A MUSCLE-FORCE MODEL WITH PHYSIOLOGICAL BASES

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INTRODUCTION
We developed a model for describing the generation of isometric muscle force that is based on verifiable physiological concepts and data. It is a continuation of preliminary work done by Adam [1]. The model provides a direct relationship between the excitation to the motoneuron pool and the force output of the muscle. It is based on knowledge of motor unit firing behavior that has evolved over the past three decades and data which have been observed by our Precision Decomposition technology [2,3]. It employs the phenomenon of Common Drive which states that the excitation modulation to the motor units within a muscle and across muscles occurs in unison [4]; the Onion Skin principle, which describes a progressively hierarchical relationship between the recruitment threshold and the firing rate of motor units, with the later recruited motor units having lower firing rates [4,5]; and an Excitation Plane that describes the firing rate behavior of the motor units as a function of recruitment threshold, including the initial and maximal firing rates.

METHODS
The input consists of an excitatory signal common to all the motor units in a motoneuron pool, upon which is imposed a 0.8 Hz oscillation representing the Common Drive. The excitation plane provides the linear relationship between the recruitment threshold and the initial firing rate; and the non-linear relationship between the firing rates and force output of the muscle. This plane is obtained by decomposing the EMG signal detected during force-increasing contractions into the constituent motor unit action potentials. The number of motor units in a muscle and the 100 distribution of the recruitment threshold of the motor units are obtained from the literature. As the excitation increases, the number of active motor units increases and the firing rates of all the motor units increase according to the Onion Skin Principle. For each motor unit, a pulse train is generated. Noise is added to each pulse train by modeling the inter-pulse intervals (IPI) as gaussian random variables with the mean given by the predicted IPIs and with a constant coefficient of variation. The time-varying force produced by the individual motor units is computed by convoluting the impulse train with the motor unit force-twitch. Force twitches are generated by using a mathematical equation which allows the peak amplitude, the rise time, and the relaxation time to be set independently [6]. The amplitude and time characteristics of the force twitch are varied as a function of time to represent the early potentiation and subsequent diminution which occur during sustained contraction. The total muscle force is computed by summing the individual motor unit responses. The force is compared to the target force and the error modifies the common excitation to the motor units.

RESULTS AND DISCUSSION
We have modeled the force characteristics of the First Dorsal Interosseous and the Vastus Lateralis muscles. As the force-twitch characteristics of the muscle change during a contraction, the excitation to the motoneuron pool is modified to maintain the force output constant. In so doing, the firing rate and the number of active motor units is altered according to the characteristics of the excitation plane. The model predicts the increased force fluctuation that occurs during sustained contractions. It predicts the initial decrease and subsequent increase in the firing rates, along with the necessary recruitment of motor units required to sustain a constant-force contraction. These results underscore the fundamental importance of force twitch potentiation and diminution during contractions. It reveals that the higher threshold motor units do not tetanize, even at maximal force contractions, when they fire maximally, and that their force-fluctuations contribute, and likely induce, the observed force fluctuation of muscle contractions (Figure 1).

It is expected that the model may explain why motor unit firing rates decrease in the elderly; why they increase as a consequence of exposure to microgravity; and why different muscles have different firing rate/recruitment characteristics. It has the potential to describe the time course of the amplitude of the force twitches, if the firing rate behavior is known. And it holds promise for identifying the influence of high threshold motor units in the execution of precision force production as is required in skilled tasks, and various other questions concerning the generation of muscle force.

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