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ADAPTATION TO VESTIBULAR DISORIENTATION: XI. THE INFLUENCE OF SPECIFIC AND NONSPECIFIC GRAVI-RECEPTORS ON NYSTAGMIC RESPONSES TO ANGULAR ACCELERATION

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ADAPTATION TO VESTIBULAR DISORIENTATION: XI. THE INFLUENCE OF SPECIFIC AND NONSPECIFIC GRAVI-RECEPTORS ON NYSTAGMIC RESPONSES TO ANGULAR ACCELERATION

I. Introduction.

During aircraft maneuvers, pilots frequently experience combined linear and angular accelerations. That such combination might modify the responses ordinarily identified with one or the other stimulus has been suggested by several recent investigations. These studies have cited the possible influences of nonspecific and specific gravi-receptors, particularly the otoliths (detectors of linear acceleration), on reactions usually attributed solely to the activity of the semicircular canals (detectors of angular acceleration). Thus, the failure of habituation of vestibular responses to transfer from one stimulus modality (e.g., caloric) to another (e.g., rotation) in cats,[2 3 4 15] and from one quadrant of head movements to another in human coriolis studies,[8 10] has been attributed to possible differences in the pattern of stimulation contributed from several sources including the otoliths. Data obtained from rabbits which had undergone nerve resections led Owada and Okubo[17] to conclude that the otoliths exert some regulatory functions on nystagmus, while studies with centrifuges showed that otolithic stimulation influenced the magnitude of nystagmus obtained from humans as a result of both calorizations[1] and angular accelerations.[14] Linear accelerations produced by parallel swings have caused nystagmus in humans and rabbits when the eyes of the subjects were deviated laterally,[11 12 13 18] and horizontal nystagmic reactions have been reported for humans exposed to periodic linear accelerations.[16] Additionally, the augmentation or reduction of nystagmus during rotation of human subjects about an earth-horizontal axis was attributed by Guedry[9] to the changing location of the gravity vector.

Collins[5] examined the possible influence of gravi-receptors on habituation of nystagmus in cats. Cats placed on their sides were given a series of angular accelerations which significantly reduced their nystagmic reaction. However, when the position of each cat was changed by 180° (thereby keeping the same sets of canals in the plane of rotation), no habituation effects were apparent during subsequent testing.

With few exceptions,[e.g., 19 20] studies of vestibular habituation in birds have been concerned with head nystagmus rather than with ocular responses to stimulation of the semicircular canals. The present study was designed to examine the process of habituation of ocular nystagmus in birds and to explore further the possibility of an interaction between gravi-receptors and semicircular canal activity in the habituation process.

II. Method.

Subjects. Habituation of horizontal nystagmus was examined in a group of six African parrots. Sixteen dwarf parrots were used to examine the influence of the position of specific and nonspecific gravi-receptors on the habituation of vertical nystagmus. Each bird was restrained by means of a band of gauze which served both to keep the wings against the body and to secure a special arched, cloth-covered brace which extended from the back of the bird around the top of its head. The beak of the bird was taped closed and secured (in approximately the position of normal carriage relative to the bird's body) to the edge of a metal container in which the bird was placed. Additional tape extended across the cloth-covered brace from one side of the container to the other and provided

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The 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, United States Department of Health, Education, and Welfare, Public Health Service, March 1963. We gratefully acknowledge assistance rendered by Sue Downs Brown and Nancy Rice during the conduct of this study.

complete immobilization of the subject. Needle electrodes were inserted on each side of each eye of the African parrots, and above and below each eye of the dwarf parrots so that separate recordings of either horizontal or vertical components of nystagmus were obtained from the right and left eye of each bird. Recording from both eyes separately but simultaneously permitted a choice of tracings for scoring and provided additional assurance that a complete set of tracings would be obtained even though a recording problem (e.g., a pulled electrode) might develop. The recorder was an Offner Type R Dynograph with 3 sec. time constants. Animals were tested in groups of two or three by means of a tier arrangement on the Huffman Rotation Device.[6 7] A variety of auditory stimuli was presented during response periods to help maintain alertness in the birds.

African parrots: Lateral-canal stimulation. African parrots were tested with their lateral canals in the plane of rotation and with their heads (and bodies) positioned over the turning axis of the rotator. Two pre- and two post-habituation trials, immediately preceding or following the habituation series, were conducted as indicated in Table 1; stimuli comprised accelerations and decelerations of 5°/sec.^{2} for 12 sec., separated by 2 min. of constant velocity. The habituation series comprised 15 accelerations of 5°/sec.^{2} for 12 sec., followed by 1 min. of constant velocity and subthreshold decelerations (0.15°/sec.^{2} for 400 sec.). An additional pair of post-tests, conducted 2 weeks after the initial pair, examined the question of retention of habituation. All trials were in total darkness; rest intervals between trials (i.e., with the rotator at a standstill) were from 3 to 5 minutes in room illumination.

TABLE 1.—Outline of test procedure for stimulation of the lateral semicircular canals in six African parrots. Pre- and post-habituation stimuli were accelerations and decelerations of 5°/sec.^{2} for 12 sec., separated by 2 min. of constant velocity. Habituation stimuli comprised accelerations of 5°/sec.^{2} for 12 sec. (decelerations were subthreshold).

African parrots	Pre-trails (accel. and decel.)		Habituation series (15 trials; accel. only)	Post-trials (accel. and decel.)	
	1	2		1	2
A-1, A-2, A-3	CW	CCW	CW	CW	CCW
A-4, A-5, A-6	CCW	CW	CW	CCW	CW

Dwarf parrots: Vertical-canal stimulation. In the major portion of the study, dwarf parrots were placed in a tilted position with their heads over the axis of rotation. Two body placements were used: "beak down" and "beak up." For the "beak down" position, the container holding the birds was tilted 90° forward and approximately 45° to the left of the birds (from the restrained, upright position); the "beak up" position represented a change of 180° from "beak down." In these positions, a brisk vertical nystagmus could be elicited. By visual observation of birds used in pilot studies, the direction of the eye-movement responses tended to be somewhat oblique and the direction of the fast-phase in one eye was opposite to that of the other eye.

The 16 dwarf parrots were divided into four groups according to body placement and to direction of rotation during habituation trials (see Table 2). Thus, two groups received habituation trials in a "beak down" position; one with CW (clockwise) and the other with CCW (counterclockwise) rotation. The remaining two groups were habituated with "beaks up," one during CW and the other during CCW rotation. The habituation series for all birds comprised 15 accelerations of 10°/sec.^{2} for 12 sec.; each acceleration was followed by 1 min. at constant velocity and a subthreshold deceleration (0.15°/sec.^{2} for 800 sec.). Two pre- and two post-tests were conducted immediately before and immediately after the habituation series. Within each

group of birds the first pre- and post-test rotations were conducted with "beak down" for two birds (one CW, the other CCW), and with "beak up" for the remaining two birds (one CW, the other CCW). The second pre- and post-test were in the same direction of rotation as the first for a given bird, but the animal's position was changed by 180°. Pre- and post-tests comprised accelerations and decelerations of 10°/sec.^{2} separated by two min. of constant velocity. Thus, during pre- and post-tests both directions of nystagmus were elicited (one direction during acceleration, the other during deceleration) for the two head and body positions ("beak down" and "beak up"). During the habituation series, however, only one direction of nystagmus was permitted to occur and the head and body were maintained in a single position.

TABLE 2.—Outline of test procedure for stimulation of the vertical semicircular canals in 16 dwarf parrots. Pre- and post-habituation stimuli were accelerations and decelerations of 10°/sec.^{2} for 12 sec., separated by 2 min. of constant velocity. Habituation stimuli were accelerations of 10°/sec.^{2} for 12 sec. (decelerations were subthreshold).

Dwarf parrots	Pre-1 and post-1 (accel. and decel.)	Pre-2 and post-2 (accel. and decel.)	Habituation series (15 trials: accel. only)
D-1	CW—beak down	CW—beak up	All CW (beak down)
D-2	CW—beak up	CW—beak down	
D-3	CCW—beak down	CCW—beak up	
D-4	CCW—beak up	CCW—beak down	
D-5	CW—beak down	CW—beak up	All CW (beak up)
D-6	CW—beak up	CW—beak down	
D-7	CCW—beak down	CCW—beak up	
D-8	CCW—beak up	CCW—beak down	
D-9	CW—beak down	CW—beak up	All CCW (beak down)
D-10	CW—beak up	CW—beak down	
D-11	CCW—beak down	CCW—beak up	
D-12	CCW—beak up	CCW—beak down	
D-13	CW—beak down	CW—beak up	All CCW (beak up)
D-14	CW—beak up	CW—beak down	
D-15	CCW—beak down	CCW—beak up	
D-16	CCW—beak up	CCW—beak down	

Scoring. Measurements were made of slow-phase eye displacement, frequency of nystagmus, and duration of response as outlined elsewhere.[15] For the African parrots, it was possible to convert the horizontal slow-phase measurements to degrees of eye movement by means of a calibration factor obtained from the birds' responses to optokinetic stimulation.[2] Vertical eye movements could be obtained only occasionally from a few of the dwarf parrots exposed to the optokinetic stimulator, hence slow-phase measurements of their vertical eye movements were expressed in arbitrary units.

III. Results and Discussion.

Stimulation of the lateral canals. A sample of the tracings of horizontal eye movements obtained from one of the African parrots appears in Figure 1. Mean response scores for the six birds for measures of slow-phase displacement, frequency, and duration of nystagmus from the right eye are presented in Table 3 and depicted in Figure 2.

For the direction of nystagmus repeatedly elicited during habituation trials, there was a decline for all three measures (relative change scores) from the pre-test to post-1; the decline was statistically significant for slow-phase ($t=5.38$, $p<.01$) and frequency ($t=11.47$, $p<.001$) measures, but not for duration ($t=1.36$, $p<.05$ level$=2.57$). The unhabituated direction of nystagmus showed some decline from the pre-test to post-1 (except for an increase in the

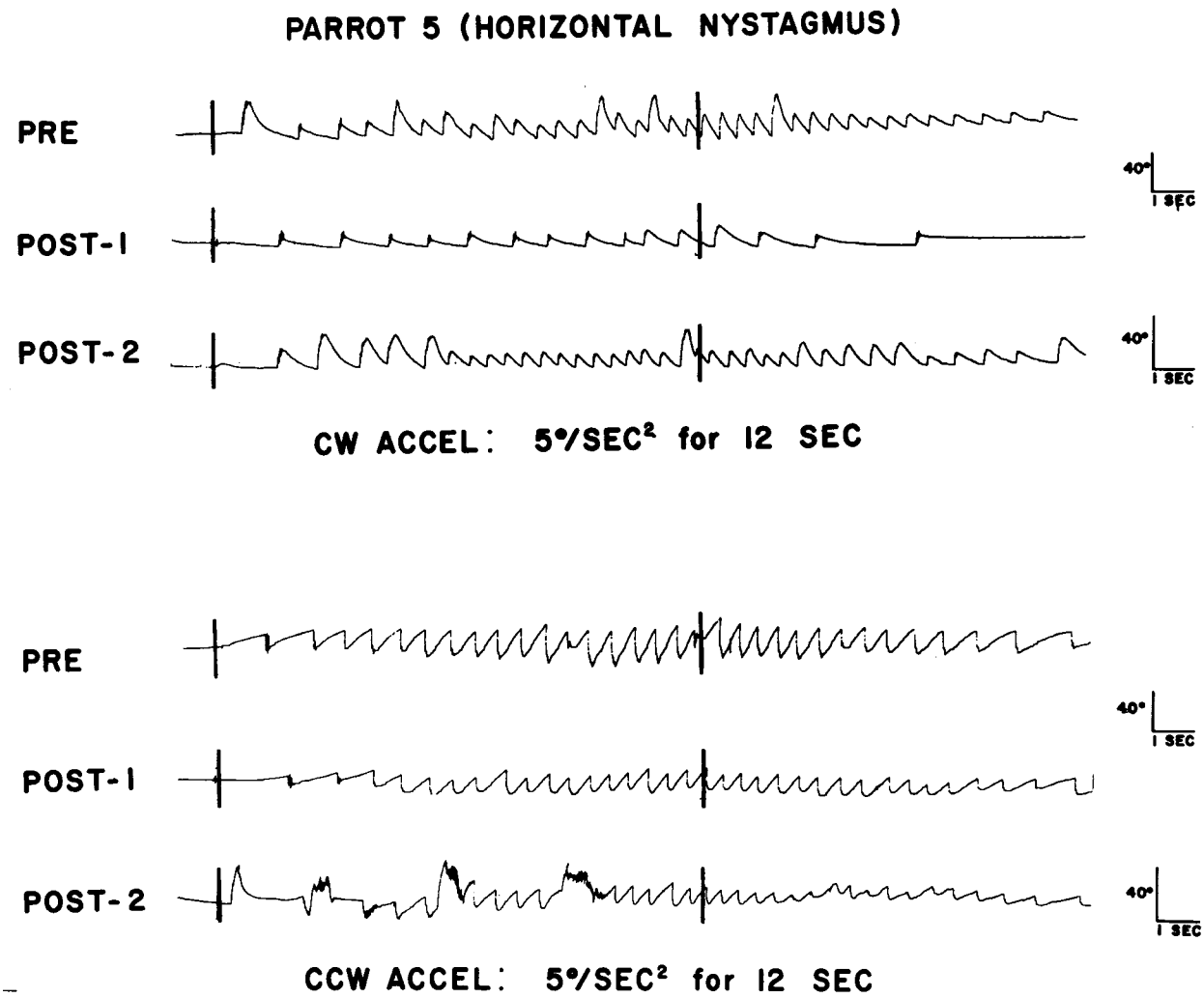

FIGURE 1. Tracings obtained from an African parrot. Vertical bars demarcate the stimulus periods; calibration markers appear to the right of the tracings. Upward deflections of the recording pen signify eye movements to the right; downward deflections signify eye movements to the left. A series of 15 unidirectional habituation trials occurred between the pre-test and post-1 tests; post-2 tests were given 2 weeks later. A clear, directionally specific reduction is evident in the post-1 tracings (CW acceleration), with a strong recovery from habituation apparent in the post-2 data.

average duration score), but the declines were not significant. Post-2 tests, conducted 2 weeks later, showed recovery of the habituated response. Nystagmus in the unhabituated direction was approximately at the same level in the post-1 and post-2 sessions, but the latter tested as significantly lower than the pre-test ($t=4.40$, $p<.01$), due to the fact that all six parrots showed some decline from the pre-test to post-2 (see Table 4).

Comparisons among relative change scores appear in Table 5. The declines of slow-phase eye movement and frequency of nystagmus in the habituated direction from the pre-test to post-1 were significantly greater than both the pre- to post-1 change for the unhabituated direction, and the pre- to post-2 change for the habituated direction. No other comparisons produced statistically significant differences.

Thus, ocular nystagmus from parrots underwent relatively rapid habituation and the response decline was (relatively) directionally specific. Considerable recovery occurred following a 2-week rest. These results are similar to those obtained from other animals,[e.g., 7]

Stimulation of the vertical canals. Tracings of the vertical component of eye movements recorded from one eye of a dwarf parrot appear

TABLE 3.—Mean horizontal slow-phase eye displacement, number of nystagmic beats, and response duration obtained from six African parrots during tests before and after a series of 15 unidirectional angular accelerations. Data represent an average of two trials per subject (CW accel. and CCW decel., or CW decel. and CCW accel.). The lateral canals were in the plane of rotation. All responses were recorded from the right eye of each bird. Pre-test and post-1 tests, respectively, were given immediately before and after the habituation series; post-2 tests were conducted 2 weeks later.

Test	Habituated direction					
	Slow-phase		Frequency		Duration	
	Degrees	% of pre-	Beats	% of pre-	Seconds	% of pre-
Pre-	469.3	----------	35.6	----------	25.8	----------
Post-1	253.7	54.1	19.2	53.9	23.1	89.5
Post-2	410.5	87.5	31.9	89.6	26.1	101.2

Test	Unhabituated direction					
	Slow-phase		Frequency		Duration	
	Degrees	% of pre-	Beats	% of pre-	Seconds	% of pre-
Pre-	472.3	----------	36.7	----------	25.8	----------
Post-1	404.1	85.6	33.8	92.1	28.3	109.7
Post-2	405.6	85.9	32.1	87.5	25.8	100.0

TABLE 4.—Results of t tests between pre-test and post-test scores for the habituated and the unhabituated direction of nystagmus.

Measure	Comparisons	Direction of nystagmus	
		Habituated	Unhabituated
Slow-phase	Pre- vs. post-1	**5.38	1.76
	Pre- vs. post-2	2.33	**4.40
	Post-1 vs. post-2	*3.35	0.04
Frequency	Pre- vs. post-2	***11.47	2.43
	Pre-vs. post-2	0.70	2.21
	Post-1 vs. post-2	*3.90	0.66
Duration	Pre- vs. post-1	1.36	1.98
	Pre- vs. post-2	0.61	0.53
	Post-1 vs. post-2	1.36	1.74

Levels of significance: *—.05, **—.01, ***—.001

in Figure 3. Mean response scores for duration, frequency, and slow-phase eye displacement, for each of the two head positions, appear in Table 6 and are graphically presented in Figure 4.

Statistical analyses (Table 7) of pre- and post-test scores indicate that nystagmus in the direction repeatedly elicited during habituation trials declined significantly for all three response measures when the birds were maintained in the same position as that imposed during the habituation series. For a change in position of 180°, however, only frequency of nystagmus showed a significant pre- to post-test decline (see Figure 4 and Table 7).

Statistical comparisons of the relative change of post-test scores from those of the pre-test appear in Table 8. The decline in nystagmic output for the habituated direction and the head-body position used during the habituation series was significantly greater (.05 – .01 levels) than the pre- to post-test changes for either direction of nystagmus in the unhabituated head position,

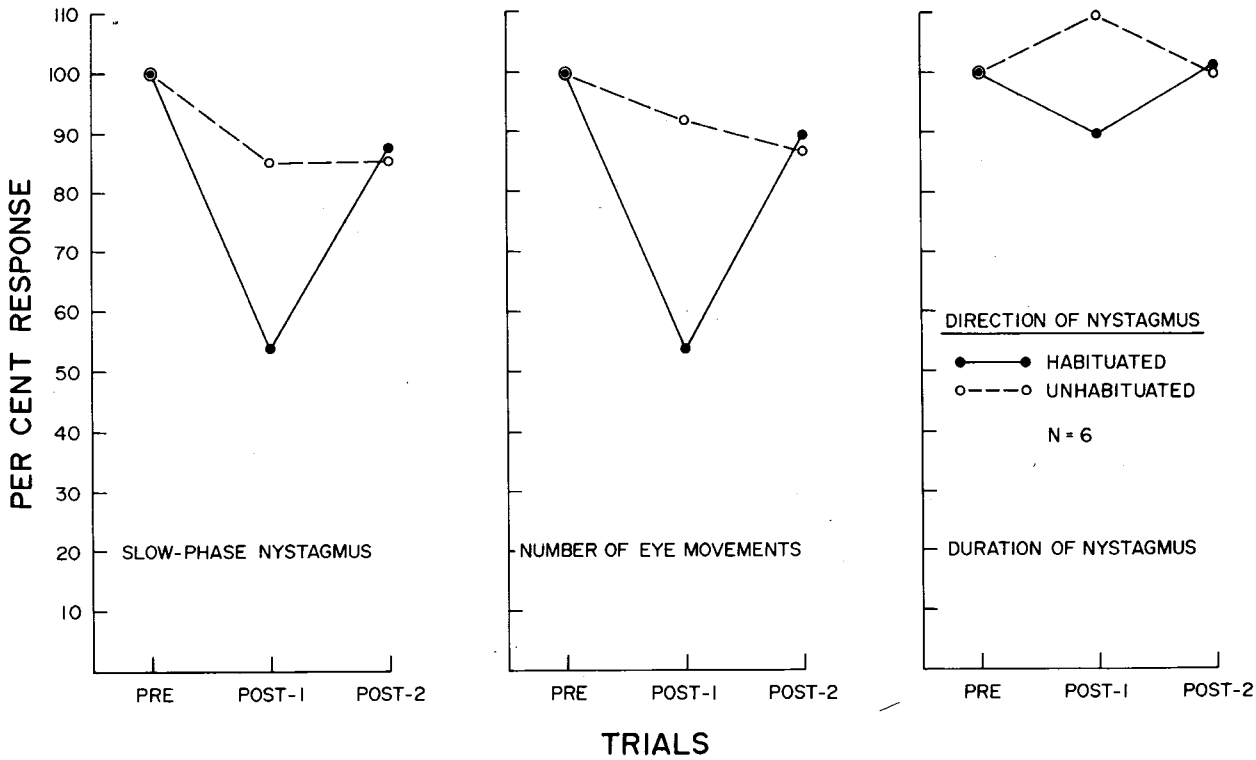

FIGURE 2. Mean change (in percent) of post-1 and post-2 scores from pre-test levels for three measures of horizontal nystagmus obtained from African parrots. Pre-test scores for the habituated and the unhabituated directions were each set at 100 percent. Directionally specific effects of the habituation series (post-1) are marked, and recovery (post-2) is clearly evident.

TABLE 5.—Results of t tests comparing the relative change in post-1 and post-2 responses from those of the pre-test for the habituated and the unhabituated directions of nystagmus.

Comparisons of relative change	Measure	t
Habituated: Pre- to post-1	Slow-phase	*3.38
vs.	Frequency	*3.70
Habituated: Pre- to post-2	Duration	1.38
Habituated: Pre- to post-2	Slow-phase	**4.18
vs.	Frequency	***10.46
Unhabituated: Pre- to post-1	Duration	1.93
Unhabituated: Pre- to post-1	Slow-phase	1.02
vs.	Frequency	0.60
Unhabituated: Pre- to post-2	Duration	1.71
Unhabituated: Pre- to post-2	Slow-phase	0.36
vs.	Frequncy	0.72
Habituated: Pre- to post-2	Duration	0.95

Levels of significance: *—.05, **—.01, ***—.001

TABLE 6.—Mean vertical slow-phase eye displacement, number of nystagmic beats and response duration during pre- and post-habituation trials for 16 dwarf parrots. Data for both the habituated and unhabituated directions of nystagmus are presented for the head position used during the 15 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 (Arbitrary Units)	Pre	148.0	172.3	165.0	160.6
	Post	99.4	181.4	227.7	162.0
Number of Beats	Pre	34.1	32.2	34.3	27.7
	Post	17.5	28.8	26.9	26.3
Duration (Seconds)	Pre	23.1	22.1	22.5	21.4
	Post	18.0	22.1	21.1	20.4

as well as for the unpracticed direction of nystagmus in the habituated head-body position. No other comparisons yielded statistically significant differences (see Table 8 and Figure 4).

Thus, habituation of vertical ocular nystagmus occurred in the birds and was confined to the direction repeatedly elicited. Moreover, the reduction in response was relatively specific to the position maintained by the animals during the habituation series, i.e., there was relatively little or no transfer of habituation when the same canals were stimulated but with the position of the animals changed by 180°. These data agree with related results obtained from cats,[5] and do not appear to be due to arousal factors caused by changing the position of the animals. In addition to the auditory stimuli used to help maintain arousal during response periods, several birds were given six or more additional trials in the "unpracticed" head-body position; the response declined in the usual fashion. The birds were then placed in the opposite position (that maintained during the original habituation series); no recovery of response from the post–1 levels was apparent. Further trials involved alternating the position of the animals. No discernible effects of the handling occurred.

The results permit two interpretations: (1) The specificity of the response reduction is due to factors generally associated with the habituation procedure, i.e., the animal becomes habituated to the general environment as well as to the acceleration stimulus, and "significant" changes in the environment (including body position) result in a failure of habituation to transfer to the new situation and; (2) the neural patterns gen-

TABLE 7.—Results of t tests between pre- and post-test scores for the two directions of nystagmus and the two head-body positions.

Condition		t		
Direction of nystagmus	Head position	Slow-phase	Frequency	Duration
Habituated	Habituated	*2.72	***4.94	**3.08
Habituated	Unhabituated	1.67	*2.58	0.98
Unhabituated	Habituated	0.41	1.60	0.00
Unhabituated	Unhabituated	0.08	1.05	1.31

Levels of significance: *—.05, **—.01, ***—.001

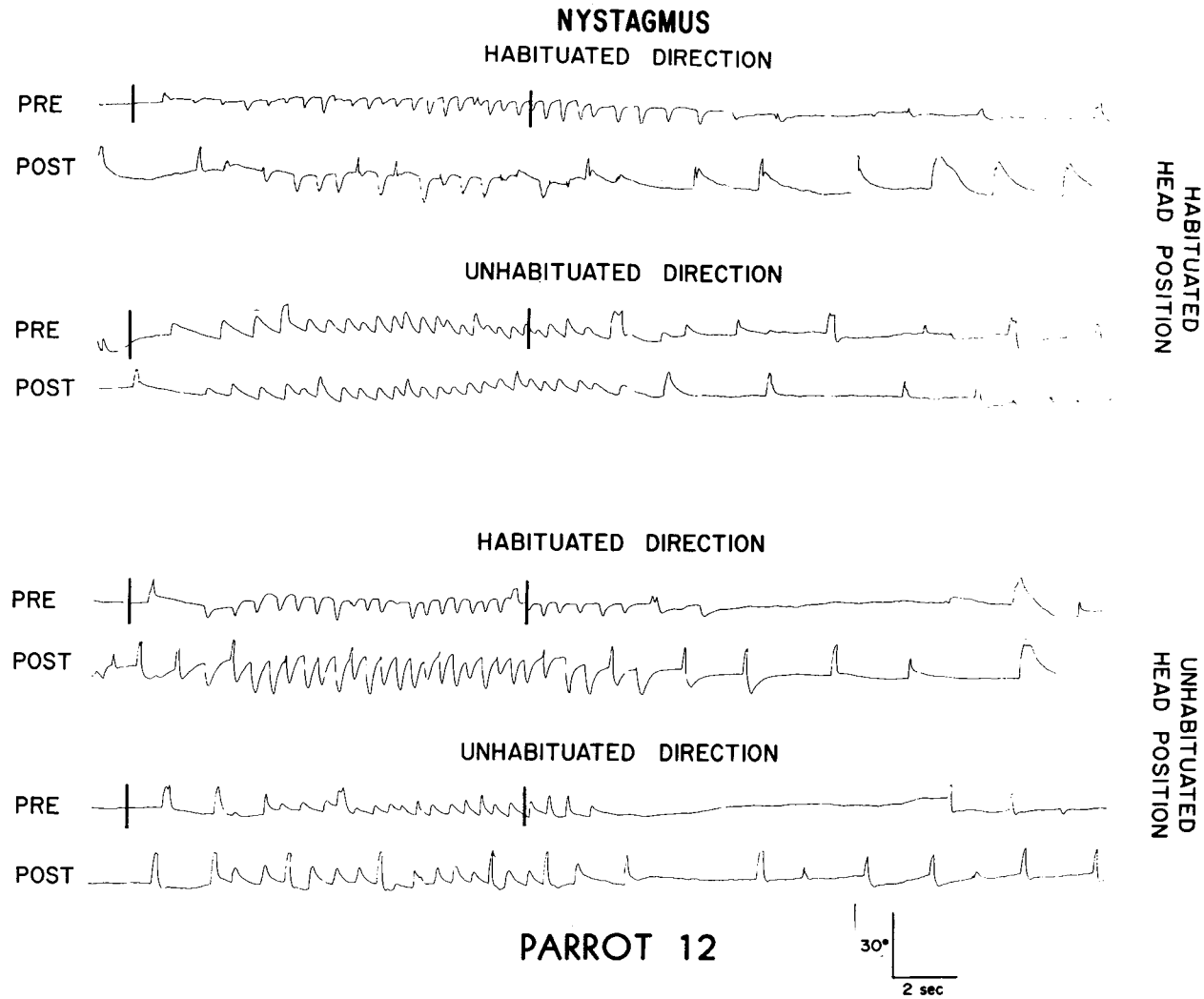

FIGURE 3. Tracings of vertical nystagmus obtained from a dwarf parrot. An optokinetic calibration was obtained for this bird. Vertical bars demarcate stimulus periods of 10°/sec.^{2} for 15 sec. Upward and downward deflections of the recording pen signify vertical eye movements in those same directions. A series of 15 unidirectional habituation trials occurred between the pre-test and post-tests. Nystagmus declined significantly for the head position used and for the direction repeatedly elicited during the habituation series. (Note the early secondary nystagmus in the topmost post-tracing.) That same direction of nystagmus is considerably enhanced during the post-test trial for the unhabituated head position.

erated by the semicircular canals, the otoliths, and other gravi-receptors interact to a considerable degree in determining habituation of nystagmus in some animals. This proposed interaction would thus be more dynamic than the previously reported regulatory effects (i.e., inhibiting or enhancing responses) of the otoliths on semicircular canal activity.

IV. Summary.

Horizontal ocular nystagmus from restrained birds was habituated in a directionally specific fashion by means of repeated angular accelerations. Substantial response recovery was evident following 2 weeks of rest. Vertical nystagmus was similarly habituated in a separate group of birds. The reduction of the latter response was obtained with the birds positioned so that vertical semicircular canals were in the plane of rotation. By changing the position of the birds 180° after the habituation trials, the same set of canals could be stimulated but with the otoliths and other gravi-receptors oriented differently. Habituation was relatively specific for the direction

of nystagmus repeatedly elicited and for the head and body position maintained during habituation trials. A dynamic interaction between gravi-receptors and the semicircular canals is suggested as a possible feature of nystagmic habituation.

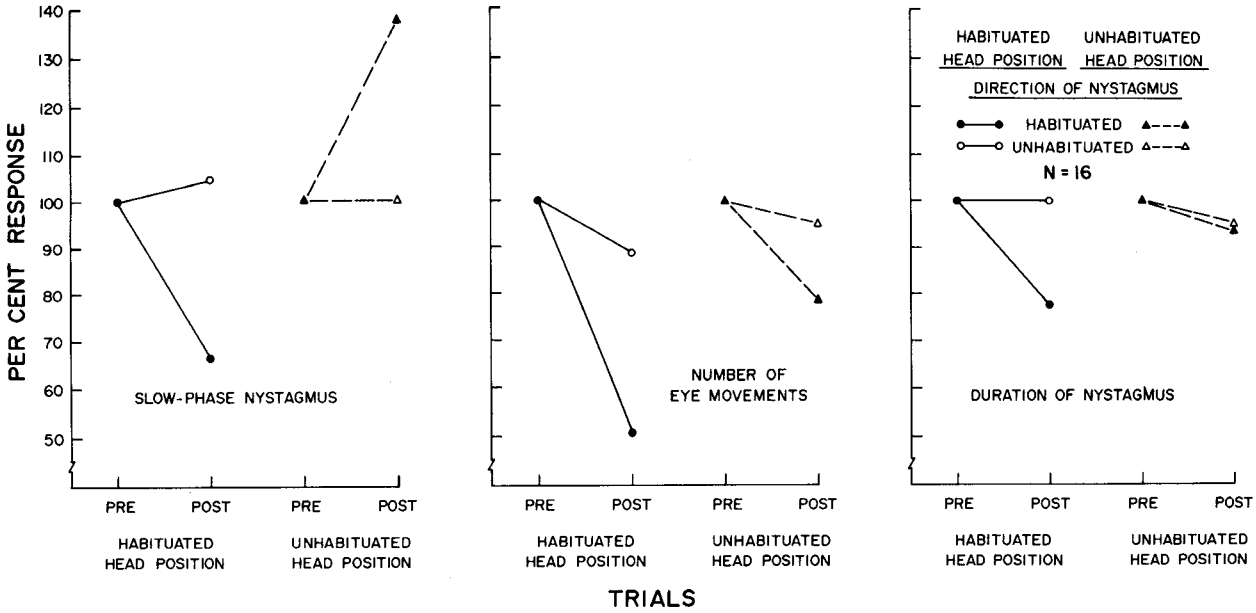

FIGURE 4. Mean change (in percent) of post-test scores from pre-test levels for three measures of vertical nystagmus obtained from dwarf parrots. Pre-test scores for the habituated and the unhabituated directions of nystagmus were each set at 100 percent. Response reduction is directionally specific and relatively specific to the head position used during the habituation series.

TABLE 8.—Results of t tests on relative change scores (pre- to post-test) between the various combinations of head-body position and direction of nystagmus (Hab=Habituated; Unhab=Unhabituated). The pre- to post-test decline for the habituated direction of nystagmus in the habituated head position was significantly greater than the pre- to post-test changes obtained for other head-position and nystagmus-direction combinations.

Comparisons					t		
Head position	Nystagmus direction	vs.	Head position	Nystagmus direction	Slow-phase	Number of beats	Duration
Hab	Hab	vs.	Hab	Unhab	**3.42	**3.94	*2.56
Hab	Hab	vs.	Unhab	Unhab	*2.34	**5.47	1.53
Hab	Hab	vs.	Unhab	Hab	**3.26	**3.10	1.51
Hab	Unhab	vs.	Unhab	Hab	0.69	1.13	1.10
Hab	Unhab	vs.	Unhab	Unhab	0.46	0.53	1.44
Unhab	Unhab	vs.	Unhab	Hab	1.35	0.90	0.05

Levels of significance: *—.05, **—.01.

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