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PHYSIOLOGY OF THE VESTIBULAR ANALYZER

Edited by V. V. Parin and M. D. Yemel'yanov

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Annotation

A broad range of problems related to the physiology of the vestibular analyzer of man and animals, located under conditions of terrestrial gravitation and applicable to space flight, is illuminated. A great deal of attention is devoted to consideration of the biological mechanisms of the functioning processes of the vestibular analyzer at different levels of development of the nervous system, to characteristics and principles of the physiological interaction of the analyzers of the body's position and motion in space, and to application of mathematics and electron microscopy in the field of labyrinthology. The book contains 24 tables and 38 figures. Responsible editors are Academician V. V. Parin and Professor M. D. Yemel'-yanov. The text is preceded by a foreword.

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Foreword

This collection, written by a collective of authors, presents 39 papers in which a wide range of problems related to the physiology of the vestibular analyzer under terrestrial conditions and applicable to space flight is illuminated.

The material is accordingly arranged by sections: the interaction of the vestibular analyzer with other analyzer systems, physiology of the vestibular analyzer, the problem of motion sickness and increased stability to vestibular effects, and development of new methods of investigating the vestibular function.

The papers of a theoretical nature interpret physiological mechanisms of the intimate functioning processes of the vestibular analyzer under various conditions, they disclose methods, characteristics and principles of interaction with other analyzers, and they consider problems of applying mathematics andelectron microscopy in the field of labyrinthology. The experience of studying the vestibular function during orbital flights, the problem of vibration and new methods of investigating the vestibular analyzer are generalized in the papers of a practical trend. Further ways of studying the analyzer function during space flights are noted.

Study of this collection will permit doctors and experimenters working in various fields to become acquainted with the most recent achievements on the physiology of the vestibular analyzer.

Academician V. V. Parin

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PHYSIOLOGY OF THE VESTIBULAR ANALYZER

V. V. Parin and M. D. Yemel'yanov

INTERACTION OF THE VESTIBULAR ANALYZER WITH OTHER ANALYZER SYSTEMS

SOME REAL PROBLEMS OF INVESTIGATING THE ANALYZER FUNCTION OF ASTRONAUTS IN FLIGHT

M. D. Yemel'yanov

ABSTRACT. A number of positions is put forward on the basis of analyzing disruptions of the analyzer function of cosmonauts in flight, and of experimental investigations under ground conditions. Illusory sensations of spatial orientation develop as a result of conflicting situations in perception of gravitational and visual conditioned reflex verticals. The illusions may be accompanied by motion sickness.

The orbital flights of Soviet and American astronauts have made it possible to accumulate the most voluminous scientific data on the effect of space flight factors on the human organism. It would apparently be useful and feasible to supply not only the results of numerous investigations in certain branches of space medicine, but also to present them in the form of critical generalizations. /5*

The fact is that there have been statements in the periodical literature and at international congresses and symposiums on astronautics which have often eliminated the state of astronauts in flight from the diametrically opposed positions.

American colleagues, for example, have more than once mentioned the presence of some kind of vegetative disorders in their astronauts, at the same time corroborating the possibility of spatial illusions developing during the transitional periods from the active trajectory of ship motion to weightlessness. On the other hand, there have been reports in the Soviet press about development of symptoms in individual cosmonauts which were similar to the initial phase of vibration.

* Numbers in the margin indicate pagination in the foreign text.

Some authors, expressing one or another hypothesis on the origin of similar phenomena, were subsequently trapped by their own assumptions. Thus, the idea of vestibular origin of vegetative disorders in cosmonauts was born and is persistently corroborated, and Lansberg introduced the term "sputnik sickness."

No less important is the problem of differentiating the effect of dynamic weightlessness on an organism from other factors of the unusual medium in which the astronaut finds himself. The equality sign is placed between space flight and weightlessness with respect to the analyzer function. We know, moreover, that the activity of the analyzers essentially reflects the state of cortical dynamics and depends directly on it. There are adequate conditions /6 during space flight, beginning with the emotions of the astronaut and ending with his executing extremely tense and varied operations, which may alter the functional state of the higher branches of the central nervous system [7].

Finally, there is some reevaluation of the results of investigations carried out on the ground or in the earth's atmosphere with the help of modeling factors of space flight. This refers mainly to simulation of weightlessness in aircraft (flight along a Keplerian parabola). In this case, forces act on a human, which generate multidirectional accelerations varying over short time intervals. Each new stimulus during g-loads or weightlessness is superimposed on the aftereffects of the preceding, and it is natural that the adaptation processes of an organism develop according to principles other than under conditions of prolonged and permanently acting weightlessness.

The following facts related to the function of the vestibular apparatus indicate how important it is to consider the period of the aftereffects of stimuli.

This author has investigated the bioelectric activity of the sacrospinal muscles upon stimulation of the vestibular apparatus by a pulsed current. The period of the aftereffect of the stimulus, similar in value to threshold values, continued for more than a minute. A number of papers [7-9, 20-22, 30] demonstratively indicate the duration (up to 100 sec) of the course of postrotational and optokinetic nystagmus, the more carefully the investigation being conducted, the more distinctly the shift in the direction of nystagmus phases being revealed.

The same phase tendency was discovered during sensory vestibular reactions by M. D. Yemel'yanov with respect to the illusion of rolling, and by O. M. Frenkel in cases of vertigo developing after rotation [13]. It is natural that such a phase tendency may leave a definite imprint on the nature and direction of the total reaction, if an additional stimulus is superimposed. Therefore, the contradictory data obtained by Ye. M. Yuganov [15] and Jackson [29] while investigating the function of the vestibular apparatus in man during flights along a Kepler trajectory are not accidental. The first established prolongation of postrotational nystagmus of the test subject, and the second, using a stronger stimulus (Coriolis acceleration) and the technique of photonystagmography in infrared light, displayed no variations of nystagmus reactions.

Consequently, the results of ground experiments with momentary variation of gravitational forces cannot be extended to prolonged weightlessness without /7 the proper stipulations and extensive analysis of the facts obtained.

Taking into account the foregoing, the author of this report decided to touch on certain problems of investigating the analyzer function of astronauts during orbital flight and to summarize the results of ground-based experiments carried out with the aim of analyzing data of space research.

The Vestibular Analyzer

As we know, G. S. Titov was the first to give a rather thorough analysis of the unpleasant sensations which he experienced during his seventh orbit and which were similar to the vibration syndrome. The leading specialists of the country, in particular otolaryngologists, were brought together to discuss this phenomenon. Their opinion is reflected to some degree in the article of G. L. Komendantov and V. I. Kopanev [10]. The specialists favored the vestibulo-vegetative syndrome, the basis of which is the accumulation of adequate stimulation of the vestibular analyzer in the form of inertial forces which produce Coriolis accelerations.

Measures were taken to prevent similar disruptions in future astronauts by intensive and prolonged vestibular training. On the other hand, the plan of orbital flights included more extensive investigations of the vestibular function; simultaneously, ground experiments were set up on the prolonged effect on the human organism of forces which are related primarily to multidirectional complex accelerations (in particular, of Coriolis acceleration).

The methods of investigating the vestibular function during space flight envisioned study first of all those reactions which are specific for the vestibular analyzer (vestibulomotor reflexes to acceleration and the equilibrium function). A number of tests were employed for this purpose which permitted direct and indirect evaluation of the effect of the vestibular apparatus on the tone of skeletal muscles and coordination of movements. One of the models was the eye with its extrinsic muscles -- the motor activity was studied with the help of an oculogram. A somewhat modified method of vertical writing [24] was employed and the test of extended arms was used. Moreover, handwriting [2, 11] and all directed movements of the astronaut in executing flight tasks were subjected to analysis. Special attention was given to this during the exit of A. Leonov from the spaceship.

Vegetative reactions unrelated to vestibular stimuli and after combining of certain stimuli (head and trunk movements) were also recorded -- respir- /8 ation and pulse rate and the bioelectric activity of the heart (especially to variations of the R-R interval). The method of determining the excitability of the vestibular apparatus with the help of galvanic current was used for the first time on the *Voskhod* spaceship. The state of higher nervous activity was evaluated from data of electroencephalography [2].

The methods enumerated were supplemented by the cosmonauts' evaluation of their own sensations at various stages of work. The following was established as a result of employing these methods: there were no expressed and prolonged nystagmus and asymmetry of ocular muscle tone in any of the cosmonauts. Significant disruptions of thin coordination of movements or deviations of outstretched arms were also not noted. The slope angles of vertical writing were contained within the limits of prethreshold values of the curves of vestibulometry.

The galvanic test carried out by B. B. Yegorov disclosed the same indicators as those on the ground. Registration of the enumerated vegetative reactions made it possible to explain certain shifts in the activity of the cardiovascular system, but unrelated to stimulations of the vestibular analyzer. Essentially no direct proof of variations in the excitability of the vestibular apparatus was obtained. The main grounds for creating various hypotheses were subjective sensations.

Before his flight, G. S. Titov was qualified as rather stable in the vestibular sense, and familiarization flights along the Kepler parabola did not elicit any unpleasant sensations in him. A high vestibular stability was achieved after prolonged vestibular training. Despite this, during orbital flight the cosmonaut experienced a number of unpleasant sensations related to the function of the vegetative nervous system. Summary data on the vestibular training of B. B. Yegorov and K. P. Feoktistov essentially hardly differed from the data of V. M. Komarov -- the time of recovery of equilibrium on an unstable platform was 5, 3, 4 and 3 sec [6]. The time of withstanding the accumulation of Coriolis acceleration for B. B. Yegorov and V. M. Komarov was 11 and 12 min. Thus, all three cosmonauts of the *Voskhod* were adequately trained for vestibular stimulations.

B. B. Yegorov describes very unusual illusions during flight which he could not interpret from the aspect of the unfitness of the vestibular analyzer function, which had repeatedly been emphasized to him. Consequently, despite the presence of illusory sensations in B. B. Yegorov and K. P. Feoktistov, it is not possible to make any conclusions about the vestibulo-vegetative deficiency of the cosmonauts.

Moreover, corresponding calculations indicated that possible Coriolis accelerations during weightlessness, which are the result of ship rotations /9
around its axis or of the earth and simultaneously of movements of the cosmonaut (head and trunk), are significantly less than the threshold stimulations of the vestibular apparatus. Consequently, it is not possible to talk about accumulation of vestibular stimulations.

Ground experiments[1] on the effect of prolonged rotations (up to seven days) on man in combination with measured amounts of Coriolis accelerations disclosed the leading role of individual tolerance.

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[1] Conducted by M. D. Yemel'yanov, R. R. Galle and colleagues.

Moreover, a very important fact was noted: preliminary investigation of the vestibular function in test subjects by methods known in otorhinolaryngological examination did not permit prognosis of the state during rotation. The characteristics of an organism's adaptation to this type of effect were determined by the excitability of the vestibular apparatus and by the functional state of physiological systems to which the vestibular reflexes were transmitted. This is expressed very clearly with respect to the cardiovascular system -- hemodynamic shifts were strongly expressed in persons with vascular lability at normal thresholds of vestibular sensitivity. Regulation of the effect of the vestibular analyzer with various physiological systems depended on the prevalence of the tone of the sympathetic or parasympathetic nervous system. In the second case the adaptational capabilities of the organism were very limited.

Upon completion of rotation, the contrast appeared among comparatively stable vestibular reactions during employment of special tests, thresholds of vestibular sensitivity according to the data of so-called cupulometry and disorders of gait and equilibrium. The impression formed was that the central regulatory mechanisms of the statokinetic analyzer system are primarily affected.

Thus, it was definitely concluded that prolonged rotation in itself and in combination with Coriolis accelerations is a stimulus, the effect of which on an organism is determined by the state of various physiological systems and their interaction, which also determines adaptation mechanisms in the final analysis.

The results of observations of cosmonauts during flight and experiments may be generalized.

1. Adequate vestibular stimulations in the form of rectilinear and angular accelerations during orbital flights are almost nonexistent during weightlessness. Coriolis accelerations may develop periodically, but upon comparison with threshold values for ground conditions [25-27] they are tens of times less, i.e. they are far beyond the limits of the physiological capabilities of a human sensing them. /10

2. Objective methods selected to investigate the vestibular function during flight disclosed no variations of the excitability of the vestibular analyzer.

3. The cosmonauts were prepared by vestibular training to specific standards of stability provided for in the training program. At a given stage of mastering space, the problem of sending cosmonauts with a varying degree of stability of the vestibular analyzer, and even more so with an inferior vestibular function, into space flight was not assigned, because the flight program included reliable investigations.

4. Adaptation to Coriolis accelerations, to which principal significance is imparted in the development of vestibulo-vegetative disorders during space

flight, is in fact determined not only and not so much by the activity of the vestibular analyzer, as it is by the interaction of afferent systems.

Thus, it is apparently impossible to regard the analyzer function of cosmonauts in orbital flight simply through the prism of the vestibular apparatus, and to link the "vibration" syndrome to its dysfunction. Moreover, physiology is disposed to facts which indicate the possibility of producing vegetative disorders and illusory sensations upon emulation of any of the sense organs. This is also confirmed by space flight itself -- optokinetic stimuli intensify vegetative displacements when following objects outside the cockpit.

The Motor Analyzer

The papers of V. I. Yazdovskiy, I. I. Bryanov et al. [18], A. I. Mantsvetova, and I. P. Neumyvakin et al. [11] indicated that under conditions of brief weightlessness there is comparatively rapid adaptation of the motor analyzer and recovery of coordination of movements. It is obvious that during orbital flights lasting up to 14 days, astronauts experience no apparent difficulties in executing motor acts. At least the activity of piloting the ship, making notes in the flight log and carrying out certain additional movements (photography) did not vary significantly. Assumptions about a decrease of proprioceptive afferentation expressed by many investigators are not without foundation, but were also not confirmed experimentally.

I. T. Akulinichev, M. D. Yemel'yanov and D. G. Maksimov [1] investigated the motor activity of the eyes with the help of electro-oculograms of the /11 cosmonauts in flight. The authors felt that the eyeball with its transverso-striated musculature is an excellent model to study the processes of development of motor reflexes during weightlessness.

Analysis of the electro-oculograms of A. G. Nikolayev, P. R. Popovich, V. F. Bykovskiy and V. V. Tereshkova indicated that none of them during their three-to-five-day stay in a state of weightlessness experienced any persistent disruptions of eye movement coordination. Obviously, adaptation of the motor analyzer is rather active. Moreover, a deep understanding of this process requires more refined and complete methods of recording the motor activity of the eyes and coordination acts during space flight. It is not excluded that the absence of expressed disruptions in the function of the motor analyzer is caused by the restriction in the motions of the cosmonauts, reaching a state of automatic performance during training for essential work operations, and also by the comparatively brief state of weightlessness. American investigators, for example, feel that sharpness of vision and distinction of brightness vary due to the high degree of immobility of the eye during weightlessness.

The problem of analyzer interaction is one of the most important in space medicine. M. D. Yemel'yanov, V. V. Baranovskiy and A. G. Kuznetsov [4] studied the characteristics of the interaction of the optical, vestibular and

motor analyzers with respect to space flight conditions. The investigations made it possible, in our opinion, to explain the following important positions.

1. Since analysis of the spatial relationships of man with surrounding objects is to a significant degree formed during the process of ontogenesis, there are no doubts whatever about the fact that this process is accomplished by conditioned reflex mechanisms of various degrees of complexity (synthetic, conditioned chain reflexes, stereotyping, etc.). In connection with this, spatial illusions are comparatively easily produced when conflicting situations are created during perception of the gravitational and visual conditioned reflex vertical. Such conflicts are created in the case when man is deprived of the possibility of maintaining static postures, is in a state of unstable equilibrium and at the same time is deprived of the possibility of fixing his eyes on immobile visual objects, i.e. we are speaking here about disorder of the statokinetic reflexes which cannot be corrected by vision. Illusions in such cases become especially vivid and continue for a prolonged period.

2. Under known conditions of the experiment, besides total disruption of spatial orientation and disordered motor reaction (with loss of equilibrium), the test subject develops expressed vegetative disorders, similar to those /12 observed during flight along a Kepler parabola or possible in astronauts in a state of prolonged weightlessness. It is obvious that in a given case we are not talking about classical vibration, but about a unique disorder of the system of complex synthetic conditioned reflexes, which provide orientation of man in space. This in turn leads to disruption of the regulatory mechanism of physiological processes from the aspect of the vegetative nervous system. Such great demands are made of the latter, under conditions of analyzer function disruptions, that its own type of vegetative crises, or vegetative neuroses develop.

3. Interaction of the analyzers may proceed according to a decrease by two-three times of the thresholds of sensory and vegetative reflexes, inherent to the vestibular or optical analyzer. Moreover, the excitability of the vestibular apparatus may not be altered. Alleviation of transmitting excitation occurs somewhere along the tract of the reflex arch. It is possible that the leading role in such cases, in the sense of the appearance of vestibulo-vegetative reflexes, is played by the functional state of the effector organ, for example, of the organ or peripheral vessels (see Galle, in this collection). An apparent effect on vestibular reflexes is exerted by the nature of proprioceptive afferentation -- inhibition takes place during stable muscular stresses (eye fixation, stress of the skeletal muscles). On the other hand, involuntary disordered and prolonged activity of the eyes, and balancing of the test subject on an unstable platform results in the opposite effect.

4. Illusions of the spatial position are undoubtedly cortical processes. Everything which contributes to generalization of cortical stimulation intensifies this phenomenon. On the other hand, illusions and accompanying vegetative reflexes may be suppressed with the help, for example, chloral hydrate.

There are adequate conditions during space flight for disrupting the activity of the spatial analyzer system, but the forms in which this disruption appears may be varied. The state of the higher branches of the central nervous system should be regarded as the common origin for all disruptions of the analyzer function. Obviously, the reasons which lead to predominance of the stimulating processes in the cerebral cortex enhance development of illusory sensations and vegetative disorders.

Thus, the adaptive mechanisms of man, which are oriented toward maintaining the analyzer function during space flight, will be determined first of all by the state of the higher branches of the central nervous system. Hence, it is natural that problems of training astronauts cannot lead only to vestibular training, but the functional characteristics of other analyzers /13 must be taken into account. It is important to train a system of analyzers. Selection, then, should provide for many sided study of the higher nervous activity of astronaut candidates.

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VARIATION OF THE ELECTRICAL ACTIVITY OF THE BRAIN OF ANIMALS AND MAN UPON STIMULATION OF THE VESTIBULAR APPARATUS

V. G. Samsonova

ABSTRACT. The effect of vestibular and light stimulations on reaction of single neurons in the visual cortex of the frog, total activity of different regions of the brain and reaction of assimilating the rhythm of light flashes in animals and man are studied. Isolated and multiple stimulation of the vestibular and visual analyzers reveal a close functional relationship between them.

This report presents experimental data of the Laboratory of Analyzer Physiology, Institute of Higher Nervous Activity and Neurophysiology of the USSR Academy of Sciences, obtained during study of the electrical activity of certain regions of the brain of animals and man under conditions of stimulation of the vestibular system. The biopotentials of single cells of the optical center, total electrical activity of various regions of the brain, and reaction of assimilation of light flashing rhythms by the brain were investigated. /14

Reaction of the neurons of the optical center to isolated stimulation of the vestibular and optical systems, and upon their simultaneous stimulation, was studied in the frog *Rana temporaria*, immobilized by tubocurarine. Drawing off of the potentials is extracellular and is accomplished by glass micropipettes less than 0.5 μ in diameter and filled with a 3-molar concentration of KCl. Stimulation of the vestibular system is carried out by the thermal method for 3-5 min. A Sylvania flash lamp with an average pulse intensity of 100 msec was used for light stimulation. Responses of two types of neurons -- those having spontaneous activity and the so-called silent cells -- were investigated.

Isolated stimulation of the vestibular apparatus elicited a significant variation of the electrical activity in the majority of spontaneously active units of the frog tectum compared with that of background activity. The effect of alleviation was observed in part of the cells of this type -- the frequency of discharges increased progressively as the period of stimulation of the vestibular system was lengthened (Figure 1a). The other, greater part of the elements responded to such stimulation by inhibition of activity, expressed by a gradual decrease in the frequency of impulses in proportion to stimulation (Figure 1b). Total inhibition of the discharges was observed /15
in some neurons. After curtailment of stimulation, the frequency of impulses returned gradually to the initial level. Only a small part of the spontaneously active cells did not react to stimulation of the vestibular apparatus.

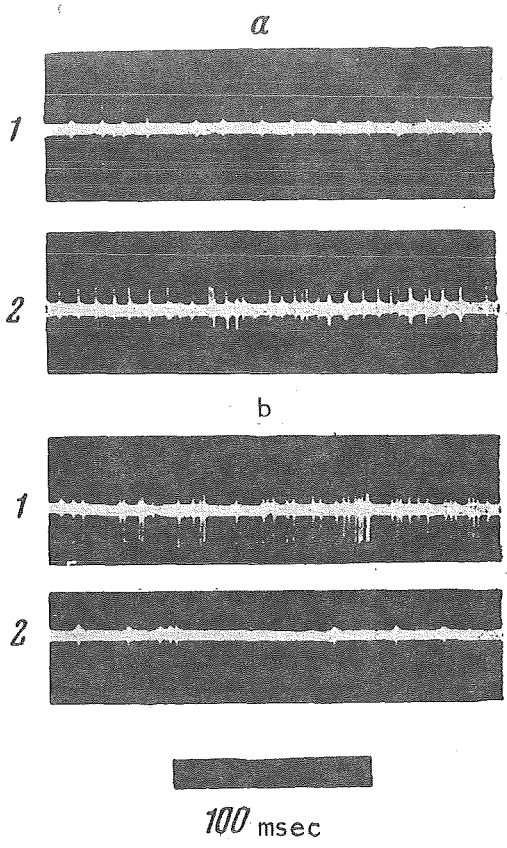


Figure 1. Spontaneously Active Neurons of the Optical Center of a Frog Responding to Isolated Stimulation of the Vestibular System. a, Intensification of discharge frequency; b, Inhibition of electrical activity; 1, Impulse activity of cell before stimulation; 2, Impulse activity of cell during stimulation of the vestibular apparatus

The reaction of the same spontaneously active units to isolated light and vestibular stimulation was atypical and often contradictory. Figure 2 shows a histogram of neuron discharges, in which the light signal increased the frequency of pulse activity, and vestibular stimulation decreased the frequency of pulsed activity. Elements are often encountered which do not respond to isolated light stimulation, and which are inhibited upon stimulation of the vestibular apparatus. /16

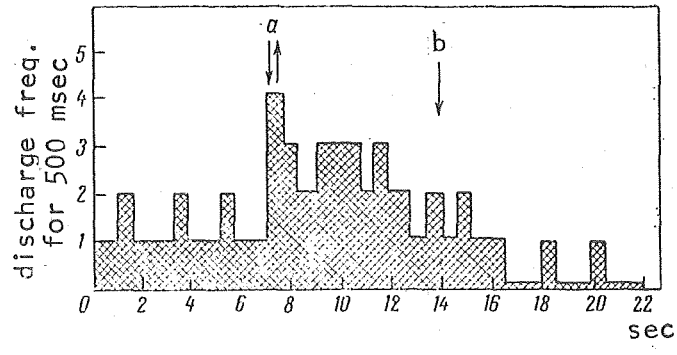


Figure 2. Frequency Distribution of Discharges in a Spontaneously Active Tectal Cell Upon Isolated Stimulation of Optical and Vestibular Systems. a, Light; b, Vestibular stimulation; c, Discharge frequency for 500 msec

Simultaneous stimulation of the vestibular and optical analyzers clearly revealed their close functional relationship. Responses of the majority of spontaneously active tectal cells to light stimulation were significantly affected by the vestibular system. This was evident in the variation of discharge frequency and the latent period of the response to the light signal in the case when it was present in the background of prolonged stimulation of the vestibular apparatus.

Light stimulation also affected the electrical activity of the neurons altered by vestibular stimuli. It is significant that in our experiments we often encountered neurons in which light stimulation removed inhibition of the activity caused by stimulation of the vestibular apparatus. Figure 3 shows two such neurons. It is obvious that significant inhibition of discharges in

one of the cells and total inhibition in the other caused by stimulation of the vestibular system was eliminated by a light stimulus. Only single spontaneously active cells did not alter their reaction to light upon addition of vestibular stimulation.

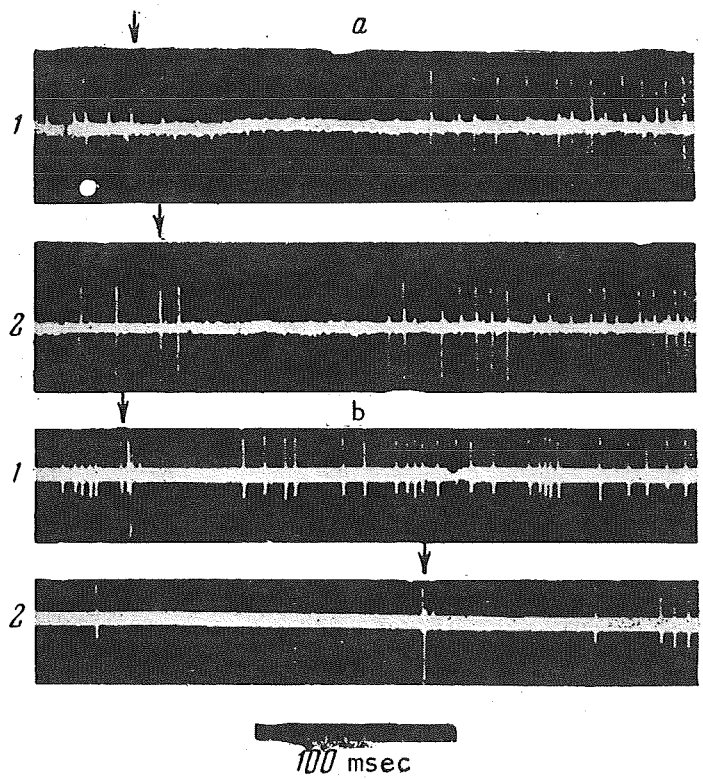


Figure 3. Reaction of Two Spontaneously Active Neurons (a and b) to Combined Stimulation of the Optical and Vestibular Systems. 1, Up to the arrow is background activity, and after the arrow is reaction to isolated light stimulation; 2, Up to the arrow is activity upon isolated stimulation of the vestibular apparatus, and after the arrow is activity upon combined stimulation of both systems. The arrow is the beginning of light stimulation.

Close functional interrelations between optical and vestibular analyzers at the neuron level were also revealed in recent years in warm-blooded animals. Polarization of the labyrinth in cats caused a significant variation in the frequency of discharges of the spontaneously active units of the optical center [7-9]. However, in distinction from results of our experiments, according to the data of a number of investigators, stimulation of the vestibular apparatus was usually accompanied by an intensification in the activity of these units. We shall dwell later on the possible reasons for disagreements in the investigations.

Tectal cells with a different type of response: the silent cells, i.e. those not having spontaneous activity, behave differently. They did not react to isolated stimulation of the vestibular apparatus, and responded only to a light flash. Units which adapt rapidly (those responding in a short burst of discharges) did not react at all to additional stimulation of the vestibular system to light stimulation (Figure 4a), and only in a small part of slowly adapting neurons (reacting to light stimulation in a long burst of discharges) did such an addition lengthen the latent period and sometimes decrease the number of discharges in response to the light stimulus (Figure 4b).

We know that cells having spontaneous activity predominate in the optical center; therefore, functional interrelations of the optical and vestibular /18

analyzers are apparently determined to a great extent by the reaction of spontaneously active rather than of silent neurons.

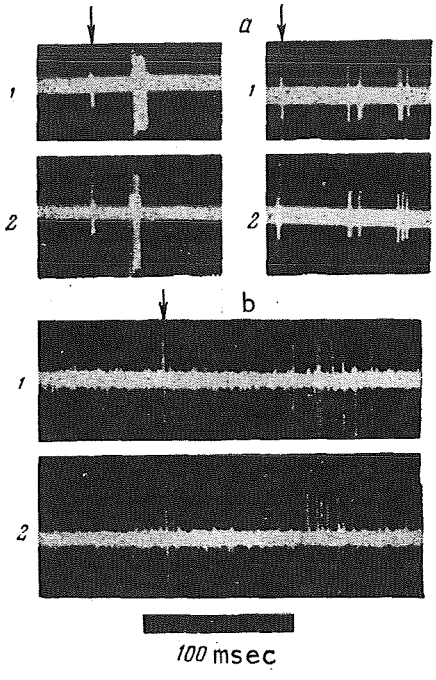


Figure 4. Responses of Silent Tectal Cells to Combined Stimulation of Optical and Vestibular Systems. a, Absence of modified reaction of the cell to light upon additional stimulation of the vestibular apparatus; b, Modified reaction of the cell upon additional stimulation of the vestibular analyzer; 1 and 2, Same as in Figure 3.

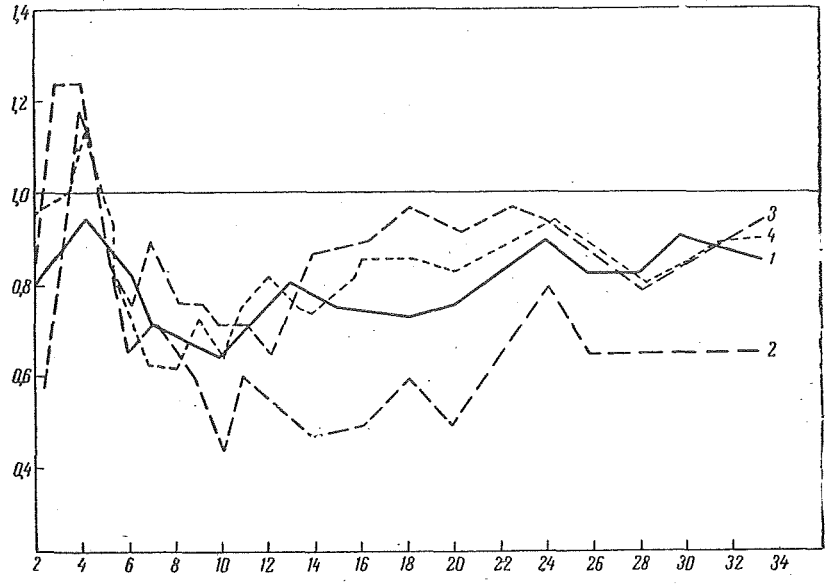
Thus, the work of different investigators on the study of cellular activity, and also the results of our experiments clearly reveal the close functional relationships of the optical center with the vestibular system at the neuron level. Cellular activity of the higher branches of the optical analyzer is under the direct or medium, but significant influence of effects issuing from the vestibular system, which in turn are regulated by processes developing in the optical center upon light stimulation.

General desynchronization of total electrical activity of the human and animal brain, caused by stimulation of the vestibular apparatus, has long been known [2-4, 6, 11]; however, only application of the methods of /19 automatic analysis of electroencephalograms (EEG) has made it possible to reveal the true nature of the variation in frequency components of the EEG during this stimulation.

It was established in the paper of N. P. Gordeyeva and V. A. Il'yanko, conducted on rabbits with electrodes implanted in the optical, parietal , motor and frontal regions of the cerebral cortex and in the reticular formation of the mesencephalon, that a variation in the electrocorticogram begins in all investigated regions of the brain upon automatic rotation of wide-awake animals in a specially equipped Barani chair (Figure 5). A decrease is observed in the amplitudes of all frequencies from 6 Hz and higher. It is expressed more sharply in the range 6-14 Hz. The amplitude of low-frequency components of the EEG increases, as a rule.

In order to explain the relationship of the variations in total electrical activity of the brain to the nature of stimulation of the vestibular apparatus, we have recently conducted similar research on rabbits with calorific stimulation of the labyrinth. According to preliminary data, the variation in the EEG frequency spectrum upon such stimulation of the labyrinth is similar to that observed during rotation of the rabbits, i.e. the amplitudes of average EEG frequencies decrease and low frequencies increase.

Comparison of the data obtained upon rotation of animals and upon calorific stimulation permits us to consider that similar variation of the total electrical activity of the animal brain is indeed caused by stimulation of the vestibular apparatus. Similar variations in the EEG spectrum of man were obtained upon stimulation of his vestibular system. M. P. Aronov [1] showed that when a man is rotated, EEG suppression begins in the frequency range of 5-20 Hz, and a significant increase of it begins at lower frequencies. It was important to clarify with what such a transfer of energy toward the low-frequency components of the EEG is related upon vestibular stimulations: whether with displacement of the dominant rhythm or with other effects. Special experiments [1, 5, 10] showed that an increase of low frequencies owed its origin to superposition onto the EEG of the electronystagmogram, caused by nystagmus synchronous in frequency with the low-frequency EEG components. This fact makes it possible to calculate the true variation of low frequencies of EEG upon vestibular stimulations. /20



frequency components of EEG, Hz

Figure 5. Mean Deviation from Background (Assumed to Be 1) of EEG Frequency Components Upon Stimulation of the Vestibular Apparatus. 1, Optical region; 2, Parietal region; 3, Motor region; 4, Reticular formation

We also analyzed the variation in the functional state of different regions of the animal and human brain, caused by vestibular stimulation, according to the reaction of the brain in assimilating rhythms of light flashes, which is a more refined indicator of the functional state of the brain than is EEG variation. A "Sonneklyat" photostimulator with a

significantly weakened flash intensity was used for rhythmic light stimulation.

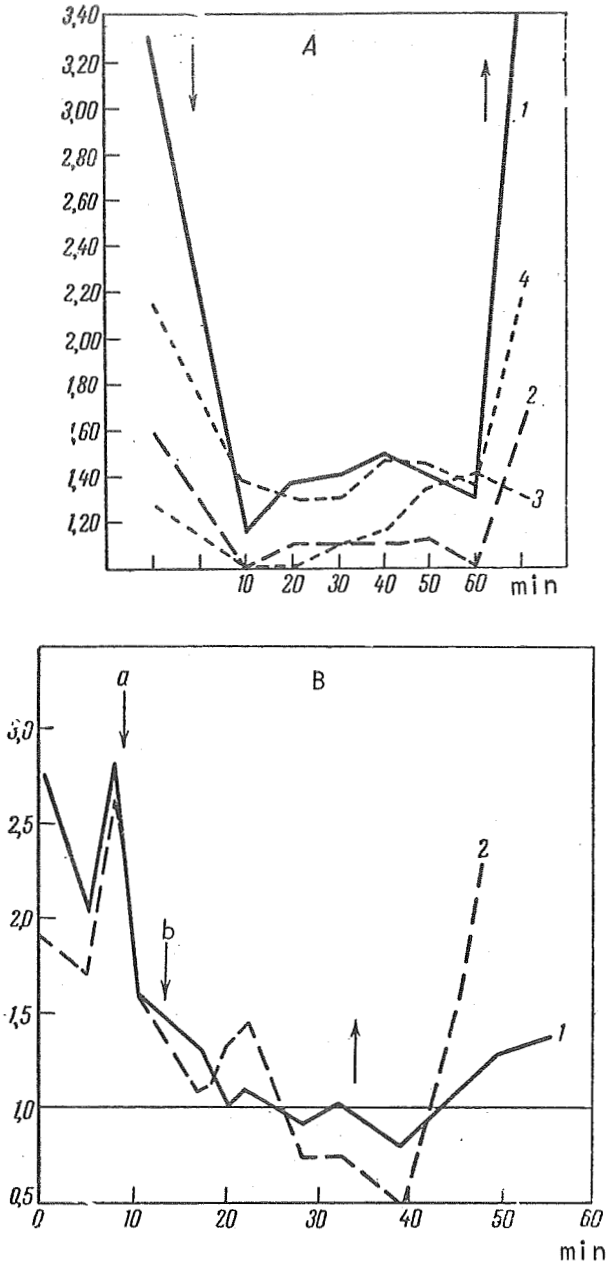


Figure 6. Variation in Reaction of the Brain Assimilating Rhythms of Light Flashes upon Stimulation of the Vestibular Apparatus. A, Average data in rabbits; B, Experiment on a human, 28 July 1964; a and b, 6 and 8 rpm; an amplitude of EEG oscillations of 7 Hz without light flashes was assumed as unity; 1, 2, 3, 4, Same as in Figure 5.

According to the data of N. P. Gordeyeva, reproduction by the rabbit's brain of the rhythms of light flashes in the background (before stimulation of the vestibular apparatus accomplished by rotating the animal) was clearly expressed in the occipital, parietal, motor and frontal regions of the cerebral cortex and in subcortical formations; moreover, the amplitude of the corresponding fluctuation was greater in the visual cortex and reticular formation, and less in the other cortical zones. Stimulation of the vestibular system caused a characteristic and significant decrease in the amplitude of the assimilated rhythm through all regions of the brain during the entire period of rotating the animal in the Barani chair (Figure 6A).

Similar variations in the reaction of the brain assimilating the rhythms of light flashes were obtained by V. A. Il'yanko and us upon stimulation of the vestibular apparatus in man (Figure 6B).

These are fundamental results of the work of the Laboratory of Analyzer Physiology of the Institute of Higher Nervous Activity and the Institute of Physiology of the USSR Academy of Sciences on the study of the effect of stimulating the vestibular apparatus of animals and man on the electrical activity of the visual center and other branches of the brain. /22

Thus, data of all the investigations mentioned here, as well as experimental data presented in this paper, indicate without doubt the significant variation of total and pulse activity of the brain caused by stimulation of the vestibular system.

It is necessary to note certain discrepancies in the results obtained by different investigators -- according to the data of some, similar stimulation causes inhibition, and according to others -- intensification of electrical activity. Consideration of the techniques used in the different papers indicates that this divergence is apparently caused first of all by the intensity, and also by the nature of stimulating the labyrinth -- weak stimulation of it causes inhibition of electrical processes, and strong stimulation causes them to increase.

A shift in electrical activity reflects a variation in the functional state of the brain which, according to the data of our experiments, survives for the entire period of stimulation of the vestibular apparatus. This variation leads to a deterioration in physiologically normal activity of both the visual center and of other regions of the brain -- to a phenomenon extremely undesirable when operating under real conditions related to unusual stimulation of the vestibular system.

Is it possible to compensate for this negative effect of vestibular stimulations? If we judge by the electrical reactions of the brain, we should seek possible compensatory mechanisms in conditions of creating a dominant focus in another section of the brain. The basis for this hypothesis is the following -- V. A. Il'yanok established that the variations described here in the reaction of the brain assimilating the rhythms of light flashes, which develop upon vestibular stimulations in both animals and man, are observed

only under conditions when the visual system is stimulated by a light of weak or medium intensity. If the visual analyzer is stimulated by bright intermittent or continuous light, the extent of this reaction remains unchanged or slightly increases upon additional stimulation of the vestibular apparatus. As indicated, stimulation of individual neurons of the visual center by light eliminated inhibition of their activity caused by vestibular stimulation. According to the data of Gorgiladze and Smirnov, suppression of all phases caused by a single light flash of potentials in the visual cortex and related to stimulation of the labyrinth was altered by recovery of their amplitude and even an increase under conditions when stimulation by a flash of the same intensity and duration was applied 10-15 times per second, i.e. when the total energy of the light was increased by an order of 1-1.5. The widely known psychophysiological investigations of the analyzer interaction of the Orbeli /23 and Kravkov school also indicate the possibility of suppressing the activity of a single analyzer by increasing the intensity of stimulation by another.

It is possible that creation of a dominant focus in some other section of the brain rather than the visual cortex may be very effective in compensating disruptions caused by unusual stimulations of the vestibular system.

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ACTIVITY OF THE PHASE AND TONIC SYSTEMS OF THE OCULOMOTOR APPARATUS IN CERTAIN VESTIBULAR REFLEXES AND IN VESTIBULAR NYSTAGMUS

D. P. Matyushkin

ABSTRACT. The phase and tonic systems of the oculomotor apparatus in rabbits during revolutions around the longitudinal axis of the body and to rotational postnystagmus is investigated. When an animal is rotated slowly around the longitudinal axis of its body in the direction of the muscle being studied, the function of the tonic system in it is intensified, and the phase system is brought into the reaction along with the tonic system upon rapid rotations.

It was assumed until recently in physiology that the motor part of the oculomotor apparatus (OMA) of mammals was constructed of functionally homogeneous units. Assumptions about their inhomogeneity have been made only in certain morphological papers [3, 6].

Physiological arguments of the duality of the motor complex of OMA, and the presence in it of special quick (phase) and slow (tonic) systems were presented in our papers published in 1961-1963. /24

With the help of electrophysiological techniques, in particular of the method of intracellular derivation of potentials, we succeeded in isolating two types of fibers, similar to those found in the skeletal muscles of amphibians, and the extrinsic ocular muscles of rabbits [1, 5]: phase type fibers generating quick (2 msec in duration) and high (80-90 mv) potentials of the effect carrying stimulation, and tonic type fibers which generate only slow (10-20 msec) and low (18-20 mv) oscillations of potentials of neuromuscular connections, not capable of carrying stimulation. In the total electromyogram, the phase fibers generate quick oscillations, usually of two-phase form, and the tonic fibers generate slow single-phase oscillations.

It was discovered that phase type fibers are innervated by α motoneurons (at a conducting rate of approximately 80 m/sec), and tonic type fibers are innervated by γ motoneurons (at a conducting rate of approximately 30 m/sec). Moreover, tonic fibers have multineuron innervation compensating their nonconductivity.

It was possible to separate the "total" contracting reactions of the ocular muscles of rabbits and cats, obtained upon electrical stimulation of their nerves, into phase and tonic components, and thus investigate the contracting properties of the phase and tonic masses of the fibers. Contractions of the phase fibers obtained upon superthreshold stimulations of α axons and subthreshold of less excitable γ axons were very rapid (the increment of

a single stress for 8-9 msec). Contractions of tonic fibers occurring upon stimulation of γ axons under conditions of selective anode blockade of α axons were much slower (increment of a single stress for 50-100 msec) and drawn out.

Our data on the dual nature of the OMA of mammals has been totally confirmed in morphological and electrophysiological investigations of the American scientists Hess and Pilar [4], who published their results after our paper was issued.

There are grounds (similarity of morphology, functional tasks, pharmacological properties, the nature of total electromyogram) to assume that the dual functional organization of OMA discovered in animals is present in man.

Calculations and experiments indicate that the phase and tonic systems of OMA have different ophthalmodynamic functions -- the phase system provides for various rapid movements of the eyes, and the tonic system provides for their slow movements and fixation. /25

Of special interest is the evaluation of the participation of phase and tonic systems of OMA in vestibular reflexes and nystagmus of the extrinsic eye muscles.

We investigated the behavior of the phase and tonic systems of OMA in vestibular reflexes to rotations around the longitudinal axis of the body (head-trunk) and in postrotational nystagmus of seven rabbits with an intact brain. During these experiments the "total" electromyogram of the outer eye muscles of the superior rectus of the extrinsic rectus were recorded and analyzed. Needle electrodes were implanted one in the venter musculi and the other in the muscle tendon; the mode of muscle function was isometric. It was possible, as a rule, to distinguish typical potential oscillations for the phase and tonic systems at a high drum rate of the electromyogram (EMG) in time.

During experiments with slow rotation of an animal around the longitudinal axis of its body toward the investigated superior musculus rectus (from a position of the paries upward), the slow electrical wave activity, i.e. functioning of the tonic system, increased in it. Upon fixation of the rotated position, the level of activity achieved was maintained and was proportional to the angle of rotation. The increase in the amplitude of slow EMG oscillations in this reflex was much greater than the increase in frequency, which probably indicates partial synchronization of γ motoneuron activity. We note that synchronization of γ motoneuron activity, innervating various sections of the same tonic muscular fibers, is feasible in a mechanical sense.

Returning the animal to its initial position decreased electrical activity of the muscle to its initial level, and rotation in the opposite direction decreased it to zero.

If rotation in the direction of the muscle being investigated is rapid (for example, at a rate of 90 deg/sec), the phase system (rapid two-phase effective potentials appeared in the EMG) became involved in the reaction along with the tonic system. From the physiological point of view, involvement of the phase system in the reaction is justified in a given case by the necessity for rapid compensation of eyeball rotation.

During postrotational nystagmus of the extrinsic musculus rectus, caused by tenfold rotation of a rabbit in a manual centrifuge at a rate of 1 rpm with subsequent sudden stopping, the EMG looked different depending on the direction of nystagmus. If the direction of nystagmus was such that the muscle being studied functioned actively in the slow phase (stress was recorded electrographically with the help of a piezocrystal), slow oscillations of ordinary single-phase form and sometimes with slight mixing of rapid oscillations, increasing in amplitude and frequency, were observed during the slow phase on the EMG; the activity terminated during the rapid phase. /26

With the nystagmus in the opposite direction, when the muscle being studied functioned actively in rapid phases, the EMG was a burst of typically rapid two-phase reaction potentials of high amplitude with a mixture of lower slow oscillations, and the EMG of the slow phase was a series of slow oscillations of low amplitude, decreasing to zero at the end of the period.

Thus, experiments indicate that slow phases of nystagmus are provided mainly by the tonic system, and rapid phases by the phase system. It should be noted that the duration of the burst of rapid reaction potentials (during rapid phases) hardly varies during damping of nystagmus, and also varies insignificantly from experiment to experiment, remaining within the limits of 0.08-0.12 sec. Apparently the activity of the period of phase system activity, during which rapid motion of the eyeballs is accomplished and the visual function is disrupted, is provided for by some special mechanism. Duration of the periods of tonic system activity under these conditions varies over wide ranges according to variations in the periods of nystagmus.

The results considered by investigating nystagmus of individual eye muscles set in the isometric mode apparently reflect basic laws of the distribution of the function between the phase and tonic systems of OMA in vestibular reflexes when they occur in a natural situation.

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ELECTROPHYSIOLOGICAL INVESTIGATION OF THE INTERACTION OF THE VESTIBULAR AND VISUAL AFFERENT SYSTEMS

G. I. Gorgiladze and G. D. Smirnov

ABSTRACT. The effect of vestibular stimulation (polarization of the labyrinth by direct current) on stimulation in the visual system and on the activity of individual neurons in the visual cortex of the cat is studied. Results of the experiments permit us to conclude that the effect of polarizing the labyrinth on the primary visual cortex of the cat is of a nonspecific nature.

The close functional relationship and interaction of vestibular reception /27 with other systems of spatial perception, first of all with the visual and somatosensory systems have been shown by numerous physiological and psychological investigations [3, 4, 11, 20, 22, 25 and 29].

Interaction between the visual, vestibular, and also the somatosensory systems should provide a subjective stability of the visible world. Disruption of this interaction, due to cessation of the flow of impulses from the vestibular apparatus [31] or due to strong vestibular stimulation, may elicit visual disorders. Study of the interaction of various analyzer systems becomes especially important to aviation and space medicine [1, 6, 19].

Diverse illusions of spatial perception [5, 10, 12-14] may develop under conditions of weightlessness, and also due to the effect of other physiological and psychic factors which accompany them or develop during space flights. It should be noted that the function of the vestibular apparatus is especially disrupted during weightlessness [18, 19].

Future development of space flights will be related to the appearance of spatial orientation mechanisms, and also to the search for means of eliminating disruption of normal interaction between different functional systems.

Electrophysiological data on the effect of the vestibular apparatus on the optical system were published comparatively recently [23, 24]. It was shown in preparations of encephale isole of the cat that stimulation of the vestibular apparatus (polarization of the labyrinth by a direct current) causes the activity of most neurons of the visual cortex of both hemispheres to intensify with a latency period of 25-200 msec; neuron reactions to light stimulation also increased, and the critical frequency of flashes was increased.

Grüsser, Grüsser-Cornehls [23] and Jung [26, 27] confirmed that, although the vestibular effect is reflected in the visual neurons after a relatively

prolonged latency period, it is also specifically different from those variations in neuron activity which are caused by stimulation of nonspecific structures of the brain stem [21, 17]. It was assumed that nonspecific reticulo-thalamic structures not only have a more general effect on the /28 cortex, in the sense of a variation in the dynamics of processes taking place within it, but it also fulfills a more complex function and may be the transfer point of a specific effect. Hence, the conclusion was made that the primary visual zone is the formation into which specific afferentation enters not only from the retina, but also from the vestibular apparatus.

In this paper we studied the effect of vestibular stimulation (polarization of the labyrinth by a direct current) on conduction of stimulation in the optical system and on the activity of individual neurons in the visual cortex of the cat.

Method

Experiments were carried out on 68 unanesthetized curarized cats under conditions of crepuscular adaptation of the eyes. The head of the animal was secured in a stereotactic device. The entire period of preparing for the experiment was carried out under a general ether anesthetic. The spots of fixation and wound areas were anesthetized by a 1% solution of novocaine. The atropinized eye was stimulated by light flashes (1/3-15 flashes per sec).

Electrical activity from the visual cortex (area 17), the corpus geniculatum laterale (CGL), the chiasm and the retina was recorded. The lead was unipolar -- an indifferent electrode was embedded in the skin of the forehead. The optic nerve in part of the experiments was stimulated by an electrical current in the region of the chiasm or CGL.

Recordings of elicited responses were carried into a "Diza Elektronik" cathode oscillograph with parallel recording on an eight-channel Alvar ink-writing electroencephalograph.

Activity of individual optic elements was recorded extracellularly from contralateral area 17 (gyrus lateralis medialis) by microelectrodes of Pyrex glass, filled with 2.7 mole % of a KCl solution (diameter of the microelectrode end was 0.5-2 μ).

Neuron activity was recorded on an "Amplior" cathode oscillograph. The ECoG was recorded simultaneously on an ink-writing electroencephalograph. A chlorinated silver electrode 0.3 mm in diameter was implanted in direct proximity to the microelectrode in order to conduct the ECoG to the surface of the cortex. An indifferent electrode was attached to the bone of the forehead.

Vestibular stimulation was elicited by polarization through an electrode placed on the osseus ring of the fenestra teres by a 0.05-0.50 ma current

[8]. In order to elicit a reaction of ECoG activation, alegesic stimulation of the skin of the front extremity by an electrical current or high-frequency stimulation of the mesencephalon reticular formation was used. /29

Results

A. Effect of Labyrinth Polarization on Conduction of Stimulation in the Optic System

1. Single light flashes. Labyrinth polarization by a 0.1-0.12-ma force (the active electrode is the cathode or anode) causes suppression of induced potentials to single light flashes in the visual cortex of both hemispheres (Figure 1). Both primary positive and negative phases (especially negative) and later components of induced potentials are inhibited. General activity of the background rhythmicity of the cortex is observed simultaneously. Inhibition of induced potentials continues during the entire period of labyrinth stimulation, and they recover completely 20-30 sec after the polarizing current has been switched off, simultaneously with disappearance of the activation pattern in the background ECoG. Suppression of induced potentials is apparently of purely cortical origin, because it is not present in other sections of the optic system -- in the retina, chiasm and CGL, although in a number of cases insignificant suppression may sometimes be observed in the CGL. This inhibiting effect of labyrinth polarization on induced potentials in the visual cortex was observed in most experiments. However, in some experiments the amplitude of induced potentials did not vary, and increased very rarely.

Variations of induced potentials upon labyrinth polarization are not limited to the visual cortex. The amplitude of induced potentials in the auditory cortex and that of the transcallosal responses (Figure 2) decreased simultaneously. Stimulation of the mesencephalon reticular formation or labular stimulation of the skin on the background of ECoG activation had a similar effect on those induced potentials.

2. Rhythmic light flashes. When the eye is stimulated by light flashes in a 10-15-per-second rhythm, a different pattern is observed. The amplitude of responses in a normal cortex drops after a certain period upon such light stimulation and a decrease of individual responses (transformation of rhythm) develops. Upon labyrinth polarization, induced potentials follow the stimulation rhythm and even increase in amplitude. This alleviation of /31
responses continues for several seconds and gradually returns to the initial background upon continued polarization (Figure 3). Alleviation of reaction to rhythmic stimulation of the eye was also observed in the background of electrical stimulation of the mesencephalon reticular formation.

3. Electrical stimulation of the optic tract. Polarization of the labyrinth results in an increase of induced potentials both to solitary and rhythmic stimulation of the chiasm or CGL. When the chiasm is stimulated,

responses may also be alleviated at the CGL level. Stimulation of the reticular formation also causes intensification of induced potentials of the cortex upon solitary or rhythmic stimulation of the chiasm or CGL (Figure 4).

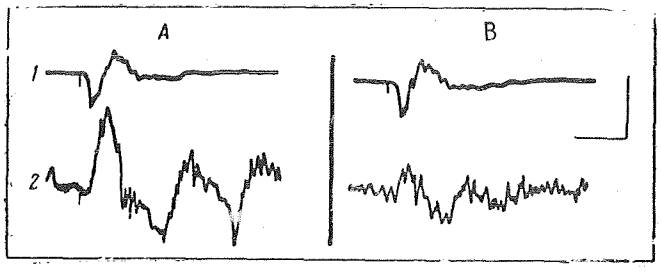

Figure 1. Inhibiting Effect of Labyrinth Polarization on Induced Potential in the Sinistral Optic Region. Right eye is stimulated by single light flashes. A, Standard, before labyrinth polarization; B, During polarization of the sinistral labyrinth (0.03-ma cathode); 1, CGL; 2, Visual region of the cortex. Calibration: 500 mcv, 100 msec

B. Neuron Reactions in the Visual Cortex to Labyrinth Polarization

A total of 125 neurons from area 17 were recorded. According to the nature of the reaction to light, these neurons correspond to five types, described earlier by Jung and his colleagues [27], no dependence of their distribution on the section of the cortex within the environs of area 17 or on the depth of microelectrode implantation being revealed.

Almost all neurons possessed /32 spontaneous activity, with the exception of two which were activated only to a light flash (C-type). Spontaneous activity is dependent on background ECoG. Spontaneous activity of the neuron is usually higher when overcoming rapid oscillations in the ECoG than that during overcoming slow waves.

Polarization of the ipsi- or contralateral labyrinth by a cathode or anode on the background of ECoG activation with a latency period of 25-250 msec activates most optic neurons. The neuron activation threshold /34 coincides with primary variations in the ECoG (0.08-0.15 ma). According to the nature of the reaction to labyrinth polarization, the neurons may be divided into three types, similar to those described earlier [23].

Type a (14%) -- lack of variations to labyrinth polarization (Figure 5A).

Type b (37%) -- intensification of activity when polarizing current is switched on, part of the neurons possessing rapid adaptation and returning to normal activity within the first 1-4 sec, the other part maintaining increased activity over the entire period of labyrinth polarization with weakly expressed adaptation (Figure 5B and C).

Type c (49%) -- activation to switching on and switching off the polarizing current; duration of activation to switching on and switching off of polarizing current varied from 2 to 20 sec (Figure 5D).

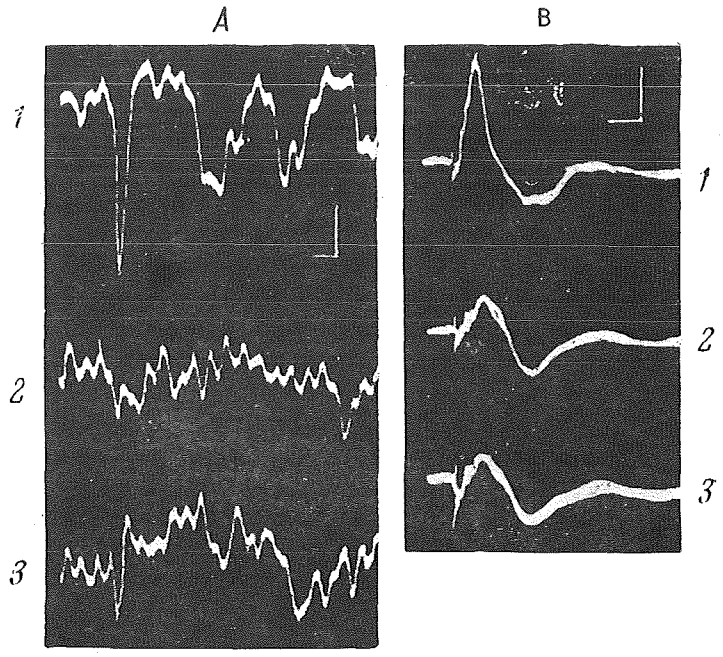

Figure 2. Effect of Polarizing the Dexter Labyrinth on Induced Potential in the Right Auditory Region of the Cortex (gyr. ectosylvius medialis) in Response to an Acoustic Click (A) and Transcallosal Response (B) in the Region of Gyr. Suprasylvius medialis. A: 1, Standard, before labyrinth polarization; 2, During polarization of the dexter labyrinth (0.3-ma cathode); 3, 25 sec later, after beginning of polarization; B: 1, Standard (15 v, 0.1 msec); 2, During labyrinth polarization (0.3-ma cathode 3, During alegesic stimulation of skin of the front paw by electrical current. Calibration, 200 μv, 50 msec

Neuron activation increases as the intensity of the polarizing current increases.

Figure 6 presents a schematic representation of these types of neurons. In no case was inhibition of neuron activity observed in the primary visual projection zone in response to labyrinth polarization.

Investigation of the same neuron reactions to alegesic stimulation of the skin indicated a total parallelism between variation of neuron activity and ECoG activations. Even in a small number of neurons, spontaneous activity did not vary, those same neurons also not being activated by labyrinth polarization (type a).

The lower the spontaneous activity of the neuron, the more distinct its activation appeared upon polarization of the labyrinth or alegesic stimulation of the skin. Simultaneous stimulation of the labyrinth and skin increased neuron activity significantly higher than each stimulation separately.

It is important to note that the existence of different types of neuron reactions to labyrinth polarization is not a unique feature of the visual cortex. We have also recorded such neuron types in other cortical sections (gyr. ectosylvius medialis and gyr. suprasylvius medialis).

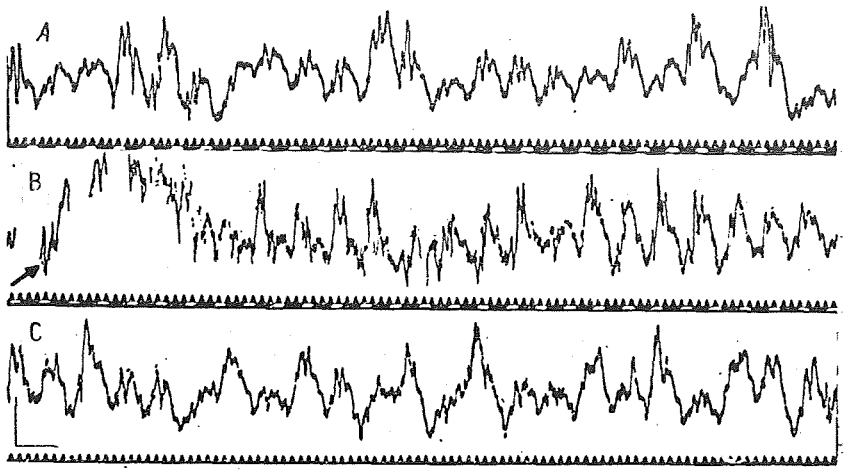

Figure 3. Effect of Labyrinth Polarization on Induced Potentials in the Optic Region of the Cortex. The eye is stimulated by light flashes at a frequency of 12 per sec. The arrow denotes switching on of polarization (0.3-ma cathode). The large deviation on the ECoG is an artifact to switching on of the direct current. Calibration, 100 μv, 100 msec; A, B, C, Individual sections of ECoG recording

It should be noted that in the motor cortex (gyrus sigmoideus anterior), in distinction from the optic region, where reaction to labyrinth polarization is expressed only in activation of neurons, inhibiting effects similar to reactions in vestibular nuclei are also observed [7]. In this region of the cortex, part of the neurons were activated to polarization of the ipsilateral labyrinth by a cathode, and inhibited by an anode; contralateral cathodization on the other hand suppressed neuron activity, and anodization activated /36
it (Figure 7).

Polarization of the labyrinth together with an increase in activity stabilizes and intensifies the neuron type to a light flash. If the neuron reacts weakly to light, or instability in the reaction develops, polarization of the labyrinth delineates very clearly the affiliation of this neuron to one or another type. Inhibitory phases usually become shorter, and the number of impulses during the active phases increases significantly. For example, Figure 8 shows two neurons from area 17 which belong to type b. A neuron with a short latency period emits a high-frequency burst of impulses to a light flash (denoted by the small arrows), after which an inhibited burst 160-170 msec in length follows. A second, somewhat more prolonged activated phase and a second inhibited phase 240-280 msec long then begin. Polarization of the labyrinth affects the induced activity of these neurons in the following manner -- the number of impulses in the first activated phase almost doubles, and the first inhibited phase is reduced to 80-120 msec.

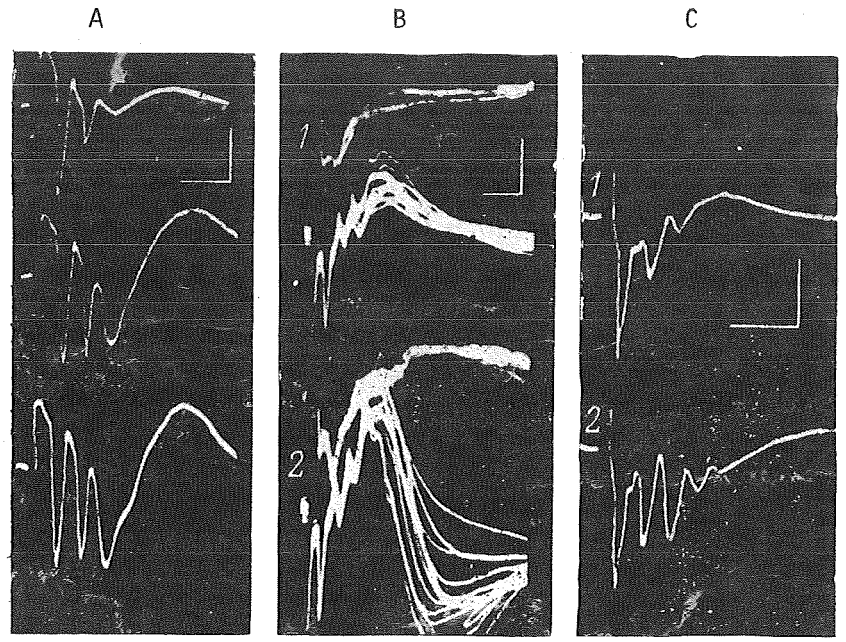

Figure 4. Alleviation of Induced Potentials in the Right Visual Cortex to Solitary and Rhythmic Stimulation of the Chiasma upon Labyrinth Polarization and Stimulation of the Mesencephalon Reticular Formation (A and B) and to Solitary Stimulation of the NKT upon Polarization of the Labyrinth (C). A, Induced potential to solitary stimulation of the chiasm (10 v, 0.1 msec): 1, Standard; 2, During polarization of the sinistral labyrinth (0.25-ma cathode); 3, During stimulation of the mesencephalon reticular formation (7 v; 250 per sec, 1 msec). Calibration, 400 μv, 10 msec. B, Induced potential to rhythmic stimulation of the chiasm at a frequency of 10 per sec: 1, Standard; 2, During polarization of the labyrinth (0.25-ma cathode). Calibration, 400 μv, 10 msec. C, Induced potential to solitary stimulation of the NKT (6 v, 0.1 msec): 1, Standard; 2, During polarization of the labyrinth (0.3-ma cathode). Calibration, 500 μv, 10 msec

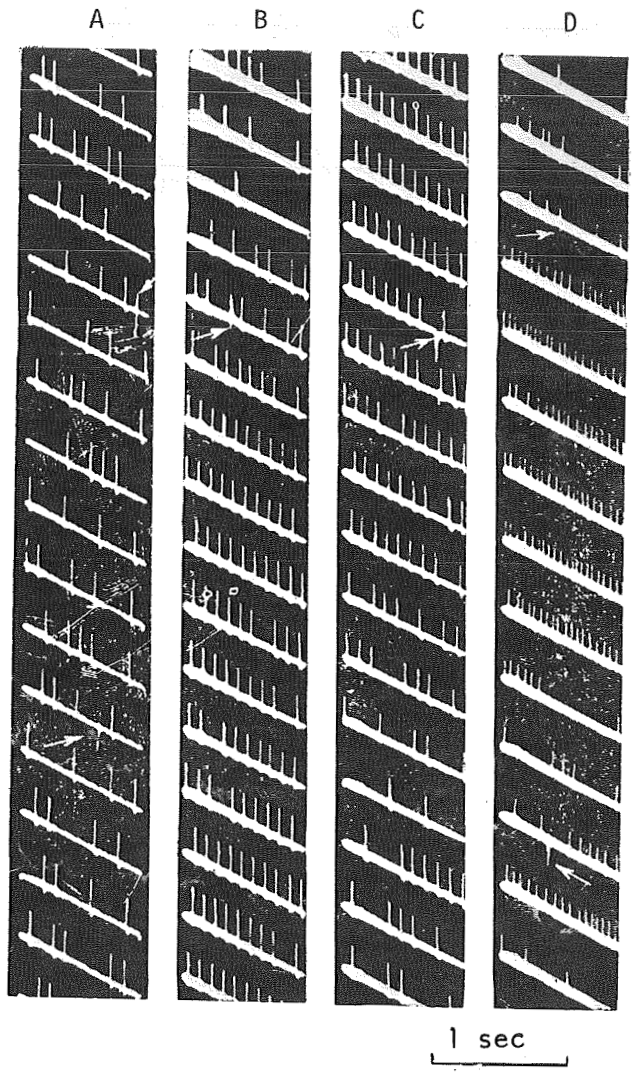

Figure 5. Different Types of Neuron Reactions of the Left Optic Region of the Cortex to Labyrinth Polarization. The right labyrinth is polarized (0.3-ma cathode). A, Neuron not reacting to labyrinth polarization (type a); B and C, Neuron activated to switching on of polarization (type b); D, Neuron activated to switching on and switching off polarizing current (type c). The arrows denote the moment of switching on and switching off the polarizing current.

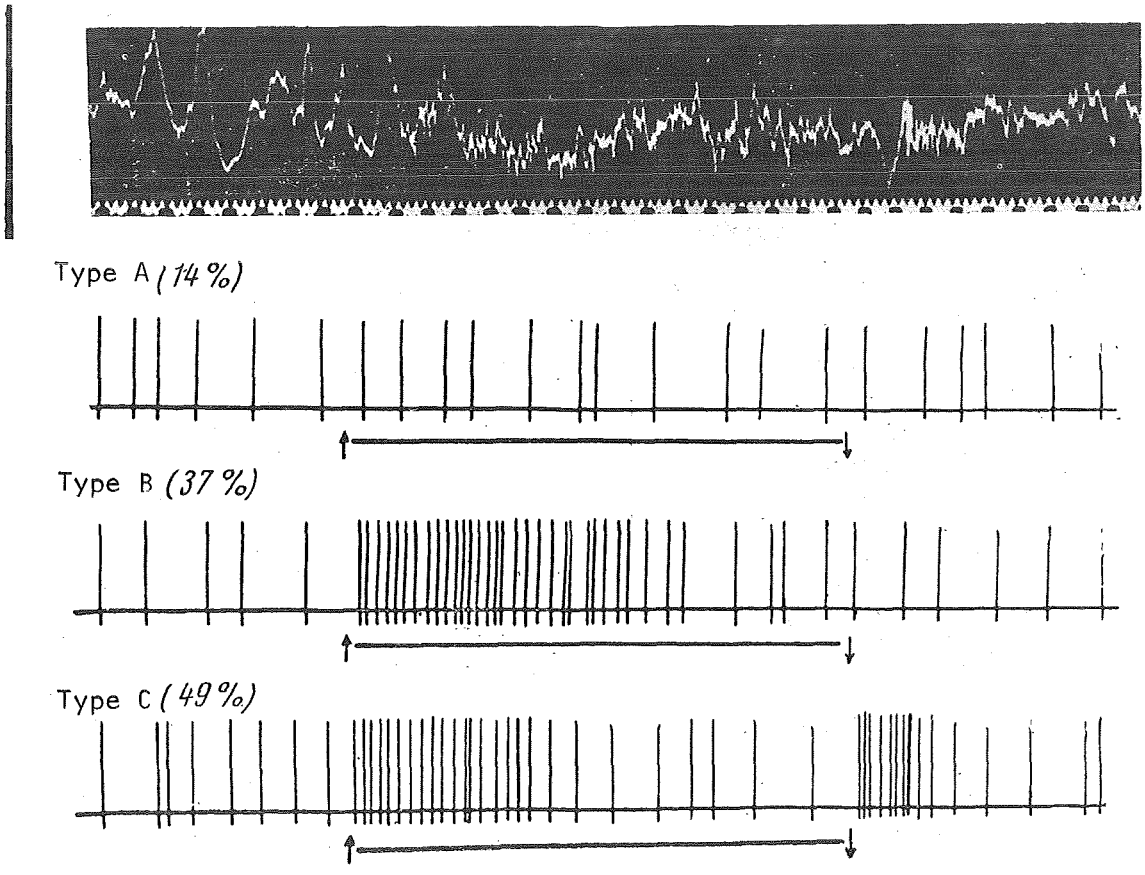

Figure 6. Schematic Representation of Three Types of Neurons of the Optic Region of the Cortex (Area 17) of the Cat As a Function of Labyrinth Polarization. The arrows indicate switching on and switching off the polarizing current. Variation of the ECoG, derived from the right gyr. lateralis medialis to polarization of the left labyrinth (0.25-ma cathode) is given above.

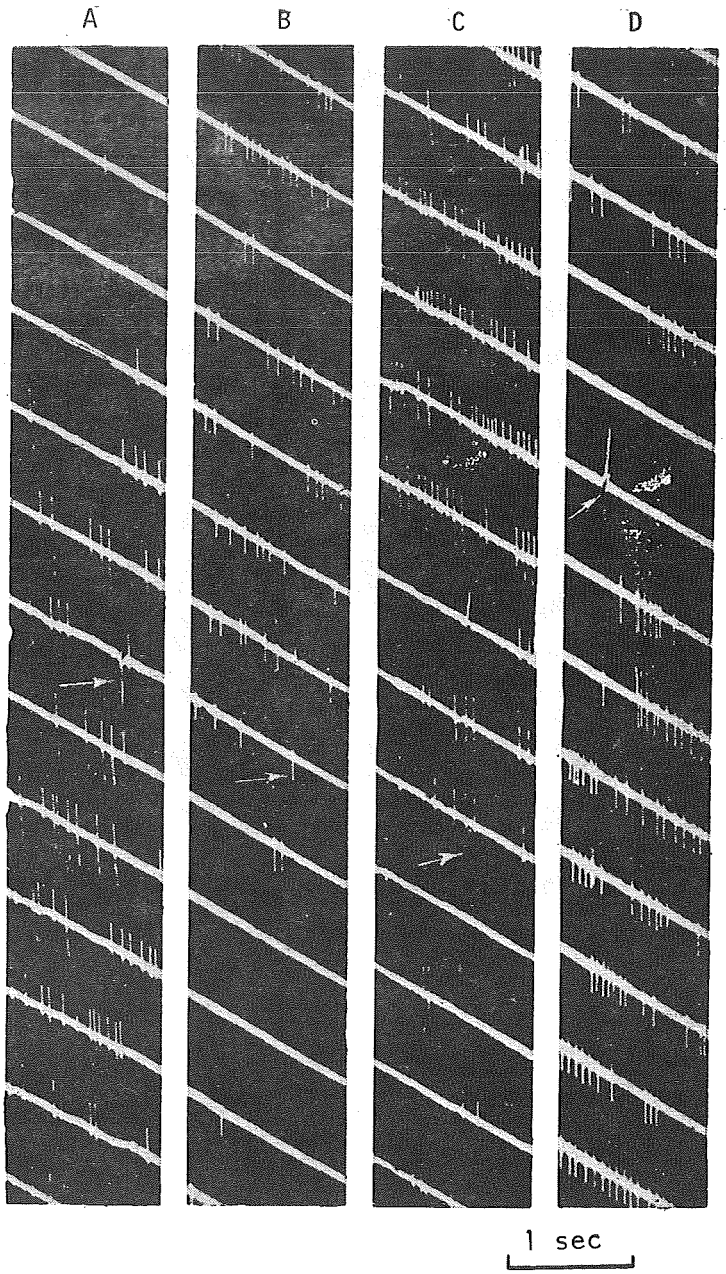

Figure 7. Effect of Labyrinth Polarization on Neuron Activity from Right Gyr. Sigmoideus Anterior. The ipsilateral labyrinth is polarized by cathode (A) and anode (B), and the contralateral labyrinth is polarized by cathode (C) and anode (D). Current intensity in all cases is 0.5 ma. The arrows indicate the moment of switching on the direct current.

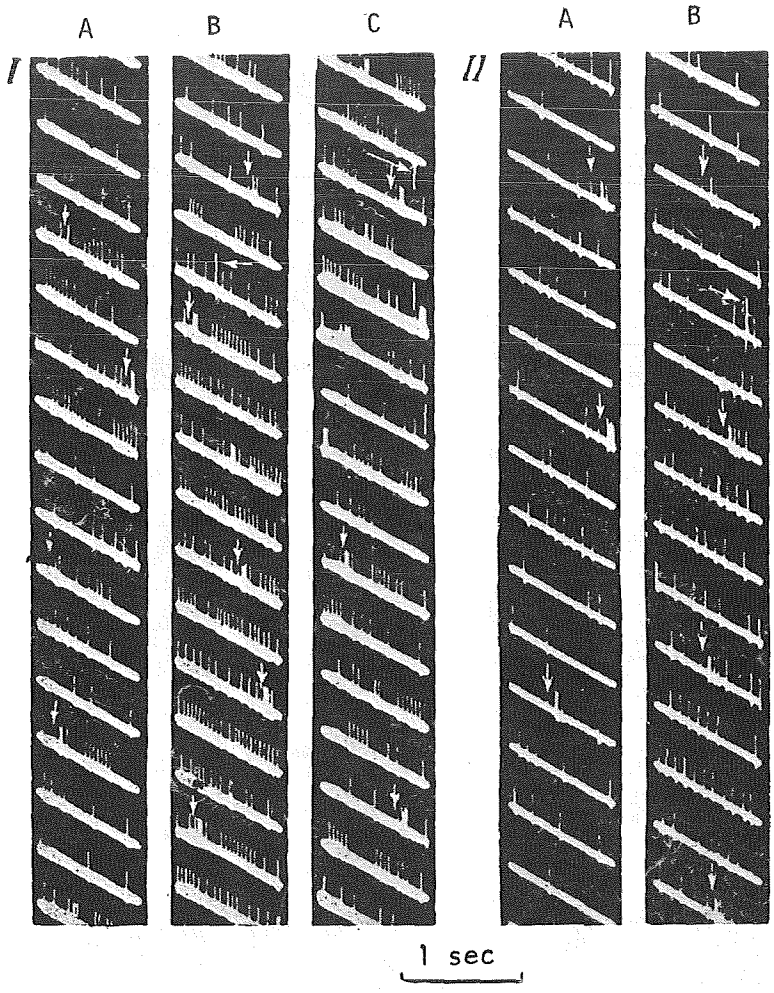

Figure 8. Effect of Right Labyrinth Polarization (0.25-ma cathode) on b-neurons of the Left (I) and Right (II) Optic Regions of the Cortex. A, Standard; B, During labyrinth polarization; C, After switching off of polarization. The small vertical arrows indicate the illumination of the left eye by solitary light flashes, and the large arrows indicate switching on and switching off of polarization.

The second activated and second inhibited phases vary in a similar manner.

During the course of polarization, neuron reaction, despite the pattern of electroencephalographic activation maintained, may return to the initial level. Labyrinth polarization, despite significant activation of neurons, often does not vary the activated or inhibited phases, but stabilizes response reactions of neurons to a series of high-frequency flashes, i.e., the lability of a given reaction increases.

There are no correlations between specific visual and vestibular types. Thus, neurons belonging to different visual types may react according to type b.

Like labyrinth polarization, alegesic stimulation of the skin intensifies or stabilizes response reactions of neurons to light (Figure 9).

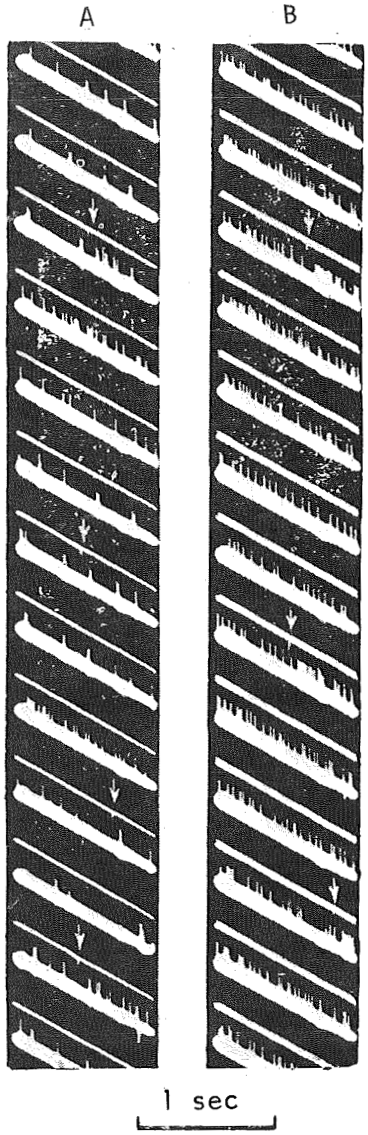

Figure 9. Effect of Alegesic Stimulation of Skin of Front Paw by Electrical Current on Induced Activity of b-Neuron in Right Optic Region. A, Standard; B, During alegesic stimulation of skin. Arrows indicate light flashes directed at left eye.

It is important to note that not once, even upon sharply expressed intensification of impulse activity in response to labyrinth polarization or to alegesic stimulation of the skin, did the reaction of neurons to light stimulation disappear. The type of reaction also did not vary, if we disregard the appearance of the reaction in several neurons of type a; these neurons begin to respond to light flashes in the background of labyrinth polarization or skin stimulation.

Discussion

The investigation carried out indicated that polarization of the labyrinth causes variation in the excitability of the optic system in the cat. /39 The basic effect in this case is noted at the level of the cerebral cortex, and consists of inhibition of induced responses to solitary light flashes and intensification upon rhythmic light stimulation. Certain variations, judging by electrical reactions, may also be observed in the CGL. It should be noted that Grüsser, Grüsser-Cornehls and Saur [24] did not observe any variations in the activity of individual nerve elements of the CGL in response to labyrinth polarization when they were being recorded. In the experiments of Jung and his colleagues [28], labyrinth polarization also increased the activity of CGL neurons, but upon condition of the cortex remaining intact. At the same time, responses to electrical stimulation of the chiasm or NKT during labyrinth polarization are alleviated upon both rhythmic and solitary stimulations. Variations in induced potentials are observed in the background of overall ECoG activation.

These results contradict the experiments of V. G. Samsonova [15], who observed a decrease in amplitudes of EEG fluctuations to rhythmic light flashes (7-33 Hz) in a human being rotated, and they contradict her conclusion about the inhibiting effect of the vestibular system on cortical structures of the visual analyzer. We showed that labyrinth polarization, by eliciting generalized ECoG activation, affects induced responses identically both in the /40 visual and auditory cortexes, and also affects the transcallosal response. On the other hand, direct electrical stimulation of the mesencephalon reticular formation or alegesic stimulation of the skin, accompanied by such ECoG fluctuations, have a similar effect on the responses.

The results of experiments carried out indicate that variations of neuron activity in the primary optic zone of the cortex and their reaction to light upon vestibular stimulation caused by labyrinth polarization are the same as for those caused during alegesic stimulation. In both cases there is a close relationship between generalized ECoG activation and variations in the reaction of individual neurons.

In distinction from the German authors [24], we were unable to find a fourth type of neuron activated only by switching off the polarizing current. The fact that the effect of vestibular stimulation on the primary optic projection zone is not specific, i.e. is not related to the feeding of information typical for a given system of receptors to the cortex, is also

confirmed by the similarity in variations of neuron activity observed under the same conditions in various regions of the brain. Moreover, the presence of neurons in the primary visual cortex, reacting differently to labyrinth polarization, and also the uniformity of reactions expressed only in activation (in distinction from the more complex pattern to stimulation of nonspecific structures of the brain stem) are one of the main reasons for the assumption that vestibular pulsation has a specific effect on neurons of area 17, and at the same time provides "regulation of perception stability of the visual world" [23, 26, 27]. This assumption was also made on the basis of generally known psychophysiological observations. But these observations may also be explained without assuming a specific vestibulo-optic coordination in the visual cortex. Thus, for example, we know that stimulation of the vestibular apparatus in man (rotation or galvanization of the mastoid processes) causes disruption not only of the visual, but also of the auditory and tactile senses [4].

Jung and his colleagues [28, 30] subsequently varied somewhat their views; they indicate that the vestibulo-optic convergence in the primary optic zone of the cortex is not a specific sensory regulation, but is expressed in the nonspecific pattern of activation.

The investigations carried out emphasize the leading role of the reticular formation of the brain stem in propagating vestibular stimulation to the cerebral cortex. In this regard our data agree with Molnar's conclusions, who proposed that the reticular formation participates in accomplishment of vestibular effects on the cerebral cortex based on the fact that artificial /41
epileptogenic foci, created beforehand in different zones of the cortex, were activated in this case. It should be pointed out at the same time that vestibular stimulation, compared to other afferent effects, was the most powerful activator of the brain stem reticular formation, and was eliminated by significantly higher doses of pharmacological substances blocking this system [9].

Our observations also indicate that neuron reactions in the visual cortex increase and become more defined in the background of vestibular or alegesic stimulation. Moreover, participation of the brain stem reticular formation in this process permits us to suggest that a decrease in the level of vestibular effects may under specific conditions be compensated due to other afferent systems.

Conclusions

1. Polarization of the labyrinth, like alegesic stimulation of the skin or direct electrical stimulation of the mesencephalon reticular formation, in most cases inhibits induced responses in the optic region to adequate stimulation of the eye by individual light flashes.

2. Induced responses to rhythmic light flashes or to individual and rhythmic stimulations of the optic track by an electrical current are alleviated in the background of those stimulations.

3. Three types of optic neurons to labyrinth polarization are distinguished; however, the same types of neurons were also discovered in nonoptic regions of the cortex.

4. Alegesic stimulation of the skin activates all those neurons which are activated by labyrinth polarization, with the exception of a small portion (14%) of neurons which do not react to labyrinth polarization. Inhibition of neuron activity to labyrinth polarization or to alegesic stimulation of the skin was not noted.

5. Polarization of the labyrinth and alegesic stimulation of the skin intensify and stabilize response reactions of neurons to light flashes on the background of electroencephalographic activation.

The identity of the effects of vestibular alegesic and reticular stimulations indicates that the effect of labyrinth polarization on the primary visual cortex of the cat has no specific character.

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A MATHEMATICAL MODEL OF THE OCULOMOTOR APPARATUS

A. A. Petrov, V. G. Sragovich and B. G. Sushkov

ABSTRACT. A mathematical model of the OMA is proposed in the form of the aggregate of neuron networks which function according to physiological principles. A qualitative explanation of certain reflex movements of the eyes is given, and results are presented of experiments on an OMA model run on an electronic computer.

Functioning of the oculomotor apparatus (OMA) has long attracted the attention of physiologists, neuropathologists and psychologists as an example of a relatively accessible motor system controlled only by nervous effects. The OMA is an indicator of vestibular effects and an example of a "vital" servosystem; therefore, it has become the object of attention of engineers trying to describe functioning of the OMA within the limits of automatic control theory. In our opinion, the language of neuron networks and of automation theory is more prospective and adequate. Numerous neurophysiological and psychophysical experiments surveyed in extensive monographs do not permit us to give the overall picture of the system which controls eye movements. /43

It was discovered in the cycle of papers of D. P. Matyushkin that the OMA of rabbits is formed by two motor systems -- T (the tonic or slow) and P (the phase or rapid), and the relationships between them have been investigated. D. P. Matyushkin presents data showing that the OMA of man also possesses a dual structure. These results are based on a proposed mathematical model of the OMA in the form of an aggregate of neuron networks which function according to principles generally accepted in physiology.

As factual data on the OMA increases, this model should be improved and should provide predictions about new effects of eye movements by stimulating experimental investigations.

1. The control system of the OMA is a multilevel system, in which each higher level controls the operation of the lower levels. This control is accomplished through variation of the states of lower levels by the diffused effect on their parts or on the entire aggregate of neurons which form them.

The lower primary level of the system is the motor complex consisting of the extrinsic eye muscles, nuclei III, IV and VI of the craniocerebral nerves and corresponding motor tracts. The primary level is the slave organ and is under the activating or coordinating effect of the second level, which is reasonable to relate anatomically to the system of the posterior longitudinal fasciculus and to sections of the reticular formation.

Higher levels of OMA control include vestibular, visual, cortical and other effects.

Let us consider the second level in more detail. Its function is to maintain the tonus of the extrinsic eye muscles and to maintain a given position of the eyes with respect to orbits which may be disrupted by various /44 random effects on the motor complex. Activation of the motor neurons of the oculomotor nuclei in order to maintain the tonus of the eye muscles is accomplished by OMA control of the motor complex activators (MCA) which make up the second level.

Due to the effect of all possible nonspecific effects[1], the MCA diffusely stimulates the tonic motor neurons (TMN) of the eye muscles. Since the model concepts presented here lay claim only to explanation of the logic of OMA function, we shall limit ourselves for simplicity to consideration of the control of two mutually antagonistic muscles in each eye (for example, intrinsic rectus and extrinsic rectus muscles). Upon analysis of the logic of OMA functioning, it is also immaterial whether the MCA of one muscle is an isolated localized nerve structure or part of some structure common for all extrinsic muscles of the eyes, or an abstract concept denoting the aggregate of all nonspecific effects of this muscle on the tonic system. Therefore, we may consider that each muscle corresponds to its MCA. We shall enumerate the four muscles we studied in the order of their natural arrangement (designating 1 as the abductor muscle of the left eye, 2 as the intrinsic rectus of this eye, 3 as the intrinsic rectus of the right eye and 4 as the abductor of the right eye).

The activity of the MCA determined by the effect of many factors has an irregular character. The simplest movements of the eyes -- tremors and drift -- are irregular and asynchronous in both eyes, and are explained by irregular stimulation of the TMN from the MCA.

The coordinating function (stabilization of a given position of the eyes) is accomplished by the second level through three reflexes acting in parallel: a) withdrawal of one or both eyes as a result of muscle contraction due to an increase in activity[2] of corresponding MCA is compensated through the interneuron network by proprioceptive junctions ("stretch reflex") which become active. However, this compensation is only partial, because according to available data the stretch reflex of the extrinsic eye muscles is relatively weak and appears with a large lag, b) an apparent simultaneous withdrawal of both eyes in the same direction due to an increase in total MCA activity of 1 and 3 (or MCA 2 and 4) is compensated by a synchronous jump (caused by the PMN) in the opposite direction (let us call this reflex nystagmoid), c) the

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[1] We understand a nonspecific effect to be that on OMA unrelated to solution of a concrete visual problem.
[2] MCA activity is determined mainly by the number of simultaneously pulsating neurons.

apparent approach or separation of the eyes as a result of an increase in total activity of MCA 2 and 3 (or MCA 1 and 4) is compensated by slow separation or approach of the eyes (convergent reflex). The enumerated reflexes are organized into interneuron networks with participation of proprioceptive afferentation. Stretch and convergent reflexes are accomplished by the T-systems of corresponding muscles, and the main role in the nystagmoid reflex belongs to the P-system. The T-systems of the antagonistic muscles ("reciprocal innervation") are suppressed during these compensating movements. Joint action of these three reflexes accomplishes rapid and reliable correction of eye position. /45

It is possible to construct many functionally equivalent systems which carry out the indicated actions. A system is briefly characterized below which is similar to physiological concepts.

Each of the reflexes is organized in a corresponding structure -- an interneuron network[1] We shall denote then as S, N and K. We shall consider in detail the assumed functioning of structure N, consisting of two symmetrical interacting neuron networks N_r and N_e. Impulses from MCA 1 and 3 enter the input of N_r, and those from MCA 2 and 4 enter the input of N_e. Stimulating effects on TMN and PMN of muscles 2 and 4, and inhibiting effects on TMN of muscles 1 and 3 proceed from the output of N_r. The output neurons of network N_e stimulate the PMN and TMN of muscles 1 and 3, and inhibit TMN 2 and 4.

Both networks, N_r and N_e, have a natural "viscosity" (spatial and time summation, intrinsic inhibiting effects) in which weak actions of the MCA become extinct. Moreover, signals entering each network, by propagating along it, transmit inhibiting effects to the other network by preventing propagation of stimuli in this network. When signals of identical intensity appear in both networks, there is mutual inhibition, and both networks are closed to these signals. When the activity of one of the two MCA groups noticeably exceeds that of the other group, the pulsation generated by it in its own network suppresses the opposite network which does not pass the signal. The inhibiting effect of this latter network on the first decreases simultaneously. Therefore, the rather intense and prolonged activity of one MCA group appears during stimulation of a certain number of output neurons of the network, which also means the PMN of the opposite group of muscles. Pulsation of the output neurons of the network results in inhibition of the cells of both networks, in order to avoid extremely partial jumps, during which the visual capability of the eyes is decreased[2].

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[1] The question of whether these structures are anatomically dispersed or integrated is of no importance to us.
[2] Apparently, organization of this inhibition is a function of some special structure.

Structure K for a convergent reflex functions in a similar manner. /46
MCA 2 and 3 act on network K_d, and MCA 1 and 4 act on network K^k. Output neurons stimulate TMN 1 and 4 and TMN 2 and 3, respectively. Impulses from the proprioreceptors of the muscles (muscular spindles) enter the input of structure S, and output neurons have an alleviating effect on the tonic system of the same muscle.

We surmise that the effect of upper levels of OMA on the lower level is accomplished through the second level by variation of the thresholds of its neurons -- by inhibition and alleviation of MCA cells and of structures N and K. Apparently there are direct tracks from above which stimulate structures N and K.

Some known reflex movements of the eyes may be explained qualitatively in the following manner.

1. The effect of visual afferentation upon fixation of an immovable point consists in leveling MCA activities and alleviating the neurons of structures N and K. Switching off the visual stimulus (open eyes in darkness) removes these effects, and eye movement becomes sweeping. Drift and jumps acquire an increased amplitude and convergent movements replace one another disorderly.

When the head is rotated slowly, for example to the right, weak pulsations from the cervical muscles and labyrinths intensify MCA 2 and MCA 4 somewhat, and weakly inhibit structure N. A compensating movement of the eyes to the left develops.

Increased pulsation from the labyrinth during caloric and vestibular testing elicits strong MCA activity and weakly inhibits structure N as before. Therefore, a smooth motion of the eyes begins in the corresponding direction ("slow phase of nystagmus"), which is replaced by a jump in the opposite direction ("quick phase"), because the high stimulation from the MCA exceeds inhibition of N.

2. In order to verify the correcting capability of the control system which functions according to the system described above, experiments were carried out on a digital computer.

In these calculations, details of the structure of neuron aggregates described above were lacking. A block diagram of a model was considered in which individual sections of the latter (blocks) possessed the required functional properties. Thus, for example, each MCA is characterized by an activity which is measured by a ($0 \leqslant a \leqslant 1$), which denotes the fraction of stimulated neurons, and $a = 1$ (maximum MCA activity) corresponds to the case when all neurons of a given MCA are stimulated, and activate all TMN of the corresponding muscles. Activity of P- and T-systems is determined in a similar manner, i.e. this value is equal to the ratio of the number of

stimulated PMN (and TMN, respectively) to the number of all PMN (TMN) of the /47
"pool"[1] The position of each eye is characterized by its deviation from a neutral position measured on a certain scale. It is assumed that this deviation is equal to zero at the initial moment. MCA act on the T-system such that activity of the latter is linearly dependent on MCA activity. Due to its effect, the eyes move at a rate proportional to the difference of TMN activities of the left and right muscles. The rate of this movement depends, moreover, on elastic resistance of the stretched muscle. Activity of the T-system of each muscle increases when the latter is stretched, and decreases when it contracts (stretch reflex). Pulsations from the activators also enter the block imitating the functioning of network N. This is where the difference between MCA activity which innervates the abductor muscle of the left eye and MCA activity of the antagonistic muscle is determined. The same difference was calculated for the right eye. If the greatest of these differences exceeds a given threshold value, it is included in the functioning of the P-system, and both eyes move suddenly in the direction where pulsations from the MCA are weaker. The rate of the jump is greater, the greater the inconsistency in MCA activity. After this the P-system of all muscles is unstimulated for a certain period. Experiments were carried out with such a simplified model in which different combinations of stimulation suppressed MCA, and eye movements to which these stimuli were applied were recorded.

These experiments permitted us to conclude that control, based on the nystagmoid nature of interaction of two OMA motor systems, is capable of correcting eye position. Moreover, behavior of the model is similar to that of a real system. Thus, in the case when MCA activity of one side (for example, MCA 2 and MCA 4) noticeably exceeded MCA activity of the other side (MCA 1 and MCA 3), which imitated an increase in activity of the right labyrinth, nystagmus began with a slow phase to the right. This similarity to oculographic recordings was observed in the characteristics of model behavior when visual stimuli appeared in darkness.

3. The object of further study is neuron networks similar to networks N_r and N_e described above. This study is of significant interest with regard to the fact that G. I. Gorgiladze discovered their existence experimentally in vestibular nuclei. The networks studied are multilayer neuron structures in which each neuron of the succeeding layer may receive stimulating impulses from adjacent neurons of the preceding layer with a greater probability, and from remote neurons -- with less probability. Experiments on the digital computer indicated that such networks reveal the required properties, in particular the "viscosity" mentioned above, i.e. damping of weak signals. /48
Interaction of two networks upon properly organized mutual inhibition also satisfies the desired requirements -- both networks do not permit incoming weak signals to pass; if the input signals differ significantly, then in time the network, at which the weak signal arrived, is in a state of inhibition,

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[1]Russian word indefinite -- "pul" or "pulo" probably meaning possibly the total of all neurons in question -- Tr.

and the other, on the other hand, is stimulated. In the case when strong and equal signals arrived at both interacting networks, complete closing of the networks did not take place, although as the number of layers in each network increases it becomes all the more apparent. Thus, the intensity of the output signal comprised approximately 60% of the signals at the input in the case of five layers, and about 40% when there were eight layers in each network.

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THE EFFECT OF POSTURE ON THE SENSORY-MOTOR COORDINATION OF MAN

A. A. Koreshkov and G. M. Aboyan

ABSTRACT. Results are presented of experiments, in which test subjects executed complex movements during different positions of the body in space. Severe changes in the movements of the subjects were revealed, especially in the horizontal position. The data obtained in the experiments are considered with respect to the interaction of the vestibular, visual and motor analyzers.

Numerous papers of Russian and foreign psychologists and physiologists have established that orientation of man in space and execution by him of coordinated acts is provided by the combined activity of the vestibular, visual, kinesthetic and other analyzers.

Deep theoretical analysis of the problem of the interrelation of analyzers was presented in the papers of the outstanding Russian physiologist A. A. Ukhtomskiy [2]. This problem acquired especially important significance with regard to development of aviation and astronautics. It became quite obvious that any form of motor activity in man under different conditions of an external medium, including space, is guaranteed by coordinated activity of the organs of locomotion, vision and equilibrium. One of the concrete forms of such activity is the effect of initial operating posture on the quality of sensory-motor reactions. We know, for example, that even slight variation of a comfortable working posture of man (erect sitting or standing) affects the /49 accuracy of visual perception and the nature of movements. Thus, it was established [1] that a slight inclination of the head toward the shoulder from an initial vertical position decreases the accuracy of elementary motor acts of the executor. This observation agrees especially with flight practice, where incorrect posture of the pilot during flight and inclinations of the head to the side are often the reason for disruption of spatial orientation and incorrect actions which often result in an emergency situation.

The topic of our research is the problem of the effect of different inclinations of the body with respect to the horizontal on the quality of sensory-motor coordination.

The experiments were conducted in a special articulated chair. The age of the test subjects ranged from 24 to 28 years. Four working postures were employed -- erect sitting, that at an angle of 60 and 45° to the horizon, and a horizontal position. In the initial investigations, all test subjects were transferred from an erect sitting to horizontal position, and then from a horizontal position to erect sitting. Moreover, inclinations of the head to

the right and to the left at 45° were carried out in a horizontal position and at an angle of 45°. Four tasks were assigned for all positions -- the first consisted in that the test subject, having a controlled sinusoid on a paper in front of his eyes, had to construct precisely the same sinusoids along the points above and below it.

The second task consisted of executing two circles -- one of lesser and the other of greater radius than the control circle. In order to construct the assigned circles, eight points were also marked for each circle.

The third task consisted of constructing a five-pointed star without removing the pencil from the paper. The test subjects were expecially instructed to maintain the dimensions and accuracy of the control star.

The fourth task was to execute a spiral of three loops, similar in accuracy of plot and dimensions to the control spiral. The control stars and the spiral in the third and fourth tasks, since they were easiest, were shown to the test subjects only in each pose before beginning completion with instructions to maintain the dimensions of the figures.

The time required to complete the task was calculated each time during construction of the figures in one or another position. The data obtained (according to time of completion) are presented in Tables 1, 2 and 3.

TABLE 1. AVERAGE DATA ACCORDING TO TIME (IN SECONDS) OF EXECUTING TASKS IN EXTREME POSITIONS -- FROM ERECT SITTING TO THE HORIZONTAL

Position	Assigned figures			
	Sinusoids	Circles	Star	Spiral
Erect sitting	25,5	21,0	16,6	12,3
Horizontal	22,5	18,5	18,0	11,6

Tr. Note: Commas indicate decimal points.

The data of Table 1 reflect the results of the first series of experiments where the test subject began to complete the tasks in an erect sitting position and was transferred through intermediate positions at an angle of body inclination of 60 and 45° to a horizontal position.

The success of completing the tasks in this series is undoubtedly /50
reflected not only by the position, but also by the lack of training of the test subjects, who were completing for the first time a task unusual for them.

TABLE 2. AVERAGE DATA ACCORDING TO TIME (IN SECONDS) OF EXECUTING TASKS IN EXTREME POSITIONS -- FROM THE HORIZONTAL TO ERECT SITTING

Position	Assigned figures			
	Sinusoids	Circles	Star	Spiral
Horizontal	28,25	20,15	21,3	13,5
Erect sitting	23,00	20,25	20,0	11,7

Tr. Note: Commas indicate decimal points.

This may explain the fact that an average of 25.5 sec was expended in drawing sinusoids in an erect sitting position, 21 sec for drawing circles, and 22.5 and 18.5 sec, respectively, for drawing the figures in a horizontal position.

In the second series of experiments the same test subjects began to execute the tasks in a horizontal position and completed them in an erect sitting position.

As is obvious from the data of Table 2, different results were obtained in this series of experiments. The time for drawing circles was approximately /51 the same as in the erect sitting position, as it was in the horizontal position. Whereas an average of 23 sec was expended when drawing the sinusoids in an erect sitting position, and 28.25 sec in a horizontal position.

TABLE 3. AVERAGE DATA ACCORDING TO TIME (IN SECONDS) OF EXECUTING TASKS DEPENDING ON POSITION IN I AND II SERIES OF EXPERIMENTS COMBINED

Position	Assigned figures					
	Sinusoids		Circles		Star	Spiral
	Upper	Lower	Inner	Outer		
Erect sitting . .	26,5	22,0	24,7	16,5	19,0	12,0
Horizontal . .	27,2	23,7	21,6	17,0	19,5	12,8

Tr. Note: Commas indicate decimal points.

Approximately the same relationships also occurred when executing the other two tasks.

Although the number of experiments conducted was small (a total of 48 sinusoids, 48 circles and an equal number of stars and spirals were drawn by three test subjects), the results obtained may be interpreted from the point of view of the dependence of temporary characteristics of executing tasks on posture.

In an additional series of experiments the same test subjects accomplished tasks of drawing sinusoids and circles in two positions -- erect sitting and at an angle of 45° to the horizontal with inclinations of the head to the right and to the left at 45°. Accomplishment of the task on drawing a circle in the erect sitting position was better than that at an inclination at an angle of 45°

Drawing of the sinusoids was more successful in the erect sitting position.

The results obtained are inadequate in a quantitative aspect to formulate any definite conclusions. However, when executing a more complex task -- such as drawing sinusoids, the test subjects in all experiments mastered it more successfully in the erect sitting position.

Preliminary analysis of accuracy also indicates the same tendency.

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ON THE INTERACTION OF CERTAIN ANALYZERS UPON FORMATION OF MOTOR REACTIONS OF ANIMALS DURING WEIGHTLESSNESS

L. A. Kitayev-Smyk

ABSTRACT. Reactions to brief periods of weightlessness are described in cats and rabbits which are healthy, have one- or two-sided labyrinthectomies, or which are deprived of vision. The tonic and motor components are distinguished in the motor activity of the animals. Behavioral reactions of animals during weightlessness develop due to the effect of two competing information flows -- from the gravireceptors and from the visual analyzer.

The papers of Soviet authors have indicated that different analyzers, linking the organism to the surrounding medium, function in close interaction as physiological systems. Due to this fact, the capability of living creatures to adapt to a rather broad range of variations in the external medium under conditions of terrestrial existence is guaranteed. /52

The development of space flight has presented the problem of man and the animals accompanying him in flight adapting to conditions either not encountered on earth, or significantly different from terrestrial conditions in the level of their effect on organisms. The first group refers to variations in gravity. During weightlessness or reduced weight, variations in the nature of information proceeding from the gravity receptors apparently elicit rearrangement of the activity of an organism's analyzer systems. Numerous facts are presently known, obtained during flights along a parabolic trajectory and in satellites, which indicate that this rearrangement in man and in animals is far from painless.

The first investigators discovered the development of expressed unrest in animals during weightlessness, and an increase in motor activity and discoordination of movements was noted. Sensory disruptions in the form of spatial illusions accompanied by emotional reactions (fear, euphoria, etc.) developed in a large number of people upon encountering weightlessness, motor activity increased, in particular, grasping reactions developed, and vegetative disorders appeared, in a number of cases very sharply expressed [2-4, 7].

On the basis of a number of papers, we may consider that an important role in -the formation of similar reactions during weightlessness belongs to the vestibular analyzer [2-4, 7]. Little attention has until the present been given to investigation of the significance of other analyzers during weightlessness.

In this report, the results are presented of investigating the interaction of the visual and vestibular analyzers during formation in animals of adapting to the repeated effects of brief periods of weightlessness.

Method

The state of weightlessness was created in the cabin of an aircraft while flying along a parabolic trajectory. Duration of each regime of weightlessness was 25-30 sec. Weightlessness was preceded and also followed by a G-load up to 1.8 g, lasting 15-18 sec. In a number of cases, controlled experiments were carried out, in which weightlessness was created directly after the natural force of gravity.

During each flight (not more than once a day) 6-8 regimes of weightlessness were carried out.

The experiments were conducted on 24 rabbits 8-10 months old without regard to sex, and on 18 cats without regard to age or sex. A special compartment was outfitted in the cabin of the aircraft to conduct the experiments, in which the animals were able to float freely in the air. /53

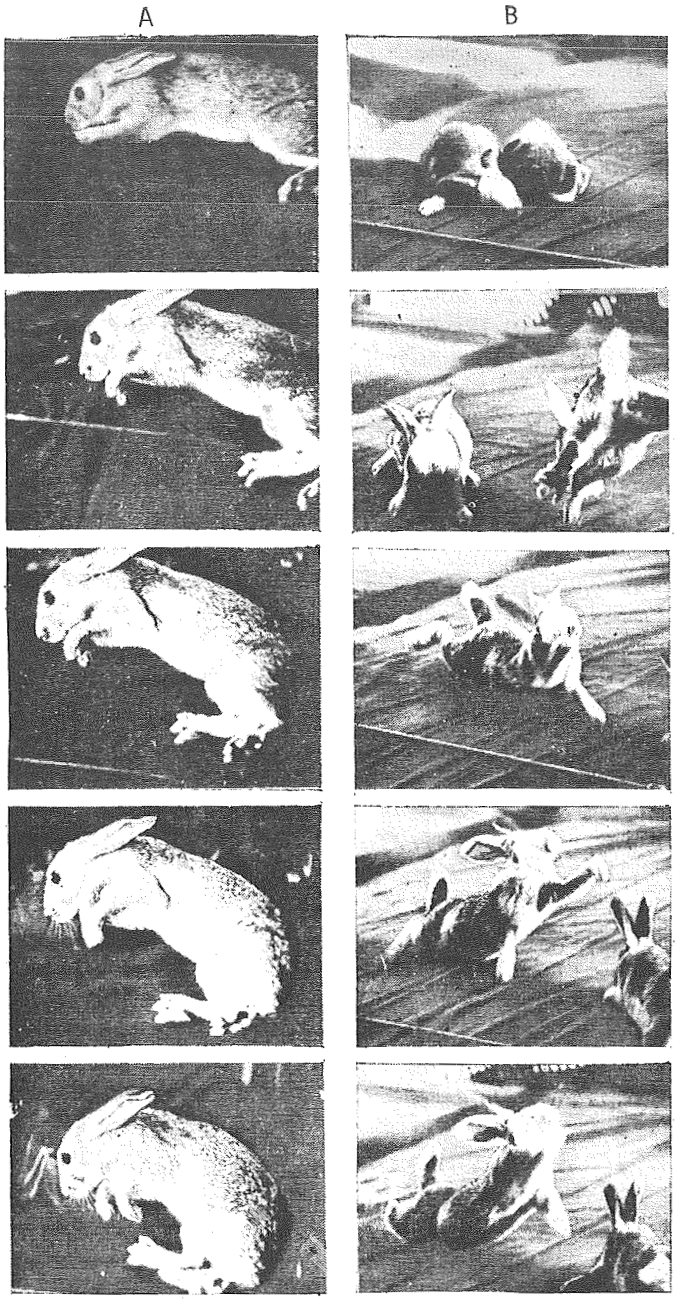
Behavioral and postural reactions of the animals were recorded with the help of motion picture filming with subsequent frame-by-frame interpretation (see the illustration).

Cutting off the vision of the animals was accomplished by using special lightproof masks placed over the eyes of the animals; the vestibular apparatus were cut off in the rabbits by the method of A. B. Tsypin and Yu. G. Grigor'yev [6], and those in the cats by the method of Klein.

Six series of experiments were carried out: the first series on healthy animals (six rabbits and three cats), the second series on six rabbits and three cats with vision cut off during the flights, the third series on three rabbits and three cats delabyrinthized 1-2 days before the experiments, the fourth series on three rabbits and three cats delabyrinthized 1-1.5 months before the experiments, the fifth series on three rabbits and three cats delabyrinthized 1-1.5 months before the experiments with their vision cut off during flight, and the sixth series with three rabbits and three cats delabyrinthized on one side. A total of 210 experiments were conducted.

Results of the Experiments

During the first and second seconds of weightlessness, motor activity of healthy animals increased sharply. Observation and analysis of the movie film indicated that movements of the animals consisted of several motor components.



Rabbits During Twentieth Regime of Weightlessness. A, Healthy animal; B, Animal with vision cut off. Sequence of the frames is from top to bottom.

Initially, the most noticeable were movements similar to running: "jumps" and "drumming" movements of the extremities. The cats also developed rotary movements of the tail, as if the animal were describing a funnel with it, the body beginning to turn in the opposite direction. An increase in motor activity was always accompanied by psychic stimulation -- by screams and dilation of the optic fissure in the rabbits, and by an expressed grasping reaction in the cats.

At the beginning of the period of weightlessness (upon multiple repetition) the jumps and then the drumming movements of the paws disappeared. Psychic stimulation of the animals decreased simultaneously. The cats stopped rotating the tail, but continued to maintain it extended upward with respect to the body.

After motor reactions had disappeared, extension of the extremities and body was maintained, becoming more pronounced. The extensory reaction disappeared in the fifteenth to twentieth regime of weightlessness in rabbits and in the sixth to twelfth regime in the cats. Subsequently, in the absence of /55 gravity, the animals hung in the air, pressing their paws to the abdomen and extending them only in order to grasp at some object which happened to be near by.

The behavior of the cats differed from that of the rabbits by a more rapid onset of adaptation to weightlessness and by a greater diversity of individual reactions. Cutting off vision (see the table) sharply increased the motor activity of the animals during weightlessness, and prolonged the period of adapting to it. If motor stimulation in healthy animals disappeared during the sixth to eighth regime of weightlessness, in those animals in which vision was cut off during the flights, the jumps and drumming movements of the paws were maintained through the thirty-sixth regime. Beginning with the thirty-seventh regime, their eyes were uncovered, and only during the fortieth regime of weightlessness did motor reaction disappear. The masks cutting off vision were again placed on them, but motor stimulation no longer occurred. Cutting off vision in rabbits which had undergone weightlessness eight to ten times with covered eyes did not cause an increase in motor activity when gravity disappeared; in certain cases of the observations, their movements were sluggish and disappeared rapidly.

In animals delabyrinthized in the absence of visual compensation of lost functions, when the experiments were conducted two to three days after the operation, motor activity during weightlessness developed; however, extension of the extremities and body was not noted. Cutting off vision under condi- /56 tions of weightlessness was hardly reflected in the behavior of these animals.

Delabyrinthized animals, in which compensation of lost functions was to a significant degree formed by vision, floated in the air quietly without movements after beginning of weightlessness. If the vision of these animals was cut off, then, as a rule, 1.5 sec after the beginning of weightlessness vigorous movements in the form of jumps began, and adaptation did not occur even after multiple repetitions of the experimental regimes.

THE PERIOD REQUIRED FOR ADAPTATION TO WEIGHTLESSNESS IN RABBITS AND CATS WITH THEIR VISION AND VESTIBULAR APPARATUS CUT OFF

Animal	Motor Reaction		Tonic Reaction	
	Rabbits	Cats	Rabbits	Cats
Healthy	desappears at 6-8th regime	disappears at 3-8th regime	disappears at 15-20th regime	disappears at 6-12th regime
with cut-off vision	does not disappea for 36 regimes	does not disappear for 24 regimes	disappears at 20th regime	disappears at 10th regime
delabyrinthized without terrestrial visual compen-	does not disappear for 24 regimes.		no reaction	
delabyrinthized with terrestial visual compensation	no reaction		no reaction	
one side delabyrinthized	does not disappear for 36 regimes	accompanyied by rotation	does not disappear for 36 regimes	accompanyied by rotation
delabyrinthized with terrestial visual compensation and cut off vision	does not disappear for 36 regimes	accompanied by rotation	no reaction	

In the animals with one side delabyrinthized, vigorous movements developed during weightlessness in the form of asymmetrical jumps with both covered and uncovered eyes, independently of the periods which passed after the operation. As a result, a rather rapid rotation of the animals in the air (1.5-2 revolutions per second) followed. The animals with one labyrinth also did not adapt to weightlessness upon repeated exposure to it.

Discussion

Various living creatures undergo the effect of weightlessness rather often under conditions of terrestrial existence. Moreover, two characteristics, to a significant degree determining the reaction of animals, are inherent to such weightlessness: a) development of weightlessness under conditions of free falling, which is always related to signaling the danger of a possible impact against the ground, and b) shortness of one to two seconds.

Comparing the motor reactions of animals during free falling and during weightlessness created during flight experiments, we can see a definite similarity. In the second case, the experiments indicated an increase in healthy animals of motor activity, in which two components may be distinguished: tonic extensory reaction of the extremities and body, and motor reaction, developing in a number of cases at the second second of weightlessness and being manifested in rotary movements of the tail and in jumping and running movements. During free falling under ground conditions, a similar tonic "lifting" reaction develops, which guarantees a safer posture upon impact against the ground, and rotary movements of the tail which stabilize the falling animal in the air.

However, being under conditions of weightlessness for more than one to two seconds is a phenomenon unfamiliar and extraordinary for inhabitants of the earth. The absence of gravity continues to be perceived as falling, as indicated by the animals maintaining the extensory reaction and rotary movements of the tail for several regimes of the flight; the significance of /57
weightlessness as a danger signal elicits an intense defensive reaction of "running away" in this case. The extreme expression of such a reaction may be regarded as the result of disinhibition of the subcortical formations: reciprocal movements of the extremities are characteristic for the embryonic period, prior to formation of inhibiting functions of the cortex [5].

Conditions of weightlessness created in the cabin of an aircraft cause a contradiction between signals entering from the gravity receptors and visual information. While the vestibular and musculocutaneous analyzers are "reporting" of falling, i.e. of dangerous disruption of normal stability of the surrounding environment, the vision indicates the absence of spatial variations -- the same walls, floor and ceiling are all around, and there is no visible falling.

And if the signals from the gravity receptors cause formation of the described behavioral reactions expressed in motor stimulation of the animals and hypertension of the extensors of the extremities and body, visual information contributes to the disappearance of these reactions and the development of adaptation to weightlessness. Cutting off vision, as indicated by experiments, disrupts the process of adaptation to new gravitational conditions.

Behavior in delabyrinthized animals in the absence of terrestrial visual compensation (replacement) of labyrinth functions is formed in accordance with information entering from the musculocutaneous analyzer and, possibly, from the visceral receptors. Signals on disappearance of gravity cause motor stimulation of the animal. The visual analyzer in a given case has no decisive effect on the process of behavior formation; not being dominant in animals, it may even lose its significance during development of adaptation due to disruption of the functional wholeness of the analyzer system from the position of the body moving in space.

When there is terrestrial visual compensation after a labyrinthectomy and maintaining of visual function during flight, motor stimulation during weightlessness does not develop. In a given variant of the experiment the visual analyzer, becoming dominant, provides information in spatial analysis about the stability of the surrounding environment during weightlessness, which excludes the development of motor stimulation.

The experiments with a labyrinthectomy on one side also support the given opinion about the interaction of analyzers during weightlessness. Due to rotation developing in animals in the absence of support during weightlessness, the organ of vision becomes independent in evaluating the stability of surrounding objects; moreover, the functional asymmetry of the labyrinths is /58 an additional reason for spatial distortions. As a result, vigorous motor reaction develops in these animals after disappearance of gravity without any sign of adapting after repeated regimes of weightlessness.

It should be noted that cutting off the vision of healthy animals which have experienced weightlessness with uncovered eyes does not cause that extent of motor stimulation which is inherent to animals which have always been under these conditions with covered eyes. Consequently, not only visual signals, but also visual memory about the stability of the surrounding environment may contribute to adaptation to weightlessness.

In conclusion it should be noted that the nonuniform period of adaptation to weightlessness in rabbits and cats is in our opinion the consequence of different significance of vision in the spatial analysis of these animals. Due to the higher evolutionary level of development and ecological characteristics of cats as carnivores, their vision is of greater significance than that of rabbits. On the other hand, the vestibular analyzer of cats possesses superior adaptive capabilities when compared to rodents [1].

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INVESTIGATION OF THE ADJUSTABLE REFLEXES OF ANIMALS DURING WEIGHTLESSNESS

L. A. Kitayev-Smyk

ABSTRACT. Experiments on cats and rabbits during weightlessness in a parabolic trajectory showed the following: 1) a sequential vestibular adjusting reaction which brings about the "rotation reaction" after disappearance of gravity; 2) a vestibular adjusting reaction which stabilizes the position of the head in space during weightlessness; 3) a cervical adjusting reaction which causes straightening of the head and body with respect to the axis of the animal.

The constant effect of gravity determined to a significant degree the /59
structure of organisms inhabiting the earth, as well as their capabilities for locomotion. The motor apparatus of animals permits them to overcome terrestrial gravity, the direction of the force of gravity serving in this case as the most important spatial orienting point. The complex system of motor reflexes which guarantees normal vital activity of animals and man under conditions of natural gravitation has been rather well studied at present. As space flight has developed in recent years, the necessity for prolonged normal functioning of the motor apparatus of man during weightlessness has arisen.

A special case of this problem is study of how the adjustable reflexes, i.e. the reflexes instrumental in stabilization of an organism with respect to any gravitational orienting point (under earth conditions with respect to vertical direction), are accomplished after gravity has disappeared.

We know that during the very initial period of the effect of weightlessness (under earth conditions this occurs during free falling) animals retain the capability to orient themselves with respect to the vertical. Thanks to this the "rotation reaction" and landing "on the feet", i.e. in a position less dangerous upon impact with the ground, are realized. When falling is more prolonged, orientation of an animal right side up is enhanced by rotary motions of the tail which stabilize the animal with respect to the counterflow of air.

When the force of gravity is partially decreased and an animal restrained by the body is dropped, the so-called "lifting reactions" develop: animals straighten their extremities, spread their toes and raise their heads -- a position less dangerous upon landing [9].

Gerathewohl and Stallings [7] reported that during experiments when flying in an aircraft along a Kapler parabola, the "rotation reaction" in cats was retained for 20-22 sec of weightlessness, after which it disappeared, in the opinion of the authors as a result of adaptation to weightlessness. When

investigating reactions to progressive motions in cats during weightlessness, Schock did not detect them under these conditions. Many authors have shown that the typical position for animals during weightlessness is that similar to /60 a "lifting" motor reaction, i.e. extension of the extremities and body is observed; rotary movements of the tail and significant agitation are also noted [6, 8].

Thus, the position and nature of motor activity of animals indicates their perception of weightlessness as free falling. However, disappearance of gravity for more than one to two seconds for inhabitants of the earth is an unfamiliar phenomenon. During prolonged weightlessness, adjustable reactions which develop during its initial effect must undoubtedly undergo changes which may be reflected in the characteristics of an animal's entire motor function.

This paper is devoted to investigating the characteristics of development of adjustable reactions of animals during weightlessness created during parabolic flights. It was necessary to explain how long the orienting effect of gravity continues to affect the adjustable reactions of an animal after it disappears, which is an orienting point for adjustable reactions during weightlessness.

We regard the "Hellungreflex" of Magnus [3] as "adjustable reactions"; we recall that some Russian authors translate this term as "rectifying reactions" (for example, Samoylov and Komendantov).

Method

The state of weightlessness was created in the cabin of an aircraft during flights along a parabolic trajectory. Duration of each period of weightlessness was 25-30 sec. Weightlessness was preceded and also followed by a g-force of 1.5-1.8 g lasting 15-18 sec. Six to eight periods of weightlessness were accomplished during each flight. The flights were conducted no more than one per day.

The experiments were carried out on three healthy cats and six healthy rabbits, and on two delabyrinthized cats and three delabyrinthized rabbits. All animals were adapted to the effect of weightlessness, i.e. their motor activity did not vary when gravity disappeared.

The following series of experiments was conducted.

1. Before the onset of weightlessness the animal was restrained by the body and head in an upside-down position. During the periods of weightlessness, after different intervals, the animal was freed from its restraint. The presence of the "rotation reaction" was determined.

2. In the absence of gravity, the animal restrained by the body rotated around its longitudinal axis. Adjustment of the head was determined. /61

3. Before the onset of weightlessness, the animal was restrained by the body and the head, the head being turned 90° with respect to the body around its longitudinal axis. During weightlessness the animal was freed from restraint, and the characteristics of straightening were ascertained.

4. In the absence of gravity, observations were carried out on animals floating near the floor, walls or ceiling of the aircraft cabin. The presence of visual adjusting reactions was ascertained.

5. During periods of weightlessness, reactions to progressive movements were investigated -- a) of the head, b) lifting reactions, and c) readiness to jump.

6. Within ten to fifteen seconds after the beginning of weightlessness, the animal was restrained by the body and head, was rotated within 0.3-0.5 sec by 180° around the longitudinal axis of the body and immediately freed. The ensuing reaction of the animal was ascertained.

The state of the vestibular analyzer in all animals was determined under the natural force of gravity before and after the flight experiments. A total of 240 experiments was conducted under conditions of weightlessness, and 170 under natural gravity. An opaque mask was placed over the eyes of the animals during all experiments on the cats, with the exception of investigating visual adjustment during weightlessness. The experiments on the rabbits were carried out with and without vision being cut off.

The results of all the experiments were recorded on movie film (with sequential frame interpretation), and were also controlled visually.

The Results of the Experiments

The first series. The "rotation reaction" developed in healthy animals upon release from restraint no more than 4-5 sec after the beginning of weightlessness. This reaction was absent in delabyrinthized animals.

The second series. During forced rotation during weightlessness of an animal with intact labyrinth, its unrestrained head lagged the body in rotation. The head stopped rotating, coming to a straight-line position with respect to the body, within one to three seconds after the body had stopped rotating. Lag of the head during rotation of the animal was not observed after delabyrinthization (Figure 1).

The third series. When a healthy animal with the head rotated beforehand /64
is released during weightlessness, the head remains immobile, and the body rotates to a straight-line position with respect to the head. On the other hand, a delabyrinthized animal rotates the head while the body remains immobile (Figure 2).

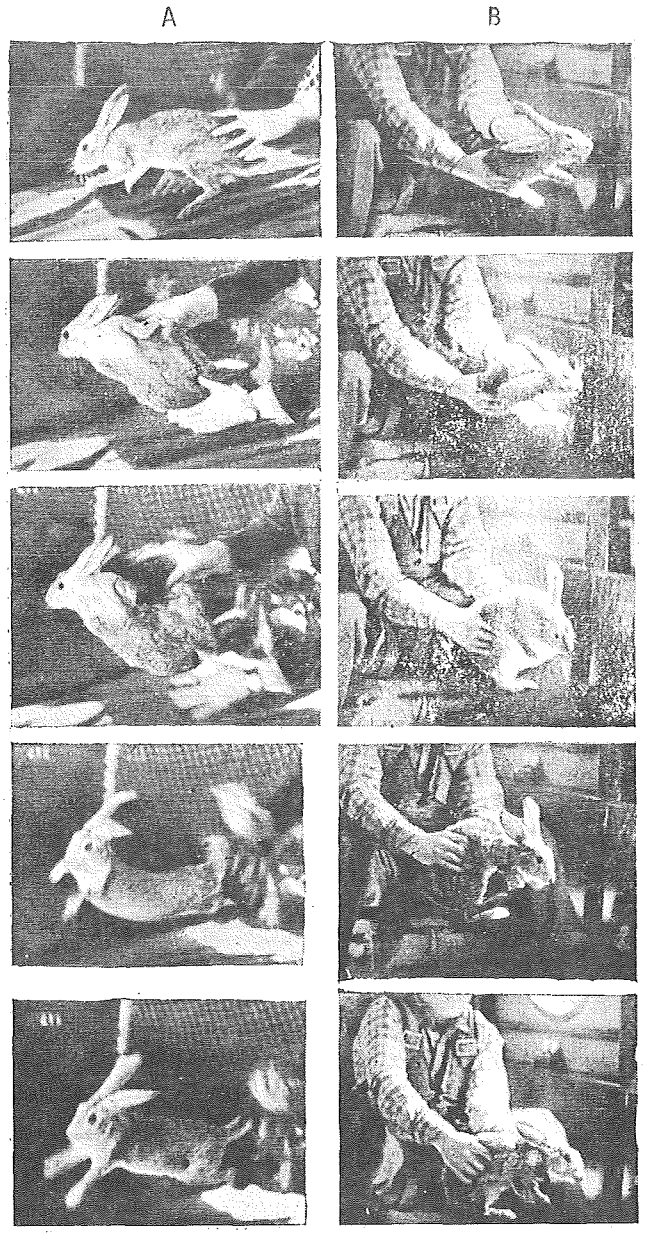

Figure 1. Experiment of the Second Series. A, Healthy animal; B, Delabyrinthized animal. Sequence of frames is top to bottom. Explanations are in the text.

The fourth series. Visual adjusting reaction during weightlessness in the form of rotation, after which the legs of the animal were directed toward the nearest surface (independent of whether it was the floor, wall or ceiling), was manifested in all animals. It was more expressed in cats. This reaction in rabbits appeared in cases when they floated not more than 10 cm from any surface (Figure 3).

The fifth series. Reactions to progressive movements during weightlessness were not detected in our experiments.

The sixth series. If an animal with intact labyrinths was released in weightlessness after rapid (within 0.3-0.5 sec) rotation by 180°, it developed motions which rotated it in an opposite direction and which continued until the end of the period (15-20 sec). Removal of the mask intensified these movements. Disordered movements, not resulting in rotation, appeared in delabyrinthized animals upon their release after rapid rotation.

Rotations of animals upon "rotation reaction" during visual orientation and during experiments of the sixth series were accomplished with the help of "twisting" movements of the entire body, which began at the head, then the front part of the body was drawn into this movement, and finally the caudal part.

The presence of rotary movements of the tail, in which it described a cone, should also be noted in cats in the absence of /65 gravity (before they begin to adapt to weightlessness). These movements are always accompanied by rotation of the body in the opposite direction.

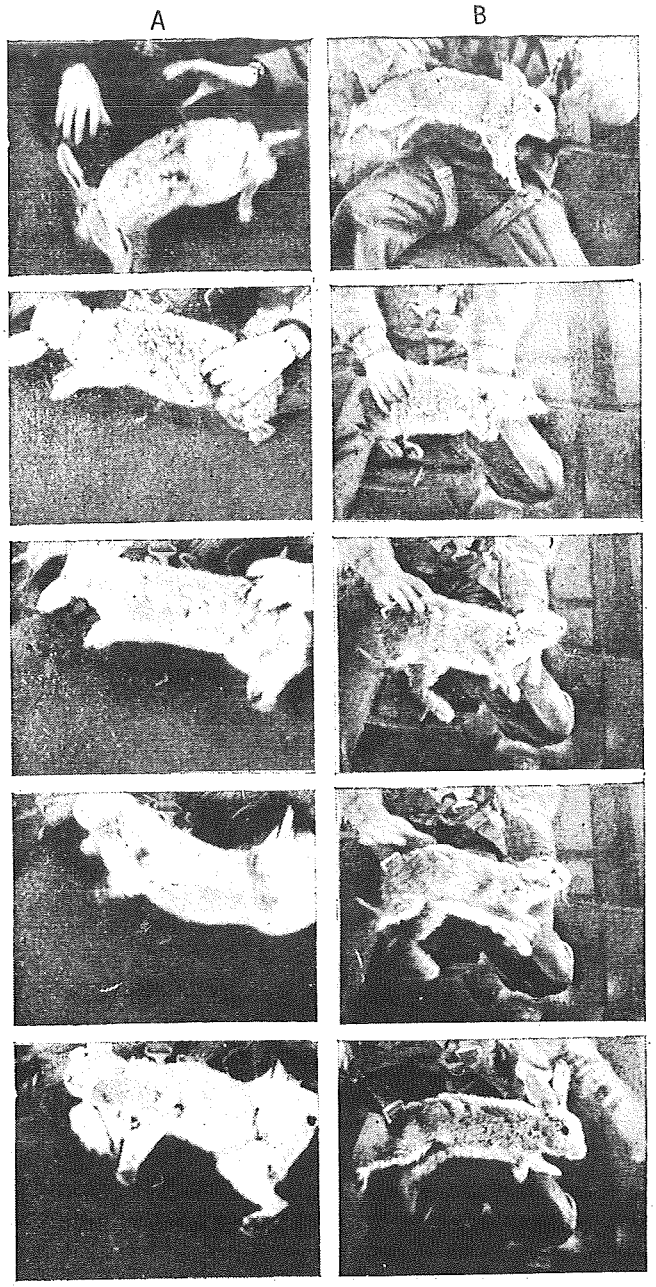

Figure 2. Experiment of the Third Series. The notations are the same as in Figure 1.

Movements of the tail ceased as the cats adapted to the absence of gravity, but the tail remained straightened in a dorsal direction for some time.

No deviations from preflight conditions were observed upon examination of the vestibular status of animals after the experimental flights. Signs of fatigue and an increase in defensive reactions were noted in cats after the flights.

Discussion

In both ground conditions and during the first seconds of parabolic flight, the "rotation reaction" of animals is manifested when accelerations do not affect the gravity receptors, because the reaction of footing is lacking during free falling and weightlessness. The triggering mechanism of the "rotating reaction" is apparently the sequential effect of stimulation of the otoliths by forces of gravity, which occurs before onset of weightlessness. The following fact supports this viewpoint: the "rotating reaction" appeared in animals only during the first four to five seconds of weightlessness, and was absent in delabyrinthized animals.

If the stimulus (gravity) was absent for 4-5 sec, the "rotation reaction" did not develop. Moreover, upon forced rotation of the animal's body, its head maintained its previous position for some time, i.e. there were effects which prevented rotation of the head and which stabilized it in its initial position; in delabyrinthized animals the head rotated together with the body. This means that besides

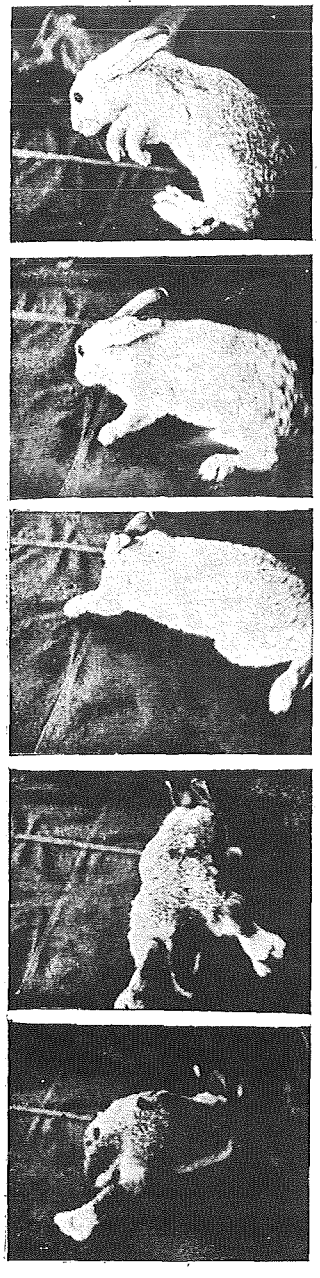

Figure 3. Experiment of the Fourth Series (Visual Adjusting Reaction of Healthy Animal). Sequence of the frames is top to bottom.

the indicated sequential adjusting "rotation reaction" during prolonged weightlessness, vestibular reflexes which stabilized the head in space, and cervical reflexes which maintain the straight position of the head and body with respect to each other take place. Both types of reflexes must overcome the "rotation reaction". Their effect begins to be reflected at the fourth or fifth second of weightlessness, probably, in proportion to attenuation of the sequential effect of gravity. If the head and body of an animal are arranged in a single sagittal plane during weightlessness, labyrinthine and cervical reflexes act in the same direction, stabilizing the position. In the case when the head is rotated with respect to the body, they are in conflict. If in this case the animal floats freely in the air, the vestibular reaction is predominant -- the body rotates while the head remains /66 immobile. When the body is restrained, the head rotates after one to three seconds (to a straight position with respect to the body), i.e. the cervical adjusting (rectifying) reaction predominates upon prolonged stimulation of the proprioceptors of the cervical muscles.

Attention is drawn to the disagreement of data about time, during which the "rotation reaction" is retained in animals during weightlessness, in this paper and in that of Gerathewohl and Stallings [7]. In connection with this one should consider the experimental method of the American authors. As they reported, during weightlessness the experimenter grasped the animal by the skin of the back, rotated it by 180° around the longitudinal axis, then released it. The animal thus rotated independently in the air, assuming its previous position. The experimenter caught the animal by the back and repeated the manipulation, after which the same reaction followed. The actions of the experimenter were repeated eight to twelve times for 20-22 sec, after which the animal stopped rotating independently in the air. It seemed that intense agitation of the animal was observed during the experiment. Disappearance of the "rotation reaction" in the experiments of the authors cited is in our opinion least of all related to adaptation of the animals to conditions of weightlessness. The return of the animal to its initial position occurred for a number of reasons. Gerathewohl and Stallings noted that the head of the animal lagged during rotation of the body, which was being rotated by the experimenter. Consequently, the reverse rotation,

beginning at the fifth or sixth second of the period of weightlessness, was apparently accomplished due to the adjusting vestibular and cervical tonic reflexes described in this paper. Moreover, the vigorous rotation of the animal may cause the reaction of counter rotation also described in this report. Finally, the vision of the animals in a number of experiments by the American authors was not shut off; thus, the "rotation reaction" could still develop due to the visual adjusting reaction retained and well expressed in cats during weightlessness.

The question arises as to why the animals stopped rotating to their initial position after their forced rotation at the twentieth to twenty-second second of weightlessness. First, reactions of cats to vestibular stimulation disappear after several rotations, in distinction, for example, from rodents, in which these reactions are very stable [1]. Secondly, the singularity of the state of weightlessness, frequent touching of the animal and repeated rotations of it, which were especially verified during parabolic flights in our experiments, at first evoke intense stimulation, and then rapid fatigue of the animal. Even after conducting experiments by the Gerathewohl and Stallings method during two to three periods of weightlessness within a /67 single flight, the tendency of cats to hide, which at first occurred during the breaks between the periods, disappeared; they lay apathetically on the floor, breathing hard, and from time to time meowing loudly. Motor reactions, including the "rotation reaction" in such a state, could undoubtedly be suppressed. Thus, the "rotation reaction" in the experiments of Gerathewohl and Stallings apparently disappeared not as a result of the animal's becoming adapted to weightlessness, but due to overfatigue and the development of internal inhibition.

The report of Schock [10] was mentioned above, about the absence of reactions to progressive movements during brief periods of weightlessness. We also did not detect these reactions. But they apparently may not be expected during weightlessness in their usual form, because when an animal is dropped right side up (in the ventral direction) under ground conditions, the pressure of the otolith on the sensory filament of the utricles decreases, and during weightlessness transfer of the animal to a ventral direction causes the sensory filaments to be extended, rather than a decrease of pressure on them. The absence of apparent motor reactions to progressive movements may indicate a decrease in muscular reactivity during conditions of weightlessness in animals which have become adapted to these conditions [5].

Development of the counterrotation reaction in the absence of gravity indicates that the cupular function is retained under these conditions. Preservation during weightlessness of the central integrative functions of the nervous system of animals adapted to weightlessness is indicated by the activity of their behavior, and by the development of visual adjusting and grasping reactions under these conditions.

Thus, the data of this report indicate the existence of 1) a sequential vestibular adjusting reaction which brings about the "rotation reaction" within 4-5 sec after the disappearance of gravity, 2) the vestibular adjusting

reaction which stabilizes the position of the head in space during weightlessness, and 3) a cervical adjusting reaction which causes the head and body to straighten with respect to the longitudinal axis of the animal. The vestibular reaction is dominant during free floating of the animal; the cervical adjusting reaction predominates when the body is restrained. Both of these reactions inhibit the "rotation reaction," contributing to its suppression in proportion to attenuation of sequential stimulations in the vestibular analyzer.

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ON THE PROBLEM OF THE INTERACTION MECHANISMS OF THE VISUAL AND VESTIBULAR ANALYZERS

N. G. Medvedeva

ABSTRACT. The problem of the possible mechanism of interaction of the visual and vestibular analyzers is considered. The bioelectric potential of various regions of the brain and retina are recorded in a state of rest, and during single and rhythmic light stimulations in healthy and mute subjects. The author concludes that interaction of these analyzers takes place at the level of the cortical-subcortical analyzer systems.

Since the introduction and founding of the term "interaction of afferent systems" by L. A. Orbeli, this problem has been on the mind of both Russian and foreign scientists.

While concerned with study of the interaction mechanisms of the analyzers, S. V. Kravkov [3] recognized the following possible methods of transmitting stimuli: 1) the ephaptic method -- direct transfer of stimulation from one nerve fiber to another (this possibility was shown in amyelinic nerve fibers [15-17, 18]), 2) intercentral connections, 3) the vegetative method [3, 17, 19], 4) the humoral method, and 5) sensory conditioned reflexes -- the cerebral cortex [3].

Long known vestibular tests, accompanied by variation of the motor activity of the eyes, are related to the area of interaction of the visual and vestibular analyzers.

The work of Ye. M. Belostotskiy et al. [2] indicated that stimulation of the vestibular analyzer in people with normal hearing alters the light sensitivity of an eye adapted to darkness.

It has become of particular interest to explain the nature of the variations in different sections of the visual analyzer upon stimulation of the vestibular analyzer, which was also the task of the given investigation.

When studying the variations of the functional state of the analyzers due to the influence of different effects, different methods of research, including electrophysiological, are utilized [2, 4, 7, 8-14].

In order to solve the stated problem, the electrophysiological complex /69
method of investigation was utilized -- simultaneous registration of bioelectric potentials of the retina and the cerebral cortex. Bioelectric currents of the brain from the frontal, parietal, occipital and temporal regions with biopolar derivation, and biopolar potentials of the retina in a

state of relative rest as well as upon transmission of singular and rhythmic light stimulations (frequency from 5 to 30 Hz, duration of 5-8 sec with an interval of 5-8 sec) were recorded. Recording was conducted on a multichannel electroencephalograph before and after rotation of the test subject on a Barani chair (ten revolutions per 20 sec). Research was carried out on 58 subjects -- 11 healthy and 47 deaf[1]. The results of variations in the electroretinogram (ERG) were processed by the statistical method of Student for small samples. ERG recording was accomplished by the method described previously [5, 9, 10].

Indices of the functional state of the cerebral cortex were the frequency and amplitude of the rhythm of rest and the reaction of biocurrent rearrangement in response to rhythmic light stimulus and a single light. Indices of the functional state of the retina were the nature of the ERG (the amplitude of wave b, its period, culmination, and latency period), and also assimulation of the retina of rhythmic light flashes.

Analysis of the data obtained indicates that normal α rhythm at a frequency of 9-10 oscillations per second and an amplitude of 25-40 μv was observed in healthy subjects examined before rotation in a Barani chair (Figure 1 A). The rhythm of light flashes within ranges from 8-10 to 16-20 Hz were assimulated in the EEG primarily in the occipital and parietal regions. It was possible to delineate in the ERG wave b with an amplitude of 150-200 μv having a period, culmination and latency period within the range of the norm.

A normal, clear α rhythm (with closed eyes) through the entire cortex with an amplitude of 25-50 μv, varying with a rapid and difficultly reducible rhythm upon opening of the eyes (Figure 2 A), was detected in the EEG of 35 deaf subjects (of 47). The reaction of biocurrent rearrangement in response to rhythmic light was observed in 34 subjects (of 47), 24 assimulating the rhythms having a frequency from 8-10 to 20-24 Hz, and 10 subjects assimulating the rhythms within ranges from 8-10 to 13-16 Hz. The test subjects became accustomed to singular light flashes slowly (ten or more stimulations before cessation of "tremor reaction"), and the appearance of one or two high-amplitude slow waves (the K complex) was recorded in some individuals [1]. All this indicated a decrease in the tonus of the cortex, diminishing its lability somewhat. The ERG of deaf subjects was within the norm, and all rhythms of light flashes supplied were assimulated in it.

[1] V. A. Ryabichev participated in the experiments with deaf subjects.

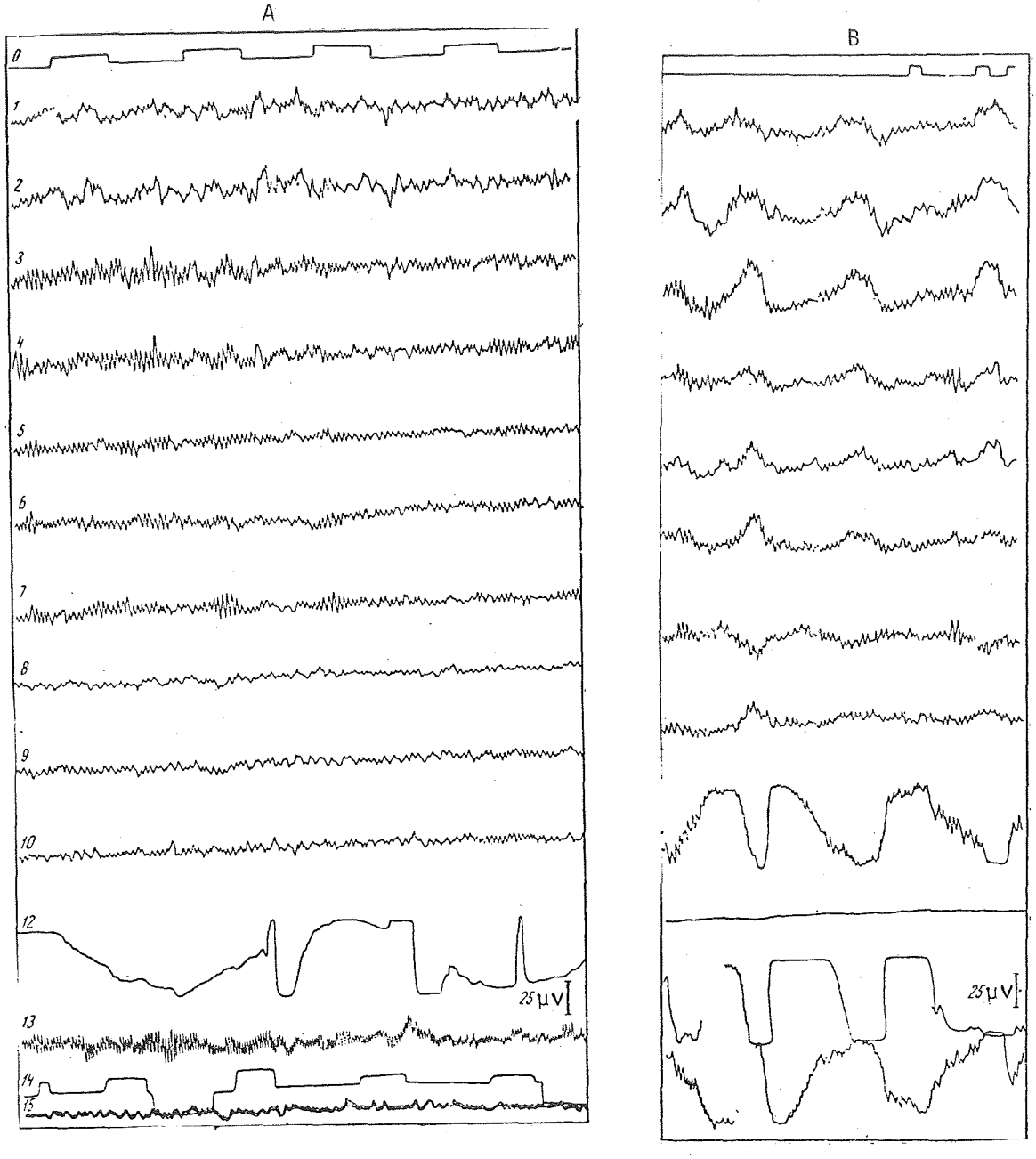

Figure 1. Electroencephalogram (EEG) of a Subject with Normal Hearing Before (A) and After (B) Stimulation of the Vestibular Analyzer. Leads into the EEG: 1, Frontal, right side; 2, Frontal, left side; 3, Parietal, right side; 4, Parietal, left side; 5, Parietal-occipital, right side; 6, Parietal-occipital, left side; 7, Occipital, right side; 8, Occipital, left side; 9, Occipital right and left sides; 10, Temporal, left side; 11, Sensory motor reaction; 12, Electroretinogram; 13, Occipital, monopolar, right side; 14, Integrator; 0, Marker of light stimulation

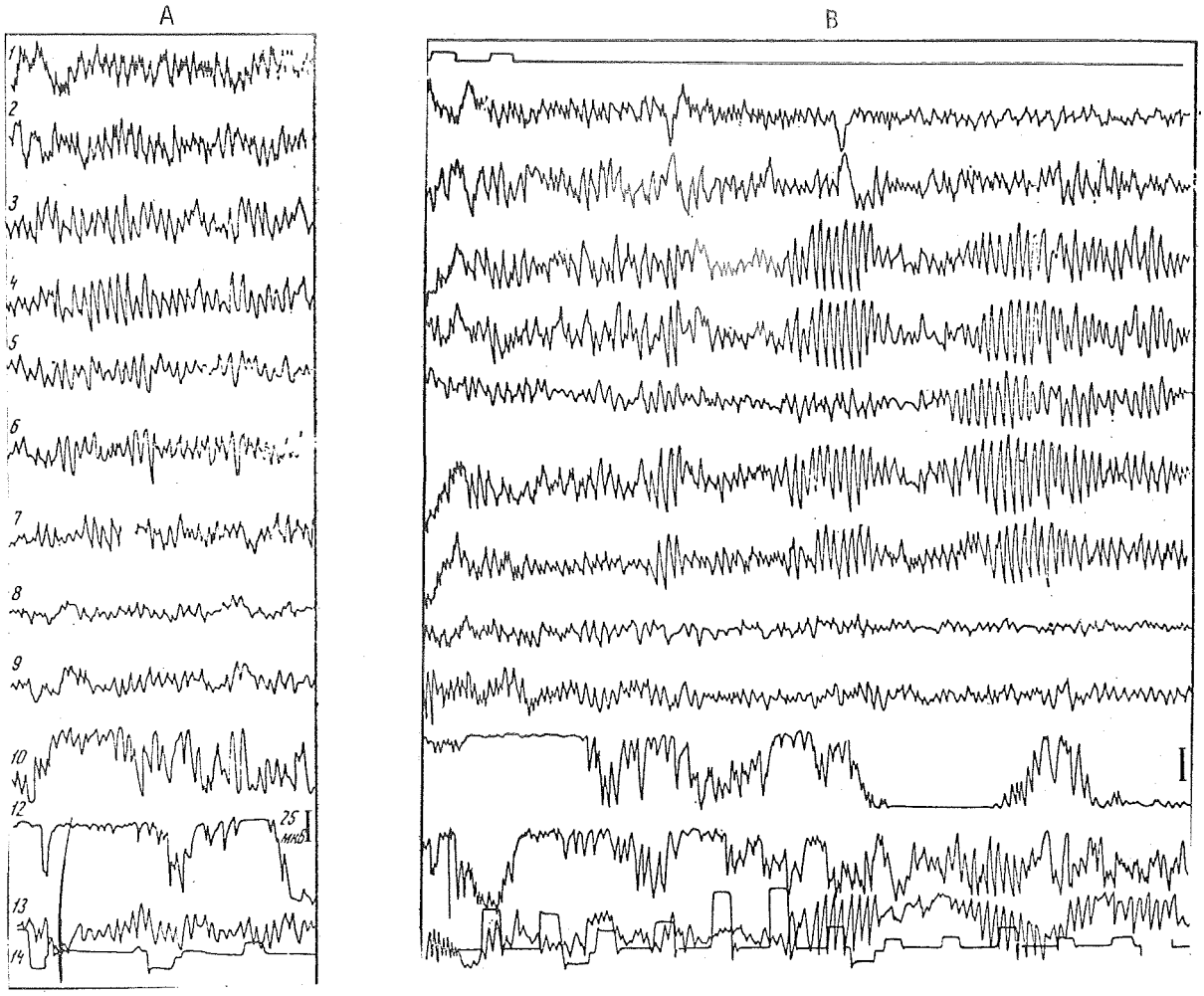

Figure 2. Electroencephalogram (EEG) of a Deaf Subject Before (A) and After (B) Vestibular Stimulations. Leads are the same as in Figure 1.

The disappearance of α rhythm, rather rapidly reducible (from 20-25 to 150 sec), but unstable in frequency (8-12 oscillations per second), and with a somewhat diminished amplitude (see Figure 1 B), was noted in the EEG of normal subjects due to rotation in a Barani chair. Four individuals (of eleven) displayed sharp vegetative reactions in the form of perspiration, the skin of the face becoming pale, nausea, and significant nystagmoid movements of the eyes. Discernible variations were not noted in the reaction of biocurrent rearrangement in response to rhythmic light; single flashes of light caused the appearance of the slow K complex in four test subjects. Nystagmoid phenomena, and statistically barely reliable variations in amplitude and the /72

latency period of wave appearance were observed in the ERG (making its recording and analysis difficult) (Figure 3 B).

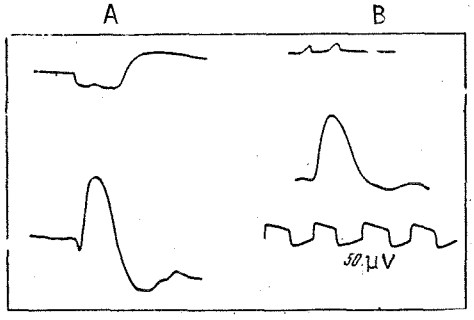

Figure 3. Electroretinogram of a Normal Test Subject Before (A) and After (B) Vestibular Stimulations

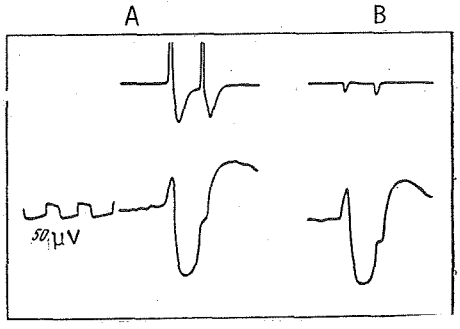

Figure 4. Electroretinogram of Deaf Subjects Before (A) and After (B) Vestibular Stimulations

No significant variations in EEG (see Figure 2 B) and rearrangement reaction were noted in deaf subjects upon stimulation of the vestibular apparatus; an absence in variations of wave c and assimulations of rhythm were observed in the ERG, and weak nystagmoid movements were noted (Figure 4 B).

The data obtained permit us to think that the interaction of visual and vestibular analyzers under a given experimental setup is brought about mainly due to their cortical sections. The diminished flow of information from the vestibular analyzer in deaf subjects is inadequate to alter the cortical mosaic of the stimulus-inhibitory process, and the decreased tonus of the cortex cannot elicit centrifugal variations at the periphery of the visual analyzer. Functional variations of the cortex of normal subjects caused by vestibular stimulations result in disruption of cortical-subcortical relationships, which in turn alters the functional states of the retina (i.e. of the /74
periphery of the visual analyzer).

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THE EFFECT OF VISUAL STIMULATION ON NYSTAGMUS, FROM DATA OF ELECTRONYSTAGMOGRAPHY, IN THE PRESENCE OF TUMORS OF THE POSTERIOR CRANIAL FOSSA

N. S. Blagoveshchenskaya

ABSTRACT. Visual stimulation may intensify or retard spontaneous and caloric nystagus even in the same patient during dynamic investigation. This depends on the intensity of the stimulation and its characteristics (rhythmic light or a single light flash), and on application of additional stimuli (the caloric test). All characteristics of spontaneous and caloric nystagmus were altered by light stimulation in patients with tumors of the posterior cranial fossa, and periods of caloric nystagmus (phase culmination) were altered.

The vestibular function may be altered under the effect of the most diverse stimuli. By using the electrographic method of recording nystagmic movement of the eyes, Mahoney, Harlan, and Bickford [11] established that various external and internal stimulations have a noticeable effect on caloric /75 nystagmus. Inhibition was observed upon sudden acoustic and alegesic stimulations. Nystagmus was intensified when the test subject was solving a mathematical problem. Mitrinoviez [15] noted an increase in the chronaxy of the vestibular apparatus during the effect of acoustical stimulation on the organ of hearing. M. D. Yemel'yanov and A. G. Kuznetsov [2] emphasize that disruption of the interrelationships of the vestibular, visual and proprioceptive analyzers is of great importance during development of illusory sensations in pilots.

There is an especially close anatomical and functional interrelationship between the vestibular and visual analyzers. Thus, nystagmic movements of the eyeballs logically develop during vestibular stimulation. On the other hand, we often observed in the clinic that prolonged visual stimulation with objects flashing in front of the eyes (the bright striped hue of a fabric, investigation of optokinetic nystagmus, a bright flashing light) may cause a paroxysm of vestibular vertigo and nausea in patients with an unstable vestibular apparatus.

Guedry [9] carried out vestibular stimulation of pilots; in one group of test subjects, this study was conducted in darkness, and in the second group problems were assigned in which the subjects were required to follow an image on a flashing screen. Nystagmus and vegetative reactions were more defined in subjects completing a visual assignment during vestibular stimulation.

S. F. Shteyn [5] pointed out the close relationship of the vestibular apparatus with the eye; moreover, in his opinion, stimulation of the vestibular apparatus may cause 1) nystagmus, 2) distortion of the eyeballs,

3) inadequacy of the eye muscles (diplopia and strobism), and 4) disorder of pupil lability.

Chafee, Bowie and Hampson [7] studied the electrical responses of the retina to visual stimulation, and Miles [13] disclosed the differences in potentials of the eye of man in darkness and in light.

N. S. Blagoveshchenskaya [1] sometimes noted the appearance of temporary doubling in the eyes after a rotation test, and intensification of "nystagmus" of the upper eyelids upon vestibular stimulation in the presence of tumors of the posterior cranial fossa. M. V. Kulikova noted the variation in the nature of the electroencephalogram and nystagmogram due to the effect of certain external stimuli (light and sound) and of medicinal substances (glucose, mercusal and caffeine).

Electronystagmography permits us to ascertain the phenomenon of nystagmus inhibition. Mc-Lay [12] observed a patient who could inhibit caloric nystagmus. Certain external factors (music) intensified nystagmus inhibition. A correct concept about the state of the vestibular apparatus is possible on the condition that central nystagmus inhibition be eliminated /76
[12]. He achieved this with the help of such substances as alcohol, conversation with the patient during the investigation and simultaneous recording of speech audiometry.

According to S. V. Kravkov [3], variation of excitability in the organs of sense may occur due to transition of stimulation from the nerve tracks of one sense organ to those of another, anatomically similar to it. This transition may be brought about by the central links between afferent systems, through the vegetative nervous system, and also by establishing temporary links of the conditioned reflex type. Consequently, the transition may take place in both subcortical formations as well as in the cerebral cortex.

The literature contains various points of view about the nature of the effect of visual stimulation on vestibular nystagmus. Most authors observed inhibition of vestibular nystagmus upon application of visual stimulation [4, 6, 14, 17]. Some authors noted intensification of vestibular nystagmus after visual stimulation [10]. Individual authors feel that vestibular nystagmus may be inhibited or intensified by visual stimulations, depending on which nystagmus -- rotary or post-rotary -- is affected [16].

The task of this paper was to study the effect of light stimulation on nystagmus. It was also necessary to explain which components of nystagmus are affected by light stimulation. A total of 38 patients with disease of the posterior cranial fossa were examined, in which forty composite recordings of electronystagmograms and electroencephalograms were made; 10 healthy subjects were examined at the same time. Light stimulation in 17 observations was applied not only by single light flashes, but also by rhythmic flashes of different frequency with the help of a photostimulator (the effect of rhythmic light on nystagmus has hardly been covered in the literature). Rhythmic light stimulation was not applied to 16 patients because of weak vision or for

technical reasons, but recording of electronystagmograms and electroencephalograms was carried out in darkness and in light.

Electronystagmography has substantial advantages over visual observation when studying the interaction between the vestibular and other analyzers, because it permits accurate and objective recording of the slightest deviations in variation of vestibular nystagmus, and they may be analyzed at any point of the study. It is often very difficult and sometimes impossible to follow precisely all the small variations in rhythm, amplitude and characteristics of phase shift of nystagmus during the visual observations.

Data which we obtained during simultaneous recording of electronystagmograms and electroencephalograms during simultaneous application of rhythmic light stimulation are promising in the theoretical and practical sense. Moreover, we managed to record objectively the close functional relationship and interaction of the visual and vestibular analyzers. /77

Nystagmus recording and electroencephalography were carried out on a 20-channel electroencephalograph of the "Alvar" system. Electrodes were attached near the external sections of both eye sockets and one above the bridge of the nose in order to record horizontal nystagmus. One electrode was placed above the eye and another below it to record vertical nystagmus. Calibration of movements was carried out to 20°, and paper speed was 3 cm/sec. When recording nystagmus to the right, and also nystagmus upward, the peak of the waves on the nystagmogram was aligned upward. During recording of nystagmus to the left, or downward, the peak of the waves was directed downward. A caloric test was carried out by pouring 100 mℓ of water at a temperature of 19° for 10 sec into the external acoustical duct.

In the case of clear asymmetry of caloric nystagmus, calorization with hot water (100 mℓ water at a temperature of 49°) was carried out. Extensive neurological and otoneurological examination of the patient in the hospital was carried out prior to electronystagmography.

There was the following localization of the pathological process in the patients studied: neurinoma of the auditory nerve -- 9, arachnoidal endothelioma of the lateral cistern of the pons -- 2, tumor or encephalitis ~~in~~ in the region of the pons Varolii and the medulla oblongata -- 10, tumor of the medulla oblongata -- 1, tumors of the vermis and IV ventricle -- V, tumors of the cerebellum -- 8, tumors of the IV ventricle -- 5, tumor of the mesencephalon -- 1, tumor of the III ventricle with ingrowing into the aquaeductus Sylvii and effect on the regions of the posterior cranial fossa -- 1, and normal -- 10 patients. A total of 50 examinations were conducted (two patients were examined twice).

The effect of single light flashes and of rhythmic light of different intensity and frequency on spontaneous and caloric nystagmus was studied in the patients; combined stimulation of the vestibular apparatus by a caloric test was employed, on the background of which single and rhythmic light

light flashes and acoustical stimulations were carried out. Variations in nystagmus with opened and closed eyes were analyzed.

Light stimulation had a different effect on nystagmus. Single light flashes usually were barely reflected in nystagmus, sometimes altering one of its waves at the moment of the flash. On the other hand, rhythmic light affected nystagmus more often and more intensely, which was found to be a direct function of the frequency of the flashes. Thus, at a rhythm of six /78 to eight flashes per second there was often an intensification of nystagmus: its frequency increased and a more uniform amplitude developed. More frequent flashes, 12-16 per second, could result in sharp inhibition and even total disappearance of nystagmus in this same patient. Opening the eyes during normal illumination of the room or closing the eyes as the light was switched off could also have a strong effect on nystagmus. Fixation of the gaze often inhibited nystagmus.

Acoustical stimulation, according to data of electronystagmography, had a much smaller effect on nystagmus than visual stimulation.

According to our data, all components of vestibular nystagmus (rhythm, amplitude and characteristics of phase shift) were varied and rearranged under the effect of rhythmic light. Moreover, these variations differed substantially in both different patients, as well as in the same patient, with application of diverse functional loads (either a single light of varying frequency, or combined stimulations -- rhythmic light plus caloric test).

Light stimulation in eleven observations resulted in inhibition of spontaneous, optokinetic and caloric nystagmus, in four observations -- to intensification of nystagmus, and different indices were recorded in five patients at different functional light loads -- intensification at one and inhibition of nystagmus at another functional load.

Inhibition of vestibular nystagmus due to the effect of light developed in eleven patients in the following manner -- the rhythm of nystagmus was retarded, its amplitude decreased, duration was reduced, and phase shift varied as the long phase lengthened. The rhythm of spontaneous and caloric nystagmus decreased to almost total disappearance under the effect of light. Slower light pulses sometimes caused retardation of nystagmus, and more rapid ones caused total disappearance. Nystagmus again developed after cessation of the effect of rhythmic light.

The rhythm of nystagmus in patient K decreased sharply during rhythmic light stimulation (at first it was 20 impulses per 10 sec, then 16, 10 and 6 with gradual disappearance of nystagmus). Spontaneous and caloric nystagmus could be temporarily inhibited sharply with subsequent recovery on the background of light stimulation when rhythmic light stimulation was switched on.

Light stimulation could significantly diminish the amplitude of nystagmus (thus, the amplitude of nystagmus in one patient decreased from 22-10° to 10-5° under the effect of rhythmic light) or could reduce the duration of

nystagmus -- when recording caloric nystagmus with closed and opened eyes it was often clearly obvious on the nystagmogram that caloric nystagmus is less prolonged and lower in amplitude with open eyes than it is with closed eyes.

Rhythmic light could alter the relationship of nystagmus phases; the /79 nature of nystagmus became slower and more drawn out, with a lengthened slow phase.

Nystagmus stimulation under the effect of light stimulation was noted much more rarely (in four patients) and appeared either at the onset of spontaneous nystagmus which was not present prior to this, or in an increase of amplitude and frequency of the rhythm; finally, rhythmic light stimulation could lead to greater normalization of nystagmus phase shift with a reduction in the duration of the slow phase.

Upon stimulation with rhythmic light, a number of patients assimulated to a certain degree the rhythm in the electronystagmogram -- an increase in frequency of nystagmus rhythm upon increase in frequency of the rhythm of light flashes and retardation upon a decrease in the rhythm of the flashes.

The characteristics of nystagmus during rhythmic light stimulation often became irregular in rhythm and amplitude; two- and three-humped peaks of the waves were noted. Nystagmus assumed a more uniform amplitude after cessation of rhythmic light.

That there is close interaction between the vestibular and visual analyzers is reflected by data on the effect of visual stimulation and fixation of the gaze on nystagmus phase shift. Thus, patient S with incephalitis of the brain stem (or a tumor of the stem in the posterior cranial fossa) experienced pendulum-like nystagmus without a clear phase shift, but the pendulum-like nystagmus gradually converted to phase nystagmus upon fixation of the eyes.

Rhythmic light could cause rough nystagmus of the upper eyelids in the presence of various illnesses.

The same stimulus (rhythmic light) could stimulate nystagmoid movements of the eyes (in the initial background) in some cases, and could inhibit them in others in a single patient at various functional states. For example, rhythmic light sharply inhibited spontaneous nystagmus in the initial background in patient P with tumor of the pons Varolii, while rhythmic light caused a clear temporary increase in frequency of the rhythm of caloric nystagmus on the background of the caloric test.

Switching on rhythmic light at the beginning of caloric nystagmus may sharply alter its rhythm and culmination characteristics. The course of caloric nystagmus cycles may be altered sharply -- two culminating rises in frequency of rhythm may be obtained.

The effect of light stimulation on nystagmus was especially clear if there was no very rough destruction of vestibular nuclei and vestibulo-oculomotor bonds in the brain stem.

When there was functional variation of the vestibular analyzer, we could /80 often see that if a single stimulus -- rhythmic light -- were applied, it may cause an intensification of nystagmus in the form of an increase in the frequency of its rhythm and phase normalization. But if two stimuli, caloric test plus rhythmic light, were applied to the same patient, rhythmic light would be a too-strong stimulus on the background of the caloric test, and would result in inhibition of nystagmus with sharp retardation of its rhythm.

Rhythmic light intensified caloric nystagmus in two patients (it became more regular in rhythm); when the rhythm of light stimulation was increased in frequency, nystagmus became irregular in rhythm, and upon retardation of light flashes, nystagmus again became more regular in rhythm. Thus, we have in the data of observation a state approaching a phase state, because more intense stimulations (more frequent light flashes) caused a decrease in the function, while weaker stimulations (slower flashes) intensified nystagmus.

It is appropriate to pose the question, where does the interaction of the vestibular and visual analyzers take place? Obviously, at different levels in both the stem section of the brain and in the cortex. Proof of the latter is the variation, from data of electroencephalography, in the functional state of the cortex of the occipital lobe due to the effect of rhythmic light before and after vestibular stimulation by caloric test. Upon rotation of test subjects with eyes opened and closed, no substantial difference was noted on the electroencephalogram, with the exception of weak depression of the α rhythm in the temporal region immediately after closing of the eyes; this depression disappeared after rapid rotation [16].

In contrast with these data, assimilation of rhythmic light in the electroencephalogram in many of our patients was much worse after vestibular stimulation than it was initially. In other patients rhythmic light before caloric tests did not alter the characteristics of the EEG, while high-amplitude bursts of the α rhythm and epileptoid symmetrical impulses, expressed more in the occipital-temporal regions, developed on the background of rhythmic light after caloric tests.

All this indicates that stimulation of the vestibular apparatus leads to functional variations in the cortex of the occipital region of the cerebellum -- the cortical section of the visual analyzer. Consequently, there is also a close interrelationship between the vestibular and visual analyzers at the level of the cerebral cortex.

Variations on the electronystagmogram due to the effect of visual stimulation are a clear example of objective recording of the interaction of the visual and vestibular analyzers. These data disclose in more detail the /81

interaction of the cortical-stem functional interrelationships, showing how an unconditioned reflex is affected by visual stimulation, by altering all characteristics of nystagmus.

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THE EFFECT OF PROLONGED SLOW ROTATION ON HEARING

I. Ya. Yakovleva, E. I. Matsnev and V. P. Baranova

ABSTRACT. A study was made of the effect of the prolonged stay of man (3 and 10 days) in a rotating room at a velocity of 40 and 10 deg/sec on the functional state of the auditory analyzer. Variations in hearing were found which exceed the individual spread of the norm, and functional shifts were more severe after 3-day rotation at a velocity of 40 deg/sec, and were maintained for 5-6 hours after the experiment.

Studies of the physiological effects arising upon the prolonged influence of Coriolis accelerations under conditions of slow rotation were first begun in 1958 by a group of American scientists [6, 7].

After two-day rotation of a test subject in a slowly revolving room approximately 5 m in diameter at angular velocities of 1.7, 2.2, 3.8, 5.4 and 10 revolutions per minute, symptoms of the so-called "illness of the canals" were observed. Moreover, general dysphoria, apathy, vertigo, headache, somnolence, nausea and sweating were noted, and vomiting occurred at high velocities. /82

Our investigation was directed toward further study of the physiological effects arising upon prolonged presence in a slowly rotating room (SRR).

Experiments of Yu. G. Grigor'yev and colleagues (1962-1964) revealed a significant variation in the functional state of the auditory analyzer after a stay in an SRR for 24 hr at a velocity of 10.6 and 21.2 deg/sec.

American scientists [6, 7], investigating the work capability of man in an SRR for two weeks at a velocity of three revolutions per minute, noted a "high variability of the results of auditory testing."

Study of the functional state of the auditory analyzer under the effect of high rotation velocities in the SRR has not been illuminated in available literature, and may be of interest during training for prolonged space flights. In connection with this we conducted a study of the influence of the indicated effects on the functional state of the auditory analyzer. Examination was carried out one to three days before the experiment, and five to six hours after its termination. Exo-endoscopy was carried out by generally accepted methods of otorhinolaryngological examination.

Investigation of the functional state of the auditory analyzer included monaural determination of thresholds of auditory sensitivity during air conduction for frequencies of 125, 250, 1000, 1500, 2000, 3000, 4000, 6000,

8000 and 10,000 Hz. In order to compare the data obtained, the study of hearing was carried out at all stages on the same audiometer (audiomatic AUG-60) at the same time of day (from 11 a.m. to 4 p.m.).

The investigations were carried out during these hours in accordance with Neuberger's data [10]. The author noted the least spread of auditory thresholds due to the daily cycle at this time of day. During study of more complex functions of the auditory analyzer, the differential thresholds of sound intensity were determined, and auditory adaptation was investigated. Differential thresholds to a tone at 1000 Hz were determined monaurally by Lusher's method [9].

Auditory adaptation for tones at 500, 1000 and 10,000 Hz of threshold intensity was also determined monaurally by the method of Carhart and Hood [5, 8]. Indices of all investigations were obtained on the basis of triple measurements.

Investigation was conducted on six test subjects -- on two before and after rotation in the SRR for seven days at a rotation velocity of 10 deg/sec, and on four subjects (two series of experiments) before and after rotation for /83 three days at a rotation velocity of 40 deg/sec.

All test subjects were acknowledged to be healthy upon otorhinolaryngological examination. There were no illnesses of the otorhinolaryngological organs during anamnesis. Fluctuations of the tonal thresholds of hearing during air conduction, according to the data of B. Ye. Sheyvekhman and colleagues [4], did not exceed the individual spread of this indicator in the norm.

The investigations carried out indicated that after rotation in the SRR at a velocity of 10 deg/sec, fluctuations of tonal thresholds are noted, primarily in the zone of low and high tones (125, 250 Hz and 6000-10,000 Hz). An increase in thresholds (of the sensitization type) was observed in subject N (Figure 1). Fluctuations of tonal thresholds were within ranges of 5-20 db, which (according to the data of B. Ye. Sheyvekhman and colleagues [4]) slightly exceed the daily fluctuations of the thresholds.

Investigation of differential thresholds for both frequency and intensity did not reveal deviations from the norm. Auditory adaptation in test subject N was disrupted for low, middle and high tones for the first day after the experiment. On the second day a variation in adaptation was observed only for high tones. We did not note any disruptions of adaptation in test subject G.

After rotation in the SRR at a velocity of 40 deg/sec, two of the four subjects examined complained of a sensation of blocking of the ears and of noise in the head and ears for 6-8 hours after termination of the experiment. The indicated phenomena disappeared after sleep.

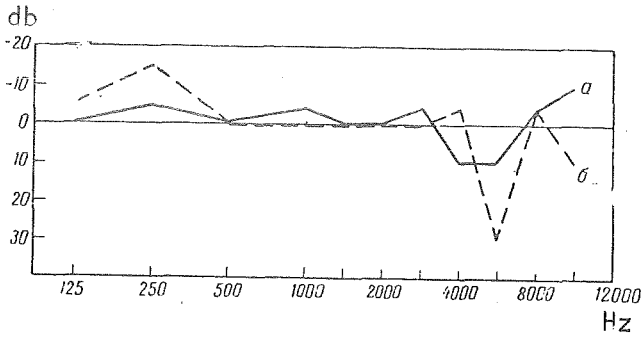

Figure 1. Audiogram of Test Subject N-n. Rotation at a velocity of 10 deg/sec; a, Before rotation; b, After rotation

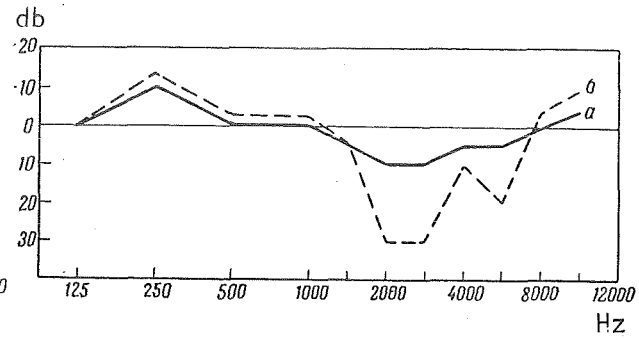

Figure 2. Audiogram of Test Subject R-v (40 deg/sec). The notations are the same as in Figure 1.

Investigation of tonal thresholds of hearing after the experiment disclosed a significant increase in thresholds (15-20 db) to high tones (2000, 3000 and 6000 Hz) in three of four subjects examined (Figure 2).

Differential thresholds of sound intensity during background examination, /84 according to data of the literature [2, 9], corresponded to the individual spread of this indicator in the norm. After rotation in the SRR three subjects displayed a significant decrease of differential thresholds exceeding the individual spread of this indicator in the norm.

No disruptions of adaptations during background examination in our test subjects were noted; after the experiment we noted in one of four subjects examined a variation in auditory adaptation to high tones, within the limits of variations of the adaptogram within the norm sometimes observed [3, 5].

Thus, the investigations indicated that prolonged rotations in a SRR at velocities of 10 and 40 deg/sec may cause variations in the functional state of the auditory analyzer.

Functional shifts are characterized subjectively by a sensation of noise in the head and ears, by an objectively significant increase of auditory thresholds to high tones, and by disruption of the function of loudness. The appearance of auditory variations within five to six hours after termination of the experiment indicates the relative persistence of disruptions of the functional state of the auditory analyzer. The variations noted may be caused by a complex of effects -- prolonged stay in a closed space of limited volume, by the effect of the noise background of the installation and by rotation itself.

Comparisons of our data with the results of investigations by Yu. V. Krylov [1] and with data of the investigation of hearing after seven

days' rotation at a velocity of 10 deg/sec permit us to conclude that the controlling factor in variation of hearing with regard to a stay in the SRR is the velocity of rotation and its duration. Yu. V. Krylov [1] did not observe /85 significant variations of hearing in controlled experiments without rotation in this installation and at a rotation velocity of 5.3 deg/sec. These variations were noted by him upon increasing rotation velocity of the installation to 10.6 deg/sec.

In our investigations, functional variations of hearing were more expressed after three-day rotation at a velocity of 40 deg/sec than after seven-day rotation at a velocity of 10 deg/sec. Apparently, increasing the velocity of rotation has the greater effect.

The mechanisms of indicated variations of hearing are probably related to central neurodynamic shifts.

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THE PHYSIOLOGY OF THE VESTIBULAR ANALYZER

THE EFFECT OF CENTRIFUGAL FORCE ON CALORIC NYSTAGMUS

V. A. Kislyakov and I. V. Orlov

ABSTRACT. Variations in the thresholds of caloric thermal nystagmus in pigeons due to the effect of centrifugal force (0.1-1.0 g), acting in the tail-head or head-tail direction, were studied. Characteristic variations in the thresholds (both an increase and decrease) and the direction of nystagmus were found, depending on the magnitude and direction of the effect of centrifugal force.

Generally accepted at present is the point of view, according to which the semicircular canals sense angular accelerations, and the otolithic apparatus senses linear accelerations, the effect of centrifugal force and variations in gravitation. /86

However, this view was not immediately established, and some prominent scientists have proved that the semicircular canals may react to rectilinear accelerations [2, 10]. In 1952, Szentagothai [11] presented the foundation of this point of view.

There is a hypothesis, on the basis of which one may assume that interaction of the atrium receptors and semicircular canals is brought about through the nerve centers [3]. At the same time microelectrode investigations of Gernandt [9] showed that the effect of centrifugal force substantially distorts the reaction of the semicircular canals to angular acceleration, analyzed by the activity of individual elements of the eighth nerve. The conditions of Gernandt's experiments permitted him to regard these facts from the point of view of the effect of centrifugal force on the cupulo-endolymphatic system without drawing in interaction with the otoliths.

Regardless of the attitude toward one or another point of view, it should be acknowledged that the general property of both the semicircular canal system, as well as that of the atrium is their organization on the principle of inertial systems [6]. This circumstance has made it possible to find such conditions in experiment in which linear accelerations or the effect of gravity may affect the cupulo-endolymphatic system of the semicircular canals. Barany's caloric test was essentially the first such experiment [5].

Barany's basic concept of the mechanism of caloric vestibular reactions. was that about endolymph convection currents arising due to the effect of temperature effects on the semicircular canal. Convection currents are

the result of variation in the specific gravity of the endolymph in this section of the canal, where it is heated or cooled. The effect of the caloric test depends on the orientation of the canal with respect to the vector of gravity. Convection currents do not develop, according to Barany's theory, in a horizontally positioned canal. The assumption follows from this theory that caloric reactions should vary due to the influence of altered gravitation. This was often proved by Bergstedt [7] during experiments in which caloric nystagmus in humans were intensified during rotation in a centrifuge. An increase in the duration of caloric nystagmus due to the effect of g-forces was observed by Ye. M. Yuganov [4]. /87

In our research we studied variations in the thresholds of thermal caloric nystagmus in pigeons under the effect of centrifugal force. Cervical caloric nystagmus was caused by local heating of the right lateral semicircular canal by a method developed in our laboratory [1]. Heating temperature was recorded with the help of a microthermistor connected to the pons. The method permitted us to determine the threshold of caloric stimulation by simultaneous recording of nystagmus and the curve of the temperature increase of the canal. Nystagmus was recorded electromyographically. The threshold of caloric reaction was regarded as the minimum increase in temperature at which nystagmus developed. Various gradations of centrifugal force were obtained on a rotating stand with programmed automatic control. The pigeon was placed in a special stand at a distance of one meter from the center of rotation, with the head pointed toward the periphery. The bird and the stand were inclined forward (nose downward) by 15-20° in order to place the lateral semicircular canals in a horizontal position. The functional indicator of the horizontal position of the canal was cessation of background nystagmus, which occurred after exposure of the canal due to a decrease in its temperature (to 33°). Convection currents in a canal oriented in this manner ceased, which indicated the disappearance of cold nystagmus.

In our experiments, heating of a canal oriented horizontally was accompanied by caloric nystagmus, which apparently developed due to expansion of the endolymph, rather than due to convection currents. It was assumed that the effect of the caloric test should vary under the effect of centrifugal force because of the variation in the specific gravity of the endolymph at the point of heating with respect to the remaining mass of the endolymph.

Two main series of experiments were carried out. In the first of them, centrifugal force was applied in the direction of the tail-head. Thresholds of caloric nystagmus varied before and during rotation at a constant angular velocity with the following values of centripetal accelerations -- 0.1, 0.2, 0.3, 0.5, 0.75 and 1.0 g. Measurements were taken 30 min after positive acceleration equal to 0.5 deg/sec^2. The intervals between measurements were 10 min. Moreover, characteristic variations of thresholds and the directions of caloric nystagmus were revealed (all data were processed statistically by the Fischer-Student method). Thresholds within the range to 0.2 g, inclusive, increased on the average by 1.5 times with respect to the initial level measured before rotation. Upon acceleration equal to 0.3 g, caloric nystagmus did not develop even at an increased temperature by 7°, whereas before /88

rotation the threshold was 2.4 ± 0.23° (the zero point of the reading was assumed to be the temperature of the exposed semicircular canal). Upon acceleration equal to 0.5 g, reversion of the direction of caloric nystagmus was observed, which may be explained by variation in the direction of endolymph flows in the canal. A further increase in acceleration caused a decrease in the thresholds of reversed caloric nystagmus. At an acceleration of 0.75 g it decreased by 2.5 times, and at 1.0 g -- by 8 times with respect to the value corresponding to acceleration of 0.5 g.

In the second series of experiments, centrifugal force was applied in the head-tail direction. In this series the dependence of caloric thresholds on centrifugal force was different. At acceleration of 0.5 g, the threshold decreased to 70%, and at acceleration of 1.0 g -- to 22% (the threshold before rotation is assumed to be 100%). No reversal of the direction of nystagmus was observed during these experiments.

Finally, additional experiments with rotation, during which the pigeon was positioned on a tangent to the periphery, indicated that under such conditions centrifugal force does not affect the thresholds of caloric nystagmus.

We attempted during the experiment to study the described phenomena from the point of view of hydrodynamic properties of the cupulo-endolymphatic system of the semicircular canal. The hypothesis is expressed about development of endolymph shifts in the ring system of the semicircular canals due to the effect of centrifugal force. Variations in the thresholds of caloric nystagmus, and also its reversal under the effect of centrifugal force, are regarded as the result of algebraic summation of endolymph shifts in the semicircular canal due to the effect of caloric activity and centrifugal force.

The data obtained may at first glance seem artificial, occurring only under conditions of a specially set up experiment and rather improbable in the natural life of an organism. However, there is the hypothesis that the difference in the specific gravity of the endolymph and cupula by 0.0001 may be significant, which causes superthreshold deviation of the cupula due to the effect of gravitational acceleration [8]. In our experiments the difference of the specific gravities in the endolymph of the semicircular canal was created by local heating of a section in its lateral region. Moreover, centrifugal force clearly altered the results of the caloric test.

In modern aviation and space flights, in which the vestibular apparatus, /89
along with other systems of the organism, is under conditions removed from the ground range of effects, the probability increases that unusual reactions will appear.

The proposed model of experiments with a combination of temperature and rotational tests is a convenient method of studying the function of the labyrinth in an alternating gravitational field.

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CHARACTERISTICS OF THE FUNCTIONAL STATE OF THE OTOLITHIC APPARATUS UNDER CONDITIONS OF VARIABLE WEIGHT

Ye. M. Yuganov and A. I. Gorshkov

ABSTRACT. The functional state of the otolithic apparatus was studied under conditions of weightlessness and G-loads using galvanometry and a method of direct otolithometry developed by the authors. It was revealed that under conditions of brief periods of weightlessness, thresholds to current and linear acceleration increase uniformly, on the basis of which it is concluded that weightlessness is a specific stimulus of the vestibular apparatus. The article has eight references.

There is at present no single opinion about the mechanism and nature of the effect of weightlessness on the vestibular analyzer. There are various concepts, each of which is based on general theoretical ideas and extrapolation of data of the overall physiology with respect to conditions of decreased weight. Regarding the question of the physiological mechanisms of space motion sickness, the authors relate its development to disruption of the functional arrangement of various analyzer systems [1], to the effect of Coriolis accelerations which develop when the head is moved with respect to the center of possible rotation of a spaceship [2], to an increase in the stimulation of the receptor formations of the semicircular canals, and to the consequence of alleviation of inhibiting effects from the otolith apparatus due to its functional cutoff in weightlessness [2, 6-8]. In connection with /90 that presented above, it is important to study the characteristics of the function of the otolith apparatus under conditions of variable weight. This would make it possible to explain whether this factor is a specific stimulus of the neuroreceptor formations of the otolithic apparatus, or whether weightlessness is a state equivalent to the absence of a stimulus. If weightlessness is the absence of a stimulus, by taking as a basis the reasoning of V. A. Ukhtomskiy's concept of dominance, we may consider that there is a decrease in the thresholds of stimulation of the otolithic apparatus during weightlessness with respect to the effect of adequate stimulations. Being guided by the theory of V. I. Voyachek and K. L. Khilov on the interaction of the otolithic and cupular organs of the vestibular analyzer, one should assume that in this case, in connection with a state similar to physiological otolithectomy, there is disruption of the functional arrangement between various parts of the analyzer, which should be manifested in the known "splitting" of the reactions -- activation of vestibular nystagmic reaction and inhibition of vestibulo-vegetative reflexes.

Determining the nature and degree of variation in the sensitivity of the otolithic and cupular organs of the vestibular analyzer and their functional state during weightlessness is extremely important not only from a general theoretical point of view, but also in practice for medical guarantee of

space flights. Study of this problem is beneficial for refining methods and criteria of vestibular selection, training and processing of certain other means of preventing vestibular disorders during orbital flight, in particular of the problem of artificial weightlessness.

During the course of solving this problem, our investigations under normal ground conditions and during increased weight were controlled. Moreover, study of the nature of vestibular reactions due to the effect of centrifugal forces also assumes an independent significance -- the duration and amount of g-loads acting on the organism of the pilot have increased significantly in aviation and space flights.

Study of the functional state of the otolithic apparatus under conditions of weightlessness and g-loads was carried out by means of galvanometry and by the method of direct otolithometry proposed by us. The latter method makes possible direct determination of sensitivity thresholds of the otolithic apparatus to linear accelerations. The sensitivity threshold was assumed to be the minimum value of linear acceleration, under the effect of which the test subject with closed eyes experienced the sensation of motion.

Thresholds were determined under ground conditions, under conditions of weightlessness, and under the influence of g-loads with the help of the so-called stand of acceleration sensitivity developed by A. I. Gorshkov. The /91 stand makes it possible to study sensitivity thresholds of the otoliths within acceleration ranges from 0.0001 to 0.1 g at various positions of the test subject. However, during present experiments in weightlessness, the test subject is placed in a reclining position, and the platform of the stand is alternately positioned in the head-feet and feet-head direction.

Controlled experiments under ground conditions were conducted on 212 subjects. The studies indicated that sensitivity thresholds of the otolithic apparatus in subjects clinically healthy in the otorhinolaryngological sense under ground conditions are within the limits of 0.001-0.03 g.

Similar studies under conditions of brief weightlessness were conducted on part of these subjects using an acceleration stand, which was installed in a laboratory aircraft, making it possible to develop weightlessness of 25-30 sec duration in parabolic flight. Thresholds were measured at the tenth and twenty-second seconds of weightlessness, and in those cases when this period was inadequte to measure the threshold, -- under the repeated effect of weightlessness. The results of the studies obtained under ground conditions and weightlessness were compared, which made it possible to judge the extent and direction of variation in sensitivity thresholds of the otolithic apparatus during flight.

One hundred ninety-five experiments were conducted in weightlessness with participation of 51 subjects. The investigations indicated that in all cases without exception, sensitivity threshold values of the otolithic apparatus under conditions of weightlessness increased by 1.4-2.1 times with respect to their "ground" values. It is important to note that in an

overwhelming number of cases the sensation of motion during weightlessness developed in the subject when movement was in the direction from head to feet.

Investigations of the sensitivity thresholds of the otolithic apparatus during the effect of g-loads were conducted at a g-load value of two units with participation of 35 subjects. In this case, the acceleration stand was mounted on the platform of a centrifuge having a radius of 7.25 m, such that its platform was shifted perpendicular to the vector of g-load effect.

Results of the experiment indicated that under the effect of g-loads, the sensitivity thresholds of the otoliths to linear accelerations increase by 1.5-2 times.

In the second series of experiments, the state of sensitivity thresholds of the otolithic apparatus to galvanic current was studied. The thresholds were measured with the help of a series EI-1 electric pulsating device. A galvanic current with an intensity of 0.5-6.0 ma having a three-second duration of exposure was employed. So-called transverse galvanization was conducted. The negative electrode was attached to the skin of the face in front of the tragus of the left ear, and the positive electrode at the /92 same point near the right ear. A minimum current intensity, at which the illusion of rolling in the direction of the anode developed, was specified in the studies. This value of current was assumed to be the threshold value. Thresholds were studied with the subject having his eyes closed under ordinary conditions, under the effect of g forces and weightlessness. Two hundred forty-eight experiments were carried out on 22 subjects.

The data of the experiments indicated a uniform increase of sensitivity thresholds of the otolithic apparatus to current, both during the period of g-load effect and during weightlessness.

Taking as a basis A. A. Ukhtomskiy's concept of dominance and I. P. Pavlov's study on the irradiation and concentration of nervous processes in the cerebral cortex, we assume that stimulation of the otolithic apparatus by weightlessness creates a dominant stimulation of corresponding regions of the brain, and according to the law of dominance causes inhibition of impulses arising due to the effect of linear accelerations on the otolithic apparatus. One may assume that this hypothetical mechanism is the basis and determines the uniform increase of stimulation thresholds of the vestibular analyzer to current and linear accelerations under these conditions.

The experiments conducted make it possible to obtain the necessary data on the extent and direction of variation in sensitivity thresholds of the otolithic apparatus under brief effects of weightlessness and g-loads. However, they in no way permit determination of the specific nature of stimulation processes arising under these effects. The latter fact was established with the help of averaged methods and primarily by recording the main indicators of post-rotational and caloric nystagmus under these conditions.

The experimental data indicate that duration of nystagmic reaction during weightlessness decreases, and the duration of vestibular nystagmus under the effect of g-loads increases. The nature of the variation in cupular reactions permits us to assume that weightlessness and increased weight of man are states of the organism, each of which is characterized by specific stimulation of the otolithic apparatus.

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MICROELECTRODE INVESTIGATION OF THE VESTIBULAR NEURONS OF THE MESENCEPHALON

I. I. Leshchinyuk and V. A. Kislyakov

ABSTRACT. The effect of afferent vestibular pulsation on neuron activity of the inferior tubers of the lamina quadrigemina was investigated under conditions of direct current polarization and acoustical and caloric stimulation of the labyrinth. The experiments were conducted on decerebralized cats. The presence of neurons in the inferior corpus bigeminum was shown. The type of reaction of neurons studied is broader than that in the vestibular neurons of the medulla oblongata.

Much attention is being given at present to study of the functional organization of the central sections of the vestibular system. Most investigations are devoted to study of the processes of information processing in the bulbar [3, 9] and cortical sections of the brain [2, 7, 8, 10, 12].

Some authors attempted to solve the problem of representing vestibular afferent systems at the level of the mesencephalon.

Gernandt [5], employing adequate vestibular stimulation, observed variations in neuron activity in the lower tubers of the lamina quadrigemina.

We undertook the present research for the purpose of studying the effect of afferent vestibular pulsation on neuron activity of the mesencephalon, in particular of the lower tubers of the lamina quadrigemina.

Method

The experiments were conducted on decerebralized cats. The tendons of the occipital muscles were sectioned along the crest of the occipital bone, and an access was opened to the right and left bulla. Both bullas were exposed. After the craniotomy a transcortical section of the brain was made along a line passing 2 mm from the front edge of the upper tubers of the lamina quadrigemina (a trans-mesencephalic section), and the tentorium and the upper section of the cerebellum were separated. The animal was administered a myorelaxant, transferred to artificial respiration and fixed in a stereotactic device. At first the microelectrode was inserted under visual control. Later shifting of the electrode was accomplished in accordance with the stereotactic coordinates of the atlas of the cat brain of Snider and Niemer [11]. During the entire experiment the animal was warmed artificially by an attachment fed from a water ultrathermostat. /94

Potentials were led off extracellularly and were fed through a cathode repeater to the input of a UBP1-01 amplifier. Recording of potentials was accomplished from the screen of an OK-21 cathode oscillograph.

The background rhythmic activity of individual neurons of the corpus bigeminum were recorded, and variations in their rhythm in response to ipsi- and contralateral polarization of the wall of the round fenestra by a direct current of 100-200 μa were studied. Moreover, acoustic (white noise) and caloric stimulation were employed. In the latter case the round fenestra was irrigated by 10 mℓ of cold water (12°).

Results of the Investigation

Single neurons investigated in this paper were recorded in the lower tubers of the lamina quadrigemina. Ninety-two spontaneously active and eight mute neurons were studied. The main pulse activity of the neurons was in the form of constant discharge of two-phase peak potentials, primarily of irregular rhythm. Monophase peaks, both positive and negative, were recorded along with two-phase peaks. The frequency of discharges of the spontaneously active neurons of the lower tubers of the lamina quadrigemina fluctuated over broad ranges from 0.1 to 60 pulses per second. The majority of spontaneously active neurons, and also silent neurons recorded responded to polarization of the labyrinths by a definite variation in a background rhythm.

Moreover, of 92 spontaneously active units, 20 neurons did not respond to polarization of the labyrinths. The type of reactions of the remaining neurons developing in response to ipsi- and contralateral polarization of the labyrinths could be classified as a function of the variations in background rhythmic activity.

Variations in spontaneous rhythm upon ipsilateral polarization were studied in 52 neurons. The results of these experiments indicated that spontaneously active cells respond differently to the effects of direct current of positive or negative sign. They may be subdivided into several types according to the nature of the reaction to polarization.

In most neurons (20) spontaneous activity was suppressed by the anode and intensified by the cathode. We include in the second group 11 neurons in which activity was elicited by the anode and disappeared upon polarization of the cathode.

We may include in the third type nine neurons which were inhibited by current of any polarity.

The fourth group includes six neurons, the pulse activity of which /95
increased upon polarization by current of any polarity.

Besides neurons having spontaneous rhythmic activity, eight silent neurons were discovered which displayed their own activity upon cathodization.

As we know, the vestibular apparatus is a dual organ and has dual representation at different levels of the central nervous system. The most distinct position is demonstrated at the level of vestibular nuclei of the bulbar complex and the cerebral cortex [1, 3, 4, 6, 13].

In connection with this we investigated the interaction between vestibular nuclei of the left and right tubers of the posterior corpus bigeminum. It should be emphasized that in order to conduct these experiments, the method of polarization which made it possible to selectively stimulate only one labyrinth was extremely valuable. Both labyrinths are activated upon adequate stimulation.

In the given series of experiments, the reaction of 28 spontaneously active neurons were investigated according to their responses to ipsi- and contralateral stimulation of the labyrinth. Of them 10 neurons responded reciprocally to ipsi- and contralateral polarization. Their activity was suppressed upon polarization by an ipsilateral anode, and was intensified upon polarization by the cathode. Polarization by the anode of the contralateral labyrinth caused an increase in rhythmic activity, and polarization by the cathode resulted in inhibition.

Six neurons were activated by both ipsilateral and contralateral polarization of current of any sign.

An opposite type of reaction to polarization was observed in two neurons. Two neurons were activated by an ipsilateral anode and contralateral cathode. The effect of the ipsilateral cathode and contralateral anode inhibited their activity. One neuron was inhibited by the ipsi- and contralateral anode and activated by two-way cathodization. Two neurons did not alter their rhythm to contralateral polarization, but responded to ipsilateral polarization. One neuron was activated by contralateral polarization (cathode and anode) and by an ipsilateral cathode, but suppressed by an ipsilateral anode. Reaction of two other neurons was characterized by suppression of rhythmic activity to both anodes and absence of reaction to cathodization.

Besides the described types of reactions of neurons to polarization of the labyrinths, neurons were also observed in which polarization caused an initial increase in spontaneous rhythm, but inhibition at the end of stimulation. In some neurons the reaction to polarization proceeded according to the on-and-off effect.

The caloric test was applied to seven neurons reacting reciprocally to /96
labyrinth polarization. In five neurons investigated, reaction of the ipsi- and contralateral round fenestra to irrigation by cold water was also reciprocal, and in two neurons reaction was single-valued (inhibited).

Acoustic stimulation of a number of neurons indicated that there are neurons in the lower corpus bigeminum which react not only to polarization and acoustic stimulation, but to both effects.

Conclusion

The results of this paper indicate that there are neurons in the lower corpus bigeminum which receive afferent pulsation from the vestibular apparatus.

The types of neuron reactions to ipsi- and contralateral polarization of the labyrinths presented partially agree with the types of neuron reactions of the bulbar complex. However, in our experiments we obtained a wide range of neuron reactions of the posterior corpus bigeminum compared to types of neuron reactions presented in the literature for vestibular neurons of the medulla oblongata [1, 4].

It should be noted that neuron reactions of the lower corpora bigeminum to stimulation of different modalities indicate the presence in them of mono- and bisensory elements.

Analysis of neuron reactions of the lower corpus bigeminum to labyrinth polarization and reciprocal relationships between neurons of the ipsi- and contralateral sides permits us to express the assumption about the presence of direct and intersecting links of the labyrinth with formations of the mesencephalon.

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MICROELECTRODE INVESTIGATION OF NEURON REACTIONS OF THE VESTIBULAR NUCLEI IN THE CAT UPON POLARIZATION AND CALORIC STIMULATION OF THE LABYRINTHS

G. I. Gorgiladze

ABSTRACT. Activity of vestibular neurons and the nature of their reaction to stimulation of the ipsi- and contralateral labyrinths, and also the effect of intravenous administration of strychnine to explain the nature of the interaction between vestibular nuclei are investigated in detail. It is concluded that interaction between contralateral vestibular nuclei is brought about by direct commissural connections. The article contains three tables, 36 references and seven illustrations.

In the preceding paper [3], devoted to study of the dual function of the vestibular apparatus, we discovered reciprocity in reactions between neurons of the vestibular nuclei of the medulla oblongata in the cat to direct current polarization of the ipsi- and contralateral labyrinths. Stimulation of most vestibular neurons of one side was accompanied by inhibition of neurons of the opposite side. Upon polarization of both labyrinths by current in a single direction, reciprocity was disrupted -- neuron activity of both the left and right sides was altered in the same manner. On the basis of these data we proposed a scheme explaining the interaction between vestibular nuclei by the presence of neurons with inhibited functions between them. Interaction between vestibular nuclei of both sides may be brought about by both direct commissural bonds existing between them [15, 21], as well as by efferent regulation at the receptor level [30, 31]. /97

The proposed paper studies in detail activity of vestibular neurons and the nature of their reactions to stimulation of the ipsi- and contralateral labyrinths, and also explains the effect of intravenous introduction of strychnine on the nature of interaction between vestibular nuclei.

Method

The experiments were run on 28 adult decerebellized cats under nembutal anesthesia (60-100 mg/kg intraperitoneally). The animals were additionally curarized by Remiolan (3-5 mg/kg) and transferred to artificial respiration. Activity of single neurons of the vestibular nuclei was monitored by microelectrodes of pyrex glass having an end diameter of 0.5-2 μ and filled with a 2.7-molar solution of KCl. The indifferent electrode was attached to the skin of the forehead. Pulsation was prevented by flooding the brain with a dense solution of agar-agar. In a number of cases, a small plexiglass disk with an aperture in the center (1 mm), through which passed the end of the

microelectrode, was lowered to the brain and lightly pressed. The heads of the animals were rigidly fixed in a Delle stereotactic device. The angle of inclination of the oral fissure to the horizontal plane was -135° (according to Magnison). Extracellular peak neuron activity was recorded at a constant /98 time of 0.5 msec on an "Amplior" cathode oscillograph. Intracellular recording of neuron activity was also carried out on two neurons. The location of the electrode end was determined after fixation of the brain in formalin and flooding in paraffin in the sections stained according to the Nissle method, with use of the atlas of vestibular nuclei [13]. The vestibular apparatus was stimulated by direct current [5] and calorically. One labyrinth (monaural stimulation) or two labyrinths were polarized by current of different direction (binaural stimulation) or by current of a single direction (equal stimulation). For caloric stimulation both bullae osseae exposed previously were irrigated by 3 mℓ water of varying temperature (hot water of 40-65° and cold water of 16-18°) for 10 sec.

Results

The activity of 98 neurons of the right and left vestibular nuclear complexes of the medulla oblongata to labyrinth polarization by direct current (galvanic test) and 52 neurons to irrigation of the bullae osseae by water of varying temperature (caloric test) was studied.

1. Monaural polarization. Several types of neuron reactions to polarization of the ipsi- and contralateral labyrinths, presented in Table 1, were discovered.

As follows from the table, most neurons (71) are activated to polarization of the ipsilateral labyrinth by the cathode and inhibited by anodization of the same labyrinth. The activity of a small number of neurons (14) could be suppressed by the ipsilateral cathode and intensified by the ipsilateral anode. Cathodization of the contralateral labyrinth inhibited activity of the suppressing part of the same neurons (66 of 71), which were activated by the ipsilateral cathode. The same neurons were activated by the contralateral anode. Thirty neurons were activated by the contralateral cathode and inhibited by the contralateral anode.

We can isolate two neurons individually which reacted to the ipsilateral cathode by an initial brief activation, being altered by prolonged suppression of activity, and by brief initial suppression with subsequent prolonged activation by anodization of the same labyrinth.

In their effect, ipsi- and contralateral polarization do not have the same physiological influence -- the ipsilateral cathode usually activates neurons much more intensely than does the contralateral anode, and on the other hand, activity is more strongly suppressed by the contralateral cathode /99 than by the ipsilateral anode (Figure 1).

TABLE 1. DIFFERENT TYPES OF NEURON REACTIONS OF VESTIBULAR NUCLEI TO POLARIZATION OF THE IPSI- AND CONTRALATERAL LABYRINTHS BY DIRECT CURRENT OF DIFFERENT DIRECTION

Type of reaction	Number of neurons	Ipsilateral		Contralateral	
		Cathode	Anode	Cathode	Anode
I	66	+	—	—	+
II	14	—	+	+	—
III	5	+	—	+	—
IV	11	0	0	+	—
V	2	+—	—+	Not investigated	

Note. + denotes neuron activation;- denotes inhibition of activity; 0 indicates absence of reaction to polarization (also for Table 2).

The contralateral effect is retained completely after section of the ipsilateral VIII nerve. Section of the contralateral VIII nerve causes a rather significant and prolonged increase in the activity of those neurons which are inhibited by the contralateral cathode (Figure 2).

It is typical that no relationship was discovered in neuron distribution with different types of reactions in different vestibular nuclei or within the /101 limits of a single nucleus.

Upon intracellular registration of two neurons of the I type with low spontaneous activity, stimulation of the contralateral VIII nerve by a single pulse of electrical current caused a distinct inhibiting postsynaptic potential having a latency period of 3.5-4 msec, an amplitude of 20 mv and duration up to 30-40 msec (Figure 3 A).

2. Binaural polarization. Reaction of neurons of I type to simultaneous polarization of both labyrinths depends on the direction of current -- if the cathode is applied to the ipsilateral labyrinth and the anode to the contralateral labyrinth, the neuron is activated much more intensely than would be the case during monaural stimulation, i.e. in the case of an ipsilateral cathode or contralateral anode (Figure 4 B). When the direction of current is reversed, i.e. when the anode is applied to the ipsilateral labyrinth and the cathode to the contralateral labyrinth, suppression of neuron activity was greater than would be the case with the current in the same direction, but with monaural stimulation. Neurons of the II type reacted exactly opposite to the same stimulations of the labyrinths. Neuron activity of the III type varied identically in both cases of binaural stimulation.

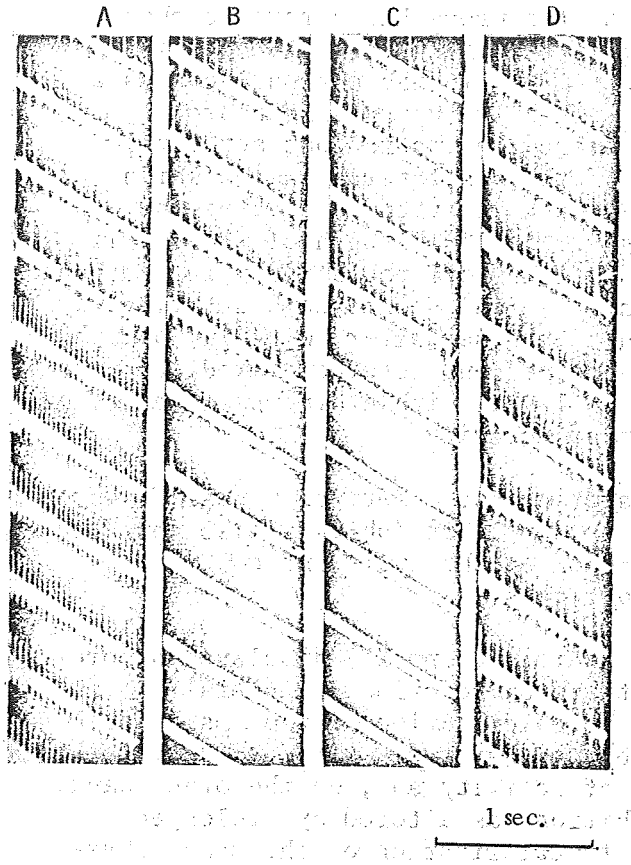

Figure 1. Neuron Reaction from the Right Nucl. Lateralis to Polarization of the Ipsilateral Labyrinth by Cathode (A) and Anode (B), and the Contralateral Labyrinth by a Cathode (C) and Anode (D). Intensity of the Polarizing Current Is 0.25 ma. The Arrows Denote the Moment of Switching on the Current.

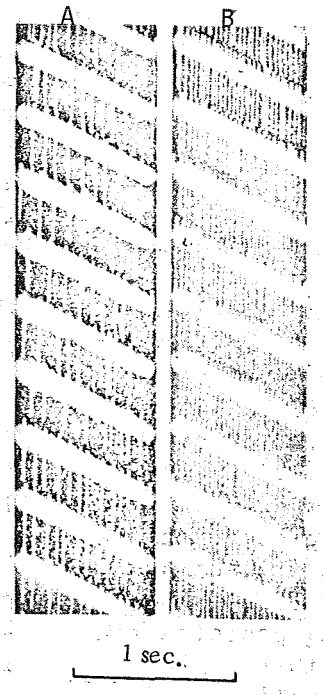

Figure 2. Effect of Sectioning the Contralateral VIII Nerve on Spontaneous Neuron Activity of the First Type from the Nucl. Inferior. Spontaneous Activity Vefore (A) and After (B) Sectioning of the Contralateral VIII Nerve

3. Equal polarization. Upon simultaneous polarization of both labyrinths by current of identical intensity and a single direction (cathode or anode to both labyrinths, a different pole to the indifferent electrode), activity of most neurons of vestibular nuclei of either side was suppressed in the same manner (Figure 4 C). An exception were the neurons of III type, the activity of which increased upon simultaneous cathodization and decreased upon simultaneous anodization of both labyrinths.

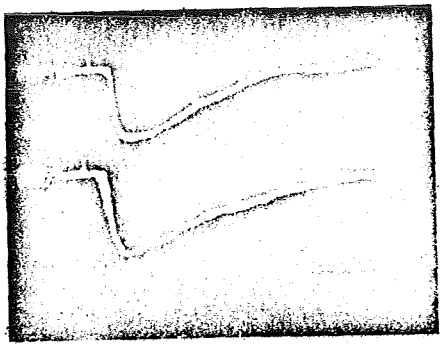

Figure 3. Intracellular Registration of Vestibular Neuron Response of the Nucl. Medialis to Electrical Stimulation of the Contralateral VIII Nerve (10 v, 0.15 msec). A, Inhibiting postsynaptic potential before administration of strychnine; B, Inhibiting postsynaptic potential within 7 min after introduction of strychnine nitrate (0.3 mg/kg intravenously); calibration, 10 mv; 20 msec

4. Effect on switching on polarizing current. Reaction to switching on polarizing current in most neurons has a reverse characteristic; if the ipsilateral cathode is applied, switching off the current acts as a weak anode, slightly suppressing neuron activity compared to spontaneous activity. Switching off the ipsilateral anode, which suppresses neuron activity, activates the neuron (Figure 5). The length of these variations to switching off the stimulating current is different. Normal spontaneous activity may return within 3-20 sec after switching off the current. Some neurons returned immediately to their initial level, without intensification or suppression of activity.

5. Caloric test. Several types of neuron reactions, presented in Table 2, also appeared to calorization of the ipsi- and contralateral labyrinths.

Three neurons (type XI) displayed a more complex pattern of reaction -- initial brief activation to calorization of the ipsilateral /103 labyrinth by hot water was altered by prolonged inhibition of activity and, on the other hand, brief inhibition was altered by prolonged activation to calorization of the same labyrinth by cold water (Figure 6).

It is obvious from the data of the table that in most cases calorization of the contralateral labyrinth by hot water causes inhibition of neuron activity, it being maintained even after sectioning of the ipsilateral VIII nerve.

6. Polarization and calorization. Two types of stimulation were applied /106 on several neurons. In some cases there was agreement of reactions to polarization and calorization of labyrinths. Thus, a neuron reacting to polarization of the labyrinths of type I could also react to calorization of labyrinths according to a similar type I.

In other cases, disagreement could be observed in reactions to these stimulations -- a neuron reacting to polarization of labyrinths of type I could react to calorization of labyrinths of type II, III, etc.

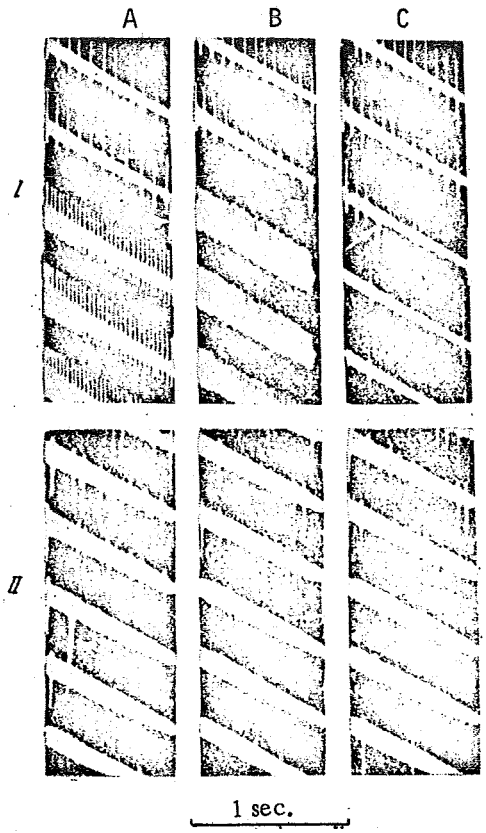

Figure 4. Reaction of Two Neurons of the Right (I) and Left (II) Nucl. Lateralis to Monaural (A), Binaural (B) and Equal (C) Polarization of the Labyrinths. A, Right labyrinth is polarized by the cathode; B, Cathode is applied to right labyrinth and the anode to left; C, Cathode is applied to both labyrinths. Intensity of polarizing current is 0.3 ma. Arrows denote moment of switching on the current.

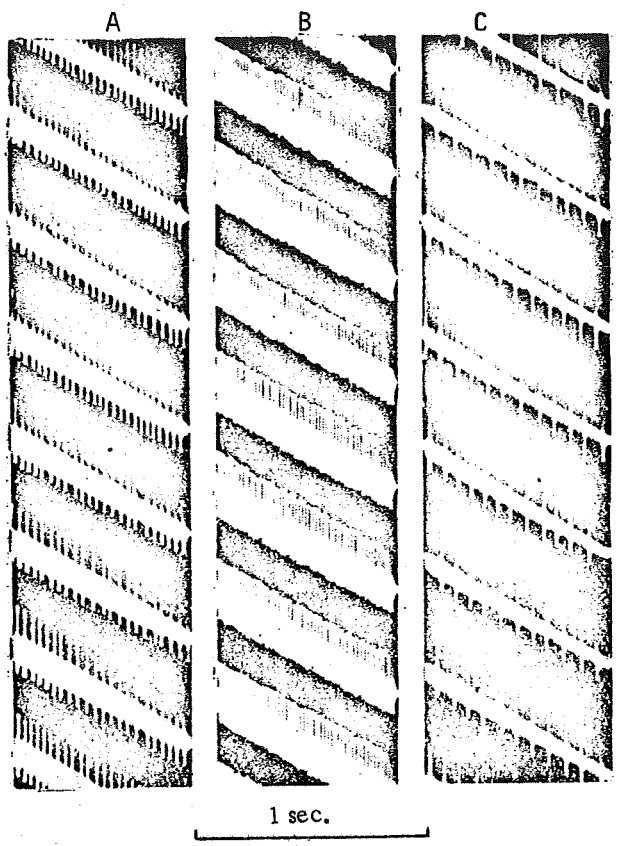

Figure 5. Neuron Reaction from Nucl. Superior to Switching Off Polarizing current. A, Spontaneous activity; B, Activation to cathode polarization of the ipsilateral labyrinth (0.35 ma); C, Suppression of activity to switching off the cathode

Upon maximum suppression of neuron activity due to application of the caloric test, cathode polarization of the ipsilateral labyrinth is ineffective during the first seconds; it is no longer in a state to activate the neuron. However, 25-30 sec after application of the caloric test, the ipsilateral cathode does activate the neuron, although spontaneous activity is still absent. On the other hand, intensification of neuron activity caused by the

caloric test could at first be suppressed by the ipsilateral anode; however, once maximum activity was achieved, the ipsilateral anode was no longer able to suppress such intense activation of the neuron (Figure 7).

TABLE 2. DIFFERENT TYPES OF NEURON REACTIONS OF VESTIBULAR NUCLEI TO CALORIZATION OF THE IPSI- AND CONTRALATERAL LABYRINTHS BY WATER OF DIFFERENT TEMPERATURE

Type of reaction	Number of neurons	Ipsilateral calorization		Contralateral calorization		Type of Reaction	Number of neurons	Ipsilateral colorization		Contralateral calorization	
		Hot	Cold	Hot	Cold			Hot	Cold	Hot	Cold
I	12	+	—	—	+	VII	5	—	+	—	0
II	4	—	+	+	—	VIII	1	+	0	—	0
III	11	+	—	+	—	IX	1	+	0	0	0
IV	5	—	+	—	+	X	2	0	0	+	—
V	3	—	—	—	+	XI	3	+—	—+	Not investigated	
VI	5	—	+	—	—						

7. Pharmacological investigation. After intravenous introduction of 0.2-1 mg/kg strychnine nitrate, the inhibiting effect of the contralateral labyrinth is completely retained (see Figure 3 B).

Discussion

We managed to distinguish several types of neurons reacting differently to polarization and calorization of the ipsi- and contralateral labyrinths. It turned out that the polarization of the same labyrinth by current of a different direction yields opposite effects of variation in neuron activity of vestibular nuclei. Upon calorization, neurons were found which react identically to irrigation of one labyrinth with water of varying temperature (types V and VI). The reverse pattern is also observed in most cases upon separate polarization of the ipsi- and contralateral labyrinth by current of a single direction. This reciprocity was intensified upon binaural and absent upon equal stimulation of the labyrinths. Only in five neurons (type III) was reciprocity absent -- cathode polarization of the ipsi- or contralateral labyrinth increased, and anode polarization suppressed activity of these neurons. Upon calorization, a greater number of neurons was revealed which reacted identically to irrigation of the labyrinths with water of identical

temperature. A total of 11 neurons of 98 reacted only to contralateral polarization, two neurons of 52 reacted to contralateral calorization, and one neuron reacted only to ipsilateral calorization by hot water. The overwhelming majority of neurons reacted to stimulation of both labyrinths. /107

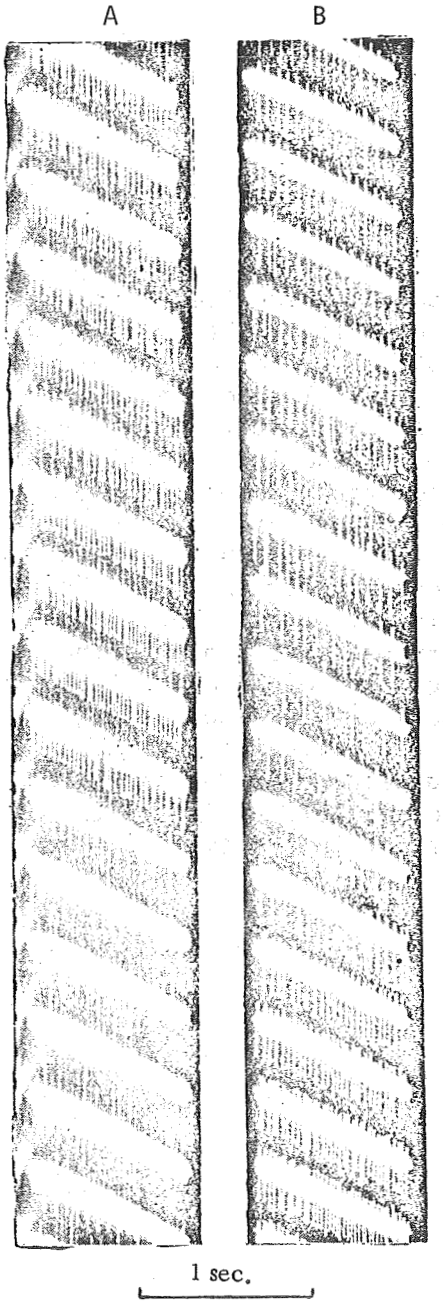

Figure 6. Two Neurons (A and B) of the Nucl. Medialis, Reacting to Calorization of the Labyrinth According to Type XI. A, Inhibition of neuron activity after brief activation to ipsilateral calorization by hot water; B, Neuron activation after brief suppression of activity to ipsilateral calorization by hot water. The arrows denote the moment of the beginning of calorization.

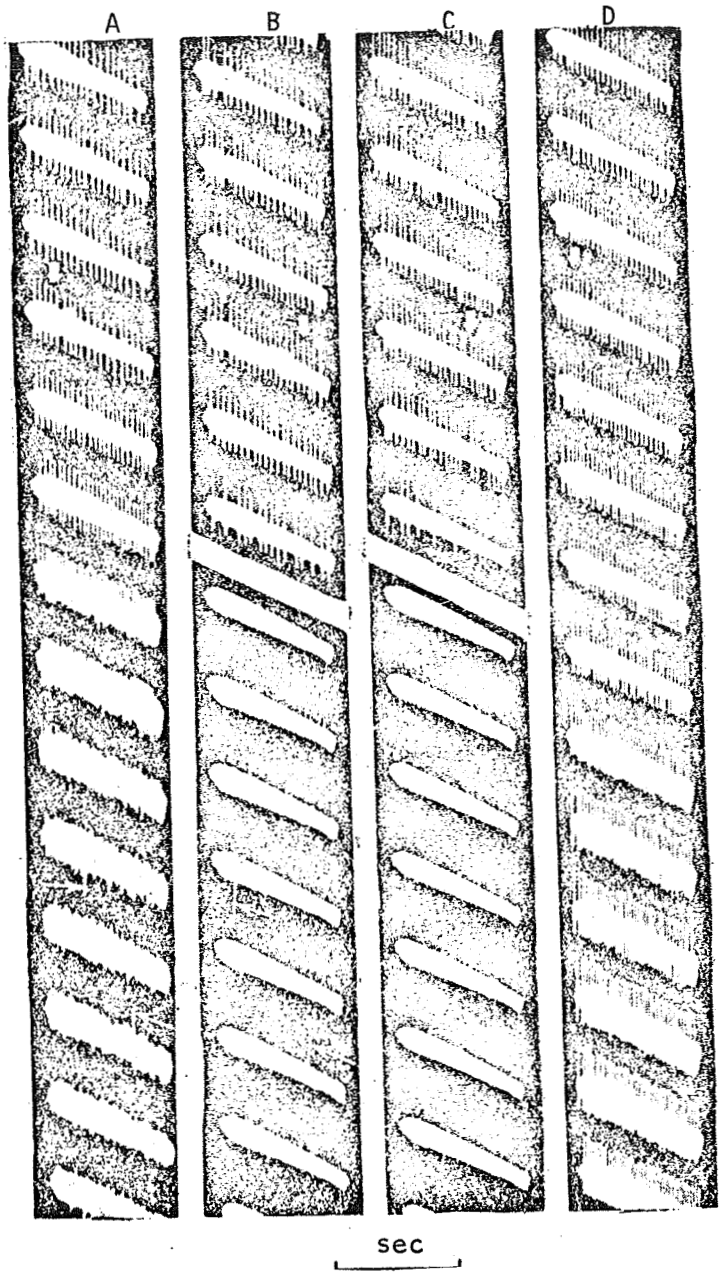

Figure 7. The Competing Effect of Caloric and Galvanic Stimulations on Neuron Activity of the First Type of the Nucl. Inferior. Reaction to irrigation of the ipsilateral round fenestra with hot (A) and cold (B) water; reaction to irrigation of the contralateral round fenestra with hot (C) and cold (D) water. The large vertical arrows denote the beginning of calorization. The small arrows denote switching on and switching off anode (A) and cathode (B) polarization of the ipsilateral labyrinth. Current intensity is 0.3 ma.

Reciprocal relationships between vestibular nuclei upon adequate stimulation of the vestibular apparatus were shown in cats [11, 26], rabbits [19] and fish [33]. Thus, an intensification of activity during rotation in the direction of lead-off and inhibition during rotation in the opposite direction were noted in all neurons recorded by Eckel [20] in rabbits. Most neurons of the vestibular nuclei in fish reacted in the same manner to inclinations in different directions. A small number of neurons reacted identically with activation or inhibition to the same stimuli [33]. Whether this reciprocity was caused only by purely peripheral phenomena (increase of pulsation from one labyrinth and suppression from another) or by central phenomena could not be resolved upon application of adequate stimulation affecting both labyrinths simultaneously. Pulsation from one labyrinth may affect the neurons of the vestibular nuclei of the opposite side. The possibility of such a cross effect is shown by morphological papers [14, 15, 21, 29]. B. N. Klosovskiy [7] assigns these cross links an important role in realization of mutual inhibition of vestibular nuclei of both sides during vestibular nystagmus, and calls them inhibiting elements. S. N. Khechinashvili [9, 10] attributes important significance to them in reciprocal variations of the electrical activity of vestibular nuclei of both sides begin upon polarization of one labyrinth by direct current, assuming in these reciprocal variations V. M. Bekhterev's concept of the reason for the dual function of the vestibular apparatus [1]. It is true that a number of authors [23-26] were unable to determine their functional significance.

De Vito and colleagues [34] studied the neuron reactions of vestibular nuclei in cats to separate polarization of the ipsi- and contralateral labyrinths. The ipsilateral cathode and contralateral anode rendered the activating effect, and the ipsilateral anode and contralateral cathode rendered the inhibiting effect on activity of vestibular neurons.

This problem was recently studied in greater detail by Weber and Steiner [35] in anesthetized cats. Calorization and polarization of the labyrinths revealed several types of reactions basically similar to ours. In distinction from us, they also found neurons which reacted identically (by activation or inhibition) to stimulation of both labyrinths by water of different temperature. Also like us, they did not find any correlation between the different types of reactions and localization of neurons.

The similarity of our data with the results of the authors cited above permits us to conclude that almost every neuron of the vestibular nuclei is /108 under the influence of both the right and left labyrinths. Unfortunately, the question of the functional organization of the vestibular nuclei still remains open. In order to explain the reciprocal reactions, we assumed [3] that the commissural fibers existing between the vestibular nuclei of both sides are linked with inhibiting neurons. It is possible that such elements are neurons which are activated by the contralateral cathode or by contralateral calorization by hot water, and inhibited by the contralateral anode and by contralateral calorization by cold water; stimulation of the ipsilateral labyrinth had no effect on their activity.

Inhibition of neuron activity in vestibular nuclei is by its very nature postsynaptic. Intracellular recording in two neurons showed development of clearly expressed inhibiting postsynaptic potential (IPSP) to electrical stimulation of the contralateral VIII nerve.

It was shown that reaction to switching off the polarizing current has a different character -- for example, if the neuron is activated by the ipsilateral cathode, when the current is switched off neuron activity may fall below initial spontaneous activity and return to it 3-20 sec after the current is switched off. Apparently, to this fact is related the fact that generalized activation of the EEG caused by labyrinth polarization continues after cessation of stimulation by approximately the same amount of time [6]. The fact that caloric and galvanic stimulation of the labyrinths often generates different reactions which do not coincide in the same neurons, should indicate that different vestibular receptors or even different nerve formations may be activated by these stimulations. These types of stimulation have a great advantage over adequate stimulation, since they permit individual stimulation of each labyrinth, but they also have great disadvantages. Thus, calorization may cause generalized activation of the EEG in individuals having unexcitable labyrinths, since in this case the temperature and mechanical receptors of the skin are stimulated [2]; as a temperature stimulus, it may also cause prolonged variation in the excitability of vestibular receptors [23]. The question on the nature of the effect of direct current is debatable. Galvanovestibular reflexes may also develop after labyrinthectomy [10]. In all probability, the decisive factor is the intensity of the stimulating current. We showed that after chemical shut-off of the labyrinth, polarization no longer activates the EEG, but with large current intensities the EEG pattern may vary and persist even after intracranial sectioning of the VIII nerve [4]. The competition which we discovered between caloric and galvanic stimulation of the labyrinth permits us to assume that at comparatively low intensities, direct current may alter the vestibular afferentation, having a direct effect on the generator potential of the receptors. /109

It was no accident that we used strychnine to clarify the nature of contralateral inhibition of the neurons of vestibular nuclei. It is known that strychnine prevents development of IPSP in motor neurons of the spinal cord and is thus an arrester of inhibiting synapses [19]. Strychnine prevents the inhibiting effect of stimulating crossed and noncrossed oligo-cochlear efferent fibers on the nerve component of the microphone effect of the cochlea [17, 18, 22] and blocks an increase in direct potential (direct current resting potential) of the labyrinth to stimulation of the efferent tract of the vestibular nerve [31]. But it does not block inhibition of mitral cells of the plexiform layer of the bulbus olfactorius to stimulation of the lateral olfactory tract in the anterior commissura [27], of Purkinje's cells of the cerebellum [12, 16], of the pyramidal cells of the hippocampus and cells of the ventrobasal complex of the thalamus [12], and of Betz's cells of the cortex [16].

We showed that strychnine does not eliminate contralateral inhibition of vestibular neurons. Consequently, chemism of inhibiting synapses which bring about a given type of inhibition in vestibular nuclei should differ from that in those formations where the blocking effect of strychnine on inhibition of the synapse has been proved experimentally.

Interaction between vestibular nuclei may also be brought about by means of efferent fibers making up the vestibular nerve and linked to the pre- and postsynaptic structures of the receptors [36]. It has been shown that activation of this tract may alter afferent pulsation from the vestibular receptors of the opposite labyrinth [28, 30, 31].

Efferent regulation of receptor afferentation is apparently brought about through the multisynaptic tract, since it appears with a high latency period [30, 31] and is suppressed by small doses of nembutal [32]. It is also eliminated by intravenal introduction of subconvulsive doses of strychnine [31].

The interaction between vestibular nuclei of both sides described in our experiments was in all probability brought about by direct commissural connections existing between them, since it 1) was also observed after sectioning of the ipsilateral VIII nerve, 2) it was retained under deep nembutal anesthesia (60-100 mg/kg intraperitoneally) and 3) it was not eliminated by intravenous introduction of significant doses of strychnine.

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EXPERIMENTAL INVESTIGATION ON MODELING DIFFERENT TYPES OF NEURONS

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A. N. Razumeyev and V. Yu. Davidenko

ABSTRACT. A mathematical model of a system, is proposed as an example of the electrical activity of vestibular neurons. The model makes it possible to overcome many methodological difficulties of electrophysiological experiments, and to model conditions of the experiment and to introduce them as a disrupting effect.

Analytic investigation of the vestibular apparatus under conditions of high G-loads and weightlessness is fraught with extreme methodological difficulties. Development of objective methods of quantitative analysis of functional variations in the neurons of the vestibular apparatus is also in itself a complex problem. This paper proposes to expand the method of modeling various types of neurons developed by us to analysis of the electrical activity of vestibular neurons. /111

The basis of our method is investigation of the nonlinear characteristics of stimulated membranes. This study showed that the functional arrangement shown in Figure 1 successfully reproduces all basic electrophysiological characteristics of various types of neuron activity. These characteristics may be described by a nonlinear differential equation which may be presented in operator form as the following:

$$\begin{aligned}\{[T^2p^2+2\xi Tp+1][(1+pT_{dl})(1+pT_{il})-F(U_{out})\cdot pK_{dl}K_{il}]+\\ +K_{dl}\cdot K_{il}(1+pT_{dl}\}\cdot K_{out}(P)-\\ -K_{cl}\cdot K_{il}\cdot(1-pT_{dl})\cdot U_{out}(p)=0,\end{aligned} \tag{1}$$

where K_{cl} is the amplification factor of the link imitating the cell body; T is the time constant of this link; K_{il} is the amplification factor of the link imitating the passive elements of the base of the axon monticulus; T_{il} is its time constant; K_{dl} is the amplification factor in the differentiating link of the regenerative circuit; T_{dl} is its time constant; and F_{out} is the nonlinearity of the regenerative process.

Analysis of the processes taking place in a system, carried out by the method of harmonic linearization, makes it possible to obtain basic relationships, which determine variations in frequency and amplitude of oscillations upon variation of the parameters of the system and of external effects, in the form:

$$A_1 = (\pi D)^{-1} \cdot (2C_1)^{1/2}[C_1 + \{C_1^2 - [\pi D (b - x_4^0)]^2\}^{1/2}]^{1/2} \tag{2}$$

$$\left.\begin{aligned}
&\Omega = [(\alpha_1 + \pi\beta_1 \cdot f(x_4^0) \cdot [\Theta_1 \cdot f(x_4^0) - (b - x_4^0)^2]^{-1/2}\gamma_1^{-1}]^{1/2}, \\
&\alpha_1 = K_{il} \cdot K_{36} \cdot K_8;\ \beta_1 = K_8 \cdot K_{il} \cdot T_{dl} + 2\xi T + T_{il} + T_{dl}; \\
&\gamma_1 = \alpha_1 T^2;\ \Theta = \frac{2C_1}{\pi^2 D^2};\ f(x_4^0 = C_1 + \sqrt{C_1^2 - [\pi D (b - x_4^0]^2}; \\
&D = \frac{B - \sqrt{B^2 - 4AC}}{2A};\ B^2 > 4AC;\ A = 2\alpha_1^3 \xi T; \\
&B = \alpha_1^2 [F + G];\ C = FG;\ G = T^2 + \\
&\qquad + 2\xi T T_{il} + 2\xi T T_{dl} + T_{il} \cdot T_{dl}; \\
&F = 2K_8 \cdot K_{il} \cdot K_{cl} \xi T T_{dl} + 8\xi^2 T^2 + 4\xi T T_{il} \cdot 4\xi T T_{dl};
\end{aligned}\right\} \tag{3}$$ /112

$$\left.\begin{aligned}
&g = \frac{2C_1}{\pi A_1}\sqrt{1 - \left(\frac{b - x_0^4}{A_4^0}\right)}; \\
&x_4^0 \geqslant b - \frac{C_1}{\pi D};
\end{aligned}\right\} \tag{4}$$

$$\alpha'' x_4^0 + \beta' x_4^0 + x_4^0 (K_{il} \cdot K_{cl} \cdot K_8 + \rho_0) + \dot{I} = K_{il} \cdot K_{cl} f(t). \tag{5}$$

In equation (5), ρ_0 is the linearized transfer coefficient of the nonlinear link for a constant component.

It is obvious from these relationships that there are three representative areas of the dependence of oscillation amplitude on the level of the input signal. /113

Upon unrestricted increase in the amplitude of the input signal of nonlinear link A_1, its standardized equivalent complex amplification factor

$$q_0\left(\frac{A_1}{b - x_4^0}\right) = \frac{2}{\pi} \frac{\sqrt{1 - \left[\frac{\frac{1}{A_1}}{b - x_4^0}\right]}}{\frac{A_1}{b - x_4^0}} \tag{6}$$

approaches zero, which is equivalent to suppression of the regenerative addition in neuron response. In practice when the input signal is too high, $\frac{A_1}{b - x_4^0} \gg 1$, neuron response becomes gradual; moreover, pulse oscillations which are established and supported in the system when the critical level of depolarization is exceeded are suppressed. This phenomenon has assumed the title of cathode depression in physiological literature.

When input signals are low, $\frac{A_1}{b - x_4^0} = 1$, i.e. at subthreshold levels of depolarization, regenerative processes in the system are also impossible. They develop abruptly when the amplitude of the input signal slightly exceeds response threshold. Moreover, the amplitude of oscillations remains practically unchanged, and their frequency, as can be seen from the relations increases as the level of depolarization increases if the constant component of oscillations caused by asymmetry of nonlinearity of the regenerative process does not exceed the level corresponding to disruption of oscillations in the system and to the onset of cathode depression.

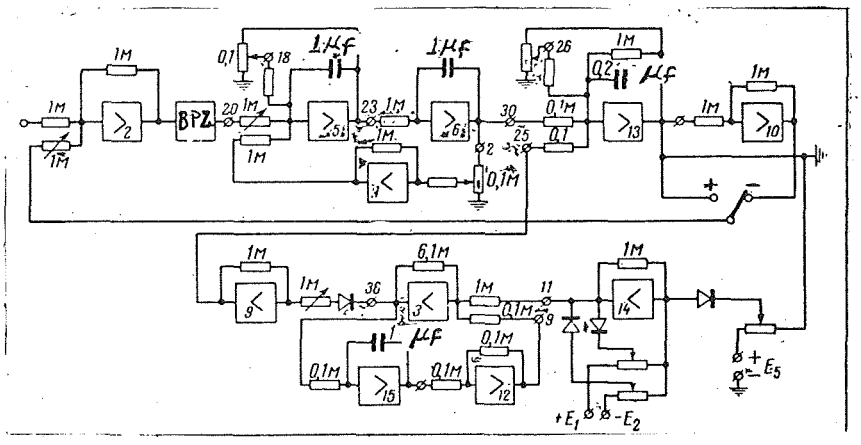

Figure 1. Block Diagram for Solving a Problem on the MN-7 Machine. The devices connected between points 7 and amplifier output 10 model passive transmission of electrical signals along the cell body (between points 7 and 30) and the base of the base of the axon monticulus (the remainder). The feedback circuit (between points 25 and amplifier output 13) models the nonlinear regenerative process of stimulation.

The threshold of neuron response is determined by the value of the threshold of rest and the constant component of disrupted oscillations x_4^0

and is equal to $(c - x_4^0)$. In a state of rest $x_4^0 = 0$; x_4^0 is the solution of one of the equations (5) presented. x_4^0 is a time function. Solution of this equation is determined by the parameters of the stimulated membrane.

Under the defined relationships, the nonlinearity asymmetry of the membrane characteristics leads to slight overcontrols of x_4^0. Because of this, the frequency of neuron responses, as can be seen from the expression presented, will increase at the initial moment of switching on the voltage drop, and will then slowly decrease. Depending on the level of input signals in the neurons, we can follow the entire range of responses from on to on-off and adaptation.

When the hyperpolarizing effects are switched off, neuron responses are /114
possible only in those cases when $x_4^0 > b$. This is explained by the comparative ease of elliciting anode-breaker responses in the intermediate neurons, in which rest threshold b is relatively low, and also in several depolarized motor neurons. At low values of b, switching off the hyperpolarizing effect on the neuron may be accompanied by a series of discharges. The relationships given above make it possible to predetermine the nature of responses which depend on a creation of depolarizing and hyperpolarizing effects on the neuron, and make it possible to determine them quantitatively by experiment. The theoretical relationships presented here are well illustrated by experimental data.

This paper considers neuron reactions to direct stimulation. The singular exception is the example of the indirect or synaptic effect shown in Figure 2.

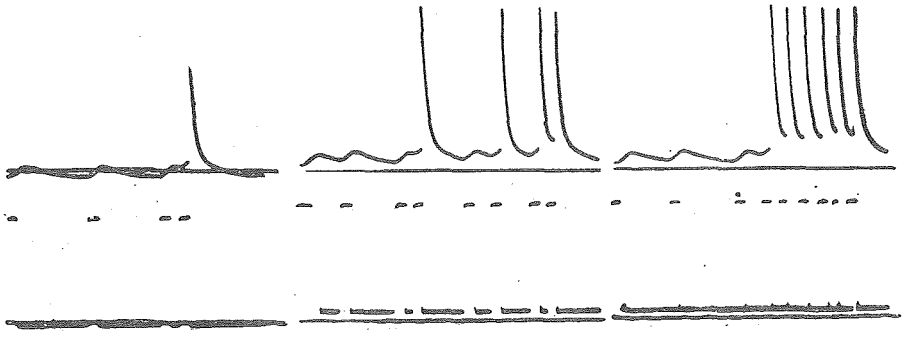

Figure 2. Neuron Response to Orthodrome Stimulation, Summation of Postsynaptic Stimulating Potentials, and Generation of Action Potentials

In this case the postsynaptic stimulating potential (PSSP) and its temporary summation are imitated. It is obvious in oscillogram 1 that two stimuli eliciting identical PSSP separately, sufficiently separated in time,

do not cause the regenerative process. The same two stimuli, closer in time, are summarized; total PSSP reaches a threshold, and the regenerative process, the expression of which is the appearance of a single peak, develops immediately behind the gradual reaction. It is further shown in oscillograms 2 and 3 how individual PSSP are summarized as a function of the relationship of stimulations in time and the duration of their effect. Moreover, it is implied that the duration of stimulation does not exceed the time of PSSP. It is obvious from the oscillograms that an increase in the frequency of /115 stimulations results in an increase in frequency of discharges, to a certain decrease in subsequent peaks and to an increase in the level of depolarization, from which begins the second, adjacent peak (the last peak in oscillogram 2, and the second and fifth in oscillogram 3).

The threshold properties of the neuron are illustrated by responses to direct stimulation (Figure 3). Oscillogram 1 shows subthreshold response to rectangular stimulus with a sloping posterior front. In this case the reaction is of a gradual nature and is not accompanied by the regenerative process; the descending portion of the response corresponds to the falling portion of the input signal.

Further (oscillogram 2), as the input signal increases, the gradual response increases, and five peaks appear with a large delay, i.e. the regenerative process develops, as is the case in living neurons. Typical here is the fact, as in real intermediate neurons, that transition from gradual to regenerative reaction is abrupt, i.e. instead of a single peak the number of peaks increases to eight and nine (oscillograms 3 and 4, respectively) upon a slight increase in stimulation. As stimulation increases, the latency period of discharges decreases, and their frequency in the rectilinear section of the stimulation remains almost unchanged. Only in the descending section does the frequency decrease somewhat (oscillograms 4 and 5) due to the prevalent slight increase in frequency of discharges. And further (oscillogram 6), the frequency of discharges becomes even more irregular, and at the same time their amplitude varies sharply, which indicates the beginning of the development of cathode depression. The phenomenon of cathode depression progresses through a stage of discharges (oscillogram 8) different in amplitude, but /116 relatively constant in rhythm to total cessation of their generation in the middle part of stimulation (oscillograms 9 and 10). However, there are discharges at the beginning and end of stimulation, which indicates in the first case the stage before development, and in the second the stage after development of cathode depression in the section of decrease in input signal.

Even in this series of oscillograms there appears an interesting property of the discharges -- frequency and amplitude vary even in the rectilinear section of stimulation; separate series, separated by comparatively large intervals, appear in the overall response; after these series, the first peaks usually have a high amplitude. It is also important that in the overall response the initial level of peaks is different -- large peaks are generated at a low level of depolarization, and small peaks at a high level. This unique transformation of initial rhythm, and also peak amplitudes and the

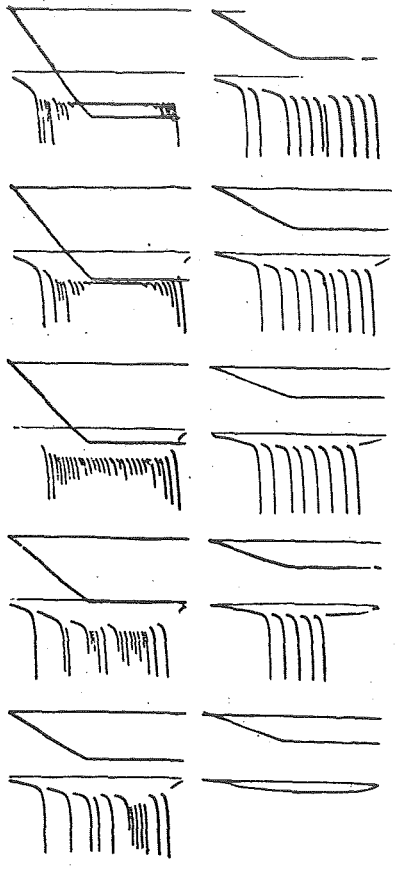

Figure 3. Neuron Response to Direct Stimulation by Rectangular Stimulus with a Sloping Posterior Front and Various Stages of Cathode Depression

level of their generation obtained upon the direct effect, may indicate an important characteristic of electrogenic properties of the neuron model -- but determination of these responses by the internal properties of the system itself.

When a bold analogy with a living neuron is made, in our opinion many of the reactions of central neurons may be explained, without resorting to complex reservations and references on the nature of synaptic connections, their functional significance, etc. Everything may be reduced first of all to the properties of the surface membrane of neurons, and then to its interrelationships with various effects, and to the combination of these effects on the membrane. With such an approach we should again strictly analyze the question of the relationship of rapid and slow electrical reactions in central neurons.

The dependence of response frequency on the nature of stimulation is best of all followed during rhythmic stimulation. In this case, depending on the frequency and amplitude of the input effect, we can already see the noted characteristics of discharges.

Figure 4 shows responses to sinusoids of different frequency.

The length of a series of impulses generated by the analog of the neuron in the range of low frequencies is proportional to the length it exceeds threshold level (oscillogram 11). In the range of medium frequencies, the neuron response with a single action potential (oscillogram 2) to each positive half-wave of the sinusoid. Upon further increasing the frequency of the input signal, transformation of the rhythm begins, caused by commensuration of the period of external oscillations with that of neuron refractivity. Moreover, only individual peaks in a series of responses may drop at first. Then, upon definite relationships of amplitude and frequency of input stimuli, this transformation progresses more and more, the responses consist of two or /117 three peaks separated by a period of "silence," then each third response diminishes (the oscillogram) and, finally, each second response diminishes (oscillogram 4). An increase in amplitude of the input signal may restore neuron responses of type I:I, as was the case in experiments on real neurons, where all these transitions are more difficult to observe.

Results were obtained on the model, which are observed in intermediate neurons at different amplitudes and time relationships of depolarizing and hyperpolarizing signals entering the neuron through the microelectrode implanted in it.

These results are very important to understand such electrophysiological phenomena as cathode depression, anode-breaker response, the appearance of gradual reactions after the peak, double peaks and an increase in hyperpolarization after such double peaks.

The phenomenon of cathode depression has already been demonstrated by the oscillograms of Figure 3.

It is further expedient to consider the so-called anode-breaker response. A great deal of attention has recently been given to analysis of this phenomenon in physiological laboratories.

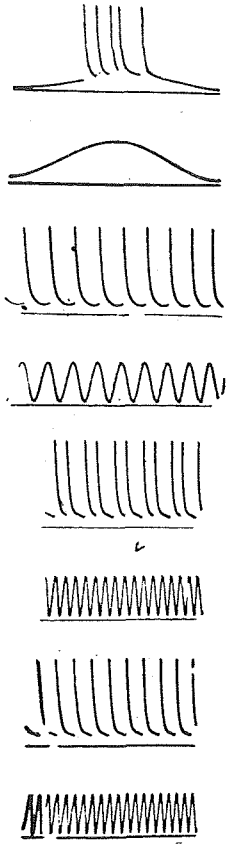

Figure 4. Transformation of Rhythm As a Function of Stimulation Frequency

Oscillogram 1 (Figure 5) shows the response of a neuron analog, first depolarized by very frequent stimulations, to switching off and switching on a prolonged hyperpolarizing current. As can be seen, switching off the current causes a large peak followed by a very small abortive peak. This indicates the high level of depolarization after switching off the current. If, as indicated in oscillogram 2, the neuron is first depolarized to a higher level, switching off the same hyperpolarizing pulse now causes rhythmic responses, which indicates the optimum level of polarization for development of autorhythmic properties of the system. This tendency to autorhythm of neurons which have first been depolarized is best shown in /118 controlled effects, when hyperpolarization causes different depth and length.

We also wanted to dwell on the phenomenon of response doubling, which is often observed in physiological experiments and is explained differently in different cases. We feel that it also depends on the combination of depolarization and hyperpolarization of the membrane, caused by incoming signals.

Oscillogram 3 shows the case of high depolarization of the neuron by frequent rectangular stimuli. Switching on and switching off hyperpolarization yields a known pattern of rhythmic responses. But the fifth and sixth peaks in oscillogram 3 are adjacent, and begin like response doubling. The same is true of oscillogram 4 (the third and fourth peaks). Moreover, it is important to note that this response doubling is accompanied by an

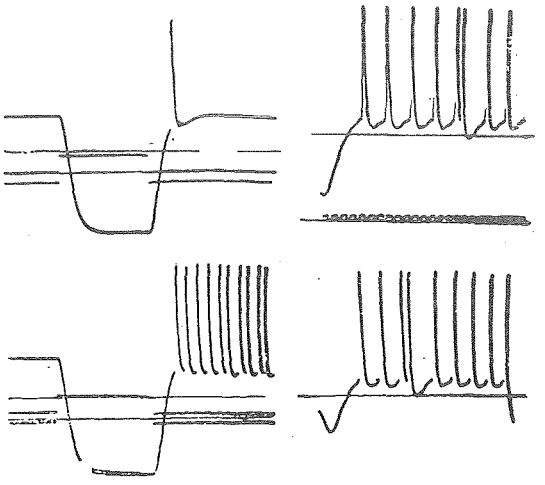

Figure 5. Different Types of Anode-Breaker Responses

increase in subsequent polarization, as can be seen in the oscillograms presented.

We feel that the results presented make it possible to overcome many methodological difficulties of electrophysiological experiments. Obviously there is no requirement for nonnumerical experiments on the study of the components of the activity of vestibular neurons under extreme conditions. It is sufficient to model these conditions in a suitable manner, and to introduce them as the disturbing effect in the model considered here, and to further verify in real experimentation only the most interesting results from the point of view of the problem considered.

ON THE FUNCTIONAL RELATIONSHIP BETWEEN THE SEMICIRCULAR CANALS AND THE OTOLITHIC APPARATUS

A. Ye. Kurashvili and V. P. Babiyak

ABSTRACT. It was established that when the combined effect of angular and centrifugal accelerations act on man and animals (rabbits, cats and dogs), the angular velocity of eye movement increases during the slow phase of pulses of rotational nystagmus. An increase begins at the moment G-loads take effect and continues until rotation reaches a constant velocity. An attempt is made on the basis of the data obtained to explain the effect of weightlessness on man. The article contains one table and eight references.

The papers of a number of authors [1-6, 8] have shown a close functional /119 interrelationship between the ampullar and otolithic receptors.

The investigations have shown that if an adequate stimulus of the otolithic apparatus -- rectilinear acceleration -- is added to the stimulus of the semicircular canals -- angular acceleration, -- reflexes on the part of the semicircular canals vary significantly. It turned out that the duration of postnystagmus is decreased after combined stimulation of the semicircular canals and otolithic apparatus.

The investigations mainly concerned postrotational nystagmus, and the principles of variation during rotation upon simultaneous stimulation of the receptors of the semicircular canal atrium were studied very inadequately.

In order to study these principles we utilized the modern method of recording nystagmus -- electronystagmography -- which makes it possible to obtain total characteristics of its main parameters -- amplitude, angular velocity of eye motion during the slow phase, and the frequency of pulses and their duration. The experiments were conducted on animals (rabbits, cats and dogs) and on humans.

A rotating chair-centrifuge was used to reproduce angular and centrifugal accelerations in animals, and a 2.3-m centrifuge was used to study humans.

The animals were at first subjected to angular acceleration, and then to the combined effect of angular and centrifugal accelerations. The magnitude of angular acceleration in both experiments was identical, and the G-load recorded by an appropriate sensor was from one to three units. Experimental conditions were similar during study of humans.

Experiments on animals and the data of laboratory studies of humans indicated that upon simultaneous stimulation of the semicircular canals and

the otolithic apparatus, amplitude, angular velocity of eye motion during the slow phase and the pulse frequency of rotational nystagmus increase noticeably within known limits of G-load effect. This increase begins from the moment of /120 G-load effect, and continues until rotation reaches a constant velocity.

The nystagmogram, obtained when a rabbit is rotated in the center of a circle, when only angular acceleration was acting on it, describes a uniform curve with slight angular acceleration of the slow phase (6.2 deg/sec).

The second nystagmogram was recorded during rotation of the rabbit on the edge of the centrifuge when angular and centrifugal accelerations were acting on it. It is obvious from this nystagmogram that the amplitude and velocity of the slow phase (14.5 deg/sec) increase significantly at the moment of rotation as G-load increases, but subsequently diminish noticeably when G-load reaches a level of approximately one unit, and uniform acceleration is achieved.

A similar pattern is observed upon examination of the nystagmograms of a rabbit, experimental dog and during testing of humans.

Statistical analysis of individual parameters of nystagmus indicated that the value of total amplitude, angular velocity of eye motion during the slow phase and pulse frequency of rotational nystagmus increase noticeably due to G-load effect (see table).

VARIATIONS IN PARAMETERS OF ROTATIONAL NYSTAGMUS DURING ROTATION OF TEST SUBJECTS IN THE CENTER AND ON THE PERIPHERY OF A CENTRIFUGE

Nature of effect	Statistical index	Overall amplitude	Velocity of slow phase deg/sec	Pulse frequency
Rotation in center of centrifuge	$\bar{x}$	181	8,7	40
	$\pm\sigma$	16,6	7,0	7,4
	$\pm m$	4,05	1,6	1,7
Rotation on periphery of centrifuge	$\bar{x}$	283	16,3	46
	$\pm\sigma$	54,3	10,5	12,4
	$\pm m$	13,7	2,4	2,5
	t	7,8	3,4	2,7

Tr. Note: Commas indicate decimal points.

The data obtained provide the basis for confirming that there is an intensification of the indices of rotational nystagmus due to combined stimulation of the semicircular canals and the otolithic apparatus. This intensification is apparently caused by the fact that rectilinear acceleration has an additional effect on the cupulae, causing great deformation of them compared to the effect of only angular acceleration.

Controlled experiments with animals in a centrifuge indicated that switching off the otolithic function noticeably affects the nature of rotational nystagmus, which develops upon a decrease in its intensity. /121

The reason for this may be the effect of shutting off the function of the otolithic apparatus, which under normal conditions of interaction with the ampullar receptor intensifies its function, or the traumatizing effect of centrifuging on the function of the ampullar receptor.

New data which we obtained verify the opinion expressed by some authors that the receptors of the semicircular canals and otoliths function as synergists rather than as antagonists.

If we proceed from this position, we may explain correctly certain facts observed during weightlessness. Thus, according to investigations of Ye. M. Yuganov [5] and other authors, a decrease in frequency of nystagmic reaction and a decrease of all other animal and vegetative reflexes from the semicircular canals is observed under conditions of brief weightlessness. The author, relying on previous concepts about the functional relationship between the semicircular canals and otolithic apparatus, explains this by the fact that weightlessness acts as a strong stimulus on the otolithic mechanism, which under these conditions is as if it exerts an inhibiting effect on the function of the semicircular canals.

This explanation of the author leaves the following questions unresolved.

1. Why, during stimulation of the otolithic apparatus under ground conditions, is only the nystagmic reaction inhibited (we are talking about duration of nystagmus), the remaining somatic and vegetative reactions from the semicircular canals intensify, and when, according to Yuganov, during weightlessness there is stimulation of the otolithic apparatus, not only is nystagmus reduced, but all remaining vestibular, somatic and vegetative reflexes are also reduced?

2. Why, during our experiments, does combined stimulation of the otolithic apparatus and semicircular canals increase the intensity of rotational nystagmus, while stimulation of the otolithic apparatus during weightlessness, according to Yuganov, decreases nystagmus?

These questions, according to the data of our experiments, may be explained in the following manner.

As already noted above, the semicircular canals and otoliths function as synergists, i.e. otolithic stimulation intensifies reflexes from the semicircular canals. During brief periods of weightlessness, the otoliths lose their weight while preserving their mass. Under these conditions, the function of the otolithic apparatus apparently diminishes, i.e. during the process of synergism one of its links is functionally diminished, as a result of which weakening of the reflexes from the semicircular canals also begins.

Thus, a decrease in the function of one of the links in the synergistic /122 process causes weakening of the reflexes from the semicircular canals under conditions of weightlessness rather than new stimulation of the otoliths.

The otolithic function under conditions of weightlessness may not be diminished for the following reasons.

The otolithic receptors in all inhabitants of the earth are arranged such that the ponderable otolithic membrane shifts when there is a variation in the direction of gravity, or due to the effect of rectilinear acceleration, and signals the position of the body in space. Such arrangement of the otolithic receptor is determined by the constant effect of gravitational forces directed toward the center of the earth. All living creatures have become adapted to these conditions of existence during the process of phylogenic development.

But when an animal or man finds himself under conditions of weightlessness, the otoliths lose weight, and this means that the otolithic receptors are deprived of their normal conditions in their reflector activity. Can the otolithic receptors function normally under conditions when the accustomed system of activity is disrupted?

We must assume that loss of weight of the otoliths has a noticeable effect not only on the function of the otolithic receptors, but also on the function of the semicircular canals, since their activity is closely interrelated.

On the basis of our data we may assume that weakening the reflexes from the semicircular canals during weightlessness is caused by a decrease in the function of the otolithic apparatus in connection with weight losses of the otoliths.

If under conditions of ground experiments, switching off the otolithic function weakens expression of reflexes from the semicircular canals, and, on the other hand, their simultaneous stimulation intensifies these reflexes, then under conditions of weightlessness all reflexes from the semicircular canals should be diminished in a similar manner in connection with disruption of the otolithic function.

However, decreasing the reflexes from the semicircular canals still does not mean a decrease in sensitivity of the vestibular analyzer. Under conditions of weightlessness, disruption of the accustomed interrelationship

of the ampullar and otolithic receptors apparently has a negative effect on the combined activity of many analyzers, to which the vestibular analyzer is connected, which upon accumulation of stimulations may result in undesirable vestibulo-vegetative shifts in an astronaut's organism.

We know that signs of discomfort observed in some astronauts did not begin immediately, but within several hours after their presence in a state of weightlessness.

During prolonged space flights, the most effective means of preventing motion sickness should obviously be to create conditions of artificial gravity for the crew members of a spaceship.

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ON THE FUNCTIONAL STATE OF THE VESTIBULAR APPARATUS OF RATS DURING HYPOTHERMY

I. I. Voinova

ABSTRACT. The characteristics of post-rotational nystagmus in rats were studied during the dynamics of developing artificial hypothermy at a body temperature of 37-20°. When body temperature was lowered to 33-34°, the intensity of nystagmus was increased; cooling the rats to 28-27° and below caused post-rotational nystagmus to diminish, and the reaction disappeared completely at 20°.

Functional characteristics of the vestibular apparatus under conditions of variable reactivity of an organism have been barely studied, and are of specific interest for biology and medicine. There is limited information in the literature which indicates that the vestibular reaction varies when an organism is cooled. According to the data of Innocenti [2], the duration and frequency of nystagmus to rotational stimulation of guinea pigs and rabbits cooled to 28° at first increase, then at 26-24° decrease, and disappear at a body temperature below 20°.

It was established during study of post-rotational nystagmus in guinea pigs that it is inhibited when animals are cooled [3].

In our paper we studied the characteristics of post-rotational nystagmus in rats during development of hypothermy and recovery of vital function to its initial level.

Method

The experiments were carried out on 62 white rats, in which post-rotational nystagmus was studied according to the norm, upon cooling and heating of the animals. The animals were restrained right side up on the surface of a special table rotating at different angular velocities -- 18, 30, 60, 120, 180, 240, 300, 360, 420, 480, 540, 600, 660, 720, 1080 and 1440 deg/sec. /124

Each rotation continued for 20 sec at an interval of one to two minutes and a stop of one second. Recording of nystagmus was accomplished using electrodes positioned near the external angles of the eyes bitemporally on a 4EEG-1 four-channel encephalograph. The experiments were conducted in a cooling chamber in which it was possible to maintain a temperature to -20°.

Body temperature was measured rectally. The state of hypothermy in 48 rats was obtained by the hypercapnia-hypoxia method (the modified method of Zhiyya-Andzhuas).

For comparison, eight experiments were carried out in which cooling of the rats was accomplished after premedication (20 mg/kg of promedole and 25 mg/kg of pipolphene).

Reaction of the vestibular apparatus was studied at a body temperature of 35-37, 33-34, 31-29, 27-28, 25-26, 23-24 and 20-22° and within 17-18 hr after total recovery of vital function. Digital experimental material was processed according to Student's method.

Results of the Investigations

Experimental results indicated that duration of post-rotational nystagmus according to the norm, and also under conditions of cooling the animals depends on the rate of acceleration (Figures 1 and 2) and varies within limits from 0 to 22 sec.

Stimulation of the labyrinth by rotating the animal at an angular velocity from 18 to 60 deg/sec according to the norm yielded a gradual increase in sensitivity of post-rotational nystagmus (see Figure 1). Rotation of rats at an angular velocity from 240 to 600 deg/sec caused a more defined reaction. Duration of nystagmus increased 8-14 times compared with minimum accelerations. Maximum intensity of rotation (1080-1440 deg/sec) caused a two- to threefold decrease in vestibular reaction.

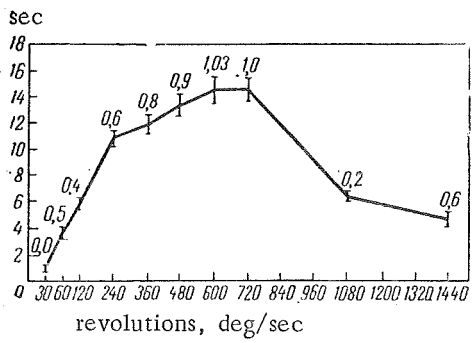

Figure 1. Variation in Duration of Nystagmus As a Function of Acceleration at Normal Body Temperature

Cooling rats according to the hypercapnia-hypoxia method (see Figure 2) to a body temperature of 33-34° resulted in a 1.5-fold increase in duration of post-rotational nystagmus compared with the control.

Duration of nystagmus at 29-31° did not differ substantially from that of control animals. A further decrease in body temperature to 26-27° caused a decrease in duration of the reaction by 1.5-2 times. When the rats were cooled to 23-24°, a slight reaction in response to stimulation of the labyrinth by rotation of the animals at an angular velocity of 240-600 deg/sec was noted in a number of experiments (see Figure 2). Movements of the eyeball to rotational stimulation ceased in rats cooled to a body temperature of 20°. /125

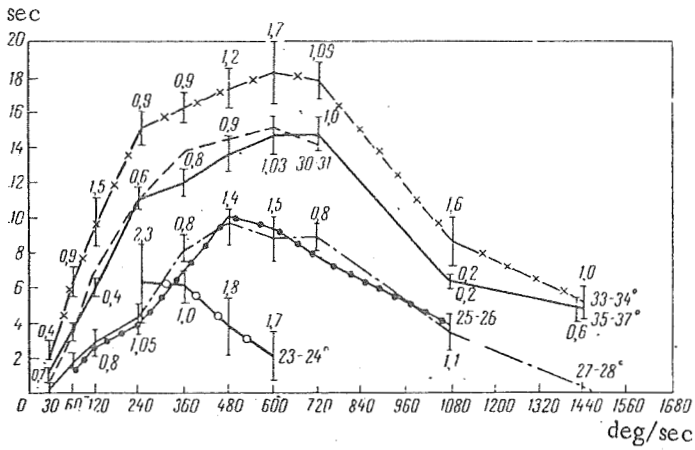

Figure 2. Variation in Duration of Nystagmus in Rats During Development of Hypothermy

A decrease in reaction was observed in all experiments under conditions of cooling with preliminary premedication at a body temperature of 33-34°. Variation in post-rotational nystagmus at 30-31° in this group of animals was irregular. However, at a /126 temperature of 26-27° there was an expressed tendency for reaction to decrease in comparison with control animals.

It is necessary to note the fact that even at deep levels of hypothermy, when nystagmus disappears completely, adjusting reflexes of the head and body are rather clearly maintained and disappear only at a body temperature below 16°.

Results of controlled experiments (body temperature of 36°), in which observation was carried out of the variation in duration of post-rotational nystagmus as a function of repeated stimulation of the labyrinth, indicated negligible adaptation of the vestibular reaction. It is obvious from Figure 3 that the difference in duration of nystagmus between the first and second and the first and third rotations is negligible, but is more clearly expressed upon comparison of the first rotation of the animal with the fifth and sixth rotations.

Thus, the results of our investigations indicated that the functions of the vestibular apparatus are not in direct dependence on the depth of hypothermy and on the level of tissue metabolism compared to the other functions of the organism.

Function of the vestibular apparatus even increases at specific stages of hypothermy, when body temperature is decreased to 33-34°, and at 29-31° it is maintained at a level near that of intact animals. Cooling rats to a body temperature of 28-27° and below causes inhibition of reaction from the semicircular canals, and at 20° the reaction disappears completely. However, the otolithic apparatus still continues to function under these conditions.

Obviously, the data obtained may be explained, on the one hand, by elimination of the inhibiting effect of the higher branches of the central nervous system during hypothermy, which is confirmed by studies of Magnus [7], /127 which showed the inhibiting effect of the cerebrum and cerebral cortex on functions of the vestibular apparatus. On the other hand, we may assume that

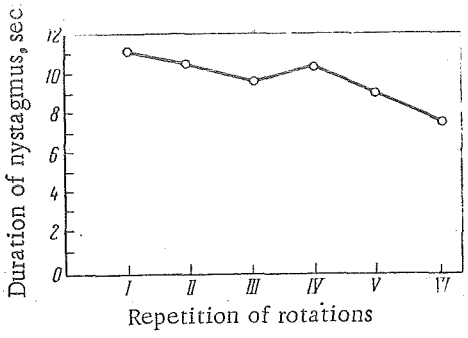

Figure 3. Variation in Duration of Nystagmus upon Repeated Rotation. Rotation velocity is 360 deg/sec.

the vestibular apparatus and its reflex tracts under these conditions are more stable to cooling as apparatus which are phylogenically more ancient. Very curious is the fact that the vestibular apparatus itself and its various branches are not uniformly stable to cooling. Thus, the otolithic apparatus retains its function under deeper levels of hypothermy, while the adjusting reflexes of the head in our experiments were rather well defined even at a body temperature of 18-16° and below, and post-rotational nystagmus related to the function of the semicircular canals disappeared completely at 23-20°.

Conclusions

1. Duration of nystagmus during hypothermy in rats when rotated at angular velocities from 18 to 1440 deg/sec depends on the method and degree of cooling the animal.

2. In hypothermy, obtained by the hypercapnia-hypoxia method, duration of nystagmus at various stages of cooling the animal (34-32°) increases by 50%, returns to its initial level upon further cooling (31-29°), and then decreases at a body temperature of 28-23° and disappears completely at a rectal temperature of 20°.

3. The vestibular otolithic function related to adjusting reflexes is retained during the entire period, even to a body temperature of 17-16°.

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SENSORY MOTOR REACTIONS OF MAN UNDER THE EFFECT OF ROTATION ON A LOW-RADIUS INSTALLATION

S. S. Markaryan, V. G. Terent'yev and V. S. Fomin

ABSTRACT. Investigations were carried out on a special stand which permits variation in the position of a subject's body with respect to the vertical rotation axis. Rotation around an axis passing through the region of the pelvis with the subject in a vertical position is acceptable for no more than 20 min at a velocity of 1.5-2.0 rps. Rotation around axes passing through the region of the head, heart and feet are tolerated much worse.

Not only rectilinear, but also centripetal accelerations, the rotation axis of which passes through different parts of the body, may act on the organism of a pilot under certain flight conditions. Therefore, it is important to study the maximum capabilities of man under these conditions with regard to controlling the craft and executing specific coordinated movements. We have not succeeded in finding similar papers in the literature. /128

We assigned ourselves the problem of studying certain indicators of sensory motor reactions of man under conditions of maximum permissible centripetal accelerations during rotation around axes passing through different parts of the body, and with the body being in different positions with respect to the vertical axis of rotation.

Method

The investigations were conducted on a special stand which rotated at constant velocities from 0.25 to 2.0 revolutions per second at relatively constant angular velocities of 1 deg/sec^2 during periods of acceleration and braking. Two series of experiments were carried out depending on the position of the test subject with respect to the vertical axis of rotation. In the first series the rotation axis passed through the region of the pelvis, and the trunk was in a vertical position or inclined forward at 20, 30, 45, 65, 80 and 90°. In the second series of experiments the test subject was fixed in a horizontal position such that the rotation axis passed through the region of the head, heart or feet. Investigations began at extremely low accelerations, and the effect of maximum permissible accelerations was subsequently studied, in which definite functional shifts developed in the organism of the test subject, and his work capability was noticeably disrupted. Duration of rotation in all cases was identical -- 20 min. A total of 86 experiments was carried out with participation of 16 healthy test subjects with high vestibular stability.

Study of the sensory motor reactions was conducted according to a method, the essence of which is contained in the following -- the test subject, sitting in the chair of the stand, followed the readings of two instruments during rotation (milliammeters with a central zero). When the command was given, he altered the readings of these instruments to a previously known /129 reading, for which he executed appropriate movements of the right arm (manual drive control) and the feet (foot pedal control). Signal lamps of three colors, to which the test subject responded with the same movements as to voice commands (right, left and straight), served as conditioned stimuli. For this purpose, preliminary training under conditions of rest was carried out. Indicators of motor reaction were the latency period from the time the signal or command was supplied until the beginning of motor activity and duration of the reaction, i.e. the time of achieving a given goal. Study of the sensory motor reaction was carried out before and during rotation, and immediately after the stand was stopped. The experiments were repeated five to six times to verify average indicators.

Recording of stimulation and reciprocal motor reaction was accomplished in the form of curves on the photographic tape of a loop oscillograph, which was guaranteed thanks to the presence of a collector device on the rotation stand.

Results of the Investigations

After preliminary training under conditions of rest, the test subjects were given stable indicators of latency periods within the ranges of 0.5-0.9 sec. The length of reactions (time of reaching a given goal) in various subjects ranged from 0.7 to 2.5 sec. During investigations in the third minute of rotation and immediately after the stand was stopped, an increase in the indicators of the sensory motor reaction was, as a rule, much greater than during the process of total rotation. This is apparently related to intensification of afferent pulsation from the receptors of the vestibular apparatus, caused by positive and negative accelerations at the moment of gaining velocity and braking (the appearance of nystagmus, "flashing" of the instrument panel in front of the eyes, false sensation of body position in space, etc.). Latency periods and length of motor reactions during rotation at a constant velocity were increased with definite characteristics depending on the conditions of the experiments. In the first series of the experiments, the greater the angle of inclination of the trunk with respect to rotation axis and the greater the angular velocity, the higher were both indicators of sensory motor reactions. In the second series, an increase in the length of latency periods and motor reactions depended on the position of the body with respect to rotation axis, and also on the magnitude of angular velocity.

The table presents average data of the increase in latency periods (the first figure) and the length of motor reactions (the second figure) for the entire period of 20-min rotation (in percentages with respect to initial

ndicators) depending on the position of the body with respect to rotation /131
xis and on angular velocity.

VERAGE INDICATORS (IN %) OF INCREASE IN LATENCY PERIODS AND LENGTH OF MOTOR EACTIONS AS A FUNCTION OF ANGULAR VELOCITIES AND BODY POSITION WITH RESPECT TO THE VERTICAL AXIS OF ROTATION

Position of test subject	Angular Velocity, revolutions per second						
	0,25	0,50	0,75	1,00	1,25	1,50	1,75
First series: rotation axis passed through the region of the pelvis, and the body was inclined							
by 0°		10/20		20/45	15/45	25/35	42/51
20°		2/10		13/22	30/54	41/33	
30°				5/44		16/48	51/63
45°				32/20	44/39		
65°		28/24	16/32	52/40			
80°		48/22	59/43				
90°	23/36	62/31					
Second series: test subject was fixed in a reclining position, and rotation axis passed through the region of the							
head	12/10	19/0	0/14	0/19			
heart		0/21	24/33	42,33			
feet	58/7	17/12					

NOTE: The first figure is the indicator of increase in latency periods, and the second is that of the length or motor reactions.

It is obvious from the table that in the first series of experiments an ncrease in the indicators of sensory motor reactions by 40-50% began at lower otation velocities as the angle of inclination of the body increased with espect to the vertical axis of rotation. The most unfavorable conditions n the second series were those in which the axis of rotation passed through he region of the feet.

It should be noted that the highest angular velocities in our experiments were maximum not only according to indicators of sensory motor reactions, but also in the degree of disruptions in the functional state of the cardiovascular system (according to data of E. V. Marukhanyan) and of the visual analyzer (A. B. Flekkel', 1963).

Comparison of the indicators of latency periods and duration of motor reactions with results of mathematical calculations and the magnitudes of centripetal accelerations indicated the presence of a regular inverse function between the degree of the variations in sensory motor reactions and the values of longitudinal components of these accelerations in the head-pelvis direction.

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THE PROBLEM OF MOTION SICKNESS AND INCREASED SENSITIVITY TO VESTIBULAR EFFECTS

ON THE PROBLEM OF VESTIBULO-VEGETATIVE REFLEXES DUE TO THE EFFECT OF CORIOLIS ACCELERATION

A. S. Kiselev

ABSTRACT. Studies on 40 subjects revealed that the severity of vestibulo-vegetative and vestibulo-somatic reactions is greater during acitve tilting backward and forward than during tilting forward and backward. On this basis a new test which determines the degree of vestibular resistance to Coriolis acceleration is proposed for vestibular selection and conditioning of cosmonauts.

In his time, Purkinje discovered that a man sitting quietly during uniform rotation loses the sensation of rotation, but it again appears when he inclines the head. /132

In 1908, V. I. Voyachek [1] explained Purkinje's phenomenon by the development of acceleration which arises upon rotation of the body in two mutually perpendicular planes. The magnitude of this acceleration is calculated by Coriolis's formula.

According to published data, some cosmonauts experienced the state of motion sickness during orbital flight around the earth [2, 4].

The spaceship and the cosmonaut revolve around the earth, and also develop rotational movements around their own axes. Under such flight conditions, any movement of the head or body of the cosmonaut contributes to development of Coriolis acceleration. Although this acceleration does not reach high values, when it accumulates during a prolonged flight it may lead to development of vestibulo-vegetative reflexes. The latter circumstance dictates the requirement in selecting cosmonauts, of investigating their sensitivity to Coriolis acceleration, especially its cumulative effects.

We know that the sensitivity of the vestibular analyzer to this acceleration is determined by the classical experiment of V. I. Voyachek. Moreover, animal reaction -- inclination of the body of the test subject upon its extension from a forward inclined position -- is recorded during uniform rotation.

However, considering that the body of a cosmonaut is inclined backward during flight and he must more often straighten himself in a backward-forward direction, it would be more correct in V. I. Voyachek's experience to carry out similar straightening of the body, i.e. backward-forward, and of course registration of vegetative rather than animal reaction is more significant.

Relying on the data of V. G. Strelets [5] and I. S. Usachev [6], which /133 indicate greater definition of vestibular reactions during backward inclined rotation than during forward inclined rotation, we may assume that straightening from the backward-forward position during rotation (we shall arbitrarily call it "backward Coriolis") displays more defined vestibular reaction than during straightening from the forward-backward position (we shall arbitrarily call it "forward Coriolis").

Our experiments performed according to this scheme on 40 test subjects confirmed this assumption. Both vestibulo-somatic and vestibulo-vegetative reactions during the "backward Coriolis" experiment were more defined than those during "forward Coriolis" experiment. Thus, inclination of the head-body during "backward Coriolis" was on the average 40°, and during "forward Coriolis" was 24°, respiration increased in frequency during "backward Coriolis" by an average of 5, and during "forward Coriolis" by 2 cycles per minute; pulse increased during "backward Coriolis" by 11 strokes, and during "forward Coriolis" by 6 strokes per minute, and the temperature varied on the average during "backward Coriolis" by 0.7°, and by 0.4° during "forward Coriolis."

The data of the investigation were accomplished by the single-stage experiment of V. I. Voyachek, the purpose being only one, namely to prove greater definition of vestibular reactions during "backward Coriolis" compared to "forward Coriolis." However, we spoke earlier about the fact that accumulation of the indicated vestibular stimulations is possible during flight. Therefore, further investigations were directed toward study of vegetative reflexes arising upon accumulation of the effect of Coriolis acceleration, obtained when the body is straightened from a backward inclined position during rotation, i.e. upon accumulation of the so-called "backward Coriolis."

However, such an experiment is endured very poorly by test subjects when repeated; therefore, we decided to limit active movements during rotation to only single inclinations of the head from a backward to vertical position.

This method of investigation, more similar to reality, differs from proposals of other authors who have recorded the vestibulo-vegetative reflexes during inclinations of the head forward and to the side [3, 7].

Method

Test subjects were used in the experiments, who had never before experienced vestibular disorders under normal conditions (while driving automobiles, during airplane flights and sea travel).

At first initial control experiments were set up. Pulsopneumograms, skin temperature and perspiration were recorded in a state of rest, and then the same reflexes were determined after cessation of rotation, carried out at a /134 velocity of a single revolution every two seconds. Vegetative reactions were also recorded with the subject's head inclined without rotation. The results of these investigations indicated that variations in temperature and perspiration did not begin due to the effect of negative acceleration alone, respiration varied, but increased in frequency by only two cycles per minute, and pulse increased by four strokes per minute. When the head was inclined without rotation, respiration, temperature and perspiration remained unchanged, and pulse increased in frequency by two strokes per minute. Thus, we did not actually observe any clearly expressed vegetative reactions during the initial experiments, i.e. due to the effect of negative acceleration alone or of inclinations of the head alone.

Having obtained initial data, we turned to the experiment with Coriolis acceleration. The test subject with head thrown back and eyes closed was rotated in a Barani chair at a rate of one revolution every two seconds. After the sensation of rotation had disappeared, the test subject on command began to move the head from backward inclination to the vertical and back, completing one inclination every second.

When signs of motion sickness (paleness, perspiration, etc.) appeared, the experiment was stopped and recording was made of the indicated reflexes. When visual signs of motion sickness were absent, the experiment continued for 10 min. Experiments were conducted on 100 subjects according to the method described above.

We divided all test subjects into four groups according to the degree of definition of visually determined vegetative reactions arising in response to accumulation of the effect of Coriolis acceleration during continuous rotation.

The first group includes those subjects in which vestibulo-vegetative disorders appeared during the first three minutes (paleness and perspiration). When the experiment was continued for more than three minutes, the test subjects of this group began to display definite vegetative reactions (cold sweat, nausea, vomiting). We shall call this accumulation of the third degree.

The second group included test subjects in which the symptoms indicated above appeared during the fourth to sixth minute (accumulation of the second degree).

The third group consisted of subjects in which vegetative disorders began during the seventh to ninth minute (first degree accumulation).

And the fourth group included subjects who endured the entire experiment for 10 min (zero degree accumulation).

As the experiments indicated, there were 22 subjects with third degree accumulation, 9 with second degree, 23 with first degree and 46 with zero degree accumulation. Thus, vestibulo-vegetative symptoms noted visually /135 appeared in 54% of the investigations.

When analyzing data obtained as a result of recording pulsopneumograms, we may note that a variation in the frequency of respiration and pulse began in response to the effect of accumulation of Coriolis acceleration. Moreover, an increase in frequency of the indicated reaction was noted in most cases. Thus, respiration increased by 64%, and pulse increased in 58% of the cases. A decrease in frequency of respiration was noted in 19%, and a decrease in pulse rate was noted in 13% of the cases. Respiration and pulse rates in the remaining test subjects did not vary significantly.

Variation in respiration and pulse did not always proceed simultaneously. Combined variation of pulse and respiration was noted only in 42% of the cases.

When considering variation in respiration and pulse rate in the test subjects displaying various degrees of sensitivity to Coriolis acceleration, we may note the following: if variation of respiration and pulse rate among those inured to Coriolis acceleration (with zero degree accumulation) had no definite uniformity and, moreover, pulse did not vary by 50%; in test subjects displaying increased sensitivity to Coriolis acceleration (second and third degree accumulation), these variations appeared as a rule in an increase in pulse and respiration rate. Thus, pulse in individuals with third degree accumulation increased in 91% of the cases, and respiration rate increased in 73%, the degree of definition of these reactions being significant.

Regarding variation in body temperature, here the dependence of this reaction's definition on the degree of sensitivity of test subjects to Coriolis acceleration is especially noticeable. Thus, if a decrease in temperature among all groups was noted at 58%, temperature decreased by only 20% in the group with zero degree accumulation, and a decrease in temperature was noted in 91% of the cases in subjects with first, second and third degree accumulation, the extent of decrease in body temperature also being more defined in those groups, reaching 1-2°. An increase in body temperature was noted in only 11% of the cases, mainly in subjects with zero degree accumulation.

We were unable to discern significant differences and regularities in variation of perspiration among groups having a different degree of sensitivity to Coriolis acceleration.

The data presented permit us to propose a unique stand for passive training to this type of acceleration. With the help of this stand it is possible to obtain a prolonged effect of Coriolis acceleration on a test subject, without resorting to active inclinations of the body and head, and consequently such training may be continued for a longer period.

Conclusions

1. Vestibulo-animal and vegetative reactions due to so-called "backward Coriolis" are more defined than those due to "forward Coriolis." /136

2. The proposed method of investigation -- "backward Coriolis" -- most nearly approximates the real conditions of cosmonaut flight.

3. This test makes it possible to reveal the degree of vestibular stability to accumulation of Coriolis acceleration, and to obtain defined vestibulo-vegetative reflexes in subjects with increased sensitivity to this acceleration.

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THE EFFECT OF PROLONGED ROTATION AND CORIOLIS ACCELERATIONS ON THE VESTIBULAR FUNCTION OF MAN

R. R. Galle

ABSTRACT. Fourteen experiments wer conducted in a rotating chamber at a velocity of 10 and 40 deg/sec lasting up to 7 days. Some results of investigating the function of the vestibular analyzer during rotation are presented. It is proposed that prolonged rotation tests be used as diagnostic tests to determine the tolerance of man to vestibular effects.

The analyzer function varies significantly under conditions of space flight. The main reason for these variations, in the opinion of most authors, is the effect of unusual conditions of weightlessness on the organism.

One of the manifestations of analyzer function disruption is development of spatial orientation illusions and of the motion sickness syndrome.

We know that accumulation of vestibular analyzer stimulations plays a leading role in the genesis of motion sickness under ground conditions. The assumption that the vestibular analyzer is of no less significance in the development of the motion sickness syndrome during space flight is natural, especially when we consider disruption of its functional state under conditions of weightlessness.

One of the most probable vestibular stimuli which may occur during orbital flight is Coriolis acceleration. It occurs when man moves inside the /137 cabin of his ship while the latter is rotating. Calculations indicate that the physical magnitude of this stimulus does not exceed $3 \cdot 10^{-5}$ g. This makes it necessary to treat the function of the vestibular analyzer very carefully under conditions of weightlessness, especially when it is necessary to increase the load on it.

The possibility of a significant increase in the intensity and duration of vestibular stimuli is related to prospective creation of artificial gravity during interplanetary space flights in order to prevent undesirable consequences of the prolonged stay of man under conditions of weightlessness.

The most realistic method of creating artificial gravity at present is to apply rotation to the spaceship, as a result of which a centrifugal force develops at a definite radius, which in the opinion of the authors of such schemes, should make up for the gravity lost.

According to the data of certain American authors [2], in order to create artificial gravity equal to 0.25 g in this manner, the spaceship must be given an angular velocity of rotation of approximately 18 deg/sec within a radius of 25 m. This rotational velocity is approximately 300 times greater than the angular velocity of a spaceship's rotation in orbit. Correspondingly, Coriolis acceleration is increased by the same amount.

In connection with the foregoing, a number of questions arises, on solution of which will depend the possibility of rational utilization of rotation of the spaceship or orbital stations. First of all they include the question of the possibility of the prolonged stay of man in a rotating system without detriment to health and work capability. It is often necessary to determine optimal angular velocities of rotation which do not cause development of severe vestibular disruptions, and also to determine maximum endurable rotation velocities.

It was established in investigations of Graybiel [3] and other authors, conducted in a slowly rotating room, that rotation at a rate of 18 deg/sec with a 2.5-m radius does not lead to disruption of state of being and work capability of man during the course of 14 days. Slight vestibular disruptions, which disappear completely during the first one or two days, are observed at this velocity of rotation [2].

Rotation at greater angular velocities leads to development of the definite syndrome of motion sickness. Results of experiments in a slowly rotating room at an angular velocity of 60 deg/sec and a cycle of 12 days were published in one of the most recent papers [3]. Despite careful selec- /138
tion of test subjects, all of them developed the definite syndrome of motion sickness, and not one of them became adapted. These experiments permitted the American authors to consider a rotation velocity of 60 deg/sec within a small radius as the maximum endurable. In their opinion, the leading role in development of the indicated disruptions is played by the vestibular analyzer, and Coriolis accelerations play the role of stimuli.

Similar investigations were conducted in the Soviet Union by a collective of authors under the direction of A. V. Lebedinskiy, Yu. G. Grigor'yev and M. D. Yemel'yanov (1963-1964). The experiments were set up in a unique domestic installation, the "slowly revolving room" (MVK-1), having a radius of approximately one meter with rotation velocities of 5.3, 10.6 and 21.2 deg/sec and a cycle up to three days.

The results of the investigations indicate that initial symptoms of motion sickness begin at a velocity of 10.6 deg/sec, and that all test subjects developed severe signs of motion sickness at a velocity of 21.2 deg/sec. Moreover, adaptation developed more slowly, and in a number of cases did not begin at all.

Research in the slowly revolving room is continuing at present by a collective of scientific workers under the direction of M. D. Yemel'yanov to establish the regularities and mechanisms of man's adapting to prolonged periods in a rotating system under the condition of his active occupation.

This report is devoted to analysis of certain characteristics of variations in reactivity of the vestibular analyzer under the effect of the indicated factors. Moreover, we shall touch upon questions of objective analysis of man's endurability to prolonged rotation, and the Coriolis accelerations which develop.

A total of 14 experiments were set up on six healthy subjects distinguished by a different degree of vestibular stability. Two speeds of rotation were employed -- 10 and 40 deg/sec at a cycle of seven days.

During the experiments, observation was conducted of variations in vestibular reaction without additional effects, and also upon proportioned prolonged stimulation by Coriolis acceleration. The latter was created by active rhythmic inclinations of the head forward at the rate of one movement per second. The direction of inclination coincided with the radius of rotation.

Vestibulo-sensory reactions were analyzed for the presence of illusory sensations of motion and for variations in the motion of visual sequential image (B. B. Bokhov). Electronystagmography and a number of neurological tests were utilized to display vestibulo-somatic reactions.

The vegetative component of vestibular reactions was studied with the help of data obtained from subjective analysis of the state of being, and also /139 by analysis of variations in a number of indices of the functional state of the cardiovascular system, external respiration and galvanocutaneous reaction. Moreover, observations were made of the work capability of the test subjects.

Reactions were then analyzed for the presence of "spontaneous" vestibular disorders and for variations in the reactivity of the vestibular analyzer during experiments on the VU-2 electrically rotating chair.

Experiments at an angular velocity of 10 deg/sec had almost no effect on the state of being and work capability of the subjects. Moreover, reactions were recorded in them which indicated stimulation of the vestibular analyzer (slight illusions of swaying, horizontal nystagmus, disruption of statics, etc.). A uniform decrease in indicated reactions with time was esbalished, which indicates good adaptability to the loads applied. However, a tendency to irregular pulsating variations in a number of indicators during a seven-day experiment was noted in one test subject (who, according to preliminary data, was stable to vestibular loads). Aftereffect reactions (severe vertigo, illusion of swaying at inclinations, spontaneous nystagmus, disruptions of gait, a sharply positive Ashner symptom, compensating-paradoxical reactions during vestibulometric investigation) were more sharply defined in him.

Much more sharply expressed variations were observed during the experiments at an angular rotational velocity of 40 deg/sec. Six subjects took part in these experiments. Vestibular disruptions were observed in all of them right up to symptoms of motion sickness. The reactions were intensified during movements. Moreover, three groups of test subjects (according to the degree of endurance of the effects) were revealed.

The first group was characterized by the presence of weakly expressed symptoms of motion sickness and their comparatively rapid regression, beginning at approximately the third or fourth hour of the experiment. The dynamics of vestibular reactions in these subjects indicated a uniform decrease in the excitability of the vestibular analyzer. Work capability was not disrupted during the experiment. Aftereffect reactions were slightly expressed, and during the first four to five hours were subject to reverse development.

Investigation of the vestibular function after the experiment revealed a moderate increase in vestibular stimulation to angular and Coriolis accelerations upon emergence from the SRR with preservation of normal relationships between the extent of the stimulus and the response reaction. Vestibular excitability subsequently returned to its initial level, and even decreased.

The second group was characterized by more expressed signs and a longer period of the symptoms of motion sickness (more than 6-7 hr), during which /140
there was significant disruption of work capability.

The subjects of this group also became adapted to rotation in the SRR according to subjective signs, but 24-30 hr later. According to objective indicators of the state of the vestibular function, the process of adapting was distinguished by irregular pulsation, and according to certain signs (reaction of sequential image, nystagmus, galvanocutaneous reaction) adaptation did not begin at all. Aftereffect reactions were more sharply expressed and prolonged. One of the subjects of this group developed a definite syndrome of motion sickness during the aftereffect.

Variations in vestibular stimulation are characterized by the presence of paradoxical reactions to individual stimuli, which may indicate significant disruptions in the central sections of the vestibular analyzer. On the whole, an increase in vestibular reaction to angular and Coriolis accelerations was noted.

The third group was characterized by development of sharply defined symptoms of motion sickness. The comparatively short duration of the experiment (up to 24 hr) and significant decrease in the work capability of the test subjects did not make it possible to follow in detail the dynamics of the development of vestibular disruptions. However, we may say they did not begin adaptation during the experiment, neither according to subjective nor objective signs.

Of practical interest is comparison of initial data on the degree of vestibular stability, obtained when using generally accepted methods for professional sampling (testing for accumulation of Coriolis accelerations [1]) with endurance of experiments in the SRR. Agreement is observed only in the group of subjects with decreased vestibular stability. In the remaining cases, the results of experiments in the SRR include significant corrections upon analysis of vestibular stability from the point of view of forecasting endurance of prolonged rotation. Test subject G-e with normal vestibular stability endured the experiment much better than test subjects N-n and G-n, who were analyzed as subjects with increased vestibular stability.

Thus, on the basis of the foregoing, we may make the following conclusions:

1) prolonged stay of man in the SRR during his active occupation leads to disruptions in the function of the vestibular analyzer, definition of which increases as the angular velocity of rotation increases;

2) the test subjects are divided into three groups according to the dynamics of variation in vestibular reaction during the experiment:

a) those with a steadily developing adaptation process; /141
b) those with irregular fluctuation rate of adaptation;
c) those lacking signs of adaptation.

According to this, endurance of the test subjects of prolonged rotation and Coriolis accelerations may be analyzed as good, satisfactory or poor;

3) investigations of the vestibular function during rotation in the SRR and during the aftereffect may supplement presently existing methods of determining the vestibular stability of man.

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INVESTIGATIONS OF SLEEP IN MAN UNDER CONDITIONS OF PROLONGED ROTATION

F. D. Gorbov and V. I. Myasnikov

ABSTRACT. Rotation of test subjects at an angular velocity of 10 deg/sec over a period of days had no significant effect on the quality of nocturnal sleep. Relatively superficial sleep was determined by factors of a circumstantial nature (uncomfortable bed, temperature discomfort, vibrations, etc.) rather than by rotation. Seven-day rotation at the same velocity decreased the depth of sleep (according to EEG data) without disrupting wellbeing.

Symptoms of space motion sickness, noted during the flight of some Soviet cosmonauts indicate that weightlessness as a complex pathogenic factor may cause the phenomenon of vestibular discomfort in a number of cases. It is known from published data that vestibulo-vegetative disorders, combined under the concept of motion sickness, have resulted in deterioration of the state of being and a decrease in the work capability of crew members of spaceships [4, 5]. Many authors feel that the most effective means of preventing harmful effects of weightlessness on an organism is to create ships with artificial gravity, which may be achieved with the help of rotating spaceships [12]. However, in this case Coriolis accelerations will act on the crew members [6]. The experimental investigations of Graybiel, Clark and Zarriello [8, 10] indicated that when humans stay in a room rotating at a velocity of 5-10 revolutions per minute, they develop symptoms of motion sickness. In the literature available to us, we have not found data on the effect of motion sickness on the sleep of an astronaut or test subject, other than information presented in the paper of Yu. G. Grigor'yev and colleagues [1]. In connection with this we felt it expedient to study the characteristics of sleep in man during prolonged rotation in a slowly rotating room (SRR) at a strictly proportioned rate of angular rotation acceleration and duration.

Method

The investigations were conducted with participation of five healthy subjects of different ages in a SRR [1] with an angular velocity of 10 and 40°. Duration of rotation varied within the limits of one to seven days. The characteristics of experiments with rotation in which investigations were carried out on sleep are presented in the table. /142

Duration of sleep, according to the order of the day, was 8 hr. Two air mattresses were arranged as beds by the test subjects on a rotating platform parallel to each other on both sides of the axis of rotation. The position of

the subjects during sleep was such that the head and feet were located near the outer edge of the rotating platform.

CHARACTERISTICS OF EXPERIMENTS WITH ROTATION (1965)

Test subject	Date	Duration of Rotation, days	Velocity of rotation, deg	Study of Sleep		
				Before experiment	During experiment	After experiment
R-v E. V.	11.II	1	10	—	+	—
N-n A. M.	18.II	1	10	—	+	—
G-le R. R.	22—29.II	7	10	+	+	—
N-n A. M.	22—29.II			+	+	—
K-n M. P.	21.IV	1	40	+	+	—
R-v E. V.	21.IV			+	+	—
R-v E. V.	15—18.II	3	40	+	+	+
G-le R. R.	15—18.II			—	—	—
G-n A. V.	8—11.II	3	40	+	—	+
N-n A. M.	8—11.II			—	—	—

The data from questioning and results of medical observation, results of electroencephalographic studies of the bioelectric activity of the brain, and data of experimental study of the depth of sleep were utilized as analysis criteria.

Each test subject was instructed to give a subjective analysis of sleep during rotation, and to record the results in a notebook of self-observations with detailed characteristics of depth of sleep, characteristics of dreams, speed of falling asleep and waking up, etc.

The EEG was recorded from symmetrical sections of the head with a bipolar (frontal-occipital) lead. Recording was carried out in darkness during the entire night every 15 min.

The basis for experimental study of the depth of sleep was the principle of "physiological probing," which consisted in the fact that the frequency of /143 a sound signal causing a "wakeup reaction," variation in the EEG pattern during the effect of acoustical stimulation or during its aftereffect and the appearance of the galvanocutaneous reflex (GCR) were calculated. Pure tones of different frequency, applied discretely in sequence of 12,000, 11,000, 10,000, ..., 4,000, 3,000 and 2,000 Hz, were utilized as a stimulus. The acoustical signals were applied from a ZG-33 audiogenerator every 10-15 sec with vibration lasting 3-5 sec.

Results of the Experiment

Controlled study of sleep was carried out in a special chamber, isolated from external sources of light and noise, on each of the five test subjects before the experiment in the SRR. It was determined as a result of these investigations that the conditions of the experiment had a definite effect on the sleep of the test subjects, disrupting the process of falling asleep and deteriorating the quality of nocturnal sleep. This was indicated by the data from conversations with the subjects, results of studying the bioelectric activity of the brain, and experimental study of the depth of nocturnal sleep. The difficulty of falling asleep and poor sleep was, in the opinion of the test subject, caused by the presence of an unusually large amount of electrodes attached to the body and by realization that one is in an experimental chamber and is being observed without interruption. The latter was the subject of emotional experiences and the reason for dreams. For example, subject G-n A. V., relating the content of his dream, reported that "someone enters and says: 'Don't sleep, everything is translucent here, you are being studied!'" A more detailed description of nocturnal sleep in the chamber was given by subject K-n M. P. on 21 April 1965: "... I did not fall asleep right away because of the unaccustomed high pillow and the presence of the electrodes. However, I slept soundly without dreaming for the first half of the night. I awoke once during the night (he doesn't indicate the reason), after which I could not fall asleep for a long time: I was distracted by the knot of the bandage attaching the electrodes to my head, and noise from the fan operating (when the air touched the pillow, it seemed that the bed gave the sound of the fan some kind of overtone). I don't remember when I fell asleep. Toward morning I dreamed something neutral in content. I awoke immediately after the 'reveille' signal. I slept well. I felt fine after sleep."

Study of the EEG during the process of falling asleep indicated that the dynamics of the bioelectric activity of the brain of the test subjects was characterized by a gradual decrease in the amplitude and index of dominating rhythm with subsequent alteration of the EEG pattern (Figure 1).

As can be seen from the figure, the bioelectric activity of the brain of /144
subject K-n M. P. was characterized before beginning of sleep by the presence of an α rhythm with a frequency of 10 oscillations per second and an amplitude to 75 μv on the EEG. The α rhythm index was 87%. Within 10 min after the light was switched off in the chamber, a gradual decrease in the amplitude and index of α rhythm was observed. Subsequently, the dominating rhythm was replaced by an indefinite one, with gradual increase in the number and amplitude of slow EEG components, until the latter assumed the character /145
of a "sleep" curve (within 60 min after sounding of the signal).

Bioelectric activity of the brain during sleep was distinguished by irregularity of the EEG pattern, when the periods of indefinite rhythm of low amplitude with total absence of dominating frequency were replaced by periods of slow activity.

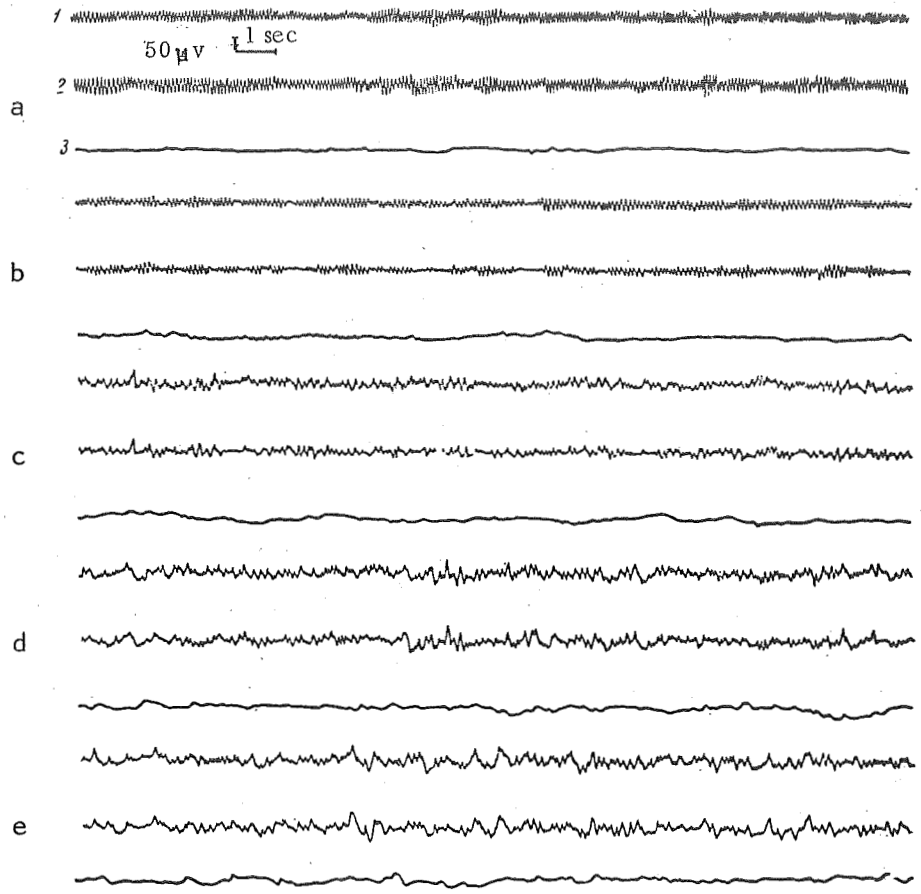

Figure 1. Dynamics of the Bioelectric Activity of the Brain of Subject K-n During the Process of Falling Asleep. 1, EEG -- frontal-occipital, left; 2, EEG -- frontal-occipital, right; 3, Oculogram; a, EEG recorded during stimulation; b, c, d and e, EEG recorded during falling asleep within 30, 40, 50 and 60 min, respectively, after sounding of the signal

Experimental investigation of the depth of sleep indicated that acoustical stimuli applied on the background of indefinite rhythm caused a reaction of waking up with a frequency of the acoustical signal of 12,000-9,000 Hz, and when there were diffused slow waves on the EEG, variations of cortical rhythm developed to sound, shifted in the direction of lower frequencies (8,000 Hz and below), i.e., upon an increase in the level of the natural loudness of sound (during sleep) by 2-2.5 times. Curves of the depth of sleep were obtained as a result of these investigations (Figure 2).

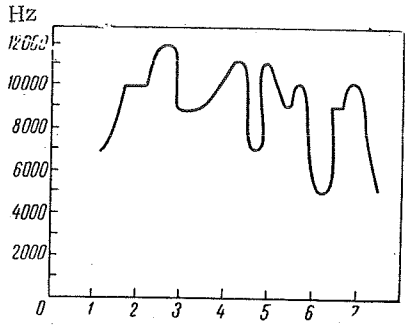

Figure 2. Curve of the Depth of Nocturnal Sleep of Subject R-v in a Special Chamber.

As can be seen in the curve, phases of deep and superficial sleep interchange, the depth of sleep of the subject increasing toward morning. Deviation of the curve from the "standard"[1] was caused, in our opinion, by a number of reasons -- on the one hand, details, being on duty, and participation in marches accustomed the subject to broken sleep, and on the other hand, the relatively shallow depth of sleep during the first half of the night was caused by the effect of circumstantial factors of the experiment. In some cases the effect of circumstantial factors was so sharply defined, that some subjects, for example, G-le R. R. and G-n A. V. were almost unable to fall asleep during the entire night. For example, an indefinite rhythm with an amplitude of bioelectric potentials within limits of 10-20 μv was recorded in the EEG of subject G-le R. R., recorded at various periods of sleep (Figure 3). Reaction of waking up in the form of bursts of α rhythm of different degrees of definition and duration developed in response to acoustical signals of 12,000-11,000 Hz.

Thus, circumstantial factors had a significant effect on the nervous-psychic sphere of the subjects, causing, in certain cases, emotional tension, /146
individual expression of which was determined by a number of circumstances, in particular by typological and characterological properties of the personality. It would not be necessary to dwell on the significance of this circumstance, if we did not consider the fact of sleep disruption in test subjects in the chamber and anamnestic data, according to which the conditions of work activity of the subjects in the past were very similar (being on duty, details), as a result of which, in their opinion, they acquired in one degree or another habits of broken sleep, sleep in a noisy and unaccustomed situation, uncomfortable position, etc.

Rotation during the day at an angular velocity of 10 deg/sec did not cause disruption in the quality of sleep. Relatively superficial sleep at night was caused not by rotation as an adequate stimulus of the vestibular apparatus, but by factors of circumstantial nature -- uncomfortability of the bed, temperature discomfort, vibrations, etc.

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[1] A normal curve, according to Kohlschütter [13], is characterized by rapid falling asleep and an increase in the depth of sleep, reaching a maximum within 1-1.5 hr after beginning of sleep, after which there is a more or less sequential transition to superficial sleep.

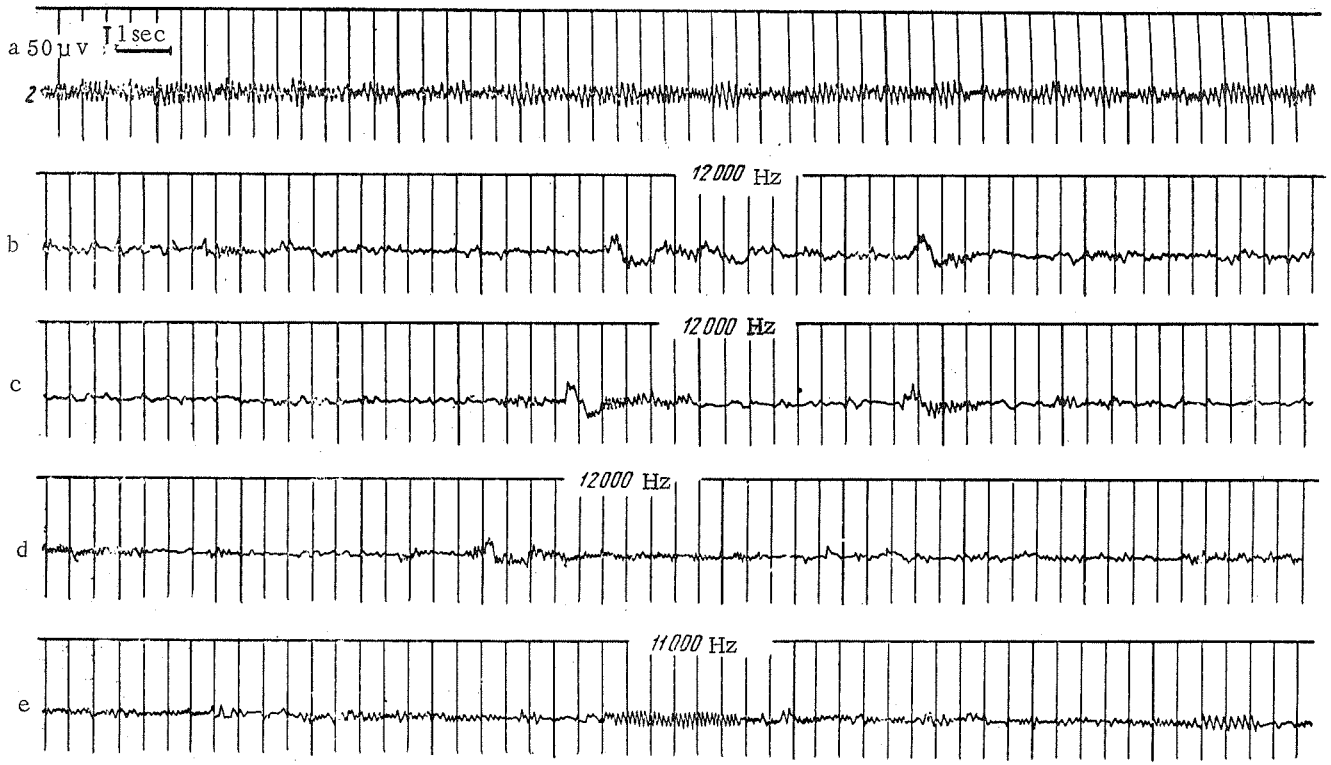

Figure 3. The EEG Component of the Reaction of Test Subject G-le Awakening in Response to Sound at Various Times of Nocturnal Sleep. a, EEG recorded during stimulation; b, c, d, and e, EEG recorded during sleep at 2:30, 2:40, 2:50, and 5:40 a.m., respectively, 1, Stimulus marker; 2, EEG frontal-occipital left

Lack of defined symptoms of stimulation of the vestibular analyzer during seven-day rotation, on the contrary, did not provide occasion to confirm that rotation as a pathogenic factor did not occur. Despite the relatively good state of being and quality of nocturnal sleep (according to the test subjects), at different periods from the beginning of rotation they displayed paradoxical EEG reactions. Application of acoustical stimuli in a sequence provided by the method of investigation caused inhibition of cortical rhythm in their aftereffect, the degree of inhibition being increased in proportion to the decrease in frequency of the acoustical signal. Regarding EEG reactions to the fact itself of applying stimulus, its pattern to sound of different frequency barely changed (upon visual analysis) compared to the initial EEG curve (Figure 4). Whether the presence of paradoxical reactions was caused by variation in the depth of sleep as a result of rotation is difficult to say; however, similar dynamics of the bioelectric activity of the brain in the subjects during controlled studies of sleep in the chamber was not observed. They were also not observed during subsequent days of rotation.

As an additional indicator of the depth of sleep, the percentage relationship of indefinite rhythm and slow activity in the EEG recorded at various times of the experiment was studied. It turned out that in a percentile relationship, indefinite rhythm has a tendency to increase in proportion to rotation.

EEG processing indicated that of 50-57 min of the total time of recording, the indefinite rhythm in subject G-le R. R. occupied 86% during the first and 90% during the sixth night of the experiment, while slow activity was only 5.5 and 4%, respectively. Indefinite rhythm in subject N-n A. M., compared to that of subject G-le R. R., was 76.5% during the second and 85.0% during the seventh night of rotation, and slow activity, on the /149 other hand, diminished from 20.0 to 14.0%. Thus, the relationship of indefinite rhythm and slow activity in the EEG as an index of the depth of sleep indicates that nocturnal sleep of the subjects during a seven-day experiment with rotation was relatively superficial. This agrees with data of other authors [2, 7, 11], in the opinion of which deep sleep of man is characterized by the presence of diffused slow waves on the EEG.

Rotation of subjects in the SRR at an angular velocity of 40° had a serious effect on the organism. The subjects developed vestibule-vegetative disorders with subsequent development of phenomena of fatigue, the degree of which, despite individual differences, depended on the period of rotation from the moment of their appearance and until beginning of sleep. Fatigue, appearing subjectively as a sensation of tiredness, was obviously, in conjunction with the above enumerated factors, one of the reasons for sleep disruption from the point of view of both its depth, and its duration. The depth of sleep, increasing rapidly, soon decreased, and became superficial and sensitive with frequent interruptions, especially during the first night. As an example, let us cite a portion of a simultaneous EEG recording of subjects G-le R. R. and R-v E. V. during the first day of rotation (Figure 5). As is obvious in Figure 5, the EEG's of subjects within an hour after "taps" (a)

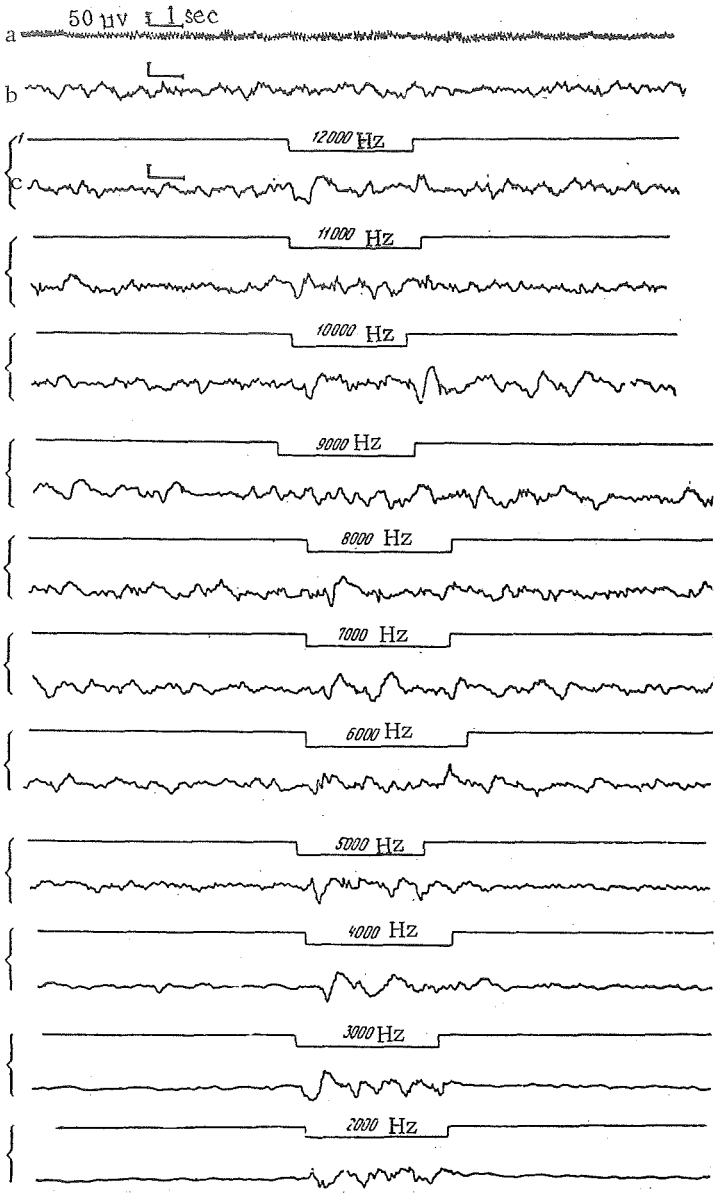

Figure 4. Paradoxical EEG Reaction of the Cerebral Cortex of Subject G-le During Sleep to the Second Day of Rotation in the SRR. a, EEG recorded during stimulation; b, EEG recorded during sleep and before application of acoustical stimulus; c, Dynamics of bioelectric activity of the brain to acoustical stimuli during sleep; 1, Stimulus marker; 2, EEG, frontal-occipital, left

differed significantly from each other not only in frequency, but in the amplitude of biopotentials. θ and δ rhythm with an amplitude of individual waves to 80-90 μv is recorded in the EEG of subject R-v E. V. (1), while a jagged rhythm of low amplitude is observed in the EEG (2) of subject G-le R. R. Bioelectric activity of the brain of the same subjects, but recorded 4 hr (b) after beginning of sleep, differ in their low jagged rhythm, typical for shallow sleep or the period of falling asleep [9].

However, despite its relatively shallow depth, sleep had a favorable effect on the well-being of the subjects and on their work capability. Definition of vestibulo-vegetative disruptions after sleep diminished sharply, and movements of the subjects became freer and their appetite improved, which in turn was reflected in the quality of sleep on subsequent nights. Sleep during the second day was deeper than during the first night, but more shallow than during the third day of the experiment.

As an example we can cite notes from the notebook of subject G-n A. V., who, during the first day of rotation, displayed a poor appetite, heaviness in the pit of the stomach, urges to to vomit, increased perspiration and vertigo.

Despite this, "I fell asleep rapidly, but on the whole I slept poorly -- I awoke three to four times during the night (I have the impression that I am not sleeping but simply dreaming). I feel better in the morning, and feel no /150 unpleasant sensations. After breakfast, the heaviness in the pit of the stomach appeared, but passed within about 3-4 hr. I slept somewhat better the second night -- I fell asleep immediately and did not awaken during the night. The next morning, I awoke from the signal of the experimenter. I experienced no unpleasant sensations, neither during the morning nor during the day. The third night I slept soundly, and even slept through reveille (according to the order of the day) for 15 min."

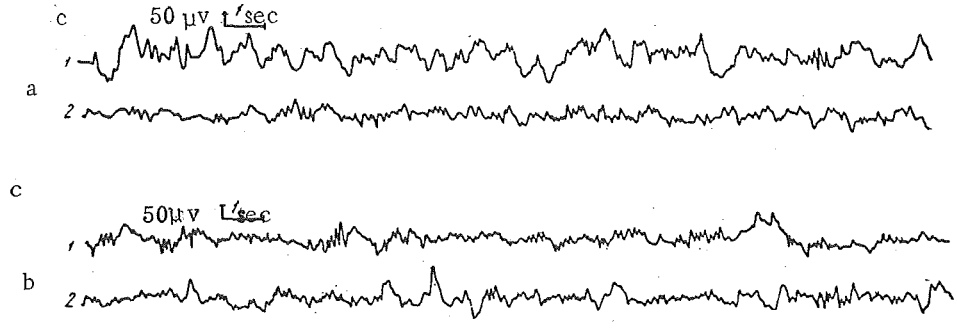

Figure 5. Dynamics of the Bioelectrical Activity of the Brain During Sleep of Subjects R-v (1) and G-le (2) During the First Day of Rotation in the SRR at an Angular Velocity of 40°. a and b, EEG's recorded within 1 and 4 hr, respectively, after taps; c, Frontal-occipital, left

It was determined from the experiments conducted that rotation at an angular velocity of 40° caused vestibulo-vegetative disruptions similar to motion sickness in some test subjects, and sleep had an alleviating effect on the severity of these disruptions.

This is obviously explained by the fact that during sleep excitability of the nerve cells of the vestibular analyzer at all levels of the reflex curve diminishes sharply. Moreover, restriction of motor activity during sleep almost totally excludes the effect of Coriolis accelerations as an adequate stimulus of the vestibular analyzer, and weakening of the muscles which provide an active position of the body during various positions and movements of subjects during waking hours, and the labyrinth apparatus responsible for bringing abour tonic reflexes is released. These circumstances in the final analysis resulted in a decrease in the severity of vestibulo-vegetative disorders, and in an improvement in well-being and work capability of the subjects. Without going into details of discussing the central mechanisms of the alleviating effect of sleep on development of

vegetative disorders during rotation, it should be said that obviously the latter is related to restriction of motor activity and weakening of the postural muscles, and also to a decrease in vestibular "reactivity" during sleep. All this not only reflects the complex process of adapting to prolonged, in particular, vestibular effects, but it also indicates ways of developing methods of regulating sleep under the indicated conditions. /151

Conclusions

1. Circumstantial factors of the experiment disrupt the quality of nocturnal sleep and the process of falling asleep (according to EEG data and experimental study of the depth of sleep).

2. Rotation at an angular velocity of 10° over a period of days has no substantial effect on the quality of nocturnal sleep. Relatively superficial sleep is determined not by rotation, but by circumstantial factors -- an uncomfortable bed, temperature discomfort, vibration, etc.

3. Seven-day rotation at an angular velocity of 10° has a definite effect on the sleep of test subjects, decreasing its depth (according to EEG data) without disrupting well-being.

4. Rotation of subjects at a velocity of 40° results in vestibulo-vegetative disorders and development of fatigue. Sleep has a favorable effect on the severity of vestibulo-vegetative disorders, well-being and work capability of test subjects.

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SOME DYNAMIC INDICATORS OF THE VESTIBULAR ANALYZER UNDER THE EFFECT OF CORIOLIS ACCELERATION

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and S. V. Zhadovskaya

ABSTRACT. The effect of prolonged Coriolis accelerations on rated athletes was studied. Vegetative reactions, and also shifts in static and dynamic equilibrium, post-rotational nystagmus and dynamometry were recorded. Grouping according to professional affiliation (flying or technical personnel) did not reveal any substantial differences between the groups.

One of the important problems of aviation and space medicine is the study /152
of the effect on man of long-acting angular accelerations, which under specific conditions cause the phenomenon of accumulation, manifested by sensory, animal and vegetative disorders.

The efforts of some Soviet and foreign authors, studying the interaction of afferent systems under conditions of increased stimulation of the vestibular analyzer, indicate that hyperergistic stimulations which develop in it are capable of disrupting the activity of other analyzers, and also various pathological reflexes on the part of the vegetative nervous system.

Most contemporary papers, devoted to the problem of the effect of long-acting angular accelerations on the vestibular analyzer, concern the vegetative aspect, while still insufficient attention is given to the question about the effect of this stimulus on the vestibulo-somatic function of the analyzer. Moreover, this very aspect of the activity of the analyzer (on condition of vestibulo-vegetative stability) is most important in the flying profession, since all purposeful motor acts of the pilot and especially of the astronaut in unsupporting space are determined by the stability and adequacy of reactions of the vestibulo-animal sphere.

On the basis of the foregoing, we undertook complex investigation, analysis of the results of which primarily concerns the vestibulomotor function of the organism.

A model of long-acting angular accelerations, which change direction unceasingly, were Coriolis accelerations developing during five-minute uniform circular rotation of a test subject (one revolution every 2 sec) and simultaneous inclinations, at a frequency of one inclination -- straightening every 4 sec [2].

The following physiological indicators were recorded:

a) pulse frequency and the magnitude of arterial pressure for the vegetative nervous system;

b) indicators of pedography, ichnography and the phenomenon of residual bending of the head were determined with the help of a saggital indicator of the vertical position of the head for systems which control body equilibrium during orthograde standing and in motion (the vestibular and proprioceptive analyzers).

The method of pedography is based on determination of the stability with /153 regard to constant fluctuations of the center of gravity of the human body under conditions of natural comfortable standing. The pedograph is constructed on the principle of an integrator of oscillations which emits ready information on the degree of stability which has developed during a segment of specific time (usually not less than 20 sec, but not more than the slowest oscillations [1]).

Ichnography is a method based on determination of body equilibrium during walking, and determines the angle of inclination, or the "spread of the gait," from an average line.

Determination of residual bending of the head consists in recording the angle of inclination from the sagittal plane after one or several oscillatory movements of the head in the frontal plane.

Rotational and post-rotational nystagmus were determined from separate indicators, specific for the vestibular analyzer, by the electronystagmography method and duration of the illusion of counterrotation. The velocity of uniform rotation was 20 deg/sec and the duration was 60 sec.

The indicator of muscular-tonic function was carpal dynamometry; along with this, physiological tremor was also recorded, for which a seismograph was used in combination with an amplifying and recording device of an ink-writing electromyograph.

Analysis of motor activity was accomplished by the latency period of motor reaction to sounds of varying intensity. The test of critical frequency of fusing light flashes (CFFLF) was employed to determine the state of the visual analyzer. The entire complex of investigations was carried out both before and after vestibular loading.

The authors felt it feasible to present only the main assumptions of the investigation, and to make the most essential conclusions from them.

Seventy-one subjects were studied, of them 32 were flight and 39 were technical personnel. All were athletes of class I and II in various sports. The study was conducted during sporting competitions. The purpose of including athletes in the group of test subjects was to determine the effect

of sports on the adaptation function of the physiological systems being studied during the prolonged effect of angular accelerations on the vestibular analyzer.

According to the investigations of V. G. Strelets [4] and other authors, of great importance in raising the professional skills of pilots are physical exercises conducted under ground conditions, and namely such of the more /154 dynamic sports as basketball, gymnastics, soccer, etc.

The effect of athletic training was reflected in increasing the stability of the vestibular analyzer and in fine differentiations of the motor-coordination skills of the proprioceptive system.

Data of the investigation indicated that as a result of vestibular stimulations, 22 subjects displayed distinct symptoms of motion sickness, which made it necessary to curtail stimulation before the end of the period. Personnel having an unstable vestibulo-vegetative system (the motion sickness syndrome) were divided according to types of sport in the following manner: 6 of 20 basketball players (30%), 2 of 11 gymnasts (18%), 9 of 22 soccer players (41%), 1 of 5 volleyball players (20%), 2 of 6 track athletes (33%), and 2 of 7 swimmers (28%).

Analysis of the results of this study indicated that after vestibular stimulation a more distinct shift of vegetative indicators developed in basketball players, gymnasts and soccer players -- there was an increase in arterial pressure and a drop in pulse rate.

The CFFLF and dynamometry indicators decreased in soccer and basketball players, and the latency period of motor reaction increased. After stimulation, some disruption in the function of equilibrium in the orthograde position was noted in soccer and basketball players, track athletes and volleyball players; this function remained unchanged in swimmers, and improved in gymnasts.

Ichnography detected deterioration of equilibrium in soccer, basketball and volleyball players, and it was unchanged in gymnasts, swimmers and track athletes.

The results given above indicate that extreme stimulation of the vestibular analyzer by an adequate stimulus causes significant shifts in various systems of the organism, which may be reflected in the work capacity of the human who is under the given conditions. On the other hand, analysis of the results obtained for athletes in various sports indicated that the greatest shifts in static and dynamic equilibrium, and also in CFFLF, dynamometry and motor reaction were noted in basketball, soccer and volleyball players and track athletes.

However, it must be noted that from the point of view of statistical analysis, the grouping according to types of sports used, due to the small

number of subjects in the different groups, diminishes the reliability of differences between these groups according to the indicators studied. Therefore, analysis of electronystagmography data was carried out with respect to the whole aggregate of observations (71 subjects), and also for groupings by succeptibility to motion sickness and professional affiliation.

Grouping according to professional affiliation (flying and technical personnel) did not reveal any significant differences between these groups, i.e. variations in nystagmographic and other signs discovered were almost uniformly distributed among these groups. This is apparently explained by the fact that flight school cadets, due to their brief flying experience (on the average not more than 100 flight hours), in effect had not yet acquired sufficiently high professional skills to affect conditioning of the vestibular function. On the other hand, involvement in sports contributed to equalizing the degree of training of the vestibular analyzer between both groups. /155

Training according to susceptibility to motion sickness (see table) is specific for nystagmographic indicators, since under given conditions the common reflexogenic source for both vegetative reflexes as well as for nystagmus and the illusion of counterrotation are the receptors of the semicircular canals.

Analysis of nystagmography and the duration of the illusion of counterrotation indicate the following.

1. Duration of postnystagmus both before and after accumulation exceeds the duration of the illusion of counterrotation by more than twice. This difference is valid for both groups. Comparison of data with results of the investigation conducted earlier indicates that the duration of illusion in untrained personnel is almost coincidental with that of postnystagmus.

2. Duration of rotational nystagmus exceeds that of post-rotational nystagmus (before accumulation) in subjects who endure well vestibular stimulation for an average of 8.3 sec; in subjects with motion sickness symptoms, this difference was not so great and is statistically unreliable.

3. After stimulation, all subjects displayed equalization of the length of rotational and post-rotational nystagmus.

4. The frequency of nystagmus due to the effect of stimulation did not vary significantly; the amplitude of rotational nystagmus has the tendency to decrease after the accumulation test, the difference reaching an average of 1.9° for all subjects.

5. Significant differences between the amplitude of nystagmus and postnystagmus is not noted before accumulation.

After accumulation, there is a tendency toward predominance of the amplitude of post-rotational nystagmus. This variation in pilots is

INDICATORS OF NYSTAGMUS AND THE ILLUSION OF COUNTERROTATION IN THOSE SUBJECT TO AND NOT SUBJECT TO MOTION SICKNESS

Group of test subjects	Before stimulation							After stimulation						
	Acceleration			Deceleration				Acceleration			Deceleration			
	+Ny	F	A	−Ny	F	A	Ill	+Ny	F	A	−Ny	F	A	Ny
Those subject to motion sickness	41,8	3,8	9,6	34,8	3,2	9,5	14,8	38,0	3,4	7,2	35,6	3,5	9,5	12,7
	10,6	1,7	4,9	8,6	1,0	4,0	8,6	11,9	1,5	4,3	9,4	1,3	3,9	9,0
	2,27	0,37	1,04	1,84	0,23	0,86	1,83	2,55	0,31	0,93	2,01	0,28	0,84	1,92
Those not subject to motion sickness	41,3	3,2	11,4	32,9	2,7	10,4	13,0	36,6	3,3	9,0	33,3	3,0	9,5	12,5
	3,2	1,4	5,9	10,4	0,9	5,0	10,6	12,3	1,6	5,7	12,2	1,0	4,8	12,5
	0,46	0,22	0,84	1,49	0,12	0,71	1,51	1,76	0,22	0,82	1,74	0,14	0,69	1,78

Note. Ny is the duration of rotational and post--rotational nystagmus, F is frequency, A is amplitude and Ill is the duration of the illusion of counterrotation.

Tr. Note: Commas indicate decimal points.

insignificant, in technicians the difference is 1.5°, in those subject to motion sickness it is 2.3°, and it is insignificant in those not subject to motion sickness.

Thus, the facts given above indicate specific variations in the reflex activity of the ampullar receptor, which develop due to the prolonged effect of angular accelerations.

The most typical for the test subjects with stable analyzer function was /157 the predominance of the duration of rotational over post-rotational nystagmus. A significant lag in the duration of counterrotation illusion compared to duration of postnystagmus was common for all test subjects. Least variable were such parameters of nystagmus as frequency and amplitude.

Conclusion

The dynamics of indicators of experiments on equilibrium, dynamometry, tremorography, determination of CFFLF and the latency period of motor reaction, which develops under prolonged effect of angular accelerations on an organism, indicates a different effect of the latter on the mechanisms of integrating the vestibular analyzer in the system of the cerebrum, visual, auditory and proprioceptive analyzers.

Special investigation of the dynamics of certain indicators of vestibular nystagmus and duration of counterrotation illusion made it possible to establish the phenomenon of dissociation of duration of rotational and post-rotational nystagmus in subjects with a stable vestibulo-vegetative region, which is related to the adaptation function of the analyzer.

The significant lag in duration of counterrotation illusion from corresponding postnystagmus, typical for athletes, indicates that due to training, the most defined temporary shifts occur in the cortical activity of the analyzer, which apparently has a direct relationship to the regulatory mechanisms of the latter.

On the whole, data of the given investigation have again demonstrated the effect of the vestibular analyzer on the function of other afferent systems.

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ON THE PROBLEM OF DEVELOPMENT OF LATENT FORMS OF MOTION SICKNESS

A. N. Petrov

ABSTRACT. Motor responses to light signals were studied in 77 subjects with the help of a special device mounted on a two-beam swing. The time of complex sensory motor reactions, the amount of information perceived and processed and the capacity of the visual analyzer were determined. Statistically reliable variation of the indicators determined was revealed in seven subjects with the absence of visible signs of motion sickness.

Some investigators [1, 3, 4] have stated the possibility of development /158
of so-called latent forms of motion sickness, the characteristic feature of which is the absence of the usual vegetative symptoms (nausea, vertigo, vomiting), but at the same time deviations in the activity of a number of systems and organs of man are observed. These deviations often are not essentially reflected in well-being, but may be reflected in work capacity, by decreasing it. Especially great attention must be given to the appearance of such forms of motion sickness when selecting flight personnel.

The requirement for quantitative analysis of the work capacity of man under conditions similar to the activity of one operating an aircraft arises. Unfortunately, tests used at present to evaluate the work capacity of man cannot completely satisfy the investigator, because they hardly reflect the real structure of the work process. Three main elements may be distinguished in the activity of a pilot in flight, as in control of any other craft:

1) receiving information from the machine (readings of various instruments) is a sensory function of control;

2) processing the information obtained and making decisions in controlling the machine is an intellectual function of control;

3) controlling actions toward the machine are motor functions of control [2].

It is necessary to find such methods of analyzing work activity, in a single complex of which would be given the characteristics of all three elements of operator activity (the pilot) in controlling the craft. We have attempted in this paper to find and classify such criteria with the help of certain elements of information theory.

Motor responses to light signals were taken as the basis of the model of human activity. Moreover, we proceeded on the fact that such a model approximates to some degree human activity near a control panel, in particular the activity of a pilot, when he is required to make the necessary decisions, and correspondingly to carry out specific motor manipulations in response to the light signals of his instruments (flashes of signal lamps).

For this purpose, a special instrument was mounted on two-beam Khilov swings. Different colored lights, each of which the subject had to extinguish immediately in a specific, previously assigned manner (for example, by a switch arranged in the right or left hand, or installed under the foot in the form of a pedal), burned on light panels positioned in front of the eyes of the test subject. Reaction time from the moment of the lamp flash until its being extinguished, and also correctness of the manner of extinguishing it were recorded on the tape of a loop oscillograph. Activity of the subjects during this was evaluated according to three points: /159

1) the time of complex sensory motor reaction (the reaction of choice);

2) the amount of information supplied in the form of light signals perceived and processed;

3) the extent of visual analyzer capacity.

According to a previously arranged program, the test subject was supposed to extinguish each burning lamp according to the specific method for it. In the case of incorrect selection in the manner of extinguishing, the erroneous response was also recorded on the tape of a loop oscillograph. The time of this reaction was calculated as the speed of selection reaction. The amount of information perceived and processed consisted of the total amount of correct and erroneous responses to the light flashes. If there were no errors the information was maximum, and if there were incorrect responses the amount of information decreased correspondingly. In the case of incorrect responses, information equaled zero. Calculation of the amount of information perceived and processed was accomplished by Shannon's formula $I = t \log_2 p$, and the amount of information was calculated in bits.

We assumed that the time of complex sensory motor reaction characterizes the speed of psychic processes of man, and the amount of information perceived and processed, depending on the number of correct and erroneous decisions, characterizes those processes from the qualitative aspect. It was necessary to have another indicator which would combine the two enumerated tests in a single complex, i.e. would make it possible to evaluate the amount of information received and processed in time. This indicator was capacity -- a value expressing the ratio of information to the time during which this information was perceived and processed. Capacity was calculated by the formula $C = I/t$, where I is the amount of information (in bits), and t is the time interval (in sec) during which this information is perceived and processed.

It is obvious from the formula that capacity depends on the time of complex reaction and on the number of errors committed by the test subject. The capacity of the visual analyzer was calculated by our method. Moreover, the fewer errors committed by the test subject and the shorter the time of complete sensorymotor reaction, the higher was capacity, and vice versa. /160

It follows from the data presented that the tests which we used may to some extent characterize quantitatively the state of man's work capacity. When work capacity decreases, the number of erroneous actions increases, the time of complex sensory motor reaction lengthens, and the amount of information received and processed and capacity decrease. As work capacity improves, these indicators vary in the reverse direction.

In our paper we set the goal of studying how these values vary under conditions of experimental motion sickness. During the course of the experiment the time of complex sensory motor reaction and the amount of information perceived and processed were determined in a subject in a calm state, and the value of visual analyzer capacity was calculated. These indicators were subsequently determined during motion sickness and compared with control values obtained before rocking.

Seventy-seven subjects were studied. Rocking was continued until definite vestibulo-vegetative reactions (paleness, vertigo, nausea and vomiting) appeared in the subjects. In case there were no appearances of motion sickness, the swaying was stopped after 60 min.

Determination of work capacity during rocking was accomplished in unstable test subjects with the appearance of the first unpleasant sensations (slight nausea, slight vertigo), and in the remaining (stable) subjects -- at the thirtieth to fortieth minute of rocking.

In accordance with the results obtained, all test subjects could be divided into two main groups: those resistant to prolonged restimulation of the otolithic region of the vestibular apparatus and those who were unstable. The first group included 33 subjects (43%), and the second group included 44 subjects (57%). Personnel of the first group displayed no external indications of motion sickness during the 60 min of rocking (and in some cases for a longer period), and they made no complaints of deterioration of well-being. Subjects of the second group, as a rule, displayed definite vegetative symptoms (paleness, cold sweat, increased salivation and vomiting) during the first 25-30 min of rocking. The subjects of this group complained of vertigo, headache and nausea. We established very definite (statistically reliable) lengthening of the time of complex sensory motor reaction and a decrease in the amount of information perceived and processed, and in the capacity of the visual analyzer in subjects of the second group. We expected that motion sickness in subjects of the second group should cause distinct disruption of work capacity. Therefore, of great interest was investigation of subjects of the first group, who displayed no external indications of motion sickness, according to the tests which we selected. Investigation of the work capacity

in subjects of the first group indicated that 26 of 33 subjects displayed no statistically reliable variations in the time of complex reaction, the amount of information perceived and processed and the value of visual analyzer capacity, i.e. work capacity hardly varied. At the same time, in seven subjects who lacked external indications of motion sickness, we determined a statistically reliable increase in the time of complex sensory motor reaction by 13% ($p < 0.02$) and a decrease in the value of visual analyzer capacity by 19% ($p < 0.05$). The amount of information perceived and processed in the subjects hardly varied, although there was some tendency for it to decrease (observed variations were not statistically reliable) ($p > 0.05$). Thus, the so-called latent form of motion sickness was observed in seven subjects (out of 77 tested, i.e. approximately 10% of the cases). Moreover, it should be emphasized that a decrease in work capacity developed mainly due to an increase in the time of complex sensory motor reaction and, to a lesser extent, due to erroneous responses to given signals. These data permit us to conclude that in the latent forms of motion sickness the speed of psychic processes suffers primarily, while no deep qualitative variations expressed in disruption of stimulus differentiation develop. One may assume that retardation of the speed of complex reaction is the initial phase of latent forms of motion sickness, which precedes deeper disruptions of the complex coordinating and differentiating activity of man. The latter may apparently be developed upon more prolonged periods of stimulating the vestibular apparatus.

Conclusions

1. The time of complex sensory motor reaction, the amount of information supplied in the form of light signals perceived and processed, and the value of visual analyzer capacity may characterize the state of human work capacity in the quantitative sense.

2. So-called latent forms of motion sickness, in which definite objective symptoms (vegetative disorders) and disruption of work capacity are lacking, develop in some subjects (approximately 10%) under conditions of experimental stimulation of the otolithic system.

3. Deterioration of work capacity under conditions of stimulating the /162
vestibular apparatus for an hour occurs mainly due to a decrease in the speed of motor reactions, and to a lesser degree due to erroneous reactions.

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ON THE INTERRELATIONSHIP OF THE FUNCTIONAL TOLERANCE OF THE VESTIBULAR ANALYZER AND THE STATE OF ARTERIAL PRESSURE DURING MOTION SICKNESS

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ABSTRACT. The effect of the tenfold otolithic test on arterial blood pressure (BP) and pulse rate was investigated. BP, measured by the oscillographic method in persons resistant to motion sickness, remains unchanged or increases briefly upon vestibular stimulation. Hypotonia (57%) was noted in most persons prone to motion sickness.

With the new achievements in aviation and space technology, the requirements for adaptational capabilities of an organism are increasing significantly, because modern means of transportation are coupled with accelerations unusual for man, which often lead to motion sickness.

Among the physiological processes undergoing changes during motion sickness, greatest attention is given to the activity of the cardiovascular system.

Studying the effect of medicinal substances during artificial motion sickness in man, we turned our attention to the fact that the state of arterial pressure of test subjects affects the state of the vestibular analyzer and the defensive effect of medicinal substances against motion sickness. A great deal of literature has been devoted to the state of the cardiovascular system during brief periods of vestibular stimulation. On the basis of a number of studies [1, 3, 5, 7, 9, 10-15], a distinct reaction has been determined. On the part of the cardiovascular system in response to stimulation of the vestibular analyzer, an interrelationship has been established between the excitability of the vestibular analyzer and arterial pressure. However, we have not encountered in the literature available to us special studies devoted to explaining the effect of arterial pressure on the functional tolerance of the vestibular analyzer during motion sickness and the defensive effect of medicinal substances against motion sickness.

We assigned ourselves the task of conducting a detailed study of the following problems.

1. What are the characteristics of the physiological level of arterial /163
pressure in subjects slightly resistant and resistant to motion sickness?

2. What changes in the state of vascular tonus take place during vestibular stimulation in subjects resistant to and subject to motion sickness?

3. Is there a correlation between the degree of tolerance of the vestibular analyzer and the level of arterial pressure?

4. How does the functional capacity of the vestibular analyzer vary under the effect of medicinal substances against motion sickness in persons subject to motion sickness, who have normal and decreased arterial pressure?

The study was carried out on 730 test subjects.

The functional tolerance of the vestibular analyzer was determined by the number of otolithic reactions conducted repeatedly at intervals of 30 sec until the appearance of definite vegetative symptoms of motion sickness (paleness, cold sweat, nausea or vomiting). The group of subjects susceptible to motion sickness included those in which definite vegetative symptoms of motion sickness developed before ten otolithic reactions. The criterion of resistance against motion sickness in our studies was the absence of vegetative symptoms after ten otolithic reactions.

Of 730 subjects, 145 displayed vegetative symptoms of motion sickness before ten otolithic reactions (those subject to motion sickness). The remaining subjects underwent ten otolithic reactions at intervals of 30 sec without any unpleasant sensations and vegetative symptoms (those resistant to motion sickness).

Arterial pressure was studied by means of an arterial oscillograph. Triple measurement of arterial pressure at intervals of 5 min was conducted before stimulation of the vestibular analyzer. After stimulation, arterial pressure was again measured at intervals of 5 min (after ten otolithic reactions in personnel resistant to motion sickness, and after the appearance of vegetative symptoms of motion sickness in those subject to it).

We conducted detailed analysis of the state of arterial pressure and pulse during motion sickness on 100 youths subject to it, and on 100 resistant to it. The control group (those resistant to motion sickness) consisted of 100 youths in whom the doctors found no illnesses of any kind. Upon questioning they did not complain of a decrease in work capacity, headaches, and all withstood rocking well and did not experience motion sickness when using transportation (automobile, aircraft, boat, etc.).

Before stimulation of the vestibular analyzer, arterial pressure in the /16
overwhelming majority of subjects of the control group was normal: 130/80 -- 130/60 -- 120/80 -- 120/60 mm Hg at a pulse rate of 60-80 beats per minute. Arterial pressure in four subjects was somewhat higher: 140/60 -- 140/80 mm Hg at a pulse rate of 60-74 beats per minute. And, arterial pressure in two subjects was diminished: 110/50 mm Hg at a pulse rate of 60-64 beats per minute.

These subjects were divided into five groups after stimulation of the vestibular analyzer by ten otolithic tests at intervals of 30 sec, depending

on the fluctuation in arterial pressure. There were no fluctuations in maximum and minimum arterial pressure in 40 subjects (the first group), pulse rate did not fluctuate in 28 subjects, and 12 subjects displayed an increase in pulse rate to 10 beats per minute.

An increase in arterial pressure by 10-20 mm Hg (only minimum or maximum, or simultaneously minimum and maximum) was observed in 56 subjects (second, third and fourth groups). An increase in pulse rate by 20 beats per minute was noted in 30 of 56 subjects. And, a drop in arterial pressure by 10-20 mm Hg was observed in only four subjects (the fifth group).

Upon analysis of the oscillograms of arterial pressure in the control group, one could note that arterial pressure remains unchanged or briefly increases in those resistant to motion sickness during stimulation of the vestibular analyzer of ten otolithic reactions at intervals of 30 sec.

The group of those subject to motion sickness consisted of 100 persons. Thirty-eight of them complained of rapid physical and mental fatigue, headaches and poor sleep; 82 persons during childhood poorly withstood swinging or were subject to motion sickness in one or another means of transportation. All subjects of this group were healthy, and displayed no illnesses. Arterial hypotonia was revealed in 57 subjects prior to stimulation of the vestibular analyzer: it was 100/60 -- 100/40 mm Hg in 38 subjects, 90/55 -- 90/40 in 17 subjects, and 85/50 mm Hg in two subjects at a pulse rate of 54-80 beats per minute. We considered maximum arterial pressure of 105-100 mm Hg and below, and a minimum of 65-60 mm Hg and below as arterial hypotonia. Arterial pressure in 43 subjects was normal at a pulse rate of 60-80 beats per minute.

After stimulation of the vestibular analyzer by determining otolithic reactions at intervals of 30 sec, prior to the appearance of vegetative symptoms of motion sickness of the second degree, the subjects were divided into five groups depending on the fluctuation of arterial pressure. Fluctuations in maximum and minimum arterial pressure were not observed in 23 subjects (the first group); an increase in pulse rate by 12 beats per minute was noted in eight subjects, and a decrease in arterial pressure by 10-20 mm Hg was observed in 54 subjects (fourth and fifth groups). Moreover, /165
a decrease in pulse rate by 20 beats per minute was noted in 24 subjects, pulse rate did not fluctuate in 20 subjects, and there was an increase in the pulse rate by 20 beats per minute in ten subjects. An increase in arterial pressure by 10-20 mm Hg was noted in the remaining 23 subjects (the second and third groups) with an increase in the pulse rate of ten subjects by 20 beats per minute, and fluctuations of pulse rate were not observed in 13 subjects.

Upon analysis of the oscillograms of persons subject to motion sickness, one could note that their reaction of arterial pressure was more prolonged (up to 30 min) compared to those resistant to motion sickness. These reactions were often observed after stimulation of the vestibular analyzer -- a drop in arterial pressure within several minutes was replaced by an increase, and vice versa.

The data presented indicate that if arterial hypotonia was present in 57 of 100 subjects susceptible to motion sickness, it was present in only two subjects among 100 resistant to motion sickness.

If a decrease in arterial pressure was observed in 54 of 100 subjects susceptible to motion sickness after stimulation of the vestibular analyzer, this decrease was noted in only four subjects out of 100 resistant to motion sickness.

In the group of subjects susceptible to motion sickness, we compared the tolerance level of the vestibular analyzer to that of arterial pressure. It developed that among subjects susceptible to motion sickness, 2 of 43 subjects having normal arterial pressure developed motion sickness after one otolithic test, 3 developed motion sickness after two tests, and 7 developed sickness after three tests. Thirteen of 57 subjects with arterial hypotonia developed motion sickness after one otolithic test, nine after two tests, and ten after three tests.

As can be seen from further analysis, a vestibular stimulus equal to one to three otolithic reactions caused motion sickness in 28% of the subjects with normal arterial pressure and in 56% of those with arterial hypotonia. After four to six otolithic reactions, 52% of the subjects with normal arterial pressure and 38% with arterial hypotonia developed motion sickness. After seven to nine otolithic reactions, 20% of those with normal arterial pressure and 6% of the subjects with arterial hypotonia developed motion sickness.

Tolerance of the vestibular analyzer after inception of 1 mg of scopolamine in those subject to motion sickness, with arterial hypotonia, and the defensive effect of scopolamine are much more weakly expressed than that in subjects having normal arterial pressure. Thus, symptoms of motion sickness developed after 1-15 otolithic tests in 47 of 57 subjects with arterial hypotonia, despite inception of 1 mg of scopolamine, after 16-20 otolithic tests in eight subjects, and only two subjects did not display the vegetative /166
symptoms of motion sickness after 20 otolithic tests. Vegetative symptoms after 20 otolithic tests were not observed in 21 of 43 subjects with normal arterial pressure, and after 16-20 otolithic tests in 22 subjects. Consequently, when the tolerance of the vestibular analyzer is identical, 1 mg of scopolamine defends subjects with decreased arterial pressure much worse than it does those having normal arterial pressure.

On the basis of the investigations conducted, we can make the following conclusions.

1. There is an interrelationship between the functional tolerance of the vestibular analyzer and arterial pressure during motion sickness.

Arterial hypotonia is a factor predisposed to motion sickness:

a) arterial hypotonia is observed in 57% of subjects susceptible to motion sickness, and in 2% of those resistant to motion sickness;

b) upon stimulation of the vestibular analyzer, a decrease in arterial pressure was noted in 54% of those subject to motion sickness, and in 4% of those resistant to motion sickness;

c) comparison of the reactivity of the vestibular analyzer with the level of arterial pressure during motion sickness indicated that reactivity of the vestibular analyzer is much higher in those subjects with arterial hypotonia than in those resistant to motion sickness;

d) the defensive effect of scopolamine (1 mg) against motion sickness in subjects with arterial hypotonia is less expressed than in those with normal arterial pressure.

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ON THE ROLE OF THE ADAPTATION FUNCTION OF SYMPATHETIC INNERVATION IN PREVENTION OF MOTION SICKNESS

V. P. Fomina-Kosolapova

ABSTRACT. Testing the effect on the excitability of the vestibular apparatus of a rabbit using sympatholytic (sympatholytin, piperoxane and pyridoxiphene), sympathomimetic (adrenaline and ephedrine) substances was carried out. Sympathomimetics caused a decrease in the number of nystagmic pulses during rotation and a reduction in post-rotational nystagmus. The sympatholytics, except for piperoxane, have the opposite effect. The article contains one table, 15 references and three illustrations.

That the vestibular apparatus affects the vegetative nervous system is not disputed by anyone at present. It has been convincingly shown clinically and experimentally that stimulation of the vestibular analyzer causes changes in the state of the cardiovascular system, respiration, the smooth muscles of the stomach and intestines, in perspiration and salivation, causes variations in body temperature, etc. [2-5, 9-12].

With respect to the effect of the vegetative nervous system on the vestibular apparatus, much still remains disputable and unknown. Available literature sources on this problem often contain inconsistent information [8, 9].

Ye. B. Babskiy and V. Ye. Vinogradov [1] establish a decrease in the excitability of the vestibular analyzer on the operated side in six patients who for different reasons underwent cervical sympathectomy on one side. The clinical observations of K. L. Khilov [11] also indicate variation in the sensitivity of the vestibular analyzer as a result of a wound in the superior cervical sympathetic ganglion.

A study was conducted of the effect on the vestibular reflexes of various pharmacological substances which vary the sensitivity of the sympathetic and parasympathetic fibers. Adrenaline decreased the excitability of the vestibular analyzer. G. L. Komendantov indicates that administration of adrenaline first leads to inhibition, and then to an increase in vestibular reflexes. Acetylcholin, according to his data, stimulates the function of the vestibular apparatus. N. N. Lozanov, I. P. Baychenko and A. N. Krestovnikov [6, 8] tested the effect of atropine and picrotoxin on the vestibular apparatus (picrotoxin inhibits the sympathetic nervous system and atropine inhibits the parasympathetic system). The results of their investigations indicate that inhibition of the sympathetic and parasympathetic nervous systems has no /168 apparent effect on vestibular reflexes.

For this a test was conducted of the effect of various pharmacological substances, which change the tonus of the sympathetic nervous system, on the excitability of the vestibular apparatus. In particular, sympatholytin, pyridoxiphene, and piperoxane were tested. All these substances have the property of blocking the adreno-reactive systems, and also of weakening or eliminating the effect of noradrenaline and adrenaline administered from without on the organism. Adrenaline and ephedrine of the sympathomimetics were tested. The experimental studies were carried out on rabbits. The method of investigation was as follows: animal (nystagmus) and vegetative (respiration) reflexes were recorded in the animals during rotation on a chair before and after administration of the above-enumerated pharmacological substances. Nystagmus was recorded with the help of an electronystagmograph according to A. Ye. Kurashvili [7], and respiration was recorded with the help of a carbon monitor. Recording was made on an MPO-2 oscillograph. Besides respiration and nystagmus, the number of revolutions of the chair and a time marker were also recorded.

A total of 71 studies was carried out on 12 rabbits, in which adrenaline was tested 22 times, ephedrine 8 times, sympatholytin 22 times, pyridoxiphene 7 times and piperoxane 12 times.

Upon analysis of the nystagmograms obtained, the number of nystagmic impulses and the duration of post-rotational nystagmus were determined, and upon analysis of the respiration curves, the frequency of respiration before rotation (at rest), during rotation and after introduction of the pharmacological substances was determined. The results of the investigations are presented in the table.

The data of the table indicate that the sympathomimetics (adrenaline and ephedrine) caused a decrease in the number of nystagmic impulses during rotation and a recession of post-rotational nystagmus (Figure 1). The sympatholytics increased the number of nystagmic impulses, and intensified rotational and post-rotational nystagmus, which apparently may be regarded as the appearance of increased sensitivity of the vestibular analyzer (Figures 2 and 3). An exception was only piperoxane, which in just two of twelve studies caused intensification, and in ten caused a recession in nystagmic reaction. It is possible that this preparation has, in addition to its adreno-blocking property, the capability of selectively and uniquely affecting the tonus of the vestibular analyzer. The small number of studies which we carried out does not permit us to favor this preparation categorically, but, apparently, /169
the characteristic of piperoxane to affect the tonus of the vestibular analyzer in an inhibiting manner should be studied.

The data of the table also indicate that an increase in respiration rate was observed in rabbits during rotation. At rest, an average of 80 to 90 respirations per minute was observed. During rotation, the number of respirations per minute increased on the average from 117 to 140, respiration having become saccadic. After administration of the sympathomimetics, respiration rate during rotation increased less, on the average to 90-100 per

minute. After introduction of the sympatholytics, respiration rate during rotation was on the average the same as before administration of the medicinals.

VARIATIONS IN NYSTAGMUS AND RESPIRATION UNDER THE EFFECT OF SYMPATHOMIMETICS AND SYMPATHOLYTICS (AVERAGE VALUES)

Medicinal substance	Dosage, mg/kg	Nystagmus				Respiration			
		Before admin		After admin		Before admin		After admin	
		Number of impulses	Duration of post-rotational	Number of impulses	Duration of post-rotational	At rest	During rotation	At rest	During rotation
Adrenaline hydrochloride (0. 1% solution)	1,0	60	12,6	54	10	90	132	75	90
Ephedrine Hydrochloride (5% solution)	1,0	64	8,4	61	7,6	81	117	81	100
Symapatholytin	10	48	6,7	59	10,2	80	140	72	130
Piperoxane	3	51	6,5	41	5	84	120	85	100
Pyridoxiphene	30	59	5,3	61	7,4	85	140	88	150

Tr. Note: Commas indicate decimal points.

Results of the studies permit us to state that definition of vestibular reactions depends on the tonus of the sympathetic nervous system. Upon introduction of sympatholytics, an intensification of vestibular reactions was observed, and vestibular reactions were less defined upon introduction of sympathomimetics. It is known that stimulation of the parasympathetic section of the vegetative nervous system occurs during stimulation of the labyrinth. In such a state, adrenaline or some other sympathomimetic administered from without inhibits excessive stimulation, adapts it for normal perception and renders stimulation adequate. When the effect of the sympathicus is excluded (for example, when it is blocked with drugs or eliminated by cervical sympathectomy), reactions of the parasympathetic nervous system will not be adaptive, which we also observed in our studies.

Consequently, upon administration of sympathomimetic drugs into the /173
organism, the tonus of the sympathetic nervous system is enhanced, and at the same time its adaptational role is intensified. The results of our studies permit us to recommend sympathomimetic substances to prevent motion sickness.

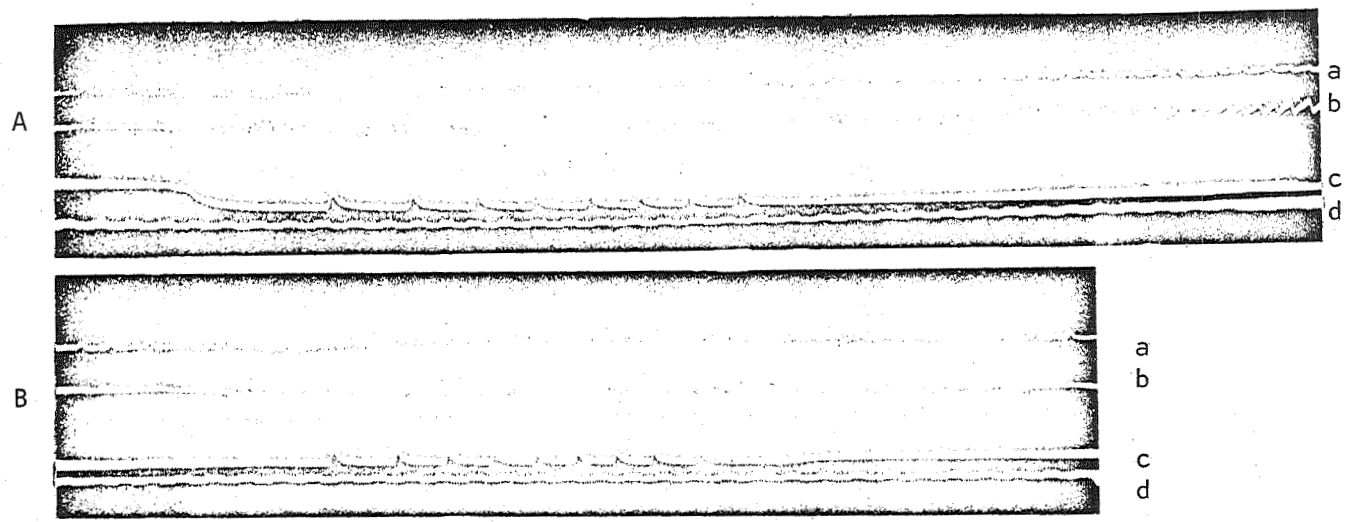

Figure 1. Nystagmus in Rabbits During Rotation Before (A) and After (B) Administration of Adrenaline. a, Respiration; b, Nystagmus; c, Revolutions of the chair; d, Time marker

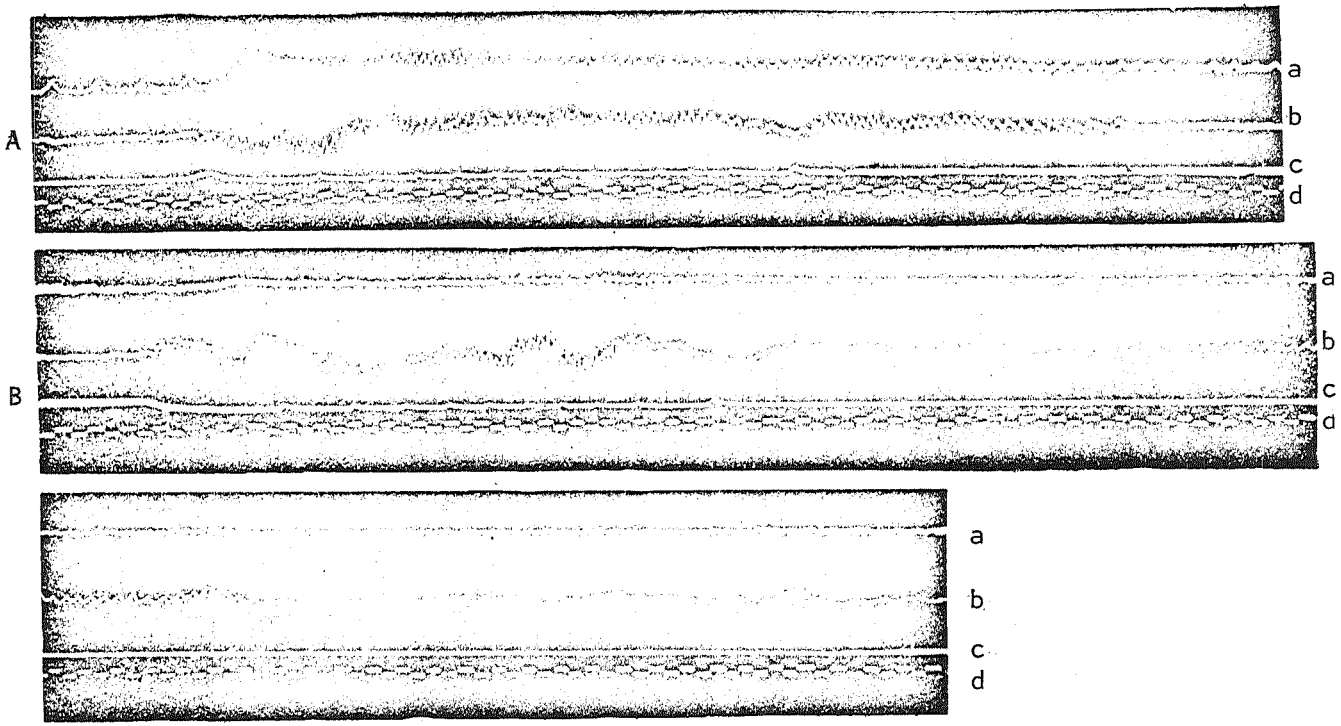

Figure 2. Nystagmus in a Rabbit During Rotation Before (A) and After (B) Administration of a Sympatholytic. a, b, c and d, Notations are the same as in Figure 1.

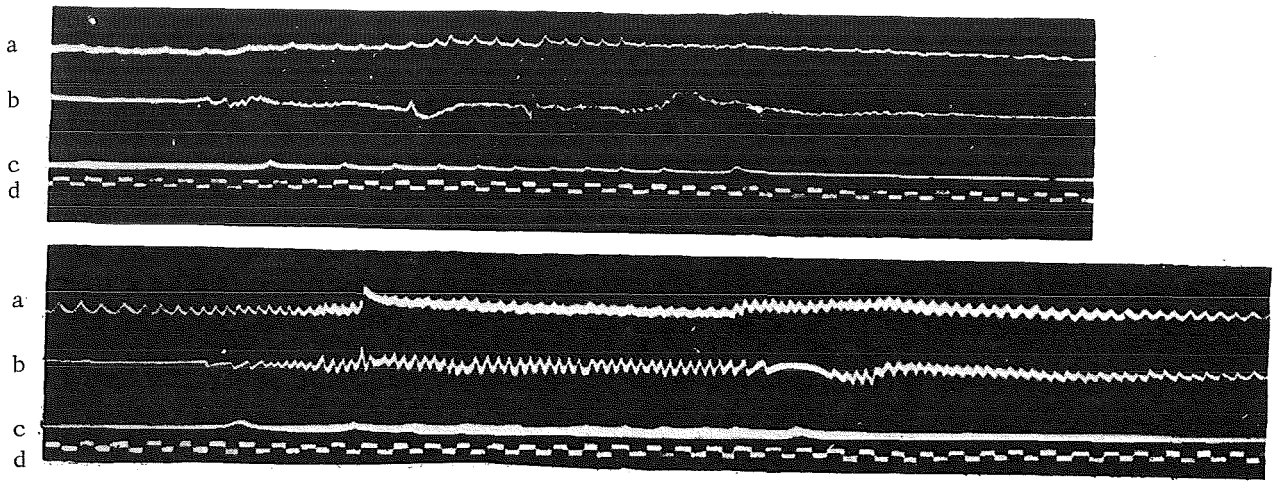

Figure 3. Nystagmus in a Rabbit During Rotation Before (A) and After (B) Administration of Pyridoxiphene. a, b, c and d, Notations are the same as in Figure 1.

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VESTIBULAR TRAINING OF TEST PILOTS BY PASSIVE METHODS

N. I. Popov, F. A. Solodovnik and G. F. Khlebnikov

ABSTRACT. The problem of conditioning men to rotation with transfer to an unstable platform, rocking, rotation with active tilting of the head and body, balancing, and to complex vestibular and visual stimuli is considered. An increased tolerance of man to the enumerated effects was achieved in all cases after conditioning.

A number of unpleasant factors related to motion of the ship (G-load, weightlessness, vibration, noises, etc.) under conditions of space flight act on the organism of the astronaut. In a state of weightlessness, the function of the analyzers, in particular of the vestibular analyzer, is disrupted [2-9]. There is a change in the reciprocal interrelationships between the otolithic and cupulo-endolymphatic systems, and on this background various accelerations, in particular Coriolis accelerations, have negative effects on an organism [1-3, 10]. /174

Despite their insignificant magnitude, the accelerations may have a cumulative effect and gradually lead to development of a definite pattern of motion sickness.

One of the warning indicators in development of motion sickness during space flight is increased sensitivity of the vestibular analyzer to adequate stimuli under ground conditions with the help of special training. We carried out active and passive vestibular training of test pilots.

Active training was basic and was conducted according to a system of physical training with the use of special apparatus and stands. We shall not undertake to describe them. Passive vestibular training supplemented active training -- we set ourselves the task of affecting the otolithic and cupulo-endolymphatic systems of the labyrinth, and also certain other afferent systems which control spatial orientation.

The following methods were employed:

1) rotation in a special chair with transition to an unstable support;
2) rocking in a four-beam Khilov rocking device;
3) training in a rolling device with optokinetic stimulation;
4) rotation in a chair with simultaneous sequential inclinations and straightening of the body and head to assigned limits;
5) balancing in a chair with an unstable support.

Prior to the beginning of the training cycle, the functional state of the vestibular analyzer was examined. The data obtained made it possible to decide in each individual case which stimuli cause greatest stimulation of the vestibular analyzer. Training was planned and carried out with regard to these characteristics. In order to evaluate the results of training after termination of the cycle, repeated studies of the functional state of the vestibular analyzer were made.

Studies and training stability of the vestibular analyzer against the effect of angular accelerations were carried out in a rotating chair with transition to an unstable support. The extent and duration of the vestibulo-somatic reaction to measured stimulation were determined during recovery of equilibrium. The data obtained are presented in Table 1.

TABLE 1. AVERAGE TIME OF RECOVERY OF EQUILIBRIUM TO MEASURED STIMULATION (IN % OF INITIAL)

Test subject	Before training	After training
A	180	60
B	420	60
C	300	30
D	300	80
E	480	60
F	220	110
G	150	110
H	200	60
I	240	120

Stability of the vestibular analyzer against Coriolis acceleration apparently depended on a number of factors (fatigue, lack of sleep, an over- /175
full stomach, etc.), and also on the state of the central nervous system (poor frame of mind, uncertainty, etc.). Individual characteristics of the organism and physical capabilities to adaptation played a definite role. Various unfavorable factors had an ever diminishing effect in proportion to the increase in stability.

It is obvious from the table that the period of equilibrium recovery after conditioning was reduced in all subjects, and consequently, vestibulo-somatic reactions to the same effect were reduced.

As a result of conditioning conducted on a four-beam Khilov rocking device, an absence of definite vestibulo-vegetative reactions in all subjects was revealed, which may be explained by the high stability of the vestibular apparatus to rectilinear accelerations.

Stability of the vestibular analyzer against Coriolis acceleration was evaluated according to the time of development of vestibulo-vegetative reactions (variation in pulse rate, perspiration, paleness of the face, nausea, etc.). The extent of the indicated effect varied as a function of the status of the vestibular apparatus and its stability at a given moment. Conditioning was stopped when vestibulo-vegetative reactions developed, or when the well-being of the subjects deteriorated. Definite vestibulo-vegetative reactions in proportion to conditioning developed with significantly greater effects, and subsequently were not revealed by the methods of study used. It should be noted that conditioning did not begin in all subjects at the same point in time. In some cases, definite vestibulo-vegetative reactions developed with each conditioning period only in a greater effect, and in other cases an increase in stability at the beginning of the conditioning cycle was replaced by a brief decrease. Conditioning of subjects of the latter group began more slowly, and required a greater number of conditioning periods.

During the course of the studies and conditioning to complex stimuli in /176
an optokinetic drum and in a chair with an unstable support, the results were evaluated according to the presence of illusory sensation, their duration, and the number of definite oscillations of the body with respect to the center of gravity, controlled with the help of a stabilograph. The results of these studies are presented in Table 2.

TABLE 2. DEVELOPMENT OF ILLUSIONS BEFORE AND AFTER VESTIBULAR CONDITIONING

Test subjects	Before condition		After condition		Test Subjects	Before condition		After condition	
	Presence of illusions	No. of oscillations	Presence of illusions	No. of oscillations		Presence of illusions	No. of oscillations	Presence of illusions	No of oscillations
A	+	2	—	0	F	+	0	—	0
B	+	35	—	7	G	+	48	—	0
C	—	4	—	0	H	—	0	—	0
D	+	23	+	0	I	+	85	—	0
E	—	22	—	0					

As can be seen from the data of the table, illusions of rotation before conditioning developed in only six of eight subjects, and after conditioning in only one subject.

The range of definite oscillations of the body during optokinetic stimulation before conditioning was within limits from 0 to 85 per minute. Similar oscillations were not observed in only two subjects. After

conditioning, the oscillating movements diminished sharply in one subject and were absent in eight subjects.

Disappearance of illusions of rotation and significant oscillations of the body during complex stimulation on afferent systems which control spatial orientation indicates the possibility of adapting man to unusual conditions of existence -- it is possible to maintain one's body in a given position when afferentation in the system of analyzers controlling spatial orientation is varied.

It should be noted in conclusion that conditioning carried out by the indicated methods increases stability of the vestibular analyzer against the effect of some unfavorable factors of space flight.

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ON THE NONSPECIFICITY OF VESTIBULAR CONDITIONING

B. B. Bokhov

ABSTRACT. Results presented are obtained in rabbits, which indicate the nonspecific nature of acclimatization to vestibular stimulation. After the animals had been conditioned to a single stimulus, a weakening was observed in the reaction of nystagmus in response to stimuli which were greater or less in value than the conditioning stimulus.

The problem of nonspecific increase in the adaptability of an organism to /177 a number of unfavorable factors by increasing its stability to one of them attracts the attention of investigators of various branches of medicine. This phenomenon takes on special significance for seamen, pilots, and to a greater extent astronauts, when true conditions cannot be totally reproduced during training. In practice, programming of training of indicated contingent is accomplished by taking into account its nonspecific nature. However, a comparatively small number of studies has been devoted to the theoretical basis of a system of measures to increase the stability of man against the effect of angular and rectilinear accelerations. In particular, selection of the type, extent, overall number and duration of individual vestibular stimuli during training is not always sufficiently well founded.

Moreover, experimental observations indicate that post-rotational nystagmus may again appear after its total elimination, if rotation velocity is increased [2, 3, 18]. This information is verified by data from practice, when personnel stable against stimulation under ground study and training develop motion sickness due to the effect of stimuli acting under real conditions [9, 13], and also by data on the development of unpleasant sensations in experienced pilots while conducting standard rotational tests [1, 7, 14].

The purpose of this paper was to study the development of acclimatization to superthreshold stimuli of the vestibular apparatus, and to establish its specificity.

The experiments were conducted on rabbits. The VU-2 electrorotating device was used as a stimulus [6]. Recording of response reactions was /178 accomplished on a "Petit" electroencephalograph.

In the first series of experiments the effect of repeated rotation at a velocity of 120 deg/sec on duration of nystagmus, developing after rotation of a rabbit at a velocity of 10, 20, 30, 60, 70, 90, 120, 150 and 180 deg/sec, was studied. A stop-stimulus of 120 deg/sec was selected as one of the

maximum stimuli which still elicit a gradual reaction of the vestibular apparatus [4, 17].

Conditioning of the nine rabbits was preceded by two test recordings of the reactivity curve for nystagmus and simultaneous recording of pulse rate for all nine stimuli. During the succeeding six to seven days, stable reduction in postnystagmus to stop-stimulus of 120 deg/sec was achieved. After termination of conditioning, two reactivity curves were again recorded.

Only four reactivity curves, every two at an interval of five to seven days, were recorded in the control animals. The control group (11 rabbits) was selected such that the duration of post-rotational reaction in them during the first rotation would correspond to similar figures of experimental animals. This permitted us to compare the relative rate of eliminating reaction during the course of four studies in both groups.

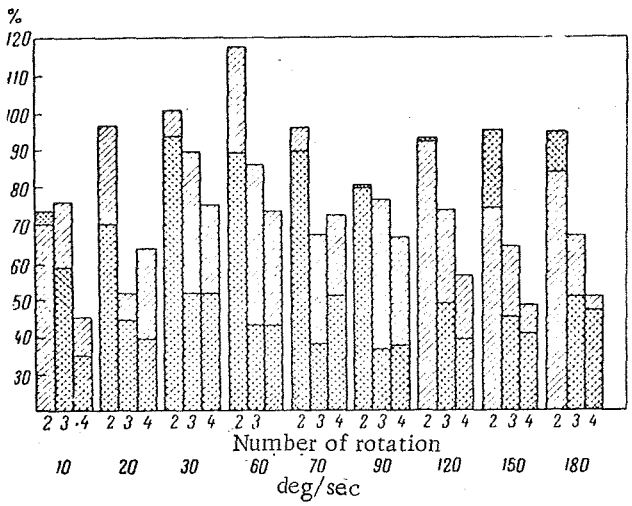

Figure 1. Reduction of Nystagmic Reaction in Experimental and Control Groups After Quadruple Repetition of Series Rotation. Duration of nystagmus during first rotation was assumed to be 100%.

Figure 1 shows elimination of post-rotational nystagmus. The difficulty of evaluating the experimental data obtained was that even double or triple application of vestibular stimulus causes a reduction in duration of postnystagmus [5, 8, 11]. Actually, judging from the data obtained, there is an obvious reduction of nystagmic reaction to all stimuli in both experimental and control animals. However, the course of the curves of nystagmic reduction is not identical in groups.

First, the steepness of the reduction curves (the rate of nystagmic reduction) from the second to the third study is somewhat greater in the experimental group; secondly, the duration of nystagmus between the third and fourth studies continues unchanged in the control group compared to the experimental group. Both comments refer to the reduction curves to stimuli within the range 30-180 deg/sec. Consequently, repeated rotation at a velocity of 120 deg/sec alters reaction to stimuli of both greater and lesser intensity. According to the results obtained, regression curves were plotted and their reliability evaluated[1].

[1] Statistical processing of the experimental data was carried out by V. S. Novoselov on the Ural-2 computer.

A second series of experiments was carried out in order to refine the data obtained. In these experiments, only two stimuli of 120 and 60 deg/sec, which are maximum for the cupulometric range, were employed. The experiment /179 consisted of sixfold rotation of the animals at a lesser velocity, and within an hour a sixfold rotation at a higher velocity (first group). The order of rotation was reversed in the second subgroup. Duration of post-rotational nystagmus, and also pulse and respiration rates for 20 sec were calculated. After termination of the experiments, a comparison was made of the somatic and vegetative reactions to the same stimulus in the various subgroups.

It was discovered during comparison of the data of nystagmic reaction frequency in response to a stop-stimulus of 60 deg/sec, that the overall tendency in variation of this indicator was identical in both groups (Figure 2). The greatest frequency of nystagmus is observed during the first seconds after stopping, then there is a gradual decrease in frequency. However, the representative feature of nystagmic variation in the second group is a sharper drop in frequency. Mathematical processing proved its total statistical reliability. If rotation at a velocity of 120 deg/sec was preceded by repeated rotation at a velocity of 60 deg/sec, the frequency of nystagmus in response to a stop-stimulus of 120 deg/sec was reduced. However, no statistically reliable difference in the subgroups was detected. In a given case, one may assume that there are not only effects of intense stimuli on reaction to lesser stimuli, but also the reverse effect, which is more weakly expressed.

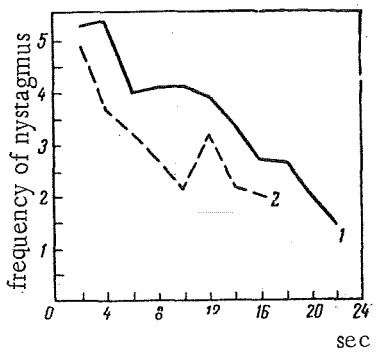

Figure 2. Dynamics of Variation in Nystagmic Frequency (Number of Nystagmic Impulses During Each 2 sec of Reaction) After Stop-Stimulus of 60 deg/sec in Various Subgroups (1, 2)

Turning to vegetative indicators, one should /180 note that respiratory reaction to variable stimuli consisted of a latency period, respiratory pause, and a subsequent increase in respiration rate. Length of the latency period (0.19 sec) and respiratory pause (0.6-0.9 sec) to stop-stimuli of 60 and 120 deg/sec hardly differed from each other in the different groups.

With regard to an increase in respiration rate, this component of the reaction diminished noticeably after sixfold stimulation by a stop-stimulus of 60 deg/sec in both the first and second subgroups.

Variation in heartbeat in response to a stop-stimulus of 120 deg/sec included a sharp increase in the R-R interval (retardation of heartbeat) and gradual return of the index to the norm during the first second after stimulation.

The pulse reaction described above to a stimulus of 120 deg/sec became more distinct in both subgroups during the sixth rotation than during the first rotation.

However, a valid difference between data of the first and sixth rotation was established only in the second subgroup (rotation without preliminary conditioning).

The results of the investigations conducted may be generalized in the following manner.

1. Conditioning to angular acceleration may be generalized.

2. Acclimatization is transferred to reactions which develop in response to stimuli exceeding and inferior in value to the conditioning stimulus.

We did not manage to obtain data with respect to translation of the effect of conditioning to vegetative reactions.

Reports of other authors, who studied transfer of acclimatization from intense to weak stimuli and vice versa, agree with available data on nystagmus [16]. However, it should be emphasized that the concern should apparently be /181 directed toward transfer of acclimatization only to a limited number of stimuli located within a specific range. There is no doubt that we are concerned here with a general physiological phenomenon which has been detected in the most diverse functional systems during conditioning and elimination of various reactions [10, 12].

Introduction of the concept of limited generalization of acclimatization explains the seeming contradictions between those observations which are in favor of the specificity of acclimatization and those against it. The deciding factor in these cases is the extent of agreement of spatial and time characteristics of usual and "unusual" stimuli acting for the first time.

Important conclusions in the practical sense ensue from the concept of limited selectivity of acclimatization to a vestibular stimulus -- first, optimum stimuli must be found which have a more clearly expressed property to transfer or generalization of acclimatization; and secondly, conditioning programs must be planned with regard to the magnitude and type of stimuli which will act on man under real conditions.

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THE EFFECT OF MOTION SICKNESS ON THE FUNCTIONAL STATUS OF THE HYPOPHYSIS-CORTEX SYSTEM OF THE ADRENAL GLANDS

N. I. Kastrov and O. A. Nakapkin

ABSTRACT. The effect of stimulating the vestibular apparatus on the content of regular elements of the blood was studied. It was established that rocking healthy subjects in a Khilov swing for 15 minutes leads to a distinct reduction in the eosinophiles in the blood within 4 hours.

Establishing the genesis of motion sickness is important in the study of the effect of various types of accelerations on the human organism. /182

The research of V. I. Voyachek and K. L. Khilov [2, 8] has shown that the initial link in the chain reaction of motion sickness is stimulation of the otolithic apparatus. The extent of its sensitivity may be judged by the definition of vegetative reactions in response to vestibular monotonic stimulations and the time of their onset. The process of motion sickness may be presented schematically in this manner -- stimulation of the vestibular apparatus stimulates specific regions of the cortex and subcortical vegetative centers which also determine the development of vegetative reactions. One of the leading vegetative centers is the inion, which is connected to the hypophysis through the hypothalamic region.

According to the theory of Sel'ye and other authors, the hypophysis and the cortex of the adrenal glands determine the overall adaptational reaction of an organism to a stimulus -- the stressor --unusual in intensity or quality. According to Sel'ye's theory, which we used in conjunction with the papers of I. P. Pavlov, I. M. Sechenov, A. A. Orbeli, A. D. Speranskiy and other Soviet scientists, a complex neurohumoral reaction is observed in an organism subjected to a stress effect. An extreme stimulus, by stimulating the central nervous system, causes release of adrenaline to its sympathetic region. This together with the effect of the hypothalamic region in turn stimulates production by the hypophysis of so-called stressor hormones: somatotropic (STH) and adrenocorticotropic (ACTH). With quantitative predominance of ACTH, there is intensified release of glucocorticoids, in particular of cortisone, by the adrenal glands, which causes various types of changes in the organism, including eosinopenia [1, 4, 7, 11]. Such a stressor may be manifested by the effect of acceleration on the human organism.

On the basis of this concept, we hypothesized a specific role of the hypothalamus-hypophysis-cortex system of the adrenal glandsin the genesis

of motion sickness. We selected calculation of the number of eosinophiles in peripheral blood as a test to confirm this hypothesis.

Motion sickness in test subjects was accomplished on a four-beam Khilov swing within 15 min. The following reactions to motion sickness were recorded: subjective sensations, tint of facial skin, and variation in pulse rate. Calculation of the leucocytic formula, total number of leucocytes, and the absolute number of eosinophiles was accomplished before and within 4 hr after motion sickness (on an empty stomach) at 8-9 a.m. and at 12-1 p.m.). The absolute number of eosinophiles was calculated in a Goryayev counter. Hinkelman liquid dye was used to dilute the blood. Eosinopenic reaction to motion sickness was considered positive upon a 50-percent or greater decrease in the number of eosinophiles. /183

We studied a total of 113 subjects, of which 25 served as control, 41 received ACTH (the Thorn test), and 47 were subjected to motion sickness.

Results of the study showed that within 4 hr after laboratory inducement of motion sickness there was a significant reduction in the absolute number of eosinophiles ($x = 106$ and 1 cm^3 of blood) compared to the initial level ($x = 189$). The indicated differences are statistically reliable, because $p = 0.002$. Similar data are observed within 4 hr after intramuscular administration of 25 units of ACTH. Moreover, the absolute number of eosinophiles is 142 and 240, respectively. The difference in average values is significant ($p < 0.002$). The control study indicates that during the course of 4 hr (in the state of rest), from 9 a.m. to 1 p.m., there is some reduction in the number of eosinophiles of the peripheral blood (from 160 to 119), but these differences are not statistically reliable.

Results of the studies are presented in Table 1.

Thus, there is distinct eosinopenia similar to that noted after intramuscular introduction of 25 units of ACTH in response to vestibular motion sickness.

It is important to emphasize that the extent of decrease in the absolute number of eosinophiles in the peripheral blood increases in proportion to the increase in intensity of motion sickness symptoms. Test subjects subjected to motion sickness were divided into two groups according to the degree of severity of otolithic reaction (according to V. I. Voyachek and K. L. Khilov): 19 subjects with vegetative reaction of 0-I degree, and 28 subjects with vegetative reaction of II-III degree. /184

It was discovered during study of the eosinopenic reaction in these two groups of test subjects after motion sickness that a very significant decrease in the absolute number of eosinophiles ($\bar{x} = 87$) compared to the initial level ($\bar{x} = 210$, $p = 0.001$) is noted in subjects with vegetative reaction of II-III degree. A reduction in the absolute number of eosinophiles (from 159 to 134) was also observed in a subgroup with a less severe reaction to motion

sickness (vegetative reaction of 0-I degree), but this decrease was not reliable (Table 2).

TABLE 1. EOSINOPENIC REACTION IN RESPONSE TO VESTIBULAR MOTION SICKNESS IN CONTRAST TO THE THORN TEST

Statistical index	Control		ACTH		Motion sickness	
	9 a.m.	1 p.m.	9 a.m.	1 p.m.	9 a.m.	1 p.m.
n	25		41		47	
$\bar{x}$	160	119	240	142	189	106
$\pm\sigma$	102	102	142	95	135	87,7
$\pm\sigma/\bar{x}$	20	20	22	14	19,8	12,9
t	1,6		3,3		3,5	
p	0,1		0,002		0,002	

Tr. Note: Commas indicate decimal points.

TABLE 2. VARIATION IN ABSOLUTE NUMBER OF EOSINOPHILES AS A FUNCTION OF DEGREE OF MOTION SICKNESS

Atatictical index	Group subject to motion sickness		Group not subject to motion sickness	
	9 a.m.	1 p.m.	9 a.m.	1 p.m.
n	28		19	
$\bar{x}$	210	87	159	134
$\pm\sigma$	118	81	97,9	99,3
$\pm\sigma/\bar{x}$	22	15	22,7	23,1
t	4,6		0,78	
p	0,001		0,5	

Tr. Note: Commas indicate decimal points.

Thus, analysis of the data obtained permits us to conclude that subjects with a severe degree of motion sickness indicated sharper "stressor eosinopenia" compared to that after administration of ACTH. An insignificant eosinopenic reaction developed in subjects not subjected to motion sickness. Our data agree with the results of experimental studies of MacLanghlin and Gray [10], who observed an increase in the level of corticosteriods in the blood after rotation of animals.

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MOTION SICKNESS IN DOGS BEFORE AND AFTER INTRAVENOUS ADMINISTRATION OF SODIUM HYDROCARBONATE

A. G. Kuznetsov and V. N. Barnatskiy

ABSTRACT. The effectiveness of intravenous administration of hydrocarbonate ad a prophylactic substance during motion sickness (vertical linear accelerations) was studied in three dogs. A two-time administration of 10 mℓ of a 5% solution at two-week intervals had a positive effect, which was expressed in a decrease in the frequency and severity of motion sickness symptoms.

Presently effective substances which reduce vegetative disorders during motion sickness are cholinolytic and antihistamine preparations in various combinations [3]. However, these preparations together with their positive effect have a very significant deficiency -- in dosages used, they cause inhibition in various branches of the central nervous system. In 1949, Hasegawa proposed a new method of counteracting motion sickness -- intravenous administration of a solution of sodium hydrocarbonate. Unfortunately, Hasegawa's method has still not achieved general recognition. Without assigning ourselves the task of explaining the mechanism of the effect of soda solutions upon intravenous administration, we decided to verify the effectiveness of the given method in our studies.

The experiments were run on three dogs. In the dog, arbitrarily named D-9, the electrical activity of the muscular layer and nerve stems of the stomach was studied (on an EGS-3 electrogastrograph), and in dog D-11 the electrical activity of the pyloric sphincter and nerve stem in the small bend of the stomach was studied (with the help of a UBP-1 amplifier and MPO-2 oscillograph). Moreover, salivation, nausea, vomiting and behavior of the animals were also recorded (only the latter reactions in dog D-14)[1]. The dogs /186 were subjected to rocking in a vertical plane on a specially designed stand for 20 min; accelerations which developed during this period were ±0.3.

The animals (weighing 10-11 kg) were administered 10 mℓ each of a 5% solution of sodium bicarbonate. The preparation was again administered within two weeks. The studies were begun within three days after administration of the preparation. Severe disorders, which were manifested in repeated paroxysms of nausea and vomiting, were observed upon rocking of dog D-11 before administration of the soda solution. Motor inhibition was noted during rocking and during the aftereffect. Within three days after administration, fewer attacks of nausea and vomiting were observed in it, although rocking

[1] We understand the state of nausea to be salivation and single regurgitation accompanied by motor unrest.

was continued five minutes longer than during the control. Within two weeks, a second administration of 10 mℓ of a 5% sodium solution was accomplished, after which the dog hardly responded to motion sickness. For three and four months after first administration of the soda, the animal was again subjected to rocking: the dog stood quietly, and did not display any motor unrest, agitation, nausea and vomiting.

Weakly defined vegetative disorders, which manifested themselves in single attack of nausea and motor inhibition for several minutes during the aftereffect, were noted during rocking of dog D-9 before administration of the soda solutions. Motion sickness symptoms were not noted after the first administration of soda; the effect continued for two months.

Severe vegetative disorders, which manifested themselves in repeated attacks of nausea and vomiting, were observed during rocking of dog D-14 before administration of the soda. After the second administration of soda, vegetative disorders during rocking were insignificant, and were not noted after two weeks. The positive effect of administering soda continued for a year.

Motor activity of the stomach of dog D-9. There was inhibition of the motor activity of the stomach, which was maintained during the aftereffect of the stimulus for several minutes, began during rocking of the dog during the control experiment. The same pattern was noted three days after administration of the soda. On the fourth day during rocking, a sharp intensification of motor activity began, which was replaced within several minutes by inhibition. From the sixth day after administration of the soda, motor activity of the stomach was inhibited only during rocking.

Motor activity of the pyloric sphincter of dog D-11. Periodic reductions /187
and weakening of the pylorus were noted in a hungry animal without rocking in control experiments. Rocking caused intensification and increase in the rate of reductions of pylorus, which is also maintained during the aftereffect for 10-15 min, i.e., a pattern was observed counter to the activity of stomach musculature. Intensification of pylorus reductions was observed during rocking after administration of soda solutions; during the aftereffect its reduction displayed the same characteristics as before rocking.

Before administration of soda, the amplitude and frequency of bioelectric potential fluctuations in the nerve cords increased during rocking, and a significant reduction in activity for several minutes was observed during the aftereffect. After administration of soda, the amplitude and frequency of bioelectric potential fluctuations in the nerve cords increased insignificantly during rocking; this increase in electrical activity according to the indicated parameters was maintained for several minutes after the stand was stopped. An increase or decrease in amplitude and frequency of biopotential oscillations in the nerve cords and muscular layer of the stomach occurred at the same time during the experiment. No correlations were established between the electrical activity of the pyloric sphincter and nerve cords of the stomach investigated in our experiments.

Analyzing the data obtained, we concluded that dogs endure motion sickness much more easily after administration of solutions of sodium hydrocarbonate.

The positive effect of Hasegawa was at first explained by dissolving of the otoliths, as a result of which much less information is supplied to the central nervous system from the otolithic apparatus during rocking than takes place before administration of the soda. This author has recently abandoned this position, and has introduced the concept of the antiangiospastic effect of sodium hydrocarbonate. Criticizing the views of Hasegawa, Ye. A. Vinnikov [2] indicated that the otoliths are not dissolved upon administration of the soda. However, this is still not proof that the otolithic mass is not altered after intravenous administrations of soda solutions. In order to answer this question, experiments are needed on quantitative analysis of the calcareous otoliths. It is noted in the papers of Bladergren [1] and U. Neuman [4] that upon intravenous administration of sodium bicarbonate solutions, changes are observed in the relationship of the bicarbonate and phosphate buffers, in particular in the increase of Na_2HPO_4 in the blood, which leads to mobilization of calcium ions. They also indicate that the strength of the bond with calcium is different in different tissues of the organism.

The foregoing permits us to suggest that intravenous administration of /188
sodium bicarbonate contributes to washing out calcium ions from the otoliths while maintaining calcium stability in the bony tissue. As a result of this, the otolithic mass is diminished, which may apparently also be the reason for the decrease in the impulse from the otoliths when an organism is subjected to accelerations.

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DEVELOPMENT OF NEW METHODS OF INVESTIGATING THE VESTIBULAR FUNCTION

THE ADI TEST AND ITS SIGNIFICANCE FOR FUNCTIONAL INVESTIGATION AND CONDITIONING OF THE VESTIBULAR ANALYZER

A. Kh. Min'kovskiy

ABSTRACT. The combination of quantitative and qualitative characteristics of vestibulo-somatic, vegetative and sensory reactions, observed as a result of using measured angular accelerations, decelerations and tilting (the ADI test) in various planes, provides broad possibilities for correct analysis of the functional state of the vestibular analyzer.

Since Egmond, Groin and Jongkees proposed using measured positive and negative angular accelerations ("cupulometry") to investigate the function of the semicircular canals, there has been increased interest in this test. /189

Introduction of measured accelerations and decelerations in the practice of labyrinthology undoubtedly contributed to expansion of knowledge about the function of the vestibular analyzer; however, so-called cupulometry cannot give a total concept about the state of this function, since the state not only of the semicircular canals, but also of the otolithic apparatus must be taken into account.

In 1958, we proposed a method of investigating the function of the vestibular analyzer by applying accelerations, decelerations and inclinations (in the frontal and sagittal planes) -- the ADI test. Due to inclining the chair, variation in the direction of gravitational acceleration develops in the test subject, which as we know is one of the adequate stimuli for the otolithic apparatus, inclinations in the sagittal plane (i.e. forward and backward) determining the predominant variation in the position of the utricular otoliths, and inclinations in the frontal plane (i.e. to the right and left) determine variation in the position of the saccular otoliths. This principle advanced by Quicks in the 1920's was applied by us in 1939 to study gait ("utricular" and "saccular" gait).

The combination of measured accelerations and decelerations with measured inclinations or without them is apparently the most complete method at present in studying the effect of various angular accelerations and Coriolis accelerations on the function of the vestibular analyzer.

In 1958, a chair was constructed according to our technical requirements, with the help of which we could achieve measured angular accelerations within /190 the range from 0.05 to 25.6 deg/sec^2 and angular velocities from 2 to 180 deg/sec, and also inclinations in the frontal and sagittal planes at a rate of approximately 4 deg/sec.

The use of only inclinations of the chair, or only of measured rotations, or of combinations of them (i.e. rotations and inclinations simultaneously) makes it possible to study both the separate and total effect of these stimuli on different parts of the vestibular analyzer. The effects of different variants of Coriolis accelerations may also be studied using this method.

The latest models of this type of chair differ significantly by a much wider range of possible angular accelerations, angular velocities and inclinations; improvements have also been made in the automatic control of the chair (G. S. Chernorutskiy and A. P. Sibrin).

During the period 1959-1965, numerous studies conducted with the help of the new type chair were carried out in the vestibulometric laboratory of the Department of Otorhinolaryngology at the Chelyabinsk Medical Institute. The method used to study the function of the otic labyrinth made it possible to resolve a number of problems important for theoretical and practical labyrinthology. In particular, values of threshold stimuli were refined for vestibulosensory reactions, it turning out that they may be very low: 0.05 deg/sec^2, in distinction from thresholds of nystagmic development: 6.4 deg/sec^2 [1, 3-16].

The distinctive and most important characteristic of the studies conducted in the new type chair is the possibility of quantitative and objective recording of vestibulo-somatic and vestibulo-vegetative reactions by means of sensors connected by contact rings and subsequently to the recording device. The presence of a rotating device may provide simultaneous recording of 20 different reactions.

In a number of papers which we completed during the period 1959-1965 jointly with Professor V. V. Skryabin [8-13], external respiration was studied during stimulation of the otolithic apparatus, which was achieved by inclining the chair in the frontal, and some time later in the sagittal plane (inclinations in each of these planes were carried out for two minutes). Respiration was recorded simultaneously with the tilting by the method of spirography using a metabolimeter with ink recording. As a result of studies made on 35 subjects (17 were healthy and 18 had disruptions in the function of the middle or inner ear), it developed that respiration rate did not vary, and depth of respiration increased noticeably, in the majority of healthy subjects when they were tilted in the sagittal plane. When they were tilted in the frontal plane, the respiration rate of almost half the subjects increased, and the depth of respiration in most subjects also increased. Variations in /191 respiration were expressed somewhat more weakly in well conditioned subjects (athletes). Thus, as a result of the studies conducted, we can hypothesize

about the presence of a functional interrelationship between the receptors of the otolithic apparatus and respiration.

Our colleague V. M. Bagmanov proposed, in 1964, a new method of investigating pulse during the effect of angular and Coriolis accelerations varying in value and direction -- micropulsography. Time markers in seconds were received on the pulsogram from the beginning of the effect of angular acceleration until its termination. Variations in pulse were calculated for each second of the effect of angular acceleration, and a "microphotograph" as it were of the pulse was obtained. An increase in pulse rate was prevalent during the effect of Coriolis acceleration, and a decrease in pulse rate was noted during the effect of negative angular accelerations. After the effect of Coriolis acceleration had ceased, a decrease in pulse rate was observed in most test subjects. If pulse rate before the beginning of the affect of angular accelerations was 100 beats per minute, which corresponded to the upper limit of the range of fluctuations in pulse rate, at the beginning of the effect of angular acceleration a decrease in pulse rate was observed, which was independent of the rate of angular acceleration. If pulse rate was 50-60 beats per minute (the lower limit of the range of fluctuations in pulse rate), then an increase in pulse rate was noted in all subjects at the beginning of angular acceleration.

Study of the extent of oxygen saturation of the arterial blood during variation in the functional state of the otolithic apparatus, i.e. during tilting in the frontal and sagittal planes, was carried out by us jointly with Professor V. V. Skryabin. A drop was observed in the oxygen content in the arterial blood, and was more persistent upon stimulation of the utriculus. The rate of blood flow during stimulation of the otolithic apparatus increased in most subjects, which apparently indicates the adapting nature of this reaction. A decrease in the rate of blood flow and a decrease in oxygen saturation of arterial blood below 84% was noted in subjects poorly resistant to sea rolling [8-12].

Variations were detected in the oxygenation and rate of blood flow (A. Kh. Min'kovskiy and V. V. Skryabin) during application of positive and negative angular accelerations, a decrease or increase in blood flow being detected during application of positive angular accelerations. Stable oxygenation and an increase in the rate of blood flow were observed in athletes under the effect of positive angular acceleration; a decrease in the rate of blood flow was often observed during negative angular acceleration.

The state of oxygenation due to the effect of different rates of angular /192
accelerations may be evaluated as stable and slightly disruptive [8-12].

T. A. Nadimova studied the sensory thresholds of the excitability of the otolithic apparatus, and thresholds in sensing tilting in the frontal and sagittal planes. It was shown that these thresholds are not always identical for the frontal and sagittal planes. If there were a change in the functional state of the otoliths of the sacculus (which was achieved by tilting in the frontal plane), the sensation of tilting developed more rapidly in some

subjects (i.e. within 2-15 sec), than during variation in the functional state of the otoliths of the utriculus (tilting in the sagittal plane), when the sensation of rotation developed within the range of 2-25 sec. Study of the qualitative and quantitative characteristics of otolithic-sensory, otolithic-somatic and otolithic-vegetative reflexes in combination with study of cupulosensory, cupulosomatic and cupulovegetative reflexes gives a more total concept about the functional state of the vestibular analyzer. As a result of studies which we conducted, we can consider that subjects who undergo the effect of negative angular accelerations well rarely suffer vertigo or other symptoms of discomfort during rapid movement, changes in velocities or direction in motion, location at altitudes, and rapid ascents and descents.

It was undoubtedly of interest to study Coriolis acceleration by the ADI method. Nystagmus developing as a result of the effect of Coriolis forces differs from that developing during stimulation of the semicircular canals [14-16].

Yu. V. Tatukov, A. L. Lobanov and G. I. Chevychalov used the ADI method to study variations in labyrinth reactions in subjects undergoing different types of athletic conditioning. The data obtained by these authors permits us to conclude that the ADI test is useful in controlling the state of the vestibular analyzer in subjects undergoing athletic training.

Analysis of electronystagmograms is quite complex, because until now there has been no single method of interpreting the data obtained. For this purpose we have proposed the principle based on determining the latency (L) period of nystagmus (in seconds), amplitude (A) of the fast component (in microvolts), of the slow (M)[1] component, duration (P)[1] and frequency of nystagmus and acceleration (A) (visual analysis of the effect of angular acceleration), and the number of nystagmic pulses (LAMPA). This integral index (LAMPA) should be calculated for each value of angular acceleration applied, for example, for an angular acceleration of 6.4, 12.8 deg/sec^2, etc. B. B. Sharov calculated the following values of LAMPA components for angular /193 acceleration of 12.8 deg/sec^2 (7-8 sec): L = 0.12 sec, A = 120-230 μv, M = 0.37-0.2 sec, P = 35-50 sec, and A = 120-140 nystagmic impulses per minute. The figures presented should be regarded as average values, because some deviation may be observed both in the direction of an increase and in the direction of a decrease.

Ye. A. Kupryashkin [4] reported oscillographic variations in subjects during various angular accelerations. He showed that most subjects displayed a decrease in maximum and average dynamic and minimum oscillatory pressure during the effect of negative subthreshold angular acceleration, and these indices did not vary in most subjects during the effect of positive subthreshold angular acceleration. Under the effect of positive and negative

[1] M: from Russian "medlennyy," slow; P: from Russian "prodolzhitel'nost'," duration. Letters M and P used to form index word "LAMPA" -- Tr.

angular acceleration of higher value, there was a decrease in the maximum and average dynamic and minimum oscillatory pressure.

A six-year study (1959-1965), conducted in the vestibulometric laboratory of the Department of Otorhinolaryngology at the Chelyabinsk Medical Institute, permits us to consider that the ADI test is totally compatible with requirements set forth at present for precise and detailed "microscopy" of labyrinth reactions. Combination of quantitative and qualitative characteristics of vestibulo-somatic, vestibulo-vegetative, and also of vestibulosensory reactions, observed during application of measured angular accelerations, decelerations and tilting in different planes, presents broad possibilities for correct analysis of the functional state of the vestibular analyzer.

The significance of the ADI test for conditioning purposes in clinical or athletic practice consists in the fact that selective and adequate effects, differing in a quantitative and qualitative aspect, may be used as desired for various parts of the vestibular analyzer, depending on the nature of the illness or the type of athletic conditioning.

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CERTAIN REFLEXES OF THE SEMICIRCULAR CANALS WITH RESPECT TO PROFESSIONAL SELECTION AND EVALUATION OF FLIGHT PERSONNEL

V. I. Babiyak

ABSTRACT. The author proposes investigating the vestibular function with the help of positive and negative angular accelerations of 20 deg/sec^2. A definite relationship was discovered between illusions and nystagmus. The phase nature of variations in the indicators analyzed is emphasized.

Flying under complex weather conditions creates favorable conditions for development of spatial sensations in pilots. These sensations may be the reason for total loss of spatial orientation and flying accidents.

Most authors [1-5] acknowledge the significant role of the vestibular analyzer in forming various illusory sensations; however, the mechanism of their development has not yet been explained.

One of the reasons for this situation is insufficient objective analysis of vestibulosensory reactions and imperfection of certain rotational tests (the Barani test), which can no longer satisfy modern requirements of vestibulology.

In our opinion (K. L. Khilov and colleagues), the severity of defensive vestibulo-somatic reflexes is determined by the functional state of the cortical region of the analyzer; therefore, recording of the corresponding somatic reflexes must be provided for objective analysis of sensory (cortical) reactions.

These ideas stimulated us in turning to the study of the illusory sensations of a vestibular nature using new methods, namely: applying strictly measured rotation with simultaneous recording of nystagmus (by the electronystagmography method) and subjective readings of the test subjects (by means of photo recording).

The rotation method consisted of the following: angular acceleration at a constant rate (± 20 deg/sec^2) for 4 sec, and a period of uniform rotation for 3 min. A total of 115 healthy subjects ranging in age from 16 to 36 years, primarily males, who had previously undergone no vestibular conditioning, were studied.

The dynamics of vestibular reactions was developed in the following manner: appropriate sensory and nystagmic reactions developed in the subjects

at the beginning of rotation. After a certain time, different for different subjects, these reactions disappeared, and the illusion of "immobility" developed. Seventy-three subjects (assigned to the third group) displayed no further sensations upon continuation of uniform rotation until rotation was stopped, and the remaining 42 subjects displayed a new illusory sensation, smooth rotation in a direction opposite that of real rotation, on the background of uniform rotation. In 17 (first group) of the indicated 42 subjects, the illusion was repeated twice during three-minute uniform rotation, and this state developed only once in 25 subjects (second group).

Illusory sensations of rotation in most subjects had a diverse qualitative aspect -- swaying, rolling, etc. -- and all this on the background of overall directed vertigo.

Nystagmogram data of the indicated 42 subjects showed that during uniform rotation, nystagmic reaction, coinciding in direction with that of vertigo, developed with the appearance of illusory sensation. For example, if it seemed to the subject that he was rotating to the left (while actually rotating to the right), the rapid component of nystagmus was directed to the left.

Analysis of the oral report of the subject and of nystagmograms indicated that each subsequent illusory sensation and the nystagmus accompanying it /196 vary their direction by 180° with respect to preceding vestibular reactions; consequently, these reactions are of a phase nature, and since they develop whether or not there are accelerations (during uniform rotation), they may be characterized as inadequate for the vestibular analyzer.

Apparently these paradoxically developing reactions are the result of imperfection of central neurodynamic processes which participate in regulation of the analyzer function.

Results of the investigation (Table 1) indicate that along with significant individual fluctuation in duration of the illusion and nystagmus there is close agreement between them.

Thus, nystagmic reaction, developing jointly with an illusory sensation, may in this case be an objective indicator.

The appearance of phase states made it possible to hypothesize that they have a significant effect on the severity of post-rotational reactions, which is reflected in the accuracy of analyzing the results, considered during professional selection and evaluation, conducted by the rotation method.

The mechanism of the effect of phase stimuli which develop paradoxically during uniform rotation on post-rotational reactions is as follows: if the direction of paradoxical reflexes (vertigo and nystagmus) coincides with that of post-rotational reflexes, the latter are intensified; on the other hand, if the reflexes of interacting stimuli are mutually opposed, post-rotational reactions are weakened. These situations are confirmed by the second study

conducted on the same groups according to the following method. The value and time of the effect of angular acceleration is the same (±20 deg/sec^2 every 4 sec). The variable value was the time of uniform rotation, which was equal in each individual experiment to 25, 60, 120 and 180 sec. Under these conditions the possibility was created for interaction of post-rotational reflexes with phase stimuli at various times from the beginning of rotation. /197

Analysis of comparative data of nystagmograms on three groups of subjects (Table 2) showed that the above-indicated paradoxical reactions significantly affect the duration of post-rotational nystagmus and the sensation of counter-rotation. It is obvious from the data of Table 2 that the more severe variations in duration of postnystagmus began in subjects of the first group (17 subjects), were less expressed in the second group (25 subjects) and were not expressed in the third group (42 subjects).

TABLE 1. NYSTAGMIC AND ILLUSORY REACTIONS DURING VESTIBULAR STIMULATION

Group of test subjects	Statistical index	First phase		Second phase	
		Illusion	Nystagmus	Illusion	Nystagmus
1-я	$\bar{x}$	61,7	68,2	24,0	23,2
	$\pm m$	7,4	7,1	2,8	2,5
	$\pm \sigma$	±29,9	±28,6	±11,2	±10,0
2-я	$\bar{x}$	33,7	36,6	—	—
	$\pm m$	3,6	3,8	—	—
	$\pm \sigma$	±17,6	±18,7	—	—

Tr. Note: Commas indicate decimal points.

TABLE 2. COMPARATIVE ANALYSIS OF NYSTAGMOGRAMS

Group of test subjects	Statistical index	Time of uniform rotation, sec.							
		25		60		120		180	
		+Ny	-Ny	+Ny	-Ny	+Ny	-Ny	+Ny	-Ny
1-я	$\bar{x}$	26,8	31,0	30,5	36,8	30,1	34,6	30,6	21,1
	$\pm m$	0,42	0,74	1,09	0,97	1,12	1,04	1,14	0,65
	t	4,79		4,36		4,54		7,18	
	$\bar{x}$	20,4	22,5	20,3	22,7	20,5	23,9	20,6	18,4
2-я	$\pm m$	0,90	0,73	0,85	0,74	0,88	0,66	0,96	1,00
	t	2,13		2,00		3,05		1,52	
	$\bar{x}$	12,5	12,5	12,2	12,3	12,3	12,0	10,7	12,2
3-я	$m \pm$	0,22	0,22	0,19	0,21	0,18	0,13	0,2	0,17
	t	0,1		0,3		0,4		5,5	

Tr. Note: Commas indicate decimal points.

Simultaneous analysis of the configuration of nystagmograms showed that when the direction of paradoxical and post-rotational nystagmus coincides, the latter was more prolonged that the rotational nystagmus corresponding to it. Interaction of nystagmus when their direction is mutually opposed caused a decrease in duration of post-rotational nystagmus.

The greatest expression of dependence revealed was noted in subjects of the first group. Thus, at an average value in duration of rotational nystagmus equal to 30 sec, duration of postnystagmus on the average increased to 35 sec ($t \approx 4.0$) in the case of interaction of concommitant reactions; the duration of postnystagmus decreased to 21 sec ($t \approx 7.0$) upon interaction of antagonistic stimuli.

This characteristic was less expressed in the second group, and not /198
expressed at all in the third group.

The foregoing permits us to conclude that using the method of measured stimulation of the vestibular analyzer in combination with recording of sensory and nystagmic reflexes has made it possible to define a group of subjects (17 of 115 subjects), susceptible to formation of repeated illusory reactions. Such a state of the vestibular analyzer is determined as an expression of vestibulosensory instability, apparently caused by an imperfection in regulation of its functions on the part of the higher branches of the central nervous system. The paradoxical reactions which develop during this state apparently have as their basis known mechanisms of irradiation and concentration of stimulation, and related phenomena of spatial and time-sequential induction. In this regard, primary stimulation of the vestibular apparatus by an adequate stimulus (positive angular acceleration) may be regarded as the triggering mechanism of reactions, which develop during subsequent uniform rotation.

The second group (25 subjects) is a transitional link between the first and third groups, and apparently does not require such close attention of the medical commission during professional selection as that required by the first group. Personnel making up the third group (73 subjects) were regarded as stable in a vestibulosensory respect.

The use of illusory sensations in the study with simultaneous recording of nystagmus indicated that electronystagmography under conditions of the types of rotation proposed may be a reliable objective indicator of illusory reactions, which may apparently be applied for purposes of the evaluation of flight personnel.

Use of the indicated method in discovering the dependence of post-rotational reactions on phase stimulations, not yielding to calculation by the Barani test and certain others, explains the significant difference between results of different authors who determined time characteristics of post-rotational reactions.

The studies carried out indicate the timeliness of using new methods capable of providing calculation of paradoxical reactions which develop during uniform rotation. In this regard the method used may be suggested as a basis for developing new electronystagmographic methods to study the vestibular analyzer by the rotation method.

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ANALYZING THE RAPID COMPONENT OF NYSTAGMUS IN NYSTAGMOGRAPHIC INVESTIGATIONS

M. M. Levashov

ABSTRACT. The nature of the rapid component of nystagmus is investigated with the help of photonystagmography. An attempt is made to give the quantitative characteristics of the rapid component of nystagmus. It is proved that the rapid component depends on afferent pulsation of the ampullar apparatus and may serve as a valuable indicator of the dynamics of the cupula. For total analysis of one cycle of nystagmus, it is recommended that the average harmonic velocity of the rapid and slow phases be used.

Vestibular nystagmus of the eyes is one of the more important objective vestibulo-somatic reactions by which, to one degree or another, it is possible to analyze the vestibular function in the clinic and in experiments. Despite the fact that nystagmus has been known from the time of Purkinje, it is not possible at present to consider it thoroughly studied. Thus, in particular, there is no single opinion about the genesis of the rapid component, or about the fact whether the rapid component is only a passive compensatory phase which develops in response to monitoring the eyes during the slow component, or whether it is related to afferent pulsation, fed from the receptor. The answer to this question should be first of all sought in careful analysis of nystagmographic data. Some studies provide indirect evidence counter to the passive nature of the rapid component [6, 10].

The method of photographic recording of nystagmus [1-5] developed by us has made it possible to reveal principles inherent to the rapid component, and which indicate that the rapid component is directly affected by afferentation from the receptors of the semicircular canal [1-4].

Discovery of the relationship of the rapid component to the vestibular apparatus dictates new requirements in analysis of nystagmus. The requirement for careful quantitative measurements of the rapid component in experiment, in the clinic and in evaluation has arisen -- the requirement for complex evaluation of nystagmic impulse which would make it possible to calculate the characteristics of the dynamics not only of the slow, but of the rapid component. This report, the data of which were obtained in experiments on rabbits, attempts to find such criteria.

Nystagmograms recorded during rotational tests indicated that the rapid /200
component of horizontal vestibular rotational and post-rotational nystagmus (in particular, the velocity of the rapid component) does not remain constant and unchanged during the course of nystagmic reaction, but varies within a range so broad that its lower limit is often within the limits of the velocity range of the slow component.

The nature of the variations in the rapid component differs from that of the variations in the slow component. Differences in dynamics are detected, for example, when comparing the histograms of the velocities of slow and rapid components. In the velocity histogram of the slow component there is left asymmetry, which is the result of the fact that nystagmic reaction consists of two different parts -- starting and sequential. The starting part, relatively short, is determined directly by stimulation of the ampullar apparatus, and the related mechanical processes in the semicircular canal and ampule, by the afferent flow of pulses being fed along the vestibular nerve from the cupula to the centers. The sequential part of nystagmic reaction is related in origin to gradually damping processes of stimulation in the centers, and may in time significantly exceed the starting part. Division of nystagmic reaction into these two parts is of course of an arbitrary nature, and to clearly restrict one part from another is not possible. Therefore, in our studies on the starting part we referred to those nystagmic impulses which occur within the first two to three seconds from the beginning of nystagmus. The concept that the processes in the receptor apparatus are only a triggering mechanism of vestibular reflexes has been reflected in the literature [7], and it satisfactorily explains the disagreement between the duration of nystagmic reaction (seconds) and that of the effect of the stimulating stimulus (fractions of a second). The rate of the slow component is proportional to the value of the active stimulus, and consequently, to the frequency of afferent pulsation [5, 8]. Therefore, slow components with high rates taking place in the relatively brief starting part of nystagmus occupy a small fraction in the overall distribution pattern.

The histogram of the rate of the rapid component differs in that it is not only asymmetrical (left asymmetry), but bimodal with a negative excess (asymmetry and excess are statistically reliable: $t_A = 10.0$ and $t_e = 9.4$).

The difference in histograms of the rates of the slow and rapid components requiresspecial consideration. Variations in the rate of the rapid component (its decrease or increase when compared to the rate in the preceding impulse) are often opposite in sign compared to the variations in the rate of /201 the slow component. In other words, when, for example, the rate of one component increases, that of the other decreases and vice versa. However, such an opposite phase, comprising approximately 23% of variations, does not explain the differences in the histograms. The presence of an excess and the bimodality are explained by the characteristics of the rapid component in starting nystagmic impulses, and the very existence in the initial part of nystagmus of two maximums in the rate of the rapid component observed at stable time intervals [2, 3]. The nature of the variations in the rates of the slow and rapid components in the initial part of nystagmus differs substantially. The envelope of the rate of the slow component in the initial part has one maximum, and the envelope of the rate of the rapid component has two maximums, of which the first begins earlier and the second later than the maximum of the slow component rate. The minimum of the rapid component's rate corresponds to the slow component rate in time. The curve of the rapid component rate has a double-peaked form. The probability of detecting these two maximums of the rapid component rate in nystagmus is great: $p = 0.86$ for

the first and p = 0.94 for the second. It is just the characteristics of the variation in rapid components in the initial part, where in the course of a comparatively short period the maximum values of the rate are observed twice, which explains the bimodality of the histogram of the rapid component rate.

The rapid component depends on afferent pulsation of the ampullar apparatus, which is confirmed by experiments with direct local rhythmic electrostimulation of the cupula [5]. These experiments indicate the existence in the centers, controlling the rapid component, of "tuning" to a certain frequency, which is optimal. It is this optimum frequency of the afferent flow of pulsation which causes nystagmic impulses, in which the rapid component has its greatest rate. Frequencies lesser and greater than optimal have a lesser effect. "Tuning" is rather fine: at frequencies differing from optimal by ±10 Hz, the rate of the rapid component is 25% less than it is during the optimal frequency. Experiments with local electrostimulation of the ampullar apparatus serve as a model of deviation of the cupula.

Explaining the dependence of the rapid component of nystagmus on vestibular afferentation requires attention to quantitative analysis of the rapid component, which may be a valuable indicator for evaluating the dynamics of the cupula. Hence, the requirement to develop for purposes of diagnostics and evaluation such a complex analysis of nystagmus, in which not only the dynamics of the slow component, which is already done at present [9], but also the dynamics of the fast component would be considered. Individual recording /202 on two independent channels of the rates of the slow and fast components [10] with subsequent comparison of them is of course possible. It is more desirable to obtain analysis of each nystagmic impulse immediately on the two components in the form of a single value. As one of these values we may use the average harmonic value employed in statistics when averaging variable velocities.

The average harmonic velocity of each nystagmic impulse may be expressed as a simple averaged harmonic for two indicators -- the velocity of the slow component and the velocity of the rapid component:

$$H = \frac{n}{\sum \frac{1}{V}}; \quad H = \frac{2}{\frac{1}{V_1} + \frac{1}{V_2}}, \quad \text{i. e.}$$

$$H = \frac{2 \cdot V_1 V_2}{V_1 + V_2}, \quad \text{O.P. } H = \frac{2A}{T_1 + T_2},$$

where A is the amplitude of the nystagmic impulse, V_1 and V_2 are velocities, and T_1 and T_2 are the durations of the slow and fast components. Moreover, the difference in distances (rotation angles), traveled by the eye during the slow and rapid components, is not considered. This difference could be determined by calculating the weighed average harmonic velocity rather than the simple velocity, but there is apparently no need for this, because, according

to data of photonystagmographic studies, the difference in amplitudes is rarely significant.

The average harmonic was used to analyze the reaction of extinguishing nystagmus during repeated rotation tests. The curve of the envelope of the average harmonic velocity reflects the characteristics of the velocity envelopes of the slow and rapid components. The shape of the curve of the average harmonic velocity is maintained upon extinguishing of nystagmus, despite the fact that the duration of nystagmus, the number of impulses and the absolute values of the velocities of the slow and fast components decrease.

The most widely used and universal method of recording nystagmus is electronystagmography, but "in pure form" it gives the investigator comparatively little. An attempt at qualitative recording of one component (the slow component) usually has a negative effect on the quality of recording the other (rapid component). Moreover, manual processing of nystagmograms is extremely labor-consuming. In connection with this it is desirable to develop a device for automatic analysis of nystagmus, which would provide one or another complex indicator of nystagmus at output. This problem could be partially answered by an electronic device which would provide average harmonic velocity at the output, i.e. a simultaneous complex characteristic of /203 each nystagmic impulse according to two indicators -- the velocities of the slow and rapid components.

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ELECTRONYSTAGMOGRAPHY AND ITS PROSPECTS

A. Ye. Kurashvili and V. I. Babiyak

ABSTRACT. Electronystagmography is a simple and accurate method of recording eye movements. It may be used in the study of pathological states in the vestibular analyzer. It is used to establish a correlation between oculomotor nuclei and vegetative centers, and also to study the interaction between the vestibular and visual analyzers. The article contains 13 references.

Nystagmus of the eyes is an important indicator for objective analysis of the vestibular function.

Graphic recording of nystagmus makes it possible to study such indicators as amplitude, angular velocity of the slow phase, duration, pulse frequency and direction of nystagmus.

There are a number of methods of nystagmography: mechanical [1, 3, 5], optical [2], and photokinographic [6, 8, 13]. Electrographic recording of nystagmus was first accomplished by Schott in 1922. Subsequently, studies on electronystagmography were published in a number of papers [4, 5, 6, 9].

Electronystagmography has a number of advantages over other methods of recording nystagmus and makes it possible to obtain the total characteristics of nystagmic reaction. Electronystagmography is based on bioelectric phenomena in the eyeball.

According to studies of Morier, Rush and Muller, conducted in 1936, /204
electrical processes are always taking place in the retina of the eyes, even in darkness. The retina is charged negatively, and the cornea is charged positively; consequently, the eye is a unique dipole, where the electrical and optical axes converge. The constant electrical potential between the cornea and retina (the corneal-retinal potential) is found on the surface of the skin near the outer edge of the orbit.

During nystagmic movements of the eyeball, there is fluctuation in the potential difference, recording of which gives a graphic picture of nystagmus. The essence of electronystagmography consists of intensifying the biopotential difference which develops with subsequent recording of it on standard oscillographs (the N-102, MPO-2, K-12, etc.).

The value of the recorded potential difference in warm-blooded animals and man fluctuates within the range of 50-500 mv; consequently, an amplifying device should have a high amplification factor and good antinoise qualities.

We used an ac amplifier designed by our department, the parameters of which make it possible to record nystagmus without distortion. The frequency characteristics of the amplifier are linear within the range from 0.22 to 200 Hz with a variation factor in the boundary sections not less than ±10%, a time constant not less than 1.5 and not greater than 2.5 sec, an amplification factor not less than 2,500,000. The amplifier is made according to the differential layout with positive balancing of the input, which provides a significant reduction in noise level.

The dimensions of the amplifier make it possible to attach it directly on the rotating chair, which gives a number of advantages: it decreases the noise level, and eliminates the requirement for long shielded leads.

Electronystagmography is accomplished by using various rotational methods, which, by meeting the requirements of modern experiment, should correspond to the basic requirement of strict dosimetry of adequate stimulus in the value and time of the effect. It is no secret that automatic rotation devices are available only in several scientific centers of the country, and the best models are extremely large and expensive. In our department we developed and designed an automatic electronic layout with a programming device, which makes it possible to carry out rotation according to triangular, trapezoidal, and multistage (with subthreshold acceleration on the order of 0.1 deg/sec) programs.

Among the advantages of the device should be included its portability, total automation of given modes of rotation, the possibility of connecting it /205 to other chairs which rotate with the help of an electric motor, and its low cost.

The technique of electronystagmography is simple and consists of attaching a pair of special sensors, made of any nonoxidizable metal, on the cleaned skin of the subject near the external angles of the eyes. A third grounding electrode is attached to any part of the skin. Attaching the sensors is accomplished either with the help of adhesive plaster or by a pressure spring which makes it possible to remove them very rapidly and again apply them.

In order to record horizontal nystagmus, the sensors are attached near the external angles of the eyes, and for recording vertical nystagmus they are attached near the upper and lower edges of the orbit. A combination of these positions is possible when using a two-channel amplifier. For recording nystagmus in experimental animals (rabbits, cats and dogs) similar sensors are used: two of them are attached either to the lower eyelids with the help of adhesive plaster or BF type glue, or needle electrodes are implanted in the skin near the external angles of the eyes. A grounding electrode is attached to a shaved portion of the skin.

Multiple use in electronystagmography of proportioning and recording apparatus permits not only qualitative, but also quantitative analysis of individual parameters of nystagmus, overall duration of the relationship of

its different phases in time, of frequency, amplitude and angular velocity of eyeball movement in the slow component phase. The most labor-consuming process is determination of the amplitude and angular velocity of the slow component.

Calibration of the amplitude of nystagmus according to a standard pulse with a voltage of, for example, 100 mv yields a significant deviation from true value, since this method does not take into account the individual fluctuation of the corneal-retinal potential. In our department we apply a method based on the principle of electro-oculography.

Deviation of the gaze from a midline in the horizontal plane by a standard angle (for example, 10°) causes a vertical shift in the oscillation of the oculogram which corresponds to a given angle of deviation. Proportional comparison of the extent of calibrated oscillation with the amplitude of nystagmus provides expression of the latter directly in angular degrees.

The above method of calibrating nystagmus is a necessary step in determining the angular velocity of nystagmus in the phase of the slow component.

Many Soviet and foreign authors attribute great importance to this parameter, which more completely expresses the functional state of the vestibular analyzer; however, known methods of calculating it differ in their great complexity and require additional methods and optical means, which /206 undoubtedly diminishes the practical value of this parameter.

The angular velocity of nystagmus is determined according to the following formula:

$$W = \frac{A \cdot 10^\circ}{K \cdot t},$$

where A is the amplitude of nystagmus (in mm), K is the amplitude of calibrated oscillation (in mm) which corresponds to rotation of the eyeballs by 10°, and t is the time of their movement in the slow phase.

These parameters are determined by direct measurements on oscillograms, but the complexity of this procedure is obvious. Some simplification of the formula is achieved in the case when t is made equal to one second, then parameter A by an additional geometric construction is brought into agreement with parameter t, and the formula assumes the following form:

$$W = \frac{A \cdot 10^\circ}{K}.$$

Another, simpler method of determining the angular velocity of nystagmus in the slow phase of the component is possible, based on measuring angle α, formed by an isoline, and the oscillation of the slow phase, and on the condition from trigonometry that the value of an acute angle in a right triangle is directly proportional to the opposite and inversely proportional to the adjacent leg. It follows from this that angle α is directly proportional to the amplitude of nystagmus and inversely proportional to the rate of tape feed. The formula of angular velocity has the following form:

$$W = \frac{\tan \alpha \cdot 10^\circ \cdot V}{K},$$

where V is the rate of tape feed, and the remaining parameters are known. Both the described methods are impractical in a wide area because of their complexity.

On the basis of the foregoing, one of the authors worked out a new method to determine the angular velocity of nystagmus, based on the principle of optokinetic nystagmus.

Analysis of the mechanism of development of optokinetic nystagmus and experimental data indicated that the angular velocity of the slow phase of optokinetic nystagmus when the gaze is directed horizontally is equal to the angular velocity of rotation of the test subject. Therefore, recording optokinetic nystagmus by the electronystagmographic method at a standard angular velocity of chair rotation, for example, of 10 deg/sec, with subsequent comparison of corresponding angles of nystagmograms of optokinetic and vestib- /207
ular nystagmus yields a direct expression of the angular velocity of vestibular nystagmus in degrees. The formula of this method is extremely simple:

$$W = \frac{\alpha'' \cdot 10 \text{ deg/sec}}{\alpha'},$$

where α'' and α', respectively, are angles formed by oscillation of the slow phase, of vestibular and optokinetic nystagmus, and 10 deg/sec is the angular velocity of chair rotation.

Calculation of the frequency, amplitude and angular velocity of nystagmus by various authors has been accomplished at different time segments of nystagmic reaction.

We practice calculation of these parameters for rotational nystagmus during the first 10 sec of reaction with subsequent derivation of an average for a given time segment, and during the first 20 sec of reaction for caloric nystagmus.

Some foreign authors include in the number of calculated parameters of nystagmus such values as the total number of nystagmic pulses, total amplitude of the entire reaction and others, but all these methods, including those described above, are extremely labor-consuming. Therefore, there is a pressing need to create an ideal nystagmograph with analyzing and integrating devices, capable of providing finished information about the various characteristics of nystagmus.

The method of electronystagmography has a number of advantages over other methods by its simplicity and independence from external conditions. With its help it is possible to record caloric, galvanic, vestibular, optokinetic and spontaneous nystagmus. It may be used under both field and operational conditions, and at the bedside of the patient. It is possible with its help to study the various psycho-physiological aspects related to motor activity of the eyes, without hampering the activity of the subject. However, the universality of this method is limited by its unsuitability for studying the fast component of nystagmus. For this purpose the optical principle of recording nystagmus should be used.

The value of electronystagmography is determined by the importance of nystagmus in expressing the functional state of various physiological systems, disruption of the function of which is manifested by a nystagmic reaction typical for them. This includes the various pathological states of peripheral, conducting and central branches of the vestibular analyzer, the cerebellum, and certain subcortical formations, at the level of which integration of efferent oculomotor tracks takes place.

The close relationship of the oculomotor system to the vestibular nuclei, and of the latter with the vegetative centers makes it possible to seek correlational relationships in the activity of the animal and vegetative /208 systems. An expression of this correlation may be nystagmic reaction, while the value of its individual parameters in expressing this correlation may be different.

Interaction of the visual analyzer with the oculomotor system and of the latter with the vestibular centers permits seeking laws of interaction of the visual and vestibular analyzers, which are the most necessary factor of adequate spatial orientation of man and animals.

Finally, study of various parameters of nystagmus with respect to analysis of vestibular reactivity makes it possible to develop precise electronystagmographic tests, which more fully reflect the somatosensory stability of the vestibular analyzer under extreme conditions.

As one of the most accurate methods of investigating the vestibular function, electronystagmography, when processed properly, under conditions of precise dosimetry of an adequate stimulus, in conjunction with various electrophysiological methods may contribute to discovery of central neurodynamic laws which control the function of the analyzer, and may in fact prove

the unfitness of certain mechanical theories of the peripheral genesis of vestibular instability.

Thus, electronystagmography may be used with great benefit both in the clinic and in various physiological studies on the vestibular analyzer with respect to the interaction of afferent systems.

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NEW INSTALLATIONS FOR INVESTIGATING THE VESTIBULAR ANALYZER

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ABSTRACT. The four-beam swing used at present is simultaneously a stimulator of the otoliths and semicircular canals. An installation is proposed in which the horizontal component of acceleration is eliminated in order to reduce to a minimum stimulation of the semicircular canals. A motor is used to oscillate the cabin. The installation makes it possible to study the effects of optokinetic stimuli.

The appearance of vegetative disruptions and illusory sensations about the position of the body in space during orbital space flights contributed to the increased interest of physiologists and otolaryngologists to the pathogenesis of motion sickness. The hypothesis was made on the basis of numerous observations and studies [1, 5-7] that vegetative disorders and various illusions of the position and motion of the body in space are the result of disruption of the interaction of afferent systems when making a spatial analysis under unusual conditions of the external medium (instrument flights on aircraft and space flights). Moreover, the vestibular analyzer has been given an important role in the pathogenesis of the indicated phenomena. It was revealed at the same time that certain methods of investigating the vestibular apparatus (the Barani chair and the four-beam swing) do not completely satisfy the requirements of space flight. Thus, it is difficult to make a separate study on them of the effect of inertial forces on an organism, and to alter their direction and magnitude. There are no attachments on the installations to vary the functional state of the visual and proprioceptive analyzers. The foregoing provided us the basis to propose new installations for investigating the vestibular analyzer. /209

A horizontal component of accelerations on the four-beam swing with respect to sensitivity thresholds of the semicircular canals is quite important. We know that the sensitivity thresholds of the semicircular canals to accelerations are on the average 0.5-5 deg/sec^2. According to calculations made by formulas of theoretical mechanics, during rocking on a four-beam swing (when T = 4 sec, beam length is 4 m and the angle of inclination of the beam from the vertical is ±45°), the horizontal component of acceleration varies sinusoidally from 0 to ±0.65 g.

If a_{max} is the maximum horizontal component of acceleration, ρ is the mass density of the endolymph, r is the radius of the semicircular canal, ε is angular velocity in radians, l is the length of the semicircular canal, L is /21

the distance between the cupula and the most distant point of the semicircular canal in the direction of oscillations, then

$$a_{max} \cdot \rho L = \rho \cdot r \cdot \varepsilon \cdot l,$$

hence $a_{max} = \frac{r \cdot l}{L} \cdot \varepsilon.$

The given equation provides the specifics of the anatomical structure of the semicircular canal. Moreover, the value of the horizontal component of acceleration acting on the cupula is in direct dependence on angular acceleration, which varies in radians, the radius and length of the semicircular canal and in inverse dependence on the distance between the cupula and the most distant point of the semicircular canal in the direction of oscillations.

If we assume a threshold value for angular accelerations of 5 deg/sec^2, $r = 5$ mm, $l = 20$ mm, and $L = 10$ mm, the threshold value for the horizontal component of acceleration will be

$$a_{max} = 0.001 \text{ m/sec}^2, \text{ or } 0.0001 \text{ g}.$$

Consequently, during rocking on a four-beam swing, the horizontal component of accelerations is higher than the stimulation threshold of the semicircular canals. When the head is tilted or rotated, these accelerations act on one or another semicircular canal depending on the angle formed by the plane of the semicircular canal and the direction of acceleration. The vertical component of linear acceleration acts on the semicircular canals in a similar manner due to the shift in the vertical plane.

Thus, there is combined stimulation of the vestibular analyzer on a four-beam swing.

A. V. Lebedinskiy [6], L. T. Zagorul'ko [4], G. V. Gershuni [3] and others established that adequate subthreshold stimulations of any afferent system may accumulate according to the principle of interaction, and alter the functional state of other systems, at the same time affecting the final reaction. On this bases, we decided to reduce to a minimum stimulation of the semicircular canals with simultaneous stimulation of the otolithic apparatus. In order to do this, stimulation of the vestibular analyzer was accomplished on a specially designed device in which the horizontal component of acceleration was eliminated. The installation consists of a cabin for the test subject, devices for rocking and a control panel. The rocking device may be assembled from steel springs, rubber shocks or a hydraulic attachment. The /211
drive mechanism in small compartments may be a system of blocks and steel cables. In order to vibrate the cabin, a motor with an off-centered mass

attached to its shaft is used. We recommend the following parameters of operating the installation -- a two-second oscillating cycle and ±4 g acceleration; additional modes of operating the installation provide the same oscillation cycle and acceleration -- 0.05, 0.1, 0.2 and 0.3 g. Variation of the functional state of the visual analyzer is accomplished in the cabin with the help of a blackout device. The front wall of the cabin must be glassed in to study the effect of optokinetic stimuli.

Rocking of the test subject in the cabin is possible in a standing, sitting and lying position. Terminal blocks for 30 terminals are mounted in the cabin and outside it in order to connect measuring equipment and to illuminate the chamber.

In order to study the interaction of proprioceptive and vestibular analyzers, it is recommended that a chair for rotation with transition to an unstable position be included. Chair rotation is accomplished in both directions, acceleration of both sides from 0.01 to 80 deg/sec^2 with fixation at one or another level, and also stop-stimuli being provided. Transition of the chair to an unstable position is accomplished by a special mechanism sensitive to shifts in the center of gravity of the subject within limits of tilting of 0.1 cm from the gravitational vertical. In order to study the effect of the visual analyzer on the vestibular analyzer, a cylinder rotating around the chair is mounted additionally, with black and white strips being glued to the inner surface. Rotation of the cylinder is accomplished at the same parameters as is the chair.

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ON THE PROBLEM OF METHODS OF STUDYING THE VESTIBULAR FUNCTION IN A SPACESHIP

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ABSTRACT: Some ways and methods of investigating the vestibular analyzer under conditions of weightlessness are proposed. Adequate stimuli in this case may be the various movements of the cosmonaut's head and body, and rotation of the spaceship itself. The importance of complex investigation of the vestibular analyzer with recordings of EOG, EMG and EEG is emphasized.

Space flights of man have indicated the extreme importance of studying the vestibular function of the astronaut. /212

We know from the literature that under conditions of prolonged weightlessness, illusory sensations of spatial position and vegetative disorders similar to the motion sickness syndrome develop. In connection with this, special investigations of the vestibular function have been carried out during orbital space flights of Soviet cosmonauts.

Movements of the cosmonaut's head and body measured for speed, amplitude and direction served as adequate stimuli. The program of investigation included the following tests:

1) a test to determine muscular tonus of the arms (maintaining equilibrium of the outstretched arms with closed eyes);

2) the finger-to-the-nose test;

3) a test to determine fine coordinated movements (correctness of sketching geometrical figures -- spirals, stars, and two pairs of parallel lines);

4) study of the tonus of the ocular muscles and coordination of eye movements.

An electro-oculogram was used additionally, which made it possible to record nystagmus during expressed vestibular effects and asymmetry in the function of the right and left vestibular apparatus.

As a result of the investigations, an absence of vestibulo-somatic disorders and disruptions of coordinations of movement was noted; vestibulo-vegetative and vestibulosensory phenomena which occurred in certain cases had a functionally reverse character.

However, the enumerated methods did not permit analysis of the functional state of the vestibular apparatus and its role in the indicated disorders separately from other statokinetic systems of man (visual, cerebellum, and proprioception).

Data obtained during study of the vestibular function under conditions of prolonged weightlessness cannot answer several questions: how are the sensitivity and stimulation thresholds of the vestibular apparatus altered, are there elements of adaptation, what are the mechanisms in disruption of spatial orientation, and what are the characteristics of interaction of the vestibular, motor and visual analyzers which form the spatial concept in man.

It is also necessary to consider that investigations of the vestibular function were conducted with the incomplete objective of recording reactions. Thus, the problem of the role of the vestibular analyzer in space flights has been insufficiently studied, and the hypotheses mentioned have not been confirmed by experimental data. /213

The special conditions of the vital function of a cosmonaut during flight in a spaceship are a significant barrier to study of the vestibular function, because not one of the existing present methods of investigating the vestibular analyzer is suitable without radical changes. The difficulties of studying are also included in the fact that weightlessness and adequate stimuli (angular and Coriolis accelerations) during space flight have a complex effect on the vestibular analyzer in various combinations and sequences. It is very difficult to imitate the factors of space flight, and impossible to imitate weightlessness under laboratory conditions.

We propose certain ways and methods of investigating the vestibular analyzer under conditions of prolonged weightlessness. Adequate stimuli may be the various movements of the cosmonaut's head and body and rotation of the spaceship itself. Moreover, it is possible to study the role of Coriolis accelerations in development of motion sickness according to a specially developed program with regard to cumulative effects. We suggest galvanic and pulsed current of different characteristics as inadequate stimuli.

Electrophysiological study of the vestibular analyzer enjoys an almost 150-year history. The first experiments with electrical stimulation of the vestibular apparatus date back to the beginning of the past century (Ritter and Purkinje, 1820).

We know that electrical current, which is the universal physiological stimulus, by acting on the vestibular analyzer, may produce the same reactions as those during adequate stimulations of the vestibular analyzer or with the caloric test.

In clinical practice, the so-called galvanic test is reaction to passing a direct current through the head, and is accompanied by the total sum of characteristic vestibular reactions -- sensory, motor, and to a lesser extent vegetative. Reactions of tilting the head and body, which are more

convenient to observe and record, developed more rapidly and easiest of all during electrical stimulation of the vestibular analyzer. The nature of motor reactions is determined by the direction, intensity and form of the stimulating current. Thus, for example, during crossgalvanization of the head, /214 tilting of the body and falling always take place in the direction of the anode.

Many Soviet and foreign scientists have been concerned with electrophysiological studies of the vestibular function in man and animals for the purpose of a theoretical basis and practical analysis of the model [11, 23, 35-37, 57, 59, 61, 70, 82, 85, 96, 97].

Among galvanovestibular reactions, study has been made of tonic reflexes to the ocular and cervical muscles, galvanic nystagmus, variations in the reflex tonus of the extremities, falling, and also reflex variations in respiration and blood pressure.

While the methodology of the galvanic test has been rather well developed, many theoretical aspects of this investigation such as the mechanism of the effect of current, the origin of galvanic nystagmus and others remain unexplained. The least studied problem is the point of applying the electrical stimulus within the environs of the vestibular analyzer. There is an opinion on the effect of current on the entire vestibular analyzer as a whole, but with the majority of the effect being on the cord of the vestibular nerve, its nucleus in the medulla oblongata, and the central branches in the cortex.

However, most investigators feel on the basis of experimental research that electric current acts primarily on the peripheral branch of the analyzer, i.e. on the receptor apparatus of the labyrinth, innervating the nerve fibers and the Skarpovskiy ganglion. According to Barani [49], galvanic current acts on the vestibular centers in the medulla oblongata, and on the Deygers nucleus.

It was established in experiments on pigeons that the galvanic reactions remain even after two-sided extirpation of the labyrinths, which is related to stimulation of the brain centers. According to Marinesco and Kreindler [96], the total time of the pulsed current and value of the interval between pulses are indicators of the excitability of the bulbar vestibular centers. During an electrical test, according to Quix [98], both the ampullar and otolithic apparatus are stimulated simultaneously. Dohlman [68] suggests that the galvanovestibular reflexes are caused by the effect of direct current on the otolithic receptors and the fibers of the vestibular nerve connected to them which come from the Skarpovskiy ganglion.

S. N. Khechinashvili [37, 38] in his well known research writes that electrical current acts on the neuroepithelium of the semicircular canals. Mackenzie [94], and then Junger [84], attempted to investigate galvanic nystagmus quantitatively. Galvanic current was used as a stimulus of the vestibular analyzer by Ye. M. Yuganov and colleagues on subjects during /215

flights along a Kepler parabola. The reactions obtained hardly differed from vestibular reflexes which developed during brief periods of weightlessness or upon stimulation of the semicircular canals by the rotational test.

Hennbert (1950), reviewing the status of this problem, says that in an undamaged vestibular analyzer sensitivity to galvanic current decreases from the periphery to the center. Upon disruption of the receptor, stimulation may begin at the Skarpovskiy ganglion and then propagate toward the central branches.

The galvanic test may cause reactions upon total destruction of the labyrinth, which has been proven by many authors on the basis of clinical observations [63, 95, 97] and experimentally on monkeys [102] and pigeons [83].

Thus, despite the indicated difficulties and deficiencies of the method of studying the vestibular function with the help of electrical current, this method may be very valuable in practical and theoretical aspects. The use of electrical current to investigate the vestibular analyzer generally and, in particular, during orbital flight in a spaceship has a number of advantages:

a) the possibility of using given, strictly proportioned (beginning from threshold) and precisely measured effects (stimulus control);

b) the universality of the stimulus in the sense of its capability of eliciting opposite reaction;

c) its safety;

d) the possibility of using portable and small-size instruments.

Proceeding from known tenets of electrophysiology and the study of lability, pulsed current is more of a physiological stimulus than is galvanic; it may be used more effectively under conditions of weightlessness as the most optimum electrostimulus for investigating the sensitivity and reactivity thresholds of the vestibular analyzer. Investigations should be carried out with the help of a special portable on-board device -- a generator of electrical stimuli.

With regard to caloric investigation, its significance is difficult to evaluate. It is well known that caloric investigation is one of the most widely used methods for studying the vestibular analyzer. During the past decade, many authors have introduced various modifications into the methodology of the caloric test.

Mechanisms of the effect of caloric stimulation and the ensuing vestibular reactions, in particular nystagmic reaction, until the present have not been fully explained.

One of the most important problems in development of caloric investigation is working out a method of caloric analysis of the excitability of the vestibular analyzer. Many authors [25, 64, 89] attribute only a qualitative significance to the caloric test. However, Barse [52], Arslan [48] and Langraf think it is possible to develop a standard quantitative method of caloric testing. /216

Until the present, the problem of criteria for analyzing the excitability of the vestibular analyzer according to developing reactions has not been resolved in caloric investigation. N. M. Aspisov [4], M. F. Tsitovich [43], A. I. Shchadrin [40], Brünings [62], Boenninghaus [58] and others have analyzed the excitability of the vestibular analyzer by the amount of water required to obtain nystagmus. Some investigators determine the threshold according to the time of onset of caloric nystagmus [11, 42, 46, 67, 100]. Many authors [14, 19, 83] judge the status of vestibular function by the duration of caloric nystagmus. M. F. Tsitovich [43], F. M. Ioselevich [19], I. A. Sklyut [34], Fitzgerald and Hallpike [72], Wodak [105], and Carmichael, Dix and Hallpike [65] have used caloric reactions for the purpose of explaining the relationship of the vestibular analyzer to the cerebral cortex, and to explain the reasons for vestibular asymmetry.

Conducting caloric investigation during space flight would be of great scientific importance in both a practical and theoretical sense. The essence of the former is included in control of the functional state of the vestibular analyzer at various stages of space flight by determining the thresholds of its sensitivity and excitability.

The theoretical aspect of the investigations is an explanation of the mechanism of the caloric reaction from the point of view of the significance of temperature convection in the labyrinth for development of vestibular reactions.

We know that the physical theory of caloric nystagmus is based on the phenomenon of natural temperature convection. According to Benedict [54], during weightlessness natural convection in liquids is lacking with preservation of a much less active mechanism of molecular heat conductivity. Thus, if the processes of natural convection in the endolymph are the basis of the mechanism of caloric testing, vestibular reactions during caloric testing in weightlessness should be absent or appear in some unusual form.

It is proposed to conduct investigations with the help of a miniaturized instrument especially developed for this purpose, the basis of which is electrical heating and cooling of an olive-shaped insert in the acoustic duct. The device permits precise proportioning and measuring of the temperature of the labyrinth during the study, which makes it possible to obtain a /217
comparative qualitative and quantitative analysis of the excitability of the vestibular analyzer.

Methods of recording and analyzing vestibular reactions carried out with the help of telemetry, and also directly on board the spaceship, should be as

precise and objective as possible. However, the importance of subjective sensations of the cosmonaut, and also medical monitoring on board the spaceship are not excluded.

Greatest attention should be given to using electrophysiological methods to record physiological functions, making it possible to reveal the slight variations in the functional state of the vestibular analyzer in somatic and vegetative reflexes.

1. Sensory reactions. Illusory sensations of position and motion of the body in space, and the nature and direction of Purkinje's visual sequential image. Study of the interaction of the vestibular and visual analyzers is accomplished with the help of the visual image. According to the literature, there is a more individual distinction in formation of a visual sequential image, which is expressed by a different latency period and overall duration, which correspondingly characterizes the state of the inhibiting and stimulating processes of the central nervous system. According to S. P. Narikashvili [29] and L. T. Zagorul'ko [15, 16], characteristic variability of the visual image reflects individual characteristics (the type) of higher nervous activity.

Many authors [56, 69, 75, 81, 90, 101] consider the variability of the sequential image from the point of view of the interdependence of the peripheral visual apparatus and central branches of the visual analyzer. In connection with the overall problem of the interaction of afferent systems put forth by L. A. Orbeli, a significant position is occupied by study of the functional interrelationships of the organs of sense during development of aftereffect phenomena in them. The sequential image has been used by a number of authors [2, 6, 15-17, 29] to study characteristics of the interaction of various analyzers.

The investigations of L. T. Zagorul'ko [15] indicated that due to the effect of stimulating the vestibular apparatus, characteristic variations take place in the sequential image in the direction of motion: it is shortened and clouded. Study of the visual sequential image was carried out on an aircraft while executing various flight maneuvers, and also when flying along a Kepler parabola [77]. As a result of the investigations, definite characteristics were revealed: as G-loads increase, the image moved downward, and it /218 moved upward during partial or total weightlessness. This direction of movement of the visual image is apparently related to the effect of the otolithic apparatus on the visual analyzer, which is confirmed by ground experiments.

It is obvious that correct analysis of the results obtained during study of the sequential image is possible only upon a correct concept of those elements of the analyzer which are a substratum for development of similar processes.

In the opinion of some investigators, the location of development of sequential sensations is the peripheral areas of the analyzers. Others feel

that the sequential sensations develop in connection with processes of the aftereffect which occur in the cerebrum; the receptor is the source of stimulation pulses.

There are two methods of obtaining the visual sequential image upon adequate stimulation of the retina -- by brief (fractions of a second) and prolonged (tens of a second) exposures to light [18, 22, 77]. The advantage of the first method is the possibility of obtaining very precise time data; however, the second method is much simpler and more convenient, because it requires no complex apparatus.

It was noted in the investigations of B. B. Bokhov [8], who used the method of prolonged stimulation, that the most indicative variation of visual sequential image during vestibular stimulations is the movement of the image.

2. Motor reactions. These include the following tests: tilting of the head, body and arms, the vertical writing test, study of the motor activity of the eyes, electronystagmography and electromyography.

A number of authors [27, 33, 50, 78, 104] has been involved in developing methods of investigating vestibulospinal reflexes. The investigators proposed their methods of graphical recording of the pointing test which permit objective analysis of this reaction; however, they have not gained sufficient dissemination.

Until the present, Barani's indicating test has been used in the clinic, which is a complex motor reaction related to a coordinated function of the motor analyzer, i.e. with conscious activity of man.

The reactions of tilting the arms and reactions of arm tonus described by Wodak and Fischer more objectively reflect the nature and degree of tonic reflex during vestibular stimulation.

The vertical writing test, which is a variation of the indicating test, was proposed by the Japanese otorhinolaryngologist Fukuda [74]. The test is a /219 method of graphical recording of vestibulospinal reflexes which take place upon disruption of the so-called labyrinth equilibrium.

The indicator of disruption of tonic effects, originating from the right and left labyrinths, is redistribution of the tonus of body musculature, in particular of the upper extremities, which is expressed in asymmetrical inclination of the arms in one or another direction. According to Fukuda, vertical writing is characterized by purely objective results of recording, and is a sensitive test, revealing prenystagmic vestibulospinal reflexes upon weak stimulation of the vestibular apparatus.

The test reveals changes in muscle tonus upon various functional and organic disruptions of the vestibular analyzer. It is expedient to use the vertical writing test as modified by B. B. Bokhov [8] for investigations under special conditions.

Electromyography under conditions of weightlessness is of great interest for study of the nature of vestibular reactions. Selection of a rational method of monitoring and electrophysiological measurements of the biopotentials of corresponding muscles is an important condition for objective recording of somatic reflexes, reflected in variation of muscular tonus of the neck, body, extremities and eyes.

3. Vegetative reactions. These are pulse and respiration rate (electrocardiography), pneumography and the galvanocutaneous reflex.

Electroencephalography (EEG) occupies a special position among electrophysiological methods of investigation. The vestibular function has for many years been studied with the help of electroencephalography, which has played an important role in revealing localization of the cortical region of the vestibular analyzer and interrelationships of the cortex and subcortical formations [4, 5, 7, 12, 20, 21, 24].

The papers enumerated above illuminate the problem of EEG fluctuation due to the effect of vestibular stimulations, and indicate the role of the cerebral cortex in forming vestibular reactions. Consequently, the use of EEG to record vestibular reactions during space flight is quite well founded.

The specific conditions in a spaceship require restriction of weight, size and power requirements of the on-board equipment, and protection of it from the harmful effects of space flight. Other requirements which the /220 equipment must satisfy are reliability in operation, resistance to interference and high-quality recording.

The most feasible for use on board a spaceship are compact, composite instruments which permit several types of investigation and recording. Thus, for example, investigation of the motor activity of the eyes, vertical writing and visual sequential image tests are all carried out on the same special small-size instrument.

Much attention must be given to development and use of appropriate electrodes which should satisfy the conditions of space flight. Thus, the urgent problems of space medicine are investigation of the vestibular function during space flight with the aim of revealing the mechanisms of vestibular disruptions, study of the characteristics of interaction of vestibular and other analyzers, and creation of stable vestibular resistance by concerted action to vestibular reactions.

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ON THE PROBLEM OF THE IMPORTANCE OF PARABOLIC FLIGHT TO REPRODUCE BRIEF PERIODS OF WEIGHTLESSNESS IN VESTIBULAR EVALUATION OF COSMONAUTS

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ABSTRACT. The possibility of using parabolic flights to create brief periods of weightlessness for vestibular selection of cosmonauts is considered. It was shown that parobolic flights reveal persons who are prone to motion sickness. The use of additional vestibular stimulation during weightlessness helps to reveal persons with latent forms of motion sickness.

As a result of the successful flights of Soviet and American astronauts, extensive scientific data has been obtained on the effect of a complex of space factors on the human organism, which indicate that the organism on the whole adapts rather well to conditions of prolonged weightlessness [3, 8, 9].

However, it is difficult to say whether the work capability and functional activity of both systems and organs vary during weightlessness.

Facts indicate that the vestibular analyzer during space flight endures the most intensive and prolonged specific effects compared to the other organs and systems, and it requires more careful study when selecting and training cosmonauts for space flight.

Real prospects for distant flight are connected with more prolonged stays of cosmonauts under conditions of weightlessness; therefore, the problem of more careful vestibular selection and training of cosmonaut candidates becomes very relevant. Vestibular selection of airmen and seamen was given great attention in its time [2, 5-7, 10-12], as a result of which effective methodology of selecting and training was worked out.

The flight of G. S. Titov aboard *Vostok 2*, which lasted more than 25 hr, indicated that existing methods of investigating the function of the vestibular analyzer do not quite satisfy requirements set forth for selection of crew members of modern spacecraft. For this purpose we have attempted to find additional methods of vestibular selection of cosmonauts, based on their /224 maximum similarity to conditions of actual space flight. Selection centered on parabolic flights carried out in jet aircraft, which produced brief periods of weightlessness lasting 20-45 sec. There were two reasons for the basis of this.

During flight along a parabolic curve, the subject encounters the same factors as during space flight, but for very much shorter periods of time and they are less severe. Noise, vibration, positive linear and angular accelerations, Coriolis accelerations developing during tilting of the body and turning of the head when flying an aircraft, weightlessness, etc. act on the cosmonauts.

Reaction of the otolithic region of the vestibular apparatus during flight of a jet aircraft along a parabolic curve is similar to that of subjects during rocking on a four-beam swing; the difference consists of the fact that the gravitational effect in the swing varies over a lesser range (±0.4 g) during ascent and descent of the platform, and during flight along a Kepler parabola -- within the range 4-5-0 g, i.e. several times more intense.

Study of the functional state of the vestibular analyzer was made before the flight, under conditions of brief periods of weightlessness and after the flight. Parabolic flight for weightlessness was arranged such that the "humps" of weightlessness followed each other. Moreover, G-loads were created before and after weightlessness.

The vestibular analyzer was studied for three basic groups of reactions -- the sensory component (subjective sensations), vegetative component (pulse rate, respiration rate, overall hyperhydrosis, and skin color), and the animal component (reactions observed during the Barani rotational test). The study was conducted on subjects who had undergone vestibular selection according to the usual method with good results.

Analysis of the data obtained during the flights for weightlessness indicates that basic changes in the sensory components are observed at the moment G-loads take effect and upon transition from G-loads to weightlessness. Sensory reactions were somewhat less expressed during the period of stabilized weightlessness and at the moment of return to positive G-loads. Subjective sensations observed during the period of G-load effect were normal, and indicated a weight increase of the subject. A completely different picture was observed during the transition period from G-loads to weightlessness, when the vestibular apparatus received unusual stimulation for ground conditions. At this moment, 95% of the subjects displayed disruptions of spatial orienta- /225
tion in the form of an illusion of changing position (a sensation of sharp ascent upwards, falling downward, flying upside down, on the side and on the back, etc.), sensations of "heart failure" and contraction of the field of vision.

It is characteristic that the greatest number of cases of unusual negative sensations was felt by the group of nonflying personnel (63.6%), and somewhat less by pilots with comparatively brief flight training.

The vegetative component of vestibular reactions during parabolic flight also underwent unique changes, which included the following.

Pulse and respiration rate during the effect of G-loads increased sharply, and it reached 130-140 beats and 28-30 breathing cycles per minute in subjects who withstood parabolic flight poorly. At the moment of transition from G-loads to weightlessness there was a decrease in pulse and respiration rates on the background of unusual sensory reactions. It is natural that in personnel who withstand flight well, pulse and respiration normalize rapidly; in those who do not withstand weightlessness well, it is very slow, and often pulse and respiration remain at a high level right to the end of the period of weightlessness compared to initial data obtained during the horizontal portion of the flight.

The time of pulse and respiration normalization during the portion of stabilized weightlessness is very important for diagnostic purposes. It was established that in subjects who withstand conditions of parabolic flight well, normalization of pulse and respiration begins by the tenth second, in subjects with average resistance -- by the fifteenth to twentieth second, and in those who withstand the flight poorly -- by the thirty-first to forty-fifth second. For diagnostic purposes, it is important to know how unstable were the indicators of pulse and respiration during weightlessness. The presence of severe lability of pulse indicates a predisposition to motion sickness. No less important in analyzing vestibulo-vegetative reactions were sensations of discomfort -- general weakness, sluggishness, somnolence, headaches, increased salivation, nausea, paleness of the face, cyanosis of the lips, and general increased perspiration.

In our research of a large number of subjects who earlier underwent vestibular selection and training during parabolic flight, we noted vestibulo-vegetative reactions in only one pilot and in four nonflying subjects.

It was established upon analysis of the results of conducting a rotational test before and after the flights that in subjects who withstood parabolic flight well, the illusion of counterrotation and post-rotational nystagmus became 3-5 sec shorter after the flight compared with initial data. In those cases when vegetative disorders were observed during flight, which indicated the presence of explicit or latent forms of motion sickness, the /226 illusion of counterrotation and post-rotational nystagmus either did not vary, or lagged initial data by 2-5 sec (in five subjects). In order to verify the given situation, we conducted an additional tenfold Barani rotational test during flight under conditions of weightlessness with the single difference that the rotation velocity was two times greater than on the ground.

Analysis of data obtained during the flight indicated that in subjects who withstand parabolic flight well, the illusion of counterrotation and post-rotational nystagmus are reduced by 4-6 sec, compared to data under ground conditions. This in itself confirms the correctness of our preliminary assumption about the diagnostic value of the modified Barani test before and after flights for weightlessness.

Besides all the foregoing, we also managed with the help of the indicated test to establish severe vestibulo-vegetative reactions (pronounced paleness

of the skin, cyanosis of the lips, general hyperhydrosis, nausea, hypersalivation, etc) in four subjects who had earlier withstood flights for weightlessness well. It is characteristic that the indicated subjects had earlier passed vestibular selection and special vestibular conditioning successfully.

The use of the rotational test during weightlessness made it possible to determine subjects prone to motion sickness in time, and to show methods for further conditioning of the vestibular apparatus.

Data of the observations clearly show the diagnostic value of the given method in selecting personnel prone to motion sickness during weightlessness. Thus, phenomena of vestibulo-vegetative discomfort under conditions of flight without additional vestibular stimulation were discovered in five subjects, and in four subjects after tenfold rotation during weightlessness (a total of 21.9%).

The advantage of the given method of vestibular selection consists in the fact that on the background of a periodically changing gravitational field, from 4-5 to 0 g and reverse, any angular movements lead to rapid accumulation of Coriolis accelerations and severe vegetative reactions; this method is used to check the stability of the otolithic region of the vestibular analyzer to minus stimulation.

Reviewing the foregoing, we may make the following conclusions.

1. Flights in aircraft to reproduce weightlessness make it possible to ascertain those persons subject to motion sickness.

2. The use of additional tenfold rotation under conditions of weightlessness permits determining those persons with latent forms of motion sickness.

3. The criteria for the tendency to motion sickness in the given method /227
are:

a) negative subjective sensations (illusions of inverted position, heart failure, sensations of helplessness and fear);

b) high lability of vegetative reactions (jumps in pulse and respiration rates, rapid change in skin color);

c) retarded (to 31-45 sec) reaction of pulse and respiration recovery under conditions of zero gravity;

d) lengthening of the period of illusion of counterrotation and post-rotational nystagmus during the rotational test in weightlessness and after flight for weightlessness compared to initial data.

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THE SIGNIFICANCE OF CERTAIN VESTIBULOMETRIC TESTS IN MEDICAL FLIGHT EXAMINATION OF PERSONNEL PREDISPOSED TO ILLUSORY SENSATIONS DURING FLIGHT

I. A. Sidel'nikov and I. I. Bryanov

ABSTRACT. A chair with an unstable platform, pulsed current, a rotating chair with unstable platform and a rotating cylinder for optokinetic stimulation were used to study proneness to illusions of spatial orientation. It was discovered that increased susceptibility to pulsed current indicates a high probability of development of illusory sensations.

It is known that illusory sensations of spatial orientation develop /228 during flight in many pilots at different periods of principal activity. This prevents fine execution of the flight mission and, according to the data of foreign authors, is in 14% of the cases the reason for flight mishaps [16]. A great deal of attention has also been given to this problem in Soviet literature [1, 2, 4, 10-15].

Illusory sensations of spatial orientation during flight are most difficult when solving problems of an expert nature, because medical flight examination has not previously had sufficiently effective methods of investigation which permit forecasting the possibility of development of illusions, to reveal the mechanisms of disruptions in spatial orientation, and to determine the degree of their severity and persistence.

This is why attempts are undertaken constantly to study these disorders, and why there are unceasing attempts to find new methods which permit simultaneous diagnosis and warning of the development of disruptions in spatial orientation during flight.

Papers have appeared in recent years [4, 5] which relate disorientation in space and, in particular, the development of illusions during flight to characteristics of the interaction of analyzers which play an important role in the formation of spatial concepts in man. In this regard we used a combination of methods [4, 5] directed toward the study of the interaction of analzyers in personnel predisposed to illusory sensations, and in personnel stable in this sense (the control group).

Below is presented a short description of all vestibulometric studies used in this paper.

1. A test to determine the capability of the subject to maintain equilibrium with closed eyes in a special chair with unstable support.

2. A test with pulsed current to determine the excitability of the vestibular apparatus with closed and open eyes in a subject who was in a chair with unstable support (when his eyes were open, the subject fixed his gaze on an immobile visual object). With the help of the given test, a minimum value /229 of stimulation was determined (in this case, current intensity), which caused tilting reaction, and the extent of inhibiting effect on the vestibular apparatus of the visual analyzer.

3. A test in a rotating chair with unstable support which made it possible to determine the capability to recover equilibrium after a specific amount of stimulation of the vestibular apparatus under conditions of balancing. This test was designed to ascertain the capability of inhibiting vestibular reactions on the part of the motor analyzer under conditions, when the functional interrelationship of the analyzers of position and body motion in space was disrupted artificially.

4. A test to determine characteristics of the development of the optokinetic illusion of motion. For this a rotating cylinder was used (height and inner diameter of 1500 mm) with black and white strips (100 mm wide) attached to the inner surface at an angle of 60° to the vertical. The subject was placed in front of the cylinder. The optokinetic effect was achieved by rotating the cylinder at a velocity of 136 deg/sec. Illumination at the level of the strips was 50 luxes. The latency period of illusion, the period of the aftereffect and motor reaction to the optokinetic stimulus were determined. Motor movements of the body (by means of tensometers and nystagmus) and vegetative (pulse and respiration rates) reactions were recorded. Moreover, detailed characteristics of sensory reactions were provided on the basis of oral reports of the subject.

5. A rotational test which permitted determination of post-rotational nystagmus and the duration of the sense of counterrotation.

Vestibulometric investigation was combined with general clinical investigation.

A total of 86 subjects, of whom 75 were fighter pilots, 7 were bomber pilots and 4 were from transport aviation, were studied. Illusions of spatial orientation were noted in 46 subjects. The remaining 40 subjects displayed no illusory sensations during the flights and comprised the control group.

In the opinion of a number of authors [17-21] concerning the dominant role of the vestibular apparatus in genesis of illusory sensations, the hypothesis may be quite valid that in personnel prone to illusory sensations, vestibulo-vegetative reactions during rocking in a swing will be detected in a greater number of cases. Therefore, all subjects were subjected to rocking in a Khilov swing, and the OR and OR_{10} tests were conducted. Examination showed that only 18 of 86 subjects displayed vestibulo-vegetative reactions of /230 various degrees of severity during rocking in the swing and during the OR_{10} test.

It is important to emphasize that in 12 of 18 subjects illusions in anamnesis were noted during flight. In 6 subjects there were no illusory sensations during flight. No correlation between the degree of severity of vegetative reactions and the extent of illusory sensations during flight were noted in any of these subjects. Thus, subject I-ev each time displayed a sharply expressed vestibulo-vegetative reaction during rocking in the Khilov swing, while he developed illusory sensations during flight very rarely and suppressed them easily by changing position and fixing his gaze on the instruments. Similar data were noted in P-t, V-v and others.

On the other hand, moderately severe vestibulo-vegetative reactions (motion sickness in the swing, the OR test) were encountered in personnel with sharply expressed sensory and vegetative reactions during flight. No apparent vegetative reactions during rocking in the swing were noted in a significant part of the subjects who experienced the effect of illusion.

Thus, data obtained as a result of investigating vestibulo-vegetative resistance, cannot be used fully to explain the reasons and mechanisms of illusory sensations, and also to determine their type, severity, duration, etc.

Investigations of post-rotational nystagmus, illusions of counterrotation, and OR results also do not permit establishing a causal relationship between the degree of severity of vestibular reactions during these tests and predisposition to illusions during flight. Thus, prolonged illusions of counterrotation and nystagmus were observed in both pilots with false spatial sensations during anamnesis, as well as in those who had never experienced them.

On the other hand, even at the first stage of investigation attention was turned to the fact that in personnel with illusory sensations during flight, an increased excitability of the vestibular apparatus to pulsed current was detected. In 37 of 46 cases, excitability was increased, which was characterized by a value of pulsed current of 1-0.5 ma. At the same time, in pilots not subject to illusory sensations, excitability was determined by a threshold value of 1.5-2.5 ma.

Thus, for example, in subject Sh-v, who often complained of recurring illusory sensations during flight, the stimulation threshold of the vestibular apparatus with closed eyes was 0.5 ma, and in subject S-n, who did not observe similar phenomena during flight, it was 2.5 ma.

The low stimulation threshold of the vestibular apparatus to pulsed current was also detected in pilots without illusions during anamnesis, but /231 who were subject to motion sickness both during the experiment and during flight.

Thus, a certain generality is noted in reactions of the vestibular apparatus to pulsed current in personnel prone to illusions of spatial orientation.

The minimum values of current causing response reactions of the vestibular apparatus with a fixed gaze in pilots experiencing false sensations during flight were different, but the loss of equilibrium or motor reaction continued for a prolonged period in all subjects. It was especially prolonged in those subjects who indicated development of complex illusions -- inverted positon of the aircraft and sharp rolling. It should be noted that in some of these subjects asymmetry of excitability was observed upon stimulation of the right and left vestibular apparatus. Excitability of the vestibular analyzer when the gaze was fixed varied within the limits of 0.5-3 ma.

In subjects having no false sensations during flight, it was not possible to cause losses of equilibrium (with fixed gaze) by pulsed current of the indicated intensity, or it was extremely brief.

Upon comparison of the investigation results, a certain generality was revealed of reactions in specific groups of personnel. Thus, those with increased sensitivity to pulsed current (with closed and open eyes), as a rule, withstood rotation poorly in combination with balancing on an unstable platform and optokinetic stimulations. Comparing the data obtained with anamnestic data, one may be convinced that in these subjects illusory sensations developed very easily during flight and, what is especially important, the illusions, being very severe in nature, did not disappear upon attempts to eliminate them by one or another method. Fixing the gaze on the instruments did not help.

Thus, in this group (26 subjects) there was a definite physiological characteristic -- increased vestibular sensitivity with weak inhibition of the effect of stimulations of the visual and motor analyzers on the vestibular analyzer under conditions of variable functional effect of the latter.

Let us cite several examples. Pilots K-un, Z-kiy, and S-in were selected for the study in connection with often developing and prolonged various illusions of spatial orientation during flight. They displayed increased sensitivity of the vestibular apparatus to pulsed current (0.5-1 ma) with closed and open eyes, prolonged recovery of equilibrium (32-102 sec) with loss of orientation in space after rotation and subsequent transition to an unstable platform, a short latency period (to 5 sec) and a long period of /232 aftereffect of optokinetic illusion of motion (40-48 sec). Apparently, an important role in the mechanism of the development of illusions in the pilots named was played by the characteristics of physiological interaction of the analyzers in space orientation, which are typified by weak inhibiting effects on the part of the visual and motor analyzers on the vestibular analyzer.

We assume that, with respect to such pilots, the question must be raised about changing their profession or of removing them from instrument flights.

The subjects of the other group (11 subjects) differ significantly. Typical of them are increased sensitivity of the vestibular apparatus to pulsed current (0.5-1 ma) with closed eyes and normal or decreased sensitivity with open eyes and fixing of the gaze on a visible object. This is

characterized by a brief period of equilibrium recovery on an unstable platform after rotation (0-30 sec), a prolonged latency period (greater than 15 sec), and brief period of aftereffect of optokinetic illusion (4-5 sec).

Pilots of this group are also distinguished by the circumstance that some of them develop motion sickness under experimental conditions with closed eyes. Stimulation of the visual and motor analyzers (balancing), on the other hand, helps to inhibit vestibular reactions. Anamnestic data are in agreement with experimental results: they arbitrarily inhibit illusions during flight not only when ground orientation points fall within their field of vision, but even when fixing the gaze on a light source inside the cabin. Demonstrative in this regard are the results of the study of V-v, who suppressed illusions during flight by fixing his gaze on a signal lamp.

Thus, in a given case the significant factor determining pathogenesis of illusions during flight should be considered the increased sensitivity of the vestibular analyzer with the relatively high inhibiting effect on it of the visual and motor analyzers.

Additional data, which make possible clarification of the capability of the inhibiting effect of stimulations of the visual analyzer on vestibular reactions, are the results of investigating the optokinetic illusion of motion.

The prolonged period of the aftereffect of optokinetic stimulus (6-5 sec) indicates weak inhibition, and a short period (0-5 sec) indicates a strong inhibiting effect of stimulations of the visual analyzer.

For the two groups described one should also note the significance of the /233 results of rotational tests on an unstable platform in analysis of the severity of false sensations which develop during flight. It has been noted that in personnel with severe and persistent spatial disruptions of vestibular origin, equilibrium after rotation is not recovered for a prolonged period: for 35-102 sec. This is often related to the sensation of total disorientation in space.

Evaluation of the fitness of pilots of the second group for professional activity under complex weather conditions should be accomplished with regard to the effectiveness of special conditioning directed toward increasing resistance against stimulations of the vestibular analyzer and improvement of physiological systems and mechanisms which determine inhibition of vestibular reactions (strengthening the muscular apparatus, balancing skills, learning to fix the gaze on the instruments, etc.).

Results of vestibulometric tests in the third group of subjects (nine men), who experienced illusory sensations during flight, did not differ in the characteristics which were common to the first two groups.

It was possible to observe in these persons normal, increased or decreased sensitivity of the vestibular apparatus, and disagreement between

results of investigating the sensitivity of the vestibular apparatus with a pulsed current and data obtained by other methods. In some pilots, results of investigating the vestibular apparatus typified his normal sensitivity. However, functional disorders of the nervous system, diagnosed by clinicians as a neurotic state, were established in all these persons. Obviously, this circumstance may be explained by development during flight of various disorders of spatial perception in the latter group of subjects.

Upon examination of pilots having no illusions during anamnesis (the control group), no deviations were ascertained in the function of the vestibular apparatus or in the characteristics of interaction of vestibular, visual and motor analyzers.

Conclusions

1. The proposed complex of methods to study the vestibular function, based on study of interaction of the vestibular analyzer with motor and visual analyzers, provides great opportunities for determining and clarifying the mechanisms of spatial disruptions in flight personnel.

2. Increased sensitivity of the vestibular analyzer to pulsed current in conjunction with the weakened inhibiting effect of the proprioceptive and visual analyzers on vestibular reactions should be regarded as an unfavorable diagnostic symptom when selecting personnel for flying under complex weather conditions. /234

3. The combination of increased sensitivity of the vestibular apparatus with a high inhibiting effect of the visual and motor analyzers may be regarded as a favorable diagnostic indicator with respect to flight activity, but for flights under complex weather conditions it is desirable to conduct special conditioning.

4. The proposed complex of vestibulometric tests in conjunction with general clinical examination makes it possible to isolate personnel in whom illusory sensations have a nonvestibular genesis, and, thus, provides the opportunity to approach diagnostic evaluation of flight personnel having false sensations of spatial orientation during flight in a discriminating manner.

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COMPARATIVE ANALYSIS OF VESTIBULOMETRIC METHODS OF EXAMINATION USED FOR PURPOSES OF PROFESSIONAL SELECTION

S. R. Raskatova

ABSTRACT. Three tests were compared in order to find more sensitive methods of vestibulometry during medical flight examination. Examinations of 900 subjects indicated that DPK is the simplest and most economical method timewise, revealing increased sensitivity of the vestibular apparatus to the effect of adequate stimulation when other methods are less indicative.

Vestibulometry occupies one of the leading positions among methods used in medical flight examination.

Moreover, examination of candidates in flight schools, and also selection of personnel for special purposes is a very difficult matter. The diagnostician must determine in a single examination not only the explicit pathology, but also latent disruptions of the otorhinolaryngological organs, and, moreover, a large number of personnel is generally examined within a very limited time. In this regard it is necessary to note which methods of investigating the function of the vestibular apparatus (the Khilov swing and OR_{10} experiment) acceptable at present are extremely labor-consuming.

Practice indicates that testing in a Khilov swing requires on the average no less than 18 min, and the OR_{10} experiment no less than 25 min. This is why until the present searches go on for new methods of vestibulometric examination, which are more suitable for purposes of professional selection. In connection with manned flights into space, even more attention has recently been given to studies in the field of labyrinthology.

This report presents results of comparing different vestibulometric methods, used for purposes of medical flight diagnosis (the Khilov swing, OR_{10}), with a method developed by I. I. Bryanov on which is based the cumulative effect on the vestibular apparatus.

The test for endurance of accumulation of Coriolis forces is conducted in the following manner. The subject assumes the same position in a Barani chair as in the OR test (body inclined 90° with respect to the vertical plane). The chair then begins to rotate uniformly at a velocity of two revolutions per second (eyes closed). The subject straightens and tilts his body on the background of the constant uniform rotation of the chair. So that the rate of straightening is controlled by the subject himself, it is suggested that he

pronounce aloud two-digit figures. For example, when straightening at an assigned velocity of 3 sec, the subject pronounces "twenty-one, twenty-two, twenty-three," and during this counting straightens his body. Tilting and straightening are continued throughout uninterrupted rotation every 5 sec on command from the doctor. The test continues for one minute, then the chair is stopped. The pause continues for one minute. During this time, the doctor /236 determines vegetative reactions and questions the subject about subjective sensations. After the minute's pause, in the absence of expressed vegetative reactions, the test is continued for the same period, but the chair is rotated in the opposite direction. Thus, the entire test is run for three minutes. A preliminary experiment of running the test for accumulation of Coriolis forces permitted us to assume that personnel who withstand the above test well should withstand the test in the Khilov swing and the OR_{10} experiment, and those persons who display vegetative reactions during rocking in the Khilov swing and the OR_{10} experiment should be exposed with the help of this test. The active effect of Coriolis forces in the above test continues for two minutes (DPK).

Comparison of the methods was conducted on flying personnel, candidates of flying schools and cadet pilots of the All-Union Aviation School. The data presented provide the opportunity to follow the results of vestibulometric studies on all age groups. A total of 153 subjects were tested.

When conducting vestibulometric studies, we adhered strictly to identification of the conditions and sequence of tests run. Thus, vestibulometric testing was conducted between 12 and 2 p.m. in persons who were not involved in any other tests, including stimulation test. The interval between subsequent vestibular testing was 1-2 days. Thus, all tests were run under different conditions.

TABLE 1. DISTRIBUTION OF TEST SUBJECTS BY AGE AND PROFESSIONAL ACTIVITY

Group of test subjects	Total	Up to 30 years	From 31 to 40 years	Above 40 years	Above 50 years
Flying personnel	94	37	49	7	1
Cadets	9	9	—	—	—
Non-flying personnel	50	38	12	—	—
Total	153	84	61	7	1

Table 1 shows distribution of test subjects by age and professional activity.

Table 2 shows the comparative characteristics of vestibulo-vegetative reactions in the test subjects depending on the manner of stimulating the vestibular apparatus.

TABLE 2. COMPARATIVE CHARACTERISTICS OF VESTIBULO-VEGETATIVE REACTIONS OF TEST SUBJECTS DEPENDING ON THE METHOD OF STIMULATING THE VESTIBULAR APPARATUS

Group of test subjects	DPK Test			Khilov swing			OR_{10}		
	Good	Average	Poor	Good	Average	Poor	Good	Average	Poor
Flying personnel	43	38	22	68	25	10	82	18	3
Non-flying personnel	18	20	12	37	10	3	36	14	—
Total	61	58	34	105	35	13	118	32	3
Total	153			153			153		

Thus, with the help of the DPK test (a two-minute test for accumulation of Coriolis forces), 34 subjects were revealed with very severe vegetative reactions and 58 with an average degree of reaction, while only 13 subjects /237 with very severe and 35 with moderately severe reactions were revealed during testing in the Khilov swing; less effective was the OR_{10} experiment, which revealed very severe vegetative reactions in only three subjects and moderately severe in 32 subjects.

TABLE 3. COMPARATIVE CHARACTERISTICS OF VESTIBULO-VEGETATIVE DISORDERS IN SUBJECTS DURING TESTING IN THE KHILOV SWING AND THE DPK TEST

Khilov swing	DPK Test			Total
	Good tolerance	Moderately severe vegetative reaction	Very severe vegetative reaction	
Good tolerance	58	34	13	105
Moderately severe vegetative reaction	3	17	15	35
Very severe vegetative reaction	—	7	6	13

Table 3 compares results of tolerance of the same personnel during testing in the Khilov swing and the DPK test.

Thus, 105 subjects endured the swing without vegetative reactions. When examined by the DPK method, only 58 subjects (out of 105) did not display vegetative reactions. Various degrees of vegetative reaction were revealed in 47 subjects (34 and 13). The OR_{10} experiment (Table 4) revealed vegetative reactions in 14 subjects, and 91 subjects displayed no vegetative reactions.

TABLE 4. COMPARATIVE CHARACTERISTICS OF VESTIBULO-VEGETATIVE DISORDERS IN SUBJECTS DURING TESTS IN A KHILOV SWING AND THE OR_{10} TEST

Khilov swing	OR_{10}			Total
	Good tolerance	Moterately severe vegetative reaction	Very severe vegetative reaction	
Good tolerance	91	14	—	105
Moderately severe vegetative reaction	23	11	1	35
Very severe vegetative reaction	4	7	2	13
Total	108	42	3	153

At first glance one forms the impression that there are many discrepancies between the Khilov swing and OR_{10} test. However, analysis of the data on average and poor tolerance to the Khilov swing in 48 subjects (35 and 13) /238 shows that only three persons did not reveal vestibulo-vegetative disorders during the DPK test. In the remaining 45 subjects, the DPK test revealed vegetative reactions of moderate and very severe nature. Regarding the OR_{10} experiment, this test did not reveal vestibulo-vegetative reaction in 27 subjects (23 and 4) of 48.

Comparing results of tolerance to the OR_{10} experiment and DPK test (Table 5), we also note a definite characteristic which indicates that the OR_{10} experiment is a weaker test to reveal the degree of tolerance of the vestibular apparatus. Thus, 59 subjects of 118 who tolerated the OR_{10} test well displayed vegetative reactions when tested by the DPK method. On the other hand, in almost all cases, when the OR_{10} experiment revealed decreased tolerance of the vestibular apparatus, the two-minute test confirmed it.

TABLE 5. COMPARATIVE CHARACTERISTICS OF VESTIBULO-VEGETATIVE DISORDERS IN SUBJECTS DURING OR_{10} AND DPK TESTING

OR_{10}	DPK			Total
	Good tolerance	Moderately severe vegetative reaction	Very severe vegetative reaction	
Good tolerance	59	46	13	118
Moderately severe vegetative reaction	2	12	18	32
Very severe vegetative reaction	—	—	3	3
Total	61	58	34	153

Similar data were obtained in the studies of a number of air force doctors. /239

The greatest number of coincidences in the degree of severity of vegetative reactions is in testing in the Khilov swing and the DPK test (Table 6).

TABLE 6. COMPARATIVE CHARACTERISTICS OF VESTIBULO-VEGETATIVE REACTIONS IN CANDIDATES IN THE ALL-UNION AVIATION SCHOOL, DEPENDING ON THE METHOD OF STIMULATING THE VESTIBULAR APPARATUS

Degree of otolithic reaction	Khilov swing	DPK	Otolithic reaction
0	—	—	48
I	—	3	5
II	5	6	3
III	51	47	—
Total	56	56	56

Of special interest is the analysis of the data of Table 7, which shows the comparative characteristics of vestibulo-vegetative reactions in cadets beginning flight training (I. L. Litmanov).

TABLE 7. COMPARATIVE CHARACTERISTICS OF VESTIBULO-VEGETATIVE REACTIONS IN A GROUP OF CADETS DEPENDING ON THE METHOD OF STIMULATING THE VESTIBULAR APPARATUS

Degree of vegetative reaction	Khilov swing	OR_{10}	DPK	OR
0	145	132	106	148
I	5	14	29	2
II	—	2	11	—
III	—	2	4	—
Total	150	150	150	150

Thus, testing in the Khilov swing revealed hardly any vestibulo-vegetative disorders, while the DPK test revealed 15 subjects with II and III degree vegetative disorders.

Moreover, it is important to emphasize that these 15 subjects with II and III degree vegetative reactions also revealed one degree or another of vegetative reaction during flights. On this basis we can assume that the /240 nature of vestibular stimulation in the DPK test is most similar to stimuli which occur under real flight conditions of all the vestibulometric tests. We can agree with this assumption, since adequate stimulations in the DPK test are not continuous or monotonic, but with pauses, i.e. the same as occurs under real flight conditions.

Among the advantages of the DPK test should be included the fact that stimulations are strictly proportioned, and the one-minute break (between the two rotations) makes it possible to determine more accurately the nature and degree of severity of vegetative reactions occurring after each minute of stimulation. Moreover, the minute break is a unique test for fluctuation in the rhythm of stimulation, i.e. it permits us to judge the adaptability of the organism and its adaptational capabilities. The fact is that some persons withstand very prolonged and monotonically active stimulation quite satisfactorily, as if they are adapting to the intensity of the stimulus and its rhythm, but should they come under conditions when this rhythm is disrupted, they begin to react vigorously by severe vestibulo-vegetative reactions. It is quite natural that for professional activity of a pilot, and even more so when selecting cosmonaut candidates, it is preferable to select personnel with high mobility of adaptational mechanisms.

Thus, on the basis of the comparative analysis of three vestibulometric methods given, a definite characteristic is noted which indicates that the OR_{10} experiment is the weakest test to reveal the degree of tolerance of the

vestibular apparatus, and the DPK method is the most effective, responsive to problems of professional selection.

Conclusions

1. DPK (a two-minute test for tolerance to accumulation of Coriolis forces) is a simple and economic method timewise, which makes it possible to determine the stability of the vestibular apparatus to the effect of adequate stimuli.

2. DPK makes it possible to reveal increased sensitivity of the vestibular apparatus in those cases when this is not possible by other methods of vestibulometry used in medical flight diagnosis.

3. DPK may be used as a method of conditioning the vestibular apparatus, and as a control of its effectiveness.

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