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Accuracy of gastrocnemius muscles forces in walking and running goats predicted by one-element and two-element Hill-type models

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ABSTRACT

Hill-type models are commonly used to estimate muscle forces during human and animal movement—yet the accuracy of the forces estimated during walking, running, and other tasks remains largely unknown. Further, most Hill-type models assume a single contractile element, despite evidence that faster and slower motor units, which have different activation–deactivation dynamics, may be independently or collectively excited. This study evaluated a novel, two-element Hill-type model with "differential" activation of fast and slow contractile elements. Model performance was assessed using a comprehensive data set (including measures of EMG intensity, fascicle length, and tendon force) collected from the gastrocnemius muscles of goats during locomotor experiments. Muscle forces predicted by the new two-element model were compared to the forces estimated using traditional one-element models and to the forces measured *in vivo* using tendon buckle transducers. Overall, the two-element model resulted in the best predictions of *in vivo* gastrocnemius force. The coefficient of determination, r^2, was up to 26.9% higher and the root mean square error, RMSE, was up to 37.4% lower for the two-element model than for the one-element models tested. All models captured salient features of the measured muscle force during walking, trotting, and galloping (r^2=0.26–0.51), and all exhibited some errors (RMSE=9.63–32.2% of the maximum *in vivo* force). These comparisons provide important insight into the accuracy of Hill-type models. The results also show that incorporation of fast and slow contractile elements within muscle models can improve estimates of time-varying, whole muscle force during locomotor tasks.

1. Introduction

Muscle models that accurately reproduce time-varying muscle forces are crucial for evaluating motor performance and key to interpreting muscle-driven simulations of movement. Hill-type models, which estimate a muscle's force based on length-tension and force–velocity properties (*e.g.*, Zajac, 1989; Winters, 1990), are arguably one of the most widely-used tools in biomechanics—yet the accuracy of the forces predicted by Hill-type models during walking, running, and other motor tasks remains largely unknown. In this study, we examined the ability of several different Hill-type models to reproduce *in vivo* gastrocnemius forces measured in goats during locomotion.

Rigorous validation of Hill-type models requires experimental measures of fascicle lengths and muscle excitations, which are typically used to drive the models, as well as direct measures of muscle or tendon force. Most previous tests of muscle models have relied on *in situ* stimulation experiments in animals, where the neural excitation and fascicle strain values are not generally representative of *in vivo* dynamic behavior (*e.g.*, Brown et al., 1999; Brown and Loeb, 2000). Only a few studies have assessed the performance of Hill-type models under more realistic conditions (Sandercock and Heckman, 1997; Perreault et al., 2003). Varying results in the errors in force prediction by muscle models, and the paucity of validation studies based on *in vivo* data, warrant further investigation. In particular, models must be tested during dynamic tasks that involve time-varying excitations, both to refine interpretation and to identify limitations that need to be addressed.

One limitation of traditional Hill-type models is their failure to account for different mechanical properties of the fiber types recruited. Muscles are comprised of different types of muscle fibers, broadly classified as slow to fast, that have different activation–deactivation rates, and force development. Most previous Hill-type models assume either that fiber type within the muscle is homogeneous (*e.g.*, Zajac, 1989) or that orderly

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recruitment occurs (*e.g.* Umberger et al., 2003; Van Soest and Bobbert, 1993). However, previous analyses of motor unit recruitment in rats (Hodson-Tole and Wakeling, 2009), humans (Wakeling, 2004), and goats (Lee et al., 2013) have revealed that the recruitment patterns of slow and fast fibers can vary depending on the motor task. Recently, we showed that a Hill-type model could more accurately predict gastrocnemius forces in goats during *in situ* isometric contractions when the model incorporated both fast and slow contractile elements, and when the contractile elements were activated in a manner consistent with measured electromyographic (EMG) recordings (Wakeling et al., 2012). Some other muscle models have incorporated different fiber-type properties, but have also been limited to simulations of isometric contractions (Bol et al., 2011; Fuglevand et al., 1993). Therefore, a secondary aim of this study was to test—for *in vivo* locomotor tasks—whether a Hill-type model with fast and slow contractile elements (*i.e.*, a "two-element model" or "differential" model) yields more accurate predictions of whole muscle force than traditional one-element models. We compared our recently developed, two-element model (Wakeling et al., 2012) to three commonly used Hill-type models that have been applied in a wide range of biomechanics applications. *In situ* and *in vivo* experiments were conducted on the lateral and medial gastrocnemius (LG and MG) muscles of goats, as these muscles are known to comprise both slow and fast fibers (Lee et al., 2013). These experiments yielded simultaneous recordings of fascicle length, excitation, and time-varying tendon force, providing a comprehensive and informative data set for testing the predictive accuracy of the different models. The models in this study relied on measured fascicle lengths, rather than on scaled fiber lengths derived from the muscle-tendon lengths (*e.g.*, Zajac et al., 1989); this allowed us to evaluate modeling assumptions related to properties of the fiber types recruited, which was our main goal, while minimizing uncertainty in the models' force–length properties, which also influence the predicted force.

2. Methods

Six African pygmy goats (*Capra hircus* L; 3 males, 3 females; age 21.0 ± 15.5 months, mass 25.85 ± 6.20 kg) were tested at Harvard University's Concord Field Station. The experimental protocol involved four main steps over a three-day period: surgical implantation of transducers, *in vivo* testing, surgical implantation of nerve cuffs, and *in situ* testing. All experimental protocols are described elsewhere (Lee et al., 2011; Wakeling et al., 2012; Lee et al., 2013; also see Supplementary materials) and are reviewed here in brief.

2.1. Experimental data collection

(1) Goats were trained to walk, trot and gallop on a motorized treadmill, and they performed these gaits on level and inclined surfaces as part of a larger study. Our previous analysis showed that the level trials elicited the most pronounced differences in recruitment (Lee et al., 2013). Thus, the level trials were used in the current study to test the different muscle models.

(2) The MG and LG were instrumented with fine-wire EMG electrodes to measure muscle excitation (Lee et al., 2011), sonomicrometry crystals to measure fascicle length (resolution=0.3 μm Lee et al., 2011), and "E"-shaped tendon buckle transducers on the Achilles tendon were used to measure tendon force (calibration yielded $r^2 > 0.99$, Biewener and Baudinette, 1995). *In vivo* lateral and medial tendon forces were estimated from the total *in vivo* tendon force, measured by the single tendon buckle on the tendon, using the ratio of the maximum forces measured from the *in situ* recordings of the lateral and medial gastrocnemius muscles from the two tendon buckles (see below). Tendon forces were normalized by the maximum force recorded during incline trotting, $F_{\max}$, consistent with previous analyses (Lee et al., 2013).

(3) *In vivo* recordings were made while goats walked, trotted, and galloped on the treadmill. Between 15 and 20 strides were recorded for each condition, and data were recorded at 5000 Hz (Lee et al., 2013). Sufficient rest was given between trials to ensure the goats could complete the experiments.

(4) An additional force transducer was surgically attached on the medial portion of the Achilles tendon prior to the *in situ* experiments. *In situ* recordings were made to measure the muscles' active and passive force–length relationships, using tetanic stimulation, for a range of ankle angles and muscle lengths. A series of different nerve stimulation protocols were used to elicit twitches from different motor units, enabling identification of the twitch profiles for slow and fast motor units (Lee et al., 2011).

2.2. Experimental data processing

(5) To extract information about motor unit recruitment that could be used to drive the muscle models, the major components of the EMG signal corresponding to signals from slow and fast motor units were identified using wavelet analysis (Von Tscharner, 2000; Lee et al., 2011). Optimized wavelets were derived to identify recruitment patterns of slow and fast motor units (Lee et al., 2011; Wakeling, 2005; Hodson-Tole and Wakeling, 2008). The EMG signal was characterized by its total intensity and by the intensities at the low- and high-frequency bands, corresponding to signals from the whole muscle and from slower and faster motor units, respectively (Fig. 1). The final step in the intensity calculation was applying a Gauss filter to the intensity envelope. The filter width was set to have the same time resolution (75 ms) for all measures of intensity so that temporal-based comparisons could be made between the different models (see Supplementary materials for more details).

(6) The EMG intensities were used as excitations for a series of coupled first-order differential equations, constituting transfer functions (Eq. (1)), that enabled estimation of the active state of each muscle. Transfer functions were derived for the whole muscle as well as for the slower and faster motor units (Figs. 1 and 2; Lee et al., 2011); in particular, constants $\tau_{\mathrm{act}1,2,3}$ and $\beta_{1,2,3}$ were identified for the different motor units (Table 1) and were determined from *in situ* data pooled from the six goats. Details are described elsewhere (see Supplementary materials, Lee et al., 2011).

$$\begin{aligned}
&\frac{d}{dt}(a_1) + \left[\frac{1}{\tau_{\mathrm{act1}}}(\beta_1 + [1-\beta_1]EMG(t-t_{\mathrm{off}}))\right]a_1(t) = \left(\frac{1}{\tau_{\mathrm{act1}}}\right)EMG(t-t_{\mathrm{off}})\\
&\frac{d}{dt}(a_2) + \left[\frac{1}{\tau_{\mathrm{act2}}}(\beta_2 + [1-\beta_2]a_1(t))\right]a_2(t) = \left(\frac{1}{\tau_{\mathrm{act2}}}\right)a_1(t) \qquad (1)\\
&\frac{d}{dt}(a_3) + \left[\frac{1}{\tau_{\mathrm{act3}}}(\beta_3 + [1-\beta_3]a_2(t))\right]a_3(t) = c\left(\frac{1}{\tau_{\mathrm{act3}}}\right)a_2(t)
\end{aligned}$$

Activation levels of the slower and faster motor units were scaled in amplitude such that summation of the two levels equaled the activation level of the whole muscle (*i.e.*, the total activation, Fig. 2). This simplified comparison of the one-element and two-element models.

2.3. Muscle models

Three one-element muscle models and a novel two-element model (Wakeling et al., 2012) were used to estimate time-varying forces produced by the MG and LG during the different locomotor conditions (Fig. 1). The three one-element models generated similar predictions of muscle force so only one is presented here; the other one-element models are described in the Supplementary materials. The output of each model, the total muscle force F_{m}, was estimated by:

$$F_{\mathrm{m}} = c[\hat{F}_{\mathrm{f}} + \hat{F}_{\mathrm{P}}(l)]\cos\theta \qquad (2)$$

where $\hat{F}_{\mathrm{f}}$ is the active component of the muscle fiber force and $\hat{F}_{\mathrm{P}}$ is the passive component of the force as a function of fiber length (l). Constant c and the pennation angle, θ, scaled the fiber force to the whole muscle force. In particular, constant c scaled the predicted force from its normalized value to the measured force for each goat. Thus, c reflects the maximum isometric force generated by the muscle. The pennation angle was calculated at each time step as a function of fiber length (l) from the resting pennation angle and the fascicle length, assuming that the thickness of the muscle remained constant (Zajac, 1989; Millard and Delp, 2012; van den Boger et al., 2011; see Table 2 for mean and standard deviation values of optimal and resting fascicle length and pennation angle). The inputs to each model included the time-varying fascicle lengths, which were also used to calculate fiber contractile velocity and pennation angle, and the activation states (Figs. 1 and 2). The activation states were normalized to the maximum activation during incline trotting, consistent with our procedure for normalizing the measured tendon forces. Other parameters used in the models (Fig. 1 and Table 3) were either derived from experimental measurements or taken from the literature, and were not optimized to "fit" the *in vivo* forces.