MASSACHUSETTS INSTITUTE OF TECHNOLOGY

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BIOPHYSICAL EVALUATION OF THE HUMAN VESTIBULAR SYSTEM

Principal Investigators: Professor J. L. Meiry
Professor L. R. Young

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Status Report on NASA Grant NGR 22-009-156 for the period July 1969 to September 1970

MAN-VEHICLE LABORATORY
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CENTER FOR SPACE RESEARCH
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I. THE HUMAN VESTIBULAR SYSTEM

Research on the function and importance of the vestibular system continues to be central to the Man-Vehicle Laboratory. Our research efforts fall under the following broad categories:

1. quantitative modelling of vestibular function including interaction with the visual system.

2. the underlying physiological and neurophysiological mechanisms responsible for observed vestibular and visual responses.

3. clinical diagnosis of disorders based on our research on vestibular function.

I.1 Models for Thresholds in the Vestibular System (C. Oman)

One of the persistent conceptual difficulties with the mathematical models for the dynamic characteristics of the vestibular system is the representation of the threshold of perception. This operator relates the applied angular or linear acceleration to the measured human response and defines the range of input stimuli which will be undetected. Clearly a simple dead zone applied directly to the input acceleration has to be ruled out since this presentation will imply onset of sensation immediately after the stimulus exceeds the magnitude of the dead zone. Massive experimental evidence classified as the Muelder product supports the notion that the onset of sensation is related to the magnitude of the angular acceleration input. To reconcile these experiments with the tendency to describe thresholds as dead zones Meiry in his 1965 version of vestibular models included a dead zone on the cupula deflection although he noted that this representation should not be taken literally. The 1968 vestibular adaptation model of Young and Oman reinterpreted the threshold to be a dead zone operator acting on the cupula signal after an adaptation operator, with the input to the dead zone having the dimension of angular velocity. This configuration certainly facilitates the correlation of model prediction with available latency time data however cannot account for the experiments of Malcolm, Outerbridge, and Jones on secondary nystagmus which show that postrotary slow phase nystagmus velocity decays smoothly to zero with no evidence of threshold.

One of our primary problems in formulating a viable model for threshold is that consistent data is lacking, and is only gradually becoming available. Clark has pointed out that measured thresholds vary from .035 deg/sec^2 to 8.2 deg/sec^2, but that a large amount of the variability in the measurements may in fact be related to differences in the experimenter's definition of threshold, and the modality used to measure it. It is generally conceded that the most reliable estimator of semicircular canals threshold may be results from tests of oculogyral illusion, but there is some inconsistency in measured values for this threshold as well.

One must also keep in mind the fact that threshold is a statistical measure, and not a sharp physical boundary. If indeed the endolymph could be classified as non-Newtonian fluid the finding will have an enormous effect on the vestibular models especially when used to describe response to inputs in the vicinity of a threshold.

The correct mathematical quantification of the threshold phenomenon is of great importance to the analytical design of appropriate motion cues for moving base simulators. Current methods of applying washout to motion cues indicate requirements for overdesign of motion capability in many cases. Precise descriptions of vestibular thresholds are required to use the vestibular models in the analytical design procedure of simulators, however. With this target objective we have initiated a comprehensive series of investigations to provide a consistent and viable vestibular threshold model.

Our program has commenced with an extensive effort to accumulate and classify all experimental data which has any bearing on the threshold phenomenon. This data base has been categorized according to modality of input, measured variable and method of measurement. We have concluded that the base has to be supplemented with a series of new experiments involving measurements of subjective, nystagmus, and postural reflex thresholds with open and closed eyes moving and stationary visual fields. The experimental design effort specifically uses "hypothesis testing" to validate or negate data and models. With the completion of this effort we intend to carry out an investigation into the properties of the endolymph since the validation of the non-Newtonian hypothesis will have a significant impact on the measurement methods used to determine thresholds. Viscosity measurements extending those which Steer performed in our laboratory will be attempted.

I.2 Eye Movements and Visual Perception (S. Yasui)

The relation between eye movements and the visual perception of motion can be regarded as a process described by one of the following alternatives:

1. Mutual interaction, i.e., the eye movement command is generated on the basis of the visually perceived word and in turn the resulting eye movements affect the subjective perception of the target.

2. Unidirectional interaction where visual perception commands eye movements.

3. Unidirectional connection with eye movements affecting perception.

4. The oculomotor system and the perceptual process are completely decoupled.

The experimental verification of the prevailing alternative involves the simultaneous acquisition of eye movements, psychophysical response and objective target behavior. This correlation of data has to be carried out during a rather extensive repertoir of visual tracking of real targets and after images. A rather attractive method of attack would be to employ illusory targets such as the oculogyral, elevator and other illusions with the actual visual tracking task. However we believe that the mechanism of these illusions and their relation to the oculomotor system is not clearly understood. Thus our experimental program seeks to establish a solid basis of understanding visual illusions while investigating the relation between eye movements and visual perception of motion. On the basis of preliminary experiments we favor the proposition that the oculomotor system and the perceptual process are decoupled.

Another aspect of this investigation is the study of the optokinetic nystagmus, of particular importance is the evaluation determining what portion of the oculomotor system is shared by the slow phase optokinetic nystagmus and the smooth pursuit tracking eye movement.

We have carried out an experiment where a visual fixation target of a small stationary dot was superimposed onto the striped pattern. Contrary to some previous findings the eye movement record has shown that the fixation effort eliminates almost any trace of the optokinetic nystagmatic eye movement unlike fixation during vestibular simulation. If the fixation target is moved to the direction opposite to the motion of the field pattern, the eye movements become somewhat different from the case of the ordinary visual tracking with no such background pattern, indicating the persistent presence of some degree of the optokinetic nystagmus command and its interference with the tracking eye movement.

I.3 Extravehicular Attitude Control by Use of Head Motions (L. Von Renner)

Despite a vast expenditure of time and talent in the field of EVA operations, a few important problems remain. One of these is clearly the need for a simple controller by which an astronaut could order a change in his attitude or, alternatively, could resist change if he so desired. Those controllers which are currently receiving most attention require the use of one or both hands, a serious inconvenience if one is engaged in the fine adjustment of an orbiting telescope, for example. Or they include in their design "arm rests" which add volume to the overall system and do, themselves, restrict motion. Of the many alternate controllers which have been conceived, that of the head provides an enticing picture. To effect a ninety degree left turn by, for example, simply turning the head left would be a simple, natural control which, when provided with a lockout device for those times when head motions are not for the purpose of attitude change, appears attractive. Can the head be utilized effectively as a controller of one's attitude? The concept for this system stems from our work on the human vestibular system and space orientation, in which it is clear that all the postural control loops act to stabilize the head and body in space. Thus a system which would drive the astronaut's trunk to a given position with respect to his head should be quite satisfactory.

Preliminary experiments were performed to seek appropriate muscle sets for control purposes. Surface electrodes were applied to a number of proposed sites on the neck, facial area, and upper back. Signals were received and rough processed by filtering, rectifying, and low-pass filtering.

Proceeding in this fashion, three independent sets of muscles were located which, in addition to satisfying the requirements of decoupled and controllable EMG signal output, also were somewhat logical choices for attitude control. They are 1) the left and right sterno-cleido-mastoideus at a point just above the common carotid artery, 2) the left and right trapezius at a point along the top of the shoulder and at the base of the neck, and 3) the combination of the facial muscle of the forehead and that of the platysma immediately above the collarbone. Signals for the first set were independently induced by simple left-right flexion of the head; a leftward motion generated an output from the right sterno-cleido-mastoideus. Motions as slight as fifteen degrees would be registered as EMG output. The left and right trapezius recorded signals when either the left or right shoulders, respectively, were raised upward toward the neck. These two signals were found to be independent of each other and of the motions which generated an output from the previously discussed pair. The forehead source was active when the subject "wrinkled" his forehead by raising his eyebrows. The platysma generated a response when the subject exercised his lower neck as if in response to a tight collar. Needless to say, these motions are independent of each other and of those previously described.

Proportional control was roughly possible for all six sites; a subject could learn to control the position of the pen recorder for any muscle being tested. As a result of these tests, it seemed reasonable to suggest that use of the sterno-cleido-mastoideus be made for left-right attitude control (yaw) because of the desirable self-compensating effect of this particular head motion with respect to axis controlled. Trapezius control, which is to say shoulder flexion upward, was regarded as practical to assume for roll control. The "upward eyebrow" would be assigned control of pitch up; the playtsma would generate pitch down.

Experiments were performed in which subjects attempted to control their yaw attitude while seated in a chair free to rotate about its vertical axis. A random input signal was sent to the chair's torque motor which resulted in left-right rotations. Each subject attempted to counteract this motion and keep the chair stationary by sending a compensating control signal to the chair. Control signals were generated by both a conventional stick and by electromyographic impulses induced by left-right head movements.

Subjects were able to control their attitude using electromyographic signals. While performance was worse than with simple stick control, a measure of "performance index" was found to be in the same order of magnitude in both cases.

On the basis of collected data in one axis, attitude control by means of head motions appears feasible. The main problem encountered was that of a significant "dead zone" of electrical inactivity from +45 degrees to -45 degrees of head angle.

Details are given in the M.Sc. thesis by Lonnie C. Von Renner, entitled "Extravehicular Attitude Control by Use of Head Motions."

I.4 Galvanic Stimulation and the Perception of Rotation
(J. Tole)

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.

I.4.1 The Experimental Method

The intent of this research was to study the relationships between modes of application and intensities of galvanic stimuli and a subjects' 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 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 adapted 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 100μa, 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 make a total of eight runs per subject. The controls were added not only to discover, if possible, any overall effect on this norm after the combined experiments.

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

Once the basic experiment was decided upon, a suitable experimental design was required in order to study a number of different variables in a systematic way. A design was sought which would incorporate all of the following features: 1.) all six possible modes of unipolar and bipolar galvanic stimulation, 2.) a number of different intensity levels, 3.) yield as much information as possible about effects of galvanic stimulus, 4.) employ as few subjects as possible, 5.) balanced for the elimination of order effects.

Since there were six possible modes, it was decided arbitrarily to use six intensity levels in the experiments. If each subject were run at every mode and intensity, however, thirty-six runs per subject would have been required to include all of the possible combinations. In order to reduce the number of runs required per subject and in order to achieve the randomness of application desired, a slightly modified form of the Graeco-Latin square experimental design was employed.

I.4.2 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 inpregnated with electrode paste was included in the electrode in order to avoid metal to skin contact and to obtain a relatively uniform current distribution. 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.

All three contact areas on the subject were treated with electrode paste before the runs in an effort to achieve a nominal inter-electrode D. C. resistance of 2-3K ohms.

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.

I.4.3 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 800μa 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 800μa significant effects were apparent. A threshold for current effect between 400 and 800μa 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.

I.4.4 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.

Details are given in the M.S. thesis by John R. Tole, entitled "Galvanic Stimulation and the Perception of Rotation".

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

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.

Because of the inherent complexity of the posture control system, analysis is simplified by considering only control of forward and backward rotational motions of the body about the ankle joint, hereafter termed body sway or body angle motion. Body sway motion represents the critical mode in control of posture because of the inherently unstable "inverted pendulum" characteristics of the body. Therefore, this simplification is justified. Relative motion between upper body segments is of considerably less consequence during <u>quiet</u> standing and may be neglected here. Hence, the goal of the postural control system in this simple task is to assess the current status of body sway motion and generate appropriate ankle reaction torques to maintain stability.

The research is divided into three segments. First, a general posture control model is assembled, given current models for motor and sensory components and the general properties of neural processing described in the literature. This general model then forms the basis for a series of experiments. Finally, experimental observations are combined with the general physiological model to develop specific models for the sensory-motor interface.

In both the design of the experiments and development of the final models, the highly adaptable and non-stationary characteristics of the system are recognized. Experiments use transient disturbances which probe the states of the system at specific instances in time or during very short periods in which characteristics remain relatively constant. The models also define transient rather than continuous control processes.

Sensory deprivation techniques are employed during experiments to isolate characteristics of the individual sensory feedback modes. These methods allow observation of a number of control strategies and enable a more complete determination of the range of adaptability of the various sensory feedback modes.

II.1. Reflex Control of Posture

Two direct mechanical mechanisms resist length changes in flexor and extensor muscles. During constant stimulation, muscle tensions vary in proportion to small length changes about a median length (13, 17). Rate of stretch also affects tension of the muscle under constant stimulation (5). Both the length-change and velocity induced tensions act to resist overall change in muscle length. It should be noted that the sensitivity of both of these mechanisms varies in response to the activation level of the muscle itself.

In addition to the "mechanical" mechanisms varying tension to resist muscle length change, there is active resistance initiated by muscle spindle reflexes.

Stretching skeletal muscle produces a corresponding stretch of the muscle spindle fibers interspersed throughout the muscle. Stretching a muscle spindle increases its afferent discharge, which then acts through the alpha motoneuron pool to contract skeletal muscle fibers in the region of the stretched spindle. Increase of muscle tension is achieved by a combination of the recruitment of additional motor units and increased activation of units already firing.

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

1. Muscle "mechanical" properties are dependent on the level of muscle activation (10, 13).
2. Muscle spindle feedback "gains" are controlled by higher center commands (8).
3. Higher centers may act on the alpha-motoneuron pool, exercizing direct control over the activation level of the muscle.

In describing control mechanisms of the reflex arc, physiologists have recognized its likeness to a position servo-mechanism. Only recently, however, have investigators integrated functional descriptions of the individual physiological components into models of the reflex control system (7, 9, 13).

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. Further investigations of posture control mechanisms described in this paper begin with these premises.

The reflex control mechanism, including proprioception feedback pathways and higher center inputs, is illustrated in Figure 1 . Components 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 excercise independent control of both phase and position feedback gains.

Reflex Responses During Quiet Standing

The following is a description of the experiment conducted to determine specific values of the parameters for the ankle stretch reflex control loop. The reflex response parameters obtained are then formulated into a model which quantifies the contribution of the ankle reflex control loop to overall postural stability, providing the basis for further experiments exploring the strategy of reflex parameter adaptation to changing control conditions.

The subject stands relaxed on the experimental platform, arms folded above the waist and feet ten to twelve inches apart. The platform detects the subject's reaction torques and his sway angle about the ankle joint. A hydraulic position servo allows rotations of the platform about an axis colinear with that of the subject's ankle joints. The ankle stretch reflex is excited by small steps of the platform.

During each test run the subject is asked to stand relaxed with his eyes opened. To prevent fatigue, each test run is limited to 16 step samples, or approximately 3 minutes. Seven test runs are conducted for each of five step sizes: 1/10, 1/4, 1/2, and 1 1/2 degrees. A test run consists of one step size only. The ordering of step size test runs is random. Responses are characterized by a peak within 80-125 milliseconds, a compensatory response peak at 400-800 milliseconds, then gradual return to equilibrium.

The reflex response amplitude, defined as the maximum response occurring within 80 to 125 milliseconds after initiation of the step disturbance, is determined for each step response. Reflex gain is defined as response amplitude divided by the ankle step size. The composite average gain as a function of step size is shown in Figure 2. Variation among subjects is statistically insignificant, $p > 0.1$.

To examine the later compensatory phase, average responses of each subject to the 1/4 and 1/2 degree steps are computed. These response groups are further subdivided according to initial reflex gain into three levels. Variations among the three subjects are statistically insignificant, $p > 0.1$. As an example, Figure 3 shows the response averages for one test case.

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 1/4 to 1/2 degrees are considerably below that necessary for postural stability (2 ft-lb/degree versus 7 ft-lb/°) suggests that reflex control alone may fully stabilize the body for disturbances below 1/10°. This is substantiated by current physiological evidence.

Evidence of large gain increases in muscle responses to small length changes is found in the work of Hill (6) and Joyce et al (11). Similar gain increases in reflex responses are shown by Brown et al (1) and Matthews (14).

Recordings of ankle torque and body angle responses during quiet standing indicate that the reflex loop fully stabilizes very small amplitude sway motions. All subjects exhibit frequent periods of five or more seconds duration in which no motion within measurement resolution (T = ± 0.10 ft-lb θ_B ± 0.02 degrees) can be observed. All higher center feedback controls are limited by thresholds considerably larger than the measurement resolutions. (Results, Sections 3 and 4). Therefore, reflex feedback control must be responsible for these stable periods.

On the basis of forementioned physiological and experimental evidence, 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°. Reflex feedback gain is sufficient for complete postural stability for deflections less than 0.05°.

The compensatory response is initiated by higher center commands. Observed delay time, about 200 milliseconds, agrees with physiological evidence for higher center response delay; it also agrees with vestibular response delays measured by the author.

Figure 4 shows the compensatory response natural frequency as a function of the initial reflex disturbance amplitude. Included in the figure for comparison is the response characteristics as a function of gain for the following system: an inverted pendulum stabilized with a rate compensated feedback, with system dynamics roughly equivalent to those of the body reflex control system. Results suggest that higher centers enhance the total reflex gain during a transient disturbance in proportion to the perceived disturbance amplitude. Reports of several investigators also indicate reflex gain control as a likely higher center control mechanism.

Kim and Partridge (12) show that total reflex gain (Δ tension/Δ length) in cat soleus muscle is enhanced by factors of two to three times when the vestibular nerve is stimulated continuously. They note that neck rotations also enhance reflex gain. In a further study, Partridge and Kim (16) find that isometric tension varies less than 1% of maximum muscle tension during sinusoidally modulated vestibular stimulation.

Gernandt et al. (4) have shown that vestibular stimulation in anesthetized cats strongly effects the dorsal to ventral root response amplitude at the cervical and lumbrosacral levels of the spine.

In summary, vestibular and extereoceptive stimulation is shown to enhance reflex responses, establishing this mechanism as a probable method for higher center control of postural disturbances. The fact that vestibular responses do not act as length commands gives further support to this conclusion. Two physiological mechanisms for reflex enhancement are proposed; multiplicative increase in the dorsal to ventral reflex gain, and control of the tension levels of muscle. Functionally the mechanisms are equivalent.

The strategy of gain enhancement shows an excellent combination of higher and lower levels of sensory information. The higher center gain command involves no complex processing and can be effected with a minimum of delay. Additional corrective computation takes place at the spinal level through enhanced resistance of body displacements. This mechanism is a crude one, but in most situations a good "first guess." More complex higher level mechanisms requiring longer processing time may intervene somewhat later to fine-tune the initial crude corrections.

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.

The following experiments explore fully the relationship of reflex and higher center control strategy, illustrating reflex gain during a variety of circumstances which alter the effectiveness of the reflex control loop. Test conditions are designed to determine the effects of the following on feedback parameters:

1. visual feedback: enhancement and elimination
2. conscious posture set

3. random ankle angle disturbances
4. elimination of ankle position feedback

All subjects clearly demonstrate adaptation of the reflex gain in response to changes in posture control conditions. Subjects are able to increase reflex gain when asked to exert special effort to minimize sway. They all reported, however, that this condition was quite uncomfortable if maintained for more than a few minutes.

When given a high sensitivity visual display of body angle, subjects' reflex gain decrease only slightly compared to normal gain. Subjects reported that this condition too was tiring after several minutes.

When small random disturbances are introduced, reflex gain decreases to nearly one-half the normal gain.

The median gain is nearly zero when the reflex control loop is fully suppressed by opening the position feedback loop.

Elimination of visual feedback has little effect on reflex control strategy under any of the tested conditions.

The availability of the supporting surface for body and inertial reference information determines the reflex gain setting. Reflex gain is reduced as the reflex control loop becomes a less effective mode of stabilization. Changes in the state of higher center feedback sensors seem to have no effect on the strategy for reflex gain setting.

II.2. Vestibular Control of Posture

The vestibular organs, the utricles, the saccules, and the semicircular canals are the prime motion sensors in the human. Vestibular cues contribute important sensory information for the regulation of posture.

Characteristics of the vestibular system are well documented (15, 19, 20). A complete description can be found in the references listed above; a review of the details pertinent to posture control is given here.

Angular acceleration in three dimensional space is sensed by three approximately orthogonal semicircular canals in each inner ear. The utricle otoliths, one in each inner ear, are multi-dimensional linear accelerometers. They sense specific forces (linear acceleration plus gravity) in a plane rotated 30 degrees with reference to the horizontal plane of the head. Hence, combined canal receptors sense all relevant angular motions of the body; utricle otoliths sense the summation of all linear and gravitational forces.

The canals are heavily damped accelerometers, with perceived output corresponding to angular velocity. The threshold of perception of angular velocity is heavily dependent on the sensory mode in which it is measured. A discussion of this point is included in the following paragraphs. The utricle otoliths are also heavily damped accelerometers, sensing both tilt angle and linear velocity.

Angular acceleration threshold values for the semicircular canals reported in the literature vary over a wide range. Meiry (15) estimates a linear acceleration threshold of 0.005g, equivalent to a 0.30° threshold for subjective orientation. Clark and Stewart (2) find detection of steady state angular accelerations with the oculogyral illusion at values ranging from 0.04 to $0.28°/sec^2$. The illusion does not involve a direct sensation of movement, rather the subject, seated in a dark enclosure during angular acceleration, perceives movement of a light spot which is actually fixed with respect to him. The illusion of movement is believed to be caused by the action of canal output responses on the visual system. Their results show that canal responses influence visual sensation at levels of angular acceleration significantly below the levels which can be detected subjectively.

Vestibular Stimulation by Body Angle 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 posture control model to be developed here considers only quiet standing during which the upper body remains relatively rigid, equivalence of body angle and pitch angular accelerations may be assumed.

Stimulation of the utricle otolith organs by body sway motions is considerably more complex since both gravitational and linear acceleration reaction forces act as inputs. During uncontrolled sway divergence of the body, gravitational (f_g) and tangential acceleration reaction force (f_t) act in opposite directions, Figure 5.

$$I_B \ddot{\theta}_B = m_B \, g h_{cg} \, \theta_B + T_A \qquad 3.1$$

The net reaction force on the otolith is:

$$f_o = \theta_B \left[g - \frac{m_B g h_{cg} d}{I_B} \right] \qquad 3.2$$

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, (i.e. it is opposite to the force on the otolith due to gravity alone). If the body diverges with partial resistence from postural responses, the net force acting on the otolith may be negative, zero, or positive depending on the intensity of postural resistence. Recalling that reflex responses oppose body sway with a torque roughly proportional to angular deflection of the ankle joint, the following relations demonstrate the ambiguity of the sign of the linear motion sensor:

$$T_A = -K \, \theta_B \qquad 3.3$$

$$f_o = \theta_B \left\{ g - \frac{m_B g h_{cg} d_o}{I_B} + \frac{K d_o}{I_B} \right\} \qquad 3.4$$

Using body parameter values (18) we find that:

$$f_0 > 0 \quad \text{if } K > 4 \text{ ft-lb/degree}$$

$$f_0 < 0 \quad \text{if } K < 4 \text{ ft-lb/degree}$$

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

Postural Response to Vestibular Stimulation

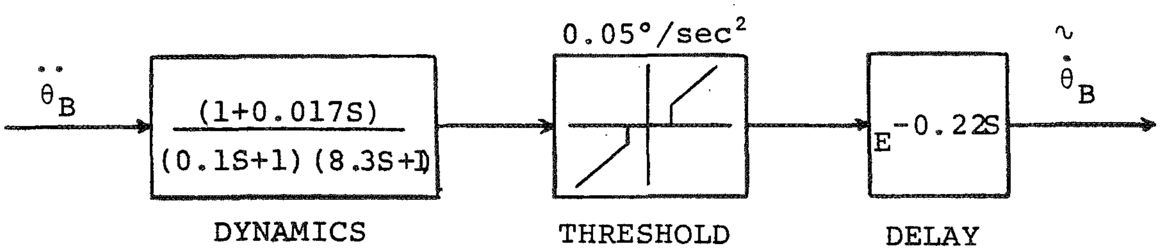
The subject stands relaxed on the experimental platform. Sway is induced using small forward or backward platform displacements at constant velocity, introduced by the experimenter when the subject shows no movement. The platform disturbance induces a step change in body angular velocity.

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 extereoceptive 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 extereoceptive cues. Subjects are tested with eyes open and eyes closed to determine effects of visual cues on vestibular detection of body sway.

Figure 6 shows typical postural responses to rapid and to slow induced body motion stimuli. Responses are characterized by an initial period during which the body angle begins to increase while the ankle torque remains unchanged. When the motion is detected by the vestibular sensors, ankle reaction torque increases rapidly, returning the body to a stable position. Threshold of the vestibular feedback sensors is defined in terms of the time after initiation of motion at which the ankle torque level has increased 0.25 foot pounds above its initial level.

<u>Conclusions - The Vestibular Model</u>

Threshold characteristics for forward and for backward sway are identical. Variations among the subjects and among the test conditions are statistically insignificant, $p > 0.1$ for all samples. Composite threshold functions for the three test conditions are compared to the semicircular canal model threshold characteristics in Figure 7 . 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 $0.05°/sec^2$ 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 (19) 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 (ω_B = 3 r/sec) is fast compared to the very slow dynamics of the otolith organs.

The role of linear and angular acceleration cues in posture regulation are made clear by observing the frequency ranges at which each component of the vestibular apparatus is most effective in responding to sinusoidal postural sway. Figure 8 shows the sinusoidal body angle amplitude necessary to achieve detection of motion as a function of sway frequency. Note the clear separation of the functional range for each sensor. The thresholds for each sensor within its frequency range of maximum sensitivity are approximately the same.

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, $p > 0.1$.

The inverted pendulum configuration of the human body is stabilized with a combination of body sway and body angle and body angle rate feedback. Two modes of vestibular sensation provide dynamic feedback information of body angle. The semicircular canals provide a good estimate of sway rate for frequencies above 0.1 cps, while the otoliths indicate sway angle below 0.1 cps. Because of frequency response limitations of each sensor, the canal feedback control loop is unable to respond to rapid sway divergence. Thus, stability can only be attained through the combination of two frequency selective feedback loops, each of which in isolation is unable to provide stability.

In the proposed vestibular control model, the canal output, body angle rate, is used for an initial estimate of both body angle rate and, through neural integration, body angle. The low frequency utricle otolith estimate of body angle updates the initial canal estimate. The model configuration is shown in Figure 9 .

The goal of the vestibular control model is to predict the response characteristics of a single cycle in the regulation process. Discrete response characteristics of the complete body-motor sensory model are shown in Figure 10 . The presence of canal feedback alone shows the expected low frequency divergence. Stability is achieved when utricle otolith feedback is included to correct this.

Note that the stimulation results can be compared to actual responses only during the first cycle, since no provision is made in the model to "reset" the vestibular thresholds.

II.3. Visual and Extereoceptive Senses

General models for visual and extereoceptive 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 extereoceptive responses cannot be observed in isolation.
2. Present physiology does not permit construction of detailed models of the visual and extereoceptive senses.

Posture Regulation with Vestibular, Visual and Extereoceptive Senses

Effects of including visual and/or extereoceptive cues during vestibular control of posture are considered. Subjects stand on the experimental platform under the following conditions:

1. eyes open; platform rotates to maintain the ankle angle at zero degrees
2. eyes closed; platform rigid
3. eyes open; platform rigid

In each of the above conditions, posture control follows the same basic pattern seen during vestibular feedback control: quiet period, body divergence, transient responses, and re-establishment of quiet stability.

The basic strategy of control in case 1, vestibular and visual cues only, is similar to control strategy with vestibular cues only. Control strategies in cases 2 and 3, however, 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 - enhancement of reflex gain during transient disturbances. Subsequent analysis develops each of these control models to include effects of visual and extereoceptive cues.

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.

Extereoceptive/Reflex Control

Basic changes in control are evident when extereoceptive 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 extereoceptive cues are added, (case 2), dropping from 0.36° to 0.13°. Variations in the extereoceptive 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.

Models for Extereoceptive and Visual Control

The model for reflex/extereoceptive control follows the strategy of gain control developed in Section 1. The model is shown in Figure 11 .

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

The model is simulated. Figure 12 compares responses predicted by the model with experimental observations.

A visual feedback loop is added to the vestibular control model presented in Figure 9 . The visual sense is modeled as a linear feedback controller with prediction (rate compensation) and transmission delay of 0.40 seconds.

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 extereoceptive and visual senses. Extereoceptive cues provide rapid, low threshold detection of body sway divergence. Visual cues effect well damped, high resolution correction of the slow phase drift.

II.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.

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.

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, Figure 13 . 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.

Average reflex gain of the vestibular defective subject increases markedly when eyes are closed, Figure 14 . The average reflex gain for extension, 12.35 ft-lb/deg, is large enough to achieve "rigid" postural stability.

This experiment tests the ability of the subject to detect sway divergence of reflex control and extereoceptive 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 extereoceptive 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.

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 continusouly during quieter periods. During these quiet periods, body angle drifts continusouly 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.

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/extereoceptive control model described in section 4. They confirm two major characteristics of the model:

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

II.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.

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.

Posture Control with Vestibular and Visual Senses

When reflex/extereoceptive 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.

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, extereoceptive cues, is normal. Reflex gains are somewhat higher than normal. It may be concluded that extereoceptive 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.

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.

References

1. Brown, M. C., Goodwin, G. M. and Matthews, P. B. C., "After Effects of Fusimotor Stimulation on the Response of Muscle Spindle Primary Afferent Endings," J. Physiol., Vol. 205, 1969, 677-94.

2. Clark, Brant, "Factors Influencing the Perception of Angular Acceleration in Man," Second Annual Status Report, NASA NGL-05-046-002, 1969.

3. Eccles, R. M. and Lundberg, A., "Supraspinal Control of Interneurons Mediating Spinal Reflexes," J. Physiol., Vol. 147, 1959.

4. Gernandt, B. E., Magdolna, I. and Livingston, R. B., "Vestibular Influences on Spinal Mechanisms," Experimental Neurology, Vol. 1, 1959.

5. Hill, A. V., "The Heat of Shortening and the Dynamic Constants of Muscles," Proceedings of the Royal Society of Britain," Vol. 126, 1938.

6. Hill, D. K., "Tension Due to Interaction Between the Sliding Filaments in Resting Striated Muscle. The Effect of Stimulation," J. Physiol., Vol. 199, 1968.

7. Houk, J. C., "Mathematical Model of the Stretch Reflex in Humans," S.M. Thesis, M.I.T., 1963.

8. Jansen, J. K. S. and Matthews, P. B. C., "The Central Control of the Dynamic Response of Muscle Spindle Receptors," J. Physiol., Vol. 161, 1962.

9. Johnson, A. R., "The Servo-Analysis of Postural Reflexes," Ph.D. Thesis, M.I.T., 1960.

10. Joyce, G. C. and Rack, P. M. H., "Isotonic Lengthening and Shortening Movements of Cat Soleus Muscle," J. Physiol., Vol. 204, 1969.

11. Joyce, G. C., Rack, P. M. H., and Westbury, D. R., "The Mechanical Properties of Cat Soleus Muscle During Controlled Lengthening and Shortening Movements," J. Physiol., Vol. 204, 1969.

12. Kim, J. H. and Partridge, L. D., "Observations on Types of Response to Combinations of Neck, Vestibular, and Muscle Stretch Signals," J. Neurophysiology, Vol. 32, 1969.

13. McRuer, D. T., Magdaleno, R. E. and Moor, G. P., "A Neuromuscular Activation Systems Model," Third Annual NASA-University Conference on Manual Control, 1967.

14. Matthews, P. B. C., "Evidence that the Secondary as Well as the Primary Endings of the Muscle Spindles May be Responsible for the Tonic Stretch Reflex of the Decerbrate Cat," J. Physiol., Vol. 204, 1969.

15. Meiry, J. L., "The Vestibular System and Human Dynamic Space Orientation," NASA-CR-628, 1966.

16. Partridge, L. D. and Kim, J. H., "Dynamic Characteristics of Response in a Vestibular Reflex," J. Neurophysiology, Vol. 32, 1969.

17. Roberts, T. D. M., Neurophysiology of Postural Mechanisms, Plenum Press, Butterworths, England, 1967, 90-120, 81-89, 120-175.

18. Webb, Paul, Bioastronautics Data Handbook, NASA SP-3006, 1964.

19. Young, L. R. and Meiry, J. L., "A Revised Dynamic Otolith Model," Aerospace Medicine, Vol. 39, 1968.

20. Nashner, Lewis M., "Sensory Feedback in Human Posture Control," Sc.D. Thesis, M.I.T., 1970.

Details are given in the Sc.D. thesis by Lewis M. Nashner entitled, "Sensory Feedback in Human Posture Control."

III. PUBLICATIONS

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

Sensory Feedback in Human Posture Control

by
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".

Extravehicular Attitude Control by Use of Head Motions

by
Lonnie Charles 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 ($\pm 45°$ 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 head position as a control signal source.

Galvanic Stimulation and the Perception of Rotation

by
John Roy Tole

M.S. Thesis, M.I.T., June, 1970

Abstract

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.

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

Model for Vestibular Adaptation to Horizontal Rotation

by
Laurence R. Young and Charles M. Oman

Presented at the 4th Symposium on the Role of the Vestibular Organs in Space Exploration, Pensacola, Florida, September 1968; Aerospace Medicine , October, 1969.

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

Modeling Adaptation in Human Semicircular Canal Response to Rotation

by
Laurence R. Young and Charles M. Oman

Presented at a meeting of the Section of Instrumentation on January 13, 1970; Transactions of the New York Academy of Sciences, April, 1970.

One of the persistent difficulties with the simple, second-order mathematical model for semicircular canal response which has concerned investigators for many years is the lack of a suitable mathematical description for adaptation. Close examination of data for several types of experiments in which humans are rotated in the dark indicates that both involuntary compensatory eye movements (nystagmus) and subjective sensation are fundamentally different in form from those predicted purely on the basis of a second-order differential equation. Short-term adaptation effects are seen in both types of responses. The mathematical model's response to horizontal rotation can be improved by the addition of two adaptation terms (time constants of approximately 0.5 minute for sensation and 2 minutes for nystagmus) to the overdamped second-order description of the cupula dynamics. Adaptation is represented as a shift of reference level based on the recent history of cupula displacement. While the adaptation model is of the nonrational parameter type, it accounts for the measured consistent difference in time constants between nystagmus and subjective cupulograms, "secondary" or "nach-nach" nystagmus, and also decreased sensitivity to prolonged acceleration. Although the dynamics of the adaptation are now known, quantitatively, the physiological origins of the process remain to be explained.

Sensory Feedback in Human Posture Control

by
Lewis M. Nashner and Jacob L. Meiry

Presented at the Sixth Annual Conference on Manual Control, April, 1970.

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.

Vestibular Models

by
Laurence R. Young

Presented at the 1969 Joint Automatic Control Conference of the American Automatic Control Council, August, 1969.

The vestibular system, comprising the membranous non-auditory labyrinths in the inner ear, serves as a fast, rough, inertial system to enable man to adjust his posture to avoid falling down, to sense his position and velocity, and to direct and stabilize his eyes in order to take in visual information while moving. Most of us are aware of this motion-sensing system only when it causes difficulty. In addition to motion sickness (which may be attributed to visual-vestibular conflict), we are concerned with vestibular contributions to disorientation and vertigo, and nystagmus (rhythmic motion of the eyes which may interfere with reading displays.) We must also consider the long-term adaptation effects possible with the unusual motion environment under weightlessness, reduced gravity, or in a rotating spacecraft. On the positive side, it is important to note that the presence of vehicle motion (as opposed to "fixed base" simulation) generally makes any vehicle easier to fly and aids pilot performance. To be specific, the motion cues seem to aid pilot performance most for vehicle motions in the frequency range of high sensitivity of the vestibular system.

For all of these reasons, as well as for its possible clinical value, we are developing a quantitative mathematical model for the vestibular system, relating the time history of linear and angular motions to nonvisual perception of orientation, motion, and nystagmus. The models we are developing are "input-output" models; however, in each case we attempt to relate the parameters of the model to known physiological characteristics. The engineering interest in the vestibular system, as a component in man's "attitude control system," has led us also to build a physical analog of the vestibular system, using gyros, accelerometers, gimbals, and a special-purpose analog computer.

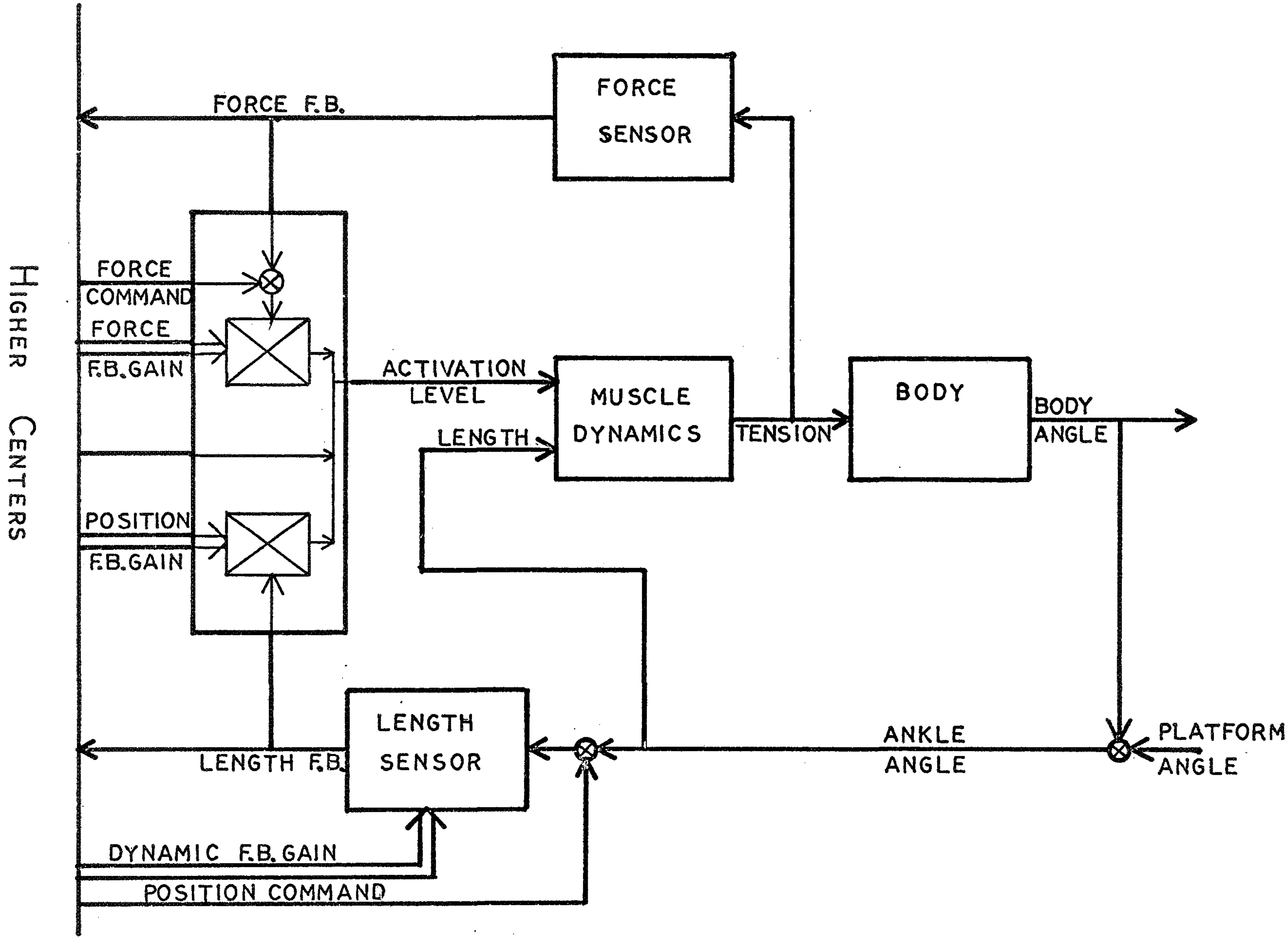


FIGURE 1 THE REFLEX CONTROL SYSTEM

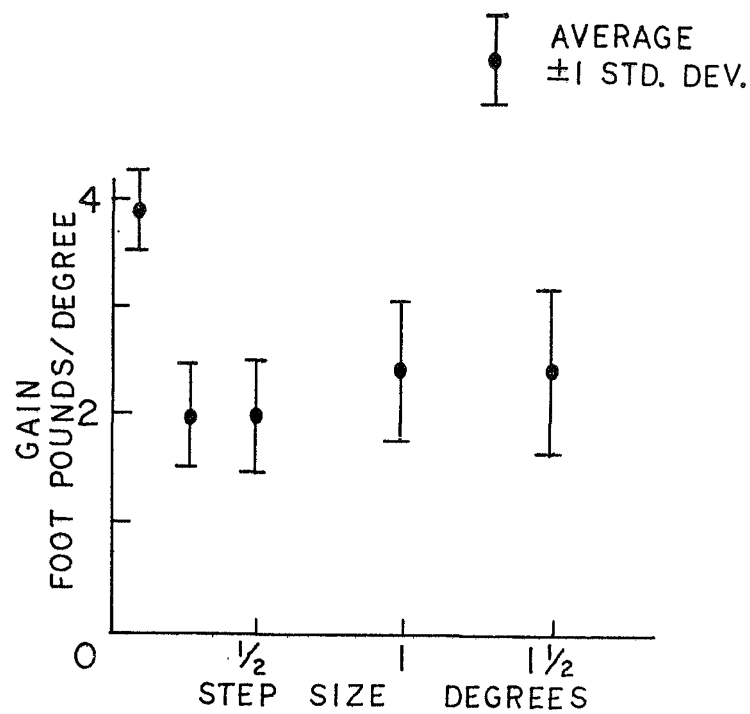


FIGURE 2 AVERAGE ANKLE REFLEX GAIN AS A FUNCTION OF STEP SIZE

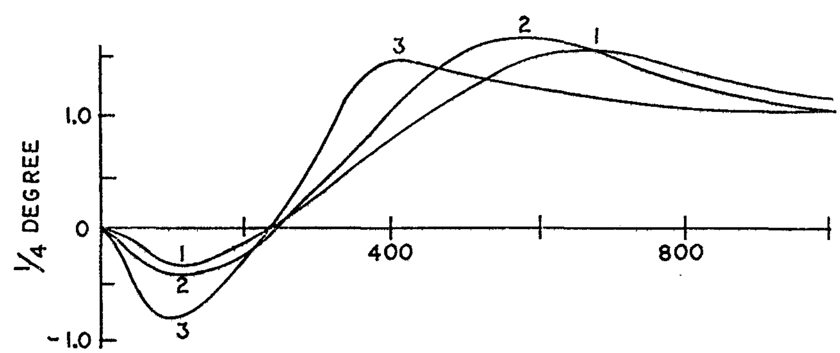


FIGURE 3 AVERAGE ANKLE REFLEX RESPONSES GROUPED ACCORDING TO GAIN FOR 1/4 DEGREE STEPS FLEXING THE ANKLE

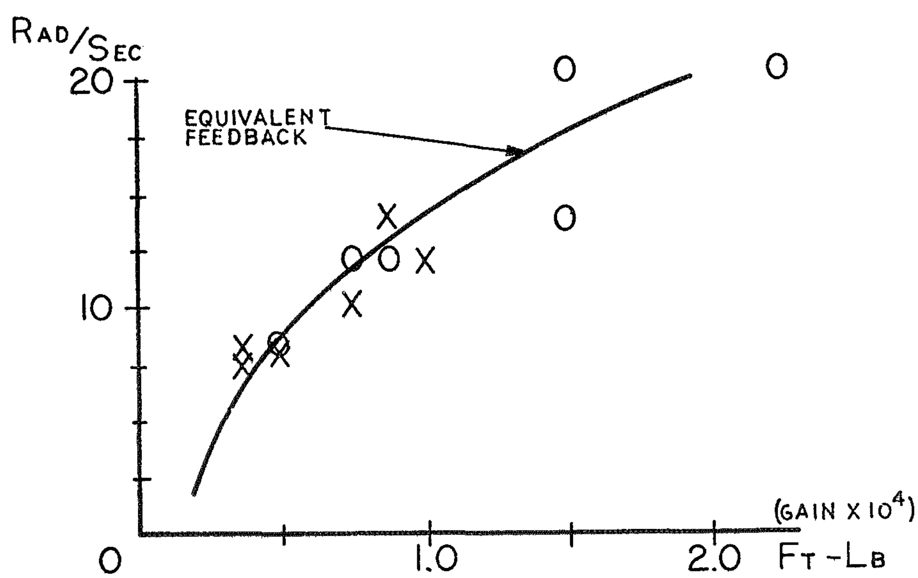


FIGURE 4 NATURAL FREQUENCY AS A FUNCTION OF REFLEX AMPLITUDE, COMPENSATORY RESPONSE

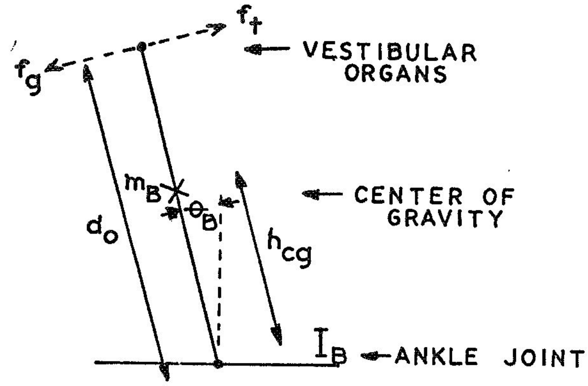


FIGURE 5 THE BODY AND ITS SWAY DYNAMICS

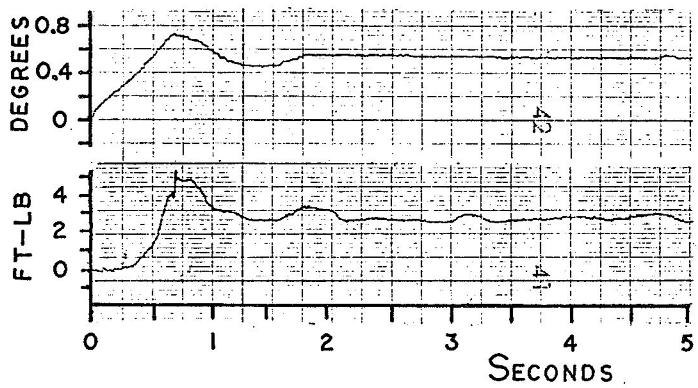


FIGURE 6 A TYPICAL POSTURAL RESPONSE TO INDUCED SWAY MOTION

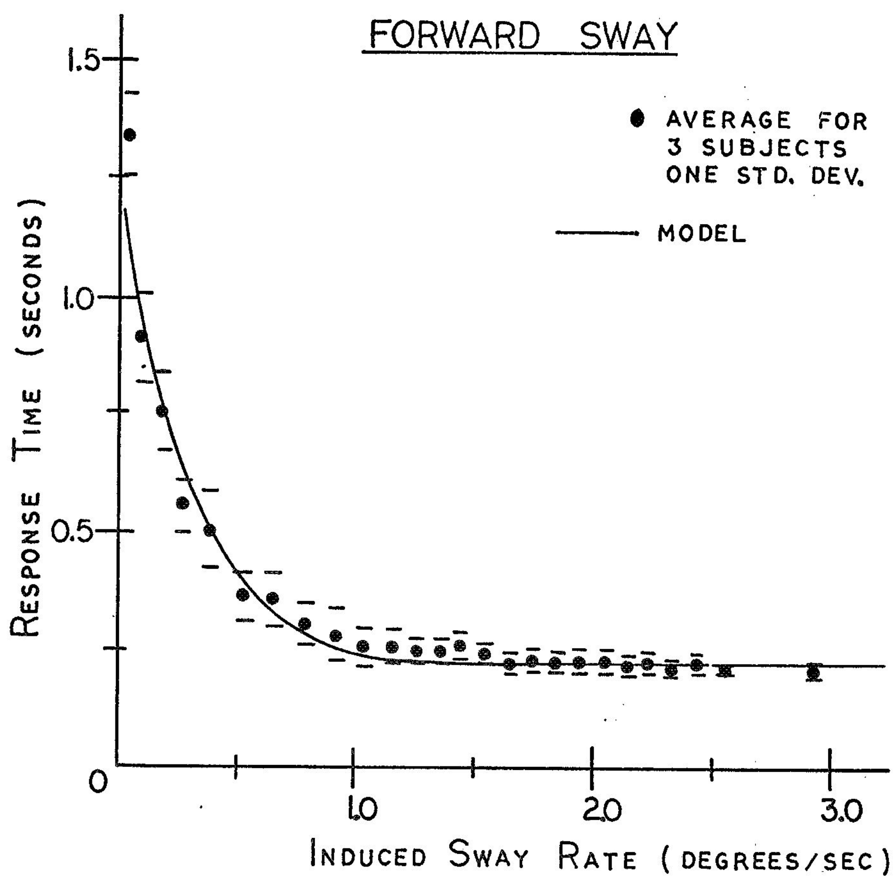


FIGURE 7 VESTIBULAR THRESHOLD RESPONSE CHARACTERISTICS TO INDUCED SWAY MOTION

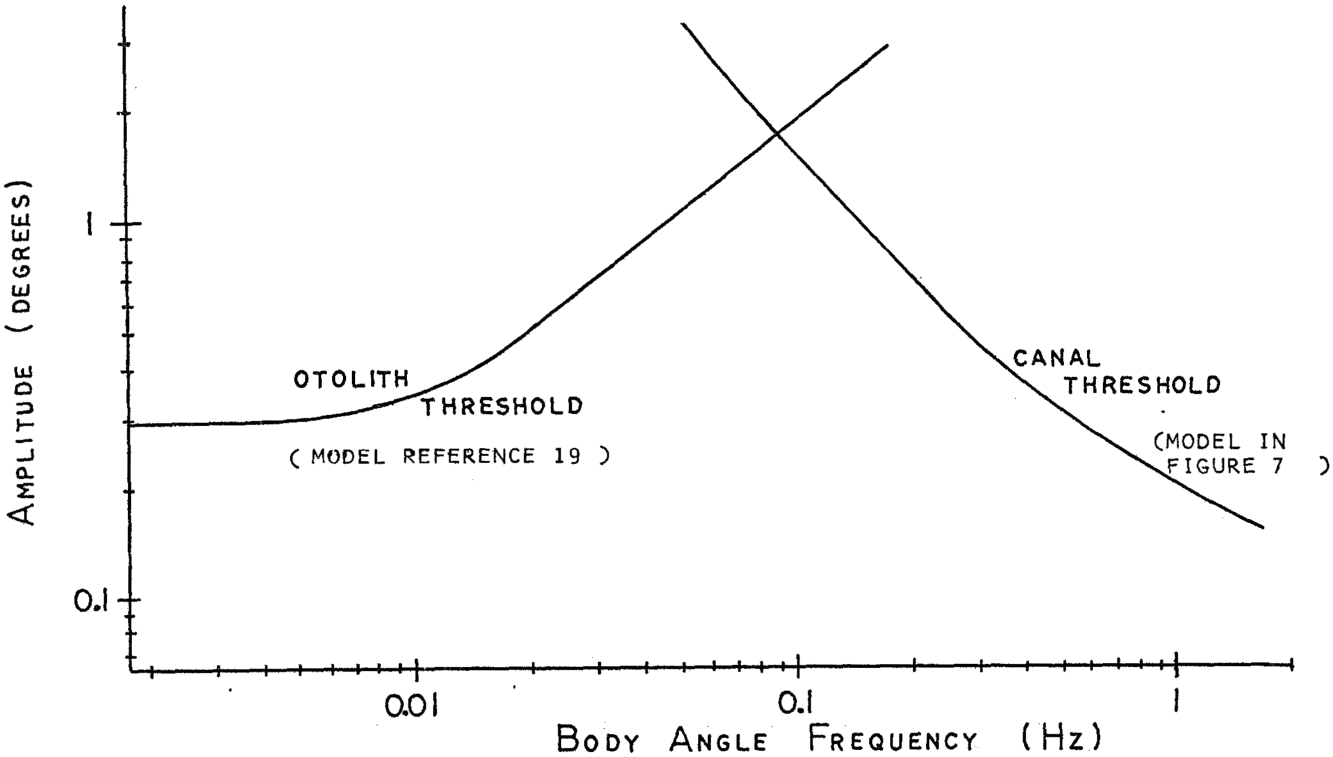


FIGURE 8 THE AMPLITUDE OF OSCILLATION JUST NECESSARY TO TO PRODUCE A THRESHOLD RESPONSE IN EACH VESTIBULAR ORGAN AS A FUNCTION OF SWAY FREQUENCY

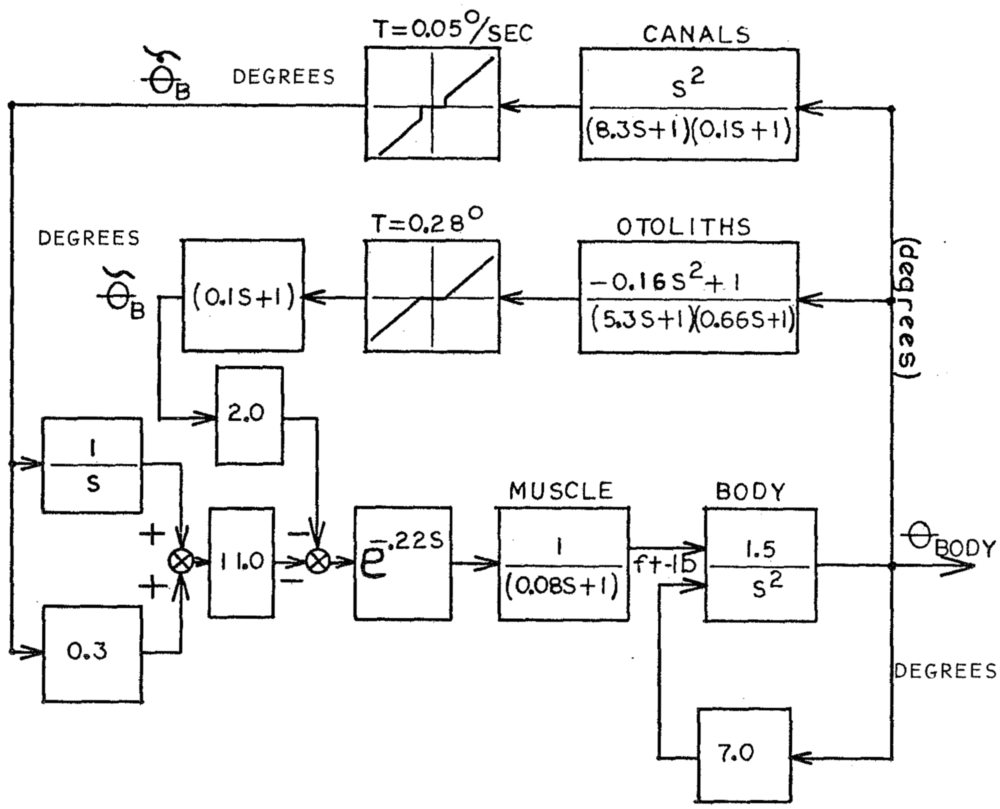


FIGURE 9 MODEL FOR VESTIBULAR REGULATION OF POSTURE

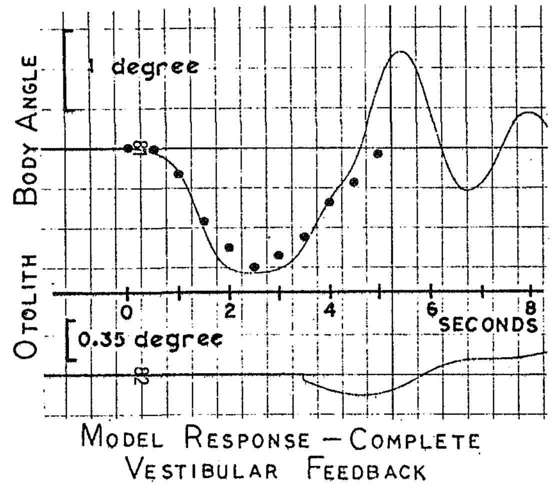


FIGURE 10 VESTIBULAR CONTROL MODEL CHARACTERISTICS COMPARED WITH EXPERIMENTAL DATA

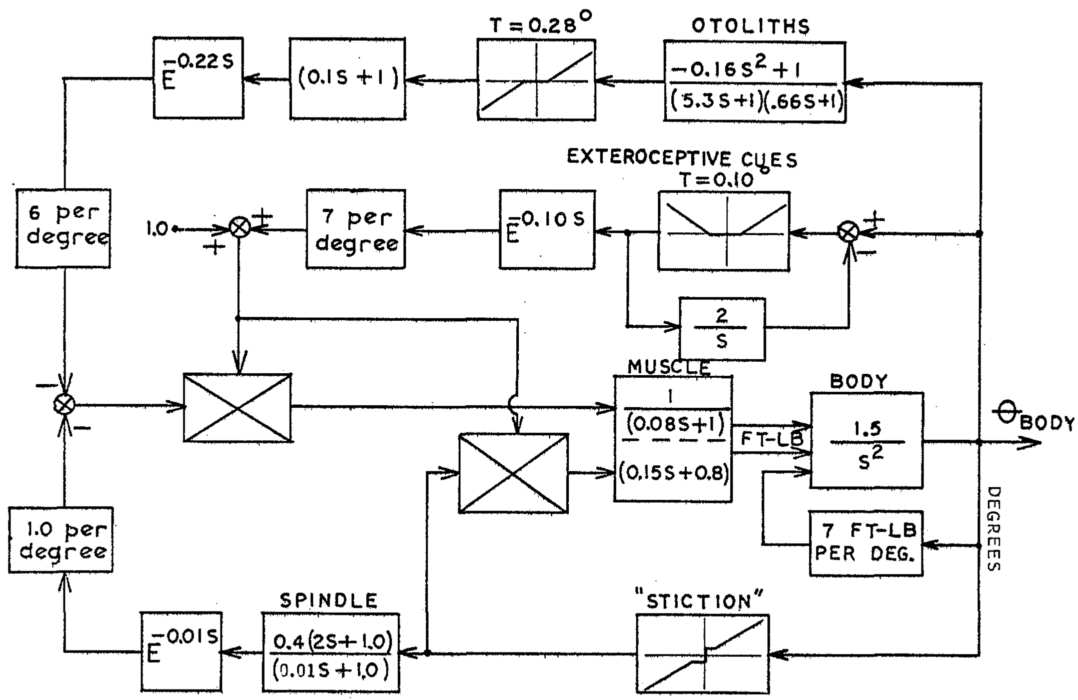


FIGURE 11 REVISED MODEL FOR REFLEX CONTROL OF POSTURE INCLUDING AND UTRICLE OTOLITH FEEDBACK LOOPS

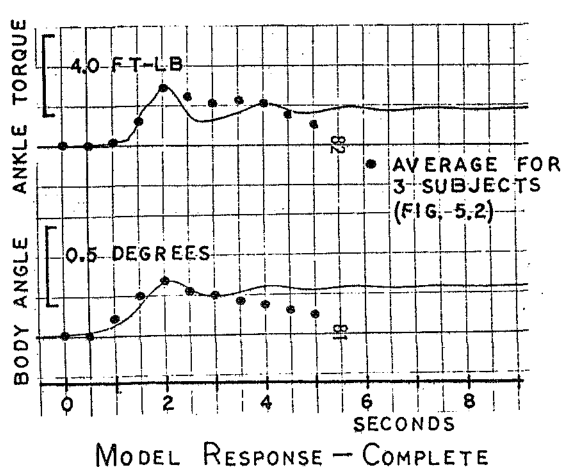


FIGURE 12 CHARACTERISTICS OF THE REFLEX/KINESTHETIC CONTROL MODEL COMPARED WITH EXPERIMENTAL DATA

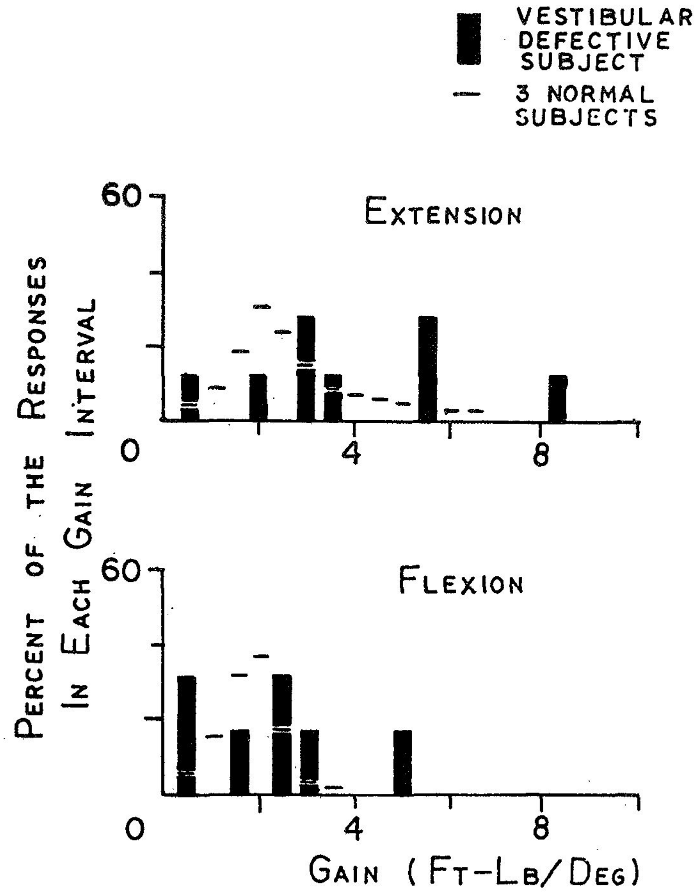


FIGURE 13 DISTRIBUTION OF REFLEX GAINS FOR 1/4 DEGREE STEPS, VESTIBULAR DEFECTIVE SUBJECT STANDING WITH EYES OPEN

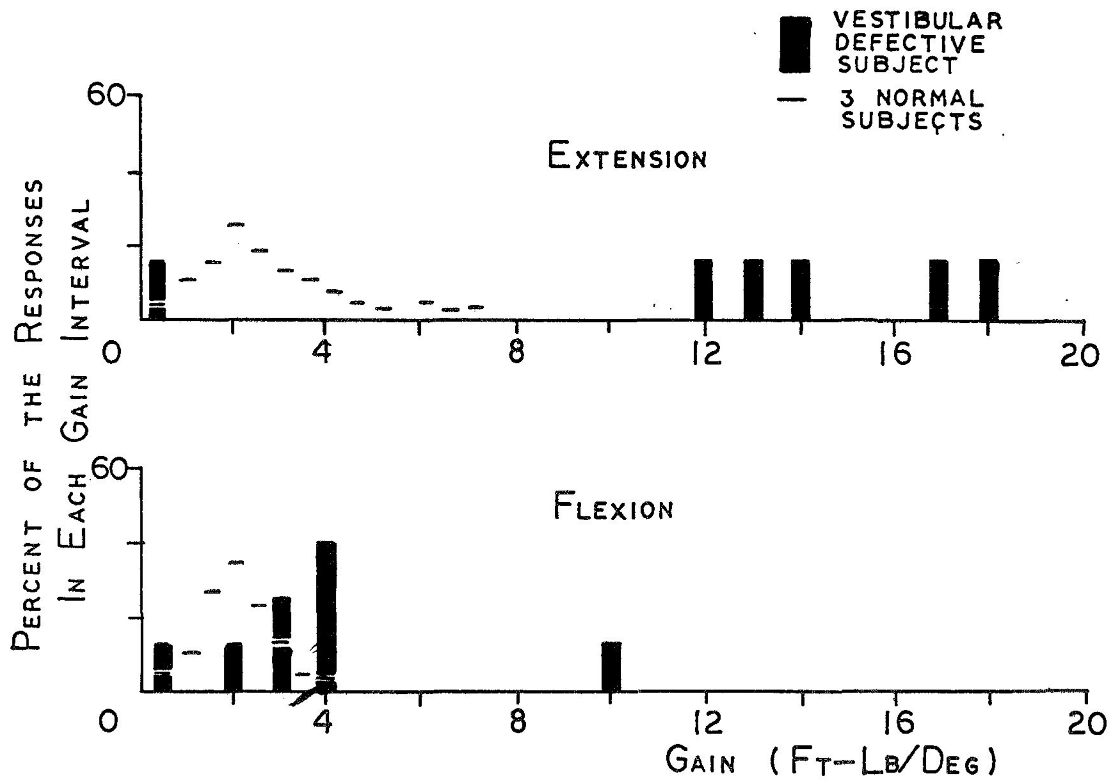


FIGURE 14 DISTRIBUTION OF REFLEX GAINS FOR 1/4 DEGREE STEPS, VESTIBULAR DEFECTIVE SUBJECT STANDING WITH EYES CLOSED