A GENERALIZED TRANSFER FUNCTION FOR DESCRIBING MECHANONEURAL SE--ETC(11)

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subsequently, movement of the head. Fluorens established many vestibular physiologists. In order to describe the dynamics of the semicircular canal system, Steinhausen's hypothesis from those which describe other phenomena such as "adaptation":

**INTRODUCTION**

Rotational head movements stimulate the sensory and motoric of the semicircular canals of the inner ear, causing compensatory eye movements (nystagmus), appropriate to the plane of rotation, via a vestibular reflex arc. However, the sensory epithelium of the semicircular canals, the cristae ampullares, are relatively inaccessible for direct functional study during normal physiological head movements. In the first place, they lie deep within the skull, enclosed by synovial and perineural sheath and the meninges. Secondly, any technique which exposes the hair cells of their nerve supply for neurobiological experimentation necessarily disrupts the vascular supply to the neuroepithelium and interferes with the ionic balance between the perilymph and endolymph. Thirdly, even when the neuroepithelial area is exposed, it is difficult to perceive the extent to which the normally invisible cupula covers the cristae and fills the ampulla of the duct. (It is the cupula which couples the mechanical energy of head motion to the receptor hair cells of the crista for transmission into neural impulses at the afferent terminals.) Thus, it is not surprising that, for over a century, the dynamic response characteristics of the semicircular canals have not been completely elucidated despite continuous investigation by many vestibular physiologists.

Historically, until the time of Fluorens (11), the semicircular canals were associated with the perception of sound. By sectioning the membranous semicircular canals in the pigeon and the rabbit, Fluorens established that eye, head, and body movements always occur in the same plane as that of the tilted canals. Votsis (16), also investigating the pigeons, first associated these canals with bodily equilibrium. Breuer (5), from Brown (9), and Mach (6) suggested that the cristae ampullares respond to rotational accelerations of the head. Moreover, they also hypothesized that the motion of the endolymph within the canal was responsible for exciting the neural activity in the nerve endings (hydrodynamic theory). (Mach, however, later appears to have favored a hydraulic theory, i.e., the pressure in the adequate stimulus--see refs. 14, 28.) Ewald (ii), using an "hydraulic hammer", produced artificial endolymphatic movements in the canals of pigeons and demonstrated that the direction of head movements was dependent upon the direction of endolymph flow. Ewald's "law" was placed on a firmer footing when Lewenstein and Sand (7) established that the action-potential (spiral) frequency in fibers innervating the cristae varied according to the direction of angular movement of the head.

In order to describe the dynamics of the semicircular-canal system, Steinhausen (16, 17), and, subsequently, Edmond, Green and Jones (10), proposed the so-called torsion-pendulum model. In this model, the instantaneous angular deflection of the cupula, \( \Theta(t) \), caused by an instantaneous angular acceleration of the head, \( a(t) \), is governed by the linear differential equation

\[
\Theta(t) = \frac{1}{2} a(t) - \Theta(t) \frac{d}{dt}
\]

where \( \Theta(t) \) is the effective moment of inertia of the endolymph in the semicircular canal; \( a(t) \) is the linear acceleration of the head relative to the wall of the semicircular canal; \( \Theta(t) \) is the elastic-restoring moment per unit angular displacement of the endolymph relative to the semicircular canal; and \( \Theta(t) \) is a constant of proportionality relating endolymphic displacements between the cupula and the canal endolymph. The transfer function of Eq. (1) can be written as
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The head plane was coincident with the plane of rotation (10). The tape recorder was used to trigger a physiological signal analyzer (Nicolet Instruments Inc.) to count and store the taped, entrained action potentials in preselected appropriate time periods (bins) for up to 5046 sequential bins (see Fig. 1 for typical binned response). Fourier techniques were used on the binned neural data to obtain the magnitude of the peak amplitude of the response and the temporal (phase) relationship between the angular acceleratory stimulus and the fundamental component of the neural response.

Amplitude- and phase-values were used in a curve-fitting program on a PDP-11/40 minicomputer (Digital Equipment Corp.) to provide a distinct mathematical expression for the best-fitting transfer function for a linear system. (The steady-state frequency response for a linear system to a sinusoidal input angular acceleration may be found from axial,

\[ |G(f)| = |\text{Re} \{G(f)\}^2 + |\text{Im} \{G(f)\}|^2 \],

and phase,

\[ \phi(f) = \tan^{-1} \left( \frac{\text{Im} \{G(f)\}}{\text{Re} \{G(f)\}} \right) \],

spectra [pole plots—see ref. 36], where \( \text{Re} \{G(f)\} \) and \( \text{Im} \{G(f)\} \) are the real and imaginary parts of \( G(f) \), respectively.)

The method employs techniques in non-linear, least squares approximations and is applicable to both high- and low-order transfer functions (4). In the final interpolation in the program, the least squares error, LSE, of the best-fitting transfer function is obtained as

\[ \text{LSE} = \| Y - X \| \]

where \( Y \) is a residuals matrix \( (Y^T) \) transpose of \( Y \) which is made up of error terms that express the differences between the experimental data and the model which is to be fitted. The mean square error,

\[ \text{MSE} = \text{LSE}/(2L - 8) \],

compares the goodness-of-fit of the derived transfer function to that of the experimental data \( (2L - 8) \) number of real and imaginary components of the data points, and \( 8 \) number of parameters in the transfer function.

A more detailed description of the methodology may be found in a special monograph (7) and elsewhere (6, 21).

RESULTS AND DISCUSSION

The simplest transfer function that fitted the data for all units is of the form,
CV = \frac{\text{mean} - \text{median}}{\text{median}}

(8)

where \( \sigma \) is the standard deviation of the units' response time intervals, \( \mu \) is the mean time interval, and \( k \) is a gain constant with units in impulse/s. The ratio \( CV \) has previously been defined as the transfer function of the adaptation operator (27, 28). The coefficient of variation, CV, was determined as the ratio of the standard deviation of intervals \( k = M \beta \left( \sum_{i=1}^{n} \frac{1}{i} \right) \)

(9)

where \( k \) and \( \beta \) are constants, \( M = 1 \) in theory, but finite when fitting Eq. (10) via a digital computer, and \( i = 1 \) and \( i = 2 \) are time constants (14). Interestingly, when \( M = 1 \), Eq. (10) becomes

\[
\frac{\text{CV}}{\text{CV}_{\text{pure}}} = \frac{1}{1 + \text{CV}_{\text{pure}}}
\]

(10)

which has previously been defined as the transfer function of the adaptation operator (27, 40). Thus, \( \text{CV} \) appears to be a form of adaptation. A work by Thorson and Hiedeman-Thorson (39) suggests that \( \text{CV} \) represents a distributed relaxation process which is inherent in the sensory-adaptation mechanics of limulus photoreceptors, vertebrate retinal receptors, chemoreceptors, and other mechanoreceptors. Investigations by Taglietti, Nussi, and Cassella (8) further suggest that \( \text{CV} \) likely represents a relaxation phenomenon consisting of a time-varying intracellular electrogenic process, the components of which are summed with the generator potential in the receptor hair cell.

The coefficient of variation, \( CV \), was determined as the ratio of the standard deviation of intervals to the mean interval, as obtained from interframe-interval distributions of spontaneous single-unit activity. When a regression of \( CV \) on \( k \) was made for 78 units, a statistically-significant product-moment correlation \( (r = 0.22, P = 0.05) \) was obtained (21). Thus, the larger the \( CV \), the larger the value of \( k \) and, consequently, the amount of adaptation. Other work by Goldberg and Fernandez (15), in squirrel monkeys, shows that the \( CV \) is statistically correlated with semicircular-canal afferent fiber conduction rates. The thicker fibers have faster conduction rates and larger \( CV \). Together, these findings suggest that sensory adaptation phenomena are directly dependent on the innervation pattern of the afferent fibers.

The transfer function, \( G'(s) \), differs also from that of \( G'(s) \) in that \( k \) is not single-valued as it is in the torsion-pendulum model; rather, it is unit dependent, taking on values from \( k \approx 4.65 \) to 22.17 as seen in Fig. 4B (10). The stress between \( k \) and \( v \), would account for none of the five-fold range of values that were determined for \( k \). However, there is sufficient indication from other studies (13) that the response dynamics of nodal groups of contiguous hair cells are quite different from those of other groups. Realizing that the hair-cell tufts are stiff (14), that their lengths vary according to their position on the sensory epithelium (crista) (22), that the number and thickness of the stereocilia can be variable (23), and that the mechanical properties of the cupula are not necessarily uniform across the crista (29), then it is plausible that \( v \) could have a regional distribution.

The form

\[
G(s) = \frac{C_k}{(1 + s)(1 + s)}
\]

(12)

was fitted to published afferent-response data in the squirrel monkey (Saimiri sciureus) (12), the frog (Rana esculenta and R. temporaria) (1), the nevilia (Orelia auriculata) (33), and the guitarfish (Myliobatis antarcticus) (33). The parameter \( k \) is high frequency time constant which results from both the displacement and the rate of displacement of the cupula. Such a term has been obtained from analysis of vestibular-driven eye movements in man (Beenen and Sternfeld, cited in ref. 1), and primary afferent (1) responses in the squirrel monkey (12) and the electric eel fish (26). Table 1 lists \( k \), \( k_{1,2} \), \( t_1 \), and \( t_2 \) for these four species and for unit responses to white-noise stimuli obtained from pigeons that were primarily enucleate isochromatic. For all species listed in Table 1, the MSE using Eqs. (12) or (11) was comparable to or smaller than that obtained with other models. Further details are given elsewhere (8).
TABLE 1: Parameters of a linear relationship (Eqs. (1), (11)) describing semicircular-vestibular dynamics in five species.

<table>
<thead>
<tr>
<th>Species</th>
<th>m</th>
<th>n</th>
<th>Frequency range, ( f ) (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Squirrel monkey</td>
<td>1.0</td>
<td>1.0</td>
<td>0.015-0.5</td>
</tr>
<tr>
<td>Gerbil</td>
<td>1.0</td>
<td>1.0</td>
<td>0.015-0.5</td>
</tr>
<tr>
<td>Frog</td>
<td>1.0</td>
<td>1.0</td>
<td>0.015-0.5</td>
</tr>
<tr>
<td>Guitarfish</td>
<td>1.0</td>
<td>1.0</td>
<td>0.015-0.5</td>
</tr>
<tr>
<td>Pigeon</td>
<td>1.0</td>
<td>1.0</td>
<td>0.015-0.5</td>
</tr>
</tbody>
</table>

In Table 1, the frequency range of 0.015-0.5 Hz is restricted in the frog and guitarfish to utilize an adequate value of \( m \). In accordance with the biophysical properties of the membranous vestibular receptors and the dimensions of the pertinent anatomical features of the membranous vestibular receptors, Hartmann and colleagues have found that there should be an upper break frequency at \( f > 0.5 \text{ Hz} \) for semicircular-vestibular dynamics in semicircular-vestibular afferents. Regarding the frequency range up to 0.5 Hz, Hartmann and colleagues have found in the same range as those determined empirically for \( 0.015 \text{ Hz} \).

REFERENCES


Fig. 1. Typical binned neural response. Bin widths are 0.0, (for $f = 0.01$ Hz), 0.1 (for $f = 0.05$ to 0.5 Hz), 0.05 (for $f = 1.0$ Hz), and 0.01 s (for $f = 5$ Hz).
Fig. 2. Node plot of Unit 3170 re angular acceleration and fits of models to data.

Fig. 1. Node plot of Unit 3170 re angular acceleration and fits of models to data.
Fig. 4. Bode plot of Unit 92270 for angular acceleration and fits of models to data.

Fig. 5. Bode plot of Unit 102269 for angular acceleration and fits of models to data.