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Relation between Perception of Vertical Axis Rotation and Vestibulo-ocular Reflex Symmetry

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Running head: Rotational perception and VOR

Abstract

Subjects seated in a vertical axis rotation chair controlled their rotational velocity by adjusting a potentiometer. Their goal was to null out pseudorandom rotational perturbations in order to remain perceptually stationary. Most subjects showed a slow linear drift of velocity (a constant acceleration) to one side when they were deprived of an earth-fixed visual reference. The amplitude and direction of this drift can be considered a measure of a static bias in a subject's perception of rotation. The presence of a perceptual bias is consistent with a small, constant imbalance of vestibular function which could be of either central or peripheral origin. Deviations from perfect vestibulo-ocular reflex (VOR) symmetry are also assumed to be related to imbalances in either peripheral or central vestibular function. We looked for correlations between perceptual bias and various measures of vestibular reflex symmetry that might suggest a common source for both reflexive and perceptual imbalances. No correlations were found. Measurement errors could not account for these results since repeated tests in the same subjects of both perceptual bias and VOR symmetry were well correlated.

Key Words: Vestibular - Vestibulo-ocular reflex - Motion perception - Manual control

Introduction

Self-motion perception is derived from a variety of sensory sources including visual, vestibular, somatosensory, and auditory cues (1-3). Vestibular contributions to the perception of rotation about an earth-vertical axis have been studied extensively (4). When subjects are in an upright position, rotations about an earth-vertical axis stimulate primarily the horizontal semicircular canals. Signals from these canals are processed in the central nervous system to produce the sensation of rotation and to generate compensatory eye movements through the vestibulo-ocular reflex (VOR).

Because both self-motion perception and the VOR are thought to rely on the same neural structures, attempts have been made to correlate different properties of the VOR and self-motion perception in order to verify this hypothesis. Various investigators have quantified the dynamic properties of rotational sensation following transient rotational motions (4,5) and during sinusoidal oscillations (6-8). Their results have generally confirmed a close correspondence between the dynamics of the VOR and sensation. For example, these studies have identified a 10-20 s time constant that characterizes the time course of the decline of sensation following a step change in rotational velocity. A similar range of time constant values characterizes the dynamic properties of VOR induced eye movements (9). The semicircular canal time constant, however, is shorter than the VOR time constant (in monkeys (10,11), and presumably in humans). This difference between canal and VOR time constants indicates the participation and possible shared use of a central velocity storage mechanism (12) in the processing of canal signals for both sensation and the VOR.

Attempts to correlate other shared properties of the VOR and self-motion perception have been limited by the methods for measuring motion perception such as self reports of direction changes and estimates of perceived velocity (4). To overcome these limitations, Zacharias and Young (13) developed another method for the quantification of rotational perception. In their method, the subject has control over his rotational velocity, and is instructed to null out rotational motion perturbations introduced by the experimenter so that the subject perceives that he is at zero velocity. This protocol places the subject in a closed loop control system which we refer to as perceptual feedback. This technique has the advantage that quantitative estimates of both the static and dynamic properties of rotational perception can be obtained.

The static properties of rotational perception are of particular interest in that they may be related to measurable characteristics of VOR responses. Static properties refer to the long term, or DC responses of perceptual and reflex systems. For rotational perception, a static response might correspond to a sustained sensation of turning when in fact there is no motion. For the VOR, static properties might be indicated by an average deviation of slow phase eye velocity from zero during stimulation with a zero-mean rotational motion.

Using the perceptual feedback technique, static properties of rotational perception are determined by measuring the average rate of change of the subject's rotational velocity during a perceptual feedback experiment. More specifically, Zacharias and Young found that when subjects were deprived of visual motion cues, their rotational velocity linearly increased throughout the course of the stimulus presentation. This drift, a constant acceleration, can be accounted for by the presence of a static, directional bias in the subject's perception of his rotational velocity. The term perceptual bias will refer to this static bias signal and the associated drift in velocity during the perceptual feedback test.

Zacharias and Young speculated that the source of this bias is an imbalance between the neural activity from the semicircular canals in opposite ears. This hypothesis assumes that the central nervous system acts as a simple comparator of activity from the semicircular canals in opposite ears. Any difference in activity between the two ears signals that the head is turning and is accompanied by a perception of rotation. Because the semicircular canals have the response characteristics of an accelerometer at low frequencies of head motion, a subject who is controlling his own rotation would have to accelerate in order to generate a constant change in activity from the semicircular canals. The subject would perceive himself to be at rest when the change in activity generated by the constant acceleration canceled the inherent difference in activity between the ears. The magnitude of the acceleration would be proportional to the difference in activity that exists when the subject is stationary.

It is often assumed that deviations from perfect VOR symmetry are related to an imbalance between the two ears. This is clearly the case in subjects following an acute unilateral loss of vestibular function. These subjects have asymmetric VORs that reflect the imbalance between the two ears (14-17). However, the central nervous system is able to adapt to chronic imbalances in vestibular function and to restore VOR symmetry to normal limits (14,16,18). Similarly for motion perception, the spinning sensation following an acute unilateral loss of vestibular function gradually subsides even though the peripheral vestibular asymmetry remains.

The adaptive mechanisms associated with the compensation for unilateral deficits are presumed to be active in normal subjects. These mechanisms are required to calibrate VOR gain and to adjust for central and peripheral imbalances or changes in function that occur over time due to aging and various disease processes.

Given the constant influence of the central adaptive systems, it seems unlikely that VOR asymmetries and perceptual bias are only related to imbalances of peripheral vestibular inputs. Rather, a residual asymmetry measured in a normal subject could potentially be influenced by the imperfect functioning of a central adaptive system. Therefore residual VOR and perceptual asymmetries may be related to peripheral asymmetries, to central asymmetries (associated with the central adaptive mechanism), or to some combination of the two.

Is there a single symmetry adjustment mechanism which serves both reflex and perceptual processes? If perceptual and reflex measures of symmetry were correlated, this would suggest a common source signal (perhaps the simple imbalance in activity between the two ears) or at least covarying central mechanisms of symmetry adjustment. Alternatively, uncorrelated perceptual and reflex measures of symmetry would suggest more complex central processes which might include separate symmetry adjustment mechanisms, or separate sources of perceptual and VOR bias following a common symmetry adjustment mechanism.

Methods

VOR and perceptual feedback tests were performed by 20 normal human subjects, 11 male and 9 female, aged 22 to 44 years. The test session lasted about 45 minutes, including a three minute break in the middle of the session. The subjects were given the option to stop the session at any time. Two of the 20 subjects did not finish the test sequence due to motion sickness symptoms, and their data are not included.

Subjects sat in a chair mounted on a 108 N·m velocity servo-controlled motor (Contraves Goerz Corp, Model 824) and were rotated about an earth-vertical axis. The axis of the chair was at the center of a 2.1 m diameter circular room. The circular room was used for the projection of visual stimuli during some of the perceptual feedback tests. Three VOR tests were performed (referred to as pre-test VOR), followed by twelve perceptual feedback tests, and then the same three VOR tests (post-test VOR) were repeated.

All procedures were in accordance with standards set by the Institutional Review Board of Good Samaritan Hospital & Medical Center.

VOR Test

Test Conditions. Subjects performed tests of VOR function with eyes open in a dark room. Horizontal and vertical eye movements were recorded by electrooculographic (EOG) techniques (bandwidth DC to 80 Hz) using silver/silver chloride electrodes. Horizontal EOG was recorded using bitemporal electrodes. Vertical EOG was recorded by electrodes placed above and below the right eye. EOG calibrations were made before and after each VOR test. Stimulus delivery and data collection were controlled by computer (DEC LSI 11/73). Horizontal and vertical EOG, and the chair's tachometer signal were digitized (12 bit resolution) and stored for later analysis. Digitizing rates were 200 per second for the horizontal EOG and 50 per second for the vertical EOG and the chair's tachometer.

Stimuli for VOR tests consisted of single frequency sinusoidal rotations at 0.05, 0.2, and 0.8 Hz with peak velocities of 60°/s. The duration of the sine tests were 100 s (5 cycles) for 0.05 Hz, 45 s (9 cycles) for 0.2 Hz, and 26.25 s (21 cycles) for 0.8 Hz. The first cycle in each test was considered a transient response and was not included in the data analysis. Subjects were given verbal tasks throughout the VOR tests to maintain a constant level of alertness. The tasks consisted of alphabetically naming places, cars, foods, etc.

VOR Data Analysis. Figure 1 shows an example of the VOR data analysis. Eye position data were differentiated to calculate eye velocity. Fast phases of the nystagmus were identified and eliminated using a method similar to that of Barnes (19). For each stimulus cycle, a judgment was made about the quality of the data and the analysis based on the consistency of eye movements and on the success of the analysis in detecting fast phases. Poor quality cycles were rejected. Curve fits were made to each cycle of the remaining slow phase eye velocity data. The curve fits were of the form:

$$r(t) = B_r + A_r \sin(2\pi f + P_r)$$

where B_r is VOR bias in °/s, A_r is response amplitude in °/s, P_r is response phase in degrees, and f is the stimulus frequency in Hz. Curve fit parameters were averaged to give final estimates of VOR response parameters.

A directional nonlinearity of the VOR was quantified by separately calculating the slopes of the slow phase eye velocity, after removing the relative phase shift between stimulus and response, versus stimulus velocity data for chair rotations to the right and left. The slopes were calculated by a least squared error fit of a two segment line to the data (Figure 1, lower right). One line segment was for positive and the other for negative stimulus velocities. The two line segments were constrained to intersect one another at zero stimulus velocity.

The two-part linear curve fit yielded three parameters: the reflex gain for slow phase eye movements to the right, G_R, the gain for slow phase eye movements to the left, G_L, and VOR offset defined as the eye velocity at zero stimulus velocity. A measure of VOR gain asymmetry was calculated by the formula $100*(G_R-G_L)/(G_R+G_L)$.

VOR bias, offset, and gain asymmetry parameters are collectively referred to as VOR symmetry measures. For a normal population, the ranges of these symmetry measures are about ±6°/s for VOR bias and offset, and ±15% for VOR gain asymmetry (20).

Since the VOR symmetry measures were highly correlated across the three test frequencies, individual subject averages of the symmetry measures were used for comparisons of pre- and post-test results, and for comparisons of VOR symmetry measures with motion perception results. For example, a subject's average pre-test VOR bias refers to the average of the VOR bias obtained at 0.05, 0.2, and 0.8 Hz from the VOR tests given prior to the perceptual feedback tests. A subject's average VOR bias refers to the average of VOR bias measures obtained both pre- and post-test at all three test frequencies.

Perceptual Feedback Tests

Test Conditions. Perceptual feedback tests immediately followed the first three VOR tests. Auditory cues to motion were masked by a white noise stimulus during all perceptual feedback tests. A potentiometer (pot) was attached to the arm of the chair and adjusted to rest comfortably at the subject's fingertips. The knob on the pot did not provide any tactile cue for a zero position. The subject was asked to continuously adjust the pot to compensate for the experimenter-delivered disturbance signal in order to make himself "feel stationary" throughout the test. Figure 2 shows a schematic block diagram of the perceptual feedback experiment.

Each subject was given a practice session just prior to the perceptual feedback tests to become accustomed to the control of rotation using the potentiometer. After the practice session, twelve perceptual feedback tests were performed. The second, third, and eighth tests were rotations in the dark. The fifth test was a rotation with an earth-fixed, full field visual pattern projected onto the wall of the circular room. This test served as a control trial which tested the ability of the subject to regulate his motion when both vestibular cues and earth-referenced visual cues were available. The other eight tests involved various visual and visual-vestibular interactions. A three minute break was given immediately prior to the last rotation-in-the-dark test. The results of rotations in the dark are of primary interest to this paper, and will be referred to as perceptual feedback tests 1, 2, and 3 (numbered in the order in which they occurred in the test sequence).

The disturbance signal for all the perceptual feedback tests was a zero-mean pseudorandom signal consisting of the summation of six discrete sinusoidal frequencies with a period of 81.92 s. The eight frequencies were 0.037, 0.085, 0.183, 0.378, 0.720, and 1.550 Hz. The nominal amplitudes of the lowest two frequencies were 7.8°/s, the middle two were 3.9°/s, and the highest two were 1.95°/s. If the subjects had not been able to adjust their rotational motions, the highest instantaneous chair velocity would have been about 25°/s. Two complete cycles of the pseudorandom stimulus were given. The total duration of each perceptual feedback test was 204.8 s which included 20.48 s of an earth-fixed visual pattern before and after the 163.84 s presentation of the pseudorandom stimulus.

Chair tachometer and potentiometer signals as well as horizontal and vertical EOG were digitized (100/s) and stored for later analysis.

Data Analysis. Perceptual feedback results were quantified by calculating the average drift of the subject's rotational velocity away from zero. The second cycle (last 81.92 s) of each test was analyzed to determine the magnitude and direction of drift. The second cycle was selected to avoid any possible transient effects at the beginning of the test. The drift (in $^\circ/s^2$) was determined by calculating the average change of chair velocity with time using a linear regression to the chair velocity data. By convention, a negative sign indicated drift toward the subject's left and a positive sign indicated drift to the right.

As demonstrated by Zacharias and Young, when the dynamic properties of the various components in the feedback loop in Figure 2 are taken into account, the presence of a drift in rotational velocity away from zero is consistent with the presence of a constant bias signal introduced into the loop.

Results

VOR Responses

VOR response parameters were consistent with those obtained from a large normal population (20). In particular, a total of 540 VOR parameter values were measured in the 18 subjects. Only 18 of the 540 values (3.3%) were outside of the 95% confidence limits previously established for a normal population.

In Figure 3 (left column), average pre-test and average post-test measures of VOR bias, offset, and asymmetry are compared. Similar results were obtained with comparisons of pre- and post-test VOR symmetry measures at the individual test frequencies. Correlations between pre-test and post-test VOR parameters ranged from 0.58 to 0.87 (Table 1). All correlation coefficients in Table 1 were individually significantly different from zero ($P<0.02$). The lowest correlations were between pre-test and post-test VOR gain asymmetry measures at 0.05 and at 0.2 Hz, and the significance of these two correlations were lost when the P values were adjusted to account for multiple comparisons (Bonferroni adjustment, (21)).

The 95% confidence limits on the linear regressions between pre- and post-test VOR symmetry measures were consistent with a unity slope, suggesting that no significant VOR response changes occurred during the experiment.

Perceptual Feedback

Figure 4 shows a subject's performance during two perceptual feedback tests, one in the light within an earth-referenced visual field and the other in the dark. If the subject had not exerted control over his rotation by adjusting the potentiometer, the subject's rotational velocity would have been equal to the pseudorandom disturbance signal. For rotations in the light, the time course of the potentiometer signal was approximately equal and opposite to the disturbance signal. Since the subject's rotational velocity was controlled by the sum of the disturbance and potentiometer signals, the subject's actual rotational motion (chair velocity) showed less variation than the disturbance signal, and the subject's average velocity remained near zero throughout the test. The same was true for the perceptual feedback test in the dark except that there was a long term drift in the baseline of the potentiometer and chair velocity signals. This drift showed an approximately linear trend with time.

Measurement of average baseline drift over the last half of each perceptual feedback test quantified the presence of a static bias in a subject's perception of his rotational motion. When earth-referenced visual cues were available, drifts were small, ranging from -0.029 to 0.015°/s^2 with a mean of -0.0015 and standard deviation of 0.0092°/s^2. The mean of the absolute value of drift was 0.0060°/s^2.

When perceptual feedback tests were performed in the dark, drifts were larger in general than those recorded when earth-referenced visual cues were available. The magnitude of drift during 80% of the rotation-in-the-dark trials was larger than the ±2 s.d. range of drifts recorded when visual motion cues were available. For the three rotation-in-the-dark tests, drifts ranged from -0.33 to 0.57°/s^2 with a mean of -0.0083 and standard deviation of 0.16°/s^2. The mean drift was not significantly different from zero ($P>0.7$) indicating an equal tendency of subjects to drift right and left. The variance of the population's drift on the three rotation-in-the-dark tests was significantly larger ($P<0.001$) than the variance when earth-referenced visual cues were available. The mean of the absolute value of drift was 0.11°/s^2.

Figure 3 (center column) compares repeated measures of drift from the three rotation-in-the-dark tests. Correlations were 0.77, 0.47, and 0.57 for test 1 vs 2, 1 vs 3, and 2 vs 3, respectively. All of these correlations were individually significantly different from zero ($P<0.05$) although the 1 vs 3 correlation lost significance when the P values were corrected for multiple correlations (21). However, statistical analysis showed that one outlying point in the 1 vs 3 drift comparison (circled in Figure 3, data from the same subject are also circled in other two drift comparison plots) had a disproportionately large influence on the 1 vs 3 regression analysis than did other points. When this subject's data was excluded, the 1 vs 3 and 2 vs 3 correlations increased to 0.76 and 0.67, respectively, and the 1 vs 2 correlation was unchanged. All of these correlations were significantly different from zero ($P<0.01$ with the Bonferroni adjustment). No reason could be found to explain the presence of this outlying point.

Correlations between VOR and Perceptual Feedback Results

Correlations between perceptual feedback drift and the various measures of VOR symmetry were low (Table 2). For this comparison, each subject's average drift was calculated from the three rotation-in-the-dark perceptual feedback tests, and average VOR parameters were calculated from pre- and post-test results. Similar patterns of correlation were obtained from comparisons between the three individual perceptual feedback drift measures, and pre-test and post-test VOR parameters. The correlation between drift and the 0.2 Hz VOR gain asymmetry measure is the only individually significant correlation ($P=0.027$) in Table 2.

Figure 3 (right column) shows average drift versus average VOR symmetry measures. One subject's data (circled) had a disproportionate influence on the regression analyses. When this subject's data were not included, there were small, but insignificant, negative correlations between drift and the various average VOR symmetry measures (correlations in parentheses in Table 2 do not include this outlying data point).

Discussion

Perceptual bias, measured by the drift in velocity during perceptual feedback tests, appears to be unrelated to various measures of VOR response symmetry. Because drift and VOR symmetry measures were repeatable, measurement errors cannot account for the poor correlations between them.

The only suggestion of a relation between perceptual bias and VOR symmetry was the small negative correlation between drift and VOR symmetry measures (after removing an outlying data point). However, the sign of the correlation between drift and VOR symmetry should be positive if an imbalance in function between the semicircular canals in the two ears were responsible for both perceptual bias and VOR symmetry. For example, if average activity in the left canal were greater than the right, this would signal a rotation to the left and would produce slow phase VOR eye movements to the right (a positive VOR bias). Left canal activity greater than the right would also produce a sensation of turning to the left. Perceptual feedback tests would result in a positive (to the right) drift. This constant acceleration to the right would have the effect of increasing the average activity level of the right canal and decreasing the left in order to achieve a sensation of zero velocity rotation which occurs when right and left canal activities are equal. Therefore a simple model that presumes that rotational perception and VOR symmetry are related to imbalances in activity between the two ears, predicts a positive correlation between drift and VOR bias.

The fact that drift and VOR symmetry measures were not positively correlated suggests that there are other influences on motion perception bias and/or VOR symmetry. A candidate for the source of this influence is the central adaptive mechanisms that provide compensation for various lesions, and may play a role in the processing and integration of vestibular signals with motion cues from other sensory systems. The effect of these adaptive mechanisms have been more extensively studied in the VOR system than in motion perception. However it is known that the spinning sensation associated with acute lesions of the peripheral vestibular system declines with time even though the lesion remains. This suggests that a central adaptive network exists for perceptual as well as for reflex processes. The extent to which the perceptual and reflex systems share the neural network responsible for adaptation is not known.

Figure 5 shows a simple model which is consistent with our results. This model is intended to represent the static or low frequency behavior of pathways, rather than their dynamic properties. The model does not exhaust all possibilities, but rather illustrates a functional mechanism that could result in uncorrelated measures of perceptual bias and VOR symmetry even though there may be extensive sharing of central perceptual and reflex pathways.

The model includes a single "central symmetry adjustment mechanism" which acts upon a central neural network that receives vestibular signals from the two ears. The purpose of this mechanism is to compensate for long term imbalances in neural activity from the two ears. Even in normal subjects this symmetry compensation mechanism may not achieve perfect balance. The net result would be a non-zero "residual bias" which could contribute to both perceptual and VOR biases.

If the residual bias were the only contributor of static motion information to both perceptual and VOR systems then perceptual bias and VOR symmetry would be positively correlated. In order to explain the experimental finding of uncorrelated drift and VOR symmetry measures, the model postulates the presence of additional separate sources of bias for the motion perception and VOR systems. If these separate bias sources were not related to one another, and at least one of them was large relative to the residual bias, then there would be little or no correlation between motion perception bias and vestibular reflex symmetry measures.

If an individual were to lose vestibular function in one ear, the central symmetry adjustment mechanism in the model would be temporarily overwhelmed by the large peripheral bias. This would produce a residual bias that would likely be large relative to the separate central motion perception and reflex biases. Therefore the expectation is that motion perception and reflex symmetry measures would be positively correlated until the symmetry adjustment mechanism was able to reduce the residual bias to a small value. Once the residual bias were reduced to a small value relative to either of the separate sources of bias, then perceptual and reflex biases would again appear uncorrelated.

It is interesting to speculate on the reason why it may be useful for the brain to control symmetry in different ways in the motion perception and the VOR systems, and therefore on the reason why separate central sources of perceptual and reflex bias may be necessary. When a subject is in the dark, the VOR, whose purpose is to promote clear vision during head movements, is of no functional utility. The presence of a VOR bias in the dark therefore would not disrupt the functional purpose of the VOR. In contrast, a false perception of motion would have relevance to a subject even in the dark. That is, a spinning sensation in the dark would likely disrupt normal motor control. When visual cues are absent, somatosensory signals probably play an important role in providing the sensory information necessary for the motion perception system to compensate for any biases which would otherwise produce a spinning sensation. Although somatosensory cues clearly influence VOR function (3,22), they are probably less important than visual feedback in the control of VOR symmetry. The different functional consequences associated with biases in perception and in the VOR provide a plausible reason for the need of at least partially separate adaptive mechanisms.

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Table 1. Correlation Coefficients: Pre-test vs. Post-test VOR Measures (N=18).

VOR Parameter	0.05 Hz	0.2 Hz	0.8 Hz	3 Frequency Average
Bias	0.79	0.79	0.86	0.87
Offset	0.81	0.76	0.73	0.85
Gain Asymmetry	0.58	0.58	0.71	0.64

Table 2. Correlation Coefficients: Average Drift vs. Average of Pre- and Post-test VOR Symmetry Measures*

VOR Parameter	0.05 Hz	0.2 Hz	0.8 Hz	3 Frequency Average
Bias	0.10	0.28	0.16	0.19 (-0.23)
Offset	0.08	-0.01	0.25	0.11 (-0.21)
Gain Asymmetry	0.13	0.52	0.01	0.32 (-0.16)

*N=18 except for correlations in () where N=17.

Figure Legends

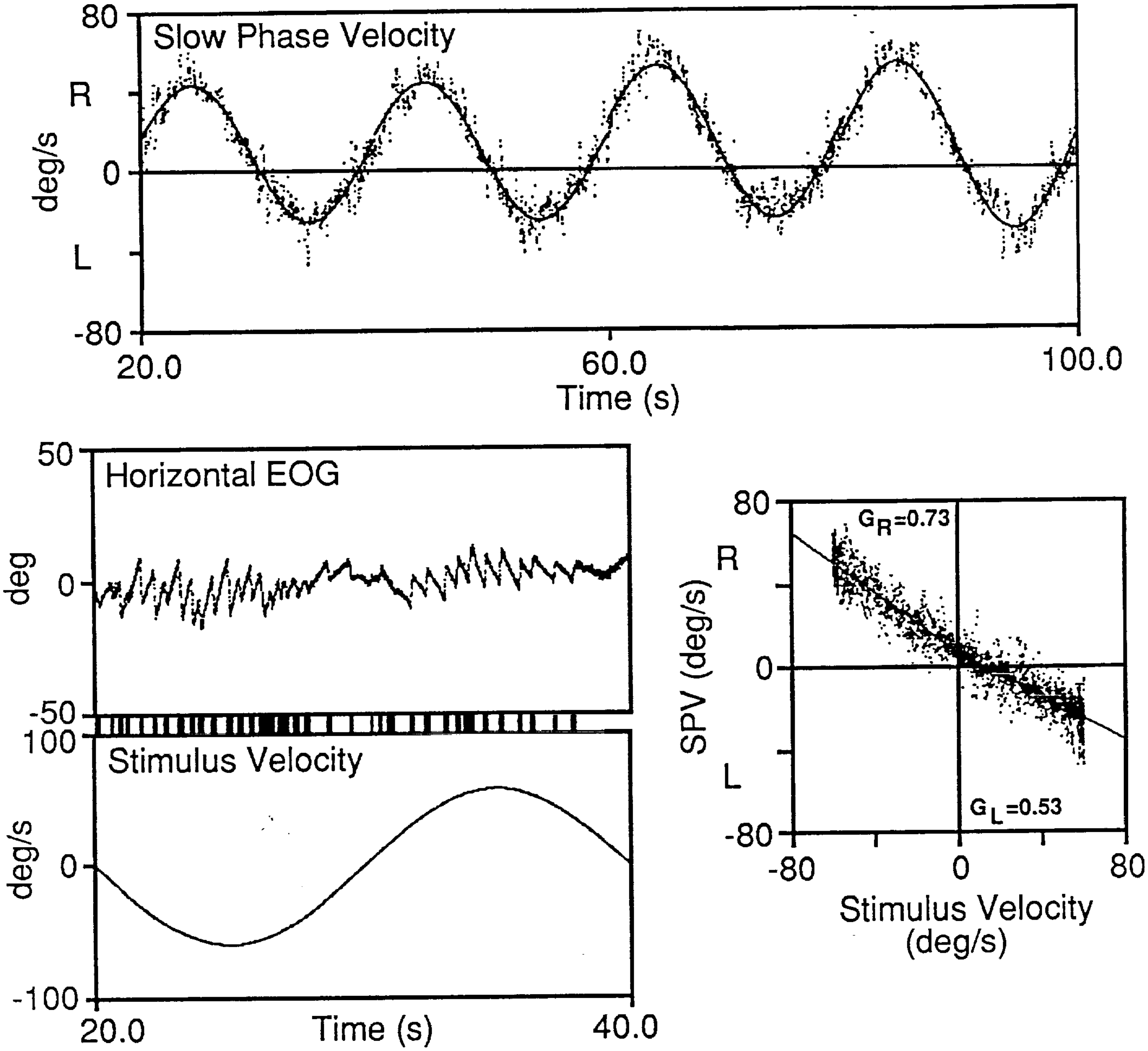
1. Example of a VOR response to a sinusoidal rotational stimulus. Upper trace: Slow phase eye velocity vs time from the last 4 cycles of a 0.05 Hz stimulus. The solid lines through the data points are curve fits to each cycle of the response. Lower left: Horizontal plane eye movements evoked during the first analyzed cycle of the data. Vertical bars between the EOG and stimulus velocity traces indicate the identified fast phases of nystagmus. Lower right: Slow phase eye velocity vs stimulus velocity plot. Solid lines are linear regression fits (constrained to intersect at zero stimulus velocity) from which VOR offset and gain asymmetry parameters are calculated. This particular data was from the subject with the largest 0.05 Hz VOR bias recorded in this study.

2. Block diagram of the perceptual feedback experiment.

3. Comparisons of VOR symmetry measures and perceptual feedback test drift. Left column: Average pre-test vs average post-test VOR symmetry measures. Center column: Comparison of repeated measures of drift from perceptual feedback tests performed in the dark. Right column: Comparison of average drift from perceptual feedback tests performed in the dark and average VOR symmetry measures. In the center and right columns, the circled points are from an individual (a different individual in each column) whose data had a disproportionate influence on at least one of the linear regressions in that column. The regression results (with 95% confidence limits) do not include the circled points.

4. Examples of perceptual feedback test results showing the time course of the pseudorandom disturbance signal (lower trace), the subject's adjustment of the potentiometer, and the chair rotational velocity during a rotation in the dark (upper) and with a stationary earth-referenced visual field (center).

5. A model suggesting central nervous system mechanisms and sources of bias which influence the static properties of motion perception and vestibular reflexes.



Slow Phase Velocity
80
R
deg/s
0
L
-80
20.0
60.0
100.0
Time (s)
Horizontal EOG
50
deg
0
-50
100
Stimulus Velocity
deg/s
0
-100
20.0
Time (s)
40.0
80
G_R=0.73
R
SPV (deg/s)
0
L
-80
G_L=0.53
-80
0
80
Stimulus Velocity
(deg/s)

Figure 1

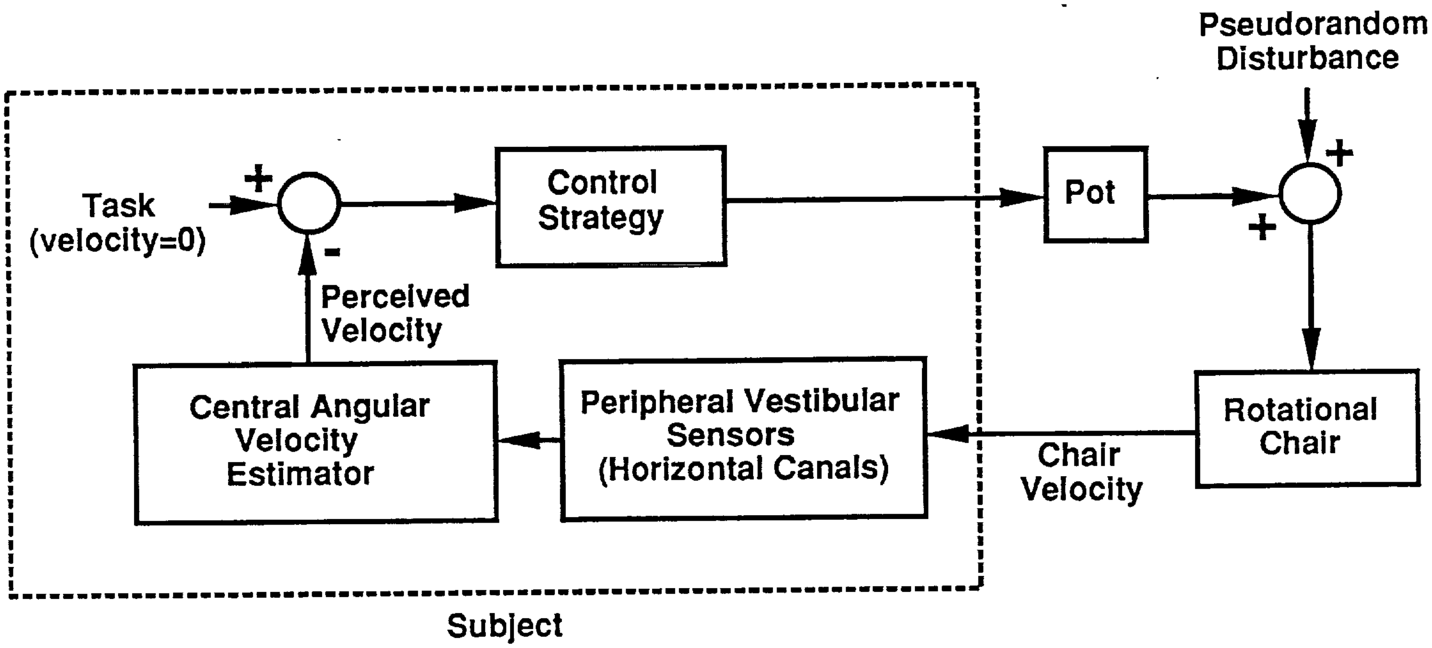

Pseudorandom Disturbance
+
+
Task (velocity=0)
+
-
Control Strategy
Pot
Perceived Velocity
Central Angular Velocity Estimator
Peripheral Vestibular Sensors (Horizontal Canals)
Rotational Chair
Chair Velocity
Subject

Figure 2

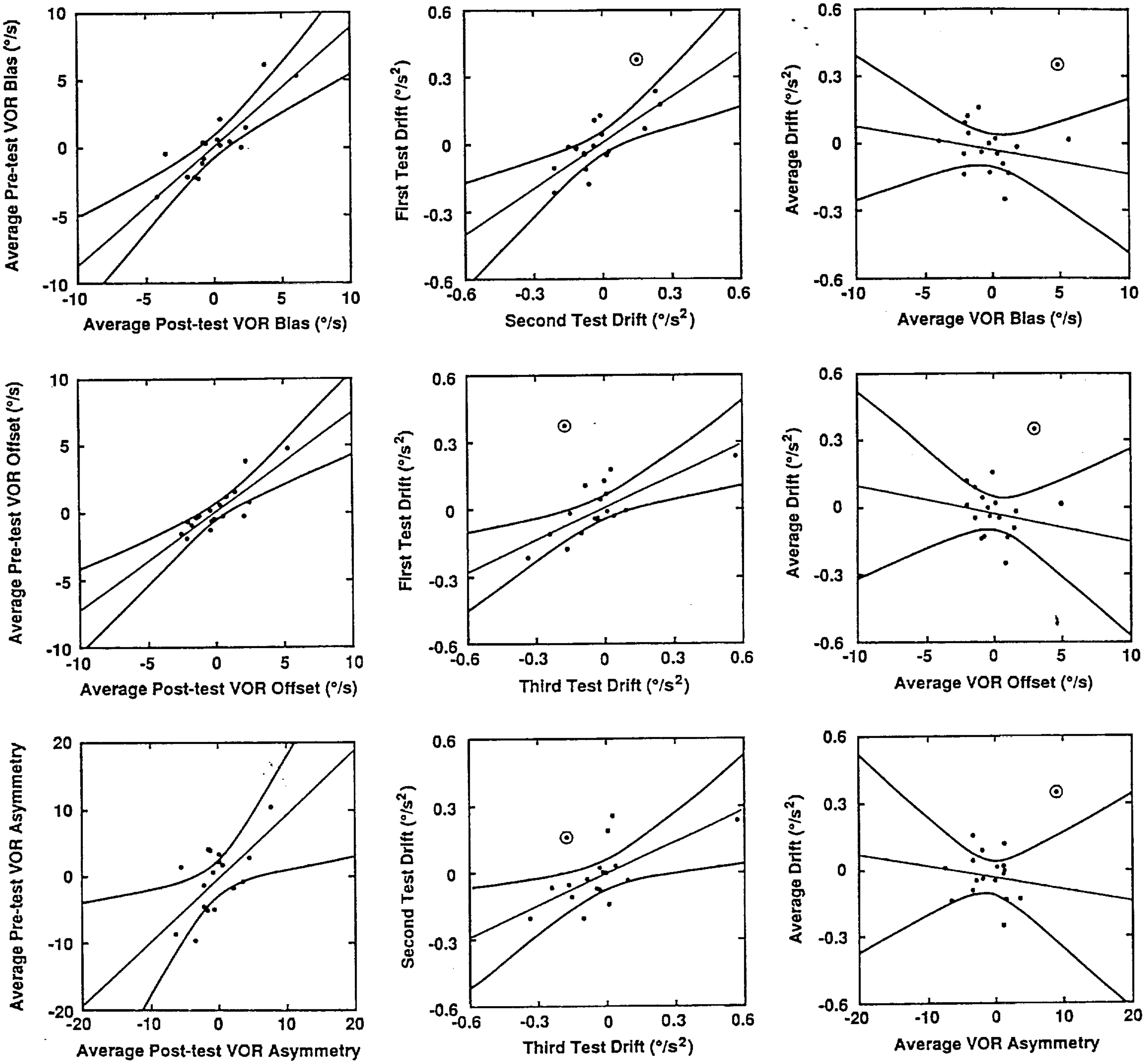

Average Pre-test VOR Bias (°/s)
Average Post-test VOR Bias (°/s)
10
5
0
-5
-10
First Test Drift (°/s²)
Second Test Drift (°/s²)
0.6
0.3
0
-0.3
-0.6
Average Drift (°/s²)
Average VOR Bias (°/s)
Average Pre-test VOR Offset (°/s)
Average Post-test VOR Offset (°/s)
First Test Drift (°/s²)
Third Test Drift (°/s²)
Average Drift (°/s²)
Average VOR Offset (°/s)
Average Pre-test VOR Asymmetry
Average Post-test VOR Asymmetry
20
10
0
-10
-20
Second Test Drift (°/s²)
Third Test Drift (°/s²)
Average Drift (°/s²)
Average VOR Asymmetry

Figure 3

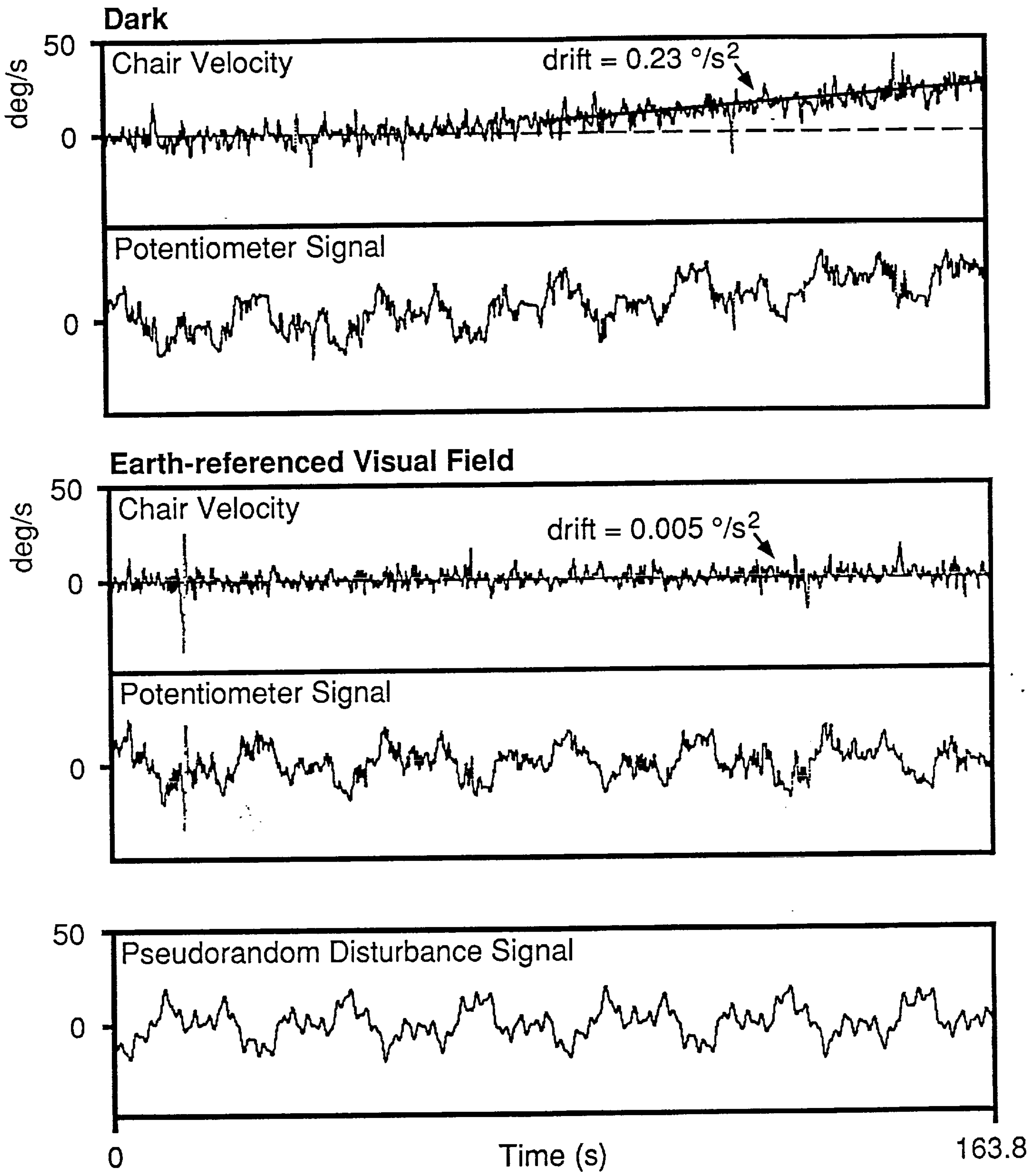

Dark
50
deg/s
0
Chair Velocity
drift = 0.23 °/s2
Potentiometer Signal
0
Earth-referenced Visual Field
50
deg/s
0
Chair Velocity
drift = 0.005 °/s2
Potentiometer Signal
0
50
0
Pseudorandom Disturbance Signal
0
Time (s)
163.8

Figure 4

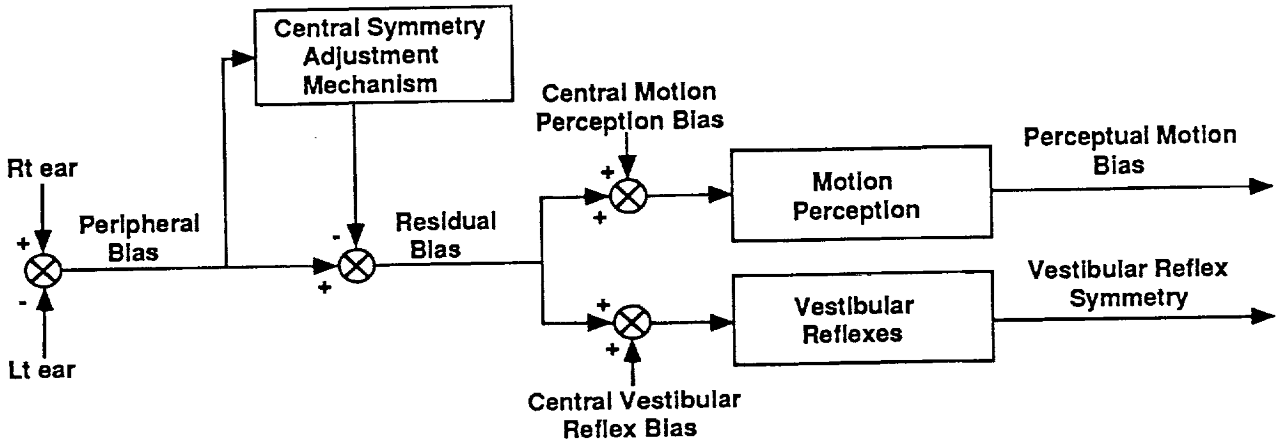

Central Symmetry Adjustment Mechanism
Rt ear
Lt ear
+
-
Peripheral Bias
-
+
Residual Bias
Central Motion Perception Bias
+
+
Motion Perception
Perceptual Motion Bias
+
+
Vestibular Reflexes
Vestibular Reflex Symmetry
Central Vestibular Reflex Bias

Figure 5