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MATHEMATICAL MODEL FOR INTERACTION OF CANALS AND OTOLITHS IN PERCEPTION OF ORIENTATION, TRANSLATION, AND ROTATION

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ABSTRACT

A computer model with six degrees of freedom was developed in which linear acceleration along each axis is detected and directed along two channels. Output of one channel is perceived as a signal that was generated by gravity, produces no perception of translation, and is used to determine body orientation with respect to earth-vertical. Output of the other channel is perceived as a signal generated by transient linear acceleration and produces a perception of translational motion. Attenuation of signals in these channels is controlled by computations that compare the angular velocity signal generated by the canals with the angular velocity of the input linear acceleration vector. The difference between these velocities serves as an error signal that increases the attenuation of the orientation channel and decreases the attenuation of the translation channel. Orientation channel outputs attenuate orthogonal canal signals that provide angular sensation and ocular reflexes. The model computes the following results that are consistent with empirical data reported in the literature: (1) For off-vertical rotation: bias and modulation components of nystagmus, faster decay of postrotatory nystagmus, attenuation of postrotatory turning sensations, and perceived conical translation; (2) For pendular centrifuge: vertical ascent and tumbling during deceleration; (3) For non pendular centrifuge: delay in perception of roll: and (4) For passive roll: no delay in perception.

INTRODUCTION

Off-vertical rotation experiments (6,8,12) indicated that gravity which normally does not induce a perception of motion was converted into a linear acceleration that did induce a perception of motion. Those experiments indicated separate channels for orientation and translation accelerations. Data passing through the orientation channels determined orientation with respect to the earth's gravity and did not induce a perception of translation. Data through the translation channels induced a perception of translation.

Centrifuge experiments (4,7) in which subjects were fixed upright and indicated perception of vertical as the centripetal acceleration increased showed that perception of the gravito-inertial resultant was delayed. The exponential delay had a time course similar to the exponential decay of postrotatory nystagmus (2,3). Those experiments indicated that the angular acceleration of the centrifuge produced a Z-axis canal output that attenuated the flow of centripetal acceleration data through the Y-axis orientation channels.

Off-vertical rotation experiments in which continuous horizontal nystagmus correlated with rotation rate (1-3,5,16-18) indicated that the vestibular processing system derived rotation data from the changing direction of input linear acceleration vectors. Increasing perception of linear translation (12) and increasing amplitude of the nystagmus modulation component (1,16,5) as the off-vertical rotation rate increased indicated that rotation data derived from changing linear acceleration vectors reduced data flow through the orientation channels and increased data flow through the translation channels.

Experiments in which subjects indicated perception of vertical while being passively rolled (15) showed no delay in perception. Accurate perception of passive roll indicated that agreement between rotation data from the canal angular accelerometers and rotation data derived from changing linear acceleration vectors attenuated data flow through the translation channels and enhanced data flow through the orientation channels. Decreased time constants for decaying nystagmus and decaying sensation of rotation during the postrotatory phase of off-vertical rotation (1-3) indicated that data from orientation channels attenuated the effects of angular rotation data from the orthogonal canals.

These interactions between canal and otolith data were simulated with a mathematical and computer model that processed linear and angular acceleration input data to produce outputs that conceivably account for the experimental results. Perception and eye-movement data from these experiments determined the mathematical functions and their coefficients. The model represents a mathematical simulation of one possible method of data processing within the vestibular system. Results of this processing may serve as inputs to the visual, proprioceptive, or cognitive systems, but the model does not simulate data processing within those systems.

METHODS

The computer model was developed using simulation software (Extend, Imagine That, Inc., San Jose, CA) running on a Macintosh computer. Blocks and connections shown in Fig. 1 controlled the flow of data for the simulations. Nomenclature and mathematical conventions were in accordance with those established in reference (11). The programming language was structured like the "C" programming language. The symbol * denotes multiplication, ^ denotes exponentiation, and exp() returns the number e raised to the argument.

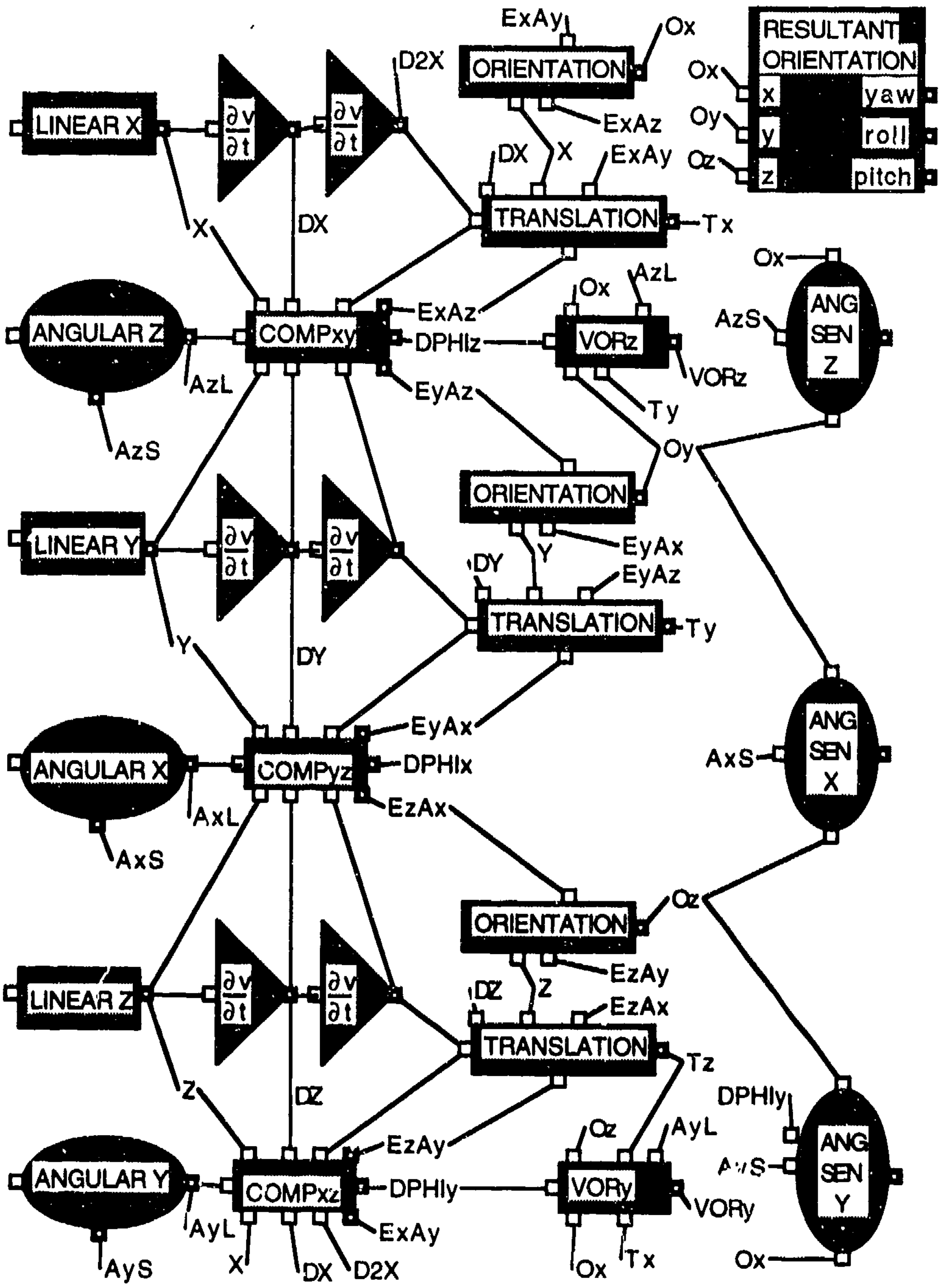

Figure 1. Blocks and connections that interact with the simulation software and control the flow of data in the model. Open squares on the edges on the blocks are inputs. The darker squares are outputs. Data flow is represented by a line drawn from an output to an input. Outputs connected to an abbreviated name transmit data to all inputs with the same name anywhere in the model. The angular and linear acceleration drivers used for simulating experimental inputs were connected to the appropriate linear and angular X, Y, and Z inputs shown on the left side of the figure. Graphic plotters were connected to outputs to observe the responses of the model to the acceleration inputs.

Nystagmus and turning sensation decay at different rates following postrotatory deceleration (3). These different decay rates are generated in the angular blocks for X, Y, and Z axes by using two equations that respond to the same angular acceleration input, but they have different time constants. The long time constants for the Y and Z axes were derived from postrotatory nystagmus data (2,3) and a review of canal dynamics (9). The long time constant for the X-axis was set equal to the Y-axis. The short time constants for the X, Y, and Z axes were derived form the post rotatory sensation times for rotation about these axes when they were vertical (2). These blocks have two outputs with a suffix L or S corresponding to the long and short time constants. The Extend software requires that input variable names contain "in" as a suffix and output variable names contain "out" as a suffix.

Equations for these blocks are:

For the ANGULAR X block:

```
AxLout=AxLout*exp(-deltaTime/7.2)+7.2*ALPHAin*(1-exp(-deltaTime/7.2));
AxSout=AxSout*exp(-deltaTime/3.3)+3.3*ALPHAin*(1-exp(-deltaTime/3.3));
```

For the ANGULAR Y block:

```
AyLout=AyLout*exp(-deltaTime/7.2)+7.2*ALPHAin*(1-exp(-deltaTime/7.2));
AySout=AySout*exp(-deltaTime/2.5)+2.5*ALPHAin*(1-exp(-deltaTime/2.5));
```

For the ANGULAR Z block:

```
AzLout=AzLout*exp(-deltaTime/16)+16*ALPHAin*(1-exp(-deltaTime/16));
AzSout=AzSout*exp(-deltaTime/5.5)+5.5*ALPHAin*(1-exp(-deltaTime/5.5));
```

The second term in each equation computes the change in angular velocity during the interval deltaTime in response to the angular acceleration ALPHAin. The variable deltaTime is the length of the simulation sampling interval in seconds. If the experimental input drivers were free of mathematical discontinuities, a sampling interval of 0.01 s was adequate for the experimental simulations used in this development. Coefficients for this term were set equal to the time constant so that stimuli in the normal physiological frequency range would produce outputs corresponding to velocity. The first term accumulates the incremental changes in velocity and decrements the output at a rate proportional to the accumulation. This term determines the decay rate of the output after the input acceleration returns to zero.

Time constants for response of the otolith linear acceleration transducers were assumed to be short compared to rates of change used in this development so the script for the LINEAR X, LINEAR Y, and LINEAR Z input blocks was: LinearOut=LinearIn. Outputs of these blocks were differentiated twice using blocks from the electronics library in the Extend software. The linear input and the derivatives were used in other blocks in which the first and second derivatives have the prefixes "D" and "D2," respectively.

The blocks labeled COMP, with a suffix, compared the angular velocity of the linear acceleration vector in the plane defined by the suffix with the output of the angular acceleration block orthogonal to the plane. The equations for the COMPxy block are:

```
DPHIzOUT=(Xin*DYin-Yin*DXin)/(Xin^2+Yin^2+0.000001);
ExAzOUT=realABS(DPHIzOUT*(1-exp(-20*SQRT(DXin^2+D2Xin^2)))+AzLin);
EyAzOUT=realABS(DPHIzOUT*(1-exp(-20*SQRT(DYin^2+D2Yin^2)))+AzLin);
if (currentTime<deltaTime) {DPHIZout=0; ExAzOUT=0; EyAzOUT=0;}
```

The DPHIzOUT function computes the angular velocity of the linear acceleration vector in the XY plane. The small constant in the denominator of the DPHIZout function prevents a discontinuity when both X and Y components are zero. The term AzLin is the angular velocity indicated by the output of the ANGULAR Z block. The long time constant output was used because the time constant for the exponential delay in perception of the gravito-inertial resultant (4,7) corresponded closely to the time constant for postrotatory nystagmus about the Z-axis (2,3). When the directions of DPHIz and AzLin are in agreement, the algebraic signs are opposite. The absolute value of their sum was used to compute the error signals, ExAzOUT and EyAzOUT. (The function realABS() returns the absolute value of the argument; sqrt() returns the square root of the argument.) If one of the linear components, for example Xin, was not changing in magnitude, the derivatives DXin and D2Xin would be zero, and the DPHIZout term would be zero in the error computation for ExAzOUT. The "if" statement prevents a discontinuity on the first simulation step (derivatives require values from the previous and current steps). Equations for the COMPyz and COMPxz blocks are similar to the COMPxy block and have corresponding variable names for axes in those planes.

All the ORIENTATION blocks have the following equations:

```
TotalError =sqrt(ErrorAin^2+ErrorBin^2);
ORIENTATIONout = LINEARin*EXP(-1.9*TotalError);
```

Each axis lies in two planes; therefore, the total error is the vector sum of error signals from each of the COMP blocks corresponding to these planes. The exponential factor varies from one to zero as the total error increases. Using a simulation of the gravito-inertial delay experiment (4,7), the coefficient 1.9 was adjusted until the computed roll closely matched the empirical data reported by Graybiel (7). In that experiment subjects were fixed upright facing tangentially on a centrifuge and indicated perceived vertical as the centrifuge accelerated and maintained constant velocity Fig.(2). Results of that experiment are shown as open squares in Fig. 2. The computed roll using the outputs of the Y and Z-axis orientation blocks is the dark solid line. The coefficient 1.9 was adjusted until the computed roll closely matched the perceived roll reported for that experiment (7). The computed roll was delayed by the slowly decaying error signal that originated in the ANGULAR Z block and attenuated the centripetal acceleration in the Y-axis ORIENTATION block.

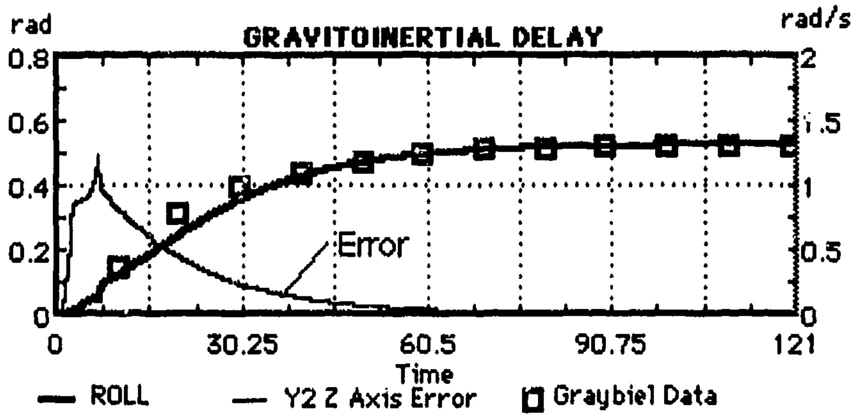

Figure 2. Roll output of the RESULTANT ORIENTATION block during simulations of the gravito-inertial experiment (4,7). Time is in seconds.

Equations for all the TRANSLATION blocks are:

```
TotalError=sqrt(ErrorAin^2+ErrorBin^2);
TRANSLATIONout=LINEARin*(1-exp(-1.9*TotalError))*(1-exp(-20*sqrt(D)));
if (currentTime <=2*deltaTime) {D=0;} Else D=DLinearIN^2+D2LinearIN^2;
```

The second factor in the translation function is the complement of the corresponding factor in the orientation block and varies from zero to one as the error signals increase. The coefficient 1.9 was set equal to the corresponding error coefficient in the ORIENTATION block so that the sum of the second factors in the two blocks always equals one. The third factor varies from zero to one as the derivatives increase. The coefficient of 20 was set high so that the sum of outputs from the ORIENTATION and TRANSLATION blocks would equal the linear input, except for very low frequency components of the linear input. More empirical data are needed to properly adjust this coefficient which determines the low frequency characteristics of this block:

The equations for the RESULTANT ORIENTATION block are:

```
YAWout= - ATAN2(OyIN,OxIN);
ROLLout= - ATAN2(-OyIN,OzIN);
PITCHout= - ATAN2(OxIN,OzIN);.
```

The function ATAN2 returns the angle whose tangent is the first argument divided by the second. These equations compute body orientation with respect to outputs from the ORIENTATION blocks as if those outputs were components of the vertically oriented gravity vector.

The VORz block computes a vestibular ocular reflex driver that simulates the vestibular output to the oculomotor system for further data processing that results in compensatory eye movements about the Z-axis. The output represents the interaction of linear and angular accelerations to generate a vestibular output only and does not account for any gain or phase effects of the visual system or other influences on eye movements. Equations for this block are:

```
VORzOUT=-AzLin*EXP(-0.22*sqrt(OxIN^2+OyIN^2))
        +DPHIzIN*(1-EXP(-0.22*sqrt(OxIN^2+OyIN^2)))
        -0.0145*TRANSLATIONyIN;
```

The first term is driven by the long-time-constant output of the ANGULAR Z block and is attenuated by the vector sum of the outputs from the ORIENTATION blocks in the XY plane. Coefficients in this attenuation factor were adjusted using published off-vertical rotation and postrotatory suppression data (2). The simulation of those experiments are shown in Fig. 3. The subjects were rotated about their Z-axis, which was vertical. Angular acceleration was 5.23 rad/s^2 and angular velocity was 1.047 rad/s. After sufficient time for the canal cupulae to return to equilibrium position, they were decelerated at 5.23 rad/s^2 to a stop. One or two seconds after stopping they were reoriented such that their Z-axis was horizontal. The time constant for decay of postrotatory nystagmus was measured. In the simulation, deceleration began at 80 s, and reorientation occurred between 81 and 83.5 s. The simulations were repeated while adjusting the coefficient for the attenuation factor until the VORz decay time constant was 8.67 s, which closely compares to 7.1 - 9.7 measured experimentally (2). The second term is driven by the DPHIz input from the COMPxy block where it was the computed rate of rotation of the linear acceleration vector in the XY plane. The second factor in this term varies from zero to one as the outputs from the ORIENTATION blocks in the XY plane increase. Coefficients in this term were set equal to the corresponding coefficients in the first term; therefore, the sum of the attenuation factors in these two terms always equals one. If the orientation block output is low, VORz will be determined by the angular Z input. Conversely, if the orientation block output is high, VORz will be determined by the computed angular velocity of the linear input in the XY plane. The third term is driven by the output of the Y-axis TRANSLATION block. The coefficient for this term was adjusted using modulation component data from off-vertical rotation experiments (1,5,16,17).

The VORy block computes the vestibular driver for compensatory eye movements about the Y-axis. Equations for this block are:

```
VORy=-AyLin*EXP(-0.078*sqrt(OxIN^2+OzIN^2))
    +DPHIyIN*(1-EXP(-0.078*sqrt(OxIN^2+OzIN^2)))
    +0.0042*TRANSLATIONzIN + 0.0055*TRANSLATIONxIN + 0.003*Oz;
if (VORy>=0) {VORyOUT=VORy;} Else VORyOUT=0.6*VORy;
```

The first and second terms are similar to the corresponding terms in the VORz block. The coefficient 0.078 was adjusted to fit postrotatory VORy data derived previously (2). Those experiments were similar to those for the VORz except the subjects were initially rotated about their Y-axis that was vertically oriented. After stopping, they were repositioned such that their Z-axis was vertical. The model value was 5.83 s compared to the experimental values of 5.8-5.9 s.

The third and fourth terms are driven by outputs from the TRANSLATION blocks in the XZ plane. Paige and Tomko (14) reported that compensatory eye movements about the Y-axis could be driven by linear acceleration along the X or Z-axis. Coefficients for these terms were adjusted using modulation component and phase data from Wall and Petropoulos (18). They reported that the VOR about the Y-axis was asymmetric. This asymmetry may be associated with the visual rather than the vestibular system; however, to adjust the relative contribution of the X and Z components that provided the best simulation of the experimental data, an "if" statement was added to change the overall gain of the VORy block depending on the polarity of the computation. The final term and the second "if" statement provide a driver that may account for the vertical nystagmus reported during high Gz centrifuge experiments (10).

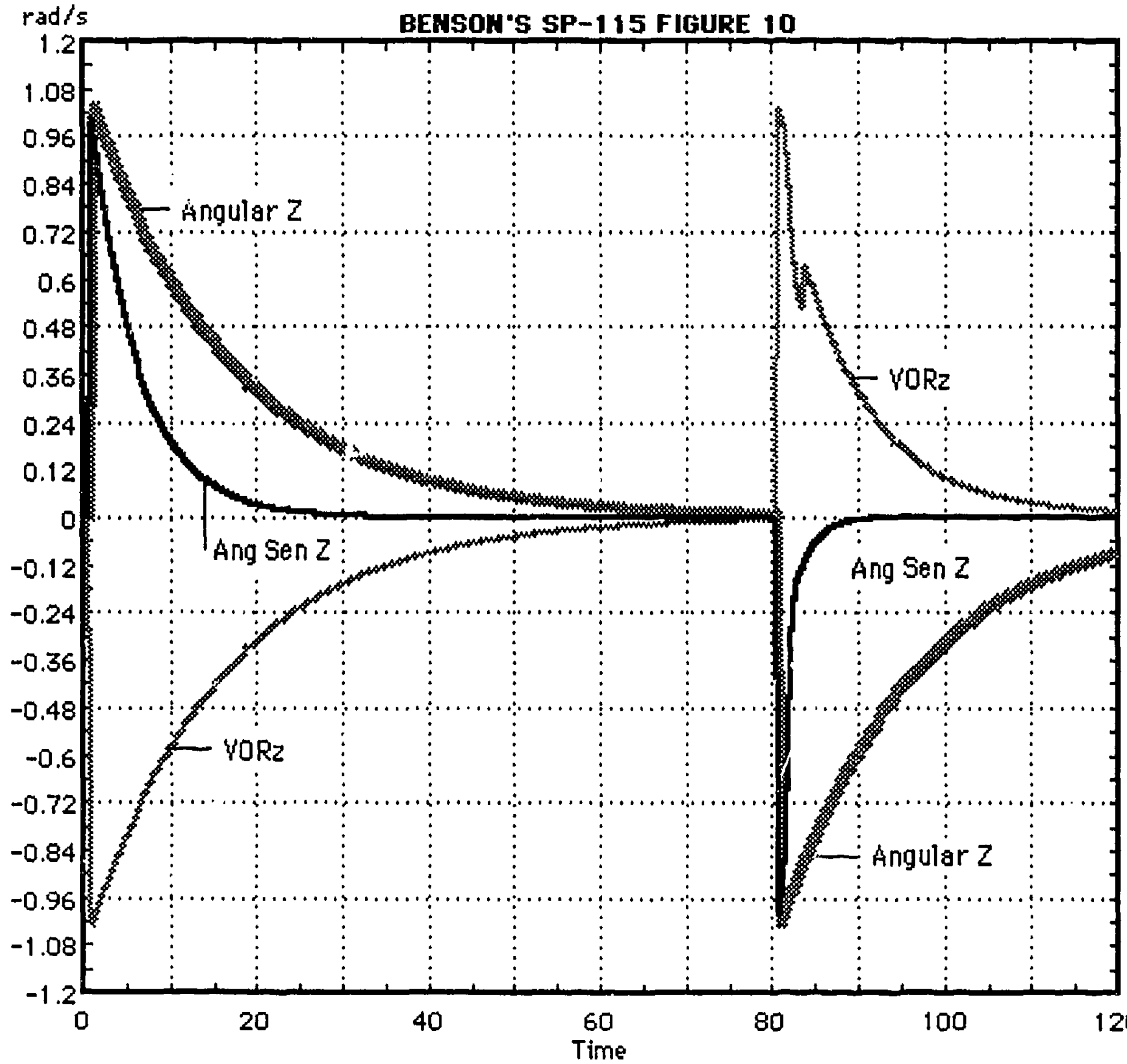

Figure 3. Output of the Angular Z, VORz, and the AngSen Z blocks during a simulation of the experiment reported elsewhere (2). From a vertical position subjects were accelerated about their Z-axis to an angular velocity of 60 deg/s. At 80 s, subjects were decelerated to a stop. Between 81 and 83.5 s, they were tilted 90 deg.

The ANG SEN Z block computes an output that simulates a vestibular driver which could be used by other systems to generate a sensation of angular velocity about the Z-axis. The equation for this block is:

```
AngSenZout=AzSin*EXP(-1.25*sqrt(OxIN^2+OyIN^2));
```

The function is driven by the short-time-constant output of the ANGULAR Z block and is attenuated by the vector sum of ORIENTATION block outputs in the XY plane. The coefficient of the attenuation factor was adjusted to fit the postrotatory sensation times reported for deceleration impulses following constant angular velocity about the Z-axis (2,3). The experiment was the same as described above for VORz. Output of the AngSenZ is also shown in Fig. 3. The attenuation coefficient was adjusted until the time at which the output had fallen to 0.01 rad/s equaled 8.56 s, which compares closely to the experimental value of 8.7 reported by Benson (2).

The ANG SEN X block computes a vestibular driver for generating a sensation of angular velocity about the X-axis. The equation for this block is:
AngSenXout=AxSin*exp(-0.182*sqrt(OzIN^2+OyIN^2));
The function is driven by the short-time-constant output of the ANGULAR X block and is attenuated by outputs of the ORIENTATION blocks in the YZ plane. The attenuation coefficient was adjusted to fit the postrotatory sensation times reported for deceleration impulses about the X-axis (2). The model value was 11.98 s compared to the experimental value of 12.1 s.

The ANG SEN Y block computes a vestibular driver for generating a sensation of angular velocity about the Y-axis. The equation for this block is:
AngSenYout=AySin*EXP(-0.2*SQRT(OzIN^2+OxIN^2));
The function is driven by the short-time-constant output of the ANGULAR Y block and is attenuated by outputs of the ORIENTATION blocks in the XZ plane. The attenuation coefficients were adjusted to fit the postrotatory sensation times reported for deceleration impulses about the Y-axis (2). The model value was 9.56 s compared to the experimental value of 9.5 s.

With all the model parameters fixed, the following experiments were simulated: Benson's off-vertical rotation at 10, 20, 40, and 60 deg/s (1); Correia and Guedry's off-vertical rotation at 180 deg/s (5); Lackner and Graybiel's off-vertical rotation from zero to 180 deg/s (12); Stockwell and Guedry's passive roll (16); and Guedry et. al. pendular centrifuge at 3 Gz (10).

RESULTS

Figure 4 shows the output of the Y-axis orientation and translation blocks during an off-vertical rotation simulation that began with the subject supine. Angular acceleration about the Z-axis was 1.047 rad/s^2 to an angular velocity of 1.047 rad/s, and at 90 s deceleration was 1.047 rad/s^2. The orientation block output declined exponentially while the translation block output increased. These changes in amplitude were driven by the Z-axis error signal shown in the lower part of the figure. During the acceleration phase, output of the angular Z block closely matched the angular velocity of the linear input vector in the XY plane, thus producing a low error signal. As the output of the angular Z block decayed, the error signal rose exponentially to equal the angular velocity of the linear vector. During the deceleration phase, the angular velocity of the linear vector decreased in magnitude but did not change direction while the output of the angular Z block increased in the opposite direction. At the end of deceleration, the angular velocity of the linear vector was zero so the error signal was thereafter driven by the decaying output of the angular Z block. During this decay phase, the error signal attenuated the orientation Y block so the output rose slowly to equal the earth's gravity component along the Y-axis, which was a function of the final angular position. Output of the translation block was zero at end of deceleration because the derivative factor in the translation block equation was zero.

The curves shown in Fig. 5 were generated during the same off-vertical simulation shown in Fig. 4. The VORz output was initially driven by both the long-time-constant output from the angular Z block and the angular velocity of the resultant linear input vector computed in the COMPxy block. As the output of the Y-axis translation block, (Fig. 4) increased, it produced the modulation component. As the angular Z output decayed, the VORz decreased until it was driven only by the angular velocity of the resultant linear input vector. The constant bias component was not equal to the actual angular velocity of the input vector because the output of the X and Y orientation had decreased and thus attenuated the DPHIz term in the VORz block. After the deceleration phase, output from the orientation blocks reduced the time constant for decay of the VOR.

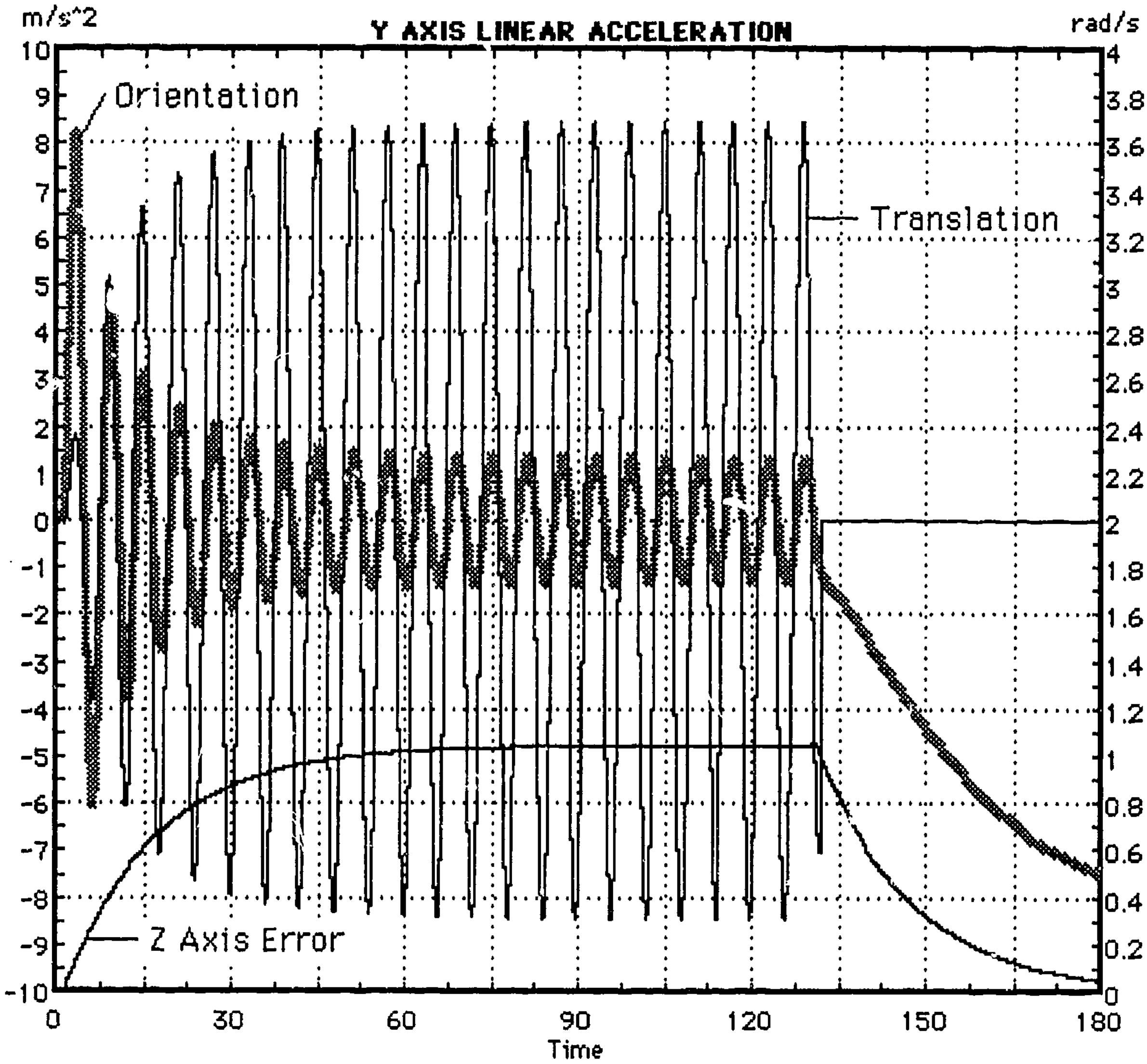

Figure 4. Output of the Y-axis orientation and translation blocks during an off-vertical rotation simulation that began with the subject supine. The angular acceleration and deceleration about the Z-axis were 1.047 rad/s^2. The maximum angular velocity was 1.047 rad/s. Deceleration began at 130 s. Ordinate axis for Z-axis error is on the right. Time is in seconds.

The output of the angular sensation Z block shown in Fig. 5 was driven by the short-time-constant angular z output but was attenuated by outputs of the X and Y orientation blocks. As shown in Fig. 4, the orientation components were high during the acceleration and early part of the constant velocity phase and were sufficient to suppress the output of the angular sensation block to negligible levels. During the deceleration phase, the orientation block output was low and the angular Z output was high enough to slightly override the suppression for a few seconds.

Figure 6 shows the computed values (open squares) of the bias and modulation components for off-vertical rotation simulations at angular velocities from 10 to 180 deg/s about a horizontal Z-axis. Additional data points were derived from other studies: crosses (1), triangle (17), closed square (16), and diamond (5). The bias component was driven by the DPHIz term in the VORz block. At low angular velocities, the error signal was low allowing outputs from the orientation blocks to be high enough that the DPHIz term in the VORz block was not significantly attenuated. The bias term was then linearly proportional to the angular velocity of the input resultant vector in the XY plane. At high angular velocities, the large error signal attenuated the outputs of the orientation blocks and thus attenuated the DPHIz term. The opposing effects of these two factors produced a peak bias component. The modulation component was controlled only by the output of the Y-axis translation block and continued to rise as the error signal increased the gain of the translation block.

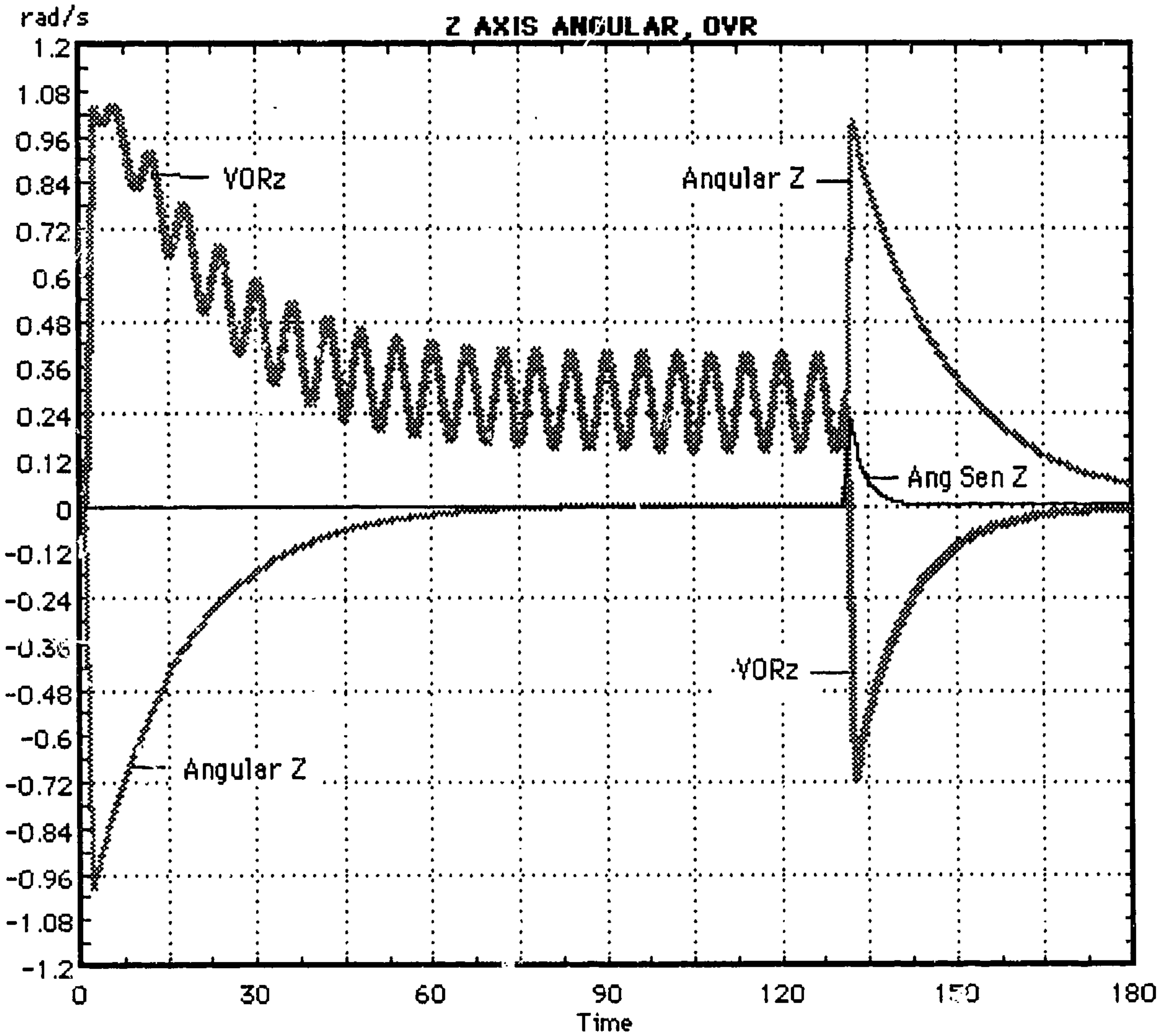

Figure 5. Outputs from Angular Z, VORz, and Ang Sen Z blocks for the same simulation as in Fig. 4. Time is in seconds.

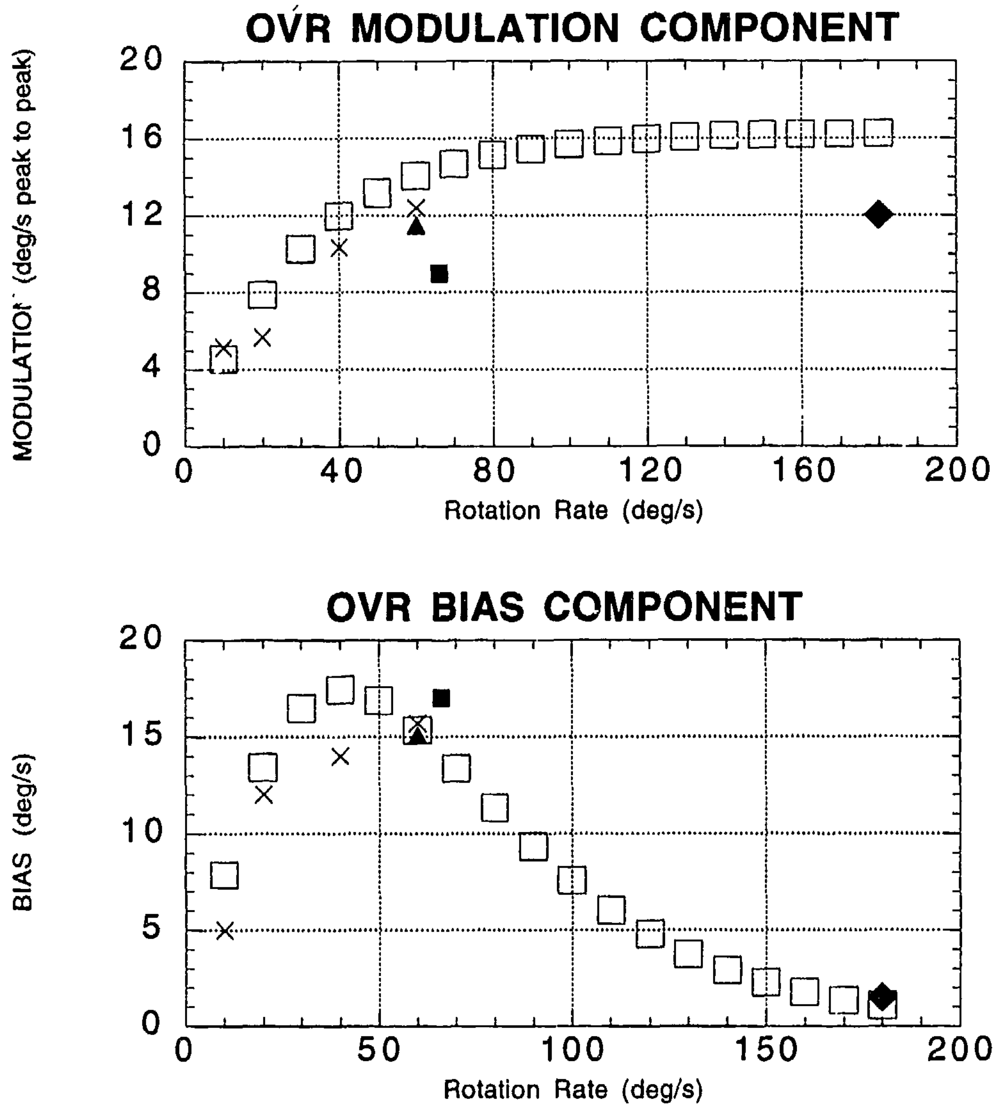

Figure 6. Bias and modulation components of horizontal nystagmus for off-vertical rotations with Z-axis horizontal. The squares were derived from the VORz computed by the model. Additional data points were derived from other studies in the following references: crosses (1), triangle (17), closed square (16), and diamond (5).

Figure 7 shows the outputs from the Z-axis orientation and translation blocks during a simulation of a pendular centrifuge experiment (10). The centrifuge accelerated at 0.112 rad/s^2 to an angular velocity of 2.13 rad/s and at 100 s decelerated at the same rate. The subject was facing tangentially with the center of rotation on the right. As the centrifuge velocity increased, the pendular restraint system rolled such that the resultant acceleration along the Y-axis was always zero. This roll relative to the centrifuge plane of rotation generated a coriolis angular acceleration applied to the angular Y input block. The Y-axis error signal was large for both the acceleration and deceleration phases because the output of the angular Y block was large compared to the angular velocity of the resultant input linear acceleration in the XZ plane. This error signal decreased the orientation block output and increased the translation block output.

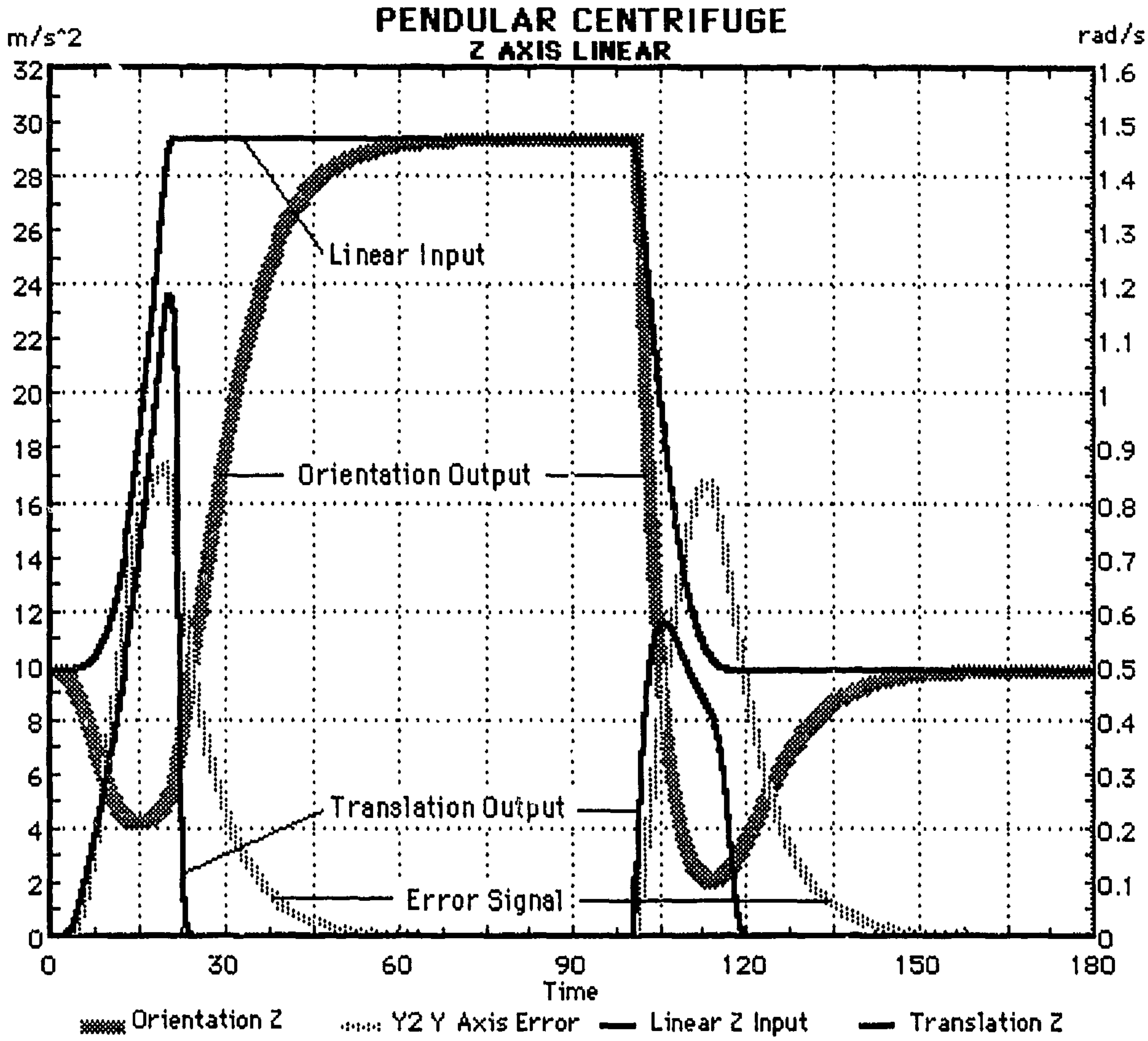

Figure 7. Outputs from the Z-axis orientation and translation blocks during a simulation of a pendular centrifuge experiment. Time is in seconds.

Figure 8 shows the output of the Y and Z angular sensation blocks for the same centrifuge simulation. During acceleration, the sensation of turning about the Z-axis was in the same direction as the centrifuge velocity and began before the sensation of pitching up about the Y-axis. These computed angular sensations and translation upward along the Z-axis (Fig. 7) are consistent with the actual motion generated by the accelerating centrifuge, and subjects generally do not report confusion (10). During deceleration, translation upward rose sharply followed by the sensation of pitching down about the Y-axis. The Y-axis amplitude during deceleration was greater than during acceleration because the attenuating effect of the orientation output was less. After the small Coriolis acceleration, the Z-axis output indicated an angular velocity outward opposite from the angular velocity of the centrifuge. All of these sensations during deceleration and the translation upward were reported previously (10).

Figure 9 shows the output of the VORz and VORy blocks during the pendular centrifuge simulation. The VORy is driven by the long-time-constant output of the ANGULAR Y block and the TRANSLATION Z output. These components are in the same direction during the acceleration phase and in the opposite direction during the deceleration phase. The peak amplitudes shown in Fig. 9 are close to the experimental values (10). This reference was used to adjust the coefficient of the ORIENTATION Z input term in the VORy block so that the VORy would have a small value during the constant velocity of the centrifuge. The VORz in Fig. 10 has the same wave form as the experimental values (10), but the amplitude is higher. These higher simulation values may have been the result of incorrectly assuming that the Linear Y input was zero, which would be true only if the vestibular organs were located at the inertial centroid of the combined subject and pendular restraint system. An output of the ORIENTATION Y block would have attenuated the VORz.

For comparison Fig. 2 is repeated as the upper panel in Fig. 10; the lower panel depicts passive roll simulation in which the subject was rotated about the X-axis to the same angle 0.524 rad. The linear Y and Z inputs were at the final values within 4.5 s. The X-axis error signal was very low because the output of the angular X block was congruent with the computed angular velocity of the linear input acceleration in the YZ plane. This low error signal allowed the Y and Z-axis orientation blocks to pass the input accelerations without significant delay or attenuation. The open squares are the experimental results of perceived roll reported by Stockwell and Guedry (15).

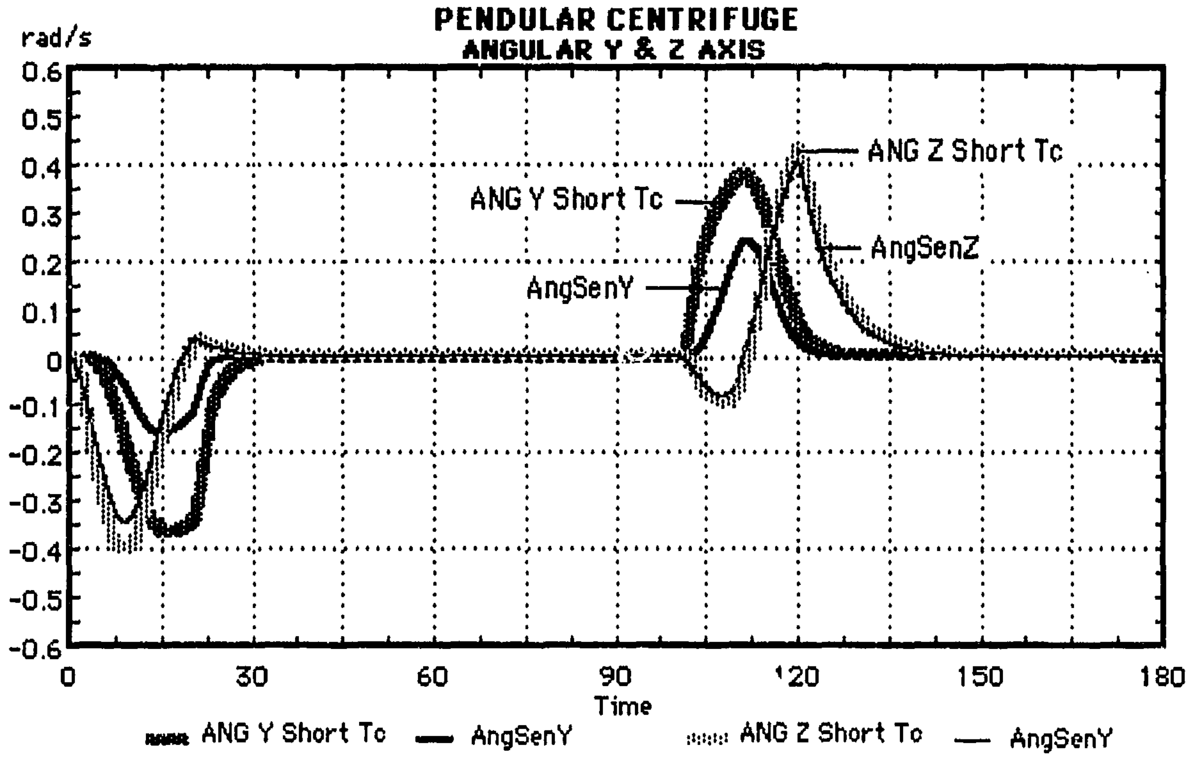

Figure 8. Outputs from the angular Z, angular Y, angular sensation Y, and angular sensation Z blocks during the same simulation of a pendular centrifuge experiment as in Fig. 7.

Figure 11 shows the result of a simulation of an off-vertical rotation experiment in which the angular velocity gradually increased for 90 s (12). The Z-axis error signal was initially low so outputs of X and Y-axis orientation blocks were maximum during the first rotation. At this low acceleration rate, the output of the ANGULAR Z block does not correspond to angular velocity so the difference between the angular Z output and the computed angular velocity of the input acceleration vector generated an increasing error signal during the acceleration phase. This increasing error signal attenuated the X and Y orientation blocks and decreased the attenuation of the X and Y translation blocks. In the actual experiment (12), the subjects initially perceived clockwise rotation about the Z-axis. As higher rotational velocities were achieved, they perceived a counterclockwise spiraling outward about a central axis while still rotating clockwise. The perception of spiraling outward is consistent with the increasing amplitude of the translation block output. The angular sensation output driven by the canal signal was initially suppressed by the orientation output. Perception of clockwise rotation about the Z-axis may have resulted from the position change of the orientation vector in the XY plane, which would be simulated in the model by the yaw output of the resultant orientation block. By the time the actual rotation rate reached 120 deg/s, the subjects no longer perceived rotation about their own body axis. They only perceived counterclockwise orbital motion. At 120 deg/s, which corresponds to 60 s on the time axis, the simulation shows that the orientation output was very low and the translation output was very high. The amplitude and phase of the X- and Y-translation outputs are consistent with the perceived counterclockwise orbital motion.

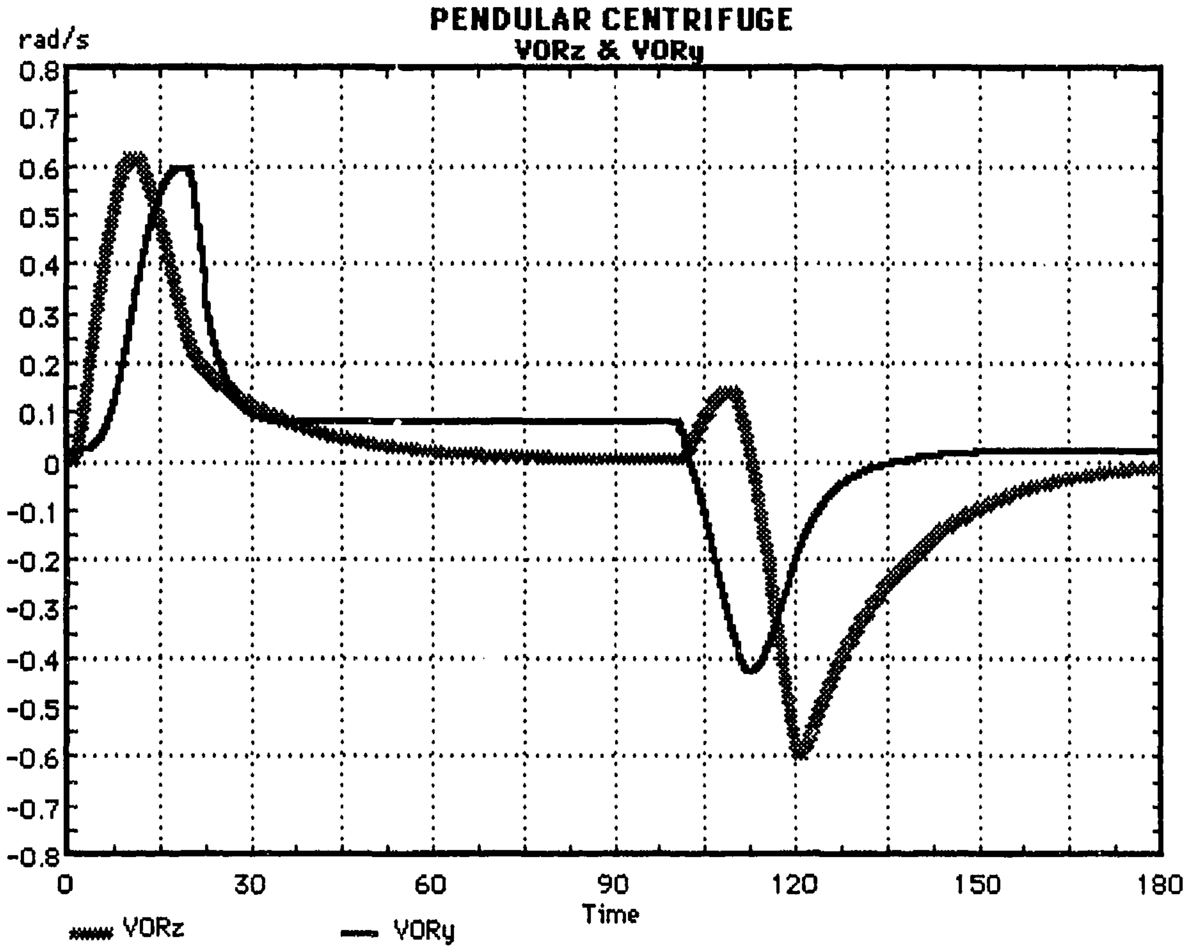

Figure 9. Output of VORy and VORz blocks during the same pendular centrifuge simulation simulation as for Figs. 7 and 8. Time is in seconds.

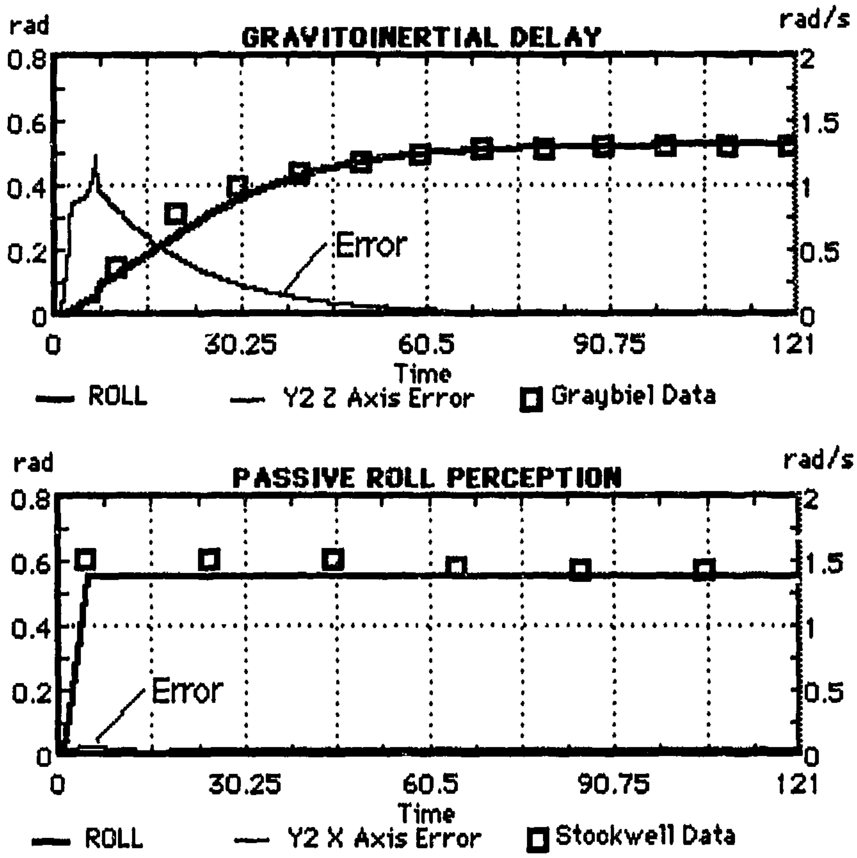

Figure 10. Roll output of the resultant orientation block during simulations of the gravito-inertial experiment reported earlier (4,7) and the passive roll experiment reported elsewhere (15). The open squares were derived from the reference data. Subjects in the gravito-inertial experiment were fixed upright on a centrifuge and indicated perceived orientation. The centrifuge reached constant velocity within 8 s. Time is in seconds.

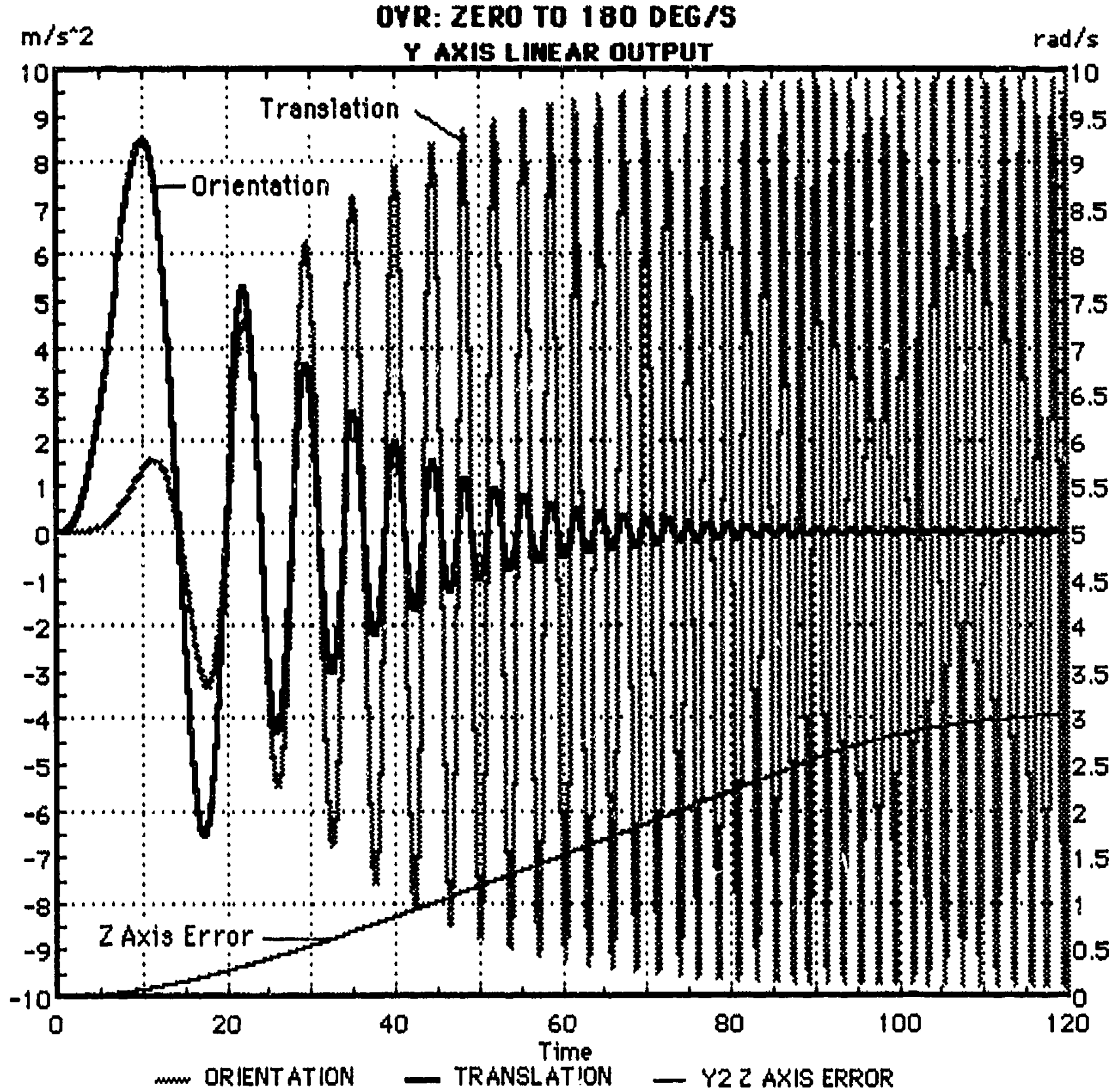

Figure 11. Output of the Y-axis orientation and translation blocks during a simulation of a Lackner and Graybiel's experiment (12). From a supine position, subjects were accelerated clockwise about their Z-axis at 2 deg/s^2 to an angular velocity of 180 deg/s. Constant velocity was reached at 90 s. The ordinate axis for the error signal is on the right. Time is in seconds.

DISCUSSION

One of the fundamental concepts that determined the structure of this model is that it is physically impossible to have rotation about an axis and to simultaneously have a stationary orientation vector in the orthogonal plane. In this model, those conditions are mutually inhibitory through proportional analog processes as opposed to all-or-none suppression of one by the other. When the angular output and the rotation velocity of the input orthogonal linear vector are not in agreement, an error signal proportional to the magnitude of the discrepancy reduces the flow of linear acceleration data through the orthogonal orientation channels and increases the flow though the translation channels. Conversely, orientation block output data affects orthogonal angular data by attenuating outputs of the VOR and the angular sensation blocks.

Clark and Graybiel's studies of the gravito-inertial delay (4,7) provided the data that showed quantitatively how an angular input attenuates a linear input. Those data established the mathematical relationship between the error and the proportion of the linear input that would pass through the orientation channel. The complementary function was then used in the translation block so that the sum of the gains in corresponding orientation and translation channels would equal one. Those experiments need replication for the Y-axis, and corresponding data are needed for the X and Z axes.

Benson's experiments on postrotatory sensation times and nystagmus decay rates (2) provided the data to quantify the concept that stationary orientation vectors are incompatible with canal-driven nystagmus and perceptions of angular velocity about an orthogonal axis. Those data established the function and coefficients for the VOR and the angular sensation blocks. Benson's off-vertical rotation data over a range of low-rotation rates (1), Correia's data at mid- and high-rotation rates (5), and Stockwell's data over a range of tilt angles (16) provided the clue that output of the orientation channels affects the gain of the otolith driven bias component. Those experiments need replication, with a large population, over a wide range of rotation rates and at intervals that will establish the peak and shape of the curve for bias as a function of rotation rate.

With the parameters and coefficients established through iterative simulations that produced the best overall agreement with data from those foundation experiments, the model was then used to simulate other reported experiments. Simulation of Stockwell and Guedry's passive -roll experiment (15) was consistent with their experimental data and showed that the angular velocity signal from the angular X input was balanced by the computed angular velocity of the linear YZ plane input vector, and that the low-error signal correctly allowed the changing linear input accelerations to pass through the orientation channels.

Simulation of Guedry and colleagues pendular centrifuge experiments (10) provided a quantitative rationale for some of the reported perceptions. During deceleration, the large Y-axis canal output results in an error signal that directs part of the Z-axis linear input acceleration to pass through the translation channel, which could provide the basis for the reported perceptions of ascent from the earth. The same error signal reduces the orientation output and allows the large Y-axis canal signal to pass through the angular sensation block, which may account for the reported sensation of forward tumbling.

The simulation of Lackner and Graybiel's off-vertical rotation experiment with a gradually increasing rotation rate (12) provided the quantitative basis for their subjects' perception of an increasing spiral outward to an orbital motion in the opposite direction to the actual motion. Outputs from the X and Y translation blocks have the magnitude and phase to account for that motion.

In simulations at low off-vertical rotation rates, the angular sensation block was suppressed while the experimental subjects correctly reported rotation position about their Z-axis (1,5,12). This result raises the possibility that when a gravity vector is present, the sensation of angular rotation about axes other than gravity may be determined by the rate of change of yaw, pitch, and roll, derived from orientation channel outputs, and the canal outputs serve to generate the appropriate error signals.

In this model, vertical oscillation parallel to gravity does not generate an error signal, because the linear input vector changes in magnitude but not direction. With no error signal, the oscillating linear input signal passes entirely through the orientation block. The translation block would provide no cues for direction of movement. This result is consistent with Malcolm and Melvill Jones experimental results (13). They conducted a series of experiments in which the subjects were oscillated vertically and instructed to indicate their direction of motion. Although subjects responded as though they were aware of movement, their ability to correctly indicate direction was little better than chance.

CONCLUSION

A mathematical model was developed for the interaction of angular and linear acceleration data within the vestibular system. The parameters and coefficients were established to provide an overall best fit to data reported for gravito-inertial delay and off-vertical rotation experiments. Although perceptual and eye-movement data from the literature were used to adjust the coefficients, the model is limited to a mathematical simulation of data processing within the vestibular system before the outputs interact with the visual, proprioceptive, or cognitive systems.

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13. ABSTRACT *(Maximum 200 words)*

A computer model with six degrees of freedom was developed in which linear acceleration along each axis is detected and directed along two channels. Output of one channel is perceived as a signal that was generated by gravity, produces no perception of translation, and is used to determine body orientation with respect to earth-vertical. Output of the other channel is perceived as a signal generated by transient linear acceleration and produces a perception of transnational motion. Attenuation of signals in these channels is controlled by computations that compare the angular velocity signal generated by the canals with the angular velocity of the input linear acceleration vector. The difference between these velocities serves as an error signal that increases the attenuation of the orientation channel and decreases the attenuation of the translation channel. Orientation channel outputs attenuate orthogonal canal signals that provide angular sensation and ocular reflexes. The model computes the following results that are consistent with empirical data reported in the literature: (1) For off-vertical rotation: bias and modulation components of nystagmus, faster decay of postrotatory nystagmus, attenuation of postrotatory turning sensations, and perceived conical translation; (2) For pendular centrifuge: vertical ascent and tumbling during deceleration; (3) For non pendular centrifuge: delay in perception of roll: and (4) For passive roll: no delay in perception.

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