TASK—CONTROL OF AROUSAL AND THE EFFECTS OF REPEATED UNIDIRECTIONAL ANGULAR ACCELERATION ON HUMAN VESTIBULAR RESPONSES

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AVIATION MEDICAL SERVICE
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Wendt (1951) has indicated that habituation (a response decline) of human nystagmus may depend upon the conditions under which the response is repetitively elicited. He says ". . . visual stimuli tend to inhibit the vestibular nystagmus, and with repetition these stimuli become increasingly dominant. Such habituation is probably not preventable." In the absence of visual stimulation, he has indicated that the loss of nystagmus ". . . is preventable by keeping the subject attentive to the external surrounds and avoiding inward-directed revery states."

Hence, in addition to specifying the importance of the conditions of elicitation, Wendt (1951) has distinguished between two kinds of habituation. One of these is a loss of a state of attentiveness toward, or interest in the surrounds. The other, and the more usual way of regarding the phenomenon, refers to a real change in the properties of the system that should be independent of fortuitous subjective variations such as attitudinal or attentional factors.

Wendt's concern with the importance of subjective states has been amply vindicated in recent studies which have shown that simple instructions regarding mental activity can markedly modify nystagmic behavior and that a high state of arousal, attention, or alertness, regardless of where it is focused, results in a vigorous nystagmic response (Collins, Crampton & Posner, 1961; Collins & Posner, 1963; Guedry & Lauver, 1961, Lidvall, 1962; Mahoney, Harlan, & Bickford, 1957). Further, it has been demonstrated that all of the characteristics of "habituation" can appear as early as the first exposure of individuals to rotatory stimulation by simply instructing them to relax and daydream (Collins, 1962). Such instructions literally abolish the response from some subjects and markedly reduce it from most.

Apparently, with vision not permitted and in the absence of instructions or techniques designed to maintain attention, subjects soon become relaxed and lapse into reverie states. Concomitantly, nystagmic activity declines and may eventually cease. This type of response decline, then, is readily demonstrable and equally readily reinstatable (cf. Collins & Guedry, 1962; Guedry, Collins & Sheffey, 1961).

The present study was designed to examine the effects of repeated mild angular accelerations in total darkness on human nystagmus while subjects performed a number of attention-demanding tasks. The latter were employed in an effort to obviate the influence of declining alertness and to "drive" the response on every trial. Further, "habituating" stimuli were limited to CW accelerations; decelerations were sub-threshold. Thus the question of whether nystagmus habituation could be directionally specific was examined. As a further point of interest, data pertaining to the subjective experience of rotation were collected to determine: (a) if subjective habituation could occur in the absence of visual cues; (b) if such habituation could be made directionally specific; and (c) if it could occur as a result of repeated stimulation while the subject's attention was directed elsewhere.

Apparatus and Procedure

Apparatus

Rotatory. The turntable has been described by Guedry and Kalter (1956). It was located in a light-proof enclosure and was equipped

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[1] Study conducted with the skillful technical assistance of Kenneth J. Gall and Kenneth E. Swain while the author was at the U. S. Army Medical Research Laboratory, Fort Knox, Kentucky. Additional assistance in data reduction rendered by Carolyn Roulston, Mary Jayne Capps, Joseph E. Duchon, and H. Gerald Hobelmann is gratefully acknowledged.

with a slip-ring system to permit recording in an adjoining room.

Task-stimulators. A Hewlitt-Packard 205A9 Oscillator was used to provide stimuli for most of the tasks assigned to the subjects. The oscillator was a source of both auditory and vibratory stimuli. The former were presented to the subject by means of a pair of standard earphones. Vibration was applied to the subject's forefinger by a Goodmans (4-ohm) Model V58 vibrator. The plastic extension of the vibrator protruded slightly through the hole in the left arm-rest of the subject's chair.

In all cases, the oscillator-frequency for the auditory stimulus was 700 cps; that for the vibratory stimulus was 250 cps. Stimulus intensity was maintained at a 30dB level above the subject's absolute threshold (obtained daily) during experimental sessions. A set of 3 interconnected Hunter Timers provided control over the duration of stimulus presentation.

Recording. All data were recorded on an Offner Type-T Electroencephalograph. A 1.4 sec RC time constant was used in amplification for nystagmus tracings. These tracings were obtained by means of a pair of electrodes taped by the outer canthi; an indifferent electrode was located on the mastoid process. Subjective responses were recorded (DC) by means of a telegraph key positioned on the right arm-rest of the chair. Depression of the key produced a pen deflection on the recorder; release of the key returned the pen to its original base-line. Similar deflections were produced by the timers, thereby indicating the duration of a given task-stimulus. Acceleration periods were recorded in a like manner.

Tasks

Subjects were given a period of instruction concerning the tasks and received actual practice in all but that requiring estimation of subjective velocity. In the latter case, they were given several demonstrations (with the experimenter performing the role of the subject) and asked to use only vestibular information in making their judgments.

Reaction time. At frequent points throughout a trial, subjects were presented with a tone, or with a vibratory stimulus, of one-half sec duration. Subjects were instructed to respond to the stimulus as quickly as possible by depressing the telegraph key.

Temporal estimation of stimulus-filled intervals. Subjects were presented with a series of tones or vibrations during a trial. Each stimulus lasted for a period ranging between 0.5-6.5 sec (in 1-sec intervals). At the conclusion of a stimulus, subjects were to reproduce its duration by depressing the telegraph key for the same period of time as that occupied by the tone or the vibration.

Temporal estimation of stimulus-bounded intervals. Brief (one-half sec) tonal or vibratory stimuli were presented to indicate the onset and conclusion of an intervening period of no stimulation. The intervening periods (unfilled intervals) ranged in duration from 0.5-6.5 sec in 1-sec steps. Thus, e.g., a half-sec tone would be followed by 4.5 sec of silence, and then by another half-sec tone. The subject would then reproduce the duration of the silent (unfilled) interval by depressing the key for his estimate of the length of time between the two tones. A series of these stimuli were presented throughout a trial.

Estimation of subjective velocity. Subjects were instructed in the technique of estimating angular displacement from their subjective experiences (Bekesy, 1955; Guedry & Lauver, 1961). Specifically, they were required to signal, by depressing the telegraph key, the onset, cessation, and each experience of 90° rotation. A warning signal was presented 10 sec prior to the initiation of an acceleration to alert the subject to the impending stimulus. When the subject signalled cessation of experienced rotation, he was instructed to remain attentive for any further rotatory sensations, however weak, which he might experience (e.g., a secondary reaction — a sensation of turning in the opposite direction without an adequate stimulus — Guedry, Cramer, & Koella, 1956). Such experiences were to be reported at the conclusion of the trial. Ten sec prior to deceleration (1 min and 50 sec after termination of acceleration) a second signal was presented which notified the subject that he could close his eyes and relax until the conclusion of the trial. This task was used only in the preliminary and post-tests.

TABLE 1

Procedural Outline for the Pre- and Post-Test Trials. Decelerations Were Always Sub-Threshold (0.18°/Sec^2). MA Refers to Mental Arithmetic Tasks, and ESV to Estimates of Subjective Velocity. The Rest Period Between Trials 4 and 5 Was 15 Minutes Long.

	TRIALS								
	1	2	3	4	REST	5	6	7	8
ACCELERATION	CW	CCW	CW	CCW		CW	CCW	CW	CCW
TASKS	MA	MA	MA	MA		ESV	ESV	ESV	ESV

Mental arithmetic. Subjects were required to do arithmetic problems consisting of silent, continuous division (Collins, 1962). A problem was assigned just before a given trial and a signal to begin work was presented 10 sec prior to acceleration. A second signal, to stop work, was presented 10 sec prior to deceleration (1 min and 50 sec after termination of acceleration). Subjects jotted down their final answer (in darkness) on a pad secured to the arm-rest of the chair. They then closed their eyes and relaxed until the conclusion of the trial. This task was employed during the preliminary and post-tests, and for trials 1, 2, 199, and 200 during the habituation series.

Subjects

The 10 subjects were all male volunteers, experimentally naive, physically healthy, and without any past history of ear difficulties, dizziness, or unusual reactions to linear or angular motion. They ranged in age from 19-26 years with a mean of 22.8. They were cautioned to maintain normal sleeping hours, to abstain from alcohol, and to report the intake of any medicinal drugs during the course of the experiment. Subjects were well motivated and it is unlikely that any of these factors influenced the results.

Procedure

Subjects were seated upright on a chair mounted on the rotating platform. A biteboard positioned their heads so that the horizontal semicircular canals were approximately in the plane of rotation. Earphones were worn during all trials and series of angular accelerations were administered in total darkness over 13 daily sessions. Twelve sessions were on consecutive days; the thirteenth occurred exactly 4 weeks after the twelfth.

The first, twelfth, and thirteenth sessions were termed, respectively, preliminary (pre), post-1, and post-2 sessions. Each of these consisted of 8 trials (a trial is defined as a complete acceleration cycle, i.e., acceleration to constant velocity to deceleration to stop). The acceleration direction for each of these trials was alternately clockwise (CW) and counterclockwise (CCW). During the first 4 trials, subjects were assigned mental arithmetic problems; during the last 4, they made estimates of subjective velocity (see Table 1).

Sessions 2 through 11 each consisted of 20 trials (habituation sessions). For this total of 200 accelerations, rotation was always in a CW direction. Tasks were assigned prior to each trial (see Table 2). In all of these trials, a signal was presented to the subject 10 sec prior to deceleration (1 min and 50 sec after termination of acceleration) to indicate that his task was completed and that he could close his eyes and relax until the conclusion of the trial.

All trials comprised the following: (1) 30 sec at a constant velocity of 1 rpm; (2) an acceleration of 4.15°/sec^2 for 13 sec; (3) 120 sec at a constant velocity of 10 rpm; (4) a deceleration of 0.18°/sec^2 for 333 sec to zero velocity. Rest periods of 3-5 min with the room illuminated separated the completion of one trial and the beginning of the next. Thus, acceleration stimuli were separated by a total of 11-13 min. An additional 15-min rest period

TABLE 2

ORDER OF TASK-PRESENTATION FOR THE 200 HABITUATION TRIALS. THE 10 SESSIONS, EACH COMPRISING 20 TRIALS, WERE HELD ON CONSECUTIVE DAYS. SOUND WAS USED AS THE STIMULUS DURING ALL TRIALS IN THE ODD-NUMBERED SESSIONS: VIBRATION WAS USED DURING ALL TRIALS IN THE EVEN-NUMBERED SESSIONS. MA REFERS TO MENTAL ARITHMETIC, RT TO REACTION TIME, AND FI AND BI TO FILLED AND BOUNDED INTERVALS, RESPECTIVELY.

	SESSIONS									
TRIALS	I	II	III	IV	V	VI	VII	VIII	IX	X
1	MA	FI	BI	BI	FI	FI	BI	BI	FI	FI
2	MA	FI	BI	BI	FI	FI	BI	BI	FI	FI
3	FI	FI	BI	BI	FI	FI	BI	BI	FI	FI
4	FI	FI	BI	BI	FI	FI	BI	BI	FI	FI
5	FI	FI	BI	BI	RT	RT	BI	BI	FI	FI
6	FI	RT	RT	RT	RT	RT	RT	RT	RT	RT
7	FI	RT	RT	RT	BI	BI	RT	RT	RT	BI
8	RT	BI	FI	FI	BI	BI	FI	FI	BI	BI
9	BI	BI	FI	FI	BI	BI	FI	FI	BI	BI
10	BI	BI	FI	FI	BI	BI	FI	FI	BI	BI
REST	15 MINUTE REST PERIOD									
11	BI	BI	FI	FI	FI	FI	FI	FI	BI	BI
12	BI	BI	FI	FI	FI	FI	FI	FI	BI	BI
13	BI	BI	FI	FI	FI	FI	FI	FI	BI	FI
14	BI	RT	RT	RT	FI	FI	RT	RT	RT	FI
15	FI	FI	BI	BI	RT	RT	BI	BI	FI	FI
16	FI	FI	BI	BI	RT	RT	BI	BI	FI	RT
17	RT	FI	BI	BI	BI	BI	BI	BI	FI	FI
18	FI	RT	RT	RT	BI	BI	RT	RT	RT	FI
19	FI	FI	BI	BI	BI	BI	BI	BI	FI	MA
20	FI	FI	BI	BI	BI	BI	BI	BI	FI	MA

during which the subject was permitted to leave the turntable separated trials 10 and 11 (see Table 2). Immediately prior to each trial, calibrations of the horizontal displacement of the subject's eyes were made and subjects were encouraged to be attentive and accurate in the performance of their tasks.

Scoring

All nystagmus records were analyzed into 3 measures: duration of response, slow-phase displacement, and frequency of beats. For the latter two, records were scored in 5-sec intervals throughout the course of the reaction. Durations were calculated from the onset of acceleration to the concluding phase of the last beat of primary nystagmus. Slow-phase eye deviation was scored by summing the slow-phase displacements of each nystagmic beat, from peak to base-line, per 5 sec interval. These values were converted to degrees of eye movement by means of the calibration factor. Frequency of nystagmus was determined simply by counting the number of beats within each interval.

Of the 2,080 trials conducted, only 5 records were not scored. Two of these were from the habituation series and, due to technical difficulties, no records were obtained. The remaining 3 were one pre-test (Trial 1 for RW) and 2 post-2 trials (Trials 1 and 2 for LM). In these cases, failure of a timing mechanism to perform properly resulted in interrupted stimulations. The obtained nystagmus was not scored for these incomplete accelerations.

Results

Effects of Stimulus Repetition

Some examples of recorded nystagmus appear in Figure 1. The post-test tracings clearly indicate a brisk nystagmus in spite of the preceding 200 acceleration exposures. However, the form of the response differs from that displayed in the pre-test. The intervening series of habituating trials induced an overall decline in the amplitude of nystagmus, and an increase in its frequency during the early seconds of the response. Figure 2 presents this relationship more clearly. For both the practiced and unpracticed directions of response, the first post-test shows a decline in slow-phase output relative to the pre-test performance. A further drop is evident in post-test-2, given one month later with no intervening trials. Noteworthy differences were evident in the frequency measures for both the practiced and unpracticed directions. Specifically, during the first 20-25 seconds of the response, the frequency of nystagmus increases from the pre- to the post-tests. However for the remainder of the response curve, the frequency shows a drop in post-test-1 and, although still below its original level, some recovery in post-test-2.

Figure 3 provides a direct comparison of the effects of the habituation series on post-test responses in the practiced and the unpracticed directions. There are negligible differences between the two directions in the pre-test, with the exception of the markedly longer duration for the CW direction. This difference is attributable to a single subject (RB) who yielded a 2-minute response to his first acceleration. Slow-phase output declined for both directions in post-test-1. However, it apparently declined differentially: relatively more for the unpracticed direction during the stimulus period, and relatively more for the practiced direction during the remainder of the response. The relationship between the slow-phase data for the two directions in post-test-2 resembles more closely the pre-test, although a further overall drop is evident.

The frequency plots in Figure 3 are of particular interest. With no significant pre-test differences evident between the two directions, the post-tests demonstrate an increase in frequency of nystagmus during the stimulus period, and a depression of activity after that time. This increase is clearly greater for the practiced direction. One month later (post-test-2), an overall frequency increase is evident for both directions, particularly during the stimulus period.

Plots of average total output appear in Figure 4. It is clear that some drop in the total slow-phase activity and the average response duration occurs for both directions from the pre-test to post-test-1. An additional decline is evident in post-test-2 despite the lack of any subsequent intervening stimulations. For frequency measures, little change in total activity is evident for the practiced direction; the unpracticed direction tends to decline by about

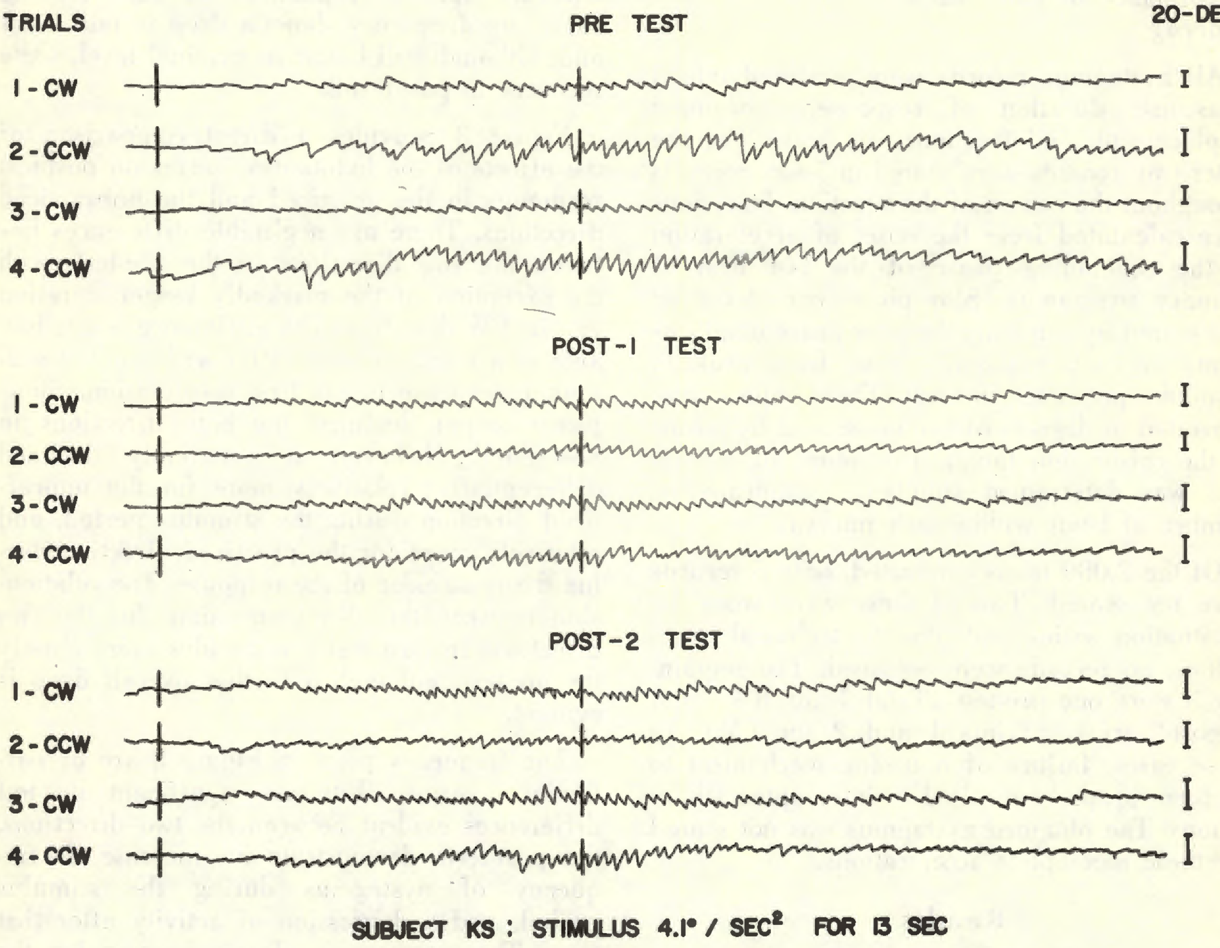

FIGURE 1. Nystagmus recorded during pre- and post-test mental arithmetic tasks. Vertical bars through records demarcate the stimulus period. Eye calibrations are at the right of each tracing. Note the increased response frequency in post-1 trials following 200 CW stimulations. Post-2 trials show no evidence of recovery to the pre-test level although one month with no intervening trials had elapsed between post-1 and post-2 tests.

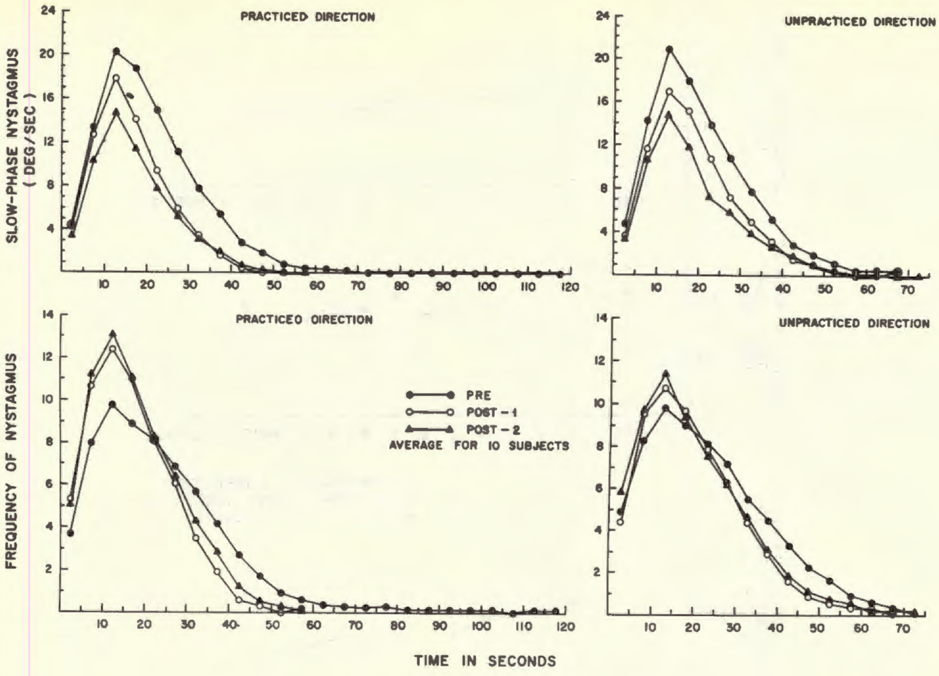

FIGURE 2. Average nystagmus slow-phase and frequency curves for pre- and post-test data plotted in 5-sec intervals. An overall depression of slow-phase output is evident for both the practiced and unpracticed directions. For frequency data, a depression affects only the tail of the curve; an increased frequency response occurs during the stimulus period and for a few seconds thereafter.

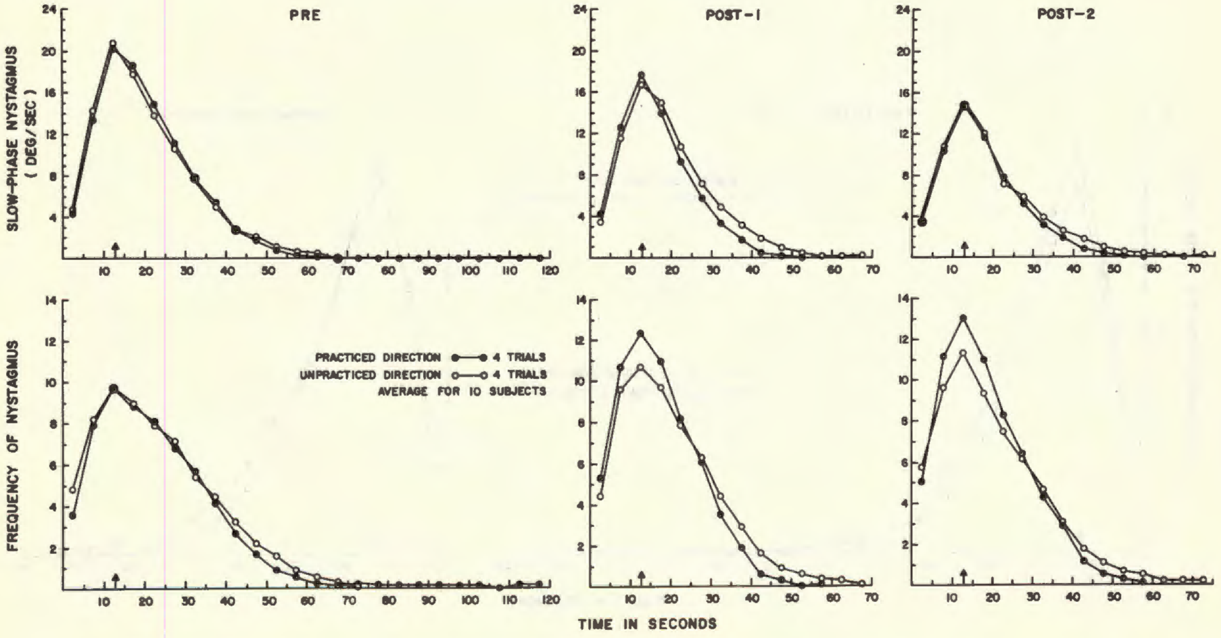

FIGURE 3. A time-course comparison of frequency and slow-phase nystagmus responses in practiced and unpracticed directions during the pre- and post-tests. The clearest differences appear in the post-test frequency responses during, and for a few seconds after, the stimulus period favoring the practiced direction. Compare with Figure 2.

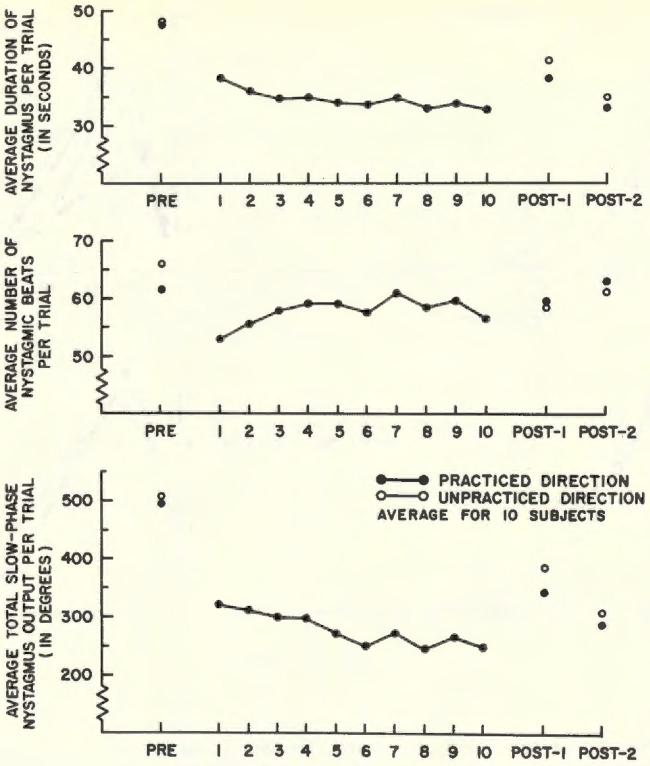

FIGURE 4. Average response-per-trial for each of the 13 experimental sessions. A gradual decline during the 10 habituation sessions is evident for both slow-phase and duration data; an increase occurs in frequency of nystagmus. Pre- to post-test declines in slow-phase and duration of nystagmus are somewhat greater for the practiced direction; overall frequency of nystagmus shows little change.

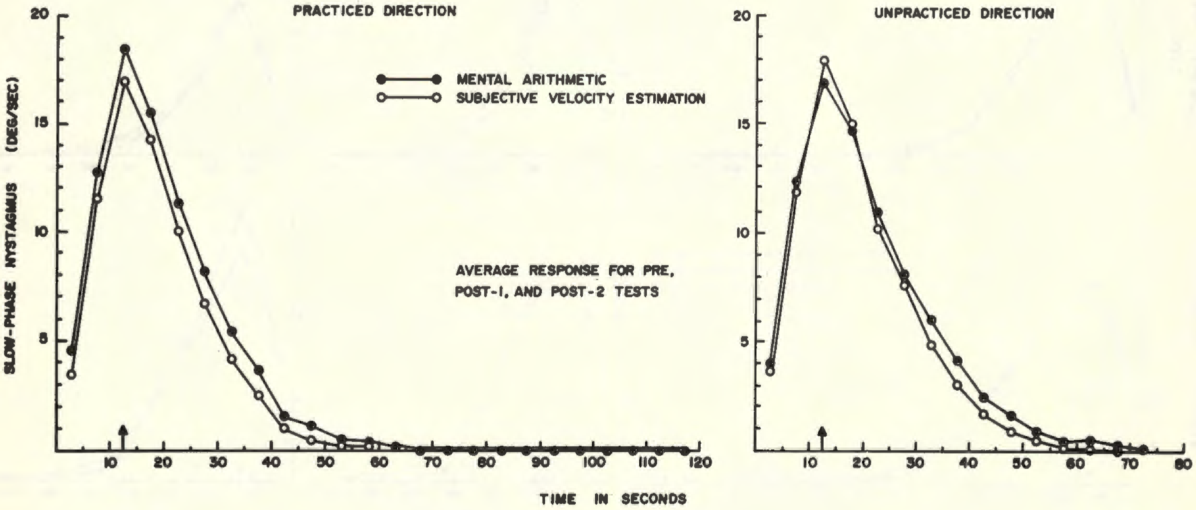

FIGURE 5. A time-course comparison of pre- and post-test nystagmus output to mental arithmetic trials and to trials in which subjects estimated angular velocity. Since separate curves for pre-, post-1, and post-2 tests all showed the same relationship favoring output during the arithmetic trials, curves were averaged over the 3 sessions.

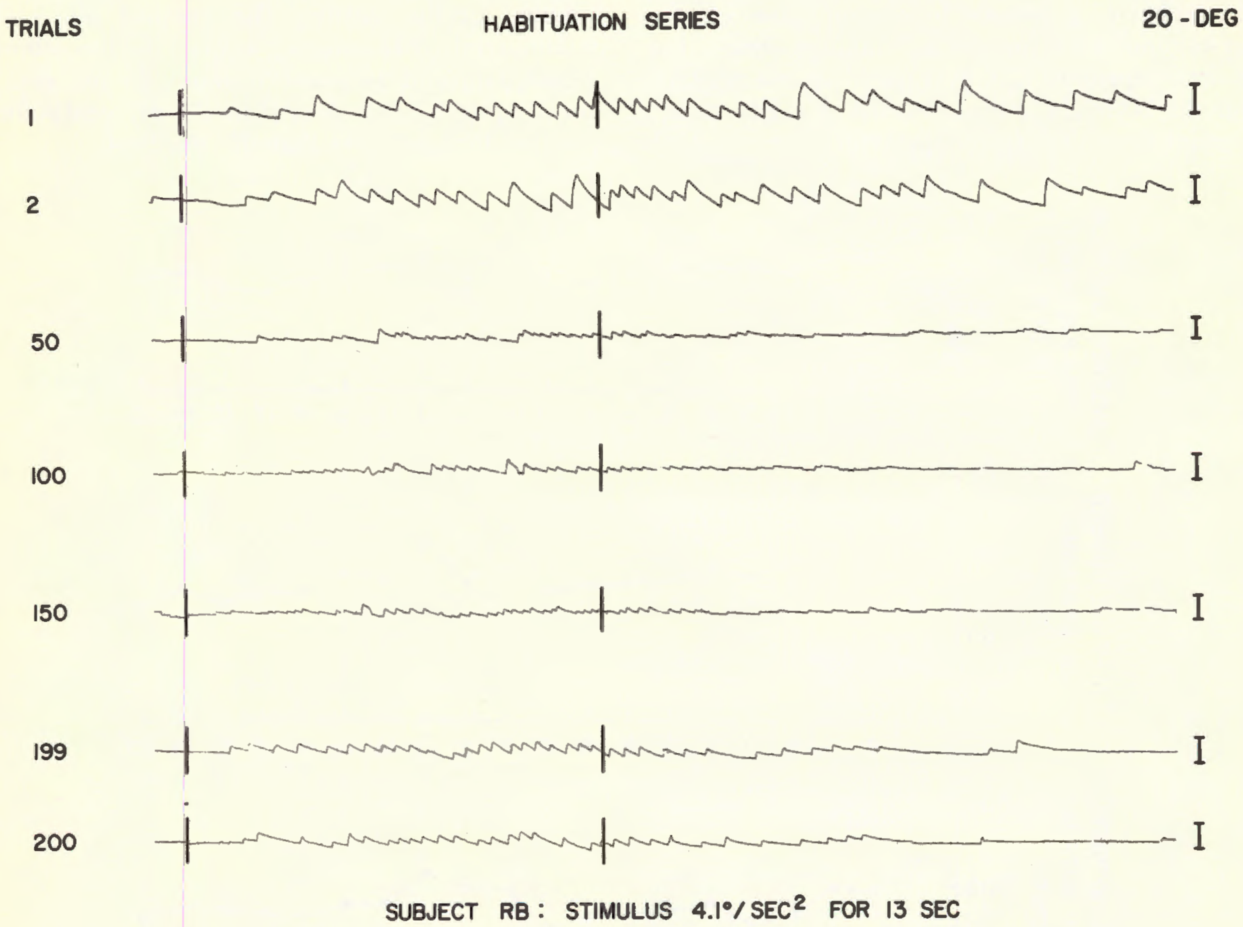

FIGURE 6. Nystagmus tracings obtained during the habituation series. Trials 1, 2, 199, and 200 comprised mental arithmetic tasks. The middle 3 tracings were obtained while the subject was engaged in making estimations of temporal intervals. Markings are the same as in Figure 1.

10 per cent. Thus, the overall frequency counts show little pre- to post-test change and thereby mask the selective effects of the habituation series on the frequency response during, and for a few seconds after the angular acceleration (Figures 2 and 3).

There was no large difference evident between the output of nystagmus obtained during the mental arithmetic (MA) tasks and during those in which estimates of subjective velocity were made (Figure 5). However, differences slightly favoring MA trials were consistent for each of the pre- and post-tests.

The Habituation Series

In addition to pre- and post-test data, Figure 4 provides a session-by-session plot of the nystagmus data for the habituation series. The points represent the average response-per-trial for the 20 trials in each session. A fairly steady decline is evident from session to session in both duration and slow-phase measures. For frequency, an increase occurs. In all cases, the maximum change is approximately 20 per cent. It should be noted that the differences in output levels between pre-test data and those of the habituation series are due primarily to the rather rapid decline within the first few habituation trials (Figure 6).

Figure 7 provides an indication of the course of the various response outputs over trials. In this case, each point represents an average of the 10 sessions. Gradual declines are evident for all 3 measures from trials 1 through 10. Increased output occurs in all cases for trial 11 (after a rest period) following which another gradual decline occurs. The greatest range of trial-to-trial differences occurs in the slow-phase data and amounts to about 25 per cent; for frequency, it is less than 20 per cent; and for the duration, less than 15 per cent.

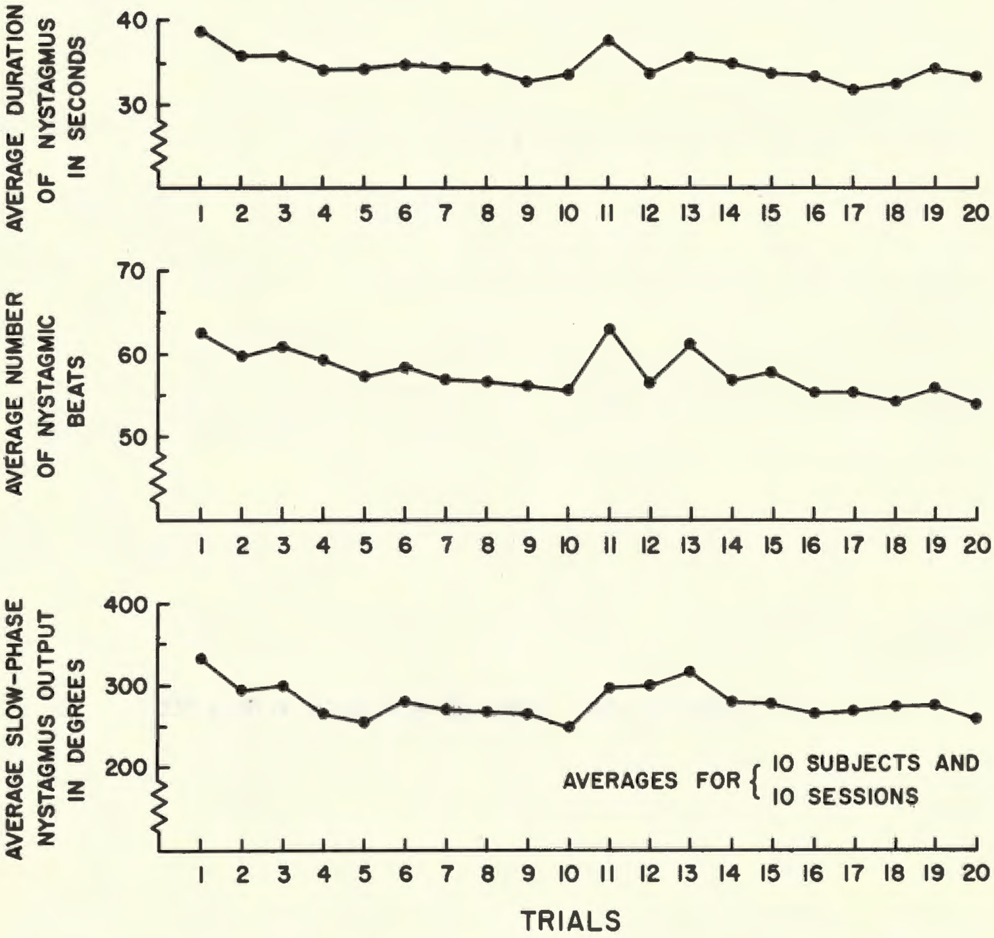

FIGURE 7. Analysis of nystagmus output during the 20 daily trials. Each point is an average for the 10 habituation sessions. Trial-to-trial declines are not marked and an increased output occurs uniformly for trial 11 after a 15 min rest period.

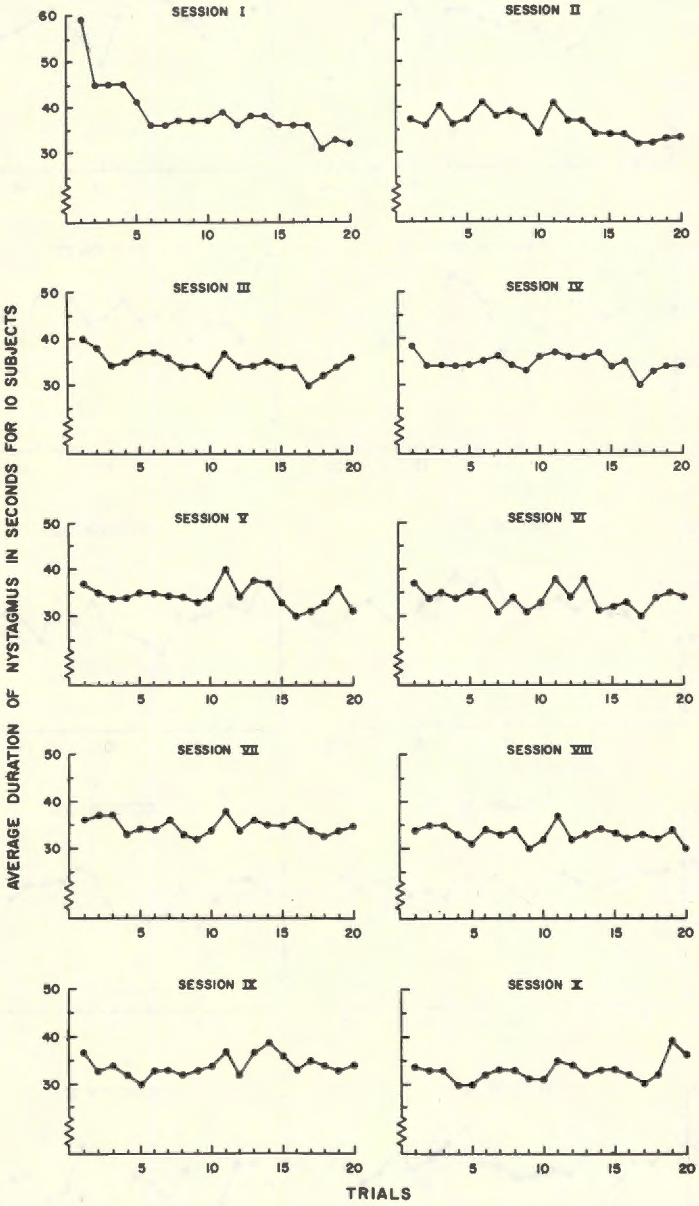

Figure 8. Trial-by-trial plots of nystagmus durations for the habituation series.

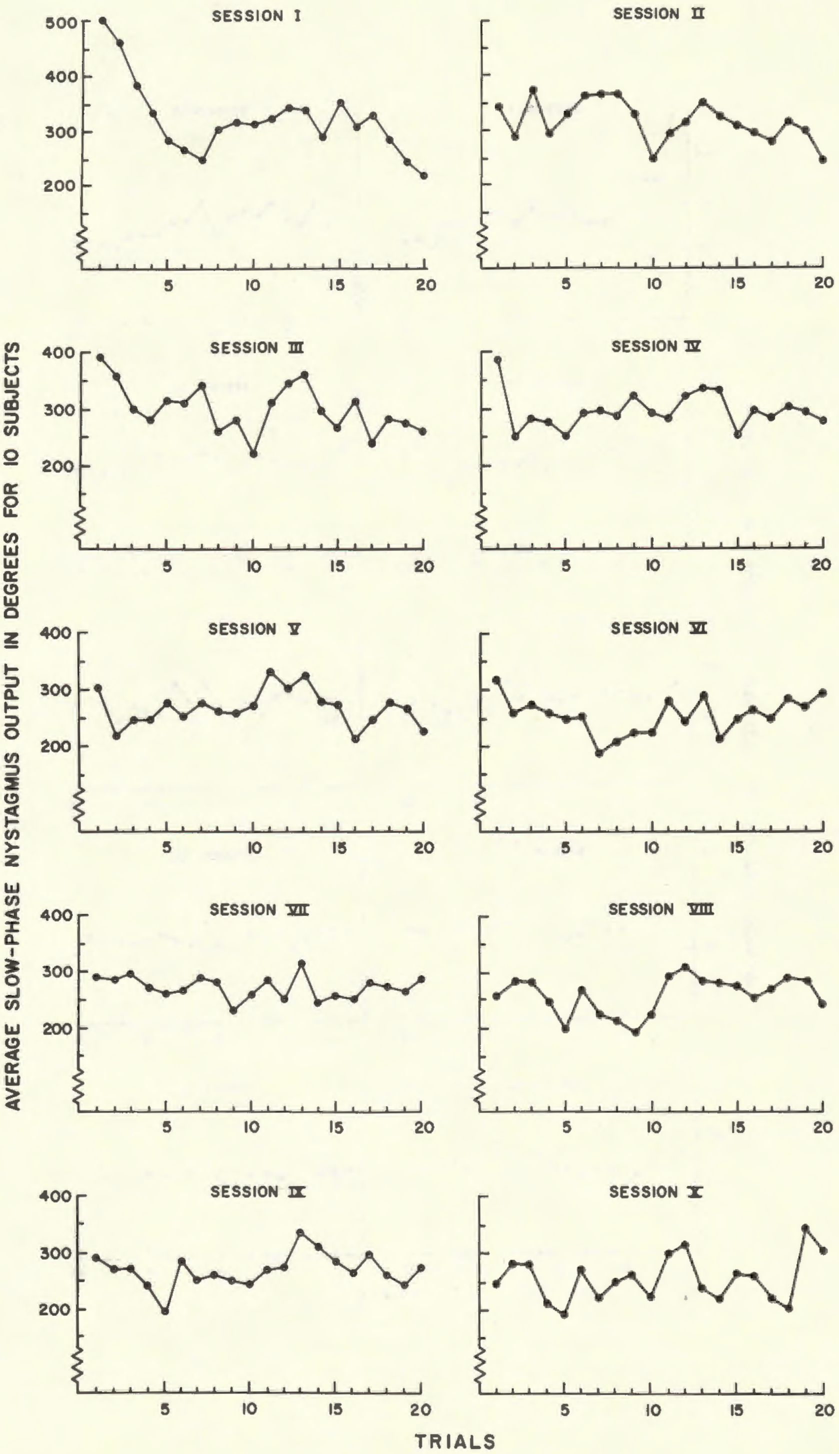

FIGURE 9. Trial-by-trial plots of slow-phase nystagmus output for the habituation series.

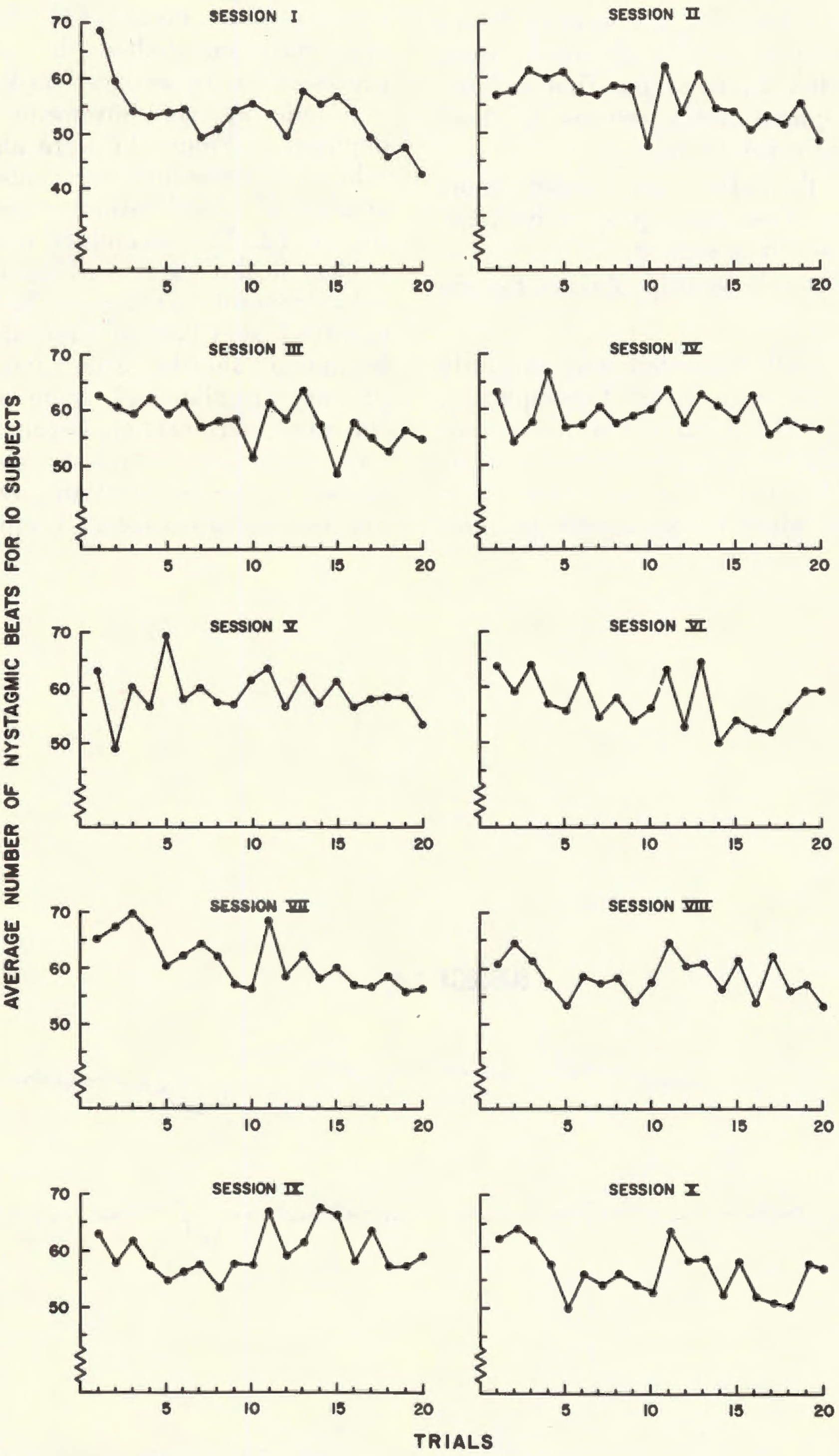

FIGURE 10. Trial-by-trial plots of the nystagmus frequency data for the habituation series.

The average trial-by-trial data for each session appear in Figures 8, 9, and 10 for duration, slow-phase, and frequency respectively. These graphs indicate that:

(a) The most significant and striking losses in slow-phase output and in duration occur within the first few trials of the first session. The average response never returns to those early levels in any future trial.

(b) Changes thereafter are much more gradual and there is no sharp, progressive trial-to-trial decline within a session.

(c) A different relationship obtains for the frequency data.

Subjects were well motivated and carefully instructed prior to each trial. Consequently, only 19 of the 2,000 habituation series records showed the wandering eye movements characteristic of loss of attention. In each case, these changes occurred while subjects were estimating temporal durations. Nystagmus was immediately re-instated by simply presenting a new sound or vibratory stimulus while the subject was in the process of responding to a previous one (Figure 11). Such a procedure apparently marshalled the subject's attention processes to the assigned task.

Wandering eye movements similar to those depicted in Figure 11 were also seen when deceleration recordings were obtained. Other examples of deceleration responses appear in Figure 12. The secondary nystagmic reactions evident in the tracings of the latter figure were not infrequent occurrences. Such responses were observed in 1,058 of the habituation records, beginning shortly after termination of the primary reaction and, quite often, still apparent when deceleration began. On some occasions, secondary responses seemed to be enhanced by the deceleration (see Figure 12), but this was not a consistent finding.

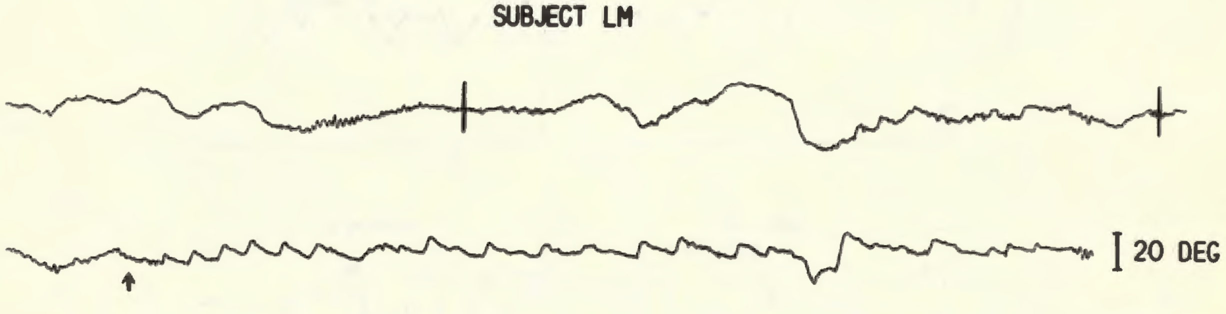

FIGURE 11. One of the 19 instances in which wandering eye-movement and unclear nystagmus were obtained. The subject was engaged in estimating temporal intervals. The arrow indicates the point at which a new task stimulus was presented while he was still in the process of responding to a previous one. Nystagmus was immediately restored. Markings are the same as in Figure 1.

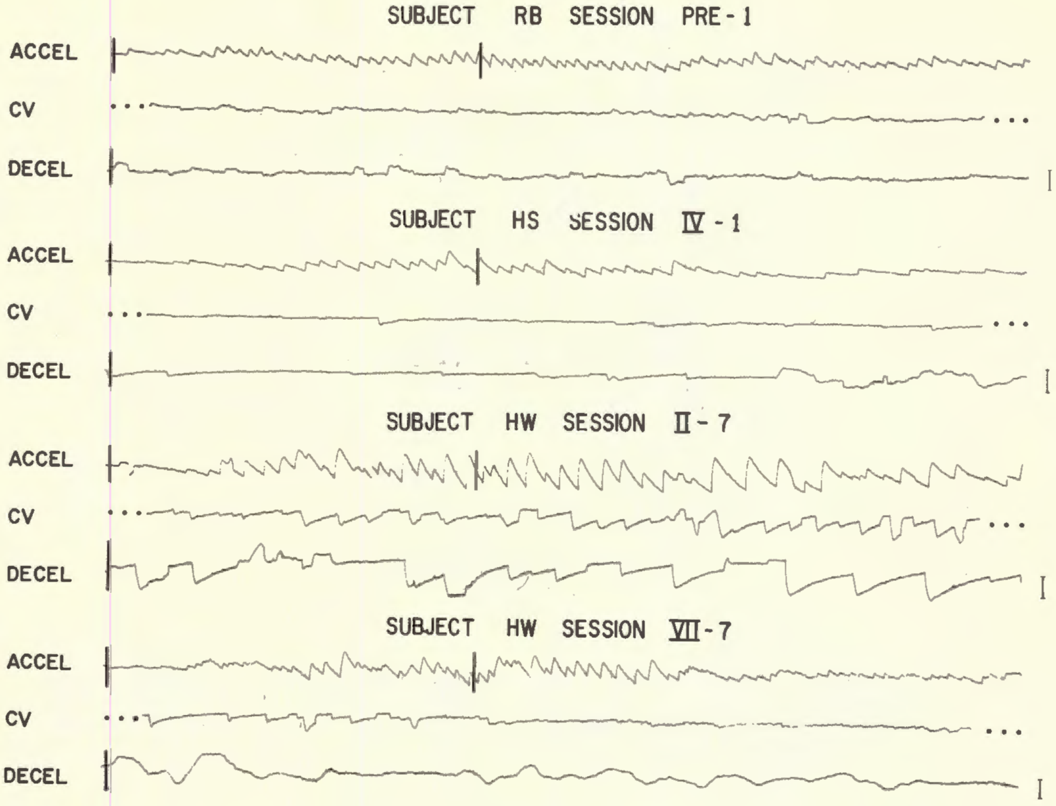

FIGURE 12. Some examples of secondary nystagmus and of deceleration responses. The tracings are not continuous but are interrupted where the 3 dots appear. Other markings are the same as in Figure 1. RB shows no secondary reaction and no directionally specific activity during deceleration. Secondary nystagmus is present for both HS and HW. Such responses were frequently still in progress when the period of constant velocity (CV) ended, but in only some cases did they appear to be enhanced by the deceleration stimulus (as in the HW, Session II-7 record).

Subjective Angular Velocity

Subjective responses were scored by measuring the amount of subjective displacement, signalled by the key pressing technique, within each 5-sec interval. Since each signal represented 90° of experienced angular movement, the measurements were readily converted to degrees of displacement.

Four trials each in the pre-test and the two post-tests provided subjective rotatory data for both CW and CCW accelerations. Plotted results appear in Figure 13 for 8 of the 10 subjects. For the pre-test, no essential difference between the two curves is apparent. However, post-test-1 indicates a clear decline for the CW direction and post-test-2 shows some recovery, albeit not complete, after one month with no intervening stimulation. From Figure 14 it is clear that the subjective impressions of angular velocity in the CCW direction were not at all affected by the 200 CW habituation trials.

Data from two subjects are not included in Figures 13 and 14. Both gave abnormally long subjective responses during the pre-test and, to prevent possible distortion, their data were not included in the average curves. It is possible that they may have responded to non-vestibular cues or, perhaps, that they fell into a rhythm of key pressing although their sensation had diminished. The latter effect has been noted in the training of subjects (F. E. Guedry, personal communication).

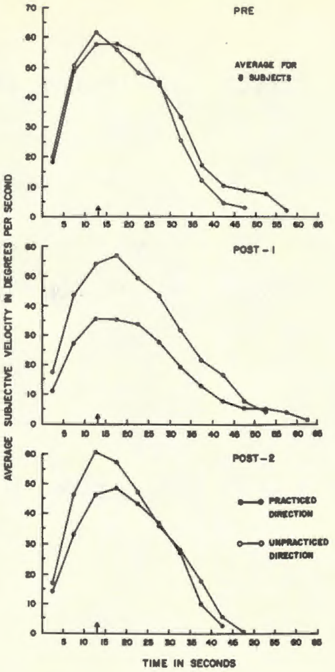

FIGURE 13. Subjective velocity estimated during pre- and post-tests. Each point represents an average of 2 trials per subject. Arrows indicate moment of stimulus termination. Intensity of the subjective reaction is considerably diminished in post-1 for the practiced direction. Post-2 test shows some recovery.

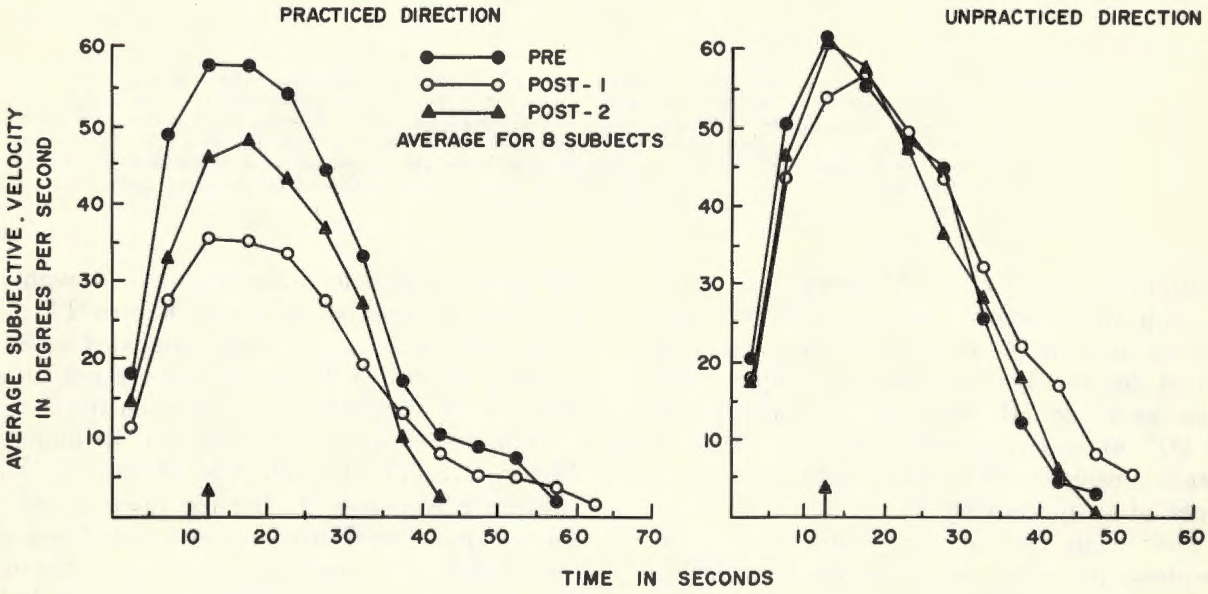

FIGURE 14. A direct time-course comparison of pre- and post-test output for the practiced and for the unpracticed directions. The latter shows little or no change. The practiced direction shows a substantial decline in amplitude from the pre-test to post-1. Recovery is evident in the second post-test given 1 month later. Note that the duration of the subjective response is not reduced after the 200 accelerations interposed between the pre- and post-1 tests.

Discussion

Human Nystagmus Habituation

Rotation studies. Griffith (1920b) employed 10 rotatory trials per day for approximately 4 weeks and found an average response loss in 16 subjects of 79 per cent for both frequency and duration of nystagmus. His data showed a major decrease in the first few trials and he noted that, when subjects had organic disturbances or had just undergone physical exertion, nystagmus improved temporarily. Griffith (1924) reported his own response to be still below its original output level some 4 years later, with no intervening stimulation. However, in his study, as well as in those of Holsopple (1923; 1924) who also found nystagmus habituation, visual fixation was permitted.

Dodge (1923) subjected himself to 114 rotation trials per day for 6 days. He recorded nystagmus with eyes closed and reported eventual abolishment of the response to his deceleration stimulus (which was initiated while the acceleration response was going on) and a 50 per cent transfer effect when the direction of rotation was reversed. He also noted that "the rotation experiment had a soothing soporific character . . ."

In a less extensive study, Mowrer (1937) examined the influence of vision during rotation by 12 trials alternately with and without fixation opportunities during rotation. Vision was always permitted at the stop and it was here that the data were obtained. He reported no significant evidence of habituation.

Suzuki and Totsuka (1960) measured the duration of post-rotatory nystagmus during approximately 20 trials for 4 groups of subjects. Nystagmus was recorded from closed eyes and, although alertness may have been a factor in producing some marked trial-to-trial variability, no clear pattern of habituation was obtained.

More recently, Guedry, Collins and Sheffey (1961) gave experienced subjects 10 rotation trials per day for 5 days. Stimuli were 14.6°/sec^2 for 5 sec. Odd-numbered trials were entirely in darkness. Even-numbered trials were also in darkness with the exception of a 5-sec period (2 sec after the stop) during which visual fixation was permitted. They reported a decline of nystagmus from day-to-day as well as within days, but noted that much of the decline appeared due to an alertness factor.

Caloric studies. In unilateral caloric studies, Loch and Haines (1946) reported that duration of nystagmus was unaffected when subjects were irrigated once daily for 5 or 6 days while wearing Frenzel glasses. However, they noted changes in the form of the response. Lidvall (1961a, b; 1962) used a small number of stimuli (4-6) and found nystagmus habituation regardless of whether the interstimulus intervals were short (6-8 minutes) or long (1-25 days). Fluur and Mendel (1962a, b) reported reduced nystagmus from a series of 12 unilateral irrigations. In the studies of Lidvall and of Fluur and Mendel, eye movement recordings were obtained from behind closed eyes. These studies differ significantly from those of rotation in that the canals on one side only are stimulated. In this regard, Lidvall (1961b) has stated that diminution of responses so elicited "should not prove surprising" in view of recovery patterns following unilateral labyrinthectomies.

Present results. The present data indicate that, when subjects are kept in an alert state, 200 stimulations will not abolish nystagmus to a 4.1°/sec^2 acceleration applied for 13 sec. That the response can disappear as a function of declining alertness (and be immediately reinstated by appropriate techniques) has been demonstrated in previous papers (cf. Collins, 1963a) and was evident in several of the records obtained here (Figure 11).

Although nystagmus in the practiced direction was not abolished, the total slow-phase output and the duration of the reaction were reduced by 30.5 and 19.4 per cent respectively, from the pre-test to post-test-1. Total frequency declined only 3.2 per cent. However, the form of the response was strikingly changed. During the stimulus period and for a few (5-7) seconds thereafter, the amount of slow-phase displacement declined while the frequency of the beats increased. The remainder of the response became depressed for both measures and the duration was shorter. These data may indicate how an apparently complete abolishment of nystagmus occurs. Repeated elicitation of the eye-movement response may result in increased activity of the central mechanism which controls the fast-phase of the reaction. True habituation in an alert subject may then come about by increased activity of the fast-phase center in interrupting the slow-phase drift of the eyes at earlier and earlier times so that, eventually, there is a very high fast-phase frequency and extremely little slow-phase displacement. Such a mechanism could, eventually, completely cancel out nystagmus.

These data provide no indication of whether nystagmus is differently influenced under conditions of visual fixation. They indicate that in an alert subject, in total darkness, with the response permitted to run its course, nystagmus is not easily abolished to this mild level of stimulation. The previously cited studies of human habituation did not control for these factors. Thus, Griffith (1920b; 1924), Holsopple (1923; 1924), and Mowrer (1937) all obtained their data under conditions of fixation. Although Dodge (1923) did not permit vision, there are indications that alertness was a factor and, in addition, his acceleration and deceleration responses overlapped. Declines of nystagmus obtained by Guedry, et al. (1961) were reported to be substantially affected by alertness. A similar factor may account for the variability obtained by Suzukí and Totsuka (1960).

The reductions in response obtained in the present study from pre-test to post-test-1 do not approach the declines reported in the earlier studies. Further, the reduction does not have any striking directional specificity. Although it is possible that the 0.18°/sec^2 deceleration stimulus was not completely sub-threshold, it seems unlikely that it would produce an almost identical amount of response decline as a 4.1°/sec^2 stimulus while leaving the subjective reaction unaffected. Further, the subjects were permitted to relax and close their eyes prior to and during the deceleration period in a further effort to reduce any potency of the deceleration stimulus. It should be noted, however, that since a secondary nystagmus was frequently in progress when deceleration was initiated, some interaction of this ongoing response with the deceleration stimulus might have occurred on some trials (see Figure 12).

The second post-test, given after one month of rest, indicates that there was little, if any, recovery of the nystagmic reaction. A further drop in duration and slow-phase activity is evident. Frequency of nystagmus showed a slight overall increase. These changes were true of both the practiced and unpracticed directions. Hence, the changes which the repeated stimulation induced are not attributable to simple fatigue nor are they readily reinstatable. A similar permanency of change was reported by Griffith (1924) and Guedry et al. (1961). It is interesting to note that a brief (15 min) rest during a series of successive rotations resulted in a temporary elevation of the nystagmic response whereas a far lengthier rest-period (1 month) had no significant restorative effect.

The tasks. Previous short-term studies of alertness and vestibular function (Collins, 1962; Collins, Crampton & Posner, 1961) indicated that timing tasks could lose their attention-value. Several records obtained here showed wandering eye-movements or dysrhythmia during response periods while subjects were making temporal estimations. However, the subjects were extremely well motivated and such occurrences were remarkably few.

It is of interest that the 2 mental arithmetic (MA) trials inserted at the conclusion of the tenth and final habituation session did not restore nystagmus to its original level (Figures 4 and 6). This indicates that differences in output level between pre- and post-tests and the habituation series (Figure 5) can not be accredited solely to differences in task. It seems clear that MA is an extremely effective means of eliciting a vigorous, long-duration nystagmus to both angular acceleration (Collins, 1962; Collins & Poe, 1962) and caloric irrigation (Collins, Guedry & Posner, 1962). However, the major difference between the pre-test output-level and that for the habituation series seems due to the rapid decline of nystagmus which occurs within the first few trials. Remaining differences appear attributable to (a) a more vigorous response during MA and subjective rotation tasks, and (b) fewer pre- and post-test trials.

Use of the tasks apparently prevented the frequently reported, sharp decline of nystagmus from trial-to-trial (e.g., Griffith, 1920b; Guedry et al. 1961). That some such reduction in response occurred is clear, but as Figure 7 illustrates, it is remarkably slight, is greatest from the first to the second trial, and is at least temporarily reinstatable by a few minutes of rest (Trial 11). Figures 8, 9, and 10 illustrate, with the exception of the first session, that the pattern is not at all a regular one and the within-session declines are generally not great in alert subjects.

Some comparative data. Nystagmus habituation has been demonstrated for a number of infrahuman species. Repeated vestibular stimulation under a variety of conditions has produced marked response declines in the pigeon (Fearing, 1926; Mowrer, 1934), the squab (King, 1926), leghorns (Fukuda, Hinoki & Tokita, 1958), white rats (Griffith, 1920a), rabbits (Dunlap, 1925; Maxwell, Burke & Reston, 1922, Hood & Pfaltz, 1954), and cats (Collins, 1963b, c; Crampton, 1962a, b; Crampton & Schwam, 1961; Henriksson, Fernandez & Kohut, 1961; Henriksson, Kohut & Fernandez, 1961).

The present data may be compared with results obtained from a group of 10 cats exposed to one session of 15 unidirectional rotations under acceleration conditions identical to those reported here (Collins, 1963c). The cat shows a marked and rapid nystagmus habituation. Initially, its response is shorter in duration and lower in frequency than that of man. Within a series of 15 trials, duration declines by about 50 per cent and frequency and slow-phase output each by about 70 per cent. The habituation occurs even when alerting stimuli are introduced (Crampton, 1962a; Crampton & Schwam, 1961). Further, the character of the habituation process seems different from that of man. There appears to be simply an overall depression of activity with the maximum loss of response occurring after termination of stimulation. Crampton (1963) has referred to this as a "tailoring" of the cat's response to the stimulus. Other data indicate that nystagmus habituation in the cat is directionally specific (Collins, 1963b; Crampton, 1962a; Henriksson, Kohut & Fernandez, 1961).

Subjective Rotation

Earlier findings. Griffith (1920b) in addition to his reports of nystagmus decline, noted attenuation in the sensation of apparent motion which followed cessation of rotatory stimulation. Under his test conditions, visual fixation was permitted.

Hallpike and Hood (1953) and Hood (1960) reported a directionally specific decline in the duration of the rotatory sensation elicited from subjects with closed eyes. Their technique differed from the usual stimulating conditions in that they applied a standard test stimulus (e.g., $4°/sec^2$ for 6 sec) before and after a prolonged (e.g., $2°/sec^2$ for 75 sec), constant angular acceleration. The latter effected a notable decline in the post-test response when both stimuli deflected the cupula in the same direction. When the post-test caused a cupula deflection in the opposite direction, responses were normal.

Guedry, Collins & Sheffey (1961) had subjects estimate subjective velocity during a 5-day test series of 10 daily trials. Trials were alternately: (a) in total darkness, and (b) in total darkness with the exception of a 5-sec period in illumination with opportunities for visual fixation. The average total subjective displacement dropped by approximately 50 per cent when tests given 1 day before and 1 day after the habituation trials were compared. An additional post-test 9 days later showed recovery such that the amount of subjective displacement rose from 1/2 to 2/3 of its original level.

Lidvall (1961a, b) reported declines in both the intensity and duration of the rotational experience actuated by repeated unilateral caloric irrigation. However not all subjects are able to specify a directional component to the subjective experiences occasioned by such stimulation (Preber, 1958).

Subjective aspects of rotation have been frequently studied in terms of the oculogyral illusion i.e., the apparent motion of an object (usually a spot of light in an otherwise darkened room) which is actually in a fixed position relative to the subject; the object appears to move in a definite sequence during vestibular stimulation. van Dishoeck, Spoor, and Nijhoff (1954) and Vogelsang (1961) have related the illusion to sensation rather than nystagmus.

Brown and Guedry (1951) noted no decline in the duration of the oculogyral illusion (OGI) as a result of a series of stimulations in total darkness, although a similar series with the target light present, and a third series with room illumination resulted in marked declines. Guedry (1950) found a trial-to-trial attenuation in the duration of the illusion by alternating trials in total darkness with those in full-room illumination. Later, he reported declines in duration of the illusion which were specific to the direction of nystagmus when room illumination was introduced (Guedry, 1953a, b). These studies emphasized the importance of visual fixation in habituation of the OGI response.

In a later study, Guedry and Ceran (1959) employed prolonged, constant angular accelerations of low magnitudes. Although their primary concern was in the decline of subjective velocity (using a target light as a reference point) *during* an extended stimulus period, they also noted a reduction in subjective velocity as a function of stimulus repetition. The reduction of the subjective response *during* a single prolonged stimulus (Guedry & Beberman, 1957; Guedry, Cramer & Koella, 1958; Guedry & Lauver, 1961) represents an adaptation process which probably differs from that under consideration here.

Present results. The data obtained for subjective rotatory experiences provide a clear indication that the decline in the sensation of angular movement is specific to a practiced direction of stimulation. The 200 CW habituation trials produced virtually no change in the magnitude and duration of the subjective reactions to CCW acceleration. However, for the practiced direction, total subjective displacement declined by about 37 per cent, and peak subjective velocity by about 39 per cent from the pre-test to post-test-1. After one month without intervening rotation trials, recovery was evident. Total subjective displacement was now only 27.5 per cent less, and peak subjective velocity only 16.5 per cent less, than the pretest values. A decline in rotatory sensation with repetition of stimulation and a subsequent indication of recovery after several days of rest was also reported by Guedry, Collins & Sheffey (1961).

In addition to the importance of demonstrating that the subjective decline can clearly be made directionally specific and that visual fixation is not a necessary condition for such an occurrence, these data provide an indication that subjective vestibular habituation may occur in the absence of attending to the rotational stimulus. Reports from the subjects seemed to indicate that they were generally unaware of rotatory sensations during the habituation series and were attending, instead, to the assigned tasks.

Some Related Studies

Occupation-induced habituation. The performance of individuals in certain occupations would seem to require at least some forms of vestibular habituation. Figure skaters, for example, undergo extremely vigorous rotatory experiences with no apparent disorienting effects. Examination of such people in the laboratory is reported to indicate a lack of both vertigo and nystagmus when they are stimulated either by rotation or by caloric irrigation (McCabe, 1960).

Since World War I, the study of vestibular habituation has been closely related to aviation medical problems. Indeed, questions concerning the vestibular function of pilots provided the impetus for many of the early studies. Recent investigations have examined groups of pilots to determine the effects of flying experience on their responsivity to vestibular stimulation. Aschan (1954) employed rotational stimuli and reported lower-than-normal values for both sensation and nystagmus durations in a group of Swedish fighter pilots. There was no apparent directional specificity for the reduced sensation, but directional differences in nystagmus appeared related to the direction in which the pilot preferred to "roll" his plane. Long periods of reduced flying activity resulted in a "normalization" of the vestibular response, particularly with respect to nystagmus.

Caporale and Camarda (1958) examined 4 acrobatic jet pilots with rotation tests of nystagmus. They noted a vestibular asymmetry in each pilot that was correlated with the lateral position of the man in the acrobatic V-formation most frequently used.

Preber (1958) tested a group of trainee pilots before and after flight training. He divided them into 3 groups (no airsickness; airsick once or twice; severely airsick several times) on the basis of a questionnaire given after 4-6 months in the course. In re-examining his vestibular findings obtained before training began, he noted large differences between the "no airsickness" and the "severely airsick" groups. The latter showed greater maximum slow-phase eye speed and longer duration of sensation to both rotation and caloric irrigation. A follow-up examination of the "severely airsick" group after they had adapted to the flying situation and had shown no further symptoms indicated that their sensations of turning and the maximum eye-speed of nystagmus had declined for the rotatory and caloric tests.

Groen (1962) mentions a study by Krijger which indicated that both the sensation and the nystagmic response to rotation were inhibited in experienced test pilots when their data were compared to those of a control group. After several weeks of flying inactivity, their responses returned to normal.

Observations during an aircraft maneuver were made by Dearnaley, Reason, and Davies (1962). Subjects reported the duration of the vestibular after-sensation following one-minute long, 45-degree banks. Duration of the sensation was markedly shorter for experienced pilots than for trainees whether their eyes were closed or visual references were available.

The studies cited above indicate that the repeated vestibular stimulation occasioned by some occupations results in a recoverable modification of the vestibular response. That the reduction of sensation was not found to be directionally specific (Aschan, 1954) while that of nystagmus was (Aschan, 1954; Caporale & Camarda, 1958), and that recovery of the oculomotor reaction occurred after several weeks of inactivity (Aschan, 1954; Groen, 1962) differ from findings in the present study. However, several reconciliating explanations are possible: (1) Only duration of the sensation was reported in the cited studies. Present data show little effect on the duration but a marked effect on the intensity of the subjective reaction. Further, the pilots were exposed to angular movements in more than one direction. This may have had an equalizing effect. (2) Habituation of the vestibular response for these occupational groups is occasioned by efforts to overcome sensations which intrude on performance. Further, opportunities for visual fixation are present. It is possible that the mechanism of habituation differs depending upon whether combinations of intention and visual references are present, or whether the reaction is simply elicited repetitively (Guedry, 1964). The latter condition may more accurately represent Hood and Pfaltz's (1954) "non-meaningful stimuli" than does the former.

Unusual vestibular stimulation. Responses to passive rotation about the center of a vertical axis with the head held in a fixed position, characteristic of the test situation reported here, differ markedly from the vestibular reactions elicited as a result of head movements during constant rotation. The subjective experience produced by such stimulation can be extremely uncomfortable and disorienting, and the nystagmic reaction comprises both horizontal and vertical components. Habituation of these Coriolis phenomena, both subjective and ocular, was noted by Guedry and Montague (1961), while Graybiel, et al. (1961) reported a reduction in the oculogyral illusion as a result of repeated head movements in a rotating room.

Analysis of Coriolis nystagmus habituation indicated that a compensatory response, opposite in direction to the responses elicited as a result of head movements in the rotating room, was built up over time to counteract the disorienting reactions and produce a state of adaptation (Guedry & Graybiel, 1962). Further studies indicated that, when head movements were restricted to a particular quadrant, there was no transfer to the unpracticed quadrant (Guedry, Graybiel & Collins, 1962; Guedry, Collins, & Graybiel, 1963).

The vestibular habituation attendant to adapting to head and body movements in a constantly rotating environment appears different from the mechanism by which nystagmus was reduced in the present study. However, there are notable differences in the experimental conditions. In the Coriolis studies, all 3 pairs of semicircular canals were stimulated, otolith and proprioceptor activity was marked, visual fixation was permitted, and, as in the occupational studies cited above, intention was involved as the subjects tried to inhibit the uncomfortable reactions.

Overview

Data obtained in the present study indicate that a bidirectional decline in nystagmic output occurs in man as a result of repeated unidirectional angular accelerations in total darkness. Nystagmus, however, is not readily abolished to these mild levels of stimulation if subjects are maintained in an alert state. Rather, the character of the response becomes altered, apparently by increased activity of the central mechanism which controls the fast-phase of the reaction. This modification of the central nervous system is not capricious; the response shows little or no recovery toward its original intensity and form after a month of rest.

The decline in the subjective rotatory experience has four aspects of interest. (1) Whereas nystagmus was bidirectionally modified, the reduction of the sensation of rotation was specific to the direction of the habituation trials. (2) The reduction occurred in the absence of visual references. (3) The reduction apparently occurred without the attention of the subjects being focused on their sensations of movement. (4) A pattern of recovery of subjective intensity was evident after 4 weeks with no intervening stimulation.

It is possible, indeed even likely, that the reduction of the subjective reaction might have been greater had appropriate visual stimuli been employed. It has been demonstrated that under certain conditions, visual information can obviate the sensation of movement while nystagmus is relatively unaffected (Guedry, Collins & Sheffey, 1961). The present study provides additional confirmation of the separate nature of the oculomotor and the subjective aspects of the vestibular response.

An evaluation of this and other studies (cf. Crampton, 1962b) seems to indicate that no single term, such as "habituation," "response decline," "central suppression," or "adaptation," can completely connote the effects of repeated stimulation upon vestibular function. Rather, there is more than one type of habituation, to use the classical term, and the types apply to both sensation and nystagmus.

One of these, as Wendt (1951) noted, refers to alertness or arousal. If a subject is not in an alert state, nystagmus output shows a marked reduction and, in some cases no nystagmus may be present. Such a state probably occurs with repetition of stimulation as the subject becomes habituated to the environmental conditions including the stimulus and the novelty of the situation. This type of habituation appears to influence both the slow- and fast-phases of nystagmus, although the latter activity appears more significantly reduced (Collins & Guedry, 1962). The subject who is not alert may also have no subjective rotatory experience.

Related to the above is the direction of the subject's attention. The present study indicates that an alert subject need not attend to rotation in order to produce changes in the subjective and in the eye-movement responses. However, if a subject does attend to the rotational stimulus, nystagmus may decline as a function of decreasing subjective experiences (Guedry & Lauver, 1961). In this situation, however, the reduction of the sensation probably results in a reduction in arousal with its consequent attenuation of nystagmus.

A second type of habituation is evident in the present study. Here repeated simple stimulation of alert subjects reduced nystagmus by apparently increasing the activity of the central mechanism controlling the fast-phase of the reaction. The subjective response was also reduced although subjects, engrossed in their assigned tasks, reported that they were unaware not only of their eye-movements, but also of the accelerations.

A third type of vestibular habituation is the conditioned compensatory nystagmus to Coriolis stimulation (Guedry & Graybiel, 1962). Here a complex array of sensory and volitional impulses are repetitively elicited and a reduction of undesirable reactions occurs by means of a centrally produced reaction, opposite in sign, which cancels them out.

In addition to their theoretical implications, the present data have practical significance. The changes in vestibular reactivity as a result of repeated stimulation, whether by experimental, occupational, or avocational means, point up the need for caution in the clinical evaluation of vestibular function and in the selection and specification of subjects used in experimentation. The fact that directionally specific subjective modifications can occur may be worth considering when changes in certain occupational routines are required. Thus, for safety purposes, an individual who has habitually performed precision tasks involving primarily unidirectional vestibular input (e.g., an acrobatic crew pilot — Caporale & Camarda, 1958), may require a period of practice if his routine is shifted so that stimulation from the opposite direction is incurred.

Summary

Ten subjects were each exposed to a habituation series of 200 CW accelerations in total darkness while performing a number of attention-demanding tasks. Decelerations were subthreshold. Preliminary and post-tests indicated that slow-phase nystagmus and duration of the ocular response declined bidirectionally as a function of the habituation trials. That the total reduction in response was not as great as that reported in earlier studies seems due to the task-control of alertness. A marked change in the form of the response occurred. Specifically, stimulus repetition produced an increase in frequency of nystagmus during the stimulus period and for a few seconds thereafter. The remaining "tail" of the response showed an overall depression. These changes were approximately equal for both CW and CCW stimulation.

Measurements of subjective velocity were obtained during several pre- and post-test trials but never during the habituation series. A decline in the intensity of the sensation to CW acceleration was produced by the habituation series but the subjective experience to CCW acceleration was unaffected. Thus, a directionally specific decline in the subjective vestibular response occurred in the absence of attending to the rotatory sensation in the habituation trials and without visual cues.

A second post-test given after one month with no intervening stimulation showed little or no restoration of nystagmus. However, the subjective reaction demonstrated a clear, albeit incomplete, pattern of recovery.

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APPENDIX A

RESPONSE SCORES FOR THE PRE- AND POST-TESTS. EACH VALUE IS A MEAN FOR TEN SUBJECTS EXCEPT PRE TRIAL 1 AND POST-2 TRIALS 1 AND 2 (NINE SUBJECTS).

	Duration (Seconds)			Frequency			Slow-Phase (Degrees)		
Trials	**Pre**	**Post-1**	**Post-2**	**Pre**	**Post-1**	**Post-2**	**Pre**	**Post-1**	**Post-2**
1	53.1	39.9	34.0	66.5	60.3	60.1	546	365	305
2	50.2	40.1	34.3	65.7	55.9	59.6	527	387	316
3	46.1	37.7	38.0	64.2	60.6	60.9	506	376	327
4	49.2	42.5	38.3	65.6	63.0	63.3	475	404	376
5	44.6	37.0	35.9	56.8	56.5	64.3	468	336	264
6	48.0	44.9	35.2	65.7	59.2	56.3	529	393	274
7	45.8	38.1	32.9	61.9	61.0	67.9	485	317	261
8	44.0	37.8	32.7	65.9	58.1	66.6	516	360	274
Mean	47.6	39.8	35.2	64.0	59.3	62.4	506	367	300

APPENDIX B

RESPONSE SCORES FOR THE PRE- AND POST-TESTS. EACH VALUE IS A MEAN FOR EIGHT TRIALS EXCEPT PRE- SCORES FOR RW (7 TRIALS) AND POST-2 SCORES FOR LM (6 TRIALS).

Sessions	Subjects									
	MB	PB	LB	RB	JH	LM	HS	KS	RW	HW
	Mean Duration of Nystagmus (Seconds)									
Pre	51.4	52.4	39.6	47.5	37.3	60.6	36.4	53.5	51.1	52.9
Post-1	41.1	41.6	39.4	33.6	32.8	46.8	27.4	40.3	44.4	49.8
Post-2	40.8	38.0	21.7	31.8	24.8	50.0	29.9	41.1	41.8	47.1
	Total Slow-Phase Displacement (Degrees)									
Pre	510	506	336	321	333	639	231	593	610	1062
Post-1	229	437	345	211	201	577	188	486	259	744
Post-2	276	282	171	238	124	516	166	350	342	660
	Total Frequency of Nystagmus									
Pre	69.8	91.9	58.6	47.5	56.5	75.3	33.0	91.6	55.0	68.6
Post-1	77.0	67.0	62.8	37.3	44.1	69.5	33.1	84.1	51.5	67.8
Post-2	90.8	82.6	49.1	38.5	48.9	93.0	34.5	80.3	53.6	76.0
	Frequency of Nystagmus During First 20 Seconds									
Pre	34.0	31.0	44.3	27.6	30.6	23.8	27.1	32.1	45.5	19.1
Post-1	52.4	40.1	42.9	33.7	34.2	25.6	28.1	32.4	53.1	26.9
Post-2	57.2	36.1	50.1	39.3	38.7	25.7	29.9	34.1	54.0	26.3

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1. Vestibular Function
2. Adaptation
3. Nystagmus
4. Psychology
5. Sensory Psychology

Subjects were exposed to a 10-day habituation series of 200 CW accelerations in total darkness while performing attention-demanding tasks. Decelerations were sub-threshold. Preliminary and post-tests indicated that slow-phase nystagmus and duration of the ocular response declined bidirectionally as a function of the habituation trials, but frequency of nystagmus increased during the stimulus period and for a few seconds thereafter. These changes were approximately equal for both CW and CCW stimulation. Measurements of subjective velocity were obtained during several pre- and post-trials but never during the habituation series. A decline in the intensity of the sensation to CW acceleration, but not to CCW stimulation, was produced by the habituation series. A second post-test given after one month with no intervening stimulation showed little or no restoration of nystagmus. However, the subjective reaction demonstrated a clear, albeit incomplete pattern of recovery.

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