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Hill's Model for Muscle Physiology and Biomechanics

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Synonyms

Hill's model; MATLAB; Muscle

Definition

Computational models of muscles serve as important tools to understand the musculoskeletal physiology and biomechanics. Such models have been widely implemented in a variety of simulation platforms and incorporate varying degrees of physiological details. This entry summarizes a simplified two-component biomechanical muscle model, first described by A. V. Hill in 1938, popularly known as the *Hill's muscle model*. The Hill's model provides thermodynamically constrained quantitative relationships between muscle length, shortening velocity, force, and heat released during a muscle contraction. The model description, simulations, and MATLAB script provided here highlight the computational features of the Hill's muscle model.

Detailed Description

Biomechanical Components of Muscle Force Generation

Muscle cells contract to produce movement. During a contraction, the shortening of a muscle cell results in tension or force production. The basic structural components involved in force production consist of a *series elastic element* and a *contractile element*. The series elastic element is composed of tendons and aponeurosis. Tendons are tough extensions of the muscles, and aponeurosis is thin sheets of tissue that attach the muscle to the bone. The contractile element is composed of sarcomeres which consist of thin actin filaments and thick myosin filaments. The sarcomeres form subunits called myofibrils which are long filaments bundled into muscle fibers (see Fig. 1). The myosin heads of the thick filament form crossbridges with the adenosine triphosphate (ATP) binding sites on the thin actin filaments. To produce force in the muscle cell, the filaments slide past each other when bound to ATP. More details on muscle biology, molecular mechanisms, and dynamics of force generation can be found in (Enoka and Pearson 2013).

In his seminal paper (1938), A.V. Hill details his extensive experiments measuring the length, velocity, force, and the energy released during

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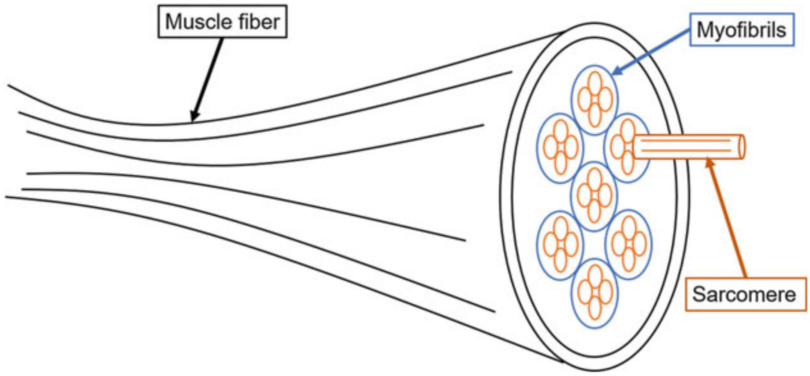


Hill's Model for Muscle Physiology and Biomechanics, Fig. 1 Structural components of a muscle. Schematic illustrating the main structural components of a muscle

muscle contractions (Hill 1938). Based on such physiological measures, Hill proposed a mathematical relationship between energy, force, and velocity of muscle shortening/lengthening (also see (Holmes 2006)). It is noted that the details of muscle biology were unknown at that time.

Model Description

A Two-Component Biomechanical Model for Force Production

A highly simplified biomechanical muscle model conceived by A.V. Hill consists of series elastic and contractile elements as shown in Fig. 2.

The series elastic element is assumed to be a spring-like structure with length, L_{se}, and the length of the contractile element is given by L_{ce} such that, the total muscle length, L, is:

$$L = L_{ce} + L_{se}$$

During an isometric contraction, the L_{ce} gradually reduces to mimic shortening of the contractile element. In parallel, the L_{se} gradually increases (muscle stretch), to account for the constant muscle length. The contraction force of L_{ce} is exactly the same as the stretching force of L_{se}. Such a force, P is assumed to be proportional to the stretch in L_{se} (Hooke's Law) as given below (also see Loiselle et al. 2008).

$$P = \alpha(L_{se} - L_{se}(0))$$

where α is the spring contant and $L_{se}(0)$ is the length of the series elastic element before the contraction. The rate of change in L is therefore:

$$\frac{dL}{dt} = \frac{dL_{ce}}{dt} + \frac{dL_{se}}{dt} = v_{ce} + \frac{dL_{se}}{dt}$$

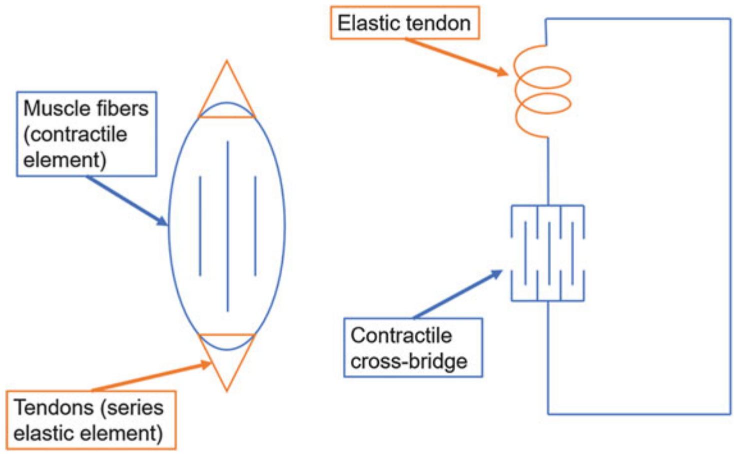
where v_{ce} is the shortening velocity of the contractile element. Similarly, the rate of change of P is given by:

$$\frac{dP}{dt} = \alpha\frac{dL_{se}}{dt}$$

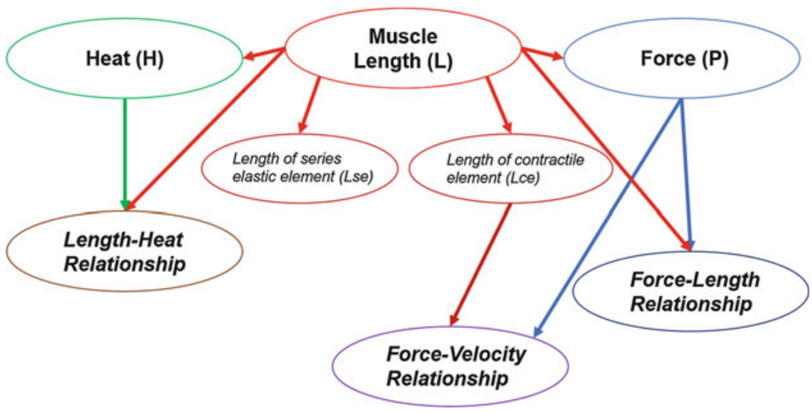
From the above, it is noted that during length changes, the force P responds to length change primarily in L_{se}. For isometric contractions, in which the total muscle length is held constant, the contractile element subsequently readjusts to restore the L_{se} and therefore the force, P.

Heat Released and Force-Velocity Relationship

The original formulation for the force-velocity relationship given by A.V. Hill was based on the measurements of heat released during muscle shortening. The heat released depends on the distance (x) and velocity (v) of shortening. To measure these relationships, Hill's experiments consisted of testing the effect of different shortening velocities on the heat released during shortening. To achieve a consistent initial condition, he began at the tetanic force, P_0, during an isometric contraction and subsequently measured the heat released during muscle shortening for varying loads (P) (also see Figs. 4, 5, and 6). The heat released during muscle shortening is given as ax,



Hill's Model for Muscle Physiology and Biomechanics, Fig. 2 Biomechanical components of a muscle. A schematic showing the biomechanical equivalence of the structural components of a muscle



Hill's Model for Muscle Physiology and Biomechanics, Fig. 3 A flow chart of the computational steps of Hill model. The model input is the assumed muscle length (L), and outputs include lengths of the series elastic and contractile elements, velocity, force, and heat released. The ovals indicate computational steps

g.cm, where *a* was experimentally determined to be a constant and has the unit of force. Next, if *P g* of load is lifted by the muscle, the work done is given as *Px*, *g.cm*.

The total energy in excess of the isometric contraction is given as:

$h = (P + a)x$, in *g. cm*

The rate of change in energy is therefore written as:

$$\frac{dh}{dt} = (P + a)\frac{dx}{dt} = (P + a)v$$

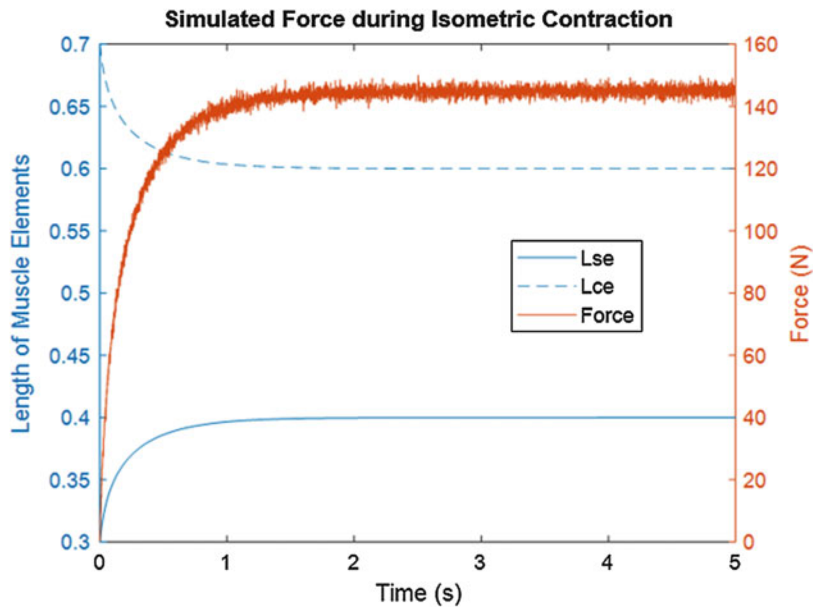
Experimentally, Hill found that this rate of change of energy release increased linearly as the load, *P*, diminished such that it was zero when $P = P_0$. This relationship is known as the famous Hill equation and relates the rate of heat released during muscle shortening to the corresponding load/force, as given below:

$$(P + a)v = b(P - P_0)$$

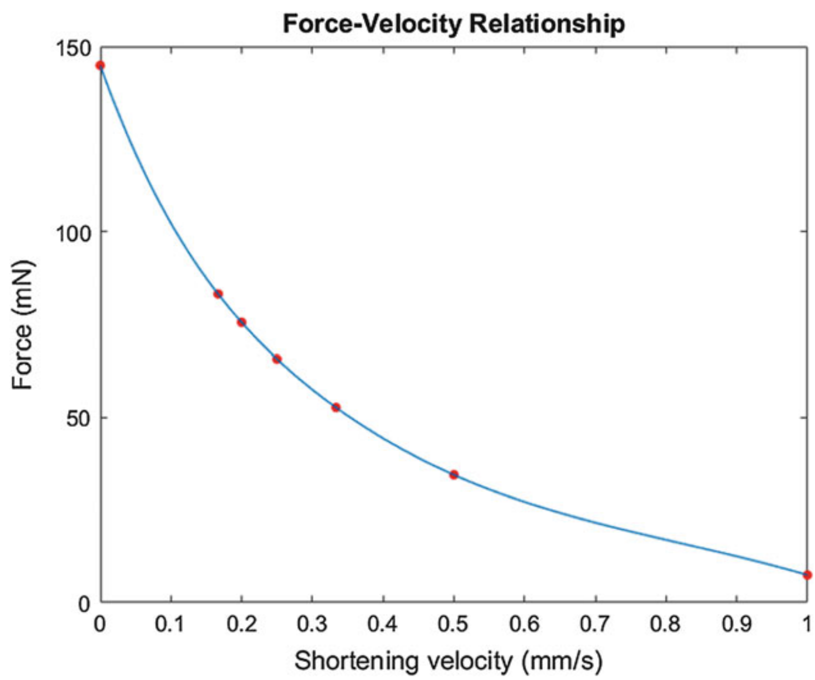
where *b* is the slope of the above linear relationship. The constant *b* is defined as the absolute rate of energy liberation.

Model Simulations

Figure 3 illustrates a flow diagram of the computational steps of the two-component biomechanical muscle model. The changes in muscle length (*L*) are translated into force (*P*) and heat production (*H*). The model reproduces known physiological relationships between these quantities. The description here is restricted to isometric conditions where the muscle length is held



Hill's Model for Muscle Physiology and Biomechanics, Fig. 4 Force-Length Relationship. In the above simulation, L_{se} was set to 30 % of the total muscle length, L. The simulation included motor noise in order to more realistically model physiological force production

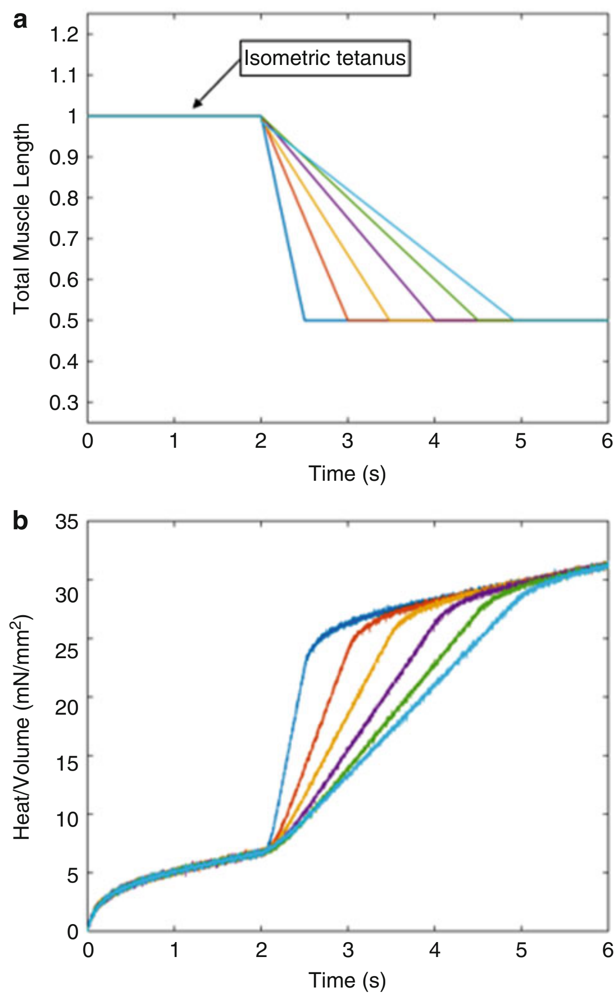


Hill's Model for Muscle Physiology and Biomechanics, Fig. 5 Relationship between force and shortening velocity. Red circles show the steady-state force for different values for shortening velocity in individual simulations. The blue line shows a regression fit highlighting an inverse force-velocity relationship

constant to generate a corresponding steady-state force.

Force-Length Relationship

Figure 4 illustrates the force generation during an isometric contraction. In this simulation experiment, the initial length L_{se} is set 30% of the total length L at rest, such that the L_{ce} is at 70% of L; note that the force is zero. To mimic muscle shortening during an isometric contraction, the value of L_{ce} is reduced to 60% of L. Note that this change in length is not



Hill's Model for Muscle Physiology and Biomechanics, Fig. 6 Force-Velocity and Length-Heat Relationships. (**a**). The muscle was held in isometric tetanus for 2 s, after which it was subject to different shortening velocities. From right to left, the shortening velocities shown are 1 mm/s, 0.50 mm/s, 0.33 mm/s, 0.25 mm/s, 0.20 mm/s, and 0.17 mm/s. After undergoing a period of shortening, all of the simulations ended at the same final length, which was ½ of the original length of the muscle at isometric tetanus. (**b**) The heat released by the muscle for the different shortening velocities in (**a**) is plotted (heat responses are color matched with traces in **a**). Over shorter periods of shortening, the rate of energy released is higher or reaches the maximal level more quickly; for this simulation, the end length was the same and notes that the energy released at the end of shortening is the same across all trials

instantaneous but has an initial transitory phase as L_{ce} shortens and L_{se} increases to ensure L is constant. Correspondingly, the force, P, increases. After stabilization of L_{ce} and L_{se}, the force P saturates at the steady-state value of the isometric contraction. A white noise was added to the force function in these simulations to match realistic conditions.

Force-Velocity Relationship

Hill empirically demonstrated that when held at the tetanic condition during an isometric contraction, subsequent increases in muscle load, P, decreased the shortening velocity, v, of the muscle over a distance, x, cm. Such experiments can be simulated in the model to reproduce this force-velocity relationship. As shown in Fig. 5, beginning at an isometric force of 150 mN, the shortening velocity, v mm/s, was changed from a value 0 to 1 in repeated simulations to compute the resulting steady-state force. This inverse force-velocity relationship is summarized by an exponential regression fit as shown in the figure.

Length-Heat Relationship

Hill demonstrated that the heat released during muscle shortening is independent of the shortening velocity. This critical aspect on the thermodynamics of isometric contraction is illustrated by the simulations in Fig. 6. The muscle model was released from an isometric tetanus at 2 s and was subject to different shortening velocities as shown in Fig. 6a. The corresponding heat liberated as shown in Fig. 6b depends only on the shortening distance x (here, $x = 0.5$ mm) and not on the shortening velocity. Specifically the total amount of heat released due to muscle shortening was the same across all of the simulations, despite varying shortening velocities. These results demonstrate that the shortening distance x is a crucial determinant of the energy released by the muscle. When held in completely isometric conditions, the energy released is zero because there is no change in distance.

Conclusion

Computational models of muscles help explain the principles of muscle physiology and force generation. The Hill model described here offers insights into the relationships between muscle length, force, velocity, and heat released based on the classic experiments by A. V. Hill (1938). The model is useful to begin understanding the quantitative aspects of muscle physiology and biomechanics.

Cross-References

► Muscle Physiology and Modeling

Appendix

Model Implementation Using MATLAB

```
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%      Hill Muscle Model       %%%%%
%%%%%    Jakob von Morgenland      %%%%%
%%%%%   The Hill Muscle Model and its
Implementation (JVM and SV)    %%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
```

Preparing Inputs for the Hill Function

```
t=0:0.001:5;
% time from 0 to 5 seconds with 0.001
time step
L=ones(length(t),1);
% initializing length of muscle to 1
L2=ones(length(t),1);
m=[-1,-0.5,-1/3,-0.25,-0.2,-1/6]
% theoretical slopes for linear
velocity equations
yint=[3,2,1.66,1.5,1.4,1.32]
% calculated y-intercepts for linear
velocity equations
vel=[1,0.5,1/3,0.25,0.2,1/6,0]
% theoretical velocity values derived
from slope calculations
% not used in rest of simulation,
included for reference for force-
velocity graph
force=[7.437,34.51,52.68,65.71,
75.52,83.16,144.9]
% calculated force values derived from
simulations using theoretical velocity
values
```

Input-Output Relationship for Hill Model

```
[P,H,Lse,Lce] = hill(L,t);
% Inputs = muscle length (L) and time (t)
% Outputs = force (P), heat (H), and the
individual element lengths (Lce and Lse)
```

For Loop to Determine Force-Velocity Relationship

```
for j = 1:length(m)
    for i = 1:length(t)-1
        if t(i)<2
            L2(i)=1;
        else
            if t(i)>= 2
               L2(i)=yint(j)+m(j)*t(i);
            end
        end
        if L2(i) < 0.5
            L2(i)=0.5;
            i=length(t);
        end
    end
    [P2,H2,Lse2,Lce2] = hill(L2,t);
    Pss(j)=P2(length(t)-1);
end
```

Hill Function

```
function [P,H,Lse,Lce] = hill(L,t)
```

Model Parameters

```
a = (380*.098);    % shortening and heat
excess proportionality constant
b = 0.325;   % excess energy and steady-
state force proportionality constant
P0 = a/0.257;    % initial force in
isometric contraction
alpha = P0/0.1;   % spring constant for
series elastic element
Lse0 = 0.3;   % initial length of the
series elastic element
k = a/25;   % heat production constant
```

Initialize Arrays for Outputs

```
Lse = zeros(length(t),1);
Lce = zeros(length(t),1);
Lse(1,:) = Lse0;
Lce(1,:) = 1-Lse0;
H = zeros(length(t),1);
P = zeros(length(t),1);
```

Solver for Length Input into Hill Model

```
for j = 2:(length(t))
    dt = (t(j)-t(j-1));
    dL = (L(j)-L(j-1));
    dP = alpha*((dL/dt)+b*((P0-P(j-1))/
(a+P(j-1))))*dt;
    P(j) = P(j-1)+dP;
    H(j) = H(j-1)+(k+a*b*((P0-P(j-1))/
(a+P(j-1))))*dt;
    Lse(j) = Lse0+P(j-1)/alpha;
    Lce(j) = L(j)-Lse(j);
end
```

Creates Noise for More Realistic Output

```
for i = 1: length(H)
     H(i) = H(i)+(k/10)*randn(1);
     P(i) = P(i)+(P0/100)*randn(1);
end
end
```

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Further Reading

Nature-Springer Encyclopedia of Neuroscience