Inappropriate interpretation of surface EMG signals and muscle fiber characteristics impedes progress on understanding the control of neuromuscular function.

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As the final common pathway from the nervous system to muscle, the motor unit transmits an activation signal generated by the nervous system to engage the contractile proteins and produce the muscle forces needed for reflex responses, automatic behaviors, and voluntary actions (11). The net force exerted by muscle depends on the amount and timing of motor unit activity, the contractile properties of the activated muscle fibers, and the mechanical characteristics of the connective tissues that transmit the muscle fiber forces to the skeleton. Neuromuscular function, therefore, is often characterized in terms of motor unit activity and the contractile properties of single muscle fibers. The purpose of this viewpoint is twofold: (1) to underscore the limitations in deducing motor unit activity from interference electromyographic (EMG) recordings; and (2) to emphasize the dissociation between motor unit characteristics and muscle fiber types.

The activation signal generated by the nervous system for an intended action can be characterized with either the times at which individual motor units discharge action potentials or the algebraic sum of many motor unit action potentials (Figure). From the discharge times of multiple concurrently active motor units (≥8), it is possible to identify the neural drive to muscle—defined as the control signal transmitted via the final common pathway—that establishes the amplitude and time course of the force to be exerted by the muscle (9, 17). In contrast, the amplitude of the interference EMG signal, which depends on both the synaptic inputs received by the motor neurons and the muscle fiber electrical properties, comprises the summation of motor unit action potentials and provides an index of muscle activation (16).

Due to the exponential distribution of innervation number across the motor units comprising a single muscle (12), the number of motor unit action potentials is not directly related to the number of muscle fiber action potentials that contribute to an EMG signal (see Fig. 5 in Ref. 10).
Consequently, the amplitude of an EMG signal does not provide a direct index of the neural drive to muscle (15), especially during the many actions that involve changes in muscle length (13) and during fatiguing contractions (10, 16). Nonetheless, the amplitude of a surface EMG signal can provide a useful approximation of the amplitude component of the neural drive to muscle during some controlled conditions (8, 18).

Due to the 5-fold range in twitch contraction times and the 100-fold range in peak tetanic forces among the motor units innervating a single muscle (22), the force exerted by a muscle depends on the contractile properties of the involved motor units (11). Pioneering work in characterizing these properties, largely involving animal models, classified motor units into discrete categories based on their contractile properties. The most popular scheme used two tests to identify three types of motor units (3). The first test involved a qualitative evaluation of the shape of an unfused tetanus that was elicited by stimulating the axon of a motor unit for 0.5-2.0 s at a rate of 1.25x its twitch contraction time. Motor units that produced a monotonic increase in force during the unfused tetanus were classified as slow (type S), whereas those that displayed a depression (sag) in the middle of the response were considered to be fast (type F). The second test assessed the level of fatigability for the type F motor units by measuring the decline in submaximal force across repeated trains of electric stimuli (40 Hz for 330 ms) for 2-6 min. Those units that exhibited a substantial decrease (≥75%) in force were classified as fatigue-sensitive (type FF), whereas motor units with lesser reductions in force (≤25%) were categorized as fatigue-resistant (type FR). The Burke scheme, therefore, classifies motor units as slow or fast on the basis of the shape of the unfused tetanus and not according to differences in twitch contraction time.
Even in their original work, Burke and colleagues found that twitch contraction times for motor units in cat hindlimb muscles are distributed continuously (Fig. 4 in Ref. 4) and did not cluster into discrete categories of slow- and fast-twitch motor units (24). Studies of human muscles have confirmed these results and found that the twitch contraction times of motor units do not exhibit a bimodal distribution, but rather approximate a normal distribution (26, 30). Moreover, the Burke scheme was unable to identify discrete types of motor units in human muscles (1). Taken together, these results indicate that it is not appropriate to categorize motor units as either slow or fast twitch on the basis of contractile properties.

In contrast, the single-fiber electrophoretic technique has demonstrated that it is possible to classify distinct types of muscle fibers on the basis of myosin heavy chain (MHC) isoform content (2, 5, 6). There are three such isoforms in adult human muscle: type I, type IIA, and type IIX. In a seminal study, Bottinelli and colleagues demonstrated that the contractile properties of fiber segments from the vastus lateralis muscle of men varied with the content of MHC isoforms (2). For example, they found that maximal shortening velocity (fiber lengths/s) was slowest for type I fibers (0.25 ± 0.08), fastest for type IIX fibers (2.39 ± 0.8), and intermediate for type IIA fibers (1.11 ± 0.36). The slower shortening velocity for type I fibers is attributed to smaller step sizes and longer attachment times during the crossbridge cycle (6). Such single-fiber characterizations are often used to explain the variance in whole-muscle function (19, 23, 25, 29).

Despite the existence of discrete types of muscle fibers, two factors confound the translation of this distinction into the continuous distribution of motor unit properties: coexpression of MHC isoforms as detected by gel electrophoresis and lateral transmission of muscle fiber force. In addition to muscle fibers that can be characterized as containing only one of the three MHC isoforms, there are muscle fibers that coexpress two of the MHC isoforms (7, 27) and they have...
contractile properties that are intermediate between those for the fibers with only one of the
MHC isoforms (2, 6). In an extensive survey of rodent muscles, Caiozzo and colleagues found
the proportion of muscle fibers coexpressing MHC isoforms varied across muscles but was
typically present in at least 40% of the muscle fibers (5). Such polymorphisms attenuate fiber-
type differences in contractile properties (see Fig. 1 in Ref. 6). Moreover, the homogeneity of
the coexpression profile among the muscle fibers comprising a single motor unit is unknown.

The other factor that disables the translation of muscle fiber types into motor unit types is the
pathway by which force is transmitted from the crossbridges to the skeleton (21, 31). In a classic
demonstration of this effect, Street (28) compared the force transmitted longitudinally by single
muscle fibers (frog semintendinosus) with that transmitted laterally via surrounding connective
tissues and neighboring muscle fibers. She found that the single fiber force transmitted laterally
was only slightly less (87 ± 2%) than that transmitted longitudinally. The rate of increase in
tetanic force, however, was slower for lateral than for longitudinal force transmission.
Moreover, the compliance of the surrounding tissues is greater for the fibers that are activated
first during a contraction and declines as muscle force increases. Much of the force generated by
individual muscle fibers, therefore, must be transmitted laterally across the sarcolemma and into
interfiber connective tissues that modulate the force dynamics. Consequently, the force
contributed by a single muscle fiber to whole-muscle force depends on both its contractile
properties and its unique association with the surrounding connective tissues and neighboring
muscle fibers (21, 31). Nonetheless, differences in cross-bridge kinetics and specific tension of
single muscle fibers from vastus lateralis, but not fiber-type proportions, are able to account for
some of the age-related reduction in the maximal power production of the knee extensors (25).
Taken together, these findings indicate that caution is necessary when attempting to deduce the neural drive to muscle from interference EMG recordings and the lack of discrete motor unit types poses a translational challenge to those studying the functional significance of differences in the properties of single muscle fibers.
DISCLOSURES

The authors declare no conflicts of interest, financial or otherwise.

AUTHOR CONTRIBUTIONS

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References


Figure Legend

The force exerted by muscle depends on the characteristics of the activated motor units. In response to synaptic input from descending pathways and peripheral sensory receptors, motor neurons located in the ventral horn of the spinal cord or brain stem generate action potentials that are transmitted along motor axons to muscle fibers and subsequently activate the contractile proteins. The muscle image represents the orientation of the fascicles along the length of the muscle with the distal attachment at the bottom of the image and the muscle fibers attaching to superficial and deep aponeuroses. The forces produced by the activated muscle fibers are transmitted via associated connective tissues to the aponeuroses and then exert a pulling force on the skeleton. The cross-section through the muscle (left of muscle) shows the mosaic pattern of intermingling muscle fibers with different myosin heavy chains isoforms as identified by histochemical assays (only types I, IIA, and IIX are shown). The Motor unit force indicates the twitch force exerted by a single motor unit in response to a single stimulus, whereas the Net motor unit force indicates the attenuating influence of the surrounding tissues on the motor unit twitch force. The activation signal received by the muscle during a voluntary contraction can be recorded as an interference EMG signal that is either rectified and integrated to provide an index of muscle activation or decomposed into the discharge times of individual motor units (9 are shown) to derive a key control signal for muscle activation. The decomposition of surface EMG recordings into single motor unit activity is most effectively accomplished with high-density surface electrodes (16). The control signal derived from the decomposed signal can be estimated from the cumulative train of action potentials discharged by concurrently active motor units (17). Note the similarity in fluctuations in the control signal derived from the motor unit discharge times and the force fluctuations during a steady submaximal contraction (15).