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The Labyrinthine Posture Reflex (Righting Reflex) in the Cat during Weightlessness

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ALTHOUGH it is generally accepted that linear acceleration is the physical stimulus for the otolith organ, its function during periods of increased and decreased gravity has not been clarified.[3,8,15] In 1952, Slater[16] discussed the probable response of the otoliths to the weightless condition by drawing some tentative conclusion from morphologic data and electrophysiologic experiments made by Adrian[1] and Lowenstein[9], and by Lowenstein and Roberts.[10] The experiments in this report deal with the otolith functions of the cat. The findings are thought to throw some light on the vestibular processes during subgravity and zero-gravity.

The means of sensing the effect of gravity, which is actually a linear accelerative force, is provided by a set of mechanically affected organs of the inner ear known as otolith organs. They are located in the utricle and the saccule which are filled with endolymph and contain the very specialized structure of macula and otoliths. The otolith apparatus consists of a plaque of hair cells covered with a mucus layer, which carries a large number of very small particles of calcium carbonate, the so-called otoliths. When the head is in an upright position, the macula of the utricle lies approximately in a horizontal plane, that of the saccule in a vertical plane. The planes of the two saccular maculas form an angle opening forward and downward.

The probable response of this organ to weightlessness has been discussed elsewhere.[6,8] Because of their physical characteristics, the otoliths are "gravireceptors." They can move within the macula under the pull of their own weight, or in response to accelerative forces and their inertial effects. This movement bends or pulls, or shears the epithelial hairs, thus distorting the

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sensory cells and producing a stimulus. Depending upon the position of the head in the state of rest, the end organs of the utricle and saccule are affected in a certain way. The forces of gravity and acceleration, caused by voluntary and involuntary motion, are also conveyed to the brain in the form of impulses traveling along the vestibular nerve. These impulses are all of the same intensity but they vary in frequency depending upon the direction and mode of acceleration.

The weight or movement of an otolith distorts the cell or cells closest to it. Minimal stimulation occurs when the maculas are horizontal and the otoliths rest on the hair cells; maximal stimulation is obtained when the otoliths hang from the cells or, with normal head position, when they are pushed upward. Now, in the weightless state, the otoliths are deprived of their weight, too, and this should result in a minute change of the cell structure. This then will bring forth an alteration of the impulse rate of the vestibular nerve.

It is the opinion of many investigators that the force of gravity exerts the most fundamental influence upon our spatial orientation.[2,7,11,14] However, there is no need for the organism to obtain a conscious knowledge of the direction and amount of gravity. The basic need is for a mechanism that adapts the body automatically to their effects. This is done by means of the so-called postural reflexes which are thought to serve to maintain or restore the "normal" position and posture of the body. This group of reflexes, which includes the static and statokinetic reflexes of the body, reveals that gravity has an essential effect upon animal life. This effect is very difficult to assess but relatively easy to demonstrate.

One of the best-known reflexes of this sort is the postural righting reflex of the cat. Since the pioneer work of Magnus,[12,13] this reflex has been studied under various conditions. If a cat is first held in any other than normal position and then dropped, the animal immediately turns into the normal posture so that it always lands on its feet. A similar reaction occurs when the cat, lying on its back with its head held in an almost normal position, is moved vertically downward. However, this reflex does not seem to function when the cat is moved upward. Adrian's experiment on the cat has shown that changes in head position were associated with an alteration of the impulse rate, which was caused either by the act of tilting or by the angle of tilt as such. He found that pressure toward the macula did not increase the stimulus. This may account for the lack of postural righting reflex during movement in the upward direction.

From a practical viewpoint the question was asked how the righting reflex of the cat would work during subgravity and zero-gravity. Would the cat turn around when held upside down or would it stay in this position? Is there a time factor involved which may indicate adjustment and adaptation? How will other cues—for instance, visual orientation—affect the functioning of the reflex? The answers to these questions were sought not only to satisfy our own curiosity, but to clarify the role of the otolith organ during weightlessness.

METHOD

Eight cats were used in the experiment; all were healthy young animals born in the School of Aviation Medicine cat and dog kennels, and raised from three different litters. Four of the kittens were about three weeks old when used in the experiment; two of the kittens were about eight weeks, and two young cats were about twelve weeks of age. The experiments were conducted as follows:

Each of the three sets of experimental animals first was taken into the School of Aviation Medicine film studio and placed on a table. The animals were then lifted up individually and held upside-down in a long stretched position. They were released unexpectedly and dropped from an altitude of about 20 inches. When the three-week-old kittens were employed, the table was covered with a rubber pad. In some of these experiments the animals were blindfolded to exclude visual orientation. The behavior of the animals was recorded on film. This experiment was repeated several times so that its result could be considered conclusive.

The animals were then taken into the air and exposed to short periods of weightlessness. Virtual weightlessness, or a state of reduced gravity, was produced by flying a jet type aircraft (T-33 or F-94) along a Keplerian trajectory.[4,5] The ascent to 20,000 feet was made at a rate of climb of 2,000 feet per minute. The cabin pressure at that altitude was about 9.5 psi, which is equivalent of an altitude of approximately 12,000 feet. The pilot of the craft (H.D.S.) flew the ascending arc of the parabola at full throttle and the descending part with about 75 per cent rpm in order to obtain weightlessness for about 25 to 35 seconds. Absolute weightlessness or zero-gravity occurred for only a few seconds during each of these maneuvers due to the small accelerative forces present. These unavoidable accelerations were of an estimated magnitude of about 0.03 to 0.05 G. The weightless state was indicated and controlled by the conventional G-meter installed in all fighter type aircraft. Before entering into the parabola and during recovery from the dive, accelerations of 1.25 G were not to be exceeded because it was observed during the first flight that the cats were extremely sensitive to an increase of acceleration. Five or six parabolas were performed during each experimental flight.

The small kittens were taken along in pairs and kept in a container until the working altitude was reached. The older animals were used one at a time and carried on the arm of the experimenter in the aircraft (Fig. 1). The cats were turned upside-down and released after periods of 1, 5, 10, 15, 20 and 25 seconds after entering the weightless state. The behavior of the animals was studied under both blindfold and nonblindfold conditions and recorded on film.

Motion pictures were made using a 16 mm. Filmo camera, model 70 H, with a 13 mm. lens, f = 1.5, and a film speed of 24 frames per second. Kodachrome film with a Kodak No. 83 filter, and one Eastman Panchro-

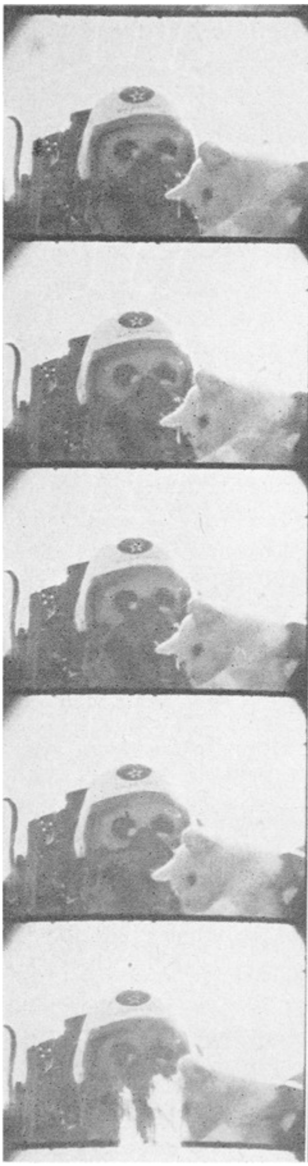

Fig. 1. Photograph of cat before the experiment in the T-33 aircraft.

Fig. 2. Prompt righting reflex of cat immediately upon entering the weightless condition.

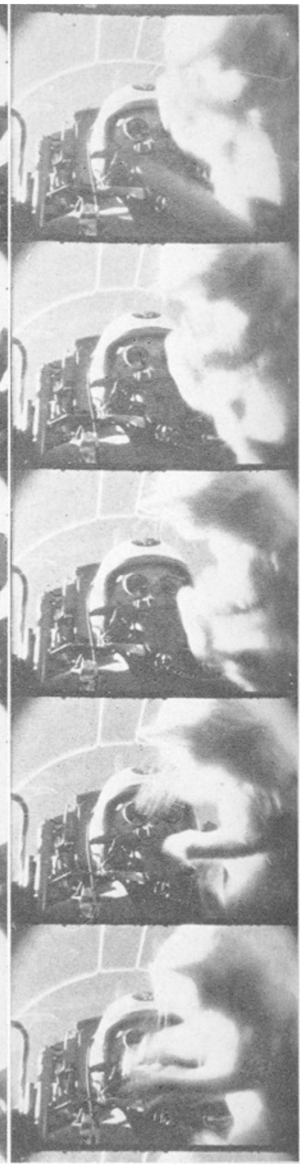

Fig. 3. Delayed reflex: the cat turns slowly after a certain delay.

Fig. 4. Postural righting reflex fails completely; the cat floats in an inverted position.

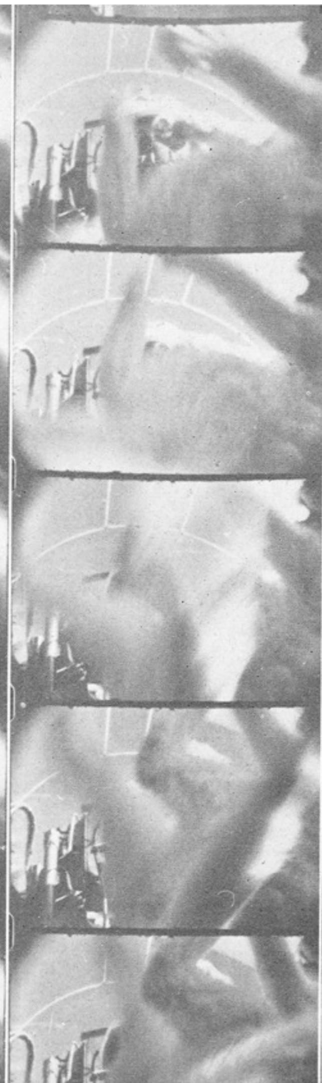

Fig. 5. Disturbed reflex associated with slight tumbling.

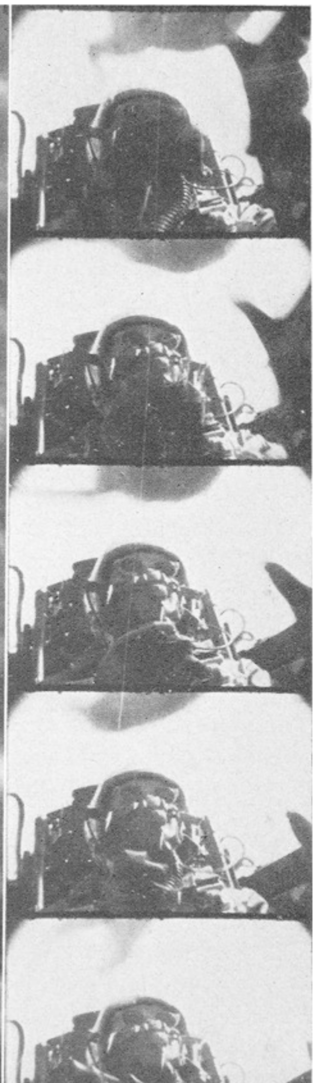

Fig. 6. No righting reflex. The animal floats slowly upwards due to acceleration in this direction (so-called "negative G").

matic black-and-white film for illustration purposes, was used. The camera was attached to the airframe on top of the instrument panel between front and rear seat of the T-33 aircraft, and focused at a distance of about 100 cm. In the F-94 aircraft the camera was installed below the rear panel and focused slightly upward at a distance of about 75 cm. It was switched on shortly before each parabola and stopped at the end of it. Some illustrations of the results are given in Figures 2, 3, 4, 5 and 6. Unfortunately, the animal is only partly visible in these pictures because of the small field size and the limited elevation of the camera.

The evaluation of the films consisted of an analysis of the moving pictures as well as the stills by describing briefly the behavior of the animals with regard to promptness or delay of the righting reflex under the conditions of reduced gravity. To this end, the films were run at normal speed and additional checks of each scene of exposure of the cat were made by looking at each individual frame when the film was moved by hand. The observations were then tabulated; the reflex response was related to the length of time spent in the weightless condition. Thus, some numerical results were obtained which must be considered for what they are worth.

RESULTS

Even before the experiments were started it was observed that the four younger animals fell straight down when they were dropped on the ground. We found that the postural righting reflex of the cat develops during the fourth till sixth week after birth. Hence, in describing the behavior of our animals we must distinguish between (1) the three-week-old kittens whose postural righting reflex was not developed, and (2) the eight and twelve-week-old ones whose reflex was well established. We can summarize the behavior of the first group very briefly.

The motion pictures of the younger kittens made on the ground and in the air show very clearly that in not a single case did the animals turn around after they were released. They fell or floated in an inverted position under normal gravitational and under subgravitational conditions, respectively. Since the righting reflex was not developed, blindfolding was meaningless, of course. The responses of this group of animals were not tabulated due to the uniformity of behavior.

The behavior of the older animals, on the other hand, showed considerable differences under the various experimental conditions. On the ground, the reflex functioned promptly and so unanimously that the results were not tabulated either. The responses of the four older animals upon exposure to weightlessness, however, were tabulated and are given in Tables I and II. In the first table, the behavior of the two eight-week-old kittens is described. As can be seen in this table, the animals turned back into their normal posture at the first exposure to weightlessness. This reflex seems to be delayed or disturbed in the later trials. Table II contains the description of the two oldest animals. Again, the general impression is that the cats turn

TABLE I. BEHAVIOR OF THE ANIMAL WHEN EXPOSED IN AN UPSIDE-DOWN POSITION TO SHORT PERIODS OF WEIGHTLESSNESS AT VARIOUS INTERVALS AFTER THE SUBGRAVITY STATE BEGINS

Animal	Parabola	No. of Exposure	Condition	Time	Response
Grey kitten A	1	1	Eyes open	Immed.	Prompt righting reflex
		2	Eyes open	5	Delayed righting reflex
		3	Eyes open	10	No righting but tumbling due to wild motor response
	2	1	Eyes open Normal position	Immed.	Floating upward and delayed turning upside-down due to accelerations acting in the opposite direction (negative g's).
	3	1	Eyes open	10	No righting
		2	Eyes open	15	No righting and floating upside-down for a few seconds
		3	Eyes open	20	No righting reflex
		4	Eyes open	25	No righting reflex
	4	1	Hood	10	No righting reflex
		2	Hood	15	No righting reflex
		3	Eyes open	20	No righting but tumbling
		4	Eyes open	25	No righting but floating
		5 (?)	Eyes open	30 (?)	No righting, floating upward
	5	1	Hood	5	No righting, floating upward
		2	Hood	10	Righting, tumbling
		3	Hood	15	No righting; floating upward and tumbling
Grey kitten B	1	1	Eyes open	Immed.	Righting reflex somewhat delayed
		2	Eyes open	5	No righting, floating upward
	2	1	Hood	Immed.	Righting, floating upward, turning again upside-down
		2	Hood	10	No righting, floats upward and downward upside-down
	3	1	Eyes open	5	Righting and turning about longitudinal axis
		2	Eyes open	10	Delayed righting
		3	Eyes open	15	Righting reflex
	4	1	Hood	Immed.	Righting
		2	Hood	5	No righting but tumbling into vertical, then normal
		3	Hood	10	Delayed reflex
		4	Eyes open	20	Floats downward, then delayed reflex
	5	1	Hood	5	Floats upward, tumbling
		2	Hood	10	Floats upward, tumbling and turning in normal position
	6	1	Eyes open	10	Righting
		2	Eyes open	15	Delayed righting and tumbling

into the normal position during the first exposures; but that the reflex is delayed or does not occur at all toward the end of the experiments.

To obtain a clearer picture of the occurrence and mode of the righting reflex, particularly in regard to the time factor, the responses of the four older animals were tabulated (Table III). In this table, the beginning of the exposure of the cat to be weightless condition is indicated by time values from one to twenty-five seconds, which are approximations because of the awkward situations which sometimes occurred when the animal refused to be released or clung to a foothold in the cockpit. In column 2, the given number of parabolas varies from five to six for the respective animal. Column 3 is subdivided in responses obtained under blindfold and nonblindfold conditions; the first number being smaller because the animal succeeded in stripping off the hood on several occasions.

An inspection of Table III confirms the observations made in the aircraft and the general impression obtained from Tables I and II. Upon release immediately, or not later than about 5 seconds, the animal turned into the

TABLE II. BEHAVIOR OF THE ANIMAL WHEN EXPOSED TO SHORT PERIODS OF WEIGHTLESSNESS IN AN UPSIDE-DOWN POSITION AT VARIOUS INTERVALS AFTER THE SUBGRAVITY STATE BEGINS

Animal	Parabola	No. of Exposure	Condition	Time	Response
Black and white cat	1	1	Hood	5	Prompt righting reflex
		2	Hood	10	Prompt righting reflex
	2	1	Hood	5	Prompt righting reflex
		2	Hood	10	Normal position, turning upside-down due to acceleration in opposite direction (negative g's)
		3	Hood	20	Delayed righting reflex and turning
	3	1	Eyes open	10	No turning, floating upward, grasps top string
	4	1	Hood	Immed.	Righting reflex
		2	Hood	5	Righting reflex
	5	1	Hood	Immed.	Righting reflex
		2	Hood	5	Righting reflex
		3	Hood	10	Floating, no reflex
		4	Hood	15	No righting reflex
		5	Hood	20	No righting reflex
	6	1	Hood	Immed.	Righting reflex
		2	Hood	5	Floating upward, no turning, grasps top string
White cat	1	1	Eyes open	5	Floating upward, delayed righting reflex
	2	1	Eyes open	5	Prompt righting reflex
		2	Eyes open	10	Prompt righting reflex
		3	Eyes open	15	Prompt righting reflex
	3	1	Eyes open	5	Righting reflex
		2	Eyes open	10	Floating upward, no righting
		3	Eyes open	15	Floating upward, tumbling but no righting reflex
	4	1	Eyes open	5	Floating upward, no righting reflex
		2	Eyes open	10	Floating upward, no righting reflex
		3	Eyes open	15	Floating briefly, no righting reflex
	5	1	Eyes open	Immed.	Righting reflex
		2	Eyes open	5	Delayed righting reflex
		3	Eyes open	15	Righting reflex, slightly delayed

normal position eleven times when visual cues were available, and ten times when they were blindfolded. After a latency of about 15 or 20 seconds, the righting reflex occurred or failed about the same number of times when the cats were not blindfolded. When the hood was used, the same ratio of responses was already obtained after 10 seconds. From this time on the reflex failed in five cases. With eyes open no righting response was observed among the few cases exposed after a period of twenty-five seconds. By and large, we found that the postural righting reflex ceased to function after a stay of more than twenty seconds in the weightless state; and that visual cues did not seem to affect the reflex to a marked degree.

DISCUSSION

Magnus[12] has demonstrated that normal animals acquire and maintain posture by various static and statokinetic reactions. In our experiments, both types of reflexes will also be activated because the cat normally does not like to lie on its back, nor to be moved in this position in a vertical direction. When a cat is held back downward and then allowed to fall, the otolith reflex acting upon the neck muscles turns the head of the animal rapidly into its normal position. The contraction of the neck muscles, which rotate the head, activates the myotatic neck reflexes which affect the muscles of the body by turning the thorax and then the pelvis into the normal posture. This reaction can be seen in pictures

TABLE III. OCCURRENCE OF RIGHTING REFLEX AT VARIOUS INTERVALS AFTER THE SUB- AND ZERO-GRAVITY STATES BEGIN

Animal	Parabola	Beginning of Exposure of Animal in Seconds: With Eyes Open						With Hood					
		1	5	10	15	20	25	1	5	10	15	20	25
Grey kitten A	1	+	±	−									
	2	x*											
	3			−	−	−	−						
	4					−	−			−	−	−	
	5								−	+	−		
Grey kitten B	1	+	−										
	2							+		−			
	3	+	+	+									
	4				+	+		+	−				
	5								−	±			
	6			+	±								
Black and white cat	1							+	+				
	2							+	x*	±			
	3			−									
	4							+	+				
	5							+	+	−	−	−	
	6							+	−				
White cat	1	±											
	2	+	+	+									
	3	+	−	−									
	4		−	−	−								
	5	+	±	±									
Righting reflex (+)		6	2	3	1	1		7	3	1			
Delayed reflex (±)		1	2	1	1					2			
No righting reflex (−)			3	5	2	2	2		4	3	3	2	

*Animal was held in normal position and an acceleration opposite to the direction and stronger than the force of gravity was employed.

of a promptly functioning righting reflex (Fig. 2).

Although we have enough evidence to assume that the postural righting reflex was generally produced by an otolith response, this reflex can be reinforced by exteroceptic or visceral stimulation. Because the animal was symmetrically supported in our experiments, reinforcement of the postural righting reflex by the so-called "body righting reflex" can be neglected. However, there is the possibility of a certain reinforcement through the loss of touch and grip pressure during the release of the animal. This may account for some of the reflex actions in an advanced state of weightlessness.

Because visual cues play a prominent role for the orientation of the cat, the occurrence of the so-called "optical righting reflex" was controlled by means of the hood. This reflex was observed in those cases in which the animal turned or stretched itself in order to grasp the top or the side of the canopy. There is some evidence from Table III that blindfolding changed the reflex pattern but slightly.

Naturally, we cannot expect the righting reflex to occur before it has been developed. After this was accomplished, the reflex should fail only if there is a complete lack of stimulation. During the transition from the normal state of gravity into subgravity, the gravireceptors are stimulated.

This may have caused the righting response of the animal when released immediately upon entering the weightless state. On the other hand, if the animal was in this state for a certain period of time and was then released, the reflex was delayed or failed. It should have failed completely if true weightlessness were obtained. Hence, it seems that the righting reactions observed toward the end of the parabola were caused by the slight changes in acceleration, which unfortunately occurred during most of our weightless periods.

The response pattern obtained in our experiments must be attributed to the changed stimulus pattern of discrepant gravitational, visual and tactile cues which caused spatial disorientation. This may be the main reason why the animal became so confused and fought against being exposed to the weightless condition, and why the postural reflex was disturbed. These experiments also show that the otoliths most probably are not stimulated by acceleration as such, but by the changes of acceleration. In the weightless condition of our experiment the animal is subjected to the constant acceleration of gravity, but this force does not seem to activate the postural righting reflex. Physiologically, this is understandable because it is the initial change of the physical state of the otoliths that produces an inertial effect to elicit the sensory stimulus indicating the alteration of the physical condition. Thereafter, the otoliths "move along" with the maculae, and only the alteration of this condition by deceleration brings forth the inertial effects that will stimulate the gravireceptors again.

How powerful this stimulation can be was demonstrated by the two exposures of the cats to accelerations producing centrifugal forces different from the direction and stronger than the force of gravity. The black and white cat tended to turn in the apparent direction of gravity, but the reflex was delayed and incomplete due to the almost normal position of the head. The grey kitten turned immediately from the normal position upward and landed in an inverted position at the top of the canopy. In this case, the physiologic condition was very similar to that when the kitten was dropped in the upside-down position. Because the posture of the head was inverted from one condition to the other, the inertial effect on the otoliths is the same when the direction of acceleration is reversed. The inverted righting response occurred although visual cues were available.

SUMMARY AND CONCLUSIONS

Experiments on the postural righting reflex were made using (1) four young kittens before the reflex was developed, and (2) four older kittens with the reflex well established. On the ground, the animals were dropped in upside-down position from an altitude of about twenty inches, and later in the air exposed to periods of about twenty to thirty seconds of practical weightlessness. The reflex was studied in T-33 and F-94 aircraft under both blindfold and non-blindfold conditions. The behavior of the cats was recorded on 16 mm. film.

The motion pictures were evaluated by repeatedly watching the film, and by an analysis of the individual frames. On the ground, the younger animals fell straight down; the older ones turned upright immediately after release without exception. In the air, the younger kittens floated upside-down during weightlessness; the older ones turned upright at the beginning of the weightless state, but their reflex failed after several exposures. By and large, it was observed that the postural righting reflex of the cat ceased to function after a period of about twenty seconds of practical weightlessness; and that the available visual cues did not affect essentially the reflex pattern.

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Importance of Aircraft Sanitation

Domestic airlines today are spending more money to feed their passengers than they spent not many years ago to fly them. Airline catering has become a specialized trade. In compliance with good sanitation standards, galley equipment is designed to facilitate cleaning—corners are rounded, seams are tight, and parts are removable. Although the primary aim of sanitation is to prevent the spread of communicable disease, an immediate benefit in air travel is that protection of the pilots' health enhances safety. A pilot suffering from severe nausea, vomiting, headache, diarrhea, or cramps would be a hazard to the safety of his plane, its passengers, and its crew.—HEALTH ALOFT: *Physician's Bulletin,* October, 1956.