



Biomechanical benefits of the onion-skin motor unit control scheme



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ABSTRACT

Muscle force is modulated by varying the number of active motor units and their firing rates. For the past five decades, the notion that the magnitude of the firing rates is directly related to motor unit size and recruitment threshold has been widely accepted. This construct, here named the After-hyperpolarization scheme evolved from observations in electrically stimulated cat motoneurons and from reported observations in voluntary contractions in humans. It supports the assumption that the firing rates of motor units match their mechanical properties to “optimize” force production, so that the firing rate range corresponds to that required for force-twitch fusion (tetanization) and effective gradation of muscle force. In contrast, we have shown that, at any time and force during isometric voluntary constant-force contractions in humans, the relationship between firing rate and recruitment threshold is inversely related. We refer to this construct as the Onion-Skin scheme because earlier-recruited motor units always have greater firing rates than latter-recruited ones. By applying a novel mathematical model that calculates the force produced by a muscle for the two schemes we found that the Onion-Skin scheme is more energy efficient, provides smoother muscle force at low to moderate force levels, and appears to be more conducive to evolutionary survival than the After-hyperpolarization scheme.

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1. Introduction

Muscle force is modulated by varying the number of active motor units and their firing rates. The manner in which motor units are controlled determines the characteristics of the force generated by the muscle that in turn determines the manner in which we interact with our environment and each other.

There is general agreement that, as the excitation to the motoneuron pool increases to produce more force, motor units are recruited in order of increasing size, as described by the “Size Principle” (Henneman, 1957; Hu et al., 2013). As for the firing rate, over the past five decades there has been a common acceptance of the notion promulgated dominantly by Eccles et al. in 1958 that higher-threshold motoneurons have greater firing rates than lower-threshold ones. This notion stems from the observation that, when the nerves of anesthetized cats are *electrically stimulated*, the larger-diameter (higher-threshold) motoneurons exhibit a shorter after-hyperpolarization (AHP) and greater firing rates than the smaller-diameter (lower-threshold) ones.

The lower-threshold motor units have wider and smaller amplitude force twitches than the higher-threshold motor units and require lower firing rates to tetanize (produce twitch fusion). By inference, this arrangement would “optimize” the force generating capacity of the muscle since each motor unit would fire at rates producing twitch fusion and thus contributing its greatest individual force. This hypothesis, which we will refer to as the AHP scheme, was supported by Kernell (1965, 2003) and has been tacitly accepted by many thereafter and adopted in support of their observations in humans (Grimby et al., 1979; Moritz et al., 2005; Oya et al., 2009, among others). However, the empirical studies that reported a linear relation between recruitment threshold and firing rates grouped motor unit data from different subjects and contractions performed on different days or at different force levels (Gydikov and Kosarov, 1974; Grimby et al., 1979; Moritz et al., 2005; Tracy et al., 2005; Barry et al., 2007; Oya et al., 2009; Jesunathas et al., 2012). But, we make note that this approach is known to introduce inter-subject variability and errors in the analysis (De Luca and Hostage, 2010; De Luca and Contessa, 2012; Hu et al., 2013, 2014b).

We (De Luca et al., 1982; De Luca and Hostage, 2010; De Luca and Contessa, 2012) and others Seyffarth, 1940; Person and Kudina, 1972; Masakado et al., 1995; Stock et al., 2012; Hu et al., 2013, 2014b; De Luca et al., 2014; among others) have shown that, at any time and force during *voluntary constant-force contractions* in

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humans, earlier-recruited motor units maintain higher firing rates than later-recruited ones, providing an inverse orderly hierarchy of nested firing rate curves resembling the layers of the skin of an onion. We refer to this construct as the Onion-Skin scheme (De Luca and Erim, 1994).

In this work, we applied a novel model of muscle force generation (Contessa and De Luca, 2013) to compare the force characteristics produced by the two schemes during constant-force contractions. We did so for two muscles: the first dorsal interosseous (FDI) of the hand and the vastus lateralis (VL) of the thigh. These muscles were chosen because they have different properties: the FDI is a smaller muscle commonly involved in precise low-force level activities, and the VL is one of the largest muscles in the body that generates large forces.

2. Methods

The model used for the simulation of the firing rate and force behavior of motor units is a modified version of that developed by Contessa and De Luca (2013) for the FDI and VL muscles. The input–output relationship at the motoneuron level, describing the firing behavior of motor units, and the firing rate to force transduction at the muscle fiber level, describing the mechanical properties of motor units, are modeled separately. The model is based on the concept of Common Drive (De Luca et al., 1982), which describes an excitation, consisting of the sum of all excitatory and inhibitory inputs from the Central and Peripheral Nervous Systems, driving the firing behavior of all motor units in the motoneuron pool of a muscle. The Common Drive will be referred to as the “input excitation”, φ , to the model. It ranges from $\varphi=0$, when no motor unit is active and no force is produced, to $\varphi=1$, the maximal level of input excitation required to exert maximal force output.

The motoneuron pools of the FDI and VL contain approximately 120 and 600 motor units, respectively (Feinstein et al., 1955; Christensen, 1959). Motor units are activated when the input excitation is greater than or equal to their recruitment threshold value, τ . The range of motor unit recruitment thresholds is between 0 and 67% maximum voluntary contraction force (MVC) in the FDI and between 0 and 95% MVC in the VL (De Luca and Hostage, 2010). Smaller motor units are recruited at lower input excitation levels, and as the input excitation increases, higher-threshold motor units are progressively recruited, as described by the following equation derived by De Luca and Kline (2012):

$$\% \text{activeMUs}(\varphi) = 0.0058s\varphi(1 - 360e^{-5.9\varphi}) + 100(1 - e^{-9.8\varphi}) \quad (1)$$

where s is the number of spindles in the muscle, with $s=34$ for the FDI (Smith and Marcarian, 1966) and $s=440$ for the VL (Voss, 1959).

The input excitation also determines the firing rate value λ_i of each active motor unit i . The Onion-Skin scheme describes a hierarchical inverse relationship between the recruitment threshold τ_i and the firing rate λ_i of each motor unit at any input excitation level during a voluntary contraction, thus formulating the “Onion Skin” property (De Luca et al., 1982; De Luca and Erim, 1994). The AHP scheme formulates an opposite arrangement where both the minimal and maximal firing rates of motor units are directly related to recruitment threshold. See the set of trajectories in Fig. 1, referred to as the firing rate spectrum, which represents the firing rate pattern of motor units as a function of increasing input excitation in the two schemes and muscles.

The equations describing the Onion-Skin scheme were derived by fitting empirical data of motor unit firing rates obtained during voluntary isometric linearly-increasing and constant force contractions in humans with mathematical equations. λ_i is modeled as a function of the input excitation φ and the motor unit recruitment threshold τ_i , as described by the following equations (Contessa and De Luca, 2013) for the FDI:

$$\lambda_i(\varphi, \tau_i) = 19 + 8.0\varphi - (21 + 116e^{-\varphi/0.2})\tau_i - e^{-(\tau_i - \varphi)/(0.16\tau_i + 0.04)} \left[9.9 + 8.0\varphi + (-14.7 - 116e^{-\varphi/0.2})\tau_i \right] \quad (2)$$

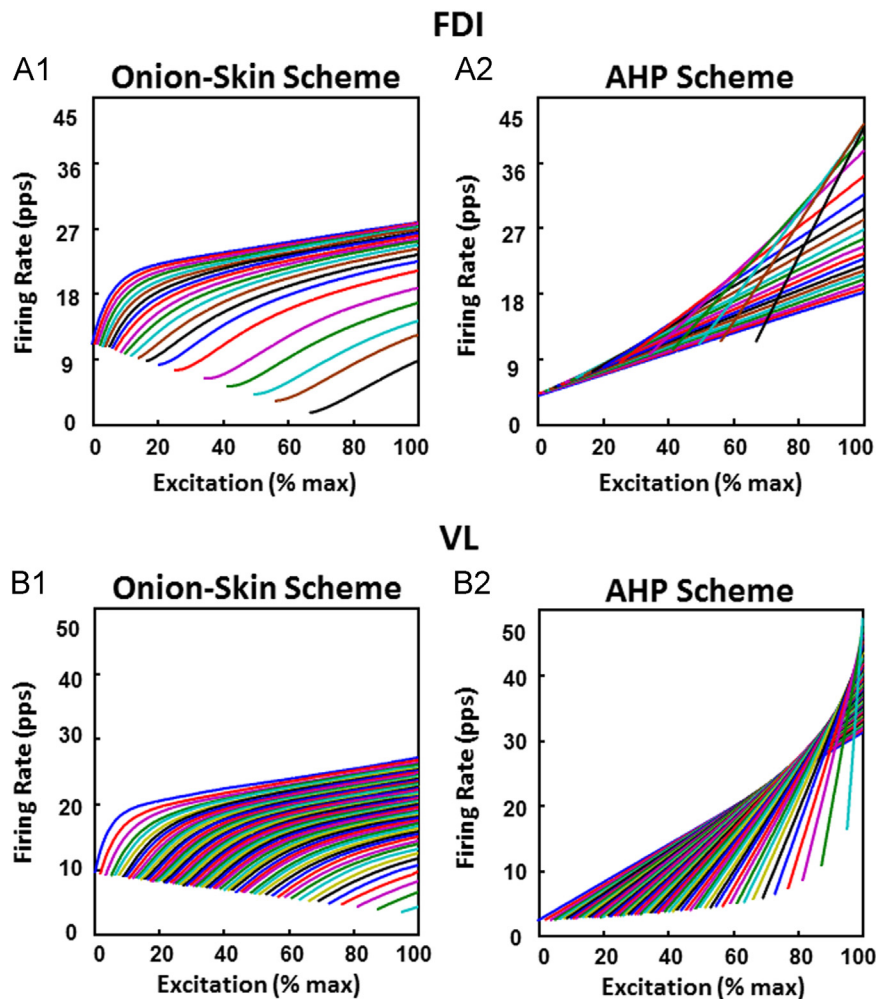


Fig. 1. Firing rate spectrum for the Onion-Skin scheme and for the After-hyperpolarization (AHP) scheme. Simulated motor unit firing rate as a function of increasing input excitation to the motoneuron pool of the FDI (top) and VL (bottom) muscles in the Onion-Skin (A1 and B1) and in the AHP (A2 and B2) scheme. This set of trajectories is referred to as the firing rate spectrum. Note that one out of six motor units is shown for clarity.

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