SUMMARY
Several muscle models based on common and new approaches were used to test the idea that muscle force depends on the recruitment of its different fibres and elucidated the optimal way to predict force development from whole muscle. The model where slow and fast contractile elements acted in parallel and were activated independently most accurately predicted muscle force through a series of strict and robust validation tests. This model supports the idea that preferential recruitment of faster motor units is a mechanically appropriate strategy for tasks that require fast contraction-relaxation cycles.

INTRODUCTION
Mammalian skeletal muscle is comprised of a mixture of different motor units that have different contractile properties. Thus, it is expected that the force developed by the whole muscle depends on the recruitment and activation pattern of the different motor units within it. Current Hill-type muscle models calculate force based on factors such as length, velocity, and activation level [1,2]. Common assumptions such as constant activation-deactivation rates and homogenous fibre population hinder the development of more advanced models that should include the intrinsic properties of slow and fast fibres. Furthermore, robust validation of these models can only be conducted if the muscle forces are measured directly and under various conditions.

The objectives of this study were to 1) examine how the different fibre-types influenced whole muscle mechanics, 2) test different models where the material properties varied in accordance with different physiological criteria, and 3) develop a model where independent contractile elements acted in parallel and could be activated independently.

METHODS
Five different types of muscle models were tested. Homogenous model A was comprised of fibres with homogenous properties with v_e taken from maximum intrinsic speeds of different fibre-types weighted by their fractional cross-sectional area within the muscle. The value for k, curvature of the force velocity relation, was set as an intermediate value between the slow and fast fibre limits where

\[ k = 0.1 + 0.4p \]  

where \( p \) is the fractional area occupied by the fast muscle fibres [3]. Hybrid model B was the same as homogenous model A except that \( v_e \) represented the fastest fibres and \( k \) was calculated from the composite force-velocity relation taken from the combination of fast and slow fibres with force proportional to their fractional fibre area following Hill [4]. Orderly recruitment model C assumed that as the level of activation increased, then the active muscle took the characteristics of progressively faster fibre types [5]. \( v_o \) was scaled to equal that of the slowest fibres at the lowest activation levels. \( k \) was calculated using equation 1. Reverse recruitment model D assumed that as the level of activation increased, then the active muscle took the characteristics of progressively slower fibre types. Again, \( k \) was calculated using equation 1 and \( v_o \) was activation dependent in an opposite manner to the orderly recruitment model C. For models A-D, the activation state as determined from the total EMG intensity following [Lee et al., ISB 2011]. The total muscle force \( F_m \) was given by:

\[ F_m = c_1(F_f + F_p(l)) \cos \beta \]  

where \( \beta \) was the pennation angle (assumed constant for isometric contractions), \( F_p(l) \) was the passive component of the force-length relationship, \( F_f \) the active force from the fibres, and \( c_1 \) scaled the fibre force to the whole muscle. Differential recruitment model E contained fast and slow contractile elements in parallel that could be differentially activated. The activation levels were determined from the EMG intensity at specific frequency bands previously optimized to detect fast- and slow-motor unit activity Lee et al. [ISB, 2011].

The muscle models were then tested against physiological data measured in situ from four African pygmy goats at Harvard University’s Concord Field Station. All surgical and testing procedures followed IACUC approval. Fine-wire EMG, Achilles tendon force buckles, and sonomicrometry crystals were implanted to measure muscle activity, tendon force, and fascicle length and pennation angle, respectively. Unfused tetanus trials were obtained by stimulating the nerve at 5, 10, 20, and 40 Hz.

The models were evaluated with a set of variants that bracketed the possible fibre-type proportions and intrinsic speeds for these muscles. The coefficient of determination, \( r^2 \), was calculated between the predicted and measured forces. The predicted forces were tested using ANOVA against the following factors: model, goat, muscle, fibre-type proportion, and stimulation frequency.
RESULTS AND DISCUSSION

The ANOVA showed that there was a significant effect of choice of $v_0$, and stimulation frequency on the modeled forces. This is to be expected. Despite the muscle-tendon unit being held isometrically, fluctuations in the length of the elastic element resulted in a fluctuation in strain rate in the muscle fibres, and thus the models would be sensitive to the $v_0$ selected. At the low stimulation frequencies there were large fluctuations in force, and thus the instantaneous force values were very sensitive to stimulation frequency. The models differ in their calculation of the activation dynamics and this is reflected in the rates of force development and relaxation.

Figure 1: Coefficients of determination between predicted and measured forces (mean + s.e.m.) from five different muscle models for tetanic contractions between 5 to 40 Hz stimulation frequency. Note how the differential model accounts for fluctuations in motor unit recruitment and results in a better fit between the predicted and measured forces.

The tetanic contractions were stimulated by a standardized stimulation to the nerve. The amplitude of the motor unit action potentials appeared similar for all stimuli, but there was considerable variation in the amplitude of the EMG intensities and activity levels for the fast and slow motor units. This demonstrates that, even for this seemingly controlled and repeatable contraction, there was a fluctuation in the motor units being recruited. The ANOVA showed that there was a significant effect of model type on the predicted force. The new differential model $E$ had the highest $r^2$ for all stimulation frequencies (Fig. 1), choices of $v_0$ and fibre-type proportions. Thus, the ability of differential model $E$ to track and accommodate the fluctuations in motor unit recruitment resulted in better prediction of the muscle force.

Would It is to be expected that motor unit recruitment show even greater fluctuations during natural behaviours where contractions are submaximal and voluntary. Additionally, during locomotion the strain rates of the fibres may be expected to exceed those found in isometric tetanic contractions. Therefore, is should be expected that the differential model $E$ will show even greater improvements over traditional muscle models when it is used for in vivo conditions.

CONCLUSIONS

The models presented here provide insight into how the contributions of different fibres influence whole muscle mechanics. The model that contained independent slow and fast contractile elements that could be differentially activated most accurately predicted muscle force through a series of validation tests. The models support the idea that the exact recruitment pattern of fibres within a muscle influence the mechanics of the whole muscle, and thus that appropriate recruitment is required for optimal mechanical output of a muscle.

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