

# Neuromechanics of Human Motion

## Motor Units and Muscle Function

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Joshua Cashaback, PhD

# Recap — Bayesian Integration

$$p(A|B) = \frac{p(B|A) \cdot p(A)}{p(B)}$$

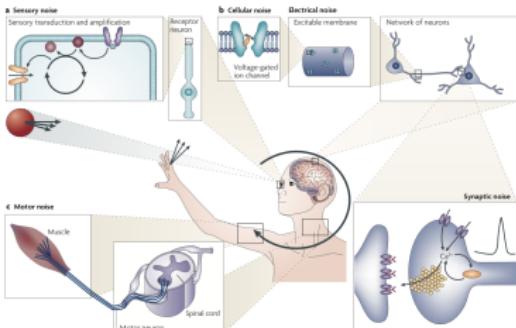
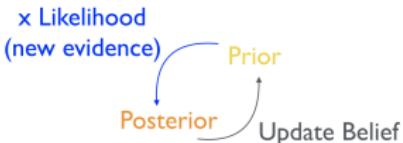
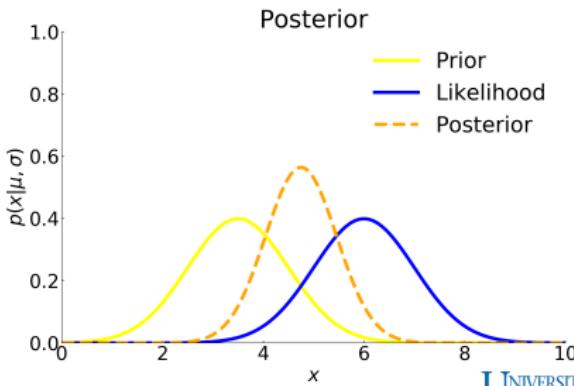


Figure 1 | Overview of the behavioral noise cascade at which noise is present in the nervous system. a) Sensory noise include the transduction of stimuli, such as photons falling on a receptor and the signal-amplification cascade. b) Sources of cellular noise include the ion channels of excitable membranes, synaptic noise and network interactions (see BOX 2). c) Sources of motor noise include motor neurons and muscle. In the behavioral task shown (catching a ball), the nervous system has to act in the presence of noise in sensing, information processing and movement.



# MODULE 2

## Muscle and Limb Dynamics (Outputs)

# Lecture Objectives — Motor Units and Muscle Function

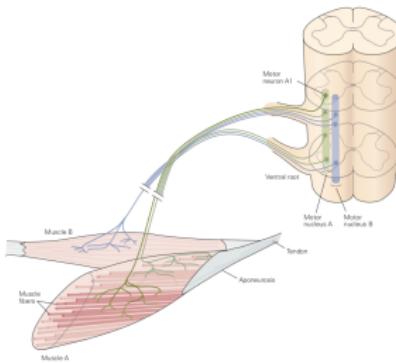
1. Motor Unit and Muscle Contraction
  - a. Motor neuron
  - b. Recruitment and discharge rate
  - c. Neuromuscular junction, sarcoplasmic reticulum
  - d. Cross-bridges
  - e. Force-Length curve (active and passive)
  - f. Force-Velocity curve
  - g. Tendon compliance

# Muscle Contraction

# Motor Unit

## Motor Unit

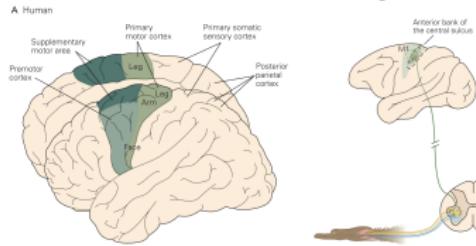
A motor neuron and the skeletal muscle fibers innervated by that motor neuron's axonal terminals.



One motor neuron will innervate a few to 1000s of muscle fibers  
Motor neurons dictate muscle force

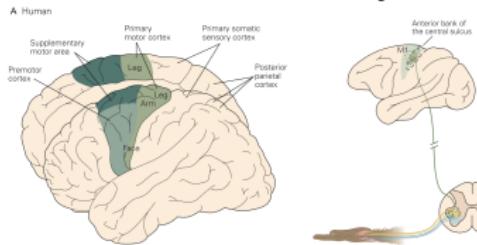
# Origin of Motor Neuron Action Potentials

## Motor Cortex - Voluntary Actions

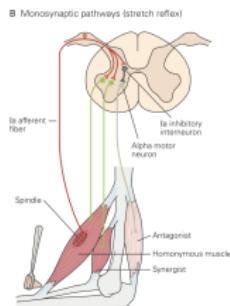


# Origin of Motor Neuron Action Potentials

## Motor Cortex - Voluntary Actions

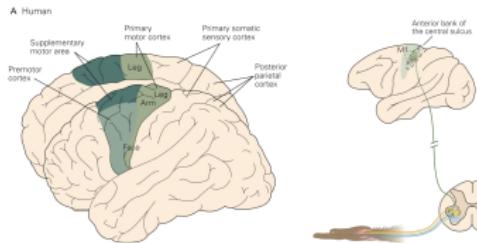


## Spinal Reflexes - Involuntary Actions



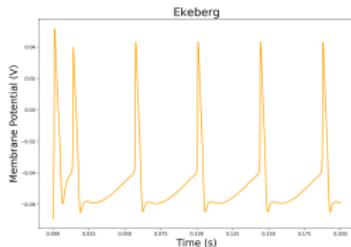
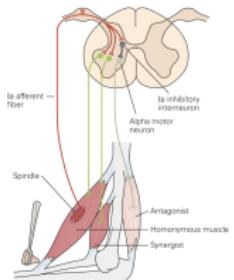
# Origin of Motor Neuron Action Potentials

## Motor Cortex - Voluntary Actions



## Spinal Reflexes - Involuntary Actions

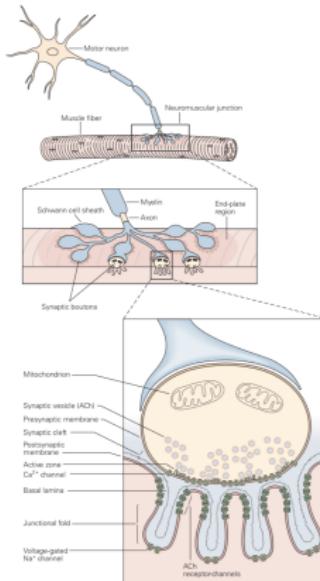
B Monosynaptic pathways (stretch reflex)



MN action potentials travel toward the muscle  
Neuromechanics - BMEG 467/667

# Neuromuscular Junction

## Synapse from Motor Neuron to Muscle



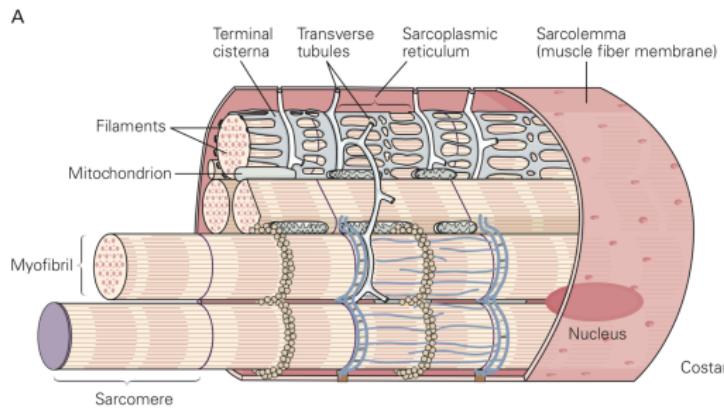
Acetylcholine (ACh) is a neurotransmitter

# Neuromuscular Junction

## From Motor Neuron to Muscle

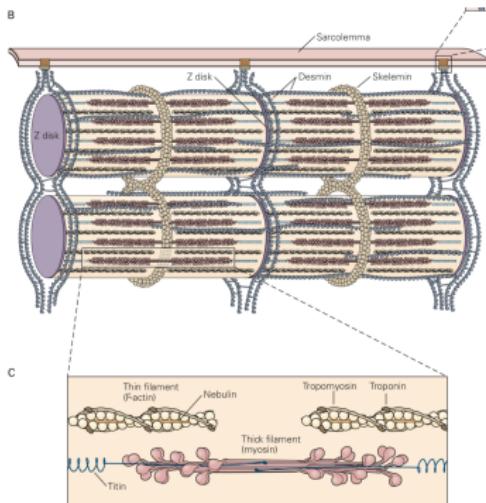
1. The action potential reaches the axon terminal.
2. Calcium ions flow into the axon terminal.
3. Acetylcholine is released into the synaptic cleft.
4. Acetylcholine binds to postsynaptic receptors.
5. This binding causes ion channels to open and allows sodium ions to flow into the muscle cell.
6. The flow of sodium ions causes an action potential along the sarcolemma (EMG).

# Sarcoplasmic Reticulum & T-Tubules



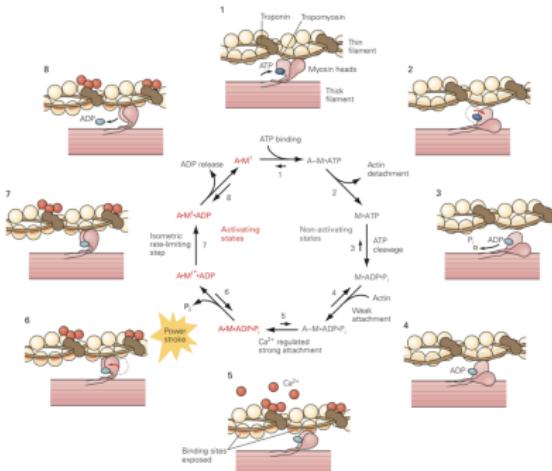
1. Sarcoplasmic Reticulum & transverse tubules absorb and store  $\text{Ca}^{2+}$
2. AP along the sarcolemma causes the SR and TT to release  $\text{Ca}^{2+}$
3.  $\text{Ca}^{2+}$  allows cross-bridges to move and generate muscle contraction

# Sarcomere — Cross Bridges



1. Myosin (thick filament) binds to Actin (thin filament)
2. Myosin heads move and cause muscle contraction

# Cross Bridge Cycle



**Figure 34-9** The cross bridge cycle. Several nonactinating states are followed by several actuating states triggered by the cycle of actin filament movement. After entry of adenosine triphosphate (ATP) into the myosin head, the myosin head detaches from actin step 2. ATP is hydrolyzed to pyrophosphate (PP<sub>i</sub>) and actin step 3, and the myosin becomes bound to actin again. Pyrophosphate release from actin causes tropomyosin to slide over actin and enables the myosin head to close step 5. This results in the release of PP<sub>i</sub> and the extension of the myosin neck, or power stroke of the cross bridge. Each cycle of actin filament movement of about 2 nm during a step (see step 7) and the release of adenosine diphosphate (ADP) (step 8), strong binding, weak binding, M', cross bridge force of myosin; and M'', cross bridge force of actin. (Reprinted, with permission, from Gordon, Binder, and Homsher 2001.)

$\text{Ca}^{2+}$  from the SR allows myosin to strongly bind to Actin  
 $P_i$  release causes **power stroke** — myosin head moves (muscle contraction)

# Motor Neurons Modulate Muscle Force

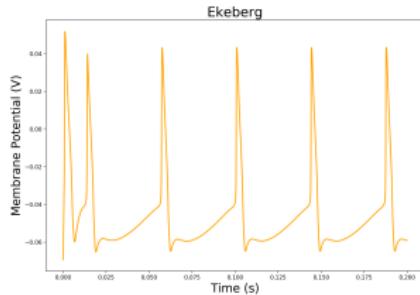
# Motor Neuron — Modulating Muscle Force

## 1. Recruitment

- . thresholds
- . size principle

## 2. Discharge Rate

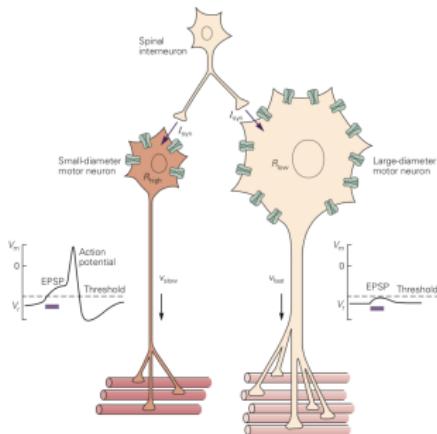
- . low vs. high firing rates



# Motor Neuron — Recruitment

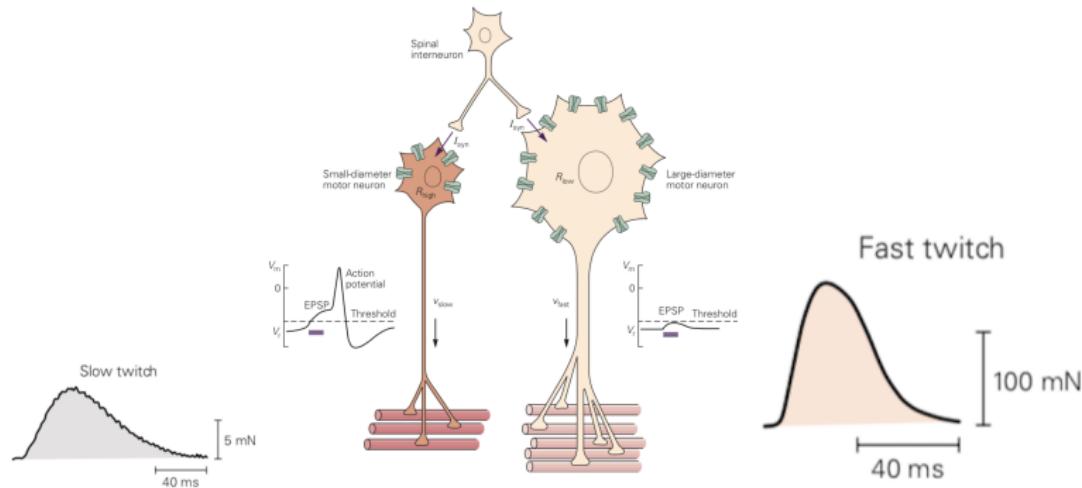
## Henneman's Size Principle

Motor neurons with small cell bodies generate action potentials (are recruited) before motor neurons with large cell bodies



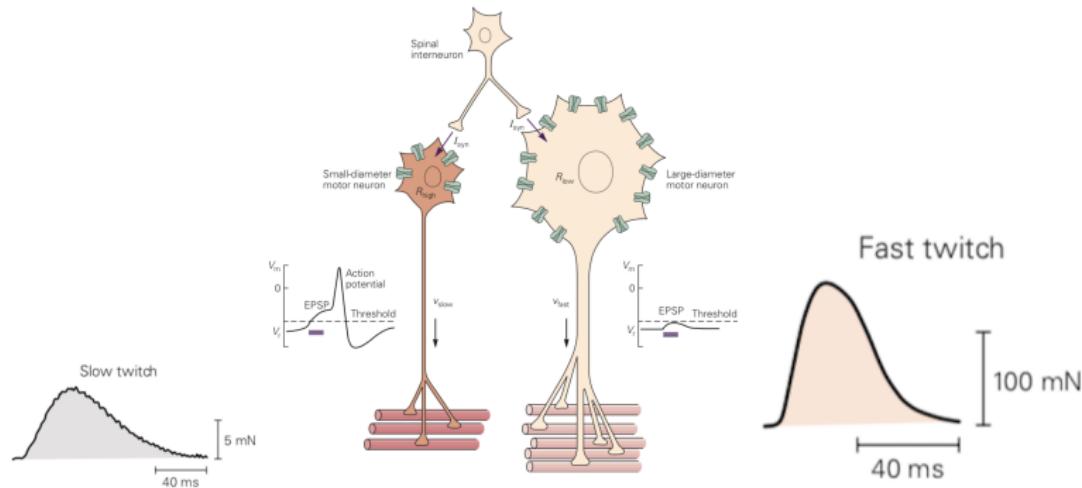
Inverse relationship between excitability and size

# Motor Neuron — Slow vs. Fast Fibers



1. Small diameter motor neurons recruit slow-twitch muscle fibers
2. Large diameter motor neurons recruit fast-twitch muscle fibers

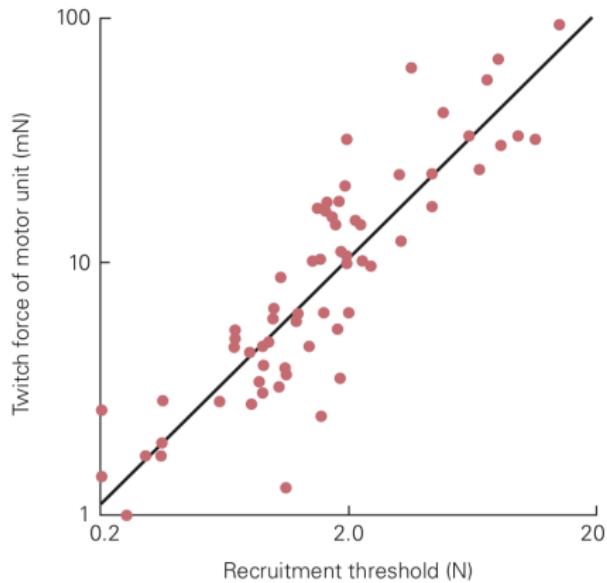
# Motor Neuron — Slow vs. Fast Fibers



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# Motor Neurons — Threshold vs Force

C Recruitment of 64 motor units in one muscle



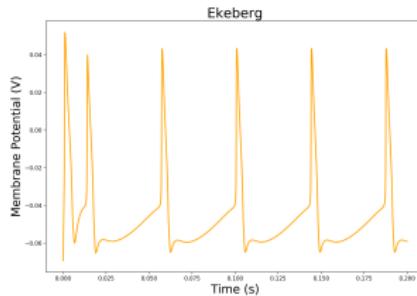
# Motor Neurons—Modulating Muscle Force

## 1. Recruitment

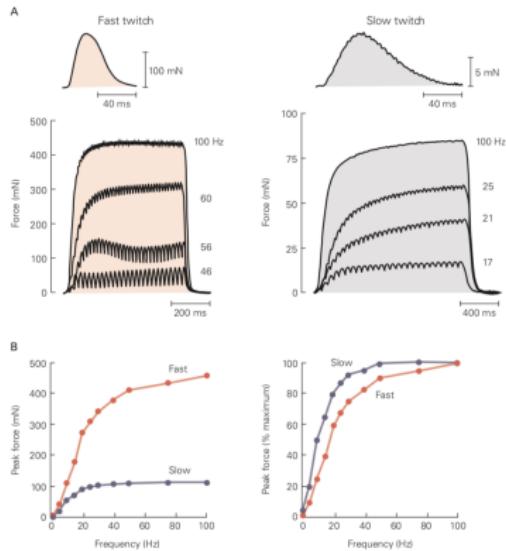
- . thresholds
- . size principle

## 2. Discharge Rate

- . low vs. high firing rates



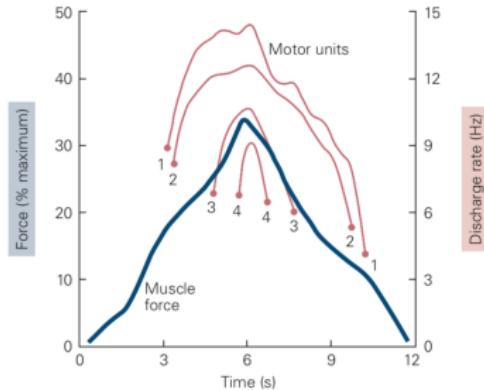
# Motor Neuron — Discharge Rate



Greater motor neuron discharge rate leads to greater force

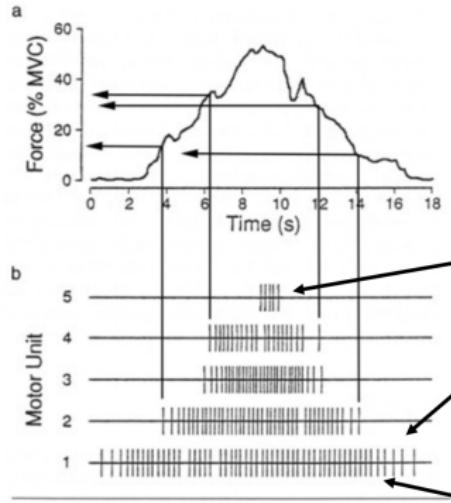
# Recruitment and Discharge Rate

**Figure 34–6** Muscle force can be adjusted by varying the number of active motor units and their discharge rate. A gradual increase and then a decrease in the force (blue line) exerted by the knee extensor muscles involved the concurrent activation of four (out of many) motor units. The muscle force was changed by varying both the number of motor units that were active and the rate at which the motor neurons discharged action potentials. Motor unit 1 was activated when muscle force reached 20% of maximum. Initially the motor neuron discharged action potentials at a rate of 9 Hz. As force increased, the discharge rate increased up to 15 Hz, when both the force and discharge rate declined, and the motor unit was inactivated at 14% of maximal force. Motor units 2, 3, and 4 were activated at greater forces but discharge rate was modulated similarly. (Reproduced, with permission, from Person and Kudina 1972.)



Muscle force modulated by both the recruitment and discharge rate of motor neurons

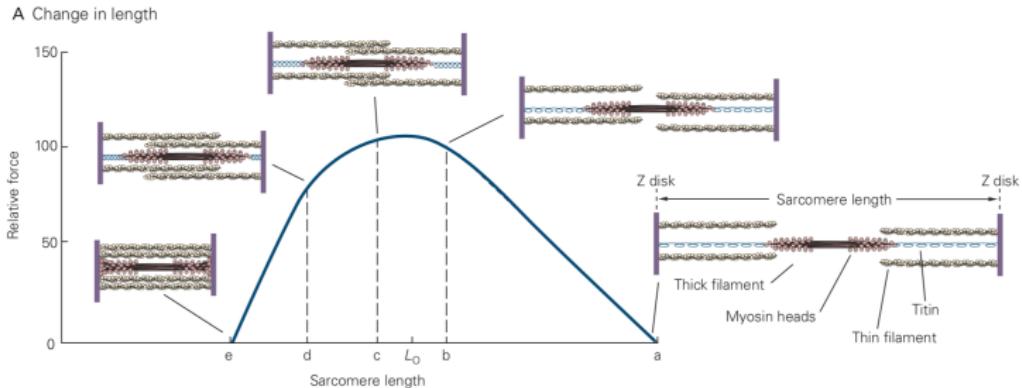
# Recruitment and Discharge Rate



Muscle force modulated by both the recruitment and discharge rate of motor neurons

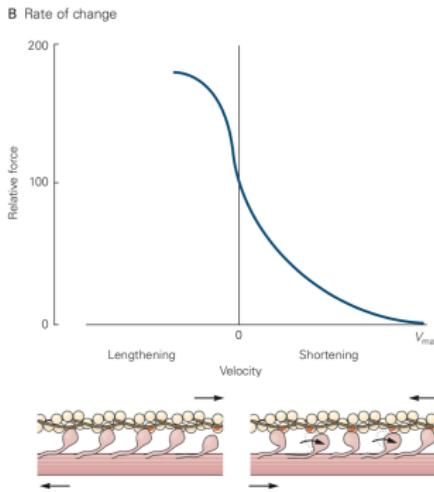
# Cross Bridge Binding Influences Muscle Force

# Active Force Length Curve



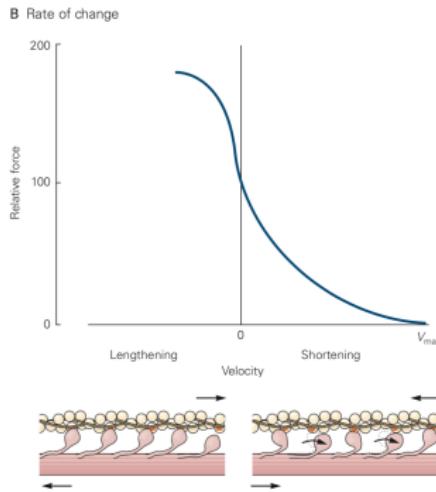
1. Optimal length ( $L_0$ ) = maximal actin and myosin overlap
2. Stretched muscle = cross bridges can't form
3. Shortened muscle = extreme overlap reduces number of potential attachment sites

# Force Velocity Curve



1. Shortening: myosin heads spend more time near the end of their power stroke, causing less force (active state) and more time detaching, reposition, and reattaching (inactive state)

# Force Velocity Curve

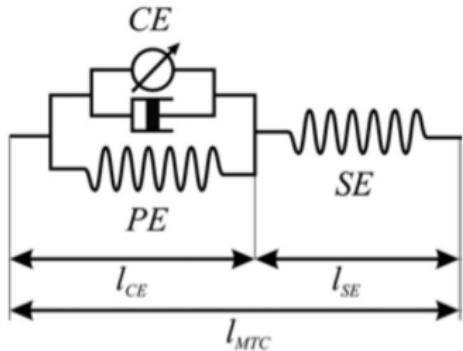


1. Lengthening: myosin heads spend more time stretched and little time unattached because they do not need to reattach

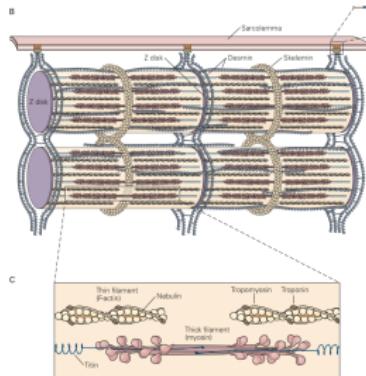
# Introduction to Muscle Modelling

# Different Types of Muscle Models

Hill (Phenomenological) vs Cross-bridge (Mechanistic)



Schematic of a Hill-type muscle model.



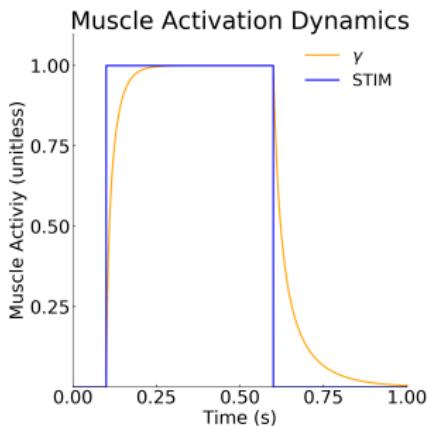
Fundamental difference relates to how the contractile element generates force

# Considerations

Factors to consider:

1. Electrical
  - . Stim-driven vs. EMG-driven
  - . Activation dynamics
2. Mechanical
  - . active force length curve
  - . passive force length curve
  - . force velocity curve
  - . tendon compliance
  - . pennation angle

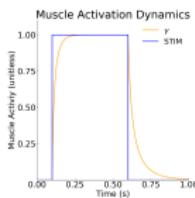
# Stim Driven



*STIM*: stimulating the muscle

- neuromuscular junction via  $\alpha$ mn OR electrical stimulation
- $\gamma$ : free  $Ca^{2+}$  concentration (drive cross-bridge cycling)
  - rise = release, fall = uptake into sarcoplasmic reticulum

# Stim Driven



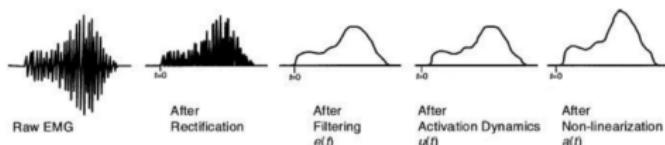
$$\dot{\gamma} = \frac{(STIM - \gamma)}{\tau} \quad (1a),$$

$$\tau = \begin{cases} \tau_{act}(0.5 + 1.5\gamma); & STIM > \gamma \\ \tau_{deact}/(0.5 + 1.5\gamma); & STIM \leq \gamma \end{cases} \quad (1b),$$

$$\tau_{act}(0.015), \tau_{deact}(0.05) \quad (1c).$$

note: minimal STIM set to 0.0001 for numerical stability

# EMG Driven

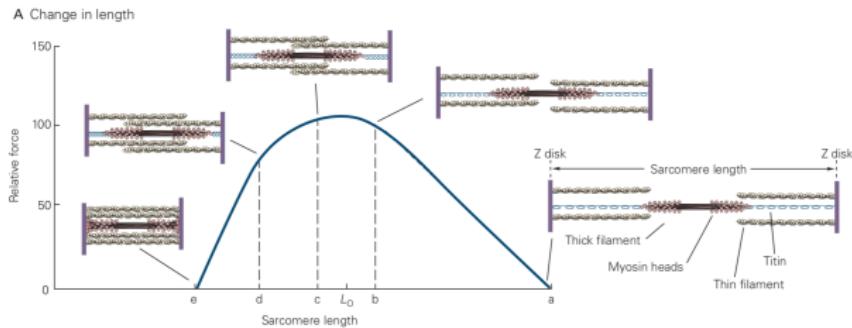


**Figure 3.**

Muscle activation dynamics: Transformation from EMG to muscle activation.

1. EMG is a measure of the electrical activity spreading across the muscle, causing it to activate.
2. electromechanical delay
3. non-linear EMG to Force relationship
4. Buchanan et al., 2004
5.  $\gamma = a(t)$

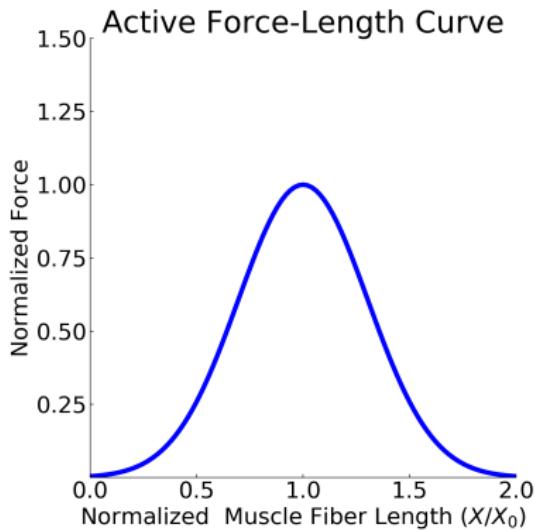
# Active Force Length Curve



## Modelling:

1. piece-wise linear
2. polynomial
3. Gaussian

# Active Force Length Curve

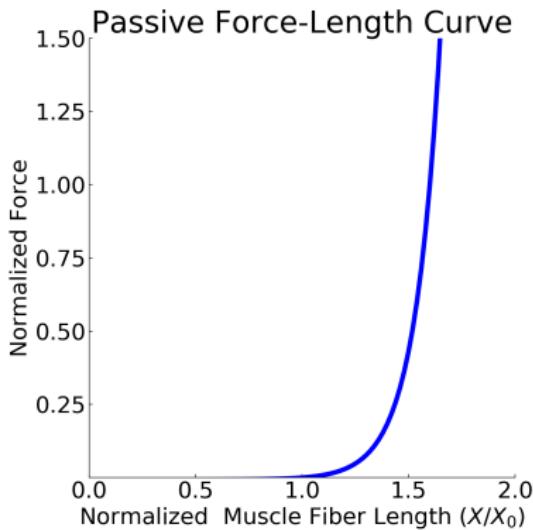


$$\alpha = e^{-(X/X_0 - 1)^2/\nu}$$

$\alpha$ : normalized active force capacity

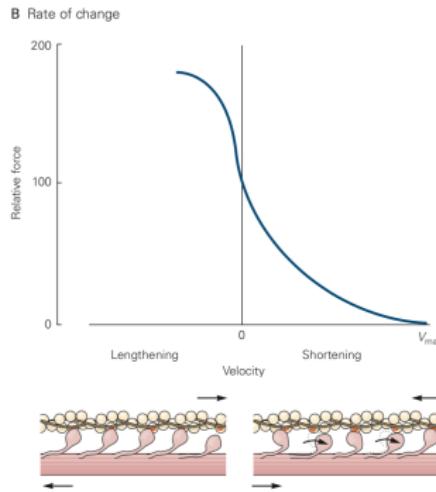
$\nu(0.185)$ : width parameter

# Passive Force Length Curve

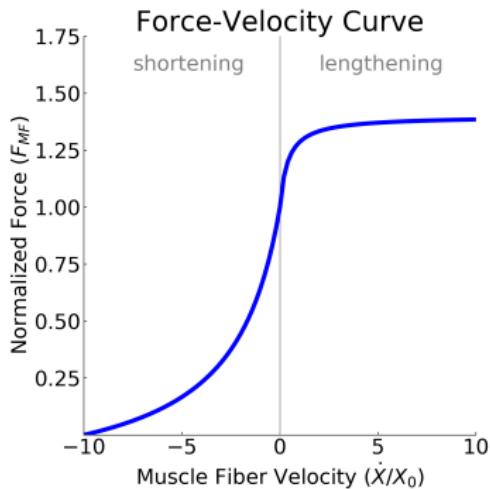


$$F_{PE} = \frac{e^{k_{PE}(X/X_0 - 1)/\varepsilon_{PE}} - 1}{e^{k_{PE}} - 1}$$
$$k_{PE}(5.0); \varepsilon_{PE}(0.6)$$

# Force Velocity Curve



# Force Velocity Curve



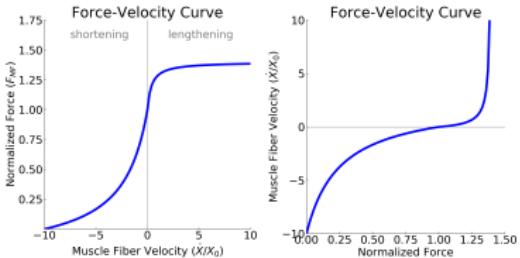
Defined in terms of normalized muscle fiber velocity

$$\left(\frac{\dot{X}}{X_0}\right) = (0.25 + 0.75\gamma) V_{MF}^{\max} \frac{F_{MF} - \gamma\alpha}{b}$$

$V_{MF}^{\max}(10.0)$ : maximum shortening velocity

Note:  $\gamma = 1$ ,  $\alpha = 1$ ,  $\frac{\dot{X}}{X_0}$  is an input  $[-10, 10]$  for plotting

# Force Velocity Curve



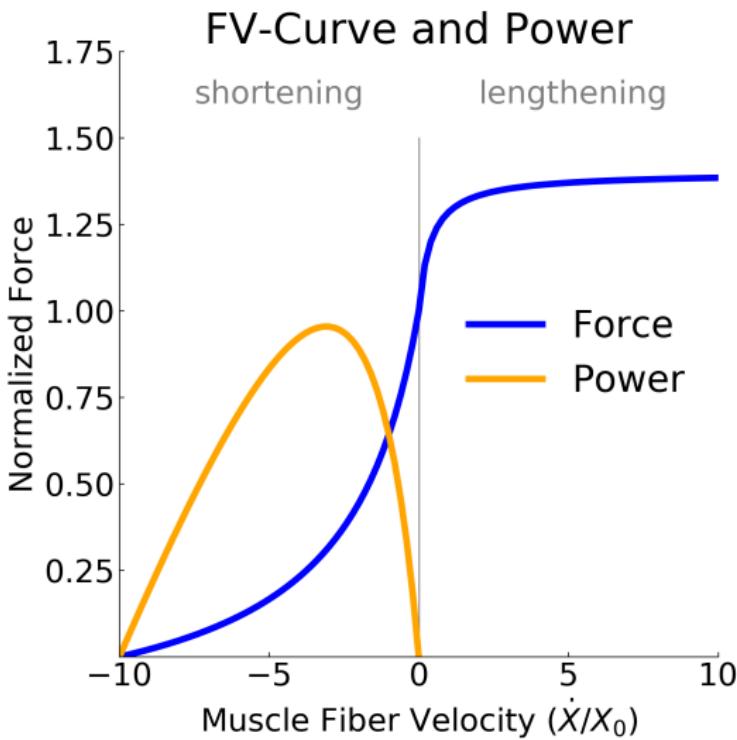
$$\left( \frac{\dot{X}}{X_0} \right) = (0.25 + 0.75\gamma) V_{MF}^{\max} \frac{F_{MF} - \gamma\alpha}{b} \quad (1a),$$

$$b = \begin{cases} \gamma\alpha + \frac{F_{MF}}{A_f}; & F_{MF} \leq \gamma\alpha \\ \frac{(2 + \frac{2}{A_f})(\gamma\alpha F_{MF}^{\max} - F_{MF})}{(F_{MF}^{\max} - 1)}; & F_{MF} > \gamma\alpha \end{cases} \quad (1b), \quad (1c).$$

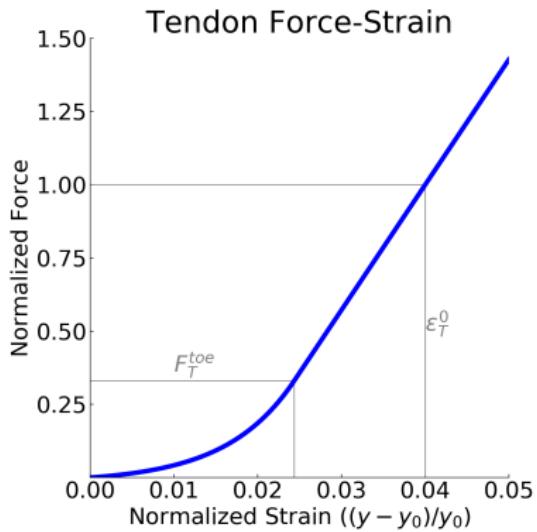
$F_{MF}^{\max}$  (1.4); influences peak lengthening force

$A_f$  (0.25): shape parameter

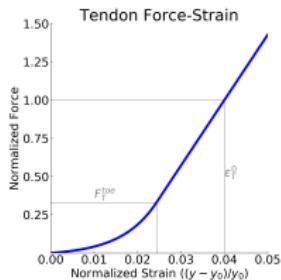
# Power



# Tendon Strain-Force Curve



# Tendon Strain-Force Curve

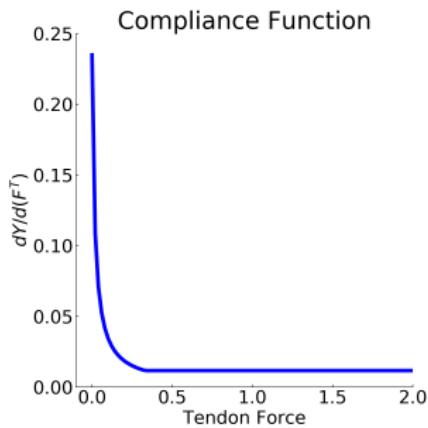


$$F_T = \begin{cases} \frac{F_T^{toe}}{e^{k^{toe}} - 1} (e^{k^{toe}[(Y - Y_0)/Y_0]/\varepsilon_T^{toe}} - 1); & \frac{Y - Y_0}{Y_0} \leq \varepsilon_T^{toe} \\ k^{lin}([(Y - Y_0)/Y_0] - \varepsilon_T^{toe}) + F_T^{toe}; & \frac{Y - Y_0}{Y_0} > \varepsilon_T^{toe} \end{cases}$$

$Y_0$ : tendon slack length

$$F_T^{toe}(0.33); k^{toe}(3.0); e_T^0(0.04); \varepsilon_T^{toe}(0.609e_T^0); k^{lin}(1.712/e_T^0)$$

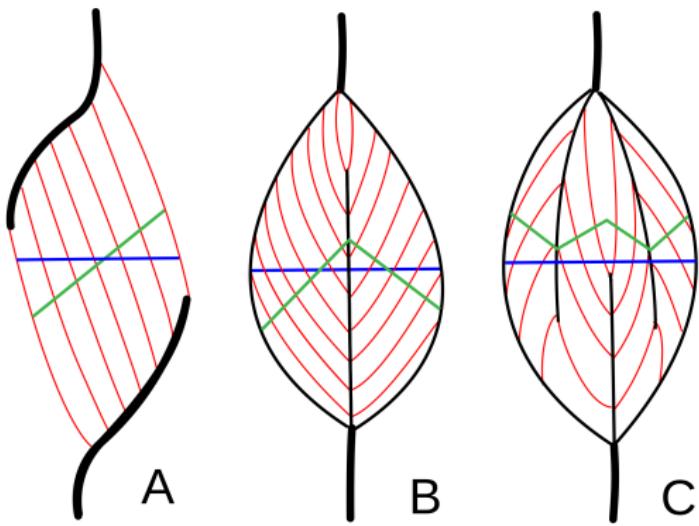
# Tendon Compliance



$$\frac{dY}{dF_T}$$

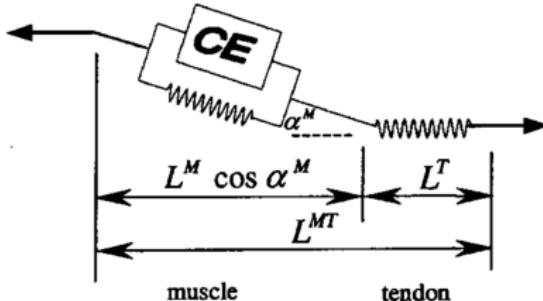
some muscle models want tendon mechanics defined in terms of compliance

# Muscle Pennation



unipennate, bipennate, multipennate

# Pennation Angle



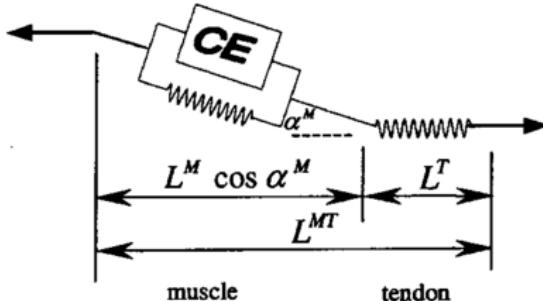
Don't confuse  $\alpha$  here with active FL curve in previous slides

I personally use  $\theta$  for pennation angle

Models: no, static, dynamic pennation angle

$$L_{MT} = L_T + L_{MF} \cos(\theta)$$

# Pennation Angle



Don't confuse  $\alpha$  here with active FL curve in previous slides

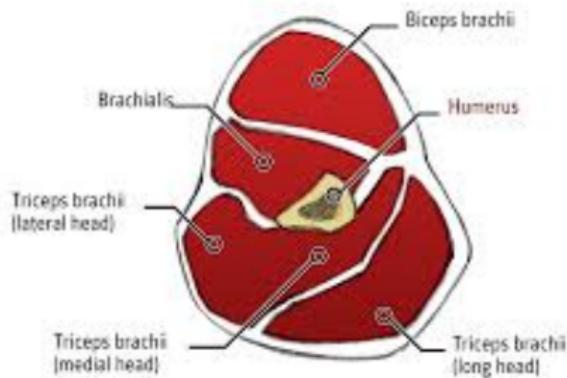
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Models: no, static, dynamic pennation angle

$$L_{MT} = L_T + L_{MF} \cos(\theta)$$

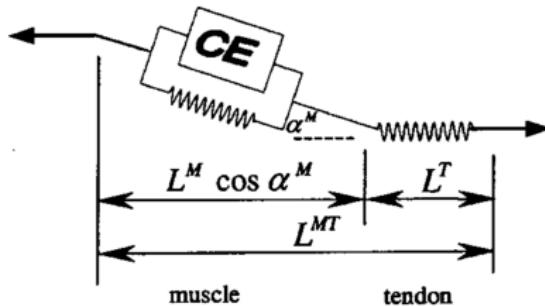
$$L_{MT} = Y + X \cos(\theta)$$

# Physiological Cross-Sectional Area & Stress



PCSA: bigger muscles generate more force  
 $\sigma$  (muscle stress,  $N/cm^2$ ): quite variable (35.0)

# Muscle-Tendon Force



$$F_{MT} = F_T = F_{MF} \cos(\theta) + F_{PE} \cos(\theta)$$

$$F_{MT} = F_T = PCSA \cdot \sigma (\gamma \cdot \alpha \cdot FV + F_{PE}) \cos \theta$$

# Summary

1. Motor Unit and Muscle Contraction
  - a. Motor neuron
  - b. Recruitment and discharge rate
  - c. Neuromuscular junction, sarcoplasmic reticulum
  - d. Cross-bridges
  - e. Muscle and Tendon Mechanics

Questions???

# Homework

Plot:

1. Active Force Length Curve
2. Passive Force Length Curve
3. Velocity-Force (x-axis) Curve
4. Force (x-axis)-Velocity Curve
5. Tendon Strain-Force Relationship
6. Tendon Compliance
7. Activation Dynamics
8. Thelen, D. G. (2003). J Biomech Eng, 125(1), 70-77.

# Next Class

1. Hill-type Model
2. Distribution Moment Approximation Model

# Acknowledgements

Dinant Kistemaker