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US ARMY MEDICAL RESEARCH LABORATORY

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REPORT NO. 764

ADAPTATION TO PROLONGED CONSTANT ANGULAR ACCELERATION

(Progress Report)

by

James H. Brown, Ph. D.

and

James W. Wolfe, Ph. D.

31 January 1968

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Fort Knox, Kentucky 40121

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ABSTRACT

ADAPTATION TO PROLONGED CONSTANT ANGULAR
ACCELERATION

OBJECTIVE

These studies were designed to determine the extent of adaptation in vestibulo-ocular reflex responses to prolonged constant angular acceleration, and to compare the magnitude of the decrements with that found for subjective responses to similar stimuli.

METHOD

Two independent groups of normal human subjects (total N = 25) were exposed to a number of long-duration (up to 96 sec), relatively high-intensity (up to $24^\circ/\text{sec}^2$), constant, angular accelerations. Electrically recorded nystagmus was scored for second-by-second slow-phase output.

RESULTS

Nystagmic slow-phase decrements during stimulation were clearly evident. The decrements appeared to be initiated at about the same time after stimulus onset (30-35 sec) for all accelerations used.

CONCLUSIONS

Adaptation may simply reflect a central habituation process. Exploration of this possibility might be directed toward the sinusoidal, infra-slow variations evident in subjective responses, eye movements, and recordings from various loci in the vestibular system.

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ADAPTATION TO PROLONGED CONSTANT ANGULAR ACCELERATION

INTRODUCTION

Response measures of stimulation of the vestibular apparatus may be organized into three general categories: (a) reflexive eye-movements (e. g., vestibular nystagmus and counterrolling); (b) electrophysiological recordings; and (c) subjective measures of angular velocity including both indirect measures such as the oculogyral (16), oculogravic (15), and audiogyral (1) illusions, and more direct psychophysical measures such as numerical magnitude estimation (4) and key-press estimates (18) of velocity.

One of the most meaningful approaches to the understanding of vestibular function is the systematic comparison of these different responses during similar stimulus manipulations (10, 12, 13). This approach provides an emphasis on interactions of the vestibular system with other sensory systems, thus facilitating integration and meaningful application of data, as well as defining the most important future research problems. For example, although the various intersensory illusions resulting from exposure to accelerative stimulation have been extensively studied, the pervasive influence of vestibular stimulation upon other sensory system responses does not appear to have been generally appreciated. However, when electrophysiologic, nystagmic, and subjective responses to accelerative stimulation are jointly evaluated, it appears that the cerebellum is intricately involved in both the organization of vestibular inputs and the integration of vestibular information with other sensory systems (28). Koella (22) points out that "The cerebellum with its intensive supply of vestibular, proprioceptive, tactile, optic, and acoustic impulses certainly is a structure uniquely capable of integrating these afferent signals, there is good electrophysiological evidence that convergence of heteromodal volleys does occur in the cerebellum." Clearly, determination of the basic mechanisms involved must include an integration of data from these three general response categories.

The biophysical model for the semicircular canals, a torsion pendulum analog (27), has provided a fruitful model for evaluating the varied responses to angular acceleration (2, 24). Primary limitations of the model are its inability to handle either the systematic influence of arousal level upon nystagmic responses (5, 11) or the occurrence of extensive adaptation (a response decline during stimulation)

during long-duration, constant, angular acceleration. With regard to the question of adaptation, clear discrepancies exist in comparisons of subjective and nystagmic responses to angular acceleration. For example, subjective responses involving both key-press estimates (18) and magnitude estimates (3, 4, 8) demonstrate extensive adaptation. On the other hand, Collins and Guedry (9, 10) reported no adaptation in human nystagmic responses to long-duration constant angular accelerations (1.0 and 1.8°/sec²), when arousal level was carefully controlled. Other investigators have reported declines in both subjective and nystagmic responses (20, 25). Collins and Guedry (10) suggest arousal level as a primary explanation for experimental differences with regard to nystagmic adaptation at low intensities, but these authors also discuss the possible involvement of higher threshold, quicker adapting receptor units to account for adaptation at higher intensity levels than they examined. Evidence from electrophysiological recordings from the vestibular nuclei during angular acceleration are ambivalent (12, 13, 21). Although the frequency of discharge from some units appeared to decline under prolonged stimulation, most of those sampled did not decline to any significant extent. What decrement is evident might simply be a reflection of overshoot in a non-critically damped receptor system (7). However, since these data were obtained under barbiturate anesthesia, the failure of the units to exhibit any significant adaptation also might be attributed to influences of the anesthetic upon central inhibitory mechanisms (6). In any case, in view of the complete loss of nystagmus under barbiturate anesthesia (14), these data are difficult to interpret relative to adaptation.

The primary purpose of the present studies was to determine the extent of adaptation in vestibulo-ocular reflex responses to long-duration, relatively high-intensity, constant, angular accelerations, and to compare the magnitude of the decrements with that found for subjective responses to similar stimuli.

METHOD

Apparatus

Rotary Device. The rotary apparatus consisted of an angular acceleration device, driven about the vertical axis by an electrohydraulic motor control system (5). Constant angular accelerations of precise duration and intensity were programmed from control equipment outside the room which housed the accelerator. The subject was enclosed in a light-tight removable capsule. Electronic voice communication through slip rings permitted continuous contact with S. An

adjustable bite-board maintained S's head in a fixed position over the axis of rotation.

Recording. Electrodes were taped near the outer canthi of the eyes with an indifferent electrode placed in the center of the forehead. EOG signals for summated horizontal eye movements were led through slip rings to a Grass ink-writing recorder in the adjacent control room. Eye-movement potentials were amplified with a 3.0-sec, RC, time constant and displayed with a 25 mm/sec paper speed. For calibration purposes three lights were placed in front of S such that the left and right light subtended a 10° visual angle from the center. Prior to each S's first trial and again following his last, the lights were turned on. A 10° voluntary movement of the eyes was recorded to obtain a calibration relating actual angular displacement of the eyes to mm of recorded eye movement. Periods of acceleration also were recorded.

Procedure for Experiment 1. All testing was conducted in total darkness and each S was instructed to keep his eyes open and generally directed straight ahead. Fifteen Ss were given a counterbalanced series of six experimental trials which consisted of six different angular accelerations: (1) $3^\circ/\text{sec}^2$ maintained for 88 sec; (2) $5^\circ/\text{sec}^2$, for 53 sec; (3) $8^\circ/\text{sec}^2$, for 30 sec, (4) $12^\circ/\text{sec}^2$, for 20 sec; (5) $17^\circ/\text{sec}^2$, for 14 sec; and (6) $24^\circ/\text{sec}^2$, for 10 sec. All accelerations were presented symmetrically around zero velocity from either 20 RPM (8° , 12° , 17° , and $24^\circ/\text{sec}^2$) or 22 RPM (3° and $5^\circ/\text{sec}^2$) in a CCW direction, through zero velocity, to 20 RPM or 22 RPM in a clockwise direction. A preliminary trial of $24^\circ/\text{sec}^2$ and 10-sec duration provided a check for proper functioning of the recording equipment, and served to acquaint S with the experimental procedure. The 15 Ss were young men 19-22 years of age, with normal labyrinthine function. All Ss had been previously exposed to laboratory angular accelerations and were selected for the present study on the basis of their nystagmic records and high motivation. A high level of arousal was maintained by requiring S to accomplish mental arithmetic problems during the trial (both successive multiplication and division). Approximately 15 sec before stimulus onset, S was assigned a problem which he continued to work until asked for the answer and told to relax by the experimenter. A minimum of 5 min of constant velocity was programmed between trials to decrease the confounding of responses by secondary nystagmus from the previous acceleration.

Results and Discussion - Experiment 1. Nystagmic responses for all trials except the preliminary trial were scored by hand. The

vertical magnitude of the slow-phase sweep of each primary nystagmus beat was measured in mm for each 1-sec segment of the record, and then converted to degrees of slow-phase by means of the calibration taken at the end of each session. Logarithmic transformations of each \underline{S} 's nystagmic output for each second of every trial were made, the logs then summated across \underline{S} s and geometric means computed for each second of each of the six trials.

The averaged, second-by-second, slow-phase output is plotted for the six angular accelerations in Figure 1. Adaptation (a decline

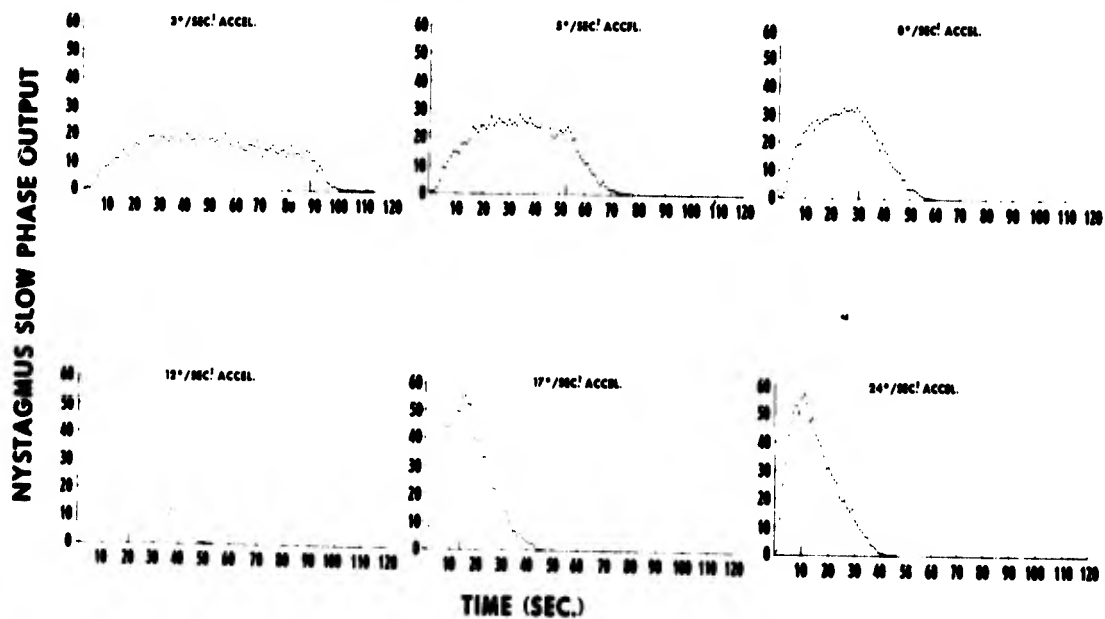


Fig. 1. Nystagmus slow-phase output ($^{\circ}/\text{sec}$) for the six angular accelerations. The vertical bars on the baseline denote termination of the accelerations.

in output during the period of stimulation) is clearly evident in responses to the longer duration, but lower intensity accelerations ($3^{\circ}/\text{sec}^2$ and $5^{\circ}/\text{sec}^2$). Despite the considerable second-to-second variation in the nystagmic responses (a typical finding when slow-phase is plotted in this manner) lines of best fit drawn by eye for these two accelerations have a negative slope from the points of peak sensitivity after approximately 35 sec of stimulation. However, this decline must be described as only moderate, as compared to the nearly complete adaptation found in subjective estimates of angular velocity to similar accelerations (3, 4).

It is interesting to note that the nystagmic decline from peak output was initiated at approximately the same time (35 sec after the onset of acceleration) for both stimuli, in spite of the much longer duration of the $3^\circ/\text{sec}^2$ stimulus. None of the other stimuli were maintained past this apparently critical point for onset of nystagmic adaptation, and no adaptation was evident.

It would be of interest and considerable significance to determine if the time of onset of adaptation is in fact common to a wide range of angular accelerations. To the extent that this could be demonstrated, vestibular adaptation would not appear to be a phenomenon of peripheral origin. Adaptation to sensory stimulation has been traditionally viewed as a peripheral not a central phenomenon (26). But, in terms of the mechanical characteristics of the semicircular canals, it is highly unlikely that adaptation to constant angular acceleration reflects changes in the dynamics of the cupula-endolymph system (27). Lowenstein's work with the ray (23) indicates that adaptation could have a peripheral locus since different neural units apparently are initiated during cupula deflection and higher threshold units appear to adapt more readily. If in fact this were the mechanism for adaptation, response declines during prolonged stimulation should be more quickly initiated and have a steeper slope with higher intensity stimuli. That is, after 30-35 sec. the cupula would be deviated considerably more and the assumed higher threshold faster adapting units more quickly brought into play for an acceleration of $12^\circ/\text{sec}^2$ than for one of $3^\circ/\text{sec}^2$. Experiment 2 was designed to help answer this question.

Procedure for Experiment 2. The methods and procedures were essentially the same as that in experiment 1, with the exception that all stimulus durations were maintained as long as feasible within the limitations of maximum RPM. All accelerations were presented symmetrically around zero velocity from 40 RPM in a CCW direction to 40 RPM in a CW direction. Each of 10 experienced subjects received four angular accelerations in a partially counterbalanced order: (1) $5^\circ/\text{sec}^2$, 96 sec; (2) $8^\circ/\text{sec}^2$, 60 sec; (3) $10^\circ/\text{sec}^2$, 48 sec; and (4) $12^\circ/\text{sec}^2$, 40 sec. Arousal level was maintained by mental arithmetic tasks.

Results and Discussion for Experiment 2. Again, geometric means were computed for slow-phase output for each second of the four accelerations. These data are shown in Figures 2-5 on the succeeding pages. Several aspects of these data require comment. A significant response decline during periods of stimulation is clearly evident in nystagmic responses to each of the accelerations. Lines of

Figs. 2 - 5. Nystagmus slow-phase output ($^{\circ}/\text{sec}$) for the four angular accelerations. Vertical bars on the baseline define the time of stimulus termination.

$5^{\circ}/\text{SEC}^2$

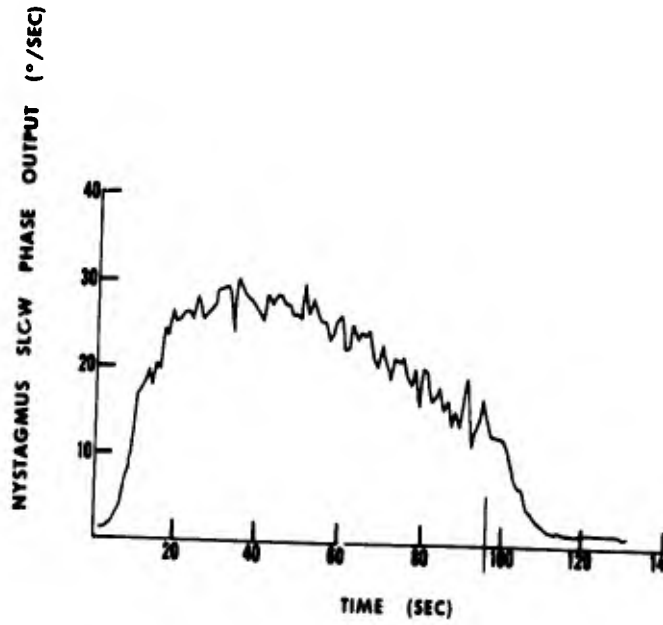


Figure 2

$8^{\circ}/\text{SEC}^2$

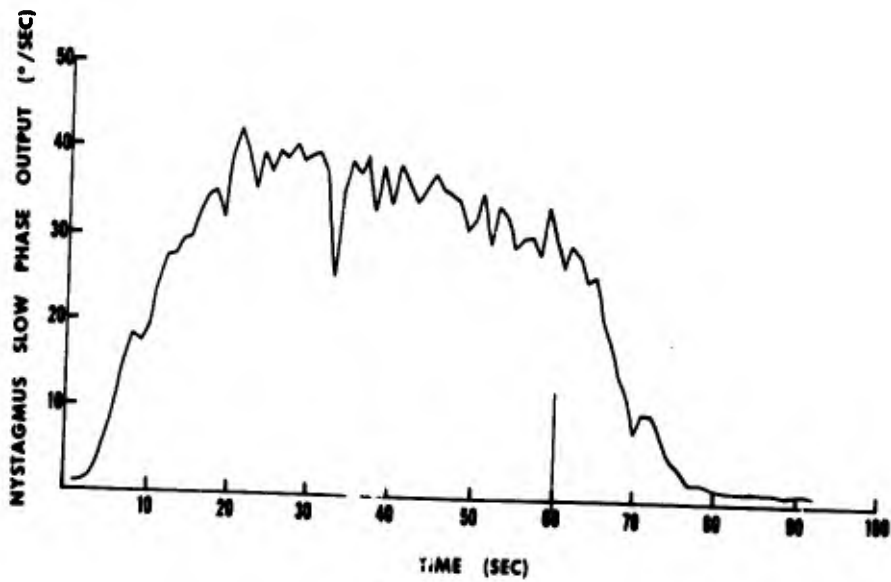


Figure 3

10°/SEC²

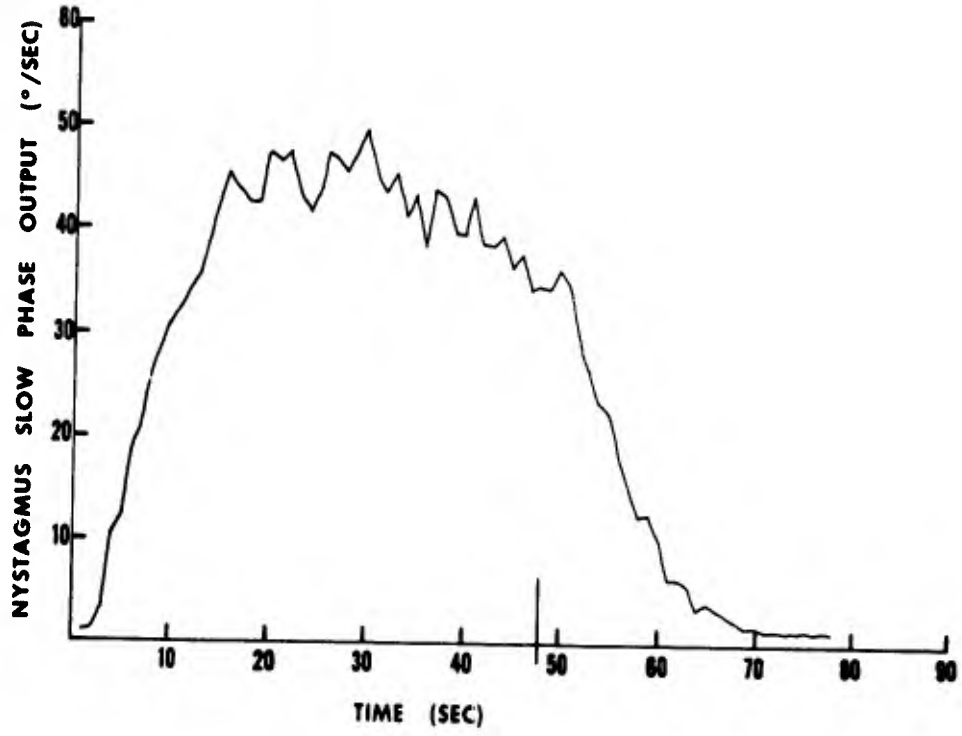


Figure 4
12°/SEC²

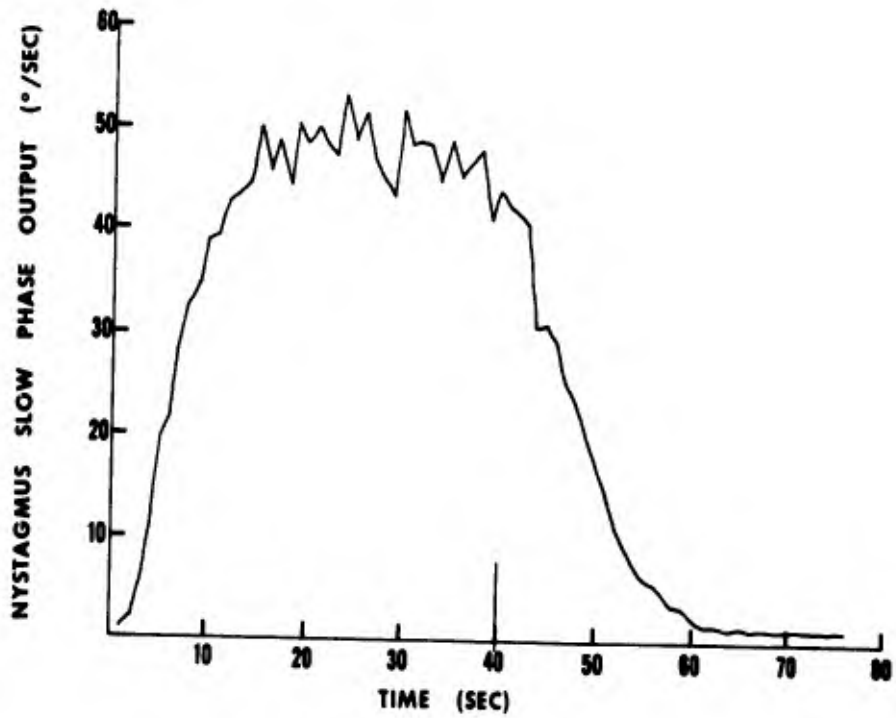


Figure 5

best fit were drawn by eye for each of these declines. The slopes of these lines, the intercepts at approximate peak output, and the percentage decrements are shown in Table 1. The general trend is

TABLE 1
Slopes and Percent Decrement from Nystagmic
Peak Output

Acceleration	Slope	Amount of Decrement	Peak Output (Intercept)
5°/sec ²	-.25	51%	32 sec
8°/sec ²	-.30	28%	28 sec
10°/sec ²	-.70	30%	30 sec
12°/sec ²	-.56	19%	30 sec

for the slopes to become more negative as the intensity of the acceleration increases. These data clearly indicate that, once initiated, nystagmic output declines more quickly for more intense accelerations. However, it would appear that the onset of the decrement is initiated at approximately the same time following stimulus onset (25-30 sec), apparently independent of the intensity of the stimulus. The systematic changes in percentage decrements are readily understood when one considers the shorter periods during which a decrement can occur for the more intense stimuli. For example, even though responses to the 12°/sec² stimulus were declining with a slope of -.56, it was possible to maintain the acceleration for only 8 sec after peak output (32 sec) resulting in only a 19 percent decrement. On the other hand, responses to the 5°/sec² stimulus, although exhibiting a shallower decline, -.25, were accumulated over a much longer time period, allowing a considerably larger percentage drop.

In both experiments, a nystagmic decrement was clearly evident during acceleration. Further, this decrement was initiated at about the same time for all accelerations used and, the more intense the acceleration, the greater the slope of the decrement. Although it is conceivable that the reported decrements are due to decreases in arousal level during stimulation, as Collins and Guedry (10) suggest, in view of both the assigned mental arithmetic tasks and the relatively large decrements found, arousal level would not appear to be a satisfactory explanation of the phenomenon. While manipulation of arousal level

evidently can compensate for "adaptation" of nystagmic responses to low-intensity accelerations (10), yet, a decrement is evident despite high arousal level in response to more intense stimuli, if the accelerations are maintained past an apparently critical duration of 30-35 sec.

This close, time-locked relationship between the onset of nystagmic adaptation and duration of stimulation, which appears to be essentially independent of stimulus intensity, is difficult to explain. However, the same general time relations are evident in the onset of adaptation for subjective responses (3, 4, 8), i. e., adaptation occurs only after 25-35 sec of stimulation, regardless of the intensity of the acceleration. Both of these responses appear to be reflecting a generally similar course for onset of a decline during protracted stimulation. Wolfe (28) has shown that infra-slow potentials from the cerebellar vermis of cat reflects peaks which may vary in period from as short as 10 sec to as long as 5 min. Controlling conditions appear to be how much stimulation S has received and arousal level. In cats, there is a slow conjugate shifting of the eyes in addition to the nystagmic response which seems to bear a direct relationship to these infra-slow potentials (28). Slow but systematic phase displacements of the eyes are not uncommonly encountered in human EOG recordings, and, furthermore, Clark (8) has reported a similar "waxing and waning" of subjective responses during long-duration angular acceleration. One might speculate that either the vermal potential or the phase displacement of the eyes could provide the necessary neural activity to initiate a response decline. Exploration of this intriguing possibility will require comparison of cerebellar potentials and infra-slow eye movements with the nystagmic and subjective decrements.

In conclusion, even though nystagmic responses do show a clear decrement during constant angular acceleration, yet, the vestibulo-ocular reflex does not decline as rapidly or as much as do subjective responses to comparable accelerations (3, 4). In addition to "adapting" more quickly, subjective responses also appear to "habituate" and recover from habituation more quickly than do nystagmic responses (2, 17, 19). In view of the previous discussion, it is tempting to speculate further that the response decline during stimulation, operationally a classical example of adaptation, is, in fact, only another reflection of a central habituation process.

SUMMARY

Two independent groups of normal human subjects were exposed to a number of long-duration (up to 96 sec), relatively high-intensity

($3^\circ/\text{sec}^2$ - $24^\circ/\text{sec}^2$), constant, angular accelerations. Nystagmic decrements during stimulation were clearly evident. The decrements were initiated at about the same time after stimulus onset (30-35 sec) for all accelerations used. The decrements in the nystagmic responses were compared to related findings for both subjective and electrophysiological responses.

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13. ABSTRACT

Two independent groups of normal human subjects were exposed to a number of long-duration (up to 96 sec), relatively high-intensity ($3^\circ/\text{sec}^2 - 24^\circ/\text{sec}^2$) constant, angular accelerations. Nystagmic decrements during stimulation were clearly evident. The decrements were initiated at about the same time after stimulus onset (30-35 sec) for all accelerations used. The decrements in the nystagmic responses were compared to related findings for both subjective and electrophysiological responses. (U)

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