Abstract  Transparent motion is a visual stimulus condition that generates multiple motion vectors on the retina that can differ in speed, direction, and/or luminance. Transparent motion creates a conflict for retinal stabilization. In this study we investigated the effect of transparent visual motion on the oculomotor reflexes that provide retinal stabilization in the rabbit. In the first experimental condition, the animals were stationary. We presented one stationary and one oscillating visual pattern to the animals while varying the luminance of the patterns. We found that the optokinetic eye movement responses were fully determined by the luminance of the individual visual inputs, weighted for the total luminance. No effect of absolute stimulus intensity was found. In the second experimental condition we oscillated the animals, while using an identical visual stimulation paradigm. The contribution of the vestibulo-ocular reflex enhanced the response to the visual pattern, which was in agreement with the vestibular stimulus. This effect of vestibular stimulation was independent of the absolute intensity of the visual stimuli. From this result we conclude that the weighting process of the transparent visual patterns occurs upstream from the site of the visual-vestibular interaction. Both the visual weighting and the visual-vestibular interaction were dependent on stimulus frequency. In line with the properties of the visual and vestibular stabilization reflexes in isolation, the contribution of the vestibular system increased, whereas the influence of the optokinetic system decreased with increasing stimulus frequency.

Key words  Transparent motion · Optokinetic reflex · Vestibulo-ocular reflex · Eye movements · Models · Rabbit

Introduction

During transparent optic flow, two or more visual motion patterns are simultaneously present on the retina. In daily life, such transparent motion is encountered when one looks at moving objects through a visual medium (e.g. snow, bushes, or a dirty window). Furthermore, in an environment where not all visual objects are at the same visual distance, self-motion generates motion parallax, during both translation and rotation about an axis that does not intersect both eyes. Parallax can also give rise to transparent optic flow vectors on the retina.

In order to stabilize the visual world on the retina, all vertebrate species are provided with oculomotor stabilization reflexes. The most important are the vestibulo-ocular reflex (VOR) and the optokinetic reflex (OKR; Baarsma and Collewijn 1974). The VOR originates in the semicircular canals whose output represents the angular velocity of the head. It elicits compensatory eye movements, which are opposite in direction relative to the head movements. The OKR is triggered by retinal slip (movement of the visual world relative to the retina), which elicits reflexive compensatory eye movements with a slow component that has the same direction as the moving image.

During transparent visual stimulation, eye movements are not capable of compensating all retinal image motion, since the various motion components cannot all be compensated for simultaneously. In humans, transparent visual stimuli cause eye movements to (alternately) follow one visual pattern while ignoring the other (Kowler et al. 1984; Howard and Gonzales 1987; Niemann et al. 1994). It is likely that foveal pursuit mechanisms play a role in this behavior. The distinction between the contribution of involuntary global OKR and voluntary foveal pursuit in the eye movement response remains an issue, even when the contribution of the pursuit system is minimized (Niemann et al. 1994; Mestre and Masson 1997).

The rabbit does not have a fovea and does not possess a smooth pursuit system (Collewijn 1977). Therefore,
since slow eye movements in the rabbit are generated as part of postural reflexes, the rabbit is an ideal model in which to study compensatory reflexive eye movements in response to transparent visual stimulation.

In this paper we describe how horizontal OKR and the combined horizontal vestibulo-optokinetic reflex (VOKR) of the rabbit are affected by full-field transparent optokinetic stimulation. The purpose of this study is to investigate how the OKR in response to a transparent visual stimulus depends on the luminance of the individual flow components and in what way this relation is affected by concurrent vestibular stimulation.

Preliminary results of these experiments have been published in abstract form (Mathoera et al. 1997).

Materials and methods

Animal preparation

Six young adult female pigmented Dutch belted rabbits were used. About 1 week prior to the experiments, the rabbits were implanted with permanent scleral search coils in both eyes for eye movement recording. A coil of five turns of insulated stainless steel wire (Teflon-bioflex wire, type AS 632; Cooner Sales, Chatsworth, Calif.) was woven underneath the conjunctiva, the superior and inferior rectus muscles, and the inferior oblique muscle. Also skull screws were mounted for fixation of the head.

Surgical procedures were carried out under general anesthesia, induced by ketamine (100 mg/ml Nimetek; AUV, Holland), 1% acepromazine (10 mg/ml Vetravanil; Sanofi, Holland), and 2% xylazine hydrochloride (22.3 mg/ml Rompun; Bayer Germany). Initial doses of 0.7 mg/kg of a mixture of ketamine and acepromazine (1:1 in proportion by volume) and, in separate injection, 0.25 ml/kg of xylazine hydrochloride were given intramuscularly. These initial doses, which maintained a good anesthesia for about 1 h, were supplemented as necessary.

All surgical procedures, as well as the experimental protocols that are described below, were in accordance with guidelines set by the ethics committee of the medical faculty of Erasmus University and Principles of laboratory animal care (NIH publication no. 86–23, revised 1985).

Experimental procedure

The rabbit was restrained in a linen bag that was tied down on a small board. The head bolts were fastened to a head holder mounted on the board. The head was fixed with the nasal bone at an angle of about 35° off-vertical, which brings the horizontal semicircular canals perpendicular to the direction of gravity (Soodak and Simpson 1988). The rabbit on the board was placed on an earth-horizontal circular turntable (diameter 70 cm) with the middle of the interaural axis in the axis of rotation.

Two experimental protocols were performed: the intensity protocol and the frequency protocol.

Intensity protocol

In this protocol two visual patterns were presented to the rabbit. Both patterns consisted of light spots on a dark background. One pattern was stationary relative to the head of the rabbit, whereas the other moved sinusoidally about the yaw axis with a frequency of 0.1 Hz and an amplitude of 2.5° for 11 cycles. To investigate the influence of the luminance of the two patterns, we varied the intensity of the stationary and the moving pattern independently. The five intensities, which were used in all combinations, were 0.0, 0.75, 1.5, 2.25, and 3.0 cd/m², resulting in 25 conditions.

To investigate the effect of simultaneous vestibular stimulation, these 25 conditions were applied twice: once where the head of the rabbit did not move (optokinetic stimulation) and once where the rabbit moved with an amplitude and phase that was identical to the moving visual stimulus (vestibulo-optokinetic stimulation). Thus, in the latter condition, the pattern that oscillated relative to the world was stationary relative to the head of the rabbit, while the earth-fixed stationary pattern moved relative to the head. Note that as a consequence the visual stimulation relative to the head in both vestibular conditions was identical. In the remainder of this paper, the pattern that was stationary relative to the rabbit will be referred to as the “S pattern” and the pattern that moved as the “M pattern” (Fig. 1).

The intensity protocol, consisting of 50 stimulus conditions (two vestibular and 5 times five spot luminance levels) was performed using three rabbits (animals C, F, and J). All stimuli were presented in random order. Between trials, it took less than 20 s to store the data on hard disc and to adjust stimulus parameters according to the protocol.

Frequency protocol

All six rabbits were exposed to 11 luminance levels (76.0, 36.0, 30.0, 16.0, 9.3, 6.0, 4.0, 2.7, 1.7, 1.0, 0.4, and 0.0 cd/m²) of the M pattern, while the luminance of the S pattern was set at a fixed level (4.0 cd/m²). As in the previous protocol, each visual stimulus was also presented in combination with vestibular sinusoidal stimulation with the same frequency, amplitude, phase, and direction as the moving component of the transparent visual stimulus. The 22 conditions were tested for three stimulus frequencies: 0.05, 0.1, and 0.2 Hz for 11 cycles. Amplitudes were chosen in such a way that the maximum velocity that was obtained was 1.7°/s for all three frequencies. These amplitudes were 5°, 2.5°, and 1.25°, respectively. Again all 66 conditions were presented in random order.

Eye position recording

Horizontal components of eye position were measured with the magnetic induction method, with ocular sensor coils in an earth-fixed rotating magnetic field (1300 Hz), based on phase detection. (Collewijn 1977). The position of the left eye and the right eye were recorded simultaneously. Eye position data were gathered by a data acquisition unit (CED 1401 PLUS) operated by a Pentium PC at a sample frequency of 250 Hz.

Stimulus generation

Vestibular stimulation

The platform on which the rabbit was placed was oscillated about the yaw axis, driven by a servomotor (Mavilor-DC motor 80). The driving signal, which specified the required position, was computed and delivered by the CED unit. Actual position of the platform was measured by an angular displacement transducer (Trans-Tek 600) whose output was recorded by the CED unit and stored along with the eye position and visual stimulus position data for off-line analysis.

Transparent optokinetic stimulation

The rabbit has an almost panoramic visual field, with an optokinetic responsive area for each eye that extends from about 100° anterior to 75° posterior, and 10° inferior to 50° superior (Dubois and Collewijn 1979). Therefore a panoramic visual stimulus was used (Fig. 1) for optimal visual stimulation. The visual stimulus consisted of a translucent dome (90 cm in diameter) with a plain white inner surface, which was centered around the head of the