CONTROL OF MOTOR UNITS DURING VOLUNTARY FORCE-PRODUCTION: IMPLICATIONS FOR EXERCISE

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We have recently developed a technology that enables studies of the firing properties of a large set (typically 30 to 40) of concurrently active motor units during isometric voluntary contractions ranging from low force levels to maximal voluntary contractions (MVC). With this technology we have executed studies to investigate the behavior of the firing rates of motor units as a function of their recruitment properties during contractions at various force levels. We found that the firing rates have a hierarchical structure wherein the firing rate value of motor units is inversely related to their recruitment threshold, with earlier recruited motor units having greater firing rates at any time and any force level during a contraction. This relationship does not support the opposite notion that has been generally held for the past five decades. Knowing the structure of the firing behavior of motor units during voluntary contractions provides guidance for understanding the performance of muscles during exercise and sports.

Over five decades ago, Eccles et al. (1958) reported that fast conduction velocity motoneurons (higher-threshold, larger-diameter motoneurons) exhibited faster spike potentials (faster after-hyperpolarization) and faster force twitches than lower-threshold, smaller-diameter motoneurons. They posited that the firing rate of motoneurons is regulated by the after-hyperpolarization and matches the force twitch, so that higher-threshold motoneurons would fire faster than lower-threshold motoneurons. Such a construct would provide a fused tetanus of "optimal" size to both low-threshold, slower-twitch motor units and to high-threshold, faster-twitch motor units that would maximize the force production of a muscle. This hypothesis was supported later by Kernell (1965), who reported an inverse relationship between the after-hyperpolarization and the firing rate of electrically stimulated motoneurons. We questioned this supposition when De Luca et al. (1982) found the opposite behavior in voluntary contractions; that is, during constant force isometric contractions higher-threshold motor units fired at lower firing rates than lower-threshold motor units.

The technology used in our earlier work was limited to identifying the firings of only a few (<5) motor units during a contraction. We have now developed a technology capable of automatically decomposing surface EMG signals into their constituent individual action potential trains. Presently the technology can identify the firings of up to 60 active motor units with an average accuracy of 95%, and at times reaching 97% in contractions up to 100% MVC. We have also developed a test that can verify the accuracy of all the identified firing instances (Nawab et al., 2010).

In De Luca and Hostage (2010), we used this technology to study motor unit control during voluntary isometric contractions and found that there exists a hierarchical inverse relationship between the recruitment threshold and the firing rate of motoneurons in a pool during a contraction. That is, the greater the recruitment threshold, the lower the firing rate of a motor unit. We have referred to this behavior as the "onion skin" property (De Luca et al., 1982; De Luca and Erim, 1994). This inverse relationship describes an "operating point" that remains invariant for the motoneurons in a pool, and it is modulated by the excitation to the pool, measured by the force generated by the muscle.

Next, in De Luca and Contessa (in review) we studied the behavior of the motor unit firing rates as the force increased linearly during voluntary isometric contractions. The firing rates of each motor unit increased as exponential functions. Again we found a hierarchical inverse relationship between the recruitment thresholds and the magnitude of the firing rates. The time constant, which determines the rate of increase of the exponential functions, was directly related to the recruitment threshold. Given that the recruitment thresholds are directly related to the size of the soma, it follows that both recruitment and the firing behavior of motor units is a direct consequence of the intrinsic physical properties of motoneurons.

Taken together, these observations indicate that the higher-threshold, larger-size, faster-twitch, faster-fatiguing, mostly-glycolitic motor units fire slower that the lower-threshold, smaller-diameter, slower-twitch, slower-fatiguing, mostly-aerobic motor units. This control scheme is not structured to maximize the force production of a muscle, as hypothesized by Eccles et al. (1958) and Kernell (1965, 2003). Their work taught us that under the unnatural condition of electrical stimulation, higher-threshold motoneurons can be forced to fire faster than lower-threshold ones, but it does not teach us that they do so in voluntary contraction. Thus, the notion of a match between the firing rate and force twitch of motor units to increase the force output of a muscle is not supported by our data. Even allowing for their contention that high-threshold motor units with higher-amplitude shorter-duration force twitches would tetanize at higher firing rates; the greater muscle force thus produced would only last for a brief period of time, because the faster-twitch fibers would fatigue quickly. Thus, the higher force could be sustained only a few seconds.

In contrast, the “onion skin” control scheme is organized to enhance a combination of force and time-to-sustain the force. It is well suited to support the fight-or-flight response over a sustained time sequence, a useful feature to possess for surviving life-threatening circumstances. It also provides an effective economy of force-generation for the earlier-recruited lower-force twitch motor units because their firing rates rise quickly and reach tetanization at relatively low force levels. Thus, providing their maximal contribution at the lower end of the force range and reducing the need to recruit higher threshold motor units during relatively low level contractions, leaves the largest most-fatigable motor units for use during extreme force requirements. The progressive deceleration of the firing rates during linearly increasing force contractions, most dominantly seen in faster-firing lower-threshold motor units, limits the firing rates so that acetylcholine at the neuromuscular junction is not wasted in generating action potentials that would produce force twitches which would not be added to the already achieved tetanization force of the muscles fibers. In so doing, it prolongs the fatigue resistance of the lower-threshold motor units.

Concerning exercise, our findings indicate that the determining factor in the control of motor units during isometric voluntary contractions is the size of the soma of the motoneuron. It appears that fast twitch and slow twitch fibers are regulated by the size and thus by the physical property of the motoneurons. Thus, slow twitch fibers, found in early recruited motor units always participate in a contraction. Fast twitch fibers typically found in relatively high-threshold motor units cannot be accessed without first recruiting slow-twitch fibers. Consequently they cannot be exercised independently of slow twitch fibers during isometric contractions. The best one can do is to perform fast increasing contractions to high force levels. In this paradigm the low-threshold fast-firing slow-twitch motor units would tetanize quickly and the high-threshold slower-firing fast-twitch motor units would be recruited only a fraction of a second later and receive the high level excitation that generates the high force level.

It is useful to remember that the above discussion applies to isometric contractions. Motor unit control schemes for dynamic contractions have not been studied due to technical difficulties in decomposing the EMG signal. However, we tend to believe that it will be the same as that for isometric contractions.

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