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TRANSFER AND RETENTION OF EFFECTS FROM TWELVE DAYS OF
ROTATION AT 10 RPM

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Research Report

HABITUATION TO COMPLEX VESTIBULAR STIMULATION IN MAN:
TRANSFER AND RETENTION OF EFFECTS FROM TWELVE DAYS OF
ROTATION AT 10 RPM*

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U. S. NAVAL SCHOOL OF AVIATION MEDICINE
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PENSACOLA, FLORIDA

SUMMARY PAGE

THE PROBLEM

To study the transfer and retention of some of the effects produced by twelve days of almost continuous rotation in one direction.

FINDINGS

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In three experimental runs, a total of nine men rotated at 10 RPM for twelve days. Eight control subjects were tested at comparable intervals. Rotating chair tests conducted before and after the twelve-day run demonstrated that nystagmus and subjective effects produced by head movements during the accustomed direction of rotation (CCW) had diminished markedly. In the unaccustomed rotation direction (CW) one hour after cessation of room rotation, nystagmus and subjective reactions approximately equaled reactions prior to the twelve-day run. The unequal reduction of reactions was attributed to conditioned compensatory reactions which would facilitate reactions during CW rotation and counteract reactions during CCW rotation. Two days after the twelve-day run, responses to both rotation directions were suppressed as compared with initial levels of response; compensatory reactions had apparently dissipated. Some response decline was still present three weeks after the twelve-day run, but tests after three months revealed considerable recovery toward initial response levels. Reactions to passive whole-body angular acceleration were not greatly altered by the twelve-day run.

Author

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The author is deeply grateful to the men who served as subjects in these experiments, to R. S. Kennedy, LT, MSC, USN, who served as on-board experimenter during the twelve-day run, and to Ashton Graybiel, CAPT, MC, USN, who initiated the three experimental runs.

INTRODUCTION

Graybiel, Clark, and Zarriello (10) introduced a new form of the sensory "rearrangement" experiment when they studied reactions of men living in an enclosed slowly rotating room (SRR). This experiment involved systematic alteration of vestibular sensory input attending movement of the head and body. Many other experiments on sensory rearrangement have systematically altered visual information by optical methods (21,25,27), while proprioceptive and labyrinthine sensory input attending body movement remained unmodified. Most subjects in these optical studies have achieved a degree of adjustment to rearranged visual input as demonstrated by improved accuracy of visually-guided motor performance and by "aftereffects" upon return to a natural environment. In regard to aftereffects, removal of the optical distortion produced "errors similar to but in the opposite direction to those initially induced by the rearrangement" (21, p.29).

Held has concluded (21, p.28) that compensation for optical rearrangement requires reafference, a term introduced by von Holst (28,29), to designate patterns of afferent impulses resulting from natural voluntary movement which are compared by central mechanisms with patterns preset by the voluntary command to act. As evidence for the reafference concept, experiments have been cited indicating that active (voluntary) movement was effective and passive movement was ineffective in producing compensation (21), and this concept has been related to vestibular function by Groen (14). Also considered important to the development of compensation is consistency of "... atypical relations between movement and contingent reafferent stimulation"(21, p.29). Each movement has a pattern of reafferent stimulation which, though unnatural, is unique for the particular movement. "Progressive shifts in coordination compensate for the errors induced by these atypical conditions" (21, p.29).

Within the closed rotating room almost any movement would involve a rearranged pattern of sensory input. During each movement relative to the room kinesthetic receptors respond to the curvilinear motion of the body relative to the earth, while the visual estimates which gauge the intended movement do not register the curvilinear path. In other words, movement in a straight line relative to the floor of the room appears visually to be in a straight line even though it is really in a curved path relative to the earth, and kinesthetic receptors register only the curved path. Even in the absence of vision, proprioceptive information from the limbs is still anomalous. An attempted movement of the hand or foot in the plane of rotation results in a force proportional to the Coriolis acceleration which is directionally parallel to the floor of the room* and at right angles to the direction of the movement. Hence, information fed back from the muscles and joints does not correspond with that usually received

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*actually parallel to the plane of rotation

when similar intentional movements of the limbs are consummated under natural conditions. In addition, and of considerable significance to the over-all effects produced in the SRR, is the fact that, when the head is tilted to rotate about an axis (head-tilt axis) which is orthogonal to the axis of rotation of the room (ω -axis), each endolymph ring in the semicircular canals undergoes a change in angular momentum. The stimulus thus produced may be conceptualized as an inertial torque about a third axis which is approximately orthogonal to both the head-tilt and ω -axes (1, 19, 26). Angular accelerations about the head-tilt axis would be effective in stimulating the semicircular canals during the movement*, but at termination of head tilt, their net effect would be negligible due to the temporal proximity and opposite signs of the acceleration and deceleration. Hence, upon completion of a forward head movement#, for example, the residual effect would derive from the stimulus about the third axis, resulting in deflected cupulae signaling lateral head tilt. The sensory rearrangement in the SRR is, therefore, both extensive and realistic in that several senses are involved and subjects are unencumbered by restrictive apparatus attached to the body. Moreover, active movements can be used during the adjustment period, and there is a unique though atypical pattern of sensory input for each particular movement in the SRR. In other words, conditions considered important to development of compensation for sensory rearrangement in other lines of research are also present in the SRR.

The results of experiments in the SRR show many characteristics in common with other rearrangement experiments. At first, subjects experience difficulty in maneuvering. Here the accurate visual information on fixed spatial relations within the room conflicts with the kinesthetic proprioceptive information derived from the curvilinear motion of the body relative to the earth. With head movements, particularly tilting motions, apparent motion sensations of vestibular origin are experienced (11, 15, 19), nystagmus may be recorded in darkness (15, 18-20), and after only short exposure nausea is reported by many subjects. With prolonged exposure (several days) most subjects demonstrate marked changes in most of these effects. Walking and other psychomotor skills improve substantially (2, 12); nausea, nystagmus, and the vestibular illusions diminish (11, 18). As in other rearrangement experiments, after prolonged adjustment to unnatural stimulation, return to a natural environment reinstates many of these effects. For example, nausea (and even vomiting) occasionally reappears; head movements, which prior to exposure gave no effect under natural conditions, now may elicit apparent motion sensations (11, 15, 20) and nystagmus reactions (18) which are opposite in direction to reactions produced initially by the same head movement during rotation. These may be interpreted as signs of compensation, conditioned during the rotation exposure (18).

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*with or without concomitant rotation of the room

#forward relative to the body with the subject standing upright

The present paper describes tests conducted before and after a period in which men lived aboard the SRR for twelve days while it rotated at 10 RPM in a counter-clockwise (CCW) direction. The tests consisted of recording nystagmus and subjective impressions produced by head movements during 10 RPM CCW rotation (the accustomed direction of rotation) and during 10 RPM CW rotation. Tests were given at several intervals after the prolonged rotation exposure to trace the retention of response modification. Many other facets of the over-all effects produced during the rotation exposure were recorded and these results will appear in a general report (12). The present report is restricted to nystagmus and subjective motion phenomena recorded before and after the prolonged rotation exposure and to the same response measures recorded from control subjects who were not rotated for twelve days or otherwise exposed to unusual vestibular stimulation.

PROCEDURE

SUBJECTS

Subjects in the experimental runs were eight officers in the naval aviation training program and one naval enlisted man. All men were within the age range of 19 to 25 years. In the first run four officers who had completed the acrobatics stage of flight training served as subjects; in the second, four officers in pre-flight training were subjects. The ninth subject was a man who had had a number of short runs (totaling about fifty hours) in the SRR and who served as an experimenter's aide in a third run conducted primarily to study subjects with bilateral labyrinthine loss. His exposure during this run was identical to that received by the men in the first two runs; thus, his results are included in this report. The results obtained from the subjects with labyrinthine deficits are part of another investigation and are not included in this report. In addition, eight men within the age range of 18 to 26 years participated in the control tests made at intervals corresponding to the test intervals of the experimental runs.

Throughout Run 1 and during the daylight hours of Runs 2 and 3, there was one onboard experimenter, RK, who supervised and observed the various activities of the subjects in the SRR.

APPARATUS

Tests before and after the twelve-day ride in the SRR were conducted with a Stille-Werner rotating chair, described elsewhere (17). The chair's rotary structure was enclosed with heavy blackout cloth to reduce light cues and air currents. In addition, subjects wore foam rubber eye covers designed to exclude light while their eyes remained open.* A bracket supporting a biting board on a swivel was mounted

*Many subjects in the dark with eyes open yield nystagmus which is of better quality and intensity than responses they yield when the eyes are closed in the dark (19, p.491).

on the chair to restrict head movements to 45-degree arcs in the frontal plane. Head movements were recorded by use of a potentiometer attached to the axis of the bite-board assembly. An Offner Preamplifier Type 481B (time constant -- 1.0 sec) was used to amplify corneoretinal potential, and an Offner Type R Dynograph recorder was used for recording movement of the head and the chair. Silver electrodes were taped near the outer canthus of each eye and above and below one eye to detect horizontal and vertical components of eye movements. Visual stimuli were always excluded during recording of nystagmus.

Habituation to continuous rotation was accomplished in a room which rotated in a counterclockwise direction at 10 RPM. The first group of subjects lived in SRR I, described in a previous report (2). This is a nearly-circular multisided room, 15 feet in diameter, completely enclosed, and capable of virtually vibration-free constant angular velocity for prolonged periods. The remaining subjects received their habituation run in SRR II, part of a new device called the Coriolis Acceleration Platform described elsewhere (24) in detail. Although SRR II has many features not available in SRR I, the principal difference in regard to the present experiment is its larger diameter, 20 feet, and the absence of a center post. Both of these features increase the available space for locomotion within the room, but this increased space probably did not influence the amount of spontaneous voluntary movement for several days (two to three days), i.e., until nausea and general discomfort associated with movement in the room subsided. Because most of the testing equipment was arranged around the outer circumference of SRR II, the effective radius of SRR II was reduced to about 8 feet; hence, differences in maximum centripetal accelerations routinely encountered in the two rooms were probably inconsequential.

METHOD

The general plan of the experiment, shown in Figure 1, was to compare results of CW and CCW rotation tests given in the Stille-Werner chair before and at several intervals after a twelve-day period of almost continuous CCW 10 RPM rotation in the SRR.

These tests consisted of lateral head tilt toward the right shoulder and a return movement to upright followed by a similar sequence toward the left shoulder while the chair rotated at 10 RPM. Head movement consisted of 45-degree angular displacements accomplished in about two seconds. Each head position was maintained until nystagmus dissipated plus an additional thirty seconds. Head movements were commenced one minute after the chair attained constant angular velocity. Angular accelerations of 15 deg/sec^2 maintained for four seconds were used in starting and stopping the chair. Four of the subjects received the CW test first and the remainder received the CCW test first. In addition to rotation tests, all subjects were given "static" tests in which the same sequence of head movements was made while the chair was stationary.

INITIAL TESTS		HABITUATION PROGRAM		POST TESTS	
CHAIR ROTATION		ROTATION IN SRR - 10 RPM, CCW		CHAIR ROTATION	
HEAD TILTS		DURATION OF RUN - 12 DAYS		HEAD TILTS	
DURING CW ROTATION 10 RPM	DURING CCW ROTATION 10 RPM	VOLUNTARY MOVEMENTS DURING NORMAL ROOM ILLUMINATION		DURING CW ROTATION 10 RPM	DURING CCW ROTATION 10 RPM
RESPONSES:		9 SUBJECTS		RESPONSES:	
1. NYSTAGMUS				1. NYSTAGMUS	
RECORDED IN DARKNESS				RECORDED IN DARKNESS	
WITH EYES OPEN WITH ASSIGNED MENTAL ARITHMETIC				WITH EYES OPEN WITH ASSIGNED MENTAL ARITHMETIC	
2. SUBJECTIVE RATINGS OF INTENSITY OF EFFECTS				2. SUBJECTIVE RATINGS OF INTENSITY OF EFFECTS	
TIME:				TIME:	
1 DAY BEFORE				1-HR., 2 DAYS, 3 WKS., 3 MOS.	
12-DAY RUN				AFTER 12-DAY RUN	

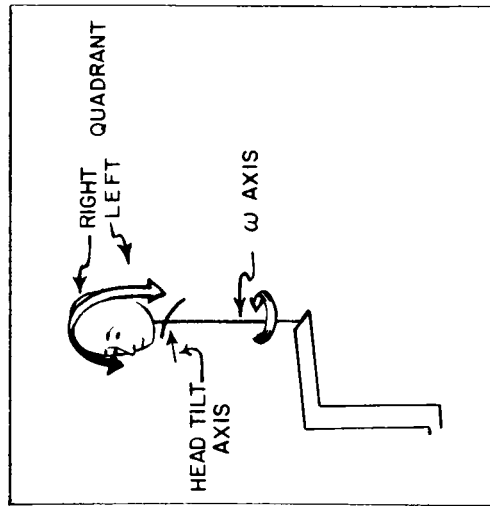


Figure 1

Summary of Conditions in the Experimental Runs

Inset figure illustrates axes of head and whole-body movements during chair tests.

During each test session nystagmus and reports of subjective effects were recorded. Nystagmus was recorded in darkness but with the subjects' eyes open. Just prior to each stimulus, subjects were given arithmetic problems to be solved during the course of the vestibular reaction to the stimulus. It is well known that nystagmus dissipates in some subjects after only a few stimuli and that assigned mental tasks tend to prevent this form of nystagmus decline (4,6). The plan of the present experiment was to eliminate loss insofar as possible by assigned mental tasks and thus to test for any residual changes.

In regard to subjective reports, subjects were asked to compare the strength of subjective reactions during CW tests with those during CCW tests. In the tests after the prolonged run, they were asked for this comparison again and, in addition, were asked to compare each test with previous tests.

These tests were given one or two days prior to commencement of the twelve-day run, the Initial Test, and again one hour, forty-eight hours, and three weeks after the end of the twelve-day run. In addition, the second group of four subjects were tested three months after the twelve-day run.

During the twelve-day run, a number of tests, behavioral and physiological, were conducted and these are described in another report (12). Some of these tests required that the SRR be stopped to accommodate test personnel. The SRR was stopped three or four times per day for such purposes. Typical stops were five minutes or less in duration, but occasionally stopping time was as long as fifteen minutes. During stops, subjects were required to remain motionless in the room to prevent readaptation to a natural environment. These other tests also have significance for the present paper in that they required subjects to move about while the room was rotating. Subjects were busy with test procedures and routine chores for approximately eight hours per day. However, during the first three days of each run, some subjects greatly restricted their movements and participation in tests due to sickness. In the first run, to conserve time for some of these other tests (cf. 12) during the recovery period after the twelve-day run, subjects were tested only in one head-tilt quadrant for each direction of chair rotation*.

RESULTS

NYSTAGMUS PRODUCED BY HEAD MOVEMENTS DURING ROTATION

The general findings are summarized by Figures 2 and 3 which are bar graphs based upon results of Runs 1 and 2, respectively. To facilitate comparison of response magnitude for the two rotation directions, total slow-phase displacement of nystagmus

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*during the Post 1-hr Test and the Post 48-hr Test

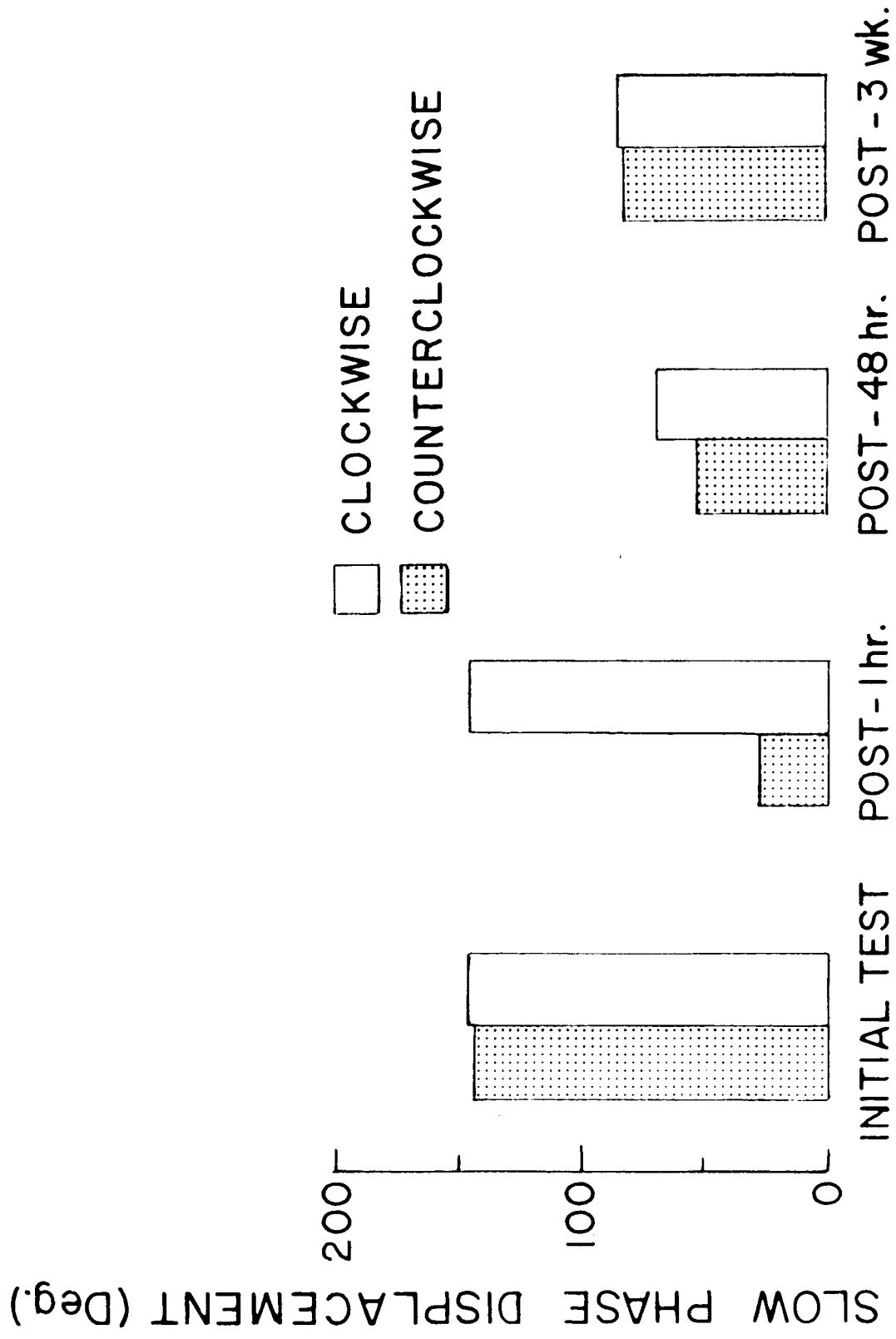


Figure 2

Average Total Slow Phase Displacement of Nystagmus Produced by Head Movements during Rotating Chair Tests in Run 1

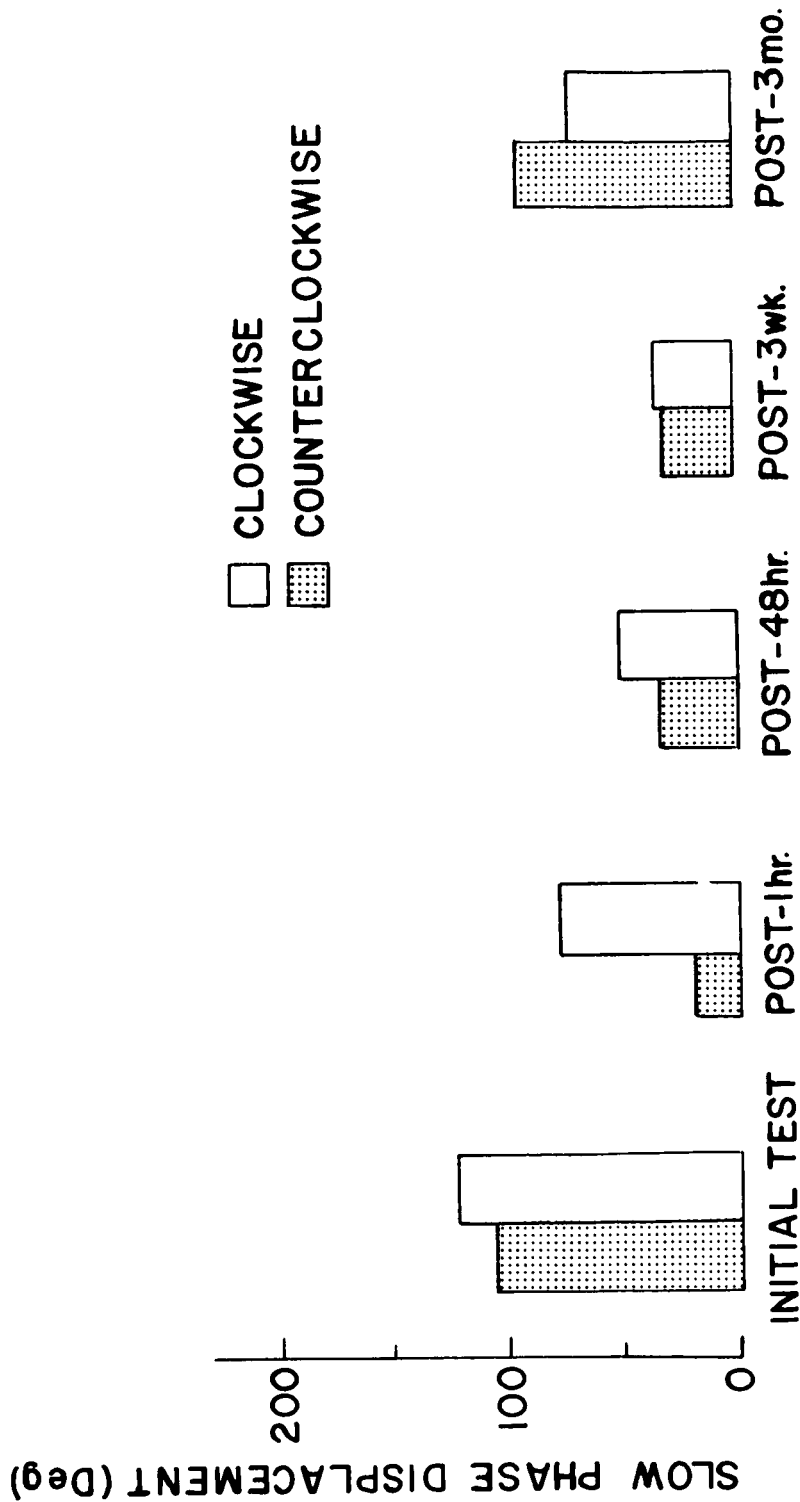


Figure 3

Average Total Slow Phase Displacement of Nystagmus Produced by Head Movements during Rotating Chair Tests in Run 2

.(calculated from the vectorial resolution of vertical and horizontal components of eye movements) was averaged for each rotation direction without regard to response direction.

It is apparent from Figures 2 and 3 that in both Runs 1 and 2, nystagmus produced by head movements during the accustomed rotation direction (CCW) is greatly reduced during the Post 1-hr Test, given one to two hours after the twelve-day run, whereas in the CW rotation direction, there was little nystagmus reduction. In four of eight possible comparisons in Run 1, nystagmus was increased during the CW Post 1-hr Tests. (For individual results, see Figure 10, P. 19.) In Run 2, eight of the sixteen responses yielded by the four subjects during the CW Post 1-hr Test were either approximately equal to or greater than the responses to the same stimuli during the Initial Test, but the remainder of the responses were declines, some sufficiently great to give the average decline apparent in Figure 3. (For individual results, see Figure 11, P. 20.)

During the Post 48-hr Test, responses to head movements during both CW and CCW tests were less than their counterparts during the Initial Tests. Moreover, responses to CW tests were considerably less during the Post 48-hr Test than during the Post 1-hr Test. Responses during the CCW test had recovered slightly from the Post 1-hr Test, and thus responses for the two rotation directions were more nearly equal and all responses were suppressed as compared with the initial response level.

During the Post 3-wk Tests of Run 1 the average nystagmus reaction elicited by head movements was nearly equal for the two directions of rotation, and there was some recovery from the level of the Post 48-hr Test, but responses were still suppressed as compared with the level of the Initial Test. In Run 2 there was no average recovery during the Post 3-wk Tests for either CW or CCW rotation; moreover, the average response to the CW tests, the "unaccustomed" rotation direction, showed further decline from the level of the Post 48-hr Tests, a result which deviates from the average responses in Run 1.

The subjects of Run 2 were available for a Post 3-mo Test (actually Post 11-wk). This test revealed considerable recovery toward the initial levels of response for head movements during both CW and CCW rotation, but there was still some suppression as compared with response levels of the Initial Test.

Nystagmus results from Runs 1 and 2 are shown also in Figures 4 and 5, respectively, which present continuous time plots of average response magnitude for stimuli produced by head movements during CCW rotation (solid lines) and during CW rotation (dotted lines). Data were combined for the averages shown in Figure 4 on the basis of

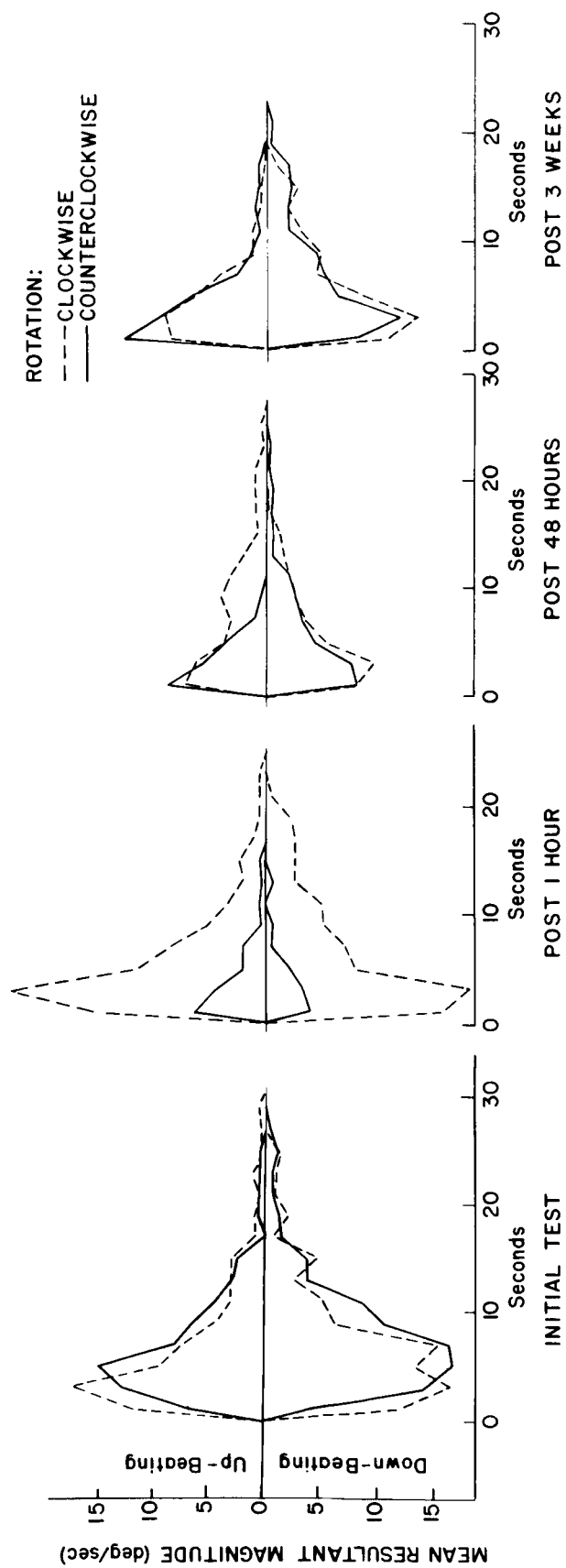


Figure 4

Magnitude of Slow Phase Velocity of Nystagmus throughout the Course of Reactions to Head Tilts during Chair Tests in Run 1

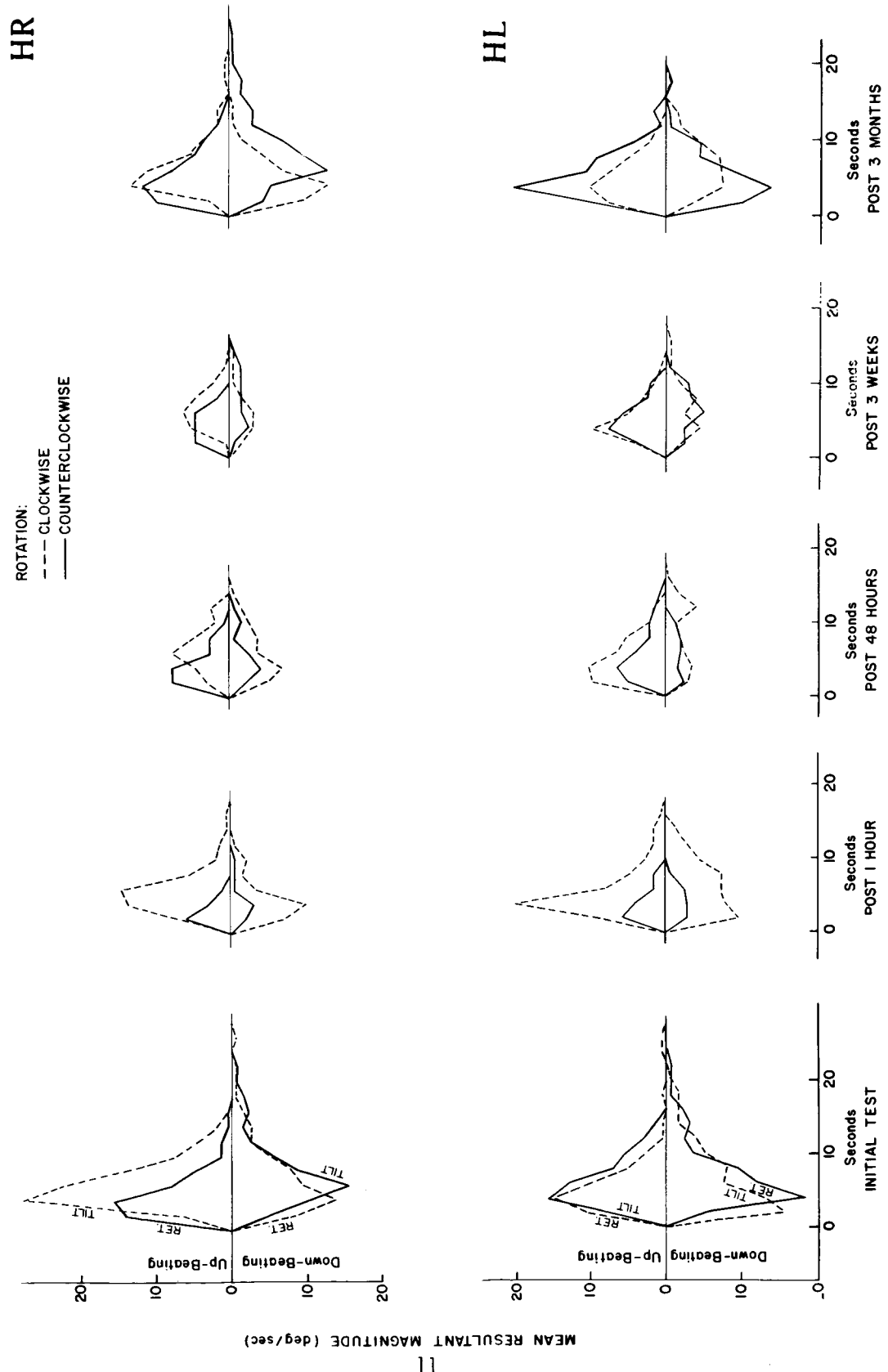


Figure 5

Magnitude of Slow Phase Velocity of Nystagmus throughout the Course of Reactions to Head Tilts during Chair Tests in Run 2

the direction of the vertical component of nystagmus.* For example, nystagmus with fast phase up was produced during CCW rotation by head tilts to the left in two subjects and by head returns to upright from the right in the other two subjects, and these data were combined to obtain the average upward beating nystagmus represented in Figure 4. Each subject made head movements in both left and right quadrants during each test session of Run 2. Hence, separate averages for left and right quadrants were available from Run 2, and these are presented in Figure 5.

SENSATIONS PRODUCED BY HEAD MOVEMENTS DURING ROTATION

Prior to the twelve-day run, head movements produced reactions adjudged to be of about equal intensity irrespective of the direction of rotation of the chair. In the Post 1-hr Test, the four subjects of Run 1 and three of the four subjects of Run 2 reported no subjective reaction at all to head movement during CCW rotation. The fourth subject of Run 2 reported very weak sensation during CCW rotation. In the CW tests, six of eight subjects of Runs 1 and 2 reported that sensations were as strong as or stronger than those experienced during CW tests prior to the twelve-day run. The other two subjects reported sensations to be slightly less than those experienced during the Initial Test.

During the Post 48-hr Test, seven of the eight subjects of Runs 1 and 2 reported a slight return of sensation during the CCW test, as compared with the Post 1-hr Test, but much weaker sensations than those experienced prior to the twelve-day run. In the CW Post 48-hr Test, six of the eight subjects reported sensations to be much weaker than those experienced during either the Post 1-hr Test or during the Initial Tests prior to the twelve-day run. The other two subjects felt that the effects were about the same as during the Post 1-hr Test, but less than the Initial Test.

During the Post 3-wk Test, the four subjects of Run 1 reported a return of vertiginous sensations set off by head movements during chair rotation in either direction. However, there was no feeling of nausea associated with the stimulus in subjects who initially had reported nausea. This was substantiated by a two-hour CCW 10 RPM ride in the SRR. Whereas initially three of the four subjects had experienced nausea within the first two hours of rotation in the SRR, now none reported any symptoms related to motion sickness. In general, results of the subjects of Run 2 were similar in the Post 3-wk Test, with perhaps less reported return of vertigo. These subjects did not receive a two-hour ride in the SRR at this time.

*As shown in Figure 7, P. 15, the nystagmus produced by these head movements is principally vertical, but the horizontal components are directionally opposite. This method of data averaging was used because time considerations did not permit the complete testing schedule in the Post 1-hr Test or in the Post 48-hr Test. Two subjects made head movements in the left quadrant during CW rotation and in the right quadrant during CCW rotation; the other two subjects made right-quadrant head movements during CW rotation and left-quadrant movements during CCW rotation.

After three months, the subjects of Run 2 were again tested. Three subjects estimated the subjective effects to be less than those experienced initially, i.e., prior to the twelve-day run. The fourth estimated that the effects had returned to initial intensity. On the average, the subjective effects apparently had not returned to the Initial Test level after a three-month rest.

COMPENSATORY NYSTAGMUS

In Run 1, static tests were conducted about fifteen to 45 minutes after the twelve-day rotation ended. In three of the four subjects, a given lateral head tilt without concomitant whole-body rotation now produced nystagmus opposite in direction to nystagmus produced by a like head movement during CCW body rotation initially, i.e., before the twelve-day run. The fourth subject showed compensatory nystagmus in only one of four recorded head movements during the static test, and this was a weak response. The other subjects exhibited compensatory nystagmus in at least three of the four head movements; some of these responses were of good quality and persisted for ten or twenty seconds after the head movement. None of the subjects exhibited "compensatory nystagmus" in static tests before the twelve-day run. Similar results were obtained in Run 2. All four subjects exhibited compensatory nystagmus between one and two hours after the twelve-day run, but one subject who initially gave very little response during rotation also gave very weak compensatory nystagmus in the static "Post Test." Examples of compensatory reactions are shown in Figure 6.

DIRECTIONS OF NYSTAGMUS ELICITED BY THE FOUR HEAD MOVEMENTS DURING THE TESTS

The four head movements were a 45-degree lateral tilt toward the left shoulder and a 45-degree return to upright position, a 45-degree lateral tilt toward the right shoulder and a 45-degree return to upright position. The planes and directions of nystagmus relative to the skull elicited by these four head movements are shown in Figure 7. For example, an arrow directed upward and to the reader's left designates nystagmus with fast phase up and to the left relative to the subject's skull. Figure 7 shows the average direction and magnitude of the fast phase of nystagmus for the first ten seconds of reactions to head movements in the four subjects of Run 1 prior to the twelve-day run. It is important to note that nystagmus of essentially the same plane and direction can be produced by either CW or CCW rotation; e.g., nystagmus up and left is produced by head tilt to the right during CW rotation and by head return from right tilt during CCW rotation. Hence, reactions of closely corresponding planes and direction were differentially influenced by the habituation run, as shown in the results of the CCW and the CW Post 1-hr Tests.

NYSTAGMUS PRODUCED BY ANGULAR ACCELERATION OF THE CHAIR

Bar diagrams in Figure 8 show total slow phase output of nystagmus produced by the angular accelerations of 15 deg/sec^2 used in starting and stopping the chair in tests before and after Run 1. In Run 1, the twelve days of rotation had little influence

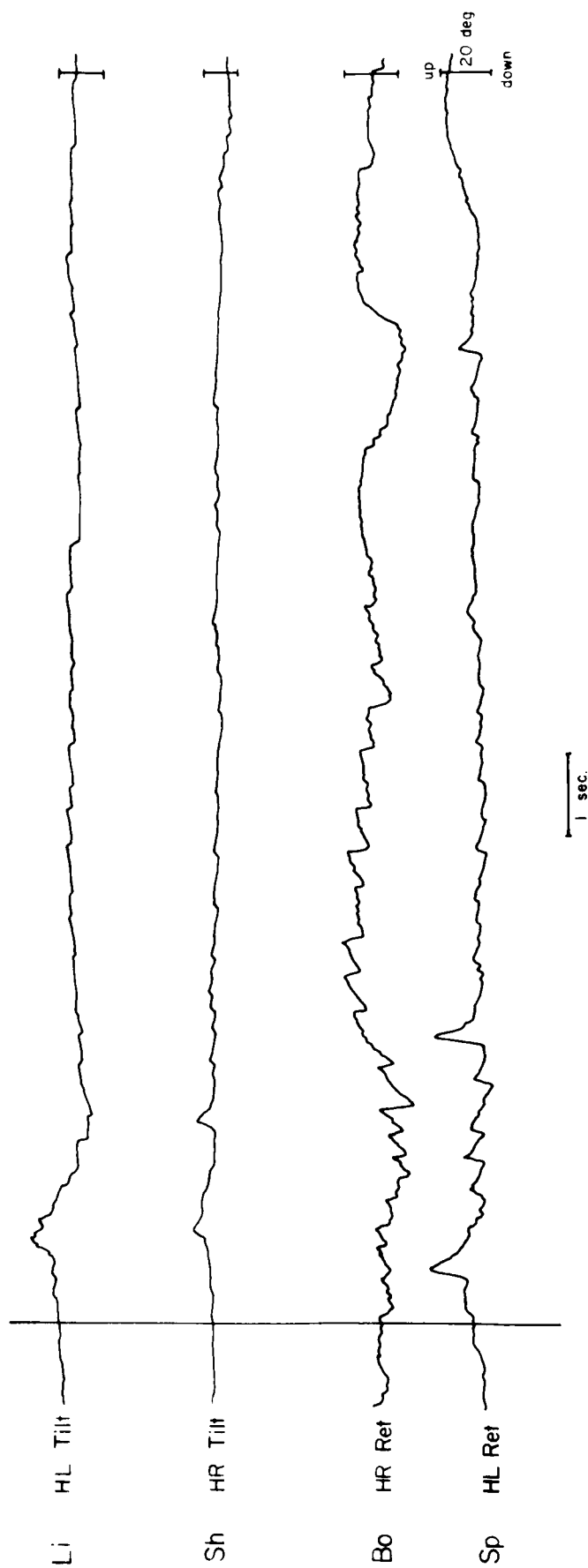


Figure 6

Tracings of Conditioned Compensatory Nystagmus (Vertical Component) Produced by Lateral Head Movements during Static Tests about One Hour after Twelve-Day Rotation Run

Li and Sh are from Run 1; Bo and Sp from Run 2. Vertical line marks beginning of 2-sec head movement. Note that reactions are opposite in direction to those recorded during CCW rotation as shown in Figure 7.

10 RPM CLOCKWISE TEST

10 RPM COUNTERCLOCKWISE TEST

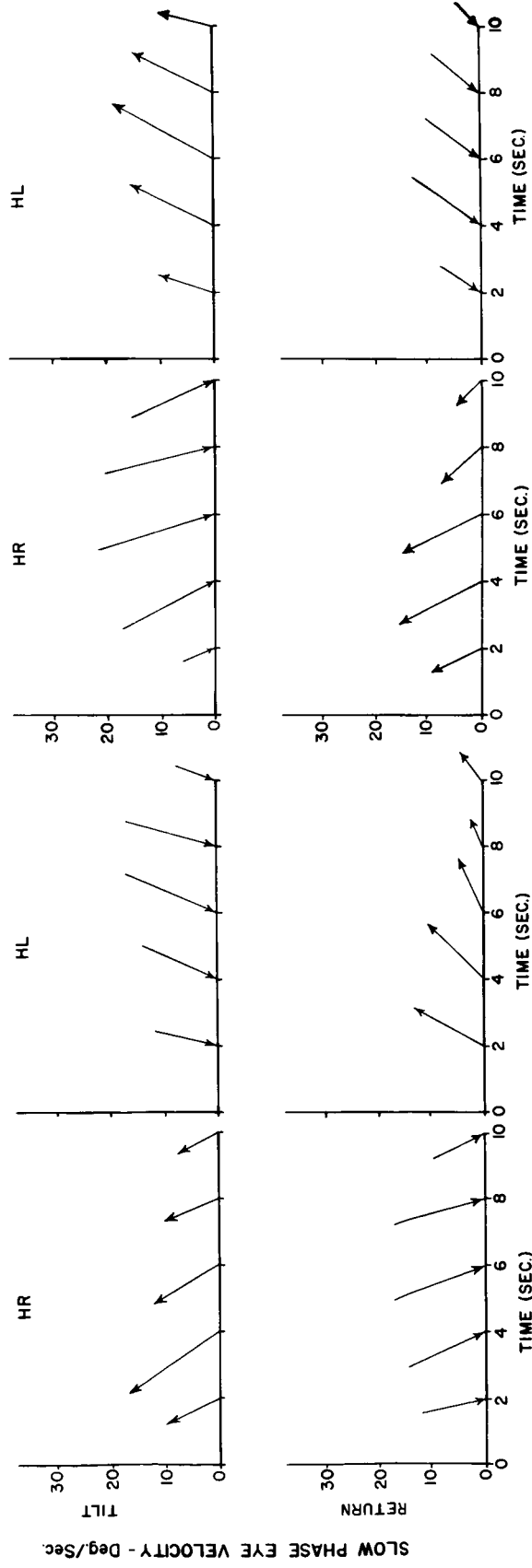


Figure 7

Vectorial Representation of Nystagmus at 2-sec Intervals throughout Course of Reactions Produced by Head Movements during Initial Rotation Tests of Run 1

Length of arrow indicates slow phase velocity (magnitude) in deg/sec; direction of arrow indicates direction of fast phase relative to sagittal plane of skull. An arrow upward and to the reader's right designates nystagmus up and to the right of the subject's sagittal plane.

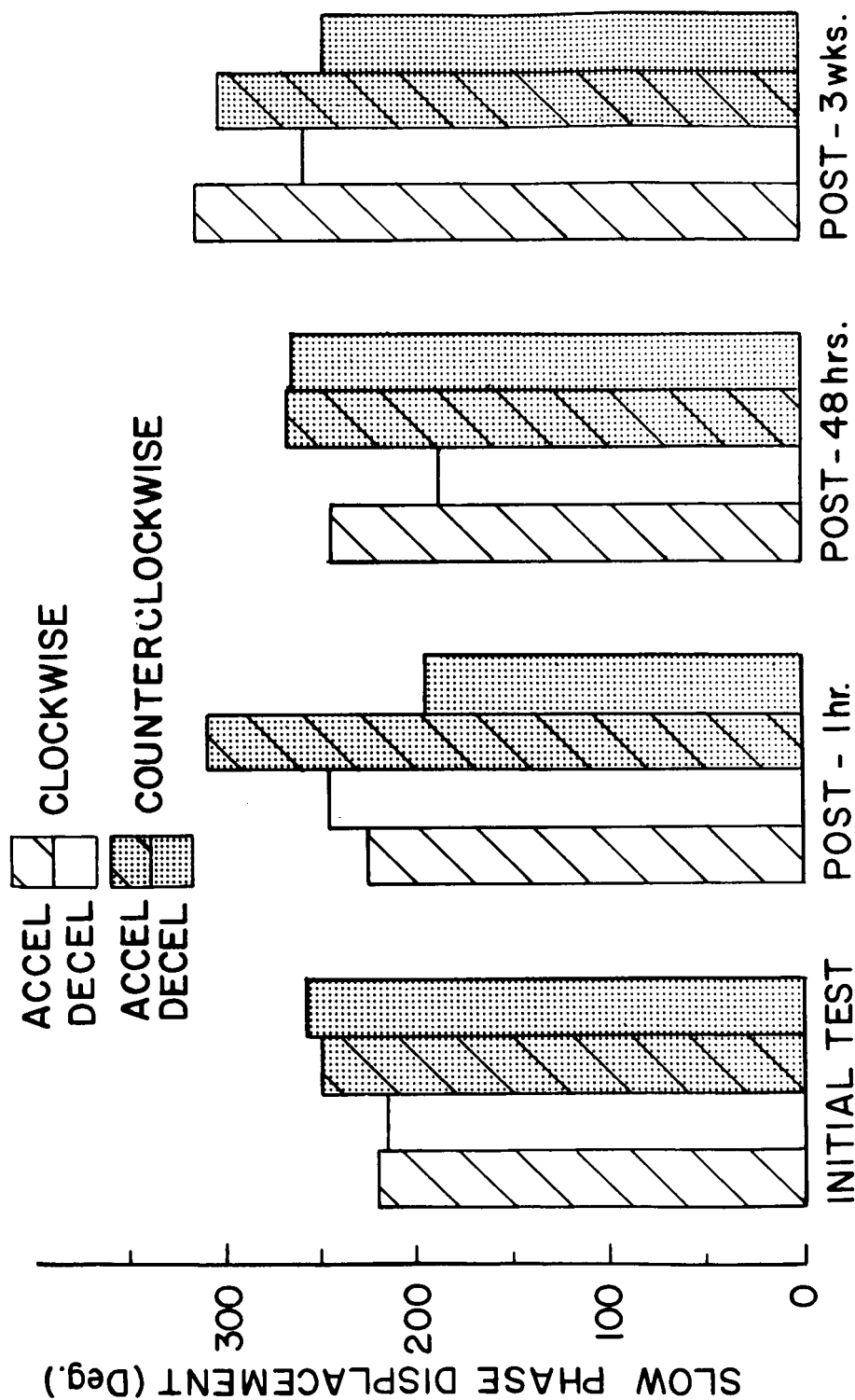


Figure 8

Average Total Slow Phase Displacement of Nystagmus Produced by 15 deg/sec^2 Angular Accelerations Used in Starting and Stopping the Chair Tests of Run 2

- on nystagmus produced by passive whole-body angular acceleration of the chair before and after the period of prolonged rotation. Results of similar tests in Run 2 are presented in Figure 9. In Run 2, the group average was strongly influenced by two subjects with strong reactions who also showed a pronounced order effect in the Initial Test session, the first response being much greater than the fourth. These same two subjects received the CW test first while the other two subjects, with weak reactions, received the CCW test first. Hence, the group average in the Initial Test, was influenced markedly by these two subjects, but considering the average level attained by the end of this session, there was little response decline to angular acceleration attributable to the twelve days of rotation, and the slight average declines could easily be attributable to the starts and stops during the twelve-day run.

INDIVIDUAL DIFFERENCES

Results obtained from individual subjects are shown in Figures 10 and 11. The single subject of Run 3 whose data are included are shown under De in Figure 10. This subject had very little nystagmus to any stimulus at the beginning of the experiment, possibly due to his previous runs in the Post 1-hr Test; his responses to head movements during CCW rotation were almost completely absent but responses to head movements during CW rotation had increased substantially. In the Post 48-hr Test, responses returned toward the level of the Initial Test, the responses to head movements during CW rotation showing considerable decline from the response level of the Post 1-hr Test. In the Post 3-wk Test, responses appeared to be less in intensity than those of the Initial Test.

During the Post 1-hr Test period, static tests revealed compensatory nystagmus in subject De.

Individual differences were prominent in several respects. First, the subjects differed markedly in their initial nystagmus reactions produced by head movements during rotation. Some subjects had vigorous reactions while others gave very weak nystagmus responses to head movement stimuli. Of four subjects with very weak nystagmus responses (Ev, Lu, De, and Mo), Mo was adjudged to be among the most severely affected by rotation in regard to motion sickness and malaise; some of the stronger "nystagmus-responders" were clearly less disturbed. However, there was a significant rank order correlation ($\rho = .57$; $P < .001$) between total nystagmus output during head movements in the Initial Test before the twelve-day run and degree of disturbance (motion sickness) during the twelve-day run as rated by the onboard experimenter, RK, who was unaware of the nystagmus results at the time he made his ratings.

As shown in the individual results depicted in Figures 10 and 11, all subjects showed clear response declines to head movement stimuli during CCW rotation, but there were individual differences in amount of decline during CCW tests and also individual differences as to whether or not declines occurred during CW tests.

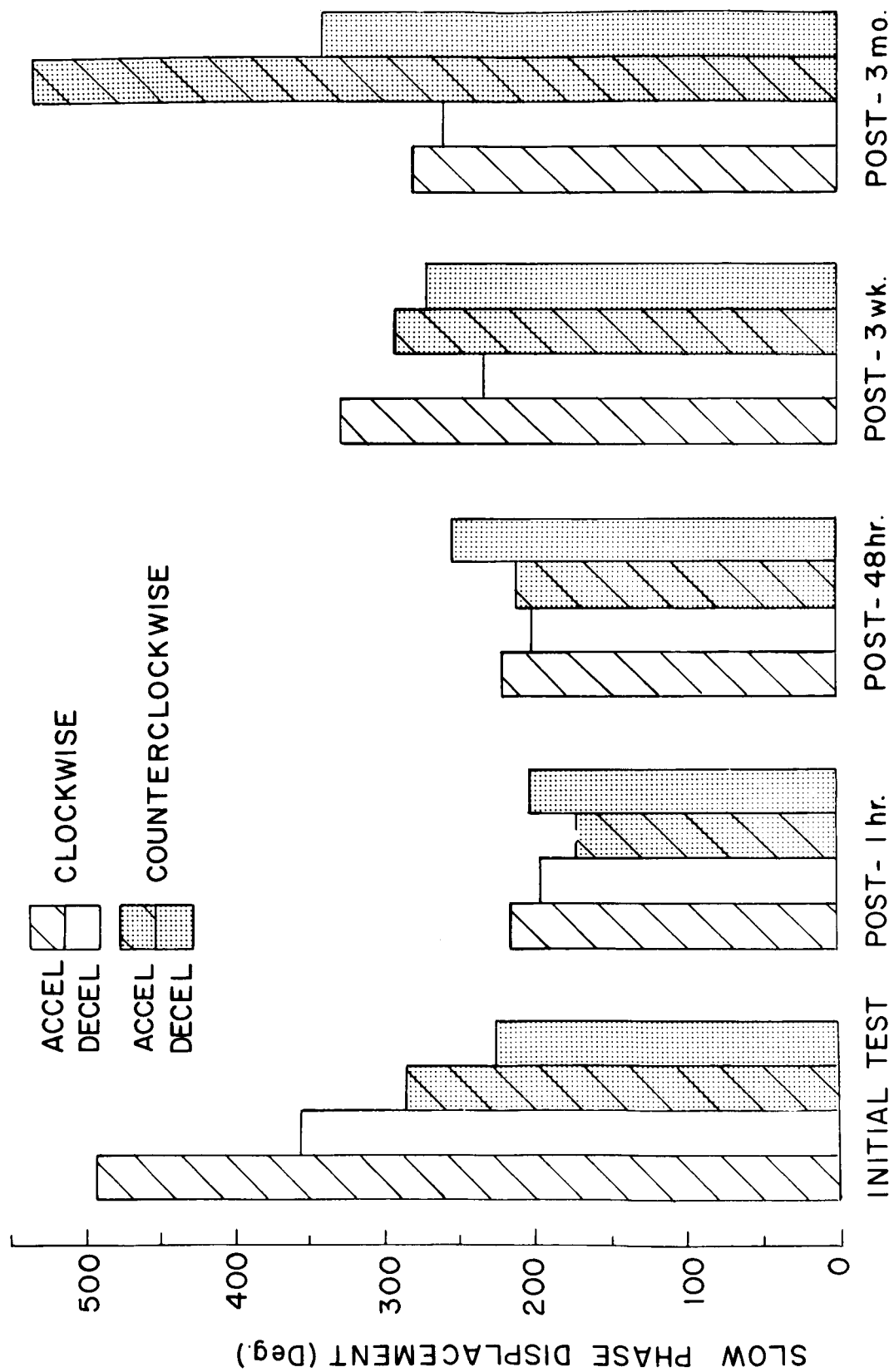


Figure 9

Average Total Slow Phase Displacement of Nystagmus Produced by 15 deg/sec² Angular Accelerations Used in Starting and Stopping the Chair Tests of Run 2

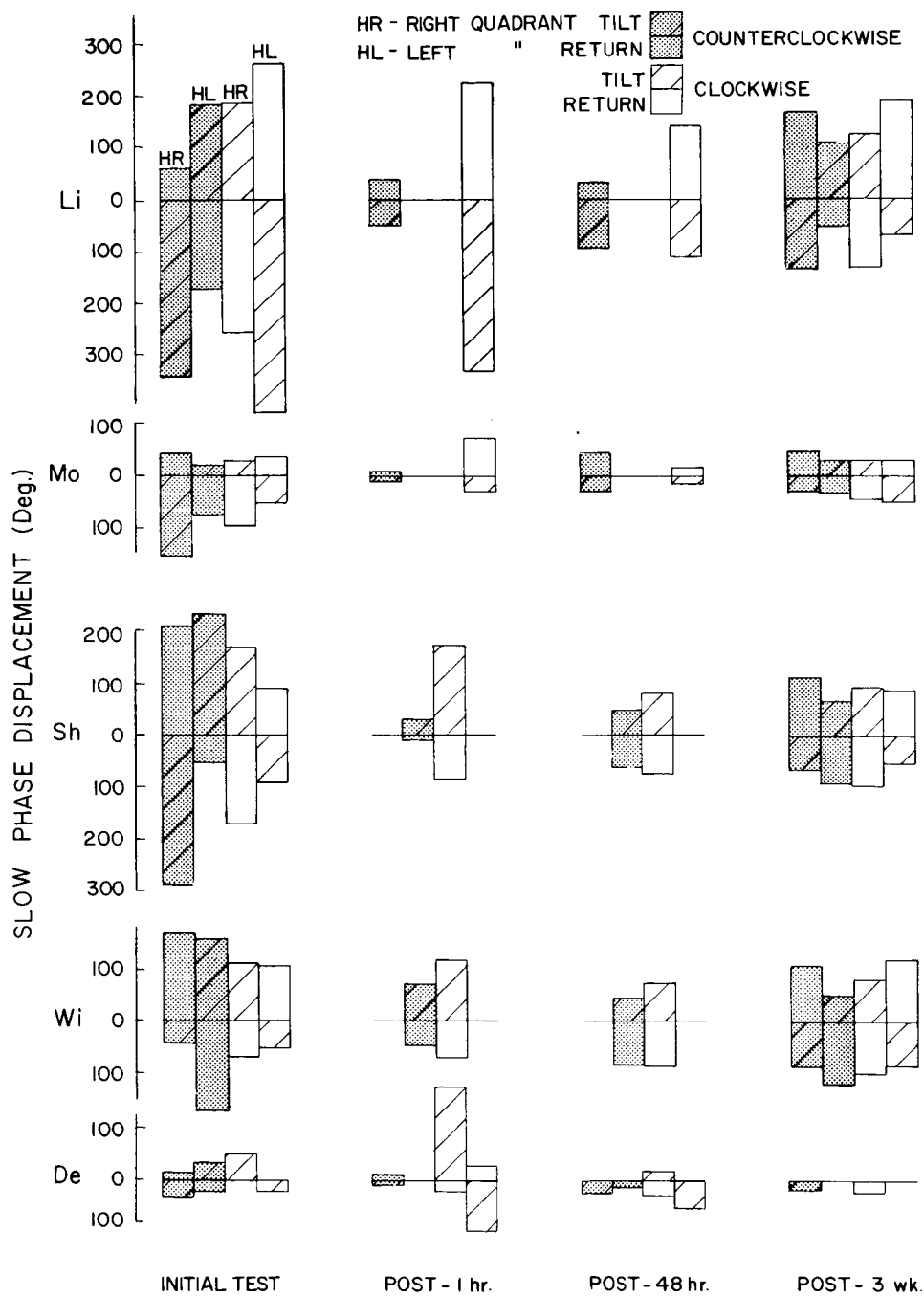


Figure 10

Individual Subjects' Total Slow Phase Displacement of Nystagmus Produced by Head Movements during Rotating Chair Tests of Runs 1 and 3. De is from Run 3.

No departure from baseline signifies absence of certain responses in De. No departure from baseline signifies no test given for subjects Li, Mo, Sh, and Wi.

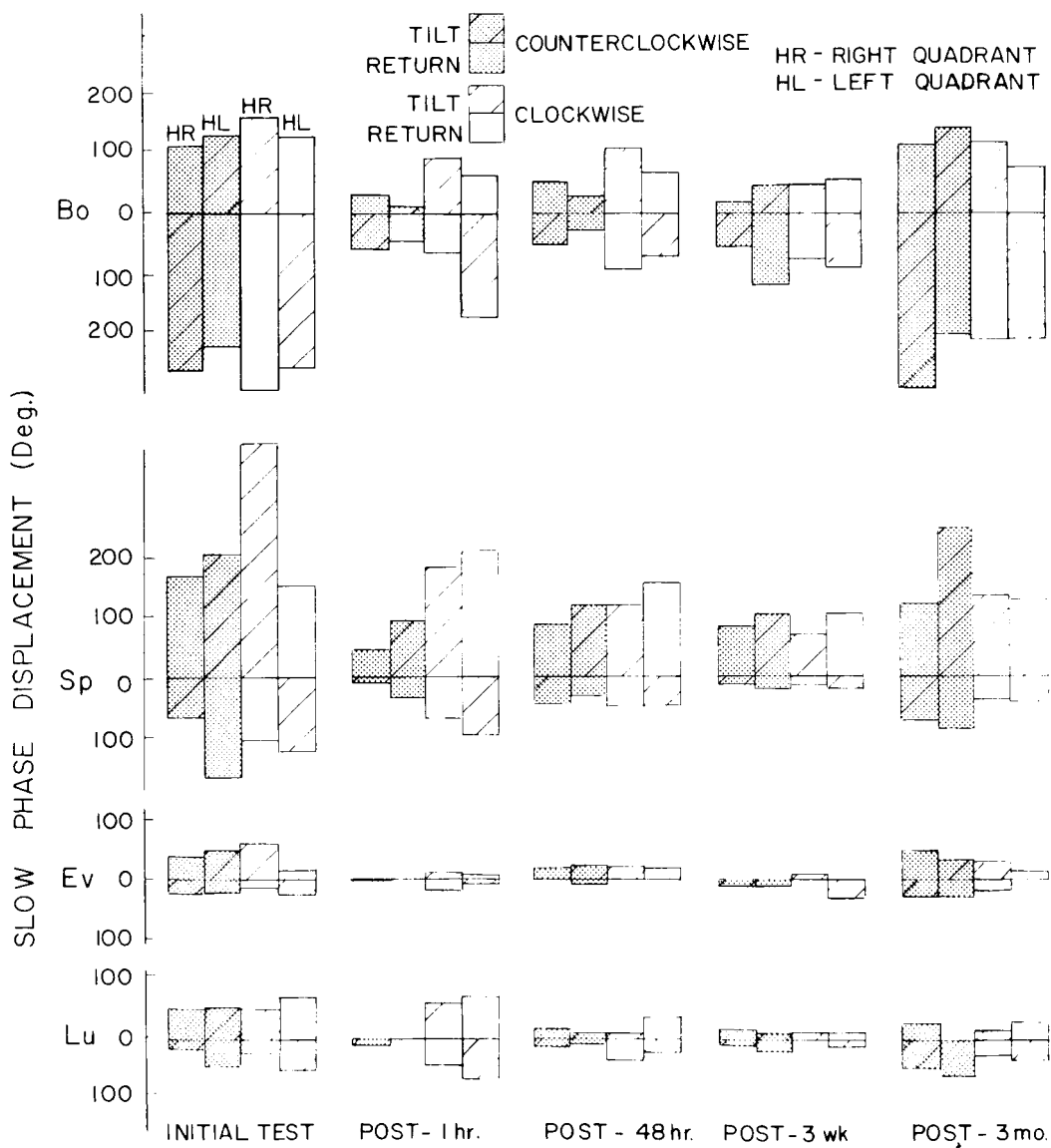


Figure 11

Individual Subjects' Total Slow Phase Displacement of Nystagmus Produced by Head Movements during Rotating Chair Tests of Run 2

No departure from baseline signifies absence of certain responses for Ev and Lu.

Different subjects chose different methods of adjusting to the SRR. Some remained very still in reclining positions, making only required movements for several days until adjustment occurred, whereas others chose to move about in spite of frequent nausea and vomiting. All subjects adjusted in that they moved about freely and without nausea after about the third day of the twelve-day run. However, some subjects spent more time in a reclining position than others after adjustment, and this may have significance for individual differences because particular head movements relative to the body give different stimuli to the canals in upright and in reclining positions (16). In addition, the four subjects of the second run seemed to have less enthusiasm for the experimental tasks than the first group toward the end of the run. Whereas the first group expressed willingness to participate in similar future experiments, the second group indicated that they would not volunteer again. Whatever the reason for differences between groups, the attempts to maintain alertness during nystagmus testing may have been adversely influenced by lowered motivation in the second run.

CONTROL RUN

Tests in the Stille-Werner chair were given to a control group of eight men. The temporal separation of these tests corresponded with the schedule used in Runs 1, 2, and 3, but the control subjects were not exposed to the twelve-day period of rotation at 10 RPM or to any other unusual vestibular stimulation between tests. Following the first control test, other tests were given after intervals of 13 days, 15 days, and 34 days to correspond respectively to the Post 1-hr, Post 48-hr, and Post 3-wk Tests of the experimental runs.

Results from the control run are shown in Figures 12 and 13. In Figure 12, it is apparent that there is little or no decline in nystagmus produced by head movement during 10 RPM rotation in "post 1-hr" and "Post 48-hr" Tests. The average declines in the "Post 3-wk" Tests are of questionable statistical significance ($t_{ccw} = 1.3$; $df = 7$ $P > 0.2$; $t_{cw} = 2.1$; $df = 7$ $p > .05$). Figure 13 represents nystagmus produced by whole-body angular acceleration, and it appears that here also there were no significant declines in nystagmus.

DISCUSSION

In the Post 1-hr Test of the experimental runs, it appears reasonable to attribute the marked inequality of responses to head movements during CW and CCW rotation to the presence of conditioned compensatory reactions (rather than to a lack of transfer of habituation). Compensatory reactions have been observed previously following exposure to prolonged rotation (18), and in the present experiments each of the subjects during the static tests just after the twelve-day run revealed compensatory reactions in the form of nystagmus or subjective reactions or both. For particular head movements, these compensatory reactions are directionally the same as reactions elicited during CW rotation and opposite to reactions which would be elicited by CCW rotation.

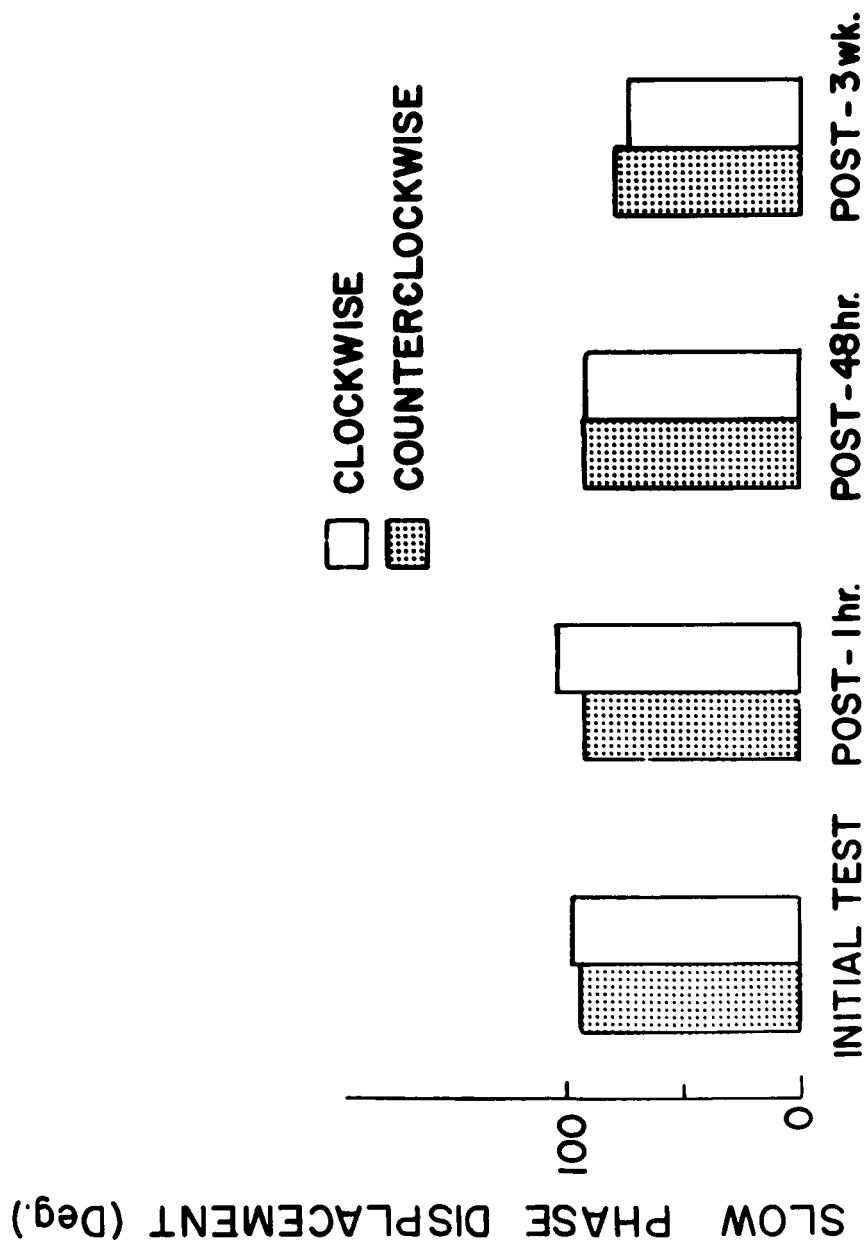


Figure 12

Control Group Average Total Slow Phase Displacement of Nystagmus Produced by Head Movements during Rotating Chair Tests

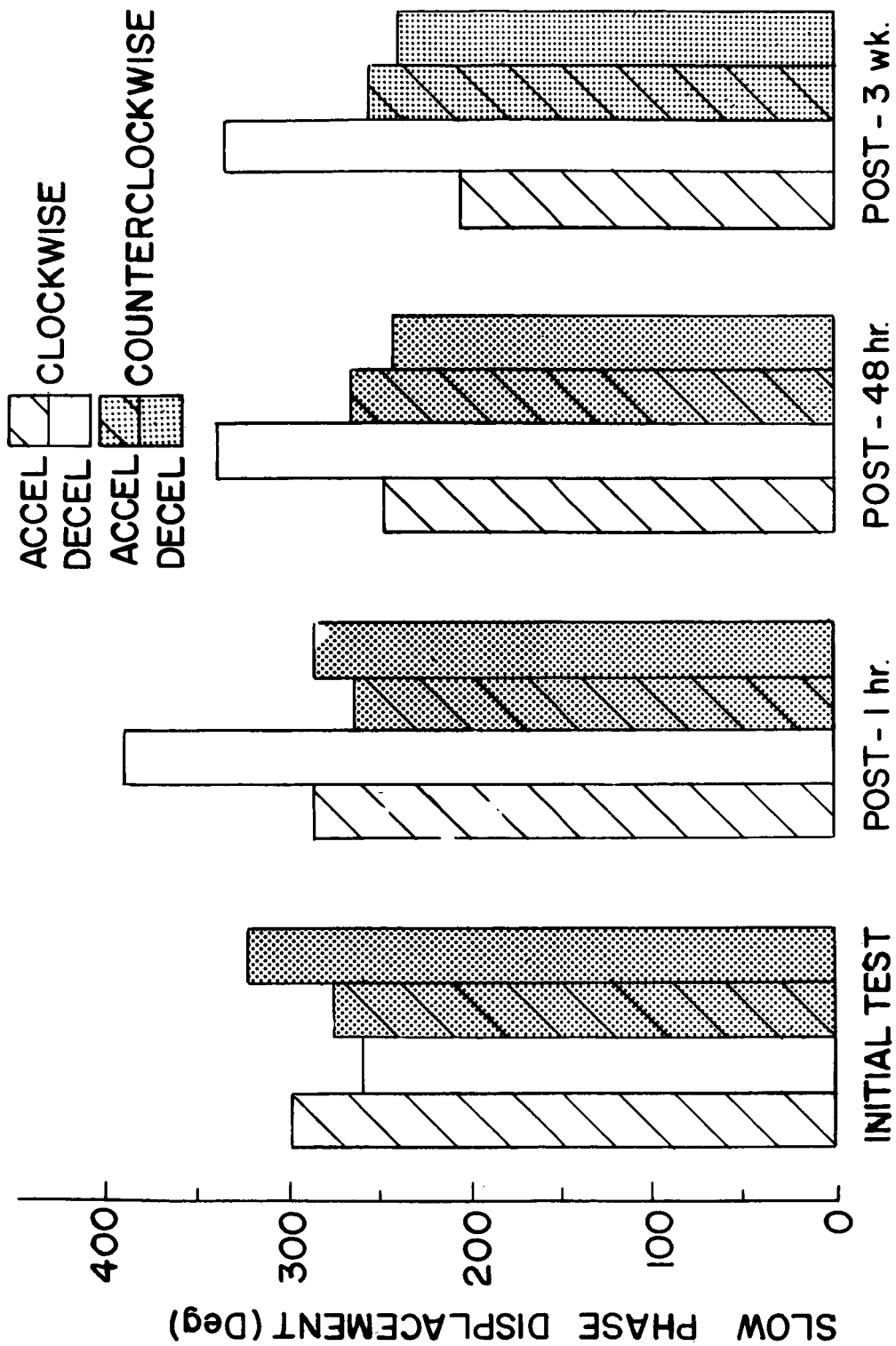


Figure 13

Control Group Average Total Slow Phase Displacement of Nystagmus Produced by 15 deg/sec² Angular Accelerations Used in Starting and Stopping the Chair Tests

In the Post 48-hr Test the responses to head movements during CW rotation were almost all below the level exhibited in the Initial Tests or in the Post 1-hr Test. At the time of the Post 48-hr Test the compensatory reactions were no longer in evidence in the static condition. It is reasonable to expect that compensatory reactions would dissipate fairly quickly upon return to a natural environment by virtue of natural head movements which would elicit the now-inappropriate conditioned response until extinction occurred. The fact that during the Post 48-hr Test, responses to head movements were below the Initial Test level irrespective of direction of rotation suggests a more general response suppression for this kind of stimulus which persists long after the compensatory reactions have been extinguished. Presumably, then, the absence of a response decline during the Post 1-hr CW Test was attributable to a compensatory factor which partially in some cases and completely in others counteracted the suppression during the CW test, and this suppression would have reduced all reactions to head movements during rotation, CW or CCW, in the Post 1-hr Test if it had not been counteracted by the compensatory factor during the CW test.

The lowered responses to head movements during rotation three weeks after the twelve-day run suggest that suppression is retained for long periods.

It is not clear that this "general suppression" generalizes to other forms of vestibular stimulation. For example, the nystagmus produced by passive angular acceleration of the entire body was not reduced at all in some subjects after the twelve-day run, and the average decline was not more than one might expect from the number of starts and stops of the SRR during the twelve-day run. The major response decline seems to have been restricted to the unnatural antisynergic sensory input occasioned by head movements during whole-body rotation.

In the past there have been questions raised as to whether habituation "transfers" from one vestibular stimulus to another (9, 13). Recent studies have indicated that habituation (in cats) may be specific to the direction of response repeatedly elicited during habituation (8, 23). Habituation to repetitive unidirectional caloric stimulation of one ear transferred to caloric stimuli producing ipsidirectional responses but did not transfer to caloric stimuli which produced contradirectional responses, irrespective of the ear stimulated (23). Similarly, habituation induced by repetitive rotational stimuli which elicited only one direction of response did not transfer to similar stimuli producing responses of opposite sign (7) or different planes (8, 15, 20).

In the present experiments the apparent specificity of habituation (during the Post 1-hr Test) to the practiced direction of rotation was interesting because nystagmus of closely corresponding planes and directions may be produced during either clockwise or counterclockwise rotation (see Figure 7). Hence, the Post 1-hr Test results appeared to be indicative of habituation specificity which was independent of direction of response. Although this particular conclusion does not hold for the results of the Post 48-hr and Post 3-wk Tests, Collins (5), in a less complex experiment, also noted that habituation may fail to transfer when directions of responses elicited by different forms of stimulation are directionally the same; viz., caloric habituation did not

- transfer to rotational stimuli and rotational habituation did not transfer to caloric stimuli. Apparently, transfer of habituation cannot be predicted in two stimulus situations, the one practiced and the other unpracticed, solely on the basis of the similarity of the nystagmus originally produced by the two situations.

Further evidence of habituation specificity was found in a previous study (20) of human subjects following repetitive elicitation of the Coriolis vestibular reaction. While rotating in the SRR, subjects made head movements restricted to one quadrant of one plane, e.g., left lateral tilt and return movements. Tests conducted in darkness just before and just after habituation series of 100 or more tilt-return cycles revealed nystagmus declines which were much more pronounced in the practiced than in the unpracticed quadrant. Subsequent static tests indicated subjective compensatory reactions which were fairly well restricted to the practiced quadrant. These findings were confirmed by a later experiment (15) which further indicated that visual tasks performed during the habituation series were influential in the development of the conditioned compensatory reactions. It is hypothesized that stimuli from several sources (the otolith system, the proprioceptor system of the neck, the "intention" involved in the voluntary head movements) may have been conditioned to release particular response patterns in the CNS appropriate to compensate for particular antisnergic canal inputs for head movements in the practiced quadrant. Head movements in the unpracticed quadrant would not produce these patterns of conditioned stimuli, possibly accounting for a lack of compensatory reactions during movements in this quadrant.

Hence, the minimal transfer to the unpracticed quadrant in this previous SRR study (15) may have been attributable to a failure to release compensatory reactions in that quadrant, whereas in the present study, the apparent lack of transfer of habituation to the unpracticed rotation direction (in Post 1-hr Tests) was probably a consequence of compensatory reactions augmenting responses produced during CW rotation.

The present experiments have practical implications for certain conditions which might be encountered in space operations. The immediate aftereffects of prolonged rotation training would be undesirable. Any head movement could release false sensations of motion, and these would be particularly accentuated if the departing space vehicle introduced maneuvers involving rotation in opposite sense. However, the fact that responses to head movements during rotation in either direction were suppressed forty-eight hours to three weeks after the twelve-day run is noteworthy. It is possible that these reduced responses are indicative of a suppression which will transfer to similar types of stimulation, i.e., to stimuli in which head movements induce unnatural patterns of canal responses which conflict with other kinesthetic sensory input, and hence afford a generalized protection against such stimulation for some time after the rotation training. The situation in a rotating space station is not likely to cause a specific set of conditioned reactions to head movement which would generalize to conditions outside the space station because a particular head movement relative to the body when a person stands *in the plane of rotation* would release

different nystagmus reactions for each direction the person faces (cf. 16). It is possible that active head movements are important to the development of compensatory reactions (21,22). The situation most apt to yield active head movement, i.e., situations in which the person is sitting or standing upright, will not yield consistent responses for each head movement. Hence, development of a particular set of compensatory reactions would depend upon specific visual orientation cues within the space station which indicate the direction the person faces relative to the direction of rotation. The question which is of concern here is whether or not the additional complexity of this situation in the space station would lead to deterioration of performance as has been indicated in sensory disarrangement experiments in which the distortion of sensory feedback is disorderly and hence unlearnable (3,21,22). In the space station the sensory rearrangement would be orderly but more complex during active movements than in the rotating room on earth.

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