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Motor Control of Low-Threshold Motor Units in the Human Trapezius Muscle

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Westgaard, R. H. and C. J. De Luca. Motor control of low-threshold motor units in the human trapezius muscle. *J Neurophysiol* 85: 1777–1781, 2001. The firing pattern of low-threshold motor units was examined in the human trapezius and first dorsal interosseous (FDI) muscles during slowly augmenting, low-amplitude contractions that were intended to mimic contractile activity in postural muscles. The motor unit activity was detected with a special needle electrode and was analyzed with the assistance of computer algorithms. The surface electromyographic (EMG) signal was recorded. Its root-mean-square (RMS) value was calculated and presented to the subject who used it to regulate the muscle force level. In the trapezius, there was minimal, if any, firing rate modulation of early recruited motor units during slow contractions ($\leq 1\%$ EMG_{max}/s), and later recruited motor units consistently presented higher peak firing rates. As the force rate of the contraction increased (3% EMG_{max}/s), the firing rates of the motor units in the trapezius approached an orderly hierarchical pattern with the earliest recruited motor units having the greatest firing rate. In contrast, and as reported previously, the firing rates of all motor units in the FDI always presented the previously reported hierarchical “onion-skin” pattern. We conclude that the low-threshold motor units in the postural trapezius muscle, that is the motor units that are most often called on to activate the muscle in postural activities, have different control features in slow and fast contractions. More detailed analysis revealed that, in the low force-rate contractions of the trapezius, recruitment of new motor units inhibited the firing rate of active motor units, providing an explanation for the depressed firing rate of the low-threshold motor units. We speculate that Renshaw cell inhibition contributes to the observed deviation of the low-threshold motor units from the hierarchical onion-skin pattern.

INTRODUCTION

Many studies have shown that the average firing rates of motor units during force-varying contractions have a hierarchical organization, with higher firing rates for early recruited units (De Luca and Forrest 1973; De Luca et al. 1982; Person and Kudina 1972; among others). When mean firing rates of motor units with different recruitment threshold are plotted for a contraction with a trapezoid force profile, the complement presents the appearance of an “onion skin.” That is, at any given force level, the lower-threshold motor units fire at greater rates than the higher-threshold units. It has been hypothesized that this phenomenon is the result of the hierarchical response of individual motor units to a “common drive” of the motoneu-

ron pool from supraspinal motor centers (De Luca and Erim 1994; De Luca et al. 1982), either caused by graded intrinsic cellular properties (e.g., input resistance), or graded efficacy of synaptic input to motoneurons, or both. This hypothesis is attractive in that it provides a simplified scheme for the control of force output from a muscle. However, it can be argued that the common drive control scheme is not advantageous for postural muscles, which must generate a sustained force output. By this scheme, low-threshold motor units are required to maintain elevated firing rates over long time periods even at moderate force levels, which may cause premature fatigue to these motor units.

It is known that the human trapezius muscle is commonly involved in sustaining prolonged contractions from postural demands (Jensen et al. 1993a). We know from our previous work that this muscle has shown evidence of the unusual motor control feature of motor unit substitution, which presumably helps to delay motor unit fatigue (Westgaard and De Luca 1999). Conceivably, there may also be adaptations to the motor control scheme in force-varying contractions that act to delay fatigue. We have therefore examined the firing behavior of low-threshold trapezius motor units during force-varying contractions of low force and long duration.

METHODS

Twenty experiments [12 on the trapezius, 8 on the 1st dorsal interosus (FDI)] were performed by 11 healthy subjects, 9 males and 2 females, whose age ranged from 25 to 51 yr. Each subject read and signed an informed consent form approved by the local Institutional Review Board before participating in the study.

Trapezius experiments

The subjects were seated in a chair. Straps were placed over the shoulders and connected to force transducers below each shoulder. The subjects were asked to generate force by elevating the shoulders. The contractions were performed bilaterally, but experimental data were only collected from the right trapezius. The contraction level was controlled by tracking a target signal consisting of a visual display of the root-mean-square (RMS) value of the detected surface electromyographic (EMG) signal. The RMS value of the EMG signal is more variable and therefore more difficult to use for tracking purposes than the shoulder elevation force. However, the synergies of large muscles

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that potentially contribute in shoulder elevations allow considerable inter- and intra-individual variation in the association between motor unit firing rates and force output. The control of contraction level by the surface EMG signal recorded from the same muscle region as the trapezius motor units was therefore preferred. Contractions with ramp and trapezoidal surface EMG force profiles were performed. However, all experiments did not contribute data for all force profiles, either because motor unit firing rates could not be successfully determined in some contractions or because force profiles were excluded in consideration of the overall duration of the experiment. The overall duration of the experiments was limited to approximately 2 h, to avoid undue strain of the subject and possible late fatigue effects in the firing rates of the low-threshold motor units. The number of experiments with the successful implementation of a specific procedure is listed in RESULTS.

The surface EMG signal was detected with an active parallel-bar (1 by 10 mm in size and located 10 mm apart) differential electrode. The electrode was positioned with the medial bar 20 mm lateral to the midpoint of the line between the C₇ spinous process and the acromion (Jensen et al. 1993b). The surface EMG signal was band-pass filtered at 10–1,000 Hz and the RMS value calibrated as a percentage of the EMG activity detected at the maximal voluntary contraction (%EMG_{max}) level. The intramuscular EMG signal was recorded by a quadrifilar wire electrode, consisting of four strands of 50- μ m diam, nylon-coated Ni-Cr wire bonded together and cut transversely to expose only the cross section of the wires. The wire bundle was placed in a 27-gauge needle, and a hook was formed at approximately 1 mm from the exposed end of the wire. The needle was inserted to a depth of approximately 10 mm, at a point approximately 10 mm medial to the midpoint of a line between the C₇ 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 a FM tape recorder.

The intramuscular EMG signals were decomposed into the individual motor unit firing trains using the Precision Decomposition technique (De Luca 1993; De Luca and Adams 1999; Le Fever 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 were obtained by passing the time series of the inter-pulse intervals through a Hanning window and inverting the output. The Hanning window has a low-pass filtering effect, attenuating fast, transient changes in motor unit firing rates.

FDI experiments

The subjects were comfortably seated with their forearms resting on a flat surface with the hand and forearm secured in a restraining device (De Luca et al. 1982). The device immobilized the hand and wrist by means of a finger mold and a strap. The FDI was held at maximum length by fixing the thumb at nearly 90° angle to the index finger. A quadrifilar needle was used for intramuscular recording (De Luca et al. 1982). (For this muscle a needle electrode is preferred in that it allows more flexibility in searching for low-threshold motor units.) The surface electrode, which was the same as for the trapezius experiments, was placed in the middle of the muscle (Erim et al. 1996). The muscle contraction level was controlled in the same way as the trapezius experiments, by tracking the visual display of the RMS value of the detected surface EMG signal. The intramuscular EMG signals were decomposed into the individual motor unit firing trains by the same procedure as described for the trapezius muscle.

RESULTS

The majority of the experimental procedures consisted of contractions of low force and slow modulation of the force

level, similar to those observed during normal use of the trapezius (e.g., Jensen et al. 1993a). Figure 1 shows results of low-contraction-level experiments on the trapezius and FDI muscles, tracing a trapezoid EMG activity profile that reached levels of approximately 10 and 20% EMG_{max}. Figure 1, A–C, illustrates the typical motor unit activity pattern in the trapezius experiments, observed in all of 10 experiments with low-contraction level and a trapezoidal force profile. Each panel includes an example of a motor unit recruited at a very low threshold (<2% EMG_{max}) and which maintains a lower firing rate than later recruited units during the trapezoid contraction. Note that the later recruited motor units in Fig. 1C, where a force profile with faster rise time and higher amplitude is used, tend to follow the onion-skin pattern, and the lowest threshold motor unit presents a firing rate behavior that is approaching the onion-skin pattern. The corresponding panels of Fig. 1 (D–F) show that motor units of the FDI muscle, detected at similarly low thresholds, attain the highest firing rates and present the orderly onion-skin phenomenon. This firing rate pattern is consistent with previous reports of FDI motor units in trapezoid contractions with faster rise time and higher contraction levels (De Luca and Erim 1994; De Luca et al. 1982).

The firing behavior of low-threshold motor units was also examined in contractions where a trapezoidal force profile

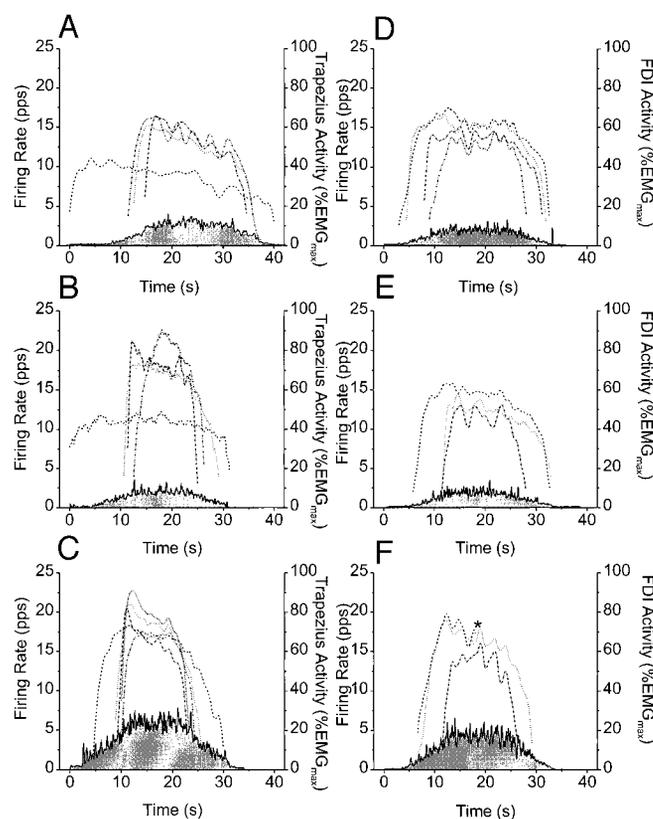


FIG. 1. Root-mean-square (RMS) detected surface EMG activity pattern (fully drawn lines with shading underneath) and firing rates (broken lines) of trapezius (A–C) and first dorsal interosseous (FDI; D–F) motor units during 30-s contractions tracing a trapezoidal activity profile. Electromyographic (EMG) amplitude levels reach approximately 10 (A, B, D, and E) and 20% (C and F) EMG_{max}. The firing rates are low-pass filtered at 0.5 Hz. The left y-axis is calibrated to show firing rate in pulses per second (pps); the right y-axis shows RMS-detected surface EMG activity in %EMG_{max}. Asterisks in this figure and in Fig. 3 mark points where a motor unit no longer is identified with certainty.

reaching approximately 20% EMG_{max} was superimposed on a low-amplitude constant-force contraction of 7% EMG_{max} , to mimic an activity pattern observed in trapezius during normal usage. Results from one trapezius and one FDI experiment are shown in Fig. 2. The firing behavior of trapezius and FDI motor units in this procedure conforms to the pattern shown in Fig. 1. In the trapezius muscle, new motor units recruited during the trapezoidal contraction have higher firing rates than units already active (Fig. 2A, observed in all of 5 experiments). The new recruited FDI motor units have lower firing rates, and the onion-skin appearance of the firing rates is preserved (Fig. 2B). This behavior was observed in all of four experiments.

Firing behavior was further examined in sustained ramp contractions (Fig. 3). Figure 3, A–C, is from the trapezius muscle and shows firing rates of motor units during ramp contractions at 0.05, 1, and 3% EMG_{max}/s . Figure 3, D–F, shows firing rates of FDI motor units for ramp contractions at similar force rates. In case of the slow ramp contraction of 0.05% EMG_{max}/s (reaching 10% EMG_{max} in 3 min), the motor units of the trapezius muscle showed little evidence of rate modulation, and later recruited motor units had higher firing rates than early recruited motor units (observed in all of 6 experiments). In contrast, FDI motor units in the same slow ramp contraction showed a weak, but clear firing rate modulation and preserved the onion-skin control pattern (Fig. 3D). This behavior was observed in all of seven experiments. In ramp contractions with a force rate of 1% EMG_{max}/s , there was cross-over of firing rates of early recruited motor units for the trapezius muscle (Fig. 3B); however, later recruited motor units

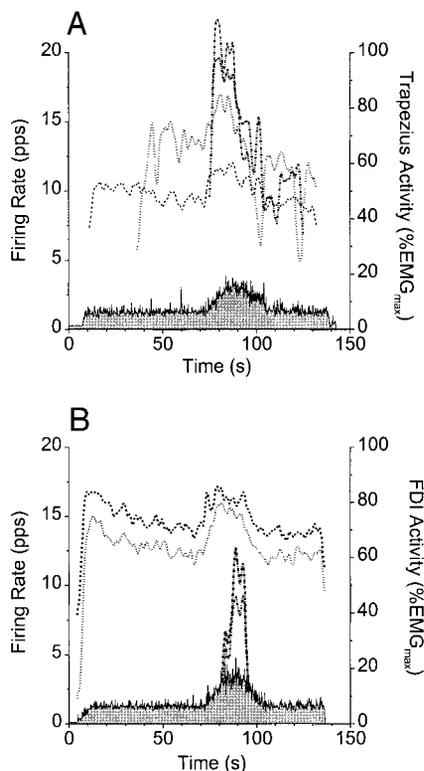


FIG. 2. Trapezius (A) and FDI (B) experiments with a trapezoidal EMG activity profile (rate of increase 1% EMG_{max}/s to reach 17% EMG_{max}) superimposed on a static contraction (7% EMG_{max}). RMS-detected surface EMG activity pattern (fully drawn lines) and low-pass filtered motor unit firing rates (broken lines) are shown. The firing rates are low-pass filtered at 0.5 Hz and adjacent averaged with a window of 0.5 s to improve clarity.

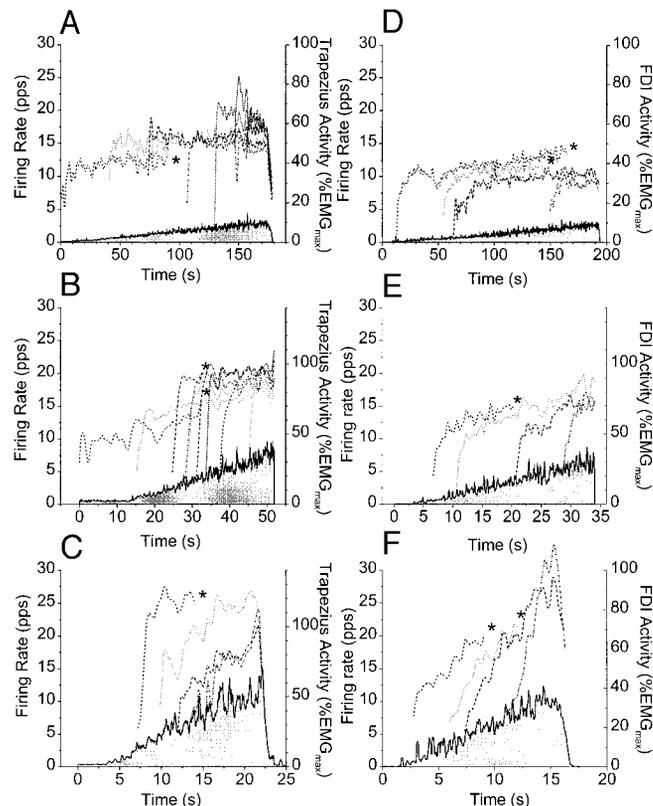


FIG. 3. EMG activity pattern (fully drawn lines) and motor unit firing rates (broken lines) in ramp contractions. Three trapezius and 3 FDI contractions with rates of incline 0.05% EMG_{max}/s (A and D), 1% EMG_{max}/s (B and E) and 3% EMG_{max}/s (C and F) are shown. Vertical axes as in Fig. 1. All firing rates are low-pass filtered at 0.5 Hz. Adjacent averaging is performed with time windows of 0.5 s (A and D) and 0.25 s (B, C, E, and F) to improve clarity.

tended to follow the onion-skin control pattern. In contrast, the FDI motor units followed the onion-skin control pattern (Fig. 3E). At the moderately fast rate of force increase of 3% EMG_{max}/s , motor units of both muscles responded with firing rate increase according to the onion-skin control pattern (Fig. 3, C and F). This behavior was observed in all of five ramp contractions with the trapezius muscle and is a common observation in studies of the FDI.

Firing rates of trapezius and FDI motor units recruited below 10% EMG_{max} are summarized in Table 1. In contractions with force rates $\leq 1\%$ EMG_{max}/s , the trapezius motor units recruited between 5 and 10% EMG_{max} (denoted as later recruited motor units) reach higher peak firing rates than motor units recruited below 5% EMG_{max} (denoted as early recruited motor units). Firing rates on recruitment are, however, quite variable, especially in slow ramp contractions (note large SD and range). Firing rate modulation in ramp contractions is particularly evident when the rise time changes from 1 to 3% EMG_{max}/s (Fig. 3C and Table 1); however, the few motor units tracked for sufficient length of time with the “fast” rate of rise make the firing rate statistics less certain than for the other protocols. The contrast between trapezius and FDI motor unit firing behavior is evident for both the slow and fast ramps. In slow ramps the firing rates of the FDI motor units are markedly lower than the corresponding trapezius motor unit firing rates. There is only marginally higher firing rates of FDI motor units in ramps with rate of rise 3% compared with 1% EMG_{max}/s .

We commonly observed depression in firing rates of active

TABLE 1. Firing rates of trapezius and FDI motor units recruited in ramp contractions, 4 s after recruitment (defined as sustained firing rate >3 pps)

Category	<i>n</i>	Firing Rate, pps
<i>Slow contraction (0.05% EMG_{max}/s)</i>		
Trapezius		
Early MUs*	12	11.0 ± 3.6 (5.1–15.7)
Later MUs†	13	16.2 ± 4.7 (7.6–24.8)
FDI		
Early MUs*	31	7.7 ± 2.4 (4.0–13.4)
Later MUs†	17	7.8 ± 1.6 (4.9–10.9)
<i>Moderate fast contraction (1% EMG_{max}/s)</i>		
Trapezius		
Early MUs*	11	15.7 ± 2.3 (11.9–19.0)
Later MUs†	16	19.0 ± 1.5 (17.1–22.1)
FDI		
Early MUs*	17	14.3 ± 3.6 (9.3–22.2)
Later MUs†	10	14.0 ± 3.0 (12.0–21.1)
<i>Fast contraction (3% EMG_{max}/s)</i>		
Trapezius		
Later MUs†	5	28.2 ± 2.8 (23.9–31.1)
FDI		
Early MUs*	8	16.5 ± 2.0 (14.6–19.2)
Later MUs†	10	17.3 ± 2.9 (13.1–23.0)

Values are means ± SD with range in parentheses; *n* is number of motor units. FDI, first dorsal interosseous; EMG, electromyograph; MU, motor unit. * MUs recruited $<5\%$ EMG_{max}. † MUs recruited between 5 and 10% EMG_{max}.

trapezius motor units following the recruitment of new motor units. (This phenomenon was more easily observed in contractions whose force increased $<2\%$ EMG_{max}/s.) Figure 4A shows a segment of the data in Fig. 3A at higher resolution. The firing rates of three early recruited motor units are shown, while vertical arrows indicate time of recruitment of the late units. A marked depression in the firing rate of the unit recruited at 105 s follows the recruitment of motor unit 6 at 145 s. Later, there is a depression in firing rates of all three units, following the near simultaneous recruitment of two more units (units 7 and 8 at 155 s). Depression of early recruited trapezius motor units in force-varying contractions is further strikingly illustrated by the firing rate behavior in short-duration spontaneous “glitches,” observed several times in this experimental series. In Fig. 4B the firing rate of two trapezius motor units reversed into a depression halfway into the rising phase of a 2-s glitch. In contrast, the firing rate of FDI motor units traced the envelope of the RMS value of the surface EMG during similar force glitch (Fig. 4C).

DISCUSSION

The onion-skin motor control behavior is a consistent finding in force-varying contractions of extremity muscles. It has been demonstrated for FDI (De Luca and Forrest 1973; De Luca et al. 1982), deltoid (De Luca et al. 1982), flexor pollicis longus, extensor pollicis (De Luca and Mambrito 1987), tibialis anterior (De Luca et al. 1996; Stashuk and de Bruin 1988), rectus femoris (Person and Kudina 1972), abductor digiti minimi (Tanji and Kato 1973), brachialis (Kanouse et al.

1979), and the lower limb muscles in the cat (Hoffer et al. 1987). Proximal extremity muscles show less firing rate modulation than distal muscles, but the control scheme with first recruited units reaching the highest firing rate has been consistent in all these studies.

We have shown that the FDI follows the same onion-skin motor control strategy in low-level, slowly augmenting ($<1\%$ EMG_{max}/s) contractions typical of postural activity, as has previously been demonstrated for force-varying contractions with faster rise time (De Luca and Erim 1994; De Luca et al. 1982). The trapezius muscle shows a motor unit recruitment

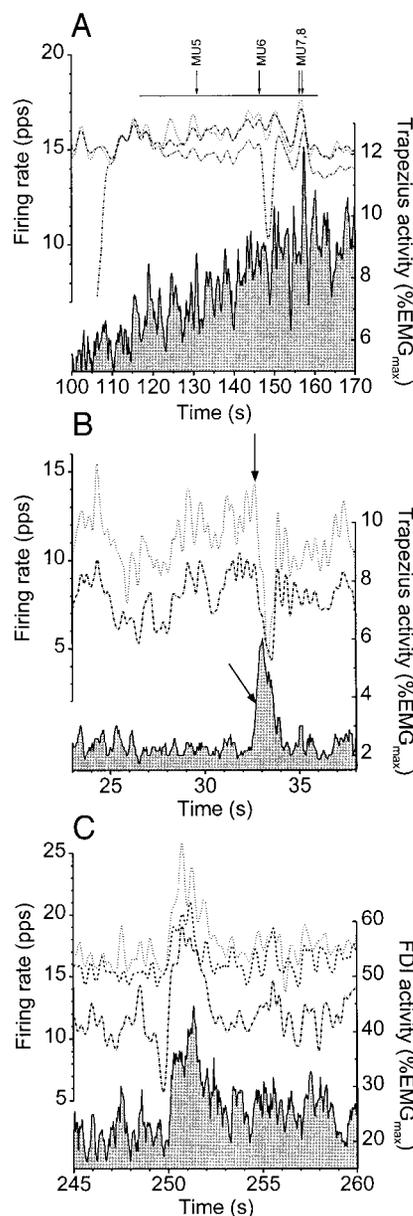


FIG. 4. A: expanded view of contraction in Fig. 3A. Fully drawn line shows RMS-detected EMG amplitude level; broken lines show firing rates of early recruited motor units. Vertical axes as in Fig. 1. The vertical arrows indicate time of recruitment of higher threshold motor units. B and C: sections of recordings with transient increases in RMS amplitude at high time resolution, from the trapezius muscle (B) and FDI (C). The 2 arrows in B identify the corresponding time points in the recordings of RMS amplitude and motor unit firing rates. The firing rates are low-pass filtered at 0.5 Hz and adjacent averaged with time windows of 0.5 s (A) and 0.1 s (B and C).

pattern that conforms to the onion-skin control behavior during relatively fast force-varying contractions, but reverts to a qualitatively different motor control scheme during slow contractions. Under the latter conditions, which represent a typical operating mode of the trapezius muscle, there is minimal, if any, rate modulation of early recruited motor units and the later recruited motor units reach higher firing rates than units already active.

Trapezius is the only muscle among those listed that must meet predominant postural task requirements. The deviant motor control features, observed during mimicked postural contractions make the trapezius better adapted to provide a sustained force output, in the sense that low firing rates delay fatigue in the low-threshold motor units.

The firing rate behavior of trapezius motor units in slow augmenting contractions may be understood in terms of the observed depression in firing rates of active units when new motor units are recruited. A negative feedback that suppresses the effect of an increased excitatory drive is indicated. A similar phenomenon is reported by Broman et al. (1985) in the tibialis anterior muscle, a muscle whose firing rates show weak sensitivity to force. The depression of firing rates in this muscle was, however, of much shorter duration than was observed for the trapezius motor units.

The suppression of firing rates may involve a peripheral feedback loop with muscle receptors, and/or recurrent inhibition by Renshaw cells. We consider negative feedback through muscle receptors unlikely, as the depression in firing rates is observed during constant-force contractions at very low force levels, when there is little muscle afferent activity, especially in humans (e.g., Prochazka and Hulliger 1983). Furthermore, a marked decline in firing rates of muscle spindles during sustained voluntary contractions has been reported (Macefield et al. 1991). Recurrent inhibition through Renshaw cells appears the more likely mechanism, since Renshaw inhibition is a prominent feature in motor control of neck muscles, including the trapezius in the cat (Brink and Suzuki 1987; Rapoport 1979). Renshaw inhibition is more pronounced in proximal than in distal muscles of the human (Katz et al. 1993; Rossi and Mazzocchio 1991), and is stronger in low-threshold than in high-threshold motor units of the same muscle (Hultborn et al. 1988; Pompeiano et al. 1975). Renshaw inhibition would depress the active motor units in the trapezius muscle on recruitment of new units, reducing the sensitivity of motor unit firing rates to increased force output; and this effect would be greatest on the low-threshold motor units. However, the remarkably stable firing rates of trapezius motor units in slow force-varying contractions may be difficult to achieve through Renshaw feedback alone. Other spinal control circuitry and/or descending command signals likely contribute and different intrinsic characteristics of trapezius and FDI motoneurons can be another contributing factor to the different control features of the two muscles.

This apparent deviant behavior of the low-threshold motor units in the trapezius muscle does not contradict the concept of the common drive because it can be explained by superimposing the influence of a preferential inhibitory factor on the common drive.

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