

Short Communications

Unusual motor unit firing behavior in older adults

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(Accepted 11 October 1988)

Key words: Motor unit; Aging; Electromyography; Firing rate; Cocontraction; Myoelectric signal

Motor unit firing behavior was studied in the first dorsal interosseus (FDI) and tibialis anterior (TA) muscles of 10 aged subjects during slow, isometric contractions. Previous study in younger individuals had shown that motor units are recruited and derecruited in an orderly manner whereby the early-recruited units are the last to be derecruited. However, there were several examples in the old subjects in which some high-threshold motor units were derecruited at much lower levels of force. Concurrent antagonist firing in an effort to maintain the required precision is considered a likely candidate for such prolonged motor unit activation.

An analysis of the morphological characteristics of motor unit action potentials (MUAPs) by traditional needle electromyography in aged individuals often reveals a number of abnormal findings. The potentials tend to be large in amplitude¹⁰ and the shapes are often complex and polyphasic with occasional satellite potentials²⁰. The duration of the motor unit action potential is usually longer in the aged^{2,3}.

While concentric needle recording has been useful in documenting morphological features of aged motor unit action potentials, a description of motor unit firing behavior and a study of the central motor command has not been previously presented, due to the inherent difficulty of recording a reasonable sample of MUAPs at moderate contraction levels. However, the development of accurate decomposition techniques for the identification of MUAP firing occurrences during moderate force exertion has increased our understanding of motor unit behavior. One such procedure, described by De Luca and co-workers^{14–17}, uses recordings obtained from a specially designed electrode in conjunction with an algorithm which incorporates both template matching and motor unit firing history to identify individual motor unit firing occurrences with considerable accuracy.

Previous experiments using this MUAP identification procedure have reported generally faster firing rates and greater use of rate coding in small muscles than in large muscles, an orderly pattern of motor unit recruitment/derecruitment⁵ and a common modulation of motor unit firing rates for units within a single muscle^{4,6,7}. In this section, we describe some aberrant motor unit firing behavior in normal older subjects. A preliminary report of these results has been presented elsewhere¹³.

The procedure used for recording motor unit activity and obtaining the firing times of individual motor units has been previously described^{14–16}. Briefly, we use a quadrifilar needle electrode consisting of 4 platinum-iridium wires (either 50 or 75 μm diameter) placed in a 25-gauge cannula and exposed at a side port with an interelectrode distance of 200 μm . Three channels of electromyographic information were obtained from this recording configuration. The signals were bandpass-filtered (1–10 kHz) and stored on FM tape along with the force from a transducer. The EMG signals were later digitized off-line at 50 kHz. An operator-interactive decomposition algorithm using both template matching and motor unit firing statistics was used to identify individual motor unit firing times. Earlier studies had demonstrated that this technique

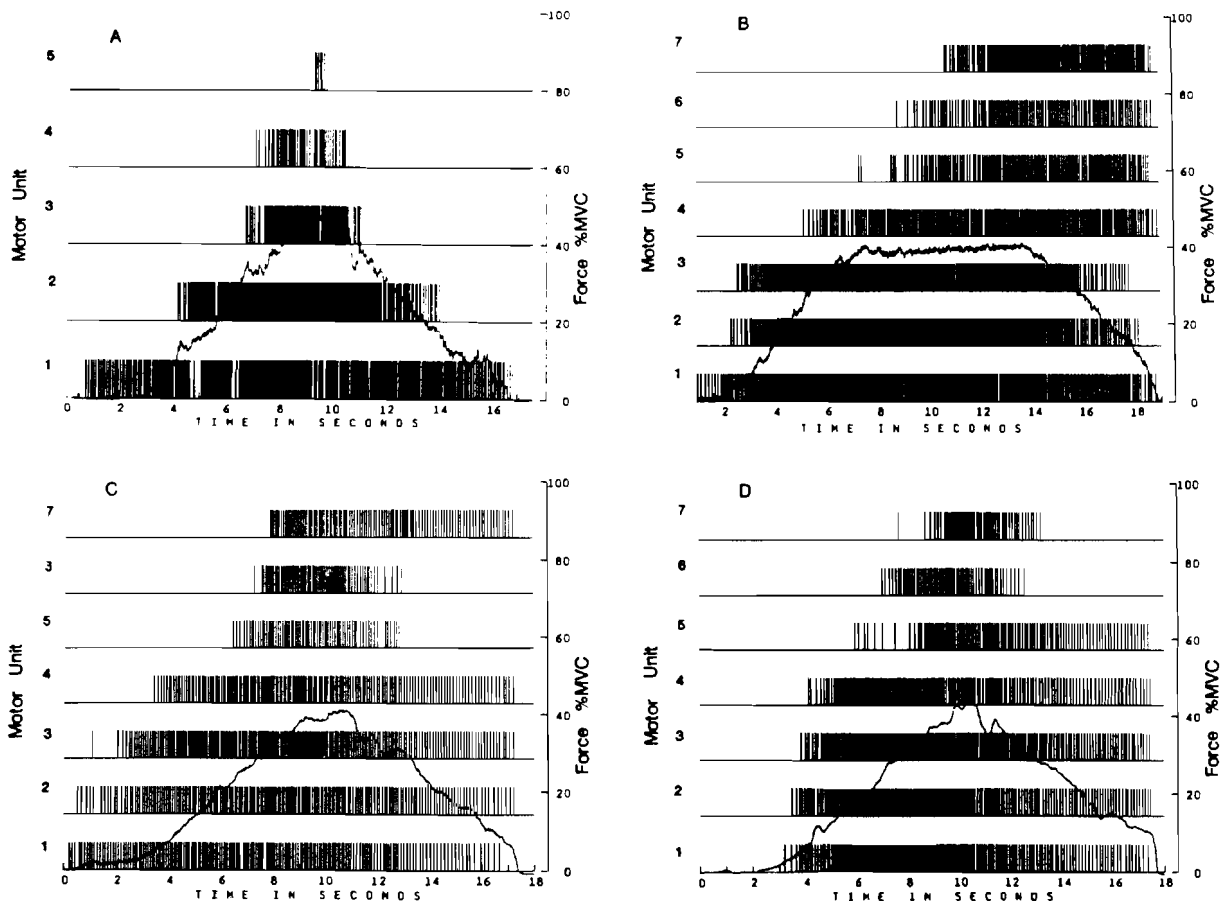
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yields motor unit firing times with an accuracy approaching 100%^{14,15}.

Motor unit activity was recorded in 10 aged individuals (mean age 75.1 ± 10.1) with no known neuromuscular disorders. Recordings were made from the first dorsal interosus (FDI) while the subject isometrically abducted the index finger and from the tibialis anterior (TA) muscle during isometric ankle flexion. A PDP-11 computer was used to present force trajectories on a monitor. Two different trajectories were generally used. In one condition, the trajectory required the subject to reach 50% of maximal voluntary contraction (MVC) in 5 s (10% MVC/s), remain at 50% MVC for 8 s, and then relax the contraction over a 5-s period. The second condition involved a triangular contraction,

requiring the subject to reach 50% MVC in 8 s and then return to the zero force level in 8 s. Each individual was required to track the force trajectory as accurately as possible. Several practice trials were given before recording motor unit activity.

Typical results are presented in Fig. 1. In Fig. 1A, a normal pattern of recruitment/derecruitment can be observed in which the earliest-recruited motor units were also the last to be derecruited as the force was slowly graded to 50% MVC. Unusual motor unit behavior in a 63-year-old subject during contraction of the FDI muscle is seen in Fig. 1B. The first 3 units recruited exhibited normal behavior and were recruited and derecruited in an orderly manner. However, the last 4 units recruited all continued firing until nearly the end of the contraction. Of



1. Motor unit firing patterns. Each vertical tic represents one motor unit firing. The force is indicated by the solid line (force level on right ordinate). A: normal pattern from FDI muscle in 67-year-old subject. Firing times of 5 motor units are shown. The early-recruited motor units are also the last to be de-activated. B: FDI muscle in 63-year-old subject. Note that some of the high-threshold units were not derecruited until the end of the contraction. C: same subject as in B. TA muscle. D: again, same subject as in B and TA muscle. This contraction was recorded later in the same test session.

particular interest is unit #7 which began firing during a steady 40% MVC force plateau and increased its firing rate after 1–2 s. This unit was among the last to be derecruited.

These instances of unusual motor unit behavior were not confined to the FDI muscle. An example from the TA is presented in Fig. 1C. Here the task was to produce a slow increase in force to 50% MVC and then a slow relaxation. All older subjects had more difficulty tracking these trajectories than the younger individuals tested in previous studies. In this contraction, the subject did not reach the 50% MVC level before the trajectory required relaxation, and did not relax fast enough. Consequently, a sudden drop in force was produced at 10% MVC. Nevertheless, motor unit 7 was recruited at 33% MVC and was still firing at 12% MVC during the relaxation phase at which time it was derecruited with a final doublet firing (two firings with a short interpulse interval).

This tendency for late-recruited units to be derecruited at low force levels was observed in 3 of the 10 subjects tested, but not during every contraction. For example, Fig. 1D shows the firing times of 7 motor units from the same subject and muscle as in 1C, and recorded several minutes later. Although there is some difference between the recruitment and derecruitment thresholds of motor units 6 and 7, the difference is on the order of a few percent of maximal force and does not resemble the gross discrepancy seen in Figs. 1B and 1C.

In normal, young adults, the earliest recruited units are generally the last to be derecruited in these types of slow, isometric contractions⁵, providing indirect support for the size principle of motor unit recruitment in humans¹¹. The data presented in this paper indicate that a different pattern of recruitment/derecruitment may exist in older adults. There are several possible explanations which could account for these data.

Fatigue. It does not seem likely that these contractions were fatiguing. Each contraction was less than 20 s in duration, at a peak intensity of 40–60% MVC which was only maintained for a few seconds before the subject began the relaxation phase. Moreover, the available studies indicate that older adults generally manifest as much muscular endurance (on a relative force level) as do younger

individuals²². Finally, the results presented in Fig. 1C and D tend to negate a fatigue-related explanation. Although Fig. 1D (which follows Fig. 1C in the same test session) has some peculiarities, the 'run-on' behavior typical of motor unit 7 in Fig. 1C is not observed in Fig. 1D. Thus, a contraction in which motor units are recruited/derecruited in a reasonably normal fashion can follow one in which the later-recruited units are turned off later than usual.

Accuracy of decomposition. An obvious question is whether these results represent an accurate identification of the motor unit firing times. This issue has been the topic of previous papers which have demonstrated that in our hands, the decomposition technique used can accurately identify several motor unit action potential trains^{15,17} in an active contraction. Moreover, in the present series of experiments, some high-threshold units would have had to have been continually (and mistakenly) identified to produce this 'run-on' behavior. This is highly unlikely, and in any event, should have been observed in earlier studies with younger subjects. Thus, it seems highly unlikely that the observed behavior is due to methodological problems associated with accurate decomposition.

Abduction vs flexion. The FDI does function primarily to abduct the index finger, but also serves as a synergist for flexion of the second digit. Thus, an additional explanation for these data is that the subjects were performing pure abduction during the initial phase of the contraction, but a combination of abduction and flexion during the relaxation phase. We cannot eliminate this possibility of a mixed abduction–flexion contraction, as we did not record flexion force during the contraction. However, this explanation seems unlikely for several reasons. The threshold for recruitment/derecruitment has been reported to be different in FDI units depending on whether the muscle is used as a flexor or as an abductor⁸. More recent evidence, however, has failed to support the idea that the direction of force production alters recruitment threshold in FDI motor units²¹. Also, the needle used in these experiments is quite selective and it does not seem likely that we could be recording from units in both flexor and abductor FDI heads at the same time. In aged muscle the two heads of the FDI are more anatomically distinct than in younger muscle. So this

abnormal pattern of motor unit behavior is less likely to be seen from the same electrode in older adults. We have observed that the absolute force level for recruitment can differ somewhat from that for derecruitment⁵ and some minor deordering of derecruitment threshold at very closely spaced force levels can occur (unpublished observations). However, the gross failure to cease motor unit activity at a force level close to that for recruitment (as seen in Fig. 1) has not previously been observed in younger subjects, nor has the dramatic modification in derecruitment order been previously reported.

Antagonist co-contraction. Perhaps the most plausible explanation is that these subjects who exhibited the motor unit 'run on' behavior were co-activating antagonists in an effort to maintain precision. All of the subjects tested in this experiment had considerably more difficulty executing accurate contractions than younger subjects performing the same tasks. Younger subjects were able to track these trajectories accurately after only one or two practice trials, and were often able to follow two trajectories (requiring simultaneous contraction of two different muscle groups) after only a few practice trials¹². The loss of motor units which accompanies the aging process^{1,3} is one explanation for the reduction in ability to produce precisely controlled force. The motor units that remain are larger and less capable of finely grading force. One strategy for maintaining precision would be to increase the activation of functional antagonists (the second dorsal interosseus and first palmar interosseus in the case of the FDI, and soleus-gastrocnemius group for the TA).

Such a 'stiffening movement' or '*Versteifungsbewegung*' was reported as early as 1926 by Wachholder and Altenburger^{23,24} and has been reviewed by others⁹. As an extreme example, one can envision a situation in which considerable motor unit activity occurs in muscles on both sides of a joint, with little or no external force produced. There is some indication that one of the early phases of skill acquisition may be accompanied by increased co-contraction¹⁹. Increased co-contraction would allow the subject to increase the net force more slowly and also relax more slowly than might be possible without antagonist activity. In the context of the present results, if increased antagonist activation occurred during the relaxation phase, it would

explain the need to maintain motor unit activity in some motor units at force levels well below recruitment threshold. This behavior would be particularly evident in the relaxation phase, where the ability to maintain precision in the force output is more challenging^{5,6}.

The antagonist co-contraction explanation does not fully explain the aberrant behavior evident in Fig. 1B. Here, the early-recruited, low-threshold motor units exhibit rather normal recruitment-derecruitment behavior, however, the late-recruited units evidence patterns of abnormal derecruitment. Within the same muscle, then, while some units behave 'normally', other motor units demonstrate irregular firing patterns. Thus, it seems that the aging process might affect motor unit behavior within muscles as well as possible modifications to control strategies involving agonist-antagonist pairs.

Inasmuch as there is a gradual process of denervation and reinnervation in aged muscle¹⁸, it is tempting to suggest that these aberrant units represent reinnervating motor units. However, this would still fail to explain the unusual firing behavior. If these aberrant fibers are innervated by small motoneurons which have increased their territory by innervating other muscle fibers, why were these motor units not recruited earlier in the contraction? Similarly, if these aberrant fibers are innervated by large motoneurons containing degenerating axonal twigs, why does the unit activity persist so long in the contraction?

We have described an abnormal pattern of motor unit behavior in aged adults, whereby the order of motor unit derecruitment is different than the order of recruitment. Moreover, in some high-threshold units the threshold force of recruitment differs from the threshold force of derecruitment. Whatever the explanation for this unusual motor unit activity, these results demonstrate that motor unit behavior during voluntary activity in older individuals can indeed be markedly different from that observed in young subjects.

We are grateful for the assistance afforded by Dr. D. Stashuk. This work was supported by NIH NIA NRSA 1 F33 AG05405-01 and the Liberty Mutual Insurance Company.

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