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THE PROBLEM

1. To measure otolith activity as indicated by ocular counterrolling in response to body tilt within a force field of zero G, one-half G, and standard G.

2. To determine the effect of extralabyrinthine factors upon ocular rotation under these gravitational conditions.

FINDINGS

Six individuals with bilateral labyrinthine defects and seven normal persons served as subjects. Transient periods of subgravity force (0.5G, zero G) were produced by parabolic flight maneuvers in a specially equipped C-131B aircraft which accommodated a tilt chair and accessory apparatus for recording ocular counterrolling response at upright and with body tilt (±25°, ±50°). Testing under 1.0G conditions was accomplished during period of straight and level flight. The labyrinthine-defective (L-D) group revealed results which were qualitatively similar to those from the normal group but markedly reduced in magnitude. This demonstrated that extralabyrinthine factors were not significantly influencing extraocular muscle tonus, and therefore ocular counterrolling served as a valid and sensitive indicator of otolith activity under hypogravic conditions. In the normal subjects zero G induced a physiological deafferation of the otolith organs as indicated by the lack of any significant counterrolling response when the subjects were tilted rightward or leftward up to 50°. When the gravitational force equalled approximately 0.5G, the magnitude of counterrolling fell substantially below the level midway between the zero and Earth standard gravity response. The nonlinear relationship between otolith activity and subgravity force that is implied in these data and confirmed in a follow-up study is discussed.

ACKNOWLEDGMENTS

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The authors, furthermore, acknowledge with pleasure the excellent combined support given by Navy and Air Force personnel. In particular, they wish to cite Mr. Edward L. Ricks, Jr., for his invaluable technical assistance in carrying out the experiment aloft.
INTRODUCTION

Man's normal environment includes the everpresent accelerating force of gravity which is sensed by means of mechanical distortion of various sensory receptors, i.e., the Pacinian corpuscles around joints and tendons, pressure receptors in the area of the body being supported and those sensing shifts in the viscera, and particularly important, the specialized (otolith) organs of the inner ear. In space exploration man is exposed to an environment without gravitational stimulation although equivalent inertial forces would be generated during head or vehicular movement. As in the case of other parameters of the total Earth environment, it has been suggested (4, 11) that important physiological problems might arise from the prolonged absence of normal otolithic stimulation.

During the initial Mercury man-in-space program only limited scientific and medical investigations were possible. Even so, the subjective reports (12) of the Project Mercury astronauts clearly indicated that, at least for missions up to five days' duration and for highly selected individuals, no gross difficulties were encountered which could be readily attributed to the vestibular apparatus. The flight reports (3) of the Russian cosmonauts, on the other hand, have indicated that certain disturbances of probable vestibular origin have occurred and persisted after their return to a normal gravitational condition. Basic individual differences (5, 9), duration of exposure, and amount of stimulation to the vestibular system by free head movements or the maneuvers of the orbiting vehicle could account for the variance in symptoms reported among these space pilots. The question of the effects of weightlessness upon man is therefore still not satisfactorily answered and must await until man is more adequately tested during his future extended space missions that will include increased exposure to angular and linear accelerative forces.

It has fortunately not been necessary to await the availability of time and space for an experiment onboard an orbiting capsule or rotating space laboratory to determine certain characteristics of basic otolithic behavior under weightlessness and other reduced G loadings. The two main procedural requirements for such a quantitative investigation were met by having methods available to 1) measure accurately and specifically the activity of these organs of the inner ear and 2) counteract the Earth's gravitational pull in known amounts and for a duration greater than the response lag of the labyrinthine-oculomotor system. The first requirement was met by precise measurements of the reflex of ocular counterrolling using a recently developed photographic technique; the second, by parabolic flight trajectories in a specially equipped aircraft which was large enough to accommodate a tilt-test apparatus. Under transient hypogravic conditions the counterrolling response was particularly suitable as an indicator of otolith activity since this ocular adjustment to a change in magnitude of force was found to occur much more rapidly than in even the relatively short durations of reduced G loads that were induced by ballistic flight maneuvers. As a result of these factors it was possible for the first time to measure certain basic physiological effects upon the otolith receptors of reducing and completely eliminating its adequate stimulus.
PROCEDURE

SUBJECTS

Six deaf subjects with severe or complete bilateral loss of the semicircular canals plus little or no otolith organ function, as measured by counterrolling (14, 17) and subjective illusions (7, 15, 16), served as the labyrinthine and specifically otolithic defective group. Seven experienced military pilots with normal hearing and normal vestibular organ function as measured by thermal stimulation and counterrolling formed the test group. These normal subjects were also selected on the basis of having normal or less than normal sensitivity to motion sickness as exhibited in tests carried out in the Pensacola Slow Rotation Room. This screening was done in order to avoid the complications of severe symptoms that commonly arise from parabolic flight maneuvers, especially since a dental bite was used by the subject. The labyrinthine-defective (L-D) individuals were ideal subjects in this respect since their loss of vestibular function rendered them completely insensitive to sickness induced by this type of motion.

APPARATUS

The tandem tilting device used in the experiments is portrayed in Figure 1 with the subject and experimenter in position for photographically recording ocular counterrolling. The device consists essentially of two opposing chairs which are fixed to a common base that can be tilted to ±50° by means of a hand crank. On a chest-high metal plate connecting the two chairs, a 35mm camera, electronic flash unit, and fixation light are mounted. Supportive devices were provided to hold in rigid alignment the subject's head and body and to secure him to the chair. The height of the chair was adjustable by an electric motor drive. A bite-board extending from the camera mount fixed the subject's head position relative to the camera. The experimenter was less rigidly held by a padded ring surrounding the chest, plus shoulder and seat belt supports, which allowed him to carry out the photographic recording of eye position. The photographic equipment including the electronic flash and fixation target were identical to that used and described in detail in other studies (14, 17).

The base plate of the tilt device was bolted to the floor slightly aft of midships of a C-131B aircraft. This aircraft was specially equipped with an accelerometer computer system which provided an instrument display for guiding the pilot in flying specific Keplerian trajectories, viz, for inducing zero and 0.5G.

METHOD

The flight maneuver designed to counteract normal gravitational acceleration completely or halfway is portrayed in Figure 2 with a photograph of the aircraft type (C-131B) used. After the initial pull-up and push-over of the aircraft a period of null-G was executed which lasted approximately five seconds. Following this weightless period, there was a rather rapid (about one second) transition into the period of 0.5G which was maintained about six seconds before the terminal pull-up state of the maneuver was
Figure 1

Diagram of Apparatus with Subject and Experimenter in Position for Photographically Recording Ocular Counterrolling
Figure 2

Diagram of the Parabolic Flight Maneuver Designed to Provide Periods of Zero and One-Half G Force Using the C-131B Type Aircraft
made. Usually, but not always, two such maneuvers were flown in succession. The computer guidance system was always used by the pilots in performing this maneuver, but since no accelerometer tracings were made during the maneuvers it has been assumed that the pilot error did not exceed \( \pm 0.05G \) on any given maneuver. Based upon the previous records of parabolic flights of this airborne laboratory this assumption appears reasonable, particularly when highly trained and experienced pilots control the maneuvers as in this study.

When airborne the subject and experimenter were seated facing each other in the tilting device and the supportive straps secured. The dental bite was adjusted so that when the subject was fixating the target provided, his right eye appeared precisely centered within the field of view of the camera. The electronic flash unit was angled inward and upward close to the outer canthus of the subject's right eye; his left eye was covered with an opaque patch. Several minutes before the test, one drop of pilocarpine hydrochloride 1% was instilled in the right eye of each subject to reduce the size and physiological oscillations of his pupil. The use of the miotic drug was found to be particularly important in these experiments since it was found that the stimulation associated with the parabolic flight maneuver produced abnormally great amounts of fluctuation of the pupil size. The photographic recording of a smaller and relatively constant pupil size had been found previously under terrestrial conditions to increase the ease and speed with which the test and standard film images of natural iris landmarks could be superimposed and aligned, although the accuracy (within \( \pm 5 \) minutes of arc) was not appreciably improved by this procedure. Details of the photographic method of precisely measuring cycloversional eye movement have been described elsewhere (14). Throughout the period of experimentation, particularly after each change in body tilt, the experimenter verified the correctness of the focus and the subject's fixation as indicated on the ground-glass screen of the camera.

Just prior (about thirty seconds) to the start of each trajectory maneuver the following procedure was followed: The tandem tilt device was hand-cranked slowly to one of five body positions with respect to the gravitational vertical in the following order: 0°, -50°, +25°, -25°, +50°. Each angle of inclination was maintained throughout two consecutive trajectories; then the subject was returned to the upright position before proceeding to the next tilt position. A single photograph of the eye was taken at the end of the zero and the 0.5G period of each Keplerian trajectory. A total of ten parabolas constituted a single test for one subject. In most cases the subject was retested in the aircraft by the same procedure. The same test under normal gravitational conditions was conducted during straight and level flight or on the ground, and as a result, unlike the hypogravity procedure, a period of increased G did not immediately precede the 1.0G test period.

RESULTS

The data are summarized graphically in Figure 3. Mean counterrolling values in minutes of arc as a function of body tilt up to \( \pm 50 \) degrees are shown in the Figure for both normal and labyrinthine-defective (L-D) groups of subject tested under the three
Counterrolling as a Function of Magnitude of Gravitational Force (0 G, 1/2 G, 1 G) and Body Position with Respect to Direction of Force in Normal and Labyrinth-Defective Subjects

NORMAL SUBJECTS

L-D SUBJECTS

Figure 3
gravitational conditions (zero G, 0.5G, 1.0G). The curves of each subject were similar to those of their respective group but were less regular in form. This result was expected since characteristically (2, 6, 8, 14, 17) a certain amount of variability in the torsional position of the eye is manifested which appears to be independent of body position. If a sufficient number of recordings are taken on a given individual, the occasional, large random fluctuations do not significantly bias the mean values. Under terrestrial conditions these extraordinary rotary movements appear to be spontaneous but aloft they could also be due to slight vibrations and translational motion that sometimes occur during a maneuver. Since a strict limitation was placed upon the number of parabolas to be flown for this experiment and therefore the number of recordings, the choice was made to use the combined test results of several normal and of a comparable number of L-D subjects rather than to base the study on more expansive data obtained from only one or two persons of each group. This choice had the effect of minimizing intra- and interindividual differences in counterrolling response.

The L-D group responded in a qualitatively similar fashion to the normal group (Figure 3), i.e., decreased counterrolling with reduction in gravitational force, but quantitatively intergroup differences were great. Since the L-D group was composed of individuals with little or no residual otolith function even at the 1.0G level, an appreciable quantitative effect upon otolith activity of reducing the G loading could not be expected and was not found. These results are important in that they demonstrate the absence of significant influence of tonic innervation to the extraocular muscles from extralabyrinthine sources and, furthermore, they allow the assumption that counterrolling under conditions of this experiment is a valid indicator of otolithic activity in hypogravic states.

The normal group of subjects when exposed to complete and partial (0.5G) weightlessness manifested marked reduction in amplitude of counterrolling. During the transient period of zero G the data indicate that the otolith organs were deafferentated to such an extent that no significant counterrolling occurred in tilting these subjects rightward or leftward up to 50°. When the gravitational force equalled approximately half of Earth standard, the characteristic counterrolling response appeared, but its value was much less than at 1.0G and, in fact, below that which would fall midway between the values of zero and the normal magnitude. These data suggest that the relationship between otolith activity and G force is nonlinear at least between zero and 1.0G. On the basis of this finding a follow-up study (19) was made using hypogravic levels which were continuously and accurately recorded during the maneuvers. The results of the second study corroborate the nonlinear function over the entire range from zero to normal G, yet indicate a Fechnerian logarithmic function (18, 19) from approximately 0.6G to 1.0G and probably beyond.
DISCUSSION

The results of this initial study of hypogravic effects upon compensatory counter-rolling response indicate that 1) the magnitude of counterrolling to a given head tilt can be a valid and specific indication of otolith activity under hypogravic as well as normal (14, 17) and hypergravic conditions (1, 22); 2) the time period of the counter-rolling in response to a change in magnitude of force occurs well within the hypogravic phase of the trajectory flight pattern used (approximately five seconds' duration); 3) essentially no counterrolling occurs in weightlessness; 4) a nonlinear relationship exists between otolith activity and G force (zero to normal); specifically, halving the normal gravitational load yields substantially less than one-half the normal counterrolling response.

Several studies (1, 20, 22) have been concerned with the change in otolith activity with increased G. These in general have shown that normally the counterrolling response is stimulus bound. An increase in gravitoinertial force produces a corresponding and an essentially linear (1) increase in counterrolling response. By extrapolation (1) or by considering only the lateral component of the acting force (22), otolithic activity was predicted to be a linear function of the hypogravic force. These approaches are vitiated by the nonlinear character of the response found in the present study as well as in the later one (19) under actual hypogravic conditions for which the direction of force was held constant with respect to the otolithic receptors. The compliance with and violation of Fechner's law by the counterrolling versus log G force is discussed in detail in another report (18).

Success in using counterrolling in this study depended to a great extent upon the speed with which the vestibulo-ocular adjustments to new levels of gravitational force occurred since the transient hypogravic periods that were available for this experiment were relatively short. The results would seem to indicate that the lag period in the otolith-oculomotor system responsible for counterrolling movements was not violated and, in fact, probably is very much less than the time actually allowed after reaching the hypogravic phase of the maneuver before recordings of eye position were made. This assumption is strengthened by anatomical data (21) which demonstrate the existence of simple bisynaptic neural pathways linking the vestibular organs (cristae) with the oculomotor system. We have recently been collecting data in an attempt to determine the duration of lag in this response.

In weightlessness the otolith system was deafferentated to the extent that it failed to respond significantly to tilting as manifested by ocular counterrolling. This evidence of physiological deafferentation produced by the no-gravity condition should not be regarded as equivalent to total deafferentation that, for example, would result from transection or complete functional loss from disease of the VIIIth nerve, even though a physiological mimics a pathological loss of otolith action as indicated by counterrolling. Exposed to weightlessness the normal subject unlike the totally labyrinthine-defective person possesses an otolith system which would still be potentially active, poised to sense inertial forces, and thus capable of bringing its influence to bear upon the behavior of the space traveler. While the data of the present study may be of practical
rvolve in space flight problems, they also provide for the first time information concern-
ing the basic physiological behavior of the otolith organ in man when the adequate
stimulus is reduced and eliminated. Since the follow-up study provides a more detailed
description of the stimulus-response relationship in hypogravic levels, a discussion of
basic function of the otolith organs from a biological point of view is reserved for that
report.

It would appear from the data collected during weightlessness that if any change
occurs in the resting discharge of the otolith apparatus under at least transient exposure
and other conditions of the test, it does not appreciably affect counterrolling. Ad-
ditional data on man, however, will be required to investigate specifically the possi-
bility of unusual spontaneous otolithic nerve discharges, as found in the frog (10, 13),
during a ballistic weightless flight. It should also be considered that the otolithic
gravireceptor organ may be subject to some form of adaptation in response to the lack
of normal stimulation. It is conceivable that, if the exposure is sufficiently long, its
sensitivity may increase as do to the photoreceptors of the eye deprived of photic
stimulation. If this occurs, the otolith apparatus would become more sensitive to head
and space vehicle movements, and disproportionate responses to these stimuli could be
expected. The overload sustained on re-entry into the Earth’s atmosphere, for example,
might become a special problem.

Carefully controlled experiments yielding quantitative data over more extended
orbital periods are required to settle whether man’s behavior will be influenced by
abnormal vestibular stimulation occurring during prolonged weightless periods. If a
defense against weightlessness is found to be necessary, it has been proposed that the
vehicle be rotated to produce sufficient amounts of artificial gravity. The level of
centripetal force that would have to be generated for adequate otolithic stimulation
would depend upon the otolith activity versus G force relationship. As indicated in
this study, the relatively large drop in magnitude of counterrolling with one-half re-
duction in G force suggests that greater forces will be required for a given level of
otolith activity than if a linear relationship existed.
REFERENCES


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Otolith organs
Vestibular apparatus
Weightlessness
Subgravity forces - physiological effects
Counterrolling
Ocular movement
Space travel - vestibular effects