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THE EFFECTS OF VISUAL INFORMATION ON VESTIBULAR NYSTAGMUS HABITUATION

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

THE EFFECTS OF VISUAL INFORMATION ON VESTIBULAR NYSTAGMUS HABITUATION

The receptors of the auditory and vestibular systems lie in a bony labyrinth in the dense, petrous part of the temporal bone. The vestibular portion of each labyrinth, which appears to respond to angular and linear acceleration and position with respect to gravity (and may also be sensitive to certain auditory stimuli) consists of three semicircular canals and two membranous sacs, the utricle and the saccule. The part of the vestibular system which is responsive to angular accelerations consists of three pairs of semicircular canals so oriented that the members of a functional (though not nominal) pair lie in opposite labyrinths in approximately parallel planes and so that the three pairs are at approximately right angles to one another. At one end of each semicircular canal is an ampullar swelling within which a small gelatinous mass, the cupula, is attached along one edge like a swinging door. The utricle, a membranous sac, is attached to both ends of all three canals of a single labyrinth, so that a circuit through a canal and back through the utricle to the starting point is unobstructed except by the cupula. The membranous labyrinth is filled with endolymph, a liquid similar to cerebrospinal fluid. Because of its inertia, the endolymph tends to retain its instantaneous angular velocity, so that an angular acceleration of the head results in head movement relative to the fluid. The cupula is thus displaced by the fluid, exerting a shearing force (Engström, Lindeman, & Ades, 1966) on hairs projected into the cupula from receptor cells at its base.[1] For a more complete description of the anatomy of the vestibular system, see Wendt (1951, pp. 1191-1197); Camis and Creed, (1930, pp. 12-17) or Groen (1956). A discussion of receptor organs is given by Engström et al (1966).

Steinhausen (1931) observed that the mechanics of the semicircular canal are such that it should behave as a heavily damped torsion pendulum. Angular acceleration results in a displacement of the endolymph in the canal, and therefore, a displacement of the cupula. The elasticity of the cupula provides a force tending to return the entire system to its initial state, while the viscosity of the endolymph resists this movement, allowing the cupula to return slowly. Assuming that the neural discharge rate is a monotonically increasing function of cupular deflection, the torsion pendulum might be expected to provide a useful mathematical model of vestibular

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[1] This widely accepted theory of semicircular canal function was independently proposed by Mach, Breuer, and Crum Brown in the period 1873-74, and is called the Mach-Breuer-Brown theory. A discussion of the historical development of the evidence for this theory is presented by McNally and Stuart (1942) and by Boring (1942, pp. 535-544). There is still controversy regarding the exact mechanisms of semicircular canal function. See Camis and Creed (1930); Wendt (1951). Due to the introductory nature of this description, no further discussion of this controversy will be presented.

responses to angular stimulation. The necessary physical constants and the solution of the differential equations for the system have been provided by van Egmond, Groen, and Jongkees (1949). Since the canals are oriented in approximately orthogonal planes, the three canals constitute a fairly efficiently structured device for the resolution of a single rotatory vector (the angular accelerative stimulus) into three orthogonal rotatory vectors. The transformation is isomorphic, and the mathematics involved is well known (Summers, Morgan, & Reimann, 1943).

Along with kinesthetic and proprioceptive receptors throughout the body, the vestibular system is responsible for reflex movements of the limbs, body, head, and eyes, and for the perception of motion and position. Neural impulses from the vestibular receptors are distributed primarily via four vestibular nuclei. Two of these, the medial and superior vestibular nuclei, are connected to the three ipsilateral and three contralateral oculomotor nuclei via the medial longitudinal fasciculus, and perhaps via the reticular formation. These pathways appear to be the mechanism for a reflex compensatory eye movement called vestibular nystagmus (Gernandt, 1959). When the semicircular canals are stimulated (normally by an angular movement of the head), a reflex deviation of the eyes in the opposite direction (the "slow-phase" movement) has the effect of maintaining the eyes in a more or less fixed position relative to the visual field. The system functions much like an inertial platform, stabilizing the retinal image. When the eyes are sufficiently deviated from a central position, a second reflex movement (the "fast-phase" movement) rapidly returns them to center, and a new cycle begins (Wendt, 1936a). Another reflex eye movement, optokinetic nystagmus, is of similar form, but is caused by visual stimuli. In the absence of some such compensatory deviation of the eye, virtual blindness would prevail during some head movements because of the retinal "smear" thus induced (Melvill Jones, 1965). It is for this reason that vestibular nystagmus is often thought of as an adaptive mechanism serving to assist vision. Although there is not complete agreement, the best evidence suggests that slow-phase eye movements are related directly to semicircular canal activity (Dodge, 1921) while the fast-phase movements seem to be central in origin (Gernandt, 1959; Groen, 1960).

With repeated stimulation of the vestibular system, nystagmic activity declines (see Crampton, 1964; Guedry, 1965a; Wendt, 1964). This response change seems to fall into two basic categories: habituation due to loss of arousal (more specifically, loss of the alerting property of the stimulus), and changes due to conditioning of opposing response tendencies (Guedry, 1965a). Nystagmus habituation due to loss of arousal occurs quite readily when the subject's task is passive, but the nystagmus is readily reinstated by any alerting change (Wendt, 1951). This type of habituation appears to involve the substitution of autogenous wandering eye movements for nystagmic beats, and often results in highly erratic patterns of nystagmus. Many early studies report nystagmus habituation which probably resulted from an arousal loss. If it is desired to investigate factors resulting in nystagmus habituation due to conditioning of an opposing or inhibiting response, it is necessary to minimize the effects of loss of arousal. The subject must be made to perform a task which is alerting, but not necessarily a task related to rotation (Collins, Crampton, & Posner, 1961; Collins, Guedry, & Posner, 1962; Collins, 1962). Of several simple tasks evaluated by Collins (1962) and by Collins and Guedry (1962) for the purpose of maintaining arousal, mental arithmetic was found to be most effective.

The possibility of vestibular habituation due to the conditioning of opposing response tendencies was noted by Dodge (1923) and elaborated upon by Wendt (1936b). It has been suggested (Collins, 1966) that this type of habituation accounts for reductions in vestibular response observed in such groups as aircraft pilots (Aschan, 1954) and figure skaters (McCabe, 1960). Basically, the implication is that this type of habituation of nystagmus results from increasing dominance of ocular control by visual mechanisms. Habituation of this sort is an active, learned response serving to assist the functional adaptation of the organism to its environment. Habituation induced by stimulation of cats in one direction has been found by many investigators to transfer only partially, if at all, to the other direction (Capps & Collins, 1965; Collins, 1964a; Crampton, 1962a; Henriksson, Kohut, & Fernández, 1961).

If one takes a functional view of the organism and of vestibular nystagmus as an adaptive mechanism serving to facilitate vision, it is reasonable to expect that habituation of nystagmus might vary as a function of the visual characteristics of the environment. For example, in an experimental situation in which nystagmus aids vision, one would generally expect little or no habituation because the normal nystagmic response is quite adequate and the habituation would itself be maladaptive. On the other hand, in an experimental situation in which the nystagmus is detrimental to vision, one might expect nystagmus, a relatively maladaptive response, to decline.

A number of studies have provided support for these expectations. Mowrer (1934) found essentially no habituation when pigeons were allowed to see a fixed environment during rotation. Pigeons exposed to a visual environment which rotated with them evidenced a decline in head nystagmus, however. In the latter situation, of course, head or eye movements interfere with vision (Guedry, 1968a) and are thus maladaptive. In a later study (Mowrer, 1937), however, humans exposed to a fixed visual environment during rotation on every other trial (vestibular nystagmus aids vision) showed only slight habituation in duration of post-rotatory nystagmus. There are some difficulties associated with these studies involving vision of a fixed visual field during acceleration and protracted rotation, and/or deceleration and a protracted period at rest. During the acceleration from rest and for a short time thereafter, the vestibular stimulus and the visual stimulus are completely synergic; during rotation, after the vestibular system recovers from the effect of the acceleration, the two systems provide conflicting inputs, since the visual information still implies motion. Upon deceleration with vision allowed, the two inputs are asynergic, implying motion in opposite directions. When the subject has stopped, the vestibular system is still in a stimulated state so that the two inputs still conflict until the vestibular system again recovers, at which time both systems indicate that the subject is at rest. It is difficult to study the interaction of two stimuli under such complicated circumstances. Two relatively easy means exist for inducing by a rotatory stimulus vestibular nystagmus which is always detrimental to vision: Coriolis[2] stimulations with the interior of the rotating platform visible to the subject; and sinusoidal oscillation while viewing a visual field rotating with the subject.

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[2] A Coriolis stimulus to the vestibular system results when a subject makes a head movement while in a rotating environment. During such a head movement, an imbalance develops (due to gyroscopic precession) in the forces operating on those semicircular canal(s) which are not aligned with the axes of rotation of the environment or of the head movements. As a result, the stimulus to the vestibular system elicits responses ordinarily associated with a canal or canals not in the plane of head-tilt.

Guedry and Graybiel (1962) reported a study of the effects of Coriolis accelerations on nystagmic habituation of seven men who lived in a room rotating at 5.4 r.p.m. for 64 hours. The room was illuminated and the subjects allowed to move around freely. In the process of moving about the room, of course, the subjects experienced repeated Coriolis stimulations. Nystagmus resulting from such head movements is not adequate in the sense that it compensates for actual motion relative to the visual field--it is, in fact, in the wrong direction. And, as might be expected, Guedry and Graybiel observed the development of a compensatory reaction which tended to counteract the nystagmus. When the subject was returned to a stationary environment, head movements elicited nystagmus opposite in direction to that observed during similar head movements while rotating. This nystagmus was not present prior to the habituation procedure. Several other studies by these investigators have produced similar results (see Guedry, 1965a). It is impossible to attribute this compensatory reaction entirely to the influence of vision, however, since the Coriolis stimulus involves a conflict of the semicircular canal system not only with vision, but also with the otolith organs, kinesthetic receptors of the head and neck, and with the subject's knowledge of the nature of the movement attempted.

In a later Coriolis study (Guedry, 1964), subjects performed restricted head movements in only one quadrant of the frontal plane. Two groups of ten subjects each performed 100 head-tilt cycles consisting of a head-tilt, 20 seconds rest, a return to an upright position, and 20 seconds rest, while rotating at 7.5 r. p. m. Including rest periods, this procedure took about four hours. One group performed the head movements in the dark, while the second group was required simultaneously to solve visually presented mechanical comprehension problems. This served to maintain alertness and to force the subject to attend to his visual environment, presumably requiring the subject to exercise voluntary control of eye movements to inhibit nystagmus. Similar previous studies (Guedry, Graybiel, & Collins, 1962; Guedry, Collins, & Graybiel, 1964) in which subjects were merely passively exposed to their visual environment had shown wide variation in degree of habituation. In this study, however, all subjects in the vision group showed a clear decline in nystagmus in the practiced quadrant, with little transfer to the unpracticed quadrant. Little decline was evidenced in either direction by the no-vision group. In this experiment, the two groups were comparable in the degree of conflict among vestibular and kinesthetic cues, differing only in the presence or absence of visual cues, attention to the visual environment, and general level of alertness. The most appealing, and probably the most parsimonious, explanation is that a compensatory reaction or conditioned suppression of nystagmus developed to overcome the detrimental effect of nystagmus on vision. A conceivable alternative is that compensatory reactions due to vestibular and kinesthetic conflicts develop only in alert subjects, irrespective of vision.

The plausibility of this alternative explanation is reduced by the discovery of a similar compensatory reaction with simple passive rotation which involves minimal vestibular-kinesthetic conflict. Guedry (1965b) exposed subjects to visually-presented problems only upon deceleration from rotation (subjects were in the dark during acceleration and rotation at constant velocity) in a habituation procedure which comprised 80 trials in four hours. He obtained direction-specific nystagmus habituation, i. e., specific to the direction which required vision.

There have been negative findings, also. Brown and Crampton (1966) used only eight cycles of vestibular stimulation, each consisting of ten seconds of acceleration at 24 deg/sec^2, five minutes of rotation at constant velocity, a deceleration equivalent to the acceleration, and five minutes at rest. Four groups of 20 subjects each were exposed to the six-cycle habituation series (the first and last cycles were pre- and post-habituation measures of subjective and nystagmic response) under different visual conditions. The different groups experienced the habituation series under conditions of darkness, a fixation light rotating with the subject, an illuminated capsule interior rotating with the subject, and vision of the fixed external room. No differences were observed in nystagmus habituation. It should be noted, however, that this study involved very large vestibular stimuli and a short habituation series. It also involved the varying vestibular-visual interaction previously described in connection with Mowrer's studies, although this situation occurred only in the group exposed to the external room. Perhaps most important, it involved only passive exposure to the visual fields described. It is suggested that there was no functional need for nystagmus to habituate, since precise vision was not required by the experimental procedure. The absence of active participation in the visual environment may also explain negative findings with repeated rotation of animals with vision allowed (e. g., Crampton, 1962b), although a number of other explanations are plausible.

Although some of these results can be explained by simple conditioned suppression, these studies considered as a whole are suggestive of the existence of a mechanism whereby a compensatory reaction develops to inhibit nystagmus when that nystagmus has repeatedly proven to interfere with vision. These studies also suggest that active visual participation may be the key element in eliciting such a habituative response. Several characteristics of an optimum study of the differential effect of vision on nystagmus habituation readily suggest themselves. The procedure should involve passive rotation about a single axis, to provide a vestibular stimulus without the complicating characteristics of Coriolis accelerations due to voluntary head-tilts. The procedure might well incorporate sinusoidal acceleration since such stimulation results in vestibular activity in one direction or the other almost all the time, eliminating lengthy rest periods and shortening the procedure. The visual task should be a demanding one, possibly at very low levels of illumination, so that voluntary inhibition of nystagmus is required. Even when a visual task is required of the subject, he might be able to perform without suppression of nystagmus if the task is sufficiently easy.

Guedry and Benson (1969) attempted a procedure with many of the desired characteristics, although it was not designed as a habituation study. Six men were subjected to sinusoidal oscillation resulting in vertical nystagmus (specifically, horizontal oscillation while lying on one side) while performing a continuous compensatory tracking task. This tracking task required the subject to monitor a meter which rotated with him, and to null out deflections of the meter needle by appropriate movements of a control (Gilson, Benson, & Guedry, 1970). In spite of the fact that the vestibular stimuli were equal in the two directions, a directional difference in habituation of slow-phase velocity was found, with a greater reduction in slow-phase velocity occurring in fast-phase-up nystagmus. Nystagmus with fast-phase-up was also found to be readily inhibited by visual fixation, while nystagmus with fast-phase-down was not, repeating a finding of Hixson and Niven (1969). Thus, the conditions hypothesized to produce habituation due to vision existed only in the fast-phase-up direction, and the obtained result might well be attributable to vision. However, factors other than vision might also explain this finding. Several differences are known to exist between fast-phase-up and fast-phase-down nystagmus. In addition to differences in susceptibility to inhibition by visual fixation, a difference in absolute magnitude of slow-phase velocity has been observed, with a greater mean slow-phase velocity associated with fast-phase-down nystagmus (Guedry & Benson, 1969; Hixson & Niven, 1969). Because of these differences, one cannot dismiss the possibility that there is also a directional difference in habituability of vertical nystagmus which is independent of vision.

The present experiment was performed in an attempt to determine whether a direction-specific habituation of nystagmus might be elicited by exposure to a difficult visual task during horizontal oscillatory stimulation of an upright subject. Because it incorporated stimulation of the horizontal canals, the response of which is thought to be essentially symmetrical at least as regards susceptibility to inhibition by visual fixation, the present experiment avoided possible artifacts due to inherent directional differences. Basically, it was hypothesized that performance of a visual task during rotation in one direction would result in a significantly greater reduction in the magnitude of the nystagmic response than would result from rotation in the dark in the opposite direction. Secondarily, it was hypothesized that when the tracking task was repeated at reduced illumination after habituation, less nystagmus and better performance would be observed in the direction previously associated with the visual task than would be observed in the opposite direction.

METHOD

Subjects

Twenty commissioned Naval pilot candidates served as subjects for this experiment. These subjects are an unusually homogeneous, intelligent, healthy and highly motivated group. They are all college graduates who have volunteered for duty as Naval Aviators. They have passed a rigorous physical examination and have made passing scores on the Naval Aviation Selection Battery, which includes the Aviation Qualification Test (a test of general intelligence), the Mechanical Comprehension Test, and the Biographical Inventory (a test which contains some personality items as well as some personal history). Their ages range from 20-29 years, with a mode of 22.

Equipment

A somewhat modified Stille-Werner rotating chair (Figure 1) driven by a Servomex waveform generator provided continuous, sinusoidal vestibular stimulation, with peak velocities of 90 deg/sec in each direction, and a 25.5-second period. Control of the chair was accomplished by a feedback circuit serving to minimize differences between the (sinusoidal) input waveform and the output of a velocity transducer (tachometer) associated with the drive shaft of the motor driving the chair. In order to determine any irregularities of motion

Figure 1. Modified Stille-Werner rotating chair, showing position of headrest, hand controller, and visual display (behind projection from panel on right).

which might not be reflected in the tachometer output (also used to record chair velocity on experimental records), an angular accelerometer was mounted on the chair at its axis of rotation and a recording of both velocity and acceleration (Figure 2) was made with a 184 lb. pilot subject aboard. The acceleration of the chair was found to be in general uniform and symmetrical. A discontinuity observed at approximately zero velocity probably resulted from the high wind resistance of the chair assembly and appeared to be equal in the two directions of rotation. The discontinuity did not result in a perceptible jerk, as judged by the experimenter. A 0.8-second lag between the velocity indicated by the tachometer and the actual motion of the chair (as reflected by the accelerometer) probably resulted from drive-shaft play and must be taken into account in interpreting the temporal relation between stimulus and response.

The subject's head was located at the axis of rotation and tilted forward to place the horizontal canals approximately in the plane of rotation. A headrest was used to maintain this position and to minimize motion of the head relative to the chair.

An aircraft cross-pointer indicator was placed in a position approximately 80 cm. away from, laterally centered with, and at an angle 36 degrees below the subject's eyes, and remained fixed relative to the subject at all times. At this distance, the meter face (4.0 cm. in diameter) subtended

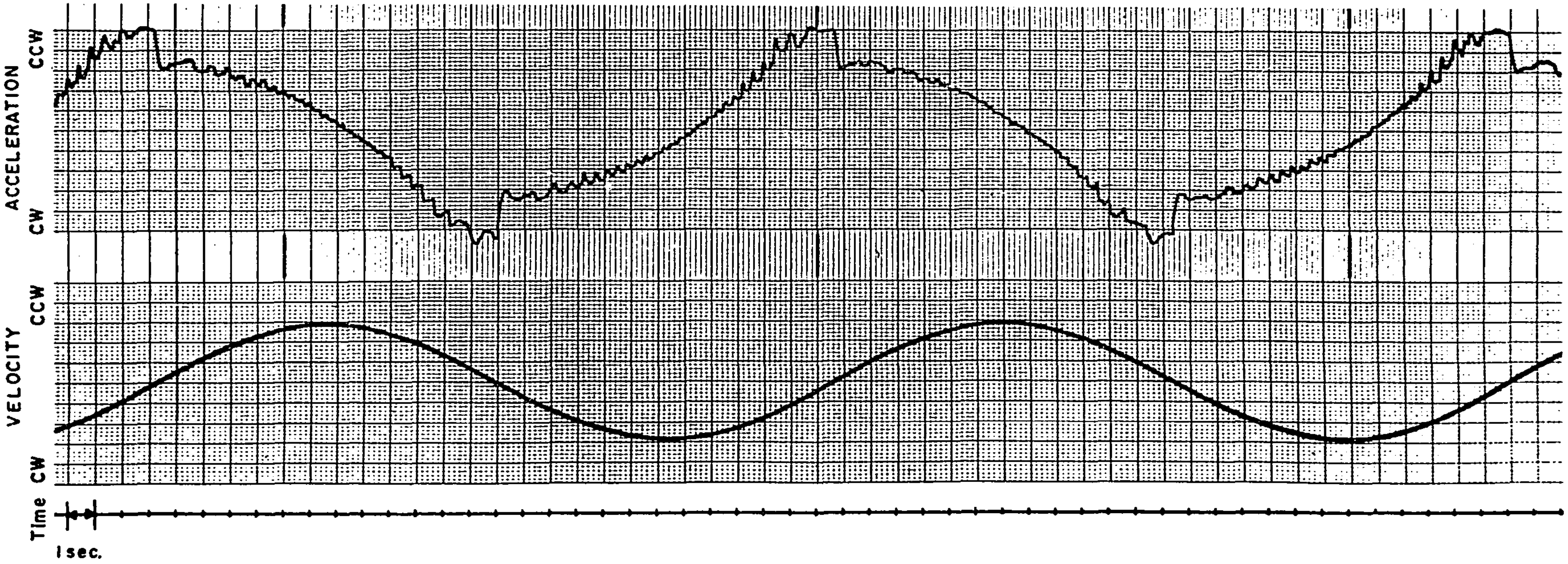

Figure 2. Acceleration profile of sinusoidal stimulus, displayed with tachometer (velocity) record.

a visual angle of 2.9 degrees. The meter could be illuminated at a luminance of 0.0270 foot-lamberts, 0.0126 foot-lamberts, or could be made dark. The horizontal needle of the instrument was maintained in the central position, while the vertical needle was deflected by an electrical forcing function consisting of the sum of four sine waves with periods of 4, 13, 17, and 31 seconds and amplitudes proportional to their periods. These component waveforms were selected to provide an unpredictable stimulus and to minimize coincidence with the 25.5-second vestibular stimulation cycle. During all periods of meter illumination, the subject was required to null deflections of the pointer by appropriate fore-aft movements of a hand controller similar to an aircraft "joystick." The joystick was placed at a comfortable height and centered between the subject's legs. The absolute value of the resulting pointer deflection (error) was integrated over one-second periods, converted to digital form by a digital voltmeter, and recorded by a paper-tape printer (Gilson et al, 1970).

The levels of illumination, frequencies of pointer oscillation, and gain selected were found in a pilot study to result in a fairly easy visual task while the subject was stationary. When horizontal nystagmus was induced by oscillation, however, the task became quite difficult, and was, for very short periods of peak nystagmus velocity, impossible for some subjects. Selection of a low level of illumination and a meter needle perpendicular to the plane of the subject's eye movements resulted in maximum interference with visual perception (eye movements essentially parallel to a moving needle would, of course, interfere very little with the subject's ability to determine the position of the needle). The primary level of illumination (0.0270 foot-lamberts) was selected on a subjective basis as the lowest luminance which still allowed performance of the task, although with considerable effort, during oscillation.

Horizontal nystagmus was recorded by the corneo-retinal potential method (Marg, 1951; Young, 1963) using Beckman silver-silver chloride electrodes. An 8-channel Sanborn recorder made AC recordings of nystagmus with a 2.5-second time constant, along with recordings of chair velocity, the compensatory tracking stimulus, and the integrated tracking error. Two small calibration lights were located immediately above the meter and at a horizontal distance equivalent to 20 degrees of visual angle. At appropriate intervals, these lights were illuminated alternately and the subject was instructed to follow the movement with his eyes, providing a reference eye movement of known magnitude on the nystagmus record.

Changes in level of illumination are known to produce changes in the corneo-retinal potential. Specifically, an overdamped oscillation with approximately a 25-minute period is induced (Homer & Kolder, 1966). Artifactual changes in recorded nystagmus which might result from this oscillation may be prevented by preceding an experiment with a prolonged period of dark adaptation. In the present experiment, however, the resulting loss of arousal might well have presented a greater problem than the corneo-retinal potential changes since: (1) directional differences, rather than absolute magnitudes of nystagmus, were of the greatest significance, and (2) no point in the critical (pre- and post-habituation) nystagmus measures was more than 90 seconds removed from a calibration. For these reasons, no effort was made to control or to correct for corneo-retinal potential changes.

Although every effort was made to make the room as light-tight as possible, additional protection against the effects of extraneous illumination was provided by a cloth surrounding the subject on all sides. The cover served the additional function of reducing noise and wind cues. Post-procedure questioning indicated that no subject ever detected any extraneous light.

Procedure

Electrodes were placed on the subject's forehead and adjacent to the outer canthus of each eye: a few minutes were allowed to elapse before recording was attempted, in order to insure good electrode contact. During this period, the subject was told about the general nature of vestibular research, nystagmus, and electro-oculography. He was then shown the controlling and recording equipment and allowed to ask questions.

The subject was taken to the room containing the rotating chair and placed in the chair. The headrest was adjusted until, in the experimenter's judgment, a line between the external auditory meatus and the outer canthus was horizontal, assuring approximate horizontality of the lateral semicircular canals. Electrode connections were made and it was ascertained that the subject was reasonably comfortable. The subject was told that the experiment would consist of four sessions of oscillation; sessions one and four would be in the dark, while sessions two and three would require intermittent performance of the compensatory tracking task, which was explained at this time. The need for constant alertness and the effect of loss of alertness on nystagmus were explained. The subject was requested to remain as alert as possible throughout the experiment. He was told that he would be required to perform mental multiplication of two digit numbers throughout sessions one and four, to assist him in maintaining alertness and to provide a measure of his alertness and general performance capability. He was told that the tracking task would serve the same function during sessions two and three. The function of the calibration lights was explained, and the experimenter darkened the room and left. The subject was allowed two minutes to practice the tracking task at the normal level of illumination (0.0270 foot-lamberts). His performance under these static conditions provided a baseline measure of tracking performance.

The procedure consisted principally of four experimental periods, each consisting of an eye-movement calibration, a period of continuous oscillation, and another eye-movement calibration. A two minute rest period was allowed between experimental periods. The entire procedure occurred in complete darkness except during periods of calibration and use of the meter lights. Figure 3 illustrates the temporal characteristics of the experimental procedure.

Sessions one and four provided pre- and post-habituation measures of nystagmus in complete darkness. Each of these experimental periods included seven 25.5-second cycles of oscillation. Nystagmic responses were scored during five cycles commencing after 31.9 seconds (1 1/4 cycles) of oscillation. This initial unscored period was included to allow the nystagmus to assume its normal "steady state" phase relationship to the stimulus.[3] An attempt was made during periods one and four to maintain the subject in a state of alertness by asking him to

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[3] During sinusoidal oscillation, the response of the vestibular system is approximately sinusoidal in form. The damping in the semicircular canals has the effect of allowing the vestibular system to integrate the force applied as a result of angular acceleration (Groen, 1960), in much the same way that a shock absorber integrates linear forces. Thus, the vestibular response is approximately proportional to the velocity of the chair, rather than to the acceleration, although the response is slightly phase-advanced relative to the chair velocity. Since the eye-movement calibration was performed after peak counterclockwise velocity was reached, and the oscillation was then begun, the vestibular system was partially adapted to counterclockwise stimulation, and a short period of oscillation was required before the normal phase relationship was established.

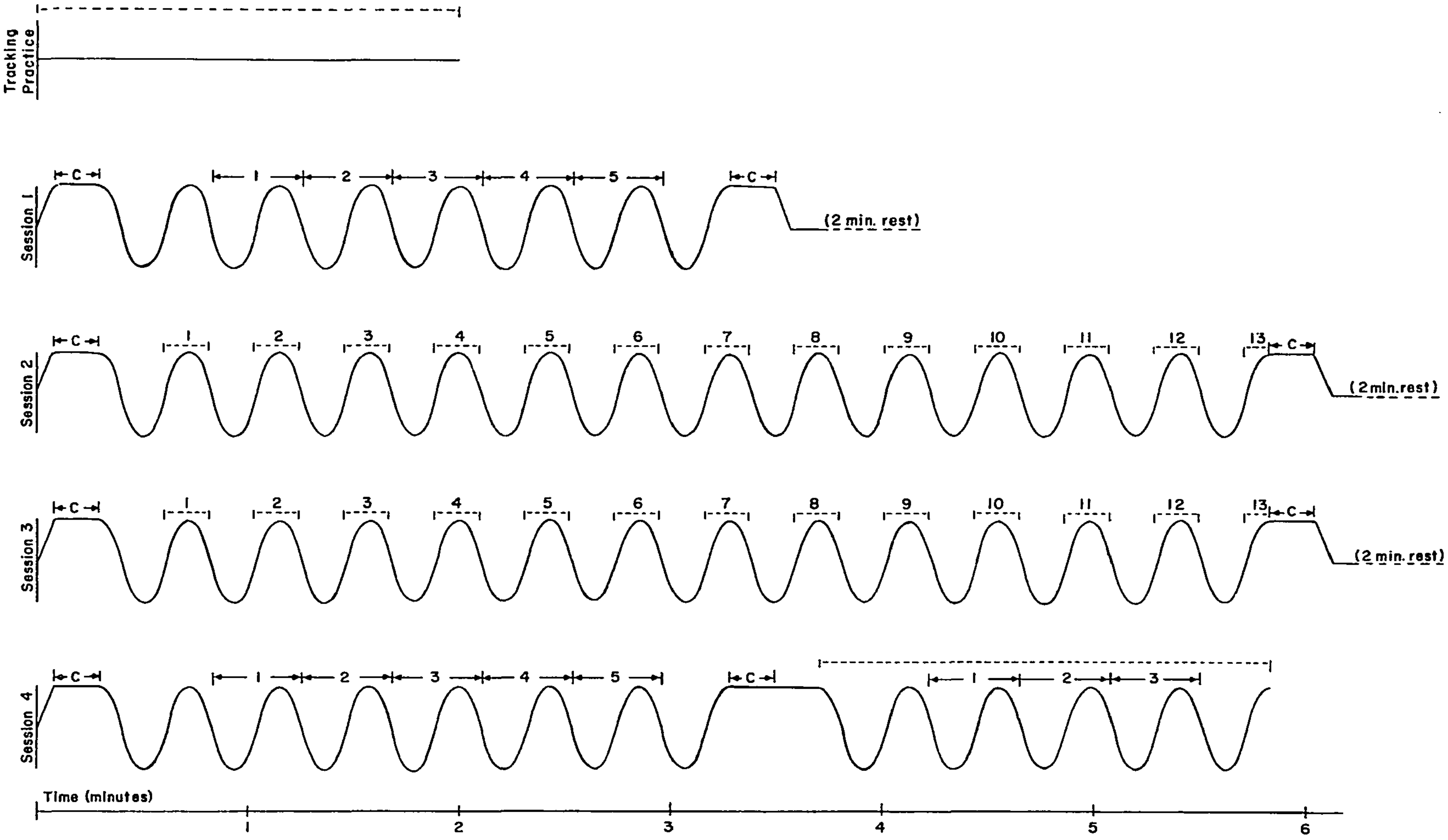

Figure 3. Temporal profile of experimental procedure for Group B. Eye-movement calibrations are designated "C". Solid line shows chair velocity as a function of time; up is CCW; peaks are ±90°/sec. Scored cycles of nystagmus are designated and numbered in Sessions 1 and 4. Dotted lines indicate compensatory tracking task performance. Group A procedure was identical except that periods of tracking in Sessions 2 and 3 occurred one-half cycle later.

perform mental multiplication of two-digit integers throughout these periods. The two-digit numbers ranged from 12 to 23; problems were not chosen randomly, but were continuously selected by the experimenter according to the performance of the subject. When an incorrect response was made, an easier problem was selected; when a correct answer was given in less than about 15 seconds, a more difficult problem was presented. On those occasions, early in the experiment, when a subject seemed to blurt out an answer quickly and without a real attempt at calculation, the same problem was repeated once and the subject encouraged to take his time and obtain the correct answer.

Sessions two and three constituted the habituation series. Each of these sessions included thirteen 25.5-second cycles of oscillation. During one-half of each cycle, the meter was illuminated at a luminance of 0.0270 foot-lamberts and the subject was required to perform the tracking task. The half-cycle chosen for visual stimulation was slightly phase-advanced relative to the velocity of the chair, so that it corresponded to that entire portion of a cycle in which the vestibular system was stimulated in one direction, as indicated by points of nystagmus reversal in pilot subjects. Tracking performance during habituation was recorded, as was nystagmus.

The direction of vestibular stimulation during the performance of the visual task was counterbalanced across subjects, yielding two experimental groups. Group A performed the visual task during clockwise vestibular stimulation (i.e., during nystagmus with fast phase to the right), while Group B performed the visual task during counterclockwise vestibular stimulation. It should be noted that the procedures administered to these groups were identical in every other respect, including the vestibular stimulation schedule, and that they are both experimental groups. Each subject served as his own control by virtue of his exposure to vestibular stimulation with visual suppression of nystagmus in one direction and without visual suppression of nystagmus in the other direction. Subject assignment to groups was in randomized blocks of two subjects, in order to avoid artifacts due to any gradual unintentional change in procedure.

Following the final eye-movement calibration (Session 4), the subject performed the tracking task at reduced illumination (0.0126 foot-lamberts) during five 25.5-second cycles of oscillation. Performance and nystagmus were scored for three cycles commencing after 31.9 seconds (1 1/4 cycles) of oscillation. The reduced luminance level was selected intuitively as providing a task which was quite difficult, so that in the absence of nystagmus habituation, eye movements would interfere with performance to a considerable degree. In this way it was hoped to detect any difference in performance of the visual task which might result from directionally specific nystagmus habituation. Since the tracking was continuous during this final period, a measure of performance was obtained during vestibular stimulation in each direction.

RESULTS

The use of an AC amplifier in the recording of nystagmus resulted in a continuous correction for long-term lateral eye displacement. Thus, the record may be thought of as representing the instantaneous horizontal deviation of the eye from its current "average" position. Since the time constant employed (2.5 sec.) was large relative to the duration of a single nystagmic beat, the recording provides reliable information concerning horizontal eye position throughout a beat (Tursky & O'Connell, 1966). Slow-phase nystagmic velocity was obtained from this position record by determining the slope of the eye position during the slow portion of a beat with a tangent potentiometer (see picture, Guedry, 1968b, p. 182). The output of this potentiometer was modified by a linear operational amplifier previously adjusted in gain to correct for the subject's corneoretinal potential, as determined by the 20° calibration procedure. The resulting output, slow-phase velocity in degrees per second, was translated to digital form by a digital voltmeter and printed by a paper tape printer. An earlier version of this scoring device was described by Guedry and Turnipseed (1968).

Slow-phase nystagmic velocity was obtained in this manner at one-second intervals throughout the five scored cycles of oscillation in Session One and the corresponding period in

Session Four. Corresponding points of the five cycles in each session were then summed to obtain a single mean response curve for each group for each of Session One and Four (Figure 4). Those scores above the abscissa were then summed, as were those below the abscissa, to obtain approximations to the integrals of the positive and negative portions of the curve, respectively. These scores represent the total amount of slow-phase nystagmic movement with fast-phase right[4] and fast-phase left, respectively, over five cycles of stimulation. The means and standard deviations of these total slow-phase movement scores are shown in Table 1 by group, session, and direction of nystagmus.

In order to correct for initial individual differences in total nystagmic output, and for differences in the two directions within a subject, it was intended that an analysis of covariance (Winer, 1962) be applied, using initial nystagmus scores as the covariate, with final scores as the criterion (Cochran, 1957). However, the comparison of groups by the analysis of covariance technique is appropriate only when (among other things) there are no differences between the corresponding populations on the covariate--in this case the initial score. An analysis of variance performed on the initial

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[4] It is conventional to indicate the direction of nystagmus by the direction of the fast-phase movement relative to the subject. Thus, left-beating nystagmus, or nystagmus to the left, involves slow-phase movement to the right and fast-phase movement to the left, and might result from angular acceleration to the left.

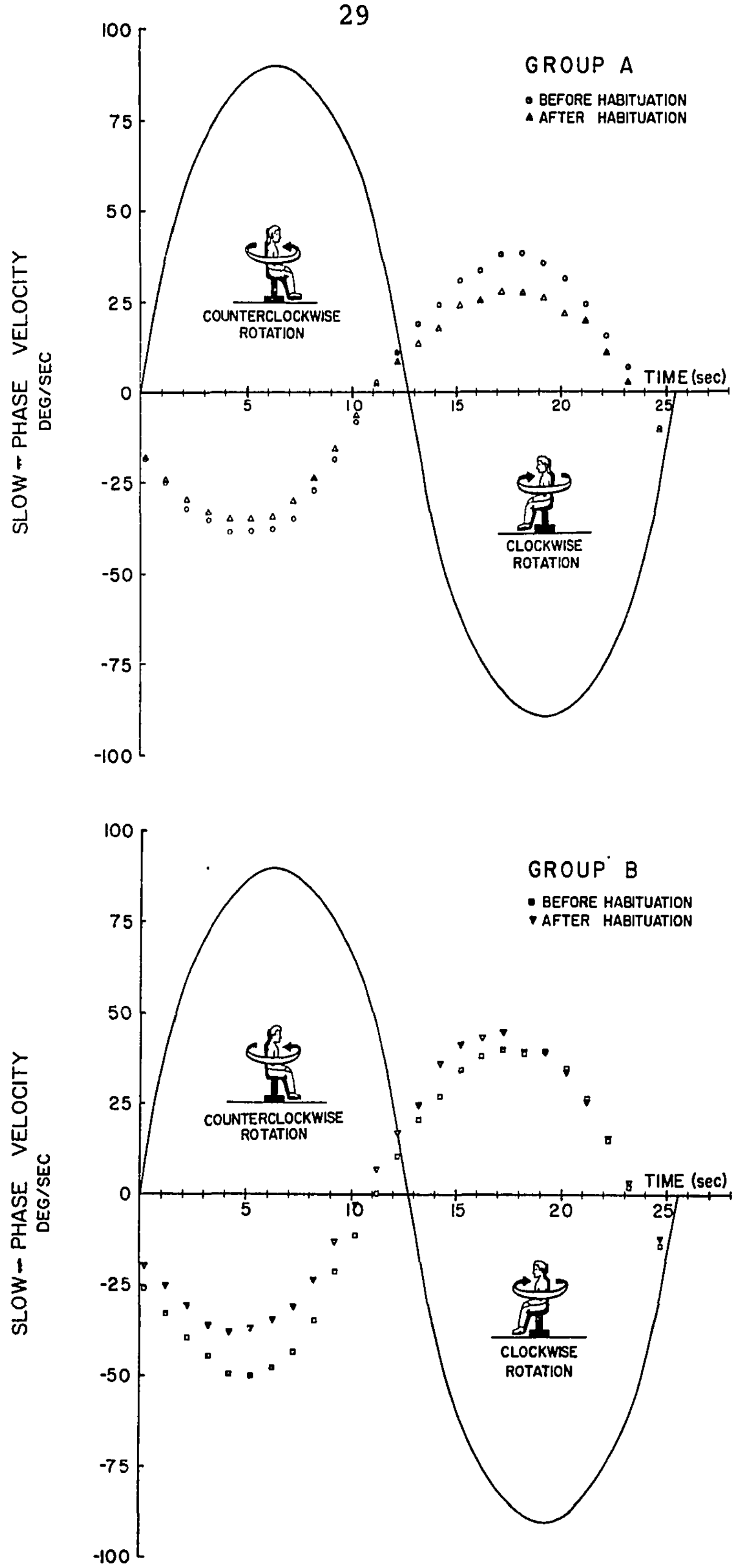

Figure 4. Slow-phase eye-movement velocity, by group, before and after habituation. Each point is an average of slow-phase velocity at corresponding points in five consecutive cycles of rotation. Solid line represents chair velocity.

TABLE 1

Means and Standard Deviations[a] (in Parentheses) of Total Slow-Phase Eye Movement in Degrees, by Group, Direction of Fast Phase, and Session.

Session	Group A		Group B	
	Nystagmus Left	Nystagmus Right	Nystagmus Left	Nystagmus Right
1	1567	1487	2017	1616
	(439)	(264)	(406)	(371)
4	1380	1073	1451	1781
	(400)	(276)	(278)	(386)

[a] $S = \sqrt{\frac{\Sigma x^2}{n}}$

scores (Table 2) shows that such an assumption cannot be made in this case. A greater amount of slow-phase movement was found in left-beating nystagmus than in right-beating nystagmus, confirming a finding of Gilson et al (1970). There was a tendency for Group B to exhibit more nystagmus than Group A, and for Group B to exhibit a preponderance of nystagmus to the left which Group A failed to exhibit. These tendencies, while not statistically significant (i. e., $p > .05$), prevent the assumption that the groups were homogeneous with respect to initial scores.[5]

Since the initial Group x Direction interaction was in the opposite direction to that predicted to occur _after_ treatment, neither difference scores nor a repeated-measures analysis of variance could be employed; the "initial values effect" (regression toward the mean) would tend to lend artifactual support to the hypothesis. An analysis of variance was performed on the final scores alone (Table 3). Since regression toward the mean of a single population cannot result in a _reversal_ of the initial difference, the analysis of variance of final scores is a conservative test for the hypothesized directional change. The interaction was, in fact,

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[5] Since the experimenter's hypothesis is in this case associated with the "alternative" hypothesis, rather than with the "null" hypothesis, it is not α but β , which is the appropriate measure of significance. β cannot be calculated without unwarranted assumptions regarding the underlying sampling distribution. It should be clear, however, that the "null" hypothesis cannot be confidently _accepted_.

TABLE 2

Analysis of Variance of Initial Total Slow-Phase Displacement Scores, by Group and Direction of Nystagmus.

Source	df	MS	F	η^2
Groups	1	615020.9	3.8859*	.1776
Subj. w/i Groups	18	158268.2		
Direction	1	379435.9	7.1387**	.2840
Group x Direction	1	194379.1	3.6570*	.1689
Residual	18	53151.9		

*$p < .10$

**$p < .05$

TABLE 3

Analysis of Variance of Final Total Slow-Phase Displacement Scores, by Group and Direction of Nystagmus.

Source	df	MS	F	η^2
Group	1	1173435.3	8.3931***	.3180
Subj. w/i Groups	18	139809.6		
Direction	1	4657.8	0.0835	.0046
Group x Direction	1	879665.3	15.7630*	.4669
Residual	18	55805.7		

*$p < .10$

***$p < .01$

significant in the predicted direction.[6] That is, Group A had less slow-phase movement in right-beating nystagmus than in left-beating nystagmus, while Group B showed a difference in the opposite direction. The proportion of variation (η^2) explained by this interaction (.47) is probably an underestimate of the effect of the experimental variable, since only the final scores were analyzed. In addition, Group A had significantly less slow-phase displacement than Group B, regardless of direction. This does not represent a change from the initial condition, since an almost significant difference occurred in the same direction initially.

For Group B (and for some extreme subjects in Group A), the pattern of change in total slow-phase movement was that which would be expected if a conditioned compensatory nystagmus had developed. That is, not only was the slow-phase velocity reduced in the direction suppressed during habituation, but an increase occurred in the slow-phase velocity in the opposite direction, along with a phase shift (Figure 4). These effects can be seen quite clearly in the raw eye-movement records. Records are shown in Figure 5 for one extreme and one typical subject from each group, both before and after habituation. Record I of Figure 5 shows an extreme subject in Group B. Nystagmus to the left (first half of record) declined in slow-phase velocity, while nystagmus to the right

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[6] All statistical tests reported in this paper are non-directional (two-tail) tests.

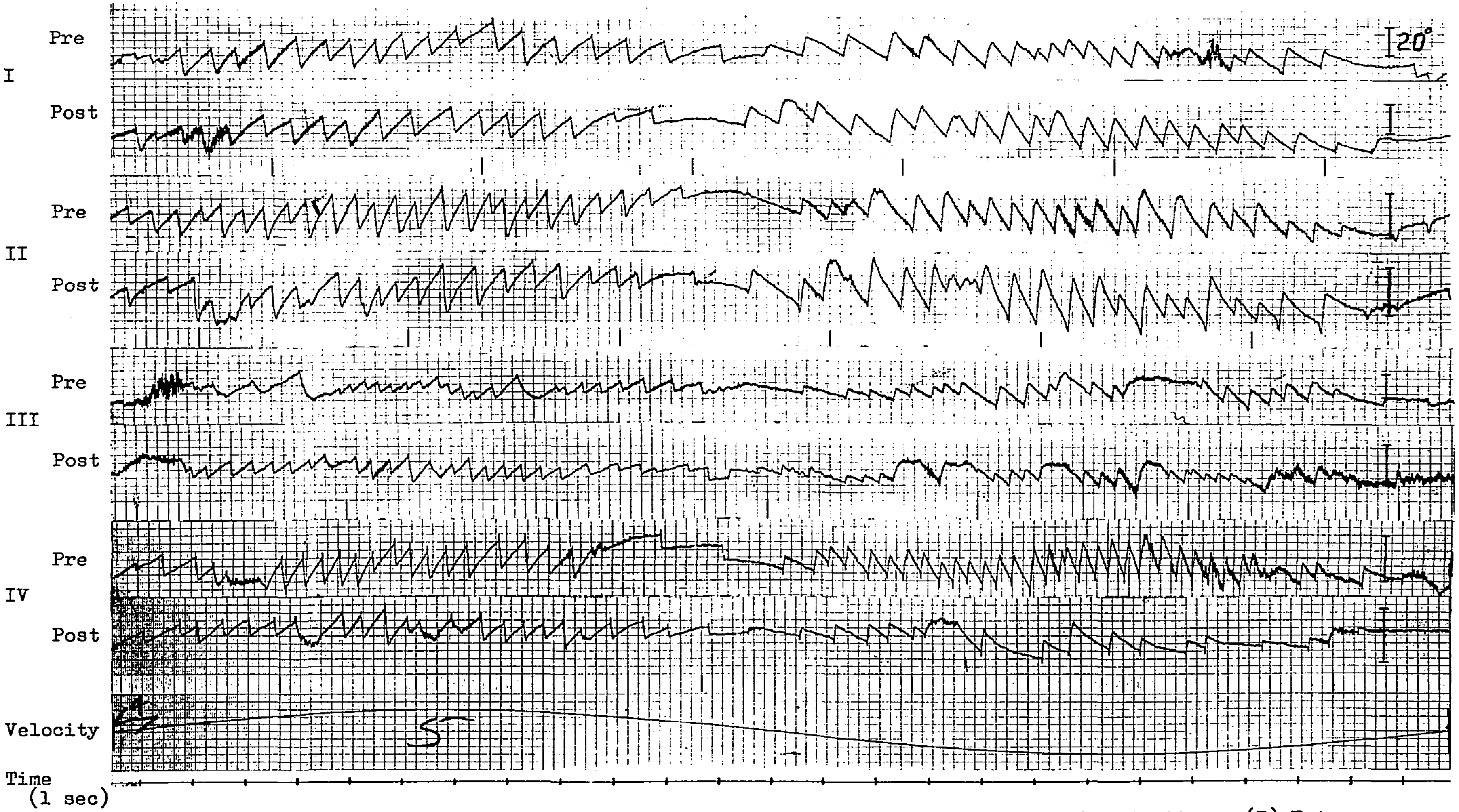


Figure 5. Sample eye-movement recordings for four subjects, before and after habituation. (I) Extreme subject, Group B. (II) Typical subject, Group B. (III) Typical subject, Group A. (IV) Extreme subject, Group A. Stimulus cycles are superimposed to give same time-base. Last pair of records (IV) is from scored cycle 4 of pre- and post-tests; all others are from cycle 3.

increased in slow-phase velocity, began earlier, and ended later after habituation than before. These same effects can be noted in Record II, a typical Group B subject, though to a lesser degree. A typical Group A subject (Record III) showed a small direction-specific change which is not readily discernible by visual inspection. An extreme Group A subject (Record IV), however, showed an increase in slow-phase velocity of left-beating nystagmus, accompanied by a reduction in velocity, later initiation, and earlier termination of the slow-phase component of right-beating nystagmus. This phase shift is not typical of Group A, but did occur in a few subjects. It should be noted that these records were selected as typical or extreme examples of their respective groups on the basis of slow-phase activity only. Record IV, if examined in terms of fast phase, shows a phase shift in the opposite direction to that indicated by the points of reversal of slow-phase velocity. The particular point at which a fast-phase movement occurs is probably more closely related to instantaneous ocular deviation than to the vestibular response *per se*; in any case, a visual inspection of all records indicates that the point of reversal as defined by fast-phase beats is highly inconsistent and that that shown in Record IV is not typical.

In order to determine whether habituation occurred which was independent of treatment or nystagmus direction, a separate analysis of variance was performed in which Group was represented as an independent factor, while Direction of nystagmus and Session (pre-, post-habituation) were represented as repeated measures. The main effect due to Session was significant (F=18.9752; df=1, 18; $p < .01$). The reduction in total nystagmic output accounted for 51 per cent of the otherwise unexplained variation in pre- to post-habituation nystagmic differences and represented a 15 per cent decline from initial nystagmic output. The remainder of the analysis is not reported here since the other factors were contaminated by initial differences between the groups.

Since identical procedures were administered to both groups during Session 1, it is concluded that the trend toward an initial group difference and a Group x Direction interaction resulted from a chance difference due to random subject assignment to groups. The initial presence of a significantly greater slow-phase output in left-beating nystagmus than in right-beating nystagmus is another matter, since this directional difference was found regardless of treatment group. Before it can be concluded that a directional difference in nystagmic response probably exists in the population from which the subjects were drawn, the possible contributions of a procedural asymmetry must be considered. For all subjects, the initial rotation of each session was in the counterclockwise direction. After the peak velocity had been reached in this direction, an eye-movement calibration was obtained (Figure 3). During the calibration procedure, the subject continued to rotate counterclockwise at a constant velocity of 90°/sec. By the time oscillation was begun following the calibration, partial cupular return (and neural adaptation) had occurred. If the 31.9-second interval of oscillation prior to the scored period were inadequate for these adaptive effects to disappear, partial adaptation to counterclockwise stimulation would still have been present during the scored cycles of oscillation. The result would have been a reduction in response to counterclockwise stimulation during the early cycles of oscillation. Such an abnormality did in fact occur during the first half-cycle of scored nystagmus, as evidenced in Figure 6. It cannot account for the observed difference in directional response, however, since the artifactual effect of the asymmetry is both small and in the opposite direction to the overall initial difference observed. It should be noted that a period of oscillation is also required before the nystagmic response assumes its normal phase relationship to the stimulus, regardless of the state of adaptation. Failure to allow an adequate interval for the assumption of this "steady state", however, would have resulted only in an abnormal stimulus-response phase angle, without a directional difference in slow-phase velocity. Since the known procedural asymmetry has been demonstrated not to account for the observed initial directional difference in nystagmic response, it is concluded that a directional difference exists in the population from which the subjects were drawn.

The total number of nystagmic beats was obtained, by subject, for each Direction of nystagmus and Session (1 and 4).

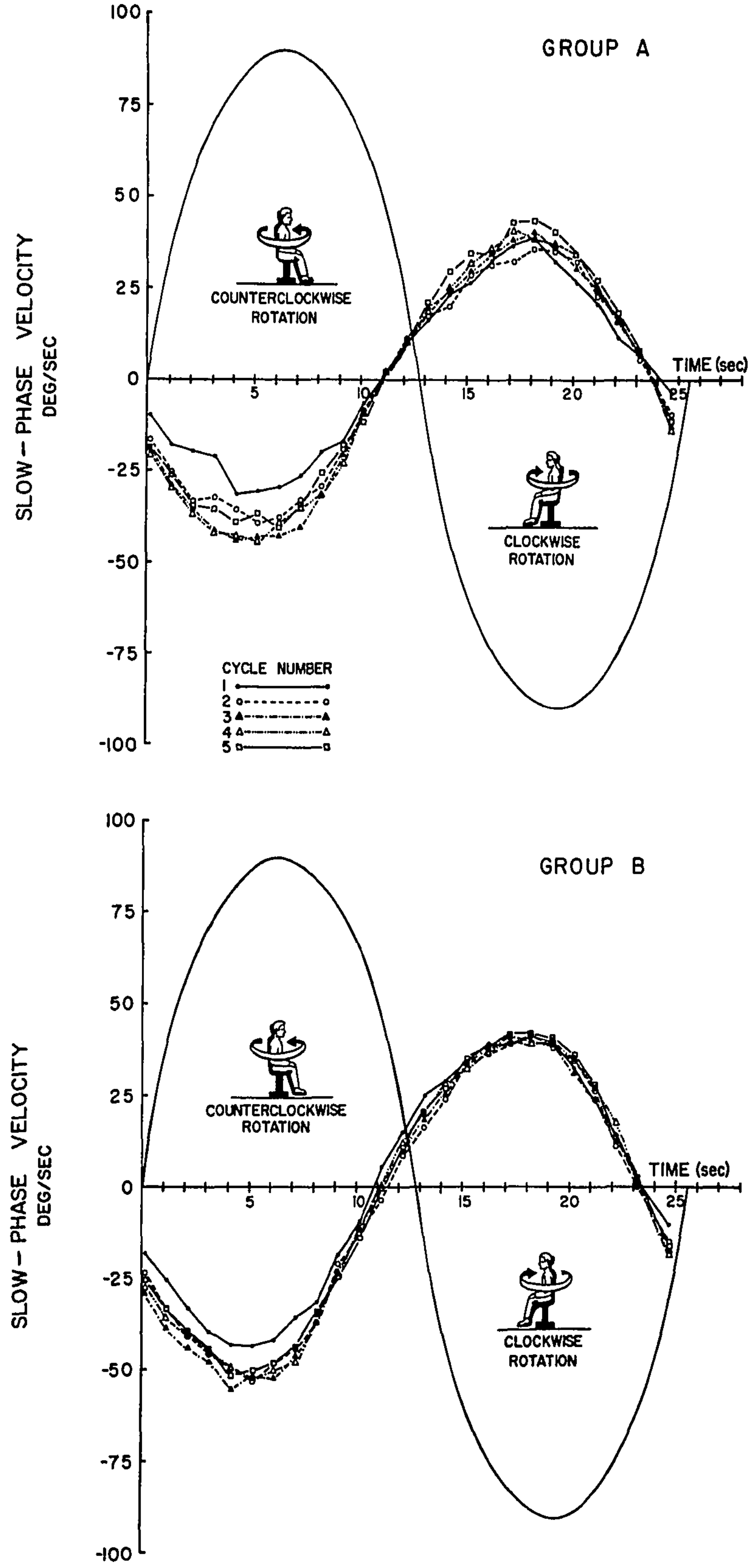


Figure 6. Slow-phase eye-movement velocity during initial measurement, by group and cycle. Solid line represents chair velocity.

Means and standard deviations of these nystagmic frequencies are shown in Table 4. Because an initial group difference and a Group x Direction interaction were observed with this variable also, an analysis of variance of final scores was performed (Table 5). No experimental effect was observed, although a significant group difference occurred, with Group A exhibiting a higher nystagmic frequency than Group B.

Mean ocular deviation scores were obtained, by subject, direction of nystagmus, and session, by dividing each total slow-phase deviation score by the corresponding nystagmic beat frequency. Means and standard deviations of the resulting scores are shown in Table 6. An analysis of variance was performed (Table 7). Since the group with the lower mean total slow-phase deviation in Session 4 also had the higher frequency, the group difference in mean ocular deviation is quite significant. Additionally, the Group x Direction interaction, which is the relevant measure of experimental effect, accounted for 62% of the relevant variation in mean ocular deviation, as opposed to 47% of the relevant variation in slow-phase velocity. This increase in effect probably reflects a correlation of frequency with total deviation across subjects, with a consequently reduced error variance when mean ocular deviation scores are considered.

Total slow-phase deviation scores are illustrated in Figure 7 by half-cycle throughout the entire experimental procedure. During the habituation series (Sessions 2 and 3),

TABLE 4

Means and Standard Deviations[a] (in Parentheses) of Nystagmic Frequencies, by Group, Direction of Fast Phase, and Session.

Session	Group A		Group B	
	Nystagmus Left	Nystagmus Right	Nystagmus Left	Nystagmus Right
1	140 (31)	139 (16)	136 (16)	113 (6)
4	141 (29)	125 (19)	118 (14)	116 (9)

[a] $S=\sqrt{\frac{\Sigma x^2}{n}}$

TABLE 5

Analysis of Variance of Final Nystagmic Frequencies, by Group and Direction of Nystagmus.

Source	df	MS	F	η^2
Group	1	0.2624	5.0994**	.2208
Subj. w/i Groups	18	0.0515		
Direction	1	0.0774	2.7054	.1307
Group x Direction	1	0.0476	1.6632	.0846
Residual	18	0.0286		

**$p < .05$

TABLE 6

Means and Standard Deviations[a] (in Parentheses) of Mean Ocular Deviations, by Group, Direction of Fast Phase, and Session.

Session	Group A		Group B	
	Nystagmus Left	Nystagmus Right	Nystagmus Left	Nystagmus Right
1	11.4 (2.5)	10.8 (1.8)	14.9 (2.7)	14.3 (3.3)
4	9.9 (2.5)	8.5 (1.4)	12.4 (2.1)	15.3 (3.0)

[a] $S = \sqrt{\frac{\Sigma x^2}{n}}$

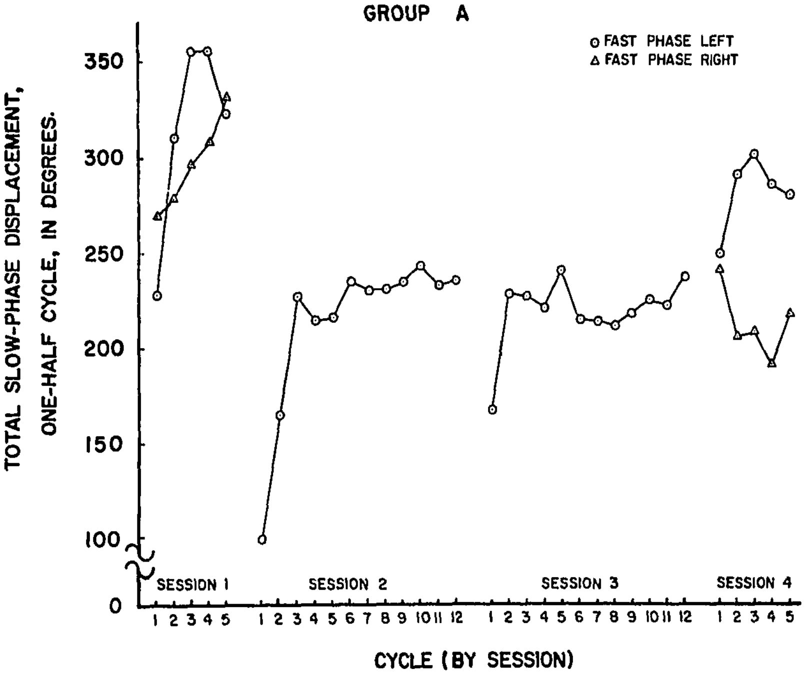
TABLE 7

Analysis of Variance of Final Mean Ocular Deviation Scores, by Group and Direction of Nystagmus.

Source	df	MS	F	η^2
Group	1	1501175.1	21.0415***	.5390
Subj. w/i Groups	18	71343.5		
Direction	1	43494.1	3.9038*	.1782
Group x Direction	1	327790.0	29.4207***	.6204
Residual	18	11141.5		

*$p < .10$

***$p < .01$



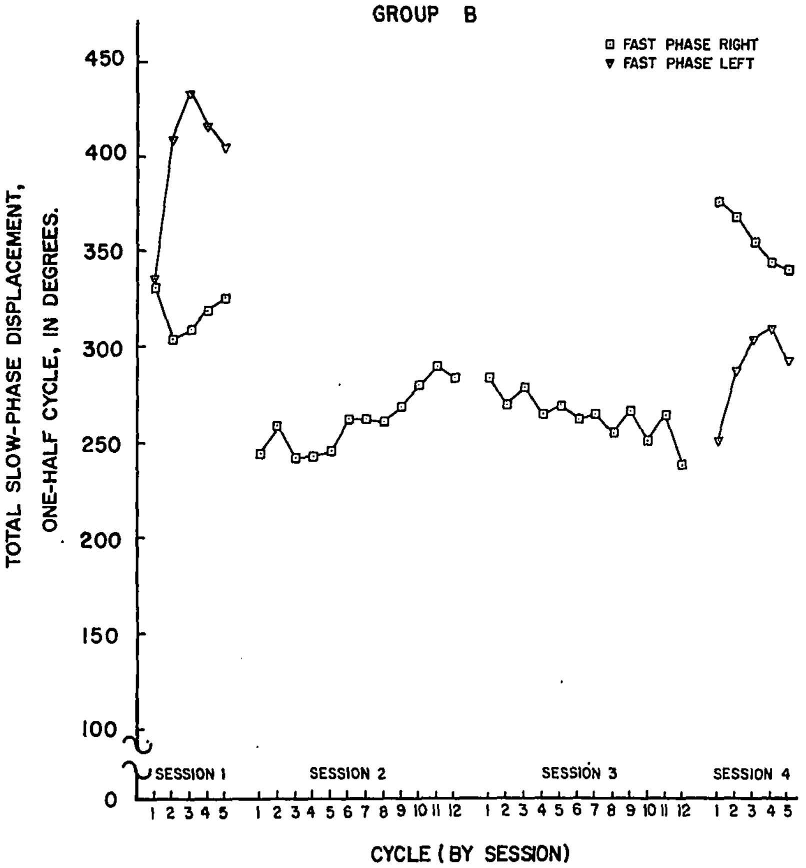


Figure 7. Total slow-phase eye displacement, by half-cycle throughout experimental procedure. Nystagmus during visual suppression in Sessions 2 and 3 was not scoreable, and is therefore not depicted.

nystagmus was, of course, suppressed by the visual task during rotation in one direction, so that only nystagmus in the other direction is plotted. The first scored cycle of nystagmus in each habituation session occurred after the first exposure to the visual task for Group B, but prior to the first exposure for Group A, so that the low level of nystagmic activity observed in Group A at the beginning of each habituation session probably results from a lack of arousal. Both groups show a clear tendency for nystagmus in the unsuppressed direction to increase throughout Session 2. A gradual decline in Group B's nystagmus during Session 3 is not clearly observed in Group A. Both groups show an overall reduction in nystagmic activity, relative to Sessions 1 and 4, throughout the habituation series, probably because of the residual effects of fixation during half of each cycle. It is known that still fixation results in a reduction in slow-phase velocity for a considerable period after darkness is reinstated, at least in the case of a nystagmic response to a vestibular stimulus preceding the still fixation (Collins, 1968).

Following the post-habituation oscillation in the dark, the subject performed the tracking task at reduced illumination while both nystagmus and tracking performance were recorded. Because nystagmus was suppressed by visual fixation during this period of oscillation, it was necessary to resort to a subjective rating scale as a measure of nystagmic activity. Specifically, each subject received one rating for his nystagmus in each direction (two scores per subject), on a 10-point scale. This rating was then divided by the subject's calibration deflection to obtain a calibration-corrected score. Means and standard deviations for these scores, and for the subjects' tracking performance during the corresponding periods, are shown in Table 8. The magnitudes of both scores should be considered arbitrary. High scores represent high nystagmic activity and large tracking errors, respectively.

An analysis of variance of the nystagmus ratings (Table 9) yielded a significant Group x Direction interaction accounting for 36% of the relevant variation. As predicted, each group demonstrated a reduction in nystagmus in that direction which, during habituation, was associated with the visual task. An analysis of covariance of the tracking performance scores using the baseline tracking scores as the covariate (Table 10) yielded no significant effects, although the directional differences were in the predicted directions for both groups. An analysis of variance performed on these same scores was virtually identical, indicating that the initial and final tracking scores were uncorrelated; it is assumed, therefore, to be an unreliable measure, and no further analyses of tracking performance were attempted.

TABLE 8

Means and Standard Deviations[a] (in Parentheses) of Calibration-corrected Nystagmus Ratings and Tracking Performance (Error) during Final Period at Reduced Illumination, by Group and Direction of Fast Phase.

Group	Nystagmus Ratings		Tracking Performance	
	Nystagmus Left	Nystagmus Right	Nystagmus Left	Nystagmus Right
A	124	62	3850	3206
	(78)	(53)	(1999)	(678)
B	83	131	3409	3659
	(69)	(120)	(878)	(1154)

[a] $s=\sqrt{\frac{\Sigma x^2}{n}}$

TABLE 9

Analysis of Variance of Nystagmus Ratings During Final Period (Tracking at Reduced Illumination), by Group and Direction of Nystagmus.

Source	df	MS	F	η^2
Group	1	2030.5	0.1611	.0089
Subj. w/i Groups	18	12602.0		
Direction	1	525.9	0.1759	.0097
Group x Direction	1	29975.7	10.0250***	.3577
Residual	18	2990.1		

***$p < .01$

TABLE 10

Analysis of Covariance of Tracking Performance During Final Period at Reduced Illumination, by Group and Direction of Nystagmus, with Practice Session Tracking Error as Covariate.

Source	df	MS	F	η^2
Groups	1	27285.5	0.0091	.0005
Subj. w/i Groups	17	2988060.3		
Direction	1	388860.0	0.5090	.0275
Group x Direction	1	1994559.9	2.6108	.1267
Residual	18	763963.8		

DISCUSSION

A further elaboration of the two categories of "habituation" (loss of arousal, conditioning of opposing response tendencies) previously outlined will now be undertaken. A qualitative behavioral model based on the simultaneous operation of these two factors will be presented in an attempt to reconcile a number of conflicts in the literature and to elaborate further the results of the present study.

With repeated presentation, many stimuli elicit progressively lower magnitudes of response. This is the phenomenon appropriately referred to as habituation, although it should be understood that an exact usage requires that the stimulus-response relationship be established as an unlearned one (Harris, 1943). The presence of vestibular nystagmus in neonates (Peiper, 1963, p. 150) implies that this response is innate. It will be seen, however, that some of the alterations of this response which have been reported to result from repeated vestibular stimulation may not, in fact, result from habituation to the vestibular stimulus.

Arousal

If a subject is repeatedly exposed to vestibular stimulation, a decline is observed in his nystagmic response to stimuli equivalent to the repeated stimulus. Wendt (1951) has attributed this decline to the development of a state of "reverie." Presentation of any alerting stimulus results in a resumption of the response (Wendt, 1951), although the resumption is not complete (Crampton & Schwam, 1951), and it is this property which primarily suggests arousal as a mechanism. It should be noted, however, that this property of "dishabituation" (Thompson & Spencer, 1966) is also found in lower organisms such as amoeba (Harris, 1943) and in spinal reflexes (Thompson & Spencer, 1966), so that a more general mechanism is apparently involved. Thompson and Spencer (1966) have suggested that this mechanism is synaptic in organisms with a central nervous system. Hernández-Peón (1960) has presented considerable evidence for the existence in mammals of two primary mechansims of habituation, both of which are reticular and are related to arousal. Habituation of non-specific arousal probably results from inhibition of the diffuse thalamic projection system by the dorsal midbrain reticular formation. It should be noted that this type of habituation is specific to the stimulus; "non-specific" refers to the response which is habituated, that is, to the orienting reflex, or general cortical recruitment produced by the diffuse thalamic projection system. The second mechanism is also stimulus-specific, but results in habituation of activity which is specific to the stimulus modality involved. In this case, habituation probably results from centrifugal inhibitory activity of the mesencephalic reticular formation. No attempt will be made to distinguish operationally between these forms of habituation due to loss of the alerting properties of the vestibular stimulus; the existence of separate specific and non-specific habituation mechanisms must be kept in mind, however.

The traditional view has long been that the entire reduction in nystagmic response which occurs as a result of repeated simple vestibular stimulation is due to vestibular habituation. It should be recognized, however, that another factor may account for a portion of this response loss (e. g., Collins, 1964b). At the time a naive subject experiences his first artificial vestibular stimulus in a habituation experiment, he is likely to be in a relatively high state of arousal as a result of the novelty of the experimental situation. As the experiment progresses, the subject's level of alertness declines as a result of habituation to the experimental situation as a whole. Since nystagmic response is known to be a sensitive measure of instantaneous arousal (Collins et al, 1961; Collins & Posner, 1963), a decline in nystagmus is an expected consequence of this primarily <u>non-vestibular</u> habituation. The primary objection which can be raised to this point of view is that the vestibular stimulus is itself quite alerting, so that a very high level of arousal and attention to the vestibular stimulus results from the first such stimulation. Subsequent declines in nystagmic response may therefore be felt to result almost entirely from a decline in the alerting value of the vestibular stimulus. If the subject were initially in a low state of arousal, so that only the vestibular stimulus contributed to his alertness, and he was subsequently habituated, this would undoubtedly be true. However, if to a significant degree the initial level of arousal of a subject in a vestibular habituation experiment results from other than vestibular stimuli (the experimental situation), and if habituation to those stimulus conditions occurs, then a reduction in nystagmic response due to factors other than vestibular habituation can be expected. In the present author's view, it is this general habituation which most closely fits Wendt's description of a state of "reverie."

The aim of this argument is not to suggest methodological studies, but to make it clear that instantaneous arousal may very well exert an effect on the magnitude of the nystagmic response, independently of vestibular habituation, though not, of course, independently of all habituation. It is not suggested that a reduction in response which results from vestibular habituation can readily be distinguished from that due to habituation to the experimental situation. To do so would be very difficult indeed, since it would require very precise control over nonspecific arousal mechanisms. The only apparent method for achieving such control is through drugs which probably also affect the habituation mechanisms. Operationally, then, declines in nystagmic activity as a result of repeated vestibular stimulation will be referred to as vestibular habituation.

Directional Balance

The second category of response change to be considered is that involving the conditioning of a compensatory response which is superimposed upon or substituted for the normal response. A response change of this sort is not, of course, habituation, although it will be seen that some response changes of this type may have been attributed to habituation. While the general characteristics which such a mechanism might exhibit are not well established, the most predominant characteristic of such response changes as elicited in the laboratory is an apparent conditioned shift in a directional balance mechanism (Howard & Templeton, 1966, pp. 131-133). As a result, nystagmus in one direction is suppressed, while nystagmus in the other direction is enhanced. Large intra-individual directional differences in nystagmus were reported as typical by Fluur and Mendel (1962a) and were found in the present study. The operation of the directional balance mechanism is suggested in Figure 7. Spontaneous shifts of a reciprocal nature are observable in Session 4 for Group A, and in both Sessions 1 and 4 for Group B.

Fluur and Mendel (1962a) have suggested that shifts in the directional balance mechanism occur by a simple negative feedback mechanism whereby reticular and other vestibular pathways act upon efferent fibers to adjust receptor threshold reciprocally in the two labyrinths, the threshold in the adequately stimulated labyrinth being increased. In the case of a cold-water unilateral caloric[7] stimulation, of course, the threshold of the opposite labyrinth to hot-water stimulation is increased. While the neural pathways cited are fairly well established (Gernandt, 1967; Engstrom et al, 1966), it does not seem parsimonious to assume that a simple habituative feedback mechanism is in operation here. In the present study and others involving both rotatory and caloric stimuli (e. g., Collins, 1965; Guedry, 1965b; Guedry & Graybiel, 1962), direction-specific effects have been obtained as a result of vestibular-visual interaction, and clearly not as a result of simple stimulus repetition. It seems likely that in these cases the directional shift is a mechanism for the resolution of intermodal conflict (Howard & Templeton, 1966). Likewise, direction-specific effects have been obtained in human subjects in the absence of vision, both with rotatory (Collins, 1964b; Fluur & Mendel, 1964) and with caloric stimuli (Fluur & Mendel, 1962a, 1962b). While these results have often been attributed to simple repeated stimulation, it is apparent that they, also, involve an intermodal conflict. In the case of caloric stimulation, for example, none of the stimuli which normally accompany

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[7] Introduction of hot or cold water into the external auditory canal causes thermal convection currents in a canal or canals which are oriented approximately vertically. The resulting deflection of the cupula constitutes a stimulation of the semicircular canal, and is called a caloric stimulus. The effects of hot and cold water are opposed, so that, for example, stimulation of the left ear with cold water or of the right ear with hot water while the head is tilted back to orient the horizontal canals in a vertical direction results in nystagmus with fast-phase right.

vestibular stimulation during movements are present.

It is fairly easy to specify in a gross manner a set of stimulus patterns which are ordinally related with regard to their degree of intersensory discordance. This term, intersensory discordance, is taken from Howard (1968), but will be used throughout the remainder of this paper in a more general sense than usual. It will include, of course, those instances in which conflicting information is provided by different sensory modalities, including reafferent information. For a want of a better term, it will also be taken to encompass conflicts between reafferent information and information regarding intended movements, in those instances in which voluntary movement is involved. Such conflicts are probably detected by a comparison of neural feedback of efferent signals with reafferent information regarding actual movements completed (von Holst & Mittelstaedt, 1950). Conflicts involving the absence of one of a pair of normally associated stimuli are also included. Several factors are involved in the determination of the degree of intersensory discordance associated with a given stimulus pattern. Among the most obvious are the number of discordances (e. g., in the case of caloric stimulation with vision allowed, a visual-vestibular discordance is added to those others already mentioned, resulting in a higher degree of overall discordance with the vestibular information), their magnitudes (a function of both quality and intensity), and their type. This last factor refers to the specific modalities involved. For example, when another modality conflicts with vision, vision usually provides more veridical information, so that the resulting perceptual adaptation primarily involves changes associated with the non-visual modalities (Howard & Templeton, 1966). Thus, even though vision is not dominant in a single Coriolis stimulation, visual information prevails with repeated stimulation.

With these considerations in mind, a ranking of a few of the common experimental vestibular stimulation conditions will now be presented, where the ordinal position of any single stimulus pattern is based on the degree to which an intersensory discordance affecting vestibular responses might be expected. It is immediately obvious that active Coriolis stimulation is a most extreme intersensory discordance of the sort under consideration. All other available information, including exafferent information, reafferent and other proprioceptive information, and visual information, if present, conflicts with the information provided by the semicircular canals. Passive Coriolis stimulation is not quite so extreme, since there is no opportunity for a conflict between vestibular and exafferent-reafferent information. There is likewise no opportunity for such conflicts with caloric stimulation. It should be noted that the conflicts which do occur during caloric stimulation are of a different type than those produced by Coriolis stimulation. Caloric stimulation involves the absence of stimuli normally associated with the experienced vestibular sensation, whereas Coriolis stimuli involve mutually contradictory inputs from vestibular and other sensors (and even among vestibular sensors). It is suggested on an intuitive basis that the type of discordance represented by a Coriolis stimulus is a more severe discordance than that associated with caloric stimulation. As with Coriolis stimulation, caloric stimulation with vision involves a higher order of intersensory discordance than caloric stimulation without vision. The final entry in a hierarchy of normal experimental conditions is passive rotation. In the absence of vision, the degree of intersensory discordance during passive rotation is very low, since all information is concordant. The only source of discordance is the absence of voluntary movement normally associated with rotation, and it is likely that this discordance is of a very low order. If the subject is allowed to see a visual field rotating with him, as in the present experiment, passive rotation results in a fairly intense intersensory discordance, involving as it does a conflict between two primary spatial sensory modalities.

It is suggested, then, that passive rotation, caloric stimulation, and active Coriolis stimulation involve progressively higher levels of intersensory discordance, and that in each case the presence of conflicting visual information results in a considerably higher degree of discordance than occurs with the same stimulus pattern administered without vision. If, as postulated previously, the repetition of a stimulus pattern involving vestibular stimulation and conflicting information from other senses results in a conditioned shift in the directional balance mechanism, the degree of that shift is expected to vary directly with the level of discordance associated with the stimulus pattern.

The Basic Model

Two mechanisms for the alteration of the nystagmic response as a result of repeated vestibular stimulation have now been outlined. The first mechanism, habituation due to loss of arousal, involves a reduction in nystagmus which arises as a function of repeated simple stimulation and is postulated to be fairly non-specific with regard to direction (i.e., habituation transfers readily to stimulation in the opposite direction). The apparent discrepancy with experimental findings will be clarified later. The second mechanism involves a conditioned shift in the directional balance mechanism which is postulated to result not from repeated stimulation *per se*, but rather from repeated exposure to an intersensory conflict involving vestibular stimulation. As will be demonstrated, a considerable portion of the existing body of experimental data on habituation can be explained by assuming that these two mechanisms are as postulated and that they operate simultaneously and fairly independently in all habituation studies incorporating caloric, passive rotatory, or Coriolis stimulation, with or without vision. The existence of these factors has been recognized by many past authors, but they appear to be rarely considered in combination.

The proposed model postulates that habituation due to loss of the ability of the vestibular stimulus to arouse the subject operates under all the conditions of repeated stimulation previously mentioned, and that the degree to which habituation occurs is assumed not to vary with different stimulus patterns (provided the same pattern is repeatedly administered), so that a vestibular stimulus of the same magnitude results in the same degree of habituation due to loss of arousal whether it is administered by Coriolis, caloric, or passive rotatory means. Habituation of this sort is assumed to manifest itself by equal reductions in the nystagmic response to stimulation in both directions; that is, habituation due to loss of arousal precipitated by repeated stimulation in one direction is assumed to transfer completely to stimulation of the same type in the exactly opposed direction.

The model further postulates that response changes due to a conditioned shift in the directional balance mechanism are superimposed upon response changes due to habituation in an additive, non-interactive fashion. To the degree to which directional shifts occur, it is evident that they result in a further reduction in response to stimulation in the same direction as that of the repeated stimulus. With regard to stimulation in the opposite direction, the shift in directional balance opposes the tendency, resulting from habituation, for the response to decline. In situations involving little intersensory discordance, such as passive rotation in the dark, a minimal shift of directional balance is produced with repeated stimulation, so that nearly complete transfer of habituation to oppositely directed stimulation is predicted to occur. In experimental conditions with progressively higher degrees of intersensory discordance, progressively greater declines in response are predicted for stimuli in the same direction as the habituation series, with smaller and smaller response reductions in the opposite direction. On an empirical basis, standard caloric stimulation (30°C or 44-45°C) would appear to involve a level of intersensory discordance in which the two opposed response-change tendencies for stimulation in the opposite direction cancel one another, so that no net transfer of the response change to stimulation in the opposite direction is observed. With intersensory discordance of sufficient magnitude, an *increase* in response is predicted for the direction of stimulation opposite to that of the repeated stimulus. A shift of directional balance of sufficient magnitude might even result in spontaneous nystagmus. These effects have been observed after active Coriolis stimulation with vision by Guedry and Graybiel (1962).

Empirical Observations Relevant to the Model

The evidence for the operation of two factors in the present experiment is quite strong. Obviously, simple habituation fails to account for the effects of vision in the present study, particularly the increase in response (in Group B) to a repeatedly presented stimulus. The implication is also fairly strong that the second factor (in addition to simple habituation) is a conditioned shift in the directional balance mechanism. Conditioned suppression of the nystagmic response to stimuli repeatedly associated with vision would explain the observation of a larger decline in response to rotation in the direction associated with vision than in the opposite direction. This explanation fails to account for the increased response in the opposite direction (in Group B). In any case, no obvious alternative explanation is available for the temporal response changes observed. In Group B and for some subjects in Group A, the habituation series resulted in an earlier onset and later cessation of response to stimulation in the direction not associated with the visual task during habituation. Thus, in Group B, a slow-phase response to the left was observed after habituation, during portions of the oscillation cycle in which a response in the opposite direction was elicited before habituation.

The present experimental results seem to suggest that the temporal characteristics of the two mechanisms are different. In Figure 7, Group B (the phenomenon is not so clear for Group A), a gradual increase in the nystagmic activity in the visually unsuppressed direction (that direction involving the lesser degree of intersensory discordance) is observed throughout most of Session 2, followed by a gradual reduction in nystagmus throughout the remainder of the habituation series. During the latter part of the habituation series, dysrhythmia and highly erratic nystagmus were frequently observed. In several instances a dishabituating stimulus (click) was presented, eliciting in every case a resumption of regular nystagmus and an increase in slow-phase velocity. These phenomena are common characteristics of nystagmic response reduction due to loss of arousal.

Fluur and Mendel, in procedures involving unilateral unidirectional caloric habituation, (1962a, 1962b) and unidirectional rotatory habituation (1964) of human subjects in the absence of vision (i. e., eyelids closed), described their results in terms of two types of subjects. Group I showed direction-specific nystagmus changes (a reduction in the duration of nystagmus in the direction elicited during stimulation, with an increase in the duration of the nystagmic response to stimulation in the opposite direction). Group II showed a decline in nystagmus duration in both directions. In all of these studies the Group I type of response was highly predominant. Proctor and Fernández (1963), in a study of unidirectional unilateral caloric habituation in cats, also obtained responses of both types, although they did not report their results in this manner. In the latter study, it was the bidirectional response reduction which predominated. As a result, these authors reported a decline in nystagmic slow-phase velocity in the habituated direction in all subjects, with inconsistent changes in the opposite direction (i. e., some subjects showed a reduction, some an increase). If only the means are considered, Proctor and Fernández found a reduction in nystagmus in the habituated direction, and no change in the opposite direction. Similar results have been reported by Collins (1964a) for unidirectional unilateral and Capps and Collins (1965) for unidirectional bilateral caloric habituation in cats, and by Collins, Mertens, and Schroeder (1969) for unidirectional unilateral and bilateral caloric habituation in humans. Since these authors reported only means, it is not possible to determine whether they obtained inter-subject differences similar to those described previously. Such individual differences may, of course, occur regardless of mean changes. Since individual differences are so prevalent in vestibular habituation studies, and since such differences may represent different adaptive mechanisms, it would appear desirable that they be reported.

The pattern of response changes obtained in the present study was quite similar to that reported by Fluur and Mendel (1962a, 1962b, 1964) in that a direction-specific change was predominant, with some subjects (in fact, Group B in general) demonstrating an apparent directional balance shift involving increased response in one direction, and some subjects (and Group A in general) demonstrating a different degree of response decline in the two directions. This group difference in pattern response changes apparently did not result from the experimental procedure. The subjects in Group B tended in general to have initial directional differences in nystagmic response. Group A, on the other hand, had several subjects with no noticeable initial directional difference. The only fortunate result of this chance difference between groups is that it suggests that those subjects most apt to show a predominance of direction-specific changes in nystagmus under these experimental conditions may also be apt to have an initial directional imbalance, as if their directional balance mechanism were relatively unstable or perhaps pliable. Even within Group A, there appears to have been a tendency for those subjects with initial directional differences to show the greatest directional change (compare Figure 5, parts III and IV, for example).

Fluur and Mendel (1962a) interpreted their results in terms of two mutually exclusive mechanisms, so that a subject showed either one or the other type of response change. However, their data (and certainly the present data) suggest that the two mechanisms operate simultaneously. Even those subjects indicated by Fluur and Mendel as belonging to Group II often showed a greater decline in nystagmus in the habituated than in the non-habituated direction.

The major discrepancy between the caloric studies of Fluur and Mendel (1962a, 1962b) and Collins et al (1969) and between the rotatory studies of Fluur and Mendel (1964) and Collins (1964b) is that in each case the former investigators found the direction-specific mechanism to predominate, while the latter authors found a reduction in nystagmus in the habituated direction, with little change in the non-habituated direction. Fluur and Mendel's results may well have been a procedural artifact. They made a major logical error in that they based the validity of their experiment on the assumption concerning the nature of the phenomenon they were studying. Specifically, they assumed that there exists no mechanism for vestibular habituation other than the directional balance mechanism. They employed a repetitive caloric testing procedure prior to the experiment in order to determine the normality of their subjects' vestibular responses. Assuming that only direction-specific habituative mechanisms exist, they alternate the direction of stimulation during this procedure, so that the effects of the opposed stimuli would cancel one another. Since habituation is known to occur most rapidly in the first few trials (e. g., Collins, 1964a), these pre-experiment vestibular stimulations may very well have resulted in a significant degree of habituation, and thus bidirectional reduction in response. Under such circumstances, the model proposed in the present paper would predict that shifts in the directional balance mechanism would be more predominant than usual, even though not quantitatively greater, due to the lesser degree of bidirectional habituation occurring during the study. Consider the extreme case in which all habituation has occurred prior to the study; under these circumstances, no further bidirectional change would occur during the study, and the model would predict equal and opposite response changes in the two directions as a result of the intersensory discordance associated with the repeated unidirectional stimulation.

The proposed model would predict that repeated exposure to vestibular stimulation in alternating directions would result in no directional balance shifts, since conditioned shifts in the directional-balance mechanism would continuously cancel one another. A bidirectional habituation of nystagmus would be expected, however, and has in fact been reported for caloric stimulation with vision in cats (Henriksson et al, 1961) and for rotatory stimuli in darkness, both in cats (Collins, 1967) and in humans (Brown & Crampton, 1966; Guedry, 1965b). The latter two studies were concerned with the effects of vision, but reported control groups habituated in the dark. Brown and Crampton reported a larger nystagmus reduction than did Guedry, in spite of the fact that their procedure was shorter (habituation is generally found to increase with a greater number of stimulations) and involved a larger stimulus (habituation generally varies inversely with stimulus intensity; Thompson & Spencer, 1966). However, Guedry specifically alerted the subjects during the pre- and post-habituation tests, while Brown and Crampton had their subjects perform the same task (subjective reports) throughout the experiment, so that a portion of the nystagmus reduction might have been due to greater immediate lack of arousal (as opposed to habituation) in their study than in Guedry's.

Gonshor and Jones (1969) reported an experiment in which no habituation occurred to sinusoidal rotatory stimulation. It is possible, of course, that oscillation differs from alternating opposed stimulation in the degree of habituation induced. It seems more likely, however, that the absence of habituation in this experiment resulted from the low intensity of the stimuli used (60° amplitude, 6-second period). It is quite possible that habituation is minimal to experimental stimuli of normal physiological magnitudes (Henriksson et al, 1961); such habituation might be expected to have already occurred as a result of normal movements.

The results of the present study suggest very strongly that an active participation in the visual environment is an important element in the effectiveness of a vestibular-visual discordance for the elicitation of a conditioned shift in the directional balance mechanism. The total exposure to simultaneous visual and vestibular stimulation in the present experiment was on the order of five minutes, which is extremely short in comparison with other experiments which have reported changes in the nystagmic response as a function of vision. There is every indication that the readiness with which conditioning was achieved is a result of the difficulty of the visual task and the consequent requirement that nystagmus be suppressed in order that the task be performed.

The present experiment has demonstrated the development of a direction-specific conditioned compensatory nystagmic response (i. e., a directional shift) due to the effect of vision during simple passive rotatory vestibular stimulation. A similar compensatory nystagmus was demonstrated to result from active Coriolis stimulation by Guedry and Graybiel (1962), who concluded that

> several factors are of likely importance in conditioning a demonstrable compensatory nystagmus: a) otolith and proprioceptor positional sensory information prior to and during the stimulus which elicits the canal response; b) an acceleration environment which yields a consistent sensory influx from each stimulus-producing movement; c) intention in the stimulus-producing movements; and d) visual inhibition of vestibular sensations.

The present experiment has demonstrated a similar effect (though to a much lesser degree) in the absence of voluntary movement. Thus, it has been demonstrated that intention and the exafferent-reafferent information associated with voluntary movement, though facilitatory, are not necessary for the development of a compensatory response shift. Visual suppression of nystagmus, which depends in part on self-observation reafference (as opposed to locomotor reafference) is clearly important.

Most studies of the habituation of vestibular nystagmus induced by caloric and rotatory stimuli without vision have concluded that habituation occurred in the stimulated direction with little transfer to stimulation in the opposite direction (although greater transfer occurs with rotatory than with caloric habituation). If only these studies are considered, it is parsimonious to assume that only a single mechanism is involved, i. e., a stimulus-specific habituation with only a small degree of stimulus generalization to opposed stimuli. The model proposed earlier in this paper has the advantages that additional and conflicting experimental evidence obtained under similar conditions of habituation may be explained, many of the effects of vision and other sources of intersensory discordance on the habituation of nystagmus can be accounted for, and the difference in degree of directional transfer between rotatory and caloric stimulation is explained. It is quite likely that the proposed model is an oversimplification. In particular, it is quite possible that the effects of repeated intersensory discordance are not completely direction-specific, as suggested in the model. It is, however, possible to account for most of the results reviewed, at least on a gross level, without introducing this additional complication into the model.

An Inadequacy of the Model

Guedry (1965b) and Collins (1965) performed studies of the effects of vision on nystagmus habituation using caloric and rotatory stimuli respectively. While the results were somewhat as predicted by the model, the observation in both studies of a greater overall decline in response in subjects performing a visual task than in non-vision control subjects is inconsistent with the model in its present form and merits further attention.

Guedry (1965b), whose subjects performed a difficult visual task during accelerations in one direction and had no vision during equal accelerations in the opposite direction, obtained slow-phase velocity reductions of 50 per cent and 20 per cent, respectively. The resulting directional difference (nearly 40 per cent) is much greater than that obtained in the present study. Guedry's 4-hour experimental procedure involved 80 one-minute exposures to a visual-vestibular discordance, whereas the present experiment involved only about 5 minutes of exposure to visual-vestibular interaction. It is interesting that Guedry obtained a decline in response of about 20 per cent in both directions in control groups habituated in the dark, both with and without auditory alerting tasks. That is, the response decline evidenced by the non-vision control groups was about the same as that shown by the vision group to stimulation in the direction not associated with vision. This finding is not consistent with the proposed model, which predicts that the mean decline for each group should be the same, with a difference in directional preponderance. Guedry's results also seem inconsistent with the present results, and it is probable that the considerable difference in experiment duration and resulting arousal effects is responsible, at least in part, for this discrepancy. In this connection, it should be emphasized that the present experimental procedure was very short and that the effects on the nystagmic response were quite small relative to those reported in most habituation studies. The duration of exposure to simultaneous visual and vestibular stimulation apparently was, as intended, on the borderline with regard to the development of conditioned responses. Guedry's experiment, on the other hand, was quite long.

Collins (1965) with vision allowed during 40 unidirectional unilateral caloric stimulations over a four-day interval, obtained results which parallel Guedry's. When subjects were tested after repeated cold caloric stimulation of the right ear while attempting to fixate a visual target, they evidenced a 25 per cent reduction in slow-phase displacement for unilateral stimuli equivalent in direction to the habituating stimulus, and only a 10 per cent decline for opposed stimuli. A control group habituated in the dark with an auditory alerting task showed no consistent change in slow-phase displacement. The post-tests were administered the day after the final habituation trials, so that the lower absolute magnitude of response change is not surprising. The fact that the pattern of response change parallels that resulting from Guedry's quite different procedure is significant.

Two plausible explanations must be considered for the greater reduction in response with vision in these two studies. Obviously, one possibility is that a conditioned suppression of nystagmus has occurred, rather than a shift of directional balance. Such a response change would be adaptive with regard to the visual task, and would not be at all surprising. As mentioned previously, however, the present results are not compatible with a unidirectional conditioned suppression of nystagmus as a result of visual stimulation. The experimental conditions of the present study do not differ from those of Guedry's or Collins' studies in any way which would readily explain the operation of two basically different response-change mechanisms as a result of the visual-vestibular interaction.

The alternative explanation which seems most worthy of consideration is that the vision and non-vision groups in Guedry's and Collins' studies differed on some secondary variable. Specifically, it is suggested that the subjects performing visual tasks were in a higher state of arousal throughout the habituation procedure than were the control subjects aroused only by auditory tasks (or not at all). If it is postulated that the rate at which habituation occurs varies directly with the subject's level of arousal during habituation, then in prolonged procedures visually aroused subjects would be expected to show a greater overall response decline than subjects not visually aroused as a result of their higher level of general arousal during habituation.

The choice between these two possible explanations (and perhaps others) for these specific findings of Guedry (1965b) and Collins (1965) will require further research. Experiments in which subjects with and without visual tasks are equated in degree of arousal are indicated, but the problems associated with such equation of arousal are of considerable magnitude. Studies of the effects of arousal _during_ habituation have not been performed satisfactorily in human subjects, and should clearly be undertaken.

Further Research

The model has a number of experimentally verifiable implications, and several methods for conducting further research suggest themselves. A unidirectional caloric habituation study incorporating similar visual conditions to those in the present experiment should produce a greater degree of directional balance shift than a unidirectional rotatory study with approximately equal vestibular stimulus intensity, since the overall degree of sensory discordance between vestibular and other modalities is greater with caloric stimuli. Vision during oscillation (either rotatory oscillation or caloric stimulation with sinusoidally changing temperature--the latter method apparently has not yet been tried) should affect nystagmus no differently than similar stimulation in the dark, provided both groups are aroused equally. Such equation of arousal is, of course, a difficult methodological problem. An active interaction between subject and experimenter might be used to achieve a high state of arousal in both vision and no-vision groups. The overall degree of discordance associated with rotatory vestibular stimulation should be manipulable independently of vestibular stimulus intensity by use of a visual field capable of moving independently of the rotation of the subject. Vision might be made to affect habituation of nystagmus in cats by use of visual stimuli known to be highly alterting.

Perhaps the most critical test of the model would be provided by investigating the effects of several unidirectional habituation series, alternating in direction of habituation. Capps and Collins (1965) performed a unilateral caloric habituation series on cats, followed by a similar habituation series in the contralateral direction, and found that the response in the original direction was still habituated. It is possible, though slightly awkward, to account for these results within the proposed framework. According to the model, during the first habituation series two factors were in operation. Both served to reduce nystagmus in the stimulated direction (direction A, say), but were in opposition with regard to the other direction (b), with little net change resulting. That is, with repeated stimulation in direction A, habituation operated to decrease the response to stimulation in direction B, while a shift in directional balance tended to increase response in direction B. In the case of standard caloric stimulation, these changes seem to be approximately equal, cancelling each other. During the contralateral habituation series (stimulation in direction B), the same two factors operated, but in this case they cooperated to reduce the nystagmic response to stimulation in direction B, while the two factors opposed one another in their effects on the originally habituated direction (A). If the effects of these two factors in direction A were again approximately equal, no net change in this direction would be expected to result from the contralateral habituation series. With repeated alternating habituation series, the model predicts a breakdown in this stair-step phenomenon. As the degree of bidirectional habituation approaches its asymptote, only the directional shift should remain. At this point, a habituation series should result in an increase in nystagmus in the unstimulated direction. Suggestive evidence for this is found in Fluur and Mendel's (1962b) report of such an increase upon secondary contralateral habituation under conditions in which bidirectional habituation may have occurred to a significant degree prior to the experiment.

SUMMARY

Several previous studies have suggested that vision affects the course of vestibular nystagmus habituation, and have further suggested that a critical variable in the elicitation of such an effect is the nature of the visual task. A visual task which requires suppression of nystagmus for its performance and which requires a high level of attention to the visual environment might be expected to have a considerable effect on changes in the nystagmic response with repeated stimulation.

Accordingly, two groups of 10 subjects each were exposed to identical series of sinusoidally oscillating horizontal rotation with peak angular velocities of ± 90°/sec and a 25.5-sec period. Each group was required to perform a compensatory tracking task using a visual display at low luminance and a hand controller. This visual task was performed only during one-half of each rotation cycle, with the two groups performing the task during oppositely directed nystagmic responses. Habituation involved a total of 306 seconds of vestibular stimulation during this conflicting visual task. Pre- and post-habituation measurements of nystagmic slow-phase velocity incorporated the same sinusoidal stimulus in total darkness. The visual task resulted in a conditioned compensatory change

in the pattern of nystagmic response, with a reduction in total slow-phase eye movement occurring in the direction associated with the visual task and, in most subjects, some increase in response in the opposite direction. Variability of response change was greater in the latter direction, with some subjects showing a reduction in response in both directions. During a subsequent period of visual tracking at even lower luminance, the same directional difference in nystagmic activity was observed.

A qualitative behavioral model is proposed to account grossly for the observed effects of repeated vestibular stimulation, with or without vision. The model postulates the simultaneous operation of two factors: a bidirectional reduction in response resulting from repeated vestibular stimulation and depending upon arousal mechanisms, and a highly direction-specific change in response resulting from repeated inter-modal sensory conflict and depending on a shift in the interlabyrinth directional-balance mechanism. Operation of the latter factor results in a decrease in nystagmic activity in one direction and a simultaneous increase in the opposite direction. The model explains several discrepancies in the literature, accounts for many (though not at present all) of the effects of vision, provides a mechanism for the explanation of individual differences in habituation observed in the present and other studies, and may account for the failure of some investigators to obtain a change in habituation due to vision.

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