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Human eye movement response to *z*-axis linear acceleration: the effect of varying the phase relationships between visual and vestibular inputs

Abstract We investigated the effect of systematically varying the phase relationship between 0.5-Hz sinusoidal z-axis optokinetic (OKN) and linear acceleration stimuli upon the resulting vertical eye movement responses of five humans. Subjects lay supine on a linear sled which accelerated them sinusoidally along their z-axis at 0.4 g peak acceleration (peak velocity 1.25 m/s). A high-contrast, striped z-axis OKN stimulus moving sinusoidally at 0.5 Hz, 70°/s peak velocity was presented either concurrently or with the acceleration stimulus or alone. Subjects' vertical eye movements were recorded using scleral search coils. When stimuli were paired in the naturally occurring relationship (e.g., visual stripes moving upward paired with downward physical acceleration), the response was enhanced over the response to the visual stimulus presented alone. When the stimuli were opposed (e.g., visual stripes moving upward during upward physical acceleration, a combination that does not occur naturally), the response was not significantly different from the response to the visual stimulus presented alone. Enhancement was maximized when the velocities of the visual and motion stimuli were in their normal phase relationship, while the response took intermediate values for other phase relationships. The phase of the response depended upon the phase difference between the two inputs. We suggest that linear self-motion processing looks at agreement between the two stimuli – a sensory conflict model.

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Introduction

Under natural conditions, vestibular information combines with visual information to provide us with a stable visual environment as well as an internal representation of spatial orientation. These functions require cooperation between the vestibular and visual systems, since individually neither system can provide all the information required for an unambiguous interpretation of the sensory flow. The classical approach to studying the response to vestibular stimulation both in the research laboratory and in clinical environments has involved a comparison of the eye movement response to head movements in the dark with the response to stimulation in the presence of visual information. This technique has provided a good understanding of the response to angular head movements (Niven et al. 1965; Hixson 1974; Hydén et al. 1982; Baloh et al. 1984). Unlike angular movement, effective compensation for linear movement is dependent on viewing distance and target eccentricity (Paige 1989; Paige and Tomko 1991; Schwarz and Miles 1991; Snyder and King 1992). The effect of linear acceleration on gaze stabilization can thus only be meaningfully assessed in the presence of the necessary distance cues, i.e., vision.

Compensatory vertical eye movements during rostrocaudal (z-axis) linear acceleration in the dark, have previously been shown in cats (Fukushima and Fukushima 1991), monkeys (Paige and Tomko 1991), and humans (Tokita et al. 1981; Baloh et al. 1988). Combining linear acceleration that changes in direction and amplitude with visual information has been effective in enhancing horizontal (y-axis) optokinetic (OKN) response (Veenhof 1965; Tokunaga 1977; Buizza et al. 1980; Mendoza and Merfeld 1993; Merfeld et al. 1994), vertical (z-axis) OKN response (Fukushima and Fukushima 1991; Wall et

al. 1992a, b), and smooth pursuit eye movements (Yasui and Young 1975; Shelhamer et al. 1991).

Pairing sinusoidal linear motion with a sinusoidal visual stimulus allows us to mimic what happens during vertical movements outside the laboratory, e.g., during walking, when *down*ward head translations are accompanied by *up*ward visual motion and vice versa. We have shown this combination to produce a robust, compensatory response during *z*-axis acceleration that is greater than the response to visual motion alone (Wall et al. 1992a, b). However, when we paired the peak velocity of *up*ward head translations with the peak velocity of an *up*ward visual motion, the response was unchanged from vision alone. From this, we suggest that otolith-driven eye movements may be functionally useful only when they are combined in a meaningful way with simultaneous signals from other senses such as an integrated otolith signal combined with visual velocity in order to reduce retinal slip.

Two possible ways to achieve an otolith-visual signal combination are through "arousal" or through "interaction". In this context, arousal means that otolith input simply increases the gain of the OKN system. Thus, the phase relationship between the visual stimulus and eye movement response does not depend upon the otolith input. In contrast, interaction means that the visual and otolith inputs combine to produce the response. Thus, the phase of the response depends upon the phases of both inputs. By varying the phase relation of the maximum otolith signal and the maximum required eye velocity, we can distinguish between arousal and interaction. If the response is interactive, then we can determine the phase relationship that produces the maximum response.

Materials and methods

Linear acceleration device (sled)

We used the MIT Man-Vehicle Laboratory linear acceleration "sled": a human-rated cart mounted on a 4-m-long track. The sled was driven by a velocity servo-controlled motor with a performance envelope up to 2.0 Hz and 0.7 g. A 386 personal computer calculated the command signal and sent it to the sled through a 12-bit digital to analog (D/A) converter at 200 samples per second. The analog signal was low-pass filtered (3 Hz) to eliminate D/A quantization on the command signal. The use of the filter introduced an effective time delay, between the velocity command and actual sled velocity, of 175 ms (32° at 0.5 Hz). Sled velocity was measured using the tachometer signal and had a sensitivity of 1.59 V/m per second. Sled velocity and eye movement data were sampled at 200 Hz through a 12-bit (±10 V) A/D converter by a 386 computer. Sled vibration was attenuated through helmet and body padding.

Visual stimulator

The visual stimulator was a continuous loop of alternating fluorescent yellow and black high-contrast stripes and was mounted on the cart. The subject had an unobstructed view of the 40°×40° visual field, which was fixed at 52 cm at the straight-ahead position.

The stripes were 4.5 cm wide. The windowshade velocity was controlled independently of the sled through another velocity feedback servo. Visual stimulus velocity was measured directly from the motor-mounted tachometer having a sensitivity of 10.3 V/m per second and was sent to the 12-bit (±10 V) A/D converter sampled as above.

Subjects

This study was approved by the MIT Committee On the Use of Humans as Experimental Subjects and subjects were given written and verbal explanations of all test procedures. Informed consent was obtained before testing all five subjects (three men, two women), who varied in age from 22 to 27 years. Subjects had no visual or vestibular anomalies, except for one subject with mild myopia. Subjects' corneas were examined before and after the experiment. There was no instance of a corneal abrasion. All subjects had had considerable experience with this or similar equipment and were paid for their participation.

Eye movement recording and calibration

Robinson-type C-N-C search coils were mounted on the sled in a frame with dimensions 25″ height×31″ width×30″ depth. Medical grade silastic annuli with imbedded copper coils (Skalar) were placed on the sclera of the subject's eyeball in order to record horizontal and vertical eye position. Subjects wore the eye coils for a maximum of 30 min. The C-N-C system was calibrated to 0.2 V/°. System noise was less than 0.1°. Eye position signals were sent to the 12-bit (±10 V) A/D converter, sampled, and stored as above for subsequent analysis.

Eye movements were calibrated at the beginning and the end of each session using three 5-mm-diameter targets, 53 cm from the subjects' eyes, separated by 10°. The center target was located at the primary gaze position.

Experimental procedure

Subjects lay on their backs and were linearly accelerated along their rostrocaudal or *z*-axes. They viewed the visual optokinetic stimulus mounted on the sled. Their heads were stabilized with a tight-fitting aviator's helmet (David Clark) and chin strap as well as a body harness. The helmet and harness were attached to the sled. During runs, sound isolation was provided through a noise-cancellation headset (BOSE) and an additional white noise.

The characteristics of the visual and vestibular stimuli were the same for all conditions – only the phase relationship between them was varied. The sled had a peak acceleration of 0.4 g at 0.5 Hz (peak velocity 1.25 m/s). The optokinetic stimulus had a peak velocity of 0.62 m/s at 0.5 Hz. Maintaining a stabilized retinal image in the primary gaze position during optokinetic stimulation would thus require a peak eye velocity of 70°/s. Maintaining a stabilized retinal image of an earth-stationary target during the vestibular stimulation would have required a peak eye velocity of 140°/s. These amplitude and frequency conditions were chosen because they had produced a robust eye movement response in previous experiments (Wall et al. 1992a,b). All trials were 30 s long (10 cycles at 0.5 Hz plus 5 s of ramp-up and ramp-down). The instructions were the same for each trial. Subjects were told to keep their gaze straight ahead and not to follow one particular stripe but to notice or count the stripes as they went by. Subjects were also given a simple distracter task such as naming objects using successive letters of the alphabet.

There were a total of nine conditions: one with OKN stimulus alone and eight which paired OKN with linear acceleration in various phase relationships. The relationship was varied in 45° steps. The resulting stimulus configurations are illustrated in Fig. 1. Our convention was that 0° phase difference corresponded to the natu-

Fig. 1 An example of the eye position signal is shown at the *top*, with the corresponding de-saccaded slow-component eye velocity *below*. *Upward trace deflections* represent upward eye movements. The visual stimulus velocity is shown in relation to each of the sled stimulus velocity conditions. The phase relationship of the two stimuli are indicated by the *arrows*. The condition nomenclature, e.g., 45, 90, indicates a phase lead of the visual stimulus with respect to the sled stimulus velocity
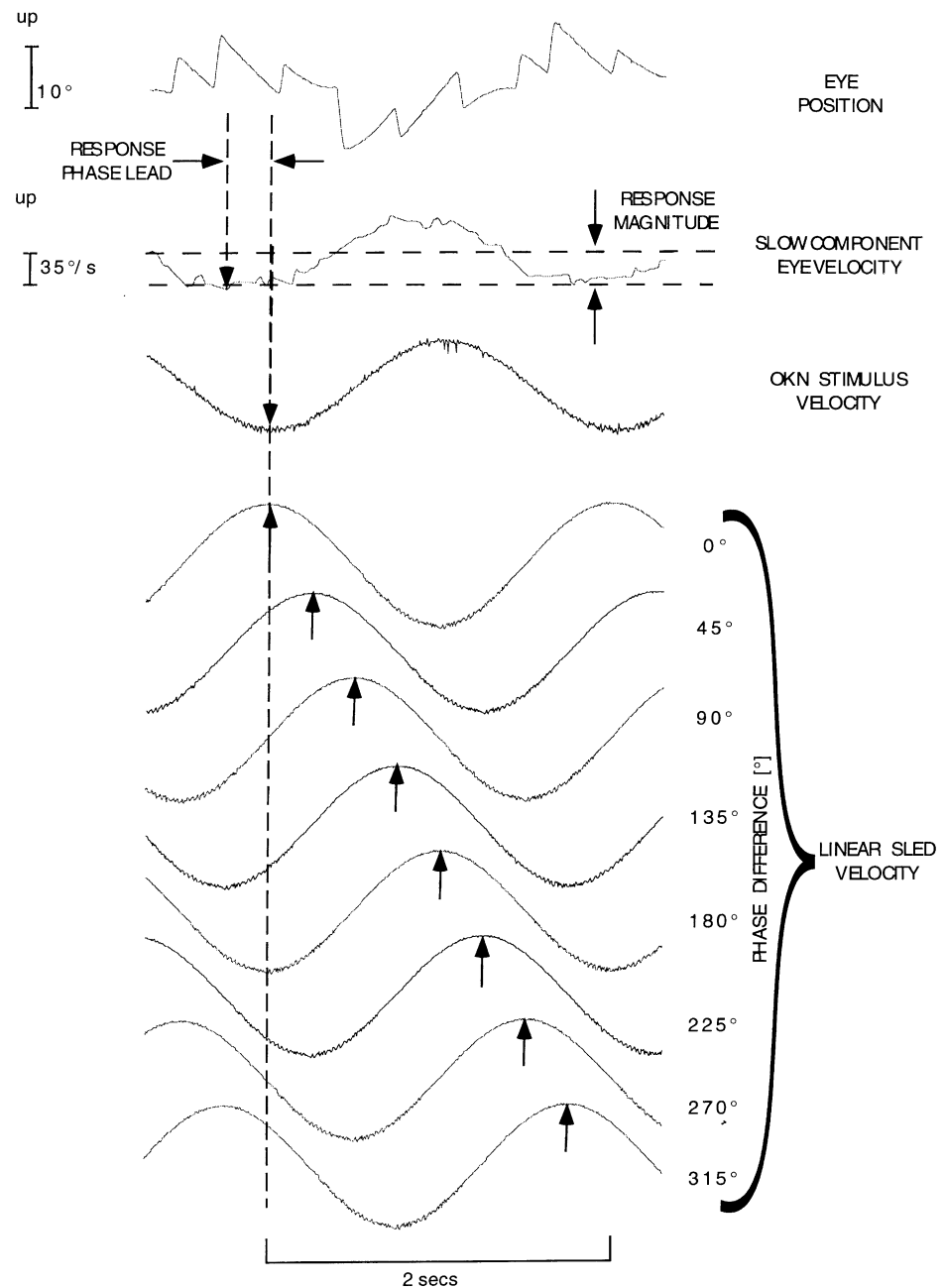
ral relationship of the stimuli (upward vision paired with downward physical motion). A positive phase difference corresponds to a phase lead of the visual stimulus velocity with respect to the sled motion's peak velocity. After the data had been collected, it was discovered that the analog filter used in the sled controller had added an additional 32° lag. The actual phase differences used for the experiment were therefore 32°, 77°, 122°, 167°, 212°, 257°, 302°, and 347°, which we refer to as condition 32, condition 77, etc.

We controlled for order effects and fatigue using a modified Latin square design (Zar 1984). We ran four trials each of the 32°, 122°, 212°, 302°, and vision alone conditions, spaced throughout the session. Due to time constraints imposed by search coil use (as per manufacturer's instructions), we ran one trial each of the 77°, 167°, 257°, and 347° conditions, for a total of 24 trials.

Data analysis

Slow-component velocity extraction

The digitally stored eye position, sled velocity, and OKN velocity signals were analyzed using locally developed Matlab-based programs. Fast components were identified using an acceleration-based algorithm that sets a threshold for each run, allowing maximum separation of the bimodal distribution of slow and fast components (Oman and Balkwill 1993). The fast components so detected were then removed from the velocity trace and the gaps filled with a ramp representing a linear interpolation of the surrounding slow-component velocities (SCVs). The continuous measure of SCV was used for subsequent analysis. The experimenter verified deletion of the fast components and manually deleted any missed by the computer. The algorithm was successful in deleting approximately 95% of saccades/fast components.
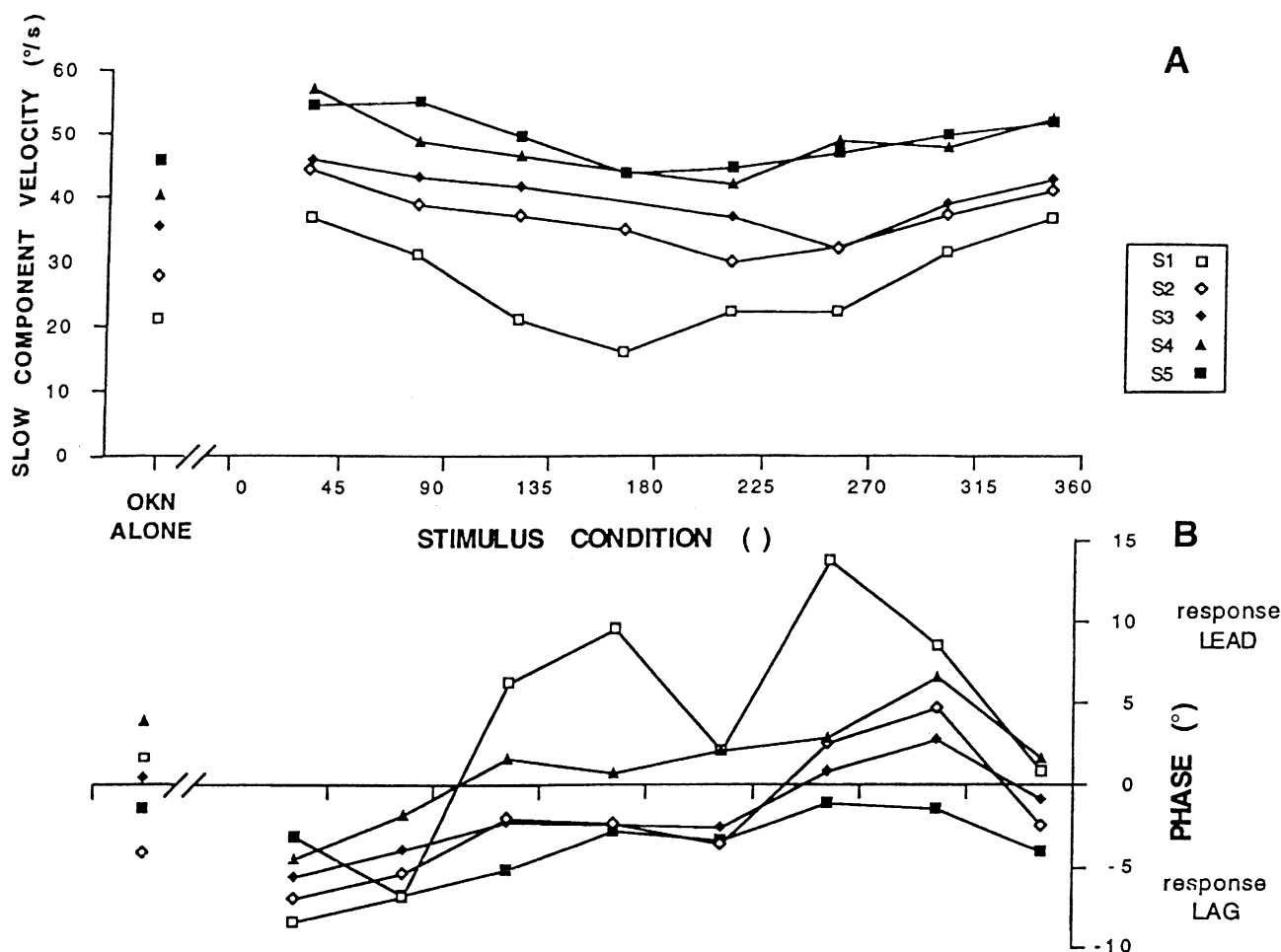
Fig. 2A,B Variation in magnitude (**A**) and phase (**B**) of the eye movement response as a function of stimulus conditions (see text). Positive-phase slow-component velocities (SCVs) indicate a phase lead with respect to the visual stimulus. The response to optokinetic stimulation alone is shown on the *far left* for comparison. *Error bars* for individuals are not shown for clarity, but are always <2.5°/s for magnitudes and <1.5° for phases

A z-parameter test (Zar 1984) was used to compare the responses obtained in trials that were scattered through our data collection period but which had identical stimulus conditions. This was to look for patterns indicating subject drowsiness or an order effect within each subject. No significant variations of these types were found and so the responses elicited by all trials for any one condition were pooled.

Quantifying the slow-component velocity

Frequency analysis of the SCV was performed using Gauss' method of least squares. The values of the d.c. component as well as the stimulus frequency and its first three harmonics were determined by our analysis method. The data of each trial resulted in a vector which represents the magnitude and phase of the fundamental frequency sine fit to all 10 cycles. Within one trial, the vector mean of the cycles typically had a standard error of less than 1°. Thus we only consider the variability between ensemble means of pooled responses. A multivariate statistical method (Hotelling's T^2; Johnson and Wichern 1982) was used to calculate the two-dimensional 95% confidence region.

Results

Slow-component velocity response

Figure 1 shows an example of a typical vertical eye position and resulting SCV trace evoked by the combination of visual and vestibular stimulation used. It also illustrates our convention for the measures of "phase" and "slow-component velocity amplitude" and shows the typical noise levels of our records. The lower part of the figure illustrates the various phase relationships between the linear sled velocity and OKN velocity that were used in this experiment.

The mean magnitude and phase of the SCV response are plotted in Fig. 2 for each subject for all phase relationships tested and averaged across subjects in Fig. 3. The 32, 77, and 347 conditions were significantly different from the OKN-alone response in the majority of subjects (see Table 1). Although there was considerable intersubject variability, the magnitude of the SCV response for each subject varied with the phase relationship between the visual and vestibular stimulus components. Each subject showed an increase in magnitude compared with their OKN-alone response (Fig. 2A, left) when the phase difference between the visual and vestibular inputs was small (close to the natural relationship). The magni-

Fig. 3A,B The means of the SCV magnitudes (**A**) and phases (**B**) for all five subjects are shown with *standard error bars*. The *hatched area* represents the mean OKN response. *Stars* indicate those points that are significantly different from the OKN-alone responses in more than three subjects (see Table 1). The magnitude of the eye movement response was enhanced by sled motion except when the sled's motion was out of its natural relationship with vision. However, the response never went below the OKN-alone response. Conventions as for Fig. 2
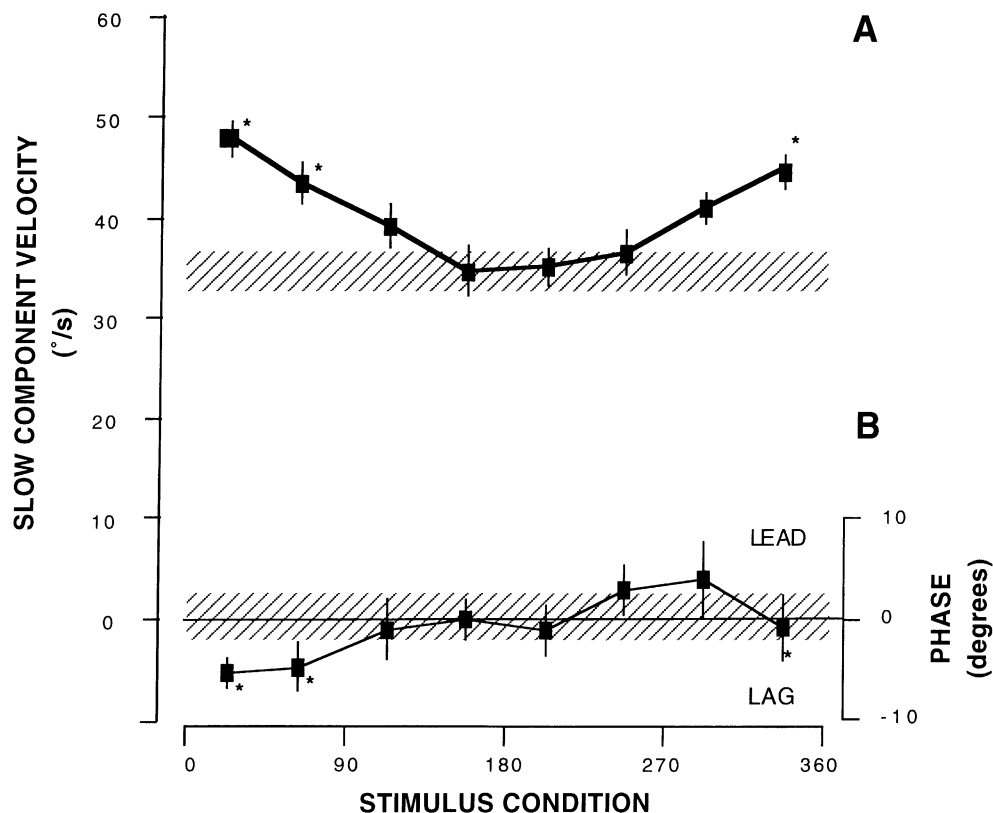
tude became closer to the OKN response for phase differences around 180° (stimuli opposed).

The phase of the SCV response with respect to the visual stimulus velocity is shown in Fig. 2B. A response phase lag (negative SCV phase with respect to the visual stimulus) was found for visual stimulus phase leads of between 347 and 122; a response phase lead was found for conditions around 270.

Hotelling's T^2 test (see Materials and methods) was used to plot the 95% confidence regions of the vector means across subjects. Some of the conditions (OKN alone, 32, 122, 212, and 302) are illustrated in Fig. 4. Figure 4B shows a comparison of the OKN-alone condition with conditions 32 and 212. The change in magnitude and phase from the OKN-alone condition when the sled velocity was paired with the visual velocity stimulus in the natural relationship (as in condition 32) is evident. In contrast, condition 212, an unnatural relationship between visual and vestibular cues, was not significantly different from OKN alone. Figure 4C shows a comparison of four conditions, each 90° apart. The polar plot representation clearly shows the phase-dependency of the response. The response changed from a lead to a lag when the sled stimulus velocity changed from a lead (condition 302) to a lag (condition 32) with respect to the visual stimulus velocity.

All conditions with vestibular inputs were compared with the OKN-alone condition using Hotelling's T^2 to determine the level of statistical significance. Table 1 summarizes these results. There was a progression of the

number of subjects that are significantly different from the OKN-alone condition. Conditions 32 and 77 evoked eye movements that were significantly different from OKN alone in all subjects, eye movements evoked by condition 212 were not different in any subject, and, between these peak conditions, the subjects vary in their transition point for significance of the difference from the OKN-alone response. The analysis presented in Table 1 indicates that each individual subject showed the same trends as the mean (Figs. 3, 4). This is despite the fact that the individual subjects show considerable variation in the gain of their response to visual stimuli presented alone (Fig. 2A, left-hand side). The subjects are therefore adding a vestibular component to optokinetic systems that are operating at a range of efficiencies.

Discussion

These experiments have shown that for z-axis (head-to-toe) linear movement, simultaneous visual and vestibular stimulation can alter both the phase and the amplitude of the oculomotor response compared with the response elicited by a linearly moving OKN stimulus presented to a stationary observer. Peak enhancement of the eye movement response occurred when the peak velocity of the visual stimulus was in phase with the peak head velocity, that is when peak upward visual stripe velocity occurred at the same time as peak downward body velocity, or peak downward visual stripe velocity occurred at
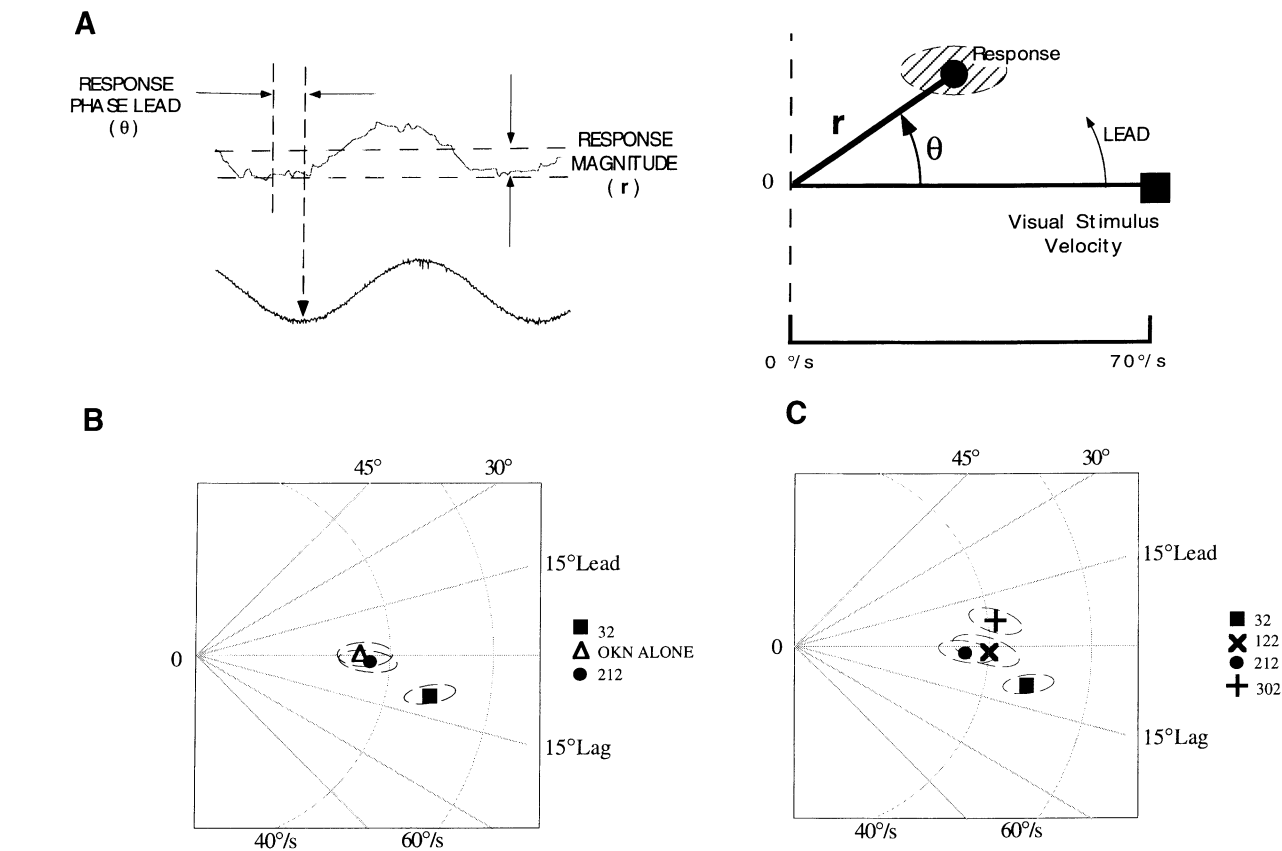
A

RESPONSE
PHASE LEAD
(θ)

RESPONSE
MAGNITUDE
(r)

Response

r

θ

LEAD

0

Visual Stimulus
Velocity

0 °/s   70°/s

B

45°   30°

15°Lead

■ 32
Δ OKN ALONE
● 212

0

15°Lag

40°/s   60°/s

C

45°   30°

15°Lead

■ 32
✖ 122
● 212
➕ 302

0

15°Lag

40°/s   60°/s

Fig. 4A–C Variations in slow-component velocity (SCV) plotted as vectors. **A** Slow-component velocity response phase and magnitude are shown on the *left*, as in Fig. 1. The visual stimulus velocity is represented on the *right* as a vector of 70°/s magnitude and 0° phase. A schematic of a mean response vector is also shown at 35°/s and 40° phase lead. The *hatched area* around the response represents the 95% confidence region for the mean vector (see Materials and methods). **B** The vector means and their error ellipses are shown for OKN-alone and the 32 and 212 phase conditions. The OKN-alone response was in phase with the visual stimulus velocity with a SCV response magnitude of about 35°/s. Condition 32 produced a phase lag and an SCV magnitude increase from the OKN-alone condition, whereas Condition 212 showed no change. **C** Four phase conditions are shown, conditions 32 and 212 from **B** and conditions 122 and 302. Condition 122 is not significantly different from 212, whereas condition 302 shows a significant phase lead

Table 1 Eye movement responses evoked by each visual/vestibular stimulus pairing compared with OKN alone (no sled movement) using Hotelling's T^2 test for multidimensional analysis. The *P*-values for each subject are shown. The number of subjects that show a significant change from their own OKN-alone response at the $P<0.05$ level is shown for each condition in the *far right column*

Condition	S1	S2	S3	S4	S5	Subjects (n)
32	0.003*	0.040*	0.039*	0.043*	0.033*	5*
77	0.006*	0.019*	0.024*	0.028*	0.002*	5*
122	0.660	0.050*	0.302	0.171	0.002*	2
167	0.032*	0.092	–	0.373	0.329	1
212	0.247	0.814	0.372	0.464	0.193	0
257	0.110	0.015*	0.704	0.002*	0.822	2
302	0.201	0.015*	0.123	0.023*	0.092	2
347	0.005*	0.029*	0.158	0.001*	0.014*	4*

* Significantly different from OKN alone at $P<0.05$

the same time as peak upward body velocity. This is the natural phase relationship between visual and body movement. It was *not* the case that peak enhancement occurred when maximal otolith stimulation (peak body acceleration) was in phase with maximal visual velocity. The phase requirement of the maximum enhancement indicates that the otolith signal, which is proportional to the imposed linear acceleration of the head (Fernandez and Goldberg 1976), was integrated resulting in an otolith-visual system directed toward the goal of maximizing eye velocity to reduce retinal slip. This integration may happen at the level of the vestibular nuclei, where all of the cells that responded to both vestibular and visual stimuli were found to be related to an otolith-*velocity* signal (Xerri et al. 1988). In fact, these neurons were

stimulated maximally by a visual stimulus that was synergistic with the *velocity* of the body movement (e.g., our condition 0).

Although maximal enhancement of the response occurred when the velocities of the stimuli were synergistically paired, that is, when they were in their natural phase relationship, surprisingly there was never a significant *reduction* of the response below the OKN-alone level, even when the physical motion was in the most unnatural relationship with the visual movement (directly opposed).

Fig. 5A–D Four conceptual models. On the *left* is shown the block diagram for each model and corresponding SCV equation. On the *right* is the theoretical response for each model. **A** The linear model vectorially adds the integrated head velocity to the OKN velocity input to produce the SCV output. **B** Otolith input turns up optokinetic gain. **C** The selective arousal model predicts that if the OKN and otolith inputs "agree", i.e., the difference in their phases ($\phi_{oto}-\phi_{OKN}$) does not exceed some threshold, , then the OKN gain is increased. If the difference exceeds the threshold, then the output is the OKN output response alone. **D** The scaled-enhancement sensory-conflict (*SESC*) model uses a "conflict detector" to compare the two inputs. The output of this conflict detector, $g(\phi)$, depends upon the difference in phase between the two inputs. The otolith signal is added vectorially to the OKN signal, but in proportion to the amount the two signals agree
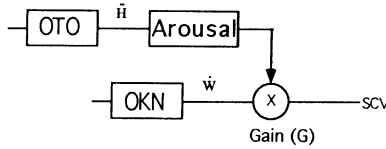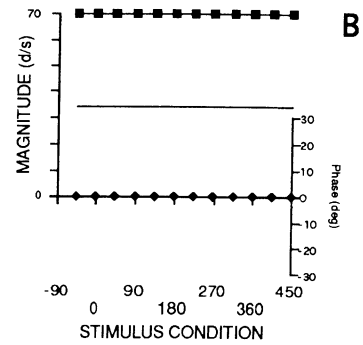
1: Linear   model
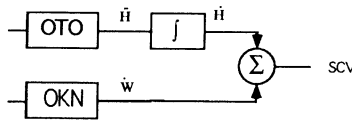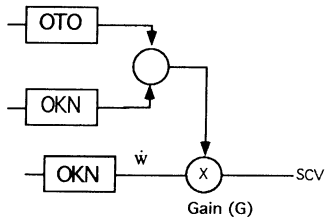
$$SCV = OKN + \int OTO$$
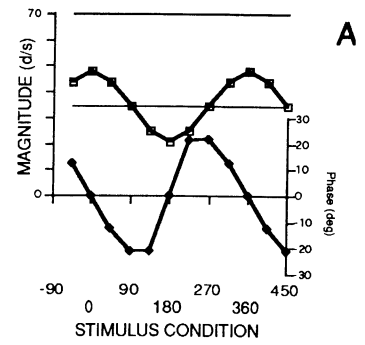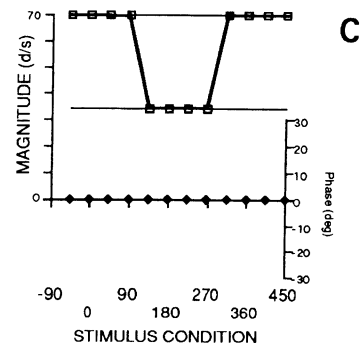
2: Arousal   model
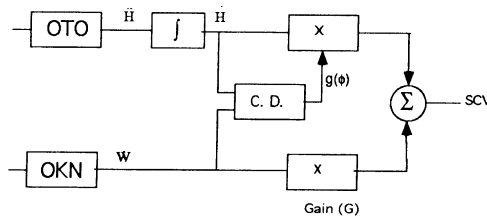
$$SCV = G \times OKN$$

3: Selective   arousal   model

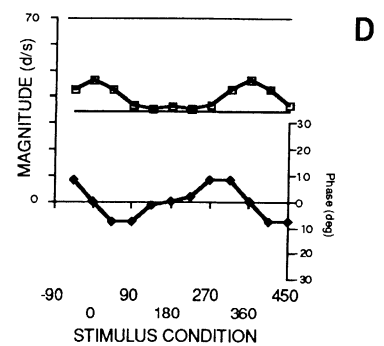$$SCV = G \times OKN, \text{ if } (\phi_{oto}- \phi_{OKN}) < \theta$$
$$(\theta = \text{some threshold})$$

4: SESC   model

$$SCV = G \times OKN + g(\phi) \times \int OTO$$
$$\text{where, } g(\phi) = 0.5\ (R_{xy}(\phi) + 1)$$

The eye velocity required to maintain fixation on an earth-fixed target during linear translation depends on the distance of the target. If the target is close, the eyes need to move with a high velocity, if the object is very distant, such as a star, no eye movement is required at all. Compensatory eye movements evoked by linear motion have been shown to be sensitive to distance of the target (Baloh et al. 1988; Israel and Berthoz 1989; Paige 1989; Schwarz and Miles 1991). Target distance might be obtained from accommodation or vergence angle (Schwarz and Miles 1991; Demer 1992). All our stimuli were at the same viewing distance (52 cm) and differed only in the phase relation between the visual and vestibular components. There is no reason to suppose that some combinations caused the visual target to be perceived as being closer or evoked more vergence than others. The fact that there was an enhancement when the signals agreed and no enhancement when they disagreed indicates that the interaction cannot be explained by a simple summation between visual and vestibular responses, but can, however, be explained by a sensory conflict model.

Vector addition models

A simple linear model has been proposed previously to describe eye movement responses to linear acceleration and visual stimuli (Buizza et al. 1980). Model 1 of Fig. 5 describes this otolith-visual system that produces the SCV response through simple vector addition of the velocity inputs. Buizza et al. suggested this model to characterize visual-vestibular interaction with upright subjects sinusoidally linearly accelerated along their interaural axis (y-axis) while using a constant velocity optokinetic (OKN) stimulus. They found that the horizontal OKN response showed a superimposed oscillation at the same frequency as the concurrent sinusoidal linear acceleration. Others have confirmed this result (Mendoza and Merfeld 1993; Merfeld et al. 1994). This mode of interaction is similar to that proposed for canal-visual interaction (Koenig et al. 1978; Schmid et al. 1980).

However, this summation model predicts a reduction in the SCV response, from the OKN-alone response, that we do not see during z-axis stimulation (Wall and Furman 1990; Wall et al. 1992a). Also, the change in the phase of the SCV predicted by this model is much larger and of a different pattern than the change in the data reported here. Therefore our data suggest that z-axis otolith-visual interaction is quite different from that of canal-visual interactions and the otolith-visual y-axis system investigated by Buizza and others. The differing results may also be due to the types of stimuli used. Buizza et. al. (1980) and Merfeld et. al. (1994) used a constant-velocity visual stimulus paired to a sinusoidal linear acceleration. Such a stimulus puts the visual stimulus in a natural relationship with concurrent vestibular stimulation for only half the acceleration cycle (e.g., condition 0) and is in conflict (e.g., condition 180) during the other half. This type of stimulus would not be able to distinguish between an "arousal" or "interactive" model of otolith-visual stimulation, since no phase change is predicted at the conditions tested (0 and 180).

Arousal models

The most general arousal model of otolith-visual interactions is that otolith input turns up optokinetic gain (Tokunaga 1977). This model (shown as model 2 in Fig. 5) predicts that otolith vestibular inputs always enhance the OKN response regardless of the phase between the inputs.

This model was already shown to be inadequate in our previously published data (Wall et al. 1992a), which demonstrated an enhancement from the OKN-alone response for some visual-vestibular phase relationships, but no change in the eye movement response for others. However, an arousal model could still be used to explain previous and current data at conditions 0, 180, and OKN alone by hypothesis that only a "synergistic" pairing would enhance the OKN response while an "antagonistic" pairing left the OKN-alone response unmodified. The "selective arousal" model shown in Fig. 5C increases the OKN response only when difference in the phase of the two inputs ($\phi_{oto}-\phi_{OKN}$) does not exceed some threshold θ.

A variation on this model, not shown in the figure, would be to make the arousal gain (G) a function of the phase difference ($\phi_{oto}-\phi_{OKN}$). This might explain the magnitude of the SCV response in our eight-phase comparisons, but it cannot account for change in the phase of the OKN-alone response when paired with linear acceleration. The sensitivity of the phase of the response to the stimulus inputs indicates that the otolith and visual signals are *interactively* combined. Note that the "linear model" (Fig. 5A) is interactive, but was ruled out for other reasons. The "selective arousal" model predicts no phase change in the SCV response, so this model is not interactive and cannot account for the results for all the phase conditions.

Sensory conflict models

"Sensory conflict" has been used in the literature for some time to describe a disagreement between at least two sensory systems (Guedry 1965a, b). Specifically, sensory conflict detection models have been used to describe the effects of otolith inputs on ocular motor responses when put in conflict with canal responses such as during postrotatory tilt in monkeys (Merfeld et al. 1993) and in humans (Benson 1966) or during off-vertical axis rotation (OVAR) in monkeys (Raphan et al. 1981), cats (Harris 1988), and humans (Harris and Barnes 1987).

A sensory conflict model predicts that visual and vestibular information are weighted proportionally to the usefulness of that information. The "scaled-enhancement

sensory conflict (SESC) model" in Fig. 5D contains a "conflict detector", which compares the integrated otolith input, i.e., velocity, with the OKN velocity signal. The output of this conflict detector depends upon the difference in phase between the two inputs, i.e., the extent to which they are in temporal agreement. This is analogous to the mathematical operation of cross-correlation which measures the resemblance between one signal and a delayed version of the other. In our case, the smaller the phase difference between the otolith and visual drives, the higher the correlation. Evidence that the brain performs neural cross-correlations have previously been used as an explanation for stereopsis (Tyler and Julesz 1978), as a possible mechanism for sound localization (Yin et al. 1986) and as a possible mechanism for the generation of the bias component in the eye movement response to OVAR (Raphan and Schnabolk 1988).

The conflict detector implemented in the SESC model uses the correlation-coefficient $R_{xy}(\phi)$, where x is otolith signal, y is the optokinetic signal and ϕ is the phase difference between them. $R_{xy}(\phi)$ is simply the cross-correlation $s_{xy}(\phi)$, normalized by subtracting the product of the means of x and y and dividing by the product of their standard deviations. Since x and y are sine waves, $R_{xy}(\phi)$ is a cosine wave with amplitude ± 1. The conflict detector raises the cosine to fall between 0 and 2 and then scales it to output values of $g(\phi)$ between 0 and 1:

$$g(\phi) = 0.5(R_{xy}(\phi) + 1)$$

where

$$R_{xy(\phi)} = \frac{S_{xy}(\phi) - \mu_x\mu_y}{\sigma_x\sigma_y}$$

and

$$S_{xy}(\phi) = \int x(t)y(t + \phi)dt$$

For the in-phase condition 0, the output is maximal (1). When the inputs are out of phase (condition 180) the detector's output is zero. At a 90° phase disagreement the output is 0.50. The conflict detector signal controls a variable gain element in the otolith signal pathway. The otolith signal passing through that stage is added vectorially to the OKN signal, but in proportion to the amount the two signals agree. The SESC model produces an SCV response whose magnitude is augmented when the drives are in phase but equal to the OKN input when the drives are out of phase. The phase of the SCV response depends upon the difference in phase between the otolith and OKN inputs. Both these features are in agreement with our results. The prediction of the SESC model is shown superimposed on the data in Fig. 6. One unresolved discrepancy between this model and our data is that the peak of the actual vertical SCV is offset 32° from the optimal phase relationship predicted by the model. This may be because the theoretical optimal phase relationship of 0° was not actually tested.

Although a sensory conflict model had not been applied previously to oculomotor responses to linear acceleration, a sensory conflict model had been used to de-
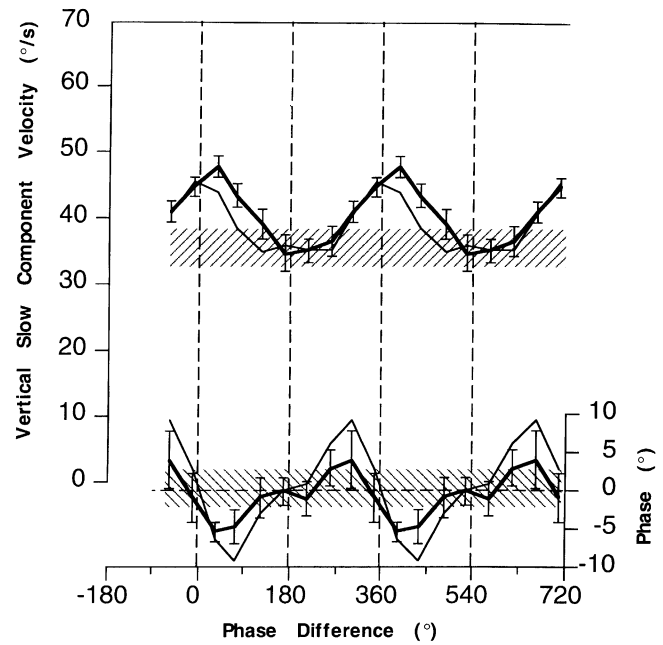

Fig. 6 The prediction of the scaled-enhancement sensory-conflict (SESC) model (*thin line*) is shown superimposed on the data (*thick line with SE bars*). Conventions as for Figs. 2 and 3

scribe human perception and control of linear motion (Zacharias and Young 1981; Huang and Young 1987) and vestibular neuron response in the cat to simultaneous otolith and visual stimulation (Xerri et al. 1988). Xerri et al. (1988) found that simultaneous otolith and visual stimulation of neurons in the lateral vestibular nuclei (related to postural control) led to a nonlinear interaction that was frequency dependent. Below 0.25 Hz, the visual response dominated. Between 0.25 and 0.5 Hz, the response to both inputs looked like the otolith response alone. Very few units showed a linear addition of otolith and vision responses alone. They related these responses to the results of Zacharias and Young (1981) and Huang and Young (1987), who showed that for human perception of *body motion* the visual system dominates at lower frequencies, while at higher frequencies the vestibular system dominates. A nonlinear interaction had been similarly used to describe the effect of linear acceleration stimulation on the perception of visual *image motion* (Pavard and Berthoz 1977).

Others have reported a response in the vestibular nuclei of the cat that is dependent on the phase of the stimuli rather than the frequency (Daunton and Thomsen 1979; Daunton and Christensen 1992). They found two types of cells that responded differently to the same sensory pairing of visual and acceleration stimuli. One population of cells increased their firing to synergistic visual and vestibular inputs (e.g., condition 0) and the other population, "antagonistic" cells, decreased their firing to the same inputs. Our data would predict that the latter cells would fire maximally during our antagonistic behavioral condition (condition 180). The dynamics of the

two populations of cells may contribute to nonlinearities in the behavioral response.

Conclusions

We have shown that the otolith-visual system is an interactive system that works in a velocity coordinate framework. We have extended the concept of sensory conflict detection previously used to describe responses to linear movement, in perceptual tasks and single-unit recording, to include an oculo motor task described by the SESC model. This paradigm provides a functional, physiological measure for describing otolith-visual interactions.

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