TITLE

DEGRADATION OF VISUAL PURSUIT DURING SUSTAINED +3 Gz ACCELERATION

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ORIGINAL RESEARCH

Degradation of Visual Pursuit During Sustained $+3\ G_z$ Acceleration

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Background: During positive acceleration, there is a diminished flow of blood to all regions above the heart. This is manifested by the commonly described loss of peripheral vision, greyout and blackout, which have been investigated extensively. The ability to select appropriate scanning patterns and to efficiently process visual information is one of the important determinants of scan effectiveness. This study investigates the performance of the smooth pursuit system under sustained $+3\ G_z$ before any signs of loss of vision. ***Methods:*** Eleven subjects with no known oculomotor and vestibular anomalies participated in the study. Horizontal and vertical pursuit at amplitudes of 10 and 20° were investigated in each of the subjects over 4 separate days. During each test session, pursuit targets of a predictable sine wave, oscillating at 0.2, 0.4, 0.8, 1.2 and 1.6 Hz were presented to the subjects in a random order. Horizontal and vertical eye movements were recorded using the El-Mar eye tracking system. The subjects were tested in 4 trials: 1) at 1 G before exposure to increased acceleration; 2) during sustained $+3\ G_z$; 3) immediately after the $+3\ G_z$ exposure; and 4) 5 min after the $+3\ G_z$ exposure. ***Results:*** Breakdown in smooth pursuit in response to horizontal and vertical sinusoidal stimuli during $+3\ G_z$ is indicated by a statistically significant decrease in gain and an increase in phase lag ($p < 0.01$). This is most obvious when the stimulus frequency is greater than 0.4 Hz. Qualitatively, the pursuit response during acceleration was ataxic and disorganized in appearance. ***Conclusion:*** It is postulated that degradation of pursuit gain and phase could be due to central hypoxia, and that the increase of G loading on the vestibular system could affect the neural integration of the pursuit signal in the vestibular nuclei with its direct output to the oculomotor system.

Keywords: ocular pursuit, eye movements, acceleration.

TODAY'S HIGH PERFORMANCE aircraft can generate increased, prolonged accelerations during dive pull-outs and banked turns. Exposure to increased accelerations affects the body in a number of ways; for example, motor coordination skills are impaired, the cardiovascular and respiratory systems are stressed, and the vestibular system is stimulated in a manner that may result in various gravitational-inertial illusions.

In contrast to other sensory modalities, vision is profoundly affected by acceleration (4). From the psychophysiological point of view, dimming, peripheral light loss, greyout, and blackout are the most commonly used indices of vascular stress resulting from increased $+G_z$. Unfortunately, these indices are crude and do not, for example, provide useful answers about the effects of accelerations at levels below the limit of varying degrees of vision loss on the visual-vestibular system. Moreover, these indices do not lend themselves to the determination of changes in vision that are ancillary to cardiovascular disturbances associated with acceleration.

Depending on the subject, within the range of +3 to $+7\ G_z$, it was reported that a stage is reached where there is a limitation of ocular motility (7) with the subject's eyes coming to rest in the primary position. However, this ocular immobility can be overcome by voluntary effort but the superseding movements are ataxic. The mechanism of this limitation of ocular motility is hypothesized to be a dysfunction of the normal oculomotor control systems caused by cerebral hypoxia. However, the quantitative analysis of performance and disruption of the oculomotor control system under sustained $+G_z$ acceleration, and the direct effect of sustained $+G_z$ acceleration on the vestibulo-oculomotor system remain relatively unknown.

Eye movements are of two principal types: those that stabilize gaze to keep images steady on the retina and those that shift gaze to direct the line of sight at an object of interest. The function of the smooth pursuit system is to generate smooth eye movements that keep the image of a moving target on the fovea from slipping across the retina (11). It has been reported that general disorientation due to acceleration stress in the centrifuge situation could affect the sensory integration of the most experienced observer (5). This study investigated the quantitative effect of acceleration on the performance of visual pursuit at $+3\ G_z$ before the development of the aforementioned behavioral symptoms that will lead to loss of vision.

METHODS

A group of 11 subjects (2 females and 9 males) ranging in age from 23 to 42 yr participated in the study. They had no known history of ophthalmologic, oculomotor, or vestibular disorders, and they had no spon-

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taneous nystagmus nor a Romberg sign with eyes opened or eyes closed. All subjects obtained medical approval to participate from a Defence Civil Institute of Environmental Medicine (DCIEM) physician. The research protocol and procedures were reviewed by the DCIEM Human Ethics Committee and the subjects were asked to review and sign the Human Experimentation Subject Volunteer Consent Form before their participation. All subjects were instructed to strictly abstain from alcohol, tobacco (cigarette smoking), and over the counter and prescribed medication for at least 24 h prior to the experiment, as these substances may affect their visual pursuit tracking ability. All except three subjects had previous experience as participants in human centrifuge study.

Motion Stimulus

The experiment was conducted using the DCIEM man-rated centrifuge, which consists of a rotating arm 6.1 m long from the center of rotation to the pivoting point of the gondola. The gondola is passively coupled to the G_z vector and pivots on self-aligning trunnion bearings. The gondola swings out freely during rotation, such that the resultant vector of gravitational and centrifugal acceleration is always orthogonal to the floor of the gondola. Consequently, subjects inside the gondola experience an increased downward-pulling force in the direction of their spinal (z) axis thus achieving a $+G_z$ centrifugation. In the present study, the resultant force either equaled Earth's gravity ($+1\ G_z$; centrifuge stationary) or exceeded it by a factor of 3 ($+3\ G_z$; centrifuge rotating at approximately 20 rpm).

Subjects were seated and secured in the gondola facing the forward direction of motion of the gondola. A gradual onset rate of $0.1\ G \cdot s^{-1}$ was employed on relaxed subjects not wearing anti-G suits until it reached the target of $+3\ G_z$ level, and was maintained at $+3\ G_z$ for the designated pursuit trial. At the end of the trial, the centrifuge decelerated to $+1\ G$ at $1\ G \cdot s^{-1}$.

Binocular horizontal and vertical eye movements were recorded simultaneously using the El-Mar video-based binocular eye-tracking system (El-Mar Inc. Series 2020, Downsview, Ontario) mounted on a CF (Canadian Forces) standard flight helmet. The El-Mar eye tracking system has a linear range of ±25° on the vertical meridian and ±30° in the horizontal, and a maximum resolution of 0.1° when measured with an artificial eye based on previous studies (1). The helmet-mounted eye tracking system and thus the head of the subject was immobilized by a head restraint mechanically attached to the seat inside the gondola. The head restraint design positions the subject's head so that the plane of the lateral semicircular canals is approximately parallel to the horizontal axis. The design also allows a maximum of 3 cm vertical translation of the subject along the spinal (z) axis. This is necessary because increased acceleration tends to cause the subjects to sink into the seat. The translation along the spinal axis is in the range of a few millimetres. However, translations along the x and y axes, as well as movements along the roll, pitch, and yaw planes were not possible. Two-way audio communication and closed-circuit video monitoring of the subject were available from the centrifuge control room.

TABLE I. TARGET MOVEMENT CHARACTERISTICS FOR BOTH HORIZONTAL AND VERTICAL PURSUITS.

Stimulus Frequency (Hz)	Amplitude (degrees)	Peak Velocity ($° \cdot s^{-1}$)
0.2	10	12.5
	20	25
0.4	10	25
	20	50
0.8	10	50
	20	100
1.2	10	75
	20	150
1.6	10	100
	20	200

Visual Stimulus

Visual pursuit was performed with the subjects tracking a sinusoidally moving target from a light-bar. The light-bar, 70 cm long, mounted 1 m in front of the subject, was custom-built for the centrifuge gondola with no moving parts, so that any pursuit deficiencies observed can be attributed to the deficiencies in the smoothness of eye movement recordings. The light-bar system is similar to commercially available clinical optical stimulators, which provide precise control of optical stimuli. Depending on the mechanical mounting configuration, horizontal and vertical sinusoidal stimuli could be displayed in different sessions. The waveform used was a predictable sine wave. Sinusoidal stimuli provide the opportunity to study the effects of increasing peak velocity and peak acceleration of the stimulus on gain (eye velocity/target velocity).

Stimulus Conditions

Horizontal and vertical pursuit with peak-to-peak amplitude of 20 and 40°, respectively, were investigated. A total of four stimulus conditions were investigated on separate days: horizontal 10°, horizontal 20°, vertical 10° and vertical 20°. Target amplitude was kept constant so that an increase in target frequency was accompanied by an increase in peak acceleration and in peak velocity.

For each stimulus condition, pursuit targets at 0.2, 0.4, 0.8, 1.2, and 1.6 Hz were presented randomly to the subject. The frequencies and amplitudes were chosen to cover a broad dynamic range. Increasing target frequency corresponds to increasing levels of tracking difficulty. Target movement characteristics for the horizontal and vertical pursuit are shown in **Table I.** Each stimulus condition lasted less than 2 min.

Test Procedure

The elevator illusion is an apparent elevation of a visual target, which has been shown to depend on both the intensity of the gravitational inertial forces and the orientation of the head (6). In order to suppress the "elevator illusion" that subjects might experience under increased acceleration in the centrifuge, a target at the center of the light bar is on at all times. Subjects were instructed to fixate on the LED target during the onset of acceleration and before the pursuit trials were to begin.

Before each trial, the subject indicated to the experimenter that they were prepared and had directed their eyes on the target and were instructed to visually follow the target. The experimenter then triggered the stimulus without further warning to the subjects. A minimum of 8 cycles of data was recorded for each stimulus frequency.

After dark adaptation and calibration of the eye tracker, the trial sequence was administered to the subject at 1 G before the acceleration, and will be referred to from here on as "PRE" trial. A gradual onset rate of 0.1 $G \cdot s^{-1}$ was employed on relaxed subjects not wearing anti-G suits until it reached the target of $+3$ G_z level. After waiting for another 60 s for the decay of transient vestibular responses, the same sequence was administered to the subject, and is referred to as the "TEST" trial. During the preliminary trials we varied the waiting period from 30, 45, and 60 s, and in no case did any of the subjects complain of disorientation sensation due to Coriolis effects, nor did they exhibit any spontaneous eye movements. At the end of the sequence, the centrifuge decelerated at 1 $G \cdot s^{-1}$. When the gondola came to a full stop, the same sequence was repeated and is referred to as the "POST" trial. The sequence was repeated again 5 min later and is referred to as the "POST5" trial. The entire test session lasted about 15 min, including the 5 min of rest between POST and POST5. This order was used to separate effects and after-effects of hypergravity from purely time-related phenomenon such as fatigue or learning. A normal subject could perform the tests without undue fatigue. During debriefing, subjects were to report any experience of elevator illusion, greyout or blackout, episodes and symptoms of motion sickness.

Data Collection and Analysis

Horizontal and vertical eye positions from both eyes of the subject and the pursuit stimulus position were recorded. Analog eye positions from the EL-MAR system were digitized by computer sampling at 120 Hz and digitized with 16-bit resolution over a 45° peak-to-peak range. Digitized data was then displayed on a graphics monitor for review and subsequent analysis.

The eye position recorded represents the total tracking response of the subject pursuing the target. It consists of slow (smooth pursuit) and fast (saccadic) components. The eye position signal was differentiated to yield instantaneous eye velocity. The first one half cycle of data was always discarded. All measurements were based on an average of 8 consecutive cycles that represented the subject's best response. The fast component represents the re-fixation eye movements that are required to re-fixate on the target when the pursuit system fails to provide adequate tracking of the target. The fast components were identified by their direction and characteristic velocity profile, and were removed. A fast Fourier transform was then performed giving a DC offset term, the magnitude and phase of the fundamental, and the percent harmonic distortion was expressed as follows: [magnitude of the first 7 harmonics divided by (magnitude of fundamental + magnitude of the first 7 harmonics × 100]. This algorithm is similar to that used by Baloh et al. (2). During the smooth pursuit of a target moving sinusoidally, the measurements made to evaluate the responses are gain and phase. The gain of the slow pursuit eye movements is defined as the magnitude of the fundamental divided by the peak target velocity. It was calculated with an algorithm which selected and analyzed the slope of each eye movement (slow phase eye velocity) and compared it with the stimulus over the duration of the experimental session. Phase is defined as a measure of the temporal synchrony between the target and the eye. The phase lag between the eye movement response and the stimulus was measured by the distance between the points at which the stimulus acceleration was zero to the transition point at which the slope of eye displacement was zero (velocity of slow phase eye velocity was zero). Ideally, during normal pursuit response, the gain is close to 1 and the eye does not lag behind the target, therefore phase lag should be minimal.

The mean gain and phase lag of the pursuit response in PRE, TEST, POST, and POST5 trials were compared using analysis of variance, repeated measures design followed by Planned Comparison Post-hoc Analysis. The multiple comparison significance level was set at 99% (0.01). P-values for factors with more than two levels were adjusted using the Greenhouse-Geisser's epsilon correction factor to provide a more conservative F-value.

RESULTS

The data from our naive subjects (subjects who had no prior experience in the centrifuge) showed no overt difference from the others and, therefore, all data were analyzed in the same manner. All 11 subjects completed the horizontal pursuit trials. However, due to severe motion sickness and disturbance from disorientation during the decelerating phase of the centrifuge, 1 of the 11 subjects withdrew his participation from the vertical pursuit trials. None of the subjects reported any visual symptoms such as darkening of the visual field or loss of peripheral vision under sustained $+3$ G_z.

Our attempts to suppress the "elevator illusion" appeared to be successful. Only one of the subjects reported this apparent elevation of target on a single occasion and it lasted for a few seconds during the transition phase to $+3$ G_z. Eye tracking data were recorded from each eye separately. Visual inspection of the polygraph tracings and plots of slow component velocity from both eyes revealed identical responses from the right and the left eyes of all subjects. This also applies to both horizontal and vertical pursuits. Although pursuit gain and phase shift of both eyes were extracted, only the data from the right eye of all subjects was statistically evaluated to determine if there were any significant differences between the various frequencies, amplitudes and G-levels.

On inspection of the position tracings, as expected, the pursuit responses showed considerable inter-sub-

TABLE II. PHASE AND GAIN AS A FUNCTION OF +GZ LEVEL AND STIMULUS FREQUENCY.

+Gz Level	Stimulus Frequency (Hz)				
	0.2	0.4	0.8	1.2	1.6
Gain					
PRE	0.900 ± 0.009	0.872 ± 0.008	0.817 ± 0.015	0.737 ± 0.021	0.649 ± 0.026
+3 Gz	0.874 ± 0.008	0.801 ± 0.001	0.723 ± 0.020	0.62 ± 0.023	0.516 ± 0.029
POST	0.887 ± 0.012	0.882 ± 0.008	0.829 ± 0.017	0.729 ± 0.021	0.614 ± 0.090
POST5	0.890 ± 0.014	0.824 ± 0.017	0.824 ± 0.017	0.739 ± 0.024	0.636 ± 0.030
Phase					
PRE	1.96 ± 0.150	4.29 ± 0.346	11.1 ± 0.512	23.24 ± 1.167	35.54 ± 2.323
+3 Gz	2.86 ± 0.262	6.51 ± 0.379	16.74 ± 0.719	30.99 ± 1.568	47.46 ± 2.295
POST	1.99 ± 0.204	4.56 ± 0.343	12.54 ± 0.653	24.77 ± 1.412	38.72 ± 2.543
POST5	1.92 ± 0.152	3.92 ± 0.195	12.23 ± 0.583	25.4 ± 1.5270	39.78 ± 2.382

$\alpha = 0.01$; ±SE, PRE = trial at +1 G before exposure to acceleration; TEST = test trial at sustained +3 Gz; POST = trial at +1 G immediately after the +3 Gz exposure; POST5 = trial at +1 Gz 5 min after completion of POST.

ject variability. Inspection of the tracings also revealed that within each subject during horizontal pursuit there were no differences between the mean gain of right and left pursuit, nor during vertical pursuit were there differences between the mean gain of upward and downward pursuit. At the lowest target velocities, some subjects could produce a clear signal with little distortion, while others often had frequent superimposed saccadic eye movements. As the target velocity increased all subjects used saccades inter-mixed with attempts at smooth pursuit. At the highest target velocity some subjects relied primarily on saccades to follow the target.

Effects of Sustained $+G_z$ on Visual Pursuit

A 4 ($+G_z$ level) × 2 (direction: horizontal and vertical pursuit) × 2 (amplitude) × 5 (frequency) repeated measures ANOVA was performed on both the gain and phase pursuit parameters. Following epsilon correction the analyses revealed the following identical effects for the gain and phase parameters respectively: significant main effects for the $+G_z$ level [(F3, 27) = 45.39608 $p \leq 0.000001$, $\epsilon = 0.68788$; (F3, 27) = 68.6645, $p \leq 0.000001$, $\epsilon = 0.65964$)] and the stimulus frequency [(F4, 36) = 37.73177 $p \leq 0.000001$, $\epsilon = 0.30838$; (F4, 36) = 113.0137, $p \leq 0.000001$, $\epsilon = 0.37344$)] and significant interactions between $+G_z$ level and stimulus frequency [(F12, 108) = 8.24745 $p \leq 0.000001$, $\epsilon = 0.33227$; (F12,108) = 12.9624, $p \leq 0.000001$, $\epsilon = 0.34148$)]. There were no significant effects involving either the direction or amplitude of the pursuit stimulus. The two-way interactions involving $+G_z$ level and stimulus frequency for the phase and gain parameters are presented in **Table II**. Inspection of the gain results (top of Table II) reveals that as stimulus frequency increased gain decreased, and that across the stimulus frequency levels the greatest decrement in gain occurred at the $+3\ G_z$ level. On the other hand, as stimulus frequency increased the phase lag increased (bottom of Table II), and that across all stimulus frequency levels the greatest increase in phase lag occurred at $+3\ G_z$. In both the gain and phase, the PRE and POST values where similar.

Subsequently, two 3-way interactions involving $+G_z$ level, direction, and stimulus frequency, illustrated in **Fig. 1**, were used to examine of the following pursuit parameters: horizontal gain, vertical gain, horizontal phase and vertical phase. Fig. 1A and 1B illustrate the effect of $+3\ G_z$ level on gain during both horizontal and vertical pursuit. Regardless of the direction (horizontal or vertical) of visual pursuit, as stimulus frequency increased the gain decreased, and that across the stimulus frequency levels the greatest decrement in gain occurred at the $+3\ G_z$ level.

Planned comparisons (**Table III**) revealed that, with the exception of vertical pursuit at 0.2 Hz, the decrease in gain was significantly lower at $+3\ G_z$ than at the PRE, POST, and POST5 trials regardless of the direction of visual pursuit. Further planned comparisons between the PRE and the two post trials in the horizontal gain and vertical gain parameters revealed no significant differences.

Fig. 1C and 1D illustrate the effect of $+G_z$ level on phase lag during both horizontal and vertical pursuit. Regardless of the direction of visual pursuit, as stimulus frequency increased the phase lag increased, and across all stimulus frequency levels the greatest increase in phase lag also occurred at $+3\ G_z$. Planned comparisons (**Table IV**) revealed that, with the exception of vertical and horizontal pursuit at 0.2 Hz, the increase in phase lag was significantly greater during $+3\ G_z$ than at the PRE, POST and POST5 trials regardless of the direction of visual pursuit. Further planned comparisons between the PRE and the two post trials during horizontal pursuit in the phase parameter revealed no significant differences within the frequencies tested. However, during vertical pursuit in the phase parameter planned comparisons revealed the presence

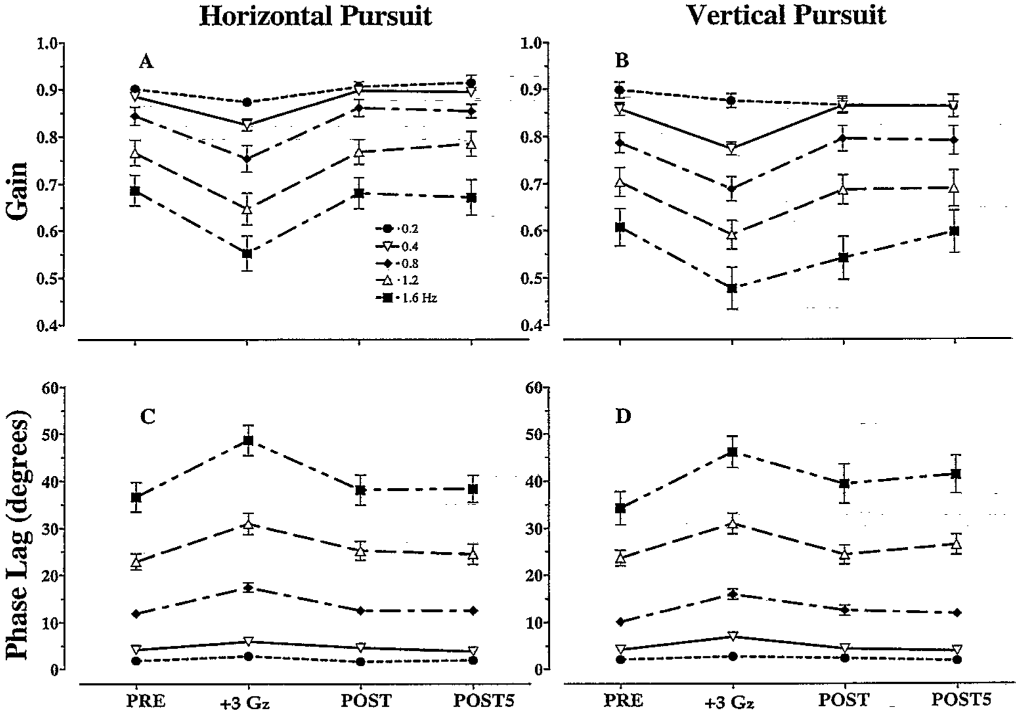

Fig. 1. Summary of mean gain decrease (1A-horizontal, 1B-vertical) and mean phase increase (1C-horizontal, 1D-vertical) as a function of +Gz level and stimulus frequency. (PRE = test trial at +1 Gz before exposure to acceleration; TEST = test trial at sustained +3 Gz, POST = test trial at +1 Gz immediately after the +3 Gz exposure, POST5 = test trial at +1 Gz 5 min after completion of POST1. Bars represent SEM and may not be visible due to size of symbol). As stimulus frequency increased the gain decreased, the phase increased and that across the stimulus frequency levels the greatest decrement in gain and increment in phase occurred at the +3 Gz level.

of significant difference between the PRE trial and POST5 trial at 1.6 Hz (p = 0.00349).

DISCUSSION

To our knowledge, there has not been any quantitative study investigating visual pursuit performance under +Gz stress. Most of the literature concentrates on how increased acceleration severely impairs the retinal circulation causing greyout, loss of peripheral vision and progresses to complete loss of visual function when the systolic pressure at eye level falls to around 20 mm Hg. Duane et al. (7) reported that eye motion under high G-loading is perfectly feasible. Trained centrifuge subjects were physically capable of voluntarily moving their eyes on all axes of motion if sufficient effort was made, although the movements were ataxic in nature. The authors further proposed that the most probable explanation for ocular ataxia is that a loss of sensory feedback from the retina occurs. The other possibility for the ataxic eye movements is gaze nystagmus during extreme lateral gaze.

For complete knowledge of how well the eye is following at the target, the phase relation between target and eye movements must be investigated. Even with considerable loss of amplitude, it is still possible to see the target reasonably well, providing there is no phase lag. In this case, at each velocity mode the image must temporarily be stationary on the retina. If the eye is appreciably phase shifted relative to the target, as demonstrated in our data, the image will never be stationary on the retina. To be stationary without phase-lag, the image must be foveal in smooth pursuit, especially with +3 Gz load at high stimulus velocities. Although our study involves pursuit tracking in a less complex environment than actual flying, it offers a significant challenge to the pursuit tracking system in the majority of our subjects. At frequencies greater than 0.4 Hz, both

TABLE III. PLANNED COMPARISONS: SIGNIFICANT DIFFERENCES IN GAIN AT +3 GZ COMPARED TO THE PRE, POST, AND POST5 +GZ LEVELS IN EACH FREQUENCY TESTED.

Stimulus Frequency (Hz)	Horizontal Gain (+3 Gz vs. PRE, POST & POST5)	Vertical Gain (+3 Gz vs. PRE, POST & POST5)
0.2	p=0.000281	n.s.
0.4	p≤0.000001	p=0.000026
0.8	p=0.000040	p=0.000003
1.2	p=0.000005	p=0.000002
1.4	p=0.000012	p=0.000002

TABLE IV. PLANNED COMPARISONS: SIGNIFICANT DIFFERENCES IN PHASE LAG AT +3 GZ COMPARED TO THE PRE, POST, AND POST5 +GZ LEVELS IN EACH FREQUENCY TESTED.

Stimulus Frequency (Hz)	Horizontal Phase (+3 Gz vs. PRE, POST & POST5)	Vertical Phase (+3 Gz vs. PRE, POST & POST5)
0.2	n.s.	n.s.
0.4	p=0.00004	p≤0.000001
0.8	p≤0.000001	p=0.000013
1.2	p=0.000027	p=0.000001
1.4	p≤0.000001	p=0.000002

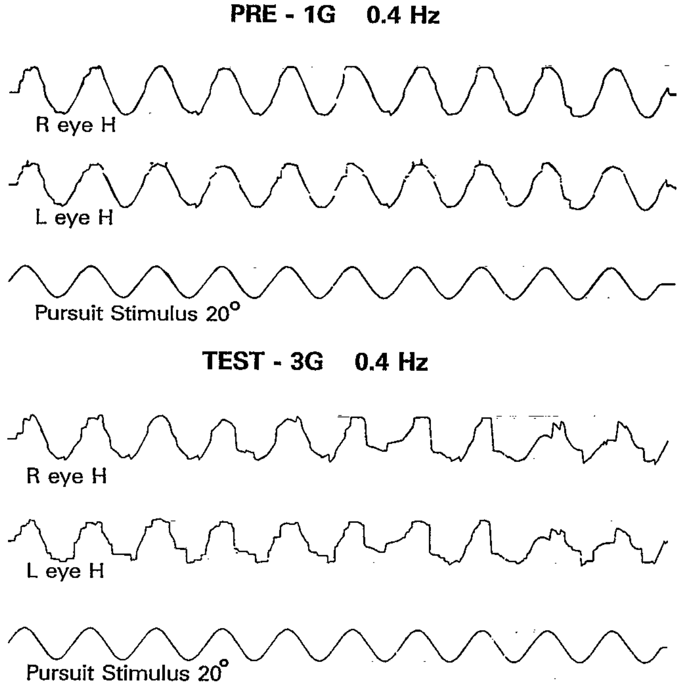

Fig. 2. Position tracing of a subject exhibited ataxic and disorganized pursuit during horizontal pursuit at 0.4 Hz at 20°. Fig. A (Upper) was performed under 1G. Fig. B (Lower) was performed under +3 Gz condition. (R eye H = Right eye horizontal position; L eye H = left eye horizontal position).

horizontal and vertical pursuits showed substantial impairment during sustained +3 Gz acceleration. This impairment is exemplified by a significant decrease in gain and a significant increase in phase lag.

From the polygraph tracing, the breakdown in smooth pursuit is identifiable by its ataxic and disorganized appearance. The smooth tracking capacity was substituted by saccadic eye movements of varying degrees in some subjects. The subjects' eye position fell behind the moving target briefly, then retrieved it with a saccade. **Fig. 2A** and **2B** illustrate the typical response of a subject tracking at a frequency of 0.4 Hz and amplitude of 20° during PRE +1 Gz and +3 Gz levels, respectively. The corresponding velocity plots for Fig. 2A and 2B, eye velocity vs. stimulus velocity during horizontal pursuit at 0.4 Hz at amplitude of 20° between +1Gz and +3Gz, are shown in **Fig. 3A** and **3B**, respectively.

It has been well established that the pursuit reflex breaks down when either the velocity of the target movement is too great, $> 40-60° \cdot s^{-1}$, or when the frequency of a direction changing movement is too high, > 1–2 Hz (9). The rapid decline in the gain of the pursuit reflex and the development of large phase lag at frequencies above 1 Hz has been shown both by recording the eye movements of subjects attempting to follow an oscillating target (18) and by measurement of visual performance (3). Our data is consistent with previous findings regarding the general characteristics of horizontal and vertical pursuit with increasing frequency and amplitude. In addition, our data indicated a significant increase in phase lag and a significant decrease in mean gain at all stimuli during +3 Gz as compared with all other +1 G conditions.

Contrary to previous findings (2), we did not observe a significant difference between horizontal and vertical pursuit within the gain or within the phase pursuit parameters at the frequencies and amplitudes tested. Our observations also do not support the finding that asymmetries may occur during vertical pursuit within the gain and phase pursuit parameters in normal subjects with both up and down preponderance (2). Nor did we observe any asymmetries during horizontal pursuits (left and right) in the gain and phase pursuit parameters.

What are the possible mechanisms underlying the decrease in pursuit performance under sustained acceleration? Previous studies (8,18) have speculated that acceleration has a direct mechanical effect on the eyeball. For example, Steinbach (16) has proposed that gravity appears to influence the resting eye position based on the observation that the center of mass of the human eye is behind the center of rotation. If this is the case, we should expect some asymmetry in the gain and phase characteristics of the upward pursuit and downward pursuit under sustained gravity. However, under sustained +3 Gz we did not observe any asymmetries during horizontal pursuit within the gain and phase pursuit parameters within and across subjects at the

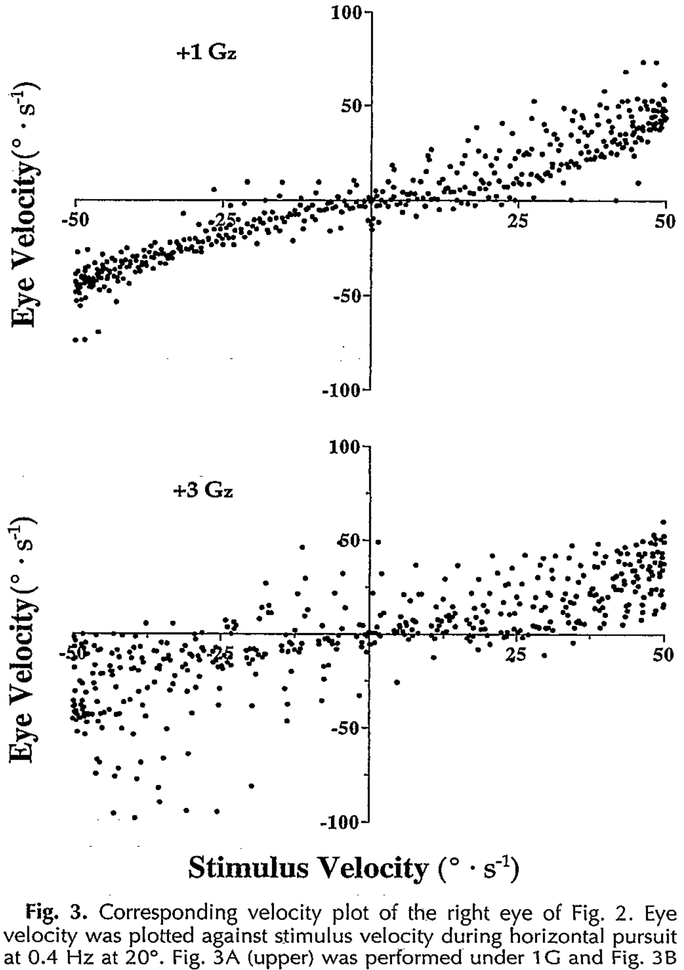

Fig. 3. Corresponding velocity plot of the right eye of Fig. 2. Eye velocity was plotted against stimulus velocity during horizontal pursuit at 0.4 Hz at 20°. Fig. 3A (upper) was performed under 1G and Fig. 3B (lower) was performed under +3 Gz condition.

frequencies and amplitudes tested. This speculation of a mechanical effect is further refuted by previous study showing that ocular ataxia disappeared during the application of negative pressure while the relative weight of the eyes remained constant at a given G level (6) and that there was a re-gain of sensory feedback from the retina. The mechanics of target tracking probably play a secondary role in acquiring, identifying and tracking a moving target in a realistic situation. Various cognitive factors conditioned by experience and practices are probably more important than the mechanics itself.

Increased acceleration on human subjects decreases the efficiency of gas exchange, causing arterial desaturation, and increases the possibility of cerebral hypoxia despite adequate perfusion. The underlying mechanisms of the aforementioned phenomena involve an acceleration-induced steepening of the pulmonary perfusion gradient and a decrease in central blood volume due to venous pooling in the dependent veins (9). It has been shown that at $+3\ G_z$, the alveolar-arterial oxygen difference rises enough to cause significant arterial desaturation, both in unprotected subjects (13,14) and in those wearing anti-G suits (12).

Cerebral hypoxia produced by positive acceleration was postulated to produce a dysfunction in the normal oculomotor and pupillary control systems that lead to ocular fixation and pupillary dilatation. There is some evidence that the gain of smooth pursuit eye movements seems to be affected by changes in oxygen partial pressure. For example, the occurrence of limitation of ocular motility appeared to be related to the subjective sensations of greyout and blackout (7). This limitation of ocular motility closely parallels similar observations reported in other forms of anoxia. It was reported that during acute arrest of cerebral circulation using a cervical cuff, the eyes of the subject fixated and were incapable of following the examiner's finger moving rhythmically from side to side in the horizontal plane (15).

Evidence on the effect of hypoxia on the oculomotor system is scarce. Urbani et al. (17) reported that six subjects who underwent 30 min acute exposure to hypobaric hypoxia at 5000 m demonstrated a decrease in smooth pursuit gain. Eye movements were recorded with an EOG technique before, during, and after hypoxia, and analyzed for peak velocity gain. The authors concluded that the observed decrease in gain and its time course might be interpreted as an adaptive change within the nervous system in response to the hypoxic stress.

On exposure to sustained acceleration, one could encounter hypoxic hypoxia due to the impaired gas exchange in the lungs resulting in inadequate tension of the oxygen in the arterial blood and hence in the capillary blood. Stagnant (circulatory) hypoxia could also be produced by a fall in cardiac output and arterial BP when exposed to sustained positive acceleration. The oxygen contents and tension of the blood fall more rapidly than normal as it flows through the capillary bed, so that oxygen tension at the venous ends of the capillaries is inadequate to maintain tissue oxygenation. Although the literature on hypoxic effects at less than $+5G_z$ acceleration is unclear, it is likely that the observed degradation of visual pursuit is a result of hypoxia during positive acceleration.

However, we cannot completely rule out the possibility that the increase G-loading on the vestibular system affects the neural integration of the pursuit signal in the vestibular nuclei, which has direct output to the oculomotor system. The reason is as follows. The effects of sustained linear acceleration along the G_z axis act on the otoliths. Anatomically, retinal information on the speed and direction of a moving target cascades through the visual cortex, the medial superior temporal visual area, and to the lateral (LVN), descending (DVN) and medial (MVN) vestibular nuclei. Although all three vestibular nuclei receive inputs from the utricular and saccular otoliths, the DVN is a major recipient of otolith fibers and many tilt sensitive neurons were found in the MVN. The vestibular nuclei probably perform the necessary neural integration of signals before the pursuit command is finally sent to the oculomotor nucleus. The underlying mechanism of the observed pursuit degradation under acceleration awaits further investigation.

In 79 out of 80 Planned Comparisons, there was no significant difference between pre and post trials, which is in agreement with the observation that there was no learning effect in the pursuit performance. If this were not the case we would expect many more significant increases in gain and decreases in phase lag toward the end of the trials. Similarly, there appeared to be no effects from fatigue, in which case, we would expect further decreases in gain and further increases in phase lag in the POST and POST5 conditions.

CONCLUSIONS

In conclusion, when the smooth pursuit system was studied as a function of sustained acceleration the gain decreased and the phase lag increased. Smooth pursuit was most sensitive to sustained acceleration when these systems were stressed to their frequency limits. Operationally, the question remains whether the performance on visual pursuit under sustained acceleration could be improved by practice.

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