As people move about, they perceive changes in their orientation and position in the environment, and can update these values with respect to significant locations in space. Analytically, self-motion can be decomposed into two components: (1) observer rotation, which has a direction (pitch, yaw, roll), an angular speed, and a total angular displacement; and (2) observer translation, which also has a direction of motion (or heading), a linear speed, and a total linear displacement. However, the problem of perceiving self-rotation and translation is complicated by the fact that the human form is not a rigid body, but a hierarchy of segments consisting of mobile eyes in a mobile head on a mobile trunk on a pair of legs.

To determine the attitude and motion of each segment, a family of perceptual systems comes into play. The orientation of the eye in the head may be determined from extraretinal signals such as efference to or proprioception from the extraocular muscles. The motion of the head in three-dimensional-space can be determined via the vestibular organs, including semicircular canals sensitive to angular acceleration and otoliths sensitive to linear acceleration, including gravity. Temporal integration of these signals can yield information about head velocity and displacement. The orientation of the head on the trunk is specified by neck proprioception, and the trunk’s position and motion with respect to the ground by podokinetic or substratal information, a compound of proprioceptive and efferent signals from the legs and feet. In principle, these body-based senses allow for a chain of coordinate transformations between reference frames for each segment, but as we will show, they appear to be relied upon in a task-specific manner. Finally, the visual system may detect rotation and translation of the eye with respect to environmental objects on the basis of optic flow or the displacements of landmarks, bypassing such coordinate transformations.

In the present chapter, we review psychophysical and behavioral evidence regarding the perception of rotation and orientation, briefly describe the perception of translation and heading, and discuss the combination of the two in path integration.
Perceiving Rotation and Orientation

Vestibular and Proprioceptive Systems
The semicircular canals are the only sensors that are stimulated specifically and exclusively by angular head motion, so it can be claimed that they are dedicated to the detection of self-rotation. Indeed the vestibulo-ocular reflex (VOR) works properly only when the semicircular canals and the corresponding neural networks are intact. However, there is no conscious percept of vestibular stimulation, and we become aware of this sense only when we experience motion sickness, inner ear pathology, or postrotatory sensations. On the other hand, the semicircular canals are never stimulated in isolation, leading many researchers to investigate vestibular interactions with other senses and the multisensory perception of self-motion.

The perception of self-rotation from vestibular and proprioceptive information has been investigated psychophysically using estimates of either angular velocity or angular displacement. The latter has been achieved by obtaining retrospective estimates of the total angular displacement after a rotation—or concurrent estimates of one’s change in orientation during a rotation—which we will describe in turn. Studies of vestibular thresholds for rotational velocity and acceleration have also been performed, but will not be reviewed here (see Benson et al., 1989; Benson and Brown, 1989).

Retrospective Estimates of Angular Displacement One method for testing the vestibular perception of angular displacement is by comparing it with the performance of the vestibulor-ocular reflex (VOR). When a normal human subject is briefly turned in total darkness while trying to fixate a target in space, the VOR produces slow-phase compensatory eye movements that tend to hold the eyes on target. While this response is generally too weak for accurate compensation, it seems to be corrected by supplementary saccades in the compensatory direction (Segal and Katsarkas, 1988), even in the dark (VOR + saccade). To measure the perceived angular displacement, a retrospective estimate can be obtained using the vestibular memory-contingent saccade (VMCS) paradigm (Bloomberg et al., 1988), in which, after a brief passive whole-body rotation in the dark, the participant must saccade to a previously seen target based on a vestibular estimate of the total rotation. Bloomberg et al. (1991) found that the VMCS response measured after rotation was indeed indistinguishable from the combined VOR + saccade response measured during rotation, even when the latter was adaptively modified by prolonged visual-vestibular conflict (Bloomberg et al., 1991a). Israël et al. (1991) repeated the VMCS paradigm with different delays between the end of body rotation and the saccade. They found that vestibular information about the rotation amplitude can be stored without significant distortion for 1 min, longer than the time constant of the semicircular canals. The retrospective performance thus probably involves storing an estimate of the angular displacement in spatial memory.
Israel et al. (1993) compared these two measures during yaw and pitch rotations. They found, first, a strong correlation between VMCS + saccade and the VOR responses, with a slightly greater accuracy in the former (figure 16.1). The finding that a concurrent response (VOR) is less accurate than a retrospective one (VMCS) is well known in subjective magnitude estimation (Young, 1984), and it is classically attributed to the concurrent task that is interfering with the perception being estimated (Guedry, 1974; Stevens, 1960). Second, a greater accuracy was observed with yaw than with pitch rotation, consistent with thresholds for angular motion perception (Clark and Stewart, 1970), despite the fact the imposed rotations were well above threshold. Third, there was an unexplained greater accuracy for rotations that did not stimulate the otoliths.

The perception of angular displacement from neck proprioception has been investigated in a paradigm similar to VMCS. Nakamura and Bronstein (1993) assessed the perception of trunk rotation about a stationary (earth-fixed) head by having participants make eye saccades in the direction of trunk orientation. Normal subjects could accurately identify trunk orientation independent of trunk velocity and total displacement. The authors concluded that trunk orientation is perceived veridically and that neck-spinal afferents carry a tonic signal that is accessible by the ocular motor system. Mergner et al. (1998) had participants saccade to a previously seen target following passive rotations of the head and/or trunk. Saccades based on vestibular input from full-body rotation fell short at low

**Figure 16.1**
VOR and VMCS for rotations on the Z (body vertical) and Y (interaural) axes. The gain is the ratio of the eye saccades amplitude (E) over the head rotation angle (H). D0, VOR; D2, delay of 2s before the saccade (in the VMCS); D12, delay of 12s; V, subject's head in the vertical plane before the rotation; H, in the horizontal plane; Z, Y, rotation axes; L, low acceleration (gray pictograms). The only trials without otoliths stimulation are those at the left (VZ) and right (HYL) extremities. (Adapted from Israel et al., 1993, with permission.)
stimulus frequencies, but the addition of neck proprioception, produced by passive rotation of the head on an earth-fixed trunk, improved response accuracy.

It is well known that the prefrontal cortex (PFC) plays a primary role in visual spatial memory (Funahashi et al., 1993). To determine whether this role extends to vestibular spatial memory, Israël et al. (1995) recorded VMCS (as well as visual memory-guided saccades) in patients with various cortical lesions. It was found that (1) the PFC is involved in the memorization of saccade goals encoded in spatiotopic (absolute spatial) coordinates, whether stimuli are visual or vestibular, (2) the supplementary eye field but not the frontal eye field is involved in the control of the vestibular-derived, goal-directed saccades, and (3) the parietotemporal cortex (i.e., the vestibular cortex) but not the posterior parietal cortex is involved in the control of such saccades. Therefore it was concluded, first, that the role of the PFC includes both visual and vestibular spatial memory, and second that two different cortical networks are respectively involved in the latter and in the control of memory-guided saccades made to visual targets. These networks have only the PFC in common, which could control VMCS. This provides a physiological basis for distinguishing the cognitive processing of ego- and exocentric space.

However, in the classical VMCS paradigm the initially viewed target is directly in front of the subject, so that the expected saccade is a simple reproduction of the head or body rotation in the reverse direction. It was subsequently found that the saccade accuracy greatly decreases when the target is eccentric rather than straight ahead (Blouin et al., 1995, 1995a, 1997, 1998, 1998a). The data suggest that these errors stem not only from an underestimation of rotation magnitude, but also from an inability to use passive vestibular signals to update an internal representation of the target position relative to the body. Neck proprioception is more effective in this task.

Intrigued by this result, Israël et al. (1999) studied memory-guided saccades in three conditions: visual-memory guided saccades (the visual target was at 10° or 20°, right or left), saccades to the remembered spatiotopic position of the same visual target after whole-body rotation, and saccades to the remembered retinotopic position of the visual target after whole-body rotation. Visual feedback presented after each trial allowed eye position correction, as in Bloomberg et al.'s experiments. The results extend those of Blouin et al., and indicate that vestibular information contributes to updating the spatial representation of target position when visual feedback is provided.

Extending such target manipulations, Mergner et al. (2001) thoroughly examined the interactions between visual, oculomotor, vestibular, and proprioceptive signals for updating the location of visual targets in space after intervening eye, head, or trunk movements. They presented subjects in the dark with a target at various horizontal eccentricities, and after a delay in darkness asked them to point a light spot (with a joystick) to the remembered target location. In the “visual-only” condition, pointing accuracy was close to ideal (the slope of the estimation curve was close to unity). In the “visual-vestibular” condition, subjects were rotated during the delay; after a 0.8 Hz (28.8°/s) rotation, pointing was close
Vestibular, Proprioceptive, and Visual Influences

to ideal, but after a 0.1 Hz (3.6°/s) rotation, the slopes of the estimation curves were below unity, indicating underestimation of body rotation (figure 16.2). The eccentricity of the target further reduced the slopes. In the “visual-vestibular-neck” condition, different combinations of vestibular and neck stimuli were administered during the delay (head fixed on the rotating body, head fixed in space on the rotating body, and synergistic and antagonistic vestibular-neck combinations). As long as these rotations were fast (0.8 Hz), the mean accuracy was close to ideal, but with 0.1 Hz rotations of the trunk about a stationary head, a shift toward the trunk occurred (i.e., the slope decreased), whereas head rotation on the stationary trunk yielded slopes close to unity irrespective of the frequency, suggesting that the effects summed and the errors cancelled each other. Variability of the responses was always lowest for targets presented straight-ahead. The authors concluded that, (1) subjects referenced “space” to prerotatory straight-ahead, and (2) they used internal estimates of eye, head, and trunk displacements with respect to space to match current target position with its remembered position—in effect inverting the physical coordinate transformations produced by the displacements. While Mergner et al. (2001) developed a descriptive model of human orientation in space, they specifically admitted that the model could not reproduce the drop in performance with eccentric targets found by Blouin et al., which was partly attributed to the low frequency components of Blouin’s vestibular stimulation.

Estimates of angular displacement and angular velocity have been used interchangeably to characterize vestibular perception of self-rotation, on the assumption that the two estimates are equivalent because perceived displacement is simply the time integral of perceived velocity. Mergner et al. (1996) tested this hypothesis by directly comparing displacement and velocity estimates. Participants were presented with whole-body yaw rotations in the dark, with one group estimating peak velocity and the other group estimating total displacement. Experimenters then used the velocity estimates to predict the displacement estimates by assuming that the velocity signal decayed exponentially from the reported peak value (reflecting the dynamics of vestibular mechanisms) and mathematically integrating it. Predicted and reported displacements were similar for a time constant of 20s, in good agreement with earlier studies. The authors concluded that displacement estimates can indeed be considered equivalent to velocity estimates of self-rotation over the range of stimulus parameters tested.

However, Becker et al. (2000) found that the vestibular perception of angular velocity and displacement are differentially affected by seated or standing posture. Sinusoidal rotations in the horizontal plane were delivered to subjects sitting in a rotating chair or standing on a rotating platform, and judgments were obtained by retrospective magnitude estimation. While displacement estimates did not depend on posture, velocity estimates were more accurate for sitting than for standing, particularly with large amplitude stimuli. Posture had no effect upon the vestibular detection threshold. This demonstrates that perceived displacement does not always equal the time integral of perceived velocity. In addition, the persistence of nearly veridical displacement estimates at constant velocities
Visual-vestibular-neck interactions in delayed pointing after passive rotation. Superimposed in each panel are the results for the four stimulus combinations: VEST (solid circles), NECK (open circles), VEST + NECK (solid squares), and VEST-NECK (open squares). Thin dashed 45° lines, “ideal” performance. Heavy dashed 45° lines, hypothetical performance of subjects with absent vestibular function (applies only to VEST). (A) Pictographic representation of the four vestibular-neck stimulus combinations used (view of subject from above). (B) Stimuli of 18° at 0.8 Hz. (C) Stimuli of 18° at 0.1 Hz. Note that the estimation curves for VEST + NECK fall very close to the ideal 45° lines, both at 0.8 Hz and 0.1 Hz, while those for VEST-NECK show the largest offset from these lines. Insets give across-trials standard deviation (in degrees) for the four stimulus combinations (averaged across all target eccentricities). (VEST, whole-body rotation (the orientation of the head-in-space, HS, equals that of trunk-in-space, TS). NECK: trunk rotation with head kept stationary (stimulus, head-to-trunk, HT). VEST + NECK, head rotation on stationary trunk. VEST-NECK, head and trunk rotation in space in same direction, but trunk with double amplitude to maintain HT constant). (Adapted from figure 4 of Mergner et al., 2001, with permission.)
over extended durations (when vestibular signals have stopped) suggests the intervention of cognitive processes.

**Concurrent Perception of Angular Displacement** When investigating multisensory self-motion perception, the kinematics of motion and response characteristics of the different sensory channels should also be taken into account. This is why concurrent self-rotation perception tests are also frequently used.

As we have noted earlier, in order to determine trunk motion in space, the vestibular signal of head motion in space must be combined with neck proprioception about the trunk-to-head excursion. Mergner et al. (1991) studied the vestibular-neck interaction with a concurrent tracking task, in which the subjects manipulated both a head-pointer and a trunk-pointer to indicate their perceived rotation during passive sinusoidal yaw rotations of the trunk and/or head in the dark. For the perception of trunk rotation in space, rotation was underestimated with vestibular stimulation alone (whole-body rotation) and with neck stimulation alone (trunk rotation under an earth-fixed head). The gains were low, only about 0.7 at 0.4 Hz and decreasing at lower frequencies. Judgments were similarly erroneous for other vestibular-neck combinations, with one noticeable exception: during head rotation on a stationary trunk, subjects veridically perceived the trunk as stationary. For the perception of head rotation in space, vestibular stimulation yielded the same frequency characteristics as for the trunk. Neck stimulation (trunk rotation under a stationary head) induced an illusion of the head rotating in space, but with head rotation on a stationary trunk, perception became almost veridical. The neck contribution reflected the sum of two components: the nonideal neck signal that contributed to the perception of “trunk in space,” and the nearly ideal neck signal produced by head rotation on a stationary trunk.

Mergner et al. (1993) investigated the interaction of vestibular signals and leg proprioception in seated subjects. Stimulation consisted of sinusoidal and transient whole-body rotations in space (vestibular stimulation) and rotations of the feet relative to the trunk, induced by a moving platform (leg proprioception). Responses were obtained with a pointing procedure similar to that described above, in which the subject manipulated both a feet-pointer and a trunk-pointer. First, the perception of relative motion between feet and trunk was veridical across the frequencies tested and had a low detection threshold (0.2°/s). Rotation of the feet under the stationary trunk evoked an illusion of trunk turning, which reached a considerable magnitude at low frequencies. Second, the perception of trunk rotation from vestibular stimulation was underestimated, especially at low frequencies, with a detection threshold close to 1.0°/s. Third, with combinations of vestibular stimulation and leg proprioception, perception varied monotonically as a function of both inputs. Rotation was underestimated except during trunk rotation about stationary feet, when it was approximately veridical and the threshold dropped to 0.2°/s, suggesting that it was essentially determined by leg proprioception.
To elucidate the role of the “starting point” in perceiving angular displacement, Israël et al. (1996) passively rotated subjects on a motor-driven turntable. Subjects then had to return to the starting point by using a joystick to control the direction and velocity of the turntable in total darkness. The starting point could be defined prior to rotation by an earth-fixed, visual target, or given by the initial body orientation. Subjects succeeded in returning to the starting point in all conditions, but had lower variability when the target was visually presented. The larger scatter in the other conditions was directly related to variations in the peak return velocity, whereas there was no relationship between return amplitude and velocity with the visual target. These results suggest that visual presentation of an earth-fixed starting point facilitates real time integration, improving accuracy during self-controlled motion in the dark.

A related observation was reported by Israël et al. (1995a), who instructed subjects to use push buttons to rotate the turntable through angles of ±90°, 180°, or 360° (outward), and then to rotate back to the initial position (return), in complete darkness. On average, participants undershot the specified angle on the outward rotation, but the variability was lower on the return rotation. (No corrective rotation was imposed prior to the return.) The data suggest that subjects maintained an internal representation of the starting point (the initial body orientation), which served as a clearer goal (for the return) than did a specified rotation angle (for the outward rotation), in an environment devoid of any spatial reference.

Yardley et al. (1998, 1999) sought to determine whether significant attentional resources are required to monitor vestibular information for changes in body orientation. To provide interference, participants either counted backwards during rotation (Yardley et al., 1998) or performed a dual-task paradigm (Yardley et al., 1999). The results indicate that a small but significant degree of attention or cognitive effort is necessary to accurately monitor the direction and amplitude of self-rotation, during both passive and active locomotion.

To investigate the role of gaze stabilization during the control of whole-body rotation, Siegler and Israël (2002) tested subjects seated on a mobile robot that they could control with a joystick. They were asked to perform 360° rotations in the dark while maintaining their gaze, when possible, on the position of a visible (at the beginning of the rotation) or imagined (after about 110° rotation) earth-fixed target. This required active head rotations. Subjects performed better on a 360° whole-body rotation in the dark when asked to stabilize gaze in space than when no specific instruction was given. Furthermore, performance was significantly related to head stabilization in space. These results revealed the importance of head-free gaze control for spatial orientation, insofar as it involves spatial reference cues and sensory signals of different modalities, including efferent copy and neck proprioceptive signals. The benefits of free head movements amply confirm the findings of Mergner et al. (1991; 2001) about the role of neck proprioception on self-rotation estimate.
When subjects actively step about the vertical axis without vision, there are two sources of information about the angular displacement: the vestibular signal and the podokinetic or substratal signals. To investigate the podokinetic contribution, Jürgens et al. (1999) had participants either stand passively on a rotating platform (vestibular) or actively step about their vertical axis on a stationary platform (podokinetic and vestibular). Rotations consisted of short acceleration epochs followed by constant velocity periods, which participants had also learned to produce when actively turning. Perceived displacement was either verbally estimated or indicated by stopping when a specified displacement had been reached. The results showed that perception of angular displacement is more precise during active turning (see also Yardley et al., 1998), and that the intention to achieve a specified displacement modifies the perception of passive rotation but not that of active turning.

Becker et al. (2002) investigated how vestibular and podokinetic signals are fused in the perception of angular displacement. They compared three conditions: (1) passive rotation, standing at the center of a rotating platform (vestibular only); (2) treadmill stepping opposite to the rotating platform, so that the body remained fixed in space (podokinetic only); and (3) active turning, stepping around the stationary platform (vestibular and podokinetic). Angular velocity varied across trials (15–60°/s) but was constant within a trial. Participants signaled when they thought they had reached a previously specified angular displacement, ranging from 60° to 1080°. The error was smaller during active turning than during passive rotation and treadmill stepping. The authors found this to be compatible with the idea that vestibular and podokinetic signals are averaged, but only for the case of fast rotation. Finally, participants could estimate large angular displacements surprisingly well during passive rotation, even though the duration of motion far exceeded the conventional vestibular time constant of 20 s. This indicates that the initial velocity estimate based on the vestibular signal can be maintained long after the signal itself has decayed (a result similar to that found by Becker et al., 2000).

Mittelstaedt and Mittelstaedt (1996) and Mittelstaedt (1995) also investigated the perception of angular displacement over long time intervals. Participants were positioned in darkness face forward or backward on a rotating platform, at radial distances of \( r = 0 \)–1.6 m, and accelerated to a constant angular velocity \( (\omega = 0.35–0.87 \text{ rad/s or } 20–50^\circ/\text{s}) \) within 0.8 s. They successively indicated when they felt they had turned through another 180°. Fairly veridical at first, these reports lagged progressively as though perceived velocity declined exponentially to zero. When \( r = 0 \), the data revealed idiosyncratic time constants (20–90 s) that were independent of disk velocity, confirming the results of Becker et al. (2002) for passive rotation. But at other radial distances the time constants increased with \( r*\omega \), and hence depended on centrifugal force. After at least 2 min, the rotation was stopped and participants continued to indicate 180° turns at successive intervals as before. The deceleration force induced a postrotatory aftereffect with time constants that were independent of radius and disk velocity, as would be expected if the prolonged time constants during rotation were due to the added orthogonal (centrifugal) force.
Illusions  Multisensory illusions have also been used as tools to increase our understanding of the mechanisms of self-motion perception.

Gordon et al. (1995) and Weber et al. (1998) exposed participants to between 30 min and 2 h of walking on the perimeter of a rotating platform, such that the body remained fixed in space. After adaptation, participants were blindfolded and asked to walk straight ahead on firm ground. However they generated walking trajectories that were curved, and continued to do so, with gradually decreasing curvature, over the next half hour (figure 16.3). The angular velocities associated with these trajectories were well above vestibular threshold, yet all participants consistently perceived themselves as walking straight ahead. On the other hand, when the blindfolded participants were asked to propel themselves in a straight line in a wheelchair, postadaptation trajectories showed no change from before adaptation. Thus, sensory-motor adaptation appears to have been limited to the podokinetic components of gait. Such findings may have implications for the diagnosis and rehabilitation of locomotor and vestibular disorders.

Jürgens et al. (1999a) asked whether this podokinetic after-rotation (PKAR) is due to (1) an intersensory recalibration triggered by the conflict between the visual signal of stationarity and the somatosensory signal of feet-on-platform rotation, or (2) an adaptation of the somatosensory afferents to prolonged unilateral stimulation, irrespective of the visual stimulation. Participants turned about their vertical axis for 10 min on a stationary or a counterrotating platform (so they remained fixed in space), under visual conditions of either darkness, optokinetic stimulation consistent with body rotation, or a head-fixed optical pattern consistent with no rotation. After adaptation, they tried to step in place on a stationary platform without turning, while in darkness. All adaptation conditions that included active stepping without optokinetic stimulation yielded the PKAR effect. With consistent optokinetic stimulation during adaptation, PKAR increased, indicative of an optically induced afterrotation (oPKAR) that summed with the standard PKAR. This oPKAR could also be demonstrated in isolation, by passively rotating subjects in front of the optokinetic pattern, yielding an afterrotation in the contralateral direction. Not unexpectedly, when the optokinetic pattern was illuminated, the PKAR was rapidly and totally suppressed because subjects could control a straight course on the basis of visual information. Surprisingly, however, when darkness was restored, PKAR smoothly resumed, and within about 1 min appeared to continue the course it had been following prior to illumination. This report therefore extends the previous observations by showing: (1) that PKAR follows any situation involving prolonged unilateral podokinetic circling, (2) that it cannot be “discharged” by brief periods of straight stepping under visual control, and (3) that a second type of oPKAR is induced by optokinetic stimulation. The authors concluded that PKAR does not result from an adaptation to sensory conflict, but occurs because the somatosensory flow of information partially habituates to long-lasting unilateral stimulation, so that asymmetrical stimulation is taken to correspond to straight stepping.
Vestibular, Proprioceptive, and Visual Influences

Figure 16.3
Adaptation to 2 h walking on the perimeter of a rotating disc. Locomotor trajectories of three subjects. Top lines show the trajectories of pre-adaptation attempts at walking “straight ahead” with eyes blindfolded. Representative of all subjects, roughly straight trajectories were achieved. In marked contrast, the central set of curved lines and data points shows a complete set of post-adaptation trajectories for subject EH. The actual starting points of trials were in different locations of the room, but for the purpose of illustration they are superimposed. The top left inset plots calculated radial distances of individual points on a given curve from the calculated “best center” of curvature, against angular deviation of these radii from that of the starting point. The close approximation to straight horizontal lines indicates the constancy of trajectory curvature. The progressive increase of average radius from one trajectory to the next illustrates the trend of readaptation to normal conditions. Bottom lines reproduce trajectories of straight line attempts in the self-propelled wheelchair pre- and postadaptation. Characteristically, there were no significant postadaptation changes in these trajectories. Selected postadaptation trajectories from two additional subjects are shown on the right side, exemplifying attempts which could not be completed due to approaching physical obstructions. (Adapted from figure 1 in Gordon et al., 1995, with permission.)
Many studies have investigated whether the self-movement signals that serve to stabilize gaze are also sent upstream to inform perceptual systems. Howard et al. (1998) measured postrotatory ocular nystagmus and sensations of body rotation in standing subjects after 3 min of adaptation in the following conditions, all in the dark: (1) passive rotation about the vertical axis (vestibular only), (2) active turning (vestibular and podokinetic), and (3) stepping about the vertical axis on a counterrotating platform, so body orientation remained fixed in space (podokinetic only). Following passive rotation, slow phase postrotatory nystagmus occurred in the same direction as the rotation (i.e., sensations of self-rotation were opposite to the direction of previous movement), and after active turning it was reduced in velocity. Surprisingly, after stepping in the absence of body rotation, nystagmus also appeared and was in the opposite direction of intended turning, an effect known as the antisomatogyrical illusion. Rieser et al. (1995) also showed that humans rapidly adjust the calibration of their motor actions to changing circumstances. Siegler et al. (2000) examined whether postrotatory effects alter the perception of self-motion and eye movements during a subsequent rotation. Blindfolded participants seated on a mobile robot first experienced a passive whole-body rotation about the vertical axis, and then reproduced the displacement angle by controlling the robot with a joystick. The reproduction began either immediately after the passive rotation (no delay), or after the subjective postrotatory sensations had ended (free delay). Participants accurately reproduced the displacement angles in both conditions, though they did not reproduce the stimulus dynamics. The peak velocities produced after no delay were higher than those after the free delay, suggesting that postrotatory effects biased the perception of angular velocity in the no-delay condition. Postrotatory nystagmus did not reflect the postrotatory sensations, consistent with the results of Mittelstaedt and Jensen (1999) for 2D rotations.

DiZio et al. (1987a, 1987b) sought to determine whether gravitoinertial force magnitude influences oculomotor and perceptual responses to coriolis, cross-coupled stimulation (making head movements about an axis other than that of rotation elicits a complex pattern of stimulation of the vestibular system known as coriolis, cross-coupled stimulation). During the free-fall and high-force phases of parabolic flight, blindfolded participants were passively rotated about the yaw axis at constant velocity while they made standardized head movements. The characteristics of horizontal nystagmus and the magnitude of experienced self-motion were measured. Both responses were less intense during the free-fall periods than during the high force periods. Although the slow phase velocity of nystagmus reached the same initial peak level in both force conditions, it decayed more quickly in zero G during free fall. These findings demonstrate that the response to semicircular canal stimulation depends on the background level of gravitoinertial force.

During natural movements, visual and vestibular information are complementary. Cue conflict experiments help to understand the relative importance of these signals and how they are combined. As illusions, sensory conflicts have been used as tools to help under-
standing the mechanics of self-motion perception. The vestibular-ocular reflex (VOR) and perception of angular displacement were compared by Ivanenko et al. (1998) before and after adaptation to inconsistent visual-vestibular stimulation. During adaptation, participants were exposed to 45 min of repeated passive whole-body rotations of 180°, combined with visual rotations of only 90° in a virtual reality display of a room. In postadaptation tests in the dark, large inter-individual variability was observed for both the VOR gain and estimates of angular displacement. The individual VOR gains were not correlated with perceived angles of rotation either before or after adaptation. Postadaptation estimates of angular displacement decreased by 24% when compared with preadaptation estimates, while the VOR gain did not change significantly. These results show that adaptive plasticity in VOR and in self-rotation perception may be independent of one another.

With two participants who had demonstrated a great capacity for adaptation in this last experiment (symmetrical visual-vestibular stimulation), Viaud-Delmon et al. (1999) examined adaptation to asymmetrical incoherent visual-vestibular stimulation. The authors sought to obtain separate (and different) adaptation to right and left stimulations. The test was similar to that mentioned earlier, but to achieve a 90° rotation in the virtual room the subject had to be rotated by 180° to the right, or by 90° to the left. Strikingly, after 45 min of asymmetrical left-right stimulation, perception of angular displacement in dark decreased equally for rotations to the right and to the left. This finding indicates that the calibration of vestibular input for spatial orientation did not undergo a directionally specific control.

In this section we have seen that the vestibular contribution to perceived rotation is accurate only in the simplest situations: when the head is rotated on the stationary upright trunk, with no distracting visual targets and no trunk or leg movements. However, in more complex situations estimates are much better when the vestibular system works in concert with the proprioceptive system. These sensory systems are typically coactivated, both on earth and in weightlessness, and they display a similar frequency dependence under rotation. Both convey only internal idiographic information, and are thus susceptible to illusions, i.e., erroneous interpretations of the motion of the mobile segments of the head, trunk, and legs hierarchy. Vestibular and proprioceptive contributions to spatial orientation are thus highly sensitive to other influences from the visual, motor, and cognitive systems.

**Visual System**

A rotation of the observer’s eye in a visible environment generates a global pattern of motion on the retina, known as the rotational component of retinal flow. Specifically, yaw or pitch produces a parallel lamellar flow pattern (see figure 16.4b), whereas roll about the line of sight produces a rotary flow pattern. The direction of flow is opposite the direction of observer rotation, and its angular velocity is equivalent to the observer’s rotation rate, independent of environmental depth. Thus, the observer’s rotation in a stationary
Figure 16.4
The instantaneous retinal velocity field for self-motion over a ground plane. Each vector represents the retinal velocity of a point on the ground plane, where the point is the tail of the vector. (A) Translational component: radial flow field produced by observer translation toward the "X," parallel to the ground plane. "X" denotes the focus of expansion. (B) Rotational component: lamellar flow field produced by observer rotation to the right about a vertical axis. (C) Rotation and translation: flow field produced by translation toward the "X" while rotating about a vertical axis to fixate the "O", which is attached to the ground plane. This field is the vector sum of (A) and (B). Note that the same velocity field can be produced by travel on a circular path.
environment is fully specified by the retinal flow. Here we focus on yaw rotation about a vertical axis, because it is most relevant to spatial orientation in terrestrial animals.

**Circular Vection and Angular Velocity** Consistent with the facts of optic flow, a large-field display of lamellar motion, such as that produced by a cylindrical drum rotating about a stationary observer at a constant velocity, can induce a strong sensation of self-rotation in the opposite direction known as circular vection. The latency for the onset of circular vection (CV) is typically about 2–3 s (Brandt et al., 1973), whereas complete vection, in which the rotating drum appears stationary and all motion is attributed to self-rotation, is often not achieved until 8–12 s. Presumably, the latency is due to a conflict between optic flow and the absence of vestibular stimulation at the onset of drum rotation, which indicates that no angular acceleration occurred; complete vection might then be achieved only after a delay related to the vestibular time constant, the duration ordinarily required for the canals to stabilize after acceleration to a constant velocity and the vestibular signal to decay. The delay is reduced by simultaneous vestibular stimulation, either smooth or impulsive acceleration of the observer platform in a direction opposite the visual motion (Brandt et al., 1974). This finding suggests that brief vestibular stimulation is sufficient to specify angular acceleration at the onset of self-rotation, which can then be sustained by constant-velocity optic flow. Conversely, platform acceleration in the same direction as visual motion eliminates vection (Young et al., 1973), even though the subject is actually rotating! Thus, the two sources of information can cancel each other. The delay to achieve complete vection also depends on the initial optical acceleration of the rotating drum. With accelerations below $5^\circ/s^2$, vection is complete at onset, whereas at higher visual accelerations there is an increasing delay (Melcher and Henn, 1981). Such findings are consistent with the view that the optokinetic response has low-pass characteristics and is sensitive to constant-velocity stimulation, whereas the vestibular signal has high-pass characteristics and is sensitive to acceleration or initial velocity, but not to sustained velocity, with a time constant of around 20 s (Young, 1981; Howard, 1986).

The perceived speed of circular vection corresponds closely to that of the visual display over a wide range of speeds, consistent with the fact that the optic flow rate specifies the speed of self-rotation. This relationship is linear up to a saturation velocity of about $120^\circ/s$, whereupon perceived speed levels off (Brandt et al., 1973). Surprisingly, Wist et al. (1975) reported that perceived speed increases with the perceived distance of the display, despite the fact that angular velocities do not vary with distance. They suggest that yaw rotation may be partially interpreted as lateral translation, for which the speed of self-motion does increase with distance, due to the similarity of their corresponding flow patterns. As the rotating drum is accelerated, Melcher and Henn (1981) found that perceived speed closely tracks the visual velocity at low accelerations ($\leq 2^\circ/s^2$), but it initially lags the display at high accelerations ($10^\circ/s^2$). Conversely, with vestibular stimulation provided by a rotating chair in darkness, perceived speed corresponds to the actual speed at high accelerations,
but increasingly underestimates the actual velocity at lower accelerations. With a rotating
chair in the light, however, perceived and actual speeds are linearly related with a gain
near 1 up to 60°/s at all accelerations tested. This result again reflects the complementary
frequency responses of the visual and vestibular systems, such that their combined per­
formance yields accurate estimates over a wide range.

Restricting the field of view in such experiments has shown that a smaller visual angle
of stimulation reduces the subjective strength and perceived speed of both circular and
roll vection (Brandt et al., 1973; Held et al., 1975; Allison et al., 1999). This finding is
consistent with Gibson’s (1950) observation that a global transformation of the optic array
corresponds to self-motion, whereas local transformations tend to correspond to the motion
of objects. However, vection can also be induced with small fields of view, less than 15°
in diameter (Andersen and Braunstein, 1985; Howard and Heckmann, 1989). A case in
point is the train illusion, in which an observer looking out the window of a stationary
train experiences self-motion when the train on the adjacent track begins to move. Note
that, in this case, the motion is produced by a more distant surface within a small, bounded
region of the array.

Subsequent research has found that such foreground-background relationships have a
strong influence on vection. Self-motion generally occurs within a stationary environ­
mental frame of reference, and thus generates optic flow from background surfaces. In
contrast, moving objects generally move in front of a stationary environmental background
(Gibson, 1968). Brandt et al. (1975) originally reported that presenting stationary bars in
front of a moving pattern had little effect on circular vection, but greatly reduced vection
when they were perceived as being in the background. This result was confirmed by Ohmi
et al. (1987), who monocularly presented two layers of dots moving in opposite directions,
which spontaneously reversed their order in depth. The pattern that was perceived to be
in the background determined the direction of circular vection. Howard and Heckmann
(1989) tested a central display that was either nearer or farther than a surround display, as
specified by binocular disparity. They concluded that the effect of motion is greater when
it is in the background than the foreground, and that both visual field size and depth order
influence vection. Note that Zugaro et al. (2001) similarly observed that background cues
preferentially anchor head direction cells (see chapter 4). It has also been observed that
the presence of a stationary foreground enhances the vection produced by a moving back­
ground (Howard and Howard, 1994; Nakamura and Shimojo, 1999). This is likely due to
relative motion with the foreground increasing the perceived speed of the background,
thereby enhancing vection.

It was originally believed that the retinal locus of stimulation also influenced vection;
specifically, that the periphery dominated the perception of self-motion, whereas central
vision dominated the perception of object motion (Brandt et al., 1973; Dichgans and
Brandt, 1978). However, it has subsequently been shown that both circular and linear
vection can be induced in central vision, and that there are no differences in the subjec-
ative strength or perceived speed of circularvection once central and peripheral stimulation are equated for area (Andersen and Braunstein, 1985; Post, 1988; Howard and Heckmann, 1989).

To investigate how visual and vestibular signals are combined, Mergner et al. (2000) obtained verbal estimates and pointer indications of perceived self-rotation in three viewing conditions. Subjects were presented with sinusoidal yaw rotations of an optokinetic pattern alone or in combination with rotations of a Barany chair. With pure optokinetic stimulation, specific instructions yielded different perceptual states: (1) when normal subjects were primed with induced motion (i.e., the illusory motion of a stationary target, opposite to the direction of the real motion of the inducing stimulus; thus normal subjects were primed with a stationary target superimposed upon the optokinetic moving display), the gain of circular vection was close to unity up to frequencies of 0.8 Hz, followed by a sharp decrease at higher frequencies; (2) when they were instructed to “stare through” the optokinetic pattern into far space, CV was absent at higher frequencies, but increasingly developed below 0.1 Hz; and (3) when they tracked the moving pattern with eye movements, vection was usually absent. In patients with loss of vestibular function, vection showed similar dynamics to those of normal subjects in the primed condition, independent of instructions. With vestibular stimulation alone (rotation in darkness), self-rotation judgments in normal subjects showed high-pass characteristics, falling from a maximum at 0.4 Hz to zero at 0.025 Hz. With combined visual and vestibular stimulation, perception of self-rotation in the “stare through” condition showed a clear modulation in association with the optokinetic stimulus, and therefore it did not correspond to the actual body rotation at low frequencies; this modulation was reduced in the tracking condition. The authors concluded that self-motion perception normally takes the visual scene as a reference, and vestibular input is simply used to verify the kinematic state of the scene. If the scene appears to be moving with respect to an earth-fixed reference frame, the visual signal is suppressed and perception is based on the vestibular signal (see also Berthoz et al., 1975).

Angular Displacement and Orientation If the velocity of vection can be accurately perceived, then in principle the total angle of displacement could be visually determined by mathematically integrating the optic flow over time. Alternatively, in an environment with distinctive stable landmarks, the angle of self-rotation is given by the angular displacement of the landmarks, and one’s current spatiotopic orientation is defined by the directions of visible landmarks.

To investigate the perception of active angular displacement, Bakker et al. (1999) asked participants at the center of a rotating platform to turn through a specified angle (in increments of 45°) either by stepping or by using an automated manipulandum. With optic flow alone, presented in a head-mounted display of a three-dimensional forest of trees (24°H × 18°V), target angles were greatly undershot with a gain factor of about 0.6. With vestibular information alone, the gain was about 0.7, and with vestibular plus podokinetic
information, turning was most accurate, about 0.9 (see also Jürgens et al., 1999; Yardley et al., 1998). Chance et al. (1998) similarly observed that learning object locations in a virtual environment was more accurate when participants actively turned (visual, vestibular, and podokinetic information) than when they were passively presented with a visual display.

This undershooting of total displacement with vision alone suggests that angular speed may have been overestimated. The suggestion that such errors stem from a small, head-mounted display seems unlikely because small fields of view tend to reduce, not increase, the perceived speed of rotation (Brandt et al., 1973). Schulte-Pelkum et al. (2003) tested a larger random-dot field on a cylindrical screen (86° H x 64° V) and found that target angles were still undershot, but with a higher gain of 0.85. These findings suggest that temporal integration of optic flow tends to underestimate the total angular displacement.

Jürgens et al. (2003) examined the perception of angular displacement during passive rotation over a much wider range, up to 900°. Participants on a platform in a large-field rotating drum experienced a brief acceleration followed by three different velocities, and reported when a target angle had been reached. There was a linear relationship between the perceived and target displacement and the average performance was quite accurate: a gain near 1.06 with vision alone, 0.94 with vestibular alone, and 1.02 with both, with lower variability in the visual conditions. However, in the vision alone condition, target angles were greatly undershot at the low rotation rate (15°/s), suggesting that speed was overestimated, while angles were overshot at the high rotation rate (60°/s), suggesting that speed was underestimated. Similar effects were observed when the lights were turned off after the first 90° and subjects pushed a button to signal each successive 90° rotation. Interestingly, the angular estimates did not depend upon a subjective experience of vection. The authors concluded that the temporal integration system can extrapolate the initial perceived velocity, based on early visual and/or vestibular information, in order to determine the total angular displacement. They also proposed that the perceived velocity is biased toward the mean of recent experienced or expected velocities. They argue that the vision-based undershoot reported by Bakker et al. (1999) may result from their head-mounted display being less “potent” than a rotating drum, but this seems contrary to the fact that it apparently induced higher perceived speeds. Alternatively, the undershoot might be due to the relatively low rotation velocity of about 9°/s generated by the participants in the Bakker et al. (1999) study.

Becker et al. (2002a) investigated circular vection using four viewing conditions of an optokinetic drum, turning at 15, 30 or 60°/s: participants (1) attentively followed the visual details of the moving optokinetic pattern (FOL) (similar to the “tracking with eye movements” instruction of Mergner et al., 2000), (2) stared at the pattern (STA) (similar to the stare through instruction), (3) voluntarily suppressed their optokinetic reflex (SUP) (maintaining gaze at an imaginary stationary point), or (4) suppressed the optokinetic reflex by fixating a stationary fixation point (FIX). To quantify CV, subjects pressed a button to indi-
cate each successive perceived rotation of 90°. The total apparent angular displacement increased gradually in the order FOL < STA < SUP < FIX; vection latency (5 to 55 s) decreased in the same order. Slow eye velocity (ranging from 3 to 50°/s; measured to confirm that subjects followed the viewing instruction and to quantify the retinal slip) was the same in FOL and STA, but lower during SUP. The authors concluded that (1) the influence of eye movements on circular vection depends on whether these are intentional (FOL) or not (STA); (2) the increase in circular vection (cumulated 90° indications) during voluntary suppression of the optokinetic reflex (SUP) suggests that afferent motion cues such as retinal slip are processed with larger gain than efferent motion cues such as eye-movement signals; hence (3) the enhancement of circular vection during fixation (FIX) is not, or not solely, due to induced motion of the fixation point opposite the direction of optic flow (see Mergner et al., 2000).

Thus, estimates of angular displacement from integrating optic flow appear to be approximately veridical, but are subject to influences of rotation velocity, fixation, and possibly display size and distance. On the other hand, an environment containing visual landmarks may permit quite accurate orientation judgments. Riecke et al. (2002) presented a virtual display of Tübingen’s market square on a cylindrical screen and trained participants to locate 22 target objects. They were then physically rotated to random orientations and asked to point to unseen target objects, yielding mean absolute errors of only 16.5° (variability 17°). Removing vestibular information did not significantly affect performance when landmarks were available, but reduced performance when optic flow had to be integrated. This indicates that spatial orientation can rely on salient visual landmarks, bypassing the temporal integration of optic flow.

Perceiving Translation and the Direction of Self-Motion

Vestibular and Proprioceptive Systems

There is an extensive literature on the sensitivity of the vestibular system to linear acceleration, often investigated with centrifuges so as to avoid linear space limitations (Anastasopoulos et al., 1996; Angelaki, 2003; Bles and Degraaf, 1993; Young, 1981; Böhmer and Mast, 1999; Clarke and Engelhorn, 1998; Furman and Baloh, 1992; Merfeld et al., 2001; Seidman et al., 2002; Tribukait, 2003; Wearne et al., 1999) as well as other protocols (Angelaki and McHenry, 1999; Baloh et al., 1988; Benson and Brown, 1989; Berthoz et al., 1975; Bles et al., 1995; Bronstein and Gresty, 1988; Gianna et al., 1997; Glasauer, 1995; Glasauer and Israël, 1995; Golding and Benson, 1993; Harris et al., 2000b; Hlavacka et al., 1996; Melvill-Jones and Young, 1978; Paige et al., 1998; Pavard and Berthoz, 1977: Walsh, 1961; Wertheim et al., 2001). In this section we merely highlight some recent work on the perceived displacement and direction of translational motion, as it ties in with our closing discussion of path integration.
Linear Displacement  The magnitude of linear displacement can be quite accurately determined over short distances from otolith signals. Israël and Berthoz (1989) applied the VMCS paradigm with lateral body displacements along the interaural axis in darkness. Although the linear VOR per se was very small, subjects could stabilize their gaze on a previously seen straight-ahead target with VOR + saccades. When subjects were instructed not to move their eyes during self-motion (VMCS), most of them could still correctly reproduce the head movement amplitude with saccades. This indicates that linear head displacement was perceived and stored with the adequate metrics and could be used to drive the saccadic system. Bilabyrinthectomized patients could not perform any adequate gaze stabilization, showing that the observed performance required vestibular signals.

Over longer distances, Berthoz et al. (1995), Israël et al. (1997), and Grasso et al. (1999), found that participants who are passively accelerated through a target distance along the anterior-posterior (AP) axis can accurately replicate that distance when traveling at a different acceleration (all without vision). This suggests that vestibular information allows consistent within-modality estimates of linear displacement. During active walking, participants are highly accurate at reproducing a travel distance as long as the walking speeds on the target and test paths are the same (Mittelstaedt and Mittelstaedt, 2001). They can also accurately walk to a static visual target without vision, and estimate this distance on the basis of either vestibular or podokinetic information alone, as long as they travel at a normal walking speed, step length, and frequency. This suggests that the path integration system is calibrated for normal walking. As observed for angular displacement, podokinetic signals are the most accurate and appear to be dominant during linear displacement.

Direction of Heading Telford et al. (1995) compared vestibular, podokinetic, and visual judgments of the direction of self-motion, or heading. The participants were passively transported at an acceleration above the otolith threshold, actively walked from a standstill with a sub-threshold acceleration, and/or viewed optic flow from a three-dimensional array of vertical rods in a head-mounted display. The task was to align the head in the perceived direction of self-motion. Visual judgments were an order of magnitude more precise than podokinetic or vestibular judgments. When the visual heading and the vestibular heading were misaligned by 30°, pointing judgments were completely determined by optic flow; when the visual and podokinetic headings were misaligned by 30°, judgments were in between them (Ohmi, 1996). Thus, it appears that heading direction can be determined in any modality, but optic flow allows for the most precise judgments. Vestibular heading estimates are highly variable and strongly dominated by visual information. (See Duffy, et al., this volume, for more on visual and vestibular influences on the neural estimation of heading.)
Visual System
Translation of the observer's eye through the environment generates a radial pattern of motion known as the *translational component* of retinal flow (see figure 16.4a). The **focus of expansion** in this flow pattern corresponds to the current direction of heading (Gibson, 1950). The radial structure of the pattern depends solely on the observer's direction of heading, whereas the rate of flow depends upon both the observer's speed and the distance of environmental surfaces.

**Linear Vection** The characteristics of linear vection are quite similar to those of circular vection. In this case, an experience of self-translation, usually along the AP axis, is induced by lamellar flow presented laterally (Berthoz et al., 1975) or radial flow presented in the frontal plane (Lishman and Lee, 1973). The latency for linear vection is about 1–2 s, and it has low-pass characteristics with a frequency cutoff of 0.5 Hz and a time constant of about 1 s (Berthoz et al., 1975; Berthoz and Droulez, 1982). In contrast, the otolith system has high-pass characteristics, with sensitivity to linear acceleration only at frequencies above 1 Hz (Melvill-Jones and Young, 1978). This is again consistent with a division of labor between the visual and vestibular systems.

**Linear Displacement** Perceiving the total displacement from optic flow is more problematic during translation than rotation, because the flow rate is inversely proportional to the distance of environmental surfaces. Thus, determining one's speed or displacement from optic flow depends on perceived distance. With a display of a moving grating at a fixed distance, the speed of linear vection has been found to be linear up to a saturation velocity of over 90°/s (Berthoz et al., 1975; Carpenter-Smith et al., 1995).

In experiments on perceived displacement, Bremmer and Lappe (1999) asked participants to judge whether a display of self-motion over a textured ground plane depicted a greater travel distance than a standard display, while they held eye height and depth structure constant. They obtained a gain of 0.98, even when the speed of self-motion was varied between standard and test. Frenz et al. (2003) determined that such relative judgments remain reasonably accurate despite variation of the visually specified eye height and viewing angle of the ground plane, leading them to conclude that distance estimates are based on the perceived speed of self-motion through the environment rather than simply on proximal image velocities. Interestingly, when asked to reproduce the travel distance in a sample display by controlling optical speed with a joystick, most participants regenerate the velocity profile of the sample display (constant velocity, sinusoidal, or a sequence of velocity plateaus) (Bremmer and Lappe, 1999). A similar pattern has been observed for the vestibular-based reproduction of passive displacements (Berthoz et al., 1995; Israël et al., 1997), suggesting that self-motion may be encoded as a velocity history rather than as a temporally integrated distance value.
On the other hand, Harris et al. (2000a, b) reported large misestimates of travel distance using a static visual target in a virtual corridor. Subjects first viewed a target, then experienced visual stimulation (motion presented in a head-mounted display) or vestibular stimulation (passive mechanical displacement in the dark) corresponding to acceleration down the corridor, and were asked to indicate when they passed the target. With visual stimulation alone, performance was quite accurate (distance gain of 1.04), but with vestibular stimulation alone subjects undershot the target distance (gain of 0.5), as previously reported by Israël et al. (1993a). In contrast, when the target was first specified by mechanically accelerating the subject through the target distance, judgments were accurate with vestibular stimulation of the same or a different acceleration (distance gain of 0.96), but they greatly overshot the target distance with visual stimulation (gain of 4.3). These results suggest that visual and vestibular estimates of travel distance are not well-calibrated, so that visual distance is underestimated and vestibular distance is overestimated relative to one another. Subsequently, Redlick et al. (2001) found that judgments of visually determined travel distance actually depend on the acceleration of the visual display: subjects undershot a static target with accelerations less than 0.1 m/s² (including constant velocities) whereas gains were close to 1 at accelerations above 0.2 m/s² (which is above the vestibular threshold). However, it is difficult to interpret this set of results, because the displays contained no binocular disparity and were presented at optical infinity, had stripes on the walls but no texture on the floor, and were simulated with an unusually low eye height—any of which could have led to errors in perceived distance and hence in perceived self-motion.

There is thus some difference of opinion regarding the perception of linear displacement from optic flow. Relative judgments of travel distance over a ground surface appear to be quite good, but there may be errors at low accelerations or miscalibration with respect to vestibular estimates.

Direction of Heading The instantaneous direction of translation is specified by the radial optic flow pattern, in which the focus of expansion (FOE) corresponds to the heading direction. The location of the FOE in relation to environmental landmarks thus provides information about the orientation of the locomotor path in the environment. We briefly describe some basic findings on the perception of heading (for recent reviews, see Lappe et al., 1999; Warren, 2004; and chapter 15 by Duffy et al., in this volume).

Observers can judge their direction of translation from random-dot displays of radial flow with an accuracy of 1° of visual angle (Warren et al., 1988). Accuracy is similar in various three-dimensional environments, such as a ground plane, a frontal plane, or a cloud of dots, but decreases as the number of dots is reduced. Such results indicate that the visual system spatially integrates local motion signals to estimate the heading direction (Warren et al., 1991; Burr et al., 1998).
However, the perception of heading is complicated by the fact that the eye can also rotate during translation, a common occurrence when one fixates a point in the world during locomotion. If the eye is simultaneously translating and rotating in space, the flow pattern on the retina is the sum of the rotational (lamellar) and translational (radial) components, and can be quite complex (see figure 16.4c). To determine the instantaneous heading, the visual system must somehow analyze the translational and rotational components.

There are two general approaches to this rotation problem. First, it is possible that extraretinal signals about the rotation of the eye and head are used to estimate the rotational component of self-motion, which is then subtracted from the retinal flow to recover the translational component of self-motion (Banks et al., 1996). Second, it is theoretically possible that heading can be determined from the retinal flow alone, because motion parallax in the flow pattern corresponds to observer translation, whereas common lamellar motion corresponds to observer rotation. Thus, the visual system might (1) determine the heading directly from motion parallax (Rieger and Lawton, 1985; Royden, 1997), (2) first estimate observer rotation from the lamellar flow and subtract it to determine the heading (Perrone, 1992), or (3) possess templates for the set of flow patterns produced by combinations of translation and rotation (Lappe and Rauschecker, 1993; Perrone and Stone, 1994).

The psychophysical evidence on the rotation problem is mixed. Warren and Hannon (1988; 1990) initially reported that heading judgments were similarly accurate with an actual eye rotation (flow and extra-retinal signals specify rotation) and a display that simulated the optical effects of an eye rotation (flow specifies rotation, extra-retinal signals specify no rotation), indicating that heading can be perceived from retinal flow alone, even when it is in conflict with extra-retinal signals. However, the simulated rotation rates in these experiments were low (<1°/s). Royden et al. (1992) and Banks et al. (1996) subsequently found that heading judgments were increasingly inaccurate at faster rotations (1 to 5°/s), with errors in the direction of simulated rotation, consistent with the extra-retinal hypothesis. Royden (1994) argued that observers actually based their judgments on a perceived curved path of self-motion rather than on the instantaneous heading direction. Observers are more accurate under conditions designed to elicit estimates of the instantaneous heading: (1) when judging the direction they are skidding while traveling on a circular path (Stone and Perrone, 1997), (2) when asked to base heading judgments on the illusory motion of the fixation point during simulated rotation (van den Berg, 1996), or (3) when asked to judge heading in short displays (<500ms) of simulated rotation (Grigo and Lappe, 1999). These results suggest that the visual system can estimate instantaneous heading, although observers tend to judge their perceived path of self-motion.

Such observations raise the question of how the visual system recovers the path of self-motion over time from complex retinal flow patterns, which is known as the path problem.
The problem is that the flow field is ambiguous with respect to the observer's path: the same instantaneous flow field can be generated by a straight path of self-motion with an eye rotation about the vertical axis, or by a circular path of self-motion (see figure 16.4c). This ambiguity can be resolved in more realistic environments with distinct objects. Li and Warren (2000; 2002) found that when displays contain reference objects, path judgments are quite accurate, even at high simulated rotation rates (see also Cutting et al., 1997; Wang and Cutting, 1999). They proposed that the visual system determines the instantaneous heading with respect to objects in the environment (the object-relative heading), and then recovers the path of self-motion by tracking the object-relative heading over time. For example, if the path is straight, the heading point will remain fixed in the scene, whereas if the path is curved, it will shift relative to objects over time.

The data thus indicate that both retinal flow and extra-retinal signals contribute to detecting the path of self-motion. This may account for the mixed results in the heading literature. Crowell and Andersen (2001) reported that the role of extra-retinal signals is merely to gate the interpretation of the lamellar component of flow from a three-dimensional scene as being due to an eye rotation or to a curved path of self-motion. With distinct objects in the scene, the retinal flow appears to dominate extra-retinal signals in determining the path of self-motion (Li and Warren, 2000). The direction of the locomotor path in the environment can thus be determined whether or not the eye is simultaneously rotating.

**Combining Rotation and Translation in Path Integration**

The literature we have reviewed shows that, considered individually, estimates of angular displacement, linear displacement, and the direction of locomotion are all quite veridical, at least at normal walking speeds under full-cue conditions or within a single modality. Given that this is the case, one might expect that a path integration system could combine these linear and angular estimates to perform accurate navigation. A number of models of path integration describe how linear and angular displacements might be combined (Maurer and Seguinot, 1995), enabling an observer to return to their starting location in a homing task. One approach continuously updates a homing vector that preserves only the direction and distance to the home location (Fujita et al., 1990); alternatively, a record of the traveled paths or velocity profiles may be preserved (Fujita et al., 1993). It is thus somewhat surprising that path integration in humans appears to be rather coarse, with large constant and variable errors.

To examine interactions between angular and linear displacements in the vestibular system, Ivanenko et al. (1997) had blindfolded participants undergo passive whole-body motion in the horizontal plane, including pure rotations in place, corner-like trajectories, and arcs of a circular trajectory. Stimulation of the semicircular canals was the same for all trajectories, but was accompanied by otolith stimulation during the arc motion. When
subjects used a pointer to reproduce the total angular displacement after the motion. They consistently overestimated their rotation angle on all trajectories. However, when they continuously pointed toward a distant unseen target during the motion, pointing was highly accurate and matched the dynamics of angular motion. It was concluded that (1) the brain can distinguish and memorize the angular component of complex two-dimensional motion, despite a large inter-individual variability; (2) in the range of linear accelerations used, no effect of otolith-canal perceptual interaction was shown; and (3) angular displacements can be dynamically transformed into matched pointing movements.

In a similar experiment, Ivanenko et al. (1997a) tested passive rotation in place, passive linear motion, and a semicircular trajectory. Body orientation in the horizontal plane was controlled independently of the trajectory, so that different combinations of otolith and canal stimulation were produced. Participants had to point toward a previously seen target during the motion, and in a second session had to make a drawing of the perceived trajectory at the end of the movement. The movement of the pointer closely matched the dynamics of the rotational component of the planar motion. This suggests that, in the range of linear accelerations tested, there was no interference of otolith input on canal-mediated perception of angular motion. The curvature of the drawn paths could largely be explained by the input to the semicircular canals, without taking into account the directional dynamics of the otolith input during passive motion. Thus, the reconstruction of the trajectory in space does not appear to involve integrating the linear and angular components of the motion into a unified two-dimensional representation. This result suggests that rotational and translational motions may not be accurately combined to recover one’s path (also see chapter 17 by Hicheur et al.).

One test of path integration that combines linear and angular displacements is a homing task such as triangle completion. The participant starts at a home location, travels actively or passively along two specified legs of a triangle, and is then asked to return home along the third leg of the triangle. Loomis et al. (1993) found that blindfolded subjects with only vestibular and podokinetic information performed triangle completion with surprisingly poor accuracy. Absolute (unsigned) errors were 24° for the final turn toward home, and 1.68 m for the length of the return path, or about 30% of the triangle’s third leg on average. Constant (signed) errors revealed a compression in the range of responses, such that participants tended to overshoot on short legs and undershoot on long legs, and overturn small angles and slightly underturn large angles. The authors suggested that this regression toward the mean of a set of tested triangles is consistent with a path integration system that preserves some record of traveled paths rather than simply updating the homing vector. With optic flow alone, Peruch et al. (1997) found even less accurate triangle completion performance in subjects using a joystick in a simple virtual environment. In contrast to active walkers, their subjects consistently underturned all final angles.

Surprised by these results, Nico et al. (2002) submitted blindfolded subjects to passive linear displacements along the two equal sides of a triangular path. Subjects were then
oriented toward the starting point and asked to complete the triangle by driving straight to the starting point, either blindfolded or with full vision in a small (7 x 6 m) or a large (38 x 38 m) room. Room dimensions exerted a significant effect on performance: in the smaller room blindfolded responses were always too short, although subjects correctly reached the starting point when visual feedback was allowed (figure 16.5). In contrast, in the larger room, subjects correctly responded while blindfolded but drove significantly farther than required with full vision. These data show that vestibular navigation is highly sensitive to both stored (knowledge of environment) and current visual information.

Figure 16.5
Triangle completion with self-driven transport while seated on a mobile robot. The circles containing plus signs indicate the starting and expected arrival points. Triangle legs (black solid lines) show the passively traveled trajectories in darkness (stimulus), before the actively controlled straight transport in light (response: dotted lines). The empty dots (±SD) each show subject’s responses; subjects had not seen the start/end point. These data are from the smaller experimental room used. Responses were too long (overshoots) when the same task (with the same “stimulus dark-response visual” condition) was performed in the larger room, and too short (undershoot) when executed in darkness (“stimulus dark-response dark” condition).
In order to compare optic flow and vestibular/podokinetic information in the same setup, Kearns et al. (2002) tested triangle completion in a large virtual environment. Participants walked freely within a 12-m by 12-m area while wearing a head-mounted display (60° H × 40° V). To test optic flow alone, a seated observer steered with a joystick in a virtual texture-mapped arena, which resulted in large variable errors in final angle (SD = 33°) and path length (SD = 1.5 m, 28% of the required path length). Constant errors reflected underturning of most final turns, similar to Péruch et al. (1997), as well as undershooting of long legs and slight overshooting of short legs. When participants actively walked in the virtual environment, performance was more consistent and exhibited a different pattern of constant errors, with or without optic flow. Variable errors in final angle (SD = 20°) and path length (SD = 1 m, 22% of the required length) were somewhat smaller, whereas constant errors reflected consistent overturning of the final angle rather than underturning. This pattern of results indicates that observers can perform path integration using optic flow if necessary, but they rely predominantly on vestibular/podokinetic information during active walking.

Kearns (2003) measured the relative contribution of visual and vestibular/podokinetic information by selectively manipulating the visual gain of the translational or rotational flow during active walking. Thus, for a given walked distance, the observer appeared to travel through a greater (150%) or shorter (67%) visual distance in the virtual arena; turning angles were manipulated similarly. The relative contribution of vestibular/podokinetic information to triangle completion performance was about 85% overall, but there was a significant contribution of about 15% from optic flow. It thus appears that the temporal integration of optic flow makes a small but reliable contribution to path integration, even during active walking. Overall, however, the large errors in triangle completion suggest that relatively veridical estimates of rotational and translational displacements are not accurately combined during path integration.

On the other hand, when Kearns (2003) added five landmarks near the two outbound legs, accuracy improved dramatically, and the visual contribution increased to 50% for the translational gain and 60% for the rotational gain. The landmarks appear to provide a visual reference frame within which the observer can update position more accurately than by integrating the optic flow. Yet there still remains a strong contribution of vestibular/podokinetic information to updating position. However, when landmarks are positioned near a target location, subjects completely rely on them as beacons for navigation (Foo et al., in press) (figure 16.6). During triangle completion, if a landmark near the home location is surreptitiously shifted as the subject walks the first two legs of the triangle, the change goes unnoticed and elicits corresponding deviations in the final turn. It has recently been found that this is the case for shifts of as much as 28°, well above the resolution of vestibular/podokinetic path integration (Foo et al., 2004). This suggests that the visual system relies heavily on local landmarks, when available, rather than path integration mechanisms in order to remain oriented in the environment.
Shortcuts between two learned locations in human walking. During training (left panels), subjects repeatedly walked from home (H) to location A and back, turned through angle H, and walked from home to location B and back. They were then tested on the novel short-cut from A to B (right panels). Traces represent individual trials from a representative subject. (a) Desert world: With no visual landmarks (only a textured ground plane), accumulating errors are characteristic of path integration. (b) Forest world: With a random array of colored posts, errors accumulate until local landmark configuration is visible, then subjects home in on target location. (c) Local landmarks: When landmarks near the target location are shifted by 9° on catch trials (gray traces), subjects follow them completely. Complete dominance of local landmarks also occurs with shifts up to 28° in a continuous triangle completion task. (Adapted from Foo et al., in press.)
Conclusion

The results reviewed in this chapter point to the conclusion that whole-body rotation and translation at typical locomotor speeds, including angular and linear displacements, are veridically perceived and reported on the basis of visual, vestibular, and podokinetic information. These abilities allow for the accurate control of self-motion, and should in principle provide a reliable sensory basis for maintaining one’s orientation to the environment and for path integration over longer paths of locomotion. Yet paradoxically, path integration performance in a simple task such as triangle completion is quite unreliable and inaccurate. These observations imply that difficulties may reside in combining estimates of angular and linear displacement to determine a complex path, a process that deserves further study. Fortunately, it appears that the visual system has developed an alternative orientation system based on visual landmarks, which allows for highly accurate and precise orientation and navigation within a heterogeneous environment. In the absence of distinctive landmarks, the system can fall back on a coarse path integration system, which may suffice to bring the observer within range of another landmark.

References


Vestibular, Proprioceptive, and Visual Influences


