

Vestibular reactions during prolonged constant angular acceleration

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GUEDRY, F. E. AND L. S. LAUVER. *Vestibular reactions during prolonged constant angular acceleration.* J. Appl. Physiol. 16(2): 215-220. 1961.—Six human subjects received stimuli of 2 deg/sec.² for 45 seconds and 1.5 deg/sec.² for 60 seconds. Direct-coupled amplification of corneoretinal potential was used to record eye movements. Although some subjects occasionally showed a rise and decline in the velocity of nystagmus during constant angular acceleration, typically, near-maximum velocity was attained in about 30 seconds with little subsequent gain or loss until acceleration ended. Routinely, nystagmus outlasted the subjective afterreaction. Departures from previous results seem attributable to maintenance of alertness by requiring continuous estimation of subjective events. Theoretical implications of the divergence between the subjective and oculomotor aspects of the reaction are discussed.

A DECLINE IN VESTIBULAR REACTION during or shortly after a single prolonged period of low-magnitude stimulation has been considered to be indicative of adaptation in the vestibular system (1-4).¹ The magnitude of the subjective aspect of the vestibular reaction, estimated by several techniques, first rises and then declines during the course of prolonged constant angular acceleration (3).² Recently this finding has been independently confirmed (5).

Although most of the evidence for vestibular adaptation has been derived from the subjective aspect of the reactions, electrophysiological evidence for peripheral adaptation has been indicated. Lowenstein (6) has reported that increasing the intensity of stimulation of the ampullar mechanism initiates neural activity "in one after the other previously silent units of higher

threshold." These elements of higher threshold often adapt themselves rather rapidly and fire over a limited range of stimulus intensity, while the spontaneously firing elements 'are delicately poised' to react to near-threshold stimulation and are either nonadapting or slowly adapting. There is also some evidence for vestibular efferents (7) which could place the peripheral activity, to some extent, under central control. Albeit, irrespective of the source, if peripheral activity is reduced it is reasonable to expect that vestibular nystagmus as well as the subjective aspect of the vestibular reaction should be reduced.

The present experiment is designed to examine the velocity of the slow phase of nystagmus during the course of prolonged constant angular acceleration and to determine whether the time characteristics of any rise and decline in velocity of nystagmus correspond to the previously established (3) time characteristics of the subjective reaction.

METHODS

The rotary device used to produce the vestibular stimulation consisted of a large turntable (8) centered in a light proof room. The subject was positioned with his head at the center of rotation and with the plane of the lateral semicircular canals approximately in the plane of rotation.

Nystagmus was recorded by the 'corneoretinal potential' technique. Silver, silver-chloride electrodes prepared by the method of Ford and Leonard (9) were taped alongside each eye near the outer canthus to detect horizontal eye movements; a reference electrode was taped high on the forehead near the hairline. The signals generated by horizontal eye movements were led into two channels of an Offner type-T EEG recorder. One channel was set for D-C recording and the other for a recording time constant of 1.2 second.³ The latter

³ The instrument is chopper-stabilized to produce the desired features without amplifier drift, of a truly direct-coupled (D-C) amplifying system. It also provides a switch to insert one of several coupling condensers in series with the input to any channel when the input signal may have unwanted 'D-C drift'; this is referred to herein as RC (resistor-condenser coupled) amplification with, in this case, a 1.2-second time constant.

Received for publication August 19, 1960.

¹ The effects of a constant angular acceleration are balanced eventually by the spring action and friction of the cupula-endolymph system. Cupula position would then be maintained as long as the acceleration endures. With certain assumptions about cupula control of vestibular reactions, the magnitude of the reaction should also be maintained, without decline.

² In 1921 Dodge (4) reported a decline and reversal of the subjective reaction during prolonged angular acceleration. In his situation, the decline could have been due to a diminishing acceleration, but the reversal could not be similarly explained. Dodge considered a central compensatory mechanism.

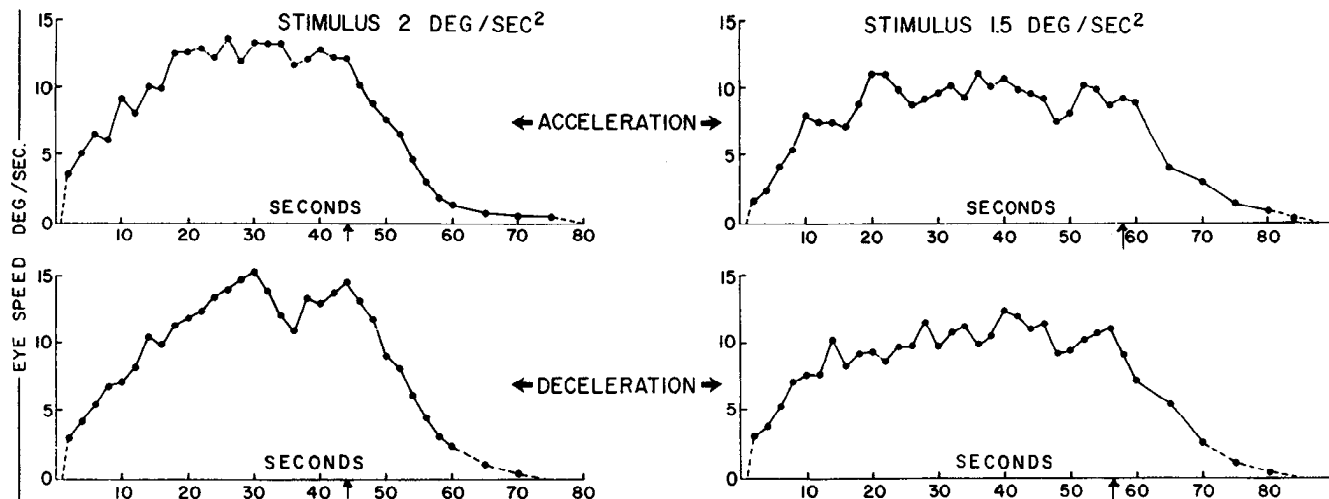


FIG. 1. Slow-phase nystagmus eye speed averaged for 6 subjects. Arrows on *x*-axes denote termination of stimulation.

provided an auxiliary record in the event that D-C drift emanating from sources other than the eyes would cause loss or distortion of a record. This was a rare occurrence and the only case in which the D-C record was unusable was probably attributable to skin abrasions caused by overzealous cleaning of the skin.

The experimental room was in darkness whenever vestibular nystagmus was recorded. Subjects were instructed to keep their eyes open throughout each trial. Calibration records of 20-degree eye movements were obtained before and after each trial to permit conversion of recorded pen deflections to angular displacements of the eyes.

Preliminary experiments demonstrated that stimuli in the 1.0–2.0 deg/sec.² range did not always elicit systematic nystagmic eye movements, particularly after several periods of stimulation, unless the experimenter frequently reminded the subject to remain alert. When nystagmus diminished it was frequently replaced by slow wandering eye movements as noted by previous investigators (10). To avoid this difficulty subjects were carefully instructed to remain alert and the number of stimuli in each experimental session was restricted.

In spite of these precautions the nystagmic reaction failed to develop during the third stimulus of the first session in the first experimental subject (*DN*). As a result of this problem and the fact that several preliminary subjects, while making repeated angular displacement estimates, had demonstrated clear nystagmic reactions throughout prolonged stimuli, it was decided to require the signaling of subjective events for all of the remaining experimental trials.

The task given the subject was to signal by a telegraph key the onset of rotation and, thereafter, each time he felt he had rotated through 90 degrees. This method of estimating the magnitude of the subjective reaction throughout its course has been used by several investigators (3, 11, 12), but it requires careful training of subjects. It was used in this experiment principally to

maintain the active participation of the subjects while nystagmus was being recorded.

Each of six men participated in two experimental sessions which were separated by a 1-week interval. Two magnitudes of prolonged constant angular acceleration were used, 2.0 deg/sec.² applied for 45 seconds and 1.5 deg/sec.² applied for 60 seconds. Rotation was maintained at a constant rate for 90 seconds before deceleration was started. Deceleration was of the same magnitude as acceleration for any given trial. Two trials with the 2.0 deg/sec.² stimuli were used in the first session and two trials with the 1.5 deg/sec.² stimuli were used in the second session. Within sessions trials were separated by a 4-minute rest interval.

Record measurement. The D-C records were divided into 1-second intervals and the slow-phase slopes of nystagmic beats within these intervals were measured by use of a drafting instrument. When more than one beat occurred within an interval slopes were averaged arithmetically. A dead pen on one of the unused channels provided a base line for 'zeroing' the drafting instrument and a scale was attached to the instrument so that slopes could be read as tangents. The constancy of slope of the individual beats recorded on the D-C channel made this measurement technique feasible. However, the 1.2-second channel usually gave good representation of eye displacement with respect to time. Examples of the correspondence between the nystagmic eye-movement records given by the D-C channel and the 1.2-second channel are shown in figure 7 below.

RESULTS

Figure 1 shows the average nystagmic reaction throughout its course, during and after the 2.0 deg/sec.² stimuli and the 1.5 deg/sec.² stimuli of the two experimental sessions. The records of each subject for a given stimulus magnitude were subdivided into 2-second intervals, starting with the onset of stimulation. The

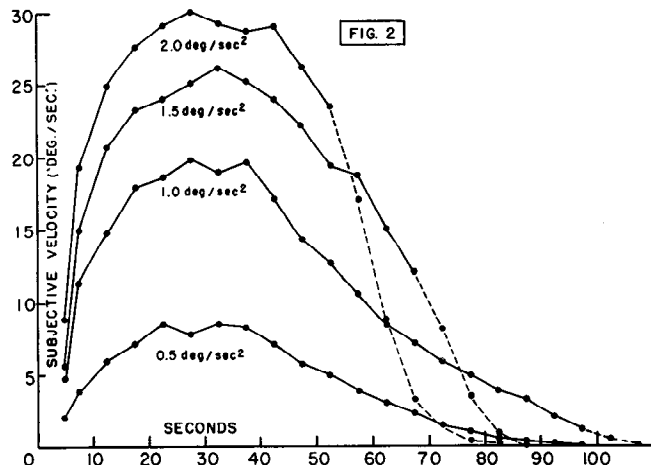


FIG. 2. Subjective velocity averaged for 10 subjects. Dotted lines denote point at which constant angular acceleration terminates.

velocity of nystagmus (slow phase) within temporally corresponding intervals was averaged over subjects throughout the duration of the stimulus and after-reaction. It is clear, from this representation of the data, that there is little, if any, systematic decline in the velocity of nystagmus as averaged for the group during the course of either of these prolonged constant angular accelerations.

These data can be compared with the changes in the average magnitude of the subjective reaction recorded in similar circumstances. Subjective estimates of 45-degree angular displacements were made by 10 subjects, well-trained in the technique of estimating subjective angular displacement during vestibular stimulation. The results of this experiment, detailed in a previous report (3), are reproduced in figures 2 and 3. Within the range of stimuli applied (0.5 deg./sec.^2 – 2.0 deg./sec.^2) the maximum subjective velocity attained and the rate of change of subjective velocity up to this maximum are directly related to the magnitude of the constant angular acceleration applied. However, after about 30 seconds of constant angular acceleration the subjective reaction declines even though the angular acceleration remains constant. It is to be noted that these subjective data were averaged for trials and subjects by matching corresponding time intervals marked off from the start of each stimulus, and that this is the same method used for averaging the velocity of nystagmus presented in figure 1.

Hence, whereas average subjective velocity rises and declines in the course of prolonged constant vestibular stimulation, the average slow-phase velocity of ocular nystagmus rises but does not clearly decline in the course of constant vestibular stimuli of comparable magnitude and duration.

That the averaged data as presented in figures 1, 2 and 3 are apparently representative of individual results was checked by plotting individual curves for each subject for each condition. Examination of the indi-

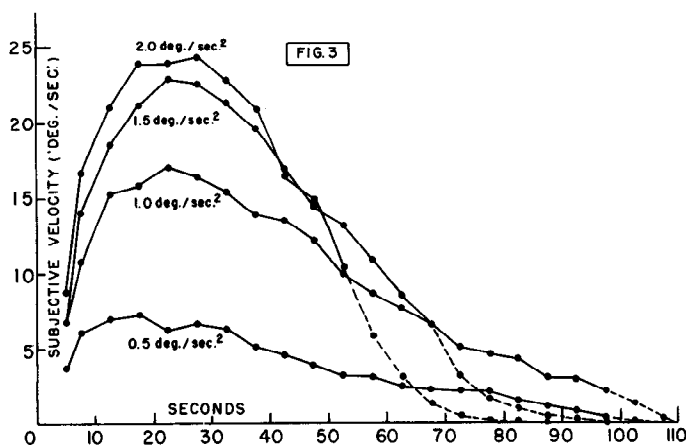


FIG. 3. Subjective velocity averaged for 10 subjects. Dotted lines denote point at which constant angular deceleration terminates.

vidual subjective data revealed a peak magnitude and start of a decline within the interval 25–40 seconds during constant angular acceleration, in spite of auditory and vibratory cues to velocity. These extraneous cues had the effect of prolonging the interval before the peak subjective velocity was attained (fig. 2), but the individual results showed the rise and decline during the acceleration. These cues had the opposite effect during deceleration, as would be expected (cf. figs. 2 and 3).

The individual plots of nystagmic eye-movement data collected under these conditions do not routinely show a rise and decline in eye velocity during the course of either the accelerations or decelerations used in the present experiment. The more typical finding in the individual graphs is for the nystagmus velocity to very nearly reach a maximum in roughly 30 seconds and then to hold at this value, with a little gain in some cases, until the stimulus is terminated. There are, however, individual exceptions to this, in which the nystagmic response shows a rise and decline somewhat comparable to that of the subjective reaction. Unaveraged data for individuals demonstrating these several types of nystagmus reactions are presented in figure 4.

The task of key-pressing to signal subjective events had several interesting interrelations with nystagmic eye movements.

a) A clear rise and decline in nystagmus during prolonged acceleration (or deceleration) was obtained from *subject DN* during session 1 when he was not signaling subjective reactions (but after he had been alerted by the experimenter). The nystagmic response was clear throughout the duration of the acceleration, but the velocity of the slow phase of nystagmus peaks at about 25–30 seconds and then clearly declines during the remainder of the constant stimulus, as shown in figure 5 and in the left-hand graph of figure 6. In session 2 when the same subject was actively signaling the subjective reaction, his nystagmic response does not show

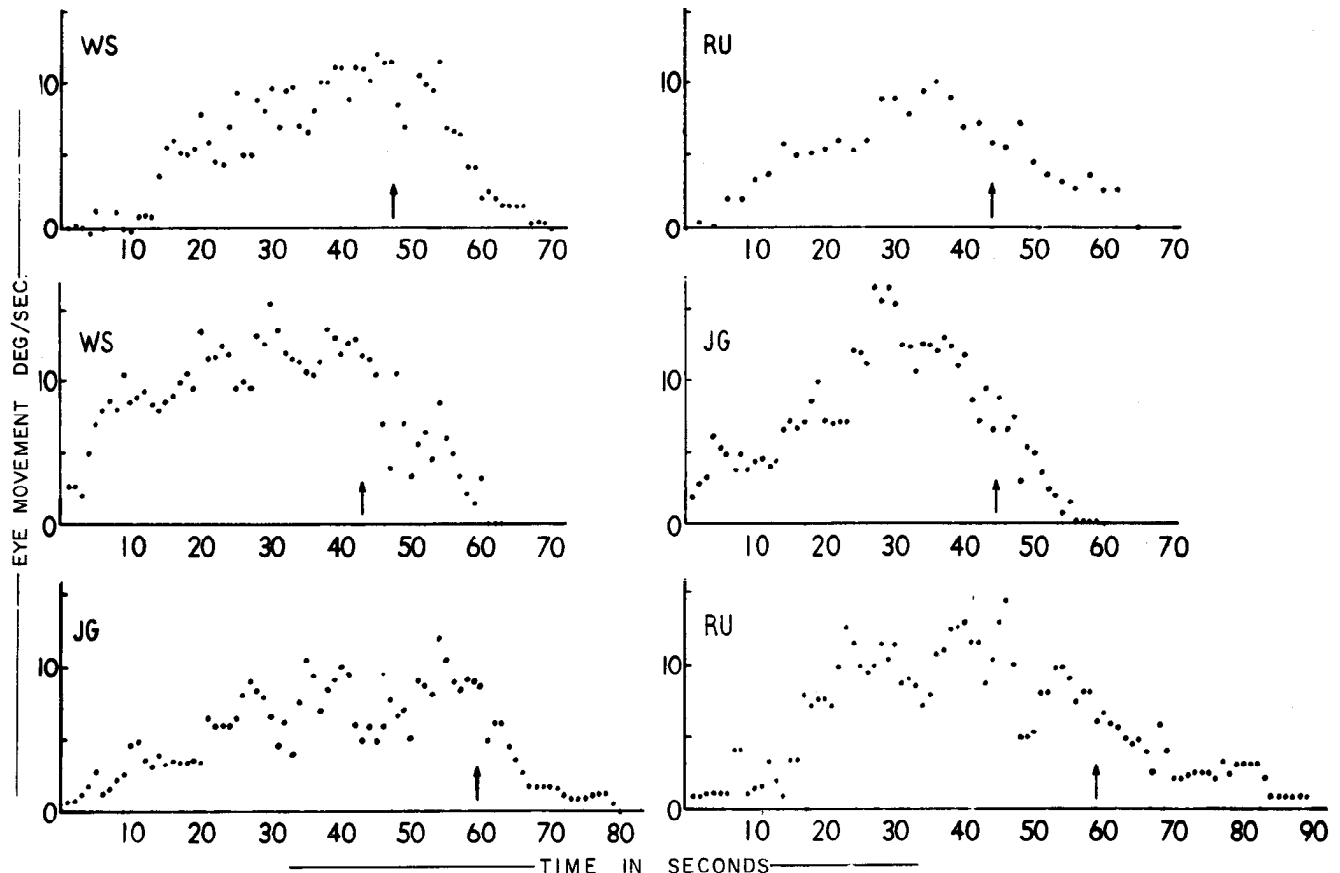


FIG. 4. Three examples (*right*) of nystagmic reactions which show rise and decline of slow-phase eye speed during constant angular acceleration and three examples (*left*) of reaction which

a clear decline during acceleration or deceleration (right-hand graph fig. 6) even though the stimulus was maintained longer and was of lower magnitude than those in session 1.

b) Nystagmus was always in progress when subjects signaled the end of the subjective reaction, and nystagmus usually continued for some time thereafter. An example of this is shown in figure 7.

c) Soon after subjects signaled cessation of the subjective reaction the nystagmic reaction occasionally dropped abruptly in amplitude and then from the lowered amplitude ran its course to termination.

d) The unsystematic wandering eye movements in the upper record of figure 8 started during a period of constant angular velocity and continued throughout a 45-second period of constant 2 deg/sec.² deceleration. The systematic nystagmus of the lower record occurred during the same magnitude deceleration of the following trial, after the experimenter had alerted the subject (*DN*) between trials. In the second session, when this subject was signaling subjective events during a lower magnitude and more prolonged stimulus, the nystagmic response remained systematic. As a matter of fact, after the key-press technique was instituted there was no

did not decline until stimulus terminated. *Arrows* above *x-axes* denote point of stimulus termination.

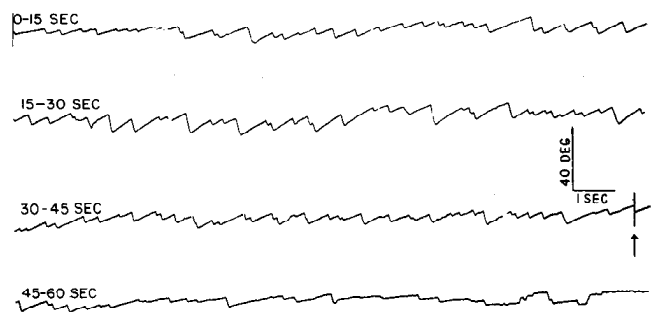
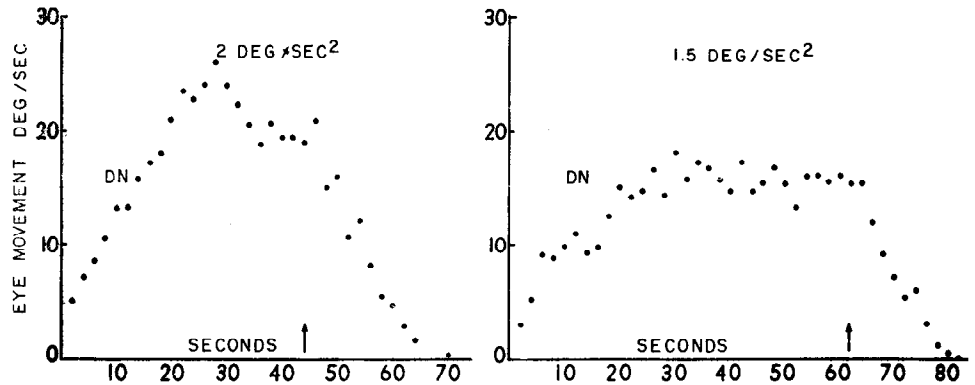


FIG. 5. D-C recordings of nystagmus obtained during 2 deg/sec² acceleration after *subject DN* had been alerted by experimenter. Subject was not signaling subjective reaction during this session. Note lessening slopes after 30 sec. Arrow at 45 sec. denotes onset of constant velocity.

further occurrence of the replacement of nystagmus by the wandering unsystematic eye movements which are characteristic of sleep or reverie states (10, 13); systematic nystagmus accompanied the 'adequate vestibular stimulus' throughout the remainder of the experiment without the necessity of repeated instruction to the subject regarding alertness.

FIG. 6. Slow-phase eye speeds obtained from *DN* during one stimulus of session 1 (left) and during a more prolonged stimulus of session 2 (right). Arrows denote point of stimulus termination.



DISCUSSION

Wendt (13), Mowrer (14) and Buys (15) have reported that primary nystagmus may terminate during the course of a prolonged constant magnitude angular acceleration. Recently Ek *et al.* indicated (5) that nystagmus shows principally the same characteristics as the subjective reaction during prolonged constant angular acceleration and they indicate a decline in the subjective reaction after 30-40 seconds of constant stimulation. However, there have been several indications that the time course of the subjective and the oculomotor reactions are not the same (16, 17), particularly during prolonged reactions, and that nystagmus may persist for more than 30 or 40 seconds during constant angular acceleration without declining (18, 19).

A decline in nystagmus during prolonged low-magnitude constant angular acceleration was not demonstrated for the group of subjects in the present experiment, although there were individual cases where a decline occurred. It is quite possible that the subjective reporting technique, used previously to demonstrate the rise and decline of the subjective reaction during prolonged constant acceleration (3), was instrumental here in preventing the decline of nystagmus. The intrusion of large amplitude unsystematic eye movements which had occurred frequently in preliminary trials was no longer a problem after instituting the subjective signaling technique.

Subsequent experiments by Collins, Crampton and Posner (20) and Collins (21), involving higher-magnitude, shorter-duration stimuli than those used herein, have demonstrated clearly that mental effort, whether induced by requiring the subject to repeatedly signal subjective events or to perform mental arithmetic, is sufficient to produce significantly more nystagmus than is obtained in 'reverie states.' These subsequent experiments, the findings of the present study, and the observations of Wendt (10, 13) point to a nystagmic reaction which may decline during prolonged constant acceleration when the subjective reaction declines, but perhaps only when the subject starts to drift into a reverie state as the sensation of rotation subsides. In this case the nystagmus follows the subjective vestibular

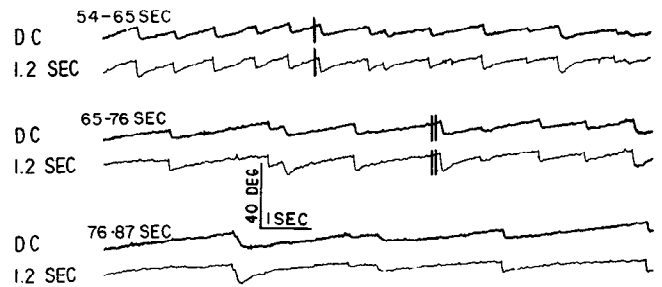


FIG. 7. Simultaneous recordings (*subj.* RU) of nystagmus using D-C amplification and RC amplification (1.2-sec. time constant). Single vertical line in 54-65-sec. interval denotes end of 1.5 deg/sec² stimulus. Double vertical line in 65-76-sec. interval denotes end of subjective reaction.



FIG. 8. D-C records obtained from *subject DN* during decelerations of two successive trials. Lower record obtained after subject was 'alerted' by experimenter.

reaction as a result of a fortuitous change in the subject's state of alertness. If, on the other hand, the subject is maintained in an 'alert state' during prolonged acceleration, then the subjective reaction declines but the nystagmic reaction apparently does not, during stimuli of 60-second duration.

With very prolonged low-magnitude constant angular accelerations, e.g. 1 deg/sec² for 50 seconds, Aschan (19) has indicated that the "nystagmic reaction terminates at the moment when acceleration ceases. At higher accelerations a reduction of speed up to 50% is obtained within a second." This was not routinely observed in the present experiment. There were instances of rapid decline in speed of the slow phase of nystagmus soon after the cessation of stimulation but the more typical course of events is reflected by the curves presented in figure 1. These curves show negative exponential decay in response with time-constants approximating those to be expected from the work of Groen *et al.* (12) and Van Egmond *et al.* (22). In no case was there cessation of nystagmus immediately upon cessation of acceleration

or deceleration, although the subjects frequently signaled cessation of the subjective reaction shortly after (and occasionally shortly before) deceleration terminated. The persistence of the nystagmic afterreaction may be attributable to the fact that 1.5 deg/sec.² was the lowest magnitude stimulus used herein, whereas Aschan reported immediate nystagmus termination immediately upon cessation of a 1.0 deg/sec.² stimulus. However, another possibility is that the maintenance of active participation of the subject by requiring repeated estimates of subjective events resulted in a greater nystagmic output in the present experiment.

A decline in the subjective aspect of the vestibular reaction without a corresponding decline in the nystagmic reaction suggests several possibilities which are not mutually exclusive.

1) The subjective reaction is selectively attenuated by a central mechanism which does not directly influence the oculomotor centers. This has been previously suggested (4, 23) and is perhaps the most likely possibility.

2) The adaptation demonstrated in the subjective reaction is attributable to peripheral adaptation, consistent with Lowenstein's electrophysiological evidence (6), but is not manifest to the same degree in the nys-

tagmic reaction. Assuming that peripheral adaptation is present, possible mechanisms for the divergence in these two aspects of the reaction are:

a) The most rapidly adapting peripheral elements are supplied with neural connections which terminate in centers influencing the subjective reaction exclusively. Lorente de No (24) has indicated a separation of fibers near the ganglion from all three ampulla into three bundles; one containing fine fibers, one containing medium fibers and a third containing thick fibers. Lowenstein (6) has indicated a possible differential adaptation between different sensory elements within the canals and Hallpike and Hood (1) have suggested that the fine fibers are of the nonadapting variety. However, there is no indication, to the authors' knowledge, that the vestibular cortical projection pathways take their origins principally from the 'adapting thick fibers.'

b) The oculomotor nystagmic reaction may be supplied with a self-perpetuating mechanism within the oculomotor system which maintains the nystagmic reaction despite a decline in peripheral, vestibular activity. Evidence supporting this possibility can be adduced, but if this is a factor in the results it is clear that the self-perpetuating mechanism itself is dependent upon the mental activity of the subject.

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