

MASSACHUSETTS INSTITUTE OF TECHNOLOGY

FINAL REPORT OF RESEARCH ON
BIOPHYSICAL EVALUATION OF THE
HUMAN VESTIBULAR SYSTEM

NASA Grant NGR 22-009-156

Principal Investigator: Prof. L.R. Young



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Department of Aeronautics and Astronautics
Center for Space Research
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Cambridge, Massachusetts

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INTRODUCTION AND SUMMARY

The research conducted under NASA Grant NGR 22-009-156 has been aimed at increasing our understanding of vestibular function by the combined approach of advanced measurement and mathematical modelling. Fundamental measurements of some physical properties of endolymph and perilymph, combined with nystagmus measurements and fluid mechanical analysis of semicircular canal function furthered the theory of canal mechanical response to angular acceleration, caloric stimulation and relating linear acceleration. The effects of adaptation seen at low frequency angular stimulation was studied and modelled to remove some shortcomings of the "torsion pendulum" models. Otolith function was also studied experimentally and analytically, leading to a new set of models for subjective orientation.

Applications to special problems of space, including the case of rotating spacecraft were investigated and one line of research - the illusion of self-movement created by rotating visual scenes - is being exploited for flight simulation and possible space application. The interaction of visual and vestibular cues and their relation to proprioceptive information was explored relative to postural control.

Several areas of clinical interest were explored as by-products of this research, including the investigation of caloric tests, galvanic stimuli for vestibular diagnosis, and postural stability, and the etiology of motion sickness. Some of the nystagmus reduction instrumentation and programs should have clinical utility.

Research under this grant was used for the preparation of 3 Ph.D. theses and 5 M.S. theses. The research was directed by Professor Laurence R. Young, Director of the Man-Vehicle Laboratory, with Professor Y.T. Li. Professor Jacob L. Meiry played a major role in the research from 1965 to 1970. Professor Renwick Curry participated in the modelling activity and Professor Charles Oman was active in most phases of the research, as graduate student in 1967 and more

recently as a faculty member. Our principal medical collaboration has been with Alfred M. Weiss, M.D., who is also Head of Otoneurology at the Massachusetts Eye and Ear Infirmary.

This research was under the overall technical supervision of Walton Jones, M.D. of NASA Headquarters.

SECTION ONE

PHYSICAL PROPERTIES OF THE LABYRINTHINE FLUIDS

Contents

- 1.0 Introduction
- 1.1 Microviscometer
 - 1.1.1 Description of microviscometer
- 1.2 Measurements
 - 1.2.1 Density measurements
 - 1.2.2 Thermal Coefficient of Expansion
 - 1.2.3 Coefficient of thermal conductivity

Related Publications:

Steer, 1967

Steer et al, 1967

I. PHYSICAL PROPERTIES OF THE LABYRINTHINE FLUIDS

1.0 Introduction

To provide the best foundation for our study of the vestibular apparatus, a detailed knowledge of the physical properties of the labyrinthine fluids was essential. The chemical properties of these fluids, the endolymph and the perilymph are known and tabulated, but the data on the physical properties was scarce and very limited in scope. Consequently, an experimental program to measure the relevant characteristics of the fluids was outlined and the following properties were measured: density, coefficient of volume expansion, viscosity, thermal coefficient of viscosity, and thermal conductivity (Steer, 1967).

Because of the necessity of performing measurements with very small samples, on the order of one microliter, standard instrumentation was inadequate and the adaptation of existing measurement techniques to the task involved recalibration of the instruments and construction of a precise microviscometer. This also made necessary the use of modified sample handling procedures.

1.1 Microviscometer

The microviscometer built was designed along the principle of the rolling ball viscometer of Flowers. The viscosity of a fluid measured with this viscometer is determined to a first order approximation by the formula

$$\mu = \frac{K}{v} [\rho_B - \rho_F] = At[\rho_B - \rho_F]$$

where

ρ_B = density of ball

ρ_F = density of fluid sample

v = terminal velocity of ball in the fluid

t = time for ball to travel a fixed distance

K, A = gain constants of the instrument

To further improve the accuracy of the measurement of the velocity of the rolling ball, in our viscometer, the velocity is measured over a small (1 cm) distance at the end of the tube, long after the terminal velocity has been reached. One source of error arises from the variation of the gain constant of

the instrument, A, with temperature. This variation, however, is taken into account by careful calibration of the instrument with known fluids at several temperatures.

1.1.1 Description of the Microviscometer

The basic velocity (or time) measurement unit is an epoxy block with two miniature lamps and photodiodes to measure the time of travel of a tungsten carbide sphere in a miniature pipette. A modified 5 μ l lambda pipette containing the sample is mounted in such a manner that both light beams are broken by the rolling sphere and the time interval as presented by the outputs of the photodiodes are recorded by external electronic circuitry. The epoxy block is mounted on a hinged platform at an angle of twenty degrees from the horizontal and is provided with an external cable to tilt the platform to return the ball to the beginning of the tube. The inclined plane is mounted on a ten inch triangular plate which is provided with two levels and two adjustable legs for leveling and power resistors for control of fluid temperature. The sample temperature is monitored by a thermocouple mounted in the epoxy block. Open loop temperature control will be applied unless measurement accuracies require a closed loop controller. The entire apparatus is confined by a plexiglass case for temperature stabilization and cleanliness. Time measurements are made via an electronic counter to an accuracy of 10^{-6} seconds.

In practice, it was found to be necessary to modify some of the original design features of the microviscometer. The first of two major changes was the inclusion of a closed loop temperature controller to maintain the sample within 0.1° C of the desired temperature. It was also found to be necessary to include an electrostatic shield in the design of the instrument to eliminate the effects of the electrostatic force field on the rolling sphere.

1.2.1 Density measurements

The measurement of viscosity by the "rolling sphere" viscometer requires knowlege of the density of the fluid measured. However, since the tungsten carbide sphere used in our micro-viscometer has a density near 13, and the labyrinthine fluids have densities near 1, then the absolute accuracy of their

differences is relatively insensitive to errors in the density measurement of the fluids. It is sufficient for this purpose to measure densities to an absolute accuracy of $\pm 2\%$.

Using a precision chemical balance to weigh a calibrated micropipette empty, filled with water, and filled with cat or human endolymph or perilymph, it was found that the labyrinthine fluids' density is indistinguishable from that of water to an accuracy of $\pm 2\%$.

1.2.2 Thermal Coefficient of Expansion

To calculate the torque on the endolymph due to caloric stimulation, it is necessary to know the change in the density of endolymph due to variations in temperature. For this purpose it is useful to recall that:

$$\frac{\partial V}{V \partial T} = \frac{-\partial \rho}{\rho \partial T}$$

where

- V = volume
- ρ = density
- T = temperature

The coefficient of expansion ($\frac{\partial V}{V \partial T}$) was obtained by measuring the change in length of a 0.500 inch column of fluid in a glass capillary. A microscope equipped with a micrometer adjustable table having a resolution of 0.05×10^{-3} inches was used for the readout instrument. By measuring the change in length for a 10°C change in temperature and taking into account the expansion of the glass pipette, the coefficient of expansion was found to be $4.4 \times 10^{-4}/^\circ\text{C}$ for cat and human endolymph and perilymph. Error analysis bounds the measurement accuracy to $\pm 5\%$.

1.2.3 Coefficient of Thermal Conductivity

A device to measure the thermal conductivity of small samples was constructed. It measured the time constant of decay of the thermal gradient between two insulated bodies connected by a tube of fluid.

SECTION TWO

FLUID DYNAMIC ANALYSIS OF THE CUPULAR-ENDOLYMPH SYSTEM

Contents

- 2.0 Introduction
- 2.1 The Endolymph as a Newtonian Fluid
- 2.2 Analysis of Flexible Canals
 - 2.2.1 The Flexible Semicircular Canal as a Roller Pump
 - 2.2.2 A Model for Canalicular Response to Rotating Linear Acceleration Stimuli
- 2.3 Rotating Linear Acceleration Stimulation Experiments
 - 2.3.1 Conclusions
- 2.4 Pressure Differences and Cupula Deflections
- 2.5 Summary

Related Publications:

- Katz, 1967
- Steer, 1967
- Young, 1969
- Young and Oman, 1970

2.0 Introduction

The dynamic response of the semicircular canals as measured by rotatory nystagmus or subjective estimation of angular velocity was in disparity with theoretical models of the canals. Approximate analytical attempts to evaluate the characteristics of the canals in terms of time constants of the transient response resulted in estimates of these characteristics outside the range observed experimentally. In an attempt to resolve the gap between theory and experiment in this area of vestibular research, we initiated an analytical effort to solve the Navier-Stokes equations associated with the flow of endolymph in the canals. With the knowledge of the physical properties of the labyrinthine fluids, the exact formulation of these equations is feasible (Steer, 1967).

Our research activities in this area of fluid dynamics proceeded along two parallel directions. One approach considered the laminar flow of a Newtonian fluid in a solid, inflexible tube when subjected to angular accelerations. The solution of these Navier-Stokes equations, either in a closed form or by successive iterations, should present an analytical transfer function of the semicircular canals relating skull rotation to cupular deflection.

The second effort attempted to analyze the fluid flow in the semicircular canals assuming a flexible wall structure. This investigation was carried out in order to determine whether linear accelerations can induce fluid rotation in a flexible tubular angular accelerometer. This was an attempt to establish analytically the sensitivity of the semicircular canals to linear accelerations based on several assumptions about canal structure.

2.1 The Endolymph as a Newtonian Fluid

From the results of our measurements of the labyrinthine fluids, it is clear that the assumptions of a Newtonian Fluid undergoing laminar flow are indeed valid. The validity of the assumption of a "rigid" tube may, however, be questioned. Since the measured densities of the endolymph and perilymph are very

nearly identical, the canal system must be very nearly neutrally buoyant and thus not appreciably distended by the application of linear or angular acceleration.

Although the Navier-Stokes equations are simple in form, they are difficult to apply in practice. For preliminary analysis, it is expedient to use a conformal mapping technique to expand the closed circular tube into an infinitely long straight tube of radius r and to solve the Navier-Stokes equations in cylindrical coordinates, rather than in spherical coordinates. The transformation can later be inverted, if necessary. To further justify such a temporary simplification, the ratio of radii of the torus of the semicircular canal is 20 to 1 and thus the "thin ring" approximations are very applicable.

The equation to be solved in cylindrical coordinates can be reduced to the form

$$\frac{\partial^2 v(r,t)}{\partial r^2} + \frac{1}{r} \frac{\partial v(r,t)}{\partial r} = \frac{1}{\mu} \frac{\partial P(t,\ell)}{\partial z} + \frac{1}{\nu} \frac{\partial v(r,t)}{\partial t} - a_z(t)$$

μ = viscosity

$a_z(t) = \alpha(t)R$

ν = kinematic viscosity

$\alpha(t)$ = angular acceleration

R = long radius of torus

$v(r,t)$ = velocity of fluid

r = short radius of torus

$P(t,\ell)$ = pressure in fluid

t = time

ℓ = length along duct

subject to the boundary condition

$$v(a,t) = 0$$

If the cupular damping term is ignored, then the solution of the above equation for $a_z(t) = -4c$ (where c is a constant) becomes

$$v(r,t) = ca^2 \left[1 - \frac{r^2}{a^2} - 8 \sum_{i=1}^{\infty} \frac{J_0(\lambda_i r)}{(\lambda_i a)^3 J_1(\lambda_i a)} e^{-\lambda_i^2 \nu t} \right]$$

Since cupular displacement is proportional to the integral of the flow through the tube, it is convenient to evaluate the average of $v(r,t)$ over the cross sec-

tion of the tube. Then:

$$\bar{v}(t) = \frac{ca^2}{2} \left[1 - 32 \sum_{i=1}^{\infty} \frac{e^{-\lambda_i^2 vt}}{(a\lambda_i)^4} \right]$$

where λ_i 's are the solutions of the 'zero' order Bessel function, $J_0(\lambda_i a) = 0$.

Further consideration of the equation in cylindrical coordinates with the inclusion of the cupular damping terms leads to the results that the dynamic behavior of the semicircular canals can, in fact, be described by a transfer function of the form:

$$\frac{\theta}{\alpha} C(s) = \sum_{i=1}^{\infty} \frac{A_i}{s^2 + 2\zeta_i w_i s + w_i^2}$$

Note that this analytical model is of the form measured experimentally. The evaluation of the constants A_i , ζ_i , and w_i , although difficult, could be carried out once the 'spring constant' for cupular deflection is known.

Ninety-six per cent of the effect in the flow drag:inertia ratio is accounted for by the first term, which is the only term present in the simple torsion pendulum model. Furthermore, the effects of the other Bessel functions are even more rapidly damped out than the major one. An additional important contribution to the damping term is the viscous drag of the cupula as it is displaced by the ampulla. The short time constant (0.002 seconds) is thought to be associated with cupula drag.

2.2 Analysis of Flexible Canals

Nystagmus in the presence of counter-rotating motion poses the question of whether or not the semicircular canals, because of their flexibility, are subject to excitation by rotating linear acceleration. It is shown by the simple counter-rotation of a glass filled with liquid that a circulation can be induced in the fluid. This can be shown qualitatively to be the result of the free surface of the fluid, and that it follows from the initial transient motion. Classical concepts of the vestibular sensors predict only a transient nystagmus which

decays to zero for a constant velocity rotation about any axis, However, experimental observations have shown that rotation of subjects at a constant angular velocity about a horizontal longitudinal axis provokes continuous vestibular nystagmus and subjective sensation of rotation. Thus it became necessary to investigate the classical concepts to determine which receptors are responsible for this mode of stimulation.

2.2.1 The Flexible Semicircular Canal as a "Roller Pump"

From histological studies, the position of the membranous labyrinth relative to the bony labyrinth has been accurately measured. Observations indicate that the duct of the membranous canal is attached by fibrous connections along its outer periphery to the bony canal; however, the inner periphery is relatively unattached and flexible. In pigeons the duct is denser than either the endolymph or perilymph that surrounds it. Under the influence of pure angular acceleration about an axis in the direction of the gravity field, the duct flexibility and density will have no significant consequences. However, if the gravity field is not colinear with the axis of rotation, a component of the gravity field will act upon the mass and possibly produce a movement of endolymph within the duct.

A flexible duct immersed in and containing an incompressible fluid will be distended by the influence of a linear acceleration if its density is different from that of the fluid, and a density difference between the interior and exterior fluids will further accentuate this distension. As shown in figure 2.2.1, a flexible circular duct which is attached along its outer periphery to a rigid structure and is denser than the fluid surrounding it, will have a constricted cross-sectional area where the acceleration field pushes against its support, and it will be expanded where the acceleration pushes it away from its support.

Further, if the linear acceleration vector (\bar{a}) is slowly rotated at a constant angular velocity w , the constriction will move along the outer periphery of the duct in phase with the rotation of the acceleration vector. The effect of the moving constriction is then to move or pump the fluid in the duct in the direction of rotation. This pumping action works against the viscosity and inertia of the fluid, and at high angular rotation rates, the fluid that is being pushed by the

moving constriction cannot be displaced fast enough. It builds up a pressure gradient which expands the duct back toward its original uniform shape. Thus, for high angular rotation rates of the linear acceleration vector, the mass of fluids acts as a hydro-mechanical filter, which reduces the duct constriction and, along with it, the pumping action of the flexible tube.

For a flexible tube with an elastic flow restraint such as the cupula of the semicircular canals, the fluid is initially pumped against and displaces the elastic restraint which then produces a pressure differential across the tube. A static equilibrium state is then reached where the displaced elastic restraint provides sufficient pressure feedback to inhibit further flow. Thus, for a constant velocity of rotation in a linear acceleration field, a constant cupula displacement can be maintained by this flexible roller pump action.

2.2.2 A Model for Canalicular Response to Rotating Linear Acceleration Stimuli

For constant rotation of the semicircular canals, the steady state displacement of the elastic cupula provides a pressure differential across the cupula which inhibits further flow. All of the fluid displaced by the moving constriction must therefore flow back through the constriction, and the pressure drop of this "back flow" must exactly balance that caused by the displaced cupula.

The average velocity of the backflow is given by the equation

$$\frac{A_c}{v} = \frac{(A - A_c) W R}{A}$$

where

A = the cross sectional area of the unrestricted portion of the duct

A_c = the cross sectional area of the constricted portion of the duct

W = rotation rate of the linear acceleration vector

R = radius of the torus

The static pressure differential ΔP which can maintain an average flow of endolymph can be calculated from fluid dynamic analysis to be:

$$\Delta P = \frac{16\pi\mu}{a^2g} \left(1 - \frac{A_C}{A}\right) W R$$

Further, it can also be shown that a pressure differential across the membranous duct produces a cupular response which is related to angular acceleration stimulation α by the equation

$$\Delta P = 2\pi R \rho g \alpha$$

From the last two equations we can obtain the relationship between the rate of angular rotation, the magnitude of the duct restriction, and the equivalent constant angular acceleration that would produce the same steady state cupular displacement.

$$\alpha_{\text{equiv}} = \frac{8\mu W}{a^2 \rho g^2} \left(1 - \frac{A_C}{A}\right)$$

where

$$a = 0.015 \text{ cm}$$

$$R = 0.3 \text{ cm}$$

$$\rho = 1 \text{ gm/cm}^3$$

$$\mu = 0.0085 \text{ poise}$$

$$g = 980 \text{ cm/sec}^2$$

$$\alpha_{\text{equiv}} = 0.3 \left(1 - \frac{A_C}{A}\right) W \text{ radians/second}$$

To establish the applicability of the roller pump principle to the semicircular canal, the relative magnitudes of the bias component of slow phase nystagmus from rotation in a linear acceleration field and the steady state nystagmus stimulated by constant angular acceleration can now be compared to determine how large a distension of the duct is necessary to produce a significant physiological response.

Experimental data has shown that a $6^\circ/\text{sec}$ bias component of vestibular nystagmus is related to a 1 rad/sec rotation about a horizontal longitudinal axis. Several experiments have shown that such a $6^\circ/\text{sec}$ slow phase velocity would also

result for several seconds during $0.6^\circ/\text{sec}^2$ constant angular acceleration.

Solution of the equation for the value of A_c/A when $W = 1 \text{ rad/sec}$ and

$\alpha_{\text{equiv}} = 0.01 \text{ rad/sec}^2$ yields $A_c/A = 0.97$.

This shows that a mere 3% constriction in duct area, or correspondingly, a 1.5% contraction of the radius of the membranous canalicular duct can produce sufficient roller pump action to account for the observed bias component of

nystagmus which results from constant rotation at 1 rad/sec in a 1 g acceleration field.

The rotation rate W_r at which the roller pump action diminishes is determined by the elasticity and strength of the fibrous attachments of the duct, and is not readily calculable. However, this cut-off frequency can be accounted for by adding a high frequency lag term to the equation for α_{equiv} to provide for a diminished response at higher rates of rotation. From this we obtain:

$$\alpha_{\text{equiv}} = \frac{8\mu}{a^2 \rho g^2} \left(1 - \frac{A_c}{A}\right) \left(\frac{W}{\left(1 + \frac{W}{W_l}\right) \left(1 + \frac{W}{W_r}\right)} \right)$$

2.3 Rotating Linear Acceleration Stimulation Experiments

To investigate the variation of the bias and the amplitude of the sinusoidal component of vestibular nystagmus as a function of rotation rate, the M.I.T. Instrumentation Laboratory Precision Centrifuge with a rotating platform (9.7 meter radius) was fitted with the Man-Vehicle Laboratory rotating chair simulator and six experimental subjects were rotated at 5, 7.5, 10, 20, 30, and 40 rpm in a 0.3 g horizontal acceleration field. Nystagmus was measured with eyes open in the dark by means of a pulsed infrared eye movement monitor. From the nystagmus records, the slow phase nystagmus velocities were calculated and plotted. The results show a persistent sinusoidal component at the period of rotation for all subjects at all rotation rates. For most subjects, a clear bias component is observed for 5 and 7.5 rpm and for some, it still exists at 10 rpm; however, for 20, 30, and 40 rpm, it is not observable in any of the subjects tested. The amplitude of the sinusoidal component increases with increasing rate of rotation.

To compare the results with those of the horizontal rotation experiments it is necessary, even though the assumption of linearity is tenuous, to normalize the results of our experiments with respect to a 1 g gravity field. In figure 2.3.3a and b our normalized results are plotted along with those of Benson and Guedry. The model predicted bias component is also plotted in figure 2.3.3a for an assumed upper break frequency of $W_r = 7.5$ rpm.

It does appear that the predicted responses from the "roller pump" model are borne out by the data in that, at low and high rotation rates, the bias component is not observable, and there is a general shape of measured response that does conform to the predicted second order system. Further, the experimental data show that the upper break frequency which we were unable to calculate because of insufficient data, is in the range from 5 to 10 rpm.

2.3.1 Conclusions

In summary, these experiments, which provide a slightly different vestibular stimulation than the "barbecue spit" experiments of Guedry and Benson or the "revolution without rotation" experiments of Money, further verify the hypothesis that rotation at a constant velocity in a linear acceleration field does provoke vestibular nystagmus. The results of the analysis presented here show that a duct area constriction of only 3% provides sufficient roller pump action to generate the observed bias component of nystagmus. In addition, the upper cut off frequency W_r was found experimentally to be in the range between 7.5 and 10 rpm.

2.4 Pressure Difference and Cupula Deflections

A pressure difference occurs across the cupula when endolymph in the canal is accelerated. The resulting force, considered in the head fixed coordinate system of the vestibular apparatus, can be created either by an angular acceleration stimulus applied to the head, or by natural or artificially created density gradients in the endolymph ring due to temperature gradients across the canal.

Since the density and temperature coefficient of expansion of endolymph are known, and the morphology of the membranous canals has been extensively studied, one can calculate the pressure gradient across the cupula in the steady state for both the caloric and acceleration stimuli.

Calculations suggest that the semicircular canals sensory areas are enormously sensitive to pressure gradients, one can only assume that experiments aimed at observing the range of cupula motions by fenestration might easily traumatize the cupula. Unfortunately, the cupula is practically invisible under bright field microscopy.

However, using the theoretical model for the canal hydrodynamics, a useful estimate can be made of the range of cupula displacement. The results of these calculations, show that for accelerations of the 0.0 deg/sec^2 level associated with behavioral thresholds, the cupula should deflect 0.177×10^{-4} radians (0.001°). This corresponds to a deflection of the midpoint of the cupula of approximately 10^{-2} millimicrons. This is roughly three orders of magnitude less than the size of the hair cells in the crista, and a thirtieth the diameter of the kinocilium. It is approximately the same dimension as the thickness of the unit membrane in the hair cells.

Another implication of this calculation is that the dynamic range of cupula deflections is constrained to less than a third of a degree for long term accelerations of less than $30^\circ/\text{sec}$. Actually, almost all long duration dynamic tests of canicular response to sustained acceleration are performed at acceleration levels considerably less than this. Acceleration levels considerably higher than $30^\circ/\text{sec}$ are commonly encountered in normal quick head movements, or in the cupulogram impulsive stop. However, the duration of these motions is sufficiently small that large cupula deviations are never achieved. This is understandable because, as is well known, the cupula position is approximately proportional to the time integral of the stimulus angular acceleration, over the first several seconds after stimulation. Specifically, solution of the torsion pendulum equation indicates that over the normal range of velocities used in the cupulogram experiment (up to $50^\circ/\text{sec}$), the cupula should move less than 0.025 deg . The midpoint of the cupula would move less than a quarter of a micron.

The cupula of the human horizontal semicircular canal constitutes an important link in an enormously sensitive biological pressure transducer, one which is probably quite easily subject to trauma in research preparations or otological surgery. Subjective behavioral thresholds to rotation are likely associated with

cupula pressure differences of 10^{-4} dyne/cm². This small pressure is approximately equivalent to the acoustic threshold at the tympanic membrane. A pressure difference of 10^{-3} dyne/cm² is probably required to produce nystagmic response to rotational or caloric stimuli. In the course of everyday life peak pressures should rarely exceed 10^{-2} dyne/cm². Hence, the application of even 10^{-4} cm of water pressure across the ampulla (10^{-1} dyne/cm²) would subject the cupula to a distinctly unphysiologic steady state pressure.

Calculations indicate that the dynamic range of motion about the midpoint of the cupula is from about 10^{-2} millimicrons at threshold up to about 3 millimicron at the upper limit of self induced sinusoidal head motions. The presence of a torque saturating characteristic in the cupula for large displacements could limit the upper end of the dynamic range to smaller values, however. Nonetheless, the dynamic range of motion calculated here is generally consistent with results obtained from the lateral line organs. No conclusion is reached with respect to whether the cupula moves angularly or linearly or both, except that it should be noted that all modes are possible, because of the small dynamic range of motions that are required.

The question of what constitutes the "physiologic" behavior of the cupula has been a subject of debate for some time. Considerations based on calculation of the moment of inertia of endolymph in the membranous semicircular canal and on known behavioral responses to angular accelerations suggest that the pressure across the cupula associated with behavioral thresholds must be less than 10^{-4} dyne/cm². Calculation of the density gradient pressures resulting from threshold level caloric stimulation yields results consistent with this figure. These calculations result directly from the known morphology of the canals, and involve no assumptions with respect to cupula stiffness or cupula drag. They suggest that the cupula constitutes a biological pressure transducer with a threshold of the same order as that of the auditory system. The calculations also suggest that it would be extremely easy to traumatize the cupula structure by exposing it to pressure gradients far beyond its normal range of dynamics in the course of experimental preparations designed to visualize cupula motion.

An estimate of the range of cupula motion is also obtained from theoretical considerations. Conservative calculations indicate that the cupula midpoint moves

only about 10^{-2} millimicron at the $0.1^{\circ}/\text{sec}^2$ acceleration levels commonly associated with behavioral thresholds. Accelerations of $30^{\circ}/\text{sec}^2$ or velocity changes of $600^{\circ}/\text{second}$, typical of maximal self-induced head motions should produce cupula midpoint motions no greater than about 3 millimicron. Because of the small dynamic range of cupula motions, modes of cupula deflection other than rotation about the crista cannot be ruled out, because they are indistinguishable from a dynamic point of view.

solve the disparity between the calculated and observed responses of the semi-circular canals.

Further examination of the structure of the membranous canal duct showed it to be flexible, denser than the surrounding endolymph and perilymph, and attached by fibrous connections along its outer periphery to the bony canal. The distension of the duct under the influence of linear acceleration, which acts on the density differences between the duct and the fluids, was shown to be responsible for a "roller pump" action when the canal is rotated about an axis orthogonal to the linear acceleration field. This roller pump action produces a steady state cupula deviation in response to a constant rotation in an acceleration field and offers a realistic physical explanation for the observed bias component of neural discharge from cat canalicular neurons when the animals are subjected to counter-rotating motion. We have shown that less than a 3% constriction in duct cross-sectional area can produce the bias component of vestibular nystagmus that has been observed in two types of experiments; those in which subjects were constantly rotated about a horizontal longitudinal axis, and experiments in which subjects were rotated about a vertical axis in a lateral acceleration field by use of a rotating chair mounted on the boom of a centrifuge.

This canicular response to rotation in a linear acceleration field is of some consequence in that it gives the human a significant vestibular input of the same physiological character as angular acceleration. If rotating environments are to be used for gravity simulation or space station stabilization, then man's ability to correctly interpret and to adapt to this new vestibular information must be carefully considered.

2.5 Summary

Hydromechanical analysis of the semicircular canals as a rigid torus filled with fluid and subjected to a constant angular acceleration showed that the damping to inertia ratio of the canaliculâr duct was an order of magnitude higher than is calculated from the observed objective and subjective responses of man to angular accelerations. Investigation of the influence of viscous drag of the cupula on the membranous ampulla showed that for the dimensions of the cupula and the clearance between the cupula and the ampulla that is observed from histological studies, the cupula drag could contribute as much damping to the semicircular canals as the hydro-dynamic drag of the endolymph in the canalicular duct. These results re-

SECTION THREE

GALVANIC STIMULATION AND THE PERCEPTION OF ROTATION

Contents

- 3.0 Introduction
- 3.1 The Experimental Model
- 3.2 Galvanic Stimulation Equipment
- 3.3 Experimental Results
- 3.4 Subject's Reported Sensations
- 3.5 Galvanic Vestibular Stimulation and Neck Rotation Interaction with
the Ankle Stretch Reflex
 - 3.5.1 Method
 - 3.5.2 Discussion of Results

Related Publications:

Tole, 1970

Young, 1970

Weiss and Tole, 1973

3.0 Galvanic Stimulation and the Perception of Rotation (Tole, 1970; Weiss and Tole, 1973; Young, 1970)

Clinical interest in the vestibular system centers around the responses of the system to rotation and disorders related to rotation or movement. In the clinic the most common stimuli to the vestibular system have been rotation and caloric stimulation with the former allowing only binaural excitation while caloric irrigation can be used to examine the response of one labyrinth at a time.

Another means of stimulation has been observed to produce disorientation effects similar to those experienced during rotation. It has been known for some time that direct current passed through the head gives rise to a swaying or rotary sensation. The galvanic vestibular reaction as this effect is called has been studied with varying interest since the late 1880's. However, due to problems of instrumentation and localization of the action site of the current, this method of stimulation has not gained acceptance.

Although the action site is not known exactly, it is currently believed that galvanic stimuli do not act at the same points as rotational or caloric inputs. Rather the current is thought to act closer to the central nervous system than on the peripheral organ. To facilitate the evaluation of the suitability of galvanic stimulation as a clinical tool we have conducted a study to establish quantitatively the effects of current intensity and polarity on subjective sensation and on nystagmus. The primary objective of the experiments was to determine whether galvanic stimulation can indeed bias the threshold for rotary sensation. Secondary objectives were to determine how current intensity levels and electrode locations influenced the aforementioned measurements.

3.1 The Experimental Method

The intent of this research was to study the relationships between modes of application and intensities of galvanic stimuli and a subject's perception of rotation. Thus an experiment was sought which would employ both rotatory and galvanic stimuli administered independently of one another.

The experiment which was used consisted of the following. The subject was placed in a darkened rotatable chair and a zero-mean random position input was applied to the chair. The subject was provided with a three state controller of changes in chair velocity and was given the task of countering

any sensations of motion which he experienced. That is, if he felt he was moving to the right he should press his controller to the left until he no longer sensed motion and so on. Assuming that the random signal indeed has a zero mean and that the subject has no directional preponderance, one would expect, theoretically, that the subject would counter any motion above his threshold and that the chair would not move more than slightly away from the reference position.

If a galvanic stimulus is applied to the subject together with the random input to the chair, one would expect the subject's motion sensation to be altered in some manner. This approach was adopted with the postulate that the galvanic stimulus would bias the threshold for rotation perception. The measure of response would be the deviation of the chair position over the course of a run.

The experiment thus places the subject in an active role as opposed to the passive role of similar experiments previously conducted. The three state controller was employed since it appeared important that the subject respond only to a sensation of motion in the direction of rotation and not to the magnitude as he might were a graded controller such as a joy stick used.

Each subject was to be run with each of the six possible modes, unipolar right cathode and right anode, unipolar left cathode and right cathode and bipolar left cathode and right cathode, and at six different intensity levels.

The lowest intensity level was chosen at $100\mu\text{a}$, consistent with Dzendolet's reported objective threshold for low frequency sinusoidal vestibular stimulation. Successive intensity values were doubled up to a maximum of 3 ma. in order to cover as wide a range as possible and still remain within pain and safety levels.

In addition to six runs with combined rotational and galvanic stimulus, two control runs, one at the beginning and the other at the end of the session were added to discover any overall effect on this norm after the combined experiments.

Eye movements were monitored in addition to the subjective response in an attempt to obtain an involuntary measure of response.

3.2 Galvanic Stimulation Equipment

Galvanic stimulation was applied through two specially designed circular electrodes approximately one inch in diameter affixed to the subjects' mastoid processes. A layer of wetted gauze impregnated with electrode paste was included in the electrode in order to avoid metal to skin contact and to obtain a relatively uniform current distribution and a nominal 2-3K resistance. The two electrodes were mounted on a standard headband.

An indifferent electrode consisting of a 2 inch by 3 inch gauze pad was placed on the back of the subject's neck and held in place with surgical tape. This electrode was used as the common in unipolar tests.

The positioning of the three electrodes on the subject was either across the two mastoid processes or from one mastoid process to the nape of the neck. D.C. current was obtained from an Electronics for Life Sciences Constant Current Stimulator Model CCS-1A. This stimulator is battery powered and has a maximum output capacity of 10 ma. at 90 volts. The maximum current to be used was 3 ma.

3.3 Experimental Results

The experiments described above produced two types of data: eye position and chair position versus time for each two minute run. In order to estimate the average drift away from the zero reference position, it was decided to calculate the mean value of chair position and of cumulative slow phase eye position over each run. The latter was used since it represents total amplitude of eye deviation during the experimental run.

The mean, variance, and standard deviation for chair position and cumulative slow phase eye position for each run were calculated.

In order to determine which of the parameter groups among subjects, order, modes, and intensities had significant influence on the data, a standard analysis of variance was performed.

The data on chair position indicates a significant difference between anodic and cathodic mode effects with anodic stimuli seemingly producing larger effects. However, if control runs are taken into account, the effects of the two mode types become nearly equal.

Intensities below the 800 μ a level appear to have no effect on the results with responses being approximately the same as for the control runs. At intensity levels at and above 800 μ a significant effects were apparent. A threshold for current effect between 400 and 800 μ a was thus suggested.

Analysis of the eye movement data was rather non-conclusive. Thus no definite conclusions may be drawn concerning the influence of the experimental conditions on eye movements.

One interesting observation can be made on the eye data however. The modes had the highest variance ratio and in comparison of the means of each mode with the corresponding means in the chair data analysis certain similarities can be noted. All right cathodic modes have negative (toward the cathode) mean responses while all right anodic modes have positive mean responses. In addition, the anodic effects have larger magnitudes than the cathodic as in the chair data. This suggests that a similar net effect due to modes is being observed in both chair and eye movement data.

The peculiarities of the experimental scheme may well have masked the eye movement data. Only relatively low angular accelerations, were present which would naturally decrease eye deviations due to rotation. Eye drift (other than that due to the galvanic stimulus) may have decreased the ability to measure the deviations due to the current. It is possible that a fixation point might aid this latter problem, or it might further inhibit galvanic nystagmus.

3.4 Subject's Reported Sensations

The subjects reported several sensations during the experiments. These included disorientation, head tilt, and one report of the sensation of "spinning in two directions simultaneously." Several subjects also reported an after-effect following stimulation at 3 ma. This manifested itself in a spinning sensation but died out before the beginning of the next run five minutes later.

3.5 Galvanic Vestibular Stimulation and Neck Rotation Interaction with the Ankle Stretch Reflex. (Burr, 1973).

Postural reactions to galvanic vestibular stimulation varies from tilting of the head to, as current intensity increases, pronounced swaying and falling. These effects are dependent on current polarity and intensity. This investigation was intended to further define the postural reaction to this type of stimulation. The experiment was based on the assumption that changes in muscle tone resulting from the galvanic vestibular stimulation would alter parameters of the stretch reflex in the affected muscles. The muscles involved in rotation about the ankle joint were chosen because of their role in posture maintenance. We were able to test the reflex while the subject was standing by using the posture control experiment platform.

Six normal subjects were tested under different stimulation and head position conditions. Training tests were conducted with eyes open. The eyes were closed for all other tests to heighten the stimulation effect by removing visual cues for orientation.

3.5.1 Method

Separate recordings of the torque exerted on the platform by each foot, hip displacement, and electromyographic (EMG) activity were made. From the recorded reflex responses, parameters were designed which were used to perform a statistical analysis on the effects of the galvanic vestibular stimulation. The latency and duration of the initial burst of reflex EMG activity were used to determine the timing of the response, while the maximum torque exerted in the direction of the reflex response and the time until the torque returned to the initial levels were used to define the torque response. A rough measure of the final change in position following stimulation was made by measuring hip displacement five seconds after the reflex stimulation.

3.5.2 Discussion of Results

The experiment yielded no evidence to support the hypothesis that galvanic vestibular stimulation has a tonic effect on the ankle stretch reflex, at least in normal conscious subjects. Several explanations for this result can be offered.

First, there is serious question whether a tonic effect on reflexes can be elicited in the normal conscious human. Encephalization may provide the ability to control muscle tone to the extent that the tonic reflex effects are completely masked. A different effect of encephalization, which could have affected the results, is based on the fact that the stretch reflex destabilizes the subject when the platform moves during the test. The stretch reflex may have been inhibited to reduce this destabilizing effect. Such inhibition is considered unlikely, however.

There was obviously a transient effect on muscle tone caused by the stimulation as evidenced by the swaying or falling reactions. However, sway prevents simple measurement of stretch reflex response. The stability requirement before initiation of the stimuli effectively meant that the subjects needed to accommodate to the stimulus effects before testing began. This idea is supported by the absence of a trend of increasing stability as a sequence effect in the stability measurements. Unfortunately, the time spent waiting for stability before the first stimulus could not be measured. This would have give a rough estimation of the adaptation time to the galvanic vestibular stimulation effects.

Two unpredicted minor results deserve discussion. there was a significant constant difference in peak torque between the left and right leg. The left leg showed larger responses. The only explanation other than calibration error is a tendency for subjects to stand with more weight on the left leg than on the right.

The asymmetry of the final hip displacement is due to the stresses at the ankle joint. When a person is standing, the vertical projection from his center of gravity passes in front of the ankle joint. The portion of the ankle anterior to the joint is in compression; the portion posterior, particularly the Achille's tendon, is in tension. After platform rotation, the hip moves to a position which is a compromise between the initial hip position and the hip position that maintains the initial ankle angle. In the experiment, the hip returned closer to the initial position after plantarflexion. Dorsiflexion increases the ankle compression. The compression is eased by making less of a return to the initial hip position. Conversely, after ankle compression is decreased by plantarflexion, the hip can return nearer the initial hip position.

CHAPTER FOUR

CALORIC RESPONSE OF THE SEMICIRCULAR CANALS

Contents

- 4.0 Introduction
- 4.1 Adaptation to Unilateral Caloric Stimulation
 - 4.1.1 Caloric Stimulation
 - 4.1.2 Experiments
 - 4.1.3 Results
 - 4.1.4 Model
 - 4.1.5 Summary

Related Publications:

- Steer, 1967
- Oman, 1968
- Steer, 1969

4. CALORIC RESPONSE OF THE SEMICIRCULAR CANALS (Steer, 1967; Steer, 1969; Oman, 1968)

4.0 Introduction

The phenomenon of caloric stimulation of the semicircular canals is well known and used extensively both in research and for clinical diagnosis. Observed nystagmus response during periods of caloric stimulation is explained in terms of convection currents which set up fluid flow in the semicircular canals. Although sufficient evidence in favor of such a "convection current" model exist, a modeling effort had not yet been undertaken.

In particular, the relation between fluid temperature input at the tympanic membrane and equivalent angular acceleration on the semicircular canals has not been evaluated.

Our research activities in the area of caloric stimulation drew heavily upon the knowledge which we gained from experimentation and analysis on the properties of the labyrinthine fluids and the dynamics of the fluid flow. The initial emphasis was on an effort to establish analytically the similarity between caloric stimulation of the semicircular canals and excitation with angular acceleration.

It has been clearly shown by the work of Cawthorne and Cobb that the application of a thermal input to the tympanic membrane results in a temperature gradient across the horizontal semicircular canal. This temperature gradient gives rise to a convection current of fluid in the canal and results in a nystagmus output from the subject.

The transfer function of the temperature gradient across the canal as a result of caloric stimulation has been computed by a minimum mean squared error fit of the data from the measurements of Cawthorne and Cobb to a first order dynamic lag model and the results were found (Steer, 1967) to be:

$$\frac{\Delta T}{T} = \frac{K}{\tau s + 1}$$

where $K = 0.1$

$\tau = 20 \text{ sec}$

$s = j\omega$

$T = \text{temperature of tympanic membrane above body temperature}$

$\Delta T = \text{temperature gradient across canal above body temperature}$

To transfer the observed temperature gradient to a torque on the fluid of the semicircular canals and thus to an angular acceleration, the following simple model was used.

When a vertical ring of inviscid fluid is placed in the field of a constant uniform temperature gradient, a given torque is exerted on the fluid. The same torque may be exerted by angular acceleration of the ring. The relation between this angular acceleration (α) and the corresponding externally applied temperature (T) is given by the relationship

$$\alpha = \frac{1}{4R} \left(\frac{\Delta\rho}{\rho\Delta T} \right) g \frac{kT}{\tau s + 1}$$

where

$$\frac{\Delta\rho}{\rho\Delta T} = \text{relative change in density with temperature}$$

$$R = \text{radius of the ring}$$

$$g = \text{acceleration of gravity}$$

For water as a fluid and for a ring of the horizontal canal

$$k = 0.1$$

$$\tau = 20 \text{ sec}$$

$$g = 980 \text{ cm/sec}^2$$

$$\frac{\Delta\rho}{\rho\Delta T} = 0.4 \times 10^{-3}/^{\circ}\text{C}$$

$$\alpha = \frac{0.0327}{20s+1} T$$

To compare the thresholds of angular acceleration and caloric stimulation, consider a typical threshold temperature of $T = 0.2^{\circ}\text{C}$ resulting in

$$\alpha = 0.374^{\circ}/\text{sec}^2$$

Since a typical threshold angular acceleration is of the order of $0.2^{\circ}/\text{sec}^2$ the agreement is reasonable. The factor of two disparity is attributable to the computation of the gain k . The data of Cawthorne and Cobb was taken during surges and obtained by a thermocouple inserted into one half of the horizontal canal then by displacing about half of the endolymph in the canal. This could well result in a higher temperature gradient than actually exists.

4.1 Adaptation to Unilateral Caloric Stimulation

4.1.1 Caloric Stimulation

This section describes the results of a series of experiments on human subjects. Analysis was done on measurements of eye movements resulting from thermal stimulation of the vestibular system. The stimulus was delivered by irrigating the external ear canal with hot and cold water, and modulated by changing the orientation of the subject with respect to gravity. By varying the time between the onset of irrigation and the change of body position, it was determined that the adaptive behavior evident in the response was essentially independent of prior irrigation time. Therefore, if caloric adaptation is of vascular origin, it must be related to the tilt stimulus itself, or associated with the level of vestibular response. Results of modeling head fixed caloric test results suggest that the former is not the case. Instead, certain aspects of the adaptation were observed to be similar quantitatively, to that observed in human responses to rotational stimuli. It seems more likely, therefore, that the observed adaptation is of vestibulo-ocular rather than vascular origin. A model for nystagmus response to caloric stimulation is proposed, and its implications with respect to interpretation of clinical caloric tests results are discussed.

4.1.2 Experiments

The basic protocol used in these experiments involved irrigation of the subject's right ear with water at 30 or 44 degrees C. All tests were conducted in the dark, usually with the subject's eyes open. Subjects were told to push the subjective response button when (1) they first felt water reach their eardrum (2) when they first felt subjective rotation and (3) every 90 degrees of rotation thereafter. Rotations about the horizontal axis of the body were to be reported by giving one or two clicks of the switch, depending upon direction of rotation. If rotation was felt about any other but a longitudinal axis, three clicks were to be used.

During the run the experimenter observed the eye position on the oscilloscope and made small step changes in the EOG preamplifier to compensate for drift. This had no effect on the slow phase velocity.

During irrigation, the subject was maneuvered by means of chair rotation into a face up position, and later returned to the original position. This was usually repeated later in the experiment. Eye movement calibrations were taken before and after the tests.

Reactions of the subjects varied. Most agreed that the test was not a particularly pleasant one, but the incidence of malaise due to motion sickness varied from subject to subject. None ever vomited or felt that vomiting was immediately imminent.

Forty tests were conducted on seven subjects over a six month period.

4.1.3 Results

From the earliest phases of the experimentation, a pattern in the responses was observed. Initial responses were consistent with the model proposed by Steer, a small initial component of nystagmus, with a latency of 20 to 30 seconds was usually observed. When the chair was tilted back, nystagmus increased in rapid crescendo, just as it would do in response to a step in angular acceleration. The direction of the component responding to tilt, face up, was always such that hot water produced ipsilateral beating nystagmus, and cold water produced the reverse. The small initial component was not always beating in the same direction as the tilt response. Behavior up to this point, obviously is predicted by Steer's model.

As shown in figure 4.1.1, however, response beginning 30 to 40 seconds after the application of the tilt stimulus deviates from the predicted behavior in that the slow phase velocity response (SPV) peaks, and then gradually decays over the next two to three minutes. No artifacts due to rotation in the median plane were observed.

It would seem that the response to the first tilt stimulus is apparently unrelated to time since onset of irrigation, at least within the limits in which this was considered. It seemed reasonable to presume that adaptation was likely of vestibulo-ocular origin and proceed to systematically study its relationship to the descriptions of adaptation developed for (bilateral) rotational stimuli. The only other alternative, that adaptation was of thermal origin but related to body position or the level of vestibular response, rather than irrigation time, seemed

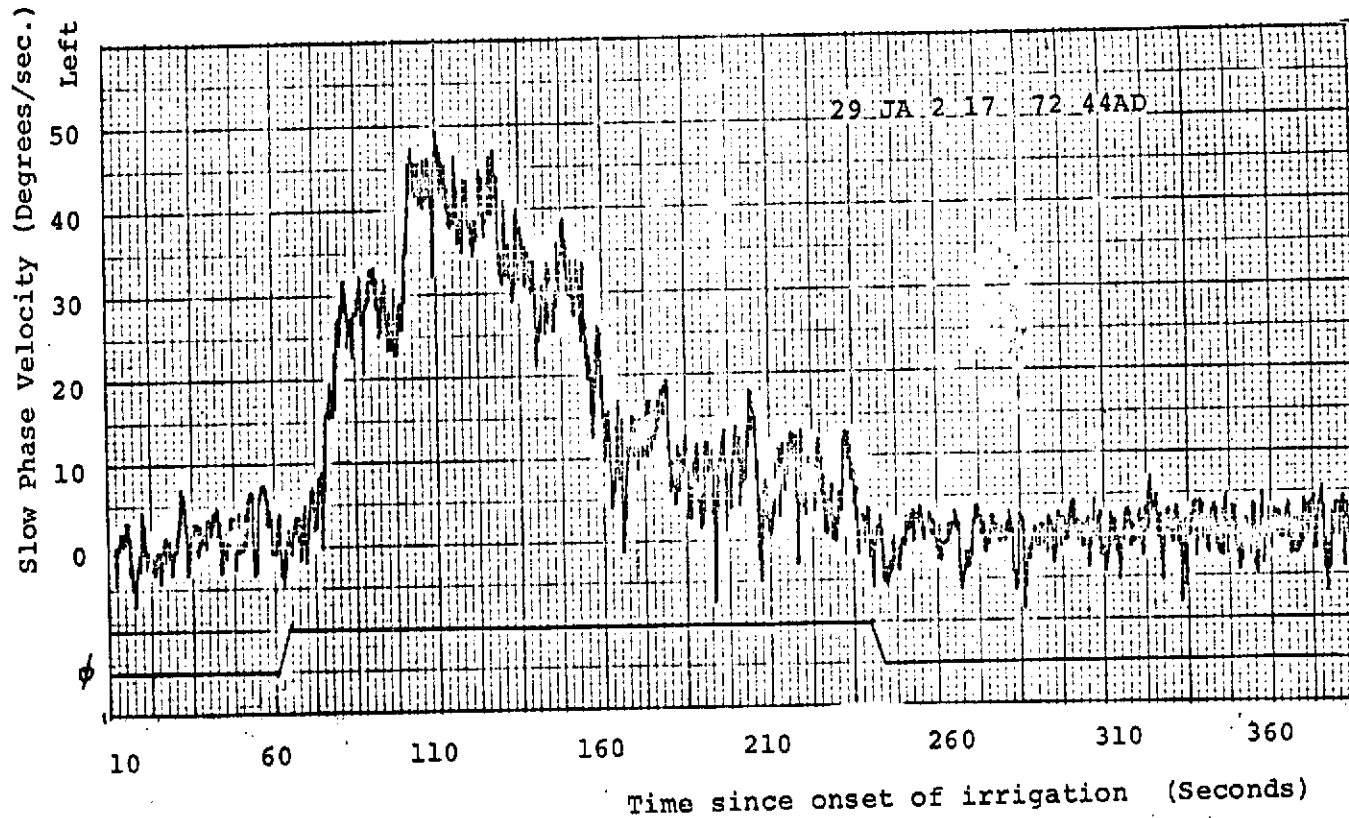


Figure 4.1.1 Nystagmus SPV response to tilt stimulus applied after one minute of irrigation with water at 44 Deg.C (Right Ear)

unlikely. One could argue that vasodilation might be modified by the effects of blood pressure, but here the legs were not elevated above the labyrinth. In order to meaningfully compare caloric adaptation to rotational responses, it was necessary to quantify the adaptive caloric behavior. Quantification is also necessary if a model for caloric response was to be developed which would relate the various types of tests.

4.1.4 Model

If the tilt stimulus is interpreted as the equivalent of a truncated ramp in angular velocity applied unilaterally, it can be shown that the adaptation of the caloric response can be predicted quite well by the adaptation operator developed for rotational responses. The fit is nearly exact until the tilt stimulus is terminated, at which point the behavior of caloric and rotational responses differ. In rotational tests, slow phase velocity rapidly reverses direction after the velocity ramp has been truncated, while the reversal in caloric testing appears to be suppressed.

The proposed model includes the following assumptions:

1. That the dynamics of thermal transmission are similar to those described by Steer (1967)
2. That the Steinhausen model adequately describes the viscoelastic mechanical dynamics of the cupula/endolymph system
3. That somewhere in the physiology, a homeostatic adaptive process is taking place similar to that described by Young and Oman (1968)
4. That due to the unilateral nature of the stimulus, nystagmus reversals are blocked in a direction opposite to that of initial response.

The solutions shown in figure 4.1.2 were determined (by computer) using the following values for the model parameters:

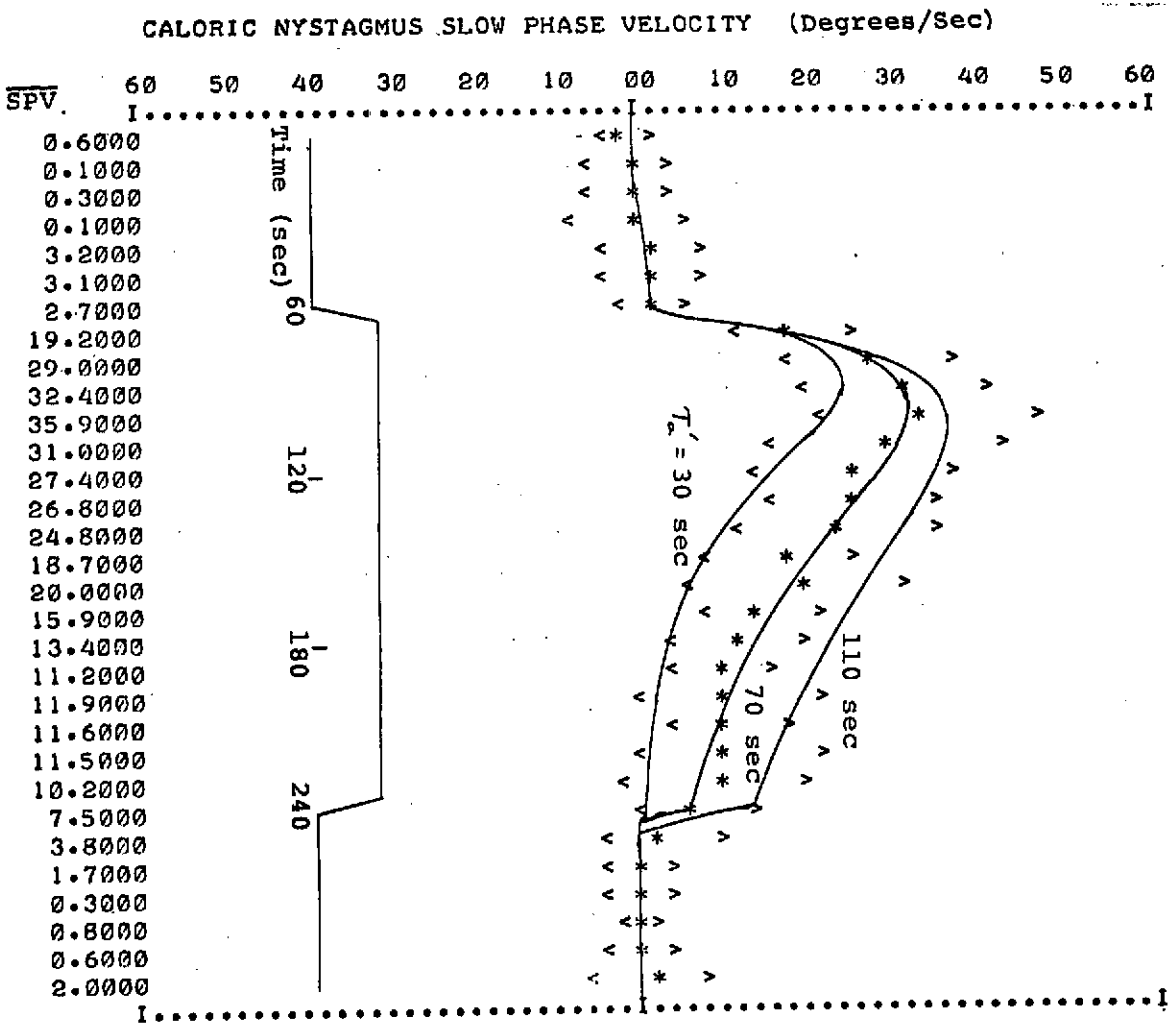


Figure 4.1.2 Fit of Combined Data with Model shown for three different values of adaptation time constant.

$$\begin{aligned} \tau_c &= 25 \text{ seconds} \\ \Pi/\Delta &= 20 \text{ seconds} \\ \tau'_a &= 70 \text{ seconds} \end{aligned}$$

The time course of the initial response shown in figure 4.1.2 was predicted by assuming that, in the experiments, the horizontal canals were pitched up by an average of four degrees from the vestibular reference plane. While this assumption gives reasonable fit to the data, it should be kept in mind that one cannot rule out other hypothesis on the basis of this alone.

As shown in the figure, the peak magnitude of the expected SPV response is heavily dependent on τ'_a . It would seem that much of the variance in the data could be accounted for if this varied from subject to subject or run to run. However, such a concept cannot account for the observed fluctuations in the detailed response decline. Neither can it account for the observed variance in responses in the eyes level portions of the experiment. Since mean variance over the eyes level portion was 29 (deg/sec)^2 , and that of the face up portion was 107 (deg/sec)^2 , it seems more reasonable to describe the variance, for modelling purposes, as being composed of two components:

1. An additive pseudo-white noise component $N(t)$ of zero mean and variance of 29. This component could presumably be due to both physiological and instrumentation noise.
2. Effects due to random variables controlling overall response magnitude, which once determined, were constant from run to run.

The adaptive behavior of the mean caloric SPV fits that predicted by the homeostatic adaptation operator well, except for the absence of overshoot. This provided the strongest motivation for assuming that homeostatic effects occur internally in caloric experiments which are blocked at the behavioral output. If one adopts an alternative hypothesis, that the decay of caloric SPV is roughly exponential because of a gradual stimulus (as opposed to temperature) related decrease in the gain of the response pathway, one can account for the fact that overshoot is not observed. However, there is no simple explanation to be had on

on a synergistic basis for the overshoot observed in data from rotational experiments.

4.1.5 Summary

Adaptation has been observed in horizontal nystagmus slow phase velocity responses to caloric tilt testing. It is thought that the slope of the initial rise in nystagmus slow phase velocity resulting from the tilt stimulus is primarily determined by the long time constant of the viscoelastic physical dynamics of the horizontal canal itself. The subsequent decay of nystagmus, which cannot be accounted for on the basis of commonly accepted models of canal dynamics, is attributed to adaptation.

It was found that the time course of slow phase velocity response to a face up rotation is essentially independent of the interval between the start of irrigation and the application of the interval between the start of irrigation and the application of the tilt stimulus, provided this interval is greater than one minute, and also that small, consistent responses to the thermal stimulus in the eyes level position are allowed for. The origin of these initial responses remains uncertain, because the precise orientation of the horizontal canals in the skull of each subject was not known. One would conclude from this that the adaptive behavior of the slow phase velocity during the eyes up portion must be related to the application of the tilt stimulus, and not attributable to those adaptive dynamics of temporal bone heat transfer which are solely related to the time history of irrigation temperature.

Although it is at least conceptually possible that thermal adaptation might be determined partly by the level of vestibular response via efferent projections to the vasculature of the temporal bone, the striking similarity between adaptation observed in step responses to angular acceleration and responses to face up tilt stimuli makes this hypothesis seem unlikely. It seems much more probable that the adaptive behavior observed in rotational and caloric testing result from a common mechanism in the vestibular/oculomotor pathways. It is shown that fitting a homeostatic adaptation model proposed by Young and Oman in 1968 to mean caloric SPV responses elicited by face up tilt (after prior irrigation) yielded a mean

adaptation time constant of seventy seconds.

It is important to note, however, that the caloric response deviates from that expected on the basis of comparison with responses to truncated ramps in angular velocity at the point where tilt is terminated. Reversals of nystagmus which occur during ramp termination are entirely absent in the caloric tilt case. It is tentatively hypothesized that this lack of reversal results from the blocking of nystagmus reversals by a response dependent nonlinearity in the unilateral response pathway. Presumably, this nonlinearity is not evident in responses from angular acceleration stimuli because of the bilateral nature of the stimulation. It remains a distinct possibility that the dynamics of adaptation are fundamentally nonlinear in nature, but that responses to rotational stimulation are somehow linearized as a result of synergistic combination of information from each pair of canals. The data obtained, however, seem to indicate a slightly different interpretation: It was observed that the character of the eyes-up/eyes-down tilt stimulus appeared to support the notion that linear, homeostatic adaptation does take place as a consequence of unilateral as well as bilateral stimulation, but that slow phase nystagmus responses in a direction opposite to that elicited by the first tilt stimulus are blocked by some central mechanism. A model based on this concept was used to successfully predict observed responses to caloric tilt tests, and certain aspects of the response to stimuli applied in head fixing testing. In particular, the model successfully predicts the duration of nystagmus in the Hallpike clinical caloric test, provided tests are performed with the eyes open and no opportunity for fixation. The observed constancy of nystagmus duration over a wide range of irrigation temperatures in Hallpike testing is also accounted for.

It is not to be concluded from this work, however, that vasodilation due to temperature change does not produce weaker responses than cold in face up testing. Rather the implication is that these are not predominant factors in determining the dynamics of the response, and probably exert greater influence on indirect measures of vestibular response such as latency duration, and peak slow phase velocity.

SECTION FIVE

LOW FREQUENCY RESPONSE OF THE SEMICIRCULAR CANALS

Contents

- 5.0 Introduction
- 5.1 Experiments
 - 5.1.1 Results and Discussion
- 5.2 Vestibular Adaptation to Horizontal Rotation
- 5.3 Low Frequency Linear Stimulation
 - 5.3.1 Experimental Procedure
 - 5.3.2 Results and Discussion
- 5.4 Directional Preponderance (Bias) in the Semicircular Canals
- 5.5 Visual-Vestibular Interaction
 - 5.5.1 Anti-Vertigo Display
- 5.6 Interaction of Semicircular Canal and Otolith Information in Subjective Orientation
- 5.7 Nystagmus Processing Instrumentation
 - 5.7.1 Nystagmus Processing Program
 - 5.7.2 Analog Analysis

Related Publications:

- Katz, 1967
- Oman, 1968
- Young and Oman, 1968
- Young and Oman, 1969
- Young, 1969
- Oman, 1972
- Young and Oman, 1970
- Ormsby, 1974
- Ormsby and Young, 1974

5. LOW FREQUENCY RESPONSE OF THE SEMICIRCULAR CANALS
(Katz, 1967; Oman, 1968; Young and Oman, 1968, 1969; Young, 1969; Oman, 1972)

5.0 Introduction

The dynamic properties of the semicircular canals are generally modelled as a torsion pendulum quantitatively described by a linear second order differential equation. This model is characterized by two time constants, the values of which are well known, both for subjective response to angular accelerations and for objective response as measured by eye nystagmus. While the assumption of linearity is warranted for a wide range of frequencies, Hixon and Niven (1962) found that nystagmus elicited at low frequencies (0.02 and 0.04 Hz) appears to be dependent upon the magnitude of peak angular acceleration.

To examine further this apparent nonlinearity of the semicircular canal response, a series of experiments was carried out to measure the subjective and objective response to angular sinusoidal accelerations of predominantly low frequencies (0.01 Hz to 0.1 Hz) (Katz, 1967).

5.1 Experiments

Experiments were performed on four subjects. Each subject was seated in the cab of the Man-Vehicle Laboratory rotating chair, in darkness. Within easy reach of his right hand was a simple directional switch to be used to indicate the subjective feeling of rotation direction.

Eye movements relative to the skull were measured by the pulsed infra-red photoelectric method.

The matrix of frequency and peak amplitude of sinusoidal acceleration presented to each subject is given in Table 5.1. All of the data points except those at 0.01 Hz and 0.02 Hz were run for a length of time (several cycles) such that the results from ten cycles of readable data could be collected and averaged. The first sixty seconds of all records were disregarded to allow the transient response of the canals to attenuate. At 0.01 Hz and 0.02 Hz, the peak angular velocity was great enough to cause discomfort for the subject if he was exposed to oscillation at these frequencies for any protracted length of time (greater than 5 minutes). We attempted to collect five or six cycles of readable data on two or three different runs at the same data point.

The subjective response of the subject to angular acceleration was indicated by means of the directional switch previously mentioned. The subjective switches and the transition point from left to right beating nystagmus could readily be compared with the actual zero angular velocity points of the chair.

5.1.1 Results and Discussion

Plotting the subjective and objective phase shift results of these experiments against the theoretical description of the horizontal semicircular canals results in the graphs shown in figures 5.1.1 and 5.1.2. In figure 5.1.1, most of the data falls below the theoretical curve, while in figure 5.1.2, most of the data is above the theoretical curve. This confirms the observation that the objective nystagmus response exhibits more phase lead than the subjective response at identical stimulus conditions. In the past, however, the two responses were elicited and recorded separately, here, they were recorded simultaneously. It is heartening to note that although there is a very wide spread, the locus of the center of gravity of the data for the subjective response does lie but slightly below the theoretical curve.

F (Hz)	α_m deg/sec	10	15	20	25	30	35	40
.01		x	x					
.02				x	x	x	x	x
.04				x	x	x	x	x
.08				x	x	x	x	x
.10				x	x	x	x	x

Matrix of Data Points Presented

Table 5.1

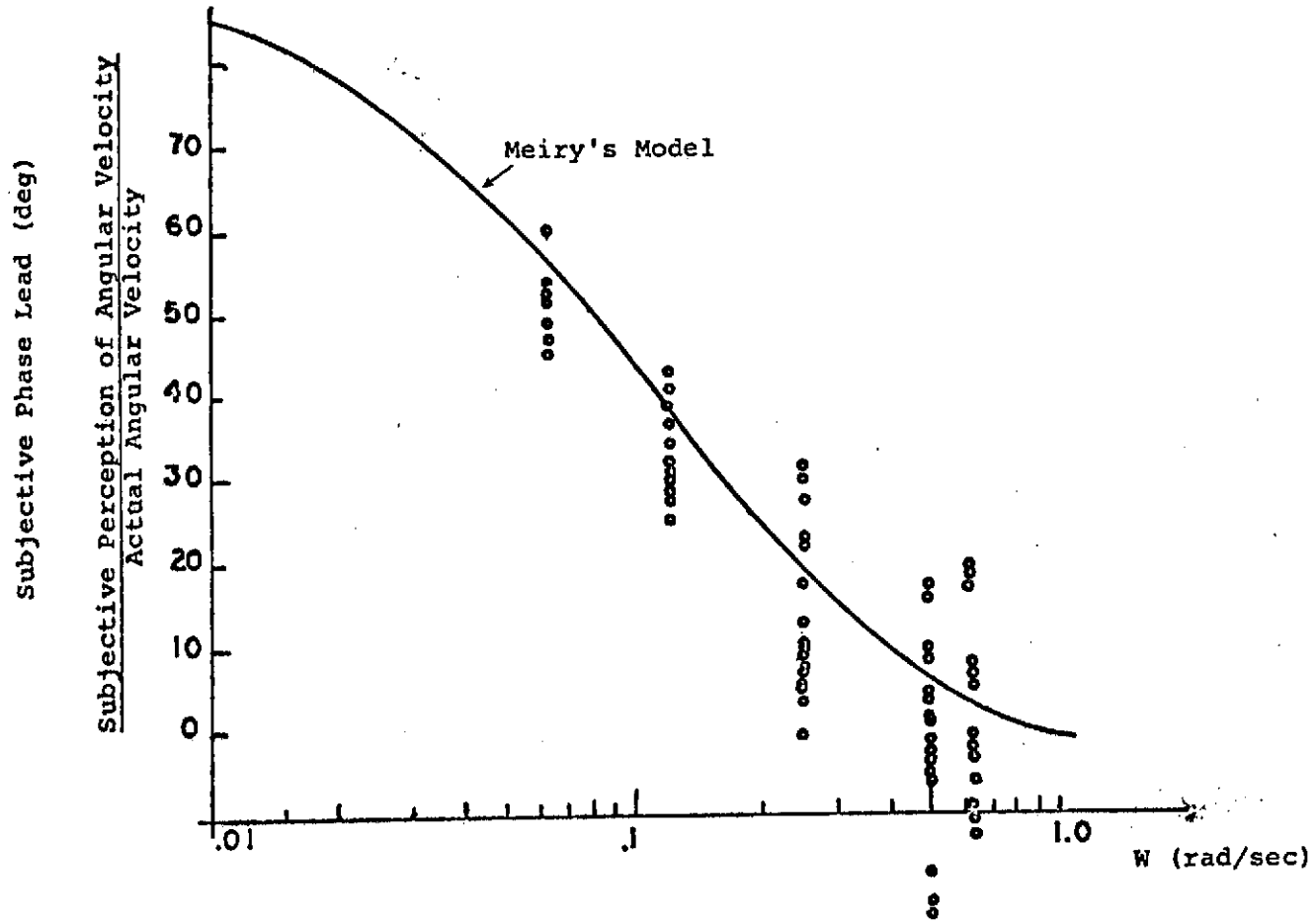


Figure 5.1.1

Subjective Measurements

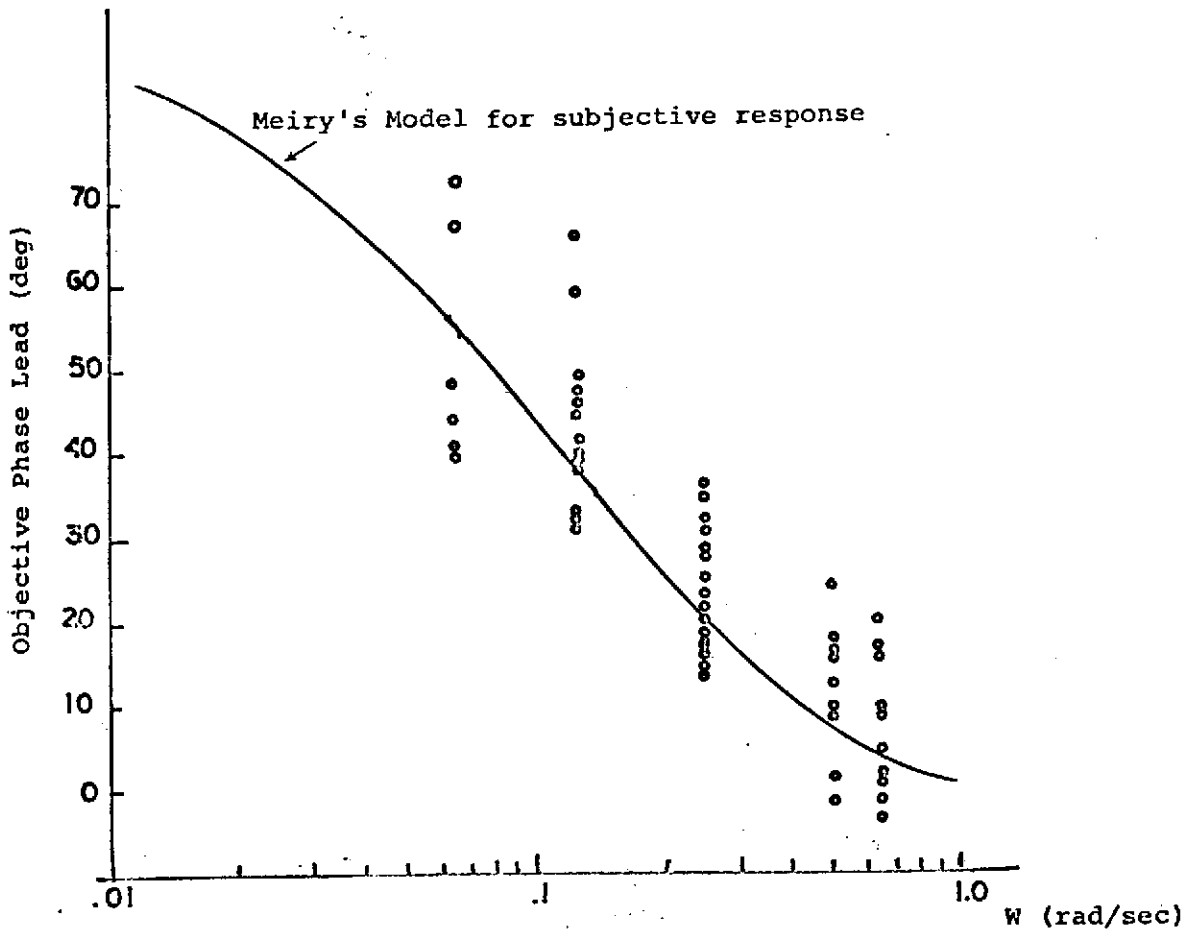


Figure 5.1.2

Objective Measurements

5.2 Vestibular Adaptation to Horizontal Rotation (Oman, 1968; Young and Oman, 1968, 1970)

The lack of a suitable mathematical descriptor for adaptation and habituation had been a persistent difficulty with the simple, second order torsion pendulum mathematical model for semicircular canal response. In particular, data of rotation experiments indicate that both the nystagmus and the subjective response are fundamentally different from that predicted purely on the basis of a second order model. The notable discrepancies are:

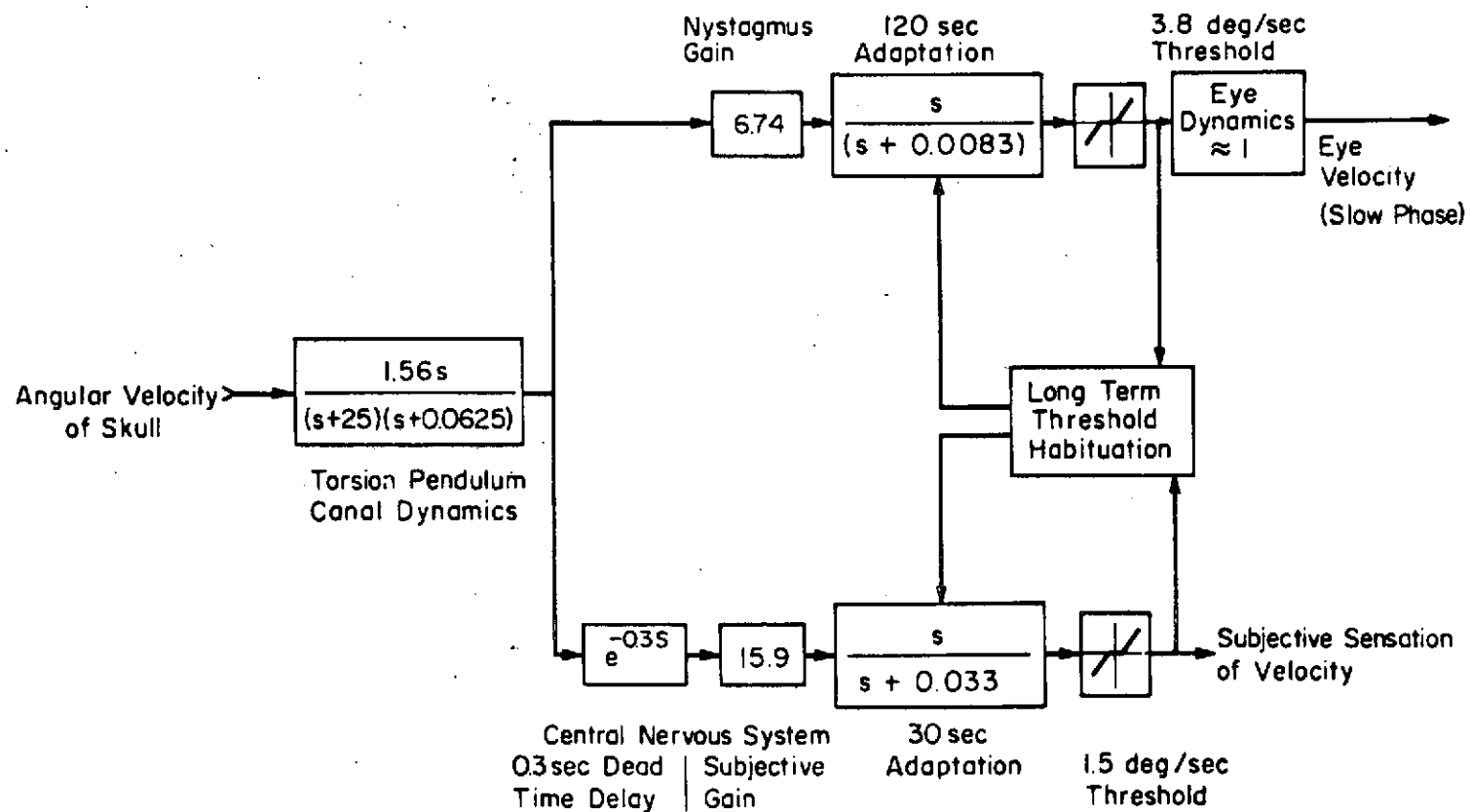
a. The sensation of rotation to sustained constant angular acceleration has been shown to decay, whereas the model predicts a constant steady state sensation of angular velocity and nystagmus.

b. The response to a sudden change (step) in angular velocity has been observed to overshoot, whereas the model predicts an exponential decay to the threshold level.

c. There is ample evidence that the dynamics of the subjective velocity response are fundamentally different from those of the nystagmus: A consistent difference appears in the time constants conventionally determined for the second order canal model depending upon whether they are estimated from eye movement recording or from measurements of subjective sensation of rotation (cupulograms.)

To eliminate these discrepancies a model was developed which cascaded an adaptation operator for nystagmus and for subjective response with second order dynamics representing the physical behavior of the cupula itself, as shown in Figure 5.2.1. This approach accounts for all the previously mentioned difficulties with the second order formulation. The model was developed to fit average response data from a number of sources, and allows a reinterpretation of the results from classical experiments on nystagmus and subjective response.

The fundamental assumption in the model is that adaptation has associated with it a short term homeostatic mechanism which results in a shift in the zero sensation and nystagmus velocity response reference levels. We hypothesize that the cupula response signal undergoes more rapid adaptation in the subjective path than in the nystagmus path. It should be emphasized, however, that despite the



Model for Subjective Sensation and Slow Phase Nystagmus Velocity for Rotation About a Vertical Axis

Figure 5.2.1

success of the model in accounting for the differences between nystagmus and subjective response, little should be inferred directly from the mathematical adaptation operator about the underlying physical mechanism associated with this process.

The input-output transfer function of the adaptation operator itself appears as:

$$\frac{R(s)}{\xi(s)} = \frac{s}{s + \frac{1}{\tau_a}}$$

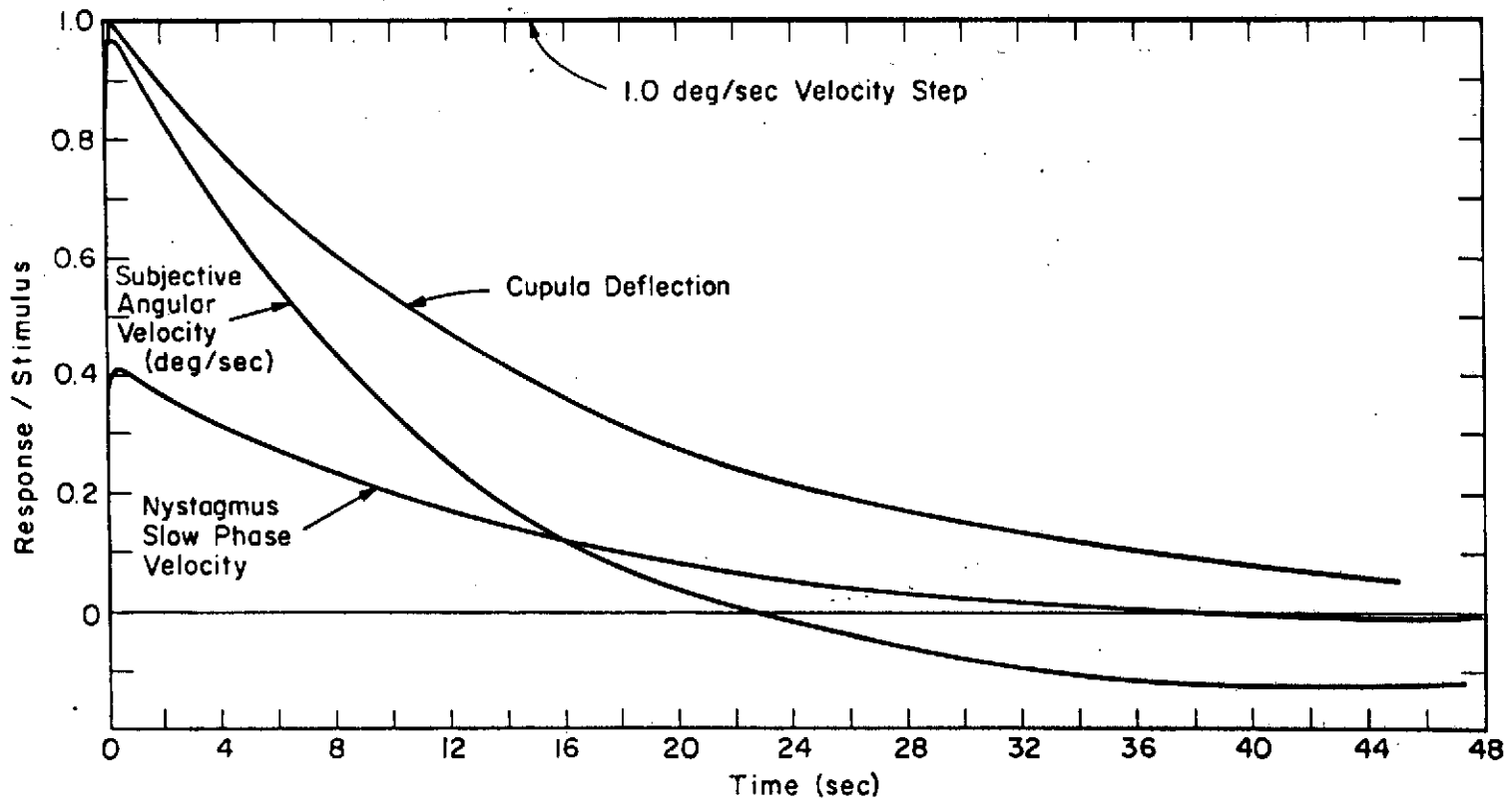
in Laplace transform notation. The adaptive dynamics represented by the expression in the equation exhibit a simple exponential decay with a time constant τ_a in response to a step deflection of the cupula.

As a model of the dynamics of the physical end organ we maintain the torsion pendulum form. Steer's rigorous fluid dynamics analysis has given support to the adequacy of the over-damped second order transfer function. Our approach was to hypothesize two paths for the model output; one for the subjective response and one for the nystagmus slow phase velocity. Different adaptation time constants for each pathway were determined and placed in a series with a second order cupula transfer function resulting in the model shown in Figure 5.1.1.

Groen and others point out that the long period time constant of the cupula return phase is estimated at approximately ten seconds for the horizontal plane by subjective cupulometry, but it is estimated at 16 to 20 seconds based on the nystagmus cupulogram. A fundamental assumption behind the second order model is that both the subjective sensation of rotation and the angular velocity of slow phase nystagmus are proportional to cupula displacement. Thus one would expect that they should follow a similar time course of decay until passing through their respective threshold levels, thus indicating the ratio of viscous damping to cupula spring constant.

For our model the cupula phase time constant of the second order physical dynamics was chosen to be 16 seconds. Figure 5.2.2 illustrates the response of the subjective path of this model to a step change in angular velocity such as that used in the cupulogram test. The predicted cupula response is also shown. Note

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Velocity Step Response of MIT Semicircular Canal
Linearized Model to 1 deg/sec Step in Horizontal Plane

Figure 5.2.2

that the predicted subjective angular velocity decays more rapidly than the cupula return and overshoots slightly.

Also shown in Figure 5.2.2 is the nystagmus response which exhibits the relatively weak 120 second time constant adaptation dynamics ($s/(s+.008)$) in the oculomotor loop of the model. The nystagmus curve decays with practically the same time constant as does the cupula deflection. When the model nystagmus data taken for several different velocity step magnitudes is examined in terms of the duration of post rotation nystagmus or, equivalently, the time until the model curve passes below threshold, it indicates a long time constant of about 16 seconds. If the subjective angular velocity is similarly treated, however, and the time duration of subjective response is estimated as though the entire system were second order, the apparent time constant is approximately 10 seconds. These two values agree very closely with the observed objective and subjective time constants derived from cupulometry. Thus, the effect of the adaptation operator in the subjective loop is to shorten the apparent (second order) time constant, and to explain the important discrepancy mentioned earlier.

The linearized subjective response overshoot is also shown in Figure 5.2.2. A large enough acceleration impulse will cause the magnitude of the overshoot to exceed threshold and a "second effect" or subjective reversal of direction is predicted. This reversal has been noted on many occasions. The adaptation model also predicts an overshoot for nystagmus response to velocity steps, but its magnitude is not nearly as great as that of the subjective overshoot.

It should be noted that the time constant and threshold specified for the model are the result of a fit of a particular set of average response data. Data from individual subjects may deviate somewhat from the responses predicted here. In this regard, however, it is interesting to note that working independently, Jones and Malcolm of McGill University have measured nystagmus response for long duration angular accelerations, and also observed that their results were at variance with the second order model. An adaptation operator for the nystagmus pathway was hypothesized, and an analog computer was used to match the model with the experimental data. The resulting model showed remarkably good fits for indi-

vidual experimental data, as well as for average response. Significantly, while the assumptions made in the derivation of the adaptation operator were quite different in the McGill study, they lead to a dynamic expression for an adaptation operator identical in form with that of our study.

5.3 Low Frequency Linear Stimulation

The revised dynamic otolith was based on tests conducted on subjects placed in a linear accelerator. At low frequencies, the simulator track available is not sufficiently long to permit accelerations which will exceed the otolith threshold.

One way to compensate for this difficulty is to apply the low frequency sinusoidal angle input to the roll motion of a rotation simulator. In this case, care must be taken to avoid stimulation of the semicircular canals. The requirements are that for a given frequency the amplitude must greatly exceed the threshold of perception for an upright head (0.005g) and the maximum angular acceleration must be less than the threshold for the vertical semicircular canals ($.5 / \text{sec}^2$).

The experimental design called for the following stimulations

Sinusoidal Rotation Stimulation

<u>rad/sec</u>	<u>amplitude($^{\circ}$) (zero to peak)</u>
0.02	6
0.04	6
0.06	6
0.08	6
0.10	6
0.12	6
0.16	6
0.20	6
0.40	3
0.50	2

Several problems were encountered in adapting the Man-Vehicle NE-2 simulator for use in this experiment. The main difficulty was that of producing a smooth cab position output in response to a sine wave command. This problem was finally resolved by adding a dither signal of 28 cps to the low frequency input.

5.3.1 Experimental Procedure

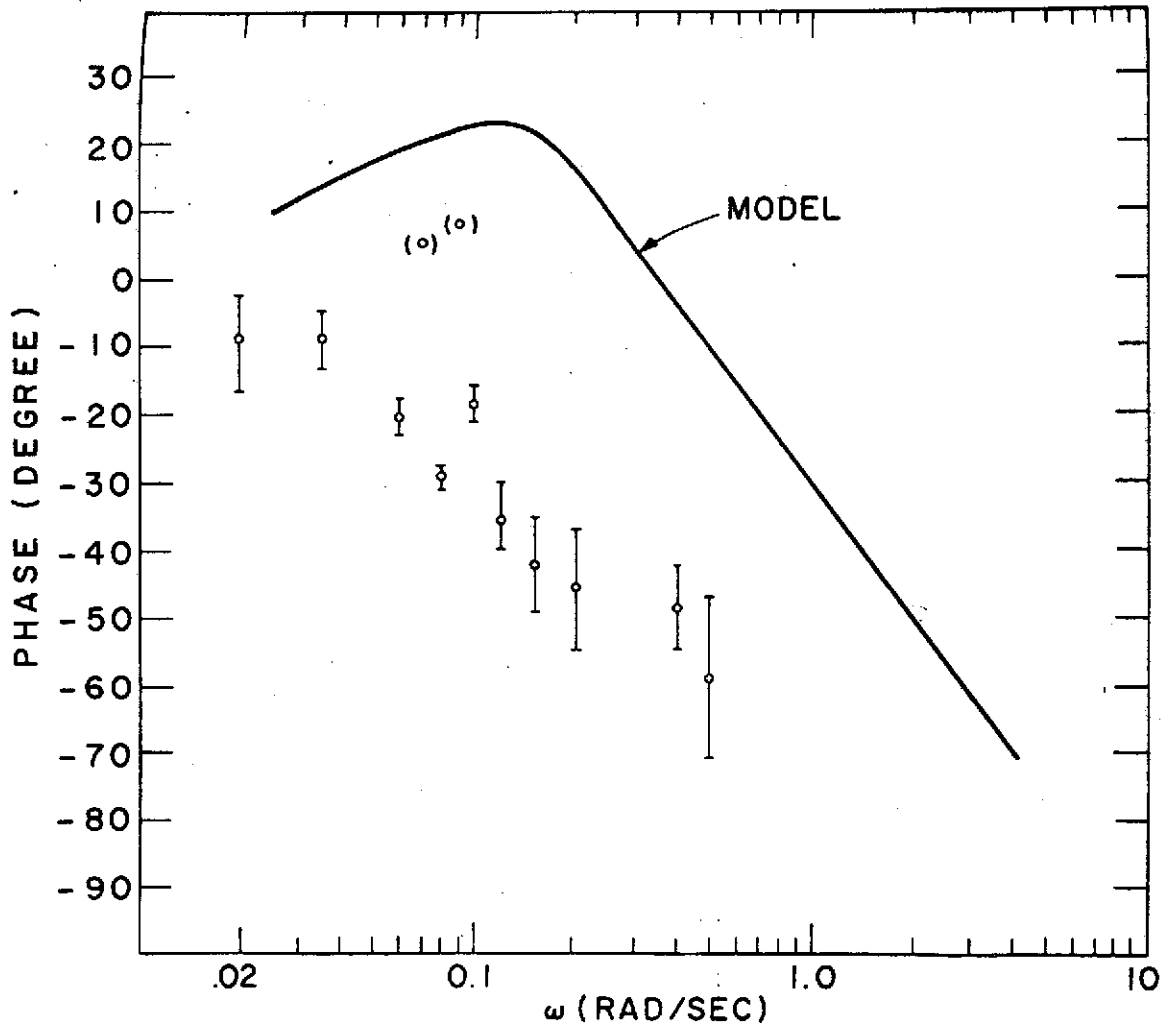
The subject was seated upright in the cab, and seat and harness straps were secured. No head restraint was provide; however, the subject was instructed to keep his head erect, stationary, and facing the front of the cab. The operator was instructed to indicate by means of a stick control on the right-hand armrest, the direction of his motion; at times of uncertainty, the stick was to remain upright. No restriction was placed on the means by which the subject was to make his decision, except to warn him that the acceleration of the cab in response to the dither signal had an envelope which was roughly sinusoidal, but with nodes that did not correspond to the maximum position displacement of the cab. The canopy was covered with an opaque cloth, and the trials began.

Generally, a signal of moderate frequency (0.08 rad/sec) was first applied. This permitted the subject to get a "feel" for the experiment. After three cycles, the lowest frequency to be considered (0.02 rad/sec) was applied and subsequent frequencies applied in ascending order to the maximum value (0.5 rad/sec). Six subjects were tested, four in this manner and two with trials in random order. The data for these two subjects did not differ statistically from that of the ordered sequence, suggesting that the order of stimulation was not of much significance.

5.3.2 Results and Discussion

The experimental data was analysed for intersubject variations which were found to be insignificant. Subsequently, the mean and standard deviation of the 40 data points per frequency were obtained.

The results are presented in figure 5.3.1 along with the predicted results of the otolith model. Clearly, the shape bears close resemblance and the anticipated levelling off of phase lag at low frequencies resembles the model. However, the phase shift of roughly fifty degrees which separates the model from the data makes exact interpretation of the results difficult. Such a shift might be expected because the experiment differed considerably from that upon which the model was



PHASE LAG (LEAD) OF SUBJECTIVE RESPONSE TO A CHANGE IN VELOCITY DIRECTION

Figure 5.3.1

based. One important difference was that of a high frequency dither signal which was applied as an additive input to the experiments. Its purpose was to provide smooth roll motion of the cab, but it may also have caused a continuous and randomly oriented shear acceleration to the sensory cells of the macula. This in turn could yield a delay in the subjective sensation of the velocity vector.

In retrospect, it is very likely that the semicircular canals were also stimulated to further complicate the nature of the measured response.

5.4. Directional Preponderance (Bias) in the Semicircular Canals

During voluntary control of the position of our vertical axis rotating chair, subjects have a tendency to drift in a preferred direction of rotation in the absence of non-vestibular stimuli. Some experiments have been done which investigated and quantified this phenomenon.

Subjects were seated in a chair free to rotate about a vertical axis. They were requested to keep their heads vertical so that the excitation of the otolith organs was minimized. The rotating chair was enclosed in a darkened compartment to prevent any external cues. The subject was provided with a control stick with which he could control the movement of the chair. The rotating chair was given a random input in angular motion and the subject was asked to keep the chair stationary.

The results of the experiment showed that the subject did have a tendency to rotate in a preferred direction without being aware of the fact. Of the seven subjects tested, three subjects always drifted in one direction, and the rest drifted in a preferred direction at least 80% of the time. It was further noted that the subjects tended to drift in the preferred direction at an approximately constant angular acceleration. The mean of average angular accelerations of the subjects in their preferred direction of rotation was $0.1625 \text{ radians/sec}^2$, with standard deviation of $0.067 \text{ radians/sec}^2$.

The subjects were examined by Dr. A.D. Weiss of the Massachusetts Eye and Ear Infirmary. They were given a general vestibular examination such as the ones usually given to patients with ear defects. Of particular importance in the

vestibular examination was the caloric testing with both hot and cold water irrigation. From the recording of the nystagmus, the duration of nystagmus was noted. Appropriate analysis of this data in turn gave the reduced vestibular response in one ear, as compared with the other, and the directional preponderance in one direction of nystagmus, as compared with the other direction, both in duration and slow phase velocity.

Although high correlation was not observed between Dr. Weiss' tests and those run on the rotating chair, there seemed to be significant binary correlation between the reduced vestibular response, with eyes open, and the bias as measured with the rotating chair. Five of the six subjects tested by Dr. Weiss showed reduced vestibular response in the ear corresponding to the direction of bias rotation. This would mean that subjects who tended to drift to the left also usually show their left ear more sensitive to the caloric testing.

5.5 VISUAL-VESTIBULAR INTERACTION

5.5.1 Anti-Vertigo Display

An outgrowth of our efforts to develop valid mathematical models for the semicircular canals and otoliths using the techniques of control theory was an attempt to define and investigate the etiology of vertigo, and the interaction between visual and vestibular motion cue inputs. We concluded that the one basic circumstance associated with most cases of vertigo is that a conflict arises as a man attempts subconsciously to continue the process of establishing a conception of his dynamic orientation in space in the presence of contradictory visual and vestibular cues. We believe that the occurrence of disorientation resulting from conflicting sensory modalities might be alleviated by a system which shows a vertiginous subject a display of the outside world oriented with respect to him so that it would agree, on the average, with his subjective prediction of the orientation of the outside world based only on his nonvisual modalities. In essence, the conflict between the visual and the vestibular input, presumably the major source of sensory modality conflict in most situations, would thereby be resolved.

Experiments were therefore undertaken to investigate the interaction of visual and vestibular motion cues. The laboratory's rotating chair was modified to include

a rotating drum projector to produce a moving stripe display on a screen inside the cab. Subjects were seated in the closed cab and stimulated so as to experience a simple form of vertigo, "dizziness", which results from lingering sensations of rotation after the cessation of angular velocity. A nonrational parameter computer model for human vestibular response to angular acceleration in a horizontal plane was used to control the moving bar display, thus creating a visual input which could be made to agree or to disagree with the theoretical subjective sensation of motion relative to the outside world. The system is diagrammed in figure 5.5.1.

Preliminary investigations involving four types of tests on five subjects were performed. A typical velocity profile is shown in figure 5.5.2. Subjects were asked to indicate the onset of sensation of rotation in a given direction by pushing a bi-directional switch, and to signal each ninety degrees of subsequent rotation in that particular direction. In addition, subjects were told to indicate directly when they felt confused in that they could no longer determine their angular velocity. The results of the experiments indicated that in the presence of a conflicting visual cue subjects either became unable to assess their angular velocity or reported subjective velocities which were primarily vestibular in origin. No confusion was reported when the display was driven so that the visual cue was sympathetic to the theoretical subjective angular velocity profile, even though it was not identical with the actual chair velocity. However, every subject reported confusion either when the display was anti-sympathetically driven or when the visual input was driven so that it was stabilized with respect to the outside world.

5.6 Interaction of Semicircular Canal and Otolith Information in Subjective Orientation (Ormsby, 1974; Ormsby and Young, 1974)

To broaden the approach to the vestibular role in spatial orientation beyond the simple case of pure linear or pure angular acceleration stimuli we developed a model for orientation under combined stimuli. This research, begun under the subject grant, was continued under grant NGR 22-009-701 for applications to flight simulation.

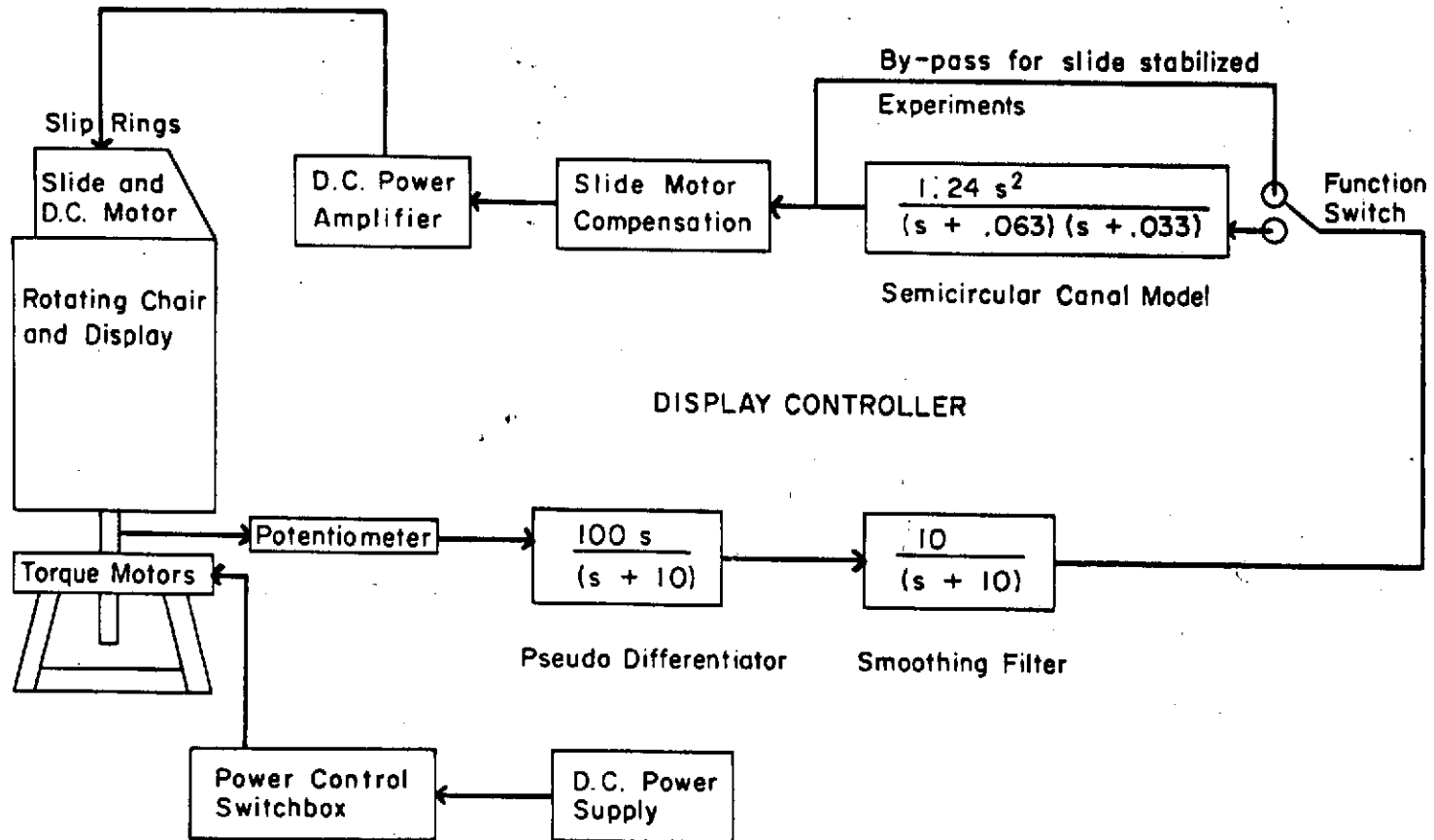
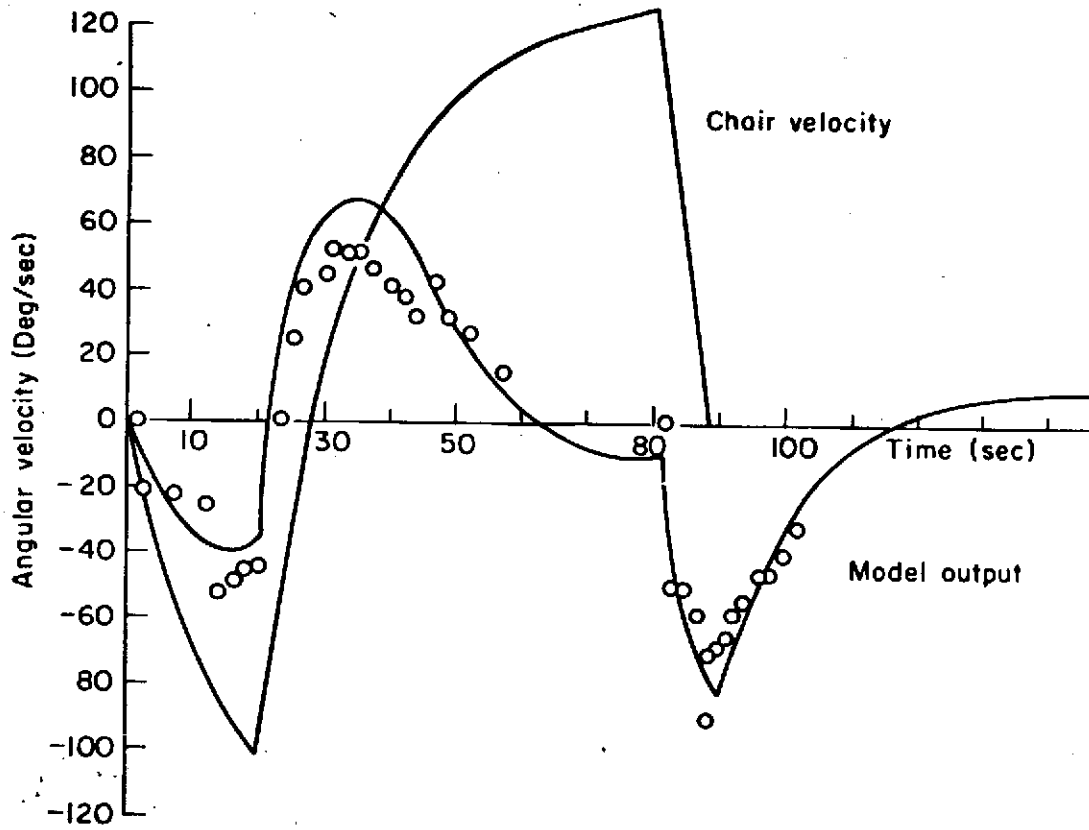


Figure 5.5.1

Anti-Vertigo Display System Schematic



SUBJECT : LVR
 MODEL DRIVEN + CCW
 RUN 3

Figure 5.5.2

5.7 Nystagmus Processing Instrumentation

In conjunction with our research project requirements for rapid, accurate on-line reduction of nystagmus records, we have developed a series of nystagmus devices and programs. These can have application to the clinical setting as well as the research laboratory.

5.7.1 Nystagmus Processing Program

MITNYS was developed using a Digital Equipment Corporation PDP-8 computer. The program uses one A/D converter channel to sample the input eye position record and up to six available D/A channels to output cumulative eye position, slow phase velocity and other response indices at a rate of 80 per second. The program is made to cycle once every 12.5 milliseconds by using an external analog clock. It uses approximately 2K of available memory.

The basic approach is as follows: The sampled eye position record is monitored by a fast phase detection routine. When a fast phase portion of the record is encountered, the eye position record is parabolically extrapolated across the fast phase interval based on slow phase eye velocity and acceleration. At the end of the fast phase, the difference between the current eye position and the extrapolated position is taken and added to a running sum, the total fast phase height. By subtracting this running sum from the input eye position, slow phase cumulative eye position is calculated; i.e. each fast phase segment is removed and the slow phase segments are pieced together. The program detects the dominant feature of the fast phase interval, the slope sense change, by comparing the sign of the difference with the sign of an average slow phase velocity. When slow phase velocity is low, the program disables the slope sense criterion, since a reversal of slow phase component may well occur and substitutes a modified velocity test. The other dominant feature of the fast phase interval, the reversal in the polarity of the velocity or a significant change in magnitude, by calculating the absolute value and the sign of the difference between two successive eye position samples. The absolute value is used as a criterion by comparing it with a minimum estimated fast phase velocity which is set as a function of the current

slow phase velocity.

5.7.2 Analog Analysis

A parallel development effort was begun with the limited objective of creating a low cost analog circuit which would act as an electronic differentiator for the slow phase portion of a caloric nystagmus record, and suppress the effect of the fast phase. Cumulative eye position, fast phase frequency, and other parameters were not required.

The concept evolved around the notion of constructing a device which effectively extrapolated across the fast phase interval in the eye velocity record by a simple low pass filtering. It was clear that treating the fast phase component as noise and low pass filtering of the total eye velocity record would not be appropriate as a low pass filter would effectively smooth the slow phase portion of such a record, the response of the filter to the fast phase portion significantly biases the intervening slow phase response.

Linear filters effectively screen "noise" which has zero mean value, but will not remove the fast phase from the total eye velocity record because the fast component, considered alone, does not have zero mean. However this condition could be satisfied, and the fast phase effectively filtered out if a "counterspike" of equal shape but opposite polarity were added to the total eye velocity at the smoothing filter input, as soon as a fast phase component is detected. To effectively achieve a smooth record, the fast phase/counterspike pair must be separated in time by an interval which is substantially smaller than the filter time constant. Over such a short time interval, a low pass filter acts essentially as an integrator. Hence, the requirements on the shape of the "counterspike" can be relaxed. It is only really necessary that the time integral of the counterspike be equal to that of the fast phase velocity.

A prototype design based on the foregoing principle was developed in the laboratory. The prototype has been successfully used in numerous analyses of caloric nystagmus. It became apparent that one of the advantages of the use of the fast phase filter is the simple physical compression of slow phase velocity data onto a

single page. If only a more traditional electronic differentiator is used, the data must be output on a chart recorder at a speed such that the fast and slow phase components can still be distinguished and runs of more than several minutes duration must extend over many feet of chart paper. The investigator must perform the pattern recognition function and is faced with the tedious task of recording his slow phase velocity determinations.

The prototype design generates the required counterspikes by a procedure which is satisfactory only when caloric records are being analyzed. The counterspike injected prior to the output low pass filter is merely a truncated and inverted version of the fast phase component formed by passing the difference between the current total eye velocity and a current slow phase velocity estimate through a deadzone element. The design has the advantage of simplicity, and exploits the fact that the caloric slow phase velocity response changes only slowly. A potential positive feedback instability exists should the actual slow phase velocity change sufficiently rapidly such that the difference between it and the feedback velocity estimate is greater than the deadzone value. For a given input position gain and signal/noise ratio, satisfactory values of deadzone and slope must be found by trial and error. Current efforts are focussed on developing an alternative low cost counterspike generation method using a delayed version of the velocity signal in order to circumvent the stability problem, and to make the filter usable for all types of inputs.

SECTION SIX

CONTROL OF POSTURE IN MAN

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- 6.0 Introduction
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 - 6.1.1 Reflex Responses during Quiet Standing
 - 6.1.2 The Role of Ankle Reflexes in Postural Stability
- 6.2 Vestibular Control of Posture
 - 6.2.1 Stimulation by Body Motion
 - 6.2.2 Postural Response to Vestibular Stimulation
 - 6.2.3 Conclusions - The Vestibular Model
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 - 6.5.3 Posture Control without Vestibular Senses
 - 6.5.4 An Overall Summary

Related Publications:

Nashner, 1970

Nashner, 1971

Young, 1970

Burr, 1973

6. Control of Posture in Man
(Nashner, 1970, 1971; Young, 1970; Burr, 1973)

6.0 Introduction

The control of forward and backward rotational motions about the ankle joints during quiet standing tasks was studied using a series of experiments designed to test how a human uses multiple feedback sensors to control his orientation. The goal of the postural control system in this simple task was assess the current status of the body sway motion and generate appropriate ankle reaction torques to maintain postural stability.

In both the models and the experiments, transient disturbances which probe at the state of the system at specific instances in time are treated, rather than continuous control processes. Sensory deprivation techniques were applied to isolate characteristics of the different feedback modes.

6.1 Reflex Control of Posture

The two direct mechanical mechanisms which resist change in flexor and extensor muscles are the rate of stretch and the muscle tension. In addition to the mechanical mechanisms varying tension to resist muscle length change, there is active resistance initiated by muscle spindle reflexes.

Higher center activity influences the reflex feedback functions in the following ways:

1. muscle mechanical properties are dependent on the level of muscle activation
2. muscle spindle feedback gains are controlled by higher center commands
3. higher centers may act on the alpha motor neuron pool, exercising direct control over the activation level of the muscle.

These studies demonstrate the validity of mathematical reflex control models. Most importantly, they show that linearized component models and equivalent bilateral muscle models can predict postural responses. Components of the postural reflex system include postural muscles responsive to both active neural stimulation and to mechanical stretch and position feedback via the muscle spindles which respond in proportion to length and rate of stretch. The higher centers exercise independ-

ent control of both phase and position feedback gains.

6.1.1 Reflex Responses during Quiet Standing

An experiment was conducted to determine specific values of the parameters of the ankle stretch reflex control loop, which were then used to formulate a model which quantified the contribution of the ankle reflex control loop to overall postural stability. The experiment consisted of the subject standing relaxed upon a platform which detected his reaction torques and sway angle about the axis joint. Excitation of the ankle stretch reflex was by small steps of the platform about an axis colinear with that of the ankle joints.

The reflex response amplitude was determined for each step response. Reflex gain is defined as response amplitude divided by the ankle step size. A significant feature of the reflex control loop is the large increase in gain for disturbances of very small amplitude. While gains for steps of $\frac{1}{4}$ to $\frac{1}{2}$ degree are considerably below that necessary for postural stability (2 ft-lb/degree versus 7 ft-lb/degree) this suggests that reflex control alone may fully stabilize the body for disturbances below 1/10 degree. This is substantiated by current physiological evidence. Evidence of large gain increases in muscle responses to small length changes and similar gain increases in reflex response have been found. Recordings of ankle torque and body angle responses during quiet standing indicate that the reflex loop fully stabilizes very small amplitude sway motions. All higher center feedback controls are limited by thresholds considerably larger than the measurement resolutions, therefore, reflex feedback control must be responsible for the stable periods observed during quiet standing.

On the basis of this discussion, a reflex gain function is defined in which both muscular and reflex responses show gain increases due to stiction for deflections less than 0.15 degree. Reflex feedback gain is sufficient for complete postural stability for deflections less than 0.05 degree. The compensatory response is initiated by higher center commands. Observed delay time, about 200 msec agrees with physiological evidence for higher center response delay; it also agrees with vestibular response delays.

In summary, vestibular and exteroceptive stimulation is shown to enhance

reflex responses, establishing this mechanism as a probable method for higher center control of posture disturbances. The fact that vestibular responses do not act as length commands gives further support to this conclusion. Two mechanisms are proposed for reflex enhancement: multiplicative increase in the dorsal to ventral reflex gain and control of the tension levels of muscle.

6.1.2 The Role of Ankle Reflexes in Postural Stability

The ankle stretch reflex feedback helps stabilize body sway motion. In many circumstances however, independent reflex control cannot perform this function. On non-rigid surfaces, inertial information is lost and the higher center sensory loops (eyes and vestibular organs) must mediate or override the reflex responses to provide postural stability. Experiments were run to explore the relationship of reflex and higher center control strategy. Test conditions were designed to determine the effects of visual feedback (enhancement and elimination), conscious posture set, random ankle angle disturbances, and elimination of ankle position feedback on the feedback parameters.

6.2 Vestibular Control of Posture

The vestibular organs, the utricles, the saccules, and the semicircular canals are the prime motion sensors in the human. Characteristics of the system are well documented and reviewed elsewhere in this report.

6.2.1 Stimulation by Body Motion

Angular acceleration of a rigid human body about the ankle joints is directly equivalent to the accelerating input to the pitch axis semicircular canals. Since the model considered here considers only quiet standing, equivalence of body angle and pitch angular accelerations may be assumed. Because the utricle otolith organs are located well above the center of mass of the body, the net reaction force on the otolith is negative during free fall sway divergence of the body. If the body diverges with partial resistance from postural responses, the net force acting on the otolith may be negative, zero, or positive depending on the intensity of postural resistance. Recalling that reflex responses oppose body sway with a torque

roughly proportional to angular deflections of the ankle joint, the following relations demonstrate the ambiguity of the sign of the linear motion sensor.

$$T_A = -K \theta_B$$

$$f_O = \theta_B \left(g - \frac{m_B g h_{cg} d_O}{I_B} + \frac{K d_O}{I_B} \right)$$

Using body parameter values we find that:

$$f_O > 0 \text{ if } K > 4 \text{ ft-lb/degree}$$

$$f_O < 0 \text{ if } K < 4 \text{ ft-lb/degree}$$

During stabilization postural responses, tangential and gravitational forces on the otolith are always of the same sign.

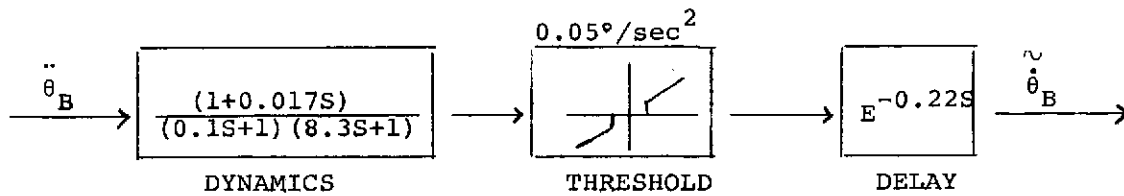
6.2.2 Postural Response to Vestibular Stimulation

The subject stands relaxed on the experimental platform. Sway is induced using small forward or backward platform displacements at constant velocity, introduced by the experimenter when the subject shows no movement. The platform disturbance induces a step change in body angular velocity.

Elimination of all other modes of sensory feedback is necessary to insure that postural responses to the induced sway are vestibular in origin. To remove reflex responses and exteroceptive cues, the platform is rotated to track the motions of the body; thus, maintaining an ankle angle of zero. Nulling ankle angle during body angle motion effectively opens the reflex position feedback loop but does not interfere with the subject's ability to generate isometric ankle control torques. Removal of reflex feedback also eliminates any advanced exteroceptive cues. Subjects are tested with eyes open and eyes closed to determine effects of visual cues on vestibular detection of body sway.

6.2.3 Conclusions - The Vestibular Model

The following semicircular canal model predicts the observed threshold characteristics over the complete range of induced sway rates.



Linear dynamic characteristics of the semicircular canal model compare closely with Meiry's canal model. The addition of a very small lead term is necessary to predict the minimum response time characteristics for large impulsive inputs. This term has no effect on threshold response properties within the dynamic range of normal body angle motions. New values are derived for the pitch semicircular canal acceleration threshold and response transmission time delay. The $0.05^\circ/\text{sec}^2$ acceleration threshold is considerably less than those observed with subjective reports.

Linear motion sensors play no role in the detection of postural responses during free-fall divergence. Simulation of the otolith dynamic model indicates that the linear acceleration threshold must be an order of magnitude less than the lowest values reported in the literature, even in the limit, as the initial body angle offset amplitude approaches zero. The utricle otolith organ threshold is sufficient to account for observed response threshold levels only in the static or nearly static range, since the body free-fall divergence rate ($\omega_B = 3 \text{ r/sec}$) is fast compared to the very slow dynamics of the otolith organs.

6.2.4 Postural Regulation with Vestibular Feedback

Posture control with vestibular feedback alone is observed. Subjects stand with eyes closed on the experimental platform. Ankle angle is maintained at zero by rotating the platform to track body angle motion. Ankle reaction torque and body angle are recorded continuously. A typical response sequence, is composed of the following stages:

1. stable period with no movement lasting several seconds
2. sway divergence begins
3. threshold is reached; ankle torque increases to restabilize body
4. one or several oscillations occur before quiet standing is re-established.

The transient response patterns are consistent among subjects. Average canal threshold is 0.36° . Variations among subjects are insignificant, $p > 0.1$.

In the proposed vestibular control model, the canal output, body angle rate, is used for an initial estimate of both body angle rate and body angle. The low frequency utricle otolith estimate of body angle updates the initial canal estimate. Stability is achieved when utricle otolith feedback corrects the expected low frequency divergence found when canal feedback alone is considered.

6.3 Visual and Extereceptive Senses

General models for visual and extereceptive feedback are developed which indicate the ways that these senses modify vestibular responses. Analysis is limited to more general models for the following reasons: (1) in normal subjects visual and extereceptive responses cannot be observed in isolation; (2) present physiology does not permit construction of detailed models of the visual and extereceptive senses.

6.3.1 Posture Regulation with Vestibular, Visual and Extereceptive Senses

Effects of including visual and/or extereceptive cues during vestibular control of posture were considered. Subjects stood on the platform under the following conditions: (1) eyes open; platform rotates to maintain ankle angle at 0 degrees; (2) eyes closed; platform rigid; (3) eyes open, platform rigid. In each of the conditions, posture control follows the same basic pattern seen in vestibular feedback control: quiet period, body divergence, transient responses, and re-establishment of quiet stability. The strategy of control in (1) above, visual and vestibular cues only, is similar to that found with vestibular cues only. In (2) and (3), the strategies are different, since the rigid platform enables full activation of the reflex control loop. Here control follows the pattern observed in the reflex response experiments. Subsequent analysis develops each of these control models to include effects of visual and extereceptive cues.

6.3.2 Vestibular and Visual Control

Average threshold values for the vestibular response during divergence are slightly smaller when eyes are open, 0.29° , than when eyes are closed, 0.36° . In both cases, eyes open and eyes closed, variations among the three subjects are statistically insignificant, $p > 0.10$. Visual cues, however, do not appear to directly effect the vestibular response threshold. The body angle threshold for

vestibular response is dependent on the divergence rate of the body, which is more rapid when eyes are closed. This effect is found to account for the difference between eyes open and eyes closed response thresholds.

6.3.3 Exteroceptive/Reflex Control

Basic changes in control are evident when exteroceptive cues and the reflex feedback loop are combined with vestibular regulation of posture. The following paragraphs explain these changes.

When reflex feedback control is included, the percentage of time during which subjects show static stability (i.e., when changes in reaction torque and body orientation cannot be detected) increases from an average of 20% to 40%. This increase is the result of "stiction" in the reflex loop.

The threshold for detection of body sway decreases significantly when exteroceptive cues are added, (case 2), dropping from 0.36° to 0.13° . Variations in the exteroceptive threshold value among subjects is statistically insignificant, $p > 0.10$. Amplitude of the transient response is reduced in proportion to the nearly threefold decrease in detection threshold.

Natural frequency of the transient response increases when the reflex feedback loop is added. Natural frequency with reflex stabilization is 0.35 Hz, significantly higher than that with only vestibular feedback control, 0.20 Hz.

Addition of visual cues, (case 3) shows slightly improved damping characteristics during the slow phase correction. Threshold for detection of sway remains virtually unchanged.

6.3.4 Models for Exteroceptive and Visual Control

The model for reflex/exteroceptive control follows the strategy of gain control developed in Section 6.1.

The exteroceptive sense is modeled as a low threshold sway detector with habituation. Otolith cues provide slow phase correction due to habituation of exteroceptive cues. Because quiet standing with reflex and exteroceptive cues is inherently very stable, little effect is noted when visual cues are added.

The model assumes that visual feedback participates in posture control only intermittently. Visual control is suppressed during stable periods and activated only after vestibular detection of divergence.

The basic strategy of separating dynamic and static feedback control functions applies to exteroceptive and visual senses. Exteroceptive cues provide rapid, low threshold detection of body sway divergence. Visual cues effect well damped, high resolution correction of the slow phase drift.

6.4 Posture Control Without Vestibular Cues

Posture regulation of a subject with complete loss of vestibular function is observed. The subject, age twenty years, has complete loss of vestibular and auditory function due to bilateral transection of the eighth nerve. The subject's motor-sensory functions in the lower limbs are normal. Vestibular loss occurred about two years prior to the author's tests. Since loss of vestibular function, the subject has remained active and has compensated for the sensory deficiency to the extent possible.

6.4.1 The Tests

The subject was observed standing quietly with eyes open and eyes closed. The following test was performed:

1. reflex response gains; eyes open and eyes closed
2. induced sway threshold tests; eyes open only
3. continuous recording of postural response and body angle motion.

6.4.2 Reflex Response Gains

Recalling earlier conclusions, the average gain of the stretch reflex response induced by small rotations of the ankle joint is shown to be about one-third that necessary for postural stability. During quiet standing with eyes open, the vestibular defective subject demonstrates reflex responses at gains somewhat larger than those of normal subjects, The level of gain, however, is still well below that necessary for postural stability. The subject is most likely using the same strategy for control as normal subjects.

This experiment tests the ability of the subject to detect sway divergence of reflex control and exteroceptive cues. Body sway is induced using backward and forward deflections of the platform at constant velocity. As sway is induced, the platform is rotated to track the rotation of the body, thus eliminating reflex and exteroceptive detection of sway via deflection of the ankle joints.

The observed response is similar to that seen in normal subjects: body angle begins to increase without a corresponding increase in ankle torque; motion is detected and torque increases rapidly; stability is re-established.

6.4.3 Threshold for Detection of Induced Sway

The minimum body angle subtended before motion is detected is about 0.35 degrees. The angle threshold increases continuously as the rate of induced sway increases, while normal subjects with the aid of vestibular cues show a constant threshold of 0.29 degrees for induced rates up to 0.80 degrees per second.

With eyes open, control strategy of the vestibular defective subject is the same as that observed for normal subjects. Records show periods of "stiction" stability and frequent diverging transients. Threshold for detection of the divergence transients is about the same as that observed for normal subjects, 0.10 degrees. Corrections of the transient disturbance, however are less consistent. Resulting divergence body angles are larger, 0.5 degrees versus 0.25 degrees for normals, and corrections are often underdamped.

When eyes are closed, the entire strategy of control changes significantly. No periods of "stiction" stability are present, rather small, higher frequency oscillations (about 3/4 to 1 Hz) are present almost continuously during quieter periods. During these quiet periods, body angle drifts continuously at rates ranging from 0.2 to 1.0 degrees per second. A rough estimate of the threshold for detection of this slow phase drift is about 2 to 4 degrees.

When slow phase drift is detected, larger transient responses are initiated. Characteristics of these responses are very erratic. Many of them are very poorly damped, showing many large oscillations at frequencies above 1 Hz.

6.4.4 Conclusions

A vestibular defective subject is able to regulate posture during a quiet

standing, eyes open task using the same control strategy as normal subjects. A radical shift in strategy, however, is necessary to maintain stability when the vestibular defective subject closes his eyes. Results are consistent with the reflex/exteroceptive control model described in section 6.4. They confirm two major characteristics of the model:

1. Habituation of the exteroceptive gain control mechanism results in poor static stability of the reflex/exteroceptive control loop.
2. Gain of the reflex loop may be increased to achieve static "rigid" stability.

6.5 Conclusions

The posture control model can be subdivided into two basic parts: regulation with stretch reflex position feedback (standing on a rigid surface), and regulation relying on higher center feedback sensors (standing on a surface which rotates to track body angle motions, nulling ankle angle continuously.)

Posture control strategy in these two extreme cases is fundamentally different. Evidence is presented, however, which suggests that for a large class of conditions between these extremes of a perfectly rigid flat surface and a surface with special compliant properties, a combination of these two control strategies can be expected.

6.5.1 Posture Control on a Rigid, Flat Surface

During quiet standing on a rigid, flat surface, the ankle stretch reflex gains are about one-third that necessary for posture stability. Small "stiction" forces acting between fibers within both intra- and extra-fusal muscle, however, supplement this reflex gain, and together they provide a gain adequate for complete stability for very small ankle deflections.

6.5.2 Posture Control with Vestibular and Visual Senses

When reflex/exteroceptive feedback is removed, the subject must rely completely on higher center motion sensors, the vestibular and visual systems. With eyes closed, vestibular cues are sufficient to provide postural stability. In this case, the utricle otoliths and the semicircular canals operate as frequency selective feedback sensors. Canals, the higher frequency motion sensors, detect body divergence and initiate postural responses.

6.5.3 Posture Control without Vestibular Senses

Posture control without vestibular function is nearly normal when a defective subject stands on a rigid surface with eyes open. Detection of body divergence, exteroceptive cues, is normal. Reflex gains are somewhat higher than normal. It may be concluded that exteroceptive detection of divergence and visual correction of slow drift are sufficient.

When eyes are closed, a radical change in control strategy is evident. Since neither visual nor utricle otolith static senses are available, reflex gain is increased about sixfold to enable "rigid" stability.

6.5.4 An Overall Summary

Posture control is seen as a multiloop system in which a number of specialized feedback sensors contribute to the generation of commands. Proprioceptive sensors contribute to the generation of commands. Proprioceptive sensors and neural processing at the lowest levels enable crude but fast acting responses based on information from body centered frames.

"Inertial" sensors and higher center processing provide more accurate, adaptable control but with longer processing delays. Hence, posture control is a highly non-stationary process in which responses to transient disturbances are initiated at the lowest levels. Allocation of control then "radiates" upwards to the higher centers where successive corrections based on more complete information, fine tune the initial responses.

GALVANIC STIMULATION AND THE PERCEPTION OF ROTATION

John R. Tole, M.S. Thesis, M.I.T., June, 1970

The influence of galvanic vestibular stimulation on the perception of rotation was investigated. The study was intended to lay the groundwork for future, more detailed study of the galvanic reaction. Of particular interest are possible clinical applications in the treatment of vertigo and the diagnosis of certain vestibular disorders.

A set of experiments were designed to measure the gross effects of current intensity and point of application on a subject's perception of rotation. An approximate threshold for the intensity effect was determined. Among points of application only polarity differences could be shown to be significant. A tentative linear relation between the bias in perception threshold and the intensity of current was found. The galvanic reaction of one vestibularly abnormal subject is also discussed.

Comparisons were made between galvanic stimulation and other common means of vestibular stimulation. Current mathematical models of vestibular function were reviewed and the extension of these models to include the galvanic reaction was examined.

Possible future directions for research in this area are also discussed.

EXTRAVEHICULAR ATTITUDE CONTROL BY THE USE OF HEAD MOTIONS

L.C. Von Renner, M.S. Thesis, M.I.T., June, 1970

Abstract

On the basis of a survey conducted on existing techniques for astronaut extravehicular attitude control in space, experiments were performed to determine the usefulness of bioelectric currents generated in muscle tissue as a control signal source.

Muscle sites were identified on the neck and biocurrents (electromyographic signals or EMG's) were detected using surface electrodes. Raw signals were generated by turning the head right or left with respect to the body; subsequent conditioning was performed using a hybrid computer. Motion cues (yaw) were provided by a rotating chair which a subject attempted to control by moving his head. Performance levels based upon integrated squared error were compared for two separate plant dynamics between electromyographic and conventional pencil-stick control.

Examination of the data revealed that control of yaw attitude using EMG;s was a practical means of providing hands-off control. However, EMG performance was in all cases poorer than equivalent tests conducted using a stick. This probably resulted from the large deadband ($\pm 45^\circ$ normally) which existed in the physical angle of turn required of the head to produce a measurable signal. Recommendations are made for describing function analysis of the data and the investigation of other, mechanical methods for using the head position as a control signal source.

THE EFFECTS OF GALVANIC VESTIBULAR STIMULATION AND NECK ROTATION ON THE ANKLE
STRETCH REFLEX

Charles Roger Burr

S.M. Thesis

January 1973

ABSTRACT

The postural effects of galvanic vestibular stimulation (GVS) were investigated in normal subjects. Neck rotation effects were also studied because of the dependence of postural GVS reactions on head position. Motivation for the investigation derived from an interest in possible clinical applications of GVS.

The ankle stretch reflex was examined as an indicator of muscle tone. Changes in muscle tone resulting from GVS and neck rotation would lead to alteration in the reflex response timing and/or magnitude. The stretch reflex was elicited with the subject standing, by small rapid platform rotation steps about the ankle axis. Parameters were selected from ankle torque, hip displacement and EMG records. Statistical analysis of the parameter values showed no significant tonic effects of GVS or head position.

Vestibular anatomy and physiology and relevant posture physiology were reviewed. Experimental evidence concerning the action site of GVS was examined.

INFLUENCE OF ADAPTATION ON THE HUMAN SEMICIRCULAR CANALS AND THE ROLE OF SUBJECTIVE ANGULAR

VELOCITY CUES IN SPATIAL ORIENTATION

Charles M. Oman, S.M. Thesis, M.I.T. September 1968

The role of the semicircular canals in human dynamic spatial orientation was studied. A working definition for vertigo was developed based on the assumption that conflicting sensory modalities are the primary etiological factor.

Experiments were undertaken to investigate the interaction between visual and vestibular motion cue inputs. A nonrational parameter computer model for human vestibular response to angular acceleration in a horizontal plane was used to control a moving bar display which showed subjects seated inside a rotating chair cab a visual input which could be made to agree or to disagree with the theoretical subjective sensation of motion relative to the outside world.

The study led to an improvement in the mathematical model for subjective response and compensatory eye velocity by including the effects of short term adaptation. By assuming that the physical canal dynamics were second order and that the adaptation mechanism involves a short term homeostatic shift in the zero response reference level, some of the persistent difficulties of the classical "torsion" pendulum model were overcome. Differences in nystagmus and subjective cupulograms, as well as phase and time course data were explained. Experimentally observed "subjective undershoot" and "secondary nystagmus" were accounted for.

The results of display experiments involving four types of tests on five subjects indicated that in the presence of a conflicting visual cue, subjects either became unable to assess their angular velocity, or reported subjective velocities which were primarily vestibular in origin. No confusion was reported when the display was driven so that the visual cue was sympathetic to the theoretical subjective response. However, every subject reported confusion when visual input was driven so that it was stabilized with respect to the outside world.

SENSORY FEEDBACK IN HUMAN POSTURE CONTROL

Lewis Michael Nashner Sc. D. Thesis, M.I.T., June, 1970

Abstract

Current models for physiological components and a series of experiments on human subjects form the basis for a multiloop control model which describes how a human uses multiple feedback sensors to control his orientation. Particular emphasis is placed on defining functional interfaces between the feedback sensors and postural responses. Because of the inherent complexities within the posture control system, analysis is simplified by considering only control of forward and backward rotational motions about the ankle joints during quiet standing tasks.

The research effort is divided into three segments. First, a general posture control model is assembled given current models for motor and sensory components. This general model forms the basis for a series of experiments with human subjects using a specially designed two-degree-of-freedom simulator. Finally, experimental observations are combined with the general model, developing specific models which predict the observed postural responses.

During quiet standing on a rigid surface, ankle reflex gain is about one third that necessary for postural stability. Ankle reflexes, however, are adequate to fully stabilize very small deflections due to the presence of 'stiction' forces acting between fibers in intra- and extra-fusal muscle fibers. Quiet standing is punctuated by frequent transients during which the subject "breaks out" of static reflex stability and begins to diverge. A kinesthetic threshold is reached, commanding a transient multiplicative increase in reflex gain proportional to disturbance amplitude. A static sense, either vision or utricle otolith is necessary to correct slow drift of this reflex/kinesthetic control loop.

When reflex and visual feedback are removed, the vestibular sensors are able to fully stabilize posture. The utricle otoliths and semicircular canals act as frequency selective feedback sensors. The canals detect sway divergence and initiate corrective postural responses. The utricle otoliths provide a static vertical reference to stabilize slow drift of the canal control loop. Otolith cues are shown to be ambiguous at higher frequencies because of interactions between linear motion and gravitational stimuli.

Control strategy is observed in one subject with complete loss of vestibular function but with normal motor control. When eyes are open, the subject shows reflex/kinesthetic control strategy which is very nearly normal. The subject is also able to stand with eyes closed; however, this required great effort. Tests show eyes closed control strategy to be radically different. Extensor reflex gains were increased six-fold, allocating almost complete control of function to reflex rigidity.

PERCEPTION OF ROTATION - NYSTAGMUS AND SUBJECTIVE RESPONSE AT LOW FREQUENCY STIMULATION

Gerald B. Katz

M.S. Thesis

January, 1968

Abstract

A rotating chair was built to submit subjects to sinusoidal angular accelerations at various combinations of frequencies (0.01 cps to 0.1 cps) and peak angular accelerations ($10^{\circ}/\text{sec}^2$ to $45^{\circ}/\text{sec}^2$) for the purpose of studying the human subjective and objective response to rotation at low frequencies. Each of four subjects was seated in the completely dark chair with the axis of rotation passing through his head.

His subjective response was measured by means of a directional switch; his objective nystagmus eye movement response was simultaneously measured and recorded. A study of the resultant phase differences between both subjective and objective perceptions of angular velocity and actual angular velocity leads to the following conclusions:

1. The phase lead of both objective and subjective response exhibited no simple functional dependence upon amplitude of acceleration.
2. The amount of phase lead in both cases is inversely proportional to stimulus frequency.
3. The objective phase lead is larger at any stimulus condition than the corresponding subjective phase lead.
4. Intersubject response differences were very evident, irregular, and relatively great.
5. The data presented agrees in a gross manner with the data of Hixon and Niven.

DYNAMIC RESPONSE OF THE SEMICIRCULAR CANAL AND LATERAL LINE ORGANS

by

Ph.D. Thesis

Charles M. Oman

1973

Abstract

The mechanical dynamics of the peripheral sensors and adaptation in response to stimulation were studied in the human semicircular canals and in the free-standing lateral line organs of the mudpuppy, Necturus maculosus.

The pressure sensitivity and the dynamic range of physiologic motion were estimated for the human semicircular canal cupula. Behavioral thresholds were expected to create cupula pressure differences of 10^{-4} dyne/cm², and displacements to be on the order of 10^{-2} microns, or less. In everyday life, motions of the center of the cupula probably do not much exceed 3 microns.

Adaptation was studied in eye movement responses to unilateral caloric stimulation by changing body orientation during prolonged irrigation of the ear with hot or cold water. Response decline was found to be unrelated to the time history of irrigation temperature, per se, and therefore not likely due to local reflex vasodilation. The value of seventy seconds found for the caloric adaptation time constant by modeling average responses implicates adaptive mechanisms in vestibulo/ocular pathways. However, unilateral response dynamics appear nonlinear in that nystagmus reversals observed in corresponding rotational testing, usually attributed to the effects of adaptation, did not occur in caloric responses.

The cupula of the freestanding lateral line organ in Necturus was examined histologically and found to contain a structurally distinct outer sheath and an inner core of longitudinal filaments. Stiffness of the cupula was measured by applying lateral forces near its top. Cupula displacement dynamics were predicted to approximate those of a second order overdamped dynamic system in response to local water flow velocity. The time constants of these dynamics were expected to change significantly as the cupula grows in length.

Afferent and efferent nerve activity was studied in Necturus in response to direct mechanical stimulation of the cupula. Efferents were observed to respond to touch stimuli, and not to afferent stimulation. Possibly because of the relaxing agent used, efferents did not appear to modify afferent response. Afferents were found to respond in a direction sensitive manner linearly proportional to cupula velocity, rather than to displacement. Behavior of this type has not previously been reported.

THE INFLUENCE OF ANGULAR AND LINEAR ACCELERATION AND THERMAL STIMULATION ON THE HUMAN SEMICIRCULAR CANAL

Robert W. Steer

Ph.D. Thesis

August 1967

Abstract

The hydrodynamic properties of the human semicircular canal system were studied to determine its dynamic characteristics and their relationship to observed subjective and objective vestibular responses to various motion inputs. Four topics of particular importance in current vestibular research were examined in detail.

The density, coefficient of expansion, and viscosity of the labyrinthine fluids, endolymph and perilymph, have been measured to provide precise values for the coefficients of the dynamic model. A microviscometer was designed, built, calibrated, and used to measure the viscosity of 1-2 microliter samples of endolymph and perilymph. Density measurements were made via precision balance scales and accurate volume measurements and coefficients of expansion were made by microscopic measurements of the volume of the fluids at several temperatures.

The semicircular canal is modelled as a rigid torus of fluid, with the cupula acting as an elastic and viscous restraint. A system transfer function is evaluated for cupula displacement as a function of angular acceleration. It is shown that the cupula's viscous drag on the wall of the membranous labyrinth accounts for the majority of the damping in the system and resolves the disparity between previous calculations of damping, which only considered the hydrodynamic drag of endolymph in the canalicular duct and measured damping coefficients.

Caloric stimulation of the vestibular apparatus is examined, and a model is proposed based on the published measured time history of the temperature gradient across the lateral canal when the external auditory meatus is irrigated with water above or below body temperature. The presence of a thermal gradient across the lateral canal is shown to produce the physiological equivalent of an angular acceleration because of the torque which acts on the endolymph as a result of its thermal coefficient of expansion. Caloric experiments were performed which attest to the validity of the model.

The influence of linear acceleration on the semicircular canals was investigated. Human objective and subjective responses to rotation about a horizontal axis, to counter-rotation, and to stimulation by a rotating acceleration vector were examined. The observed responses of long duration nystagmus and continuous sensation of rotation are not in conformity with classical models of the vestibular system and there has developed a sizable body of experimental evidence which attributes a significant portion of these unusual responses to the semicircular canals. It is shown through the distensibility of the canalicular duct under the influence of linear acceleration, that the observed bias component of nystagmus can be attributed to a first order nonlinearity of the semicircular canal dynamics. Experiments were performed on a centrifuge equipped with a rotating chair to show the relationship between the magnitude of the acceleration field, the rotation rate of the subject, and the slow phase velocity of vestibular nystagmus.

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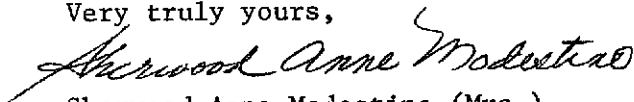
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Gentlemen:

We submit herewith five (5) copies of the Final Report of Research on Biophysical Evaluation of the Human Vestibular System in fulfillment of the technical report requirements under the reference grant.

This research was conducted under the direction of Professor Laurence R. Young, Principal Investigator and Director of the Man-Vehicle Laboratory, Department of Aeronautics and Astronautics.

Very truly yours,



Sherwood Anne Modestino (Mrs.)
Secretary to Professor L. R. Young

/s

CC: NASA Bioresearch Office
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