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FINAL REPORT FOR NASA GRANT NAG 2-445

VISUAL-VESTIBULAR INTERACTION

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June 1994

(NASA-CR-196097) VISUAL-VESTIBULAR
INTERACTION Final Report (MIT)
9 p

N94-35379

Unclass

G3/53 0013753

FINAL REPORT

Introduction

Significant progress was achieved during the period of this grant on a number of different fronts. A list of publications, abstracts and theses supported by this grant is provided at the end of this section. The completed studies focused on three general areas.

1. Eye movements induced by dynamic linear acceleration.
2. Eye movements and vection reports induced by visual roll stimulation.
3. The separation of gravito-inertial force into central estimates of gravity and linear acceleration.

Eye movements induced by linear acceleration in humans were studied for acceleration aligned with the inter-aural (y-axis) direction (Shelhamer, 1990; Shelhamer & Young, 1991; Christie, 1992; Merfeld et al., 1992b) and with the longitudinal (z-axis) direction (Polutchko & Merfeld, 1993). Investigations of ocular torsion induced by linear acceleration aligned with the inter-aural direction have also been completed (Law, 1992; Teiwes et al., 1993a & b).

A second set of studies focused on the visual vestibular interaction induced by visual roll stimulation. One study measured the influence of tactile cues applied to the shoulder on vection (Standish, 1990; Young & Standish, 1990) while another recorded torsional eye movements in humans using the new search coil system in both upright and supine orientations (Jackson, 1992).

A third set of studies investigated the eye movements of squirrel monkeys during simultaneous canal and otolith stimulation in an attempt to determine how the CNS resolves sensory conflicts. One of these studies looked at the three-dimensional eye movements observed following post-rotatory tilt (Merfeld et al., 1993a), while another investigated three-dimensional eye movements during eccentric rotation (Merfeld, 1990; Merfeld et al., 1991). Both studies provided evidence that the CNS might resolve the otolith measurement of gravito-inertial force into estimates of gravity and linear acceleration.

Based on some of these findings, two new models were developed to help explain the complex sensory interactions associated with multisensory integration. These models are based upon observer theory (Merfeld, 1990; Merfeld et al., 1993b) and optimal observer (Kalman filtering) theory (Shelhamer, 1990; Shelhamer & Young, 1991).

Furthermore, as documented in more detail below, the MIT linear sled facility (hardware, software, measurement techniques and analysis algorithms) was significantly improved, and the system is well prepared for the proposed studies.

Experimental Studies

Effect of Linear Acceleration on the Tracking of Imaginary Targets

A set of studies was designed to measure the ability of subjects to track a hidden earth fixed target during linear translation (Polutchko & Merfeld, 1993). Subjects watched a real target (LED) that was hidden from view by a barrier only during sled motion so the subject received no feedback regarding their performance. Tests were performed with acceleration along the inter-aural (y-axis) direction in upright subjects and along the longitudinal body (z-axis) axis in supine subjects. Similar to previous studies (Israel et al., 1989), the subjects nearly exclusively tracked the targets using saccadic eye movements. In the y-axis the responses were essentially symmetric. However, the z-axis tracking showed a significant asymmetry with linear motion toward the head (eye movement downward) yielding larger eye movements than linear motion toward the feet (eye movement upward).

Linear Acceleration and Pursuit Eye Movements

Human horizontal eye movements were studied under several stimulus conditions (Shelhamer & Young, 1991). The linear VOR response in the dark was highly variable and led to the subsequent study of other facets of otolith-stimulated compensatory horizontal eye movements. Tracking of a fixed retinal afterimage during linear acceleration increased the gain by a factor of 2 to 10 over the dark linear VOR, providing further support for our theory in which oculomotor efferent copy information is used to reconstruct an internal representation of target velocity, which is then tracked by the oculomotor system. Studies of smooth pursuit confirmed the earlier results of reduced phase tracking of predictable target motion. Addition of the vestibular information indicating translation while tracking an earth-stationary target led to improved pursuit performance.

Linear Visual-Vestibular Interaction

Investigation of the effect of lateral horizontal whole body linear acceleration on ongoing lateral OKN was investigated by Christie (1992). Using the window shade sled combination, Christie conducted a series of experiments which showed that modulated OKN is a reproducible response to the presentation of simultaneous visual and vestibular stimuli. All subjects had modulation that increased significantly with the stimulus frequency. The phase lag also increased with increasing frequency. At 0.25 Hz, the amplitude of modulation of the slow phase velocity using the cycle-by-cycle method was typically around 10°/sec with a 45° phase lag. At 1.00 Hz, the amplitude had increased to 15°/sec and the phase lag had increased to 75°. Based on these results, it is clear that vestibular inputs and visual inputs can be combined by the CNS to produce complex eye movement patterns.

Ocular Torsion Induced by Dynamic Linear Acceleration

Ocular torsion during dynamic linear acceleration was recorded in six subjects, with four different frequencies, and two different maximum accelerations (Law, 1992). All of these tests were conducted with the subject in the erect position. The data showed that Counterrolling saccades were consistently present. Because of the presence of these saccades, ocular counterrolling position cannot be used as the only indicator of torsion. We therefore also determined the slow phase velocity (SPV) of the torsional eye motion. The cumulative eye position (CEP), which is the position of the eye without the saccades, was then found by integration of the slow phase velocity. Gains and phases for OCR position and cumulative eye position were found. The experimental data showed that, for both the OCR position and the cumulative eye position, the gain decreased and the phase lag decreased with increasing frequency. The cumulative eye position data was fit by a first order transfer function of the form

$$\frac{K(s + \omega_c)}{s}$$

The gain constant, K, for the experimental data was between 0.4 and 1.2 and the cutoff frequency, ω_c , ranged between 1.0 rad/sec and 5.9 rad/sec (0.2 Hz and 0.9 Hz). With a decreasing phase lag and a flattening of the gain at higher frequencies, the above model contradicts previous models of OCR, such as those presented by Hannon et al. (1966), Young and Meiry (1968), and with results from Lichtenberg (1979), Lichtenberg et al. (1982) and Arrott (1982, 1985), which were based on OCR position.

Influence of Tactile Cues on Roll Vection

Construction of a device for use with our rotating dome which makes possible the application of graded tactile cues against the shoulders - constant force and various spring constants was accomplished. Measurements of effects of localized and generalized tactile cues on the onset and strength of vection, body sway, and head tilt were carried out (Standish, 1990).

Ocular Torsion Induced by Visual Roll Stimulation

Ocular torsion was measured during roll optokinetic stimulation ("rotating dome") (Jackson, 1992). Subjects were tested in both the erect and supine positions. Stimuli were clockwise and counterclockwise rotation of the dome at four different speeds between 15 and 60°/sec. After-effects (OKAN) following visual stimulation were studied under three conditions: in the light, in the dark with a fixation LED, and in complete darkness. The slow phase roll OKN gain was shown to be quite low and highly variable, and to decrease with increasing stimulus velocity. Contrary to prior expectations, the majority of subjects demonstrated lower OKN gains supine than erect. This decline from erect to supine may have resulted from habituation, as adaptive effects were observed over the course of each session. Contrary to previous studies, mean torsional eye position was found to deviate in the direction of the fast phase during OKN as it does for horizontal OKN. Tonic deviation increased with increasing SPV. While a single line through the origin best related ocular deviation to SPV for supine runs, the linear fits were translated in the direction of the slow phase for erect tests. The shift may have resulted from static ocular counterrolling induced by a central recomputation of the gravity vector. Time constants of SPV decay during OKAN were found to average 2.4 seconds. OKAN time constants were shortened by both otolith suppression and visual information. The short time constant of SPV decay indicates that velocity storage is generally underdeveloped for torsion in human subjects. Cross-correlation of roll vection with torsional SPV and eye position demonstrated further that the perceptual and eye movement processes are not closely linked. Consistently greater eye deviation in the direction of the fast phases during vection indicated that vection and OKN may share some basic mechanisms.

Squirrel Monkey Eye Movements Following Post-Rotatory Tilt

Three-dimensional squirrel monkey eye movements were recorded during and immediately following rotation around an earth vertical yaw axis (Merfeld, 1990; Merfeld et al., 1993a). To study interactions between the horizontal angular VOR and head orientation, post-rotatory VOR alignment was change relative to gravity by tilting the head out of the horizontal plane (pitch or roll between 15 and 90 degrees). Results showed that in addition to post rotatory horizontal nystagmus, vertical nystagmus followed tilts to the left or right (roll) (as previously shown by Raphan et al., 1981 and Harris, 1987) and torsional nystagmus followed forward or backward (pitch) tilts. When the time course and spatial orientation of eye velocity were considered in three dimensions, the axis of eye rotation always shifted toward alignment with gravity, and the post-rotational horizontal VOR decay was accelerated by the tilts. These phenomena may reflect a neural process that resolves the sensory conflict induced by this post-rotatory tilt paradigm. A model, based on this concept of sensory conflict, was developed to simulate these data (Merfeld, 1990; Merfeld et al., 1993b). This model predicted the axis shift and other aspects of the data.

Squirrel Monkey Eye Movements during Eccentric Rotation

The vestibulo-ocular reflexes (VOR) are determined not only by angular acceleration, but also by the presence of gravity and linear acceleration. This phenomenon was studied by measuring three dimensional nystagmic eye movements, with implanted search coils, in six male squirrel monkeys. Monkeys were rotated in the dark at 200°/s (centrally or 79 cm off-axis) with the axis of rotation always aligned with gravity and the spinal axis of the upright monkeys. The monkey's orientation (facing-motion or back-to-motion) had a dramatic influence on the VOR. These experiments (Merfeld, 1990; Merfeld et al., 1991) show that: a) the axis of eye rotation always shifted toward

alignment with gravito-inertial force; b) the peak value of slow phase eye velocity was greater with the monkey facing-motion than with back-to-motion; and c) the time constant of decay was smaller with the monkey facing-motion than with back-to-motion. All of these findings were statistically significant ($p < 0.05$) and consistent across monkeys.

The eccentric rotation results indicate that the VOR may consist of two components: a linear reflex and a rotational reflex. The angular component is known to depend upon semicircular canal dynamics and central influences. The linear component of the response decays rapidly with a mean duration of only 6.6 s, while the axis of eye rotation rapidly aligns (< 10 s) with gravito-inertial force. As discussed elsewhere (Merfeld, 1990; Merfeld et al., 1991), these results are consistent with the hypothesis that the otolith measurement of gravito-inertial force is resolved into central estimates of linear acceleration and gravity such that the central estimate of gravity minus the central estimate of acceleration approximately equals the otolith measurement of gravito-inertial force. If this hypothesis is correct and can be verified using other paradigms, it will provide an alternate mechanism to explain the high-pass/low-pass filtering of otolith stimulation that has previously been reported and discussed (e.g., Mayne, 1974; Paige & Tomko, 1991a & b).

Modeling Projects

Observer Model

As discussed previously our experiments will be driven by our models. Two related, but quite different, models have been developed as part of our continuing investigation of multi-sensory integration. One model (Merfeld et al., 1993b), based on observer theory (Luenberger, 1971; Oman, 1982), was developed following a set of eye movement studies measuring the eye movements of squirrel monkeys during simultaneous stimulation of the semi-circular canals and otoliths (Merfeld, 1990; Merfeld et al., 1991; 1993a). The primary hypothesis represented in the model is that the central nervous system of the squirrel monkey incorporates information about body dynamics and sensory dynamics to develop an internal model of these dynamics.

As discussed in the introduction, the model successfully predicts "velocity storage" during rotation about an earth-vertical axis. The model also successfully predicts that the time constant of the horizontal vestibulo-ocular reflex is reduced and that the axis of eye rotation shifts toward alignment with gravity following post-rotatory tilt. Finally, the model predicts the bias, modulation, and decay components which have been observed during off-vertical axis rotations (OVAR). Recently, the model of Merfeld et al. (1993b) was extended to simulate responses during eccentric rotation. The model qualitatively predicted the responses (axis shifts, effect of the orientation of centrifugal force, etc.; Merfeld et al., 1991) that were observed during constant velocity eccentric rotation with no changes to the model parameters or organization. In other words, a model developed to predict responses in a 1-g environment, surprisingly, also predicted the responses in the hyper-g environment during eccentric rotation very well.

Optimal Observer ("Kalman Filter") Model

A independent set of experimental studies investigating eye movements during linear acceleration (Shelhamer, 1990; Shelhamer & Young, 1991) led to a model of the linear vestibulo-ocular reflex based on optimal observer (Kalman filtering) theory. In essence, the model contains a central pattern generator which predicts the target motion and hence enhances the response during predictable stimulation (e.g., sinusoidal stimulation). This model helped explain the eye movement responses obtained during predictable linear stimulation and explained the continuing response oscillations that were observed following cessation of sinusoidal stimulation.

Facilities and Instrumentation

During the period of this grant we have successfully upgraded our sled system and have also greatly enhanced our eye measurement capabilities with the addition of a search coil and video analysis systems. We also have developed some algorithms which allow us to more accurately calculate three-dimensional eye orientation and eye velocity from three-dimensional coil recordings.

Sled System

Our linear sled control system, which previously was based in a very old PDP-11 computer, was upgraded and is now completely controlled by a computer program running on a dedicated DOS compatible computer. The new control program is highly interactive and allows selection of a wider range of sled motions than the previous program. Numerous sled motion profiles (including sine, sum-of-sines, damped position steps, acceleration steps, etc.) have been implemented and tested for various protocols. In addition to controlling the sled, the system can also control a second external device that operates using an analog voltage signal such as our optokinetic display ("window shade"). Our linear optokinetic display was redesigned and rebuilt to provide more consistent behavior and a closed-loop control system was implemented to yield better stability. New students are now qualified to run the sled and begin research after only a brief training period.

Coil System

To measure eye orientation more accurately, especially eye torsion, we purchased and installed a C-N-C search coil system on the sled including a new seat arrangement with a non-metallic head/neck restraint system which conforms to C-N-C's specifications. We also implemented the system as part of our rotating dome apparatus. The system is fully operational and a number of experiments have been completed (Law, 1992; Christie, 1992; Jackson, 1992; Teiwes et al, 1993a & b; Polutchko & Merfeld, 1993, Mendoza et al., 1993).

Video System on Sled

We recently purchase an ISCAN video system which measures horizontal and vertical eye position from a video image of the eye. In conjunction with this purchase, we developed a head-mounted biteboard system to provide well-stabilized eye images. This system has been completely tested and is fully operational and provides an additional measurement option to enhance our coil recordings.

Eye Movement Algorithms

Mathematical analyses (Westheimer, 1957; Haustein, 1989) and models (Tweed & Vilis, 1987; Hepp, 1990) have shown the importance of considering the three-dimensional nature of eye kinematics. For eye movements that do not deviate far from the primary position, the search coil detector circuits accurately indicate yaw, pitch, and roll of the eye. However, as the eye deviates from the primary gaze position, a number of nonlinear errors become important (Robinson, 1963; Ferman et al., 1987). These errors are worsened by any misalignment of the search coils on the globe. We developed an algorithm that corrects for these errors to yield better and more accurate estimates of eye orientation and eye velocity (Merfeld & Young; 1992). This method is an exact solution of the kinematic and kinetic problems. The resolution is limited only by the accuracy of the calibration procedures and by the inherent measurement limitations (nonlinear magnetic fields, measurement noise, etc.).

List of Publications, Abstracts and Theses Supported by This Grant

Papers

NAG 2-445

Merfeld, D.M., Young, L.R., Oman, C.M. & Shelhamer, M.J. "A multidimensional model of the effect of gravity on the spatial orientation of the monkey", accepted for publication in the Journal of Vestibular Research, in press, 1993.

Merfeld, D.M., Young, L.R., Paige, G.D. & Tomko, D.L. "Three dimensional eye movements of squirrel monkeys following postrotatory tilt", accepted for publication in the Journal of Vestibular Research, in press, 1993.

Merfeld, D.M. & Young, L.R. "Three-dimensional eye velocity measurement following post rotational tilts in monkeys", in Sensing and Controlling Motion, Annals of the New York Academy of Sciences 656:783-794, May 1992.

Young, L.R. & Standish, G. "Influence of tactile cues on visually induced postural reactions", chapter 89, The Head-Neck Sensory-Motor System, 555-559, Berthoz, A., Graf, W. and Vidal, P.P., eds., Oxford University Press, New York, 1992. Originally presented at the International Symposium on the Head Neck System, Fountainebleau, France.

Merfeld, D.M., Christie, J.R.I. & Young, L.R. "Horizontal and vertical eye movements in humans during inter-aural linear acceleration", Proceedings of the XVII Barany Society Meeting, Prague, Czechoslovakia, June 1992.

Wearne, S.L., Curthoys, I.S., Merfeld, D.M. and Halmagyi, G.M., "Deviation of the Axis of Eye Rotation During Rotation in Yaw Following Unilateral Vestibular Deafferentation." Proceedings of Barany Society Meeting, Prague, Czechoslovakia, 1992.

Merfeld, D.M., Young, L.R., Tomko, D.L. & Paige, G.D. "Spatial orientation of VOR to vestibular stimuli in squirrel monkeys", Acta Otolaryngologica Supplement 481:287-292, 1991.

Shelhamer, M., & Young, L.R. "Linear acceleration and horizontal eye movements in man", Acta Otolaryngologica Supplement 481:277-281, 1991.

Manuscripts (in final preparation)

Merfeld, D.M., Young, L.R., Paige, G.D. & Tomko, D.L. "Vestibulo-ocular reflex of the squirrel monkey during eccentric rotation", To be submitted to: Experimental Brain Research.

Shelhamer, M., Merfeld, D.M. & Mendoza, J.C. "Vergence alone does not control the gain of the linear VOR", To be submitted to: Journal of Vestibular Research.

Merfeld, D.M., Wearne, S.L., Curthoys, I.S., Halmagyi, G.M., "Human Perceptual and Eye Movement Responses during Eccentric Rotation." To be submitted to: Journal of Vestibular Research.

Wearne, S.L., Curthoys, I.S., Merfeld, D.M., Halmagyi, G.M., "The Human Linear and Angular Vestibulo-ocular Reflexes during Centrifugation in the Tangential Orientation. To be submitted to: Journal of Neurophysiology.

Wearne, S.L., Curthoys, I.S., Merfeld, D.M., Halmagyi, G.M., "The Human Linear and Angular Vestibulo-ocular Reflexes during Centrifugation in the Radial Orientation. To be submitted to: Journal of Neurophysiology.

Abstracts

Polutchko, K.A. & Merfeld, D.M. "Using voluntary eye movements to quantify the estimation of linear translation", abstract, accepted for the May 1993 meeting of the Aerospace Medical Association.

Mendoza, J.C., Merfeld, D.M. & Young, L.R. "Interaction of optokinetic nystagmus (OKN) and linear vestibulo-ocular reflex (LVOR)", abstract, accepted for the May 1993 meeting of the Aerospace Medical Association.

Teiwes, W., Clarke, A.H., Merfeld, D.M., Oman, C.M., Scherer, H. & Young, L.R. "Comparison of the 3 dimensional video-based eye movement measurement technique video-oculography (VOG) with the scleral search coil technique (SSC)", abstract, accepted for the May 1993 meeting of the Aerospace Medical Association.

Teiwes, W., Clarke, A.H., Merfeld, D.M., Oman, C.M., Scherer, H. & Young, L.R. "Otolithic contribution to torsional eye movements during dynamic linear acceleration, abstract, accepted for the May 1993 meeting of the Aerospace Medical Association.

Merfeld, D.M. "Spatial orientation in the squirrel monkey: an experiment and theoretical investigation", dissertation abstracts, accepted for publication in the Annals of Biomedical Engineering, 1993.

Merfeld, D.M., Wearne, S.L., Curthoys, I.S. & Halmagyi, G.M. "Perceptual tilt responses in humans during eccentric rotation: a comparison to eye movement responses", abstract, 73-4, XVII Barany Society Meeting, Prague, Czechoslovakia, June 1992.

Christie, J.R.I., Merfeld, D.M. & Young, L.R. "Horizontal and vertical eye movements in humans during lateral interaural linear acceleration", abstract, 19-20, XVII Barany Society Meeting, Prague, Czechoslovakia, June 1992.

Wearne, S.L., Curthoys, I.S., Merfeld, D.M. & Halmagyi, G.M. "Human 3-D oculomotor responses to yaw-axis centrifugation", abstract, p. 125, XVII Barany Society Meeting, Prague, Czechoslovakia, June 1992.

Merfeld, D.M., Young, L.R., Tomko, D.L. & Paige, G.D. "Effect of gravity on monkey vestibulo-ocular reflex", abstract, New York Academy of Sciences conference, Sensing and Controlling Motion: Vestibular and Sensorimotor Function, Palo Alto, CA, July, 1991.

Young, L.R. & Standish, G. "Influence of tactile cues on visually induced postural reactions", Presented at the International Symposium on the Head Neck System, Fountainebleau, France, 1990.

Merfeld, D.M., Young, L.R. & Tomko, D. "Spatial orientation of VOR to combined vestibular stimuli in squirrel monkeys", abstract, Barany Society, Tokyo, Japan, May 1990.

Shelhamer, M.S. & Young, L.R. "Linear acceleration and horizontal eye movements in man", abstract, Barany Society, Tokyo, Japan, May 1990.

Theses

Merfeld, D.M., "Spatial Orientation in the Squirrel Monkey: An Experimental and Theoretical Investigation", MIT Ph.D. thesis in Biomedical Engineering, January 1990.

Shelhamer, M., "Linear Acceleration and Horizontal Eye Movements in Man", MIT Sc.D. thesis in Biomedical Engineering, January 1990.

Standish, G.J., "Influence of Generalized Tactile Cues on Motion Sensation and Postural Control", MIT S.M. thesis in Aeronautics and Astronautics, June 1990.

Law, G.W., "Measurements of Ocular Counterrolling during Linear Accelerations Using an Electromagnetic Scleral Search Coil System", MIT S.M. thesis in Aeronautics and Astronautics, August 1991.

Christie, J.R.I., "Modulation of Optokinetic Nystagmus in Humans by Linear Acceleration and the Effects of Spaceflight", MIT S.M. thesis in Aeronautics and Astronautics, February 1992.

Jackson, D.K., "Characterization of the Torsional Optokinetic Response to Rolling Visual Fields in Humans", MIT S.M. thesis in Aeronautics and Astronautics, February 1992.