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Sensorimotor adaptations to microgravity in humans

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Summary

Motor function is altered by microgravity, but little detail is available as to what these changes are and how changes in the individual components of the sensorimotor system affect the control of movement. Further, there is little information on whether the changes in motor performance reflect immediate or chronic adaptations to changing gravitational environments. To determine the effects of microgravity on the neural control properties of selected motor pools, four male astronauts from the NASA STS-78 mission performed motor tasks requiring the maintenance of either ankle dorsiflexor or plantarflexor torque. Torques of 10 or 50 % of a maximal voluntary contraction (MVC) were requested of the subjects during 10 ° peak-to-peak sinusoidal movements at 0.5 Hz. When 10 % MVC of the plantarflexors was requested, the actual torques generated in-flight were similar to pre-flight values. Post-flight torques were higher than pre- and in-flight torques. The actual torques when 50 % MVC was requested were higher in- and post-flight than pre-flight. Soleus (Sol) electromyographic (EMG) amplitudes during plantarflexion were higher in-flight than pre- or post-flight for both the 10 and 50 % MVC tasks. No differences in medial gastrocnemius (MG) EMG amplitudes were observed for either the 10 or 50 % MVC tasks. The EMG amplitudes of the tibialis anterior (TA), an antagonist to plantarflexion, were higher in- and post-flight than pre-flight for the 50 % MVC task. During the dorsiflexion tasks, the torques generated in both the 10 and 50 % MVC tasks did not differ pre-, in- and post-flight. TA EMG amplitudes were significantly higher in- than pre-flight for both the 10 or 50 % MVC tasks, and remained elevated post-flight for the 50 % MVC test. Both the Sol and MG EMG amplitudes were significantly higher in-flight than either pre- or post-flight for both the 10 and 50 % MVC tests. These data suggest that the most consistent response to space flight was an elevation in the level of contractions of agonists and antagonists when attempting to maintain constant torques at a given level of MVC. Also, the chronic levels of EMG activity in selected ankle flexor and extensor muscles during space flight and during routine activities on Earth were recorded. Compared with pre- and post-flight values, there was a marked increase in the total EMG activity of the TA and the Sol and no change in the MG EMG activity in-flight. These data indicate that space flight, as occurs on shuttle missions, is a model of elevated activation of both flexor and extensor muscles, probably reflecting the effects of programmed work schedules in flight rather than a direct effect of microgravity.

Key words: chronic electromyography, microgravity, motor control, force estimation, antagonist co-activation, space flight.

Introduction

The structural and functional properties of the neuromotor system of terrestrial animals have evolved with a variety of design strategies that facilitate mobility in the gravitational environment of Earth. Experiments performed over the last century demonstrate that many of the details of the neural control of movement accommodate this gravitational environment by extensively using ‘automatic’ neural control strategies (Grillner, 1981). Not only are these neural strategies tightly linked to the structural features of the musculoskeletal system of a given species, but in effect these neuromotor features are linked to Earth’s gravitational forces. It is often assumed that the degree to which humans depend on their automaticity of neural control to accommodate Earth’s gravity ($1\,\boldsymbol{g}$), particularly during postural locomotor tasks, is far less than that of other terrestrial animals. In effect, we know little of how Earth’s gravitational forces have impacted the evolution of neuromotor systems, including that of humans (Chekirda et al., 1970; Baker et al., 1977; Kozlovskaya et al., 1981; Clement et al., 1985; Kozlovskaya et al., 1988; Fisk et al., 1993; Edgerton and Roy, 1996).

To gain further understanding of how the human neuromotor system accommodates to gravity, we studied the activation of motor pools before, during and after a 17-day space flight while performing well-defined motor tasks and compared the activation properties of extensor muscles with that of their flexor antagonists. We also examined the chronic activity levels of selected leg flexor and extensor motor pools that work directly against gravity to maintain an upright position. The results suggest that the space flight environment imposes acute [e.g. elevated soleus (Sol) electromyographic (EMG) amplitude during plantarflexion on the first flight day] and chronic [e.g. persistently high tibialis anterior (TA) EMG during dorsiflexion] effects on the activation properties of motor pools that have different 'antigravity' functions on Earth.

Materials and methods

Subjects

Four healthy male astronauts, with no previous space flight experience, participated voluntarily in the present study, one component of the National Aeronautics and Space Administration (NASA) Life and Microgravity Spacelab Shuttle Transportation System 78 (STS-78) mission. The mean age of these subjects was 43.8±3.8 years (mean ± S.D.). The study was approved by the NASA and UCLA Ethics Committees.

Experimental protocol

The control of ankle plantarflexion and dorsiflexion was tested using a torque-velocity dynamometer (TVD; Laboratory of Swiss Federal Institute of Technology). Test days were 30 and 12 days before launch (L−), flight days (FD) 2 or 3, 7 or 8 and 13 or 14 and 0, 2, 8 and 15 days after flight (R+).

EMG activity of the Sol and medial gastrocnemius (MG), two primary plantarflexors, and the TA, a primary dorsiflexor, was recorded using bipolar skin surface electrodes (Multi Bio Sensors Inc., 2.5 cm center to center). Electrodes were placed directly over the belly of the muscles at locations marked with permanent ink. EMG signals were amplified using custom-made amplifiers with a gain of 1000 that were attached around the waist. The EMG leads were secured to the legs as they projected from the amplifier. Each series of motor control tests was performed with the same electrode placement as was used to record normal routine activities. During TVD testing, the signals were sampled with 12-bit resolution at a sampling rate of 1 kHz and stored on an IBM ThinkPad hard drive.

Motor control testing paradigm

For all motor control testing, the subjects were secured in a supine position with the head slightly elevated. The center of rotation of the TVD was aligned with the axis of rotation of the ankle. The TVD output signals were proportional to the torque and angular movement of the joint. When testing the ankle, the right knee was fixed at approximately 160 °. The ankle was positioned at 120 ° (i.e. slightly plantarflexed) for testing of the dorsiflexors and at 90 ° for testing the plantarflexors. Subjects were first requested to provide a series of isometric sub-maximal and maximal voluntary contractions (MVCs, three trials at five levels of MVC). The computer detected the force generated during the highest MVC and used this value as a basis for feedback to the subject during the test. MVCs were obtained approximately 15–20 min prior to the constant torque tests.

The experimental task consisted of maintaining a targeted torque output while a 10 ° peak-to-peak passive sinusoidal motion (±5 ° from the previously stated joint angles) was imposed on the ankle joint for eight cycles at 0.5 Hz. The subjects were prompted *via* a computer monitor to 'push' (plantarflexor activation) or 'pull' (dorsiflexor activation) and maintain either 10 or 50 % MVC. The subjects were provided momentary force feedback on the computer screen, i.e. the target torque was displayed for 2 s at the beginning of each test. The same series of tests was repeated with a constant visual display of the target torque (data not shown). The exact sequence of the commands was (i) 'push' at 10 % MVC, (ii) 'pull' at 10 % MVC, (iii) 'push' at 50 % MVC and (iv) 'pull' at 50 % MVC. The TVD repositioned the ankle after each test. The duration of each test was 24 s followed by 8 s of rest as the TVD was repositioned.

Data processing

Rectified EMG signals were averaged across each individual task using customized software developed in-house using LabVIEW (National Instruments, Austin, TX, USA). These values were normalized to the maximal EMG value for the corresponding muscle recorded during an isometric MVC for that same test day. Normalized EMG amplitude was plotted *versus* test day for each task. The average torque in newton-meters (N m) across the eight cycles for each task, e.g. 'push' 10 % MVC at 0.5 Hz, was calculated and expressed as a percentage of the MVC.

EMG data were also recorded on analog tape for 24 h periods using an analog tape recorder (TEAC model HR-401 TEAC Corp., Montebello, CA, USA; mass 588 g). One tape was required for each 12 h recording period. The recordings were digitized later at 1000 Hz and archived on CDs. The EMG data files were then processed using customized LabVIEW software. All the data were initially reviewed using interactive software to display the EMG signals on a computer monitor. Periods of interference were identified and entered into a spreadsheet file. These periods amounted to only a few seconds each day. A spreadsheet file of the data was used by a second program to identify and analyze acceptable EMG data from the subjects. The analysis program rectified the EMG data, calculated averages for successive 40 ms segments throughout the day and constructed amplitude histograms from the averages. The averaging process approximated a low-pass filter with a cut-off of 12.5 Hz. Integrated EMG levels were calculated by summing the product of the amplitude represented by each bin and the bin count. Histograms of baseline noise were used to determine which bins represented zero activity. This was typically the first two or three bins of the histograms. Counts in the remaining bins were used to calculate the duration of the activity.

Statistical analyses

Differences in torque output and normalized EMG amplitudes during motor control tasks and chronic EMG amplitudes were compared using repeated-measures analysis of variance (ANOVA). Multivariate ANOVA (MANOVA), which adjusts for the correlation due to repeated measurements on the same subjects, was not possible because the number of repeated measures exceeded the total number of subjects. Therefore, univariate analyses were performed using the Huynh–Feldt procedure, which corrects for repeated measurements by adjusting the *F*-value prior to the probability estimate. For incomplete data sets (see figure legends), the mean of the three available subjects was used as the missing value to compute the ANOVAs; however, all figures depict means ± S.E.M. for the available subjects. No plantarflexor torque is reported for the first day of flight because of technical problems on that test day. If recordings were made on fewer than three subjects on any test day, no data are reported. Because we also were interested in the acute adaptations to and recovery from space flight, contrasts were used to compare specific test days. Similarly, linear combination contrasts were used to compare the combined pre-flight, in-flight and post-flight test days. All analyses were performed using SuperAnova statistical software (Abacus Concepts, Berkeley, CA, USA) and Apple Macintosh microcomputers.

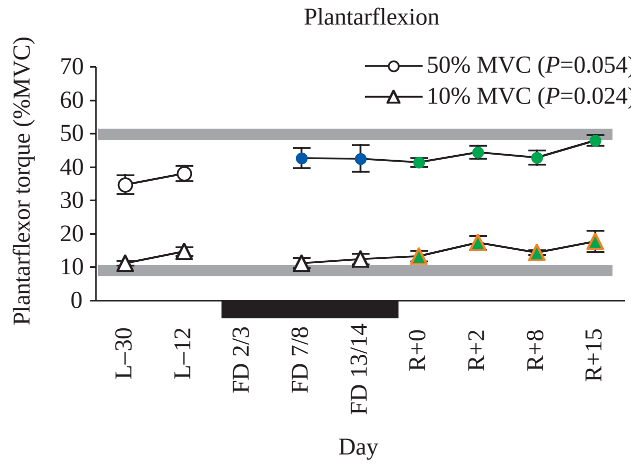

Fig. 1. Mean torque during plantarflexion motor control tests performed at 10 and 50 % maximal voluntary contraction (MVC) on test days pre-flight (L–30 and L–12), in-flight (F7/8 and F13/14) and post-flight (R+0, R+2, R+8, and R+15). The filled bar on the *x*-axis indicates flight days. Values are means ± S.E.M.; *N*=4 at each time point. Blue symbols indicate a significant difference between pre- and in-flight values. Green symbols indicate a significant difference between pre- and post-flight values. Orange symbols indicate a significant difference between in- and post-flight values. For 10 % MVC, post-flight was elevated over pre-flight (P=0.03) and in-flight (P=0.009) values. For 50 % MVC, pre-flight values were lower than in-flight (P=0.02) and post-flight (P=0.002) values. The P levels for the ANOVA main effects are shown.

Results

Plantarflexor torques

When attempting to maintain 10 % MVC against an oscillating lever, the actual plantarflexor torques relative to the targeted torques were lower pre- and in-flight than post-flight (Fig. 1). During the 50 % MVC tasks, both the in- and post-flight torques were higher than the pre-flight torques. The mean torques on the various in-flight days were similar, suggesting no chronic effects of space flight.

EMG amplitudes for the Sol, MG and TA during plantarflexion

During both the 10 and 50 % plantarflexion MVC tests, the EMG amplitudes in the Sol were lower pre- than in-flight and not significantly different from post-flight values (Fig. 2). The only significant change between days occurred during the first flight recording (P=0.001). No changes in the MG EMG amplitudes were observed for either the 10 or 50 % MVC tasks during plantarflexion. There were no flight effects for the TA at 10 % MVC. During the 50 % MVC test, in- and post-flight TA mean EMG amplitudes were higher than pre-flight values and there was a significant increase in EMG amplitude in the first flight recording (P=0.03).

In six out of six cases, the mean EMG amplitudes of the TA in-flight were above the highest pre-flight value (Fig. 2). In five of the six cases, the in-flight TA EMG mean amplitudes exceeded all post-flight values. In five of the six comparisons of the first flight day tests with the pre-flight tests (the three muscles tested at 10 and 50 % MVC for plantarflexion), the mean EMGs were higher in-flight. For similar comparisons between the last in-flight and first post-flight days, the mean EMG amplitudes were lower post-flight in six of six cases.

Dorsiflexor torques

When the subjects attempted to maintain a constant level of dorsiflexion torque at 10 or 50 % MVC during the oscillating tasks, the torques exerted were not significantly different pre-, in- or post-flight (Fig. 3).

EMG amplitudes for the TA, Sol and MG during dorsiflexion

For the TA mean EMG amplitude, there were no overall significant main effects. However, the mean EMG amplitude was higher in- than pre-flight for both the 10 and 50 % MVC tasks and remained higher post- than pre-flight for the 50 % MVC tasks (Fig. 4). All 12 mean TA EMG amplitudes in- and post-flight were higher than the four pre-flight means. Both the Sol and MG EMG amplitudes were higher in- than pre-flight for both the 10 and 50 % MVC dorsiflexion tasks. There were no pre/post differences in the mean EMG amplitudes of the Sol or MG at either 10 or 50 % MVC. In six out of six cases (the three muscles tested at 10 and 50 % MVC for dorsiflexion), the mean EMG amplitudes were elevated on the first flight day

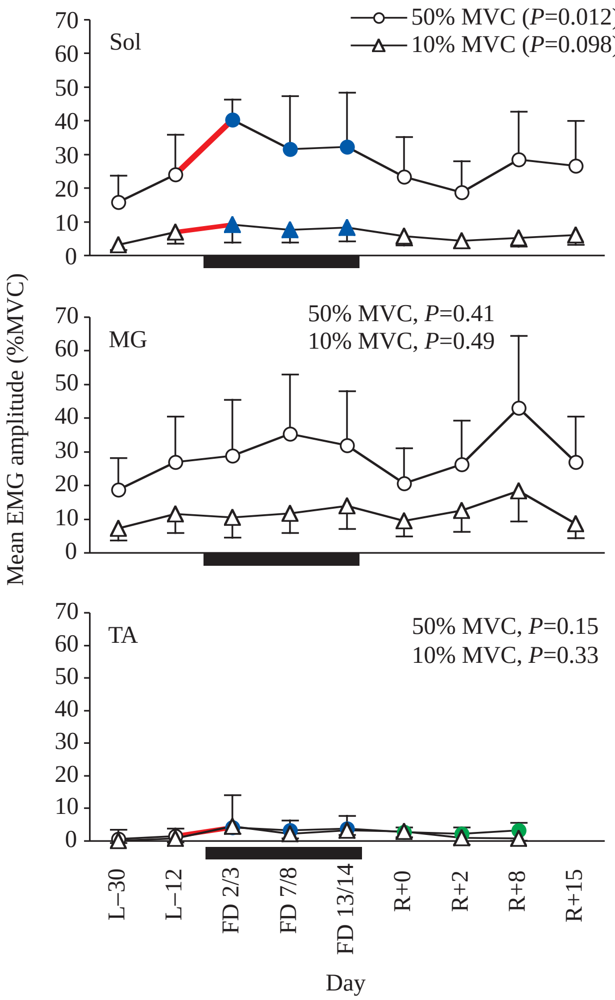

Fig. 2. Mean electromyographic (EMG) activity of the soleus (Sol), medial gastrocnemius (MG) and tibialis anterior (TA) muscles relative to maximal voluntary contraction (%MVC) during plantarflexion motor control tests performed at 10 and 50 % MVC. The *x*-axis is labeled as for Fig. 1. Values are means ± S.E.M.; *N*=4, except for F2/3 (*N*=3). R+15 was excluded for the TA as only one subject's recordings were valid. Colored symbols indicate significant differences as in Fig. 1. Red lines identify significant contrasts between pairs of adjacent data points. For the Sol, in-flight EMG amplitude was elevated above pre-flight values for both the 10 % (P=0.02) and 50 % MVC (P=0.002) tasks. No differences were observed in MG EMG amplitude. For the TA, in-flight (P=0.01) and post-flight (P=0.05) EMG amplitudes were elevated above pre-flight values for the 50 % MVC task. The P levels for the ANOVA main effects are shown.

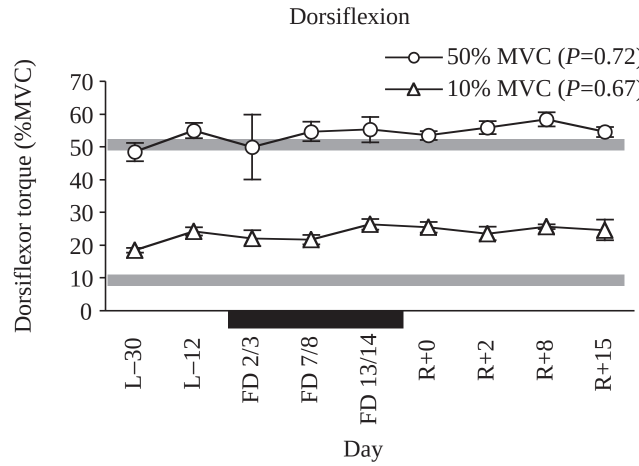

Fig. 3. Mean torque during dorsiflexion motor control tests performed at 10 and 50 % maximal voluntary contraction (MVC). The *x*-axis is labeled as for Fig. 1. Values are means ± S.E.M.; *N*=4, except for F2/3 (*N*=3). No significant differences were observed. The P levels for the ANOVA main effects are shown.

compared with pre-flight, and in six out of six cases the mean EMG amplitudes were lower on the first post-flight test than on the last flight test.

EMG activities during routine daily activities

The effects of space flight on the relative EMG activities of selected flexor and extensor motor pools of the legs were studied by recording from all subjects for up to 24 continuous hours with the subjects fully ambulatory. The mean total activity levels per day for the Sol were more than twice as high in- than pre- and post-flight (Fig. 5). The total period during which some Sol EMG activity, i.e. activity above baseline noise, was detected showed patterns similar to those for the total daily activity, i.e. more than double (Fig. 6). There was a significant increase in the Sol integrated EMG on the first day of flight (P=0.05) and a significant decrease on the first recording day after flight (P=0.01). The MG EMG total activity per day (Fig. 5) and the duration of 'on-time' (Fig. 6) during the pre-, in- and post-flight conditions were similar. The total activity in the TA was more than six times higher in- than pre- or post-flight (Fig. 5). The total 'on-time' for the TA was more than ten times higher in- than pre- or post-flight (Fig. 6). There was a significant increase in the TA integrated EMG (P=0.002) and duration (P=0.0001) on the first day of flight and a significant decrease on the first recording day after flight for integrated EMG (P=0.007) and for duration (P=0.0001).

Discussion

Alterations in the motor pool strategies to maintain constant torque

Although some changes in motor control strategies occurred among the crew members in the present study as a result of the changing environmental conditions, the subjects executed the requested tasks remarkably well during flight. In general, these observations reflect the ability of the central nervous system to accommodate quickly to the changing physical environments linked to space flight. However, what may intuitively seem to be small effects in motor control tests could be critical in determining whether a difficult motor task is executed successfully and safely. In accommodating these varied gravitational environments, some acute effects were apparent because significant changes occurred in the EMG levels on the

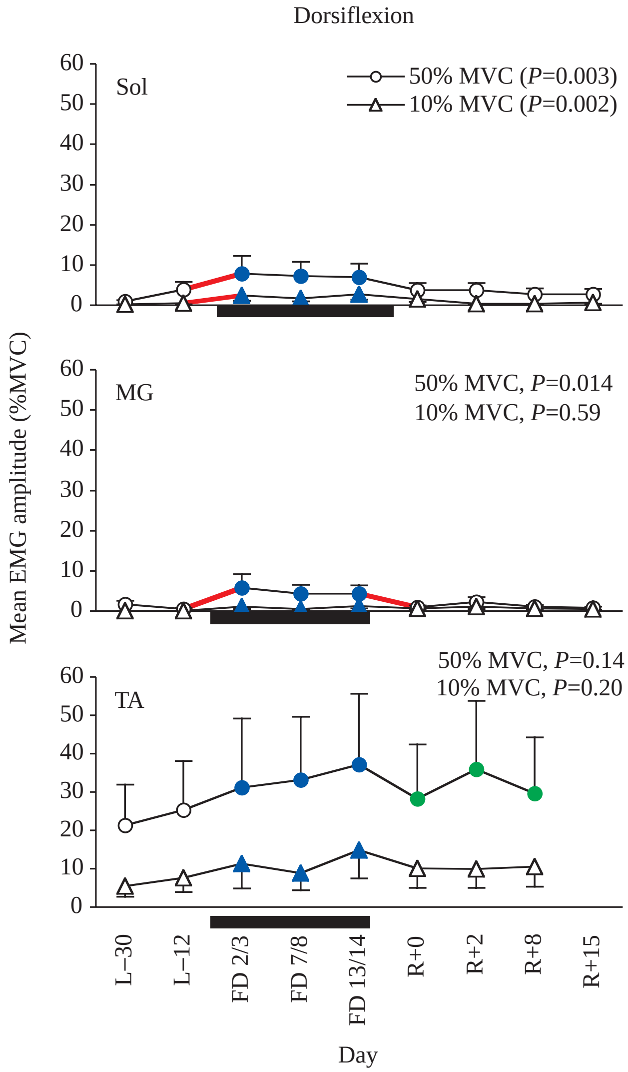

Fig. 4. Mean electromyographic (EMG) activity of the soleus (Sol), medial gastrocnemius (MG) and tibialis anterior (TA) muscles relative to maximal voluntary contraction (%MVC) during dorsiflexion motor control tests performed at 10 and 50 % MVC. The *x*-axis is labeled as for Fig. 1. Values are means ± S.E.M.; *N*=4, except for F2/3 (*N*=3). R+15 was excluded for the TA as only one subject's recordings were valid. Colored symbols and lines indicate significant differences as in Fig. 2. The Sol mean EMG amplitude was lower pre- than in-flight for the 10 % (*P*=0.0001) and 50 % (*P*=0.0002) MVC tasks. The MG mean EMG amplitude was lower pre- than in-flight for the 10 % (*P*=0.05) and 50 % (*P*=0.002) MVC tasks. The TA mean EMG amplitude was lower pre- than in-flight for the 10 % (*P*=0.03) and 50 % (*P*=0.02) and lower pre- than post-flight for the 50 % (*P*=0.05) MVC tasks. The *P* levels for the ANOVA main effects are shown.

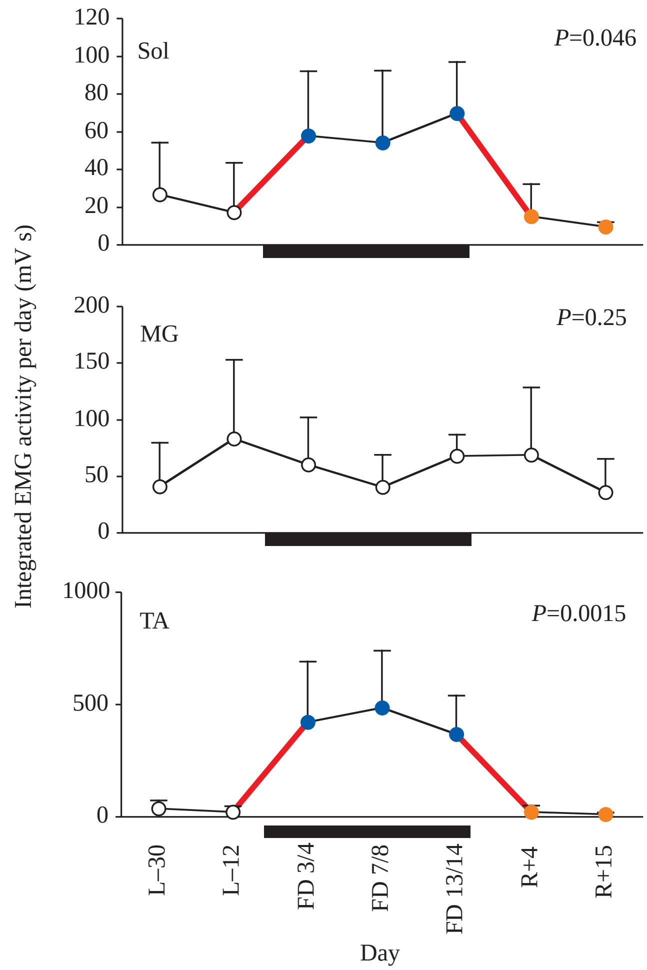

Fig. 5. Mean integrated electromyographic (EMG) activity (mV s) observed over the entire recording day for the soleus (Sol), medial gastrocnemius (MG) and tibialis anterior (TA) muscles. The *x*-axis is labeled as for Fig. 1. Only subjects with full data sets were used in determining mean values. Values are means ± S.E.M.; *N*=4, except for F7/8 (*N*=3). Colored symbols and lines indicate significant differences as in Fig. 2. The in-flight values for the Sol (*P*=0.07) and TA (*P*=0.002) for each day were greater than the pre- and post-flight values. No differences were observed for the MG EMG activation levels. The *P* levels for the ANOVA main effects are shown.

first day of flight recordings and again on the first day of recording post-flight. Some chronic effects were also suggested by the persistent differences between pre- and post-flight performances. The significance of these effects for the ability to perform motor tasks safely during flight and upon return to Earth cannot be determined at the present time. The present data suggest that a shift in the level of excitation of selected motor pools occurred when performing a given motor task, depending on whether the subject is or has been exposed to the space flight environment. The ability to maintain constant torque output during oscillatory movements could have been altered as a result of any one or a combination of adaptations in the sensorimotor system to space flight.

A differential effect of microgravity on perception of force during plantarflexion versus *dorsiflexion*

A fundamental assumption in the design and interpretation of the present experiments is that the generation of a force with the intent to match a requested or targeted force in the absence of continuous feedback reflects the perceived level of effort as

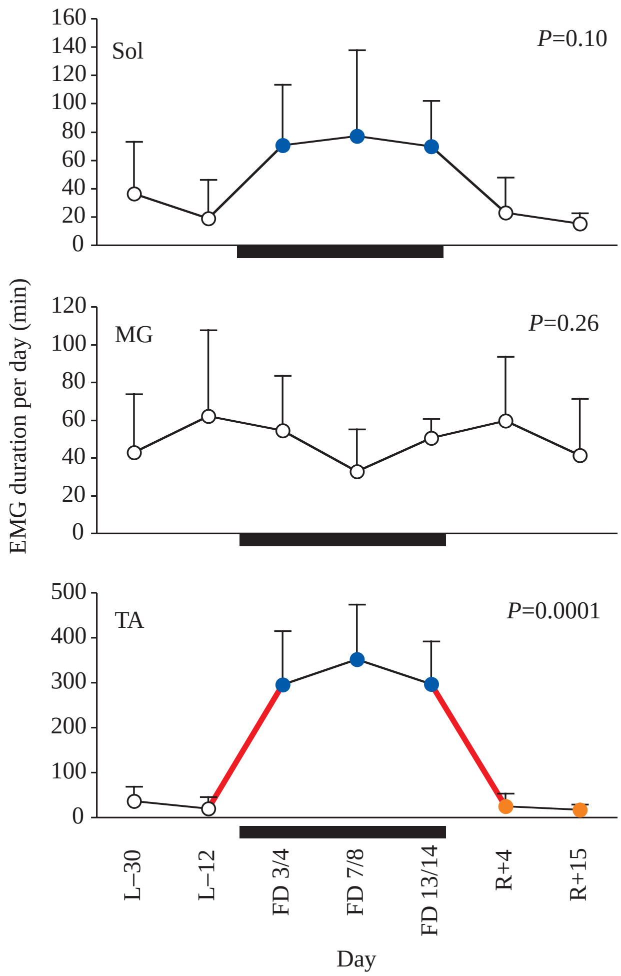

Fig. 6. The duration of electromyographic (EMG) activity (min) observed over the entire recording day for the same muscles as in Fig. 5. The *x*-axis is labeled as for Fig. 1. Values are means ± S.E.M.; *N*=4, except for F7/8 (*N*=3). Colored symbols and lines indicate significant differences as in Fig. 2. The duration of activity for the Sol in-flight was greater than pre-flight (P=0.03). No differences in the duration of the active EMG periods were observed for the MG. The in-flight TA EMG duration was greater than pre- or post-flight values on each test day (P=0.0001). The P levels for the ANOVA main effects are shown.

well as the ability of the muscular components to respond to a given motor command. The perceived levels of force generated are presumably a function of the ensemble of proprioceptive afferent feedback from the entire body, although the predominant input is probably derived more directly from the working joints and associated muscles and tendons (Jones, 1986). Assuming that no changes occurred in the muscular components over time, then the altered force output observed in the present study could reflect space-flight-induced changes in afferent input and its 'interpretation'. Although some decrement in the force potential, as measured from single muscle fibers, was reported for these subjects during this space flight mission (Widrick et al., 1999) and Narici et al. (Narici et al., 1997) found a reduced peak torque following electrical stimulation of the plantarflexors, the MVC torques that we measured during plantarflexion were unaffected (McCall et al., 1999). It does not appear that the present results can be explained by a change in the muscle output potential, given that the predominant changes observed in all the measurements taken occurred on the first flight day and on the day of return to Earth from flight. Further, it has been reported that muscle spindle activity is attenuated in microgravity in response to tonic vibration (Lackner and DiZio, 1992). These authors also suggested that microgravity results in reduced muscle co-activation and joint stiffness through modulation of muscle spindle activity *via* otolith, somatosensory and proprioceptive receptors. We suggest that the present results are attributable to alterations in the sensory information and/or the central processing of this information rather than to a change in the muscle output potential.

The EMG responses reflect several changes that seem to have been part of the neural strategy to adjust to the imposed gravitational environments. There was no evidence in the present study that activation levels shifted towards the faster motor pools, i.e. from the Sol to the MG, and away from the slower motor pools as was found in the rhesus monkey after approximately 2 weeks of space flight (Recktenwald et al., 1999; Roy et al., 1996). In the 50 % MVC plantarflexor tasks, the Sol EMG amplitudes were higher in- than pre- or post-flight. However, the level of activation of the TA was also elevated during some of the plantarflexion tasks during flight (Fig. 2). This, in itself, might be considered evidence of a persistent flexor bias during flight except that during dorsiflexion tasks there was also an elevated level of activation of the antagonist muscles, i.e. the Sol and MG. In general, it appears that the adaptive strategy to perform either the plantarflexor or dorsiflexor tasks during flight was to generate a stiffer ankle joint by increasing the level of co-activation of agonists and antagonists. Theoretically, the higher levels of contraction of a muscle could improve the ability to perceive joint position accurately (Gandevia and McCloskey, 1977a; Gandevia and McCloskey, 1977b; McCloskey et al., 1983; Gandevia, 1987).

Numerous approaches have been used to study the accuracy of the perception of muscular efforts (Gandevia and McCloskey, 1977a; Gandevia and McCloskey, 1977b; Cafarelli and Bigland-Ritchie, 1979; Cooper et al., 1979; Jones and Hunter, 1982). Subjects have been asked to estimate muscle output as a percentage of maximum while pushing isometrically or by way of a contralateral force-matching task (Gandevia and McCloskey, 1977a; Gandevia and McCloskey, 1977b; Cafarelli and Bigland-Ritchie, 1979; Jones and Hunter, 1982). Our approach differs from the above-mentioned studies in that the subjects were asked to maintain a constant and targeted level of torque output while the joint was oscillated passively over a 10 ° range of motion and the task was to match a torque perceived from the limb performing the task. Thus, to maintain a constant plantarflexor or dorsiflexor torque, the subject had to activate a muscle group in alternating concentric and eccentric contractions. It should be noted also that the torque output was maintained without continuous visual feedback of the actual torque output being generated. However, a brief cue on the computer screen for the appropriate torque was given for 2 s at the beginning of a series of sine-wave cycles. One might have predicted that the more complex task of maintaining a targeted torque while the limb position was oscillating and to maintain a constant torque regardless of whether the muscular effort was in an eccentric or concentric mode would have manifested a much greater impairment in the ability to exert a targeted torque as a result of space flight than was actually observed.

How does space flight on the shuttle change routine activity patterns in plantarflexors and dorsiflexors of the ankle?

One factor that might be expected to affect how the neuromuscular system adapts to a microgravity environment is how the environment alters the pattern of use of a muscle. In other words, to what extent are the adaptations a use-dependent phenomenon? From this perspective, a major limitation in understanding the mechanisms of adaptation of the neuromuscular system to space flight in any animal has been the dearth of information associated with how the microgravity, or more generally the space flight, environment affects the activity patterns of the neuromuscular system. For this reason, we studied the levels of activation of two muscles that serve as plantarflexors and one that serves as a dorsiflexor during routine activities on Earth and during flight. It is often assumed that space flight is a model of ‘disuse’ of muscles. The present results clearly demonstrate that this is not the case. When we unloaded the hindlimbs of rats for 4 weeks (Alford et al., 1987), the amount of EMG activity in the TA was elevated markedly, whereas the activity levels in the MG and Sol were reduced slightly, but these extensor muscles remained modestly active. Long-term recordings in the human subjects of the present study were similar to those observed in the hindlimbs of these chronically unloaded rats, particularly with respect to the TA.

We suggest that the elevated EMG activity in the TA is due, in part, to a lack of reciprocal inhibition that is routinely derived from the activation of extensors during weight bearing (DeLuca and Mambrito, 1987). It is also likely that some of the elevated activity in the TA can be attributed to the motor tasks performed routinely during flight, i.e. securing the body in a given position using foot loops. Activation of the dorsiflexors occurs routinely when the foot is placed in these loops. However, on the basis of both the total integrated EMG activity and the duration of all the periods when EMG activity was present, it would appear that the use of the loops cannot be the only explanation for the elevated activity in the TA.

It is also of interest that there was no reduction in the level of total daily activation of the MG or Sol during space flight and, in fact, Sol activity was higher during flight. Some of the EMG activity in these muscles must be attributed to the busy work schedule of each crew member during flight, during which there must be some alternating flexion and extension movements just to maintain the necessary body positions during spontaneous or programmed activities. It also is important to understand that numerous experiments on this particular flight involved extensive neuromuscular testing as well as participation in varying levels of daily exercise routines. From this perspective, the activation levels recorded cannot be attributed solely to the microgravity environment. The data more accurately reflect how the activation patterns of the neuromuscular system respond to a series of programmed motor tasks in a microgravity environment.

Concluding remarks

The ability to estimate and execute a requested ankle plantarflexor or dorsiflexor torque during a dynamic task was altered by space flight, which induced a flexor bias in routine, and perhaps in programmed motor tasks. These results show that, during routine daily activities in-flight, the dorsiflexors become hyperactive, whereas the plantarflexors maintain a normal or elevated level of activation. To understand better how animals adapt to microgravity, future studies need to carefully document detailed activity patterns of multiple motor pools controlling limb, trunk and head movements during flight compared with those occurring on Earth. Because of the large quantity of exercise performed during flight in the present study, a clear understanding of the true effects of microgravity cannot be gained and generalized to all studies of microgravity.

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