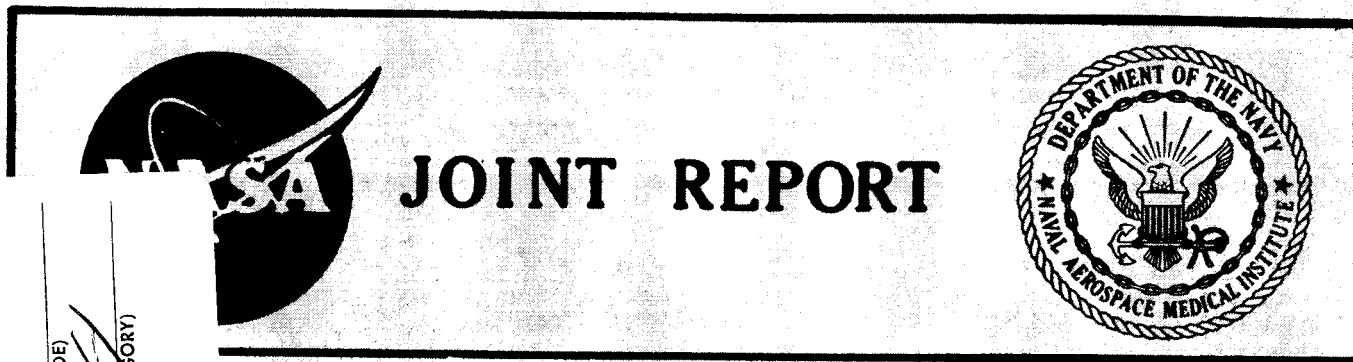


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ILLUSION IN NORMAL AND LABYRINTHINE-DEFECTIVE SUBJECTS

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SUMMARY PAGE

THE PROBLEM

To determine the separate and combined influences of otolith and nonotolith sensory inputs on perception of the oculogravic illusion. By manipulating the visual and gravito-inertial force environments it was possible to investigate the separate and combined contributions of 1) field force receptors in the vestibular organs and 2) nonvestibular proprioceptors stimulated by external contact support, which influenced the visually perceived direction of extrapersonal space.

FINDINGS

Under the conditions of this experiment the findings suggest that in normal persons, the vestibular contribution is predictable in terms of the changes in direction of the gravito-inertial force vector but that the nonvestibular contribution varies; it may be relatively great or small. In persons with bilateral labyrinthine defects a nonvestibular contribution was always present but there was great individual variance. The significance of the findings in terms of tests measuring the function of the otolith organs is discussed.

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INTRODUCTION

This report describes an experiment in which sensory inputs influencing the visually perceived direction of space were measured. A person is poised to perceive these influences if, for example, he is subjected to centripetal force while in a fixed position on a human centrifuge. The change in direction of the gravito-inertial vertical with reference to his body is rightly interpreted as a tilt away from the upright, and the visual framework tends to tilt concordantly. The latter phenomenon is a form of apparent motion which for convenience has been termed the oculogravic illusion (1).

This illusion, first described by Purkinje (2), was the object of investigation by Mach (3) who reasoned that it must have its genesis in a sensory organ in the skull, and the nonacoustic labyrinth was implicated. Kreidl (4) regarded the illusion as having its origin in the vestibule (otolith apparatus) when 13 of 62 "deaf mutes" failed to perceive it. Our early experimental findings (5) using deaf persons with bilateral labyrinthine defects (L-D subjects) seemed to confirm Kreidl's work with minor qualifications. Later, in a systematic study the settings of ten L-D subjects were compared with those of nine normal subjects under identical conditions (6). The normal subjects readily perceived the apparent rotation of the target (oculogravic illusion), and their estimates bore a meaningful relation to the angular changes in the gravito-inertial horizontal. Individual variance in these subjects was manifested chiefly in their overestimation of the illusion when they were exposed to relatively large changes in direction of the force vector. None of the L-D subjects made settings comparable to those of the normal subjects. The only consistent L-D performers were four who perceived little or no illusion; the others expressed varying degrees of difficulty in making the settings which were characterized by interindividual and intraindividual variance.

Although the inferior performance of the L-D subjects was ascribed to loss of otolith function, there was no correlation between the magnitude of the settings and the degree of ocular counterrolling, a measure of otolith function (7, 8). It was hypothesized that the differences among the L-D subjects in perceiving the oculogravic illusion might be explained by residual otolith function, by inputs from nonotolith proprioceptors, or by a combination of both.

The present experiment was designed to test this hypothesis by exposing normal and L-D subjects to centrifugation, under dry condition and when immersed in water. Field force receptors in the otolith organs would not be affected by the immersion while nonotolith proprioceptors, mechanoreceptor systems, would be minimally stimulated.

Two classes of phenomena relating to visual space perception can be studied while systematically manipulating the force environment. One class deals with "interactions" in which cues to a visual frame of reference are available, the other with "influences" in which visual cues are either lacking or inadequate. In the present experiment we took advantage of the extraordinary circumstance in which a dim line of light in darkness is an inadequate cue, yet can be manipulated to indicate the visually perceived

direction of space. In using such a visual target, "influences" are being studied. Their threshold of effect, i. e., the threshold for perception of the oculogravic illusion under ideal conditions, is a change in direction of the gravito-inertial horizontal of approximately 1.5° (9).

PROCEDURE

SUBJECTS

Four naval aviators and four deaf persons with bilateral labyrinthine defects participated. The four L-D subjects were in good general health; their significant clinical findings are summarized in Table I. All had suffered from meningitis in childhood, one at pre-school age. Their otolith function was determined by means of ocular counterrolling. The counterrolling index (CI) is defined as one-half the sum of the maximum rightward and leftward ocular counterroll when the subject is tilted 25° , 50° , and 75° from the upright. Typical values for normal and L-D subjects do not overlap (10). The L-D subjects were thoroughly familiar with all aspects of the experiment except those dealing with centrifugation under water.

The aviators, 26 to 32 years of age, were in excellent health and performance had met the stringent medical requirements for duty involving flying. None had a history of middle ear disease. Routine hearing and caloric tests revealed no significant abnormality. Their counterrolling indices, obtained at 50-degree maximal tilt, ranged from 241 to 434. All were experienced in taking tests of many kinds, but none was familiar with the procedures in this experiment.

APPARATUS

The heavy duty centrifuge at General Dynamics Astronautics (San Diego, Calif.) was modified for our purpose. It was hydraulically driven, with adequate performance characteristics and excellent rotary coaxial connections. A gondola was fabricated that consisted of a cylindrical tank and observer's platform mounted in a trunnion 18.08 feet from the center of rotation (Figure 1). It was equipped with a suitable water heater, closed-circuit television, and voice communication system. By means of a pneumatic piston the whole assembly could be rotated about the trunnion pins through an arc of 45 degrees in a period of thirty seconds with the centrifuge stationary or rotating. Inside the tank a metal seat was fitted to a rail system and could be removed, along with the subject, by means of a hoist. Bolted to the seat was the rear half of a Fiberglas body mold prepared for each subject; the front half was secured by "quick release" metal locks.

A visual test goggle (VTG) was devised which represented a modification of a visual target device used previously (11). On the right side of the device a red Maddox lens illuminated by a collimated light shining through a pinhole aperture produced a line against a dark background; the left side was an opaque eye covering. The lens could be rotated clockwise or counterclockwise about its center by means of a

Table I

Clinical Findings in Four Deaf Subjects With Bilateral Labyrinthine Defects

Subject	Age	Age Onset Meningitis	Cochlear Function* R L	Semicircular Canal Function + R L	Otolith Function Body Tilt +50° +75°
JO	36	7½	NIL NIL	NIL NIL + at 60 sec	126 176
MY	26	8	NIL NIL	NIL NIL	63 82
PE	35	12	NIL NIL	NIL NIL	21 30
ZA	23	3½	+ ≥ 135 db	+ ≥ 130 db	14 36

*Response to white noise up to 160 db.

+Response to irrigation with water at 3°C + 1° for 3 minutes.

**Ocular counterrolling index. (See text.)

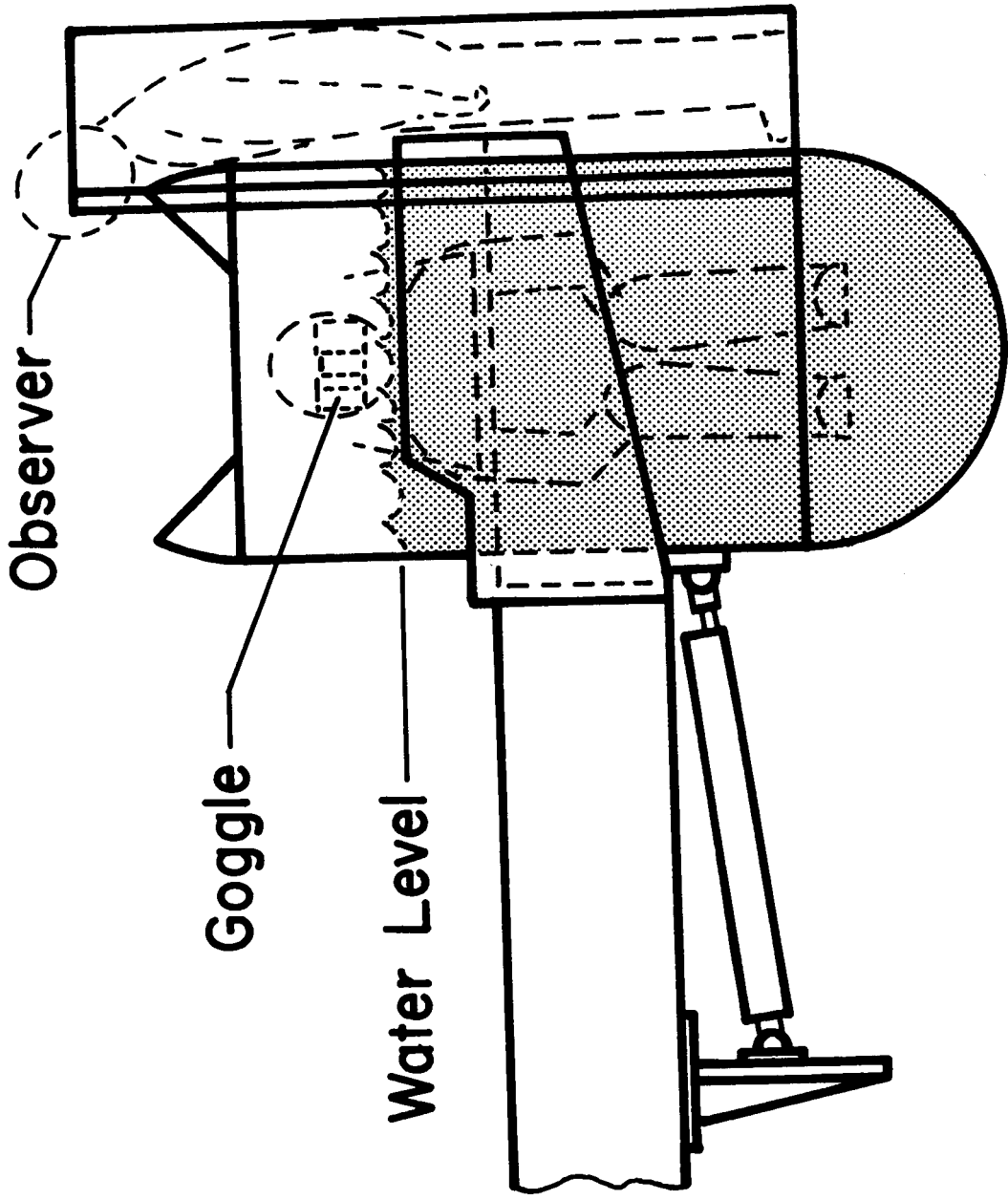


Figure 1

Gondola for Human Centrifugation Under Wet and Dry Conditions

knurled knob. An external counter on the VTG displayed the meridional position of the target line to the nearest 0.1 degree which was relayed via a closed-circuit television system to the control room.

METHOD

The subjects' task, described elsewhere in more detail (6), consisted essentially in setting the target line, on demand, to the horizontal of extrapersonal space. It should be noted that under all wet conditions, the subject's head was out of water and he raised one hand above water level in adjusting the knob on the VTG; in other words, there was not total immersion. Under stationary conditions the experimenter offset (rotated) the target, switched on the light, and the subject set it to the horizontal and signaled completion. The average of five such settings under prerotation conditions was used as the "perceived horizontal" (PH) with which to compare subsequent settings. The centrifuge then was brought up to speeds causing a change in direction of the gravito-inertial horizontal (GIH) of 10° , 20° , or 30° in periods of never less than twenty seconds. The order of exposure involving the three changes in GIH was varied randomly among the eight subjects and among the five test sessions for any given subject. After constant rotation for at least an additional twenty seconds the target light was switched on and the subject was signalled to make the first of the five settings.

Five series of trials, either under "wet" or "dry" conditions, were conducted in the following order: In the first two the subjects wore bathing trunks, and the tank was filled with water up to their necks; this was termed the water or "wet-BT" condition. In the third and fourth series the subjects wore bathing trunks, and the tank was empty; this was referred to as "dry" or "air" conditions. A fifth series under wet conditions, not originally contemplated, required the subjects to wear a foam rubber suit. This was termed the "wet-RS" condition.

Manipulating the force environment is neither easy nor precise if comparison is made with manipulation of visual or auditory environments. In the present experiment the use of individually fitted molds ensured good positioning of the subject in the force environment under all conditions and excellent contact with his support under dry conditions.

RESULTS AND DISCUSSION

The actual settings made by all subjects under all conditions in this experiment are shown in Table II. Positive and negative values indicate, respectively, rotation of the target in the same and opposite direction to that of the gravito-inertial horizontal during positive accelerations.

It is seen in Table II that the settings of the normal subjects demonstrate a consistent and regular dependence on changes in the GIH in three but not in the fourth

Table II

Perception of Oculogravic Illusion in Normal and Labyrinthine-Defective Subjects:
 Mean and Standard Deviation of Five Settings to the Gravitoinertial Horizontal

Conditions	Change in Gravitoinertial Horizontal	Normal Subjects					Labyrinthine-Defective Subjects										
		CU	DI	HU	LI ⁺	JO	MY	PE	ZA								
		\bar{x}	σ	\bar{x}	σ	\bar{x}	σ	\bar{x}	σ	\bar{x}	σ	\bar{x}	σ				
Wet-BT Series I	0	*	1.1	*	0.5	*	1.2	*	1.0	*	1.8	*	0.8	*	5.0	*	1.3
	+10	+3.8	2.9	+10.1	1.9	+9.0	1.7	+6.8	1.7	+1.9	1.2	+3.6	1.7	+8.3	4.8	-4.1	2.7
	+20	+17.3	3.7	+23.8	1.3	+19.8	1.7	+6.5	4.7	+1.5	1.1	+2.0	5.0	+4.1	3.6	+10.5	2.2
	+30	+40.3	4.9	+36.1	1.8	+23.8	1.2	-1.4	6.4	+3.7	1.6	+2.0	3.9	-0.2	3.2	+16.0	3.1
Wet-BT Series II	0	*	1.4	*	0.9	*	0.5	*	0.7	*	0.8	*	1.8	*	1.9	*	0.9
	+10	+8.3	2.0	+14.0	0.8	+9.0	0.8	-13.9	1.5	-1.8	0.8	+2.1	2.8	-13.0	7.7	+8.4	1.4
	+20	+20.6	1.6	+25.4	0.6	+20.8	1.5	-14.8	1.8	-2.8	0.9	+2.2	3.9	-21.0	3.4	+17.3	2.3
	+30	+34.9	4.9	+37.3	1.1	+32.1	2.5	-16.6	1.8	-1.1	1.0	+2.5	1.8	-14.7	3.9	+20.0	1.6
Wet-RS	0	*	2.6	*	0.9	*	1.0	*	1.1	*	0.9	*	1.7	*	2.0	*	2.0
	+10	+15.4	6.0	+8.4	1.2	+6.8	0.6	+4.6	1.6	+3.5	2.0	+1.0	1.9	+6.1	0.9	-2.1	2.4
	+20	+20.2	4.8	+26.4	0.9	+22.8	2.0	+16.4	2.1	+3.6	1.9	+9.1	1.8	+1.8	1.9	+5.1	0.5
	+30	+39.5	5.0	+37.2	0.5	+39.8	1.5	+8.4	2.6	+6.8	1.5	+7.7	4.2	+10.1	1.5	-2.9	2.8
Dry Series I	0	*	1.0	*	0.4	*	0.5	*	0.9	*	2.2	*	1.3	*	3.4	*	1.9
	+10	+19.0	3.8	+12.7	1.0	+6.9	1.2	-21.5	0.8	-1.1	1.2	+5.6	2.0	+8.2	1.6	+7.8	1.4
	+20	+35.3	2.8	+27.7	1.0	+18.9	1.5	-20.1	1.9	0.0	1.4	+5.9	0.3	+6.8	1.3	+27.9	2.8
	+30	+47.5	3.6	+38.7	1.0	+33.3	2.1	-10.3	1.8	+4.4	3.5	+11.7	1.5	+17.4	1.8	+44.4	2.8
Dry Series II	0	*	0.7	*	1.2	*	0.4	*	3.1	*	1.1	*	2.0	*	2.6	*	1.3
	+10	+11.2	5.1	+14.1	1.1	+9.4	1.5	-16.8	2.3	+3.3	1.3	+1.0	2.9	+2.2	1.1	+10.0	2.9
	+20	+36.2	1.8	+25.1	0.6	+21.1	1.7	+16.1	2.9	+6.7	1.0	+9.0	3.4	+11.5	2.0	+22.6	1.9
	+30	+54.9	2.7	+37.9	0.7	+34.7	4.8	+15.5	4.0	+13.7	1.4	+14.7	2.7	+22.7	3.1	+35.4	3.3

* Perceived horizontal.

† Subsequently dropped from the normal group. See text and Figure 2 B.

subject, LI. The bizarre settings in the case of LI were wholly unexpected, requiring individual consideration and necessitating his removal from the normal group.

In Figure 2 A is shown a comparison between the means of the settings made under dry and wet conditions by each normal subject. All subjects demonstrated an increasing tendency toward higher values in their settings for equivalent increases in change of direction of the GIH. This well-known tendency has been termed the "magnitude effect" (6), reflecting the progressively greater increase in magnitude compared with increasing angle of the gravito-inertial force vector, the positive acceleration of the curve depicting magnitude becoming substantial at 15° and rising rapidly after 30° . Only CU demonstrated significant differences between the settings made in dry and wet conditions. In the former he greatly overestimated the angular change in GIH at all three levels, while under wet conditions the overestimation was made only at 30° and the amount was moderate. Thus, it would appear that water immersion reduces the magnitude of the oculogravic illusion by reducing nonotolith sensory inputs. Stated differently, nonotolith sensory inputs contributed significantly to the perception of the illusion by CU but not by DI or HU.

The bizarre settings in the case of LI are depicted in Figure 2 B. When questioned, he stated that he had experienced no difficulty in making the settings and considered his performance satisfactory.

The four L-D subjects manifested such great interindividual and intraindividual variances that they are considered separately. The settings made by JO are depicted in Figure 3 A. The curves representing the values under wet-BT conditions indicate that he did not perceive the illusion; hence, there is no evidence, using this indicator, that he possesses residual otolith function. Under wet-RS conditions the settings suggest that he may have perceived the oculogravic illusion. In the first series of trials under dry conditions the only evidence that JO may have perceived the illusion was the apparent magnitude effect at 30° . The curve representing the second series under dry conditions clearly indicates that JO perceived the illusion. Although this ^{LATTER} later curve shows values far below the expectation for normal subjects, its configuration is typical of one from a normal subject. Among our entire group of L-D subjects (ten), JO is one of two persons whose behavioral responses least resemble those of the normal, although he has the highest counterrolling index (10).

The findings in the case of MY, Figure 3 B, clearly indicate that he perceived the illusion under dry but not wet-BT conditions. His settings made under wet-RS conditions are irregular but suggest that he may have perceived the illusion. These results evince the fact that otolith influence on the illusion was not present but that there was evidence of influences from nonotolith sensory inputs under dry and possibly under wet-RS conditions.

The settings made by PE, Figure 3 C, demonstrate that he readily perceived the illusion under dry conditions. When submerged, PE stated that, at times, he was confused and did not know which way was up; this was reflected in the greater variance in

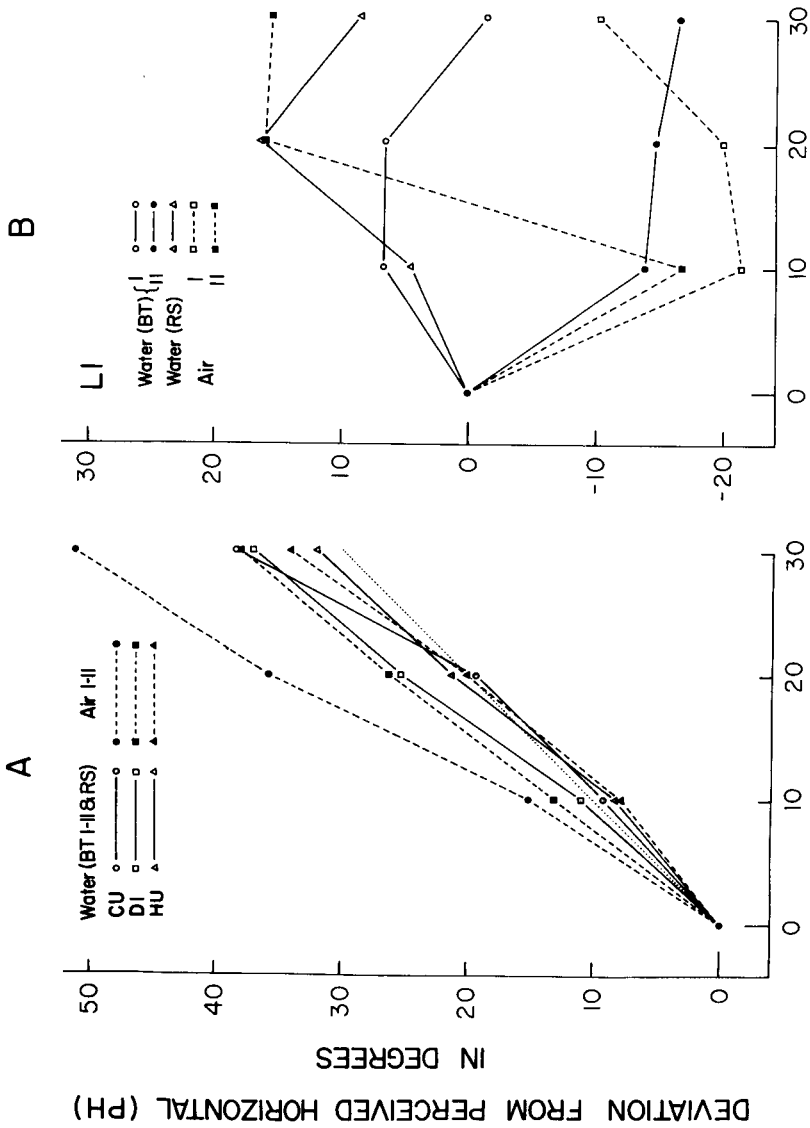


Figure 2

Subjects' Estimates of the Horizontal Plotted Against Changes in the GravitoInertial Horizontal During Centrifugation Under Dry and Water Immersion Conditions

Subjects were exposed to a change in direction of the force vector with reference to themselves in the frontal plane. They indicated the horizontal by rotating a dim line of light in darkness.

A. Settings made by three subjects constituting the normal group. Each point under wet conditions represents the mean of 15 settings in three experimental trials and under dry conditions the mean of 10 settings in two trials.

B. Atypical settings in one subject with normal vestibular functions as indicated by caloric tests and ocular counterrolling.

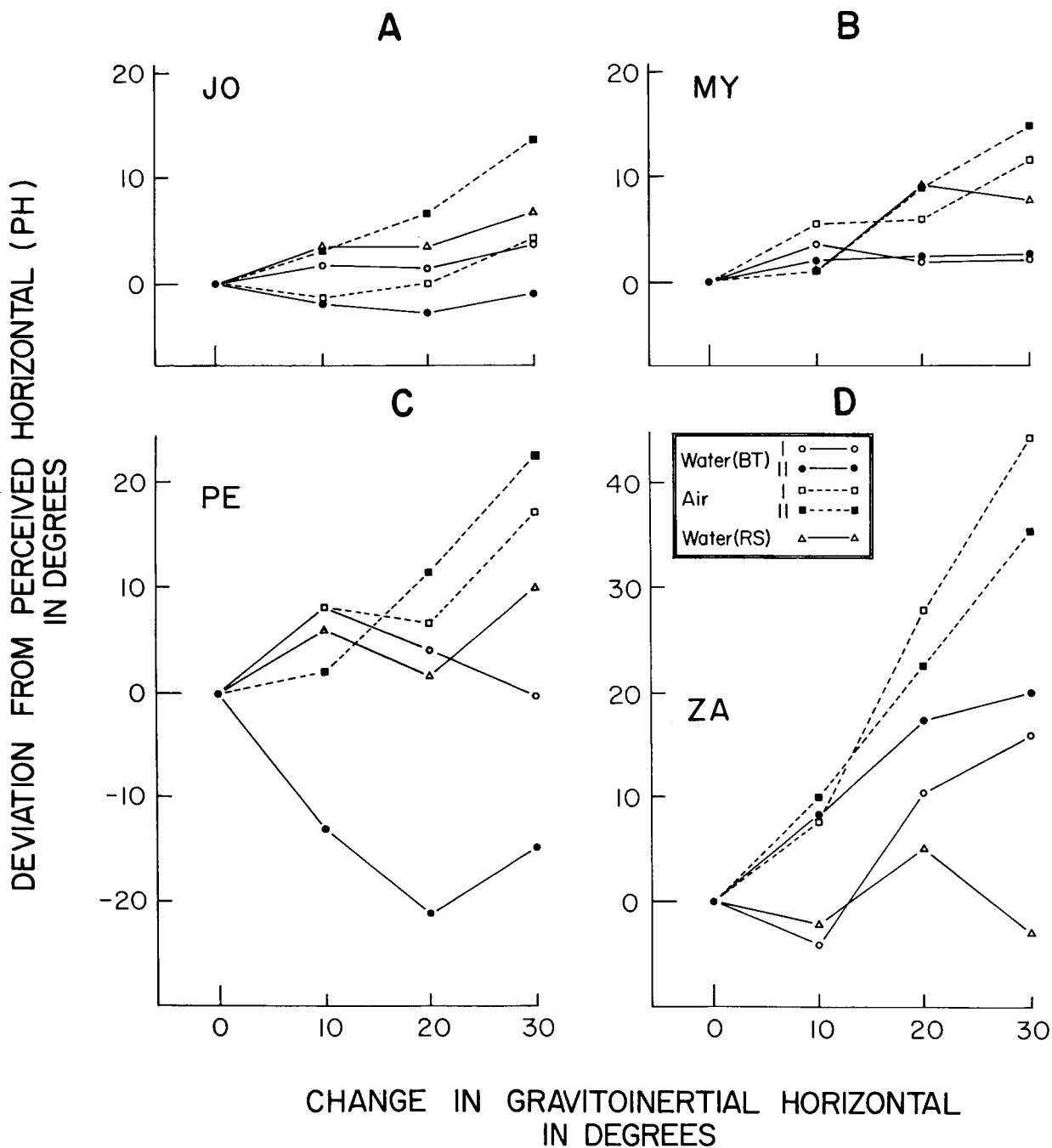


Figure 3

Estimates Made by Four Deaf Subjects With Bilateral Labyrinthine Defects (L-D)

Conditions the same as described for Figure 2. Each point represents the mean of five settings.

his settings than in those of the others. Under wet-BT conditions the curve depicting his first series of trials indicates that the illusion may have been perceived minimally at 10° and 20° but not at 30° , while in the second series his settings were discordant. In the wet-RS series PE probably perceived the illusion at 10° and 30° but not at 20° . These findings under wet conditions suggest a loss or reduction of nonotolith influences on perception of the illusion. The loss of "contact" cues caused disorientation which may have contributed to irregularities in his making the settings.

ZA's settings (Figure 3 D) under dry conditions show that, not only did he perceive the oculogravic illusion, but also his estimates were similar to those of the normal subject CU. Under wet-BT conditions he perceived the illusion but considerably underestimated the change in angle in the gravito-inertial horizontal. Under wet-RS conditions he did not perceive the illusion at 10° and 30° and whether he perceived it at 20° is doubtful. Among all of our L-D subjects, ZA's responses most nearly resemble the normal. This similarity was not apparent initially when he was a participant in our other experiments but seems somehow to have been acquired as a result of practice. That he was the youngest among all the L-Ds at the time he acquired his vestibular defects (3 1/2 years) may have been a factor.

In Figure 4 A are the results of earlier experiments (Pensacola) which were similar in design to that of the dry series in the present study (San Diego). The curves drawn with solid lines compare the mean settings made by nine normal medical students with those made by the normal control subjects (three) used in this experiment, indicating that the latter are fairly representative of a larger group.

The dashed lines in Figure 4 A represent settings made under dry conditions by the four L-D participants in this experiment and those made by the larger group of which they are a part. Comparison between means of the settings made by the entire group and by the group fragment on the previous occasion (Pensacola) indicates that the settings of the small group were substantially below those of the large group. When the settings made by the small L-D group in Pensacola are compared with those made by them in San Diego, higher values in the present study are seen except when the change in the GIH was 10 degrees.

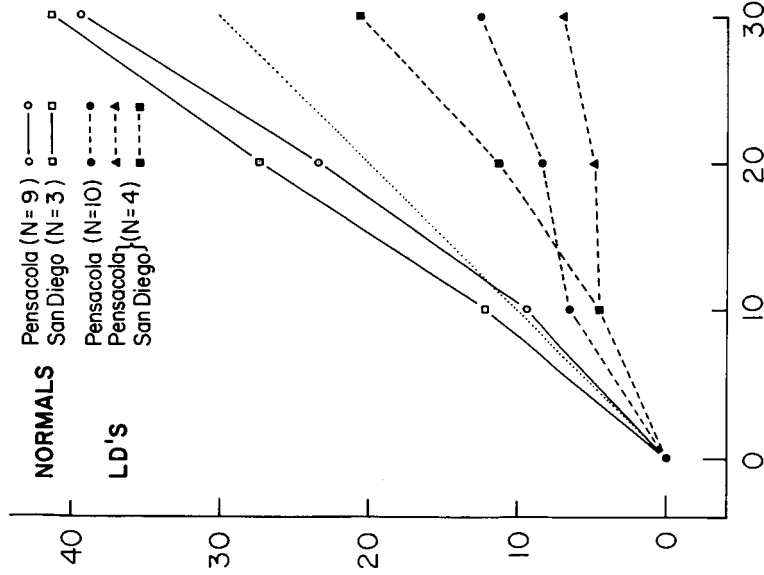
Figure 4 B summarizes all of the findings of the present experiment in terms of group differences between dry and wet conditions in the three normal and four L-D subjects.

GENERAL DISCUSSION

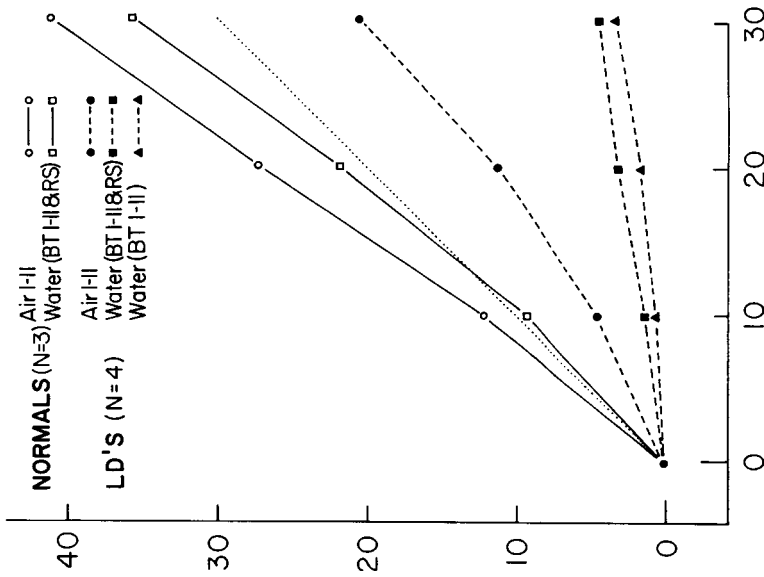
In this experiment an attempt was made to control otolith and nonotolith sensory inputs which might influence the perceived direction of space as indicated by the apparent rotation of a line of light in the dark when the subject was exposed to a change in direction of the gravito-inertial horizontal with respect to himself. With regard to nonotolith receptors, stimulation was greatly reduced, although not perfectly controlled, by immersing the subjects in water up to the neck. Otolith inputs could only be controlled by selecting subjects with or without loss of otolith function; there was no

DEVIATION FROM PERCEIVED HORIZONTAL (PH)
IN DEGREES

A



B



CHANGE IN GRAVITATIONAL HORIZONTAL IN DEGREES

Figure 4

A. Comparisons between settings made under dry conditions in San Diego and Pensacola. Solid lines compare two normal groups composed of different subjects. The four L-D subjects participating at San Diego were part of the larger Pensacola group.

B. Comparison between mean settings made by normal and L-D subjects under wet and dry conditions.

possible way of reducing the effects of gravito-inertial forces on the field receptors in the vestibule. It is important to emphasize that, in every experimental trial, there was full opportunity for any influences having their origin in the otolith organs to become manifested, whereas there was not the same level of assurance that nonotolith inputs were completely excluded. Consequently, the lowest values of the settings obtained in any series of trials under water immersion conditions still registered the maximal otolith influence. These lowest values for the three normal subjects were not far different from their values under dry conditions, with the exception of those of CU where the difference in magnitude under wet and dry conditions was greater than the magnitude of the illusion perceived under dry conditions by the L-D subjects JO and MY and not far below that for PE. Stated differently, the demonstration that nonotolith sensory inputs may or may not contribute to the perception of the oculogravic illusion in normal subjects explains, at least in part, individual variance in its perception among L-D subjects. To the extent that nonotolith contributions (to the illusion) can be demonstrated in normal subjects, they subtract from the need to invoke the phenomenon of "compensation" to account for the perception of the illusion in L-D subjects.

When the L-D subjects were exposed under water immersion conditions, any residual otolith receptors were inescapably stimulated while nonotolith receptor systems were never completely suppressed. Under these conditions the lowest values of the settings in the case of JO and MY indicate that they did not perceive the illusion, and, judged by this test, there was not evidence of residual otolith function. The comparable "lowest values" in the case of PE and ZA indicate that they perceived an illusion, but the likelihood that this was due to residual otolith function is small because the absolute values are small, inconstant, and far below the values under dry conditions.

At all events there is proof that nonotolith sensory inputs were mainly or entirely responsible for the perception of the illusion in L-D subjects and that the individual variance was great. For subject ZA the curves representing settings under dry conditions were similar to the values obtained with normal subjects. Under wet conditions the values were far lower than in the normal controls although still greater than those obtained from L-D subjects. The likelihood that these large nonotolith values in the case of ZA would be matched by the nonotolith values of a normal subject would seem to be small based on our findings; it would require a setting of 70° when the force vector was at 30° . This small likelihood is supported by the fact that, over the years, ZA has shown a strong tendency toward marking higher estimates of the illusion.

The bizarre settings by LI under wet conditions seem to implicate neural connections between the otolith and visual pathways. The small differences between wet and dry conditions suggest that nonotolith sensory inputs were not previously involved. The ranks of the normal and L-D subjects within their groups with respect to their ocular counterrolling index did not have an apparent significance in terms of the perception of the illusion. Among the L-D subjects, JO had the highest value, an index of 176, yet the proof that he had lost all otolith function, as determined by lack of perception

of the illusion under immersion conditions, was good. Moreover, as mentioned earlier, among the entire group of L-D subjects he was one of two whose behavioral responses least resembled the normal. If the relatively large compensatory roll of the eyes in his case had its genesis in the otolith organs, then it measures a residuum of function with no easily demonstrable useful purpose.

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13. ABSTRACT <p>The separate and combined influences of otolith and nonotolith sensory inputs upon perception of the oculogravic illusion were investigated by manipulating the visual and gravito-inertial force environments. By comparing the visually perceived direction of space by four naval aviators and four deaf persons with bilateral labyrinthine defects when dry and when immersed in water up to neck level, the contributions of 1) field force receptors in the vestibular organs and 2) nonvestibular proprioceptors stimulated by external contact support could be differentiated. Under these various conditions it was found that in normal persons, the vestibular contribution is predictable in terms of the direction of the gravito-inertial force vector but that the nonvestibular contribution varies; it may be relatively great or small. In persons with bilateral labyrinthine defects a nonvestibular contribution was always present but there was great individual variance. The significance of the findings in terms of tests measuring the function of the otolith organs is discussed.</p>			

Unclassified

Security Classification

14. KEY WORDS	LINK A		LINK B		LINK C	
	ROLE	WT	ROLE	WT	ROLE	WT
Gravitoinertial force environment						
Labyrinth defects						
Oculogravic illusion						
Perception						
Sensory inputs						
Water immersion						