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An Analysis of Heading towards a Wall

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Navigating towards a desired spatial location is an easy task, provided that you are capable of seeing your environment. Vision will guide your movement and allow you to reach your goal successfully. Vision in this situation encompasses various signals: the pattern of image motion on the retina (the *retinal flow field*), the variations in image motion of points in different distances in the environment (*motion parallax*) and the depth information itself relayed by cues such as texture gradients or binocular disparity. Sensory information is received from many other senses besides vision by the brain during locomotion. The vestibular organs transmit information about acceleration and orientation of the head relative to the ground, proprioception signals the posture of the limbs relative to the trunk, and the oculomotor reference signal yields information about the movement of the eyes.

It has been a long-lasting discussion whether visual information alone is sufficient to specify the direction of one's movement in space, or the *direction of heading*. Gibson (1950) was the first to investigate the visual motion that results from self movement through a structured environment. He introduced the term *optic flow* to refer to the temporal changes in the visual environment around a moving observation point (Gibson, 1950, 1966). This idealized observation point is thought to lie in front of an observer's eye. The optic flow therefore describes the visual movement that surrounds the moving eye. The movement pattern arising in the eye, i.e. on the observer's retina, is referred to as *retinal flow*. The retinal flow is the sum of the image motion resulting from self movement and the image motion resulting from rotation of the observer's eye. Both optic and retinal flow patterns can be illustrated by vector fields

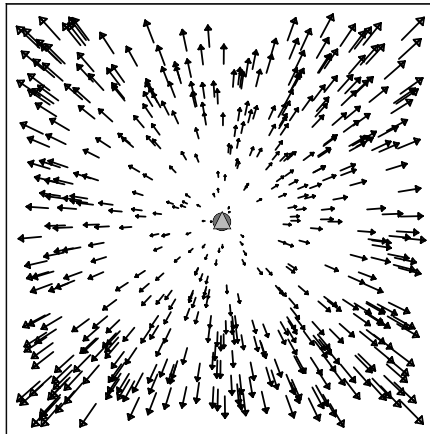


Fig. 5.1. When an observer approaches a vertical wall along the wall normal (i.e. on a path perpendicular to the wall) a radial optic flow pattern is created. In this vector plot of the optic flow pattern, each vector gives the optical velocity of a single point on the wall. The heading direction is marked by a triangle. It is located in the center of the radial motion pattern. It represents the focus of expansion of the optic flow field.

in which each vector gives the optical velocity of a point in the environment relative to the head or eye respectively (see for example Figure 5.1). Based on geometrical considerations on optic flow fields, Gibson (1950, 1966) suggested a way to determine the direction of heading. During linear translation, the heading direction becomes a singular point in the optic flow field. The movement of all other image points flows radially out from this point. It is therefore called the *focus of expansion*.

Figure 5.1 illustrates an optic flow field that arises when an observer moves perpendicularly towards a vertical wall. A vertical wall is a special case because all the points are in a plane. This means that the velocity and direction of all points can be accurately predicted from only a few parameters that describe the orientation of the wall. This is unlike the motion of points that make up a normal three-dimensional environment which do not have this redundancy. Around the heading direction, which is indicated by the triangle, a radial flow pattern appears with the focus of expansion marking the heading direction. With the discovery of the focus of expansion a direct solution seemed to be found to explain the visual control of self-motion. The maintenance of a course would require locating the focus of expansion in the visual field, adjusting it to the desired aiming point, and then maintaining the coincidence between the focus of expansion and the desired goal during locomotion (Gibson, 1950, 1966).

First approaches to the heading detection problem

During the decade after Gibson's initial work, these concepts were applied in theories that tried to explain the human ability to steer cars or to land air planes. In the seventies, the first experiments were performed to determine how accurate humans could locate the focus of expansion in an optic flow field. In these experiments, human subjects were presented with expanding random dot patterns with the focus of expansion at different locations on the display. Random dot patterns were used instead of natural scenes to avoid interference by object recognition processes and to restrict the information content of the stimulus to pure velocity fields. Because the real-time computer graphics used today were not available at that time, the experimental setups needed to be more inventive.

Llewellyn (1971) painted dots or glued circular discs on glass plates which were held in front of a point light source. The dots cast shadows on a translucent screen viewed by the subjects. To create expansion, the glass plate was moved towards the light source. After the movement had stopped the subjects had to adjust the light of a torch to the location on the screen where they had perceived the focus of expansion. Llewellyn (1971) found very poor accuracy with mean errors between 5° and 10° . A similarly disappointing result was found by Johnston, White, and Cumming (1973) who used an animated movie of a random dot pattern. A digital computer calculated the positions of dots seen from a moving vehicle approaching a vertically oriented, dotted surface. Single frames of that motion were then photographed from a visual display on to 16-mm film. This film was projected by a fisheye lens on a spherical dome 28 ft in diameter. The subject was seated at the center of this dome. When indicating the center of the projected expansional motion, subjects exhibited errors of 8° to 13° . Johnston, White, and Cumming (1973) as well as Llewellyn (1971) concluded that the precision in identifying the focus of expansion was too low to satisfy the locomotion strategy proposed by Gibson and hence called his proposal into question. They pointed out that in real life locomotion takes place in surroundings with real objects of specific shapes, sizes and colors, the knowledge, recognition and observation of which during self-motion could help navigating (see also Cutting et al. (1992) and Vishton and Cutting (1995) in this regard).

Later, Warren, Morris, and Kalish (1988) examined the heading detection performance from flow fields, simulating translational movements towards a wall with computer generated real-time simulations displayed on a video screen. In contrast to the earlier studies, they found mean detection errors

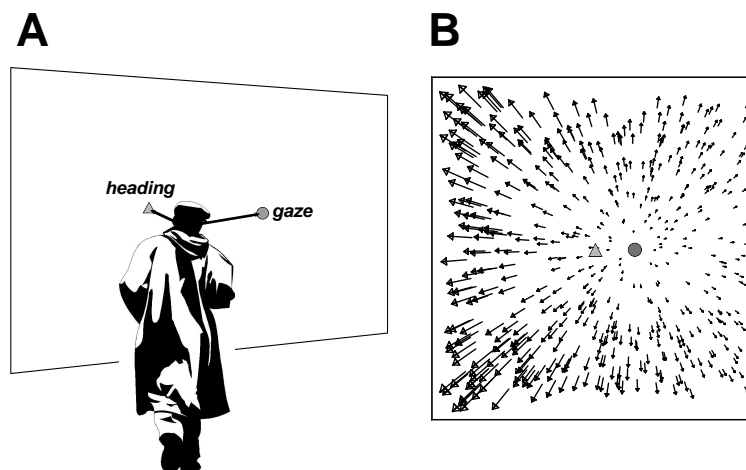


Fig. 5.2. A: While an observer moves towards a vertical wall his gaze may not be directed to a point on the wall that coincides with his heading direction. However, if he intends to keep gaze on another point on the wall during his forward motion, an appropriate tracking eye movement is required. B: The retinal flow pattern in this situation contains radial motion flowing away from the fixation point (circle) instead of from the direction of heading (triangle). The heading direction no longer corresponds to the focus of expansion. The gaze direction becomes a pseudo-focus of expansion.

of only about 1° . Besides the advanced experimental setup which should allow higher accuracy, Warren, Morris, and Kalish (1988) attributed the much better performance which they reported to the two-alternative forced-choice (2AFC) discrimination task they used instead of a pointing task. In a pointing task subjects have to judge absolute locations whereas in a 2AFC task they give their judgements relative to a target. However, it has to be considered that in such a discrimination task the average detection error depends on a threshold for percent correct, which has to be defined. Warren, Morris, and Kalish (1988) used a threshold of 75%. This means that 75% of the answers were better or equal to 1° . As proposed by Gibson (1950, 1966), they suggested that moving observers rely on the radial structure in the optic flow field to determine heading.

But is this radial structure really a good cue for the visual determination of heading during locomotion? When one considers retinal flow, i.e. the flow pattern that actually appears in the eye, the answer must be no. The best demonstration for this comes from considering the retinal flow arising from movement towards a fronto-parallel wall.

Retinal flow and the problem with eye movements

Regan and Beverly (1982) examined the retinal flow pattern that arises when an observer fixates and tracks a point on the wall that is offset from the direction in which he is heading. Such a movement is illustrated in Figure 5.2A. The observer walks towards the wall while directing his gaze to a point on the right of the heading direction. Regan and Beverly demonstrated that the radial expansion which indicates the heading direction in the optic flow field, is replaced in the retinal flow pattern by a quasi expansional structure with its center at the fovea. This flow is illustrated in Figure 5.2B. The retinal flow field is shown that is created when the observer fixates a point to the right of the direction of heading. In this case the heading direction, indicated by the triangle, no longer corresponds to a focus of expansion. Instead, a quasi-expansional structure appears around the gaze direction, which is indicated by the circle. We will refer to this point as the *pseudo-focus* of expansion. Near the center of the retinal expansion, the motion pattern differs only slightly from the pattern that would have been observed during real translation towards the direction of gaze (Figure 5.1). However, the deviation becomes stronger in the peripheral parts of the visual field.

This special case of movement towards a wall is a powerful demonstration that the radial structure in a retinal flow field does not simply indicate the direction of heading. The question then is: How is the heading direction deduced from the retinal flow when eye movements are involved?

Heading detection during eye movements: The need for depth or extraretinal information

To examine the influence of eye movements on heading detection, several authors (Rieger & Toet, 1985; Warren & Hannon, 1990; Royden, Banks, & Crowell, 1992; Royden, Crowell, & Banks, 1994; Banks, Ehrlich, Backus, & Crowell, 1996) used the paradigm of simulated eye rotations. They presented a flow field corresponding to translational movement of an observer, together with a rotation of the viewpoint and instructed subjects to fixate a stationary target. The retinal stimulus in this case should be the same as the retinal flow experienced during real translation and real eye movement. Rieger and Toet (1985) added various 3D rotations to flow fields that simulated an observer's

approach to one or two vertical random-dot planes. However, the added rotations in this case did not actually simulate tracking eye movements but were varied in orientation and speed independent of the visual scene. Subjects had to judge the heading direction in a 4AFC task relative to the fixation point on the screen center. Rieger and Toet (1985) found that when the scene consisted of two planes separated in depth, subjects performed acceptably well. With only one plane, corresponding to heading towards a wall, heading detection was at chance.

The basic finding of all these studies was that depth differences in the environment help the visual system to interpret retinal flow in the presence of eye movements. It has been suggested that the observer relies on the relative optical motion of elements in different depths. The so called *motion parallax* contains information about the relative magnitudes of translational and rotational components in the movement. Whereas the observer's translational movement results in visual motion that depends on the depth layout of the scene, the velocity field resulting from an observer's rotation or eye movement is independent of the element distances. Therefore, if the retinal flow results from motion within a richly three-dimensional world, the translational and rotational components can, at least theoretically, be separated (Rieger & Lawton, 1985; Koenderink & van Doorn, 1981; Longuet-Higgins & Prazdny, 1980). A wall is a very sparse three-dimensional world which makes the separation much more difficult.

Warren and Hannon (1990) used computer displays to present flow fields simulating an observer's linear forward motion combined with a tracking eye movement. They created different environmental scenes including a single vertical plane textured with dots, a 3D cloud of dots and a more natural scene of a dot covered ground plane to walk over. The geometry they employed in simulating movement towards a single plane is sketched in Figure 5.3A. The observer approaches the plane perpendicularly with a speed v . A specified point on the right or left from his heading direction is tracked during a movement of duration t . During the movement, the angle ν between the gaze and the heading direction changes from ν_0 to ν_t . Subjects viewed the simulated movement on a computer screen and subsequently had to judge the simulated heading direction. They were instructed to fixate a point which was either moved across the screen or was stationary. In the first case the subjects performed a real eye movement, whereas in the latter case such an eye movement was simulated within the flow field display.

Warren and Hannon (1990) found no differences in the subjects' ability to

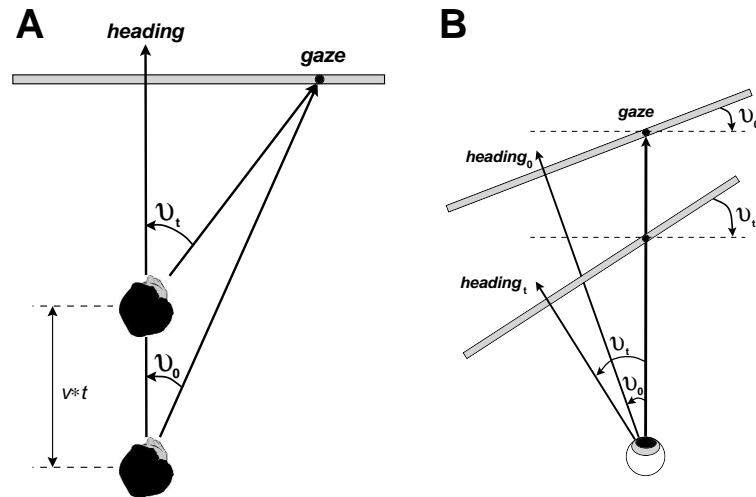


Fig. 5.3. A: Illustration of the movement simulated in the heading detection experiments. An observer approaches a vertical wall in direction of the wall normal while fixating a point to the right (or left) of the heading direction. He moves with a speed v for a time t . The angle between his direction of heading and the direction of gaze is ν_0 in the beginning and ν_t at the end of the movement. B: The same movement seen by the eye. During the approach towards the wall the eye holds gaze upon a specified point on the wall. The slant of the wall with respect to the line of sight changes because of the increasing retinal heading angle ν between the direction of gaze and the direction of heading.

determine the simulated heading direction in both the simulated and real eye movement condition, provided there were depth variations in the simulated environment. When a movement towards a single plane was combined with a tracking eye movement in the simulation, subjects responded at chance, similar to the findings of Rieger and Toet (1985). Warren and Hannon (1990) reported that in this case subjects tended to perceive themselves as heading towards the fixation point. As mentioned above and illustrated in Figure 5.2B, in the single plane layout the fixation point becomes a pseudo-focus in the retinal flow field. Warren and Hannon suggested that subjects misperceived this pseudo-focus as the direction of heading. Thus, when heading towards a wall subjects seem to rely on expansion in the flow field as the indicator of their heading.¹

¹As soon as depth is introduced in the environment the fixation point of course remains a singular point but does no longer show a clear expansional structure that could be mistaken for a focus of expansion. The fixation of a point on a floor as an observer walks over it for example, results in a spiral structure around the fixation point in the retinal flow field. When determining heading from such a flow field, subjects are forced to use cues other than

Royden, Crowell, and Banks (1992) and Royden, Banks, and Crowell (1994) performed similar experiments to Warren and Hannon's with varying environmental layouts and simulated as well as real eye movements. In their experiments, the eye rotation was not limited to a visual tracking of an object in the scene. Some conditions simulated the tracking of an independently moving object not attached to the scene. Consistent with Warren and Hannon (1990), Royden et al. (1992, 1994) found that during real eye movements, heading detection was possible and accurate. On the other hand, when the eye rotation was simulated, subjects always made large errors, except in 3D environments with very low rotation rates of below $1^\circ/\text{sec}$. In the simulation of heading towards a single wall with simulated eye movements, heading detection was not possible at all. Royden et al. (1992, 1994) concluded that to analyze retinal flow, extraretinal eye velocity information is necessary for the brain. When an oculomotor reference signal is available, the eye rotation can be compensated for and the flow field is analyzed correctly.

The view that emerges from these studies is the following: Heading detection from retinal flow fields simulating a linear approach to a vertical wall combined with a simulated tracking eye movement fails because of the lack of depth in the environment and the lack of an extraretinal signal. The retinal flow field contains a pseudo-focus of expansion at the fixation point. Because extraretinal input is absent no information is available to distinguish the pseudo-focus from a real focus of expansion. The approximately radial structure around the fixation point is taken as an indicator for the heading direction and leads to the systematic misjudgment.

In the following, we will describe experiments that require a revision of this view.

Heading towards a wall: New considerations

When an observer approaches a vertical plane, minimal depth variations occur when the plane is perpendicular to the line of sight. If the plane is slanted at some angle with regard to the line of sight, parts of the plane will be nearer to the observer than others. If the observer performs an eye movement during his forward motion, the line of sight will change, and in consequence the slant of the plane will change, too. Sketched in Figure 5.3B is the orientation of the plane with respect to the eye of the observer in Figure 5.3A. The fixation of a point on the wall in a direction different from the wall normal, results in

radial structure.

a slant ν of the wall with respect to the line of sight. During a movement of duration t the eye approaches the wall. At the same time, the angle ν between the direction of heading and the direction of gaze becomes larger and so does the slant of the wall. Thus, if such a movement is presented over time, some subtle depth variations will inevitably occur. The question is: Is it possible to use these subtle changes to obtain a correct estimation of heading even during eye movement?

Given a homogeneously textured wall, depth information or information about the slant of the wall can be obtained from several visual cues. One is the visual density of points on the wall at different distances, i.e. the texture gradient. A second one is the speed gradient, i.e. the fact that points at different distances move at different retinal velocities. Third, if the scene is watched with both eyes, binocular disparity also yields depth information. Let us concentrate on the monocular cues first.

The importance of a large field of view

In Figure 5.4 (left) a retinal flow field originating from the movement sketched in Figure 5.3 is shown. The wall is represented by a plane of dots which are projected on a visual field of $90^\circ \times 90^\circ$. The fixation point is projected on the fovea, that is on the center of the visual field, here marked by the circle. It remains fixed on the fovea while the images of the other dots move depending on the observer's movement. The figure shows the trajectories of the dot images during a typical movement. Each point indicates the position of a single dot image after a single frame. The thick black line marks the heading direction which also moves on the retina during the course of movement. The final angle between heading direction and gaze direction is 6° . Around the fixation point, a clear expansional structure, the pseudo-focus, appears. Information about the slant of the wall relative to the eye is also available. A speed gradient can be observed since the velocities of the dots on the right side, which is the more distant side of the wall, are lower than of those on the left side. This can be recognized by the smaller spacing between points on a trajectory on the right side. Warren and Hannon (1990) as well as Royden et al. (1992, 1994) used a display consisting of homogeneously distributed dots which therefore, like our display, also contained texture and speed gradients. However, the strengths of both of these cues depend on two parameters. The first is the slant of the wall, which is directly related to the retinal heading angle ν between heading and gaze direction. The second is the size of the field of view.

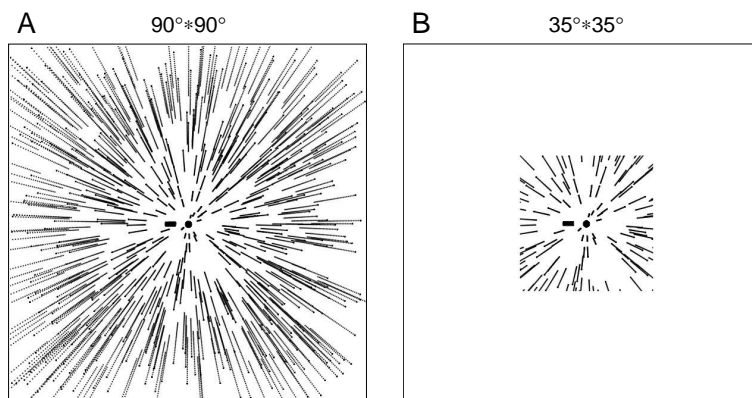


Fig. 5.4. Retinal motion resulting from a movement towards a random-dot plane in the direction of the plane normal in combination with a tracking eye movement. Displayed are the trajectories of the dot images during the movement. Each point indicates the position of a single dot image after a certain time interval. The circle marks the fixation point which is always projected on the fovea, i.e. on the center of the visual field. Also shown by the thick black line is the heading direction. It shifts from close to the direction of gaze at the beginning of the movement to 6° to one side in both cases. A shows a field of view of $90^\circ \times 90^\circ$, B shows a field of view of $35^\circ \times 35^\circ$.

The displays in the described experiments presented a field of view of $40^\circ \times 32^\circ$ (Warren & Hannon, 1990) and $30^\circ \times 30^\circ$ (Royden et al., 1992, 1994). The unrestricted visual field of a human observer covers roughly $180^\circ \times 150^\circ$. The flow field in Figure 5.4 (left) extends $90^\circ \times 90^\circ$. In comparison, Figure 5.4 (right) shows a field of view of $35^\circ \times 35^\circ$. It is difficult to observe texture or speed gradients in the small field of view. Therefore an extension of the field of view might be expected to influence the heading detection performance, as a larger field of view should be associated with a greater range of three-dimensional variation and therefore might make the task easier. This suggestion has been made previously on the basis of computer simulations of an ideal observer (Koenderink & van Doorn, 1987). However, surprisingly, an enlargement of the field of view up to $60^\circ \times 40^\circ$ in experiments of Banks et al. (1996) did not lead to significant improvements of the heading judgements.

We confirmed this negative result even with a field of view as large as $90^\circ \times 90^\circ$. We simulated a perpendicular approach towards a homogeneously dotted wall together with an eye movement that kept gaze on a point on the wall (Figure 5.3). The stimuli were generated on a Silicon Graphics workstation and were displayed by a video projector on a large tangent screen 60 cm in front of the subject. Subjects had to fixate in the middle of the screen. To re-examine the experiments of Warren and Hannon (1990) we chose parameters

similar to theirs. The retinal heading angle ν , i.e. the angle between the direction of heading and the direction of gaze, was varied horizontally between -6° and 6° . The simulated speed of the observer was 2.0 m/sec. The stimulus presentation lasted for 3.2 seconds. However, we used a pointing task instead of the 2AFC task. After the movement had stopped, subjects were instructed to point at the location on the screen where they thought they would hit the wall if the movement had continued.

Despite of the large field of view subjects were not able to judge the simulated heading direction correctly. Instead, their judgements were strongly biased towards the fixation points. Some subjects even pointed directly at the fixation point.

Warren and Hannon (1990) described that subjects erroneously perceived the direction of gaze as their heading. In our case, however, only an intermediate bias towards the fixation point occurred. This difference is most probably due to the size of the field of view. Our display contained greater texture gradients appearing mainly in the periphery and helping to convey the changing slant of the wall relative to the line of sight.

We conclude that depth cues provided by an enlargement of the field of view alone are not sufficient to allow correct heading detection. We next asked whether binocular disparity might be exploited as a cue in this situation.

Does stereoscopic vision help?

Stereo vision has been shown to contribute to heading detection from optic flow by introducing more depth cues. Stereo vision improves heading judgements from noisy optic flow fields in conditions where monocular observers perform only poorly (van den Berg & Brenner, 1994). A direct demonstration of an influence of disparity-based depth order can be observed in an "illusory optic flow" stimulus (Grigo & Lappe, 1998). In this illusion, subjects perceive a shift of the center of an expanding optic flow field when it is transparently superimposed on a unidirectional motion pattern (Duffy & Wurtz, 1993). This illusory shift can be explained by the visual system taking the presented flow pattern as a certain self-motion flow field and then determining the direction of heading as if the transparent translational motion had resulted from an eye rotation (Lappe & Rauschecker, 1995). The magnitude of the illusory shift depends strongly on the depth order of the two superimposed motion patterns. When the translating pattern is presented in front of the expanding pattern, a highly significant decrease of the illusory shift occurs, down to 25 percent of

its magnitude at zero disparity. When the translation is presented behind the expansion, the illusory shift decreases only slightly (Grigo & Lappe, 1998).

We wanted to test whether binocular disparity can also help in perceiving one's movement towards a wall. We presented the same simulated observer movement as before, only now in a stereoscopic projection that contained realistic binocular disparities of the moving dots. We used active LCD shutter glasses for the stereoscopic perception. We found no improvements in the heading detection results compared to the experiments using monocular presentation. Presumably the disparities are too small and too evenly distributed compared to those of a rich three-dimensional stimulus.

Stimulus duration as a critical parameter

A further aspect of the experimental condition that could potentially influence heading judgements is the temporal duration of the simulated movement. As can be seen in Figure 5.4, the simulated heading direction shifts on the retina during an observer's movement towards a wall whilst tracking a point on the wall off to one side. The magnitude of the shift depends on the duration of the stimulus. Similarly, the magnitude of the change of the slant of the wall also depends on the stimulus duration. Therefore, we performed the experiment with a very short simulation time. Instead of 3.2 seconds as before, we used a stimulus duration of 0.4 seconds. The final retinal position of the direction of heading at the end of the trials was the same as in the previous experiments with the long presentation time. The initial retinal heading angles at the start of the trials were accordingly adjusted for the shorter stimulus presentations. Thus, the short trials effectively presented the last 0.4 seconds of the longer trials. Subjects had to indicate the final heading angle in the display.

Surprisingly, with these very short movement times, subjects were suddenly successful in detecting the direction of heading as being distinct from the direction of gaze and the pseudo-focus of expansion. However, this was only possible with the large field of view: with the short simulation time but only a small field of view, performance remained poor. Subjects verbally reported low confidence in their heading judgements in all conditions, but found the short stimulation condition easier to perform. Thus, there seem to be two main constraints on successfully detecting heading direction in a simulated movement towards a wall: the field of view has to be large and the presentation time has to be short.

Surprised by this finding, we measured the relationship between stimulus duration and heading detection performance. We presented optic flow patterns

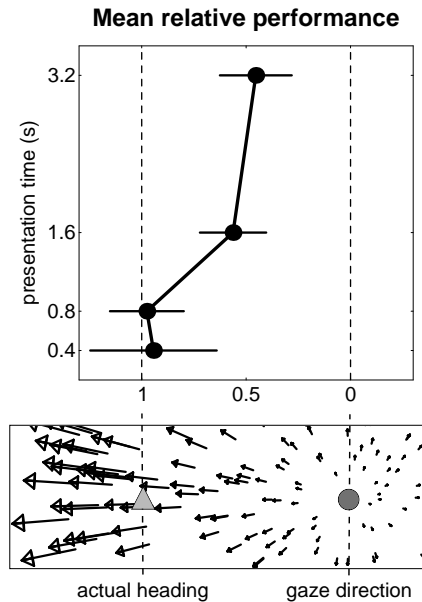


Fig. 5.5. Dependence of the accuracy of heading judgements on the duration of the stimulus. The final difference between the heading direction and the fixation direction was varied in five steps between -6° and 6° . The relative performance is the slope of the regression line of judged heading direction against actual heading direction. A value of 1 corresponds to correct heading detection. A value of 0 indicates pointing towards the direction of gaze. The responses for each heading angle were averaged over 9 subjects. Performance clearly drops for prolonged movement times as a bias towards the fixation point appears. Whereas with short presentations subjects performed correctly, with stimulus durations greater than one second, they pointed closer to the fixation point.

with durations between 0.4 and 3.2 seconds. The final angle between the direction of gaze and the direction of heading was varied in five steps between -6° and 6° . Each combination of presentation time and heading angle was displayed five times. Nine subjects participated in the experiment. For the analysis, the responses for each heading angle were averaged over the subjects. Then the relative performance was calculated as the slope of the regression line over the five heading angles. A slope of unity indicates correct heading perception and zero corresponds to pointing towards the pseudo-focus at the fixation point.

The results are displayed in Figure 5.5. We found that with movement times over about one second the tendency to point closer to the fixation point increased dramatically. With stimulus durations less than one second subjects performed very well, but with longer simulated movements, subjects confused heading directions with the fixation point.

These results indicate distinct temporal dynamics in the process of heading detection from retinal flow. Previous studies had linked the erroneous percept of moving along the direction of gaze to the absence of extraretinal input, because heading detection was accurate when real eye movements were performed, i.e. extraretinal input was available (Warren & Hannon, 1990; Ryoden et al. 1994). However, in these experiments the stimulus duration always exceeded 1 sec. In contrast, with durations below 1 sec heading detection is possible without the help of extraretinal oculomotor signals. The visual system obviously relies on the visual input during brief stimulus exposures. In the line of previous reasoning, the gradual development of the error would suggest that the visual system puts increasingly more emphasis on the extraretinal signal as time progresses. In the first few hundred milliseconds either the visual system ignores extraretinal eye movement information, or the extraretinal signal is not yet fully developed. Support for this hypothesis comes from a study of the Filehne illusion, which is supposed to measure the strength of the eye movement reference signal during smooth pursuit. Wertheim (1987) described that for a brief exposure of the stimulus (300 msec) the eye movement reference signal was much smaller than for an exposure of the stimulus for 1000 msec. Therefore, in the case of the Filehne illusion, the visual system compensates for a pursuit eye movement and analyzes the visual input correctly only after a certain exposure time. In our case of simulated eye movement during actual fixation, the visual system may use a signal that no eye movement takes place and confuse the center of the radial structure in the flow field with the direction of heading also only after a certain duration.

But what would be the implications of that dynamical change in the importance of the extraretinal eye movement signal in natural movement conditions? For this question it is important to consider the possible origin of the eye rotations. Slow eye rotations like those simulated in our stimuli can result from either voluntary smooth pursuit eye movements usually generated when we want to track a moving object with the eyes. Or they might be generated by reflexive, involuntary mechanisms that are active during normal self-motion. The vestibulo-ocular, the optokinetic, and the ocular following reflexes induce eye movements that try to stabilize spatial vision during movements of the head.

Both types of eye movements, voluntary pursuit and stabilization reflexes, could lead to the eye rotation that was simulated in our experiments. However, the two types of eye movements typically have very different dynamical properties. Smooth pursuit is characterized by the tracking of a moving target

over an extended period of time, i.e. as long as the subject is interested in following the target. Smooth pursuit eye movements can therefore last up to a few seconds. On the other hand, smooth pursuit takes about 100 msec to be established. In contrast, stabilization reflexes occur very fast (10–20 msec for the vestibulo–ocular reflex, 60 msec for ocular following) and without voluntary attention. During typical oculomotor behavior saccadic eye movements direct gaze to new targets about 2 or 3 times per second. This leaves about 300–500 msec time between two saccades. For a moving observer, after each saccade a new flow field occurs on the retina that differs from the one experienced before the saccade. Reflexive gaze stabilization mechanisms induce eye movements during the intersaccadic interval. Thus, in natural behavior eye movements during the first 300 msec after the saccade are most often generated by involuntary stabilization mechanisms. At later times, it is more likely that the smooth pursuit system is involved. A longer intersaccadic interval is evidence of a voluntary process that keeps gaze directed at a target of interest.

It is a long standing question whether an extraretinal eye movement signal is present during reflexive eye movements. It has been suggested (Post & Leibowitz, 1985) that only voluntary eye movements generate an extraretinal signal. A possible lack or even an incompleteness of the extraretinal signal during involuntary eye movements could explain the dynamic use of visual and extraretinal cues. During short stimulation periods that last about the length of a typical intersaccadic interval a potential eye rotation might be the result of an involuntary eye movement. Since the extraretinal signal might not be indicative in this case, the brain ought to rely more on visual cues. In contrast, long periods of uninterrupted flow stimulation are more likely to contain eye rotations that result from smooth pursuit. In this case, the extraretinal signal is reliable and can be used to compensate for the eye movement induced visual rotation.

Conclusion

Previous research has suggested that in the case of movement towards a wall human subjects tend to falsely associate their direction of heading with the pseudo–focus of expansion that is introduced by a simulated eye movement. Our experiments confirmed this tendency when the same parameters as in previous experiments were used for the stimuli. However, when the field of view was extended to $90^\circ \times 90^\circ$ and the presentation time of the stimulus was reduced to below 1 second, subjects were able to perform the task correctly. The larger field of view provides stronger texture and speed gradients that

carry information about the slant of the wall. This information can be used to overrule the pseudo-focus and to correctly determine the direction of heading provided presentation time is small. With prolonged presentation duration the lack of extraretinal information about the involved eye movement causes the subjects to again confuse the heading direction with the fixation point. This possibly reflects the result of a dynamical use of the extraretinal eye movement signal by the visual system in the interpretation of retinal flow fields. This dynamical change might be related to different kinds of eye rotations occurring in natural situations.

Acknowledgements

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References

- Banks, M. S., Ehrlich, S. M., Backus, B. T., & Crowell, J. A. (1996). Estimating heading during real and simulated eye movements. *Vision Res.*, *36*, 431-443.
- Cutting, J. E., Springer, K., Braren, P. A., & Johnson, S. H. (1992). Wayfinding on foot from information in retinal, not optical, flow. *J.Exp.Psych.: Gen.*, *121*(1), 41-72.
- Duffy, C. J., & Wurtz, R. H. (1993). An illusory transformation of optic flow fields. *Vision Res.*, *33*, 1481-1490.
- Gibson, J. J. (1950). *The Perception of the Visual World*. Houghton Mifflin, Boston.
- Gibson, J. J. (1966). *The Senses Considered As Perceptual Systems*. Houghton Mifflin, Boston.
- Grigo, A., & Lappe, M. (1998). Interaction of stereo vision and optic flow processing revealed by an illusory stimulus. *Vision Res.*, *38*, 281-290.
- Johnston, I. R., White, G. R., & Cumming, R. W. (1973). The role of optical expansion patterns in locomotor control. *Am.J.Psychol.*, *86*, 311-324.
- Koenderink, J. J., & van Doorn, A. J. (1981). Exterspecific component of the motion parallax field. *J.Opt.Soc.Am.*, *71*(8), 953-957.

- Koenderink, J. J., & van Doorn, A. J. (1987). Facts on optic flow. *Biol.Cybern.*, *56*, 247–254.
- Lappe, M., & Rauschecker, J. P. (1995). An illusory transformation in a model of optic flow processing. *Vision Res.*, *35*, 1619–1631.
- Llewellyn, K. R. (1971). Visual guidance of locomotion. *J.Exp.Psych.*, *91*, 245–261.
- Longuet-Higgins, H. C., & Prazdny, K. (1980). The interpretation of a moving retinal image. *Proc.Royal.Soc.London B*, *208*, 385–397.
- Post, R. B., & Leibowitz, H. W. (1985). A revised analysis of the role of efference in motion perception. *Perception*, *14*, 631–643.
- Regan, D., & Beverly, K. I. (1982). How do we avoid confounding the direction we are looking and the direction we are moving?. *Science*, *215*, 194–196.
- Rieger, J. H., & Lawton, D. T. (1985). Processing differential image motion. *J.Opt.Soc.Am.A*, *2*, 354–360.
- Rieger, J. H., & Toet, L. (1985). Human visual navigation in the presence of 3-D rotations. *Biol.Cybern.*, *52*, 377–381.
- Royden, C. S., Banks, M. S., & Crowell, J. A. (1992). The perception of heading during eye movements. *Nature*, *360*, 583–585.
- Royden, C. S., Crowell, J. A., & Banks, M. S. (1994). Estimating heading during eye movements. *Vision Res.*, *34*, 3197–3214.
- van den Berg, A. V., & Brenner, E. (1994). Why two eyes are better than one for judgements of heading. *Nature*, *371*, 700–702.
- Vishton, P. M., & Cutting, J. E. (1995). Wayfinding, displacements and mental maps: Velocity fields are not typically used to determine ones's aimpoint. *J.Exp.Psychol.: Hum.Percept.Perform.*, *21*, 978–995.
- Warren, Jr., W. H., & Hannon, D. J. (1990). Eye movements and optical flow. *J.Opt.Soc.Am.A*, *7*(1), 160–169.
- Warren, Jr., W. H., Morris, M. W., & Kalish, M. (1988). Perception of translational heading from optical flow. *J.Exp.Psychol.: Hum.Percept.Perform.*, *14*(4), 646–660.

Wertheim, A. H. (1987). Retinal and extraretinal information in movement perception: How to invert the Filehne illusion. *Perception*, *16*, 299–308.