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# GOODYEAR

# GOODYEAR AEROSPACE

## CORPORATION

### ARIZONA DIVISION
#### LITCHFIELD PARK, ARIZONA

August 23, 1965

GERA-1056

# THE FUNCTIONAL PARAMETERS
# OF THE SEMICIRCULAR CANALS

Robert Mayne
Manager
Advanced Systems and Technologies Division

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# ACKNOWLEDGEMENTS

# INTRODUCTION AND SUMMARY

Goodyear Aerospace Corporation is conducting a study of "Spatial Orientation in a Weightless Environment" under contract to NASA Manned Spacecraft Center, Houston, Texas. An objective of the program is to investigate how the system of spatial orientation may function or malfunction in a weightless environment and may initiate motion sickness-like disturbances. A further objective is to consider the possibility of designing an analog of the system with the expectation that it may assist in the prediction of the disturbances which may occur under given environmental conditions. A first report entitled "Functional Aspects of the System of Spatial Representation in the Control of Body Movements. Part I. General Considerations" described the over-all system and outlined a proposed hypothesis regarding the nature of motion sickness. The objective of further reports will be to amplify upon this outline. The present report investigates the functional parameters of the semicircular canals and how these parameters may be adapted to provide suitable control of body movements.

Semicircular canal end organs are found in a wide variety of species, including mammals, birds, fish, and reptiles. The basic operating principles of these organs seem to be the same and their configuration similar in all animals. The adaptation to various species requires, however, the modification of certain parameters of the system. An investigation of these variations should provide a significant insight into the operation of the canals and should contribute to the detailed understanding of the canal system which is necessary to the fulfillment of the broad objective of the program.

Jones and Spells[10] (1963) conducted such a study. They made measurements of the critical dimensions of the canals in some 87 species and determined an

empirical relation for the dimensions of the internal radii and the radii of curvature as a function of the weight of the animals. Using dimensional analysis, they computed the likely relation between the maximum angular velocity of the head and the weight of animals. Their conclusions were that the very small changes observed in the dimensions of canals were sufficient to adjust the canal characteristics to the computed variations of head velocity as well as to the sensitivity requirements of different species. The application of frequency response and elementary information theory to the analysis was discussed in private correspondence with Jones and is utilized in this paper.

The present analysis confirms the broad findings of Jones and Spells, but indicates that other variable parameters in addition to canal dimensions must be provided to achieve suitable flexibility of adaptation to various species.

## THE FREQUENCY RESPONSE OF THE SEMICIRCULAR CANALS

The history of the evolution of the theory of the semicircular canals is too well known to bear repetition here. Suffice it to say that Steinhausen[17](1933) expressed the behavior of the canals by an equation of the form:

$$\ddot{\theta} + L\dot{\theta} + P\theta = 0. \tag{1}$$

With oscillatory motion impressed on the head, the equation becomes:

$$\ddot{\theta} + L\dot{\theta} + P\theta = A\omega^2 \sin \omega t \tag{2}$$

where

$\theta$ = angular displacement of the endolymph
fluid relative to the canal

$$L = \frac{\phi}{I} \qquad\qquad P = \frac{\Delta}{I}$$

and

$\phi$ = the moment of viscous friction exerted on the
endolymph per unit angular velocity

$I$ = moment of inertia of the endolymph

$\Delta$ = elastic moment exerted on the endolymph per
        unit angular displacement

A = maximum angular displacement of the head

$\omega$ = circular frequency of the oscillation.

The system is greatly overdamped and the theory expressed by Equation (1) has been called that of the "overdamped pendulum. "

Van Egmond, et al. [19, 20](1948-1949), Groen, et al.[4](1952), explored numerous aspects of the behavior of the canals of man and of the ray on the basis of the above formulation and calculated the constants of the equation. Mayne[11](1950) computed the frequency response of the canals for frequency ranges said to represent normal body movements.

The behavior of a system defined by Equation (1) can be expressed as a ratio of output-to-input or by a so-called "frequency response function. " This function may be in terms of endolymph displacement output to canal acceleration, velocity, or displacement input. It can be assumed that cupular displacement and, therefore, semicircular canal output signals, are proportional to endolymph displacement. Figure 1 shows a plot of the three frequency response functions for the canals of man on the basis of constants computed in reference 11. It will be noted that there are ranges of frequency where the response is flat for each of the three forms of input. Obviously, a highly desirable characteristic of a measuring instrument is a flat response to the quantity to be measured. This permits a direct reading of the quantity without complicated corrections. A flat response is particularly important in the case of the measurement of transient phenomena since without it a different correction would be required for every frequency component of the transient. The semicircular canals operate, therefore, in different frequency ranges as accelerometers, velocity meters, or seismographs.

The range of frequencies or "bandwidth" where the response to velocity input is reasonably flat is roughly from 0.04 cps to 4 cps. This appears to cover the range of body movements. In contrast, flat responses to acceleration and displacement lie in ranges below 0.002 cps and above 100 cps, respectively.
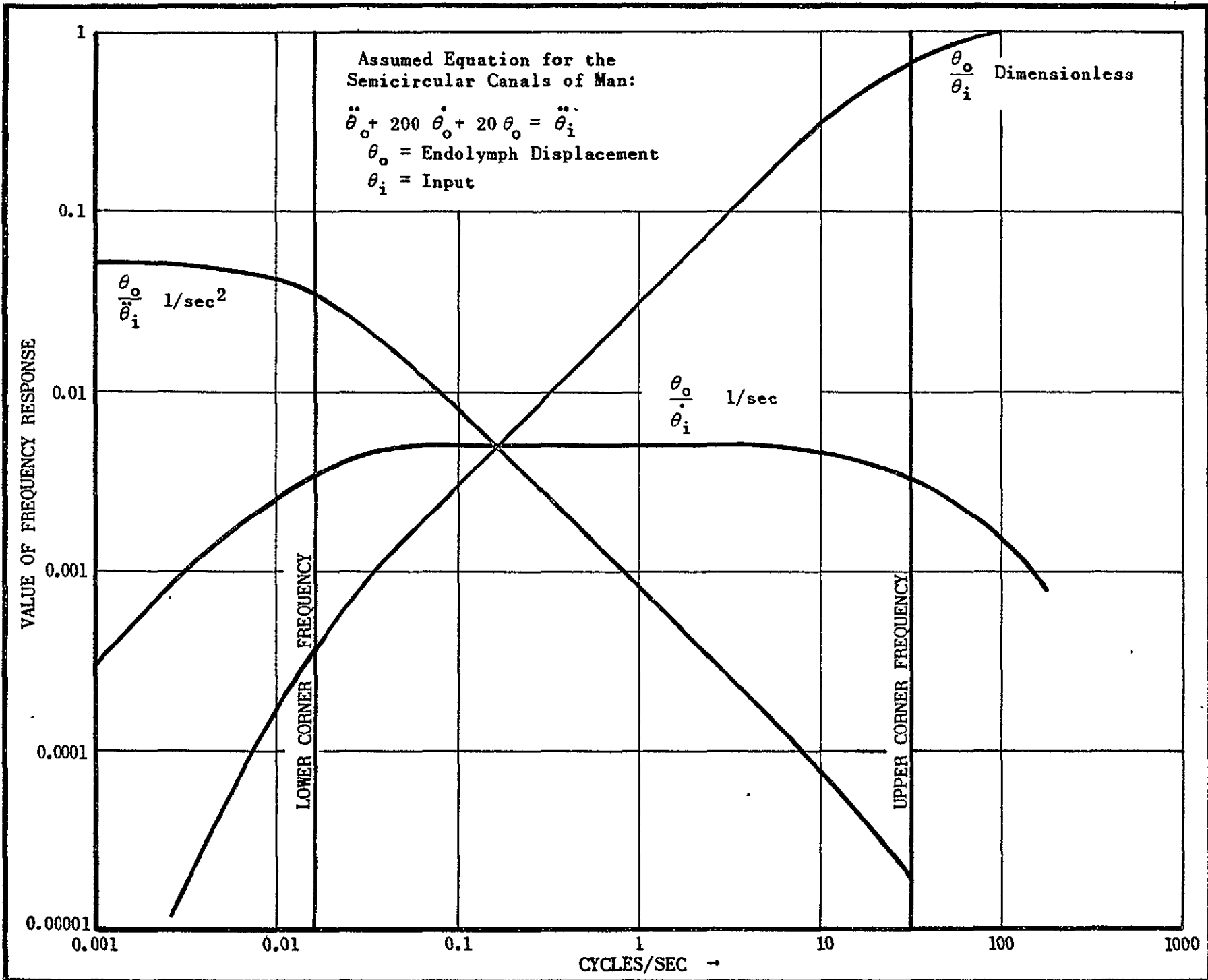
Figure 1 — Frequency Response Functions of the Semicircular Canals of Man for Acceleration, Velocity, Displacement Inputs

The figure contains the following labeled text:

Assumed Equation for the Semicircular Canals of Man:

$$\ddot{\theta}_o + 200\,\dot{\theta}_o + 20\,\theta_o = \ddot{\theta}_i$$

$\theta_o$ = Endolymph Displacement

$\theta_i$ = Input

$\dfrac{\theta_o}{\theta_i}$ Dimensionless

$\dfrac{\theta_o}{\ddot{\theta}_i}$ 1/sec$^2$

$\dfrac{\theta_o}{\dot{\theta}_i}$ 1/sec

Axis labels: VALUE OF FREQUENCY RESPONSE (vertical), CYCLES/SEC → (horizontal)

LOWER CORNER FREQUENCY

UPPER CORNER FREQUENCY

Obviously, oscillations having a period of more than eight minutes, or less than ten milliseconds, are not within the range of normal body movements. It can be said, then, that the semicircular canals are adapted to measure the velocity of the body's transient movements within a range of frequencies and to the accuracy defined by the frequency response curve of Figure 1. Van Egmond, et al.[20] (1948) wrote, "... the function of the semicircular canals is to control body movements by indicating the attained velocity and the angle of rotation executed." The statement agrees with the present view although obviously "the angle of rotation executed" is not given directly by the canals, being the result of further neural computations, but the statement is ambiguous unless the limits of frequencies for which it is true to a given accuracy are indicated as in Figure 1. The same conclusions are reached in a recent paper by Jones and Milsum[9] (1965) in which they published a frequency response curve similar to that of Figure 1. Experimental data, as in the measurement of slow phase nystagmus, or in the determination of subjective velocity during a post-rotational period, show that semicircular canal signals are interpreted as velocity even when they do not correspond to objective reality. While acceleration is the initiating stimulus of the canals, its value is lost in the processing. In a similar manner the displacement of an automobile on a highway is the initiating stimulus to a speedometer but the value of this displacement is lost in this instrument and must be retained in another instrument: the odometer.

It is well known that any transient phenomenon such as the sound of music, or a body movement, can be expressed as a summation or a spectrum of pure sinusoids of various frequencies, amplitudes, and phases, by a so-called Fourier transform. The frequency spectrum of body movements of various animals may be expected to vary with their size and it is the purpose of this investigation to determine how well this spectrum corresponds to the bandwidth of the frequency response of the canals and what parameters must be adjusted to achieve such a "match."

The over-all response of the semicircular canals must include the sensory end organs.  This response is usually determined experimentally on the basis of eye movements, which are known to be controlled by the semicircular canals.[7,8] Experimental data show that the response is only defined approximately by Equation (1) and is modified by a number of factors, including the limit of linearity of cupula elasticity,[8] the value of threshold cupula movements,[3] adaptation,[5,6] mental sets,[1,2] and possibly by a variable cupula stiffness.[6] It is believed, however, that the equation is reasonably accurate for movements within the normal range of body activity.  Three numbers are mainly significant in defining canal behavior within this range: the upper range of the frequency band, the lower range of the frequency band, and the resolution.  Linear dynamic range and information rate may also be included as significant factors of over-all canal response.  The parameters which influence these characteristics will be discussed subsequently.

## SUMMARY

The semicircular canals are adapted to measure the angular velocity of head movements.  The measurement is accurate only within a bandwidth of frequencies corresponding to normal body activity.  The signal issued by the canals, even when in error, is always interpreted as velocity by the central nervous system.  While acceleration is the initiating stimulus to the canals, its value is lost in the processing.  The simple formulation by Equation (1) is modified by a number of factors, including non-linearity of elasticity, threshold, adaptation, and mental sets.  It is believed that these disturbing factors can be neglected for the normal range of body movements.  The report will attempt to discover a relation between the frequency response of the canals and the predicted frequency spectrum of the movements of various animals.

## UPPER RANGE OF THE FREQUENCY BAND

The upper and lower limits of the frequency response of the canals to a velocity input may be defined in terms of the so-called corner frequencies. These frequencies define a point in the spectrum where the response is 0.707 of the flat response and the phase shift is 45 degrees. The corner frequencies do not correspond to the usable bandwidth as the distortion is considerable at those values, but they are convenient points of reference. The upper corner frequency ($f_u$) of a highly overdamped system such as the semicircular canals is expressed to a close approximation by the formula:

$$f_u = \frac{L}{2\pi} \text{ cps.}$$ (3)

L can be computed from hydrodynamic considerations and the Hagen-Poiseuille law of laminar flow in small circular pipes.

Schmaltz[15] derived the formula

$$L = \frac{8\eta}{\rho r^2},$$ (4)

where

$\eta$ = coefficient of viscosity of the endolymph

$\rho$ = density of the endolymph

$r$ = internal radius of canals.

Van Egmond, et al.[19] (1949), altered the formula to:

$$L = \frac{4\eta}{\rho r^2},$$ (5)

on the ground that the canals include only half a circumference, the remaining portion consisting of the very much enlarged utricle. It appeared to them that viscosity in the utricle could be neglected because of the enlarged size of the canal. However, it can be shown that the inertia of the fluid can also be neglected in the utricle for the same reason. The alteration of the formula therefore

cannot be justified on the ground of the enlarged canal dimension. The formula is valid, however, in showing that the top corner frequency, and therefore the maximum frequency $\omega_{\text{max canals}}$ to which the canals can respond properly, is expressed by:

$$\omega_{\text{max canal}} \propto f_u \propto \frac{1}{r^2} : \tag{6}$$

Jones and Spells developed an empirical formula relating $r^2$ to the mass m of mammals. This formula can be written as:

$$r^2 \propto m^{0.14 \pm 0.04} , \tag{7}$$

Thus,

$$f_u \propto m^{-0.14 \pm 0.04} . \tag{8}$$

We turn to an investigation of the maximum frequency of oscillation of the heads of various species as a function of their weight in the hope of finding a meaningful relation with Jones and Spells' empirical data. _A_head movement may be with respect to the body or as the result of an over-all body movement. The semicircular canals are believed to play a role in both cases, but we will consider only movements of the head with respect to the body for the sake of simplicity. Also, we will limit this first investigation to mammals for reasons to be discussed later.

The head-muscle system may be considered as an oscillatory system with moment of inertia, restoring moment, and damping. The moment of inertia is that of the head; the restoring moment is provided by the servo system. If the servo is linear, the restoring force is proportional and opposite to displacement as in the case of a spring. The restoring force per unit displacement or "stiffness" is variable, however, depending upon "gain" which in turn depends on the "desired" speed of movement. The damping is usually provided in a servo system by a so-called lead function, which produces a force proportional and opposite to velocity, corresponding to a viscous force in an oscillating system.

Typically, the damping is critical. Servo mechanisms sometimes include more complex controlling functions, but only a simple second-degree system need be considered here.

To determine the maximum frequency of oscillation of the head with respect to the body, likely relations must be established between the weight of animals, the moment of inertia of their heads, and the maximum moment which the muscles can exercise.

First we assume, with Jones and Spells,[10] geometrical similarity between all animals; in other words, we assume that all dimensions of an animal of a certain size are related to those of another animal of a different size by the same ratio, and that the weight of all parts of their anatomy is related as the cube of the dimension ratio. If $\ell$ is a typical dimension of an animal of mass m, the moment of inertia of the head would then be:

$$I \propto m\ell^2 \propto m^{5/3}. \tag{9}$$

Under the assumption of geometric similarity, the weight of the neck muscles would be proportional to the weight of the animals. If we assume, further, that the power which can be exerted by muscles is proportional to their weight, we have, since the power or energy rate is equal to the moment times the velocity,

$$\dot{E}_{max} = \left[M\dot{\theta}\right]_{max} \propto m \tag{10}$$

where

$\dot{E}$ = energy rate or power

M = moment applied to the head

$\dot{\theta}$ = angular velocity.

For a sinusoidal oscillation,

$\theta$ = A sin $\omega$t, and

$\dot{\theta}$ = A$\omega$ cos $\omega$t (11)

where A is the maximum amplitude of angular movement assumed to be a constant for all animals and $\omega$ is the circular frequency.

But the moment is equal to the acceleration times the moment of inertia, or, for a sinusoidal oscillation,

$$M = I\ddot{\theta} = AI\omega^2 \sin \omega t. \qquad (12)$$

Substituting the value of M into Equation (10),

$$\dot{E} = -\frac{1}{2}A^2\omega^3 I \sin 2\omega t,$$

giving

$$\dot{E}_{max} \propto m \propto \omega^3_{max} I \qquad (13)$$

and, therefore,

$$\omega_{max} \propto \sqrt[3]{\frac{m}{I}} . \qquad (14)$$

Substituting the value for I gives

$$\omega_{max} \propto \sqrt[3]{m^{-\frac{2}{3}}} = m^{-0.222} . \qquad (15)$$

Jones and Spells,[10] using somewhat different assumptions, obtained an expression for maximum head angular velocity of $\dot{\theta} \propto m^{-\frac{1}{3}}$. (It will be noted from Equation (11) that the maximum head velocity is proportional to $\omega_{max}$ and that the two are numerically equal for an amplitude of oscillation of one radian.) They argued that such a relation would provide too rapid an increase of angular velocity of the head as the weight of animals is reduced. While the angular velocity of the body movements of a cat, for instance, can be expected to be higher than that of a tiger, the above relation would call for an increase corresponding exactly to the reduction in linear dimension so that the cat could move his paws at the same linear speed as a tiger. The difficulty, as pointed out by Jones and Spells, is in the assumption of dimensional similarity. There is no reason to expect, actually, that the same ratio of total weight of animals can be allocated to muscles in animals of widely varying weights. It is more likely that a larger proportion of weight must be allocated to portions of the body other than muscles, such as skeleton and various organs, as the animals become

smaller. Equation (15) gives a somewhat slower increase of the speed of angular movement or of frequency with reduced weight of animals, but is believed subject to the same criticism as that of Jones and Spells.

Jones and Spells then reasoned that, to keep gravitational stresses on the neck constant, more muscle must be provided as the animal increases in size than predicted by dimensional similarity and more muscle is then available to turn the head. On the basis of this assumption, they obtained the relation;

$$\dot{\theta}_{max} \propto m^{-\frac{1}{12}} . \tag{16}$$

They felt that this exponent provided too small an increase for angular velocity as a function of reduced weight and argued that the true exponent should be between $-\frac{1}{3}$ and $-\frac{1}{12}$.

We adopt here a different criterion in the determination of the maximum frequency of oscillation of the head; namely, that maximum inertial stresses caused by the oscillation should be constant for all animals. This appears as a reasonable assumption since biological materials, such as brain tissues, are similar in all animals. Inertial stresses in an angular oscillation are of two types: those caused by reversal and those caused by centrifugal force. The maximum stresses from these two causes can be expressed as;

$$S_{max} \propto A\omega^2 \ell \quad \text{for reversal}$$

$$S_{max} \propto A^2\omega^2 \ell \quad \text{for centrifugal force.}$$

The two are numerically equal for an amplitude of oscillation of one radian and, since A is a constant, we can write for both types of stresses:

$$S_{max} \propto \omega^2_{max} \ell \tag{17}$$

where $S_{max}$ is taken as constant in accordance with the previous assumption.

The value of the maximum frequency of oscillation of the head $\omega_{max \; canals}$ can be expressed by:

$$\omega_{max \; canals} \propto \sqrt{\frac{1}{\ell}} = \sqrt{\frac{1}{m^{\frac{1}{3}}}} = m^{-0.167} \quad . \qquad (18)$$

It will be noted that there is good agreement between this value and the empirical formula of Equation (8) relating the maximum frequency response of the canals and animal weight. It appears, therefore, that a good match obtains between canal dimensions and the dynamics of head movements of various species insofar as maximum frequency of oscillation is concerned.

There are, however, rather wide variations of canal sizes for animals of the same weight. These individual variations may result from the adaptation of different species to different environments. The present generalized investigation can only give average results. For better correlation, the investigation must proceed to the experimental determination of the frequency spectrum of head movements of specific animals.

SUMMARY

Using data obtained by Jones and Spells, good correlation was found between empirically determined upper frequency of canal response and theoretically determined maximum frequency of the head movements of various species. The results are in substantial agreement with those obtained previously by Jones and Spells. The investigation appears to confirm the effect of internal canal dimension in the maximum frequency response of the canals.

## LOWER RANGE OF THE FREQUENCY BAND

The upper corner frequency of the canals is a measure of the maximum frequency at which the canals give reliable velocity information. Similarly, the lower corner frequency is a measure of the lowest utilizable frequency. As mentioned above, the corner frequencies are convenient points of reference but do not represent the limits of the usable bandwidth, which is much narrower. Some body motions may utilize the higher portion and others the lower part of the bandwidth. A diver, for instance, may utilize the upper range in the control of a 1-1/2 turn from a low board and depend on the lower limit in a swan dive from a high board. The canals of an airplane pilot in a turn are operating below their normal range of frequencies and may cause abnormal sensations.

The lower corner frequency is given to a close approximation by the equation

$$f_\ell = \frac{1}{2\pi\tau} ,$$
(19)

where $\tau$ is the time constant represented by

$$\tau = \frac{L}{P} = \frac{\phi}{\Delta} .$$
(20)

Van Egmond,[20] et al., showed that, from elementary hydrodynamic considerations,

$$\phi = 8\pi^2 \eta R^3 ,$$
(21)

where $\eta$ is a constant as defined in Equation (4), and R is the radius of curvature of the canals.

Jones and Spells give

$$\Delta = \pi r^2 \mu R ,$$
(22)

where $\mu$ is the coefficient of elasticity which they assumed to be constant.

From these two relations they derived

$$\tau \propto \frac{R^2}{r^2} \ .$$  (23)

This formulation of Jones and Spells, if true, together with Equation (19), would define the manner in which the low frequency response of the canals should vary with the dimensions r and R and therefore, using their empirical relations, with animal weight. To check this relation we have to derive some likely relation between the weight of animals and the lowest frequency component of their head movements as we have previously derived a similar relation for maximum frequency.

We assume tentatively that the low frequency must vary as the same function of animal weight as the high frequency; in other words, that the ratio $\frac{f_u}{f_\ell}$ must remain constant for all animals. This condition is nearly realized by Equation (23) as an average because if, as stated by Jones and Spells, $r^2$ and R vary as similar functions of m,

$$R \propto r^2 \propto m^n$$

and

$$\tau \propto \frac{R^2}{r^2} \propto m^n \propto r^2 \propto R;$$  (24)

and, from Equations (6) and (15),

$$\frac{f_u}{f_\ell} = C.$$  (25)

However, Jones and Spells' measurements show that $r^2$ and R are only approximate functions of the same power of m. Further, the relations between canal dimensions and mass represent only averages for a large number of animals, and there are wide variations for species of the same weight. While Equation (24) may be nearly true as an average, it does not necessarily apply even approximately to a specific specie. It gives, for instance, values at wide variance from the experimentally derived time constants for man and for a ray.

It should be expected, also, that a plot of $f_\ell$ and therefore $\tau$ vs weight of animals should show a statistically significant relation similar to that of $f_u$ or $r^2$. But the plot of $\frac{R^2}{r^2}$ shows no such relation. It would seem better, therefore, to express the probable value of the time constant directly as

$$\tau \propto r^2 . \tag{26}$$

This would ensure that $f_\ell$ and $f_u$ would vary as the same function of m in accordance with our previous assumption. This relation can be achieved with proper adjustment of cupula stiffness. We investigate the manner in which it must vary to give this relation. We assume that ampullae and cupulae of different sizes are geometrically similar. The total force on the cupula is equal to the pressure P times the cupula area which may be taken as

$$V^{\frac{2}{3}} ,$$

where V is the volume of the ampulla. We can then write the relation

$$M\varepsilon \propto \frac{1}{2}P\, V^{\frac{2}{3}}\, V^{\frac{1}{3}} \propto PV, \tag{27}$$

where

M = elastic moment per unit deflection of cupula

$\varepsilon$ = angular deflection of cupula.

But we can also write from equality between the volume of endolymph displaced in the canal and that swept by the cupula;

$$\theta\, r^2 R \propto \varepsilon\, V^{\frac{1}{3}} V^{\frac{2}{3}} \propto \varepsilon\, V. \tag{28}$$

Combining Equations (27) and (28) gives

$$P = \frac{\theta\, M r^2 R}{V^2} . \tag{29}$$

But $\Delta$ is the moment on the endolymph per unit displacement so that

$$\Delta \propto \frac{Pr^2R}{\theta} \; ; \tag{30}$$

or, from Equation (29),

$$A \propto \frac{Mr^4R^2}{V^2} \; . \tag{31}$$

From

$$\tau = \frac{\phi}{\Delta}$$

and Equation (21), we derive

$$\tau \propto \frac{RV^2}{Mr^4} \; , \tag{32}$$

and from Equation (26),

$$M \propto \frac{RV^2}{r^6} \; . \tag{33}$$

Equation (33) indicates how M should be adjusted to other dimensions of the canals to make $\tau$ proportional to $r^2$.

It must be clear that the assumption by Jones and Spells that $\mu$ is constant in Equation (22) does not imply a constant elastic moment coefficient of the cupula. The constancy implied by their formulation is for the quantity

$$\mu = \frac{\Delta}{\pi r^2 R} \; . \tag{34}$$

We may compute how hinge moment must vary to satisfy their assumption. From Equations (30) and (22) we have

$$\mu = \frac{Mr^4R^2}{\pi V^2 r^2 R} \; ; \tag{35}$$

and, since $\mu$ is assumed to be a constant,

$$M \propto \frac{V^2}{r^2 R} \; . \tag{36}$$

Equation (36) expresses the variable hinge moments implied by Jones and Spells' formulation.

It appears, therefore, that cupula stiffness must be introduced as one of the adjustable parameters in the semicircular canals and that Jones and Spells' formulation does not avoid this complication. If cupula stiffness is adjusted according to Equation (33), the lower frequency of the bandwidth will be the same function of mass as the upper frequency except for a constant of multiplication. While this may seem reasonable enough, it must be pointed out that Van Egmond, et al.,[19] found a different time constant for clockwise and counter-clockwise rotation in subjects with a unilateral labyrinthine loss. This would indicate that the time constant does not depend always uniquely on canal dimensions. The formulation must be taken, therefore, as a tentative approximation, pending availability of further experimental data.

Table I shows some values of time constants $f_u$ and $f_\ell$ computed on various bases and compared with some experimental results. The formulation of $\tau$ in terms of $\frac{R^2}{r^2}$ gives a value of 7.4 for the ray against an experimental value of 35.[4] The formulation in terms of $r^2$ gives a value of 55, which is of the same order of magnitude as the experimental value. The ratio of $f_u$ to $f_\ell$ is constant when $\tau$ is taken as proportional to $r^2$ as must be expected since the stiffness of the cupula was adjusted to achieve the result. Other computed characteristics do not appear unreasonable.

SUMMARY

The low corner frequency $f_\ell$ is a measure of the lowest frequency at which the semicircular canals give accurate data about velocity. It is inversely proportional to the time constant. A formulation for the time constant which would result in a constant ratio $\frac{f_u}{f_\ell}$ was developed. This formulation was shown to require a variable stiffness of cupula. The limited available experimental data seem to fit the proposed formulation.

## TABLE I – COMPUTATIONS OF $\tau$, $f_u$, AND $f_\ell$ ON VARIOUS BASES

| | Man | Ray (skate) | Mammal (3) | Fish (3) |
|---|---|---|---|---|
| Mass (Kg) | 70 | 10 | 10 | 10 |
| R (3) | 3.15 | 6.3 | 2.30 | 6.00 |
| $r^2 (mm)^2$ (3) | 0.02 | 0.11 | 0.014 | 0.053 |
| $f_u$ (cps) $= \dfrac{0.64}{r^2}$ | 32 | 5.8 | 45.7 | 11.60 |
| $\tau_1 = 0.02 \dfrac{R^2}{r^2}$ | 10 | 7.34 | 7.6 | 13.5 |
| $f_{\ell 1}$, based on $\tau_1$ | 0.159 | 0.0216 | 0.021 | 0.01175 |
| $f_{\ell 2}$, based on $\tau_2$ | 0.0159 | 0.00289 | 0.0228 | 0.00578 |
| $\tau_2 = 500\, r^2$ | 10 | 55 | 7.0 | 27.5 |
| Experimental $\tau_e$ | 10 (1) | 35 (2) | | |
| $f_\ell$, based on $\tau_e$ | 0.0159 | 0.0046 | | |

The constants in the computation of $f_u$, $f_\ell$, and $\tau$ are taken to give proper values for the canals of man as shown above.

(1) Van Egmond, et al.[20]

(2) Groen, et al.[4]

(3) From Jones and Spells[10]

## RESOLUTION

Resolution, or "sensitivity" of a measuring instrument may be defined as the reciprocal of the size of a resolvable element which may be, in turn, taken as a measure of the limit of accuracy of the instrument. A navigational system, for instance, which measures velocity to an accuracy of plus or minus three feet per second may be said to have a resolvable element of six feet per second. Another characteristic of a measuring instrument is the ratio of the maximum amplitude of the quantity it measures to the size of the resolvable element. This ratio is usually expressed in db and is designated as the dynamic range of the instrument.

Physiological sensors can be assumed similarly to possess the characteristics of resolution and dynamic range. Fechner is generally credited with the pioneering work in the determination of the size of the resolvable elements of various sensors or "just noticeable differences" (jnd). His studies indicated that the jnd must be specified in statistical terms. More recently, his work has come under considerable scrutiny with an application of statistical theory of signal recognition (Swets, John H).[18] Seashore attempted to correlate the jnd in pitch variations, time measurement, and sound intensity with musical ability. It is likely, similarly, that a high angular velocity resolution is a factor in accurate body control in various acts of skill.

The experimental determination of jnd generally involves the statement by a subject that he does or does not perceive a change in a sensation, be it the pitch of a tone, the weight of an object, or the intensity of a light when the stimulus is increased gradually. The experimental situation involves, therefore, higher neural or mental functions in the way of conscious perceptions and their verbalization. The work of Swets, et al.,[18] has been directed in part toward the isolation of the physiological reaction from the "noise" created by these higher functions. Following adaptation, the semicircular canals normally operate autonomically in the control of body movements without conscious sensations. It would seem that their resolution should be determined on the basis

of the analysis of thoroughly habituated motions in which higher functions have no part. Any golfer needs no demonstration that higher mental functions can introduce severe "noise" in the control of body movements and will work hard to acquire a mechanical, so-called "grooved swing" as independent as possible from any conscious interference.[11] This value may also be a function of mental sets or the state of arousal, as indicated by various experimental data.[1,2]

For the purpose of this study, we will assume there exists a semicircular canal resolvable element. We recognize that this element should be expressed statistically, and we associate it with the autonomic control of body movement, free from the interference of higher functions. Within these limitations we let

$$\frac{\dot{\theta}_{i\,max}}{n} = \Delta\dot{\theta}_i \, , \tag{37}$$

where

$\dot{\theta}_{i\,max}$ = the maximum amplitude of a sinusoidal velocity input of the head within the limit of linearity of the canals

$n$ = number of resolvable elements in the maximum velocity input

$\Delta\dot{\theta}_i$ = the size of a resolvable element of velocity.

The maximum number of resolvable elements processed per second is then

$$\dot{n} \propto f_u n \, , \tag{38}$$

where $f_u$, as defined earlier, is proportional to the highest frequency component $\omega_{max\,canals}$ of a head movement.

There is a similar expression in communication engineering: the so-called "Hartley Law," which differs mainly from the above in its logarithmic formulation. The physical justification for the formulation of the Hartley Law is that it expresses a measure of the required complexity of a channel which is

needed to handle a given rate of yes and no pieces of data assuming optimum coding. The nature of the physiological coding of sensor data is not known in the way of "trade-offs" made between simplicity of coding and simplicity of channels. The formulation of Equation (38) is left purposely loose so as to be free from any implications in this regard. It should correspond, nevertheless, to an adequate physical concept for the purpose of this paper.

The so-called "Fechner Law" states that as the stimulus is increased, the increment of stimulus necessary to produce a noticeable difference of sensation increases logarithmically. The compression of sensory data has a close parallel in physical equipment. An engineer finds himself frequently with the need of using such compression when the range in the magnitude of the data he wishes to measure exceeds the dynamic range of his instrument. In the recording of the radar image of ground targets, for instance, the dynamic range of the radar return far exceeds that of the processing equipment and of the photographic film on which it is recorded. The engineer finds, however, that by compressing his data he obtains useful imagery and, as likely as not, he will utilize a logarithmic compression although he has never heard of Fechner's Law. A television picture similarly must use considerable compression of the range of light intensity, particularly in an outdoor scene. In the design of other instruments, however, there can be no compromise with linearity. In an inertial system, for instance, the accelerometers must be as completely linear as possible. Dynamic range must simply be limited to the range where linearity obtains within tight limits. The vestibular system is a close biological parallel to a physical inertial system. If the semicircular canals are to fulfill their functions as components of such a system, they, too, must be linear within their normal range of operation. Much experimental data on the canals can be interpreted as evidence that such is the case. The Fechner Law, therefore, probably does not apply even qualitatively to the detection of velocity by the semicircular canals. The size of the resolvable stimulus should remain constant regardless of the magnitude of the stimulus within the normal range of operation. There are, of course, techniques by which

non-linear components can be paralleled to produce an over-all linear response. Jones has suggested that non-linear right and left canals are paralleled in push-pull to give an over-all linear response over a greater dynamic range. It is possible, also, that the semicircular canal data are operated upon by an inverse transfer function of the hydromechanical system to extend the limits of linear response. We are speaking here, of course, of the linearity of over-all response of the canal system, including the hydromechanical system and the sensory end organs.

We must next investigate how n, $\dot{n}$, and $\Delta\dot{\theta}_i$ are related to the weight of animals on the basis of previous assumptions. From the assumption of linearity it follows that throughout the normal range of operation of a specific canal system the deflection of the cupula must increase by the same increment $\Delta\varepsilon$ to produce a detectable velocity increment $\Delta\dot{\theta}_i$. We now assume as a first approximation that the increment $\Delta\varepsilon$ is the same for all animals. The increase of velocity input $\Delta\dot{\theta}_i$ necessary to cause such a threshold variation $\Delta\varepsilon$ is then the resolvable element of the system. We must try to determine how the magnitude of $\Delta\dot{\theta}_i$ necessary to produce a deflection $\Delta\varepsilon$ of the cupula varies as a function of the dimensions of the canals and the weight of animals.

The solution of Equation (1) for a region within the bandwidth of canal response gives:

$$\Delta\theta_e \propto \frac{\Delta\dot{\theta}_i}{L} \, , \tag{39}$$

where $\Delta\theta_e$ is an incremental displacement of the endolymph.

Since, from Equation (5),

$$L \propto \frac{1}{r^2} \, ,$$

we have

$$\Delta\theta_e \propto \Delta\dot{\theta}_i r^2 \, , \tag{40}$$

The increment of volume $\Delta V$ of endolymph delivered to the cupula for an incremental displacement of endolymph $\Delta\theta_e$ is expressed by

$$\Delta V \propto \Delta\theta_e Rr^2 \propto \Delta\dot{\theta}_i Rr^4 \quad . \tag{41}$$

The cupula deflection $\Delta\varepsilon$ is then

$$\Delta\varepsilon \propto \frac{\Delta V}{V} \propto \frac{\Delta\dot{\theta}_i Rr^4}{V} \quad , \tag{42}$$

where $V$ is the volume of the ampulla.

We then have

$$\Delta\dot{\theta}_i \propto \frac{V}{Rr^4} \quad , \tag{43}$$

and, since $\Delta\varepsilon$ is assumed to be a constant for all animals with, from Equation (6),

$$f_u \propto \frac{1}{r^2} \quad , $$

we can also write

$$\Delta\dot{\theta}_i \propto f_u \frac{V}{Rr^2} \quad . \tag{44}$$

If we take $V \propto Rr^2$ as found to be approximately true empirically by Jones and Spells, we have

$$\Delta\dot{\theta}_i \propto f_u \quad . \tag{45}$$

We next assume that the amplitude of oscillation of head angular movement A is the same for all animals so that we can write

$$\dot{\theta}_{i\ max} \propto A\omega_{max} \propto f_u \quad . \tag{46}$$

The number n of resolvable elements is then

$$n = \frac{\dot{\theta}_{i\ max}}{\Delta\dot{\theta}_i} \propto \frac{f_u}{f_u} \quad , \text{a constant.} \tag{47}$$

The information rate is then

$$\dot{n} f_u \simeq f_u \; . \tag{48}$$

Under previous assumption we conclude therefore,

1. From Equation (45) that the size of a resolvable element increases in direct proportion with the maximum frequency of head oscillation, and therefore that the sensitivity to velocity is greater for a large animal than for a small animal.

2. From Equation (47) that the number of resolvable elements or the dynamic range is the same for all animals.

3. From Equation (48) that the information rate increases with the frequency and therefore with a reduction of animal size.

Conclusion 1 appears reasonable. It indicates that the resolution or sensitivity of the head angular velocity becomes greater as the weight of the animal increases. Jones and Spells had come to a similar conclusion. Conclusion 2, however, is questionable. It would seem that the dynamic range should increase with the size of animals. The problem seems to be with the assumption that the same incremental cupula deflection corresponds to a resolvable element of velocity in all animals. This would not be the case if a greater number of sensory elements were present in the crista of larger animals. If we assume for the sake of illustration that the number of sensory cells increases in direct ratio to ampulla volume, and that because of random stimulation the size of a resolvable element is inversely proportional to the square root of the number of cells, we would have, with Jones and Spells' findings that $V \propto r^2 R$ approximately, from Equation (43),

$$\Delta\dot{\theta}_1 \propto \frac{1}{r \sqrt[3]{R}} \; , \tag{49}$$

from Equation (47),

$$n \propto \sqrt{Rr^2} \quad , \text{ and} \tag{50}$$

from Equation (48)

$$\dot{n} \propto \sqrt{\frac{R}{r^2}} \quad . \tag{51}$$

Or, retaining the volume V of the ampulla in the equations,

$$\Delta\dot{\theta}_1 \propto \frac{\sqrt{V}}{Rr^4} \quad , \tag{52}$$

$$n \propto \frac{1}{\sqrt{V}} \quad , $$

and

$$\dot{n} \propto \sqrt{\frac{R}{r}} \quad . \tag{54}$$

It would be interesting to determine histologically whether or not there is an increase of sensory cells in the cristae of larger animals. The determination of the meaningful information rate in a bundle of fibers must await more detailed knowledge of the mechanism of excitation of individual cells and the organization of the resulting action potentials in ganglions and terminal points in the CNS. Equation (51) gives a somewhat greater information rate in the case of smaller animals. The higher frequency of motion appears to over-compensate for the lower resolution.

SUMMARY

On the basis of certain specified assumptions, relations were obtained between canal dimensions, resolution, dynamic range and information rate of the canal system. The analysis shows an increased velocity resolution and dynamic range for larger animals. It appears that a variable number of sensory cells must be included in the adjustable functional parameters of the canals.

## THE SEMICIRCULAR CANALS OF FISH

Jones and Spells point out that the dimensions of r and R for fish are relative-ly large compared to those of mammals. The contrast of these dimensions is shown in Table II, together with computation of relative values of $f_u$, $f_\ell$, $\Delta\dot{\theta}_i$, n, and $\dot{n}$ in fish and mammals of the same weight.

TABLE II - COMPUTATION OF RELATIVE VALUES OF SEMICIRCULAR CANAL CHARACTERISTICS ACCORDING TO FORMULAS DERIVED IN TEXT

(Dimensions of canals from Jones and Spells)

| Animal class | r (mm) | R (mm) | $f_u$ | $f_\ell$ | $\Delta\dot{\theta}_i$ | n | $\dot{n}$ |
|---|---|---|---|---|---|---|---|
| Mammals | 0.12 | 2.3 | 100 | 1 | 100 | 100 | 100 |
| Fish | 0.23 | 5.9 | 27 | 0.27 | 9 | 310 | 83 |

Experimental data as given in Table I show. that the canals of a ray with a weight one-seventh that of man has a time constant three and one-half times greater. The dimensions of the canals and the experimental data show that both $f_u$ and $f_\ell$ are much lower for fish than for mammals, while the velocity resolution and the dynamic range are much greater for fish than mammals. It is easy to visualize why this should be so.

The head of the fish is fixed to the body without a connecting neck; the rotation of the head can only take place with a rotation of the body. The preceding analysis of head movements is therefore not applicable. There is nothing in the turning of a fish which corresponds to a turning movement of the head or the body. The fish must have forward motion in order to turn, and in this characteristic it resembles a ship, an airplane, or an automobile. There may be small restoring rolling moments when the fish is stationary, but these appear rather inconsequential. The fish applies the bulk of its power to gain

forward motion and then needs to exercise only small control forces to effect a turn. The angular speed of the turn depends on the linear velocity of the fish as it enters the turn, the amount of control forces that can be exercised, and is limited by fluid dynamic considerations such as the stalling of control surfaces under excessive lift, and probably by stresses on the body and control surfaces. There is no correspondence between this situation and that of a mammal where estimated muscle power and moment of inertia determine a frequency of oscillation. It is easy to see why Jones and Spells found no statistically significant relations between canal dimensions and the mass of fish.

In a previous report[12] we considered a leap over a ditch as a typical body movement requiring vestibular data in the case of man. In the case of a fish a more typical movement would be a pursuit maneuver in attacking another fish, or an evasive one while under attack. These maneuvers find a parallel in missile or airplane controls. They require an accurate measurement of very small variations of velocity over relatively long periods of time. This, in turn, calls for a low $f_\ell$, high resolution, and dynamic range. Table II indicates that these requirements are met by the canals of fish. The relative size of the canals for mammals and fish is one of the best illustrations of the match of these sensors to biological systems. It may be noted that the above discussion applies also in some degree to birds as their canals have larger dimensions than mammals of the same weight. It is found, for instance, that the time constant and therefore the low corner frequency of the canals of pigeons are similar to those of man. The difference is less, however, for birds than for fish because birds must be adapted for movements on the ground as well as for flight, and their maneuvering in the air probably calls for higher rate of turn than for fish in the water.

## DISCUSSION AND CONCLUSIONS

The present investigation, as far as it goes, confirms the broad findings of Jones and Spells[10] regarding the matching of the semicircular canals to the requirements of various species. While Jones and Spells considered mainly two adaptable characteristics of the canals – maximum head angular velocity and sensitivity – we considered here five such characteristics: high limit of frequency response, low limit of frequency response, resolution, dynamic range, and information rate. We found, also, that five adjustable parameters may be required to provide an adequate flexibility of adaptation to various species. These parameters were said to include: the internal diameter of the canal, the radius of its curvature, the volume of the ampulla, the stiffness of the cupula, and the number of sensory cells in the crista. The various schemes possible to extend the linear dynamic range may also be included. The next step in the investigation should be one of experimental measurement of body movement, canal characteristics, canal dimensions, and attempted correlation of the data for specific animals. While the assumptions made in the computations may not hold when such data are available, it is hoped that the computations may have provided some objectivity to the discussion.

The manner in which the functional parameters of the canals may be adjusted to achieve a certain performance may be illustrated by visualizing how a similar problem would be handled in an engineering organization. A system group would specify the desired characteristics $f_u$, $f_\ell$, $\Delta\dot{\theta}_i$, n and $\dot{n}$ to a design engineer. The latter would set down the equations for the first three independent characteristics as follows.

$$f_u = c_1 \ \frac{1}{r^2} , \tag{55}$$

$$f_\ell = c_2 \ \frac{Mr^4}{RV^2} , \tag{56}$$

$$\Delta\dot{\theta}_i = c_3 \ \frac{\sqrt{V}}{Rr^4} , \tag{57}$$

where the constant of proportionality would have been established. He would first select $r^2$ from Equation (55) to give the desired $f_u$ and would substitute the values in Equations (56) and (57) giving,

$$f_\ell = c_4 \ \frac{M}{RV^2} \ ,$$

(58)

$$\Delta\dot\theta_i = c_5 \ \frac{V}{R} \ .$$

(59)

From Equation (59) he would obtain, since $\Delta\dot\theta_i$ is known,

$$V^2 = c_6 \ R^2 \ .$$

(60)

Substituting in Equation (58) would give

$$\frac{M}{R^3} = c_7 \ ,$$

(61)

since $f_\ell$ is also specified. Suitable values could then be selected on the basis of good design practice based on past experience. It would then be possible to compute V from Equation (59). A check would then be made regarding the number of fibers to be provided and of the linearity of the system within the desired dynamic range n. Some schemes may have to be provided to extend the range. It may be found, also, that the specified characteristics could not be met and a readjustment of requirements, including over-all performance, may have to be made.

All of this is fairly straight-forward. The more difficult portion of the job would be in the specifications of canal characteristics to achieve good match of the canals to other body characteristics such as power available in muscles, body inertia, information handling capacity of central processes, and of muscle control, resolution of time, resolution of force and of position sensing, etc., not forgetting, of course, the expected body environment. None of these elements can be assumed to be fixed. They are all adjustable to achieve an over-all match.

The expectation that components of a biological system are matched is at the root of the motivation to undertake investigations such as the present one. It originates from an assumption of efficient design and economy in the configurations of nature.

An overdesigned component in a system is wasteful in that its performance is lmted to that of other components. An underdesigned component is also wasteful as it limits the performance of all other components. But the most remarkable match of all is that of reason to the understanding of the work of nature. This trait of reason is not entirely irrelevant to our major objective of developing a theory of motion sickness as will be indicated in subsequent reports.

In the history of human thought and experience three agencies have been either proposed or observed to produce matched designs: God, evolution, and an engineering organization. It does not seem inappropriate to examine conceptually, as we have done here, how the one agency open to our examination would have undertaken the design of the simpler portion of one of nature's complex creations.

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