

OPTIC FLOW AND EYE MOVEMENTS

Markus Lappe and Klaus-Peter Hoffmann

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

- I. Introduction
- II. Gaze during Self-Motion
 - A. Gaze during Driving
 - B. Gaze during Walking
- III. Ocular Reflexes during Self-Motion
 - A. Ocular Compensation for Rotational Movements
 - B. Vestibuloocular Compensation for Translational Movements
- IV. Optic Flow Induced Eye Movements
 - A. Optokinetic Tracking Movements
 - B. Saccades and Optokinetic Quick Phases
 - C. Voluntary Tracking
 - D. Vergence Responses
- V. Implications of Eye Movements for Optic Flow Processing
- VI. Conclusion
- References

I. Introduction

Eye movements are an integral part of many visually guided behaviors. We typically shift our gaze to a new object of interest twice every second. These gaze shifts are used to obtain essential visual information through foveal vision. During self-motion, eye movements have a further important function for visual perception. Because self-motion induces image motion on the retina, eye movements are needed to counteract the induced visual motion and stabilize the image of the object that is fixated. Eye movements during self-motion have important consequences for the processing of optic flow. On the one hand, they may help optic flow analysis in a task-dependent manner. On the other hand, they introduce complications for optic flow analysis because they add further retinal image motion. In the following, we will first look at the distribution of gaze during self-motion. Then we will review work on gaze stabilization, mainly during linear (forward) motion. Finally, we will describe the consequences of eye movements on the retinal flow pattern during self-motion.

II. Gaze during Self-Motion

Reliable and accurate recording of gaze direction during self-motion is a difficult technical problem. First of all, many eye movement recording systems cannot be easily taken along with a moving subject. Second, the gaze movements of freely moving subjects are composed of movements of the eye in the head, movements of the head on the trunk, and movements of the trunk with respect to the feet. It is quite challenging—but not impossible, see Solomon and Cohen (1992a, 1992b)—to measure all these components simultaneously. A way to circumvent this problem is to measure the position of the eye in the head along with a headcentric view of the visual scene by a camera fixed to the head (Land, 1992; Patla and Vickers, 1997).

Presumably because of the technical problems involved only a few studies have examined eye movements during active self-motion. Naturally, most interest in the allocation of gaze during self-motion and the percentage of time spent on different parts of the visual field has come from applied psychological research on driving behavior in automobilists (Shinar, 1978). The next section presents some basic results of this research. After that, studies of gaze measurements during walking are reviewed.

A. GAZE DURING DRIVING

Basic results early on showed that gaze during open road driving is typically directed straight ahead, or to the far scenery on the side, to other vehicles, or (very infrequently) to the near parts of the road (Mourant *et al.*, 1969). The percentage of time spent in these gaze directions increases in this order. But it also depends on the scene and on the task or objective of the driver. More gaze shifts to eccentric positions are made when the driver is asked, for instance, to attend to all the road signs, memorize the travel area, and the like (Mourant *et al.*, 1969; Hughes and Cole, 1988; Luoma, 1988). Frequent and large gaze shifts occur when crossing an intersection (Land, 1992).

During straight driving, gaze stays mostly close to the focus of expansion or the heading of the car (Mourant *et al.*, 1969; Land and Lee, 1994), presumably because it is important to monitor constantly the way ahead, particularly at the high travel speed in a car. A further characteristic and consistent relationship between gaze direction and driving behavior has been described for the negotiation of curves (Land and

Lee, 1994). While approaching and driving through a curve, gaze is directed toward a specific point at the inner edge of the road. This point has been termed the tangent point because it is the point where the tangent to the edge of the road reverses direction. It is also the innermost point of the road edge seen from the driver. The tangent point is a characteristic point of the visual projection of the curve in the driver's display, not a fixed point on the curve in space. As such, the tangent point moves on the edge of the road as the driver continues to pass the curve. During driving in a curve, gaze is directed toward the tangent point on average 80% of the time. Land and Lee propose that this gaze strategy eases the task of steering because the motion and position of the tangent point provides visual information to estimate the curvature. Thus the fixation of the tangent point could be a special visual strategy for the requirements of driving.

B. GAZE DURING WALKING

Locomotion on foot is composed of entirely different visuomotor characteristics and requirements than driving a car. The important parameter that needs to be controlled is the placement of the foot in the step cycle. Hollands *et al.* (1995, 1996) and Patla and Vickers (1997) reported that gaze in walking human subjects was mostly directed toward future landing positions of the feet. Hollands *et al.* (1995, 1996) measured eye movements in human observers who had to traverse a course of stepping stones. The subjects were required to place their feet on particular predetermined target positions. Gaze alternated between left and right targets in correlation with the step cycle. Patla and Vickers (1997) recorded gaze direction in a task where subjects had to step over small obstacles along their locomotor path. Most of the time, gaze was directed to a location on the ground several steps ahead of the current position. Only 20% of the time did subjects fixate an obstacle immediately before stepping over it. They concluded that information about the stepping positions is obtained well ahead of time.

Wagner *et al.* (1981) investigated the gaze behavior of walking humans in an outdoor environment. Rather than measure gaze positions with an instrument, they simply asked their subjects to report what they looked at as soon as a certain auditory signal was sounded. They took 58 measurements from each of 16 subjects. The results indicated that most often gaze was directed to objects close to the observer. The maximum of the distribution of gaze points lay between 1.5 and 3 m from the observer. From an analysis of this distribution, one might conclude

that only a small proportion ($< 10\%$) was near the focus of expansion. The majority of gaze directions deviated quite substantially from the focus of expansion (median deviation about 20°). Wagner *et al.* also classified the types of objects at which gaze was directed. In almost half of the cases, subjects looked at moving objects such as other people, vehicles, or animals. Thirteen percent of gazes were directed to the ground in front of the subject.

Solomon and Cohen (1992a,b) studied eye movements of walking monkeys. They used a setup in which the monkey ran on a circular platform, being tethered to a radial arm that could move about a centered pole. They simultaneously recorded eye-in-head, head-on-body, and body-in-space positions. The direction of gaze in space could be recovered from these measurements. The two monkeys in these experiments usually fixated a point in the environment and kept their gaze directed toward this point for a period of several hundred milliseconds. Then they shifted gaze to a new target.

From these studies, one may conclude three basic findings. First, normal self-motion is accompanied by a large number of eye movements. This is not surprising since eye movements are an integral part of many behaviors and are needed to obtain necessary visual information to guide these behaviors. Second, the distribution of gaze depends on the task that is required from the observer. Third, and related to the second point, the pattern of gaze movements is different for driving a car and for walking. In the first case, there is a consistent relation between driving parameters and gaze direction. Gaze is kept near the focus of expansion for straight driving and near the tangent point of the curve during turns. In contrast, during walking, gaze is typically not directed at the focus of expansion but rather more variably at objects in the near vicinity along the path of travel.

III. Ocular Reflexes during Self-Motion

Section II concerned the distribution of gaze and of fast, saccadic gaze shifts during self-motion. A further concern are slow eye movements that occur between gaze shifts. During self-motion, the visual image of the world on the retinae of the eyes is also in motion. This retinal image motion creates a problem for stable vision. In order to perceive the environment accurately, it is desirable to have a clear and stationary visual image. Several types of compensatory eye movement reflexes exist that attempt to counteract the self-motion-induced visual motion and

to keep the retinal image stable (Carpenter, 1988). These gaze stabilization eye movements use vestibular, proprioceptive, or visual signals to achieve this task.

Rotations and translations of the head in space induce corresponding signals in the semicircular canals and otholiths of the vestibular organs. These signals are directly used to move the eyes opposite to the movement of the head. These eye movements are called the rotational and translational vestibuloocular reflexes. The cervicoocular reflex uses signals from the neck muscles to determine head movement and the corresponding compensatory eye movement.

The optokinetic and ocular following reflexes in contrast use the retinal image motion directly. In this case, the eye movement follows the motion on the retina in order to minimize retinal image slip and generate a stable image. The optokinetic reflex (OKR) acts as a feedback loop system which adapts eye velocity to the velocity of the retinal image motion. The ocular following reflex (OFR) describes the initial (60–150 ms) ocular reaction to the onset of motion of a visible scene. In this case, the eyes follow the visual motion of the scene in an open loop manner. A recent review of the properties of these reflexes in relation to self-motion can be found in Miles (1998).

The requirements for gaze stabilization are very different for rotational and translational self-movements. Because the rotation is the simpler part, we will first look at reflectory eye movements induced by self-rotation and then proceed to eye movements induced by self-translation and the associated expansional optic flow.

A. OCULAR COMPENSATION FOR ROTATIONAL MOVEMENTS

For rotations of the head or body, the entire visual scene moves with a single angular velocity. The rotational vestibuloocular reflex (rVOR) compensates for rotations of the head by rotating the eyes opposite to the head rotation. The speed of the eyes in the rVOR closely matches the speed of the head movement such that very good image stabilization is achieved. This is particularly true for fast head movements (e.g., head oscillations in the 2- to 8-Hz range). For slower head movements, ocular compensation increasingly relies on the optokinetic reflex. The optokinetic reflex tries to null retinal image motion by adjusting the eye speed of the visual motion. It works best for low visual speeds. A combination of the two reflexes, which is the normal situation during active movement, results in almost complete image stabilization during head rotations.

B. VESTIBULOOCULAR COMPENSATION FOR TRANSLATIONAL MOVEMENTS

Translations of the head in space also induce vestibularly driven compensatory eye movements. This is called the translational vestibuloocular reflex (tVOR). For lateral or up-and-down head shifts, the eyes are again rotated against the head movement. Unlike in the case of head rotations, however, the required speed of the eye movement cannot be determined from the head movement alone. Accurate image stabilization in this case requires to take into account the geometry of the visual scene. If one considers, for instance, lateral head movements in front of a large object, the induced visual speed of the object depends on its distance from the eye. If the object is close to the eye, the same head movement would induce a much larger visual motion than if the object is farther away. Hence to achieve accurate image stabilization, the compensatory eye speed must be different, depending on the viewing distance.

This situation has been investigated by Schwartz et al. (1989, 1991). They recorded eye movements of rhesus monkeys placed on a sled that moved laterally in the dark. Immediately before the movement, the animals were required to fixate a small spot of light that could be placed at various distances from the animal. This fixation target was extinguished before the sled movement started and merely served to enforce a defined state of vergence at the beginning of the movement. Nevertheless, the speed of the induced vestibuloocular eye movements changed with the viewing distance such that compensation for head movement was always near the optimum. A similar scaling of eye speed with viewing distance also occurs for the ocular following reflex (Busetini *et al.*, 1991). Both findings have been confirmed for humans (Busetini *et al.*, 1994).

The requirements for gaze stabilization become even more complicated when forward movement is considered instead of lateral or up-and-down movement. During forward motion, it is physically impossible to stabilize the entire retinal image. Forward motion induces an expanding pattern of optic flow in the eyes (Fig. 1). Points in different parts of the visual field move in different directions. Hence it is only possible to stabilize part of the visual image. This should be the part at which gaze is directed. For motion along a nasooccipital axis, the tVOR of squirrel monkeys indeed depends on the viewing direction. Eye movement is rightward when gaze is directed to the right and leftwards when gaze is directed to the left (Paige and Tomko, 1991). The speed of the tVOR eye movements in this situation varies with viewing distance and with gaze eccentricity. This variation is consistent with the increasing speed of the optic flow at eccentric locations (Paige and Tomko, 1991).

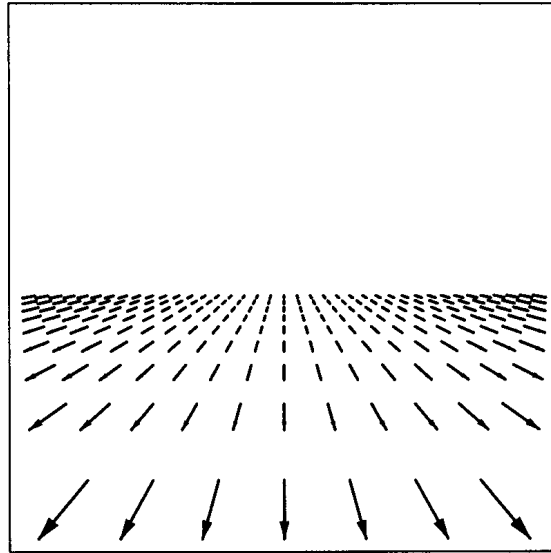


FIG. 1. Optic flow field for linear forward movement over a flat ground plane.

IV. Optic Flow Induced Eye Movements

The aforementioned studies suggest that the translational vestibuloocular reflex is well adapted to the requirements of gaze stabilization during linear motion. We have recently demonstrated the existence also of optokinetic responses to radial optic flow fields, which are associated with linear forward translation (Lappe *et al.*, 1998, 1999; Niemann *et al.*, 1999).

We recorded spontaneous optokinetic eye movements of humans and macaque monkeys that were watching a large-field radial optic flow stimulus presented on a large projection screen in front of them. The stimulus simulated movement across a ground plane (Fig.1). The typical oculomotor response in this situation is shown in Fig. 2. It consists of regularly alternating slow tracking phases and saccades, or quick phases, at a frequency of about 2 Hz. In the following discussion, we will first describe the properties of the slow phases and then those of the saccades.

A. OPTOKINETIC TRACKING MOVEMENTS

During the visual scanning of a radial optic flow stimulus, the visual motion pattern arriving on the retina depends on the direction of gaze.

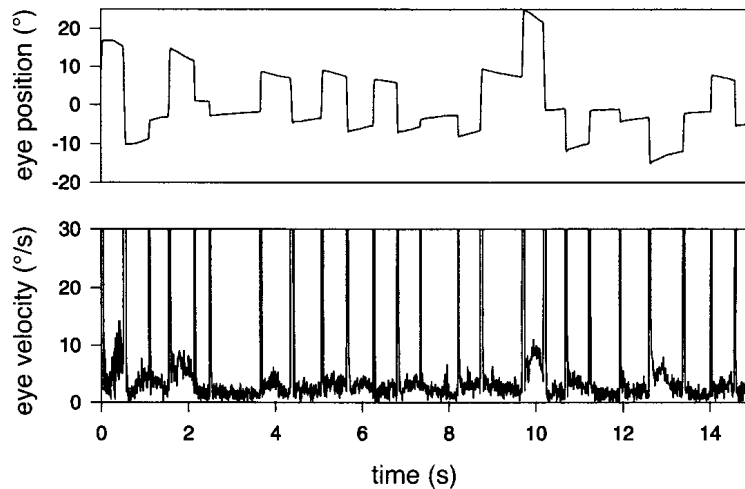


FIG. 2. Horizontal eye position and eye velocity recorded from a monkey that watched a radial optic flow stimulus. The stimulus in this case consisted of a contraction corresponding to backward movement. A regular pattern of alternating tracking phases and saccades can be seen. The eye movement in the tracking phases follows the stimulus motion in gaze direction. Eye movement direction depends on gaze direction. All tracking phases move toward the center.

For instance, if one looks directly at the focus of expansion, the visual motion pattern is symmetric, and there will be no motion in the direction of gaze. If one instead looks in a different direction, retinal slip on the fovea will occur, the direction and speed of which will depend on the gaze direction. Therefore, the eye movement behavior needs to depend on the direction of gaze, too.

Eye movements in the slow phases follow the direction of motion that is present at the fovea and parafovea. The slow phases stabilize the retinal image in a small parafoveal region only. Figure 3a shows a vector field plot of the optokinetic tracking phases of a monkey viewing a radial flow pattern. Each line depicts the direction and speed of a single slow phase eye movement that occurred while the animal looked at a specific location in the flow pattern. Figure 3b shows for comparison the optic flow stimulus (i.e., the visual motion vectors that occurred at these positions in the stimulus). One can see a nice correspondence of eye movement direction and local motion direction in most cases. This close correspondence was confirmed in several quantitative measurements regarding the deviation of the eye movement direction from the local motion direction, all of which indicated a very low deviation (Lappe *et al.*, 1998).

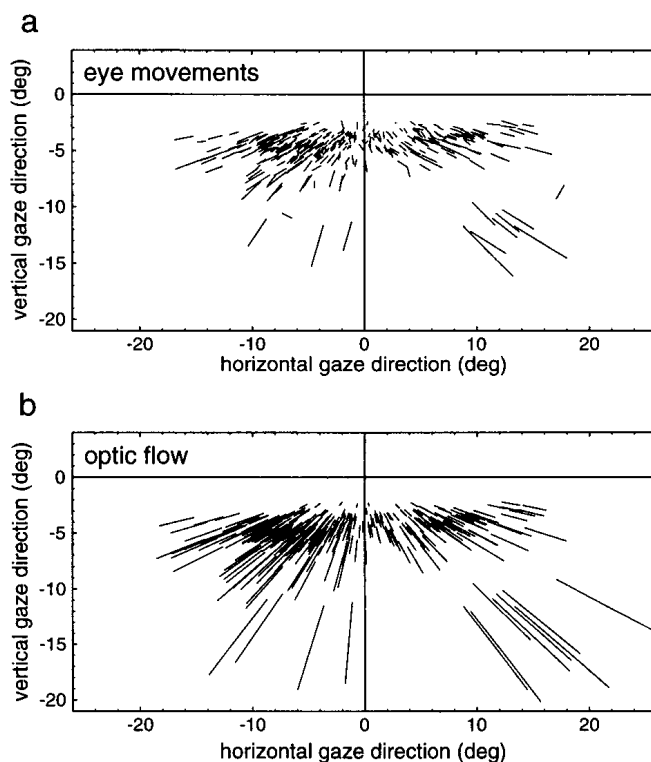


FIG. 3. (a) Vector field illustration of eye movements of a monkey that watched an expanding optic flow stimulus. This stimulus simulated movement over a ground plane consisting of a flat layer of random dots. (b) The visual motion that occurred in the stimulus. Each line in panel a indicates starting position, mean direction, and mean speed of a single optokinetic tracking movement. Each line in panel b represents the local speed and direction in the stimulus at a given eye position from panel a. One can observe that the direction of eye movement is in very good agreement with the local motion in the direction of gaze. The differing vector lengths demonstrate that eye speed is often lower than the corresponding stimulus speed.

However, it is also apparent from Fig. 3 that the speed of the eye movement is often considerably lower than the corresponding local stimulus speed. We defined the gain of the eye movement as the ratio between the eye speed in the direction of the local flow on the fovea and the speed of the foveal motion, averaged across the entire slow phase eye movement. On average, the gain reached a value of 0.5 in both humans and monkeys (Lappe *et al.*, 1998; Niemann *et al.*, 1999). Thus, eye speed was only about half as fast as the speed of the local, foveal image motion.

This discrepancy is resolved, however, if one considers not only the foveal motion but also the motion from within the parafoveal region.

The optokinetic system is known to integrate visual motion signals from throughout the visual field with a special emphasis on the fovea and a parafoveal area of up to 5 or 10° eccentricity (Hoffmann *et al.*, 1992). Thus the visual input that drives these eye movements most likely consists of the spatial average of motion signals from the fovea and parafovea. For a ground plane flow field, this averaged motion signal has a substantially smaller speed than the foveal motion (Lappe *et al.*, 1998). Therefore, the low gain with respect to the foveal motion might be explained from an integration process in the optokinetic system. A much higher gain (close to unity) can be observed, however, when subjects are instructed to actively perform a smooth pursuit movement to follow a single element of the flow field (Niemann *et al.*, 1999).

To summarize, the direction of involuntary optokinetic tracking movements elicited by radial optic flow stimulation well matches the direction of the foveated part of the flow field. The speed of these eye movements is predicted by the averaged speed from the motion in a foveal and parafoveal area.

B. SACCADIC AND OPTOKINETIC QUICK PHASES

When optokinetic nystagmus is normally evoked by presentation of full-field uniform motion or by a drum rotating around the subject, slow phase tracking movements and saccadic quick phases are very stereotyped. An initial saccade against the direction of the stimulus motion is followed by a slow phase that tracks the stimulus motion in order to stabilize the retinal image. After the eye has moved a certain distance, another saccade against the stimulus motion occurs; it repositions the eye and compensates for positional change during the slow phase. Saccades in this situation serve two functions (Carpenter, 1988). The first is to orient gaze toward the direction from which the stimulus motion originates. The second is to reset eye position after the slow phase tracking movement.

In the case of radial optic flow stimulation, the slow phase tracking movements largely reflect this passive, stereotyped behavior. They are mainly determined by the local stimulus motion. In contrast, the saccades do not share the reflectory nature of the slow phases but rather support an active exploration of the visual scene (Lappe *et al.*, 1999). During forward locomotion, it is necessary to monitor the environment constantly and to identify possible obstacles along the path. Saccades in this situation must serve the ocular scanning of the visual scene instead of merely resetting the eye position.

We calculated that less than 20% of the total distance covered by all saccadic amplitudes in our experiments were required to compensate the positional changes resulting from the tracking phases (Lappe *et al.*, 1999). Hence, most saccadic activity must be attributed to exploration behavior. The distribution of saccades and gaze directions depended on the direction of simulated self-motion (the location of the focus of expansion) and the structure of the visual scene.

Gaze clustered near the horizon and was biased toward the location of the focus of expansion (Lappe *et al.*, 1998, 1999). This bias was stronger in human subjects than in monkeys (Niemann *et al.*, 1999). But in both cases, gaze often deviated by several degrees from the focus location. When we presented a flow field simulating movement through a tunnel instead of a ground plane, the pattern of saccadic directions changed accordingly. While in the ground plane environment, most saccades were directed parallel to the horizon, for the tunnel environment saccade directions were equally distributed in all directions (Lappe *et al.*, 1999).

More recent experiments in human subjects showed that the pattern of saccades and the distribution of gaze depend very much on the task given to the subject. In this study, we used a flow stimulus that simulated movement across a textured ground plane. On this plane, a number of black 2-D shapes that simulated holes in the surface were placed. In the simulation, subjects were driven along a zig-zag course over the surface such that the direction of self-motion changed unpredictably. In successive trials, three different instructions were given to the subjects: (a) passive viewing with no specific task to do, (b) active tracking of the direction of self-motion by pointing gaze toward the focus of expansion, and (c) identifying whether self-motion is toward any of the holes in the surface. This latter condition combines the task of heading detection with the task of obstacle detection.

When the subjects merely viewed the flow stimulus without any specific task, gaze was clustered near the focus of expansion. The same was found when the subjects were explicitly instructed to look into the focus. In contrast, when the subjects were required to identify obstacles along the simulated path of self-motion, saccades were directed to the obstacles or to the ground plane immediately in front of the subject. Virtually no saccade was directly targeted at the focus of expansion. An example scanpath is shown in Fig. 4.

Saccadic parameters are affected by optic flow. Saccadic latencies to the onset of independent object motion are higher during optic flow stimulation than for a stationary background (Niemann and Hoffmann, 1997). Saccades directed to the focus of expansion typically undershoot

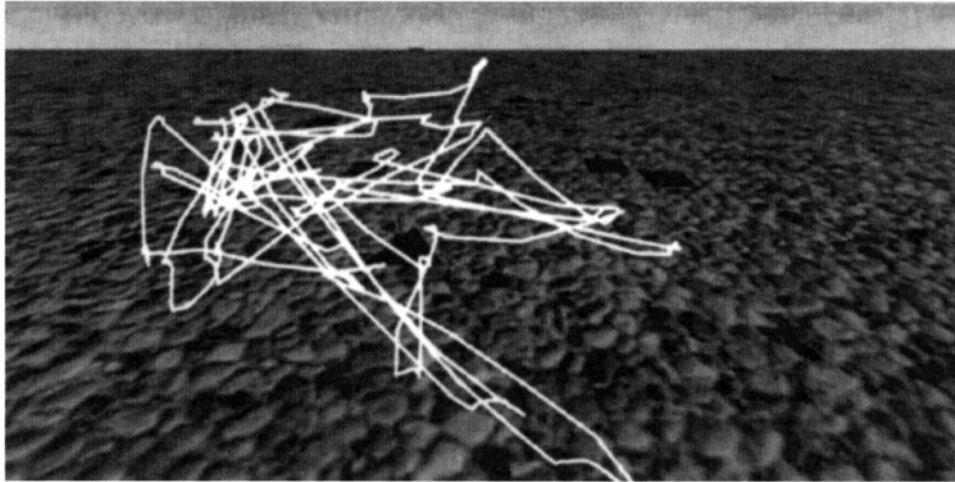


FIG. 4. Scan path of gaze of a subject performing a combined heading detection and obstacle avoidance task. The subject viewed an optic flow stimulus that simulated movement on top of a textured ground plane on which a number of black 2-D shapes were attached. The figure shows a static frame of the stimulus. In the simulation, subjects were driven along a zig-zag course over the surface such that the direction of self-motion changed unpredictably. The task of the subject was to monitor constantly whether self-motion was toward any of the black elements. The white line gives the gaze directions of the subjects over the course of the trial. One can see that gaze was mostly directed to the part of the plane immediately in front of the subject. The focus of expansion was never looked at.

the distance by as much as 40% (Hooge *et al.*, in press). These saccades are much less accurate than those toward a target in front of a stationary background. A sequence of several saccades is required to orient gaze directly into the focus of expansion.

The visual scanning of the optic flow field by saccadic eye movements also introduces complications for the gaze stabilization eye movements between two saccades. With each saccade, the direction and speed of the visual motion on the fovea changes. The dependence of stimulus motion on gaze direction demands a rapid adjustment of eye velocity after each saccade. Due to the latency of signals in the visual system, such an adjustment cannot be done instantly. Appropriate parameters for the eye movement after the saccade can be determined only after a delay of several tens of milliseconds. Within the first 50–100 ms after a saccade, the direction of the eye movement is inappropriate for accurate gaze stabilization (Lappe *et al.*, 1998). Deviation of up to 180° between the local motion direction and the eye movement directions were observed in individual cases. the mismatch seems to occur because of a tendency for the eye to (a) keep the direction of motion that was used before the saccade and (b) direct the eye movement after the saccade in an opposite

direction of the saccade itself. Both factors are reminiscent of the oculomotor behavior during regular optokinetic nystagmus evoked by large-field unidirectional motion. In regular optokinetic nystagmus, slow phases are always in the same direction and always opposite in direction to the quick phases.

C. VOLUNTARY TRACKING

Passive viewing of radial optic flow fields elicits reflectory optokinetic tracking movements with a low gain of about 0.5. A much higher gain is observed when human subjects are asked to pick a single point of the flow field and actively track it with the eyes (Niemann *et al.*, 1999). In this case, the targets can be pursued almost perfectly. This is remarkable for two reasons. First, the motion of each dot within a flow field is accelerating over time. The eye movements nicely match this acceleration. Second, each dot in a flow field is surrounded by many other dots which move with different speeds and directions and might be considered a source of noise for the pursuit system. Nevertheless, the motion of the chosen point is tracked accurately. These results show that the gain of the tracking eye movements is under voluntary control. The higher gain for voluntary pursuit compared to reflectory optokinetic responses could reflect the restriction of the stabilization to a smaller, more foveal area instead of a parafoveal integration.

D. VERGENCE RESPONSES

Radial optic flow is normally associated with forward movement. In this case, the distance between the objects in the environment and the eyes of the observer become smaller over time. Hence accurate stabilization of gaze onto an environmental object requires not only the tracking of the motion of that object by version eye movements but also by vergence eye movements to keep both eyes aligned on the object. Interestingly, radial optic flow stimuli elicit such vergence eye movements even in the absence of a distance change. Busetini *et al.* (1997) used a brief, two-frame expansion stimulus to elicit transient open-loop oculomotor responses. Such an expansion step resulted in short-latency vergence eye movements. Vergence changes began approximately 80 ms after the motion step and peaked 30–50 ms later. These findings demonstrate that gaze stabilization reflexes are truly adapted to motion in a three-dimensional environment.

V. Implications of Eye Movements for Optic Flow Processing

The eye movements that occur during self-motion and that are induced by the optic flow in turn influence the structure of the optic flow that reaches the retina. Any eye movement induces motion of the retinal image. Thus, on the retina, movements of the eye superimpose onto movements in the optic flow. The retinal motion pattern during forward movement hence becomes a combination of radial optic flow with retinal slip induced by eye movement.

A consequence of this is that the motion pattern of the retina might look very different from the simple expansion that one normally associates with optic flow. In particular, eye movements usually destroy or transpose the focus of expansion on the retina (e.g., Regan and Beverley, 1982; Warren and Hannon, 1990). It is therefore appropriate to distinguish retinal flow from optic flow clearly and define retinal flow as the actual motion pattern seen on the retina during combined self-motion and eye movement (Warren and Hannon, 1990). Retinal flow is the starting point for any process of flow field analysis in the visual system.

Figure 5 illustrates how eye movements modify the structure of the retinal flow even when self-motion remains constant (following Lappe and Rauschecker, 1994, 1995). Several examples essentially depict the same observer translation but with different types of eye movement. Figures 5a and b depict the general scenario. The observer moves across a ground plane. In this and all following plots, the direction of observer movement is identified by a cross. During the movement his gaze (indicated by a circle) could be pointed to different locations in space. The direction of gaze defines the center of the coordinate system in which the retinal flow is represented.

Figure 5b shows a view of the optic flow field in a body-centered coordinate system. This is the flow which would be seen by a body fixed camera pointed along the direction of travel. All motion is directed away from the focus of expansion which coincides with the heading of the observer. The projection of this flow field onto the retina of the observer, the retinal flow, depends on the direction of gaze and on the motion of the eye. The examples in Figs. 5c-f correspond to four different combinations of gaze and eye movement. The points at which gaze is directed in these four situations are indicated by circles in Fig. 5b and labeled in correspondence with the associated figures. Three of the points (c, d, f) are located at the horizon. One point is located on the ground close to the observer (e).

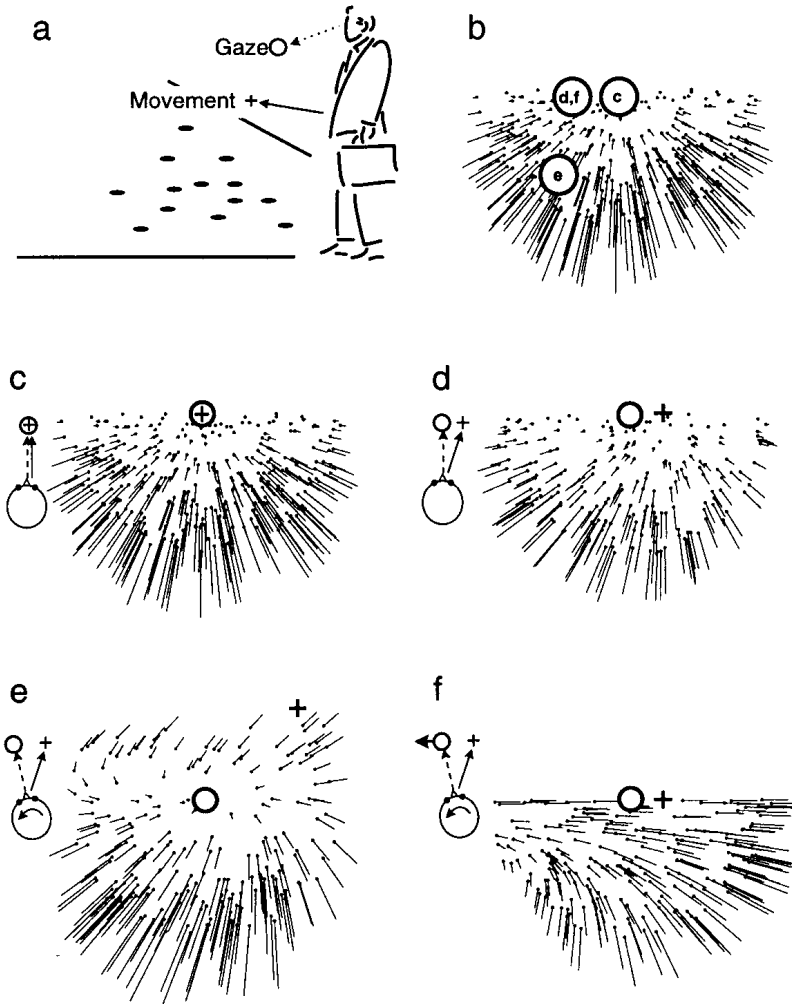


FIG. 5. The influence of gaze direction and eye movements on the structure of the retinal flow field. See text for a detailed explanation.

Figures 5c and d show the results of a gaze shift on the retinal projection of the optic flow. They mainly consist of an offset or shift of the full visual image. Figure 5c shows the retinal flow when the direction of gaze and the direction of movement coincide (i.e., when the observer looks straight ahead into the direction of movement). In this case, the focus of expansion is centered on the retina. In Fig. 5d, the observer now looks off to the side from the direction of movement. Gazing at some fixed point on the horizon allows him to keep his eyes stationary

(i.e., no eye movements occur). Again, the focus of expansion is visible and indicates heading, but now it is displaced from the center of the visual field.

Figure 5e shows a situation in which the observer's gaze is directed at some element of the ground plane located in front of him and to the left. There are two consequences of this change in gaze direction. The first is an opposite displacement of the retinal image. The horizon has moved up in the visual field. The second, more serious consequence is that the point at which the gaze is directed is now in motion. This is unlike the situation in Figs. 5c and d, where gaze was directed toward the horizon, which is motionless in the optic flow. The visual motion in gaze direction now enforces a rotation of the eye in order to track the foveal image motion and stabilize gaze on this point. Direction and speed of this eye movement are related to the observer's movement. Since direction is determined by the direction of the flow on the fovea, it is always away from the focus of expansion. Eye speed, however, might be less well defined, depending on the gain of the eye movement (see Sections IV.A and IV.C).

The eye movement induces full-field retinal image motion in the opposite direction. This retinal image motion is combined with the radial motion pattern of the optic flow. The resulting retinal flow field somewhat resembles a distorted spiraling motion around the fovea. The focus of expansion is lost as an indicator of heading. The retinal flow field instead contains a new singular point which is related to the stabilizing eye movement. Perfect stabilization gaze (unity gain) would result in a singular point located exactly on the fovea (circle in Fig. 5e). For an optokinetic tracking movement with lower gain, the singular point would lie about midway between the heading point and the fovea.

In the case of gaze stabilization, the eye movement is linked to the motion and the scene. This is different when the observer looks at a target that undergoes independent motion, such as a moving vehicle or another moving person. In Fig. 5f the observer is assumed to track an object that moves leftward along the horizon. In this case, the retinal flow again has a different structure. This leftward pursuit induces rightward retinal image motion. The combination with the radial optic flow results in a motion pattern that resembles a curved movement. No focus of expansion is visible.

These examples show that the visual signal available to a moving observer can change fundamentally during eye movements, although self-motion remains unchanged. Therefore, mechanisms of optic flow processing that want to recover self-motion must deal with the presence of such involuntary eye movements. For a presentation and discussion of

these mechanisms, the reader is referred to van den Berg (this volume), Andersen *et al.* (this volume), and Lappe (this volume).

The close interaction between gaze stabilization eye movements and optic flow is reflected in an overlap of the neural pathways for optic flow processing and eye movement control. For both purposes, the medial superior temporal (MST) area in macaque cortex plays an important role. Different aspects of the involvement of area MST in optic flow processing are discussed in several chapters in this volume (Andersen *et al.*, this volume; Bremmer *et al.*, this volume; Duffy, this volume; Lappe, this volume). But area MST is also an important structure for the generation and control of various types of slow eye movements (recent review in Ilg, 1997). The contribution of area MST to the generation of reflectory gaze stabilization in the ocular following paradigm is presented in detail in Kawano *et al.* (this volume). In this paradigm, the responses of MST neurons closely parallel the generation of ocular following eye movements, their dependence on the vergence state of the eyes, and the generation of short-latency vergence responses to radial optic flow. Area MST also contributes to the optokinetic reflex. The main pathway of the optokinetic system is through the pretectal nucleus of the optic tract (NOT) (Hoffmann, 1988) and the nuclei of the accessory optic system (AOS) (Mustari and Fuchs, 1989). Besides direct retinal afferents, this pathway receives specific cortical input from the middle temporal area (MT) and area MST (Hoffmann *et al.*, 1992; Ilg and Hoffmann, 1993). Currently unpublished experimental results suggest that neurons in this pathway also respond to radial optic flow stimuli.

VI. Conclusion

Eye movements are common during self-motion. Saccadic gaze shifts are used to scan the environment and to obtain important visual information for the control of self-motion. The scanning behavior depends on the requirements of the motion task. During car driving, the location of the focus of expansion is important for straight driving, and the tangent point along the road edge, for driving in a curve. During walking or stepping over obstacles, gaze is directed at the ground in front of the observer.

Between gaze shifts, reflectory eye movements stabilize gaze on the fixated target and reduce retinal image motion in the center of the visual field. Different types of gaze stabilization eye movements are driven by vestibular signals and by visual motion in the optic flow. These eye

movements in turn induce additional retinal image motion and thus influence the structure of the retinal flow field. On the retina, the uniform visual motion originating from the eye movement is superimposed on the radial motion pattern of the optic flow. The combination leads to complicated nonradial flow fields which require complex mechanisms for their analysis.

Acknowledgment

This work was supported by the Human Frontier Science Program and grants from the Deutsche Forschungsgemeinschaft.

References

- Busettoni, C., Masson, G. S., and Miles, F. A. (1997). Radial optic flow induces vergence eye movements with ultra-short latencies. *Nature* **390**, 512–515.
- Busettoni, C., Miles, F. A., and Schwarz, U. (1991). Ocular responses to translation and their dependence on viewing distance. II. Motion of the scene. *J. Neurophysiol.* **66**, 865–878.
- Busettoni, C., Miles, F., Schwartz, U., and Carl, J. (1994). Human ocular responses to translation of the observer and of the scene: Dependence on viewing distance. *Exp. Brain Res.* **100**, 484–494.
- Carpenter, R. H. S. (1988). "Movement of the Eyes," 2nd ed. Pion Ltd., London.
- Hoffmann, K.-P. (1988). Responses of single neurons in the pretectum of monkeys to visual stimuli in three dimensional space. *Ann. NY Acad. Sci.* **545**, 180–186.
- Hoffmann, K.-P., Distler, C., and Ilg, U. (1992). Callosal and superior temporal sulcus contributions to receptive field properties in the macaque monkey's nucleus of the optic tract and dorsal terminal nucleus of the accessory optic tract. *J. Comp. Neurol.* **321**, 150–162.
- Hollands, M., and Marple-Horvat, D. (1996). Visually guided stepping under conditions of step cycle-related denial of visual information. *Exp. Brain Res.* **109**, 343–356.
- Hollands, M., Marple-Horvat, D., Henkes, S., and Rowan, A. K. (1995). Human eye movements during visually guided stepping. *J. Mot. Behav.* **27**, 155–163.
- Hooge, I. T. C., Beintema, J. A. and van den Berg, A. V. (1999). Visual search of the heading direction. *Exp. Brain Res.*, in press.
- Hughes, P. K., and Cole, B. L. (1988). The effect of attentional demand on eye movement behaviour when driving. In: "Vision in Vehicles II." (A. G. Gale, Ed.), Elsevier, New York.
- Ilg, U. J. (1997). Slow eye movements. *Prog. Brain Res.* **53**, 293–329.
- Ilg, U. J., and Hoffmann, K.-P. (1993). Functional grouping of the cortico-pretectal projection. *J. Neurophysiol.* **70**(2), 867–869.
- Land, M. F. (1992). Predictable eye-head coordination during driving. *Nature* **359**, 318–320.
- Land, M. F., and Lee, D. N. (1994). Where we look when we steer. *Nature* **369**, 742–744.

- Lappe, M., Pekel, M., and Hoffmann, K.-P. (1998). Optokinetic eye movements elicited by radial optic flow in the macaque monkey. *J. Neurophysiol.* **79**, 1461–1480.
- Lappe, M., Pekel, M., and Hoffmann, K.-P. (1999). Properties of saccades during optokinetic responses to radial optic flow in monkeys. In: “Current Oculomotor Research: Physiological and Psychological Aspects” (W. Becker, H. Deubel, and T. Mergner, Eds.), pp. 45–52. Plenum, New York.
- Lappe, M., and Rauschecker, J. P. (1994). Heading detection from optic flow. *Nature* **369**, 712–713.
- Lappe, M., and Rauschecker, J. P. (1995). Motion anisotropies and heading detection. *Biol. Cybern.* **72**, 261–277.
- Luoma, J. (1988). Drivers’ eye fixations and perceptions. In: A. G. Gale (Ed.), “Vision in Vehicles II.” Elsevier, New York.
- Miles, F. A. (1998). The neural processing of 3-d visual information: Evidence from eye movements. *Eur. J. Neurosci.* **10**, 811–822.
- Mourant, R. R., Rockwell, T. H., and Rackoff, N. J. (1969). Driver’s eye movements and visual workload. *Highway Res. Rec.* **292**, 1–10.
- Mustari, M. J., and Fuchs, A. F. (1989). Response properties of single units in the lateral terminal nucleus of the accessory optic system in the behaving primate. *J. Neurophysiol.* **61**, 1207–1220.
- Niemann, T., and Hoffmann, K.-P. (1997). Motion processing for saccadic eye movements during the visually induced sensation of ego-motion in humans. *Vision Res.* **37**, 3163–3170.
- Niemann, T., Lappe, M., Büscher, A., and Hoffmann, K.-P. (1999). Ocular responses to radial optic flow and single accelerated targets in humans. *Vision Res.* **39**, 1359–1371.
- Paige, G. D., and Tomko, D. L. (1991). Eye movement responses to linear head motion in the squirrel monkey. II. visual-vestibular interactions and kinematic considerations. *J. Neurophysiol.* **65**, 1184–1196.
- Patla, A. E., and Vickers, J. N. (1997). Where and when do we look as we approach and step over an obstacle in the travel path? *NeuroReport* **8**, 3661–3665.
- Regan, D., and Beverley, K. I. (1982). How do we avoid confounding the direction we are looking and the direction we are moving? *Science* **215**, 194–196.
- Schwarz, U., Busetini, C., and Miles, F. A. (1989). Ocular responses to linear motion are inversely proportional to viewing distance. *Science* **245**, 1394–1396.
- Schwarz, U., and Miles, F. A. (1991). Ocular responses to translation and their dependence on viewing distance. I. Motion of the observer. *J. Neurophysiol.* **66**, 851–864.
- Shinar, B. (1978). “Psychology on the Road.” Wiley, New York.
- Solomon, D., and Cohen, B. (1992a). Stabilization of gaze during circular locomotion in darkness: II. Contribution of velocity storage to compensatory head and eye nystagmus in the running monkey. *J. Neurophysiol.* **67**(5), 1158–1170.
- Solomon, D., and Cohen, B. (1992b). Stabilization of gaze during circular locomotion in light: I. Compensatory head and eye nystagmus in the running monkey. *J. Neurophysiol.* **67**(5), 1146–1157.
- Wagner, M., Baird, J. C. and Barbaresi, W. (1981). The locus of environmental attention. *J. Environ. Psychol.* **1**, 195–206.
- Warren, Jr., W. H., and Hannon, D. J. (1990). Eye movements and optical flow. *J. Opt. Soc. Am. A* **7**(1), 160–169.