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16. Abstract

Vestibular and visual mechanisms are critical sensing systems in spatial orientation and in spatial disorientation. In aviation or space environments in particular, the role of the vestibular system is central to the problems of spatial disorientation and "pilot's vertigo." A question of significant concern in this regard has been centered around the possibility of abolishing or reducing undesired vestibular responses (inaccurate experiences of motion and eye movements which could blur vision) by repeated exposure to appropriate stimulus conditions. The present report reviews research conducted on this question. The review is generally restricted to activity and responses from the semicircular canals of the vestibular system. Methodological problems are presented briefly and the influence of arousal on vestibular responses is detailed. Data obtained from animals and from man are treated separately. At least for man, the term "habituation" may be better defined by a dynamic change in the form of vestibular responses than by a simple response reduction.

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or undulating movements of the eyes. Such spontaneous responses do not occur with eyes open in total darkness.[92] Under the open-eyes condition in darkness, a large-amplitude nystagmic eye-movement signal is obtained by corneo-retinal potential techniques. However, subjects rapidly become unaware of the position of their eyes and it is possible that they may even close their eyes without realizing it. Further, dark adaptation has been shown to influence the corneo-retinal potential,[75 76] the method most frequently used to record nystagmus, and the fidelity of tracings obtained by this technique is not always true.[31] All in all, there are problems associated with any of the methods used; therefore, the method must be kept in mind when considering reports of results. Further, in evaluating changes in the nystagmic reaction, the measure used may be of considerable significance. Although duration of nystagmus has been traditionally the most commonly used means of assessing vestibular reactivity, particularly in clinical situations, it is also probably the least indicative of changes. A thorough assessment requires some combination of measures of slow-phase eye displacement, velocity of eye movement, frequency of nystagmic beats, and duration of the response.

III. The Problem of Arousal.

A. *Animals.* Fearing and Mowrer[85] examined the effects of anesthesia on habituation of rotation-induced head nystagmus in pigeons. They reported no habituation for anesthetized animals and a clear reduction in nystagmus for undrugged birds. From incidental observations made during the study, Mowrer[167] became probably the first investigator to attempt to manipulate arousal factors and examine their influence on vestibular responses. Working with pigeons, Mowrer[167] differentiated between "excited" and "unexcited" conditions, depending upon how the birds were prepared for rotation trials, and reported longer durations of nystagmus for the "excited" condition. His interpretation, based also on previous studies, was that "excitement" influenced the vestibular reaction but that it could not account for all of the reduction produced by repeated stimulation. Similarly, Wendt[201 202] noted that immobilized animals might go into sleep-like states ("animal hypnosis") and that various types of stimuli (e.g., auditory or tactual) could restore alertness and reinstate an apparently suppressed nystagmus. Hood and Pfaltz[140] like Mowrer[167] reported temporary increases in frequency of nystagmus from rabbits when they appeared excited, and, further, noted that injections of adrenalin in rabbits which had shown substantial response declines to repeated rotation produced a partial recovery of nystagmus. Similar results were obtained by Hernandez-Peon and Brust-Carmona[134] with acoustic startle and by Crampton and Schwam[70] who used intermittent electric shock and auditory signals as excitatory stimuli during repeated rotation of cats.

Drugs have also been used to affect alertness. Crampton[68] introduced the use of d-amphetamine in an effort to maintain arousal levels in the cat; recorded amplitude of nystagmus was increased but the usual rapid reduction of nystagmus occurred with repeated rotation. Dowd[78] reported an increase in recorded amplitude but no change in phase relationships of nystagmus during sinusoidal acceleration of cats treated with d-amphetamine; sodium pentobarbital depressed the response. On the other hand, Cenacchi, Fenu, and Gabrielli[34] reported decreased nystagmus from rabbits with various amounts of amphetamine.

Wolfe[207] has noted that the dosage levels of d-amphetamine that have been used to maintain animal alertness may have some undesirable side effects; some animals become ataxic and appear to have vestibulo-cerebellar impairment. In addition, the influence of the drug on eye-movement calibrations has been neglected. The importance of the latter was noted by Jongkees and Philipszoon[144 145] who reported enhancement of rabbit nystagmus with hyoscine and also a slight increase in the (corneo-retinal potential) eye-calibration signal. Other drugs such as chlorpromazine and cinnarzine, which have a soporific effect, have been shown to reduce rabbit nystagmus[19 144 145] without altering the eye-calibration signal.[144 145]

B. *Man.* Although a number of early investigators[e.g., 9 10 106 125 189] had noted effects on vestibular responses of "indifference," "nervousness," or "arousal," Wendt[202] was apparently the first to attempt a definition of "excitement" or "arousal" in terms of conditions basic to the state

of the subject, and to relate these to the problem of habituation. He cited two factors in habituation: in one case, repeated rotatory stimulation under conditions that provided opportunities for visual fixation would result in an increasing dominance of the visual stimuli and thereby inhibit nystagmus; in the other case, under conditions of darkness, an "inward orientation of attention" would account for nystagmus reduction while an "environment-directed orientation" would restore nystagmus or prevent its decline.

Based primarily on Wendt's[202] notions regarding mental or attentional states, Collins, Crampton, and Posner[54] evaluated several instructional procedures aimed at controlling alertness during rotational stimulation of human subjects (tested with eyes open in total darkness) and demonstrated that both quantity and quality of nystagmic output could be manipulated in the same subject by instructions regarding mental activity. If subjects were asked to relax, daydream, and pursue no particular line of thought ("reverie"), relatively weak nystagmic responses were recorded; vigorous nystagmus was obtained when the same subjects performed continuous mental arithmetic (successive division) or signalled turning sensations in 90° intervals.[c.f., 12 109] Several other studies[120 150 156] reported that mental tasks or increased alertness would produce a regular nystagmus in place of dysrhythmic responses (see Figure 1), or would prevent apparent adaptation from occurring.[55 123]

The results of subsequent research[39 40 43 45 60] pointed to the fact that inward- vs. outward-directed orientations probably do not account for the influence of the instructions on nystagmic output since both "reverie" and mental arithmetic may be classified as "inward-directed."

STIMULUS: BILATERAL IRRIGATION FOR 15 SEC

FIGURE 1. The effect on caloric nystagmus of alerting a subject. The vertical bar indicates the end of the irrigation; the arrow denotes the point at which the subject (eyes open in darkness) was told to alert himself. The tracing comprises 42 seconds of recording.

What appears to be of importance is that the subject be in a sufficiently aroused or active mental state, whether the arousal arises from attending to his sensations, pursuing a particular line of thought, performing mental calculations, or responding to auditory or other stimuli. It should be noted that not all instructions are effective in this regard. Some tasks, such as counting, may not produce any noticeable effect on nystagmus,[152] while others, such as tasks involving timing behavior, appear to require relatively little attention with repetition.[39] A point of additional interest made by Collins, Crampton, and Posner[54] was that EEG alpha activity was not blocked as a result of angular accelerations nor did it appear to be affected by different instructions regarding alertness, although nystagmus was markedly influenced by the latter. These EEG-nystagmus findings were confirmed in a later study[60] which concluded that, at least under some conditions, EEG monitoring might be a less sensitive indicator of states of alertness than are vestibularly-induced eye movements. Pendleton and Paine[176] made a similar observation with newborn infants, and Lidvall[152] noted stable alpha activity and lack of blocking during caloric vestibular stimulation. More recently, Goto, Tokumasu, and Cohen[100] concluded that (excluding barbiturates or deep sleep) "the frequency and velocity of rapid eye movements are among the most sensitive indices of alertness of any, including the EEG."

That assigned tasks or instructions regarding mental activity are important in maintaining vigorous nystagmus or restoring a deteriorated response has been confirmed in a number of studies.[e.g., 11 17 24 79 99 147 158 192 196 198] Instructions have been effective with caloric irrigations,[40 45 57] with drugs,[16 59] with alcohol,[190 191] with positional alcohol nystagmus,[129] and when used in conjunction with hypnosis[7] although, in one report,[142] hypnotized subjects showed suppressed nystagmus (and, frequently, slow pendular eye movements) in spite of assigned tasks. Under some laboratory conditions, mental tasks appeared effective in reducing or preventing motion sickness occasioned by unusual vestibular stimulation.[64 65 114] Further, the absence of alertness or

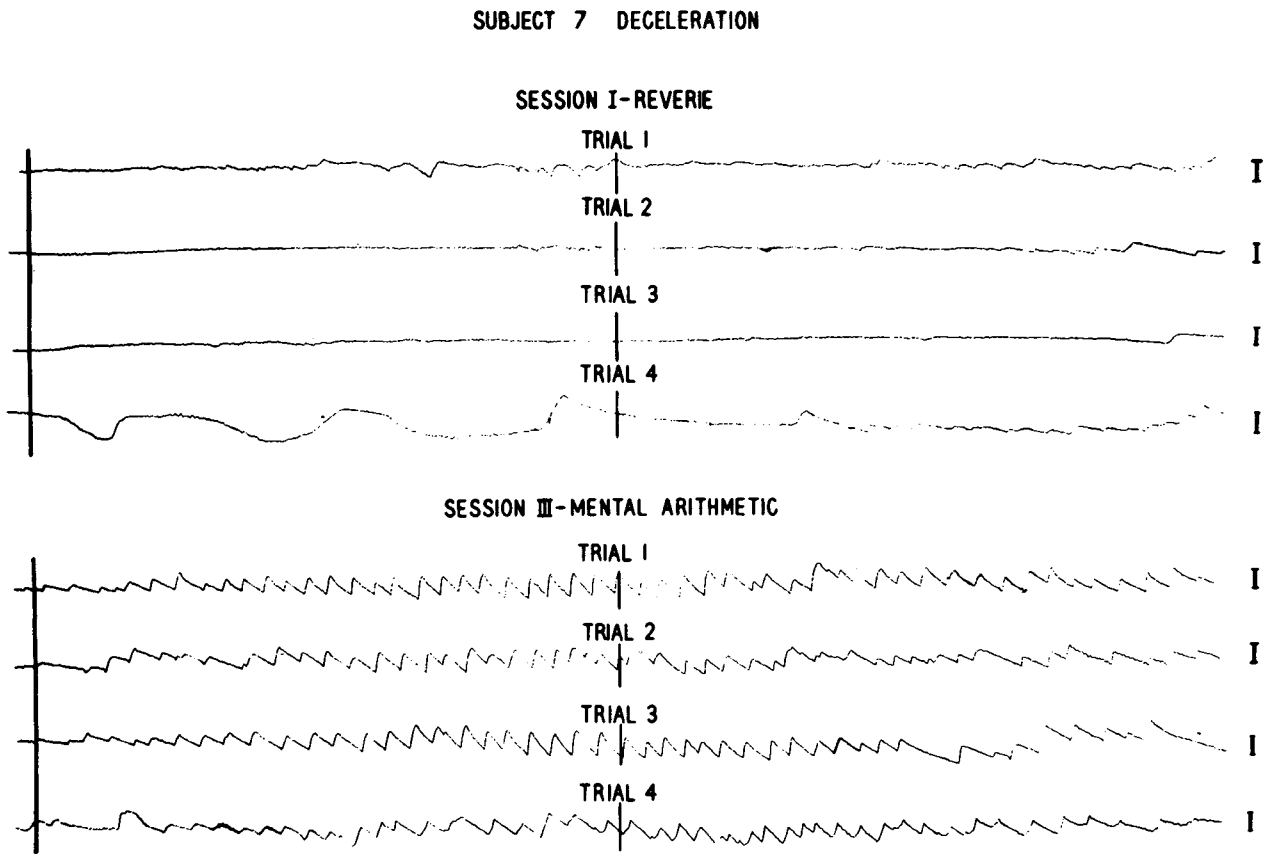

FIGURE 2. The influence of instructions on vestibular nystagmus (see text). Vertical bars through the tracings demarcate a 15-second period of angular stimulation at 4.5°/sec². Markers at the end of each tracing indicate 20° eye calibrations. Recordings were obtained from the subject with eyes open in total darkness. Sessions were held on separate days; trials were consecutive on a given day. The "reverie" task was given during the subject's first exposure to laboratory vestibular stimulation. (Reprinted with permission from the *Journal of Experimental Psychology*.[39])

arousal, whatever its neuro-psychophysiological cause, is probably a major factor in vestibular findings which indicate substantial or total suppression of nystagmic responses in schizophrenic patients.[e.g., 2 37 38 181] Patients who show these sub-normal vestibular reactions are frequently characterized as apathetic, indifferent, lacking in initiative, and showing a poverty of mental content. More recent work with autistic children has shown a similar depression of nystagmus.[187] However, the latter deficit has been attributed to vestibular dysfunction in a scheme which assigns to the vestibular system the role of regulating the mutual interaction of sensory input and motor output during the waking state and in REM sleep.[173]

It is sometimes suggested that the use of mental tasks to maintain arousal level represents an artificial means of preventing or interfering with the habituation process. That is, in the absence of structured mental activity, an overall suppression of nystagmus rapidly appears. It is quite apparent that a decline of nystagmus can occur with relatively few stimulus repetitions in total darkness when subjects are uninstructed regarding arousal. It is equally apparent that any inadvertent alerting of such subjects will result in the reappearance of a vigorous nystagmus.[120] However, since "reverie" assignments can result in almost no nystagmus to an otherwise adequate rotational stimulus during the first exposure to laboratory angular accelerations,[39] it would seem proper to differentiate between situational or perhaps psychological habituation as opposed to habituation of the vestibular system *per se*. If interest centers around true changes in vestibular functioning as a result of repeated testing, it would appear to be an experimental prerequisite

to attempt to effect some control over the mental state of the subject. This is particularly true when subjects are repeatedly tested in total darkness or with their eyes closed; the tendency to doze under such conditions is probably very strong.

IV. Survey of Studies of Animals.

A. *Nystagmus: Rotation-Induced.* Abels[1] apparently began experimental evaluation of the habituation of head after-nystagmus in pigeons. Using a cage suspended from cords which were twisted and then allowed to unwind, Abels observed the intensity of the jerks of nystagmus following an abrupt stop of the rotation under conditions either permitting or excluding vision. He noted a marked habituation with repetition under the former condition, and a considerable but lesser response reduction under the latter condition. Abels[1] reported that the reduction was directionally specific; after repeated rotation in one direction, a reversal of direction would elicit a vigorous response.

The reduction of head after-nystagmus from pigeons tested in the light was confirmed by King[146] and by Huddleston.[141] Huddleston[141] indicated that the decline was more rapid for squabs than for older pigeons and noted that head after-nystagmus could be completely inhibited by visual stimuli in combination with voluntary movements of the head. Further, although birds rotated in the dark showed a compensatory head movement upon which nystagmus of relatively low amplitude was superimposed, birds rotated in the light showed little compensatory positioning of the head and a relatively higher amplitude of nystagmus.

King[146] confirmed Abel's[1] finding of the lesser reduction of nystagmus with vision excluded by testing blind birds, while Fearing,[82] rotating hooded pigeons alternately clockwise and counterclockwise, reported significant reductions in frequency and duration of head after-nystagmus with no apparent effect of one direction of stimulation upon the other (i.e., the responses for each direction appeared to decline independently). In later studies, Fearing[83 84] massed the habituation trials (61 stimulations in a single session) for one group of birds and spaced the habituation trials (10 trials per day for 14 successive days) for other birds; the animals were then subdivided into smaller groups, each retested at a different interval ranging from two to 32 weeks. The data led Fearing[84] to conclude that spacing the habituation trials led to greater retention of habituation than did massing the trials in a single session. Brown[25] confirmed this effect with ocular nystagmus from cats.

King's[146] study also introduced a finding which has yet to be experimentally resolved, i.e., in tests following habituation stimuli, the number of nystagmic head movements declined more when the pigeons' heads were fixed (restrained) during the habituation series than when they were free to move in the horizontal plane (vision permitted in all cases). Lumpkin,[155] rotating a single rabbit in the light in an extensive series of tests (142 days), used a head-holder for most of the trials, but tested the animal with its head free on specific occasions. He found considerable differences in the frequency and duration of ocular nystagmus for the two conditions (although both showed habituation) and concluded that head-fixed and head-free habituation were not the same. Earlier, Maxwell, Burke, and Reston[160] claimed that ocular nystagmus was reduced more in the light when rabbits' heads were free as opposed to fixed. However, they simply noted the results of the habituation series for their animals (i.e., there was no pre- to post-test comparison of the groups under the same conditions) and, initially, the head-free group had durations which were approximately 30% shorter and frequencies of nystagmus which were about 50% less than the head-fixed group.

Mowrer's[168] study of the influence of vision on habituation of head nystagmus in pigeons also contained differences related to head-free stimulus conditions. Mowrer[168] reported that pigeons tested in darkness showed little or no habituation of the duration of after-nystagmus following a large number of rotations with heads free in illumination, and a clear (directionally specific) decline when the heads were fixed and the room was illuminated during the habituation series. Similarly, when vision was permitted and a striped drum forming a wall around the turntable was rotated with the turntable during the habituation series (thereby preventing optokinetic nystagmus), only a slight bidirectional reduction of head after-nystagmus was obtained during post-tests in darkness (use of the striped-drum also produced very little after-nystagmus

during light trials and repeated stimulation resulted in abolition of the response). However, when the habituation series was in darkness, bidirectional nystagmic reductions were obtained for both the head-fixed and head-free conditions although, contrary to results reported by King[146] for tests in which vision was always permitted, response attenuation was greater for the latter condition. The complete lack of a decline of nystagmus in the dark following repeated head-free stimulation in the light and a directionally specific decline in the dark following head-fixed stimulation in the light are difficult to explain since Mowrer[168] employed approximately equal rates of acceleration and deceleration during the habituation trials. However, the experiment was a complex one since it involved: fixed vs. free head conditions; ocular nystagmus with and without head nystagmus; optokinetic nystagmus enhancing vestibular nystagmus in one direction, and opposing it in the other; compensatory head positioning allowed to occur with free heads and prevented with fixed heads; and the possibility that head position varied among the conditions. Mowrer[169] later examined the effects of interacting vestibular and optokinetic stimulation with pigeons. He indicated that, when vision was permitted during and after rotation, after-nystagmus was inhibited by: (1) the tendency to fixate visually on some object, (2) the tendency for an optokinetic response to persist after cessation of rotation, and (3) the tendency for optokinetic head movements during rotation to stimulate the semicircular canals in a way which counteracted the vestibular stimulus occasioned by a deceleration.

King[146] had also reported that decerebrate pigeons with heads fixed in the light showed less habituation than did normal birds. Halstead[127] and Halstead, Yacorzynski, and Fearing,[128] using hooded pigeons, found a significantly greater decline in duration of head after-nystagmus from normal birds than from those with cerebellar lesions. Another group of normal birds received a similar series of rotations and demonstrated the same response reduction; half of the birds were then subjected to cerebellar operations. Two weeks later, birds with cerebellar lesions showed significant recovery of nystagmus; those which had not been operated on showed no change from the habituated level. Similar findings were obtained from yet another group with a 4-week interval. In both control and cerebellar birds, some habituation was still present after a 3-month interval. Moreover, substantial (control birds) to complete (birds with lesions) "transfer of habituation" was obtained to rotation in the opposite direction. The latter result confirmed the findings of Mowrer[168] although "transfer" may be an inappropriate term since the acceleration stimulus used during habituation trials almost surely was of high magnitude and brief duration.

The question of "transfer of habituation" to the opposite direction of turning as cited by Halstead[127] and by Abels[1] involves some confu-

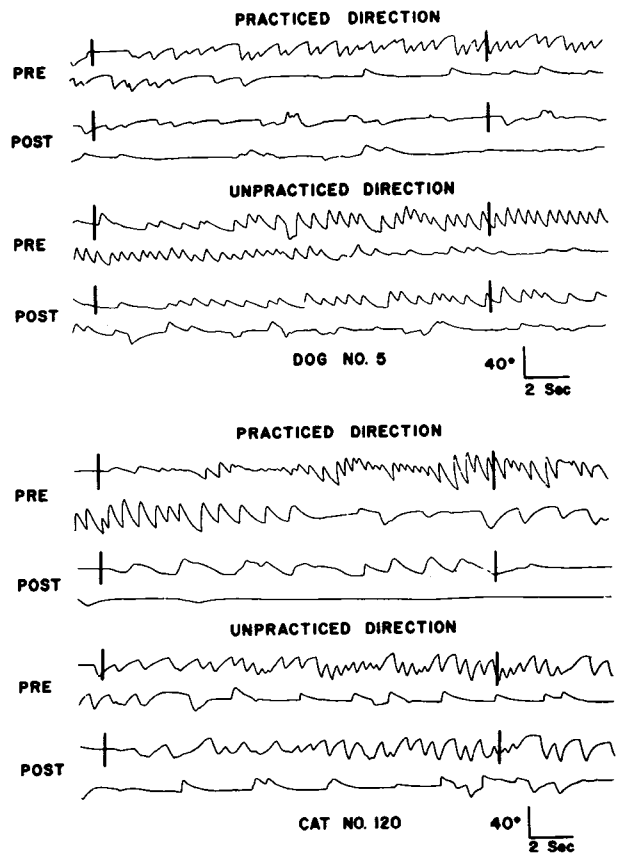

FIGURE 3. Directional specificity of habituation of ocular nystagmus in a cat and a dog. A series of 15 CW angular accelerations (decelerations were subthreshold) was administered between the pre- and post-tests. A directionally specific reduction is evident. The animals were rotated under head and body restraint in total darkness.[cf., 132] Vertical bars demarcate the stimulus period; optokinetically-derived calibration markers indicate 40° eye excursions. Similar effects are obtained from other animals. (Reprinted with permission from *Acta Otolaryngologica*.[62])

sion regarding stimulation (compare Figures 3 and 4). Early investigators sometimes overlooked the fact that a rotating subject brought to an abrupt stop actually received vestibular stimulation in both directions (in one direction during acceleration, and in the opposite direction during deceleration). In Abel's[1] situation, the acceleration rate was probably of lower magnitude than that of the deceleration (brake stops); with Halstead,[127] the rates were probably approximately equal. In examining only deceleration responses, and in reversing the direction of turning after an habituation series, one would expect an equally reduced response if the rates of acceleration and deceleration during habituation had been approximately equal (see Figure 4) or, if the rate of the latter were higher, the "unhabituated" direction might be expected to yield a relatively stronger response than that finally evidenced in the "habituated" direction. Data from the two studies support these expectations, and the expectations themselves are based on studies by Griffith[105] with white rats and by Maxwell, Burke, and Reston[160] with rabbits, which showed a considerable reduction in frequency and duration of ocular nystagmus following repeated abrupt stops of rotation. When the stopping was then attempted from a faster rate of motion, a more vigorous and longer-lasting nystagmus was elicited (however, even this response was less than that obtained from an identical stimulus prior to the habituation trials).

Most of the investigations cited above have examined habituation of head after-nystagmus. Before beginning a more thorough look at the habituation of ocular nystagmus, one further study might best be considered here. Fukuda, Hinoki, and Tokita[96] rotated unrestrained, blindfolded leghorns on perches. During accelerations, these birds showed the usual head deviation opposite to the direction of turn followed by an appropriate head nystagmus. Upon stopping, the head deviation and nystagmus were in the opposite direction. In tests following repeated exposure to rotation in both directions, the birds still showed a head deviation opposite to the direction of acceleration, but now nystagmus was very brief; moreover, this attenuated nystagmus was followed by a deviation of the head in the direction of the turn. The head remained in this position until rotation ended; the head then

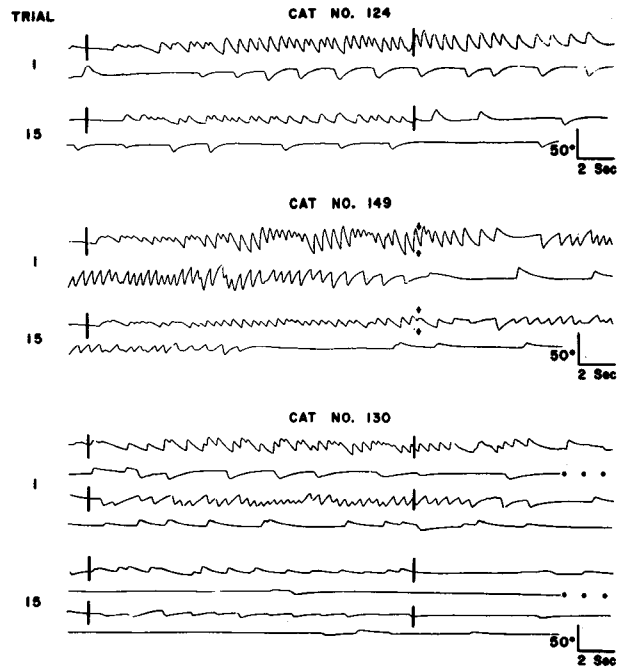

FIGURE 4. Equal rates of repeated accelerations and delecerations produce equal reductions in both dinections of nystagmus (cat no. 130). Responses need not be permitted to run their course in order for the reductions to occur; cat no. 149 received 15 accelerations which were followed within 0.6 seconds by decelerations (arrows). Cat no. 124 shows the usual reduction in all phases of the nystagmus response as a result of 15 unidirectional stimulations; strong secondary nystagmus is also evident during the first trial. Vertical bars demarcate the stimulus periods; dots in the lower tracings indicate approximately 80 seconds of recording not shown.[47]

deviated even further in the direction of the previous turning, a brief nystagmus occurred, and the head returned to the mid-line. These opposite reactions, conditioned by practice, were accompanied by improved equilibrium during rotation.

As noted earlier, Maxwell, Burke, and Reston[160] reported reductions of ocular nystagmus from rabbits as a result of repeated rotation with vision permitted. Maxwell,[159] Pilz,[179 180] Lumpkin,[155] and Henderson[130] confirmed this finding. Maxwell and Pilz[161] compared nystagmic reductions for groups of rabbits (their heads apparently were fixed) rotated in the light and total darkness. A greater percentage of decline in number of eye movements was obtained for the latter group. However, these findings simply reflected the results of the habituation series and optokinetic stimuli were present throughout the

light trials. Henderson[130] noted that rabbits which no longer showed after-nystagmus following repeated stimulation in the light would evidence a vigorous response if they were then blindfolded. Some further tests led him to agree with the conclusions of Mowrer[169] regarding the influence of optokinetic stimuli.

Maxwell, Burke, and Reston[160] also reported that, following habituation to rotation, rabbits gave "normal" responses to caloric irrigations. Hood and Pfaltz[140] made a similar observation with rabbits tested in the dark, and Collins[42] obtained the same results from cats. However, the animals' heads were fixed at different angles for rotation as opposed to caloric trials in the latter two investigations, and head position was not specified in the Maxwell, Burke, and Reston[160] study. It has been suggested[41 52 166] that differences in the orientation of specific and nonspecific gravi-receptors for the two types of test situations might account for the failure to obtain transfer of habituation from rotational to caloric stimulation.

Hood and Pfaltz[140] also reported that the response decline obtained by repeated rotation did not show recovery upon retest two weeks later. Other tests showed that the interval between stimulations did not affect the course of habituation, i.e., that the number of stimulations performed was critical regardless of the interval between tests.

More recent investigations have dealt primarily with ocular nystagmus from the cat and have probably effected better overall control of stimulus conditions. Although Prince[183] reported no change in the duration of after-nystagmus from cats subjected to over 1000 rotation tests, all later investigations show clear response reductions following repeated rotatory or caloric stimulation. In all of the studies cited below, the heads of the cats were fixed by special restraining techniques (almost invariably that of Henriksson, Fernandez, and Kohut[132]) and electronystagmographical methods were used to record eye movements. Unless otherwise indicated, rotatory stimuli comprised accelerations and decelerations separated by one to three minutes of constant velocity. Unidirectional rotatory stimulation involved deceleration at stimulus rates below the threshold for eliciting nystagmus.

Crampton and Schwam[70] and Crampton[68] reported a marked reduction of ocular nystagmus from cats during the course of a 12-trial series of angular accelerations in darkness. Auditory stimuli or electric shock interspersed throughout a trial produced only partial recovery of habituated nystagmus. The response decline occurred both within a 12-trial series and over the course of similar series administered once a week for six weeks. Fairly strong doses of d-amphetamine injected into previously untested cats appeared to produce a higher-than-normal amplitude of nystagmus throughout habituation trials, but the response showed the same form of reduction as that of undrugged cats subjected to the same tests.[68] The drug does not appear to affect the time-course of nystagmus.[56]

McCabe and Gillingham[163] reported no habituation of ocular nystagmus in anesthetized cats subjected to strong bidirectional stimuli (360°–720°/sec^2). However, unanesthetized cats showed marked reductions in the eye-movement response. Ablation experiments conducted on cats with suppressed nystagmus were effective in restoring nystagmus (i.e., releasing suppression) when the superior and lateral vestibular nuclei were destroyed; the releasing effect was most pronounced when both nuclei together were eliminated.

Crampton,[68] Collins,[42] and McCabe and Gillingham[163] have defined the reduction of nystagmus in the cat as an overall suppression. The greatest decline occurs within the first five stimulations; slow-phase eye velocity is sharply reduced, duration of the response becomes attenuated, frequency declines, and secondary nystagmus (a response which follows and is opposite in direction to the primary response[cf., 5]) begins earlier and is of lower output with stimulus repetition. The same effects occur with prolonged angular accelerations (36 seconds) and a progressively earlier peaking of the response with a declining output during angular acceleration becomes clearly evident with repeated tests.[56 118]

Crampton[66] also subjected groups of cats treated with d-amphetamine to a unidirectional series of six habituation trials in total darkness. An evaluation of pre- and post-tests which comprised stimulation in both directions led Crampton to conclude that habituation was directionally specific. Brown and Marshall[29] confirmed these results with d-amphetamine but reported com-

plete recovery of nystagmus after one week. They related the latter point to Fearing's[83 84] work on "massed" and "spaced" practice with pigeons and to a study by Brown[25] in which separate series of unidirectional angular accelerations in darkness were administered to groups of cats. The series for each group were presented at different intervals (one to 14 days). An additional series was given to all cats two weeks later, and a final series was presented one month after that. The acquisition of habituation occurred equally for all groups in spite of the different time between series, but recovery (partial) after rest intervals was clearly affected. Groups with the shortest intervals between series showed the most recovery; those with the longest intervals between series showed no recovery.

Response reductions were also obtained by Collins and Updegraff[62] from both cats and dogs subjected to unidirectional habituation trials in total darkness. Duration, frequency, and slow-phase measures of nystagmus all showed declines, with duration yielding the least reduction and slow-phase eye movement the most (see Figure 3). Responses to stimulation in the opposite direction were more vigorous, but such that the authors concluded that habituation might be only relatively specific to direction. Following one week of rest, only partial response-recovery was obtained.[62] Similarly, Winget and Smith[204] reported a reduction in the duration of ocular after-nystagmus from restrained chickens (eyes closed) repeatedly decelerated from 32 rpm. Winget, Smith, and Kelly,[205] however, indicated that such steady declines did not occur if animals were exposed to long periods of centrifugation (1.5–2.0g) between habituation stimuli. These authors suggested that centrifugation might alter the functional characteristics of the labyrinth by inducing structural or chemical changes.

Crampton[67] examined the influence on habituation of optokinetic stimuli (room lights were on during accelerations and for 30 seconds thereafter) during unidirectional rotatory stimulation of cats. Whether the optokinetic response enhanced (one group) or opposed (another group) the vestibular nystagmus, the same amount of habituation was evident in pre- and post-tests conducted in total darkness as occurred with a group of cats given the same habituation series (eight rotations) in total darkness.

Later, Crampton and Brown[69] reported that repeated unidirectional rotatory stimulation of the vertical semicircular canals (in darkness) had no effect on responses of the horizontal canals, i.e., there was no transfer of effects from vertical canal stimulation to the horizontal canals. Although these authors apparently did not record the vertical nystagmus, Collins[52] demonstrated habituation of all aspects of that response in a series of unidirectional habituation trials in darkness with the animals restrained and placed on their sides. Pre- and post-tests showed that the habituation was relatively specific to the direction of nystagmus elicited during practice and, moreover, was relatively specific to the position of the otoliths and other gravi-receptors (see Figure 5); the latter pre- to post-test comparison was accomplished by placing the animals on the side opposite that maintained during habituation (i.e., changing their positions by 180°), thereby stimulating the same set of canals, but with the otoliths and other gravi-receptors in a new position. A similar study by Collins and Updegraff[63] demonstrated in parrots the same possibility of the specificity of habituation of vertical canal responses to the position of gravi-receptors.

Collins[47] noted no significant effect on habituation of nystagmus in darkness when physically equivalent accelerations and decelerations followed each other within less than a second, i.e., the deceleration stimulus was applied during the peak of the nystagmic response to acceleration, thereby interrupting that response; nystagmus occasioned by deceleration was permitted to run its course. Habituation was obtained for both directions of response (evaluated in separate unidirectional pre- and post-tests) and was of the same magnitude as that obtained both from a group of cats exposed to 2-minute periods of constant velocity between accelerations and decelerations (both directions of response were permitted to run their course) in a similar habituation series, and from another group which received unidirectional habituation (subthreshold decelerations). The latter group also confirmed the relative directional specificity of habituation (see Figure 4).

B. *Nystagmus: Caloric-Induced.* With the exception of Dunlap's[81] use of unilateral ice water irrigations with two rabbits, caloric hab-

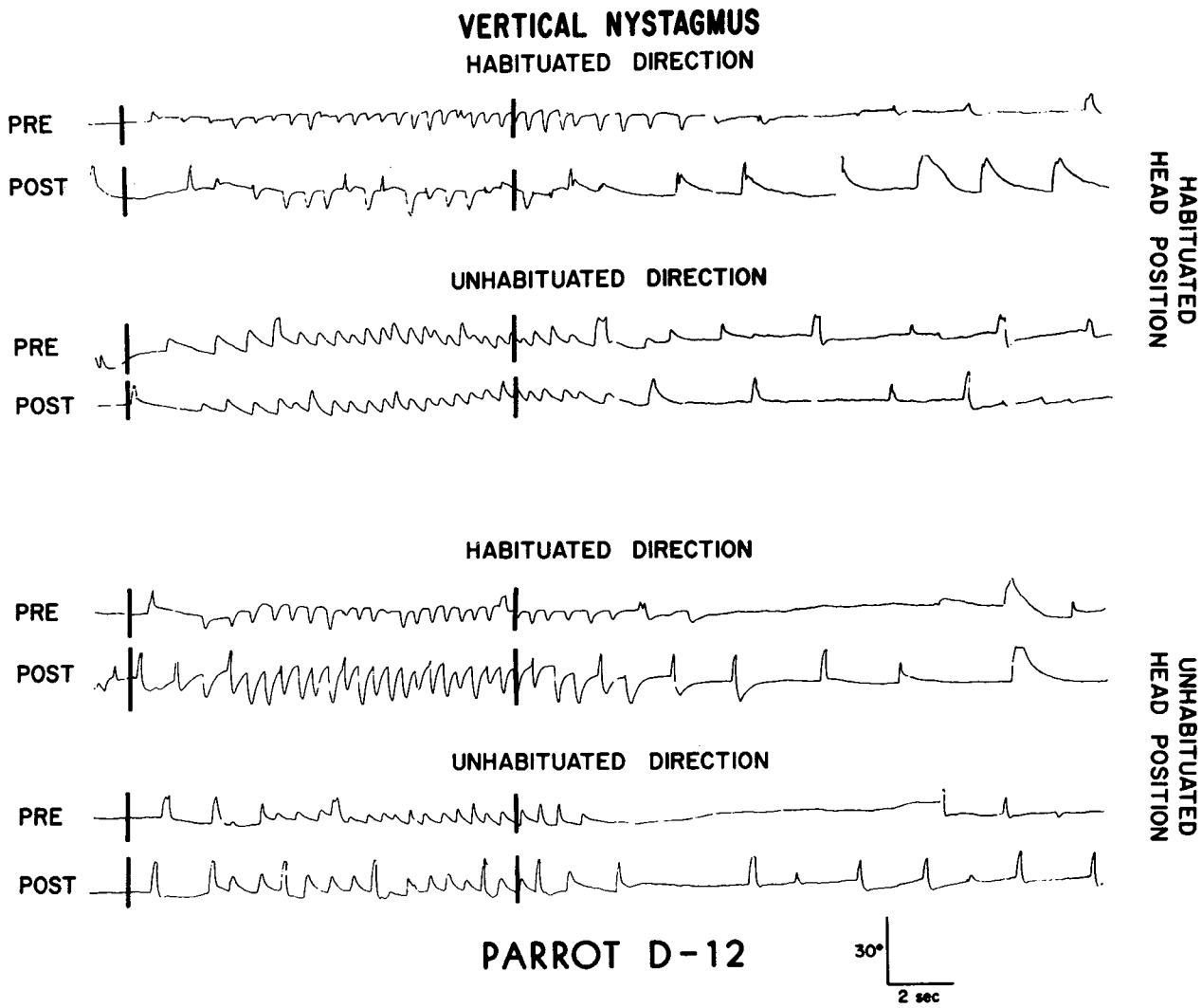

FIGURE 5. Specific and non-specific gravi-receptors interact with the semicircular canals in the reduction of vertical nystagmus by repeated rotation of birds[63] and cats.[52] The ocular tracings above were obtained from a parrot which was exposed to 15 unidirectional accelerations with its head and body fixed in a "beak down" position. Pre- and post-tests involved both directions of rotation with the beak down (habituated head position) and both directions of rotation with the beak up (unhabituated head position). Nystagmus reduction was relatively specific to both the head position used and the direction of nystagmus elicited during the habituation series. Vertical bars demarcate the acceleration period; a calibration marker appears at the bottom right of the chart. (Reprinted with permission from *Acta Otolaryngologica.*[63])

ituation studies of animals have been largely restricted to cats. Dunlap[81] calorized a single ear of each rabbit in the light three times daily every other day for a total of 39 to 48 trials. No ocular nystagmus was elicited following the 24th trial in one animal and the 33rd trial in the other. Retests a month later showed recovery; nystagmus was obtained during the first five to six days of this new series which was continued for one to two months. The opposite ear was then irrigated and yielded some response, but the reaction was clearly weak; several days of irrigation eventually abolished this nystagmus. The rabbits next were rotated and showed no nystagmus to stimulation of the horizontal or of the vertical (animals were placed on their sides) semi-circular canals. Retested six months later, the rabbits showed no caloric nystagmus, but both gave vigorous responses to rotation. The heads of the animals may have been in the same plane for both caloric and rotatory stimulation.

Henriksson, Fernandez, and Kohut[132] calorized cats in the light and reported a reduction of nystagmus (particularly maximum eye-speed)

following several stimulations. In another study which permitted vision,[133] 10 irrigations, alternately warm to one ear and cool to the other (each driving nystagmus in the same direction), produced more habituation and at a faster rate than that obtained by 10 irrigations of one ear with a single temperature of stimulus; a following irrigation drove nystagmus in the opposite direction and produced vigorous nystagmus, i.e., there was no transfer of habituation to the unpracticed direction of responses. In another series of tests, cats were given 10 irrigations of one ear alternately with cool and warm water; another group received a single temperature of stimulus alternately to each ear. Both procedures reduced maximum eye velocity, but the second procedure seemed more effective, in agreement with the related finding noted above. Further tests showed that the same pattern of habituation was obtained whether 10 irrigations were separated by 5-minute intervals or by 24-hour intervals, and that response declines persisted for two to three weeks. Transfer of unidirectional habituation was extensively examined. Different groups were given 10 calorizations of a single ear with cool or with warm water; the same ear was then irrigated with the opposite stimulus temperature (driving nystagmus in the unpracticed direction); normal responses were obtained. Other animals received 10 cool stimuli in the right ear and then, in separate tests, warm water to the same ear and both warm and cool water to the left ear. Non-equivalent stimuli (i.e., stimuli which would drive nystagmus in the unpracticed direction) produced vigorous responses, regardless of the ear tested; equivalent stimuli produced a reduced response. When animals were given 10 irrigations alternating warm and cool water to one ear or using cool water alternately presented to each ear (in both cases, nystagmus was driven alternately to the left and the right) a bidirectional decline was obtained and any following irrigation stimulus (cool or warm applied to either ear) revealed complete transfer of habituation. Fernandez and Schmidt[86 87] noted that the reduction of nystagmus was particularly apparent in the frequency of eye movements and in velocity of the slow and fast components, while duration and amplitude of nystagmus might not be affected. Habituation was also obtained from cats with total ablation of the necortex, with unilateral or bilateral ablation of the temporal lobes, and with hemidecortication.[86 87]

Proctor and Fernandez[184] examined blindfolded cats with unilateral irrigations and obtained a clear response decline in frequency and amplitude of nystagmus (the latter was not obtained in the studies which permitted vision), and in the velocity of both the slow and fast components. After habituation, blindfolds were removed and an additional test was conducted. Neither direction, nor frequency, nor total number of eye movements was affected (i.e., they were still at the habituated level), but both amplitude and velocity of nystagmus were increased. Pre- and post-tests indicated transfer of habituation for an equivalent stimulus presented to the non-habituated ear; non-equivalent stimuli presented to either ear showed some response reduction (partial transfer). Tests conducted two to 12 days later showed only partial response recovery.

Collins[41] confirmed the response reduction with unilateral caloric irrigations in the dark and noted that the greatest decline occurred within the first five trials. The relative directional specificity of reduction was also confirmed by use of equivalent and non-equivalent unilateral stimuli following habituation. Further, unidirectional rotation tests in total darkness, conducted before and after the habituation series, showed only a small change in nystagmic output. Thus, contrary to Dunlap's[81] findings with rabbits, the response decline following caloric stimulation did not show significant transfer to rotational stimuli. However, the animals' heads were positioned differently for the two stimulus conditions in Collins'[41] study.

In other transfer experiments, Capps and Collins[33] and Mertens and Collins[166] employed both bilateral (simultaneous stimulation of one ear with warm, and the other with cool water) and unilateral irrigations in total darkness. A 15-trial series produced significant decrements in slow-phase eye movement and frequency of nystagmic beats (duration was not markedly affected) for either unilateral or bilateral stimulation (see Figure 6). Retention tests were conducted one to four weeks later and showed partial recovery which appeared somewhat greater after four weeks than after two weeks; however, nystagmus appeared to decline more

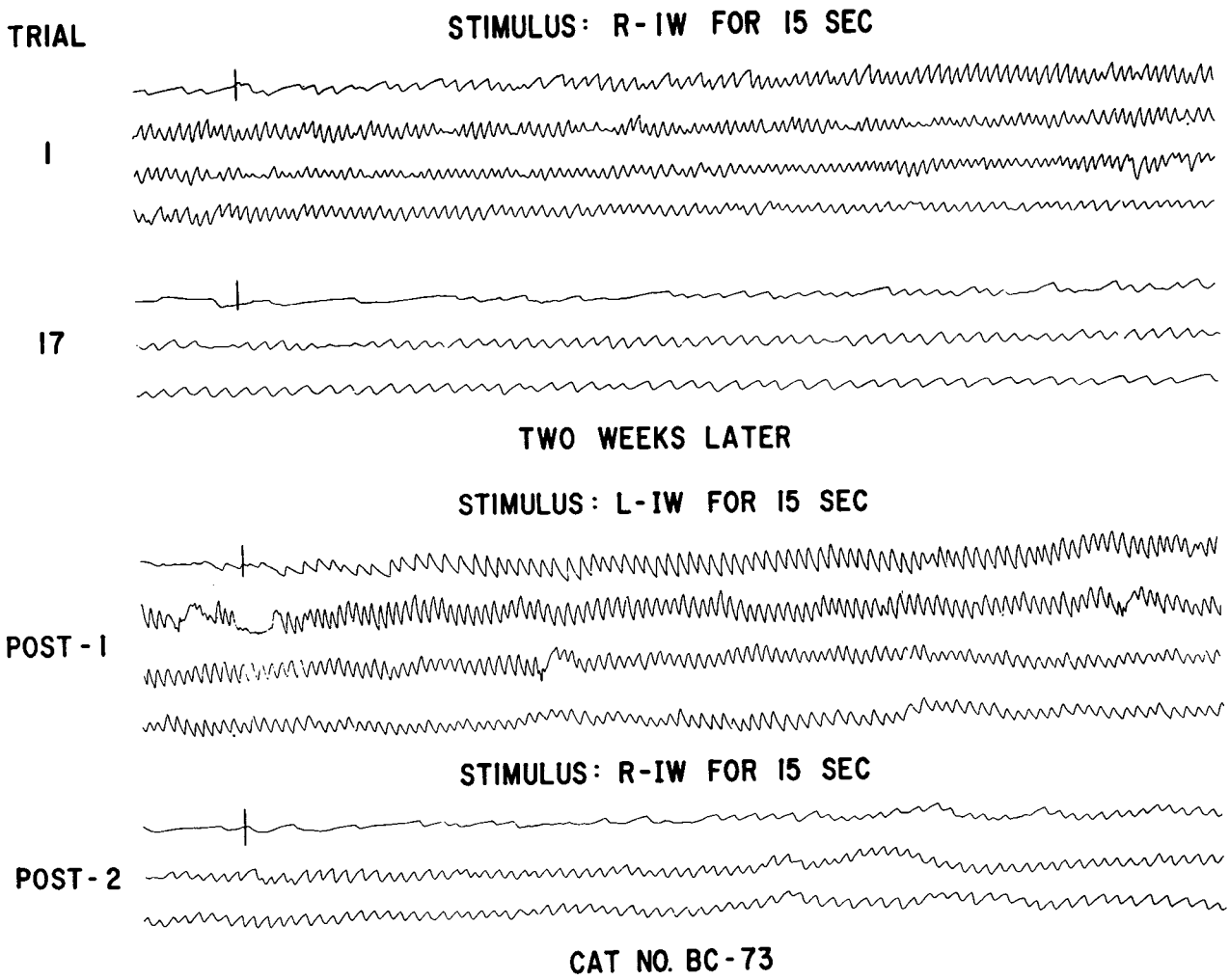

FIGURE 6. Caloric nystagmus during the first and last trials of a 17-trial series of unilateral ice water irrigations of the right ear. The response is clearly reduced following the caloric habituation series. After two weeks, there is some recovery of the responses from the right ear, but the directional specificity of the reduction is still evident when comparisons are made with responses from the left ear. Vertical bars indicate the end of the irrigations; optokinetically-obtained calibration markers appear at the right, below each pair of tracings. (Reprinted with permission from *Acta Otolaryngologica.*[33])

rapidly with several repetitions of the retention-test irrigations. In examining transfer, Capps and Collins[33] gave three groups of cats a pre- and post-test comprising a mild unilateral stimulus (26° C. to the right ear); one group received an habituation series of 15 such irrigations, the other two groups received a bilateral series (26° C. to the right and 50° to the left ear) of 15 habituation trials for a duration of 25 seconds in one case, and 30 seconds in the other (increasing the duration of a bilateral stimulus up to at least 30 seconds produces a stronger nystagmus[50]). Responses to the post-test unilateral stimulus were reduced to an approximately equivalent level for all three groups. Thus, habituation to bilateral calorizations transferred to a unilateral stimulus of less intensity. Similarly, three new groups received a strong unilateral stimulus (ice water) during pre- and post-tests; one group was exposed to unilateral ice water habituation, the other two were habituated with bilateral irrigations of 15 and 20 seconds duration, respectively. Although bilateral stimuli produced weaker responses initially than did the unilateral ice water irrigation, responses to the post-test unilateral stimulus were reduced approximately equally for all groups. Thus, habituation to bilateral calorizations transferred completely to a unilateral stimulus of greater intensity.[33] Further, no effect of the

habituation series was evident for optokinetic responses (rotation of a striped drum).

Later, three different intensities of unilateral stimulation were applied to three groups of cats in a 15-trial habituation series.[166] Pre- and post-tests indicated that all of the unilateral habituation stimuli produced as great a response reduction to bilateral caloric stimuli as did a series of 15 bilateral irrigations. Thus, unilateral caloric habituation transferred to bilateral caloric stimulation. Additional pre- and post-tests involved rotation. Bilateral caloric habituation appeared to have relatively little effect on responses to rotation. Similarly, a group of cats exposed to a series of unidirectional rotations were given pre- and post-tests with bilateral calorizations (all driving nystagmus in the same direction): habituation was obtained to the rotatory stimulus, but no significant effects on caloric nystagmus were obtained.[166] These results confirmed previous findings by Collins[41 42] which showed relatively little inter-modal transfer of habituation (head position was different for caloric and rotational trials in these studies), but did not agree with Dunlap's[81] results.

A study by Collins[44] examined the effects of "double irrigations" (simultaneous binaural irrigation with water of equal temperatures) on habituation in the dark. The "double irrigation" drives the cupulae in opposite directions, thereby cancelling horizontal nystagmus (weak vertical nystagmus may sometimes be produced, cf.,

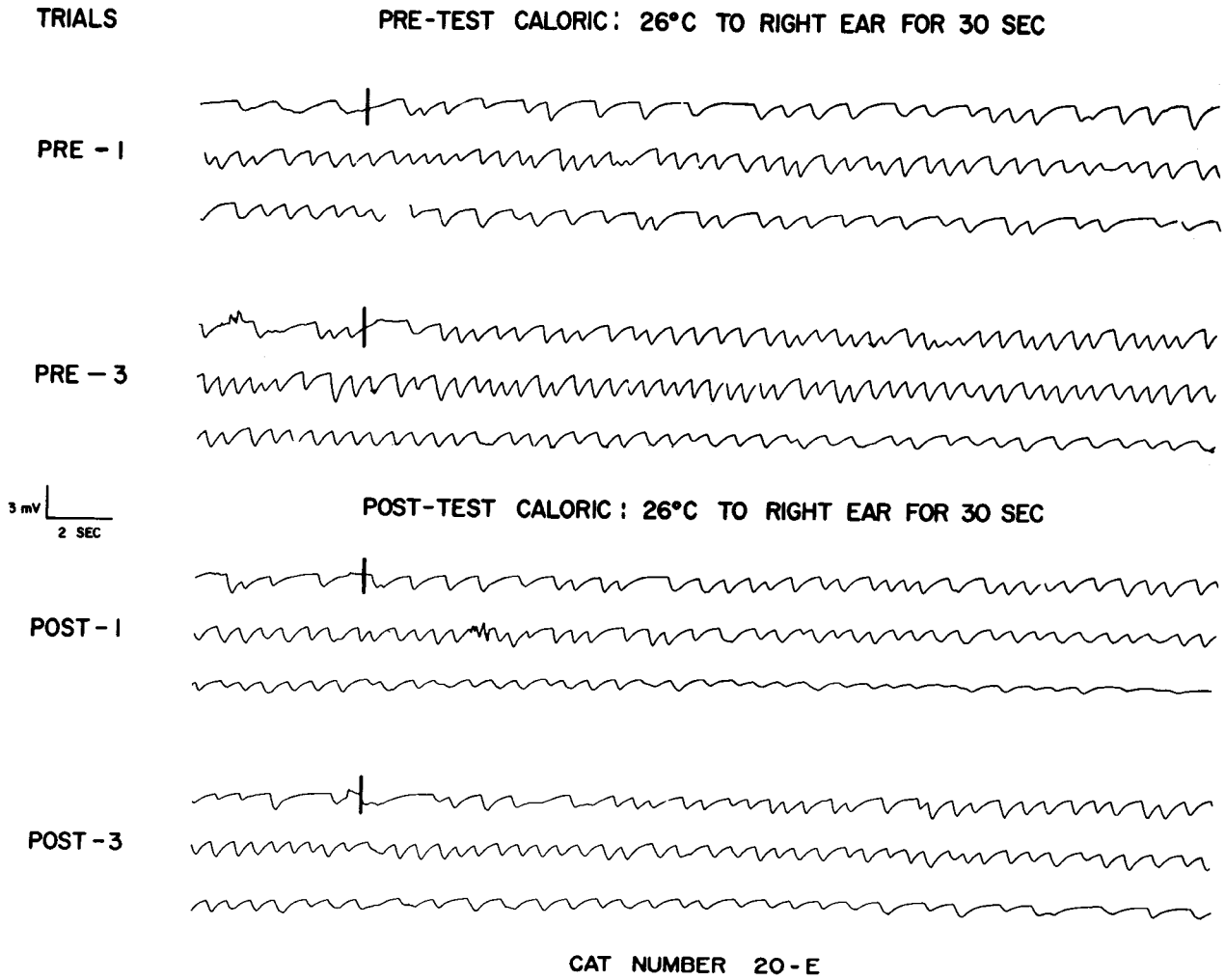

FIGURE 7. Repeated peripheral stimulation does not necessarily cause a reduction of vestibular nystagmus. The tracings depicted above are from a cat which received 15 "double irrigations" (administration of 26° C. water to both ears simultaneously) between the unilateral pre- and post-tests. Vertical bars denote the end of the irrigation period; all trials were in total darkness. (Reprinted with permission from *Acta Otolaryngologica.*[44])

Riesco-Mac-Clure[186]). Pre- and post-tests with unilateral irrigations of the same stimulus temperature indicated that the series of "double irrigations" produced no nystagmic habituation (see Figure 7).

V. Survey of Studies of Man.

A. *Nystagmus: Rotation-Induced.* As noted earlier, Ruppert[189] and Bárány[10] reported a unidirectional reduction of nystagmus from dancers who habitually whirled in one direction. In more recent times, Fukuda, Tokita, Hinoki, and Kitahara[98] have cited shorter-than-normal durations of nystagmus not only for dancers but for athletes as well. School boys[98] and gymnasts[188] involved in vestibular programs of self-stimulation in play activities or prescribed physical training are reported to show progressively attenuated nystagmus which is interpreted as an improvement of the labyrinthine function by training; athletic ability is concomitantly enhanced.[98 188]

In laboratory studies, Griffith[106] rotated subjects (including himself) in the light and reported attenuation of the duration of nystagmus and of the number of eye movements both within a daily series of tests and from day-to-day; only minor recovery was evident after two months of rest. He also noted that, when a rotating subject was stopped and then moved back one-quarter turn, a markedly reduced nystagmus duration was obtained (this probably has implications for "head-free" rotation studies of animals). Four years later, with no intervening tests, Griffith[107] conducted another series of rotations on himself in the light and reported some recovery of nystagmus duration and number of eye movements (the response had been abolished after 135 trials in the earlier study), but the nystagmus was not as vigorous as it had been initially and now only 35 trials were required to abolish the response.

Six subjects in another study[104] were given a daily series of rotations. After-nystagmus was timed in the light following one revolution of the turning device; when subjects no longer showed any nystagmus, the number of revolutions was increased to two, then to three, and so on. Progressively more trials were required to inhibit after-nystagmus completely as the number of revolutions increased from one to two, two to three, and so on to nine to ten. None of the subjects experienced vertigo at any time and, at the end of the study, none showed past-pointing. Griffith[103] also reported that visual far-fixation after a brake deceleration produced twice the duration and frequency of nystagmus as did near-fixation. Subjects with their gaze directed laterally (in the direction of the fast-phase) showed an enhanced duration, but this, too, became attenuated with repeated practice. Preventing visual fixation (e.g., with 20-diopter lenses) doubled the duration of after-nystagmus. However, even in the absence of visual fixation, duration of nystagmus declined with repeated elicitation.

Holsopple[137] reported attenuation of after-nystagmus with repeated practice in the light for several rates of deceleration. Subjects were then rotated while wearing 20-diopter lenses and, although they showed an increased nystagmus time, durations were still below initial reactions. One subject was then blindfolded and the duration of his sensation timed; it showed little difference from pre-habituation levels. Holsopple[137] also reported that rotation in the opposite direction yielded vigorous after-nystagmus. He attributed this to the fact that acceleration and deceleration stimuli were not separated by a sufficient period of time. He restated this view in another paper[139] and particularly emphasized the importance of nystagmus running its course (i.e., that the response must not be interrupted by an opposing stimulus) for habituation to occur. More recently, Brown[26] obtained significant response reductions for both directions of nystagmus during a series in which accelerations were immediately followed by decelerations in total darkness. Collins[47] reported a similar finding with cats; however, the form of the habituated response curve appears different in comparing cat and man. Holsopple[138] also noted that nystagmus time may be seriously affected by position of the head and that "practically every subject exhibits some tendency toward head movements during rotation."

Dorcus[77] rotated a group of subjects with heads fixed, and another with heads free. Duration of after-nystagmus was observed during 50 rotations over a 10-day period. For both groups, duration declined with repetition; responses in the opposite direction, however, were not affected. The "head-fixed" group clearly showed a greater reduction than did the "head-free" group. Ad-

ditional trials were then conducted by fixing the heads of those previously rotated with heads free, and freeing the heads of those previously rotated under the "head-fixed" condition. The response-level which had been reached at the end of the habituation series was not changed by changing the head condition. Dorcus[77] concluded that the two types of habituation were different.

Mowrer[170] braked subjects to a stop from 12 rpm and observed the duration of after-nystagmus. During 12 trials, in a room with striped walls, subjects were alternately required (1) to keep their eyes always open, and (2) to have eyes closed during rotation but open when the chair stopped. The latter condition produced greater after-nystagmus than the former, but no decrease with repetition, while the former condition produced some reduction of response duration. Mowrer[170] then gave another series of 12 rotations to two groups of subjects. Trials were alternately conducted with (1) eyes closed during rotation but open when the chair stopped, and (2) eyes open and the subject fixating on the top of his finger (one group) or eyes open but a drum over the subject's head (the other group). Both of the latter conditions prevented optokinetic nystagmus and permitted visual still-fixation. There was no difference among the conditions with respect to duration of after-nystagmus. Mowrer[170] concluded that the reduction of after-nystagmus was due to the post-stimulus persistence tendency of the optokinetic response (i.e., optokinetic after-nystagmus).

Dodge[74] conducted the first extensive habituation study in which visual stimulation was excluded by subjecting himself to over 600 rotation trials during a 6-day period. Using sudden starts and stops separated by approximately 15 seconds of rotation at 20 rpm, he recorded nystagmus with eyes closed and reported abolition of the response to deceleration. By changing the direction of rotation, he found a 50% reduction of nystagmus from pre-habituation levels. However, there were complicating factors present: decelerations were introduced while the response to acceleration was still in progress, and alertness was probably uncontrolled. With respect to the latter, Dodge[74] noted that "the rotation experiment had a soothing soporific character . . . (that) did not carry over into reversed rotation or accidental interference with the customary speed."

Cupulometric data from 320 normal subjects tested with Frenzel-type glasses were obtained by Aschan, Nylen, Stahle, and Wersäll.[8] Duration of nystagmus was directly observed. Using four to six stimulus rates, the authors noted a directional preponderance which depended upon whether subjects were first rotated to the right or to the left for each stimulus rate. The durations of nystagmus to the first direction of rotation were significantly longer than those obtained to the second direction of rotation for all but the highest stimulus value (52°/sec). No such effect was noted for the duration of the after-nystagmus.

Suzuki and Totsuka[194] used standard cupulometric procedures, and recorded nystagmus from behind closed lids. Subjects were given a series of 10 or more abrupt stops from constant velocities of five or of 10 rpm. No decline in response duration was reported for the higher stimulus rate, while the lower rate showed considerable trial-to-trial variation; in addition, irregular nystagmus was frequently associated with the shorter durations (probably due to arousal factors). However, Fluur and Mendel[93] reported a reduction in the duration of recorded nystagmus (closed eyes) after 10 to 12 brake decelerations from 14 rpm. No technique for controlling alertness of the subjects was noted. Additional subjects were braked to a stop from 5 rpm, but no indication of habituation was evident after 10 trials. Unilateral caloric stimuli administered before and after the 15 rpm rotation series showed reduced durations for the direction of nystagmus elicited during the habituation series, and a longer nystagmus time for the opposite direction in most subjects. Several subjects showed a pre- to post-test decline in duration to all unilateral caloric stimuli. Similar results were reported by Pfaltz and Arx[177] who obtained a reduction in nystagmus during the course of 10 unidirectional rotations in darkness. Post-tests elicited both directions of nystagmus and showed a preponderance favoring the non-practiced direction; the difference was still evident two weeks later.

Collins[43] gave 10 subjects each a series of 200 unidirectional accelerations (decelerations were subthreshold) over a 10-day period. Nystagmus was recorded with eyes open in total darkness and subjects were assigned a variety of tasks to be performed during stimulation. Tests con-

ducted the day before and the day after the habituation series indicated that there was not so much a decline in nystagmus as there were changes in the form of the response. Specifically, for the "practiced" direction, slow-phase eye displacement declined (30%) throughout the response. However, the number of eye movements increased throughout the stimulus period and for several seconds thereafter (although total frequency showed a slight decline); the response also appeared more regular and perhaps better "tuned" to the stimulus (see Figure 8). These changes were somewhat greater for the "practiced" direction, but were clearly evident for both directions, and were still present one month later with no intervening trials.

Wendt[203] reported a similar finding using oscillatory stimulation: with repeated testing (subjects' eyes were closed), the amplitude of slow-phase eye movements declined and the number of fast phases increased until, finally, the original form of the nystagmus was lost. Both Collins[43 51] and Wendt[203] have noted that repeated elicitation of nystagmus from alert subjects in darkness produces, as one major effect, increasingly greater fast-phase activity which modifies the form of the response until, conceivably, the nystagmic aspect may no longer be evident following a very large number of stimulus repetitions. More recently, Torok[197] and Johnson and Torok[143] noted an increased frequency of nystagmus following repeated angular stimulation.

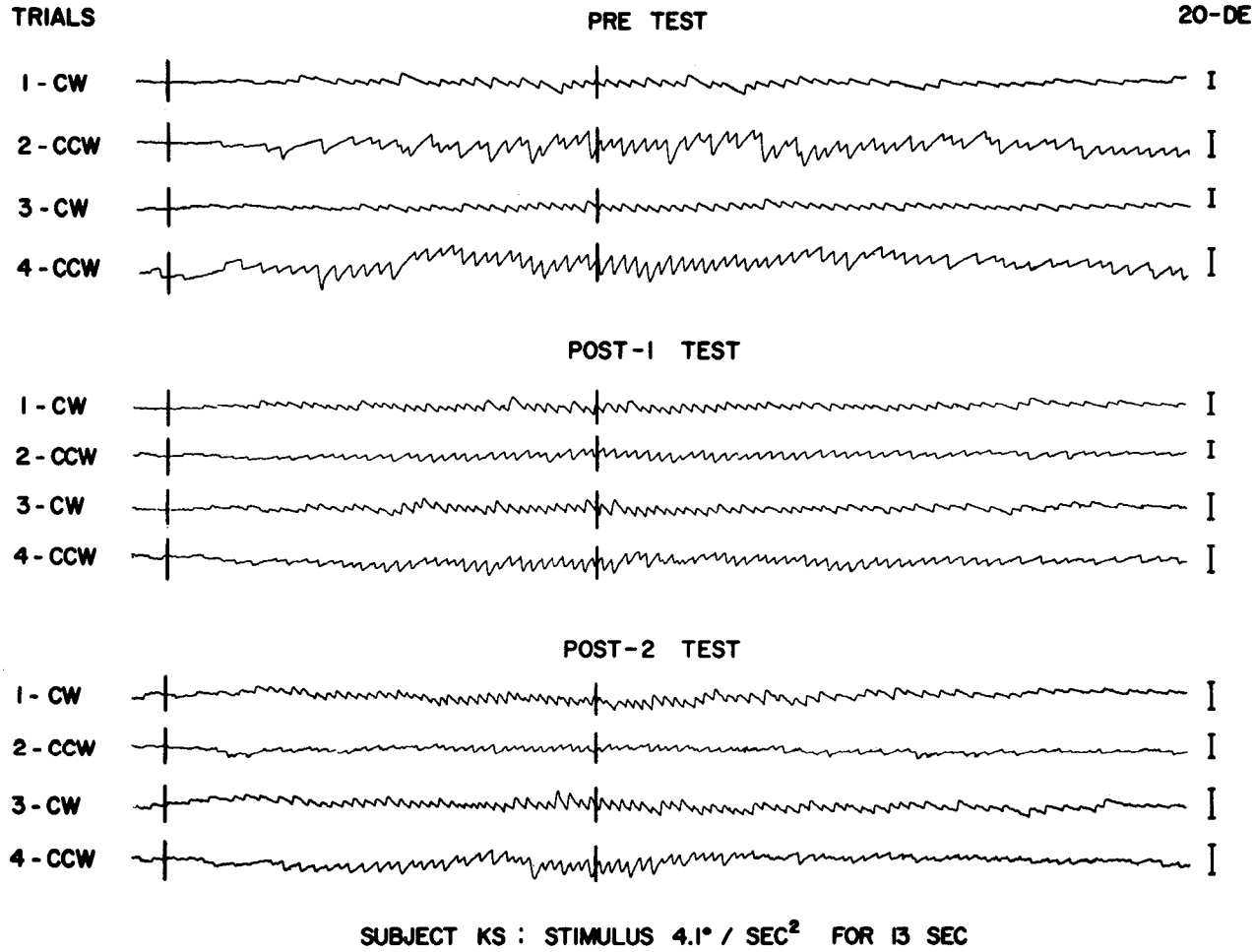

FIGURE 8. Tracings of nystagmus obtained from a subject performing mental arithmetic with eyes open in darkness. A 10-day series of 200 CW accelerations (all decelerations were subthreshold) occurred between the pretest and the post-1 test and produced an increase in the frequency of eye movements. Post-2 tests were conducted one month later with no intervening trials. Vertical bars demarcate the period of acceleration; 20° calibration markers are at the end of each tracing. (Reprinted with permission from *Acta Otolaryngologica.*[43])

Perhaps the most striking examples of the effects of repeated angular accelerations on human nystagmic responses may be found with figure skaters. Skaters have been regarded both anecdotally and as the result of some evaluations[162 168] as having acquired considerable or complete vestibular suppression as a result of their spinning experiences. When tested in total darkness, however, skaters gave vigorous nystagmic responses to a variety of angular stimuli.[46 51] When compared with ordinary subjects tested in the laboratory (in total darkness), the skaters showed significantly less slow-phase eye displacement and as high or higher a frequency of nystagmus during the early part of the response than did the ordinary subjects.[51] Tracings also appeared more regular for the skater group. These comparisons between skaters ("practiced" subjects) and non-skaters ("unpracticed" subjects) show considerable similarity to the findings discussed earlier in which pre- to post-test comparisons of the same subjects were made after 200 unidirectional rotations.[43] Apparently most figure skaters spin CCW on ice (there are notable exceptions, and few, if any, either practice or develop a facility for spinning well in both directions. Since their on-ice spinning rate is too high to permit "visual spotting," they use visual fixation almost invariably during one direction of eye-movement (i.e., following deceleration). However, no consistent directional differences appeared for skaters in duration of nystagmus, slow-phase eye displacement, or frequency of eye movements as a result of angular acceleration in total darkness.[51]

These results indicate that vestibular nystagmus (in the absence of visual stimulation) is not readily suppressed in alert subjects as a result of considerable experience with angular accelerations, whether that experience occurs in darkness or with opportunities for visual fixation. The response appears modified, but in a dynamic fashion rather than as the result of an overall suppression.

As noted earlier, Wendt[202] claimed that nystagmus generated in total darkness would not be abolished in alert subjects. However, he indicated that, with opportunities for visual fixation, the visual stimuli would eventually become predominant and markedly interfere with nystagmus. A number of studies in which subjects were allowed opportunities for visual fixation have reported significant declines (or abolition) of nystagmus.[77 106 138 139] Perhaps the best example of such habituation can also be found with figure skaters. Both in the laboratory (caloric and rotational stimulation) and following on-ice spins, skaters demonstrate almost total suppression of vestibular nystagmus when they have fixed visual references.[46 162] The longest duration of nystagmus recorded (by means of telemetry) from skaters following on-ice decelerations from 235–278 rpm was about five seconds; other skaters gave just a few beats of nystagmus before

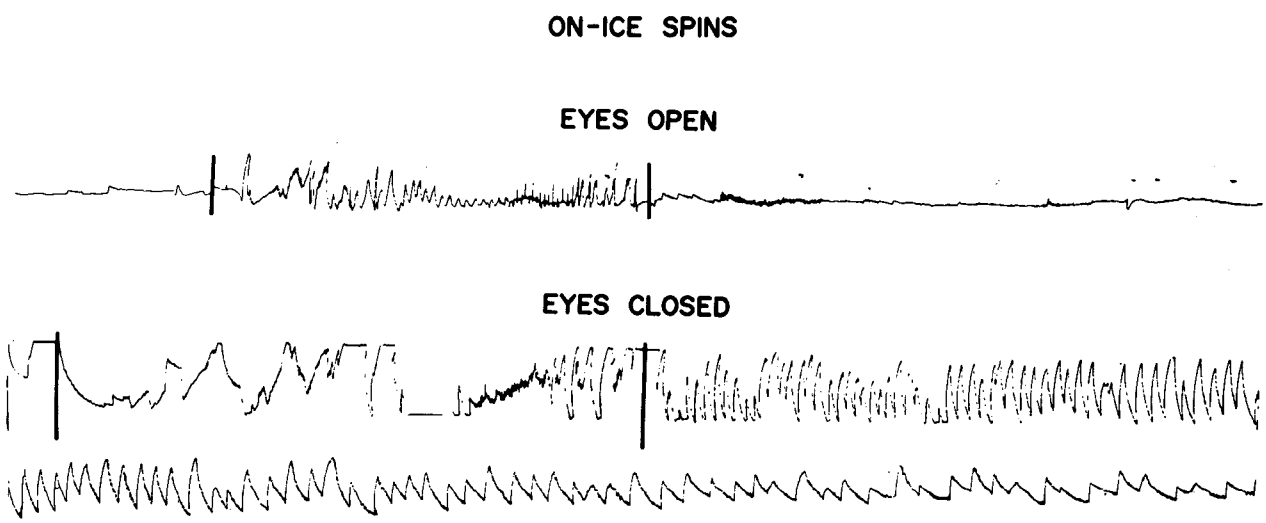

FIGURE 9. Eye-movement tracings obtained by means of telemetry during on-ice spins performed by a figure skater. Each strip of tracings represents 33 seconds of recording. Vertical bars demarcate the period of spinning. After-nystagmus is markedly suppressed during visual fixation.[cf., 46]

visual fixation terminated any apparent eye movement.[46] However, removal of the opportunities for visual fixation by means of eye closure would reinstate a vigorous nystagmic response (see Figure 9). More recently, Fukuda, Tokita, Aoki, Watanabe, Hishida, Tashiro, Miyata, and Mazuoka,[97] Osterhammel, Terkildsen, and Zilstorff,[174] Dix and Hood,[73] and Tokita, Aoki, Watanabe, and Miyata[196] reported no after-nystagmus (or only a beat or two of eye movement) from ballet dancers whose eyes were open following their pirouettes, but vigorous nystagmus when their eyes were closed. Previously, Tschiassny[199] had noted that a post-rotatory nystagmus could be obtained from a ballet dancer if "visual spotting" was not permitted.

The findings with figure skaters might lead one to conclude that total or almost total suppression of nystagmus may require repeated vestibular stimulation with opportunities for visual fixation. Such suppression is visual inhibition of the response rather than vestibular inhibition, and the ability to exercise substantial control over vestibular eye movements does not seem to generalize completely to situations in which vision is not permitted.* In fact, one study[27] reported no influence on nystagmic responses in darkness of several types of visual stimulation during repeated rotation (a small, dim target light, an illuminated enclosure, and full room lighting). However, the habituation series for the several tested groups comprised only six trials for a given direction of nystagmus and the angular accelerations used (24°/sec^2 for 10 seconds) induced incidents of nausea and vomiting when either the room or the enclosure was lighted.

In evaluating the relative lack of generalization of eye-movement control by figure skaters from the on-ice condition (vision permitted) to the laboratory situation (vision excluded), several factors must be considered: (1) during on-ice spins skaters actively coordinate control of rotation, while in the laboratory they are passively rotated; (2) the stimulus rates during on-ice spins are considerably higher than those generated in the laboratory; (3) some laboratory findings with ordinary subjects[117] and with aerobatic pilots[3 4 32] show directionally specific effects related to visual stimulation.

With respect to the latter, Aschan[3 4] reported a directionally specific shortening of the duration of nystagmus (cupulometry) from fighter pilots, with the reduction related to the direction in which the pilots most frequently rolled their aircraft during various flight maneuvers. Caporale and Camarda[32] obtained a similar finding from acrobatic pilots using accelerations and decelerations of 1°, 3°, and 6°/sec^2 separated by 90 seconds of constant velocity at 15 rpm. Recordings from behind closed eyes showed a clear directional difference in intensity of nystagmus. Pilots who flew on the left during various aircraft formations (and therefore kept their heads turned to the right during flight to maintain visual contact with the aircraft ahead of them) showed weak left-beating and normal right-beating nystagmus. Pilots who flew on the right side of formations (with their heads, therefore, turned to the left) evidenced the reverse of this directionally specific difference. Other studies of pilots have not noted such consistencies.[22 23 178]

Guedry[117] controlled arousal by tasks and used total darkness during one direction of nystagmus (e.g., CW acceleration), while visual stimulation occurred during the other direction of the response (e.g., CW deceleration). Subjects were given 80 such rotation trials within a 4-hour period. Tests before and after the 80-trial series were conducted entirely in darkness; results indicated a pre- to post-test decline in slow-phase nystagmus of about 20% for the direction repeatedly elicited in darkness (in good agreement with the results obtained in darkness by Col-

* Generalization of nystagmic modifications from dark to light conditions is also minimal, at least after a short series of habituation stimuli. Marshall and Brown[158] rotated subjects in an illuminated enclosure before and after a series of 10 habituation trials employing identical stimulus rates. One group received the habituation series with the enclosure illuminated (and visual still-fixation possible), the other group was in total darkness. During all trials, subjects signalled their estimates of turning velocity. Both groups showed a significant reduction in slow-phase eye displacement during the habituation series. In the post-test (enclosure illuminated), the group habituated in total darkness showed no significant change in slow-phase output from the pre-habituation level; the group habituated in illumination, of course, had significantly reduced scores. This lack of transfer from "dark" to "light" conditions might be accounted for by the fact that, of itself, visual fixation on objects produces a marked decrease of the slow-phase excursion of the eyes, and the reduction obtained after a short series of rotations in the dark may not be sufficient to influence noticeably the greater attenuating effects of visual still-fixation.

lins[43]) and a pre- to post-test decline of about 50% for the direction of nystagmus repeatedly inhibited by visual stimulation.

The findings of Aschan,[3 4] Caporale and Camarda,[32] and Guedry[117] do not appear to agree with results obtained from figure skaters, who show equivalent nystagmus regardless of direction when tested in the laboratory, although on ice they make use of visual information only (or at least primarily) during deceleration responses. The lack of agreement may be due not only to active vs. passive rotation and to marked differences in stimulus rates, but also to the fact that the skaters do perform on-ice turning maneuvers in both directions and the rate of these turns (as opposed to rates during their free-style spins) may be equivalent to laboratory stimuli. In addition to these factors, (1) it is possible that visual stimulation may simply speed up the habituation process for the practiced direction of turn and, with many repetitions, transfer of the nystagmic response modification may become complete so that both directions of nystagmus are equivalently modified; and (2) the sensory pattern is different for skaters spinning on ice as compared with laboratory rotations. In the latter case, nystagmus was always elicited with the cupula in its resting position. On ice, skaters build up their acceleration until they feel it has reached its peak and then bring themselves to a stop; the deceleration (followed by visual still-fixation) is thus introduced with the cupula away from its resting position, perhaps at a point of maximum deflection.

All of the above has been concerned with what Guedry[117] has termed "simple vestibular stimulation," i.e., stimulation by angular acceleration about a vertical axis primarily of a single pair of semicircular canals. "Complex vestibular stimulation" may involve simultaneous activation of other pairs of canals and of specific and non-specific gravi-receptors. In this regard, mention should be made of studies involving rotation about a horizontal axis[14 15 64 65 116] and combinations of angular and centripetal accelerations.[18 48] Nystagmus is clearly affected by these conditions. In the former case, nystagmic eye movements did not cease during constant velocities ranging up to several minutes in duration, and a relatively abrupt termination of nystagmus and sensation occurred upon stopping. In the latter cases, the intensity, plane, and direction of nystagmus changed as centripetal acceleration increased with the lateral canals in the plane of rotation. Bergstedt[20 21] has shown that the intensity of both positional and caloric nystagmus is increased with increasing g: the latter finding was confirmed by Orlov[172] and by Yuganov,[209] with Yuganov also reporting a decrease in post-rotational nystagmus during weightlessness. Thus, it is clear from these and other studies[e.g., 52 63 164 175] that nystagmus can at least be affected by other motion- or position-sensing systems and, indeed, horizontal nystagmus can even be elicited by periodic linear accelerations.[171]

"Complex vestibular stimulation" can also be accomplished by means of simultaneous motion about more than one axis[cf., 136] or by active or passive head movements during rotary motion.[121 124] Such simultaneous stimulation of more than one pair of semicircular canals, the so-called Coriolis vestibular effect, produces (in addition to sensations) nystagmus with a predominantly vertical component. It should also be noted that there is a lack of congruency between signals from the semicircular canals and those from other sensory systems (e.g., otoliths and proprioceptors) under these unusual stimulus conditions. In examining the question of habituation, most "Coriolis studies" have been conducted with opportunities for visual fixation. Subjects have been permitted to move about freely in a rotating room,[121] or have made restricted head movements during rotation according to set procedures,[114 119 122] or have been exposed to passive movement (chair tilts) as well as making active head tilts.[80]

Subjects learn to adapt to the unusual vestibular effects produced by moving about in a lighted rotating room. During long-term studies (64 hours to 12 days) standard head-movement tests with control of arousal were introduced during the course of the prolonged rotational period as well as before and after rotation (i.e., with no rotation). Nystagmus was recorded in total darkness during these standard tests and showed an overall decline during rotation.[121] Following cessation of rotation (in a static situation) subjects demonstrated spontaneous compensatory nystagmus as a result of head movements.[115 121] That is, following the adaptation period, while at a standstill, standard head movements produced a nystagmus opposite in direction to that which should have occurred had the same head

movement been made during rotation. Retention and transfer of habituation effects were examined by Guedry,[115] who tested subjects in darkness before and after a 12-day exposure to living in a CCW rotating room. A clear attenuation of nystagmic responses to head tilts during CCW rotation was obtained in post-habituation tests; little pre- to post-test change was obtained for head tilts during CW rotation. Additional post-tests were conducted two days, three weeks, and three months later. Nystagmic responses to head movements during CCW rotation showed progressive but incomplete recovery; however, nystagmus obtained as a result of head movements during CW turning fell well below the pre-test values in these later tests, to a level approximately equal to CCW responses, as if to establish a balance at the habituated level.

Studies of Coriolis effects with restricted head movements (in one quadrant of the frontal plane only) have been of shorter durations (four to seven hours). Although a large number of head movements was made in the lighted room by the subjects, no spontaneous compensatory nystagmus was obtained following the rotation periods.[119 122] However, standard head-movement trials in darkness during rotation were conducted after about 200 head movements in the light and showed a general pre- to post-test suppression of nystagmus for the practiced direction of head movement, but there was no effect of the habituation trials on nystagmus generated by head movements in the unpracticed quadrant.

Further research confirmed and expanded these findings. Guedry[114] had a group of subjects tilt their heads and return them to upright at set intervals with their eyes closed. Other subjects performed the same head movements but were required to solve problems with multiple-choice answers which were projected on a screen during the head movements. All head movements were made in a single quadrant with most subjects completing 100 tilts and 100 returns. Before and after the 100-cycle series, subjects performed mental tasks in darkness and made head movements in both the practiced and unpracticed directions. A clear pre- to post-test reduction in recorded nystagmus (approximately 70%) occurred in the practiced quadrant for subjects who performed the visual problem-solving tasks; the unpracticed quadrant showed only a 15% reduction. A similar quadrant-specific reduction was evident in pre- to post-test comparisons for the group which had performed the head movements with eyes closed, but the reduction in the practiced quadrant was only about 12%; the unpracticed quadrant showed essentially no pre- to post-test change.

B. *Nystagmus: Caloric-Induced.* Although angular acceleration is the adequate stimulus for the semicircular canals, the most frequently used method of eliciting nystagmus in clinics is that of thermally-produced endolymph movement in the canals. The recommended procedure is to use water of temperatures 7° C. above and below body temperature.[88] Cool water (30° C.) drives nystagmus (fast-phase) away from the irrigated side, warm water (44° C.) drives it toward the irrigated side. Although the stimulus is a gross one, it has the advantage of permitting the testing of each ear separately.

Almost all studies of the effects of repeated caloric irrigations on nystagmic reactions have involved unilateral stimulation. Loch and Haynes[154] timed nystagmus from subjects wearing Frenzel glasses and reported no decline as a result of irrigations performed once daily for five to six days, although they noted a change in the form of the response (nystagmus became more regular). With subjects' eyes closed, Stahle[193] found no clear response decline for four irrigations, two of which drove nystagmus to the left and two to the right. However, he noted that dysrhythmia might occur with repeated stimulation. Lidvall[149 150 151 152] performed a series of studies which indicated that a relatively small number of stimuli (four to six) would significantly shorten nystagmus duration (recorded from behind closed eyes) and reduce the frequency of nystagmus, while increasing latency and dsyrhythmia, whether the intervals between stimuli were short (six to eight minutes) or long (one to 25 days).

Fluur and Mendel[90 91] also recorded eye movements from behind closed lids and obtained significant reductions (about 30%) in response duration (increasing dysrhythmia made quantification of other aspects of nystagmus impractical) following a series of eight to 12 irrigations. In their first study, subjects received unilateral habituation trials. In post-habituation tests, the majority of subjects showed a response reduction from pre-test levels for unilateral stimuli to

either ear which drove nystagmus in the habituated direction, and a longer nystagmus time for unilateral stimuli which drove nystagmus in the opposite direction. Other subjects showed a pre- to post-test decline for either cool or warm stimulation in either ear. In the second study,[91] subjects were habituated with eight to 12 unilateral stimulations of one ear; post-tests yielded the same results as that obtained from the majority of subjects in the previous study. Next, a new series of unilateral stimuli drove nystagmus in the opposite direction. Post-tests indicated a decline for that direction of nystagmus irrespective of the ear irrigated, but responses in the opposite direction (habituated in the first series of stimulations) were now back to the initial, pre-habituation levels. The authors concluded that "in a person already habituated by repeated monaural irrigation with hot water it is not possible to superimpose a habituation to cold water in the same ear without influencing the response to the primary habituation." They theorized that habituation influenced the spontaneous activity levels in the two labyrinths and disrupted the balance between them.

However, Pfaltz and Arx[177] obtained a directional preponderance of nystagmus following a series of unidirectional rotations, and reported no reversal of this difference following a series of unilateral caloric stimuli which drove nystagmus in the opposite direction, although the caloric response declined with repetition (all tests in darkness). They noted that a shift in the ratio between the two directions of nystagmus could be obtained by repeated unidirectional angular accelerations, but not by repeated unilateral caloric irrigations ("Eine Verschiebung des quantitativen Verhältnisses zwischen Rects-und Linksnystagmus kann im Gegensatz zur widerholten Dreheizung nicht mittels aufeinanderfolgender monauraler thermischer Reize erzielt werden."). A series of binaural irrigations, on the other hand, produced a preponderance of nystagmus favoring the unpracticed direction of eye movement.

Forssman, Henriksson, and Dolowitz[95] and Forssman[94] investigated the effects on caloric habituation of 12 consecutive irrigations in darkness and in illumination (the first and twelfth trials were always in darkness). They reported approximately equivalent reductions in duration and velocity of nystagmus for the two conditions (25% for duration; 55% for velocity). In addition, laterotorsion (i.e., deviation of the head[cf., 131]) declined by approximately 40%. Dysrhythmia during light trials was considerable (probably due to only intermittently effective visual inhibitation), but during dark trials was very moderate.

In the above investigations only Lidvall[152] reported the use of any alerting technique. After demonstrating a progressive decline in the number of eye movements during four irrigations, Lidvall[152] noted that an additional trial during which subjects performed mental calculations resulted in an immediate restoration of the response. A study by Collins[45] examined the influence of an extensive series of unilateral irrigations (10 daily for four days) on responses to both unilateral and bilateral irrigations. One group of subjects was tested in total darkness while performing various tasks; the other group actively sought to control nystagmus by fixating on ceiling markers in a lighted room. During pre- and post-tests, each subject received six irrigations; two were bilateral (warm and cool water simultaneously presented to the two ears), one driving nystagmus to the left, the other to the right; the remaining four were unilateral irrigations with cool and warm water presented to each ear successively. Results indicated essentially no effect of the habituation series on the duration of nystagmus for either group. For the group habituated in total darkness, no significant decline in slow-phase eye displacement but a significant overall increase in eye-movement frequency appeared (see Figure 10). For the group habituated in the light, no pre- to post-test change in frequency of nystagmus occurred, but slow-phase measures declined significantly. For both groups, changes were somewhat greater for the three stimuli provoking responses in the same direction as that of the habituation trials. For the light group no recovery of the slow-phase loss was evident after one month of rest; similarly, for the dark group, the increase in frequency of nystagmus was still evident upon retest a month later.

Collins, Schroeder, and Mertens[61] performed a similar series of 40 irrigations with subjects actively fixating on ceiling markers; one group was given unilateral irrigations, the other bilateral stimulation; nystagmus was driven to the left in both cases. During pre- and post-tests,

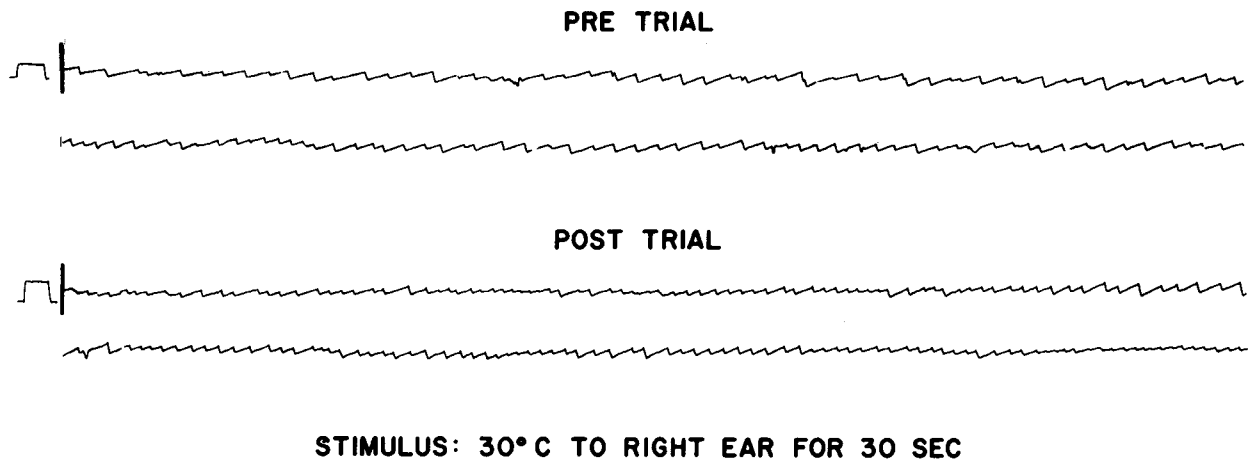

FIGURE 10. Caloric nystagmus recorded before and after an habituation series of 40 unilateral irrigations (all trials in darkness with the subject's eyes open). Dysrhythmia and an overall reduction of nystagmus are not necessary consequences of repeated vestibular stimulation; an increase in the number of eye movements, as depicted above, may occur. Vertical bars indicate the end of the irrigation; 20° calibration markers appear at the beginning of each tracing. Each strip of tracings represents 33 seconds of recording.[cf., 45 61]

subjects received the series of six cool and warm unilateral and bilateral stimulations noted above. Results indicated that, for both groups of subjects, nystagmus declined unidirectionally. A control group received only the pre- and post-test irrigations and showed no change.

The same study also included four rotation trials prior to any pre-test irrigations; the rotations were repeated after all post-test irrigations. No significant changes were evident in nystagmic output for either direction of rotation-induced nystagmus as a result of the caloric trials.

C. *Subjective Reactions: Rotation-Induced.* The sensations of motion accompanying semicircular canal stimulation appear to be more readily affected by repeated exposure to either angular accelerations or calorizations than are nystagmic eye movements. Of considerable interest is the fact that they may follow a time-course different from that of nystagmus.

Griffith,[104 106] who reported attenuation of nystagmus following cessation of rotatory stimulation in a lighted room, also noted a decline in the sensation of apparent motion with repeated stimulation. Although Hallpike and Hood[126] found an attenuation of turning sensations that was directionally specific (subjects were rotated with eyes closed), their findings may be more closely related to adaptation effects than to habituation. These investigators used a short test stimulus before and after a prolonged stimulus (e.g., $2°/sec^2$ for 75 sec) and found that, when the post-test stimulus was in the same direction as the prolonged stimulus, rotary sensations were shorter than the pre-test level; when the post-test stimulus was in the direction opposite that of the prolonged stimulus, reactions were of normal (pre-test) duration.

A single subject with eyes covered and head approximately erect was given two series of CW rotations by Meda.[165] The first series covered 40 days and comprised 290 trials (stops and starts were sudden and apparently separated by one minute of constant velocity at 30 rpm). A fairly systematic decline in the duration of the sensation following deceleration was obtained both within days and from day-to-day. Tests conducted before and after habituation showed little or no change in (1) the duration of after-sensations with the head anteverted so that the lateral canals were perpendicular to the plane of rotation, (2) the duration of sensations occasioned by head movements either during rotation or immediately after deceleration, and (3) the duration of after-sensations following CCW deceleration. The lack of transfer of habituation from one set of semicircular canals to another set, or between reactions from one set of canals and Coriolis-induced responses has been confirmed in other studies of nystagmus from man and cat.[52 69 115 119] However, the failure to obtain a reduction to CCW deceleration is surprising since the subject was apparently exposed to an

equivalent stimulus (CW acceleration) during the habituation series, at an equivalent rate (sudden starts and stops) under identical visual conditions (eyes covered). A second series was initiated with the subject's head ventrally flexed. After 100 rotations the after-sensation was reduced by about 50%. Tests with head movements during and following rotation showed no clear effect of the habituation series on the duration of these Coriolis sensations. Additional tests conducted at intervals of one to three months with the subject's head erect finally showed full recovery of the duration of the after-sensation.

In comparing the technique of cupulometry to the Bárány test procedure, Groen and Jongkees[108] demonstrated that the sensation cupulogram obtained before and after a set of three CW and three CCW Bárány spins (stops from 30 rpm) showed a marked decline. They felt that the Bárány-type stimulus damaged the vestibular organ and that a maximum velocity of only 10 rpm should be used prior to braking subjects to a stop. However, Brand[24] obtained response declines for post-rotational turning sensations both within a daily series of brake decelerations from 10 rpm (or less) and from one test day to the next.

Aschan,[3] using cupulometry, reported reduced durations of sensation to rotational stimuli from fighter pilots. Unlike the directionally specific reductions in nystagmus which he found for this group, sensations for both directions of angular stimulation were attenuated. Similarly, Dearnaley, Reason, and Davies[71] reported shorter durations for experienced pilots than for trainees in the vestibular sensations occasioned by 1-minute long, 45-degree banks in an aircraft; within each group there was no difference between left and right turns. The differences between pilots and students were present whether subjects' eyes were closed or visual references were available, although increasing the amount of visual information decreased the sensation for both groups. Preber[182] had examined pilot trainees before flight training and followed-up a group which showed severe airsickness during the training period. These subjects, as a group, had longer durations of sensation during turning tests conducted prior to flight training than did trainees who did not get air sick; however, after adapting to the flying situation, tests showed a decline in duration of sensation. Previously, de Wit[206] had reported progressively greater cupulogram slopes in comparisons of a group of sailors who had never been seasick, a group of students, and a group of sailors who were chronically seasick.

Guedry, Collins, and Sheffey[120] performed a 50-trial habituation series spaced over five days with trials alternately in total darkness and with a 5-second period of room illumination following deceleration. Pre- and post-tests in total darkness showed a decline of approximately 50% for total subjective displacement. Partial recovery was evident nine days later with no intervening trials.

Benson[13] gave subjects (closed eyes) impulsive decelerations and, three seconds after they had reached a stop, had them shake their heads for two seconds. The duration of post-rotatory sensations was reduced after the head-shaking period. With repetition, post-rotatory sensations declined both with and without head shaking, but declined independently. There was no difference between non-aerobatic aircrew and ordinary subjects.

Collins' study,[43] employing 200 unidirectional habituation trials in total darkness with subjects performing various attention-demanding tasks, showed a directionally specific reduction of 39% in peak subjective velocity and 37% in total subjective displacement for the practiced direction of angular acceleration. There was no pre- to post-test difference for the unpracticed direction (see Figure 11). One month later, with no intervening trials, total subjective displacement was only 27.5% less, and peak subjective velocity only 16.5% less, than the pre-test levels for the practiced direction; the unpracticed direction still showed no change from the pre-test level. Thus, the subjective reaction declined in a directionally specific fashion, without the subjects attending to the sensation, and in the absence of vision; the response showed partial recovery after one month of rest.

Professional figure skaters report some initial dizziness when they resume spinning routines after vaction periods of one to three months. In skating trim, they appear to experience only very mild and brief dizziness following on-ice spins, but if they close their eyes upon stopping, clear vertiginous sensations occur. Similarly, while

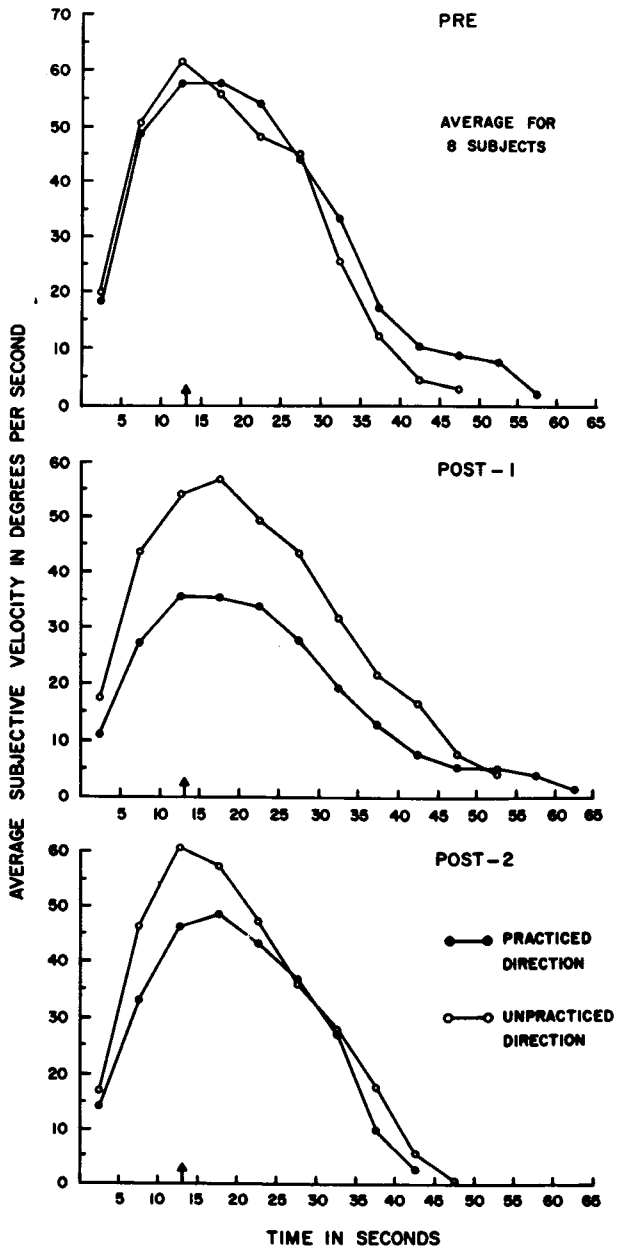

FIGURE 11. Subjective velocity estimates made by subjects before (pre) and after (post-1) a series of 200 CW accelerations (all decelerations were subthreshold). Post-2 tests were conducted one month later with no intervening trials. The habituation series produced a clear, directionally specific reduction in the intensity of the turning sensation (but not in its duration); a month of rest produced considerable recovery. (Reprinted with permission from *Acta Otolaryngologica.*[43])

they can perform gracefully with open eyes following such spins, closing their eyes produces a loss of balance and an inability to maneuver.[46] In laboratory tests (total darkness) of figure skaters, clear turning experiences were reported to rotation and there was no difference in the duration of left vs. right turning sensations.[51] When compared with ordinary subjects, however, skaters had significantly shorter durations to stimuli ranging from $5°/sec^2$ for 18 seconds to $90°/sec^2$ for one second. It is of considerable interest that the differences between the two groups were proportionately greater for the higher rates of angular acceleration.[51]

D. *The Oculogyral Illusion.* During rotational stimulation, an object with a minimal visual surround (a small dim light source in an otherwise dark room) appears to move in a definite pattern although it and the observer are in fixed positions.[102] This apparent motion, the oculogyral illusion (OGI) has been identified with the sensation of turning rather than with nystagmus[30 72 203] (however, see also reference 36). Brown and Guedry[28] examined the duration of the OGI before and after short series of rotations (1) in total darkness, (2) with a target light present, and (3) with five seconds of room illumination following cessation of rotation (target light present). Marked declines in OGI duration occurred for the latter two conditions. Previously, Guedry[110] had reported a successive shortening of the duration of the illusion during a series of trials in which conditions of total darkness and of brief illumination of the test room (shortly after deceleration) were alternated. Directional specificity of this decline in the condition which employed vision was noted in later studies[111 112 113] and it was observed that a decline of the OGI at one stimulus rate produced a greater response reduction to a stimulus of lesser intensity and a lesser response reduction to a stimulus of greater intensity.[112] Subsequently, Clark and MacCorquodele[35] reported no shortening in the duration of the OGI in three trained subjects who observed the illusion with a more complex visual stimulus (the lighted outline of a cube) during 276 accelerations and 276 decelerations. A recent study by Brown and Crampton[27] showed no differential effects on duration of the OGI of rotating subjects in total darkness, with the OGI, with an illuminated enclosure, or in full-room illumination; however, only six habituation trials were conducted for each group in the direction under consideration.

E. *Coriolis Vestibular Sensations.* The OGI has also been used in studies of habituation of Coriolis vestibular responses produced by head movements during constant rotation. The array of effects which occurs depends to some extent upon the kind of visual information available during the head movements.[48] The sensations produced (as well as the apparent movement of a target light) are combinations of displacement and acceleration (see Figure 12 and reference 53), e.g., tilting the head to the right during CW rotation produces a sensation of tilting backward and accelerating upward (much like a sharp climbing maneuver in an aircraft). Guedry and Montague[124] reported reduction of the apparent displacement of a target light with repeated head movements. Graybiel, Guedry, Johnson, and Kennedy[101] rotated subjects in the light for a 64-hour period during which they made voluntary head movements or were passively tilted in a special chair. Tests during the experiment involved the OGI (the lighted outline of a cube) with the room otherwise dark. Magnitude estimates of the illusion declined for all subjects. In addition, a conditioned compensatory reaction was obtained; when the room was at a standstill at the end of the experiment, subjects made head movements and reported OGI effects which were opposed in direction to those which would have been produced had the same head movement been

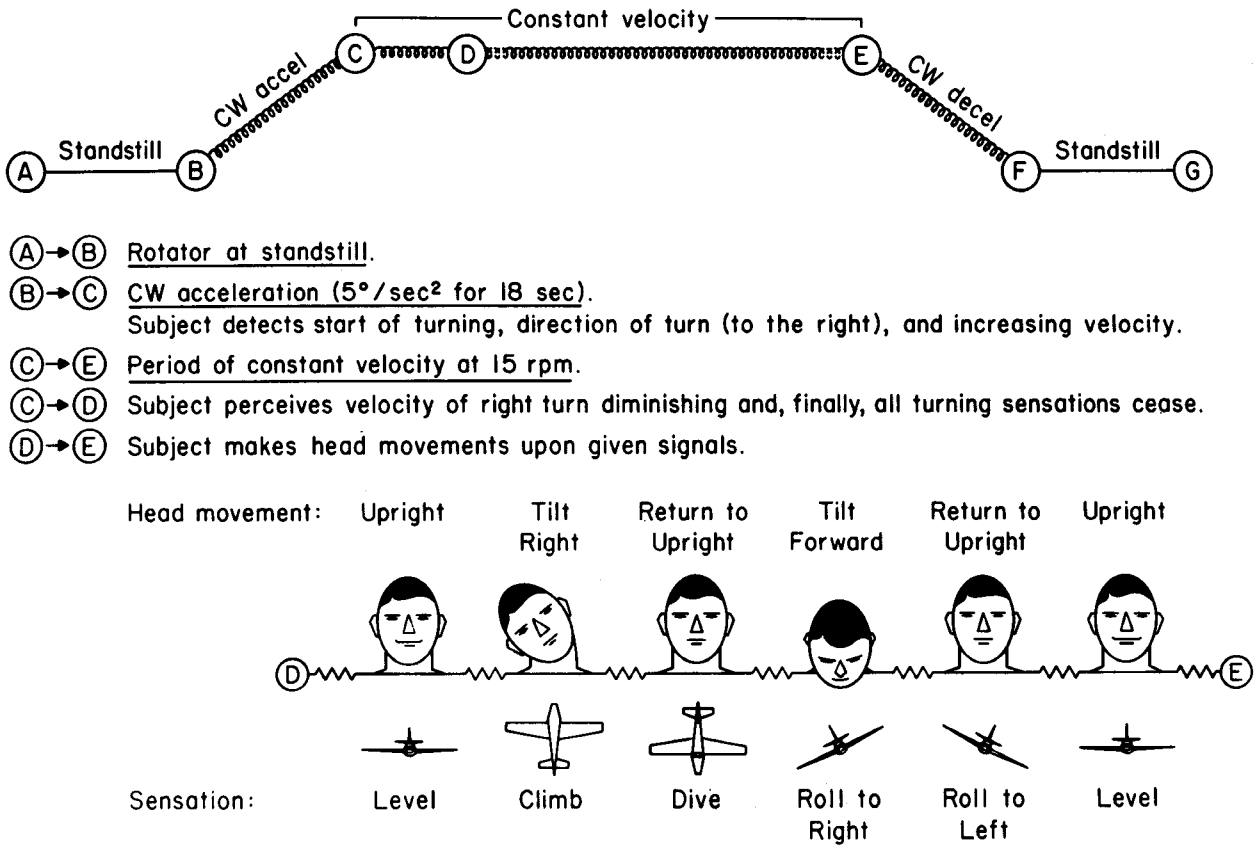

FIGURE 12. The subjective reactions occasioned by angular accelerations, angular decelerations, and head movements during rotation.[53] Note that: The sensations are reversed if CCW rotation is used; returning the head to upright from a tilt to the right is equivalent to tilting the head to the left; the sensation experienced as a result of deceleration is directionally opposite that resulting from the acceleration and is perceived as a speeding up rather than a slowing down.

made during rotation. Similar conditioned compensatory reactions were obtained for nystagmus.[121] Further evidence was obtained for conditioned OGI effects in studies of shorter duration (four to eight hours of rotation) with voluntary head movements restricted to a single quadrant in the frontal plane.[119 122]

Guedry[114] exposed two groups of subjects to a 100-cycle series of head movements restricted to a single quadrant; one group performed the movements with eyes closed, the other group solved problems projected on a screen during the head tilts. Tests were conducted before and after the 100-cycle series (1) during rotation and (2) in a static situation. During rotation, there were clear pre- to post-test reductions in OGI for head movements in the practiced quadrant and a lesser reduction for the unpracticed quadrant among subjects in the "vision" group; the "darkness" group showed less reduction. In static post-tests, the "vision" group reported OGI effects principally in the practiced quadrant; the "darkness" group evidenced little or no OGI reactions.

Related to the above, but without using the OGI, Guedry[115] gave pre- and post-tests in darkness to subjects who had lived in a lighted, rotating room (10 rpm CCW) for 12 days. The subjects rated the intensity of sensations occasioned by specific head movements during both CW and CCW rotation. Little or no post-test sensations were obtained during CCW rotation; sensations from head tilts during CW rotation were as strong or stronger than the pre-test levels. Additional post-tests conducted two days, three weeks, and three months later showed recovery, but not to the pre-test levels.

F. *Subjective Reactions: Caloric-Induced.* Sensations generated by caloric irrigations are not uniform among subjects and may even differ from one irrigation to the next for the same subject.[45] Frequently a directional component of the experience cannot be specified.[182] Although bilateral stimulation (simultaneous presentation of cool water to one ear and warm to the other) frequently produces sensations of apparent angular motion about an earth-vertical axis, both bilateral and, more often, unilateral calorizations will result in experiences of tilting, floating, dizziness, "arcing" (successive apparent motion through a relatively small angle), combinations of these, or even apparent turning about an earth-horizontal axis.[45]

Lidvall[149 150 151 153] reported a considerable decline in "vertigo" with as few as four unilateral irrigations and noted that the decline was specific to the direction of cupula deflection in the irrigated ear,[150] i.e., after vertigo habituation of one ear with a cool stimulus, a warm stimulus applied to that ear, or any stimulus applied to the opposite ear would produce a strong vertigo response. Forssman, Henriksson, and Dolowitz[95] and Forssman[94] noted declines in vertigo ratings exceeding 80% after 12 irrigations, whether subjects were tested in darkness or in an illuminated room. Hinchcliffe[135] obtained ratings of caloric vertigo induced by unilateral stimulation and reported marked declines in intensity ratings following five irrigations; a second series administered on the following day showed partial recovery for the first trial and a rapid decline for the remaining tests (subjects' eyes closed).

Collins[45] kept subjects alert during a 40-trial habituation series (one group was tested in total darkness, another group was engaged in active visual fixation) and tested responses in total darkness before and after the habituation trials. Since the pre- and post-tests involved all combinations of irrigations (unilateral and bilateral, cool and warm), the effects of the 40-trial series (cool water to the right ear) on responses in the same and in the opposite "directions" could be evaluated. For both groups of subjects, directionally specific effects were evident. There was an average increase in latency of the sensation, and a decline in its duration and rated intensity for all stimuli eliciting responses in the same direction as the habituation trials. Responses in the opposite direction were either less affected (although showing some decline) or, in the case of subjects who received the 40-trial series in darkness, unilateral stimulations produced ratings of greater intensity than the pre-test levels. For both groups, a 1-month rest interval resulted in some recovery or complete recovery of the response.

Collins and Mertens[58] expanded and partially replicated the above study. Using the same caloric pre- and post-test procedures, they examined two groups which engaged in active visual fixation during a 40-trial habituation series (one group received unilateral stimulation, the other bilateral stimulation) and a control

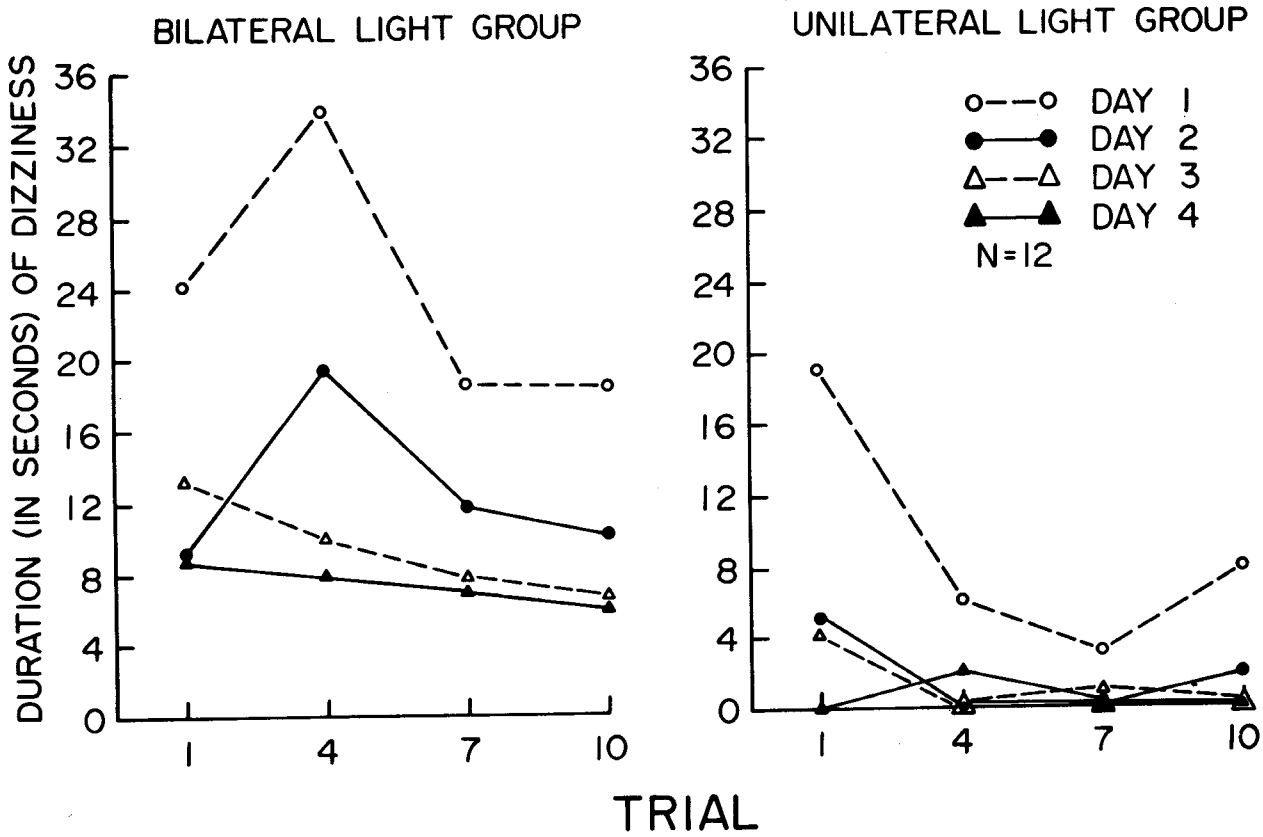

FIGURE 13. The mean duration of dizziness calculated from the reports made by 12 subjects in each of two test groups during caloric irrigations. Subjects fixated on a ceiling marker throughout each of 10 calorizations per day for four consecutive days. The bilateral group received simultaneous irrigations of the two ears (right 30° C.; left 44° C.); the unilateral group received 30° C. irrigations of the right ear only. The subjective reaction shows considerable decline over the test series.[cf., 88]

group which received only the pre- and post-tests. During the 40 visual-fixation trials, the duration of "dizziness" and of the apparent movement of the fixation point showed an irregular but progressive decline during each 10-trial day, and over the four test days (see Figure 13). The pre- and post-test data (obtained in darkness) showed essentially no change in sensation ratings made by the control group. In agreement with previous work,[45] repeated unilateral stimulation (cool water to the right ear) produced relatively little pre- to post-test change in sensation-intensity for caloric stimuli which elicited responses in the direction opposite those of the habituation series. Post-test responses to the unilateral and bilateral stimuli which involved cool water in the right ear showed significant declines; warm water to the left ear (a stimulus "equivalent" to that used in the habituation series) did not produce a decline in sensation. This latter result (a lack of transfer) does not agree with the previous finding of Collins,[45] but does agree with Lidvall's report[150] that unilateral caloric habituation of vertigo is specific to the cupula deflection of the repeatedly stimulated ear. The group which received bilateral habituation demonstrated significant declines in vertigo (49–62%) for all three stimuli which produced reactions in the same direction as the habituation series, and a uniform increase (22–32%) in sensation ratings for the three non-equivalent stimuli.

G. *Special Effects of Brief Periods of Visual Fixation on Vestibular Responses.* Only a few studies have examined the effects of brief periods of visual stimulation on nystagmic and subjective reactions. Brown and Guedry[28] and Guedry,[111] [112] [113] as indicated earlier, used brief periods of illumination in studies of the oculogyral illusion. Wendt[202] noted that, although post-rotational

nystagmus was inhibited during a period of visual fixation, the response was quickly reestablished during a succeeding period of darkness. Guedry, Collins, and Sheffey[120] confirmed Wendt's[202] statement, but found that the response was not restored to the level of an uninterrupted reaction and that the sensation of turning showed no recovery.

Collins[51] introduced three seconds of room illumination one second after various rates of de-

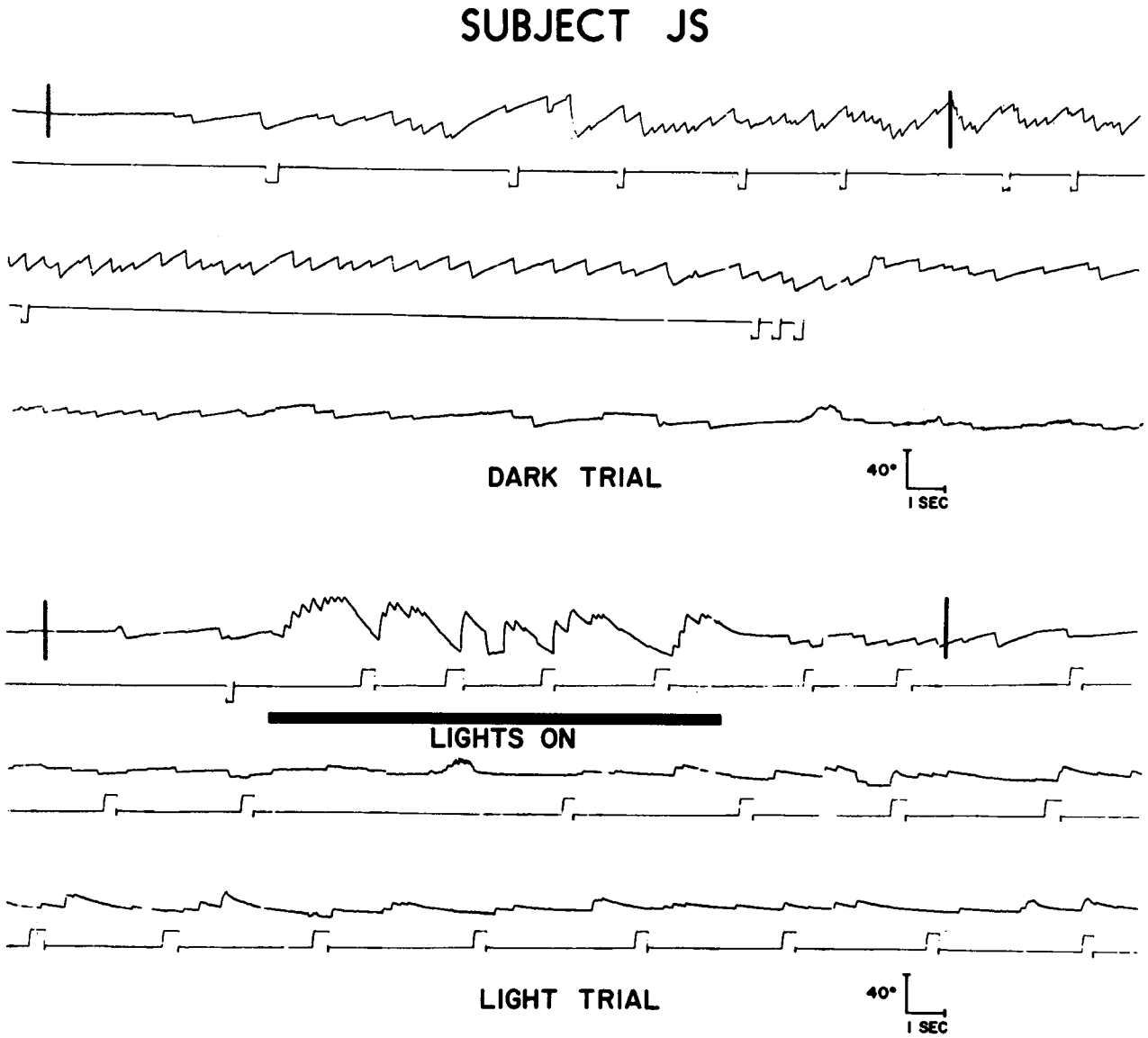

FIGURE 14. The influence on nystagmus and subjective turning of a period of room illumination during a CW deceleration. Vertical bars through the tracings demarcate the deceleration period. The deflections on the lines just below the nystagmus tracings represent the recorded signals of turning[cf., 12 109] experienced by the subject; downward deflections indicate a sensation of turning left, upward deflections indicate a sensation of turning right. Note in total darkness the prolonged primary nystagmus, the lack of secondary nystagmus, and the indication of the usual left-turning sensation from this subject. The period of room illumination during the light trial produces a reversed (optokinetic) nystagmus and a reversal of the indicated direction of turn. Subsequent extinguishing of the lights reverses the direction of primary nystagmus for only a few seconds; the primary response is then replaced by a long-lasting secondary nystagmus. Moreover, this subject did not experience the leftward turning which the canals would have been signalling after the lights were turned off; a long-duration right-turning sensation was reported (subjects called out the direction of turn in addition to manual signals). Other subjects reported no sensation for several seconds after the period of room illumination, and then experienced strong sensations of turning to the right.[cf., 49]

celeration; trials were otherwise in darkness. Subjects actively fixated on wall markers during illumination and attempted to control completely their eye movements. Room illumination (subjects were at a complete standstill) substantially reduced on-going nystagmus; during the subsequent period of darkness, nystagmus recovered, but never to the level of an uninterrupted response. Of perhaps greater significance, the shortened primary nystagmus was frequently replaced very quickly by a secondary nystagmus which appeared more vigorous than the secondary reactions obtained (but much later in time) during trials in total darkness (see Figure 14). (Markaryan[157] has also noted strong secondary nystagmic reactions following angular stimulation and a period of visual fixation.) The sensation of turning was suppressed during the visual stimulation and, during the subsequent period of darkness, was reinstated (although considerably reduced) in only a small percentage of cases.

More recently, using "prolonged" angular stimuli (20 seconds or more), Collins[49] introduced room illumination for various durations during the deceleration period; the final six seconds of deceleration and the subsequent period at a standstill were always in total darkness. Under these conditions, subjects could see themselves decelerating (although in darkness the vestibular signals would have produced a sensation of accelerating in the opposite direction; see Figure 12), and an optokinetic nystagmus was generated opposite to the nystagmus which the semicircular canals would have initiated. Room lights were turned off during the last few seconds of deceleration, and vestibular nystagmus quickly replaced the optokinetic response. However, in comparison with an uninterrupted response, nystagmic output was at a much-reduced level, was significantly shorter in duration, and more frequently was succeeded by a vigorous secondary nystagmus. Following the period of room illumination (during the last six seconds of deceleration in darkness) many subjects reported no sensation; some reported a brief sensation of turning in the true direction (in opposition to the vestibular signals). Very shortly after the termination of deceleration a marked and prolonged "secondary" sensation was reported by almost all subjects.

These data have been interpreted as indications that secondary reactions are of central origin, in agreement with Aschan and Bergstedt.[5] In addition, it has been suggested that they may occur as a result of "prolonged" neural activity in the primary direction,[49] that secondary reactions are processes which oppose primary reactions (perhaps occurring as the consequence of a central imbalance produced by "prolonged" unidirectional activity), and that visual information (under some conditions) is centrally integrated and enhances this already on-going process, thereby attenuating the primary response.[49 51]

VI. A Modified View of "Habituation."

The term "habituation" has been used throughout this report to identify a series of repeated stimulations or to describe the effects of such a series on various responses. Most investigators carefully restrict the meaning of the term to "response reduction" or, considering habituation to represent a valid class of learning, cite Thorpe's[195] definition ("a tendency merely to drop out responses"). Although vestibular research findings appear to share many of the general characteristics ascribed to other habituation phenomena,[74 127 185] such definitions fail to describe adequately the dynamic processes of change which are evident as a result of repeated vestibular stimulation under at least some conditions. For example, repeated exposure of man to Coriolis stimulation in the light reduces nystagmus and subjective reactions in both light and darkness; an overall suppression appears to occur. However, closer examination indicates that a conditioned compensatory reaction has developed to oppose these responses.[114 121] There is no simple dropping out of responses; instead there is a gradual inhibition of the original response as the opposed reaction becomes more fully developed. These opposed reactions have appeared most clearly under two nonexclusive conditions: (1) when there is an element of conflict between vestibular and visual signals (and perhaps others of a sensory nature), (2) where the organism is attempting to adapt to an unusual vestibular environment. In darkness, nystagmus repeatedly elicited by simple vestibular stimulation is not simply reduced in alert subjects; the form of the response is changed and the change appears to be due to increased activity of the fast phase of the eye movement which,

concomitantly, reduces the amount of slow-phase eye excursion.[41 51] With very brief responses, such as those elicited by mild turns of short arc, increasingly more frequent fast phases may gradually obliterate the original form of nystagmus.[203] "Active modification" would more closely describe the effects of repeated stimulation on human vestibular responses.

The above suggests the possibility of more than one kind of vestibular "habituation." In the section concerned with arousal, presented at the beginning of this paper, the notion of psychological or situational "habituation" was discussed in terms of arousal factors. In addition, repeated vestibular stimulation of animals produces some effects apparently different from those obtained from human subjects. Cats, for example, show a very rapid reduction of all measures of ocular responses (in darkness or in light) similar to what might occur with a non-alert human subject, even though this overall reduction occurs in animals which seem alert, or which have received an analeptic drug, and in which various sensory methods of arousal do not significantly restore nystagmus. Thus, in spite of a rich history of research, there remain considerable gaps in knowledge concerning specific effects of repeated stimulation on vestibular reactions and, moreover, there remain important questions regarding the extent to which changes in the reaction patterns of animals can be generalized to human response patterns. It is suggested, however, that central processes are activated as a result of repeated vestibular stimulation, and that limiting the term "habituation" to a "simple dropping out of responses" masks dynamic changes and interactions which occur in humans as these responses become modified.

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33505