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Judgements of Heading

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To study the contribution of vision to the perception of ego-motion, one often dissociates the retinal flow from the corresponding extra-retinal information on eye, head and body movement. This puts the observer in a conflict concerning the experienced ego-motion. When the retinal flow of a translating and rotating eye is shown to a stationary eye, observers often perceive ego-motion on a curved path. In contrast, when they receive the same retinal flow with a rotating eye subjects correctly perceive the simulated rectilinear ego-motion. Thus, different visual representations of ego-motion gain precedence when using the conflict stimulus and when using conditions in which the visual and extra-retinal information accord. Because the flow-pattern can be decomposed in many different ways, the brain could represent the same flow-pattern as a rotation about an axis through the eye plus rectilinear ego-motion or a rotation about an axis outside the eye (corresponding to circular ego-motion) plus motion towards the axis of rotation. The circular motion path percept minimizes the conflict with extra-retinal eye movement information if the axis of rotation is placed at the fixation point. However, in simulated eye rotation displays subjects also perceive illusory motion in depth of the stationary fixation point. This illusory motion is argued to reflect the ego-centric decomposition. Errors are small when subjects judge their heading on the basis of this illusory motion. For the same displays much larger errors are made, however, when subjects judge heading from the entire motion pattern, which often results in perceived ego-motion on a curved path. This indicates that subjects can choose between two different representations of ego-motion resulting in different perceived heading. Copyright © 1996 Elsevier Science Ltd.

Optic flow   Heading   Motion   Attention

INTRODUCTION

Recently, a number of studies have addressed the question whether humans can perceive their direction of heading purely on the basis of retinal image motion or whether there is a need for extra-retinal signals. This question is of theoretical, as well as neurophysiological interest because its answer gives constraints on the sort of visual motion processing that occurs in the brain. Moreover, it bears on the more general question how the brain transforms retinal signals into a format that is appropriate for merging with information from other sensory modalities like vestibular and kinaesthetic information.

There is general agreement that eye movement signals are essential for accurate heading perception under conditions where the visual motion pattern is ambiguous, like observer motion towards a fronto-parallel plane (Rieger & Toet, 1985; Warren & Hannon, 1990). However, for more natural conditions like motion across the ground plane, conflicting results have been obtained. In the prototypical experiment observers view a motion display that presents the retinal motion of an eye that is moving along a straight line across the plane while simultaneously rotating so as to fixate a point on the plane (Warren & Hannon, 1988, 1990). Because the eye rotation is simulated in the display, the subject's eye does not move. Thus, the visual information concerning the rotation is present but the extra-retinal information related to the eye movement is absent. Figure 1 shows four snapshots of the motion pattern presented on the screen. When the fixation point (which is located slightly to the right of the observer's simulated path) is distant, the motion pattern is radiating outward from the direction of heading (H). This condition corresponds to Gibson's focus of outflow hypothesis for heading perception (Gibson, 1966). As the fixation point is approached, the simulated rotation increases and the motion pattern contains an increasingly faster rotational component which displaces the centre of the pattern from H to the fixation point (F). Thus, to perceive H the observer needs to discount the rotational component in the retinal flow. Can subjects do so on the basis of purely visual information?

Warren and Hannon (1988, 1990) concluded that humans can. They found accurate discrimination of heading direction (about 1.5 deg). Accuracy was not significantly different for conditions in which the subjects

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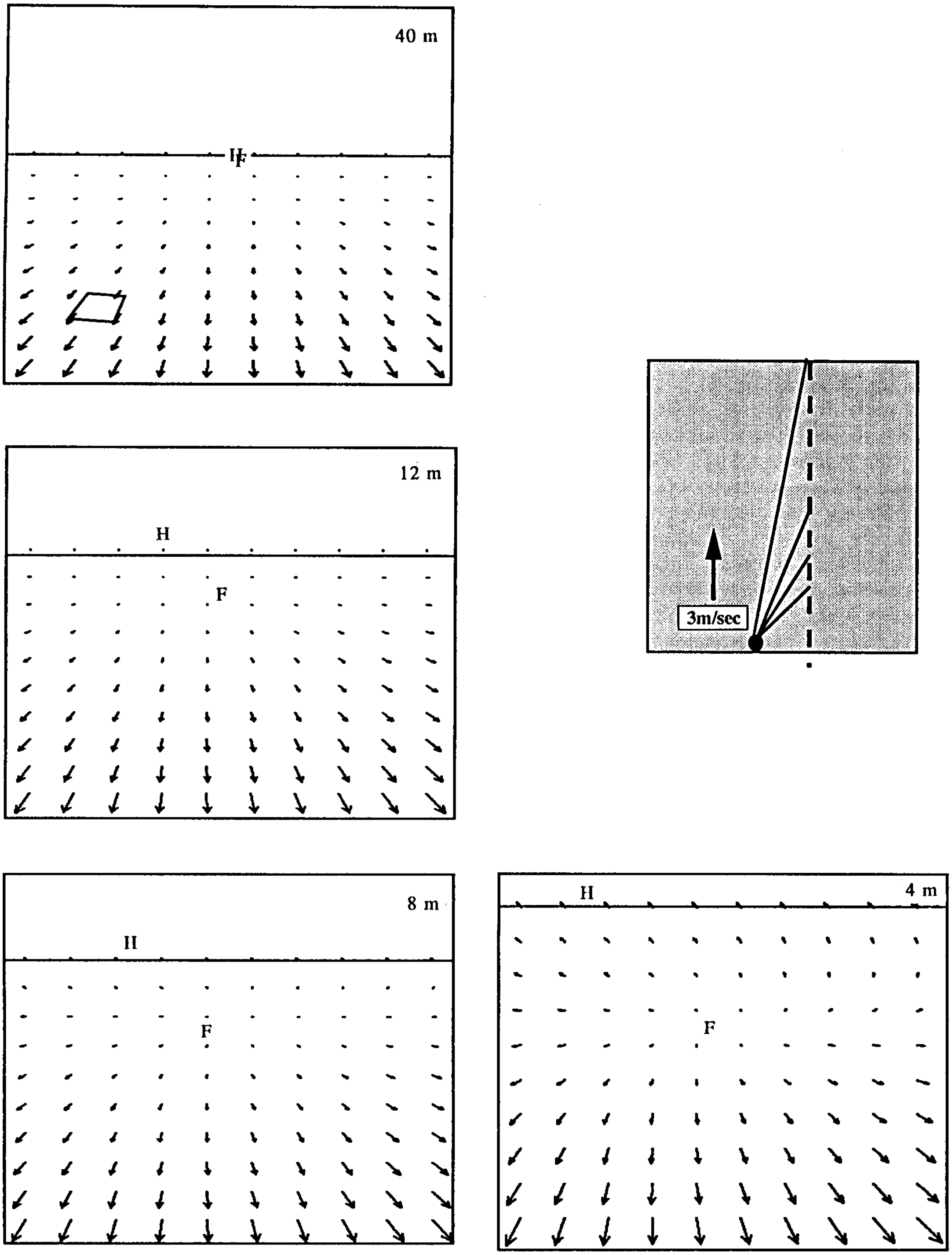

FIGURE 1. Four snapshots of the retinal flow of an observer, moving past the point F in the plane with a constant velocity (3 m/sec). F is located to the side of the heading direction H. The fifth panel shows a top view of the simulated ego-motion. Each snapshot shows the instantaneous flow-field for a particular distance to the fixation point, which is indicated in the upper right corner. Clearly, while approaching the rotational velocity increases. This causes a change in the structure of the flow-field from radial and centred on the heading direction (40 m) to spiralling and centred on the fixation direction (4 m).

made eye rotations to fixate a point of the simulated environment, or conditions that simulated these rotations.

In a series of studies, Royden and colleagues (1992, 1994) came to the conclusion that, in general, humans cannot discount eye rotations visually. When the simulated eye rotation was small (similar to Warren and Hannon's (1988, 1990) study, i.e. <1.5 deg/sec), they found accurate heading perception in their subjects. Thus, Royden *et al.* concluded that heading perception requires extra-retinal information on the eye movement, except perhaps for slow rotations.

van den Berg investigated the robustness of heading perception when the flow field was corrupted by noise. In some experiments the noise consisted of incoherent motion of a fraction of the points (van den Berg, 1992). In other studies the noise consisted of a noise velocity component that was added to the flow of *each* point in the simulated environment. Subjects could tolerate significant amounts of noise in both cases even when the egorotation was simulated. Performance depended on the presence of depth cues from other sources than the optic flow, like depth from perspective (van den Berg & Brenner, 1994a) or stereoscopic depth (van den Berg & Brenner, 1994b). Absence of such cues significantly reduced the noise tolerance. Simulated eye rotation could exceed 5 deg/sec (van den Berg & Brenner, 1994a,b), yet, even for noisy displays subjects were able to perceive the direction of heading, albeit with reduced accuracy.

What is the cause of the conflicting outcomes? Procedures as well as displays showed slight differences in the different studies. These differences were analysed by Royden *et al.* (1994) for their potential to explain the different outcomes. On the basis of their experiments they rejected differences in the simulated ego-translation as the cause. They also rejected van den Berg's suggestion (van den Berg, 1993) that the use of a fixation point that moved independently of the environment in one study and the use of a point that was part of the rigid environment in another caused the difference. Royden suggested that van den Berg's (trained) subjects had used a special cue of which the relevance for normal heading perception may be limited: the alignment of a strip of motion vectors. This alignment only occurs for the flow-vectors between the fixation point and the destination point. The intersection of this strip with the horizon indicates the correct heading direction. Below I will refer to this strategy as the "horizon strategy". In correspondence with this idea her untrained subjects performed poorly for rotation rates of 2.5 or 5 deg/sec when this cue was removed as in the case of simulated motion through a cloud of dots.

For a number of reasons I believe that the use of the strip of aligned flow-vectors is not the right explanation for subjects' performance in van den Berg's studies. First, van den Berg (1992) using a similar paradigm, found heading discrimination thresholds of about 2 deg for average horizontal rotation rates up to about 3 deg/sec. Secondly, in a study of the noise sensitivity of heading perception, performance was in many cases accurate even when the noise component in each flow vector was of equal magnitude (but with random direction) as the unperturbed local flow vector (van den Berg & Brenner, 1994a). Obviously, such perturbation seriously disrupts the alignment of the flow-vectors, masking the proposed cue. Thirdly, van den Berg and Brenner (1994b) found accurate heading perception in two subjects (RG and EB, their Fig. 3) for simulated rotation and translation through a cloud. Noise resistance was best when the presentation contained stereoscopic depth, but for low noise levels little difference in performance was found for monocular and binocular presentations. Because in this case no horizon is visible the cue would be absent altogether.

Interestingly, Royden's subjects often perceived quite a different sort of self-motion than what was simulated. Rather than motion on a recti-linear track combined with an eye rotation, her subjects often reported that they saw themselves moving on a curved path. In a subsequent analysis Royden (1994) showed that the pattern of heading errors could be explained by assuming that the subjects had based their decision on the nearest visible point on the curved path. It is well known that the retinal flow has a similar structure for simulations of ego-motion on a curved path or for motion on a straight path combined with ego-rotation (Warren *et al.*, 1992). Royden suggests that extra-retinal information on the eye movement normally is used to distinguish between these two cases; when presented to a stationary eye, the perceived ego-motion is curved, but when presented to a moving eye the same retinal flow pattern leads to a percept of rectilinear motion. This begs the question, whether the simulated rotation display is indeed a valid method to analyse the performance of the visual system in representing the direction of heading. Because subjects confound the two types of motion pattern, we cannot decide on the basis of the heading errors whether the brain's visual representation of the heading direction is not accurate or whether an accurate representation exists, but that it is overruled by the curved ego-motion representation, because of the conflicting extra-retinal signals.

van den Berg and Brenner (1994a) reported a phenomenon that may shed some light on this question. Many of their subjects perceived a clear motion in depth of the fixation point in the simulated eye-rotation condition despite the fact that this point was stationary on the screen. Similarly, Warren and Hannon (1990) reported that their subjects could not distinguish between the simulated and the real eye movement conditions, suggesting that these subjects too perceived motion of the fixation point. Possibly, the induced motion in depth of the fixation point reveals the activity of the system that we are looking for: the visual representation of rectilinear heading combined with ego-rotation. If true, the induced motion of the fixation point would reflect the retinal flow after *visual* correction for the ego-rotation component. In this study I investigate this hypothesis. Using instructions that direct the subject's attention to the induced motion of the fixation point, I find much more accurate heading perception in six naive subjects than when they are asked to indicate the destination point in the display as judged from the entire motion pattern.

METHODS

Subjects

Six subjects (three males, aged 27–34 yr; three females, aged 29–48 yr) participated in this study. Subjects wore corrective spectacles or contact lenses during the experiments. One subject (AL) had previously participated in a few pilot experiments on the perception of heading. The other persons had participated in other types of psychophysical experiments (JP, WD, DL, RM and DE). All subjects were naive as to the hypothesis under study.

Procedures

Data were collected in two or three sessions, which lasted about 40 min at most. The subject was seated and his head stabilized with a chinrest and a forehead support. Computer-simulated motion sequences were dichoptically presented at a framerate of 120 Hz. Alternate frames were presented to the left and the right eye using spectacles with LCD-shutters, synchronized with the graphics display. All presentations provided stereoscopic depth information. At the viewing distance of 2 m the screen subtended 60 deg horizontally × 50 deg vertically.

Each session started with a calibration procedure, to determine the positions of the subject's eyes relative to the screen with a triangulation technique (see the Appendix). These positions were used to present the images in the right perspective for each eye. Subsequently, about 20 trials were done in which horizontal motion across the ground plane was shown. Only observer translation was simulated. Subjects pursued with an eye movement a red dot that was part of the simulated ground plane. Perceived heading in this *real eye movement* condition was used as a benchmark to interpret the bias and scatter in the subject's responses in the other conditions, which were presented subsequently, and which all involved *simulated* eye rotations. Subjects did not receive feedback in any of the conditions.

Stimuli

The simulated environment consisted of 256 randomly located white dots which were configured in a horizontal plane or in a cloud. The simulated world extended in depth from 1 to 20 m in front of the subject's eyes. In case of the cloud, the points were randomly located in the viewing frustrum, that was defined by the borders of an imaginary screen with dimensions 1.5 times larger than the actual screen and at the same viewing distance. This ensured that the majority of the points was visible throughout the motion sequence and that the horizontal and vertical boundaries of the simulated world remained invisible. One red dot served as a fixation point. This simulated point was in all experiments but the last located within a horizontal plane 0.675 m below the eyes, which was also the height of the simulated ground plane.

The first frame of the motion sequence was shown for 1 sec to acquire stable fixation of the red dot. Simulated ego-motion (speed 1.5 m/sec) was then shown for 2 sec. Simulated ego-rotation was variable and depended on the angle between the heading direction and the fixation direction. The last frame remained visible and a triangular pointer appeared in a random direction at the same simulated distance as the fixation point. Subjects adjusted the position of this stereoscopically presented pointer within the ground plane so as to indicate the perceived direction of heading. The trial was terminated by the subject's response (a mouse click). Between trials a blank white screen was shown for 1 sec to maintain a moderate level of light adaptation of the eyes.

The simulated translation was always along a straight line. In the real eye movement condition the fixation point appeared in a random direction on the screen at a simulated distance of 8 m. The initial direction of heading was randomly chosen but varied no more than 12.5 deg in direction with respect to the fixation direction. In the other conditions involving simulated eye rotation the fixation point always appeared at the midline of the screen. Its simulated initial distance was 5.5 m and the final simulated distance was about 2.5 m (some variation occurred depending on the simulated direction of heading). If the eye rotation were not simulated these distances would correspond to viewing directions of 7 and 15.1 deg below eye height. We chose a compromise position for the fixation direction of 9.6 deg below eye height. The range of heading directions was the same as in the real eye movement condition. These conditions contained simulated eye rotations up to about 7 deg/sec.

Instructions

The subjects were told that the first set of trials (in which the real eye movement condition was presented) served as a training procedure to familiarize them with the task. They were informed that ego-motion parallel to the ground was simulated and they were asked to indicate their perceived direction of motion relative to the plane with the pointer, when it appeared. No further instruction was given as to the sort of information to attend to.

Subjects never experienced vection when observing the displays, probably because the presentation time was too short for such percepts to build up. Yet, a clear impression of relative motion between the self and the simulated environment was experienced. When the simulated eye rotations were investigated, the subjects were told that the presented motion sequences could vary in direction as well as curvedness of the motion path and were given precise instructions concerning the information to use for their judgement.

In one condition they were asked to base their judgement of heading on the perceived motion in depth of the red fixation point, i.e., to estimate their self-motion relative to the fixation point. None of the subjects was aware that the motion of the red point was an illusion and all perceived it as rigidly attached to the simulated environment. They were asked to set the pointer at that location relative to themselves that they would have hit if they had continued their motion relative to the fixation point. If the perceived motion of the fixation point changed during the trial they should indicate the average direction.

In a second condition subjects had to indicate the position at the furthest visible distance in the display where they were to arrive if the motion would have continued. Thus, subjects indicated the destination point at the end of their perceived (curved or straight) path. In this case they were asked to set the pointer at that location which was perceived as located at the straight line between themselves and the perceived destination point. Subjects were told that no special attention should be given to the motion of the fixation point.

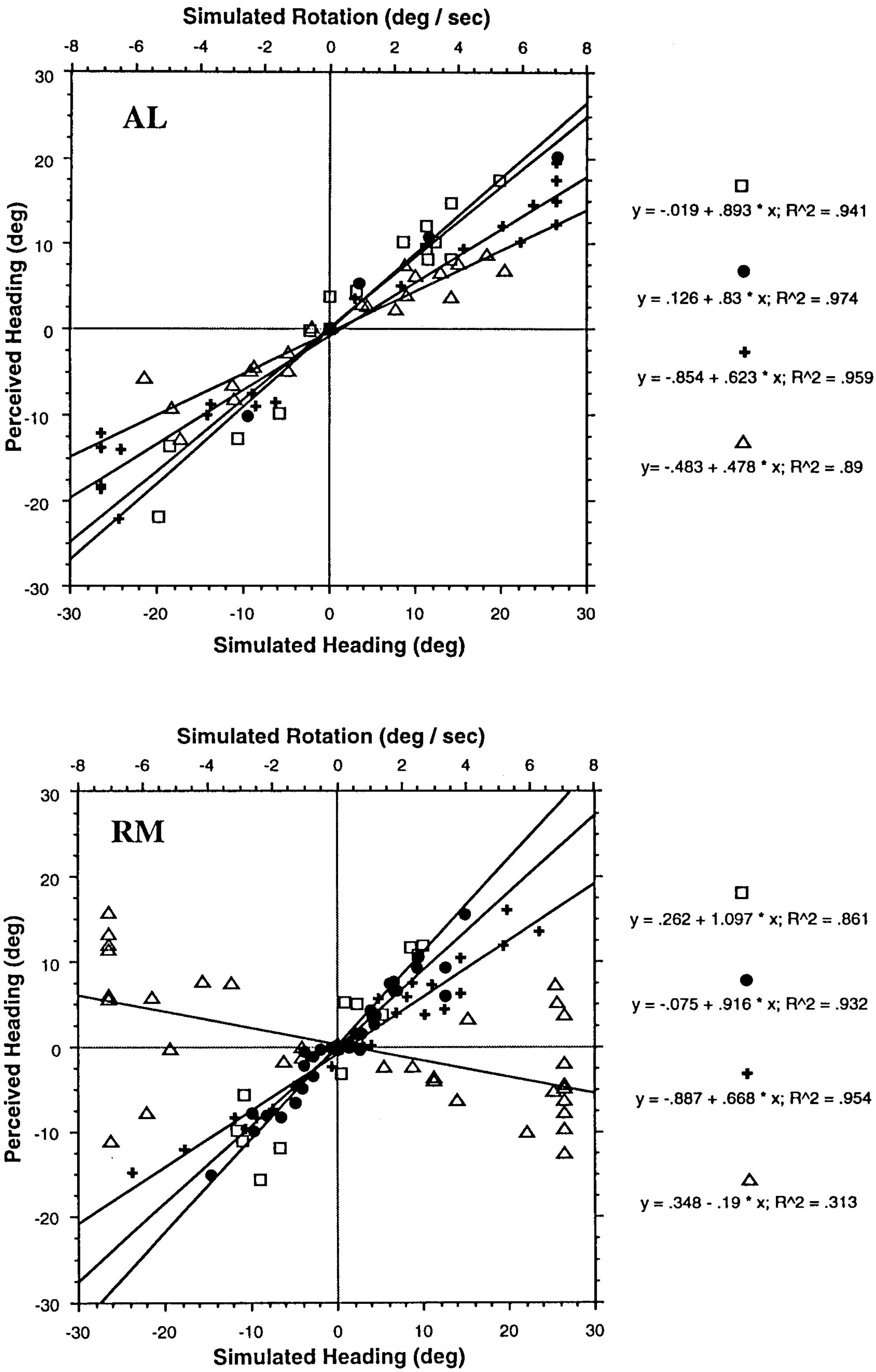

FIGURE 2. Perceived heading as a function of the simulated heading direction for two subjects (AL and RM). Both quantities are with reference to the fixation direction. The upper axis indicates the magnitude of the simulated eye rotation. Different symbols refer to different instructions and simulations. Four conditions are shown: (1) no instruction, simulated translation across the ground plane (□); (2) simulated translation and rotation, ground plane and the instruction to indicate the destination point at the horizon (△); (3) simulated translation and rotation, ground plane and the instruction to attend to the motion of the fixation point (●); and (4) simulated translation and rotation, cloud and the instruction to attend to the motion of the fixation point (+). Subject AL collected only a few data for the third condition (●) in the session whose data are shown. Full data for this condition were obtained in another session. The summary data shown in Fig. 3 reflect the result of that second measurement.

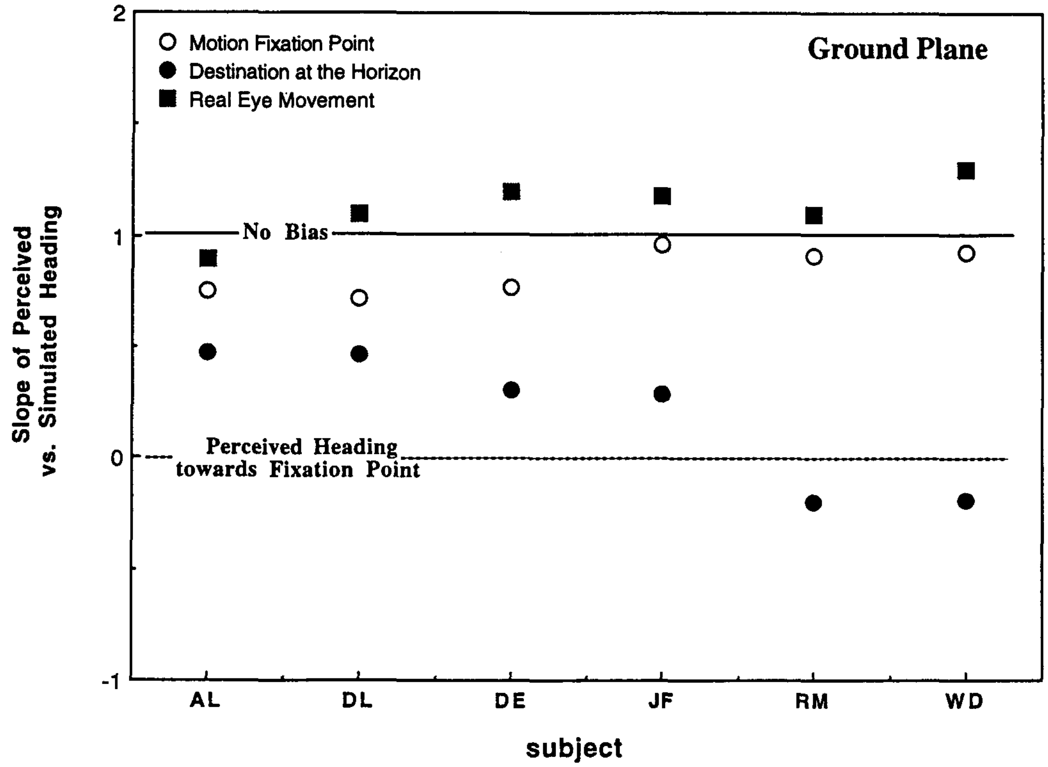

FIGURE 3. The slopes of the regression lines relating subjects' perceived heading to simulated heading across the ground plane are shown. Accurate heading perception (slope close to 1.0) was found in all subjects when a real eye rotation was made (■). For simulated eye rotations (○, ●) the bias in the perceived heading depended on the instruction: to indicate the destination at the far border of the simulated environment (●) or to judge heading on the basis of the motion of the fixation point (○).

In three subjects data collection was started with the first instruction (DE, JF and RM); in the other subjects (AL, DL and WD) the other instruction was used first.

RESULTS

Pointing responses of two subjects (AL and RM) are shown in Fig. 2. Perceived heading is indicated as a function of the simulated heading direction. Both quantities are indicated relative to the fixation direction at the end of the trial. Thus, a point at the origin of the graph indicates that the subject correctly perceived heading towards the fixation point. Each point in the graph indicates the result of one trial. When the points scatter along a straight line with slope 1.0, heading perception is unbiased. If all points were located close to the horizontal axis (slope = 0.0), perceived heading would be directed towards the fixation point irrespective of the simulated heading direction. Different symbols are for data with different simulations and instructions.

Clearly, both subjects correctly perceived the heading direction for a wide range (about 50 deg, lower axis) of simulated heading directions when a real eye movement was made. The slope of the regression line was close to 1.0 in both subjects. As indicated by the upper axis, corresponding average horizontal eye rotation could be as large as 7 deg/sec.

When the eye rotation was simulated subjects' performance strongly depended on the instruction that was given. When the subjects judged their direction of heading from the induced motion of the fixation point, I found only a small bias towards the fixation point of the perceived heading. Especially for simulated motion across the plane the bias was small; the slope exceeded 0.8. With the instruction to estimate the aimpoint close to the visual horizon, the subjects made much larger errors. The slope of AL decreased to 0.5. Subject RM systematically misjudged the location of the aimpoint even with respect to the fixation point. In many cases she perceived motion along a curved path towards a target to the left of the fixation point, whereas simulated aimpoint was to the right of the fixation point and vice versa. This is revealed by the negative slope. In both subjects, the scatter of pointing increased when they were asked to indicate the endpoint of their path rather than the heading direction as judged from the perceived motion of the fixation point.

As shown in Fig. 3, this pattern of results occurred in all subjects. The largest bias was found when subjects had to *indicate their destination at the furthest points in the display*. For this instruction idiosyncratic differences among the subjects were also largest. Bias was smallest in the subject who had previously participated in experiments on the perception of heading (AL), whereas the subject with the least experience in psychophysical experiments made the largest errors (RM).

Several subjects complained that indicating their destination point was a much more difficult task than

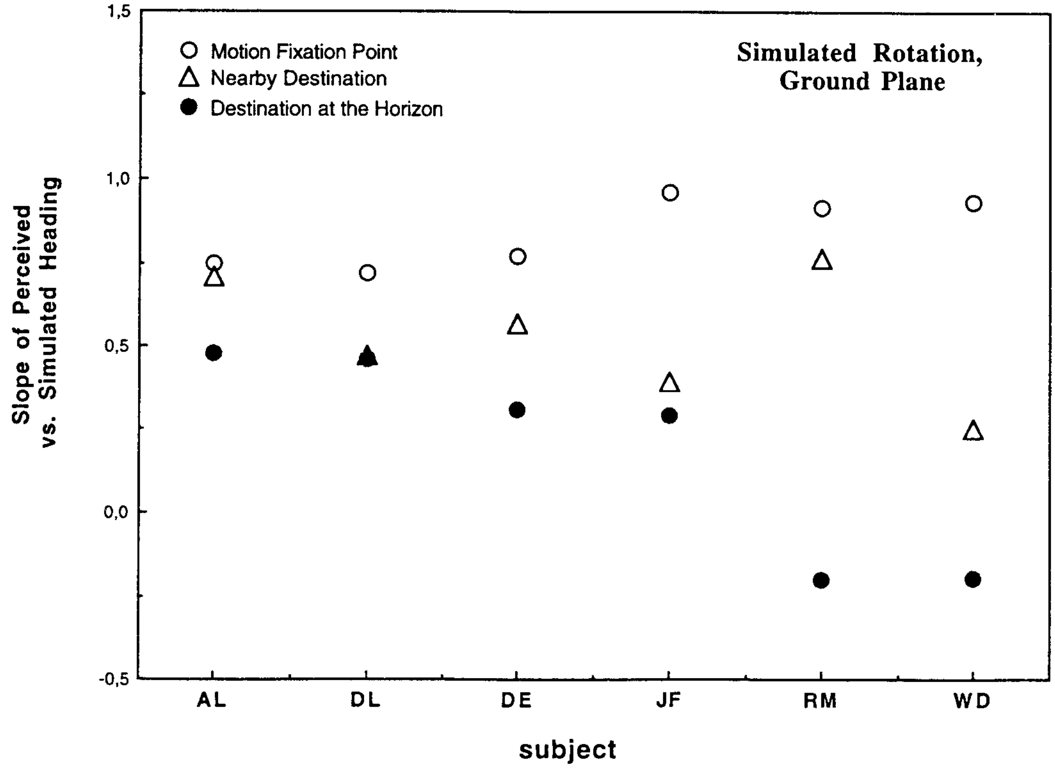

FIGURE 4. The slopes of the regression lines relating subjects' perceived heading to simulated heading across the ground plane are shown. Eye rotation was simulated in the display. The effect of three instructions on the bias in the perceived heading direction is shown.

judging their ego-motion from the perceived motion of the fixation point. This led me to investigate whether the increased bias was caused by the subject's inability to correctly indicate the destination point in the distance. Thus, I asked subjects to indicate the point on the floor, which was located at the same (ego-centric) distance as the pointer, and that they would hit if their motion (curved or straight as perceived) had continued. Again, attention was not directed to the motion of the fixation point but to the whole motion pattern. This task appeared to be easier for the subjects and the bias was correspondingly decreased. Nevertheless, the bias was still larger in all subjects than when the motion of the fixation point was used (Fig. 4).

Apparently, the instruction has a strong effect on the subject's performance. It is possible that my subjects attained better performance when asked to use the motion of the fixation point because this instruction could have stimulated them to use the "horizon strategy" (cf. Royden *et al.*, 1994; van den Berg, 1992). When the simulated environment did not contain a visible horizon (the cloud) Royden's subjects made large heading errors (Royden *et al.*, 1992) when eye rotation was simulated in the display. van den Berg and Brenner (1994b) found much better performance for comparable conditions in two subjects. Thus, a failure of the "horizon strategy" in the cloud cannot explain all the relevant data in the literature. One wonders what Royden and colleagues' (1992, 1994) instruction, to indicate the target in the distance that was nearest to the perceived heading direction, may have contributed to their subject's errors. This instruction is similar to indicating the end point of the perceived ego-motion path. It might have directed the subjects' attention away from the illusory motion of the fixation point. On the other hand, in many experiments van den Berg and Brenner (1994a) used stimuli in which the local flow vectors were perturbed by noise. This applied to all points in the display but the fixation point, because for each point the noise was proportional to its unperturbed angular motion, whereas the angular motion of the fixation point was zero. This may have caused—without the instruction to do so—a tendency in their subjects to attend most to the fixation point and its illusory motion.

If my suggestion is correct, that the instruction to attend to the motion of the fixation point is more likely to reveal the activity of a system that indicates the perceived rectilinear heading after visually discounting the ego-rotation, one could find improved accuracy of pointing, even for the cloud.

To test this idea the previous experiment was repeated with the points distributed in a cloud. Simulated motion parameters as well as the simulated initial distance and height of the fixation point were as for the previous experiments.

Subjects did not perceive themselves as heading towards the fixation point when judging the heading on the basis of the illusory motion of the fixation point.

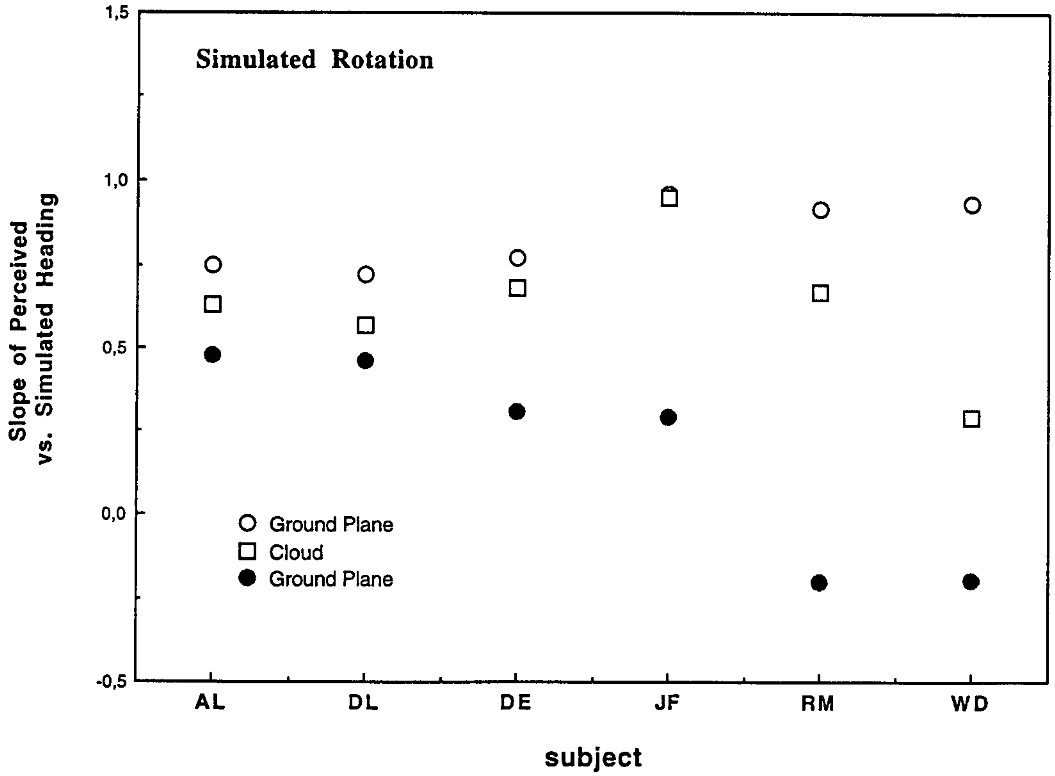

FIGURE 5. The slopes of the regression lines relating subjects' perceived heading to simulated heading are shown. The effect of the structure of the environment (ground plane or cloud) on the bias in the perceived heading direction is shown. Eye rotation was simulated in the display. Subjects judged their heading on the basis of the motion of the fixation point (open symbols) or based their judgement on their destination near the horizon (●).

There was a bias, however, and it was larger than for simulated motion across the plane with the same instruction. As shown in Fig. 2 the slope was <0.7 in AL and RM. Thus, significant heading errors were made. For example, perceived heading was shifted towards the fixation point by about 8 deg, when the heading direction was 20 deg to the right or left of the fixation direction (corresponding to a simulated rotation rate of >5 deg/sec). Nevertheless, the bias was still smaller than for the simulated motion across the plane with the instruction to indicate the destination point near the horizon. As shown in Fig. 5 all subjects showed larger systematic heading errors (reduced slopes) for simulated motion through the cloud. In some cases the difference was large (WD), in others negligible (JF). In the latter subject, pointing was practically unbiased.

As Royden *et al.* (1994, experiment 7) used monocular stimuli, whereas my displays contained stereoscopic information, a firm conclusion as to the effect of the instruction as a possible cause for the different outcomes is premature.

In three subjects (DE, JF and RM) we repeated the last measurement providing a synoptic presentation of the motion through the cloud. In this case, the flow-patterns received by the two eyes were identical and corresponded to the motion pattern that would have been received by an eye at the bridge of the nose. Thus, the information was essentially monocular. Even in this case pointing by the subjects was reasonably accurate, with slopes of perceived vs simulated heading of 0.67 (RM), 0.69 (DE) and 1.1 (JF) when they attended to the motion of the fixation point. However, subjects' pointing showed larger scatter (especially for rotation rates in excess of about 3 deg/sec) and the slopes of the perceived vs simulated heading were smaller, when the subjects indicated their far destination point in the cloud, while attending to the entire motion pattern (Fig. 6, ●). In this case pointing errors of 15 deg (bias towards the fixation point, cf. lower panels) were common in all three subjects when the simulated rotation rate was 5 deg/sec, not unlike the performance of the subjects of Royden *et al.* (1994, their Fig. 13). In contrast, I found smaller errors and in one subject (JF) even a bias in the other direction, when the subjects judged their motion relative to the fixation point (open symbols).

However, even in this case subjects may have capitalized on the fact that the fixation point was located in the same horizontal plane below the eye as in the experiments using the ground plane. One might argue that they could have used a virtual horizon at eye height. The intersection of a line through the fixation point parallel to its illusory motion (i.e. in the projection on the screen) defines an intersection with this virtual horizon, that could determine the perceived heading.

To investigate the potential of this explanation in terms of a variant of the "horizon cue", I investigated in two subjects (RM and DE) a condition in which the fixation point's simulated position was located at eye height and

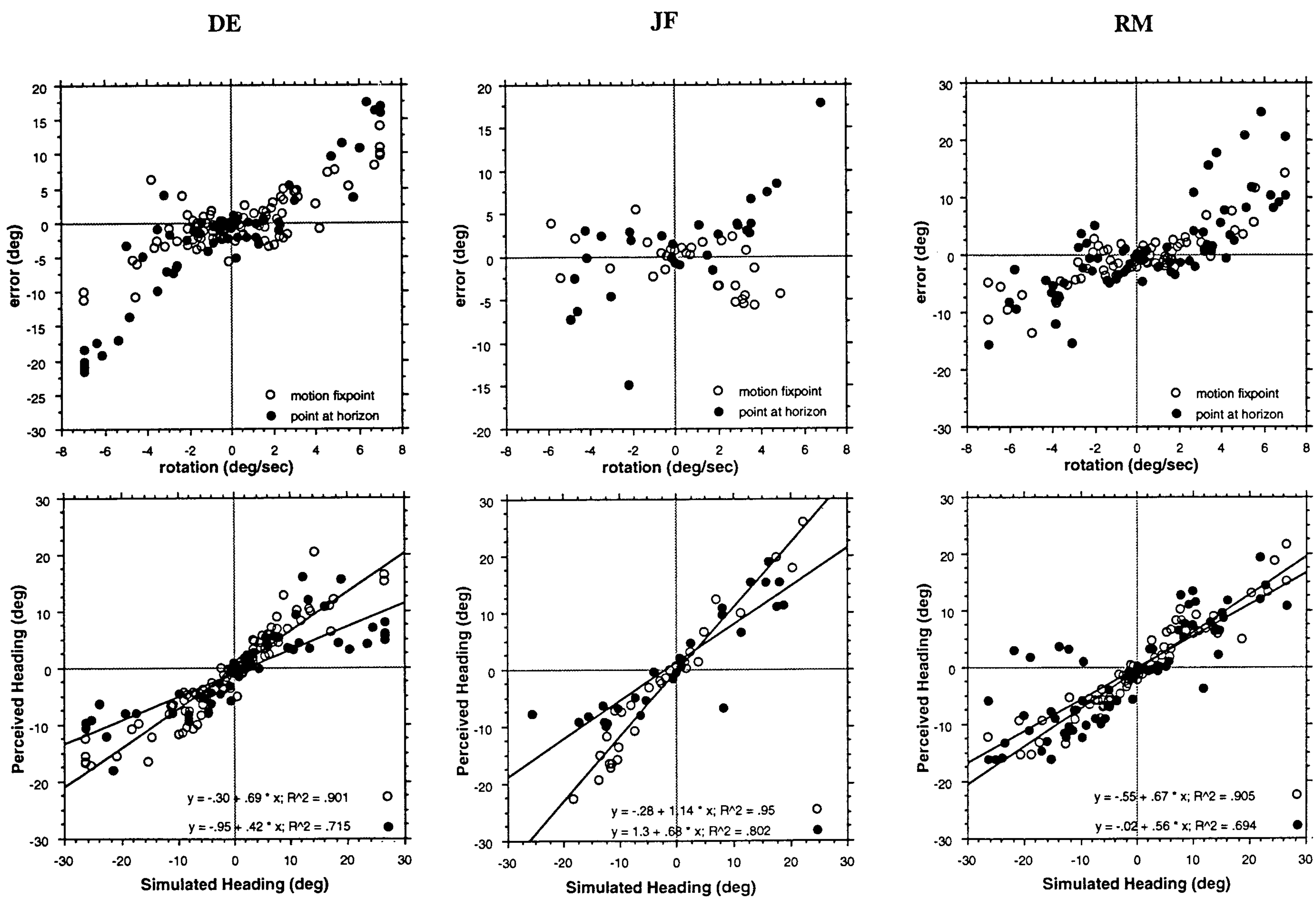

FIGURE 6. Pointing responses for three subjects (DE, JF and RM) when motion through the cloud was simulated. During the motion sequence the presentation was synoptic. Prior to and after the motion sequence the display was stereoscopic. Lower panels show the perceived heading as a function of the simulated heading direction in the same format as in Fig. 2. Upper panels show the heading errors (perceived minus simulated heading direction) as a function of the average horizontal simulated ego-rotation. Results for two conditions are shown: (1) the instruction to indicate the destination point at the far end of the cloud; and (2) the instruction to attend to the motion of the fixation point.

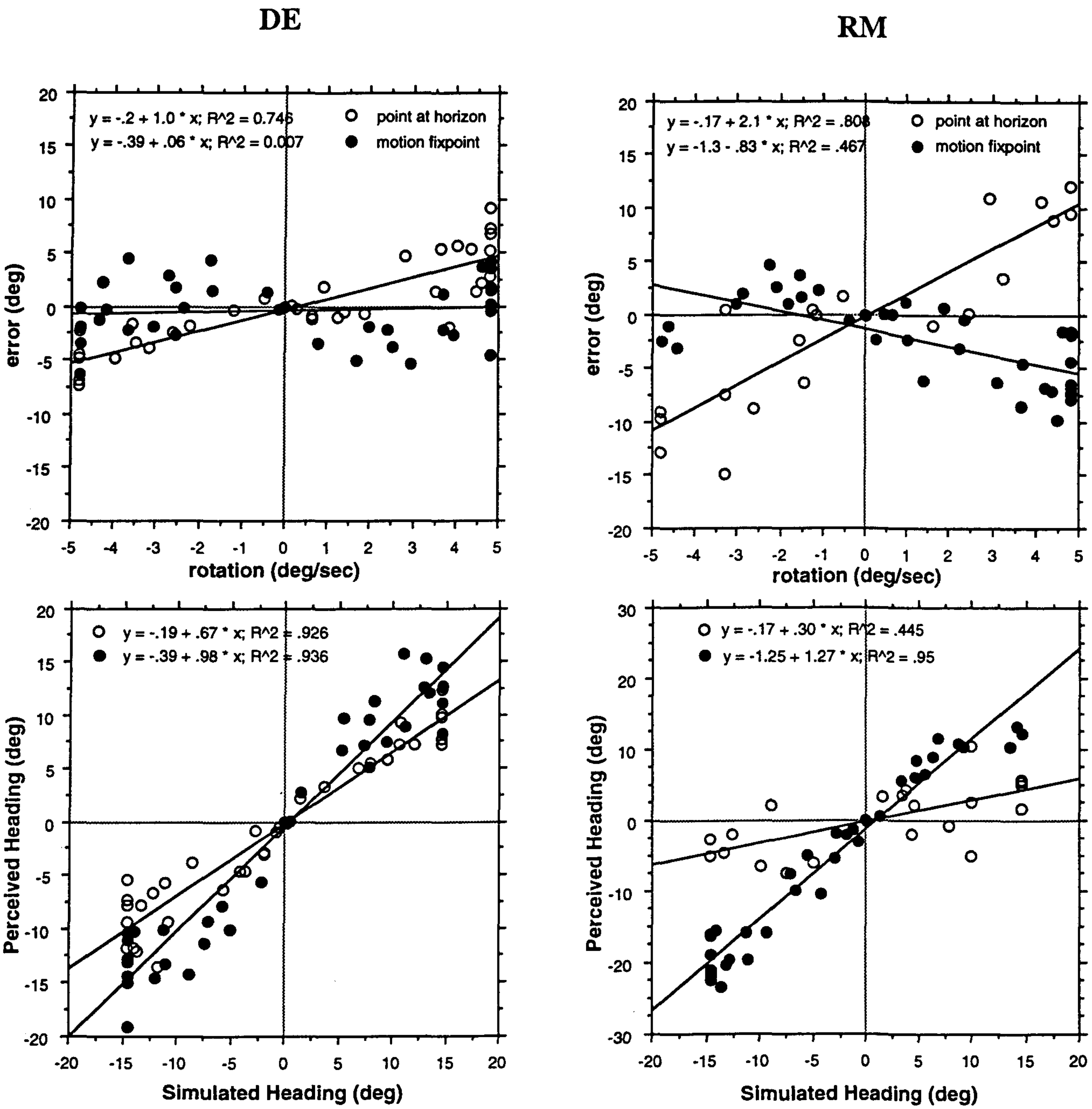

FIGURE 7. Pointing responses for two subjects (DE and RM) when motion through the cloud was simulated. The fixation point was located at eye level, so that the simulated rotation was about a vertical axis. See the legend to Fig. 6 for further explanation.

presented at the screen's centre. In addition, the fixation point's initial simulated distance was reduced to 4.5 m and its eccentricity relative to the simulated heading direction (translatory speed 1.5 m/sec) was randomly chosen, but always <5 deg. Synoptic motion was presented for 2 sec. These conditions resulted in pure horizontal simulated eye rotations of up to 5 deg/sec.

Both subjects reported that perception of heading was easier in this case because they perceived only horizontal illusory motion of the fixation point. They found the vertical rotational component in the previous simulations of self-motion through the cloud confusing. Also, the final eccentricity of the simulated heading direction was smaller than in the previous experiments which may have simplified the task. Their performance testified to that subjective impression, because perceived heading was accurate, with slopes of perceived vs simulated heading direction close to one, when self-motion relative to the fixation point was indicated (Fig. 7, lower panels (●)). Up to rotation rates of 5 deg/sec heading errors were usually <5 deg (Fig. 7, upper panels) and a bias was absent (DE; slope ≈ 1.0, lower panel) or away from the fixation point (RM; slope >1.0, lower panel). In contrast, when subjects pointed towards the endpoint of their path through the cloud (○), errors were larger, >10 deg in some cases, and pointing was always biased towards the fixation point (slopes<1.0 in the lower panels).

The last experiment strongly indicates that subjects' good performance does not only rely on the application of a "horizon strategy", because when the perceived motion of the fixation point was parallel to the horizon good performance was still found.

DISCUSSION

The main result of this study is that the perceived heading during simulated eye rotation is dependent on the type of information that subjects select to use. When subjects based their heading estimate on the perceived motion of the fixation point, the estimate could be quite accurate up to simulated rotation of about 7 deg/sec. When subjects did not pay special attention to the fixation point and indicated the destination point near the far border of the simulated environment, perceived heading was strongly biased towards the fixation direction. This means that subjects have access to at least two strategies to "solve" the heading perception task. I speculate that these two strategies reveal the activity of two parallel visual processing stages that, without specific instruction, compete to determine the subject's response.

The effect of simulated eye rotation on the perception of heading

The ability to judge heading with reasonable accuracy up to simulated ego-rotation of 7 deg/sec is remarkable, because the simulated translation was only 1.5 m/sec. Accurate heading perception was reported until now only for rotation rates up to about 6 deg/sec. In that case faster ego-translation was simulated (3 m/sec) and observers were experienced (van den Berg, 1993; van den Berg & Brenner, 1994a). Other studies reported large heading errors for rotation rates in excess of 1.5 deg/sec (Royden *et al.*, 1992, 1994). The performance of any system that aims to decompose the flow-field into translatory and rotatory contributions is set by the ratio of translation and ego-rotation for a given measurement accuracy of the flow (Koenderink & Van Doorn, 1987). Thus, the performance of my naive subjects surpasses that found in any previous report. Subjects in van den Berg's earlier studies reported spontaneously the motion of the fixation point as a piece of information guiding their responses or confirmed its use on debriefing. I do not know whether Royden and colleagues' subjects (Royden *et al.*, 1992, 1994) were aware of this cue and, if so, to what extent they used it. The present results suggest that the different performance in the different laboratories for fast simulated rotations may in part have been caused by the subjects' choices concerning the type of information used. I should point out here that none of my subjects perceived themselves as heading towards the fixation point, when they attended to its induced motion. Neither was their performance totally unbiased. This means that part of the ego-rotation was visually compensated, even when the "horizon strategy" would fail, as is the case for simulated translation and rotation through the cloud.

When attending to the motion of the fixation point the subjects reported that the fixation point appeared to move on a curved trajectory in just a few trials, and none of the subjects experienced difficulty in estimating their straight path motion relative to the fixation point. On the other hand, when attending to the entire flow-pattern the impression of ego-motion on a curved path was often very strong. Thus, there appears to be a concurrent presence of two incompatible percepts concerning the (implied) ego-motion path, which is revealed in the wide difference in estimated heading direction depending on the instruction.

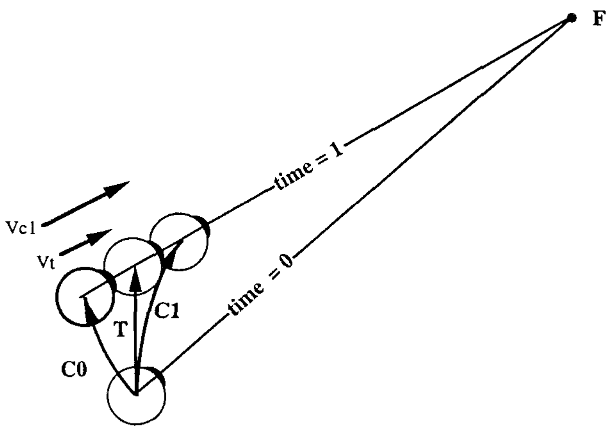

FIGURE 8. The straight motion path (T) during a time step, while simultaneously rotating to keep the line of sight directed towards the target (F), can be equated to motion on a circular path "C0" combined with a motion (Vt) towards the fixation point. Similarly, the curved motion path C1 can be equated to motion on a circular path plus a faster motion towards the fixation point (Vc1).

The curved motion path percept

The retinal flow has a similar structure for simulations of ego-motion on a curved path and for motion on a straight path combined with ego-rotation (Warren *et al.*, 1992). In fact, the instantaneous flow-field of a curved trajectory can be equated to that of rectilinear motion plus ego-rotation. For our purpose, however, it is more revealing to analyse the equivalence in the reverse direction. Given a rectilinear motion path and an eye rotation, which curved motion path gives the same instantaneous flow-field? As shown in Fig. 8, the translatory motion relative to the fixation point can always be decomposed into a motion component parallel to the viewing direction, and a motion component in a direction perpendicular to the viewing direction. Obviously, if the observer moved along a circular trajectory concentric with the fixation point the latter component would be constant (in retinal coordinates) in time (the former component being zero), and the observer would maintain fixation on the same target without need for an eye rotation. Thus, the equivalent of a rectilinear motion with an eye-rotation to fixate a point in the environment is a circular motion path concentric with the fixation point, combined with an ego-motion towards the axis of rotation through the fixation point.

These two representations of the same observer motion are connected with quite different decompositions of the flow-field. The translation plus eye-rotation corresponds to a decomposition in a radial flow-field *emanating from* *the direction of rectilinear heading* plus a uniform flow-field, with constant image motion in all viewing directions. The circular motion path plus motion towards the fixation point would lead to a decomposition of the flow in terms of a radial flow-field *emanating from the fixation point* plus a flow component due to rotation of all the points in the environment about an axis through the fixation point. The latter motion leads to opposite directions of image motion for points in front of and behind the fixation point (circular motion in depth).

In principle the brain could decompose the retinal flow along both lines simultaneously. Notice that the rectilinear motion interpretation is compatible with extra-retinal information on the eye movement if the eye is actually rotating. Conversely, the circular path interpretation is compatible with the extra-retinal information if the eye is stationary in the head. Thus, if the brain seeks to minimize the conflict between visual and extra-retinal information on the eye rotation, one might expect the circular motion decomposition to prevail when the eye rotation is simulated in the display. Of course, the conflict between visual and vestibular information remains, because semi-circular canal and otolithic information corresponding to the simulated ego-motion is absent.

Is there evidence to support the notion of a decomposition into circular motion and motion towards the fixation point? As a first step we can note that when we fixate a tree through the side window when driving a car it clearly appears to spin about its stem. Thus, the rotation of the environment about the fixation point can be perceived during forward motion. Affine flow analysis (Koenderink & Van Doorn, 1991) would seem an appropriate way to obtain an estimate of this object spin (of which the angular velocity equals that of the circular ego-motion component). There are indications that humans use affine flow to perceive structure from motion (Todd & Bressan, 1990) and to discriminate impending collision with moving objects from pass-by (Cutting *et al.*, 1995). Whether humans do so in order to perceive heading is an open question to me. A theoretical treatment of the possible use of affine flow for that purpose has been published recently (Beusmans, 1993).

Proof for the idea of a decomposition of the retinal flow in circular motion in depth and expansion centred on the fixation point is currently hard to find but there are some observations that tally well with this notion. Theoretically one can argue, that for such a decomposition the depth relative to the fixation point (derived from stereoscopic information) is sufficient. Unless combined with horizontal vergence signals, stereoscopic depth does not provide ego-centric distances or even ego-centric distance ratios which would be required to aid an ego-centric decomposition [but, the depth order helps if used to select the most distant points for estimation of the ego-rotation by an optimal observer (van den Berg & Brenner, 1994a)]. The fixation point centred decomposition can benefit from all information provided by sterescopic depth cues, whereas the ego-centric decompositions can only benefit from the depth order provided by the stereo cues. It is known that a certain class of cells in area MST of the monkey has opposite preferred motion directions depending on the depth of the moving objects relative to the fixation point (Roy & Wurtz, 1990; Roy *et al.*, 1992). This area has been implied as contributing to the analysis of ego-motion. Several lines of research have indicated that the relative rate of expansion (the inverse of the time-to-contact) is used by many organisms to time their actions [for a review, see Lee & Young (1985)] to approaching objects. Thus, behavioural as well as neurophysiological evidence supports at least the possibility that humans could analyse the flow so as to estimate heading direction from a combination of the spin of the environment about the fixation point and the relative rate of expansion.

The illusory motion of the fixation point

The perceived motion of the fixation point could reflect its relative motion to the other points in the display. Notice, however, that the fixation point was perceived as moving in depth, not as moving on the screen. This suggests that the percept is not simply some form of the Duncker illusion (Duncker, 1929). Probably, it reflects the activity of a part of the visual system that aims to remove the effect of the eye's rotation on the retinal flow and not a manifestation of the "horizon cue". My last experiment provides the best support for this suggestion, because it is difficult to conceive how in that case, when horizontal illusory motion of the fixation point was perceived, an intersection with a virtual horizon could determine the perceived heading. Yet, pointing was very accurate in this case. Somehow subjects were able to connect the perceived illusory motion of the fixation point with a particular heading direction. My interpretation is that the illusory motion reflects the activity of a system that removes the rotational component from the retinal flow in the entire field of view, and that this system computes a heading direction from the remainder by means of the detection of a focus of outflow in that reduced flow field. This does not necessarily mean that the *perceived motion* of each point in the display is consistent with that reduced flow, because subjects did not report perception of a pure expansion flow-field (which you would expect for complete cancellation of the rotational component, which the results in Fig. 7 would seem to suggest). The removal of the ego-centric rotation manifests itself in the *perceived flow* at least locally around the fixation point, but possibly not so in more eccentric parts of the visual field.

Many studies have shown that the flow component caused by an eye rotation is encoded neurophysiologically. In the rabbit it is known that whole field retinal motion is encoded in the cerebellum in a way that closely matches the sensitivity axes of the semi-circular canals [for a recent review, see Simpson *et al.*, (1990)]. Thus, at least in the rabbit visual processing of motion seems to fulfil requirements for seemless integration with vestibular signals. Also in the monkey, cells sensitive to whole field motion have been found in area MST. This area is believed to play a role in the perception of ego-motion. It contains cells sensitive to a diversity of motion patterns ranging from simple uniform shifts of the image to expanding motion or rotations in the image plane (Tanaka *et al.*, 1986; Tanaka & Saito, 1989; Duffy & Wurtz, 1991; Graziano *et al.*, 1994; Orban *et al.*, 1992). Some cells respond preferentially to one motion pattern, others to combinations of motion patterns. Graziano *et al.* (1994) have argued that collectively the cells appear to encode a stimulus space of motion patterns that can be characterized by various amounts of expansion and rotation, resulting, in general, in spiralling motion. Spiralling motion stimuli are similar to the retinal flow of an observer moving across the ground and fixating a point to the side.

Eye movements do not only affect MST responses through visual pathways but also through oculo-motor areas [see Wurtz *et al.*, (1990) for a review]. In some cells of MST this results in activation by relative motion irrespective of what caused the relative motion. For example, downward perceived motion of a point target can be evoked under various conditions: (1) during pursuit of a downward moving point on a dark background; (2) during fixation of a stationary point while another point moves downward; and (3) while moving upward a large field background pattern when fixating a stationary point. Some cells in MST respond similarly in all three conditions (Wurtz *et al.*, 1990). Thus at the level of these cells already an analysis of the motion pattern has occurred such that the relative motion between the fixation point and the environment is encoded, irrespective whether this relative motion occurs because the eye moves, the point moves or because the environment moves. In a similar vein the motion of the fixation point in depth might activate some cells in MST similarly for three analogous conditions. That is, (1) when a single point moving in depth is pursued with an eye movement, (2) when the same target motion is presented to a stationary eye as part of a translatory flow-field, or (3) when fixating the stationary target that is part of a compound flow-field corresponding to an eye that turns so as to fixate a point in the environment while translating.

For now, I merely remark that the illusory motion of the fixation point supports a decomposition of the flow-field into ego-centric motion components. Most recent models of heading perception (Perrone & Stone, 1995; Lappe & Rauchecker, 1993, 1994; Hildreth, 1992) attempt to embody such a decomposition by means of more or less physiologically realistic schemes. In neither of these schemes, however, is the perceived motion of the fixation point explicitly accounted for, so the relation of this phenomenon to those models remains as yet obscure.

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APPENDIX

To provide the subject with a motion sequence in the right perspective for each eye we measured each eye's position relative to the centre of the screen, using a triangulation technique. The subject was seated inside a cubicle with sides of 70 cm. The head was stabilized with chin and head supports. These supports were adjusted so as to ensure that the subject's eyes were level with the ground plane.

The cubicle was positioned at a fixed distance from the screen with its frontal plane parallel to the screen. A perspex strip with three vertical calibration lines was placed at the frontal plane of the cubicle. The line connecting the central marker of this strip and the centre of the screen was perpendicular to the screen. The subject aligned monocularly a target that was drawn on the screen, with the right or the left marker line on the perspex strip. These two settings define two lines, which intersect at the eye's centre of rotation (Fig. A1). The horizontal position (x_e) and the distance to the screen (z_e) of this point are computed from these settings using the following formulae:

$$z_e = \frac{D(x_R - x_L)}{(x_R - x_L - 2d)}$$

and

$$x_e = x_R + z_e(d - x_R)/D.$$

In these equations, x_L and x_R denote the target's position on the screen, when it is aligned with the left and the right marker line, respectively; d indicates the (unsigned) distance between the marker lines; and D is the (unsigned) distance between the frontal plane of the cubicle and the screen.

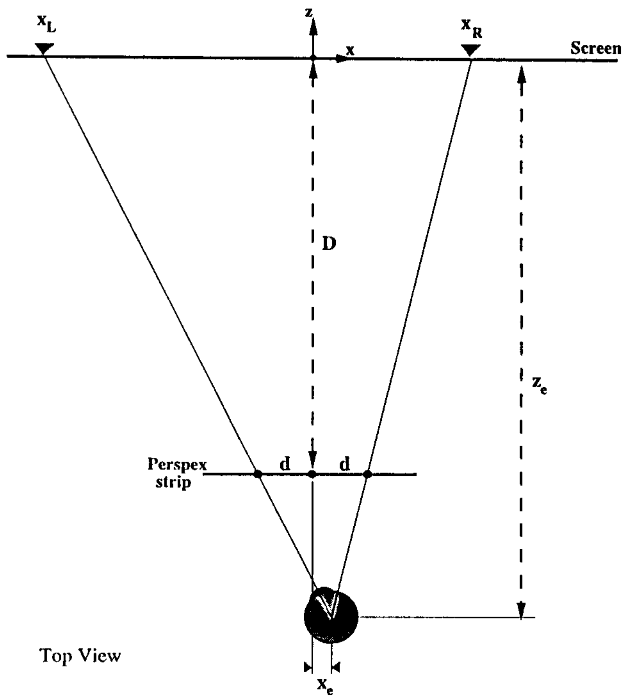

FIGURE A1. Top view of the stimulus arrangement during calibration. The perspex strip carries three equidistant marker lines (●). Each triangle at the screen indicates the horizontal position of the target (x_R or x_L) for which it is aligned with one of the marker lines. The centre of rotation of the viewing eye is indicated by the position (x_e, z_e) relative to the screen's centre. The distances between the markers (d) and between the screen's centre and the central marker (D) are also indicated.