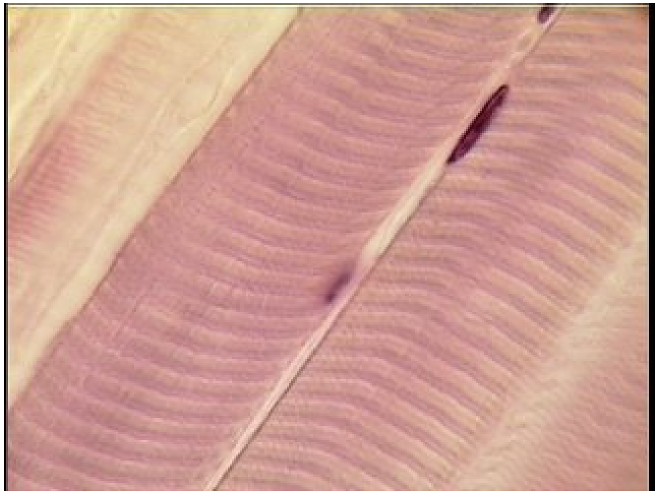
Skeletal muscle

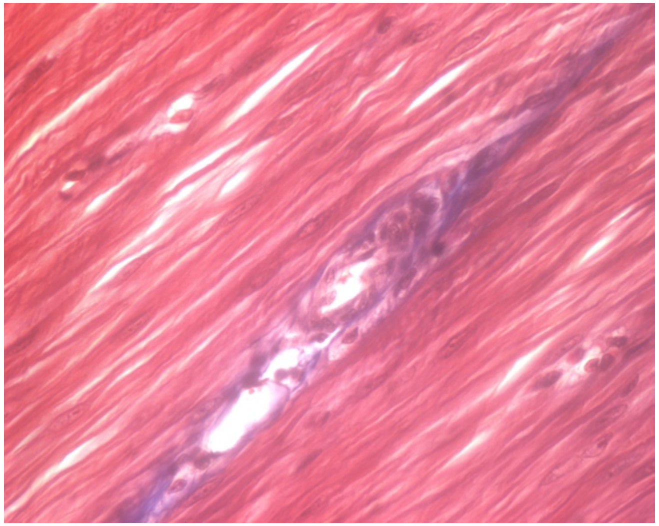
Biomechanics lecture

Muscle types

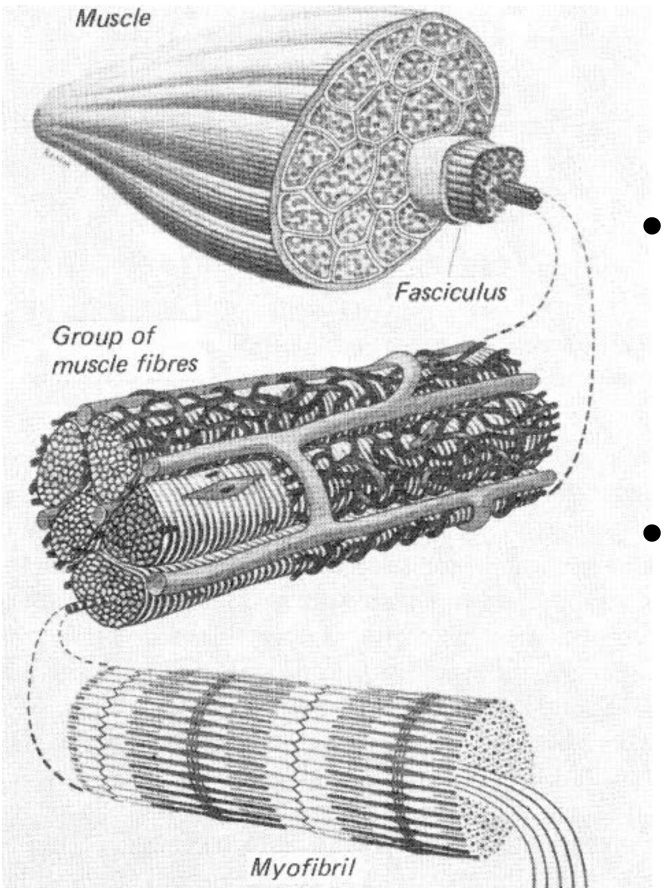
- Striated:
  - Skeletal muscle (voluntary)
  - Heart (involuntary)



- Smooth
  - intestines, blood vessels, etc. (involuntary)



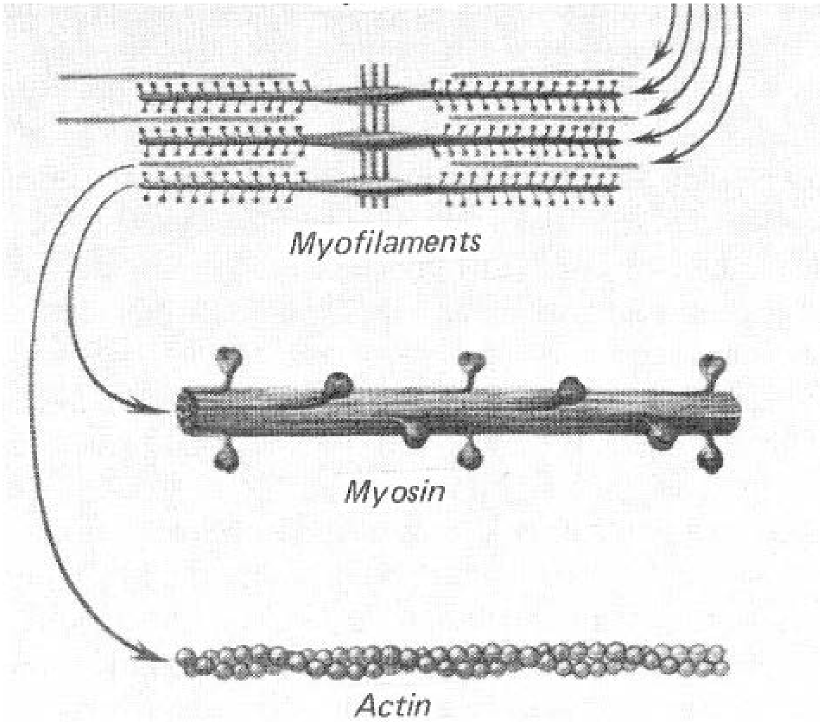
Structure of skeletal muscle



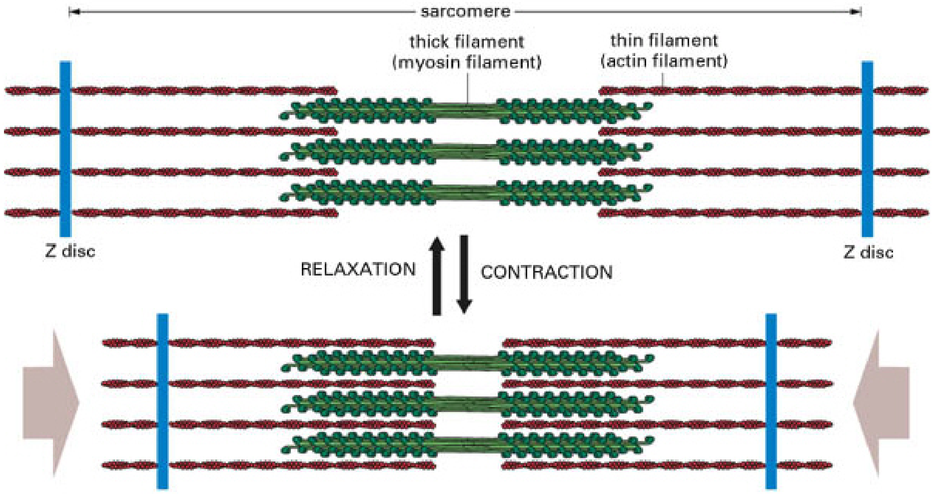
- Muscle consists of bundles of muscle fibres
- Connective tissue fills the spaces between the fibres and the sheath surrounding the muscle.
- Muscle fibre:
  - Diameter ~10-60μm (hair ~100 μm).
  - Length of fibres depend on length of muscle. From a couple of mm, to 30 cm in long muscles.

The sarcomere

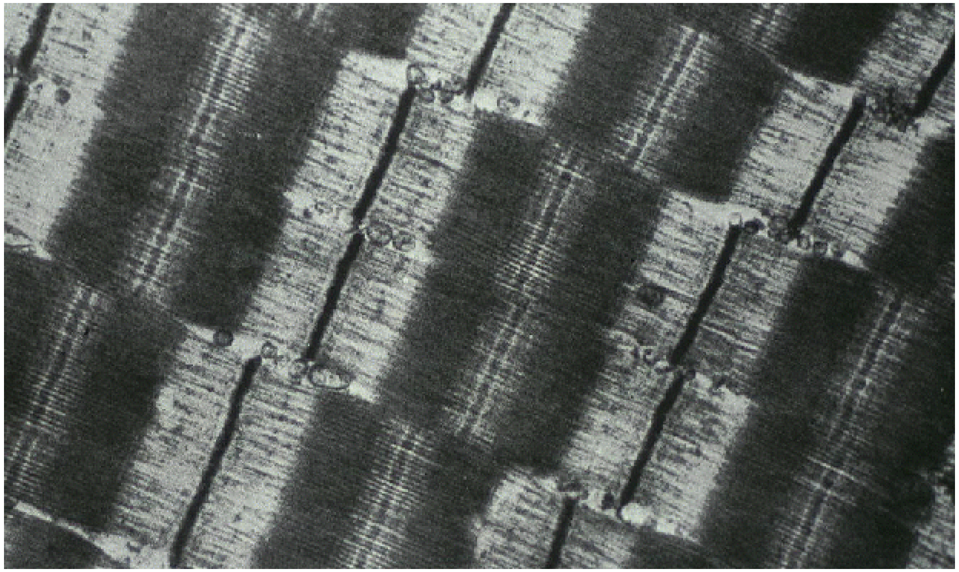
- Diameter on the nanoscale (10^{-9} m)
- Slack length ~ 2.2 µm



- When inactive the filaments can slide in and out.

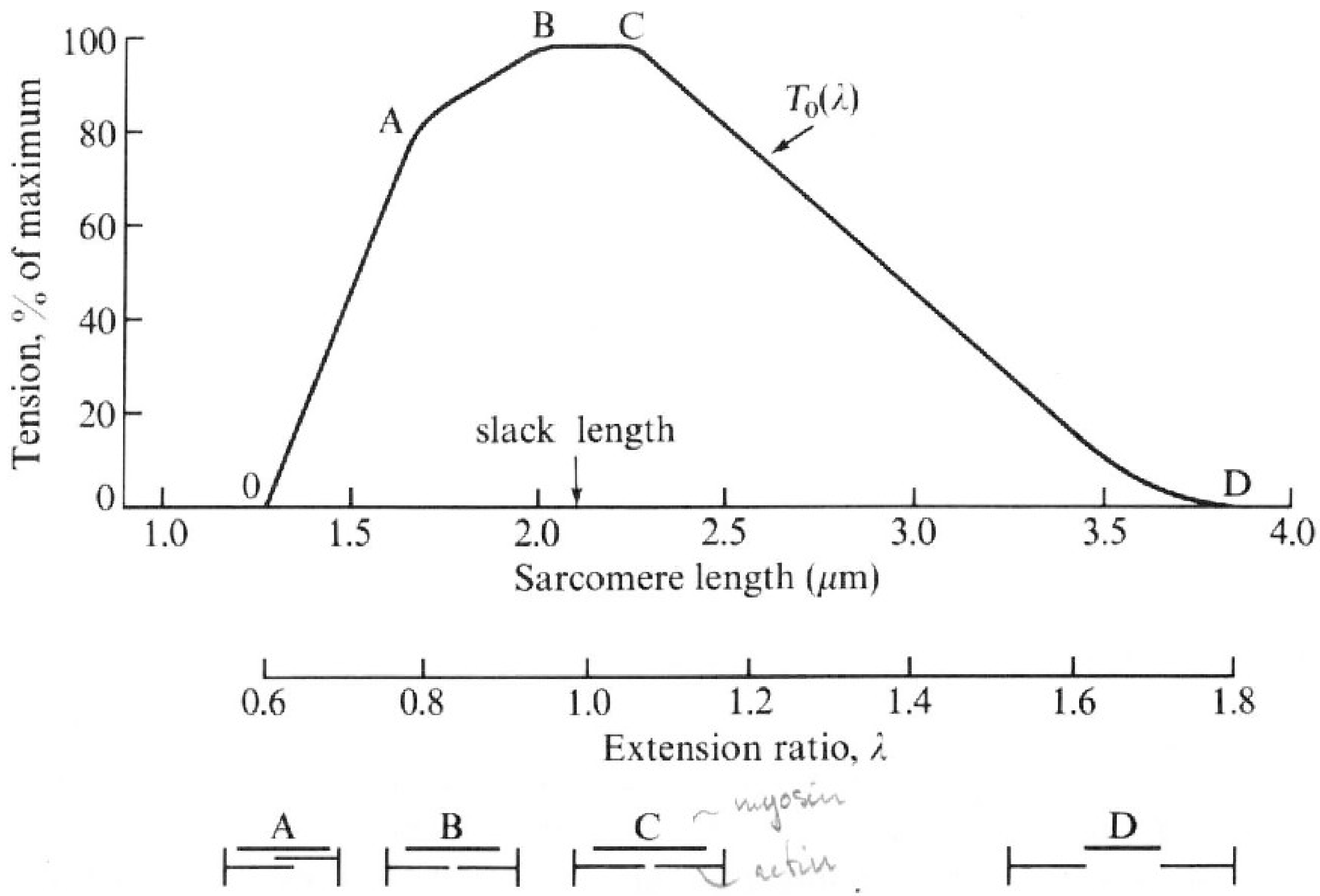


- When active, the ”fingers” of the myosin filament climb on the actin filament.



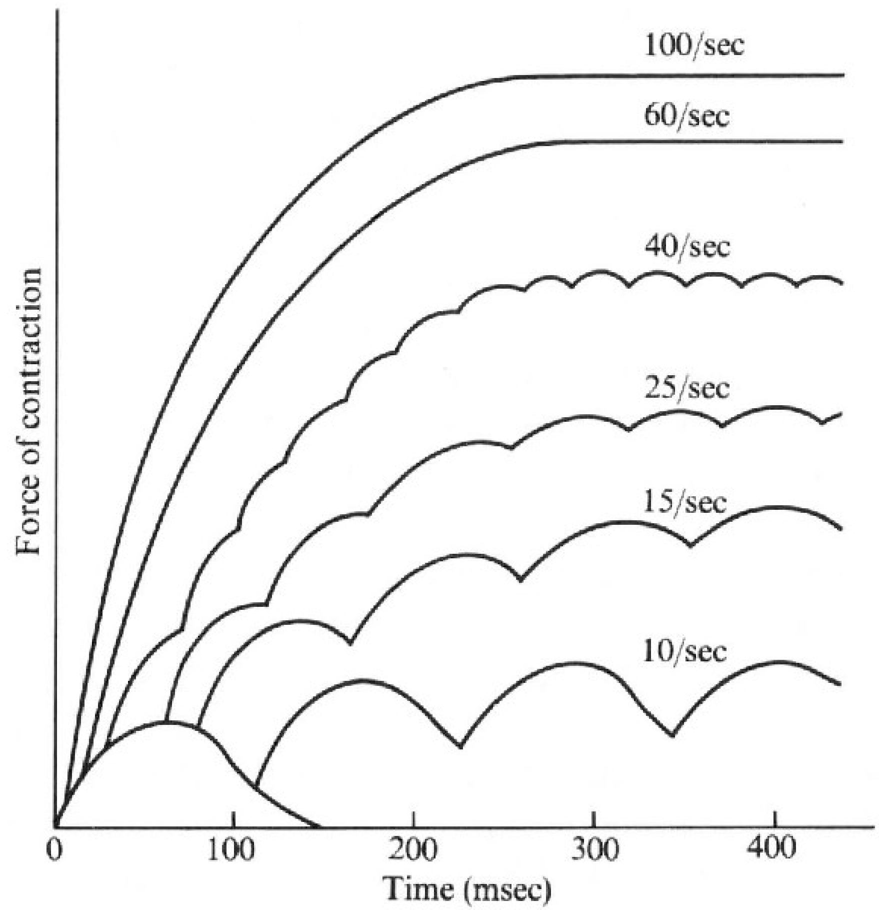
- Each sarcomere is able to shorten by approximately 30 %

Tension vs stretch



Contraction in muscle fibres

- Muscle fibers operate in twitches
- Wave summation
- When the muscle has reached a critical frequency, the muscle force smoothens
    - **Tetanized state.**
- **The tetanized force represents the maximum force of the muscle fibre (T_0)**



Contraction of muscle bundles

- Fibres organised in *motor units*
- A motor unit may consist of only 2-3 fibres or thousands of fibres
- Total muscle force depends on the total amount of fibres stimulated

Types of active contractions

- **Concentric contraction:**
  - Lifting a weight.
  - Muscle is active and allowed to shorten.
  - Load < T_0,
- **Eccentric contraction:**
  - Putting down a weight
  - Muscle is active, but is lengthening.
  - Load may exceed T_0
- **Isometric contraction:**
  – Holding a weight
  – Muscle is active, but remains at constant length
  – Load = T_0

Hill's model

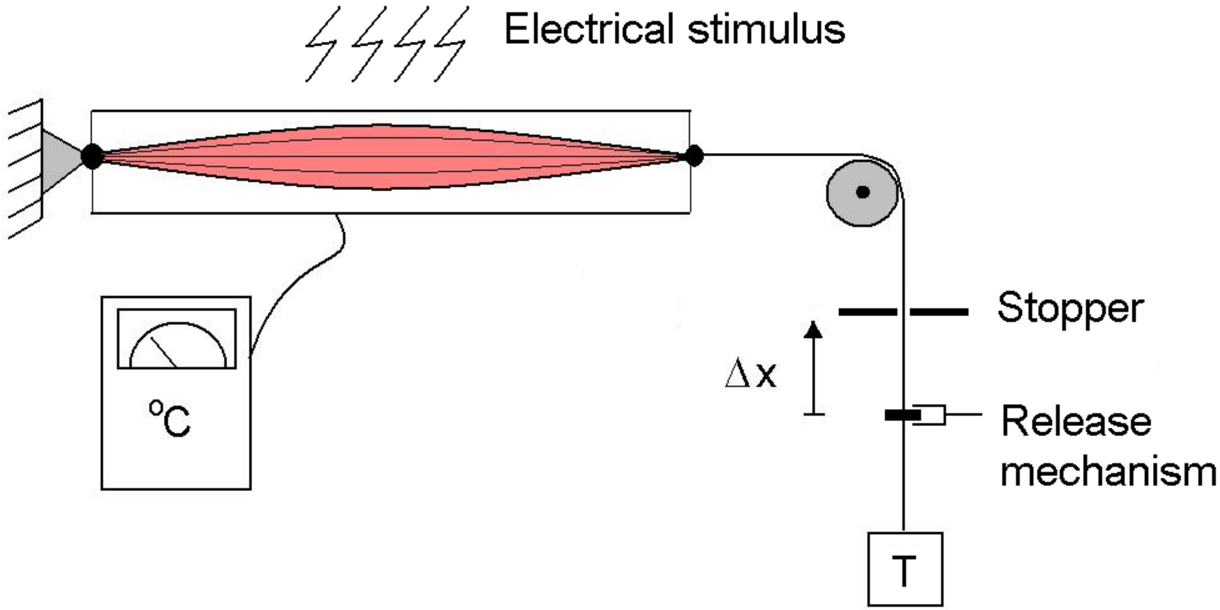
Includes two parts:

1. A relationship between max. muscle force (T_0) and velocity (v) in quick release from isometric contraction (Hill's equation)

2. *Lumped parameter model* to represent contraction and elastic stiffnesses in muscle

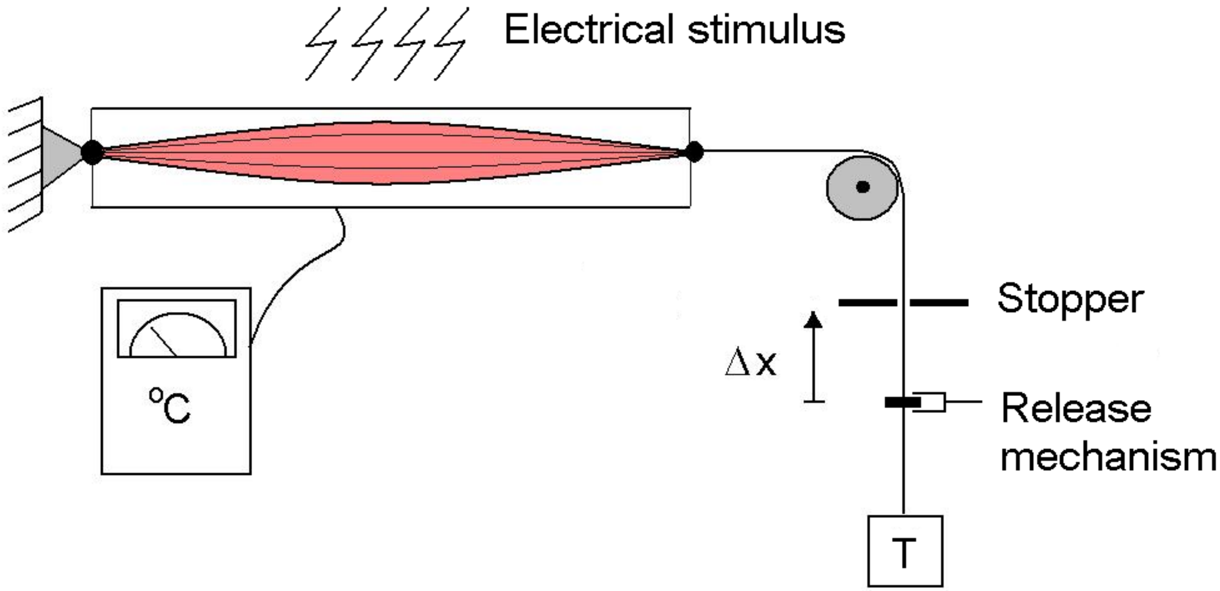
Hill,A.V., *The heat of shortening and the dynamic constants of muscle*, Royal Society of London (1938)

Hill's equation



- Measured the heat from the muscle and the work during contraction.
- Used energy balance to describe contraction of a tetanized muscle

Hill's equation



Muscle tetanized under isometric conditions, and released under isotonic conditions.

- **Isotonic contraction**: muscle force remains constant
  Load (T) < T_0

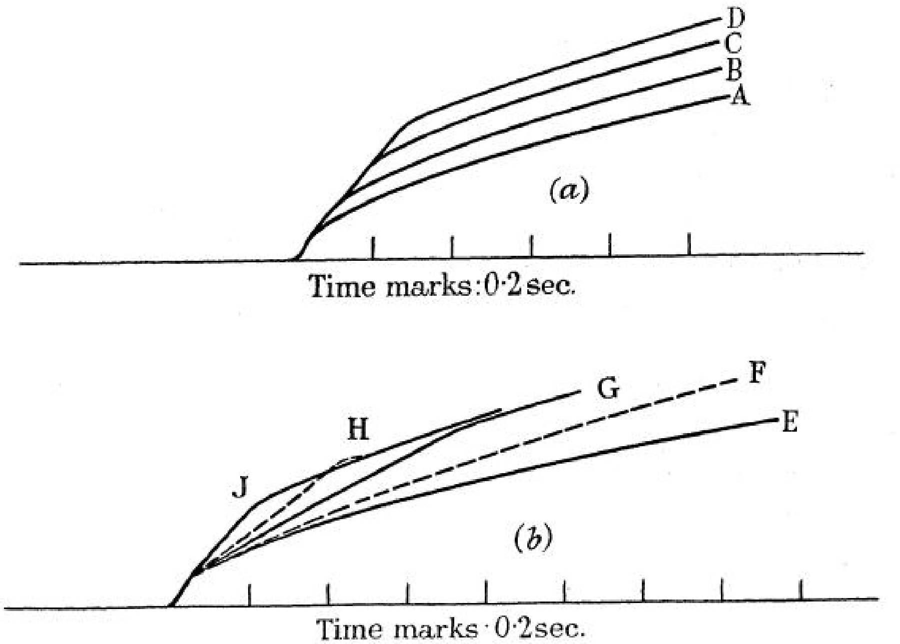
Energy balance

- Total energy: $E = A + H + W$
- A – activation heat during isometric contraction
- H – extra heat released during isotonic contraction
- W – work done by the muscle

The heat of shortening

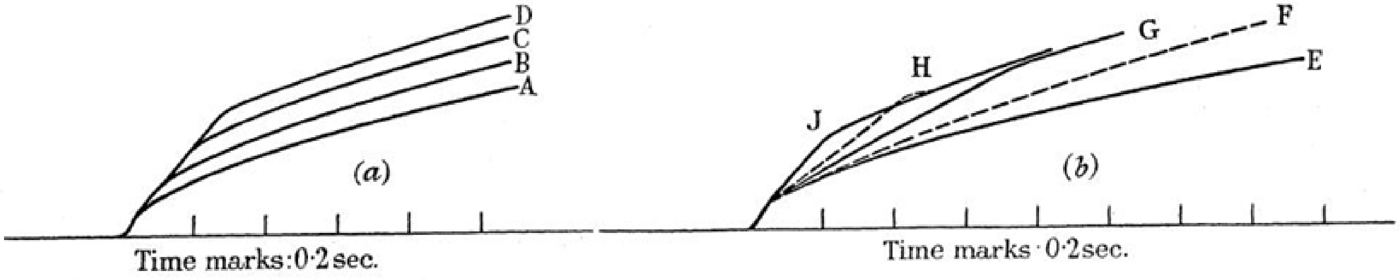
a) Different shortening distances under constant load

b) Constant shortening distance under different loads



Allowing the muscle to contract gives an extra energy release.

The heat of shortening



- The extra heat is proportional with the contraction length:

  $$H = a*dx$$

- The rate of extra energy release is proportional with difference in force between isometric and isotonic state:

  $$d(H+W)/dt = b*(T_0-T)$$

$$\frac{d}{dt}(H+W)=b\cdot(T_0-T)$$

$$H=a\cdot dx \Rightarrow \frac{dH}{dt}=a\cdot v$$

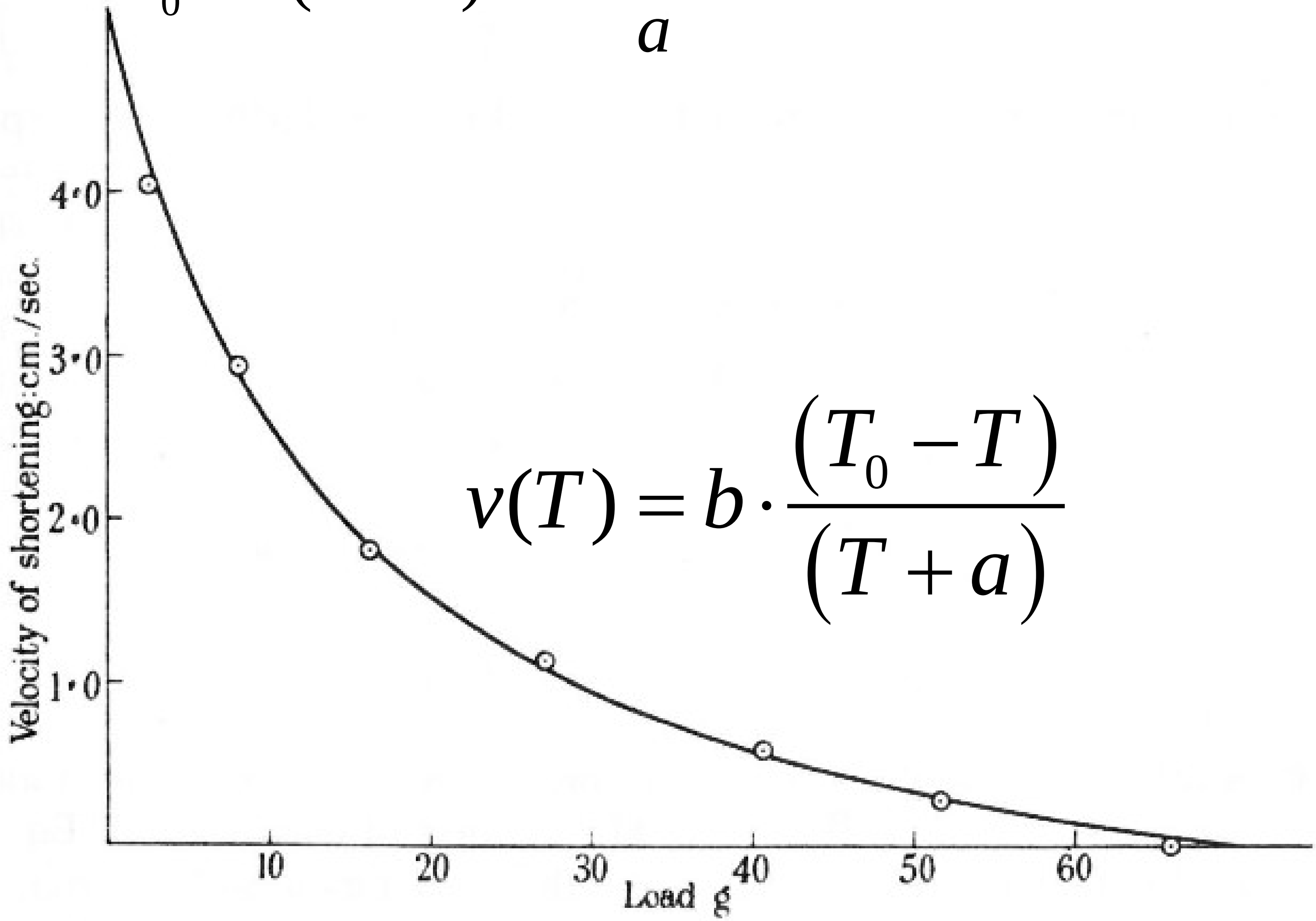
$$W=T\cdot dx \Rightarrow \frac{dW}{dt}=T\cdot v$$

$$\Rightarrow (T+a)\cdot v=b\cdot(T_0-T)$$

Hill's equation:

$\Rightarrow$ $\underline{(T+a)*(v+b) = (T_0+a)*b=\text{constant}}$

$$v_0 = v(T=0) = b \cdot \frac{T_0}{a}$$



$$v(T) = b \cdot \frac{(T_0 - T)}{(T + a)}$$

a [dimension force] :

- ”resistance” of shortening (Hill, 1938)
- depends on the cross-sectional size of the muscle
- $a/T_0 \sim 0.25$ (constant) (Hill, 1938)

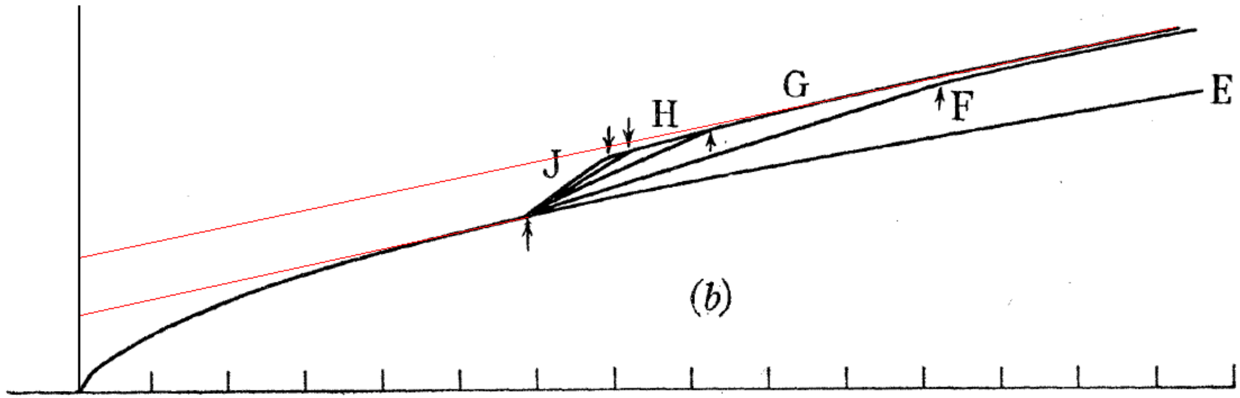
b [dimension velocity] :

- defines rate om energy release during shortening
- depends on the length (L) of the muscle
- b/L = constant at constant temperature (Hill, 1938)

Limitations of the Hill's equation

- Only valid for fully tetanized muscle
- Only describes shortening
- Applies only to quick release
- All data at or near muscle slack length (L_0)

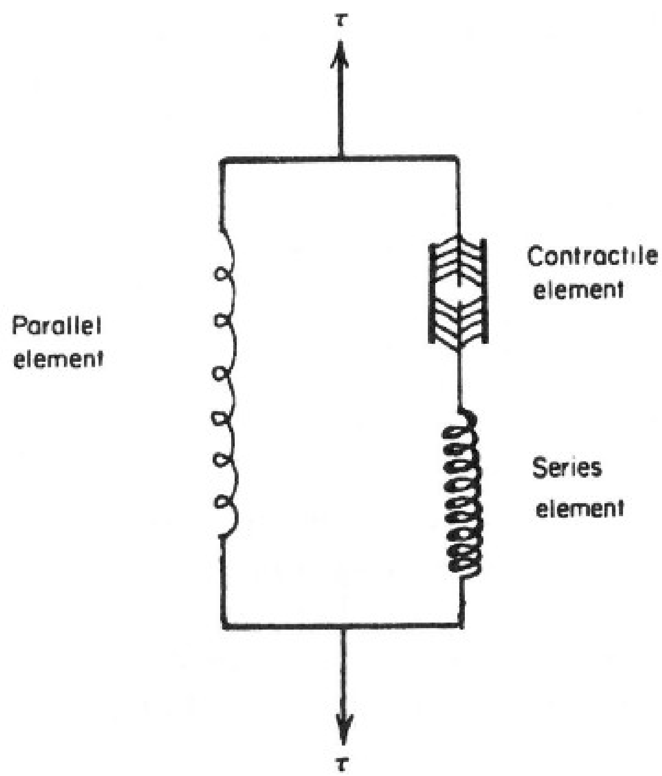
Hill's three-element model



"Shortening heat and relaxation heat during an isometric contraction. In the heat records of isometric contractions in figs. 6, 7, 8, 13 and 14, the upstroke at the beginning is very similar to that in records of contractions in which shortening is permitted: but smaller."

Hill,A.V., *The heat of shortening and the dynamic constants of muscle*, Royal Society of London (1938)

Hill’s three-element model

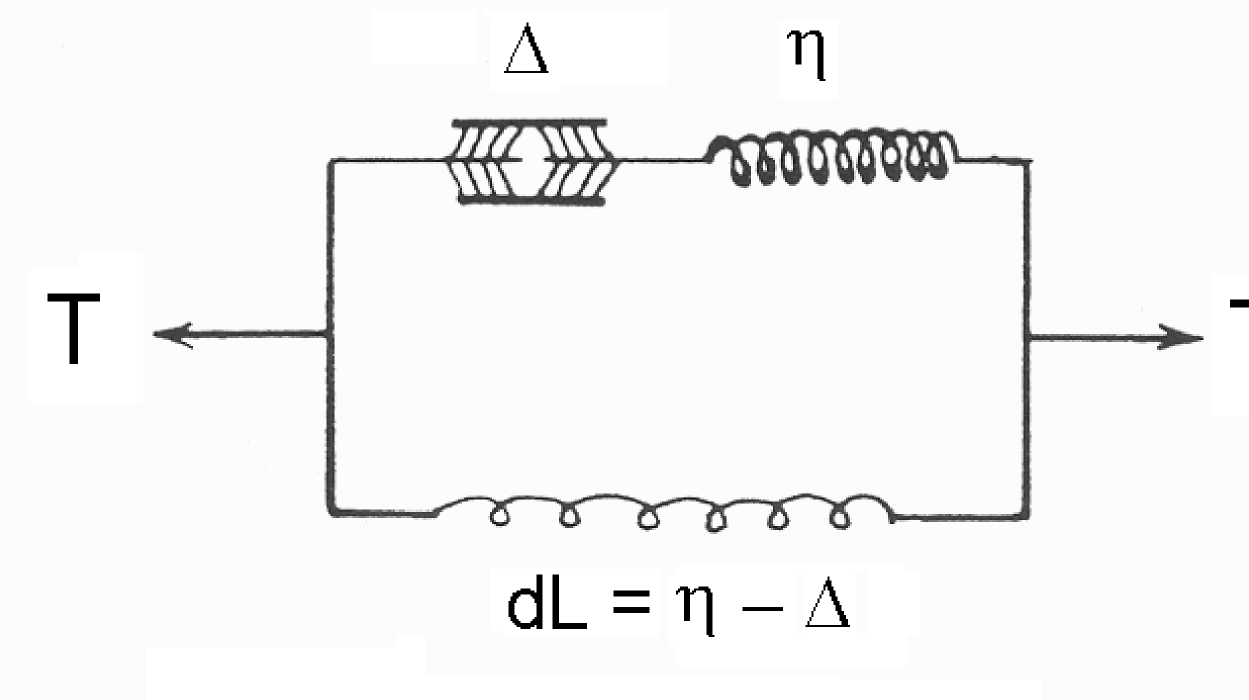


Contractile element:
the sarcomeres

Series element:
the elasticity of the actin and myosin filaments

Parallell element:
the elasticity of the surrounding connective tissue

Hill’s three-element model



$$v = \frac{dL}{dt} = \frac{d\eta}{dt} - \frac{d\Delta}{dt}$$

Forces in the three-element model

- Parallel spring element: $T^{(PE)} = P(dL)$, where $dL = L - L_0$, and L_0 is the slack length. => $T^{(PE)} = P(L)$
- Serial spring element: $T^{(SE)} = T^{(CE)} = S(\Delta,\eta)$
  - Contractile element slides freely if muscle unstimulated => $S = 0$
  - $\mathrm{sign}(S) = \mathrm{sign}(\eta)$
- Total muscle force: $T = P(L) + S(\Delta,\eta)$

Determining spring stiffness

We can measure total shortening/extension (dL) and total force (T) on the muscle, but not Δ or η:

- **Parallel spring element (k_P=dP/dL):**
  - can be determined directly from measurement at unstimulated state (T=P)
- **Serial spring element (k_S=dS/dη):**
  - must be determined indirectly by contraction measurements at stimulated state (f.ex. the *Isometric-Isotonic change over method*)

Dynamic equation of Hill's model

$$\frac{dT}{dt} = \frac{d}{dt}P(L) + \frac{d}{dt}S(\eta, \Delta) =$$

$$= \left(\frac{dP}{dL} + \frac{\partial S}{\partial \eta} \right) \cdot \frac{dL}{dt} + \left(\frac{\partial S}{\partial \eta} + \frac{\partial S}{\partial \Delta} \right) \cdot \frac{d\Delta}{dt}$$

Dynamic equation of Hill's model

- Isometric contraction: L is constant, dL/dt=0

$$\frac{dT}{dt} = \left(\frac{\partial S}{\partial \eta} + \frac{\partial S}{\partial \Delta} \right) \cdot \frac{d\Delta}{dt}$$

- Isotonic contraction: T is constant, dT/dt=0

$$\left(\frac{dP}{dL} + \frac{\partial S}{\partial \eta} \right) \cdot \frac{dL}{dt} + \left(\frac{\partial S}{\partial \eta} + \frac{\partial S}{\partial \Delta} \right) \cdot \frac{d\Delta}{dt} = 0$$

Isometric-Isotonic change over method

- Stimulate isometrically until $T=T_{aft}$:

$$\frac{dT}{dt}=\left(\frac{\partial S}{\partial \eta}+\frac{\partial S}{\partial \Delta}\right)\cdot\frac{d\Delta}{dt}$$

- Release and let contract isotonically at $T=T_{aft}$:

$$\left(\frac{dP}{dL}+\frac{\partial S}{\partial \eta}\right)\cdot\frac{dL}{dt}+\left(\frac{\partial S}{\partial \eta}+\frac{\partial S}{\partial \Delta}\right)\cdot\frac{d\Delta}{dt}=0$$

- Assumption:
  - $d\Delta/dt$ is a function of the tension S, insertion Δ, length L, and time t.

=> at the time of release:

$$\left.\frac{d\Delta}{dt}\right|_{isometric,T=T_{aft}}=\left.\frac{d\Delta}{dt}\right|_{isotonic,T=T_{aft}}$$

Isometric-Isotonic change-over method

$$\left.\frac{d\Delta}{dt}\right|_{Isometric,T_{aft}} = \frac{1}{\left(\dfrac{\partial S}{\partial \eta}+\dfrac{\partial S}{\partial \Delta}\right)}\cdot\left.\frac{dT}{dt}\right|_{T=T_{aft}} = -\frac{\left(\dfrac{dP}{dL}+\dfrac{\partial S}{\partial \eta}\right)}{\left(\dfrac{\partial S}{\partial \eta}+\dfrac{\partial S}{\partial \Delta}\right)}\cdot\left.\frac{dL}{dt}\right|_{T=T_{aft}} = \left.\frac{d\Delta}{dt}\right|_{Isotonic,T_{aft}}$$

$$\Rightarrow \left.\frac{dT}{dt}\right|_{T=T_{aft}} = -\left(\frac{dP}{dL}+\frac{\partial S}{\partial \eta}\right)\cdot\left.\frac{dL}{dt}\right|_{T=T_{aft}}$$

$$\Rightarrow \frac{\partial S}{\partial \eta} = -\frac{dP}{dL} - \frac{\left.\dfrac{dT}{dt}\right|_{T=T_{aft}}}{\left.\dfrac{dL}{dt}\right|_{T=T_{aft}}}$$

- Parallel spring stiffness (dP/dL) measured at unstimulated state.
- Tension rate (dT/dt) is measured during isometric contraction.
- Contraction rate (dL/dt) is measured during isotonic contraction.

Problems with the Hill’s model

- The spring stiffness of the serial element is difficult to determine
- Assumes the contractile element to slide freely when unstimulated
- Assumes the spring elements to be purely elastic