ALTERATIONS IN HUMAN NEUROMUSCULAR ACTIVATION DURING OVERGROUND LOCOMOTION AFTER LONG-DURATION SPACEFLIGHT

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Layne, C.S., A.P. Mulavara, P.V. McDonald, C.J. Pruett, I.B. Kozlovskaya, and J.J. Bloomberg. Alterations in human neuromuscular activation during overground locomotion after long-duration spaceflight. *J. Grav. Physiol. 11(3):1-16, 2004.* – Spaceflight impacts humans in numerous ways, including compromised postflight locomotor control. In this first systematic evaluation of the impact of long-duration spaceflight on neuromuscular locomotor control, we examined the electromyographic (EMG) activity of four lower limb muscles during overground walking before and after spaceflight aboard the Mir space station. Six subjects traversed a walkway at three different speeds while surface EMG was collected from the medial gastrocnemius, tibialis anterior, biceps femoris and rectus femoris. Several measures obtained from individual subject average gait cycle EMG waveforms were used to identify potential preflight versus postflight modifications in neuromuscular activation. Although subjects were able to adequately reproduce their preflight cadence metrics after flight, they generally displayed significant alterations in the spatial and temporal features of muscle activation and increased with-in day activation variability. An "adaptability index" measure revealed that modifications in activation characteristics associated with changing cadence were significantly modified by spaceflight. These findings indicate that neuromuscular activation during overground locomotion is modified by long-duration spaceflight. It is likely that the inability to reproduce preflight patterns of muscle activation contributes to the previously reported gait and postural control problems experienced by astronauts returning from spaceflight.

Key words: EMG, Muscle, Walking, Proprioception, Adaptation

INTRODUCTION

Humans adapt remarkably well to the opportunities and constraints imposed upon them when living and working in the weightlessness of space. Almost immediately after entering space, humans develop motor control strategies that allow for effective functional behavior and these behaviors are continually refined throughout the flight. However, upon return to Earth, the adapted motor strategies used during flight are often ineffective for accomplishing goal-directed terrestrial behavior. Additionally, returning astronauts experience many physiological changes such as altered vestibular and proprioceptive functioning and muscle atrophy. These changes contribute to decrements in motor control of crewmembers returning to Earth. Of particular interest are the decrements in postflight locomotor control that could jeopardize crew health and safety either during an emergency egress from the landing craft, or during activities of daily living within the first month after flight. Documented locomotor problems after short-duration spaceflight include the adoption of a wide base of support, increased vertical projections of the center of mass (17), increased variability in ankle and knee joint motion (6, 28) and alterations in head-trunk control (5).

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There are numerous sensorimotor changes resulting from spaceflight that contribute to postflight locomotor difficulties. Postflight alterations in vestibular information processing contribute to loss of preflight levels of head control and associated oscillopsia during locomotion (5). Loss of muscle strength and tone, (see 12 for a review), changes in spinal circuitry function suggested by altered H, otolith-spinal and stretch reflex characteristics (16, 35, 38) and modifications in proprioceptive functioning (20, 37) all converge to contribue to the inability of returning astronauts to develop the precise neuromuscular control necessary to generate safe and efficient locomotor patterns.

Surface EMG has often been used to assess muscle activation patterns during both normal and abnormal locomotion (18, 22, 23, 26, 32, 34, 40, 41). The development of muscle tension and the resulting joint angular accelerations developed throughout the gait cycle are positively correlated with EMG activation waveforms (19, 40). Thus, analysis of EMG activation waveforms is an effective method to identify subtle changes in neuromuscular activation following spaceflight and may provide insights into underlying physiological processes associated with modified activation features (32). Measures of muscle co-contraction have also been used to assess the cooperative effects of segmental joint muscle pairs in regulating stiffness around a particular joint (9). Modifications in muscle physiological functioning and loss of strength associated with spaceflight can be expected to alter muscle co-contraction parameters.

Decrements in postflight locomotor control following short-duration Shuttle flights of 9-16 days have previously been reported (5, 22, 28). Earlier reports by our group have focused on postflight locomotor control deficits observed during motorized treadmill locomotion. In contrast to treadmill locomotion, overground locomotion presents a different set of task parameters that the motor control system must respond to in order to successfully accomplish the task. To our knowledge, Chekirda et al.'s 1971 report is the only published comparision between pre- and postflight human lower limb EMG waveforms obtained during overground locomotion (6). In this report we focus on modifications in postflight overground locomotion EMG activity associated with varying cadences after long-duration spaceflight (3-6 months in flight). In addition to documenting the modifications in neuromuscular patterning resulting from extended stays in weightlessness, we explored how changes in muscle activation patterns were associated with the stepping cadence of the astronauts. Using an adaptation index, we assessed how long-duration flight affects activation patterns that are associated with disruption of the normal mechanics of stepping during different walking speeds.

METHODS

Subjects

Six male astronauts who flew aboard the Russian Mir space station for 3-6 months participated as subjects in this investigation. Their mean age was 43.3 (SD - 6.7) years and all had previous spaceflight experience. Each subject provided informed consent, as required by the NASA Johnson Space Center Committee for the Protection of Human Subjects.

Data collection

The following collection procedures were employed approximately 10 days prior to flight and one day after flight (R+1). The subjects entered the testing room and donned sleeveless shirts, shorts, athletic socks and running shoes. After the skin was cleansed with alcohol wipes, preamplifier surface electrodes where placed over the bellies of the right biceps (BF) femoris, rectus femoris (RF), tibialis anterior (TA), and medial gastrocnemius (GA). Exact electrode placement during pre- and postflight testing was assured by using a cloth measuring tape and bony anatomical landmarks as reference points. The electrodes were secured with two-sided tape and elastic leg wraps were used to prevent electrode movement across the skin. The running shoes were instrumented with electronic foot switches so that the events of heel-strike and toe-off could be determined.

During the preflight data collection, subjects traversed a wooden walkway three times at a self-selected, comfortable walking cadence. The walkway was 8.5 x 2 meters. The subjects' "preferred" cadences were determined by averaging the data obtained from the three baseline trials. The preferred cadence was used to calculate a "slow" cadence that was 80% of the preferred cadence and a "fast" cadence that was 120% of the preferred cadence. Footswitch and EMG data were then collected as the subjects completed four trials for each of the three cadence conditions. During data collection, each trial consisted of 3-4 strides, depending upon the subjects' stride length and cadence. These procedures resulted in data being obtained for a total of 12-16 strides for each cadence. It has been reported that as few as three strides can accurately reflect an individual's normal EMG activation profile for a given muscle (3), therefore we are confident that a representative sample of each subject's neuromuscular activation profile, for a given day, was obtained. The data collected during this preflight session was considered the subject's "normal" performance and was used as a comparison standard for the postflight data. A metronome was used during data collection to assist the subjects in maintaining the proper cadence for a given condition. Within a given cadence condition, the metronome was set at the same frequency during both pre- and postflight testing. This constraint enabled us to better ensure that the subjects produced similar cadences during pre- and postflight testing. It was expected that the use of the metronome assisted the subjects in maintaining the expected cadence. This may have reduced the amount of variability observed in the EMG waveforms (29). However, it was important to control for possible variations in cadence between the pre- and postflight testing. Different cadences are associated with different EMG patterns (33), therefore if pre- and postflight cadence had not been controlled for, comparisions between pre- and postflight EMG waveforms would have been problematic. Due to safety concerns, the order of cadence conditions was always preferred, slow and then fast, during both pre- and postflight testing. Raw data from the footswitches and electrodes (bandpassed 30-300 Hz) were collected at 1000 Hz and stored on a desktop personal computer.

Data reduction

To determine the average stride time within a given cadence condition, footswitch signals from each condition, for each subject, were averaged over consecutive right heel-strikes. The duty cycle for each subject and condition was also calculated using the footswitch signals. Duty cycle is the percentage of the gait cycle spent in the stance phase and provides a basic gait kinematic coordination measure (28).

The following procedures were applied to the pre- and postflight EMG signals obtained for each muscle of each subject. The muscle activation waveforms were full-wave rectified and then averaged using consecutive right heel-strikes as synchronization points. The data were then amplitude normalized by dividing each data point in the averaged waveform by the peak voltage obtained during the three cadence conditions for the pre- and postflight data collection sessions, respectively (42). This procedure enabled comparisons of relative amplitude activation between the pre- and postflight activation waveforms. Concerns regarding acute muscle injuries either prior to flight or immediately upon return to Earth, prevented the collection of EMG associated with maximal voluntary effort contractions. Thus, amplitude normalization to the EMG associated with a maximum voluntary effort was not possible. However, our comparisons of relative amplitude enabled us to determine if the postflight neuromuscular activation across the gait cycle was relatively similar to that observed preflight. Differences in relative activation suggest modifications in underlying activation processes during pre- and postflight locomotion. To facilitate quantitative analysis, the averaged, normalized waveforms were then reduced to 50 epochs, with each epoch representing 10-15 ms of data, depending upon a given subject's cadence (8, 40). This time-normalization procedure facilitated both intra- and intersubject comparisons within and across data collection sessions.

Data analysis

For each muscle, of each subject, Pearson product-moment correlations were calculated for the preflight versus postflight waveforms. This procedure allowed us to evaluate the similarity of the phasic features between the two waveforms (8, 7, 18, 43). Pre- versus postflight waveform comparisons with Pearson r values less than or equal to 0.71 were considered to have activation features that were functionally different. The Pearson r of 0.71 has been used by several authors as a threshold that suggests enough dissimilarity between waveforms that these differences contribute to kinematic (i.e. functional) differences in the two performances (7, 8, 13). The coefficient of multiple correlation (CMC), which has been used to assess the similarity between waveforms collected within a single collection session was also calculated to gain additional information regarding the similarity of the pre- and postflight waveforms. Differences in within-day waveform variability would suggest pre- to postflight differences in neuromuscular activation characteristics. Kadaba et al. (18) provide a detailed description of the calculation of the CMC. Values closer to 1 represent less stride-to-stride variability than values closer to 0. Another measure of activation variability, the coefficient of variation (CV), was also calculated across each of the waveforms. The calculation of the CV followed the convention of Winter (40) in that it was equal to the root mean square standard deviation over the stride period divided by the mean ensemble average over the entire stride.

Several additional measures designed to represent neuromuscular activation features and relationships between muscles were obtained. The sum of the relative amplitude across the waveform for each muscle and condition, for each subject, was computed. Cross-correlations and co-contraction measures between the antagonist muscle pairs at the shank (TA-GA) and thigh (BF-RF) were computed to assess whether spaceflight affected the activation relationship between the muscle pairs. To evaluate the magnitude of change in activation amplitude as subjects changed cadence, an "adaptability index" (AI) (23) was calculated for each data epoch using the following equations for the slow to preferred cadence (AIs) and preferred to fast cadence (AIf), respectively:

$$\mathrm{AI\,s} = \left(\frac{\text{Slow - Preferred}}{\text{Preferred}}\right) * 100$$

$$\mathrm{AIf} = \left(\frac{\text{Preferred - Fast}}{\text{Fast}}\right) * 100$$

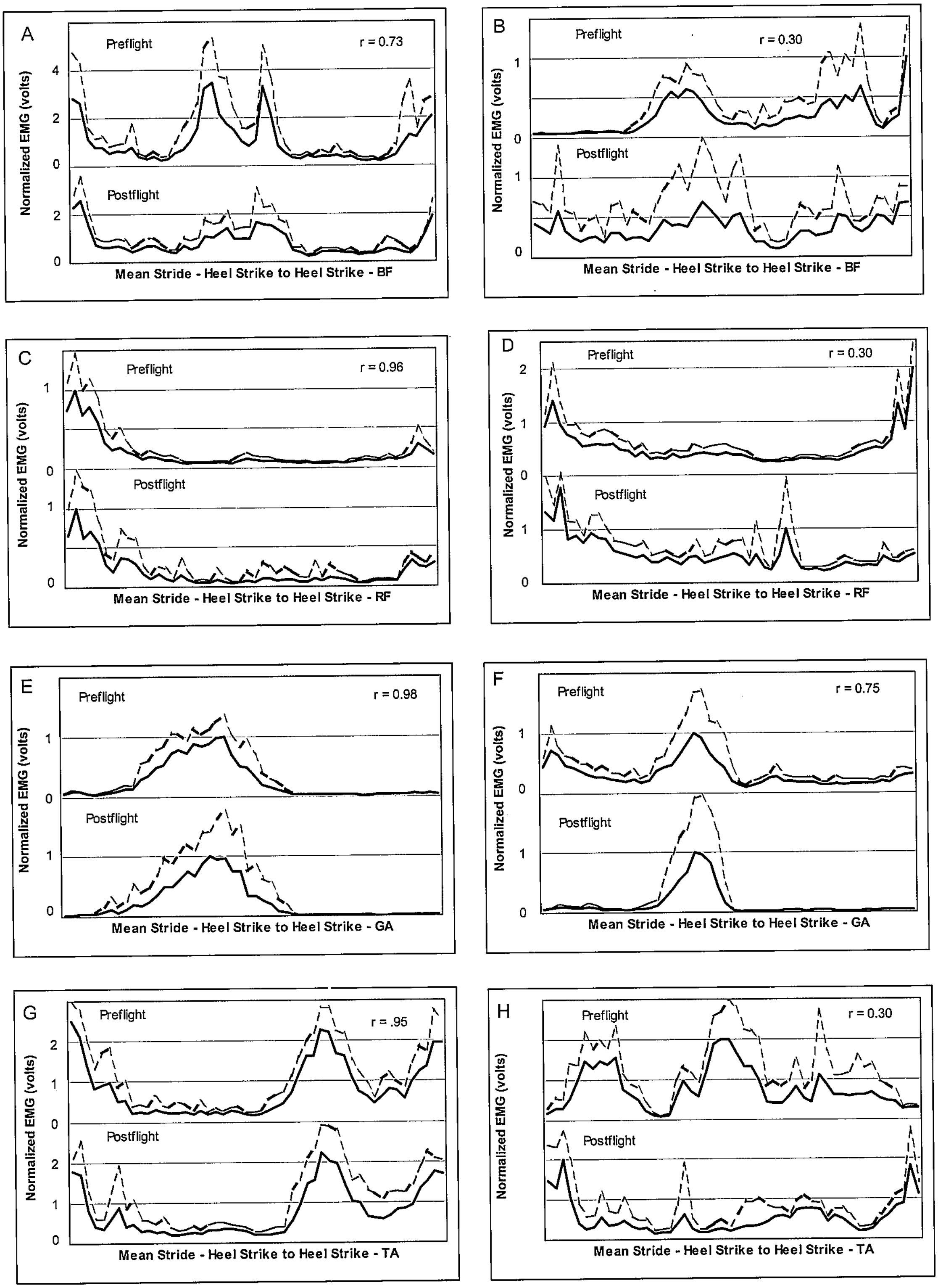


Figure 1. Single subject rectified and reduced pre- and postflight EMG averaged waveforms (+ 1 standard deviation) representing a high degree of phasic similarity (A, C, E, G) and a low degree of phasic similarity (B, D, F, H). Each waveform represents the average activation from right heel-strike to right heel-strike. The top panel of each graph displays the muscle's activation waveform and its associated variability obtained during preflight overground locomotion and the bottom panel represents that muscle's waveform obtained after spaceflight. The correlation coefficient value represents the relationship between the two displayed waveforms.

Table 1. Correlation coefficients representing the degree of similarity between pre- and postflight activation waveforms for each subject and muscle, within cadences. #Data from Subject C in the slow cadence condition were not obtained due to technical reasons.

	BF	RF	TA	GA
Subject A				
Slow	0.53	-0.04	0.84	0.91
Preferred	0.18	0.13	0.70	0.90
Fast	0.67	0.57	0.76	0.87
Subject B	BF	RF	TA	GA
Slow	0.67	0.92	0.88	0.96
Preferred	0.66	0.96	0.75	0.96
Fast	0.75	0.94	0.90	0.98
Subject C	BF	RF	TA	GA
Slow	-	-	-	-
Preferred	0.77	0.77	0.92	0.91
Fast	0.65	0.72	0.81	0.89
Subject D	BF	RF	TA	GA
Slow	0.73	0.33	0.92	0.91
Preferred	0.70	0.56	0.95	0.96
Fast	0.48	0.83	0.87	0.94
Subject E	BF	RF	TA	GA
Slow	0.44	0.78	0.86	0.68
Preferred	0.81	0.80	0.72	0.52
Fast	0.75	0.89	0.76	0.75
Subject F	BF	RF	TA	GA
Slow	0.04	0.44	0.10	0.60
Preferred	0.30	0.36	0.30	0.79
Fast	0.11	0.20	0.25	0.76

This procedure enabled us to quantify how subjects modified their neuromuscular activation as cadence was changed and to determine if the adaptation process observed postflight was similar to that observed preflight (23).

RESULTS

Our previous investigations of preflight versus postflight locomotor control (5, 22, 23, 28) and other reports concerning the impact of spaceflight on humans (21, 31, 39) have consistently found individualized adaptation patterns, particularly during whole-body, goal-directed, tasks. Therefore, to facilitate identifying the wide range of adapted responses associated with spaceflight, we assessed the data from each subject separately as opposed to the more traditional approach of developing group means. This approach is consistent with that of other authors all of whom displayed individual astronaut data throughout their reports of the physiogical and behavioral effects of long-duration spaceflight (2, 5, 21, 24, 28, 39). Paired Student *t*-tests were used to test for potential individual subject pre- to postflight changes in many of the measures. An alpha level of 0.05 was adopted for these tests. The values displayed in Tables 4, 5 and 6 are mean values obtained from the calculation of the respective measures. For example, the individual subject data for a particular muscle and condition in Table 3 represents the mean of the entire amplitude normalized EMG waveform. However, when the *t*-tests were performed, all 50 data points that comprised the respective preflight EMG waveforms were compared with the complete postflight waveform. In the case of the variables whose calculation yielded a single measure (i.e. Pearson *r* correlation coefficients, cross correlation coefficients, CVs, and CMCs) no statistical tests were performed. Although this statistical approach limits generalizations across subjects, it enabled us to more fully characterize the individual responses of our subjects.

Gait metrics

As expected, during both preflight and postflight testing all subjects displayed a descending pattern of strides times as cadence was increased from slow, to preferred, to fast. During both preflight and postflight testing, the subjects were able to modulate their gait with the aid of a metronome such that there were three distinct cadence conditions (i.e., slow, preferred, fast). Spaceflight did not significantly impact stride times or duty cycle (i.e., the percent of the gait cycle spent in the stance phase). The successful manipulation of both pre- and postflight cadence ensured that the neuromuscular features associated with adaptation to different walking speeds could be assessed without concern for the impact of significantly different speeds between pre- and postflight testing.

Modification of phasic neuromuscular activation

Figure 1A-H graphically displays pre- versus postflight average EMG waveforms (+ 1 standard deviation), that provide examples of waveforms that are highly correlated (A,C,E,G) and those that had lower Pearson *r* correlation coefficients (B,D,F,H). Table 1 presents Pearson *r* correlation coefficients for each subject and muscle at each cadence. Although no clear pattern emerged, either across subjects or conditions, there was a greater tendency for the phasic activation features of the thigh musculature to be modified after flight than for the shank musculature.

Table 2 A-L. Pre- and postflight coefficients of multiple correlation (CMC) and coefficients of variation (CV) for each subject, muscle and cadence. Greater CMC values represent less variability while higher CV values represent greater variability. #Data from Subject C in the slow cadence condition were not obtained due to technical reasons.

A

Preferred		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
BF	A	.64	.48	60	74
BF	B	.86	.58	35	52
BF	C	.69	.67	56	58
BF	D	.63	.58	73	61
BF	E	.63	.58	77	65
BF	F	.64	.26	77	96

B

Preferred		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
RF	A	.84	.69	49	74
RF	B	.89	.62	26	50
RF	C	.83	.56	43	67
RF	D	.72	.28	54	90
RF	E	.70	.72	53	59
RF	F	.68	.46	60	84

C

Preferred		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
GA	A	.79	.65	59	83
GA	B	.93	.89	27	32
GA	C	.72	.81	68	48
GA	D	.87	.81	45	55
GA	E	.44	.50	113	124
GA	F	.80	.48	60	122

D

Preferred		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
TA	A	.62	.48	71	74
TA	B	.90	.84	31	33
TA	C	.68	.66	52	54
TA	D	.84	.75	40	52
TA	E	.56	.63	83	59
TA	F	.71	.69	66	69

E

Slow		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
BF	A	.87	.33	32	85
BF	B	.67	.54	74	46
BF	C	#	#	#	#
BF	D	.86	.74	34	68
BF	E	.49	.38	86	98
BF	F	.90	.49	54	74

F

Slow		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
RF	A	.92	.76	30	64
RF	B	.91	.73	42	45
RF	C	#	#	#	#
RF	D	.77	.73	42	45
RF	E	.75	.74	51	51
RF	F	.83	.74	32	47

G

Slow		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
GA	A	.87	.33	23	66
GA	B	.95	.82	23	48
GA	C	#	#	#	#
GA	D	.85	.81	49	58
GA	E	.67	.50	59	117
GA	F	.89	.73	36	81

H

Slow		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
TA	A	.90	.56	29	64
TA	B	.90	.66	29	66
TA	C	#	#	#	#
TA	D	.77	.76	45	48
TA	E	.76	.72	54	58
TA	F	.90	.80	29	50

I Fast		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
BF	A	.72	.48	49	81
BF	B	.65	.43	66	96
BF	C	.73	.79	52	55
BF	D	.52	.59	81	63
BF	E	.66	.43	85	100
BF	F	.75	.72	68	41

J Fast		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
RF	A	.86	.76	45	68
RF	B	.67	.27	54	93
RF	C	.91	.60	29	73
RF	D	.73	.64	55	63
RF	E	.67	.65	62	69
RF	F	.68	.86	64	31

K Fast		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
GA	A	.86	.69	45	80
GA	B	.75	.51	56	84
GA	C	.93	.83	31	.48
GA	D	.85	.74	49	70
GA	E	.61	.53	70	125
GA	F	.80	.87	63	41

L Fast		CMC	CMC	CV	CV
Muscle	Subject	Pre Within Day	Post Within Day	Preflight	Postflight
TA	A	.70	.61	61	65
TA	B	.73	.37	48	90
TA	C	.82	.65	33	54
TA	D	.82	.67	44	61
TA	E	.63	.62	78	61
TA	F	.69	.78	67	39

There was also a tendency for the slow condition to be associated with the greatest change between pre- and postflight phasic activation features. Table 2A-L displays the CMC and CV measures for each subject, muscle and cadence. These measures indicate that, in most cases, the postflight EMG waveforms across strides were more variable than the preflight waveforms. Across all subjects, muscles and conditions 86.7% (59/68) of the CMC comparisons indicated the postfight waveforms were more variable than preflight. Eighty percent of the CV comparisions (55/68, 1 pre- and postflight comparison was identical) showed the postflight waveforms to be more variable than preflight.

An additional measure designed to reflect potential changes in the phasic activity of the muscle was that of ankle and thigh agonist-antagonist muscle pair cross correlation coefficients. These coefficients are displayed in Table 3. In general, there were few large pre- versus postflight changes in the cross correlation coefficients for either the TA-GA or BF-RF antagonist pairs. However, of the 17 BF-RF comparisons, 12 displayed shifts in the lead/lag relationship of at least 18 points. Given that each point represents 2% of the gait cycle, the observed shifts can be considered significant modifications in the phasic activation relationships between the thigh musculature. Conversely, only 3 of the 17 TA-GA lag/lead comparisons displayed relatively large shifts.

Modification of relative amplitude

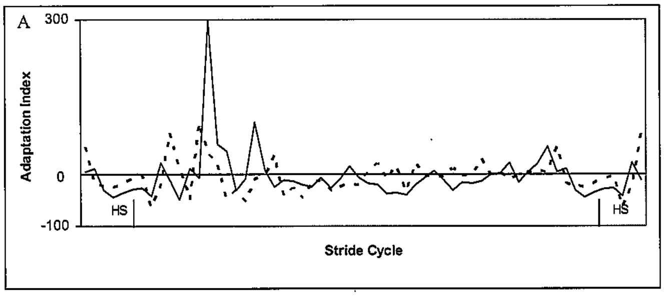
Table 4 displays the average relative amplitude of each subject and muscle for each cadence. The percentage change between the pre- and postflight waveforms is also listed. An examination of this table reveals that 66% (44/68) of the relative amplitude comparsions were significantly different. Forty-two percent of the postflight waveforms (29/68) had greater relative activation. Conversely, 24% (16/68) of the muscles displayed less relative amplitude after flight. Although the high percentage of significant changes in relative amplitude indicates that the muscles were being activated in a different manner pre- versus postflight, there was no dominant trend regarding the direction of change.

Agonist-antagonist relationships

Co-contraction measures were calculated to assess the relationship between the EMG obtained from the two shank muscles and the two thigh muscles. Results of the pre- versus postflight BF-RF comparisons, and GA-TA are displayed in Table 5A-B. When the data are collapsed over cadence and subject, 47% (8/17) of the BF-RF comparisons were significantly different, while 82% (14/17) of the GA-TA comparisons were significantly different. Consistent with relative amplitude comparisons, the direction of change was not consist across comparisons. Concordant with other measures, the co-contraction indices suggest that spaceflight is associated with substantial modifications in the activation relationships between traditional antagonist muscle pairs of the lower limb.

Adaptability index

To provide an indication of how subjects adapted their neuromuscular activation patterns to produce different cadences, adaptability indices were computed. The pre- and postflight indices were then compared using paired t-tests, for each muscle and subject, as the subjects modified their cadence from preferred to slow and preferred to fast (Table 6). Figure 2a-b displays individual subject average waveform plots of adaptation indices across the gait cycle. Figure 2a is an example of a muscle activation pattern that varies only slightly as the subject moves from a slow to preferred cadence and the adaptation is unaffected by spaceflight. Figure 2b is representative of an activation pattern that is modified as the subject changes cadence from preferred to fast. Fifty seven percent of pre- to postflight comparisons of the AI index values (25 of 44) reached significance. Consistent with the correlation comparisons, there was a trend for the thigh musculature to be more impacted by spaceflight than the shank muscles. The many differences in the pre- versus postflight AIs suggest that the neuromuscular adaptive processes associated with changing gait cadence are significantly impacted by spaceflight.



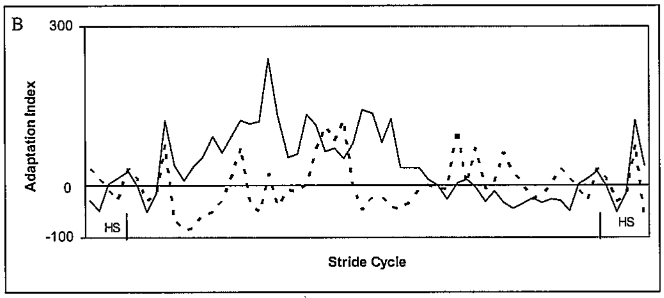


Figure 2. Single subject exemplar average AI values displaying a subject (A) whose preflight (solid line) and postflight (dotted line) TA AI remains generally stable throughout the gait cycle as he changes cadence from slow to preferred. Note that the postflight AI values are generally similar to preflight, indicating that spaceflight had minimal impact on this subject's ability to produce similar activation patterns in this muscle as those observed preflight. In contrast, 2B displays exemplar average TA AI values for a subject whose activation pattern is modified as cadence changes from preferred to fast during preflight testing and whose cadence adaptation process is affected by spaceflight. A value of zero indicates that there was no change in EMG amplitude between cadence conditions at a particular point in the stride cycle.

Taken together, the data clearly indicate that long duration spaceflight impacts neuromuscular activation during overground locomotion. The lack of a systematic response to spaceflight across subjects is not unexpected given the complex interplay between the multiple underlying physiological systems that support overground locomotion.

DISCUSSION

This report describes many alterations in human neuromuscular activation characteristics of four lower limb muscles during overground locomotion after long-duration spaceflight. All subjects displayed substantial modifications in several of the measures used to characterize neuromuscular activation as measured by surface EMG. While no constellation of activation measures served to identify a common pattern of change across astronauts, each subject exhibited significant changes in several of the measures. Overall, the various measures indicate that long-duration spaceflight resulted in significant modifications of lower limb neuromuscular activation during walking at different cadences. The majority of the reported measures reflect pre- versus postflight muscle activation characteristics and relationships between muscles within a given cadence. However, the adaptation indices provide information regarding the dynamic process of how these activation characteristics were modified as subjects changed cadence and how spaceflight impacted this process. As suggested in the Methods section, our underlying assumption is that the neuromuscular activity collected during preflight testing represents each subjects' optimal and/or preferred muscle activation pattern during the different cadence conditions. Since gait metrics were unchanged between pre- and postflight testing, substantial modifications from the preflight activity patterns were interpreted to have resulted from extended stays in weightlessness.

Table 3. Pre- and postflight cross correlation coefficients and corresponding lag/leads between antagonistic muscle pair activation waveforms at the ankle (TA-GA) and thigh (BF-RF). Data from Subject C in the slow cadence condition were not obtained due to technical reasons.

	Preflight		**Postflight**	
	***r* value**	**lag**	***r* value**	**lag**
Subject A				
Preferred				
TA-GA	0.56	19	0.53	16
BF-RF	0.49	-45	0.70	-2
Slow				
TA-GA	0.56	19	0.55	-17
BF-RF	0.60	19	0.58	1
Fast				
TA-GA	0.43	-17	0.50	18
BF-RF	0.45	-44	0.63	3
Subject B				
Preferred	*r* value	lag	*r* value	lag
TA-GA	0.53	19	0.45	17
BF-RF	0.64	-19	0.51	-20
Slow				
TA-GA	0.51	19	0.59	18
BF-RF	0.49	-19	0.51	-20
Fast				
TA-GA	0.57	19	0.65	18
BF-RF	0.47	1	0.44	-20
Subject C				
Preferred	*r* value	lag	*r* value	lag
TA-GA	0.68	20	0.63	20
BF-RF	0.34	-46	0.50	-43
Fast				
TA-GA	0.61	18	0.62	17
BF-RF	0.46	1	0.45	-43

	Preflight		**Postflight**	
	***r* value**	**lag**	***r* value**	**lag**
Subject D				
Preferred				
TA-GA	0.52	19	0.39	20
BF-RF	0.57	-19	0.49	2
Slow				
TA-GA	0.49	19	0.43	20
BF-RF	0.39	30	0.47	1
Fast				
TA-GA	0.42	-15	0.42	20
BF-RF	0.49	27	0.39	-14
Subject E				
Preferred	*r* value	lag	*r* value	lag
TA-GA	0.62	18	0.66	18
BF-RF	0.37	-43	0.41	-43
Slow				
TA-GA	0.55	20	0.52	21
BF-RF	0.40	24	0.36	-38
Fast				
TA-GA	0.65	19	0.63	18
BF-RF	0.44	-44	0.51	-44
Subject F				
Preferred	*r* value	lag	*r* value	lag
TA-GA	0.43	19	0.59	19
BF-RF	0.59	7	0.27	-45
Slow				
TA-GA	0.46	19	0.44	16
BF-RF	0.47	-16	0.25	27
Fast				
TA-GA	0.37	16	0.61	17
BF-RF	0.61	8	0.60	-40

Modified activation patterns

We have previously used the Pearson r correlation coefficient to assess the degree of EMG pre- versus postflight waveform similarity obtained from astronauts performing treadmill locomotion after short- (22) and long-duration (23) spaceflight. Unlike our previous reports, the current data suggests substantial modifications in neuromuscular activation features associated with long-duration spaceflight during overground locomotion. This was evident in the large number of correlation coefficients in the present study that were below 0.71. In comparison, we previously reported that only 8% of coefficients fell below 0.71 during treadmill locomotion after either short- (6 of 78) or long-duration (2 of 26) spaceflight. Moreover, in this investigation a large majority of pre- versus postflight CMC and CV comparisons indicated that activation variability was substantially increased after flight as compared to prior to flight. Thus, the data indicate that the average phasic features of neuromuscular activation used during overground locomotion are altered as a result of having experienced long-duration spaceflight.

Overground locomotion requires that the motor control system successfully organize to produce coordinated gait patterns in response to a different set of task parameters when compared with the more restrictive motorized treadmill gait. In particular, visual flow patterns must be integrated while traversing the walkway without the aid of a safety har-

Table 4. Mean relative activation values in amplitude normalized units across the entire average pre- and postflight waveforms. The percentage change in the two values is also displayed. Asterisks represent a significance at $p < 0.05$. #Data from Subject C in the slow cadence condition were not obtained due to technical reasons.

	Slow			Preferred			Fast		
Subject A	Pre	Post	% Delta	Pre	Post	% Delta	Pre	Post	% Delta
BF	28.9	11.4	-60.6*	15.2	28.7	88.8*	19.5	35.6	82.6*
RF	30.3	13.3	-56.1*	8.7	40.3	363.2*	9.2	35.5	285.9*
TA	24.6	23	-6.5	29.6	33.1	11.8	30.3	29.2	-3.6
GA	25.2	19.9	-21.0*	29.9	30.2	1.0	30.4	20	-34.2*
Subject B	Pre	Post	% Delta	Pre	Post	% Delta	Pre	Post	% Delta
BF	24.9	33.8	35.7*	33.5	49.9	49.0*	31.1	41.4	33.1*
RF	12.1	9.8	-19.0*	15.2	10.4	-31.6*	18.5	15	-18.9*
TA	19.1	25.5	33.5	24.8	27	8.9	28.8	33.5	16.3
GA	20.6	18.1	-12.1*	23.1	22.8	-1.3	25.7	24.1	-6.2
Subject C	Pre	Post	% Delta	Pre	Post	% Delta	Pre	Post	% Delta
BF	25.6	#		41.2	27.9	-32.3*	31.7	36.8	16.1
RF	13.7	#		21.3	26.5	24.4*	28.7	36.5	27.2*
TA	25.6	#		30	38	26.7*	34	52.7	55.0*
GA	13	#		16.9	26.9	59.2*	16.8	28.1	67.3*
Subject D	Pre	Post	% Delta	Pre	Post	% Delta	Pre	Post	% Delta
BF	28.8	28.9	0.3	20.7	35.7	72.5*	21.6	32.6	50.9*
RF	16.1	22.2	37.9*	19.3	28.9	49.7*	30.1	41.5	37.9*
TA	21.1	26.9	27.5*	24.1	28	16.2*	29.3	36.6	24.9*
GA	19.3	23.8	23.3*	20.8	22.6	8.7	21.3	23.2	8.9
Subject E	Pre	Post	% Delta	Pre	Post	% Delta	Pre	Post	% Delta
BF	20.5	18.3	-10.7	25.2	24.3	-3.6	32.6	33.5	2.8
RF	18.8	17.5	-6.9	25.5	28.4	11.4	29.2	35.8	22.6*
TA	25.9	22.2	-14.3*	26.9	30.8	14.5*	37.9	43.8	15.6*
GA	19.9	7	-64.8*	31.7	13.2	-58.4*	31.4	18.1	-42.4*
Subject F	Pre	Post	% Delta	Pre	Post	% Delta	Pre	Post	% Delta
BF	24.7	39.7	60.7*	25.3	36	42.3*	24.6	42	70.7*
RF	24.6	21.4	-13.0	34.9	30.6	-12.3	39.3	32.1	-18.3*
TA	24.9	16.1	-35.3*	33.3	17.8	-46.5*	31.3	27.6	-11.8
GA	21.3	39.2	84.0*	26.7	17.5	-34.5	28.6	21.8	-23.8

ness. Responding to these different task parameters is made more difficult after long-duration flight when loss of muscle strength, cardiac adaptations, and altered vestibular and proprioceptive system functioning combine to compromise bipedal postural control (36, 24). Therefore, assembling efficient postflight coordination modes while experiencing altered physiological conditions is problematic. The significant decreases in the correlation coefficients indicate that, although the subjects were able to walk, they often activated the monitored muscles using phasic features that were different than those observed preflight. Thus, while the subjects assembled new neuromuscular coordination modes to complete the postflight tasks, they generally were unable to use the more familiar activation patterns associated with preflight walking. Additionally, the increase in activation variability after spaceflight suggests that the ability to precisely generate stable neuromuscular activation was impeded. The present results are consistent with those of Recktenwald et al. (34) who reported significant differences in neuromuscular activation patterns during quadrupedal stepping in two Rhesus monkeys after 14 days of spaceflight.

Table 5. Pre- and postflight co-contraction values for lower limb antagonist muscle pairs for each subject and cadence. The asterisks indicate significant pre- versus postflight differences. #Data from Subject C in the slow cadence condition were not obtained due to technical reasons.

			Slow		Preferred		Fast	
			Pre	Post	Pre	Post	Pre	Post
A	BF-RF	Subjects						
		A	10.3	9.0	12.7	10.4*	16.0	12.9
		B	10.2	9.0	12.1	10.4	14.1	12.9
		C	11.2	#	17.7	15.8	20.9	21.2
		D	14.3	18.5*	13.5	25.0*	19.1	25.8*
		E	11.6	9.4*	12.5	12.3	16.0	20.6*
		F	15.9	18.0	18.3	25.2*	19.0	25.0*
B	GA-TA	Subjects						
		A	12.0	7.5*	17.4	9.7*	15.5	8.4*
		B	6.5	7.5	7.9	9.7*	7.5	8.4
		C	8.3	#	10.8	15.5*	10.3	19.3*
		D	5.5	6.8*	5.0	6.9*	5.8	8.9*
		E	11.4	3.5*	18.1	4.8*	21.1	10.3*
		F	9.5	12.9*	14.2	5.9*	12.9	10.3

The many differences in activation amplitude across the different cadences indicate that the relative level of muscle activation was modified as a result of spaceflight. These modifications also factored into the observed changes in antagonist muscle co-contraction measures and adaptation indices. Since different levels of pre- versus postflight relative activation were produced throughout the gait cycle at the different cadences, the co-contraction and adaptation indices reflected these differences. Collectively, the measures used to characterize neuromuscular activation during gait across different cadences indicate that long-duration spaceflight results in altered neuromuscular activation features. Although extended exposure to spaceflight did not systematically modifiy neuromuscular activation across subjects, each subject displayed a constellation of pre- to postflight changes that strongly suggests that their ability to produce stable spatio-temporal activation patterns, as generally observed preflight, was impaired after flight. The fact that the subjects could navigate the walkway at the required cadence suggests the neural circuits that produce the activation necessary to locomote are robust enough to adequately function despite the adaptations that occur in many other physiological systems that support locomotion. However, many of the crewmembers whose data are reported here, were unable to perform unassisted locomotion less that 24 hours prior to the formal testing procedures (C. Layne, personal observation). The fact that these crewmembers were able to undergo formal testing on R+1, emphasizes the (re)adaptive properties of the human motor control system.

The general purpose of this report is to broadly characterize changes in neuromuscular activation features associated with postflight overground locomotion. However, we discuss several physiological systems that have previously been identified as being affected by exposure to microgravity and can logically be expected to influence the neuromuscular activation process. Undoubtedly confluences of physiological modifications combine to produce the modifications in postflight EMG activity displayed by our subjects.

Loss of muscle strength

Decrements in postflight muscle strength may have been a factor in altered postflight neuromuscular activation characteristics. It is well documented that there are significant losses in volume in the lower limb and back musculature (11, 45, 39, 25). These losses are positively correlated with losses in muscle force production. Strength losses of approximately 35% relative to preflight during plantar and dorsiflexion movements following long-duration spaceflight have been reported (14, 21). Muscle atrophy, particularly of the anti-gravity muscles, occurs partially as a result of the unloading associated with spaceflight (12). Laboratory-based resistance training studies, that have typically related torque production to EMG amplitude measures, have reported increases in amplitude associated with hypertrophy (15, 27). Additionally, there are reports that 6 weeks of bed rest results in both lower limb muscle atrophy and

Table 6. Pre- and postflight mean adaptation indices associated with changes in cadence. For the slow to preferred comparisons, negative values indicate that the average amplitude associated with the slow condition was less than for preferred. For the preferred to fast comparisons, negative values indicate that average amplitude for the preferred conditions was less than for fast. The asterisks indicate significant pre- versus postflight differences at $p < 0.05$. #Data from Subject C in the slow cadence condition were not obtained due to technical reasons.

	Pre Slow-Preferred	Post Slow-Preferred	Pre Preferred-Fast	Post Preferred-Fast
Sub A				
BF	137.6	-56.7*	-19.9	7.8*
RF	336.7	-63.6*	-1.2	28.2*
TA	-4.8	-29.6*	-11.2	38.4*
GA	-4.3	-34.7*	-13.9	54.4*
Sub B				
BF	-15.2	-26.0	36.8	50.1
RF	-13.6	-9.2	-7.6	-7.6
TA	-12.0	-0.9	-6.8	-7.5
GA	-11.6	-25.7*	-2.5	22.4
Sub C				
BF	-54.5	#	35.8	-7.2*
RF	-36.5	#	-17.1	-16.1
TA	-13.4	#	-5.0	-10.8
GA	-16.6	#	9.7	0.7
Sub D				
BF	60.9	-19.3*	-2.4	22.0*
RF	-4.3	-20.4*	-28.4	-13.0*
TA	-0.2	-3.6	-5.5	-23.5*
GA	2.7	6.8	9.7	0.6
Sub E				
BF	3.4	-18.1*	-18.8	-23.2
RF	-8.9	-21.0*	-12.9	-28.1*
TA	-15.2	-24.8	-25.8	-33.6
GA	-27.5	-22.5	5.2	-26.6*
Sub F				
BF	78.8	23.1*	10.9	-0.1
RF	-20.5	-32.5*	-4.2	18.4*
TA	-12.5	-0.1*	15.6	-34.5*
GA	-18.5	679.9*	-5.2	14.7

decreased EMG amplitude during maximal voluntary efforts (4). It is therefore reasonable to suggest that modifications in muscle fiber size may influence muscle activation patterning, such as was observed in the current study.

Perhaps as important as the loss of muscle strength in postflight locomotor decrements is the increase in postflight musculotendinous stiffness at the ankle (21). To develop efficient postflight locomotion strategies the changes in ankle stiffness presumably experienced by our subjects would need to be overcome. This could possibly be accomplished through the use of modified neuromuscular activation features of the ankle musculature, as observed in our subjects. Conversely, failure to account for changes in ankle stiffness could result in modified gait characteristics, as has been documented in previous reports of pre- versus postflight gait kinematic analyses (28, 6).

Alterations in neural drive

Another factor that has been suggested to contribute to postflight neuromuscular activation modifications is that of neural drive to the motoneurons. Lambertz and his colleagues (21) found a 39% mean decrease in normalized RMS triceps sura EMG after long-duration spaceflight when compared to preflight values. Antonutto et al. (1) reported decreases in explosive leg power beyond that which was predicted based solely on the loss of muscle mass after 21 days of spaceflight. This finding, combined with the significant reduction in postflight quadricep EMG, led to the suggestion that alterations in neural drive are likely to contribute to the modification in postflight motor control (1). Moreover, muscle disuse has been associated with a decrease in maximal motoneuron firing rate, with low-threshold units being most affected (10). Thus, there is supporting evidence for the suggestion that modifications in the neuromuscular activation features observed in the present study may, in part, stem from alterations in neural drive. With specific regard to the triceps sura, Edgerton et al. (11) and others (25, 39) have reported preferential loss of soleus mass relative to the gastrocnemius and preferential loss of slow type I fibers relative to the type II fibers. Thus, overall the soleus appears to experience greater changes than the gastrocnemius as a result of spaceflight. Therefore it is reasonable to suggest that the differential changes in the calf musculature impacts the manner in which the gastrocnemius functions during gait. This suggestion is consistent with the modifications in gastrocnemius neuromuscular activation features observed in this study.

Changes in proprioception

Modifications in proprioceptive functioning associated with spaceflight could also contribute to the observed changes in neuromuscular activation properties. Changes in postflight stretch reflex responses (16) and the inability to precisely track ankle joint motion (20, 37) indicate proprioceptive functioning is altered by spaceflight. These changes could logically be expected to ultimately impact neuromuscular activation features. It has been suggested modifications in Rhesus monkey postflight locomotion may have resulted from alterations in load-related proprioceptive feedback (34). Returning crewmembers often report heightened cutaneous sensitivity from the soles of the feet (C.S. Layne, personal observation, W.H. Paloski, personal communication) that could also be expected to contribute to modified neuromuscular activation patterns. Additionally, alterations in vestibular system functioning, with its direct role in postural equilibrium through reflex loops and inputs to motoneuron pools, could affect muscle activation properties (30, 35, 44).

The impact of countermeasures and flight duration on neuromuscular activation

The degree to which neuromuscular activation was modified after flight was unrelated to the crewmembers self-reported use of in-flight countermeasures (C. S. Layne, personal communication with crewmembers). This is not particularly surprising given that the countermeasures aboard Mir were primarily designed to attenuate loss of muscle mass and cardio-vascular fitness. As discussed, neuromuscular activation is impacted by a number of physiological processes that may not be targeted by traditional countermeasures. Also of interest is the fact that modifications in postflight neuromuscular activation were not related to the amount of time spent in flight. This suggests the possibility that there may be a "threshold" effect in that once a crewmember has spent a certain amount of time in flight (i.e., months) his or her postflight responses will be more affected than after short-duration flight (i.e., 8-20 days) but the modifications will reach a plateau until the crewmember has spent considerably more time in flight (i.e., years). In other words, there appears to be a non-linear relationship between flight duration and the degree of modifications in postflight neuromuscular characteristics relative to preflight. Given the paucity of data currently available, it is impossible to evaluate this suggestion. Moreover, much of the existing data regarding physiological adaptations to spaceflight suggest space scientists will ultimately observe individual physiological profiles in response to flight duration as a broader range of flight lengths become more common.

Conclusions

This report details many changes between pre- and postflight neuromuscular activation features during overground locomotion at different cadences after long-duration spaceflight. Although there were no systematic patterns of change across the astronauts, each astronaut displayed modified activation features after returning from flight. It is suggested that these modifications in activation features stem from changes in other physiological systems that impinge upon the ability of the neural circuits responsible for neuromuscular patterning during locomotion to produce the stable activation patterns observed during preflight testing.

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