Ocular responses to radial optic flow and single accelerated targets in humans

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Abstract

Self-movement in a structured environment induces retinal image motion called optic flow. Optic flow on one hand provides information about the direction of self-motion. On the other hand optic flow presents large field visual motion which will elicit eye movements for the purpose of image stabilization. We investigated oculomotor behavior in humans during the presentation of radial optic flow fields which simulated forward or backward self-motion. Different conditions and oculomotor tasks were compared. In one condition, subjects had to actively pursue single dots in a radial flow pattern. In a second condition, subjects had to pursue single dots over a dark background. These dots accelerated or decelerated similar to single dots in radial optic flow. In a third condition, subjects were asked to passively view the entire optic flow stimulus. Smooth pursuit eye movements with high gain were observed when dots were actively pursued. This was true for single dots moving over a homogeneous background and for single dots in the optic flow. Passive viewing of optic flow stimuli evoked eye movements that resembled an optokinetic nystagmus. Slow phase eye movements tracked the motion of elements in the optic flow. Gain was low for simulated forward self-motion (expanding optic flow) and high for simulated backward movement self-motion (contracting optic flow). Thus, voluntary pursuit and passive optokinetic responses yielded different gain for the tracking of elements of an expanding optic flow pattern. During passive viewing of the optic flow stimulus, gaze was usually at or near the focus of radial flow. Our results give insights into the oculomotor performances and needs for image stabilization during self-motion and in the role of gaze strategy for the detection of the direction of heading. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Radial optic flow; Acceleration; Eye movements; OKN; Smooth pursuit

1. Introduction

When an observer moves through a natural environment a characteristic pattern of image motion (optic flow) occurs. Optic flow contains information about the movement of the observer. This information can be used for estimating the direction of heading and thus for the guidance of self-motion. However, self-motion and the retinal image motion generated by it will elicit eye movements that aim to stabilize the retinal image. Such eye movements will be driven by the optokinetic system (Lappe, Pekel & Hoffmann, 1998). However, an active observer might also intend to actively keep gaze towards objects of interest during self-motion. In this case, the smooth pursuit system might be involved.

Both types of eye movements induce retinal image motion which is in turn superimposed on the optic flow. This changes the structure of the retinal flow pattern and has implications for the analysis of the optic flow and for the determination of heading. Psychophysical studies investigated human performance in heading estimation from optic flow with or without tracking eye movements (Warren & Hannon, 1988; Warren, Morris & Kalish, 1988; Warren & Hannon, 1990; van den Berg, 1992, 1993; Royden, Crowell & Banks, 1994). However, these experiments always assumed perfect tracking performance. No investigation so far has tested the quality of tracking performance of humans in radial optic flow fields.

Radial optic flow presents a challenge to the oculomotor system for two reasons. First, in radial optic flow fields all visual motion moves away from the focus of expansion, or FOE (Gibson, 1950). Optic flow therefore

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contains simultaneous visual motion in many different directions. Second, the motion of individual elements in the optic flow accelerates or decelerates as the observer moves forward or backward. We were interested in how the oculomotor system copes with this complex image motion.

Several studies investigated eye movements in humans during driving (Mourant, Rockwell & Rackoff, 1969; Gale, Freeman, Haslegrave, Smith & Taylor, 1985, 1988; Gale, Brown, Haslegrave, Moorhead & Taylor, 1991; Land, 1992; Land & Lee, 1994). However, these studies were mainly interested in fixation strategies and not in the quality of tracking or gaze stabilization. Here, we were mainly interested in the basic properties of image and object stabilization in a situation that simulates movement through a virtual environment. We presented optic flow fields simulating forward and backward motion. The environment presented a virtual ground plane. It was formed either of random dots or of a texture pattern which gives a more realistic impression (Fig. 1).

Lappe et al. (1998) described optokinetic reflexes to radial optic flow in monkeys. They found that these eye movements had a rather low gain of about 0.4–0.5. We wanted to know whether this is also true for humans, and whether the gain depends on the subject's intention to perform an active pursuit. Thus, we also recorded eye movements when subjects passively viewed the entire flow pattern. Eye movements in this case very much resembled optokinetic responses normally obtained for stabilization of unidirectional moving stimuli. The characteristics of the ocular responses evoked by radial optic flow in humans were very similar to those found in monkeys. Additionally, we also investigated eye movements when subjects were instructed to actively pursue single elements on the ground plane or single elements on a homogeneous dark background. Motion parameters were the same in both cases. Typical smooth pursuit responses were observed in both conditions. Thus, depending on the instruction given to the subjects different types of eye movements could be observed during optic flow presentation.

2. Methods

2.1. Subjects

Four subjects ranging in age from 25 to 33 years participated in the experiments. All subjects had normal or corrected-to-normal vision and prior experience in psychophysical experiments. Two subjects (BK, HF) were inexperienced in eye movement recordings. Three subjects (BK, HF, AG) were naive with regard to the purpose of the present study.

2.2. Eye movement recording

Horizontal and vertical movements of the left eye were measured by a video-based eye movement recording system using custom miniature cameras and high-resolution digital image processing (EyeLink, SMI). Sampling rate was 250 Hz. A neck support was used and subjects were instructed to keep their heads still. Any apparent miniature head movements were detected and compensated by the EyeLink system. Gaze position was automatically calculated from eye and head position. Gaze position was calibrated and validated with an EyeLink routine presenting nine fixation targets at specific locations on the screen in random order. Validation was accepted when absolute precision was below 0.5° of visual angle.

2.3. Visual stimuli

The stimulus was generated on a Silicon Graphic Indigo2 computer and back projected onto a transparent screen with a video projector (Electrohome ECP 4100). Spatial resolution was 1280×1024 pixels with a display refresh rate of 72 Hz. The size of the stimulus was 90×90 deg^2. The distance of the subject to the screen was 63 cm. The ambient luminance of the laboratory was below 0.01 cd/m^2.

Two types of stimuli were used. The first consisted of an optic flow simulating forward or backward self-motion over a virtual horizontal ground plane 1.1 m below
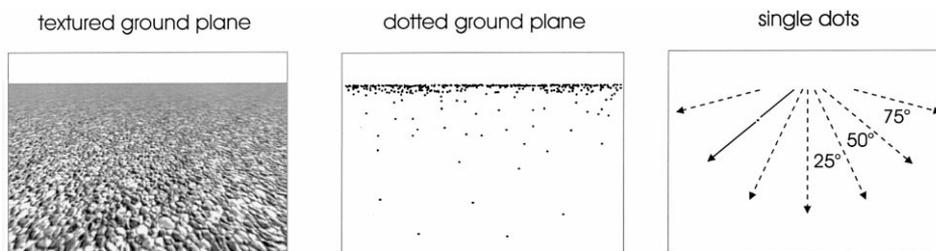

Fig. 1. Screen projections of the stimuli used in the experiments (reversed contrast). Left and center panels show the textured and dotted ground planes. The right panel shows the single dot condition: motion direction of the dot on the screen could be 0, ± 25, ± 50, or $\pm 75°$ away from the vertical meridian. Thus, the dot was placed on the ground plane either on the trajectory of the simulated movement of the observer or 0.46, 1.19, or 3.73 m to the left and to the right of the observer's trajectory.

eye level. The virtual ground plane was either covered with about 250 white dots on a dark background or with textured elements which covered it entirely (Fig. 1). The projection of the ground plane was clipped at a virtual distance of 40 m. This resulted in a visible horizon located 1.6° below the horizontal meridian of the screen. Dot size was constant at 0.5°.

In the second stimulus type only one single white dot was placed on an otherwise black virtual ground plane. The motion of this dot exactly equaled the motion of a single dot in the optic flow. By placing this dot on different locations on the ground plane we could generate different trajectories of dot motion on the screen (Fig. 1). The distance of the dot from the observer varied between 0 and 10 m.

2.4. Experimental procedure

Simulated observer speed and direction were varied independently in different trials.

1. The simulated observer velocity was either 3 or 6 m/s.
2. The simulated movement of the observer could be forward or backward. This resulted in expanding or contracting optic flow, respectively.
3. The horizontal position of the focus of radial flow was varied in order to simulate different self-motion directions. Focus position was either 0, or 10, or 20° to the left or to the right.
4. In the single dot condition the position of the dot on the ground plane was either on the trajectory of the simulated movement of the observer or 0.46, 1.19, or 3.73 m to the left and to the right of the observer's trajectory. This results in motion directions of the dot on the screen of 0, 25, 50, or 75° away from the vertical meridian of the screen, respectively (Fig. 1).

Presentation time was 20 s for each stimulus. The stimuli were viewed binocularly. Acceleration of dots ranged from 1.1 to 818 deg/s^2.

In different blocks of trials, different instructions were given to the subjects.

1. Active, selective smooth pursuit. The subject was instructed to actively follow a single dot with the eyes. The dotted ground plane or the stimulus with the single dot were used. In the case of the dotted ground plane, subjects were instructed to choose any one dot out of the set of visible dots, pursue it until it disappeared, and then choose a new one at random. Only stimuli with a central focus of radial flow (0°) were used.
2. Passive viewing of the entire optic flow stimulus. The subjects should not fixate any particular area or detail. They were instructed to simply view the stimulus (dotted or textured plane) and direct their attention to the entire pattern.

2.5. Data analysis

Recorded eye position were first filtered with a Gaussian of 4 ms width. Eye velocity was obtained by digital differentiation of the eye position data. Saccadic eye movements were detected by a velocity level criterion which was set to 35 deg/s. With this criterion some of the small saccades ($\leq 0.4°$) will be missed. This could result in an under-reporting of saccades (especially catch-up saccades in the active pursuit trials) which may change the gain. However, in a small number of trials a control analysis was carried out by manually deleting any saccade that was missed by the 35 deg/s criterion with a keyboard-controlled cursor. The gain difference (calculated as described below) between both procedures was less than 1%.

For each interval of slow eye movement (ISEM) the direction of the change of eye position (movement direction), the duration, velocity and gain were calculated. The direction and velocity of the eye movement during the ISEMs were calculated from a linear regression over all eye position data from within one ISEM. The gain (ratio of eye vs stimulus velocity) of steady-state responses during the ISEMs was defined as follows: In a radial optic flow the motion of individual elements accelerates and the direction of the element motion varies across the visual field. Therefore, standard measurements of the gain cannot be used. But for each eye position the optic flow motion and velocity that occurs at that position can be calculated from the observer motion and the spatial layout of the environment. In that way a unique optic flow vector can be assigned to each gaze position. We defined the gain of the eye movement with respect to this flow vector.

1. For each sampling point, the direction of gaze (horizontal x and vertical y eye position) in a co-ordinate system defined by the projection screen was determined.
2. The optic flow velocity $f = (f_x, f_y)$ at that visual direction was calculated from the parameters of the simulated observer motion and the visual environment used for the stimulation. In the optic flow, the motion of points $R = (X, Y, Z)$ of the three-dimensional world is projected onto the two-dimensional screen. This gives the optic flow motion at position $p = (x, y)$ on the screen. With a focal length of 63 cm R is projected onto

$$p = \binom{x}{y} = 0.63 \left(\frac{X/Y}{Y/Z} \right).$$

The motion of p on the screen is determined by the motion of R in the simulated 3D space. It results from the translation and rotation of the observer. The 3D motion F of point $R = (X, Y, Z)$ is $F = -T - \Omega \times R$ in general and $F = -T$ if we assume only a linear translation T.
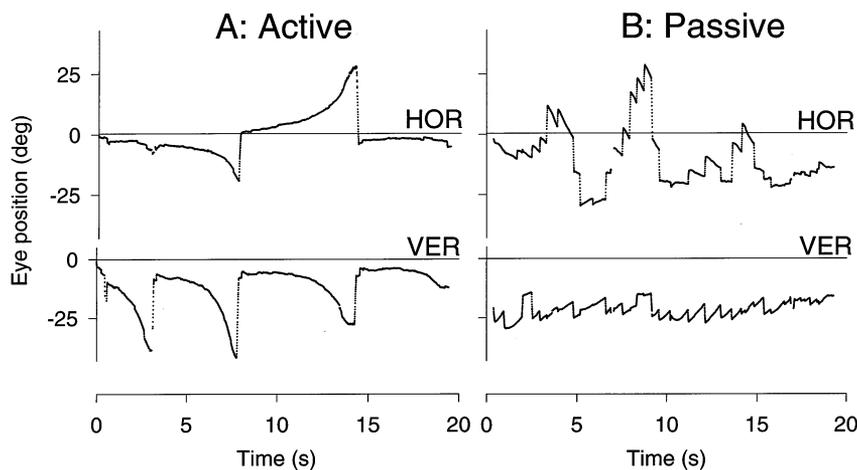
Fig. 2. Horizontal (upper trace) and vertical (lower trace) eye position during active voluntary pursuit (A) and passive optokinetic tracking (B) of a radial optic flow stimulus simulating a movement over a ground plane. In (A) forward movement with centered focus of expansion (FOE) (0°) was simulated. In (B) the optic flow stimulus simulated backward movement with a focus of contraction (FOC) 20° to the left. Simulated observer velocity was 3 m/s.

By differentiating p the motion f of p on the screen is available:

$$f(x, y) = \frac{dp}{dt} = 0.63 \begin{pmatrix} (\dot{X}Z - X\dot{Z})/Z^2 \\ (\dot{Y}Z - Y\dot{Z})/Z^2 \end{pmatrix}$$

With the perspective projection and the 3D motion F, this results in:

$$f(x, y) = \frac{1}{Z} \begin{pmatrix} -0.63T_X + xT_Z \\ -0.63T_Y + yT_Z \end{pmatrix}$$

Next the distance Z has to be expressed as a function of gaze position $p = (x, y)$. For the ground plane

$$Z = 0.63 \frac{h}{y}$$

with h as height of the observer (1.1m in our set-up).

3. The eye velocity ($v = (v_x, v_y)$) for the single sampling point was calculated from the eye position data. This was done by taking the positional difference between the current sampling point and the previous one and dividing it by the sampling interval.
4. For each single data point a gain g was calculated by taking the ratio between the component of the eye velocity in the direction of the optic flow vector and the speed of the optic flow vector:

$$g = |v|/|f|\cos \alpha$$

where α is the angle between the eye movement direction and the optic flow direction.

5. Finally, the mean gain was determined by averaging over all single gain values within one ISEM.

In the case of smooth pursuit of a single dot an additional analysis was carried out. Gain of the steady-state responses was calculated by means of the ratio of eye velocity and target velocity at any instance in time.

Eye movement trials for a specific target trajectory of all subjects were aligned to the onset of target motion and averaged. The ratio of the mean eye velocity and the target velocity was then calculated for each sampling point and averaged over the duration of the smooth pursuit.

3. Results

Depending on the instruction to the subject (active or passive) the eye movements exhibited distinct differences (Fig. 2). Fig. 2A shows a typical example of eye movements when a subject followed actively, single dots in an optic flow stimulus. Long pursuits occurred which were sometimes interrupted by catch-up saccades for positional correction (e.g. first pursuit in Fig. 2A). These pursuits showed an accelerating behavior reflecting the accelerating characteristics of optic flow elements (see also Fig. 5). Fig. 2B shows a typical example of eye movements when a subject passively viewed the entire flow stimulus. Eye movements showed a pattern of slow phases and saccades comparable to that of a typical optokinetic nystagmus (OKN), normally elicited with unidirectional coherent moving patterns.

3.1. Active tracking of optic flow elements

We investigated the gain of smooth pursuit eye movements for different observer velocities and directions (Fig. 3). In general, gain was near or at unity showing perfect object stabilization during active pursuit. When data for each subject was accumulated across velocity and stimulus type a slightly higher gain was observed when pursuing elements out of a contracting stimulus compared with an expanding stimulus

(subject AG, non-significant; BK, $P \leq 0.05$; HF, $P \leq 0.01$; ML, $P \leq 0.01$; $N < 80$; U-test. Averaged data Σ, $P \leq 0.01$; $N = 16$; U-test). Note that this difference was not always present in all conditions. No significant gain difference was found with active pursuit of individual dots in an optic flow stimulus and single dots on a dark background (individual data $N < 40$, averaged data $N = 8$; U-test).

Fig. 4. Smooth pursuit gain during active tracking of single dots. The definition of the gain was either based on the foveal velocity of optic flow (position, open symbols, taken from Fig. 3), or based on the time course of the velocity of the target (velocity, filled symbols). For the second definition, eye velocity was first aligned to the onset of target motion. Then the gain was calculated for each sampling point and finally averaged (see also Fig. 5B, D as an example). Error bars indicate standard deviations.

3.2. Active tracking of single dots

In the above definition of the pursuit gain in optic flow fields the stimulus motion had to be calculated from the eye position data (position-based gain definition, see Section 2). In conventional definitions of the gain of pursuit the stimulus motion is used directly (velocity-based). In the experiments that used single dot, stimulus motion at any time is known precisely. This gives us the opportunity to compare our definition of the pursuit gain in optic flow to a more conventional definition.

In the single dot condition each sampling point of eye movement data can be related to the velocity of the dot at the same point in time. This allows to evaluate the gain directly from the velocity of the stimulus. Fig. 4 compares the gain obtained in this way with the gain obtained with the position-based method that was introduced for the optic flow measurements. The position-based pursuit gain for single dots is based on the evaluation of the local velocity of optic flow from the eye position data. It is taken from Fig. 3 (position-based, see Section 2, open symbols). Both definitions of the gain gave very similar results.

Fig. 5 shows both methods of evaluation in more detail. Two examples are given. In one case, the target accelerated (forward movement of the observer, Fig. 5A). In the other case, the target decelerated (backward movement, Fig. 5C). Fig. 5A and C show the accumulated eye position of all subjects (thick line) and the position of the target over time (thin line). Subjects quite accurately pursued the target. A slight lag of the gaze behind the target was observed when the accelerated target was pursued.

Fig. 5B and D show the accumulated eye velocity of all subjects (thick line), the velocity of the target (thin
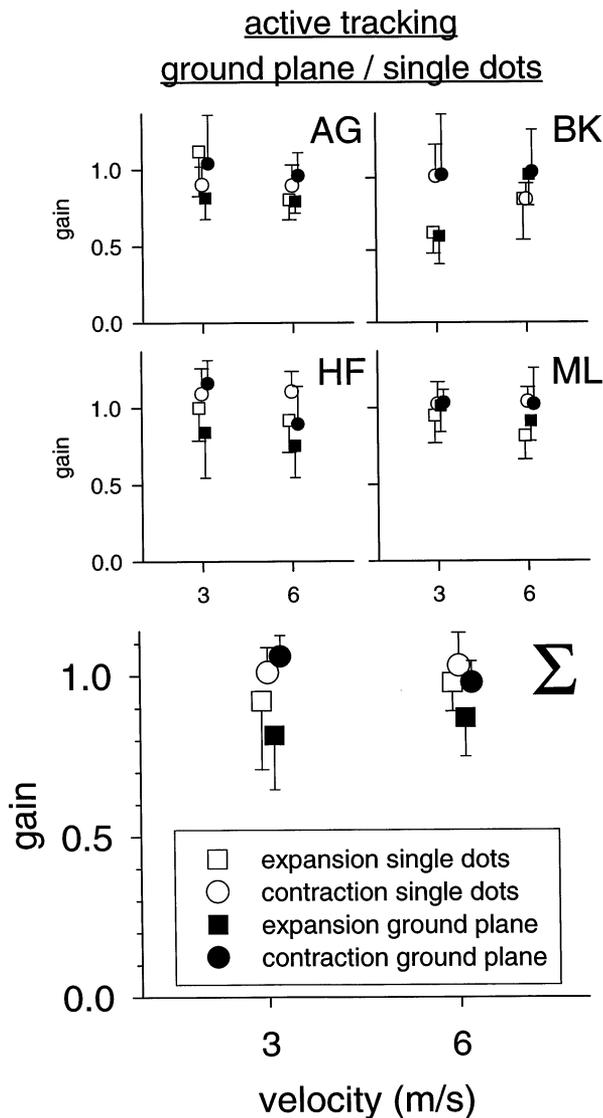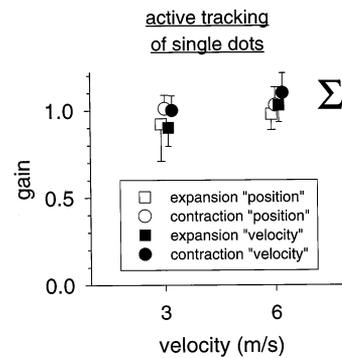

Fig. 3. Smooth pursuit gain during active tracking of dots in an optic flow field (filled symbols) or of single dots on a dark background (open symbols). Different observer velocities and movement directions are shown (forward, squares □/■; backward, circles ○/●). The gain (ratio of eye and stimulus velocity) was calculated by comparing the foveal velocity of the optic flow with the eye velocity (position-based, see Section 2 for details). Small panels show the results of individual subjects (AG, BK, HF, and ML). The large panel below shows the averaged data. Error bars indicate standard deviations.

line), and the optic flow velocity computed from the actual eye position (see Section 2, dotted line). In general, the velocity of the eye nicely matches the velocity of the target in both movement conditions. This corresponds to a high gain pursuit. An overshoot of the eye velocity with respect to the target velocity was observed in the beginning of the pursuit. Later (approximately 1 s after the start of the pursuit) the eye velocity dropped slightly below target velocity. One can also see that the evaluation of the gain based on the local velocity of optic flow computed from the actual eye position gives reliable results. This is exemplified by the velocity trace (dotted line shown in Fig. 5B and D). Although it is computed from the actual eye position it is very similar to the real velocity of the dot (thin line).

In summary, accelerated and decelerated objects (or objects during forward or backward self-motion) can be pursued almost perfectly with high gain near or at unity.

3.3. Passive tracking of optic flow

We next evaluated the gain of passively evoked eye movements. In the monkey, Lappe et al. (1998) have
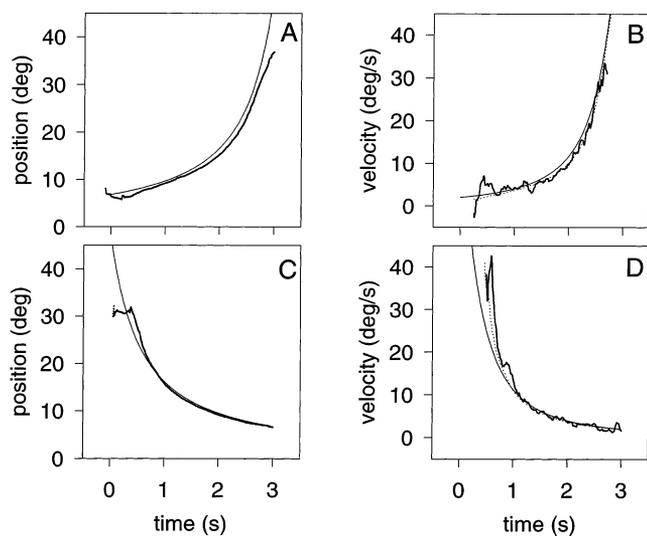
Fig. 5. Example of an averaged eye position and eye velocity signal during active pursuit of a single dot on a dark ground plane during forward (A and B), and backward movement of the observer (C and D). The dot was placed 0.46 m besides the trajectory of the observer. Observer velocity was 3 m/s. Averaged values includes all trials of all subjects. (A and C) Averaged eye position. The thin line indicates the trajectory of the target. (B and D) Averaged eye velocity. The dotted line is the velocity of the optic flow in the direction of gaze, i.e. the foveal motion velocity (taken from A and C, respectively, for further details see Section 2). The thin trace shows the velocity of the target. The two traces are not perfectly aligned because the eye is not perfectly aligned with the target trajectory (see panel A and C). The resulting velocity difference in panel B and D of the dotted and thin traces is given in peak (max) and mean differences (mean) (panel B: max 4.91 deg/s, mean 1.12 deg/s, rms error 1.34 deg/s; panel D: max 9.34 deg/s, mean 0.13 deg/s, rms error 2.03 deg/s).
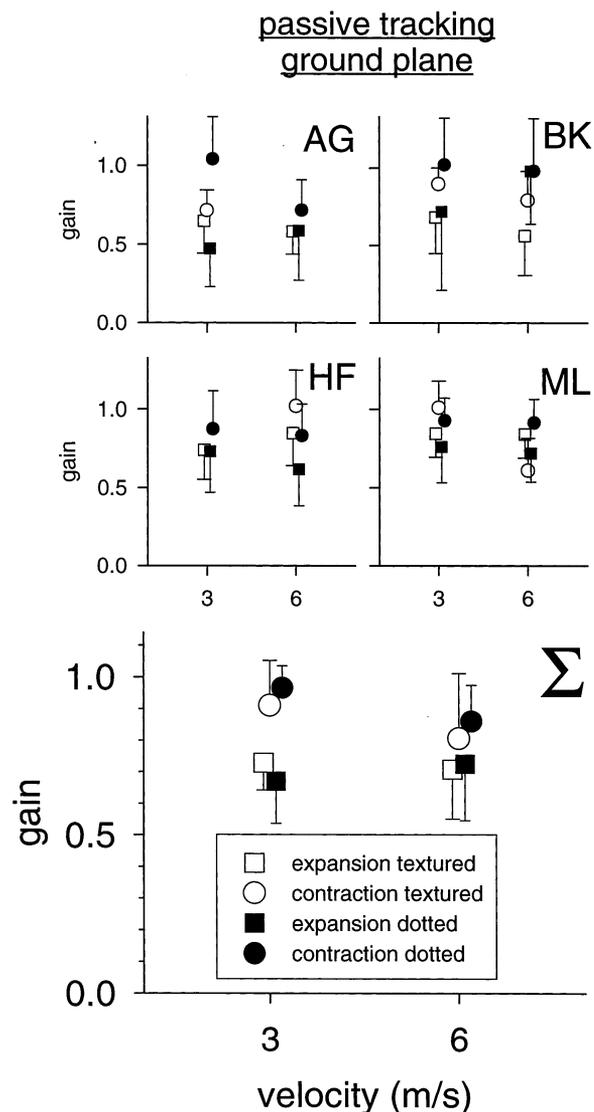
Fig. 6. Gain during optokinetic tracking of optic flow stimuli with different observer velocities, movement directions (forward, squares $\square$/$\blacksquare$; backward, circles $\bigcirc$/$\bullet$) and virtual environments (dotted, filled symbols $\blacksquare$/$\bullet$; textured, open symbols $\square$/$\bigcirc$). Error bars indicate standard deviations. The gain (ratio of eye and stimulus velocity) was calculated by comparing the velocity of the foveal optic flow at each sample point with the eye velocity (see Section 2 for details). Small panels show the results of individual subjects (AG, BK, HF, and ML). The large panel below shows the averaged result. Note that some data from AG and HF had to be discarded because of insufficient quality of eye movements (too many blinks, missing attention to the stimulus).

described that radial optic flow stimuli induce optokinetic eye movements with a rather low gain. The gain was smaller for expanding than for contracting optic flow. When data for each subject was accumulated across velocity and stimulus type human subjects in our study also showed higher gain for the contracting stimuli than for the expanding stimuli (Fig. 6; subject AG, $P \leq 0.01$; BK, $P \leq 0.01$; HF, $P \leq 0.01$; ML, $P \leq 0.01$; $N < 160$; U-test. Averaged data Σ, $P \leq 0.01$; $N = 16$;

Table 1
Mean foveal optic flow velocity and mean distance of eye position to the focus of radial flow during passive tracking[a]

		Observer-velocity (m/s) 3	6
Expansion	Local flow velocity (deg/s)	7.57 ± 17.4	9.97 ± 3.56
Contraction	Local flow velocity (deg/s)	10.6 ± 7.5	14.9 ± 12.2

[a] Data includes all subjects.

U-test). Note that this difference was not always present in all conditions. Thus, an asymmetric gain was observed that depended on the direction of simulated observer movement (forward or backward). The gain during passive tracking was generally lower than during the active smooth pursuit condition (averaged data Σ, $P \leq 0.01$; *U*-test). With increasing observer velocity the gain slightly decreased. We compared the gain obtained with the dotted ground plane to that obtained with the textured ground plane. In general, for both types of stimuli the gain was very similar (Fig. 6, filled symbols vs open symbols).

The asymmetry of the gain for expansion versus contraction was investigated in more details. As will be shown below, during viewing of expanding optic flow gaze is oriented preferentially towards the focus of expansion whereas for the contracting optic flow gaze is oriented more towards eccentric positions. Thus, the resulting mean velocity of foveal optic flow is smaller for the expanding optic flow than for the contracting optic flow (Table 1). Slower foveal optic flow leads to slower eye movement responses and hence to more uncertainty in the recording of eye movement direction.

This could result in lower gain values when considering the alpha term in the gain calculation (see Section 2). Moreover, stimulus artifacts such as directional quantization and pixel creep of slow moving dots may induce additional inaccuracies for gain measurements. Taken together, the observed gain difference between expansion and contraction might simply be due to the different distribution of gaze and the resulting differences in foveal stimulus speed and differences in the effect of stimulus artifacts. To investigate whether this is true, the gain for expansion and contraction was analyzed with respect to identical intervals of velocities of foveal optic flow (Fig. 7). Independent of speed, the gain for contraction was always higher than the gain for expansion. Thus, the gain differences in Fig. 6 are not artifactual but must be related to the expansion–contraction condition.

Next, we investigated the dependence of the gain on the direction of eye movement. Fig. 8 shows a polar plot of the gain averaged across all subjects and stimuli. It reveals an up–down asymmetry with the upward direction having a higher gain than the downward direction. Furthermore, the horizontal component of pursuit is stronger for contracting than for expanding flow. Also, for expanding flow a left/right asymmetry can be seen which is, however, not significant (*U*-test).

We further quantified the angular difference between the direction of the foveal optic flow and the direction of the eye movement. Fig. 9 shows the distribution of this angular difference for different conditions. The direction of the foveal motion is defined as the direction of the local optic flow vector on the fovea. Most often the direction of the slow phase eye movement coincides very well with the direction of the foveal optic flow. The difference angles accumulate around 0°. The range
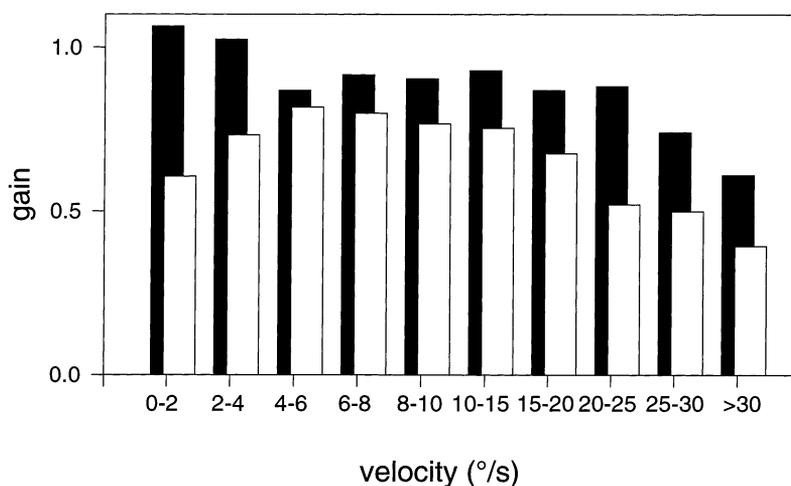

Fig. 7. Median gain during optokinetic tracking for different foveal optic flow velocities. Black bars indicate the gain with backward movement (contraction), white bars with forward movement (expansion). The foveal optic flow velocities were divided into several bins. Because most of the pursuits have been executed on low foveal optic flow velocities, bin width is set to 2 deg/s for foveal velocities lower than 10 deg/s and to 5 deg/s for higher velocities.
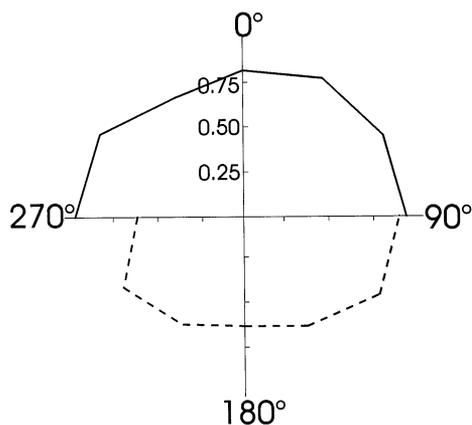
Fig. 8. Polar plot of median gain across subjects for expanding (dotted line) and contracting (solid line) optic flow stimuli. For this figure, the distribution of eye movement direction was divided into 12 bins (0, 30, 60°,...) and the median gain was determined for each bin.

of angular differences varied across different conditions: For the passive tracking of the textured ground plane and the active tracking of the ground plane and
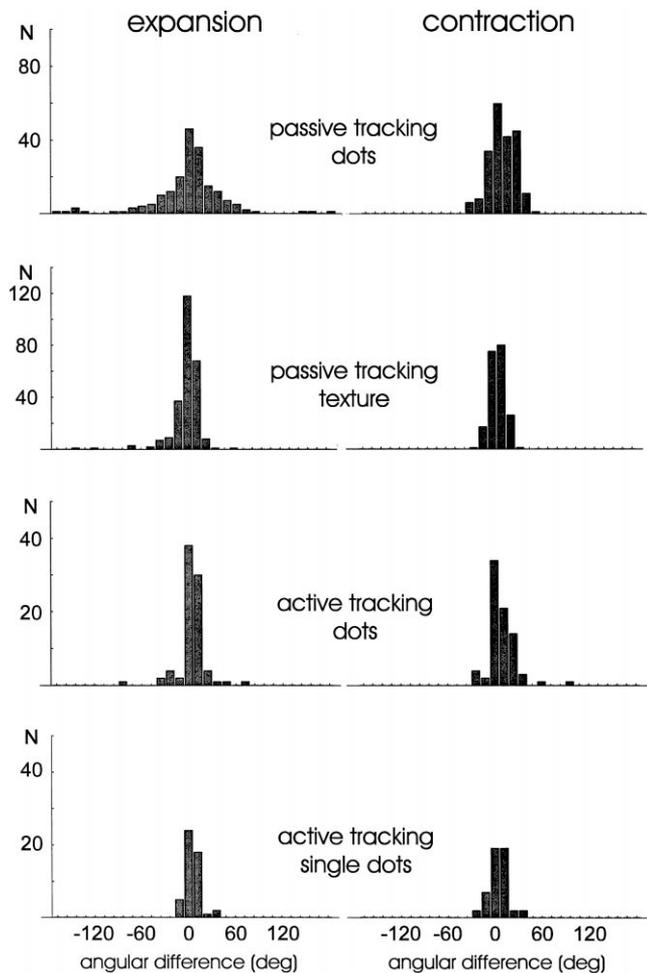

Fig. 9. Distribution histograms of angular differences between the direction of pursuit and the direction of foveal motion.

the single dots, the distribution is sharper than for the dotted ground plane ($P \leq 0.01$, F-test), indicating better directional following in these cases.

3.4. Spatial distribution of gaze

Fig. 10 shows a vector field plot of the eye movements of one subject during presentation of an expanding and a contracting optic flow stimulus. Arrows indicate the start position, the direction, and the speed of the eye movements. The vector field plot of the eye movements resembles that of an optic flow field. With increasing eccentricity of gaze eye speed increases in correspondence with the increasing speed of local elements of the optic flow. For the expanding optic flow the gaze is oriented significantly more towards the focus than for contracting flow (all subjects; mean deviation from the focus of expansion: $7.50° \pm 4.36$ S.D., mean deviation from the focus of contraction: $9.23° \pm 5.35$ S.D.; $N < 480$, $P \leq 0.001$, U-test).

We analyzed the distribution of gaze during passive tracking. Fig. 11 shows contour plots of the spatial distribution of gaze with forward and backward movement and different focus positions. The data is shown for all subjects and observer velocities. The black area reveals the area with the highest frequency of gaze. Thus, gaze was not distributed evenly across the stimulus. Rather it was concentrated in one or two areas of the stimulus, which depended on the placement of the focus of expansion or contraction (Fig. 11). The peak of the distribution of gaze position shifted in accordance with the shift of the focus. In general, gaze position was preferably oriented at or near the focus. Sometimes, for an eccentric focus position, a second peak was observed near the center of the screen or stimulus (0°).

4. Discussion

The results show that oculomotor behavior during viewing of radial optic flow depends on the instruction to the observer. When subjects actively pursued single elements in an optic flow pattern, the eye movements exhibit long tracking phases, sometimes interrupted by catch-up saccades, with high gain. This is typical of smooth pursuit eye movements. When subjects passively looked at the entire flow pattern the evoked eye movements consisted of shorter tracking phases that were frequently interrupted by saccades and had a slightly lower gain. This pattern of eye movements resembles that of an optokinetic nystagmus.

We found no difference in gain for active pursuit of optic flow elements compared to the pursuit of single dots placed on a dark background. Evaluating the smooth pursuit gain for single dots with two different
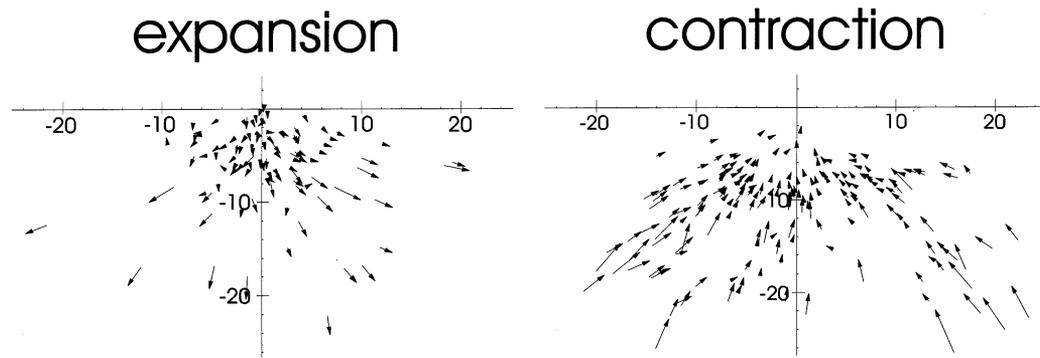
expansion   contraction

Fig. 10. Vector field plot of direction and velocity of slow phase eye movements during passive optokinetic tracking. The position, direction, and length of each vector corresponds to the average eye position, eye movement direction, and speed during a single slow phase. The subject viewed an optic flow stimulus simulating forward (expansion, left panel) or backward (contraction, right panel) movement over a dotted ground plane with 6 m/s observer velocity and centered focus of radial flow.

methods, one based on the foveal motion of optic flow, the other based on the velocity profile of the dot motion, yielded no differences. Thus, gain of active smooth pursuit of optic flow elements can be reliably estimated with the method based on the foveal motion of optic flow.

Our results clearly show that accelerating or decelerating targets can be pursued almost perfectly with high gain. However, we found a slightly higher gain for upward pursuit (pursuing elements in a contracting optic flow) than for downward pursuit (pursuing elements in an expanding optic flow). This was also, although not consistently, observed by Rottach, Zivotofsky, Das, Averbuch-Heller, Discenna, Poonyathalang et al. (1996) for vertical sinusoidal target motion. Thompson and Stone (1997) described an up–down asymmetry in speed perception. Upward motion was often seen faster than downward motion. This might be related to the observed oculomotor behavior. However, initial pursuit along a vertical axis shows no clear up–down asymmetry (Tychsen & Lisberger, 1986; Rottach et al., 1996). This might indicate separate mechanisms, one in response to visual motion and one for the prediction of target motion, contributing to the smooth pursuit system.

Open-loop responses of smooth pursuit to acceleration have been investigated in human and non-human primates (Krauzlis & Lisberger, 1994; Watamaniuk & Heinen, 1995). However, both paradigms differed in some aspects to the one we used. Whereas Krauzlis and Lisberger (1994) presented targets which accelerated smoothly for about 125 ms and then moved with constant velocity, Watamaniuk and Heinen (1995) used targets moving with constant acceleration and different initial velocities. Both investigated the open-loop response of pursuit. They found it mainly a function of target velocity rather than of target acceleration, although Krauzlis and Lisberger (1994) found some sensitivity also to acceleration. In contrast, the acceleration

and deceleration of targets in our study was variable in accordance with the movement definition of optic flow elements. Watamaniuk and Heinen (1995) showed that the smooth pursuit system is quite insensitive to changes of target acceleration. In our measurements the change of acceleration amounts to several 100 deg/s^2 during one trial. The accelerations range from 1 to 818 deg/s^2. This signal might be strong enough to contribute to a near perfect stabilization of accelerating targets. Moreover, the acceleration or deceleration in our stimuli represents the natural motion of static objects relative to a moving observer. Miles (1994) proposed that for frontal-eyed animals the visual stabilization of objects during self-motion is probably the most common form of visual tracking in everyday life. He suggested that smooth pursuit developed especially for this purpose. This specifically requires to be able to stabilize objects with accelerated or decelerated motion characteristics resulting from self-movement of the observer. Different psychophysical studies in humans investigated the detection of optic acceleration (Gottsdanker, 1956; Snowden & Braddick, 1991; Werkhoven, Snippe & Toet, 1992). Werkhoven et al. (1992) found that the detection is probably not based directly on the acceleration signal (temporal derivative of velocity) but rather on a low-pass temporal filter process followed by a variance detection stage. Thus, the detection of acceleration is based on the amplitude of a velocity modulation signal. Recently, Lisberger, O'Keefe, Kahlon, Mahncke and Movshon (1995) reported neural responses specific to target acceleration in the middle temporal area (MT) of monkeys. Area MT is part of the parietooccipito-ponto-cerebellar circuit for smooth pursuit (Lisberger, Morris & Tychsen, 1987; Komatsu & Wurtz, 1988; Newsome, Wurtz & Komatsu, 1988; Keller & Heinen, 1991). Thus, this area might contribute to the execution of smooth pursuit of accelerating or decelerating target motion.

When subjects passively viewed an optic flow stimulus, the characteristics of eye movements were similar to a typical stare nystagmus. They exhibited short following phases frequently interrupted by saccades. This suggest that the optokinetic system is responsible for the generation of these eye movements.

Lappe et al. (1998) described similar optokinetic eye movements elicited by radial optic flow in monkeys. The eye movements had a rather low gain of about 0.4–0.5. They proposed that the low gain resulted from spatial averaging of motion signals in a parafoveal summation area of the optokinetic system. The optokinetic responses during passive viewing in our experiments also had a low gain for expansion but not for contraction (Fig. 6). Several properties of the optokinetic system might contribute to the gain reduction. The many different visual motion directions in radial optic flow might be a source of inhibitory mechanisms for the optokinetic system, thus resulting in low gain. Niemann, Ilg and Hoffmann (1994) reported a greatly reduced gain of optokinetic responses to a transparent stimulus consisting of two counter-moving transparent random dot patterns. Inhibitory interactions on motion perception have also been found with patterns moving in orthogonal directions (Snowden, 1989). Thus, it seems likely that different motion directions in radial optic flow may have inhibitory influences on the optokinetic system. However, optokinetic responses to unidirectional motion presented in the central or the peripheral areas of the retina revealed a superiority of the central retina in driving the OKN (Dubois &

Collewijn, 1979; Howard & Ohmi, 1984; Murasugi & Howard, 1989). In spite of velocity vectors of many different directions in an optic flow field the preponderance of the central retina in driving the optokinetic responses results in fewer inhibitory influences from different motion directions.

But a parafoveal averaging of motion signals in our optic flow stimuli leads to a reduction of the speed signal to the optokinetic system. The ground plane contains progressively more slow motion signals from distant elements, because the density of visible points increases towards the horizon. Therefore, the average motion in a parafoveal summation area is slower than the motion on the fovea. The magnitude of the speed reduction depends on the size of the summation area (Lappe et al., 1998). Therefore the difference between the human and non-human primates may be due to a difference in the size of the retinal areas or the visual field from which motion information is integrated. The human optokinetic system might integrate motion signals from a smaller, more foveal area of the visual field than the monkeys.

Optokinetic stabilization was in general lower for expanding than for contracting optic flow stimuli. This was true for both the horizontal and vertical vector components (see Fig. 8). Lappe et al. (1998) made comparable observations in monkeys. In humans, the gain of the optokinetic nystagmus (OKN) for vertical movement is asymmetric (van den Berg & Collewijn, 1988; Murasugi & Howard, 1989). Upward moving patterns yield a higher gain than downward moving
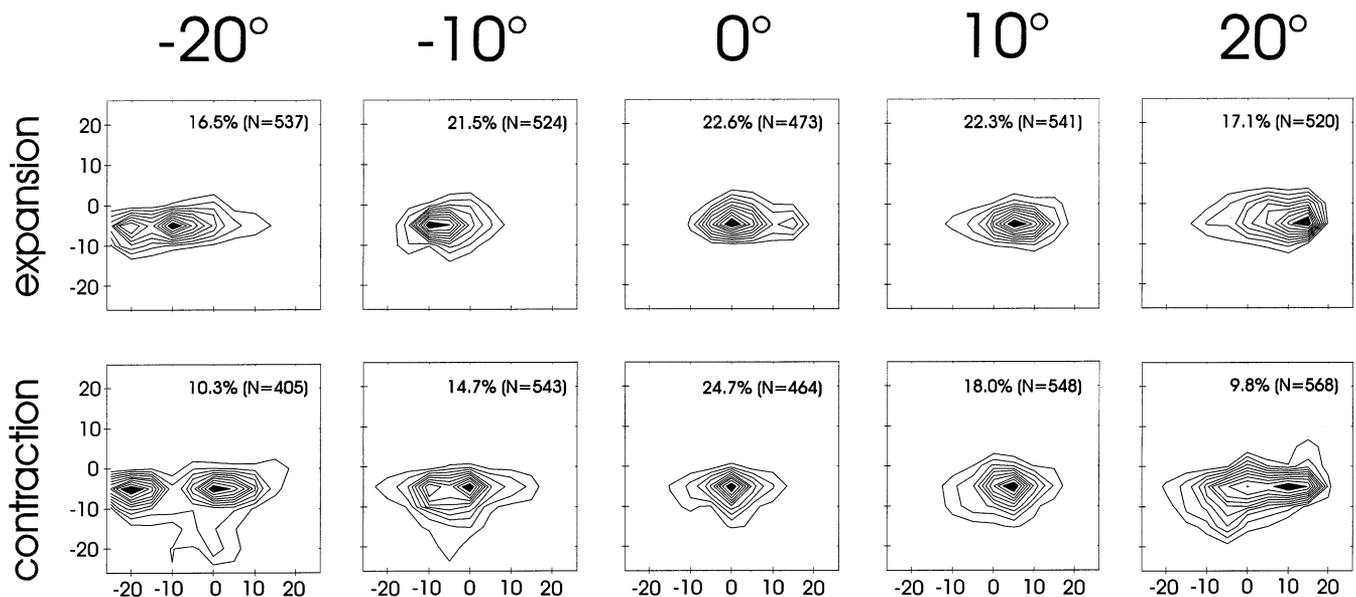

Fig. 11. Contour plots of the spatial distribution of gaze during passive tracking of optic flow stimuli with different movement directions (forward, upper row; backward, lower row) and focus positions (± 20, ± 10, $0°$). Initial eye position of each interval of slow eye movements (ISEM) was accumulated for all subjects and observer velocities. Gaze position data was divided into $5°$ bins. Lines indicate levels of similar frequency. The black area reveals the area with the highest frequency of gazes. The relative maximum frequency (%) and the number of measurements (*N*) are given for each focus position and movement direction.

patterns. In an optic flow simulating a forward movement over a ground plane all motion has a downward component whereas with backward movement the vertical component of all vectors is upward.

However, an asymmetric gain depending on forward or backward movement was also observed for horizontal eye movements during passive viewing of optic flow. The foveopetal/foveofugal asymmetry in horizontal smooth pursuit and optokinetic responses found in human and non-human primates might explain the gain asymmetry in the horizontal component of eye movement responses to optic flow (Naegele & Held, 1982; Lisberger & Westbrook, 1985; Westall & Schor, 1985; Ohmi et al., 1986; Tychsen & Lisberger, 1986; Niemann & Hoffmann, 1997). On the neuronal level, the nucleus of the optic tract (NOT) might be responsible for these asymmetries (Lappe et al., 1998). The NOT is a subcortical structure and important for the generation of the horizontal OKN (Hoffmann & Distler, 1986).

In conclusion, both the vertical and the horizontal vector component might result in lower gain for an expanding optic flow stimulus.

Gaze during passive tracking was clustered at or near the focus of expansion or contraction. Gaze strategies during self-motion have been investigated during real self-motion in bicycle and car drivers (Mourant et al., 1969; Rockwell, 1972; Shinar, 1978; Gale et al., 1985; 1988; 1991; Land, 1992; Land & Lee, 1994). Mourant et al. (1969) and Rockwell (1972) reported that approximately 90% of all saccades were oriented to an area $\pm 4°$ around the focus of expansion. This corresponds quite well to our observation of gaze distribution under laboratory conditions with visual simulation of self-motion. The following explanations might account for this oculomotor behavior: Firstly, Shinar (1978) argued that the preferred proximity of gaze near the focus might give the maximum time to the driver to take in the information on the preceding road. Secondly, the error for the calculation of direction of heading increases with increasing angle between gaze and the focus of radial flow (Warren & Kurtz, 1992). Thus, when holding gaze at a position near the focus of radial flow this error can be kept low. Thirdly, it was observed that optokinetic responses to unidirectional motion stimuli with different velocities in general match the slowest velocity in the visual field (Abadi & Pascal, 1991; Mestre & Masson, 1997). Mestre and Masson (1997) argued that this strategy of the optokinetic system might contribute to the perception of heading: the zone around the focus of radial flow has the slowest motion in optic flow while also corresponding to the direction of self-motion. Thus, the gaze strategy with the orientation to the focus might reflect a conscious process of active obtaining information or an unconscious process for a precise judgment of heading direction under both the laboratory and real self-motion situations.

However, sometimes two peaks were observed in the distribution of gaze. One was near the position of the focus of contraction, the other was near the vertical meridian. A similar effect has been described in the ocular responses to radial flow in monkeys (Lappe et al., 1998). It has been linked to the shift of the optokinetic Schlagfeld in regular OKN (Jung & Mittermaier, 1939). For the expanding optic flow, this shift is towards the location of the focus. For the contracting optic flow it is away from the location of the focus. The two peaks in the distribution of gaze for contracting optic flow therefore suggest the presence of two competing mechanisms that drive gaze position in this situation. The peak near the vertical meridian may be related to the shift of the Schlagfeld while the peak near the position of the focus may be related to an orientation towards the axis of observer motion.

Cortical and subcortical areas may generate the described eye movements. It was already emphasized that subcortical structures may play a crucial role for the generation of eye movements when the optic flow is passively tracked. While the NOT is important for the execution of the horizontal OKN in non-human primates, the accessory optic system (AOS) is concerned with the execution of the vertical OKN (Hoffmann & Distler, 1986; Mustari, Fuchs, Langer, Kaneko & Wallman, 1988). In higher mammals, the NOT and AOS receive a binocular input from MT and the medial superior temporal area (MST) in addition to the direct retinal afferents (Hoffmann, Distler & Ilg, 1992). As MT and MST are part of the parietooccipito-ponto-cerebellar circuit for smooth pursuit, the optokinetic and smooth pursuit system share common main inputs (Lisberger et al., 1987; Komatsu & Wurtz, 1988; Newsome et al., 1988; Keller & Heinen, 1991). Neurons of the subcortical structures NOT and AOS respond to fronto-parallel moving stimuli (Hoffmann & Distler, 1986; Mustari et al., 1988). Neurons of area MST also respond to fronto-parallel moving stimuli. But in addition they also respond to expanding, contracting and rotating stimuli (Tanaka & Saito, 1989; Duffy & Wurtz, 1991; Kawano, Shidara, Watanabe & Yamane, 1994; Lappe, Bremmer, Pekel, Thiele & Hoffmann, 1996). Moreover, radial flow induces also short-latency vergence movements which might also be mediated by area MST (Busettini, Masson & Miles, 1997). Therefore, slow eye movements in response to optic flow stimulation might be driven by both subcortical and cortical motion sensitive areas. However, for correct optic flow analysis during eye movements the effects that the eye movements in turn impose on the optic flow have to be taken into account, too. Indeed, extraretinal feedback during pursuit is found in MST neurons (Newsome et al., 1988; Erickson & Thier, 1991; Ilg & Thier, 1997) potentially aiding the analysis of optic flow during pursuit (Duffy & Wurtz, 1994; Bradley, Ehrlich, Backus

& Crowell, 1996; Lappe, 1997, 1998). Moreover, pursuit eye movements during forward self-motion may lead to retinal image motion resembling a spiraling pattern around the fovea (Lappe et al., 1998). MST neurons also respond to spiraling motion (Graziano, Andersen & Snowden, 1994; Duffy & Wurtz, 1997). This might reveal a specialization for these retinal image patterns during natural oculomotor behavior.

In conclusion, we have shown that radial optic flow fields elicit passive optokinetic eye movements in humans. These passive eye movements have a comparatively low gain for expansion. The gain is higher for voluntary smooth pursuit of optic flow elements. In this case, accelerated motion usually occurring in optic flow can be pursued almost perfectly.

Acknowledgements

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