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Short review

Posture, locomotion, spatial orientation, and motion sickness as a function of space flight

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Abstract

This article summarizes a variety of newly published findings obtained by the Neuroscience Laboratory, Johnson Space Center, and attempts to place this work within a historical framework of previous results on posture, locomotion, motion sickness, and perceptual responses that have been observed in conjunction with space flight. In this context, we have taken the view that correct transduction and integration of signals from all sensory systems is essential to maintaining stable vision, postural and locomotor control, and eye-hand coordination as components of spatial orientation. The plasticity of the human central nervous system allows individuals to adapt to altered stimulus conditions encountered in a microgravity environment. However, until some level of adaptation is achieved, astronauts and cosmonauts often experience space motion sickness, disturbances in motion control and eye-hand coordination, unstable vision, and illusory motion of the self, the visual scene, or both. Many of the same types of disturbances encountered in space flight reappear immediately after crew members return to earth. The magnitude of these neurosensory, sensory-motor and perceptual disturbances, and the time needed to recover from them, tend to vary as a function of mission duration and the space travelers' prior experience with the stimulus rearrangement of space flight. To adequately chart the development of neurosensory changes associated with space flight, we recommend development of enhanced eye movement systems and body position measurement. We also advocate the use of a human small radius centrifuge as both a research tool and as a means of providing on-orbit countermeasures that will lessen the impact of living for long periods of time with out exposure to altering gravito-inertial forces. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Posture; Locomotor; Motion perception; Space motion sickness; Space flight

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1. Introduction

At the system level, our window into the neural processes that mediate human spatial orientation and adaptive changes occurring to the stimulus rearrangement encountered during orbital flight is primarily obtained through second order responses. We measure eye movements with the head stationary or moving (active/passive), posture following manipulation of the support surface, and locomotor behavior during walking or running. Importantly, verbal reports of perceived self-orientation and self-motion provide ancillary data which enhances and complements conclusions drawn from the analysis of oculomotor, postural, and locomotor responses. It is the purpose of this paper to provide new work by the Neurosensory Laboratory, Johnson Space Center within a historical context. Specifically, this new work will be reviewed along with the relevant literature associated with our understanding of human responses to space flight derived from detailed measurement of posture, locomotion, illusions, spatial orientation, and motion sickness. Additional reviews, that are extremely comprehensive in nature are available [17,140,142].

2. Posture and locomotion

2.1. Posture

Assessments of postural ataxia associated with exposure to microgravity have included testing where astronauts balanced on rails of variable width, [32,61,62,70] stabilometry, [14,43] exposure to base of support movement [2,19,30,70,107] voluntary arm or toe rises, [18,93] bending at the waist, [96,97,137,141] deep knee-bends, [16,18,19,79,96-98,139,173,174] measurement of muscle potentials from the antigravity muscles, [6,30,43,76,138,139,143,148,173,175] vibrating selected antigravity muscles, [145-147] and postural tests designed to selectively eliminate visual, proprioceptive, or vestibular information [120,122,123,169]. The results from these varied and complex experiments suggest that in earth orbit, where gravitational field strength is negligible, the structural and anatomical systems that allow upright orientation and movement on earth are at best not required and at worst inappropriate. Within this framework, a multiple subject study of postural equilibrium where the mechanisms of sensory-motor balance control were assessed under normal, reduced, and/or altered (sway-referenced) visual and

somatosensory input conditions in a group of 45 astronauts has been recently undertaken. In this study, the six sensory organization test conditions used were: (1) eyes open Romberg, (2) eyes closed Romberg, (3) sway-referenced vision (sway-referencing was accomplished by servo-controlling the pitch orientations of the force plate and/or visual surround to follow the subject's center of mass sway), (4) sway-referenced support surface, (5) sway-referenced support surface with eyes closed, and (6) sway-referenced support surface with sway-referenced vision. In tests 5 and 6, the only accurate orientation information was provided by the vestibular system. When these complex sensory interaction tests were performed immediately after landing, balance control decrements were observed 1.6-4.5 h after flight in every astronaut studied. Under the standard Romberg conditions (tests 1 and 2) and the simple sensory conflict conditions (tests 3 and 4), the sway amplitudes increased after flight by less than 1.0 deg. But, under the complex sensory conflict conditions (tests 5 and 6) the sway became stability treating and more often than not, the test subjects would, during at least one trial, initiate a ballistic fall. The time course for recovery of postural stability followed a double exponential path: a very rapid stability improvement over the first 8 to 10 h after flight, followed by a more gradual return to preflight stability levels over the next 4 to 8 days. Furthermore, since the performance recovery was associated primarily with improvements in conditions 5 and 6, the results also suggest that postflight postural ataxia is mediated primarily by alterations in the vestibular (presumably otolithic) feedback loop. Ankle proprioceptive feedback loop was also altered in some subjects (test 5), perhaps as a result of decreased postural loading or new movement strategies developed during space flight, and most subjects had increased reliance on the visual feedback loop during the recovery process (tests 5 and 6), perhaps in partial compensation for the degraded performance of the other two feedback systems during space flight [11].

When comparisons were made between the rookie and veteran astronaut groups, significant differences were observed in those postflight conditions in which vestibular inputs provided the only reliable spatial orientation reference cues (tests 5 and 6). Rookies exhibited greater sway than veterans after flight. In a separate analysis of overall postural stability based on the Equitest composite equilibrium score, first-time fliers had the lowest scores on landing day, second time fliers had significantly higher scores than the first-time fliers, and third time fliers had higher scores than second time fliers.

In addition to the earlier studies [18,93] where voluntary perturbations were initiated by an arm or toe rise, a recent investigation [82] using longer duration microgravity exposure has shown, consistent with previous studies, a redistribution of ankle musculature tonic activity when crewmembers initiated a voluntary arm motion (arm raise) and were secured to the support surface at their feet. Unlike earlier investigations, this redistribution of tonic activity reverted to the terrestrial pattern of activity (i.e., ankle extensor greater than flexor tone) when these subjects were secured to the support surface with bungee cords extending from their waists. This finding suggests that biomechanical constraints are influential in the expression of tonic muscle activation. Additionally, this study demonstrated that rapid arm raises are accompanied by lower limb and trunk neuromuscular activity which precedes the onset of arm movement which retains the same temporal and spatial characteristics as that observed during voluntary arm raises on earth. The impact of space flight on bipedal postural stability in response to self-generated perturbations has been further assessed [82,83] with two astronauts and six cosmonauts who performed rapid, unilateral arm raises prior to and after 3-6 months aboard the Mir. Surprisingly, there was a drastic decrease in arm acceleration during the arm rises (i.e., perturbation) that was linked to significant increases in their postural sway postflight. Moreover, post-flight lower limb muscle activation patterns were modified relative to preflight such that the spatial and temporal activation patterning was significantly disrupted after the acceleration phase of the arm movement, indicating that the subjects had difficulty generating the required neuromuscular activation patterns necessary to maintain postural stability in response to the perturbation. Inflight, six crewmembers performed the rapid arm raise task while freefloating to assess the impact of increased somatosensory input on the magnitude of preparatory neuromuscular activation during the freefloating arm raise. Pressure boots (special shoes designed to increase pressure on the soles of the subject's feet, but probably increased pressure over the entire surface of the feet) were used to increase the

amount of somatosensory input from the feet. This condition was compared directly to trials with the crewmembers performing the task in their stocking feet. The results confirmed previous findings that the preparatory activation of the lower limbs is attenuated when subjects perform arm raises while freefloating without pressure on the feet [84-87]. The addition of the foot pressure resulted in enhanced preparatory activation (Fig. 1).

2.2. Locomotion

During normal terrestrial locomotion the head is actively stabilized relative to space with relatively high precision [10,131]. In light of these results Berthoz and Pozzo [10] and Pozzo et al. [131] have hypothesized that postural and gait motor control mechanisms may utilize a 'top-down' control scheme to ensure head stability during body movement. Such a strategy is advantageous because a stable head facilitates the maintenance of gaze stability during locomotion. Grossman et al. [15], have determined that during walking and running, the peak velocities of head rotations in yaw, pitch, and roll are generally maintained below $100^\circ/s$ and are thus below the saturation velocity ($350^\circ/s$) of the vestibulo-ocular reflex [132]. Grossman et al. [47] have characterized gaze stability during locomotion and have found that the angle of gaze is maintained relatively stable during walking and running. However, individuals with loss of vestibular function and neurological disease experience increased oscillation of the head and instability of gaze during locomotion leading to impaired acuity and instability of the visual scene during locomotion [42,48,130,154-156]. These results underscore the importance of head stability in aiding gaze stabilization during terrestrial locomotion.

Angular head movements can actually contribute to gaze stabilization during locomotion. In humans, both during treadmill and free locomotion, pitch head rotations (in the sagittal plane) aid in the stabilization of gaze by compensating for the vertical translation of the trunk that occurs with each step during locomotion [12,13,58,131].

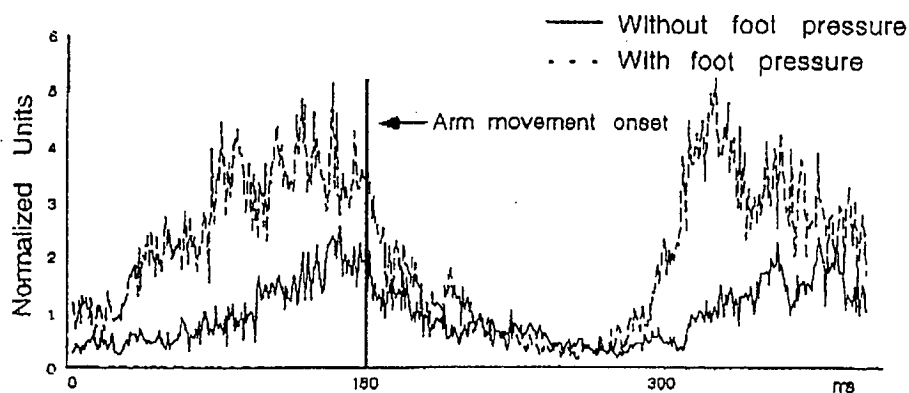


Fig. 1. Representative right biceps femoris EMG record from one subject displaying the increased neuromuscular activation associated with the use of foot pressure while performing rapid arm movements while freefloating.

Thus, coordinated head and trunk movements play a central role in maintaining clear vision during natural body movements, and they may have a strong influence on the organization of postural and locomotor control patterns.

Recently, Bloomberg et al. [12] have investigated whether exposure to the microgravity environment encountered during space flight adaptively modifies head–trunk coordination strategies during postflight locomotion. A total of 23 astronaut subjects were asked to walk pre- and postflight (6.4 km/h, 20 s trials) on a motorized treadmill while visually fixating on a centrally located earth-fixed target positioned either 2 m (far) or 30 cm (near) from the eyes. Head and trunk kinematics during locomotion were determined with the aid of a video-based motion analyzing system. Fig. 2 shows data from one subject illustrating the relationship between vertical translation of the trunk that occurs during each step and the corresponding pitch angular head movement during the near target condition. The preflight response is depicted in Fig. 2a while Fig. 2b presents an example in the same subject acquired 4 h following the return to earth. During preflight testing pitch head movements act in a compensatory fashion to oppose vertical trunk translation during locomotion: as the trunk translates upward, the head pitched forward/downward, thereby assisting maintenance of target fixation. Following space flight there was a significant alteration in coordina-

tion between compensatory pitch angular head movements and vertical trunk translation. This is evidenced by a breakdown in the smooth, sinusoidal nature of pitch head movements into a number of sub-components.

The degree of association between vertical trunk translation and corresponding compensatory pitch head movement was characterized using the coherence function. The coherence value can vary between zero and unity. If a perfect linear relationship exists between the two signals at some specific frequency, then the coherence function will be equal to unity at that frequency. If the two signals are completely unrelated, the coherence function will be zero over all frequencies. The coherence between pitch head and vertical trunk movements during gaze fixation of both far and near targets was significantly reduced following space flight indicating decreased coordination between the head and trunk during postflight locomotion (see Fig. 3). These modifications in the efficacy of head movement control may account for the reported disruption in gaze performance during locomotion and may contribute to postflight postural and gait dysfunction by disrupting descending control of locomotor function [12]. The association between postflight changes in head–trunk control and disruptions in locomotor function reflect the importance of top–down hierarchical control of posture and gait stability [130,131].

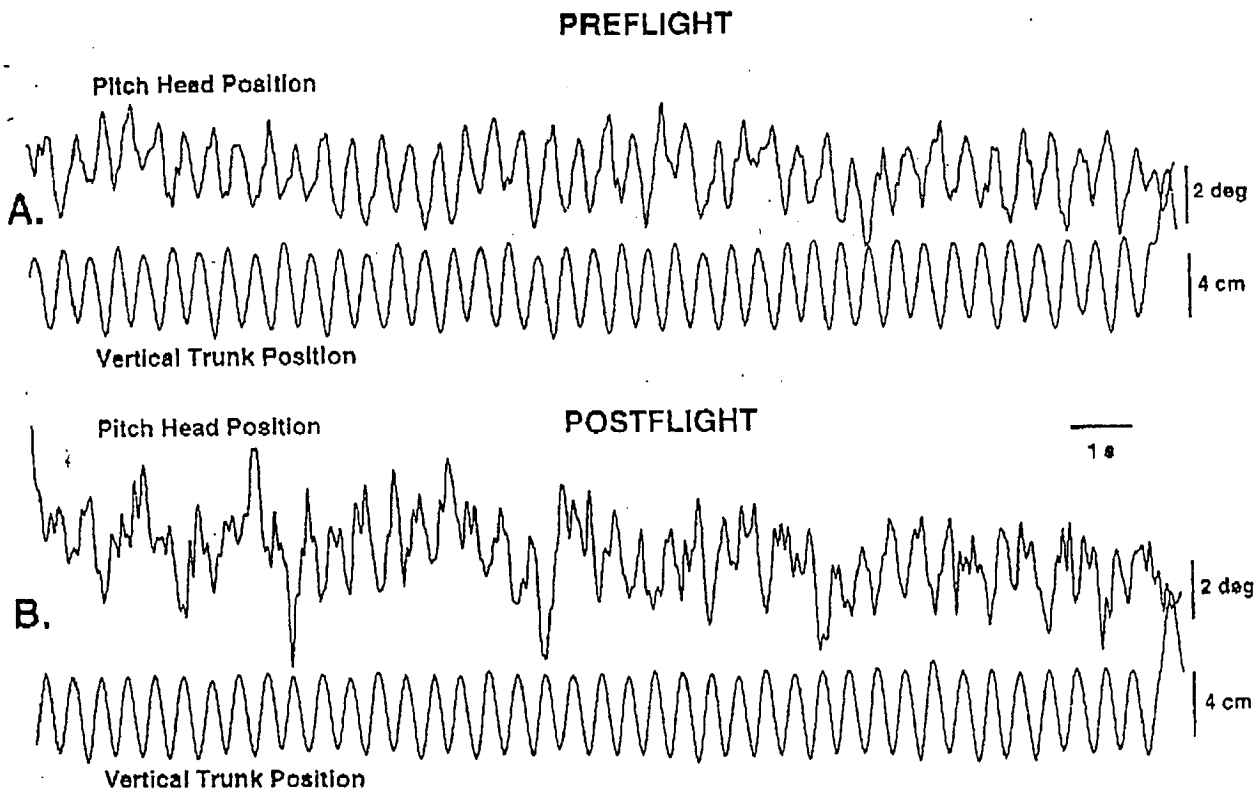


Fig. 2. Head–trunk waveforms from one astronaut showing the relationship between vertical translation of the trunk and corresponding pitch angular head movement for pre (a) and postflight (b) treadmill locomotion at 6.4 km/h.

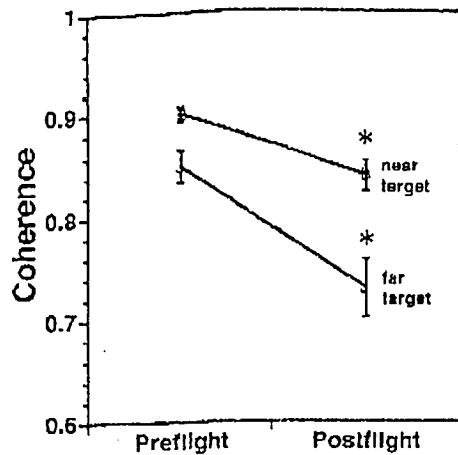


Fig. 3. Mean (+1 S.E.) pre and postflight coherence values relating vertical trunk translation and corresponding pitch head movement for all subjects combined during treadmill locomotion at 6.4 km/h. Stars denote a significant difference ($p < 0.05$) between pre and postflight mean coherence values.

Both the far and near target conditions show postflight decrements in coherence, however, the decrease is greater during the far target condition. The apparent difference in head-trunk coordination between the far and near ocular fixation conditions may be a result of subjects gaining enhanced visual feedback of the head-trunk coordination breakdown during the near target condition. During near target fixation, the degree of apparent target motion will be greater than during far fixation. Greater sensitivity to apparent target motion during near target fixation may provide enhanced visual cues that improve head movement control during this condition. Similarly, enhancement in postural stability using near and far visual contextual cues has been observed by Dijkstra et al. [29] in standing human subjects asked to maintain postural stability in a moving visual environment.

In the same series of experiments Bloomberg et al. [12] determined that astronauts showed varying postflight responses in the frequency spectra of pitch head movements. The variability in subjects' response patterns may reflect discrete head movement control strategies intended to maximize the central integration of veridical sensory information during the postflight recovery process. Head movement strategies adopted during locomotion may reflect specific task constraints and the requirement for reliance on specific sources of sensory information required for the effective organization of coordinated movement. Nashner [113] has described two possible head-trunk coordination strategies observed during the maintenance of dynamic postural equilibrium. The first strategy ('strap down') calls for the head to be fixed to the trunk during body movement, so that in essence the head and trunk can be considered a single unit. Adopting this strategy means that

head-trunk control is simplified; however, the ability to resolve complex movements into their linear and angular components by the otoliths and semi-circular canals becomes complex. Alternatively, the 'stable platform strategy' fixes orientation of the head with respect to the gravitational force vector, essentially stabilizing the head in space while the body moves underneath. The advantage of this strategy is that larger sustained rotations of the head are actively nulled, permitting the simplification of the otolithic process responsible for detecting linear acceleration and static orientation of the head. The 'cost' incurred by this strategy is that complex head-trunk patterns of coordination are required to successfully execute this control scheme.

The significant postflight reduction in predominant frequency amplitude of pitch head movements during locomotion observed in some subject may be caused by these subjects' attempts to reduce the amount of angular head movement during locomotion, and therefore reduce potential canal-otolith ambiguities during the critical period of terrestrial readaptation. This, in turn, may further simplify the coordinate transformation between the head and trunk, presumably allowing an easier determination of head position relative to space. Head movement restriction during locomotion is also shown by patients suffering from vestibular deficits [71] and by children prior to development of the mature head stabilization response [3]. However, this strategy may not be optimal for gaze stabilization because it results in a disruption in the regularity of the compensatory nature of pitch head movements during locomotion. This strategy also restricts behavioral options for visual scanning during locomotion. Consequently, there may be trade-offs between head movement strategies depending on the imposed constraints. Once significant readaptation takes place, then a decrease in constraints on the degrees-of-freedom of head movement likely occurs, returning performance back to preflight levels.

Examination of lower limb kinematics during postflight locomotion have revealed evidence for subtle yet consistent changes in segmental coordination following space flight of 8-9 days [3]. Analyses which focused on the moment of heel strike and toe off during walking have identified significant increases in variability of phase plane dynamics of the knee and hip joints during postflight treadmill locomotion [103]. Differences between loading histories experienced in 1 g and weightlessness are potentially sufficient to stimulate adaptation in mechanical impedance of the musculoskeletal system [104,115]. As a consequence, the ability to appropriately attenuate energy flow, especially at heel contact phases of human walking and running, is impaired. The forces generated at this contact phase have been shown to travel through the body resulting in head vibration [92]. We suspect these vibrations may challenge gaze stabilization and visual and vestibular function given the already vulnerable nature of the visual-vestibular systems postflight.

Consistent with the changes in segmental motion after flight are the modifications in the neuromuscular activation characteristics of the lower limb. Layne et al. [28] reported that the relative amplitude of muscle activation was modified by space flight particularly around the behavioral events of heel-strike and toe-off. Additionally, the temporal relationship between the inhibition of the gastrocnemius and the activation of the tibialis anterior around toe off was disrupted after space flight. The neuromuscular coordination between the gastrocnemius and tibialis anterior is critical to obtain adequate push-off and subsequent toe clearance. This disruption in lower limb neuromuscular activation patterning may have contributed to alterations in the body's management of the foot to head energy flow during walking. This change could impact the ability to maintain stable head movement control during locomotion, exacerbating on-going alterations in visual-vestibular control of movement.

3. Spatial orientation

Spatial orientation depends on perception of position, orientation, and motion of external objects as well as on perception of one's own position, orientation, and motion. In physics, a coordinate system which can be used to describe the position, orientation, and motion is called a 'reference frame'. The particular reference frame which a given observer takes to be stationary is called the 'rest frame' for that observer. It has been suggested that people select 'internal rest frames' which are used to create the subjective sense of spatial orientation [55]. During adaptation to alterations of environmental conditions, such as microgravity, internal rest frame construction may be altered. Further, like other mental constructs, subjective rest frames may be incorrect or inappropriate; inappropriate rest frame formation may result in illusory, visually-induced self-motion perception (vection).

Discussions with shuttle crew members and analyses of transcripts recorded during space flight investigations suggest that in microgravity, astronauts select from two basic rest frames, to determine their self-orientation and self-motion [53,140]. On earth, the spatial orientation rest frame is based primarily on gravity (detected by graviceptors including those in the vestibular apparatus, the viscera, and the skin) and visual scene polarity (visual environment features that normally align with gravity such as trees, houses, etc.). In microgravity, the astronaut's rest frame may be based on visual scene polarity cues provided by the shuttle and spacelab interiors as well as other crew members, and on the internal head and body Z-axes (sometimes called 'ideotropic vectors'). This suggests that astronauts' microgravity spatial orientation rest frames can be situated on a continuum between one determined by the visual scene (V-S) to one determined by internal Z-axis

vectors (I-Z). Rather than a continuum, however, it seems more likely that rest frame selection is bi- or multi-stable and may switch depending on variables such as the task being performed [53]. Based on discussions with 24 of the crewmembers who have participated in DSO 604-011 (Motion Perception Reporting), it was found: (1) 46% were classified as Type I-Z, (2) 46% were classified as Type V-S, and (3) 8% were classified as mixed Type I-Z/V-S [53,55,140].

3.1. Postural illusions

Vibrating muscles in order to elicit illusory limb movement during parabolic flight enhanced the illusion of arm motion during 1.8 g and diminished it during the free-fall phases of parabolic flight [77]. The investigators concluded that muscle-spindle receptor output per unit stretch of spindle is influenced by gravity as follows: Unloading the otoliths in microgravity decreases their descending modulation of α and γ motoneurons, resulting in decreased tonic vibration reflexes. Alternatively, the increased gravitational load on the arm may have been equivalent to resistance. This concept was tested when subjects, restrained with back support, experienced vibration of the soleus and anterior tibialis [146,147]. One cosmonaut reported enhanced tilt (relative to preflight) early in flight while two others reported the sensation of rising from the deck later in the flight, and when the back brace was replaced with axial restraint in the Z-axis the cosmonauts reported a return to the preflight tilt sensation when the postural muscles were vibrated. The investigators concluded that a new model of sensory-motor relationships is developed in weightlessness and that the sensory-motor context determines which model (terrestrial or microgravity) is used to interpret proprioceptive messages and to effect postural and perceptual responses [145].

The position receptors in the cervical column of the neck also play an important role in somatosensory function. During the Spacelab D-1 mission, a crew member's neck receptors, without vestibular input, were stimulated by bending the subject's trunk passively to the side or forward while the head was fixed to the floor of the Spacelab [166,169]. These manipulations produced the surprising response of illusory rotation of a head-fixed target seen in that crew member's helmet [68,164]. One explanation proposed that the missing otolithic input is supplanted by the neck receptors in flight [164]. The Austrian-Russian mission assessed the influence of the neck receptors on verticality by using neck bends and horizontal arm movements. On earth, stimulating the neck receptors by assuming various head positions (rotation, bending to the side) normally causes a slight change in horizontal arm movement. In microgravity, bending the head to the right caused the arm's horizontal movement pattern to turn counterclockwise in a frontal plane. This phenomenon increased on FDS, returned to normal after landing, and

was interpreted as an expression of disturbance in body scheme [9].

In addition to the muscle vibration and neck rotation experiments, proprioceptive illusions have been noted during and after shuttle flights. Crewmembers, performing otolith-spinal reflex tests after landing, reported sensations of the floor moving up and down under them as they hopped up and down [174]. Rhythmic deep knee bends and arm flexes resulted in a feeling of alternatively pushing and pulling (feet restrained) the space craft away or toward themselves [79]. During 'drops' (in which the crewmembers were pulled to the floor of the space craft with bungee cords attached around their waists and adjusted to have a pull equal to their body mass) astronauts have reported that in flight the fall associated with being accelerated toward the deck of the shuttle felt more like a translation than a fall (particularly late in the flight), and that postflight the floor would rise to meet their feet. Never did they report falling [139,174,187]. Several possibilities exist as to the source of proprioceptive illusions. The data of Watt et al. [174] suggest that changes in proprioceptive function caused by microgravity are expressed as a sensory deficit. Sensory-motor programs also could be altered due to different modes of locomotion in weightlessness. Finally, the system that compares motor commands with resulting sensory inputs may not be able to distinguish correctly between self-motion and movement of the world. The latter interpretation fits well with the theory of tilt-translation reinterpretation (see Section 4.2 below), and has been proposed by others to account for illusions of self- or surround-motion experienced by returning astronauts [106,127,137,139,187].

3.2. Visual illusions

On orbit and immediately after landing, astronauts frequently report that head movements produce illusions that their visual surroundings are moving [41,94,135]. These illusions, related to disturbances in the gaze-control system, known as oscillopsia, refer to apparent displacement of visual targets during passive or voluntary head movement. Oscillation of visual targets was first reported by Skylab astronauts [41]. The Spacelab-1 crew experienced significant oscillopsia for several hours after landing [119].

The term 'vection' refers to the illusion of self-motion induced in a stationary individual viewing optical flow imagery of the type that normally would be seen with true motion. Visually induced illusions become stronger in space, perhaps because the otolith organs neither confirm nor deny body tilt in microgravity. Rotating-dome experiments performed with a roll (looking inside of a rotating drum with visual markers moving about the subjects' X-axis) visual stimulus conducted with subjects from Spacelab-1 [188], D-1 [30], and SLS-1 [184-186] showed that most subjects experienced increased vection intensity in microgravity, with some reporting complete rotatory

(saturated) vection during flight. Results from SLS-1 and TML-1 suggest that visual and tactile cues are weighted differently for each subject such that preflight strategies are different from postflight ones, and none are consistent across subjects [172].

Linear vertical vection induced by a portable visual stimulator was investigated with one cosmonaut during the 8-day Austrian-Russian mission [111], and later with two others aboard Mir [112]. Initially, the onset of linear vection was, as expected, earlier than that seen preflight. However, when measured as late as 175 days into flight, vection was delayed and of a lower magnitude. Of particular interest was the occurrence of a response difference between upward going vs. downward moving pattern where episodes of inverted vection were observed [112].

Illusions of self-motion or unusual surround-motion have been addressed in several studies. Perceived translational self-motion was reported during passive roll stimulation in darkness 1 to 3 h after shuttle landing [137]. Unexpected illusory translation of either the subject or the visual surround was reported by two crew members who performed voluntary pitch or roll head movements during atmospheric entry and again after the shuttle had stopped [137]. These observations, and similar ones reported by Young et al. [187], support the hypothesis that signals from receptors that respond to linear acceleration are reinterpreted during adaptation to weightlessness [127].

Almost all crew members perceive themselves or their surroundings to move when they move their heads during flight, during re-entry, and after landing. The intensity of the on-orbit disturbances seems to increase with length of time in flight: the longer the flight, the more illusory phenomena are reported. Results currently are limited to flights lasting 10 days or less; however, the intensity and duration of illusory motion seem to reflect mission length, prior spaceflight experience, and perhaps the volume of the spacecraft (e.g., the middeck vs. the larger Spacelab module) [140].

Even though individual experiences vary, common input-output motion perception disturbances are of three types: (1) *gain disturbances*, in which perceived self/surround motion seems exaggerated in rate, amplitude, or position after the head or body movement; (2) *temporal disturbances*, in which the perception of self- or surround-motion either lags behind the head-body movement, persists after the real physical motion has stopped, or both; and (3) *path disturbances*, in which angular head and body movements elicit perceptions of linear or linear and angular self- or surround-motion [140]. These perceptual disturbances seem to be most intense or compelling during atmospheric entry, less so immediately after wheel-stop, lesser still late in flight, and weakest shortly after achieving orbit. Also, a given head or body movement usually induces perceptual disturbances of more than one type. For example, one crew member reported that sinusoidal roll head movements made late in flight resulted in self-transla-

on (path), that the translation was greater than the roll put (gain), that there was a delay between the roll input and the self-translation, and that self-translation persisted after the roll input ceased (temporal).

4. Space motion sickness

4.1. Symptoms, incidence, duration, correlates, and individual differences

Exposure to provocative real or apparent motion leads to the progressive cardinal symptoms of terrestrial motion sickness which typically include pallor, increased body warmth, cold sweating, dizziness, drowsiness, nausea, and vomiting. The signs and symptoms of space motion sickness (SMS), when considered with the time course of symptom development and the movements encountered upon exposure to microgravity, suggest that sickness experienced during spaceflight, while similar to terrestrial motion sickness, may differ slightly from those exhibited during terrestrial motion sickness. In particular, sweating has been the least frequently reported inflight symptom, and flushing is more common than pallor [65,136]. Nearly universal are malaise, loss of appetite, loss of initiative, and irritability. Stomach awareness, vomiting, headache (perhaps due to headward fluid shifts), impaired concentration, lack of motivation, and drowsiness are reported more frequently in microgravity than during acute motion sickness on earth [25,63,119,158]. Vomiting is usually sudden, infrequent, and may not be accompanied by prodromal nausea. Bowel sounds are decreased or absent, and gastrointestinal symptoms appear minutes to hours after the spacecraft achieves orbit. Illusions which may have contributed to SMS have been reported by 80% to 93% of Russian cosmonauts [31,100], as well as by American crews [54].

As on-orbit mobility has increased, the incidence of SMS has also increased. Hypersensitivity to angular head motions is common, particularly in the pitch plane [119,158]. Excessive movements made early during flights tend to increase symptoms with resolution occurring within 72 h [39,158]. Although not observed during the U.S. Shuttle program, adaptation to provocative motion during the Skylab flights proved to convey some immunity to motion sickness immediately after the flights [40]. Overall, SMS has been reported by 48% of the cosmonauts over the course of the Russian space program [31]. In the U.S. program no motion sickness was reported during the U.S. Mercury and Gemini programs, [59] but 35% of the Apollo crew members and 60% of the Skylab crew members developed symptoms [25]. Symptom occurrence during 24 of the space shuttle flights was no different for career vs. noncareer astronauts, commanders or pilots vs. mission specialists, males vs. females, different age groups, or first-time vs. repeat flyers. Overall, it is estimated that

approximately 80 to 90% of all shuttle crewmembers experience some symptoms of motion sickness, and a very small percentage never recover or become symptom-free for the duration of the flight. Potential predictors of SMS previously reviewed [69,142] have included susceptibility to ground-based motion stressors [136], measures of ocular torsion in hypo- and hypergravity (based on the otolith-asymmetry hypothesis) [27,28,95], correlations of various biochemical indices before, during, and after spaceflight with SMS susceptibility and symptom severity [11,45,46,73,89,90,168], and physiological parameters [50,51,56,134,135,151-153,157]. Prediction based on susceptibility during a first flight appears at this time to be the best indicator, correctly predicting an individual's susceptibility during a second flight in 77% of the cases [25]. This finding is consistent with the observation made by Diamond and Markham [26,27] and Diamond et al. [28], Parker [124], and Mittelstaedt and Glasauer [109], that there are stable factors associated with individual differences which can make prediction feasible. Symptom recurrence at landing reportedly afflicts 27% of Russian cosmonauts after short flights (4 to 14 days) and 92% of those returning from longer missions [31], but does not necessarily correlate with inflight SMS. 'Readaptation syndrome' seems to affect a similar percentage of U.S. crews [25].

4.2. Theories and hypotheses that address SMS and sensory-motor adaptation to microgravity

Two of the major theories advanced to account for SMS are fluid shifts and sensory conflict, the latter also known as neural mismatch, sensory mismatch, or sensory rearrangement.

A *fluid shift* mechanism has been proposed to explain how a headward fluid shift could produce concomitant changes in intracranial pressure, the cerebrospinal-fluid column, or the inner ear, thereby altering the response properties of vestibular receptors, could produce SMS [34,35,125,128]. It has also been suggested that a shift may change angiotensin activity and produce SMS by altering the hormonal or neurotransmitter balance in the chemoreceptor trigger zone [7]. Russian investigators recently have begun to change their emphasis from fluid shifts to sensory-motor conflict as the primary cause of SMS [75], although some continue to investigate the role of cephalad fluid shifts as an etiological factor [99]. Individual susceptibility to SMS thus far has not been predicted with this hypothesis [60].

The *sensory conflict theory* advanced by Reason and Brand [135] is the most parsimonious theory. It assumes that human orientation in three-dimensional space, under normal gravitational conditions, is based on at least four sensory inputs to the central nervous system: (1) the otolith organs, (2) the semicircular canals, (3) the visual system, and the touch, pressure, and kinesthetic systems. When the environment is altered in such a way that information from

the sensory systems is not compatible and does not match previously stored neural patterns, motion sickness results. Shortcomings of the sensory-conflict theory include its lack of predictive power, inability to explain those situations in which conflict exists without sickness, failure to include sensory-motor conflict, inability to explain specific mechanisms by which conflict actually gives rise to vomiting, and failure to address the observation that adaptation is not possible without conflict. Several modifications to the conflict theory may be helpful in overcoming some of these weaknesses, including the evolutionary hypothesis of Treisman [110,159], the concept of otolith imbalance [26-28,74,78,165,167,168], the concept of sensory compensation (input from one sensory system is attenuated and signals from others are augmented) [54,126,137,141,187], and the otolith tilt-translation reinterpretation hypothesis (OTTR) [118,127,189] suggesting that: (1) weightlessness is a form of sensory rearrangement to which people adapt, (2) graviceptors signal both orientation with respect to gravity (tilt) and linear acceleration, which is perceived as translation, and (3) in weightlessness, graviceptors do not respond to static pitch or roll, but do respond to linear acceleration. Because stimulation from gravity is absent during spaceflight, interpretation of the graviceptor signals as tilt is meaningless. Therefore, during adaptation to weightlessness, the brain reinterprets all graviceptor output to indicate translation, and this interpretation is carried as a compensatory response when astronauts return to the earth's surface.

5. Countermeasures

Only limited success has been achieved in controlling SMS or preventing neurovestibular disturbances associated with space flight. Research has proceeded along four broad lines of inquiry: (1) training, (2) selection, (3) pharmacologic, and (4) the use of mechanical or electrical devices. Preflight vestibular training in the Russian space program has concentrated on the use of Coriolis (cross-coupled angular) acceleration [81], and training with stimuli designed to interact across sensory and motor modalities [1,72].

Training to prevent sensory-motor disturbances in the U.S. flight program in the context sensory-stimulus rearrangement uses postulates derived from the OTTR hypothesis. Specifically, two trainers are used to present a variety of stimulus rearrangements: the Device for Orientation and Motion Environments (DOME) designed to achieve graviceptor stabilization, and the Tilt-Translation Device (TTD) designed to enhance perceived translational movement induced via linearvection and tilt [51,52,54,108,121,144]. Recent findings indicated that several stimulus-rearrangement conditions in both training devices produced perceptual experiences similar to those of flight [54,94]. The U.S.

has also used autogenic feedback training to reduce SMS both in the shuttle program and in conjunction with the Russians [20-22].

Selection as a countermeasure has not been used in the U.S. flight program, however, preflight vestibular training (or attempts made to *select* individuals) in the Russian space program has concentrated on the use of Coriolis (cross-coupled angular) acceleration [81], and training with stimuli designed to interact across sensory and motor modalities [1,72].

Pharmacological countermeasures for SMS directed against motion sickness have proven somewhat effective, although caution in prescribing medications must be exercised [181]. In ranking drugs with respect to their effectiveness in preventing symptoms of motion sickness [178], it has been found that drugs tended to be grouped according to their principal pharmacological action [4,33,36-38,44,66,67,78,80,91,102,116,117,133,149,150,160-180,182].

Antimotion-sickness drug research reviewed by Reschke et al. [142] and Wood [176,177] shows that the vast majority of antimotion-sickness drugs have been administered orally. In conjunction with space flight, oral administration presents a problem due to the reduction in gastric motility and the gastric emptying characteristic of acute motion sickness [135,183]. For this reason, alternate routes of administration, such as transdermal application [4,8,37,38,64,66,91,102,116,117,133,162], suppositories [23], and intramuscular injections (IM) [8,16,25], have been investigated. NASA is currently using promethazine as the drug of choice with IM injection as the primary route of administration [5,24].

Mechanical and electrical devices as countermeasures have been explored almost exclusively in the Russian space programs as means of alleviating motion sickness. The Cubans have developed boots or shoe like devices (typically referred to as the Cuban Boot or sandals) that have been used to hydraulically apply pressure to the bottom of the feet. This approach (see Section 2 of this paper for the approach undertaken by investigators in the U.S./Russian program regarding the Cuban boot) has apparently met with limited success [57] as have load suits (Penguin Suits) with adjustable elastic bands that produce tension over the chest, back, abdomen, side, and leg seams [49,171], and a neck pneumatic shock absorber device (cap with elastic cords) that imparts a cervical load to vertebrae, stretching neck muscles as the head is forced upright [100,101]. Occlusion cuffs worn at the hip to reduce or prevent the headward shift of body fluids, and applying lower body negative pressure also reportedly had a positive influence on cosmonaut health by decreasing dizziness, illusions, nausea, and the sensation of head pulsations [31,100]. The use of weak electrical currents (electroanalgesia) has been explored to prevent or treat space motion sickness but has been effective in increasing resistance to experimentally induced motion sickness [105,114,129].

5. Future research

Contributions that can be made from the neurological, neurovestibular, and sensory-motor community should be directed by a four-fold research program with the ultimate aim of providing not only a better scientific understanding of how individuals adapt to the environment of space flight, but also of determining how we can best protect space travelers who may be exposed to very long periods of life without gravity. First, a better understanding of individual differences and how individuals adapt to the flight environment needs serious consideration. Second, we need to stress the interactive nature of adaptability and the maintenance of homeostatic well-being including interactions of neurovestibular and cardiovascular responses to space flight. Third, we need to obtain a better understanding of spatial orientation in space flight. Fourth, research should be directed toward the development of effective countermeasures.

One of the hallmarks of human space flight experimentation has been the apparent wide diversity of sensory-motor adaptive and readaptive responses experienced by space travelers in any single study. This diversity may reflect the unique multifactorial and multisystem impact imposed by space flight. Future research will need to focus on the root causes of this response diversity to both understand the phenomena and to design effective countermeasures to mitigate their negative consequences. Indeed, we will probably need to tailor the complement of countermeasures provided to each crewmember based on their unique configuration of responses to microgravity. In order to achieve this we will need to support research that provides good predictors of individual performance that will enable us to implement the appropriate countermeasure prescription for each crewmember's specific constellation of microgravity induced responses.

Space flight research in the past has tended to focus on individual systems (i.e., vestibular, cardiovascular, bone, muscle, etc.). This approach has had the secondary effect of limiting a better understanding of interactions between those systems which must adapt to the flight environment. For example, we have come a long way in understanding changes in cardiovascular and cardiopulmonary function as the body adapts to microgravity, and we have accepted the importance of understanding calcium metabolism with its effect of bone loss and the importance of exercise in maintaining muscle mass. We have not, however, stressed the importance of top-down interactions that may play a role in all of the changes we have attributed to space flight. What role does the vestibular system have on the regulation of cardiovascular function? For example, the gravitational inertial force (GIF) is constantly monitored by the otoliths. Is this information available to assist cardiovascular reflexes? How important is the descending vestibular input in maintaining muscle tone, and consequently in maintaining muscle mass when these systems

are exposed to prolonged microgravity? How is calcium loss effected by the change in descending vestibular information and the subsequent loss of muscle tone and mass? How is autonomic function related to the complex changes observed in adaptation to the flight environment, and can we relate hormonal/endocrine changes to adaptability and function?

We have only hypothetical constructs, or at best hypotheses, underlying our understanding of spatial orientation during space flight. To date, there have been no investigations that have looked at how the descriptive information (gathered by visual, auditory, olfactory, and touch) that provides us with information about the surrounding environment and the relationship of that environment to ourselves is integrated with the sensory information (vestibular, proprioceptive and somatic sensors) which normally provides us with information about tilt, movement of the head and body relative to the earth and the magnitude of the GIF. Experiments designed to provide information on the mechanisms of spatial orientation during space flight and how our orientation changes with environmental parameters and flight durations will be necessary if we are to assure the safety of those performing EVA's and related activities where reliable sensory information is required.

With longer and longer missions being planned, sensory-motor and vestibular countermeasures will be required to insure mission success. Currently, the available countermeasures are poorly understood, and there are no effective countermeasures in place (with the exception of antimotion sickness drugs) that can be applied for beneficial neurovestibular adaptation to space flight or return to earth. Coupled with the development of effective neurosensory and sensory-motor countermeasures is the need for a reliable, effective ground-based analog for space flight. Bed rest, while appropriate for investigating many of the side effects associated with space flight, is not the answer for neuroscience. Consideration should be given to the use of various kinds of centrifuges, including slow rotation rooms for ground-based analogs.

7. Vestibular facility for international space station

Perhaps the most important neuroscience facility required for the space station will be a human rated centrifuge. As a major facility, the centrifuge should be supported with appropriate hardware for the reliable and accurate recording of eye and head movements in three dimensions, mechanisms for obtaining subject sensory-motor responses, and equipment capable of monitoring CNS and ANS responses. Prior to final design, this facility should be developed and tested aboard the shuttle/space-lab/spacehab. Overall, experiments conducted in a microgravity environment will require a centrifuge, whether it is a short-armed device or of sufficient radius to avoid

problems associated with high angular velocities, to perform studies that are counterbalanced and controlled. Suid another way, the finest improvement that we can make for experimental evaluation of vestibular function (and related physiology) in microgravity would be a switch that allowed gravity to be turned on or off. A centrifuge provides this switch.

8. Conclusion

Since the first space flights until the present, what we have learned about vestibular and sensory-motor responses to microgravity has grown substantially. We are now in the position of verifying previous experimental results where the number of subjects was small, asking new questions, and seeking new ways to improve on our base of knowledge. Regardless of advances that have been made in space flight and neuroscience, we are lacking experimental evidence which can only be gained with long duration flights. We are moving to a new era of space travel and all aspects of neuroscience must be considered to support crews for extended travel and working for long periods of time on the surface of planets beyond our earth.

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