Journal of Sports Sciences, 2002, **20**, 83–91

Taylor & Francis healthsciences

Differences in activation patterns between eccentric and concentric quadriceps contractions

MALACHY P. McHUGH,* TIMOTHY F. TYLER, SCOTT C. GREENBERG and GILBERT W. GLEIM

Nicholas Institute of Sports Medicine and Athletic Trauma, Lenox Hill Hospital, 130 East 77th Street, New York, NY 10021, USA

Accepted 16 July 2001

Previous studies analysing electromyograms (EMGs) from indwelling electrodes have indicated that fast-twitch motor units are selectively recruited for low-intensity eccentric contractions. The aim of this study was to compare the frequency content of surface EMGs from quadriceps muscles during eccentric and concentric contractions at various contraction intensities. Electromyograms were recorded from the rectus femoris, vastus lateralis and vastus medialis muscles of 10 men during isokinetic (1.05 rad·s^{-1}) eccentric and concentric knee extension contractions at 25%, 50%, 75% and 100% of maximal voluntary contraction (MVC) for each contraction mode. Additionally, isometric contractions (70°) were performed at each intensity. The mean frequency and root mean square (RMS) of the surface EMG were computed. Mean frequency was higher for eccentric than concentric contractions at 25% ($P < 0.01$), 50% ($P < 0.01$) and 75% ($P < 0.05$) but not at 100% MVC. It increased with increasing contraction intensity for isometric ($P < 0.001$) and concentric ($P < 0.01$) contractions but not for eccentric contractions ($P = 0.27$). The EMG amplitude (RMS) increased with increasing contraction intensity similarly in each contraction mode ($P < 0.0001$). Higher mean frequencies for eccentric than concentric contractions at submaximal contraction intensities is consistent with more fast-twitch motor units being active during eccentric contractions.

Keywords: electromyogram, fast-twitch fibres, maximal voluntary contractions, motor unit recruitment.

Introduction

Many studies have reported that fewer motor units are activated for eccentric than concentric contractions at the same force (Bigland and Lippold, 1954; Komi *et al.*, 1987; Tesch *et al.*, 1990; Adams *et al.*, 1992; Potvin, 1997). Additionally, studies using indwelling electrodes have indicated that there is a reversal of normal motor unit recruitment for eccentric contractions (Nardone and Schieppati, 1988; Nardone *et al.*, 1989; Howell *et al.*, 1995; Enoka, 1996). In these studies, motor units were identified as fast-twitch or slow-twitch based on the shape and amplitude of the action potentials.

The electromyogram (EMG) frequency content has also been used to provide an indirect measure of motor unit recruitment during isometric contractions in both humans (Moritani and Muro, 1987; Bernardi *et al.*, 1997) and animals (Solomonow *et al.*, 1990). An increase in mean or median frequency with increasing contraction intensity is thought to indicate increased recruitment of fast-twitch motor units (Bilodeau *et al.*, 1995; Bernardi *et al.*, 1997). Therefore, if more fast-twitch motor units are recruited during eccentric contractions, the EMG frequency content would be higher than with concentric contractions at a given submaximal intensity. In a recent study of EMG activity in exercise leading to symptoms of muscle damage, the median frequency of the hamstring muscles was markedly higher in individuals performing eccentric contractions than in those performing concentric contractions (McHugh *et al.*, 2000). This was thought to reflect greater recruitment of fast-twitch motor units for eccentric contractions. However, since comparisons were made between and not within individuals, and muscle length was not controlled during frequency computations, these conclusions are far from definitive. The observed differences could have been due to fibre

* Author to whom all correspondence should be addressed. e-mail: mchugh@nismat.org

Journal of Sports Sciences ISSN 0264-0414 print/ISSN 1466-447X online © 2002 Taylor & Francis Ltd
http://www.tandf.co.uk/journals

type differences between individuals (Gerdle *et al.*, 1988) or sampling data at shorter muscle lengths in eccentric than in concentric contractions, since mean frequency is directly affected by muscle length (Potvin, 1997).

Several studies (Moritani *et al.*, 1988; Tesch *et al.*, 1990; Nakazawa *et al.*, 1993; Potvin, 1997; Aagaard *et al.*, 2000b; Komi *et al.*, 2000) using frequency analysis of the surface EMG during eccentric and concentric contractions have failed to confirm greater recruitment of fast-twitch motor units. Together, the results of these studies indicate that fast-twitch motor units are not selectively recruited for low-intensity eccentric contractions of the elbow flexors (Moritani *et al.*, 1988; Nakazawa *et al.*, 1993; Potvin, 1997; Komi *et al.*, 2000) or maximal quadriceps contractions (Tesch *et al.*, 1990; Aagaard *et al.*, 2000b).

Previous studies comparing EMG frequency measures between eccentric and concentric contractions (Moritani *et al.*, 1988; Tesch *et al.*, 1990; Nakazawa *et al.*, 1993; Potvin, 1997; Aagaard *et al.*, 2000b; Komi *et al.*, 2000) did not measure the frequency response to increasing contraction intensity. Since normal recruitment is expected with concentric contractions (Nardone and Schieppati, 1988; Nardone *et al.*, 1989; Howell *et al.*, 1995; Enoka, 1996), an increase in frequency with increasing concentric contraction intensity can provide an insight into the sensitivity of frequency measures to detect increased recruitment of fast-twitch motor units. The aim of the present study was to compare the frequency content of the surface EMG from quadriceps muscles during eccentric and concentric contractions at various intensities.

Methods

Experimental protocol

Ten healthy males volunteered to participate in the study, each of whom provided written informed consent. The study was approved by the institutional review board. The participants' age, height and body mass were 31.0 ± 7.2 years, 1.79 ± 0.06 m and 88.6 ± 6.6 kg respectively (mean ± *s*). They performed maximum voluntary contractions (MVC) of the knee extensors followed by submaximal contractions at 25%, 50% and 75% of MVC. This sequence was performed separately in eccentric, concentric and isometric contraction modes and the order of contraction mode was randomized. This protocol was performed on two separate occasions, initially for familiarization purposes and again 1 week later for data acquisition.

For all contractions, the participants were seated in an upright position with the hips at approximately 90° flexion. The knee joint was aligned with the axis of rotation of the dynamometer (Biodex System 2, Shirley, NY) and the leg was secured to the dynamometer arm at the ankle. Eccentric and concentric contractions were performed isokinetically at a speed of 1.05 rad·s^{-1}. Eccentric contractions were performed from full extension (0°) to 100° knee flexion. The participants contracted their quadriceps in response to the initiation of movement of the dynamometer arm from the starting position (full extension). The quadriceps remained relaxed between contractions while the dynamometer returned to the starting position. A similar protocol was used for concentric contractions, which were performed from 100° to full extension. Consistent verbal encouragement was provided to ensure maximal effort. For subsequent submaximal contractions, a visual display of the target force was provided. The target force was indicated by a line using the manufacturer's software (Biodex System 2, Shirley, NY) and the participants tried to control peak torque production to match the line. Five contractions were performed at each intensity. A rest of 2 min was allowed between tests at each intensity and between tests in each contraction mode.

For isometric contractions, the knee joint was set at 70° flexion and the participants were instructed to maximally contract the knee extensors. This angle represents the optimum angle for knee extension torque production (Aagaard *et al.*, 2000a) and allows for the best comparison of maximum torque production between eccentric, concentric and isometric modes. For submaximal contractions, a visual display of the target force was provided as described above. Three 3 s contractions were performed at each intensity, at a knee flexion angle of 70°, with a 10 s delay between contractions. A delay of 10 s was used because, during the familiarization session, the participants were better able to match the target forces the shorter the time between contractions. A 2 min rest was provided between sets of contractions at each intensity.

EMG measurements

During all contractions, EMG activity was recorded from surface electrodes placed over the rectus femoris, vastus lateralis and vastus medialis muscles. The skin was shaved, cleaned and abraded before application of Ag/AgCl electrodes 10 mm in diameter. Pairs of electrodes were placed along the long axis of the muscles. For the rectus femoris, a pair of electrodes was placed midway along a line between the anterior superior iliac spine and the superior pole of the patella. For the vastus lateralis, electrodes were placed four fingerbreadths proximal to the superiolateral border of the patella along the assumed line of the fibres. For the vastus medialis, electrodes were placed two finger-breadths proximal to the superiomedial border of the patella along the assumed line of the fibres. An inter-electrode distance of 3 cm (centre to centre) was used and a ground electrode was placed on the patella. The telemetered EMGs were bandpass filtered from 10 to 500 Hz and sampled at 1000 Hz, with a common-mode rejection ratio of 130 dB (Telemyo, Noraxon, Scottsdale, AZ). Torque, velocity, angle and the three EMGs were recorded simultaneously on a personal computer.

Data processing

The EMG amplitude was quantified by computing the root mean square (RMS) of the raw signal with sliding 50 ms windows. This provided a smoothed curve from which a peak could be identified. The frequency content of the raw EMG was quantified by computing 512 point Fast Fourier Transforms (FFT) with a Hanning window function. Mean frequency was computed from the FFT. All computations were performed using software supplied by the manufacturer (Noraxon, Scottsdale, AZ). For isometric contractions, FFTs were computed on 512 ms of EMG activity (512 data points at a sampling frequency of 1000 Hz) immediately before peak torque. For eccentric and concentric contractions, FFTs were computed on 512 ms of activity between 30° and 60° of knee flexion to ensure similar muscle lengths between measures (Fig. 1). Although peak torque occurred between 60° and 80° during maximum eccentric and concentric contractions, during the submaximal contractions the target torque occurred in the mid-range, always between 30° and 60°. Therefore, we chose the activity within this range for computing the FFTs. At 1.05 rad·s^{-1}, with a sampling rate of 1000 Hz, there are 500 points in 30° of motion. The number of points in an FFT must be a power of two (e.g. 512 points). Therefore, the FFT was performed on 30.7° of motion. The mean frequency, peak RMS EMG and peak torque between 30° and 60° were recorded for eccentric and concentric contractions. Although no attempt was made to document the reliability of these EMG techniques, it has previously been shown that there is acceptable reliability

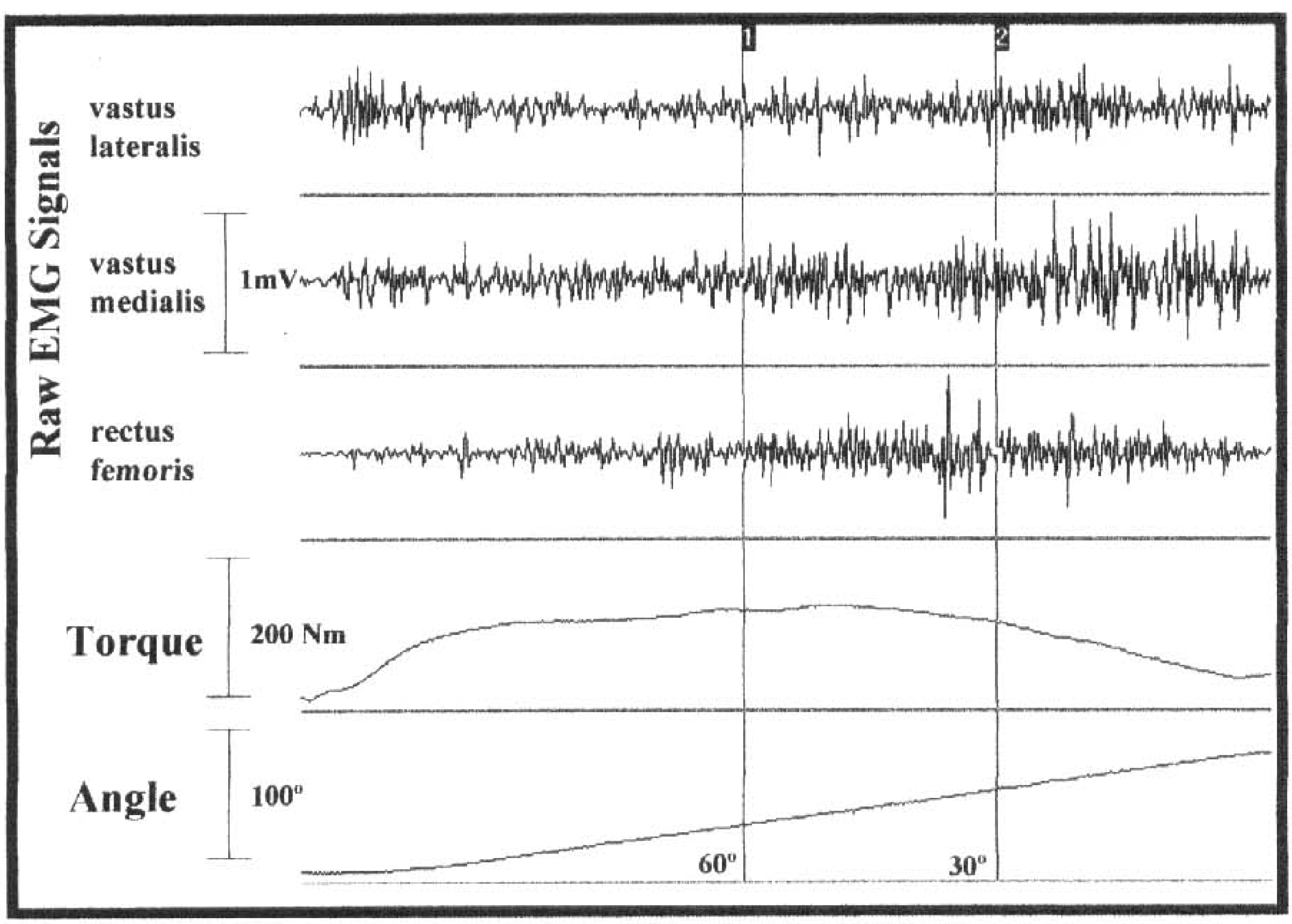

Fig. 1. Raw EMG, torque and angle recordings for one concentric contraction of the knee extensors at 50% of concentric MVC (approximately 2 s of data are shown). Fast Fourier Transforms (FFTs) were computed on the EMG activity between the perpendicular lines that identify the portion between 60° and 30° of knee flexion. The RMS EMG was computed for the same time period as the FFT.

for within-session trials (Viitasalo and Komi, 1975). Furthermore, based on previously demonstrated differences in mean frequency between contraction modes in the hamstrings (McHugh *et al.*, 2000), we estimated that a sample size of 10 would be sufficient to demonstrate a difference in mean frequency between eccentric and concentric modes.

Statistical analysis

Torque, RMS EMG and mean frequency values were averaged for each contraction intensity within each contraction mode. A 2 × 4 × 3 repeated-measures analysis of variance (ANOVA) was used to determine the main effects and interactions between contraction mode (eccentric, concentric), contraction intensity (25%, 50%, 75%, 100%) and muscle (rectus femoris, vastus lateralis, vastus medialis) on mean frequency. Isometric contractions were not included in this analysis to avoid comparison of dynamic and static contractions analysed at different muscle lengths. The main reason for collecting the isometric data was to demonstrate an effect of contraction intensity on mean frequency, thereby ensuring that the measurement technique was able to detect expected normal changes in recruitment from low-intensity to moderate-intensity contractions, as established previously for the quadriceps (Bernardi *et al.*, 1997). The effects of contraction mode, intensity and muscle on EMG RMS were analysed using a 3 × 4 × 3 repeated-measures ANOVA. Greenhouse-Geisser corrections (indicated by $_{GG}$) were applied to significant F-ratios that did not meet Mauchly's assumption of spherecity. All *post-hoc* pairwise comparisons were made with Bonferroni corrections. Significance was set at $P < 0.05$.

Results

The torque values and percentage of MVC at each contraction intensity for each contraction mode are shown in Table 1. Peak knee extension torque was significantly lower ($P < 0.001$) for concentric than for eccentric and isometric contractions. Eccentric and isometric peak torque were similar. Mean frequency was higher for eccentric contractions than for concentric contractions (mode effect, $P < 0.0001$; Table 2). The difference in mean frequency between contraction modes was greater at the lower contraction intensities (contraction mode × intensity, $P < 0.05$; Fig. 2) and more apparent in the rectus femoris and vastus lateralis than in the vastus medialis (contraction mode × muscle, $P < 0.05$; Fig. 3). Mean frequency increased with increasing contraction intensity for isometric (effect of intensity, $P < 0.001$; Table 2) and concentric ($P < 0.01$, Fig. 2) contractions, but not for eccentric contractions ($P = 0.27$; Fig. 2). For isometric and concentric contractions, mean frequency increased significantly from 25% to 50% MVC

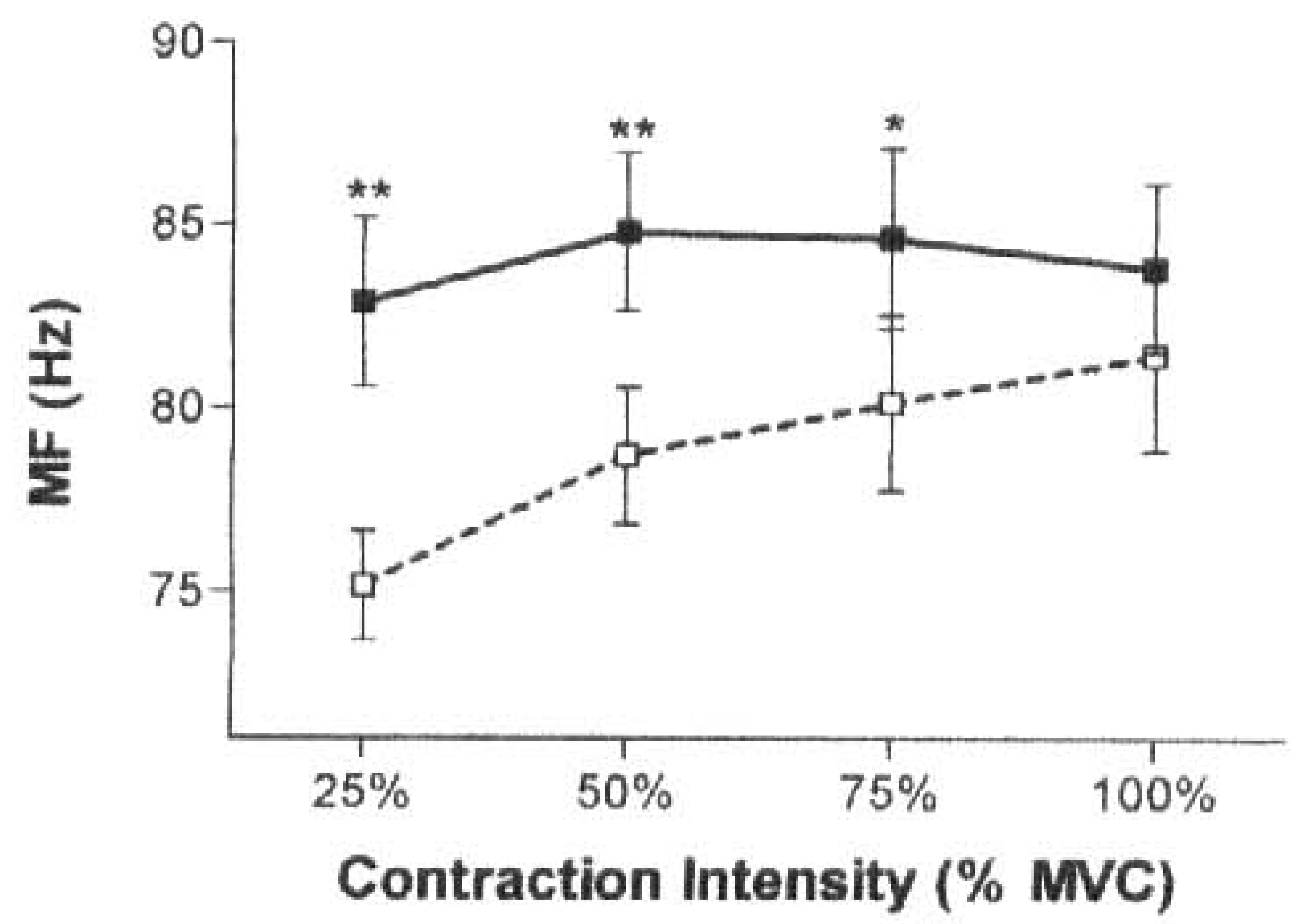

Fig. 2. Interaction between contraction mode (eccentric, concentric) and contraction intensity (25%, 50%, 75%, 100%) on mean frequency (MF) ($P < 0.05$). ■, eccentric; □, concentric. Values are averaged across the three muscles tested. The difference in mean frequency between eccentric and concentric contractions decreased with increasing contraction intensity. **$P < 0.01$, *$P < 0.05$: eccentric greater than concentric. Values are the mean ± $s_{\bar{x}}$.

Table 1. Torque and percentage MVC for concentric, eccentric and isometric contraction modes (mean ± s)

	Torque (N·m)			Percentage MVC		
	Concentric	Eccentric	Isometric	Concentric	Eccentric	Isometric
25% MVC	68.1 ± 15.2	120 ± 25.0	82.3 ± 10.8	29.3 ± 7.0	36.9 ± 6.6	26.4 ± 2.2
50% MVC	136 ± 15.2	188 ± 23.4	164 ± 27.2	58.0 ± 4.7	57.8 ± 6.0	52.7 ± 4.1
75% MVC	194 ± 30.7	259 ± 23.4	253 ± 37.3	82.9 ± 9.2	79.9 ± 12.3	81.1 ± 5.7
100% MVC	234 ± 23.7	326 ± 35.4	312 ± 44.6	100	100	100

Note: Concentric torques were significantly lower than eccentric and isometric torques ($P < 0.01$). Percentage MVC was similar between modes of contraction.

Table 2. Mean frequency for the rectus femoris (RF), vastus lateralis (VL) and vastus medialis (VM) during concentric, eccentric and isometric contractions at target intensities of 25%, 50%, 75% and 100% MVC (mean ± *s*)

	25%	50%	75%	100%
Concentric				
Rectus femoris	80.4 ± 7.3	85.0 ± 7.6	87.9 ± 12.6	89.4 ± 11.7
Vastus lateralis	74.2 ± 7.6	77.1 ± 8.9	76.7 ± 8.9	77.6 ± 8.5
Vastus medialis	70.9 ± 7.0	74.1 ± 7.6	75.9 ± 8.5	77.4 ± 10.1
Eccentric				
Rectus femoris	90.1 ± 8.9	94.0 ± 8.9	93.8 ± 9.2	93.4 ± 8.2
Vastus lateralis	81.3 ± 11.4	82.7 ± 10.8	82.9 ± 12.3	82.2 ± 12.3
Vastus medialis	77.3 ± 9.8	77.8 ± 7.9	77.3 ± 8.2	76.0 ± 8.5
Isometric				
Rectus femoris	75.7 ± 4.7	81.0 ± 5.1	83.9 ± 7.0	79.3 ± 7.6
Vastus lateralis	71.8 ± 9.5	73.5 ± 10.1	76.6 ± 10.1	74.0 ± 11.4
Vastus medialis	71.5 ± 8.9	73.6 ± 8.9	75.6 ± 10.1	73.3 ± 10.1

Note: Effect of contraction mode: eccentric > concentric, $P < 0.001$; contraction mode (eccentric, concentric) × muscle (RF, VL, VM), $P < 0.05$; contraction mode (eccentric, concentric) × intensity (25%, 50%, 75%, 100%), $P < 0.05$. Effect of contraction intensity: concentric, $P < 0.01$ (25–50% MVC, $P < 0.01$); eccentric, $P = 0.27$; isometric, $P < 0.001$ (25–50% MVC, $P < 0.01$). Effect of muscle, $P < 0.01$ (RF > VM, $P < 0.05$).

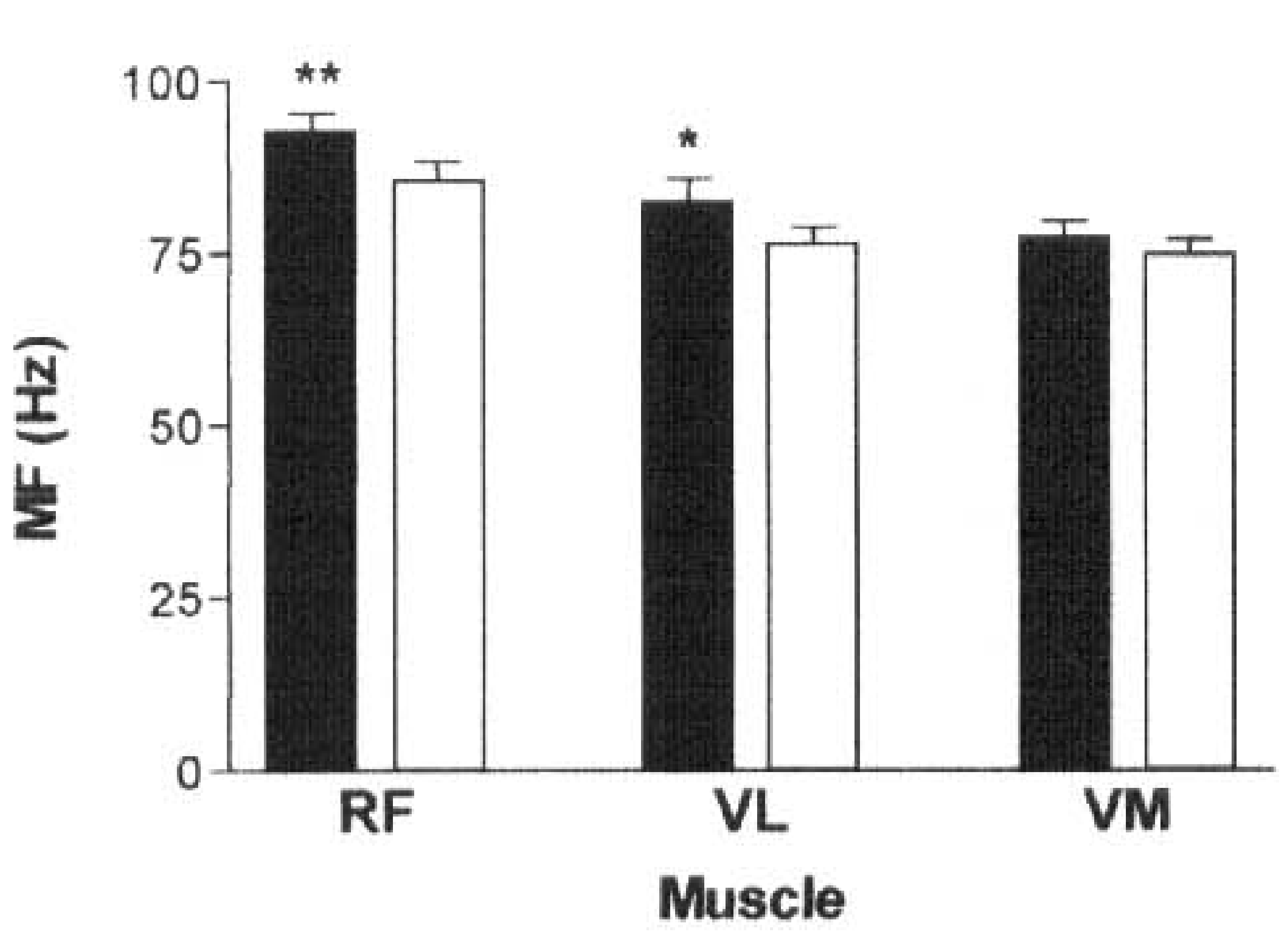

Fig. 3. Interaction between contraction mode (eccentric, concentric) and muscle (RF, rectus femoris; VL, vastus lateralis; VM, vastus medialis) on mean frequency (MF) ($P < 0.05$). ■, eccentric; □, concentric. The difference in mean frequency between eccentric and concentric contractions was significant for the rectus femoris (**$P < 0.01$) and vastus lateralis (*$P < 0.05$), but not the vastus medialis ($P = 0.33$). Values are the mean ± $s_{\bar{x}}$.

($P < 0.01$), but not from 50% to 75% MVC or from 75% to 100% MVC. There was a main effect of muscle on mean frequency ($P < 0.01$), with *post-hoc* analyses indicating a higher mean frequency for the rectus femoris than the vastus medialis across contraction modes and contraction intensities ($P < 0.05$; Table 2).

As expected, EMG RMS increased with increasing contraction intensity in each contraction mode and similarly for each muscle (all $P < 0.0001_{GG}$). The RMS EMG relative to torque was significantly lower for eccentric than concentric contractions ($P < 0.001$). The difference in RMS EMG per unit torque between eccentric and concentric contractions was more apparent at the lower contraction intensities (mode × intensity, $P < 0.05_{GG}$; 48% lower at 25% MVC, 40% lower at 50% MVC, 35% lower at 75% MVC and 30% lower at 100% MVC).

Discussion

The main finding in the present study was that mean frequency was higher for eccentric than for concentric contractions of the quadriceps femoris, across a range of submaximal contraction intensities. These results are contrary to those of previous studies, in which there was no difference or a lower mean frequency for eccentric than for concentric contractions of the elbow flexors (Moritani *et al.*, 1988; Nakazawa *et al.*, 1993; Potvin, 1997; Komi *et al.*, 2000) and quadriceps femoris (Tesch *et al.*, 1990; Aagaard *et al.*, 2000b). The only notable differences in EMG techniques were that Nakazawa *et al.* (1993) used an autoregressive model rather than an FFT to estimate the power spectrum, Moritani *et al.* (1988) used a smaller inter-electrode distance and processed the data with a Hamming window function (we used a Hanning window) and Komi *et al.* (2000) used a smaller inter-electrode distance but did not use a window function. It is important to note that these previous studies did not investigate the relationship between contraction intensity and mean frequency and, therefore, did not establish that the measurement techniques could detect the progressive recruitment of fast-twitch motor units with increasing contraction intensity.

Mean frequency was compared between contraction modes to provide an indirect indication of possible differences in motor unit recruitment. The association between mean frequency and recruitment is based on mean frequency primarily reflecting muscle fibre conduction velocity (Kupa *et al.*, 1995; Kamen and Caldwell, 1996). Since fast-twitch muscle fibres have faster conduction velocities, muscles with a high proportion of fast-twitch fibres tend to have a higher frequency (Gerdle *et al.*, 1988; Kupa *et al.*, 1995). Similarly, mean frequency increases with increasing contraction intensity as higher-threshold (fast-twitch) motor units are progressively recruited (Moritani and Muro, 1987; Bernardi *et al.*, 1997). This effect was apparent in the present study for isometric and concentric contractions, but not for eccentric contractions. The increase in mean frequency of the rectus femoris from 25% to 50% MVC during isometric contractions was 5 Hz, compared with 7 Hz in the study of Bernardi *et al.* (1997). A similar plateau in mean frequency at 60% MVC was evident (Bernardi *et al.*, 1997), but values for other quadriceps muscles were not reported. That mean frequencies decreased slightly from 75% to 100% MVC in the isometric mode contradicts this explanation. However, this effect has been demonstrated in the tibialis anterior (Broman *et al.*, 1985) and may be due to synchronization of motor unit firing rates at maximal intensities (Broman *et al.*, 1985).

In the present study, mean frequency was higher for the rectus femoris than the vastus medialis, which is consistent with the findings of Gerdle *et al.* (1988) and may reflect a higher percentage of fast-twitch fibres in the biarticular rectus femoris compared with the uniarticular vastus medialis (Garrett *et al.*, 1984). However, differences in fibre direction with respect to electrode placement between the bipennate rectus femoris and the unipennate vastus medialis may have had an effect on the results.

The increase in mean frequency with increasing contraction intensity and the higher mean frequency in the rectus femoris indicate that the technique used was able to detect differences in the proportions of active fast-twitch motor units. The increase in mean frequency with increasing intensity of concentric contractions is consistent with progressively greater recruitment of fast-twitch motor units. In contrast, that mean frequency did not increase with increasing eccentric contraction intensity could indicate that equal proportions of fast-twitch and slow-twitch motor units were recruited at each intensity. Therefore, higher mean frequencies for submaximal eccentric than submaximal concentric quadriceps contractions is consistent with a greater proportion of fast-twitch motor units being active during eccentric contractions. It follows that at 100% MVC the difference in mean frequency between eccentric and concentric contractions was minimal, since most motor units were recruited in both modes. Alternatively, the differences in mean frequency between contraction modes could be attributed to differences in motor unit firing rate. However, mean frequency is relatively insensitive to motor unit firing rates except at very low contraction intensities (Fuglsang-Frederiksen and Rønager, 1988; Solomonow *et al.*, 1990; Hägg, 1992; Kamen and Caldwell, 1996).

Other biological factors that affect the frequency content of the EMG include motor unit synchronization and muscle temperature. Motor unit synchronization decreases mean frequency regardless of the type of units firing. However, there is no evidence to suggest that higher mean frequencies for eccentric contractions could be due to less synchronization. Eccentric contractions are associated with higher intramuscular temperatures (Nadel *et al.*, 1972), which could theoretically increase mean frequency. However, having our participants perform only five contractions at each intensity, providing adequate rest between sets and randomizing contraction mode order should have eliminated any possible temperature effects.

Many technical factors affect surface EMG measurements and can lead to erroneous interpretations of results. Controlling such factors as inter-electrode spacing, electrode configuration, electrode placement with respect to the innervation zone and changing muscle length is essential for proper interpretation of mean frequency values (Kamen and Caldwell, 1996). In the present study, data were collected within a single session and, therefore, electrode spacing and configuration were consistent across all trials. That the electrode placements did not account for the innervation zones may have affected the results, since the innervation zones were moving in opposite directions during eccentric and concentric contractions. However, standard electrode placements were used, similar to those used in previous studies (Tesch *et al.*, 1990; Cesarelli *et al.*, 1999).

Given the inherent limitations of applying the FFT algorithm to surface EMGs during dynamic contractions, the present results are surprising. The continuous changes in muscle fibre lengths during dynamic contractions pose a major technical problem in analysing surface EMGs. At shorter muscle lengths, muscle fibre diameter is increased, resulting in a higher mean frequency (Potvin, 1997). Additionally, motor unit firing rate is higher at shorter muscle lengths (Christova *et al.*, 1998). In the present study, muscle length was controlled by computing mean frequency from FFTs of EMGs between 30° and 60° of knee flexion during eccentric and concentric contractions. It is also more difficult to ensure signal stationarity during dynamic than during isometric contractions. A Hanning window function was used to control signal stationarity. These limitations increase measurement variability and decrease the likelihood of detecting differences in mean frequency between contractions. However, a marked difference between eccentric and concentric contractions was apparent. This can be attributed to either a true difference in motor unit behaviour or to a fixed measurement error (bias). However, there is no apparent evidence to support measurement bias.

When comparing mean frequency between contraction modes, it is important that signal-to-noise ratios are similar. This is more important when the amplitude of the signal differs between contraction modes, since at lower amplitudes a greater proportion of the signal is due to noise. The signal-to-noise ratio can be optimized by ensuring that inter-electrode impedance is low. Although impedance was not measured in the present study, minimal noise was evident in the EMGs even at the lowest intensities (Fig. 4). Therefore, the potential for high-frequency noise to adversely affect mean frequency during eccentric contractions appears unlikely.

In general, the target torques were well matched during the submaximal contractions (Table 1). However, in the eccentric mode, the target of 25% was exceeded and the mean value was 37% of MVC. It is possible that this contributed to the observed differences in mean frequency between eccentric and concentric contractions at this target intensity. However, it should be noted that the average RMS EMG at this target intensity was similar for eccentric (178 ± 90 μV) and concentric (189 ± 91 μV) modes ($P = 0.43$). Despite similar EMG amplitudes, mean frequency was 8 ± 7 Hz lower for eccentric contractions.

In conclusion, a higher mean frequency was demonstrated for eccentric than for concentric contractions of the quadriceps femoris across a range of submaximal intensities. Higher mean frequencies for eccentric contractions is consistent with a greater proportion of fast-twitch motor units being active during submaximal eccentric contractions. These results are in line with those of previous studies using indwelling electrodes in the plantar flexors (Nardone and Schieppati, 1988; Nardone *et al.*, 1989) and the first dorsal interosseous muscle (Howell *et al.*, 1995) in humans. However, these previous studies were confined to low-intensity

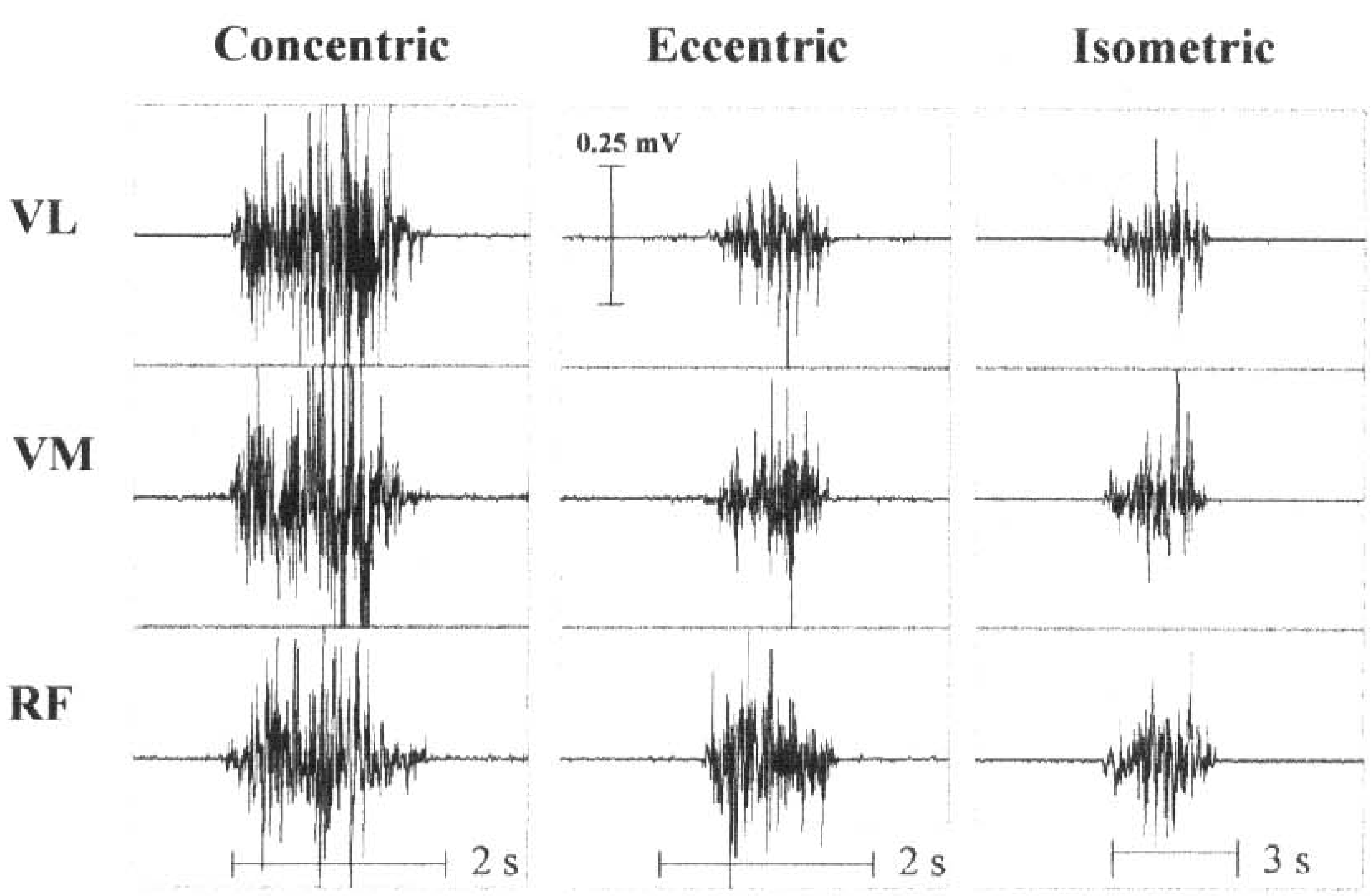

Fig. 4. Raw EMGs from the vastus lateralis (VL), vastus medialis (VM) and rectus femoris (RF) muscles during concentric, eccentric and isometric contractions at the lowest intensity tested (25% MVC) in a randomly selected participant. Note that the baseline signal noise is minimal in relation to the contractile activity.

contractions. Greater relative recruitment of fast-twitch motor units during eccentric contractions may have training implications for sports that place a high demand on fast-twitch fibre function and for rehabilitation of injuries that primarily affect fast-twitch fibres.

References

Aagaard, P., Simonsen, E.B., Andersen, J.L., Magnusson, S.P., Bojsen-Møller, F. and Dyhre-Poulsen, P. (2000a). Antagonist muscle coactivation during isokinetic knee extension. *Scandinavian Journal of Medicine and Science in Sports*, **10**, 58–67.

Aagaard, P., Simonsen, E.B., Andersen, J.L., Magnusson, S.P., Halkjaer-Kristensen, J. and Dyhre-Poulsen, P. (2000b). Neural inhibition during maximal eccentric and concentric quadriceps contraction: effects of resistance training. *Journal of Applied Physiology*, **89**, 2249–2257.

Adams, G.R., Duvoisin, M.R. and Dudley, G.A. (1992). Magnetic resonance imaging and electromyography as indexes of muscle function. *Journal of Applied Physiology*, **73**, 1578–1583.

Bernardi, M., Solomonow, M. and Baratta, R.V. (1997). Motor unit recruitment strategy of antagonist muscle pair during linearly increasing contraction. *Electromyography and Clinical Neurophysiology*, **37**, 3–12.

Bigland, B. and Lippold, O.C.J. (1954). The relation between force velocity and integrated electrical activity in human muscles. *Journal of Physiology*, **123**, 214–224.

Bilodeau, M., Cincera, M., Gervais, S., Arsenault, A.B., Gravel, D., Lepage Y. and McKinley, P. (1995). Changes in the electromyographic spectrum power distribution caused by a progressive increase in the force level. *European Journal of Applied Physiology*, **71**, 113–123.

Broman, H., Bilotto, G. and DeLuca, C.J. (1985). Myoelectric signal conduction velocity and spectral parameters: influence of force and time. *Journal of Applied Physiology*, **58**, 1428–1437.

Cesarelli, M., Bifulco, P. and Bracale M. (1999). Quadriceps muscles activation in anterior knee pain during isokinetic exercise. *Medicine and Engineering in Physics*, **21**, 469–478.

Christova, P., Kossev, A. and Radicheva, N. (1998). Discharge rate of selected motor units in human biceps brachii at different muscle lengths. *Journal of Electromyography and Kinesiology*, **8**, 287–294.

Enoka, R.M. (1996). Eccentric contractions require unique activation strategies by the nervous system. *Journal of Applied Physiology*, **81**, 2339–2346.

Fuglsang-Frederiksen, A. and Rønager, J. (1988). The motor unit firing rate and the power spectrum of EMG in humans. *Electroencephalography and Clinical Neurophysiology*, **70**, 68–72.

Garrett, W.E., Califf, J.C. and Bassett, F.H. (1984). Histochemical correlates of hamstring injuries. *American Journal of Sports Medicine*, **12**, 98–103.

Gerdle, B., Wretling, M.L. and Henriksson-Larsén, K. (1988). Do the fiber-type proportion and the angular velocity influence the mean frequency of the electromyogram. *Acta Physiologica Scandinavica*, **134**, 341–346.

Hägg, G.M. (1992). Interpretation of EMG spectral alterations and alteration indexes at sustained contraction. *Journal of Applied Physiology*, **73**, 1211–1217.

Howell, J.N., Fuglevand, A.J., Walsh, M.L. and Bigland-Ritchie, B. (1995). Motor unit activity during isometric and concentric–eccentric contractions of the human first dorsal interosseus muscle. *Journal of Neurophysiology*, **74**, 901–904.

Kamen, G. and Caldwell, G.E. (1996). Physiology and interpretation of the electromyogram. *Journal of Clinical Neurophysiology*, **13**, 366–384.

Komi, P.V., Kaneko, M. and Aura, O. (1987). EMG activity of the leg extensors muscles with special reference to mechanical efficiency in concentric and eccentric exercise. *International Journal of Sports Medicine*, **8**, 22–29.

Komi, P.V., Linnamo, V., Silventoinen, P. and Sillanpää, M. (2000). Force and EMG power spectrum during eccentric and concentric actions. *Medicine and Science in Sports and Exercise*, **32**, 1757–1762.

Kupa, E.J., Roy, S.H., Kandarian, S.C. and DeLuca, C.J. (1995). Effects of muscle fiber type and size on EMG median frequency and conduction velocity. *Journal of Applied Physiology*, **79**, 23–32.

McHugh, M.P., Connolly, D.A.J., Eston, R.G. and Gleim, G.W. (2000). Electromyographic analysis of exercise resulting in symptoms of muscle damage. *Journal of Sports Sciences*, **18**, 163–172.

Moritani, T. and Muro, M. (1987). Motor unit activity and surface electromyogram power spectrum during increasing force of contraction. *European Journal of Applied Physiology*, **56**, 260–265.

Moritani, T., Muramatsu, S. and Muro, M. (1988). Activity of motor units during concentric and eccentric contractions. *American Journal of Physics in Medicine*, **66**, 338–350.

Nadel, E.R., Bergh, U. and Saltin, B. (1972). Body temperatures during negative work exercise. *Journal of Applied Physiology*, **33**, 553–558.

Nakazawa, K., Kawakami, Y., Fukunaga, T., Yano, H. and Miyashita, M. (1993). Differences in activation patterns in elbow flexor muscles during isometric, concentric and eccentric contractions. *European Journal of Applied Physiology*, **66**, 214–220.

Nardone, A. and Schieppati, M. (1988). Shift of activity from slow to fast muscle during voluntary lengthening contractions of the triceps surae muscles in humans. *Journal of Physiology*, **395**, 363–381.

Nardone, A., Romano, C. and Schieppati, M. (1989). Selective recruitment of high-threshold human motor units during voluntary isotonic lengthening of active muscles. *Journal of Physiology*, **409**, 451–471.

Potvin, J.R. (1997). Effects of muscle kinematics on surface EMG amplitude and frequency during fatiguing dynamic contractions. *Journal of Applied Physiology*, **82**, 144–151.

Solomonow, M., Baten, C., Smit, J., Baratta, R., Hermens, H., D'Ambrosia, R. and Hiromu, S. (1990). Electromyographic power spectra frequencies associated with motor unit recruitment strategies. *Journal of Applied Physiology*, **63**, 1177–1185.

Tesch, P.A., Dudley, D.A., Duvoisin, M.R., Hather, B.M. and Harris, R.T. (1990). Force and EMG signal patterns during repeated bouts of eccentric muscle actions. *Acta Physiologica Scandinavica*, **138**, 263–271.

Viitasalo, J.H.T. and Komi, P.V. (1975). Signal characteristics of EMG with special reference to reproducibility of measurements. *Acta Physiologica Scandinavica*, **93**, 531–539.