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Motor unit recruitment during prolonged isometric contractions

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Summary. Motor unit recruitment patterns were studied during prolonged isometric contraction using fine wire electrodes. Single motor unit potentials were recorded from the brachial biceps muscle of eight male subjects, during isometric endurance experiments conducted at relative workloads corresponding to 10% and 40% of maximal voluntary contraction (MVC), respectively. The recordings from the 10% MVC experiment demonstrated a characteristic time-dependent recruitment. As the contraction progressed both the mean number of motor unit spikes counted and the mean amplitude of the spikes increased significantly ($P<0.01$). This progressive increase in spike activity was the result of a discontinuous process with periods of increasing and decreasing activity. The phenomenon in which newly recruited motor units replace previously active units is termed "motor unit rotation" and appeared to be an important characteristic of motor control during a prolonged low level contraction. In contrast to the 10% MVC experiment, there was no indication of de novo recruitment in the 40% MVC experiment. Near the point of exhaustion a marked change in action potential shape and duration dominated the recordings. These findings demonstrate a conspicuous difference in the patterns of motor unit recruitment during a 10% and a 40% MVC sustained contraction. It is suggested that there is a close relationship between intrinsic muscle properties and central nervous system recruitment strategies which is entirely different in fatiguing high and low level isometric contractions.

Key words: Motor unit – Recruitment – Prolonged isometric contractions – Fatigue

Introduction

It is a general assumption that the loss of muscle force generating capacity during a fatiguing submaximal contraction is compensated for by a progressive recruitment of additional motor units.

The concept of time-dependent recruitment has been mainly based on observations of a marked increase in the surface recorded electromyogram (EMG) during sustained, submaximal, isometric contractions (Cobb and Forbes 1923; Edward and Lippold 1956; deVries 1968; Kuroda et al. 1970). The surface EMG is, however, a questionable measure of intrinsic motor unit behaviour. Part of the observed increase in surface EMG activity during a constant force contraction may be due to a general slowing of muscle fibre conduction velocity rather than a de novo recruitment. It has been shown that an increased duration of individual motor unit potentials increases the low-frequency component of the motor unit potentials and as the body tissue acts as a lowpass filter more signal energy is transmitted to the surface and the amplitude of the surface recorded EMG increases (De Luca 1984). This factor must be taken into account and makes it difficult directly to relate changes in surface EMG to changes in motor drive or motor unit recruitment.

In a few experimental studies direct recordings from single motor units have been utilized to determine motor unit behaviour and recruitment during constant force contractions. The results are, however, not without controversy. Maton (1981) and Kato et al. (1981) have indicated that recruitment of new motor units occurred throughout an isometric contraction, while De Luca and Forrest (1973) have found no evidence of additional motor unit recuitment when a constant force contraction was in progress. The maintenance of a constant force output in the fatiguing muscle despite the absence of recruitment was, in the latter study, ascribed to an increase in twitch tension of the active units (post tetanic potentiation).

In the present experiments motor unit recruitment patterns during constant force contractions were studied using highly selective indwelling wire electrodes. The results clarified some of the previous discrepancies by demonstrating that time-dependent recruitment did exist, but was a special feature confined to prolonged

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low level isometric contractions. This observation would be an important prerequisite for distinguishing between normal motor unit behaviour and motor unit behaviour in patients complaining of pathological fatiguability.

Methods

Subjects. Eight healthy men [mean age 28.1 (SD 3.1) years] participated in the study. Voluntary consent was obtained from the subjects following an explanation of the experimental procedures and the possible risks involved. The study was approved by the local ethics committee.

Procedure. Motor unit recruitment was studied during isometric endurance experiments involving the elbow flexors. Prior to the experiments maximal voluntary contraction force (MVC) of the elbow flexors was measured with a modified Darcus strain gauge dynamometer (Bonde-Petersen 1960). The endurance experiments were conducted at relative workloads corresponding to 10% and 40% MVC, respectively. Several days of rest were allowed between experiments.

The subjects were placed in a specially designed chair in which an unchanged body position could be maintained throughout the experiment. The right upper arm was kept horizontal with a 90° flexion in the elbow and the forearm in a supinated position. Force was exerted on a small plate placed at the wrist just below the styloid processes. During the endurance experiments a constant force output was achieved by an audio-visual feedback mechanism which indicated deviations in force. Exhaustion was taken to be the point at which the subject was unable to maintain the required force level.

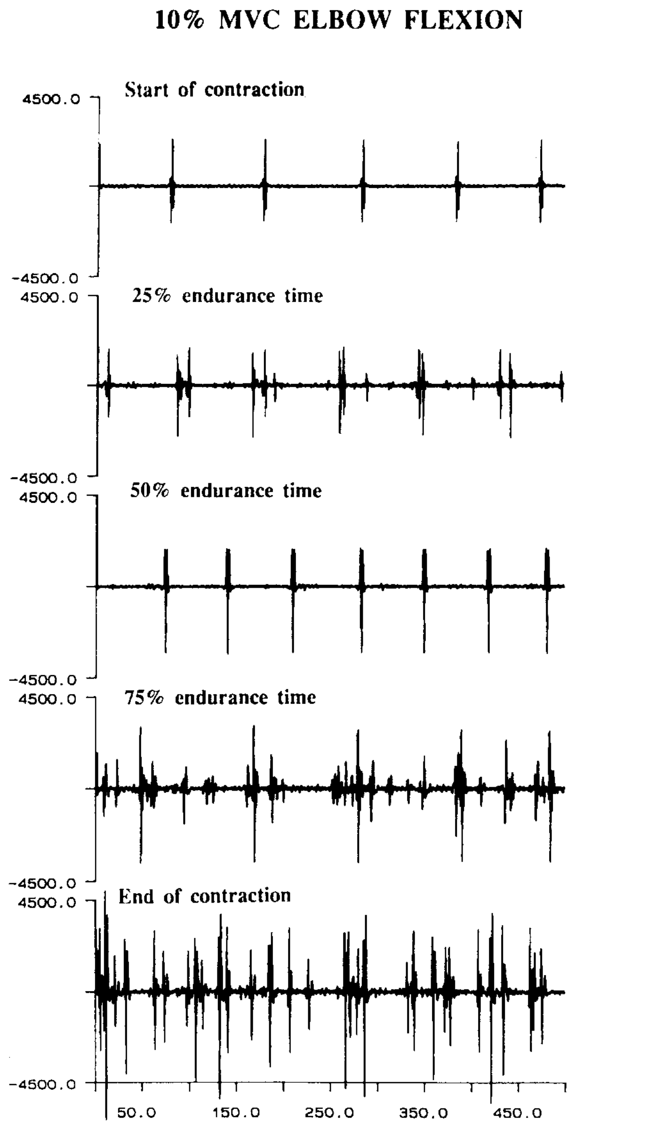

Fig. 1. Single motor unit potentials recorded from the brachial biceps muscle during elbow flexion at 10% maximal voluntary contraction (*MVC*); (isometric endurance experiment). Results from one subject demonstrating a marked time-dependent recruitment. *Panels represent from top to bottom*: start of contraction, 25%, 50%, 75% endurance time, and end of contraction (exhaustion). The recorded signals were filtered by a second order difference filter and the time period shown in each panel is 500 ms

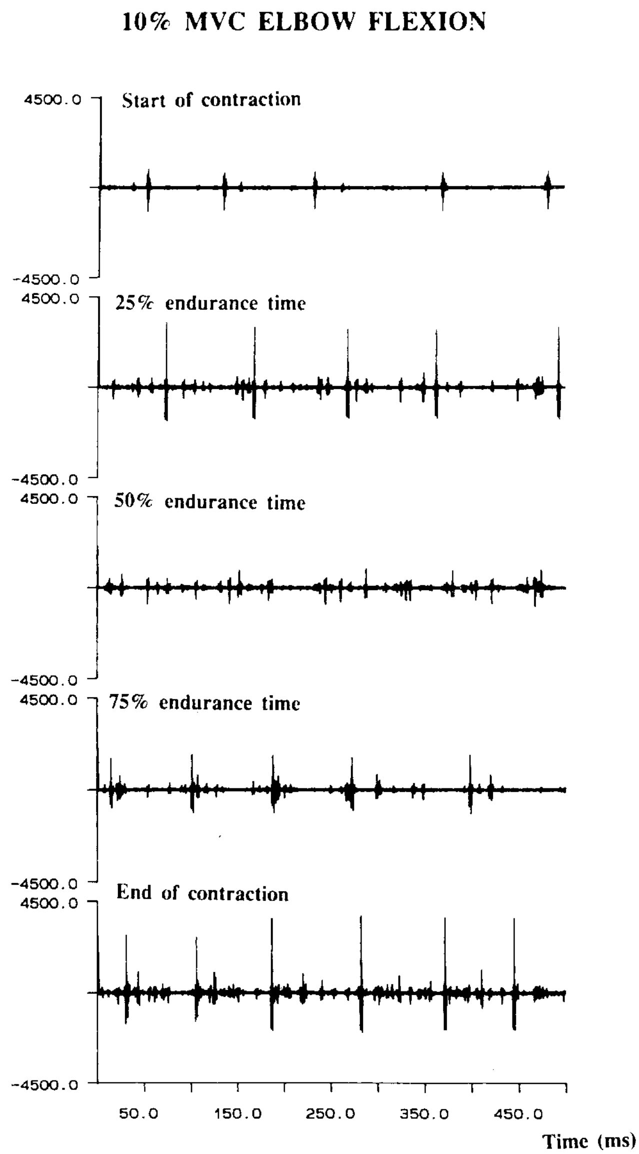

Fig. 2. Single motor unit potentials recorded from the brachial biceps muscle during elbow flexion at 10% *MVC* (isometric endurance experiment). Results from one subject, for details see legend to Fig. 1. Note the changing periods of decreasing and increasing spike activity occurring after approximately 50%–75% endurance time

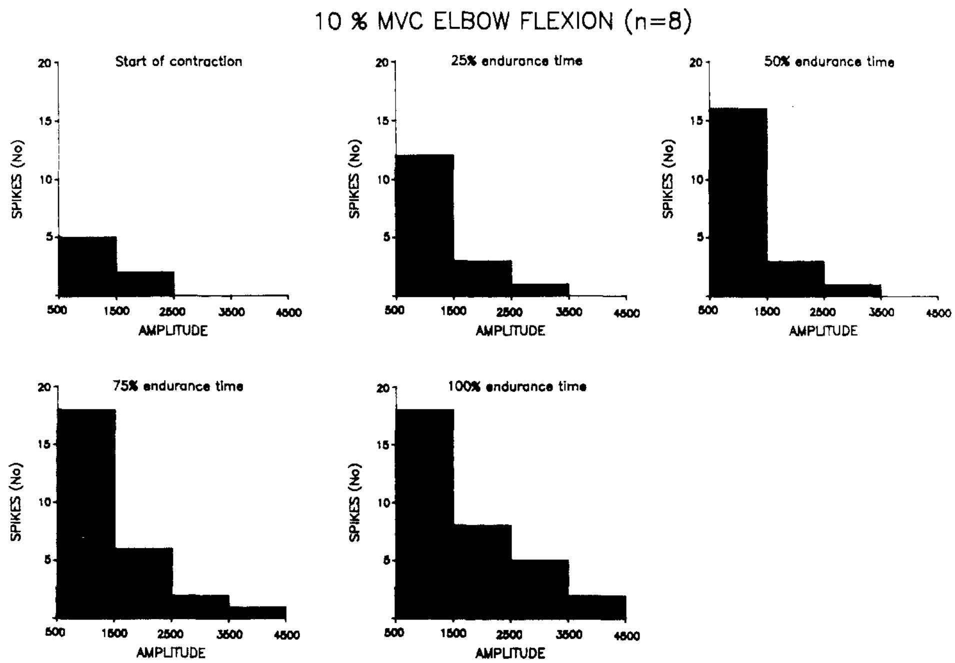

Fig. 3. Motor unit spike-amplitude histograms obtained during elbow flexion at 10% *MVC* (isometric endurance experiment). *Each bar* represents the mean of eight subjects. Values are shown for start of contraction, and 25%, 50%, 75%, and 100% endurance time (exhaustion). The calculated values in the histograms are based on individual recordings as shown in Figs. 1 and 2

EMG recordings and signal processing. Single motor unit potentials were recorded from the right brachial biceps muscle using fine wire electrodes. The bipolar electrodes were constructed from platinum wires (70 μm outside diameter) glued together with epoxy resin (Araldite) and insulated with teflon except at the cut ends. The electrodes were bent to form a hook and the recording surfaces were the wire ends. Insertion into the muscle was made with a hypodermic needle (25G) to a depth of approximately 2 cm. This region of the muscle has been shown to contain motor units with a gradation of thresholds from low to high (Elder et al. 1982).

The motor unit potentials were amplified on a multichannel EMG-amplifier (DISA 15C01, BW 20 Hz–10 kHz) and stored on magnetic tape (Brüel and Kjær 7004). To avoid noise from electrical interference the whole experimental setup was placed in a large shielded cage (2×2×2 m).

In the signal processing periods of 500 ms EMG recordings were used for analysis. In the 10% MVC experiments the first period was sampled immediately after stabilization at the target force and the subsequent periods with regular time intervals corresponding to 25%, 50%, 75%, and 100% of the individual endurance time. During the short-lasting 40% MVC experiments the sampling was reduced to the initial period, 50% and 100% endurance time. For each sample, the EMG signals were digitized at a sampling rate of 50 kHz and then filtered by a second order difference filter modified after Stashuk and De Luca (1989). This type of filtering reduces motor unit action potential duration, attenuates distant activity and thereby enhances the probability of identifying single unit potentials.

Time-dependent changes in intramuscular spike patterns were detected by a window discriminant computer subroutine. Motor unit action potential spikes above a minimal amplitude were counted according to their positive peak-amplitude in bands with a numerical increment of 1000. Mean numbers of spikes in each band were calculated and presented as spike-amplitude histograms (Moritani et al. 1986). No attempt was made to recalculate the differentiated values to their corresponding voltage values in the original EMG signal.

Statistics. Significance was tested by the Wilcoxon test for paired data and $P<0.05$ taken as the minimal level for a significant difference.

Results

Maximal torque for elbow flexion was 76.6 (SD 7.4) Nm. Endurance time at 40% MVC was 2.3 (SD 0.7) min compared to a mean endurance time of 111.3 (SD 56.1) min at 10% MVC.

Motor unit behaviour at low levels of contraction (10% MVC)

The recordings of motor unit action potential spikes during the 10% MVC contraction demonstrated a characteristic time-dependent recruitment. Figures 1 and 2 show typical recordings from two subjects. At the start of the contraction only action potentials from one or two units with a firing frequency of approximately 10 Hz were recorded. With increasing time a progressive appearance of new units with a larger spike amplitude could be observed and at the time of exhaustion the records were dominated by a large number of newly recruited motor units.

In Fig. 3, spike-amplitude histograms based on motor unit action potentials from all eight subjects are presented. The histograms quantify the pattern seen in the individual recordings. Initially – upper left panel – all spikes were counted in the two lowest bands 500–1500 and 1500–2500. The mean spike number counted was 6.3 (SD 3.3) with a mean amplitude of 1192.4 (SD 376.9). As the contraction progressed the number of action potential spikes increased and an increasing number of spikes were counted in the higher amplitude bands. At the point of exhaustion both the mean number of spikes [33.4 (SD 12.3)] and the mean amplitude [1709.6 (SD 401.5)] was significantly higher than at the start of contraction ($P<0.01$).

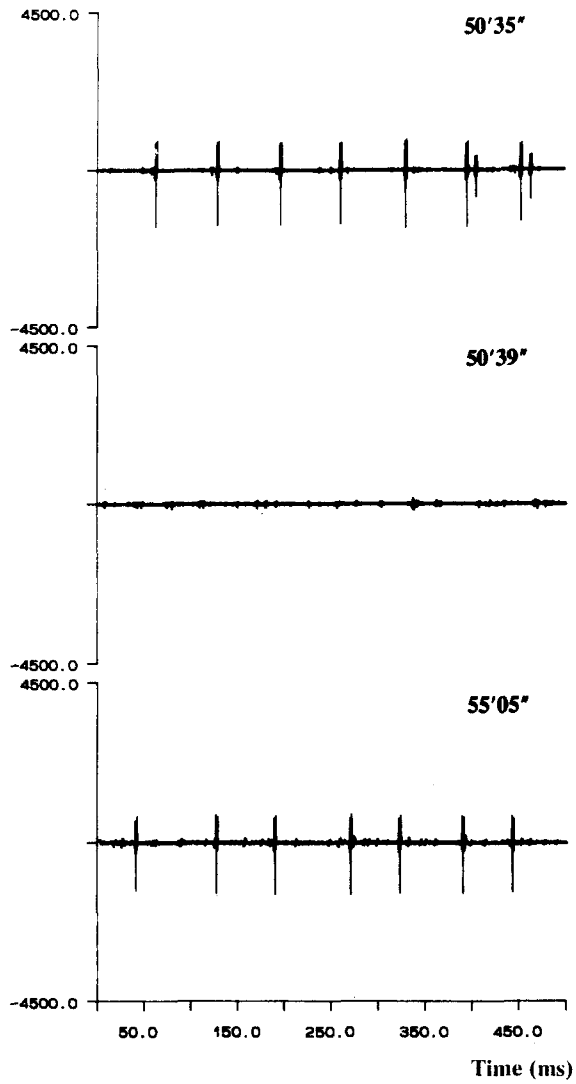

Fig. 4. Single motor unit potentials recorded during elbow flexion at 10% maximal voluntary contraction (isometric endurance experiment). Results from one subject with an endurance time of more than 2 h indicating "motor unit rotation". *Top panel*: recording obtained 50 min 35 s after onset of exercise. *Middle panel*: recording obtained 50 min 39 s after onset of exercise. *Bottom panel*: recording obtained 55 min 05 s after onset of exercise. The recorded signals were filtered by a second order difference filter and the time period shown in each panel is 500 ms

The progressive and statistically significant increase in spike activity shown in the histograms represented a recruitment pattern with rather large fluctuations in the single individuals. In Figs. 1 and 2, it can be seen that the general increase in motor unit recruitment was a discontinuous process with periods of increasing and decreasing activity. Figure 4 demonstrates a typical incidence after approximately 50 min of constant force contraction where the motor unit activity in the recording area momentarily disappeared and then reappeared minutes later. This phenomenon, where newly recruited motor units replace previously active units, is termed "motor unit rotation" and appeared to be an important characteristic of motor control during prolonged low level contractions.

Motor unit behaviour at high levels of contraction (40% MVC)

The spike-amplitude histograms for the 40% MVC contractions are depicted in Fig. 5. There was no indication of a de novo recruitment at this level of contraction. On the contrary a general loss, primarily of spikes with high amplitude, could be observed as the contraction progressed. Mean spike number counted decreased from 76.5 (SD 37.3) to 38.5 (SD 14.9) ($P<0.01$) and mean amplitude from 2954.0 (SD 2284.7) to 1462.9 (SD 265.7) ($P<0.05$) during the contraction.

This conspicuous loss of spikes was the result of marked fatigue induced changes in individual action potential waveforms. Figure 6A shows the raw EMG signals from the start and the end of a 40% MVC contraction. The signal in the fatigued muscle has a markedly slower character and a prolongation of the action potentials is clearly visible. In the difference filtered signal (Fig. 6B) spikes with a slow rise time are strongly attenuated and this appears in the spike-amplitude histogram calculated on basis of the difference filtered signal as a decrease in the number of spikes counted.

The implication is that high load contractions seem to be maintained with motor units recruited at the start of the contraction. In contrast to the de novo recruitment observed in the low level contractions no new, unfatigued motor units were seen near the point of exhaustion in the 40% MVC experiments. Instead marked changes in action potential shape and duration of the already active motor units dominated the recordings.

Discussion

The present results demonstrated that motor unit recruitment patterns during submaximal isometric contractions can be influenced by the level of contraction.

Striking differences between motor unit recruitment and firing frequencies during maximal and submaximal isometric contractions have been indicated in previous studies (Bigland-Ritchie and Woods 1984). It has, however, not been recognized that different levels of submaximal, sustained contractions could present patterns of motor unit behaviour with equally striking differences. An important methodological implication of these findings is that the familiar increase in surface EMG seen in prolonged submaximal contractions may reflect entirely different recruitment patterns in high and low level contractions. In prolonged low level contractions, the surface EMG increases in direct relation to an increasing number of newly recruited motor units. In high level contractions, however, the increase in surface EMG probably is the result of a tissue-filtering effect reflecting a change of action potential waveform and duration of the already active motor units.

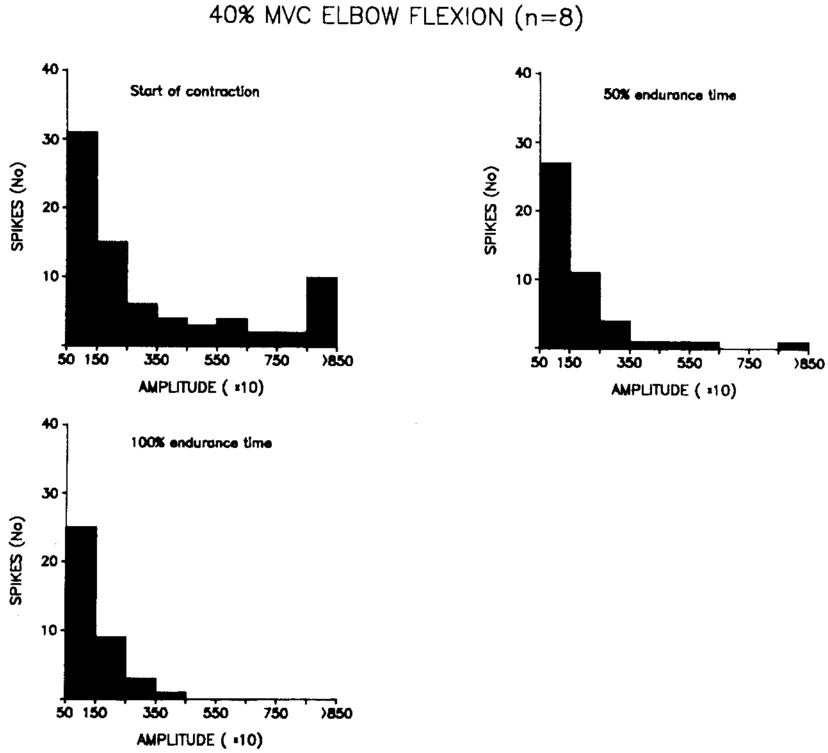

Fig. 5. Motor unit spike-amplitude histograms obtained during elbow flexion at 40% maximal voluntary contraction (*MVC*); (isometric endurance experiment). *Each bar* represents the mean of eight subjects. Values are shown for start of contraction, 50%, and 100% endurance time (exhaustion)

The characteristic features of a low level static contraction, i.e. time-dependent recruitment and motor unit rotation documented in the present study have been a matter of intense debate (De Luca 1984; Basmajian and De Luca 1985). Our data, however, substantiate the existing results from the limited number of EMG studies confined to low level static contractions. Person and Kudina (1972) for instance studied static knee extension at approximately 17% MVC with an endurance time of up to 13.5 min and found that new motoneurons were gradually recruited during a prolonged contraction at constant strength.

It is noteworthy that the de novo recruitment during fatigue from low level contractions seems to occur in a graded fashion, i.e. according to the "size principle" in which the members of a motoneuron pool are recruited in order of increasing cell size (Henneman 1957). In the 10% MVC experiment, the majority of motor units recorded towards the end of the contraction exhibited a significantly higher spike amplitude (Fig. 3). This increase in spike amplitude could theoretically have been an artefact caused by an activation of muscle fibres closer to the recording electrode. The consistency in the recordings, however, makes it unlikely that action potential spikes in the vicinity of the electrode should have been selectively recorded only near the point of fatigue in all eight subjects. It is more likely that the motor units exhibiting large amplitude spikes which we frequently recorded near the point of exhaustion belong to the phasic, fast twitch type motor unit described by Grimby and Hannerz (1977) and Gydikov and Kosarov (1974).

In comparison with time-dependent recruitment, the concept of motor unit rotation during low level contractions is even less well documented. Based on surface electromyographic recordings from multiple recording sites, Sjøgaard et al. (1986), have suggested that motor unit rotation or "alternating recruitment" occurred during a 1 h 5% MVC static knee extension. This is in line with our assumption that motor unit rotation is an important characteristic of motor control during very prolonged low level contractions. The functional gain in terms of the maintenance of optimal force is obvious and it is interesting that maximal endurance time seemed to be related to the individuals ability or capacity for motor unit rotation, i.e. the two subjects in the experiments with very long endurance times, greater than 2 h, frequently showed episodes with decreasing electric activity in the recording area (Fig. 4).

The apparent lack of time-dependent recruitment and motor unit rotation when the intensity of the contraction was 40% MVC is in accordance with observations which have been made by Stulen and De Luca (1978). In studies of relatively high intensity static exercise (deltoid muscle) they found no evidence of motor unit recruitment and ascribed the force maintenance to a potentiation of twitch tension in individual motor units as the contraction progressed. Post tetanic twitch-potentiation has been described by several authors (Burke et al. 1976; Belanger and McComas 1985) but seems to require an intense activation of the muscle (Vandervoort et al. 1983). This would indicate that the potentiation of twitch torque is an effective mechanism for force maintenance applicable only in high level static exercise. The results from the present study support the idea that no recruitment occurs during high level contractions and that force is being maintained by twitch potentiation. This has been disputed by Maton (1981) and Moritani et al. (1986) who have claimed that motor unit recruitment occurred even at high static loads of approximately 50% MVC. At pres-

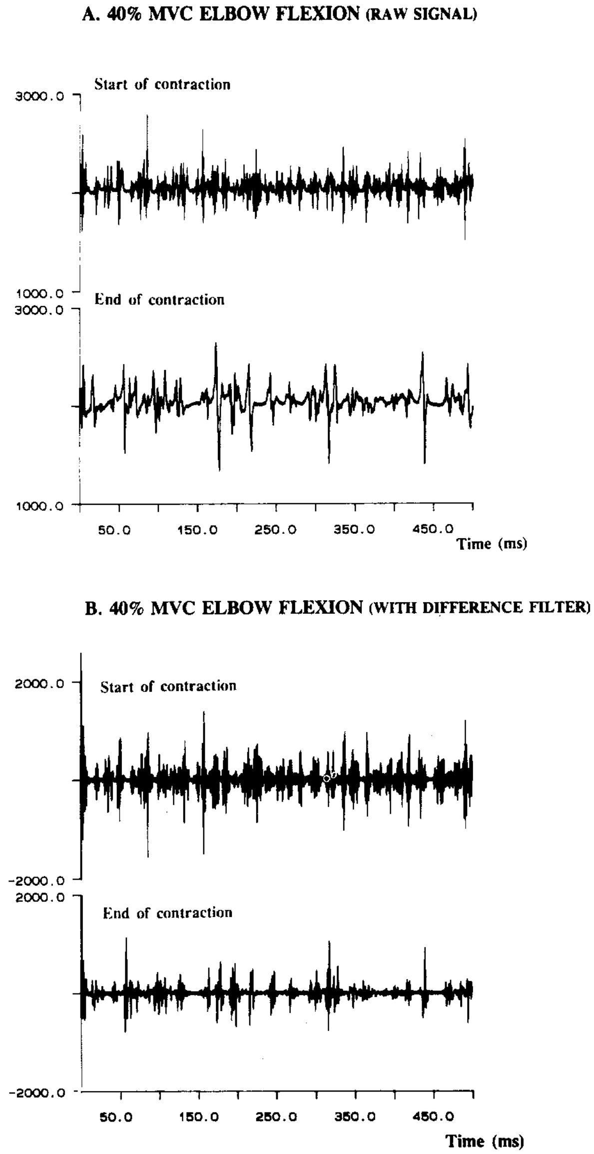

Fig. 6. Single motor unit potentials recorded at the start and at the end of a 40% maximal voluntary contraction (MVC) elbow flexion experiment (isometric endurance experiment). **A** gives the raw, unfiltered signal. Note the marked slowing and prolongation of the individual action potentials near the end of the contraction. **B** gives the same signal after filtering. A second order difference filter strongly attenuated spikes with a slow rise time and a long duration and this is seen in the filtered signal as a marked loss of spike activity

ent, the reason for this discrepancy is not clear. One possibility is that the selectivity of the recording electrodes used in the studies mentioned above was too low to ensure recordings from single motor units. If the electrode selectivity is too low the recorded signal will be an interference signal comparable to a surface EMG. In this situation an increase in EMG amplitude and activity is more likely to be the result of tissue-filtering rather than de novo recruitment.

The main implication of the present study was, however, the apparent coupling of motor unit behaviour to fatigue processes in the muscle. In the low level contractons muscle blood flow has been found to be relatively unrestricted and only minor metabolic changes in the muscle extracellular space have been found (Sjøgaard 1988). As demonstrated, the scope for de novo recruitment in this situation is large and at the point of exhaustion there are no indications of impaired muscle excitation. Action potential waveforms are unchanged and fatigue or exhaustion probably related to an impaired excitation-contraction coupling due to the vast number of stimuli delivered to the muscle. At the short lasting high intensity contraction, however, muscle blood flow has been shown to be occluded and dramatic metabolic change to take place in the muscle extracellular space (Saltin et al. 1981). In this situation, motor unit recruitment has appeared to be restricted possibly due to a reflex inhibition of motoneurons elicited from the active muscles (Bigland-Ritchie et al. 1986) or through a progressive withdrawal of fusimotor-mediated spindle support to the α-motoneuron pool (Macefield et al. 1991). Force is maintained for a short while due to twitch potentiation and modulation of motoneuron firing rates to optimize the force generating capacity of the muscle. However, exhaustion is inevitably due to a rapidly increasing failure of muscle excitation visible in the prolongation of the recorded motor unit potentials.

The results from the present study thus indicate the existence of a close relationship between intrinsic muscle properties and recruitment strategies of the central nervous system which is entirely different in fatigue from high and low level static contractions.

References

Basmajian JV, De Luca CJ (1985) Muscles alive. Their functions revealed by electromyography. Williams and Wilkins, Baltimore

Belanger AY, McComas AJ (1985) A comparison of contractile properties in human arm and leg muscles. Eur J Appl Physiol 54:326–330

Bigland-Ritchie B, Woods JJ (1984) Changes in muscle contractile properties and neural control during human muscular fatigue. Muscle Nerve 7:691–699

Bigland-Ritchie BR, Dawson NJ, Johansson RS, Lippold OCJ (1986) Reflex origin for the slowing of motoneurone firing rates in fatigue of human voluntary contractions. J Physiol (Lond) 379:451–459

Bonde-Petersen F (1960) Muscle training by static, concentric and eccentric contractions. Acta Physiol Scand 48:406–416

Burke RE, Rudomin P, Zajac FE (1976) The effect of activation history on tension production by individual muscle units. Brain Res 109:515–529

Cobb S, Forbes A (1923) Electromyographic studies of muscular fatigue in man. Am J Physiol 65:234–251

De Luca CJ (1984) Myoelectrical manifestations of localized muscular fatigue in humans. Crit Rev Biomed Eng 11:251–279

De Luca CJ, Forrest WJ (1973) Some properties of motor unit action potential trains recorded during constant force isometric contractions in man. Kybernetik 12:160–168

deVries HA (1968) Method for evaluation of muscle fatigue and endurance from electromyographic fatigue curves. Am J Phys Med 47:125–135

Edwards RG, Lippold OCJ (1956) The relation between force and integrated electrical activity in fatigued muscle. J Physiol (Lond) 132:677–681

Elder GCB, Bradbury K, Roberts R (1982) Variability of fiber type distributions within human muscles. J Appl Physiol 53:1473–1480

Grimby L, Hannerz J (1977) Firing rate and recruitment order of toe extensor motor units in different modes of voluntary contraction. J Physiol (Lond) 264:865–879

Gydikov A, Kosarov D (1974) Some features of different motor units in human biceps brachii. Pflügers Arch 347:75–88

Henneman E (1957) Relation between size of neurons and their susceptibility to discharge. Science 126:1345–1346

Kato M, Murakami S, Takahashi K, Hirayama H (1981) Motor unit activities during maintained voluntary muscle contraction at constant levels in man. Neurosci Lett 25:149–154

Kuroda E, Klissouras V, Milsum JH (1970) Electrical and metabolic activities and fatigue in human isometric contraction. J Appl Physiol 29:358–367

Macefield G, Hagbarth KE, Gorman R, Gandevia SC, Burke D (1991) Decline in spindle support to alpha-motoneurones during sustained voluntary contractions. J Physiol (Lond) 440:497–512

Maton B (1981) Human motor unit activity during the onset of muscle fatigue in submaximal isometric isotonic contractions. Eur J Appl Physiol 46:271–281

Moritani T, Muro M, Nagata A (1986) Intramuscular and surface electromyogram changes during muscle fatigue. J Appl Physiol 60:1179–1185

Person RS, Kudina LP (1972) Discharge frequency and discharge pattern of human motor units during voluntary contraction of muscle. Electroencephalogr Clin Neurophysiol 32:471–483

Saltin B, Sjøgaard G, Gaffney FA, Rowell LB (1981) Potassium, lactate, and water fluxes in human quadriceps muscle during static contractions. Circ Res 48 [Suppl I]:18–24

Sjøgaard G (1988) Muscle energy metabolism and electrolyte shifts during low-level prolonged static contraction in man. Acta Physiol Scand 134:181–187

Sjøgaard G, Kiens B, Jørgensen K, Saltin B (1986) Intramuscular pressure, EMG and blood flow during low-level prolonged static contraction in man. Acta Physiol Scand 128:475–484

Stashuk D, De Luca CJ (1989) Update on the decomposition and analysis of EMG signals. In: Desmedt JE (ed) Computer-aided electromyography and expert systems. Elsevier, Amsterdam, pp 39–54

Stulen FB, De Luca CJ (1978) The relation between the myoelectric signal and physiological properties of constant-force isometric contractions. Electroencephalogr Clin Neurophysiol 45:681–698

Vandervoort AA, Quinlin J, McComas AJ (1983) Twitch potentiation after voluntary contraction. Exp Neurol 81:141–152