MASSACHUSETTS INSTITUTE OF TECHNOLOGY

MV-69-3

BIOPHYSICAL EVALUATION OF THE

HUMAN VESTIBULAR SYSTEM

Principal Investigators: Prof. J. L. Meiry
Prof. L. R. Young
June 1969

MAN-VEHICLE LABORATORY
CENTER FOR SPACE RESEARCH
MASSACHUSETTS INSTITUTE OF TECHNOLOGY
CAMBRIDGE, MASSACHUSETTS 02139

BIOPHYSICAL EVALUATION OF THE

HUMAN VESTIBULAR SYSTEM

Status Report on NASA Grant NGR 22-009-156

for the period January 1968 to June 1969

MV-69-3

June 1969

Principal Investigators: Professor J. L. Meiry

Professor L. R. Young

MASSACHUSETTS INSTITUTE OF TECHNOLOGY

Man-Vehicle Laboratory

Department of Aeronautics and Astronautics

Center for Space Research

I.   THE HUMAN VESTIBULAR SYSTEM

The control systems engineer views the vesibular apparatus both as a potential problem and as a challenge. The problem stems from the use of vehicles to expose men to other than the normal environment for which the vesibular system was designed, resulting in such man-machine interface difficulties as vertigo, disorientation, and motion sickness. The challenge comes in attempting to recreate mechanically the elements of an attitude control system or short term inertial guidance system of the size of the non-auditory labyrinth.

Our research on the vestibular system attempts to develop mathematical models for its functioning, much in the manner of a control engineer examining the dynamic characteristics of the sensors of a feedback system. Such models, of course, indicate only average responses and are a guide to interpreting experiments. We have applied analysis and critical experiments to develop mathematical models of the semicircular canals and otoliths. These methods are typical of the techniques being used throughout the field of biological control systems. Secondly, this approach points out those special areas where the control systems analysis has raised important questions directed to the physiologist. We are involved in a constant attempt to develop a model which explains behavioral "input-output" data and is consistent with the known physiological structure. The model serves its purpose by pointing out the new areas for investigation and by posing testable hypotheses.

Perhaps the most important benefit derivable from the vestibular models is the development of better, repeatable and efficient methods of clinical diagnosis. Many of our experiments have indicated this possibility and with the appointment of Dr. A. Weiss from the Massachusetts Eye and Ear Infirmary as Research Associate in our laboratory, the effort to apply knowledge of vestibular models to diagnosis will receive new impetus during the coming year. Similarly, with the addition of Prof. R. Curry to the Man Vehicle Laboratory staff we expect to expand our activities in the area of statistical identification methods, the mainstay of biological control systems analysis.

The following material presents results of four further investigations of the human vestibular system. While the first two represent attempts to refine and verify vestibular models, the latter are efforts to bring analysis into the clinic and in vertigo prevention.

I.1   Vestibular Adaptation To Horizontal Rotation (L.Young,C.Oman)

The lack of a suitable mathematical descriptor for adaptation and habituation has 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:

-2-

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 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 empha-

sized, however, that despite the 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:

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

in Laplace transform notation. The adaptive dynamics represented by the expression in equation (1) exhibit a simple exponential decay with a time constant of 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 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 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 that the predicted subjective angular velocity decays more rapidly than the cupula return and overshoots slightly.

Also shown in Figure 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 seconds 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 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 individual 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.

I.2 Low Frequency Linear Stimulation (L. Von Renner)

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 ($.5°/sec^2$).

The experimental design called for the following stimulation:

Table I. Sinusoidal Rotation Stimulation

rad/sec	amplitude (zero to peak)
.02	6°
.04	6°
.06	6°
.08	6°
.1	6°
.12	6°
.16	6°
.2	6°
.4	3°
.5	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.

I.2.1   Experimental Procedure

The subject was seated upright in the cab, and seat and harness straps were secured. No head restraint was provided; 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 decisions, 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 by 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 (.02 rad/sec) was applied and subsequent frequencies applied in ascending order to the maximum value (.5 rad/sec). Six subjects were tested, four in this manner and two qith 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.

I.2.2.   Results and Discussion

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

The results are presented in Figure 3 along with the predicted results of the otolith model. Clearly the shape bears close resemblance and the anticipated leveling 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 based. One important difference was that of a high frequency dither signal which was applied as on additive input 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.

With the recent acquisition of Link GAT-1 by the Man-Vehicle Laboratory, we are now in the process of repeating these series of experiments with sufficient confidence of being able to avoid ambiguous stimulation.

I.3 Directional Preponderance (Bias) in the Semicircular Canals
(P. Mirchandani)

In some preliminary experiments we had observed that subjects have a tendency to drift in a preferred direction of rotation in the absence of non-vestibular stimuli. Some experiments have been completed which investigated and quantified this phenomenon.

Our subjects were seated in a chair free to rotate about a vertical axis. They were asked to keep their heads vertical such that the excitation of the otolith organs was minimized. The rotating chair was enclosed in a darkened compartment to prevent any external visual 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 noticed 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 radians/sec^2. The standard deviation of this value was .067 radians/sec^2.

The subjects were further 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 preponder-
ance 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
significant binary correlation between the reduced vestibular
response, with eyes open, and the bias as measured with the ro-
tating 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 have their left ear
more sensitive to caloric testing.

Further tests are essential before any inference can be made.
Other tests must be conducted which would distinguish whether the
bias was psychological in nature. However, there seems to be
doubt of the fact that a bias does exist in the semicircular
canals. On the assumption that a direction preponderance did
exist, the physiology of the vestibular system and the current
model of the semicircular canals were examined and an explanation
for such a bias was sought. On the basis of the existing know-
ledge of the semicircular canals four possible explanations were
obtained which could be accommodated both physiologically and
mathematically. These four explanations are given briefly be-
low.

1. The directional preponderance could be due to a permanent displacement in the cupula of the semicircular canals. In the presence of a random noise (or movement) the subject must rotate himself at a constant angular acceleration to have an average sensation of remaining stationary.

2. It has been well established that there is a threshold in the semicircular canals below which for whatever angular acceleration the subject does not feel any sensations. The directional preponderance could be due to a psychological bias of the subject to work on one side of the threshold. In this case, the subject must rotate himself at a constant acceleration (or at a uniformly increasing acceleration depending on the model of the semicircular canals adopted) in order to have an average sensation of remaining stationary.

3. The directional preponderance could be due to an asymmetry in the threshold non-linearity of the semicircular canals, the asymmetry resulting from a difference in the threshold limits in the two directions of rotation. Again, in order to have an average sensation of remaining stationary, the subject must rotate himself at a constant acceleration (or at uniformly increasing acceleration depending on the model of the semicircular canals adapted).

4. An asymmetry in the threshold of the semicircular canals could also be due to a difference in the sensitivity to rotation in the two directions. Again, the subject must rotate himself at a constant acceleration (or at a uniformly increasing acceleration depending on the model of the semicircular canals) in order to have an average sensation of remaining stationary.

-12-

The above explanations were examined mathematically and in each case it was shown how such a situation may result in the bias in angular acceleration in a preferred direction. We are pursuing further experimentation and analysis to determine which of the above four explanations, or their combination, or some other explanation, is the appropriate phenomenon which manifests itself in the directional preponderance of the human vestibular system.

Similarly, further investigation is underway to see whether our method of testing directional preponderance could be a useful diagnostic tool in hospitals and clinics and in vestibular research. It is hoped that repeatability, reliability, its low preparation time, and its low discomfort quality will make this method preferrable to some of the existing clinical techniques.

I.4   Anti-Vertigo Display System (C. Oman)

In recent months, our efforts to develop valid mathematical models for the semicircular canals and otoliths using the techniques of control theory have been reviewed in an attempt to define and investigate the etiology of vertigo, and the interaction between visual and vestibular motion cue inputs. We conclude 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

-13-

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 orienta-
tion of the outside world based only on his nonvisual modali-
ties. In essence, the conflict between the visual and the
vestibular input, presumably the major source of sensory mo-
dality conflict in most situations, would thereby be resolved.

Hence, experiments were undertaken to investigate visual
and vestibular motion cue interaction. The laboratory's
rotating chair was modified to include a rotating drum project-
or 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, "dizzyness," which
results from lingering sensation of rotation after a 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 mo-
tion relative to the outside world. The system is diagrammed
in Figure 4.

Preliminary experiments involving four types of tests on
five subjects were performed. A typical velocity profile is
shown in Figure 5. 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 addi-

-14-

tion, 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. (Figure 5 is typical.) 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.

I.5   Nystagmus Computer Program (J. Tole)

In addition to the above reported activities, an on-line hybrid computer program to analyze and process nystagmus is very nearly completed to facilitate and expedite greatly our experimental work. This computer program removes fast phase saccades from an eye movement recording to obtain the cumulative eye position. The information obtained in this manner is further processed by a psuedo-differentiator in order to derive the velocity of the slow phase nystagmus.

II.   CONTROL OF POSTURE IN MAN   (L. Nashner)

Early in 1968 the Man-Vehicle Laboratory initiated
a study to develop a quantitative description for the control
of posture in the human. The model to be developed places par-
ticular emphasis on:

1.   describing a basic configuration for the processing
of information in the nervous system

2.   describing the modes of adaptation within this con-
figuration to changing external conditions.

Initially our investigation and the model will consider
control actions about the ankle joint only. The many levels
of control feedback used in postural control will be simplified
to two, the first regulating only within the body reference
frame and the second coordinating both internally and exter-
nally referenced information to regulate the body with respect
to its external environment.

Our research effort in the area of posture control pro-
ceeds along the following lines:

a)   review of physiology

b)   design of posture experiments

c)   design and test of a moving simulator

d)   data processing and analysis design

e)   posture experiments and model synthesis

At the present time all preparatory work for the experi-
mental effort (phases (a) through (d)) has been completed. A
summary of this task follows.

II.1   Background Physiology

Sensors in all areas of the body are used in the control of posture. Some of these sensors measure within a body reference frame, while others indicate orientation of the body with respect to its external environment. Sensory processing and the generation of posture commands is also highly diffused throughout the central nervous system, the lowest level occurring at the spinal ventral roots and extending to the highest brain centers.

Although understanding of the posture control system is far from complete, many features of organization and function are understood.

II.1.1   Proprioceptor Organs

The muscles spindles and the Golgi tendon organs give feedback commands to the lowest level processing loop in the body reference frame, known as the spinal reflexes. These sensors also send collaterals to the cerebellum and to the cerebral cortex where further coordination of commands and responses takes place. Information from muscle spindles and Golgi tendon organs, however, never reaches conscious experience and is believed not to be involved in the initiation of voluntary actions.

Muscle spindles are interspersed throughout posture regulating muscles. Each measures local muscle length extending over several centimeters, with muscles involved in fine control having more spindles per unit weight than those performing only coarse movements.

The spindle is composed of several small intrafusal muscle fibers of two types, nuclear bag and nuclear chain fibers. Collaterals from a single primary group I afferent spiral around the central region of each fiber. Collaterals from a small secondary group II afferent form diffuse endings adjacent to the central region, generally on nuclear chain fibers, but also on nuclear bag fibers. The spiral endings of the primary afferent are sensitive to both the length and to the velocity of the intrafusal fibers, while the secondary endings are sensitive only to their length.

The nuclear bag fibers are innervated by small γ efferents separated functionally into two groups, γ-dynamic and γ-static fibers. Anatomically, the γ fibers are separable into three groups according to the type of ending:

1. p_1 endings; bag fibers only

2. p_2 endings; mostly bag, a few on chain

3. trail endings on both bag and chain

There is no consistent relationship between the functional and anatomical definitions.

Increased activity in the γ-dynamic efferent fiber greatly increases the velocity gain of the primary afferent fiber. The level of activity in the fibers determines the bias level of discharge for both the static and dynamic afferents.

Golgi tendon organs are muscle force transducers. Each organ is located in series with a small group of skeletal muscle fibers and measures the sum total force exerted by the group. The group of muscle fibers comprising one organ unit

are generally from different motor units; thus, each organ samples the level of activity in several motor units.

Receptors located within the joints are sensitive to the orientation angle of the joint. These receptors are not linear, rather each one has a maximum sensitivity to a unique fixed angle with the response falling off rapidly for angular deviations in either direction; thus, angle information is transmitted in the form of both frequency and the spatial distribution of responses among the many joint angle sensors.

Cutaneous and surface pressure sensors give information about the intensity and location of points of contact between the body and the external environment. As with the joint receptors, information is coded both spatially and and temporally.

II.1.2   Spinal Cord Structure

A cross section through the spinal cord reveals a butterfly-shaped grey region surrounded by a white region. The white peripheral region contains the descending and ascending tracts originating in or going to the higher brain centers. The central grey region is composed of a complex net of small nerve cells called interneurons. Each interneuron acts as a small integrating device, receiving many inputs at its cell body and transmitting the net result through one short axon to other interneurons. The axon of each interneuron is either excitatory or inhibitory to other interneurons.

Motorneurons are located at the ventral region of the grey matter. They are similar in structure to interneurons except that they are larger and their axons leave the spinal cord and innervate either skeletal or intrafusal muscle fibers. The

-19-

larger α motorneurons innervate skeletal muscle, the axon dividing and stimulating a group of fibers termed a motor unit. The smaller γ motorneuron axons stimulate intrafusal fibers in a number of muscle spindles. It appears that the effect of each motorneuron axon is exclusively dynamic or static so that independent control of the bias and gains is likely.

Afferents from the proprioceptors and commands descending in the spinal tracts enter the grey matter and impinge on the interneuron net. The structure of this interneuron net is highly complex, but it shows some definite patterns of organization with respect to the sensory inputs and commands.

The primary afferent fiber from each muscle spindle impinges monsynaptically on an α motorneuron activating the homonomous skeletal muscle. Collaterals of each primary afferent fiber also innervate higher level interneurons and ascend the spinal tracts to the higher brain centers. The simple monosynaptic feedback path acts as a position control loop, activating the muscle to oppose its extension.

Muscle spindle secondary afferents impinge on both lower and higher level interneurons with collaterals ascending in the spine to the higher brain centers. The effects of spindle secondary afferents' feedback is not understood.

Golgi tendon afferent fibers enter the dorsal roots of the spinal column and impinge on first level interneurons. These interneurons in turn inhibit the α motor neurons innervation of the homonomous muscle fibers. Collaterals from the Golgi organ afferents also innervate higher level interneurons and ascend the spinal tracts to the higher brain centers.

The Golgi tendon afferents act as accurate force transducers throughout the force range of the muscle fibers. The interaction of the simple spindle position and Golgi organ force feedback loops during posture control is not clear. It is likely that the relationship is flexible, varying with the specific posture control task at hand.

Cutaneous pressure and joint receptors have complex spinal level paths innervating skeletal muscle. These receptors are closely associated with flexor, placing and scratching reflexes.

II.1.3   Higher Brain Center Organization

Remarks about the organization of the higher brain centers must be limited to a few generalizations about the allocation of functions among the centers.

Voluntary commands are generated in the highest brain area, the cerebral cortex, where information about the states of the body and the external environment reaches conscious experience. The resulting voluntary commands are transmitted down the spinal column in the rapidly conducting pyramidal tract and less directly via the extrapyramidal tracts. The pyramidal tract axons enter the grey matter and impinge on low level interneurons or directly on motorneurons. The pyramidal tract axons are able to initiate strong, rapidly conducting activation to posture muscle.

The only proprioceptor afferents reaching conscious regions are those sensing vision, touch, deep pressure, and joint orientations. The simple body reference proprioceptors, spindles and Golgi organs, do not reach consciousness.

The cerebellum is innervated by all types of proprioceptor afferent collaterals. These collaterals are among the largest

and fastest conducting in the ascending tracts of the spine.
It appears that the sensory information remains sharply dif-
ferentiated and localized in some areas of the cerebellum.
The cerebellum also receives cerebral inputs indirectly
through mediation of the proprioceptor afferents in the In-
ferior Olive.

Generally, the cerebellum seems to be a coordinating cen-
ter. One of its functions appears to be coordination of posi-
tion and force information from posture muscle and integration
of this information with responses from the higher centers.
Removal or damage of the cerebellum results in jerky, inaccur-
ate and poorly coordinated movements.

The brain stem is a complex net of small interconnected
nerve cells. It is obviously an integrating center for sen-
sory and motor functions. This highly intercoupled and dif-
fuse structure has so far evaded any detailed functional de-
scription.

II.2   Design of posture experiments

The research seeks to define a model which consistently
describes posture control responses, including the organiza-
tion leading to the no input "remnant" response, adaptation
to changing posture control conditions, and the nature of the
response modes to outside disturbances. Early experiments
will observe subjects in the absence of outside disturbances
and voluntarily initiated movements in order to describe the
characteristics and organization giving rise to the "remnant"
response. The basic organizational insights gained in these

early experiments will be expanded in later experiments, incorporating the modes of adaptation and interaction among the feedback loops to disturbances and varied posture control tasks.

The basic features of the posture control model are stated as definitions. These definitions represent assumptions drawn from the current literature on motor-sensory physiology as reviewed in the previous section.

II.2.1   Defined Relationships in the Posture Control Model

The reflex response is defined as an ankle reaction torque resulting from commands to the lower leg muscles with intensity proportional to the ankle deflection angle and to the deflection angle rate. The gains of these two terms as well as the bias can be independently varied.

The higher center responses are defined as activity not attributable to a proportional reflex response. These responses can take the form of either transient changes in the reflex loop parameters (gains and biases) or direct activation of posture muscles. If the experiments show other forms of response these will be included.

II.2.2   Basic Operational Features of the Posture Control Model

During constant external conditions ankle angle deviations are small and the reflex feedback activation of posture muscle is assumed to be linear. The remnant response in the absence of external disturbances suggests the possible presence of several additional characteristic features of the reflex feedback loop:

1.   the existence of noise disturbances within the reflex
    control loop

2. the excitation of flexible body modes by the reflex
loop responses

3. marginal stability and very low damping in the re-
flex control loop

The higher centers can act by changing the reflex loop
gains and biases and by introducing commands directly to pos-
ture muscles. These higher center responses can be expected
to contribute significantly to the total remnant response.
Higher center characteristics likely to contribute to the rem-
nant include:

1. thresholds in the activation characteristics of higher
center responses

2. the existence of noise disturbances within the feed-
back loops

3. activation time delays

It is not likely that higher center control will demonstrate
marginal stability characteristics.

The introduction of external disturbances requires the ini-
tiation of additional responses from higher center control loops.
External disturbances can take two general forms:

1. those resulting in torque disturbances to the upper
body and requiring compensatory torque responses about the
ankle joint

2. ankle angle disturbances acting through the foot re-
quiring only compensation of the reflex loop biases.

Lateral accelerations of the standing platform introduce
torque disturbances about the ankle joint. Allocation of ad-
ditional loop "gains" and "leads" can be expected to improve
the subject's stability and prevent his reaching the instability

-24-

threshold and falling.

Rotation of the platform introduces ankle angle disturbances. The higher centers must intervene, since the reflex response, acting in a body-centered reference frame, will no longer bear a constant relationship to the gravitational frame in which torque responses must ultimately be determined. Higher center compensation in this case could take two forms:

1. Joint angle, foot pressure distribution, vestibular and visual information can be correlated to continuously update the reflex bias so that the ankle reflex response remains correlated with body motions in the gravitational frame of reference.

2. The reflex response can be suppressed by significantly lowering the gains and the control task taken over more completely by the higher centers. Since the higher centers are able to use many more forms of information, the effect of the disturbance on the higher center commands can be considerably less.

In an actual situation a combination of these two forms of compensation might be expected.

A compliant platform will reduce the apparent gain of a reflex response. So long as the compliance is not great enough to cause instability, the bias need not be changed. The compliant platform may be useful in studying the relative modes of response of the different levels of control and in determining the criteria for allocation of control among the sensory feedback loops.

II. 2.3.   The Posture Control Experiments

The principle objectives of the experiments are:

1. determine the sources of the remnant response modes, the possibilities including marginal stability for reflex control of ankle orientation

2. verify the proposed reflex control loop and develop a method for frequent sampling of the reflex loop gains.

3. develop a method to distinguish the defined higher center responses and begin to determine the logic of these responses

4. determine the criteria by which control is allocated among the levels of sensory control under varied posture control tasks

Experimental and analytical procedures are:

I. Observe subjects standing undisturbed with complete sensory information, then repeated without sensory cues including visual, motion and tactile

    A. Perform a spectral analysis of the ankle angle and torque responses

        1. At 5-10 second interval samples to observe changes in posture dynamic characteristics with time

        2. For the entire run length to observe the slow phase oscillations

    B. With 5-10 second sample lengths, compute the gains for the reflex loop which give a best fit to the observed torque data of each sample, according to the definition of the reflex response. The reflex

time delay and the characteristics of the posture

muscles will be included in the computation.

C.   Analysis of the ankle angle and torque responses

in the time domain.

II.   Observe subjects standing with transient torque and

ankle angle disturbances introduced, with and without sen-

sory deprivation.

A.   Compute the reflex gain as a function of time

using 5-10 second sample intervals, and the torque

responses not proportional to ankle angle as in I.B.

above.

B.   Compare the transient responses from disturbances

of ankle angle (platform rotation) with ankle torque

(platform lateral acceleration.)

C.   Analysis of transient responses in the time do-

main.

III.   Observe subjects on a compliant platform and with

the introduction of continuous random torque and ankle

angle disturbances, with and without sensory deprivation.

A.   The basic computational procedures here are the

same as that in I.B., except that the presence of a

continuous disturbance is an added dimension. Gain

will be determined both for the "corrected reflex"

(gain between the angle with respect to the vertical

and the torque response) and for the introduced "re-

flex disturbance" (gain between the platform motions

and the torque response.

B.   Determine responses not proportional to the reflex

responses.

C. Analysis of the responses in the time domain

II.3 Design of the Moving Simulator

The development of a platform capable of rotation about
the ankle joint without lateral disturbance to the upper leg
and capable of measuring the ankle reaction torque is com-
pleted.

The platform performs the following measurements:

1. ankle reaction torque

2. body orientation in space

3. ankle angle

In addition the platform angle can be controlled. Its
rotation axis passes through the subject's ankle joint. With
active control of the platform, the platform is used as:

1. a disturbance to the posture loop

2. a probe to measure ankle joint compliance

A mechanical system to measure ankle and hip angles, ac-
curate to one-tenth of a degree,has been developed. The sys-
tem measures lateral displacements of the hips and shoulders
and translates these outputs into ankle and hip angles.

Reaction torque is measured using four resistive load
cells, each located at one corner of the force plate on which
the subject stands. Mechanical hysteresis is approximately
±5%. The gain is .125 volts/ft.-lb. The gain varies slight-
ly with subject weight and must be adjusted using the origi-
nal calibrations.

Platform angle is controlled by a hydraulic cylinder and
Moog servo valve. At 1000 psi supply pressure and 10 degrees

peak to peak sine wave input the platform response is slightly overdamped with a natural frequency of 6 cps.

II.4 Experimental Control and Analysis

A small hybrid computer composed of a PDP-8 digital computer and a GPS 200T analog computer will be used for experimental control and analysis. The following programs have been prepared and tested:

A. DINPUT - Program Controls the Experiment and Records Data on Magnetic Tape

The four measurements, ankle reaction torque, body orientation, platform angle and ankle angle are sampled at four samples per second and stored in core memory. In addition, the program performs the following operation:

1. Computes the derivative of the reaction torque and stores the result in core

2. Initiates quarter-second torque pulses at five-second intervals. At the end of the quarter-second pulse, the change in platform angle necessary to generate the torque reaction from the ankle joint is measured and stored in core. The amplitude of the pulse is read in via the switch register at the beginning of each run.

B. CORRLN - Computes the Correlation of Two Signals in Core

To operate, the following information is loaded via the switch register:

1. The address of the first signal

2. The address of the second signal

-29-

(may be the same for autocorrelation)

3. Number of samples desired

4. The address for storage of the correlation samples
Each sample is computed by summing in triple precision
(36 bits) the product of the ith sample of signal one with
the $i + n^{th}$ sample of signal two. Each resulting sum is
scaled by dividing by the number of products.

C. EXAMIN - Examines the Data in Core Prior to Storage
on DEC Tape

The torque response, torque derivative, ankle angle
and reflex gain are reconverted to analog signals and re-
corded on pen recorder. Subsequently the correlation
spectra are recorded.

D. DATATP - Records Data in Core Memory on to DEC Tape
or Visa Versa

The operator has to specify the initial Block on DEC
tape for recording or retrieval. Data is redeposited in
core in exactly the same form and the locations from
which it was taken.

E. FRCOEF - Computes the Fourier Coefficients for Data
Stored on DEC Tape

III.   PUBLICATIONS

The following thesis has been completed in the Man-
Vehicle Laboratory through partial support of this grant:

<u>Influence of Adaptation on the Human</u>
<u>Semicircular Canals and the Role of Subjective Angular</u>
<u>Velocity Cues in Spatial Orientation</u>

by
Charles M. Oman

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

Abstract

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 conflict-
ing sensory modalities are the primary etiological factor.

Experiments were undertaken to investigate the inter-
action 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 sub-
jective 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 home-
ostatic shift in the zero response reference level, some of
the persistent difficulties with 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 vesibular 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.

The papers whose abstracts are given below presented some of the experimental efforts of the Man-Vehicle Laboratory in the area of vestibular research.

The Current Status of Vestibular System Models

by
L. R. Young

Abstract

The human vestibular system for dynamic space orientation is described mathematically, using the identification methods of control theory. The analysis by several investigators at the M.I.T. Man-Vehicle Laboratory, building on the available data, has led to a biocybernetic model which is useful in predicting man's perceived orientation in space, postural reactions, nystagmus eye movements, and piloting actions based on motion cues. The semicircular canals, which act as angular velocity sensors, have been subjected to a fluid dynamics analysis. The limitations of the torsion pendulum model of Van Egmond, Groen and Jongkees are examined, and a quantitative description of adaptation is proposed. An otolith model, responding to linear acceleration forces, is presented and shown to agree with perception of tilt and translation, eye counter-rolling, and electrophysiological data. Cross-coupling effects are discussed, including the influence of linear acceleration on the semicircular canals.

A Model for Vestibular Adaptation To Horizontal Rotation

by
Laurence R. Young and Charles M. Oman

Abstract

Short term adaptation effects are seen in subjective sensation of rotation and vestibular nystagmus. The mathematical model for semicircular canal function is improved by the addition of two adaptation terms (approximately one-half minute time constant for sensation and two minute time constant for nystagmus) to the overdamped second order description. Adap-

tation is represented as a shift of reference level based on the recent history of cupula displacement. This model accounts for the difference in time constants between nystagmus and subjective cupulograms, secondary nystagmus, and decreased sensitivity to prolonged acceleration.

Progress in Vestibular Modeling

by
Robert W. Steer, Jr.

Presented at the 4th Symposium on the
Role of the Vestibular Organs in Space Exploration,
Pensacola, Florida, September 1968.

Abstract

The intensification in vestibular research that has been stimulated by the manned space flight program has brought to light several areas of conflict between experimental data and classical concepts of vestibular function. This paper presents the objectives, assumptions, analytic evaluations and experimental data acquired during the investigations of two such topics which have been examined in some detail at the M.I.T. Man-Vehicle Laboratory.

The disparity between the experimentally evaluated time constants of objective and subjective responses to angular accelerations and the hydromechanical time constants of the semicircular canals is further accentuated by a rigorous analysis of the semicircular canals as a damped hydromechanical angular accelerometer. The dynamic response characteristics of the semicircular canals to angular acceleration are shown to be an order of magnitude faster than can be observed by nystagmus and subjective responses to vestibular stimulation. In addition, it is shown that "roller pump" action of the flexible canalicular duct can maintain an adequate pressure differential across the cupula to give it a constant deflection. This is physiologically equivalent to a constant angular acceleration stimulus, and offers a plausible explanation for the continuous nystagmus responses that are provoked by rotation at a constant angular velocity about an axis which is not colinear with an applied acceleration field.
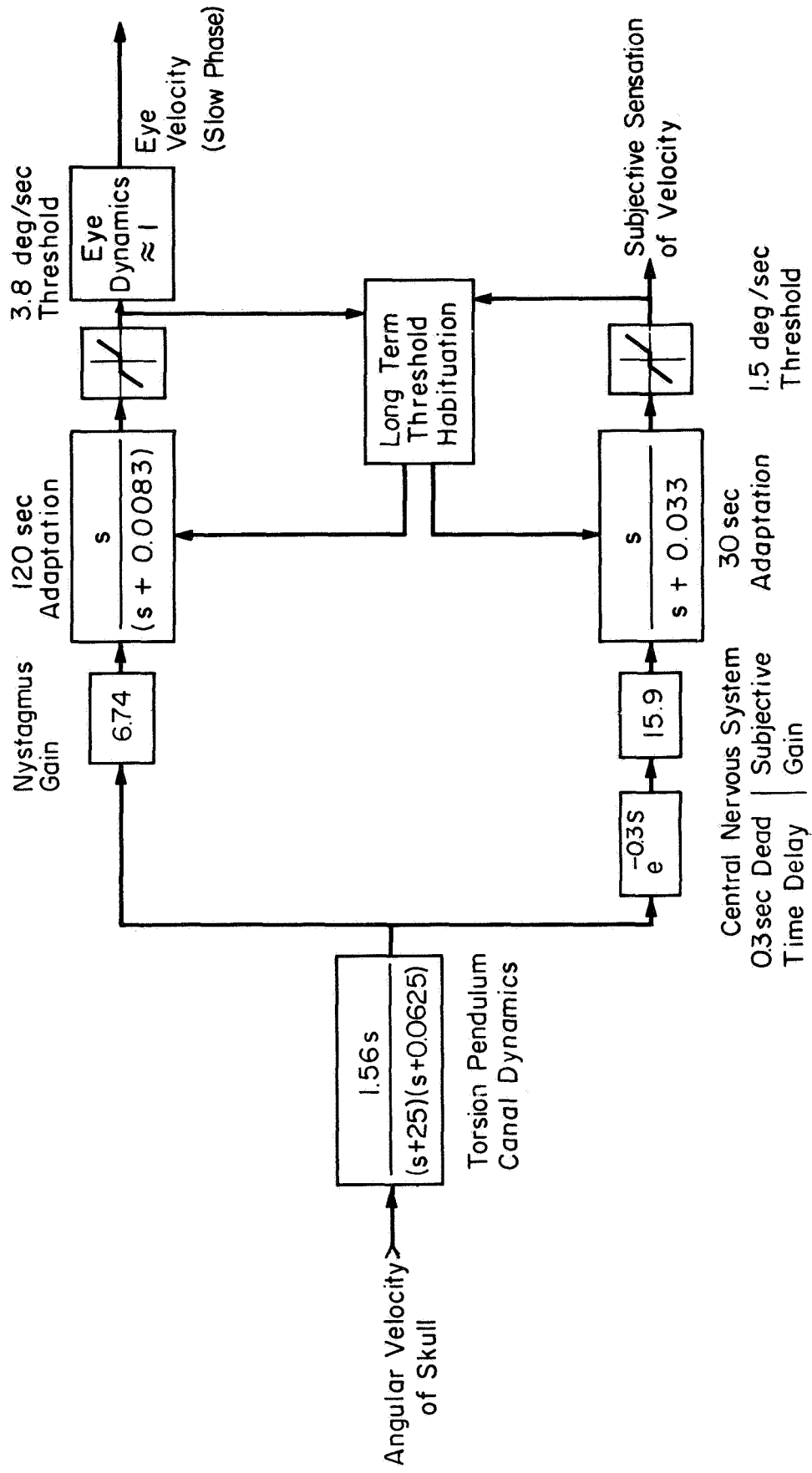
Figure 1   Model for Subjective Sensation and Slow Phase Nystagmus Velocity for Rotation About a Vertical Axis
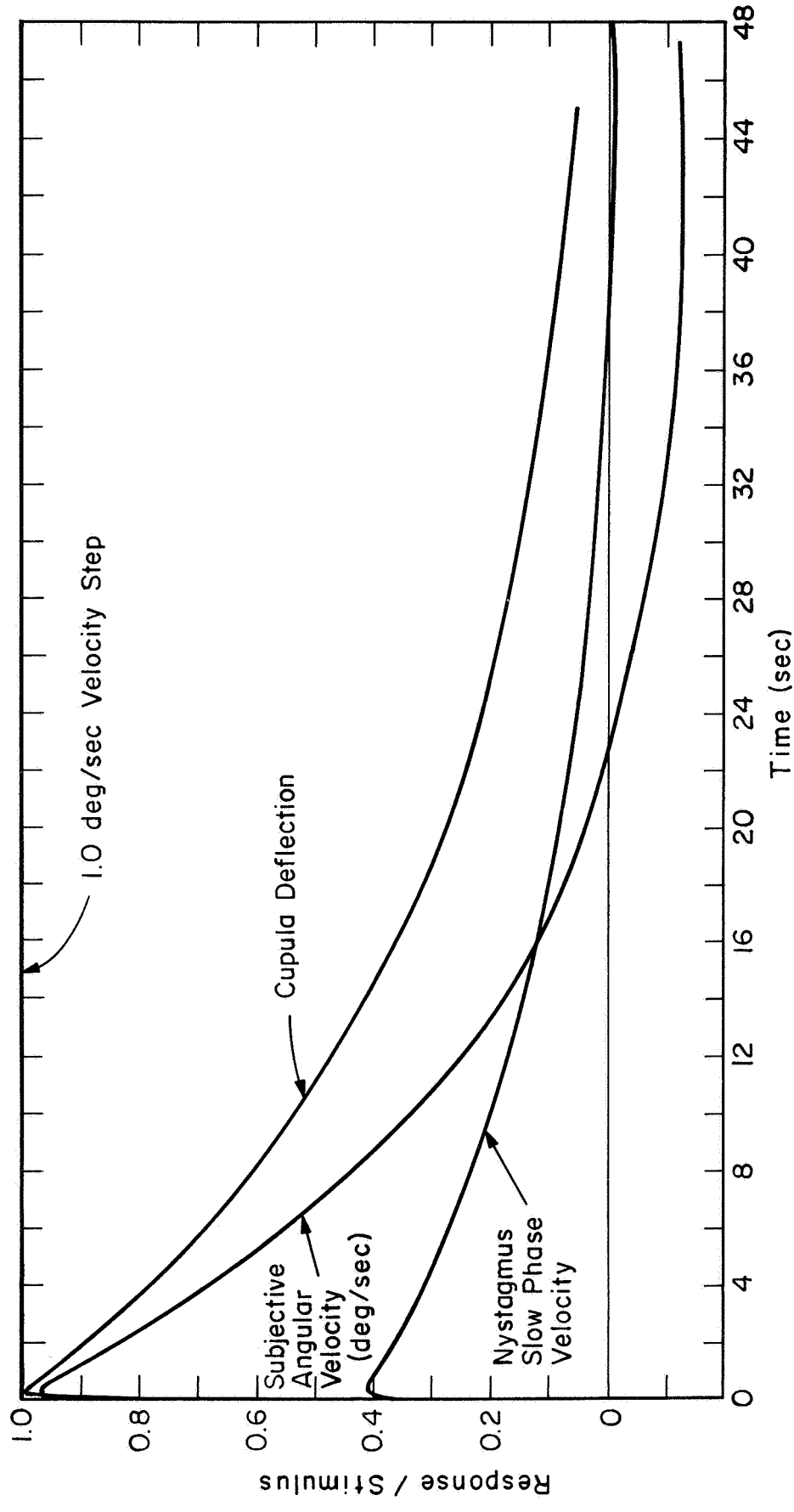
Figure 2 Velocity Step Response of MIT Semicircular Canal
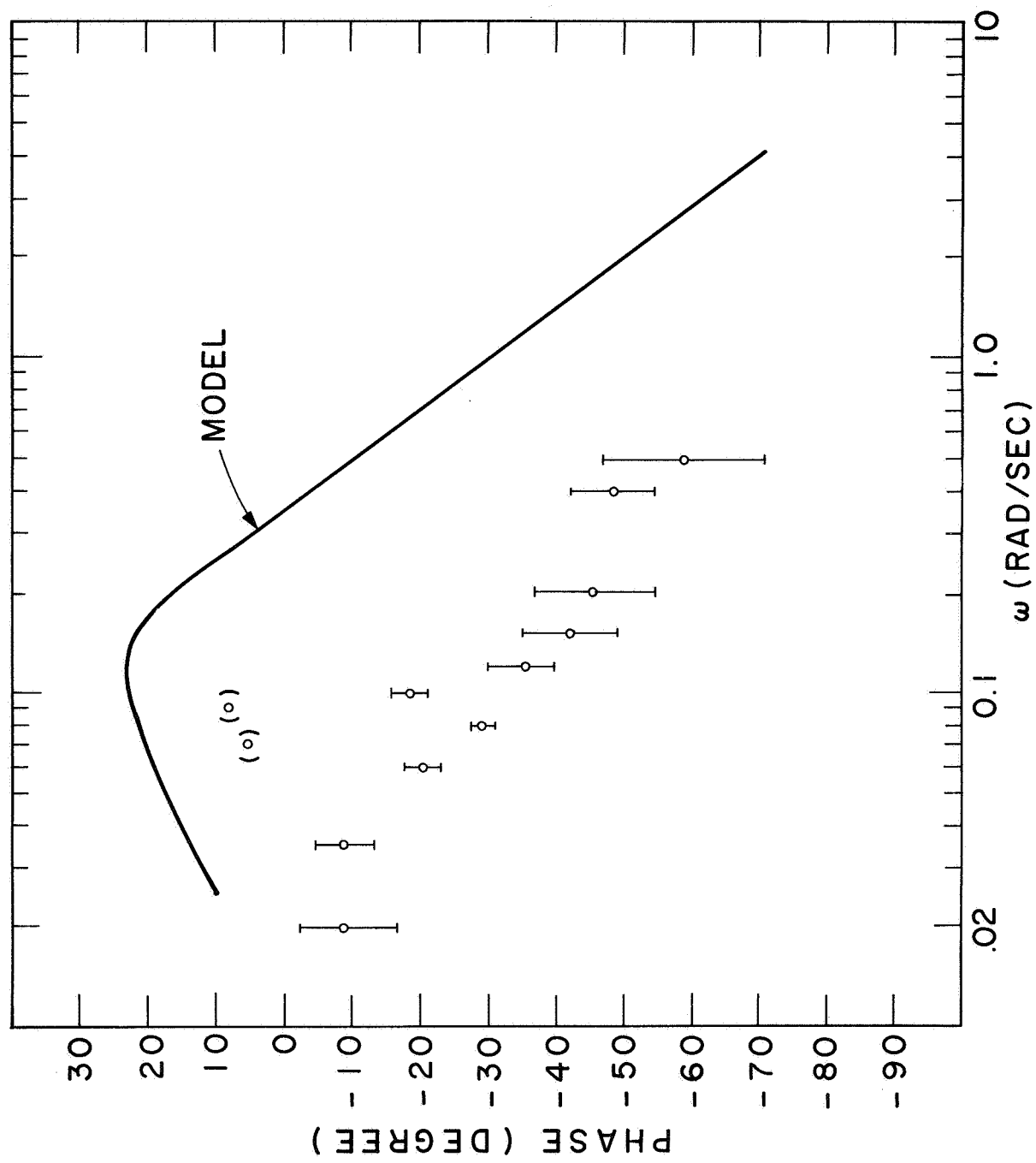Linearized Model to I deg/sec Step in Horizontal Plane

FIG. 3   PHASE LAG (LEAD) OF SUBJECTIVE RESPONSE TO A
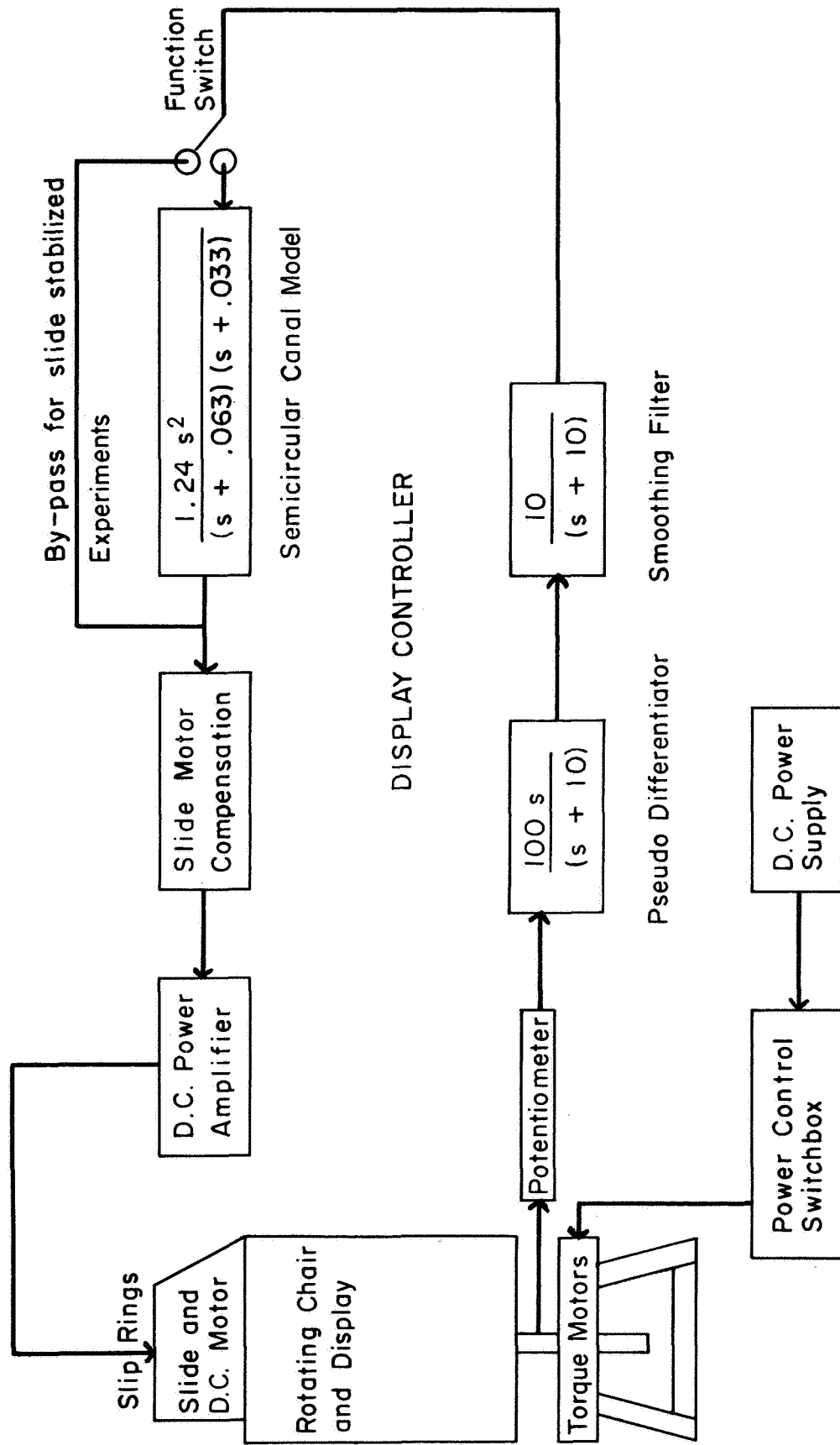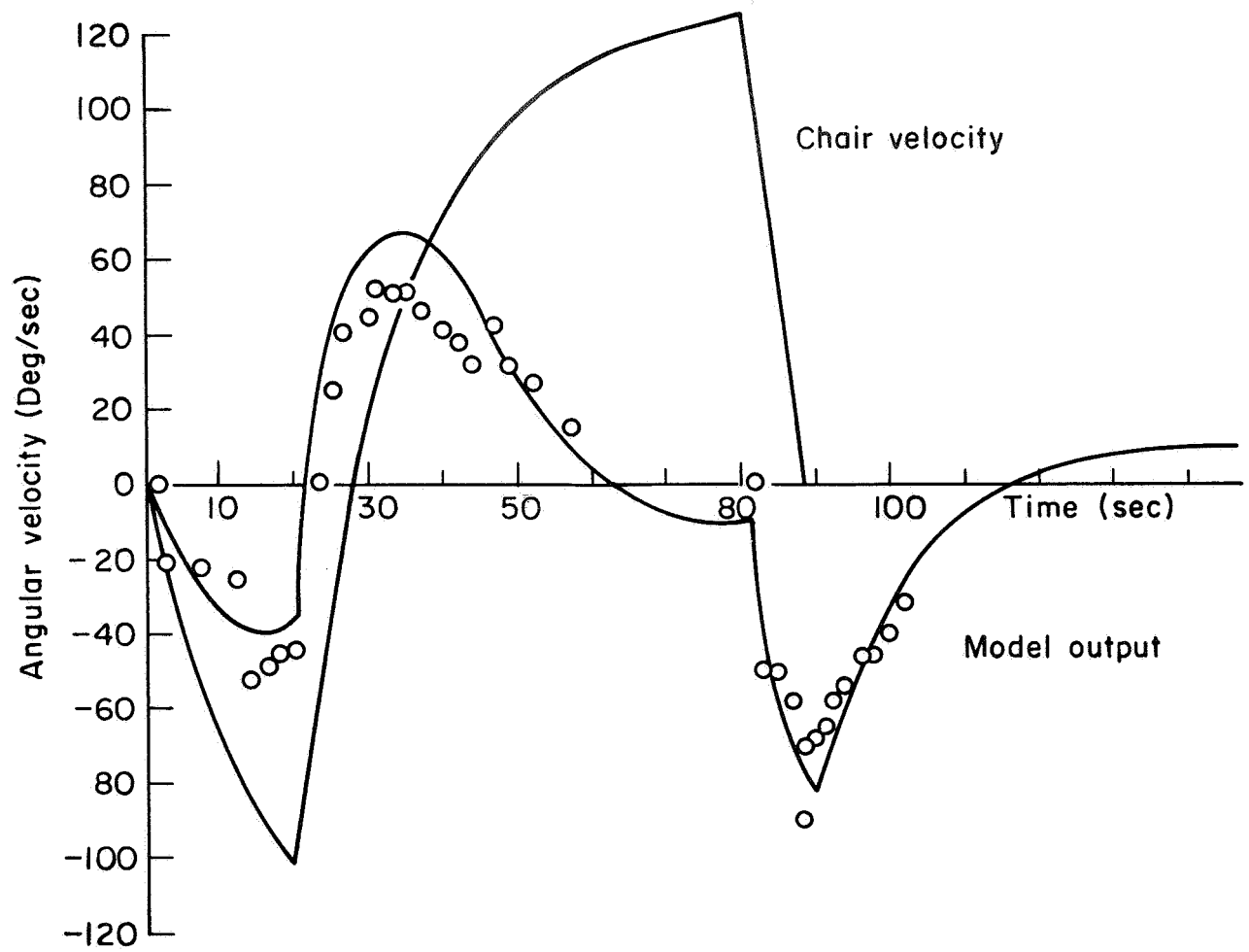CHANGE IN VELOCITY DIRECTION

Figure 4 Anti–Vertigo Display System Schematic

Figure 5
SUBJECT : LVR
MODEL DRIVEN + CCW
RUN 3