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A Comparison of the Horizontal and Vertical Optokinetic Reflexes of the Rabbit*

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Summary. The horizontal and vertical monocular optokinetic reflexes of the rabbit were measured under closed-loop and open-loop conditions. A random noise, optokinetic stimulus subtending 70 × 70 deg was presented to the left eye of rabbits placed in front of a rear projection tangent screen. The position of the right eye (nonstimulated) was measured using an infrared light projection technique. During open-loop optokinetic stimulation the eye position signal was fed back to sum with a time-integrated velocity command signal driving the optokinetic stimulus. The dynamics of eye movements evoked by horizontal and vertical optokinetic stimulation were different. Horizontally evoked eye movements never exceeded a deviation of 15 deg before being interrupted by resetting saccades, which returned the eye past the primary position. By contrast, vertical eye deviations greater than 20 deg were often maintained for intervals exceeding 10 s without resetting. The closed-loop gain of optokinetically evoked horizontal eye movements was higher for monocular posterior-anterior optokinetic stimulation than for anterior-posterior stimulation. The vertical optokinetic gain for up-down stimulation was slightly greater than the gain for down-up stimulation. The vertical up-down, open-loop optokinetic gain was greater than the down-up gain over a range of retinal slip velocities of 0.5–5.0 deg/s. Measurement of the horizontal vestibulo-ocular reflex during simultaneous horizontal optokinetic stimulation demonstrated that visual and vestibular information combine linearly to produce reflex eye movements. These data suggest that the higher gain of the horizontal optokinetic reflex may compensate in part for the reduced gain of the horizontal vestibulo-ocular reflex at lower angular accelerations of the head. An equivalent vertical optokinetic gain would be obviated by the contribution of the utricular otoliths to the vertical vestibulo-ocular reflex at low frequencies of head movement.

Key words: Optokinetic reflex – Vestibulo-ocular reflex – Rabbit – Visual-vestibular interaction

Postural stability of the head in space is achieved using information which originates from three separate sensory systems: visual, vestibular, and neck-proprioceptive. The various proportions with which these classes of sensory inputs combine to achieve postural stability depend on the frequency and amplitude of the particular forcing-function. For example, the horizontal vestibulo-ocular reflex is relatively inferior to the vertical vestibulo-ocular reflex of the rabbit in compensating for low frequency movement of the head (Barmack 1977). This difference in the low-frequency gain of these vestibulo-ocular reflexes can be attributed to a utricular otolithic contribution to the vertical vestibulo-ocular reflex. There is no equivalent otolithic input to the horizontal vestibulo-ocular reflex. In contrast, the horizontal cervico-ocular reflex appears to compensate in part for the lack of an otolithic input to the horizontal vestibulo-ocular reflex by providing low-frequency information concerning head movement relative to the body. The horizontal cervico-ocular reflex has a gain which is 2–3 times larger than the gain of the vertical cervico-ocular reflex (Barmack et al., unpubl. observ.). Since vestibulo-ocular, cervico-ocular, and optokinetic reflexes must combine to provide the rabbit with a relatively fixed spatial reference, it would appear that the horizontal optokinetic input might also be of relatively greater importance in providing low-frequency information

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useful for stabilizing the head, further compensating for the absence of an otolithic input in the horizontal plane.

The monocular horizontal optokinetic reflex of rabbits is asymmetric, with posterior-anterior stimulation evoking optokinetic eye movements of higher gains (eye velocity/stimulus velocity) than anterior-posterior stimulation (Collewijn 1969). The relative gain and asymmetry of monocular vertical optokinetic eye movements has not been measured systematically. Previous investigators have suggested that vertical optokinetic eye movements are equivalent in gain to horizontal optokinetic eye movements, but with no directional asymmetry (Collewijn and Noorduin 1972). More recently, Dubois and Collewijn (1979) have suggested that vertical optokinetic eye movements are symmetrical for the two directions of stimulation but are of lower gain than horizontal optokinetic eye movements.

In addition to differences in reflex gains, the dynamics of eye movements evoked by vertical and horizontal vestibular stimulation are different in the rabbit. Horizontal vestibular stimulation evokes compensatory eye movements which are frequently interspersed with fast resetting (saccadic) eye movements. These anticompensatory resetting saccades prevent extreme deviations of the eyes from primary position. Vertical vestibular stimulation, however, does not usually evoke these fast resetting eye movements (Barmack 1977).

The present experiment was undertaken with the aim of comparing the dynamics and gains of horizontal and vertical eye movements evoked by "open-loop" and "closed-loop" monocular stimulation. A second goal of the present experiment was to determine if eye movements evoked by vestibular and optokinetic stimulation combine linearly. We have found that (1) the dynamics of horizontal and vertical optokinetically evoked eye movements are different, (2) the gain of the horizontal (posterior-anterior) optokinetic reflex exceeds the gain of the vertical optokinetic reflex, and (3) horizontal optokinetic and vestibular reflexes combine linearly. These findings have been previously communicated as an abstract (Erickson and Barmack 1978).

Methods

Preparatory Surgery

Nineteen albino and pigmented rabbits were anesthetized with ketamine hydrochloride (50 mg/kg i.m.) and halothane. Each rabbit's head was aligned in a stereotaxic apparatus so that the lambda suture was 1.5 mm below the bregma suture. Two stainless steel screws (10–32) were anchored to the calvarium with four smaller peripherally placed stainless steel screws (2–56) and dental cement. The two larger screws mated with a steel rod which during the experiment maintained the rabbit's head at the center of a biaxial servo-controlled rate table and supported an eye position monitor. The rod was tilted in the posterior-anterior direction at an angle of 12 deg to align the plane of the horizontal semicircular canals with the horizontal plane of the rate table. Rabbits were allowed to recover from the bolt-implantation operation at least 24 h before experimentation began.

Eye Position Recording

During the experiment the body of the rabbit was firmly encased in "egg carton" foam rubber and the head was immobilized by the afore-mentioned steel rod. Eye position was monitored with an infrared light projection technique. The eye was anesthetized topically with proparacaine hydrochloride, and a small suction cup bearing a light-emitting diode (LED) was attached to the anesthetized eye. The LED projected a narrow beam of infrared light onto a photosensitive X-Y position detector (United Detector Technology, SC-50) which was mounted on the head restraint rod and located 3–5 mm from the tip of the LED. The photosensitive surface gave a continuous X-Y indication of the position of the incident centroid of infrared light. The system was calibrated by moving the eye on which the LED was mounted through known angular displacements. It was found to have a sensitivity of 60 mV/deg, and was linear to within 5% for deviations of the eye of ±15 deg. Eye velocity was determined by electronically differentiating the eye position signal.

Optokinetic Stimulation

The rate table was located 55 cm from the center of a rear-projection tangent screen which subtended 70 deg × 70 deg of visual angle. The optokinetic stimulus was constructed from a random dot stereogram; each dot subtending 10 min of visual angle. The optokinetic stimulus was rear projected onto the screen by beaming the image projected by a 35 mm slide projector off a series of first surface mirrors. Two of the mirrors were mounted on EEG pen motors which were positioned at right angles. The direction and velocity of optokinetic stimulation was controlled by supplying an appropriate voltage ramp to one of the two pen motors. A rear projection tangent screen is truly tangent at only one point on the optical axis. Consequently, linear distances and angular distances are not equivalent, and a "constant velocity" target will in fact have a lower angular velocity at the extreme edges of the screen. For the present tangent screen, the velocity of the optokinetic stimulus was about 12% lower for the most peripheral 5 deg relative to the most central 5 deg subtended by the tangent screen. Our calibrations of optokinetic stimulus velocity were based on the time required for a point to traverse the entire tangent screen, and therefore represent *average* velocities. The rabbit was aligned with respect to the tangent screen so that the optokinetic stimulus subtended the central 70 deg of the visual field. This alignment was important since optokinetic stimulation of the anterior sectors of the visual fields of albino rabbits (15–60 deg on each side of the sagittal plane) evokes an optokinetic nystagmus of inverted sign (Collewijn et al. 1978; Hahnenberger 1977). Differences in the gains of optokinetic reflexes of albino and pigmented rabbits were not observed in the present experiment probably because of minimal stimulation of the anterior visual field by the 70 × 70 deg optokinetic stimulus.

In preliminary experiments, we recorded the position of both the left and right eyes during monocular optokinetic stimulation. The eye movements evoked by monocular optokinetic stimulation

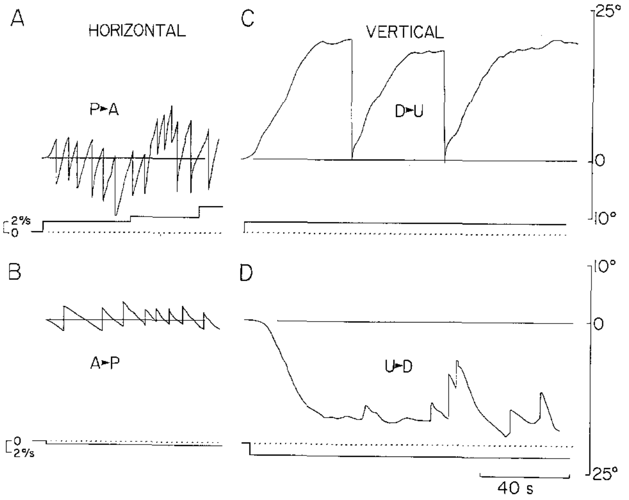

Fig. 1A–D. Horizontal and vertical eye movements evoked by monocular optokinetic stimulation. Movements of the right eye were recorded during optokinetic stimulation of the left eye. The lower trace indicates the velocity of the optokinetic target. **A** Posterior-anterior stimulation. **B** Anterior-posterior stimulation. **C** Down-up stimulation. **D** Up-down stimulation

were conjugate to within 10%, the limiting accuracy of our method of measuring the position of both eyes simultaneously. However, the suction cup which attached the LED to the eye obscured the central 50 deg of vision. Monocular optokinetic stimulation of this partially occluded eye evoked reflexes of lower *gain* than did monocular stimulation of an unoccluded eye; during which movements of the unstimulated eye were measured. Therefore, the monocular optokinetic reflexes described below were evoked by stimulating and monitoring separate eyes. Typically, the left eye was stimulated and the eye position of the right eye was recorded. Vision of the right eye was prevented by draping the entire right side of the rabbit, including the eye position transducer, with three layers of black cloth. The closed-loop optokinetic gain was defined as: peak compensatory eye velocity/optokinetic stimulus velocity. The closed-loop optokinetic gain was measured over a range of optokinetic stimulus velocities (00.1–50.0 deg/s) by starting with the lowest stimulus velocity. Each stimulus velocity was maintained until an asymptotic value of peak compensatory eye velocity was attained. This peak value was interrupted by anticompensatory resetting saccadic eye movements. An average of 2–4, intersaccadic peak compensatory eye velocities was computed for each optokinetic stimulus velocity. *Open-loop* optokinetic stimulation was achieved by feeding back the eye position signal of the unstimulated eye and summing it with the time-integrated retinal slip command signal. The summed output of these two signals was used to control the position of the optokinetic stimulus. *Open-loop optokinetic gain* was defined as: peak compensatory eye velocity/retinal slip command velocity. The procedures for measuring the open-loop optokinetic gain were similar to those used for testing the closed-loop optokinetic gain. Retinal-slip velocity was always increased from the lowest to the highest value over a range of 00.1–50.0 deg/s.

Vestibular Stimulation

The horizontal vestibulo-ocular reflex was measured in seven rabbits before and during concomitant open-loop optokinetic-stimulation. Rotation of the rate table about the vertical axis was servo-controlled, and the position output signal of the rate table was of constant amplitude for sinusoidal input signals of ±10 deg amplitude at frequencies equal to or less than 0.8 Hz. During combined optokinetic and vestibular stimulation, the left eye of the rabbit was stimulated optokinetically and the position of the right eye was measured. Open-loop monocular optokinetic stimulation during simultaneous stimulation of the horizontal vestibulo-ocular reflex was achieved by summing the eye position and table position signals with the time-integrated optokinetic stimulus velocity command signal. Horizontal vestibulo-ocular reflexes were also tested in an ascending order of frequency. These testing procedures minimized the time necessary for "steady state" reflexes to be attained. All data were recorded with an FM tape recorder and subsequently measured from a storage CRO display.

Results

Differences in Eye Movements Evoked by Horizontal and Vertical Optokinetic Stimulation

Horizontal and vertical monocular optokinetic stimulation evoked eye movements which were grossly different. For horizontal optokinetic stimulation, compensatory eye movements were evoked which were frequently interspersed with fast resetting saccadic eye movements (Fig. 1A, B). This pattern of compensatory eye movements interspersed with resetting eye movements was present for both posterior-anterior and anterior-posterior optokinetic stimulation and prevented extreme deviations of horizontal eye position. Unlike horizontal eye movements, eye movements evoked by monocular vertical optokinetic stimulation were interspersed with fewer fast resetting saccadic eye movements (Fig. 1C, D). Vertically evoked saccades were also less effective in returning the eye toward primary position. A comparison of anticompensatory resetting saccadic eye movements evoked by horizontal and vertical optokinetic stimulation demonstrates that virtually all of the anticompensatory saccades by stimuli of either posterior-anterior or anterior-posterior directions returned the eyes past primary position, whereas only a small fraction of the vertical anticompensatory saccadic eye movements achieved an equivalent result (Fig. 2). Similar plots of saccadic amplitude versus eye position were obtained from four other rabbits.

Not only were the anticompensatory saccadic eye movements evoked by vertical optokinetic stimulation less effective in returning the eye towards primary position than were horizontal anticompensatory saccadic eye movements, but vertical saccades were initiated from more extreme positions over the entire range of velocities tested. Vertical deviations

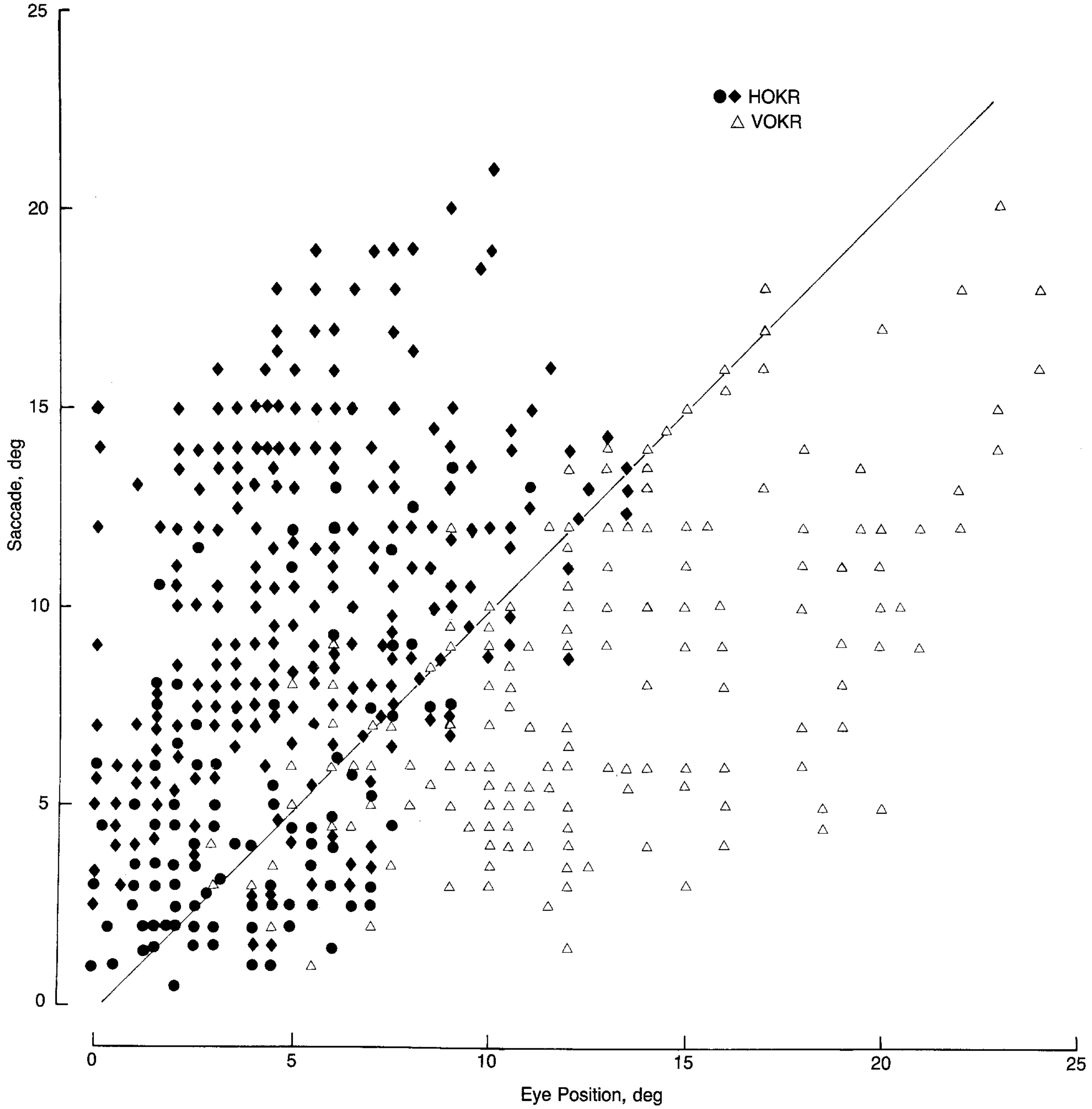

Fig. 2. Differences in saccadic compensation for vertical and horizontal eye deviation evoked by optokinetic stimulation. The amplitudes of resetting saccadic eye movements are plotted as a function of the eye positions at which saccades were initiated. Data were pooled from three rabbits. Filled circles and diamonds represent saccadic eye movements evoked by anterior-posterior and posterior-anterior optokinetic stimulation, respectively. Open triangles represent saccadic eye movements evoked during vertical optokinetic stimulation (up-down and down-up). Saccadic eye movements which returned the eyes past center position lie above the diagonal line. Saccadic eye movements which did not return the eyes to center position lie below the diagonal line

greater than 20 deg were often maintained for intervals exceeding 10 s without resetting. This was true for vertical eye movements in the down-up and up-down directions (Figs. 1–3). Thus, vertical anticompensatory saccadic eye movements were initiated from more extreme eye positions, and these eye movements were less effective in returning the eyes *past* primary position than were the anticompensatory saccadic eye movements evoked by horizontal optokinetic stimulation.

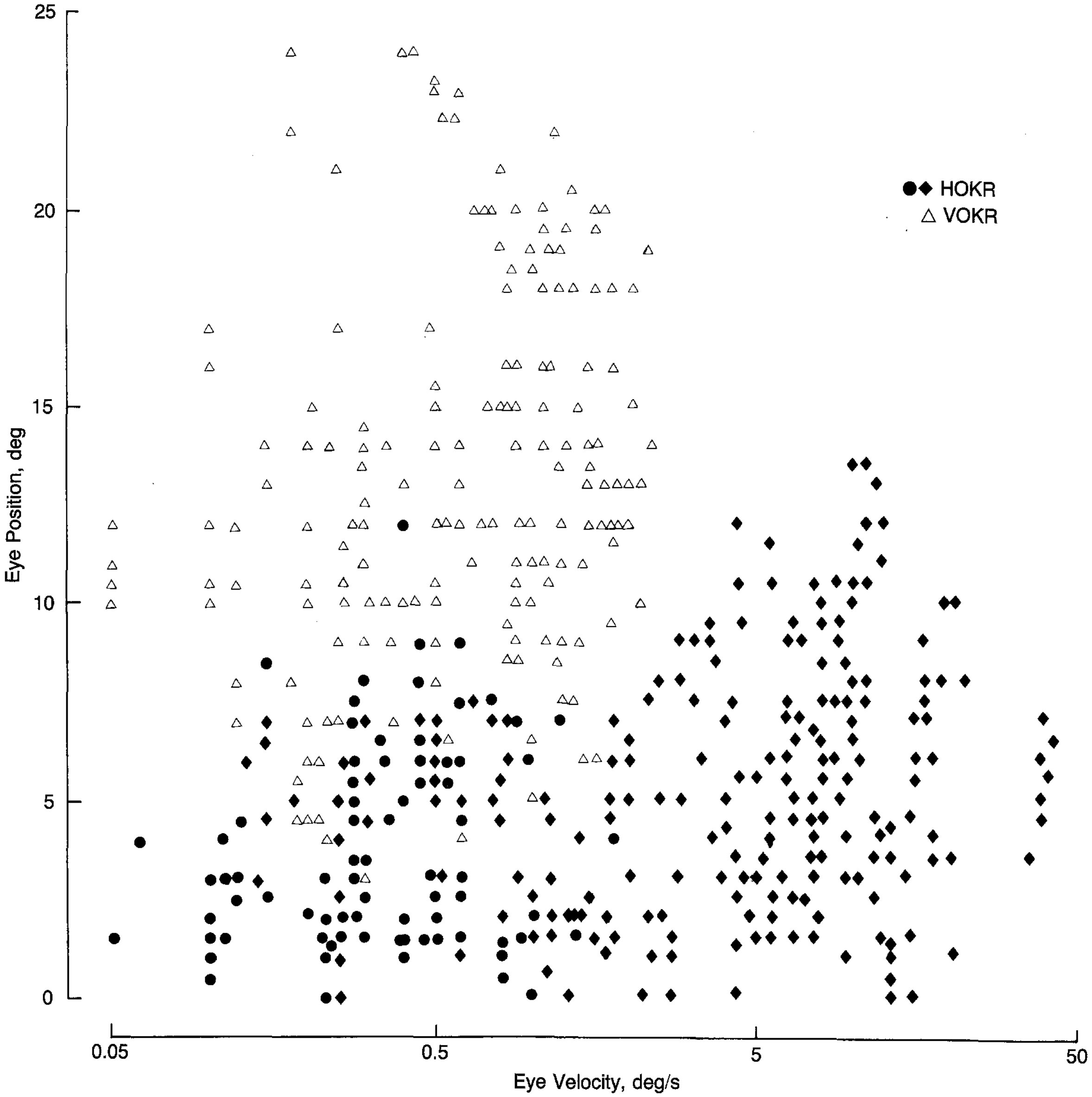

Fig. 3. Eye position and velocity at which anticompensatory saccadic eye movements are evoked during horizontal and vertical optokinetic stimulation. The eyes deviated to more extreme eye positions during vertical optokinetic stimulation (open triangles) before anticompensatory saccadic eye movements were initiated. Anticompensatory eye movements in the horizontal plane evoked by posterior-anterior (diamonds) and anterior-posterior (circles) optokinetic stimulation were initiated from less extreme eye positions. Data were pooled from three rabbits

Closed-loop Gains of Vertical and Horizontal Optokinetic Reflexes

The closed-loop gains of vertical and horizontal optokinetic reflexes were measured in 12 rabbits. Optokinetic stimulation was delivered to the left eye and movements of the right eye were recorded. The closed-loop gain of the horizontal optokinetic reflex evoked by posterior-anterior stimulation was consistently higher than the closed-loop gains of the other optokinetic reflexes (anterior-posterior, up-down, and down-up) (Fig. 4). This asymmetry in closed-loop gain for horizontal monocular optokinetic stimulation has been previously reported by others (Collewijn 1969; Collewijn and Van der Mark 1972). The closed-loop gains of vertical optokinetic reflexes were lower than the posterior-anterior gain of the horizontal optokinetic reflex, but greater than the anterior-posterior gain of the horizontal optokinetic reflex. There was a slight asymmetry in the gain of

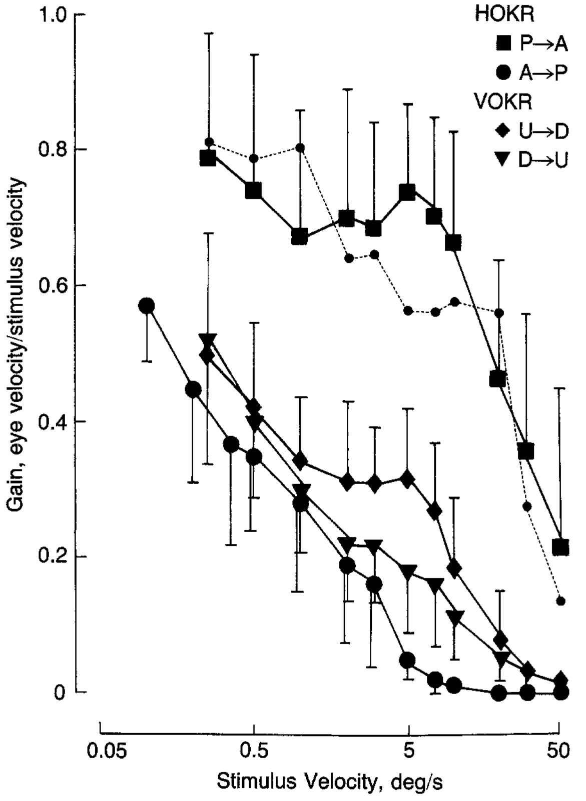

Fig. 4. Closed-loop gain for eye movements evoked by monocular optokinetic stimulation in the horizontal and vertical planes. The left eye was stimulated and movements of the right eye were recorded. Filled squares, posterior-anterior stimulation; filled circles, anterior-posterior stimulation; filled diamonds, up-down stimulation; inverted filled triangles, down-up stimulation. Each data point represents the mean gain for 12 rabbits. The smaller filled circles connected by dashed lines indicate closed-loop optokinetic gains for posterior-anterior stimulation predicted from the open-loop gains illustrated in Fig. 5. One standard deviation (+ or −) is illustrated for each data point

the vertical optokinetic reflex. Over the stimulus range of 2–20 deg/s, the gain of the up-down vertical optokinetic reflex was statistically greater (*t*-test, $p < 0.01$, N = 10) than the gain of the down-up optokinetic reflex.

Open-loop Gains of Vertical and Horizontal Optokinetic Reflexes

To determine the retinal slip velocities at which differences in the closed-loop gain of the vertical optokinetic reflex might be maximal, we compared the open-loop gain of both horizontal and vertical optokinetic reflexes during monocular stimulation. The open-loop gain of the horizontal optokinetic reflex was measured only in the posterior-anterior direction. This direction of stimulation evoked eye movements of highest gain (peak compensatory eye velocity/retinal slip velocity). There was an asymmetry in the gain of the eye movements evoked by vertical optokinetic stimulation (Fig. 5). Over a range of retinal slip velocities of 0.5–5.0 deg/s, the

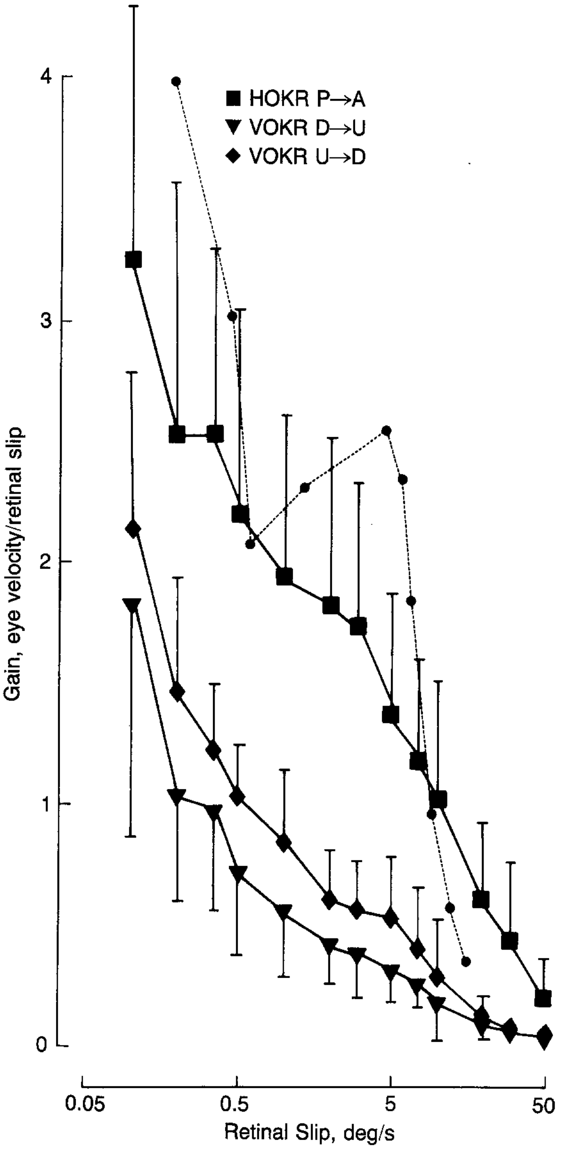

Fig. 5. Open-loop gain of optokinetic reflexes evoked by monocular horizontal and vertical stimulation. The left eye was stimulated and movements of the right eye were fed back to maintain constant retinal slip velocity. Filled squares, posterior-anterior stimulation; inverted triangles, down-up stimulation; diamonds, up-down stimulation. The open-loop gains of the up-down responses were significantly greater than the gains of the down-up responses for retinal slip velocities of 0.5–5.0 deg/s. Each data point represents the mean gain for ten rabbits. The smaller filled circles connected by dashed lines indicate open-loop optokinetic gains for posterior-anterior stimulation predicted from the closed-loop gains illustrated in Fig. 4. Standard deviations (+ or −) are illustrated for each data point

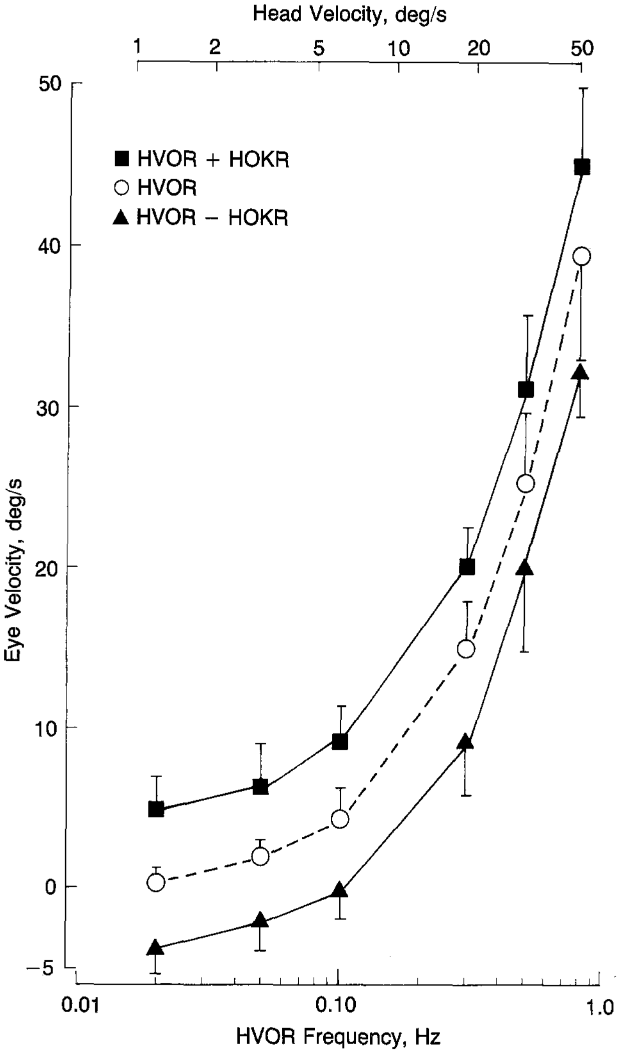

Fig. 6. Linear interaction between eye movements evoked by vestibular and optokinetic stimulation. The horizontal vestibulo-ocular reflex was evoked by sinusoidal oscillation of the rate table (±10 deg, 0.02–0.8 Hz) before and during concomitant open-loop, posterior-anterior optokinetic stimulation of the left eye at a fixed retinal slip of 3 deg/s. The position of the right eye was monitored. The open circles connected by dashed lines indicate the mean peak velocity of the right eye during stimulation of the horizontal vestibulo-ocular reflex. The filled squares and triangles indicate the mean peak eye velocity to the right and left respectively during concomitant horizontal vestibular and open-loop posterior-anterior optokinetic stimulation of the left eye. Standard deviations (+ or −) are illustrated for each data point; N = 7

gain of the eye movements evoked by up-down optokinetic stimulation was significantly greater than the gain of eye movements evoked by down-up stimulation (t-test, $p < 0.025$, $N = 10$).

It is possible to predict the closed-loop optokinetic reflex gain on the basis of the data obtained under open-loop conditions. This can be done by measuring the minimal retinal slip velocity, Rv, at each stimulus velocity, Sv, under closed-loop conditions of optokinetic stimulation. This retinal slip velocity is then multipled by the open-loop gain, Go, and divided by the closed-loop stimulus velocity. Hence, the predicted closed-loop gain $= \frac{\mathrm{Rv} \cdot \mathrm{Go}}{\mathrm{Sv}}$. This predicted closed-loop optokinetic gain function is illustrated for posterior-anterior optokinetic stimulation in Fig. 4 (dashed line). Similarly, the open-loop optokinetic gain can be predicted from closed-loop data. In this instance the eye velocity, Ev, evoked during closed-loop optokinetic stimulation is divided by the retinal slip velocity, Rv. The predicted open-loop gain = Ev/Rv. This predicted open-loop function for posterior-anterior open-loop optokinetic stimulation is illustrated in Fig. 5 (dashed line).

Linear Interaction Between the Horizontal Optokinetic Reflex and Horizontal Vestibulo-ocular Reflex

The question of how optokinetic and vestibular information combine was examined by measuring the horizontal vestibulo-ocular reflex before and during simultaneous open-loop posterior-anterior optokinetic stimulation of the left eye (Fig. 6). The HVOR was evoked in the absence of vision by sinusoidal oscillation of the rate table (±10 deg, 0.02–0.80 Hz). Open-loop, posterior-anterior optokinetic stimulation of 3 deg/s was delivered in the absence of vestibular stimulation and evoked eye movements with an average velocity of 5.1 deg/s (N = 7). Then, open-loop, posterior-anterior optokinetic stimulation (3 deg/s) was delivered to the left eye as the rabbit was oscillated in the rate table (±10 deg, 0.02–0.80 Hz). The reflex eye movements evoked by conjoint monocular optokinetic and vestibular stimulation reflected a linear combination of these two inputs (Fig. 6). However, at the three lowest frequencies examined, 0.02, 0.05, and 0.1 Hz, the average change in peak eye velocity caused by concomitant posterior-anterior optokinetic stimulation was somewhat less than would be expected; 4.2 ± 0.3 deg/s. This departure from linearity can probably be ascribed to the fact that the open-loop optokinetic stimulus occupied only the central 70 deg of the left visual field. The remaining visual field was not "clamped". At low frequencies of vestibular stimulation this "unclamped" peripheral field would tend to reduce the efficacy of the constant velocity optokinetic feedback system.

Discussion

Dynamics of Eye Movements Evoked by Horizontal and Vertical Optokinetic Stimulation

There were marked differences in eye movements evoked by horizontal and vertical optokinetic stimulation. Vertical eye movements were made at lower velocities to more extreme positions and were interrupted less frequently by anticompensatory resetting saccadic eye movements. Vertical anticompensatory resetting eye movements were less effective than were horizontal anticompensatory eye movements in returning the eyes to primary position. Anticompensatory resetting eye movements also occur with lower frequency during the vertical vestibular (roll) stimulation than during the horizontal vestibular stimulation (Barmack 1977). However, anticompensatory resetting eye movements can be increased in frequency during stimulation of the vertical vestibulo-ocular reflex by orienting the head of the rabbit "nose-up" so that sinusoidal roll stimulation about an earth vertical axis does not cause a change in the orientation of the utricular otoliths with respect to gravity (Barmack, unpubl. observ.). From these observations one might infer that a stimulus-modulated utricular signal may ordinarily prevent the occurrence of anticompensatory vertical eye movements. It is possible that a "steady state" utricular otolithic signal might also be responsible for the relative paucity of anticompensatory resetting eye movements evoked by vertical optokinetic stimulation.

Comparison of the Gains of the Horizontal and Vertical Optokinetic Reflexes

The gain of the horizontal monocular optokinetic reflex in the posterior-anterior direction exceeded that of the vertical monocular optokinetic reflexes in both the up-down or down-up directions. The higher gain of the horizontal monocular optokinetic reflex may compensate for the reduced gain of the horizontal vestibulo-ocular reflex during head movements of relatively low frequency. Equivalent vertical optokinetic gains would be obviated by the contribution of the utricular otoliths to the vertical vestibulo-ocular reflex at these lower frequencies of head movement. The present data contradict an earlier report of similar gains for horizontal and vertical optokinetic reflexes of the rabbit (Collewijn and Noorduin 1972), but agree with more recent measurements of both horizontal and vertical optokinetic reflex gains (Dubois and Collewijn 1979).

The gain of the vertical monocular optokinetic reflex in the up-down direction was slightly superior to the gain of the vertical optokinetic reflex in the down-up direction. Open-loop optokinetic reflex measurements suggested that this asymmetry in vertical optokinetic reflex gain is present over a narrow range of retinal slip velocities of 0.5–5.0 deg/s. These velocities correspond to the velocities at which direction-selective retinal ganglion cells in the rabbit are most sensitive (Oyster et al. 1972). Extensive recordings from direction-selective retinal ganglion cells have demonstrated a three-lobed distribution: (1) down-up, with a slight anterior-posterior component, (2) posterior-anterior, with a slight up-down component, and (3) up-down, with a slight anterior-posterior component (Oyster 1968). Perhaps the up-down component of the posterior-anterior lobe is responsible for the slightly enhanced gain for optokinetic stimulation in the up-down direction. A similar asymmetry for vertical optokinetic responses has been recorded during binocular optokinetic stimulation in the monkey (Matsuo et al. 1979).

Comparison of Open- and Closed-loop Optokinetic Reflex Gains

The open-loop optokinetic reflex gains which were obtained with the present experimental techniques were lower by a factor of 5–10 at the lower retinal slip velocities than open-loop gains measured previously using binocular full field stimulation in the rabbit (Collewijn 1969). Nevertheless, the open-loop gains which we measured yielded a reasonably accurate prediction of the closed-loop gains using the same 70 × 70 deg monocular optokinetic stimulus. Apparently, in the present experiment a signal from the "unclamped" retina prevented the "runaway" eye movements observed in both rabbits and monkeys during maintained full-field binocular and monocular open-loop optokinetic stimulation (Collewijn 1969; Koerner and Schiller 1972). It should be noted that the predictions of closed-loop optokinetic reflex gains based upon data obtained from full-field open-loop optokinetic stimulation are not in good agreement with measurements made of closed-loop optokinetic reflexes.

Linear Interactions Between Horizontal Vestibular and Optokinetic Stimulation

The present results directly demonstrate that simultaneous visual and vestibular stimulation evoke eye movements which reflect a linear combination of these inputs. We have not examined the range of optokinetic velocities over which this linear summation occurs. Previous single-unit studies have suggested that the vestibular nuclei might provide the site at which visual and vestibular information is combined (Henn et al. 1974; Waespe and Henn 1977, 1979). Visual information could reach the vestibular nuclei via the visual olivo-cerebellar pathway (Barmack 1979) or via a projection originating from the subparafascicular region (Barmack et al. 1979). At present, it is not known whether visual and vestibular information combine linearly at the level of the vestibular nuclei, since previous experiments have not controlled these two inputs independently. It is not necessary that visual and vestibular information combine linearly at the level of the vestibular nuclei in order for these inputs to evoke eye movements which reflect a linear combination. Nevertheless, it would seem likely that such a linear combination does occur at the level of the vestibular nuclei and that it would be revealed using stimulus conditions which allowed independent control of vestibular stimulation and retinal slip velocity.

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