

MATTERS OF SIMULATION OF THE SEMICIRCULAR CANAL SYSTEM

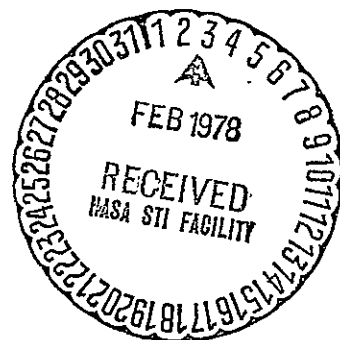
V. S. Gurfinkel' and S. V. Petukhov

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16. Abstract A scale model of the human semicircular canal system is developed based on the theory of dynamic similitude. This enlarged model makes it convenient to conduct tests on the vestibular processes and dynamics in the semicircular canals. The tests revealed hydromechanical interaction between canals, with asymmetry of the conditions of movement of the endolymph in the canals in opposite directions. A new type of vestibular reactions, occurring with angular oscillations of the head, was predicted and demonstrated using this model and human test subjects.			
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MATTERS OF SIMULATION OF THE SEMICIRCULAR CANAL SYSTEM

V. S. Gurfinkel' and S. V. Petukhov

Institute of Information Transmission Problems of the Academy
of Sciences of the USSR, Moscow

It is common knowledge that a complex of sensor signals of different modalities takes part in the formation of the concept of a human "body schematic", its position in space, and mechanisms of posture coordination and posture components of random movements [1]. An important role in this set belongs to information on the effect on the body of inertial and gravitational forces coming from the vestibular apparatus [3].

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In the last two decades, in connection with the growing interest in the vestibular function, much new data has been obtained on the structural and functional characteristics of the vestibular apparatus. The activity of the neurons of the vestibular nucleus, reticular formation, red nucleus, cerebellum, and other neuron structures in response to artificial and natural stimulation of the vestibular apparatus was studied (see review [37]).

Information on the regulation of sensitivity of the vestibular receptors is of substantial significance for an understanding of the vestibular function. Thus, it was shown in study [36], using light and electron microscopy, that the vestibular apparatus receives efferent innervation. Efferent impulses evoke depolarization of the receptor cells of the vestibular analyzer [32] and depress the frequency of impulsion of the primary sensor neuron [21,24,25].

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

The presence of efferent innervation is evidently essential for coordination of afferent flows of different modalities, for discrimination of active and passive effects on the vestibular apparatus, and also for ensuring constancy of the body schematic—an important factor in spatial orientation. In addition, efferent control of the activity of the vestibular receptors complicates analysis of the processes which take place on the level of the receptor section of the vestibular apparatus, in connection with which the necessity occurs of resorting to the method of simulating the primary processes in the vestibular apparatus.

The following essay is devoted to a description of a model of the semicircular canal system, through the use of which an attempt was made to answer the following questions. First of all comes the question of the presence of hydro-mechanical interaction between the semicircular canals, connected in considerable segments by common cavities—the utricle and common limb of the vertical canals. Such interaction was observed with rough mechanical influences on the membranous labyrinth under conditions of fenestration of the osseous labyrinth [35]. Very strong intercanal interaction was demonstrated in study [13] on a model which reproduces the shape of the semicircular canal system on an enlarged scale. Unfortunately, as shown by analysis [6], these data can not be considered conclusive, insofar as the model was constructed without consideration for the requirements of the theory of dynamic similitude. The possibility of appreciable hydromechanical interaction is also affirmed in article [4], devoted especially to the question of hydro-mechanical intercanal interaction, based on tests with local caloric stimulation of individual formations of the labyrinth of a frog. However, it is necessary to note that the utilization of the results of electrophysiological investigations of the ampullar nerves for the purpose of detecting hydro-

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mechanical intercanal interaction is made difficult because of the possibility of the presence of direct neural connections between the cupular receptors of different canals [17].

We also investigated the question of conditions for movement of the endolymph in opposite directions of by-pass of each canal. These conditions are not identical because of the structural features of the canals. This problem was first examined in study [18]. There are contradictory assertions in this regard in the literature; whereas the ampullopetal movement of the endolymph is considered weaker than the ampullofugal in [10,11], the ampullopetal movement is believed to be stronger than the ampullofugal in [13], on the other hand. Both this and the other assertion rely either on speculative reasoning or on very simplified model investigations, and do not finally solve the problem being examined.

Finally, we were interested in the possibility of spontaneous change in the direction of the endolymph flow in the canals a short time after the effect of a cupulometric "stop-stimulus" [13].

The simulation method was used by many authors for studying the functioning of the semicircular canal system as the very first steps in investigating the vestibular apparatus. The necessity of simulation is brought about by the great complexity of investigations of a natural semicircular canal system, which is small in size, included in the hard-to-reach petrosal portion of the temporal bone; its membrane is opaque and easily deformed during exposure of the labyrinth in the cranium. Another complicating factor for the experimenter is the fact that the processes which occur in the membrane of the revolving labyrinth should be subjected to study. The well-known possibility of judging the deflection of the cupulae according to the change in frequency of impul-

sation in the ampullar nerve is limited, as has already been noted, by the presence of an efferent nervous system in the vestibular analyzer, capable of changing this frequency without any deflection of the cupulae.

The models of functioning of the semicircular canals described in the literature can be conditionally subdivided into analytic and demonstration. The authors of the analytic models ([2,8,33,38] and others) attempted to describe the dynamics of the intracanal processes in the language of mathematical equations, based on individual experimental data and speculative hypotheses. These models are of great use for formulating and clarifying many questions, but they are distinguished by considerable randomness of the initial hypotheses or conscious simplicity of the description. At present, the analytic model of a semicircular canal proposed by Steinhäuser [33] is the most useful. It is based on a simplified idea of the semicircular canal as an isolated torus, having a resilient septum and filled with endolymph.

The demonstration models ([10,12-14,20,29,30] and others) usually reproduced in glass, more or less completely, the form of the semicircular canal system, and were filled with a fluid which was similar to endolymph in its properties. With rotation of these models, a flow of fluid was observed directly in the canals, which approximately reproduced the intracanal processes of the natural system. Using such models, answers were obtained to important questions on the laminar nature of the flows in the semicircular canals, on the independence of the endolymph flow from the radius of rotation, on the time of post-rotation flow of endolymph, and others. But, the possibilities of the demonstration models in the past were seriously limited by the following circumstances. The models, having the dimensions of the natural system, facilitated the investigation little, since it is difficult to establish model cupulae in a

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miniature membrane (diameter of the system is equal to 8 mm), and one can observe the flow of fluid in the canals only under a microscope. An increase in the dimensions of the membrane without a corresponding change in the remaining parameters of the system lead to the circumstance that the dynamics of the natural processes would no longer be reproduced in the model. In addition, the previously-used visual method of observing what goes on in the membrane made it possible to study only the stage of fluid movement after cessation of rotation of the model.

It is shown in the present study that the indicated difficulties are surmountable. Described below is a scale model of the semicircular canal system in man, which reproduces the dynamics of the natural processes under physical experimental conditions which are convenient for their study. In developing this model, it was necessary to take into account some requirements of the theory of dynamic similitude, to the presentation of which we will now pass.

If one thinks, as is generally accepted, that the membrane of the membranous labyrinth is smooth from within and sufficiently solid so as not to be deformed with normal rotations of the head, then the dynamics of the processes in the membrane of the semicircular canal system are determined by six physical parameters: dimensions of the membrane, which are given, with a fixed form, by any characteristic linear dimension l of the membrane; the time t of the flow of non-stationary processes in the system; the viscosity η ; the density ρ of the intracanal medium and the resilience of the cupulae α ; the angular acceleration $\dot{\omega}$ of the membrane of the system.

We will pose the question: can one change the values of individual parameters in an arbitrary manner while still maintaining the dynamics of the natural processes in the semicircu-

lar canal system unchanged? The answer, which will be obtained below using the methods of the dynamic similitude theory (see [9], for example), consists of the following: one can change three of the six indicated parameters in an arbitrary manner and maintain the dynamics of the natural processes in an enlarged membrane which is geometrically similar to the membrane of the semicircular canal system, because of the appropriate selection of the magnitudes of the three remaining parameters. For example, the values of ℓ , η , and ρ can be subjected to change and this does not have an effect on the dynamics of the processes with the appropriate selection of the scales of α , ω , and t .

Thus, it is possible, in place of the study of the processes in a natural membrane of small dimensions, filled with physiological fluid, to study those same processes in a membrane with arbitrarily larger dimensions and intracanal fluid selected through consideration of experimental convenience.

We will prove the assertion that has been made. If one designates the dimensions: length— L , mass— M , time— T , then the dimensions of density, viscosity, resilience, and angular acceleration, respectively, have the forms $[\rho]=M/L^3$; $[\eta]=M/LT$; $[\alpha]=M/T^2$; $[\omega]=1/T^2$ (the angle is considered a dimensionless magnitude). Like any other characteristics of the occurrence of processes in the semicircular canal system, the angular deflection θ , which we are especially interested in, can be written as a function of six definite parameters:

$$\theta = \theta(\ell, t, \eta, \rho, \alpha, \omega). \quad (1)$$

Of these six parameters, a total of three are independent according to dimensions, i.e. their dimensions can not be represented as a power monomial from the formulas of dimensionality for other parameters. We will choose ℓ , t , and η as independent (one can also take the other three parameters, but, with

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the given selection, the final result has a more visible form). The dimensions of the remaining values can be expressed through the dimensions of l , t , and η :

$$[\rho] = \frac{[\eta] \cdot [t]}{[l]^2}; \quad [\alpha] = \frac{[\eta] \cdot [l]}{[t]}; \quad [\omega] = \frac{1}{[t]^2}. \quad (2)$$

If the units of measurement of the values of l , t , and η are changed by β_l , β_t , and β_η times, respectively, i.e. if we change to $l' = \beta_l l$, $t' = \beta_t t$, and $\eta' = \beta_\eta \eta$, then the values of ρ , α , and ω are also transformed in the new system of units of measurement:

$$\rho' = \frac{\beta_\eta \beta_t}{\beta_l^2} \rho; \quad \alpha' = \frac{\beta_\eta \beta_t}{\beta_l} \alpha; \quad \omega' = \frac{\omega}{\beta_t^2}. \quad \text{Relationship (1) expresses some physical regularity, and, therefore, does not depend on the system of units of measurement. In the new system of units}$$

$$\Theta = \Theta \left(\beta_l l, \beta_t t, \beta_\eta \eta, \frac{\beta_\eta \beta_t}{\beta_l^2} \rho, \frac{\beta_\eta \beta_t}{\beta_l} \alpha, \frac{\omega}{\beta_t^2} \right). \quad (3)$$

The scales of β_l , β_η , and β_t are arbitrary. We will use the selection of these scales in order to reduce the number of arguments in the function of Θ . We will set $\beta_l = 1/l$; $\beta_t = 1/t$; $\beta_\eta = 1/\eta$, i.e. we will select the system of measurement so that the values of the first three arguments would be equal to one. Then

$$\Theta = \Theta \left(1, 1, 1, \frac{l^2 \rho}{\eta t}, \frac{t \alpha}{\eta l}, \omega t^2 \right). \quad (4)$$

It is not difficult to see that the arguments are dimensionless. Thus, from relationship (1) with six dimensional arguments, we arrive at the equivalent relationship (4) with three dimensionless arguments. These three dimensionless ratios

$$\frac{l^2 \rho}{\eta t}, \quad \frac{t \alpha}{\eta l}, \quad \omega t^2 \quad (5)$$

are the similitude criteria of the processes in the semicircular

canal system in man and all vertebrate animals. It is evident from (4) that the maintenance of the value of the similitude criteria guarantees reproduction of the dynamics of the natural processes in the membrane which is geometrically similar to the membrane of the initial system with the same accuracy with which the processes in the system are determined by the six physical values considered. One can change the values of the three dimensionless parameters (ℓ , η , and ρ , for example) while maintaining the dynamics of the natural processes, because of the compensating change in the remaining parameters. This possibility was also utilized by the authors to construct a physical scale model of the human semicircular canal system. The given proof is a supplement to the Π -theorem of the theory of dynamic similitude [9]) for the case of processes in semicircular canals.

We will move to the description of the constructed scale model of the human semicircular canal system (fig. 1). The data on the dimensions of the membrane of this system are basically taken from [16], and also from studies [15,23]. The constructed model¹ reproduces in glass the form of the right half of the human semicircular canal system, with linear dimensions enlarged, through consideration of experimental convenience, 49 times, as compared with the natural dimensions [5]. Glycerin was selected to fill the glass membrane, which brings about a change in density and viscosity of the intracanal medium from $\rho=1.0 \text{ g/cm}^3$ and $\eta=0.85 \cdot 10^{-2} \text{ g/cm} \cdot \text{sec}$ at 35° C in the natural labyrinth [36] to their model values $\rho=1.26 \text{ g/cm}^3$, $\eta=14.9 \text{ g/cm} \cdot \text{sec}$, at an experiment temperature of 20° C . Having designated ℓ , ρ , and η with model values from the requirement of maintaining the values of the similitude criteria (5), we obtain the relationships between the model (m) and natural (n) values of the resilience α of the cupulae, the angular acceleration ω , and the time τ of occurrence of the processes:

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$$\alpha_m \approx 4.9 \cdot 10^4 \alpha_n; \omega_m \approx 3\omega_n; t_m \approx 1.75t_n.$$

(6)

Thus, in order to reproduce the dynamics of the natural processes, the model should be rotated with a threefold lesser acceleration than that whose effect on the vestibular apparatus interests us, and the processes in it will be extended 1.75 times in time.

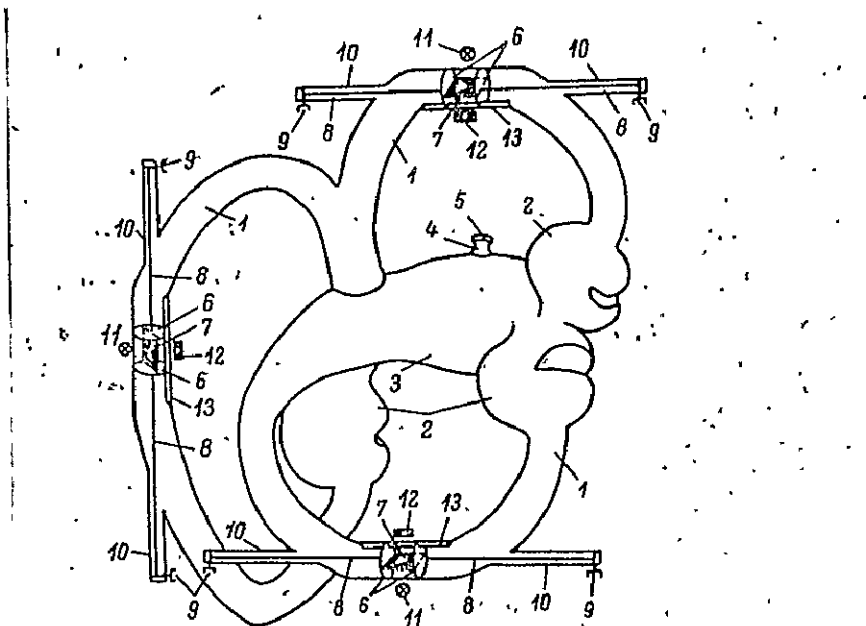


Fig. 1. Schematic of Scale Model of Human Semi-Circular Canal System.

1—semicircular canals; 2—ampullae; 3—utricle; 4,5—neck with stopper for filling the model with glycerin. The rest of the designations and the description of the model are in the text.

Insofar as the structure of the cupula can be considered unchanged with deflection of the cupular cover, and the deformation of the front of the moving fluid by the cupula can be considered insignificant, it is assumed, with simulation, that: each cupula is considered a solid movable plug, suspended in the surrounding fluid and spanning the entire cross-section of the canal; the effect of the cupula on the magnitude of the longitudinal displacement of the intracanal medium is de-

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terminated entirely because of the resilient forces which strive to return the deflected cupula to a position of rest. This concurs with the observations in study [13].

To the extent that the formulated hypothesis is correct, it is not important where the model is mounted—in the ampulla or in the semicircular canal itself, as long as the effect of resilient forces of the required magnitude on the processes in the system is maintained. (The location of the natural cupulae in the ampullae is probably explained by the fact that the range of linear functioning of the cupular receptors is limited and, in order to prevent going beyond the boundaries of this range, the cupulae are mounted in broadened ampullae, where the displacement of the medium is less than the displacement of the medium in the canal itself). It is natural that the resilience coefficient of the cupula, with its location in the canal, should be decreased by as many times as the area of the cross-section of the canal is less than the area of the cross-section of the ampulla. The displacement of the medium in the canal is precisely this number of times greater than in the ampulla, and, thus, the required magnitude of the resilient forces, equal to the product of the resilience coefficient and the displacement of the cupula, will be maintained.

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All of this was considered during the installation of the cupulae, with consideration for technological simplicity, inside of the canals which were homogenous in cross-section in small rectilinear sections, rather than in the ampullae. The model cupula (fig. 1) is a membrane, suspended in the surrounding fluid and well-fitted to the size of the canal, of two disks (6), and the average density of the membrane is equal to the density of the glycerin, which protects it directly from two undesirable effects—displacement of the model cupula under the influence of inherent weight, and the occurrence of dry

friction with movement of the cupula because of its pressure on the walls of the canal.

Stabilizing resilient forces are imparted to the cupula because of its extension on thin resilient fibers 8, the ends of which are fastened to acicular portals 9. These portals make it possible to control the magnitude of the resilient forces of the cupula by means of winding of the fibers 8 on them. The portals 9 are located in hollow glass processes 10. The inclusion of processes 10 filled with immobile fluid in the model in no way affects the dynamics of the fluid flows in the system, but makes it possible to take a resilient fiber 8 of increased initial length for broadening the range of control of the resilient forces of the cupula and, in addition, to locate the portals 9 in them, rather than in the canals themselves, where the portals could hinder the fluid flow.

It is common knowledge from the literature that the return of the deflected cupula to a position of equilibrium, under the effect of only inherent resilient forces, is approximately described by the exponent $e^{-0.1t}$ [22,28]. In the constructed model, the resilience of the cupulae was selected so that the time of return of the deflected model cupulae to a position of equilibrium was equal to the time of the natural system, determined by the exponent $e^{-0.1t}$, multiplied by the coefficient of similitude 1.7 (see relationship (6)).

The system for recording the displacements of the model system (*i.e.* the parameter which determines the signals entering the input of the nervous system from the vestibular apparatus) utilizes a light source 11 and a photoresistor 12, fastened under the cupula on the outside of the canal opposite each other. The amount of light falling on the photoresistor

from the light source 11 is determined by the position of the light-distributing screen 7 in the canal, which is fastened to the disks of the cupula. In order to prevent undesirable turns around their central axes, which can introduce distortions with the given schematic of registration of the desired longitudinal movements of the cupulae, the disks are mounted on a guide rail 13.

In order to conduct experiments, the model is placed on a rotating unit, capable of providing the required rotational conditions. With the effect of rotations, the characteristics of which correspond to physiological rotations, the movements of each of the cupulae occur within the limits of the straightened section of the canal ($1/20$ part of the circumference of the canal). The light-distributing screen 7, which shifts with each cupula, changes the amount of light striking the photoresistor 12 proportional to the shift of the cupula. The desired movements of the cupulae of the semicircular canal system are registered on the tape of an oscillograph, for example, according to the magnitude of the resistance of the photoresistor.

Through adjustment of the model, a special check was conducted of the correspondence of some functional features of the model to the features of the natural semicircular canal system. First, we checked to see whether each model cupula covered the cross-section of its canal sufficiently completely. India ink injected into the model canal on one side of the cupula practically did not penetrate to the other side of the cupula with shifts of the intracanal medium, which is correct for natural semicircular canals as well [33]. Second, it was established that changes in the position of the model relative to the vector of gravitation do not change the position of the cupulae in the canals, i.e. the model cupulae are insensitive to the effect of the force of gravity,

just like the cupulae of the natural labyrinth are insensitive to it (see review [7]). Of course, it would have been extremely desirable to compare the characteristics of the shifts of the model cupulae in some cases of accelerated rotation with the corresponding characteristics of the natural cupulae. Specifically, a similar comparison could have shown how completely the dynamics of the processes in the system are determined by the physical parameters taken into account during the derivation of the criteria of similitude of the processes in the semicircular canals. This is hindered by the absence of quantitative data in the literature, obtained in studies directly in the natural labyrinth.

We will switch to the description of experiments on the scale model of the human semicircular canal system. All of the experiments cited below on rotation of this model were carried out on the VU-4—a specialized rotation unit designed for vestibular testing of people and animals.

The placement of the model of the semicircular canals on the VU-4 required the manufacture of a special platform, which reliably fixed the model in various positions relative to the axis of rotation, which made it possible to select the required plane of rotation of the model.

In order to answer the question of hydrodynamic intercanal interaction, the model was brought from a state of rest into rotation in the most characteristic planes, with different values of constant angular acceleration from 3 to $110^\circ/\text{sec}^2$. In connection with the fact that the values of the angular accelerations should triple (see relationship (6)) with interpretation of the data of the model experiment with regard for the natural human semicircular canal system, the utilization of these accelerations corresponds to the rotation of humans with accelerations from 9 to $330^\circ/\text{sec}^2$, which covers the range

of angular accelerations used during normal vestibular studies. The degree of stimulation of each canal was judged according to the relative magnitude of the shifts of the model cupulae. Recording of the movements of the model cupulae was carried out on the N-135 oscillograph, the paper roller of which was switched on from the control panel of the VU-4 right before the beginning of rotation of the model. Also recorded, in addition to movements of the cupulae, was the signal from the VU-4 remote panel, which controls the rotation of the unit. An example of the oscillograph recording is given in figure 2. The results of rotation of the model in some planes are given in figures 3-5. With rotation of the semicircular canal system in a direction opposite to that indicated in the captions to the figures, the signs of deflection of the semicircular canals change to the opposite, and the magnitude of the deflection changes by no more than 5-7%.

Proof of the existence of hydromechanical interaction is given, for example, by rotation of the model in the plane of the horizontal canals, with which, as experiments showed, not only the horizontal canal is stimulated, but also the two vertical canals, the position of which perpendicular to the plane of rotation excludes their independent stimulation in the absence of a connection with the horizontal canal. A graph is presented in figure 3 which demonstrates the fact that deflection of the intracanal medium, of the anterior vertical canals, for example, during rotation of the model in the plane of the horizontal canals reaches 15% of the deflection of the intracanal medium of the horizontal canals. For verification of the fact that the vertical canals are actually stimulated in the given case because of the presence of movement of the fluid in the horizontal canal, plugging of the horizontal canal was carried out, which precluded movement of the glycerin in it. Under these conditions, with the examined rotation, the vertical canals also ceased to be

stimulated. With rotation in the plane of the vertical canals, the horizontal canal is almost not stimulated (see fig. 7), which corresponds to the results of electrophysiological studies [26].

On the whole, the data obtained on the model indicate that /155 it is only possible to view the system of semicircular canals as a set of isolated rings quite approximately. We did not detect changes in the direction of flow of the fluid to the opposite direction during rotation of the model with constant velocity, which differs from the results of experiments [13] on a model created without regard for the requirements of the theory of dynamic similitude.

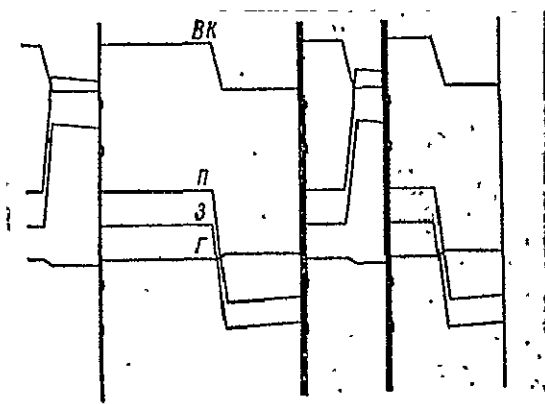


Fig. 2. Example of oscillograph recording of displacement of model cupulae during rotation of model
BK—rate of rotation of seat;
 π —displacements of cupula in anterior canal; 3—same in posterior canal; Γ —same in horizontal canal.

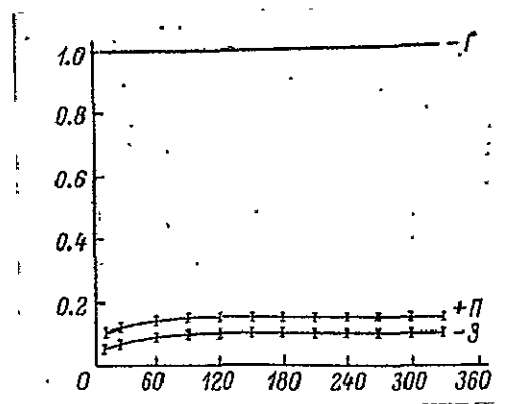


Fig. 3. Relative displacement of endolymph in three semicircular canals (π , 3, Γ) of the right labyrinth with rotation of the head in the plane of the horizontal canals on the left.

x-axis—magnitude of angular acceleration of model, multiplied by three, for coordinating the results to the case of rotation in man, $^{\circ}/\text{sec}^2$; y-axis—relative displacements of cupulae, portions of displacement of cupula of canal stimulated most in the given situation, assumed per unit; + sign—deflections of cupula, leading to an increase in frequency of ampullar impulsation in a natural labyrinth; - sign—opposite deflections.

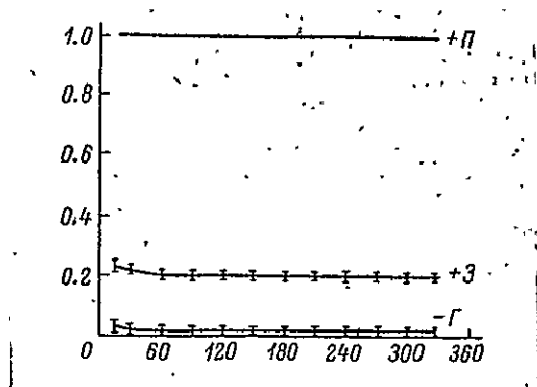


Fig. 4. Relative displacement of endolymph in three semi-circular canals of the right labyrinth with rotation of the head in the plane of the anterior right canal "forward-to the right".

Designations are the same as in figure 3

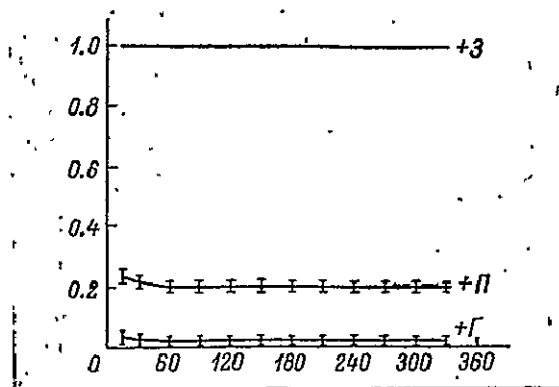


Fig. 5. Relative displacement of endolymph in three semi-circular canals of the right labyrinth with rotation of the head in the plane of the right posterior canal "backward-to the right".

Designations are the same as in figure 3.

The dismountable membrane of the physical scale model of the semicircular canal system makes it possible to carry out interchangeable installation of different parts of the membrane for studying the effect of the shape and dimensions of its individual parts on the dynamics of the processes in the system. For example, it is common knowledge that the cross-section of the common limb of the vertical canals is extremely distinctive for animals of different species. In order for verification of what kind of influence the magnitude of the cross-section of the common limb has on the processes in the system, a specially-manufactured common limb with a cross-section three times smaller than normal was installed in the model. The experiments showed that with such a change in the membrane of the system, intensification of the hydromechanical interaction between the vertical canals, and its weakening with respect to the effect of the horizontal canals on the vertical, is characteristic for rotation in the majority of the planes.

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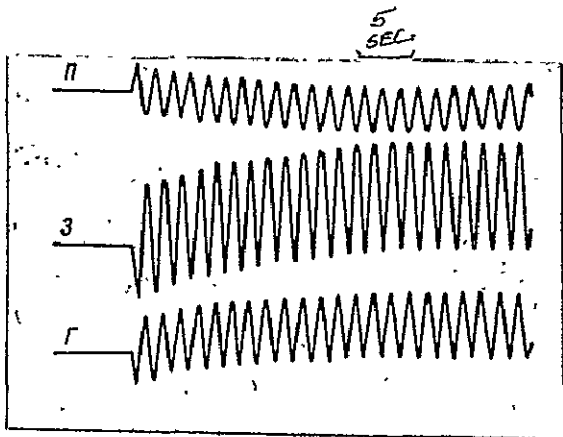
We will now turn to the functioning of the vestibular apparatus with angular oscillation of the head. We studied the behavior of the cupulae in the scale model of the human semicircular canal system with sinusoidal angular oscillations of the model on a VU-4 rotating unit. Fastening of the model to the unit and recording of the movement of the model cupulae were accomplished in the same way as in the experiments described above. Shown in figure 6 is the behavior of three

cupulae of a single labyrinth with angular oscillations of the model.

By the best approximation, the differ-

Fig. 6. Movement of cupulae with sinusoidal angular oscillations of the model of the semicircular canal system.

Displacement of any of the presented quasisinusoids upward (downward) is associated with the displacement of the corresponding cupula in the direction of an increase (decrease) in the frequency of ampullar impulsation. π —anterior, β —posterior, Γ —horizontal canal.



ence between any of the represented curves and the sinusoidal curve according to which the cupula should oscillate, according to Steinhäuser's equation, consists of the accumulation of the constant component, which strives for some maximum value with the passage of time. This maximum value is greater the greater the frequency and amplitude of the angular oscillations of the head.

We will call the accumulating constant component of the deflection of the cupula the differential deflection. This appellation is suggested on the strength of the following associations: the given accumulation is accomplished by small portions (in mathematics, a differential denotes a small increment), and its cause consists of the difference in the conditions of

f_1

movement of the endolymph in opposite directions. We will agree to consider the differential deflections positive if the cupula shifts towards an increase in the frequency of the ampullar impulsation, and negative with a shift of the cupula in the other direction. The accumulation of differential deflections of the cupulae with angular oscillations of the head probably occurs in the vestibular labyrinths of all animals, but the nature of this asymmetry should be established in each case by an individual investigation. The differential deflections of the cupulae in man, as shown by studies on our physical model of the semicircular canal system, are negative in the anterior vertical canals and positive in the horizontal and posterior vertical canals.

We would note that it was tests on a physical scale model of the semicircular canals that revealed the accumulation of the constant components of deflection of the cupulae with angular oscillations of the semicircular canals, and drew our attention to the existence of asymmetry of the conditions for movement of the fluid along the canal in opposite directions of by-pass. Recent searches in the literature made it possible to establish that this phenomenon was noted earlier in studies [11,13,19]. The assertions of these authors have already been cited at the beginning of our article. However, we did not manage to find studies in which the accumulation of the constant components of deflection of the cupulae with oscillation of the head was shown or hypothesized. /157

The indirect corroboration of the differential deflection of natural cupulae revealed in tests on our models of the human semicircular canal system can be seen in [19]. In this study, carried out on monkeys, it is demonstrated that, with angular sinusoidal oscillations of the natural semicircular canal system, the activity of the cupular afferents, modulated according to a distorted sine curve, shifts sequentially relative to the

activity level at rest with each period of time, as should be the case with the accumulation of the differential deflections of the cupulae (fig. 7). The authors point out that such a quasi-sinusoidal character can not be explained based on Stein-

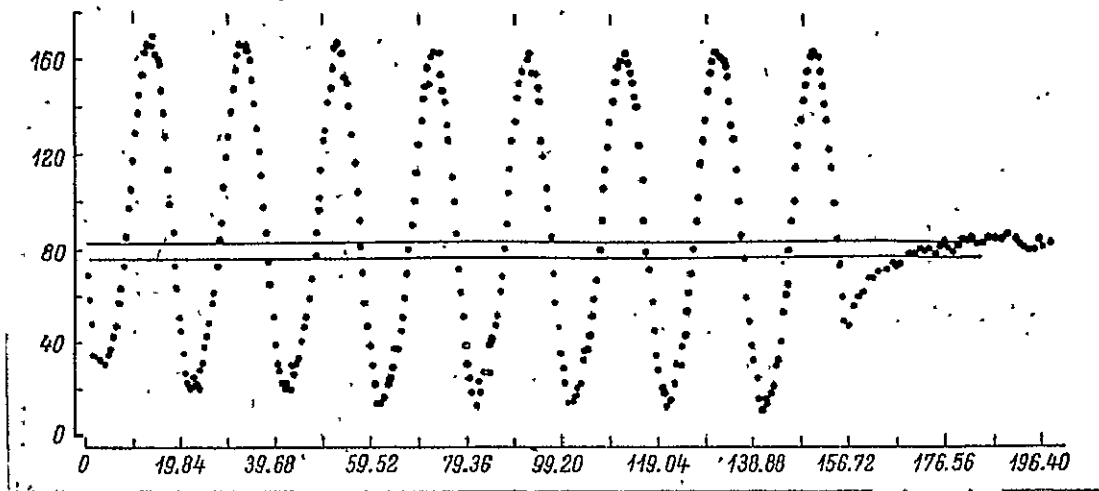


Fig. 7. Ampullar impulsation of the anterior semicircular canal of a monkey with angular sinusoidal oscillations of the head with a frequency of 0.05 Hz. x-axis—time, sec.; y-axis—frequency of ampullar impulsation, impulses/sec.; lower and higher horizontal lines on the graph—levels of impulsation at rest before and after the oscillations, respectively (according to [19]).

hausen's model, and this non-correspondence is attributed to the dynamic features of the afferents which innervate the semicircular canals. It seems to us that the gradual shift of the constant component of ampullar impulsation can be explained more simply by the accumulation of differential deflections of the cupulae, the possibility of which the authors overlooked.

One can correct Steinhausen's equation so that it would reflect the difference in hydrodynamic resistances with movement of the endolymph in different directions of by-pass of the semicircular canals. For this purpose, it is necessary to make the value of the viscosity term in Steinhausen's

equation dependent on the direction of movement of the endolymph, thereby modifying the linear equation into a non-linear equation:

$$I\ddot{\theta} + C(\text{sign } \dot{\theta})\dot{\theta} + K\theta = I\dot{\omega}, \quad (7)$$

where

$$C(\text{sign } \dot{\theta}) = \begin{cases} C' \text{ with } \dot{\theta} > 0, \\ C'' \text{ with } \dot{\theta} \leq 0. \end{cases}$$

Here, θ , $\dot{\theta}$, and $\ddot{\theta}$ are the angular shift, angular velocity, and angular acceleration, respectively, of the endolymph on the axis of the canal relative to its walls; I is the moment of inertia of the endolymph ring; K is the moment of the resilient forces per unit of angular deflection; $\dot{\omega}$ is the component of angular acceleration of the skull relative to inertial space, perpendicular to the plane of the semicircular canal; C' and C'' are the moments of the forces of friction per unit of angular velocity with movement of the endolymph in opposite directions.

The study of equation (7) on an MN-7 analog computer, with a sinusoidal character of the angular acceleration, showed the good qualitative suitability of this equation for describing the movement of the endolymph with angular oscillation of the semicircular canal. Specifically, by means of comparison with the results of angular oscillation of the physical model of the semicircular canals in the physiologically normal range, it was gathered that the value of the coefficients $P=C'/C''$ was within the interval $0.9 < P < 1$ for any of the canals.

The obtained data of the model studies have the most direct relationship to the vestibular reactions of the body, particularly with the effect of mechanical oscillations on man. Thus, based on the model results set forth, we predicted and recorded [6] the existence of a new class of so-called differential vestibular reactions, which should be displayed as a re-

sult of angular sinusoidal oscillations of the human head, and cannot be principally explained on the basis of Steinhäusen's idealized model, which represents the semicircular canal system as a set of isolated tores.

This prediction was based on the following initial thesis: the constant components of deflection of the cupulae in one of the directions with sinusoidal angular deflections of the head are interpreted by the body as a result of the effect, in addition to oscillator accelerations, of constant angular accelerations, of which there are actually none. The given hypothesis is natural, since it is well-known that one can achieve shifts of the cupulae and a change in the frequency ampullar impulsation by many inadequate methods (caloric stimulation, stimulation by electric current, etc.), but the vestibular reactions in this case will be the same as if angular accelerations, leading to a similar change in the frequency of ampullar impulsation, were acting on the semicircular canals. The taking into account by the body of non-existent constant angular acceleration with angular oscillations of the head should lead to the appearance of additional sensor-motor reactions which do not correspond to the actual situation. The features of these reactions depend on the plane and parameters of the oscillations.

In directed experiments with the participation of test subjects, we revealed [6] the following differential vestibular reactions, which had been predicted beforehand: a) differential vertical nystagmus as a result of angular oscillations of the head in sagittal-symmetric planes, frontal and horizontal, for example; b) differential oculogyral illusion of movement of a luminous target in the sagittal plane in the dark as a result of angular oscillation of the head in sagittal-symmetric planes; c) differential sagittal-asymmetric nystagmus as a re-

sult of angular oscillation of the head in planes which are mirrored-asymmetric relative to the sagittal plane; d) convergence or divergence of the eyes and accompanying illusion of splitting of objects in the field of vision parallel to the plane of the horizontal canals as a result of angular oscillations of the head.

The ideas of the asymmetry of the dynamics of the processes in the vestibular apparatus make it possible to point out the accumulation of differential deflections of the sensitive elements of the vestibular apparatus as an additional reason for the development of motion sickness in people and animals. The indicated ideas are useful during the simulation of disturbances of spatial perception and for the development of procedures for vestibular training and professional selection.

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