The perception of heading during eye movements

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WHEN a person walks through a rigid environment while holding eyes and head fixed, the pattern of retinal motion flows radially away from a point, the focus of expansion (Fig. 1*a*)[1,2]. Under such conditions of translation, heading corresponds to the focus of expansion and people identify it readily[3]. But when making an eye/head movement to track an object off to the side, retinal motion is no longer radial (Fig. 1*b*)[4]. Heading perception in such situations has been modelled in two ways. Extra-retinal models monitor the velocity of rotational movements through proprioceptive or efference information from the extraocular and neck muscles and use that information to discount rotation effects[5]. Retinal-image models determine (and eliminate) rotational components from the retinal image alone[6–12]. These models have been tested[13,14] by measuring heading perception under two conditions. First, observers judged heading while tracking a point on a simulated ground plane. Second, they fixated a stationary point and the flow field simulated the effects of a tracking eye movement. Extra-retinal models[5] predict poorer performance in the simulated condition because the eyes do not move. Retinal-image models[6–12] predict no difference in performance because the two conditions produce identical patterns of retinal motion. Warren and Hannon[13,14] observed similar performance and concluded that people do not require extra-retinal information to judge heading with eye/head movements present, but they used extremely slow tracking eye movements of 0.2–1.2 deg s^{-1}; a moving observer frequently tracks objects at much higher rates (L. Stark, personal communication). Here we examine heading judgements at higher, more typical eye movement velocities and find that people require extra-retinal information about eye position[15] to perceive heading accurately under many viewing conditions.

Experiment 1 reproduced the conditions of Warren and Hannon[13] except we used constant, faster rotation rates (actual or simulated) from 0 to 5 deg s^{-1} and a vertical axis of rotation. In addition, the fixation point was positioned slightly above the horizon and moved independently of the ground plane. At the end of a simulus presentation, seven vertical lines appeared and the observers indicated the one that corresponded most closely to the perceived heading. As in the experiments of Warren and Hannon[13,14], real and simulated eye movement conditions produced identical patterns of retinal image motion, so retinal-image models predict similar performance in the two conditions.

Figure 2 shows that both observers responded very differently

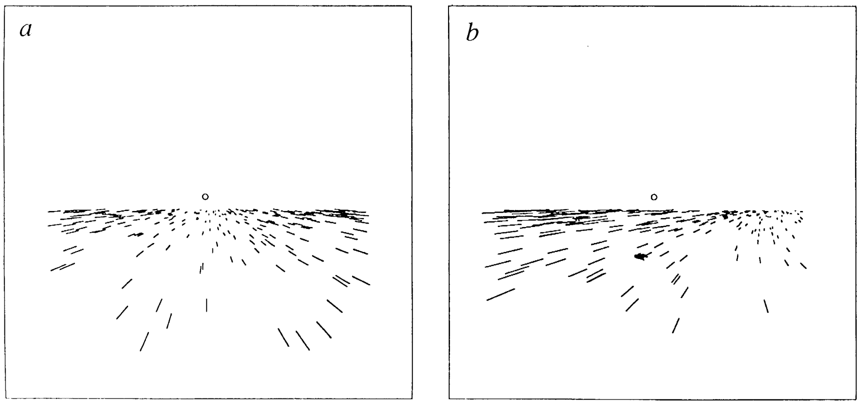


FIG. 1 Optical flow fields for an observer moving across a ground plane. *a*, Flow field for a translational movement; the observer has moved forward while holding the eye and head fixed. The circle marks the focus of expansion, which corresponds to the observer's direction of motion. *b*, Flow field for translation plus rotation; the observer has again moved forward while tracking an object moving from left to right. As before, the circle marks the observer's heading. In the real eye movement condition of experiment 1, the flow field on the display screen resembled the one in *a* and the flow field on the retina resembled the one in *b*; in the simulated eye movement condition, the flow fields on the display screen and retina resembled the one in *b*.

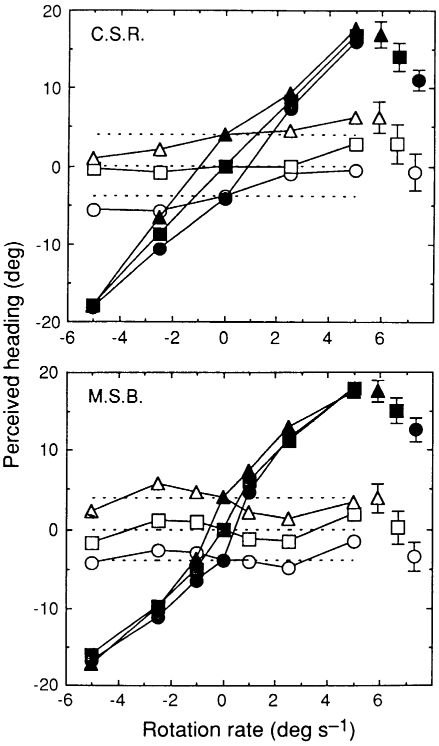


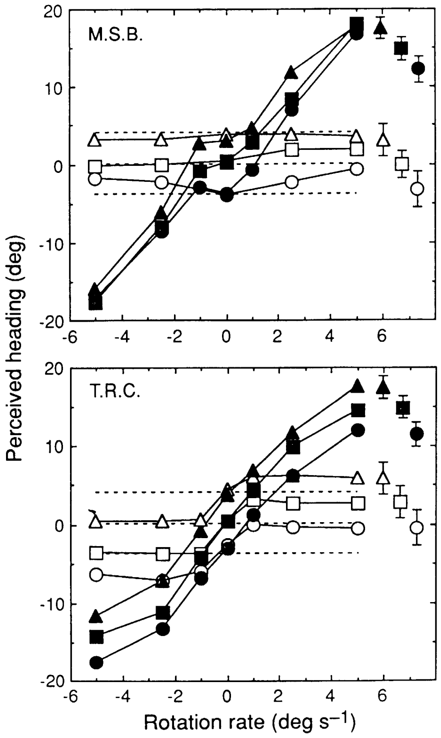
FIG. 2 Results of experiment 1: heading judgements for motion across a ground plane with real or simulated eye movements. Dot motions corresponded to the optical flow produced when an observer walks across a flat surface at a speed of 190 cm s^{-1}. Simulated eye height was 160 cm. The ground plane was truncated at a distance of 3,730 cm. Dots were distributed randomly on the plane with an average density of 0.6 dots per m^2; roughly 220 dots were visible at the beginning of a trial. The stimulus subtended 30 × 30 deg at the 30-cm viewing distance. Viewing was monocular. The fixation point was 2.5 deg above the truncated horizon. In the real eye movement condition, observers C.S.R. and M.S.B. tracked a point moving horizontally at 0, ±2.5 or ±5 deg s^{-1}. In the simulated eye movement condition, observers fixated a stationary point and the flow field simulated the effects of horizontal eye movements at 0, ±2.5 and ±5 deg s^{-1}. In addition, observer M.S.B. was tested for rotation rates of ±1 deg s^{-1} in both conditions. At the beginning of the motion sequence, the fixation point (which actually began moving 200 ms earlier) was always at the center of the display, so at that instant the heading was always towards or 4 deg to the left or right of fixation. These eccentricities were identical across the real and simulated conditions. At the end of each, 1,250-ms trial, observers indicated which of 7 target lines, equally spaced 4 deg apart, was closest to the perceived heading; the target lines were 2 deg apart when the rotation rate was ±1 deg s^{-1}. Each condition was presented 20 times. The two panels show the results separately for two observers; others yielded similar data. Open and filled symbols represent responses in the real and simulated eye movement conditions, respectively. Circles, squares and triangles represent the responses for headings of −4, 0 and 4 deg. Error bars on the right show twice the average standard deviation for each heading.

in the two conditions: they judged heading accurately in the real eye movement condition and very inaccurately in the simulated condition. When they moved their eyes, the average errors were 1.5 and 1.9 deg for rotation rates of 2.5 and 5 deg s^{-1}, respectively; when they did not, the errors increased to 9.8 and 17.3 deg. The results suggest that humans require proprioceptive or efferent information from the extra-ocular muscles to judge heading accurately in the presence of rotations. Most retinal-image models[6-8,11] fail to predict the large inaccuracies in heading judgements seen in the simulated condition.

The retinal-image models require depth variation in the scene in order to separate translational and rotational flow[6-12]. Consequently, they cannot find a unique solution for translation relative to a frontoparallel plane. To see if human observers have similar difficulties, we repeated experiment 1 using a frontoparallel plane instead of a ground plane. In experiment 2, both observers again made accurate heading judgements in the real eye movement condition (average errors were 1.1 and 1.5 deg at 2.5 and 5 deg^{-1} s, respectively) and inaccurate ones in the simulated condition (average errors were 9.1 and 16.8 deg). Thus, when extra-retinal information about eye position is available, observers make accurate heading judgements in a situation in which retinal-image models[6-12] do not.

Because our results conflict with those of Warren and

FIG. 3 Results of experiment 3: heading judgements for observer motion (observers M.S.B. and T.R.C.) through a rigid, 3-dimensional cloud of dots with real or simulated eye movements. The motion of the dots in the display simulated translation at 50 cm s^{-1} through a cloud with dots at distances of 0–3,730 cm. Roughly 615 dots were visible at the beginning of the trial. The fixation point was a member of the rigid cloud and was positioned 5 deg to the left or right of the heading at the beginning of the motion sequence. Placing it at distances of 10^7, 310, 162 and 112 cm produced average rotation rates 0, 1, 2.5 and 5 deg s^{-1}, respectively. All other display and procedural parameters are identical to those in experiments 1 and 2. The open and filled symbols represent heading judgements in the real and simulated eye movement conditions, respectively. Circles, squares and triangles represent judgements for headings of −4, 0 and 4 deg. The top, middle and bottom horizontal dotted lines show the true headings of −4, 0 and 4 deg, respectively.



Hannon[13,14], we performed an exact replication of their experiment. As they reported, observers made reasonably accurate judgements independently of whether actual or simulated eye movements generated the rotational flow. Thus, with very slow rotations and/or with the tracked object fixed to the surface, observers can judge heading accurately with simulated eye movements.

Experiment 3 tested which of these two differences in the experiments was critical. The displays simulated translation through a rigid, three-dimensional cloud of dots. The fixation point was a member of the cloud, but we varied rotation rate by placing it at different simulated distances. Figure 3 shows that heading judgements were accurate in the real eye movement condition and poor in the simulated condition. Thus, rotation rate rather than the attachment of the fixation point to the simulated three-dimensional object appears to be the critical variable. Interestingly, judgements in the simulated condition were fairly accurate at 1 deg s^{-1} so observers can judge heading well from retinal image information alone when the simulated rotation is slow[13,14].

Although these experiments were done in a dark room, the edge of the display screen was just visible. Perhaps observers did not interpret the rotational flow in the simulated condition as a consequence of eye movements because the screen edge did not move relative to the fixation point. We repeated experiments 1 and 3 under conditions in which only the dots were visible and got the same results. Therefore this possible artefact cannot explain the erroneous judgements in the simulated eye movement condition.

Observers badly misperceived their heading in the simulated eye movement conditions. When presented the frontoparallel plane of experiment 2, observers thought they were heading towards the position of zero flow in the display. With the ground plane of experiment 1, they thought they were moving along a curvilinear path in the direction of the simulated eye movement. In neither case did they perceive the specified linear motion plus horizontal eye movement. The erroneous percept in the simulated condition of experiment 1 reflects the fact that the pattern of retinal motion closely resembles the pattern created by motion on a curvilinear path[16]. Presumably, such misperceptions do not occur in the real world with observer-initiated locomotion because extra-retinal information helps distinguish linear motion plus eye/head rotation from curviliner motion. We have shown that humans require extra-retinal information about eye position to perceive heading accurately in the presence of rotation rates greater than 1 $\deg^{-1}$ s. These rates occur when an observer fixates a nearby object that is not along his or her heading, or fixates a moving object. ☐

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