Dynamical use of different sources of information in heading judgments from retinal flow

Antje Grigo and Markus Lappe

Department of Zoology and Neurobiology, Ruhr University Bochum, Bochum, Germany

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The optic flow arising in the eyes of an observer during self-motion is influenced by the occurrence of eye movements. The determination of heading during eye movements may be based on the pattern of retinal image motion (the retinal flow) or on an additional use of an extraretinal eye-movement signal. Previous research has presented support for either of these hypotheses, depending on the movement geometry and the layout of the visual scene. A special situation in which all previous studies unequivocally have agreed that an extraretinal signal is required occurs when the visual scene consists of a single frontoparallel plane. In this situation eye movements shift the center of expansion on the retina to a location that does not correspond to the direction of self-movement. Without extraretinal input, human observers confuse the center of expansion with their heading and show a systematical heading estimation error. We reexamined and further investigated this situation. We presented retinal flow stimuli on a large projection screen in the absence of extraretinal input and varied stimulus size, presentation duration, and orientation of the plane. In contrast to previous studies we found that in the case of a perpendicular approach toward the plane, heading judgments can be accurate. Accurate judgments were observed when the field of view was large ($90° \times 90°$) and the stimulus duration was short (≤ 0.5 s). For a small field of view or a prolonged stimulus presentation, a systematic and previously described error appeared that is related to the radial structure of the flow field and the location of the center of expansion. An oblique approach toward the plane results in an ambiguous flow field with two mathematically possible solutions for heading. In this situation, when the stimulus duration was short, subjects reported a perceived heading midway between these two solutions. For longer flow sequences, subjects again chose the center of expansion. Our results suggest a dynamical change in the analysis or interpretation of retinal flow during heading perception. © 1999 Optical Society of America

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1. INTRODUCTION

Optic flow is the visual motion pattern induced by self-movement. Retinal flow is the projection of this pattern onto the retina of a moving observer. Ever since the work of Gibson,[1,2] the question has been discussed whether it is possible to determine one's direction of movement (heading) simply from the retinal flow without other sensory information. In the case of pure linear forward translation, the retinal flow field consists of an expansion pattern with its center of expansion located in the direction of movement. However, if any kind of rotational movement is involved, for example, an eye or head movement or a curved motion trajectory, the retinal flow field becomes more complex. It has been suggested that for flow fields that are disturbed by eye movements, extraretinal information is necessary to perceive the movement correctly, especially for high eye-rotation rates.[3,4,5] Others, however, have described situations in which accurate heading judgment is possible without extraretinal eye-movement information.[6,7] In these cases heading estimation had to be based solely on visual information from the retinal flow field.

Many different types of visual information in retinal flow have been suggested to be important for the estimation of heading (for a review, see Refs. 6 and 8). These include global flow structure,[1] differential invariants of the flow field,[9] static monocular[10] or binocular[11,12] depth signals, and several types of motion parallax.[13,14,15] Motion parallax, in general, is the difference in the image motion of elements at different distances from the observer. We refer to local motion parallax as the relative motion of adjacent image points that result from elements separated in depth. This kind of motion parallax has also been termed differential motion and has been suggested to be important for a decomposition of translational and rotational components in the flow field.[6,16] If the environment lacks local depth variations, for example, in the case of a smooth surface, local motion parallax is hardly detectable. Differences in image motion, however, may exist between nonadjacent points. This global motion parallax may serve as a cue to detect, for instance, the slant of flat surfaces.[17]

Another important visual cue for heading estimation is the pattern of local movement directions. Each combination of translational and rotational components of self-motion results in a certain pattern of retinal flow. In particular, the completely radial structure of pure translational flow fields has been assigned a prominent role in heading judgments.[1,2,6,8] Depending on the environment and the involvement of eye movements, some other flow patterns can be classified. For example, fixation on a point on a horizontal ground plane during forward movement results in a flow field with a spiral structure around the fovea. Such a pattern can also be used to determine heading.[6,7]

To distinguish translational from rotational components of the retinal flow and determine the direction of translation, flow-field invariants could also theoretically be used.[9,18,19] One such invariant is the maximum of divergence, i.e., the maximum rate of magnification. The maximum of divergence is invariant against rotations. In particular, if the environment consists of only a single surface, the maximum of divergence can easily be determined.[9]

In our experiments we used the environment of a frontoparallel plane to investigate the significance of different types of flow-field information and the dynamics of the analysis of retinal flow. We considered a linear approach toward a frontoparallel plane combined with a tracking eye movement. This is a challenging case because the environment almost completely lacks depth. Thus local motion parallax is rarely available. However, there are small variations in the slant of the plane. Slant is defined as the angle between the normal to the plane and the observer's line of sight. Slant changes arise because the observer fixates a target attached to the plane but approaches the plane on a path different from his direction of gaze. During the observer's approach the eyes rotate by a certain amount and the slant increases. Thus slant-related texture gradients and speed gradients (global motion parallax) along the plane are available [see Fig. 1(C)].

Previous research has indicated that characteristic errors in heading estimation from retinal flow occur in this situation.[3,4,6,14] In these studies human subjects were presented with a visual motion pattern that simulated a linear, perpendicular translation toward a frontoparallel plane combined with a simulated eye movement. They were asked to locate the direction of forward movement from this retinal flow stimulus. During the stimulation subjects did not move their eyes but continuously fixated a stationary target, thereby creating a conflict between visual and extraretinal signals. Under this condition, heading estimation was impaired. Subjects misperceived themselves as heading toward the direction of gaze.

This misperception can be explained by the structure of the retinal flow field that is explained in Fig. 1. The linear forward motion itself causes a purely radial flow pattern [Fig. 1(A)]. The simulated tracking eye movement adds a retinal motion pattern that to some degree resembles a uniform translation [Fig. 1(B)]. The combination of this motion with the radial flow in Fig. 1(A) results in a shift of the center of expansion, which then appears to lie in the direction of gaze rather than in the direction of translation [Fig. 1(C)]. The retinal flow pattern therefore shows an approximately radial structure with its center at the direction of gaze. We refer to the center of this radial pattern as a pseudofocus of expansion. The previous studies have suggested that subjects rely on the radial structure in the flow field to determine heading and thus confuse the pseudofocus with a real focus of expansion.

Figure 1(D) shows the flow pattern that would arise from a purely translational movement. A closer look reveals slight deviations between the flow pattern in Fig. 1(C) and the one in Fig. 1(D). The differences are shown separately in Fig. 1(E). They result from the slant and relative rotation of the plane with respect to the line of sight in the case of Fig. 1(C). They are more pronounced in the periphery than in the center of the pattern. If observers could capitalize on these differences, they might be able to distinguish the two cases.

An important point in this respect concerns the stimulus size. The field of view in all the experiments performed so far has been smaller than 40° × 40°.[3,4,6]

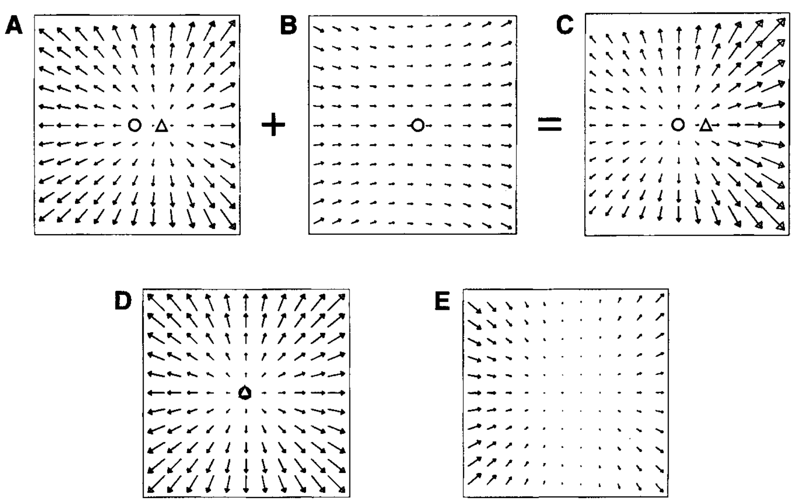

Fig. 1. Retinal flow patterns resulting from different observer motions with respect to a frontoparallel plane. Triangles, heading; circles, direction of gaze; arrows, motions of points as they are projected on the screen. (A) Retinal flow caused by a pure forward translation along the plane normal. The flow consists of a radial motion pattern with the center of expansion located in the direction of self-movement. (B) Retinal flow pattern caused by an eye rotation. The magnitude of this eye rotation is such that gaze follows the motion of the point on the plane that is projected on the fovea. (C) Forward motion during a smooth pursuit eye movement (A + B) results in an approximately radial flow pattern with its center in the direction of gaze. This motion pattern somewhat resembles the motion seen during pure forward translation in the direction of gaze. (D) Retinal flow caused by a linear forward motion when the direction of gaze coincides with the direction of translation. (E) The differences between the flow patterns in (C) and (D). They are largest in the periphery of the field of view (here 90° × 90°).

Within this small field of view the differences between the pseudofocus and a true focus of expansion are hardly noticeable. An enlarged field of view should make the differences more distinct and might allow better heading estimation performance.[20] The experiments described here tested this hypothesis by use of a large field display of 90° × 90°. The results show a clear improvement in heading estimation in this case.

The experiments performed in previous studies have all simulated a perpendicular path toward the plane. Approaching the plane on an oblique path is another interesting situation for a number of reasons. In that case, several sources of information in the flow field become separated. Heading no longer is along the plane normal. However, the pseudofocus remains in the direction of gaze. The maximum of divergence falls in between the direction of movement and the normal to the plane.[9] Furthermore, at any given instance of time, the flow field has two equivalent solutions for heading. These are the plane normal and the veridical heading.[21] We examined which visual information subjects use for heading estimation and how they deal with the ambiguity.

A further issue of our study concerns the dependence of heading perception on the duration of the simulated self-movement. In previous experiments the stimuli were presented for several seconds. Long presentation durations might improve heading estimation because temporal integration should facilitate the task and could resolve possible ambiguities in the flow field.[21,22,23] However, Crowell *et al.*[24] and te Pas *et al.* have[25] found 300 ms to be sufficient to judge translational heading accurately. Stone and Perrone[23] have simulated curvilinear motion toward two frontoparallel planes for only 400 ms and also found accurate heading judgments. In most of the experiments described here, we used stimulation durations of 400 and 500 ms. By varying presentation duration, we observed a change in the subjects' perception of heading over time.

2. GENERAL METHODS

We presented retinal flow fields that normally occur on an observer's retina when he moves toward a large frontoparallel plane while also moving his eyes. The geometry of this movement is depicted in Fig. 2. The observer approaches the plane under a certain angle φ, measured with respect to the plane normal n. During the movement he keeps his gaze directed toward a fixed point on the plane. The angle ν is the angle between the direction of gaze and the direction of movement. We will refer to this angle as the retinal heading angle. It changes slightly during the movement of the observer. The observer's speed perpendicular to the plane is denoted by v. The observer moves within the movement duration t from an initial position to his final position at a distance D from the plane. The final position is held constant across the trials, whereas the initial position is adjusted according to the speed and duration of the observer's movement. At the final position the remaining time to collision is τ. In all experiments, with the exception of experiment 6, a perpendicular approach was simulated; that is, the direction of forward movement coincided with the normal to the plane.

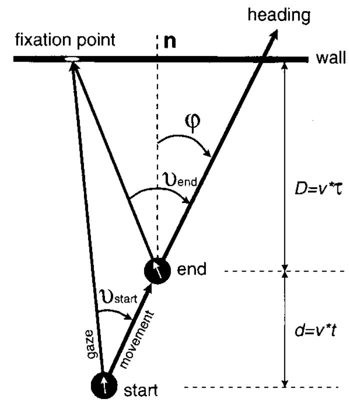

Fig. 2. Simulated movement geometry seen from the top. The observer moves toward a frontoparallel plane under a certain angle φ with respect to the plane normal n. During the movement gaze is directed to a point fixed on the plane. During the time t the observer moves with speed v to his final position, which is at a distance D from the plane. At the end of the movement the time to collision is τ and the retinal heading angle is ν_{end}.

The retinal motion of visible points on the plane was simulated on a SGI graphics computer by randomly distributed bright dots on a dark background. They were displayed by a video projector on a large tangent screen 60 cm in front of the observer. The stimuli were generated in real time. The screen refresh rate was 72 Hz, and the frame rate was 36 Hz. Screen dimensions were 90° × 90°. Dot size was 0.2° and did not change during the movement.

The stimuli simulated continuous tracking of a fixation target attached to the plane. This target was marked in red and was permanently displayed at the screen center. Subjects were required to fixate this target throughout the whole experiment. Before the onset of movement, the first frame was shown statically for 1 s to allow the subject to establish fixation. Then the movement was simulated for a certain time t. Subjects had to be attentive to the whole duration of the stimulus. After the movement had stopped, the scene remained on the screen. Then the subject's task was to adjust a previously hidden mouse pointer to that point on the plane at which the subject would collide with the plane if the movement had continued. After the subject's response the next trial started. Owing to the simulated rotation, the impact point moved slightly on the screen during the display but always remained fixed with respect to the plane. Subjects were told that the simulated movement could result in an apparent translation and rotation between plane and observer. They were not instructed to base their judgments on any specific part of the stimulus. In different parts of the experiment, different sets of stimulation parameters were used that are described in detail below. Within each parameter set, the parameters for a single trial were chosen at random. Each parameter combination was presented five to ten times.

All subjects participated voluntarily and had normal or corrected-to-normal vision. Age ranged between 20 and

35 years. Individuals and number of subjects varied from one experiment to the other. Except for the authors, who participated in some of the experiments, subjects were not familiar with the purpose of the experiments.

3. EXPERIMENT 1: HEADING TOWARD A VERTICAL PLANE

In the first experiment we used a perpendicular approach toward the plane and different directions of gaze, as sketched in Fig. 3. Retinal heading angles at the end of the movement were 0°, ±3°, or ±6°. We simulated an observer speed of $\upsilon = 2$ m/s. The movement was presented for 0.5 s. At the end of each trial, time to collision was 2 s. The continuous tracking of a target on the plane required a certain simulated eye rotation. Mean eye-rotation rates were 0°, 1.2°, or 2.4°/s for the three different absolute values of the retinal heading angle. The field of view was 90° × 90°.

A. Results

The results are shown in Fig. 4. The angle between the direction of gaze and the perceived heading is plotted against the simulated retinal heading angle ν. The means of six subjects, averaged over 10 repetitions each, are shown along with their standard deviations. Correct responses were to lie on the diagonal (dotted line). The erroneous percept of movement toward the fixation point, previously described by Warren and Hannon,[6] would result in responses that fall on a horizontal line through 0°. The solid line gives the regression through the five means. It deviates only slightly from the diagonal, showing that average heading judgments from retinal flow in this situation are quite accurate.

Figure 5 gives the results for individual subjects. For individuals, both overestimations and underestimations of the retinal heading angle can be observed. It is important to note that most subjects felt very uncertain about

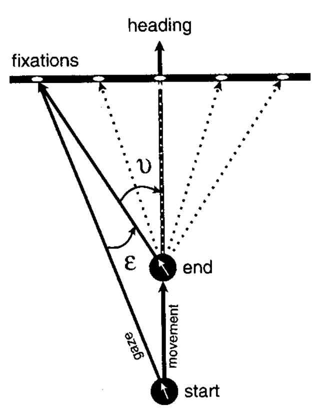

Fig. 3. Overview of the simulated movement in experiments 1 to 5. The observer moves with speed υ along the plane normal. After time t he reaches his final position. To fixate a point on the plane during the movement, the observer's eyes have to rotate about an angle ε. At the end of the movement the angle between the gaze direction and the direction of self-motion, the retinal heading angle ν, can take five different values, depending on the location of the fixation target on the plane.

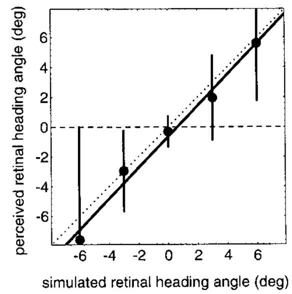

Fig. 4. Results of experiment 1. The perceived retinal heading angle is plotted against the simulated retinal heading angle, which was 0°, ±3°, or ±6°. Circles, mean responses of six subjects averaged over ten repetitions each; vertical lines, standard deviations; horizontal dashed line, direction of gaze, i.e., the location of the fixation point, which was always at 0° at the center of the screen. Correct answers must lie on the diagonal (dotted line). The regression line deviates only slightly from the diagonal, which means that heading estimation is quite accurate.

their responses. They claimed that the task was difficult and expressed little confidence in their choices. However, in spite of the subjects' uncertainty, the individual judgments are directly proportional to the simulated retinal heading angle in most cases. Only one of the six subjects (FB) consistently indicated the fixation point as the perceived heading. The responses of FB together with those of subject CS, who showed large variances in her responses, caused the large standard deviations of the means in Fig. 4. Removing these two subjects from the analysis yielded almost the same averaged regression line, only with smaller standard deviations. Yet we will use averages over all subjects in all the following experiments. This approach allows easy comparisons between the various experiments. We believe that this method provides an unbiased estimate that does not require us to formulate a criterion to dismiss any of the recorded data.

In Fig. 4 the mean results of the heading estimation task match the actual heading well. We wanted to see whether this close matching is a general result for this movement situation or whether heading estimation is impaired with larger simulated retinal heading angles and correspondingly higher rotation rates. We enlarged the simulated final retinal heading angles to ±10° and ±20°. With an observer speed of 1 m/s, a movement time of 0.5 s, and a final time to collision of 1 s, this enlargement resulted in mean rotation rates of 6.6° and 12.8°/s, respectively. Each condition was presented eight times in random order. Seven subjects participated in this experiment.

The results are shown in Fig. 6. Again, the mean perceived heading is plotted against the simulated final retinal heading angle. Again, the regression line through the responses matches the diagonal, i.e., the veridical heading, well.

B. Conclusion and Discussion

We found that heading judgments based on the visual information obtained during the linear movement toward a single vertical plane combined with a simulated eye rotation are, on average, reasonably accurate. This finding is in conflict with previous studies that had found large er-

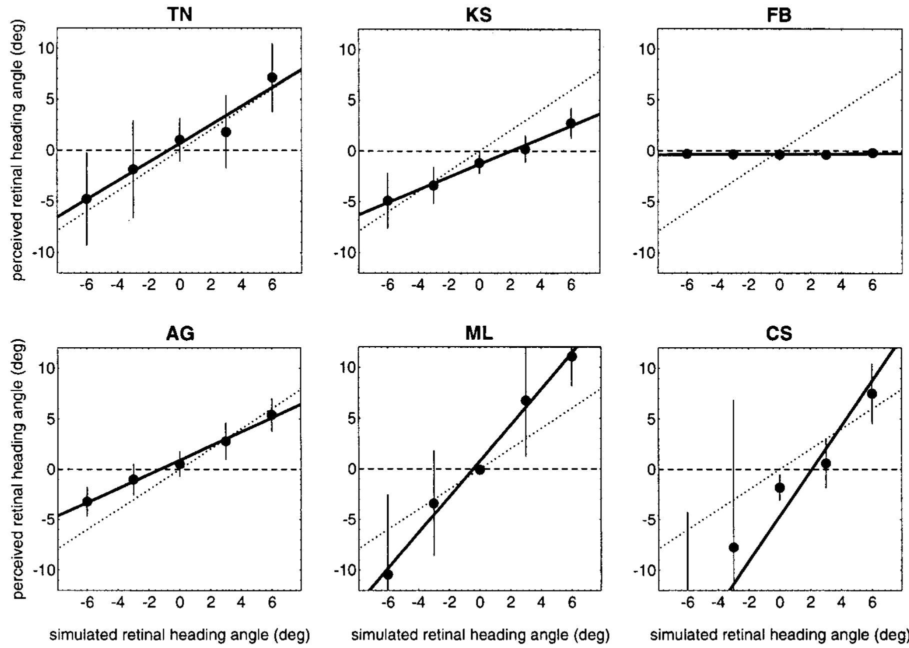

Fig. 5. Responses of individual subjects in experiment 1. Individual overestimation and underestimation of heading can be observed, which in all cases is roughly proportional to the simulated retinal heading angle. Only one subject (FB) consistently perceived the fixation point as his direction of self-motion.

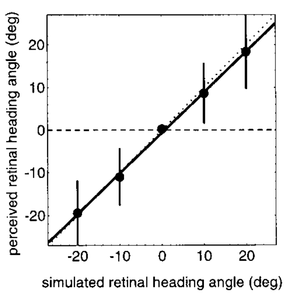

Fig. 6. Mean results for seven subjects for the heading estimation task with high rotation rates. The simulated retinal heading angle was as high as 20°. Nevertheless, subjects on average estimated heading correctly.

rors in heading judgments in this situation.[3,4,6] Warren and Hannon[6] had simulated a perpendicular approach toward a frontoparallel plane along with a pursuit eye movement and found that performance of heading estimation was near the level of chance. They had described that subjects, like FB in our case, consistently perceived themselves as heading toward the fixation point. This fixation point represents a pseudofocus of expansion in the retinal flow field (see Fig. 1). Because the experimental conditions that were used by Warren and Hannon[6] differed from ours in some aspects, we reexamined the movement situation with parameters similar to theirs.

4. EXPERIMENT 2: REEXAMINATION OF A PREVIOUS EXPERIMENT

In experiment 2 we used parameters similar to those used by Warren and Hannon.[6] Instead of a field of view of 90° × 90°, we now displayed the stimuli in an area of 45° × 35°; Warren and Hannon had used screen dimensions of 40° × 32°. Furthermore, we prolonged the presentation duration to 2 s; Warren and Hannon had presented their stimuli for 3 s. Warren and Hannon had varied the simulated heading angles from −7° to 7°; we used five discrete values of 0°, ±3°, and ±6°, the same as in experiment 1. Observer speed was again 2 m/s, and time to collision at the end of the trials was 2 s; Warren and Hannon had used 1.9 m/s and 1.9 s, respectively. The mean rotation rates were 0°, 0.7°, or 1.5°/s in our experiment and between 0.2° and 1.2°/s in Warren and Hannon's experiment. Thus, compared with the first part of experiment 1, we changed only the size of the field of view and the stimulus duration. Each simulation condition was performed five times.

A. Results

Consistent with Warren and Hannon's results, subjects were not able to determine their heading correctly. Instead, for all the subjects, heading perception was biased toward the direction of gaze, that is, toward the pseudofocus of expansion.

Compared with the first part of experiment 1, only the stimulus size and the presentation duration changed. These changes resulted in a loss of the heading estimation ability and the emergence of a characteristic error. We wanted to determine which of the two parameters is the crucial factor. Therefore we next tested two different conditions. First, we used the large field of view (90° × 90°) and a long presentation duration (2 s). Then we presented short stimuli (0.5 s) in a small field of view (45° × 35°). Varying either stimulus size or simulation duration alone did not much improve heading estimation performance. In both condition the subjects' answers were strongly biased toward the fixation point. Only the combination of short stimulus presentations and a large field of view yielded, on average, correct responses.

B. Conclusion and Discussion

Two main requirements have to be fulfilled before subjects can correctly estimate heading in the situation we studied: The field of view has to be large, and the stimulus presentation has to be brief.

The influence of the size of the field of view is easily understandable: In the central region of the flow field, the motion pattern surrounding the pseudofocus does not differ much from a real expansion pattern. The differences become more pronounced in the peripheral parts of the visual field [see Fig. 1(E)]. Owing to the observer's tracking eye movement, the plane rotates relatively to the observer's line of sight. In the peripheral field of view, cues such as texture gradients and speed gradients, which accompany the change of the slant of the plane,[17,26,27] become noticeable. These cues allow detection of the relative rotation between the plane and the observer. Theoretically, this should be even easier for larger retinal heading angles or higher rotation rates because then the change of the slant is much larger. Indeed, with high rotation rates, subjects reported a strong impression of a rotating plane.

In contrast, the small field of view does not provide enough information to detect the rotational component in the flow field.[20] The flow field might be misinterpreted as being due to a purely translational movement. Thus the pseudofocus is confused with a real focus of expansion that would indicate the direction of linear self-motion. With the large field of view, the percept of the rotation enables subjects to disregard the pseudofocus as the indicator for heading.

While the influence of the field of view was to be expected, the influence of the presentation duration was rather surprising. Therefore we next examined the dependence of the heading estimation performance on the presentation duration.

5. EXPERIMENT 3: DURATION OF THE STIMULUS

In experiment 3 we presented simulated observer movements for durations of 0.4 or 3.2 s. We used five discrete final heading angles of 0°, ±3°, and ±6°. The two duration conditions were run in separate blocks of trials. The field of view was 90° × 90°. Observer speed and time to collision was the same as in the previous experiments. The final retinal heading angles at the end of the trials were the same for the different presentation durations. The initial retinal heading angles at the start of the trials had to be adjusted accordingly. Thus the short trials effectively presented the last 0.4 s of the longer trials. We used nine subjects who were different from those used in the previous experiments.

A. Results

The results are shown in Fig. 7. Again, the perceived retinal heading angle is plotted against the simulated retinal heading angle. For a presentation time of 0.4 s the regression line of the mean answers fits the diagonal well. This means that with short simulation time the mean error was very low. In contrast, when the movement was presented for 3.2 s, the responses were clearly biased toward the fixation point. The regression line was slanted away from the diagonal and toward the horizontal by ~55%.

B. Conclusion and Discussion

For the brief presentation, average heading judgments matched the simulated heading well. With long presentation durations, responses are biased toward the direction of gaze. This may suggest that heading perception, or the analysis of the retinal flow pattern, changes dynamically over time. However, alternative explanations might be considered.

Could it be that the bias in heading estimation for longer presentation duration results from the perception of a curved motion path? At any moment in time, the retinal flow resulting from linear movement plus eye rotation about a vertical axis is equivalent to a flow field caused by movement on a curved path around a different vertical axis.[28] Royden *et al.*[4] studied heading judgments from retinal flow during forward movement over a ground plane combined with a simulated horizontal eye rotation. They found that the simulated movement was often erroneously perceived as curvilinear motion.[4,22] If our subjects had also perceived curved path motion, they would have indicated the intersection of the path with the plane. Hence the path would have had to have an initial direction toward the veridical heading with a curvature

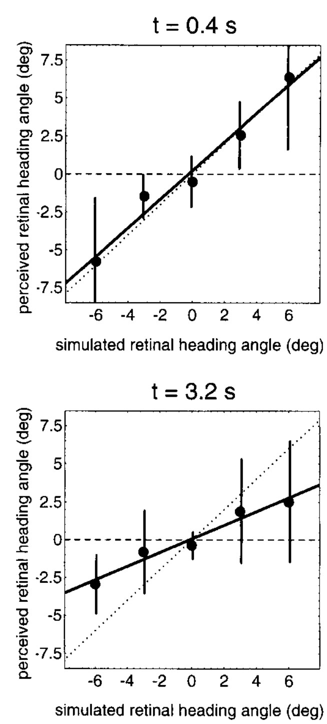

Fig. 7. Results of experiment 3. Shown is the mean perceived heading of nine subjects for trials with a presentation duration of 0.4 s (top) and 3.2 s (bottom). Vertical lines, standard deviations. The deviation of the regression line from the diagonal is much larger for the long presentation time, indicating a decrease in heading estimation performance.

toward the direction of gaze. However, depending on the presentation duration, subjects gradually changed the reported heading. This is equivalent to gradually changing the perceived point of collision with the plane. For a curvilinear movement with a constant curvature, one would expect that the collision point would remain constant. Thus a perception of a curved path alone could not explain the results. A dependence of the curvature on stimulus duration would be required. Moreover, curvilinear motion and linear movement plus eye rotation yield different trajectories of the points in the flow field as time progresses.[28] These differences become larger with longer presentation durations. Thus for long stimulus durations, subjects should be able to distinguish better between a linear and a curved path: They should reject the alternative of the curved motion path in favor of the translational motion plus eye rotation. Yet for prolonged stimulus durations, subjects bias their responses away from the veridical heading toward the fixation point. Therefore a curved path percept is unlikely to explain our results.

A much simpler explanation might be that the retinal heading angle changes over time during the simulated movement. In the above experiment we varied the presentation duration while holding all other parameters constant. Thus, for fixed final retinal heading angles of ±3° and ±6°, the initial angles between the direction of gaze and the simulated heading were different for the different presentation durations. The initial retinal heading angle is smaller for the longer presentation time, provided that the observer always moves with the same speed. In our case, for the final retinal heading angle of 6°, the initial heading angle was 5° for a movement time of 0.4 s and 2.3° for a 3.2-s movement. Thus an influence of the initial heading angle could bias the perception toward smaller angles and hence toward the fixation point for longer presentation times. In the next experiment we examined whether the dependence of the heading estimation performance on the presentation duration is related to the initial retinal heading angle.

6. EXPERIMENT 4: MAGNITUDE OF CHANGE OF THE RETINAL HEADING ANGLE

In experiment 4 we kept the angular difference between the initial retinal heading angle and the final retinal heading angle constant while varying the presentation duration. If the subjects' responses depend simply on this angular difference, the duration of the movement should have no effect.

The final simulated distance of the observer from the plane (see Fig. 2) was the same in all conditions. The final direction of gaze was ±6° or 0°. Simulated observer movement was presented for 0.4, 0.8, 1.6, or 3.2 s. To keep the initial retinal heading angle constant for all movement durations, the observer's speed was adjusted accordingly. With the fixed final distance to the plane, the different speeds resulted in different values for the time to collision at the end of the trials. We chose three possible angular differences between the initial and the final retinal heading angles. They were 1°, 1.7°, or 2.7°. We presented the stimuli in four isolated blocks sorted by presentation duration. The blocks with the trials lasting 0.8 and 1.6 s contained all three angular differences, whereas the block with the shortest trials contained only the two large angular differences and the block with the longest trials contained only the two small ones. Five subjects participated in this experiment. All of them had seen the kind of stimuli before in one of the previous experiments.

A. Results

The results are displayed in Fig. 8. The three panels show the means of the responses for the three angular dif-

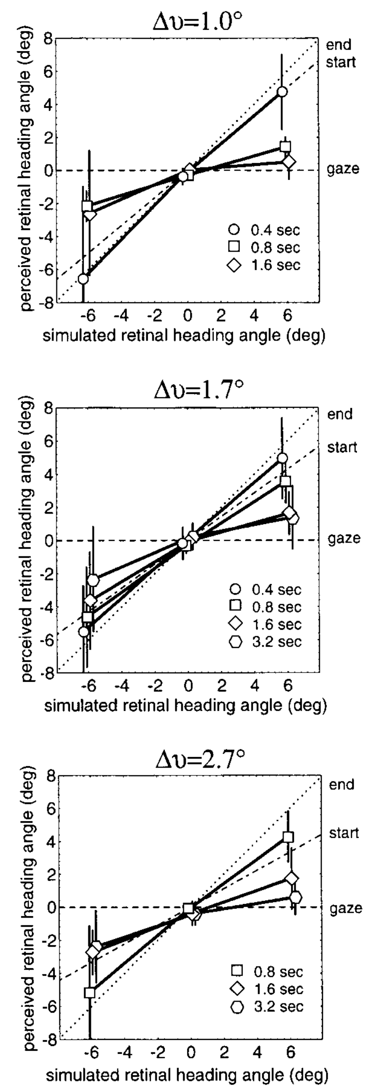

Fig. 8. Results of experiment 4. The three panels present the three angular differences $\Delta\nu$ between the initial and the final retinal heading angles. The final heading angles are 0° and ±6° in all figures. The initial retinal heading angles are accordingly different. Within each figure, the mean results of five subjects for different stimulus durations are shown together with their standard deviations. For less confusion the different means are slightly separated horizontally from one another. Overall, a significant bias toward the direction of gaze can be observed for prolonged stimulus durations.

ferences of the retinal heading angle. In each figure the mean responses for the different presentation durations are marked by different symbols and are connected by a line. For better discrimination, the different symbols as well as the corresponding standard deviations are slightly shifted sideways from one another. The dotted diagonal represents the simulated heading angle at the end of the trials. The slanted dashed line gives the heading angle at the start of the trials. The horizontal line represents the direction of gaze, or the location of the pseudofocus of expansion, which was always in the center of the screen. Evidently, the subjects' perceived heading deviates more from the veridical solution when the presentation lasts longer. A Friedman repeated-measures analysis of variance (ANOVA) on ranks confirmed a significant bias toward the fixation point for longer presentation times ($p < 0.05$). Furthermore, it can be observed that the tendency to point nearer to the fixation point is independent of the angular difference between the initial and final simulated retinal headings.

B. Conclusion and Discussion

The direction of self-motion perceived by the subjects does not depend on the retinal heading angle at the start of the trial or on the angular difference between the initial and final heading angles. In all cases, a bias toward the direction of gaze emerges for prolonged presentation durations. Only when the stimulation duration is short (0.4 s) does the perceived heading correspond to the simulated one. However, in trials with short presentation duration the simulated speed of the observer and hence the velocities in the flow were higher. At the same time, the time to collision at the end of the trial was shorter. These parameters could potentially influence the heading judgments.[29] But as experiment 3 showed, the dependence of the heading estimation on the presentation duration also occurred when the speed and the time to collision were constant.

However, in experiment 3 the short-duration trials contain the last 0.4 s of the long trials. Because flow velocity and slant angle increase over time and are greatest toward the end of the trial, observers are most likely to perform accurately with the information near the trial's end. At the beginning of the 3.2-s trial not much information can be gained from the flow velocities. If observers base their judgments on the entire stimulus duration, performance might be impaired by the lack of information at the trial's start. Indeed, a simple control experiment in which we presented only the first 0.4 s of the 3.2-s trials to three observers revealed relative heading errors roughly similar to those made with the full 3.2-s period. This is not surprising if one considers the lack of information in that part of the stimulus. Thus the poor performance in the long trials might be related to the absence of essential visual cues at the trials' start. However, this still leaves the question of why the flow-field information that is provided at the end of the long trials, and which by itself suffices to yield correct heading estimation, is not used. Evidently, the visual cues provided in the final 400 ms are not correctly evaluated when preceded by a long presentation of continuous flow. This suggests that long and short flow field stimuli may be evaluated differently. To test this hypothesis we performed a further experiment in which we divided the 3.2-s trial into short flow field sequences of 0.4 s.

7. EXPERIMENT 5: SEQUENTIAL PRESENTATION

Experiment 5 examined the hypothesis that long continuous-flow stimuli are analyzed differently from short flow field samples. To test this, we created a stimulus that presented the same entire movement as the 3.2-s stimulus in experiment 3 but consisted of several short sequences. This was realized by randomly repositioning all dots in the display every 400 ms. This resulted in seven sudden changes of the flow field that were clearly noticed by the observers. However, the simulated heading, the position of the fixation point on the plane, and hence the global motion pattern remained the same as in experiment 3. In this way, the stimulus was partitioned in eight short sequences with a total duration of 3.2 s. Our hypothesis was that each change resets the flow-field analysis. If visual perception were different for short and long flow field sequences, we might expect an improvement in heading estimation compared with that resulting from a continuous presentation of 3.2 s.

The experiment was performed with four subjects who had also participated in experiment 3. Again, their task was to indicate the perceived future point of collision with the plane.

A. Results

Figure 9 shows the results of heading judgments from the sequentially presented flow field. The regression line of the means only slightly deviates from the diagonal. The responses were reasonably accurate. Performance was much better than with a single continuous 3.2-s flow stimulus [compare Fig. 7 (bottom)].

B. Conclusion and Discussion

As in experiment 3, the presentation duration of the stimuli in experiment 5 was 3.2 s. The only difference was that the stimuli were not shown continuously but in

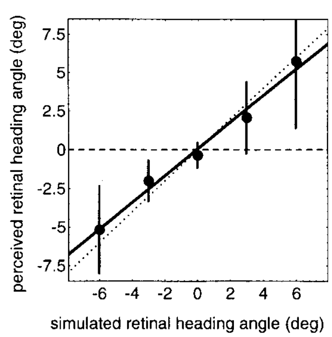

Fig. 9. Results of experiment 5, showing the mean perceived heading of four subjects. Vertical lines give the standard deviations. Trials had a total duration of 3.2 s, but the distribution of dots was randomly changed every 0.4 s. Each redistribution resulted in an interruption of the continuous flow but did not change the simulated motion. The deviation of the regression line from the diagonal is much smaller than for a single long presentation (compare Fig. 7).

consecutive short sequences of 0.4 s. A comparison of the results [Figs. 7 (bottom) and 9] reveals that only in the latter case did correct heading judgments succeed.

The results of experiments 3 to 5 can be summarized as follows: The information present in the last 400 ms is sufficient to estimate heading with reasonable accuracy. The performance gets compromised in the longer trials, i.e., when the same stimulus is preceded by a long continuous-flow presentation. With continuous presentation of 3.2 s, observers may base their judgments on the entire duration of the stimulus, yielding a decrease in performance owing to the less visual information at the start of the stimulus. For presentation of only the first 400 ms of that stimulus, roughly identical relative errors occur. Partitioning the 3.2-s stimulus into short sequences, on the other hand, enhances performance and yields approximately the same accuracy as with the final 0.4-s stimulus. This suggests that each sudden change resets the process of heading judgment. At the end of the full trial it is based on the last 0.4-s sequence.

We may conclude that optic flow fields are analyzed within sequences of several hundred milliseconds. For longer flow sequences the visual information within the additional flow duration is not optimally extracted. Thus, at least in the case of heading toward a frontoparallel plane, heading estimation seems to depend crucially on the duration of the final flow sequence. Possible reasons related to eye-movement behavior in natural situations will be discussed below.

8. EXPERIMENT 6: OBLIQUE HEADING TOWARD THE PLANE

In all experiments up to now, the observer approached the plane on a perpendicular path. In the final experiment we simulated an oblique approach toward a plane during a tracking eye movement (see Fig. 10). This has several consequences for heading judgments. In an oblique approach, several sources of information in the flow field that fall together in a perpendicular approach become separated.

First of all, the retinal flow field induced by a movement relative to a plane is ambiguous.[21] At any given instance in time, the task of determining heading from retinal flow has two mathematically equivalent solutions. The first is the true motion of the observer. The second is obtained by exchanging the normal to the plane (n) and the direction of self-motion. Also required is a change of the rotational motion of the observer. With a perpendicular approach toward the plane, the plane normal and the movement direction are identical. Therefore, in the experiments performed so far, the ambiguity did not occur. Second, the point of the maximum rate of magnification becomes separated from the plane normal and the direction of movement. For a movement toward a single plane the maximum of divergence appears in a visual direction that bisects the angle between the movement direction and the plane normal, independent of eye rotations.[9] With a perpendicular approach, it falls together with the direction of self-motion.

We examined the oblique approach for two reasons. The first was to test the percept of the subjects in the case

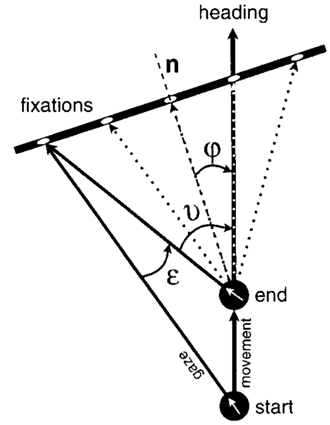

Fig. 10. Illustration of the experimental setup in experiment 6. The observer approaches the plane under an angle φ with respect to the plane normal n. During the movement the observer fixates a point to the right or left of the plane normal. This results in a retinal heading angle ν with respect to his direction of gaze.

of an ambiguous flow field. The second was to examine which information in the retinal flow subjects use for their heading judgments. Because of the ambiguity, subjects could either judge heading correctly or choose to point toward the plane normal. Besides these two mathematically correct solutions, subjects still might erroneously choose the pseudofocus, i.e., the direction of gaze, if they relied on the radial structure of the flow field. The maximum of divergence might also have some significance.

We simulated paths that deviated by an angle φ of 0°, ±10°, or ±20° from the plane normal, as illustrated in Fig. 10. At the end of the movement, the fixation point on the plane was at 0°, 10°, or 20° to the left or right of the plane normal. Note that the retinal heading angle ν now is the sum of the angle between the gaze direction and the plane normal and the path angle φ. We used only those combinations of path angles and gaze directions in which the magnitude of the retinal heading angle ν did not exceed 30°. As a consequence, the number of data points varied between conditions. The observer's speed component perpendicular to the plane was 1 m/s in all cases. Therefore absolute speed varied slightly for different path angles. Mean rotation rate was between 0°/s and 20.4°/s, and stimulus duration was 0.5 s. The presentation of conditions was randomized, with each condition presented eight times. We used the same seven subjects that had participated in the second part of experiment 1.

A. Results

The five diagrams in Fig. 11 show the mean reported heading of all subjects for the five different angles of approach. The dotted diagonal again gives the veridical heading angle. Pointing toward the pseudofocus would result in responses on the dashed horizontal line. The dashed–dotted line parallel to the diagonal indicates pointing toward the plane normal.

The slopes of the regression lines over the retinal heading angles are similar for all the angles φ. But a systematic offset can be observed. For simulated approaches that are not perpendicular to the plane, the regression

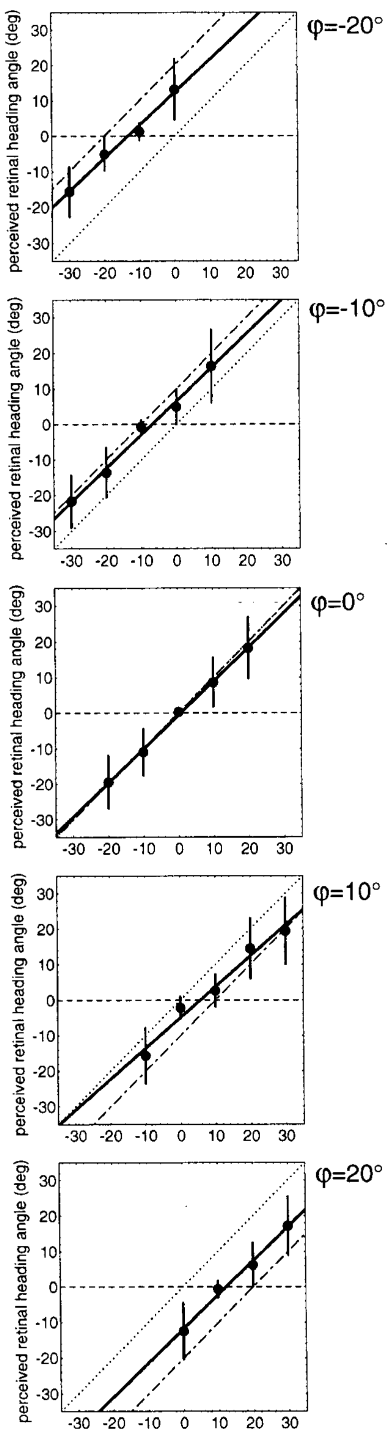

Fig. 11. Results of experiment 6. Mean responses of seven subjects are presented for different path angles φ. Dotted diagonal, simulated heading angle; dashed-dotted line parallel to the diagonal, direction of the plane normal. Whereas for perpendicular approaches ($\varphi = 0$) the subjects' judgments are correct, for $\varphi \neq 0$ a systematic offset toward the plane normal can be observed. Note that for $\varphi = 20°$ and for $\varphi = -20°$ only four data points are available. Because we wanted the magnitude of the retinal heading angle ν to remain below 30°, these conditions could not include trials in which the fixation point deviated by −20° or by 20°, respectively, from the plane normal.

line is shifted toward the plane normal. The magnitude of the shift depends on the angle of approach. Overall, the perceived heading is shifted approximately halfway toward the normal to the plane. In controls in which we presented the stimuli for 2 s, the usual bias toward the pseudofocus was observed (not shown).

B. Conclusion and Discussion

For oblique approaches toward the plane, subjects report neither the veridical simulated heading nor the other mathematically correct solution, which would be the plane normal. Rather, on average, they indicate a point between the two solutions. Because the responses are mean values, this could be due to an average of single responses, if half of the responses indicated the veridical direction and the other half indicated the plane normal. However, neither the distribution of single responses in individual subjects nor the distribution of the means of the subjects appeared bimodal. This suggests that subjects perceived themselves as moving toward a point between the veridical heading and the plane normal.

This behavior could reflect an internal compromise between the two ambiguous solutions. For a short presentation duration, no decision can be made between the two mathematically correct solutions for heading,[21] and therefore subjects may have chosen a compromise between the two solutions and reported the mean.

However, the reported location also roughly corresponds to the point of the maximum of divergence that appears midway between the simulated heading and the plane normal. The results can be explained when subjects mistakenly chose the location of the maximum of divergence to judge heading. Previously, Regan and Beverley[30] assumed that subjects used the maximum of divergence instead of the focus of expansion in heading estimation tasks. However, the stimulus used by Regan and Beverley was very different from ours. It is therefore difficult to directly compare their result with ours, except for the conclusion that the maximum of divergence may have visual significance in heading estimation.

At first glance, the result of experiment 6 seems in conflict with the results of Warren *et al.*,[8] who tested both hypotheses in pure translational approaches toward a frontoparallel plane and found support for the radial structure as being used for heading estimation. However, our control experiments show that for prolonged stimulus durations subjects bias their responses toward the pseudofocus of expansion. This in turn is consistent with the results of Warren *et al.*,[8] who presented their stimuli with durations of 3.7 s.

9. SUMMARY AND GENERAL DISCUSSION

We studied the mechanisms and dynamics of human heading estimation from retinal flow. Our experimental conditions presented to the static eye retinal flow that contained translational and rotational components. Therefore observers had the retinal flow pattern available, but extraretinal information would signal the absence of an eye rotation. We simulated an observer's movement toward a vertical plane combined with a tracking eye movement. To determine heading correctly in this situation, one has to detect the rotational component in the flow field. In natural conditions two sources of information are available: extraretinal signals and visual information. Extraretinal signals enable subjects to judge heading correctly in this specific movement situation.[3,4,6] However, in our experiments subjects did not actually execute an eye movement but fixated a stationary target on the display while an eye movement was simulated in the stimulus. Thus extraretinal information could not signal the presence of a rotation in the flow field. It might instead signal static eye position, thereby creating a conflict between visual and extraretinal signals.

Visual information about a rotational component in the flow field can come from motion parallax, i.e., from the differences in visual motion that originate from depth variations in the scene.[6,15,14,16] However, in the situation we studied, the visual scene contained very little depth variations. Local motion parallax, i.e., differences in motion between neighboring image points, was almost completely absent. Global motion parallax was available to some degree because the plane was slanted with respect to the observer's line of sight. This resulted in a gradient of image speeds along the slanted plane.

In contrast to previous studies,[3,4,6] our subjects under some conditions gave on average good heading estimates in a perpendicular approach toward the plane. We made two basic observations: First, correct heading judgments in this situation required a large field of view. Second, heading errors were larger after the presentation of a long (3.2-s) stimulus than for a short stimulus consisting of only the last 0.4 s. In these short trials, heading judgements were reasonably accurate when the field of view was large. For long stimulus durations or for a small field of view, the percept of heading was biased toward the percept of a pure linear movement. This raises two questions: (1) Why is heading estimation better in the large field of view? (2) Why does it change with time?

A. Large Field of View

The essential problem in judging heading toward a vertical plane is the nearly complete lack of depth variations and the resulting absence of local motion parallax.[3,4,6,14] However, the stimulus is not entirely devoid of depth variations. During the simulated movement of the observer, the slant of the plane relative to the observer changes. A large field of view includes changing texture gradients and speed gradients (global motion parallax) in the periphery that allow detection of the relative movement of the plane [see Fig. 1(E)]. The percept of the rotational component might enable subjects to differentiate the pseudofocus from a real focus of expansion and to evaluate the flow field in terms of observer rotation and translation.

The situation becomes more difficult when the field of view is restricted. The visual cues that specify the changing slant of the plane are strongest in the peripheral parts of the stimulus [see Fig. 1(E)]. With a small field of view there is not enough information available to detect the rotational component in the flow field.[20] Therefore the underlying self-motion is more likely interpreted as a pure translational movement. Heading in this case might be judged by the radial structure. This would lead to the observed confusion of the pseudofocus at the fixation point with a real focus of expansion.

For paths perpendicular to the plane, subjects estimated the simulated heading in the short trials on average correctly, provided a large field of view. For an oblique approach toward the plane, subjects reported a location about halfway between the veridical direction and the plane normal. Since the flow field in this situation is ambiguous, these responses might result from a compromise between the two mathematically correct solutions. In theory, the ambiguity can be resolved over time.[21] As the position of the observer changes during the movement, the plane normal intersects the plane at different points. Heading, however, always remains toward the same point on the plane. Thus the two solutions should become separable after some time. In our data the instantaneous ambiguity of the flow field might have influenced the behavior of the subjects. For the short trials, heading was perceived in a direction that might reflect a compromise between the two possible solutions. The hypothesis that the ambiguity is resolved over time, however, is not supported by our data. Instead, for the long trials, subjects biased their judgments toward the center of expansion, which suggests an entirely different response behavior. The same behavior occurs also for perpendicular approaches toward the plane, i.e., in a situation in which no ambiguity exists.

B. Dynamics of Heading Estimation

In the short trials, subjects perceived the simulated heading correctly. In the long trials, responses were biased toward the center of expansion. This bias occurred independently of the magnitude of change in the simulated retinal heading angle. This finding is rather surprising because it contradicts the common assumption that longer stimulus durations should facilitate better performance.[21,22,23]

Indeed, it seems logical that longer stimulus durations provide more visual information. However, the actual amount of information that is gained by longer presentation might be rather small. If we assume that the changing slant of the plane is relevant, then we should note that the largest change occurred toward the end of the movement. Because the long and the short trials ended in exactly the same positions, much of the information given in the long trials is also available in the short trials. Nevertheless, if heading estimation were based on the total information given during a trial, one would expect an actual improvement for longer presentations, or at least constant performance. On the other hand, the flow field at the start of a long trial contains insufficient information to determine heading correctly. Performance in the long trials would therefore be impaired if subjects base their judgments mainly on the initial part of the stimulus. This would require either that subjects ignore the information at the end of the trial or that they evaluate it in a different way than when presented alone in a short trial. We believe the former to be unlikely. First, subjects were asked to indicate their collision point with the plane after the end of the trial. Thus they had to be attentive to the end of the trial. Second, because the heading angle changes over the course of a trial, subjects needed to keep track of their heading throughout the presentation. Experiment 4 confirmed that subjects did not simply use the initial heading angle. Third, in the control experiment that presented the initial 0.4 s of the long trial, relative errors were similar to those after 3.2 s. Absolute perceived heading angles, however, were much larger after 3.2 s than after 0.4 s, corresponding to the change in heading angle during the long trial. Therefore we conclude that subjects must have interpreted the flow in the final part of the long sequences in a different way than in the short trials. This implies that the same flow-field sequence is analyzed differently when it forms the end of a longer sequence than when it is presented in isolation. Hence the way the visual system analyzes retinal flow must change dynamically over time.

At present, we can only speculate about possible reasons for such a change. Many different mechanisms and signals have been suggested for heading estimation. Because our stimuli lack several important cues and provide conflicting signals, some of these mechanisms are expected to show characteristic errors. Therefore one possible explanation could be that the system uses multiple parallel heading estimation schemes[31] and dynamically varies their relative contributions. Or it could base heading estimates on multiple parallel signals and vary their respective influences.

The percept of a pure self-translation that occurs for the long trials would require the assumption of the absence of a rotation. Therefore the different heading judgments could depend on whether the presence of an eye rotation is detected. The brain has two major sources of information to determine the presence of an eye rotation. These are the visual input and extraretinal eye-movement signals. In our case, the two signals are in conflict. The flow field contained visual evidence for a rotation, but the eyes were stationary. An extraretinal fixation signal might bias the percept toward that of a pure translation. Under this assumption, the different percepts could be explained if the strength of the contribution of these two signals varied over time. Interestingly, a change in the relative contribution of visual versus extraretinal signals over time has been reported for pursuit eye movements. In the Filehne illusion, subjects track a moving target with the eyes, and a second stationary target is presented. Although stationary, this target is perceived to move slightly in the opposite direction of the eye movement. This is regarded as evidence that the extraretinal signal underestimates the eye movement.[32] It cannot completely compensate for the eye-movement-induced retinal motion of the stationary target. The strength of the Filehne illusion depends on the duration of the presentation of the stationary target[33]: It is large for brief target presentations (300 ms) and decreases for longer durations (1000 ms). This finding suggests that the contribution of visual and extraretinal signals during eye movements changes with stimulus duration. If a similar effect occurs for fixation signals it might explain our findings.

It might also be important to observe that the long simulation trials are somewhat unusual with respect to normal behavior. During real self-motion or during inspection of optic flow fields, typical oculomotor behavior consists of an alteration of saccades and reflectory tracking movements.[34–37] The frequency of saccades is approximately 2–3 Hz.[36,37] Therefore the normal sampling of the optic flow field consists of sequences of only 300–500 ms. Eye movements in this situation are driven in part by reflectory mechanisms and are somewhat inaccurate.[36,37] Longer sequences of continuous tracking are the exception; they occur typically only for voluntary fixation of a target for an extended period of time. The eye movements in this case are much more precise.[34,37] The short trials thus present a typical visual input that often occurs during normal behavior but usually has a variable and inaccurate eye-movement component. In contrast, the long trials present an exceptional situation in which eye movement is very predictable. Maybe the system uses two different modes of operation in these two cases. The long trials might bias the system toward the percept of a constant and accurate oculomotor behavior and toward an increased reliance on extraretinal input. Because extraretinal input in our experiments could signal only a static eye, such a system must evaluate the flow field as that of a pure linear movement. In short flow sequences, in contrast, judgments are based on visual information regarding a rotation and translation of the eye; the results of experiment 5 support this view. Sudden changes of the distribution of dots partially simulate the effect of saccadic eye movements. They interrupt the continuous stream of visual motion input. These interruptions segment the flow into samples of the typical intersaccadic interval. This restarts the process of visual flow-field analysis and leads to a restoration of correct heading judgments.

Address correspondence to Markus Lappe, e-mail lappe@neurobiologie.ruhr-uni-bochum.de.

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