Motor Unit Firing Behavior in Man

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Abstract. Studies on motor unit firing behavior in man by the decomposition technique are described. The decomposition technique identifies motor unit firing with 100% accuracy at force levels of greater than 80% maximal voluntary contraction (MVC). In all muscles examined, the higher the recruitment threshold of the motor unit, the lower the rate at which it fired at the target level. Smaller muscles, such as those in the hand, recruit their motor units at 0–50% MVC and rely exclusively on firing rate increases to augment force output at 50–100% MVC. Larger muscles, such as those in the leg or arm, recruit motor units at least to 90% MVC, and possibly higher. Their firing rates have a relatively smaller dynamic swing. Thus, smaller muscles rely primarily on firing rate and larger muscles rely primarily on recruitment to modulate their force. High cross-correlation functions in firing rate behavior within a muscle were observed between individual motor unit firing rates at constant force isometric contraction. Thus the nervous system does not control the firing rate of motor units individually. Instead, it acts on the pool of homonymous motoneurons in a uniform fashion. Electrical stimulation of cutaneous receptors tends to increase the recruitment thresholds of low-threshold motor units and to decrease their firing rates, while high-threshold motor units generally exhibit a decrease in recruitment threshold and an increase in firing rate. (Keio J Med 43 (3): 137–142, September 1994)

Key words: motor unit, decomposition, recruitment, firing rate, macroelectromyography

Introduction

Although each motoneuron innervates a number of skeletal muscle fibers, individual muscle fibers are innervated by only one motoneuron. Since all muscle fibers innervated by a motoneuron contract in response to an action potential in the motor axon, in 1925 Liddle and Sherrington introduced the term "motor unit" to indicate that this combination of elements — the motor neuron and all the muscle fibers it innervates — represents the basic and smallest functional unit controlled by motor systems.

How is the force of a muscle increased? There are two ways. One way is to increase the number of active motor units within the motoneuronal pool, a mechanism termed "recruitment". Once a motor unit is recruited, further increases in its force output can be achieved by raising the discharge rate, a mechanism termed "rate coding".

The size principle first proposed by Henneman et al stated that, for a given muscle, motoneurons are brought into activity in the order of their size, with progressively increasing synaptic excitation. In short, smaller motoneurons innervating slow-twitch motor units are recruited at low force thresholds, while larger motoneurons innervating fast-twitch motor units are recruited at increasing force intensity. They also stated that derecruitment occurs in the reverse order of the recruitment. Milner-Brown et al found a positive, linear correlation between the twitch tension of a motor unit and its recruitment threshold in man and concluded that the size principle fits human muscle well.

In regard to rate coding, it has been difficult to decompose the electromyographic signal into its constituent motor unit action potential trains. A relative movement of 0.1mm between the detection surfaces of the electrodes and the active fibers may considerably modify the shapes of the motor unit action potentials (MUAPs). It is obviously difficult to record high threshold units with the concentric needles usually employed in clinical electromyography (EMG). The decomposition technique allows accurate identification of action potential trains of several motor units in an active contraction. For several
years I have been using the decomposition technique recently developed by De Luca and colleagues. This article presents the results obtained by means of the decomposition technique.

**Decomposition Technique**

The term "decomposition" has been commonly used to describe the process whereby individual MUAPs are identified and uniquely classified from a set of currently active motor unit action potential trains (MUAPTs). The process of decomposition involves breaking down the superposition EMG signal that is recorded when more than one motor units is active in the vicinity of the detection electrode. The concept of decomposition is depicted in Fig 1.13

Accurate determination of the activity of individual motor units and of groups of concurrently active motor units requires measurement of the EMG activity accompanying muscle contraction using selective multi-channel indwelling electrode configurations. Suitable detected composite EMG signals can be analyzed and separated into their constituent MUAPTs by utilizing the EMG signal acquisition and decomposition technique. During muscle contractions three EMG signal channels are detected using a quadrifilar electrode consisting of platinum-iridium wires with a bandpass of 1KHz to 10KHz. The three channels of information are used to identify individual MUAP firings from the composite myoelectric signals.8-11

Decomposition is performed by means of a computer-based operator-interactive algorithm. The algorithm scans the EMG signals and identifies MUAPs. Each MUAP is then classified as being created by a particular motor unit by comparing its shape to candidate motor unit templates. Besides template matching, the probability of each motor unit firing at the time is also considered to classify each MUAP. Probability estimates for each motor unit were calculated based on the previous firing history of that motor unit and were updated with each MUAP classification of that motor unit. Superposition of MUAPs was resolved into its component motor unit templates by special computer algorithms that at times required operator-interaction to assist in determining the composition of unknown wave shapes. The use of three channels of information to represent MUAP and motor unit template shapes is critical to the successful classification of candidate wave forms for it provides sufficiently unique representations of an individual motoneuron's MUAP to allow the firing times of each individual motor unit to be consistently and accurately discriminated. The decomposition procedure was proven accurate by independently decomposing EMG signals obtained simultaneously using two needles separately inserted into the same muscle. The decomposition program identifies motor unit firings with 100% accuracy at force levels of more than 80% MVC.10,11

The decomposition technique provides a new investigatory method to study the behavior of several concurrently active motor units and to determine their characteristics beyond those relating to individual motor units. It is also possible to search for information transmission within the nervous system beyond individual neuron-to-neuron interaction and to explore the orchestration of neural activation within and between muscles.12

**Relationship between Recruitment and Firing Rate**

Typical recruitment and firing information obtained by the decomposition technique during controlled isometric contraction is displayed in Fig 2a and 2b.

In Fig 2b, the recruitment and derecruitment order of motor units is observed, demonstrating the size principle. In Fig 2a, the low-threshold motor unit possesses a higher firing rate than the high-threshold motor unit throughout. That is, the higher the recruitment threshold of the motor unit, the lower the rate at which it fires at the target level. In animal studies, however, the maximal firing rate is higher for large motoneurons than for small motoneurons,17 because high threshold motor units tend to have shorter twitch duration and thus require higher
stimulus frequencies to produce fused contractions. The experiments in animals were different from normal voluntary contraction in man. The motoneurons were impaled with microelectrodes and stimulated with a steady current. Thus only one motoneuron was investigated and several motoneurons were never investigated simultaneously. The examples in Fig 2a represent typical observations of the firing rates of motor units in all upper and lower limb muscles.

### Firing Rate and Recruitment Interaction in Different Muscles

The weight of evidence from several recent studies suggests that small muscles, such as those in the hand, are controlled by different schemes than larger muscles, such as those in the leg or arm. Smaller muscles recruit their motor units within 0–50% MVC and rely exclusively on firing rate increases to augment force output at 50–100% MVC. The firing rates of these muscles continuously increase with the force output, reaching values as high as 60 pulses/s. Larger muscles recruit motor units at least to 90% MVC, and possibly higher. Their firing rates have a relatively smaller dynamic swing, generally peak at 35–40 pulses/s, and tend to display a plateau effect. Thus, smaller muscles rely primarily on firing rate and larger muscles rely primarily on recruitment to modulate their force.

The explanation can be found by considering the anatomy and function of the muscles. Small muscles have relatively few motor units. If recruitment were the only means by which additional force could be developed, small muscles would be incapable of smoothly contracting. Smaller muscles are generally involved in performing precise movements. Larger muscles, on the other hand, have many motor units and do not require fine force gradation to accomplish their task. Thus, the firing rates of such muscles do not require continual regulation and do not possess the highly dynamic characteristics seen in smaller muscles.

The functional requirements of the muscle coupled with the anatomical constraints on it determine the firing rate-recruitment characteristics which the nervous system engages to achieve the required task. It appears that the nervous system is configured to balance the contribution of firing rate control and recruitment control to enhance the smoothness of the force output of the muscle.

### Interaction between Motor Units Firing Rates

Figure 3 shows an example of the firing rate behavior of four units during attempted constant-force contraction of the tibialis anterior muscle. Common behavior in the fluctuations in all of the firing rates was observed even at constant force. This commonality becomes more apparent in Fig 4, which shows the cross-correlations of the firing rates at mid contraction. The high correlation values and the lack of any appreciable time shift with respect to the individual correlation functions indicates that modulations of the firing rates occurs simultaneously and to a similar degree in each motor unit. These findings indicate that the nervous system does not control the firing rates of the motor units individually. Instead, it acts on the pool of the homonymous motoneurons in a uniform fashion. The examples in Fig 3 and 4 are typical of the observations made of the firing rates of motor units in all of the upper and lower limb muscles when the muscles act in one direction regardless of where the motor units are located in any individual muscle.

In earlier reports, individual motor unit firing could
be controlled easily by training, but in recruitment and firing rate control, it appears difficult to control individual motor unit separately. With free, unsequenced selection from a pool of motoneurons, there would be innumerable possible combinations, constituting an impossible control problem.

**The Effect of Percutaneous Stimulation on Motor Unit Firing Behaviour**

Clinical observations in patients with disturbances of finger sensory function have shown that input from cutaneous receptors is important for motor control of precise hand movements. In human subjects, changes in sensory input produce considerable behavioural changes. Thus, the effect of digital nerve electrical stimulation on motor unit firing behavior was studied in the first dorsal interosseus muscle.

Stimulation of cutaneous receptors tended to increase the recruitment threshold of most of the motor units recruited under 20% MVC and decrease their firing rates, while high-threshold motor units (those recruited over 30% MVC) generally exhibited a decrease in recruitment threshold and an increase in firing rate.

The effect of digital nerve stimulation on FDI motor
units seems to be similar to the effect of sural nerve stimulation on the cat gastrocnemius and soleus muscle. Stimulation of the sural nerve, for example, produces largely inhibitory post-synaptic potentials in MG motoneurons innervating slow twitch muscle fibers but largely excitation post-synaptic potentials in motoneurons innervating fast-twitch muscle fibers.20 Thus cutaneous afferent input is not distributed in the same way to all motoneurons in both cat and man.

**Macro-EMG and Motor Unit Recruitment Threshold**

In 1980 Stalberg et al.21–23 developed a new recording method, macro-electromyography (macro-EMG). The recording electrode is a modified single-fiber EMG electrode with the cannula insulated except for a 15 mm length at the tip. Because of their large recording surface, macro-EMG electrodes are capable of measuring potentials from a larger portion of the motor unit than conventional EMG electrodes. Thus, both the amplitude and the area of the macro-EMG were found to be positively correlated with the size and number of muscle fibers in the motor unit.

For motor units recruited below 30% MCV, motor unit size measured by macro-EMG correlates well with recruitment threshold and twitch force.24,25 This relationship has not been clearly established at higher force levels, because it is difficult to identify motor unit firing accurately using standard trigger-averaging techniques.21–25 The decomposition program identifies motor unit firing with 100% accuracy at force levels of more than 80% MVC, allowing reliable recording of macro-EMG potentials. We used the decomposition technique to assess the relationship between macro-EMG size and the recruitment of high-threshold motor units.

As depicted in Fig 5, motor units with high recruitment thresholds have large macro-EMG amplitudes and yield linear correlations, probably because the high-threshold motor units have larger, or a greater number of, muscle fibers.26 Our results substantiate those of previous studies for low-threshold motor units, and confirm that the size-principle also applies to high-threshold motor units. In addition, the continuous change in the macro-EMG size and recruitment threshold suggests the presence of a wide spectrum of motor unit types with slightly different properties, rather than a dichotomous division into type 1 and type 2 motor units.

Thus, the macro-EMG is correlated with twitch force and recruitment threshold. We also found a linear correlation between the macro-EMG size and muscle fiber conduction velocity.27 Hence, the macro-EMG is linearly correlated with the recruitment threshold, twitch force, and the muscle fiber conduction velocity of the motor unit. In conclusion, the macro-EMG is a new size-principle parameter useful in clinical research to determine motor unit size.28

**Summary and Future Research**

Motor unit firing behavior has been studied extensively. However there were no correct methods to investigate it. The decomposition technique will provide an objective means for evaluating muscle and nervous dysfunction than any current electrophysiological tool available today. Moreover it will solve the remaining unsettled problems about motor unit control mechanism in health and diseases: For example, the relationship between motor unit firing behavior and motor unit type. These researches about motor units will obviously make a important contribution to rehabilitation medicine, neurology and neurophysiology.

**References**


