Biology 325 - 2005
Guest Lectures in Animal Locomotion

Lectures 1 & 2: John Gosline

- **The metabolic cost of terrestrial and aquatic locomotion;**
- **Cost of transport; scaling of metabolic cost.**
- **Mechanics of terrestrial locomotion: walking and running.**

Lectures 3 & 4: Margo Lillie

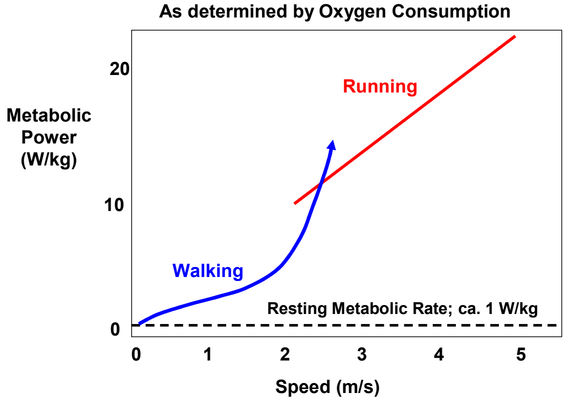
- **Mechanical properties of tendon**
- **Tendon elasticity in wallaby hopping**
- **Mechanical behaviour of muscles: positive and negative work**
- **Role of muscles in running**

Lectures 5 & 6: Bob Shadwick

- **Muscle work-loops**
- **Structure and mechanics of muscle in swimming fish**
- **Work-loop control in aquatic vs. terrestrial movement**

http://www.zoology.ubc.ca/bpg/courselinks.htm

Metabolic Power in Human Locomotion
As determined by Oxygen Consumption



NET Metabolic Power in Human Locomotion
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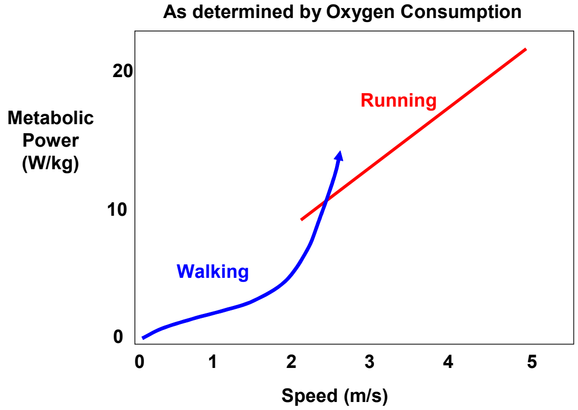
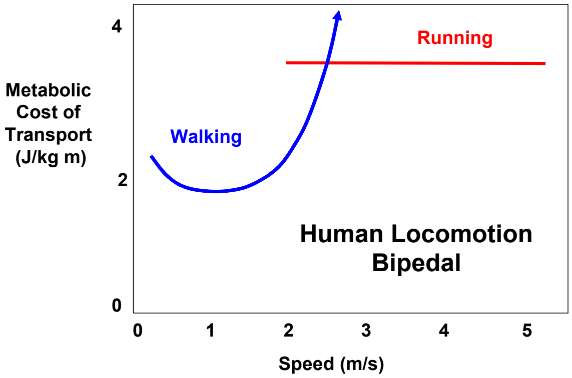


COST OF TRANSPORT

W/kg ÷ m/s = J/kg m



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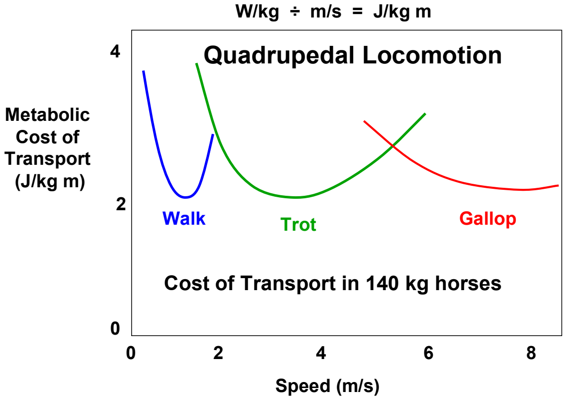
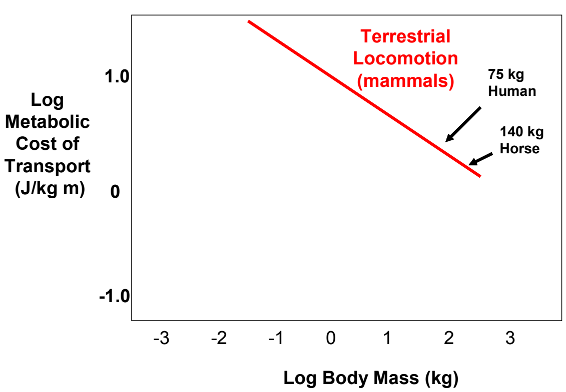
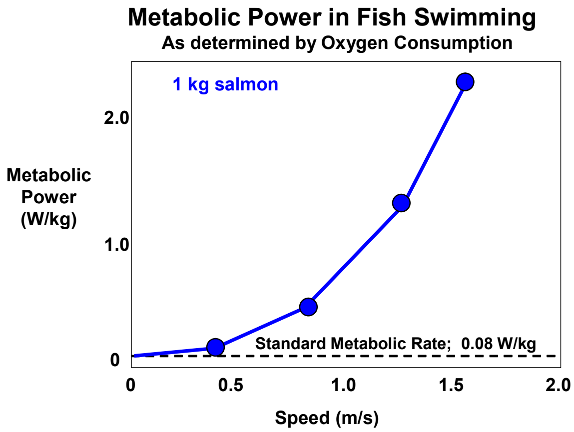
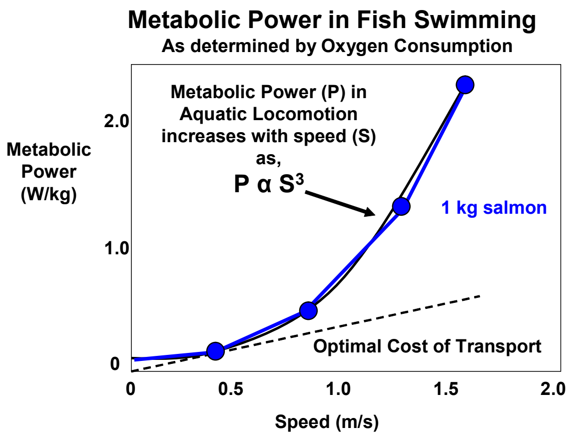


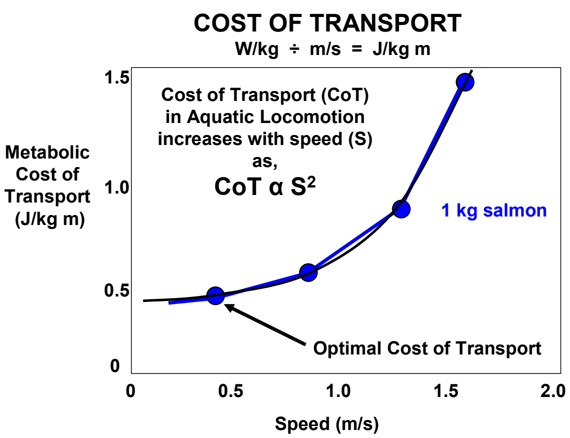
Cost of Transport Scales with Body Mass, $M^{-0.33}$





J. R. Brett,
Fisheries Research Board of Canada Biological Station, Nanaimo, B.C., Canada





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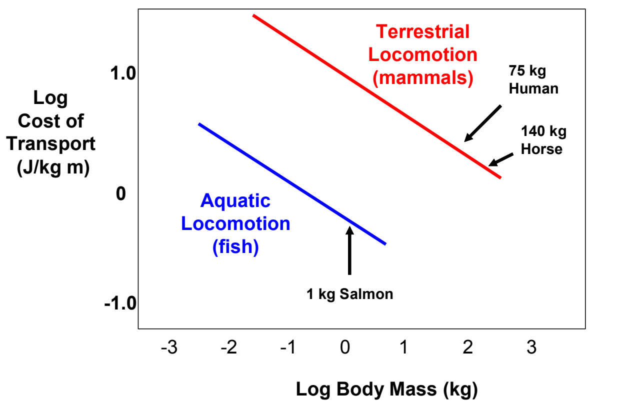


J/kg m = Nm/kg m = N/kg

The cost of transport can be expressed as the force (N) required to move a 1 kg fish at a particular speed. So for a 1kg salmon moving at 1 m/s, the metabolic "force" per kg will be about 0.7 W/kg.

Let's estimate the DRAG FORCE the fish will experience in water to see if we can account for this metabolic "force" required to move the fish at 1 m/s.

$$F_{drag} = \tfrac{1}{2} C_d \rho A V^2$$

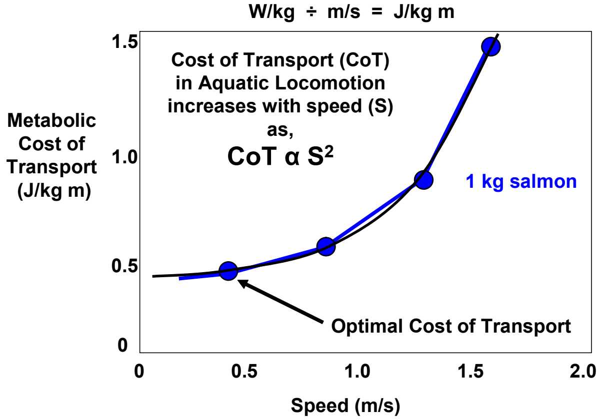
ρ_{water} = 1000 kg/m^3; V = 1.0 m/s; A ≈ 0.006 m^3

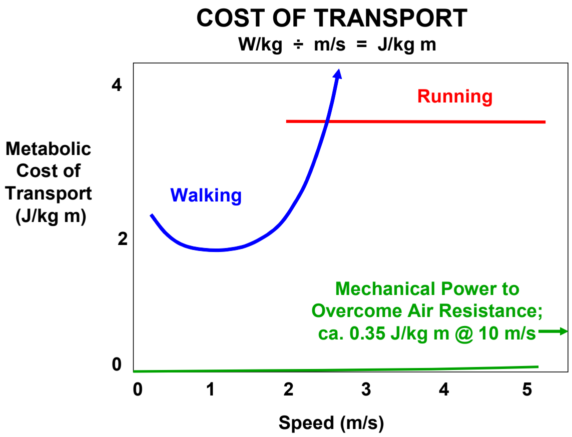
Cd = 0.45 (sphere) → 1.35 N
= 0.01 (streamlined body) → 0.03 N
≈ 0.05 (fish) → 0.15 N

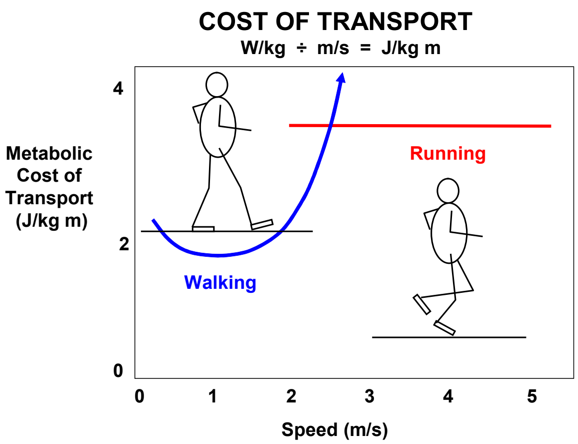
The metabolic "force" should be larger than the mechanical force because of the loss in the conversion of chemical energy (metabolism) into mechanical thrust. A reasonable guess for the efficiency of this conversion is about 20%, making the metabolic "force" roughly equal to 0.75 N/m. Note, this value is virtually identical to that shown on the graph.

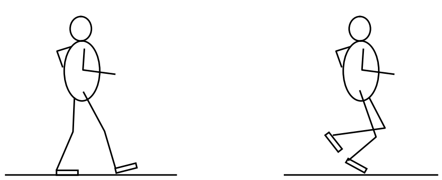
COST OF TRANSPORT

W/kg ÷ m/s = J/kg m







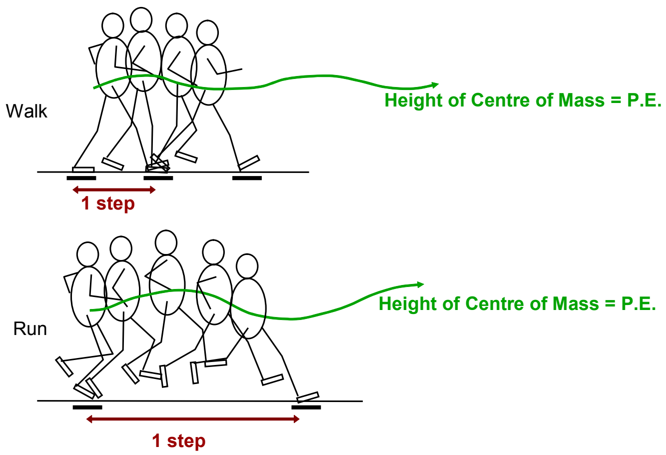


Level Walking V ≈ 1 m/s Level Running V ≈ 4 m/s

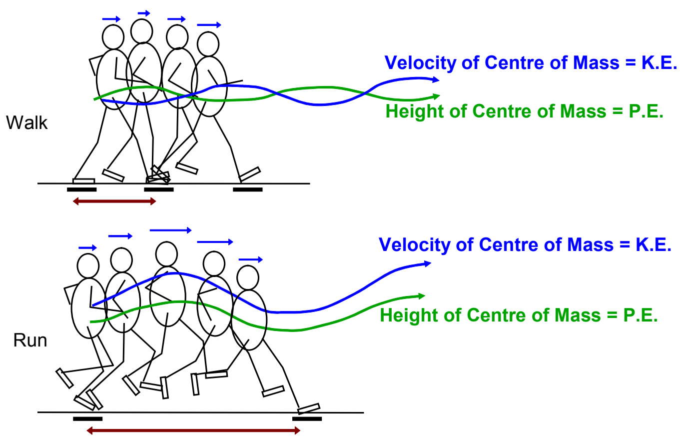
Force and Energy in Level Movement at Constant Velocity

Gravitational Force	($F_g = mg$)	⟶	weight	
Gravitational Energy	($E_g = mgh$)	⟶	$\Delta h = 0$,	$\mathbf{E_g = 0}$
Acceleration Force	($F_a = ma$)	⟶	$a = 0$,	$\mathbf{F_a = 0}$

Height is NOT Constant in terrestrial Locomotion



Velocity and Height are NOT Constant in terrestrial Locomotion



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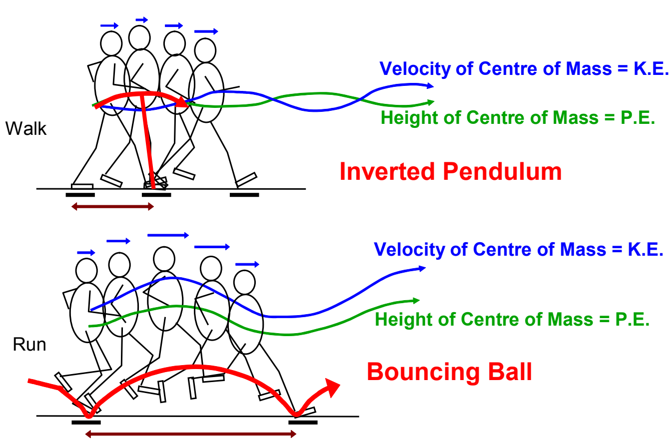
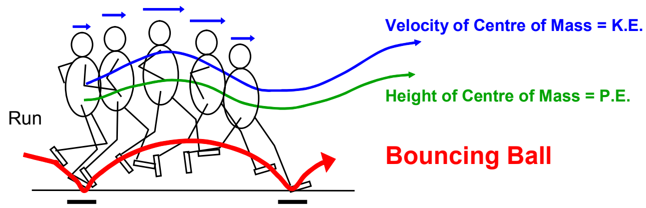
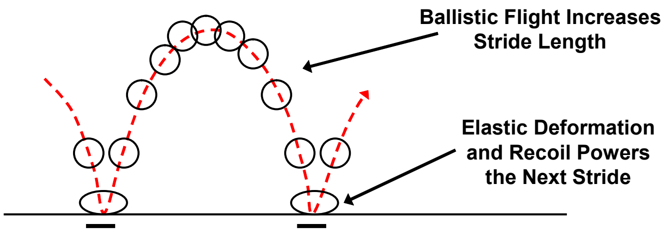
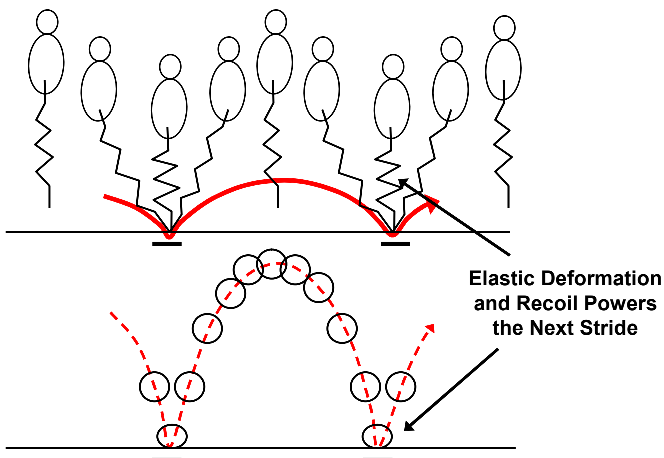
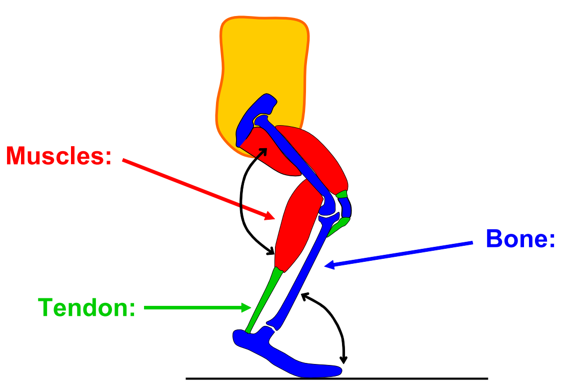








Where is Elastic Energy Stored in the Leg?



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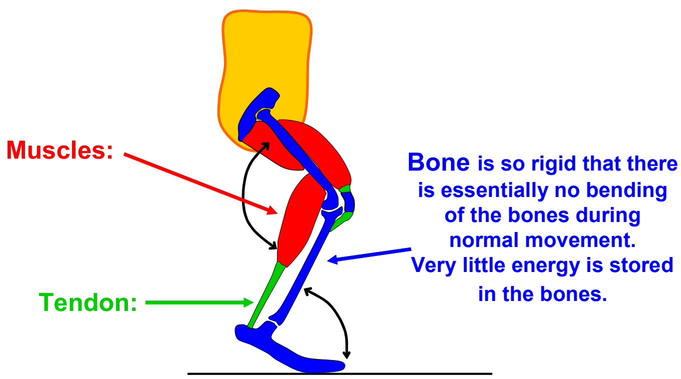
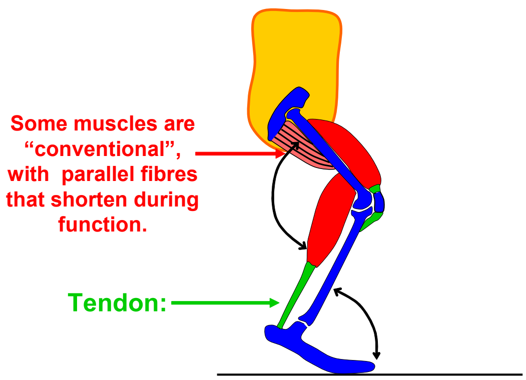


Elastic Energy is Stored Primarily in the Stretching of the Tendon-Muscle System that Controls the Extension of the Ankle



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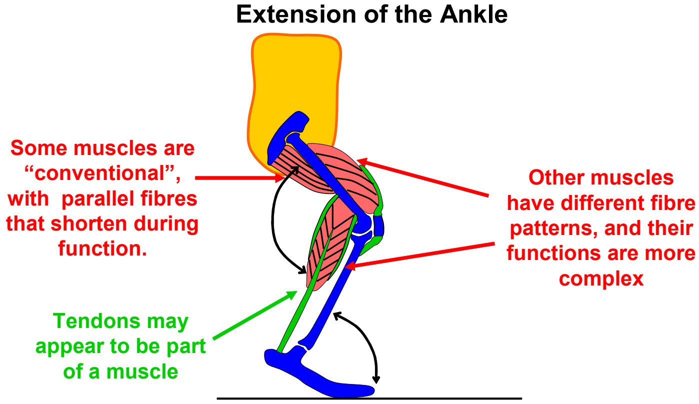

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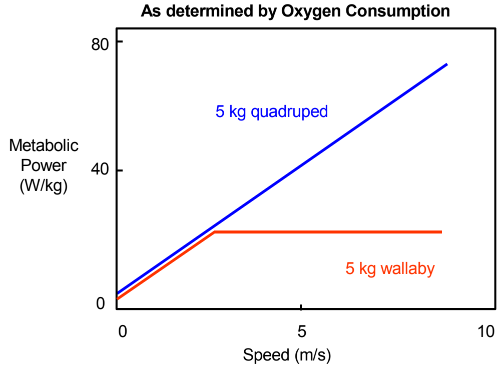
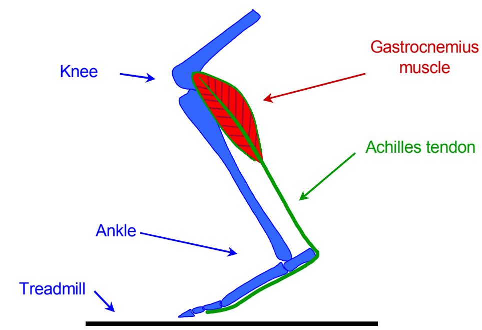
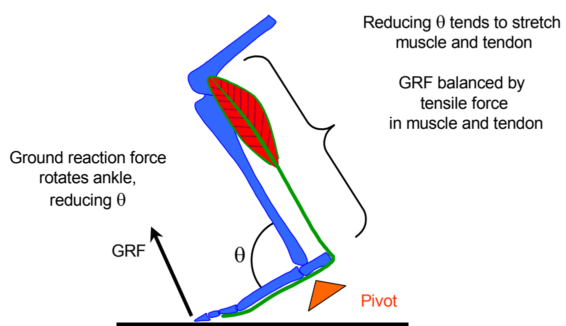
Metabolic Power
As determined by Oxygen Consumption



Simplified Anatomy of Wallaby Ankle

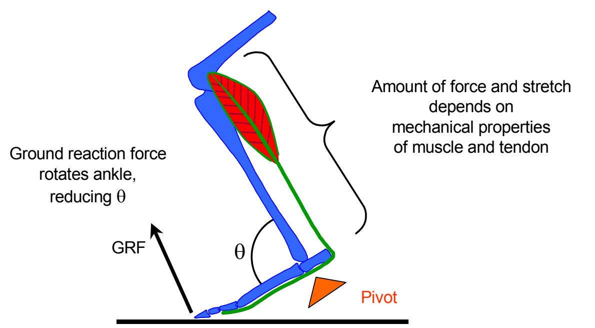


Rotation Forces on Lever at Ankle

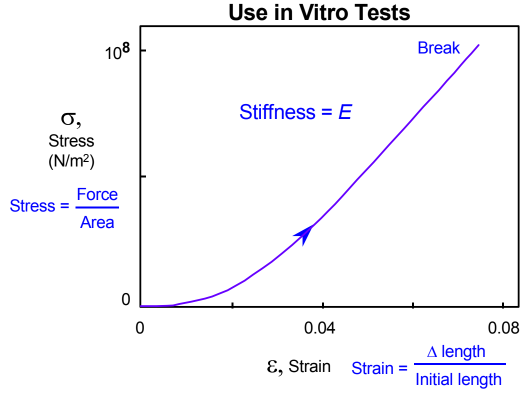


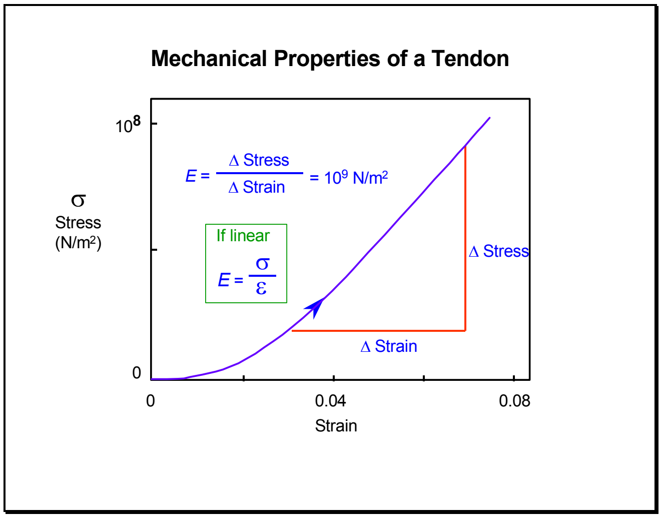
How much energy can be stored in tendon and muscle?

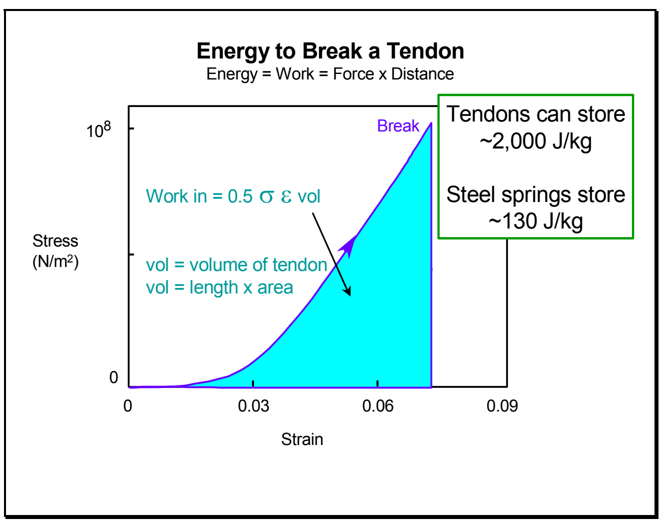
Energy = Work = Force x Length



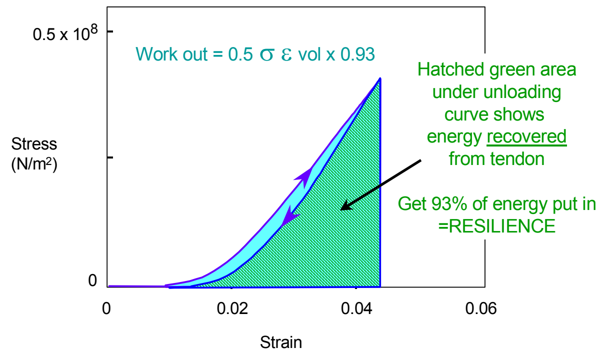
Mechanical Properties of a Tendon
Use in Vitro Tests



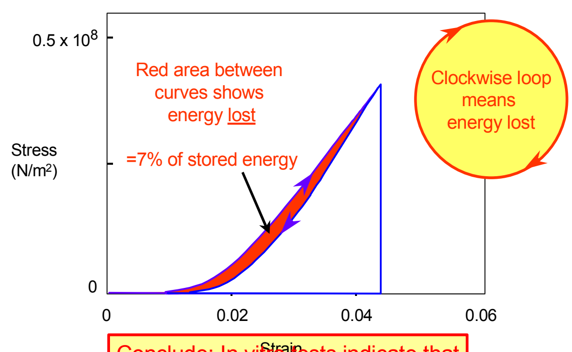

Mechanical Properties of a Tendon
σ
Stress
(N/m²)
10^8
0
E = Δ Stress / Δ Strain = 10^9 N/m²
If linear
E = σ/ε
Δ Stress
Δ Strain
0
0.04
0.08
Strain


Energy to Break a Tendon
Energy = Work = Force x Distance
Stress
(N/m²)
10^8
0
Break
Work in = 0.5 σ ε vol
vol = volume of tendon
vol = length x area
Tendons can store
~2,000 J/kg
Steel springs store
~130 J/kg
0
0.03
0.06
0.09
Strain

Using a Tendon as a Spring: Energy Recovered on Recoil



Using a Tendon as a Spring: Energy Recovered on Recoil



Conclude: In vitro tests indicate that tendons are effective springs

In Vivo Study of Wallaby Hopping

We already know that metabolic power is independent of speed.

Question:
How does mechanical work change with speed?

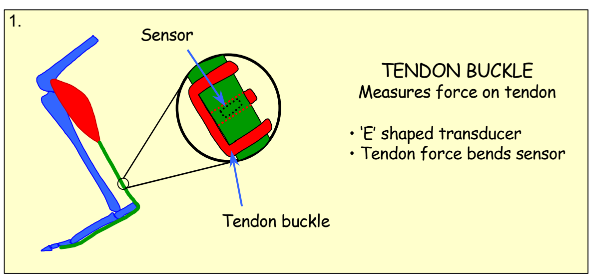
Experimental Approach:

1. Get force (stress) and length (strain) data
   i muscle
   ii tendon
2. Calculate mechanical work done

Experimental Study: Wallaby Hopping on Treadmill

Measure:

1. Force on muscle and tendon using tendon transducers
2. Tendon length and area
3. Muscle fibre length using sonomicrometer
4. Electromyography (EMG)



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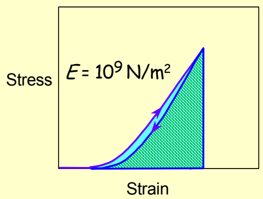
2.



CALCULATE TENDON WORK

Work out $= 0.5\ \sigma\ \varepsilon$ vol $\times$ 0.93

- $\sigma = F/A$
- $\varepsilon = \sigma/E$
- vol = length x area
- resilience = 0.93

Experimental Study: Wallaby Hopping on Treadmill

Measure:

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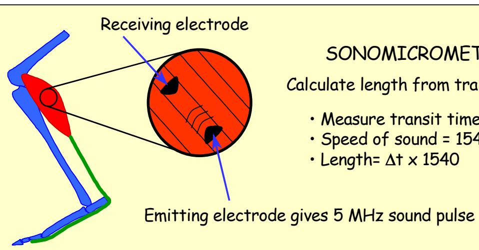
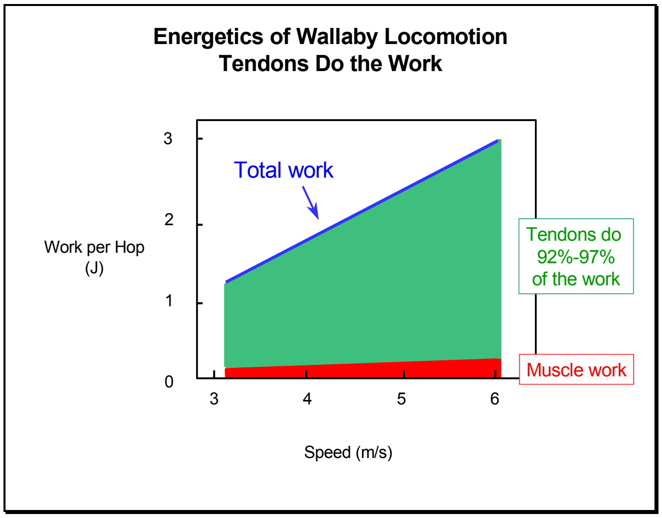
3.



SONOMICROMETRY

Calculate length from transit time

- Measure transit time, Δt
- Speed of sound = 1540 m/s
- Length= $\Delta t \times 1540$


Energetics of Wallaby Locomotion
Tendons Do the Work
Total work
Tendons do 92%-97% of the work
Muscle work
Work per Hop (J)
Speed (m/s)
0
1
2
3
3
4
5
6

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Dealing with Gravity—Using Tendons and Muscles to Improve Locomotion Energetics

- **Mechanical properties of tendon**
- **Tendon elasticity in wallaby hopping**
- **Mechanical behaviour of muscles: positive and negative work**
- **Role of muscles in running**

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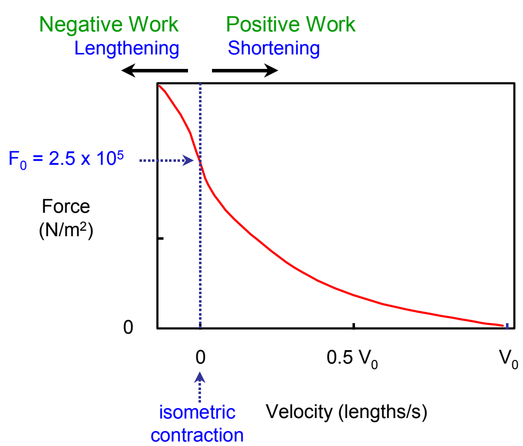
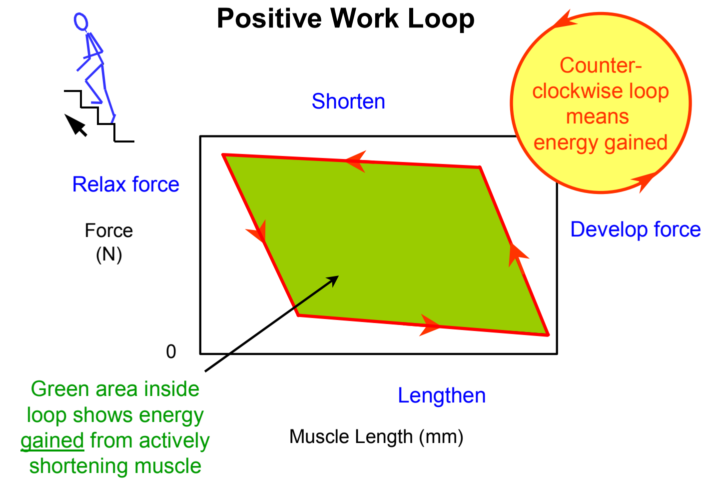
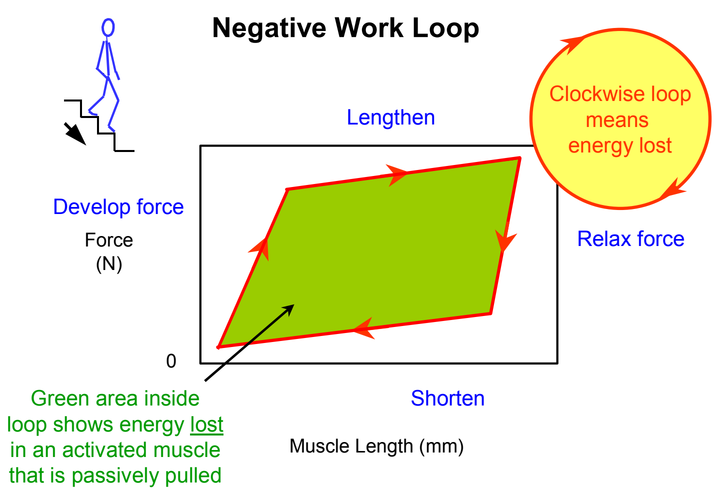
Muscle Force-Velocity Relationship

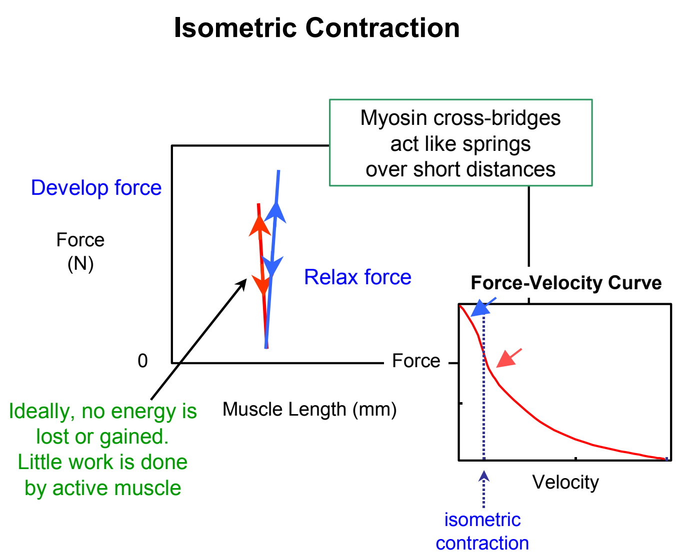




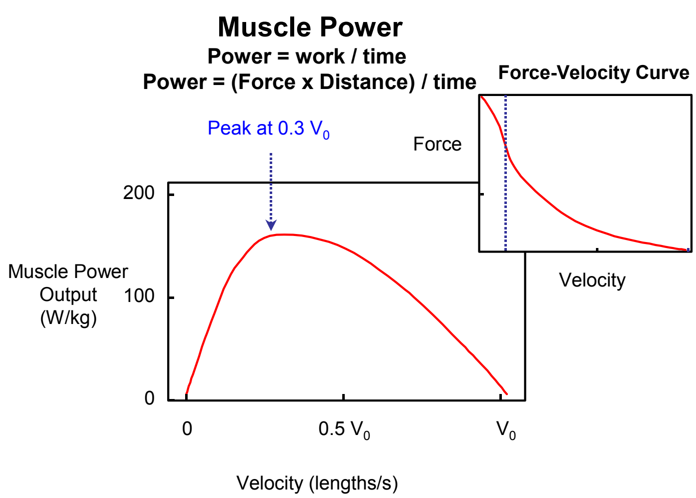
Positive Work Loop
Counter-clockwise loop means energy gained
Shorten
Relax force
Force (N)
Develop force
0
Green area inside loop shows energy gained from actively shortening muscle
Lengthen
Muscle Length (mm)



Negative Work Loop
Clockwise loop means energy lost
Lengthen
Develop force
Force (N)
Relax force
0
Green area inside loop shows energy lost in an activated muscle that is passively pulled
Shorten
Muscle Length (mm)



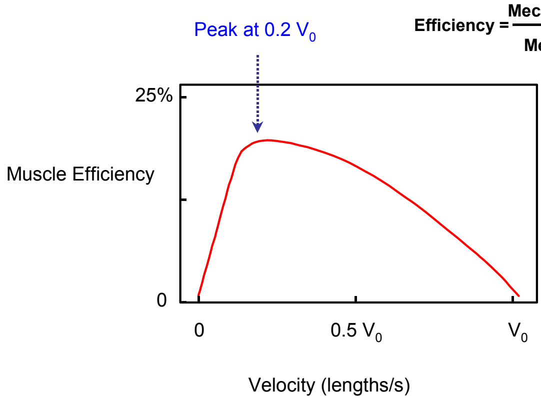
Isometric Contraction
Myosin cross-bridges act like springs over short distances
Develop force
Force (N)
Relax force
Force-Velocity Curve
0
Force
Ideally, no energy is lost or gained. Little work is done by active muscle
Muscle Length (mm)
Velocity
isometric contraction



Muscle Power
Power = work / time
Power = (Force x Distance) / time
Force-Velocity Curve
Peak at 0.3 V_0
Force
200
Muscle Power Output (W/kg)
100
0
Velocity
0
0.5 V_0
V_0
Velocity (lengths/s)

Muscle Efficiency

$$\text{Efficiency} = \frac{\text{Mechanical Power Output}}{\text{Metabolic Power Input}}$$



In Vivo Study of Turkey Running

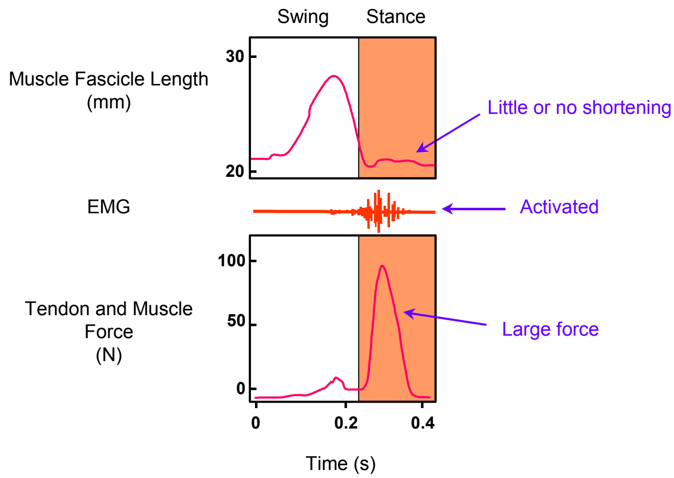
We already know that tendons supply energy for running.

Question:
What are the muscles doing in vivo?

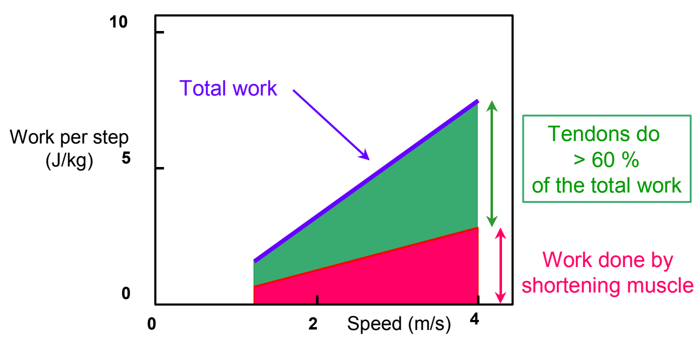
Experimental Approach:

1. Get force (stress) and length (strain) data
2. Calculate mechanical work done
3. Run turkey on level and incline

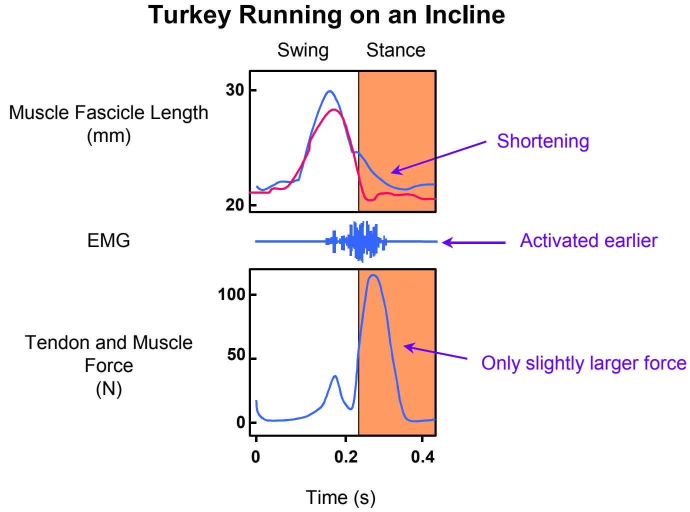
Turkey Running on Level

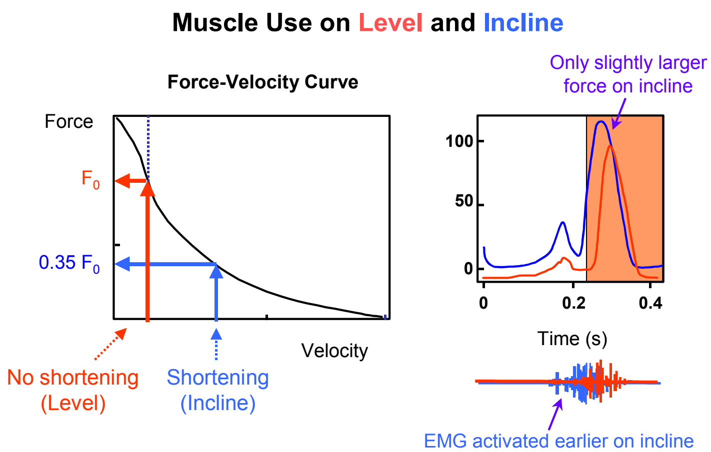


Tendon Contributes More to Total Work than Muscle



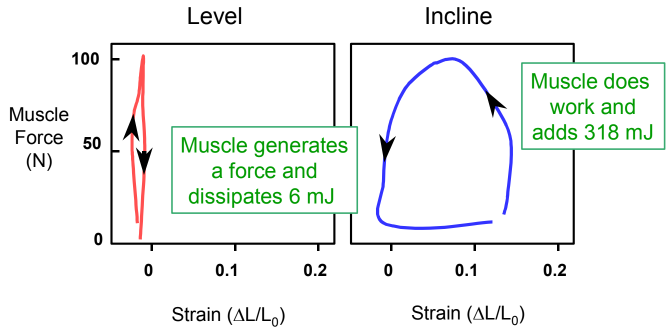
Net work = positive work (shortening) + negative work (lengthening)
Net muscle work ~ 0





Conclude: More muscle fibres must be used on incline, increasing the metabolic cost

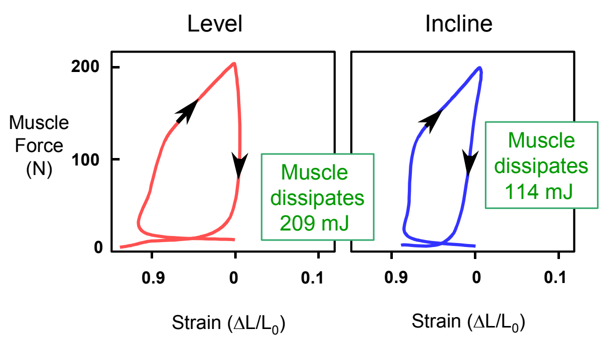
Muscle Work Loops in Stance Phase for Running Turkey



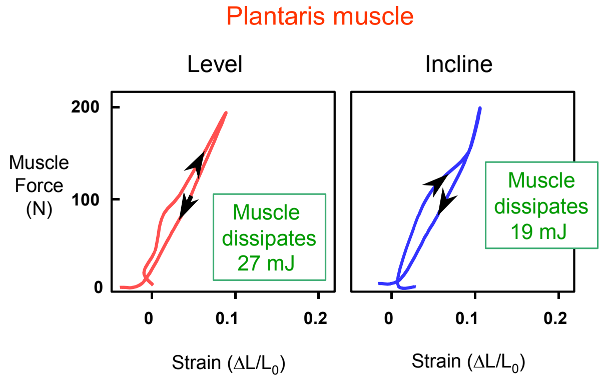
Turkey ankle muscles act as a spring on level and as a motor on incline.

Muscle Work Loops in Stance Phase for Hopping Wallaby #3

Gastrocnemius muscle



Muscle Work Loops in Stance Phase for Hopping Wallaby #2



Wallaby ankle muscles act as a spring or brake on level and on incline.
Do more proximal leg muscles act as motors on incline?

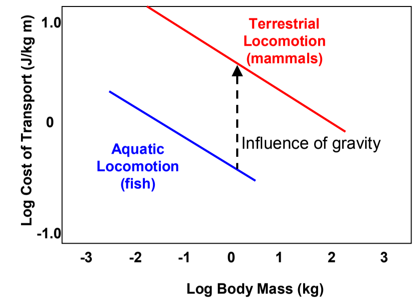
Muscle Function in Aquatic Locomotion

Fish: how are muscle and tendon organized?

How are muscles used for swimming?

Positive and negative work

Review: **Cost of Transport is Much Lower for Fish**



Dealing with Gravity is Expensive

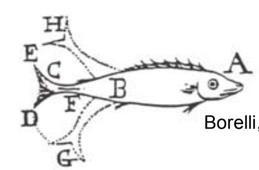
Stance phase muscles consume ~75% of energy

We have seen that legs are designed to minimize the cost to the stance phase muscles.

We might predict the musculoskeletal system in <u>fish</u> is designed to maximize power output for thrust (tendons not springs).

How fish swim: just the basics

Wag the tail:

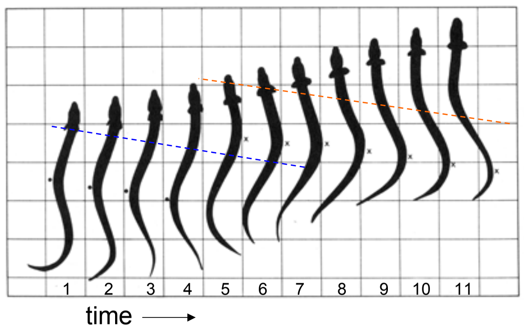


Borelli, 1680

Propulsive wave

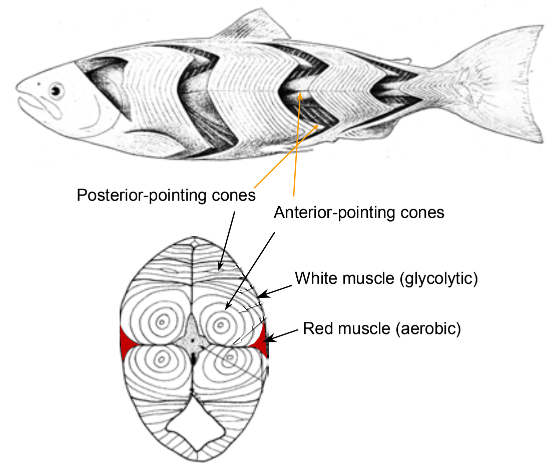
Pettigrew, 1873

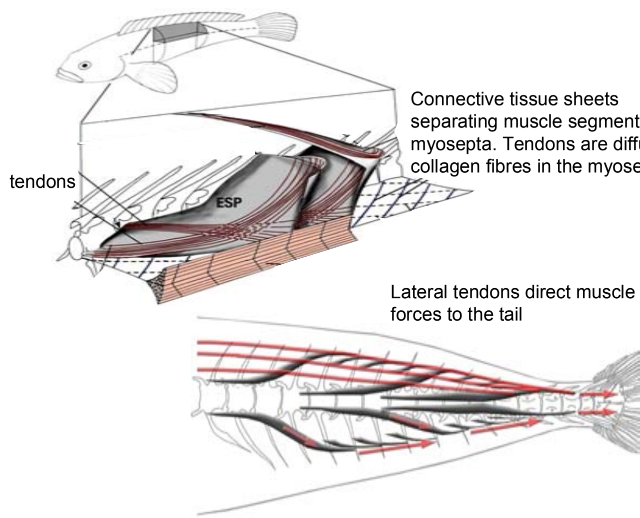
Propulsive wave generates thrust along the body



James Gray, 1933. Swimming eel

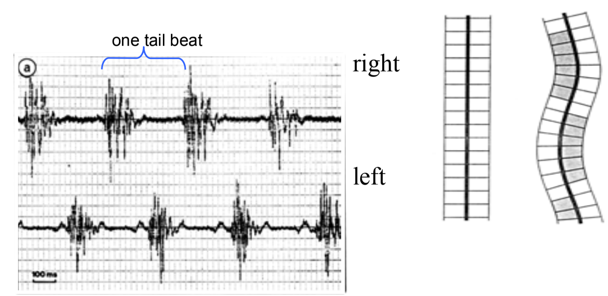
Segmented body, complex muscle architecture



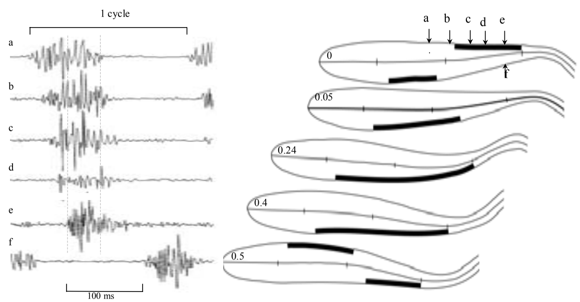


Body wave is generated by alternating waves of muscle activity propagated along the body

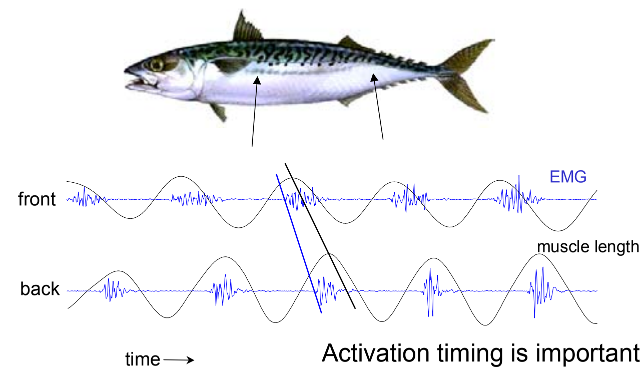
Muscle electrical activity, EMG



Waves of muscle activation cause waves of contraction



Activation wave, shortening wave, undulation



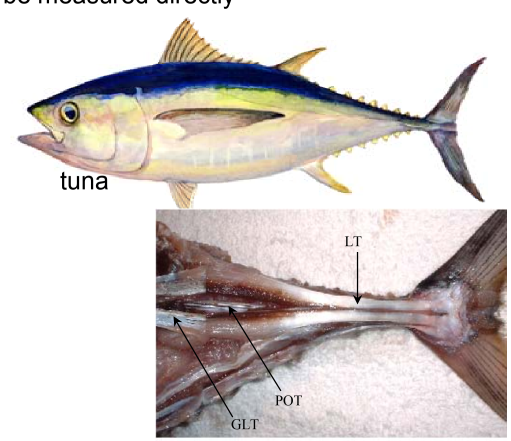
Activation timing is important

What determines whether a muscle does positive or negative work?

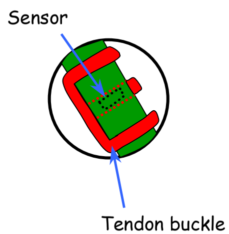
How can muscle properties measured?

How can muscle function be altered?

Only 1 type of fish that has tendons where force can be measured directly

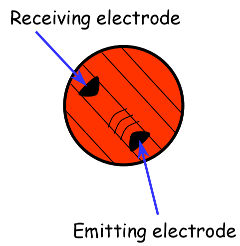


Muscle Force



TENDON BUCKLE

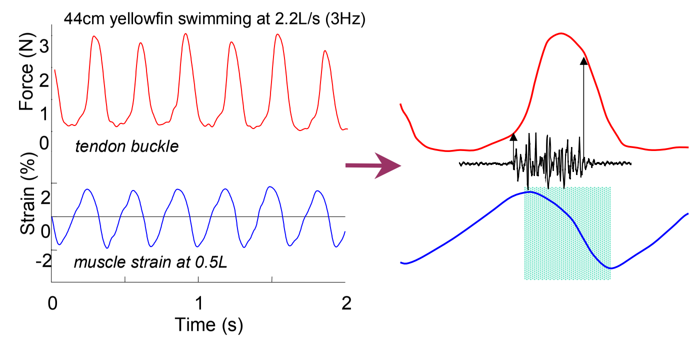
Muscle Strain



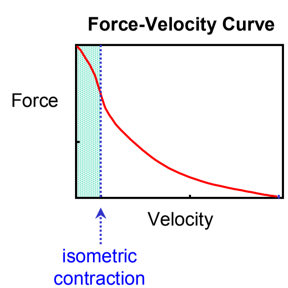
SONOMICROMETRY

***In vivo* work loops**

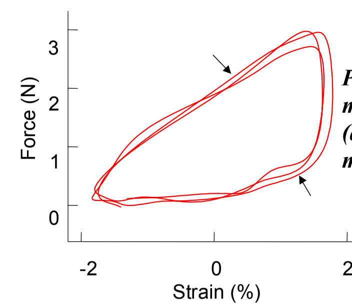
Recording of force and muscle shortening in a tuna



Remember, muscle force is enhanced by stretch activation

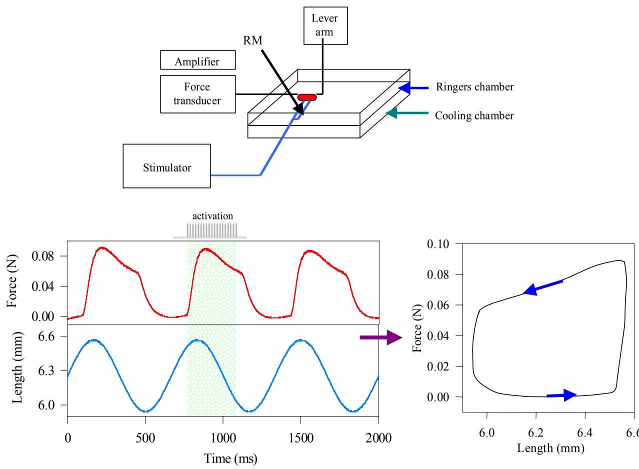


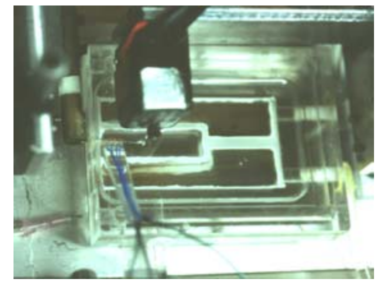
Whole body in vivo work loop

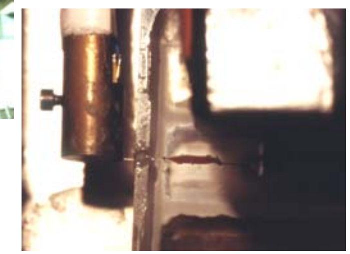


Plot of tendon force vs. muscle strain (displacement) gives muscle work loops.

Muscle Work Loop Experiments







Workloop protocol:

•Optimize starting length

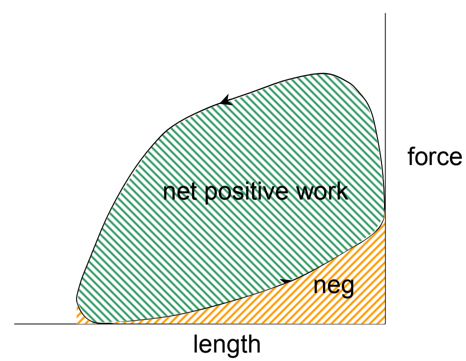
•Set muscle strain amplitude

•Set phase of activation onset

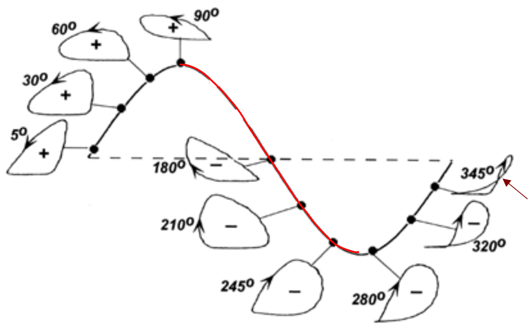
•Set duration of activation

•Set cycle frequency

•Vary parameters to optimize work, power

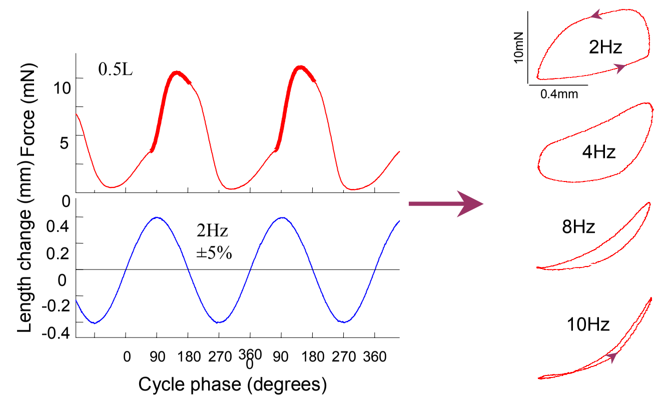


Importance of activation phase on work

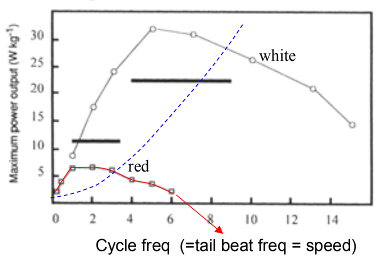


If force is developed during shortening: *positive* work
lengthening: *negative* work
Activation timing controls this

Work is dependent on cycle frequency



Muscle power in red *vs.* white fibers



Power = work/cycle X cycles/s
= work X freq

White has greater power output per kg

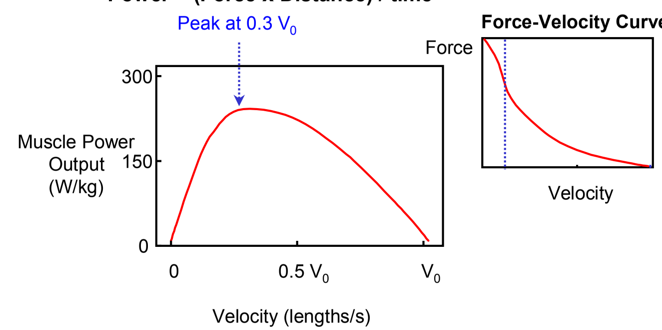
Red is optimized for low speeds, white for high speeds

*Muscle function may be altered by activation frequency

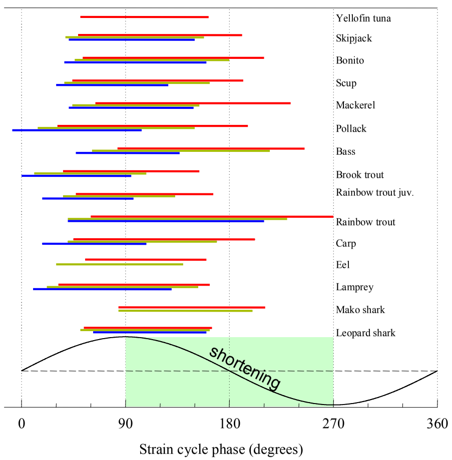
Muscle Power

Power = work / time

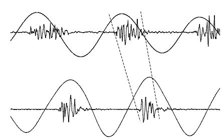
Power = (Force x Distance) / time

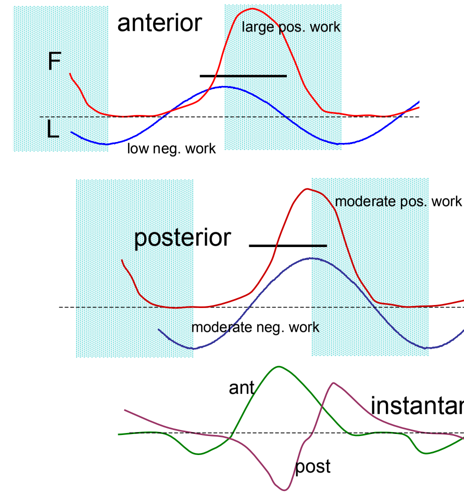


Summary of EMG activation *vs* strain for various fish



- muscle activation begins before peak length
- posterior muscle usually activated relatively earlier in length cycle
- this may result in differential muscle function

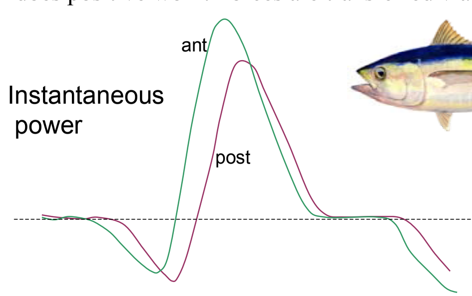




Fish such as trout:

- *differences in activation timing in anterior and posterior*
- *anterior muscle develops large positive power while posterior muscle is doing negative work*
- *this effects body stiffness*
- *may help muscles transmit forces to tail*

Tuna are different: activation wave is fast on the body, consequently the time difference between anterior and posterior is slight, activation phase is similar, most muscle does positive work. Forces are transferred via tendons.



Summary of results:

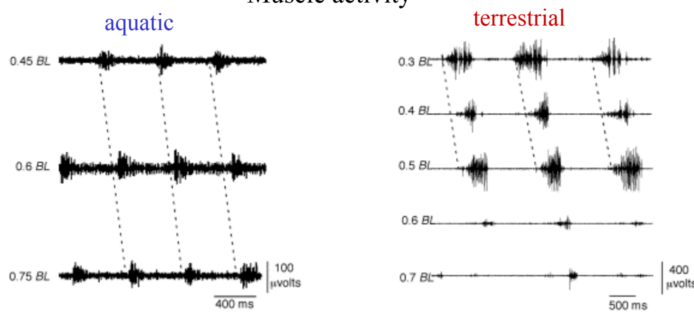
In some fish, without gravity there can still be an advantage some negative work to transmit forces along the body.

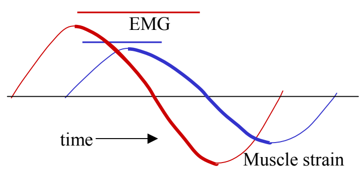
In tunas the tendons take place of stretch-activated muscle to transmit forces.

Tuna tendons do not act as energy storing springs: they are too short and too thick.

Eels on land and in water

Muscle activity

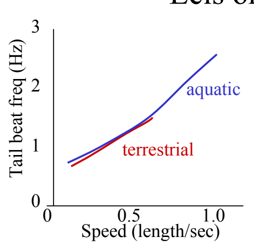


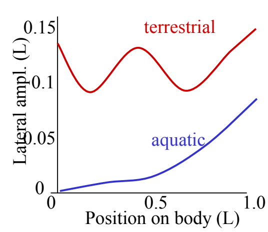


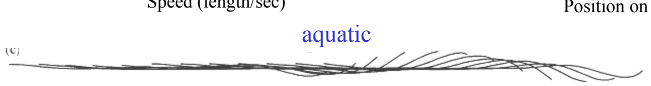
On land muscle activity and amplitude are greater.

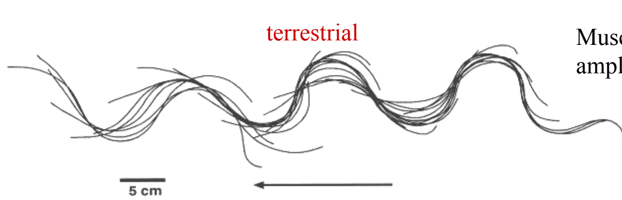
In water, there is a delay in the shortening of muscle after activation

Eels on land and in water



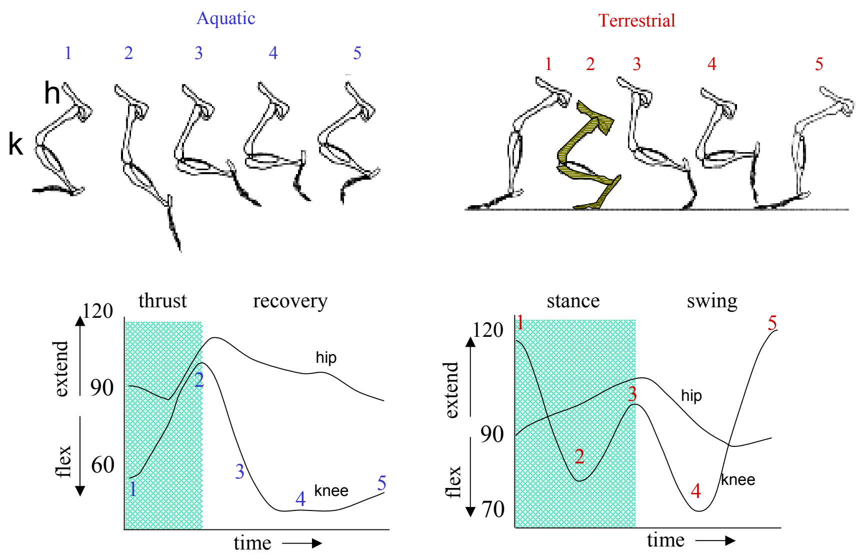




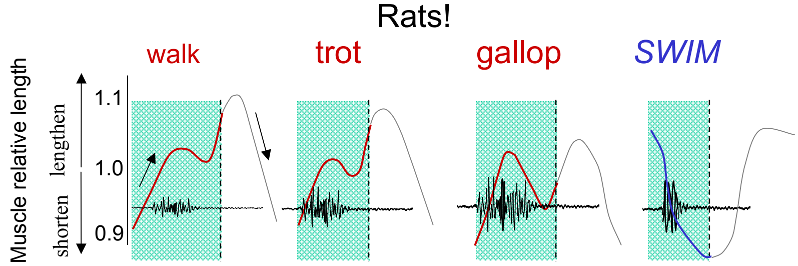


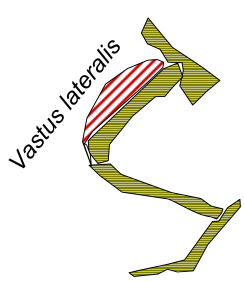
Muscles undergo larger amplitude contractions

Rats!



Rats!





on land *v. lateralis* is used as a force generator, active when lengthening, (i.e. negative work)

in water *v. lateralis* is used to generate positive contractile work

Summary:

- A major difference between aquatic and terrestrial locomotion is gravity
- Muscle performance is controlled by the phase and duration of activation
- Muscle performance is also influenced by cycle frequency or shortening velocity
-
- Muscle active primarily during lengthening absorbs energy (negative work)
- Muscle active primarily during shortening do positive contractile work
- Modulation of muscle function may occur depending on the locomotion medium (land, water)