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Heading judgments during active and passive self-motion

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Abstract Previous studies have generally considered heading perception to be a visual task. However, since judgments of heading direction are required only during self-motion, there are several other relevant senses which could provide supplementary and, in some cases, necessary information to make accurate and precise judgments of the direction of self-motion. We assessed the contributions of several of these senses using tasks chosen to reflect the reference system used by each sensory modality. Head-pointing and rod-pointing tasks were performed in which subjects aligned either the head or an unseen pointer with the direction of motion during whole body linear motion. Passive visual and vestibular stimulation was generated by accelerating subjects at sub- or supra-vestibular thresholds down a linear track. The motor-kinesthetic system was stimulated by having subjects actively walk along the track. A helmet-mounted optical system, fixed either on the cart used to provide passive visual or vestibular information or on the walker used in the active walking conditions, provided a stereoscopic display of an optical flow field. Subjects could be positioned at any orientation relative to the heading, and heading judgments were obtained using unimodal visual, vestibular, or walking cues, or combined visual-vestibular and visual-walking cues. Vision alone resulted in reasonably precise and accurate head-pointing judgments (0.3° constant errors, 2.9° variable errors), but not rod-pointing judgments (3.5° constant errors, 5.9° variable errors). Concordant visual-walking stimulation slightly decreased the variable errors and reduced constant point-

ing errors to close to zero, while head-pointing errors were unaffected. Concordant visual-vestibular stimulation did not facilitate either response. Stimulation of the vestibular system in the absence of vision produced imprecise rod-pointing responses, while variable and constant pointing errors in the active walking condition were comparable to those obtained in the visual condition. During active self-motion, subjects made large head-pointing undershoots when visual information was not available. These results suggest that while vision provides sufficient information to identify the heading direction, it cannot, in isolation, be used to guide the motor response required to point toward or move in the direction of self-motion.

Key words Heading · Optical flow · Otoliths · Sensory integration · Human

Introduction

Most empirical studies of the perception of the direction of self-motion have focused on the ability of stationary observers to identify the visual heading in an optical flow pattern. This is a purely oculocentric task which does not require subjects to align either the head or the body with the heading. Orienting the head in the direction of visually defined self-motion is a headcentric task requiring knowledge of the direction of regard of each of the eyes. Pointing with an unseen hand to the visually defined heading is a bodycentric task that requires, in addition, knowledge of where the head is on the body and of the position of the arm on the body. In addition, one may point in the direction of heading in the dark on the basis of information from either the otolith organs or from motor-kinesthesia during self-induced motion. Thus, several senses process information about headcentric and bodycentric self-motion, but few studies have examined the roles of each in spatial orientation. We will begin by briefly reviewing what is known about the directional sensitivity of each of the relevant motion senses.

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Visual heading

The visual system is an ideal heading transducer in that it consists of an array of spatially discrete neurons sensitive to the velocity and direction of flow across the retina. Gibson (1950) noted that, during locomotion, visual heading is specified by the center of radial optical flow resulting from the relative motion of stationary objects in the environment. However, the 'focus of expansion' is useful only when an observer is following a straight path and gaze is coincident with the heading (Cutting 1986; Koenderink and van Doorn 1981; Regan and Beverley 1982), conditions which rarely occur during natural motion. Retinal flow during natural motion consists not only of radial optical flow produced by linear self-motion, but also of a translational component resulting from eye movements. Heading could be derived by decomposing retinal flow into radial and translational components (Bruss and Horn 1983; Koenderink and van Doorn 1981; Longuet-Higgins and Prazdny 1980; Rieger and Lawton 1985), or by using extraretinal proprioceptive information or motor efference to monitor and subtract eye movements (von Holst 1954; Skavenski 1972; Sperry 1950). However, such computations are unnecessary when motion occurs through a three-dimensional array of objects, since heading is specified by the locus of zero parallax in the retinal flow field, i.e., by the set of objects at different distances which remain visually aligned. This cue to heading does not depend on gaze angle, since eye rotation produces very little parallax for distant targets. When gaze is centered to one side of the heading, retinal flow is asymmetrical, with higher flow rates occurring on the fixated side of the motion path. The observer merely has to make a gaze adjustment in the opposite direction to counteract the asymmetrical flow and locate the locus of zero parallax (Cutting 1986; Cutting et al. 1992; Richards 1975).

Empirical studies of visual heading have generally used computers to generate two-dimensional optical flow fields (Ahumada 1983; Cutting 1986; Cutting et al. 1992; Warren 1976; Warren et al. 1988). However, two-dimensional displays do not optimize the differential motion parallax available in the three-dimensional world. Further, such displays may not create an impression of self-motion through a stationary environment, and heading, by definition, requires self-motion. Computer-generated displays produce a conflict between vision which signals motion and other senses which signal stationarity.

Vestibular heading

The vestibular otolith organs (utricle and saccule) respond to the magnitude and direction of linear acceleration of the head. Head acceleration is encoded by the magnitude of displacement of hair cells on the sensory epithelium. Direction of linear motion is coded in terms of the pattern of activation of arrays of hair cells with different directional sensitivities (polarization axes).

Thresholds for the detection of linear head motion have been reviewed by Guedry (1974) and Gundry (1978). None of these studies measured directional thresholds of linear motion, although in some cases subjects provided verbal reports of their perceived direction of motion. Using a see-saw device to provide vertical oscillations, Walsh (1964) noted that reports of the direction of vertical motion were often out-of-phase with the actual motion, in that observers frequently reported maximal downward motion during the upswing. Benson et al. (1986) established thresholds for the detection of linear self-motion using a device in which upright or supine subjects experienced linear motion along the naso-occipital, interaural, or dorso-ventral body axes. Detection thresholds were significantly higher (0.015 *g*) for dorso-ventral motion than for naso-occipital or interaural linear motion (0.006 *g*). However, thresholds for the discrimination of different directions of motion were not obtained, since motion was restricted to two directions for each body axis.

While the otoliths provide information about the direction of head motion, they do not provide information about the direction of body motion in the absence of knowledge about the orientation of the head on the body. For example, if the head is aligned with the body and accelerated forward, the otoliths correctly interpret the forward acceleration, but if the head is turned laterally toward the left shoulder while the body is accelerated forward, the otoliths will signal rightward motion. Correct interpretation of the directions of the head and body accelerations requires inputs from proprioceptors in the neck and body.

Somatosensory heading

In addition to the signals from neck proprioceptors, during walking, information from other joint proprioceptors, foot mechanoreceptors, and sensorimotor feedback from the legs and trunk indicate which way the body is moving in bodycentric coordinates and enable an observer to point in the direction of heading. The role of these inputs in heading perception has not been examined. Walsh (1961), however, has shown that somatosensory cues have little influence on motion detection during passive motion. In subjects with high spinal lesions which destroyed sensory afferents from trunk and limb proprioceptors, thresholds for the detection of self-motion were not elevated relative to those for controls, suggesting that such cues add little to the perception of heading during passive motion.

To date, the only experiments on heading have been concerned with the visual identification of the locus of heading within an oculocentric frame of reference, and although it has been established that motion parallax facilitates judgments of heading (Cutting et al. 1992), no experiments have been done in which observers combine sensory information as they move through a 3-D environment. The present experiment examines the contribu-

tions of visual, vestibular, and proprioceptive sensory systems to the precision and accuracy of judgments of actual self-motion in both visual (oculocentric) and bodycentric coordinate systems. We used two basic tasks; a head-pointing task and a rod-pointing task. In the head-pointing task, subjects aligned the head with the direction of heading. When the lights were on, this was achieved by turning the head until a fixated, head-fixed visual target was centered on the locus of heading. This sighting task can be performed in purely oculocentric coordinates, since it does not require knowledge of either eye or head position. When the subject walked in the dark the head-pointing task was performed in bodycentric coordinates using information from the legs and from neck proprioceptors signalling the position of the head on the body. In the rod-pointing task, subjects used the hands to align an unseen rod with the direction of heading. With only visual information about heading (subjects moved passively at subthreshold accelerations in the light), the rod-pointing task requires knowledge of the position of the eyes in the head and of the head on the body. With only vestibular information about heading (subjects accelerated passively in the dark), the rod-pointing task requires knowledge of the position of the head on the body. With only proprioceptive information about heading (walking at subthreshold accelerations in the dark) the rod-pointing task requires no information about the positions of the eyes or of the head. We predict that heading judgments will be most precise and accurate when fewer in-series sensory inputs are required compared with when more sensory systems are involved. Specifically, performance should be optimal when the task is to center a visual target on the seen heading by moving the head, and when motor feedback associated with walking is available and the task is to align an unseen pointer with the unseen heading. A second prediction is that precision and accuracy should improve when several in-parallel sensory systems provide information about heading.

Materials and methods

Subjects

Five adult subjects (two men and three women) between 25 and 36 years, with normal vision or vision corrected to normal using contact lenses, participated in the experiment. None of the subjects had any known visual, vestibular, or motor abnormalities. The experiment was performed within the ethical guidelines established by York University, and informed consent was obtained from each subject prior to the start of the experiment.

Apparatus

Subjects were positioned in one of the two devices shown in Fig. 1A,B inside a hallway lined with mirrors (8.0 m long, 1.4 m wide). Diffuse illumination was provided by fluorescent overhead lights covered with a translucent Mylar sheet. The visual display consisted of approximately 360 white wooden rods (each 36 cm long, 5 cm wide) which were suspended vertically from the ceiling. The floor, the wall space below the mirrors, and all equipment

placed inside the hallway were painted flat black, and subjects wore black clothing to minimize reflections in the mirrors.

In the active motion conditions, subjects stood upright inside the walker shown in Fig. 1A. The torso was clamped within a frame on a circular bearing which could be rotated with respect to an outer frame which ran on a linear bearing down the length of the hallway. At the start of each trial, the subject and inner frame were rotated on a turntable and brought to rest and clamped at a variable angle about the Earth-vertical axis with respect to the motion path. Subjects were then instructed to walk at the same rate as the walker as it was pulled along rails located just below the mirrors at waist height (85 cm from the floor). They walked in whatever posture they happened to be clamped in the walker. For example, they walked sideways if the body was clamped at 90° to the motion path. When walking in the dark at accelerations below threshold for vestibular stimulation, subjects received only motor-kinesthetic information about the direction of motion. When walking with the lights on, they received both motor-kinesthetic and visual information.

The cart shown in Fig. 1B was used to provide passive visual, vestibular, or combined visual-vestibular stimulation. The subject sat on a padded seat which could be rotated relative to a base mounted on four wheels. After several rotations the chair was locked into a given direction relative to the motion path. The cart moved along a rail on the floor of the hallway. The chair and walker were pulled by cables running over pulleys driven by DC servo motors (EG & G Torque Systems) controlled by a Macintosh SE computer.

Visual stimulation was provided by two television monitors (Panasonic WV-5200B; 15 cm wide, 600 lines) housed side by side in a frame attached to a helmet fitted on the subject's head. The helmet was fan cooled and lined with an individually molded foam plastic insert which provided a tight coupling between the head and the optical system. The subject viewed the monitors through a pair of lenses which magnified each image to give a 60°-wide binocular field with accommodation at optical infinity. The monitors and helmet were supported on a frame which could rotate through $\pm 35^\circ$ about the mid-vertical axis of the head (Fig. 1A,B). The rotatable frame was mounted on an outer frame which ran on vertical bearings on vertical supports on either side of the subject. The helmet assembly was adjusted to the height of the subject's head and then clamped in position. The weight of the helmet assembly was carried on either the walker or the cart. In some conditions, the helmet assembly was free to rotate with side-to-side rotations of the subject's head, and in other conditions it and the head were clamped in alignment with the torso. The angular position of the helmet was recorded by a potentiometer feeding through an A/D converter into the computer.

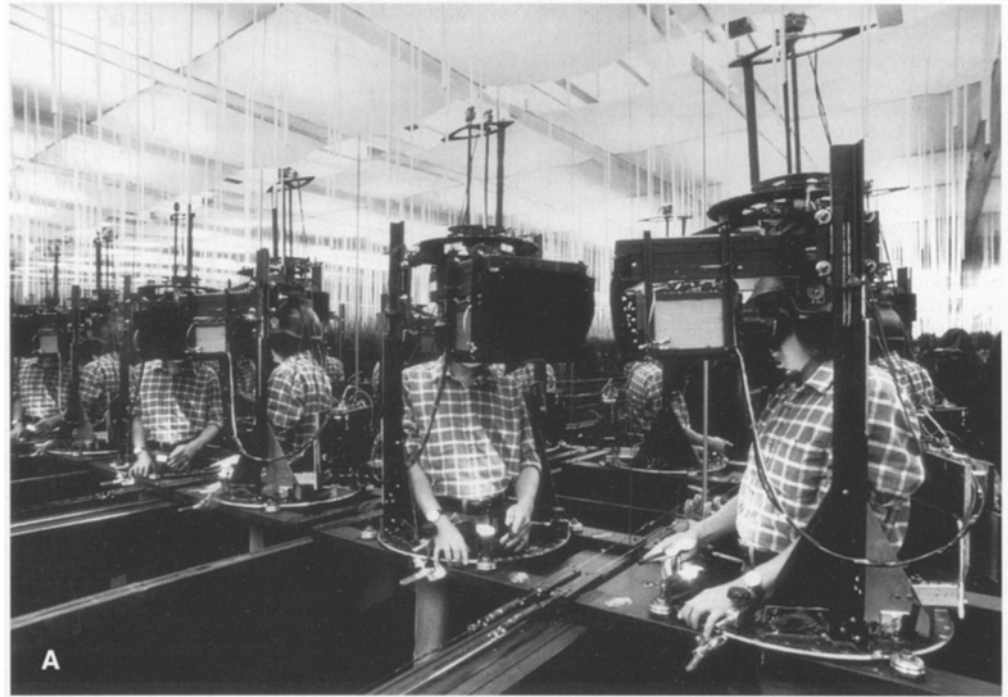
Each monitor received an input from a Panasonic video camera (5.5 cm long, focal length 7.5 mm). The cameras were mounted on stalks extending from the top of the helmet to 38 cm above the subject's head. The cameras were 6.7 cm apart center to center, a distance close to the average human interpupillary distance. Since the cameras were rigidly attached to the helmet, rotation or linear translation of the head resulted in simultaneous rotation or translation of the cameras. The roll, pitch, and vergence angles of the cameras were routinely adjusted so that calibrated displays viewed through the optical system fused into a single stereoscopic image. During visual conditions the subject saw a 60°-wide stereoscopic display of vertical rods extending to infinity in all directions.

Sound localization cues were masked by white noise transmitted to earphones inside the helmet.

Experimental conditions

Each subject was run in all five experimental conditions, three passive conditions in the cart and two active conditions in the walker. The passive conditions (visual, vestibular, and visual-vestibular) were run first using the cart. In the visual condition, the cart was accelerated (0.004 g) to a peak velocity of 0.2 m/s for 5.3 s, at which point it was decelerated to zero velocity over a further 5.3 s. These accelerations and decelerations are below the de-

Fig. 1 A The walker used to stimulate the motor-kinesthetic inputs involved in locomotion. **B** The cart used to provide passive visual or vestibular stimulation. The helmet-mounted optical system shown in the upper part of the photographs was the same for each device. Two cameras mounted above the subject's head provided video signals to two monitors directly in front of the head. As the cart or walker translated through the field of rods suspended from the ceiling, subjects viewed a 60° stereoscopic display consisting of radial optical flow due to the observer's linear motion and translational flow due to head rotation



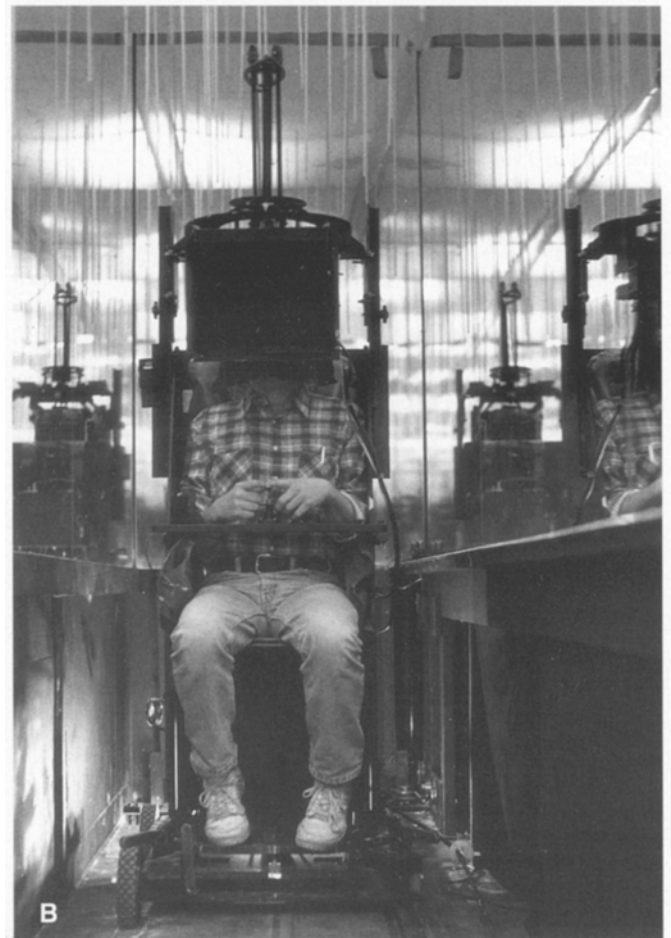
tection thresholds for the otoliths (Benson 1986; Guedry 1974; Gundry 1978). When no visual input was present, subjects detected cart vibration, but not linear translation. In the vestibular and visual-vestibular conditions, the cart was moved at a constant acceleration (0.05 g) to a peak velocity of 2.75 m/s for 5.3 s and then decelerated to zero over the last 5.3 s . This acceleration was 5–10 times higher than the detection threshold for the otoliths. In the vestibular condition, the lights were off and in the visual-vestibular condition the lights were on. In the active walking conditions, using the walker, the subthreshold acceleration profile was identical to that used in the passive visual condition. Subjects were constrained to walk at the speed of the walker. Walking trials were run in the dark, and visual-walking trials were run with lights on.

For each condition, the locus of heading was set at 0° , $\pm 5^\circ$, $\pm 10^\circ$, $\pm 15^\circ$, and $\pm 20^\circ$ with respect to the median plane of the body. These will be referred to as frontal-field trials. In non-visual conditions, an additional set of trials was run over the full 360° range (0° , $\pm 5^\circ$, $\pm 10^\circ$, $\pm 15^\circ$, $\pm 40^\circ$, $\pm 60^\circ$, $\pm 100^\circ$, $\pm 140^\circ$, 180°). Each heading angle was presented three times. The order of presentation of heading angles was randomized within a single session, and the order in which the different conditions were run was counterbalanced across subjects as much as possible. Cart and walking trials were not interspersed, as it was not practical to assemble the walker until all the cart trials were run.

For all conditions, subjects aligned an unseen rod with the heading. This is the rod-pointing task. In visual conditions, subjects also aligned a head-fixed fixation point with the visually defined heading locus by moving the head. This is the sighting task. In the walking condition, subjects also aligned the head with the heading direction. This is the head-pointing task.

Procedure

Subjects were secured in one of the two devices, and the height of the optical system was adjusted so that a black dot (0.5°) on the face of each monitor was centered on each eye. The dots could be binocularly fused to provide a fixation point at optical infinity. This minimized linear vestibulo-ocular eye movements, since eye movements are not necessary to maintain retinal image stability of objects at large viewing distances (Paige and Tomko 1991). Rubber flanges were positioned snugly against the face so that



light could not enter around the lenses. Black cloth was draped around the goggles to ensure that subjects could not pull away from the goggles to obtain visual orientation cues from the hallway.

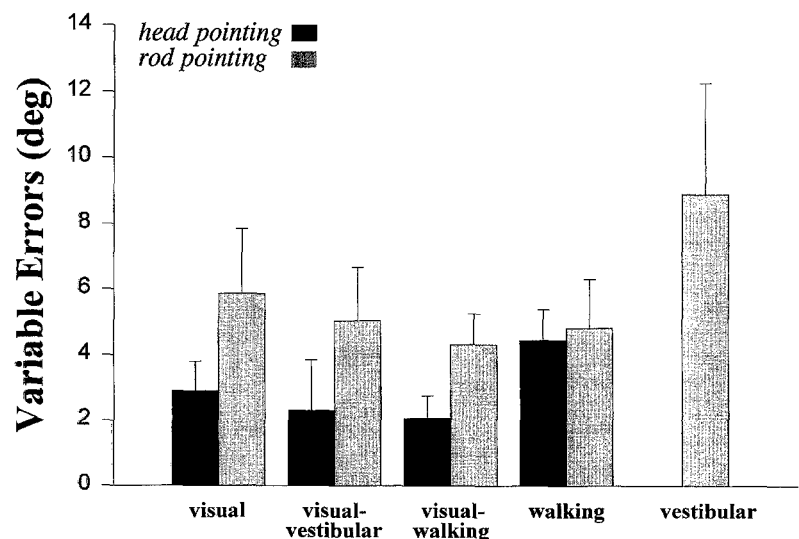
At the start of each trial, the helmet assembly was locked at 0° (head aligned with body), and subjects were rotated about the mid-body axis at subthreshold angular accelerations for approximately 40 s to ensure complete disorientation. During trials in which head rotation was allowed, subjects released a locking device on the head assembly and were thus free to move the head from side to side. In all visual conditions, subjects aligned the fixation point and the locus of zero parallax (sighting task) and then relocked the head in this position. In the walking condition, subjects aligned the head with the direction of self-motion in the dark (head-pointing task). In all of the head-free conditions, subjects performed the head-pointing task during the linear translation prior to performing the rod-pointing task. In the vestibular condition, the head was locked in line with the body to ensure that the otoliths received a linear acceleration stimulus in only one direction. In all conditions, subjects were then instructed to use both hands to align an unseen horizontal pointer with the heading direction (rod-pointing task) during the linear motion. The pointer was a rod 1 cm wide and 15 cm long mounted on a vertical shaft at waist level on the front of the cart or walker. The pointer was connected to a potentiometer calibrated with reference to the median plane of the body in the same manner as the head potentiometer. In non-visual conditions (walking and vestibular), run over the full 360° range of heading, the head was locked in line with the body (0°) and subjects made only rod-pointing responses.

In the frontal-field trials ($\pm 20^\circ$), subjects provided a verbal report of their heading direction once the cart or walker stopped moving. Three choices were given: straight ahead, forward to the right, and forward to the left. No feedback was provided during or after a trial, and subjects were asked not to pull away from the monitors to look at the hallway during or between trials. Subjects were given as many practice sessions with feedback as required to reach a criterion of three consecutive correct responses.

Measures and statistical analysis

At the end of each trial the angular head and pointer deviations from the true heading were recorded. Standard deviations of the three settings for each heading direction in each of the experimental conditions were used to determine head-pointing and rod-pointing variable errors (precision). The mean of the signed deviations of each of the settings from the true heading was used to calculate head-pointing and rod-pointing constant errors (accuracy). Values to the right of the true heading were assigned positive. Verbal heading reports were classified in terms of percentage correct. Constant and variable errors were subjected to within-subject analysis of variance. When a significant *F*-test result was obtained, post hoc analysis was performed using Tukey HSD tests.

Fig. 2 Mean variable errors ($n=5$) for each of the sensory stimulation conditions for both the head-pointing (sighting and head-pointing) and rod-pointing tasks collapsed across the nine heading directions ($0^\circ\text{--}\pm 20^\circ$). Note that the head-pointing task was not performed in the vestibular condition. Error bars represent 1 Standard deviation



Results

Precision

As shown in Fig. 2, sighting judgments were more precise ($F_{1,4}=38.72$, $P<0.005$) than rod-pointing judgments in the three conditions in which visual heading information was available (visual, visual-vestibular, and visual-walking). The variability of rod-pointing was twice as large as that of the sighting judgments (4.62° vs 2.31°). Analysis of variance of variable errors yielded a significant effect of conditions in which either the sighting or head-pointing task was performed ($F_{3,12}=5.17$, $P<0.05$). Post hoc comparisons revealed that the precision of sighting did not differ between conditions, but the precision of sighting in each of the visual conditions differed significantly from the precision of head-pointing performed in the walking condition ($P<0.05$). There was also a significant effect of conditions for the rod-pointing task which was performed in all conditions ($F_{4,16}=5.30$, $P<0.01$). Post hoc comparisons revealed that the three visual conditions and the walking condition were significantly different from the vestibular condition ($P<0.05$). There was no significant effect of heading angle for either the head-pointing or rod-pointing tasks over the frontal 40° range of heading. However, as shown in Fig. 3, in the non-visual conditions in which the experiment was run over the entire 360° range, rod-pointing precision did vary as a function of heading angle ($F_{17,68}=2.51$, $P<0.005$). There was no overall difference in precision between the vestibular and walking conditions, but there was a difference in precision as a function of heading angle. Data from leftward and rightward headings did not differ and were pooled. In the vestibular condition, rod-pointing became less precise as the angle between the median plane of the body and the heading direction increased to 90° , but precision improved as the body angle approached the position in which the subject was moving straight back. In the walking condition, rod-pointing precision was similar for headings up to 20°

Fig. 3 Mean variable pointing errors ($n=5$) for the walking and vestibular conditions for each heading angle. Variable errors represent the mean of the standard deviations of the three settings for each sensory condition and heading angle. Left- and rightward pointer settings did not differ significantly and have been pooled

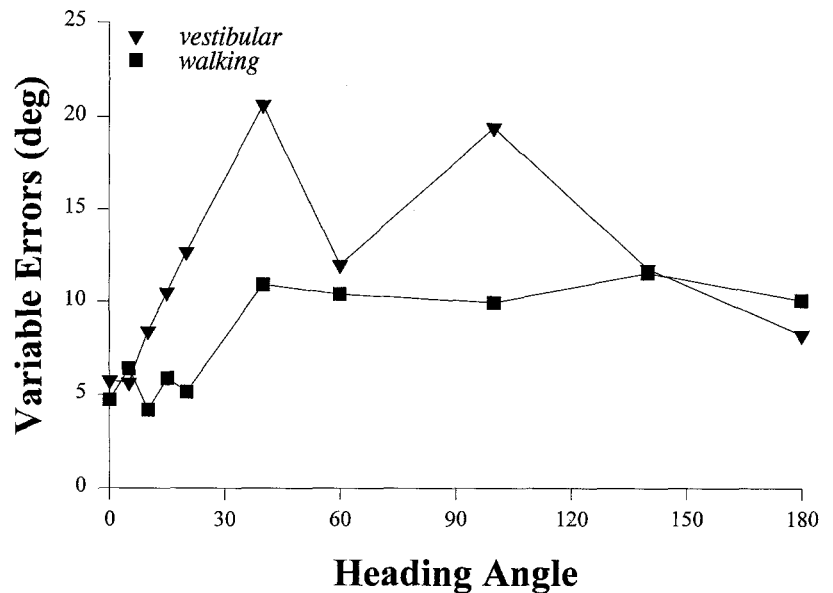
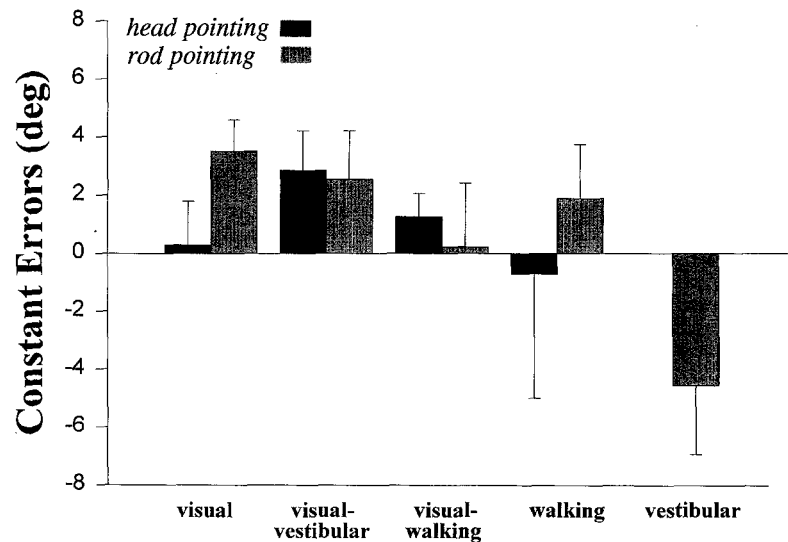


Fig. 4 Mean left-right constant errors ($n=5$) for the head-pointing and rod-pointing tasks in each of the sensory conditions. Constant errors were calculated by taking the mean of the signed deviations from the true heading for the settings made for each heading



from straight-ahead, but performance declined after about 40°.

Accuracy

Two types of constant error occurred in this experiment. In all but one of the sensory stimulation conditions, subjects judged their heading to be to the left or to the right of the actual heading for both leftward and rightward directions. These left-right constant errors are shown in Fig. 4, collapsed over heading direction for each sensory stimulation condition. In the walking condition, in which the task was to align the head in the direction of motion in the absence of visual feedback, subjects underestimated their heading angle for both leftward and rightward headings, i.e., they set the pointer to the left of rightward headings and to the right of leftward headings (mean for all subjects and headings was 3.9°). These midline errors (pointing or sighting under or overshoots relative to

the body midline) were very small for all other conditions.

The main effect of conditions was significant for both the combined sighting (visual cues available) and head-pointing (no vision) tasks ($F_{3,12}=3.85$, $P<0.05$) and for rod-pointing ($F_{4,16}=3.95$, $P<0.05$) tasks. The accuracy of sighting in the visual-vestibular condition was significantly different from the accuracy of head-pointing in the walking condition ($P<0.05$). There was a significant difference in the accuracy of rod-pointing between the vestibular and walking conditions and between the visual condition and the visual-walking and vestibular conditions ($P<0.05$). While left-right head-pointing errors were significantly larger in the visual-vestibular condition than in the walking condition, a larger response bias was actually observed in the head-pointing task in the condition in which subjects walked in the dark. Subjects underestimated the extent of their head turn for both rightward and leftward headings. This produced errors of opposite signs for each direction which effectively can-

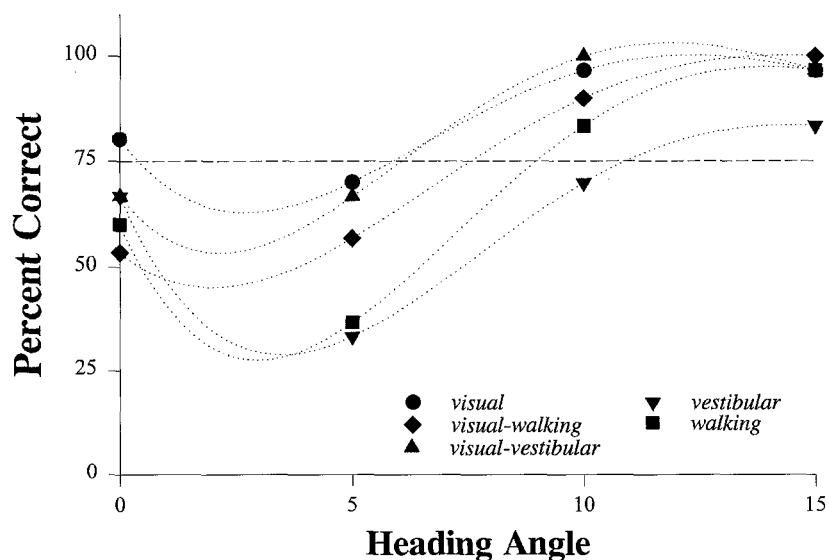
celled each other. If the undershoots obtained for each direction are signed consistently, the constant head-pointing errors were actually larger (3.9°) in the walking condition than the left-right head-pointing errors obtained in the visual-vestibular condition. The direction of left-right errors was to the right (positive values) of the heading in all but the vestibular rod-pointing task and the walking head-pointing task, in which the errors were to the left of the heading.

There was a significant interaction between heading angle and conditions for the head-pointing task ($F_{24,96}=2.34$, $P<0.005$). The head-pointing constant errors varied as a function of heading angle ($P<0.05$) only in the walking condition. In this condition, subjects did not make larger head movements as the heading angle increased, and hence errors became progressively larger.

Percent correct verbal responses

The percentage of correct verbal responses is shown in Fig. 5. A response was correct if the subject correctly indicated whether the heading direction was to the right or left or straight-ahead relative to the mid-body axis. In all stimulus conditions, the percentage of correct responses was higher for the straight-ahead position than for the 5° heading angle and increased at larger heading angles. Performance was near perfect for all but the vestibular condition at 15° . Heading thresholds were determined using a curve fitting procedure to estimate the smallest angle for which verbal heading judgments were correct on 75% of the trials. Performance was above threshold for the straight-ahead position only for the visual condition, but remained above chance in all conditions. At 5° , performance dropped to near chance levels (33%) in the two non-visual conditions. The 75% thresholds were as follows: visual 5.5° , visual-vestibular 5.7° , visual-walking 7.2° , walking 8.7° , and vestibular 11.4° .

Fig. 5 Percentage of correct verbal heading reports in each sensory condition. The 75% correct level is indicated by the dashed horizontal line. Chance performance is 33%



Discussion

The present experiment was performed to elucidate the relative contributions of multisensory inputs to the perception of heading direction. Our measures of performance were chosen to reflect the reference system used by each sensory modality. In the head-pointing task with lights on (sighting task), subjects rotated the head to align a fixation point with the locus of zero parallax in the optical flow field. In the head-pointing task with lights out, subjects aligned the median plane of the head with the heading perceived non-visually. In the rod-pointing task, subjects aligned an unseen pointer with the heading, perceived either visually or non-visually. The accuracy and precision of performance were quantified by measures of constant and variable errors, respectively. Our results indicate that during passive motion in which only visual cues were available, sighting was superior to rod-pointing. However, rod-pointing was more accurate than sighting when combined visual-walking information was available in the active-motion condition.

These results reinforce the fact that each sensory system codes information about the direction of self-motion with reference to an independent coordinate system. For example, the locus of zero parallax in the optical flow specifies heading in retinal coordinates. If the locus of heading happens to be imaged in the visual periphery, subjects should have no difficulty turning the eyes to foveate the image of the zero-parallax locus. In our sighting task, subjects fixated a target spot fixed to the head and simply rotated the head until the spot was superimposed on the locus of zero parallax. Information about the position of the eyes was not needed because subjects fixated a target attached to the head. With well-defined visual stimuli, this task should be performed as precisely as a vernier acuity task. When only visual information was available, sighting judgments were accurate to within $18'$ of arc, and precision was within 3° . Thus, accuracy in the sighting task was much better than the 3.7°

which Cutting et al. (1992) calculated would be required to avoid collisions with objects when moving at a speed of 2 m/s, a speed considerably higher than the 0.2 m/s in the visual condition of the present experiment. Sighting precision was well below the level of vernier acuity, but performance was limited by the low resolution of the monitors, by the variability of alignment of rods with the heading direction, and by confusion between a number of overlapping rods in the neighborhood of the locus of zero parallax (crowding, see Westheimer and Hauske 1975). In a vernier task, there are only two well-defined and spatially separated lines. Cutting (1986) has reported that errors in judging heading decline when visual field elements are arranged regularly, rather than randomly, as in the present experiment.

Pointing with an unseen arm to a visually defined heading and sighting are very different tasks. Since the arms that adjust the rod are attached to the torso, subjects must be aware of the orientation of the eyes in the head and of the head on the torso. In the visual condition, variable pointing errors were twice as large as variable sighting errors, and constant pointing errors were 12 times larger than constant sighting errors. The motor-kinesthetic system stimulated by walking is capable of directly encoding the orientation of the body relative to the motion path, and the positions of the eyes or the head need not be known. Our results, however, show only slight, non-significant improvements in rod-pointing accuracy and precision in the walking condition in the dark relative to the visual condition. If subjects were allowed to view the heading while walking, pointing accuracy was significantly better than that in the visual condition (0.23° vs 3.5°). Thus, combined visual and motor inputs facilitate pointing judgments relative to unimodal stimulation. We expected that motor-kinesthetic input from walking would alone provide enough information to allow subjects to point in the direction of motion. However, this input does not provide the requisite resolution for highly accurate pointing. Body orientation had to be deviated almost 9° from the motion path before subjects could consistently report their direction of motion. Heading thresholds were 60% lower in the visual condition. Thus, the visual system is a higher resolution system and allows the most accurate guidance of self-motion.

It is clear from the present experiment that vestibular inputs are not necessary for accurate judgments of heading, since rod-pointing and sighting judgments were reasonably accurate and precise during combined visual-kinesthetic stimulation when subjects moved at subthreshold accelerations. If otolithic contributions were necessary for heading judgments, we would be lost at subthreshold accelerations and during constant velocity motion. The otoliths may, however, contribute to the perception of the direction of body motion during the accelerative phases of self-motion, or when either visual or motor cues are absent. However, the significantly higher constant and variable rod-pointing errors in the vestibular condition in the dark indicate that the vestibular system is significantly inferior to both the visual and motor-

kinesthetic systems in specifying the direction of motion. A possible criticism of this experiment is that pointing does not adequately assess vestibular performance, since the vestibular system senses the direction of head, not of body acceleration. In the absence of head-on-body information, subjects should not be able to make accurate rod-pointing responses. Subjects were not allowed to move their heads in the vestibular condition, as this would have stimulated the semicircular canals and otoliths and changed the otolithic stimulus. However, we argue that the pointing task is a useful measure of the directionality of the vestibular system if the orientation of the head on the body is known, because knowing the direction of head motion can then be used to derive the direction of body motion and thus support an accurate pointing response. Since a major function of the vestibular system is to maintain postural stability, it must have access to information about the orientation of the head on the body with respect to gravity. If this were not the case, the vestibular system would not be able to maintain posture when the head is turned. Since postural stability is maintained in the presence of horizontal head turns (Fox and Paige 1991) and during head tilt (Diener et al. 1986), vestibular signals must be interpreted with reference to the orientation of the head on the body. We also obtained similar results from analysis of the verbal reports of heading. In the vestibular condition, subjects could consistently report heading direction only when the head and body were turned more than 11° relative to the heading, and perfect performance was obtained only when the angle between the subject's median plane and the heading exceeded 100° . This heading threshold was twice that obtained in the visual condition.

Vestibular inputs also did not augment heading judgments when vision was available. While subjects showed a slight, non-significant improvement in sighting and rod-pointing precision and in rod-pointing accuracy in the visual-vestibular condition relative to the visual condition, the percentage of correct verbal responses was unchanged. Sighting accuracy was actually worse in the visual-vestibular condition than in the visual condition, even though the rate of optical flow was higher in the visual-vestibular condition, since the visual condition was run at accelerations below vestibular threshold. Increased rates of optical flow have been shown to facilitate judgments of heading (Warren et al. 1989). In fact, subjects in our experiment did report that the locus of zero parallax was easier to identify in the visual-vestibular condition than in the visual condition. Ahumada (1983) conducted a study in which subjects identified the instantaneous aimpoint of an aircraft landing on a runway and similarly found that faster optic flow reduces accuracy, despite improved discriminability. The reason for this bias is unclear. Perhaps the more noticeable flow asymmetry that occurs when the head is not aligned with the locus of zero parallax was heightened in the faster visual-vestibular condition, resulting in a sighting bias. Even if the faster visual flow did not facilitate sighting, the presence of vestibular stimulation should have enabled sub-

jects to move the head in the direction of motion, even when visual stimulation was absent.

These results suggest that vestibular inputs cannot, by themselves, be used to determine the direction of self-motion. However, vestibular inputs may still play a role in heading perception under some circumstances. Vestibular inputs may be critical in conditions of high spatial uncertainty. For example, if observers become completely disorientated, vestibular cues could at least enable them to distinguish between forward, backward, and sideways trajectories. This may be sufficient to drive the appropriate gaze adjustments to bring vision into its optimal operating range in order to make an accurate final judgment. Physical limitations of the apparatus prevented us from using linear accelerations over 0.1 g. Perhaps the vestibular system operates with greater precision and accuracy at higher levels of acceleration, although this seems unlikely in view of the fact that we normally do not accelerate at levels higher than 0.1 g.

These findings emphasize the importance of the dependent measure used to assess performance. Several studies of visual heading have reported that humans cannot use information in the optical flow field to accurately determine their heading direction (Ahumada 1983; Johnston et al. 1973; Llewellyn 1971). A major reason for poor performance may be that, in these experiments, subjects used a hidden pointer or one positioned only after the display stopped moving, so direct visual feedback was absent. Since pointing is not accurate without visual feedback, it is not surprising that performance was relatively poor in these studies. Warren et al. (1988) and Cutting (1986) have shown that humans can verbally report heading direction with an accuracy of 1°.

During self-motion, several sensory systems work in concert to signal the magnitude and direction of self-motion. We have assessed the basic sensitivity of each. Our results suggest that each of the senses plays a different role in identifying and guiding locomotion. Vision can be used to accurately identify the heading in oculocentric coordinates, but in order to point or walk toward that heading, additional information is required from proprioceptors in the eyes, neck, and legs. Motor-kinesthetic information from the legs during walking in the dark at subthreshold accelerations or at constant velocity allows us to point in the direction of heading with slightly less accuracy and precision than the visual system. Vestibular information during passive acceleration in the dark allows for the least precise and accurate performance.

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