

AM-64-14

**EFFECTS OF BILATERAL CALORIC HABITUATION
ON NYSTAGMUS RESPONSES OF THE CAT**

MARY JAYNE CAPPS, M.S.
and
WILLIAM E. COLLINS, Ph.D.
Psychology Laboratories

Approved by

Stanley R. Mohler

STANLEY R. MOHLER, M.D.
DIRECTOR, CARI

Released by

M. S. White

M. S. WHITE, M.D.
FEDERAL AIR SURGEON

FEDERAL AVIATION AGENCY
Office of Aviation Medicine
Civil Aeromedical Research Institute
Oklahoma City, Oklahoma
September 1964



EFFECTS OF BILATERAL CALORIC HABITUATION ON NYSTAGMUS RESPONSES OF THE CAT

MARY JAYNE CAPPS and WILLIAM E. COLLINS

It has been suggested that the decline (habituation) of the nystagmus response to repeated vestibular stimulation is a form of learning in that it possesses the necessary features of a learned behavior—acquisition, retention, and transfer (Halstead, 1935). Acquisition of habituation is evidenced through the progressive reduction of the response with repeated stimulation, while retention has been reported for periods as long as several weeks (Halstead, 1935; Henriksson, Kohut, & Fernandez, 1961).

Transfer of unilateral caloric nystagmus habituation was shown to occur when a previously non-stimulated ear was irrigated with a stimulus provoking a response in the same direction as that elicited during habituation of the contralateral ear, responses elicited in the unhabituated direction were reported to be vigorous (Collins, 1964a; Henriksson, Kohut, & Fernandez, 1961). This apparent directional specificity of transfer has also been shown for (bilateral) habituation to mild angular acceleration (Crampton, 1962). However, studies have generally reported a failure to obtain

transfer of habituation from one means of stimulation (e.g., rotatory) to another (e.g., caloric), in spite of the fact that both types of stimuli evoked responses in the same direction (Collins, 1964a, b; Hood & Pfaltz, 1954; Maxwell, Burke & Reston, 1922). The single study reporting a stimulus-transfer effect (from caloric to rotatory stimulation) used extensive irrigations of ice water to abolish completely the nystagmus response (from each ear separately) before the rotation trials were administered (Dunlap, 1925).

The present study was designed to examine some aspects of transfer of nystagmus habituation. Bilateral caloric irrigations (warm water in one ear, cool in the other) were employed to provide simultaneous deflection of the cupulae. Transfer of the response decline was checked by administering unilateral irrigations following different series of bilateral calorizations. Subsequent testing permitted an evaluation of various other aspects of vestibular habituation.

METHOD

Sixty cats, unused in previous experiments, served as subjects. The animals, restrained by the method of Henriksson, Fernandez, and Kohut (1961) and with their heads elevated to an optimal position, were divided into 6 equal

¹ A major portion of the data presented here was submitted by the first-named author to the Psychology Department, University of Oklahoma, in partial fulfillment of the requirements for the degree of Master of Science. Grateful acknowledgement is made of the assistance rendered by Joseph E. Duchon, Billy P. Updegraff, Stanley Evans, and Mary Ellen Allen.

groups. Each group underwent caloric habituation to different stimulus conditions.

Stimulation. Three water baths were used. One was filled with ice water at a temperature of 4°C ($\pm 0.5^{\circ}\text{C}$), while the remaining 2 were equipped with Bronwill constant temperature circulators which maintained water temperature at 26°C and 50°C ($\pm 0.01^{\circ}\text{C}$) respectively (approximately 12°C above and below the cats' body temperature). Rubber tubing with attached irrigation nozzles provided the means for introducing the stimuli to the ears of the animals. The rate of flow (and, therefore, the total volume of water) was high (approximately 12 cc/sec) to permit a ready monitoring by touch of the return flow from the ear and assure delivery of the stimulus in total darkness.

Recording and Scoring. Nystagmus recordings were obtained with an Offner Type T Electroencephalograph (time constant: 3 sec), located in an adjoining room. The corneoretinal potentials were detected by needle electrodes inserted at the outer canthi of the cats' eyes.

Records were scored from the point of stimulus termination for number of beats, duration of nystagmus, and slow-phase displacement of the eyes. The number of nystagmic eye movements (beats) was simply counted for each trial. Response duration was measured from the termination of the irrigation to the last beat of the primary nystagmus.

The amount of slow-phase eye-movement was obtained in millimeters by measuring the vertical displacement of each nystagmic beat from the peak to the base line. These values were summed for each trial and transformed into degrees by means of calibration constants obtained with an optokinetic stimulator. The latter consisted of a drum, 2 1/2 ft high and 4 ft in diameter, driven by a DC motor. Alternate black and white vertical stripes covered the interior of the drum. Eye-movements induced by a constant rotatory velocity (4 rpm) of the drum were recorded and scored for each animal to obtain a calibration value relating degrees of eye-movement (assuming perfect following) to millimeters of pen deflection.

Procedure. The 6 habituation procedures are shown in Table 1. Each procedure comprised

18 trials; a pretest, 15 habituation trials, a post-1 test (identical to the pretest), and a post-2 test of a different intensity. In each case, a nystagmus to the left was induced. The pre-, post-1 and post-2 tests were unilateral irrigations, applied in all cases to the right ear. All trials were administered on the same day, at 20 min intervals. The irrigation and recording periods were always in total darkness, but animals were in full-room illumination for a period not less than 5 min before a trial began.

Four groups (AI, AII, BI, BII) were habituated to a series of 15 simultaneous bilateral irrigations of 50°C in the left ear and 26°C in the right ear. In order to obtain some information concerning the effects of time-of-irrigation on response magnitude, the duration of the bilateral habituating stimulus was different for each of these groups (BI: 15 sec; BII: 20 sec; AI: 25 sec; AII: 30 sec).

The bilateral habituation stimuli for groups AI and AII were used to produce responses of greater magnitude than the unilateral irrigation (26°C for 30 sec) administered as a pre- and post-1 test. Groups BI and BII received bilateral habituation stimuli which were selected to produce less vigorous responses than a pre- and post-1 test of ice water (4°C for 15 sec).

Two control groups (AC and BC) were habituated to unilateral irrigations identical to the pre- and post-1 test stimulus of their respective groups (AC: 26°C for 30 sec; BC: 4°C for 15 sec). These control animals provided a measure of the level of response after unilateral habituation. Therefore, comparison of the post-1 test responses of one set of experimental (AI and AII) and control (AC) groups provided the basis for examining the question of transfer of habituation from a bilateral caloric series to a less intense unilateral stimulus. Likewise, comparisons of post-1 test responses of BI and BII with those of BC indicated the extent of transfer from a bilateral habituation series to a more intense unilateral stimulus.

The post-2 test stimulus for the A groups was the same as the pre and post-1 test stimulus of the B groups. The B groups received post-2 tests identical to the pre- and post-1 tests of the A groups.

TABLE I

Schedule of Test Stimuli for Each Group

Group	Test			
	Pretest (1 trial)	Habituation (15 trials)	Post-1 (1 trial)	Post-2 (1 trial)
AC	Unilateral 26°C – 30 sec	Unilateral 26°C – 30 sec	Unilateral 26°C – 30 sec	Unilateral I W – 15 sec
AI	Unilateral 26°C – 30 sec	Bilateral 25 sec	Unilateral 26°C – 30 sec	Unilateral I W – 15 sec
AII	Unilateral 26°C – 30 sec	Bilateral 30 sec	Unilateral 26°C – 30 sec	Unilateral I W – 15 sec
BC	Unilateral I W – 15 sec	Unilateral I W – 15 sec	Unilateral I W – 15 sec	Unilateral 26°C – 30 sec
BI	Unilateral I W – 15 sec	Bilateral I W – 15 sec	Unilateral I W – 15 sec	Unilateral 26°C – 30 sec
BII	Unilateral I W – 15 sec	Bilateral 20 sec	Unilateral I W – 15 sec	Unilateral 26°C – 30 sec

Note.—All unilateral trials were administered to the right ear. Bilateral trials consisted of simultaneous irrigations of 26°C (right ear) and 50°C (left ear). IW indicates ice water (4°C).

RESULTS AND DISCUSSION

I. Effects of bilateral caloric habituation on responses to unilateral stimulation.

A GROUPS

The experimental groups (AI and AII) received habituation trials of greater intensity than the pretest and post-1 test. Figure 1, nystagmus tracings from an animal in group AII, shows the variation in response magnitude to the bilateral and unilateral stimuli.

Habituation Series. Figure 2 shows the declining mean response-per-trial of the A groups plotted as percentages of the pretest score. Analyses of variance were conducted on those data for trials 1 and 15 (see Table 2). For the three A groups, the habituation series produced a statistically significant reduction in slow-phase displacement and number of beats (.001 level), but not in response duration. Previous studies have indicated that duration tends

to be the least reliable measure of response decline (Fernandez & Schmidt, 1962; Henriksson, 1956; Ward & Fernandez, 1963).

Significant differences were also found among the groups for slow-phase displacement (.05 level) and number of beats (.01 level). Multiple comparisons were made (.05 level) with the Duncan test (Edwards, 1960). These comparisons showed that the control group yielded fewer beats and less slow-phase output than did either experimental group. Although the experimental groups did not differ significantly from each other in slow-phase displacement, group AII tended toward greater slow-phase output, and produced a significantly greater number of nystagmic beats than did AI. These relations are evident in the curves of Figure 2 in which there are 3 distinct levels of response in the number-of-beats graph, 2 in the slow-phase graph, but no distinct differentiation of the groups in the duration data.

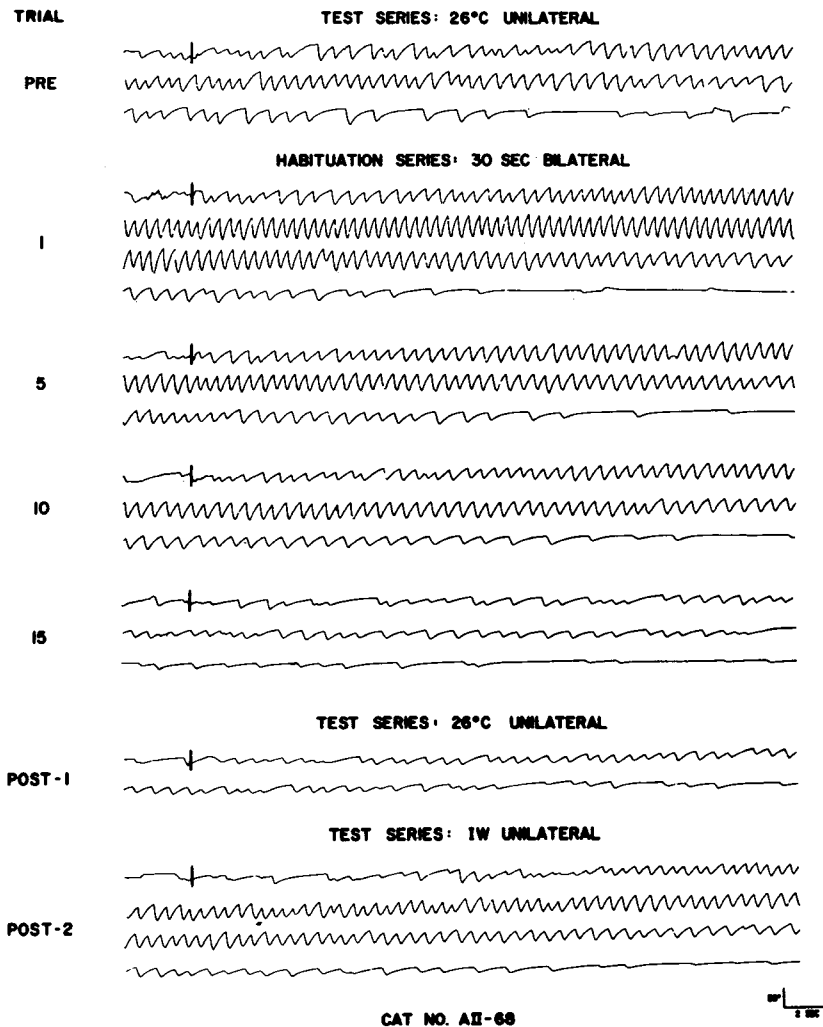


FIGURE 1. Recorded nystagmus from a cat in group AII. Upward deflection of the pen denotes a movement of the eyes to the right; downward deflection to the left. Vertical bars through the tracings mark the termination of the stimulus. The bilateral habituating stimulus was more intense than that of the unilateral pre- and post-1 tests.

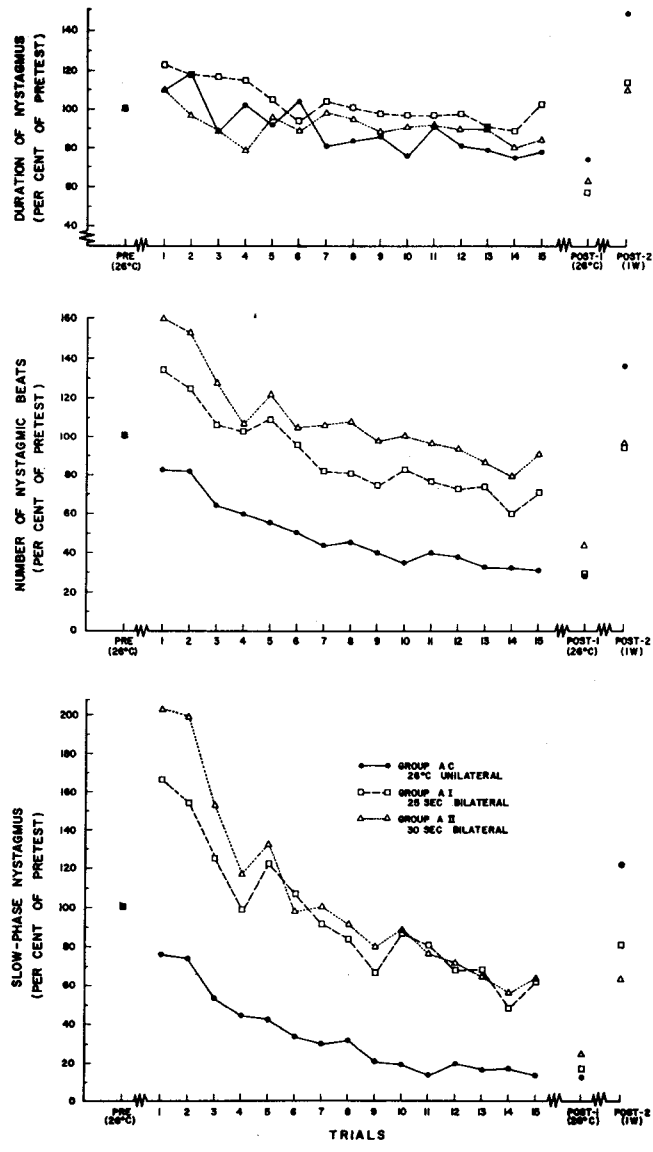


FIGURE 2. Mean slow-phase eye-movement, number of beats, and response duration of the A groups plotted as percentages of the pretest score. Groups AI and AII received bilateral habituating stimuli of greater intensity than the unilateral habituating stimulus applied to AC.

TABLE 2
Results of the Analyses of Variance on Percentage-of-Pretest Nystagmus Scores for Habituation Trials 1 and 15 of the A Groups

Source	df	Nystagmus Measure					
		Slow-Phase		Frequency		Duration	
		MS	F	MS	F	MS	F
Groups (G)	2	27454.59	4.51*	15730.84	7.29**	1714.02	.78
Subjects within G	27	6089.20		2158.45		2190.74	
Trials (T)	1	115246.92	34.12***	51205.13	36.47***	11056.84	.86
T X G	2	3477.10	1.25	101.90	.73	547.29	.42
T X Ss within G	27	91195.37		1403.88		12902.60	

*p < .05, **p < .01, ***p < .001.

All groups exhibited the greatest amount of decline in the first 5 trials of the habituation series (Fig. 2). Other studies have noted this characteristic of the response curves of habituation to unilateral caloric stimulation and to angular acceleration (Collins, 1964a, b; Griffith, 1920).

Pretests and post-1 tests. The stimulus for the pre- and post-1 test for all A groups was a 26° C unilateral irrigation for 30 sec. In order to determine the influence of the bilateral habituation trials on responses to the less intense unilateral stimulus, analyses of co-variance were conducted on the pre- and post-1 test scores for the slow-phase, number of beats, and duration measures (see Table 3). No significant differences were found among the three A groups on any measure. That is, habituation to bilateral caloric stimulation transferred to a unilateral irrigation of lesser intensity.

Post-2 tests. The post-2 stimulus for the A groups was a 15 sec unilateral ice water (IW) irrigation. For all groups, the response to the IW trial was greater than that to the post-1 (26° C) stimulus (see Fig. 2). The increased amount of response to the IW trial was notably marked for the AC (control) group.

B GROUPS

The experimental groups (BI and BII) received pretests and post-1 tests of greater intensity than the habituation trials. Nystagmus tracings depicting this relation appear in Figure 3.

Habituation series. Reduction of the nystagmic response occurred in each group as a result of the repeated trials of the habituation series. In Figure 4 the data are plotted as percentages of the pretest response and statistical analyses were conducted on these scores for trials 1 and 15 (see Table 4). Reductions in response significant at the .001 level were found for slow-phase displacement and number of beats. Duration data which were highly variable yielded no significant differences. The significant interaction effect (.05 level) appears to be a result of differences in the slopes of the habituation curves (see Fig. 4).

Differences significant at the .01 level were found among the B groups on all 3 nystagmus measures and multiple comparisons were made (.05 level) with Duncan's test (Edwards 1960). These comparisons showed that the control group produced a significantly greater number of nystagmic beats and more slow-phase out-

TABLE 3

Results of the Analyses of Covariance on Pretest and Post-1 Test Nystagmus Scores for the A Groups

Source	df	Nystagmus Measure					
		Slow-Phase		Frequency		Duration	
		MS	F	MS	F	MS	F
Treatments	2	118,270.6	.95	560.8	1.16	884.4	.87
Error	26	125,130.3		483.0		1,018.9	
Total	28						

$[F_{.95(2,26)} = 3.37]$

put than did either experimental group; the experimental groups did not differ from each other in nystagmus production. Duration scores were significantly different among all groups with BC greater than BI or BII, and BI greater than BII. These differences are evident in the curves of Figure 4 which show 3 levels of duration scores and 2 levels (control and experimental) for the slow-phase data and the number of beats.

Pretests and post-1 tests. The stimulus for these tests (15 sec unilateral IW irrigation) was of greater intensity than the habituation stimuli for the experimental groups (Figs. 3 and 4). Analyses of covariance were conducted on the 3 types of nystagmus scores (see Table 5). No significant differences were found among the groups. Thus, habituation to bilateral caloric stimuli transferred to a more intense unilateral irrigation.

TABLE 4

Results of the Analyses of Variance on Percentage-of-Pretest Nystagmus Scores on Habituation Trials 1 and 15 of the B Groups

Source	df	Nystagmus Measure					
		Slow-Phase		Frequency		Duration	
		MS	F	MS	F	MS	F
Groups (G)	2	11888.78	8.56**	10348.36	8.53**	7069.34	8.83**
Subjects within G	27	1389.41		1212.54		801.02	
Trials (T)	1	13231.35	35.29***	8623.21	32.23***	914.94	2.67
T X G	2	1611.30	4.30*	839.89	3.14	236.74	.69
T X Ss within G	27	374.88		2675.20		342.07	

*p < .05, **p < .01, ***p < .001.

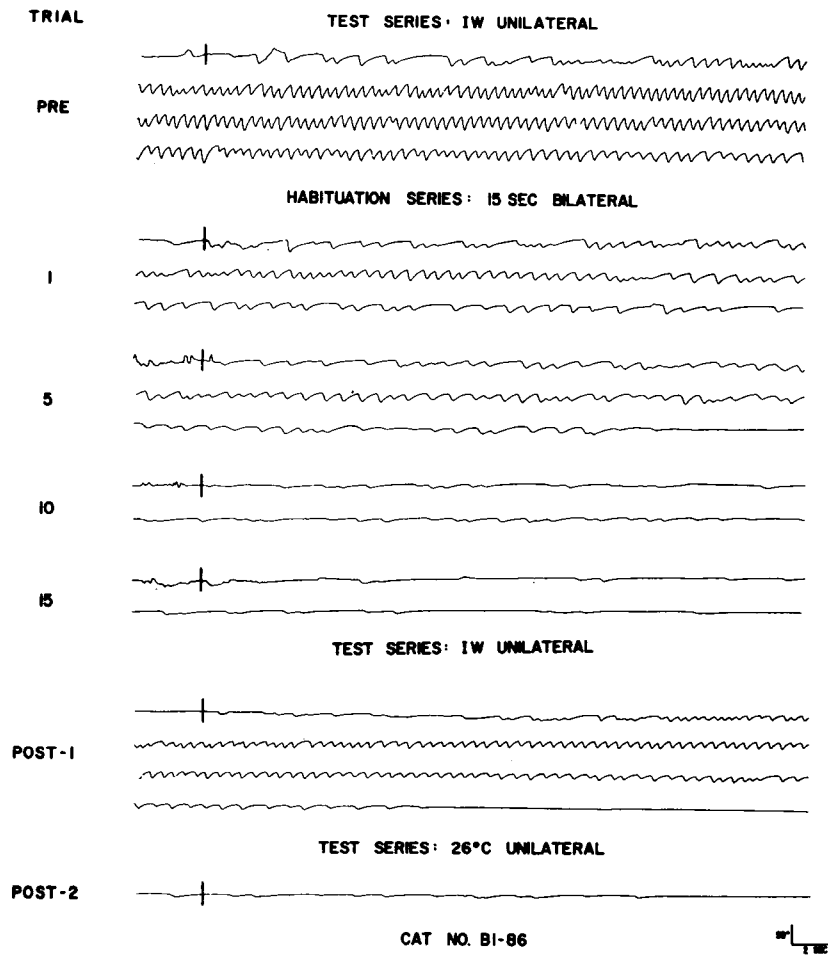


FIGURE 3. Nystagmus tracings of an animal in group BI. Markings are the same as in Figure 1. The bilateral habituating stimulus was less intense than that of the pre- and post-1 tests.

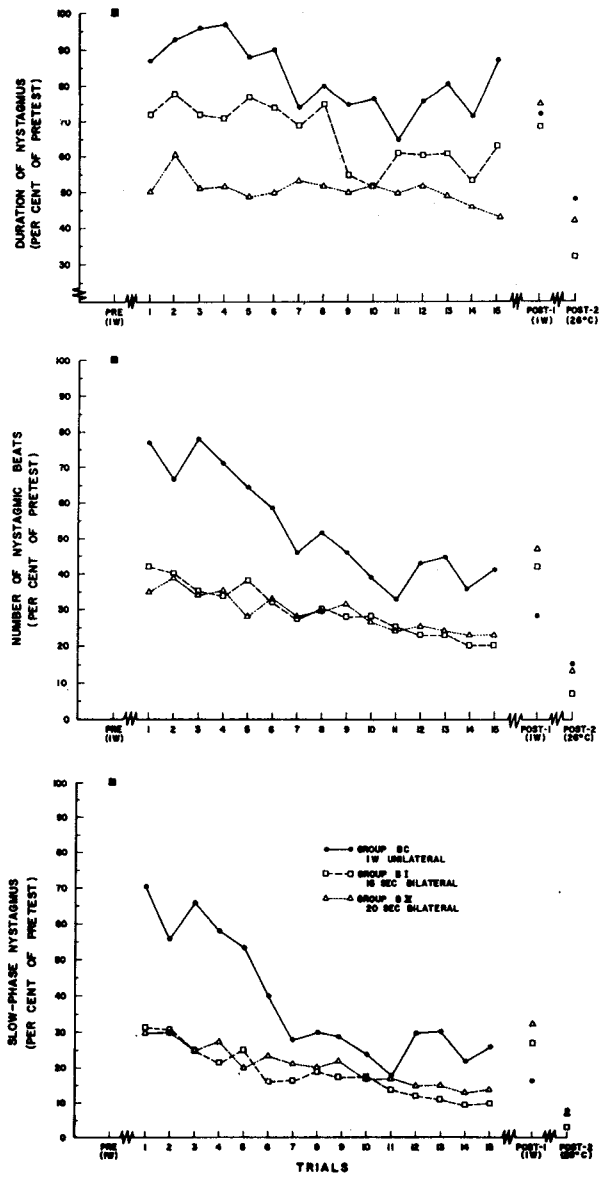


FIGURE 4. Mean slow-phase eye-movement, number of beats, and response duration of the B groups plotted as percentages of the pretest score. Groups BI and BII received bilateral habituating stimuli of less intensity than the unilateral habituating stimulus applied to BC.

TABLE 5
Results of the Analyses of Covariance on Pretest and Post-1
Test Nystagmus Scores for the B Groups

Source	df	Nystagmus Measure					
		Slow-Phase		Frequency		Duration	
		MS	F	MS	F	MS	F
Treatments	2	3,249.9	1.52	11,904.8	2.00	594.2	.15
Error	26	2,139.1		5,954.7		3,870.5	
Total	28						

[$F_{95(2,26)} = 3.37$]

Post-2 tests. The post-2 test stimulus for the B groups was a 26° C unilateral irrigation for 30 sec. This was the weakest of all group B stimuli, and it uniformly produced the least response given by these animals on any trial.

GENERAL DISCUSSION OF A AND B GROUPS

A habituation series of bilateral caloric irrigations has a pronounced effect upon the vestibular response to a unilateral irrigation, regardless of differences in intensity. Statistical analyses showed that nystagmus responses to unilateral trials after bilateral habituation were not significantly different from the response level of animals habituated to that same unilateral stimulus. This finding, indicating a transfer of habituation, differs from the studies using rotation as the bilateral habituation stimulus (Collins, 1964b; Hood & Pfaltz, 1954; Maxwell, et al., 1922). In the latter instances, habituation to rotation had no marked reductive effect on subsequent unilateral caloric irrigations. The fact that intensity differences existed between the rotatory habituation stimuli and the caloric transfer tests apparently does not account for the minimal amount or absence of transfer reported.

In the present study, intensity appears to be negligible factor in bilateral-to-unilateral transfer or caloric habituation, but it may have exerted influence in the unilateral-to-unilateral

situation. The latter effect is shown in the vigorous responses of group AC (habituated to 26° C unilateral irrigations) to the post-2 unilateral stimulus of ice water. Although probably affected to some extent by the previous habituation trials, these IW responses did not appear to be markedly reduced (Fig. 2).

The present data seem to offer some hypotheses concerning the reported failure of (bilateral) rotational habituation to transfer to (unilateral) caloric stimulation. It is possible that calorization (a gross stimulus compared to angular acceleration) activates neural elements in addition to those related to the lateral semi-circular canal; that exact placement of the head in the optimal caloric and in the optimal rotational positions is extremely critical; or that change in the position of the head significantly alters the pattern of stimulation from otolithic and proprioceptive receptors. One or a combination of these factors might cause sufficient changes in the neural patterning so that the stimulus generalization necessary for transfer of habituation does not occur (cf. Guedry, 1964).

Duration of an irrigation has been occasionally regarded as a subordinate consideration (especially to temperature effects) in caloric stimulation. However, pilot studies conducted prior to the present experiments indicated differences in response magnitude of cats to 15 vs 25 sec and 20 vs 30 sec bilateral stimuli, favoring the longer stimulus durations. The present

experiment allowed comparisons of nystagmus output to less disparate bilateral irrigations, *viz.* 15 vs 20 sec and 25 vs 30 sec. The former pair differed only in duration, and those data were highly variable. The 30 sec stimulus produced significantly more nystagmic eye movements than did the 25 sec stimulus, and although there was no statistically significant difference in the slow-phase data, there was approximately 30 per cent more slow-phase output in the first few 30-sec trials. These data indicate that the duration of irrigation may have some effect on nystagmus production even with a difference as small as 5 sec. It is possible that more pronounced effects of stimulus duration would be evident with lower rates of flow.

II. Effects of bilateral caloric habituation on subsequent tests.

DIRECTIONAL SPECIFICITY

Twenty min after receiving the treatments noted above, 2 groups, AC and BI, were given 10 additional habituation trials (with the usual interstimulus intervals) provoking responses in the direction opposite to the original habituation series. This was accomplished by stimulating the left ear of cats in the (unilateral habituation) AC group with 26° C irrigations for 30 sec, and by interchanging the temperatures (to 26° C left ear and 50° C right ear for 15 sec) for cats in the (bilateral habituation) BI group. Figures 5 and 6 show the mean response curves of both groups for the original and the subsequent habituation series for the 3 scored measures. The curves for number of beats and slow-phase eye movement exhibit a common characteristic, that is, the marked drop in response within the first 3-4 trials of the subsequent habituation series, in contrast with the more gradual decline of the original series. Responses to the first trial for each direction of nystagmus are of about the same magnitude for group AC, yet the response output drops more rapidly during the early trials in the subsequent tests. A similar effect was observed in the data obtained from group BI, although here the beginning levels of the 2 habituation series are somewhat different. Group BI received an IW pretest irrigation, and this intense stimu-

lation probably reduced the response to the first habituation trial. In spite of the differences in the initial levels, the BI curves for the second set of habituation trials exhibit the same exceptionally rapid early decline as that noted for group AC. However, the response for both groups AC and BI do not continue to drop at this rapid rate but, rather, level off so that the response to trial 10 of the subsequent series is at the same output level as trial 10 of the original series.

Previous studies (Collins, 1964a; Crampton, 1962; Henriksson, Kohut, & Fernandez, 1961) have indicated the apparent independence of direction with regard to vestibular habituation, that is, habituation of nystagmus in one direction did not appear to effect the response in the non-stimulated direction. These reports were based on a single stimulation in the previously unhabituated direction. In the present study, although the first response in the previously unhabituated direction was quite vigorous, responses to the following 2 or 3 irrigations dropped very rapidly, quite unlike the original decline. Thus, it would seem that the first habituation sequence did affect the responses in the non-stimulated direction. This apparent bi-directional effect of uni-directional habituation may be an extension of the transfer characteristic of the learning process postulated earlier (Halstead, 1935), in that the animal has learned to control the response to a method of stimulation. The absence of transfer effects on the first trial in the previously non-stimulated direction may be partly a result of the novelty of the first irrigation which deters the appearance of learning on that trial, but the effects become more apparent in succeeding trials.

It should be noted that, after the original and subsequent habituation trials, an additional trial, identical to those of the original habituation series was performed for each animal. Responses were still at the habituated level. This retention by the cat of habituation in one direction, despite subsequent habituation in the other direction, confirms the report of Henriksson, Kohut, and Fernandez (1961) but differs from findings reported for man (Fluur & Mendel, 1962a, b).

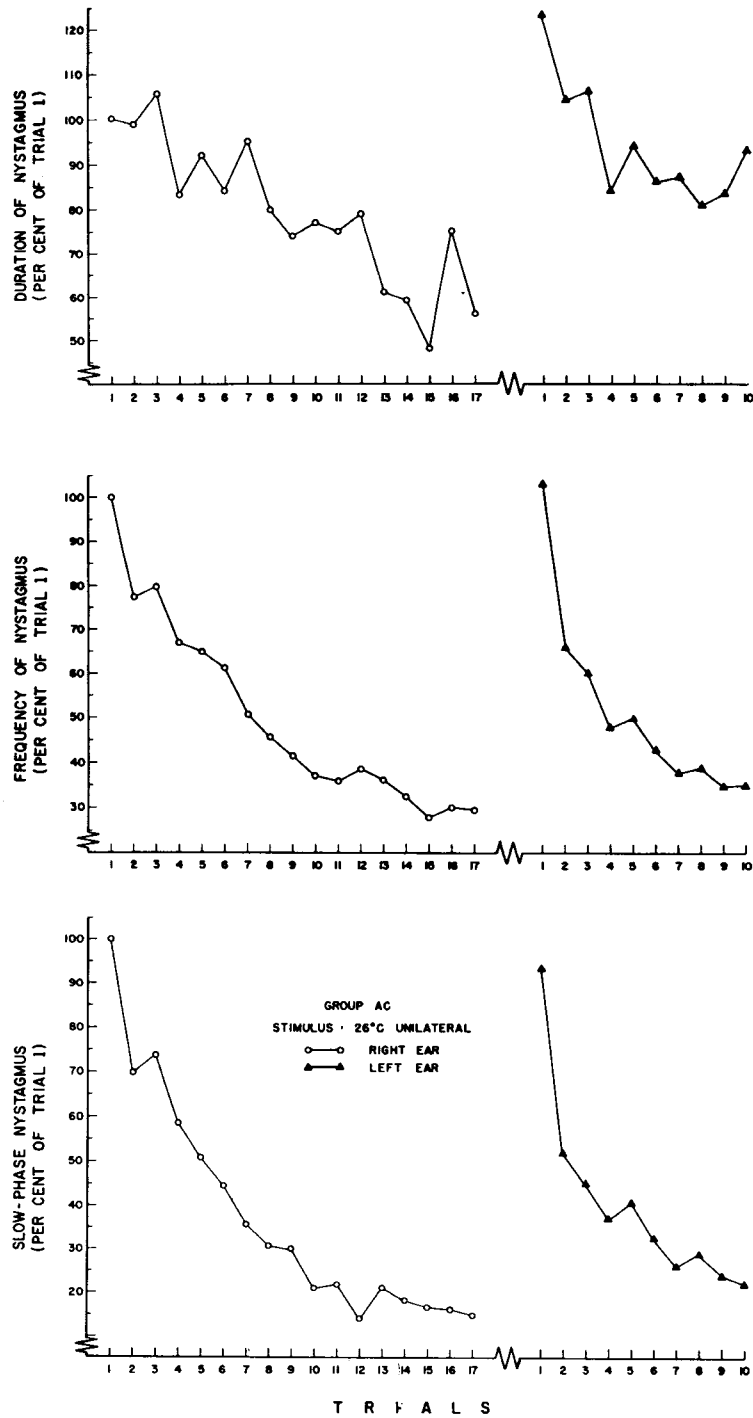


FIGURE 5. Trial-by-trial plots of nystagmus scores of group AC, in which habituation was produced for first one direction of nystagmus, and then the other. 17 unilateral irrigations of the right ear with a 26° C stimulus (and an 18th irrigation with IW not plotted) were followed by 10 left-ear stimulations. Note the high output on the first left-ear trial and then the rapid drop with succeeding trials.

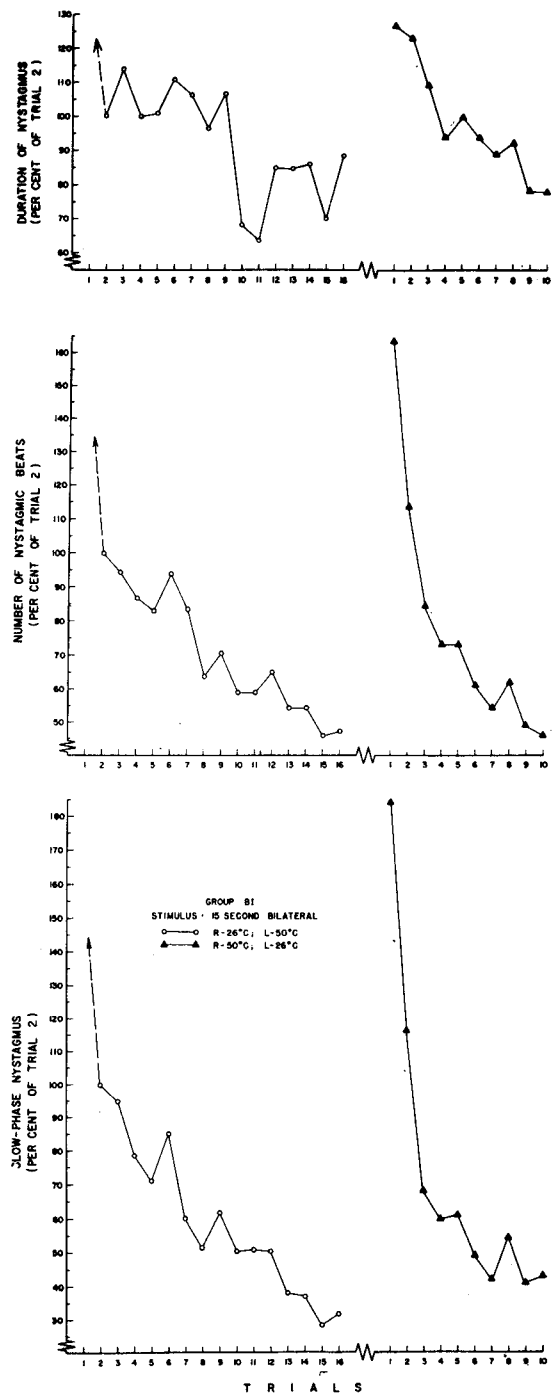


FIGURE 6. Trial-by-trial plots of nystagmus scores for group BI, in which habituation was produced for first one direction of nystagmus and then the other. A function similar to that depicted in Figure 5 for group AC is evident for BI, although here the "first" trial is probably underestimated since it was preceded by an IW irrigation (arrow).

RETENTION OF HABITUATION

Retention of nystagmus habituation has been reported for periods up to several weeks (Halstead, 1935; Henriksson, Kohut, & Fernandez, 1961). This temporal characteristic of habituation was investigated in group BC (habituated to 15 sec IW irrigations). Four animals from this group were tested one week after, and 4 other cats 2 weeks after the original habituation series (see Fig. 7). Retention was tested by 8 IW irrigations, in which the ear stimulated from alternated from trial-to-trial. Half of the animals began with a left-ear stimulation, the other half with a right-ear stimulation. Figure 8 shows the average responses on the initial series and on the retention series for the 3 scored measures. The small number of animals in each group prevented any reliable analysis of differences between the 1- and 2-week periods and, since data obtained in the retention series were similar for both groups, they were averaged to provide a single response

curve. Retention of habituation is apparent in the depicted differences for the habituated and unhabituated directions.

The course of the response decline obtained in this retention series for the unhabituated direction is very similar to that representing the previously unhabituated responses of groups AC and BI in which the question of directional specificity was examined (compare Figs. 5, 6 and 7). Thus, responses of group BC to the several trials in the unhabituated direction provided additional evidence for some bi-directional effect of unidirectional habituation.

HEAD POSITION

The direction of the nystagmic response to a caloric stimulus can be reversed by a change in head position sufficient to alter the direction of endolymph flow. Twenty min after exposure to the habituation sequence previously described, the heads of animals in groups AI and BII were lowered so that the plane of the

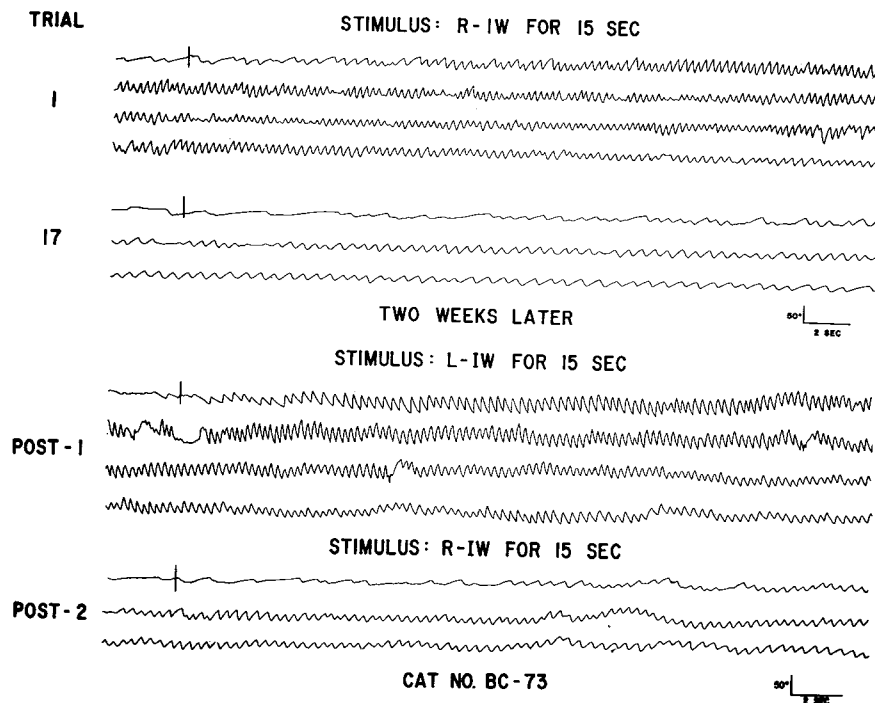


FIGURE 7. Nystagmograms from a cat which received 17 unilateral IW irrigations. When tested 2 weeks later, the response in the habituated direction shows some recovery, but is clearly weaker than that of the unhabituated direction. Markings the same as in Figure 1.

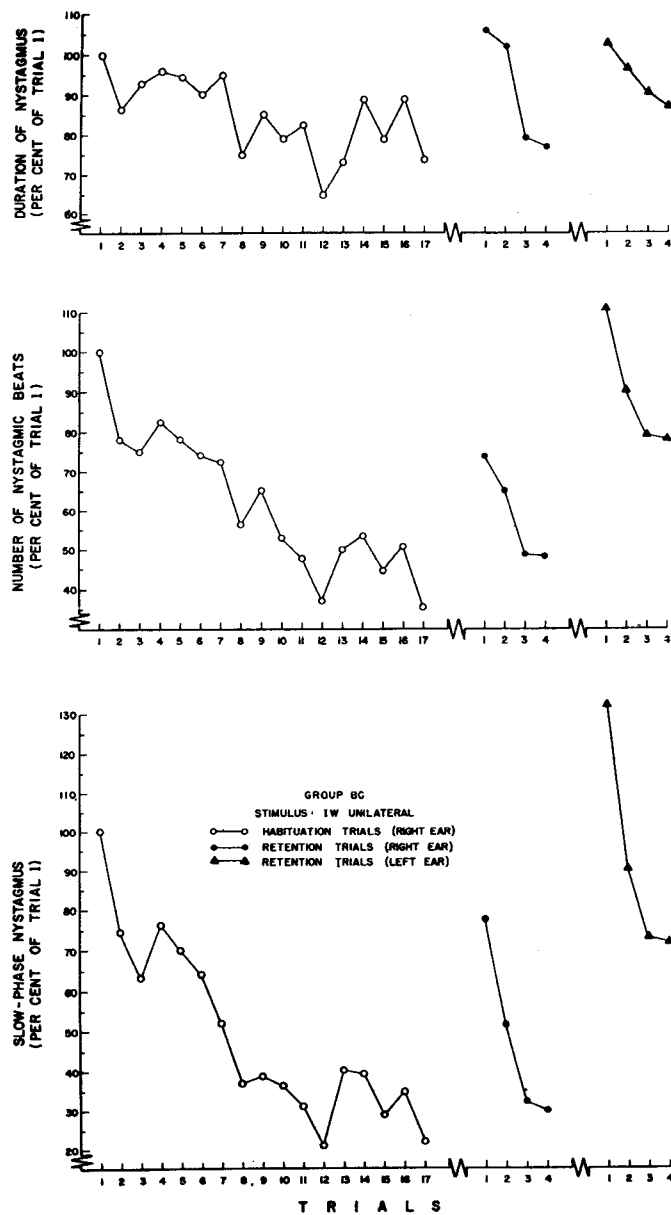


FIGURE 8. Retention of habituation in group BC. After initial unidirectional habituation (open circles), 4 cats were tested 1 week later and 4 others 2 weeks later (filled symbols) with nystagmus provoked in both directions. Data for the 1- and 2-week groups were similar and are averaged here. The habituated response shows some recovery in the subsequent testing, but declines more rapidly than it did in the original series. The unhabituated direction yields more vigorous responses.

horizontal canal was changed approximately 180° from the previous test position; and 6 trials were administered. The first 3 "head lowered" irrigations for half of the animals in each group were identical to the original habituation stimulus (right ear-26° C, left ear-50° C), while the temperatures were interchanged for the last 3 trials. The order of presentation of the 2 temperature-combinations was reversed for the remaining animals. The lowering of the head changed the direction of nystagmus previously elicited by these stimuli. That is, with the head upright, cool water in the right ear and warm water in the left produced nystagmus to the left but with the head lowered, the same stimulus produced nystagmus to the right.

Some animals did not respond to either stimulus when the head was tilted downward (perhaps, although it did not appear to be the case, due to inexact positioning). However, of the cats which did react, there was a definite directional difference as shown in Figure 9. These animals had been habituated to a stimulus provoking nystagmus to the left; when the same stimulus was administered with the head lowered, a vigorous response to the right was obtained. When the temperatures were interchanged, a reduced response in the habituated direction was elicited. The latter phenomena were also observed by Proctor and Fernandez (1963) who noted, in support of the notion that habituation is of central origin, that ". . . the mechanism underlying habituation is operating on the neural system which determines the direction of nystagmus" (p. 507). However, the responses produced with the head down in this study differed in appearance from those of the upright position, that is, the number of beats was greater and the amplitude was lower (see Fig. 9).

Another characteristic observed among groups receiving stimulation in alternating directions following habituation, was the apparent influence of the order of stimulation of the magnitude of the response. That is, there appeared to be less difference in the subsequent tests between the responses of the habituated and unhabituated directions when the first irrigation produced nystagmus in the previously habituated direction. Perhaps the novelty as-

sociated with the change of the head position served to heighten the first response elicited, regardless of the direction. However, this difference was only relative; the previously unhabituated direction uniformly yielded more vigorous responses.

DOUBLE IRRIGATIONS

Following habituation to 30 sec bilateral irrigations, animals in group AII each received 2 double irrigations (simultaneous bilateral calorizations of 26° C for 30 sec) at the usual inter-stimulus intervals of 20 min. With such stimulation, the horizontal component of nystagmus is ordinarily abolished and a vertical nystagmus usually appears. Since the horizontal component of the response had been subjected to uni-directional habituation, the double irrigations were administered to determine whether the nystagmus so elicited would evince a horizontal component in the unhabituated direction (see Fig. 10). Animals variously gave random eye movements or weak (prolonged, low velocity) responses in one direction or the other (some of which may have included a vertical component).

Following the double irrigations, both directions were tested with 30 sec bilateral calorizations of 26° C and 50° C (the temperatures were interchanged to produce both directions of nystagmus). The order of presentation of the 2 bilateral irrigations was alternated from animal-to-animal. Responses in the habituated direction remained at a reduced level while responses in the previously non-stimulated direction were vigorous.

III. Additional observations.

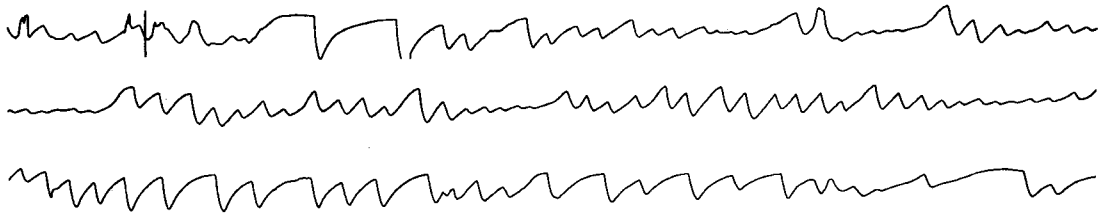
SEX DIFFERENCES

Of the 60 animals tested, 38 were females and 22 were males. Each male was matched with a female randomly chosen from the same group and *t* tests were conducted on the pretest nystagmus data (see Table 6). Female animals were found to produce a significantly (.05 level) greater amount of response as measured by both slow-phase displacement and number of beats. Although this may represent a true sex difference in vestibular functioning, it is

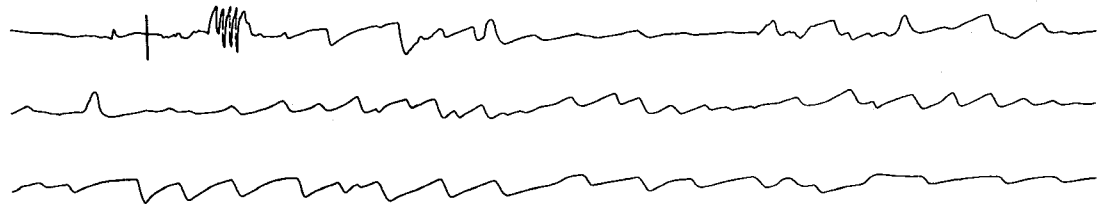
TRIAL

STIMULUS: R-26°C, L-50°C FOR 20 SEC

1



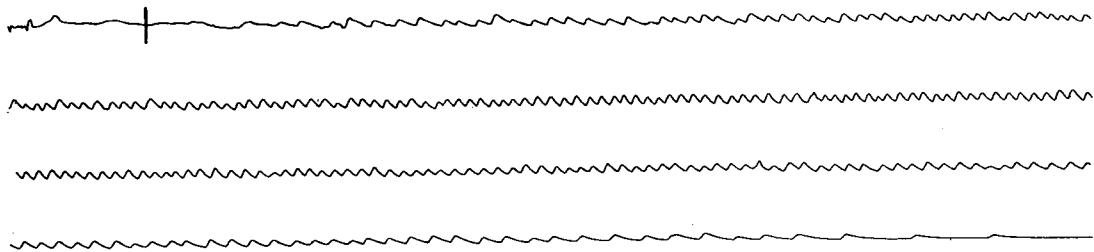
15



HEAD LOWERED

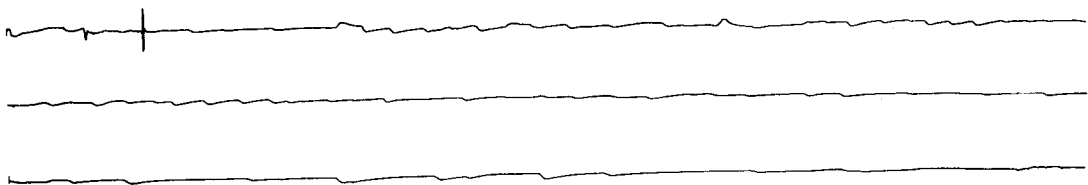
STIMULUS: R-26°C, L-50°C FOR 20 SEC

POST - 3



STIMULUS: R-50°C, L-26°C FOR 20 SEC

POST - 6



CAT NO. BII - 93

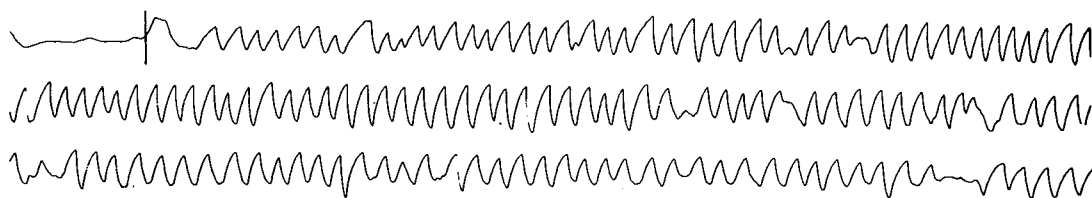
50°
2 SEC

FIGURE 9. Recorded nystagmus from a cat exposed to a habituation series of simultaneous bilateral calorizations with its head elevated. Lowering of the head changes the direction of nystagmus although the same stimulus is applied. Responses in the "practiced" direction are clearly weaker than those in the previously untested direction.

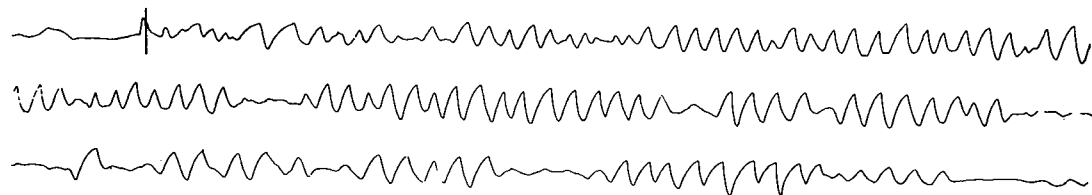
TRIAL

STIMULUS: R-26°C, L-50°C FOR 30 SEC

I



15



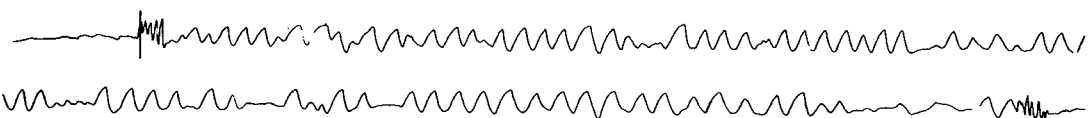
STIMULUS: R-26°C, L-26°C FOR 30 SEC

POST - 3



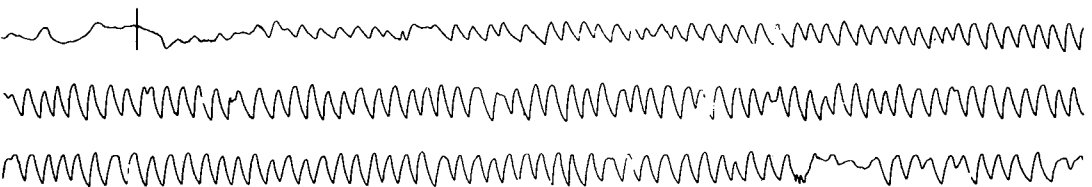
STIMULUS R-26°C, L-50°C FOR 30 SEC

POST - 5



STIMULUS: R-50°C, L-26°C FOR 30 SEC

POST - 6



CAT NO. AII - 62

50°
2 SEC

FIGURE 10. Nystagmus tracings from a cat in group AII. Post-3 and post-4 tests were "double irrigations" (simultaneous bilateral calorization with identical water temperatures) which yielded a weak and inconsistent left-beating nystagmus. Post-5 was identical to the habituation series and the response remained at its previous low level. In post-6, temperatures were interchanged, nystagmus was elicited in the opposite direction, and a vigorous response appeared.

TABLE 6

Results of *t* test Comparisons of Pretest Nystagmus Measures for 22 Male and 22 Female Cats

<u>Measure</u>	<u>t Value</u>	<u>Significance level</u>
Slow-phase	2.03	.05
Frequency	1.76	.05
Duration	1.22	---

$$t_{.05(42)} = 1.675$$

quite possibly due only to sex-related non-vestibular factors (e.g. density or mass of bone and other tissue) and may thereby be limited to caloric stimulation. There was no statistically significant sex difference in corneo-retinal potential as determined by comparison of the calibration constants

OPTOKINETIC NYSTAGMUS

Nystagmographic recordings of eye-movements elicited by both clockwise and counterclockwise rotation of the optokinetic drum were obtained before and after the vestibular trials for 49 animals. Calibration constants calculated for each of these exposures were compared statistically to examine possible effects of the habituation series on the optokinetic re-

sponse (see Table 7). No statistically reliable differences occurred as a result of the intervening vestibular stimulation, nor were any directional differences in the optokinetic responses evident. Figure 11 shows optokinetic nystagmus recordings for both directions before and after vestibular habituation. The tracings show no differences in the form or quality of the responses from one condition to another.

INVERSE RESPONSES

Two types of inverse vestibular responses were observed: secondary nystagmus and inverted primary nystagmus. Secondary nystagmus (a response following, and in the direction opposite to the primary response) has been reported as a result of both rotatory and uni-

TABLE 7

Results of the Analyses of Variance on Optokinetic Calibration Constants for Clockwise and Counterclockwise Drum Rotation Before and After Vestibular Habituation

<u>Source</u>	<u>df</u>	<u>MS</u>	<u>F</u>
Order (O)	1	12147	1.75
Subjects within O	96	6937	
Direction (D)	1	2096	.773
D X O	1	2682	.989
D X Subject within O	96	2711	

$$[F_{.95(1,96)} = 3.95]$$

OPTOKINETIC NYSTAGMUS

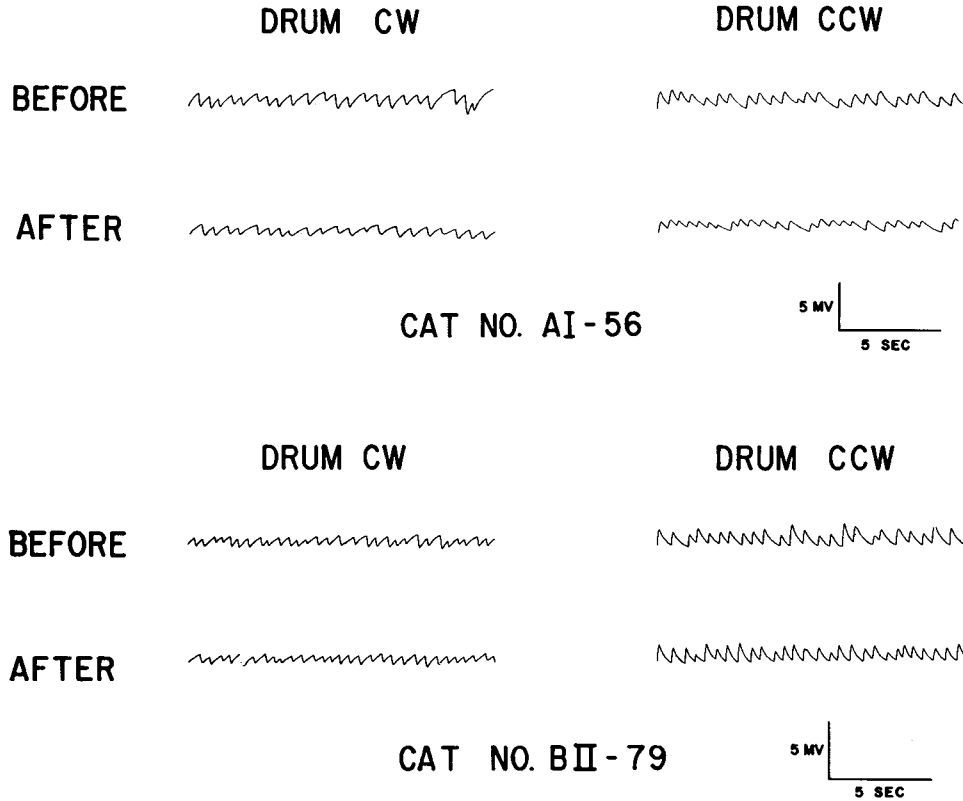


FIGURE 11. Optokinetic nystagmus obtained from 2 cats. Drum speed was 24°/sec.

lateral caloric stimulation in the cat (Collins, 1964a, b). In the present study, secondary reactions occurred frequently (322 trials) in the tracings of 51 cats. The magnitude of these reactions ranged from "strong" to "very weak", and some of the latter may have represented induced spontaneous responses similar to those reported for man by Fluor and Mendel (1961b).

The more intense stimuli appeared to elicit secondary responses more frequently, although there was no strict rank-order relation observed between stimulus intensity and number of occurrences. Fewer secondary reactions occurred as the number of trials increased. This decline of secondary nystagmus has been reported in recent studies of the cat for both rotatory and unilateral caloric stimulation (Collins, 1946a, b), but is not reported to occur in man (Fluor & Mendel, 1962a, b).

Although secondary nystagmus was not observed on every trial (a period of approximately 5 min), animals frequently exhibited a response in the direction of the secondary reac-

tion 10-15 min after a stimulation, during the recording of the response of another animal (animals were tested in pairs). These late reactions (some of which may have been induced spontaneous nystagmus) occurred without additional stimulation, after a 5 min period in illumination, and ranged from a "strong" response (Fig. 12) to only one beat every 5-7 seconds. The response shown in Figure 12 is the most vigorous of all the observed reactions of this type and therefore represents the extreme example.

Inverted primary nystagmus (a response in the opposite direction of the expected primary which appears prior to, or instead of, a response appropriate to the stimulus, Collins, 1963; Groen & Jongkees, 1949) was observed occasionally. Five animals exhibited occasional clear, though weak, inverted primary responses, in which the inverted beats were in evidence for 10-30 sec after termination of the irrigation. It is possible that these unusual responses are related to the delayed reactions noted above and depicted in Figure 12.

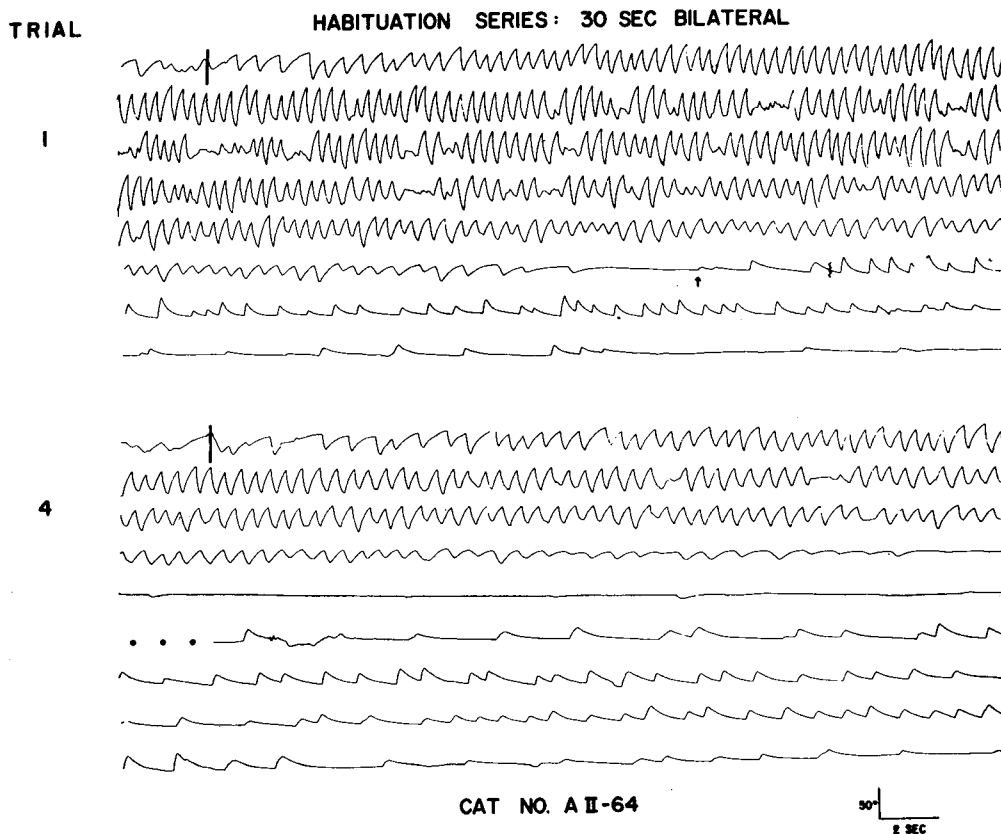


FIGURE 12. Examples of inverse nystagmus. The tracings for trial 1 show vigorous primary and secondary reactions. The arrow indicates the start of secondary nystagmus; the jagged vertical line denotes a change of paper speed from 2.5 to 1.25 cm/sec. The tracing for trial 4 shows a brisk but reduced primary nystagmus; no secondary response appeared. Dots indicate the passage of approximately 10 min (including 5 min in illumination) after which, without benefit of any additional stimulus, a vigorous response in the direction of secondary nystagmus appeared. The latter was recorded in darkness while another animal was being tested (paper speed: 2.5 cm/sec).

SUMMARY

Transfer of bilateral caloric nystagmus habituation to unilateral calorization was investigated in a group of 60 cats. Habituation to bilateral caloric irrigations markedly reduced responses to both less intense and more intense unilateral stimulation.

Subsequently testing provided information concerning the effects of caloric habituation on: (1) directional specificity of response, (2) retention of the response decline, and (3) optokinetic nystagmus. Statistical analyses also indicated a sex difference in response magnitude.

REFERENCES

- Collins, W. E., 1963: Observations on the elicitation of secondary and inverted primary nystagmus from the cat by unilateral caloric irrigation. *Aerospace Med.*, 34, 1137-1142.
- Collins, W. E., 1964a: Nystagmus responses of the cat to rotation and to directionally equivalent and non-equivalent stimuli after unilateral caloric habituation. *Acta Otolaryng.* (in press).
- Collins, W. E., 1964b: Primary, secondary, and caloric nystagmus of the cat following habituation to rotation. *J. comp. physiol. Psychol.*, 57, 417-421.
- Crampton, G. H., 1962: Directional imbalance of vestibular nystagmus in cat following repeated unidirectional angular acceleration. *Acta Otolaryng.*, 55, 41-48.
- Dunlap, K., 1925: Adaptation of nystagmus to repeated caloric stimulation. *J. comp. Psychol.*, 5, 485-493.

- Edwards, A. L., 1960: *Experimental design in Psychological research*. New York: Holt, Rinehart, and Winston.
- Fernandez, C., and Schmidt, R., 1962: Studies on habituation of vestibular reflexes. II. Effect of caloric stimulation in decorticated cats. *Ann. Oto-, Rhino-, Laryngol.*, 71, 299-320.
- Fluur E. and Mendel, L., 1962a: Habituation, efference and vestibular interplay. I. Monaural caloric habituation. *Acta Otolaryng.*, 55, 65-80.
- Fluur, E. and Mendel, L., 1962b: Habituation, efference and vestibular interplay. II. Combined caloric habituation. *Acta Otolaryng.*, 55, 136-144.
- Griffith, C. R., 1920: The organic effects of repeated bodily rotation. *J. exp. Psychol.*, 3, 15-47.
- Groen, J. J. and Jongkees, L. B. W., 1949: The measurement of the temperature at the eardrum during the caloric test of the labyrinth. *J. Physiol.*, 108, 33-36.
- Guedry, F. E., 1964: Psychophysiological studies of vestibular function: In W. D. Neff (Ed.). *Advances in Sensory Physiology*, New York: Academic Press.
- Halstead, W. C., 1935: The effects of cerebellar lesions upon the habituation of post-rotational nystagmus. *Comp. Psychol. Monog.*, 12, 1-130.
- Henriksson, N. G., 1956: Speed of slow-component and duration in caloric nystagmus. *Acta Otolaryng.*, Suppl. 125, 20 pp.
- Henriksson, N. G., Fernandez, C., and Kohut, R. I., 1961: The caloric test in the cat. *Acta Otolaryng.*, 53, 21-32.
- Henriksson, N. G., Kohut, R. I., and Fernandez, C., 1961: Studies on habituation of vestibular reflexes. I. Effect of repetitive caloric test. *Acta Otolaryng.*, 53, 333-349.
- Hood, J. D., and Pfaltz, C. R., 1954: Observations upon the effects of repeated stimulation upon rotational and caloric nystagmus. *J. Physiol.*, 124, 130-144.
- Maxwell, S. S., Burke, U. L., and Reston, C., 1922: The effect of rotation on the duration of after-nystagmus in the rabbit. *Amer. J. Physiol.*, 58, 432-438.
- Proctor, L. R., and Fernandez, C., 1963: Studies on habituation of vestibular reflexes. IV. Effect of caloric stimulation in blindfolded cats. *Acta Otolaryng.*, 56, 500-508.
- Ward, P. H., and Fernandez, C., 1963: Experimental studies on vestibular mechanisms. I. Directional preponderance of nystagmus in cats. *Ann. Oto-, Rhino-, Laryngol.*, 72, 507-528.