ORIGINAL ARTICLE

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Chronic hypobaric hypoxia does not affect electro-mechanical muscle activities during sustained maximal isometric contractions

Abstract The aim of the study was to evaluate the influence of chronic hypobaric hypoxia [43 days at 5050 m above sea level, a.s.l.] on the electrical and mechanical activities of the elbow flexor and knee extensor muscles during sustained maximal isometric contractions. Seven subjects participated in this study. The maximal voluntary contraction (MVC) of the two muscle groups was assessed. The subjects were then asked to perform a sustained MVC for 1 min, during which surface EMG and MMG signals were recorded before (SL) and after 43 days at high altitude (HA). From the time and frequency domain analysis of the surface EMG and MMG, the root mean square (RMS) and the mean frequency (MF) were then calculated. After HA exposure, in both the investigated muscle groups the results showed that: (1) the MVC did not change; (2) the maximum force decay during the sustained MVC was similar; (3) surface EMG and MMG parameters did not show any statistical difference. These data suggest that exposure to HA did not affect the electrical and mechanical properties of the two investigated muscle groups. We conclude that exposure to chronic hypobaric hypoxia seems to have no effect on the central motor drive or on muscle performance during sustained maximal isometric contractions of the active muscles.

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Introduction

The reduction of human muscle performance is a well-known phenomenon after exposure to high altitude. The decrease in muscle strength and maximal muscle power were shown to be related to a reduction of the muscle cross-sectional area (Ferretti et al. 1990) and/or to a direct effect of hypoxia on the efficiency of the muscle fibre as well as on the motor drive (Garner et al. 1990). On these bases, a change in the electrical and mechanical properties of the active motor units (MU) would be expected. At the same time, the possible alteration in motor command may determine different MU activation patterns during muscle contraction.

The possibility of evaluating the MU activation pattern by the combined analysis of surface EMG and mechanomyogram (MMG) has been suggested before (for a review, see Orizio 1993). These can both be considered as compound signals reflecting the summation of the electrical and mechanical activities of the recruited MUs. The MMG is presumably due to pressure waves generated by the dimensional variations of the active fibres during contraction, which can be detected on the muscle surface by appropriate transducers. Evidence has been presented that the amplitude (Orizio et al. 1989; Akataki et al. 2001) and the frequency content (Diemont et al. 1988; Orizio et al. 1990; Goldenberg et al. 1991; Zhang et al. 1992; Shinohara et al. 1998; Yoshitake and Moritani 1999) of the MMG signal are related to the recruitment and the average MU firing rate.

Localized muscle fatigue influences the electrical and mechanical properties of the muscle fibres of the active MUs. With fatigue, the MU action potential decreases and its duration lengthens (Basmajian and De Luca 1985; Moritani and Muro 1987). Moreover, a reduction in the amplitude of the mechanical twitch along with a prolongation of the relaxation process (Burke et al.

1973; Gordon et al. 1990; Bevan et al. 1992) take place. At the same time, the firing rate, degree of recruitment and synchronization of active MUs change significantly with fatigue (Enoka and Stuart 1992).

The aim of our study was to investigate the effect of prolonged high altitude exposure (43 days at 5050 m above sea level, a.s.l.) on the electrical and mechanical activities of the recruited MUs during sustained maximal isometric contractions by means of the combined analysis of surface EMG and MMG, together with the force signal recorded from the contracting muscles.

Experiments were carried out during a scientific expedition to the Pyramid Laboratory (Lobuche, Nepal), located at 5050 m a.s.l. Data were collected before departure and after 43 days of sojourn at high altitude.

Methods

Subjects

Seven healthy sedentary members [34 (2) years; mean (SE)] of the medical and technical staff of the expedition, after full explanation of the purpose of the experiments and the procedures to be followed, volunteered to participate in the study. The experiments were carried out in our laboratory in Brescia (Italy, 150 m a.s.l.) 1 week before departure, and after 43 days at the Pyramid Laboratory. Both the elbow flexors and knee extensors muscles were tested. The maximal voluntary contraction (MVC) of the investigated muscle groups, muscle-bone area (MBA) of arm and leg and the MVC per unit of MBA are given in Table 1. MBA was determined with anthropometric measurements according to the method suggested by de Koning et al. (de Koning et al. 1986).

On two different occasions, the subjects came to our laboratory and their preferential arm or leg were positioned in previously described (Orizio et al. 1989; Orizio and Veicsteinas 1992) ergometers, allowing isometric contractions of the elbow flexors and knee extensors at a fixed joint angle of 115° and 90° for the elbow and knee, respectively. The output force was measured by a load cell (Interface, SM-1000N, Scottsdale, USA; linear from 0 to 1000 N) that was strapped to the subject's wrist or ankle. The load cell was calibrated using known weights before each experimental session. The EMG signal was picked up by a pair of silver bar surface electrodes (1 cm long, 1 mm diameter, 1 cm inter-electrode distance) and then amplified by a differential amplifier (Hewlett-Packard 8802 A, Andover, USA; filter bandwidth 3–500 Hz). The MMG was detected by a contact sensor transducer (Hewlett-Packard 21050 A, Andover, USA; bandwidth 0.02–2000 Hz) and then amplified by a medium gain amplifier (Hewlett-Packard 8802 A; Andover, USA; filter bandwidth 2–120 Hz). The EMG and MMG signals were visualized on-line on the screen of a two-channel oscilloscope (Tektronix, mod. 2211, Beaverton, USA) to check the quality of the signals. After analog-to-digital conversion (Analog Device

RTI 815, Norwood, USA), the raw signals (EMG, MMG and force) were stored on the hard disk of a portable computer (Toshiba, T 5200, Tokyo, Japan) at 1024 Hz (EMG), 512 Hz (MMG) and 128 Hz (force), respectively.

The EMG/MMG integrated probe (Orizio 1993) with the signal detectors was positioned over the belly of the biceps brachii and vastus lateralis muscles for the elbow flexors and knee extensors exercises, respectively, and then secured to the belly of the muscle by means of an elastic band. The skin underneath the probe was previously shaved, gently abraded with fine sand paper and cleaned with ethyl alcohol.

Spectral analysis

Surface EMG and MMG analyses were performed in the time and frequency domain, and the root mean square (RMS) and the power spectrum density distribution were thus determined. For spectral analysis, the maximum entropy spectral estimation (MESE) method, with the Burg algorithm, was used and the mean frequency (MF) of each spectrum was then calculated (Diemont et al. 1988).

Experimental procedure

All subjects familiarized themselves with the experimental set-up for 1 week before the testing session. Individual MVC of the elbow flexors and knee extensors was then assessed as the maximum force that could be maintained for 3 s.

Sea level (SL)

These tests were performed in the laboratory of the Division of Human Physiology at the University of Brescia (150 m a.s.l.). After positioning of the investigated limb in the isometric ergometer and instrumentation, the subjects were asked to reach their MVC and keep the level of contraction as strong as they could for 1 min. This sequence was applied first for the elbow flexors and then for the knee extensors.

High altitude (HA)

A few days after the end of the SL experiments, the subjects flew from Milan (122 m a.s.l.) to Kathmandu (1500 m a.s.l.) and 3 days later to Lukla (2850 m a.s.l.). Then, after a 6-day trek, the high-altitude Pyramid Laboratory (5050 m a.s.l.) was reached. The data at high altitude were collected 43 days after the subjects arrived at the Pyramid Laboratory. The instruments used for the SL study were delivered by helicopter to the Pyramid Laboratory. The same experimental procedure and tests used at sea level were carried out for each subject at the same time of the day. Room temperature in the Pyramid Laboratory was constantly kept at 18–21°C and the relative humidity at 50–60%.

Table 1 Maximal voluntary contraction (*MVC*), muscle-bone area (*MBA*) and MVC per unit of MBA of the investigated muscle groups at sea level (*SL*) and after high altitude exposure (*HA*). (*n.s.* Not statistically different)

Muscle group	Conditions	MVC (*N*)	MBA (cm^2)	MVC/MBA (*N*·cm^{-2})
Elbow flexors	SL	278 (16)	62.5 (3.5)	4.48 (0.24)
	HA	293 (22)	61.1 (3.1)	4.80 (0.29)
		n.s.	n.s.	n.s.
Knee extensors	SL	584 (35)	203.2 (12.9)	2.90 (0.12)
	HA	605 (35)	202.7 (13.6)	3.03 (0.14)
		n.s.	n.s.	n.s.

Statistical analysis

A MANOVA analysis using a general linear mixed model was applied to our balanced repeated measures in order to check statistical differences in the EMG and MMG parameters between SL and HA conditions. A paired Student's t-test was performed to compare MVC and anthropometric variables before and after high altitude exposure. Statistical significance was fixed at $P < 0.05$. The values are presented as means (SE).

Results

As shown in Table 1, MVC, MBA and the MVC per unit of MBA did not change after high altitude exposure.

In Fig. 1 the decline of the generated force during sustained MVC of the elbow flexors and knee extensors is reported. Maximum force decreased by 51% and 57% during SL and HA exercise, respectively, for the elbow flexors. The degree of the force decline for the knee extensors was 53% and 57% for the SL and HA exercises, respectively. No differences were found in the force vs.
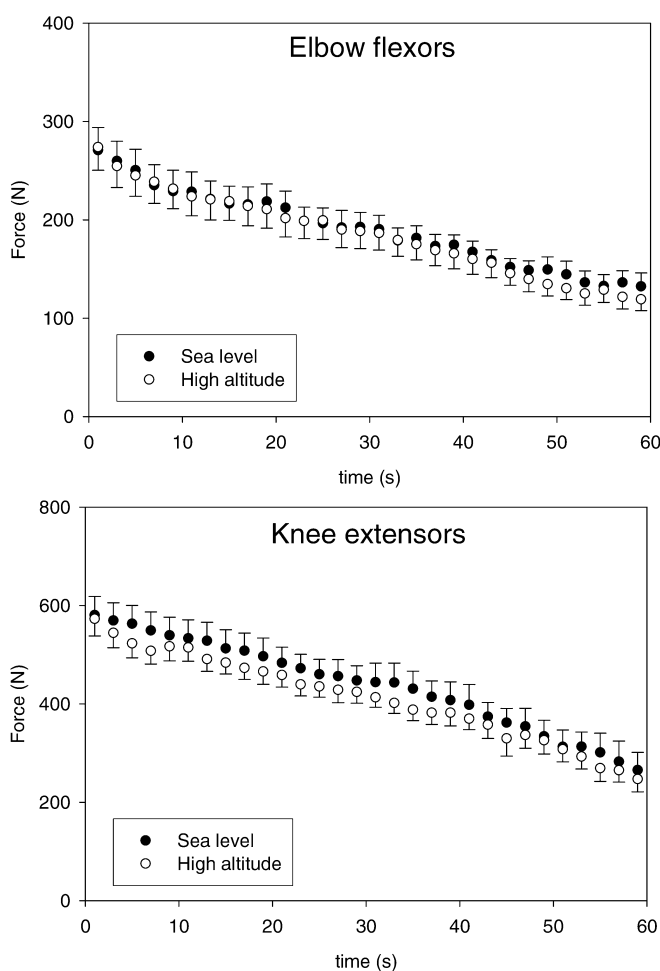

Fig. 1 Force decay during sustained maximal voluntary contraction (*MVC*) of the elbow flexor and knee extensor muscles at sea level (*SL*) and after high altitude exposure (*HA*)

time relationship between SL and HA conditions in either of the muscle groups investigated.

Biceps brachii

In Fig. 2 the MF and RMS values of the surface EMG and MMG signals are shown as a function of the contraction time during sustained MVCs at SL and HA.

At SL, the EMG MF (Fig. 2A) declined continuously from the beginning [96.5 (6.6) Hz] to the end of the exercise [46.9 (7.8) Hz; $P < 0.05$]. During exercise at HA, the trend of EMG MF over time was similar to that in SL ($P > 0.05$).

The EMG RMS (Fig. 2B) remained almost constant throughout contraction, starting with an average value of 0.47 (0.07) mV ending up at an average value of 0.32 (0.07) mV at SL. After acclimatization at HA, the EMG RMS presented the same trend as during SL exercise, starting from 0.57 (0.08) mV and decreasing to 0.36 (0.13) mV at the end of the exercise ($P > 0.05$). Although upward shifted compared to the SL values, the HA values did not differ statistically from SL values at any time.

At SL, the MMG MF (Fig. 2C) decreased significantly with fatigue from 19.4 (2.7) Hz to 9.72 (1.0) Hz ($P < 0.05$) at the end of contraction. During the HA exercise, the same trend of the MMG MF throughout the sustained MVC was observed ($P > 0.05$). The MMG MF, indeed, started from an average value of 17.3 (3.9) Hz and declined significantly to an average value of 9.1 (1.2) Hz.

During the first 20 s of the sustained MVC at SL, the MMG RMS (Fig. 2D) remained mainly constant, starting from an average value of 31.5 (4.6) mV; then, a slight decline ($P > 0.05$) took place, reaching an average value of 20.3 (6.8) mV at the end of exercise. No differences were observed during HA exercise when compared to the corresponding SL values. At the beginning of contraction, the MMG RMS was 27.7 (4.1) mV and declined progressively after the first 20 s to an average value of 18.2 (4.7) mV ($P > 0.05$) at the end of the sustained contraction.

Quadriceps

The MF and RMS values of EMG and MMG signals as a function of the contraction time during SL and HA conditions are presented in Fig. 3.

The EMG MF during the sustained MVC at SL declined significantly throughout contraction from 90.4 (10.2) Hz to 62.2 (9.9) Hz ($P < 0.05$) at the end of the exercise. At HA, a similar decrease of the EMG frequency content took place, from a value of 80.1 (8.1) Hz at the beginning of the exercise to an average value of 52.8 (6.6) Hz at the end of contraction ($P < 0.05$).

At SL, the time domain analysis of the EMG showed a decrease of the RMS with fatigue from 0.26 (0.05) mV
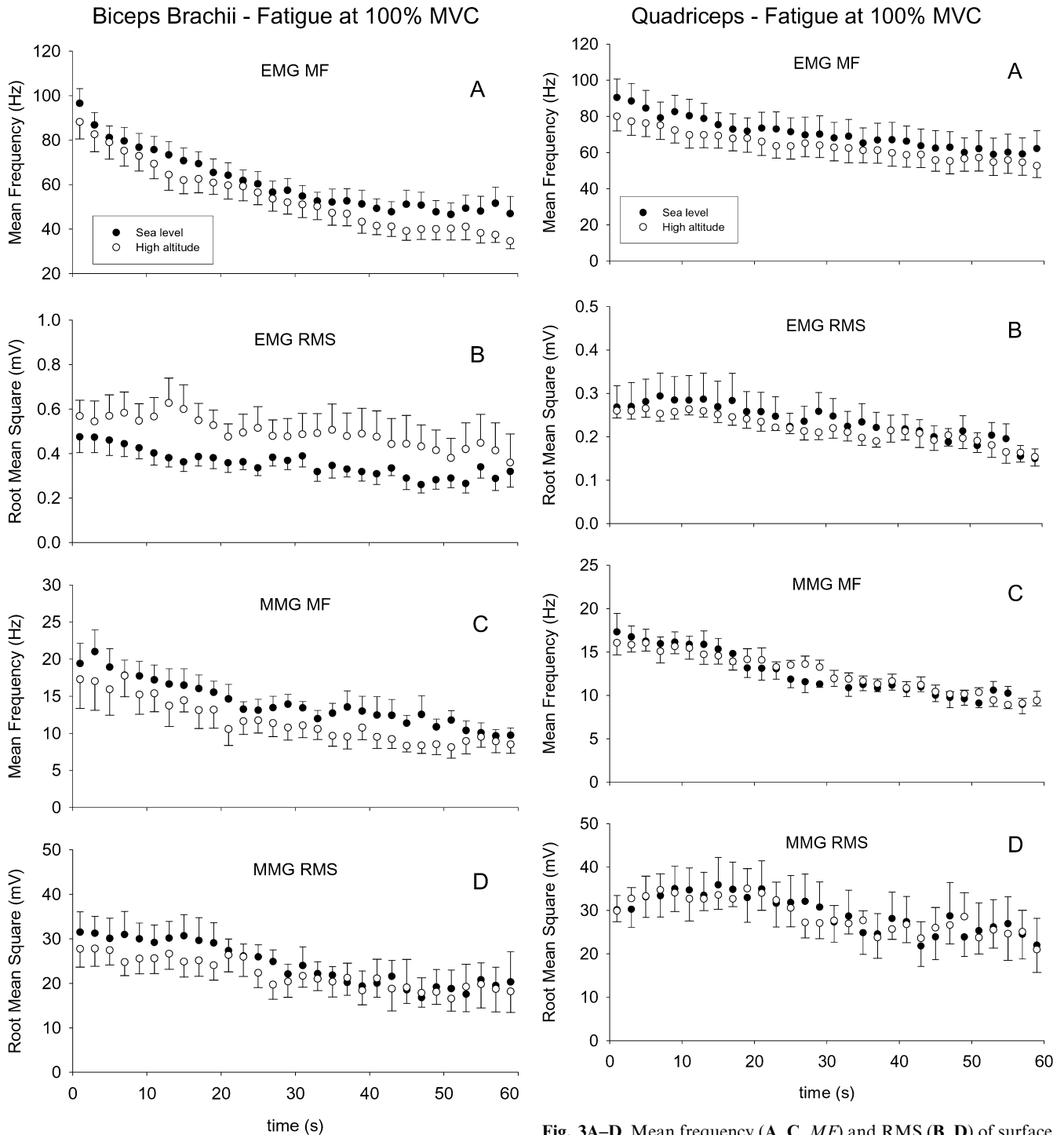
Biceps Brachii - Fatigue at 100% MVC

Quadriceps - Fatigue at 100% MVC

Fig. 2A–D Mean frequency (**A**, **C**, *MF*) and root mean square (**B**, **D**, *RMS*) of surface EMG and MMG during the sustained maximal voluntary contraction (*MVC*) of the elbow flexors at sea level and after exposure to high altitude. To detect the signals, the integrated EMG/MMG probe was positioned over the belly of the biceps brachii muscle

Fig. 3A–D Mean frequency (**A**, **C**, *MF*) and RMS (**B**, **D**) of surface EMG and MMG during the sustained maximal voluntary contraction (*MVC*) of the knee extensors at sea level and after exposure to high altitude. To detect the signals, the integrated EMG/MMG probe was positioned over the belly of the vastus lateralis (quadriceps) muscle

to 0.15 (0.02) mV ($P < 0.05$) at the end of the exercise. After acclimatization at HA, no statistical differences from the corresponding SL exercise were seen in the EMG RMS values at any time of the sustained MVC.

From the frequency domain analysis of the MMG, it can be seen that the MF presented a linear decrease throughout contraction from the beginning [17.3 (2.1) Hz] to the end of the exercise [9.4 (1.1) Hz; $P < 0.05$]. The values of MMG MF during the sustained

MVC at HA overlapped those of the SL exercise ($P > 0.05$).

Lastly, the MMG RMS at SL started at an average value of 30.1 (3.2) Hz and remained almost constant during the first 22 s of contraction. Then, a slight decline toward lower values took place (not statistical), reaching 22.0 (6.2) Hz at the end of the exercise. With fatigue at HA, no differences were found in the MMG RMS vs. time relationship. At the beginning of the sustained MVC, indeed, the MMG RMS was 29.9 (2.5) Hz; with fatigue. A not significant decrease occurred, to an average value of 21.0 (5.3) Hz at the end of contraction.

Discussion

Our data suggest that HA exposure, at least up to 43 days at 5050 m a.s.l., has no significant influence on the electrical and mechanical properties of the recruited MUs during sustained maximal isometric contractions. Indeed, no differences in MVC and in maximum force decay during sustained MVC for 1 min were assessed after HA exposure and none of the EMG and MMG parameter dynamics changed throughout the exercise in either of the muscle groups investigated.

The force production capacity of the investigated muscle groups was not impaired in our study. This finding, together with the unchanged MBA and MVC per unit of MBA, indicate that the morpho-functional properties of the investigated muscle groups were not significantly affected by other factors, such as environmental conditions or physical activity.

Our results are in agreement with the force behaviour after a 40-day exposure at 335 or 282 torr in a hypobaric chamber, reported by Garner et al. (1990), and with the preservation of the metabolic (anaerobic alactic) and mechanical functions of muscles at altitude (Ferretti et al. 1990), as well as with some studies indicating unimpaired excitability of motor neurons (Kayser et al. 1993). However, this result by itself is not enough to indicate a preserved MU activation pattern after HA exposure.

The force output of a muscle depends on the number of recruited MUs and their firing rate. Bearing in mind that, at the beginning of the sustained MVC, almost all the MUs should be recruited and working at their maximal firing rate, we should consider that with fatigue the following phenomena take place: (1) a reduction and elongation of the MUs action potential, with a corresponding slowing of the conduction velocity (CV) (Basmajian and De Luca 1985; Merletti et al. 1990), (2) an elongation of the muscle fibres' relaxation time determining a reduction of the MUs firing rate by proprioceptive feedback (Bigland-Ritchie and Woods 1984), (3) a progressive de-recruitment of fast twitch MUs (Grimby 1986) and (4) a synchronization/grouping of the active MUs (Krogh-Lund and Jorgensen 1991).

Given that EMG and MMG can be considered as interferential signals in which the single MU electrical and mechanical contribution are summated, changes with fatigue in the MU action potential and mechanical transient could be mirrored in the time and frequency domain properties of the two signals.

From the frequency domain analysis of the surface EMG, indeed, the MU recruitment and firing rate process could be retrieved. The model of Lindstrom et al. (1970) provides the basis for a direct relationship between the global muscle fibres' CV and the frequency content of the surface EMG. On this basis, the shift of the EMG power spectrum density distribution toward lower frequencies during a sustained MVC reflects the decrease in the average muscle fibre CV coupled with the alteration of the sarcolemmal action potential. In reality, the estimated CV decrease is normally much less than the EMG MF reduction, suggesting that other factors, probably related to the different MUs discharge statistics, may take part in determining the EMG frequency content (Krogh-Lund and Jorgensen 1991).

The lowering of the MMG frequency content may be partly due to the slowing of the elementary components of the MMG signal. Moreover, as suggested by previous studies from our (Orizio et al. 1990) as well as from other laboratories (Goldenberg et al. 1991; Shinohara et al. 1998; Yoshitake and Moritani 1999; Akataki et al. 2001), the frequency content of the MMG signal seems to be strongly related to the global MU firing rate. Unfortunately, to date a detailed model explaining the MMG MF vs. MU firing rate relationship is not available yet for MMG generation, as it is for the EMG MF vs. CV relationship. As previously pointed out, fatigue induces an elongation in the twitch of the whole muscle, single MU and single muscle fibre (Enoka and Stuart 1985). Thanks to a phenomenon known as "muscle wisdom" (Marsden et al. 1983), the twitch elongation would determine, via proprioceptive feedback, a firing rate reduction (Bigland-Ritchie and Woods 1984). This allows the force to be optimized with an economical activation of fatiguing muscle (Enoka and Stuart 1992).

During the 1-min sustained MVC, the force reduction was paralleled by the MMG MF in both muscle groups. Indeed, the frequency parameter continued to decrease with time, reaching statistically lower values at the end of contraction.

After HA exposure, the EMG MF at the beginning of the contraction was similar to the value found during the SL experiment in both muscle groups, and declined linearly with the same trend as in SL. Moreover, the MMG MF vs. time relationship almost overlapped the corresponding SL relationship, suggesting similar muscle activation behaviour with fatigue.

The amplitude of the EMG and MMG was expected to decrease because of the changes in the electromechanical activity of the MUs described above. This was not clearly evident in our data and the following discussion will consider other possible factors acting on the two signals with fatigue.

The EMG and MMG time domain parameters remained substantially unchanged from the beginning to the end of the exercise in both the investigated

muscles (with the only exception of a slight EMG RMS decrease during the knee extensors exercise; $P = 0.03$), indicating an almost constant level of the average electrical activity of the contracting muscles. This finding may be related to two different counterbalancing series of events, as suggested by Linssen et al. (1993). On one hand, an increase in the central drive, the elongation of the intracellular action potential duration coupled with a decrease in the average CV and a synchronization/grouping of the MU discharge would lead to an increase in the EMG power content. On the other hand, the simultaneous decrease in the amplitude of the MU action potential and in the average MU firing rate, together with de-recruitment of some highly fatigable MUs, would lead to a decrease in the EMG power content. The net effect would be a plateau of the EMG and MMG RMS vs. time relationship.

This finding is not fully in agreement with previous data on sedentary subjects (Orizio et al. 1992; Orizio and Veicsteinas 1992), showing a clear reduction of the MMG and EMG RMS with fatigue. In those papers the MVC of the subjects was higher and its reduction, over a similar contraction time, was larger than in this study. Similarly, the EMG and MMG parameter (MF and RMS) changes during the maximal effort were larger. Indeed, our results resemble the behaviour of long distance runners (Orizio and Veicsteinas 1992) and aged subjects (Esposito et al. 1996). Both these groups have a high percentage of non-fatigable slow-twitch MUs. If it is considered that the subjects actually investigated are on average 10 years older than those studied in the past, it can be hypothesized that the different behaviour of the electromechanical variables during sustained MVC may be due to some changes in the fast and slow muscle fibre MUs ratio. As an alternative, this discrepancy could be due to a greater effect of synchronization/grouping of the active MUs (Freund 1983; Datta and Stephens 1990), which may contribute to the EMG and MMG RMS increase when close to exhaustion. Indeed, this phenomenon may reduce the cancellation between elementary asynchronous contributions to EMG and MMG, with a positive contribution to the signal's amplitude, to counteract the MU action potential and mechanical twitch fatigue reduction as well as the de-recruitment of fast fatiguing MUs.

After HA exposure, the trend of EMG and MMG RMS during both the elbow flexor and knee extensor exercises paralleled, or even overlapped, the corresponding trends during the SL exercise, adding further support to the hypothesis that chronic hypoxia does not influence the MU activation pattern during fatiguing contractions.

Lastly, our results seem to indicate that the HA exposure does not influence the maximal force output, the MU activation strategy and the fatiguing process during isometric contraction of the two muscle groups investigated. Indeed, after HA exposure, the changes with fatigue of the investigated signals parameters were not different from those detected during the SL exercise, suggesting preserved muscle behaviour at fatigue. This finding could be explained by the fact that in the Pyramid Laboratory, contrary to a typical HA sojourn during mountaineering expeditions, the subjects had access to good food imported from Europe, water without any restrictions and they lived at a comfortable ambient temperature. Moreover weather conditions allowed daily physical activity. Thus, it could be argued that when a good ratio between the caloric intake and the caloric expenditure is preserved no changes in body or muscle mass take place, and also the muscular efficiency is completely preserved.

In conclusion, our data seem to exclude any effect of chronic hypoxia, at least for up to 43 days, on electrical and mechanical activities, suggesting a preserved central motor drive, as well as muscle performance, during sustained maximal isometric contractions of the two muscle groups investigated.

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