SPATIAL ORIENTATION AND POSTURE DURING AND FOLLOWING WEIGHTLESSNESS: HUMAN EXPERIMENTS ON SPACELAB LIFE SCIENCES

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Abstract—The 4 payload crew members of the Spacelab Life Sciences 9-day space flight in 1991 were subjected to limited vestibular testing in flight as well as pre and post flight. Major differences in individual “perceptual style” appeared in their reaction to the visual–vestibular stimuli in the rotating dome experiment, and especially in the extent to which nondirectional tactile cues served to anchor the subjective vertical and body postural reactions. The ability of subjects to point to remembered target positions was degraded in space, which produced a tendency to point low in some subjects in flight. The eye movements and subjective response to sudden stops and head pitching following continuous spinning (damping) were measured both in space and on the ground. Although subjective duration of inflight rotation for the dumping tests was shorter than that for the preflight tests, the postrotatory nystagmus, with or without head pitch, was lengthened in time constant relative to preflight. Ground tests, in addition to the flight experiments, investigated the changes following weightlessness in subjective and oculomotor reactions to whole body tilt, the ability to balance with eyes open and closed; leg muscle strength and stamina as related to posture; visual field dependence; and the perceptual and oculomotor reactions to horizontal linear acceleration. Several of these tests, as well as postflight measures of motion sickness susceptibility, revealed subtle evidence of neurovestibular alterations that lasted a week or more following the 10-day orbital exposure.

Keywords—vestibular; posture; perception; adaptation; human; weightlessness.

Introduction

The fact that the neurovestibular system is met with a special challenge in weightlessness, and that it is involved in a complex adaptive process that may be associated with space motion sickness, has been well established. The further readaptation required upon return to earth, or during re-entry for that matter, has also been recognized. When free floating in microgravity, the otolith organs no longer provide a vertical reference signal to the brain; rather they respond only to linear acceleration, as the astronaut propels himself about by pushing off walls, ceiling and floors. In an effort to reinterpret the meaning of the otolith signals, and to provide some sort of a reference “down” axis, required by at least some of the astronauts, the central nervous system seems to attend more to nonvestibular cues, particularly visual, tactile, and proprioceptive.

The practical aspects of this neurovestibular adaptation are the prediction, prevention, and treatment of space motion sickness, which affects over two-thirds of all space voyagers; the reduction of risk in an emergency egress in the event of an accident; and the long-term issues of human adaptation to very long duration flights en route to Mars, with or without the extra challenge of a rotating “artificial gravity” spacecraft.
The underlying research questions deal with the fundamental role of gravity in the development of specialized sense organs, the neural connections that are associated with the vestibular systems under altered environmental conditions, and the levels of the brain at which these reversible adaptive processes take place.

In order to explore the full range of neuro-vestibular adaptation, a series of human experiments was performed, each with a different combination of stimuli and neuromuscular or subjective responses. Several of the tests are refinements of investigations previously conducted on Spacelab 1 (1983) (1,2), Spacelab D-1 (1985) (3,4), or STS 41-G (1985) (5). Other tests, including the measurement of postflight fatigue in postural muscles, were initiated with the SLS-1 flight.

1. Visually Induced Roll (Young, Jackson, Grobleau, Modestino)

The alteration of the visual-vestibular interaction by loss of gravity is considered one of the possible causes of space motion sickness.

To investigate the interaction between conflicting visual, vestibular, and tactile information, the crew member places his head inside a “rotating dome” hemispherical display. During rotation of the visual surround, the subject typically experienced self-rotation, or “vection” in the opposite direction, as well as stabilizing movements of the eye, head, and trunk. The methods and results of this experiment have recently been published (6).

Beyond the previously reported tendency to increased use of visual cues for spatial orientation during and following space flight, the SLS-1 results uncovered interesting variability in individual perceptual styles. Some subjects were strongly tied to a seemingly solid anchor by the localized tactile cues from bungee cord induced foot pressure, whereas another felt a strong contribution toward self-rotation under the same circumstance. Similarly, some subjects indicated a strong inhibition of visually induced motion because of the tight grip on the bite board, although it provided no directional cues. The differences in perceptual styles may be related to the contributions of sensory and body-centered vectors in the normal and adaptive calculation of spatial orientation. In a new test for this mission, the subjects were tested pre and post flight with no biteboard or other restraint as they stood in front of the rotating dome. The increase in postflight instability, and a strong tendency to sway when the visual field rotated, was quite marked, even for subjects who felt stable and had limited reported vection. One example of this phenomenon, which lasted during the full postflight testing week, is shown in Figure 1.

2. Vestibulo-ocular Reflex (Oman, Balkwill)

The crew member was seated in a rotating chair and was rotated for a minute and then suddenly stopped. The angular vestibulo-ocular reflex (VOR), whose dynamics are known to be “g” sensitive, induced nystagmic eye movements. Eye movements were recorded in darkness using electro-oculography (EOG). In half of the tests, the head was pitched forward 90° immediately after stopping, which is known to shorten the time constant of the VOR (“dumping”). In the flight experiment, the chair was hand spun. Details of the methods and results are presented in another paper in this volume (7). All 4 payload crew members served as subjects for the experiment, which was carried out on Mission Days 3 and 4. For the inflight rotation tests, 3 of the 4 subjects showed a time constant of decay of postrotatory nystagmus that was equal to or larger than the preflight head-erect time constants. Since earlier results on brief exposure to weightlessness in parabolic flight (8) showed a shortening of apparent time constants, these results imply that yaw angular velocity storage (which increases the apparent time constant) actually increases during longer exposures to weightlessness. The ground result of sudden dumping of nystagmus was apparently not present in weightlessness, supporting the in-
Involvement of gravity and the otolith organs in the genesis of this phenomenon. In contrast, the inflight dumping rotation sensation was shorter than for the preflight tests. The gain of the yaw vestibulo-ocular reflex appeared unchanged when measured after several days in space. The results of inflight and preflight postrotatory VOR, with and without pitching, are illustrated for one subject in Figure 2.

3. Awareness of Position (Watt)

The awareness of position experiment performed on SLS-1 attempted to separate two factors that contribute to the apparent alteration in knowledge of limb and body position in space—degradation in proprioceptive function and an inaccurate external spatial map (10). It required that subjects point at 5 remembered target positions on a reference screen, with eyes closed either continuously or only during the pointing. Alterations in proprioceptive accuracy would influence both tests, and alterations in the external spatial map would be shown by the former.

Target pointing accuracy was demonstrated with a hand-held light pointer, recorded both on video and by the observer. The sequence was completed 47 times, 6 to 9 times preflight on each subject, in flight on FD 3 on all 4 subjects, and 3 times post flight.

Preflight, all subjects learned to point accurately at memorized targets, with better performance when the eyes had just been closed. Inflight pointing accuracy was very poor, with a bias toward pointing low. Performance was always better when the eyes were closed only while pointing and was unchanged preflight, inflight, and postflight under these circumstances. Mean pointing bias for each subject, before, during, and following the flight, are illustrated in Figure 3. Two subjects who were very accurate on the ground demonstrated greatly reduced performance inflight, with pronounced floorwards biasing of their points. One subject who always pointed left and down preflight, was initially more accurate inflight, but each successive point was farther from the target, leading to a mean bias similar to that seen on the ground. One subject who always pointed low preflight was more accurate inflight, beginning to drift floorwards only towards the end of the sequence. Postflight, all
subjects made greater errors than preflight, but in a similar direction. Recovery to pre-flight level of performance was nearly complete by 7 days after landing. Two subjects made several errors when trying to touch various body parts, and noted that their arms were not exactly where expected when their eyes were opened, both in and postflight.

These data suggest that in the absence of vision, the maintenance of a stable external spatial map is highly dependent on the presence of the normal gravitational force. The time course of recovery after landing suggests that this phenomenon may be mediated by the vestibular otolith organs. Proprioceptive function during an active pointing task is close to normal in weightlessness. Proprioception does become less reliable in the more relaxed limb however, and this may explain why two subjects had some difficulty touching various body parts and knowing the exact position of their floating arms.

4. Responses to Linear Acceleration (Merfeld, Christie)

The US Laboratory Sled was modified to permit testing of the astronaut responses to both lateral and longitudinal linear acceleration along an earth horizontal axis, pre and post flight. The purpose of these tests was to study the response of the linear acceleration sensors as modified by weightlessness, and to augment the inflight measurements carried out on the D-1 mission (4). Subjects were accelerated sinusoidally at high (1.0 Hz) and low
(0.25 Hz) frequencies with a peak acceleration of 0.5 g and with a series of low acceleration steps; measurements were made of horizontal and torsional eye movements, perception of acceleration, and illusions of body motion. The eye movement tests included linear visual-vestibular interaction whereby the horizontal nystagmus response to ongoing 60°/s optokinetic stimulation was modified by the sled acceleration. Finally, the crew attempted to control the sled motion, subject to known random disturbances, using only nonvisual cues.

The horizontal eye movement optokinetic/vestibular nystagmus showed the anticipated modulation by sled motion. Horizontal eye movements during lateral (Y-axis) acceleration were found to have a gain that was frequency dependent. The influence of weightlessness on the vestibular modulation of optokinetic nystagmus is not apparent, at either high or low frequencies. The amplitudes of the modulations show a strong dependence on frequency (higher gain at 1.0 Hz than at 0.25 Hz), but no clear changes in gain postflight.

The closed loop tracking results failed to replicate the improved tracking on landing day seen on earlier missions for lateral acceleration. If anything, somewhat poorer use of vestibular cues for Y-axis (inter-aural) manual control were exhibited by all subjects on the day after landing and 2 days later. For z-axis (longitudinal) acceleration, however, 2 of the
subjects showed a significant improvement in closed loop tracking ability on the day after landing, whereas 2 others showed no significant change following weightlessness.

The time to detect linear acceleration, at levels close to perception thresholds was measured for both lateral and longitudinal horizontal acceleration. The results indicate a pattern of confused and erratic response to early postflight accelerations. For lateral acceleration (Y-axis), the velocity constant (product of acceleration and time to detect) is lower post flight, representing increased sensitivity to linear acceleration. On the other hand for longitudinal (Z-axis) acceleration, the velocity constant is increased following flight.

Only 1 of the 4 subjects experienced a preflight tilt and “hilltop illusion” of body motion on the sled, with a reported preflight tilt of 20 to 30° and a depression of 12” to 24” at the ends of the track during low frequency lateral acceleration. This subject also experienced motion sickness on the sled only for these conditions. Post flight, however, this subject never reported a tilt illusion, although some vertical displacement was retained, and motion sickness symptoms were absent.

The experience of living and working in space for 10 days may alter the manner in which the nervous system deals with otolith organ signals during linear acceleration. The absence of any (expected) improvement in closed loop tracking argues against a general hypersensitivity carried over to post flight reactions to acceleration. Indeed, the possible reduction in acceleration modulation of linear optokinetic nystagmus preflight might represent some aspect of internal confusion about interpretation of otolith signals shortly after return to earth. The improvement of closed loop tracking in the longitudinal axis, however, which conforms to the trend seen following the D-1 mission, suggests a different nervous system treatment of signals from the saccus than from the utricular. The difference in the influence of weightlessness on the sensitivity to low level horizontal accelerations (more sensitive to lateral and less sensitive to longitudinal) is consistent with the conjecture that responses to primarily saccular stimuli are more disturbed by removal of the 1-g bias than are responses to primarily utricular stimuli.

5. Post Flight Postural Instability
(Roy, De Luca, Modestino)

Postural stability was severely degraded post flight, as measured by the ability to stand and walk on narrow and wide rails. Objective measurements were the time spent balancing on the rail or the number of steps in the walking task.

The decrements were very evident for all subjects when first tested on R+1, especially for standing on a narrow rail and standing eyes closed on a wide rail. Despite a feeling on the part of the crew that they were “back to normal” by R+4, the eyes-closed instability was evident for the entire postflight week.

A new postural stability measurement (11) was introduced to assess the role of muscle atrophy and fatigue on postural stability. The muscle strength, the initial median frequency (IMF), and the conduction velocity of electromyographic (EMG) signals during 30-s ankle dorsiflexion and plantarflexion, at 40% and 80% of maximum voluntary contraction (MVC), were measured before and after the flight. Muscular activity was recorded from the tibialis anterior during dorsiflexion and from the soleus and gastrocnemius muscles during plantarflexion (12).

Measurement error associated with longitudinal testing was minimized by the use of a leg-referenced device capable of relocating the EMG surface electrodes to within 2 mm. Intraclass correlation coefficients for quantifying the repeatability of preflight measurements were acceptable for all parameters measured, although the MVC and IMF parameters were more repeatable (ICC = 0.98 and 0.94, respectively) than MF slope or conduction velocity (ICC = 0.54 and 0.53).

Changes in isometric strength can be assessed by a comparison of MVC values for preflight and postflight tests. There were no changes in MVC for the tibialis anterior mus-
cle (that is, dorsiflexion) post flight compared to pre flight. Although all subjects were able to attain their preflight 80% MVC force levels during dorsiflexion, a few had difficulty sustaining it for the full 30-s duration. Plantarflexion MVC was reduced post flight by 10% to 40% and recovered to pre flight levels by R + 6. Subjects with the lowest preflight plantarflexion MVC also had the greatest relative reduction in MVC post flight.

A reduction in initial median frequency and conduction velocity can be an indication of muscle atrophy (11). All subjects except one (subject T) demonstrated a postflight reduction in IMF at R + 0 of approximately 10% to 20% with the gastro-csoleus muscles more consistently affected than the tibialis anterior. Figure 4 shows the changes in median frequency at the two contraction levels for one subject, and demonstrates the typical postflight reduction and subsequent recovery, more clearly seen for the soleus than for the gastrocnemius or for the tibialis anterior muscles. Recovery of IMF to preflight levels typically occurred at R + 4 or R + 6.

Changes in MF slope that result in larger negative values (that is, greater rate of decrease in MF during a sustained contraction) are indicative of greater fatigability of the muscle, attributable primarily to metabolite accumulation at the muscle membrane (11,12). The soleus muscle, being the most endurant, had the least negative MF slope compared to the other muscles. Changes in MF slope post flight were similar for the gastrocnemius and tibialis anterior, with greater changes and more consistency observed in the gastrocnemius, particularly at 80% MVC. Comparison across subjects did not result in any one subject appearing to have greater changes in MF slope post flight. Trials resulting in the greatest change in MF slope also resulted in the least amount of recovery. For some of these trials, the median frequency did not fully recover by R + 6.

Conduction velocity of the EMG can decrease in magnitude proportional to a decrease in muscle cross section area or accumulation of H+ ions at the muscle membrane (12). The technique of estimating conduction velocity can be problematic due to muscle inhomogeneity or extreme sensitivity to electrode positioning on the muscle (11). Conduction velocity was measured only in the tibialis anterior muscle. No consistent changes in conduction velocity were observed post flight in this muscle, except in one subject (M) who showed a decrease in the initial conduction velocity at 80% MVC. Conduction velocity slopes during a contraction were unchanged post flight. The higher variability in this parameter compared to other EMG parameters made it difficult to identify a significant effect associated with the flight.

In summary, measurable changes associated with strength and endurance were observed in the muscles of the lower limb following flight (13). Strength decrements were more muscle-specific than endurance decrements and were limited to the antigravity muscles. The few subjects with severe decrement of plantarflexion strength post flight and relatively rapid recovery may be explained as temporary inability to fully activate muscles fibers rather than as the result of severe muscle atrophy. This type of muscle insufficiency is commonly seen in patients on bed rest who can regain a large degree of strength in only a few days of practice, probably due to muscle reeducation. Although not conclusive, the changes in the EMG parameters, particularly for the IMF, which was highly repeatable preflight, support the likelihood that a mild atrophy of muscle fibers occurred, primarily in, but not limited to, the calf musculature. The increased negative slope of the MF is consistent with a type II shift in enzyme activity resulting from muscle unloading. However, in light of the relatively high variability and small number of subjects, this result is not conclusive.

Muscular atrophy as well as alteration of vestibular function contribute to the postflight instability. The wide stance and narrow "cone of stability" represent the inability to sense and recover from shifts of body axis from the apparent vertical. The special sensitivity to standing with eyes closed demonstrates the continued inability to detect and react to tilt
Figure 4. Initial median frequency of EMG, pre flight and days R+0, 2, 4, 6. Diagonal crosshatching represents 40% MVC; dotted crosshatching represents 80% MVC.
signals measured by the otolith organs following weightlessness.

Conclusions

Exposure to weightlessness influences nearly all aspects of human spatial orientation and control of head, eye, and body position. Some of the inflight phenomena that may be related to space motion sickness include the adaptive use of nonvestibular cues in setting reference frames and the degradation in accuracy of proprioception. Some of the postflight consequences extend beyond wide gait and postural instability with eyes closed to include subtle alterations of posture, visual field dependence, muscle stamina, and motion sickness that may last a week or more following a 9-day flight.

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This summary only touches some of the main points of the individual experiments. Further data and explanation of methods is provided in the “180-day report” (14) and in the formal publications of the investigators for each experiment, identified in the text.

REFERENCES