

## Human muscle modelling from a user's perspective

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### Abstract

Methods for developing mathematical models representing entire human muscles are briefly reviewed, with special emphasis on aspects of modelling velocity dependence using cross-bridge dynamics, and isometric force–length properties from myofibril lengths and muscle architecture. For each of these components, mechanistic (using basic contraction mechanisms) and phenomenological (“black-box”) models are available. Experiments on constant-velocity lengthening at different velocities were simulated using (a) a cross-bridge based model and (b) a Hill-based model. The Hill model was superior in its ability to predict muscle forces under different conditions with the same model parameters. Regarding force–length properties, myofibril overlap and muscle architecture did not correctly predict maximal isometric joint moments over the entire functional range of motion. The width of the force–length relationship of all contractile elements in a lower extremity model may be optimized to fit measured isometric moment–angle relationships. The resulting increase in width suggests that for some short-fibered muscles with complex architecture, the “effective” muscle fibre length is increased because muscle fibres may be partly connected in series as well as in parallel. It is concluded that a hybrid phenomenological/mechanistic muscle model is most likely to be practical (i.e. parameters can be estimated for human muscle) as well as accurate (i.e. correct forces are predicted for a wide range of conditions). © 1998 Elsevier Science Ltd. All rights reserved.

*Keywords:* Muscle modelling; Simulation; Force–velocity properties; Force–length properties

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### 1. Introduction

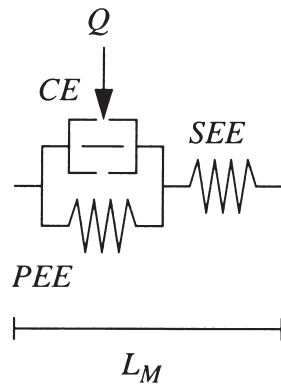
Models describing the dynamics of the human musculoskeletal system consist of equations of motion of a multi-rigid-body system coupled to equations describing the dynamics of muscle contraction. Such models allow theoretical simulations of human movement, ensuring that the results are consistent with Newtonian mechanics as well as with known properties of muscle. These are powerful tools for theoretical studies on motor control, sport performance, and joint loading [1,5,17]. A crucial component of such musculoskeletal models is the model that generates muscle forces. Specifically, it is important that muscle forces respond realistically to neural stimulation and to changes in muscle length.

The first issue when developing models for human muscle is to choose an appropriate muscle model. In gross movement simulation, Hill-based muscle models have been used almost exclusively [14]. A Hill-based muscle model typically consists of three components (Fig. 1): a contractile element (CE), a parallel elastic element (PEE), and a series elastic element (SEE). The PEE and SEE are simple nonlinear elastic elements. The CE is described by force–length and force–velocity relationships. Suitable equations describing these relationships are derived from isometric and isokinetic or isotonic contractions of skeletal muscle. In addition, the dynamics of the active state (which may be defined as the concentration of free  $\text{Ca}^{2+}$ ) of the CE is described by one or more differential equations. Such a model will always correctly reproduce the type of experiment on which the equations were based. However, the force–length, force–velocity, and activation dynamics may interact in potentially complex ways and experiments involving different contractile conditions and time-his-

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**Mechanical properties:**

$$F_{CE} = f_1(L_{CE}, V_{CE}, Q)$$

$$F_{SEE} = f_2(L_{SEE})$$

$$F_{PEE} = f_3(L_{PEE})$$

**State equation:**

$$f_3(L_{CE}) + f_1\left(L_{CE}, \frac{dL_{CE}}{dt}, Q\right) = f_2(L_M - L_{CE})$$

Fig. 1. The traditional three-component Hill muscle model, which consists of a contractile element (CE), series elastic element (SEE), and parallel elastic element (PEE).  $Q$  indicates the level of activation (“active state”) of the muscle. The state equation is a first-order differential equation with length  $L_{CE}$  of the contractile element as a state variable.

ories may not be correctly reproduced [11]. In other words: extrapolation of Hill-based muscle models to complex contractile conditions may be unreliable.

One should also consider the fact that the CE in the Hill model is described by a “black box” mathematical model. The equations merely reproduce known relationships between input and output, without making any attempt to represent the mechanism of muscle force production. Therefore, it may be argued that a model that is closer to the actual mechanisms should have the potential to correctly predict phenomena other than the observations on which the model was based. The main candidate for such a mechanistic model is based on the cross-bridge theory of muscle contraction. Several versions of this model have been developed, but the most practical one for gross movement simulation is the distribution moment (DM) model [16], which assumes that the distribution of attached cross-bridges as a function of cross-bridge length is Gaussian. It has been shown that this approximation exhibits most of the essential behavior of the original cross-bridge model and is considerably faster when solved numerically [16]. An additional advantage of cross-bridge based models is that it is based on biochemical reactions during muscle contraction. Therefore, the rate of cross-bridge cycling is related to metabolic energy consumption, which means that the energetic cost of human movement could be estimated when such models are used for simulation of movement. In the first part of this paper, we investigate whether a cross-bridge model is suitable for a specific application in gross movement simulation.

A second issue when developing models for human muscles, whether Hill-based or cross-bridge based, is the estimation of muscle properties. The classical experiments from muscle mechanics cannot be used because they require invasive measurements of isolated muscle force, while having complete control over contractile conditions (length and activation). For ethical reasons, in human muscles we are restricted to measuring joint

moments under (preferably) voluntary activation. An attractive alternative possibility is to derive muscle properties from the known properties of a single sarcomere and a scaling procedure based on morphological information about individual human muscles, possibly using fibre type distribution as well. Morphological data can be derived from cadaver measurements, or even in vivo using medical imaging techniques [3]. Models based on muscle architecture are then used to estimate the properties of the entire CE [9,11]. In the second part of this paper, we will demonstrate some limitations of a simple procedure to determine isometric force–length properties of human muscles from morphological data.

## 2. Cross-bridge dynamics

When using a musculoskeletal model for simulations of running, we considered the fact that several muscles undergo rapid lengthening during the first part of the support phase. It has been shown in experiments on isolated muscle that the muscle force may eventually drop below the isometric force when lengthening occurs at submaximal activation [8]. This so-called “yielding” effect cannot be reproduced by the standard Hill-based muscle models, but does occur in computer simulations based on the cross-bridge model [16]. In order to investigate the suitability of the DM implementation of the cross-bridge model for eccentric contractions, we carried out simulations of constant-velocity stretches in the cat soleus. The force–time response of the DM model was compared with published experimental data and a simulation using a specific implementation of the Hill model [10]. The muscle was maximally activated during all simulations, because experimental data at different velocities was only available for maximal activation [8,13]. It was expected that the force response would show short-range stiffness behavior, and no yielding. Further details of the modelling procedure have been presented elsewhere [2].

The typical response of a muscle to stretch, when starting from an isometric contraction, is an initial rapid increase in muscle force, due to stretching of cross-bridges and series elastic tissue (Fig. 2). Subsequently, cross-bridges detach and the force levels off to a steady-state value, related to the velocity of the stretch. Figure 2 shows that the Hill-based muscle model could successfully simulate both slow (Fig. 2a) and fast (Fig. 2b) stretches with a single set of parameters, while the DM model significantly overestimated the transient in the force–time history during the fast stretch. This was due to the inability of cross-bridges to detach quickly. The simulation of fast stretch could be improved by increasing certain rate constants in the DM model, but only at the expense of accuracy in the response to the slow stretch.

However, if we wait until the force predicted by the DM model reaches a steady state during the fast stretch (this takes only about 20 ms), the cross-bridges will have had time to detach and force has decreased to a value which is close to the experimental data [3]. This means

that if the DM model is evaluated by comparing it to an experimental *steady state* force–velocity relationship, the model will appear to be correct. For our application, however, which is the prediction of internal forces during a running movement, the high transient forces shown in Fig. 2b are not acceptable and could easily lead to incorrect conclusions about injury mechanisms.

### 3. Force–length properties

The force–length relationship of the contractile element in the muscle model is the result of changes in overlap between the actin and myosin filaments in a sarcomere [6]. Based on the lengths of these filaments in human muscle [12], a theoretical force–length relationship for a single sarcomere can be constructed [7]. This predicts that a human sarcomere can produce force between lengths of 1.27 and 4.24  $\mu\text{m}$ . For convenience, this force–length relationship can be modelled as a parabola with a peak at 2.76  $\mu\text{m}$  (the “optimal” length) and a *width* of 54% of optimal length. The parameter *width* is defined as the maximal amount of active shortening or lengthening, i.e. half of the active length range, relative to optimal length. This basic force–length relationship can then be transformed (scaled) into a force–length relationship for the entire CE of a muscle by taking an optimal length of  $2.76 \times n \mu\text{m}$ , where  $n$  is the average number of sarcomeres in the muscle fibres, and a maximal force of  $\sigma_{\text{max}} \times \text{PCSA}$ , where PCSA is the physiological cross-sectional area (muscle volume divided by average fibre length), and  $\sigma_{\text{max}}$  is the maximal muscle stress which is usually assumed to be the same for all muscles. The value for  $\sigma_{\text{max}}$  is somewhat uncertain and values between 20 and 100  $\text{N cm}^{-2}$  have been used [15]. Note that this scaling procedure initially neglects the effects of pennation [10,12].

This procedure was used to model the eight major muscle groups in the human lower extremity. Appropriate moment arms were then used to predict maximal isometric joint moments at each joint, for both flexion and extension, as a function of joint angles. Details of this lower extremity model and predicted isometric moments for flexion and extension of all three joints have been presented elsewhere [5]. As an example, we will consider the theoretical isometric hip extensor moment as a function of hip and knee angles (Fig. 3a). When compared to corresponding data from a human subject (Fig. 3b), it is obvious that this theoretical model leads to a very narrow moment–angle relationship. One can see the superposition of moments generated by the gluteal muscles (depending on hip angle only) and the hamstrings group (depending on hip and knee angles). The small range of joint angles where the hamstrings muscle group is producing force (Fig. 3a) is clearly not consistent with the experimental data (Fig. 3b). Note that the PEE was not included in the muscle models.

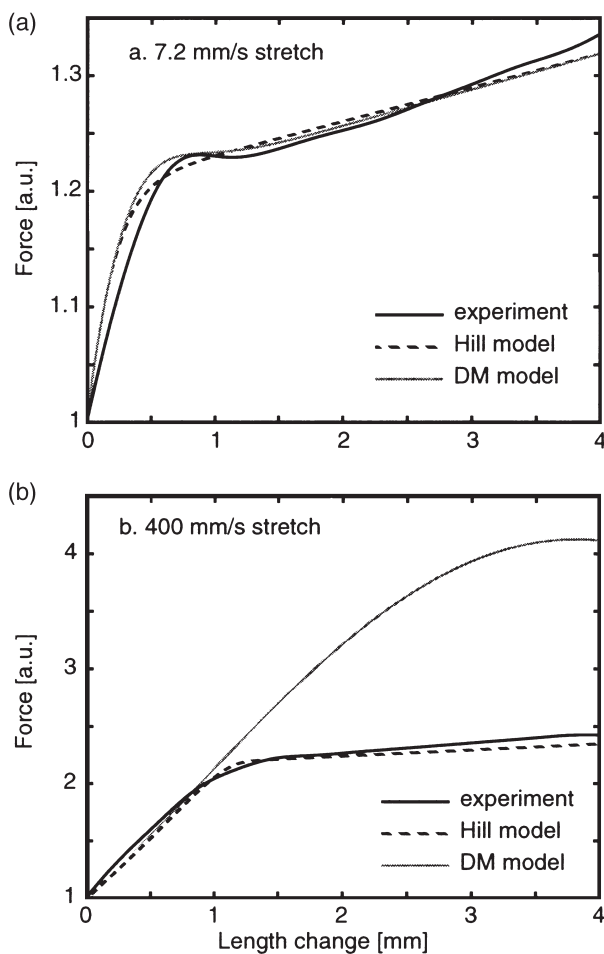


Fig. 2. Response of the cat soleus to constant velocity stretch, and simulations using the Hill model and the distribution moment (DM) model for cross-bridge dynamics. (a) Slow stretch (Joyce et al.[8]). (b) Fast stretch (Walmsley and Proske[13]). Adapted from Cole et al.[2].

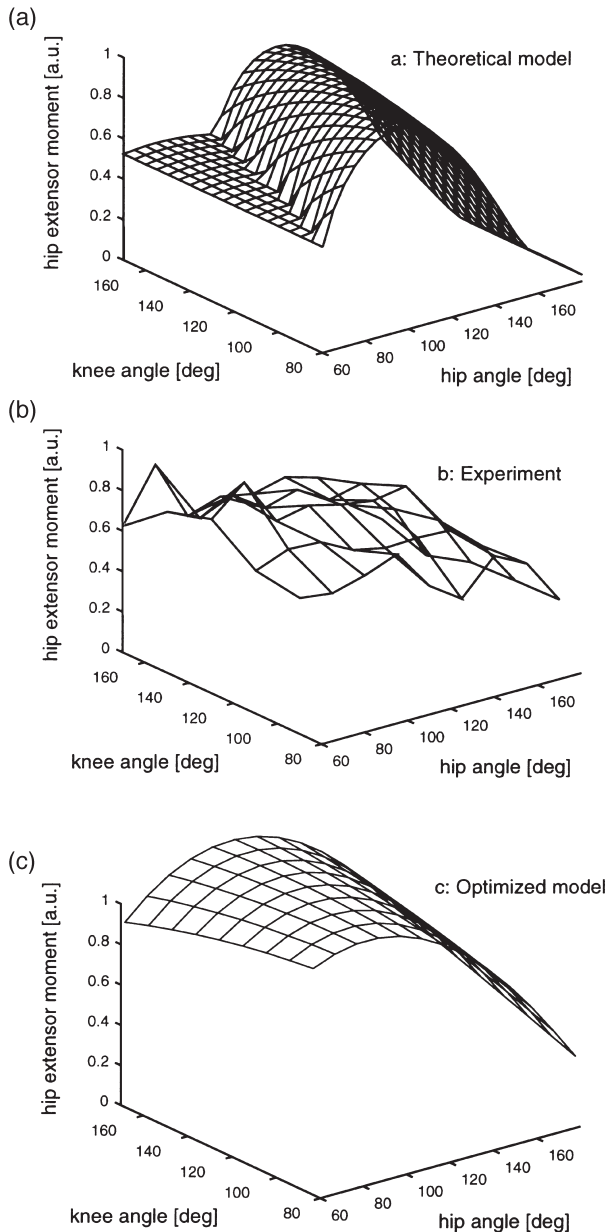


Fig. 3. (a) Predicted maximal isometric hip extensor moment using force-length properties based on myofilament overlap. (b) Corresponding measurements on a human subject. (c) Predictions using the model after optimizing the width of the CE force-length relationship and slack length of the SEE to fit data of four human subjects.

In order to reduce the difference between theory and experiment, it was decided to go towards a more phenomenological approach and the *width* parameter of the force-length relationship of the CE was optimized, together with the slack length of the SEE, to fit experimental data on all six lower extremity tasks in four subjects. Data from all six tasks (flexion and extension for three joints) were combined to obtain best fitting muscle properties for all eight muscles, since bi-articular muscle forces appear in isometric moments at two joints. Details and complete results are presented elsewhere [4]. For

several muscle groups, specifically the hamstrings, rectus femoris, and ankle plantarflexors, this optimization led to *width* values which were considerably larger than in the theoretical model. The optimized musculoskeletal model could produce realistic joint moments at each combination of joint angles. Figure 3c shows the isometric hip extensor moments predicted by the optimized model. Note that the original model (Fig. 3a) could hardly produce a hip extensor moment in the neutral position (when hip and knee angles are close to 180°).

#### 4. Discussion and conclusions

The failure of the cross-bridge model to correctly predict force transients during muscle lengthening was a serious shortcoming for our applications in simulation of human movement. It may even indicate some basic flaws in current theories of force production in muscle, but such considerations are beyond the scope of this paper. From the results shown here, the Hill model is definitely a “safer” model. In other words, it did not produce results that were far from actual muscle behavior. The cross-bridge model, on the other hand, may result in large errors in predicted muscle force during rapid lengthening. It has been demonstrated that the phenomenon of yielding, which was our original motivation for exploring cross-bridge models, can be incorporated into Hill-based models using empirical relationships [14]. In a similar way, it is possible to implement history-dependent behavior in the Hill model.

Discrepancies between theoretical and measured force-length relationships may be explained by our rather simplistic idea of muscle architecture. First, pennation was ignored. Pennation will increase *width*, but no more than about 40%, according to a simple constant volume model [9]. Second, the different muscles within the functional group, or the fibres within a muscle, may reach optimal length at different joint angles, thereby increasing the active length range of the entire muscle group. However, these optimal positions cannot be too far apart since this would imply that while one muscle is at optimal length, another muscle could be beyond its active length range, its connective tissue possibly being overstretched and injured. A third possible explanation is that optimal CE length was underestimated. If the fibres in the CE are very short relative to the muscle belly, it is almost inevitable that fibres are not only arranged in parallel, but also partly in series, due to tensile forces in tissue connecting the distal part of proximal fibres to the proximal part of distal fibres. This, effect, which is hard to quantify, would make the “effective” number of sarcomeres in series larger than initially found by counting sarcomeres in dissected muscle fibres. The same explanation has recently been proposed to explain why ankle plantarflexors have a considerably smaller

$\sigma_{\max}$  than the ankle dorsiflexors [3]. This could be due to an overestimation of the PCSA when muscle fibres are partly arranged in series. This observation is surprisingly consistent with our estimations of CE force–length relationships for these muscles from isometric moment–angle data. Soleus and gastrocnemius had much wider CE force–length relationships (*width* = 104% and 89%) than the tibialis anterior (44%) [4]. It should be noted that an increase in optimal CE length of the model would be more consistent with this explanation than an increase in *width*, as was done in our optimizations. Both modifications result in almost the same optimized isometric properties. Force–velocity properties, however, also depend on good estimates of “effective” fibre length.

In both aspects of muscle behavior (isokinetic stretch and isometric force–length properties) we had to conclude that, at this time, a phenomenological (“black box”) model is preferable to a more mechanistic model. This may be unappealing and inelegant when we are trying to understand human movement from first principles, especially when the Hill muscle model is made more and more complex by including observed phenomena on an *ad hoc* basis. On the other hand, one should consider that it is not good scientific practice to work at such widely differing levels of modelling at the same time. For instance, when studying physical chemistry, we do not incorporate the forces of nuclear physics into our models. Electrical forces suffice, and the atomic nucleus is simply regarded as a particle with given mass and electric charge. Similarly, when developing models for the purpose of understanding how muscles act together to produce well-coordinated movements, we should not at the same time try to explain how muscles work. Instead, we can be satisfied with a “black box” muscle model that describes the input–output relationships of muscle under a wide range of contractile conditions. When such simple muscle models (e.g. Fig. 1) are coupled to a multi-link representation of the human body, we can study a system that exhibits a wide range of interesting behavior. Newton’s laws of dynamics are then more important to explain the behavior of this total system than the choice of muscle model, provided that the muscle model predicts correct forces in all contractile conditions that occur during the movement.

There remain, however, important reasons for continuing to pursue modelling of whole muscles based on mechanisms of muscular force production and muscle architecture. First, such models provide the opportunity to indirectly validate theories on muscle contraction by comparing predicted muscle forces to measurements. Second, it remains very difficult to collect data for development of “black box” models for individual human muscles, mainly because *in vivo* force measurements are generally not possible. The ability to reliably predict gross muscle properties from basic mechanisms and morphological data would therefore be a great step for-

ward. At this time, we advocate a “hybrid” approach, where some muscle properties are derived from basic principles and morphological data (e.g. optimal CE length), while others (CE *width*, SEE slack length) are obtained by fitting the model to any human data that are available and may provide information about these properties [4].

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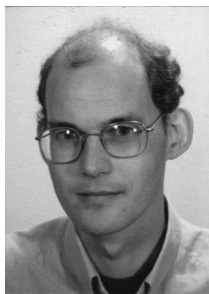
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