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M. I. T./Canadian vestibular experiments on the Spacelab-1 mission: 1. Sensory adaptation to weightlessness and readaptation to one-g: an overview

L. R. Young¹, C. M. Oman¹, D. G. D. Watt², K. E. Money³, B. K. Lichtenberg¹, R. V. Kenyon¹, and A. P. Arrott¹¹ Man-Vehicle Laboratory, Massachusetts Institute of Technology, Cambridge, MA 02139, USA² Department of Physiology, McGill University, Montreal, Quebec, Canada³ Defense and Civil Institute of Environmental Medicine, Downsview, Ontario, Canada

Summary. Experiments on human spatial orientation were conducted on four crewmembers of Space Shuttle Spacelab Mission 1. This introductory paper presents the conceptual background of the project, the relationship among the experiments and their relevance to a "sensory reinterpretation hypothesis". Detailed experiment procedures and results are presented in the accompanying papers in this series. The overall findings are discussed in this article as they pertain to the following aspects of hypothesized sensory reinterpretation in weightlessness: 1) utricular otolith afferent signals are reinterpreted as indicating head translation rather than tilt, 2) sensitivity of reflex responses to footward acceleration is reduced, and 3) increased weighting is given to visual and tactile cues in orientation perception and posture control. Three subjects developed space motion sickness symptoms, which abated after several days. Head movements, as well as visual and tactile cues to orientation influenced symptoms in a manner consistent with the sensory-motor conflict theory of space motion sickness. Six short duration tests of motion sickness susceptibility, conducted pre-flight, failed to predict sickness intensity in weightlessness. An early otolith-spinal reflex, measured by electromyography from the gastrocnemius-soleus muscles during sudden footward acceleration, was inhibited immediately upon entering weightlessness and declined further during the flight, but was unchanged from pre-flight when measured shortly after return to earth. Dynamic visual-vestibular interaction was studied by measuring subjective roll self-motion created by looking into a spinning drum. Results suggest increased weighting of visual cues and reduced weighting of graviceptor signals in weightlessness. Following the 10 day flight, erect posture with eyes closed was disturbed for several days.

Somewhat greater visual field dependence post-flight was observed for two of the crew. Post-flight tests using horizontal linear acceleration revealed an increased variance in detection of acceleration. The ability of the returned crew to use non-visual lateral acceleration cues for a manual control task appeared enhanced over their pre-flight ability for a few days after return.

Key words: Spatial orientation – Vection – Motion sickness – Vestibular – Weightlessness

Introduction

The nearly weightless (*microgravity*) environment of spaceflight provides challenging opportunities for research on sensory-motor adaptation. This paper provides an introduction to the series of interrelated experiments performed on the first Spacelab mission (SL-1) in November 1983 by a team of investigators from MIT and Canada. These investigations, most of which are described in detail in the accompanying five articles, are all aimed at assessing human vestibular and visual responses in space and are intended to clarify the presumed alteration in sensory and motor function in weightlessness. Our working hypothesis, which tied together the various experiments and against which the results are tested, is one of "sensory reinterpretation." A preliminary report was published previously (Young et al. 1984).

Our experiments were designed to help assess human sensory/motor adaptation to weightlessness and readaptation to earth's gravity, and to simultaneously examine the question: is space sickness a motion sickness? The underlying neuroscience research question is how a fully developed sensory

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

motor system, which receives redundant information from several sensory mechanisms, reorganizes to account for the environmentally imposed change in the relationship between motor commands and sensory feedback. The results of this research relate to classic studies of sensory rearrangement (e.g. Held and Freedman 1963; Rock 1966; Wallach and Smith 1972; Wallach and Bacon 1976) and to recovery from vestibular lesions (e.g. Igarashi et al. 1970; Fregley and Graybiel 1970). In particular, we ask how pitch and roll perception and postural adjustment are affected by the abnormal pattern of otolith afferent signals which must accompany sustained weightlessness. Our working hypothesis, explained below, was that in the process of sensory adaptation to weightlessness, the low frequency components of the otolith afferent signals (dependent upon head orientation in 1-g) are centrally inhibited or reinterpreted, and that visual and tactile cues consequently play an increasing role in spatial orientation.

Our research also relates directly to the etiology of space sickness, now recognized as a significant problem impacting astronaut performance, safety and well-being. Although space sickness symptoms were not reported in the smaller Mercury and Gemini spacecraft, they have been consistently reported in the Soviet space program (Matsnev et al. 1983) and experienced by Apollo and Skylab crews (Homick and Miller 1975; Graybiel et al. 1977). The incidence among Shuttle crews has exceeded 50% (Homick et al. 1985). It has been parsimonious to assume that the genesis of space sickness is similar to that of motion sickness as experienced on earth (e.g. Benson 1977; Oman 1982b), although conclusive evidence has been lacking and alternative hypotheses have been suggested (see Oman et al., this issue). The etiology of motion sickness is thought to involve the same physiological mechanisms responsible for spatial orientation and body movement control. Based on a sensory-motor conflict theory (Reason 1978; Oman 1982a), motion sickness results when incoming sensory signals no longer match expected patterns learned during previous sensory/motor experience. Because of the environmentally imposed change in graviceptor response to head movements in weightlessness, motion sickness was expected to occur in space. Space sickness would be expected to be exacerbated by real or perceived changes in body orientation, and to subside with a time course paralleling adaptation of sensory-motor systems subserving spatial orientation.

Earlier formal space flight investigations of the influence of weightlessness on human vestibular responses have included the pioneering studies of Graybiel and coworkers (1977) who observed the

absence of motion sickness susceptibility to out of plane head movements made in a rotating chair when tested after the fifth day in space. They also showed the ability to maintain a body oriented reference frame in weightlessness. Homick and Reschke (1977) reported postural instabilities with eyes closed following return of the Skylab astronauts to earth. Other tests of inflight postural stability (Clement et al. 1984) and assessment of the vestibuloocular and optokinetic reflexes have been conducted more recently (Thornton et al. 1985; Watt et al. 1985; Vieville et al. 1986). Relevant Soviet research on man in space has largely been limited, until quite recently, to assessment of motion sickness countermeasures, relationship of spatial illusions to symptoms, and post-flight studies of orientation perception, neuromuscular function and ocular counterrolling (e.g. Yakovleva et al. 1980; Matsnev et al. 1983). Spacelab-1 provided the opportunity for three teams of experimenters (European Space Agency, NASA Johnson Space Center, and MIT/Canada) to perform extensive tests on vestibular function of the same crewmembers during a mission devoted to scientific goals.

A sensory reinterpretation hypothesis for adaptation to weightlessness and readaptation to one-g

A sensory reinterpretation hypothesis formed the basis for our proposed experiments and serves as a useful tool for interpreting the results (Young et al. 1983). It assumes that the functionally appropriate physiological adaptation to weightlessness should involve a reinterpretation of afferent signals originating in the graviceptors, particularly in the otolith organs. These receptors act as linear accelerometers, and respond to the physical input of gravito-inertial force. The adequate input to the otolith organs is the force per unit mass or "specific force" (f), familiar to users of accelerometers for inertial navigation (Fernandez and Macomber 1962). This force, acting on the otolithic membranes, is equal to the vector sum of gravity (g) minus linear acceleration (a). Physically, specific force is the entity tracked by a pendulum. On earth, a non-accelerating body is subject only to the "downward" specific force vector g , and the pendulum points toward the vertical. In orbital flight, a body which is not accelerating relative to the spacecraft experiences a linear acceleration a (as the spacecraft free falls around the earth) equal to the gravitational acceleration g . The specific force acting on the otolith organs is zero, except when head movements are made. Disregarding small gravity gradient effects, a pendulum in earth orbit would assume any arbitrary orientation and velocity previ-

ously imparted to it, and would be of no use in indicating the direction of the center of the earth, or of the spacecraft floor. The otolith organs, of course, continue to provide the central nervous system (CNS) with afferent signals which are modulated by each head acceleration. We believe that on earth the signals from the saccular as well as the utricular otolith organs serve a dual function in spatial orientation and posture control – to estimate the static orientation of the head with respect to the vertical (the traditional graviceptor function) and also to estimate the linear acceleration of the head during movement. The potential ambiguity in interpretation of otolith signals (tilt vs. acceleration) is presumably resolved by CNS integration of information from the semicircular canals, other orientation senses, and knowledge of commanded motion, based on sensory-motor experience in the prevailing environment. In general, the lower frequency components of the otolith signals indicate the direction of the head relative to gravity, whereas the higher frequency components reflect both head tilt and linear acceleration.

In space, where static head orientation doesn't influence otolith organ afferent activity, each head movement produces a specific force stimulus which can swing rapidly in direction even in the absence of any head tilt. The critical question, for which space experiments are necessary, is whether the CNS adapts to accept a radically new relationship between otolith afferent signals and static and dynamic body movement – as appropriate to the new environment. If such adaptation takes place, its time course and its relationship to space motion sickness become important. The removal of a 1 g bias could, in itself, shift the otolith organs to a new portion of their nonlinear operating range, thereby altering their utility in responding to accelerations. One possibility is that the otolith signals are largely inhibited, reducing their influence on posture, eye movements and spatial orientation, and consequently leading to a decrease in the ability to sense linear acceleration of even a transient nature. An alternative hypothesis is that otolith signals are reinterpreted as the CNS learns – via sensory-motor interactions with the weightless environment – that the afferent signals now code only linear acceleration. This hypothesis assumes a robust adaptive capacity and is consistent with much previous research on adaptation to other specific sensory rearrangements (reviewed by Welch 1978). Similar hypotheses have been put forth by other groups (von Baumgarten et al. 1981; Parker et al. 1985). All of our experiments in this program were aimed in one way or another at testing this hypothesis (Oman 1982; Young 1983).

Spacelab-1 mission operations

Spacelab-1 was the first flight of the Spacelab pressurized module, a 30 foot long, manned laboratory for scientific and technical research developed by the European Space Agency (ESA) and carried into orbit in the cargo bay of the Space Shuttle. The "payload crew" of four, which performed all experiments, consisted of two NASA Astronaut Mission Specialists (one of whom had previous Skylab flight experience) and two Payload Specialists chosen by the investigators from the outside scientific community. One of the Payload Specialists was BKL, a vestibular researcher and bioengineer from our MIT laboratory. The Commander and the Pilot did not participate in flight or pre/post-flight experiments. Subjects were male, ranged in age from 35 to 53 years, and were active pilots. They were in good health and were examined and judged normal by our consulting otoneurologist. To preserve anonymity and facilitate data comparison, these subjects are referred to only by letter code A–D throughout this issue. Two crew pairs (A and B, C and D) worked alternating 12 h shifts throughout the mission. Crew circadian rhythms were shifted beginning 14 days before launch, with only partial success. After landing, circadian cycles were abruptly shifted back to local time. It was not possible to control for circadian effects in our testing.

During Spacelab missions, the payload crew lives in the Orbiter and works in the Spacelab, commuting via an access tunnel. The laboratory is maintained at normal sea level atmospheric pressure and air composition, and at comfortable temperature and humidity. Conduct of the scientific mission was substantially different from any flown previously. The investigators on the ground and their astronaut colleagues participated in extensive training, simulation and discussion of scientific goals. They performed as an integrated team, facilitated during the mission for the first time by frequent TV coverage and two-way voice communication. This flexibility permitted numerous repairs and adjustments of experiments (Garriott et al. 1984). Despite the flexibility introduced in Spacelab-1 relative to previous missions, the conduct of experiments was severely restricted in comparison to a normal ground laboratory. The competition for crew time, power, communications and other resources, and the relatively short mission duration prevented substantial extension of measurements.

For this first mission, a wide variety of experiments from the U.S., Canada, eleven European countries and Japan were included (Chappell and Knott 1984). The three closely related sets of vestibular

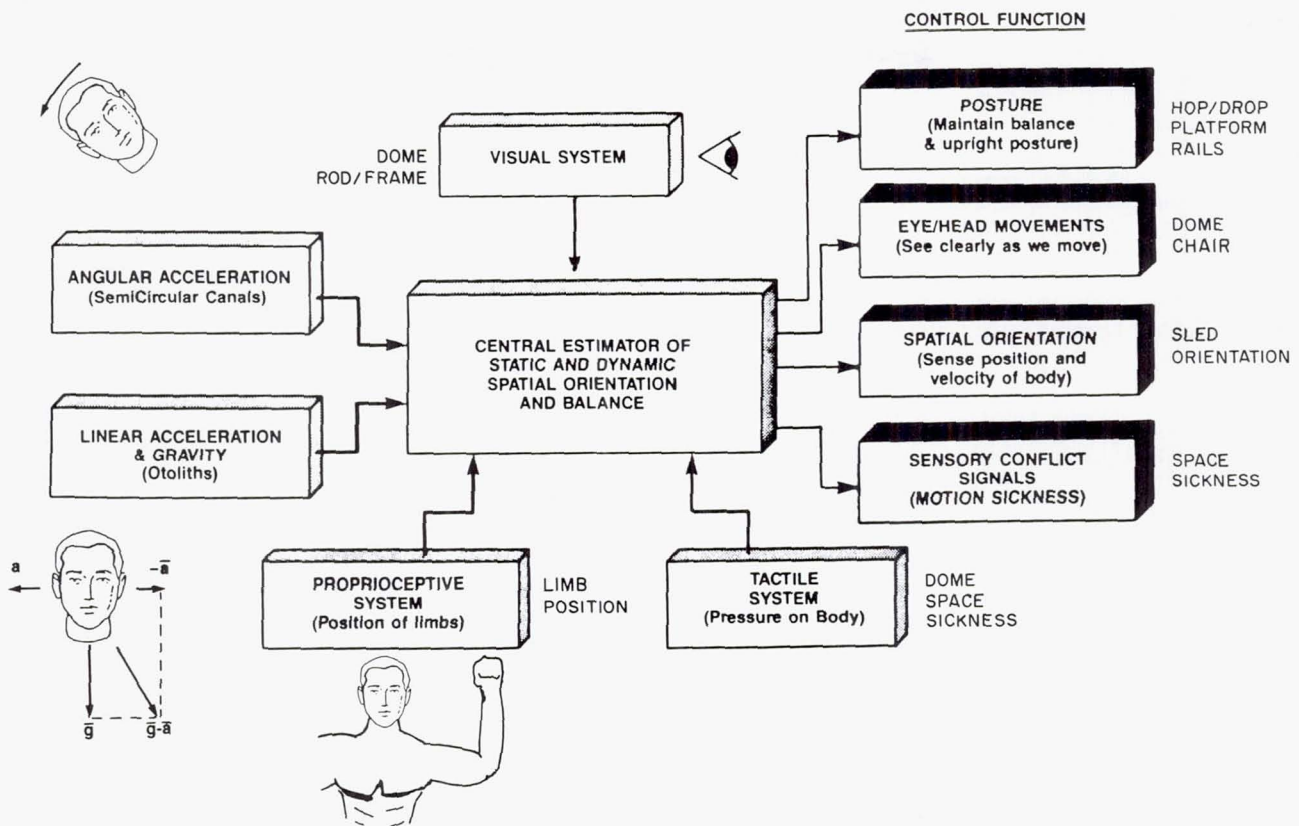


Fig. 1. Scope of the MIT/Canadian Spacelab 1 experiments, by experiment short name, relative to a schematic representation of the role of the vestibular and other senses in control of posture, eye movements and perception of orientation. Experiment short names are keyed to Table 1

lar investigations (von Baumgarten et al. 1984; Reschke et al. 1984; Young et al. 1984) required considerable crew flight time and dominated the pre- and post-flight testing.

Spacelab-1 was launched on November 28, 1983 and was extended from a planned nine days to a mission lasting 10 days, 8 h, 47 min, with a landing at Edwards AFB, California. The landing was delayed by 8 h because of computer malfunctions, severely reducing the crew availability for post-flight testing on the landing day. The NASA nomenclature used for the flight and preserved in the accompanying articles designates the pre-flight days relative to launch. "L minus one" (L-1) is the day before launch. Flight days are numbered beginning with zero. Hence Mission Day 1, or MD1, is the second 24 h in orbit. Post-flight days also are numbered from zero (R+1 is one calendar day after the return day). Mission Elapsed Time (MET) is specified in days/hours : minutes since launch.

Scope and interrelationships of the experiments

The overall scope of our SL-1 experiments and their relationship to the stimuli and outputs of the human system for spatial orientation and balance is indicated in Fig. 1. Individual experiments, investigators and SL-1 performances are shown in Table 1. Each experiment examined a different output to reveal some aspect of the way the CNS adapts to the functional equivalent of removing the gravity vector. The "Rotating Dome" experiment explored central integration of conflicting visual/vestibular/tactile sensory cues by measuring roll self-motion and compensatory eye and head movements stimulated by looking into the open end of a rolling drum. The "Rod and Frame" is a pre-post flight test of static visual field dependence. The "Hop and Drop" experiment studied the otolith-spinal reflex which normally prepares one for a landing from a fall. Electromyographic activity from the gastrocnemius and soleus

Table 1. MIT/Canadian vestibular experiments on SL-1

Experiment	Lead investigator	When performed
1. Visual-vestibular interaction (dome)	Young	Subj. A, B, MD 1, 2, 4, 5, 6, 7; C, D, MD 1 (failed) 3, 6
2. Otolith-spinal reflex (hop/drop)	Watt	Subj. A, MD 0, 1, 6; B, MD 0, 1, 6, 7
3. Awareness of orientation and limb position	Money	*Subj. B, MD 1; C, MD 8
4. Posture control (platform/rails)	Kenyon	Pre-Postflight
5. Motion sickness susceptibility (space sickness)	Oman	Subj. A, B, C, D continuous
6. Perception of linear acceleration (sled)	Arrott	Pre-Postflight (sled scheduled for D-1)
7. Ocular torsion during lateral acceleration	Young	**Subj. C, D, MD 0, MD 7
8. Vestibulo-ocular reflex nystagmus dumping (chair)	Oman	*Subj. A, B, MD 7; C, MD 3, 6

All in-flight tests were also performed pre- and post-flight

MD: Mission Day

* Data still being analyzed - not reported in this issue

** No flight data available due to equipment failure. Full test scheduled for D-1. Pre-postflight data reported with expt. 6

muscles of the leg was measured during footward acceleration provided by stretched elastic cords. The "Position Awareness" experiment measured the influence of weightlessness on both the orientation of perceived objects in the absence of a vertical and the accuracy of proprioceptive cues in determining perceived limb position. The "Space Sickness" investigation clinically characterized space sickness symptoms and studied their relationship to head movements, visual, tactile and proprioceptive cues, and to the shift of body fluids toward the head. A "Posture Platform" and narrow rails were used to measure the post-flight degradation of postural stability. The "Sled" is a linear acceleration device which was used for stimulating eye deviation and ocular torsion, as well as subjective motion during horizontal linear acceleration. A rotating chair was used to stimulate the semicircular canals for study of the horizontal vestibulo-ocular reflex and the "dumping" of post-rotatory nystagmus produced by head pitch.

The experiments conducted on Spacelab 1 were the first of a planned series of related investigations, scheduled for continuation and extension on several additional Spacelab missions in the mid-eighties. For operational reasons the experiments originally planned for use with the Space Sled, a controlled linear acceleration device, were postponed until the D-1 Spacelab mission, accomplished in November, 1985. Related tests were performed on the 1984 Shuttle 41-G Mission (Watt et al. 1985).

Pre-flight testing of the crew for the MIT/Canadian experiments was conducted from 1979 through 1983 at the experimenters' laboratories (MIT, McGill, DCIEM/Toronto) and at NASA's Johnson Space Center, Kennedy Space Center, and Dryden Flight Research Facility (DFRF). Of particular value for protocol development, training and baseline data

collection were the series of four sets of parabolic flight tests producing repeated 20-25 s periods of weightlessness in NASA's KC-135 aircraft. Pre-flight and post-flight testing by all life science experimenters was conducted at an especially constructed Baseline Data Collection Facility at DFRF at approximately 152, 122, 65, 44 and 10 days before launch. Subjects A and B were tested within hours of landing, and all four subjects were tested on 1, 2, 4 and 6 days after return. Parabolic flights to assess 0 g motion sickness susceptibility and reorientation illusions were performed pre-flight, and 3 days, and 1 year after landing.

Results and discussion

The results of our experiments on Spacelab 1, discussed in detail in the accompanying papers, must be interpreted cautiously because the experiments were conducted on only 2-4 subjects, and with fewer repetitions and frequently under less well controlled conditions than desired. These results, when taken together with findings from other related experiments, appear generally consistent with the sensory reinterpretation notion. We are aware of no evidence pointing to pathological alteration of sensory function at the end organ.

Early in the SL-1 flight 3 of 4 subjects developed space sickness symptoms, which largely resembled those of prolonged motion sickness, superimposed on the effects of fluid shift towards the head. Symptoms abated after 2-3 days. Short duration pre-flight motion sickness susceptibility tests did not predict in-flight sickness intensity. However, head movements, especially in pitch, as well as visual and tactile cues to orientation, influenced symptom level

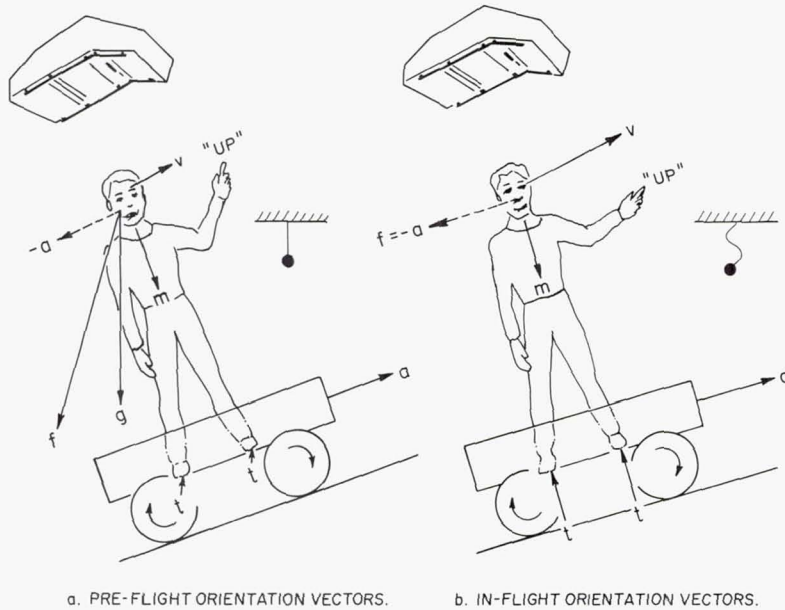


Fig. 2a, b. Schematic representation of the sensory vectors which are used in determining human spatial orientation. In **a**, the subjective zenith is arrived at by a vector sum of the various sensory contributions, but is dominated by the gravito-inertial vector (f). If the subject, shown standing on a moving wagon, were not accelerating, this would indeed be vertical (g). The subjective vertical is also biased slightly by the influence of vertical or horizontal elements in the visual field (v), by localized tactile cues (t), and by one's own body axis (m). The strength of these other cues depends on the individual. In **b**, which represents the similar situation in weightlessness, the crucial difference is that the gravito-inertial vector now represents only linear acceleration (a). The subjective zenith, or local reference axis if "up" has lost all meaning, now ignores the gravito-inertial vector in favor of the stronger visual, tactile and body centered axes. Tactile cues normal to support surfaces, such as illustrated in **b**, could be developed by a loading mechanism such as stretched elastic cords (not shown) or briefly by extension of the legs. Differences among the individual crew members in the relative strength of these vectors is reflected in the range of orientation styles

in ways consistent with the sensory conflict theory for motion sickness and with the hypothesis of sensory reinterpretation.

Changes in sensory-motor function were observed both during the flight and extensively following the landing. Otolith-spinal reflex responses to footward acceleration with head erect were inhibited when tested early in the flight, and declined further during the week in weightlessness. However, in the tests performed several hours after landing the otolith-spinal reflex had returned to pre-flight levels. Similarly, the short latency reflex reactions to destabilization of standing on the posture platform were unchanged post-flight, although the longer latency responses demonstrated postural instability, with eyes closed, on both the platform and on the rails tests. The Rotating Dome experiment data suggest increased weighting of visual cues and tactile cues, and reduced influence of graviceptor signals in determination of orientation in weightlessness. Post-flight measurements also suggested a slight increase in static visual field dependence. Proprioception may have been degraded in flight. Post-flight reaction to horizontal linear acceleration revealed a reduction in dynamic ocular counterrolling, and increased variability in the detection of low level accelerations, but an enhanced ability to use suprathreshold acceleration cues to null lateral position in a closed loop, non-visual, tracking task.

As illustrated in Fig. 2, the human estimation of body position and postural reactions is thought to change in weightlessness to make use of the varied sensory inputs in a manner which is fundamentally appropriate to the microgravity condition. In particular, it appears likely that at least three separate aspects of such reinterpretation may be present: tilt acceleration reinterpretation, reduced postural response to z-axis linear acceleration, and increased attention to visual cues. In the course of the reinterpretation, motion sickness symptoms, caused by the original sensory motor conflicts, gradually disappear.

As illustrated in Fig. 2a, for pre-flight spatial orientation, the subject relies heavily on the static gravito-inertial vector for his perception of the vertical, which can be displaced by a low frequency acceleration (e.g. Mach 1875; Howard and Templeton 1966; Schöne 1980; Young 1984). However, each individual has his perception of the upright influenced, to varying degrees, by the presence of elements in the visual field, especially those normally associated with the vertical (e.g. Witkin 1958; Howard 1982) and by localized tactile cues such as pressure on the soles of the feet. Moving visual scenes (not shown in the figure) can also create a sense of body self-motion. Furthermore, each individual has a tendency to align the perceived vertical toward the head or feet along the torso long axis.

This tendency is represented by an idiotropic body axis vector and is assumed to vary in strength among individuals (Mittelstaedt 1983).

These sensory vectors must be reinterpreted for spatial orientation in weightlessness. As shown in Fig. 2b, the gravito-inertial vector now is merely the opposite of linear acceleration relative to the spacecraft. If it were to continue to dominate the perception of tilt orientation, the astronauts would experience 180 degrees of roll or pitch each time they accelerated and decelerated while translating through the spacecraft, which was never reported. Instead, we believe that the signals from the graviceptors are reinterpreted to represent linear translation, as required for locomotion accuracy in space, and as carried over to the post flight closed loop acceleration nulling tests. In-flight postural reaction to changes in acceleration, at least along the body z-axis (Watt et al., this issue; Reschke et al., this issue) show a decrease in sensitivity, which is consistent with the absence of a need to prepare the "anti-gravity muscles" for a fall. (It remains to be determined whether this inhibition is limited to z-axis acceleration.) Upon return to earth this reinterpretation of graviceptor cues leads to a decreased ability to stand up with eyes closed, except within a very narrow cone of static stability near the upright. Actual head tilt may be perceived as a lesser tilt post-flight, combined with linear acceleration in the opposite direction, leading to destabilizing postural reactions in the wrong direction. Post-flight changes in postural control strategy may be related to this tilt/translation reinterpretation (Kenyon and Young, this issue, Reschke et al. 1984). Ocular counterrolling, which is a normal compensatory response to a tilted gravito-inertial vector, is also shown to be reduced post-flight dynamically (Arrott and Young, this issue) and statically (von Baumgarten et al. 1984; Parker et al. 1985; but not Yakovleva et al. 1980). Post-flight perceived tilt, in the dark, is reduced (Benson et al. 1984) as predicted by the hypothesized carry-over of the otolith reinterpretation, and dynamic tilt was reported on other crews to lead to a strong translation sensation (Parker et al. 1985, who independently arrived at a similar otolith tilt/translation reinterpretation hypothesis).

In the absence of usable graviceptor information regarding body orientation in weightlessness, the nervous system must pay increased attention to the remaining sensory orientation signals. Subjective reports from crew members indicate large variations in individual styles, but never a prolonged sense of absence of a reference frame or "disorientation". The increased length of the "visual" vector in Fig. 2b is intended to represent the increased weighting

given to dynamic visual inputs to self motion (the dome experiment) and to static elements such as the floor or ceiling, another crew member, or the earth (Oman et al., this issue). In many cases the relative weighting may be a complete domination by the visual, body control or tactile vector in weightlessness. Large individual differences in visual field influence in weightlessness are reflected in the post-flight increases in field dependence. Similarly, localized tactile cues, such as pressure on the feet in the Dome and the Hop/Drop experiments or on the buttocks and back when wedging into a corner, serve to take on an increasing role in determining spatial orientation and a sense of well-being. Finally, the influence of the postulated body-axis orientation vector, which could allow some crew members to orient their reference frame to their body long axis in weightlessness, is greater than pre-flight because of the reinterpretation of the graviceptor cues.

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