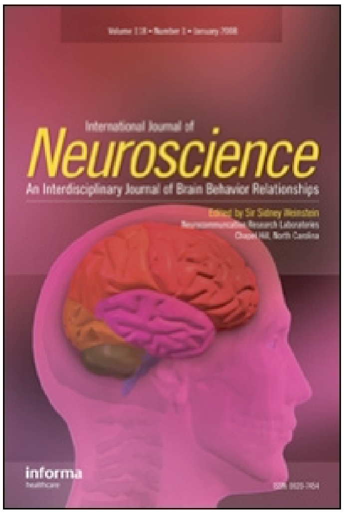

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Eye-Movements During Navigation in a Virtual Tunnel

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EYE-MOVEMENTS DURING NAVIGATION IN A VIRTUAL TUNNEL

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Eye movements were investigated amongst participants who preferentially use an egocentric or an allocentric frame of reference during navigation through computer simulated tunnels. Performance was highly accurate even though the tunnel passages contained only sparse visual flow and no differences in homing accuracy between subjects using one or the other reference frame was observed. Analyses of eye-movements revealed that gaze was centered on the tunnel's visual centroid during straight segments. However, during turns mean gaze position was directed toward the outer wall. As the angle of turn increased, the prevalence of overall eye movements and the laterality of gaze were greater than during turns of lesser angle. Even though the strategy groups reacted based on distinct reference frames, comparable patterns of eye movements were revealed for both strategies. The data describe how information during navigation through sparse visual environments is selected and

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demonstrate that the preferential use of an egocentric or an allocentric frame of reference is independent of eye-movement patterns. Thus, a purely cognitive basis for individual differences in reference frame usage can be assumed.

Keywords eye-movements, navigation, reference frame, spatial cognition

INTRODUCTION

Different strategies exist to navigate through space. Which strategy is predominately used can depend on the type of information available for the task, such as maps or verbal descriptions (Lawton, 1994, 1996; Pazzaglia & De Beni, 2001). Strategy employment can also vary according to spatial and nonspatial strategies (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003) or individual preferences pertaining to the use of an allocentric or an egocentric frame of reference (Gramann, Müller, Eick, & Schönebeck, 2005). The use of an allocentric reference frame refers to the representation of entities in space in a framework which is externally located relative to the perceiver. An egocentric reference frame is one where the holder of the reference frame represents locations with respect to him/herself. The use of distinct frames of reference as a means to represent entities in space leads to differences in the derivable primitive parameters (Klatzky, 1998). Within the allocentric representation, entities are presented as points with angular and metric distance information derivable between all interpoint connections. The construction of an allocentric locational representation does not require the updating of heading changes during navigation. In this kind of spatial representation, the navigator is represented without orientation, that is, as one point among others. Within the egocentric representation by contrast, the navigator is represented with a defined orientation at a location and other points are represented with respect to the navigator's orientation.

Preference for Allocentric and Egocentric Frames of Reference

The preference to use an allocentric or an egocentric frame of reference in spatial navigation was explored by Gramann et al. (2005), where it was demonstrated that individuals differ in their preferred use of a specific frame of reference. In a computer-simulated virtual reality (VR) task, participants navigated through tunnels which contained only sparse visual flow information. Their task was to indicate their position at the end of a passage relative to the starting point. The authors were able to categorize individuals into two distinct strategy groups. Specifically, navigators using an allocentric frame of reference, referred to as "nonturner," did not update their cognitive heading after turns and preferred to track their orientation according to their heading at the initial starting position. Those who navigated using an egocentric frame of reference, referred to as "turner," tracked changes in tunnel direction by mentally adopting them. This strategy group seemed to update changes in cognitive heading in accordance with changes in perceived heading, despite the absence of proprioceptive and vestibular cues.

In an attempt to further explore this result, Gramann, Müller, Schönebeck, and Debus (2006) reconstructed sources of brain-electrical activity associated with the process of navigation through the tunnel task based on distinct reference frames. Differences between turner and nonturner emerged during and after heading changes in the task. Specifically, navigation in the initial straight tunnel segments, when the perceived and cognitive heading of both groups was identical (see Figure 1), was associated with comparable activity within an occipital-temporal network for turner and nonturner. However, both strategy groups exhibited diverging cortical networks to be dominantly active during and after the turn; likely reflecting translational and/or rotational changes in the underlying coordinate systems. Computation of an egocentric reference frame was associated with prevailing activity within a posterior parietal-premotor network, with additional activity in frontal areas. In contrast, computation of an allocentric reference frame was associated with dominant activity within an occipito-temporal network. The results support a distinction between the ego- and allocentric frame of reference on a neuroanatomical level with the use of an egocentric frame associated with activity in a network supporting viewer-centered encoding of the environment (Committeri et al., 2004). In contrast, the use of an allocentric frame was found to dominantly activate right-hemispheric areas that are associated with the storage of an allocentric cognitive map (Burgess, Maguire, & O'Keefe, 2002; Iaria et al., 2003; Maguire et al., 1998). Thus, the assumption that the preference to use an egocentric or an allocentric frame of reference during spatial navigation is based on distinct cognitive processes is supported by electrocortical activity.

However, the contribution of perceptual factors to the preferred use of distinct reference frames remains unclear. For example, the preference to use an allocentric frame of reference, and thus, the tendency to react based on a constant heading might be associated with distinct eye-movements during and after the turn as compared to the use of an egocentric reference frame associated with the updating of heading changes during the passage.

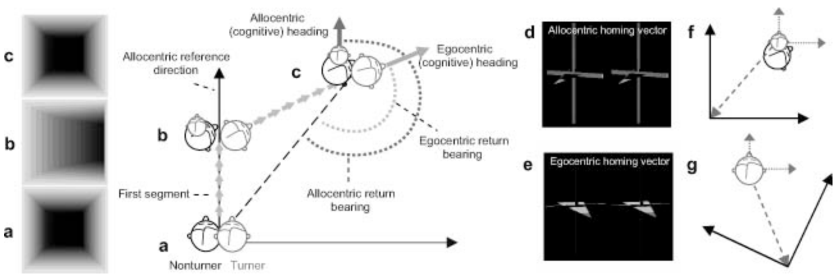

Figure 1. Depiction of a passage through a tunnel with a turn to the right. The left-most column displays the navigator's view into (a) the first straight segment, (b) a segment with a turn to the right, and (c) a straight segment after the turn. The second left column displays a nonturner (dark grey head representing the perceived heading and the small light grey head representing the cognitive heading) using an allocentric frame of reference, with the navigator's heading during (a) the first straight segment, during (b) the turn, and during (c) the straight segment after the turn. Note that the perceived and the cognitive heading diverge during the turn. On the right, a turner (light grey head representing the perceived cognitive heading which is assumed to be identical to the cognitive heading) is displayed which uses an egocentric frame of reference. During the first segment (a), the turner's heading is the same as that of a nonturner. During the turn (b), the axis of orientation changes. At the end of the tunnel, the turner's cognitive heading is different from that of a nonturner. Note that turners build up an additional allocentric frame of reference if they are forced to react based on an allocentric frame of reference. There is no depiction of an additional allocentric reference frame for turners to emphasize the preferred use of an egocentric frame of reference by this strategy group. To the right-side of the figure, examples of homing vectors are displayed with the correct angular adjustment for a tunnel with one turn of 60° to the right, with Panel d depicting the correct homing vector for nonturners, and Panel e that for turners. The right-most column displays (f) the coordinate system underlying the allocentric cognitive heading (grey dotted arrows) and the coordinate system of the video display (black solid arrows) and (g) the coordinate system underlying the egocentric cognitive heading (grey dotted arrows) and the coordinate system of the video display (black solid arrows).

Eye-Movements During Navigation

Analyses of eye-movements during simulated driving tasks demonstrate a close link between eye-movements and performance during heading changes (Land & Lee, 1994; Wann & Land, 2000; Wann & Swapp, 2001). Simulated driving experiments are similar to the tunnel experiment in the sense that visual flow is the main source of information, which is adequate to compute heading and driving distance (Lappe et al., 2000). Land and Lee (1994) have found that when steering a turn, 80% of the gaze falls on the tangent point of the curve. Wann and Land (2000) have found similar results suggesting that fixating on a particular point on the road, in this case the tangent point, simplifies the task. One year later, Wann and Swapp (2001) were able to show that the tangent point was not necessarily the only point where drivers might fixate when navigating a curve. They found that drivers were most likely to look toward the path of future travel, which often was located in the distance and in the center of the road. The authors do not claim that gaze is unimportant for steering, but do challenge the idea of whether or not any point on the road, be it the future path or the tangent point, really does have special status.

Besides the similarities in visual stimulation between driving tasks and the tunnel paradigm, the underlying research questions differ. Simulated driving studies explore eye-movement patterns during heading changes without the necessity to integrate those into a spatial representation. In contrast, the tunnel task investigates differences in spatial representation without exploring how subjects perceive heading changes. Therefore, the analyses of eye-movements during simulated driving tasks provide important information on how subjects perceive heading changes that have to be incorporated for immediate action. This approach is incorporated in the study of navigation through virtual tunnels to provide information on how subjects perceive heading changes and incorporate these into spatial representations based on distinct frames of reference.

The foremost goal of the study is to clarify the role eye-movements may play whilst navigating through the virtual space. Specifically, we aim to determine how (where and when) participants view the tunnel and to provide a detailed description of visual behavior during the virtual reality task. As a second goal, the study aims to clarify the role eye-movements play in navigation dependent on the frame of reference used, i.e., whether eye-movement patterns dissociate between navigation based on an allocentric or an egocentric reference frame. Distinct eye-movement patterns would suggest that individual differences in spatial representations are perceptually based. In contrast, comparable patterns of eye movements for turner and nonturner would support the assumption that differences in the preferred use of an egocentric or an allocentric spatial representation result from distinct higher-order cognitive processes. Finally, eye-movement analysis is also critical to ensure that previous source reconstruction (Gramann et al., 2006) has not been influenced by strategy-specific differences in eye-movement patterns during the tunnel passages.

EXPERIMENTAL PROCEDURE

Participants

Sixteen male students (8 nonturners, 8 turners) of the University of Munich, Munich, Germany, took part in this experiment. Their ages ranged from 20 to

27 years ($M = 23$ years, $SD = 1.9$) and all had normal vision without correction. Each experiment lasted approximately 1.5 hr for which volunteers were paid 9€ (or 11.50$) per hr. All participants were right-handed, with the exception of one turner.

Tunnel

Participants were seated in a dimly lit room in front of a 21-inch video display monitor at a frame rate of 100 Hz. They viewed the screen binocularly from a distance of 100 cm. The visual angle, considering the entire monitor was 14.79°, whereas the tunnel display itself had a visual angle of 4.8°. During the tunnel simulation, the navigator received visual information on translation and rotation through the rate of optic flow (see Figure 1 left panel). Tunnel passages consisted of straight and curved segments that entailed a defined number of subsegments. The subsegments decreased in size and increased in grey value toward the end instigating the impression of perspective (for a demonstration of the tunnel task please visit http://www.psy.lmu.de/exp/ma/gramann/Tunnel-Demo.html). By continuously removing one subsegment at the front and adding one subsegment at the end of the display, a smooth movement impression was elicited. At the end of a tunnel passage, the task was to indicate the end position relative to the origin of the path by adjusting an arrow. This could only be achieved by computing spatial relations among reference points. Since no reference points were visible at the end of the passage, the task had to be solved based on an internal spatial representation.

Due to the fact that the orientation of the first segment could be perceived within an allo- or an egocentric reference frame, the task's design did not influence the use of a particular frame of reference during the passage (see Figure 1(a)). Moreover, the ego- and allocentric coordinate systems were aligned at this point of the task, and therefore both the perceived and cognitive headings for both strategy groups were identical. If task performance was based on an allocentric frame of reference, the navigator's axis of orientation remained unchanged and perceived and cognitive headings diverged. In contrast, if an egocentric frame of reference was used, the navigator's axis of orientation changed over the course of a turn (see Figure 1(b)), and the cognitive heading was adapted in accordance with perceived heading changes during the turn. Tunnels with nonparallel end segments revealed differences in cognitive heading (see Figure 1(c)).

The experiment consisted of two phases. In the first phase participants were categorized into their preferred strategy. To this end, they performed 30 categorization trials including tunnels with one turn only. At the end of each trial a choice of two arrows was given, each of which pointed toward the starting point using either allocentric or egocentric coordinates. Participants made their decision with the corresponding left or right mouse button. Subsequently, they were categorized in a particular strategy group if they consistently chose an arrow representing either strategy type $\geq$70% of the time. All 16 participants who took part in the categorization phase scored sufficiently to take part in the main experiment, resulting in 8 nonturners and 8 turners. See Gramann et al. (2005) for a complete description of this stage.

In phase two, the main experimental session consisted of three blocks of 20 trials. The task was to maintain orientation during passages through virtual tunnels. Each block was elicited by the participant via mouse click which was followed by a centered fixation cross (displayed 500 ms), followed by the static display of the entrance into the tunnel (500 ms) and finally the movement through the tunnel commenced. At the end of each trial, an arrow was presented in the display center aligned with the sagittal axis of the navigator, with the arrowhead pointing away from the subject into the depth of the simulated space (i.e., the subject saw a foreshortened view of the arrow's tail side; see Figures 1(d) and (e)). As the orientation of the arrow was initially aligned with the navigator's axis of orientation, the arrow could be interpreted as a prolongation of the navigator's heading. By pressing the left or right mouse button, the navigator could rotate the arrowhead toward him- or herself, representing the homing vector. When the subjectively correct angle setting was reached, the navigator confirmed the setting by pressing the middle mouse button, and their response, alongside the correct response, was briefly shown. The next trial started after a short interval of 1,000 ms with the display of the fixations cross.

Figure 1(f) displays the coordinate system underlying the allocentric cognitive heading (grey dotted arrows) and the coordinate system of the video display (black solid arrows) at the end of an exemplified tunnel passage. Since the cognitive heading of nonturners is not updated according to perceived heading changes during the turn, both coordinate systems are still aligned at the end of a passage. By contrast, the coordinate system underlying the egocentric cognitive heading (grey dotted arrows) and the coordinate system of the video display (black solid arrows in Figure 1(g)) diverge since turners update their cognitive heading during turns. The homing arrow is interpreted as the prolongation of the navigator's sagittal axis and thus aligned with the egocentric reference frame. However, the displayed homing arrow is aligned with the video display reference frame. Therefore, the coordinate system underlying the egocentric frame of reference has to be realigned with the coordinate system underling the video display frame. When the egocentric cognitive heading is rotated back into the initial coordinate system of the monitor, the starting point of the tunnel passage is rotated accordingly, resulting in a homing vector pointing to the right of the subject (when a turn to the right was traversed as displayed in Figure 1).

All tunnels consisted of a total of five segments: four straight segments and one turn segment occurring in the middle (note however, that participants were able to see the turn coming in the second segment). The angle of the turns was systematically varied. There were three different turn angle groups altogether to prevent subjects from building categorical homing vectors for identical tunnels: (1) turn angles ranging from 83°–90° (referred hereafter as "90° turn angles"; (2) turn angles ranging from 57°–64° (referred hereafter as "60° turn angles"), and (3) turn angles ranging from 28°–35° (referred hereafter as "30° turn angles"). Eighteen trials from each turn angle group were presented pseudo-randomly to the participants, with an equal amount of turns to the left and right relative to the starting position, giving a total of 54 turns. Additionally, to deter the participants from developing a categorization of the different turn angles six filler trials were pseudo-randomly presented, thus increasing the total trial number to sixty. The filler trials were excluded from the analysis.

Performance Measures

Reactions indicating the wrong side of end position will be referred to as "side errors." To ensure that participants maintained their orientation throughout the tunnel side, the errors were analyzed. Such errors might reflect simple confusion of left and right or total loss of orientation. Side errors were analyzed separately and eliminated from further analysis.

In addition, angular fit was also calculated. This measure refers to the ability to differentiate between varying eccentricities of end position within the virtual environment. A correlation coefficient for the adjusted arrow (subjectively correct angle setting) and the expected (correct) angular vector reflects this ability to discriminate among varying eccentricities.

Finally, by analyzing the signed error, we considered possible differences in angular adjustments between turner and nonturner with respect to the direction of error (under- or overestimation). Thus, reaction tendencies like compression toward the middle can be identified.

Eye-movements were measured with an SRI Generation 5.5 Purkinje-image eyetracker (Crane & Steele, 1985) and sampled at a rate of 250 Hz.

The eyetracker provides a spatial resolution of 0.1° of visual angle. The eye-movements were recorded on a PC during sessions and evaluated off-line by custom software.

Participants were seated using a chin bar and forehead supports to stabilize and minimize head movements. They were informed that their eye movements would be recorded during tunnel navigation and that they should perform the tunnel task as naturally as possible. There was no specific task other than maintaining orientation through the tunnel. Eye-movements were recorded from the onset of tunnel movement until the end of each tunnel.

The parameters which are described in the following section were analyzed according to time. Time was binned for each trial and each binned segment covered 3,450 ms, resulting in a total of five segments. This allowed for separate analysis of different tunnel phases, such as tunnel onset, curve, and navigation after the curve.

As to the observers' oculomotor behavior, the following measures were gained from the recorded data.

Total Number of Saccades. This measure refers to the total number of saccades recorded across the tunnel passages including differing acute angled turns. Saccades were measured from the onset of tunnel movement (after the 500 ms fixation cross and after the 500 ms tunnel onset pause) to the end of the tunnel (response arrow onset). Eye-movements were not recorded when participants were adjusting the response arrow. The average total saccades were calculated separately for each tunnel phase (5 segments), taking the angle of the turn into consideration. In order to determine the latencies and amplitudes of the saccadic eye-movements, an off-line program searched the movement traces for the first point above (or below) the vectorial velocity threshold of 15°/s. The beginning and the end of the saccades were calculated as linear regressions in a 20 ms time window around these threshold points.

Average Gaze Position. This parameter reflects gaze position based on horizontal (x) and vertical (y) coordinates over time. For each saccade the x/y-start and x/y-end coordinates were recorded, along with the time of saccade onset. Average gaze positions were analyzed for each segment using the following formula:

$$(\Sigma(\text{gaze position} * \text{time})/(\text{total segment time})).$$

Navigation through the tunnel consisted overwhelmingly of horizontal eye-movements, with little and insignificant vertical eye movement activity. Therefore, data from horizontal eye-movements is exclusively reported.

Fixations vs. Slow Phase of the Optokinetic Response (spOKN). Both of these measures refer to inter-saccadic eye-movements and were determined by calculating the velocity of these movements. Fixations were defined as having velocities below 1.0°/s and inter-saccadic movements were designated as spOKN if they were 3°–5°/s. The spOKN velocity is comparable to the tunnels velocity of 5°/s. Velocities were determined using the formula:

$$v = d/(\text{t2} - \text{t1}),$$

where d (distance) is amplitude of difference between saccade$_n$ offset and saccade$_{n+1}$ onset; t2 is the time of onset of the saccade$_{n+1}$ and t1 is the time of offset of the previous saccade $_n$. We expected to find fixations in straight segments and spOKN during the tunnel curves. Therefore, once velocities were calculated, the percentage of inter-saccadic movements per segment were calculated using the formula for movements categorized as spOKN:

$$(\Sigma(\text{duration of spOKN}))/\text{total segment time},$$

and the same formula procedure was carried out during fixations. To this end, we were able to compare the total percentage of fixations to the total percentage of spOKN during the five differing tunnel segments, taking trial type into consideration. Furthermore, it is important to note that we did not distinguish between saccades and the quick phases of the OKN.

RESULTS

Tunnel Results

Side Errors. Consistent with prior experiments the total number of side errors made was $<0.01\%$. Thus, due to the low frequency of side errors, we did not subject them to further analysis.

Angular Fit. Separate correlation analyses for expected and actual angular adjustment for preferred strategy groups were made. To further ensure that both strategy groups differed in their modality of spatial representation, we computed additional correlation analyses for the angular adjustments of both strategy groups and the expected angular adjustments of the nonpreferred frame of reference, i.e., angular adjustments of turner were correlated with the expected adjustments based on an allocentric reference frame and actual adjustments of nonturner were correlated with expected angular adjustments based on an egocentric frame of reference.[1] As expected, both nonturner and turner revealed significant covariation of expected angular adjustment and actual angular adjustment within the preferred frame of reference. Nonturner, using an allocentric reference frame, demonstrated a highly significant covariation with $r(96) = .967$, $p < .001$. Turner, using an egocentric frame of reference, showed a comparable correlation with $r(96) = .959$, $p < .001$. In contrast, correlation analyses of angular adjustment and expected adjustments based on the nonpreferred frame of reference revealed a significant negative covariation for turner $r(96) = -.967$, $p < .001$ and nonturner $r(96) = -.959$, $p < .001$.

Relative Error. A ANOVA with repeated measures over the factors "Side" (left vs. right end positions) and "Eccentricity" of end position (15°, 30°, and 45°) with the between subject factor "Strategy" (nonturner vs. turner) revealed the main effect of eccentricity to be significant [$F(2,28) = 55.06$; $p < .001$]. This effect was qualified by the interaction of Strategy x Eccentricity [$F(2,28) = 4.03$; $p < .029$].

As can be seen from Figure 2, subjects overestimated less eccentric end positions and underestimated end position with high eccentricity. Nonturner revealed a stronger tendency to overestimate end positions up to 30° Eccentricity, whereas turner demonstrated a stronger underestimation of end positions with 45° Eccentricity. Highest accuracy in angular adjustments for nonturner and turner was observed for 45° and 30° eccentricities, respectively. No other factor revealed a significant influence on the signed error.

Eye-Movement Data

Table 1 gives an overview on the eye-movement data during tunnels with different turning angles, averaged over turner and nonturner.

A clear trend for increases and decreases of mean number of saccades, fixations, and slow phase optokinetic nystagmus for segments including a turn was evident. To further analyze a possible influence of the preferred strategy

[1]In the case of isosceles triangles. the expected angular adjustments for the egocentric and the allocentric frame of reference are exactly diametrical, e.g., a tunnel with a turning segment of 45° to the right would require an allocentric angular adjustment of 30° and an egocentric adjustment of −30°.

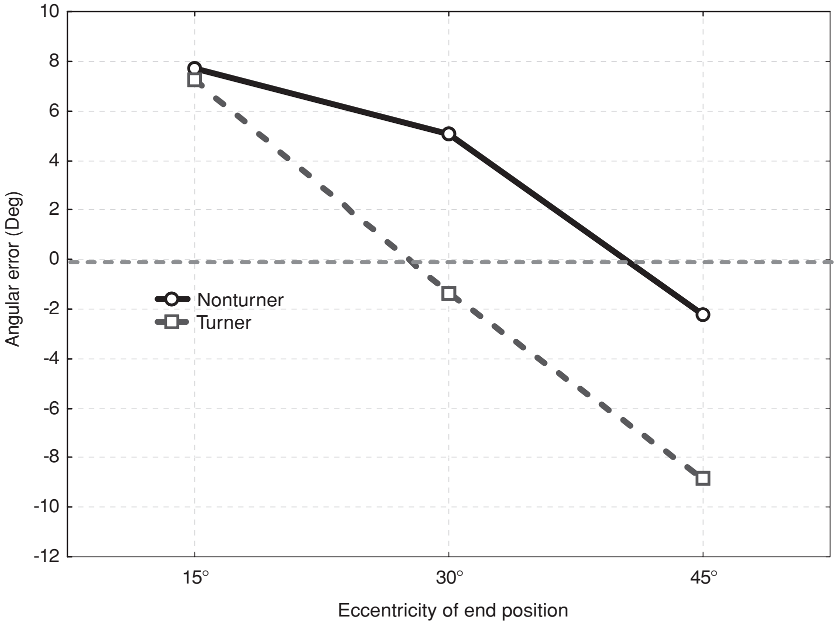

Figure 2. Relative (signed) error for nonturner (black solid line) and turner (gray dashed line) as a function of the eccentricity of end position (15°, 30°, and 45°) averaged over end positions on the left or right side relative to the starting point. The grey dotted horizontal line indicates no deviation of the subjects' reactions from the expected angular adjustment.

on eye-movement patterns, several ANOVAs were computed with the results described below.

Total Number of Saccades. The data was analyzed according to the number of total saccades occurring during one tunnel trial and averaged over trials of the same turn angle. All outliers (<.1% of data) and saccades found before tunnel movement onset were removed. Outliers were defined as saccades outside of the field of view. A 2 × 3 × 5 mixed design ANOVA with repeated measures over the factors "Side" of end position (left vs. right turns), turn "Angle" (30°, 60°, 90°), and "Segment" (1–5) and the between-subject factor of "Strategy" (nonturner vs. turner) was performed. The results revealed no significant influence of the factor side of end position [$F(8,112) = 1.95$; $p < .12$] and therefore the data were collapsed and side was no longer taken into consideration.

Table 1. Mean number of saccades, mean fixation time as percentage of segment duration, and mean percentage of slow phase optokinetic nystagmus (spOKN) in percent of segment duration for segments 1–5, collapsed over tunnels with a turn to the left or the right for different acute angled turning segments (30°, 60°, and 90°). Standard deviations (*SD*) are listed in brackets. The stimulus turn was placed in segment 3 and subjects perceived information on the upcoming stimulus turn already in segment 2

	Turn angle 30°			Turn angle 60°			Turn angle 90°		
	Saccades	Fixations	spOKN	Saccades	Fixations	spOKN	Saccades	Fixations	spOKN
Segment 1	3.49 (2.11)	3.32 (1.99)	0.17 (0.03)	3.25 (2.01)	3.07 (1.83)	0.17 (0.03)	3.33 (2.30)	3.17 (2.10)	0.16 (0.36)
Segment 2	3.99 (1.69)	3.83 (1.54)	0.16 (0.29)	3.89 (1.15)	3.73 (1.15)	0.16 (0.29)	4.39 (1.51)	4.18 (1.39)	0.21 (0.19)
Segment 3	4.60 (1.64)	2.94 (1.38)	1.66 (0.64)	5.81 (1.21)	1.83 (0.63)	1.66 (0.64)	6.62 (1.42)	1.39 (0.74)	5.24 (1.10)
Segment 4	3.82 (2.09)	3.56 (1.86)	0.26 (0.32)	3.99 (2.03)	3.45 (1.66)	0.26 (0.32)	4.13 (2.35)	3.5 (1.85)	0.63 (0.59)
Segment 5	3.89 (2.29)	3.75 (2.20)	0.14 (0.16)	4.02 (2.05)	3.89 (1.95)	0.14 (0.16)	3.95 (2.22)	3.76 (2.09)	0.19 (0.23)

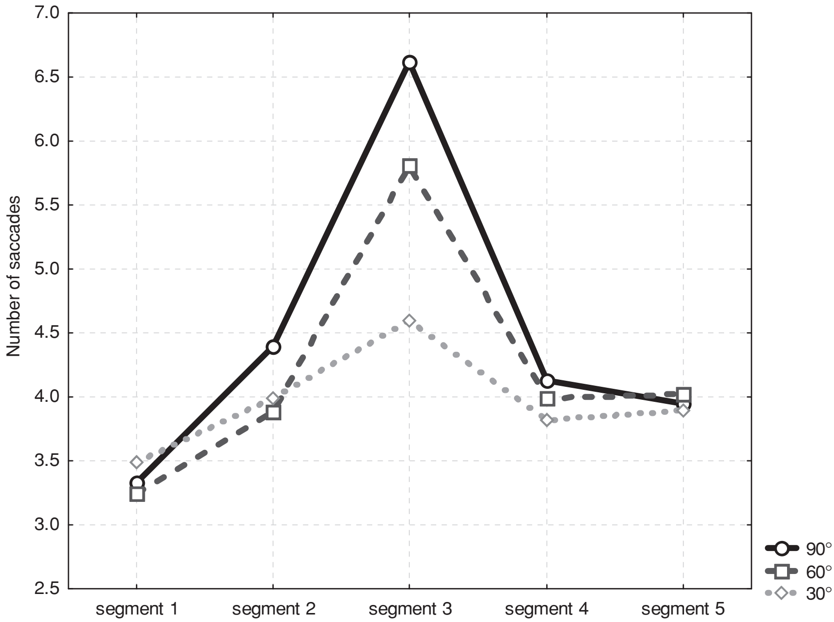

Figure 3. Mean number of saccades as a function of segment (segments 1 to segment 5; turn in segment 3) and turning angle (90°, 60°, and 30°) averaged over turns to the left and right.

A further mixed design ANOVA with repeated measures over the factors turn “Angle” (30°, 60°, 90°) and “Segment” (segments 1 to 5) and the between subject factor “Strategy” (turner vs. nonturner) was calculated. This analysis revealed no significant differences in the total number of saccades between turner and nonturner [$F(1,14) = .538$; $p < .475$]. Main effects emerged based on Angle [$F(2,28) = 11.16$; $p < .002$] and Segment [$F(4,56) = 14.93$; $p < .001$]. The most acute angled turn (90°) elicited a greater number of saccades than those of 60° (Post-hoc contrast Tukey HSD $p < .04$) and 30° ($p < .001$). The main effect of Segment was due to a significantly greater number of saccades during the turn as compared to all other segments (Tukey HSD $p < .001$). Finally, an interaction between Angle and Segment [$F(8,112) = 16.36$; $p < .001$] was observed. Increasing angles led to an increase in the number of saccades as can be seen in Figure 3. This increase in saccades was stronger during the turns as compared to straight segments before and after the turn.

Furthermore, the number of saccades increased monotonically with increasing acute-angled turns. The lowest number of saccades was observed for the first straight segment. During the second segment, where subjects saw that they approached the stimulus turn (segment 3), the number of saccades increased significantly from segment 1 to segment 2 for all three stimulus turns (Tukey HSD all $p < .04$). However, there were no significant differences in the second segment between the different turning angles that were visible already at this stage of the passage (all $p > .09$). During the stimulus turn, the number of saccades increased significantly with increasing acute angledness of the turn (all $p < .001$) and dropped back after the turn to the level of the straight segments before the turn. Again, the number of saccades in segment 4 was significantly lower as compared to segment 3 (all $p < .001$) and there were no differences in saccades within this segment based on the turning angle of the preceding segment (all $p > .08$). During the last segment no differences were observed with respect to the number of saccades dependent on the stimulus turn (all $p < .1$) or with respect to the number of saccades in the preceding segment (all $p > .99$).

Average Gaze Position. Average horizontal gaze position was analyzed by a mixed design ANOVA with repeated measures over the factors "Side" of turn (left vs. right), turn "Angle" (30°, 60°, 90°) and "Segment" (1–5), and the between subjects factor "Strategy" (turner vs nonturner). A main effect was found for Side [$F(1,12) = 11.18$; $p < .001$]. Tendencies to significance were found for Angle [$F(2,24) = 3.20$; $p < .06$] and Segment [$F(4,48) = 2.74$; $p < .06$]. Interactions were also revealed for Side and Angle [$F(2,24) = 21.12$; $p < .001$], Side and Segment [$F(4,48) = 138.08$; $p < .001$] and Side, Angle and Segment [$F(8,96) = 17.17$; $p < .001$]. The between subject variable, Strategy, was not significant [$F(1,12) = .33$; $p < .576$]. Figure 4 depicts the average x-start positions for left and right turns across segments. Eye-movements to the horizontal left are indicated by negative values, whereas eye-movements to the horizontal right are indicated by positive values.

Overall, right and left turns were significantly different (Tukey HSD $p < .001$). Also, within the stimulus turn, acute-angled turns were associated with larger average horizontal coordinates (the eye was farther to the left or right); this was significant for the comparison of 90° vs. 30° turns ($p < .03$). The post-hoc analysis of the Side x Angle interaction indicated that all left vs. right comparisons of the segment preceding the turn, as well as the stimulus turn segment were highly significant (Tukey HSD all $p < .001$). The interaction between Side x Segment revealed a diverging pattern, where all left and right turns in segment 3 revealed significantly greater laterality of eye position than all other segments (Tukey HSD all $p < .001$). Additionally, average coordinates of the segment preceding the stimulus turn were significantly more lateral than

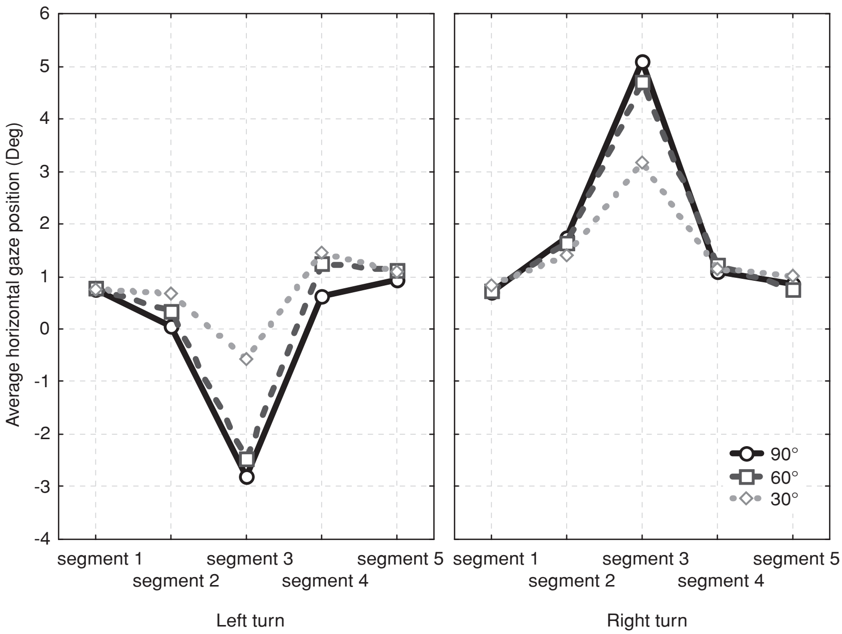

Figure 4. Average horizontal gaze position during the tunnel passages as a function of turning angle (90°, 60°, and 30°) and segment during the passage (segments 1 to 5). Leftward gaze is indicated by negative values; rightward gaze is indicated by positive coordinates.

those of the poststimulus turn segment ($p < .05$ or less). The Side, Angle, and Segment interaction showed that all differences between stimulus turns (segment 3) and all other segments were significant (Tukey HSD all $p < .001$) with the exception of the turning angles 90° and 60° regardless of side. As the eccentricities increased, so did the tendencies or significances across Segments and Sides.

The analysis of the horizontal component of the eye position has provided a concise way to define where the participants were directing their gaze over time. Figure 5 shows an example of a representative trial consisting of a right 90° turn. Horizontal eye position is depicted in black and vertical eye position in grey. The graph clearly shows little variation of eye position during straight segments, however during the stimulus turn the horizontal gaze is directed toward the outer wall. Further, a typical pattern for fixations (straight segments) and optokinetic nystagmus (turn) is clearly visible.

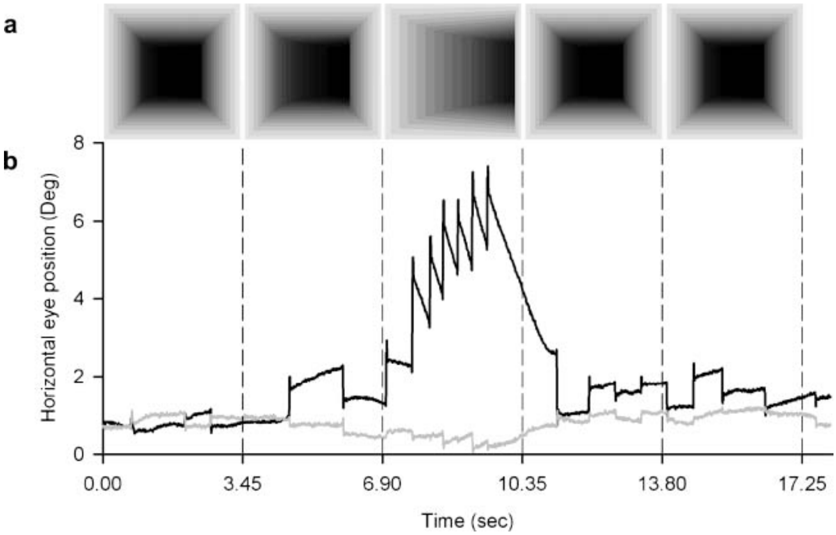

Figure 5. (a) Sequence of segments in a tunnel with a turn to the right with the first and second straight segments, the stimulus turn in segment three, and two straight segments after the turn. Note that subjects saw information on the upcoming turn already in the second straight segment. (b) Example for a typical eye movement trace for a tunnel with a 90° turn to the right. Horizontal eye position is depicted in black, vertical eye position is depicted in light grey. The *x*-axis displays the time course of the tunnel passage with a duration of each segment of 3,450 ms. The segments are indicated by the vertical dashed lines. The stimulus turn took place during the time interval from 6,900 ms to 10,350 ms. Typical pattern of fixations during straight segments (from 0 ms to 6,900 ms and from 13,800 ms to 20,700 ms) and optokinetic nystagmus during the stimulus turn (6,900 ms to 10,350 ms) is visible.

Fixations. Fixations were conservatively defined as activity between saccadic eye-movements which had a velocity below 1.0°/s. Mean eye velocity for the average fixation was less than .05°/s. A mixed design $2 \times 3 \times 5$ ANOVA with repeated measures for "Side" of end position (left, right), turn "Angle" (30°, 60°, 90°), and "Segment" (1–5) was conducted. No significant main effect or interactions including the factor Side were observed [($F(8,112) = 1.18$; $p > .32$]. Therefore, different turn angles were collapsed over the left and right side of end position. The collapsed data was entered into a mixed design ANOVA with repeated measures over the factors turn "Angle" (30°, 60°, 90°) and "Segment" (1–5) and with the between subjects factor of Strategy (turner vs. nonturner). A significant main effect was found for the factor Segment [$F(4,56) = 20.25$; $p < .001$]. Furthermore, an interaction was found between

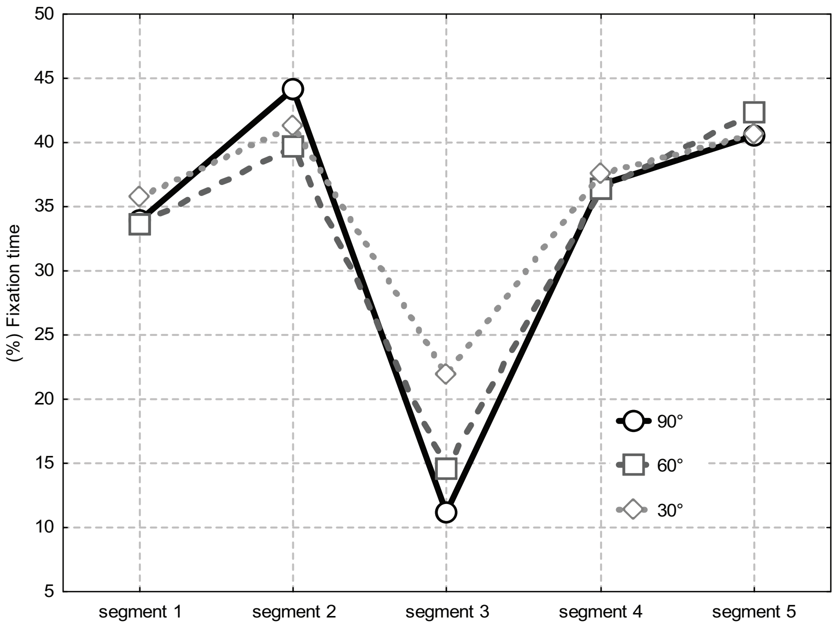

Figure 6. Mean fixation time as percentage of segment duration as a function of segment (segments 1 to 5) and turning angle (90°, 60°, and 30°), averaged over left and right stimulus turns.

Angle and Segment [$F(8,112) = 7.14$; $p < .001$]. No significant differences were found for Strategy [$F(1,14) = .218$; $p < .65$].

Similar to all the findings reported, the data diverged according to the tunnel Segment, however the data did not differ based on Angle (as fixations for the most part did not occur during the turn). The results are depicted in Figure 6. Significantly fewer fixations occurred in the stimulus turn across all turning angles in comparison to segments before and after the turn (all Tukey HSD $p < .001$).

Slow Phase of the Optokinetic Nystagmus (spOKN). spOKN was calculated in the same manner as fixations but defined as having a velocity of 3°–5°/s as described in the methods section. A mixed design ANOVA with repeated measures for "Side" of end position (left, right), turn "Angle" (30°, 60°, 90°), and "Segment" (1–5) was conducted to determine if there were any differences between left and right turns of the same eccentricities across segments. No significant differences were found [($F(8,112) = 2.26$; $p > .1$] and different turning angles were collapsed over the left and right side. A mixed

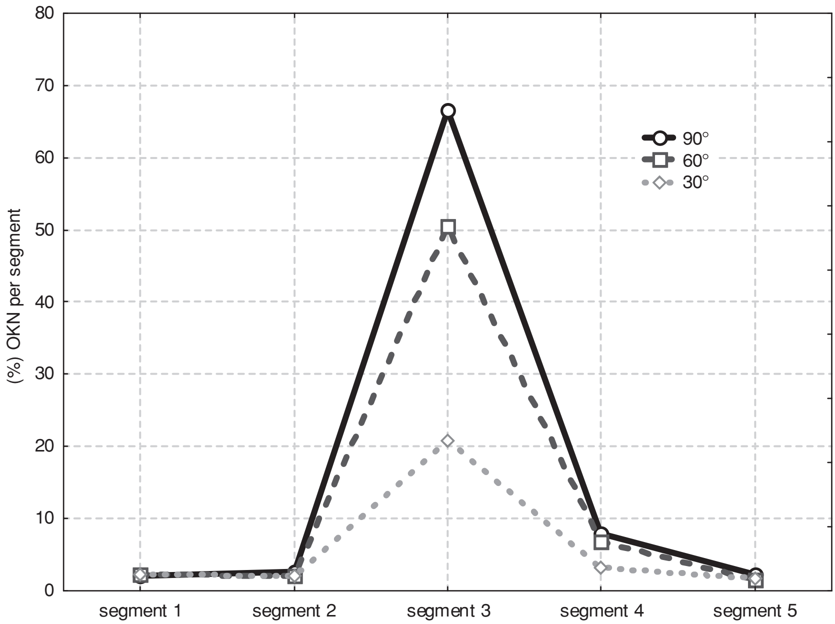

Figure 7. Mean percentage of slow phase optokinetic nystagmus (spOKN) as a function of turning angle (90°, 60°, and 30°) and segment of the tunnel passage (segments 1 to 5).

design ANOVA with repeated measures over the factors of "Angle" of turn (90°, 60°, 30°), "Segment" (1–5), and "Strategy" as the between subject factor revealed main effects for the factors Angle [$F(2,28) = 103.77$; $p < .001$] and Segment [$F(4,56) = 263.80$; $p < .001$]. Additionally, the expected interaction between Angle and Segment was also found [$F(8,112) = 128.47$; $p < .001$]. Strategy was not significant [$F(1,14) = 1.78$; $p > .2$].

Consistent with results reported thus far, as turning angle increased so did the number of spOKN produced during the stimulus turn segment, as can be seen in Figure 7.

The angle of 90°C Elicited more spOKN than the angle of 60°, which in turn elicited more than the angle of 30° (all Tukey HSD, $p < .001$). Similarly, for the main effect of Segment it was found that the stimulus turn (segment 3) contained significantly more spOKN than all other segments ($p < .001$). Again, within this segment larger turns produced more spOKN than smaller turns ($p < .001$).

DISCUSSION

To summarize, the experiment consisted of three varying tunnel types, differentiated only by the angle of the turn (30°, 60°, and 90°) in the third segment. The performance data replicated previous results showing that subjects consistently used their preferred frame of reference throughout the entire experiment, as reflected in the significant covariation of angular adjustments and the expected adjustment dependent upon the preferred frame of reference. Furthermore, the typical pattern of over- and underestimation for low and high eccentricities of end position replicated a tendency toward the middle (Gramann et al., 2005). Differences between the strategy groups revealed a tendency for nonturner to overestimate more eccentric end positions as compared to turner. The results replicate previous findings and thus allow a direct comparison of eye-movements during the task.

How is the Tunnel Perceived?

Our first goal was to determine and describe the nature that participants visually navigate and explore the tunnel passages. Therefore, total number of saccades, saccade location, fixation frequency, and spOKN frequency was analyzed. Except when analyzing horizontal gaze, there were no differences between left and right. It was found that as the turn angle increased, so did the total number of saccades during the stimulus turns. For example, an angular turn of 90° Elicited more saccades than an angular turn of 60° or 30°. The majority of eye-movements occurred along the horizontal axis, with relatively little behavior on the vertical plane. Participants consistently viewed the edge of the outer wall during turns. As the angle of the turn increased, the actual position of the edge of the tunnel's outer wall became more lateral, which was reflected in saccade position. During straight segments, the gaze remained relatively central. Overall, the participants' gaze was not centered, but there was a bias to look on the lower half of the screen and slightly to the right.

Furthermore, during straight segments, the percentage of fixations was greater than during the turn. The opposite pattern emerged for spOKN, with virtually no spOKN occurring during straight segments and with spOKN frequency spiking during the stimulus turn. Taken together, these results indicate that during the turn, participants updated heading information based on information found from the edge of the outer wall. This claim is substantiated by the recording of eye position and further indicated by the spOKN prevalence during the turn. Greater the angle of the turn was, more pronounced the spOKN activity became. Based on this finding, it can be assumed that heading calculations are more difficult with increasing acute-angle of turns and that this is reflected by gaze patterns which become more frequent and intense.

This account lends support to the belief that both turner and nonturner update their cognitive heading by extracting rotational change information during the stimulus turn and continue to track these changes thereafter. Rotational information provided by the visual flow is further computed and integrated into a spatial representation, which may differ for turner and nonturner. In addition, nonturner computed a second representation based on the allocentric frame of reference which builds the basis for their reactions (Gramann et al., 2005, 2006). Thus, both strategy groups update their cognitive heading with the perceived heading during the stimulus turn. However, only turner finally use this updated cognitive heading as the basis for their reactions and nonturner switch to an allocentric reference frame.

Task Sensitivity of Eye-Movements

The second goal of the present study was to verify whether eye-movement patterns are affected by the task demands. More precisely, we were interested in potential differences in eye-movement patterns for tasks in which visual flow information on heading changes has to be incorporated into a spatial representation (tunnel task) as compared to tasks where comparable information on heading changes is used for immediate action but not incorporated into a mental representation (driving simulation). The present experiment clearly supports the assumption that eye-movements are dependent on the task requirements. Eye-movements in a task that requires the navigator to build up a spatial representation of the environment do not replicate gaze patterns in simulated driving experiments. During a tunnel passage participants extract information on heading changes from the outer wall, whereas subjects in driving simulations most often direct their gaze to the tangent point of the curve (Land & Lee, 1994; Wann & Land, 2000). This difference directly reflects the fact that eye-movements reflect cognition (Hayhoe & Ballard, 2005) and that gaze is task dependent (Hayhoe & Ballard, 2005; Hayhoe, Shrivastava, Mruczek, & Pelz, 2003; Shinoda, Hayhoe, & Shrivastava, 2001; Yarbus, 1967). The tangent point in simulated driving tasks is the major information source for steering performance (immediate action without mental representation), whereas the outer wall of the tunnel delivers relevant information on the degree of heading changes to be incorporated into a spatial representation (mental representation with delayed reaction), i.e., during steering it is not important to know the exact angle of heading changes but rather to successfully keep the lane. In contrast, during the tunnel task the subjects are transported passively and have to extract as much information as possible with respect to the exact nature of heading changes.

Therefore, our results do not necessarily contradict simulated driving data. To further illustrate this principle, the task of the tunnel was to report the starting position relative to the end position, whereas in driving experiments there are a number of tasks ranging from instructions to pay particular attention to road signs and intersections to memorizing the landscape, all of which result in differing eye-movements (Land, 1992; Luoma, 1988; Shinoda et al., 2001). Thus, differing cognitive goals lead to differing patterns of eye-movement activity. Therefore, it can be assumed that computing heading can be done from both outer and inner curvature points, depending on the nature of the information available and the required action. Finally, the tunnel task differs from a more realistic heading estimation during locomotion in at least two important points: first, small field stimulation with only sparse visual flow information in the tunnel task differs from real navigation or driving with respect to the size of the visual field and the kind of information that can be used to estimate heading; second, during passive transportation in the tunnel task subjects are not required to actively control heading angle and eye-movements do not involve the vestibulo-ocular reflex. Thus, the paradigm used in the present study is likely to contribute to the differences in eye-movements compared to investigations using more realistic stimulation.

Eye-Movements and Frames of Reference

The final aim of the experiment was to determine if differences in eye-movements exist between participants who spontaneously adopt an allocentric frame of reference and those who prefer to use an egocentric frame of reference when navigating through the virtual tunnels containing only visual flow information. The results clearly indicate that no differences between these two strategy groups exist on the level of information uptake. Thus, we can assume that allocentric and egocentric navigators view the tunnel in the same way, and that the preference to adopt a particular strategy can be entirely attributed to differences in higher cognitive processes between these two groups. Due to the limited visual field and the sparse visual flow information potential differences in eye-movements between turner and nonturner might have been obscured. However, since identical visual stimulations were used in the past investigations (Gramann et al., 2005, 2006), the results show that differences in activation in the underlying cortical networks are due to unique cognitive strategies and that source reconstructions were not influenced by systematic differences in eye-movements between strategy groups (Gramann et al., 2006).

In summary, the presented data provide a thorough description of gaze patterns during passages through a virtual tunnel and further demonstrate the relationship between gaze and cognition. It was shown that gaze patterns changed predictably with differing angles during the stimulus turns. However, the participants performing identical tasks and utilizing differing spatial cognitive strategies to navigate through the tunnel passages did not differ in their gaze patterns. The data therefore support the claim that gaze reflects cognitive goals (in this case extracting as much information about heading changes as possible), but neither reflect nor predict the preferred use of an egocentric or an allocentric frame of reference during navigation.

REFERENCES

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron*, *35*, 625–641.

Committeri, G., Galati, G., Paradis, A.-L., Pizzamiglio, L., Berthoz, A., & LeBihan, D. (2004). Reference frames for spatial cognition: Different brain areas are involved in viewer-, object-, and landmark-centered judgments about object location. *Journal of Cognitive Neuroscience*, *16*, 1517–1535.

Crane, H. D., & Steele, C. M. (1985). Generation V dual-Purkinje-image eye-tracker. *Applied Optics*, *24*, 527–537.

Gramann, K., Müller, H. J., Eick, E., & Schönebeck, B. (2005). Empirical evidence for separable spatial representations in a virtual navigation task. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 1199–1223.

Gramann, K., Mueller, H. J., Schoenebeck, B., & Debus, G. (2006). The neural basis of ego- and allocentric reference frames in spatial navigation: Evidence from spatio-temporal coupled current density reconstruction. *Brain Research*, *1118*, 116–129.

Hayhoe, M., & Ballard, D. (2005). Eye movements in natural behavior. *Trends in Cognitive Sciences*, *9*, 188–194.

Hayhoe, M., Shrivastava, A., Mruczek, R., & Pelz, J. B. (2003). Visual memory and motor planning in a natural task. *Journal of Vision*, *3*, 49–63.

Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *The Journal of Neuroscience*, *23*, 5945–5952.

Klatzky, R. L. (1998). Allocentric and egocentric spatial representations: Definitions, distinctions, and interconnections. In C. Freksa, C. Habel, and K. F. Wender (eds.), *Spatial Cognition*, *Volume 1*. Lecture Notes in Artificial Intelligence, Vol. 1404. New York: Springer.

Land, M. F. (1992). Predictable eye-head coordination during driving. *Nature*, *359*, 318–320.

Land, M. F., & Lee, D. N. (1994). Where we look when we steer. *Nature*, *369*, 742–744.

Lappe, M., Grigo, A., Bremmer, F., Frenz, H., Bertin, R. J. V., & Israel, I. (2000). Perception of heading and driving distance from optic flow. *Proceedings of the Driving Simulation Conference DSC 2000*, Paris, France, 25–31.

Lawton, C. A. (1994). Gender differences in way-finding strategies: Relationship to spatial ability and spatial anxiety. *Sex Roles*, *30*, 765–779.

Lawton, C. A. (1996). Strategies for indoor way-finding: The role of orientation. *Journal of Environmental Psychology*, *16*, 37–45.

Luoma, J. (1988). Drivers' eye fixations and perceptions. In A. G. Gale (ed.), *Vision in Vehicles II*. New York: Elsevier.

Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S., Frith, C. D., & O'Keefe, J. (1998). Knowing where and getting there: A human navigation network. *Science*, *280*, 921–924.

Pazzaglia, F., & De Beni, R. (2001). Strategies in processing spatial information in survey and landmark-centred individuals. *European Journal of Cognitive Psychology*, *13*, 493–508.

Shinoda, H., Hayhoe, M. M., & Shrivastava, A. (2001). What controls attention in natural environments? *Vision Research*, *41*, 3535–3545.

Wann, J. P., & Land. (2000). Steering with or without the flow: Is the retrieval of heading necessary? *Trends in Cognitive Sciences*, *4*, 319–324.

Wann, J. P., & Swapp, D. K. (2001). Where do we look when we steer and does it matter? [Abstract]. *Journal of Vision*, *1*, 185.

Yarbus, A. L. (1967). *Eye Movements and Vision (B. Haigh Trans.)*. New York: Plenum Press.