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Mechanomyographic and electromyographic responses during fatigue in humans: influence of muscle length

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Abstract Mechanomyography (MMG) provides a measure of muscle mechanical changes during contractions. The purpose of this study was to quantify alterations in MMG signals during fatigue at two muscle lengths. Comparisons with electromyographic (EMG) recordings were made. A group of 13 subjects performed isometric dorsiflexions (50% of maximum for 60 s) at 40° of plantarflexion (long, l_{l}) and 5° of dorsiflexion (short, l_{s}). The mean power frequency of the EMG ($\bar{f}_{\mathrm{EMG}}$) and MMG ($\bar{f}_{\mathrm{MMG}}$) signals and the mean rectified MMG ($r\overline{\mathrm{MMG}}$) and EMG ($r\overline{\mathrm{EMG}}$) were determined over each 1-s period, normalized to the respective maximal value, regressed against time, and the resulting slopes (units = %max · s^{-1}) were analyzed. The $r\overline{\mathrm{MMG}}$ slopes were larger ($P = 0.007$) at l_{l} compared to l_{s} [mean l_{l} 0.50 (SD 0.26), mean l_{s} 0.27 (SD 0.16)], however there were no differences ($P = 0.24$) between mean $\bar{f}_{\mathrm{MMG}}$ slopes [l_{l} −0.10 (SD 0.16), l_{s} −0.16 (SD 0.11)]. Similarly, $r\overline{\mathrm{EMG}}$ slopes were larger ($P = 0.001$) at l_{l} versus l_{s} [l_{l} 0.26 (SD 0.13), l_{s} 0.08 (SD 0.15)] and there were no differences ($P = 0.89$) between mean $\bar{f}_{\mathrm{EMG}}$ slopes [l_{l} −0.15 (SD 0.14), l_{s} −0.14 (SD 0.12)]. At 5 s following the exercise to fatigue mean MVC (units = %max) were not significantly different between l_{l} and l_{s} [$P = 0.08$; l_{l} 78.8 (SD 9.1), l_{s} 85.2 (SD 6.0)]. These results showed that during fatiguing contractions, MMG and EMG amplitudes increased while frequency characteristics decreased at both muscle lengths. The change in $r\overline{\mathrm{MMG}}$ and $r\overline{\mathrm{EMG}}$ was greater at l_{l} but no differences in $\bar{f}_{\mathrm{MMG}}$ or $\bar{f}_{\mathrm{EMG}}$ slopes occurred between lengths. These results would suggest that larger increases in motor unit recruitment occur with time during fatigue at l_{l} compared to l_{s}.

Key words Exercise · Electromyography · Mechanomyography

Introduction

Several studies have shown that muscle length affects the rate of muscle fatigue, based both on the rate of force loss (Aljure and Borrero 1968; Fitch and McComas 1985; Sacco et al. 1994) as well as the rate of changes in the electromyograph (EMG) signal (Doud and Walsh 1995; Weir et al. 1996). However the mechanism(s) behind the differential rates of fatigue are not clear. Fitch and McComas (1985) have interpreted a larger loss in force production capability at a long versus short muscle length to be due to greater actin-myosin interaction at the long muscle length, resulting in greater adenosinetriphosphate (ATP) cost. However, Baker et al. (1992) and Sacco et al. (1994) have shown, using nuclear magnetic resonance spectroscopy, that ATP turnover during fatigue is similar at long and short muscle lengths.

We have previously reported, based on surface EMG responses, that differences in muscle fatigue at different muscle lengths may be due, in part, to differences in the rate of motor unit recruitment (Weir et al. 1996). Mechanomyography (MMG), which records muscle vibrations, has recently been used to examine muscle function. Mechanomyographs have been recorded during a variety of types of contraction and activities including cycle ergometry (Shinohara et al. 1997; Stout et al. 1997), voluntary isometric contractions (Ebersole et al. 1998; Orizio et al. 1990; Stokes and Cooper 1992; Stokes and Dalton 1991a), electrically elicited contractions (Chen et al. 1997; Orizio et al. 1993, 1996; Petitjean et al. 1998; Stokes and Cooper 1992; Vaz et al. 1996), concentric isokinetic contractions (Evetovich et al. 1997, 1998), and eccentric isokinetic contractions (Evetovich et al. 1998; Smith et al. 1997).

It has been suggested that the MMG signal contains information which reflects motor unit recruitment and firing rate. In addition, it may be used to differentiate

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among muscles containing different types of fibers (Marchetti et al. 1992; Mealing et al. 1996; Orizio and Veicsteinas 1992) and healthy from diseased muscle (Akataki et al. 1996; Barry et al. 1990; Orizio et al. 1997; Rhatigan et al. 1986; Rodriquez et al. 1996). Several studies have examined muscle fatigue responses in MMG signals (Barry et al. 1985; Dalton et al. 1992; Goldenberg et al. 1991; Herzog et al. 1994; Orizio et al. 1989a, 1992; Orizio and Veicsteinas 1992; Rodriquez et al. 1996; Stokes and Dalton 1991b; Zwarts and Keidel 1991) and these fatigue related changes in the MMG signal may also reflect changes in motor unit recruitment and firing rate (Goldenberg et al. 1991).

In this study, we examined changes in the amplitude and frequency characteristics of the MMG signal during fatigue at two muscle lengths to examine further the effect of muscle length on motor unit activation during fatigue. Specifically, the recording of MMG during fatigue, in conjunction with EMG, was made to verify the observation that motor unit recruitment during fatigue can vary with muscle length.

Methods

Subjects

A group of 23 subjects (12 men and 11 women) between the ages of 21 and 31 years were originally recruited as subjects for this investigation. However, 10 subjects were unable to complete the fatigue tasks as required (mean relative forces during the fatigue trials differed by $\geq 10\%$ between muscle lengths) and their results were removed from the analyses. The remaining 13 subjects [mean age 25 (SD 3) years, body mass 73.2 (SD 11.2) kg, height 176 (SD 11) cm] consisted of 8 men and 5 women. The procedures were approved by the Institutional Review Board and each subject signed an informed consent form.

Experiment protocol

The subjects reported to the laboratory on two occasions. A minimum of 48 h separated each visit. During each visit, the subjects performed a test at one muscle length and the other muscle length was tested on the next visit. The order of the test sessions was randomized. All tests were made using a KinCom isokinetic dynamometer (125E Plus, Chattecx Corporation, Chattanooga, Tenn.). Each subject was positioned supine on the dynamometer with the right knee extended and with the left knee flexed on the KinCom seat. The subjects were instructed not to use their left limbs for substitution or to increase their strength during the contraction. Additional stabilization was provided by a belt placed superior to the right knee as well as towel handles for each hand.

The subject's right foot (with shoe) was strapped into the KinCom adaptation piece by aligning the axis of rotation with the lateral malleolus. The forefoot support bar was aligned with the metatarsal heads of the foot. A toe strap and a strap positioned superior to the maleoli were used for stabilization at the ankle. The neutral ankle angle (foot in vertical position and perpendicular to the leg) was established with the aid of a carpenter's level and the long (l_l, 40° of plantarflexion) and short (l_s, 5° of dorsiflexion) positions were determined from this position.

A bipolar EMG assembly (Ag-AgCl circular electrode surfaces, diameter 2.5 cm, interelectrode spacing 2 cm) was placed on the tibialis anterior muscle (parallel to the muscle belly) at a position one-third of the distance between the inferior pole of the patella and the lateral malleolus (see Zipp 1982). The reference electrode was placed on the tibial tuberosity of the same leg. A MMG device (mass 1.5 grams, contact surface circumference 2 cm, frequency response 0.66–12,000 Hz; model 3115A piezoelectric accelerometer, Dytran Instruments, Chatsworth Calif., USA) was placed 2-cm proximal to the EMG electrode assembly and held in place with adhesive tape. The surface of the muscle was cleaned with an alcohol pad before placement of the electrodes.

At each visit, the subjects performed three maximal voluntary contractions (MVC) of the right tibialis anterior muscle at one of the two ankle joint angles. Each MVC lasted 5 s with 3 min of rest between contractions. Following the MVC determination, the subjects rested for 5 min before maintaining a fatiguing isometric contraction at 50% MVC. The subjects viewed a computer screen with a digital feedback system to facilitate the maintenance of the 50% MVC criterion. The subjects maintained the 50% MVC for 60 s and verbal encouragement was given by the testers. Directly following the fatiguing procedure the subjects were alloted a 5-s rest followed by another 5-s MVC. This same protocol was repeated for each of the two joint angles. The MMG and EMG data, described below, was collected throughout the test session and analyzed for changes in amplitude and frequency characteristics. An illustration of one 60-s trial is given in Fig. 1.

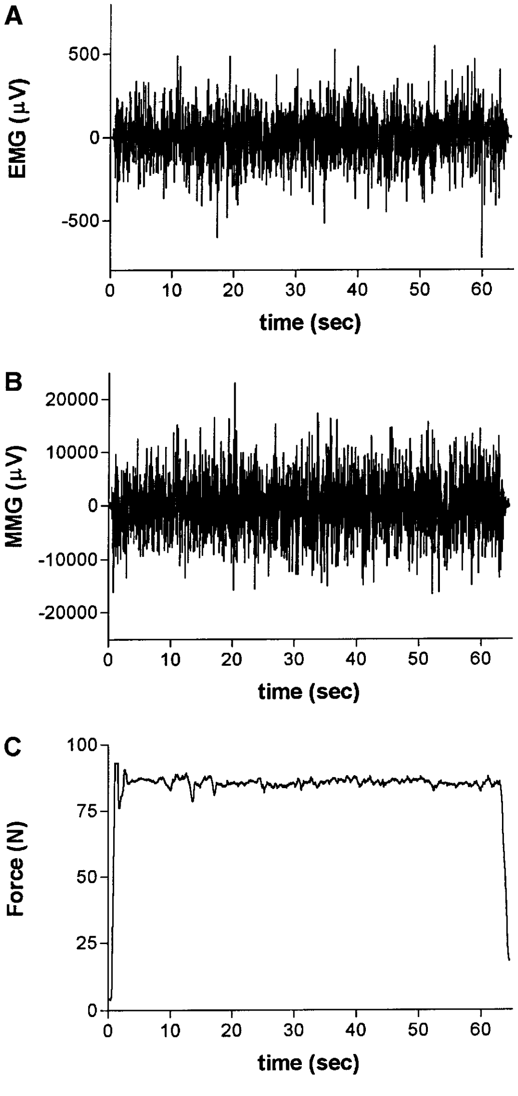

Fig. 1 Electromyogram (*EMG*) **A**, mechanomyogram **B**, and force **C** signals during a 60-s fatigue trial at short position (5° of dorsiflexion) in one subject

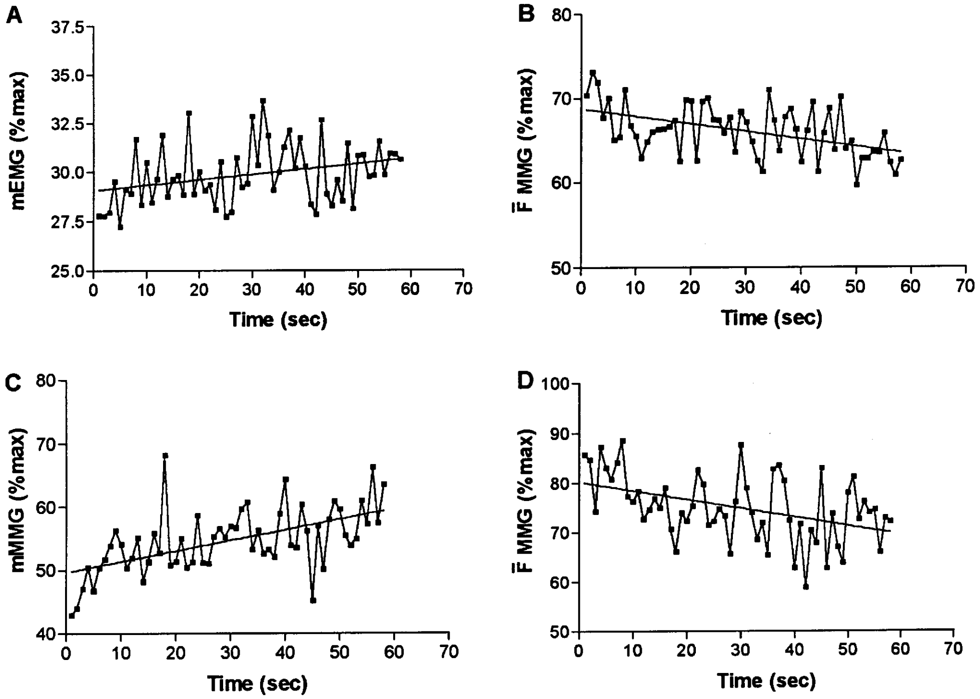

Fig. 2 Normalized mean rectified electromyogram ($r\overline{\text{EMG}}$) **A**, mean frequency electromyogram $\bar{f}_{\text{EMG}}$ **B**, mean mechanomyogram ($r\overline{\text{MMG}}$) **C**, and mean frequency mechanomyogram $\bar{f}_{\text{MMG}}$ **D** derived from the signals shown in Fig. 1. The slopes of the regression lines drawn through the data were used as dependent variables

Data acquisition and signal processing

The EMG signals were pre-amplified at the skin (gain 35×) and further amplified downstream (bandwidth 20–4000 Hz; model D-100 pre-amplifier and model EMG 55 driver amplifier, Therapeutics Unlimited, lowa City, Iowa) with the total system gain adjusted for each subject to allow maximal amplification without saturation of the analog-to-digital converter. The force, EMG, and MMG signals were fed through a low-pass filter (cutoff frequency 480 Hz at 6 dB per octave), and subsequently passed to a BNC connector board (BNC 2080, National Instruments, Austin, Tex.) interfaced with a 12-bit analog-to-digital converter (AT-MIO-16E-10; National Instruments) that amplified the MMG signal 100× and sampled each channel at 1000 Hz. The digitized data were stored on computer disks for subsequent analysis.

For the MVC analyses, a program identified the 1-s time interval in the force signal that had the highest mean. The resulting mean force from this calculation was scored as MVC. The MMG and EMG signals corresponding in time with MVC were identified for frequency and amplitude analysis (see below). The signals collected during the 50% MVC (fatigue) trials were divided into 1-s segments. Since the data acquisition period during the fatigue trials started prior to and ended after the 60-s fatigue period, the appropriate length of time for analysis was determined by computer identification of the 60 contiguous 1-s segments in the force channel that had the lowest coefficient of variation.

The resulting time window was used to identify the appropriate segments from the EMG and MMG signals for analysis. Prior to analysis, the MMG signals were digitally band-pass filtered between 2 and 100 Hz and passed through a 60-Hz notch filter (0 lag 4th order Butterworth filters). For the amplitude analyses, each segment was digxitally full-wave rectified and the mean voltage ($r\overline{\text{MMG}}$ and $r\overline{\text{EMG}}$) was determined. Similarly, for the frequency analysis, a discrete Fourier transform with a Hamming Window function was performed on each segment. From the resulting power density spectrum, the mean power frequency ($\bar{f}$) was determined using the calculations described by Kwatny et al. (1970). For both the amplitude and $\bar{f}$ analyses, the data were normalized to the respective values from the MVC trial. The normalized $\bar{f}$ and amplitude data were regressed against time with the resulting slopes (units = percentage maximum per second) used as dependent variables in the statistical analyses (see Fig. 2).

Statistical analyses

The data were analyzed with two-tailed paired student's t-tests. The independent variable was the length of the muscle and the dependent variables were $r\overline{\text{EMG}}$ slope, $r\overline{\text{MMG}}$ slope, $\bar{f}_{\text{EMG}}$ slope, $\bar{f}_{\text{MMG}}$ slope, the mean force of the 50% maximal fatiguing interval contraction, and the force of the final maximal contraction. For all analyses the α was set at 0.05.

Results

The percentage of maximal force maintained during the 60-s fatigue interval was not significantly different between muscle lengths (t = 0.06, P = 0.56; see Fig. 3), indicating that the relative effort during the fatiguing contractions was similar between conditions and any differences in the EMG and MMG responses were due

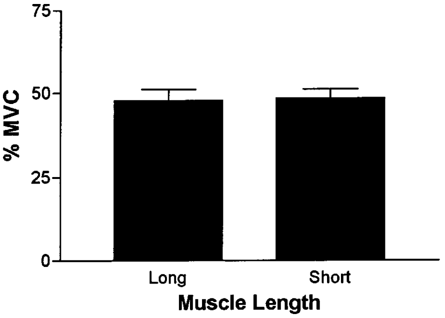

Fig. 3 Effect of muscle length on the percentage of maximal force (mean and SD) maintained during the fatigue periods. There was no significant difference (P = 0.56) between long position (40° of plantarflexion) and short position (5° of dorsiflexion) indicating similar relative force outputs at both muscle lengths. *MVC* Maximal voluntary contraction

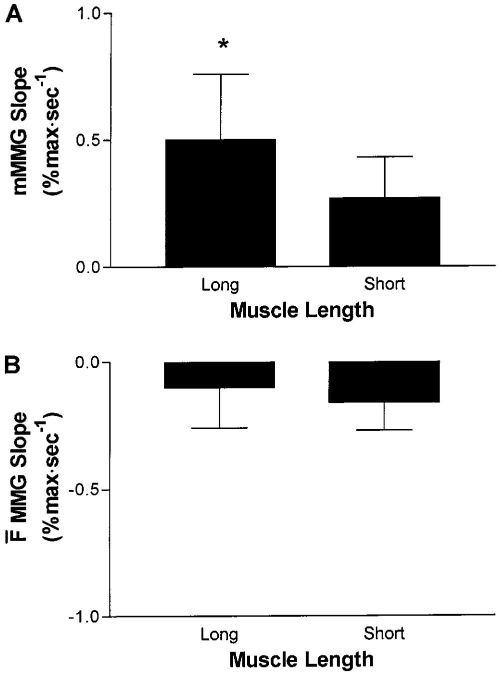

Fig. 4 **A** Effect of muscle length on $r\overline{\text{MMG}}$ fatigue slopes (mean and SD). A significantly larger slope was found at long position (l_l) compared to short position (l_s) (P = 0.007). Neither length included 0 in the 95% confidence interval (l_l = 0.35 to 0.66, l_s = 0.18 to 0.37). **B** Effect of muscle length on $\bar{f}_{\mathrm{MMG}}$ fatigue slopes (mean and SD). Differences between l_l and l_s were not significant (P = 0.24). Neither length included 0 in the 95% confidence interval (l_l = −0.20 to −0.004, l_s = −0.23 to −0.09). *Significant at $P < 0.05$. For definitions see Figs. 2 and 3

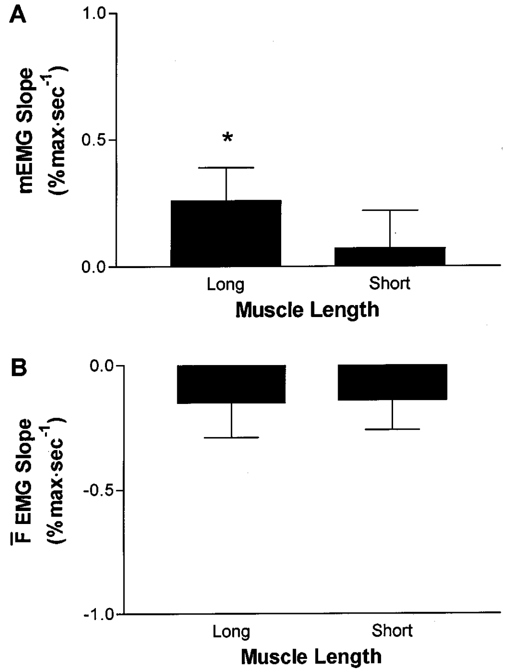

Fig. 5 **A** Effect of muscle length on $r\overline{\text{EMG}}$ fatigue slopes (mean and SD). A significantly larger slope was found at long position (l_l) compared to short position (l_s) (P = 0.001). The l_l data excluded 0 from the 95% confidence interval (0.19–0.34) while the l_s data did not (−0.01 to 0.17). **B** Effect of muscle length on $\bar{f}_{\mathrm{EMG}}$ fatigue slopes (mean and SD). Differences between l_l and l_s were not significant (P = 0.89). Neither length included 0 in the 95% confidence interval (l_l = −0.24 to −0.06, l_s = −0.22 to −0.07). *Significant at $P < 0.05$. For definitions see Figs. 2 and 3

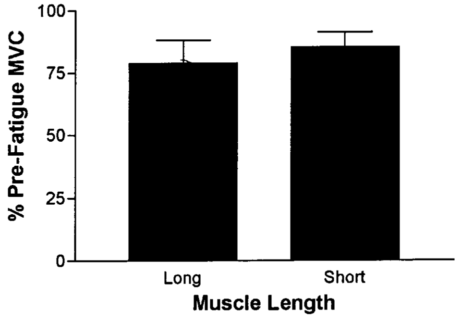

Fig. 6 Effect of muscle length on post-fatigue maximal voluntary contraction (*MVC*) force (mean and SD). Differences between l_l and l_s were not significant (P = 0.08); for definitions see Figs. 3 and 4

to the difference in muscle length. The results of the $r\overline{\text{MMG}}$ analysis showed a significantly steeper slope at l_l versus l_s (t = 3.27, P = 0.007; see Fig. 4). However, the difference in $\bar{f}_{\mathrm{MMG}}$ slope between muscle lengths was not significant (t = 1.22, P = 0.24; see Fig. 4). Similarly, the $r\overline{\text{EMG}}$ analysis showed a steeper slope at l_l vs l_s (t = 4.25, P = 0.001; see Fig. 5) while the $\bar{f}_{\mathrm{EMG}}$ slopes did not differ between l_l and l_s (t = 0.14, P = 0.89; see Fig. 5). The difference in maximal force output following the fatiguing contraction approached significance between muscle lengths (t = 1.89, P = 0.08; see Fig. 6).

Discussion

EMG Fatigue responses

The results of this investigation showed that the changes in amplitude in both the MMG and EMG signals were larger at the longer compared to the shorter muscle length. However, the changes in $\bar{f}$ in both signals were not significantly different between muscle lengths. Central to the interpretation of these data is an understanding of the mechanisms driving changes in amplitude and frequency characteristics during fatigue. With respect to EMG, the well-documented increase in amplitude during fatigue at submaximal force levels has often been attributed to increases in motor unit recruitment (Krogh-Lund and Jorgensen 1992, 1993; Moritani et al. 1986) and/or firing rate (Moritani et al. 1986). That is, during fatigue increases in recruitment and/or firing rate occur to compensate for the fatigue-related loss in force production capability of previously activated motor units, resulting in an increase in signal amplitude.

The decreases in $\bar{f}_{\mathrm{EMG}}$ have been suggested to result from a decrease in muscle fiber conduction velocity (Eberstein and Beattie 1985; Sadoyama et al. 1983) and possibly an increase in motor unit synchronization

(Krogh-Lund and Jorgensen 1992, 1993). However, it has been suggested that the amplitude and frequency characteristic changes in the EMG signal during fatigue are driven by the same mechanism. Specifically, since superficial tissue acts as a low-pass filter, the decrease in muscle fiber conduction velocity (and/or increases in motor unit synchronization) and associated changes in $\bar{f}_{\mathrm{EMG}}$ result in less signal energy being filtered by the tissues, thereby increasing signal amplitude (De Luca 1984). However, the difference in the $r\overline{\mathrm{EMG}}$ and $\bar{f}_{\mathrm{EMG}}$ responses at the two muscle lengths suggests that the primary cause of the increase in $r\overline{\mathrm{EMG}}$ is not secondary to the change in muscle fiber conduction velocity (and $\bar{f}$). Therefore, we argue that the larger increase in $r\overline{\mathrm{EMG}}$ at l_{l} compared to l_{s} is indicative of a greater increase in motor unit recruitment during fatigue at l_{l} relative to l_{s}.

The analysis of the $\bar{f}_{\mathrm{EMG}}$ slopes showed no significant difference between the two muscle lengths. In contrast, previous studies (Doud and Walsh 1995; Weir et al. 1996) have found steeper slopes at shorter muscle lengths. Although we are unable to explain these discrepancies clearly, differences in the experiment procedures are likely to be factors. For instance, our previous study (Weir et al. 1996) involved recording EMG signals over the vastus lateralis and vastus medialis muscles, both of which are pennated muscles. In contrast, the tibialis anterior is a fusiform muscle and therefore the EMG electrodes could be aligned with line of pull of the muscle fibers.

As electrode orientation has been shown to affect EMG fatigue responses (Weir et al. 1999), these anatomical differences may have contributed to the differences in the outcomes of the study. In addition, while the vastus lateralis and vastus medialis muscles have an approximately even distribution of fast and slow muscle fibers, it has been found that the tibialis anterior muscle has nearly 75% slow twitch fibers (Johnson et al. 1973). Thus, the effect of muscle length on factors affecting $\bar{f}_{\mathrm{EMG}}$ (e.g. propagation of the sarcolemma action potential) during fatigue may be diminished or eliminated in this fatigue-resistant muscle.

Further, Doud and Walsh (1995) have employed concentric contractions as opposed to the isometric contractions used in this study and they used a "task failure" condition in which they divided the central frequency signal (f_{c}) taken from the EMG recording into quartiles of an undisclosed time frame, and found that the first three quartiles of their data during the fatiguing period were not significantly different between muscle lengths. However, at the end of the contraction, or the final quartile, a greater decline in the f_{c} was observed at the shortest length. Our protocol may not have included a long enough time frame to observe findings similar to those of Doud and Walsh (1995).

MMG Fatigue responses

The interpretation of changes in the MMG responses during fatigue are similarly complicated. The MMG signal has been suggested to result from a variety of factors during muscle contraction. Among these are gross lateral movements of muscle fibers at the initiation of muscle contraction, vibration or oscillation of muscle fibers during contraction, and changes in muscle fiber dimensions during contraction (Orizio 1993). Several studies have examined the relationship between MMG amplitude and isometric force production. At least for contractions of up to 80% MVC, it has been found that MMG amplitude increases with increases in force (Orizio et al. 1989 b; Orizio et al. 1990) and may increase up to 100% MVC (Maton et al. 1990; Shinohara et al. 1998; Stokes and Dalton 1991a, b).

Differences between studies regarding MMG amplitude and force at high force levels may have been due to differences in joint angle and muscle length (Ebersole et al. 1998). Nonetheless, these responses suggest that changes in MMG amplitude reflect patterns of motor unit activation. Furthermore, electrical stimulation studies have provided additional support for the hypothesis that MMG amplitude reflects recruitment of motor units (Chen et al. 1997; Orizio et al. 1993; Petitjean et al. 1998; Vaz et al. 1996). Less data are available regarding MMG frequency characteristics and force, but $\bar{f}_{\mathrm{MMG}}$ has also been shown to increase with increases in force production (Dalton and Stokes 1993; Matheson et al. 1997; Maton et al. 1990; Orizio et al. 1990). However, it has been considered that the shape of the response may be muscle specific (Shinohara et al. 1998). These force-dependent $\bar{f}_{\mathrm{MMG}}$ changes have been suggested to reflect the firing rate of motor units (Shinohara et al. 1998), which has been supported by electrical stimulation studies (Orizio et al. 1993, 1996; Stokes and Cooper 1992). It has been suggested that increased $\bar{f}_{\mathrm{MMG}}$ with increased firing rate may have been due to increased muscle stiffness associated with increased firing rate (Vaz et al. 1997).

Relative to studies of EMG, fewer have examined MMG responses during fatigue (Barry et al. 1985; Dalton et al. 1992; Esposito et al. 1998; Goldenberg et al. 1991; Herzog et al. 1994; Orizio et al. 1989a, 1992; Orizio and Veicsteinas 1992; Rodriquez et al. 1993, 1996; Stokes and Dalton 1991b; Zwarts and Keidel 1991) and the fatigue responses have been found to vary among studies. For example, Orizio et al. (1989a) and Esposito et al. (1998) have reported decreases in MMG amplitude during constant force contractions at 80% MVC of the biceps brachii muscle. These contractions also showed decreases in MMG frequency characteristics. In contrast, Zwarts and Keidel (1991) have shown no change in MMG amplitude and median power frequency during 50% MVC isometric contractions of the biceps brachii muscle while Stokes and Dalton (1991b) have found no change in the MMG amplitude versus force relationship in the rectus femoris muscle before compared to after fatigue (fatigue was induced with repeated intermittent contractions at 75% MVC), suggesting that the MMG response did not change with fatigue.

Still other studies have shown increases in MMG amplitude with fatigue. Rodriquez et al. (1996) have found increased MMG amplitude coupled with increased power in the low frequency band (0.5–10 Hz) of MMG signals derived from the rectus femoris muscle during 40% MVC continuous contractions to exhaustion. Differences among these studies may reflect differences in motor unit control during fatigue in different muscles at different relative levels of MVC. For example, Goldenberg et al. (1991) have reported that changes in MMG amplitude during fatigue of the abductor digiti minimi muscle at constant force levels varied depending on the percentage MVC requirements of the task. At 15% and 25% MVC, maintained contractions resulted in increases in MMG amplitude. In contrast, 50% MVC trials resulted in reductions in MMG amplitude while 75% MVC trials resulted in no change in MMG amplitude.

They have noted that the abductor digiti minimi muscle is probably fully recruited at 50% MVC. Thus, the decrease in MMG amplitude may have reflected a dependence on increased firing rate to maintain the 50% MVC criterion. In contrast, their 15% and 25% MVC trials may have resulted in increases in motor unit recruitment, thus increasing MMG amplitude. Similarly, Orizio et al. (1992) have noted differential responses in both amplitude and frequency characteristics of MMG signals for the biceps brachii muscle during fatiguing isometric contractions at different intensities. The amplitude response showed decreases in root mean square MMG at 60% and 80% MVC trials while 20% and 40% MVC trials showed increases. The $\bar{f}$ response was even more intensity-dependent as both increases and decreases in $\bar{f}$ were present with time and the pattern varied by intensity level.

Our results showed that at both muscle lengths, the MMG amplitude increased while the $\bar{f}_{\mathrm{MMG}}$ decreased (all variables excluded 0 from the 95% confidence interval). In addition, the $r\overline{\mathrm{MMG}}$ response was larger at l_{l} than at l_{s} while there were no significant differences in $\bar{f}_{\mathrm{MMG}}$ between muscle lengths. Assuming that MMG amplitude reflects the recruitment of motor units and $\bar{f}_{\mathrm{MMG}}$ reflects firing rate, then these results suggest that similar decreases in firing rate occurred at both muscle lengths, but that a greater rate of increase in motor unit recruitment occurred at l_{l}. The latter point is consistent with the EMG amplitude data reported here and elsewhere (Weir et al. 1996). Therefore, both the EMG and MMG responses suggest that motor unit recruitment occurs at a faster pace at l_{l}.

Suter and Herzog (1997) have recently reported that, based on the interpolated twitch technique, muscle inhibition in the quadriceps muscle varies as a function of knee angle. It is of interest that the pattern of their inhibition response has been found to be similar to the pattern of the EMG amplitude fatigue response in the quadriceps muscle reported in an earlier communication (Weir et al. 1996). Specifically, Suter and Herzog (1997) have found inhibition to increase from 15° (0° = full extension) up to 60° of flexion with a decrease from 60° to 90°. Weir et al. (1996) have noted an increase in the fatigue slopes of EMG amplitude from 15° to 45° and a decrease from 45° to 75°. Since fatigue slopes were not determined at 60°, it cannot be determined if the peak fatigue slope from EMG amplitude coincided with the joint angle associated with peak muscle inhibition.

Nonetheless, these observations suggest that the extent of inhibition of motor units may be correlated with the change in EMG amplitude during fatigue. That is, $r\overline{\mathrm{EMG}}$ (and by extension $r\overline{\mathrm{MMG}}$) fatigue slopes derived at joint angles associated with higher levels of inhibition of motor units may be larger due to the fatigue task occurring under conditions in which a smaller percentage of the total motor unit pool is activated at a given percentage of MVC. Thus, at these angles a larger number of motor units may be available for recruitment with time, resulting in an increase in $r\overline{\mathrm{EMG}}$. While we are unaware of similar data for angle-specific muscle inhibition for the dorsiflexor muscles, we suggest that future studies examine fatigue and muscle inhibition simultaneously in different muscles at different joint angles.

With respect to firing rate, previous studies have reported that during fatigue at submaximal force levels, decreases in firing rate can occur (Garland et al. 1994). The decrease in firing rate has been suggested to result from the phenomenon of "muscle wisdom", in which fatigue-related increases in twitch duration result in decreases in the optimal firing rate required for tetanus (Marsden et al. 1983). It should be noted however, that not all studies have shown decreases in firing rate during fatigue with submaximal force levels (Moritani et al. 1986). Simultaneous recordings of motor unit firing rate and $\bar{f}_{\mathrm{MMG}}$ during fatigue are needed to examine further the relationship between $\bar{f}_{\mathrm{MMG}}$ and firing rate.

Post-fatigue MVC

The difference in the loss of relative MVC force following the fatigue trials comparing l_{s} and l_{l} was not significantly different, although there was a trend for a larger loss of relative force following fatigue at l_{l} (P = 0.084, see Fig. 6). Previous studies examining muscle length and fatigue relationships have suggested that there would be greater loss of relative force following the l_{l} versus l_{s} trials (Baker et al. 1992; Fitch and McComas 1985; Sacco et al. 1994). Our lack of significant effects may be attributed to several factors. Firstly, while previous studies have obstructed blood flow to the limb tested (Fitch and McComas 1985; Sacco et al. 1994), we did not use ischemia. Secondly, the 5-s recovery between the end of the fatigue period and the initiation of the post-fatigue MVC may have served to diminish length dependent differences in the capability for force production following fatigue, especially in conjunction with an unimpeded blood flow as noted above. Finally, a lack of statistical power may have contributed to our lack of significant effect.

Muscle length and fatigue

Collectively, both the EMG and MMG amplitude data suggest that fatigue trials at l_l resulted in greater rates of motor unit recruitment than trials at l_s. Fitch and McComas (1985) have hypothesized that a greater fatigue response at a long muscle length compared to a short muscle length was due to greater actin-myosin interaction at the long length, resulting in greater ATP cost. However, Baker et al. (1992) and Sacco et al. (1994) have reported similar ATP turnover rates at both short and long muscle lengths. Our results indicated that fatigue differences between muscle lengths may be due, at least in part, to differences in the process of motor unit recruitment during fatigue. When combined with the results of Baker et al. (1992) and Sacco et al. (1994), these results suggest that fatigue differences between muscle lengths are driven by motor control processes and not necessarily by cellular metabolic factors.

Summary

The results of this study suggest that there was a significant difference in $r\overline{\mathrm{EMG}}$ slopes at l_l compared to l_s while there were no significant differences between $\bar{f}_{\mathrm{EMG}}$ slopes at l_l compared to l_o. Similarly, the $r\overline{\mathrm{MMG}}$ slopes were significantly steeper at l_l compared to l_s while there were no significant length dependent differences in $\bar{f}_{\mathrm{MMG}}$. The amplitude data for both EMG and MMG suggest that at l_l, a greater rate of motor unit recruitment occurred than at l_s. However, the similar $\bar{f}$ slopes for EMG and MMG at l_l and l_s indicated similar rates of membrane fatigue and changes in firing rate between muscle lengths. The difference in maximal contraction between l_l and l_s following a fatiguing interval approached significance which may have been the result of the influence of muscle recovery. Differences in motor unit recruitment rates may be involved in the length dependent fatigue rates reported in previous studies.

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