



## A primer on motor unit physiology



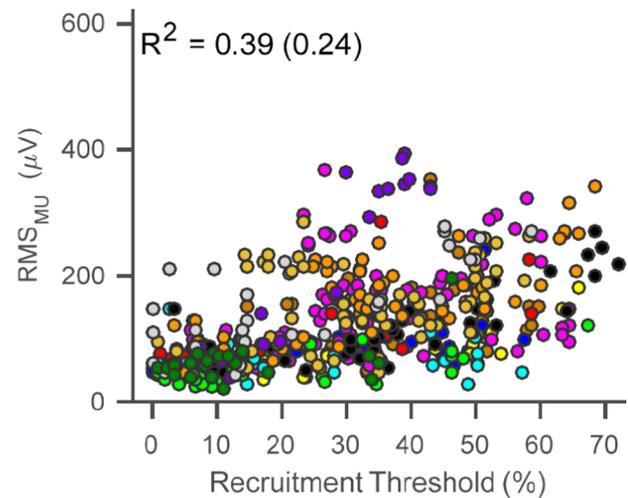
Dear Editor-in-Chief,

I would like to thank Dr. DeFreitas for taking the time to provide comments on a recent paper of mine that was published in your journal (Enoka, 2019). His main objection to my remarks seems to be that I failed to appreciate the capacity of decomposition techniques to expand our knowledge on the physiology of high-threshold motor units. In response, I provide three reasons why decomposition studies should strive to identify the discharge times of motor units that span the entire range of recruitment thresholds.

First, there is no convincing evidence that the changes in contractile function observed during aging, training, or fatiguing contractions are dominated by high-threshold motor units. The two studies cited by Dr. DeFreitas in support of a central role for high-threshold motor units in the adaptations experienced during aging and after several weeks of training are based on the false interpretation that all type II muscle fibers are innervated by high-threshold motor units. The force capacity of fast-contracting motor units—which comprise type II muscle fibers—ranges from weak to strong (Fig. 2 in Burke and Tsairis, 1974), suggesting that these motor units exhibit a range of recruitment thresholds. Moreover, there is no consensus on whether or not the remodeling of human motor units during aging is limited to those with high recruitment thresholds (McNeil and Rice, 2018) and the adaptations observed after several weeks of strength training are independent of recruitment threshold (Fig. 2 in Van Cutsem et al., 1998; Fig. 7 in Del Vecchio et al., 2019). Similarly, the concept of fatigue sensitivity as originally characterized with electrical stimulation of motor units in hindlimb muscles of cats (Burke and Tsairis, 1974) does not seem relevant to human motor units (Bigland-Ritchie et al., 1998) as even low-threshold motor units adjust their activity during fatiguing contractions (Farina et al., 2009).

Second, the association between action-potential amplitude and recruitment threshold is variable across muscles and individuals. The capacity of an algorithm to decompose an interference signal into its constituent motor unit action potentials depends on the uniqueness of the waveforms, which is a product of the configuration of the recording system and the anatomical characteristics of the muscle (Farina et al., 2008). Due to these effects, the amplitude of a motor unit action potential is not always related to its recruitment threshold and there is substantial variability in this association across individuals (Fig. 1). The findings shown in Fig. 1 also demonstrate that with appropriate editing procedures it is possible to discriminate the discharge times of motor units with a broad range of recruitment thresholds and thereby quantify the specificity of the entire motor unit pool to various interventions, such as strength training (Del Vecchio et al., 2017).

Third, although most of the literature on intramuscular recordings of motor unit activity has been obtained during low-force isometric contractions, several groups have been able to record motor unit activity during forceful contractions with intramuscular electrodes. For



**Fig. 1.** Amplitudes of motor unit (MU) action potentials in tibialis anterior as a function of recruitment threshold. Amplitude was measured as the root-mean-square (RMS) value extracted from the first 50 action potentials for each motor unit (colored circles) during gradual increases in the force exerted by the dorsiflexor muscles during isometric contractions. Each color represents the motor units for one subject. The  $R^2$  values indicate the mean (SD) of the correlation coefficients across subjects, which ranged from 0.09 to 0.87. (Reproduced with permission from Del Vecchio et al., 2017.) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

example, a number of studies have reported the discharge characteristics of single motor units during strong contractions ( $\geq 70\%$  MVC force): including Fig. 3 in Oya et al. (2009); Fig. 2 in Monster and Chan (1977); Fig. 3 in Van Cutsem et al. (1997); and Fig. 2 in Erim et al. (1996). Such reports provide the foundation for the physiological validation of the data on high-threshold motor units derived from high-density surface EMG recordings (see Figs. 1 and 2 in Enoka, 2019).

Of course, the classification of recruitment thresholds into low and high categories begs the question of what do we mean by “high threshold”? Due to the exponential distribution of innervation number within a motor unit pool, most of the motor units in a muscle are weak (Van Cutsem et al., 1998) and approximately 85% of the pool controls only half of the fibers in a muscle (Fig. 2 in Enoka and Fuglevand, 2001). Conversely, the weakest 50% of the motor units in a pool control  $< 15\%$  of the fibers in a muscle. Consequently, Carpentier et al. (2001) used a recruitment threshold of 25% MVC force to distinguish between low- and high-threshold motor units. With such a criterion, our knowledge on the discharge characteristics of high-threshold motor

units as measured with intramuscular electrodes is not as sparse as suggested by Dr. DeFreitas.

In combination with flexible editing tools, decomposition approaches should maximize the capability of this technology to identify the discharge times of motor units with a broad range of recruitment thresholds during prescribed actions.

#### Declaration of Competing Interest

The author declares no financial or other conflicts of interest.

#### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jelekin.2019.05.002>.

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