

# Eye velocity asymmetry, ocular orientation, and convergence induced by angular rotation in the rabbit <sup>☆</sup>

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## Abstract

We studied ocular asymmetries and orienting responses induced by angular rotation in rabbits with binocular video recordings. Slow phase velocities were significantly larger in the eye moving temporonasally than nasotemporally. The eyes also converged and pitched down during rotation, which increased and refocused binocular overlap in the visual fields. Eye position also shifted into the slow phase direction. Vergence and pitch outlasted the induced nystagmus, suggesting that they were generated by a separate vestibulo-oculomotor subsystem(s). Thus, mechanisms in the rabbit increase compensatory eye velocity in the eye that leads into the direction of rotation and enhance binocular vision.

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## 1. Introduction

There are considerable differences in the organization of the visual and oculomotor systems of lateral-eyed and frontal-eyed species, largely based on the different demands due to placement of the retina in visual space. The rabbit, a lateral-eyed animal, has a temporal-to-nasal preponderance in slow phase eye velocity during the optokinetic reflex (OKR) (Collewijn & Noorduyn, 1972; Tan, Van der Steen, Simpson, & Collewijn, 1993), which would produce a difference in the amplitude of excursion of the two eyes during conjugate movements. There are differences in amplitude between the movements of the eyes in the rabbit in response to otolith stimulation (Maruta, Simpson,

Raphan, & Cohen, 2001; Maruta, Simpson, Raphan, & Cohen, 2005). A temporal-to-nasal preponderance is also present in the lateral-eyed goldfish in response to rotation with steps of angular velocity in darkness (Pastor, De La Cruz, & Baker, 1992), and Collewijn, Winterson, and Van der Steen (1980) briefly noted an asymmetry in eye velocity when studying the decay profile of the aVOR in the rabbit. In this study, we posited that a similar disconjugacy would be present in the angular vestibulo-ocular reflex (aVOR) of the rabbit during rotation in darkness. A systematic study of this was the first purpose of this study.

The vestibular system not only drives the eyes to compensate for rapid head movements, but it also adjusts the field of view by orienting the eyes toward gravito-inertial acceleration, the sum of all linear accelerations including gravity (Cohen, Maruta, & Raphan, 2001). Consequently, statically tilting the head causes the eyes to counter-rotate in a wide range of species (perch, carp: Benjamins, 1918; rabbits: Fleisch, 1922; Van der Hoeve & De Keijn, 1917;

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monkeys: Dai, McGarvie, Kozlovskaya, Raphan, & Cohen, 1994; humans: Woellner & Grabiell, 1959) and influences the planar field (Listing's plane) containing the axes about which pursuit and saccadic eye movements take place in monkeys and humans (Bockisch & Haslwanter, 2001; Haslwanter, Straumann, Hess, & Henn, 1992; Hess & Angelaki, 2003). Orienting gaze shifts are also produced by the semicircular canals in response to angular acceleration. Rotating the head about a vertical axis produces a shift in the beating field of the nystagmus, i.e., in the average eye position, which is generally into the quick phase direction (humans: Hood, 1967; Siegler, Israël, & Berthoz, 1998; monkeys: Solomon & Cohen, 1992; cats: Chun & Robinson, 1978; rats: Meier & Dieringer, 1993). In contrast, this 'orienting gaze shift' (Meier & Dieringer, 1993) has been reported to be in the direction of the slow phases in the rabbit (Bartels, 1911; Lorente De Nó, 1932). The extent of the gaze shift has only been studied for eye movement in the horizontal plane, and it is not known whether the eyes orient in other dimensions. A more complete analysis of the orienting movements induced by the semicircular canals was a second purpose of this study.

Vergence is prominent after naso-occipital linear head movements (Collewyn and Noorduin; Maruta et al., 2005) or head pitch (Lorente De Nó, 1932; Maruta et al., 2001), but it is not known whether angular rotation is also associated with vergence. The consequence of a discrepancy in the movement of the two eyes in the horizontal plane is that the eyes would converge or diverge during nystagmus induced by angular head movements, depending on whether the slow phase movements were temporal-to-nasal or nasal-to-temporal. If such vergence occurred, it would change the region of binocular overlap of the visual fields.

An investigation of this was the third aim of this study. Preliminary results have been reported (Maruta, MacDougall, Simpson, Raphan, & Cohen, 2004).

## 2. Methods

### 2.1. Animal preparation

Three adult Dutch-belted rabbits weighing approximately 2.7 kg were used in this study. The experiments conformed to the Principles of Laboratory Animal Care (1996) and were approved by the Mount Sinai School of Medicine Institutional Animal Care and Use Committee. Under sterile conditions and general anesthesia (35 mg/kg ketamine, 0.35 mg/kg acepromazine, and 5 mg/kg xylazine), an acrylic pedestal was surgically implanted on the skull so that the head could be held firmly but painlessly during experiments. The head was set so that the superior border of the nasal bone inclined at  $57^\circ$  to the horizontal, the rabbit's natural posture in the freeze position (Hughes, 1971). In this position, the normals to the lateral canals are tilted back by  $7^\circ$  from the spatial vertical, while the average normal to the vertical canals is parallel to the Earth horizontal (Simpson, 1983). The animals were allowed to recover for 1 week before initial testing.

### 2.2. Coordinate frames

A head-fixed coordinate frame was defined relative to the animal's freeze position (Fig. 1A). The roll ( $X$ ) axis was naso-occipital, positive out of the nose, the pitch ( $Y$ ) axis was bitemporal, positive out of the left side, and the yaw ( $Z$ ) axis was vertical, positive up. Eye and head rota-

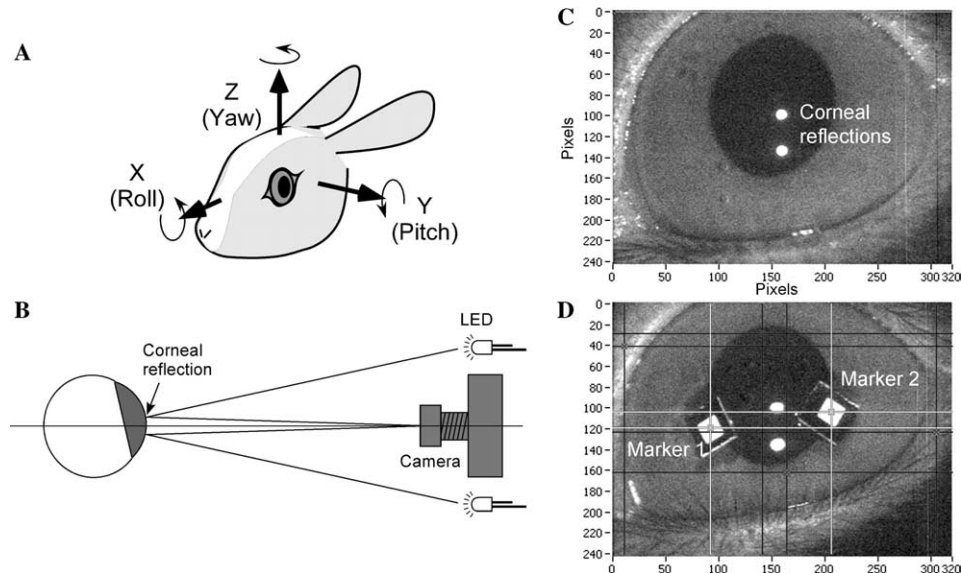


Fig. 1. (A) Head-fixed coordinate frame defined for video-oculography. (B) Placement of the video camera and light sources relative to the eye. The corneal reflections of the two LEDs illuminating the eye were used to center the camera image. At rest, the optic axis points  $13^\circ$  above the horizontal plane. (C and D) Captured images of the eye without (C) and with (D) markers on the cornea. The camera position was adjusted in a parasagittal plane so that the corneal reflections were symmetrically placed about the center of the captured image. Each of the two markers was identified as the center of the largest white area in a window defined by black lines. These lines were extended to the border of the frame in the figure (D).

tions were described with the right-hand rule using this head-fixed coordinate frame, i.e., positive eye and head rotations were clockwise ( $X$ ), down ( $Y$ ), and left ( $Z$ ) from an egocentric perspective.

### 2.3. Video-oculography

Binocular eye movements were recorded using video-oculography (Figs. 1B–D). A video camera was mounted in front of each eye in a plane parallel to the head-fixed  $X$ – $Z$  (sagittal) plane with the camera's vertical axis aligned with the  $Z$ -axis. The eyes were illuminated with infrared LEDs placed symmetrically above and below the camera lens. The positions of the camera and LEDs were adjusted en bloc in the parasagittal plane so that the corneal reflections of the LEDs fell in the center of the image field of each camera (Fig. 1C). In this condition, the camera was at the center of the corneal curvature (Fig. 1B). Image resolution was  $320 \times 240$  pixels and images were sampled at 30 frames/s. The corneas were anesthetized with 0.5% proparacaine hydrochloride and two paper markers with a white 1 mm-by-1 mm central area were placed 6 mm apart (Fig. 1D). Fixation of the markers was verified by sampling video images during the course of testing. The fixed distance between the markers was used as a reference for deriving the pixel-to-millimeter ratio in the video image. The size of the markers provided a second metric for calibrating the pixel-to-mm ratio. The stability of the corneal reflections during eye movements indicated that the center of the average curvature of the cornea converged at the center of eye rotation over the range of eye movements. Assuming a uniform sphere, the radius of the eye globe was determined by measuring the medio-lateral dimension of ten eyes from five post-mortem rabbits ( $18.13 \text{ mm} \pm 0.35$ , mean and 95% confidence interval). This is close to the value of 18.1 mm determined by Hughes (1972).

From the locations of the markers in the image field, vectors were determined relative to the origin of the corneal curvature with the average radius of the eye. An orthonormal basis for the eye coordinate frame was constructed from these vectors. The rotation of this coordinate frame relative to the head-fixed frame was computed and represented by axis angles and angular velocity vectors for analysis (Maruta et al., 2001; Raphan, 1998). The optic axis of the rabbit points  $88^\circ$  laterally and  $13^\circ$  above the horizon (Hughes, 1971), but the eye position at rest was considered to be zero in the head-fixed coordinate frame. Vergence was defined as the difference between right and left yaw eye positions. Values were positive when the eyes converged. Version was defined as the mean of the yaw eye positions of the two eyes.

### 2.4. Experimental paradigm

Animals were immobilized in a Plexiglas box. A holder attached to the box fixed the head in a posture that approx-

imated the freeze position. The box was placed in a multi-axis vestibular stimulator (Neurokinetics, Pittsburgh, PA) so that the head  $Z$ -axis was aligned with the axis of rotation. Animals were rotated with steps of velocity from  $10^\circ/\text{s}$  to  $90^\circ/\text{s}$  in  $10^\circ/\text{s}$  increments (acceleration  $85^\circ/\text{s}^2$ ). Two clockwise and two counter-clockwise rotations were given at each velocity. The order of the stimulus velocity was randomized to eliminate systematic effects of increases or decreases in stimulus velocity on gains or decay time constants of the per- and post-rotatory responses.

### 2.5. Data analysis

Saccades were identified in the velocity signal using a maximum likelihood ratio criterion (Singh, Thau, Raphan, & Cohen, 1981) and were replaced with a straight line connecting the initial and final points of the segment. The positive and negative envelopes of slow phase yaw velocities in response to velocity steps were superimposed separately for each eye, and the average decaying trajectories from the time the stimulus reached a constant velocity were fit with a single exponential function to derive estimated values of peak amplitude and time constant of decay. A linear correlation was tested for the relations between peak amplitudes and the stimulus velocity. Student's  $t$  test was used to test whether there was a difference in the average gains of slow phase velocity compensation relative to the stimulus velocity between temporal-to-nasal and nasal-to-temporal directions.

It was not necessary to remove saccades from the position records during the analysis because rabbits make few spontaneous saccades when the head is fixed (Fuller, 1980). The effect of random spontaneous saccades, if any, was negligible when averaged. The polarity of the version component during counter-clockwise per-rotation and clockwise post-rotation was mathematically inverted so that the mean trajectory of the beating fields of nystagmus could be expressed relative to the direction of the slow phases. To characterize the dynamics of the position responses in a simple form, the superimposed averages of roll, pitch, version and vergence were each fit with a decaying exponential function with the time constant  $\tau_2$  enveloped by an exponentially approaching plateau with the time constant  $\tau_1$

$$A \cdot [1 - \exp(-t/\tau_1)] \cdot \exp(-t/\tau_2) + C, \quad (1)$$

where  $t$  is the time,  $A$  is some amplitude, and  $C$  is an offset unrelated to the dynamics. A similar double exponential equation, which is equivalent to Eq. (1), was previously used to model the rise and decay profile of eye velocity in response to a step in head velocity about yaw (Raphan, Matsuo, & Cohen, 1979). The time constant,  $\tau_2$ , is a measure of the dominant time constant of the response and an indication of the inverse of the rate at which they decay to the resting state. From Eq. (1), an estimate of the peak amplitude of the trajectory and time to peak were also derived. A correlation with the stimulus rotation speed was

tested for the peak amplitude, time to peak, and  $\tau_2$  by pairing individual responses with corresponding stimulus speed.

### 3. Results

#### 3.1. Slow phase velocities

At the onset and end of constant velocity rotation, the slow phase velocity quickly reached a peak and decayed with a nearly exponential profile (Fig. 2A, panels d and e). Each eye responded to both clockwise and counter-clockwise angular accelerations in the three animals with a peak slow phase velocity that varied approximately linearly with the nine stimulus speeds between 10 and 90°/s ( $r > 0.93, p < 0.01, df = 7$ ). The movements of the two eyes

were not conjugate, and the gains at each stimulus speed were greater when the eyes were directed from temporal to nasal (Fig. 2B, “T–N” solid line) than from nasal to temporal directions (“N–T” broken line). The average gains in the nasal-to-temporal direction were 0.83 and in the temporal-to-nasal directions were 0.95, a statistically significant difference (paired  $t$  test,  $p < 0.05, N = 6$ , three animals with two directions of nystagmus). The animals had differences in average eye position in the orbit and variations in the beating field of nystagmus. Neither was related to the differences in amplitude of slow phase velocity. Thus, there was a temporal-to-nasal preponderance in response to angular acceleration about the vertical axis.

The decay profiles of slow phase velocities were fit with single exponential functions. The time constants of the fits were similar in the two eyes in each of the three animals for

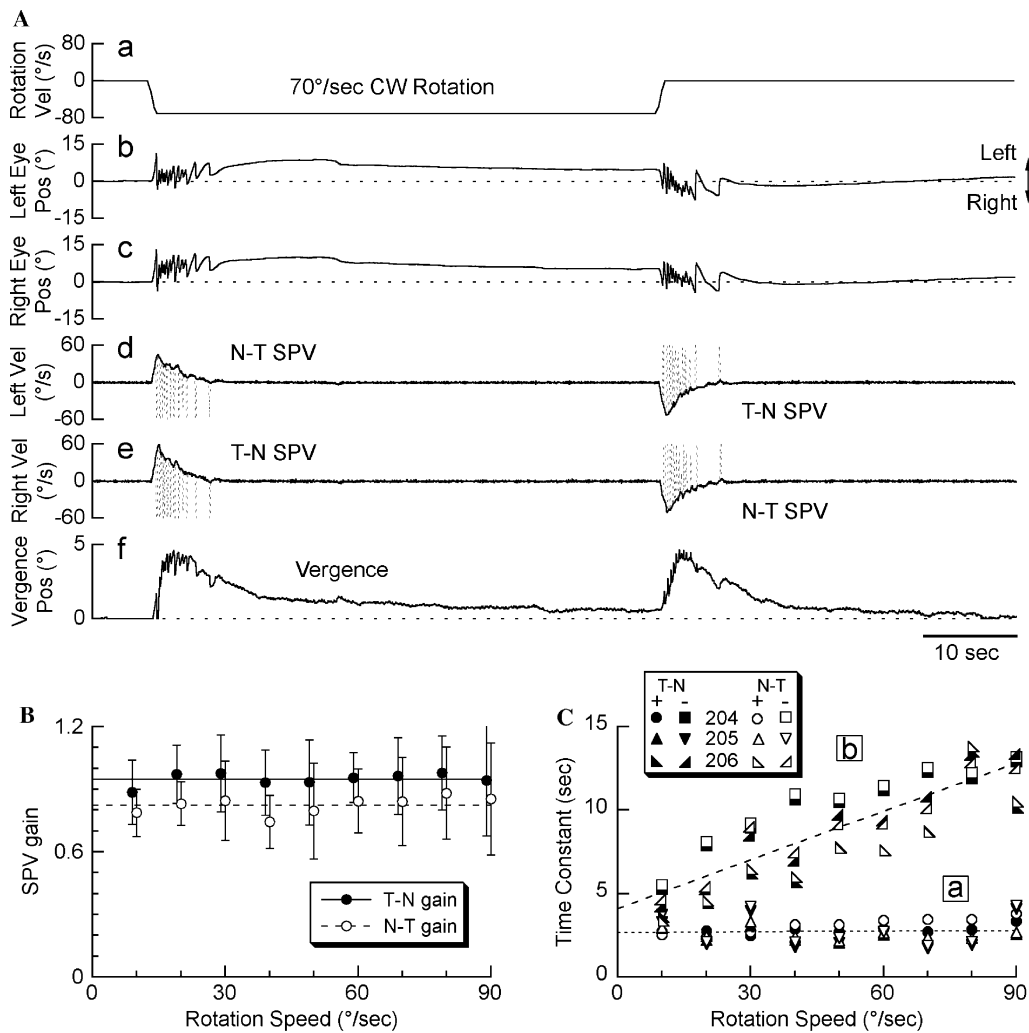


Fig. 2. (A) Positional and velocity responses to a step of 70°/s rotation (Rabbit 205). a—Stimulus velocity. b and c—Left and right yaw eye positions. The eyes drifted in the direction of the slow phases of nystagmus. Dashed lines indicate the initial eye positions. d and e—Left and right yaw eye velocities. Solid lines indicate slow phase velocities (SPV). Dashed lines indicate saccades. (T–N): temporal-to-nasal; (N–T): nasal-to-temporal. f—Degrees of vergence. The eyes converged and slowly returned to the resting positions. (B) Peak SPV gains re-stimulus speed. (C) Time constants of the decay profiles of the SPV, each fit with a single exponential function. The numbers in the inset indicate the symbols used for each animal. (+): leftward SPV; (–): rightward SPV. Two clusters of time constants that either were invariant across the stimulus speed (a, mean 2.8 s) or increased with the stimulus speed (b) were found.

all directions of rotation. In one animal (204), the decay time constants were asymmetrical, being shorter when slow phases were to the left than to the right. Another animal (205) had symmetrical but short time constants for both directions of rotation, and the third animal (206) had symmetrical but long decay profiles. The short time constants in 204 and 205 were essentially invariant across all stimulus velocities with a mean value of 2.8 s (median: 2.7 s; standard deviation (SD): 0.63 s,  $n = 54$ ; Fig. 2C, panel a). The short time constant, indicative of a lack of velocity storage, is the same as the mean time constant of the high sensitivity semicircular canal afferents in the rabbit (2.8 s, Stahl & Simpson, 1986). On the other hand, the increased time constant with stimulus velocity (Fig. 2C, panel b) that were consistent with previous studies (Collewijn et al., 1980), indicated that the central velocity storage mechanism was active in these animals.

### 3.2. Vergence

A prominent feature of the response to angular rotation was that the eyes consistently converged, unrelated to the direction of rotation. The convergence began at the onset of rotation and was maintained well beyond the duration of the induced nystagmus (Fig. 2A, panel f). Vergence responses were superimposed for each rotation speed and for each animal, and the rise and fall of the average trajectories were characterized with a double exponential function (Eq. (1); e.g., Fig. 3A). Although there was considerable variability in the peak values, when considered together, the average values increased with stimulus speed from a mean value of 1.8° at 10°/s to 5.8° at 90°/s (Fig. 3B,  $r = 0.468$ ,  $p < 0.05$ ,  $df = 25$ ), an increase of 0.07° per °/s. The time to peak following the onset or cessation of rotation was not related to the stimulus speed and had a mean value of 5.4 s (SD: 2.5 s). The decay time constants were also unrelated to the speed of rotation ( $10.9 \text{ s} \pm 4.6$ , mean and SD). Thus, vergence had the same dynamics for every rotational velocity, and these dynamics were more sluggish than the changes in slow phase velocity induced by the same rotation (Fig. 2, panels d, e, vs. f).

### 3.3. Pitch and roll positions

Roll eye position was unaffected by rotation about a vertical axis, but the pitch position of the eyes shifted downward following the onset and cessation of rotation. As for vergence, depression of the eyes followed a similar profile of rising to a peak value and then decaying to zero. There was no systematic difference in pitch between the two eyes with respect to rotation. Thus, for each rotation speed and for each animal, the binocular pitch responses were superimposed and also fit with a double exponential function (Eq. (1); e.g., Fig. 3C). The peak pitch amplitude increased with the stimulus speed from a mean value of 1.0° at 10°/s to 6.4° at 90°/s (Fig. 3D,  $r = 0.497$ ,  $p < 0.05$ ,  $df = 25$ ), an increase of 0.08° per °/s. The dynamics of

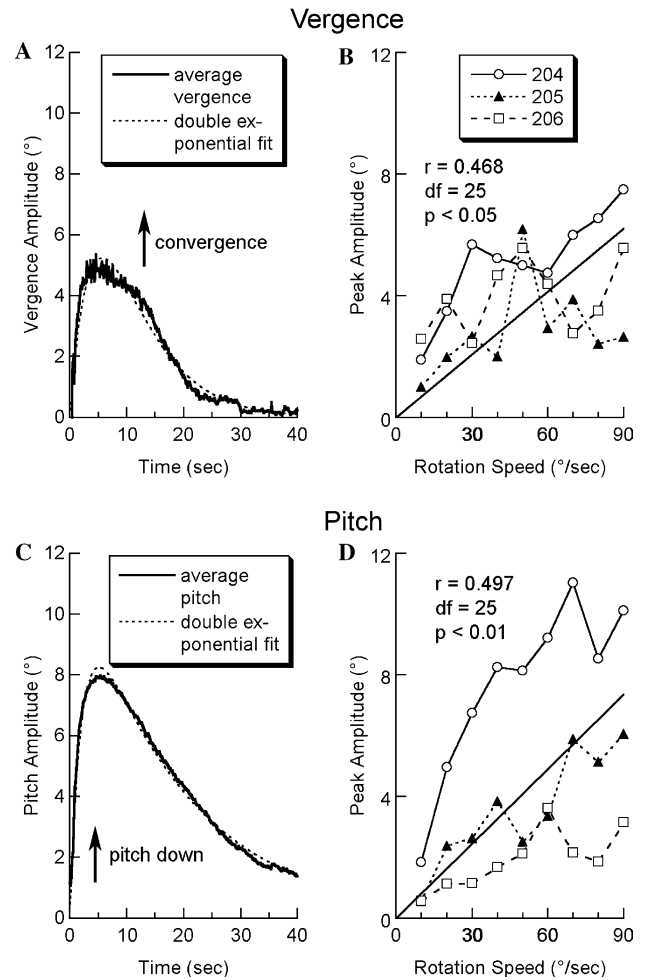


Fig. 3. (A) Superimposed average of vergence response to 40°/s rotation (Rabbit 204) with a double exponential fit (dotted line). Positive convergence. (B) Peak amplitude of vergence re-stimulus speed. The solid straight line indicates a linear fit of the means. The numbers in the inset indicate the symbols used for each animal. (C) Superimposed average of pitch response to 40°/s rotation (Rabbit 204) with a double exponential fit (dotted line). Positive down. (D) Peak amplitude of ocular pitch re-stimulus speed. The solid straight line indicates a linear fit of the means.

the pitch responses to all stimulus speeds were similar, and the peak occurred within a mean value of 4.2 s (SD: 0.9 s) after the onset or cessation of rotation. There was no significant change in the decay time constant of ocular pitch as a function of the stimulus speed, and the mean decay time constant was 12.1 s (SD: 7.7 s). Therefore, the dynamics of pitch were similar to those of vergence and more sluggish than those of the rise and fall in slow phase velocities.

### 3.4. Average beating field of nystagmus (version)

As in previous studies (Bartels, 1911; Lorente De Nó, 1932), the beating fields of nystagmus shifted in the direction of the slow phases during rotation (Fig. 2A, panels b and c). For rotation to the right, the shift in the beating field of the right eye was larger than that of the left eye and vice versa. In other words, although both eyes moved

into the slow phase direction, the movement of the leading eye toward the nose was greater than the movement of its fellow eye in the temporal direction. The difference in the movement of the two eyes was responsible for the vergence described above. In all instances, versional shifts significantly outlasted the nystagmus and the response concluded with a slow drift of the eyes back to the resting position.

The trajectories of the versional responses were fit with a double exponential function, as above (Eq. (1); e.g., Fig. 4A). The peak amplitude of the version ( $8.4^\circ \pm 2.3^\circ$ , mean and *SD*,  $N = 27$ , Fig. 4B) was unrelated to stimulus velocity. The time for the eyes to reach peak version increased with rotation speed (Fig. 4C,  $r = 0.657$ ,  $p < 0.01$ ,  $df = 25$ ), but there were differences among animals. In two of three rabbits the increase rose more slowly (Fig. 4C, circles and triangles vs. squares). There was no significant correlation between the decay time constants of version and rotation speed. At low stimulus velocities, the animals sometimes failed to return their gaze to the initial position, extending the apparent decay time constant. Excluding these extreme values ( $>30$  s), the mean decay time constant of the version was 13.8 s (*SD*: 5.5 s).

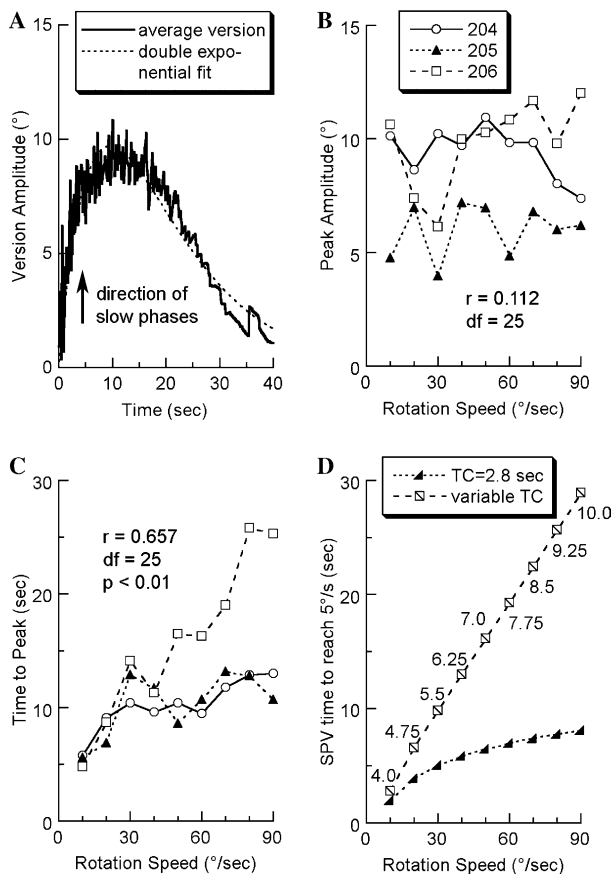


Fig. 4. (A) Superimposed average of version response to 40°/s rotation (Rabbit 204) with a double exponential fit (dotted line). Positive in the direction of the slow phases. (B) Peak amplitude of version was unrelated to the stimulus speed. The numbers in the inset indicate the symbols used for each animal. (C) Time to peak version re-stimulus speed. (D) Estimated time for the slow phase velocity to decay to 5°/s (time constant: 2.8 s, filled triangles; variable time constant: squares).

We questioned whether there was a relationship between the peak version and the level of slow phase eye velocity at which it occurred. The decay profile of the nystagmus slow phase velocities of each rabbit was simulated as a single exponential curve with a gain of unity relative to the stimulus velocity, and the time over which this exponential decayed to a threshold velocity was compared with the average time to reach peak version in the experimental data. Threshold velocities were chosen from values below 10°/s because this was the maximum slow phase velocity attained at the lowest stimulus velocities. For 206, the time constant of the slow phase velocity decay was varied linearly from 4 to 10 s for rotations from 10°/s to 90°/s (cf. Fig. 2C, panel b, triangles). In this case, there was an essentially linear increase in time to reach the threshold velocity for stimulus speeds of 10°/s and above (Fig. 4C, squares, vs. D, “variable TC,” shown for the threshold velocity of 5°/s). For rabbits 204 (right) and 205, the slow phase velocity decay time constants were invariant across stimulus velocities (2.8 s). For these animals, the time for the slow phase velocity to fall increased logarithmically as a function of stimulus speed, approximating the time increases in the experimental data (Fig. 4C, 204, 205, vs. D, “TC 2.8 s,” shown for the threshold velocity of 5°/s). Smaller or larger threshold values decreased or increased the time to reach the threshold values but did not change the dynamics. This suggests that the peak version was attained when the slow phase velocity had fallen to a threshold value during the decay.

#### 4. Discussion

The major finding of this study was that there is an asymmetry in slow phase eye velocity of the rabbit in response to angular rotation in darkness. The eye moving in the temporal-to-nasal direction has a higher velocity than the eye moving naso-temporally. Additionally, the rabbits’ eyes converge and pitch down during angular rotation in darkness. The dynamics of the vergence and pitch were similar for different rotational velocities, but the magnitudes increased with increases in the velocity of rotation. Vergence and pitch rose and fell more slowly than the slow phase velocity induced by the same stimulus, suggesting that they were produced by different vestibulo-oculomotor subsystems. Finally, there was a sustained shift of the eyes in the slow phase direction that outlasted the induced slow phase eye velocity.

The finding that there is a temporal-to-nasal preponderance of eye velocity in the rabbit in response to angular rotation in darkness has not been reported before to our knowledge, but is consistent with a similar asymmetry in eye movement in the goldfish in response to rotation with steps of velocity (Pastor et al., 1992). There is also an asymmetry in the aVOR of the squirrel monkey in response to high velocity sinusoidal stimulation (Paige, 1983). As in the other animals, the eye moving from temporal to nasal had a higher velocity than the reverse. Thus, an asymmetry

in the velocities induced in the two eyes by the aVOR appears to be widely distributed across species, although it is more apparent in lateral-eyed species.

The rabbit has a well-known temporal-to-nasal preponderance of eye velocity in response to optokinetic stimulation, which is more prominent at higher stimulus velocities (Collewijn & Noorduyn, 1972). It is possible to link both visually- and vestibularly induced asymmetries functionally. As the head turns, the VOR drives the eyes in the compensatory direction to stabilize the position of the eyes in space. For head rotation to the left, for example, the left eye, which leads into the direction of rotation, has a temporal-to-nasal movement to the right. The asymmetry that we have demonstrated in this report would enhance the gain of this movement over the nasal-to-temporal movement of the right eye. If the gain of the VOR were less than unity, there would also be slip of the visual surround on the retina to the right. This would produce a rightward OKR in which the temporal-to-nasal movement of the left eye would have a higher gain than the nasal-to-temporal movement of the right eye. Thus, the combined visual–vestibular effect would be to enhance the compensatory velocity of the eye leading into the direction of turning, so that eye would be better able to “see” in the direction of the head turn. This would be particularly valuable for the rabbit, where there is a much smaller area of binocular overlap than in frontal-eyed animals. A similar interaction of activity evoked by the vestibular and visual systems during head rotation in light is present in the activity of ‘vestibular only’ (VO) neurons in the rostral medial vestibular nuclei of the rhesus monkey (Waespe & Henn, 1977), but there was no indication that this produced an asymmetry in the velocity of the two eyes, as in the rabbit.

An asymmetry in the optokinetic response of the two eyes has also been reported in cats and monkeys after lesions in the visual cortex, presumably due to an inherent asymmetry in the subcortical visual system (Wood, Spear, & Braun, 1973; Zee, Tusa, Herdman, Butler, & Gücer, 1987). A similar asymmetry also occurs in cats whose eyes are patched before the critical period (Cynader, 1985), and in humans with strabismus (Schor & Westall, 1984). Presumably, cortical control of the nucleus of optic tract and the accessory optic nuclei in frontal-eyed animals allows symmetrical OKR during either monocular or binocular stimulation (Distler & Hoffmann, 1993). A difference in the movement of the two eyes related to visual input in the strabismic subjects is not matched by an asymmetry in the response to vestibular input, however (Fetter, Zee, & Proctor, 1988; Flandrin, Courjon, Orban, & Sprague, 1992; Schor & Westall, 1984; Tusa, Mustari, Burrows, & Fuchs, 2001). In contrast, an asymmetry in eye velocity is a normal condition for the rabbit for both visually- and vestibularly induced responses.

A significant finding was that vergence and pitch movements accompanied each rotation about a vertical axis in darkness. Concurrent vergence and pitch were first described in the rabbit by Lorente De Nó (1932) in

response to tilt relative to gravity. Baarsma and Collewijn (1975) showed that pitch is produced by forward linear acceleration, and vergence occurred when rabbits moved forward in space (Zuidam & Collewijn, 1979), but vergence and pitch have not been previously noted in response to pure angular acceleration in yaw about a vertical axis. The neural subsystem producing vergence in the primate is different from that which is involved in generating slow phase velocity or saccades (Dodge, 1903; Zhang, Mays, & Gamlin, 1992). Thus, it is not surprising that vergence might have different dynamics from the subsystem generating slow phase velocity. It is not known whether the rabbit has a high frequency vergence response ( $>1$  Hz) to linear acceleration, but it has substantial convergence to frequencies below 0.33 Hz (Lorente De Nó, 1932; Maruta et al., 2005). There were strong similarities between pitch and vergence: the two occurred together in response to naso-occipital linear acceleration and to dynamic pitch about a spatial horizontal axis, they had similar dynamics, and similar sensitivities during vertical axis rotation (pitch,  $0.08^\circ$  per  $^\circ/s$ ; vergence,  $0.07^\circ$  per  $^\circ/s$ ). Taken together, it is likely that the subsystems producing vergence and pitch are linked in the rabbit and are separate from that which produces slow phase velocity.

The low frequency characteristics of the vergence and pitch suggest that the eyes were orienting in response to angular acceleration. If correct, this broadens the concept of ocular orientation, which is usually associated with alignment to gravito-inertial acceleration (Cohen et al., 2001). The vergence and pitch movements were not directionally sensitive since they were the same whether the animals were rotating to the right or left. What could be the functional significance of these ocular orientation mechanisms during rotation? One possibility is that both pitch and vergence contribute to changes in the direction and extent of the binocular visual overlap. At rest, each monocular field extends medially over the midline by  $12^\circ$ , giving a binocular overlap of  $24^\circ$  in the horizontal plane directly in front of the animal (Fig. 5A) and an overlap of  $30^\circ$  directly overhead (Fig. 5B). Rotation at  $60^\circ/s$  evoked  $2^\circ$  of ocular adduction in each eye ( $4^\circ$  of vergence) and  $5.4^\circ$  of conjugate pitch. The vergence and downward pitch would increase the binocular overlap directly in front of the animal in the horizontal plane by about 25%, from  $24^\circ$  to  $30^\circ$  (Fig. 5C) and would give better visual acuity of the ground in front of the animal when it turns its head or moves in a circular pattern (Fig. 5D). This change in the binocularity of the visual field is consistent with the expansion of ganglion cell density in the posterior part of the visual streak (Hughes, 1971) and the larger area of representation of binocularity in the visual cortex than would be predicted by overlap of the visual fields of each eye in the freeze position (Van Sluyters & Stewart, 1974). The rabbit is myopic in frontal portions of the visual field (De Graauw & Van Hof, 1978), but the frontal part of the visual field in the rabbit is behaviorally significant (Van Hof & Lagers-van Haselen, 1973; Zuidam &

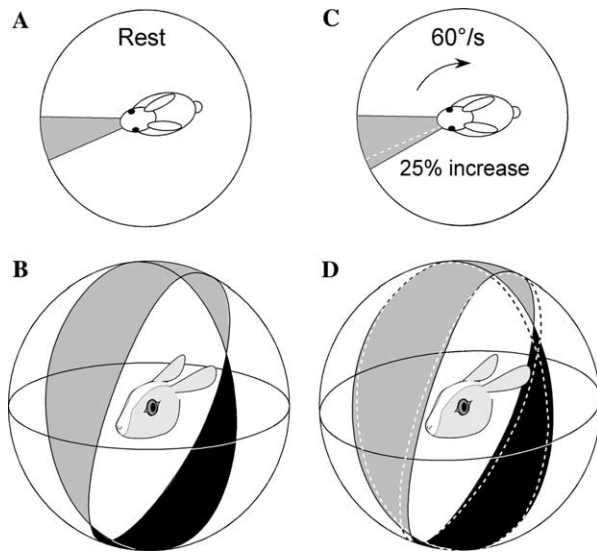


Fig. 5. Schematic binocular field of the rabbit. (A) Binocular region in the horizontal plane at rest. (B) Binocular (gray), monocular (non-shaded), and blind (black) regions at rest (adapted from Hughes, 1971). (C) Increased angle of binocular overlap in the horizontal plane during rotation. (D) The binocular overlap is increased in front of the animal and the visual streak is pitched down. The broken lines indicate the conditions at rest.

Collewijn, 1979). A mechanism that controls binocular vision in the pitch plane in the rabbit has also been suggested previously (Van der Steen & Collewijn, 1984).

The current results were taken from head-fixed rabbits. When humans or other frontal-eyed mammals move along a curved trajectory in light, there is a significant shift of the head and gaze into the direction of turning, while the slow eye velocity stabilizes gaze in space (Grasso, Prévost, Ivanenko, & Berthoz, 1998; Hicheur, Vielledent, & Berthoz, 2005; Imai, Moore, Raphan, & Cohen, 2001). In most mammalian species, a shift of the beating field of nystagmus is also in the direction of the quick phases, i.e., in the direction of turning (Chun & Robinson, 1978; Hood, 1967; Meier & Dieringer, 1993; Siegler et al., 1998; Solomon & Cohen, 1992), and is presumably an anticipatory orienting response. The rabbit makes similar anticipatory saccades during voluntary head rotation (Hughes, 1971). Were the rabbit to have a similar lead of the head into the direction of turning under natural circumstances, then the binocular overlap described here could combine with the head turn and the temporal-to-nasal preponderance in eye velocity in the leading eye to further advance visual acuity in the direction of turning.

The rabbits also had a conjugate shift of the eyes into the slow phase direction in response to rotation (Bartels, 1911; Lorente De N6, 1932). At the onset of the per- or post-rotatory nystagmus, the eyes beat across the midline, with the slow phases originating on the quick phase side. As slow phase velocity and the frequency of the quick phases declined, however, the eyes shifted into the slow phase direction. The average peak amplitude of the shift (8.4°) was not a function of the stimulus velocity, but

occurred when the slow phase velocity had decayed to  $\approx 5^\circ/\text{s}$ , i.e., when the quick phases had disappeared (Figs. 4C and D). We speculate that quick phase generation, which would oppose the slow drift of the eyes, was less in the rabbit than in frontal-eyed species, allowing for drifts into the slow phase direction. Interestingly, a slow phase velocity of  $\approx 5^\circ/\text{s}$  corresponds to the upper-limit of the effective visual stimulus velocity of on-type retinal ganglion cells, which provide primary input to the OKR (Oyster, Takahashi, & Collewijn, 1972; Simpson, 1984). Thus, the rabbit appears to be able to tolerate these retinal slip velocities from either the VOR or from OKR without generating resetting eye movements.

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