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THE TRANSLATIONAL VESTIBULO-OCULAR REFLEX (tVOR) IN PILOTS AND NORMAL CONTROLS

by

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Executive Summary

During translational accelerations of the head, the eyes must move in a compensatory fashion in order to properly stabilize images on the retina. This stabilization is necessary to allow clear vision during head movements and is accomplished by the translational vestibulo-ocular reflex (tVOR). Geometric considerations require that the size of this reflex generated eye movement be a function of both the magnitude of the applied acceleration, and the distance to a viewed visual target. The experiments described in this report were undertaken to investigate the dynamics of the human tVOR evoked eye movements to accelerations along the naso-occipital (fore-aft) axis.

Before the experiments could be begun, a suitable sled had to be designed and built and appropriate control and analysis software written. This was accomplished during the first years of the contract. The resulting linear sled, located at DCIEM, is able to apply precisely controlled linear accelerations to human subjects at frequencies up to 5Hz and with accelerations of more than 0.3g. The software package supplied is able to both control the sled and record and analyze the resulting eye and head movements. Once the sled and its associated software were in place, experiments were then carried out by accelerating subjects on the linear sled while recording the evoked eye movements using a non-contacting video tracking system. While the experiments described here only investigated eye movements induced by accelerations directed along the naso-occipital axis, the apparatus is also able to investigate the results of lateral or obliquely directed accelerations.

The major findings of this study can be stated as follows. The tVOR is a highly robust reflex particularly at high frequencies (>1Hz). Furthermore, the latency of the reflex is less than 20ms, far less than previously believed. This short latency has important consequences in flight situations. Specifically, sudden accelerations will induce reflex eye movements that will function to destabilize vision. Due to the much longer latency of visual following mechanisms, suppression of these reflex eye movements using such mechanisms, mainly smooth pursuit, will not be possible until at least 130-150ms after movement onset.

As mentioned previously, these reflex eye movements are very robust and were exhibited by all subjects. It is well known that decreases in visual acuity begin to occur once the velocity of inappropriate eye movements exceeds 5 deg/s. Since peak eye velocities of more than 80 deg/s were attained within less than 100ms following movement onset, visual degradation should be severe.

As expected from geometric considerations, the magnitude of the induced eye movements was a function of vergence angle. As subjects converged their eyes in order to view near targets, the amplitude of the eye movements evoked by the acceleration increased. Thus attempting to view a near target, such as cockpit controls, only exacerbates the situation as larger eye movements are generated and visual acuity decreases further. DR. B. Cheung is currently investigating the effects of this reflex on visual acuity under actual flight conditions.

A detailed report of the results is included and has been submitted for publication.

Responses of the Naso-Occipital Vestibulo-ocular Reflex in Normal Human Subjects

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ABSTRACT:

The naso-occipital translational vestibulo-ocular reflex (NO-tVOR) was measured in 11 normal subjects in response to sudden, high acceleration head translations. Results indicated that the tVOR is very robust and has a latency of less than 20ms. This is less than half the value previously reported using lower acceleration stimuli. The effects of target distance on the evoked eye movements were also measured. Our results showed that target distance effects were only expressed well after the onset of the eye movement. Specifically, the first 85ms of the evoked eye movement was independent of target distance. Our results imply that although the tVOR has a shorter latency than previously believed, target distance effects on reflex sensitivity must employ far longer pathways than the initial reflex itself.

INTRODUCTION:

The vestibulo-ocular reflex (VOR) functions to stabilize images on the retina during head movements. This reflex is commonly broken down into two different systems, the angular VOR (aVOR) that uses information from the semicircular canals and compensates for rotations of the head, and the translational VOR (tVOR) that compensates for head translations using otolith information. Both of these reflexes need to be subject to moment-to-moment changes in gain and even direction (for the tVOR), based on the distance and direction of viewed targets (Viirre et al, 1986; Paige, 1989; Paige and Tomko, 1991a,b).

Early experiments on the tVOR indicated that the reflex latency was quite long, around 30-40ms (Bronstein and Gresty, 1988; Snyder and King, 1992; McConville et al, 1996). However, recent experiments have suggested that the reflex latency may be much less than this, of the order of 10ms (Angelaki, 1998). However, the evidence for this short latency was indirect as it was based on fitted transfer function parameters rather than direct measurements. Nonetheless, some experiments have demonstrated a direct connection between otolith afferents and abducens motoneurons, implying that the reflex latency should be very short (Sasaki et al., 1991; Uchino et al., 1996,1997).

The naso-occipital tVOR provides a particularly difficult problem for the brain's control system as the movements of the two eyes are disjunctive and are often even in different directions (Paige and Tomko, 1991a,b). Consequently, since when the target is located on the midline the required eye movements are similar to vergence movements, the reflex might be driven using vergence pathways. Alternatively, the ascending tract of

Deiters (ATD) might be used to generate these required disjunctive movements. Since the vergence system is known to have rather sluggish dynamics, it might be possible to distinguish between these two hypotheses based on the dynamics of the movements. These experiments were undertaken in order to shed more light on these questions.

METHODS:

Experiments were performed on 11 subjects (9 male, 2 female, ages 22-52). Subjects had no previous history of vestibular or neurological disorders; none exhibited any spontaneous nystagmus. Eye movements were measured with a binocular infrared video tracker (El-Mar Ltd.) which operated at 180Hz. Head movements were measured with a pulsed magnetic field device (Flock of Birds) attached to a firmly fitted headband. Both eye and head movements were digitized at 400Hz and stored on disk for off-line analysis.

Subjects were accelerated along the naso-occipital axis using a variety of different stimulus durations ranging from 250ms to 4s (see Figure 1) while viewing targets located 20, 30, 50, and 100cm from the eyes. These target distances are the distance at the end of the translation rather than at the beginning. Thus, in each trial, the target distance was set and the sled was then backed up by a distance equal to its' total excursion. This approach was chosen to guard against the possibility of the subject striking the target, particularly at the lowest accelerations where the excursions were greatest. The head was fixed as firmly as possible to the sled using a custom made dental bite. Each experimental series consisted of 5-10 acceleration pulses delivered with each of the four profiles. Before each series, the eye movement recordings were calibrated by having subjects fixate a series of

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targets located at -10, -5, 0, 5, and 10 degrees eccentricity in both the horizontal and vertical directions.

For data analysis, only saccade free trials were used. For each of the five accelerations and four target distances, eye and head movement profiles were averaged

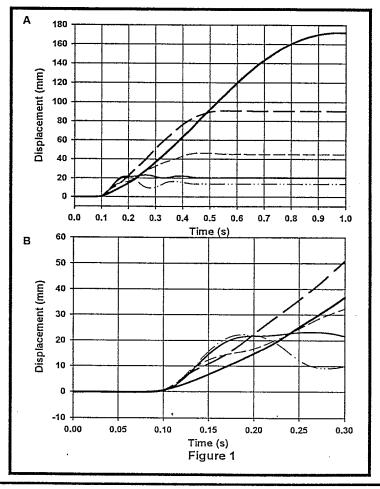


Figure 1: Representative head movements for each of the different acceleration profiles. Note that the different traces are depicted with the same line styles in both A and B. A: Complete head excursions. B: Magnified view of the first 250ms to emphasize the rapidity of the movement onset.

using a custom software package and stored for further analysis. These average files were then imported into SigmaPlot (Jandel Scientific) for further analysis and plotting. Velocity and acceleration were calculated using a four-point differentiator based on a least squares technique (Savitzky and Golay, 1964). This is similar to the familiar two-point central difference differentiator but is less sensitive to high frequency noise.

RESULTS:

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Representative head displacements are illustrated in Figure 1. The entire

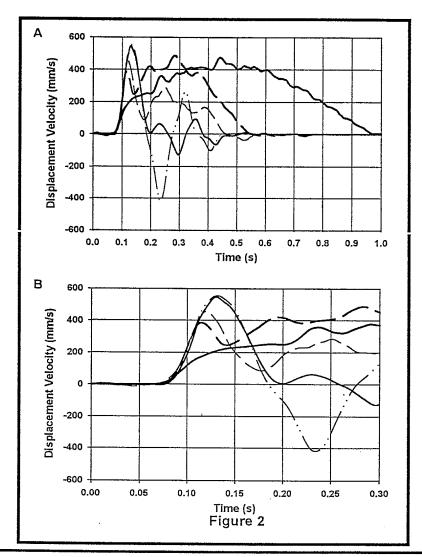


Figure 2: Head velocities corresponding to the trajectories depicted in Figure 1. Not that with the highest accelerations, a maximum velocity of over 500cm/s is achieved within approximately 100ms.

displacements profile is illustrated in Figure 1A while only the first 200ms are shown in 1B to emphasize the rapid accelerations that were produced. Head velocities were then

calculated and are illustrated in Figure 2. As can be seen, with the largest acceleration profiles, maximum velocities of nearly 600 mm/s were reached within 50ms of movement onset. This corresponds to an acceleration of more than 1.25g. Given the high

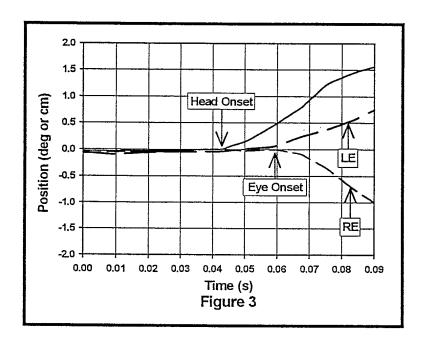


Figure 3: Eye and head movement onset. Note that the eyes begin to converge less than 20ms after the onset of the head movement.

velocities and accelerations achieved, it was possible to obtain estimates of the latency of the naso-occipital tVOR. A typical recording is illustrated in Figure 3. As can be seen in this trace, the eyes begin to converge less than 20ms after the onset of the head movement. The mean latency of the NO tVOR was found to be 19ms (11 subjects, range 16-23ms). This should be viewed as an upper limit on the tVOR latency; higher accelerations might yield lower values. Although four different target distances were used, the target distance itself had no impact on the measured latencies as target distance effects had much longer latencies.

A representative eye movement record from one subject is depicted in Figure 4.

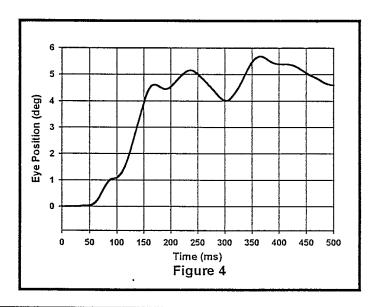


Figure 4: Representative eye movement recorded during a high acceleration trial. Note that the eye reaches a deviation of more than 4.5deg within 120ms.

Although the sled movement resulted in an oscillatory head movement during the high acceleration trials, the rapid change in eye velocity is clearly seen. Specifically, the eye excursion rises to its maximum value within approximately 100ms. Although slightly higher accelerations were used in some trials, greater eye accelerations were not observed.

The timing of the effects of target distance on the tVOR was also investigated. Accordingly, the vergence angle was calculated by subtracting the left and right eye records and then plotted for different target distances. As can be seen in Figure 5, when the eye movements generated with a target located at 20cm are compared with those generated by a target at 100cm, the trajectories are initially identical. The two traces only begin to diverge approximately 80ms after the initial eye movement onset. Since the eye movement begins approximately 20ms after the onset of the head movement, the effects

of changes in target distance are only seen about 100ms after head movement onset. This

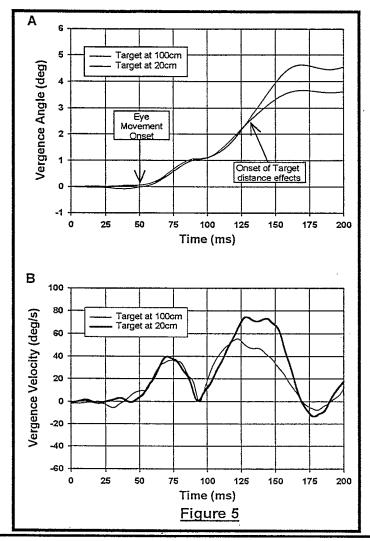


Figure 5: Comparison of eye position (A) and velocity (B) with near and far targets. Note that there is no effect of target distance until approximately 85ms after the onset of the eye movement.

value varied somewhat from subject to subject. The average latency for the expression of target distance effects was found to be 96ms (SD 8ms, range 86-107ms). Note that in order to facilitate comparison of the two traces, the initial vergence values were subtracted from the average so that both traces begin with a vergence of zero. Figure 5B illustrates the eye velocities associated with Figure 5A. Note the rapid increase in eye velocity, particularly with a near target, to a value of nearly 80 deg/s.

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Discussion:

While early papers suggested that the latency of the tVOR was quite long, this would appear to be an artifact of the relatively modest accelerations that were used. Low accelerations result in long latency estimates due to the time required to accelerate the head, and the resulting eye response, to values sufficiently higher than the inherent noise level to be detected. Indeed, the demonstration by Uchino et al. (1996,1997) of monosynaptic connections from the utricle to the abducens nucleus implies that latencies should be very short. In addition, Angelaki (1998) recently used parameter estimation techniques to calculate the latency and transfer function of the tVOR. This approach yielded a value for the latency of approximately 10ms. However, since the parameter estimation assumed that the system was linear, and it may not be, this result needs to be confirmed.

Recent experiments by Crane and Demer (1998) demonstrated that the increase in gain associated with viewing a near target during combined rotational and translational stimulation was present almost from the onset of the eye movement. Given this result, we were surprised by the relatively long latency of our target distance effects. Indeed, we only found trajectory differences occurred nearly 100ms after the onset of the eye movement. Indeed, in some subjects, latencies were so long that visual tracking mechanisms might have played a role. The reason for this difference is unclear. One possibility is that target distance effects on the disjunctive eye movements elicited by our naso-occipital accelerations may be greater than those produced by combined rotational and translational stimuli, especially as the translational acceleration in the Crane and Demer (1998) experiments was directed along the inter-aural axis. Another possibility is

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that their latency might be less than we found simply because our stimulus did not produce very high eye velocities so that more time was required before the trajectories deviated significantly from one another.

One additional area, which we attempted to investigate during these experiments, was the dynamics of the disjunctive eye movements elicited by naso-occipital motion. It is well known that excitatory afferents from the vestibular nucleus, which are responsible for the horizontal aVOR, cross the midline to terminate on both motoneurons and interneurons in the abducens nucleus. Such an arrangement will produce conjugate eye movements. The NO-tVOR when elicited with a target located close to the midline however, requires that the two eyes move in opposite directions. How this might be accomplished is unclear. One possibility is that the required vergence eye movements might be generated by otolith signals that project to the vergence system. However, given the high eye velocities generated in our experiments, this seems unlikely. Collewijn and his colleagues (1995) showed that 5 degree vergence movements attained a peak velocity of approximately 40 deg/s. In our experiments, comparable changes in vergence angle were accomplished with velocities nearly twice that. Such high velocities argue against the possibility that vergence pathways are being used. Another possibility is that the signals might travel up the medial longitudinal fasciculus (MLF) or the ascending tract of Deiters (ATD) to terminate on medial rectus motoneurons. The latter possibility is particularly attractive as Chen-Huang and McCrea (1998) demonstrated that changes in fixation distance had very strong effects on ATD neuron behaviour and concluded that ATD neurons played an important role in mediating target distance effects on the VOR.

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Since these neurons were also shown to carry otolith-related activity, they are logical candidates for mediating the disjunctive NO-tVOR.

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