Modeling Fast and Slow Twitch Skeletal Muscle Contractile Behavior Using the Hill Muscle Model

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Abstract

Skeletal muscle exhibits characteristic mechanical and energetic behaviors that differ substantially across fiber types. Slow-twitch fibers, such as those found in the soleus, are fatigue-resistant and mechanically economical, whereas fast-twitch fibers, such as those in the extensor digitorum longus (EDL), are capable of rapid shortening and high-power output. Quantitative modeling provides a means of capturing these distinctions and explaining how fundamental properties such as force–velocity behavior, series elasticity, and heat production emerge from underlying contractile mechanisms. In this study, the classical Hill muscle model was implemented and analyzed to simulate the behavior of slow and fast muscle fibers and to determine whether the model, when appropriately parameterized, can reproduce experimentally observed differences reported in Barclay's 1993 study. The governing equations of the Hill model were derived in full, including the hyperbolic force–velocity relation, the dynamics of the series elastic element, and the formulation of heat production during isometric and shortening contractions. These equations were implemented computationally and used to simulate isometric tetanus, constant-velocity shortening, and steady-state force–velocity and power–velocity relationships. Model parameters were tuned based on Barclay's experimental measurements of maximal tetanic force, the constants $a$and $b$of the Hill equation, the maximum shortening velocity, and isometric heat rates in mouse soleus and EDL. The resulting simulations produced force–velocity and power–velocity curves that closely resemble the normalized relationships published by Barclay and reproduced the markedly different heat production slopes between fiber types. The results demonstrate that the Hill model, despite its phenomenological simplicity, can be parametrically aligned with experimental data to differentiate slow and fast skeletal muscle behavior. This work illustrates the value of classical modeling approaches for gaining quantitative insight into muscle physiology and for connecting simulation results to empirical findings.

I. Objectives and Scope

The purpose of this project is to investigate whether the classical Hill muscle model can accurately represent the distinct contractile behaviors of slow-twitch and fast-twitch skeletal muscle fibers. Although the Hill model is nearly a century old, it remains a central tool in muscle biomechanics because it captures essential features of muscle contraction through a small number of interpretable parameters. Here, the model is treated not merely as a historical formulation but as a quantitative framework that can be adapted and validated against modern physiological data. The central objective of this work is to determine whether parameter tuning enables the Hill model to reproduce the experimentally measured mechanical and energetic performance of mouse soleus and EDL muscles documented in Barclay (1993) study[1]. This involves two complementary aims: first, to derive and implement the governing equations of the contractile and elastic components of muscle, and second, to adjust model parameters so that the simulations align with experimental force–velocity curves, power output, and heat production rates. By approaching the problem from a model-building and validation perspective, the project integrates physiological interpretation with quantitative simulation. The scope of the work includes derivation of the mathematical framework, implementation of numerical simulations, and direct comparison with experimental measurements. The analysis is limited to steady-state behavior under maximal activation, as this was the condition under which Barclay obtained his measurements. Activation dynamics, cross-bridge kinetics, and fatigue mechanisms are intentionally excluded to maintain consistency with the original Hill formulation and with the experimental dataset used for validation.

II. Background and Context

Skeletal muscle exhibits a remarkable heterogeneity in its mechanical, biochemical, and energetic properties, arising from distinct molecular specializations that define slow-twitch (Type I) and fast-twitch (Type II) muscle fibers. Although both fiber types rely on the same fundamental actomyosin crossbridge cycle, their contractile kinetics, calcium handling dynamics, mitochondrial energetics, and thermodynamic efficiencies diverge in ways that have profound consequences for force production and mechanical performance. Any quantitative model of muscle must therefore be able to represent these divergent behaviors in a principled and physiologically meaningful manner. The conceptual foundation for modern muscle modeling originates from A. V. Hill's seminal experiments on the heat of shortening and the dynamic constants of muscle[2]. Hill demonstrated that force and shortening velocity are linked by a hyperbolic relation and that muscle liberates additional heat when it shortens—findings that established the first quantitative description of muscle contraction. These experiments not only yielded the phenomenological "Hill equation" but also provided a thermodynamic framework that prefigured later biophysical theories of crossbridge interaction. Subsequent reinterpretations of Hill's work, have underscored the model's enduring value[3]: it offers a simplified yet surprisingly faithful description of muscle mechanics across species, temperatures, and fiber types. The slow–fast dichotomy central to vertebrate muscle physiology emerges from well-characterized molecular differences. Slow-twitch fibers express myosin isoforms with slower ATPase kinetics and display tight metabolic coupling to oxidative phosphorylation. This metabolic profile is supported by dense mitochondrial networks whose regulatory behavior has been quantified, demonstrating that slow muscle possesses a far lower apparent Km for ADP and correspondingly higher sensitivity of respiration to work demand[4]. Fast-twitch fibers, conversely, utilize myosin isoforms with high detachment rates and elevated ATPase activity, enabling rapid contraction at the cost of lower economy. These kinetic differences are reinforced by fiber-specific calcium handling characteristics: studies have shown that fast fibers exhibit accelerated SR Ca^{2+} release and uptake, allowing them to attain greater shortening velocities and more rapid force transients[5]. Energetically, slow and fast fibers differ in both their isometric heat production and their mechanical efficiency. Experimental work in amphibian and mammalian muscle, has demonstrated that fast fibers dissipate substantially more heat during both shortening and isometric contraction, reflecting their higher ATP turnover per unit force[6]. These distinctions are corroborated in mammalian muscle[1] , which shows that slow fibers operate with greater efficiency under isometric and low-velocity conditions, whereas fast fibers achieve substantially higher peak mechanical power. Despite the complex biochemical and molecular determinants underlying these behaviors, the macroscopic consequences differences in P_0, shortening velocity, curvature of the force–velocity relationship, mechanical power, and heat production, can be effectively represented using the Hill model. Its empirical parameters map naturally onto fiber-specific physiological features: the constant b reflects differences in maximal shortening velocity; the ratio a/P_0 captures fiber-dependent curvature in the force–velocity relation; and the heat constant encodes differences in energetic economy. The Hill model therefore provides an analytically tractable and physiologically interpretable framework for synthesizing these diverse experimental observations into a coherent description of fast and slow muscle behavior.

III. Existing Data and Literature Evidence

A substantial body of experimental work supports the quantitative distinctions between slow- and fast-twitch muscle fibers and provides the empirical foundation required to parameterize and validate a Hill-type model. Many of the most detailed mechanical measurements originate from isolated muscle preparations subjected to controlled shortening protocols. The classical force–velocity and heat-of-shortening relationships were first characterized by Hill's 1938[2], which established the empirical hyperbola and demonstrated that heat liberation increases in proportion to shortening velocity. These observations underpin the Hill model's differential equation for contractile dynamics and remain consistent across fiber types and species. More recent and fiber-type-specific measurements have been documented in mammalian muscle. A comprehensive mechanical and energetic comparison appear in [1] where mouse soleus and EDL muscles were evaluated under conditions of maximal activation. This study provides quantitative values for key parameters—including maximal isometric stress, Hill constants a and b, maximal power output, and isometric heat rate—that directly inform the selection of parameter values for computational modeling. Its force–velocity and power–velocity curves serve as canonical benchmarks for distinguishing slow and fast fibers. Additional evidence regarding mechanical function and intracellular calcium handling is provided [7], which demonstrates that fast fibers exhibit more rapid Ca^{2+} release and reuptake kinetics and a steeper relationship between stimulation frequency and force development. These properties correlate directly with their higher maximal shortening velocities and greater mechanical power output. The role of SR calcium release kinetics in shaping twitch and tetanus characteristics is further delineate, which shows that fast fibers achieve rapid activation through accelerated Ca^{2+} flux[8]. Energetic distinctions are equally well supported by mitochondrial studies. Slow-twitch fibers operate with tighter coupling between oxidative phosphorylation and ATP demand[4]. The much lower ADP activation threshold observed in slow fibers explains their reduced isometric heat production and higher energetic economy. Complementary thermodynamic findings reinforce that higher shortening velocities and faster crossbridge cycling in fast fibers produce proportionally higher heat liberation[6]. Several additional studies contribute mechanistic insight into fiber-type specialization[4,6,9,10]. Collectively, these works demonstrate that molecular properties—myosin isoform expression, crossbridge cycling rate, SR kinetics, mitochondrial regulation—manifest in reproducible, fiber-specific macroscopic behaviors that can be captured by a phenomenological model equipped with a small number of appropriately interpreted parameters. The consistency and breadth of these experimental findings across species and methodologies provide strong justification for using the Hill model to simulate slow- and fast-twitch muscle. They also supply the quantitative data required for model parameterization and validation. Together, they form the empirical backbone supporting the computational analyses and simulations developed in this project.

IV. Quantitative Analysis and Methods

A. Hill Muscle Model

The classical Hill muscle model provides a phenomenological yet remarkably effective framework for describing the mechanical behavior of skeletal muscle under maximal activation. Originally proposed by A. V. Hill (1938)[2], the model captures essential aspects of muscle contraction—including the well-known hyperbolic force–velocity relationship, the elastic behavior of tendon-like structures, and the energetic consequences of shortening—through a small number of interpretable parameters.

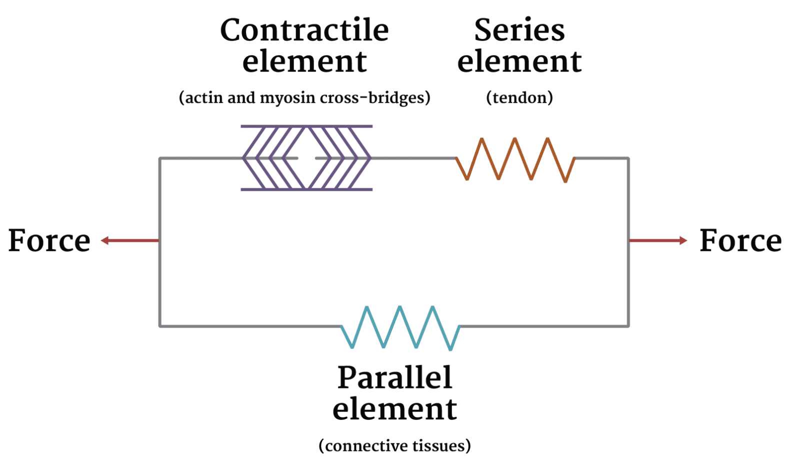

Figure 1. Representative diagram of Hill's muscle model[11]

In the present study, the Hill model was formulated mathematically in its standard two-element configuration and implemented computationally using custom Python code developed specifically for this project.

In the Hill formulation, the muscle–tendon unit is represented as a contractile element (CE) arranged in series with a series elastic element (SE). The total length of the unit, denoted $L(t)$, is therefore the sum of the lengths of its two components:

$$L(t) = L_{\mathrm{ce}}(t) + L_{\mathrm{se}}(t).$$

The series elastic element is treated as a linear spring whose extension above a slack length $L_{\mathrm{se},0}$directly determines the muscle force. The relationship between force and SE length is written as:

$$P(t) = \alpha[L_{\mathrm{se}}(t) - L_{\mathrm{se},0}],$$

where $\alpha$is the stiffness coefficient of the elastic element. This form allows the elastic contribution to be eliminated algebraically by expressing $L_{\mathrm{se}}(t) = L_{\mathrm{se},0} + P(t)/\alpha$. Consequently, the evolution of force can be described entirely by the dynamics of the contractile element and the externally imposed length trajectory.

The defining feature of the Hill model is the hyperbolic force–velocity relationship governing the behavior of the contractile element. Under maximal activation, the shortening velocity of the CE, denoted $v_{\mathrm{ce}}(t) = dL_{\mathrm{ce}}/dt$, is given by Hill's empirical equation:

$$v_{\mathrm{ce}}(t) = \frac{b(P_0 - P(t))}{a + P(t)},$$

where $P_0$is the maximum isometric force, and $a$and $b$are positive constants describing the shape of the hyperbola. An important consequence of this relationship is the expression for the maximal shortening velocity:

$$V_{\max} = v_{\mathrm{ce}}(P = 0) = \frac{P_0 b}{a}.$$

Differentiating the identity $L = L_{\mathrm{ce}} + L_{\mathrm{se}}$and combining it with the CE velocity law yields a first-order differential equation for muscle force. Substituting the expression for CE velocity and differentiating the SE relationship gives:

$$\frac{dP}{dt} = \alpha[\frac{dL}{dt} + b\ \frac{P_0 - P(t)}{a + P(t)}].$$

This differential equation governs force development in response to arbitrary length inputs and provides the basis for all model simulations performed in this work. Numerical integration was conducted using an explicit Euler method, which is sufficient for stability and accuracy under the smooth length trajectories considered (isometric and constant velocity shortening). In addition to mechanical behavior, Hill also proposed a simplified representation of heat production during contraction. Total heat rate is expressed as the sum of a baseline isometric heat term and a "heat of shortening" term proportional to the CE velocity. Using Hill's formulation, heat production during maximal activation follows:

$$\frac{dH}{dt} = k + ab\,\frac{P_0 - P(t)}{a + P(t)},$$

where k represents the isometric heat rate and the second term accounts for the additional energetic cost of shortening. This expression was integrated numerically alongside the force equation to compute heat–time trajectories under each simulated condition. All simulations performed in this study—including isometric tetanus, force–velocity protocols, power–velocity analysis, and heat production—were carried out using a custom Python implementation of the Hill model. This code reproduced the behavior of the original MATLAB model described by Holmes (2006)[3] while providing full flexibility for parameter adjustment, numerical experimentation, and figure generation. Parameters were later tuned to align the model with experimental measurements during validation (Section B), but the mathematical structure and implementation described above apply generally and independently of any specific parameter set.

B. Validation with Experimental Data

Validation of the Hill model was performed by tuning model parameters to match the experimental measurements reported by Barclay (1993)[1] for mouse soleus (slow-twitch) and extensor digitorum longus, EDL (fast-twitch) skeletal muscle. Barclay's work provides an unusually comprehensive dataset consisting of maximal isometric force, force–velocity curves, power–velocity relationships, and isometric heat production. These measurements enable a robust comparison between the simulated model behavior and the experimentally observed mechanical and energetic properties of slow and fast muscle fibers. Parameter tuning began by assigning each fiber type a value of P_0equal to the maximum tetanic stress reported in the study: 227.6 mN mm^{-2} for soleus and 172.2 mN mm^{-2} for EDL. The Hill constant $a$was determined using the ratios $a/P_0 = 0.142$for slow muscle and $a/P_0 = 0.340$for fast muscle, as provided in Barclay's analysis. The parameter b, which shapes the curvature of the hyperbolic force–velocity relation and determines the maximal shortening velocity, was set to 0.34 lengths s^{-1} for soleus and 1.97 lengths s^{-1} for EDL. These values reproduce the experimentally observed differences in shortening velocity and the overall shape of the force–velocity curve for each fiber type. The isometric heat production term $k$was selected to match the experimentally measured isometric heat rates of 26.8 mW g^{-1} for slow muscle and 134.2 mW g^{-1} for fast muscle, ensuring that differences in metabolic economy were captured appropriately. The stiffness of the series elastic element, α, was chosen so that a 10% extension of the elastic element produced a force approximately equal to P_0, consistent with previous implementations of the Hill model and with the typical compliance of muscle–tendon structures.

Force–velocity validation

The first comparison involved the steady-state force–velocity relationship, obtained experimentally by imposing constant shortening velocities and reporting the resulting steady force normalized to P_0. Simulated force–velocity curves were normalized in the same manner and plotted as P/P_0versus $V/V_{\max}$. The model successfully reproduced the principal features of the experimental curves: slow-twitch muscle exhibited a steeper decline in normalized force with increasing velocity, consistent with its smaller $b$parameter and lower $V_{\max}$, while fast-twitch muscle maintained higher relative force across a broader range of shortening velocities. When plotted side by side with the experimental curves, the simulated data followed the same characteristic hyperbolic shape and fell within physiologically reasonable bounds for both fiber types. The resulting Fig. 2 therefore serves as a direct analogue to Barclay's published force–velocity plot.

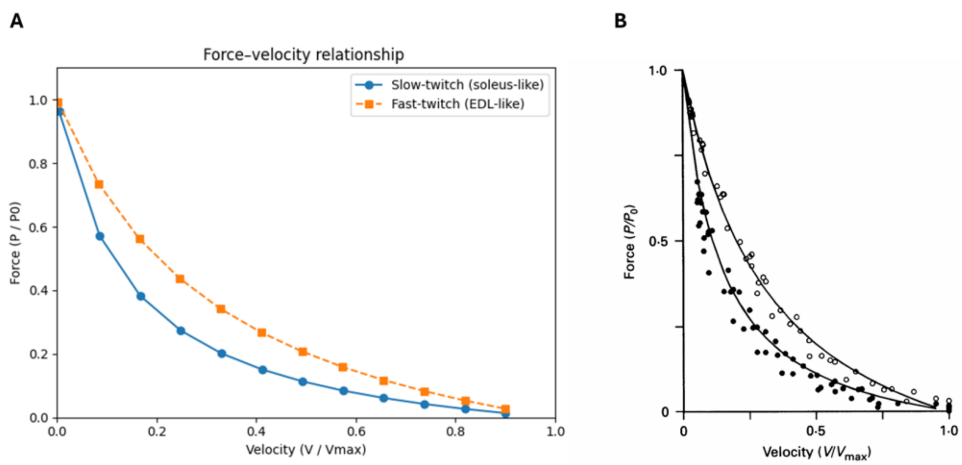

Figure 2. Force velocity graphs, (A) Hill's model prediction of slow and fast twitch muscle fibers, (B) Experimental data for fast and slow twitch muscles

Power–velocity validation

A second comparison was performed by calculating mechanical power output as the product of shortening velocity and steady-state force at each velocity tested. When normalized to muscle mass, the simulated power–velocity relationships exhibited peaks at approximately one-third of the maximal shortening velocity, consistent with classical muscle physiology. Moreover, the peak power of the fast-twitch simulation greatly exceeded that of the slow-twitch simulation, reflecting the higher $b$value and larger overall curvature of the EDL force–velocity curve. This behavior mirrors the experimental observations reported by Barclay, in which the EDL produced roughly double the normalized peak power of the soleus. The simulation results are therefore presented as Fig. 3, directly corresponding to the power–velocity plots in Barclay's study.

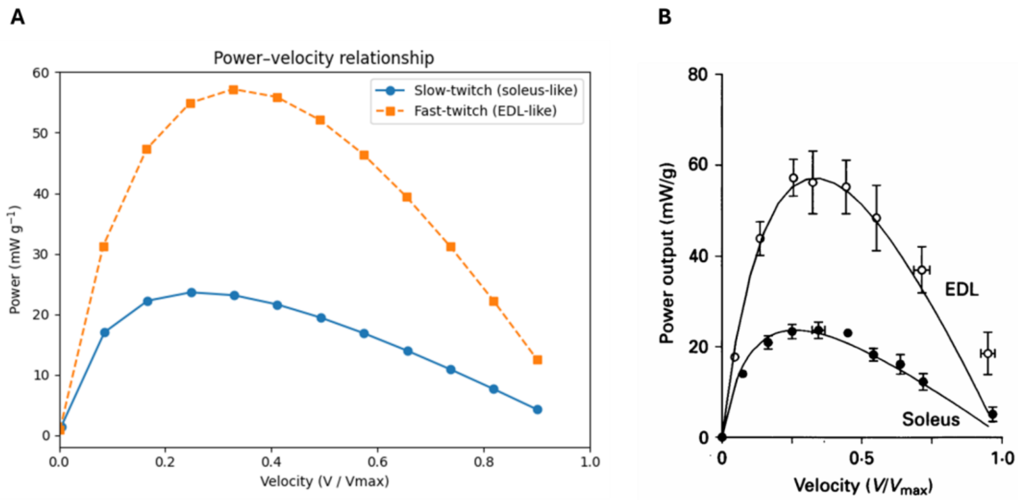

Figure 3. Power velocity graphs, (A) Hill's model prediction of slow and fast twitch muscle fibers, (B) Experimental data for fast and slow twitch muscles

Isometric tetanus and heat production validation

Finally, simulations of isometric tetanus were used to validate both force development and isometric heat production. Because the Hill model expresses heat production as the sum of a constant term $k$and a shortening-dependent term, the heat-time slope under isometric conditions is determined entirely by the baseline heat rate. By tuning k to match the empirical heat production rates, the simulated heat trajectories displayed linear behavior with slopes identical to the experimental values for slow and fast muscle. This contrast is physiologically meaningful: slow-twitch muscles are metabolically economical, whereas fast-twitch muscles consume energy—and therefore produce heat—at substantially higher rates, even under purely isometric conditions. The accompanying simulation outputs, plotted in Fig. 4, illustrate this distinction by overlaying force production and heat accumulation during an isometric tetanus for each fiber type.

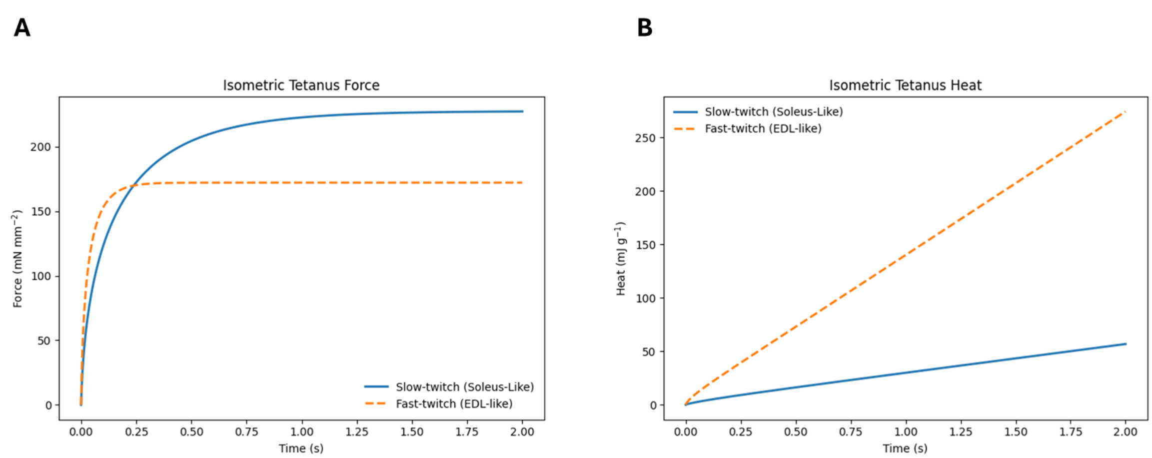

Figure 4. (A) Isometric tetanus force and (B) Isometric tetanus heat of slow and fast twitch muscles

Together, these validation results demonstrate that the Hill model, when appropriately parameterized, can capture the essential mechanical and energetic differences between slow- and fast-twitch skeletal muscle. The tuned model reproduces the canonical shapes of the force–velocity and power–velocity curves and aligns closely with the experimentally measured rates of heat production. Although phenomenological in nature, the Hill model thus provides a quantitatively accurate representation of fiber-type-specific muscle behavior and offers a useful bridge between computational modeling and experimental physiology.

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Appendix

Python code is available on GitHub:

https://github.com/Sina-M-G/Modeling-Fast-and-Slow-Twitch-Skeletal-Muscle-Contractile-Behavior-Using-the-Hill-Muscle-Model