

VESTIBULAR, PROPRIOCEPTIVE, AND HAPTIC CONTRIBUTIONS TO SPATIAL ORIENTATION

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■ **Abstract** The control and perception of body orientation and motion are subserved by multiple sensory and motor mechanisms ranging from relatively simple, peripheral mechanisms to complex ones involving the highest levels of cognitive function and sensory-motor integration. Vestibular contributions to body orientation and to spatial localization of auditory and visual stimuli have long been recognized. These contributions are reviewed here along with new insights relating to sensory-motor calibration of the body gained from space flight, parabolic flight, and artificial gravity environments. Recently recognized contributions of proprioceptive and somatosensory signals to the appreciation of body orientation and configuration are described. New techniques for stabilizing posture by means of haptic touch and for studying and modeling postural mechanisms are reviewed. Path integration, place cells, and head direction cells are described along with implications for using immersive virtual environments for training geographic spatial knowledge of real environments.

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INTRODUCTION

Thirty years have elapsed since the *Annual Review of Psychology* last included a chapter on the vestibular system. In that period, enormous progress has been made. Space flight became commonplace with the development of the U.S. space shuttle program, the Russian Mir space station, and the International Space Station. Now planning is taking place for a manned mission to Mars. A new panorama of information concerning human spatial orientation and performance in weightless and unusual force environments has emerged. In addition, important contributions of somatosensation and proprioception to orientation have been recognized as well as a contribution of cognitive factors. Falling in the elderly has become a major national and international health problem with the burgeoning numbers of older individuals. The present review provides a basic summary of vestibular function and then focuses on these new discoveries and problems.

VESTIBULAR RECEPTORS

The bilaterally symmetric labyrinths of the vertebrate consist on either side of three orthogonally oriented semicircular canals and two otolith organs.¹ Each semicircular canal is a skull-fixed cartilaginous ring filled with a fluid called endolymph.

¹For definitions of terms, see Glossary at end of text.

A gelatinous, elastic membrane, the cupula, spans the cross-section of each canal within an enlargement known as the ampulla. The cupulae encapsulate the cilia of hair cell receptors whose somas are embedded in the canal walls. Rotary acceleration of the head in the plane of a semicircular canal causes the endolymph to lag relative to the canal wall because of its inertia and low viscosity, and the resulting endolymphatic pressure deflects the cupula-hair cell complex. Bilateral parallel pairs of semicircular canals are symmetric with respect to ampulla location and are activated in push-pull fashion. Head angular acceleration causes deflection either toward or away from the ampulla, increasing or decreasing the afferent discharge rate, respectively, relative to the high tonic discharge rate when the head is stationary. Over the frequency range of natural head movements, the outputs of the canals are proportional to head angular velocity owing to the viscoelastic properties of the cupula-endolymph system. Some of the experimental procedures described below involve use of a rotating chair to create a step-like onset of head rotation followed by prolonged, constant velocity motion. Cupula-endolymph dynamics are such that the rotating chair evokes canal discharge that shows a direction and velocity-dependent sudden rise followed by a decay back to resting level.

The otolith organs by contrast are responsive to linear acceleration, be it of gravitational or inertial origin. These organs consist of aggregates of high specific-gravity crystals, or otoconia, embedded in a gelatinous membrane that also encapsulates the cilia of many hair cells whose bodies are fixed relative to the skull. Linear acceleration displaces the roughly planar otoconial masses relative to the skull, thereby bending the embedded hair cells. Hair cells collectively have a wide distribution of morphological orientations, resulting in their receptor potentials being tuned to different directions of acceleration in a plane. The utricular otolith organs are oriented roughly in the head's coronal plane and the saccular otoliths in the sagittal plane.

Different classes of hair cells and their associated primary afferent fibers of the semicircular canals and otoliths segregate angular and linear accelerations into low- and high-frequency bands. There are also efferent pathways from the CNS to the end organs, but the function of these pathways remains largely unknown. The vestibular system is illustrated in Figure 1. For a detailed review of vestibular anatomy and physiology, see Wilson & Melvill Jones (1979).

These specialized receptor systems participate in a variety of postural and oculomotor reflexes, and in the perception of body motion and orientation. Direct and indirect projections of the canal and otolith receptors to the vestibular nuclei, the "vomiting centers" in the pontine reticular formation (Miller & Wilson 1983), the cerebellum, the oculomotor nuclei, and the spinal cord have been systematically charted. Recently, vestibular projections to parietal and temporal cortical areas and hippocampus (Guldin & Grusser 1998, Kahane et al. 2003, Wenzel et al. 1996) have been identified that may underlie vestibular influences on perceived orientation and self-motion.

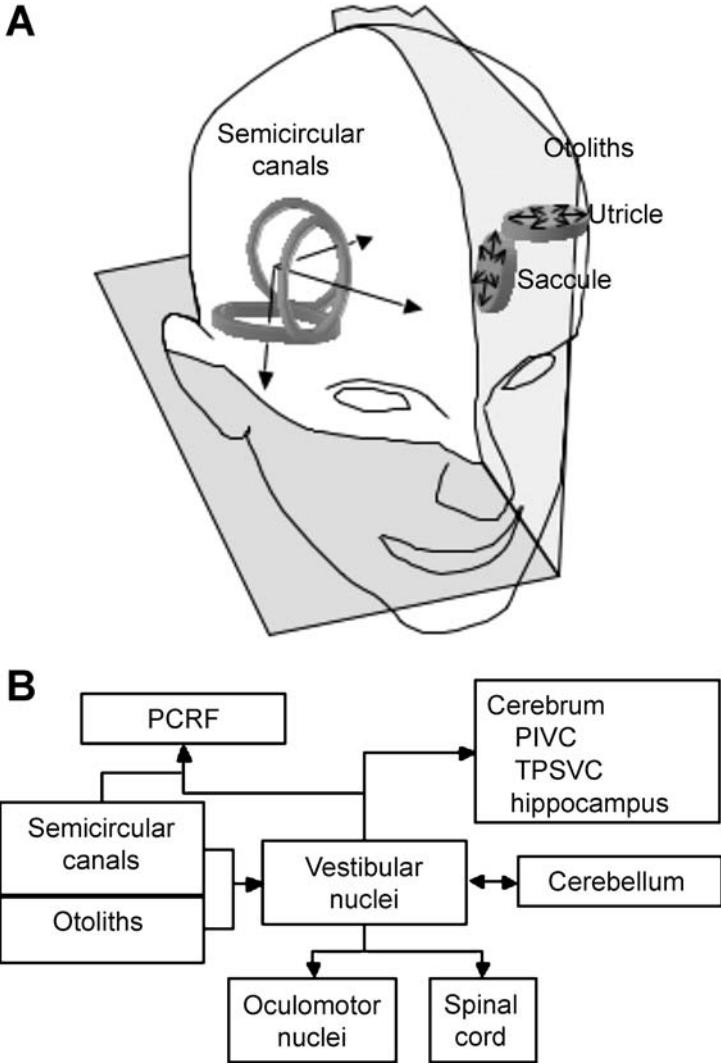


Figure 1 (A) Schematic illustration of the vestibular end organs. For clarity, the semicircular canals and the otolithic maculae are shown larger than life size and unilaterally, although both sets of organs are actually present on each side. The arrows associated with the semicircular canals indicate the head rotation vectors for which individual canals are selective; the arrows on the otolith organs are a reminder that individual hair cells on each macula are attuned to different linear acceleration directions. (B) A block diagram of connections from the vestibular organs to some important brain regions: PCRF is the parvicellular reticular formation, the electrical stimulation of which triggers vomiting; PIVC is the parieto-insular vestibular cortex; TPSVC is the temporo-perisylvian vestibular cortex.

VESTIBULAR REFLEXES

Vestibulo-Ocular Reflexes

Vestibulo-ocular reflexes and vestibulocollic reflexes are elicited both by angular and linear acceleration. During gaze shifts in which the eyes and head are oriented to a new target position, the eyes generally reach the target by a rapid saccadic movement followed by a head turn toward the target. The eyes are maintained on the target position during the head turn by a vestibulo-ocular reflex that drives the eyes in the opposite direction to the head at the same rate (see Figure 2). The vestibulocollic reflex stabilizes the head in the final position if additional passive whole-body motions are imposed. In the dark, during exposure to passive angular acceleration of the whole body, the vestibulo-ocular reflex produces a nystagmoid pattern of eye movements with a slow phase component compensatory for the direction of acceleration (“field-holding reflex”) interrupted by rapid saccades that reposition the eyes. When vision is allowed, the resulting optokinetic stimulation reinforces the vestibular compensation. During constant velocity rotation in the dark, the semicircular canal signals decay to baseline and the nystagmoid eye movements will gradually abate, but if vision is allowed the resulting optokinetic stimulation will continue to drive the eyes.

The vestibulo-ocular reflex has a three-dimensional structure (Cohen et al. 1999) that can be adaptively remapped (Dulac et al. 1995). Vestibulo-ocular reflex adaptation can be measured by comparing ocular responses to body oscillation in darkness before and after exposure to body oscillation relative to a rich visual scene. For example, a few minutes exposure to left-right rotation in synchrony with a head-fixed visual scene results in a change in gain of the vestibulo-ocular reflex such that the magnitude of compensatory eye movements in darkness is reduced. Furthermore, left-right rotation in synchrony with a visual scene oscillating up and down ultimately leads to a geometrical reorganization of the vestibulo-ocular reflex such that left-right oscillation of the body in darkness elicits vertical eye movements (Schultheis & Robinson 1981). Physiological pathways with as few as three neurons can mediate these reflexes, but higher-level inputs modulate them according to current goals. For example, a subclass of neurons in the vestibular nucleus faithfully conveys the primary afferent signals they receive about head motion in space during passive but not active head rotations (Gdowski & McCrea 1999, Roy & Cullen 1998). This task-dependent processing is based on an efferent copy of the head-to-torso rotation command (Roy & Cullen 2001).

Compensatory eye movements induced by linear acceleration include ocular counterrolling of the eyes during static roll tilt of the body (Miller & Graybiel 1962), the doll’s eye reflex (Ebenholtz & Shebilske 1975) during head pitch, and elevations and depressions of the eyes during exposure to decreases and increases in background gravito-inertial acceleration (GIA) level in the z axis of the upright head (Whiteside 1961) and to linear translations of the body (Jongkees & Philipszoon 1962). The otolith organs are responsive to GIA, the resultant of gravitational and inertial accelerations acting on the body. Under normal static conditions, GIA

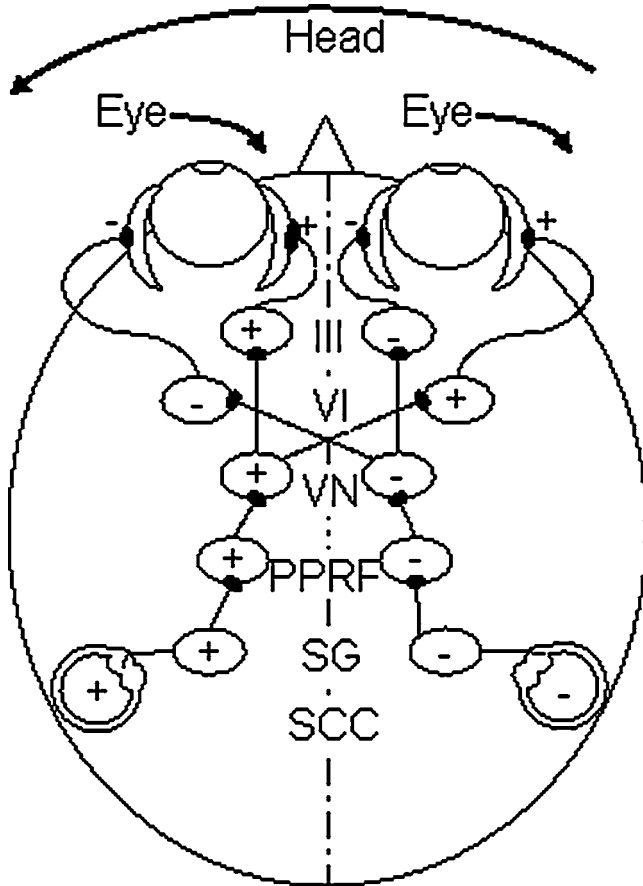


Figure 2 Schematic illustration of the circuit for an idealized unidimensional angular vestibulo-ocular reflex. A leftward head turn produces ampulopetal flow of endolymph in the ipsilateral semicircular canal (SCC) and increases the receptor potential (+*sign*); ampulofugal flow and depolarization (–*sign*) occur on the right side. Primary afferent fibers whose cell bodies are in Scarpa’s ganglia (SG) have high tonic firing rates that are increased on the ipsilateral side and reduced on the contralateral side. Excitatory synapses (filled circles) cause parallel increases and decreases in the ipsilateral and contralateral vestibular nuclei (VN) and para-pontine reticular formation (PPRF), respectively. Rightward eye movements result from a combination of ipsilateral connections to the oculomotor nuclei (III) that innervate the medial rectus muscles and contralateral excitatory input to the abducens nuclei (VI) that innervate the lateral rectus muscles. Circuitry involved in adaptation is not included.

magnitude simply corresponds to 1 g (9.8 m/s^2), the magnitude of earth gravity. Eye movements evoked by linear acceleration are rarely fully compensatory, e.g., the gain of ocular counterrolling and of the linear vestibulo-ocular reflex is about 0.1 to 0.15 (Paige & Tomko 1991). However, the linear vestibulo-ocular reflex shows sophisticated coordination with other orienting movements. For example, when an individual is undergoing left-right translation in darkness, the amplitude of lateral eye movements rapidly increases when the eyes converge to a nearer distance, as would be required to prevent visual slip of near objects if any were visible (Telford et al. 1997).

Vestibulo-Spinal Reflexes

Vestibular influences on postural control include modulation of the postural tone of the body and the antigravity reflexes that are key to maintaining without conscious effort the configuration and stance of the body vis-à-vis gravity (see Wilson & Peterson 1978, Wilson et al. 1995 for reviews). Such reflexes related to standing and balance interact in a synergistic fashion with reflexes related to the neck (tonic neck reflexes), the limbs, and the overall disposition of forces on the body (see Roberts 1978 for a review).

Loss of Vestibular Function

Progressive loss of vestibular function owing to a degenerative process may be largely unnoticed by an individual, unlike loss of other sensory functions such as hearing or vision, because of adaptive changes that occur to maintain function. The neck proprioceptive contribution to compensatory eye movements during gaze shifts, for example, increases and largely compensates for the loss of the vestibulo-ocular reflex (Bronstein & Hood 1986). Individuals with total loss of function who under normal circumstances are “fully compensated” in terms of balance and locomotion, nevertheless experience difficulty on uneven terrain or soft surfaces, e.g., sand, and under conditions of low light levels or darkness. Thresholds for perception of angular or linear acceleration are greatly increased but perception of body orientation relative to gravity may be largely intact, especially for conditions of self-support and active maintenance of posture. The preservation of accurate perception of body orientation despite loss of vestibular function is based on somatosensory, proprioceptive, efferent, and visual signals (Graybiel et al. 1968, Niven & Graybiel 1953). Loss of labyrinthine function confers total immunity to motion sickness.

EFFECT OF UNUSUAL PATTERNS OF ACCELERATION ON ORIENTATION AND SENSORY LOCALIZATION

Changes in visual and auditory localization and in perceived self-orientation are elicited by unusual patterns of vestibular stimulation. Many of these effects were initially described by Mach (1875).

Oculogyral and Audiogyral Illusions

Exposure to constant angular acceleration in a rotating chair produces changes in both visual and auditory localization (Clark & Graybiel 1949a, Graybiel & Hupp 1946). If a head-fixed visual target is being viewed in an otherwise dark chamber, it will be seen as moving with the body's changing apparent position in space but leading the body as well in the direction of acceleration. The time course and magnitude of this illusion, known as the oculogyral illusion, is related to the discharge dynamics of the semicircular canals, as described in the Vestibular Receptors section. The occurrence of the oculogyral illusion is related to the partial or complete suppression by visual fixation of the involuntary eye movements that otherwise would occur. The fixation "hold signal" to override the covert vestibular nystagmus and average shift in eye position (Schlagfeld displacement) is misrepresented as an eye deviation, thus causing an error in body relative visual localization (Whiteside et al. 1965). In the dark, a head-fixed auditory target will be heard to displace relative to the body in the direction opposite angular acceleration. The contrasting directions of the audiogyral illusion and of the oculogyral illusion have yet to be adequately explained. Figure 3 illustrates the oculogyral and audiogyral illusions.

Oculogravic, Audiogravic, and Somatogravic Illusions

Exposure to unusual patterns of GIA also leads to changes in sensory localization, in apparent self-orientation, and in apparent vehicle orientation. The oculogravic illusion is illustrated in Figure 4. During exposure to an increase in magnitude and a tilt of the GIA vector, a subject seated in a slow rotation room facing the direction of rotation, with left ear toward the center of the room, will experience rightward body tilt and see a luminous line as having displaced clockwise. If the room lights are on, the magnitude of the apparent body tilt will be decreased but a clockwise displacement of the entire room will be seen. Similar mislocalizations

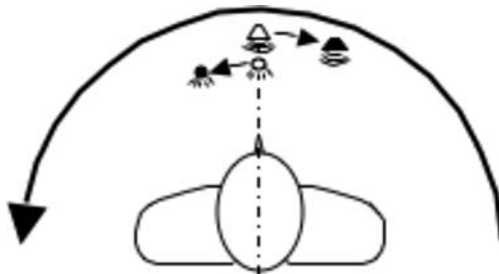


Figure 3 Illustration of the oculogyral and audiogyral illusions. The *large arrow* indicates the direction of head acceleration. The *unfilled icons* represent the actual locations of a loudspeaker and a target light fixed in the head midline (*dotted line*). The *gray icons* and *arrows* represent the perceived locations and motions, respectively, of the sound and light source.

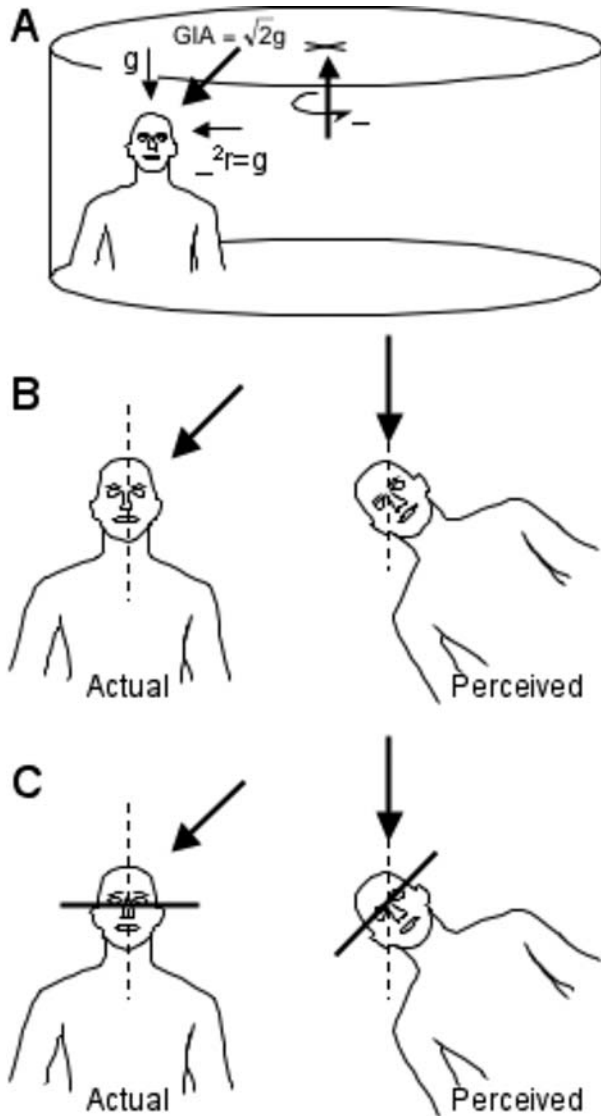


Figure 4 (A) Illustration of the gravito-inertial acceleration (GIA) experienced on a rotating room by a subject who is facing the direction of rotation, with left ear toward the center of the room, when the centrifuge acceleration is 1 g. The GIA magnitude and direction are determined by the vector sum of gravity and centrifugal force ($\omega^2 r$). (B) The somatogravic illusion refers to the apparent body tilt the subject experiences. (C) The oculogravic illusion. The subject perceives an externally presented, earth-horizontal line as tilted. If the room lights are on, the magnitude of the apparent body tilt will be decreased but a clockwise displacement of the entire room will be seen.

of auditory targets occur. The apparent body tilt is known as the somatogravic illusion (Clark & Graybiel 1949b), and the visual and auditory mislocalizations are referred to as the oculogravic (Clark & Graybiel 1949c, Graybiel 1952) and audiogravic illusions (Graybiel & Niven 1951).

These effects have sometimes been described as not illusions at all but simply accurate reflections of body and visual orientation in relation to a new vertical corresponding to the GIA orientation as sensed by the otolith organs, which cannot distinguish between inertial and gravitational accelerations (Howard & Templeton 1966). Recent experiments indicate a more complex mechanism (DiZio et al. 2001). Studies of visual and auditory localization have been carried out in which, during exposure to altered GIA direction and magnitude, subjects were required to adjust a visual or an auditory target so that it was perceived to remain in their body midline. In these circumstances, target position had to be displaced by about 15% of the GIA displacement and in the same direction in order to still be seen or heard in the midline of the head. Localization of somatosensory stimulation on the forehead was similarly affected (unpublished observation). Coincident with the altered sensory spatial localizations was a reorientation of the apparent median plane of the head. A joystick that was kept aligned with the apparent midline of the body was displaced in the direction opposite the rotation of the GIA. The time course and magnitude of this shift exactly paralleled the shifts in visual, auditory, and somatosensory localization but were of opposite sign. These localization changes are embedded in the framework of simultaneous changes in apparent orientation of the body with respect to external space.

The overall pattern of remapping of sensory localization coupled with a shift in the apparent body midline suggests that a common reference frame for body-relative localization and for localization of the body with respect to external space has been modified (see also Lewald & Karnath 2000). A potentially related finding is the observation that vestibular stimulation can alter the pattern of egocentric, unilateral spatial neglect experienced by some patients with brain injury (Vallar et al. 1990). The underlying physiological bases for these modulations remain uncertain, but temporal and parietal cortices contain projections from the relevant sensory modalities, receive vestibular projections, and are implicated in the perception of body orientation in space (Bottini et al. 2001). Thus, they represent natural sites for participation in the observed changes.

PROPRIOCEPTIVE AND SOMATOSENSORY CONTRIBUTIONS TO ORIENTATION

Muscle Spindles

The otolith organs of the inner ear provide information about the orientation of the head to the GIA. However, the ongoing sense of orientation includes the orientation of the entire body, and all of its links and segments, relative to gravity. The sense of the relative configuration of the body is commonly referred to as the body

schema. Joint receptors within the capsules of the joints were long thought to serve as potentiometers providing a fiducial representation of joint position that could contribute to an overall mapping of body configuration. However, with the advent of joint replacement surgery, it was found that accurate position sense was retained even in the absence of joint receptors (Grigg et al. 1973). About the same time, it was found that position sense was influenced by the muscle spindle fibers that are interspersed in parallel with the extrafusal muscle fibers that do the actual work of muscle contraction (cf. Matthews 1972). This arrangement means the total length of the muscle spindles is a function of overall muscle length; however, the length of their sensory region innervated by primary and secondary receptor endings is modulated by intrafusal muscle fibers innervated by gamma motoneurons in the spinal cord. The extrafusal muscle fibers are activated by the alpha motoneurons of the spinal cord. The spindle sensory signal is interrelated to the ongoing pattern of gamma and alpha activation and other signals about body loading to compute the angle and rate of change of the joint controlled by the muscle. This normal relationship can be distorted by vibrating a muscle mechanically, circa 100–120 Hz, to activate artificially its muscle spindle primary and secondary receptor endings (Hagbarth & Eklund 1966). In this circumstance, the heightened discharge is centrally interpreted as lengthening of the vibrated muscle and is referred to the joint controlled by the muscle. For example, vibration of the biceps brachii of the arm leads to the forearm feeling more extended than it actually is (Goodwin et al. 1972).

When postural muscles are vibrated, various illusions of body motion can be elicited. For example, simultaneous vibration of the Achilles tendons of a standing subject restrained in position will cause the subject to experience forward pivoting in pitch about the ankles. The subject, if in total darkness, will exhibit nystagmoid eye movements with the slow phase compensatory for the direction of apparent self-displacement. If a visual target is presented for the subject to fixate, it will be seen to move in the direction of apparent self-motion and to displace ahead of the subject in the same direction (Lackner & Levine 1979). Thus, the visual target motion has the same characteristics as the oculogyral illusion described above, and a similar physiological explanation in terms of suppression of involuntary eye movements can account for its properties.

Vibration of neck muscles leads to illusions of head rotation and displacement (Karnath et al. 1994, Lackner & Graybiel 1974, Lackner & Levine 1979). In fact, with vibration of the appropriate skeletal muscles, apparent motion and displacement of the body or its segments can be elicited in virtually any desired configuration (Lackner 1988). If visual or auditory targets are present, their positions also are remapped in the direction of apparent body motion and displacement. For example, when a small target light is attached to the hand and illusory motion of the restrained forearm is elicited by vibration of the biceps brachii or triceps muscles, the target light will be seen to displace physically in the direction of the apparent motion of the hand. This phenomenon is known as the oculo-brachial illusion (Lackner & Levine 1978).

Muscle spindle signals can be more important than vestibular cues in their influence on perceived orientation in altered gravito-inertial force environments. Subjects who move about during exposure to increases or decreases in background force level, for example during parabolic flight, experience instability of the aircraft deck and misperceive their own motion (Lackner & Graybiel 1981). When a deep knee bend is made in a greater than 1 g force level, the weight of the body is more than normal and the antigravity muscles that are undergoing eccentric contraction lengthen slightly more than for a lowering movement of the body in 1 g; in addition, an unusually high level of spindle discharge for the level of alpha-gamma motoneuronal activity likely is present. The nervous system “attributes” this unexpected lengthening to the floor moving up under the feet. With repeated deep knee bends, self-motion perception gradually becomes more accurate, and the aircraft again is perceived as stable under the feet. On return to a normal 1 g environment, aftereffects are experienced, with opposite signs. Astronauts on return to earth experience the same effects as individuals adapted to 1 g who are exposed to 1.8 g. The ground seems to move upward under their feet when they lower their body in a deep knee bend.

Somatosensation and Orientation

Proprioceptive information about limb configuration combined with somatosensory information about hand or limb contact with the body itself and with external objects is a key factor in calibration of the apparent dimensions of the body and of its relationship to external space. For example, if a subject is grasping his nose with his fingers and the biceps brachii muscle of the arm is vibrated, an illusion of arm extension will be elicited and the subject may feel his nose elongate in Pinocchio fashion (Lackner 1988). If the subject is seated with hands on the waist and arms akimbo, bilateral vibration of the triceps brachii muscles will elicit the illusion of the hands approaching one another and of the waist shrinking to become wasp-like. Such interactions indicate that the calibration of the body, in terms of its spatial dimensions, may be achieved by interaction with the hands. Control of the hands and their represented size can be calibrated by interacting with the external environment. Visual direction and the direction of regard also can be calibrated through sight of the hands.

Somatosensory stimulation influences perception of the upright and the control of posture. Receptors in the soles of the feet are important in the control of posture (Kavounoudias et al. 1998). For example, as the body leans forward, regions of the feet that are more anterior receive the most mechanical pressure in supporting the body against gravity. During passive stance, this provides a mapping of body orientation to the upright. Diabetic patients with peripheral sensory neuropathies have increased postural sway in part because of degradation of these foot-related signals. Postural control can be enhanced by the use of shoe insoles that vibrate to stimulate the plantar receptors, making it easier for the central nervous system to detect sway changes (Collins et al. 2003). Vests with tactor vibrators also have been employed with mild success to enhance balance by providing tactile stimulation

of the torso dependent on body orientation to the vertical (Kentala et al. 2003). Such systems also have been proposed for use in signaling body orientation in helicopters and high-performance aircraft (Rupert 2000).

Haptic Stabilization of Posture

Light touch cues from the hand have a powerful stabilizing influence on posture when a surface is touched with the index finger at mechanically nonsupportive force levels. In blindfolded individuals, finger contact reduces mean sway amplitude by about 50%. Even when normal sight of the surroundings is present, balance is further stabilized by light fingertip contact (Holden et al. 1994, Jeka & Lackner 1994). Labyrinthine-defective patients who cannot stand heel-to-toe with eyes closed for more than a few seconds can stand stably indefinitely when allowed light touch (Lackner et al. 1999). Finger stabilization of posture occurs in patients with diabetic neuropathy, cerebellar disease, alcoholism, and in fact, in all patient groups tested to date.

If unbeknownst to an individual, the touched surface is oscillated, postural entrainment occurs. The person will be made to sway at frequencies and amplitudes above normal detection thresholds and not be aware of it while the oscillating surface will be perceived as stationary (Jeka et al. 1997). Even when the test subject is aware that the surface can oscillate, postural entrainment will occur, albeit of lesser amplitude. However, in this circumstance, the subject will perceive the touched surface as moving and in trials in which the surface is stationary, it nevertheless may be perceived to be moving. This latter fact emphasizes the importance of cognitive knowledge and assumptions (i.e., “top-down effects”) about the environment for whether unseen touched objects will be perceived to be stationary or not.

The time course of postural stabilization by fingertip contact is remarkably rapid. When the finger is dropped to contact a surface, it will be stabilized on the surface within 100 milliseconds and a downward trend in body mean sway amplitude will be detectable within the next 100 milliseconds. By contrast, visual stabilization of posture by turning on the lights takes three or four times longer to begin and still longer to complete (JR Lackner, E Rabin, & P DiZio, submitted; Rabin et al. 2004). Touch signals from the hand also completely override the otherwise destabilizing effects of tonic vibration reflexes in leg muscles (Lackner et al. 2000). In addition, the illusions of self-displacement and aircraft displacement that occur with whole-body movements during exposure to increased or decreased background force levels in parabolic flight (see above) are virtually abolished by light contact of the hand with a stationary surface (Lackner & DiZio 1993).

The postural stabilization conferred by light touch seems to reflect a form of “precision touch” analogous to precision grip. When an object is held between the index finger and thumb and lifted, the forces at the fingertip are “automatically adjusted” to generate appropriate grip and load forces. The latency of grip adjustments, about 85 ms, is well below conscious reaction times, and reflects the

activity of a somatosensory-motor cortical control loop (Johansson & Westling 1984). During stance with maintained finger contact, the changes in the body's force at the fingertip phase lead changes in the body center of pressure and center of mass by about 300 ms. With fingertip contact, inverted pendulum sway of the body is maintained.

MODELS OF ORIENTATION

Physical sensors such as the otolith organs cannot distinguish gravitational from inertial accelerations. However, for humans, other forms of information that can disambiguate situations generally are available. One important factor is the control of the body itself in terms of the forces necessary to maintain balance or body support, and whether the body is actively moving. For example, when a person walks in a tight circle or makes a sharp turn, quite high centripetal forces are generated but body orientation is not misperceived (Imai et al. 2001). When the same forces are passively applied to the body, the same tilt of the GIA will lead to apparent roll tilt of the body (Miller & Graybiel 1966).

Internal Models and Cognitive Factors

The otolith organs have “regular” and “irregular” receptor units with different firing patterns (Fernandez et al. 1972). The regular fibers have discharges that are tuned to different static orientations of the body relative to gravity and that maintain a steady-state discharge virtually indefinitely. By contrast, irregular fibers respond to changes in acceleration and in position, but adapt over time. Regular units show a less-prominent dynamic modulation. Such frequency-dependent segregation of otolith afferent firing has been proposed as a way to distinguish gravity from inertial accelerations, especially for frequency domains that exceed those of voluntary head movements (Mayne 1974). Investigators have also proposed that the CNS uses internal models to discriminate inertia and gravity based on representations of the body's dynamics and on available semicircular canal as well as otolith input (Merfeld et al. 1999). Cognitive information also usually is available about the environment and its properties, such as whether the body is in a vehicle of some sort.

Tri-Axis Model of Spatial Orientation

A recent tri-axis spatial orientation model has been developed based on the hypothesis that the vestibular system evolved in a 1 g, Earth gravity context and that 1 g is taken as a standard relative to which all shear and deformation patterns of the otolith membranes are interpreted (Bortolami et al. 2004). The model incorporates the known structural features of the otolith organs and includes “cross talk” between the pitch and roll axes. This cross talk occurs because of the complex three-dimensional organization of the otolith membranes and their resulting displacements to shear forces (Grant & Best 1987). It accurately predicts both the

errors in spatial localization of the vertical that occur for different static orientations of the body in yaw, pitch, and roll relative to gravity, and the potential elicitation of inversion illusions in weightless conditions. A surprising prediction of the model is that when the recumbent body is in different static yaw orientations with respect to gravity, the level of resultant GIA will have negligible influences on perceived body orientation to the vertical. This prediction results from calculating yaw orientation from signals related to the pitch and roll axes and using a 1 g gravity standard to interpret these shear signals. Parabolic flight experiments have recently validated the model's predictions. The model uses somatosensory and proprioceptive cues to distinguish up and down, which is consistent with the important influence of touch and contact cues on spatial orientation in weightless conditions.

FALLING IN THE ELDERLY

Falls in the elderly have become a major health problem as longevity has increased (Maki et al. 1987). In the United States, the average survival time for a faller who has fractured a hip is about two years. Many factors contribute to falls, including reduced visual acuity, diminished vestibular function, lessened somatosensory and proprioceptive acuity, reduced muscle strength, and medications (Brown et al. 1999, Chen et al. 1996, Draganich et al. 2001, Klein et al. 1998, Lajoie et al. 1993, Leipzig et al. 1999, McIlroy & Maki 1996, Shumway-Cook et al. 1997, Thelen et al. 1996). Tripping on obstacles and when changing direction is also commonplace (Blake et al. 1988, Campbell et al. 1990, Overstall et al. 1977, Rubenstein et al. 1988). Individuals who are in the weightless phase of parabolic flight maneuvers and astronauts who are in orbital flight are actually in a state of continuous free fall; nevertheless, they do not perceive themselves to be falling (Lackner 1992). This means that otolith signals per se do not determine whether one experiences falling but that additional sensory and cognitive factors must contribute.

Experimental Tests and Models

A number of studies have investigated the role of surface features, obstacles in the walking path (Persad et al. 1995), sudden changes in direction (Mbourou et al. 2003), and visual factors (Judge et al. 1995) in predisposing individuals to lose balance during locomotion. These studies highlight the relative importance of various external factors in triggering loss of balance. Other studies have evaluated how various perturbations of the stance surface and of the visual surround affect postural recovery (Luchies et al. 1994, Pai & Patton 1997). Still others have explored the ability to recover from artificially induced forward leans of the body (Thelen et al. 1997). From these investigations, age- and gender-related changes in somatosensory, proprioceptive, and vestibular function, and muscular strength have been identified that may contribute to falling in the elderly.

Mathematical models of falling have been developed using an inverted pendulum representation of the body. The most advanced of these accurately reproduces the body's response to a Hold and Release perturbation (Bortolami et al. 2003). The individual being tested actively resists a force applied to his or her chest that is unpredictably released. For some tens of milliseconds, the body is physically in a state analogous to free fall, pivoting about the ankles. After a latency of about 50 milliseconds, compensatory postural adjustments are made to arrest falling and the body undergoes damped oscillations over 10 seconds before settling. Video recordings of the body multilink response and recovery from the perturbation, and electromyographic recordings from the postural muscles involved in the recovery, serve as observational input providing a description of the body's response. Fitting these data to a multilink inverted pendulum model allows computation of the stiffness and damping at the ankles, knees, hips, and neck, along with the recovery time to resettling. The patterning and magnitudes of muscle activation allow a snapshot of the underlying neurophysiological processes mediating recovery. It appears that postural responses to Hold and Release involve one-time, stable adjustment of stiffness and damping after a variable latency. The identified stiffness and damping parameters, as well as the latency, vary with visual and tactile sensory cues and with background GIA. The Hold and Release paradigm and model provide a useful clinical tool for experimentally studying falling and for characterizing the deficits in motor control of people prone to falling. A linear, four-link inverted pendulum model is sufficient to characterize postural recovery in patients with labyrinthine loss, those with somatosensory loss, and those with cerebellar lesions. For normal, healthy subjects only a two-link model is necessary to adequately describe recovery of balance.

MOTION SICKNESS

Motion sickness has been a persistent accompaniment of exposure to vehicles of virtually any sort: cars, trains, boats, aircraft, camels, swings, and spacecraft. The acceleration patterns in terms of amplitudes, frequencies, and durations that are most provocative are relatively well known. Many theories have been proposed to account for motion sickness, including overstimulation of the vestibular system, reaction to a perceived poison, and sensory conflict (cf. Reason 1970). None is fully satisfactory nor has adequate predictive power (e.g., the ability to distinguish which sensory conflict situations will be nauseogenic and which will not). The most certain factor known with regard to motion sickness under terrestrial conditions is that to date subjects without functioning labyrinths have not been made motion sick despite sometimes heroic efforts to do so (Graybiel 1969, Johnson et al. 1962).

Incidence and Eliciting Factors

It initially was thought that there were two general categories of responders to motion sickness, those expressing primarily "head symptoms," and those expressing

primarily “gut symptoms.” Head symptoms include headache, drowsiness, and eyestrain, whereas gut symptoms include stomach awareness, discomfort, nausea, and vomiting. It now is recognized that a person’s response to a particular form of motion depends on his or her individual susceptibility to that motion as well as to the relative intensity of the provocative stimulation. For example, making tilting head movements during constant velocity, passive body rotation at 3 rpm will elicit mainly head symptoms, whereas making tilting head movement at 30 rpm will rapidly induce nausea and vomiting for most subjects.

Space Motion Sickness

Space motion sickness, now often referred to as the space adaptation syndrome to recognize the complex pattern of changes associated with exposure to weightlessness, is an operational problem in space travel. Symptoms may develop in some astronauts and cosmonauts as early as the first hour in flight, but generally within the first day. Nearly 70% of all space travelers are affected to some extent during the first 72 hours (Jennings 1997). Pitch and roll head movements are significant etiological factors in eliciting the space adaptation syndrome (Lackner & Graybiel 1984, 1986, 1987). After return to earth, a variety of disturbances of posture, gait, and motor control are present until readaptation to earth gravity occurs. Symptoms of motion sickness may redevelop postflight as well. Astronauts generally are less susceptible in subsequent space flights and experience less severe re-entry disturbances and motion sickness as well. Severe cases of space motion sickness can be treated with anti-motion-sickness drug injections of promethazine (Graybiel & Lackner 1987, Lackner & Graybiel 1994).

It is unknown whether labyrinthine-defective subjects would be insusceptible to space motion sickness. However, they would not be immune to the postural, sensory-motor, and locomotory disturbances that occur after return to Earth. Adaptation to weightlessness involves not just adaptation of vestibularly mediated reflexive and orientation effects, but also accommodation of the entire postural and muscular control system of the body to a radically different force environment. This means that the control of body-relative movements, body movements in relation to the surroundings, and object manipulation and use involves a remapping of the motor commands to the musculature necessary to bring about the desired actions.

Under terrestrial conditions, alterations in the normal motor control patterns necessary to stabilize the head or to achieve particular movement goals can elicit symptoms of motion sickness, postural disturbances, and sensory-motor performance disruptions analogous to those occurring in space flight and after re-entry. The manipulations evoking such impairments involve changing the apparent weight and inertia of the body segments, decreasing them to mimic weightless conditions and increasing them to simulate re-entry disturbances (Lackner & DiZio 1989). Such changes are independent of vestibular function per se and point to the important role of sensory-motor control and calibration of the body to the ongoing force

environment. Motion sickness elicited in vehicles tends to be exacerbated by active maintenance of posture or by locomotion within the vehicle. Fully passive exposure with the body recumbent or not supporting itself tends to be least provocative (Lackner et al. 1991). Control over the onset and intensity of passive body motion also decreases susceptibility, e.g., the driver of a car rarely experiences carsickness even when passengers have been made quite ill.

ARTIFICIAL GRAVITY ENVIRONMENTS

For long-duration space missions lasting many months, or even several years such as a manned mission to Mars, artificial gravity produced by rotation may be necessary to reduce or prevent the loss of bone mineral content and muscle deconditioning induced by mechanical unloading of the musculoskeletal system in weightless conditions (cf. Lackner & DiZio 2000, 2004; Young 1999 for reviews).

Coriolis Forces and Disruption of Movement Control

“Artificial gravity” is the centripetal force imposed by a rotating vehicle that keeps objects within it moving in a curvilinear path. Centripetal force is proportional to the radius of rotation (r) times the velocity of rotation (in radians) squared. Accordingly, approximately 1.1 g of artificial gravity would be produced by a vehicle 1000 m in radius rotating at 1 rpm and by one 10 m in diameter rotating at 10 rpm. The latter situation is much more difficult to adapt to because when a person moves in a rotating environment, inertial Coriolis forces are generated on his or her body. These forces are larger the higher the velocity of rotation. For example, when a forward-reaching movement is made during exposure to counterclockwise rotation, a rightward Coriolis force will be generated on the arm proportional to the mass of the arm (m), the linear velocity of the arm relative to the rotating vehicle (v), and the angular velocity of rotation (ω): $F_{\text{cor}} = -2m(\omega \times v)$ (see Figure 5). This means that for a given movement of the body or a part of the body with velocity, v , the Coriolis force is linearly dependent on the angular velocity of vehicle rotation, rotation at 10 rpm will generate a tenfold greater Coriolis force than rotation at 1 rpm.

Vestibular function is one of the key factors affecting the ability of humans to adapt to rotating artificial gravity environments. For example, when a pitch head movement is made out of the plane of rotation, an unusual pattern of stimulation of the semicircular canals will result. One pair of semicircular canals will be brought into the plane of rotation and signal head rotation in the direction of vehicle rotation; simultaneously, another pair will be brought out of the plane of rotation losing angular momentum and consequently signaling head rotation in the opposite direction to that of the vehicle’s motion. The final pair will accurately signal the forward pitch of the head. The otolith organs will also be transiently stimulated by the Coriolis force generated by the head movement (see Figure 6). This bizarre pattern of vestibular activity leads to complex orientation illusions, destabilizes

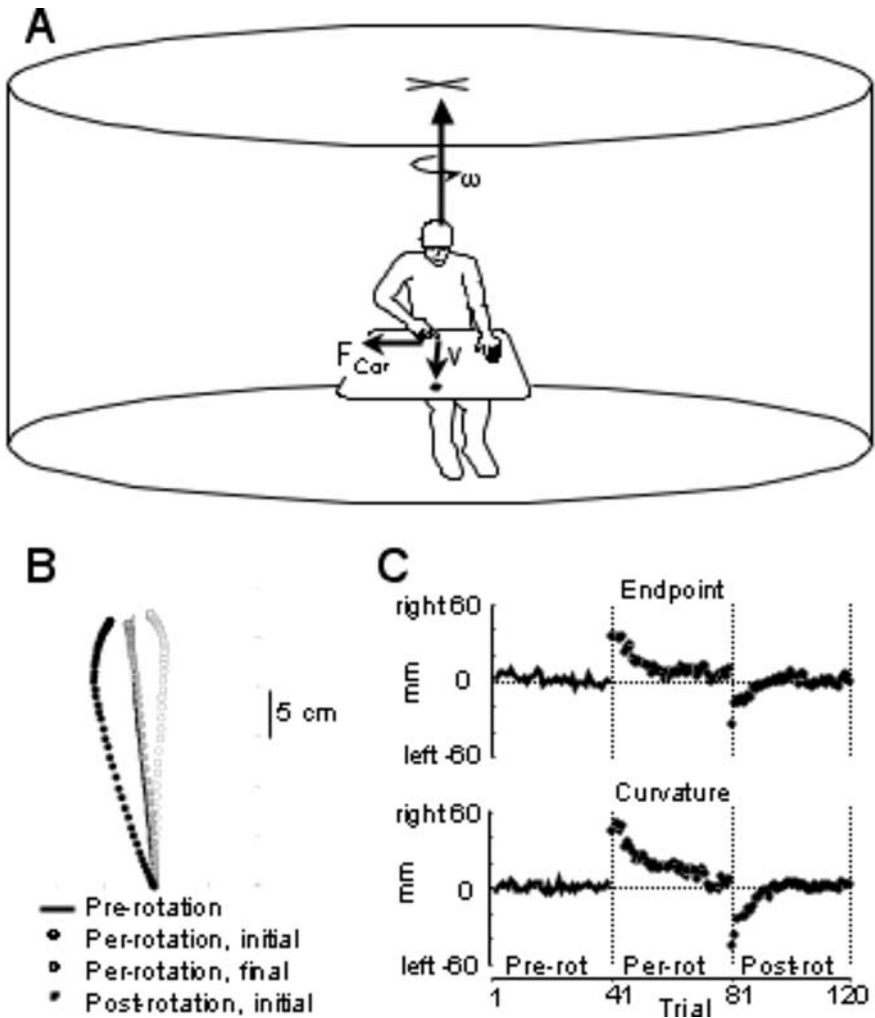


Figure 5 (A) Illustration of a subject in the center of a counterclockwise rotating room (ω) reaching forward to a target. A rightward Coriolis force, F_{Cor} , is generated while the arm is moving forward at velocity v . (B) A top view of the fingertip path shows that reaches are straight to the target before rotation starts, deviate to the right during rotation, return to baseline after additional reaches, and show mirror-image aftereffects when rotations stops. (C) Plots of the endpoints and curvatures of individual movements show that they return to baseline within 10 to 15 trials after rotation starts and stops.

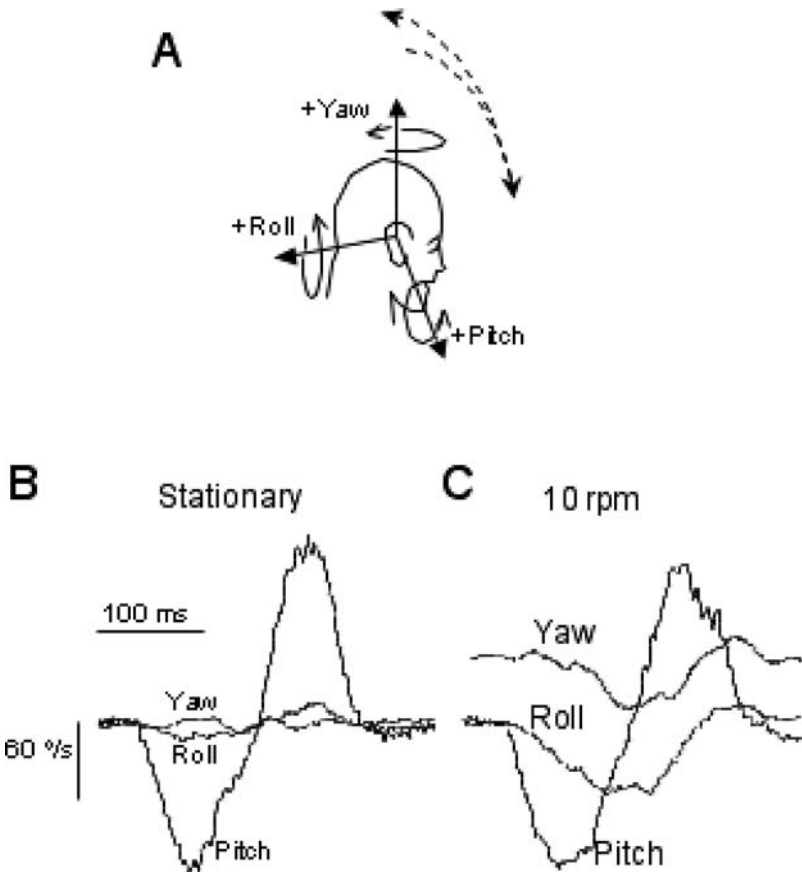


Figure 6 (A) Schematic showing the coordinate system of a set of angular rate sensors attached to the head for a movement in which the subject nods the head forward and returns immediately to the upright position (*dotted arrows*). (B) Traces from the angular rate sensors when the head movement is made in a normal stationary environment. (C) Traces recorded for a comparable pitch head movement made during 10 rpm counterclockwise rotation. Prior to the movement, the yaw axis of the head is rotating at the speed of the room; pitching the head forward reduces the yaw rate, and returning it to the upright restores it. The roll axis of the head comes into the room rotation plane during pitch forward and out of the plane during pitch up. The semicircular canals that are fixed to the head pick up these cross-coupled angular accelerations, and the subject will experience a tumbling sensation involving illusory yaw and roll motion in addition to the veridical pitch of the head.

eye movement control, and if repeated can rapidly lead to motion sickness (except in individuals without labyrinthine function). Studies of artificial gravity in slow rotation rooms in the 1960s suggested that 5 rpm was the highest rate of rotation at which people could fully adapt to the vestibular stimulation encountered (Clark & Graybiel 1961; Fregly & Kennedy 1965; Graybiel et al. 1960, 1965; Guedry et al. 1962, 1964; Kennedy & Graybiel 1962). Subsequently, this value became the “accepted” upper velocity limit for space flight artificial gravity environments. In these early studies, posture, locomotion, and arm movement control were also disrupted. On cessation of rotation, normal subjects, but not vestibular-loss subjects, experienced a recurrence of symptoms of motion sickness. Both the normal and labyrinthine-defective subjects experienced postrotation disturbances of posture, gait, and arm movement control. These aftereffects reflect the fact that motor control as well as vestibular function is affected in rotating environments.

Adaptive Accommodations and Aftereffects

Recent studies of adaptation to artificial gravity environments, however, have demonstrated that head and arm and leg movement control as well as locomotion can be adapted quite rapidly to rotational velocities of 10–25 rpm if the same movement is attempted repeatedly (Bouyer et al. 2003; DiZio & Lackner 1995, 1997, 2003; Lackner & DiZio 1994, 1998). In this circumstance, movement paths soon become straight again and movement endpoints accurate. On cessation of rotation, mirror-image errors in movement control occur, indicating that the nervous system has constructed a model of the Coriolis forces expected to be forthcoming and planned appropriate compensatory innervations to null their effect on movement paths. The persistence of this compensation even when no longer appropriate leads to the appearance of mirror-image aftereffects on cessation of vehicle rotation.

When adaptation to a rotating environment is complete, the Coriolis forces associated with movements no longer are consciously perceived. Although still present during movements, these forces become perceptually transparent. On cessation of rotation when movements are made again, a new “force” is perceived that is felt to act in the direction opposite to the original forces felt during rotation. The internally generated compensations for Coriolis forces that are no longer appropriate and that deviate movement paths and endpoints postrotation thus are perceived as external forces deviating the arm.

On Earth, the forces generated by support of the body against gravity and of body movements relative to gravity are also largely transparent. They are not felt or perceptually registered even though they are significantly above thresholds for detection. For example, to raise one’s arm it is necessary to counter the torques on the arm owing to the force of gravity. Nevertheless, the effort associated with the movement feels virtually the same even though the force generated to bring about the movement is varying greatly. Similarly, if balance is shifted from two feet to one while standing, hardly any force change on the sole of the remaining stance

foot will be felt even though the contact force has doubled (Lackner & Graybiel 1982, 1984). For a 180 lb individual it will increase by 90 lb to 180 lb, a huge change. Such observations mean that the body is dynamically tuned to its force environment, and movements within it feel virtually effortless.

Self-Generated Coriolis Forces in Everyday Behavior

The ability to adapt very rapidly and almost effortlessly to Coriolis force perturbations of head, arm, and leg movement trajectories in rotating environments was initially surprising given the restricted adaptation seen in earlier studies. However, natural locomotion generates significant linear and angular accelerations that are compensated for by automatic adjustments of the eyes and head (Imai et al. 2001). Recently, it has been shown that Coriolis forces are commonly encountered in our everyday activities (Pigeon et al. 2003a). When a natural turn-and-reach movement is made to an external object, the trunk reaches peak velocities much higher (e.g., 150–200°/s) than those ever contemplated for use in artificial gravity environments (e.g., 60–90°/s). Because turn-and-reach movements are not segmented into turn and then reach, the peak velocities of the trunk movement and of the forward velocity of the arm occur close together in time. As a consequence, very large Coriolis forces are generated on the reaching arm. Nevertheless, reaching accuracy is preserved and is independent of the peak velocity of the trunk and of whether visual feedback is available. This preservation of reaching accuracy means that the nervous system anticipates the Coriolis forces that will be generated, and it institutes appropriate anticipatory compensatory forces to eliminate their deflecting influence on movement paths.

Head and leg movements out of the plane of rotation are also common during voluntary trunk rotation and are also made accurately. Such accuracy indicates that compensation for self-generated Coriolis forces is a typical aspect of everyday motor control. It is not surprising, therefore, that individuals are able to adapt to the Coriolis forces associated with movements in passively rotating artificial gravity environments because these forces are much smaller than those generated during their everyday activities. In other words, the body when turning constitutes its own artificial gravity environment from the perspective of eye, head, arm, leg, and torso movement control. An examination of the relative straightness of arm movements and of their velocity profiles during natural turn-and-reach movements supports the view that they are planned in relation to external spatial coordinates rather than joint or intrinsic coordinates. Arm trajectories are straight and their velocity profiles are single-peaked in relation to external space, but are curved with multiple velocity peaks when plotted in relation to joint or torso relative coordinates (Pigeon et al. 2003b).

Coriolis Forces and Motion Sickness

Making pitch head movement during passive rotation is highly nauseogenic and elicits a complex, illusory tumbling sensation because it generates Coriolis

cross-coupled stimulation (CCS) of the semicircular canals (Johnson et al. 1951), as shown in Figure 6. The puzzling finding from space flight experiments is that CCS is not nauseogenic in orbital flight (Graybiel et al. 1977). These investigators were motivated by the desire to ascertain whether the limits of tolerable rotation that had been found on Earth, where CCS occurs in a 1 g force background, predict what would occur in space, where the background, artificial gravity level (centripetal force) will likely be less than 1 g. This question was and still is highly relevant for developing a feasible artificial gravity countermeasure for prolonged space flight because the severity of the side effects of rotation (motion sickness, disorientation, and disruption of movement control) as a function of background force level is a major factor that must be considered in choosing the radius and rotation rate.

Many attempts to understand the variable provocativeness of CCS have focused on putative sensory conflicts (e.g., Guedry & Benson 1978). In such theories, conflict occurs when CCS elicits semicircular canal signals encoding an off-vertical tumbling axis that is in contrast with a nonchanging otolith signal from the physically nontumbling head. Such a conflict is not possible in space flight where there is no background GIA whose direction can be encoded by the otolith afferent signals. Parabolic flight experiments have provided an alternate perspective on this problem. The duration and intensity of perceived tumbling are augmented in 1.8 g and almost eliminated in 0 g (as is motion sickness, confirming the space flight results) following the same CSS stimulation of the semicircular canals in both force backgrounds (DiZio et al. 1987). This pattern suggests that semicircular canal afferent signals encoding head velocity may be centrally integrated to produce a representation of body displacement, and that this integration process is GIA-dependent. This possibility has been confirmed recently in parabolic flight experiments. Blindfolded subjects continuously indicated their subjective self-displacement relative to external space by pointing to a fixed location with a joystick while they were exposed to seminatural, brief, suprathreshold tilts about their yaw axis. In 1 g and 1.8 g, pointing responses were nearly constant relative to the aircraft, but in zero gravity, the stick was always kept in a body-fixed orientation. Subjects verbally confirmed that they were aware of being moved in all force backgrounds but that the movement was not associated with any perceived displacement in 0 g. This means that the lack of motion sickness elicited by CCS in zero gravity may be due to a lack of internally represented body displacement. These recent findings also add to the debate about how three-dimensional spatial orientation is represented and remembered, which is surveyed in the following section.

PATH INTEGRATION

Place Cells and Head Direction Cells

The classical observations of Beritoff (1965) suggested that vestibular afferent signals during passive transport of the body could be integrated to generate a representation of the body's path through space and of its new position in relation

to the start position. These results have led to renewed interest because of the finding of “place cells” in the hippocampus that are active when an animal is in a specific location within a familiar environment (O’Keefe & Dostrovsky 1971) and of “head direction cells” that seem to code the direction in which the head is oriented with respect to extrinsic spatial coordinates (Taube et al. 1990).

Numerous experiments have demonstrated that during passive transport, spatial memory and knowledge of the trajectory and of the spatial location within the environment are maintained (Berthoz et al. 1987; Bloomberg et al. 1991; Israel et al. 1993, 1997; Mittelstaedt 1980). This is manifested in the ability to orient the head and body toward the starting position or to memorized targets, or to recapitulate the path the body has traveled. Vestibular inputs may be sufficient for such path integration because neuronal recordings show that hippocampal cells maintain their spatial tuning even during passive transport in darkness (Gavrilov et al. 1998). However, vestibular inputs are not necessary for updating spatial orientation because humans without functioning labyrinths show path integration during active walking (Glassauer et al. 1994). Path integration is also exhibited by insects lacking a vestibular system (see Wehner 2003 for a review). These creatures must rely, in the absence of vision, on monitoring motor outputs and sensory feedback to generate spatial “representations.”

COMPLEXITY OF SPATIAL REPRESENTATIONS: IMPLICATIONS FOR IMMERSIVE VIRTUAL ENVIRONMENTS

One of the most promising applications of virtual environment technology is training users to build cognitive maps of environments (Durlach et al. 2000). Through visual displays and clever “locomotion interfaces,” a user can “navigate” a large virtual space without moving around at all or while moving in very limited fashion. An example of the former would be using a joystick to navigate a virtual suite of rooms shown on a desktop display; an example of the latter would be a pilot trainee viewing a visual model of terrain he or she is “overflying” in a simulator that reproduces a portion of the inertial cues that would be present in a real aircraft. Realistic experiences can be generated in these situations, and subjects seem to acquire survey knowledge (Ruddle et al. 1997) of the virtual environment without normal vestibular inputs. An individual is considered to have survey knowledge when he or she remembers enough of the environmental layout to draw a map that indicates distances between landmarks and to give directions to destinations along novel routes (Siegel & White 1975). Acquiring survey knowledge in virtual environments is slower than in the real world (Witmer et al. 1996). It is not clear yet whether this decrement is due to lack of fidelity of the visually rendered virtual world or to the lack of normal inertial cues, including vestibular cues. However, one study has shown that spatial learning is not hindered when inertial cues are reduced or distorted (Waller et al. 2003).

Rotating room studies have demonstrated that the spatial representation and recognition of environments is dependent on the means of normally accessing them and that the subenvironment is embedded in a broader spatial representation of the spatial context (Lackner & DiZio 1998). As a consequence, entry into a particular site, e.g., a room from a direction never before experienced, can lead to a sense of unfamiliarity and strangeness in an environment that when entered from the familiar entrance seems familiar and natural.

Such observations mean that the cognitive representation of spatial environments is quite complex and is influenced by the modes of access. This has especial significance for recent developments in virtual environment technology. For example, it has been proposed that immersive virtual environments can be used to train knowledge of a real environment. This would make it possible, for example, for firefighters not to have to train in a real environment (e.g., an aircraft carrier) to know its spatial layout intimately. Training from the virtual to the real environment, however, may not transfer unless the “access” into the virtual environment is from modes of entry that are possible in the real environment.

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GLOSSARY

Afferent discharge rate – Primary afferent neurons of the mammalian vestibular system relay information from hair cells to the central nervous system. They encode head angular velocity and linear acceleration via a rate code, in terms of the number of action potentials per second.

Ampulla – An enlargement in the toroidal ring of each semicircular canal, within which resides the sensory apparatus, the cupula/hair cell complex.

Cupula – A gelatinous membrane inside the ampulla of each semicircular canal. The inertial tendency of the endolymph to lag head rotary acceleration displaces the cupula and deflects the ensheathed cilia of hair cells affixed to the ampulla base. The elasticity of the cupula causes recoil to the resting position following angular acceleration of the head.

Doll’s eye reflex – Reflexive elevation or depression of the eyes relative to the head in the direction opposite to the pitch angle of the body.

Eccentric contraction – Active production of tension in a muscle while it is being lengthened. For example, on Earth lowering the body during a deep knee bend involves eccentric contraction of the quadriceps muscle group.

Efferent copy – A duplicate of a command signal innervating muscles. For example, efferent copies of signals from brainstem nuclei to eye muscles are

thought to be involved in parcellation of visual signals into components due to self-motion and object motion.

Endolymph – The fluid that fills the semicircular canals and bathes the otolith organs. Its mass and viscosity are major factors governing the encoding of head angular velocity by the afferent signal from the semicircular canals.

Gain – The ratio of the output of a controlled system to its input. For example, the ratio of eye roll (output) to body tilt (input) in ocular counterrolling is about -0.1 .

Gravitational acceleration – Acceleration due to the force of gravity. An object at rest on the Earth's surface is being accelerated by gravity toward the center of the earth and is simultaneously accelerated in the opposite direction by the ground.

Gravitoinertial force – The vector resultant of gravitational and inertial force. The otoliths encode acceleration due to gravitoinertial forces. Einstein's equivalence principle states that no simple physical sensor can detect whether its acceleration is due to inertial or gravitational force. A very active research topic concerns how multiple sensory inputs are processed to yield separate senses of tilt relative to gravity and inertial motion.

Hair cell – Goblet-shaped sensory neuron with a bundle of cilia of graded length protruding from the cell body. Maximum depolarization or hyperpolarization is produced when the bundle is bent toward or away, respectively, from its apex, and graded responses are evoked by intermediate directions of deflection. Deflection of large arrays of hair cells is the basis of the afferent response of the semicircular canals and otolith organs (as well as other sensory systems).

Haptic perception – A type of perception derived from active touch, in contrast to the passive impressions of external stimuli impressed on the skin.

Inertial acceleration – Acceleration relative to a fixed- or constant-velocity frame of reference (such as the earth) by an external force to the object. The semicircular canals are stimulated by angular inertial acceleration and do not respond to gravity.

Inversion illusion – The experience of oneself and/or the entire seen and felt environment being upside down relative to the subjective vertical. It is often elicited upon exposure to weightless conditions.

Muscle spindle – A specialized receptor in muscle tissue producing afferent signals modulated by muscle length and rate of change in length. Its responses are modulated by the gamma motor system.

Nystagmus – Named for a sawtooth pattern involving quick jumps in one direction alternating with slower drifts in the other. Nystagmoid eye movements involve a "field fixing" pattern in which slow eye drifts compensate for self-motion in one direction alternate with rapid recentering movements.

Ocular counterrolling – Reflexive rotation of the eyes about the naso-occipital

axis in the direction opposite lateral body tilt about a parallel axis. Otolith signals related to body tilt are a major influence on this reflex.

Optokinetic stimulation – Unidirectional motion of all or part of the external visual array.

Otolith organ – Nonauditory sensory organ in the vertebrate inner ear responsible for transduction of linear acceleration and gravity. The otoliths include masses of dense crystals (otoconia) embedded in a gelatinous membrane anchored to the cilia of a skull-fixed array of hair cells. The otoconia are displaced opposite to linear accelerations of the head, thereby deflecting the hair cells and modulating their membrane potential. Different classes of spatially and temporally tuned hair cells are hypothesized to be crucial for distinguishing the inertial and gravitational parts of the net linear acceleration.

Parabolic flight – Aircraft flown in a roller-coaster path to produce alternating periods of high gravito-inertial force during the climbs, and rapid transitions to weightlessness, zero gravity, during the pushover at the top of each parabola.

Path integration – Knowledge of one's current position and heading relative to a position with which one is no longer in sensory contact. It is derived from temporal accumulation of sensory and motor signals about movement path through space.

Proprioception – The sense of position and motion of one's body segments, derived from central processing of efferent signals as well as afferent signals from muscles, tendons, joints, and skin. Some investigators include vision and audition as contributing potential proprioceptive information.

Push-pull – A traditional control theory name for the manner in which angular head acceleration in a given plane is encoded by the discharge rate of primary vestibular afferent neurons. The afferent neurons have a high resting discharge rate (about 100 imp/sec), which is increased during head angular acceleration in one direction and decreased by acceleration in the opposite direction.

Receptor potential – Graded changes in voltage across the cell body membrane of vestibular hair cells, proportional to deflection of the ciliary bundle.

Sacculles – Bilateral pair of otolith organs anatomically arranged to respond to vertical-plane linear accelerations.

Semicircular canals – Nonauditory sensory organs in the vertebrate inner ear that are stimulated by angular acceleration of the head and encode angular velocity of natural movements. The name describes the structure: three approximately orthogonal, fluid-filled toroidal tubes on either side of the head. The mechanism of the sensory response is the deflection of hair cells inside the canal by the inertial lag of the fluid during head acceleration.

Spatial neglect – Decreased probability of detection of stimuli in a circumscribed region of extracorporeal space. It can be partial or complete, and can involve multiple sensory modalities.

Utricles – Bilateral pairs of otolith organs anatomically arranged to respond to horizontal plane linear accelerations when the head is upright.

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