

M.I.T./Canadian vestibular experiments on the Spacelab-1 mission: 5. Postural responses following exposure to weightlessness

R. V. Kenyon and L. R. Young

Man-Vehicle Laboratory, Department of Aeronautics and Astronautics, Massachusetts Institute of Technology,
Cambridge, MA 02139, USA

Summary. The four science crewmembers of Spacelab-1 were tested for postural control before and after a 10 day mission in weightlessness. Previous reports have shown changes in astronaut postural behavior following a return to earth's 1-g field. This study was designed to identify changes in EMG latency and amplitudes that might explain the instabilities observed post-flight. Erect posture was tested by having the subject stand on a pneumatically driven posture platform which pitched rapidly and unexpectedly about the ankles causing dorsi- and plantarflexion. Electromyographic (EMG) activity from the tibialis anterior and the gastrocnemius-soleus muscles was measured during eyes open and eyes closed trials. The early (pre 500 ms) EMG response characteristics (latency, amplitude) in response to a disturbance in the posture of the subject were apparently unchanged by the 10 days of weightlessness. However, the late (post 500 ms) response showed higher amplitudes than was found pre-flight. General postural control was quantitatively measured pre- and post-flight by a "sharpened Romberg Rails test". This test showed decrements in standing stability with eyes closed for several days post-flight.

Key words: Weightlessness – Adaptation – Posture – Spaceflight – Electromyography

Introduction

Exposure to prolonged weightlessness produces postural changes both while weightless (Clement et al.

1984, 1985) and for several days post-flight. Astronauts display a variety of postural difficulties upon returning to earth (Homick and Reschke 1977; Homick et al. 1977). Subjects are unable to maintain stable posture with eyes closed, make wide turns around corners, use a wide stance to stand and walk, feel sensations of lateral acceleration while walking, are unable to detect small changes in head position, and experience vertigo during rapid head motions. In the absence of visual cues, quasistatic orientation with respect to the vertical and postural stability is normally based primarily on cues from the otolith organs (particularly from the utricular macula for the head erect position). Dynamic postural stabilization (especially damping) is enabled by signals from the vertical semicircular canals (Flourens 1824). Explanations for the postflight postural instabilities may lie in the changes in central processing of vestibular information that take place with long and continuous exposure to weightlessness. The effects of weightlessness on the vestibular system are not well known. Changes in postural stability may be the result of changes in any of several postural control system components.

The experiments described here were performed to document the postural responses which occur during post-flight re-adaptation and to test hypotheses which might explain the post-flight instability. Instabilities caused by delays in the EMG response to platform tilt might be reflected in latency to postural disturbances. EMG amplitudes from the muscles that control stability of the subject following a change in support surface might be altered and further destabilize the subject. Finally, delayed or sluggish long loop reactions might be reflected as changes in the characteristics of the late response, especially with eyes closed. Two postural programs were conducted – a tilting posture platform test and a modified sharpened Romberg test.

Offprint requests to: L. R. Young (address see above)

Methods

The four SL-1 payload crewmembers were tested pre- and post-flight in the Baseline Data Collection Facility, as specified by Young et al. (1986a). It was possible to test only subjects A and B within 6 h after landing.

Posture platform

Changes in standing posture were initiated by a pneumatically driven platform. It imparted a tilt up or down disturbance of 5° in 15 ms (Crites 1976). The raw EMG signals from the ankle flexors and extensors were recorded. Each EMG channel had a fixed gain (1000) amplifier followed by a bandpass filter (20–1000 Hz) a full-wave rectifier and finally a 10 Hz low pass filter. The two EMG signals were sampled for 10 s at 200 samples per second per channel by a microcomputer that also controlled the movement of the platform. If a baseline shift or other event interfered with the trial, the experimenter could stop and repeat the trial discarding the old data.

Prior to testing, the skin over the tibialis anterior (TA) and the gastrocnemius-soleus (G-S) muscles of the left leg was cleansed with alcohol and scratched with a needle at the point where two surface EMG electrodes (HP 14445A pre-jelled disposable Ag-AgCl) were placed over each muscle group (6–8 cm apart); an indifferent electrode was placed on the front of the leg over the tibia 12 cm down from the patella. Tattoos on the skin over the medial head of gastrocnemius muscle served as landmarks so that electrode placement would be consistent from one test session to the next. TA electrodes were positioned 10 cm below the bottom of the knee.

Subjects were tested under eyes open and eyes closed conditions. Initially, six trials were performed consisting of a randomized set of three up and three down tilts of the platform with eyes open, followed by a different randomized set of six trials with eyes closed. The random presentation of the platform motion was designed to reduce predictive effects that can alter postural responses. The support surface was tilted to increase the difficulty of the posture control task. As the platform is suddenly tilted proprioceptive reflexes that normally stabilize posture are inappropriate to maintain stability. This necessitates the use of other sensory systems, including vestibular, to compensate for the disturbance in posture (Nashner et al. 1982; Diener et al. 1983). Finally, eyes closed testing removes the important visual information used in low frequency stabilization of the body¹.

Subjects wore hard soled shoes and were instructed to stand on the platform with their eyes open (or closed) facing a white wall (1 m away), head erect and legs straight but knees not locked. During eyes open trials, the subject was also instructed to “look straight ahead”. The experiment room had many visual cues to the vertical but they were in the far periphery of the subject’s field of view when the eyes were directed straight ahead. The initiation of a trial was delayed for a random length of time (3 to 6 s) to reduce the predictability of the stimulus. At the end of each experiment, four EMG calibration trials were run. These consisted of the subject making maximum dorsi- or plantarflexion movements by pointing the toe up or down in alternating trials. The entire experiment took 20 min to perform.

¹ The choices of our tests were constrained by available experiment time and the postural techniques available at the time the experiment was designed. Consequently, more recent or time consuming techniques that might have more directly addressed some of the postural issues could not be used

The “Sharpened Romberg” test refers to a standardized procedure for measuring standing stability (Graybiel and Fregly 1965). This test has been used to study posture in space crews (Homick et al. 1977) and labyrinthine deficient patients (Graybiel and Fregly 1965). Results can thus be compared to other results from crews from longer duration flights both past and future. Equipment for the “rails” experiment consisted of a 1/2" × 3/4" × 8' (H × W × L) narrow rail mounted on a 2" × 4" × 8' piece of lumber and a 1/2" × 23/4" × 12" wide rail of aluminum stock (Homick and Reschke 1977).

Narrow rail walking.

The subject walked arms folded in front of him, heel to toe, along the narrow rail. (Six steps maximum).

Narrow rail standing.

The subject stood, eyes open, with arms folded, in the heel to toe position on the narrow rail for a maximum of 60 s per trial.

Wide rail standing/eyes closed.

The subject stood heel to toe on the wide rail and when stable, closed his eyes. The position was maintained for a maximum of 60 s.

Wide rail standing/eyes open.

The subject stood heel to toe on the wide rail for a maximum of 60 s, eyes open.

All trials were terminated if the subject unfolded his arms or placed a foot on the floor. Unlimited gyrations were allowed, if stable posture was regained. The operator measured the duration of the test or, in the case of the narrow rails walking, the number of steps. Individual scores for each subject were the sum of the best three out of five trials for that test. In each test, the maximum score possible was computed as the sum of three perfect scores.

Analysis

The EMG data from each subject was analyzed for latency, area from the beginning of the initial EMG response to its peak, and frequency of oscillation of the late, post 500 ms, response. Latency was measured from the platform tilt command to the start of the first EMG response, defined as a change in baseline level which exceeded the noise level by a factor of three. A peak was identified as the largest EMG amplitude (arbitrary units) that occurred within the first 500 ms after the tilt command. While this worked well with a majority of the data, some activity was so small that some judgment was necessary to identify the peak in the response. This mainly occurred for TA activity in the tilt down trials. With a sample rate of 200 per s, a precision of 10 ms was achievable. The strength of the EMG activity from the TA and G-S muscles was estimated for the initial response after the onset of the disturbance by integrating over the interval from the beginning of the initial EMG response to its peak. This single value was in proportion to the filtered EMG activity of that muscle. These response area values were scaled appropriately within each subject by using the EMG calibration data for that day’s experiment session to compensate for changes in recording sensitivity from one day to the next. Session to session variation in EMG amplitude were

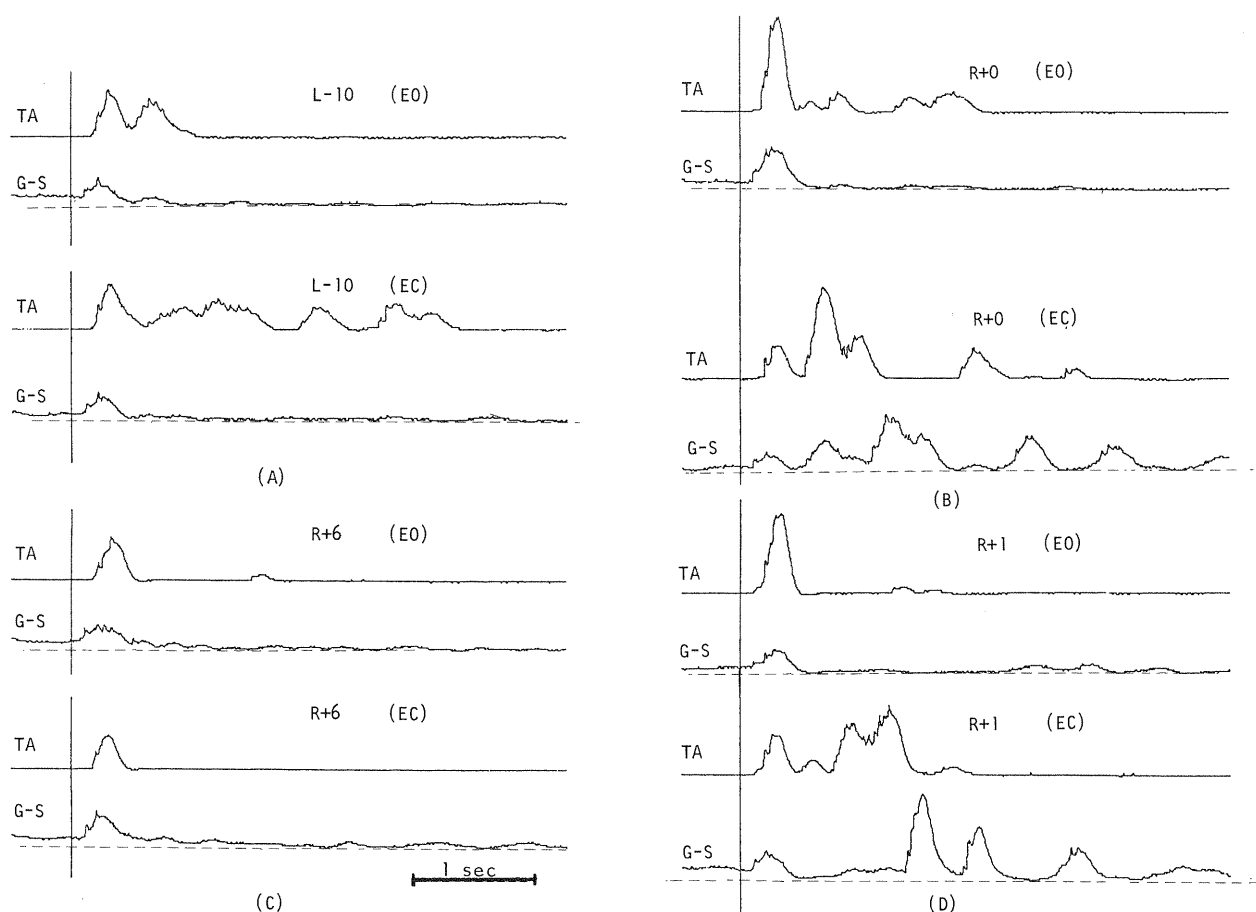


Fig. 1. A Tibialis (TA) and Gastrocnemius-Soleus (G-S) EMG responses from subject B during 5° tilt-up disturbances of the posture platform on launch -10 days (L-10), B Return plus 6 h (R+0), C Return plus 6 days (R+6), and D Return plus 1 day (R+1). The vertical line passing through the data represents the initiation of the platform tilt up. Eyes open (EO) and eyes closed (EC) responses are shown for each test day. The rectified and filtered EMG data in this figure were plotted with the same scale factor. Time markings as indicated apply to all plots. The zero baseline is indicated by a dash line on those traces where the response did not start at baseline

examined. The oscillations in the EMG activity following the initial response were measured as the time interval between the peaks in the filtered response. Observations of whole body posture were based on video recordings of subject posture made during the test.

Results

EMG activity of subject B during the first tilt up trials with eyes open and closed on test days L-10, R+0 (6 h after landing), R+1 and R+6 is shown in Fig. 1. We chose to use the last test pre-flight, L-10, since it represented the state of the subject's posture control closest to launch. We also felt that, due to the variability of the responses, a better understanding of the relationship between pre- and post-flight EMG activity would be possible by examining individual responses rather than averaged data which might

obscure some of the fine details in the response. The tilt up trials produced the most unstable condition for the subjects during both pre- and post-flight testing as they do for the normal population. The restricted dorsiflexion range of the foot caused the transfer of much of the platform tilt up momentum to the torso rather than allowing it to be absorbed by the ankle as is the case for the tilt down motion.

The eyes open (EO) tilt up responses of the TA muscle show small changes between the responses on the last pre-flight test, L-10, (Fig. 1a) and post-flight R+6 (Fig. 1c). On R+0 (Fig. 1b) and R+1 (Fig. 1d), the first response to a tilt up has a larger initial response. However, we could not find any consistent pattern of change in the initial response amplitudes within or across subjects. Often a large initial response would return to the level seen pre-flight on the following tilt up responses. This

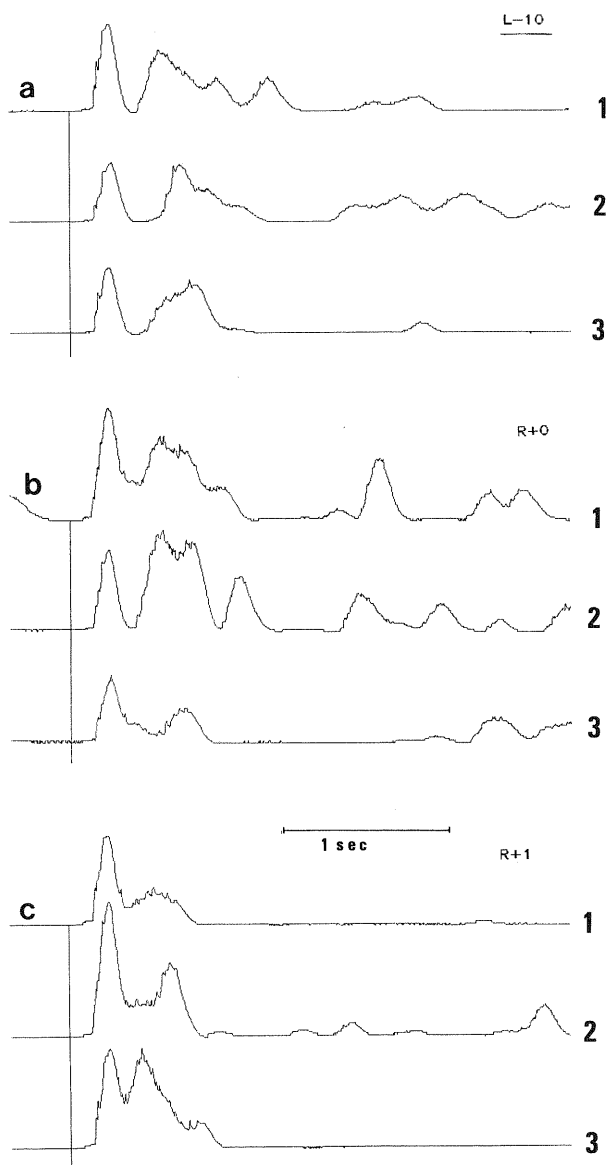


Fig. 2a-c. TA muscle EMG responses from subject A to three successive eyes closed tilt up motion of the platform on **a** L-10, **b** R+0 and **c** R+1. Numbers to the right of each response indicates precedence of responses on each test day. In each case the EMG level returns to zero at the initiation of the platform tilt-up. Time markings as indicated apply to all plots

response does not appear to be related to readaptation to 1 g since others have reported similar changes in laboratory subjects' to successive postural disturbances (Wicke and Oman 1982; Nashner 1976; Nashner et al. 1982). No similar changes were observed in the initial G-S response. The late responses have generally the same shape, being characterized by one or two peaks following the initial peak with most of the response remaining flat for the rest of the period.

The eyes closed (EC) tilt up trials qualitatively showed post-flight changes primarily in the late response. The initial peak changed very little if at all from the pre-flight level. The late response on R+0 (Fig. 1b) and R+1 (Fig. 1d) shows several large and prolonged periods of EMG activity in the TA and G-S muscles as the subject fought to maintain balance. These contractions sometimes continued throughout the trial period. Although patterns of oscillations in the muscles were also recorded pre-flight, the consistency and the amplitude of the post-flight oscillations on R+0 and R+1 were greater than those found subsequently or pre-flight. The EMG activity on R+1 (Fig. 1d) is consistent with the observation of the authors and the comments from subject B after the test, that he was still unstable on R+1 despite his comments *prior* to the testing that normal stability had returned. Successive eyes closed tilt up responses from subject A on L-10 (Fig. 2a), R+0 (Fig. 2b) and R+1 (Fig. 2c) show clear changes between pre-flight and R+0 data with less distinction on R+1. The increased amplitudes throughout the recording session clearly separated pre-flight from R+0 EMG responses in both subjects A and B. By R+4 the crew responses were not different from those pre-flight and were similar to those seen for R+6 in Fig. 1c (subject A).

The tilt down trial responses (not displayed) changed from pre- to post-flight. The eyes open (EO) and eyes closed (EC) responses on pre-flight L-10 and post-flight R+6 showed a similar pattern of TA and G-S activity. The post-flight data on R+0 and R+1 showed higher TA activity than that found pre-flight or on R+6. However, this increase in TA activity which would be inappropriate to stabilize the tilt forward of the subject produced by the platform movement, was not strong enough to cause problems since subjects were more stable during tilt down trials than tilt up both pre- and post-flight.

Latency

Tilt up trials. Despite the destabilizing nature of the tilt-up trials, pre-flight and post-flight latencies for the TA muscle were apparently unchanged within each subject. The data in Fig. 3a is representative of our subject population and shows the latencies for pre- and post-flight tests on subject B who was tested on R+0. Several aspects are notable regarding the pre- and post-flight data. Firstly, the variability of the latency is less post-flight than was found pre-flight for both the TA and G-S muscles for the tilt-up tests. Secondly, the TA latencies were consistently longer than the G-S latencies ($p < 0.001$) post-flight but not

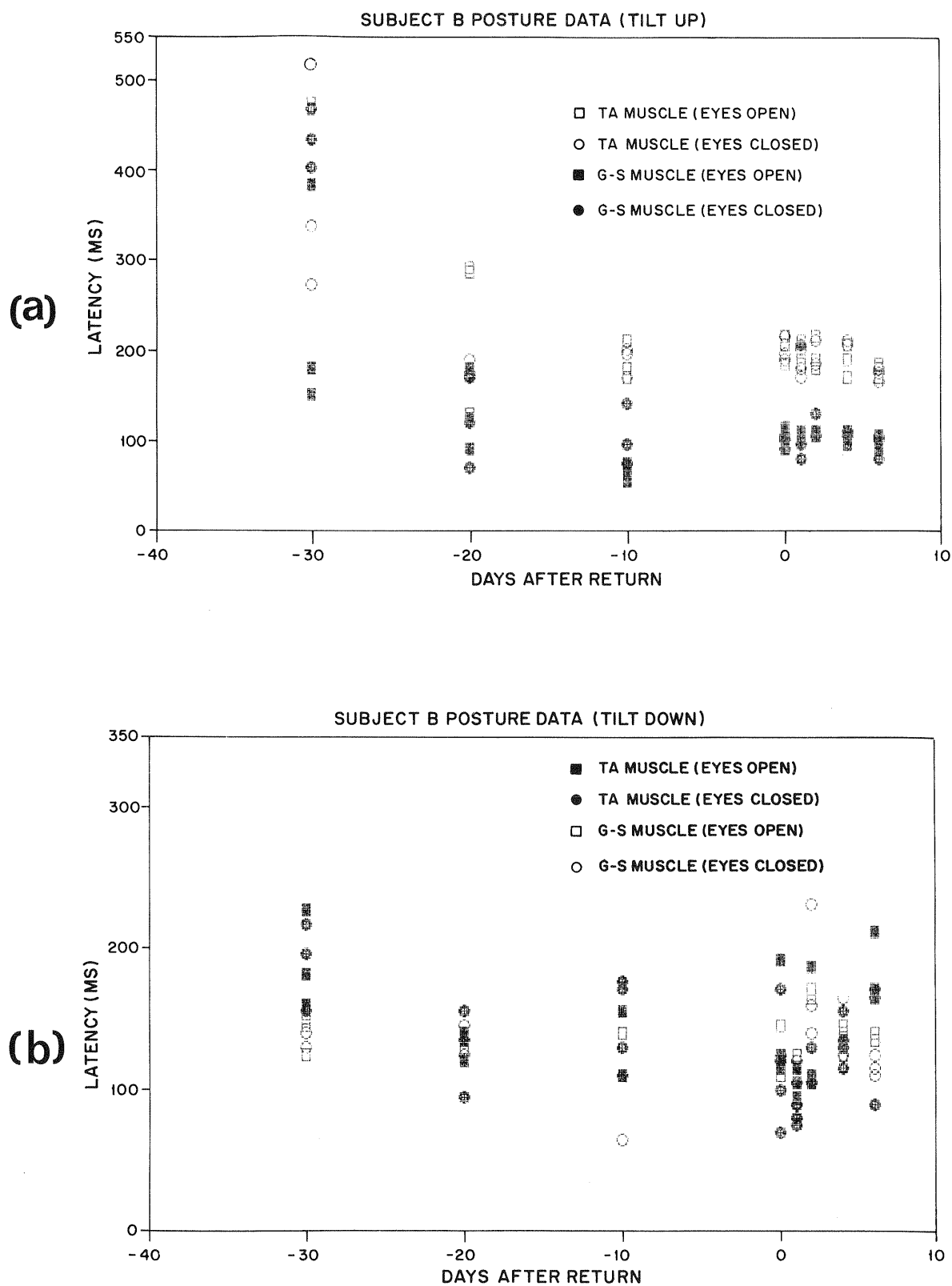


Fig. 3a, b. The latency from the command to tilt the platform 5° to the start of the EMG response for subject B. **a** Tilt up and **b** tilt down. The pre-flight data is plotted on negative days (ie. -10) and the post-flight data from 0 to 6. Closed symbols represent antagonist muscle data in this and all other such graphs

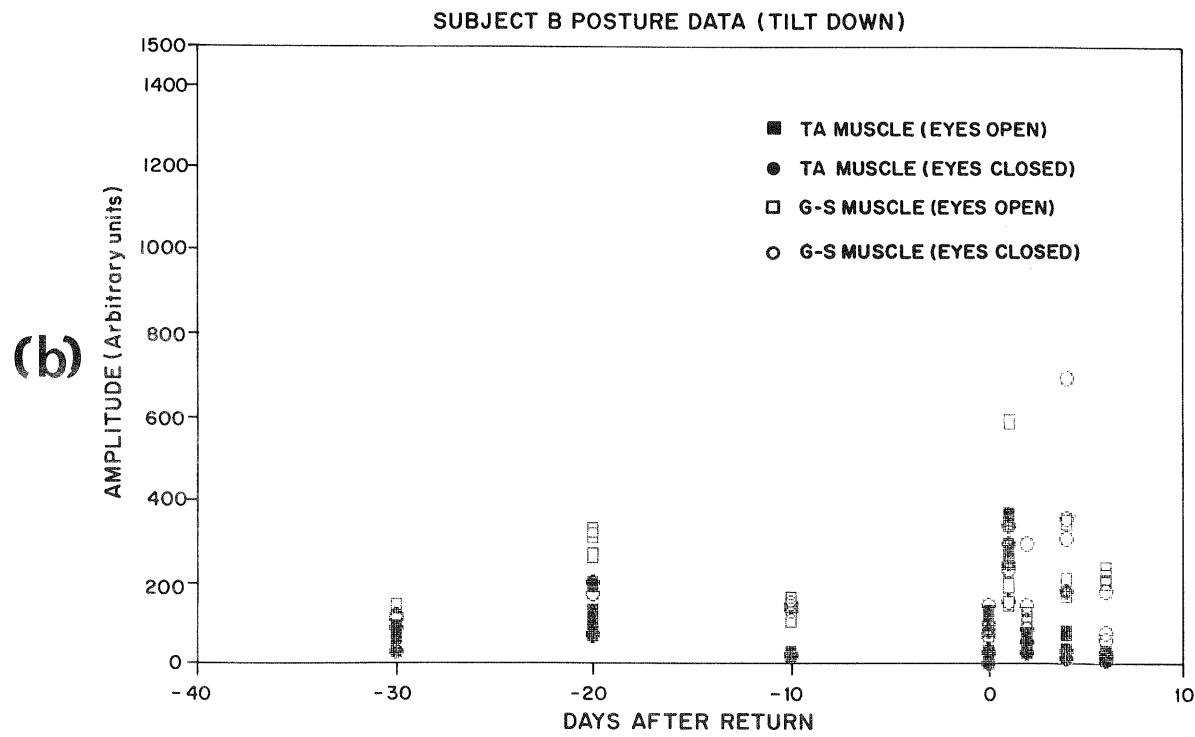
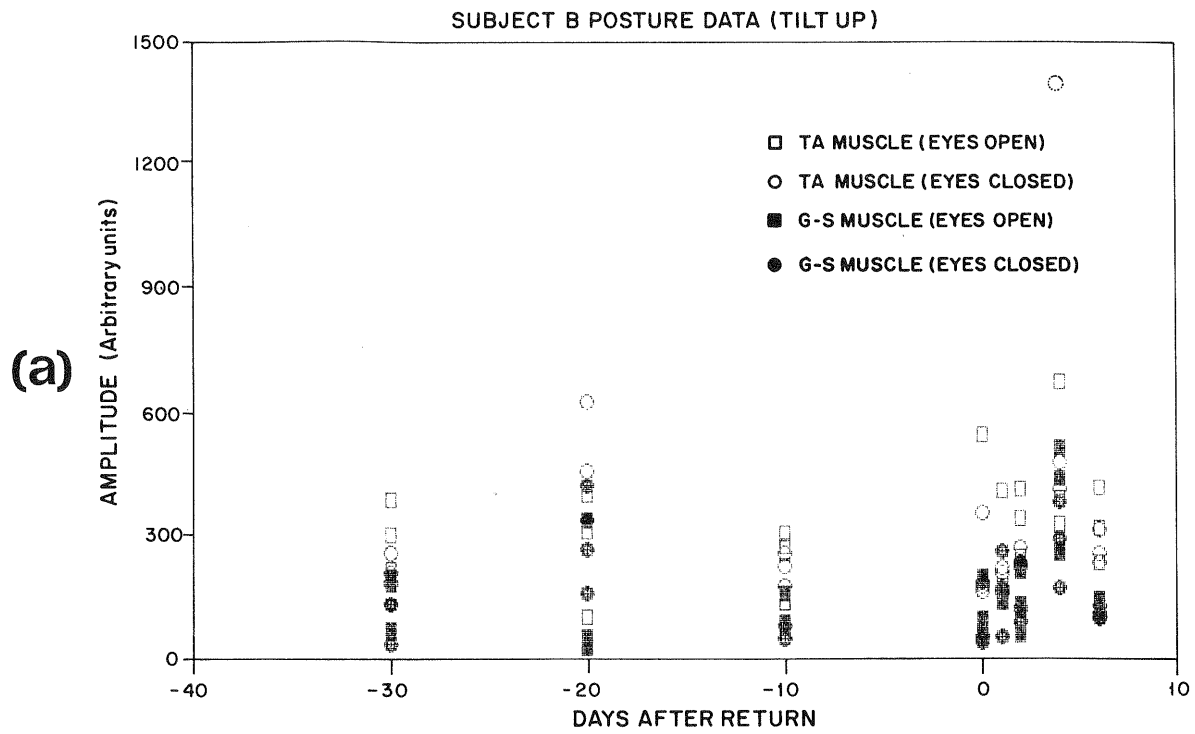


Fig. 4a, b. EMG amplitude values for the initial response from subject B. The vertical scale is given in arbitrary units since it was intended for relative comparisons of the data; a tilt up and b tilt down

pre-flight. Finally, there was no significant difference in eyes open and eyes closed latencies pre- or post-flight. These results were consistent across subjects.

The large spread of latencies pre-flight may have resulted from our indiscriminate lumping of all TA and all G-S latencies for each experiment. However, when we subtracted the latency between corresponding TA and G-S responses for each trial, pre- and post-flight relationships were similar to those shown in Fig. 3.

Tilt down trials. The tilt down data was absent of any clear separation between post-flight TA and G-S latencies as found above for all subjects. As the data in Fig. 3b show, the latencies from each muscle group are intermingled in both the pre- and post-flight trials for each subject. Similarly, the eyes open and eyes closed data showed no significant difference either within the pre-flight or post-flight data or between pre-flight and post-flight data. Taking the differences between TA and G-S muscle latencies did not show any additional relationships in timing of these contractions.

Amplitudes

Tilt up trials. The integrated EMG values plotted in Fig. 4a show a high degree of variability. The relationship between TA and G-S amplitude values were not uniform within subjects. The compensated amplitude (see Analysis) of the early response did not show any clear change pre-flight versus post-flight in any subject. Even for the two subjects who were tested on R+0 (one of which is displayed), there was no demonstrable difference within responses pre- and post-flight. The eyes open and closed trials produced similar amplitude values in each subject for pre- and post-flight testing. We could find no significant difference between pre-flight and post-flight amplitude values either eyes open or eyes closed.

Tilt down. The TA and G-S amplitudes for the tilt down trials showed no significant difference across pre- or post-flight testing nor between data from eyes open and eyes closed trials. Figure 4b is a representative display of the amplitude data from our other subjects. In general, the amplitude of the initial G-S response was smaller and more variable when it acted as the agonist (tilt-down) than the TA muscle response when it acted as the agonist (tilt-up).

To insure that our method of compensating the EMG amplitude values did not obscure some relationship across test days pre- and post-flight, we

examined uncompensated data for our subjects as well as the calibration values used on each day's data. The calibration values showed no trends or significant changes between pre-flight and the first 4 days post-flight. No additional relationships were revealed in the uncompensated data in our subjects.

Late response characteristics

In both the pre- and post-flight testing, the tilt up trials produced a measurable late response mainly in the form of oscillation of the EMG activity in the TA muscle. Consequently, we chose to analyze the late component of the posture response by examining the period and number of EMG oscillations that occurred from the end of the first EMG peak to the end of the data record. The peaks were determined as the midway point between the rising and falling slopes of the responses. The durations were measured for each set of trials (eyes open, eyes closed) for each day tested pre-flight and post-flight. The resulting data from each day was separated into eyes open and eyes closed and displayed in histogram form in Fig. 5 for subject B. The eyes open pre-flight responses show a broad range of durations with only a few observations in each bin. On post-flight days R+0 and R+1 this broad range has narrowed and is shifted slightly to shorter durations. The return to the pre-flight characteristics can be seen at R+2, R+4 and R+6. Comparison of eyes open (EO) and eyes closed (EC) data post-flight shows that the number of oscillations is increased with eyes closed over the same band of durations. Comparing pre-flight EO data to post-flight EO data shows little change. However, post-flight EC data shows the appearance of oscillations with shorter durations compared to pre-flight. For subjects A, C and D (not shown), the range of responses and the number of observations is about the same as found for subject B, but the shift towards shorter durations was less noticeable.

General observations

R+0. The two subjects tested 6 h after landing showed several postural changes from their pre-flight test sessions. Subjects were less stable, showing for the first time loss of balance on the eyes closed tilt up trials. Tilt down and eyes open tilt up trials were better tolerated with no dramatic loss of stability. Subjects showed larger sway related EMG activity when stabilizing posture after tilts post-flight. Subjects used a wider stance to stand during preparation for testing. They used aids to stand on one foot

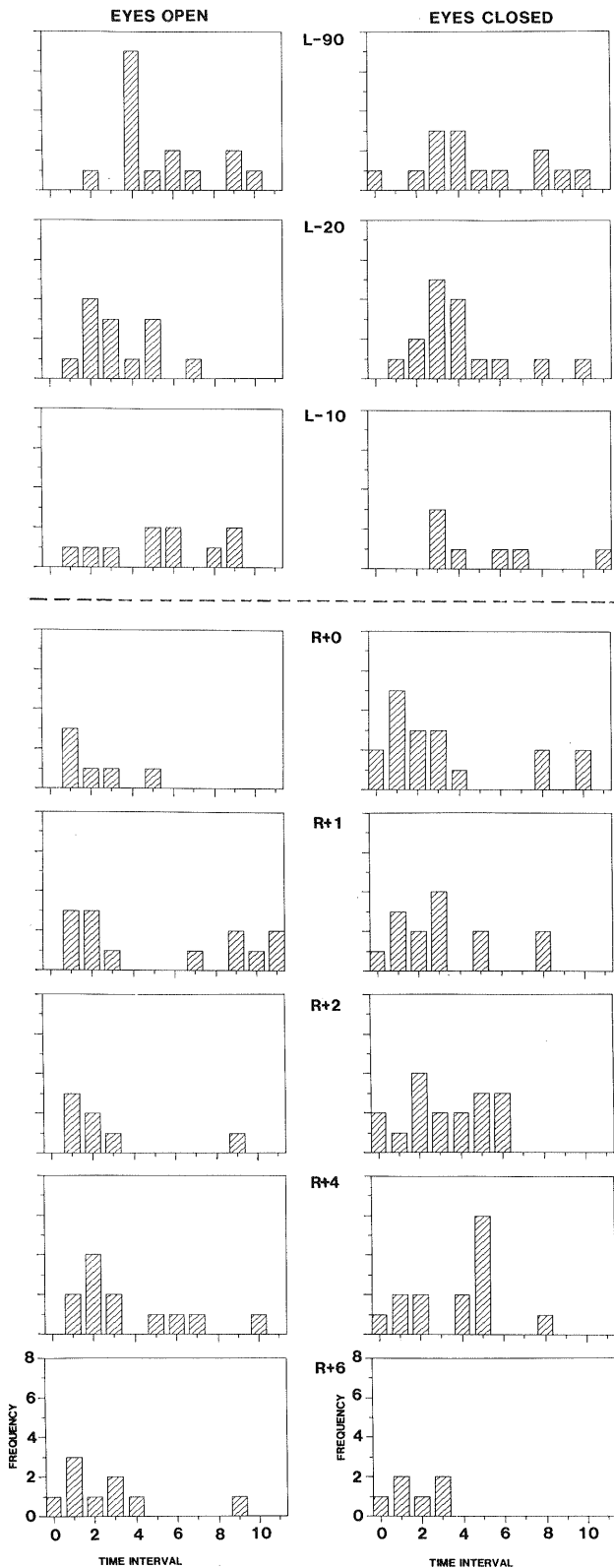


Fig. 5. Histogram plot of durations from the oscillations in the EMG activity of the late response for pre- and post-flight data in subject B. Eyes open (left) and eyes closed (right) data for TA data only. Vertical scale represents number of observations and horizontal scale is in tenths of seconds (bin widths are 100 ms wide)

during calibrations, tried to limit head movements, used a crouched posture to stand and commented that head motions seemed exaggerated. During the testing session, subjects were first unstable (mainly to tilt up trials) but by the end of the session (20 min) showed an increased ability to maintain posture during the tilts. Also, the consequences of fluid redistribution after returning to 1-g caused subject B to request a 5 min break in testing, after which he completed the tests without incident.

Prior to posture platform testing, Oman (SL-1 co-investigator) had subjects A and B make deep knee-bends². Only subject B reported an illusory motion of the floor. Subjectively, the floor appeared to come up to meet him. This subject estimated that one-third of the bending of the legs was due to apparent movement of the floor and not to the active movement on his part. The illusion was strongest with eyes open but was also present with eyes closed. Tested three hours later, the illusion was still present eyes open, but was absent when tested on R+1. A similar illusion was experienced by all subjects during the 1.7 g pullout phase of KC-135 parabolic flights conducted on R+4 and one year later.

R+1. Testing revealed that subjects were still unstable this day. On the initial tilt up trials, subjects B and D lost their balance but not to the extent experienced on R+0 for subject B. This instability was a surprise to the subjects who commented prior to the tests that their posture control had returned to normal and that they were not in any danger of losing their balance. This instability was reduced substantially on the following tilt up trial and continued to decline as the tests proceeded.

R+2. No subjects lost their balance on trials during these tests and comments from the crew indicated that they felt they were almost returned to pre-flight stability. By R+4, the subjects showed no problems dealing with the disturbances created by the platform motion. The same was true on R+6.

Quantitative measurement of whole body posture from the video tapes was not possible. However, reviewing pre- and post-flight video tapes did reveal several changes in posture strategy to handle the tilt disturbance. The differences post-flight (R+0) compared to pre-flight were that subjects A and B used more of their body to absorb the tilt disturbance. This took the form of more hip motion post-flight in an effort to minimize the motion of the head. However, we observed no change in hip motion after this disturbance, during the late response portion of

² In addition, subject B reported oscillopsia to pitch, roll and yaw head movements. Subject A reported no oscillopsia during similar head movements

Table 1. Modified sharpened Romberg test

I. Walking on 3/4" rail (number of steps, 18 maximum score)													
	L-180	L-152	L-120	L-65	L-44	L-10	Average pre-flight	R+0	R+1	R+2	R+4	R+6	Population average age adjusted
A	15	15	15	14	18	16	15.5± 1.4	[12	12]**	13	17	15	9.2± 4.0
B	18	13	15	18	18	18	16.6± 2.2	-	16	18	18	18	12.5± 2.6
C	18	18	18	18	18	17	18.0± 0.4	-	17	15	18	16	12.5± 2.6
D	15	14	11	9	12	13	12.3± 2.1	-	10	11	10	11	12.5± 2.6
II. Standing on 3/4" rail (number of seconds, 180 maximum score)													
	L-180	L-152	L-120	L-65	L-44	L-10	Average pre-flight	R+0	R+1	R+2	R+4	R+6	Population average age adjusted
A	24	12	14	13	26	8	16.0± 7.2	[12	9]*	18	10	12	13.2± 5.9
B	24	26	31	18	17	18	22.3± 5.6	-	[12	18]*	16	16	37.6±32.0
C	57	14	19	26	49	22	31.0±17.5	-	[19	15]**	18	15	37.6±32.0
D	19	8	11	11	13	9	11.8± 3.9	-	[6	8]*	9	10	37.6±32.0
III. Standing on 2 1/4" rail eyes closed (number of seconds, 180 maximum score)													
	L-180	L-152	L-120	L-65	L-44	L-10	Average pre-flight	R+0	R+1	R+2	R+4	R+6	Population average age adjusted
A	178	77	66	101	126	83	105.0±41.0	[15	22]***	48	42	151	24.2±14.0
B	98	180	55	87	127	170	119.0±48.8	-	[18	43]***	145	116	103.8±58.37
C	111	71	23	95	106	170	96.0±48.5	-	[16	43]***	46	51	103.8±58.37
D	50	63	22	15	32	14	33.0±20.0	-	[9	17]**	20	19	103.8±58.37
IV. Standing on 2 1/4" rail eyes open (number of seconds, 180 maximum score)													
	L-180	L-152	L-120	L-65	L-44	L-10	Average pre-flight	R+0	R+1	R+2	R+4	R+6	
A	180	180	180	180	180	180	180.0± 0.0	180	180	180	180	180	-
B	180	180	180	180	180	180	180.0± 0.0	-	180	180	180	180	-
C	180	180	180	180	180	180	180.0± 0.0	-	180	180	180	180	-
D	180	142	111	164	86	36	120.0±53.5	-	[80	66]***	99	76	-

Significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

the record. The static posture on 3 of the 4 subjects was not observed to be radically different *while standing steady on the platform*. However, subject C showed a change in platform posture preferring to assume a posture with knees and hip slightly flexed in his first test post-flight on R+1. This subject commented that this posture felt more stable and comfortable.

The modified Sharpened Romberg results for each test and each subject are summarized in Table 1. In general, subject A showed more postural stability and subject D less stability than the age-adjusted population norms. For all the results, statistical significance was assessed by a paired t-test comparing each subject's average pre-flight score to the first two post-flight tests on days R+0 and R+1 for A and R+1 and R+2 for B, C, and D.

Discussion

The post-flight instability in the absence of vision found on the Skylab crew (Homick and Reschke

1977) was again dramatically present on the Spacelab-1 crew after landing, and continued through at least R+2. The subjective feeling of dependence on visual cues to prevent falling, and wide stance in walking, were borne out by the quantitative ataxia tests (rails test). Subject O.G., who reported surprise at his instability, related a confirming incident that occurred on the night of R+0 and was similar to his experience after his 54 day Skylab mission. Having turned off the bedroom lights at the wall switch, he realized that he was unable to make his way to bed in the dark, and had to ask his wife to turn off the light once he had gotten safely to bed. This same subject said after falling off the wide rails with eyes closed on R+2 "at least now I can tell when I'm falling", and indicated that prior days he was "unlikely to detect an incipient fall in time to prevent it". The relatively greater attention paid to visual cues in spatial orientation post-flight, found in the visual-vestibular interaction experiments (Young et al. 1986b), was also borne out by the lesser decrement in the eyes open postural performance found in the rails and tilt platform tests. These

findings are supported by the post-flight stability results of Reschke et al. (1985) on another posture test and with the posture platform.

Despite the observed instabilities of erect posture, we found that there was no change in the early EMG latency or amplitude responses from our subjects. The small number of observations per test and the large variability of the data makes us cautious about over-interpreting these data. However, these results indicate that weightlessness for 10 days does not change the early postural control patterns as measured by EMG latency and amplitude following a disturbance in posture. Due to the multi-sensory nature of the postural control system, deficits in any one system (e.g., the vestibular system) may be masked or compensated by other systems involved in posture control. For example, while studying patients with vestibular impairments, Nashner et al. (1982) found using forward and backward movements of the support surface, that EMG latencies changed only in the most severely impaired patients and then only during eyes closed testing. This showed that congruent support surface inputs were sufficient to maintain posture control in all but the most severely impaired patients and only with eyes closed. The systems that contribute to the early postural response include the simple ankle stretch reflex (which is *destabilizing* for our disturbance) as well as vestibular connections to the spinal reflex arc. Although our tests did not allow differentiation between proprioceptive or vestibular mediated instability, changes in spinal activation seem unlikely in the light of Reschke's et al. (1984) result (post-flight) showing increased spinal activation only during free-fall. In addition, Watt and Money (1986) showed that the early otolith-spinal response to falls measured by EMG was at pre-flight levels at the time of testing post-flight despite the reduction found in flight. However, the posture disturbance used in our tests activated both otolith and semicircular canal responses. The results from tests of semicircular canal function from previous flights (Graybiel et al. 1977) and pre- and post-flight in these crewmembers, have shown no change in the VOR gain (Benson et al. 1985) and preliminary results indicate no change in phase (Oman, in preparation). Our results and those of others indicate that early postural responses to disturbances in postural equilibrium are not changed from pre-flight levels when tested 6 h post-flight. However, any change which was abolished during the first 5 h after landing (earliest test reported here was 6 h post-flight) would not have been observed. Indeed all four crew members said that they had considerable difficulty standing in the shuttle immediately after landing, and some com-

mented that they had to practice walking around the flight deck to avoid the embarrassment of falling down the stairs. Clearly, earlier post landing tests will be required. In addition, postural tests which can independently control conflicting sensory information from proprioceptive, visual, and vestibular inputs (Nashner et al. 1982) are needed to address questions of postural control that our limited tests could not answer. For example, questions remain regarding changes in the hierarchical nature of the postural control, or whether changes in posture were results of sensory adaptations or from more fundamental changes in CNS function in the brainstem.

The observed postural instability in the absence of any provable early EMG change following the disturbance stimulus may indicate that muscle atrophy, known to be associated with exposure to weightlessness (Thornton and Rummel 1977; Whittle et al. 1977), might contribute to this condition because control signals at pre-flight levels may be inadequate to control posture with partially weakened muscles. Crew members did show a loss of body weight and muscle wasting was observed but not measured. Nevertheless, there are several logical arguments against this mechanism as a major contributor to post-flight instabilities. First, the post-flight postural instability is strongest with eyes closed. One might expect to find that both eyes open and eyes closed conditions might be equally affected by muscle wasting. Secondly, if the eyes open condition did provide more stability for some reason, one would expect there to be a larger early EMG response with eyes open than with eyes closed (presumably to increase the force generated by the weakened muscle); both eyes open and eyes closed conditions showed no difference in pre- and post-flight EMG early response amplitude values. In addition, larger late EMG responses were found in eyes closed conditions post-flight. Consequently, we believe that any muscle atrophy that occurred in the crewmember's postural muscles on this mission did not play a major role in postural instability induced by inadequate early EMG response magnitudes used to stabilize posture in our subjects.

The absence of any significant change in the period of the EMG oscillations measured for the late response argues against an increase in the vestibular dead zone being responsible for the increase in sway post-flight eyes closed. Such an increase would be expected to lengthen the time to detect an off vertical position of the head/body since the sensors would need larger off vertical head and body movements in order to detect this change. One might also expect to find the period of the EMG oscillations would correspondingly increase. However, the oscillation

periods post-flight remained within the same range of periods as pre-flight and tended to be somewhat shorter on R+0 than those found pre-flight, the opposite we would have predicted with such a deficit. However, our stimulus was limited in its ability to induce consistent vestibular stimulation. Disturbances at the ankles needed to travel through several body segments prior to reaching the head. This usually results in somewhat uneven perturbations of the vestibular system. Consequently, future tests should attempt to control head movement or measure head motions during the tests. This would allow direct assessment of vestibular input to the postural control system.

Despite the small changes in duration of the late response, the amplitudes of these responses were observed to be larger early post-flight than pre-flight or on R+4 and R+6. These long-loop postural control responses are believed based on vestibular inputs and the perception of body position from proprioceptive and voluntary mechanisms. Nashner et al. (1982) have proposed a hierarchical concept by which vestibular inputs are used to gate the use of sensory information for posture control. According to this hypothesis, conflicting sensory information is referenced to signals from the vestibular system. Control of posture is mediated by that sensor which conforms to vestibular inputs. However, should the vestibular system still function but the interpretation of the incoming signals be changed, this might cause systems to focus on inappropriate sensory information to control posture. Alternatively, an unreliable vestibular system might cause the introduction of a new reference system. The increase in the late EMG response amplitude suggests that an altered estimation of body position from the vestibular or proprioceptive systems takes place immediately post-flight. However, whether this is due to a change in hierarchical control by central nervous system centers or to a change in postural strategy from control about the ankles to control about the hip, is beyond the scope of our data. Although one could presume a change in hierarchical structures to meet the required sensory rearrangement or alteration in control around the hip versus ankle, more expansive tests measuring body segment motion will be needed to substantiate such speculations.

The illusion experienced by subject B of the floor coming up to meet him while he made deep knee bends on R+0 prior to platform testing may hint at an alteration of vestibular interactions with visual and proprioceptive information during vertical accelerations. We speculate that the association between the vestibular sense of vertical accelerations and visual or proprioceptive (leg musculature) informa-

tion is different immediately post-flight than it was pre-flight. An underestimation of vertical acceleration sensed by the vestibular system coupled with veridical information from visual or proprioceptive systems could set up sensory conditions that leads to the illusion that the supporting surface is moving. Considering that this subject was exposed to 10 days of weightlessness it is conceivable that the adaptation of the saccular otoliths to weightlessness may play some part in this illusion. Inflight, the absence of a constant 1 g force may have in some manner changed the interpretation of vertical acceleration by the human from what it was pre-flight. Returning to earth and the reimposition of the 1 g force may cause the adapted individual to underestimate the magnitude of acceleration. However, a similar illusion experienced during the 1.7 g portion of parabolic flight has been explained by Lackner and Graybiel (1981) using proprioceptive mismatch between alpha and gamma motor signals. A clearer understanding of the mechanisms that are at work in the immediate post-flight period awaits further study.

All of the above observations support the conclusion that there is a definite and long lasting effect of sustained weightlessness on higher level descending postural control pathways although no post-flight modulation of the short latency ankle or otolith-spinal reflexes take place. Changes in postural strategy, as opposed to latency, support the findings of others. For example, Reschke et al. (1985) using a related posture platform test with the same subjects, also found minimal effect on EMG latency, but a change in the hip/shoulder postural stabilization strategy. These observations, along with others, are consistent with a sensory-motor reinterpretation hypothesis as an explanation for post-flight eyes closed instability (Young et al. 1984, 1986a; Parker et al. 1985; Reschke et al. 1984).

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References

- Benson A, von Baumgarten R, Berthoz A, Brandt Th, Bruzek W, Dichgans J, Kass J, Probst Th, Scherer H, Thumler R, Vieville T, Vogel H, Wetzig J (1985) Some results of the European vestibular experiments of the Spacelab-1 mission. In: Results of Space Experiments in Physiology and Medicine, AGARD Conf. Proceedings, No. 377, pp 1B-1-1B-10
- Clement G, Gurfinkel VS, Lestienne F, Lipshits MI, Popov KE (1984) Adaptation of postural control to weightlessness. *Exp Brain Res* 57: 61-72
- Clement G, Gurfinkel VS, Lestienne F, Lipshits MI, Popov KE (1985) Changes in posture during transient perturbations in microgravity. *Aviat Space Environm Med* 56: 666-671
- Crites T (1976) Pneumatic lift for posture platform. B.S. Thesis, Massachusetts Institute of Technology, Dept. Aeronautics and Astronautics
- Diener HC, Bootz F, Dichgans J, Bruzek W (1983) Variability of postural "reflexes" in humans. *Exp Brain Res* 52: 423-428
- Flourens P (1824) Recherches experimentales sur les propriétés des fonctions du système nerveux dans les animaux vertébrés. Crevot, Paris
- Graybiel A, Fregly A (1965) A new quantitative ataxia test battery. U.S. Naval School of Aviation Medicine Report NSAM-919
- Graybiel A, Miller EF, Homick JL (1977) Experiment M131. Human vestibular function. In: Biomedical results from skylab. NASA SP-377: 74-103
- Homick JL, Reschke MF (1977) Postural equilibrium following exposure to weightless space flight. *Acta Otolaryngol* 83: 455-464
- Homick JL, Reschke MF, Miller EF (1977) The effects of prolonged exposure to weightlessness on postural equilibrium. In: Biomedical results from skylab. NASA SP-377: 104-112
- Lackner J, Graybiel A (1981) Illusions of postural visual and aircraft motion elicited by deep bends in the increased gravito-inertial force phase of parabolic flight - evidence for dynamic sensory-motor calibration to earth gravity force levels. *Exp Brain Res* 44: 312-316
- Nashner LM (1976) Adapting reflexes controlling human posture. *Exp Brain Res* 26: 59-72
- Nashner LM, Black FO, Wall C (1982) Adaptation to altered support and visual conditions during stance: Patients with vestibular deficits. *J Neurosci* 2: 536-544
- Parker DE, Reschke MF, Arrott AP, Homick JL, Lichtenberg BK (1985) Thresholds for detection of linear oscillation following prolonged weightlessness. In: Results of Space Experiments in Physiology and Medicine, AGARD Conf. Proceedings, No. 377, pp 1B-11-1B-14
- Reschke MF, Anderson DJ, Homick JL (1984) Vestibulospinal reflexes as a function of microgravity. *Science* 225: 212-214
- Reschke MF, Parker DE, Anderson DJ, Homick JL (1985) Reinterpretation of otolith input as a primary factor in space motion sickness. In: Results of Space Experiments in Physiology and Medicine, AGARD Conf. Proceedings, No. 377, pp 3-1-3-18
- Thornton WE, Rummel JA (1977) Muscular deconditioning and its prevention in space flight. In: Biomedical results from skylab. NASA SP-377: 191-197
- Watt DGD, Money KE, Tomi LM (1986) M.I.T./Canadian vestibular experiments on the Spacelab-1 mission: 3. Effects of prolonged weightlessness on a human otolith-spinal reflex. *Exp Brain Res* 64: 308-315
- Whittle MW, Herron R, Cuzzi J (1977) Biostereometric analysis of body form. In: Biomedical results from skylab. NASA SP-377: 198-202
- Wicke R, Oman CM (1982) Visual and graviceptive influences on lower leg EMG activity in humans during brief falls. *Exp Brain Res* 46: 324-330
- Young LR, Oman CM, Watt DGD, Money KE, Lichtenberg BK (1984) Spatial orientation in weightlessness and readaption to earth's gravity. *Science* 225: 205-208
- Young LR, Oman CM, Watt DGD, Money KE, Lichtenberg BK, Kenyon RV, Arrott AP (1986a) M.I.T./Canadian vestibular experiments on the Spacelab-1 mission: 1. Sensory adaptation to weightlessness and readaption to one-g: an overview. *Exp Brain Res* 64: 291-298
- Young LR, Shelhamer M, Modestino SA (1986b) M.I.T./Canadian vestibular experiments on the Spacelab-1 mission: 2. Visual-vestibular tilt interaction in weightlessness. *Exp Brain Res* 64: 299-307

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