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Martin Gizzi · Theodore Raphan · Steven Rudolph
Bernard Cohen

Orientation of human optokinetic nystagmus to gravity: a model-based approach

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Abstract Optokinetic nystagmus (OKN) was induced by having subjects watch a moving display in a binocular, head-fixed apparatus. The display was composed of 3.3° stripes moving at 35°/s for 45 s. It subtended 88° horizontally by 72° vertically of the central visual field and could be oriented to rotate about axes that were upright or tilted 45° or 90°. The head was held upright or was tilted 45° left or right on the body during stimulation. Head-horizontal (yaw axis) and head-vertical (pitch axis) components of OKN were recorded with electro-oculography (EOG). Slow phase velocity vectors were determined and compared with the axis of stimulation and the spatial vertical (gravity axis). With the head upright, the axis of eye rotation during yaw axis OKN was coincident with the stimulus axis and the spatial vertical. With the head tilted, a significant vertical component of eye velocity appeared during yaw axis stimulation. As a result the axis of eye rotation shifted from the stimulus axis toward the spatial vertical. Vertical components developed within 1–2 s of stimulus onset and persisted until the end of stimulation. In the six subjects there was a mean shift of the axis of eye rotation during yaw axis stimulation of $\approx 18^\circ$ with the head tilted 45° on the body. Oblique optokinetic stimulation

with the head upright was associated with a mean shift of the axis of eye rotation toward the spatial vertical of 9.2°. When the head was tilted and the same oblique stimulation was given, the axis of eye rotation rotated to the other side of the spatial vertical by 5.4°. This counterrotation of the axis of eye rotation is similar to the “Müller (E) effect,” in which the perception of the upright is counterrotated to the opposite side of the spatial vertical when subjects are tilted in darkness. The data were simulated by a model of OKN with a “direct” and “indirect” pathway. It was assumed that the direct visual pathway is oriented in a body, not a spatial frame of reference. Despite the short optokinetic after-nystagmus time constants, strong horizontal to vertical cross-coupling could be produced if the horizontal and vertical time constants were in proper ratio and there were no suppression of nystagmus in directions orthogonal to the stimulus direction. The model demonstrates that the spatial orientation of OKN can be achieved by restructuring the system matrix of velocity storage. We conclude that an important function of velocity storage is to orient slow-phase velocity toward the spatial vertical during movement in a terrestrial environment.

M. Gizzi · T. Raphan · S. Rudolph · B. Cohen
Department of Neurology, Mount Sinai School of Medicine,
1 Gustave Levy Pl. New York, NY 10029, USA

M. Gizzi (✉)
New Jersey's Neuroscience Institute, JFK Medical Center,
98 James Street, Suite 107, Edison, NJ 08820, USA

T. Raphan
Institute of Neural and Intelligent Systems, Department of
Computer and Information Sciences, Brooklyn College,
Brooklyn, NY 11210, USA

S. Rudolph
Department of Ophthalmology, Mount Sinai School of
Medicine, 1 Gustave Levy Pl. New York, NY 10029, USA

B. Cohen
Department of Biophysics and Physiology, Mount Sinai School
of Medicine, Box 1135, 1 Gustave Levy Pl. New York,
NY 10029, USA

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Introduction

Human spatial orientation is governed by a wide variety of inputs from the visual, vestibular, and somatosensory systems (Howard and Templeton 1966; Schöne et al. 1967; Bischof 1974; Howard 1982). On Earth the vestibular system plays an important role in spatial orientation, detecting the direction of gravito-inertial vectors (Graybiel and Clark 1962; Benson 1974; Guedry 1974; Mittelstaedt 1983). Labyrinthine-defective subjects are easily disoriented in the absence of vision and cannot signal the direction of gravito-inertial forces cor-

rectly (Graybiel et al. 1968). Sensing gravity is also important for determining the height of the subjective horizon (Correia et al. 1968). Perception of the horizon shifts during centrifugation to match the combined effect of gravitational and centrifugal forces in the normal (the oculogravic illusion), even in the absence of somatosensory cues (Graybiel et al. 1968).

Perception of the orientation of external objects (Witkin and Asch 1948; Mann et al. 1949; Mittelstaedt 1986) is subject to a number of illusory effects. Tilting of the visual frame (Asch and Witkin 1948; Ebenholtz 1985, for review) or rotational visual motion (Brecher 1934; Dichgans et al. 1972; Held et al. 1975; Young et al. 1975) causes compensatory shifts in the visual vertical. Alteration of somatosensory input, either by interrupting afferent signals or by weight-loading, can cause significant shifts in the subjective vertical (Schneider and Bartley 1962). The effect of body tilt on judgement of the visual vertical or horizontal is also pronounced (Schöne 1964; Miller and Graybiel 1966; Mittelstaedt 1983).

Recently, it has been shown that gravitational information is important in determining the spatial orientation of slow phase eye velocity during optokinetic nystagmus (OKN), optokinetic after-nystagmus (OKAN; Raphan and Cohen 1988; Dai et al. 1991a,b), and vestibular nystagmus (Raphan et al. 1992) in the monkey. When animals are upright, movement of the visual field about their yaw axis gives rise to pure head- and Earth-horizontal eye velocity during OKN and OKAN. That is, the stimulus vector and eye velocity vector are aligned. When monkeys are tilted laterally into side down positions (roll tilt), vertical nystagmus appears despite optokinetic stimulation that is purely head-horizontal (Raphan and Cohen 1988; Dai et al. 1991a). Thus, the direction of the vector of the OKN velocity shifts gradually from the axis of stimulation toward the spatial vertical. During OKAN the response vector shifts further and tends to align with gravity. With forward or backward tilts (pitch tilt), torsional or roll nystagmus develops in response to the head-horizontal stimulus (Dai et al. 1991b). The appearance of vertical and/or torsional components in response to head-horizontal optokinetic stimulation has been called "cross-coupling" (Raphan and Cohen 1988; Dai et al. 1991a).

Slow-phase eye velocity during OKN and vestibular nystagmus has been modelled by two components (Cohen et al. 1977; Raphan et al. 1979; Waespe et al. 1983). A "direct" pathway generates rapid changes in eye velocity while an "indirect" pathway is responsible for the slower changes in OKN and for OKAN (Raphan et al. 1979; Waespe et al. 1983). The slow component of OKN, which is common to both the visual and the vestibular systems, has been called "velocity storage," since it stores activity related to slow-phase eye velocity (Cohen et al. 1977; Raphan et al. 1979). By generalizing the model of velocity storage to a three-dimensional dynamic system, spatial aspects can be embedded in the eigenvectors of the system matrix (Raphan and Sturm 1991). The computed direction of these vectors, which

orient the direction of OKAN, correlate well with psychophysical measures of human perception of the spatial vertical (Dai et al. 1991a,b). This suggests that these eigenvectors or "orientation vectors" may be related to the process that determines spatial orientation in humans.

Human OKN is also comprised of rapid and slow components although the rapid component predominates (Cohen et al. 1981; LaFortune et al. 1986a,b). The buildup of velocity storage during OKN has been measured by briefly placing subjects in darkness and sampling the gain of OKAN intermittently during optokinetic stimulation (Segal and Liben 1985; Tijssen et al. 1989). With this paradigm, the velocity of OKAN increases gradually over periods of 10–20 s. General characteristics of OKN and OKAN in the human are similar to those in the monkey, but parameters of the response are different. The initial jump in slow phase velocity is close to steady state velocity during OKN in humans, and OKAN does not achieve the same level as in the monkey, saturating at about 15–20°/s (Honrubia et al. 1968; Cohen et al. 1981; Jell et al. 1984; LaFortune et al. 1986a,b; Tijssen et al. 1989; Fletcher et al. 1990). The same is true for subject-vertical OKN and OKAN, where there are variable asymmetries in upward and downward slow-phase velocities (Collins et al. 1970; Schor and Narayan 1981; Baloh et al. 1983; Calhoun et al. 1983; LeLiever and Correia 1987). Time constants of human OKAN are similar to those in the monkey for full field stimuli (Cohen et al. 1977; Raphan et al. 1979; Cohen et al. 1981; LaFortune et al. 1986a,b; Fletcher et al. 1990), but they may be smaller if a restricted portion of the field is stimulated (Clement and Berthoz 1990).

Since OKAN, which is a direct measure of velocity storage, is weak in humans, it is difficult to determine the contribution of velocity storage to compensatory eye velocity during OKN. It is also unclear whether velocity storage has the same spatial orientation in the human as in the monkey. The upward component of OKN was enhanced in parabolic flight during the transition from 1.8 to 0 g, and the downward component reversed direction during the transition from 1.8 to 0 g (Clement et al. 1992). This shows that OKN eye velocity is dependent on changing gravitational fields. Whether static fields have similar effects on OKN is not clear. There is also controversy whether there is cross-coupling of human OKAN (LaFortune et al. 1989; Clement and Lathan 1991).

The purpose of this study was to determine whether there is a reorientation in the direction of OKN toward the spatial vertical in the human, as in the monkey, and whether this reorientation could be attributed to velocity storage. The latter would suggest that velocity storage makes a significant contribution to the spatial organization of visual-vestibular interaction in humans. Some of these results have been presented previously (Gizzi et al. 1992).

Materials and methods

Six adults participated in this study, three investigators (M.G., B.C., S.R.) and three subjects naive to the purpose of the study (A.Z., R.S., V.J.). None of the subjects had a history of vestibular disease. No corrective lenses were used. Every subject was tested in each condition except for R.S. (see Table 1). Tests were repeated in two subjects.

Stimulation

Optokinetic stimulation was provided by a binocular goggle system developed by M. Ehrette and A. Berthoz of the Centre National de la Recherche Scientifique; P. Simaon of the Centre National d'Etudes Spatiales and the AETA Company, Velizy, France. The subjects looked into goggles at the back of which was a belt-driven motor that presented moving 3.3° stripes. The belt velocity was measured by a tachometer, the output of which was displayed on a chart recorder and digitized for storage on disk. The stimulated portion of the field subtended an angle of approximately 88° horizontally and 72° vertically. Fresnel lenses placed in front of each eye permitted comfortable focusing, despite the nearness of the stimulus. (See Appendix B-19, Neurolab Hardware, NASA Announcement of Opportunity, AO 93-OLMSA-01 for further description.)

The orientation of the stripes could be changed by manually rotating the motor and stimulus belt on the goggles. A built-in protractor indicated the angle of stripe orientation, and the goggles were locked with a thumbscrew to maintain this angle. The stimulus velocity and orientation were set prior to each trial, and the illumination of the stripes was controlled by the computer via a digital input/output (I/O) port. Unless otherwise specified, the stimulus velocity was 35°/s. The subjects were asked to "follow the stripes" to reduce uncertainty and maximize slow-phase velocity. Each trial lasted 45 s. The lights were then extinguished, and subject remained in darkness for 30 s while any after-nystagmus (OKAN) was recorded. We also measured OKN at 20°/s and 50°/s in two subjects.

Data acquisition

Horizontal and vertical eye movements were recorded by electrooculography (EOG). Silver-silver chloride electrodes were applied lateral to each outer canthus and above and below both eyes. The vertical signals from the two eyes were added together to improve the signal-to-noise ratio. Thus, only conjugate horizontal and vertical movements of the two eyes were registered.

Cross talk between horizontal and vertical EOG channels is largely dependent on the placement of the electrodes around the eyes. We were careful to place the electrodes orthogonally to reduce the cross talk. This was checked during the calibration saccades. If cross talk was present, the electrodes were replaced. We performed horizontal and vertical saccadic calibrations on one subject with the head upright and tilted to demonstrate that ocular counter-rolling did not cause significant cross talk.

To determine the accuracy of our recording technique in signalling the vector of eye movements, we had one subject pursue a smoothly moving target with his head upright (B.C.) and one with his head tilted 45° to the left (M.G.). The target was moved sinusoidally along a straight line at angles ranging from spatially horizontal (0°) to vertical (90°) in 5° increments. The amplitude of target motion was 30° from primary position and the oscillation frequency was 0.1 Hz. Each subject tracked the target for five cycles. The horizontal and vertical eye position signals were each fit by a regression line. This regression line was subtracted from the position data to eliminate low-frequency drift. The horizontal and vertical eye positions were then plotted against each other, and a regression line was fit to the resulting scatter plot. The slope of vertical versus horizontal regression line represented the tan-

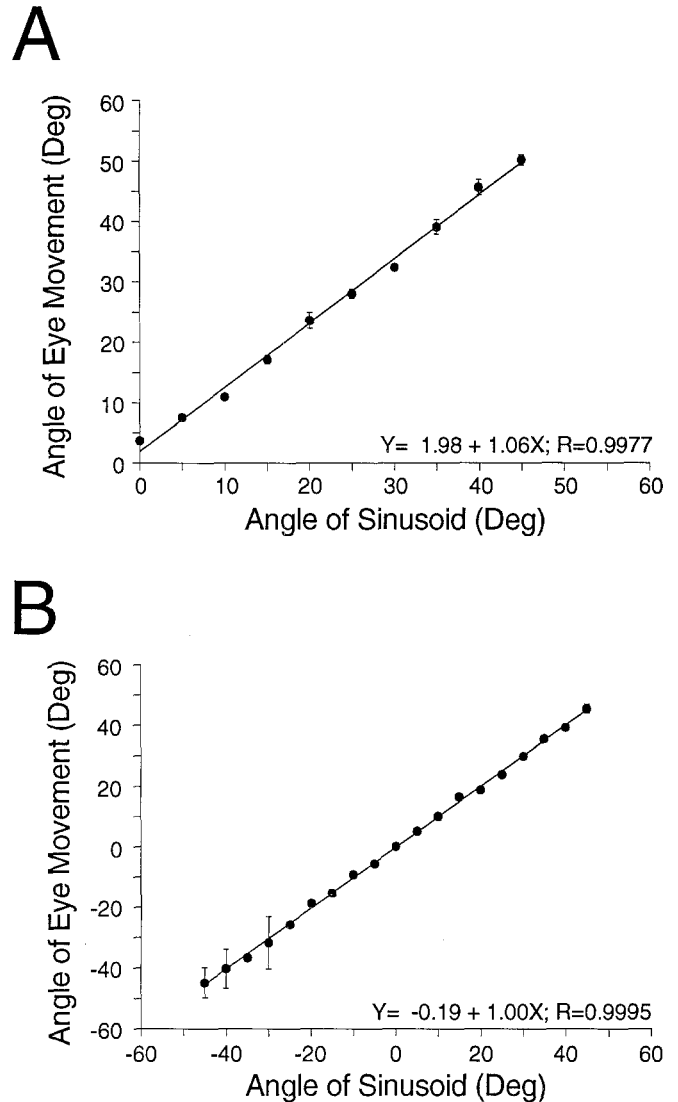


Fig. 1A, B Tracking of a spot of light at oblique angles. **A** The angle of smooth pursuit plotted versus the angle of stimulation for a subject sitting upright. The slope of the regression line was 0.99, indicating accurate tracking for angles between +45° and -45°. Differences of less than 1° could be resolved. **B** Angle of smooth pursuit versus angle of stimulation for a subject with head tilted 45° to the left. Head tilt had no influence on the accuracy of tracking. X refers to the stimulus angle, Y the response angle and R is the coefficient of correlation

gent of the angle of following. The angle of following was then plotted against each angle of stimulation.

In the head upright condition (Fig. 1A), the slope of the line representing the relationship between tracking angle and stimulation was 1.06. The angle of following had a standard error of approximately 0.2°. The angle of following matched the angle of stimulation to within 2° at up to 45° from horizontal. The resolution of angular following was therefore close to the resolution of EOG for position, which is about 0.5°. There was an offset of 1.98° reflecting either error in electrode placement or a difference between the head vertical and the stimulus vertical. With the head tilted 45° (Fig. 1B), the angle of following remained as close to the angle of stimulation as it had in the head upright condition. This indicates that our EOG recording method was sufficiently accurate for the purposes of this study and that the angle of pursuit of a two-dimensional target is unaffected by head tilt.

Torsional (roll) eye movements are not measured by EOG. Previous work on the spatial orientation of velocity storage in monkeys (Dai et al. 1991a,b) has shown that the dominant cross-coupling of OKN and OKAN was to the pitch and not to the roll axis for side down tilts. Therefore, we expected that the dominant effects in this study would be from yaw to pitch.

Eye position was calibrated every 6 min by having subjects remove the goggles and view targets presented on an 84-cm video monitor at a distance of 114 cm. High-contrast 1° square targets were presented at the central position and were sequentially displaced 10° in each direction horizontally and vertically. The values for the fixation jumps were used to scale the recordings over the next 6-min period. The optokinetic stimulator had a virtual focal distance different from the calibrating stimulus. However, because of the optics of the binocular stimulator, the stripes were presented to each eye separately, and vergence was not necessary for clear vision when following the stripes. Therefore, despite the differences in distance between the calibration and apparent optokinetic stimuli, there were no appreciable vergence differences between the two.

For the tilt conditions, subjects held their bodies upright and tilted their head 45° to either side. Head tilts were measured with a bubble clinometer that was accurate to approximately 1°. The subjects supported their head and the apparatus, which weighed 1.27 kg, when they were in the 45° head-tilted position. Since the apparatus was heavy, it contributed to damping of head movements, and there was no obvious head motion during the test. There could have been small, low-frequency variations in the an-

gle of static head tilt. Since eye velocities were measured relative to the head, however, these variations would not have affected measured eye position. Small changes in head tilt would also not cause substantial changes in horizontal to vertical cross-coupling.

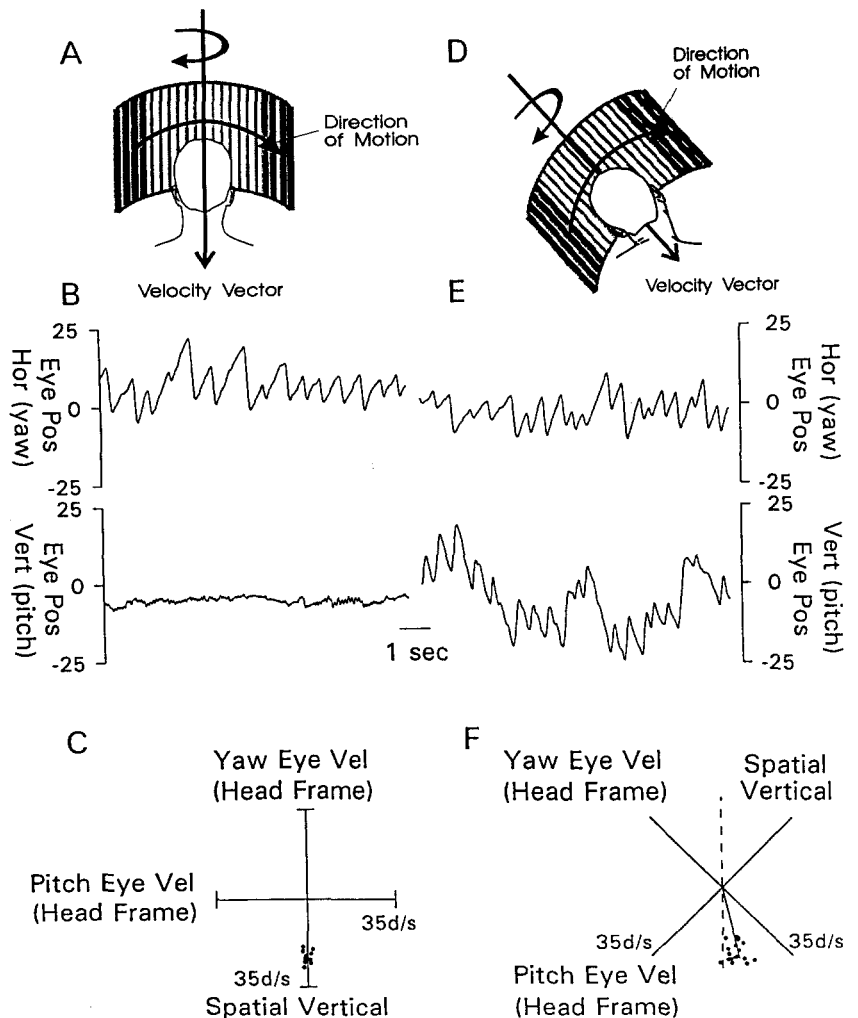
A digital computer was used to control the stimuli, take the data, and perform off-line analysis. Voltages related to eye position were recorded with a bandpass of d.c. to 30 Hz except for two subjects (S.R. and B.C.). For these, drift between calibrations made it necessary to use a low-frequency cutoff of 0.05 Hz. Eye positions and stimulus control voltages were displayed on a thermal array chart recorder, digitized at 250 samples/s and recorded on disk. The sampling rate was well beyond the Nyquist rate for the filtered signals.

Conventions for describing three-dimensional motion

Rotation of the optokinetic stimulus and the eyes are represented by axial vectors, according to a right-hand rule. For an upright subject receiving an optokinetic stimulus rotating around a head-centered axis from left to right, stimulus and eye motion are represented by a vector pointing downward along the subject's yaw axis and in space (Fig. 2A). In tilted positions, the vector of stimulus motion remains downward, along the yaw axis of the head, but is oriented at an angle with regard to the body and to the spatial vertical (Fig. 2D). A similar convention is used for eye rotations.

Fig. 2 Optokinetic nystagmus (OKN) of subject M.G. to yaw-axis optokinetic stimulation with head vertical (A-C) and head tilted left (D-F).

A,D Stimulation paradigms showing the direction of stimulus motion and its velocity vector as defined by a right-hand rule. **B,E** Horizontal (*upper*) and vertical (*lower*) eye position during visual stimulation. **C,F** The vectors of eye velocity for each slow phase over the last 10 s of OKN (*dots*) and the mean vector for the period shown (*line*). Note the tilt of the axes of eye velocity when the subject's head was tilted. (*d/s* degrees per second)



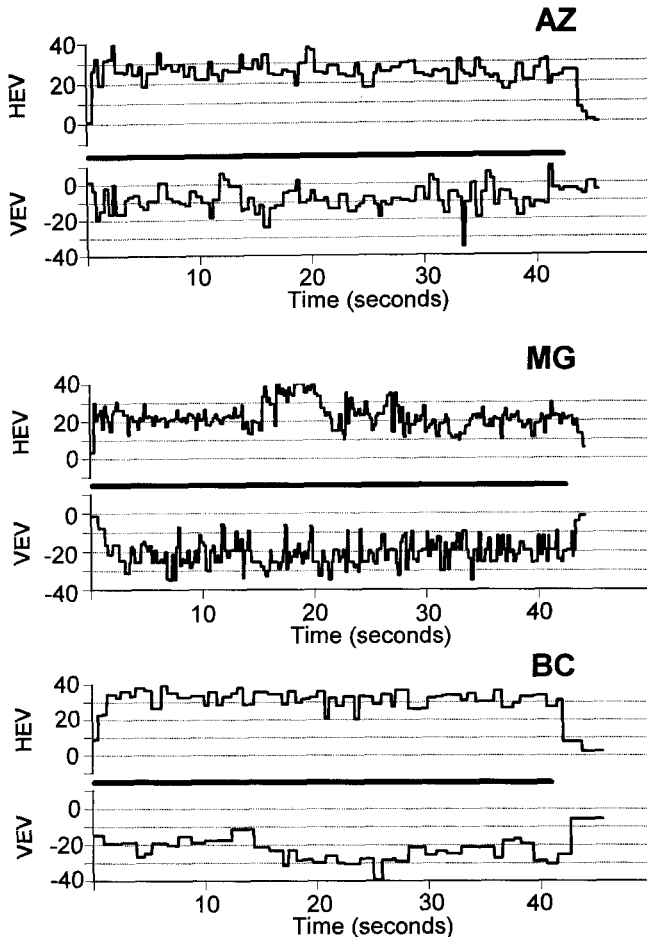


Fig. 3 Horizontal (*HEV*) and vertical (*VEV*) eye velocities induced by a head-horizontal (yaw axis) optokinetic stimulation moving at $35^\circ/\text{s}$ to the right in subjects A.Z., M.G., and B.C. A.Z. was naive to the purpose and results of the experiment. The head was tilted 45° to the left during the stimulus, causing the appearance of a prominent downward vertical eye velocity in each panel. The time of stimulation is shown by the thick horizontal bar between the horizontal and the vertical eye velocities. Eye velocities were mean values for each slow phase, derived as described in the Materials and methods. Note the rapid increase in both the horizontal and the vertical components at the onset of stimulation, the maintenance during stimulation, and the prompt fall after stimulation. There was only brief after-nystagmus at the end of stimulation

Data analysis

Data were analyzed by first identifying saccades, using a maximum-likelihood detection criterion (Singh et al. 1981). The data were then scanned on the computer terminal, and saccades missed by the program were marked by hand. Eye velocity was computed for each slow-phase by finding the slope of the best fit straight line to the sampled slow phase data, from the end of one quick eye movement to the beginning of the next, using a minimum mean square error criterion. Sample slow-phase velocities during the period of stimulation are shown in Fig. 3.

Individual horizontal and vertical slow phase velocities were averaged over a 10-s period prior to the end of stimulation. For the three sets of data in Fig. 4 we calculated the means and standard deviations of the slow-phase velocities for each of the 10-s epochs from 5 to 15 s, 15 to 25 s, 25 to 35 s, and 35 to 45 s as well as for the entire 45-s period. Variances between epochs were not significantly different, using an *F*-test at 0.1 significance. Using a

t-test at 0.1 significance, the mean of the last epoch was not significantly different from that of the entire epoch for any of the subjects. We chose the last ten seconds because they were representative of the entire period, and we could be reasonably certain that velocity storage had reached a steady state condition (in humans it is difficult to estimate the charging time of velocity storage from OKN data because of the large direct pathway gain). Using the average horizontal and vertical eye velocities as components of a two-dimensional vector, the average eye velocity response vector was computed, consistent with the methods of circular statistics (Batschelet 1981).

The Student's *t*-test was used to calculate significance measures of the rotation of the mean response vector relative to the stimulus vector. An *F*-test was performed on the ratio of the variances of the shift in the axis of eye velocity for different conditions to determine whether they were significantly different from each other. Significant differences ($P > 0.05$) would exclude use of the *t*-test as a basis for comparing the shifts in the mean stimulus and response vectors (Mendenhall 1971). Under these circumstances an analysis of variance (ANOVA) was used for comparison.

Results

Yaw-axis OKN

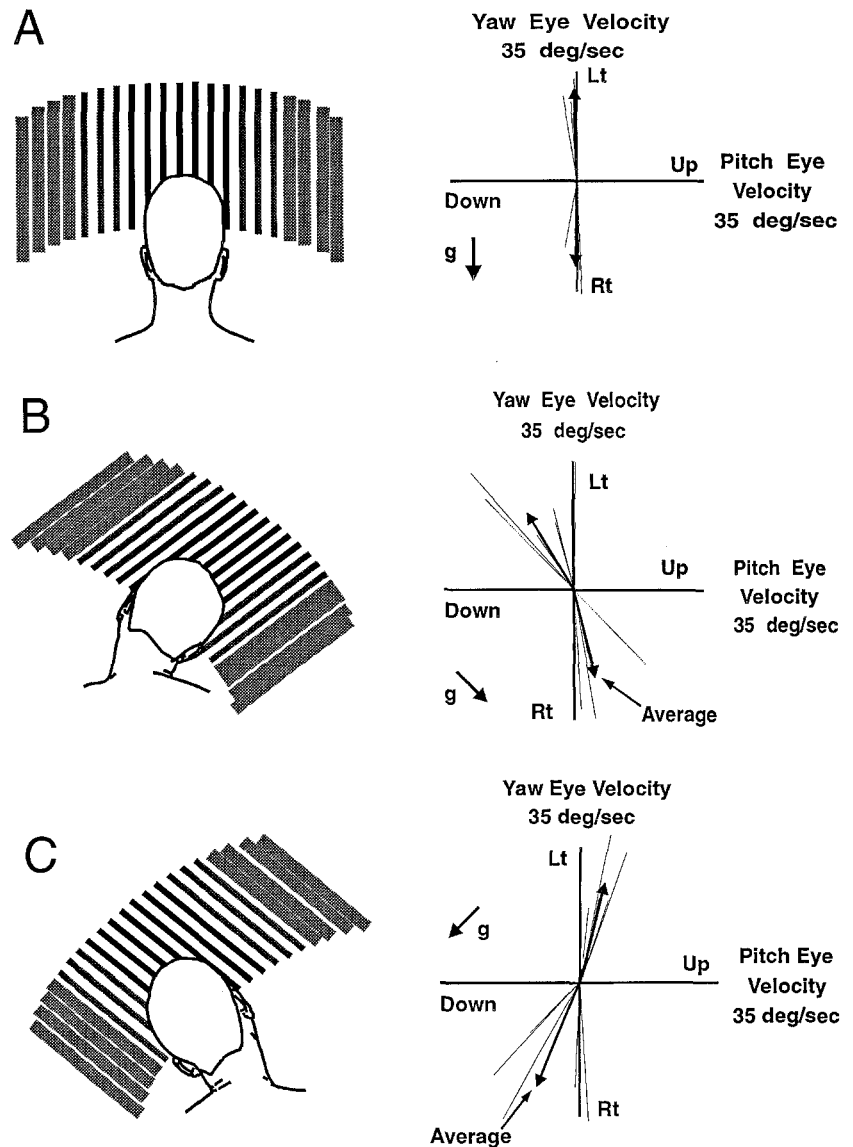
Head upright

Optokinetic stimulation at $35^\circ/\text{s}$ about a vertical axis to the right with the head upright (Fig. 2A) resulted in compensatory OKN with a mean rightward slow-phase eye velocity of $28^\circ/\text{s}$ in subject M.G. (Fig. 2B). The vector of slow-phase velocity of each beat of nystagmus during the last 10 s of the response was close to the vertical axis (dots, Fig. 2C), with the mean vector over this time being within 1° of the stimulus direction. For the six subjects the mean vector of eye velocity was within 0.5° of the spatial vertical (Fig. 4A). The standard deviation of these vectors was 1.5° , with a maximal deviation of 9° . Using a *t*-test, the 12 measurements of yaw-axis OKN were not significantly different from the stimulus axis ($t = 0.42$, $df = 11$, $P > .1$). The mean eye velocity during OKN was $28.7^\circ/\text{s}$, corresponding to a gain of 0.82. There was no asymmetry between left and right nystagmus.

Head tilted

When the head was tilted 45° left side down relative to the body and the same, right yaw-axis OKN stimulus was given opposite to the direction of head tilt (Fig. 2D), there was a downward vertical (pitch) component of slow phase eye velocity during OKN (Fig. 2E). The mean vector of the eye velocity of the nystagmus was 40° relative to the subject vertical axis, bringing it close to the spatial vertical (dashed line, Fig. 2F). Vertical eye velocity developed within 1–2 s after stimulus onset with the head tilted, and both horizontal and vertical components were maintained for the duration of stimulation (VEV, Fig. 3). Thus, despite variations in slow-phase eye velocity, the axis of eye rotation deviated early in stimulation and persisted at a fairly constant level. A few

Fig. 4A–C Effect of head tilt on yaw-axis optokinetic nystagmus (OKN). Each plot contains data from six subjects and includes the results from the two directions of stimulus motion. The axes of rotation for each figure are in a head coordinate frame of reference. The spatial vertical is shown by g . The length of the axis from the origin in each direction corresponds to $35^\circ/\text{s}$. Response means are shown as *thick lines with arrowheads*. **A** In the head-vertical condition the response was along the stimulus axis. **B** With the head tilted right the response axis shifted counter-clockwise toward the spatial vertical. **C** With the head tilted left the response axis shifted clockwise toward the spatial vertical



beats of OKAN were present at the end of stimulation, but both horizontal and vertical eye velocity decayed rapidly and had short time constants (1–2 s). None of the subjects had significant circular vection during or after stimulation, probably due to the limited visual field that was stimulated.

Head tilts to the right of 45° with *leftward* stimulation induced a *downward* component of eye velocity. The mean vector was tilted from the head's yaw axis toward the spatial vertical by 26° (Fig. 4B, upper left). *Rightward* stimulation induced an *upward* component of eye velocity with the head tilted right, and the vector shifted 14° toward the vertical (Fig. 4B, lower right). While there were individual variations in the amount of shift toward the spatial vertical, only one of six subjects had eye velocity that remained close to the yaw axis of the head.

For head tilts of 45° to the left, there was a similar shift of the mean eye velocity vector to the spatial verti-

cal by approximately the same angles, although the direction of the cross-coupling was inverted. *Rightward* slow-phase velocity induced *downward* eye velocity and shifted the vector by 21° (Fig. 4C, lower left). *Leftward* slow-phase velocity induced *upward* eye velocity with a vector shift of 11° (Fig. 4C, upper right).

Thus, the mean vector of eye velocity of the six subjects had a spatial component that tended to align eye velocity with the spatial vertical. The mean shift in the eye velocity vector as a function of head tilt was 23.5° for downward eye velocity and 12.7° for upward eye velocity. Considering the upward and downward vectors together, the mean shift was 18.0° . The axis of eye rotation for all conditions was significantly different from the axis of stimulation ($t = 5.324$, $df = 23$, $P < 0.001$).

An F -test performed on the ratio of the variances of the shift in the axis of eye velocity for the head-tilted and upright conditions showed that they were significantly different from each other at a 0.05 significance level.

Table 1 Horizontal and vertical gains of head-horizontal (yaw) and head-vertical (pitch) optokinetic nystagmus with the head upright and tilted left and right for each stimulus condition. Stimulus velocity was 35°/s in each instance. Subject R.S. became nauseated, and we were unable to obtain data for the upward vertical gain in the head-upright and -tilted positions. Differences in horizontal gain between the head-upright and -tilted conditions were statistically significant ($t=2.727$, $df=34$, $P<0.01$)

Subject	Horizontal Gain						Vertical Gain					
	Head Upright		Head Left		Head Right		Head Upright		Head Left		Head Right	
	Left	Right	Left	Right	Left	Right	Up	Down	Up	Down	Up	Down
A.Z.	1.03	0.77	0.72	0.52	0.33	0.47	0.77	0.85	0.58	0.54	0.55	0.49
M.G.	0.75	0.93	0.78	0.97	0.59	0.71	1.11	0.86	1.28	1.14	1.03	1.33
S.R.	0.70	0.94	0.40	0.63	0.50	0.43	0.49	1.12	0.42	1.55	0.38	1.35
R.S.	0.88	0.72	1.03	0.61	0.93	0.53	—	0.80	—	0.88	—	0.85
V.J.	0.83	0.88	0.56	0.42	0.55	0.56	0.67	0.53	0.52	0.49	0.67	0.68
B.C.	0.98	0.90	1.03	1.10	0.99	0.80	0.58	0.86	0.85	0.76	0.76	1.00
Mean	0.86	0.86	0.75	0.71	0.65	0.58	0.72	0.84	0.73	0.89	0.68	0.95

Table 2 Horizontal and vertical eye velocity as a function of yaw-axis stimulus velocity, head tilted 45° and upright. Rightward and leftward responses were averaged for the head-upright conditions. The conditions giving rise to upward cross-coupling (head left - motion left and head right - motion right) were averaged, as were those giving rise to downward cross-coupling (head left - motion right and head right - motion left)

	Stimulus Velocity		
	20°/S	35°/S	50°/S
Head upright			
□ Horizontal eye velocity (°/s)			
Subject B.C.	13.1	29.0	42.8
Subject M.G.	19.2	32.5	49.8
□ Vertical eye velocity (°/s)			
Subject B.C.	-0.6	-1.7	-2.3
Subject M.G.	-1.0	-1.1	+1.3
Head tilted 45° to induce upward eye velocity			
□ Horizontal eye velocity (°/s)			
Subject B.C.	18.9	32.4	46.3
Subject M.G.	17.2	25.9	32.3
□ Vertical eye velocity (°/s)			
Subject B.C.	5.9	11.0	12.1
Subject M.G.	6.4	17.9	14.3
Head tilted 45° to induce downward eye velocity			
□ Horizontal eye velocity (°/s)			
Subject B.C.	18.4	36.1	46.9
Subject M.G.	14.7	27.1	36.0
□ Vertical eye velocity (°/s)			
Subject B.C.	6.3	17.7	19.2
Subject M.G.	6.5	19.6	13.8

Thus, a t -test could not be used to compare the mean axes of rotation in the head-upright and head-tilted conditions (Mendenhall 1971). An ANOVA on the means of the two distributions indicated that the axis of eye rotation with the head tilted (Fig. 4B,C) was significantly different from that in the upright condition (Fig. 4A), despite scatter in the data ($F=21.19$, $df=2$, $P<0.0001$).

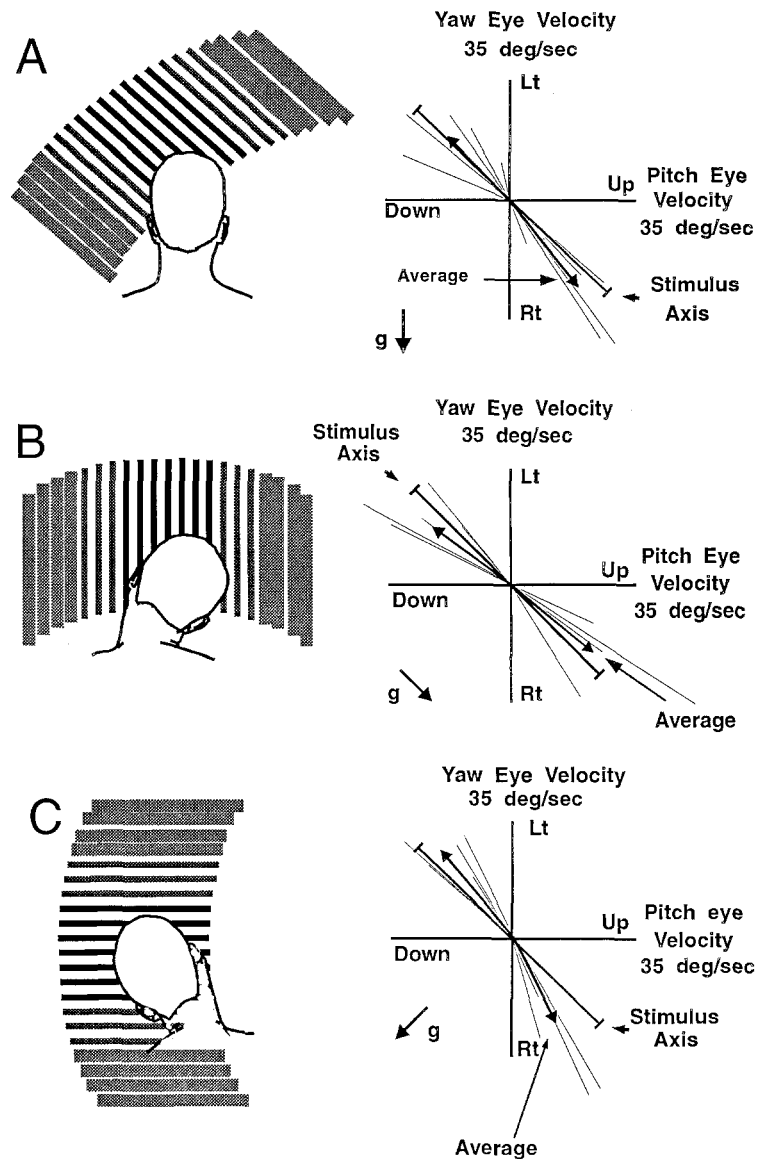
To determine how the vertical and horizontal components were altered individually by head tilt, we calculated the horizontal and vertical gains for pure head-horizontal (yaw) and head-vertical (pitch) optokinetic stimulation in head-upright and head-tilted conditions (Table 1). There was interindividual variation, but when the values for head-tilt right and left were combined, the mean gain of yaw slow-phase velocity was reduced from

a mean of 0.86 in the head-upright position to 0.67 in the head-tilted positions. This was a statistically significant difference ($t=2.727$, $df=34$, $P<0.01$). Thus, a decreased horizontal component, as well as the development of a vertical component, contributed to the shift in the angle of slow-phase velocity toward the spatial vertical when the head was tilted.

Mean gains for pitch slow-phase eye velocity were asymmetric with the head upright, downward eye velocity being greater than upward eye velocity. The gain of upward slow-phase velocity did not increase (0.72 vs 0.71) with the head tilted 45°. There was a slight increase in downward gain (0.84 vs 0.92), but the difference was not statistically significant.

We also determined whether the vertical component of eye velocity increased as a function of yaw-axis stim-

Fig. 5A–C Oblique optokinetic nystagmus (OKN) with the stimulus moving up and right or down and left relative to a head coordinate frame. Gravity and the spatial vertical were (g) aligned with the head when upright and were located at 45° when the head was tilted. **A** Head upright. Data from six subjects with the mean vectors shown as *thick lines*. The stimulus axes are indicated by *short bars*. Although shifted slightly toward the spatial vertical, the response axes were close to the stimulus axes. **B** With the head tilted right, the mean response axis shifted to the opposite side of the stimulus axis, i.e., opposite the direction of head tilt. **C** With the head tilted left the response axis shifted further clockwise



ulus velocity with the head upright and in tilted positions in two subjects (Table 2). When the head was upright, there was a maximum shift of 3° of the eye velocity vector over the full range of stimulus velocities. With the head tilted, the vertical component increased when the yaw axis stimulus velocity rose from 20 to 35°/s for the two subjects. When stimulus velocity was further increased to 50°/s, vertical eye velocity saturated, although the horizontal component rose proportionately. As a result, the shift of the eye velocity vector toward the spatial vertical was reduced at the higher stimulus velocity. This suggested that the vertical component was driven from a horizontal component that had saturated, similar to the characteristics of velocity storage in humans.

Oblique OKN, head upright and head tilted

Oblique movement of the visual field relative to the head activates both horizontal and vertical eye velocity. In the monkey the characteristics of velocity storage are different for pitch- and yaw-axis velocity, with the head upright; pitch-axis OKAN has a lower gain and shorter time constant than yaw-axis OKAN (Matsuo and Cohen 1984; Raphan and Cohen 1988; Dai et al. 1991a). As the head is tilted toward 90° in roll, the gain and time constant increase for pitch OKAN and decrease for yaw OKAN. Thus, if velocity storage was contributing to the spatial orientation of OKN, there would be effects of gravity on oblique OKN both in the head-upright and -tilted conditions.

With the head upright we induced nystagmus by optokinetic stimulation at an angle 45° relative to the head yaw axis. There was a significant shift in the mean direction of nystagmus from the stimulus axis toward the

spatial vertical. Individual variations in the axis of eye rotation from the 45° stimulus direction were greater than for stimuli that were oriented along the yaw axis (compare Figs. 4A and 5A). Taking the conditions of Fig. 5A together (stripes moving up and right, and down and left), there was a mean axis shift of 7.5° ($t = 1.79$, $df = 11$, $P > 0.1$). For the opposite oblique – up and left, or down and right – there was a mean axis shift of 10.9° ($t = 2.62$, $df = 11$, $P < 0.05$). Combining the data, there was a significant shift toward the spatial vertical of 9.2° ($t = 3.22$, $df = 23$, $P < 0.01$).

Oblique optokinetic stimulation with respect to the head produces a spatially horizontal or vertical stimulus when the head is tilted with respect to gravity (Fig. 5B,C). In contrast to the head-vertical condition where the shift in eye velocity axis was toward the spatial vertical, in the head tilted condition there was a shift of the axis of eye rotation in the direction opposite to the direction of head tilt. For instance, in the head vertical condition (Fig. 5A) the response vectors were shifted 7.5° *clockwise* relative to the stimulus (see above); with the head tilted right (Fig. 5B) the vectors shifted about 12° *counterclockwise* relative to the stimulus, which was aligned with the spatial vertical (compare “Average” with “Stimulus Axis” in Fig. 5B). With the head tilted left, the amount of *clockwise* shift was 12.4°, which was about 5° more than for the head-vertical condition (Fig. 5C). For all directions of stimulation, there was a mean shift of 5.4° of the vector of eye velocity across the midline. An ANOVA performed on the data shown in Fig. 5 confirmed a significant effect of head tilt ($F = 12.544$, $df = 2$, $P < 0.001$) on the orientation of the eye velocity vector. For an oblique stimulus in the opposite direction, there was a similar effect ($F = 5.33$, $df = 2$, $P < 0.01$).

Thus, cross-coupling from the horizontal shifted the axis of eye rotation toward the spatial vertical when the head was upright. In addition, it produced a larger shift in the axis of eye rotation during oblique stimulation with the head tilted. The shift of the eye velocity vector across the spatial vertical is similar to the effects of head tilt on perception of the spatial vertical when subjects are tilted, the “Müller effect” or “E effect” (Müller 1916).

Modelling the OKN response with regard to gravity

Description and assumptions

The three-dimensional model of the spatial orientation of OKN and OKAN in the monkey (Raphan and Sturm 1991; Raphan et al. 1992) was used as the basis for the model of the human response shown in Fig. 6. We assume that the velocity storage integrator is composed of elements that code information in semicircular canal coordinates with a fixed transformation to head coordinates. Under certain circumstances these elements produce ocular velocity responses and after-responses that are not aligned with the stimulus in three-dimensional

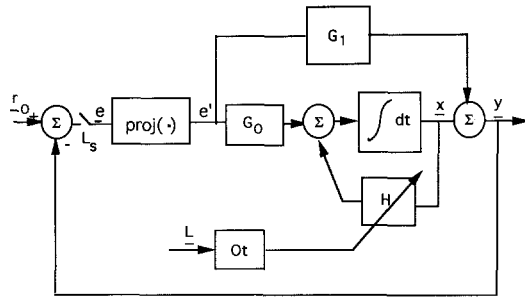
space. Thus, there must be interconnections between these various elements in order to realize the response of the integrator in three dimensions. The parameters of the **H** matrix represent the interconnections between states of the velocity storage integrator whose output components represent velocity commands to the oculomotor system along pitch, roll, and yaw directions of the head. The parameters of the **H** matrix change with gravity so as to cause an orientation of the eye velocity response to be associated with three specific vectors called eigenvectors.

When the eigenvectors are represented in the coordinate frame of the head, which is the output of the velocity storage integrator, they generate a skewed coordinate frame that is responsible for the cross-coupling. Thus, the eigenvectors of the system matrix can be viewed as orientation vectors generated by the parameters of the interconnection matrix, **H**. These are mapped by the dynamical system to the coordinate frame for eye velocity generation, i.e., the canal or head frame. In short, it is a way of mapping a geometry created by interconnection parameters to a spatial geometry.

Although the model structure was identical to that used for the monkey (Raphan and Sturm 1991; Dai et al. 1991a), there were several important differences between them. Eigenvalues, the diagonal elements of the **H** matrices, had relatively large values in the human model, reflecting the short time constants of OKAN elicited with the binocular goggles. In the monkey, time constants of OKAN were large, and the eigenvalues were almost an order of magnitude smaller for both the upright and tilted conditions.

Retinal slip was also processed differently. In the monkey, vertical eye velocity was largely suppressed during yaw-axis OKN in tilted positions (Dai et al. 1991a). Therefore, retinal slip was obtained by subtracting gaze velocity (eye velocity in these studies) from surround velocity. Vertical components were more prominent in human OKN, suggesting that there was little suppression along directions orthogonal to the stimulus. Therefore, only retinal slip along the stimulus direction was considered in the simulations, and retinal slip along an orthogonal direction was set equal to zero. The retinal slip processing is represented by the projection operator ($\text{proj}(\cdot)$), and mathematically described by the equation below the model in Fig. 6.

Because OKAN was short and difficult to measure in these experiments, parameters used in the simulations were estimated from observation of the data and from assumptions about their relationship derived from experiments in the monkey (Raphan and Cohen 1988; Dai et al. 1991a). Eigenvalues for the upright condition were taken as -2.0 for pitch and -0.4 for yaw. This corresponds to a more rapid fall in pitch than yaw eye velocity at the end of OKN (approximate time constants of 0.5 s in pitch and 2.5 s in yaw). The eigenvectors in the upright condition are along the body axis and are represented by a diagonal **H** matrix. In tilt the pitch eigenvalue was reduced to 1.5, while the yaw axis eigenvalue was



$$e' = \left\langle r_0 - y, \frac{r_0}{\|r_0\|} \right\rangle \frac{r_0}{\|r_0\|} \cdot L_s$$

MATRICES FOR HEAD UPRIGHT

$$G_1 = \begin{bmatrix} 3.2 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 1.2 \end{bmatrix}$$

$$G_0 = \begin{bmatrix} 0.8 & 0 & 0 \\ 0 & 0.8 & 0 \\ 0 & 0 & 0.8 \end{bmatrix}$$

$$H = \begin{bmatrix} -2.0 & 0 & 0 \\ 0 & -1.0 & 0 \\ 0 & 0 & -0.40 \end{bmatrix}$$

MATRICES FOR HEAD TILT

$$G_1 = \begin{bmatrix} 3.2 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 1.2 \end{bmatrix}$$

$$G_0 = \begin{bmatrix} 0.8 & 0 & 0 \\ 0 & 0.8 & 0 \\ 0 & 0 & 0.8 \end{bmatrix}$$

$$H = \begin{bmatrix} -1.5 & 0 & 1.07 \\ 0 & -1.0 & 0 \\ 0 & 0 & -0.75 \end{bmatrix}$$

Fig. 6 A model of optokinetic nystagmus (OKN) and optokinetic afternystagmus (OKAN; adapted from Raphan and Sturm 1991). The optokinetic input is r_0 . Eye velocity y is subtracted from r_0 to give retinal slip e , which becomes zero when the lights are extinguished by opening switch L_s . Retinal slip is projected onto stimulus direction ($proj(\cdot)$) to generate a signal e' . This activates a coupling matrix to the velocity storage integrator G_0 , as well as activating the direct pathway given by matrix G_1 . The state of velocity storage x summates with the signal coming over the direct pathway to produce eye velocity y . The velocity storage matrix H is controlled by otolith input O_t , which modifies the eigenvalues and eigenvectors. The matrices G_1 , G_0 , and H for head upright and for head tilt used for the simulations are shown below the model. The equation describes the transformation imposed by the projection operator

increased to 0.75, corresponding to an increase in the pitch and a decrease in the horizontal time constants (Raphan and Cohen 1988; Dai et al. 1991a).

The yaw eigenvector used to simulate the data in tilt was taken as 10° opposite the head tilt. This represents a Müller or E effect approximately equal to the shift in the axis of eye velocity in the monkey (Dai et al. 1991a) and to the perception of the vertical in humans (Schöne 1964; Middlestaedt 1986). The parameters of the velocity storage integrator were chosen as 0.8, based on an initial maximum OKAN velocity of ≈ 10 – $18^\circ/s$. The direct pathway gains were chosen as 3.2 for pitch and 1.2 for yaw, so as to give an overall gain of 0.78 for vertical and 0.77 for horizontal during OKN when the subject was upright and the stimulus was given in a pure vertical or pure horizontal direction, respectively (Table 1). The direct pathway gain matrix was the same in the tilted condition as it was in the upright. Because of the changes in the eigenvalues and the manner in which the retinal slip

was processed producing cross-coupling, however, the yaw gain was reduced to 0.7 for pure horizontal stimulation in the tilted condition. The vertical gain was maintained at 0.79 for this condition. These parameters produced an overall shift of 18° of the axis of rotation when the head was tilted, consistent with the experimental data.

Simulations

During OKN with the head upright (Fig. 7A), both the direct and indirect pathways contributed to total eye velocity, and there was no pitch eye velocity. Yaw eye velocity had an immediate jump to approximately 85% of the final value. This was followed by a slower rise to the steady state level of $27^\circ/s$, producing a gain of 0.77. The component due to velocity storage (INT) rose to $16^\circ/s$. The time constant of rise was identical to the rise of the integrator response. At the end of the response, eye velocity fell rapidly over the time course of the integrator. (The difference between total eye velocity and the contribution of the velocity storage integrator is the output of the direct pathway.) There was no vertical component. When a pure pitch stimulus was given (Fig. 7B), the steady state velocity was again $27^\circ/s$, giving the same gain, but the integrator only rose to $3^\circ/s$ because of its very small time constant. There was no horizontal component.

For oblique stimulation with the head upright (Fig. 7C), the model predicted a rotation of the eye velocity vector toward the spatial vertical of 14° . There was an initial overshoot in the vertical component, which then decayed to a steady state level of $\approx 14^\circ/s$. The integrator was only charged to about $2^\circ/s$ along the pitch axis. This is in contrast to the integrator contribution to the pitch axis during simulations with the head tilted (Fig. 7D,E) where the pitch time constant was longer and contributed more to the response characteristics.

For yaw-axis stimulation with the head tilted (Fig. 7D), there was a pitch eye velocity of $\approx 8^\circ/s$. The vertical component built up with a time constant consistent with the pitch eigenvalue, since it was not suppressed by either visual feedback or the direct pathway. While the integrator components of the response were consistent with a rotation of the eigenvector of 55° , the contribution of the direct pathway (difference between total eye velocity and the velocity storage integrator) to the horizontal component of eye velocity caused a rotation of the orientation of OKN of only 18° . The direct pathway did not contribute to the pitch response because there was no retinal slip in that direction.

Oblique stimulation with the head tilted (Fig. 7E), caused both a direct and an indirect horizontal and vertical component. The result was that the axis of eye rotation shifted across the spatial vertical by 5.2° , consistent with the data.

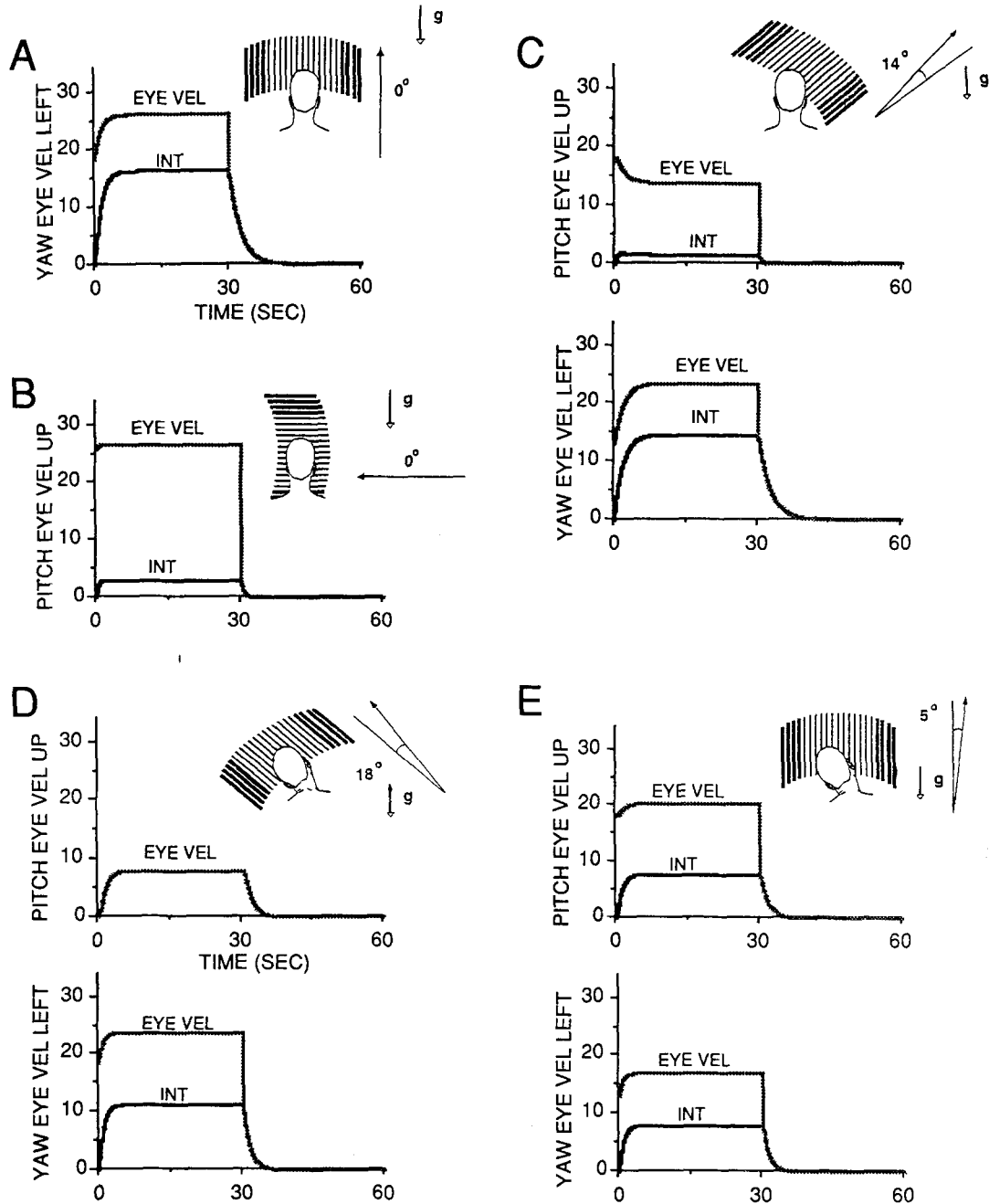


Fig. 7 A Model simulation of yaw axis stimulation with the head upright, with a $35^\circ/\text{s}$ stimulus. The corresponding experimental situation is shown in the *insert*, demonstrating head orientation and stimulus orientation. Adjacent are plotted the axis of stimulation (*line*) and the eye velocity vector (*arrow*). The angular difference between them is indicated. **A,B** The eye velocity and stimulus velocity vectors are aligned; the direction of gravity (g) is also shown. In the graphs, slow-phase eye velocity (*EYE VEL*) and the eye velocity component generated by the velocity storage integrator (*INT*) are plotted simultaneously. The simulations were performed using stimulus durations of 30 s, which were sufficient to reach steady state. Yaw optokinetic nystagmus eye velocity (*upper graph*) rose to $27^\circ/\text{s}$ and the component due to velocity storage (*INT*) rose to $16^\circ/\text{s}$. This produced a gain of ≈ 0.77 . There was no pitch component, and it was not plotted. **B** Pitch eye velocity in response to a $35^\circ/\text{s}$ stimulus in the pitch direction. The

steady state velocity was $27^\circ/\text{s}$, giving the same gain, but the integrator only rose to $3^\circ/\text{s}$ because of its very small time constant. There was no horizontal component. **D** Yaw axis stimulation with the head tilted 45° . This produced a vertical component (*upper graph*) of approximately $8^\circ/\text{s}$ due to cross-coupling in the integrator (*INT*). This produced 18° rotation of the eye velocity vector relative to the stimulus direction, in agreement with the mean experimental data. The predicted optokinetic after-nystagmus had a short time constant in accordance with the large eigenvalues in matrix **H**. **C** Model simulation of oblique stimulation with the head upright. The model predicts a rotation of the eye velocity vector of 14° toward the spatial vertical. There was also an overshoot in the vertical component, which then decayed to a steady state level of $\approx 14^\circ/\text{s}$. **E** Oblique stimulation with the head tilted. There was a shift of the vector of eye velocity 5.2° opposite the head tilt, consistent with the data

Discussion

The major finding of this study is that the yaw-axis eye velocity vector tends to align with the spatial vertical in humans during OKN when the head is tilted with regard to gravity. Despite potential artifacts in measurement of vertical components of eye velocity due to EOG, the findings were robust: a vertical component was not present in the upright position during yaw-axis OKN, but appeared in the head-tilted position, causing orientation shifts in OKN (Figs. 1–3). During yaw-axis stimulation of 35°/s, the eye velocity vector shifted a mean of 18° toward the spatial vertical, and horizontal eye velocity reached a mean of about 24°/s. Vertical eye velocity reached a mean of 8°/s, which accounted for the shift in orientation. In some subjects vertical eye velocity was substantially greater ($\approx 20^\circ/\text{s}$), causing the axis of rotation to shift nearly 45°. Thus, human OKN has a gyroscopic quality that tends to align yaw axis gaze velocity with the spatial vertical.

In addition, there were gravitational effects noted during oblique stimulation. With the head upright the axis of eye rotation shifted toward the spatial vertical, and when the head was tilted the gravitational effects on velocity storage caused the eye velocity vector to be oriented toward the side opposite the head tilt. The latter effect has also been found in the monkey (Dai et al. 1991a) and mirrors the perceived shift in the spatial vertical when human subjects are in tilted positions (Müller 1916; Howard and Templeton 1966; Schöne et al. 1967; Bischof 1974; Howard 1982; Mittelstaedt 1983). If the ocular response to yaw-axis motion relies on the same mechanism as the perception of the spatial vertical, then the spatial orientation of yaw OKN may be an objective correlate of static spatial orientation. It may also reflect the tendency of humans to align posture with gravity.

Potential sources of the vertical velocity during cross-coupling

We considered various systems that could have contributed to the orientation properties of OKN. If the head is tilted 45° to the left, there is ocular counter-rolling of about 5° to the right (Diamond and Markham 1981, 1983). As a result, a *leftward* moving stimulus relative to the head would produce retinal motion with a *downward* component, and a *rightward* moving stimulus would produce an *upward* component of movement. However, in our experiments, with head tilt to the left, *leftward* stimulus velocity induced *upward* eye velocity (Fig. 3C, upper right) and *rightward* stimulus velocity induced *downward* eye velocity (Fig. 3C, lower left). Thus, if eye velocity followed retinal motion, we would have obtained results opposite to those found in this study. Therefore, the cross-coupled components during OKN could not be attributed to the retinal effects of ocular counterrolling.

The visual system could have contributed vertical components to OKN in the tilted position by remapping the direction of the stimulus at the input stage. It has been shown that the visual fields of about 30% of neurons in the primary visual cortex of the anesthetized cat rotate as a function of head tilt with respect to gravity (Horn and Hill 1969; Bisti et al. 1972; Denney and Adorjani 1972; Tomko et al. 1981). If the shift in the orientation of human OKN were due to processing in the visual system, vertical eye velocity should have increased proportionally with horizontal eye velocity and with stimulus velocity. Instead, vertical velocities increased for yaw-axis stimulation between 20 and 35°/s, but saturated for yaw-axis velocities above 35°/s (Table 2). There was no such saturation for horizontal eye velocity. The absolute values of the peak cross-coupled vertical velocities were $\approx 20^\circ/\text{s}$, which is below the saturation range of vertical OKN (LeLievre and Correia 1987). They were approximately the saturation levels that would be predicted by the velocity storage model. Therefore, processing through the velocity storage integrator, which saturates at 15–20°/s (Cohen et al. 1981; Jell et al. 1984; Fletcher et al. 1990), is the more likely explanation. Data in the monkey are also consistent with the hypothesis that velocity storage, not processing in the visual system, is responsible for the vertical component during cross-coupling (Dai et al. 1991a; Katz et al. 1991).

Implications of modelling the spatial and temporal properties of velocity storage: comparison with the monkey

One question that needed to be resolved at the onset was whether the small amount of OKAN and its short time constant, due to the restricted field of the stimulus, could explain the relatively large orientation changes in yaw-axis OKN. From previous work in the monkey (Dai et al. 1991a; Raphan et al. 1992), it might be inferred that large OKAN time constants are necessary to generate the observed orientation properties. The model simulations (Fig. 7) demonstrate, however, that if the relative values of the parameters of the system matrix reflect differences in the time constants of yaw and pitch axis velocity storage, it is possible to predict the effects of head tilt on OKN from velocity storage despite the relatively brief OKAN.

The shift in the axis of eye rotation during OKN was greater in humans than in monkeys. In monkeys there was only about 5° of rotation of the eye velocity vector for upward coupling and no rotation for downward coupling when animals received yaw axis optokinetic stimulation when tilted 45° (Fig. 12C,D of Dai et al. 1991). In contrast, there was an average 18° shift for a 35°/s optokinetic stimulus for the same amount of head tilt in the human. According to the model, this represents an important difference in suppression characteristics of vertical eye velocity. It appears that vertically

oriented stripes, which lack vertical contrast, are not critical for the monkey to maintain its eye velocity around a yaw-axis. In humans, this lack of vertical contrast appears to play a substantially greater role in the failure of suppression of vertical velocity. The projection operator, which projects retinal slip onto the stimulus direction, appears to have modelled the process fairly accurately. One property of the model which has emerged using the projection operator is its ability to generate overshoots in the vertical response for oblique stimulation when upright (Fig. 7). This arises as a consequence of the eye velocity vector rotating away from the stimulus and allowing only the slip along the stimulus direction to determine the steady state. The orthogonal component of eye velocity is governed only by system parameters and is not under direct control of the stimulus. Thus, the model has the flexibility to predict a wide range of behavior including overshoots in eye velocity components for appropriate values of the parameters. This was observed in our data, but the dynamics were not fully explored, being beyond the scope of this study. The basis for the difference in retinal slip processing and suppression between man and monkey as suggested by the model is not clear. Whether it lies in the stimulus conditions or is a difference due to visual processing between the species remains to be determined.

In the monkey there is a striking asymmetry in pitch-up and -down eye velocity with regard to velocity storage (Matsuo and Cohen 1984; Raphan and Cohen 1988; Dai et al. 1991). The up-down asymmetry during OKN and OKAN is more variable in humans than in the monkey, and when present in this study, was stronger in the downward direction (Table 1). In the monkey, only the yaw axis vector shifted in side-down positions, and the vertical vector stayed oriented with reference to the head (Dai et al. 1992), although the gain of the vertical component increased in side-down positions for tilts of 60° or more (Matsuo and Cohen 1984; Raphan and Cohen 1985, 1988; Dai et al. 1991a). Our findings on vertical gain of OKN in 45° tilted head positions (Table 1) were generally compatible with the monkey data, suggesting that velocity storage was contributing to pitch eye velocity in tilted but not the upright position.

Thus, the study demonstrates that the orientation properties of velocity storage, together with the lack of suppression of retinal slip components orthogonal to the stimulus, are sufficient to account for the shift in the axis of rotation, as well as for other gravitational properties of OKN during oblique stimulation with the head upright and tilted. In humans the spatial aspects of velocity storage in tilted positions appear to be more significant than its temporal aspects in contributing to spatial orientation of gaze velocity. Since velocity storage in the vestibular system can be activated by relative movement between the subject and the surround, be it visual, vestibular or somatosensory (Raphan et al. 1977, 1979; Cohen et al. 1977; Raphan and Cohen 1985; Solomon and Cohen 1992), velocity storage is probably impor-

tant for orienting compensatory gaze velocity toward the spatial vertical during all types of movement in a terrestrial environment.

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