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ADAPTATION TO VESTIBULAR DISORIENTATION. III.

Influence on Adaptation of Interrupting Nystagmic Eye Movements with Opposing Stimuli

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Influence on Adaptation of Interrupting Nystagmic Eye Movements with Opposing Stimuli

Habituation of ocular nystagmus has been demonstrated perhaps most clearly and thoroughly in the cat. Under a number of test conditions, repeated vestibular stimulation of the cat has produced reductions in the duration of nystagmus, slow-phase displacement of the eyes, and number of nystagmic eye movements (e.g.[1,2,3,7]). In all of these studies, nystagmus has been allowed to run its course. Holsopple,[12] some years ago, attempted to explain directional differences found in duration of nystagmus obtained from human subjects as due to the fact that only one direction of response was permitted to run its course. Specifically, early investigators frequently obtained their data from a deceleration stimulus which followed soon after an acceleration. Nystagmus due to the acceleration was therefore interrupted as a result of the deceleration. Thus, if a subject were repeatedly rotated clockwise (CW) in this manner, a decline would occur in the nystagmic reaction occasioned by the deceleration. If the same subject were then rotated counterclockwise (CCW), the response to the deceleration (now in the opposite direction) would not show the same decline. Holsopple[12] points out that the subject would have been exposed to the same number of accelerations as decelerations during the habituation series (driving nystagmus in both directions); thus, he notes, merely reversing the direction of rotation should not produce a difference in the amount by which one response was reduced.

Although there are several possible explanations for the kinds of results noted by Holsopple[12] in this regard, the question of whether nystagmus habituation is influenced by interrupting the response is of interest.

Grateful acknowledgement is made of the assistance rendered by Bill Updegraff and Kathryn Quattlebaum during the conduct of this study.

METHOD

Apparatus. The Huffman Rotation Device[5] produced controlled angular accelerations in a light-proof room. The rotating table was equipped with tiers so that three animals could be rotated simultaneously with their heads at the center of rotation.[6]

Restraint. The method of Henriksson, Kohut, and Fernandez[11] was used to restrain the animals (see also Collins[3]). Their heads were positioned so that the lateral semicircular canals were in the plane of rotation.

Recording. An Offner Type R Dynograph comprised the recording equipment. RC time constants of 3 sec amplified horizontal eye movement signals which were picked up from needle electrodes inserted near the outer canthi.

Procedure. Prior to rotation, each cat was placed in an optokinetic stimulator and horizontal eye movements were obtained at a drum speed of 24°/sec. Slow-phase displacement measurements were made and used as calibration data. Three groups, each comprised of 10 cats, were tested. All groups received 2 rotation tests prior to (pre) and 2 rotation tests following (post) a series of 15 habituation trials. The pre- and post-tests were identical for the three groups and consisted of one CW and one CCW acceleration of 5°/sec^2 for 18 sec, in each case followed by a 2 min period of constant velocity (15 rpm) and a subthreshold deceleration (0.15°/sec^2) to zero velocity. Half of the animals in each group received CW accelerations first during the pre- and post-tests followed by CCW accelerations. The order was reversed for the remaining animals (see Table 1).

Different stimulus programs were applied to the groups for the habituation trials. Group A was given 15 trials in which CW accelerations were 5°/sec^2 for 18 sec; decelerations were a subthreshold 0.15°/sec^2 following 2 min of constant velocity (CV) of 15 rpm. For Group B CW accelerations and decelerations were both 5°/sec^2 for 18 sec and were separated by 2 min at a CV of 15 rpm. Group C was given CW accelerations of 5°/sec^2 for 18 sec followed almost

TABLE 1.—Outline of the Experimental Procedure. CW and CCW Refer to Clockwise and Counterclockwise Rotation, Respectively; CV Indicates Constant Velocity.

Animals	*Pre-test Trials (5°/sec² accel for 18 sec; 2 min CV; subthreshold decel)*	*15 Habituation Trials*	*Post-test Trials (5°/sec² accel for 18 sec; 2 min CV; subthreshold decel)*
120A–124A	1. CW 2. CCW	5°/sec² CW accels for 18 sec; 2 min CV; Subthreshold decels	1. CW 2. CCW
125A–129A	1. CCW 2. CW		1. CCW 2. CW
130B–134B	1. CW 2. CCW	5°/sec² CW accels for 18 sec; 2 min CV; 5°/sec² decels for 18 sec	1. CW 2. CCW
135B–139B	1. CCW 2. CW		1. CCW 2. CW
140C–144C	1. CW 2. CCW	5°/sec² CW accels for 18 sec; 0.6 sec CV; 5°/sec² decels for 18 sec	1. CW 2. CCW
145C–149C	1. CCW 2. CW		1. CCW 2. CW

immediately (0.6 sec later) by 5°/sec² decelerations to zero velocity. A period of 3–5 minutes in room illumination preceded each trial.

Scoring. Measures of slow-phase displacement, number of nystagmic eye movements, and duration of the nystagmic response were obtained. Slow-phase data were derived by summing the vertical distances from the peak to the base line of each nystagmic beat throughout the primary response for each pre- and post-trial. These values were converted to degrees by means of the calibration factors.

RESULTS

Samples of electronystagmographic tracings are presented in Figure 1. Mean data scores for all pre- and post-trials appear in Table 2 for each group and each direction of rotation. Mean pre-trial response values for duration, number of beats, and slow-phase output were set at 100 per cent; post-trial data were then expressed as percentages of the pre-trial. These percentage relationships appear in Figure 2.

Relative change scores (pre- to post-test) were computed for each animal and each measure for both CW and CCW stimulation and analyses of variance (partially nested design) were conducted (Table 3). Results of the analyses indicated significant pre- to post-test differences between directions of stimulation (or response) for slow-phase eye displacement, frequency, and duration of nystagmus. In this regard, it is clear from Figure 2 that CW responses showed a greater reduction than did CCW responses. Significant differences were also obtained among the groups for slow-phase and frequency measures, but not for duration scores. Further analyses were accomplished by t tests (Table 3). For CW acceleration (the "interrupted" direction for Group C), there were no significant differences among the groups in the pre- to post-test declines for the slow-phase and frequency response measures. Thus, interrupting the response did not affect habituation. For CCW accelerations, Groups B and C (both of which received stimulation in this direction during habituation trials) did not differ significantly from each other in amount of pre- to post-test decline for the slow-phase and frequency measures. Both of these groups, however, had significantly greater response reductions to CCW accelerations when compared with Group A (which received no stimulation in this direction during habituation trials).

Figure 3 contains a plot in 3-sec intervals of the primary nystagmic responses of Group C to habituation trials 1, 5, 10, and 15. The double curves show the usual features of habituation, *viz.* a steady reduction in total output and an earlier occurence of the interval of maximum eye displacement (see also Collins[4]). The data also

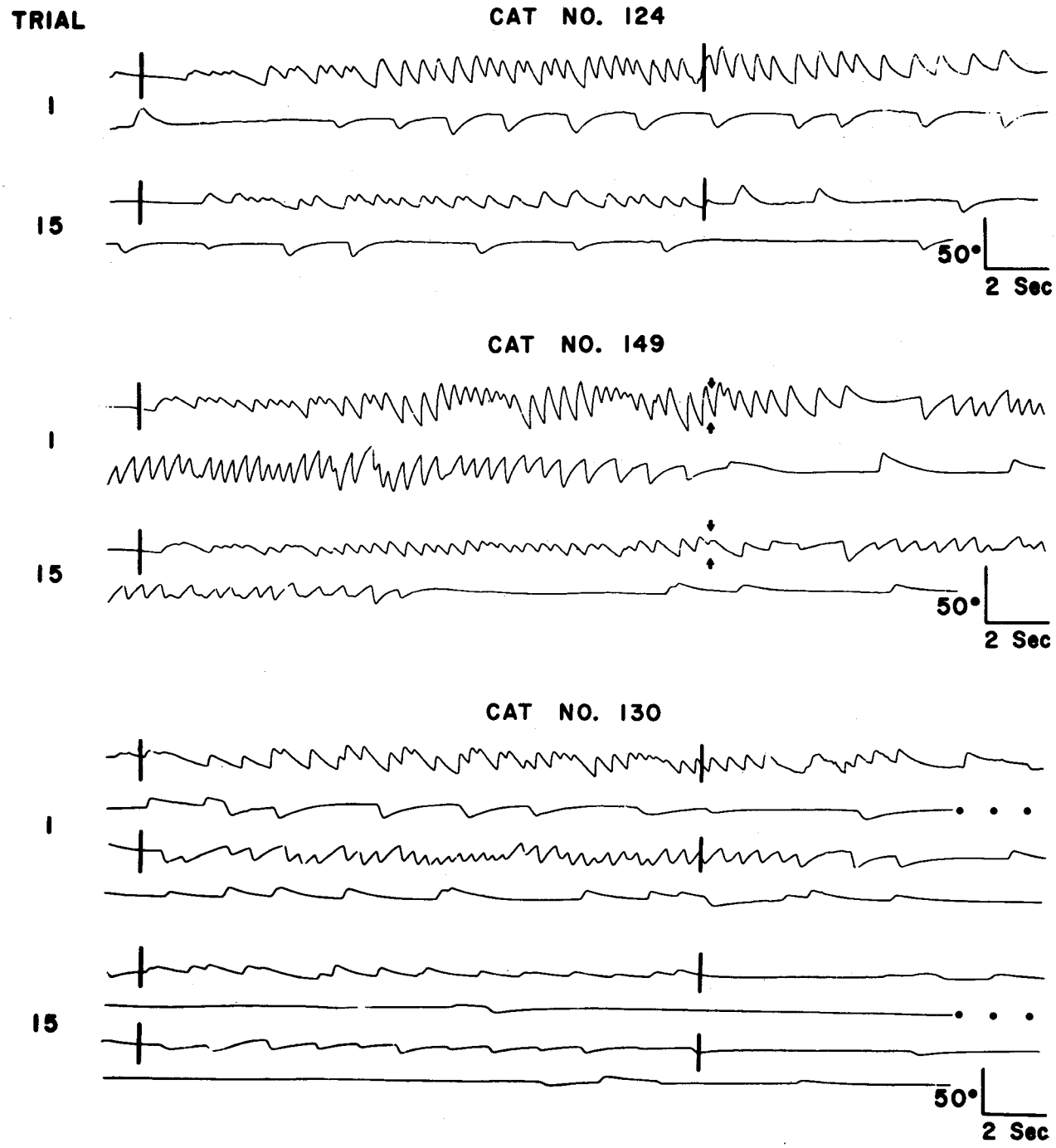

FIGURE 1.—Representative nystagmus tracings for habituation trials 1 and 15. Cat 124 (Group A) received unidirectional habituation. Cat 149 (Group C) received accelerations followed within 0.6 sec by equal rates of decelerations (arrows indicate points at which deceleration was initiated). Cat 130 (Group B) received equal rates of accelerations and decelerations separated by 2 min of constant velocity (dots in the record indicate approximately 80 sec of recording not shown). Heavy vertical bars demarcate stimulus periods and calibrations are at the end of each set of tracings. A secondary nystagmus (see Collins, 1964) is particularly prominent in tracings for Cat 124.

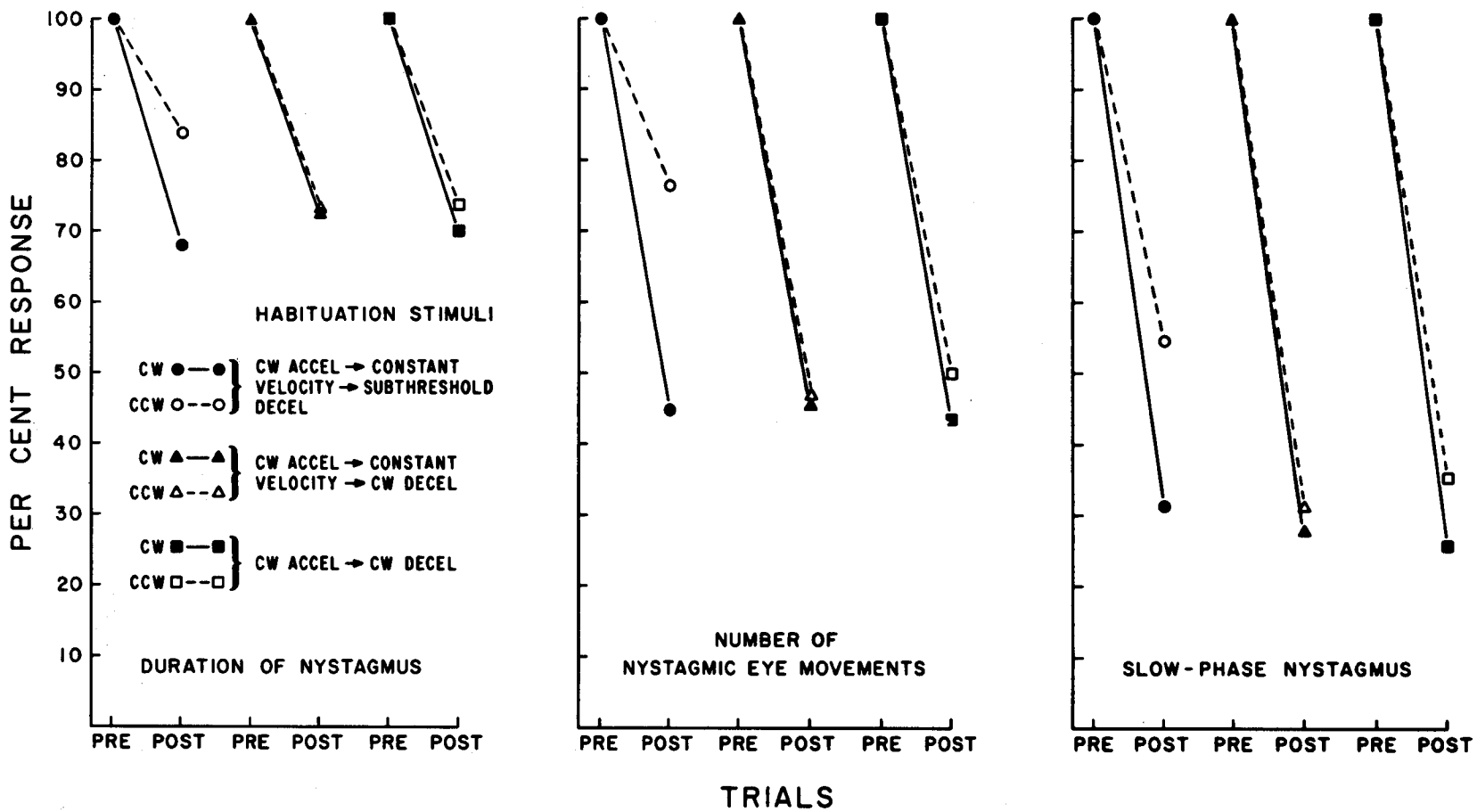

FIGURE 2.—Mean pre- to post-test declines for the 3 groups for different nystagmus measures.

TABLE 2.—Mean Response Duration, Number of Beats, and Slow-Phase Displacement of the Eyes on Pre- and Post-Trials for the Three Groups.

		Pre		*Post*	
Measure	*Group*	*CW*	*CCW*	*CW*	*CCW*
Duration in Seconds	A	31.0	29.2	21.1	24.5
	B	29.5	26.8	21.5	19.6
	C	32.7	30.8	23.0	22.7
Number of Beats	A	49.2	46.6	22.1	35.7
	B	40.6	37.4	18.6	17.6
	C	49.2	50.8	21.4	25.6
Slow-Phase Output (Degrees)	A	1078	1180	338	643
	B	661	676	171	210
	C	1012	1078	262	381

TABLE 3.—Results of Statistical Analyses of the Data.

Analyses of Variance

		Slow-Phase		*Frequency*		*Duration*	
	df	*MS*	*F*	*MS*	*F*	*MS*	*F*
Groups (G)	2	141129	5.28*	16862	4.29*	667	0.34
Direction (D)	1	29260	16.85***	28566	20.39***	7004	6.20*
GXD	2	6280	3.62*	12938	9.23**	2563	2.27
Ss within G (S/G)	27	2674		3935		1966	
SXD/G	27	1736		1401		1131	
Total	59						

t-Tests

	CW Accelerations		*CCW Accelerations*	
Groups Compared	*Slow-Phase*	*Frequency*	*Slow-Phase*	*Frequency*
A and B	0.73	0.12	3.03*	3.82**
A and C	0.91	0.57	2.60*	3.75**
B and C	0.37	0.50	0.64	0.36

* .05 level ** .01 level *** .001 level

show a progressively earlier onset of the response to deceleration. This is evidenced in the earlier crossings of the "zero output" line as the number of habituation trials is increased.

DISCUSSION

The data indicate that the pre- to post-test changes in response to CW accelerations were the same for all three groups. Further, Groups B and C did not differ from each other in the relative amount of pre- to post-test decline of nystagmus to CCW stimulation. Thus, habituation of nystagmus appeared in all cases where the response occurred during habituation trials regardless of whether only one direction of response was repetitively elicited (Group A), or both directions were elicited and permitted to run their course (Group B) or both were elicited but the response in one direction was interrupted (Group C). Significantly less pre- to post-test change occurred for the direction of nystagmus which was not elicited during habituation trials (Group A).

Results from this study demonstrate that the interruption of an on-going vestibular nystagmus from the cat during repetitive trials does not prevent response habituation in total darkness. Holsopple's[12] results could be explained by directionally specific habituation due to visual fixation following deceleration, or by arousal factors. In addition, it should be noted that by interrupting the nystagmic responses to one acceleration by means of an equal acceleration in the opposite direction, cupula deflection to the latter should be less (within certain limits), since the new stimulus is initiated while the cupula is deflected in the other direction. Thus, the "interrupting" stimulus, depending upon its duration and when it was introduced, could be a significantly weaker stimulus insofar as the vestibular system is concerned. A trend in this regard can be found in Figure 2 where the CCW acceleration ("interrupting" stimulus) for Group C shows a relatively stronger post-test response (less decline) than the CW acceleration. On the basis of the above, this might reflect the fact that the post-test stimulus was a "stronger" one than that pre-

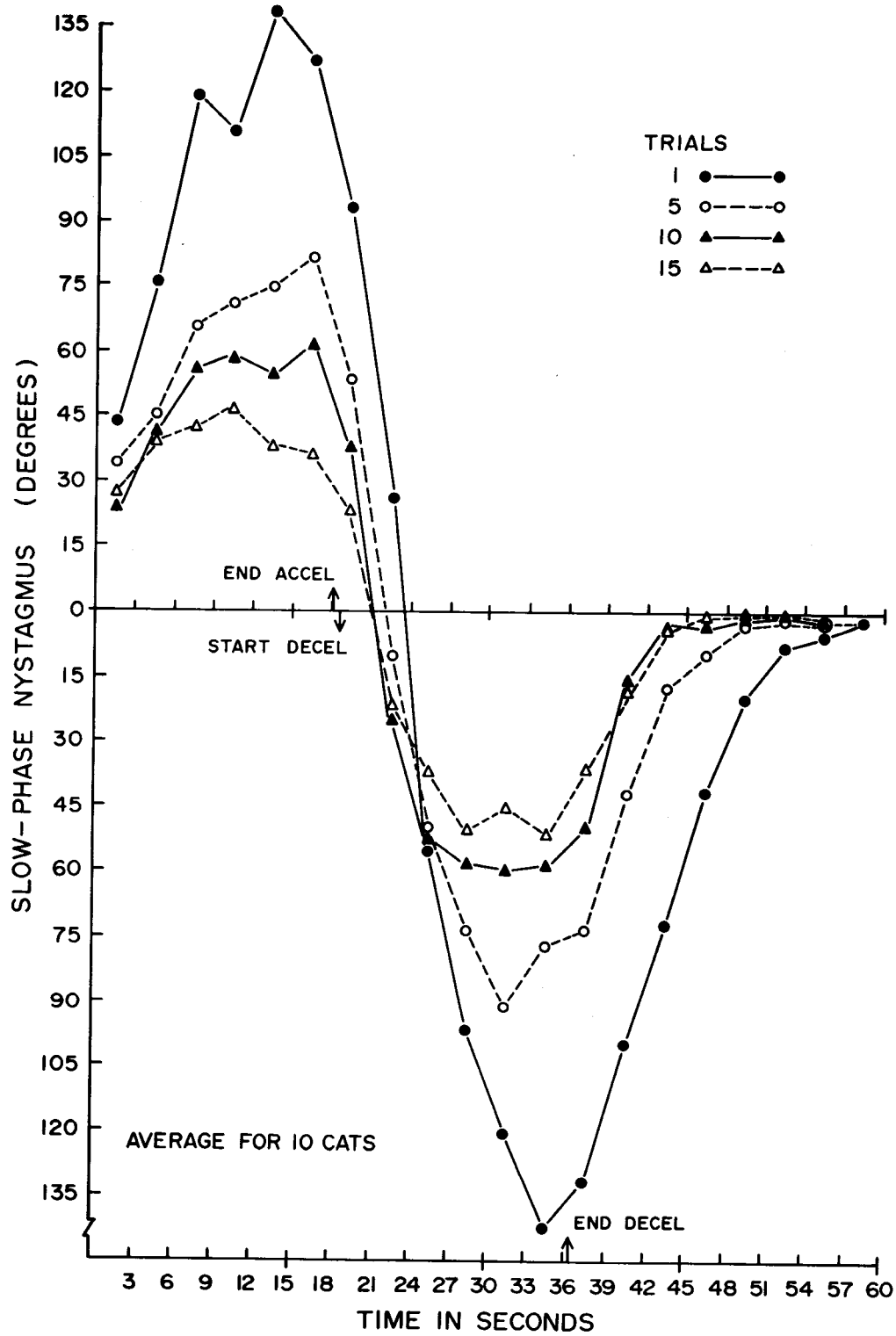

FIGURE 3.—Slow-phase nystagmus output for Group C for habituation trials 1, 5, 10, and 15. Data are plotted in degrees of eye movement for each 3-sec interval. The lower half of the graph (which includes the "tailing off" of the response) is also representative of the response declines for groups A and B.

sented during the habituation trials since, in the pre- and post-tests, the cupula was at its normal (non-deflected) position when stimulation was initiated. A similar point has been made by Guedry[10] with regard to subjective effects of rotation.

The present data also have a bearing on some of the theoretical views of habituation held by Fluur and Mendel.[8,9] Specifically, as part of their concepts of hyperpolarization, Fluur and Mendel[8] stated that if caloric nystagmus were produced in opposite directions on alternate trials, no habituation would occur in humans. Later results from a rotation study led them to reaffirm their theoretical position.[9] That this view does not hold true for the cat is evident from the results of this study as well as from an investigation of caloric habituation reported elsewhere.[4]

SUMMARY

Failure of adaptation of nystagmic eye movements to occur under certain conditions of stimulation by angular acceleration has been ascribed to a failure to allow the eye-movement response to run its course. In this study, 3 groups of subjects were tested under conditions of repeated angular accelerations in which Group A received unidirectional stimulation, Group B received bidirectional stimulation with both responses allowed to run their course, and Group C received bidirectional stimulation but the response in one direction was interrupted. Adaptation occurred for all groups in spite of the different test procedures. Other implications of the results are discussed.

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