HOW ARE THE MOTOR UNITS CONTROLLED TO REGULATE FORCE?

a personal perspective of a three decade long search

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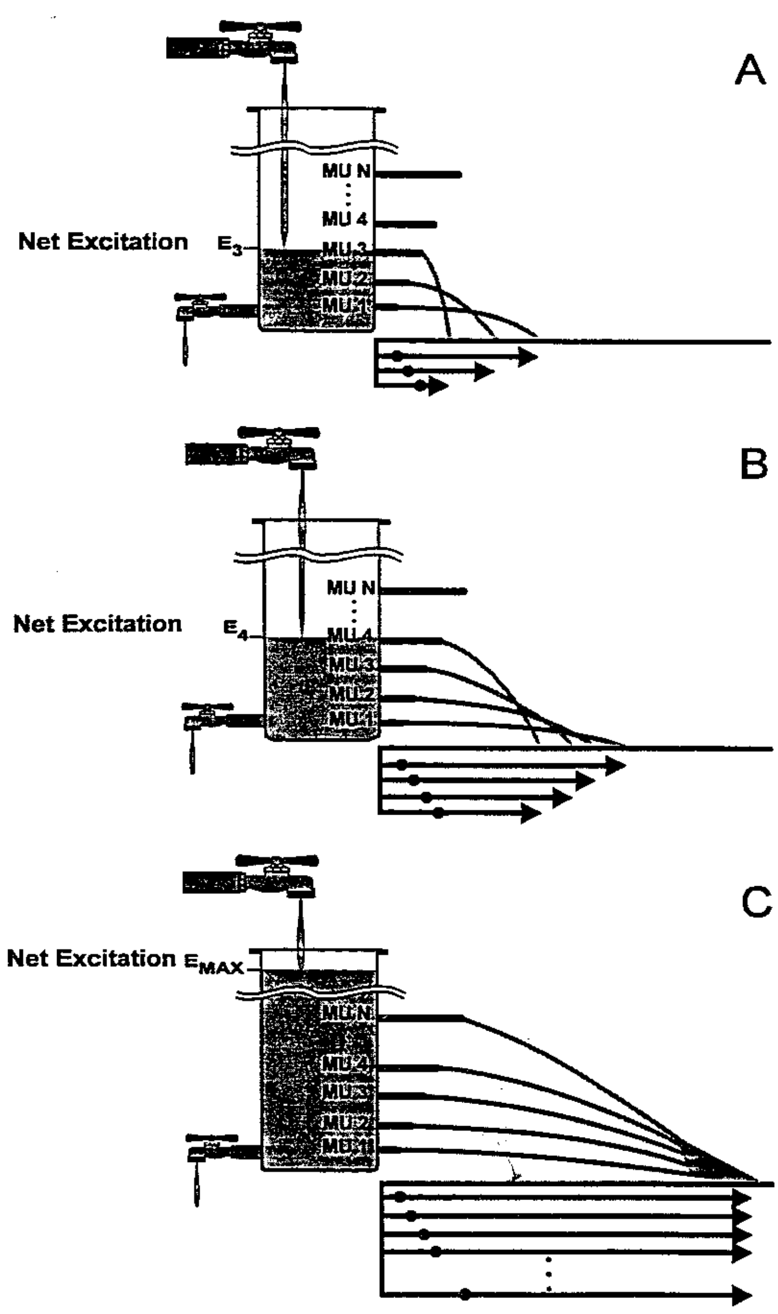
This question has been asked for approximately one century. I first became concerned with this question twenty nine years ago as a fledgling Master's student at this institution, the University of New Brunswick. The answer has been slow in coming throughout the scientific community. Certainly, the slow creep of knowledge is an indication of the complexity of the neuromuscular system and the technical limitations of the tools which are available to study the system. In a real sense, the question is one of engineering as much as one of physiology. In addition to having its own inherent physiological relevance, it also has a practical aspect for individuals interested in controlling prosthetic, orthotic and other electromechanical devices inside and outside the body.

During the past three decades, I have been fortunate to have had the assistance of many colleagues who have shared my passion for this question. One of our first achievements was to develop a method for rigorously studying several (typically 4 or 5, occasional 10) motor units simultaneously throughout the full range of contraction force, including maximal level. This is a non-trivial engineering problem which required the decomposition of a complex EMG signal into the individual action potentials of each discharge of each motor unit contributing to the detected EMG signal. The result of this effort was the Precision Decomposition technique which responds to the need by providing decomposed signals with 100% accuracy. This information provided the firing times of each of the discharges of simultaneously active motor units which, in turn, enabled us to study the behavior of the motor units during specific force-generating contractions. The one important limitation which still constrains our work is that we can only study muscle contractions which are isometric. Thus, all the following discussion is limited to isometric contractions executed at constant force or at linearly increasing forces.

The Common Drive:

Our first noteworthy finding was that the firing rates of motor units fluctuate during a contraction, even one which produces the most constant measurable force. This partially explained why the muscle cannot produce a completely constant (smooth) force. The neuromuscular system is simply not designed to do so. But even more interestingly, we observed that the fluctuations in the firing rates of all the simultaneously active motor units occurred in unison, that is, at the same time. This indicated that the motor units were being activated from a common source. We speculated that this Common Drive excited the motor units at the anterior horn in the spinal cord. This view of the control of the motor units provided a simple mechanism which enable the nervous system to accomplish a complex task.



A simple hydraulic model to summarize the rules governing the regulation of motor units in muscle-force production. The water flow into the tank corresponds to the drive to the motoneuron pool, while the outflow from the individual spouts, and the distance it travels (indicated by a horizontal arrow), corresponds tot he recruitment of a given motor unit and its firing rate. The length of each spout is representative of the initial firing rate, while the circle on the arrow representing the firing rate indicates the initial firing rate below which the motor unit cannot fire. The outlet valve on the bottom left represents the inhibition to the pool. The net accumulation of the water in the vat corresponds to the common drive (excitation-inhibition). Broken lines are used to show that vat height is much greater than the distance between individual spouts. (A) The behavior of firing rates when the drive is only enough to recruit three motor units. (B) The recruitment of a new motor unit, and the increase in the firing rates of already active motor units as the drive to the pool is further increased. (C) The convergence of the firing rates to the same value at maximal firing rates for the case of an extreme drive (water height) where the differences between the individual spout heights become negligible compared with the water level.

The Onion Skin:

The next finding was one which generated controversy. We found that during voluntary contractions, the later recruited motor units fired with a rate smaller than that of earlier recruited motor units. If one plots the firing rates of motor units as a function of time during force increasing contractions, the traces of the firing rates are nested within each other producing the appearance of the various layers of an onion. The finding was contrary to the expected behavior of the muscle if it were designed to generate the maximal possible force because the later recruited motor units produce a mechanically faster twitch and would subsequently require faster (not slower) firing rates to fuse and contribute their potential force. This does not happen, implying that under voluntary contraction the muscle has a reserve capacity to generate force. This is a useful design because if the fast twitch motor units fired fast, they would fatigue quickly. Consequently, the muscle would not be able to sustain high force levels beyond a few seconds, considerably compromising our ability for fight and flight. It appears that the nervous system has evolved to sustain relatively high force levels, but not the potentially maximal, for several seconds.

Firing Rate Behavior:

Two other observations of the firing rate which are consistent with the onion skin have also been made. The first is the existence of a direct relationship between the force recruitment threshold and the initial firing rates of a motor unit. The other is the convergence of the firing rates towards a common value at maximal force level.

The VAT Model:

All the above findings point to the inevitable conclusion that the firing characteristics of the muscle are organized in a well-structured hierarchal fashion which requires simple command forms from eh central nervous system to regulate the force production in the muscle. At least, this is the way in which the system works during isometric contractions.

All the aspects of the firing rate behavior which have been described above can be conceptually captured by a hydraulic model displayed in the accompanying Figure.

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