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Properties of saccades during optokinetic responses to radial optic flow in monkeys

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Abstract

Optokinetic eye movements stabilize vision in response to large–field visual motion. We have studied oculomotor behavior of rhesus monkeys that viewed large optic flow stimuli. These stimuli present radial motion that is normally experienced during forward self–movement. In previous work (Lappe et al., 1998) we have described that such radial optic flow stimuli also elicit optokinetic responses in the form of slow eye movements which stabilize the moving visual image on the fovea and parafovea. Here we describe the properties of saccades during unrestrained viewing of radial optic flow. We show that the saccades do not share the reflectory nature of the slow phases but rather support an active exploration of the visual scene.

Introduction

During natural locomotor behavior our eyes continuously experience global visual motion. This motion is called the optic flow. Reflectory vestibulo–ocular and optokinetic eye movements will attempt to stabilize vision during movements of the head. In the case of head rotation, an opposite movement of the eyes can almost completely cancel the visual motion and stabilize the full retinal image. This is not possible for translations of the head. Especially during forward translation, the optic flow has a radial structure in which different directions of motion are present in different parts of the visual field. Hence, eye movements can only stabilize part of the retinal image.

We have recorded spontaneous optokinetic eye movements of three macaque monkeys during unconstrained viewing of optic flow stimuli that simulated forward translation. The typical oculomotor behavior in this situation consists of regularly alternating slow phases and saccades at a frequency of about 2Hz. In a previous paper (Lappe et al., 1998) we have analysed the properties of the slow phases. Eye movements in the slow phases follow the direction of motion that is present at the fovea and parafovea. Thus, the slow phases stabilize the retinal image in a small parafoveal region only. Many of the characteristics of the slow phases can be explained by properties of the optokinetic system. In this paper we will investigate the properties of the saccades.

When an optokinetic nystagmus is elicited by a large–field unidirectional motion stimulus, slow phases and saccades are very stereotypic. First, a saccade is made against the direction of the stimulus motion. Then a slow eye movement follows the stimulus motion in order to stabilize the retinal image. After the eye has moved a certain distance, another saccade against the stimulus motion occurs which re–positions the eye and compensates for positional change during the slow phase. Saccades in this situation serve two functions (Carpenter, 1988). The first is to orient gaze towards the direction from which the stimulus motion originates. The second is to reset eye position after the slow phase tracking movement. However, during visual scanning of radial optic flow, each saccade changes the direction and speed of retinal motion on the fovea. After the saccade, the slow phase eye movement has to adapt to these changes (Lappe et al., 1998) Thus, saccades in this situation also influence tracking performance. Moreover, during forward locomotion a constant monitoring of the environment and of possible obstacles in the direction of heading is required, which might necessitate ocular scanning of the visual scene. Thus, saccades in this situation might serve different purposes than merely the resetting of eye position.

Methods

Eye movement were recorded in three awake male rhesus monkeys (Macaca mulatta). Under general anesthesia and sterile conditions a head-holder and two scleral search-coils were chronically implanted. For the experiments, the monkey was seated in a primate chair with its head fixed. Horizontal and vertical position of one eye were registered by an Eye Position Meter 3020 (SKALAR) and recorded to a PC with a sampling rate of 500 Hz. Each experimental trial lasted 15 or 20 seconds during which spontaneous and unrestrained eye movements were recorded. Several trials were performed on each recording day. Monkeys weight was monitored daily and supplementary fruit and water was supplied. All experiments were in accord with published guidelines on the use of animal research (European Communities Council Directive 86/609/ECC).

The optic flow stimuli consisted of full-field (90x90deg) computer generated sequences that were back projected onto a tangent screen, 47 cm in front of the monkey. They simulated forward or backward self–motion with respect to a large number (250) of random dots. The distribution of dots in space simulated four different virtual environments (Fig. 1). In successive trials simulated observer speed and direction was randomly varied. Observer speeds of 1, 2, or 3m/s were used. Different simulated directions of observer movement gave different horizontal positions of the focus of expansion (-20, -10, 0, +10, +20deg).

In the recorded data, saccades were separated from slow phases by a velocity level criterion, typically set at 25deg/s. Beginning and end of saccades were determined as the first and last data points which cross the criterion level,

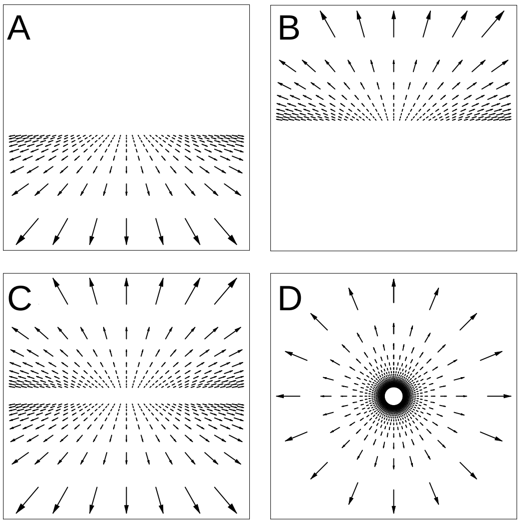

Fig. 1: Illustration of the optic flow stimuli. They simulated movement of an observer in different virtual visual environments. The first consisted of a horizontal ground plane 0.37m below eye level (A). This plane contained lit dots which moved on the screen according to the simulated observer motion. The ground plane stimulus could be inverted such that the observer moved below a ceiling (B), or two planes could be presented, one below and one above the observer (C). A fourth environment consisted of a simulated tunnel, 0.72m in diameter (D).

respectively. In addition, a minimum duration of 12ms between the start and end points was required.

Results

A typical scan path during viewing of an expanding ground plane stimulus is shown in Fig. 2A. Most of the time gaze is slightly below the horizon. Accordingly most saccades are in a horizontal direction. Saccades frequently cross the center of the stimulus. Each crossing reverses the direction of the flow that is projected onto the fovea before and after the saccade. Between saccades, optokinetic slow phase eye movements occur that follow the direction of motion on the fovea. Examples are shown in Fig. 2B, which presents the horizontal eye position as a function of time. In periods between saccades, the eye performed slow motions toward the center. These occurred because the stimulus consisted of a radial visual contraction that simulated backward motion of the monkey. Detailed analysis of the relationship between the slow phase eye movements and the optic flow stimulus revealed that direction and speed of the eye movements are linked to the foveal and parafoveal motion (see Lappe et al. 1998). Direction very closely followed the direction of the motion on the fovea. Eye speed roughly matches the average motion within the parafoveal summation area of the optokinetic system.

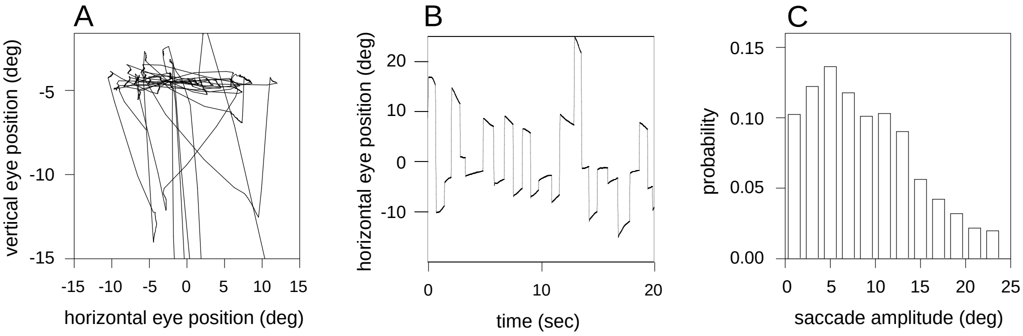

Fig.2: A: Cumulative plot of the (x,y) eye position (scan path) as the monkey viewed an optic flow stimulus such as Fig. 1A for 20 seconds. B: Example trace of the horizontal eye position over time. In this example, the stimulus was a contraction pattern simulating backward motion of the monkey. One can clearly distinguish saccades from optokinetic slow phase eye movements. C: Distribution of saccade amplitudes (Data from all animals and stimulus conditions collapsed).

To describe the saccadic behavior during optic flow stimulation we first looked at the distribution of saccade amplitudes and directions in relation to the parameters of the stimulus. Saccadic amplitude varied in a wide range (Fig. 2C). However, median amplitude, median duration, and median maximum velocity of saccades were not systematically affected by simulated observer speed or placement of the focus of expansion. The distribution of saccade directions, on the other hand, showed a clear relation to the visual environment (Fig. 3). For half–field stimuli, ground plane and ceiling, the distribution of saccade directions had clear peaks at 0 and 180deg, or rightward and leftward directions, respectively (Fig. 3A,B). This changed when full field stimuli were presented (Fig. 3C,D). In the case of the two plane stimulus, the distribution of saccade directions had four shallower peaks, which corresponded to 0, 90, 180 and 270deg. This suggests that the animal now shifted gaze also between the upper and lower stimulus fields in addition to horizontal saccades along the two horizons. For the tunnel stimulus, which is completely radial-symmetric no clear preference of any saccade direction was observed. The median temporal separation of successive saccades also depended on the simulated visual environment. Median intersaccadic interval was 415ms for half–field stimuli and 320ms for full–field stimuli.

The properties of the saccades therefore show a clear relation to the visual environment. This would be expected from typical visual scanning behavior (Yarbus, 1967). However, the slow phase eye movements between the saccades have many characteristics that link them to the optokinetic system (Lappe et al., 1998). Therefore, we wondered whether saccades during optic flow stimulation also show properties related to optokinetic quick phases. In the regular optokinetic nystagmus evoked by full–field unidirectional motion, saccades are directed against the motion of the stimulus and against the eye movement di-

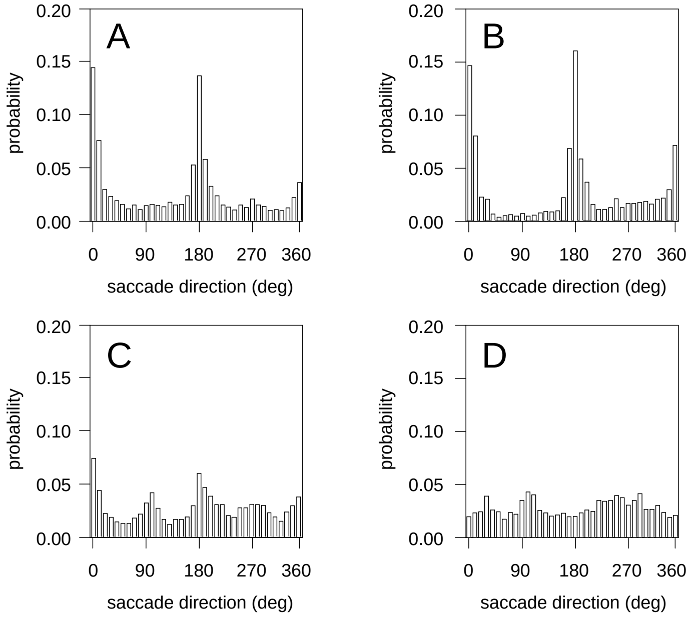

Fig.3: Distribution of saccade directions for four different environments (see Fig. 1). In ground plane (A) and ceiling (B) conditions horizontal saccades are the most frequent. This is consistent with the observation that gaze in these conditions is mostly directed towards the horizon. For the double plane (C) and tunnel (D) environments saccade directions are more equally distributed.

rection during the slow phase. We examined whether such a relationship also exists for optokinetic responses to radial motion. We compared saccade directions to the direction of the slow phase eye movement that preceded the saccade and computed the angular difference between the two. Fig. 4 shows this angular difference as a function of saccadic amplitude in scatter plots that contain data from all animals for the ground plane stimuli. For a radial flow pattern with a centered focus of expansion, saccade directions showed no correlation with the direction of the preceding slow phase eye movements (Fig. 4A). However, when the focus of expansion was 20deg eccentric on the screen the proportion of saccades in a direction opposite to the direction of the preceding slow phase increased (Fig. 4B). Evaluation of the number of saccades that were directed leftward or rightward (15deg) also showed a dependence on the location of the focus of expansion. For eccentric locations, about twice as many saccades were directed towards the focus of expansion than away from it. For contraction stimuli, this ratio was reversed. When the focus was eccentric, differences between expansion and contraction also occurred in the distribution of eye positions. Median eye position was shifted towards the focus position for expansion, but in the opposite direction, i.e. away from the focus position, in the case of contraction. This behavior might be linked to the shift of the 'Schlagfeld' of the

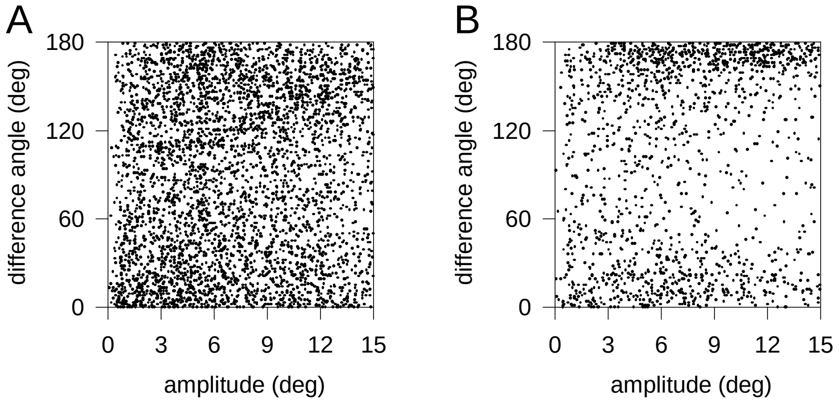

Fig.4: Distributions of saccadic amplitudes and directions relative to the direction of the preceding slow phase eye movement for central (A) and (20deg) eccentric (B) positions of the focus of expansion. Each dot represents a single saccade. Typical optokinetic quick phases would appear in the upper part of the plots because their direction would be 180deg apart from the direction of the slow phase.

optokinetic nystagmus (Lappe et al., 1998).

Optokinetic slow phases continuously change eye position. Part of the function of saccades must therefore lie in the compensation for this continuous eye drift. We quantified the proportion of saccadic amplitude that was necessary for the compensation of positional changes during slow phase eye movements. This was done by calculating the ratio between the sum of all slow phase amplitudes and the sum of all saccade amplitudes. The results are shown in Fig. 5. The percentage of saccades needed for compensation is lowest for a centered radial expansion. With increasing observer velocity or with increasing eccentricity of the focus of expansion on the screen the ratio increases. However, for expanding optic flow, which is the typical motion pattern during forward locomotion, less than 20% of saccadic amplitudes are required to compensate for slow phase eye movements. More than 80% of saccadic amplitudes is used for active exploration of the environment.

Discussion

The oculomotor behavior of monkeys that view radial optic flow stimuli consists of slow optokinetic tracking movements and quick saccadic changes of gaze direction. During slow phases the eye movement follows the motion in that part of the optic flow stimulus that falls on the fovea and parafovea. These slow phase eye movements are strongly correlated to stimulus motion. This is true for both eye movement direction and speed (Lappe et al., 1998). In contrast, most properties of the saccades did not depend on the stimulus motion. This was true for amplitude, duration, velocity, and to a large degree also for direction of saccades. Instead, saccade parameters depended strongly on the structure of

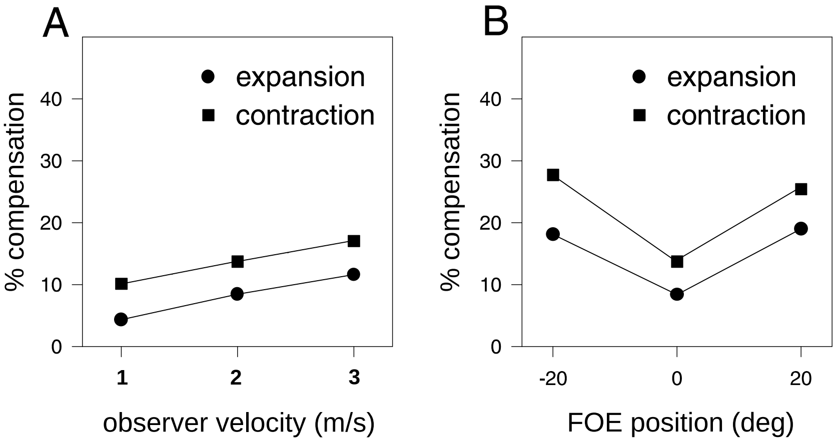

Fig.5: Proportion of saccadic amplitudes that was necessary to compensate for the positional drift of the eyes during the slow phase between two successive saccades. In A only data from stimuli with central focus of expansion were used. B contains only data from a single observer speed (2m/s).

the visual scene. The distribution of saccade directions and saccade frequency was different for half–field and for full–field stimuli. This is consistent with an ocular scanning behavior that relates to the content of the visual scene. Such ocular scanning occurs during inspection of static images (Yarbus, 1967; Burman & Segraves, 1994) but also in moving scenes during self–motion (Land, 1992; Land & Lee, 1994). Indeed, a dependence of saccade frequency on the size of the visual stimulus was also observed in humans during driving in a car (Osaka, 1991).

With fully radial optic flow stimuli, centered expansion or contraction, little support was found for the opposing hypothesis that saccades in this situation are linked with the optokinetic eye movements during the slow phases. Saccade direction was not correlated with the direction of the preceding slow phase eye movement. Saccadic amplitudes on average exceeded the distance required to compensate for the eye drift during slow phases by a factor of 4. However, this behavior changed when the focus of expansion was eccentric on the screen. In this case, saccades were more often directed against the direction of the preceding slow phase and the ratio between saccadic amplitude and the amplitude of the slow phases decreased. These observations are consistent with a greater optokinetic potential of the stimulus in this situation, which also leads to a higher gain of the slow phase eye movements (Lappe et al., 1998). As the focus of expansion becomes eccentric the stimulus motion on the screen becomes more homogeneous and more like a typical optokinetic stimulus. Saccadic properties in this case gradually change towards those observed in an optokinetic nystagmus.

While slow phase eye movements of monkeys during unrestrained viewing of radial optic flow show many properties of the optokinetic system, saccades in this situation are used to a large degree for an active exploration of the moving scene. This is unlike the stereotypic reflectory behavior of saccadic quick phases during optokinetic nystagmus. Thus, slow phases and saccades in this situation are likely generated by different oculomotor processes. The basic neuronal circuit that drives optokinetic eye movements consists mainly of subcortical structures (Hoffmann, 1986). However, lesions of the frontal eye field in rats have shown systematic effects on the saccades, but not the slow phases, of the optokinetic nystagmus (Bähring et al., 1994). Saccades in optokinetic nystagmus serve to compensate for eye drifts during the slow phases and to orient gaze towards the origin of the motion. Lesions of the frontal eye field in rats selectively impaired the orientation but not the compensation. This suggests that the frontal eye field contributes to saccadic behavior also during optokinetic nystagmus, specifically in the orientation of gaze towards novel parts of the stimulus. Such a contribution might also underlie the generation of saccades during the ocular scanning of radial optic flow.

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