Motor Unit Substitution in Long-Duration Contractions of the Human Trapezius Muscle

R. H. WESTGAARD[1,2] AND C. J. DE LUCA[1]
[1]*NeuroMuscular Research Center and Department of Biomedical Engineering, Boston University, Boston, Massachusetts 02215; and* [2]*Division of Organization and Work Science, Norwegian University of Science and Technology, N-7491 Trondheim, Norway*

Westgaard, R. H. and C. J. De Luca. Motor unit substitution in long-duration contractions of the human trapezius muscle. *J. Neurophysiol.* 82: 501–504, 1999. We examined the activity pattern of low-threshold motor units in the human trapezius muscle during contractions of 10 min duration. Three procedures were applied in sequence: *1*) static contraction controlled by maintaining a constant low level of the surface electromyogram (EMG)-detected root-mean-square signal, *2*) a manipulation task with mental concentration, and *3*) copying a text on a word processor. A quadrifilar fine-wire electrode was used to record single motor unit activity. Simultaneously, surface electrodes recorded the surface EMG signal. During these contractions, low-threshold motor units showed periods of inactivity and were substituted by motor units of higher recruitment threshold. This phenomenon was not observed during the first few minutes of the contraction. In several cases the substitution process coincided with a short period of inactivity in the surface EMG pattern. Substitution was observed in five of eight experiments. These observations may be explained by a time-variant recruitment threshold of motor units, sensitive to their activation history and temporal variation in the activity patterns. We speculate that the substitution phenomenon protects motor units in postural muscles from excessive fatigue when there is a demand for sustained low-level muscle activity.

INTRODUCTION

We were interested in exploring the behavior of motor units during long-term sustained contractions. Alterations in the recruitment and derecruitment of motor units during sustained contractions have been the subject of discussion for decades. For example, the concept of motor unit substitution has been postulated to offset the effects of fatigue (Person 1974). This concept describes a mechanism where higher threshold motor units are recruited to replace lower-threshold fatigued units that have stopped firing. A related concept, often used synonymously, is motor unit rotation (Sale 1987). By this it is meant that motor units alternate their activity in a cyclical fashion, such that substitution of one motor unit for another would be followed by back-substitution of the original unit. Although this concept is often mentioned within the clinical community, it has been reported by only a few researchers (Fallentin et al. 1993; Sjøgaard et al. 1986), and these reports have generated more controversy than conviction. Person (1974), Kato et al. (1981), and Fallentin et al. (1993) among others describe recruitment and silencing of motor units during a contraction, yet none of their studies provides evidence of constant joint torque or muscle force. De Luca and Forrest (1973) and De Luca et al. (1982) found no derecruitment during constant-force isometric contractions of moderate duration at different force levels. However, recently De Luca et al. (1996) have reported one case, where a new motor unit was recruited at the 20-s mark of a constant-force isometric contraction.

Some of the controversy may be due to the different durations of the contractions studied because altered motor unit behavior may be more evident after a contraction has persisted for some time. The inherent technical difficulties in providing assurance that the activity and inactivity phases of individual motor units are indeed monitored correctly present another source of controversy. The issue of proper motor unit identification is difficult because most investigators do not describe their identification criteria, and those that do rely on action potential shape similarities on the basis of only one electromyogram (EMG) channel. It is our experience that this approach can be prone to error, especially if the needle electrode position cannot be guaranteed to vary less than 0.1 mm.

METHODS

Four healthy subjects, three males and one female, volunteered for the study. Each subject read and signed an informed consent form approved by the local Institutional Review Board before participating in the study. We studied the trapezius muscle and detected the surface and intramuscular EMG signals. The surface EMG signal was used to indicate the level of muscle contraction; whereas the indwelling EMG signal was used to study the firing behavior of the motor units. Three experimental procedures, each of 10 min duration, were carried out in sequence: *1*) a static contraction, *2*) a manipulation task with mental concentration, and *3*) copying a text on a word processor. For the static contraction, the subject was seated; straps were placed over the shoulders and connected to force transducers below each shoulder. The subject was asked to maintain a static contraction of the trapezius muscles by elevating the shoulders. The contraction level was controlled by feedback of the root-mean-square value of the detected surface EMG signal. The contractions were performed at levels of ~4% of the signal detected at maximal voluntary contraction (EMG_{max}). In one experiment, the contraction was extended to 50 min due to a particularly favorable recording situation.

For the two other procedures, the subjects were instructed to maintain their activities without interruption, but the contraction level was not controlled. In the task with mental concentration, a two-choice reaction-time test was presented on a PC monitor (Westgaard and Bjørklund 1987). The subject was comfortably seated in an office chair in front of the monitor. An open ("frame") and a solid ("brick") quadrangle were placed in a square pattern, and an alphanumeric

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

suggestion on how to move the brick to superimpose on the frame was given. The subject responded by pressing one of two keys, "correct" or "wrong," by the right or left index finger. A new position of the "brick" and "frame" in the square pattern and a new suggestion then appeared. The typing task was performed in the same seated position on a regular word processor.

The surface EMG signal was detected with an active parallel-bar (bar size: 1 mm by 10 mm, located 10 mm apart) differential electrode (DelSys). The electrode was positioned with the medial bar 20 mm lateral to the midpoint of the line between the C_7 spinous process and the acromion (Jensen et al. 1993). The surface EMG signal was band-pass filtered at 10–1,000 Hz. The intramuscular EMG signal was recorded with specialized quadrifilar wire electrodes. These electrodes were constructed by bonding together four 50-μm nylon-coated platinum wires. The wire bundle was cut transversely, exposing only the cross section of the wires. The wire bundle was placed in a 27-gauge needle, and a hook was formed at ~1 mm from the exposed end of the wire. The needle was inserted to a depth of ~10 mm at a location ~10 mm medial to the midpoint of a line between the C_7 spinous process and the acromion. The needle was removed and the wire bundle remained lodged in the muscle. Three pairs were chosen as the differential input to the amplifiers. The signals were band-pass filtered from 1 to 10 kHz. All the EMG signals were stored on an analog FM tape recorder and were subsequently digitized.

The intramuscular EMG signals were resolved into the individual motor unit firing trains using the Precision Decomposition technique (De Luca 1993; LeFever and De Luca 1982). This technique uses template matching, template updating, firing probabilities, and superposition resolution to identify the individual firing times of the motor units with up to 100% accuracy (Mambrito and De Luca 1984). The firing rates of the motor units were obtained by passing the time series of the interpulse intervals through a Hanning window and inverting the output.

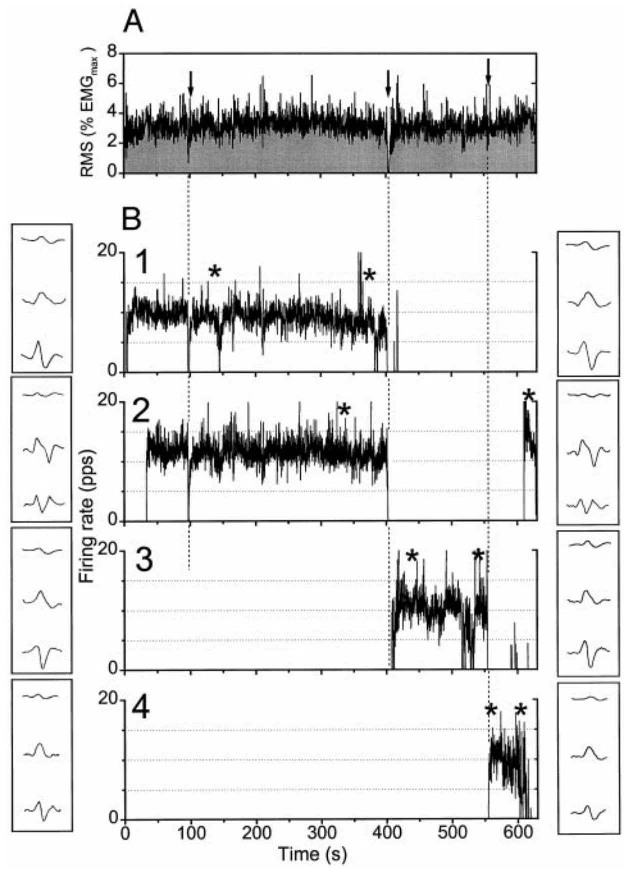

FIG. 1. Surface electromyogram (EMG) response (*A*) and firing pattern of 4 motor units (*B*) during a static, 10-min contraction. Firing rates are low-pass filtered at 0.5 Hz. Two examples of motor unit templates for each unit (shown next to the corresponding motor unit) were extracted at times marked by asterisks. Arrows and vertical dotted lines mark positions of special events in the recording (cf. text for details).

RESULTS

Three experiments with static contraction, two with mental concentration and three typing experiments were successful; i.e., at least two motor units with sustained activity patterns were identified and thereby had the potential of demonstrating motor unit substitution.

The results of a static contraction experiment lasting 10 min are presented in Fig. 1. Figure 1*A* shows the surface EMG signal; Fig. 1*B* shows the firing rates of four motor units that could be tracked during the complete duration of the isometric contraction. The *insets* next to the plots of firing rates present the templates of the motor unit action potential, as detected in the three channels of the quadrifilar wire electrode. The templates were extracted at times marked by asterisks in the firing rate plots. Note that the templates remained essentially unchanged during the contraction. This indicates that the electrode has not moved during the contraction and that the same motor unit is actually being recorded. Any slight movement of the electrode would produce noticeable changes in the shape of at least one of the templates. We have noted that with needle quadrifilar electrode having the same dimension and arrangement, a movement of 0.1 mm causes dramatic changes in the shape in at least one channel.

Figure 1 provides an interesting example of motor-unit firing behavior. Although the subject was attempting to maintain the surface EMG level constant, the amplitude of the surface EMG fluctuated throughout the contraction. *Motor unit 1* has the lowest recruitment threshold. As the amplitude of the EMG signal increases slightly, a second motor unit is recruited. At ~100 s into the contraction, an abrupt decrease occurs in the amplitude of the EMG signal (indicated by the 1st arrow and vertical dotted line), which was accompanied by a decrease in the firing rates of *motor units 1* and *2,* but both recovered without a cessation of firing. At the 405-s point, there is another abrupt decrease in the amplitude of the EMG signal (indicated by the 2nd arrow and vertical dotted line), signifying a decrease in drive to the motoneuron pool. *Motor units 1* and *2* both stop firing. Within a few seconds the excitation has recovered to the level before the depression, as evidenced by the subsequent increase of the EMG amplitude, but the two motor units are not recruited anew. Instead, a third motor unit is recruited. A little later the EMG level transiently surpasses the level previous to the decrease, and a short period of activity is observed for *motor unit 1.* At 560 s the EMG activity shows a transient increase followed by a depression and recovery (3rd arrow and vertical line). During this sequence the third unit stops firing and a fourth unit is recruited. *Motor units 1* and *2* remain silent. At 610 s the second motor unit begins firing again. *Motor unit 1* remains silent for the duration of the experiment.

Figure 2 presents an example of motor unit substitution during a test with mental concentration. This procedure is known to elicit sustained, low-level surface EMG activity in

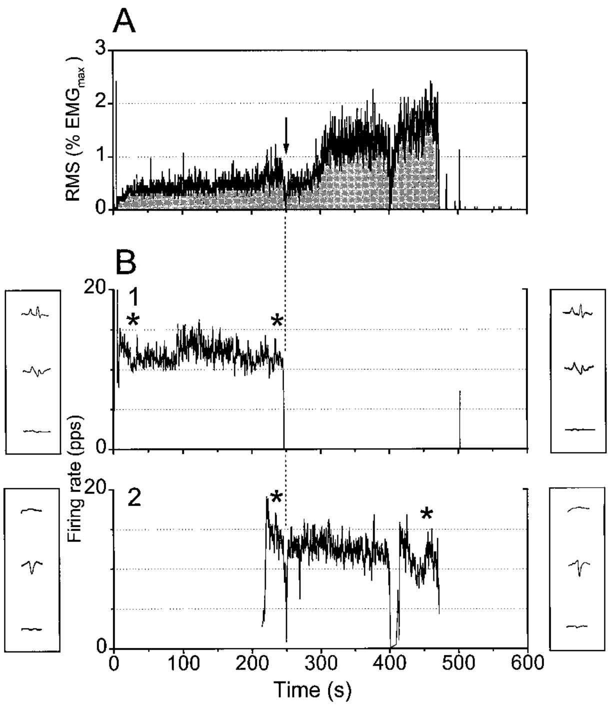

FIG. 2. Surface EMG response (*A*) and firing pattern of 2 motor units (*B*) during a 10-min experiment with introduction of mental concentration. Firing rates are low-pass filtered at 0.5 Hz. Two examples of motor unit templates for each unit (shown next to the corresponding motor unit), were extracted at times marked by asterisks. Arrow and vertical dotted line mark position of a temporary depression in the surface EMG. Note that the 1st motor unit briefly returns toward the end of the experiment.

the trapezius muscle (Westgaard and Bjørklund 1987), due to sustained activation of individual motor units (Wærsted et al. 1996). *Motor unit 1* is active at the beginning of the test. A second unit is recruited at 210 s, when the surface EMG shows a small increase. At 250 s, there is a transient depression in surface EMG (arrow and vertical line). Both motor units are silenced at the depression. The second unit recovers and continues firing, while *motor unit 1* remains silent, despite its lower activation threshold and increasing surface EMG activity during the next 3 min.

Figure 3 demonstrates motor unit substitution during typing. Five units were monitored, of which four were active from the beginning of the experiment. The first two motor units remained active throughout the experiment, while *motor units 3, 4,* and *5* were silenced during a downward trend in the surface EMG amplitude. Note that the motor unit with the lowest threshold of the three (*3*) ceases firing first, progressively followed by *4* and *5* as the EMG activity continues to decrease. *Motor units 3* and *4* remained silent for 3–4 min, before recovering. The fifth motor unit was recruited late, during a slow upward trend in surface EMG amplitude. The firing of *motor unit 5* showed short interruptions, coinciding with depressions in the surface EMG (arrows and vertical lines), but the unit was generally active during the time when *units 3* and *4* were silent.

Of the experiments that potentially were able to show substitution, substitution was observed in two of three experiments with static contraction, two of two experiments with mental concentration, and one of three experiments with typing.

DISCUSSION

Our results provide clear evidence of motor unit substitution. The system for motor unit identification, with three template representations of the motor unit action potential, provides a highly sensitive means of identification. The consistency of three different shapes rules out the disappearance and reappearance of a motor unit action potential due to electrode movement, especially as continuous monitoring of other active motor units during a pause in firing of one motor unit verifies stable recording conditions (Basmajian and De Luca 1985). A potential problem would be if the motor units are silenced and not observed again. However, in all experiments where we found substitution, at least one of the early recruited motor units that are silenced, reappears. Our data show that the template (in 3 channels) of the motor unit action potentials does not change during a contraction when the firing rate is continuously sustained. The continual presence of the surface EMG signal indicated that the motor unit firing behavior was not a consequence of the muscle turning on or off. Additionally, we present evidence of differential firing behavior among concurrently active motor units. And finally our observations cannot be attributed to the unstable behavior of higher-threshold motor units, firing only marginally above their recruitment threshold. The persistent, although erratic firing of *motor unit 5* in Fig. 3 supports this point because it sustains firing when others are silenced.

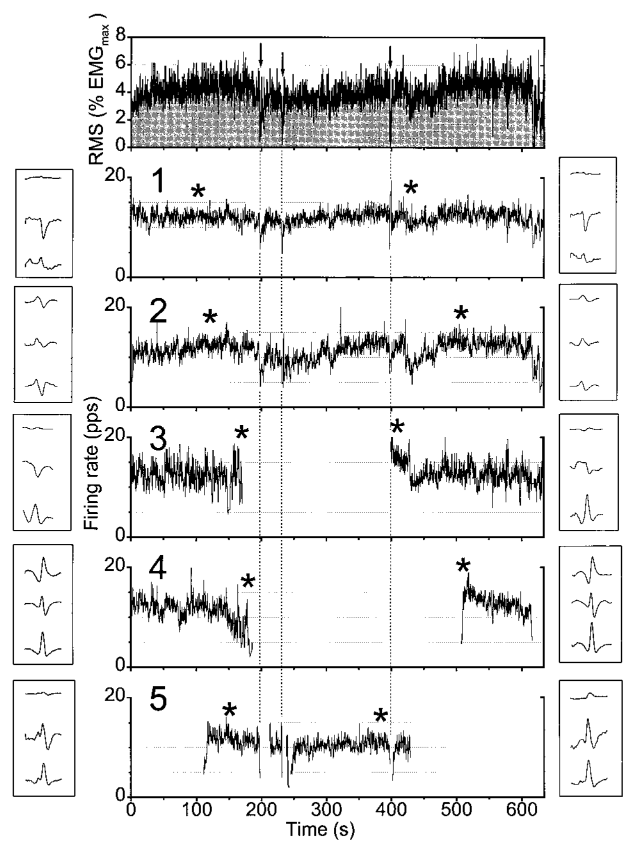

FIG. 3. Surface EMG response and firing pattern of 5 motor units during 10 min of copying text on a word processor. The firing rates are low-pass filtered at 0.5 Hz. Two examples of motor unit templates for each unit (shown next to the corresponding motor unit) were extracted at times marked by asterisks. Arrows and vertical dotted lines mark positions of special events in the recording (cf. text for details).

The complete behavior of the firing rates displayed in Fig. 1 may be explained by considering that the recruitment threshold of these relatively low-threshold motor units increases during the contraction. Apparently this adaptation is slow and is not evident at the 100-s mark of the low-level contraction we studied (Fig. 1). At the 405-s mark, when the excitation to the motoneuron pool increases after a temporary decrease, the recruitment threshold of a third motor unit (which at the beginning of the contraction was too high to be recruited) is now apparently less than the increased threshold of the first two motor units. The third motor unit is substituted by a new unit at the 550-s mark, as the recruitment threshold of the first two is still too high. In response to an increase in the excitation, at the 610-s mark the second motor unit begins to fire, presumably as a result of recovery of threshold after the 3-min period of silence. The behavior of the firing rates in Figs. 2 and 3 may be interpreted with the same explanation.

Motor unit substitution was not seen during the first few minutes of a contraction, even among units that later displayed this phenomenon. This would explain why substitution is not observed in conventional studies of motor unit firing behavior, where the contractions studied are typically <1 min (e.g., De Luca and Forrest 1973; De Luca et al. 1982). Even in our study, substitution was not observed in three of eight experiments where the phenomenon potentially could have occurred. In two of these experiments, new motor units were recruited late in the contraction, while motor units already active continued firing. It is conceivable that motor units not observed by the intramuscular electrode were silenced, to allow for the unchanged level of surface EMG.

Our observations are consistent with those of Person (1974). However, the design of our experiment now provide proof that motor unit substitution occurs during prolonged contraction. Person reported that the motor unit substitution was noticeable when the subject executed postural shifts. Our results indicate that substitution often occurs as a consequence of a decrease followed by an increase in the excitation to the motoneuron pool. A postural shift is a possible, but not a necessary inducer of such a modulation of the excitation.

It is tempting to speculate that this substitution enables the muscle contraction to be maintained longer and may possibly protect motor units in postural muscles from excessive fatigue in sustained contractions.

The technical assistance of M. Khouri is greatly appreciated. The experiments and data analysis were performed at the Neuromuscular Research Center of Boston University.

This work was supported by grants from the Liberty Mutual Insurance Company and a traveling research grant to R. H. Westgaard from the Norwegian Research Council.

Address for reprint requests: R. H. Westgaard, Div. of Organization and Work Science, Norwegian University of Science and Technology, N-7491 Trondheim, Norway.

Received 5 February 1999; accepted in final form 9 March 1999.

REFERENCES

BASMAJIAN, J. V. AND DE LUCA, C. J. *Muscles Alive.* Baltimore, MD: Williams & Wilkins, 1985.

DE LUCA, C. J. Precision decomposition of EMG signals. *Methods Clin. Neurophysiol.* 4: 1–28, 1993.

DE LUCA, C. J., FOLEY, P. J., AND ERIM, Z. Motor unit control properties in constant-force isometric contractions. *J. Neurophysiol.* 76: 1503–1516, 1996.

DE LUCA, C. J. AND FORREST, W. J. Some properties of motor unit action potential trains recorded during constant force isometric contractions in man. *Kybernetik* 12: 160–168, 1973.

DE LUCA, C. J., LEFEVER, R. S., MCCUE, M. P., AND XENAKIS, A. P. Control scheme governing concurrently active human motor units during voluntary contractions. *J. Physiol. (Lond.)* 329: 129–142, 1982.

FALLENTIN, N., JØRGENSEN, K., AND SIMONSEN, E. B. Motor unit recruitment during prolonged isometric contractions. *Eur. J. Appl. Physiol.* 67: 335–341, 1993.

JENSEN, C., VASSELJEN, O., AND WESTGAARD, R. H. The influence of electrode position on bipolar surface electromyogram recordings of the upper trapezius muscle. *Eur. J. Appl. Physiol.* 67: 266–273, 1993.

KATO, M., MURAKAMI, S., TAKAHASHI, K., AND HIRAYAMA, H. Motor unit activities during maintained voluntary muscle contraction at constant levels in man. *Neurosci. Lett.* 25: 149–154, 1981.

LEFEVER, R. S. AND DE LUCA, C. J. A procedure for decomposing the myoelectric signal into its constituent action potentials. I. Technique, theory and implementation. *IEEE Trans. Biomed. Eng.* 29: 149–157, 1982.

MAMBRITO, B. AND DE LUCA, C. J. A technique for the detection, decomposition and analysis of the EMG signal. *Electroencephalogr. Clin. Neurophysiol.* 58: 175–188, 1984.

PERSON, R. S. Rhythmic activity of a group of human motoneurones during voluntary contraction of a muscle. *Electroencephalogr. Clin. Neurophysiol.* 36: 585–595, 1974.

SALE, D. G. Influence of exercise and training on motor unit activation. In: *Exercise and Sport Science Reviews,* edited by K. B. Pandolf. London: Macmillan, 1987, vol. 15, p. 95–151.

SJØGAARD, G., KIENS, B., JØRGENSEN, K., AND SALTIN, B. Intramuscular pressure, EMG and blood flow during low-level prolonged static contraction in man. *Acta Physiol. Scand.* 128: 475–484, 1986.

WESTGAARD, R. H. AND BJØRKLUND, R. Generation of muscle tension additional to postural load. *Ergonomics* 30: 911–923, 1987.

WÆRSTED, M., EKEN, T., AND WESTGAARD, R. H. Activity of single motor units in attention-demanding tasks: firing pattern in the human trapezius muscle. *Eur. J. Appl. Physiol.* 72: 323–329, 1996.