Chapter 5

POSTURE, MOVEMENT AND LOCOMOTION

Postural activity is the complex result of integrated orientation and motion information from visual, vestibular and somatosensory inputs. These inputs collectively contribute to a sense of body orientation relative to the Earth or other support surface and, additionally, coordinate body muscle activities that are largely automatic and independent of conscious perception and, in some cases, voluntary control (Figure 5-01).

Brain structures concerning posture, movement and locomotion are hierarchically organized. Whereas local reflexes take place in local interneural circuits in the spinal cord, standing posture and equilibrium are achieved by excitation of the brain vestibular system in the midbrain and alpha and gamma motor neurons units of extensor muscles. Complex movement sequences and gait result from the activation of forebrain structures, such as thalamus and premotor or motor areas of cerebral cortex. Both voluntary and reflex pathways participate in the control of excitation of synergist and inhibition of antagonist motor neurons. Also, while the movement is underway, feedback from proprioceptors influences subsequent neuronal activity in motor centers to effect the desired movement. The cerebellum influences neuronal activity in the initiating motor centers and continuously modulates neuronal activity, based on information about motor commands and proprioceptive feedback about position and acceleration.

Figure 5-01. An astronaut in the mid-deck of the Space Shuttle is wearing sandals with suction cups to help stabilizing his body relative to the spacecraft walls when operating high-resolution photographic equipment. Photo courtesy of NASA.

Exposure to the microgravity conditions of space flight induces adaptive modification in the central processing of sensory input to produce motor responses appropriate for the prevailing gravito-inertial environment. As a result, terrestrial motor strategies are progressively abandoned, as astronauts adapt to the new demands of the zero-g environment. This is particularly true for the major postural muscles found in the lower legs. The plastic modifications in posture, movement and gait functions acquired during space flight are then inappropriate for a one-g environment upon return to Earth.

G. Clément, M.F. Reschke, *Neuroscience in Space*.
DOI: 10.1007/978-0-387-78950-7_5, © Springer Science+Business Media, LLC 2008

Difficulties with standing, walking, turning corners, and climbing stairs are experienced as astronauts re-adapt to a one-g environment, until terrestrial motor strategies are fully reacquired. These difficulties can have adverse consequences for an astronauts' ability to stand up, bail out, or escape from the vehicle during emergencies and to function effectively immediately after leaving the spacecraft after flight. Thus it is important to understand the cause of these profound impairments of posture and locomotion stability, and develop countermeasures.

1 INTRODUCTION

Homo erectus' ability to maintain stable upright posture and to move in Earth's gravitational field has evolved over many millennia. As part of this evolutionary process, numerous neurosensory and neuromuscular systems have developed to sense the orientation of the individual with respect to the gravitational field and to support and move the individual's body mass through this gravito-inertial environment. In weightlessness, the structural and anatomical systems that provide for upright orientation and movement on Earth are, at best, not required and, at worst, not appropriate for orientation and movement. As a result, part of the adaptation process involves elimination, reinterpretation, or modification of the information and control provided by these systems. One consequence is that, upon return to Earth following a sufficiently long space flight, the orientation and movement control systems of the crewmember are no longer optimized for terrestrial gravity. Indeed, disturbances in postural equilibrium and gait upon return from flight have been among the most consistently observed and reported responses associated with space flight. Careful study of these changes may provide a key to understanding how sensorimotor systems adapt to the unique environment of microgravity.

Over the past forty five years, returning crewmembers from both Russian and American space missions have reported one or more of four basic unusual sensations associated with posture or locomotion during the first few hours after landing. The first of these is the sensation of turning or lateral deviation while attempting to walk a straight path. Overcompensating for this, many crewmembers actually walk in a curved path in the opposite direction. Second is a sudden loss of postural stability, much as though the crewmember has been pushed to one side by a "giant hand", usually experienced while attempting to walk around corners. Third is the perception that the pitching and rolling head motions that accompany normal walking are greatly exaggerated. Finally, in an environment with no clear visual vertical, some crewmembers experience a sudden loss of orientation and pitch forward, or fall to the side before position awareness is regained (Young 1993).

Maintenance of a stable postural equilibrium requires constant interaction between sensory input and motor output. Disturbance of either can result in inappropriate postural responses, which lead to postural instabilities. The sensory inputs required to maintain postural stability on Earth are provided by visual, vestibular, somatosensory and proprioceptive receptors. Adaptation to microgravity apparently results in elimination, reinterpretation, or modification of the weighting of sensory information from these receptors.

The effects of weightlessness on postural stability have been examined using a number of different methods including:

a. Crewmembers' reports of changes in sensations (illusionary movement).

b. Performance on balance rails.
c. Performance on moving platforms.
d. Performance while standing following a voluntary movement (raising the arm from the side, tiptoeing, or bending at the waist) or involuntary movement (push to the chest) designed to perturb the body's center of gravity.
e. Measurement of muscle potentials from the major antigravity and weight-bearing postural muscles.
f. Application of a vibrator to selected muscles so as to elicit postural responses.
g. Performance during complex postural tests designed to selectively eliminate visual, proprioceptive or vestibular information.

Although some in-flight data have been collected (Figure 5-02), most postural stability testing has been limited to the comparison between preflight and postflight performance.

Figure 5-02. One of the engineering and technology experiments on board Skylab was a special suit instrumented to measure body motions as the wearer went through typical tasks on board the space station. One Skylab astronaut inspects such a vest during a training session on Earth. Photo courtesy of NASA.

2 IN-FLIGHT POSTURE STUDIES IN ANIMALS

The first microgravity experiment on spatial orientation and postural control was conducted some three decades ago using fish as test subjects (von Baumgarten *et al.* 1972). During the microgravity phase of parabolic flight, the animals exhibited a continuing diving response, i.e., swimming inward looping. This behavior was called "looping response." Other individuals performed spinning movements around their longitudinal body axis (von Baumgarten *et al.* 1972, DeJong *et al.* 1996). The looping behavior would result from the absence of any otolith feedback to the animals indicating completion of the maneuver. Long-axis rotation appears to be the result of the repetitive execution of the righting response, such as that observed in a falling cat (see Figure 1-09), in a situation where it is non-effective. These early experiments clearly showed that fish face severe orientation problems in a microgravity environment. Fish have not been observed to vomit under microgravity, and they may therefore be presumed not to suffer true motion sickness. Therefore, regarding fish the term *kinetosis* is more appropriate than *motion sickness*, since they do demonstrate gastro-intestinal symptoms (increased fecal output) when exposed to unusual motions outside of the water (Money 1970).

Like humans, fish also use basic visual and vestibular cues for postural equilibrium maintenance and orientation (Allum *et al.* 1976). As early as 1935 the so-called *dorsal light response* (DLR) was described (von Holst 1935). When illuminated from the side at one-g, a fish tilts its back towards the light source, but under microgravity conditions the tilt is guided by light alone. The DLR thus expresses a balance between the tilting force induced by visual information and the vestibular righting response (Watanabe *et al.* 1991) induced by tonic vestibular information. It has been suggested that the intensity of the DLR is species specific based on the finding that particular genetic strains of medakas (Japanese ricefish *Oryzias latipes*) differ in their DLR performance (Ijiri 1995). However, recent investigations have clearly demonstrated that the DLR depends on the specific ability of an individual, thus suggesting that some individuals are more “vestibular” and others more “visual,” as is the case in humans (Harm & Parker 1993, Isableu *et al.* 1997).

Like the fish, the midwater tadpoles of the African clawed-frog (Xenopus laevis) make forward somersaults when subjected to microgravity (Wassersug & Souza 1990, Wassersug 1992). However, aquatic amphibians either float randomly or make reverse (backward) somersaults when abruptly exposed to microgravity (Mori 1995). Adult non-arboreal frogs and salamander larvae rotate along their rostral-caudal axis in response to microgravity. This long axis rotation is similar to their righting reflex when inverted in normal gravity (Wassersug *et al.* 1991, Wassersug *et al.* 1993).

Arboreal frogs take up an extended-limb gliding or parachuting posture when suspended in air during microgravity (Izumi-Kurotani *et al.* 1992). A semi-arboreal snake was observed taking a stereotypic defensive posture in microgravity during parabolic flight. Pond turtles in microgravity extend their neck and limbs in an asymmetric fashion identical to their righting response when placed upside-down in normal gravity (Wassersug & Izumi-Kurotani 1993). Birds adopt a flying behavior (Oosterveld & Greven 1975) and mammals, such as hamsters or rats, frequently extend their extremities and back in-flight, similar to a flying squirrel, or spiral along their long body axis (Kalb *et al.* 2003). Some of these responses, such as in the snake, appear to be extensions of escape behavior in response to stress. However, the extension of the extremities would be the consequence from the release of the inhibitory influence exerted by the otolith organs on the antigravity muscles, the extensors (Clément *et al.* 1984, Wassersug *et al.* 1993).

The various types of neurobiological data (behavioral, morphometrical, histochemical, biochemical, and electron microscopic) using animal models for studying the signal-response chain of graviperception favor the following concept of interactions: Sudden exposure to altered gravity can induce transitionally aberrant behavior due to malfunction of the inner ear originating from asymmetric otolithic loading or, generally, from a mismatch between otolith afferents and the other sensory inputs that also provide orientation information. This aberrant behavior in different gravito-inertial environments vanishes due to a re-weighting of sensory inputs and vestibular offset and/or gain compensation, probably on a bioelectrical basis. During steady-state exposure to altered gravity, step-by-step neuroplastic reactions on a molecular basis (i.e., molecular facilitation) in the brain and inner ear possibly activate feedback mechanisms between the CNS and the vestibular organs for the regain of normal behavior (Anken & Rahmann 1999).

3 IN-FLIGHT POSTURE STUDIES IN HUMANS

In-flight studies of postural control changes associated with exposure to weightlessness in humans have been performed on both Russian and American missions. In these studies, postural equilibrium was disturbed either by a voluntary (subject initiated) movement or by an involuntary (externally initiated) movement and the postural responses to that disturbance were measured. Comparisons between in-flight and control (preflight and postflight) measurements were used to identify adaptive changes in posture control. Voluntary movement posture control paradigms included requiring crewmembers to respond when their resting position was disturbed with either a rapid arm movement, elevation of the whole body (voluntary tiptoeing), bending at the waist, or squatting (Clément *et al.* 1984, Massion *et al.* 1993). Involuntary movement posture control paradigms included displacement with a foot support platform capable of providing a forward step velocity, vibration of select muscle groups, and sudden "falls" where crewmembers were pulled to the floor of the spacecraft with elastic cords (Clément *et al.* 1984, Clément & Lestienne 1988, Roll *et al.* 1993, Reschke *et al.* 1986, Watt *et al.* 1986). The results of these investigations are described below.

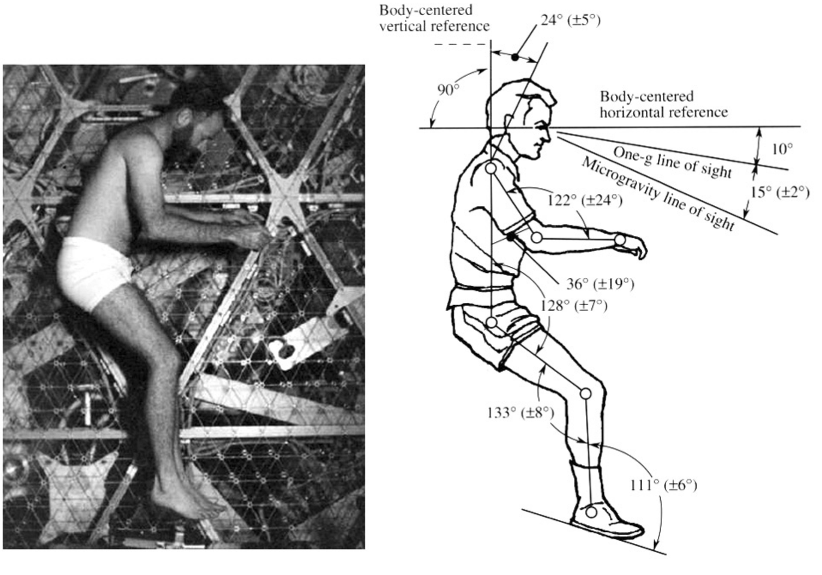

Figure 5-03. Photograph of an astronaut free-floating on board the Skylab space station (left). A series of photographs was used to construct a model of the neutral body position in weightlessness (right). Photo courtesy of NASA.

3.1 Rest Posture

Human factor studies, after investigating photographs taken during Skylab missions have led to the NASA *neutral body posture* model (Figures 1-10 and 5-03).

This model is characterized by a forward tilt of the head (with the line of sight 25 deg lower than the body-centered horizontal reference), shoulders up (like a shrug), and arms afloat, up and forward with hands chest high (Thornton 1978). However, recent investigations, taking into account body size, gender and mission duration suggest that the neutral body posture model is too generalized. Data collected on a larger number of astronauts showed that arm and shoulder positions were less bent, and there were straighter leg positions at the hip and knee than expected from the neutral body model (Mount & Foley 1999). Further studies should be made of posture in zero-g to better define not only the differences in postural response in microgravity, but to seek a more normalized picture of crew responses over different lengths of flight. Also, it is unclear how the direction of the line of sight has been evaluated from the Skylab photographs. The downward deviation of gaze in microgravity in the neutral body model is in contradiction with the results of several space experiments that actually measured the eye deviation during space flight (Clément 1998).

Frame-by-frame analysis of video recordings made during various on-board activities of crewmembers have allowed researchers to characterize prevalent orientations and stereotyped motor acts (Tafforin & Lambin 1993). Results revealed that head and body movements in yaw were more frequent in space than on the ground, and that the astronauts quickly learn to anchor their feet and use handgrips for stabilizing their posture. Head-down orientation increases in frequency as flight progresses, presumably in phase with the development of a new internal representation of the environment and the location of objects (see Chapter 7, Section 4.4).

During a standing posture in microgravity, dorsi-flexor muscles (e.g., the *anterior tibialis* leg muscle) assume a larger role in space than on Earth in regulating the orientation of the individual relative to his/her support. This is in contrast with the general use of muscle extensors on Earth, which are used to counteract gravity. This transfer of motor strategies from one muscle group to another explains the forward tilted posture of crewmembers placed in darkness when instructed to maintain a posture perpendicular to the foot support (see Figure 4-06) (Clément *et al.* 1984).

Why is there an activity in the flexor muscles in weightlessness? One explanation is that it is the result of a sudden disinhibition from the normal excitatory drive exerted by the otolith inputs (perhaps the saccule) on the extensor muscles under the influence of gravity. Another explanation has been proposed by Clément *et al.* (1988), namely that this activity is compensatory for passive resistance. In other words, the normal biomechanically neutral posture of the ankle is when the foot is slightly extended, which would bring the body backward. Therefore, in absence of apparent gravity, in order to have the feet at right angle with the leg, a small flexor tone has to be generated.

Massion *et al.* (1997) proposed that this flexor tone is aimed at maintaining a virtual vertical projection of the body's center of mass on the polygon of sustentation created by the feet. In other words, the CNS would try to recreate in weightlessness a condition similar to Earth. This interpretation is in agreement with the idea of an internal model of gravity that is oriented along the longitudinal body axis or an idiotropic vector (Mittelstaedt & Glasauer 1993, Clément *et al.* 2001). This model would allow a coherent mental representation of the body with an alignment of the longitudinal head and body axes. This internal model of gravity would also serve as a reference frame for movement, as demonstrated by the experiments detailed in the next sections.

3.2 In-Flight Postural Responses to Voluntary Movements

On the Earth's surface, gravity significantly affects most of our motor behavior. For example, when making limb movements during static balance, anticipatory responses from the leg muscles compensate for the impending reaction torques and the changes in location and projection of the center of mass associated with these movements. Similar patterns of anticipatory compensations are seen in-flight, although they are functionally unnecessary (you can not lose your balance or fall). Also, rapidly bending the trunk forward and backward at the waist is accompanied on Earth by backward and forward displacements of hips and knees to maintain balance. Since the effective torques observed in a normal gravitational environment are absent during space flight, the motor responses necessary to achieve these synergies in weightlessness are different from those needed on Earth. Consequently, movements executed in-flight must reflect reorganized patterns of muscle activation.

3.2.1 Arm Raising and Tiptoe Raising

In a joint French-Russian experiment on board Salyut-7, control of upright posture was examined during voluntary upward movement of the arm and voluntary raising on tiptoe (Clément *et al.* 1984, 1985). Early in-flight postural attitude was similar to that on Earth, but as the flight progressed, there was a forward inclination of the body, which increased when vision was stabilized, i.e., when the eyes were open but with no vision of the surrounding spacecraft. Muscle responses to sudden voluntary perturbations (raising the arm rapidly) indicated a redistribution of tonic activity between extensor and ankle flexor muscles, and a general reduction of extensor tone (Figure 5-04).

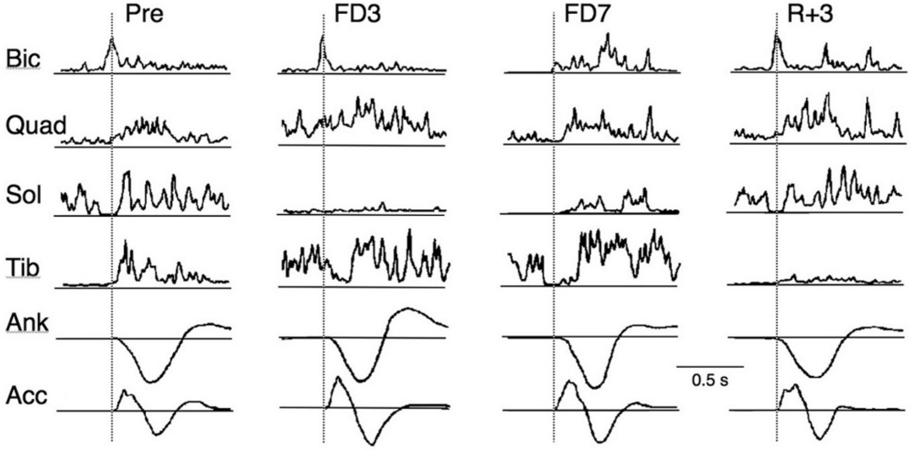

Figure 5-04. Electro-myographic (EMG) activity of leg muscles (Bic: biceps femoris; Quad: quadriceps; Sol: soleus; Tib: anterior tibialis), ankle displacement (Ank) and arm acceleration (Acc) during arm raising in one astronaut before flight (Pre), on flight days 3 (FD3) and 7 (FD7) and 3 days after (R+3) a seven-day space flight. The dashed line indicates the beginning of arm raising. On Earth, the soleus tonic activity decreases before the arm moves. In-flight, this anticipatory deactivation is seen on the tibialis muscle, which maintains the postural tone required for an upright posture in weightlessness. The EMG activity of the biceps femoris and quadriceps is not fundamentally changed in-flight. Adapted from Clément et al. (1984).

Another experiment looked at motor strategies during a rapid toe rise from a standing position. In trials conducted in normal gravity conditions, the temporal characteristics of the anticipatory activity of the postural muscles preceding the elevation to the toes showed an inhibition of the spontaneous activity of the soleus muscle followed by a burst of activity in the anterior tibialis muscle, which continued as long as the subject remained standing on his toes (Lipshits *et al.* 1981). In contrast to this rise and hold technique, if the subject immediately returned to the initial position then the anticipatory activity in the tibialis was absent. Lipshits and his colleagues (1981) proposed that this anticipatory activity functions to displace the body's center of gravity into a new stable position. When a similar toe rise experiment was conducted in-flight, results typical of those observed preflight were found on the third flight day. The finding that the sequence of motor patterns were preserved in-flight is significant and suggests that terrestrial postural programs continue to operate for a relatively long period of time in weightlessness, independent of how sensory inputs are modified (Clément *et al.* 1985).

3.2.2 Bending at the Waist

Rapid voluntary pitch movements at the waist (forward and backward) were made while the crewmember's feet were fastened to the wall of the spacecraft with Velcro bands (Massion *et al.* 1993). Kinematic analysis, in addition to confirming the forward tilt posture reported by Clément *et al.* (1985), showed that upper trunk movements were accompanied by hip and knee movements in the opposite direction, and that there was little difference between in-flight measurements and those obtained both pre- and postflight. The results of EMG analysis, like that observed during the Salyut-7 flight (Clément *et al.* 1985), showed that the early activation of the soleus muscle group observed under terrestrial conditions was replaced in-flight by an early activation of the anterior tibialis. This in-flight motor strategy was still in evidence five days following the flight.

3.2.3 Squatting

Under terrestrial conditions, upright posture is maintained primarily through tonic activity in the extensor muscles. In microgravity, simultaneous recordings of EMG activity in the tibialis and soleus muscles while the crewmember's feet were fixed to the floor of the spacecraft demonstrated that upright posture was maintained through tonic activity in the flexor muscle (Clément *et al.* 1984). This reported change prompted an investigation on STS-51G into the relationship between conscious appreciation of limb position and body position in space and muscle afferent activity. Two crewmembers were asked to lower their bodies into a squatting position, pause and then rise to a fully erect position. By the third day in-flight, the subjects reported illusions of floor motion during execution of the deep knee bends (see Figure 4-07). Similar illusions occurred following the Spacelab-1 flight (Watt *et al.* 1986, Reschke *et al.* 1986), during STS-41G (Watt *et al.* 1985), as well as during parabolic flight (Lackner & Graybiel 1981).

3.3 In-Flight Postural Responses to Involuntary Movements

3.3.1 Support Surface Translation

Using a foot support platform designed to provide sudden forward translation, postural responses to involuntary body displacements were also investigated during the

Salyut-7 flight (Clément *et al.* 1985). Preflight, when the platform was unexpectedly moved forward, the ankle joint extended (plantar flexion) and then returned to its initial position. The motor pattern in response to the sudden plantar flexion showed an initial tibialis muscle burst with latency between 80 and 120 msec. When the test was repeated (up to six times), this early burst of activity from the anterior tibialis was reduced by approximately 40%. On the second day of the flight, the initial burst of tibialis activity was similar to that observed preflight, but the level of tonic activity in the tibialis was greater than that observed on the ground. The tibialis burst of activity decreased quickly in amplitude with the repetition of the trials (Figure 5-05). On the third day after landing, the tibialis motor response returned to baseline, but the ankle rotation trajectory suggested postural destabilization. In discussing these results, the authors suggest that the early tibialis burst resembles the EMG activity of a "functional stretch reflex" mediated by supraspinal centers (Melvill-Jones & Watt 1971), and that the changes in overall EMG amplitude during flight reflect reduced output from the otoliths. These results are consistent with the findings from the Hoffmann reflex experiment (Reschke *et al.* 1986) and the otolith-spinal reflex measurements (Watt *et al.* 1986) performed on Spacelab-1 and described below.

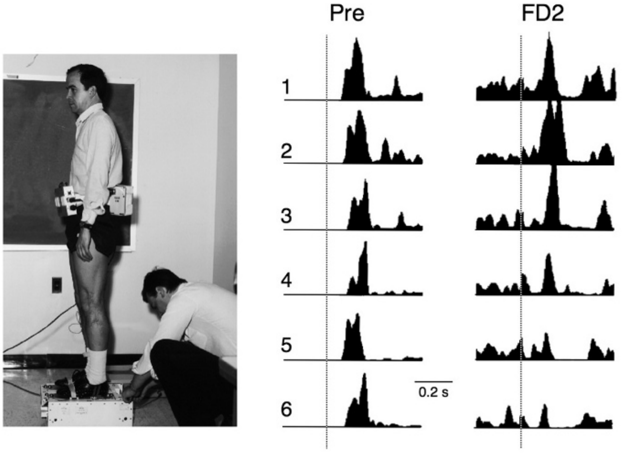

Figure 5-05. EMG reflex activity of anterior tibialis in one astronaut during six consecutive support surface forward translations before (Pre) and during space flight (flight day 2, FD2). The vertical line indicates the beginning of ankle extension. The reduction in the amplitude of the tibilialis activity burst reflex in response to this ankle extension was faster during the flight. Adapted from Clément et al. (1985).

3.3.2 Sudden Drop

In an experiment performed on board Spacelab-1, Reschke *et al.* (1986) examined the effects of weightlessness on the *Hoffmann reflex* (H-reflex). This reflex takes advantage of the anatomical pathways that link the otoliths and spinal motoneurons. Therefore, it can be used as a method of monosynaptic spinal reflex testing to assess otolith-induced changes in postural muscles.

By contrast to doctor tapping a patient's knee to produce the proverbial "knee jerk" reflex (i.e., a mechanically induced spinal stretch reflex), during H-reflex the stimulus is an electrical shock to sensory fibers coming from stretch receptors in the calf (soleus) muscle, and the response is the electrical activity mediated by the muscle motor neurons through the spinal cord and recorded from the muscle. Each time a subject is tested, the number of motoneurons that have been excited by a standard volley of sensory impulses is counted. That number is an indicator of spinal cord excitability as established by the descending vestibular output. The H-reflex data can also be related to EMG from the calf muscle (the M-wave) and self-motion reports.

Activity in this otolith pathway was elicited by exposing the subjects to unexpected drops (falls) (Figure 5-06, left). It was hypothesized that exposure to free fall would reduce the necessity for postural reflexes in the major leg muscles, and that postural modifications would reflect a change, not in the peripheral vestibular organs, but more centrally. This postural adjustment would reflect a sensorimotor rearrangement in which otolith receptor input was reinterpreted to provide an environmentally appropriate response. Early in-flight H-reflex amplitude was similar to that recorded preflight, but measurements obtained on the seventh day of flight did not show a change in potentiation as a function of the drop-to-shock intervals (Reschke *et al.* 1986). Immediate postflight H-reflex response in three of four astronauts tested showed a rebound effect. This effect returned rapidly to baseline.

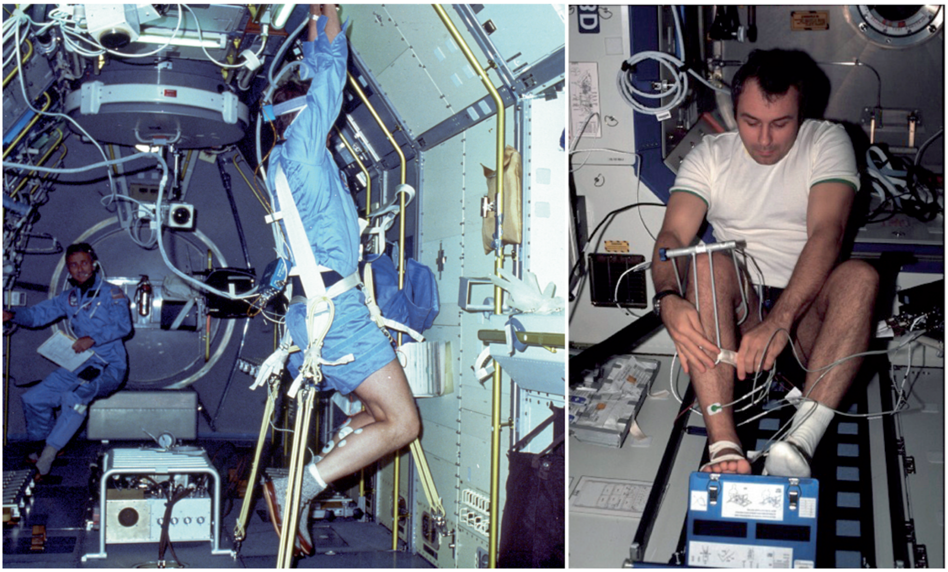

Figure 5-06. Left. H-reflex experiments on board Spacelab (left) and the ISS (right). On Spacelab, subjects were suddenly released and dropped to the floor my means of bungee cords. On Earth, during such drop the otoliths signal the muscles to prepare for jolts associated with falling. This anticipation was partially inhibited early in flight, and declined further as the flight progressed, suggesting that the brain ignored or reinterpreted otolith signals during space flight. The response returned to normal immediately after landing. During the flight, crewmembers also reported a lack of awareness of position and location of feet, difficulty in maintaining balance after hitting the floor, and a perception that falls were more sudden, faster, and harder than similar drops experienced preflight. Photo courtesy of NASA.

In-flight self-motion perception reports suggested that the early in-flight drops were perceived like those preflight. Drops later in-flight were described as sudden, fast, hard, and translational in nature. Immediately postflight, the drops were perceived like those late in-flight, with the astronauts reporting that they did not feel as though they were falling, but rather that the floor came up to meet them.

In a related Spacelab-1 experiment (Watt *et al.* 1986), otolith-spinal reflexes were elicited by sudden, unexpected Earth vertical falls. Like the H-reflex experiment, falls were executed in-flight by pulling subjects to the deck of the Spacelab using elastic cords. EMG activity recorded early in-flight from the gastrocnemius-soleus complex during the fall was of lower amplitude than that observed preflight and continued to decline as the flight progressed. These results agree with the results of the H-reflex experiment showing little or no potentiation of the monosynaptic reflex as a function of a vertical fall late in-flight (Reschke *et al.* 1986).

In astronauts tested on board the ISS (Figure 5-06, right), the spinal cord excitability decreased by about 35% in microgravity and stayed at this new level for the duration of 3-6 month missions. Although there was notable improvement in the H-reflex response the day after landing, it took about ten days back on Earth for astronauts to fully recover their muscle strength and spinal cord excitability (Watt & Lefebvre 2001, Watt 2003). This difference in excitability means that only a portion of muscle fiber units are contracting in response to signals from the nervous system and explains functionally why muscle mass declines in weightlessness, even with exercise. Reduced excitability means that there might be limits on the degree to which heart muscle strength, leg muscle tone, and bone density (for which muscle contraction is an important regulating factor) can be maintained through exercise on long-duration missions. Because this decrease in excitability is only observed on orbit and not during bed rest, an analogue for weightless space travel, the results highlight the possibility that reduced excitability with corresponding loss of muscle and bone might be partly a CNS response and not simply due to disuse of the legs (Watt 2007).

3.3.3 Muscle Vibration

The role of muscle proprioceptive receptors in control of upright posture was investigated by vibratory stimulation of the soleus and anterior tibialis muscle tendons during the Mir Aragatz mission (Roll *et al.* 1993). Two subjects participated in the experiment; one remained on-orbit for four months and was joined by a second who remained in the Mir station approximately five months.

Before flight, vibratory stimulation of the soleus resulted in backward sway about the ankle joint, whereas stimulation of the anterior tibialis resulted in forward sway. During flight, the postural responses developed differently depending on which muscle group was stimulated. Sway during stimulation of the anterior tibialis either decreased or disappeared (depending upon the subject), whereas the response to the soleus remained normal (somewhat decreased in one subject) throughout the twenty-day in-flight test period. In addition, the compensatory EMG recorded preflight disappeared in-flight even though muscle activity concomitant with the vibration was observed in both soleus and anterior tibialis (similar to the classic tonic vibratory response). No testing was possible until two days after landing. At that time, the responses of the subject who spent the least time on orbit were comparable to those obtained before flight. The same appeared to be true of the second subject, but no objective measurements were made (Roll *et al.* 1993).

The authors concluded that muscle proprioception remained intact after prolonged flight, since it was still possible to activate the muscle spindle with vibration. However, the characteristics of the response to muscle vibration changed in microgravity, indicating that adaptive sensorimotor responses occur and that these new responses were appropriate to the environment.

4 PRE- AND POSTFLIGHT POSTURE STUDIES

Owing to both the physical difficulties and constraints of performing posture studies in-flight, many investigators have chosen to test crewmembers before and immediately after flight (presumably before significant re-adaptation to one-g has occurred) in order to better understand in-flight adaptation. The first studies designed to quantify postflight postural ataxia in this fashion required astronauts, upon landing, to tandemly stand on narrow rails of various widths with their eyes either open or closed and arms folded across their chests (Berry & Homick 1973, Homick & Miller 1975, Homick *et al.* 1977, Kenyon & Young 1986). Other studies have used static force plates for stabilometry and simpler tests, such as the clinical Romberg test, a sharpened (toe-to-heel) Romberg test, and vertical posture with varying head positions, to assess postural ataxia immediately after flight (Yegorov 1979, Bryanov *et al.* 1976). Later postural performance studies have relied on dynamic posture platforms that translate the subject (Reschke *et al.* 1984, Clément *et al.* 1985, Anderson *et al.* 1986), tilt the subject (Kenyon & Young 1986, Reschke *et al.* 1991), or provide more sophisticated posture control tasks such as stabilization of ankle rotation and/or vision (Paloski *et al.* 1993). Pre- and postflight studies of vestibulo-spinal reflexes (Baker *et al.* 1977, Reschke *et al.* 1984, Kozlovskaya *et al.* 1984, Watt *et al.* 1986) and postural responses to voluntary body movements (Reschke & Parker 1987) have also been performed. A summary of the results of these studies follows.

4.1 Rail Tests

Early measurements of postural ataxia were based on the hypothesis that prolonged exposure to a weightless environment would result in changes in the sensory systems (with the possible exception of vision) necessary for the maintenance of postural stability. It was postulated that these changes would most likely originate at the periphery and involve modification of input from the receptors serving kinesthesia, touch, pressure, and otolith functions. Furthermore, as exposure time increased, adaptive responses appropriate to the new inertial environment were expected to occur at a central level. Upon return to Earth, postural instability would be manifested as a result of the in-flight neural reorganization.

The first tests of this hypothesis were performed following the Apollo-16 mission (Homick & Miller 1975) and the Skylab-2, -3 and -4 flights (Homick & Reschke 1977). Ataxia was evaluated using a modified version of a standard laboratory test developed by Graybiel & Fregly (1965). Metal rails of varying widths were provided for the crewmembers to stand on in a sharpened Romberg position (feet, heel-to-toe; arms crossed and folded across the chest) with eyes opened or eyes closed (Figure 5-07). Time before stepping (or timeout) was the performance measure of postural stability. Postflight decrements in postural stability during the eyes open tests ranged from none to moderate. However, during the eyes closed tests, postural stability was considerably decreased in all crewmembers tested. The magnitude of the change was greatest during the first postflight test. Since the Apollo and Skylab tests were not performed until the fourth and second day after landing, respectively, the magnitude of ataxia immediately postflight is believed to have been even greater than that observed at the first postflight test. As it was, one Skylab crewmember had difficulty maintaining balance with his eyes closed while standing on the floor. Improvement was slow and appeared to be related to the length of the mission.

Rail tests were repeated by another group of investigators as part of the complement of vestibular tests performed with the crew of the Spacelab-1 mission (Kenyon & Young 1986). With open eyes, performance on the narrow rail width (1.90 cm) was found to be considerably reduced postflight and did not return to preflight levels before the last test session, seven days after landing. With the eyes closed, all four crewmembers tested exhibited a significant decrement in performance immediately postflight, even while standing on the 5.72 cm wide rail. In at least one case, return to baseline had not occurred by the seventh day postflight. In addition to the static rail-standing task, crewmembers were asked to walk on the 1.90 cm rail. All subjects adopted a strategy of speed, trying to complete the test trials as quickly as possible and minimize instability. Postflight performance was in all cases below that of preflight data, but was only consistently reduced for one subject.

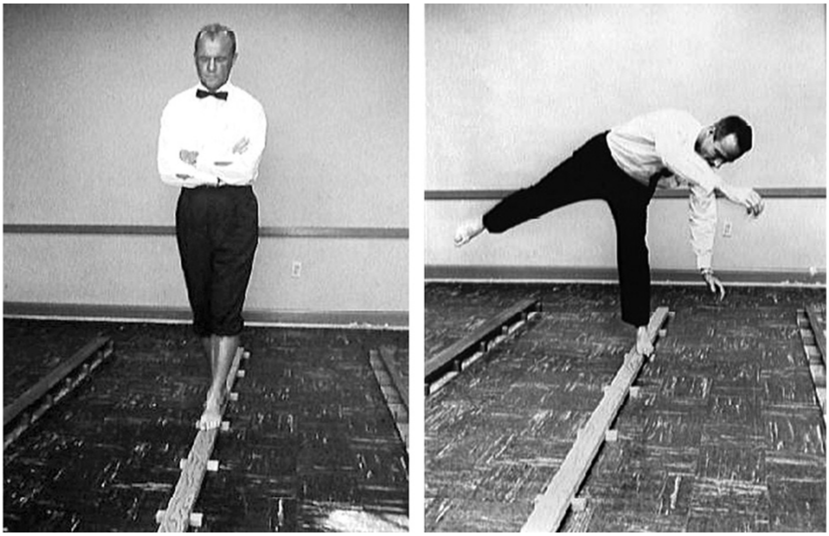

Figure 5-07. Astronauts John Glenn and Scott Carpenter during the posture rail tests performed before and immediately after their Mercury missions. Similar tests were done on Apollo, Skylab, and early Space Shuttle crewmembers. Photos courtesy of NASA.

4.2 Stabilometry

Russian investigators obtained their earliest quantification of postflight postural ataxia in a unique investigation associated with the Soyuz program. Operating under a hypothesis similar to that of their American counterparts, the Russians stressed that postural activity observed in human is based on biomechanical (support), physiological, neurological (vestibular, muscle tonus, tonic activity, coordination of movement, etc.), and psychological (perception, need, etc.) components. They postulated that space flight produces a reorganization of these components and that the subsequent return to Earth requires conscious control of these components for their restoration (Bryanov *et al.* 1976).

For many of the shorter Soyuz missions (Soyuz-3 through Soyuz-8), postural stability was measured using stabilometry 30 to 40 days before flight and at various times (9, 18, 27 hours) after flight. For longer duration flights (Soyuz-9 and Soyuz-17), additional repeated observations were collected postflight. Stabilograms were recorded for periods of one and two minutes during predetermined postural stances, including standing with the head erect (eyes open or closed), standing in the Romberg posture, and standing with the head tilted either forward or backward. Primary measures obtained from the stabilogram were the average frequency and amplitude of sway of the derived body center of gravity in both the sagittal and frontal planes. The postflight stabilographic data in all assumed postural stances were characterized by an increase of sway amplitude primarily in the frontal plane coupled with, in most crewmembers, a decrease in oscillation frequency. The magnitude of change was coupled with the length of flight, with significant changes occurring following the Soyuz-9 flight (Bryanov *et al.* 1976).

In a later study, the prime crew of the Mir Kvant expedition also participated in postural stability tests using the stabilogram technique. In this study, normal upright posture was perturbed by a calibrated force that was momentarily applied to the subject's chest. In fact, the operator pushed the subject with a stick coupled with a force transducer. Three cosmonauts participated in this study; two had been on-orbit for 151 days and the third for 241 days. Postflight testing was not initiated until six days after return of the crew. In all but one crewmember, less force was required to perturb vertical posture postflight, and in all crewmembers the time to recover from the applied perturbation increased postflight. Overall muscle activity required to maintain upright posture following the perturbation was also increased postflight. All changes observed on the sixth postflight day were still present on the eleventh day, but to a lesser degree, and were reportedly similar to those observed following other missions of comparable length (Grigoriev & Yegorov 1990).

4.3 Moving Platform Tests

4.3.1 Support Base Translation

Pre- and postflight postural stability measurements were made on four crewmembers from the Spacelab-1 mission using a dynamic posture platform that could be moved parallel to the floor in both predictable and unpredictable patterns, including sinusoids, pseudorandom and velocity steps (Anderson *et al.* 1986). In these studies, the subject attempted to maintain a normal upright stance with eyes either open or closed as the moving platform perturbed his base of support. EMG data obtained from the soleus and anterior tibialis muscles and the hip and shoulder displacements relative to the moving platform were recorded with edge detection cameras throughout the testing period. Postflight, when the subject's eyes were open and the platform was moved with a backward step function, the subject's response showed an overshoot with the shoulders and an undershoot with the hips relative to his preflight response. Also, the time required to assume a new stable position was greater after flight than before. The EMG data indicated that soleus muscle latency was greater postflight. It is interesting to note, in contrast to other posture tests, that vision appeared to degrade performance.

Another interpretation, however, would suggest that visual stabilization (i.e., gaze) was the important parameter, and that shoulder (in lieu of actual head movement measurements) tracking of the stimulus would reflect a decrease in head stability (and gaze by inference). This interesting result has never been verified with additional testing.

4.3.2 Support Base Rotation

In another dynamic posture platform study on Spacelab-1 (Kenyon & Young 1986), the crewmember's erect posture was perturbed by pitching the platform base unexpectedly about the ankle joint. EMG activity from the anterior tibialis and Gastrocnemius muscles was measured with the eyes open and closed. Postflight, the early EMG response (first 500 ms) did not change in latency or amplitude when the platform was pitched. However, the late EMG response (after the first 500 ms) was found to be higher in amplitude than that obtained preflight.

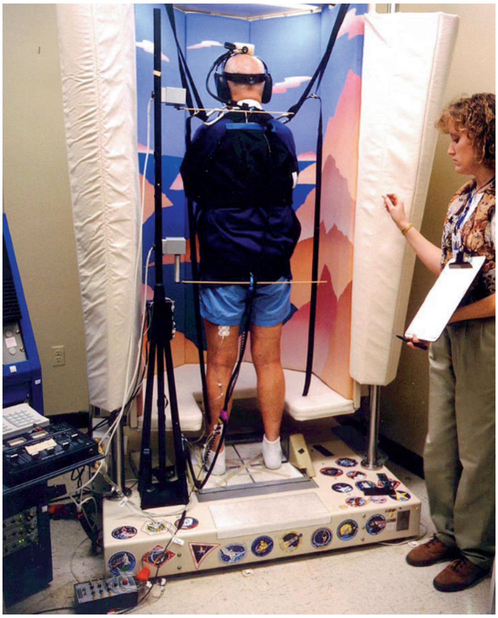

Figure 5-08. Subjects ability to stand as still as possible is investigated while standing on a platform inside a booth. The platform and the booth are designed to isolate the visual, vestibular and proprioceptive information used for balance control. For example, the booth is slaved to the body sway to prevent changes in visual information (sway-referenced vision). Similarly, information from proprioceptive receptors in the ankles is cancelled by moving the foot platform in phase with the displacements of the center of gravity (sway-referenced support). Measurements include displacements of the center of gravity, hip and shoulder; angular velocity of the head in pitch yaw and roll; and EMG activity of leg muscles. Photo courtesy of NASA.

4.4 Complex Visual, Vestibular and Proprioceptive Tests

The relative importance of visual, vestibular and somatosensory information to control of postural stability was studied before and after the seven-day Spacelab D-1 mission using a tilting room (von Baumgarten *et al.* 1986). Crewmembers stood with their feet on an Earth-fixed stabilometer anchored to the floor beneath the tilting room while body sway was measured under conditions of no visual input (eyes closed), conflicting visual-vestibular input (eyes open, room tilted with a sinusoidal motion), normal vision (eyes open, room upright), or reduced somatosensory input (foam rubber placed between the stabilometer and the astronaut's feet). Immediately postflight (a few hours after landing), two crewmembers showed an increased reliance on visual feedback for maintenance of upright postural equilibrium; stability was decreased when the room was oscillating or when eyes were closed. By the second day after landing, when three additional subjects were tested, stability under the oscillating room condition was analogous to that observed before flight. On the other hand, postural stability remained impaired for up to five days postflight when the crewmembers stood on the foam rubber or closed their eyes.

Later, a clinical posturography system (Equitest, Neurocom International, Clackamas, OR, USA) was used to assess the magnitude and recovery time course of postflight postural instabilities in returning astronauts from Space Shuttle missions (Paloski *et al.* 1993). This system consists of a platform and a visual surround scene, both of which are motorized to allow either a step input to the subject or servo-slave the platform and the scene to the subjects sway motion (Figure 5-08). Subjects complete multiple tests before and after the flight to establish stable individual performance levels and the time required recovering them. Two balance control performance tests are administered. The first test examines the subject's responses to sudden, balance-threatening movements of the platform. Computer-controlled platform motors produce sequences of rotations (toes-up and toes-down) and translations (backward and forward) to perturb the subject's balance. The second test examines the subject's ability to stay upright when visual or ankle muscle and joint information is modified mechanically. A battery of six sensory organization tests is used to assess a subject's ability to maintain postural equilibrium under normal and reduced sensory feedback conditions. The basic paradigm involves measuring hip, shoulder, head, and center of mass sway over 20-sec periods while the subject attempts to maintain a stable upright stance. Sway measurements are made three times under each of six randomly presented test conditions, including an eyes-open Romberg test, an eyes-closed Romberg test, and four other tests in which vision and/or ankle proprioceptive inputs are selectively eliminated by having the subject close his eyes or by servo-controlling the visual surround and/or support surface to the subject's center of mass sway.

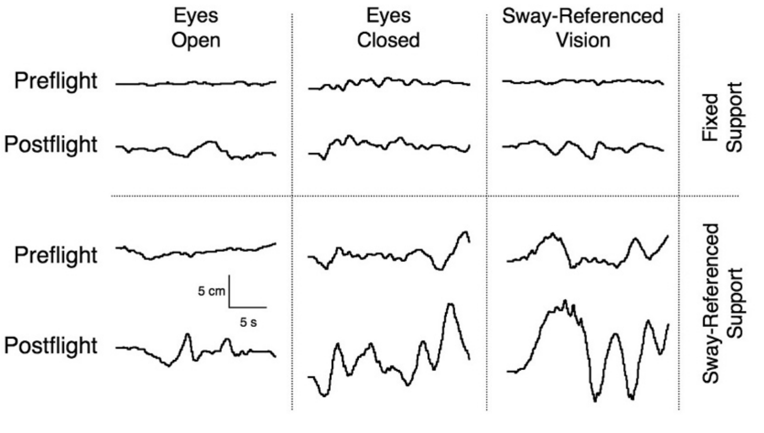

Figure 5-09. Pre- and post-flight anterior-posterior sway for a subject standing on a force platform for 20 sec. Each column and row represents a different visual and support surface condition, respectively.

The upper traces in each panel represent the preflight performances and the lower traces represent the postflight performances. After flight the subject's anterior-posterior sway amplitude increased under all test conditions compared to preflight. The increased amplitudes observed under sway-referenced support were balance threatening. When both visual and proprioceptive cues were sway-referenced, this subject's center-of-gravity oscillated between his/her forward and backward stability limits. Adapted from Paloski et al. *(1993).*

This test has the advantage of a huge clinical database against which the effects of space flight can be evaluated. Postflight measurements using this system revealed significant deviations from the results obtained before flight (Figure 5-09). The strategy used by the individuals for balance on the moving platform is modified and their behavior indicates a decrease in awareness of the direction and magnitude of the motion. On landing day, every subject exhibited a substantial decrease in postural stability. Some had clinically abnormal scores, being below the normative population 5th percentile. As dramatic as these results are, testing postural performance with the head upright may underestimate the level of disequilibrium following space flight. During a recent study, Paloski and his colleagues (2004) observed 90% fall incidence on landing day in trials during which crewmembers performed active pitch head tilts versus no falls during trials with the head held upright.

Significant differences in this complex posture test were identified between rookie (first-time space travelers) and veteran (experienced space travelers), suggesting that something learned in the adaptation/re-adaptation process is retained from one flight to the next. It was suggested that experienced space travelers are better able to use vestibular information immediately after flight than first-time fliers (Paloski *et al.* 1999). Since experienced astronauts have previously made the one-g to zero-g to one-g transitions, they may be partially dual-adapted and able to more readily transition from one set of internal models to the other.

It was also found that the recovery time course followed a double exponential path. In the 34 astronauts tested after 10-12 day Shuttle flights, an initial rapid improvement in stability during the first eight to ten hours was followed by a more gradual return to preflight stability levels over the next four to eight days (Figure 5-10). It was concluded that postflight postural instability appears to be mediated primarily by alterations in the vestibular (presumably otolithic) feedback loop and, secondarily, by alterations in ankle proprioceptive feedback, at least in some subjects (Paloski *et al.* 1999). It also appears that increased reliance on vision may partially compensate for the degraded performance of the other two feedback systems.

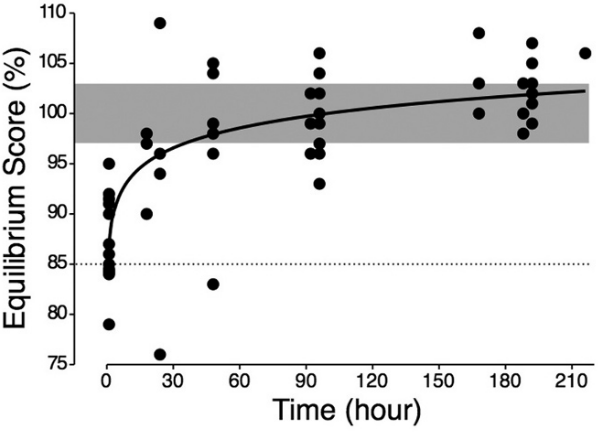

Figure 5-10. Sum of the equilibrium scores from the various sensory tests performed on astronauts after landing relative to preflight. The grey area indicates the mean (100%) and standard error measured preflight on the same subjects. A few hours after landing, the average returning crewmember was below the limit of clinical normality (dashed line). After flights ranging from 5-13 days, postflight re-adaptation took place in about four days and could be modeled as a double-exponential process, with an initial rapid phase lasting about 2.7 hours and a secondary slower phase lasting about 100 hours. Adapted from Paloski et al. *(1999).*

In a related study, Speers and his co-investigators (1998) examined changes associated with space flight in postural strategies employed by a 10-subject subset of the original 34 subjects. Using a multivariate approach, they found an increase in the relative utilization of hip sway strategy after flight and they conclude that these changes are consistent with re-weighting of vestibular inputs and changes in control strategy in the multivariable posture control system.

Postflight postural instability appears to be mediated primarily by alterations in the vestibular (presumably otolithic) feedback loop and, secondarily, by alterations in ankle proprioceptive feedback, at least in some subjects. The effects of demographic factors like age, gender and longer mission duration on these responses are currently being evaluated.

4.5 Tests of Vestibulo-Spinal Reflexes

In a number of pre- and postflight studies using the *Hoffmann reflex* (H-reflex) and the *tendon reflex* (T-reflex) techniques, it has been shown that both the alpha and gamma motor systems can be altered by space flight. In crewmembers studied during the Skylab program, the postflight T-reflex elicited by Achilles tendon percussions (mechanical stimulation) showed considerable potentiation over preflight baseline values (Baker *et al.* 1977). Before and after the Spacelab-1 mission, the H-reflex (electrical stimulation) showed a potentiation related to the selected drop-to-shock interval (see Section 3.3.2) for up to seven days postflight (Reschke *et al.* 1984).

Similar results have been obtained in the Russian space program. Kozlovskaya *et al.* (1984) demonstrated that two days after landing, the H-reflex in monkeys required a lower stimulus threshold and was potentiated over that observed before flight. In this study, it was observed that a single shock could elicit a response where the usual protocol required a double shock technique. When the double shock was employed, the second response following the conditioning shock (by 100 ms) was not inhibited, but rather enhanced. More recently, Grigoriev & Yegorov (1990) reported that the T-reflex in crewmembers who had been in orbit for up to 241 days on board Mir was characterized by a decrease in threshold and a three- to fourfold increase in amplitude over preflight values even on the sixth day postflight.

Coupled with the gradual decrease in the vestibulo-spinal reflex amplitude observed in-flight (Reschke *et al.* 1984, 1986, Watt *et al.* 1986, Watt 2001), the postflight potentiation of the H-reflex and T-reflex suggests response mediation via descending vestibular (otolith) pathways and a reinterpretation of otolith function via adaptation within the CNS in response to the stimulus rearrangement of orbital flight.

4.6 Postural Response to Voluntary Movements

In a simple test following two short-duration Shuttle missions, crewmembers provided with a visual reference (imaginary with eyes closed) were ask to bend at the waist in roll or pitch in an attempt to match a 20-deg angle (Reschke & Parker 1987). It was reasoned that if visual signals were eliminated and the otolith output was not interpreted as tilt immediately postflight, then the magnitude of the feedback signal during voluntary tilting would be reduced. Consequently, the astronauts would be expected to bend too far as they attempted to perform the roll or pitch movements. Kinematic analysis obtained from video recordings showed no significant difference in estimating the magnitude of tilt between pre- and postflight bending in either the roll or pitch plane planes. However, the basic premise may still be correct. Following the STS-41B Shuttle mission, one crewmember, attempting to test his limits of stability, demonstrated that by tilting in the roll plane there was a consistent angle at which he would lose his balance. When it was pointed out to him that most individuals would lose balance at that tilt angle, his comment was: "Yes, but I am unaware of the angle that I am leaning, even with my eyes open" (Reschke *et al.* 1991).

Another interpretation of the results is possible. While accuracy in achieving a specified tilt angle was unchanged immediately postflight, the strategy employed to maintain this accuracy appeared to involve a change in the use of the hips and shoulders. The hips were thrust backward more postflight and the angle of the head indicated that there was an attempt (or strategy) to stabilize the head in space, thus ensuring that gaze was maintained. This finding is related to the results on the translation platform, the more complex measures of postural stability and the locomotion studies described below.

4.7 Clinical Benefits

The results of space experiments on posture have put forward the remarkable plasticity in the organization of postural reactions. Prolonged exposure to a weightless environment results in changes in the sensory systems (with the possible exception of vision) necessary for the maintenance of postural stability. These changes, driven by the new complex of stimuli of microgravity, originate at the periphery and involve a subsequent reinterpretation of the sensory input from the receptors serving kinesthesia, touch, pressure, and otolith functions. Furthermore, as in-flight time increases, habituation of responses appropriate to the new inertial environment occurs at a central level, but the terrestrial motor programs are maintained. Upon return to Earth, postural instability, to a point that borders on clinical ataxia, is manifested as a result of this in-flight neural reorganization. Postflight recovery of posture is then probably related to the time it takes for the CNS to re-adapt to the appropriate interpretation of graviceptor signals. The faster re-adaptation observed in veteran astronauts on their subsequent flights opens interesting perspectives for the rehabilitation of patients after lesions of the vestibular system and countermeasures that may be developed for planetary exploration missions.

Information obtained from these investigations is promising for ground-based clinical research. A relatively large number of individuals on Earth suffer from prolonged, frequently life-long, clinical balance disorders. Disorders like Ménière's disease and traumatic injuries to the inner ear can severely influence quality of life. Falls are the leading cause of injury-related deaths in the elderly and these numbers continue to grow. Inner ear disorders are thought to account for 10-50% of falls among senior citizens. Currently, human space flight is the only means available for studying the response to sustained loss and recovery of inner ear information. Comparison between data from astronaut-subjects and similar data from patients and elderly subjects demonstrates similarities between these balance disorders. One sensible difference is that the posture problems recover in a few days for the astronauts, whereas it can take weeks (or never recover) in the patients. It is hoped that a better understanding of the strategies used during the recovery process in the astronauts and of the plasticity of this system in general, will help to improve rehabilitation treatments for patients with balance disorders on Earth.

5 LOCOMOTION STUDIES

Erect walking is a unique feature of human locomotion. Its evolutionary history indicates highly specific adaptations of the skeletal and muscular apparatus. Also, erect posture is mechanically efficient in humans because the center of body mass vaults over the supporting limb like an inverted pendulum, thereby limiting energy expenditure by means of an exchange of the forward kinetic energy with the gravitational potential energy (Cavagna *et al.* 1977).

Normal gait control depends on the acquisition of pre-programmed patterns of muscle activation and requires the continuous monitoring of external sensory input and internal reafferent signals. Locomotion pattern generators in the CNS are subject to overriding control from higher neural centers (Brooks 1986). Peripheral sensory and internal reafferent feedbacks modify patterns of activation emitted by pattern generators to improve ongoing motor performance.

Detailed postflight locomotor studies indicate that the relationship between sensory input and motor output is altered in the microgravity environment. During prolonged missions, neural adaptive processes come into play to permit new locomotion strategies to emerge in this novel sensory environment. This recalibration is associated with a time constant of acquisition and decay. The adaptive state achieved on-orbit is inappropriate for a one-g environment, leading to gait instabilities on return to Earth.

5.1 In-flight Observations

The cautious gait of astronauts descending the stairs of the “white room” docked with the Space Shuttle and walking on the runway is an obvious example of changes in sensorimotor coordination. Typically, locomotion in microgravity poses no problem and is quickly learned. However, adaptation continues for about a month. The astronauts who just visit the ISS note that the long-duration crewmembers move more gracefully, with no unnecessary motion. They can hover freely in front of a display when the new comers would be constantly touching something to hold their position (Clément 2005).

When moving about in space, the astronauts stop using the legs as they do on Earth. Instead they will increase the use the arms or fingers to push or pull themselves within the available space. For clean one-directional movements, push must be applied through the center of gravity, i.e., just above the hips for a stretched-out body. When translating though, the natural place for the arms is overhead to grab onto and push off from things as they come whizzing by. This is the worst possible place from the physics of pushing and pulling for clean movements, for by exerting forces with arms overhead, some unwanted rotations will invariably occur, which have to be compensated with ever more pushes and pulls, giving an awkward look to the whole movement. “To cleanly translate, I found it is best to keep the hands by your hips when exerting forces and boldly go headfirst. This way your pushing and pulling is directed through your body’s center of gravity and gives nice controlled motions without unwanted rotations” (Pettit 2003).

Movement in a weightless environment obeys Newton’s laws of motion. Friction forces are negligible and the angular momentum is always conserved unless acted on by an outside torque. Filmed sequences of astronauts performing a number of gymnastic moves in space were analyzed frame-by-frame. The principle of conservation for angular momentum was demonstrated as the astronauts tumbled, twisted and rotated in space. Throughout their motion and up until they entered in contact with the wall, the angular momentum was constant at 35.7 ± 1.2 kg x m^2/sec while rotating freely (NASA 1995).

5.2 Pre- and Postflight Studies

Since the legs are less used for locomotion, new sensorimotor strategies emerge in microgravity. Some of this newly developed sensorimotor program "carries over" to the postflight period, which leads to postural and gait instabilities upon return to Earth. Both U.S. astronauts and Russian cosmonauts have reported these instabilities even after short-duration space flights. Postflight, subjects experience a turning sensation while attempting to walk a straight path, encountered sudden loss of postural stability especially when rounding corners, perceived exaggerated pitch and rolling head movements while walking, and experience sudden loss of orientation in unstructured visual environments. In addition, oscillopsia and disorienting illusions of self-motion and surround-motion are observed during the head movements induced by locomotion.

In an early and intensive program, Russian investigators (Bryanov *et al.* 1976) studied locomotor behavior in 14 cosmonauts following missions lasting from 2 to 30 days in the Soyuz spacecraft (Soyuz-9, 12, 13, 14, 15, 16, and 17). Using motion picture analysis techniques, the sequential position of various body joints and limbs were recorded and analyzed to determine performance associated with walking, running, standing, long jumps, and high jumps. Distinct postflight performance decrements in gait and jumping behavior were observed with the duration of the decrements related, in most cases, to the length of the flight. Postflight gait was modified for 15 to 30 minutes after two days in space, but was affected for up to two days after flights of six to eight days. This same trend was observed for flights lasting 16 to 18 days, with performance on the Soyuz-9 (18 days) mission showing more degradation (disturbances in walking were still apparent 25 days after flight) than that observed following the sixteen-day Soyuz-14 mission (almost complete recovery two weeks postflight). Surprisingly, gait and related responses (jumping performance) following the thirty-day Soyuz-17 flight were more analogous with the postflight performances of the Soyuz-14 crew.

A typical postflight profile of the Russian cosmonauts is similar to that observed in the returning U.S. astronaut population. In walking, the cosmonauts place the legs wide apart, with the trunk held to the side of the supporting leg, and the intended path is not maintained. For greater stability, they frequently raise their arms to the side and they walk with small steps of irregular length. It is highly characteristic that in the transfer of weight during a forward step, the downward movement of the foot accelerates. At the moment of impact with the ground, the foot is "thrown" rather than being placed normally, creating the appearance of a stamping gait (Bryanov *et al.* 1976).

It is not uncommon when walking with returning crewmembers the length of the O&C Building at Kennedy Space Center, which is about 100 meters in length, to observe that they deviate to their right or left, then they realize that they had almost run into the wall, and they make a quick correction back to center. This turning sensation while attempting to walk a straight path is presumably related to the asymmetry in the re-adaptation of the vestibular system.

5.2.1 Head and Gaze Stability

Grossman *et al.* (1988) demonstrated that during walking and running in place in normal gravity, the peak velocity of head rotation in all axes is generally constrained below 100 deg/sec, and is thus below the saturation velocity (350 deg/sec) of the vestibulo-ocular reflex (Pulaski *et al.* 1981) However, the predominant frequency of head rotation during walking in place may range up to 4 Hz, and during running in place, to 8 Hz. Grossman and his colleagues (1989) have characterized gaze stability during walking and running, and have found that the angle of gaze is relatively stable. However, individuals with loss of vestibular function experience impaired visual acuity and oscillopsia during locomotion, stressing the importance of the VOR in maintaining gaze stability during locomotion (Grossman & Leigh 1990, Pozzo *et al.* 1991).

During the performance of various postural and locomotor tasks in terrestrial gravity, angular head deviation is maintained with a precision of a few degrees (Grossman *et al.* 1988, Berthoz & Pozzo 1988). Berthoz & Pozzo (1988) traced several of the figures from the classic Muybridge (1955) book showing successive photographs of human subjects engaged in a variety of different tasks. When these figures were superimposed around a common point (external auditory meatus), they noted that the head is stabilized in space within a few degrees. Berthoz & Pozzo (1988) also performed a quantitative examination of head stabilization during locomotion and found that, like the subjects photographed by Muybridge, the head did not exceed angular rotations of more than 3-6 deg in amplitude.

These ground-based results suggest that coordination of the body during locomotion is driven by the requirement to maintain head stability, and thus gaze. This concept represents a “top down” approach to the problem of gait stability. The underlying hypothesis is that gait stability is established to maintain head position in space reducing gaze error. Therefore, the maintenance of posture and gait stability is a goal-directed response designed to stabilize the head relative to the Earth’s vertical ensuring gaze stability and the maintenance of visual acuity. This “top down” approach contrasts with the concept that maintenance of posture and gait following space flight is exclusively a function of in-flight changes in locomotion, the reduction of muscle tonus and a corresponding loss of muscle strength.

This novel concept was applied to data obtained from the H-reflex experiment flown on Spacelab-1 (Reschke *et al.* 1984, 1986). Linear acceleration was provided by a vertical drop of approximately 12 cm. High speed photographs (2400 frames/sec) were taken during selected drops before and immediately after flight, and the angle of the head was computed from markers placed on the head. There was approximately twice as much angular deviation of the head three hours after landing than there was before flight (8-10 deg preflight; 20 deg postflight); by the third day postflight, a strategy had developed that allowed the subject to maintain a stable head position despite the observation that orientation of the trunk and limbs continued to be more variable than that recorded preflight. Thus, under most tasks, the head seems to be stabilized in a very precise fashion suggesting that postural and gait motor control strategies are organized around achieving this goal. During movement in the microgravity environment of space flight, the requirement to stabilize the head is presumably reduced. Thus gait and postural instabilities experienced by astronauts upon return to Earth may be caused by in-flight adaptive acquisition of new “top down” motor strategies designed to maintain head and gaze stability during body movement in microgravity. Novel and potentially unstable gait strategies may be adopted postflight in an attempt to maintain head stability in the face of conflicting sensory cues during the period of sensory recalibration on re exposure to a one-g environment.

More recently, Bloomberg *et al.* (1997) have reported changes in head pitch variability, a reduction of coherence between the trunk and compensatory pitch head movements, and self reports from crewmembers indicating an increased incidence of oscillopsia (the illusion of a visual surround motion) during postflight treadmill walking. These results are reported in greater details below.

5.2.2 Dynamic Visual Acuity

In recent experiments designed to investigate the effects of space flight on head and gaze stability during locomotion, astronaut subjects were asked to walk and run on a motorized treadmill while visually fixating a stationary target positioned in the center of view (Figure 5-11, left). Tests were conducted 10 to 15 days before launch and two to four hours after landing. A video-based motion analyzing system was used to record and analyze head movements (Bloomberg *et al.* 1999). Data from 14 crewmembers collected following their long-duration (~ 6 months) stays in space showed a decrement in dynamic visual acuity while walking. For some subjects the decrement in dynamic visual acuity was greater than the mean acuity decrement seen in a population of vestibular impaired patients collected using a similar protocol. This decreased dynamic visual acuity is presumably related to the degree of oscillopsia experienced during postflight locomotion (Bloomberg & Mulavara 2003).

It is also clear from these studies that head motion displays more variability during locomotion following space flight. Analyzing each subject's amplitude of the predominant frequency for the head angular roll, pitch and yaw movement during locomotion showed that, after space flight, there was a significant change in the head roll and pitch orientations, respectively, during walking. In contrast, only smaller percentage of subjects showed a significant change in head movement magnitudes in the yaw orientation, during walking.

Comparison between responses from astronauts who had experienced more than one space flight and first-time fliers indicated that the former demonstrated less postflight alteration in the frequency spectrum of pitch head movements than the latter. Postflight behavioral differences between astronauts based on their experience level have been previously observed in tests of dynamic postural equilibrium control (Paloski *et al.* 1993). In these tests, inexperienced astronauts show greater postflight decrements in postural stability than their more experienced counterparts. Such differences may be the result of many factors. However, they could indicate that repeated exposure to space flight leads to facilitation in formulating the adaptive sensorimotor transition from a microgravity to a terrestrial environment.

The significant reduction in predominant frequency amplitude of pitch head movements observed in astronauts postflight may be caused by attempts to reduce the amount of angular head movement during locomotion, and reduce potential canal-otolith ambiguities during the critical period of terrestrial re-adaptation. This in turn, further simplifies the coordinate transformation between the head and trunk, presumably allowing an easier determination of head position relative to space. Yet, this strategy is not 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 re-adaptation takes place, a decrease in constraints on the degrees-of-freedom of head movement likely occurs, returning performance back to preflight levels. Interestingly, patients with vestibular deficits (Keshner 1994) and children prior to development of the mature head stabilization response (Assaiante & Amblard 1993) also show head movement restriction during locomotion.

Changes in head and torso movements during locomotion postflight, predominantly in the pitch and roll planes, are presumably due to the central reinterpretation of otolith information. These changes in coordination between the head and torso, added to the changes in the performance of the vestibulo-ocular reflex (see Chapter 6, Section 2.4) would then be at the origin of the alteration in gaze stabilization during locomotion. These results support the hypothesis that changes in head stability and coordination induced by adaptive modification in "top down" motor control schemes may indeed be a contributing factor to postflight locomotor impairment.

Figure 5-11. Left. While subjects walk at 6.4 km/h on a motorized treadmill, three-dimensional full-body motion data are acquired using a video-based motion analysis system; gait cycle timing is measured using foot switches placed in the shoes and dynamic visual acuity is assessed. Right. The Functional Mobility Test *provides an assessment of the functional and operational changes in locomotor function by testing subject's ability to negotiate an obstacle course placed over a medium-density foam floor. Photos courtesy of NASA.*

5.2.3 Lower Limb Kinematics

During locomotion, foot contact with the ground, weight transfers from one foot to the other and the push off with the toe from the ground are critical phases as these interactions result in forces that create vibrations, which if unattenuated, could interfere with the visual-vestibular sensory systems in the head. The musculoskeletal system controls these vibrations: muscles and joints act as filters to minimize the perturbing effects of impacts with the ground and help to maintain a stable trajectory at the head Hence, appropriate attenuation of energy transmission during locomotion, achieved by the modulation of the lower limbs' joint configuration coupled with appropriate eye-head-trunk coordination strategies, form the fundamental features of an integrated gaze stabilization system. From this point of view, the whole body is an integrated gaze stabilization system, in which several subsystems contribute, leading to accurate visual acuity during body motion. After space flight, changes have been documented in both head-trunk and lower limb patterns of coordination, which may exacerbate the on-going visual-vestibular disturbances.

McDonald *et al.* (1994, 1996) have evaluated the variability and stability of the motion observed in the hip, knee and ankle joints during treadmill walking (6.4 km/h) following space flight. The temporal characteristics of the gait patterns were remarkably robust, and there was no significant change at both toe off and heel strike postflight relative to preflight. However, increased variability was observed after space flight in hip joint at toe off and in knee joint at heel strike.

Lower limb EMG signals were collected during treadmill locomotion after short duration space flight (Layne *et al.* 1994). In general, high correlations were found between preflight and postflight activation waveforms for each muscle and each subject. However, relative activation amplitude around heel strike and toe off changed as a result of space flight. The level of muscle co-contraction, activation variability and the relationship between the phasic characteristics of the ankle musculature in preparation for toe off were also altered by space flight (Layne *et al.* 1996). During walking after long-duration space flight, astronauts also showed modified transmission characteristics of the shock wave at heel strike and increased total knee movement during the subsequent stance phase (Mulavara *et al.* 2000).

Related studies revealed disruptions in endpoint toe-trajectory control of lower limb kinematics during the swing phase of gait cycle (Courtine *et al.* 2002), increased lateral motion of the trunk during overground locomotion suggesting instability during gait (Courtine & Pozzo 2004), and impairment in the ability to coordinate effective landing strategies during jump tasks (Newman *et al.* 1997). These sensorimotor disturbances may lead to disruption in the ability to ambulate and perform functional tasks during initial reintroduction to a gravitational environment following a prolonged transit.

5.2.4 Functional Mobility Test

To further elucidate the underlying basic sensorimotor mechanisms responsible for postflight locomotor dysfunction, Bloomberg and his colleagues also used an integrative approach. They designed a *functional mobility test* (FMT) that serves as a global test of locomotor performance that relates to activities required for emergency egress after landing. In the FMT, the astronauts walk at their preferred paces through an obstacle course set up on a base of 10-cm thick medium density foam. The foam provides an unstable surface that increases the challenge of the test. The 6.0 m x 4.0 m course consists of several pylons and obstacles made of foam (Figure 5-11, right). Subjects are instructed to walk through the course as fast as possible without touching any of the objects on the course.

The dependent measure is the time to complete the FMT. Data collected on 18 crewmembers of ISS Expeditions 5-12 indicate that adaptation to space flight led to a 52% increase in time to complete the FMT one day after landing. Recovery to preflight scores took an average of two weeks after landing. Furthermore, three of 18 subjects were unable to perform the FMT up to one day after their return from space flight. These disturbances may have significant implications for performance of operational tasks immediately following landing in case of an emergency or on a planetary surface.

5.3 Walking on the Moon and Mars

Studies at NASA Langley Research Center, Hampton VA, carried out on a simulator equipped with an inclined plane (see Figure 1-06), showed that humans walking and running was approximately 40% slower under lunar gravity conditions compared with terrestrial conditions (Pestov & Gerathwohl 1975). As the rate of movement increased, the inclination of the trunk forward increased to a greater degree under lunar gravity than under terrestrial conditions (Figure 5-12). The effects of actual lunar gravity on human activities were evaluated during the Apollo missions. Interestingly, the energy expenditures of astronauts during activities on the Moon averaged 220-200 kcal/h, about the same as walking without any equipment under terrestrial conditions. A comparison of postflight medical data showed that the astronauts who did not experience lunar gravity were physically less fit than the other crewmembers. Their weight loss was considerable, orthostatic intolerance was increased, red cell mass decrease was more pronounced, work capacity was lower, and they showed greater loss in all body fluid volumes (Berry & Homick 1973).

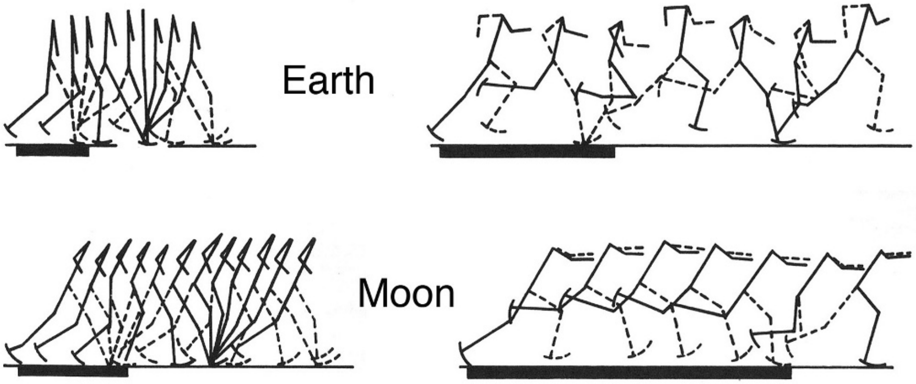

Figure 5-12. Changes in body kinematics during walking (upper diagrams) and running (lower diagrams) under lunar and terrestrial gravity levels. The heavy line shows the length of stride. Time interval between stick figures is 0.16 sec. Although more ground is covered in one single stride in lunar gravity compared to Earth gravity, locomotion is much slower. Adapted from Pestov & Gerathwohl (1975).

Despite training in ground simulations and in the one-sixth g airplane flying parabolas, falls were frequent among astronauts during extravehicular activity on the lunar surface. Eugene Cernan, Apollo-10 astronaut, on the Moon recalls “Jack (Schmitt) reached for a rock, lost his balance and toppled into a pratfall. … Jack fell again while trying to grab another Moonstone. ‘I haven’t learned to pick up rocks, which is a very embarrassing thing for a geologist,’ he admitted” (Cernan & Davis 1999, p. 323). The high and rearward center of gravity of the Apollo suit influenced upslope walking and the stiffness of the inflated suit strongly influenced gait, making it impossible to squat to retrieve dropped objects.

Different lunar gaits were tested and adopted by the crew. These included a “loping gait” in which the astronaut alternated feet, pushed off with each step and floated forward before planting the next foot; a "skipping stride," in which he kept one foot always forward, hit with the trailing foot just a fraction of a second before the lead foot, than pushed off with each foot, launching into the next glide; as well as a "kangaroo hop," which few Apollo astronauts ever employed, except playfully, because its movements were so stilted (Hansen 2005, p. 502). Learning each gait was relatively fast: Eugene Cernan, Apollo-10 astronaut, on the Moon: "I skipped around to get my sea legs in the low gravity of this strange new world. Learning how to walk was like balancing on a bowl of Jell-O, until I figured out how to shift my weight while doing a sort of bunny hop" (Cernan & Davis 1999, p. 322).

Contributing to the problem of locomotion on the lunar surface was the ruggedness of the terrain and the lower visibility. When looking out in any direction toward the horizon, the astronauts on the Moon felt a bit disoriented. Because the Moon was such a smaller sphere than the Earth, the planetoid curved much more visibly down and away than they were accustomed to. Also, because the terrain varied a good bit relative to their ability to move over it, they had to be constantly alert. "On Earth, you only worry about one or two steps ahead," Buzz has recalled (Figure 5-13). "On the Moon, you have to keep a good eye out four or five steps ahead." (Hansen 2005, p. 502). "Exacerbating the problem was the fact that astronauts really could not see their feet very well… The fact that the cables [on the ground] got dusty almost immediately also contributed to the problem" (Hansen 2005, p. 502).

In the planned Moon missions, lunar polar terrain may be more sloped than that explored by the Apollo astronauts. The polar sun angle will be far lower (1 deg, rather than 15 deg) so astronauts will be traversing areas of deeper shadow, possibly requiring the use of lights. Options for sensory supplementation during extra-vehicular activity should therefore be investigated. The effectiveness of vibrotactile cueing systems has been demonstrated in pilots and patients. They could be easily integrated in the suit. Also, night vision sensor imagery, an artificial horizon and a navigation display could be incorporated into an add-on external head-up display.

Figure 5-13. Astronaut Buzz Aldrin descends the steps of the Lunar Module *ladder as he prepares to walk on the Moon. Astronaut Neil A. Armstrong took this photograph during the only lunar extra-vehicular activity of the Apollo-11 mission. Photo courtesy of NASA.*

Ground-based simulations indicate that both the optimal walking speed and the range of possible walking speeds on Mars will be reduced compared to Earth. It was calculated that the optimal walking speed will be reduced to 3.4 km/h (down from 5.5 km/h on Earth) and the walk-run transition on Mars will occur near the optimal walking speed on Earth. However, because of the reduced gravity, the mechanical work done per unit distance to move the center of mass on Mars will be about half than on Earth (Cavagna *et al.* 1998).

6 SUMMARY

Numerous astronauts have been systematically subjected to posture and balance measurements within as little as two to four hours after landing since the very first space missions. The measurements have been obtained using standardized equipment, like balancing rails of variable width, stabilometry, and the NeuroCom EquiTest, and standard procedures, like voluntary arm or toe rises and deep knee bends. With rare exception, they all suffer from substantial disequilibrium (ataxia), especially on tests when their eyes are closed or where the support surface or the visual surroundings are caused to sway in conjunction with changes in the subject's center of mass. These situations leave the vestibular system as the only source of accurate information about orientation.

After short-duration missions, the astronauts recover rapidly for the first eight to ten hours and then gradually return to pre-mission levels over the next four to eight days. Some performance decrements are still observable weeks later. There is an inverse relationship between the initial severity of balance problems and the number of previous space flights. This indicates that one of the best countermeasures for space travel is space travel. Surprisingly, the otolith-spinal reflex appears to be no different in postflight tests than preflight performance, even though it was so greatly attenuated in microgravity. This perhaps indicates that recovery of this capacity to one-g is so rapid the problem disappears before it can be measured.

Astronauts experience substantial awkwardness, ataxia, vertigo, and slowing of gait for one week or more postflight. This is according to both anecdotal reports and controlled tests executed on a motorized treadmill, over a maze path, and on rails. A tendency to maintain a wide stance while walking, difficulty ambulating around corners, abnormal ankle angle, postural compensation for arm movements, and a substantial attenuation of the otolith-spinal reflex, which serves to prepare the body for the impact of unexpected falls, are specific problems that have been observed. About half of these aftereffects disappear within the first two to three hours after landing following short-duration missions. These aftereffects can last for much longer after long-duration missions (Figure 5-14).

Bloomberg *et al.* (1997) have reported reduced dynamic visual acuity in postflight astronauts while they were walking on a treadmill, especially for far distances. This deficit appears to be due to gaze destabilization (oscillopsia) because of a reduced ability to engage in compensatory head pitch movements during locomotion. These visual effects have been measured after two to four hours postflight and subsequently for as many as ten days postflight. This visual disability poses a potential hazard to reading cockpit displays, especially when making head movements, because it must certainly be present during the re-entry phase of the mission.

Adaptation to space flight also led to a 50% increase in time to traverse an obstacle course on landing day, and recovery of function took an average of two weeks after return. Importantly, alterations in kinematics and dynamic visual acuity were accompanied by commensurate changes in functional mobility. Such alterations in locomotion seen after space flight raise some concern about the crew capability for unaided egress from the Space Shuttle or the Soyuz in a case of emergency. Many crewmembers experience marked vertigo when making head movements during re-entry, landing and afterwards. This vertigo could be a major obstacle to successful egress if vision were impaired, as with a smoke-filled cabin.

The most significant visual-motor problems astronauts will encounter during their stay on the Moon and Mars are likely to occur when moving about in their space suits. The suits are quite large and bulky and alter the center of gravity. They will also need to learn the "lunar bounce" form of locomotion employed by the Apollo astronauts. Another possible problem will be reduced dynamic visual acuity due to changes in gait.

Our experiences on the Moon are limited and dated. Therefore, the only way to assess the effects of lunar gravity on perceptual-motor coordination is by Earth-based simulation. Partially unloading the body by means of springs or lower body negative pressure is one way to do this. This has already been done to test the effects of lunar gravity on treadmill walking (e.g., Donelan & Kram 2003). However, these procedures have no effect on the otolith organs. The one ground-based procedure that can produce all of the effects of lunar gravity is parabolic flight maneuvers, with all of the shortcomings and difficulties previously described.

Figure 5-14. A long-duration ISS crew-member (center) is being helped by ground personnel for walking after the landing of his Soyuz capsule in Kazakhstan. Photo courtesy of NASA.