

# BODY SUSCEPTIBILITY TO HIGH ACCELERATIONS AND TO ZERO GRAVITY CONDITION

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A LIVING organism, sent in a satellite, will be subjected to high acceleration at start and low or no gravity in orbit. While the former of these elements might, within limits, be varied, according to engineering capabilities, it might be worthwhile to investigate whether the no-gravity condition is really in any way detrimental to efficiency and well-being, as has been postulated by some authors (Armstrong *et al.*<sup>(1)</sup>; Gauer and Haber<sup>(2)</sup>; Haber<sup>(3)</sup>) and denied by others (Margaria<sup>(4)</sup>). In effect, once survival is assured and injuries are avoided, which is the goal current research in this field has up to now been concerned with, it is imperative in our opinion that the efficiency of the individuals manning the satellite be tested, both in their capability of directing it and of performing whatever task they have to. In this respect studies on balance and control of movements are mostly needed.

## *High Acceleration*

Previous work performed in this laboratory (Margaria *et al.*,<sup>(5)</sup> Gualtierotti *et al.*<sup>(6)</sup>, in press *a*) has shown that the effect of high acceleration forces can be greatly overcome by immersion in water: small fishes, frogs and rats in this condition had been able to stand accelerations in the order of about 500 g without suffering any visible inconvenience. Similar results have been obtained in man in a human centrifuge (Bondurant *et al.*<sup>(7)</sup>).

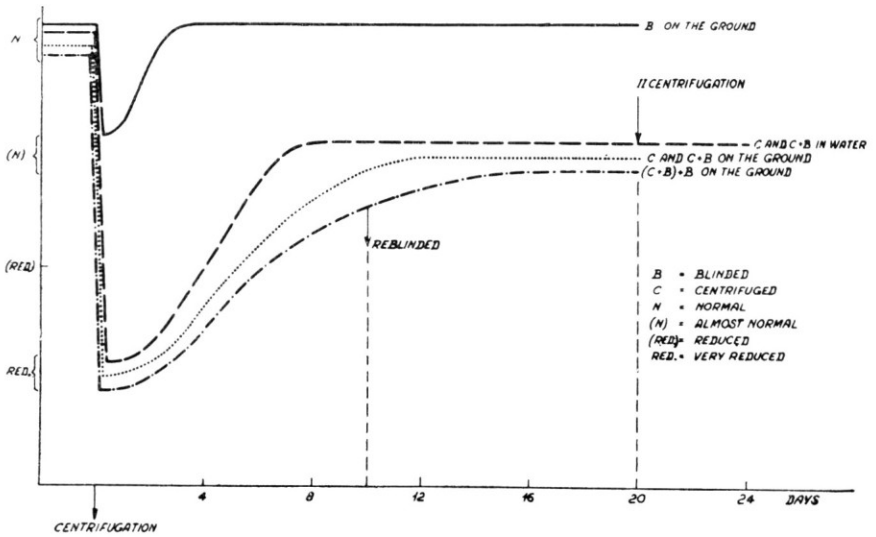
Fishes and frogs only showed an impairment of balance after 2000 g centripetal acceleration in a centrifuge for 10 min. Such loss of balance was ascribed to the destruction of the otolith system, due to violent disruption of the otoliths from their sensory cells in the inner ear: this was evidenced histologically in the fish.

As tests for balance the uprighting reflex and the behaviour in swimming and jumping were chosen. It was then found that complete recovery was

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## (a) JUMP



## (b) UPRIGHTING REFLEX

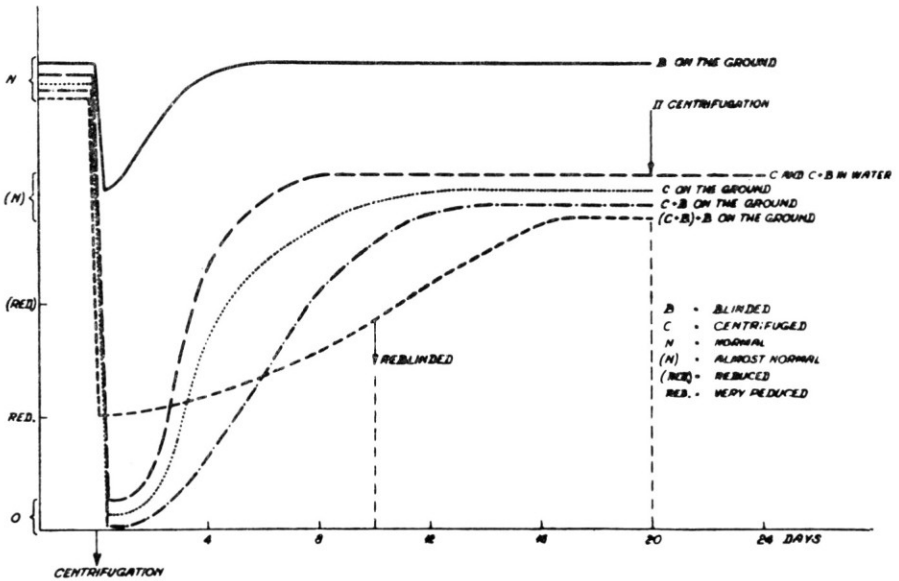


FIG. 1 (a, b). Tests performed on frogs with high  $g$  centrifugation (2000  $g$ ) for 10 min.

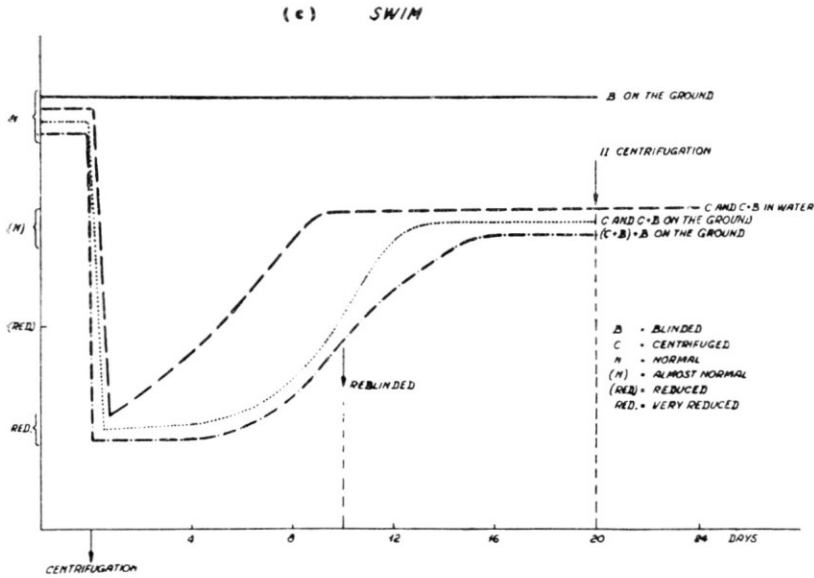


FIG. 1 (c). Tests performed on frogs with high  $g$  centrifugation (2000  $g$ ) for 10 min.

observed in the frog after 10–20 days. New experiments were devised in order to investigate the mechanism of such recovery, considering the possibility that, in absence of the otolith apparatus a vicarious function might be taken up by other sense organs such as the eye or the mechanoreceptors of the skin or muscle. A group of animals has been therefore blinded after centrifugation and in some of them the regeneration of the eye has been systematically avoided by new surgical destruction. Another group of blinded animals has been kept floating in oxygenated water to minimize the stimulation of mechanoreceptors due to the weight of the body or parts of it. All these animals recovered their sense of balance in the same time as controls; furthermore, if subjected to a second centrifugation, they did not show any impairment of the recovered sense of balance (Fig. 1).

It was then tentatively assumed that, when the ordinary sense organs were destroyed, some still unknown mechanism took over: and this would be both sensitive enough as to assure normal balance to the frog and capable to stand accelerations 2000 times higher than normal. The following experiments were devised, in order to investigate the recovery process of frogs after a well controlled surgical destruction of the labyrinths (Testa<sup>(8)</sup>, in press):

(a) Unilateral destruction of the labyrinth was performed. Tilting of the body towards the operated side was observed in 90% of the cases; jumping was deflected in the same direction, and so was swimming. Re-

covery started about 8–10 days later and nearly full recovery was reached in about 20 days.

(b) Unilateral removal of labyrinth as in (a) was followed by enucleation of the eyes. General behavior was the same as in (a) and also in this case nearly full recovery was observed in 20 days.

(c) The animals were subjected to bilateral destruction of the labyrinth. In this case only 50 per cent of the frogs showed lateral tilt. This position was however susceptible to be corrected passively, which was not the case when the destruction of the labyrinth was limited to one side only. The most remarkable alteration appeared in swimming: the animals were unable to perform efficient movements and assumed abnormal positions. Nevertheless, a recovery initiated after a few days, was completed in about 40 days. At the 20th day only occasional crises of vertigo were observed; these also decreased in number with time.

(d) The animals treated as in (c) were blinded. In this case the behavior was the same as in the previous group, but no recovery at all took place, at least up to 40 days after the surgical intervention (Fig. 2).

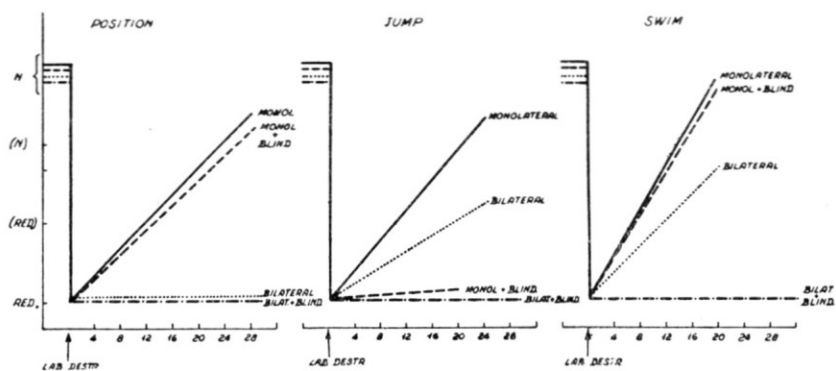
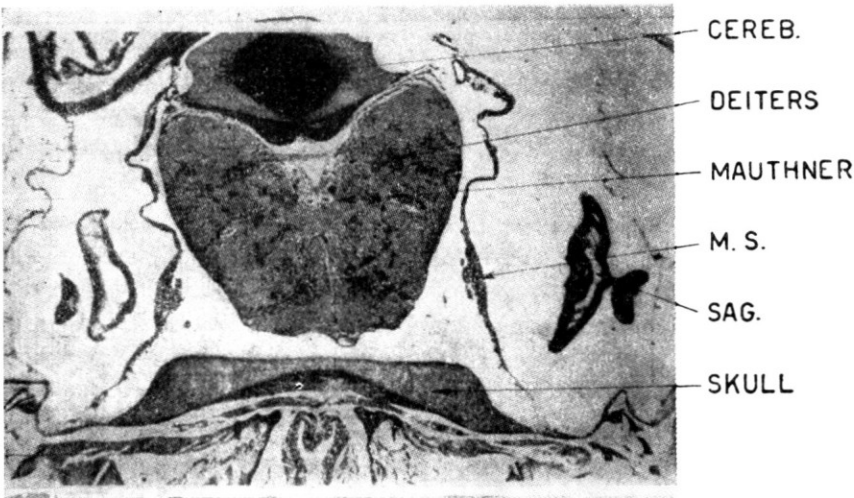
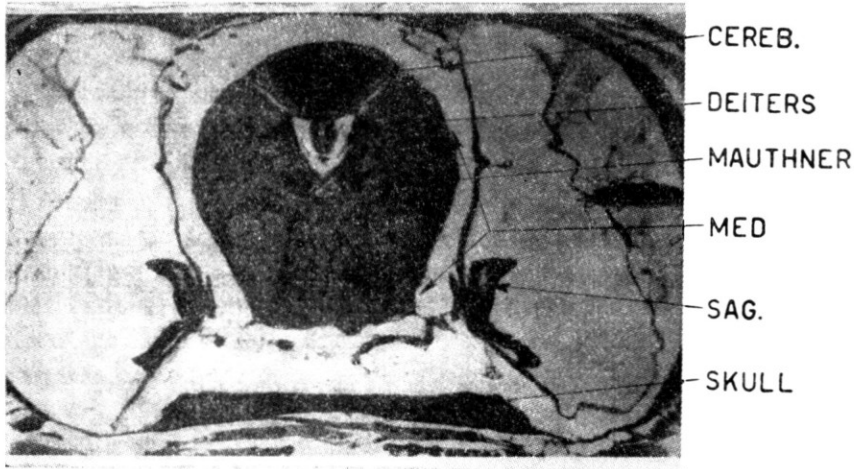


FIG. 2. Tests performed on frogs after destruction of the labyrinth.

From these results it appears that the sense of vision is the most important to compensate the destruction of the vestibular system: without vision recovery does not seem possible. Mechanoceptors are also important, as shown by the experiments in immersion (swimming) described in (c). The recovery that blinded animals showed after a long 2000 g centrifugation was evidently due to incomplete destruction of the frog's labyrinth. Surgical removal of this organ is more effective because it assures complete destruction. This explains both the recovery based on the substitute activity of the intact part of the otolith system, and the absence of a new functional impairment after a further centrifugation.

These results, on the other hand, are only observed in frogs, as previously mentioned. In fact, fishes subjected to the same high g centri-

fugation showed histologically the large otoliths disrupted from their normal sites (Figs. 3, 4). Frogs' otolith system is less liable to centrifugal injury as the otoliths are not large bodies, but they are made up of minute  $\text{CaCO}_3$  granules. It may then be clear why only some of the statoliths will be torn from their basic hairs owing to the increased weight during centri-



FIGS. 3 and 4. Section of the head of *Gambusia Hoolbrocki* performed vertically at the level of the medulla and of the otolith organ. (3) In normal fish; (4) After centrifugation. (Cereb. = cerebellum; Deiters = Deiters and lateral nuclei; Mauthner = Mauthner fibers; Med. = medulla; Sag. = sagitta; M.S. = macula sacculi; Skull = base of the skull.) Note the two sagittas in normal position in Fig. 3; detached and partially broken in FIG. 4, leaving the macula sacculi well visible. (From MARGARIA *et al.*, 1958.)

fugation, since the absolute value of such weight during high centripetal force will not always be enough to overcome the resistance of the hair and its holders. It has been demonstrated that the size of the labyrinth and the size of the mechanoreceptors connected with the otoliths are largely independent of the size of the animal, and the weight of the otoliths may vary considerably. In the table of Fig. 5 are shown the weights of

*Weights (in mg) of the Otoliths of some Fishes together with the Weight of the Fish (grams) (from DE VRIES)*

	<i>Fish</i>	<i>Sacculus</i>	<i>Utriculus</i>	<i>Lagena</i>
Pike	35	4.4	0.5	0.5
Pike	3000	51	6	6.5
Ruff	6	7	0.16	—
Ruff	—27	35	0.65	0.12

FIG. 5.

the otoliths of some fishes in mg together with the weight of the fish in grams. It might be that jumping animals, which are subjected to high deceleration when reaching the ground after the jump, have a labyrinth particularly built to stand the impact; namely, instead of having a large number of sense cells, all connected with a single otolith, as in fishes and most of the mammals, they may have a large number of otoliths, each one connected with a small number of sense cells. The resultant sensitivity would be the same in both cases as the total weight on an equal number of receptors might be the same, but the resistance to the impact would be much greater with minute otoliths. Furthermore, in emergency stress occasions involving a damage, this might be limited to only some of the otoliths and receptors: a single body otolith should be displaced instead as a whole.

Regeneration of the system and recovery of function will also be easier with a great number of small otoliths.

Small otoliths have, on the other hand, the disadvantage of being more subjected to parasite influences such as Brownian movements due to changes of temperature. This problem will be resumed again later on.

The peculiar characters of frog labyrinth might help in devising special experiments in high  $g$  studies. From the results described above, this animal seems to be particularly fit for studying conditions in which balance has to be preserved during high acceleration, namely all investigations concerned with the function of labyrinth and vestibular reflexes in such high gravity environment as to destroy this organ in mammals and other animals with large otoliths.

### Low Gravity

When normal gravity is decreased or reduced to zero, the main organs which are deprived of a normally steady stimulation are the labyrinth and the related center in the cerebellar flocculo-nodular lobe.

The skin and muscle mechanoreceptors in fact are much less important for the reception of gravitational stimuli, as shown by experiments in which the activity of these sense organs was greatly reduced by immersion in water (Margaria *et al.*<sup>(9)</sup>).

The otolith, however, is not only a static instrument, but is sensitive to any force of inertia summing vectorially with gravity; the resulting force will be interpreted subjectively as the direction of the vertical.

Experiments have been conducted in this laboratory in order to investigate the mechanism of this system and its sensitivity to acceleration, of which gravity is but an example. Cats have been used as they have a falling reflex extremely well developed which allows them, even without the help of the sight, to perform changes of position of body and legs during the fall in order to land on four paws. Such reflex is so quick that a cat can put itself upright in no more than 50–70 cm when falling back first. Cats are therefore particularly apt to give useful information in the studies of equilibrium.

Experiments have been performed (Gualtierotti *et al.*<sup>(10)</sup>, in press *b*) on curarized animals (cats) rigidly, held, in order to avoid muscular sensory inflow to the cerebellum and movements of joints which are known to constitute one of the main afferents to the cerebellum (Haddad<sup>(11)</sup>; Morin and Haddad<sup>(12)</sup>; Cohen<sup>(13, 14)</sup>, *a* and *b*). Under these conditions only a limited afferent activity outside the vestibule will reach the flocculo-nodular lobe of the cerebellum, namely the one coming from that part of the skin and those muscles subjected to the weight of the body.

By means of macro-electrodes 200  $\mu$  across, applied (1) bipolarly across the cerebellar cortex, (2) bipolarly along its surface or (3) monopolarly against an indifferent electrode, the gross responses of the flocculo-nodular lobe of the cerebellum to acceleration forces have been recorded. Recording was made comparing single sites of the medial and lateral parts of the lobe. Final analysis was made with a 5-couple microelectrode needle (Fig. 6): each couple was composed by two enameled wires 30  $\mu$  across. Thus a surface of 500  $\mu^2$  at a time could be investigated. The stimulation was given (a) by centrifuging the animal horizontally; or (b) on a plane tilted from 1.5 to 10°; or (c) by tilting the animal from the horizontal up to a maximum of 10° while the head was kept rigidly in the same position in respect to the body. Stimulation (b) results from a combination of (a) and (c).

The results obtained while recording gross activity show that cerebellar responses to static and dynamic stimulation are different. Static excitation (Fig. 7) induces an increase of amplitude of the cerebellar potentials in some sites of the cerebellum while a decrease is observed in some others,

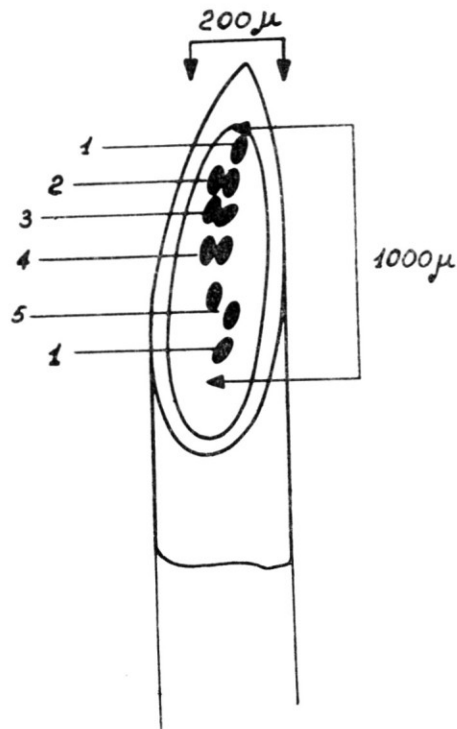


FIG. 6. A multicouple microelectrode.

maximum differences resulting from the lateral parts against the medial in the flocculo-nodular lobe. With microelectrodes such increase of amplitude is shown to be mainly due to the firing of previously quiescent units (Fig. 8) and to the increase of frequency of the already active ones.

Dynamic stimulation due to rotation mainly induced a synchronization of spontaneous cerebellar waves (Fig. 9), their frequency decreasing from 150–300 to 50–80 per sec. The amplitude of such slower potentials was much larger than that of the quiescent ones. Microelectrode recording showed however that some firing of new units took place (Fig. 10).

A finer analysis of the changes induced by acceleration can be made considering the significance of the various components of the electro-cerebellogram. When recording with microelectrodes, the spontaneous activity is composed by waves and spikes. The two show a difference of frequency and their physiological and pharmacological properties are







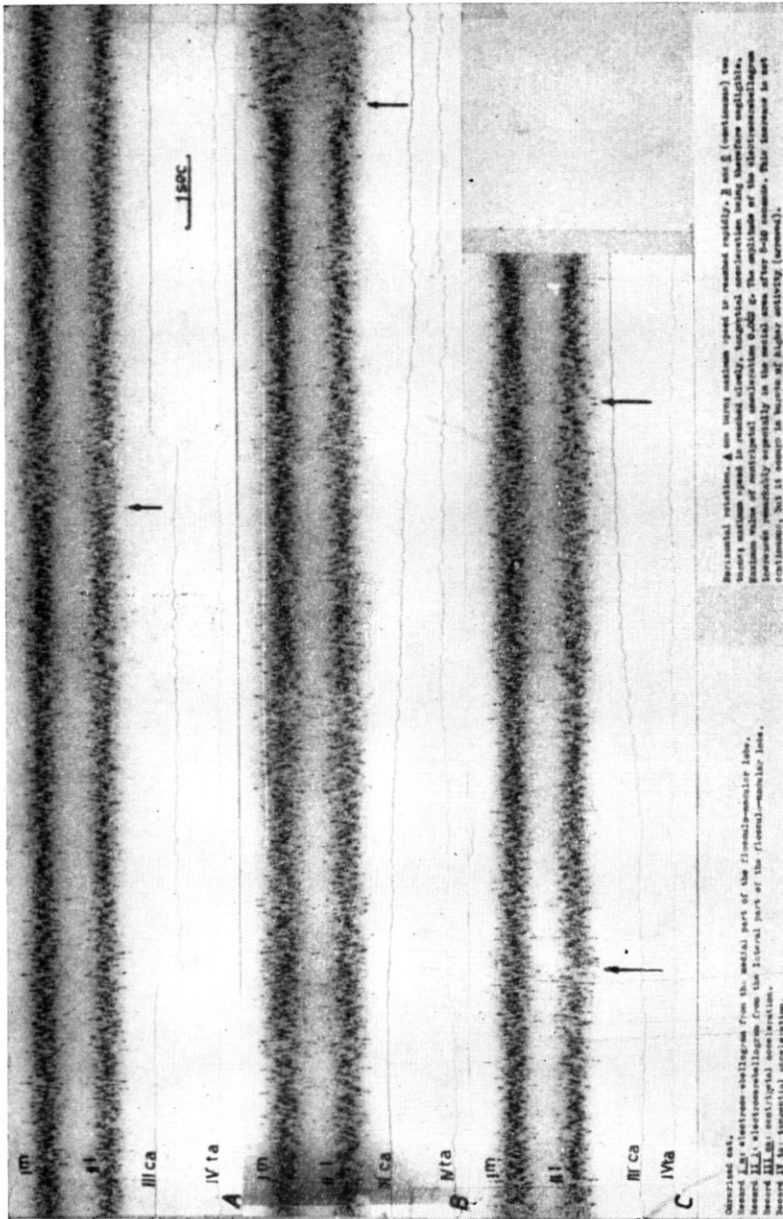


FIG. 9.



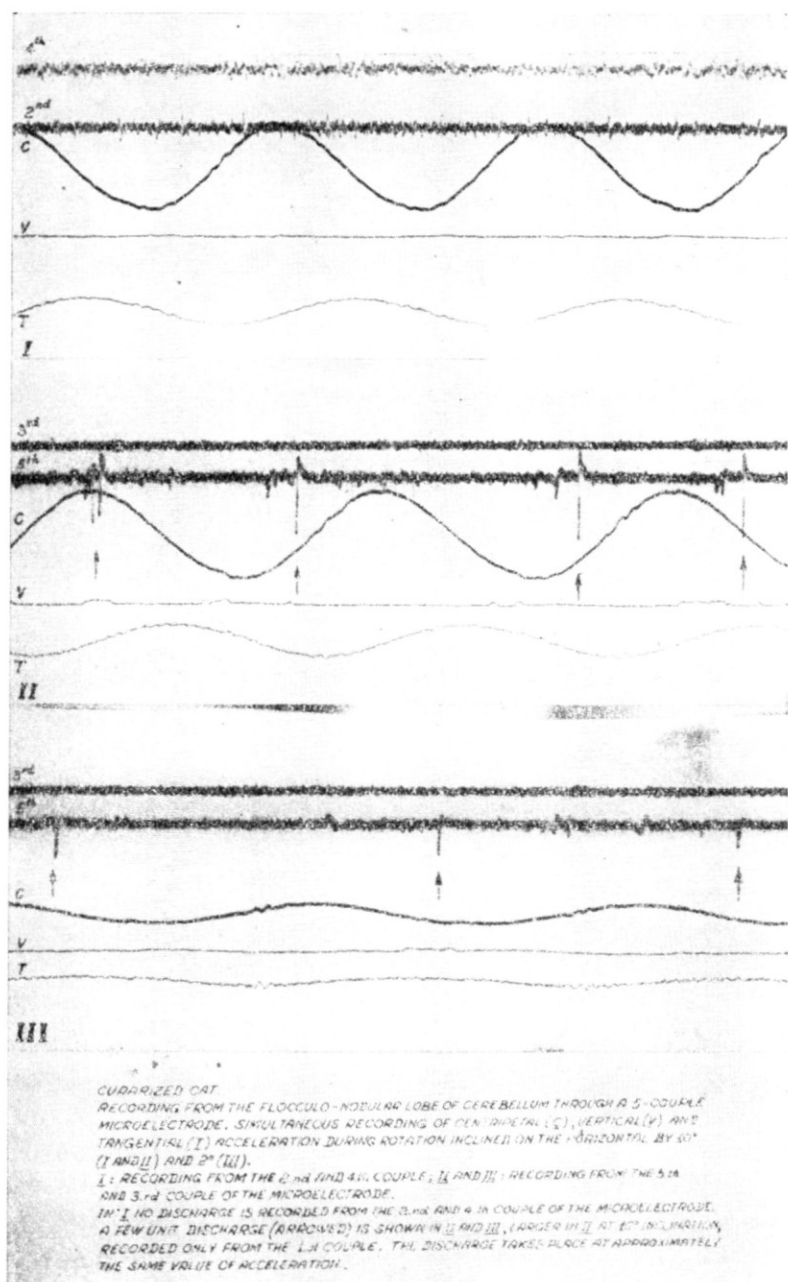


FIG. 11.



different indicating their different nature. Spikes are interpreted as being due to discharges of the axon of the Purkinje cells while the wave seems to be the result of fluctuating membrane potentials of a non-propagating nature (Bremer<sup>(15)</sup>). The spikes have normally a lower frequency than spontaneous activity. In our records their frequency in the still animal seems to be in the order of 50–80 per sec, although, owing to the technique used, it was difficult to distinguish a single unit discharge.

The wave response is very similar to the ordinary sensory response obtained from all other regions of the cortex with the appropriate peripheral stimulation. The analysis of the response in fact shows a surface-positive followed by a surface-negative potential, and the duration of the

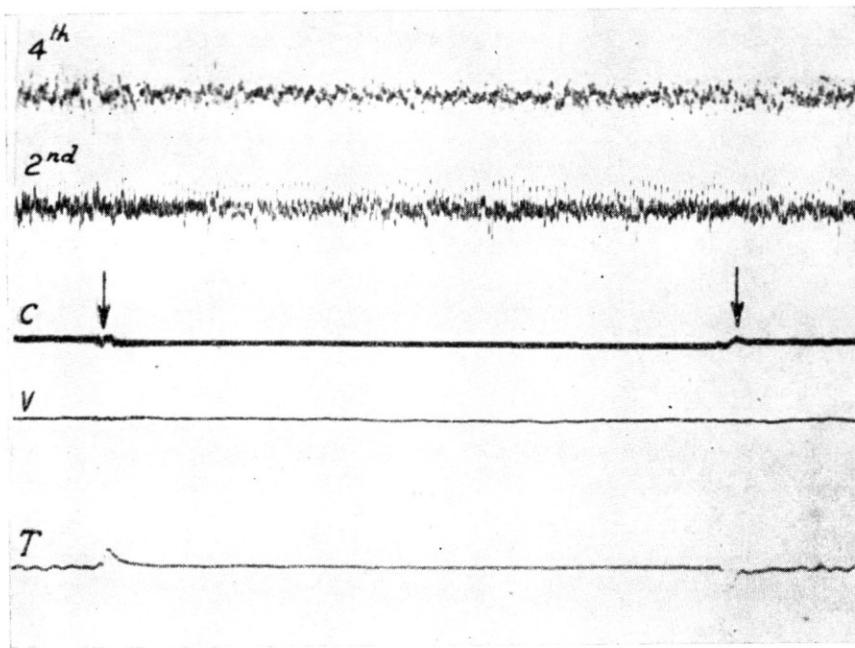


FIG. 13.

complex might last some 30–40 msec. Moreover, this response seems to diffuse to all flocculo-nodular lobe, and possibly somewhat outside it. This overlapping of responses is also typical of the general cerebellar reaction to afferent stimulation. The evoked spikes, on the contrary, seem to be strictly localized. With the multi-couple microelectrodes single or few units responses to dynamic stimulation take place at a certain value of acceleration in discrete sites, only a few tens of microns apart from a completely quiescent zone (Fig. 11).

During rotation on a tilted plan the two kinds of response, static and dynamic, are simultaneously present. In these experiments, not only both

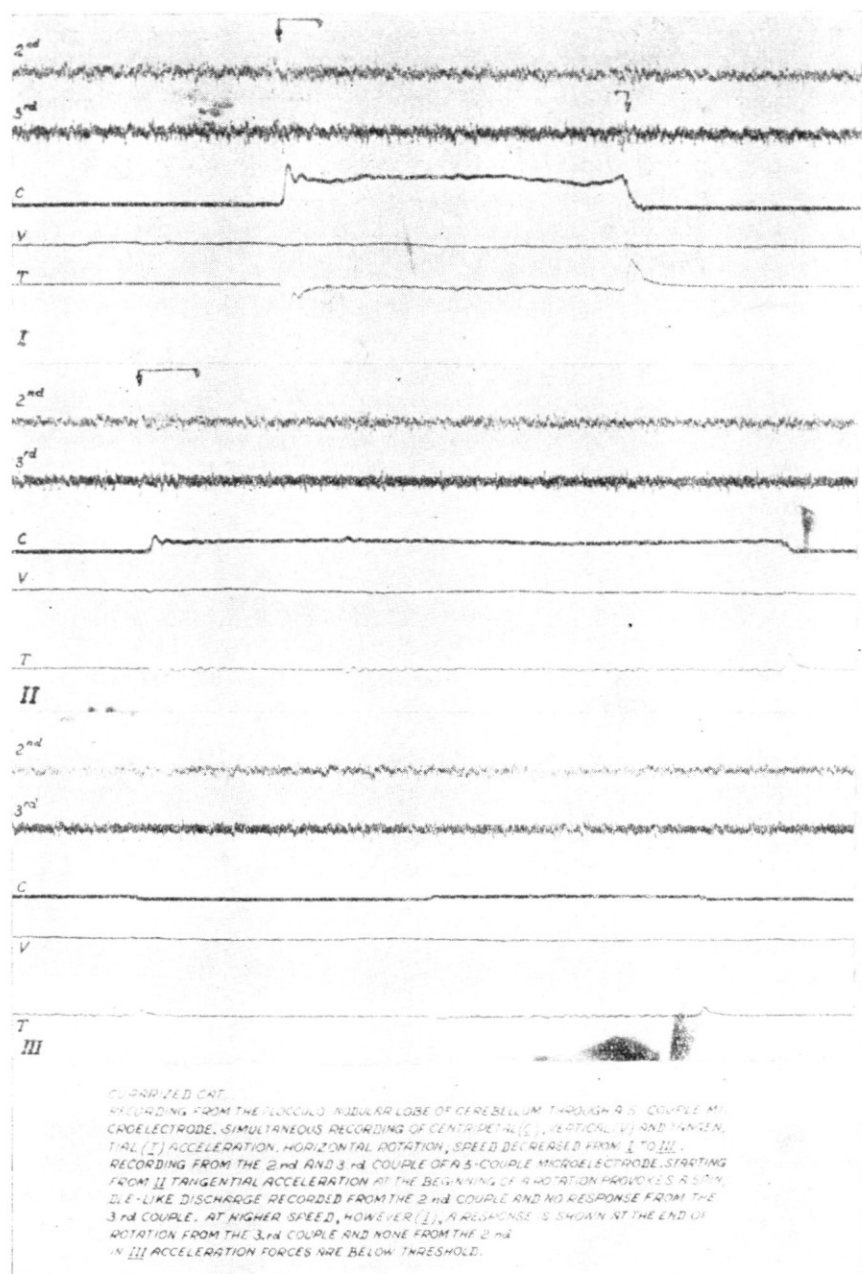


FIG. 14.



kinds of stimulation (static and dynamic) are present, but the strength of the stimulus is not constant and changes because of the summation of the earth gravitational force. In fact the direction of the gravitational component relative to the body axis changes from positive to negative depending on the position of the animal body on the plan of centrifugation (up or down, fore or aft): the resulting acceleration changes sinusoidally (Fig. 12).

Microelectrode investigation of single units in the flocculo-nodular lobe points to the existence of various kinds of units spread over the cortex. Some of these fire only at static and some at dynamic (Fig. 10), and some at both static and dynamic stimulation (Fig. 8). Some seem to respond only to the tangent acceleration that takes place at the start of rotation, but not to a similar deceleration at stop. Some units seem to fire spontaneously without any stimulus, and such firing is not altered, not even in frequency, by the onset of a dynamic or static stimulus (Fig. 13). All evoked firing shows a certain gradation of response, ampler synchronized potentials following a higher stimulus (Fig. 12). In one experiment, recording with two microelectrode couples only 100  $\mu$  apart, we were able to pick up a response to the acceleration at the start only from one couple and a response to acceleration at the stop only from the other (Fig. 14). The table of Fig. 15 shows a summary of the evoked responses according to the type, direction and mode of the acceleratory excitation used.

Stimulation	Cerebellar units									
	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>f</i>	<i>g</i>	<i>h</i>	<i>i</i>	<i>l</i>
<u>Static</u>										
Aft tilt	Spike									
Fore tilt										
Left tilt			Spike				Spike			
Right tilt										
<u>Dynamic</u>										
Centripetal		Wave		Wave	Wave					Spike
Tangential										
Accel.						Spike	Spike		Spike	
Tangential										
Decel.								Spike		

FIG. 15.

As a conclusion:

(a) Two kinds of responses may follow dynamic and static stimulation: one is a topographically widespread change of frequency and amplitude of the spontaneous waves, and is prevailing during dynamic stimulation;

the other is strictly localized, and different according to the parameters of the acceleration vectors, and consists of firing of single units.

(b) The threshold for the two responses is extremely low, of the order of 0.001 *g*.

(c) The amplitude of the response is related to the strength of the stimulus but is not a simple linear function: surprisingly, a maximum of response is obtained at a value much below 1 *g*.

The implication of these conclusions is that the vestibulo-cerebellar system has a complex structure, and is able to detect all the vectorial parameters of acceleratory forces (intensity, direction and versus). It can therefore allow measurements of displacements in space, and has such a high sensitivity that less than a change of 1/1000 of the normal earth gravity is able to induce a detectable response. Such a system can not only distinguish, with the high sensitivity indicated above, dynamic stimulations, like rotatory movements or changes of speed during the linear progression, but also static excitation like inclination of the head, quite independently from dynamic stimulation. The fact that some cerebellar units have been found to fire with both kinds of stimuli, static and dynamic, shows that in the cerebellar cortex, beside independent sensory static and dynamic central analyzers, an integrative process between these two kinds of responses takes place.

The high sensitivity of the system is rather surprising, since its order of magnitude is much lower than the normal steady gravitational pull; obviously mechanoreceptors of the requested sensitivity exist in the body.

In effect Adrian<sup>(16)</sup> had shown that less than 1° inclination of the head, corresponding to 0.017 *g* was enough to induce a significant change of frequency of the impulses of the vestibular nerve of the cat (Fig. 16). Moreover some mechanoreceptors are known to be excited by incredibly small stimulations: von Békésy and Rosenblith<sup>(17)</sup> showed that mechanoreceptors in the organ of Corti respond to vibrations of an amplitude in the order of a fraction of the diameter of the hydrogen atom. The end organs in the lateral line organ of fishes which are very similar to the otolith receptors and measure the animal's speed by the rate of flow, have such a low threshold that it cannot be determined exactly. They follow Flechner's law, the spike frequency being proportional to the logarithm of the rate of flow, and at a rate of flow of 16 mm per sec the maximal response is obtained. The gentlest tapping on the table or footstep on the floor of the laboratory stimulate the preparation (Granit<sup>(18)</sup>). The saturation of response at such a low flow (0.057 km/hr), much lower than that met during ordinary swimming, is similar to the saturation of response to acceleratory forces shown during this research. A question arises which are then the real functions of organs which seem to work only within

values that are only a fraction of the normal ones connected with the ordinary activity in a steady environment.

The high sensitivity of the system raises another question: namely, whether the parasite effect specially due to thermodynamic reactions at receptor level would not be able to produce meaningless stimulation. Convection currents in the endolymph and Brownian motion are the

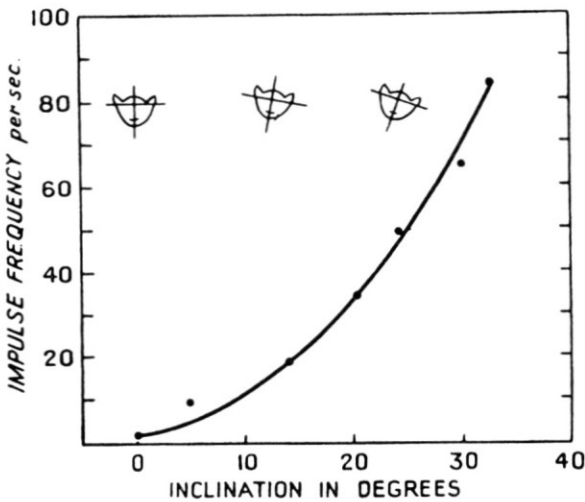


FIG. 16. Response of gravity receptors (otolith organ). Relation between tilt of head and frequency of impulses in vestibular nerve. (After ADRIAN, *J. Physiol.*, 1943, **101**, 393.) Decerebrate cat. The degree of lateral tilt of the head is shown in the upper diagrams. The impulses were recorded from the *right* nerve while the head was being tilted to the *right* (i.e. right cheek down). As the tilt was increased, the impulse frequency rose correspondingly. When the head was tilted to the *left*, the discharge in the *right* nerve ceased.

most likely disturbances if sensitivity is above a certain value. It is not difficult, however, to imagine how the labyrinth organs might discriminate between real pulses and spurious pulses, even if their receptors might be stimulated individually: real excitation in fact tends to be synchronous whereas spurious pulses do not. In the labyrinth real pulses arise from bodily displacements of the cupula when all the impulses or at least a great many of them are coincident and synchronous on the hair cell (De Vries<sup>(19)</sup>). The synchronous stimulation need not to be equally distributed for all the hair cell receptors in the cupula: some of them might be reached by more energy than others, more also than the energy involved in spurious excitations (Brownian motion or convection currents). If the mechanical stimulation were transformed in electrical energy, this could be achieved electrically: a large current would then impinge on the sense cells with lower electrical resistance.

As for the real function of the labyrinth organs, it seems that at least for the human organism, the otoliths are not so important for the conservation of the equilibrium as they are, for instance, in amphibians. In fact "the only important effect which is reported for deaf-mutes (who often have an impaired static function of the labyrinth) is that they are not subjected to motion sickness" (De Vries<sup>(19)</sup>). Thus, such organs would not be only or even mainly static instruments giving the position relative to the vertical, but more generally an index of acceleration, owing to the force of inertia on the otoliths. During the movements of the whole organism or of the head, gravity would be but one component of the forces acting on the static organ and in variable degree according to the angle with the vertical.

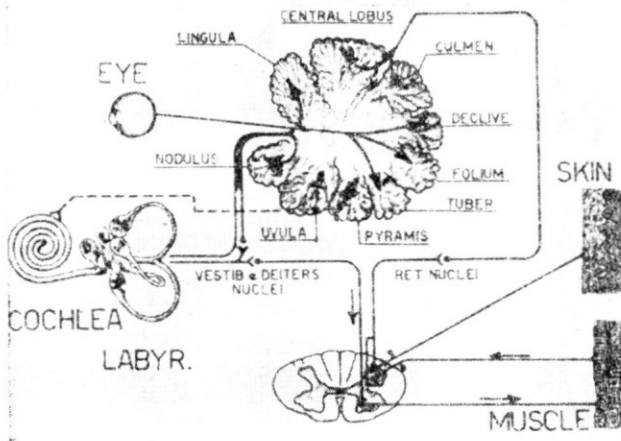


FIG. 17. Telereceptors' convergency on cerebellum (schema). Impulses due to sight, hearing, labyrinthine stimulation, general skin sensory apparatus are shown. Connections to and from intrafusal system through spinal centers are also indicated. Cerebellum is therefore a main center for long-range relationship between individual and environment. (From GUALTIEROTTI, SCHREIBER, MAINARDI and PASSERINI, 1959, *Amer. J. of Physiol.* **197**, 469.)

An evidence that the otolith apparatus is not a very fine static instrument is given by the absence of response if the gravitational field is increased by even 50 per cent or more, the direction of the force staying unchanged: this takes place, for example, in an aeroplane during turns on a horizontal plane.

A better understanding of the vestibulo-cerebellar mechanism results if the multiple connections of the cerebellum with the other parts of the organism are taken into account. The cerebellar cortex is reached by afferents coming from the deep and superficial sense organs, from the

cortex and the autonomic system (Fig. 16). The efferent activity of cerebellum and of the vestibular apparatus is particularly important in keeping the organism alert and active. The spontaneous activity both of the labyrinth receptors and of the cerebellar cortex play a significant role in the general reactions of the organism as a whole. Kempinsky<sup>(20)</sup> showed that cutting the vestibular nerve the cortical threshold to a direct stimulation is increased: movements induced by cortical stimuli are abolished. Muscular coordination is differently but remarkably altered by lesions provoked both on the labyrinth and on the fastigial cerebellar nuclei (Carpenter *et al.*<sup>(21)</sup>).

These deficit phenomena following suppression of the spontaneous activity of the labyrinth receptors and of the cerebellar cortex might be present also as an effect of the zero gravity condition met in a satellite. Experimental evidence, however, seems to show that the lack of external stimulation does not result, as a whole, in a decrease of the spontaneous activity of the corresponding organs and therefore the effect is not the same as the destruction of the organ or the cutting of its sensory nerve. For instance, absolute darkness results in an increase of the spontaneous activity of the retina, which might compensate for the physiological differentiation of the visual system due to lack of light. Very likely, the retina, even in complete absence of visual excitation, still maintains a tonic influence upon the brain (Claes<sup>(22)</sup>).

Moreover, according to Flechner's law, the response of the receptors is larger the smaller the stimulus (Granit<sup>(18)</sup>).

The tonic influence of the labyrinth may therefore persist even in absence of gravitational stimuli: this may involve only a change from the normal. By analogy with experiments on the retina, however, a possibility exists of perfect adjustment and compensation with training. For example, Stratton<sup>(23,24)</sup> studied the effect of inverting the retinal image for 8 consecutive days, in man, using a lens in front of the eye. A conflict existed between the visual information and the information given by the other sense organs. From the 5th day a nearly perfect adaptation took place. Such experiment was repeated recently by Kohler<sup>(25)</sup> with binocular inversion spectacles. At the 5th day he had complete reflex reorientation and could even perform difficult exercises such as drive a car or go skiing. Definitive removal of the spectacles took a similar time for reorientation.

A direct evidence of the adjustment of the sense of balance and of the vestibulo-cerebellar mechanism as a whole with training was shown by Geratwohl<sup>(26)</sup> (rep. by von Diringshofen, 1959) on cats during parabolic flights. The falling reflex, which is very developed in cats, was present even if very weak just entering the zero gravity condition, but after 10 seconds it disappeared completely and the animal reacted to

mechanical or visual stimulation, while floating in the air, just in the same way as normally on the ground.

As a conclusion, very probably man can easily find an adjustment to absence of gravity, as (1) gravity is but one factor and not the most important acting on the static organs of the labyrinth; (2) the energizer effect on the other nervous structures of labyrinth and cerebellum is largely independent from external stimulation; (3) most of the sensory inflow to the vestibulo-cerebellar system will be maintained through tactile, visual and deep receptor connections; (4) whatever impairment the absence of the gravitational factor may induce on the static organs, it might easily be overcome after a short training.

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This research has been sponsored by the Office of Scientific Research of the Air Research and Development Command, U.S. Air Force, through its European Office, under Contract AF 61 (052)-23.

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