AGE-RELATED CHANGES IN HUMAN VESTIBULO-OCULAR REFLEXES: SINUSOIDAL ROTATION AND CALORIC TESTS

R. J. Peterka
F. O. Black
and
M. B. Schoenhoff

Good Samaritan Hospital and Medical Center
R.S. Dow Neurological Sciences Institute and
Department of Neuro-otology
1040 N.W. 22nd Ave.
Portland, OR 97210

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Send proofs to: Robert J. Peterka
Dept of Neuro-otology, N010
Good Samaritan Hospital & Medical Center
1040 N.W. 22nd Ave.
Portland, OR 97210

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The dynamic response properties of horizontal vestibulo-ocular reflex (VOR) were characterized in 216 human subjects ranging in age from 7 to 81 years. The object of this cross-sectional study was to determine the effects of aging on VOR dynamics, and to identify the distributions of parameters which describe VOR responses to caloric and to sinusoidal rotational stimuli in a putatively normal population. Caloric test parameters showed no consistent trend with age. Rotation test parameters showed declining response amplitude and slightly less compensatory response phase with increasing age. The magnitudes of these changes were not large relative to the variability within the population. The age-related trends in VOR were not consistent with the anatomic changes in the periphery reported by others which showed an increasing rate of peripheral hair cell and nerve fiber loss in subjects over 55 years. The poor correlation between physiological and anatomical data suggest that adaptive mechanisms in the central nervous system are important in maintaining the VOR.

Key words: vestibular, eye movements, rotation testing.

R.J. Peterka, Dept. of Neuro-otology, Good Samaritan Hospital & Medical Center, 1040 NW 22nd Ave., Portland, OR 97210, USA.

INTRODUCTION

Age-related changes in the peripheral vestibular organs include loss of hair cells (1), vestibular nerve fibers (2), and Scarpa's ganglion cells (3). The rate of loss of these peripheral vestibular anatomical structures increases in subjects older than about 55 years. If reflex function depends directly on intact peripheral vestibular structures, then we might expect a decline in VOR function paralleling anatomical deterioration. Alternatively, if the central adaptive mechanisms remain intact in older subjects, then VOR function may remain relatively stable regardless of peripheral anatomical deterioration.

Literature on age-related changes in vestibular function is limited. Experiments on humans are usually performed on a small number of subjects, and these subjects are typically young adults. The exceptions to this occur in the clinical literature on caloric testing of the VOR (4,5). The results of these studies are rather ambiguous, and include both increased, decreased, and unchanged responses with increasing age. Caloric test results are therefore not consistent with the known age dependent anatomical changes in peripheral vestibular receptors and nerve fibers.

Studies on age-related changes in VOR identified using rotation testing are less complete either because the age range of subjects was limited (6,7), or because older analysis methods did not permit detailed characterization of responses to rotation (8). However, small age-related declines have been identified in these

studies. Since normal VOR function has not been studied in the same subjects using both caloric and rotation tests, it is possible that the source of this difference between caloric and rotation tests is simply related to the choice of sample test populations.

The present experiments were designed to characterize the dynamic response properties of human horizontal VOR in a normal population using passive rotational and caloric stimuli. The population was selected to provide results related to the effects of the aging process on these reflexes, and to determine if physiological changes were consistent with anatomic changes which occur with age. Optokinetic reflex and postural control function were also tested in the same subjects on the same day, and are reported in companion papers (9,10,11).

METHODS

Vestibular reflexes were tested in 216 human subjects (90 male and 126 female) aged 7 to 81 years. Ages were approximately uniformly distributed over the entire range. Subjects were required to meet the following criteria:

1. normal age-corrected auditory pure tone responses
2. middle ear reflexes present bilaterally
3. normal middle ear impedance
4. no history of head blows of sufficient magnitude to cause loss of consciousness
5. normal neurologic and otologic physical exams

6. normal corrected vision
7. no history of ototoxic drug use
8. no history of dizziness or disequilibrium
9. moderate or absent use of alcohol with instructions to abstain from alcohol and caffeine 24 hours prior to testing
10. no use of psychotropic drugs
11. no history of meningitis, encephalitis, stroke, seizure disorders, diabetes, hypertension, heart disease, or other systemic diseases.

We did not reject subjects based on the results of any of the vestibular, optokinetic, or posture tests performed.

Rotation tests. Subjects sat in a chair mounted on an 108 N·m velocity servo-controlled motor (Contraves Goerz Corp, Model 824) which rotated them about an earth vertical axis. Subjects performed tests of VOR function with eyes closed in a darkened room. Horizontal and vertical eye movements were recorded by electrooculographic (EOG) techniques (bandwidth DC to 80Hz) using silver/silver chloride electrodes. Horizontal EOG was recorded using bitemporal electrodes, and vertical EOG was recorded by electrodes placed above and below one eye. Stimulus delivery and data collection were controlled by computer (DEC LSI 11/73). Chair tachometer signals as well as horizontal and vertical EOG were digitized and stored for later analysis. Digitizing rates were 200/s for the horizontal EOG and 50/s for vertical EOG and stimulus velocity. Calibrations of the EOG were performed before and after each rotation test.

Rotational stimuli for VOR tests included both a pseudorandom stimulus (11) and single frequency sinusoidal stimuli. Sinusoidal stimuli included 0.05, 0.2, and 0.8 Hz rotations with peak velocities of 60°/s. The duration of 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 data record was considered a transient response and was ignored in the data analysis.

Subjects were given verbal tasks throughout testing to maintain a constant level of alertness. The tasks consisted of alphabetically naming such things as names, places, and foods.

Rotation Test Data Analysis. Eye position data were differentiated to calculate eye velocity. Fast phases of the nystagmus were identified using a method similar to Barnes (12). Curve fits to the remaining slow phase eye velocity data allowed the estimation of VOR response parameters. Curve fits were made to each period of the response. Periods which contained corrupted data were rejected before the final averaging of response parameter values from the remaining periods.

The curve fits to sinusoidal responses were of the form:

$$r(t) = B_r + A_r \sin(2\pi f + P_r) \qquad [1]$$

where B_r is bias in °/s, A_r is response amplitude in °/s, P_r is response phase in degrees, and f is the stimulus frequency. The recorded chair velocity data were separately analyzed to calculate stimulus velocity amplitude, A_s, and phase, P_s. The VOR gain of the reflex is defined as the ratio A_r/A_s, and the phase of the

reflex as P_r-P_s. Since the VOR is a compensatory reflex, the values of P_r-P_s were close to -180°. For the convenience of working with smaller numbers, a value of 180° was added to P_r-P_s for the VOR test. This is equivalent to inverting the horizontal eye position data.

In order to quantify nonlinear responses, the horizontal eye velocity data was shifted in time by an amount determined by the calculated phase of each period of the response. The time shift was in a direction which brought the response into phase with the stimulus. Slow phase eye velocity was then plotted against stimulus velocity to yield a scatter of points which generally lie along a negatively sloping line. An example is shown in Figure 1. The slope of the line is equal to VOR gain.

A linear VOR response is consistent with equal VOR gains for rotations in opposite directions. One type of nonlinear VOR response, sometimes seen in abnormal subjects, has unequal gains for rotations to the right and left. This type of nonlinearity was quantified by separately calculating the slopes of the eye velocity versus stimulus velocity data for chair rotations to the right and to the left. The slopes were calculated by a least squared error fit of a two segment line to the data. 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 yields 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 response

offset defined as the eye velocity at zero stimulus velocity. A measure of response asymmetry was calculated according to the formula $100*(G_R-G_L)/(G_R+G_L)$. A zero percent asymmetry is consistent with a linear system response where gain is independent of the stimulus direction.

Caloric Tests. Four irrigations of the external ear canals were made using a Brookler-Grams closed loop caloric irrigator. Subjects were in a supine position with head elevated about 30° above horizontal to assure maximal stimulation of the horizontal semicircular canals. The caloric test was not performed on subjects under 12 years, and complete data were not obtained on other subjects who became nauseated or simply chose not to continue the irrigations because of discomfort. Each ear was alternately irrigated for 45 s at 30 and 44°C. Horizontal and vertical eye movements were recorded with EOG techniques identical to those described for rotation tests. Eye movements were recorded during and after each irrigation for a total of 3 minutes. Horizontal eye movements were analyzed to calculate peak slow phase eye velocity. Caloric responses were quantified by labyrinthine asymmetry (LA), directional preponderance (DP), and average response (AR) measures defined by:

$$LA = \frac{(RW + RC) - (LW + LC)}{RW + RC + LW + LC} \times 100 \quad [2]$$

$$DP = \frac{(RW + LC) - (RC + LW)}{RW + RC + LW + LC} \times 100 \quad [3]$$

$$AR = (RW + RC + LW + LC)/4 \quad [4]$$

where RW, RC, LW, LC are the absolute values of peak slow phase eye velocities recorded during right warm, right cold, left warm, and left cold irrigations, respectively. Subjects were tasked throughout caloric testing to maintain alertness.

Visualization of Trends. In order to visualize trends in scatterplots, a robust locally weighted regression analysis (lowess fit) was used to smooth the scatterplots (13). This smoothing is similar to a moving average filter, but is less sensitive to outlying points and allows variable amounts of smoothing. A lowess smoothing parameter of 0.5 and iteration parameter of 2 were used on all data sets.

Data Quality. The overall quality of each rotation and caloric test for each subject was subjectively given a rating of good, fair, or poor. Only good and fair quality data are included in the data summaries in the results section. Quality judgments were based on the standard deviation of response parameters (such as gain, phase, and bias from rotation tests), on the consistency of the responses throughout the duration of the stimulus, and on the accuracy of the eye movement analysis in the separation of slow and fast phases of nystagmus. The actual values of response parameters were not used in judgment of data quality. The test results from about 4 percent of subjects were rated poor for each test. Poor quality data for one subject on a given test were not used to disqualify other data from the same subject on other tests.

RESULTS

The subjects showed a wide range of responses on all measures of VOR function. Age-related changes were identified in many rotation test response measures, but the magnitude of these changes was not large relative to the variability of the data. Most changes indicated a decline in function. In contrast, no obvious or consistent changes as a function of age were found in caloric test responses. There were no significant differences in reflexes between males and females.

VOR Responses to Rotation. Typical VOR rotation test results are shown in Figure 1. Population statistics for gain, phase, bias, offset, and asymmetry are given in Table 1. The small differences in N's are due to data eliminated because of poor quality. The distributions of all parameters were fairly symmetric about their means. Gain increased with increasing frequency and had lower variance at 0.8 Hz as compared to 0.2 and 0.05 Hz. The phase variance also decreased with increasing frequency. The variances of the offset distributions were somewhat less than the variances of the bias distributions at 0.05 and 0.2 Hz, and greater at 0.8 Hz.

Neither bias, offset, nor asymmetry were highly correlated across the three test frequencies. The largest correlation coefficient was 0.71 between bias at 0.2 and 0.8 Hz. Correlations comparing bias at 0.05 and 0.2 Hz, and at 0.05 and 0.8 Hz were 0.56 and 0.52, respectively. The correlation coefficients comparing response offset at the three test frequencies ranged

from 0.43 to 0.57. Asymmetry correlations across test frequencies were the lowest of all symmetry measures (range 0.10 to 0.37).

There were small changes in rotation test gain and phase responses with age (Figure 2). In particular, all gains decreased with increasing age. The gain trend was more consistent at 0.05 Hz than at 0.2 and 0.8 Hz. Phases increased with increasing age at all frequencies tested, although the effect was more pronounced at 0.2 and 0.8 Hz than at 0.05 Hz. The age-related changes in gain and phase were both roughly linear. Linear regression slopes, intercepts, and correlation coefficients are summarized in Table 2. Rotation test measures of response symmetry (the absolute values of bias, offset, and asymmetry) showed no age-related trends.

VOR Responses to Caloric Stimuli. Caloric test results were generally in agreement with those of others who reported normal ranges of LA of about 15 to 25%. Our results were consistent with a 25% upper limit of normal since 95% of our subjects had LA measures below this value. The distribution of AR had a mean of 17.0°/s (± 9.0 s.d., range 4.5 to 63.2) and was skewed toward larger values.

Age-related effects on caloric test results were ambiguous. A linear regression curve fit to AR versus age (Figure 3A) showed an average decrease with increasing age. The linear regression had an associated correlation coefficient of -0.15 which was significantly different from zero ($P<0.05$). However the lowess fit shown in Figure 3A indicated that a linear regression was probably not an appropriate description of the data. AR decreased

for subjects up to about 40 years, and then increased at a low rate for older subjects.

Figure 3B shows the absolute value of LA versus age. The lowess fit shows essentially no change over the first 6 age decades, and a slight increase in older subjects. Due to the large variance in the data, a much larger sample would be required to determine if the small increase in older subjects was significant.

Correlations Among Rotation and Caloric Parameters. Table 3 summarizes correlations among various caloric and rotation test measures. Among rotation test response symmetry measures, bias and offset were highly correlated at all test frequencies. Bias and asymmetry showed moderate correlations (about 0.6) at 0.05 and 0.2 Hz, but no correlation at 0.8 Hz. There was a small positive correlation between offset and asymmetry at 0.05 Hz, no correlation at 0.2 Hz, and a larger negative correlation at 0.8 Hz.

The correlations between response bias at all test frequencies and caloric DP were about -0.4. Offset and DP showed a similar pattern but with slightly less negative correlations. Asymmetry and DP showed small negative correlations (about -0.2) at 0.05 and 0.2 Hz, but no correlation at 0.8 Hz. There was no correlation between LA and DP, or between LA and any of the rotation test symmetry measures.

Caloric AR and rotation test gain and phase measures are known to covary in some vestibular abnormalities (14). Within our putatively normal population, there were only small correlations

between these parameters. Correlations between AR and gain at the three test frequencies ranged from 0.22 to 0.31. The correlation between AR and phase was only -0.12 at 0.05 Hz, and less at the other two test frequencies.

DISCUSSION

VOR parameter correlations. The pattern of correlation between caloric and rotation test parameters, and among the rotation test parameters themselves apparently depends on rotation test frequency. The asymmetry parameter, which measures the difference in VOR gain for rotations to the right and left, showed the most complex frequency dependent pattern. For example, the correlations between bias and asymmetry were about 0.6 at 0.05 and 0.2 Hz, but less than 0.1 at 0.8 Hz. The correlation between caloric DP and asymmetry was also higher at 0.05 and 0.2 Hz compared to 0.8 Hz. In addition, there was a shift in the correlations between offset and asymmetry from a positive value at 0.05 Hz, to a near zero value at 0.2 Hz, and then to a negative value at 0.8 Hz. Finally, the correlations between asymmetry measures made at different test frequencies were poorer than either the bias or offset parameter correlations across frequency. The poor correlation of asymmetry measures at different test frequencies and the changing relationship of asymmetry to the other caloric and rotation test symmetry measures suggests that the physiological mechanisms which control symmetry are either

frequency dependent or that separate physiological factors dominate at different frequencies of head motion.

VOR Changes with Age. We were able to identify small age effects on some VOR response measures. The direction of change of VOR gains was expected. Other age-related changes were not expected. These include increased VOR phase leads with increasing age, and the fact that VOR function measured using the caloric test did not show the same trend as VOR function measured using rotation tests.

Age-related changes in VOR function identified in this study do not follow the same time course as age-related peripheral vestibular anatomical changes identified by others. Figure 4 shows the lowess curve fit to 0.8 Hz VOR gain versus age plotted along with curve fits to data on human crista hair cell counts (1), vestibular nerve fibers (2), and Scarpa's ganglion cells (3) as a function of age. The ordinate scales are linear and are normalized to their values at a subject age of 30 years. For ages up to about 50 years there is a gradual decline in both VOR gain and the various measures of peripheral vestibular anatomic components. For the VOR gain this gradual decline continues at about the same rate through the higher age decades. However the rate of decline of all anatomic measures greatly increases after about age 60, resulting in a divergence between the anatomical and physiological data, with the VOR functioning better in older subjects than would be predicted based on changes in peripheral vestibular anatomy.

Because the subjects of this study were volunteers, it could be argued that the sample of older subjects would be biased in favor of exceptionally healthy elderly individuals who do not reflect the physiological function of a randomly selected population. This seems unlikely for several reasons: the auditory pure tone threshold functions of our subjects were consistent with the expected age-related changes (15); extended frequency audiometry (8-20 KHz) was performed on most subjects and showed consistent monotonically declining function with increasing age; the optokinetic reflex time delay showed monotonic increases with age (11); and posture test results (9) in the same subjects showed clear age effects which appeared more closely related to the time course of peripheral vestibular anatomical changes. It seems unlikely that the peripheral vestibular system of these subjects would escape distributed aging processes when other systems did not.

The increases in VOR phase leads at higher frequencies with increasing age were not anticipated. On the surface they would seem to represent a degradation of function since increased phase leads take the system response away from the goal of perfect compensatory eye movements (unity gain and zero phase). Perhaps the phase advance is an artifact of an adaptation which improves overall VOR function. For example, studies of peripheral semicircular canal function in the squirrel monkey have shown that higher gain peripheral nerve fibers have dynamic properties which include phase advances at higher frequencies (16). Phase advances indicate a sensitivity to the velocity of cupula deflection in

addition to the cupula position. In contrast, lower gain canal fibers show cupula position sensitivity and therefore, due to the integrating accelerometer characteristics of canal biophysics, the nerve responses are in phase with head velocity at higher frequencies of rotational movements.

On the basis of our results, we might postulate that in young people, low gain tonic canal fibers provide the major contribution to the VOR. As the subject ages and there is a gradual loss of peripheral canal input due to cell death, adaptive mechanisms in the central nervous system may be able to selectively increase the contribution of high gain canal nerve input. The net effect would be to maintain the gain of the VOR at a reasonable level allowing for the generation of adequate compensatory eye movements. However this mechanism of gain enhancement would be accompanied by the possibly undesirable phase leads associated with the dynamics of the high gain canal fibers. A trade-off may be occurring in favor of maintaining the desirable feature of high response amplitude at the expense of the timing of compensatory eye movements.

This hypothesis may be consistent with the multichannel model of the VOR (17) developed to explain the dynamic properties of VOR adaptation. However, assuming that human and monkey VOR adaptation occurs by similar mechanisms, there are other studies which are not consistent with this hypothesis. Minor and Goldberg (18) have shown that phasic canal fibers do not appear to contribute at all to the VOR of the squirrel monkey. If phasic fibers do not contribute to the VOR, they cannot participate in

alterations in VOR dynamics. One might argue that these phasic fibers only contribute to the VOR when they are needed for the adaptive enhancement of the reflex. However this would be inconsistent with other results which suggest that it is an enhancement of the contribution of the tonic fibers which mediates adaptive increases in VOR gain (19).

Finally, a hypothesis calling for an increased phasic fiber contribution to the VOR of older subjects may also be inconsistent with anatomical aging results which showed relatively greater hair cell loss on the crest of the crista (1), and the greatest losses of the thick fibers innervating the canal cristas (2). Since the higher gain afferent fibers, at least in the chinchilla, tend to be larger in diameter and to originate from the crest of the crista (20), the selective loss of these cells with increasing age would preclude their participation in VOR gain enhancement.

Current understanding of the mechanisms of VOR adaptation and of anatomical changes in peripheral vestibular receptors does not provide a good explanation of our VOR data. Studies of VOR adaptation, often performed in younger animals, may not adequately characterize changes which occur with age since the aging process may also effect the functionality of the central neural networks involved in adaptation. An aging adaptive neural network could contribute its own dynamic component to the VOR which differs from the dynamic properties observed in younger animals.

Clinical Significance. The presence of age-related changes in VOR function identified using rotation tests has implications for the assessment of normal function. Part of the variability of VOR

response parameters is caused by this age effect. The square of the correlation coefficient gives an estimate of the proportion of variance related to changes with age. The VOR gain versus age measures had correlation coefficients between 0.3 and 0.4. Therefore approximately 10 to 15% of the variance of gain data is accounted for by the effect of age. Measures of normal vestibular function should account for these age effects.

Since the majority of the observed response variability is independent of age, it is clear that the functional characteristics vary widely within any given age group in a putatively normal population. To the extent that aging effects are deleterious and that our reflex measures accurately characterize the general decline in function, a significant proportion of subjects within any age group look "older" than their chronological ages and may be less functional with regard to their orientation control abilities. One could hypothesize that these subjects would be more susceptible to the development of balance and orientation control problems as their vestibular function further declines with age. Perhaps there is some threshold beyond which the brain's adaptive mechanisms are not able to compensate for the declining function. After this point is reached, subjects may develop dizziness and equilibrium control complaints, or perhaps individuals will restrict their activities so as to avoid situations which stress their remaining capabilities. A longitudinal rather than a cross-sectional study would be required to test this hypothesis.

Although we did not observe large age-related trends in VOR function, it is apparent that central adaptive mechanisms cannot sustain VOR function indefinitely in the face of increasing losses of peripheral receptors and neural substrate. It will be important to extend the age limit of our study to the eighth and ninth decades, and to explore larger amplitude and higher frequency stimuli which more nearly resemble natural head motion. The point at which physiological function begins to follow the anatomical decline will define the effective functional reserve of the central adaptive mechanisms.

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Table 1. VOR response parameters for single sine stimuli. VOR phase is in degrees, bias in °/s, offset in °/s, and asymmetry in percent. Seven percentile values on the distributions of the parameters are given.

Frequency = 0.05 Hz, N = 208

	Gain	Phase	Bias	Offset	Asymmetry
Mean	0.68	10.5	-0.44	-0.35	-0.9
S.D.	0.15	4.85	3.56	2.90	7.5
2.5%tile	0.39	0.94	-8.21	-6.11	-18.8
5%	0.44	2.47	-6.34	-4.84	-15.1
25%	0.58	7.54	-2.55	-2.03	-5.7
50%	0.67	10.27	-0.36	-0.32	-0.5
75%	0.78	13.41	1.89	1.46	4.0
95%	0.96	18.10	5.00	3.84	10.8
97.5%	1.02	19.19	6.73	6.46	13.8

Frequency = 0.2 Hz, N = 208

Mean	0.75	1.62	-0.62	-0.35	-1.5
S.D.	0.16	3.17	2.91	2.32	6.6
2.5%	0.40	-4.27	-6.58	-5.00	-14.4
5%	0.51	-3.58	-5.70	-3.98	-11.7
25%	0.65	-0.36	-2.46	-1.79	-5.9
50%	0.75	1.96	-0.65	-0.33	-1.5
75%	0.85	3.97	1.32	1.09	3.2
95%	0.99	5.95	4.32	3.47	9.7
97.5%	1.02	6.39	4.88	4.49	10.4

Frequency = 0.8 Hz, N = 204

Mean	0.84	0.79	-0.28	0.04	-1.4
S.D.	0.13	2.59	2.76	3.13	5.9
2.5%	0.59	-3.95	-6.27	-6.78	-14.6
5%	0.62	-3.07	-5.30	-5.20	-11.9
25%	0.76	-0.59	-1.98	-1.62	-4.0
50%	0.84	0.74	-0.21	-0.10	-1.1
75%	0.93	2.05	1.52	1.86	1.6
95%	1.06	5.38	3.91	5.45	8.5
97.5%	1.07	6.99	5.14	6.50	10.3

Table 2. Age effects on VOR rotation test gain and phase measures. Correlation coefficients which were significantly different from zero (P<0.05) are marked with a *.

Parameter	Slope (change/year)	Intercept at 0 years	Correlation Coefficient	N
Gain @ 0.05 Hz	-0.0030	0.80	-0.39*	208
@ 0.2 Hz	-0.0026	0.85	-0.34*	208
@ 0.8 Hz	-0.0022	0.93	-0.33*	204
Phase @ 0.05 Hz	0.029	9.3	0.12	208
@ 0.2 Hz	0.042	0.0	0.27*	208
@ 0.8 Hz	0.050	-1.2	0.39*	204

Table 3. Correlations among caloric and rotation test response parameters. Data are from the 153 subjects who completed all tests with good or fair quality data.

	DP	Bias	Offset	Asymmetry
Frequency = 0.05 Hz				
LA	-0.069	0.084	0.121	-0.005
DP		-0.406	-0.373	-0.245
Bias			0.916	0.583
Offset				0.225
Frequency = 0.2 Hz				
LA	-0.069	0.138	0.125	0.071
DP		-0.394	-0.333	-0.212
Bias			0.834	0.585
Offset				0.061
Frequency = 0.8 Hz				
LA	-0.069	0.134	0.066	0.104
DP		-0.422	-0.410	0.003
Bias			0.852	0.074
Offset				-0.438

FIGURE LEGENDS

Fig. 1. Example of VOR rotation test data. Upper trace shows slow phase eye velocity response to a 0.05 Hz, 60°/s peak velocity sinusoidal rotational stimulus. Solid curve through the data is the curve fit to each cycle. Response gain, phase, and bias are obtained from these curve fits. Lower left trace shows horizontal eye movements evoked by one period of the rotational stimulus. Solid vertical bars under the horizontal EOG trace show the location of fast phase portions of the nystagmus identified in the analysis. Lower right plot shows slow phase eye velocity plotted against stimulus velocity. The two part linear fit is used to measure response symmetry of VOR gain.

Fig. 2. VOR gain and phase as a function of subject age. Data were obtained from sinusoidal rotational stimulation at 0.05, 0.2, and 0.8 Hz. Solid curves are lowess fits.

Fig. 3. Caloric test AR (A) and LA (B) as a function of subject age. Solid curves are lowess fits.

Fig. 4. Comparison of age-related changes in VOR gain and peripheral vestibular anatomical data. The 0.8 Hz VOR gain fit is the same as in Figure 2. All curve fits to anatomic data are lowess fits to published data. All fits are plotted on a linear scale normalized to 1.0 at age 30 years. The normalization factors are 0.87 for 0.8 Hz VOR gain, 6940 crista hair cells, 17450 vestibular nerve fibers, and 18135 Scarpa's Ganglion cells.

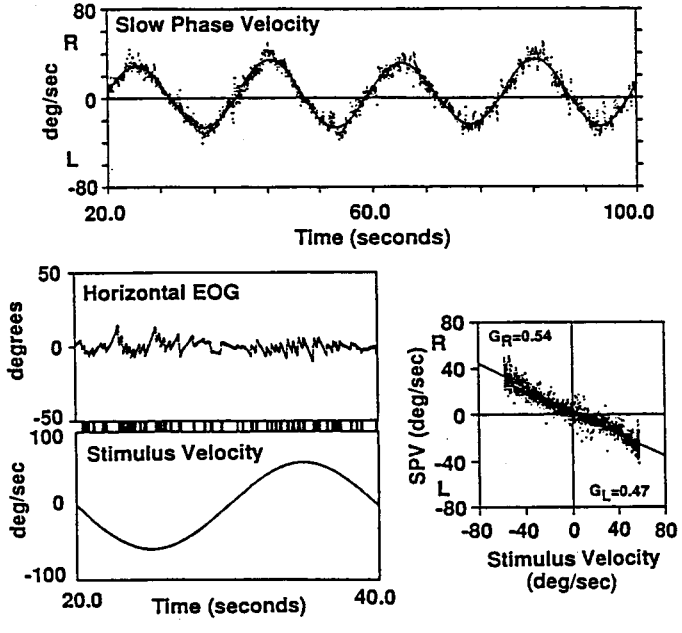

Figure 1

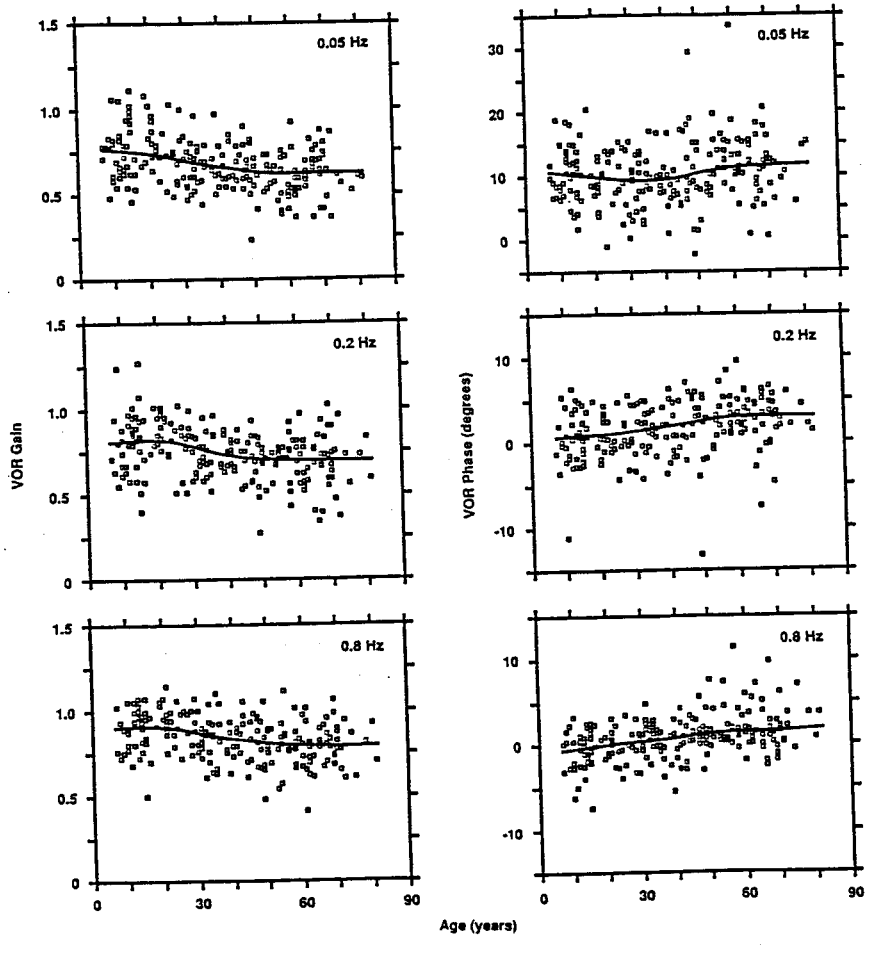

Figure 2

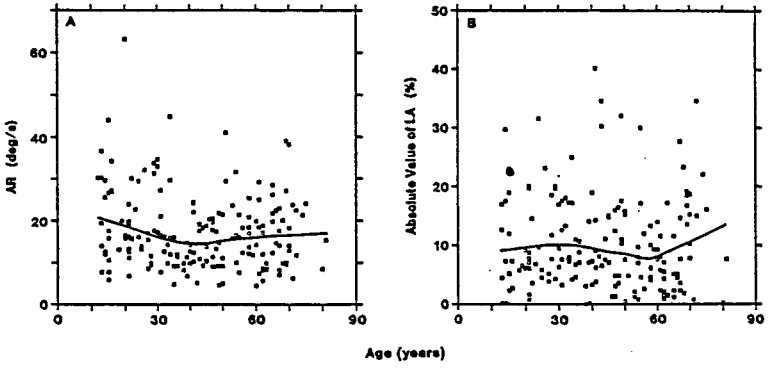

Figure 3

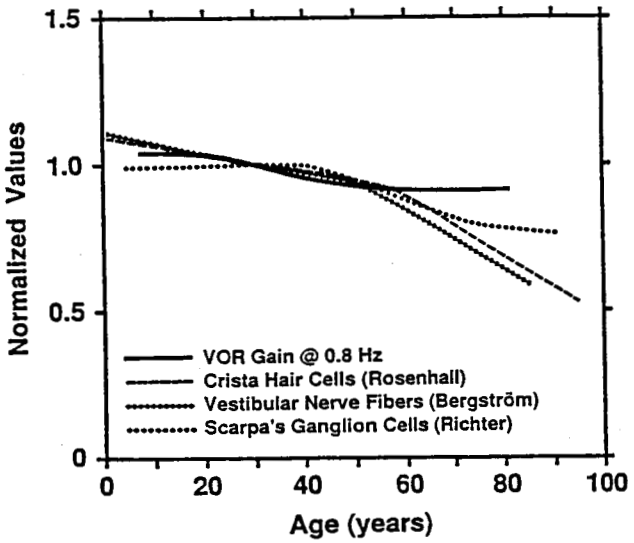
1.5
1.0
0.5
0
Normalized Values
0
20
40
60
80
100
Age (years)
VOR Gain @ 0.8 Hz
Crista Hair Cells (Rosenhall)
Vestibular Nerve Fibers (Bergström)
Scarpa's Ganglion Cells (Richter)

Figure 4