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RESEARCH ARTICLE

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Neuromuscular activation patterns during treadmill walking after space flight

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Abstract Astronauts adopt a variety of neuromuscular control strategies during space flight that are appropriate for locomoting in that unique environment, but are less than optimal upon return to Earth. We report here the first systematic investigation of potential adaptations in neuromuscular activity patterns associated with postflight locomotion. Astronaut-subjects were tasked with walking on a treadmill at 6.4 km/h while fixating a visual target 30 cm away from their eyes after space flights of 8–15 days. Surface electromyography was collected from selected lower limb muscles and normalized with regard to mean amplitude and temporal relation to heel strike. In general, high correlations (more than 0.80) were found between preflight and postflight activation waveforms for each muscle and each subject; however, relative activation amplitude around heel strike and toe off was changed as a result of flight. The level of muscle cocontraction and activation variability, and the relationship between the phasic characteristics of the ankle musculature in preparation for toe off also were altered by space flight. Subjects also reported oscillopsia during treadmill walking after flight. These findings indicate that, after space flight, the sensory-motor system can generate neuromuscular-activation strategies that permit treadmill walking, but subtle changes in lower-limb neuromuscular activation are present that may contribute to increased lower limb kinematic variability and oscillopsia also present during postflight walking.

Key words Electromyography · Adaptation · Space flight · Locomotion · Human

Introduction

Astronauts display remarkable flexibility in adapting themselves and their movements to the unique microgravity environment of space flight. Despite shifts in many physiological processes, crew members rapidly develop motor control strategies to perform tasks effectively in space. Moreover, astronauts must readapt quickly upon return to Earth in order to regain appropriate coordination strategies, particularly with regard to posture and locomotion.

Locomotor instability upon landing has been noted frequently in the US and Russian space programs (Chekirda et al. 1971, 1974; Reschke et al. 1993; McDonald et al. 1994). This instability has been manifested by: increased angular amplitude at the knee and ankle and increased vertical accelerations of the center of mass (Hernandez-Korwo et al. 1983); increased variability in lower-limb phase-plane portraits (McDonald et al. 1996); the tendency to fall to the outside when turning corners (Homick and Reschke 1977); and occasional loss of balance while locomoting (Reschke et al. 1993; P.V. McDonald, unpublished observation). Other postflight locomotion abnormalities have included unusually high impact forces at heel strike and inability to achieve proper foot clearance at toe off during postflight locomotion (C.A. Miller, unpublished observation). Although gait initiation and rhythmicity are within normal limits during postflight locomotion, many astronauts display "cautious gait" (Nutt et al. 1993), characterized by a wide base of support, short strides, long double-foot stance phase, and reduced leg and arm motion. This strategy, although it increases the dynamic stability of the body during locomotion, reduces walking speed and increases the number of steps needed to traverse a given distance. Despite the documented changes in postflight locomotor coordination strategy, the reasons for these changes have yet to be elucidated.

There are a number of physiological and neurological changes associated with space flight which could impact locomotion. Space flight has been associated with: de-

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creases in muscle strength and tone (Thorton and Rummel 1977; Kozlovskaya et al. 1981; Grigoryeva and Kozlovskaya 1987); hyperactivity in H- and stretch-reflex characteristics, increased vibrosensitivity of the soles of the feet (Kozlovskaya et al. 1981; C.S. Layne, unpublished data); changes in muscle strength-velocity profiles (Grigoryeva and Kozlovskaya 1987); and changes in proprioceptive and vestibular functioning (Kozlovskaya et al. 1981; Roll et al. 1993) and oscillopsia (Bloomberg et al. 1995). Associated with these changes are reductions in the ability to perform graded muscle contractions and decreases in muscle stiffness, particularly in the triceps surae (Grigoryeva and Kozlovskaya 1987). These neurological and physiological alterations could be expected to influence the precise neural control needed for the lower-limb muscle-activation patterns that are necessary for safe and effective locomotion.

Electromyography (EMG) has long been used to assess the neuromuscular control features associated with both normal and abnormal gait (Milner et al. 1971; Dubo et al. 1976; Winter 1984; Yang and Winter 1984a,b; Shiavi et al. 1987; Ounpuu and Winter 1989; Kameyama et al. 1990; Dickey and Winter 1992). The phasic properties of processed EMG are highly correlated with the changes in muscle tension and joint angular accelerations that occur throughout the gait cycle (Crosby 1978; Winter 1984), and a linear relationship exists between muscle tension and EMG amplitude in the range of tension levels found during normal walking (Komi 1973; de Jong and Freund 1967).

Muscle cocontraction is an important index of how effectively the sensory-motor system is able to control neuromuscular activation to regulate joint stiffness and produce effective segmental motion. Potential modifications in cocontraction after space flight can result in changes in stiffness, which may alter how the impact forces generated at heel strike are dissipated throughout the body during locomotion (M.A. LaFortune, M.J. Lake, E.M. Henning, unpublished work). At heel strike, the musculoskeletal system must effectively absorb the energy generated as the result of the sudden impact of the heel with the support medium while maintaining a kinematic strategy that ensures dynamic stability. During this "yielding" portion of the gait cycle, the hip joint angle is maintained in approximately 10° of flexion while the knee joint rapidly flexes and the ankle joint plantarflexes. This kinematic and associated neuromuscular strategy serves to keep the head, arm, and trunk segment (HAT) erect to within 1.5° and attenuates head shock during locomotion (Winter et al. 1993). This tight regulation of the HAT helps maintain the dynamic stability necessary to maintain a safe forward trajectory while contributing to stable gaze. Inefficient energy management during postflight locomotion, potentially stemming from changes in stiffness, may result in increased head motion, thereby increasing the possibility of gaze instability. The explicit link between possible changes in joint stiffness after space flight and effective segmental motion motivates an event-based analysis strategy. Heel strike introduces large amounts of energy, which must be effectively managed by the sensory-motor system. This management is achieved, in part, through precisely controlled neuromuscular activation. Therefore, in addition to evaluating neuromuscular activation patterns across the entire stride cycle, activation patterns around the behavioral events where the effective control of large energy transfers is critical to successful locomotion (heel strike and toe off) were further evaluated.

Functioning in microgravity results in crew members acquiring completely different motor control strategies than those used on Earth. Motor control strategies that efficiently transmit high-impact forces are not utilized in microgravity. However, upon landing, it is necessary to rapidly require motor strategies that effectively control high-impact forces, particular those generated during locomotion. The process of readaptation to unit gravity, combined with the above-mentioned changes in sensory-motor properties, suggests that neuromuscular activation patterns during treadmill walking may be modified after space flight.

Although much anecdotal information exists, this is the first full report of the influence of 8- to 15-day space flight on lower-limb neuromuscular activation during postflight treadmill walking. It was hypothesized that neuromuscular patterns after space flight would be modified relative to preflight patterns. These modification would take the form of changes in the timing of the phasic properties of muscle activation, increased variability of the activation patterns, and changes in the degree of muscle cocontraction, particularly around the events of heel strike and toe off. This investigation is a component of a larger study that was designed to assess possible decrements in head and gaze control during postflight locomotion.

Materials and methods

Subjects

Subjects in this study were ten astronauts (three women and seven men) who participated in Space Shuttle missions lasting 8–15 days. All provided informed consent to participate, as required by the Johnson Space Center Human Research Policy and Procedures Committee. Six of the subjects had flown previous Shuttle missions, and the remaining four were flying for the first time.

Procedures

Data were collected as subjects walked on a motorized treadmill (Quinton Series 90 Q55, Seattle, Washington) at 6.4 km/h while they fixated gaze on a small visual target centered 30 cm in front of their eyes. Subjects wore a safety harness that was suspended from an overhead metal frame and adjusted to accommodate each subject's height. The harness did not interfere with limb motion and provided no support unless the subject's trunk was displaced at least 15.24 cm downward (i.e., fall), which would activate a treadmill "stop" switch. However, none of our subjects "fell" during the testing. A "spotter" also was positioned next to the treadmill.

Subjects were outfitted with shorts, sleeveless shirts, athletic socks, and running shoes with electronic force sensors attached to

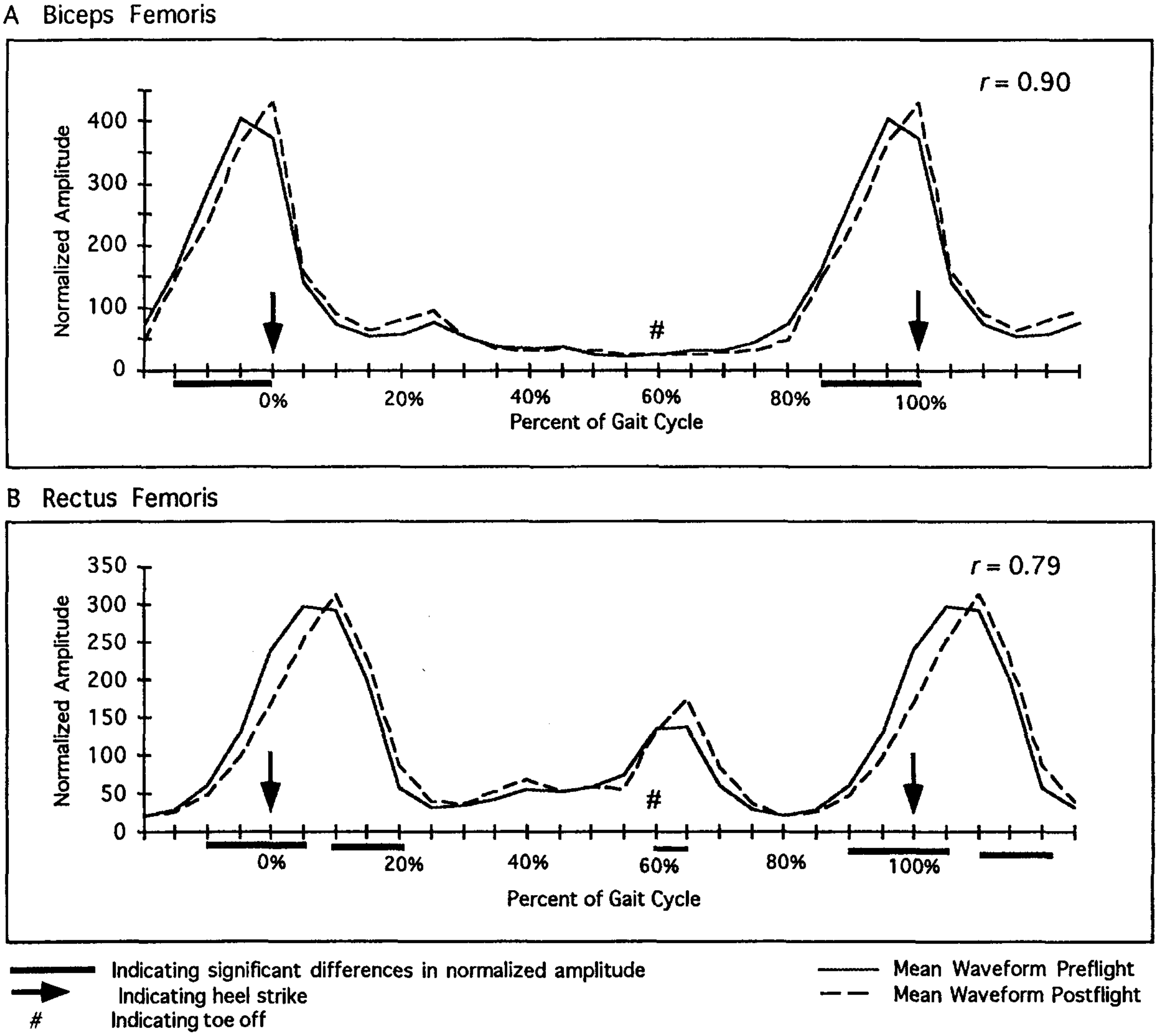


Fig. 1A, B Grand-ensemble mean preflight and postflight waveforms for biceps femoris (**A**), rectus femoris (**B**), gastrocnemius (**C**), and tibialis anterior (**D**) (*Thick lines below abscissa*, significant differences in normalized amplitude; *arrows*, heel strike; # toe off; *continuous line*, mean waveform preflight; *dashed line*, mean wave-form postflight

the heels and toes, so that times of heel strike and toe off could be determined. After the skin was cleaned with alcohol wipes, preamplifier surface EMG electrodes were placed bilaterally over the bellies of the rectus femoris (RF), biceps femoris (BF), tibialis anterior (TA), and gastrocnemius (GA) in parallel to the muscle fibers. The electrodes were attached with hypoallergenic tape and then covered with elastic leg wraps to prevent the electrodes from moving on the skin. The analog EMG data were bandpassed at 30–300 Hz before being digitized at 752 Hz. Foot-switch information, also sampled at 752 Hz, was stored within the EMG data files. Passive reflective markers were attached over various anatomical landmarks and the shoes. These markers were a component of a three-dimensional, video-based motion analysis system (Motion Analysis Corporation, Santa Rosa, California), used to obtain segmental kinematic measures. Separate manuscripts describe the influence of space flight on segmental kinematics (McDonald et al. 1996) and head and trunk coordination (J.J. Bloomberg, B.T. Peters, S.L. Smith, W.P. Huebner, M.F. Reschke, unpublished work).

After being prepared as described above, subjects straddled the treadmill until the designated treadmill speed (i.e., 6.4 km/h) was achieved, at which point they stepped onto the moving surface. Several strides were allowed until subjects became comfortable with the pace, and a 20-s data collection trial was begun on their verbal "ready." This task consisted of two explicit components, the first being to walk on the treadmill without falling, and the second to fixate a static visual target while doing so. After each trial, subjects were asked to draw the perceived motion of the target experienced during walking. Data were obtained twice before launch (at 30 days and 10 days) and four times after landing (once on landing day and again on the 2nd, 4th, and 8th days thereafter). Data analysis has focused on characterizing the influence of space flight on terrestrial locomotion as soon as possible after landing, early in the readaptation process. Thus, the data reported here compare the neuromuscular responses obtained 10 days before launch (the final data collection before launch) with those obtained between 2.5 and 4 h after landing. The time of data collection after landing could not be standardized exactly owing to individual Shuttle mission constraints which determined when the crew members arrived at the testing facility.

Data reduction

EMG data were reduced for each muscle, and for each subject, as follows. Data across stride cycles were first "time-normalized" to 100% of stride by averaging the data between consecutive right heel strikes. Next, to reduce variability among subjects, the waveforms were "magnitude-normalized" to the mean level of activation across the waveform, so that the mean level of activation

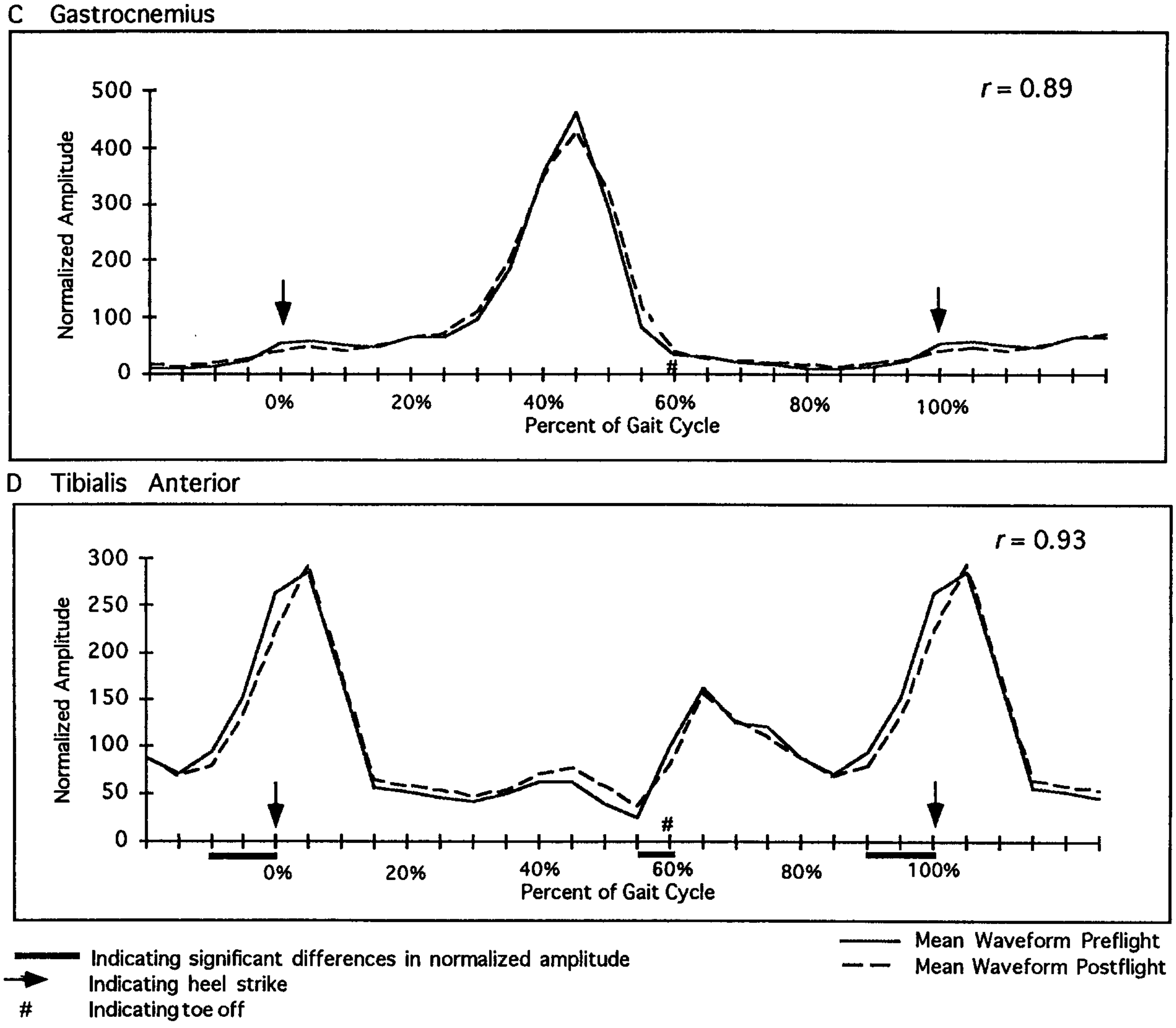


Fig. 1C, D

within the waveform was 100% (Winter and Yack 1987). The mean waveforms then were divided into 5% epochs by representing the averaged data within an epoch as a single point (Yang and Winter 1984a,b). Standard deviations and coefficients of variation across the mean waveforms also were calculated to assess activation variability. These reduction techniques produced EMG waveforms that represented the phasic features of each muscle across the stride cycle. These EMG waveforms will be referred to hereafter as "reduced waveforms."

Data analysis

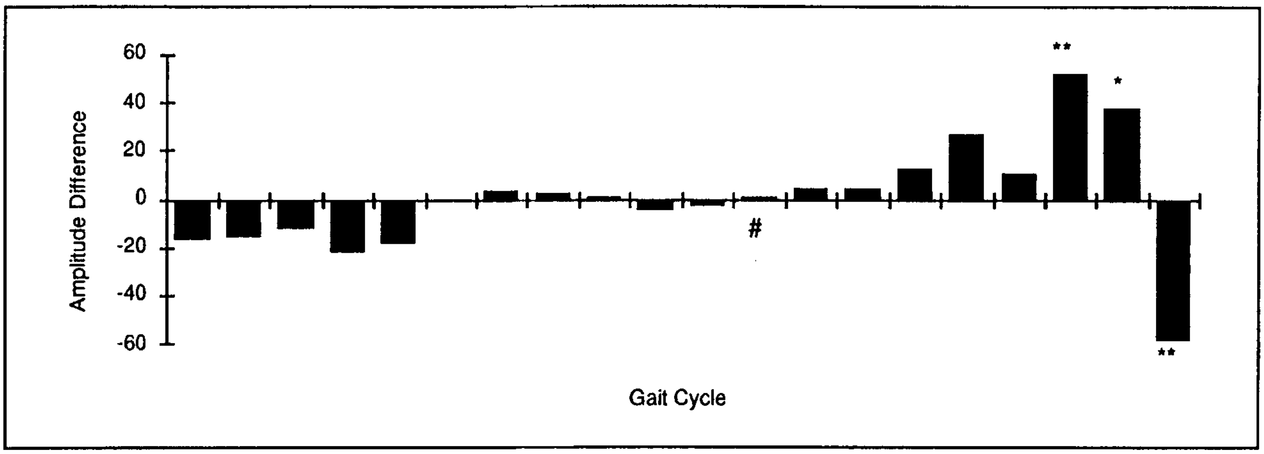
Stride time

The first step in data analysis was to determine whether space flight influenced stride time, i.e., heel strike to heel strike for the same leg, during this locomotion task. Thus, trials of 20–22 strides were averaged relative to heel strike so that preflight stride times could be compared with postflight stride times. Stride time is a function of time spent in swing and stance phases, both of which can be controlled by the locomoting subject. Thus, changes in the duty factor (the percentage of the gait cycle spent in the stance phase) could reflect changes in the neuromuscular activation patterns (Kadaba et al. 1985). Each subject's stride time and duty factor were calculated for each stride and compared before and after flight with t-tests for correlated data.

Electromyography

We addressed the question of how space flight affects the lower limb neuromuscular activation during treadmill locomotion in five ways. First, we compared reduced waveforms before and after flight using Pearson product-moment correlations for each muscle and each subject (Yang and Winter 1984a,b; Dickey and Winter 1992). This analytical approach was extended to determine the degree of activation symmetry between individual muscles of both legs before and after flight. Second, we used repeated-measures analysis of variance (ANOVA) in combination with post hoc testing to compare the preflight and postflight normalized amplitudes at each 5% epoch for each right lower-limb muscle. Third, we used full-wave rectified EMG records obtained from individual strides to characterize the phasic pattern of activation from the right lower-limb muscles. This approach was adopted to assess the potential for changes in the time of muscle activation within the time-normalized waveforms. Such changes within a stride cycle would indicate subtle, but potentially important, modifications in neural control. Fourth, we assessed potential preflight compared with postflight changes in coefficient of variation of the reduced EMG waveforms around the behavioral events of heel strike and toe off using repeated-measures ANOVA with post hoc testing. We chose to evaluate EMG variability around these behavioral events because they are associated with large segmental decelerations (heel strike) or accelerations (toe off) and therefore require precise neuromuscular control. Finally, we evaluated the degree of muscle

A Biceps Femoris



B Rectus Femoris

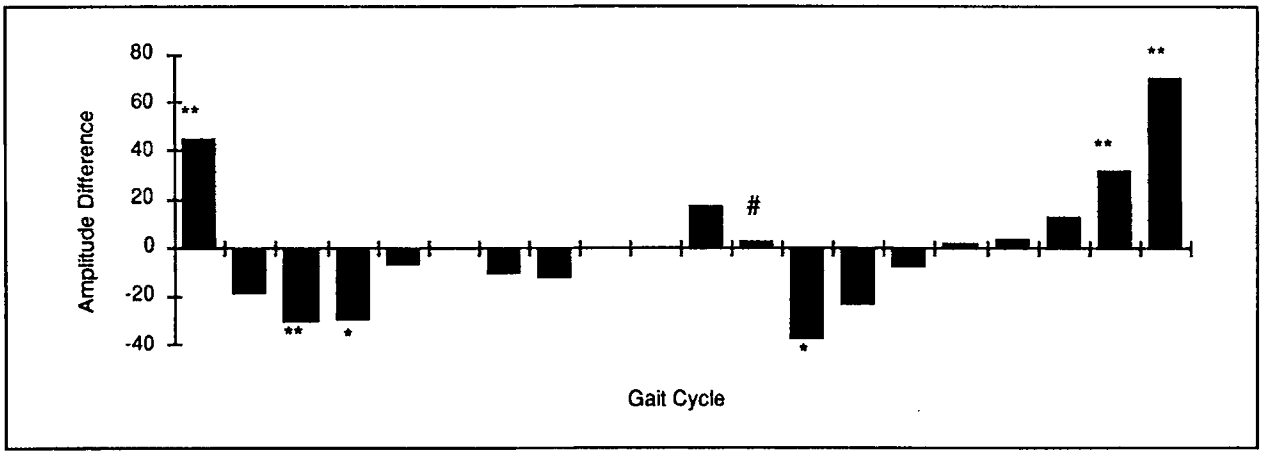


Fig. 2A, B Differences in relative amplitude between preflight and postflight grand-ensemble reduced waveforms at each 5% gait cycle epoch for the biceps femoris (**A**), rectus femoris (**B**), gastrocnemius (**C**), and tibialis anterior (**D**). Analysis epochs begin at heel strike, toe off occurs at #, *one asterisk* represents a significant statistical difference, and *two asterisks* represents a significant functional difference. See text for details

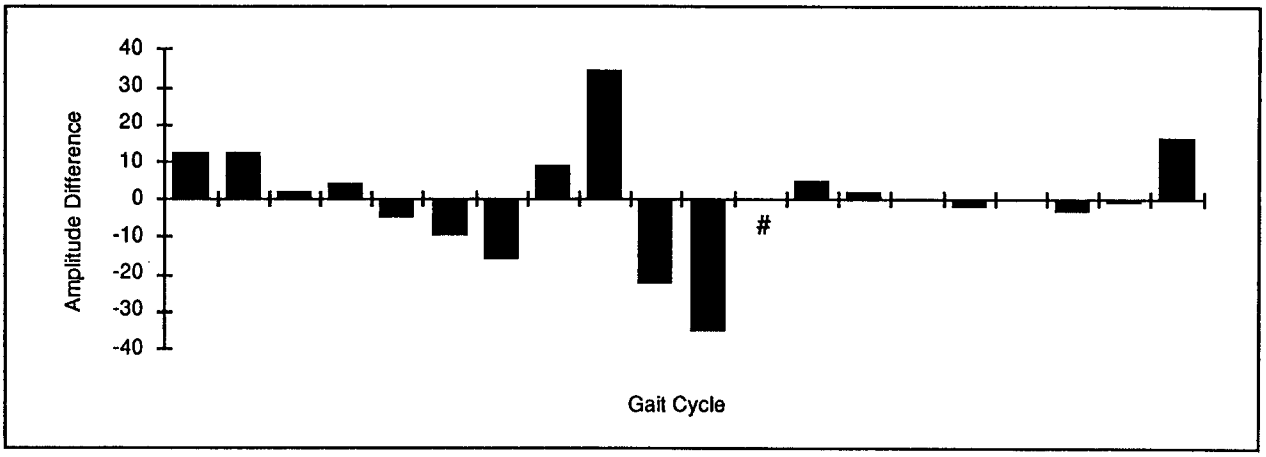
cocontraction between the traditional agonist-antagonist pairs of the BF-RF and TA-GA and evaluated potential preflight compared with postflight differences using repeated-measures ANOVAs with post hoc testing. An alpha level of $P<0.05$ was adopted for all statistical tests.

Although previous gait investigations have revealed greater variability in neuromuscular activation patterns than in limb kinematics, large changes in EMG activation characteristics have a functional effect as well (Dickey and Winter 1992). Following the convention of Ounpuu and Winter (1989), changes in relative amplitude were considered functionally significant if: (1) the difference was statistically significant at $P<0.05$; (2) the difference between the preflight and postflight measures was greater than the variability of each individual measure; and (3) the muscle was active (i.e., 20% of mean amplitude) during the analyzed epoch. Differences in preflight and postflight phasic patterns were considered functionally significant if the Pearson r value was less than or equal to 0.71 (Dickey and Winter 1992; Gabel and Brand 1994).

To evaluate the phasic activity of individual strides, we first determined what we considered to be the most significant neuromuscular control feature of each muscle during each stride, for each subject. For the RF, BF, and GA this feature was the temporal onset (relative to heel strike) and duration (as a percent of stride cycle) of the largest amplitude burst of activity (Fig. 1). For the RF and BF, the largest burst of activity occurred around heel strike. The largest burst of GA activity occurred in preparation for toe off. For the TA, the most significant neuromuscular control feature was the "silent period" present in most subjects shortly before toe off. This silent period usually corresponded to a large increase in GA activity. Thus, the temporal features of the TA silent period were thought to reflect the sensory-motor system's ability to regulate ankle musculature activity, particularly around the critical time of toe off.

The muscle-activation onset time was obtained by displaying the EMG activity of all strides simultaneously on the computer monitor. Visual inspection, in combination with interactive electronic cursors, was used to establish a computer algorithm's parameters for identification of the temporal onset of the phasic activity of interest in each stride. The algorithm was used to identify the first point of a burst that exceeded a fixed-amplitude threshold value (approximately 2 SDs above a quiet baseline) for at least 30 ms; that first point was considered the onset of muscle activation. The 30-ms minimum was selected on the basis of a report that muscle bursts that last less than 30 ms do not contribute to the force of the moving limbs during locomotion (Bogey et al. 1992). The algorithm was reversed to obtain muscle-activation offsets. Muscle-activation durations were obtained by calculating the temporal difference between the activation onset and offset. The duration of the silent period for the TA was the difference between the offset and subsequent onset of muscle activity. These temporal measures were expressed as a percentage of stride time in order to standardize the measures across data-collection sessions and sub-

C Gastrocnemius



D Tibialis Anterior

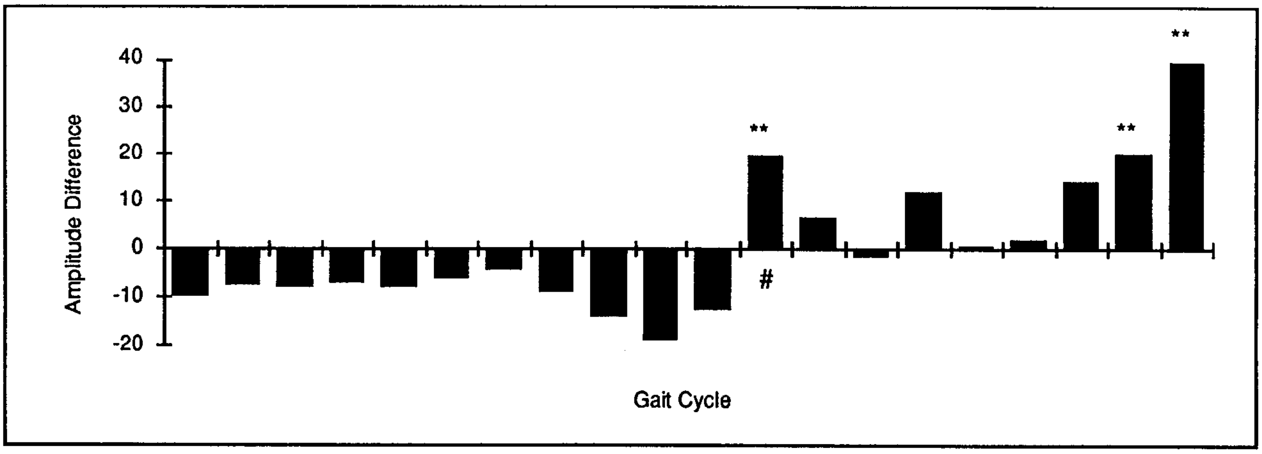


Fig. 2C, D

jects. The relationship between the ankle-joint muscle-activation characteristics in preparation for toe off was assessed by computing the temporal differences (as percentage of stride cycle) between GA offset and TA onset. Paired Student *t*-tests were used to test for preflight-to-postflight changes in the activation features of each muscle for each subject. Although this statistical approach limits generalizations to other populations, our primary intent in using these measures was to characterize the range of individual responses after space flight.

After space flight we felt it was plausible that the sensory-motor system may have had difficulty in controlling neuromuscular activation in preparation for the events of heel strike and/or toe off, as a result of these two events, or a combination of preparation for and reaction to heel strike and toe off. Therefore, we tested for preflight compared with postflight differences in the coefficient of variation during three epochs of the stride cycle: (1) the 10% preceding the event, (2) the 10% following the event, and (3) the combination of the previous two epochs (i.e., 20% of the stride cycle with the event centered in the middle of the epoch). Only muscles that were active during all three epochs around the particular event were evaluated for preflight and postflight differences.

We chose a measure of cocontraction that reflects the amount of neuromuscular activity common to antagonist pairs of muscles (Dietz et al 1994). Cocontraction values were obtained by initially summing the area under the curve of the reduced EMG waveforms and expressing the activity within each of the 20 epochs as a percentage of the summed area. These 20 epochs of the BF-RF and GA-TA antagonist pairs were evaluated and the lesser of the two values were used an indicator of cocontraction.

Results

Stride time

Neither stride time nor duty factor were affected by space flight. The group mean stride time before flight was 957.6 ms (SD 39.5), and the postflight mean was 959.1 (SD 38.2). The duty factor was 57.8% of stride cycle before flight (SD 2.2) and 58.6% (SD 1.3) afterward. Although postflight values were statistically different from preflight values for all but one subject, the magnitude of these changes were often small (1–2%). Discussions with the treadmill manufacturer indicated that treadmill belt speed could vary by up to 5% across data collection sessions. Because of this potential variation in treadmill speed, we chose to consider preflight versus postflight differences in stride time of less than 5% to be within the normal range of variation for this task. None

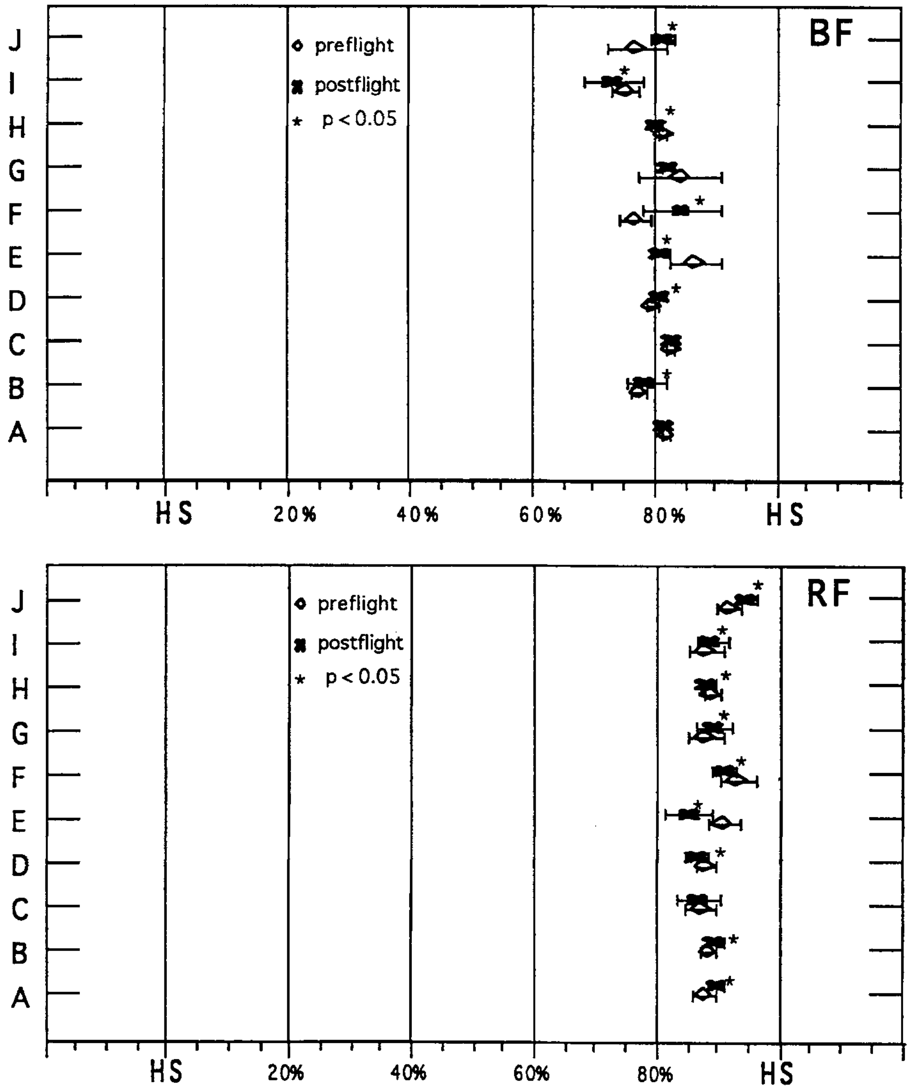


Fig. 3 Preflight versus postflight subject means (±1 SD) of biceps femoris (*BF*), rectus femoris (*RF*), and gastrocnemius (*GA*) muscle activation onsets and tibialis anterior (*TA*) offsets as a percentage of the gait cycle. Subjects are listed along the ordinate (*HS* time of heel strike)

of our subjects displayed differences approaching 5%, which indicates that subjects generally were able to reproduce the kinematic temporal features of the preflight stride cycle after flight.

Mean activation waveform correlation

In 70 of the 78 comparisons (90%), symmetry between the left and right lower limb muscle activation patterns (both before and after flight) exceeded a Pearson r value of 0.71 (Table 1). Thus, the lower-limb musculature was activated symmetrically, and this symmetry was not affected by space flight. Since there were no differences between the activation patterns of the muscles of the two lower limbs, the frequency distribution for pre and postflight activation pattern correlations were combined. Pearson r correlations between preflight and postflight muscle activation in the left and right lower limbs are summarized in Table 2. With few exceptions, preflight and postflight patterns of muscle activity were highly correlated, suggesting that the temporal features of lower-limb neuromuscular activation 2.5–4 h after landing are similar to preflight characteristics. The grand ensemble reduced-waveform patterns for each muscle before and after flight (Fig. 1) reveal few differences in the phasic characteristics of the waveforms. To make sure that our data-reduction technique did not produce artificially high correlations, correlations were assessed between the

Table 1 Frequency distribution of the right and left lower-limb muscle-activation correlation coefficients combined for pre- and postflight conditions (*BF* biceps femoris, *RF* rectus femoris, *GA* gastrocnemius, *TA* tibialis anterior)

	BF	RF	GA	TA	Total
1.00–0.91	11	10	16	12	49
0.90–0.81	6	3	1	4	14
0.80–0.71	2	2	3	2	9
0.70–0.61	0	1	0	1	2
0.60–0.51	0	0	0	0	0
0.50–0.00	1	2	0	1	4
Total no. of comparisons	20	18[a]	20	20	78

[a] Postflight RF data could not be obtained for two subjects

Fig. 3 continued

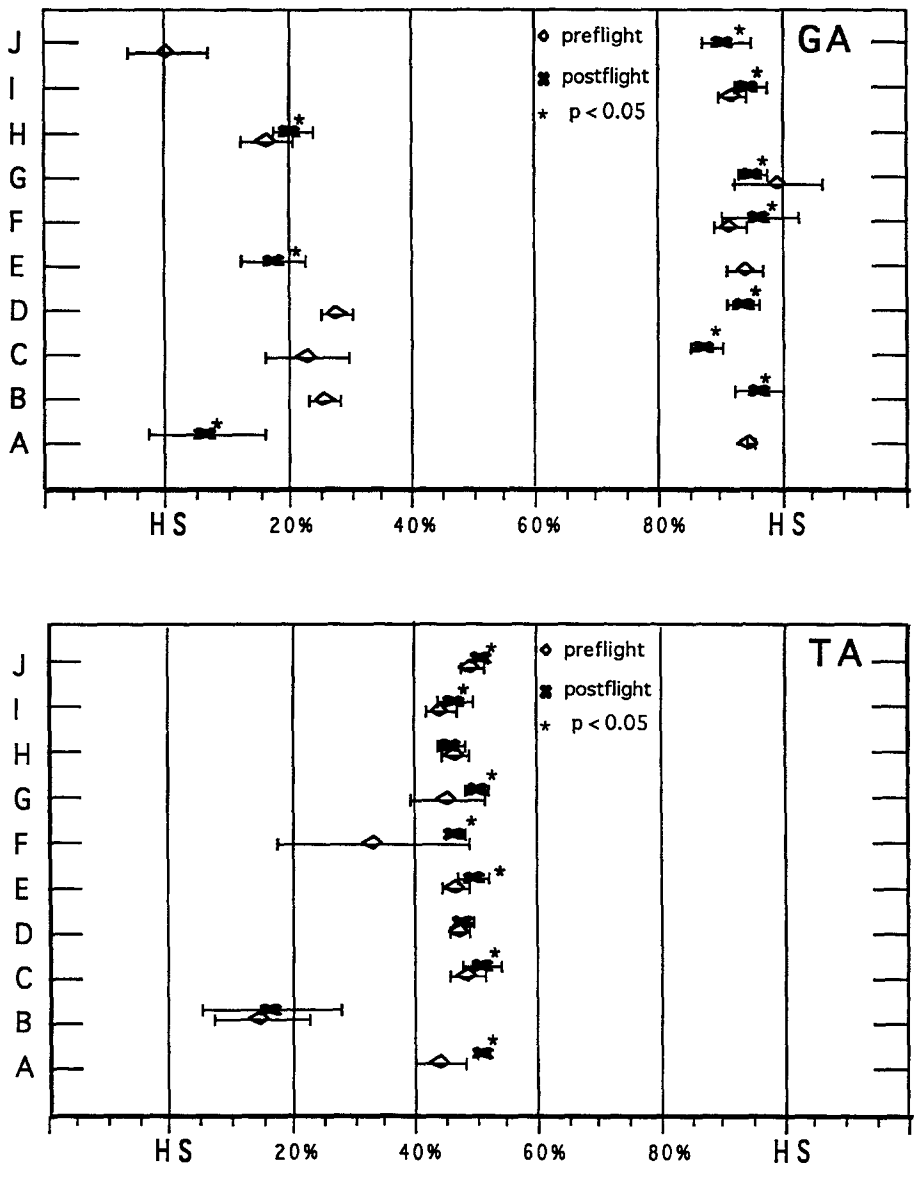


Table 2 Frequency distribution of the preflight-to-postflight muscle-activation correlation coefficients for the combination of the right and left lower limbs

	BF	RF	GA	TA	Totals
1.00–0.91	12	9	17	14	52
0.90–0.81	5	5	1	5	16
0.80–0.71	1	3	2	1	7
0.70–0.61	1	1	0	0	2
0.60–0.51	1	0	0	0	1
0.50–0.00	0	0	0	0	0
Total no. of comparisons	20	18[a]	20	20	78

[a] Postflight RF data could not be obtained for two subjects

mean waveforms developed from all of the digital samples contributing to those waveforms for three subjects. Correlations using all of the available data always revealed relationships as strong as or stronger than those found using the reduced waveforms.

Relative amplitude

Despite observing no change in the phasic features of the overall waveform, the analysis of the normalized mean amplitude of activation revealed significant functional differences before and after flight around toe off and heel strike (Fig. 2). Specifically, the RF, BF, and TA activation amplitudes were different around the heel strike, and RF and TA activations levels were different around toe off.

Single-stride activation

Muscle activation onset and duration (as percentage of stride) for the RF, BF, and GA; and the offset of activation and the duration of the TA silent period are presented in Figs. 3 and 4. Many of the preflight-to-postflight comparisons for individuals were statistically different,

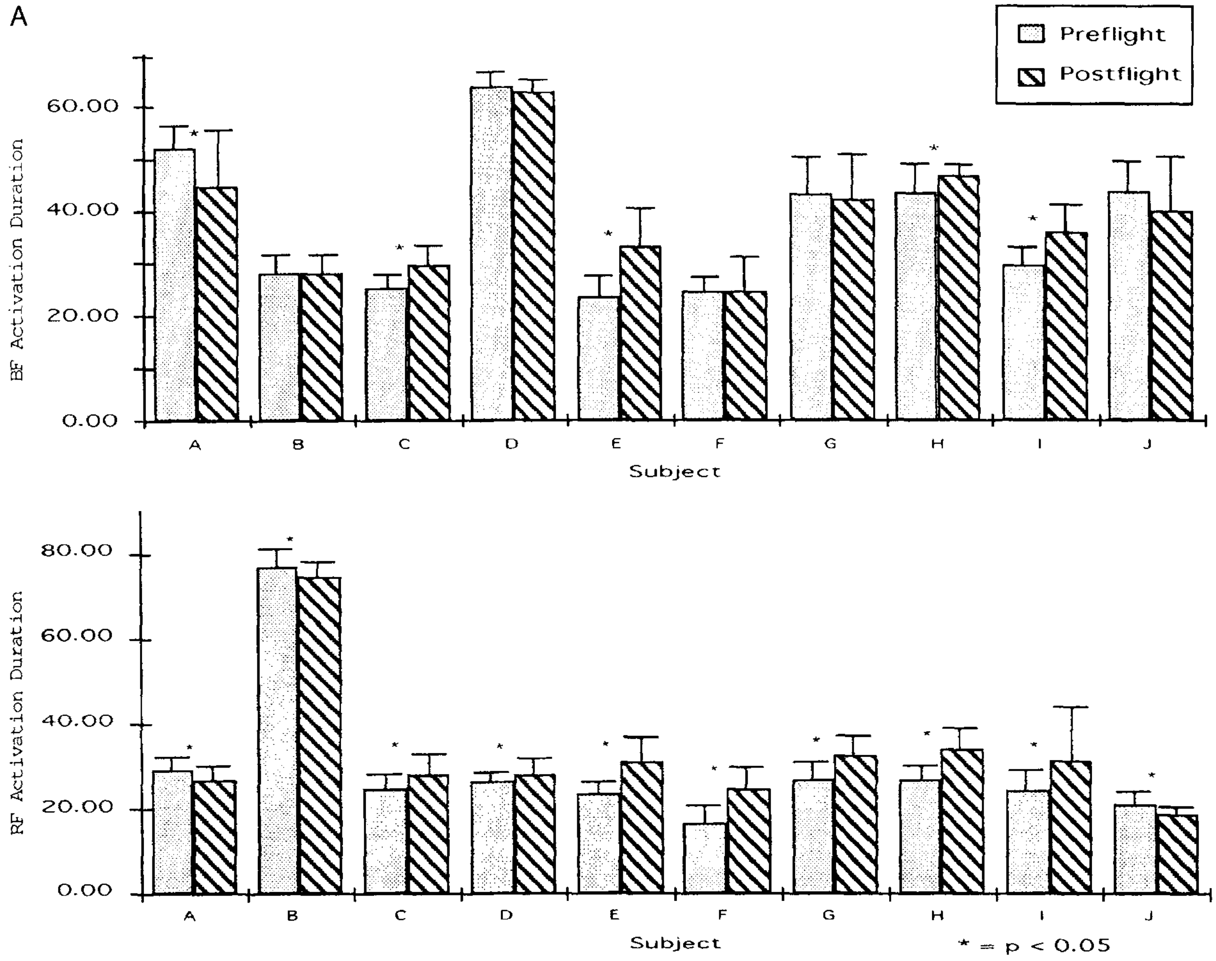


Fig. 4A Preflight versus postflight subject means (±1 SD) of the BF, RF, and GA muscle activation duration and the duration of the TA silent period

but again, the absolute differences were small. Figure 5 graphically represents the differences between GA activation offset and TA onset for the preflight and postflight sessions. All but two subjects showed changes in the postflight temporal relationship between the GA offset and the TA onset relative to preflight. For some subjects, the offset of the GA preceded the onset of the TA (i.e., the difference was negative), and for other subjects the reverse was true (i.e., the difference was positive). Moreover, the direction of the difference was changed after space flight for half of the subjects, indicating a complete reversal of the activation-deactivation sequence for the ankle musculature in preparation of toe off compared with the preflight sequence. The mean preflight-to-postflight difference in this temporal relationship was 7.1% of the stride cycle (approximately 67 ms based on mean stride time of 950 ms). Even accounting for the slight changes in stride cycle time between the preflight and postflight measures, the magnitude of this difference suggests that at least some subjects experienced considerable changes in the neuromuscular control of their ankle musculature in preparation for toe off.

Activation variability and cocontraction

Although there was a trend toward increased variability for all the active muscles around both heel strike and toe off, only the activation variability of the TA around toe off was significantly increased after space flight. After space flight the magnitude of cocontraction of the GA-TA muscles increased during the epochs immediately before toe off (i.e., at 45–55% of the stride cycle), but decreased just before heel strike (i.e., 95% of the stride cycle). Cocontraction of the BF-RF muscles increased in the two epochs immediately before heel strike (i.e., 90–100% of the stride cycle).

Discussion

In general, the overall phasic activation characteristics of the lower-limb muscles used in treadmill locomotion are only minimally affected by space flight. When analysis focused on muscle activation characteristics around heel strike and toe off, a variety of pre- and postflight differences were observed. These changes in neuromuscular activation associated with space flight are discussed below in relation to observed changes in head and lower-limb gait control strategies after space flight and the pos-

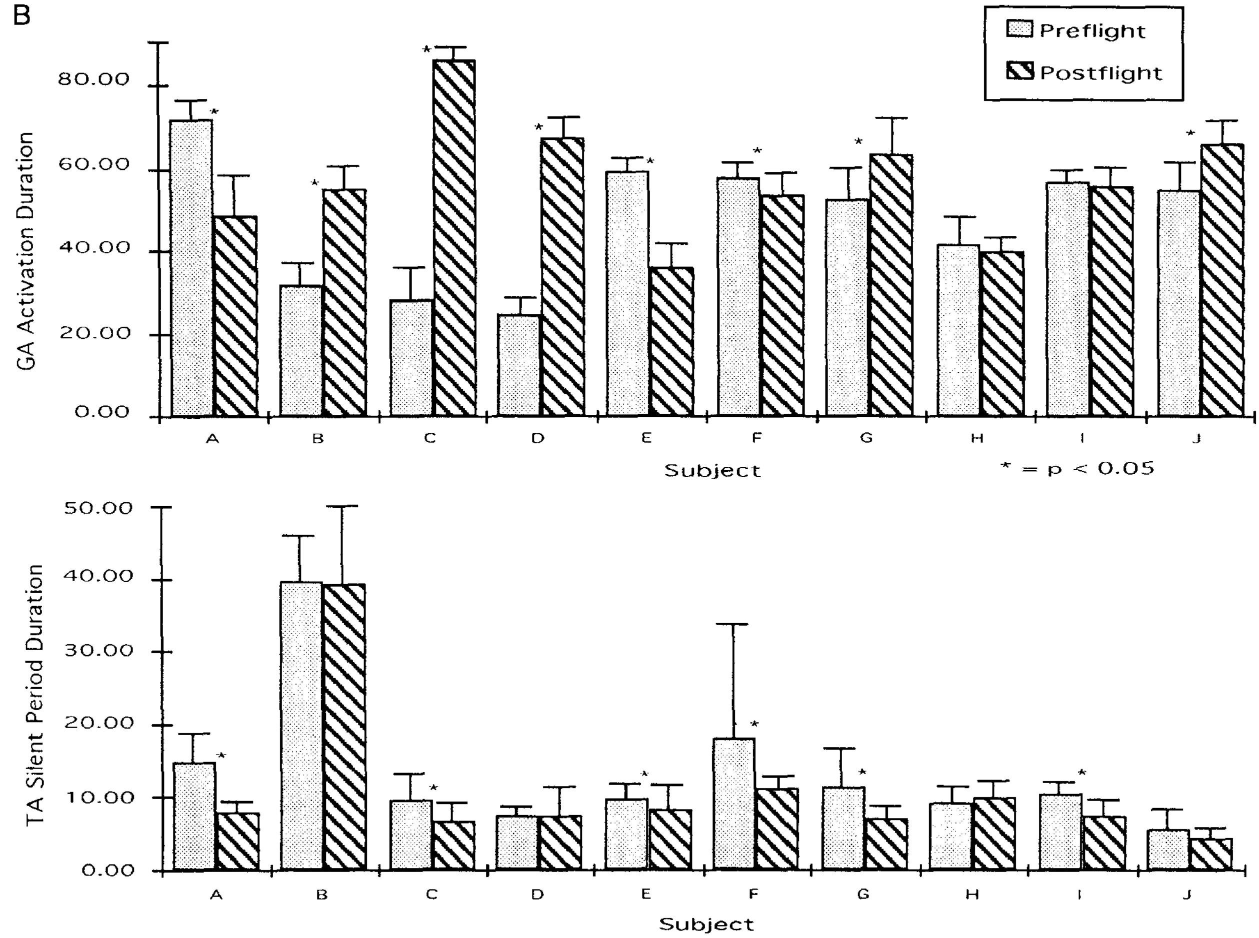


Fig. 4B

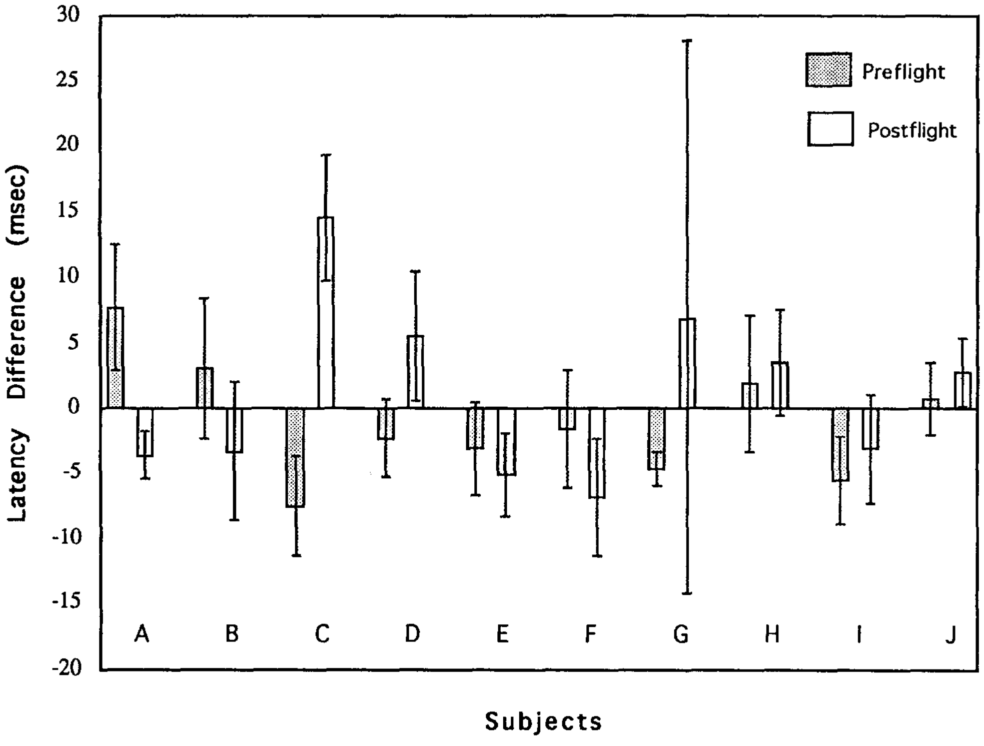


Fig. 5 Preflight versus postflight latency means (±1 1SD) differences for each subject between GA offset and TA onset. Negative values indicate that the offset of the GA preceded the onset of the TA

sible neurophysiological adaptations that contribute to these control strategies.

Pearson r correlations between muscle-activation patterns during treadmill walking before and after flight revealed that space flight had a minor impact on the overall phasic activation patterns. Dickey and Winter (1992) have recommended using an r^2 value of 0.50 (r=0.71) to indicate significant differences between muscle activation patterns. With this criterion, only 4 of the 78 single-limb muscle-activation patterns evaluated here were different before compared with after flight. Thus, the phasic characteristics of muscle activation during postflight treadmill walking were remarkably similar to preflight patterns. However, several subjects in this study had obvious postflight gait abnormalities as they entered the testing room, including widened support base, shuffling (cautious) gait, and reluctance to move their heads relative to their trunks. Interestingly, the magnitude of changes observed in the postflight activation patterns of these subjects during treadmill walking were indistinguishable from those subjects who exhibited no obvious gait abnormalities during overground locomotion. The lack of activation pattern difference was consistent with the minimal preflight-to-postflight difference in stride duration and duty factor. Evaluating single-stride phasic muscle activation characteristics as a percentage of stride duration for each subject, however, revealed many statistically significant differences between preflight and postflight locomotion. Although these changes indicate modifications in neuromuscular control strategies, these control strategies supported successful treadmill walking after space flight.

It is important to appreciate that our subjects were asked to walk on the treadmill while maintaining gaze. Thus, subjects were challenged to accommodate both criteria. Our subjects reported oscillopsia after flight, suggesting they may have exchanged clear vision for dynamic postural stability during postflight treadmill walking. This potential trade-off is not particularly surprising, given that the consequences of postural instability during this task (i.e., falling) are severe. Conversely, the consequences of unclear vision while tracking an earth-fixed target during our task were minimal with regard to safety.

The observed preflight-to-postflight neuromuscular activation stability also could reflect the task constraints inherent in walking on a motor-driven treadmill. Compared with normal overground locomotion there is minimal translation in the sagittal plane and lack of visual flow on the peripheral retina during treadmill walking. These constraints may serve to limit the variability in the lower-limb neuromuscular-activation patterns normally present in overground locomotion (Arsenault et al. 1986). Overground locomotion allows for much greater flexibility in the coordination pattern used to accomplish the task than that allowed during treadmill walking. The minimal requirement of upright treadmill walking is to coordinate body segments in a symmetrical manner that keeps the subject within a limited gait width (that of the treadmill) while keeping pace with the treadmill-belt movement. Deviations from this requirement can result in falling; moreover, the wide stance and shuffling gait used during overground locomotion after flight would be ineffective during our treadmill task.

Another potential reason for the similarity between preflight and postflight neuromuscular-activation patterns is the rapidity of readaptation after landing (Paloski et al. 1992). Many of the subjects in Paloski's study displayed clinical abnormalities in postural control 2.5 h after landing; these same subjects had improved substantially upon retesting 1 h later. Although we did not have the opportunity to retest our subjects on landing day, the magnitude of the observed effects were not related to when subjects were tested within the 2.5- to 4-h testing window. The present results substantiate numerous anecdotal reports that astronauts frequently have problems with postural control immediately following Shuttle landing, but that they adapt quickly thereafter.

Neuromuscular control during heel strike and toe off

One discrete event in the gait cycle that requires precise neuromuscular control is toe off. This fine motor skill is achieved by rapid exchanges between a large plantar flexor moment (GA activation and TA inhibition) late in the stance to a large dorsiflexor moment (TA activation and GA inhibition) at toe off. In our study, eight of ten subjects displayed a significant change in the relationship between the offset of the GA and the subsequent onset of the TA after flight relative to before. Moreover, the relative amplitude of the TA at toe off was reduced after flight relative to before, and GA-TA cocontraction magnitude was increased just prior to toe off, further supporting the idea that the precise neuromuscular control necessary to achieve proper toe clearance is compromised after space flight. These subtle changes could well explain the excessive foot-scraping on the treadmill noted during postflight testing and is consistent with the shuffling gait often noted during overground locomotion after flight.

Although the excessive foot-scraping observed in our subjects may be a maladaptive strategy that results from the inability of the sensory-motor system to efficiently activate the ankle musculature, it may also represent an exploratory behavioral mode designed to increase proprioceptive and cutaneous feedback. Pozzo et al. (1991) have suggested that patients with bilateral vestibular deficits, whose shoes displayed excessive wear on the soles, may have used such a strategy. Since proprioception is altered as a result of space flight (Kozlovskaya et al. 1981), it is plausible our subjects were scraping their feet along the treadmill belt in order to obtain increased feedback; however, the cost of this strategy is to increase the possibility of tripping during postflight locomotion.

The observed postflight differences in the relative EMG amplitudes of the RF, BF, and TA relative to preflight values and increased BF-RF cocontraction around heel strike indicates some disruption in the neuromuscular control needed to ensure optimal control around heel strike. This finding is consistent with those of McDonald et al. (1996), who reported increased kinematic variability in the lower limb around heel strike during treadmill walking after space flight. Bloomberg et al. (1994, 1995) also reported the presence of modified head control strategies after flight that may not be as effective as preflight strategies in stabilizing gaze. The presence of these strategies could indicate that the energy introduced into the system at heel strike and transmitted to the head may not be attenuated as effectively after space flight as before. Reductions in energy attenuation arising from potential changes in body segment stiffness could exacerbate oscillopsia during postflight locomotion. Subjects in this study consistently reported that the static target they were asked to visually fixate on during the locomotion task seemed to move more after flight than it did before.

As mentioned previously, several neurophysiological changes associated with space flight could be responsible for disruptions in lower-limb neuromuscular control occurring around toe off and heel strike. Crew members flying aboard the Space Shuttle experience a change in the strength ratio between the ankle plantar flexors and dorsiflexors. The plantar flexors lose significant strength while the dorsiflexors actually increase strength (Hayes et al. 1992). This change in relative strength is thought to result from the crew member's use of foot loops to maintain their orientation relative to their various work stations. The foot loops are designed such that dorsiflexor activation is primarily required to maintain the proper orientation in contrast to plantarflexor activation, which is generally used to maintain the upright position on Earth. Thus, the increase in the dorsiflexor strength and decrease in plantar flexor strength after space flight is not unexpected. These neurophysiological changes probably contributed to the inability of subjects in our study to achieve optimal transitions between the plantar and dorsiflexor muscle moments required around toe off, resulting in foot-scraping on the treadmill after flight.

Another explanation for why our subjects may have had difficulty in controlling the ankle joint musculature was alluded to above. During space flight, the dorsiflexors assume a larger role than on Earth in regulating the orientation of the individual relative to the environment. Roll et al. (1993) have suggested that these in-flight adaptations in the respective roles of the ankle musculature eventually results in the reinterpretation of ankle proprioceptive input. With increasing mission duration, ankle proprioception is no longer interpreted as coding anterior-posterior body sway while upright, but as coding either whole-body axial transportation (i.e., pushing off the support surface) or foot movement exclusively (Roll et al. 1993). Although the adaptive ankle musculature control strategy and associated sensory input reinterpretations are appropriate in weightlessness, they are maladaptive upon return to the terrestrial environment. It is quite possible that, during testing on landing day, these maladaptive ankle control strategies contribute to the disordered EMG activation characteristics observed in this study.

Although the cautious gait shown when subjects entered the testing room after flight undoubtedly reflects the effects of sensory-motor adaptations, these subjects could and did organize effective neuromuscular-activation strategies that allowed them to complete the task of treadmill walking. Nonetheless, subtle alterations were present both in temporal activation features and in relative activation levels of several muscles after space flight. These changes were particularly prominent around the important behavioral events of heel strike and toe off. Thus, although the sensory-motor system can develop and execute functional behavioral strategies effectively during the goal-directed task of treadmill walking, the changes in the neuromuscular activation characteristics observed during the task probably contribute to the difficulty in overground locomotion after landing. Efforts are underway at Johnson Space Center to characterize more precisely the influence of space flight on overground locomotion.

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