AM 67-2

ADAPTATION TO VESTIBULAR DISORIENTATION. IV.

Responses to Angular Acceleration and to Bilateral Caloric Stimulation Following Unilateral Caloric Habituation

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FEDERAL AIR SURGEON

January 1967

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I. Introduction

Thorpe[14] defines habituation as "an activity of the central nervous system whereby innate responses to certain relatively simple stimuli, especially those of potential value as warning of danger, wane as the stimuli continue for a long period without unfavourable results"; habituation, then, is learning *not* to respond. In accordance with this central concept of habituation, it has been suggested that the response declines to repeated vestibular stimulation are forms of learning, as they evidence the characteristics of learned behavior—acquisition, retention, and transfer.

Several recent investigations have been concerned with questions of transfer-effects in habituation of ocular nystagmus. One such effect is that of stimulus transfer, i.e., transfer of habituation from one type of stimulation (e.g., rotatory) to another (e.g., caloric).

Maxwell, Burke, and Reston[13] and Hood and Pfaltz[12] reported no decline in nystagmic responses to caloric stimuli after rotatory habituation. More recently, Collins[2,3] investigated transfer from rotatory to caloric and from caloric to rotatory situations and obtained minimal transfer. Dunlap[8], however, found a marked reduction in the response of rabbits to rotatory stimulation following a series of caloric irrigations with ice water. The absence of stimulus transfer-effects[2,3] has been attributed to (1) differences in intensity of response produced by caloric irrigation and by angular acceleration; (2) differences in the pattern of neural excitation to unilateral and to bilateral stimulation. A study by Capps and Collins[1] isolated certain of these differences and showed that, irrespective of the stimulus intensities used, a significant reduction in nystagmic responses of the cat to unilateral stimulation occurred after habituation to bilateral caloric irrigations. The present study was designed to examine further some questions regarding transfer of habituation while attempting to evaluate the influences of intensity, type of stimulus, and unilateral vs. bilateral stimulation.

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 acknowledgment is made of the assistance rendered by Bill Updegraff, Sue Grounds, Nancy Rice, Jeanne Heaton, and David Schroeder.

II. Methods

Subjects and Restraint. Subjects were 60 mature cats, unused in previous experiments, and assigned randomly to six equal groups. Restraint was accomplished by the method of Henriksson, Fernandez, and Kohut[11] with an adjustable restraining device. For rotation trials, the head was positioned so that a line from the outer canthus of the eye to the tragus of the ear was in the horizontal plane, placing the lateral canals in the plane of rotation; for caloric irrigations, the head was inclined 45° upward from the horizontal.

Calorization. Water baths equipped with Bronwill constant temperature circulators were used for 26°C, 30°C, and 46°C stimuli. For ice water irrigations temperature was 4°C. Rubber tubing extended from the water baths to irrigation nozzles which were inserted into the animal's ears. Rate of water flow was 15cc/sec. Irrigation periods were controlled automatically by means of solenoids connected to a Hunter Interval Timer, Model 111-C.

Rotation. The turntable[5] was situated in a light-proof room. A set of tiers allowed as many as three cats to be rotated simultaneously with their heads at the center of rotation[6].

Recording. Needle electrodes inserted at the outer canthi of the cats' eyes picked up corneo-retinal potentials, which were relayed through a terminal electrode board to the recorder. Two

Offner recorders were used, a Type TC for caloric trials and a Type R for rotation trials. A 3-sec time constant was employed in amplification.

Calibration. Prior to vestibular testing, eye movement calibrations were obtained by means of an optokinetic stimulator (a steel drum with a striped interior). Eye movements (optokinetic nystagmus) induced by rotation of the drum at 24°/sec were recorded, measured, and used to calculate calibration constants.

Scoring. For all trials, three types of measures were obtained: amount of slowphase eye displacement (in millimeters), number of nystagmic beats (frequency), and duration of response (in seconds). Slowphase displacement values in millimeters were transformed into degrees of eye movement by means of the calibration constants[1].

III. Procedure

Six groups of animals were used. A different series of 15 habituation trials was administered to each of five of these groups; the sixth group received no habituation trials (see Table 1). All animals were given identical pre- and post-tests (bilateral caloric irrigations and rotation trials). All trials, including the irrigation periods, were in total darkness.

PRE- AND POST-TESTS

For all animals, the pre- and post-test rotation trials consisted of an acceleration (5°/sec² for 12 sec), 2 min of constant velocity, and a subsequent deceleration (5°/sec² for 12 sec); half of the subjects in each group received clockwise rotations and the remaining half received counterclockwise rotations. Pre- and post-test bilateral caloric stimulation consisted of simultaneous irrigations with water at a temperature of 30°C to the right ear and 46°C to the left ear. Duration of stimulation was 20 sec.

HABITUATION TRIALS

Experimental Groups. The habituation series for the three experimental groups consisted of 15 unilateral irrigations.

Experimental Group I received an habituation series of ice water irrigations (4°C) applied to the right ear for 15 sec. The habituation trials for this group were of a greater intensity (resulted in greater response output) relative to the pre-trials than those of the other two experimental groups.

Experimental Group II received habituation trials consisting of irrigations with 26°C water

TABLE 1. Schedule of Test Stimuli for Each Group. (R=right ear; L=left ear; IW=ice water irrigation; all temperatures are in (°Centigrade)

Pre-tests	
Pre–1	*Pre–2*
Rotation (5°/sec² for 12 sec accel and decel)	Bilateral Caloric (R30°L46°C for 20 sec)
Habituation Series	
Control Groups	*Experimental Groups*
Caloric. Bilateral Caloric (R30°L46°C for 20 sec)	*I.* Unilateral Caloric (IW right for 15 sec)
Rotation. Rotation (5°/sec² for 12 sec accel; subthreshold decel)	*II.* Unilateral Caloric (R26°C for 30 sec)
Combined. No habituation trials	*III.* Unilateral Caloric (R30°C for 30 sec)
Post-tests	
Post–1	*Post–2*
Bilateral Caloric (R30°L46°C for 20 sec)	Rotation (5°/sec² for 12 sec accel and decel)

administered to the right ear for 30 sec. These trials were of an intensity intermediate to those received by Groups I and III.

Experimental Group III received an habituation series of irrigations with 30°C water applied to the right ear for 30 sec. This habituation series was the least intense of those received by the experimental groups.

Control Groups. Three control groups were used to provide a measure of the expected level of response after 15 bilateral calorizations (Caloric Control), 15 rotation trials (Rotation Control), and a period of no stimulation (Combined Control).

The Caloric Control Group received an habituation series of bilateral irrigations (30°C water to the right ear and 46°C to the left ear simultaneously for 20 sec). These 15 habituation trials were identical to the pre- and post-test bilateral irrigations received by all groups.

The Rotation Control Group received habituation trials which consisted of counterclockwise accelerations (5°/sec^2 for 12 sec), 2 min of constant velocity, and subthreshold decelerations (0.15°/sec^2). Thus, only eye movements in the same direction as those evoked by the caloric habituation trials were elicited.

The Combined Control Group received no habituation trials. The animals remained in restraint for a period of time equal to that of an habituation series.

The test schedule appears in Table 1. In all cases a time interval of 20 minutes between the start of successive trials was provided. Animals were run in groups of four for the caloric trials and in groups of three for rotation trials whenever practicable. All animals were in room illumination for at least five minutes prior to each trial.

IV. Results

HABITUATION TRIALS

Experimental Groups. All experimental groups evidenced response declines from Trial 1 to Trial 15 of the habituation series. These reductions ranged from 76–83% for slowphase displacement, from 58–74% for beat-frequency, and from 15–36% for duration of response. Response reduction was most marked during the early trials of the habituation series.

The three stimulus levels (ice water, 26°C, and 30°C) produced the expected variation in response. Ice water evoked the greatest amount of nystagmus, the 30°C irrigations produced the least, while the 26°C stimulus yielded an intermediate level of response.

Control Groups. Both the Caloric and the Rotation Controls exhibited declines from Trial 1 to Trial 15 of the habituation series. (The Combined Control Group received no habituation trials.) The Caloric Control response decline was 62% for slowphase displacement, 50% for number of beats, and 2% for duration of response. Corresponding reductions for the Rotation Control Group were 45%, 23%, and 15%, respectively.

PRE- AND POST-TEST TRIALS

Group Differences. For the six groups, analyses of covariance were conducted on pre- and post-test scores for (1) the bilateral caloric tests, (2) the rotatory stimuli eliciting responses in the direction stimulated during the habituation series, and (3) the rotatory stimuli eliciting responses in the direction opposite to that stimulated during the habituation trials. Separate analyses were executed for the three measures of nystagmus (slowphase, frequency, and duration). (1) Groups differed in pre- to post-test response decline for bilateral calorizations on all measures (.001 levels). (2) For responses to rotation in the same direction as those elicited during the habituation trials, the groups also evidenced significant differences in pre- to post-test response reduction on all measures (.05 to .01 levels). (3) No significant differences in pre- to post-test response declines were found for responses to rotation in the direction opposite to those which occurred during the habituation series.

To ascertain which groups differed significantly in pre- to post-test response decline, t tests were executed on group pre- to post-test difference scores (% decline).

Bilateral Calorizations. For bilateral caloric data, declines of the various groups were evaluated by comparing them statistically with the declines shown after a bilateral caloric habituation series (the Caloric Control Group) and with the reductions evidenced after a period of no stimulation (the Combined Control Group). For slowphase displacement, frequency, and duration of response resulting from bilateral caloric stimulation, the response declines of the three experi-

mental groups were as great as those of the Caloric Control Group. The three experimental groups and the Caloric Control Group also had significantly greater reductions in output on all measures than did both the Combined and the Rotation Control Groups (.05 to .001 levels), while the latter two groups did not differ from each other on any measure. Thus, unilateral habituation stimuli produced as great a bilateral-caloric response reduction as did a series of bilateral caloric irrigations: that is, unilateral caloric habituation transferred to bilateral caloric stimulation.

The response reductions among experimental groups were not found to differ significantly on any measure. Thus, intensity of the habituating stimulus did not appear to be a significant variable in this transfer of habituation.

The Rotation Control Group showed significantly less pre- to post-test caloric response decline than did the three experimental groups and the Caloric Control Group (.05 to .001 levels), while exhibiting a reduction no greater than that of the Combined Control Group (the group receiving no habituation stimulation). Therefore, it would seem that rotatory habituation did not transfer to bilateral caloric stimulation, although both stimuli were of a bilateral nature.

Figure 1 illustrates the group reductions in responses to the bilateral caloric irrigations for the experimental and control groups. Tracings of nystagmus during pre- and post-test bilateral caloric responses are presented in Figure 2 for the experimental groups and in Figure 3 for the control groups.

Angular Accelerations: Responses in the Direction Elicited During Habituation. For rotation-induced responses in the same direction as those elicited during the habituation series, pre- to post-test changes shown by the groups were evaluated by comparing them with the declines found after a rotatory habituation series (the Rotation Control Group) and with the changes shown by the Combined Control Group. The Rotation Control Group declined significantly more in slowphase output than did all other groups (.05 to .001 levels). (The Combined Control Group also declined significantly more than Experimental Group III.) For beat-frequency in the habituated direction, the response reduction of the Rotation Control Group was statistically greater than that of only Experimental Group III (.05 level). (Group III also declined significantly less than did Groups I and II.) The fact that the Rotation Control Group did not exhibit a greater mean decline in beat frequency was due to a large pre- to post-test increase in the number of eye movements from one animal; the post-test response consisting of a large number of low-amplitude nystagmic beats. The decline in duration of response for the Rotation Control Group was not statistically greater than that for any of the other groups. (Experimental Group I showed a significantly greater reduction in duration of response than did Experimental Group III or the Combined Control Group.) Thus, frequency and duration data allow for no unequivocal conclusion concerning caloric-to-rotatory transfer, as the decline of the Rotation Control Group on these measures was statistically no greater than that shown by the group receiving no habituation trials (the Combined Control Group). On the basis of the slow-phase data obtained, however, it would appear that habituation to caloric stimulation has little effect on rotatory responses.

Figures 4 and 5 demonstrate pre- to post-test reductions for rotation responses in both directions for the experimental and control groups, respectively.

V. Discussion

TRANSFER OF UNILATERAL CALORIC HABITUATION TO BILATERAL CALORIC STIMULATION

The data indicate that unilateral caloric habituation transfers to bilateral caloric stimulation. All three experimental groups (those groups receiving unilateral caloric habituation trials) exhibited as great a bilateral-caloric response reduction as did the Caloric Control Group (the group receiving bilateral caloric habituation trials).

While the three intensities of unilateral stimuli resulted in three different levels of response-output on early trials, the intensity factor did not appear to influence transfer of unilateral habituation to bilateral stimulation, within the intensity limits described here, as the three experimental groups did not differ in amount of post-test bilateral-caloric response reduction. This finding parallels that of Capps and Collins[1]

who indicated that intensity of the habituating stimulus was a negligible factor in their examination of bilateral-to-unilateral transfer of caloric habituation.

TRANSFER OF CALORIC HABITUATION TO ROTATORY STIMULATION

All groups receiving caloric habituation trials (the three experimental groups and the Caloric Control Group) evidenced significantly smaller reductions in pre- to post-test slowphase displacement responses to rotation in the habituated direction than did the Rotation Control Group. For slowphase displacement, the Rotation Control Group also showed a greater response reduction than did the Combined Control Group. This was not the case for reductions in beat frequency and duration of response, however. The unexpectedly small mean decline in beat frequency evidenced by the Rotation Control Group (significantly greater than the decline of only one other group) was due, as noted earlier, to depression of the mean by an atypical pre- to post-test increase, for this measure only, shown by one animal in the group (this same animal showed a 25% pre- to post-test reduction in slowphase displacement).

The values plotted in Figures 4 and 5 indicate that all groups which received caloric habituation trials (the three experimental groups and the Caloric Control Group) exhibited somewhat greater reductions for frequency and duration scores during post-test rotations which elicited nystagmus in the same direction as that elicited during the caloric habituation trials (as opposed to rotation-induced nystagmus in the direction opposite to that stimulated during the habituation series). This suggests that the caloric habituation series may have exerted some influence on subsequent responses to angular acceleration. On the basis of these data, then, it is suggested that while caloric stimulation may have some influence on responses to rotation, a series of caloric irrigations apparently does not produce nearly so great a response reduction as does an equal number of rotation trials, even though the caloric stimuli are of much greater intensity (produce a greater response output) than the angular stimuli. That this is the case whether the caloric stimuli employed activate only one labyrinth (the three experimental groups) or both labyrinths (the Caloric Control Group) indicates that differences in caloric and rotatory modes of activation may be at least partially responsible for failure to obtain transfer. Another possible explanation for lack of intermodal transfer lies in the difference between position of the otoliths during rotatory and during caloric stimulation (heads were fixed in a position approximately that of normal carriage for rotation trials and were elevated 45° for caloric irrigation). To the extent that the otoliths might influence semi-circular canal responses, transfer of nystagmus habituation might be specific to a given position of the otoliths. Data presented below in the section dealing with rotatory-to-caloric transfer of habituation appear to support either of the possible explanations offered above.

TRANSFER OF ROTATORY HABITUATION TO BILATERAL CALORIC STIMULATION

Results of the present investigation demonstrate a failure to obtain transfer of response declines from rotatory habituation to bilateral caloric stimulation. This is readily apparent in the values plotted for the Rotation Control Group in Figure 1. That no significant rotatory-to-caloric transfer was obtained is in agreement with findings of other investigators[3,12,13].

The failure to obtain transfer, however, cannot be ascribed to differential stimulation of one or both labyrinths by the rotatory and caloric stimuli, as the caloric irrigations used in the transfer tests were bilateral. Also, data already reported[1], as well as findings of this study, indicate that intensity of the habituating stimulus appears to be a negligible factor in transfer of habituation within the intensity limits employed. Specifically, in the present investigation, caloric irrigations (both unilateral and bilateral), although of a greater intensity than the angular stimuli used, appeared to have only a slight effect on responses to rotation. In addition, intensity of the habituating stimuli was found not to influence unilateral-to-bilateral caloric transfer of habituation. The present lack of transfer, therefore, cannot be explained adequately as being a result of the fact that the rotation trials (habituation series) were relatively mild stimuli in comparison to the pre- and post-test bilateral caloric irrigations. It would seem, then, that failure to obtain rotatory-to-caloric transfer may depend

more upon differences in the rotatory and caloric modes of response-activation or upon some otolithic influence than upon relative intensities or differential stimulation of the labyrinths.

ADDITIONAL OBSERVATIONS

Sex Differences. Capps and Collins[1] reported statistically significant (.05 level) sex differences (favoring female cats) in amount of slowphase output and frequency of nystagmus to unilateral irrigations. The 22 male cats in this study were compared by t test with a group of 22 female cats randomly selected from the remainder of the group. Although females were found to have greater average pre-test response output to bilateral caloric irrigation than did males (2978° *vs.* 1842° for slowphase displacement; 175 *vs.* 121 for frequency), these differences fell just short of statistical significance at the .05 level (t = 1.99 and 1.87 where $p_{.05}$ = 2.02). Female cats also showed slightly greater average responses to the pre-test rotation (673° *vs.* 610° for slowphase displacement; 33 *vs.* 32 for frequency), but these differences were clearly not significant (t = 0.71 and 0.49 where $p_{.05}$ = 2.02). The present findings thus indicate that if sex differences in vestibular functioning of the cat exist (a) they are probably limited to caloric stimulation and related more to physical factors influencing thermal conduction than to vestibular function *per se*, and (b) there is considerable overlapping of the male and female response distributions.

Double irrigations. When water of the same temperature is applied to both ears simultaneously (double irrigations), the opposing stimuli theoretically cancel any horizontal nystagmus[4]. Upon administering double irrigations to a group of cats already habituated to unidirectional bilateral calorizations, Capps and Collins[1] found no effect of the habituation series on responses. To examine further the possible influence of unidirectional caloric habituation on responses to double irrigations, animals in Experimental Group II (26°C) and the Combined Control Group (no habituation stimulation) were administered two double irrigations immediately following the post–2 trial. Half of the animals received stimulation with water of 30°C on the first trial and 46°C on the second trial. The order was reversed for the remaining animals.

Some clearly-defined nystagmus was obtained on 6 of 20 records from the Combined Control Group and on 11 of 20 for Experimental Group II. For the Combined Control Group, 3 records evidenced nystagmus in the "unhabituated" direction, 1 in the "habituated" direction, and 2 showed "reversing" responses (responses first in the unhabituated direction and then in the habituated direction). For Experimental Group II, 8 records yielded responses in the unhabituated direction, 2 were in the habituated direction, and 1 case of "reversing" occurred. Seven of the eight responses in the habituated direction were accounted for by four cats. Thus, although animals exposed to an habituation series produced more tracings with some clear nystagmus than did animals receiving no habituation stimulation, data of the present study offer no unequivocal evidence that unilateral caloric habituation influences responses to "double irrigations".

Additional post-trials. A single post-test for transfer may not always be sufficient to allow habituation transfer-effects to evidence themselves[1]. In order to explore this possibility, the Rotation Control Group was given a series of eight bilateral caloric irrigations after completion of the post–2 rotation trial. These consisted of four trials during which responses were elicited in the habituated direction (R30°L46°) and four trials during which responses in the unhabituated direction (R46°L30°) were evoked. The two stimuli were applied alternately from trial to trial; irrigation periods were 20 sec. In addition, the Caloric Control Group was given a series of five rotation trials following (and identical to) the post–2 trial. Half of the animals were rotated CW and half were rotated CCW.

As can be seen in Figure 6, responses in both the habituated and unhabituated directions fall off to about the same level after four irrigations or after five rotations (taking into consideration the pre- and post-test trials). This provides confirmation that rotatory habituation trials had little influence on responses to caloric irrigation and that bilateral caloric habituation had little effect on rotation-induced responses. Transfer-effects, therefore, were not merely "masked" by such factors as novelty due to a change of the stimulus.

Retention Trials. Reports indicate that habituation of nystagmus is retained for consider-

able periods of time[1, 11]. In order to obtain some further information regarding retention, half of the animals in Experimental Groups I (ice water) and III (30°C) were tested at one week following, and the remaining half at one month following, their habituation series. Eight bilateral caloric irrigations were administered at rates of 15cc/sec for 20 sec. Four irrigations produced responses in the direction previously habituated (R30°L46°), and four yielded nystagmus in the opposite direction (R46°L30°). The two stimuli were alternated from trial to trial.

Data obtained after one week and after one month of rest are plotted in Figure 7. As data for Groups I and III were similar, results were combined. One week after the habituation series, the first test in the habituated direction showed recovery to 60% of the original pre-test level. The "one-month" retention curves indicate more recovery (75% of the pre-test), but drop off more rapidly than the "one-week" retention curves. Unhabituated-direction slowphase responses at one month also decline more rapidly than at one week, reaching 30% of pre-test after 4 trials. Initial differences between the response curves for the habituated and unhabituated directions indicate the directional specificity of habituation. However, responses in both directions declined steadily with repeated stimulation. These cat data do not agree with the views offered by Fluur and Mendel[9, 10], based on human subjects, indicating that no habituation occurs if nystagmus is elicited alternately in opposite directions[4, 6].

VI. Summary

Transfer of nystagmus habituation from unilateral calorization and from unidirectional rotation to bilateral calorization and to bidirectional rotation was investigated in 60 subjects. Reductions in bilateral caloric responses were obtained independent of the intensity of the unilateral caloric habituating stimuli. Habituation to rotatory stimulation was found to have no effect on responses to bilateral caloric irrigations. Caloric habituation appeared to exert relatively little influence on rotation responses. Additional observations were concerned with retention of habituation, possible sex differences in nystagmic output, "double irrigations", and the influence of several post-tests on nystagmic responses in the unhabituated direction.

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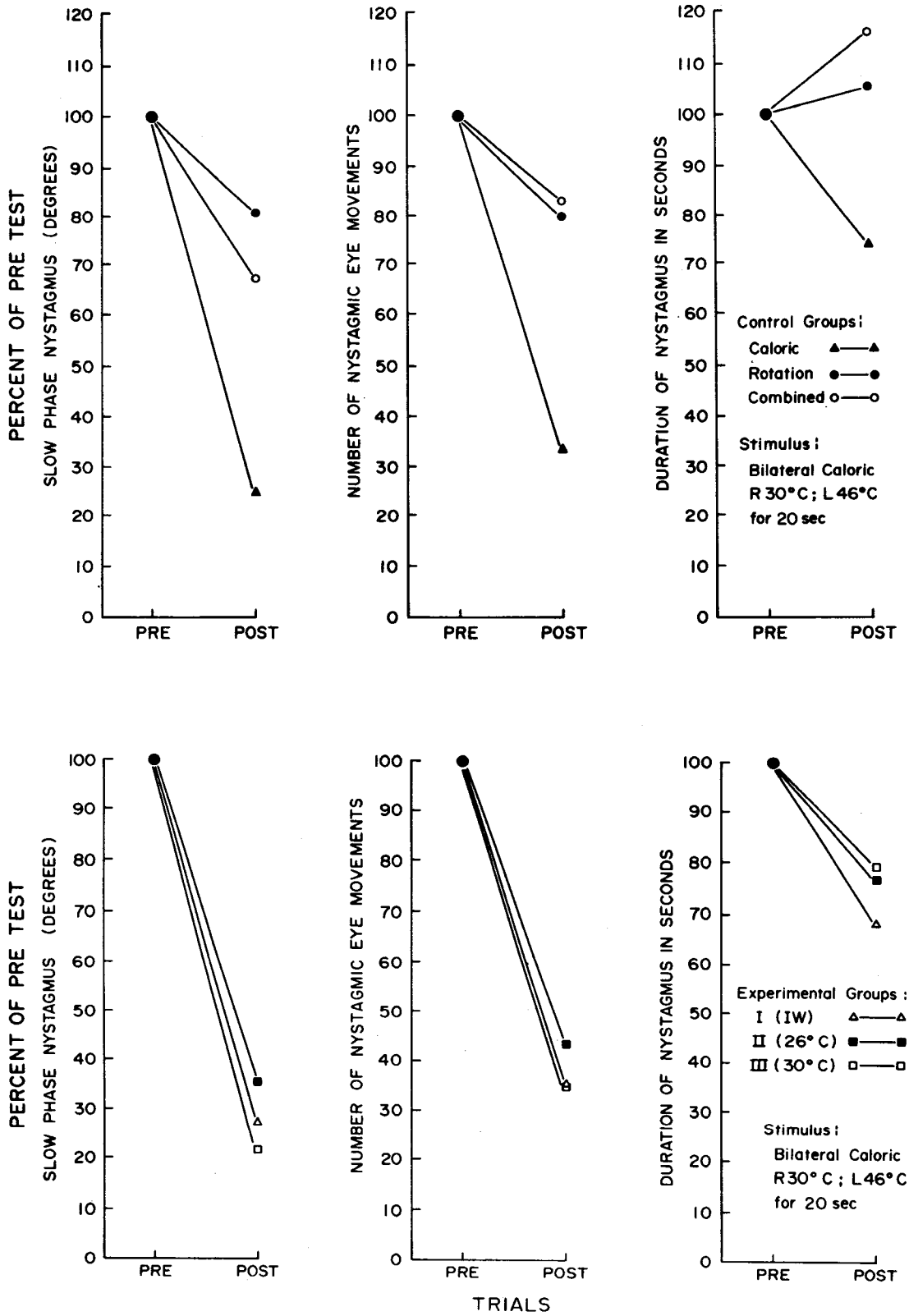

FIGURE 1. Mean pre- and post-test bilateral caloric scores for slowphase displacement, beat-frequency, and duration of response for the experimental groups and for the control groups plotted as percentages of the pre-test.

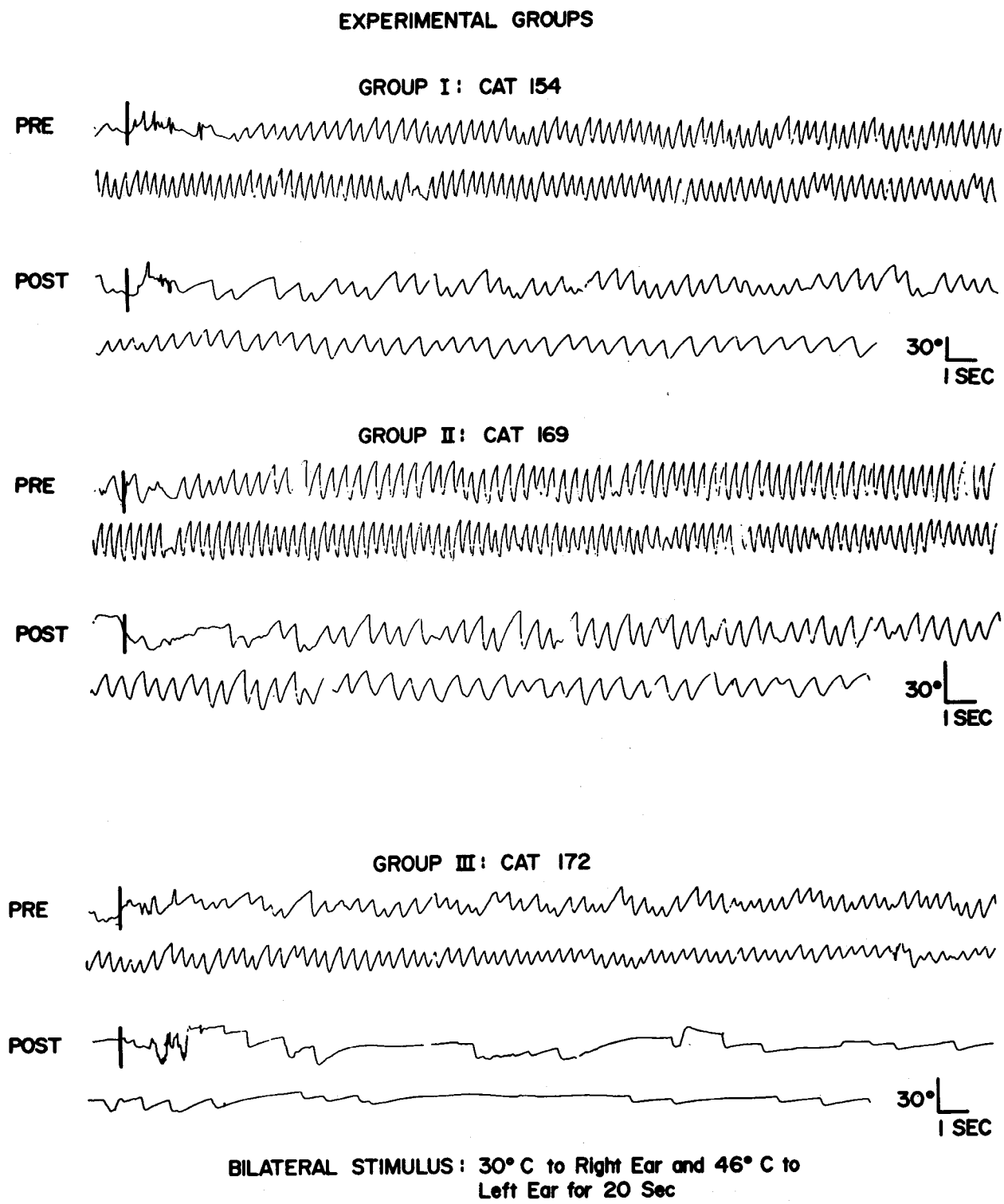

FIGURE 2. Pre- and post-test tracings of bilateral caloric nystagmus for cats in the three experimental groups. Vertical bars mark the termination of the stimulus period.

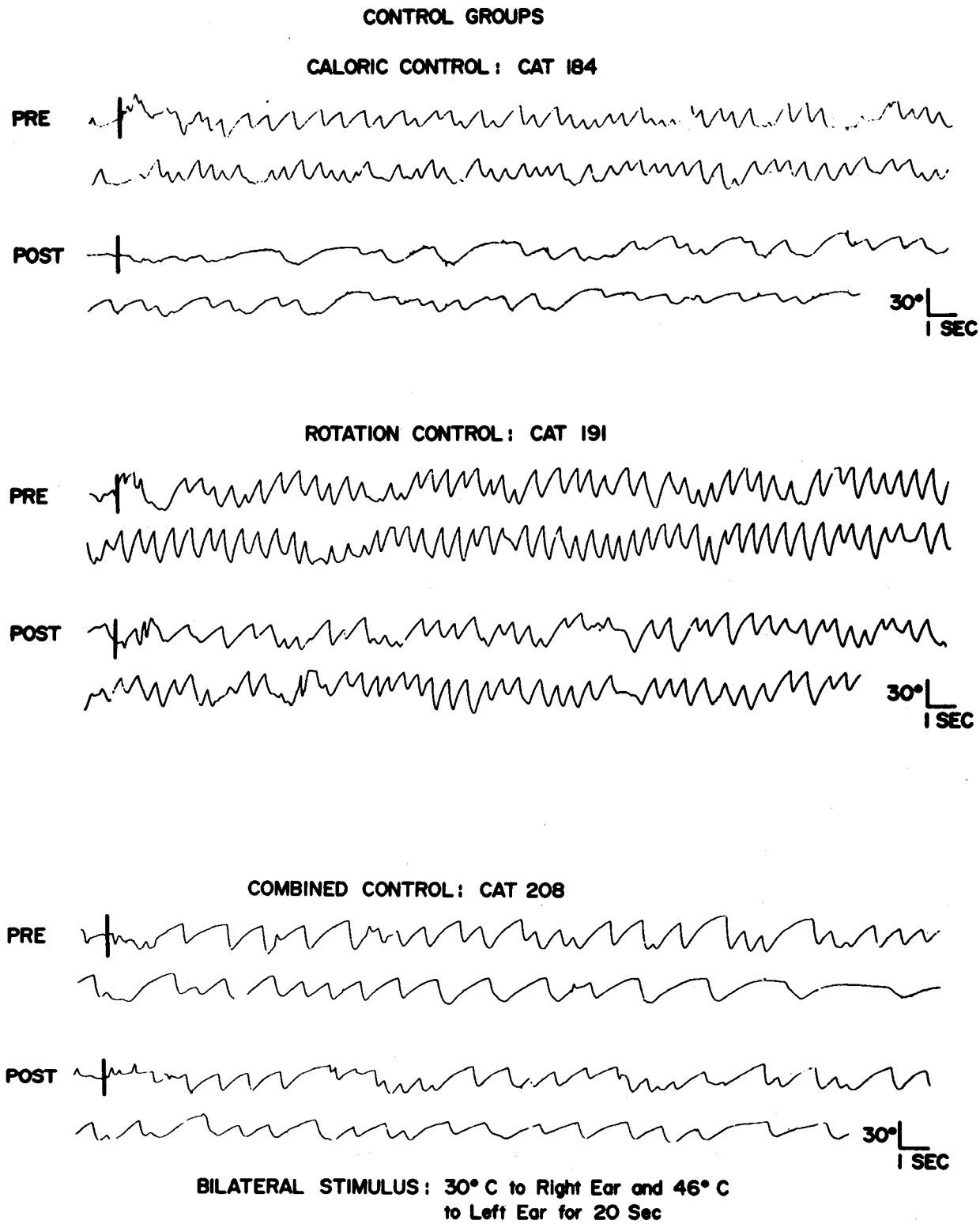

FIGURE 3. Pre- and post-test tracings of bilateral caloric nystagmus for cats in the three control groups. Vertical bars mark the termination of the stimulus period.

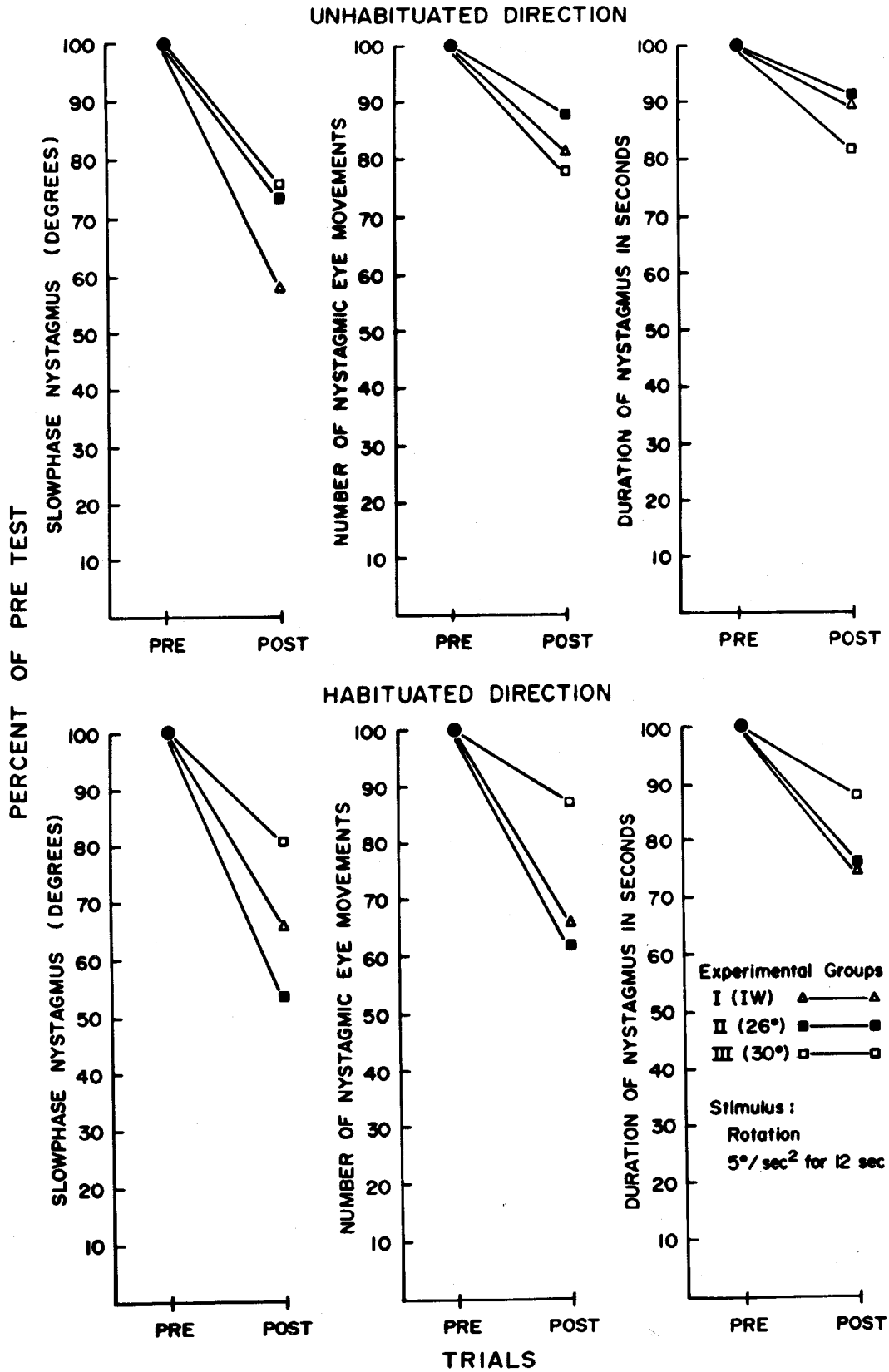

FIGURE 4. Mean pre- and post-test rotation scores for slowphase displacement, beat-frequency, and duration of response for the experimental groups plotted as percentages of the pre-test.

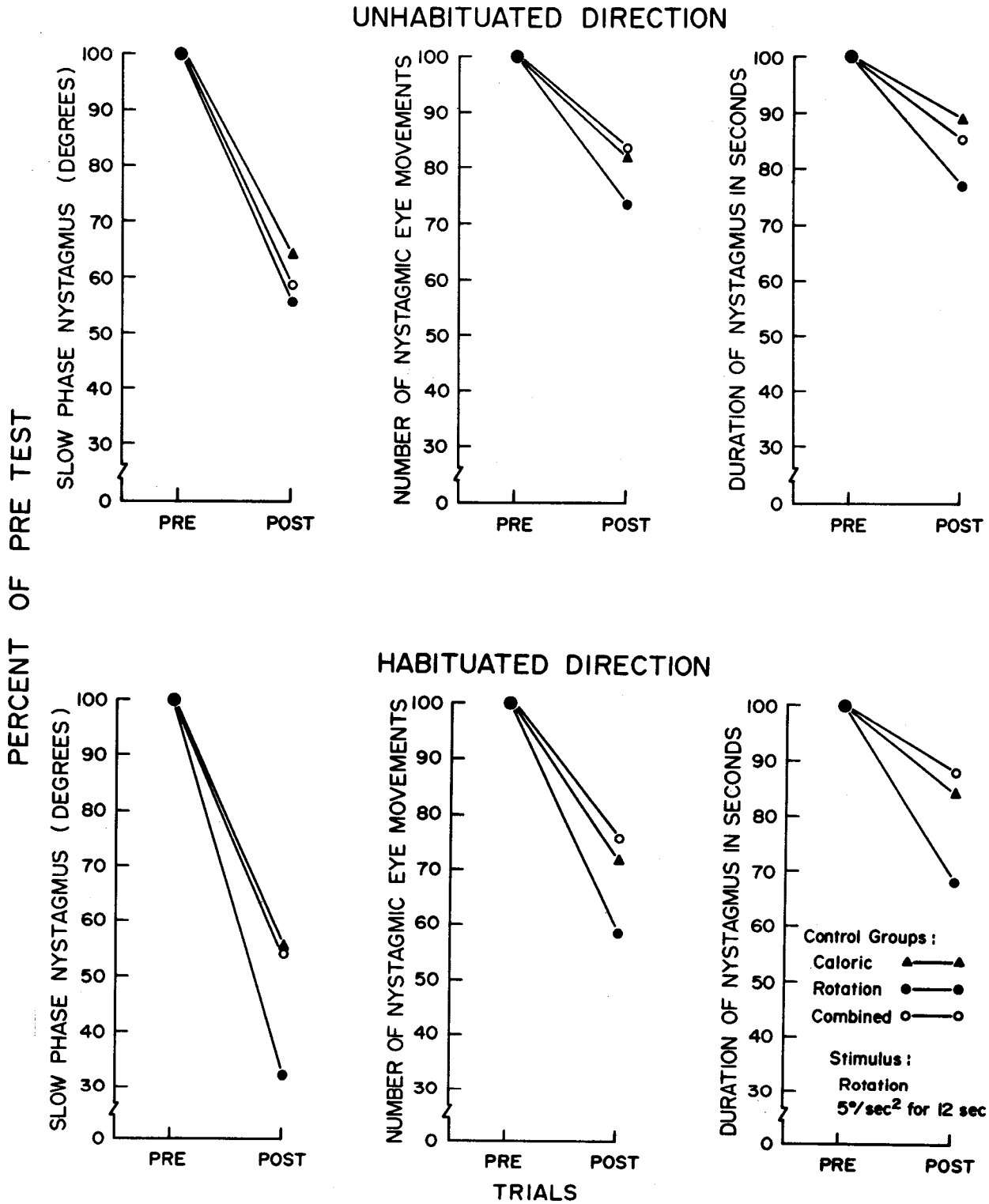

FIGURE 5. Mean pre- and post-test rotation scores for slowphase displacement, beat-frequency, and duration of response for the control groups plotted as percentages of the pre-test.

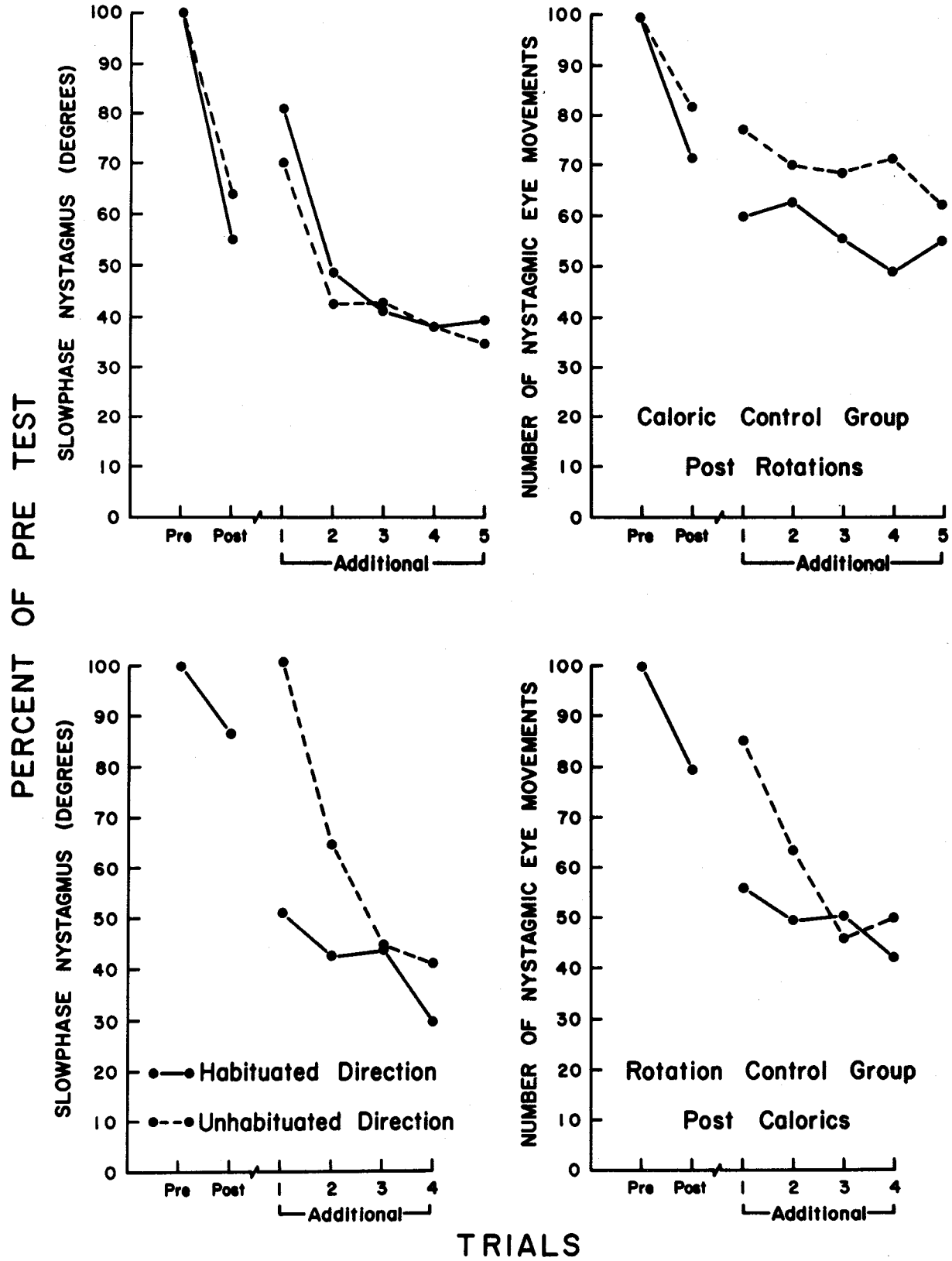

FIGURE 6. Mean slowphase displacement and beat-frequency scores for the additional post-tests plotted as percentages of the pre-test. The upper figures illustrate values for post-rotations, and the lower figures for post-calorics.

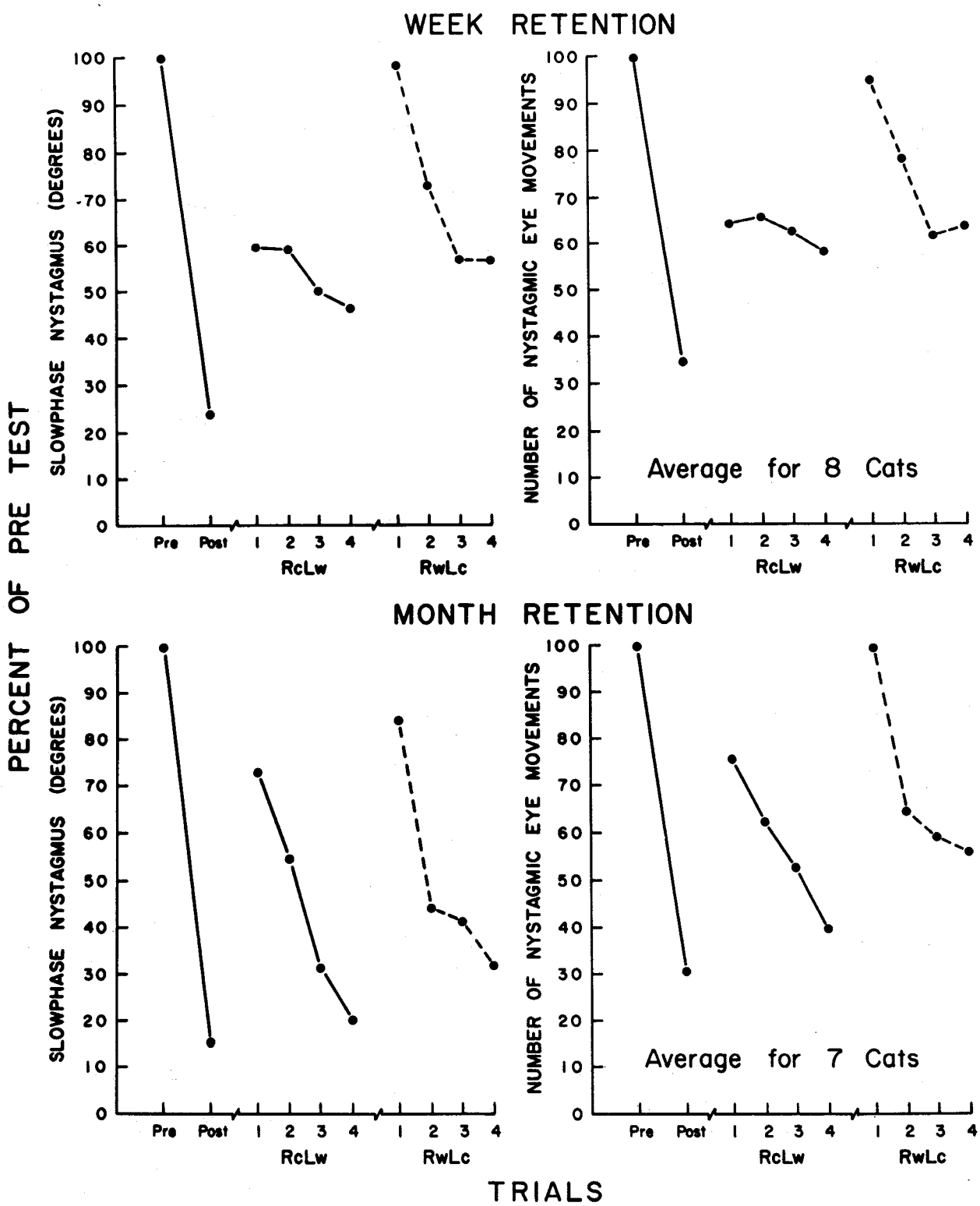

FIGURE 7. Mean slowphase displacement and beat-frequency scores at one week and at one month following the habituation series plotted as percentages of the pre-test.