Teaching from classic papers: Hill's model of muscle

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AM5510 Biomedical Signals and Systems

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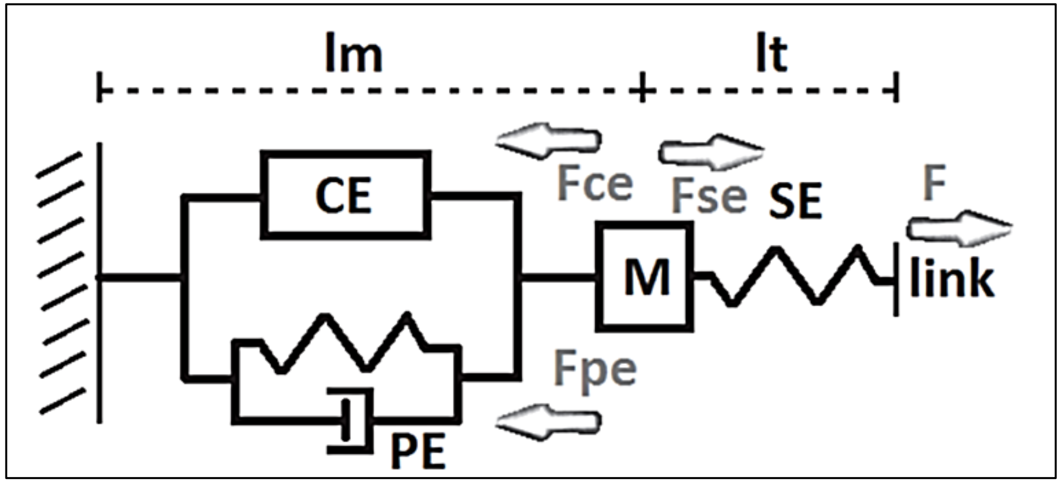
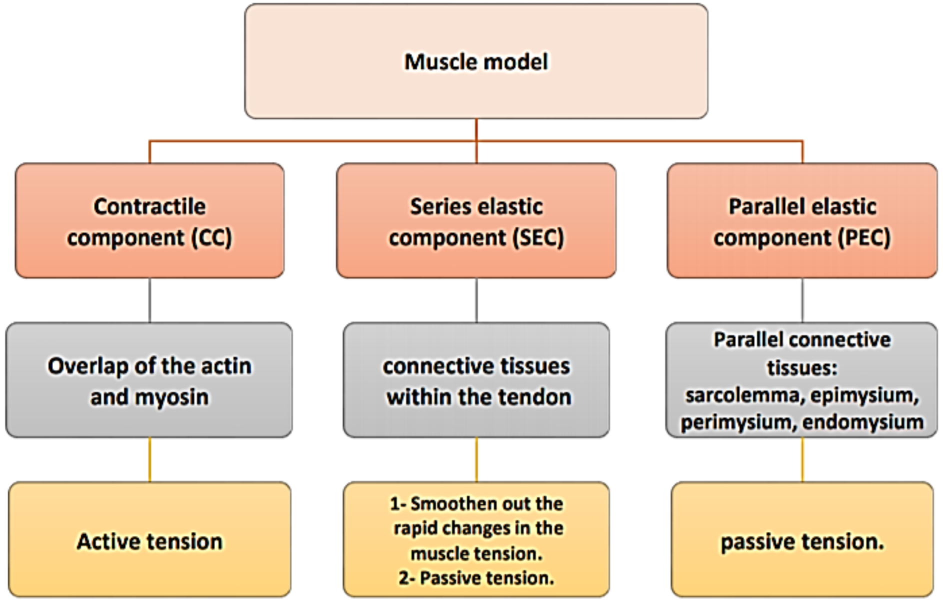
Hill's model



Hill muscle model is one of the most used models to describe the mechanism of force production.

It is composed by different elements that describe muscle behaviour:



- Force development within the CE is a function of activation kinetics (a), force-length (f-l) properties, and force-velocity (f-v) properties.
- Force developed by the PE depends on the CE length.
- Force in the SE is equal to the sum of PE and CE forces.

MATLAB code:

The MATLAB code correctly solves for the forces predicted by Hill's model assuming length is prescribed as an input and a tetanizing stimulus is applied beginning at the start of the simulation.
It does not simulate other situations in which Hill's model might be of interest, such as contractions against a constant afterload.
By choosing an arbitrary but reasonable rate of baseline heat liberation, it also produces heat tracings consistent with Hill's figures from the 1938 paper.

function hill (L,t)

```
function [P,H,Lse,Lce] = hill(L,t)
%  Teaching from classic papers: Hill’s model of muscle
%  Jeffrey W. Holmes, Department of Biomedical Engineering, Columbia University, New York

% Function hill accepts length & time inputs L(n), t(n) and computes
% following outputs assuming tetanizing impulse starts at first time point:
%     P(n) - force
%     H(n) - heat
%     Lse(n) - series elastic element length
%     Lce(n) - contractile element length
% Inputs and outputs are column vectors that must all have same length n.

% Establish constants (Hill 1938 p.174, mean data at 0¡C: a = 399*0.098, b = 0.331)
% Note that because Hill reports force with units of force/unit area and lengths in
% unitless fractions of muscle length, force and heat all have units of force/area.

a = (380*.098);         % units mN/mm2
b = 0.325;              % units lengths/sec
P0 = a/0.257;           % units mN/mm2
vm = P0*b/a;            % units lengths/sec
alpha = P0/0.1;         % units mN/mm2
Lse0 = 0.3;             % assume series elastic element is 30% of initial length
k = a/25;               % set arbitrary baseline heat rate
```

Constants have been defined in the rest of presentation

function hill (L,t)

```
% Initialize arrays
Lse = [repmat(Lse0,length(t),1)];
Lce = [repmat((1-Lse0),length(t),1)];
H = [repmat(0,length(t),1)];
P = [repmat(0,length(t),1)];

% General solver for prescribed length input to Hill model
for j = 1:(length(t)-1)
    Lse(j) = Lse0+P(j)/alpha; Lce(j) = L(j)-Lse(j);
    dt = (t(j+1)-t(j));
    dL = (L(j+1)-L(j));
    dP = alpha*((dL/dt) + b*((P0-P(j))/(a+P(j))))*dt;
    P(j+1) = P(j) + dP;
    H(j+1) = H(j) + (k + a*b*((P0-P(j))/(a+P(j))))*dt;
end
Lse(j+1) = Lse0+P(j+1)/alpha;
Lce(j+1) = L(j+1)-Lse(j+1);

% Add some noise if desired for more realistic output
H = H + (k/10)*(randn(length(t),1));
P = P + (P0/100)*(randn(length(t),1));
```

The loop solves Hill's model by stepping through the length and time inputs and using the calculated rate of force and heat rise at each time step to project the values at the next time step.

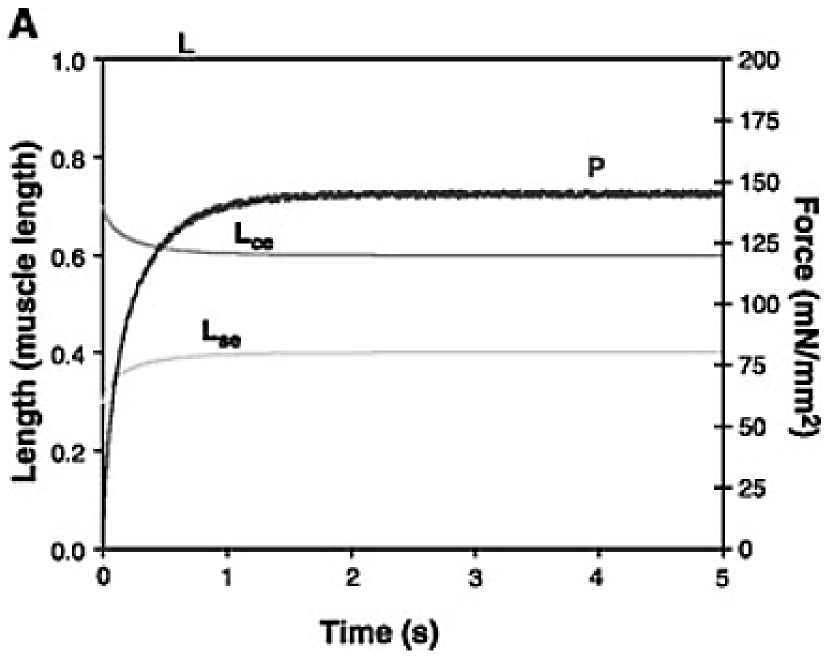
Gaussian noise is added to the computed force and heat outputs, for realistic presence of noise and to account for averaging over multiple trials.

1. Response of Hill's model to isometric tetanus

$$L = L_{ce} + L_{se} \qquad (1A)$$

$$\mathrm{P} = \mathrm{P}_{ce} + \mathrm{P}_{se} = \alpha[L_{se} - L_{se}(0)] \qquad (1B)$$

- L is muscle length,
- Lce and Lse are the lengths of the contractile and series elastic elements,
- P is muscle force,
- α is the spring constant for the series elastic element.

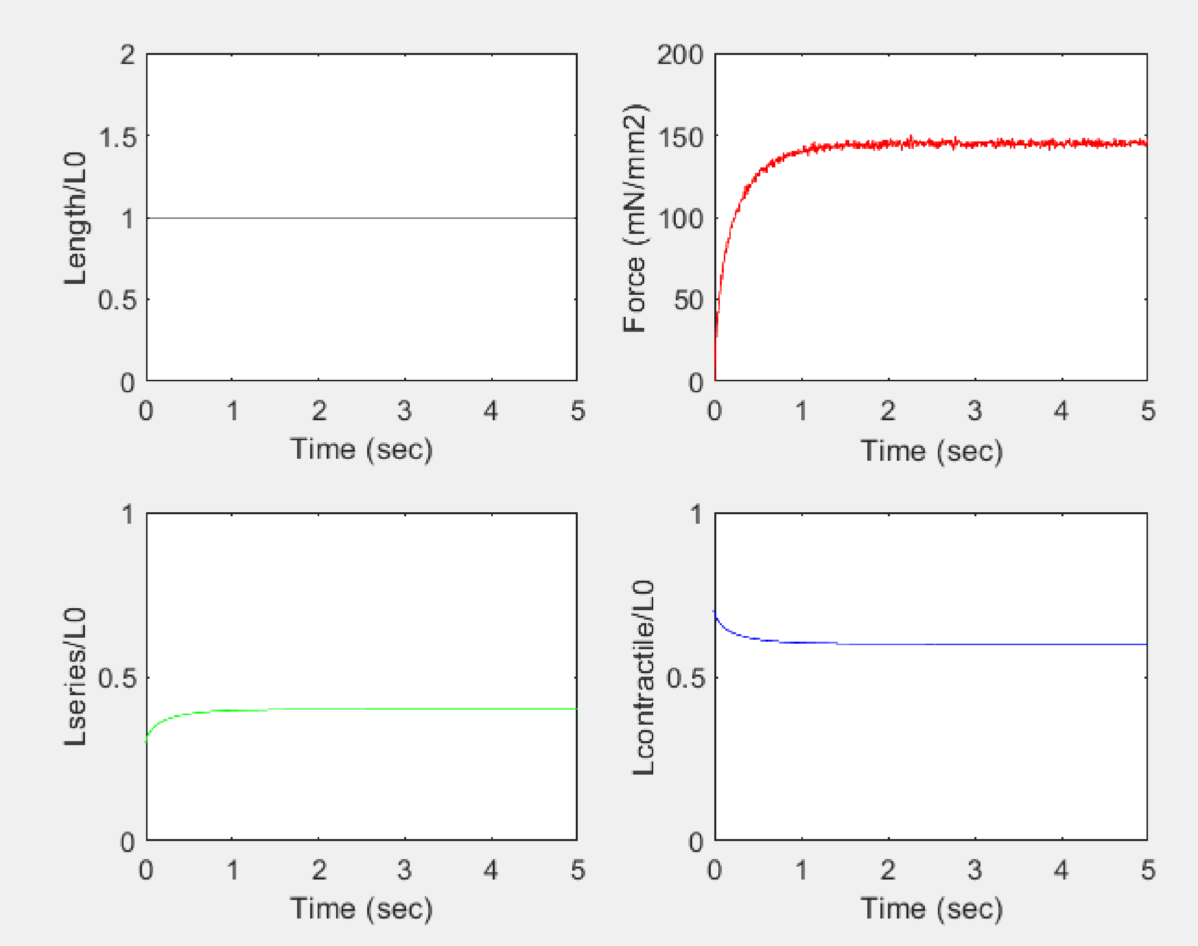


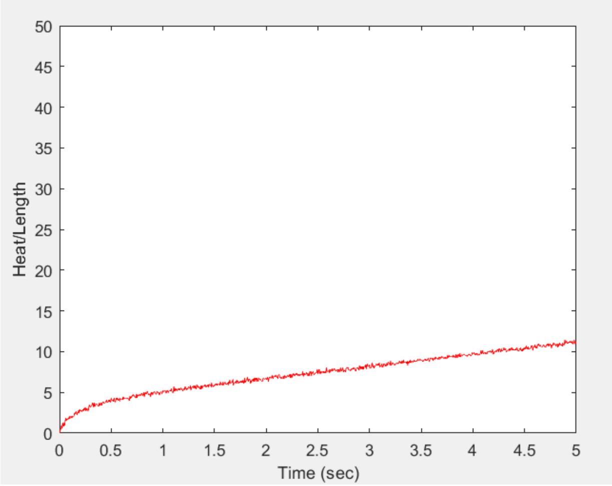
- During isometric contraction, the total length remains constant.
- The contractile element can only shorten by stretching the elastic element (in order to keep total L=const)
- To stretch the elastic element further, the contractile element must generate more and more force.
- Therefore, as Lce decreases and Lse increases, P rises.

1) Force is the same in the contractile and elastic elements because they are in series
2) Force in the elastic element is proportional to stretch

1. Response of Hill's model to isometric tetanus

```
% EXAMPLE 1: Response of Hill's model to isometric tetanus
L = ones(1000,1);          % Isometric length, (constant = 1 unit)
t = linspace(0,5,1000)';   % Time (0-5seconds)
[P,H,Lse,Lce] = hill(L,t); % Compute P,H,Lse,Lce over time

figure(1)
subplot(2,2,1);
plot(t,L,'k'); axis([0 5 0 2]); xlabel('Time (sec)'); ylabel('Length/L0');
subplot(2,2,2);
plot(t,P,'r'); axis([0 5 0 200]); xlabel('Time (sec)'); ylabel('Force (mN/mm2)');
subplot(2,2,3);
plot(t,Lse,'g'); axis([0 5 0 1]);xlabel('Time (sec)'); ylabel('Lseries/L0');
subplot(2,2,4);
plot(t,Lce,'b'); axis([0 5 0 1]); xlabel('Time (sec)'); ylabel('Lcontractile/L0');

figure(2)
plot(t,H,'r');axis([0 5 0 50]); xlabel('Time (sec)'); ylabel('Heat/Length');
```





2. Simulation of a step decrease in length imposed on a tetanized muscle

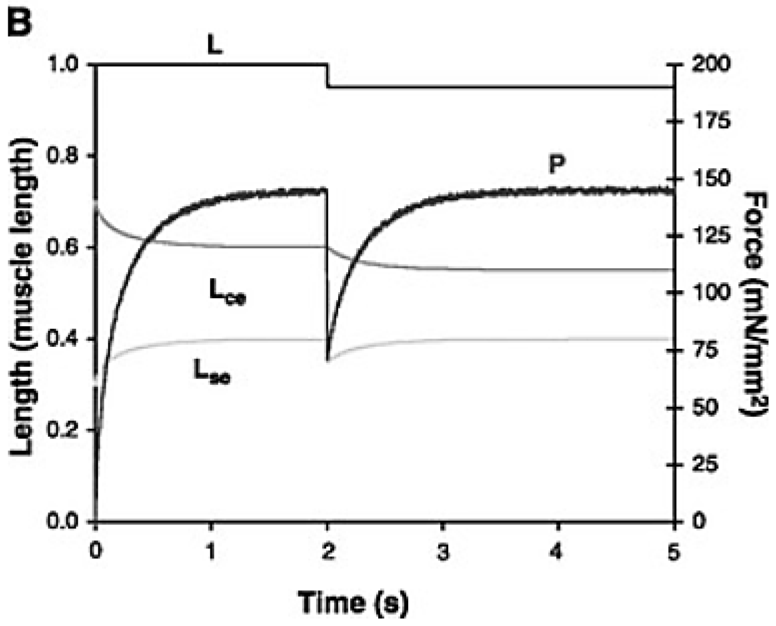
If the activated model is then subjected to a sudden change in length,

$$dL/dt = dL_{ce}/dt + dL_{se}/dt = v_{ce} + dL_{se}/dt \qquad (2A)$$

$$dP/dt = \alpha dL_{se}/dt \qquad (2B)$$

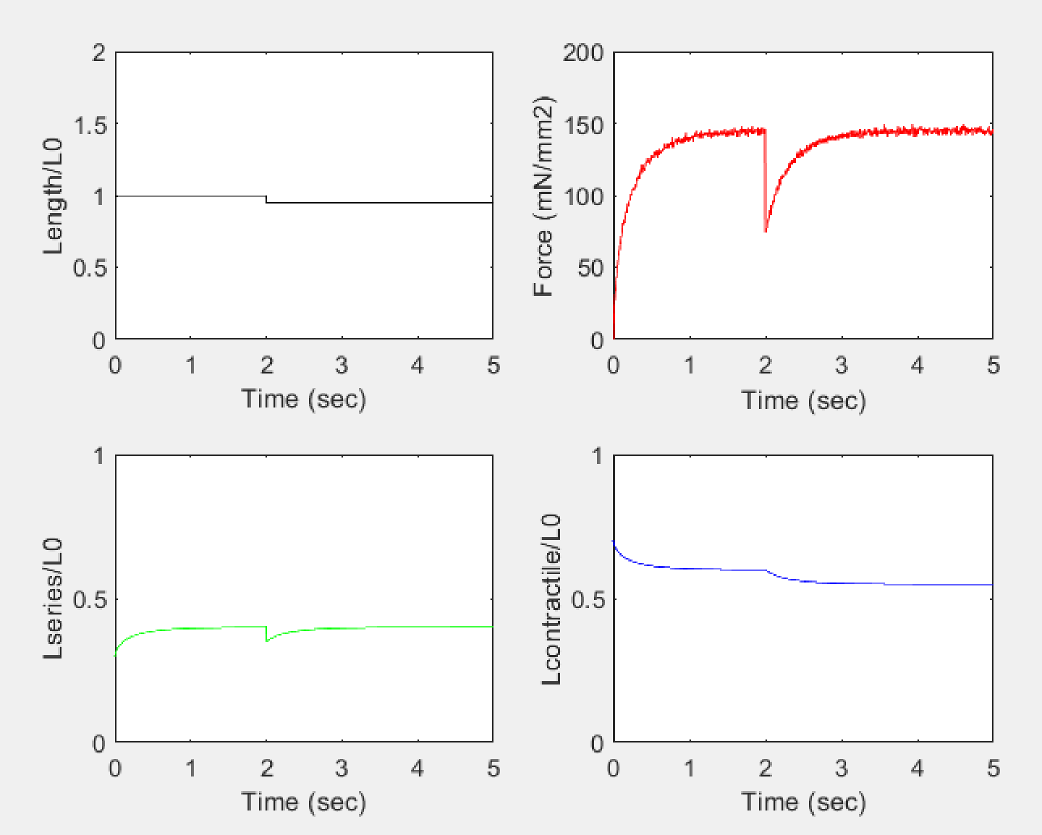
vce is the shortening velocity of the contractile element.

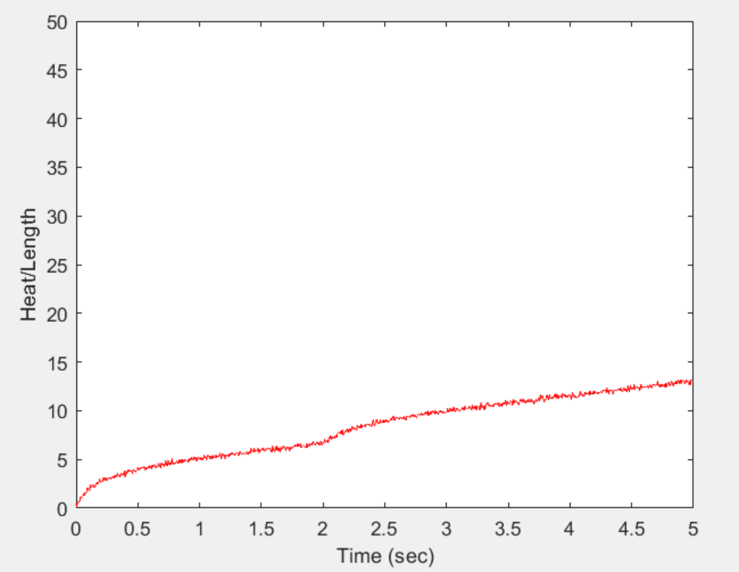
- For a sudden step decrease in length (dL/dt < 0), The contractile element has a limited maximal shortening velocity which implies that the drop is absorbed primarily by the series elastic element, with a resulting immediate drop in force.
- The force then recovers as the series element is gradually re-stretched by the contractile element.



2. Simulation of a step decrease in length imposed on a tetanized muscle

```
% EXAMPLE 2: Simulation of a step decrease in length imposed on a tetanized muscle
L = [ones(400,1); ones(600,1)*0.95];    % Step decrease in length from 1 unit to 0.95units
t = linspace(0,5,1000)';                % Time (0-5seconds)
[P,H,Lse,Lce] = hill(L,t);              % Compute P,H,Lse,Lce over time

figure(3)
subplot(2,2,1); plot(t,L,'k'); axis([0 5 0 2]); xlabel('Time (sec)'); ylabel('Length/L0');
subplot(2,2,2); plot(t,P,'r'); axis([0 5 0 200]); xlabel('Time (sec)'); ylabel('Force (mN/mm2)');
subplot(2,2,3); plot(t,Lse,'g'); axis([0 5 0 1]);xlabel('Time (sec)'); ylabel('Lseries/L0');
subplot(2,2,4); plot(t,Lce,'b'); axis([0 5 0 1]); xlabel('Time (sec)'); ylabel('Lcontractile/L0');

figure(4)
plot(t,H,'r');axis([0 5 0 50]); xlabel('Time (sec)'); ylabel('Heat/Length');
```



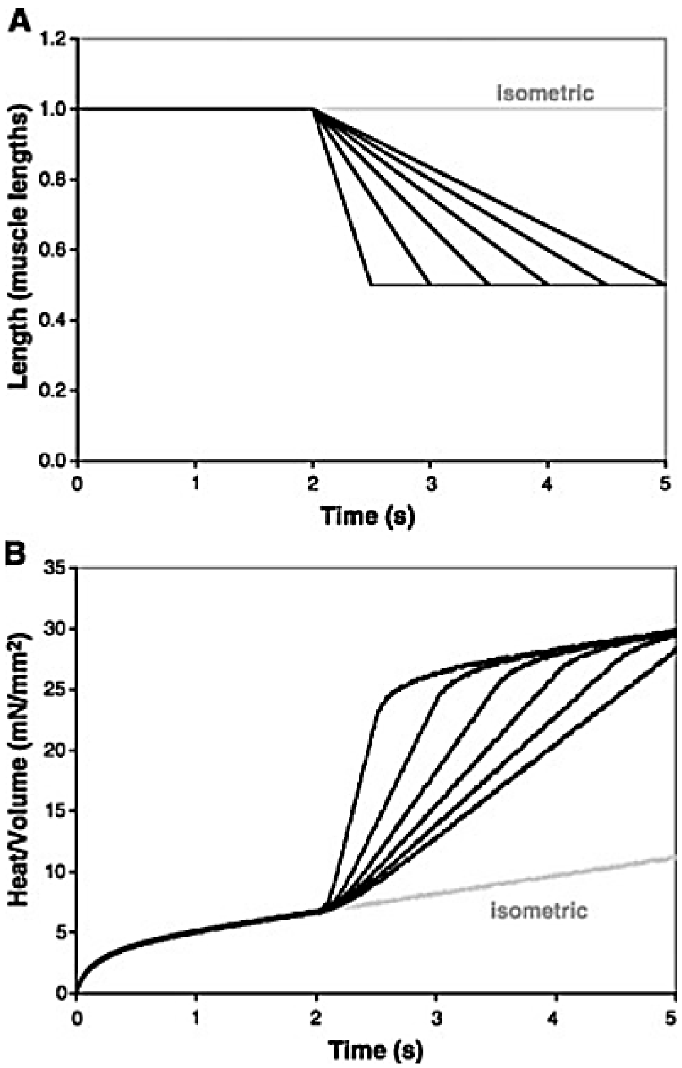


3. Dependence of rate and amount of heat liberation on the rate and distance of shortening.

- <u>Amount of excess heat</u> liberated as a result of shortening depends only on the amount shortened, not on the rate of shortening ‘v’.

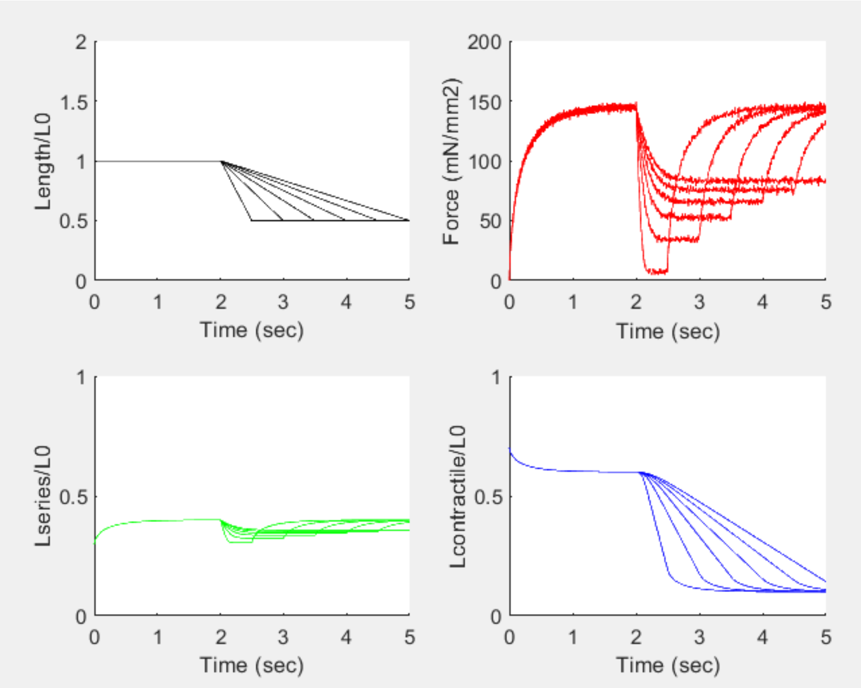
- However, <u>rate of increase in heat</u> is dependent on the velocity of shortening.

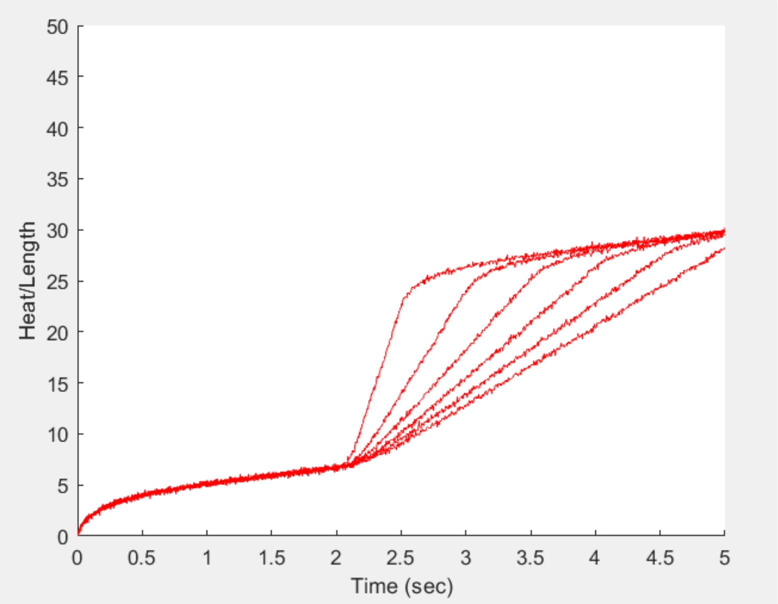
- For a more rapid change in shortening, the rate of increase in heat is more rapid (slope of the heat vs time is greater), for a brief period, before leading to saturation.



3. 1. Dependence of rate and amount of heat liberation on the rate of shortening.

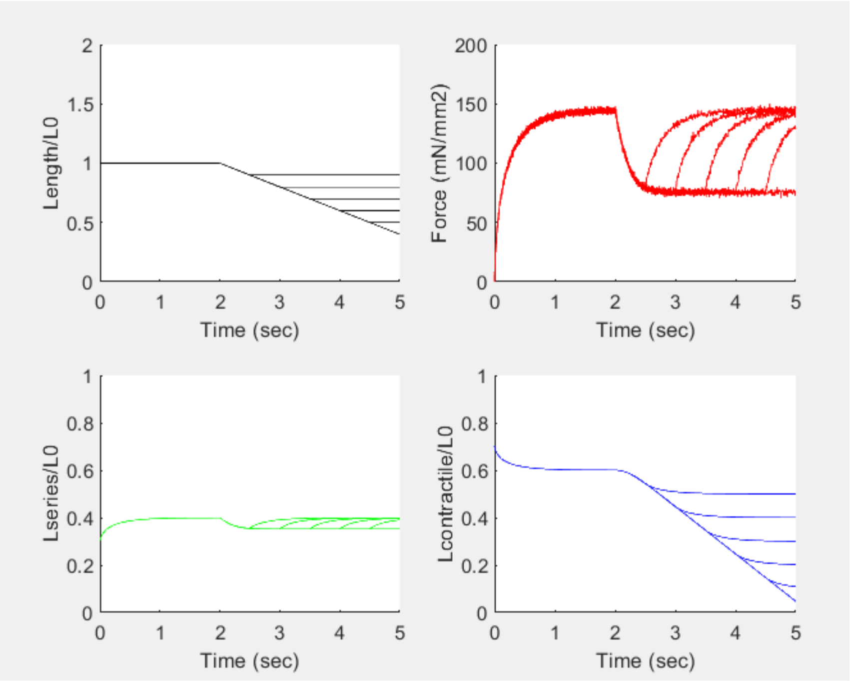
```
% EXAMPLE 3 - Dependence of rate and amount of heat liberation on the
%             rate of shortening.

for i = 1:6        % Generating 6 different rates of decrease in length
    ts = 100*i;
    L = [ones(400,1);linspace(1,0.5,ts)';repmat(0.5,(600-ts),1)];
    t = linspace(0,5,1000)';      % Time (0-5seconds)
    [P,H,Lse,Lce] = hill(L,t);    % Compute P,H,Lse,Lce over time

    figure(1)
    subplot(2,2,1); hold on;
    plot(t,L,'k'); axis([0 5 0 2]); xlabel('Time (sec)'); ylabel('Length/L0');
    subplot(2,2,2); hold on;
    plot(t,P,'r'); axis([0 5 0 200]); xlabel('Time (sec)'); ylabel('Force (mN/mm2)');
    subplot(2,2,3); hold on;
    plot(t,Lse,'g'); axis([0 5 0 1]);xlabel('Time (sec)'); ylabel('Lseries/L0');
    subplot(2,2,4); hold on;
    plot(t,Lce,'b'); axis([0 5 0 1]); xlabel('Time (sec)'); ylabel('Lcontractile/L0');

    figure(2)
    hold on; plot(t,H,'r');axis([0 5 0 50]); xlabel('Time (sec)'); ylabel('Heat/Length');
    input('')      %Press enter
end
```

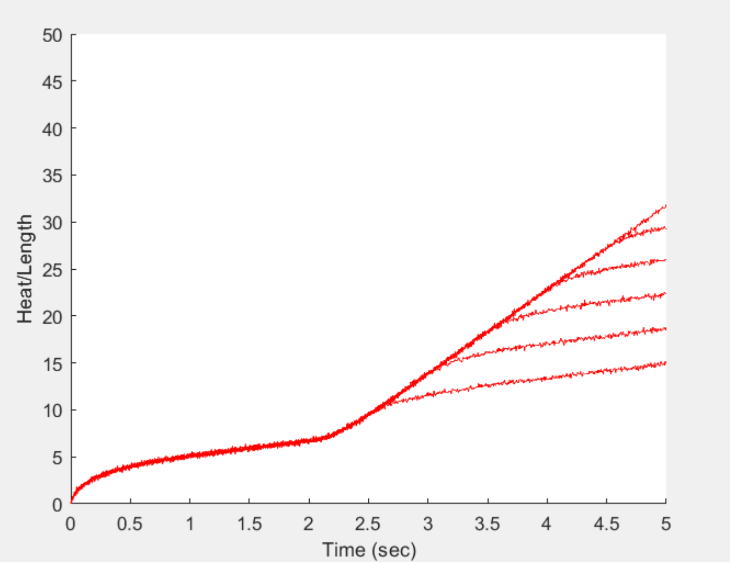




3. 2. Dependence of rate and amount of heat liberation on the distance of shortening.

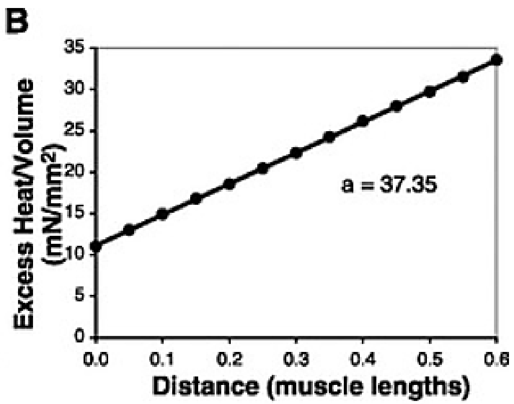
```
% EXAMPLE 4 - Dependence of rate and amount of heat liberation on the
%             distance of shortening.

for i= 0:5          % Generating 6 different final lengths with constant rate of decrease
    Lf = 0.9 - 0.1*i;
    ts = fix((1-Lf)*1000);
    L = [ones(400,1); linspace(1,Lf,ts)';repmat(Lf,(600-ts),1)];
    t = linspace(0,5,1000)';          % Time (0-5seconds)
    [P,H,Lse,Lce] = hill(L,t);        % Compute P,H,Lse,Lce over time

    figure(1)
    subplot(2,2,1); hold on
    plot(t,L,'k'); axis([0 5 0 2]); xlabel('Time (sec)'); ylabel('Length/L0');
    subplot(2,2,2); hold on
    plot(t,P,'r'); axis([0 5 0 200]); xlabel('Time (sec)'); ylabel('Force (mN/mm2)');
    subplot(2,2,3); hold on
    plot(t,Lse,'g'); axis([0 5 0 1]);xlabel('Time (sec)'); ylabel('Lseries/L0');
    subplot(2,2,4); hold on
    plot(t,Lce,'b'); axis([0 5 0 1]); xlabel('Time (sec)'); ylabel('Lcontractile/L0');

    figure(2)
    hold on; plot(t,H,'r');axis([0 5 0 50]); xlabel('Time (sec)'); ylabel('Heat/Length');
    input('')      %Press enter

end
```





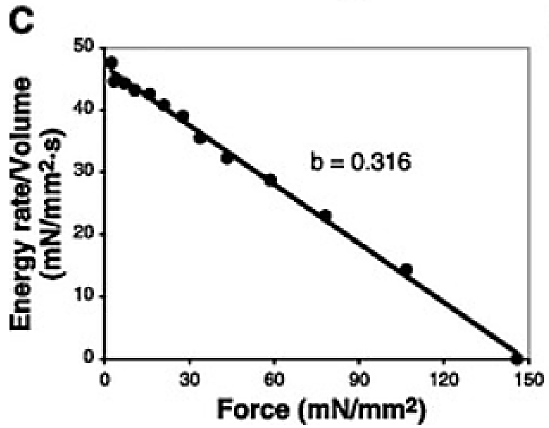
Constant a is defined as the slope of the relationship between the amount of shortening x and the amount of associated excess heat

$$\text{Shortening heat} = ax \qquad (3)$$



Excess energy released during shortening:
The mechanical work performed is force times distance;
The additional energy released beyond that of an isometric contraction is the mechanical work plus the extra heat liberated.

$$\text{Excess energy liberated} = Px + ax = (P + a)x \qquad (4)$$



Hill found experimentally that if he plotted the rate of excess energy liberation for muscles shortening at a constant load (P and a constant) against the amount of load, he obtained a straight line.
He defined constant b as the slope of the relationship between the excess energy rate and steady-state force P.

$$\begin{aligned}\text{Excess energy rate} &= (P + a)dx/dt = (P + a)v \\ &= -bP + c\end{aligned} \qquad (5)$$

Because the excess heat of shortening must be zero when there is no shortening (during an isometric contraction), c must equal bP0, where P0 is the force generated by an isometric contraction. Incorporating this fact and rearranging the equations yields the famous Hill equation.

$$(P + a)v = -b(P - P_0) \text{ or } (P + a)(v + b) = (P_0 + a) = \text{constant} \quad (6)$$

The last equation describes the classic hyperbolic force-velocity relationship of muscle, but was discovered based on considerations of energy liberation.

- Hill's equation demonstrates that the relationship between F and v is hyperbolic.
- Higher the load applied to the muscle, the lower the contraction velocity.
- Similarly, higher the contraction velocity, the lower the tension in the muscle.