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PROGRESS TOWARD A MULTIPLE INPUT MODEL OF THE VESTIBULO-OCULAR REFLEX*

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Abstract

Preliminary results of a multiple input model to describe the vestibulo-ocular reflex (VOR) during low frequency (0.01 – 0.08 Hz) sinusoidal pitch in cats are reported. A weighted sum of sinusoidal angular velocity and two jerk functions derived from the changing orientation of the animals with respect to gravity fits the major aspects of the experimental data. This indicates that the brain derives eye movement commands from a linear combination of these inputs. Several questions remain before the model can be finalized, but it provides the most complete description to date of the VOR during sinusoidal pitch.

INTRODUCTION

The function of the vestibulo-ocular reflex (VOR) is to stabilize visual fixation on a target of interest during head movements. Linear and angular accelerations of the head are detected by ten receptors, six semicircular canals and four otoliths, located in the inner ears. The semicircular canals are overdamped, fluid-filled toroids which function as integrating angular accelerometers. Three canals are arranged on nearly orthogonal planes in each inner ear. The four otoliths, two utricles and two saccules act as overdamped, three-dimensional, linear accelerometers. The utricles are primarily oriented in horizontal planes while the saccules are oriented vertically in parasagittal planes through the ears. Neural signals from these ten receptors are processed in the brainstem and used to drive the extraocular muscles.

Quantitative models of the VOR have been derived for yaw head rotations about an earth-vertical axis (*e.g.*, [1]). These are single input – single output (SISO) models and have achieved considerable success because this type of head movement generates only one input (yaw angular acceleration) and one output (horizontal eye angular velocity). Other SISO models have been developed to relate horizontal eye responses to side-to-side, sinusoidal, linear accelerations of subjects seated on a sled [2]. Again, they are valid representations of the experimental data because the stimulus consists of a single input and generates a single output. However, these models are limited in their application and attempts to use them in other conditions (*e.g.*, yaw rotations about an off-vertical axis, pitch, or roll) have been unsuccessful because they do not account for all of the stimuli which the vestibular sensors receive. For example, pitch and roll stimulate the canals, as expected, as well as the otoliths because the attitude of the head changes with respect to gravity. Off-vertical axis rotations and Coriolis accelerations also generate combinations of linear and angular accelerations. An increasing amount of experimental data are being collected using such stimuli [3-5], necessitating the development of a multiple input model to explain the results.

The ultimate goal of the present study is to develop a model which can describe reflexive eye movement responses to head motion in all linear and angular dimensions. This generalized model must have multiple inputs and multiple outputs. However, very little is known about how linear and angular signals are combined in the brainstem to produce eye movements. Therefore, as a first step, low frequency (0.01 – 0.08 Hz) sinusoidal head pitch was used as a stimulus. This simultaneously produced angular stimulation to the vertical canals and linear stimulation to the otoliths as the position of the animals' heads changed with respect to gravity. Preliminary results of a multiple input – single output model are reported here. (Note: Only vertical eye movements are generated.) This model is limited to head pitch only, but provides quantitative information about the interaction of linear and angular signals in the brain.

METHODS

Data Collection

The experimental data used here were originally collected for work reported in Tomko, *et al*. [5] and only a brief description of the data collection will be given here.

Two adult cats used as subjects were trained to accept passive restraint in an animal holder mounted to a rate table (Model 824, Contraves-Goertz, Pittsburgh, PA). The animals were sinusoidally pitched at an amplitude of 50 deg/sec over the frequency range of 0.01 – 4.0 Hz. The frequencies of interest here were those less than or equal to 0.08 Hz where angular excursion of the table was at least ± 90 degrees. This gave a strong linear stimulus due to gravity as the animals tumbled head-over-heels. Eye movements were recorded with silver/silver chloride electrodes implanted about the bony orbits of the cats. Digitized eye position data were processed by a standard algorithm which gave slow component eye velocity as its output [6]. Eye movements induced by vestibular stimulation have two components, a slow component which responds to the stimulus and a fast component which "resets" the eyes when they reach some internally-determined limit of excursion. The algorithm removes these fast components leaving only eye movements which are a direct result of the stimulus. The modelling which follows used the slow component of eye velocity.

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Derivation of Model Equations

A general form of the equation of motion of the otoliths may be written as:

$$J\ddot{x} + B\dot{x} + Kx = F \tag{1}$$

where

x = relative displacement of the otoconial mass with respect to the skull
F = effective gravitational force on the otoconia
J, B, K = effective inertial, viscous, and stiffness coefficients

The force, F, represents the force acting on the otoconial mass, m, due to the linear acceleration of gravity, a, *i.e.*, F = ma. Although the otoconial mass is not known specifically, the linear equation of motion permits the acceleration of gravity to be used as the forcing function.

The specific values of the coefficients are the subject of some debate because they cannot be measured directly and experimental results have been somewhat contradictory [7]. Nevertheless, it is known that one population of otolithic neurons fire in proportion to the displacement of the otoconial mass and a second population fire in proportion to its velocity [8]. The firing rates of the first group of neurons (known as Type 1, tonic, or regular neurons) can be determined by solving equation (1) for x, given a specific acceleration input.

The derivative of equation (1) is

$$J\ddot{v} + B\dot{v} + Kv = \dot{F} \tag{2}$$

where

$v = \dot{x}$ = relative velocity of otoconial mass
$\dot{F}$ = time rate of change of effective force on otoconia
J, B, K same as equation (1)

The forcing function, F, is equal to the product of the otoconial mass, m, and the linear jerk, j, arising from changing the orientation of the head relative to gravity. As with equation (1), the otoconial mass is not known. Thus, jerk is used as the input. Equation (2) can be solved for v giving the firing rates of the second group of neurons (Type 2, phasic, or irregular) to a specific jerk input. Therefore, tonic and phasic neurons reflect linear acceleration and jerk inputs, respectively, with their dynamic responses determined by the coefficients of equations (1) and (2).

The acceleration and jerk inputs to the utricles and saccules were calculated from the diagrams in Figure 1. Otoliths respond to shear accelerations and jerks of the otoconial mass with respect to the skull. The shear acceleration of the utricles is g sin H, where H is the angular head position (equation (3)) obtained by integrating the pitch stimulus (equation (4)).

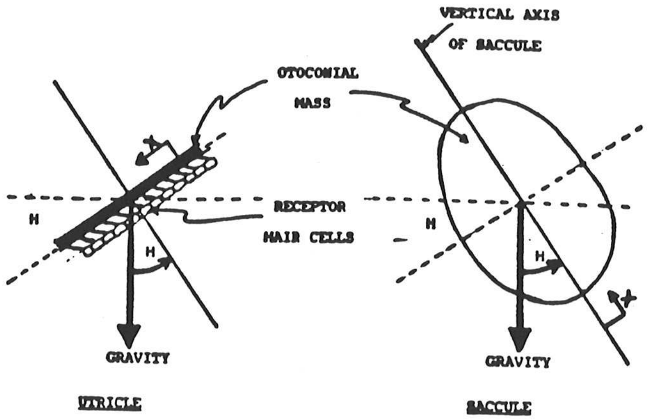

Figure 1. Lateral View of Otoliths with Head Pitched at an Angle H with Respect to Horizontal.

$$H = -\frac{A}{\omega}\cos(\omega t) \tag{3}$$

$$\dot{H} = A\sin(\omega t) \tag{4}$$

Thus, the utricle acceleration input, a_u, and its derivative, j_u, are

$$a_u = g\sin[-\frac{A}{\omega}\cos(\omega t)] \tag{5}$$

and

$$j_u = g\,A\sin(\omega t)\cos[-\frac{A}{\omega}\cos(\omega t)] \tag{6}$$

For the saccules, the gravity vector rotates in the planes of their otoconial masses. However, vertical eye movements result only from the component of the shear acceleration or jerk input along the vertical axis of the saccules. The horizontal component causes convergence or divergence of the eyes as if moving toward or away from an object, so it does not contribute to vertical eye movements. In addition, neurophysiological evidence indicates that the saccules are most sensitive to motion in the vertical direction [9]. Therefore, the saccule acceleration input, a_s, was taken to be g cos H. From equation (3),

$$a_s = g\cos[-\frac{A}{\omega}\cos(\omega t)] \tag{7}$$

Differentiating,

$$j_s = -g\,A\sin(\omega t)\cos[-\frac{A}{\omega}\cos(\omega t)] \tag{8}$$

where j_s is the saccule jerk input.

The five possible signals reaching the brainstem are the acceleration and jerk inputs to of the otoliths, equations (5) – (8), and the angular velocity of the skull, equation (4), derived from the vertical canals.

RESULTS/DISCUSSION

Although not fully quantitative, the results reflect the characteristics of the experimental data. Several possible interactions between the inputs (*e.g.*, linear, nonlinear, sums, differences, etc.) were considered, particularly because the acceleration and jerk inputs are such unusual functions.

It was realized that the influence of the two acceleration functions was small at best. Benson [10] attempted to fit acceleration inputs to similar sinusoidal data but his results do not support such a fit. Also, during pitch, acceleration inputs are translated into a signal representing instantaneous attitude of the head with respect to gravity. Jerk inputs are translated into a signal representing head velocity. Such a position signal might be expected to be insignificant compared to the angular and linear velocity signals because the function of the VOR is to stabilize visual images during head movement.

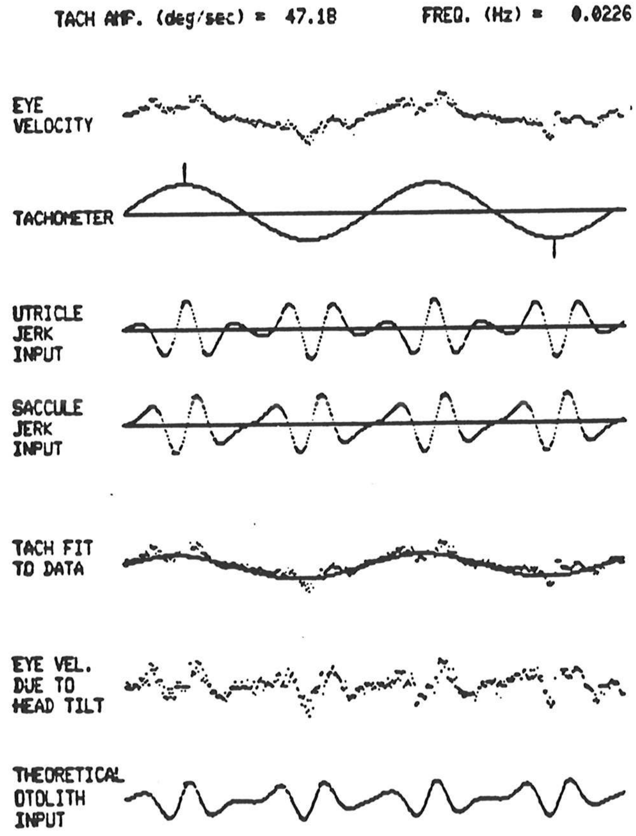

Figure 2. Experimental Eye Velocity Data and Fits of Multiple Input Model (See Text for Details).

An example of the results is shown in Figure 2. The first line contains slow component eye velocity data. Next is the rate table tachometer trace followed by the utricule jerk and saccule jerk inputs. The fifth line shows a least squares fit of the tachometer to the data. Line 6 is the eye velocity data after subtracting the sinusoidal fit of the fifth line. The tachometer fit was subtracted to remove the eye velocity due to the angular input from the remaining linear influence. Therefore, line 6 is the eye velocity generated by the changing attitude of the head with respect to gravity. The last line is a weighted sum of the utricle and saccule jerks fit by eye to the data of line 6. Similar results were obtained for data from 0.01 – 0.08 Hz. The close agreement between the last two lines demonstrates the limited influence of the acceleration inputs.

It would appear, then, that a linear combination of an angular velocity signal from the canals and linear velocity signals from the otoliths drives the eyes during head pitch. Several questions about the angular velocity response must be addressed. The angular eye velocity has a higher gain and less phase lead than expected from the dynamics of the canal response alone at the frequencies used here. Simulations with linear combinations of equations (4), (6), and (8) show that the jerk functions have little effect on the gain or phase of the angular sinusoid. That is, the gain and phase of equation (4) are preserved in the sum. The improved response may be due to enhancement by central neural mechanisms or to an additional, unidentified, peripheral response.

CONCLUSION

The preliminary results are encouraging and suggest a more detailed development of the multiple input model. Dynamic response properties of the canals and otoliths will have to be considered more fully as will several questions about the processing of the inputs in the brainstem. However, the finding that a linear combination of angular velocity and linear jerk inputs can account for the major aspects of these data indicates that it should be possible to extend the emerging model to one which is applicable for all head movements.

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