As stated by the authors, the order of motor unit activation is determined not only by axon diameter but also by the additional complicating factor of the distance between stimulating electrode and underlying axons. It is therefore encouraging that, despite these complications, a remarkable similarity is found between the findings of Trimble and Enoka and results from more easily controlled, yet analogous, animal experiments. Results from decerebrate cat experiments, in which stimulating electrodes were placed directly onto nerves and nerve rootlets, were qualitatively identical (see Fig. 8 in the article by Clamann et al1) to those of Figure 1 in Trimble and Enoka’s article. These results, from both human and animal experiments, support the conclusion that direct submaximal activation of motor neurons activates a faster-contracting population of motor units than voluntary (or reflex-generated) submaximal contractions.

The 11% average decrease in contraction times recorded during NMES, in conjunction with a 2% variability in pre- and post-NMES contraction time measurements, is convincing indirect evidence for activation of faster-contracting motor units during NMES. Demonstration of concomitant increases in peak twitch forces would have considerably strengthened this conclusion, yet twitch forces remained unchanged (Tabs. 1, 2). Resolution of this dissociation of results may reside in a more quantitative assessment of H-reflexes and M-responses relative to maximum M-response effects. A fundamental question concerns what particular fraction of the motor neuron pool was evaluated in the control and experimental conditions. Maximum H-reflexes, relative to maximum M-responses, vary widely among individuals, and interpretation of motor neuron excitability changes has been shown to be strongly influenced by the fraction of the pool that is analyzed. Resultant mechanical effects, as measured in this study, may equally be influenced by the size of reflex studied. Tables 1 and 2 reveal wide ranges of peak twitch forces, but no information relative to maximum peak twitch forces is given. If control conditions were restricted to the use of small H-reflexes, a greater proportion of higher-threshold motor neurons would be available for recruitment. Twitch force enhancement, which may be masked when larger control H-reflexes are used, such as may have occurred in this study, might therefore more readily be revealed with smaller control H-reflexes.

The results of Trimble and Enoka’s study nonetheless represent an important step in our understanding of the mechanisms underlying NMES. The lack of a concomitant increase in twitch force with decreases in contraction time warrants caution in a definitive acceptance of their conclusion and points to a need for further experimentation in this important area of clinical research.

Finally, the authors focus on the role of cutaneous afferent feedback as the principal means of altering recruitment order in these experiments. The nonselective stimulation used in NMES would be expected to activate the entire spectrum of neuron sizes, including muscle as well as cutaneous afferent fibers. Although cutaneous inputs have been shown to alter recruitment order, other factors, including muscle afferent modulated presynaptic mechanisms, may be of equal importance. The sorting out of cutaneous and muscle afferent effects is a formidable, yet necessary, task for a more complete understanding and appreciation of the underlying mechanisms associated with NMES.

References


Author Response

Despite substantial paradigmatic differences between reduced-animal experiments and studies on conscious humans, our observations on human subjects were consistent with the animal-derived hypothesis that submaximal electrical stimulation of nerve results in the activation of a faster-contracting population of motor units than that associated with submaximal voluntary activation. This conclusion, which has profound clinical implications, was based on differences in the time course of the twitch elicited by the H-reflex and the M-response and on the effect of submotor neuromuscular electrical stimulation (NMES) on the contraction...
times of the twitches associated with the H-reflex. These observations suggest that NMES may provide a therapeutic means to activate high-threshold motor units that are normally only activated under voluntary conditions at high exercise intensities.

The failure of NMES to induce a parallel increase in the peak force of the average twitch to accompany the decrease in twitch contraction time led Kukulka in his commentary to express some reservations concerning the NMES observations. Because faster-contracting motor units generally exert greater forces than slower-contracting motor units, it seems reasonable to expect that NMES-induced decreases in twitch contraction time should be accompanied by increases in twitch force. This rationale, however, assumes that a similar number of motor units were activated by the H-reflex before and during the NMES. Unfortunately, it is technically difficult to determine the proportion of the motor unit pool that is activated under such conditions. Rather, we could only conclude that the population of motor units activated during NMES was, on average, faster contracting. The absence of a change in twitch force during NMES may simply reflect the activation of fewer motor units. Although the suggestion of Kukulka to determine the proportion of the motor unit pool activated under each condition deserves consideration, the absence of this information should not detract from the significance of the conclusion based on the reduction in contraction time.

Although our results are consistent with those from animal studies, the mechanisms underlying the change in activation caused by electrical stimulation are not identical. When a nerve is placed over a stimulating electrode, as in animal studies, the activation order of the axons can be explained on the basis of biophysical principles largely related to axon diameter. In our study on human subjects, however, we demonstrated that NMES can alter the activation pattern by direct activation of faster-contracting motor units (M-response data) and by the central processing of the sensory effects associated with submotor NMES. Given the demonstrated effects of cutaneous afferent feedback on motor unit recruitment and reflexes, we favor a major role for cutaneous afferents in the sensory effects associated with NMES. Kukulka, however, correctly points out that we do not have definitive data on this issue and that it will be a challenge to determine the contributions of the various neural elements.

The observations made in this study suggest that research on NMES should proceed in two directions: one related to the mechanisms underlying the altered recruitment order of motor units (eg, role of cutaneous and other sensory feedback) and the other focused on the effects on high-threshold, fast-contracting motor units and the consequences of these adaptations for rehabilitation, including the ability to exert maximum force.

Roger M Enoka, PhD
Mark H Trimble, MS, PT

References