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Earl F. Miller, II and Ashton Graybiel

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Research Report

MAGNITUDE OF GRAVITOINERTIAL FORCE, AN INDEPENDENT VARIABLE IN EGOCENTRIC VISUAL LOCALIZATION OF THE HORIZONTAL*

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U. S. NAVAL SCHOOL OF AVIATION MEDICINE
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SUMMARY PAGE

THE PROBLEM

1. To determine the effect of different levels of magnitude of gravitoinertial force (GIF) upon egocentric visual localization (EVL) of the horizontal. Direction was held constant by utilizing the gravitational vertical and gravitoinertial vertical as the "upright," and thus measurements at the upright and at different angles of tilt from the upright were comparable in terms of direction of force.

2. To test for differences between normal and bilateral labyrinthine-defective (L-D) subjects under the above conditions.

FINDINGS

The egocentric visual localization of the horizontal of both groups of subjects was found to deviate from the gravitoinertial horizontal as a function of magnitude of the GIF. This magnitude effect was present at the upright and tended to increase with the amount of body tilt from this position; the maximum deviation of EVL of the horizontal occurred in both groups under 2.0 G conditions with a body tilt of 40° but was approximately twice as great in the case of the L-D subjects. Equally significant was the finding that the increase of GIF in the case of the L-D subjects resulted generally in an apparent rotation of the physical horizontal in a direction of the E- then A- phenomenon in contrast to the normal subjects who manifested ever increasing amounts of the E-phenomenon only. Based upon these findings and the assumption that the subjects differed under these experimental conditions primarily in otolithic function, the possible roles of otolithic and nonotolithic gravireceptor cues in EVL are discussed.

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INTRODUCTION

Numerous studies in visual orientation have been conducted in which the direction of force acting upon the subject has been considered more or less as the primary variable (1,3,4,8,14,15,17,18-21,25,and others). These studies include those in which the subject was simply tilted with respect to gravity or the direction of apparent "vertical" was changed with the addition of centripetal acceleration. Coordinate systems of reference for orientation can be established in which the vertical axis represents the gravitational force vector or if other inertial forces are present, the resultant force vector. It is convenient to define these directions of force as the gravitational and gravitoinertial verticals, and a line at right angles would be termed, respectivly, the gravitational horizontal and gravitoinertial horizontal. In reporting the present experiment, for reasons of economy the "upright" will be used for both the gravitational and gravitoinertial vertical.

As is well known, the ability to localize visually these reference axes without empirical visual cues (egocentric visual localization, EVL) is dependent upon the position of the subject relative to vertical. When upright, the estimates of horizontality (or verticality) by a normal individual are usually quite precise, but this accuracy will diminish markedly when he is tilted leftward or rightward 90°. This perceptual change with posture was first reported by Aubert (1) who observed that his vertical reference target inclined obliquely in a direction opposite that of his head or body tilt (the Aubert or, after Müller (18), the A- phenomenon). Müller in using smaller angles of tilt than Aubert sometimes observed a coinclination of target and subject which he termed the E- phenomenon. In effect, the A- phenomenon reveals an underestimation and the E- phenomenon an overestimation of the angle of tilt. A recent systematic quantitative study of these two phenomena within ± 90° of tilt from gravitational vertical has revealed that an orderly, predictable relationship exists between the relative body position and egocentric visual localization (17).

Graybiel et al. (2,5-8) in a series of studies have explored the effects on visual orientation of changing the direction of force by centrifugation. When seated physically upright at some distance from the axis of a centrifuge or carousel device, as first described by Purkinje (22) and later by Mach (10), a person will experience upon rotation a sensation of tilting in accord with the gravitoinertial vertical. This feeling of tilt is normally accompanied by an apparent displacement of objects in a structureless visual field in close correspondence to the actual change in direction of the resultant force. The visual component of this phenomenon has been termed the oculogravic illusion (5), and may be greatly reduced in labyrinthine-defective (L-D) individuals. Differences between normal and L-D subjects are found not only in the dynamic situation but also under static tilt conditions (12,13,15). These studies introduced evidence which has been extended in the present study of the differential roles played by otolithic and nonotolithic cues in visual localization.

Schubert and Kolder (23) also explored the contribution of otolithic and somesthetic systems to visual spatial orientation by placing a subject at either the gravitational or gravitoinertial vertical and requesting him to tilt, in approximately 10-degree steps, his head toward the gravitoinertial vertical or gravitational vertical, respectively. The experiments which have relevance to ours were carried out in a lighted test enclosure covered with a layer of unbleached opaque paper. They found that, when the subject was in the gravitational vertical, accuracy in localization improved as his head was tilted toward the direction of resultant force; on the other hand, no improvement in settings with head tilt from the gravitational vertical was recorded until the head reached a position about 10 degrees from the gravitoinertial vertical. They assumed from these results that otolithic information resulting in improvement under the first experimental condition was suppressed in the second by somesthetic receptor cues. The authors ruled out the A- phenomenon as a factor in their experiments because all were done under ordinary room illumination. Although these studies provided a rich background of information, none dealt with the magnitude of gravitoinertial force as an independent variable in visual space perception which is the main purpose of the investigation now to be reported. By comparing the findings on normal and L-D subjects the role of the nonotolithic gravireceptors and combined otolithic/nonotolithic gravireceptors could be compared.

PROCEDURE

SUBJECTS

Eight volunteer medical corps officers serving their Ensign clerkship training at Pensacola in 1962 constituted the normal group of subjects. All were healthy, and careful medical examination revealed no defect, disease, or disorder. In addition, each manifested normal semicircular canal response to thermal stimulation (9) and normal otolith function as measured by the counterrolling test (11, 16). Two deaf subjects with no nystagmic response to thermal stimulation of the canals with ice water, and greatly reduced counterrolling response, also served as subjects.

APPARATUS

A specially constructed tilt chair was mounted on the Pensacola human centrifuge 15' 10" from the center of rotation and housed in a light-tight metal enclosure. The chair by means of hydraulic power could be tilted leftward or rightward 90 degrees. A hollow flexible rubber appliance* fashioned like an armless "parka" coat to embrace

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*The appliance was filled with finely ground peach seeds which were separated by netting material into many small compartments. The rubber covering of the appliance was completely sealed except for an air hose connection which could be attached to a vacuum pump. Under normal ambient air pressure the seed granules within the appliance could be adjusted to conform closely to the subject's body contours; when the air was essentially removed by the vacuum pump after the fitting, the appliance became an extremely rigid support for the subject that distributed contact pressures fairly uniformly over a large area of his body.

the torso, neck, and head of the subject was developed which served as a supporting inner liner of the tilt chair. The head part of the appliance was completely encased in a large helmet which was rigidly mounted to the tilt device support. An optical system which produced a line target of collimated light was mounted so that the subject viewed it at eye level at a distance of 27 inches. A round knob providing no tactual cue of position was used by the subject to rotate the target clockwise or counterclockwise about its center. The experimenter had a similar control of the target position and the switch by which it could be illuminated. The angular position of the target and tilt chair was relayed independently by means of selsyn repeater motors to two dial readouts (smallest scale division = $1/4^{\circ}$) located at the control console near the center of the centrifuge. The right and left positions of tilt ($\pm$ 10, $\pm$ 20, $\pm$ 30, $\pm$ 40 degrees) for the different gravitoinertial verticals were calculated by subtracting and adding, respectively, the value of the angle phi. Voice and buzzer (used as a vibrator against the fingers of the deaf subjects) communication systems between the subject and experimenter were provided. A system for open voice communication with assistants and personnel operating the centrifuge was also available.

METHOD

The subject seated in the tilt chair was fitted with the appliance and, after the air was evacuated, the subject and appliance as a unit were tightly fastened to the chair with straps. The chair was then elevated until the target was at eye level. This ensured that the effective radius at the center of the head was about the same for all subjects. The selection of this point for determining a given level of force resulted in gradient of force being applied along the longitudinal body axis when it was tilted from gravitational vertical. Since the subject faced the direction of rotation, the G gradient in the cephalocaudal direction was of increasing magnitude for leftward tilt and of decreasing for rightward tilt from gravitational upright.

The procedure required the subject in darkness to make ten settings of the luminous target at nine different positions of tilt under six different levels of force (1.0, 1.2, 1.4, 1.6, 1.8, 2.0 G) Prior to each setting the experimenter offset the target between 10 degrees and 40 degrees from the horizontal either clockwise or counterclockwise in random fashion. The target was then illuminated, serving as a signal to the subject who rotated the target to what he considered to be the horizontal and signalled the experimenter to record the setting. The target light was then switched off and the next trial was begun; ten trials constituted a series.

The subject was exposed to the six different levels of force in random order, and the different degrees of tilt at each level also were randomized. The tilt chair was always moved slowly($\sim 1^{\circ}$/sec)and, except under static conditions, concurrently with the increase in centripetal force to the desired level. Settings of the luminous target were not begun until at least sixty seconds had elapsed after tilting the chair and final velocity of the centrifuge had been reached. Due to the large number (540) of settings

required and the time involved in the slow mechanical adjustments of the subject, it was impossible to complete the test in less than four to five sessions. For the sake of efficiency and comfort of the subject, no session lasted longer than two hours and was usually of 1 - 1 1/2 hours' duration.

RESULTS

Inspection of Figure 1 reveals that under ordinary gravitational conditions the mean of the normal subjects' estimates (coded in Figures 1 and 2 according to the G level) of the location of the horizontal, when they were upright, was slightly (+0.8°) clockwise from its actual position. The mean estimate at 10° and 20° leftward (-) and that at 10°, 20°, and 30° rightward (+) tilt were within 1.6° of their estimate when upright, but, at greater degrees of tilt, the E-phenomenon was clearly manifested. It is noteworthy that the shape of the curve depicting the estimates at 1.0 G differs most characteristically from the other curves in that the middle portion is nearly flat.

When the subjects were exposed to increasing levels of inertial force while positioned at the gravitoinertial upright, all of the estimates deviated counterclockwise from the gravitoinertial horizontal, but there were some exceptions to an orderly shift with increasing levels of force. With increasing degrees of leftward or rightward tilt not only did the deviations from the 1.0 G upright value become increasingly greater but they also increased with increasing levels of force. Thus, despite irregularities and right-left differences, there is a clear tendency toward increasing deviations in the E-direction with increasing magnitude of force, the most significant occurring between 1.0 and 1.2 G.

The findings on the two subjects with labyrinthine defects are summarized in Figure 2. Under normal gravitational conditions the subjects' mean estimate of the horizontal when upright was nearly 13 degrees clockwise from the gravitational horizontal. With increasing degrees of leftward tilt the estimates deviated from this value first in a counterclockwise then in a clockwise direction. With increasing rightward tilt the mean estimates deviated from the upright value in a counterclockwise direction over a relatively narrow range (+13 to +3 degrees). The curve representing these values reveals no similarity to the comparable curve in Figure 1 for the normal subjects.

With increasing levels of force while the L-D subjects were at the gravitoinertial upright their estimates of horizontality deviated in a counterclockwise direction from the upright value and tended to become more accurate with reference to the gravitoinertial horizontal until the 2.0 G level was reached. This shift in location of the visual horizontal was associated with a progressive change in the shapes of the curves depicting the estimates with leftward and rightward tilt. Thus, the curve representing the findings at 2.0 G shows that with leftward tilt the subjects' estimates deviated clockwise from the gravitoinertial upright value at first slightly then strongly; with rightward tilt the deviations were first clockwise then counterclockwise. The patterns between 1.0 and 2.0 G levels were, roughly, transitional.

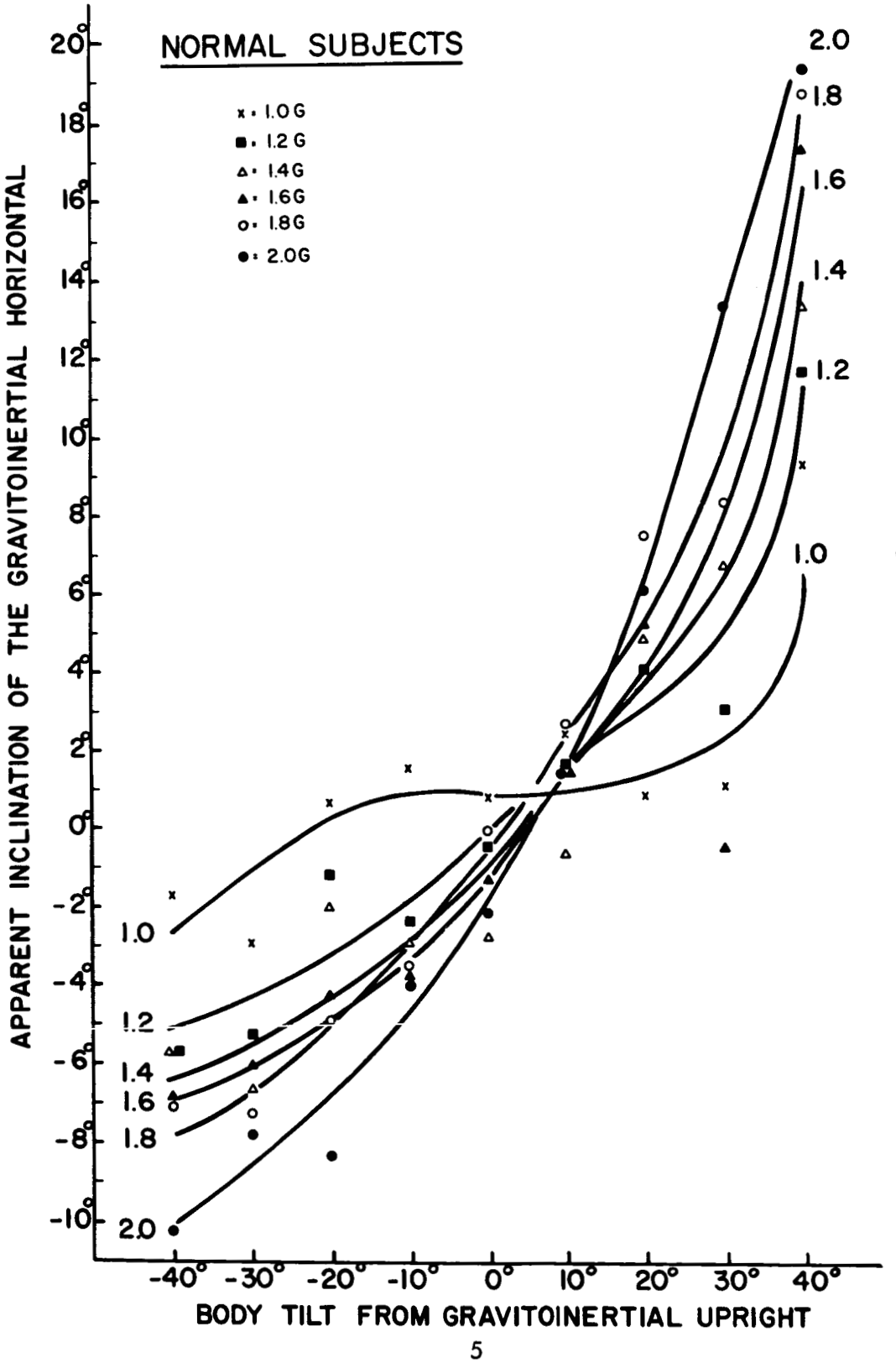

Figure 1

Visual Orientation in Normal Subjects as a Function of Magnitude of Gravitoinertial Force Acting in Various Directions with Respect to the Longitudinal Body Axis

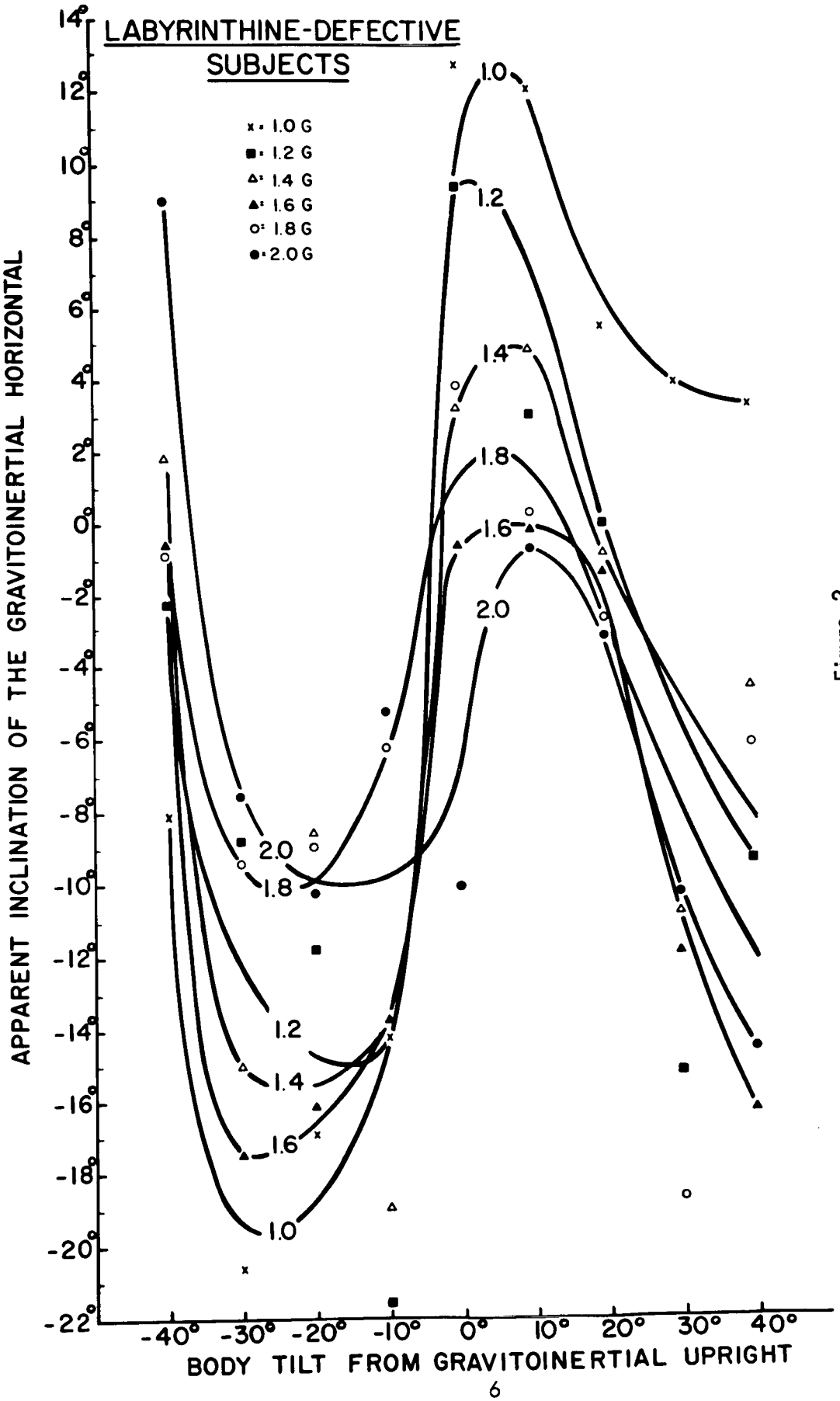

Figure 2

Visual Orientation in Labyrinthine-Defective Subjects as a Function of Magnitude of Gravitoinertial Force Acting in Various Directions with Respect to the Longitudinal Body Axis

DISCUSSION

The estimates (EVL) of the horizontal for the normal subjects under ordinary gravitational conditions are in line with previous observations using similar but not identical methods (17). The principal characteristic was good accuracy of these estimates with reference to the gravitational horizontal for the upright and small angles of tilt. With greater tilt (30° - 40°) there was an increasing tendency to exhibit the E-phenomenon. Beyond 40-degree tilt, conditions not explored in this experiment, the tendency to exhibit the E-phenomenon falls off around 65° - 70° of tilt, beyond which there is an increasing tendency toward exhibiting the A-phenomenon. Differences between leftward and rightward tilting and "irregularities" are the rule. Some of the right-left differences appear to be due to inaccurate centering of the body or the otolith organs. Asymmetry in vestibular responses has been found under different circumstances (16), and this curious phenomenon is now being explored. Some of the "irregularities" in response are the manifestation of unknown differences between series of trials under identical environmental conditions. The significance of the changing relation between vertical and lateral components of gravitational force while the subject is tilting has been touched upon elsewhere (26).

Increasing the magnitude of force in the normal subjects tended to: 1) shift the estimates of the horizontal in a counterclockwise direction when they were at the gravitoinertial upright, 2) increase the tendency toward exhibiting the E-phenomenon, and 3) exaggerate right-left differences. The "shift" could be explained if the subjects were physically tilted slightly leftward with respect to the force upright. Bodily asymmetry as a cause should have yielded more random results.

The right-left asymmetry is evident at 1.0 G and, if the high value for 40 degrees rightward tilt is accepted, relatively greater at 1.0 G than at higher levels of force. It would appear, therefore, that the gradient of G force acting only under hypergravity conditions and greater for leftward than for rightward tilts was not an important factor in the right-left differences.

The decreased accuracy in estimating the horizontal with increasing degrees of tilt is clearly evident even when using the subjects' estimates of the gravitoinertial horizontal as a baseline. Stated differently, the E-phenomenon increased as a function of increasing magnitude for a given direction of force. The influence of magnitude at higher degrees of tilt to determine its effect on the "reversal point," i.e., change from E to A tendency, was, unfortunately, not determined.

The findings on the two subjects with labyrinthine defects are interpreted with caution partly because of the small number of subjects and partly because the findings under ordinary gravitational conditions differed from previous results in that the estimates at the upright were more inaccurate (12, 15). The latter may be explained by the difference in methods used for restraint of the subjects. In this experiment contact cues were exceptionally well distributed, simulating to a small degree water immersion.

Nevertheless, the findings clearly indicate: 1) the shift phenomenon at the gravito-inertial upright, 2) a fairly regular transition of response between the 1.0 and the 2.0 G levels, and 3) a curious tendency toward manifestation of both E and A-phenomena.

The shift, as in the case of the normal subjects, was unidirectional with reference to the value obtained at 1.0 G. The stepwise changes were orderly, with reference to increasing gravitoinertial force, except for a "reversal" of the 1.6 and 1.8 G values. The shift was in the direction of greater accuracy in estimating the horizontal until the 2.0 G level was reached when the counterclockwise deviation was nearly as great as the clockwise deviation at 1.0 G. One explanation for the shift is that, with increasing gravitoinertial force, cues from contact with the chair become more reliable; the great deviation at 2.0 G, however, is out of line with this reasoning. A second explanation is the one given above for the normal subjects, namely, imperfect alignment of chair to the vertical; this would readily account for the shifting values between 1.0 and 2.0 G. If this explanation is correct, the smaller range (3.5°) of the shift in normal compared with L-D subjects (22.5°) must represent an influence of otolith over nonotolith inputs, an influence tending toward greater accuracy in estimating the EVL of the horizontal.

The regularity in the transitions in the curves (Figure 2) as a function of increasing gravitoinertial force strongly suggests that physiological factors were operating in an orderly manner in the L-D subjects. Great right-left differences are seen as a function of body tilt. The fact that the differences were as great at 1.0 G as at higher levels of force suggests that right-left differences in radii, with respect to the body position under centrifugation, were not the factor mainly responsible. As mentioned above, however, asymmetry with respect to the vertical may have been an important factor.

In an attempt to explain the directional variations as depicted by the curves we have used the L-D subject's estimate of the horizontal when he was upright as the starting point and, in a slight departure from convention, used "reversal points" as indicating a change from A to E tendency or vice versa. At least it is more convenient than to distinguish between an increasing and decreasing E- or A- phenomenon and is probably more realistic in terms of underlying mechanisms.

With leftward tilt of the L-D subjects , except at 2.0 G, the E-phenomenon was prominent at small angles and the A tendency strong at large angles; at 2.0 G only the A-phenomenon was manifested. With rightward tilt the E-phenomenon was prominent only at the 2.0 G level and a reversal occurred at 20-degree tilt. The A-phenomenon was prominent at all levels of force. If the curves are interpreted after arbitrarily setting the "upright" at a point which creates the maximum right-left symmetry, the results could be summarized as follows: 1) At small angles of tilt the E-phenomenon is prominent and at larger angles the A-phenomenon; 2) with increasing levels of force there is a decrease in the E and an increase in the A values.

The differences between the findings on the normal and L-D subjects must represent, with some reservations, the influence of the otolith organs. The reservations include: 1) the limited number of L-D subjects and observations, 2) the possibility that some residual otolith function might remain in our L-D subjects , 3) the adaptation of the L-D subjects in the direction of greater than normal use of nonotolithic gravitational cues, and 4) the extralabyrinthine factors which might have been involved (24). Assuming that these factors were not significant, it can be generally concluded that, under the conditions of our experiment and within the $\pm 40^{\circ}$ arc of tilt, visual orientation based upon nonotolithic cues is far less accurate and qualitatively different from that based upon both otolithic and nonotolithic gravireceptor cues. Otolithic cues when present would appear to dominate nonotolithic cues in suppressing the "shift" at upright, nullifying the E tendency at smaller angles of tilt, and overbalancing in the E direction for the strong A tendency at the larger angles of tilt. The dominancy of the otolithic E tendency over the nonotolithic A tendency in EVL of the horizontal would seem to be increased by increasing the magnitude of gravitoinertial force.

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