

ADAPTATION TO VESTIBULAR DISORIENTATION:

IX. Influence of Head Position on the Habituation of Vertical Nystagmus

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I. The Problem.

Interactions of linear and angular accelerations are frequently experienced by pilots during aircraft maneuvers. Recent evidence from human studies conducted on centrifuges^{1,17} has indicated that stimulation of the otoliths (detectors of linear acceleration) may influence the magnitude of nystagmic reactions initiated by the semicircular canals (detectors of angular acceleration). Data based on nerve resections in rabbits²⁰ showed that the otoliths exert some regulatory functions on nystagmus. Other studies involving rabbits and human subjects on the parallel swing (an otolith stimulator) have reported nystagmus produced by linear accelerations when the eyes of the subjects were deviated laterally, either voluntarily in humans or as the result of a compensatory reaction occasioned by placing animals on their sides.^{14,15,16,21} Niven, Hixson, and Correia¹⁹ have demonstrated clear horizontal nystagmus from humans to periodic linear acceleration and Guedry¹¹ has related these findings to his own work (involving rotation about an earth-horizontal axis) in which nystagmus produced by angular acceleration was augmented or diminished depending upon whether the gravity vector was to the left or right of the subject. Further, under conditions of bizarre vestibular stimulation of human subjects (the so-called "Coriolis" effects occasioned by head movements during rotation), failures to obtain transfer of habituation have been reported from a practiced quadrant of head movement to an unpracticed one¹² and from a practiced direction of rotation

to an unpracticed one.¹⁰ In these latter studies it was hypothesized that stimuli from several sources (including the otoliths) may have significantly influenced the development of certain demonstrated compensatory reaction patterns in ways which would result in minimal transfer of habituation.

The present study was designed to test a different aspect of the possible interactions between the otoliths and the semicircular canals. Specifically, it was desired to examine the influence of repeated semicircular canal stimulation with the otoliths in one position, on the response to stimulation of the same canals with the position of the otoliths changed. Habituation of ocular nystagmus (a response decline resulting from repeated stimulation) has been clearly demonstrated in the cat under a number of different rotatory and caloric conditions.^{e.g.,2,3,6,13,18} It has been shown that this habituation is relatively specific to the direction of response repeatedly elicited,^{e.g.,8} to the plane of the response,⁹ and to the type (rotatory or caloric) of stimulus used.^{4,5,18}

II. Method.

Eight cats, all farm-reared and of mixed breed, were each restrained by a modification of the method of Henriksson, Fernandez and Kohut¹³ prior to testing. The restraint modification involved the use of spacers to assure that head position remained invariant when the cats were placed on their sides. Fur around the left ocular orbit was shaved off and surface electrodes were taped above and below the eye. Animals were tested in pairs on the Huffman Rotation Device⁷ by means of a tier arrangement.⁸

Each animal was positioned with its head over the turning axis of the rotator and with the sagittal plane of its head and body in the plane of rotation. Two pre-habituation and two post-

¹The animals used for this experiment were lawfully acquired and treated in accordance with the "Principles of Laboratory Animal Care" issued by the Animal Facilities Standards Committee of the Animal Care Panel, U.S. Department of Health, Education and Welfare, Public Health Service, March 1963. Assistance rendered by Billy P. Updegraff and Kathryn Quattlebaum during the conduct of this study is gratefully acknowledged.

habituation trials were conducted in accordance with the schedule in Table 1. During one pre- and post-habituation trial the animals were positioned on their sides with the right half of their heads and bodies oriented upwards; in the remaining pre- and post-habituation trial the right side was oriented downwards. Pre- and post-habituation trials comprised accelerations and decelerations of $5^\circ/\text{sec}^2$ for 12 sec separated by a 2-min period of constant velocity. Half of the animals were rotated CW; the other half, CCW. Within these two groups, half of the animals received the first pre- and post-habituation test in the "right-side up" position and the second pre- and post-habituation test in the "left-side up" position; the order was reversed for the remaining animals. The use of both accelerations and decelerations permitted the elicitation of both up-beating and down-beating nystagmus under each of the two head-position conditions. Since the head position was changed 180° from the first pre- and post-trial to the second pre- and post-trial, the same sets of vertical semi-circular canals were stimulated on each occasion, but the position of the otoliths was shifted.

Habituation trials comprised 15 CCW accelerations of $5^\circ/\text{sec}^2$ for 12 sec followed by 1 min of constant velocity and a sub-threshold deceleration ($0.15^\circ/\text{sec}^2$). Half of the animals were rotated "right-side up"; the other half, "left-side up." Thus for each animal only one direction of nystagmus was elicited, with the otoliths maintained in the same position, during habituation trials.

Recording was accomplished with an Offner Type R Dynograph using 3-sec time constants in amplification. Prior to rotation each cat was placed first on its right side, then on its left side, in an optokinetic stimulator to obtain calibration data for converting slow-phase measurements of rotation-induced nystagmus to degrees of eye

movement as outlined elsewhere.¹⁸ In addition to slow-phase displacement, the number of nystagmic eye movements and the duration of the response to angular accelerations were obtained.

III. Results and Discussion.

Samples of pre- and post-test oculographic tracings are presented in Figure 1. Mean response scores for slow-phase, frequency, and duration measures of nystagmus appear in Table 2. Mean pre-test scores for the 3 measures were set at 100 per cent and the post-test data were then expressed as percentages of the pre-tests. These percentage relationships appear in Figure 2.

All post-test responses showed an average decline but the direction of nystagmus repeatedly elicited with the head (otoliths) in the "habituation" position declined more. Pre- to post-test relative change scores were computed for each animal under each condition and *t* tests were performed (Table 3). For duration values, which showed the smallest overall pre- to post-test changes, no significant differences were obtained among the comparisons. Other data have also shown that duration scores are relatively poor indicators of habituation effects.^{3,4,5}

For both frequency and slow-phase measures, the direction of nystagmus elicited with the otolith position used in the habituation series declined significantly ($p < .01$) more than: (a) the same direction of nystagmus with the otolith position changed, and (b) the opposite direction of nystagmus with the otoliths in either the "habituated" or the "unhabituated" position. There were no statistically significant differences among the remaining comparisons.

These data indicate that habituation of rotation-induced vertical nystagmus occurs in cats, but that the habituation is specific to the direc-

TABLE 1. Outline of test conditions. Pre- and post-habituation stimuli were accelerations and decelerations of $5^\circ/\text{sec}^2$ for 12 sec separated by 2 min of constant velocity. Habituation stimuli were accelerations of $5^\circ/\text{sec}^2$ for 12 sec (decelerations were sub-threshold).

Cats	Pre-1 and Post-1 (accel and decel)	Pre-2 and Post-2 (accel and decel)	Habituation Series (15 trials-accel only)
211 & 212	CW—left side up	CW—right side up	CCW—right side up
213 & 214	CW—right side up	CW—left side up	CCW—right side up
215 & 216	CCW—left side up	CCW—right side up	CCW—left side up
217 & 218	CCW—right side up	CCW—left side up	CCW—left side up

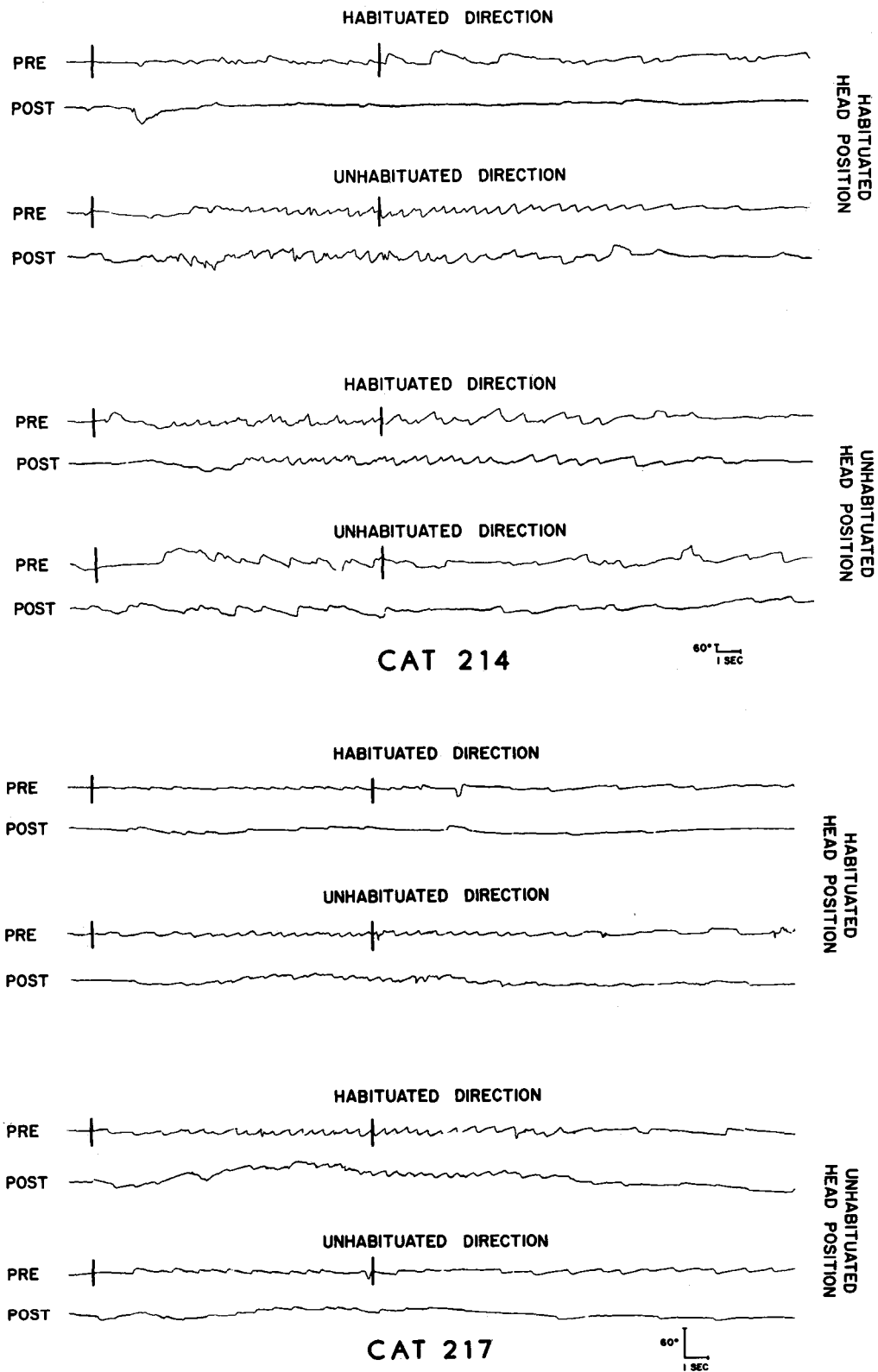


FIGURE 1. Representative tracings of vertical nystagmus from two cats. Vertical bars through the tracings demarcate the stimulus periods ($5^\circ/\text{sec}^2$ for 12 sec).

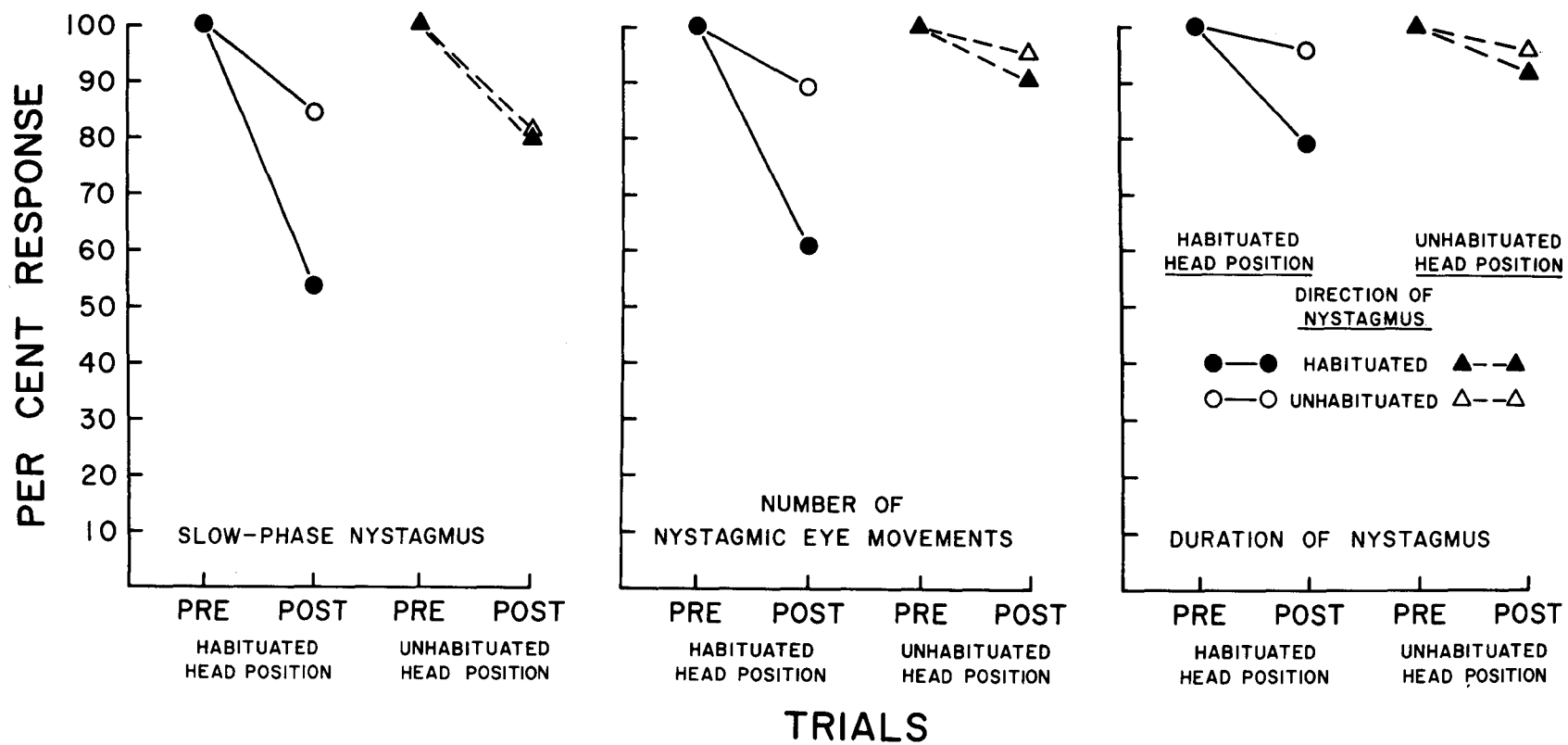


FIGURE 2. Mean pre- to post-test declines for three measures of nystagmus (N=8).

TABLE 2. Mean slow-phase displacement of the eyes, number of nystagmic eye movements, and response duration on pre- and post-habituation trials for 8 cats. Data for both the habituated and the unhabituated directions of nystagmus are presented for the head position used during habituation trials and for a 180° change in head position ("unhabituated head position").

Measure	Test	Habituated Head Position: Direction of Nystagmus		Unhabituated Head Position: Direction of Nystagmus	
		Habituated	Unhabituated	Habituated	Unhabituated
Slow-phase (Degrees)	Pre	448	372	496	325
	Post	240	311	395	264
Number of Beats	Pre	30	30	30	28
	Post	18	26	27	26
Duration (Seconds)	Pre	23	21	22	23
	Post	18	20	21	21

TABLE 3. Results of t tests for the various combinations of head position and direction of nystagmus (Hab="Habituated"; Unhab="Unhabituated").

Comparisons					t		
Head Position	Nystagmus Direction	vs.	Head Position	Nystagmus Direction	Slow- Phase	Number of Beats	Duration
Hab	Hab	vs.	Hab	Unhab	3.51*	3.07*	1.94
Hab	Hab	vs.	Unhab	Unhab	5.16*	4.39*	2.15
Hab	Hab	vs.	Unhab	Hab	3.12*	5.00*	1.89
Hab	Unhab	vs.	Unhab	Hab	0.14	1.03	0.42
Hab	Unhab	vs.	Unhab	Unhab	0.54	0.27	0.00
Unhab	Unhab	vs.	Unhab	Hab	0.45	0.07	0.32

*.01 level of significance.

tion of the reaction and to the position of the otoliths. The results do not appear due to arousal factors which might have been occasioned by changing the position of the animals; additional trials conducted with several of the cats confirmed the difference between the "practiced" and the "unpracticed" positions. The otoliths (and perhaps other nonspecific gravi-receptors) thus appear to exercise considerable influence on activity of the semicircular canals, probably by altering the neural pattern of stimulation. These results may also provide a basis for an explanation offered for the failure to obtain transfer of habituation from one mode of stimulation to another.¹⁸ It has been suggested that a possible factor in the failure of habituation of nystagmus to repeated caloric irrigations (primarily of the lateral canals) to transfer to rotational stimulation of the same canals may be due to differences in the position of the otoliths. That is, during calorization procedures, the heads of the stimu-

lated animals are placed in a position tilted back from that of normal carriage to orient the lateral canals in an optimal position for caloric stimulation. During rotation, the animals' heads are anteverted to place the lateral canals in the plane of rotation. The lack of transfer of habituation from one condition to the other may be due to the difference in the patterns of stimulation occasioned by varying the position of the otoliths. At any rate, the consistency of the results obtained from the animals tested here seems to point to an important interaction in the habituation process between specific and nonspecific gravi-receptors and responses from the semicircular canals.

IV. Summary.

Habituation of vertical ocular nystagmus by means of repeated angular acceleration was accomplished with a group of eight cats. For all habituation trials, the saggital plane of the head

and body of each animal was in the plane of rotation. By changing the position of the animals 180° after the habituation trials, the same set of semicircular canals was stimulated but the

orientation of the otoliths (and other gravireceptors) was changed. Habituation was specific to the practiced direction of nystagmus and to the practiced head (otolith) position.

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