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PRIMARY, SECONDARY, AND CALORIC NYSTAGMUS OF THE CAT FOLLOWING HABITUATION TO ROTATION

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OKLAHOMA CITY, OKLAHOMA

JULY 1963

Civil Aeromedical Research Institute, Federal Aviation Agency, Oklahoma City, Oklahoma. CARI Report 63-13, PRIMARY, SECONDARY, AND CALORIC NYSTAGMUS OF THE CAT FOLLOWING HABITUATION TO ROTATION by W. E. Collins, July, 1963.

1. Vestibular
2. Nystagmus
3. Adaptation
4. Transfer Effects
5. Sensory Physiology
6. Angular Acceleration

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PRIMARY, SECONDARY, AND CALORIC NYSTAGMUS OF THE CAT FOLLOWING HABITUATION TO ROTATION

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PRIMARY, SECONDARY, AND CALORIC NYSTAGMUS OF THE CAT FOLLOWING HABITUATION TO ROTATION[1]

WILLIAM E. COLLINS, PH. D.

Civil Aeromedical Research Institute, FAA Oklahoma City, Oklahoma

Repeated rotation of the cat in total darkness results in a marked decline of the eye-movement response (Crampton, 1961; 1962; Crampton & Schwam, 1961). Similar findings have been obtained when the stimuli were unilateral caloric irrigations performed in an illuminated environment. (Henriksson, et al., 1961). Such response diminution appears specific to the direction of the habituation trials.

It would seem reasonable to hypothesize that habituation to a specific mode of vestibular stimulation would transfer to a different stimulus modality. The evidence, however, is conflicting. In studies of rabbits, Maxwell, Burke and Reston (1922) and Hood and Pfaltz (1954) found a clear "habituation" of nystagmus to rotation, but a". . . normal response to the caloric test at the close of the series" (Maxwell et al., 1922). Dunlap (1923) found an habituation transfer-effect in rabbits from repetitive caloric irrigation to rotational stimuli.

The present study was designed: (a) to investigate the question of transfer of rotatory nystagmus habituation to caloric stimulation, (b) to depict clearly the manner in which rotatory habituation of the cat occurs, and (c) to examine the effects of stimulus repetition upon secondary nystagmus.[2]

[1] Study conducted with the technical assistance of Kenneth E. Swain while the author was at the U.S. Army Medical Research Laboratory, Fort Knox, Kentucky. The assistance of Mary Jayne Capps and Joseph E. Duchon in the process of data reduction is gratefully acknowledged.

[2] "Secondary nystagmus occurs after, and is in an opposed direction to, a primary response to a vestibular stimulus. It appears in the absence of a change in vestibular stimulation, when the primary has begun to decline" (Collins, 1963b).

METHODS

APPARATUS

Rotatory. The turntable (Guedry & Kalter, 1956) was located in a light-proof room. The acceleration program consisted of the following: (a) 30 sec at a constant velocity of 1 rpm; (b) 13 sec of CCW acceleration (4.15°/sec²); (c) 60 sec at a constant velocity of 10 rpm; (d) a sub-threshold deceleration of 0.18°/sec² for 333 sec to zero velocity. This combination of CCW threshold accelerations and sub-threshold decelerations limited nystagmus elicitation to a single direction, viz., with the fast phase to the left.

Caloric. Caloric stimulating equipment consisted of a water receptacle, an adjustable stand, tubing, a glass nozzle, and a chemical thermometer (± 0.5° C). Water temperature was maintained at 23.5° C and, whenever adjustments were necessary, they were made immediately prior to each trial. Stimuli consisted of 30 sec of irrigation of the right ear, thereby providing nystagmus with the fast phase to the left.

RESTRAINT

Animals were restrained according to the method of Henriksson, Fernandez, and Kohut (1961). Briefly, cats were anethetized and holes were drilled transversely through their canine teeth several days prior to testing. Restraint was effected by wrapping the animal in a towel, placing it in a cat-box, and inserting a strand of piano wire through the holes in the canine teeth. The wire was held securely and stretched taut by means of an adjusting device attached to the front of the box. The animal's head was thus secured in a position elevated from that of normal carriage.

RECORDING

Eye movements were recorded with an Offner Type T Electroencephalograph. A 1.4 sec RC time constant was employed in amplification. Signals were led from needle electrodes to a patch-panel on the turntable, through slip-rings, to the recorder, located in an adjoining room. Three electrodes were used with each animal. Two were positioned by the outer canthi and an indifferent electrode was located on the crown near the mid-line of the skull.

PROCEDURE

All testing took place during a single day, in total darkness, and with the animal positioned on the turntable. The preliminary and post-tests consisted of unilateral caloric irrigation (tests of transfer). Water temperature was adjusted and the nozzle inserted into the cat's ear just prior to turning off the room lights. Habituating trials were 15 CCW accelerations of 4.15°/sec². Decelerations were sub-threshold. For all rotation trials, the cat was placed with its head at the center of rotation. Electrodes were always examined and the animals alerted in illumination, immediately prior to darkening the room and initiating a stimulus. Stimulation always began within 10 sec of the onset of total darkness and rest intervals of 12-15 min (including the deceleration period) separated trials.

Data from 10 of 15 cats are presented here. Five sets of records were discarded for the following reasons: (a) responses to the preliminary test or to the first rotation were so poor as to be not quantifiable (three animals). Testing was immediately stopped. (b) Voluntary eye movements, combined with high nystagmic amplitude, blocked the recording pens on a number of trials (one animal). (c) Loss of electrode contact interrupted the stimulus series (one animal).

SCORING

Nystagmic tracings were analyzed for three types of scores: (a) slow-phase displacement of the eyes was scored by measuring the vertical distance from the peak to the base-line of each nystagmic beat. These values were accumulated for successive 3-sec intervals and translated into millivolts by means of a calibration signal. (b) Nystagmic frequency was calculated simply by counting the number of beats within the same 3-sec intervals. (c) Duration of the primary response was measured from the onset of acceleration (or the termination of the caloric irrigation) to the concluding phase of the last beat of primary nystagmus. Measurements of secondary nystagmus duration began with the first beat of the secondary regardless of where it occurred in point of time.

With this method of scoring, slow-phase displacement-measures occasionally ended in an earlier 3-sec interval than did the duration or the frequency measures (the time scale for the latter two was, of course, always identical). This apparent discrepancy is due to the fact that, toward the end of a response pattern, long, low-velocity beats appeared. Frequently only the early part of the beat contained a measurable displacement, but the beat continued into a succeeding 3-sec interval before a fast-phase brought it to termination.

RESULTS

Some examples of the recorded nystagmic activity appear in Figure 1. The decline in the eye-movement response with repeated rotation is clearly evident for both the animals depicted. When the slow-phase and the frequency measurements are plotted for trials 1, 5, 10, and 15, the manner in which the response decline occurs comes more sharply into focus (Figure 2). Initially, nystagmus "overshoots" the stimulus period, i.e., the response continues to build up for a few seconds after stimulus termination. Within the first 5 trials, however, a considerable reduction in eye movement is accomplished and the response becomes, in one sense, more "adequate," i.e., nystagmus begins to fall off sharply with stimulus termination and the duration is markedly curtailed (cf. Crampton, 1964).

Plots of the average rotatory response-per-trial (Figure 3) for the 3 measures (slow-phase displacement, frequency, and duration) are in general agreement in showing a declining func-

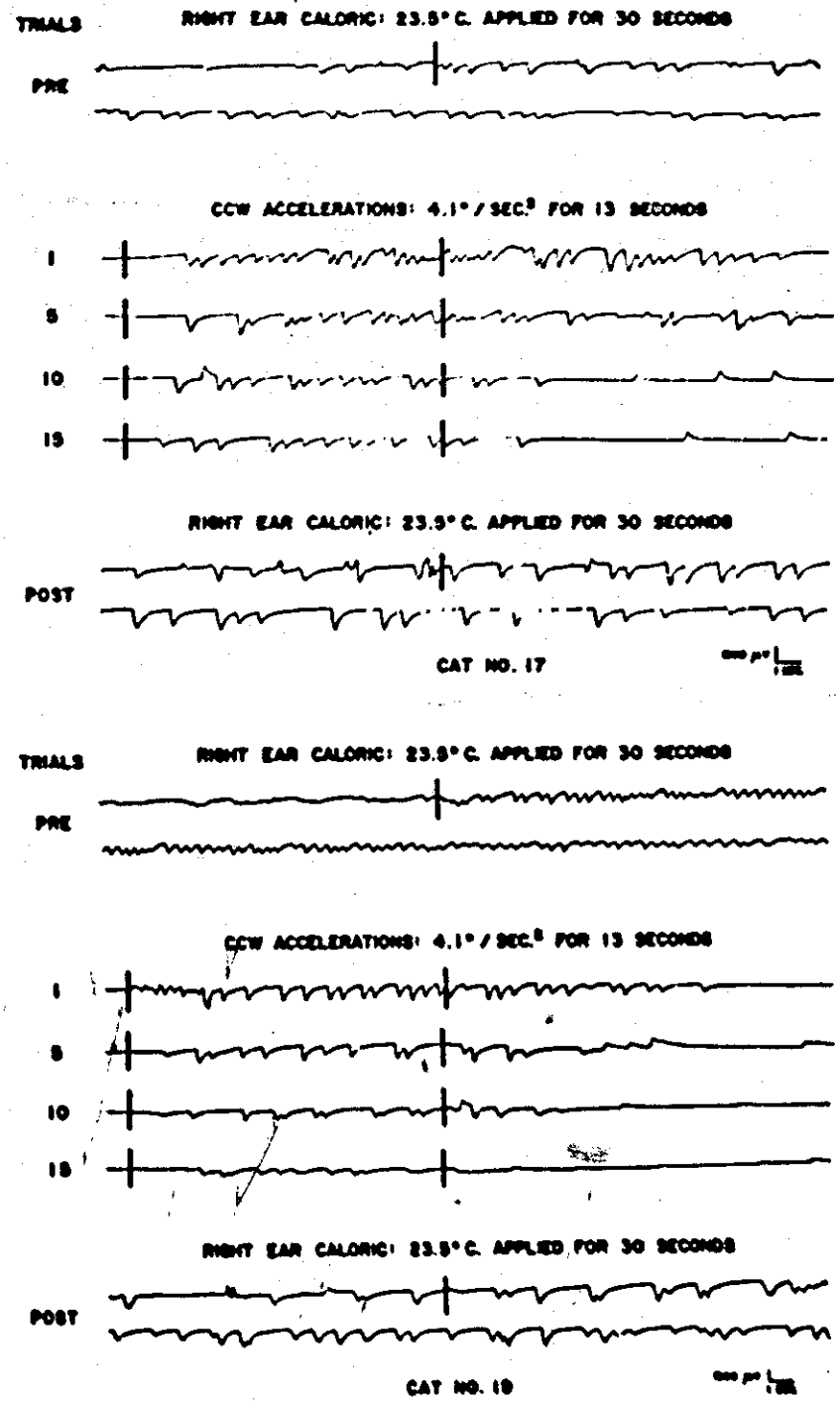

Figure 1. Nystagmus tracings obtained for two animals. The change in the form of the response from pre- to post-test, and the overall decline in rotation-induced nystagmus as a function of repeated stimulation are clearly evident. Pairs of heavy vertical bars demarcate the acceleration periods. The single vertical bars through the caloric records indicate the termination of irrigation (tracings include the last 14 sec of irrigation). Only a few beats of secondary nystagmus are evident for the rotation trials presented.

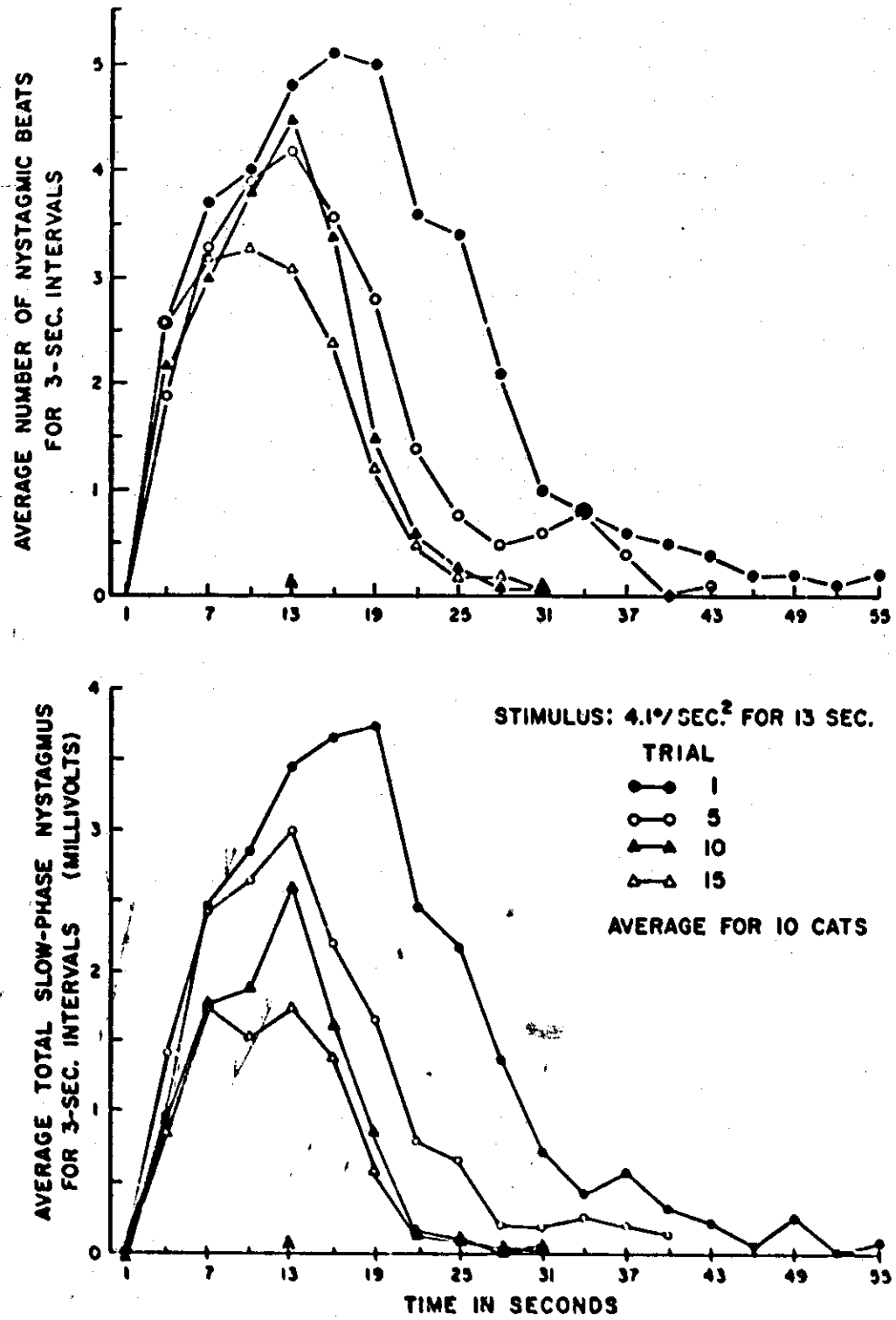

Figure 2. Alterations in the nystagmic response curve with repeated stimulation. Note the overshooting of the response in trial 1. Zero time indicates the point at which acceleration was initiated and arrows show time of stimulus termination. Data were plotted in 3-sec intervals, with the exception of the first sec.

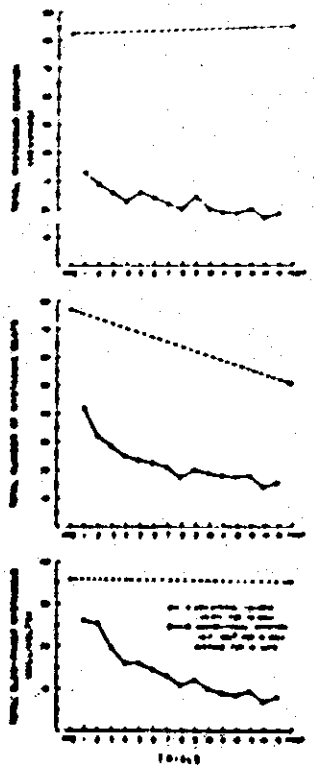

Figure 3. Average slow-phase displacement, duration, and frequency of nystagmic beats for the caloric pre- and post-tests and for the 15 rotation trials. Only the frequency measure shows a pre- to post-test decline. A steady and fairly uniform drop in the response to angular acceleration is apparent.

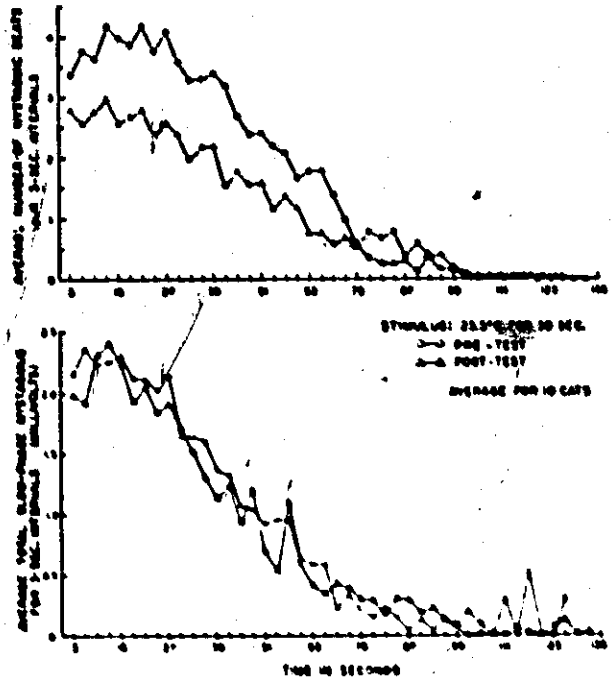

Figure 4. Time-course plots of pre- and post-test caloric nystagmus. Only the frequency has declined as a result of intervening rotations. Zero time indicates moment of termination of the irrigation stimulus.

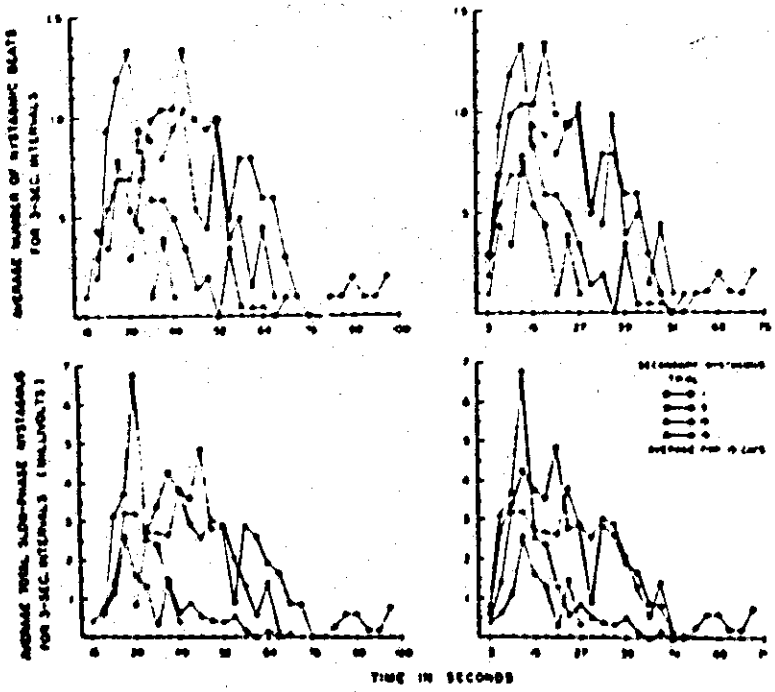

Figure 5. Decline of secondary nystagmus as a function of repeated elicitation. Graphs on the left are plotted according to true time measurements made from the point of stimulus initiation. Note that the secondary begins earlier as the number of trials increases. Graphs on the right are plotted with an arbitrary zero time, as though each curve began at the same point in time.

tion, although the least affected parameter is the duration of the response. The same consistency is not evident when the pre- and post-test caloric measures are compared. Neither duration nor total slow-phase output of the caloric response shows any indication of being affected by the series of habituating rotatory trials. However, a decline of about one-third is evident for the frequency of the caloric nystagmus. This difference between the pre- and post-test caloric trials is representatively depicted by the tracings in Figure 1, and is evident in the graphed results in Figure 4.

Plotted data for secondary nystagmus are presented in Figures 5 and 6. Although much less regular in appearance than the primary reaction, the secondary shows a similar decline as a function of repeated rotation (Figures 5 and 6). Its onset also occurs earlier as the intensity and duration of the primary are reduced (Figure 5). It should be noted that all 10 animals gave secondary responses to initial rotation trials; the number so responding was reduced to 6 by trial 15.

Data for pre- and post-test caloric secondary are included in Figure 6. These data should provide no more than a very rough guide however, since only 4 animals demonstrated a secondary during the pre-test. Of these, one gave considerably less response, one considerable more, and two gave no secondary during the post-test. In addition, two cats which had shown no pre-test secondary, gave weak responses to the post-test.

DISCUSSION

PRIMARY NYSTAGMUS

Rotational Habituation. In agreement with the findings of Crampton (1961; 1962) and Crampton and Schwam (1961), the obtained data demonstrate a clear and fairly uniform decline in the total slow-phase eye-movement response of the cat to repeated rotational stimulation in total darkness (Figure 3, lower graph). Further analysis shows that the decline is present in all three of the measures employed in this study, although the duration of nystagmus

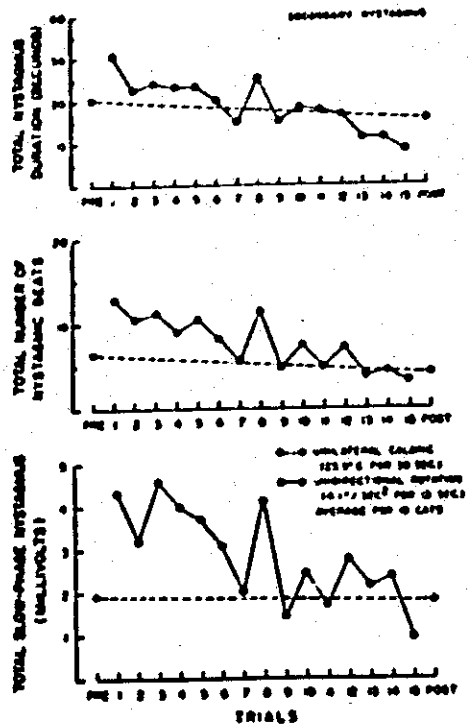

Figure 6. Average slow-phase displacement, duration and frequency of secondary nystagmus obtained during successive trials. Pre- and post-test data are based on only a few measurements. All animals gave secondary responses to rotation, however, and the decline in output with successive trials compares favorably with similar data for primary nystagmus.

is less markedly reduced than are either the frequency of the beats or the amount of slow-phase displacement (Figure 3).

The manner in which the response decline occurs is of interest. Evidence in Figure 2 indicates that: (a) During the first 4 trials, nystagmic output shows no steep decline immediately after stimulus termination; (b) by trial 5, nystagmus begins to drop sharply with the termination of acceleration; (c) a considerable amount of nystagmic decline occurs within the first 5 trials; (d) in early trials, the most affected portion of the response curve is that which occurs immediately after stimulus termination. Thus, in the cat at least, several specific changes occur early in the series of stimulations. Later trials tend to produce a more general, overall depression of the nystagmic response curve.

Transfer of Habituation. The data in Figures 3 and 4 indicate that the series of 15 rotations had only a mild influence upon the nystagmic response to caloric irrigation. The effect was limited to a reduction in beat-frequency. Thus, although a smaller number of beats occurred, neither duration nor slow-phase output showed any diminution after the intervening series of rotations. Further, this reduction in beat-frequency is no greater than that which might be obtained by 3 or 4 successive irrigations (Collins, 1963a).

Maxwell, Burke, and Reston (1922) reported a "normal" response to a "cold water douche" (of unspecified temperature and duration) after rotatory nystagmus habituation of the rabbit. However, they did not include any pre-rotation trial with which the post-rotation caloric response could be compared. Further, a fairly vigorous caloric nystagmus might well have been obtained if an ice-water irrigation was applied, due to the intense nature of such a stimulus. One or both of these factors could account for the "normal" response obtained. Some confirmation for the point regarding stimulus intensity appears in their article: ". . . when the nystagmus following rotation at the rate used in these experiments had wholly ceased to appear, a vigorous after-nystagmus could

be obtained by using a more rapid rate. . ." (Maxwell, Burke & Reston, 1922, p. 435).

Hood and Pfaltz (1954) also claimed an "unimpaired" caloric response in the rabbit after a clear rotational habituation was demonstrated. However, they relied almost solely upon the duration of the response in judging the presence or absence of such a decline. Further, both duration and frequency of the nystagmic response to their caloric tests exceeded initial rotatory responses by average factors of about 3.

Dunlap (1925) mentioned the importance of nystagmic changes other than duration of the response. Employing an extensive number of trials, he demonstrated nystagmus habituation to unilateral caloric stimuli in rabbits. Although duration was the measure which he reported, Dunlap (1925) noted that "In the later part of the series, for example, 'twenty-five seconds nystagmus' may mean only one or two jerks. The actual nystagmic adaptation against the irrigation stimulus was really, therefore, much greater and more rapid than the mere time measurements indicate" (Dunlap, 1925 p. 492). Dunlap also found an absence of rotation-induced nystagmus after the caloric habituation, i.e., a stimulus generalization. However, his stimulating technique differed from the others mentioned in that he used intense (ice water) habituating stimuli, a large number of trials, and completely abolished nystagmus to stimulation of first the left horizontal canal, and then the right, before examining the transfer effect.

The failure to obtain significant transfer effects in the present study does not appear due to a simple arousal variable, although the latter is an extremely potent factor in nystagmic output (Collins, 1962; Collins et al., 1962, Collins & Poe, 1962; Crampton & Schwam, 1961; Wendt, 1951). Several animals were given additional caloric trials subsequent to the post-test. There was no unusual drop in response with the addition of these extra trials. Hence, the high-output caloric post-test response is not due to the alerting value of a sudden change from one mode of stimulation to another. Nor can the response decline obtained as a function of repeated rotation be accredited to this factor. A steady decline in cat nystagmus has been demonstrated even when special precautions were taken to insure arousal during each elicitation (Crampton, 1961; Crampton & Schwam, 1961).

However, one or both of the following factors might account for the vigorous post-test responses obtained in this study. In addition, they provide reasons for the fact that Dunlap (1925) obtained a transfer effect while Maxwell, Burke and Reston (1922) and Hood and Pfaltz (1954) did not. (a) In this study, the caloric stimulus initiated a much more vigorous response than the mild accelerations employed, i.e., the rotational stimuli were not as intense as the caloric stimuli. As noted earlier, Maxwell, Burke, and Reston (1922) cited the importance of stimulus intensity on rabbit nystagmus. In addition, with human subjects, Griffith (1920) reported vigorous nystagmus to more intense stimuli after subjects had yielded markedly reduced responses to a practiced level, and Guedry (1953), using the duration of the oculogyral illusion as a measure, demonstrated that acceleration repetition at a given rate has less effect on reducing responses to higher levels of stimulation than it has on lower levels. (b) The induced neural patterning may differ sufficiently between unilateral and bilateral stimulation to make the habituation mechanism respond with a relative specificity that is determined by whether the canals on one side, or on both, are stimulated.

SECONDARY NYSTAGMUS

Extremely few studies have examined the characteristics of secondary nystagmus (e.g., Aschan & Bergstedt, 1954; Collins, 1962, 1963b; Collins & Poe, 1962; Hauty & Wendt, 1960). The data presented in Figures 5 and 6 indicate that the secondary, although considerably less regular in appearance, rises, peaks, and declines in a manner highly similar to the primary reaction. In addition, a decline occurs with stimulus repetition, and the function bears a close resemblance to the habituation course followed by the primary nystagmus.

Hauty and Wendt (1960) have presented measurements of the slow-phase activity of human secondary nystagmus with which some comparisons of the present data may be made.

They found from 3 subjects (one of whom demonstrated some spontaneous nystagmus), that the output of secondary nystagmus was approximately one-half that of the preceding primary response. Further, neither intensity nor duration of rotatory stimulation, separately considered, affected the intensity or duration of the secondary. A relationship was demonstrated between total output of secondary nystagmus and the product of stimulus duration and intensity.[8]

The data obtained for cats show that the total slow-phase output of secondary nystagmus was only one-fourth to one-fifth that of the preceding primary; for frequency the factor was one-third. With the exception of the last 3 trials, the durations of the primary and corresponding secondary responses were almost identical (compare Figures 3 and 6).

Of further interest is the fact that the time-course characteristics of the plotted secondary responses (Figure 5) parallel fairly closely those found for the primary reaction (Figure 2). Specifically, the secondary reaches its peak after about 18 seconds of build-up in trial 1, and after 12 seconds in trials 10 and 15. These values compare well with peak activity for the primary response during the same trials. Whether this is coincidental, or whether the build-up period for the secondary is intimately related to the time required for the primary to reach its peak, will require further investigation.

SUMMARY

Ten cats were exposed to a series of above-threshold accelerations and sub-threshold decelerations. Unilateral caloric irrigations, provoking nystagmus in the same direction as the above-threshold rotational stimuli preceded and followed the set of accelerations. A marked adaptation of nystagmus, characterized by specific changes in early trials, resulted from repeated rotation. Although neither duration nor total slow-phase eye displacement to caloric stimulation was affected, the intervening rotational experience produced some reduction in the frequency of the nystagmic beats. Two factors were proposed in explanation for the minimal transfer of adaptation from the rotational to the caloric situation. Secondary nystagmic activity was also examined and appeared closely related to preceding primary reactions. The data indicate that clinical (caloric) responses to vestibular stimulation may not give an accurate indication of a subject's state of adaptation to "practiced" levels of angular acceleration. Such findings provide cautions in the establishment of appropriate testing techniques for the analysis of vestibular function in air- or space-vehicle crew members.

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[8] It should be noted that Hauty and Wendt (1960) report no decline of human secondary nystagmus as a function of repeated elicitation. The entire question of nystagmus habituation in man is far from settled (cf. Collins, 1962, Collins, Guedry, & Posner, 1962; Wendt, 1951) and the conditions under which it will occur (e.g., Aschan, 1954, Guedry & Graybiel, 1962; McCabe, 1960; Wendt, 1951) are not yet completely defined. Apparently, under many stimulus conditions, no significant loss of response occurs

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APPENDIX A

TOTAL SLOW-PHASE NYSTAGMIC OUTPUT IN MILLIVOLTS FOR EACH ROTATORY AND CALORIC TRIAL

ROTATION TRIALS	CATS									
	10	11	12	13	14	15	16	17	18	19
1	22.5	23.2	29.3	19.4	31.0	13.1	12.4	24.4	53.0	24.6
2	32.4	16.9	24.3	10.8	26.0	11.8	6.8	13.8	33.7	18.5
3	28.3	18.0	26.4	8.5	25.1	13.8	8.0	15.4	32.5	22.0
4	19.6	20.3	22.7	14.6	20.6	10.6	7.3	11.1	21.6	11.0
5	25.8	14.0	20.6	10.6	20.7	10.1	5.6	21.0	21.6	11.6
6	17.6	16.6	19.8	8.1	13.0	10.0	5.6	23.6	13.1	17.3
7	19.3	13.0	14.7	5.8	17.4	8.8	2.9	19.3	19.0	10.3
8	14.2	11.1	17.3	9.0	12.8	9.4	3.0	10.2	13.8	8.4
9	19.7	12.0	12.7	5.2	13.0	9.2	4.0	19.7	12.9	13.2
10	17.0	11.0	9.2	5.2	12.0	9.3	5.7	7.6	15.1	8.5
11	12.0	9.3	8.3	5.8	13.6	7.2	1.4	7.9	14.2	11.4
12	15.0	11.6	5.7	5.9	12.0	4.8	1.7	8.2	12.5	7.8
13	24.0	8.6	1.0	4.6	14.0	4.9	3.4	6.3	10.7	5.6
14	11.3	10.5	4.1	3.6	8.6	6.1	1.2	7.0	8.7	4.9
15	19.2	12.0	6.7	3.4	8.3	5.9	1.6	6.9	13.2	4.4
CALORIC TRIALS										
PRE	34.6	34.6	38.2	45.6	19.1	34.2	16.1	15.9	60.2	61.4
POST	36.5	38.6	48.7	13.2	22.0	29.8	10.0	40.7	68.6	51.4

APPENDIX B

SLOW-PHASE NYSTAGMIC OUTPUT (IN MILLIVOLTS) PER 3-SECOND INTERVAL AVERAGED FOR 10 CATS. "ZERO" TIME INDICATES ON-SET OF 4.1°/SEC² CCW ACCELERATION FOR 13 SECONDS.

TIME (SEC)	TRIALS 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
0-1	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
2-4	1.0	0.9	1.4	1.1	1.4	1.0	1.1	1.0	1.0	1.0	0.8	0.7	0.7	0.6	0.9
5-7	2.5	2.4	2.1	2.1	2.4	2.5	1.8	2.1	2.2	1.8	2.0	1.8	1.8	1.3	1.7
8-10	2.9	2.6	3.4	3.5	2.6	2.6	2.5	2.4	2.4	1.9	1.7	2.0	1.6	1.8	1.6
11-13	3.5	3.0	3.3	3.0	3.0	2.5	2.5	2.2	2.3	2.6	2.0	1.8	2.4	1.4	1.8
14-16	3.7	3.2	3.9	3.2	2.2	2.4	2.3	1.9	1.5	1.6	1.5	1.4	1.6	1.2	1.4
17-19	3.7	2.8	2.2	1.8	1.7	1.4	1.6	0.7	1.4	0.8	1.4	0.5	6.6	0.3	0.6
20-22	2.4	1.8	1.5	0.8	0.8	0.9	0.7	0.3	0.4	0.2	0.4	0.2	4.2		0.2
23-25	2.2	1.4	0.7	0.7	0.7	0.5	0.3		0.4	0.1			1.3		0.1
26-28	1.4	0.8	0.5	0.3	0.2	0.2	0.2		0.2	0.1			1.6		0.0
29-31	0.7	0.7	0.5	0.0	0.2	0.2	0.2		0.0	0.0			0.0		0.1
32-34	0.4	1.0	0.1	0.0	0.3	0.1	0.1		0.1				0.0		
35-37	0.6	0.1	0.0		0.2	0.0	0.1		0.0						
38-40	0.3				0.2	0.1			0.0						
41-43	0.2								0.0						
44-46	0.1														
47-49	0.3														
50-52	0.0														
53-55	0.1														

APPENDIX C

SLOW-PHASE NYSTAGMIC OUTPUT (IN MILLIVOLTS) AND FREQUENCY OF NYSTAGMIC BEATS PER TIME INTERVAL AVERAGED FOR 10 CATS. "ZERO" TIME INDICATES MOMENT OF CALORIC STIMULUS TERMINATION (23.5° C FOR 30 SECONDS).

	SLOW-PHASE NYSTAGMUS (mv)		FREQUENCY OF BEATS	
TIME (SEC)	PRE	POST	PRE	POST
0-3	2.2	2.0	3.4	2.8
4-6	2.4	1.9	3.8	2.6
7-9	2.2	2.3	3.7	2.8
10-12	2.3	2.4	4.2	3.0
13-15	2.3	2.2	4.0	2.6
16-18	2.1	1.9	3.9	2.7
19-21	2.1	2.1	4.2	2.8
22-24	2.0	1.8	3.8	2.4
25-27	2.2	1.9	4.1	2.6
28-30	1.7	1.7	3.6	2.4
31-33	1.6	1.5	3.3	2.0
34-36	1.6	1.3	3.3	2.2
37-39	1.4	1.1	3.4	2.2
40-42	1.3	1.2	3.2	1.6
43-45	1.1	0.9	2.7	1.8
46-48	1.0	1.2	2.4	1.6
49-51	0.9	0.7	2.4	1.6
52-54	1.0	0.6	2.2	1.2
55-57	0.9	1.1	2.1	1.4
58-60	0.6	0.6	1.7	1.2
61-63	0.6	0.4	1.8	0.8
64-66	0.6	0.4	1.8	0.8
67-69	0.2	0.4	1.4	0.6
70-72	0.4	0.4	1.0	0.7
73-75	0.2	0.3	0.6	0.6
76-78	0.2	0.3	0.8	0.3
79-81	0.2	0.2	0.7	0.6
82-84	0.2	0.4	0.8	0.4
85-87	0.1	0.4	0.4	0.3
88-90	0.1	0.2	0.6	0.3
91-93	0.1	0.2	0.4	0.4
94-96	0.1	0.1	0.4	0.2
97-99	0.1	0.1	0.2	0.4
100-102	0.0	0.2	0.1	0.2
103-105	0.0	0.1	0.1	0.2
106-108	0.0	0.0	0.1	0.2
109-111	0.0	0.0	0.1	0.1
112-114	0.0	0.1	0.1	0.1
115-117	0.1	0.0	0.1	0.1
118-120	0.0	0.0	0.0	0.1
121-123	0.0	0.1	0.0	0.1
124-126	0.0	0.1	0.0	0.1
127-129		0.0		0.1
130-132		0.0		0.1

APPENDIX D

TOTAL FREQUENCY OF NYSTAGMIC BEATS FOR EACH ROTATORY AND CALORIC TRIAL

ROTATION TRIALS	CATS 10	11	12	13	14	15	16	17	18	19
1	50.5	34.0	56.0	51.0	35.0	23.8	38.0	41.8	63.8	30.5
2	55.5	26.2	41.0	26.0	25.0	12.5	22.5	33.5	42.8	28.0
3	46.0	28.5	42.5	21.0	19.0	11.5	18.5	27.5	37.0	24.0
4	34.0	26.0	41.0	23.5	18.0	17.5	22.0	29.0	31.0	11.0
5	25.5	26.0	33.5	16.5	19.0	18.0	13.0	35.8	30.8	17.0
6	28.0	22.5	38.0	20.0	11.0	17.5	17.5	35.0	24.0	23.0
7	31.0	22.5	30.0	14.5	16.0	14.5	14.0	28.5	27.5	13.2
8	18.0	21.0	31.5	15.5	13.0	14.2	10.5	17.2	19.5	15.0
9	30.0	17.0	25.2	16.2	14.0	15.5	14.0	34.5	20.5	22.0
10	23.0	21.5	20.5	14.0	12.0	19.5	19.0	15.5	29.5	16.0
11	23.5	19.0	23.5	15.5	16.0	14.5	8.5	17.0	25.5	15.5
12	21.0	19.5	19.0	14.5	13.0	14.5	9.0	15.2	27.5	17.0
13	33.5	17.5	21.5	11.5	18.0	12.0	13.0	14.0	24.2	16.5
14	18.0	15.5	16.5	12.0	11.0	12.0	11.0	14.2	20.0	14.5
15	27.0	18.0	18.5	10.0	12.0	9.0	8.0	15.0	28.8	16.0
CALORIC TRIALS										
PRE	57.0	52.0	102.0	104.5	21.0	53.0	103.0	57.2	79.0	140.0
POST	19.8	45.0	104.8	39.8	27.0	39.0	29.5	49.5	60.0	76.5

APPENDIX E

FREQUENCY OF NYSTAGMIC BEATS PER 3-SECOND INTERVAL AVERAGED FOR 10 CATS. "ZERO" TIME INDICATES ONSET OF CCW ACCELERATION OF 4.1°/SEC² FOR 13 SECONDS.

TIME (SEC)	TRIALS 1	5	10	15
0-1	0.0	0.1	0.1	0.1
2-4	2.6	1.9	2.2	2.6
5-7	3.7	3.3	3.0	3.2
8-10	4.0	3.9	3.8	3.3
11-13	4.8	4.2	4.5	3.1
14-16	5.1	3.5	3.4	2.4
17-19	5.0	2.8	1.5	1.2
20-22	3.6	1.4	0.6	0.6
23-25	3.4	1.1	0.3	0.2
26-28	2.1	0.5	0.1	0.2
29-31	1.0	0.6	0.1	0.1
32-34	0.8	0.8		
35-37	0.6	0.4		
38-40	0.5	0.1		
41-43	0.4	0.1		
44-46	0.2			
47-49	0.2			
50-52	0.1			
53-55	0.2			

APPENDIX F

DURATION OF PRIMARY NYSTAGMUS IN SECONDS FOR EACH ROTATORY AND CALORIC TRIAL

ROTATION TRIALS	CATS 10	11	12	13	14	15	16	17	18	19
1	34.0	28.3	45.4	30.0	28.8	28.0	24.2	32.2	55.0	25.0
2	39.0	31.0	34.0	23.0	21.0	21.4	20.0	28.0	37.0	32.7
3	30.2	31.7	39.0	21.0	20.7	19.0	19.0	25.0	33.5	20.2
4	22.0	26.0	32.5	21.0	20.8	19.0	20.6	25.4	28.3	15.8
5	39.7	25.8	33.6	19.4	20.9	18.0	15.0	41.5	26.0	19.8
6	29.6	25.0	39.0	19.8	15.8	17.9	16.0	32.8	25.7	18.5
7	25.9	24.0	27.0	16.0	18.2	18.8	16.0	28.8	28.0	18.0
8	18.7	26.4	30.0	18.0	16.6	19.0	15.2	19.0	24.2	18.7
9	25.8	20.7	27.2	16.2	17.0	19.0	15.6	37.0	26.8	42.1
10	26.2	21.6	21.0	17.2	16.0	19.0	16.0	18.0	29.4	19.0
11	22.0	21.7	23.2	19.8	17.4	16.0	13.0	16.4	23.5	16.7
12	18.5	18.9	21.0	16.0	16.0	17.9	14.3	22.2	22.4	18.1
13	28.2	21.0	21.3	17.2	22.0	15.0	13.8	16.7	30.1	15.8
14	18.2	19.0	19.0	14.7	15.1	16.0	15.0	19.0	28.8	14.7
15	31.2	19.0	19.0	15.1	16.0	16.0	13.0	18.4	23.7	15.2
CALORIC TRIALS										
PRE	66.4	63.8	99.8	126.2	42.0	63.4	72.0	99.0	84.9	97.0
POST	59.6	92.4	109.4	95.5	56.4	73.8	38.2	130.7	92.7	101.8

APPENDIX G

SECONDARY NYSTAGMUS: TOTAL SLOW-PHASE OUTPUT IN MILLIVOLTS FOR EACH ROTATORY AND CALORIC TRIAL

ROTATION TRIALS	CATS									
	10	11	12	13	14	15	16	17	18	19
1	5.8	7.0	3.7	1.7	2.9	4.8	5.4	5.0	5.0	3.3
2	3.3	4.0	4.2	3.5	2.8	5.0	2.9	1.7	5.8	.....
3	5.4	3.3	3.9	1.5	3.0	4.6	4.6	1.8	8.0	9.4
4	3.7	3.2	2.6	2.0	3.0	7.2	1.9	4.0	8.7	3.2
5	6.2	3.2	4.1	3.3	2.3	4.4	2.1	2.3	6.2	8.3
6	.....	4.5	0.8	3.7	2.0	4.8	7.7	2.2	1.7	2.5
7	.....	4.5	2.0	0.7	3.3	3.5	1.0	3.3	.....	1.8
8	10.3	3.9	.....	3.9	2.1	3.5	2.1	2.1	7.8	5.5
9	.....	5.1	1.0	1.3	2.2	1.1	1.7	1.4	.....	1.1
10	2.9	3.5	3.7	2.0	1.8	1.8	7.4	1.5	.....	0.9
11	1.1	3.6	0.9	1.8	2.1	1.6	1.1	1.7	.....	3.7
12	13.3	3.1	0.9	0.9	1.4	2.6	1.2	1.9	.....	1.4
13	.....	3.6	.....	0.6	0.8	2.1	1.5	1.6	.....	0.8
14	2.9	4.1	0.1	.....	1.5	1.5	0.8	2.1	.....	0.9
15	.....	2.1	.....	.....	0.8	2.9	0.3	1.8	.....	1.0
CALORIC TRIALS										
PRE	7.9	.....	.....	.....	.....	2.6	.....	.....	1.7	5.4
POST	2.1	1.6	.....	.....	0.8	.....	.....	.....	.....	13.5

APPENDIX H

SECONDARY NYSTAGMUS: TOTAL FREQUENCY OF NYSTAGMIC BEATS FOR EACH ROTATORY AND CALORIC TRIAL

ROTATION TRIALS	CATS									
	10	11	12	13	14	15	16	17	18	19
1	11	16	11	5	11	7	19	15	13	21
2	9	12	13	12	12	8	17	6	16	...
3	9	9	12	4	8	7	15	5	20	22
4	10	8	11	5	8	9	8	9	17	7
5	2	10	11	8	6	6	16	5	17	24
6	—	12	3	6	8	7	32	3	5	5
7	—	9	9	3	8	4	8	6	—	9
8	19	10	—	11	7	4	11	5	21	26
9	—	10	6	5	6	2	10	4	—	15
10	5	7	8	7	7	4	28	4	—	5
11	6	11	2	6	2	3	6	3	—	12
12	26	10	3	5	8	5	6	4	—	5
13	—	7	—	3	7	5	10	4	—	2
14	6	7	2	—	5	2	9	8	—	4
15	—	6	—	—	8	6	5	4	—	5
CALORIC TRIALS										
PRE	28	—	—	—	—	5	—	—	15	16
POST	4	2	—	—	5	—	—	—	—	30

APPENDIX I

SECONDARY NYSTAGMUS: DURATION IN SECONDS FOR EACH ROTATORY AND CALORIC TRIAL

ROTATION TRIALS	CATS 10	11	12	13	14	15	16	17	18	19
1	22.0	35.0	28.3	34.0	29.9	14.0	36.0	34.3	39.5	40.5
2	20.0	26.6	24.0	31.5	23.6	21.5	37.5	12.7	33.0	.....
3	19.0	28.0	27.0	8.5	15.0	18.5	31.0	8.0	37.5	51.5
4	17.4	31.6	27.0	19.0	13.6	24.5	20.3	32.5	36.6	13.5
5	2.7	24.7	24.7	32.2	16.0	17.0	30.0	17.5	25.0	45.2
6	.....	43.3	5.5	17.5	13.5	23.5	54.2	13.5	23.2	9.0
7	.....	20.5	26.5	14.5	24.0	12.5	14.0	15.4	.....	25.0
8	21.8	31.5	.....	37.1	20.5	9.0	20.8	13.5	39.7	60.3
9	.....	31.0	11.5	28.5	17.5	6.3	28.2	22.3	.....	6.9
10	10.0	31.1	11.5	27.4	14.0	6.0	52.0	11.2	.....	17.5
11	9.5	38.0	6.5	35.8	6.5	14.0	11.0	10.5	.....	4.2
12	29.3	40.5	10.7	20.0	18.0	15.7	9.0	8.3	.....	14.9
13	.....	26.7	.....	8.8	18.0	19.8	18.8	11.0	.....	6.8
14	10.2	24.5	8.5	.....	12.0	8.0	15.0	17.6	.....	16.2
15	.....	16.2	.....	.....	12.5	19.5	10.0	12.0	.....	13.0
CALORIC TRIALS										
PRE	67.5	.....	.....	.....	.....	26.0	.....	.....	77.0	34.5
POST	15.0	9.0	.....	.....	25.3	.....	.....	.....	.....	104.0

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2. Nystagmus
3. Adaptation
4. Transfer Effects
5. Sensory Physiology
6. Angular Acceleration

Ten cats were exposed to a series of above-threshold accelerations and sub-threshold decelerations. Unilateral caloric irrigations producing nystagmus in the same direction as the above-threshold rotational stimuli preceded and followed the set of accelerations. A marked adaptation of nystagmus, characterized by specific changes in early trials, resulted from repeated rotation. Although neither duration nor total slow-phase eye displacement to caloric stimulation was affected, the intervening rotational experience produced some reduction in the frequency of the nystagmic beats. Two factors were proposed as explanation for the minimal transfer of adaptation from the rotational to the caloric situation. Secondary nystagmus activity was also examined and appeared closely related to preceding primary reactions. The data indicate that clinical (caloric) responses to vestibular stimulation may not give an accurate indication of a subject's state of adaptation to "practiced" levels of angular acceleration. Such findings pro-

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