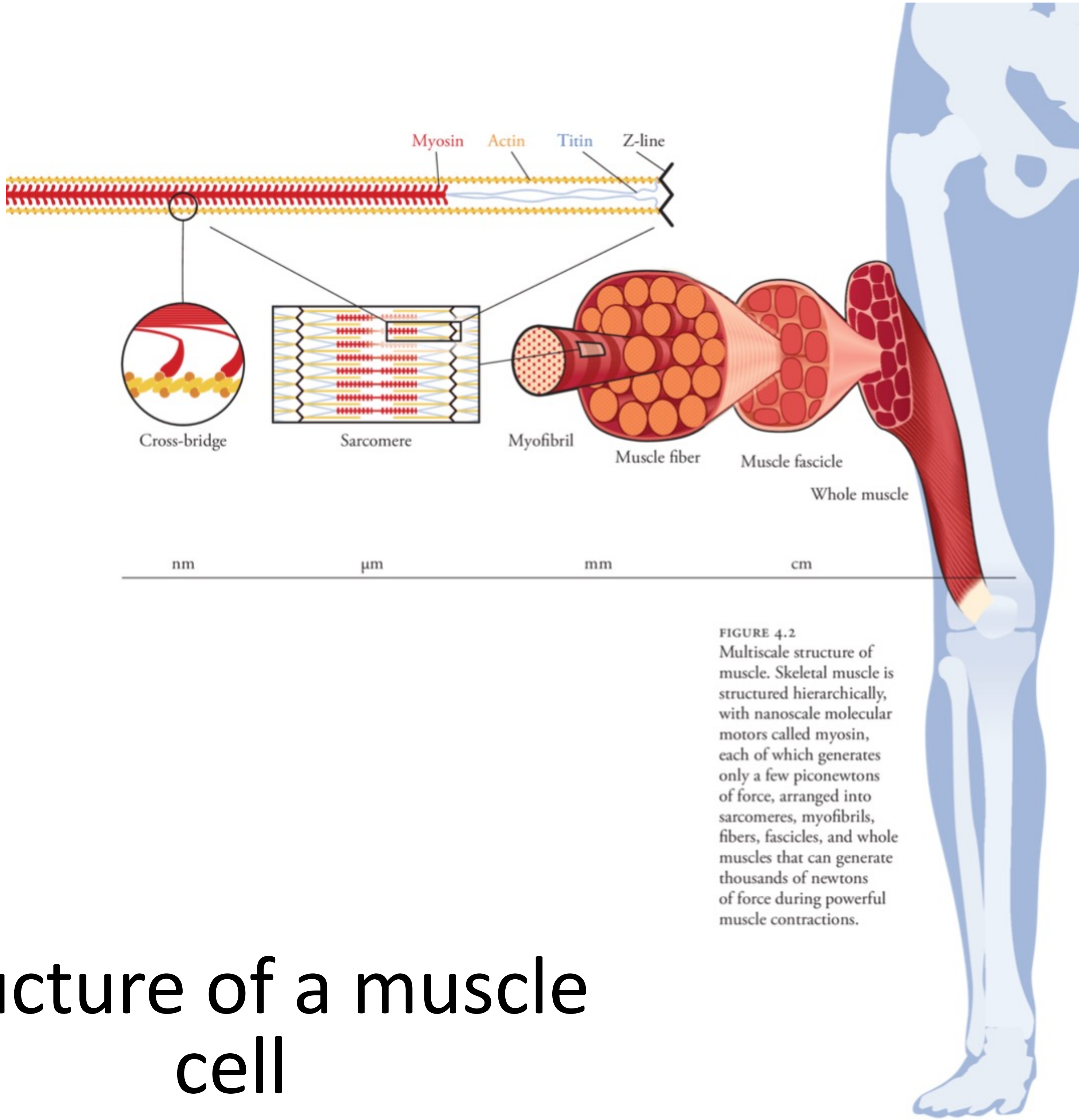
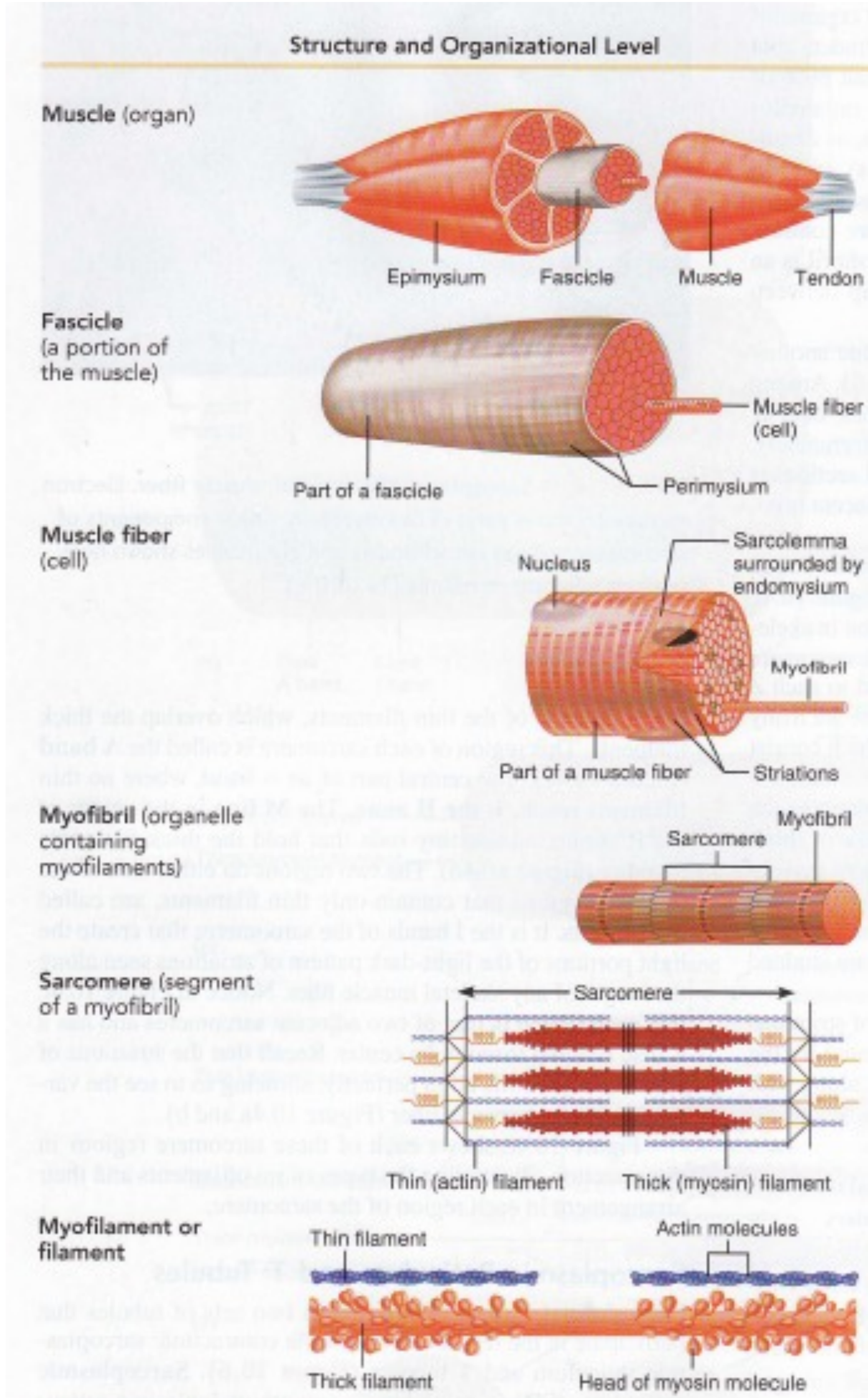


FIGURE 4.2
Multiscale structure of muscle. Skeletal muscle is structured hierarchically, with nanoscale molecular motors called myosin, each of which generates only a few piconewtons of force, arranged into sarcomeres, myofibrils, fibers, fascicles, and whole muscles that can generate thousands of newtons of force during powerful muscle contractions.

Structure of a muscle cell

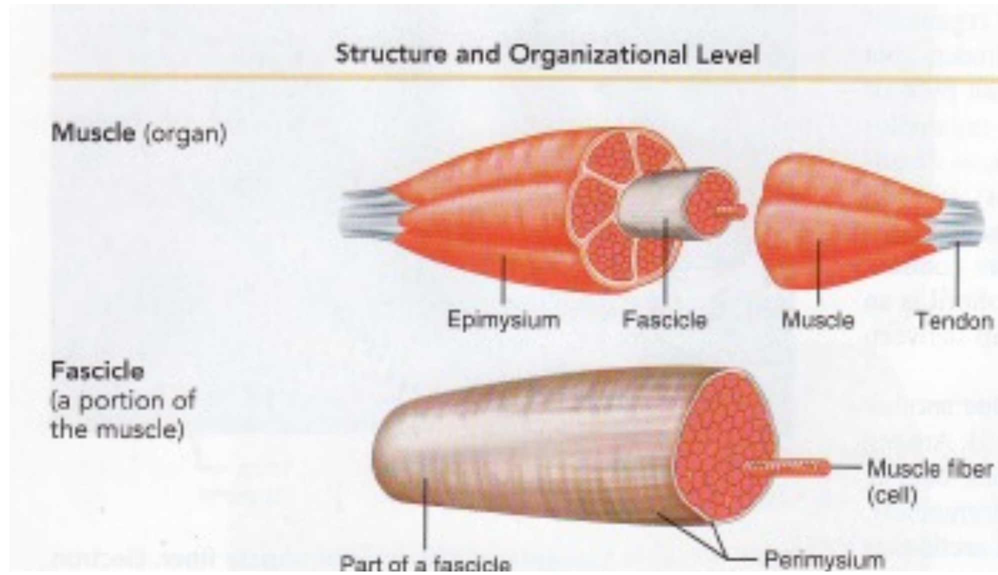
Structure of a muscle cell

A. Fascicles
  – fiber bundles
B. Fibers
  – **muscle cell**
  – bundles of myofibrils
C. Myofibrils
D. Sarcomeres (series)
E. Actin & Myosin Filaments



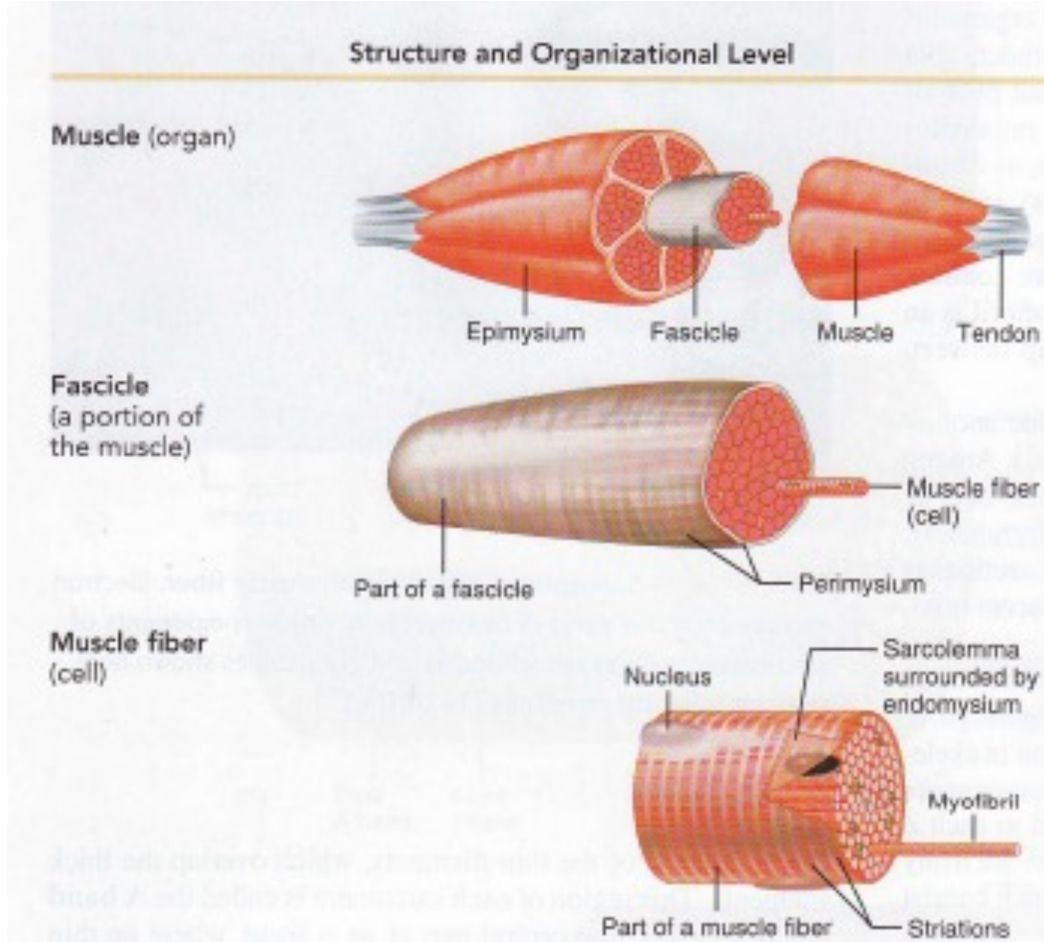
Fascicles

- A muscle is composed of multiple fascicles in *parallel*
  - A sheath of connective tissue surrounds the muscle (epimysium)
  - Each fascicle is surrounded by connective tissue (perimysium)
  - Fascicles composed of bundles of *muscle fibers*



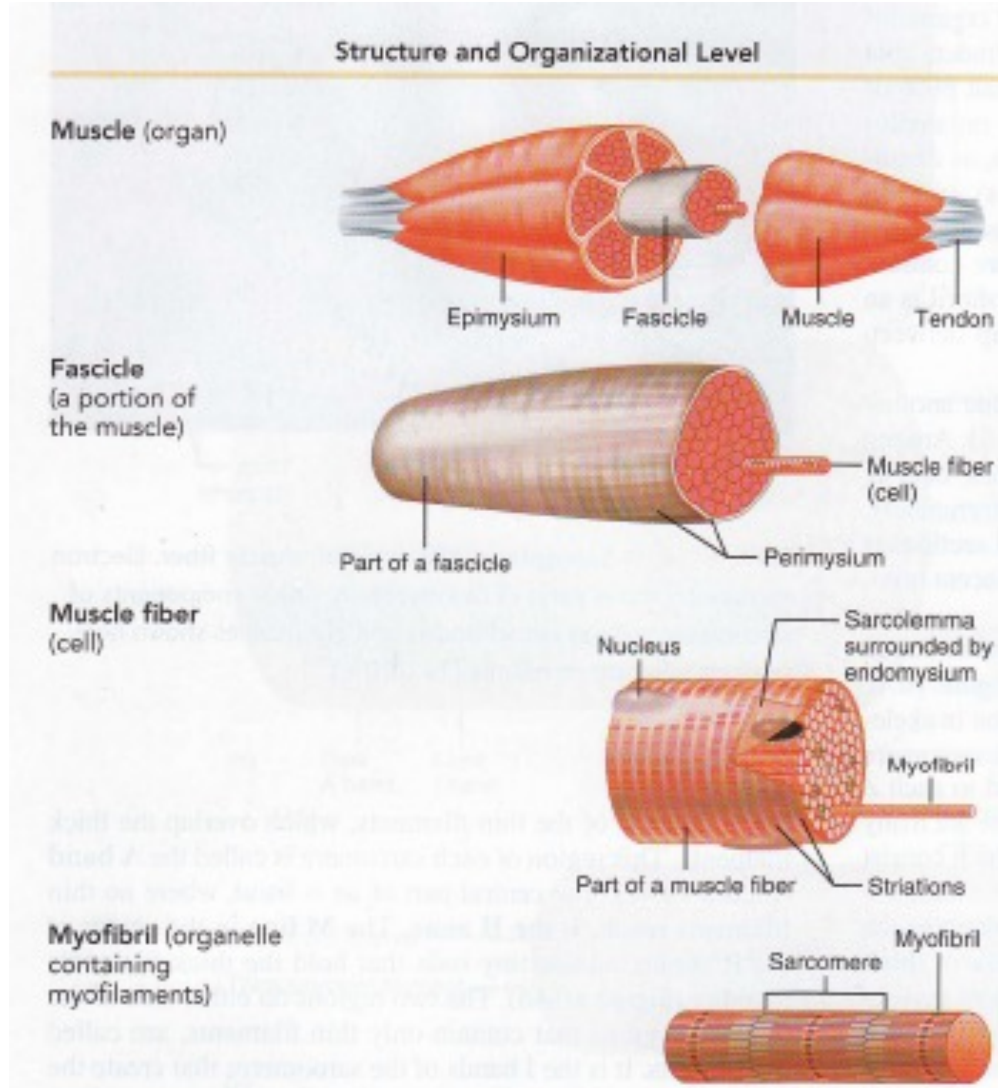
Muscle Fiber

- Muscle Cell
- Long, cylindrical, multinucleated cells
- Between fibers are blood vessels
- Surrounded by endomysium
- Composed of myofibrils



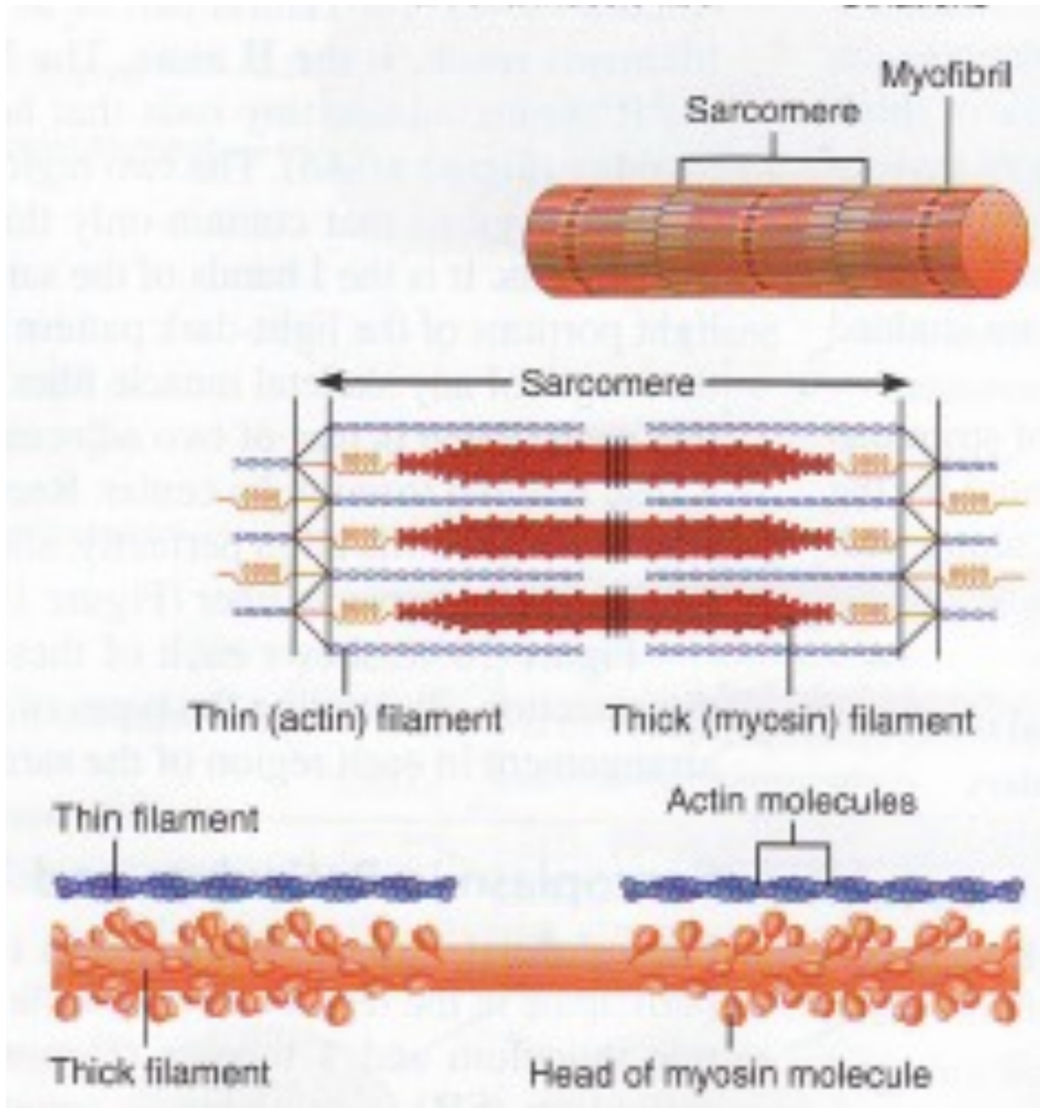
Myofibrils

- Literally (muscle thread)
- Made up of filaments
- Aligned in parallel
- Filaments make striations
  - Banding pattern
- One repeating unit is called a sarcomere
- String of sarcomeres in series



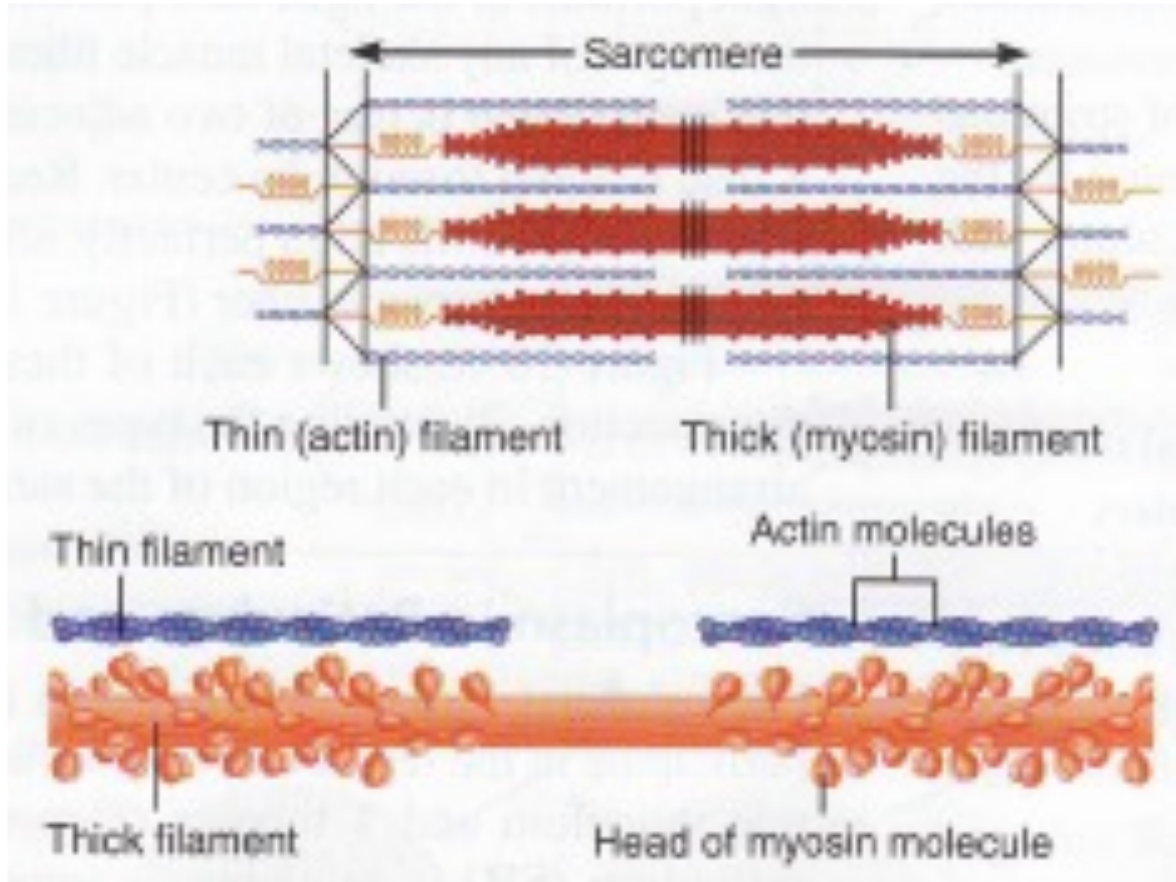
Sarcomeres

- Functional unit of muscle contraction
- Literally ‘muscle segment’
- When each sarcomere shortens the same amount, the fiber with more sarcomeres will shorten more.
- Number of sarcomeres in a fiber is very important to muscle function
- Made up of myofilaments
  - Thick and thin filaments

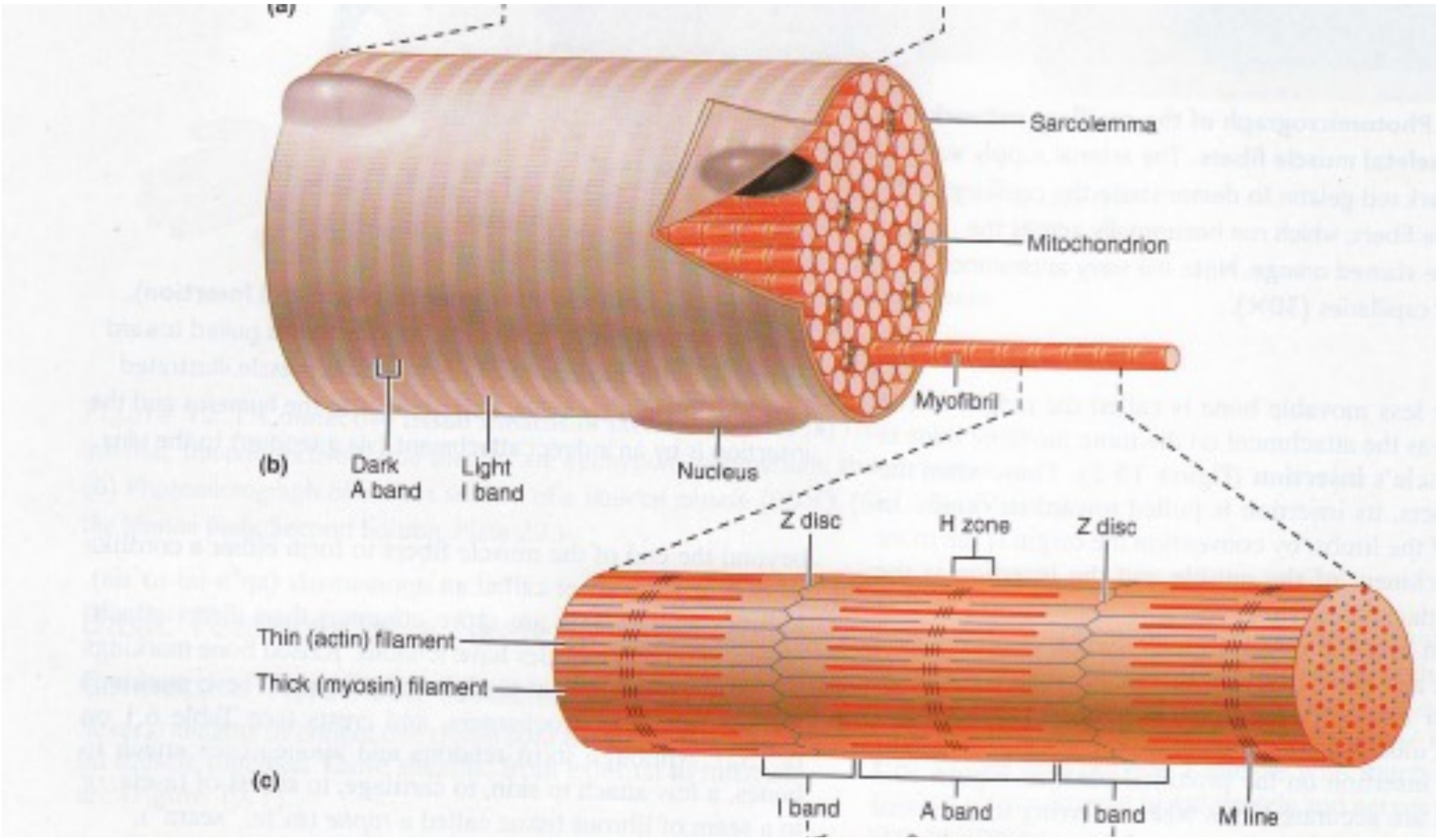


Myofilaments

- Myosin (thick)
  - In central region
  - Dark bands
  - Globular heads
  - Arranged in both directions
- Actin (thin)

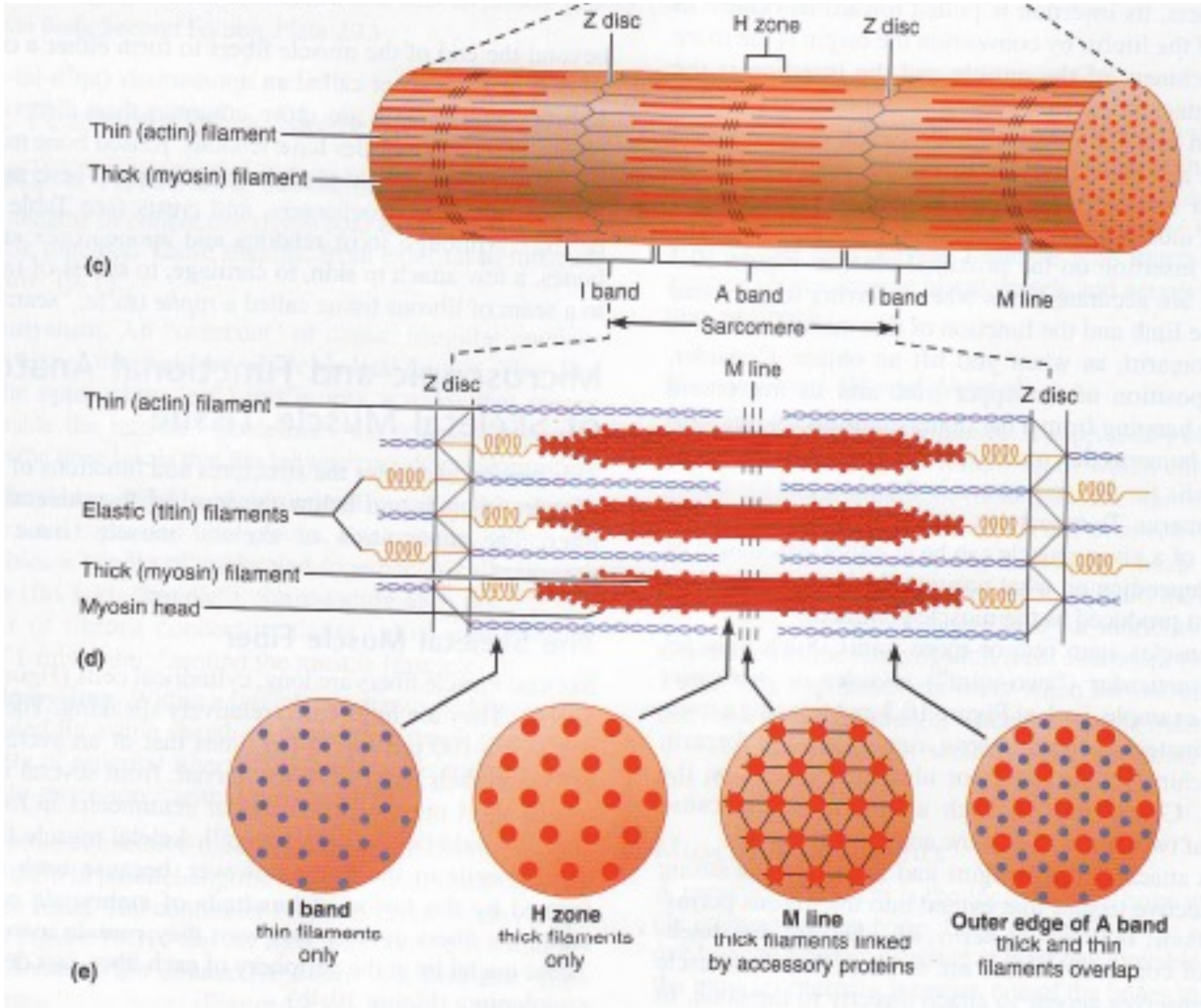


Banding Pattern



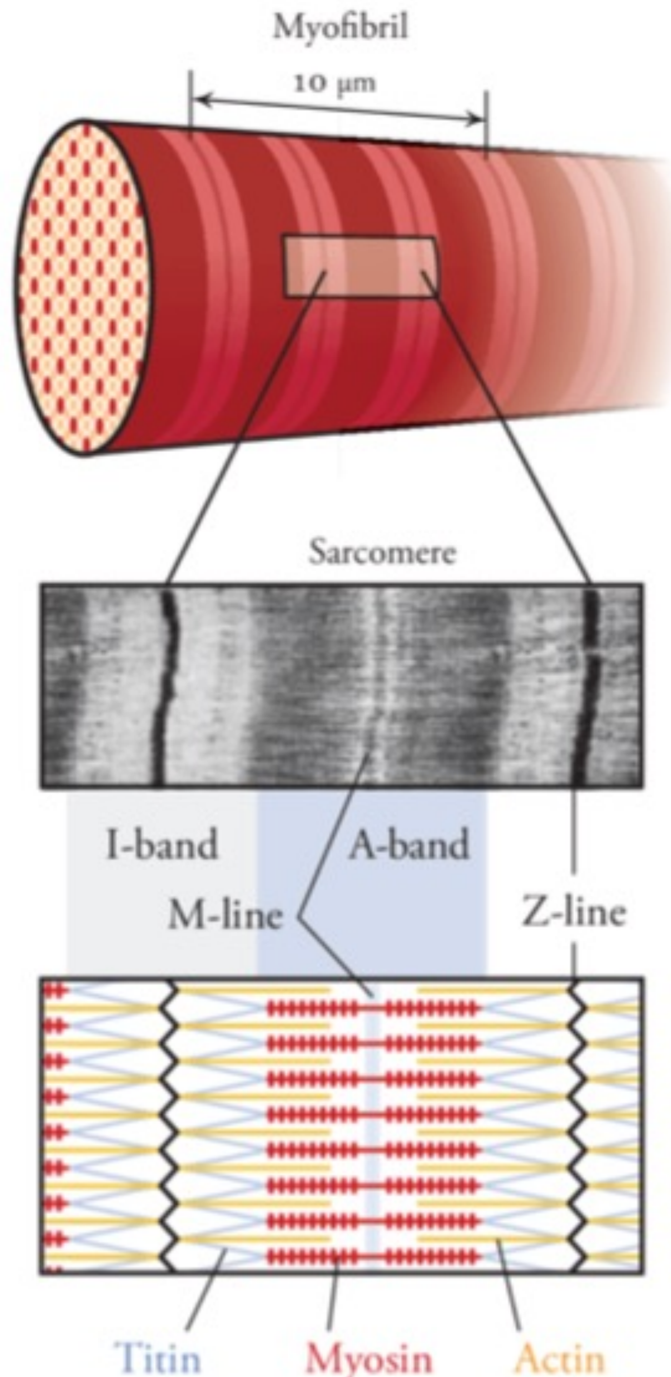
Structures based on myofilaments:

- Z-Disc
- I-Band
- A-Band
- H-Zone
- M-Line

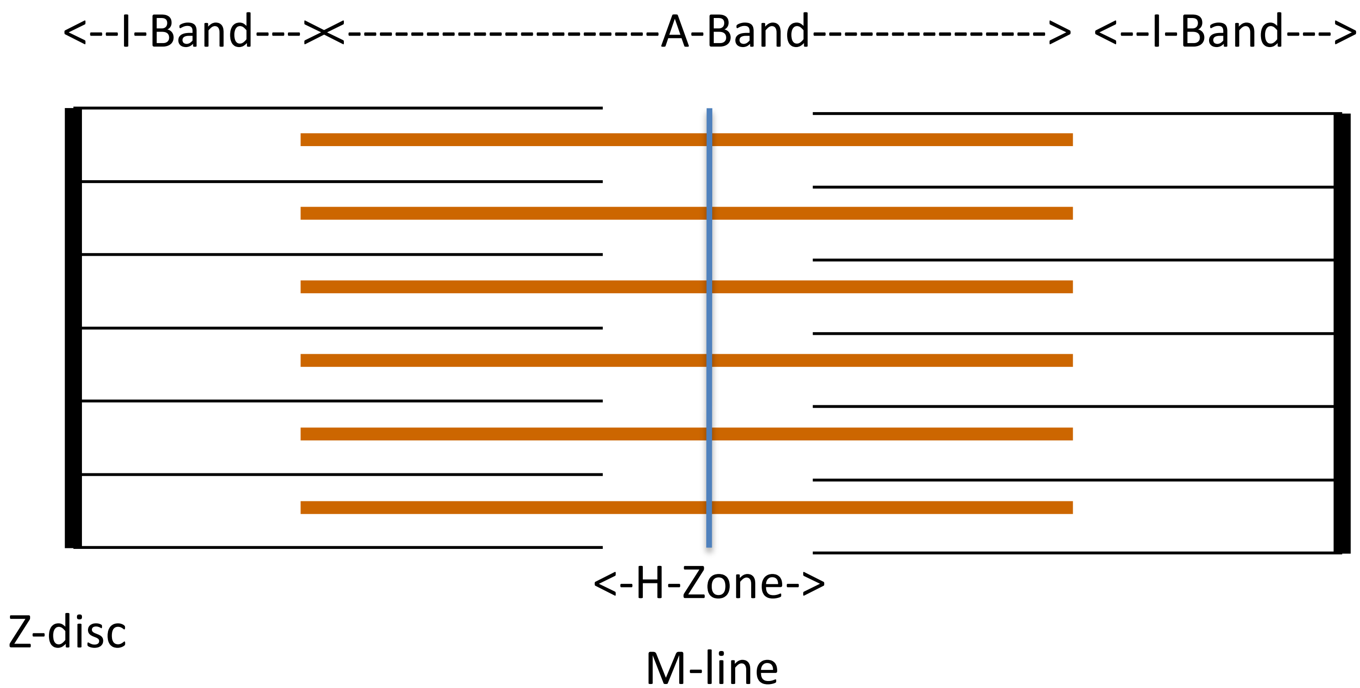


Myofibril

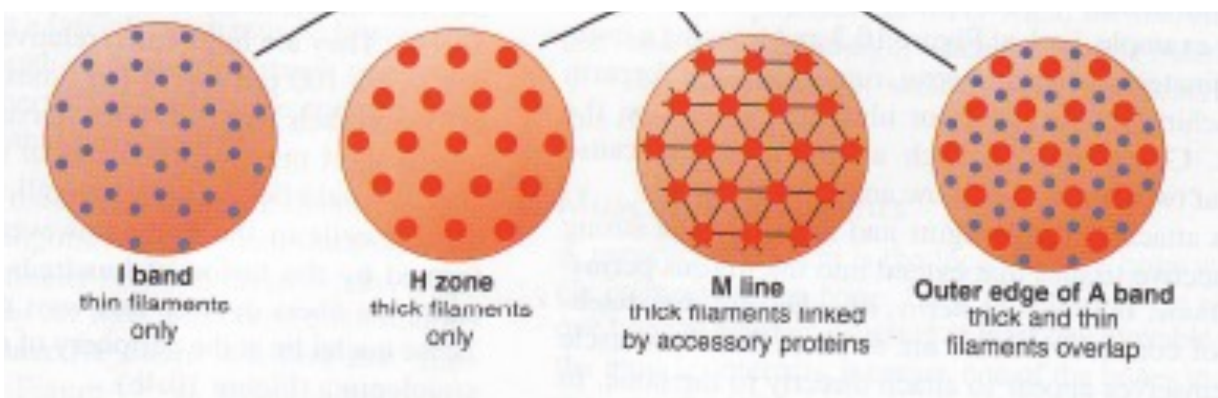
- Z-Disc
- I-Band
- A-Band
- H-Zone
- M-Line



Sarcomere:



<--I-Band---><-------------------A-Band--------------> <--I-Band--->
<-H-Zone->
Z-disc
M-line



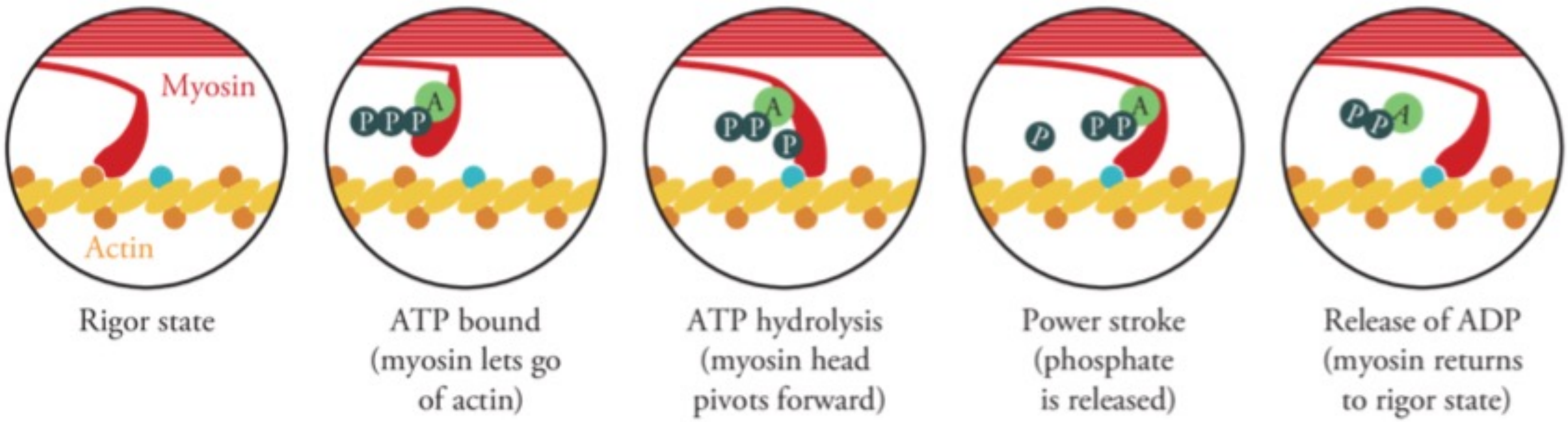
I band
thin filaments only
H zone
thick filaments only
M line
thick filaments linked by accessory proteins
Outer edge of A band
thick and thin filaments overlap

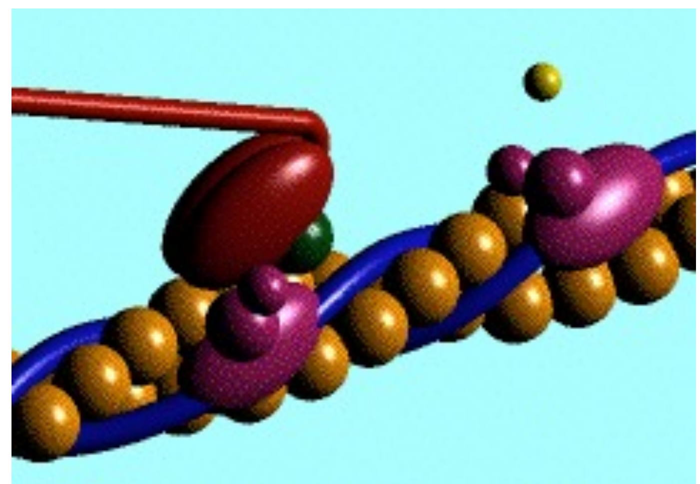
Muscle contraction

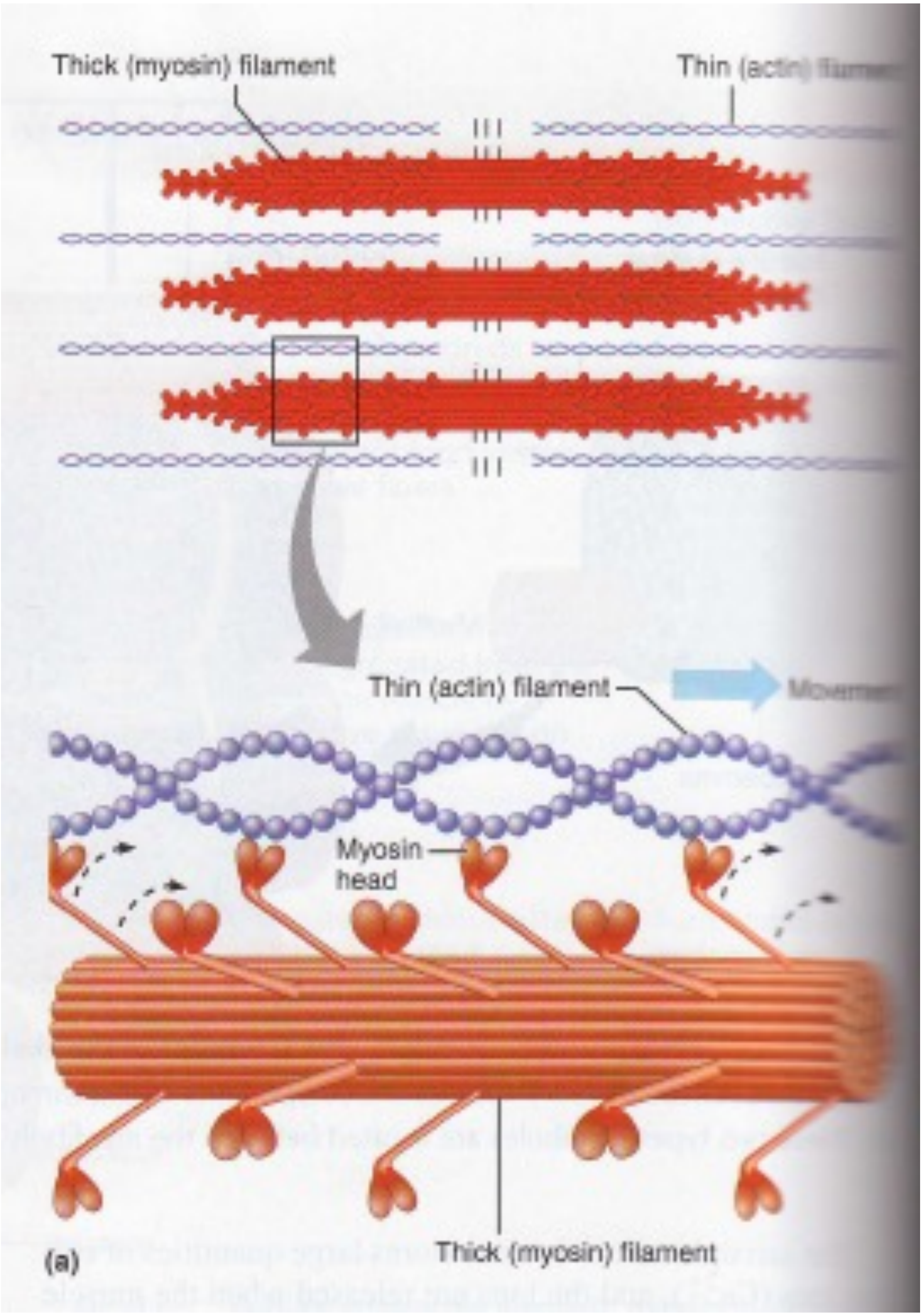
- Sliding filament theory
  - AF Huxley and HE Huxley
  - Light and Electron microscopy
  - Both published results same time in Nature (1954)
  - Does not explain lengthening contractions

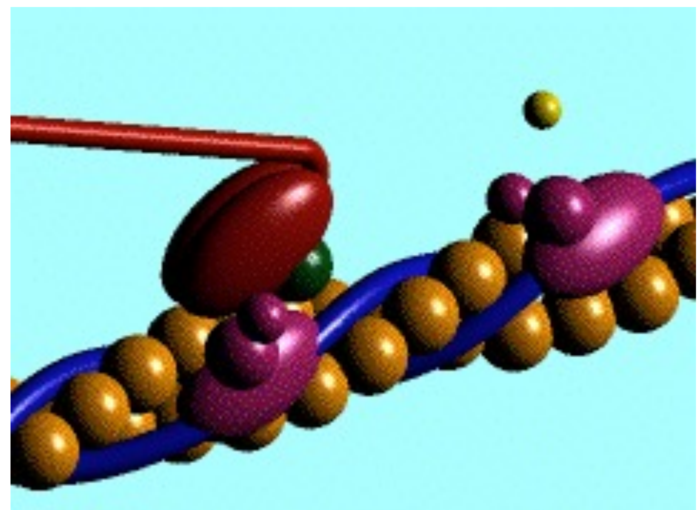

Sliding Filament Theory

- The exertion of force by muscle is accompanied by the sliding of thick and thin filaments past one another
- Commonly explained by cross-bridges


Myosin
Actin
Rigor state
ATP bound
(myosin lets go
of actin)
ATP hydrolysis
(myosin head
pivots forward)
Power stroke
(phosphate
is released)
Release of ADP
(myosin returns
to rigor state)







muscle force is proportional to the number of cross bridges attached

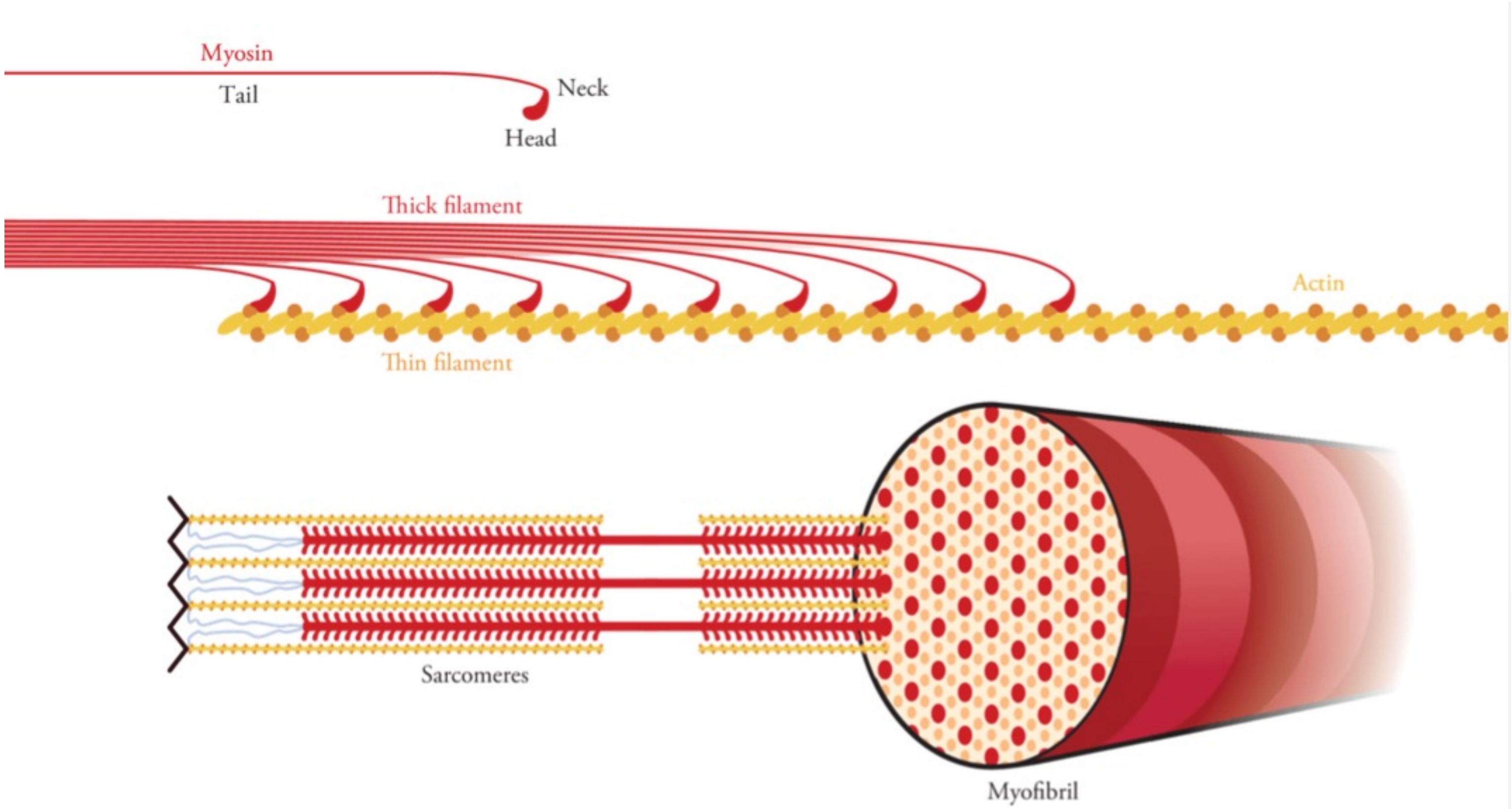
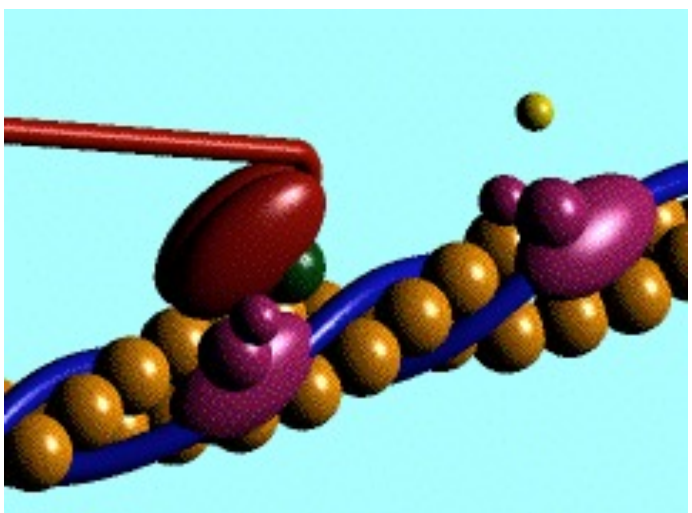


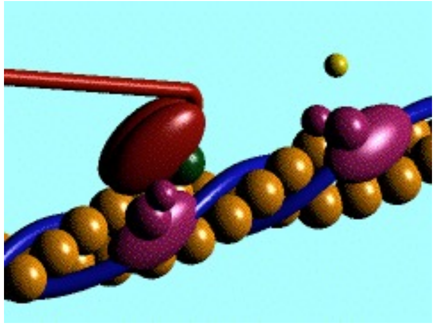
FIGURE 4.4
Schematics of myosin (top), interaction of thick and thin filaments (center), and cross-section of myofibril showing thick and thin filaments arranged in a highly organized three-dimensional pattern (bottom).



muscle force is proportional to the number of cross bridges attached

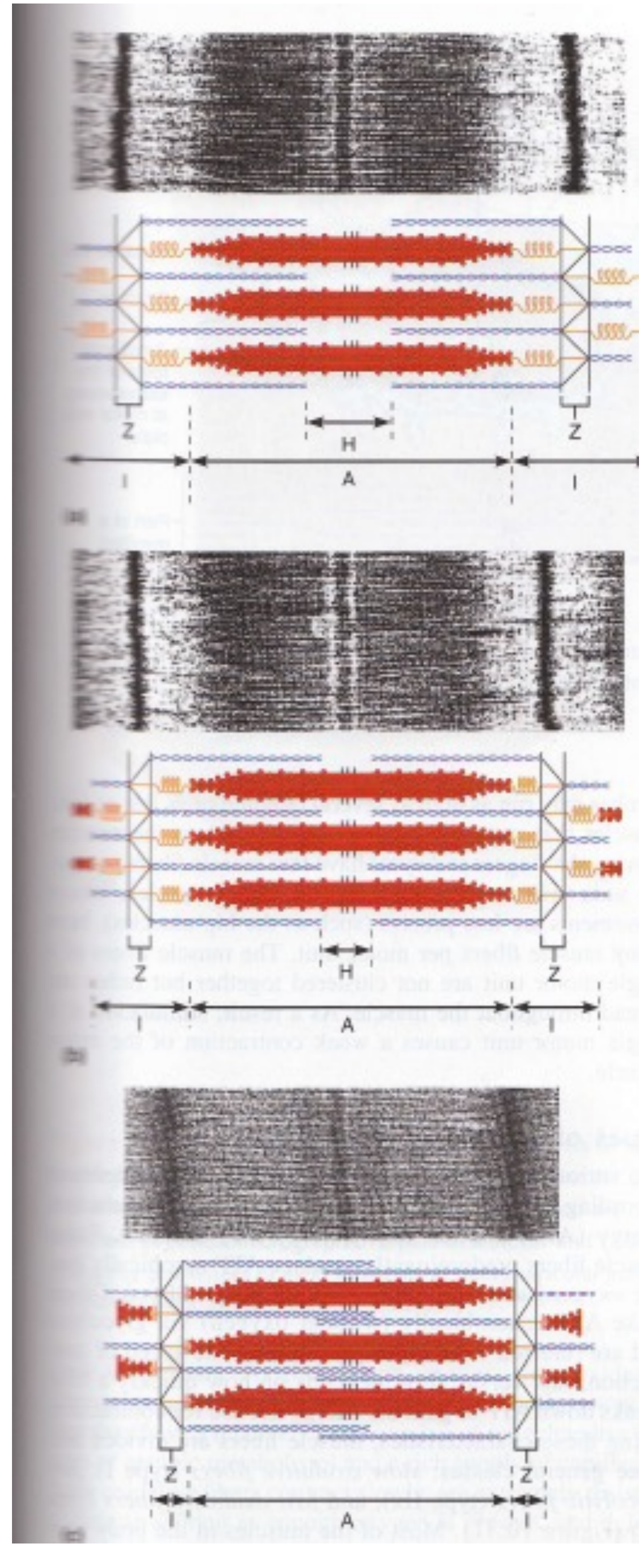
Muscle Proteins, E-C coupling

– Sarcomere: actin, myosin, crossbridges, z-disks
– Nerve stimulation
– Release of Ca++ from Sarcoplasmic-Reticulum
– Ca++ binds to troponin
– Affects tropomyosin (conformational change)
– Makes the actin binding site available
– Myosin cross bridge binds and rotates head
– Force is developed
– Re-uptake of Ca++ consumes ATP
– Detaching the crossbridge consumes ATP



Sliding filament theory

- A band stays the same
- I band shortens



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Muscle Mechanics

- Force-length
- Force-velocity

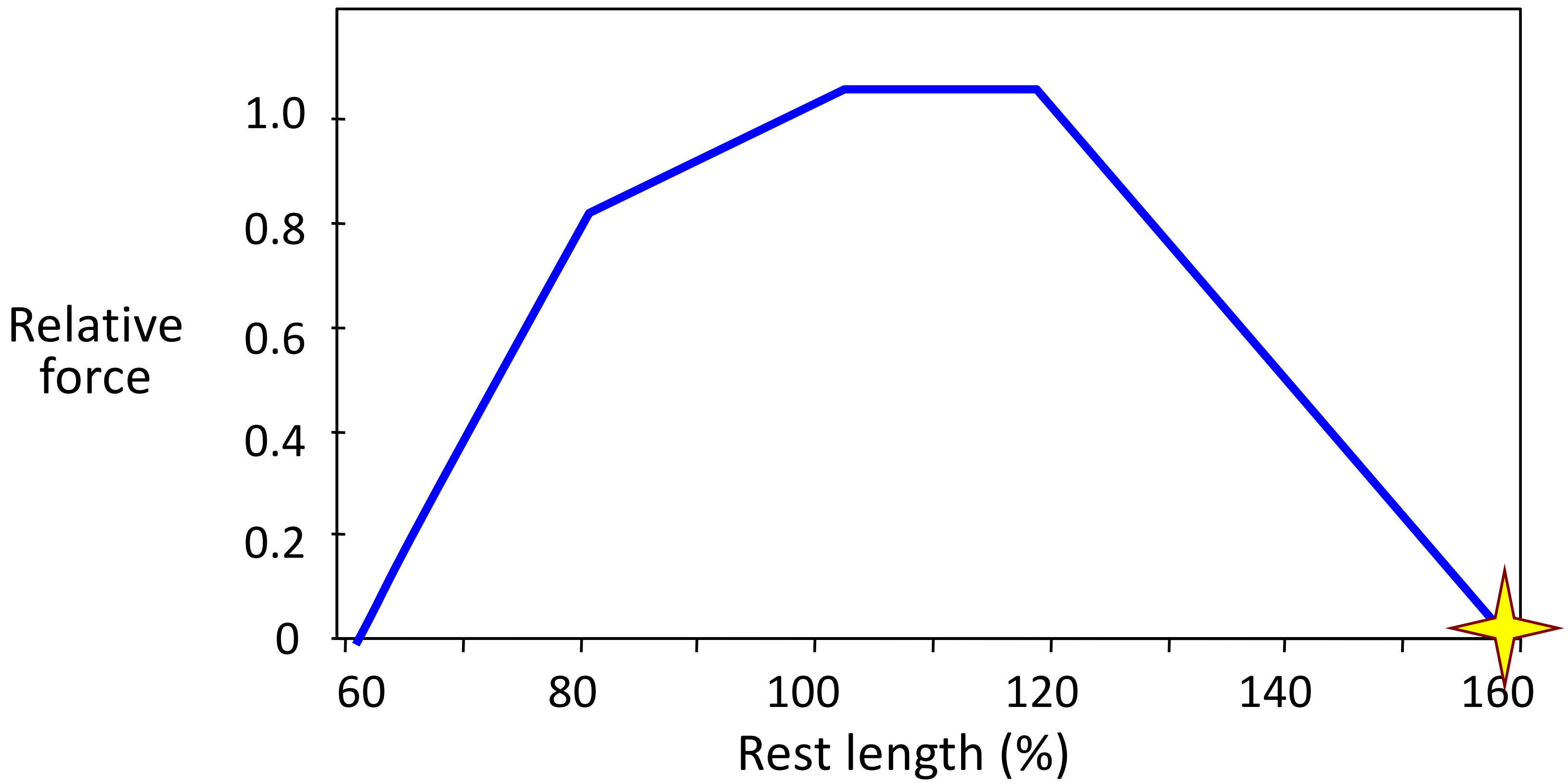
Sliding Filament Theory

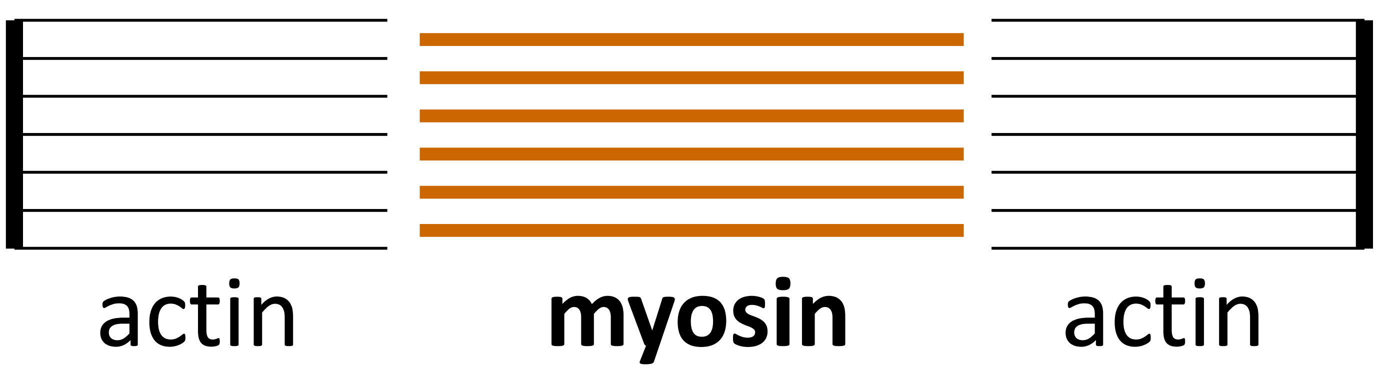
- The exertion of force by muscle is accompanied by the sliding of thick and thin filaments past one another
- Commonly explained by cross-bridges

Force-Length Relationship

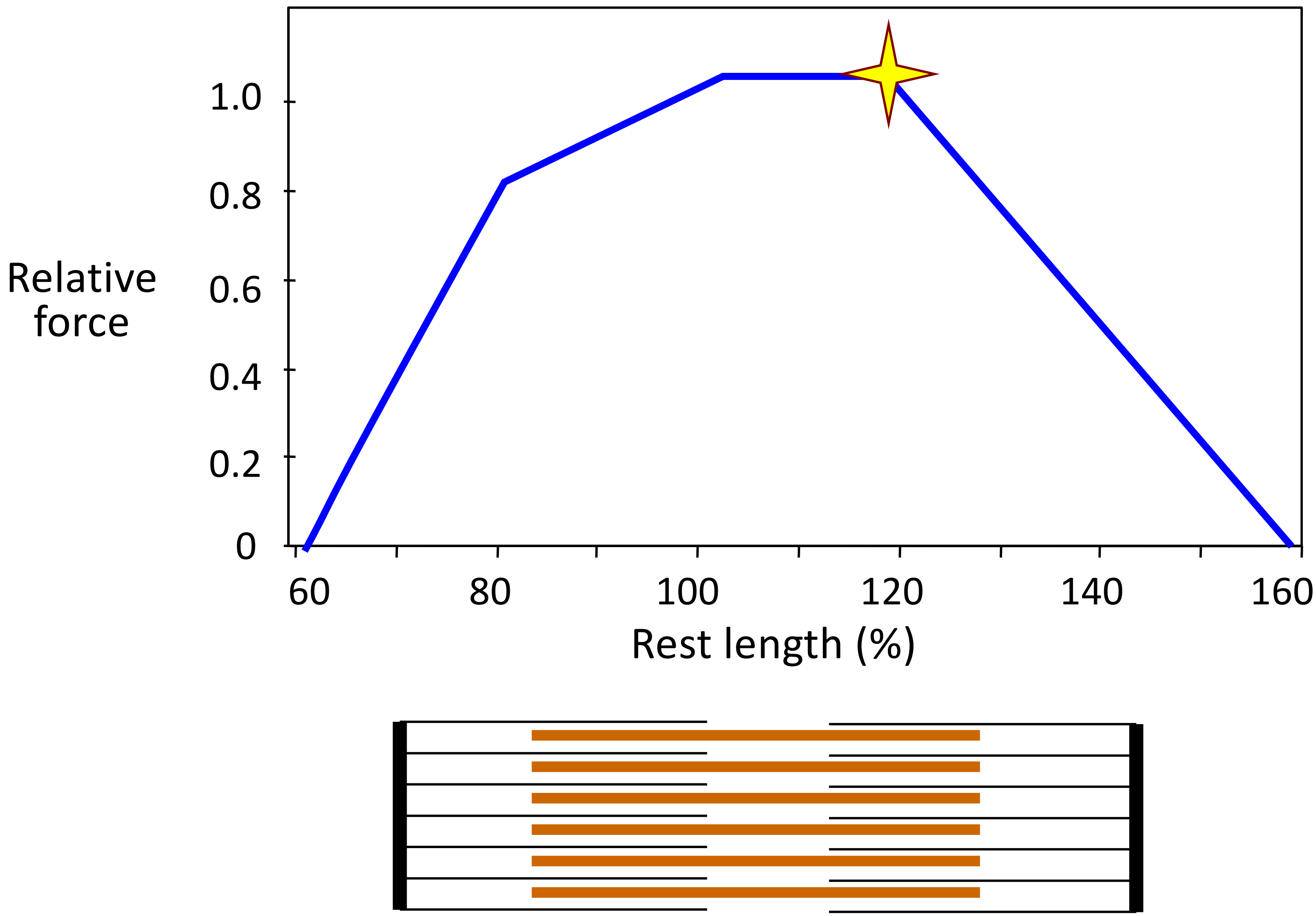
- Isometric force varies with muscle length
  - Forces generation in muscle is a direct function of the amount of overlap between actin and myosin filaments

Force-Length Relationship

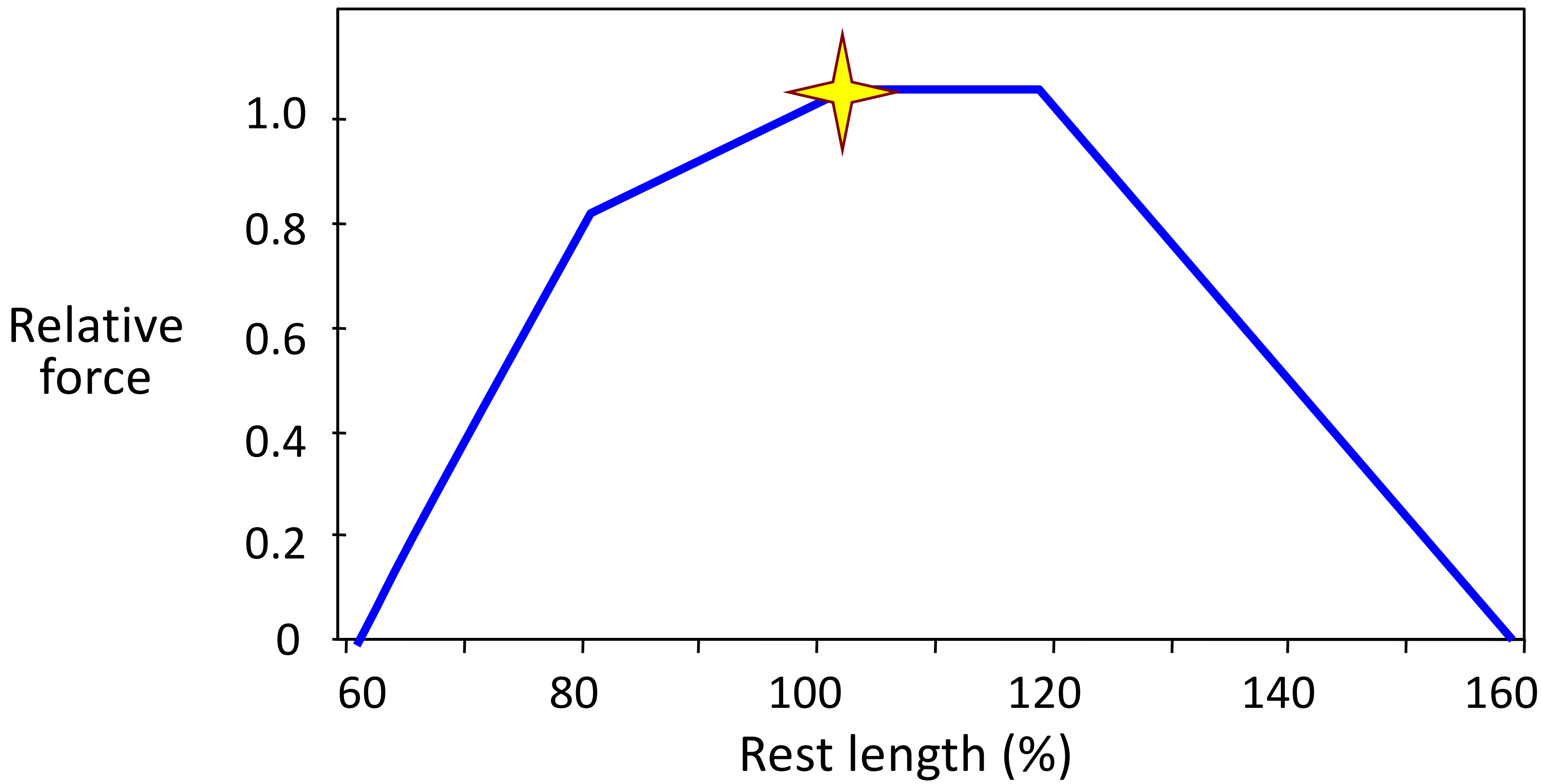


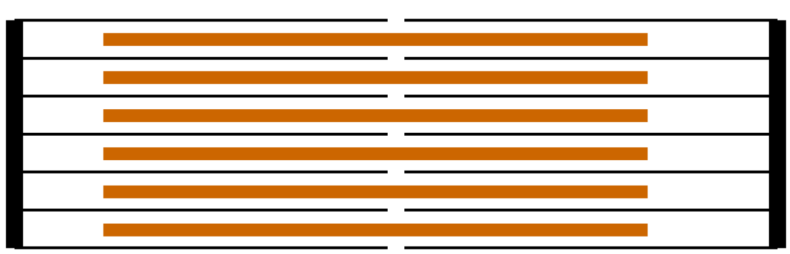


Force-Length Relationship

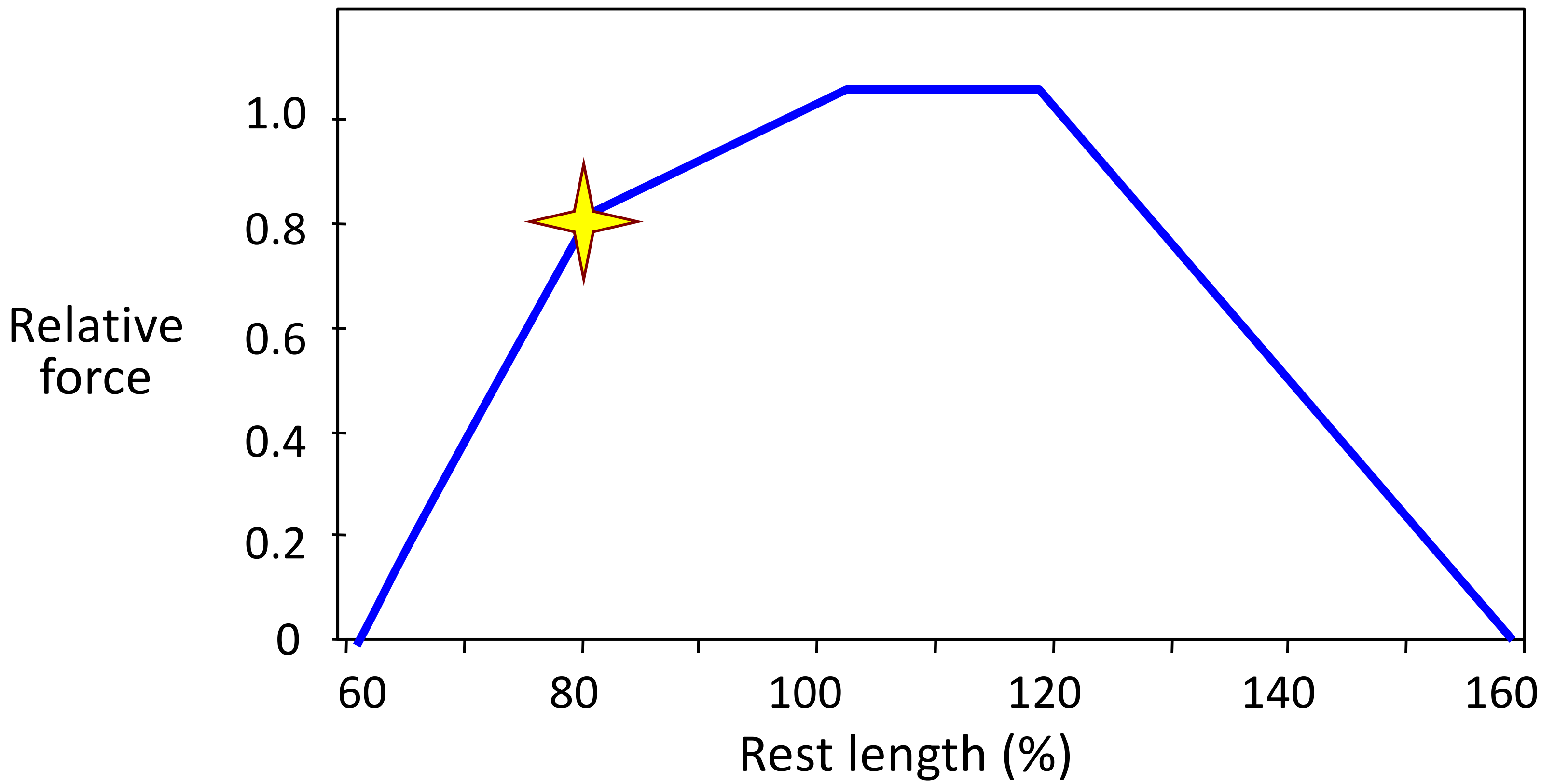


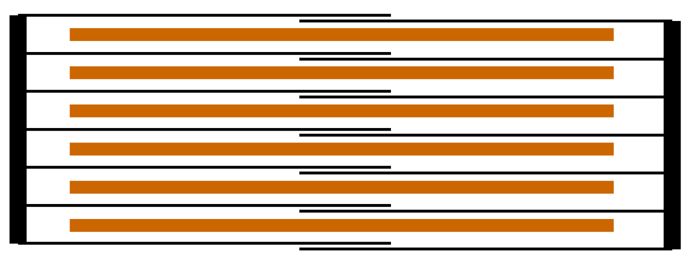
Force-Length Relationship



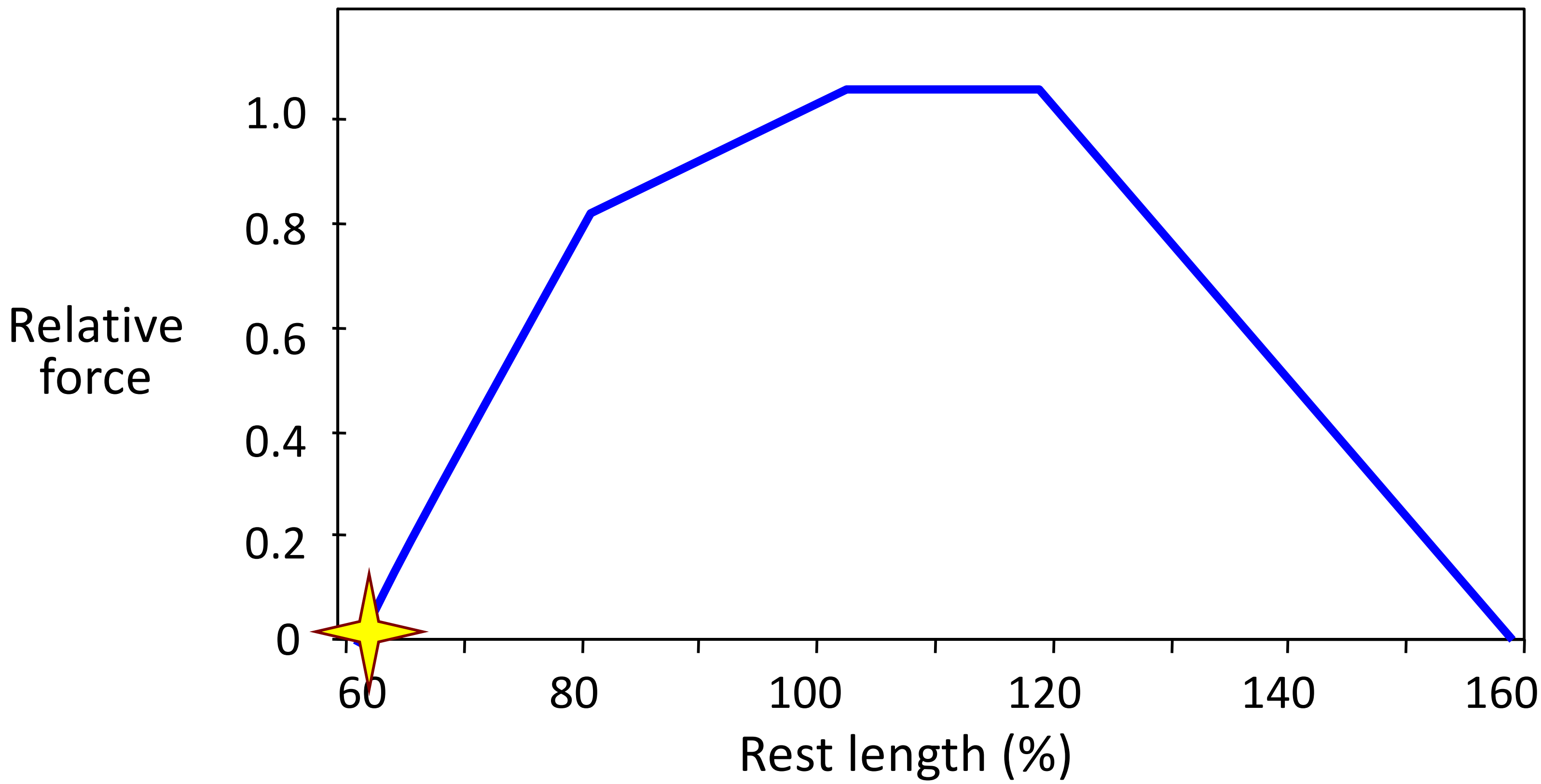


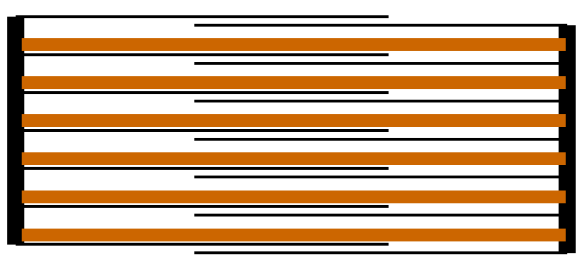
Force-Length Relationship



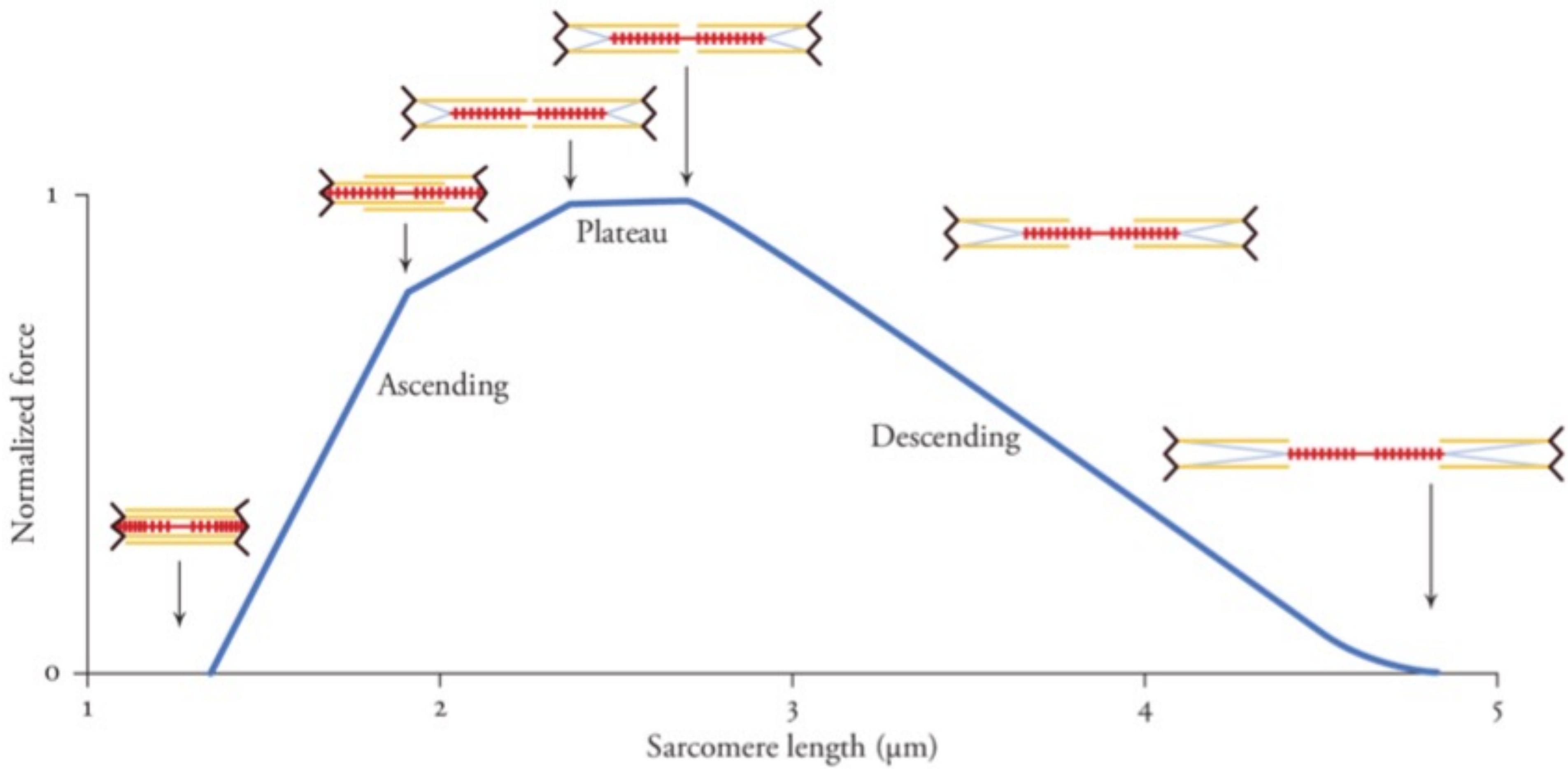


Force-Length Relationship



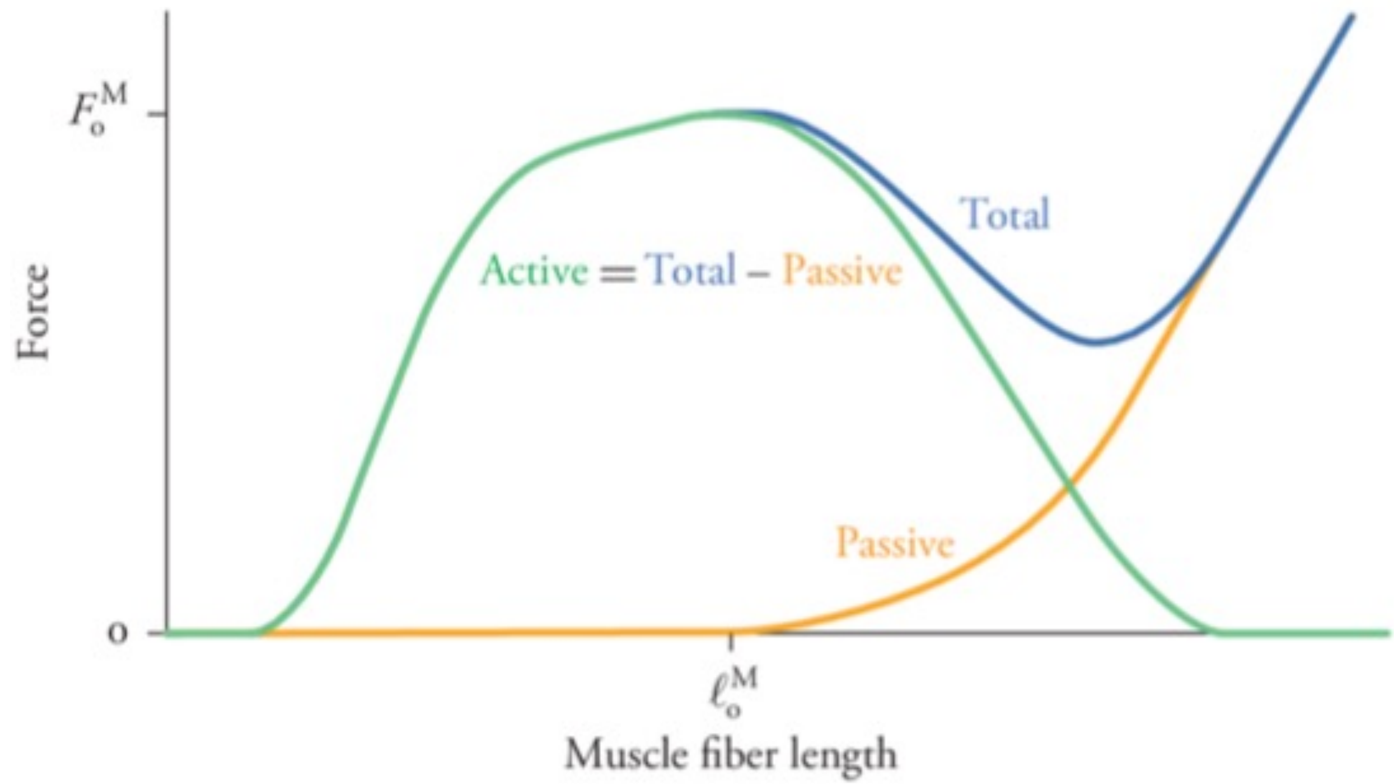


Sarcomere: Force-Length Relationship



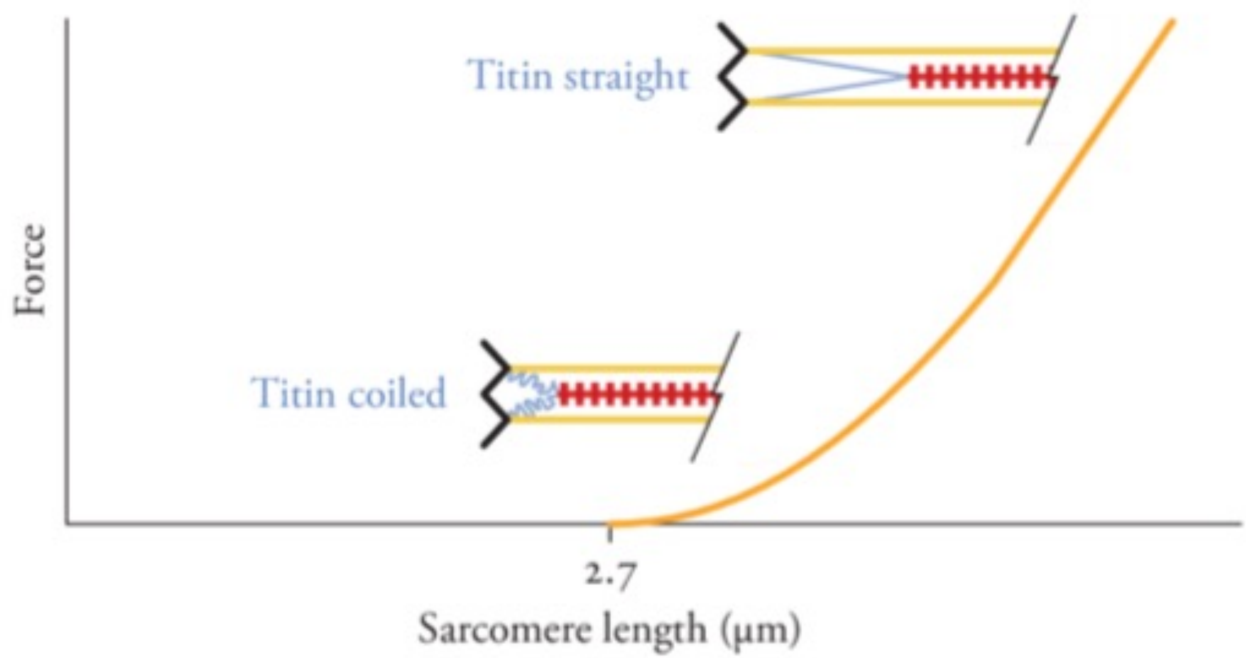
Muscle fiber: Total force-length relationship

- Active force length curve determined by subtracting measurements of the passive force from the total force.
- Peak active force occurs at the optimal fiber length
- Source of Passive force?



Titin

- Titin attaches the thick filaments to the Z-discs
- Develops force when stretched



Titin

- Cross-bridges not responsible for passive muscle tension
- Origin of passive muscle tension within myofibrils

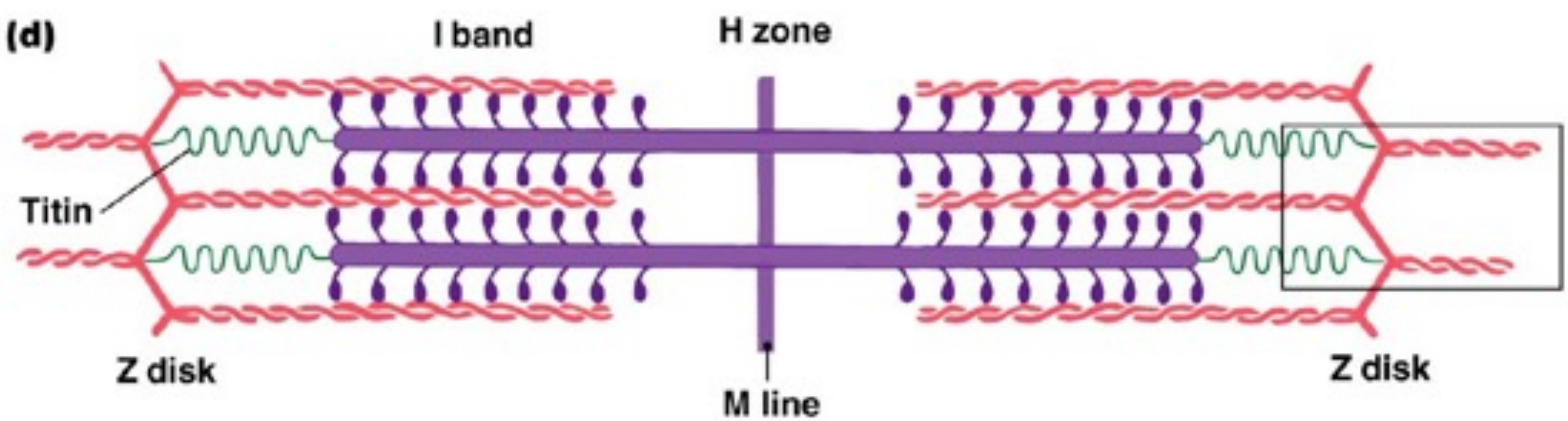
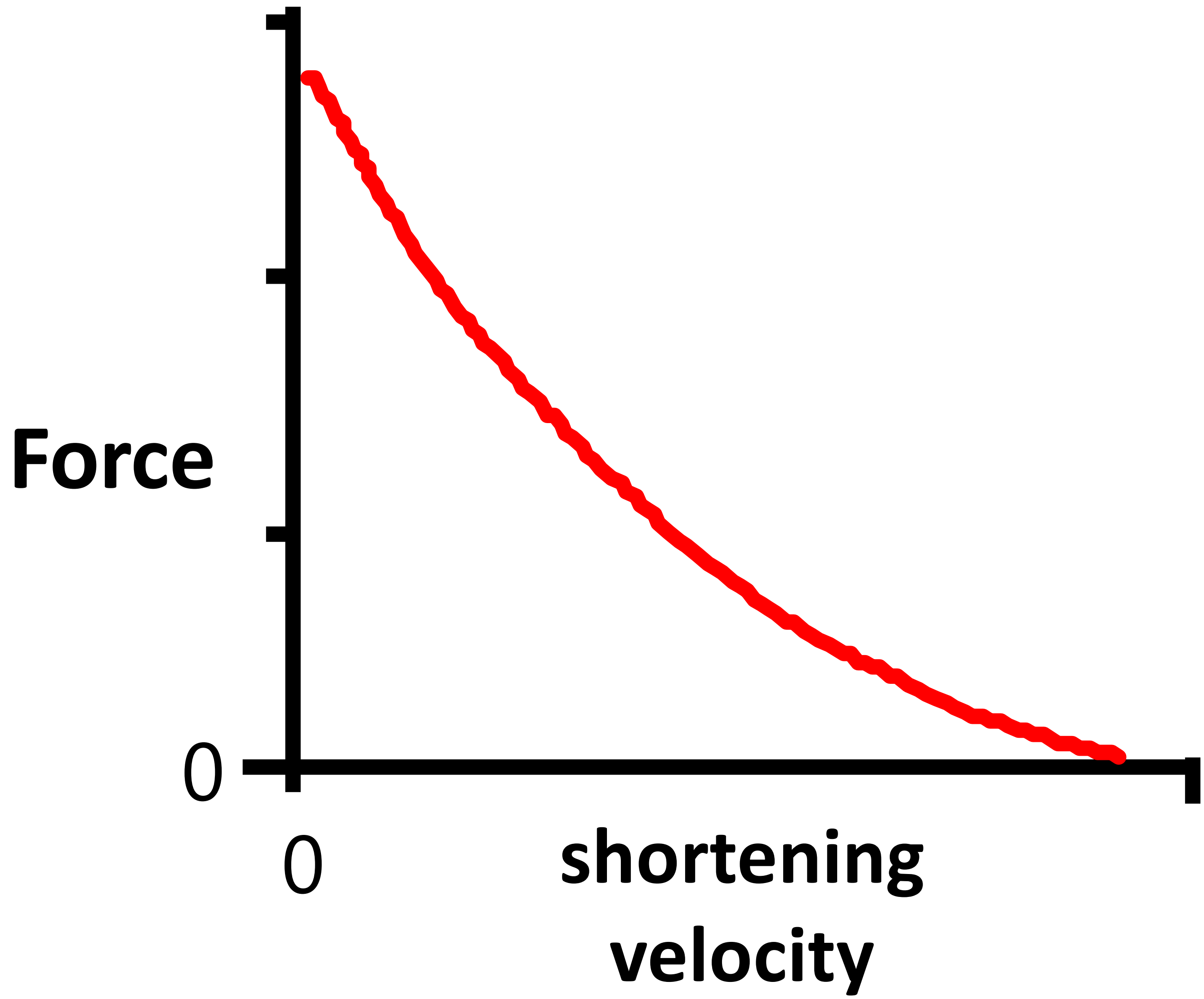


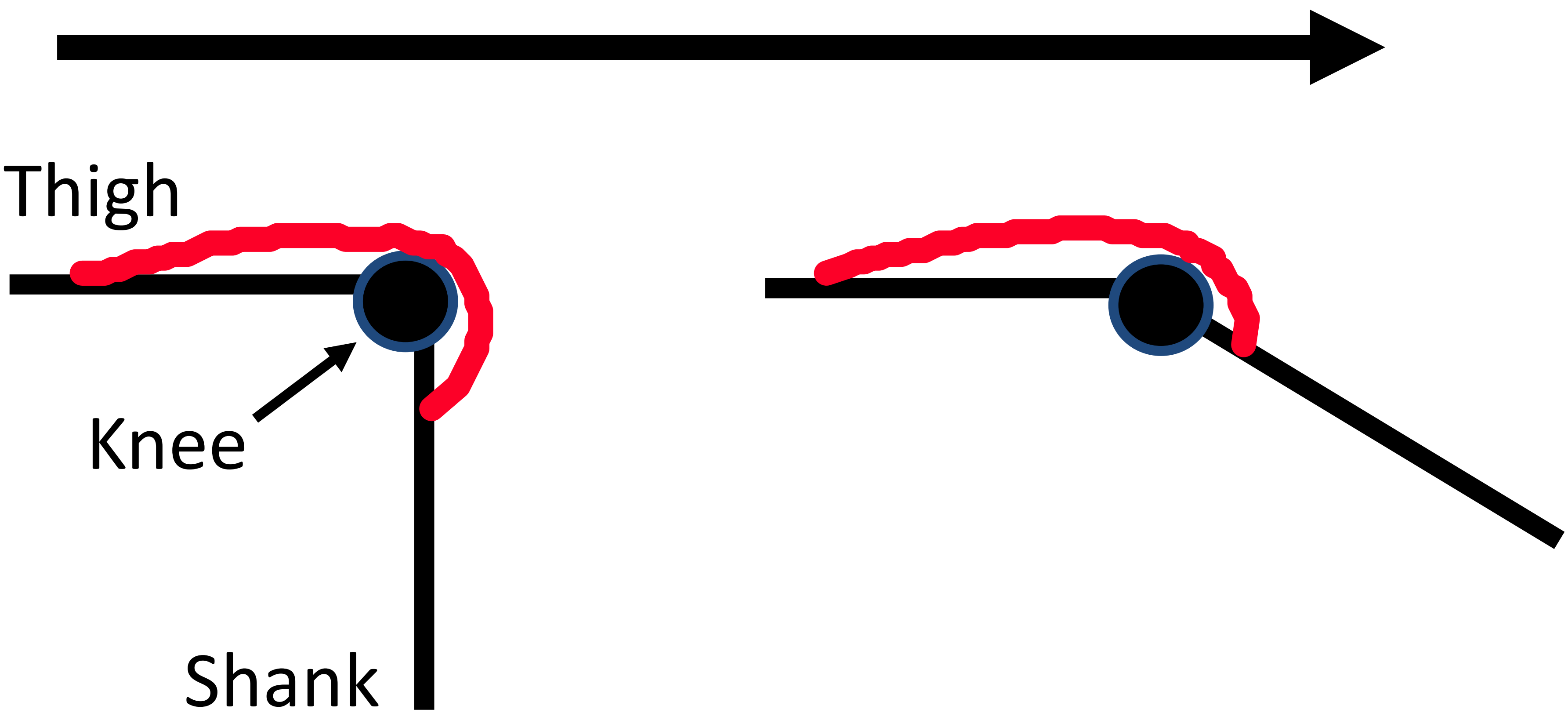
Fig. 12-3

Force-Velocity

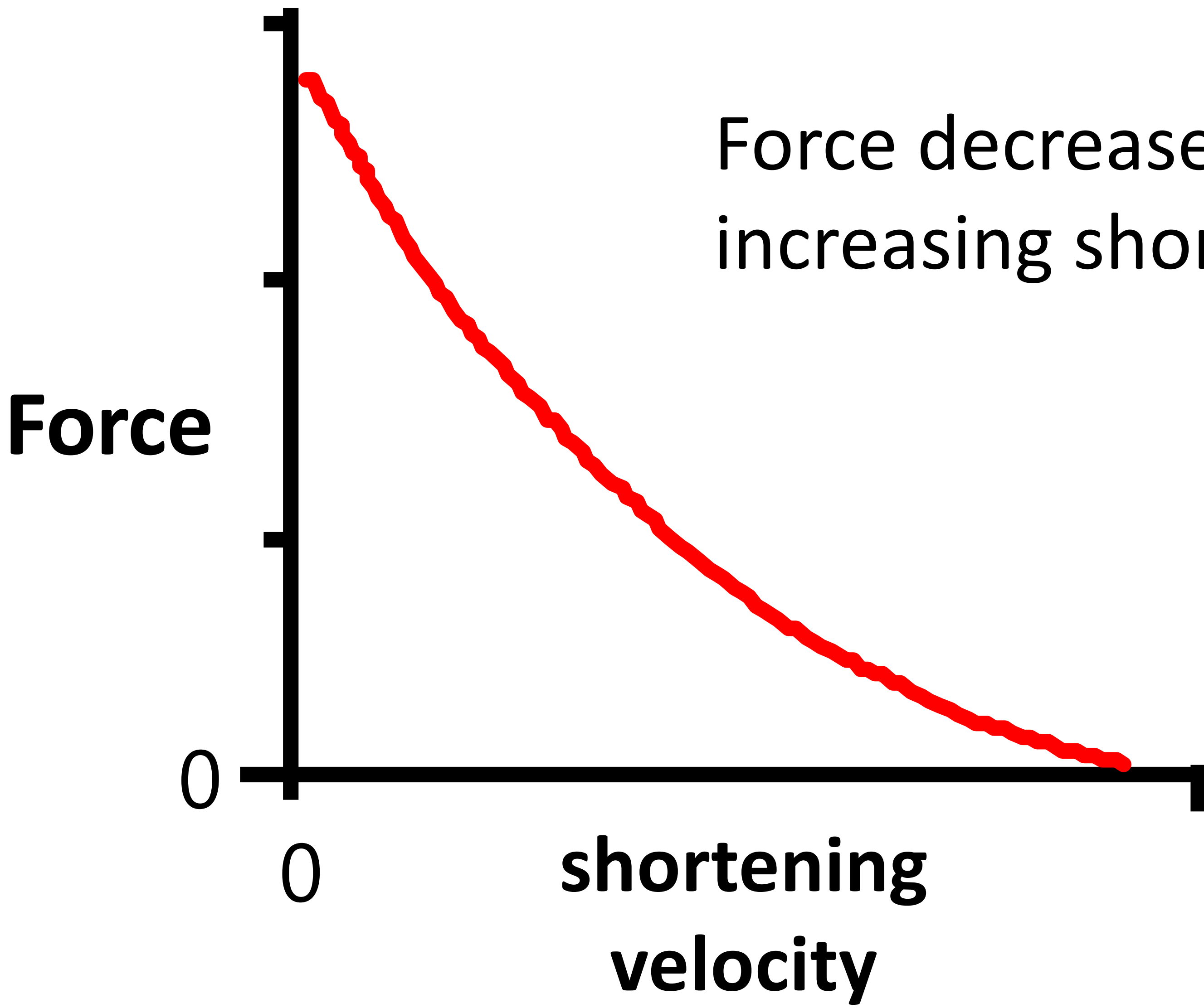


Isometric Contractions

Knee extensor muscles in shortening contraction during knee extension



Force-velocity curve

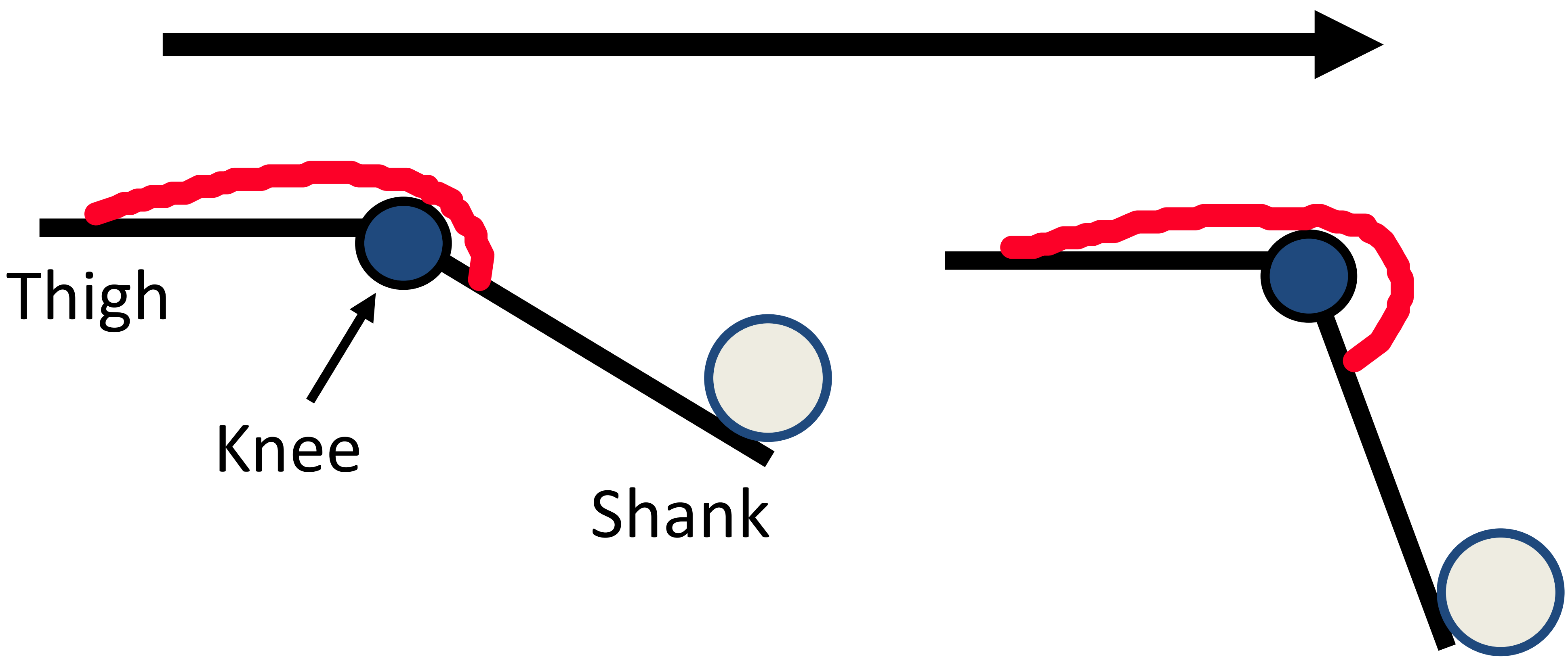


Force decreases with increasing shortening velocity

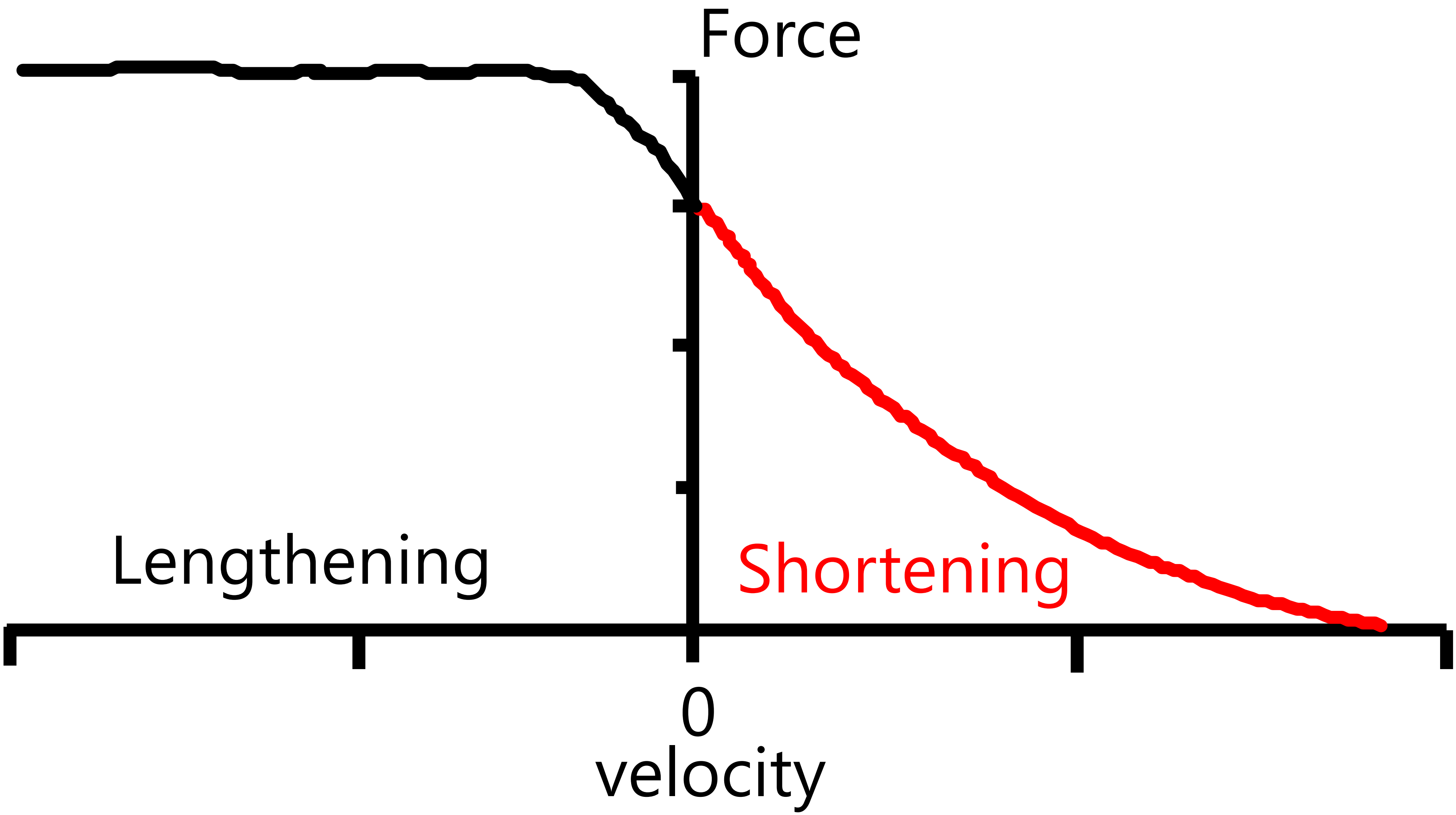
Hill's Equation:

$$(\boldsymbol{F} + \boldsymbol{a})\boldsymbol{v} = \boldsymbol{b}(\boldsymbol{F_0} - \boldsymbol{F})$$

Active and Lengthening



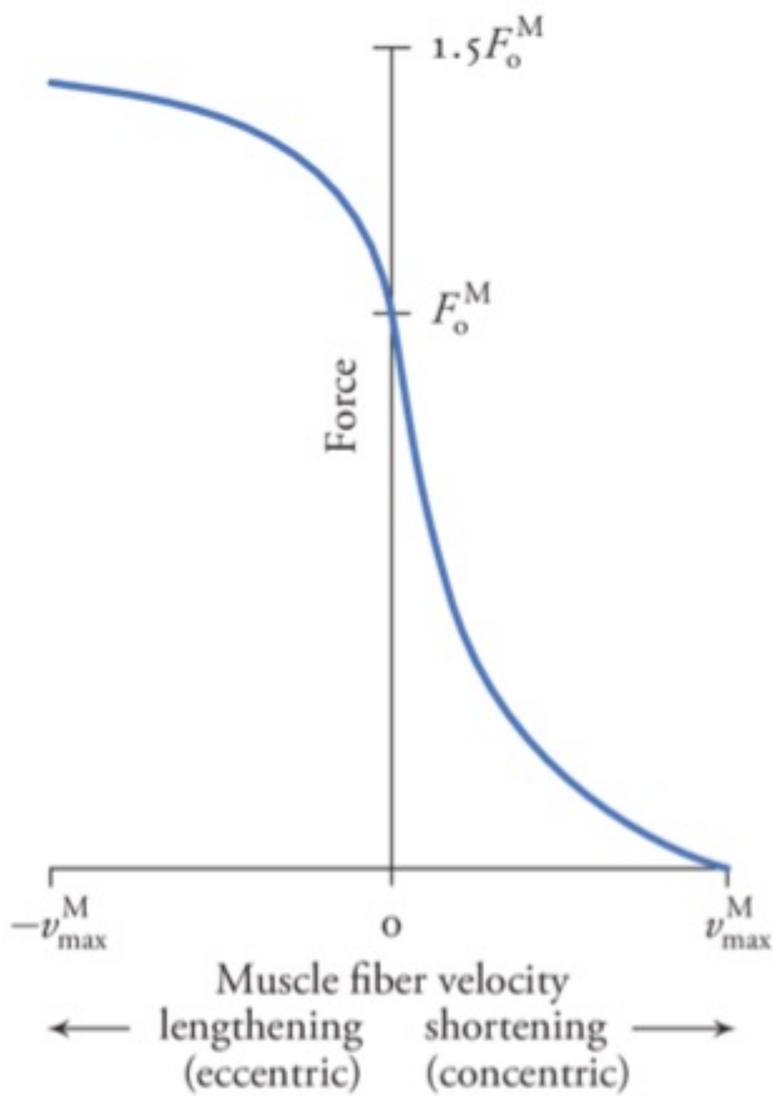
Force-velocity curve



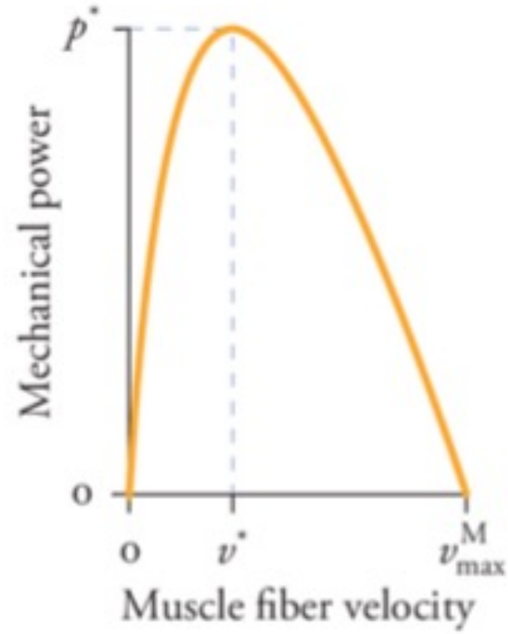
Lengthening Contractions

- Higher force (160%!)
- Velocity-independent
- Don’t know why
- Important

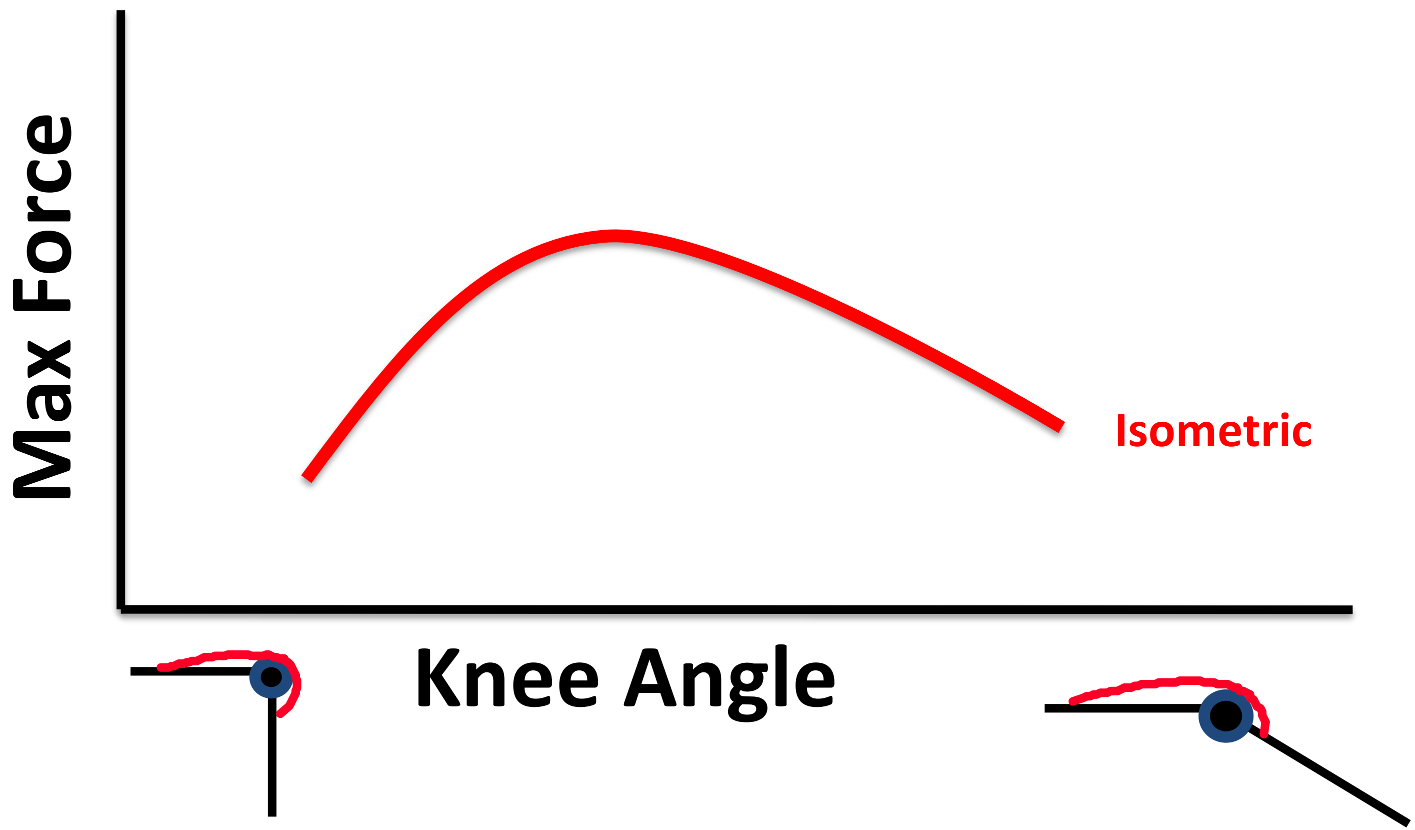
Force-velocity and Power curve



Maximum power at 1/3 maximum velocity



Problem: How will the force-angle curves change for different contraction types?



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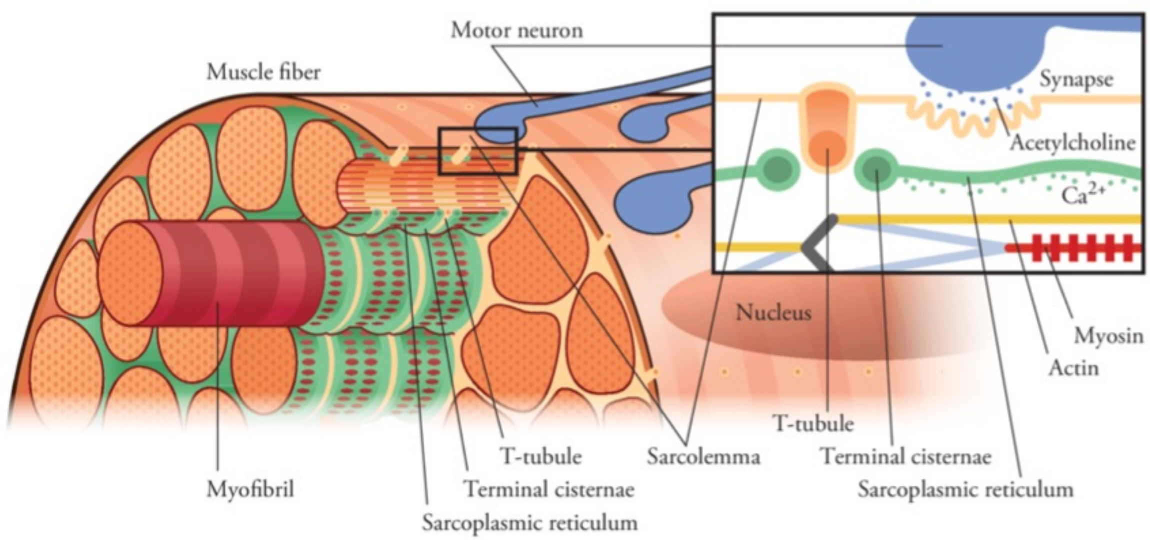
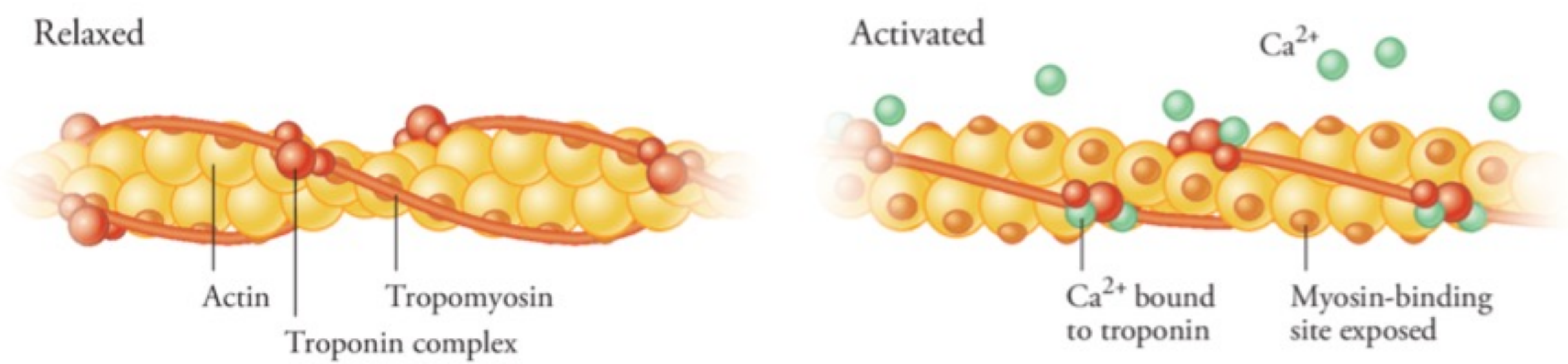
Neuromuscular Junction: E-C coupling

- Sarcomere: actin, myosin, crossbridges, z-disks
- *Nerve stimulation (acetylcholine released)*
- *Release of Ca++ from Sarcoplasmic-Reticulum*
- Ca++ binds to troponin
- Affects tropomyosin (conformational change)
- Makes the actin binding site available
- Myosin cross bridge binds and rotates head
- Force is developed
- Re-uptake of Ca++ consumes ATP
- Detaching the crossbridge consumes ATP



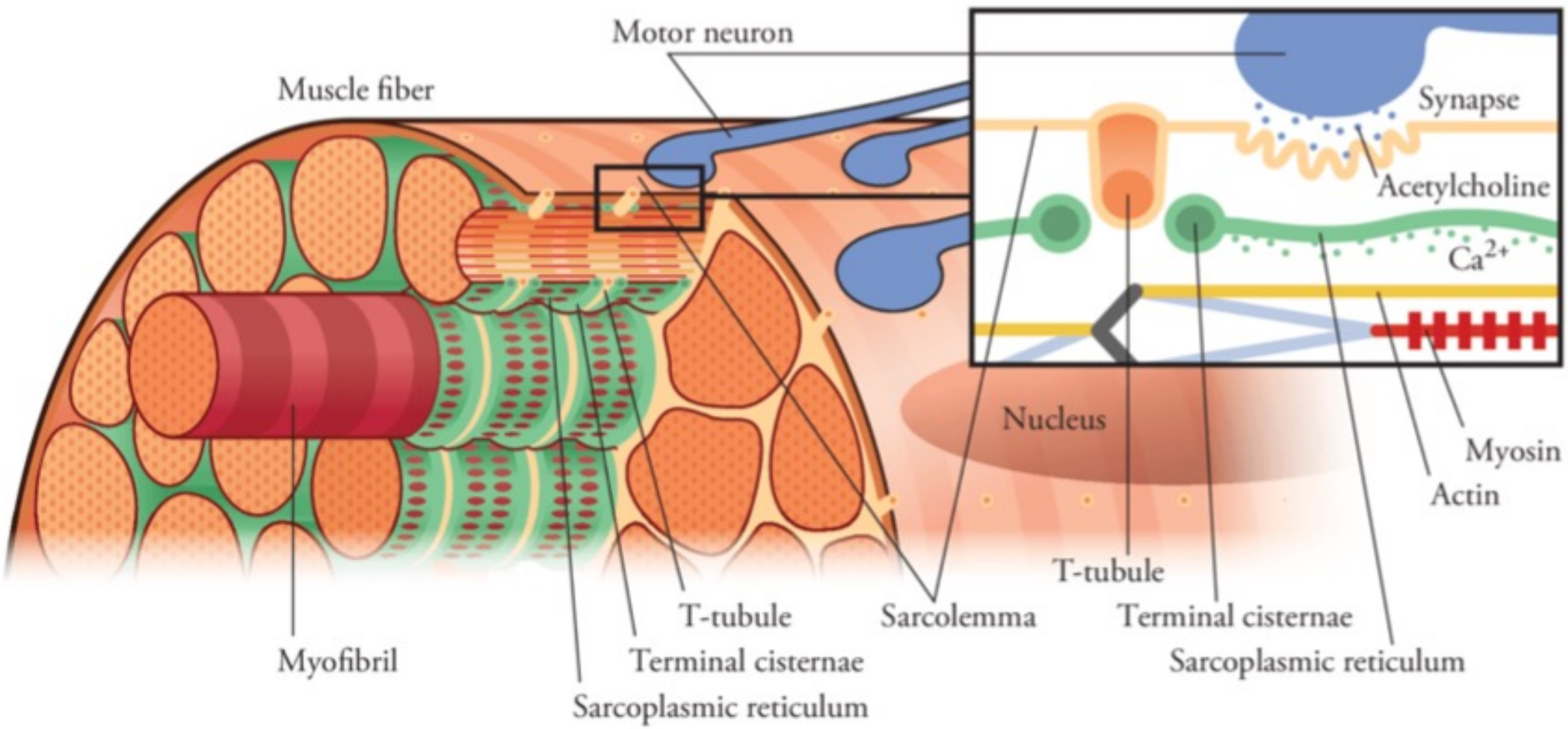
Muscle Activation

- Relaxed: Myosin binding sites on the actin filament are blocked by the tropomyosin protein
- Activated: Release of calcium ions from the sarcoplasmic reticulum bind to the troponin protein complex, causing the tropomyosin to change shape and reveal the binding sites.



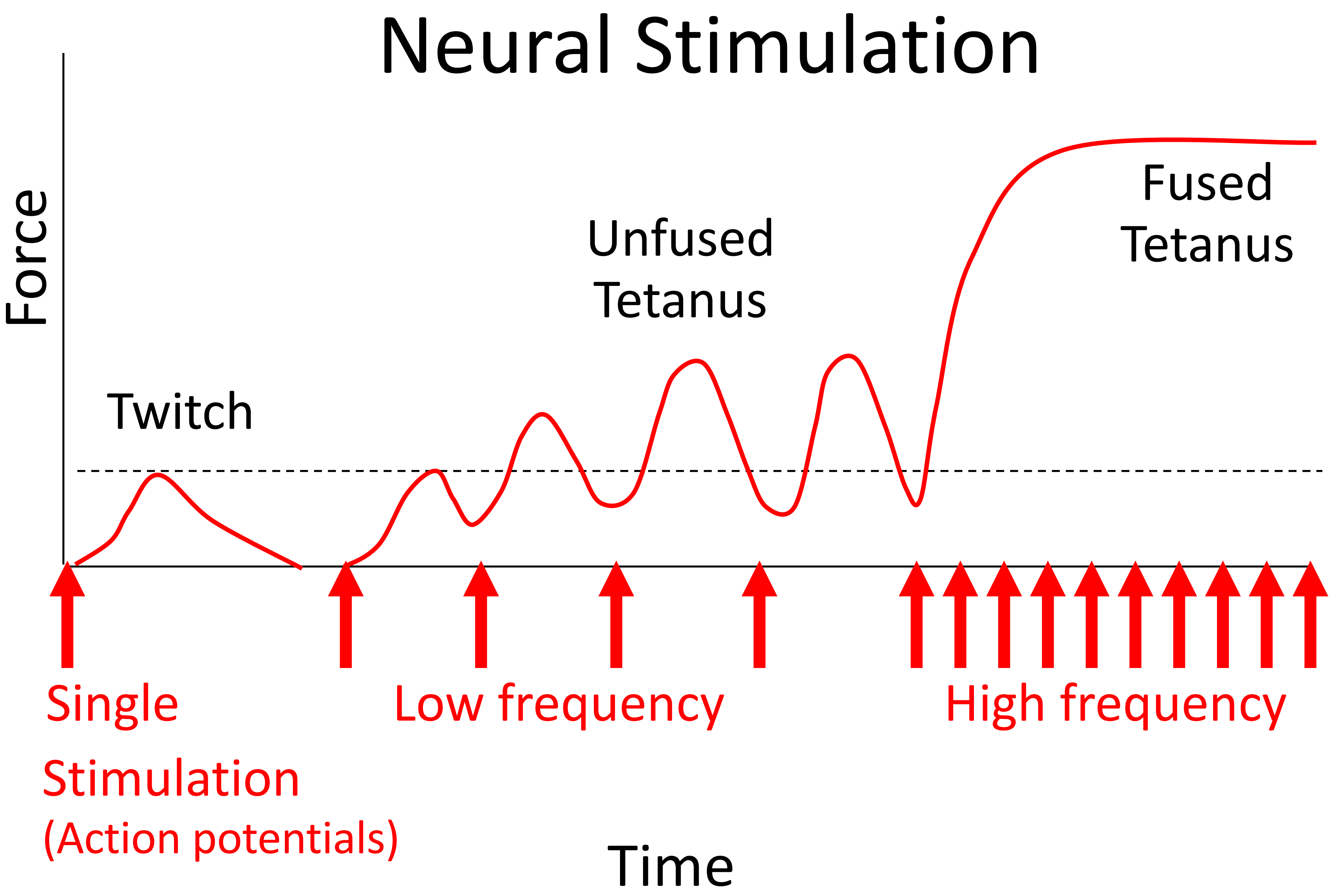
Neuromuscular Junction

- Muscle structure allows rapid progression of action potential



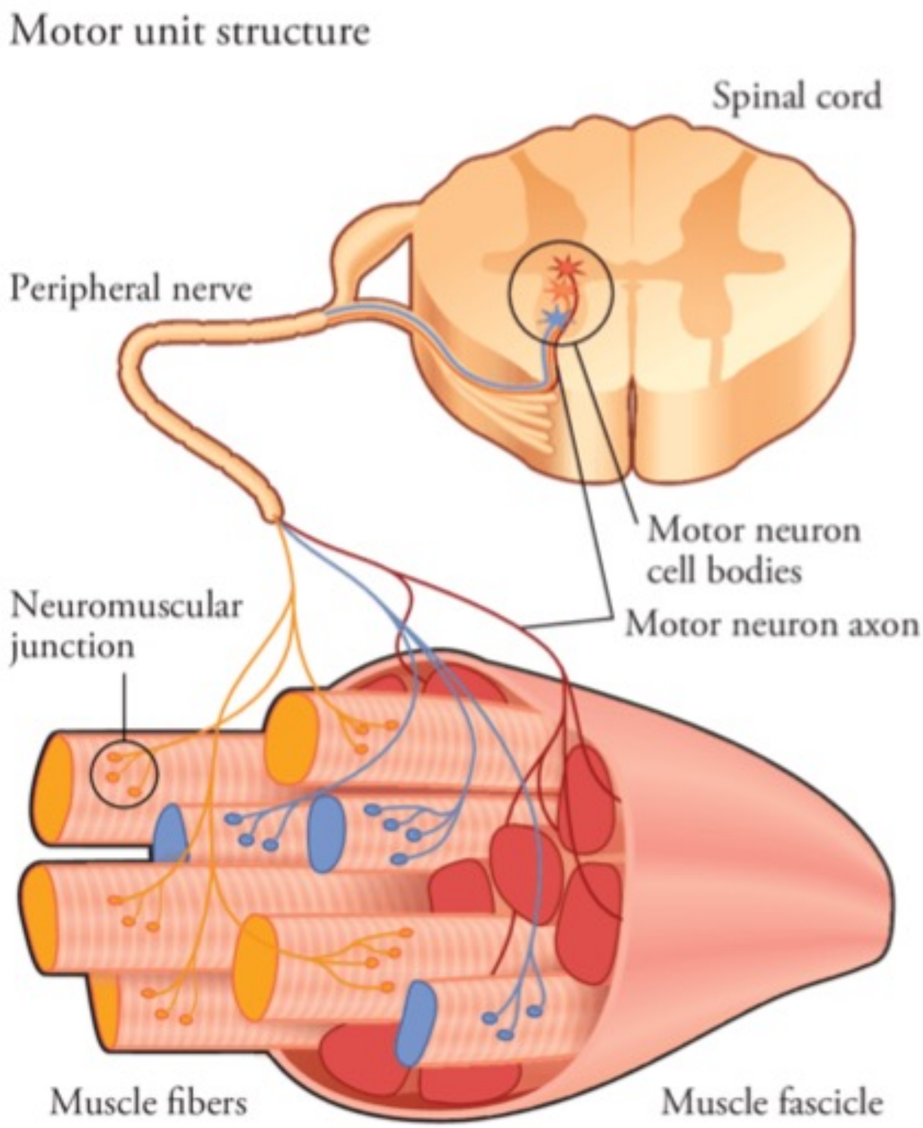
Rate encoding: Neural Stimulation

- Excitation fast (~1-2ms)
- Contraction/relaxation slow (100ms)
  - Muscle twitch lags because slack in the elastic components must be taken up.
  - Contraction time: time from start of tension to peak tension
  - Relaxation time: time from peak tension to when tension drops to 0
- Summation
  - If second impulse comes along before the first one has relaxed, they sum
  - Get more force with multiple impulses then alone
- Tetanic Summation
  - maximum tension is sustained because rapidity of stimulation outstrips the contraction-relaxation time of the muscle



Neural Stimulation
Force
Twitch
Unfused
Tetanus
Fused
Tetanus
Single
Stimulation
(Action potentials)
Low frequency
High frequency
Time

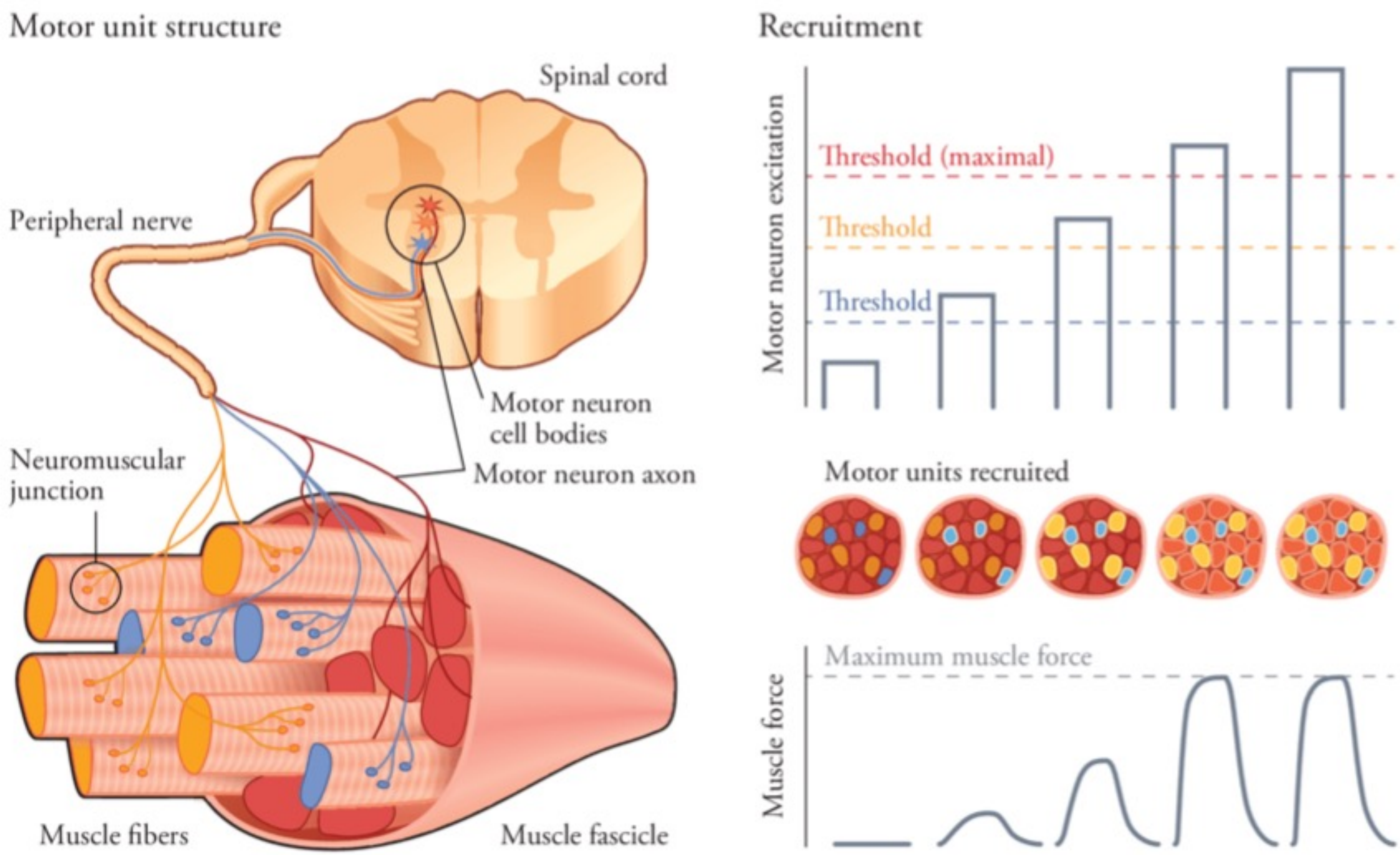
Motor unit recruitment



A motor unit comprises:

- a motor neuron,
- the motor nerve branches emanating from its axon
- the muscle fibers that are ultimately innervated.

Motor unit recruitment



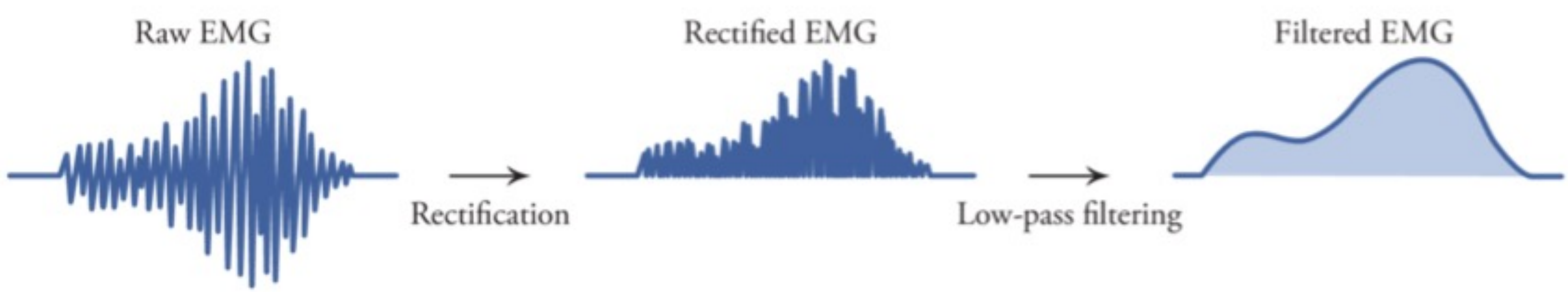
The central nervous system modulates muscle force by adjusting the number of motor units being recruited.

Henneman’s size principle

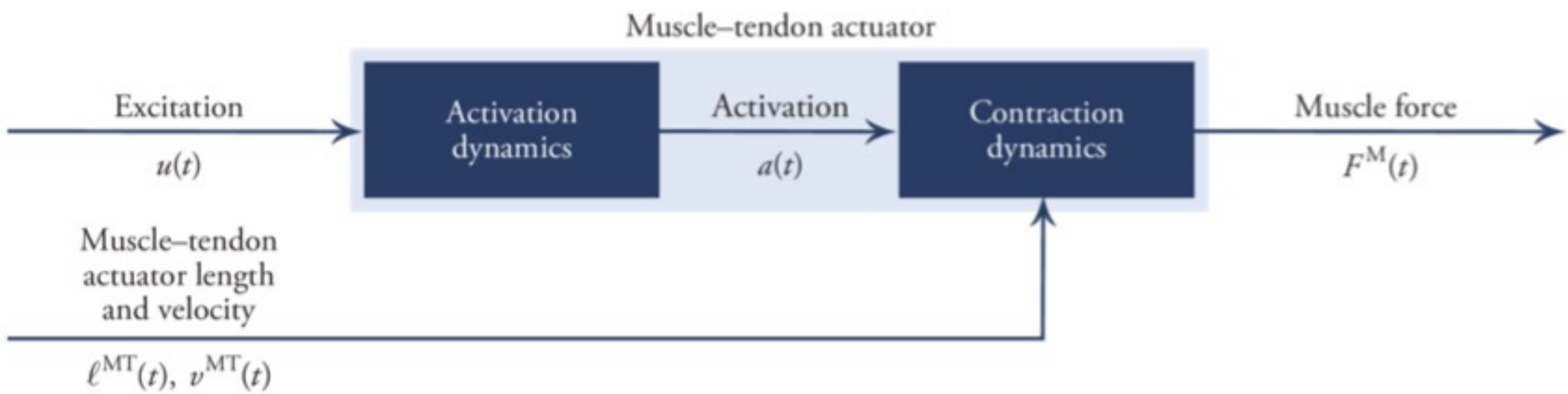
- Motor units are recruited in a particular order
  - *orderly recruitment*
  - *Henneman’s size principle*
- Small motor units recruited for small amounts of force
- With increasing force requirements, recruit progressively larger motor units

Electromyography (EMG)

- Measures electrical activity in the muscle
- Can be mounted on the skin or implanted
- Measures sum total of electrical activity in all muscle fibers
- Sensitive to electrode placement
- Does not reflect size of motor units being recruited

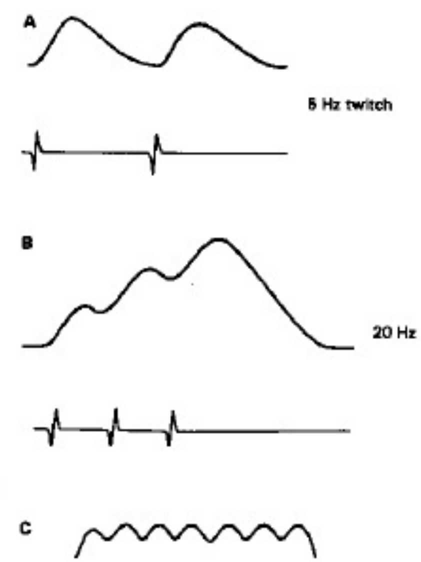


Modeling Muscle-tendon actuators



Modeling muscle activation

- Delay between excitation and activation (force development). (activation constant, τ_{act} ~10ms)
- Delay between end of excitation and muscle force decay to zero (deactivation constant, τ_{deact} ~40ms)
- Delays due to calcium dynamics: calcium release and uptake



Modeling muscle activation

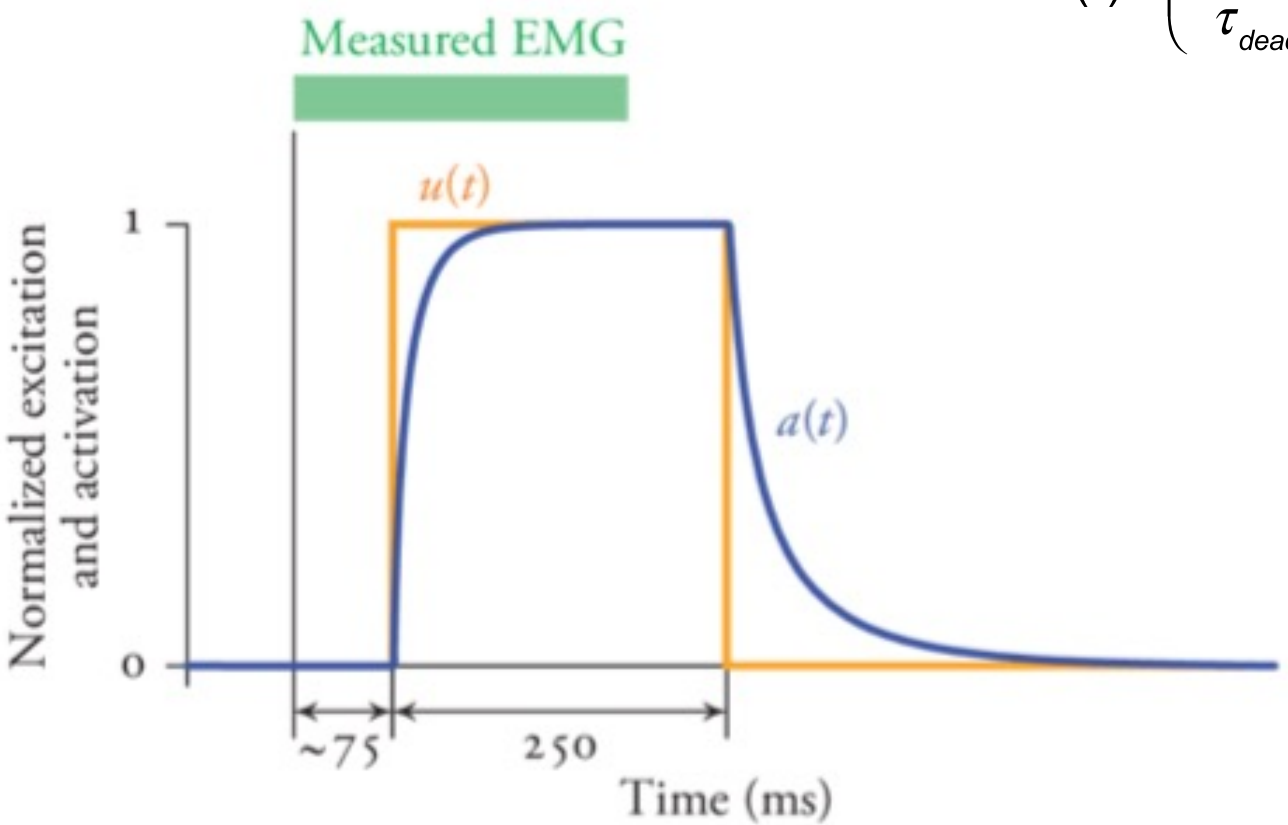
$$\dot{a}(t)+\left(\frac{1-u(t)}{\tau_{deact}}+\frac{u(t)}{\tau_{act}}\right)a(t)=\frac{1}{\tau_{act}}u(t)$$

- Excitation u(t): depolarization state of the muscle fiber
- Activation a(t): availability of calcium ions (cross-bridge cycling)

- Both vary from 0 to 1
  - 0: no CNS signal and no cross-bridge cycling
  - 1: maximum CNS signal; fused tetanus and all motor units recruited

Modeling muscle activation

$$\dot{a}(t)+\left(\frac{1-u(t)}{\tau_{deact}}+\frac{u(t)}{\tau_{act}}\right)a(t)=\frac{1}{\tau_{act}}u(t)$$



$$\tau_{act}=10ms$$

$$\tau_{deact}=40ms$$

A computational model of activation dynamics relates excitation (u(t)) to activation (a(t)) using a first-order ordinary differential equation. Excitation often lags behind a measured EMG signal.

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    - Modeling muscle activation
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Force-length-velocity-activation relationship

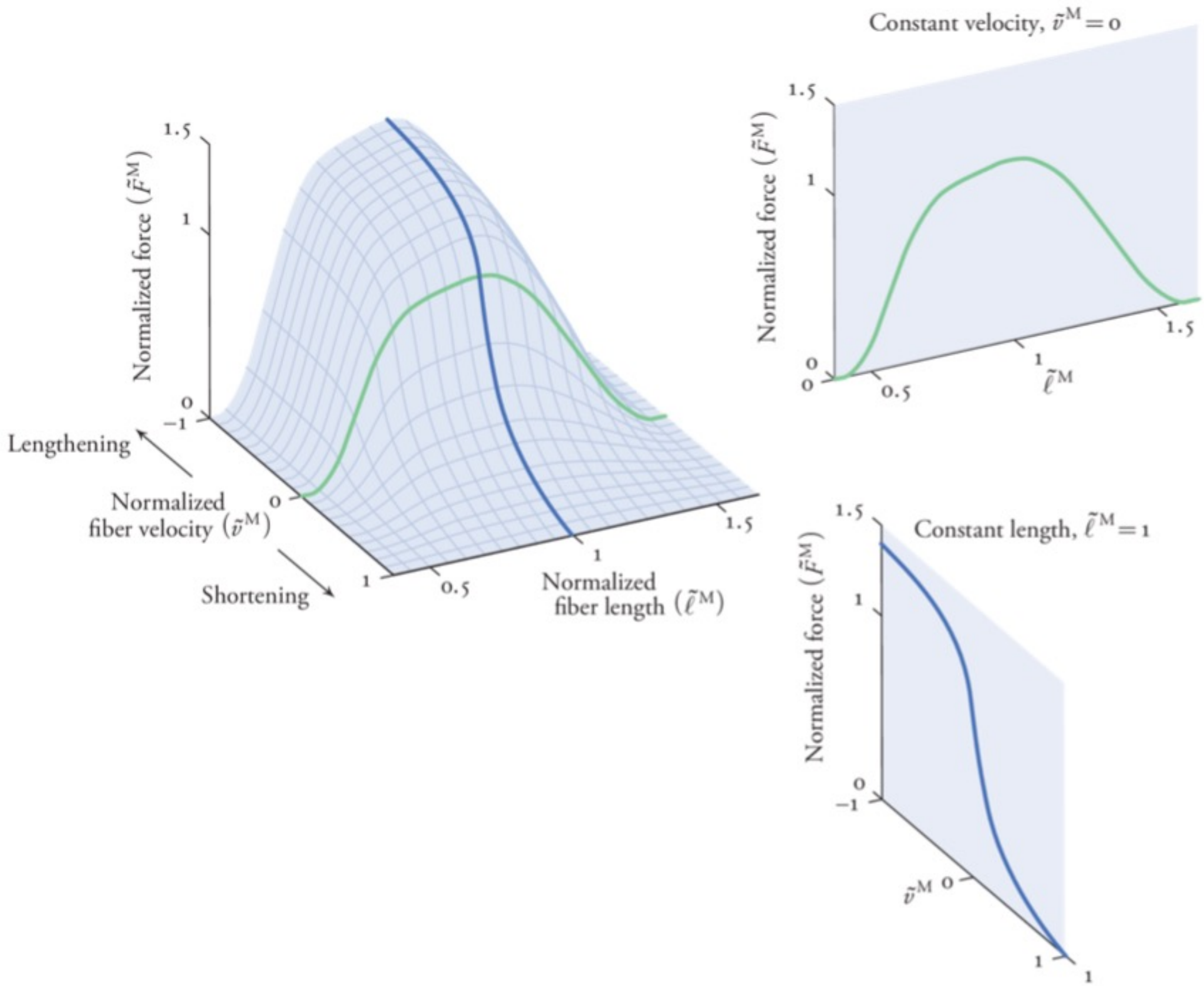
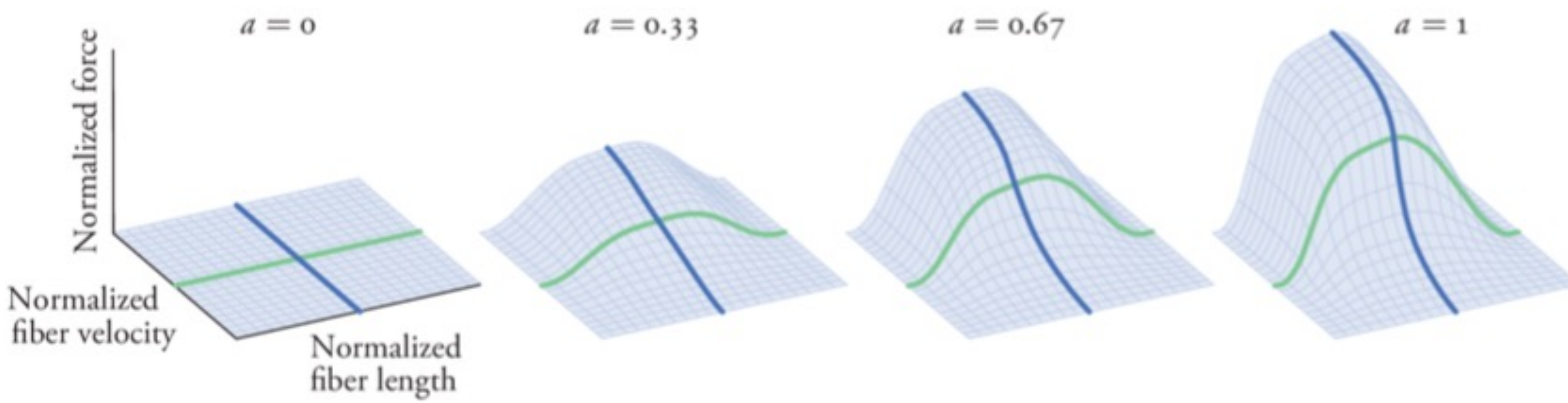


FIGURE 4.17
Muscle force-generating capacity varies with fiber length and velocity. Adapted from Lieber (2010).

Force-length-velocity-activation relationship

- The nervous system modulates muscle force through rate encoding and motor unit recruitment, collectively modeled by muscle activation.



Muscle

- Skeletal muscle
  - Unit cell structure
  - Muscle mechanics
    - Force-length relation
    - Force velocity relation
  - Activation
    - Rate encoding
    - Motor unit recruitment
    - Electromyography
    - Modeling muscle activation
  - Force-length-velocity-activation relationship