CHAPTER 3

High-density surface EMG study on the time course of central nervous and peripheral neuromuscular changes during 8 weeks of bed rest with or without resistive vibration exercise

Edwin R Mulder
Karin HL Gerrits
Bert U Kleine
Joern Rittweger
Dieter Felsenberg
Arnold de Haan
Dick F Stegeman

J Electromyogr Kinesiol (in press)

ABSTRACT

The aim of the present study was to assess the time course and the origin of adaptations in neuromuscular function as a consequence of prolonged bed rest with or without countermeasure. Twenty healthy males volunteered to participate in the present study and were randomly assigned to either an inactive control group (Ctrl) or to a resistive vibration exercise (RVE) group. Prior to, and seven times during bed rest, we recorded high-density surface electromyogram (sEMG) signals from the vastus lateralis muscle during isometric knee extension exercise at a range of contraction intensities (5-100% of maximal voluntary isometric torque). The high density sEMG signals were analyzed for amplitude (root mean square, RMS), frequency content (median frequency, Fmed) and muscle fiber conduction velocity (MFCV) in an attempt to describe bed rest-induced changes in neural activation properties at the levels of the motor control and muscle fibers. Without countermeasures, bed rest resulted in a significant progressive decline in maximal isometric knee extension strength, whereas RMS remained unaltered throughout the bed rest period. In line with observed muscle atrophy, both Fmed and MFCV declined during bed rest. RVE training during bed rest resulted in maintained maximal isometric knee extension strength, and a strong increase (~30%) in maximal sEMG amplitude, from 10 days of bed rest on. Exclusion of other factors led to the conclusion that the RVE training increased motor unit firing rates as a consequence of an increased excitability of motor neurons. An increased firing rate might have been essential under training sessions, but it did not affect isometric voluntary torque capacity.

INTRODUCTION

Body deconditioning by bed rest immobilization is an accepted Earth-based model to study neuromuscular effects of prolonged spaceflight missions [1]. The changing neuromuscular performance of individuals after a period of motor inactivity can have several causes along the chain of intention-to-move until the activation and response of the contractile machinery in the muscle. Thus, factors within the muscle itself [45], but also factors in the motor control system may contribute to the decrement in muscle performance [22;27]. Previously [33], we studied voluntary activation at maximal voluntary effort by means of the twitch interpolation technique. In spite of the above mentioned literature, we found maximal voluntary knee extensor muscle activation to be maintained during bed rest, regardless of whether the subjects participated in an exercise countermeasure program that consisted of resistive vibration exercise training (RVE, [38]). With respect to the control subjects, we previously explained this finding as the counteracting effect of the test battery performed during bed rest [33].

Although the twitch interpolation technique provides an indication of maximal voluntary force generating capacity, it presents no information regarding the underlying activation processes of motor units. Bed rest may therefore alter recruitment of motor units and/or their firing rate modulation without being detected by the twitch interpolation technique, as used in Mulder et al. [33]. In contrast, such information is contained in sEMG signals. Motor unit recruitment and firing rate both determine the amplitude of the sEMG signal. A changed relative contribution of both processes [32] can, however, be tracked down by assessing systemic differences in the relation between sEMG amplitude and voluntary muscle force. Moreover, additional information on changes in central motor drive, such as synchronization between motor units, can be obtained by analyzing the sEMG interference pattern in terms of its spectral content. For instance, there is evidence from comparative analysis of experimental and modelling data that synchronization increases the amplitude of the sEMG signal, and that it decreases the sEMG median frequency [19;28]. Diverging responses of these sEMG variables may thus be helpful to determine relative changes in neural activation more precisely. At the peripheral level, sEMG median frequency is also influenced by the velocity of propagation of action potentials along the sarcolemma, measured as mean muscle fiber conduction velocity (MFCV, [30]). To allow the separation of central factors from this peripheral influence on Fmed, it is thus necessary to also obtain MFCV estimates. To facilitate a flexible, robust derivation of the sEMG variables, we used high-density sEMG [10] with a large number of electrodes distributed over a large part of the vastus lateralis muscle.

The aim of the present study was to detect changes in motor control by assessing sEMG amplitude and median frequency during incremental isometric knee extensions in the same subjects as described in Mulder et al. [33]. Since the field of view of the surface electrodes will be smaller than the large vastus lateralis muscle studied [14], we hypothesized from our previous study that absolute sEMG amplitudes at maximal effort would remain unchanged as a consequence of bed rest, regardless whether the subjects participated in the countermeasure program. In contrast, based on previous findings following unilateral lower limb suspension and bed rest, the relation between sEMG and sub-maximal voluntary torque might be expected to change, as the required sEMG amplitude to maintain a fixed target torque increased disproportional to what may be expected based on atrophy [7;8]. It is further hypothesized that the median frequency in the control group decreases with bed rest in proportion with atrophy (i.e. muscle fiber diameter) and MFCV. Daily resistive vibration exercise training during bed rest is expected to counteract these changes. Apart from voluntary muscle activation, resistive vibration exercise is thought also to elicit muscle contractions via the stretch reflex [39]. The indirect way of muscle activation during RVE training was one of the reasons for a more detailed analysis of its effects on motor control by observing sEMG variables in this group.

METHODS

Subjects

The twenty males that volunteered to participate in the Berlin Bed Rest study were selected from a large group of applicants. All subjects were in good health conditions and were randomly assigned to either a resistance vibration exercise group, RVE (n = 10) or to an inactive control group, Ctrl (n = 10). The mean ± SD age, height and body mass were 32.7 ± 4.8 yr, 186.3 ± 8.0 cm and 86.5 ± 16.5 kg for RVE and 33.4 ± 6.6 yr, 185.4 ± 7.7 cm and 79.7 ± 10.9 kg for Ctrl. The Freiburg questionnaire [20], which assesses the metabolic units spent per week in exercise, indicated a wide range of exercise habits prior to the start of the study. There were, however, no differences in exercise intensity between the RVE (2.6 ± 2.4 hrs/wk) and the Ctrl (2.4 ± 3.6 hrs/wk) group. All subjects were familiarized with the concepts of the experiments, procedures, and the equipment during a familiarization session that was scheduled 3 days prior to the start of bed rest. The local Ethics committee of the Benjamin Franklin Hospital of the Charité – Universitätsmedizin Berlin, Germany approved the study and all participants gave their written informed consent.

General design

The study took place at the Benjamin Franklin Hospital of the Charité – Universitätsmedizin Berlin. The subjects were restricted to 56 days of horizontal bed rest, during which they were not allowed to stand up, lift their trunk in bed more than to 30° of trunk flexion, move their legs briskly, or elicit large forces with their leg muscles other than during testing or training (RVE only) sessions. Adherence to this protocol was controlled for by continuous video surveillance and by force transducers in the frames of the bed. The subjects received an individually balanced diet (details in [38]) and ingestion of alcohol, nicotine, and drugs were prohibited.

Exercised-based countermeasure

Exercises were performed in the supine position on a vibration system that was specifically developed for application under bed rest and microgravity conditions (Galileo Space, Novotec, Pforzheim, Germany, Fig. 1). The used equipment and the exercise protocol are described in full detail elsewhere [38]. In short, the vibration device consists of a vibration platform, which is vertically suspended on a trolley. Subjects remained in a supine position with feet resting on the vibration platform. Belts were attached to shoulders, hips and hands and via a spring system to the vibration platform (Fig. 1). The static force was individually adjusted to an equivalent of 2x body weight with the legs in the fully extended position. During bed rest, RVE subjects trained 6 days per week, two times each day (morning and afternoon sessions). Four dynamic exercises were performed in the morning sessions. The exercises were performed with both legs simultaneously, and were carried out in the following order: squats, heel raises, toe raises and explosive squats. During the squat exercise the knees where extended from 90º to almost complete extension in cycles of 6 seconds for each squat. The heel and toe raises were performed with the knees almost extended. During the heel raise exercise, the heels were raised to fatigue. Only then, brief rest periods (< 5 s) were allowed with the entire foot on the vibrating platform in order to recover, and subjects started to raise heels again. For the toe raise exercise a similar protocol was used, but toes were raised instead of heels. During the explosive squatting exercises, the knees were extended as quickly and forcefully as possible. Ten such 'explosive' squats were done with a rest insertion of 10 seconds in each exercise session. All exercises were performed while the platform was vibrated at a frequency of 18Hz. According to the overload principle in exercise physiology, vibration frequency and thus the applied force [39] was individually adjusted in weekly intervals, such that time to exhaustion during the squat exercise in the morning sessions remained between 60-100s (i.e. between 10 and 17 repetitions). During the afternoon sessions, the subjects exercised at a reduced intensity (70 % of the static force used in the morning sessions), but ran through the squat, heel and toe raise exercises for 60 seconds each, thereby performing as many repetitions as possible, without rest. No explosive squats were performed in the afternoon sessions. Trained staff supervised all training sessions.

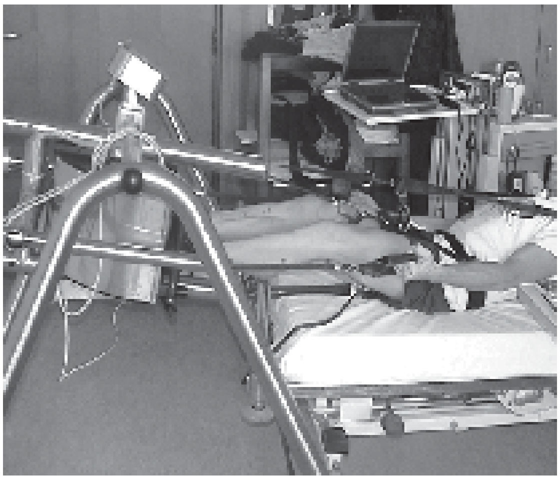

Fig. 1. The Galileo Space Device used for resistive vibration exercise (RVE) at supine position during 56 days of bed rest

Isometric knee extension

To measure the subjects' isometric knee extension torque under supine conditions, we used a custom-built supine dynamometer [33]. For each subject the optimal knee angle (either 60° or 70°, [33]) was measured at baseline and kept constant throughout the rest of the study. The hip flexion angle was set at 115° for all subjects. The subjects participated in 8 sessions. The first session was scheduled prior to the start of bed rest, but will be referred to as BR0. The remaining sessions were scheduled during bed rest at days 4, 7, 10, 17, 24, 38 and 56 (= BR4, BR7, etc.). The measurements were on the same time of the day and always before the RVE training session. This was done to exclude acute effects of vibration [34;40]. The right leg was tested.

Maximal voluntary contraction task. Following a standardized warm-up procedure [33], consisting of sub-maximal isometric contractions, the maximal voluntary torque (MVT) was assessed as the peak torque of three maximal attempts of ~3-4s in duration with a minimum of 2 min of rest in between. During the MVT attempts, the subjects were given strong verbal encouragement to achieve maximal effort. Post-contraction visual feedback was provided to achieve a higher maximal voluntary effort in a subsequent attempt.

Sub-maximal voluntary contraction task. The subjects performed in total 8 sub-maximal sustained contractions based on the MVT at the day of testing. First, contractions with low target levels (5%, 10%, 15%, 20% and 30% of MVT) were sustained for 20 s and interposed with 1 min of rest. Subsequently, contractions with high target levels (40%, 60% and 80% of MVT) were sustained for only 6 s and were interposed with 2 min of rest to minimize fatigue. The order of the trials was randomized. The large number of low contraction levels was chosen to quantify changes in motor unit recruitment or rate coding. Both the target torque and the current torque level were displayed on the computer monitor in order to provide feedback. The subjects were instructed to trace the target torque as steady as possible for the assigned durations. Display gain was the same for all torque levels.

sEMG acquisition

Concurrently with isometric knee extensor torque, sEMG signals were recorded from the vastus lateralis muscle by means of a two-dimensional, high-density sEMG system [10]. In short, the system (Active One, BioSemi, Amsterdam, The Netherlands) consists of an electrode grid of 130 gold-coated, densely spaced skin-surface electrodes. The electrodes are arranged in a 10 by 13 rectangular matrix (4.5 by 6.0 cm) with an inter-electrode distance of 5mm. The signal from each of the electrodes was recorded against a common reference electrode positioned on the patella of the tested leg (i.e. a monopolar montage). During a low intensity isometric contraction, high density sEMG signals were visualized and the electrode grid was adjusted such that the columns ran parallel to the fiber orientation. This was accomplished by utilizing the criterion that the peaks in the sEMG signal in the rows needed to be shifted in time, but had constant amplitude [37]. A representative example of 2 s of high density-sEMG data from a 20 s contraction at 20% MVT is presented in Fig. 2. The electrode grid was placed over the distal, anterio-lateral part of the vastus lateralis, such that the motor endplate zone was visible approximately halfway the columns (Fig. 2C, D). Electrode grid and amplifier were then secured in place by means of Velcro straps. The 130 pre-amplified monopolar signals were band-pass filtered (0.16-400 Hz) and simultaneously AD-converted (16 bits with a resolution of 1 μV/bit at a rate of 2048 samples/channel), and stored on hard disk. Before off-line analysis, data were high-pass filtered at 15 Hz in software.

sEMG processing

Off-line analysis was performed with customized Matlab software (Mathworks, v6.5, Natick, MA, USA). The selection of the high density sEMG variables was done on the basis of a 'go where the action is' principle [10]. Unlike a common bipolar electrode montage, the high density sEMG grid allows the spatial selection of the electrodes with the highest mean (averaged over all electrodes within a column, example of signals in a column in Fig. 2B) signal amplitude. Such spatial selection, which was separately performed for each session, assured a compensation of small variations in the placement of the electrode grid between sessions. The sEMG signals obtained during the tasks were analyzed for amplitude (root mean square, RMS) and median frequency (Fmed) from the monopolar electrode montage. RMS values were expressed as a percentage of the maximal value at the day of testing, and as a percentage of the maximal value at BR0. We used a double electrode distance (10 mm) with a single electrode pair shift distance (5mm) and the phase difference technique [6]. From the time shift away from the endplate region (e.g. between electrodes 63 and 73 in Fig. 2C and 2D) when observing subsequent bipolar recordings, muscle fiber conduction velocity (MFCV) was estimated. Estimates were obtained from all bipolar derivations for the selected column, but were accepted only when the cross-correlation between signal pairs was above 0.7 and the MFCV value below 6.5 m/s. These methodological criterions were used to reject MFCV estimates around the motor endplate zone and musculotendineous junction. For the MVC task, all sEMG variables were analyzed during one 1s epoch that yielded the highest mean torque. For each sub-maximal contraction, the sEMG variables were analyzed during one 2s signal segment (e.g. Fig. 2A). The selected segments had the lowest level of torque fluctuation (standard deviation) within the contractions.

Exclusion of data

Maximal voluntary torque levels could not be obtained for one RVE subject, because of experienced patellar discomfort during the performance of the isometric contractions. From another subject (Ctrl) we obtained unreliable baseline values, because this subject did not attend the familiarization session. Data from these two subjects were therefore discarded from the statistical analyses. MFCV values according to our criteria could not be obtained for four subjects (2 from each group). Examination of their magnetic resonance imaging data used in [33] indicated a thicker subcutaneous fat layer at baseline .

Statistical analysis

All values are expressed as means ± SEM (standard error of the mean). Statistical tests were performed with the Statistical Package for the Social Sciences software program (version 11.0, SPSS, Inc., Chicago, IL, USA). Analysis of variance (ANOVA) with a repeated measure design on bed rest duration and/or torque level with group as a co-factor was used to determine the effect of bed rest and the effect of the countermeasure. In cases where significant interactions or strong tendencies were found, post hoc analysis consisted of conducting separate ANOVAs for each group with simple contrasts. Statistical significance was set at $P < 0.05$.

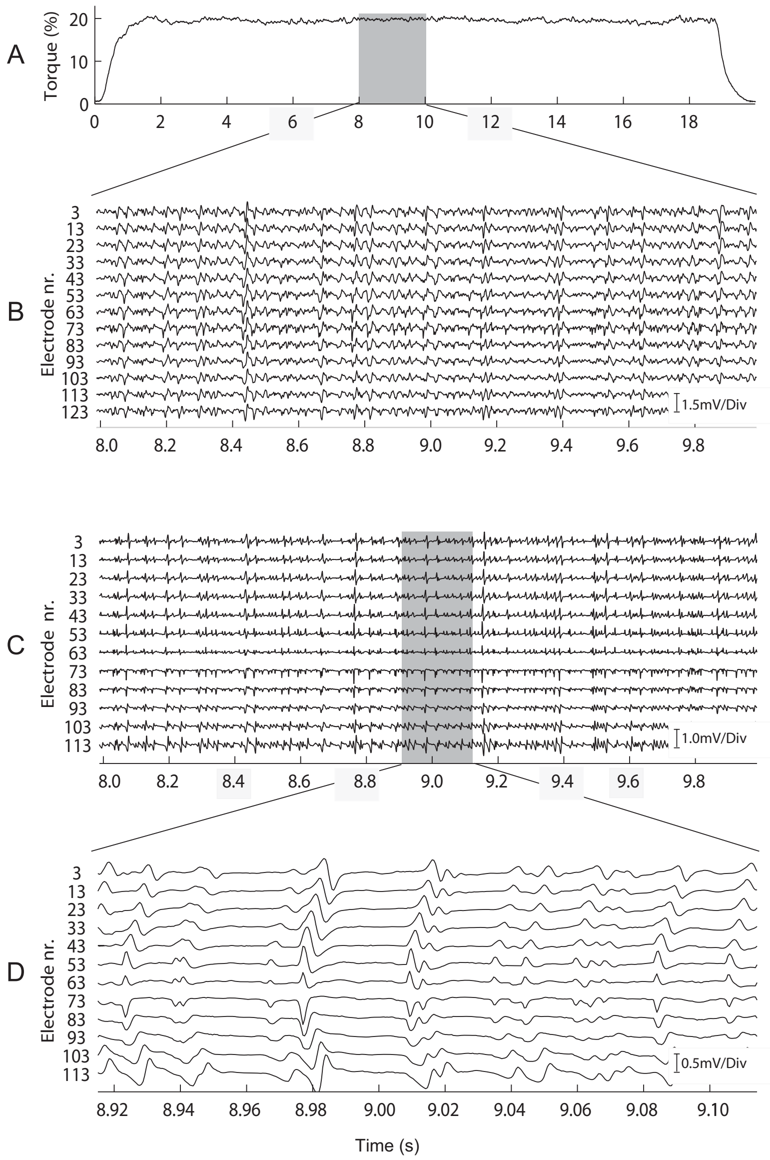

Fig. 2. Representative example of voluntary torque (A) and sEMG signals (B – D) during a sub-maximal contraction performed at 20% of actual MVT at BR0. The shaded area in A represents the 2-sec window during which torque fluctuations were minimal. During this epoch, amplitude (RMS) and median frequency (Fmed) were calculated from the monopolar sEMG signals (B). RMS was averaged over all channels within one column. The column with maximum (mean) RMS was used to average Fmed and to estimate MFCV. The latter was obtained from the bipolarly derived signal (C, D). The shaded area in C is enlarged in D. This part of the figure clearly shows the localization of the endplate region, which is characterized by the propagation of excitation in two opposing directions and a reversal of signal polarity.

RESULTS

Maximal voluntary torque
Mean group values for MVT during bed rest are provided in Fig. 3A. Bed rest resulted in a significant ($P < 0.001$) reduction in MVT for both groups. The percent reduction in MVT at BR56 was greater ($P < 0.05$) for Ctrl than for RVE, with respective values of -17.9 ± 2.5% and -9.9 ± 2.0%. Post hoc analysis revealed, however, an absence of changes in MVT from BR04 onwards for RVE, whereas a significant ($P < 0.001$) reduction in MVT (to -15.5 ± 2.7 at BR56) persisted for Ctrl.

Changes in high density sEMG signals during bed rest
sEMG amplitude. In contrast to the expected absence of changes in RMS at maximal torque level for both groups during the bed rest period, the RVE group showed a significant and strong RMS increase ($P < 0.001$) during bed rest to 130 ± 22% of the baseline value following 56 days (Fig. 3B). Post hoc analysis revealed a significant elevated RMS at BR10, 17, 24, and BR56, whereas a strong tendency towards an elevated RMS was observed at BR38 ($P = 0.054$).

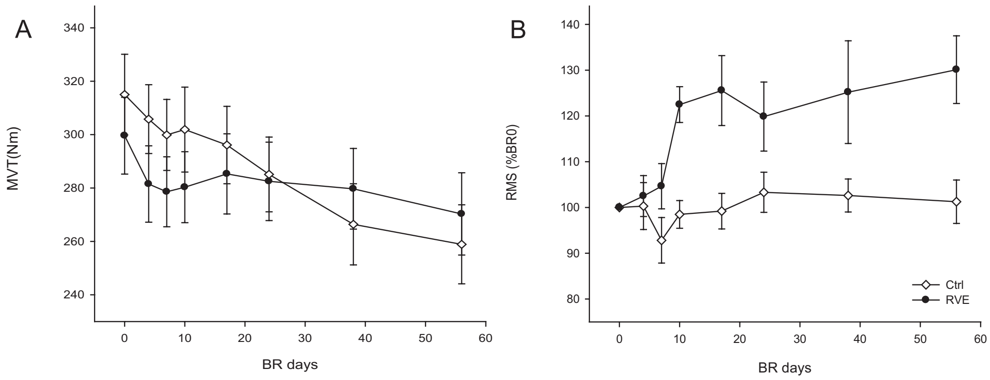

Fig. 3. Time course of maximal voluntary torque (MVT; A) and sEMG amplitude (RMS; B) at MVT during 56 days of bed rest. Data (mean ± SEM) are shown for Ctrl and RVE. RMS values are normalized for BR0. Without countermeasures, bed rest caused a significant reduction in MVT, and maintained RMS. RVE training during bed rest maintained MVT from BR04 onwards and showed an increased RMS.

In the RVE group the increase in RMS was also present at sub-maximal forces, but was most impressive at high forces (Fig. 4). To analyze the force-sEMG relationship for that group in more detail, the RMS at BR56 was also expressed as percentage of baseline RMS (BR0) for each force level (Fig. 5). The RMS at BR56 was significantly ($P < 0.05$) elevated for 15%, 30%, 40%, 60% and 100% MVT. The change in RMS at 5% and 10% MVT were significantly ($P < 0.05$) different from the increase in RMS at 100%MVT. For Ctrl, changes in RMS were also absent at the sub-maximal force levels.

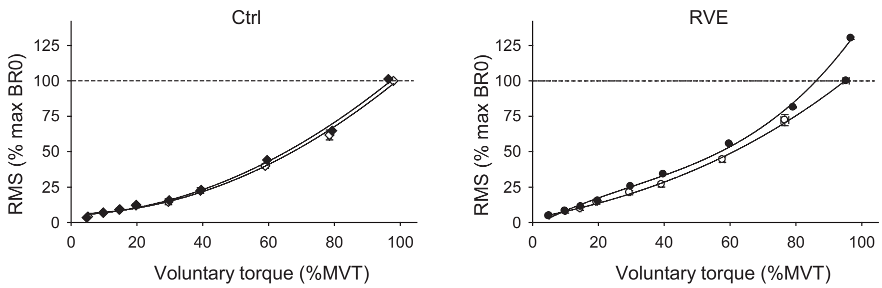

Fig. 4. Relationship between voluntary torque and sEMG amplitude for Ctrl (left panel) and RVE (right panel), pre (BR0, open symbols) and post (BR56, closed symbols) bed rest. Voluntary torque data are normalized to MVT on the day of testing. RMS data are normalized to the maximal baseline value at BR0. Each symbol represents the mean value of torque and RMS ± SEM of the corresponding group. For Ctrl, the normalized relationship remained unaltered during bed rest, whereas RVE training during bed rest resulted in a significant upward shift of this relationship. The mean relationships between RMS and voluntary torque have been fitted with a cubic equation, for clarification purposes. RMS, root mean square; MVT, maximal voluntary torque.

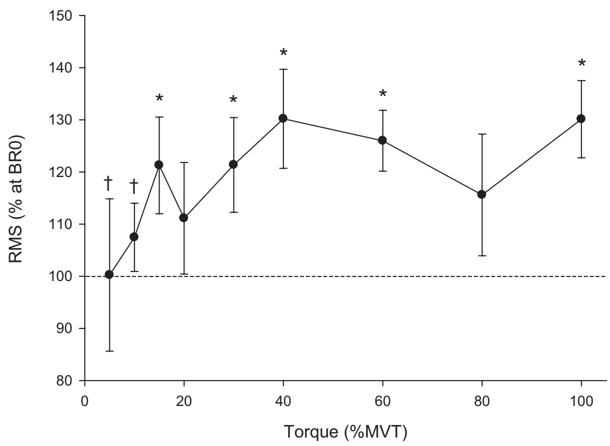

Fig. 5. Mean sEMG amplitude (RMS) values (mean ± SEM) for the RVE group at BR56, as a percentage of RMS at baseline (BR0) for the different force levels. * indicates a significantly ($P < 0.05$) increased RMS at BR56 with respect to baseline. † indicates a significant ($P < 0.05$) difference in the percentage increase in RMS with respect to the MVT level (100%) following 56 days of bed rest with RVE training.

sEMG median frequency and muscle fiber conduction velocity. In Fig. 6, the relationship between voluntary torque as a percentage of actual MVT and absolute Fmed (panels A, B) and MFCV (panels C, D) are shown for both groups. Bed rest resulted in a significant decline in both Fmed (-7.5 ± 2.3%; $P < 0.05$) and MFCV (-8.2 ± 2.6%; $P < 0.001$) across the different torque levels for Ctrl, but not for RVE.

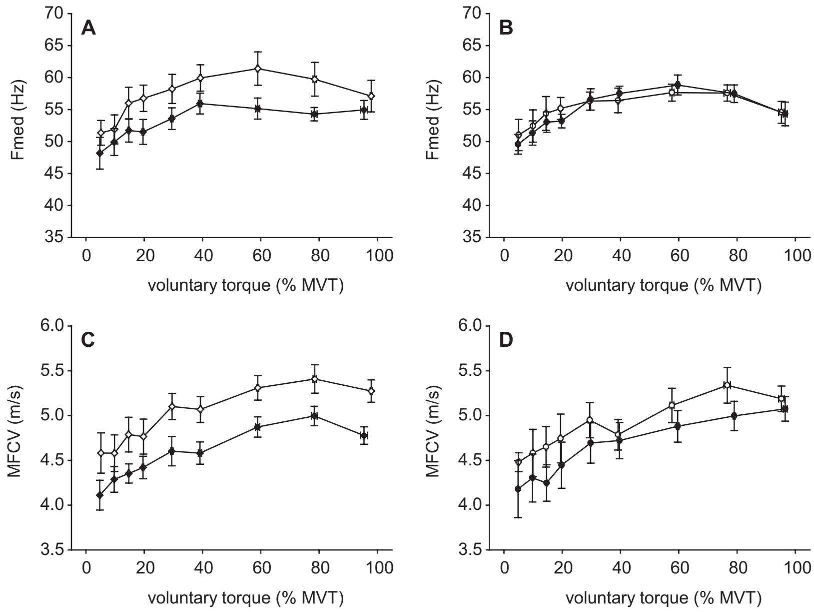

Fig. 6. Shown are the relationships between voluntary torque and sEMG median frequency (Fmed, top panels) and muscle fiber conduction velocity (MFCV, bottom panel) for Ctrl (A and C) and RVE (D and F). Depicted data (mean ± SEM) were obtained pre (open symbols) and post bed rest (filled symbols). In all panels, the voluntary torque data are normalized for the actual MVT value, i.e. the MVT of the day of testing. Without countermeasure, bed rest resulted in a significant reduction in Fmed and MFCV across the different torque levels, which was prevented by RVE training (B and D).

DISCUSSION

The effect of bed rest without countermeasures

In the Ctrl group no changes in RMS were found during the entire bed rest period. Neither did the relation between RMS and torque level change (Fig. 4). This observation indicates not only that motor unit recruitment was maintained at a maximal level [33], but also that, contrasting with initial expectations, the balance between motor unit recruitment and rate coding remained unchanged during bed rest. MFCV and Fmed (Fig. 6) declined for all force levels and by about the same percentage. Changes in Fmed are, at least in the absence of changes in motor unit firing patterns, correlated to changes in MFCV [30]. Since the MFCV is directly related to muscle fiber diameters [9], our results are well in line with quadriceps femoris muscle atrophy, measured as cross-sectional area in magnetic resonance images from the same subjects [33;43]. In contrast to previous studies [7;16;18;22;26;41], but in agreement with our previous observation that maximal voluntary torque loss could be explained by muscle atrophy alone [33], we found no evidence of change in maximum recruitment or recruitment and/or rate coding strategies, i.e. loss of neural drive capacity, as a consequence of 56 days of bed rest in the present study.

Subjects in the present study were repeatedly re-tested during the bed rest period, whereas in most previous bed rest campaigns measurements are limited to pre-post comparisons. Because of this methodological difference, we can not exclude the possibility that our testing protocol alone prevented any alteration in neural activation capacity during maximal and sub-maximal isometric knee extension exercise.

The effect of RVE training during bed rest on the peripheral level

As expected at the outset of the Berlin Bed Rest study [38], RVE was an effective countermeasure, as MVT was preserved from the fourth day of bed rest. Elsewhere, the protective effect of RVE as to muscle atrophy, measured by magnetic resonance imaging, has been described [33]. In line with these findings, no changes in the sEMG variables that could reflect muscle fiber diameter decrease (MFCV and Fmed, Fig. 6 B, D) were observed. The RVE training applied in the preset study consisted of voluntary resistive-type exercises together with externally applied vibrations to the feet. Vibration of muscles, tendons or the whole body evokes reflex contractions via the activation of primary muscle spindle afferents [36]. As said in the introduction, the indirect way of muscle activation during such training was one of the reasons for a more detailed analysis of its effects on motor control under bed rest conditions.

The effect of RVE training during bed rest on voluntary motor control

An unexpected finding was a large and rather abrupt change in RMS at maximal voluntary effort in the RVE group, which was not seen in Ctrl subjects (Fig. 3B) and has not been described in other bed rest studies that incorporated resistive exercise-based countermeasures [2;5;27]. An increase in sEMG amplitude is well recognized in resistance training under ambulatory conditions [24;29;44], though, but occurs more gradually in the course of weeks. The short time span in which the adaptations occurred in the present study might be related to the number of training sessions performed each week. In the studies cited above, subjects trained three times per week, whereas the subjects in the present study trained two times per day, for 6 days per week [38]. Furthermore, the addition of vibrations results in a large number of excitation cycles in a short time period [11]. Hence, the rapid increase in RMS during bed rest may be specific to the training regime based on RVE.

In general, an increase of RMS during a voluntary contraction could be caused by an increased number of motor unit (MU) firings per unit time, by a reduced amount of phase cancellation due to synchronization, or by changes in the MU action potential [19;31;46]. In the RVE group, MFCV and Fmed (Fig. 6) remained constant, whereas muscle cross-sectional area declined only marginally during the 56 days of bed rest [33]. Thus, changes at the muscle level can be excluded. Synchronization of MU firings is also excluded, as an increase of RMS caused by synchronization [46] would be accompanied by a decrease in Fmed [28]. The increase in RMS after about 10 days of bed rest (Fig. 3B) must therefore reflect an increased MU activation during isometric knee extension. Either more MUs were active at the same mean firing rate (recruitment), the same MUs were activated at a higher frequency (rate coding), or both. On the basis of the twitch interpolation technique, we reported also for the RVE group a high voluntary activation during maximal voluntary contractions throughout the 56 days of bed rest [33].

So, also additional recruitment of MUs can be excluded as an explanation for the increase in RMS at maximal voluntary effort in the present study.

In our view, the only remaining explanation for the increase in RMS for RVE is an increase in mean MU firing rate. In line with simulation studies of Herbert and Gandevia [25], the twitch interpolation technique as used in [33] may not have been sensitive for firing rate changes at high forces. The notion of an increased rate coding is further consistent with findings after resistance training under ambulatory conditions [17;35]. In the present study, the increase in RMS was most pronounced at the higher torque levels (Fig. 4 and 5). As mentioned in the introduction, the change in the sEMG-force relationship at high forces is compatible with a change in the maximal discharge rate of active motor units [21;32].

The details of RMS increase, in time and with torque level

Simulations of the sEMG-force relationship for a muscle with rate coding as the dominant gradation mechanism for increasing force above 50% of the maximum force predicts a curvilinear pattern, i.e., for higher forces the sEMG increases steeper than force [21]. This would explain the increase in RMS being more pronounced at the higher torque levels (Fig. 4 and 5). To explain this issue, the effects of vibration on the stretch reflex and MU firing must be considered. As mentioned, muscle, tendon or whole body vibration is believed to activate muscle spindle primary endings, which in turn, induces sustained reflex contractions in muscles at rest, known as the tonic vibration reflex [12]. When superimposed during a voluntary contraction, vibration can reinforce the excitation of motor neurons [23;42]. This may explain the increased EMG amplitude during vibration exercise [13;15]. In addition, after one single session of vibration exercise, an acute increase in stretch reflex excitability has been observed [34;40]. The increased excitability is restricted to the short-latency components [42], indicating that the plasticity is localized to the spinal level. The increase in RMS for the RVE group during voluntary isometric contractions during bed rest suggests therefore a persevering increase in excitability of the stretch-reflex loop as a consequence of eight weeks of six days per week, twice daily RVE training, even under conditions of bed rest. Although our findings are compatible with a modulation of the stretch reflex loop, modulation at higher (cortical) levels cannot be excluded. To explore the changes in excitability in more detail, other methods such as transcranial magnetic stimulation are required.

The increase in RMS had no effect on maximal voluntary knee extension strength under the isometric testing conditions. In comparison, muscle strength did increase for the same subjects during bed rest under the dynamic conditions of RVE training [38]. This can be deduced from the progressive increase in the intensity of RVE exercise during bed rest by means of augmenting vibration frequency [38]. Because the quadriceps femoris muscle atrophied slightly (up to ~5%) during the course of bed rest for the RVE group [33], the increase in dynamic knee extension strength (squat) must result from an improved neural control. In agreement with previous reports on countermeasure efficacy during bed rest [2-4], the dissociation between effects under training and testing conditions suggests that neural adaptations were task-specific and beneficial only during the RVE training itself. During isometric knee extension, the elevated

MU firing rate appears beyond the level of a substantial force increase. This may be explained by the saturating effect of firing rate on steady MU force output at high frequencies [32]. However, additional factors than little influence of increasing discharge rate on muscle force should be considered, in particular for the sub-maximal contractions. For these contractions voluntary torque should increase with increased discharge rates or motor unit recruitment. The indifferent torque responses also at sub-maximal forces might indicate that twice-daily resistive vibration exercise training altered the recruitment pattern among the different quadriceps components. The increase in activation of the vastus lateralis muscle might have been paralleled by a lesser activation of one or more of the agonist muscles. In addition, it is also conceivable that resistive vibration exercise enhanced co-activation of antagonist muscles during the isometric contractions. This would also explain why the increase in RMS in Fig. 5 in not gradual.

In conclusion, there was no evidence for a decrease in central neural drive in both groups Ctrl and RVE, in line with our previous report on the same subjects [33]. For Ctrl, this was possibly related to the repeated, albeit infrequently physical testing performed during the course of the bed rest, which might have preserved neural capabilities for this group. The decline in Fmed in Ctrl was in line with the concurrent changes in MFCV as a result of muscle fiber atrophy of the quadriceps femoris muscle. Resistive vibration exercise training during 56 days of bed rest, resulted in a significant increase in muscle activation during maximal and sub-maximal voluntary isometric knee extension in the trained subjects, as evidenced by the rapid and profound increase in RMS throughout bed rest. The increased excitation, which most likely resulted in an enhanced firing frequency of activated MUs, appeared ineffective to increase muscle strength under the isometric testing conditions. The presented data suggest that neural training effects of resistive vibration training during bed rest are highly task specific. Finally, it can be stated that this is the first study that demonstrates that the atrophy-preventing effect of resistive vibration exercise may come at the price of alterations in motor control, which appear inefficient for tasks dissimilar to the training mode itself.

REFRERENCES

[1] Adams GR, Caiozzo VJ, Baldwin KM. Skeletal muscle unweighting: spaceflight and ground-based models. J Appl Physiol 2003; 95: 2185-2201.

[2] Alkner BA, Tesch PA. Knee extensor and plantar flexor muscle size and function following 90 days of bed rest with or without resistance exercise. Eur J Appl Physiol 2004; 93: 294-305.

[3] Bamman MM, Caruso JF. Resistance exercise countermeasures for spaceflight: implications of training specificity. J Strength Cond Res 2000; 14: 45-49.

[4] Bamman MM, Clarke MS, Feeback DL, Talmadge RJ, Stevens BR, Lieberman SA, Greenisen MC. Impact of resistance exercise during bed rest on skeletal muscle sarcopenia and myosin isoform distribution. J Appl Physiol 1998; 84: 157-163.

[5] Bamman MM, Hunter GR, Stevens BR, Guilliams ME, Greenisen MC. Resistance exercise prevents plantar flexor deconditioning during bed rest. Med Sci Sports Exerc 1997; 29: 1462-1468.

[6] Beck RB, Houtman CJ, O'Malley MJ, Lowery MM, Stegeman DF. A technique to track individual motor unit action potentials in surface EMG by monitoring their conduction velocities and amplitudes. IEEE Trans Biomed Eng 2005; 52: 622-629.

[7] Berg HE, Larsson L, Tesch PA. Lower limb skeletal muscle function after 6 wk of bed rest. J Appl Physiol 1997; 82: 182-188.

[8] Berg HE, Tesch PA. Changes in muscle function in response to 10 days of lower limb unloading in humans. Acta Physiol Scand 1996; 157: 63-70.

[9] Blijham PJ, ter Laak HJ, Schelhaas HJ, van Engelen BG, Stegeman DF, Zwarts MJ. Relation between muscle fiber conduction velocity and fiber size in neuromuscular disorders 2. J Appl Physiol 2006; 100: 1837-1841.

[10] Blok JH, van Dijk JG, Drost G, Zwarts MJ, Stegeman DF. A high-density multichannel surface electromyography system for the characterization of single motor units. Review of Scientific Instruments 2002; 73: 1887-1897.

[11] Blottner D, Salanova M, Puttmann B, Schiffl G, Felsenberg D, Buehring B, Rittweger J. Human skeletal muscle structure and function preserved by vibration muscle exercise following 55 days of bed rest. Eur J Appl Physiol 2006; 97: 261-271.

[12] Burke D, Schiller HH. Discharge pattern of single motor units in the tonic vibration reflex of human triceps surae. J Neurol Neurosurg Psychiatry 1976; 39: 729-741.

[13] Cardinale M, Lim J. Electromyography activity of vastus lateralis muscle during whole-body vibrations of different frequencies. J Strength Cond Res 2003; 17: 621-624.

[14] De Luca CJ. The use of surface electromyography in biomechanics. J Appl Biomech 1997; 13: 135-163.

[15] Delecluse C, Roelants M, Verschueren S. Strength increase after whole-body vibration compared with resistance training. Med Sci Sports Exerc 2003; 35: 1033-1041.

[16] Deschenes MR, Giles JA, McCoy RW, Volek JS, Gomez AL, Kraemer WJ. Neural factors account for strength decrements observed after short-term muscle unloading. Am J Physiol Regul Integr Comp Physiol 2002; 282: R578-R583.

[17] Duchateau J, Enoka RM. Neural adaptations with chronic activity patterns in able-bodied humans. Am J Phys Med Rehabil 2002; 81: S17-S27.

[18] Dudley GA, Duvoisin MR, Adams GR, Meyer RA, Belew AH, Buchanan P. Adaptations to unilateral lower limb suspension in humans. Aviat Space Environ Med 1992; 63: 678-683.

[19] Farina D, Merletti R, Enoka RM. The extraction of neural strategies from the surface EMG. J Appl Physiol 2004; 96: 1486-1495.

[20] Frey I, Berg A, Grathwohl D, Keul J. [Freiburg Questionnaire of physical activity--development, evaluation and application]. Soz Praventivmed 1999; 44: 55-64.

[21] Fuglevand AJ, Winter DA, Patla AE. Models of recruitment and rate coding organization in motor-unit pools. J Neurophysiol 1993; 70: 2470-2488.

[22] Gondin J, Guette M, Maffiuletti NA, Martin A. Neural activation of the triceps surae is impaired following 2 weeks of immobilization. Eur J Appl Physiol 2004; 93: 359-365.

[23] Griffin L, Garland SJ, Ivanova T, Gossen ER. Muscle vibration sustains motor unit firing rate during submaximal isometric fatigue in humans. J Physiol 2001; 535: 929-936.

[24] Hakkinen K, Alen M, Kallinen M, Newton RU, Kraemer WJ. Neuromuscular adaptation during prolonged strength training, detraining and re-strength-training in middle-aged and elderly people. Eur J Appl Physiol 2000; 83: 51-62.

[25] Herbert RD, Gandevia SC. Twitch interpolation in human muscles: mechanisms and implications for measurement of voluntary activation. J Neurophysiol 1999; 82: 2271-2283.

[26] Jaweed MM, Grana EA, Glennon TP, Monga TN, Mirabi B. Neuromuscular adaptations during 30 days of cast-immobilization and head-down bedrest. J Gravit Physiol 1995; 2: 72-73.

[27] Kawakami Y, Akima H, Kubo K, Muraoka Y, Hasegawa H, Kouzaki M, Imai M, Suzuki Y, Gunji A, Kanehisa H, Fukunaga T. Changes in muscle size, architecture, and neural activation after 20 days of bed rest with and without resistance exercise. Eur J Appl Physiol 2001; 84: 7-12.

[28] Kleine BU, Stegeman DF, Mund D, Anders C. Influence of motoneuron firing synchronization on SEMG characteristics in dependence of electrode position. J Appl Physiol 2001; 91: 1588-1599.

[29] Lindeman E, Spaans F, Reulen JP, Leffers P, Drukker J. Surface EMG of proximal leg muscles in neuromuscular patients and in healthy controls. Relations to force and fatigue. J Electromyogr Kinesiol 1999; 9: 299-307.

[30] Linssen WH, Stegeman DF, Joosten EM, van't Hof MA, Binkhorst RA, Notermans SL. Variability and interrelationships of surface EMG parameters during local muscle fatigue. Muscle Nerve 1993; 16: 849-856.

[31] Merletti R, Lo Conte LR. Surface EMG signal processing during isometric contractions. J Electromyogr Kinesiol 1997; 7: 241-250.

[32] Milner-Brown HS, Stein RB. The relation between the surface electromyogram and muscular force. J Physiol 1975; 246: 549-569.

[33] Mulder ER, Stegeman DF, Gerrits KH, Paalman MI, Rittweger J, Felsenberg D, de Haan A. Strength, size and activation of knee extensors followed during 8 weeks of horizontal bed rest and the influence of a countermeasure. Eur J Appl Physiol 2006; 97: 706-715.

[34] Nishihira Y, Iwasaki T, Hatta A, Wasaka T, Kaneda T, Kuroiwa K, Akiyama S, Kida T, Ryol KS. Effect of whole body vibration stimulus and voluntary contraction on motoneuron pool. Adv Exerc Sports Physiol 2002; 8: 83-86.

[35] Patten C, Kamen G, Rowland DM. Adaptations in maximal motor unit discharge rate to strength training in young and older adults. Muscle Nerve 2001; 24: 542-550.

[36] Proske U. What is the role of muscle receptors in proprioception? Muscle Nerve 2005; 31: 780-787.

[37] Rau G, Disselhorst-Klug C. Principles of high-spatial-resolution surface EMG (HSR-EMG): single motor unit detection and application in the diagnosis of neuromuscular disorders. J Electromyogr Kinesiol 1997; 7: 233-239.

[38] Rittweger J, Belavy D, Hunek P, Gast U, Boerst H, Feilcke B, Armbrecht G, Mulder E, Schubert H, Richardson C, de Haan A, Stegeman DF, Schiessl H, Felsenberg D. Highly Demanding Resistive Vibration Exercise Program is Tolerated During 56 Days of Strict Bed-Rest1. Int J Sports Med 2006; 27: 553-559.

[39] Rittweger J, Ehrig J, Just K, Mutschelknauss M, Kirsch KA, Felsenberg D. Oxygen uptake in whole-body vibration exercise: influence of vibration frequency, amplitude, and external load. Int J Sports Med 2002; 23: 428-432.

[40] Rittweger J, Mutschelknauss M, Felsenberg D. Acute changes in neuromuscular excitability after exhaustive whole body vibration exercise as compared to exhaustion by squatting exercise. Clin Physiol Funct Imaging 2003; 23: 81-86.

[41] Schulze K, Gallagher P, Trappe S. Resistance training preserves skeletal muscle function during unloading in humans. Med Sci Sports Exerc 2002; 34: 303-313.

[42] Shinohara M, Moritz CT, Pascoe MA, Enoka RM. Prolonged muscle vibration increases stretch reflex amplitude, motor unit discharge rate, and force fluctuations in a hand muscle. J Appl Physiol 2005; 99: 1835-1842.

[43] Stegeman DF, Mulder ER, Gerrits KH, Rittweger J, Felsenberg D, de Haan A. Peripherally and centrally induced electromyographic changes in 8 weeks of horizontal bed rest with and without resistance exercise with concurrent whole body vibration. J Gravit Physiol 2005; 12: 155-156.

[44] Suetta C, Aagaard P, Rosted A, Jakobsen AK, Duus B, Kjaer M, Magnusson SP. Training-induced changes in muscle CSA, muscle strength, EMG, and rate of force development in elderly subjects after long-term unilateral disuse. J Appl Physiol 2004; 97: 1954-1961.

[45] Widrick JJ, Norenberg KM, Romatowski JG, Blaser CA, Karhanek M, Sherwood J, Trappe SW, Trappe TA, Costill DL, Fitts RH. Force-velocity-power and force-pCa relationships of human soleus fibers after 17 days of bed rest. J Appl Physiol 1998; 85: 1949-1956.

[46] Yao W, Fuglevand RJ, Enoka RM. Motor-unit synchronization increases EMG amplitude and decreases force steadiness of simulated contractions. J Neurophysiol 2000; 83: 441-452.