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AGE-RELATED CHANGES IN HUMAN VESTIBULO-OCULAR AND OPTOKINETIC REFLEXES: PSEUDORANDOM ROTATION 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) and optokinetic reflex (OKR) 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 and OKR reflex dynamics, and to identify the distributions of parameters which describe VOR and OKR responses to pseudorandom stimuli in a putatively normal population. In general, VOR and OKR response parameters changed in a manner consistent with declining function with increasing age. For the VOR this was reflected in declining response amplitudes, although the magnitude of the decline was small relative to the variability of the data. For the OKR the lag time of the response, probably associated with the time required for visual information processing, increased linearly with age at a rate of about 1 ms per year.

Key words: vestibular, visual-vestibular, eye movements.

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

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INTRODUCTION

A great deal is known about age-related performance declines in various visual perception tasks (1). These tasks are usually studied in controlled settings in which oculomotor performance is assumed not to play an important role. However in natural settings it is obvious that changes in oculomotor performance with age could have a deleterious effect on many aspects of visual perception. In particular, VOR and OKR normally function together to provide clear vision by generating compensatory eye movements which minimize image motion on the surface of the retina during head movements. It is important to know how the VOR and OKR change with age since a degradation in these reflexes could impair the acquisition of visual information during active and passive head movements.

During horizontal head rotations in the light with earth-fixed visual surrounds, the VOR and visual motion information through optokinetic and pursuit tracking systems combine to produce compensatory eye movements which facilitate clear vision by maintaining a fixed gaze direction. The combined VOR and visual tracking reflexes are effective over a bandwidth from DC to several Hertz (2).

Literature on age-related changes in vestibular and oculomotor 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 (3), in some work on age-related changes in pursuit tracking ability (4,5), and in responses to constant velocity optokinetic stimuli (6,7).

The present experiments were designed to characterize horizontal VOR and OKR dynamic response properties, and the variability of those responses in normal humans. The population was selected to provide results related to the effects of the aging process on these reflexes. Tests of VOR function using caloric and sinusoidal rotational stimuli, and tests of posture control were also made in the same subjects and are reported in companion papers (8,9,10).

METHODS

Vestibular and oculomotor 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. Details of subject selection are given in a previous paper (9). We did not reject subjects based on the results of any of the vestibular, optokinetic, or posture tests performed.

Rotation tests. Test conditions for the VOR were identical to those described earlier (9). Additionally for the OKR, the subject was surrounded by a circular cloth cylinder 1.8 m in diameter. The cylinder acted as a projection screen for an optokinetic stimulus. A full field optokinetic stimulus was provided by a pin hole type projector mounted on a 6.8 N·m servo motor (Genisco Technology Corp Model 1100) attached to the ceiling directly above the subject's head. The projector produced randomly placed vertical stripes of light against a mostly dark background.

Rotational stimuli for VOR tests included both single frequency sinusoidal stimuli (9) and a pseudorandom stimulus. The pseudorandom stimulus consisted of the summation of eight discrete sinusoidal frequencies. The frequency components were selected to minimize corruption of the results of the data analysis due to possible nonlinear responses of the VOR system (11). The eight frequencies were 0.0092, 0.021, 0.046, 0.095, 0.180, 0.388, 0.766, and 1.535 Hz. The nominal amplitudes of these components were all 15.6°/s except the highest frequency component which was 7.8°/s. The highest instantaneous stimulus velocity was about 100°/s. The duration of the stimulus was about 440 s. Transient responses were avoided by recording only the final 327.68 s of the trial.

The OKR of each subject was tested by recording horizontal eye movements evoked by a projected visual stimulus rotated around the stationary subject. The optokinetic projector moved under the control of a pseudorandom stimulus consisting of seven sinusoids with frequencies 0.018, 0.043, 0.092, 0.189, 0.360, 0.775, and 1.532 Hz. The amplitudes of the components were nominally 7.8°/s except the highest frequency component which was 3.9°/s. The peak instantaneous velocity was about 40°/s. The total stimulus duration was about 220 s. Transient responses were avoided by recording only the final 163.84 s of data. Complete OKR data were not obtained on all subjects since the stimulus induced motion sickness symptoms in some subjects, requiring the early termination of the test.

Subjects were given verbal tasks throughout the VOR and OKR rotation tests to maintain a constant level of alertness. The tasks consisted of alphabetically naming such things as names, places, or foods.

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 Barnes (12). The Fourier analysis of the remaining slow phase eye movements provided estimates of the response parameters given by the following equation:

$$r(t) = B + \sum_{i=1}^{N} A_i \sin(2\pi f_i + P_i) \qquad [1]$$

were B is bias or average slow phase velocity, with units of °/s, N is the number of sinusoidal components in the pseudorandom stimulus, A_i is the response amplitude at the i^{th} frequency f_i, and P_i is the response phase at the i^{th} frequency. A Fourier analysis of the stimulus velocity was performed to calculate the amplitudes and phases of the stimulus waveform. The reflex gains and phases at the N stimulus frequencies were computed as the ratio of response amplitude to stimulus amplitude, and the difference between response phase and stimulus phase, respectively. For the convenience of working with smaller numbers, a value of 180° was added to the calculated phases for tests of the VOR reflex so that unity gain and 0° phase represented perfectly compensatory eye movements.

The algorithms for gain and phase calculations were verified by simulating reflex responses with known electronic circuits. Before analysis, segments of the simulated responses were eliminated to simulate the patterns of missing data caused by the elimination of nystagmus fast phases from real eye movement data.

The gain and phase values of the VOR reflex were fitted with a transfer function equation of the following form:

$$H_{vor}(s) = \frac{K_v T_v s}{T_v s+1} \qquad [2]$$

where T_v is an estimate of the VOR time constant (units of seconds), K_v is the VOR gain constant, and s is the Laplace transform variable.

OKR gain and phase data for all subjects were well fit by a three parameter transfer function of the form:

$$H_{okr}(s) = \frac{K_o \exp(-T_d s)}{T_o s+1} \qquad [3]$$

where T_o is a time constant with units of seconds, K_o is the OKR gain constant relating slow phase eye velocity to stimulus velocity, and T_d is a time delay parameter with units of seconds describing the lag between visual field movement and eye movement. The $T_o s+1$ factor represents a lowpass filter which accounts for the declining gain with increasing frequency observed in some subjects. Larger values of T_o are consistent with gain declines beginning at lower frequencies. A value of zero for T_o (i.e. the transfer function reduces to $H_{okr}(s) = K_o \exp(-T_d s)$) accounts for subjects whose gain did not decline with increasing frequency. T_o is not the time constant associated with velocity storage and optokinetic afternystagmus (13).

Visualization of Trends. In order to visualize trends in scatterplots, a robust locally weighted regression analysis (lowess fit) was used to smooth the scatterplots (14). 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 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 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 was 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 and OKR function. Age-related changes were identified in almost all 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. There were no significant differences in reflexes between males and females.

VOR Responses. A sample of a typical response to a pseudorandom VOR stimulus is shown in Figure 1. The pseudorandom stimulus evokes a complex eye movement pattern (Figure 1C). However separation of slow and fast components, and calculation of slow phase eye velocity reveals the underlying compensatory motion (Figure 1B). A spectral analysis of slow phase eye velocity and the recorded stimulus velocity provides measures of response gain and phase as a function of stimulus frequency. Examples of gain and phase data from three subjects are shown in Figure 2. Typically the gain is lower at the lowest test frequency and increases with increasing frequency. In some subjects the gain monotonically increases over the frequency range tested and in others it appears to reach an asymptote. The solid lines through the data points represent curve fits of a two parameter transfer function (Equation 2) to the data of each subject.

The pattern of VOR gain and phase data of most subjects was similar in form to the data in Figure 2A, and was well characterized by the two parameter transfer function model (Equation 2). There were deviations from this pattern which are

exemplified by the data from two other subjects in Figures 2B and 2C. The low frequency data in 2B were fit well by the two parameter model but the higher frequency data showed increasing phase leads with increasing frequency. The phases of VOR responses to 0.05, 0.2, and 0.8 Hz sinusoidal rotations were 10.7°, 2.0°, and 6.9°, respectively for this subject, and therefore confirmed the general pattern. A more accurate curve fit to this data would require a higher frequency lead term in the transfer function. A transfer function of this form would be similar to the one used to describe the dynamic responses of phasic canal afferents in the squirrel monkey (15).

The VOR phase data in Figure 2C were fairly flat and greater than zero across all test frequencies. The phase of responses to sinusoidal stimuli were 3.7°, -2.8°, and 2.1° at 0.05, 0.2, and 0.8 Hz, again confirming the general pattern but with less phase lead than the pseudorandom data. The curve fit identified a long VOR time constant of 44.9 s. However the two parameter model does not describe either the low or high frequency phase data well. A transfer function fit with a s^k Laplace operator is better able to describe this type of data (16).

VOR gain and phase data from pseudorandom stimulus test results are summarized in Table 1. As with single frequency sinusoidal results (9), the variance of gain data was similar across all frequencies. The variance of phases data was larger at low frequencies than at high, probably reflecting the variance of the VOR time constant among individuals. The variance of the phase data at 1.535 Hz was larger than the variance at adjacent lower frequencies. This probably resulted from the fact that the stimulus amplitude of the highest frequency component was half that of the lower frequencies resulting in a lower signal-to-noise ratio at the 1.535 Hz test frequency.

The distributions of the VOR gain constants and time constants are summarized in Table 2. The gain constant distribution was symmetric with an average value of 0.72. The VOR time constant distribution was skewed toward longer time constants. Mean value was 24.4 s and median value was 23.0 s. Only two subjects had time constants below 10 s. One of these subjects (time constant = 8.2 s) had a partial unilateral loss of vestibular function as judged by caloric testing. A short time constant is consistent with a unilateral loss of vestibular function (17). However the other subject (time constant = 7.0 s) had normal caloric test results.

Comparison of VOR Measured by Single Frequency and Pseudorandom Stimuli. If the VOR were a linear system, then gain and phase data obtained from single frequency sinusoidal and pseudorandom stimulation should be identical within the random variability introduced by measurement errors. Statistical comparisons were made between the single frequency (9) and pseudorandom gains and **phases and are shown in Table 3. Single sine and pseudorandom** results were not significantly different at the lowest frequency (0.05 Hz). Small but consistent differences were evident at higher frequencies. In particular, the single frequency gain was higher at 0.8 Hz than the pseudorandom derived gain, and the pseudorandom phase values at 0.2 and 0.8 Hz were phase advanced by

about 3° compared to single frequency sine results. The improved phase response from sine tests may represent a small predictive effect or a response nonlinearity.

The gain value from the 0.8 Hz test was higher than the pseudorandom test result. This might also be due to a predictive effect. However, in this case it seems likely that the data analysis methods could have contributed to this higher value. During the analysis of the single frequency sine tests, data from stimulus cycles which were obviously corrupted were rejected. These corrupted data cycles could easily be identified based on gain, phase, and/or bias values which deviated greatly from the values for other cycles. There were several causes for poor data cycles including transient EMG interference, excessive blinking, gaze deviations from the horizontal plane, inattentiveness to tasking, and failure of the fast phase eye movement detection algorithm. With experience, it became a simple task to detect and correct these problems by rejecting the affected cycles. The net effect usually increased the average gain measure. Eye movement recordings were also transiently corrupted during pseudorandom testing, but we did not have a means of correcting or eliminating these problems and they were therefore averaged into the final result. **The rejection of corrupted portions of single sine** results, but not pseudorandom results, could account for the higher gains measured during sinusoidal rotations.

OKR Responses. Typical OKR test results from pseudorandom stimulation for two subjects are shown in Figure 3. Response gain was less than unity in all subjects. The gains of most subjects were approximately flat across the bandwidth of frequencies tested (0.02 to 1.5 Hz) as in Figure 3A. Phases were near 0° at the lowest frequencies and showed monotonic increasing phase lags as frequency increased. Since perfect tracking of the visual stimulus is represented by unity gain and zero phase at all frequencies, subjects demonstrated imperfect tracking in terms of both amplitude (gain) and timing (phase). The major variation on the typical OKR result was the presence of declining gain with increasing frequency in some subjects. Figure 3B shows the OKR transfer function data from one such subject.

The means, standard deviations, and ranges of OKR gain constant, time constant, time delay, and bias are given in Table 4. OKR response bias was near zero for all subjects. Both the gain constant and time delay had approximately symmetric distributions. In contrast, the OKR time constant had a highly skewed and possibly bimodal distribution with about 40 percent of the values near zero. OKR time constants near zero reflect the fact that OKR gains for these subjects were approximately constant over the frequency range tested.

The OKR pseudorandom stimulus was quite provocative in the initiation of motion sickness symptoms. Twenty subjects requested the termination of testing as a result of the onset of motion sickness symptoms. Approximately an equal number experienced motion sickness symptoms but were able to complete the 220 s duration OKR stimulus. It was not possible to calculate OKR gains and phases from incomplete trials using our current analysis methods. Therefore it was not possible to test the hypothesis

that abnormal OKR responses were related to motion sickness sensitivity in these highly susceptible subjects. However, OKR gains and phases from subjects who reported the onset of motion sickness symptoms but were able to complete the test did not show any obvious differences compared with subjects who did not report symptoms. Also comparisons of VOR rotation test results of OKR motion sickness susceptible subjects with nonsusceptible subjects did not reveal any differences.

Age-Related Changes in VOR and OKR. Several VOR and OKR response parameters changed with age (Figures 4 and 5), while the absolute values of VOR and OKR bias did not. Many of the age-related changes showed roughly linear trends. Linear regression slope, intercept, and correlation coefficients are summarized in Table 5. Both VOR time constant (Figure 4B), and OKR gain constant (Figure 5A) increased slightly in subjects up to about 30 years, and then decreased with increasing age. The OKR time delay parameter increased with increasing age, and showed the clearest age-related trend ($r = 0.53$ and slope = 1.2 ms/year) of all VOR and OKR parameters.

The age-related change in the OKR time constant was clearly not linear. Data in Figure 5B show that a large proportion of subjects between about 20 and 60 years had OKR time constants close to zero, indicating their OKR gains were constant across frequency. In contrast, there were very few subjects under 20 years and proportionally fewer subjects over 60 who had zero OKR time constants, indicating that on average their OKR gains declined with increasing frequency. The lowess curve fit indicates that age-related trends were minimal for subjects between 20 and 60 years. Subjects under 20 years showed an age-related decline in their OKR time constant with increasing age. Subjects over 60 years showed an age-related increase in their OKR time constant with increasing age.

DISCUSSION

Pseudorandom Testing. There are both advantages and disadvantages to the use of pseudorandom stimuli for VOR and OKR testing. An advantage is the concurrent testing of response dynamics over a large frequency bandwidth. The total test time is reduced compared to the equivalent testing using single frequency sinusoidal stimuli. In addition, all gain and phase measures obtained from pseudorandom responses are obtained at the same average level of subject arousal. Therefore a subject's reflex gains, which depend on alertness, can be compared across test frequencies without worry of possible alertness changes as in sequential testing at individual frequencies. A wide bandwidth stimulus can therefore reveal patterns of gain and phase changes over a range of test frequencies which are not as evident or as reliable when single frequency sinusoids are used. These detailed patterns of gain and phase changes with frequency may contain more clinically useful information than the simple summaries of response dynamics in terms of derived gain constants and time constants. In addition, a pseudorandom stimulus may provide a more "realistic" or "natural" stimulus than more predictable ones,

and therefore test the dynamics of the components under conditions similar to everyday conditions.

Pseudorandom testing has the disadvantage that the complexity of the eye movement responses makes it difficult to judge the quality of the responses. The failure to maintain subject alertness throughout the test coupled with the failure to recognize the lack of alertness would bias the gain and phase measures of reflex dynamics.

The similarity between pseudorandom and sinusoidal VOR test results suggests that information from the two test techniques is relatively interchangable. The most significant difference between VOR responses was the small 3° phase lead of pseudorandom results relative to sines at higher stimulus frequencies. However others have shown large differences in OKR dynamics when gain and phase data derived from single frequency sinusoidal tests are compared to pseudorandom results (18). In particular, OKR gains from sinusoidal tests are generally higher and show less phase lags at any particular test frequency than pseudorandom results. The simplest interpretation of these differences is that prediction plays an important role in visually driven eye movements. The mechanisms involved in this prediction are poorly understood, but it is known that the brain's predictive mechanisms influence the overall dynamic responses of pursuit eye movements even when pseudorandom visual stimuli are used (19). In particular, the predictive mechanism apparently favors the highest frequency component of the stimulus at the expense of lower frequency components causing the gains of lower frequency components of pursuit eye movements to be depressed while the gain of the highest frequency is enhanced. Although there are differences between pursuit and optokinetic response dynamics to pseudorandom stimulation (18), similar mechanisms to those which occur in pursuit tracking may influence optokinetic responses to full field visual stimuli.

The presence of a predictive mechanism as well as other nonlinear properties of visually guided eye movements does not necessarily disqualify the use of pseudorandom stimuli for OKR testing. Rather, pseudorandom stimuli may prove to be useful in quantifying the functionality of the predictive mechanism which is likely an important contributor to the control of gaze. Perhaps the larger proportion of young and old subjects with declining OKR gains at higher stimulus frequencies (larger T_o's) may indicate a less functional predictive mechanism for visually guided eye movements in these age groups.

VOR and OKR Changes with Age. We were able to identify small age effects on VOR and larger age effects on OKR reflexes. The direction of change of some reflex parameters were expected, such as declining VOR gains, declining OKR gains, and increased time delays in the OKR with increasing age. However the decreased high frequency OKR gain of the youngest and oldest subjects as compared to middle-aged subjects was not expected.

The rate at which the OKR time delay increased with age was quite large, and is similar to the changes found in pursuit latency with increasing age (4,5). If this increased time delay is representative of general changes in the speed of visual system

motion processing associated with visuo-motor tasks, this could affect tasks such as posture control, which use vision for feedback control. Longer feedback time delays generally contribute to decreased stability and poorer overall performance.

The interpretation of age-related changes in OKR time delay is complicated by the fact that the OKR time constant and time delay parameters are probably not independent. This is because the lag term T_os+1 in Equation 3 which accounts for the declining gain at higher stimulus frequencies also accounts for some of the phase lag. The larger the OKR time constant, T_o, the more phase accounted for by the lag term, and therefore the smaller the value of the OKR time delay parameter, T_d, required to explain the remaining phase lag. Since the youngest subjects had the largest T_o's, this would tend to bias their T_d's toward lower values. The oldest subjects also tended to have larger T_o's which should also bias their T_d's toward lower values. However Figure 5C shows that, despite this possible bias toward lower values, older subjects still had the largest T_d's in the population. Therefore, although the exact time course of the age-related change in time delay in Figure 5C may be distorted by the interaction with T_o, it is apparent that the oldest subjects did have the largest response delays.

Both younger (<15 years) and older (>65 years) subjects were relatively less responsive to the higher frequency components of the stimulus. The lower OKR responsiveness at higher frequencies could have functional consequences, particularly for older subjects. While it is generally appreciated that visual tracking reflexes improve visual-vestibular generated compensatory eye movements during low frequency head movements, visual motion information is apparently used to improve the dynamics of compensatory eye movements at higher stimulus frequencies associated with natural head movements (20). This would be particularly important for individuals who had VOR phase leads at higher frequencies (Figure 2B). Since older individuals had larger VOR phase leads on average than younger subjects (9), we might expect that the older subjects would need more help from their visual tracking reflexes to correct their imperfect VOR dynamics. However the sensitivity to optokinetic motion at higher frequencies declined in many older subjects making it less likely that visual tracking reflexes could correct for imperfect VOR dynamics.

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Table 1. VOR gain and phase (mean ± 1 s.d.) derived from responses to pseudorandom stimulation. N = 207 subjects.

Frequency (Hz)	Gain	Phase (degrees)
0.0092	0.58 ± 0.14	34.0 ± 8.6
0.021	0.64 ± 0.15	19.4 ± 5.6
0.046	0.69 ± 0.15	11.4 ± 3.8
0.095	0.71 ± 0.16	6.6 ± 2.9
0.180	0.73 ± 0.16	5.1 ± 2.7
0.388	0.75 ± 0.16	3.8 ± 2.7
0.766	0.75 ± 0.16	4.1 ± 3.5
1.535	0.74 ± 0.17	4.4 ± 6.2

Table 2. VOR response parameters for pseudorandom stimulus. Seven percentile values from the distributions of the parameters are listed. N = 207 subjects.

	Gain Constant	Time Constant (s)	Bias (°/s)
Mean	0.72	24.5	-0.1
S.D.	0.16	8.6	2.1
2.5%	0.42	13.6	-5.0
5%	0.48	14.2	-3.8
25%	0.61	18.4	-1.3
50%	0.73	23.1	-0.0
75%	0.81	28.1	1.3
95%	0.97	43.6	3.2
97.5%	1.02	47.4	3.7

Table 3. Comparison of single sine and pseudorandom gain and phase results. Positive differences indicate the average single sine parameter value was larger than average pseudorandom parameter value. A * indicates that the difference was significant at $P<0.05$ using a paired variable Student t-test comparison. The average differences listed are corrected for the difference in test frequencies between the single sine and pseudorandom stimuli. Gain and phase corrections were based on the VOR transfer function in Equation (2) with average time constant of 24.5 s and gain constant of 0.72. N's are smaller than those in Table 2 since comparisons were not made if either test had poor quality data.

Parameter	Single Sine	Pseudorandom	Average Difference	N	Significance
Gain	0.05 Hz	0.046 Hz	-0.011	199	-
	0.2 Hz	0.180 Hz	0.019	199	*
	0.8 Hz	0.766 Hz	0.095	195	*
Phase	0.05 Hz	0.046 Hz	-0.3	199	-
	0.2 Hz	0.180 Hz	-3.2	199	*
	0.8 Hz	0.766 Hz	-3.4	195	*

Table 4. OKR response parameters for pseudorandom stimulus. Seven percentile values from the distributions of the various parameters are listed. N = 179 subjects.

	Gain Constant	Time Constant(s)	Time Delay(s)	Bias(°/s)
Mean	0.65	0.080	0.180	-0.1
S.D.	0.12	0.080	0.043	0.8
2.5%	0.40	0.002	0.099	-1.7
5%	0.47	0.003	0.114	-1.5
25%	0.59	0.008	0.147	-0.7
50%	0.66	0.06	0.187	-0.1
75%	0.72	0.12	0.216	0.3
95%	0.81	0.23	0.248	1.1
97.5%	0.87	0.25	0.253	1.4

Table 5. Age effects on VOR and OKR response parameters. All correlation coefficients were significantly different from zero (P<0.05).

Parameter	Slope (change/year)	Intercept at 0 years	Correlation Coefficient	N
VOR Gain Constant	-0.0019	0.79	-0.24	207
VOR Time Constant	-0.062 s	27.0 s	-0.15	207
OKR Gain Constant	-0.0015	0.71	-0.26	179
OKR Time Delay	0.0012 s	0.13 s	0.53	179

FIGURE LEGENDS

Fig. 1. A 30 s sample of eye movements evoked by pseudorandom stimulation of the VOR. (A) shows the subject's rotational velocity, (B) slow phase eye velocity, and (C) horizontal EOG. Vertical bars between (B) and (C) show the locations of fast phases of the nystagmus detected by the computer analysis of the data.

Fig. 2. Examples of VOR gain and phase data from three subjects derived from responses to a pseudorandom rotation. Solid line through the data show the transfer function curve fit (Equation 2). Gain and frequency scales are logarithmic.

Fig. 3. Examples of OKR gain and phase data from two individuals derived from responses to pseudorandom optokinetic stimulation. Solid lines show transfer function curve fits to data. Equations of the curve fits are inset. Gain and frequency scales are logarithmic.

Fig. 4. VOR gain constant (A) and time constant (B) parameters as a function of subject age. Solid curves are lowess fits.

Fig. 5. OKR gain constant (A), time constant (B), and time delay (C) parameters as a function of subject age. Solid curves are lowess fits.

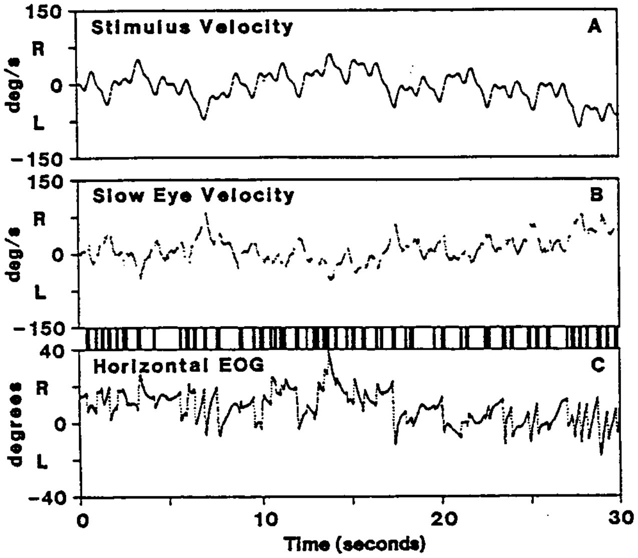

Figure 1

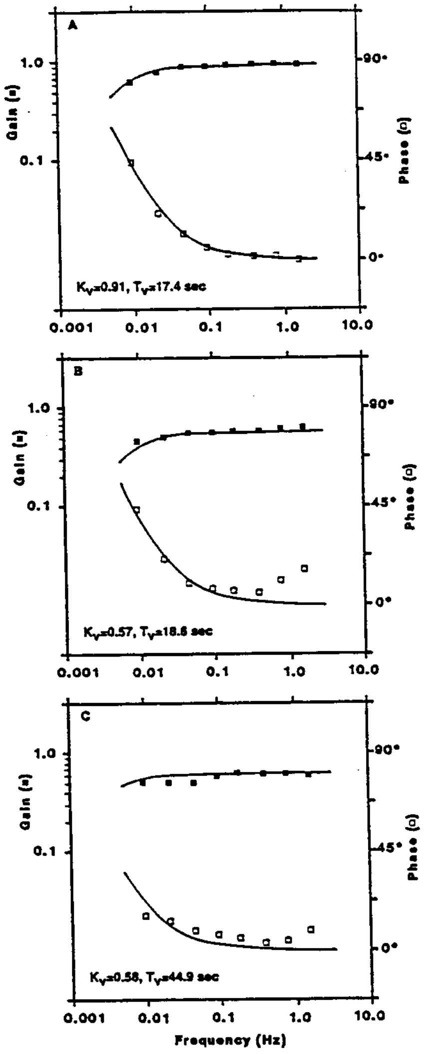

Figure 2

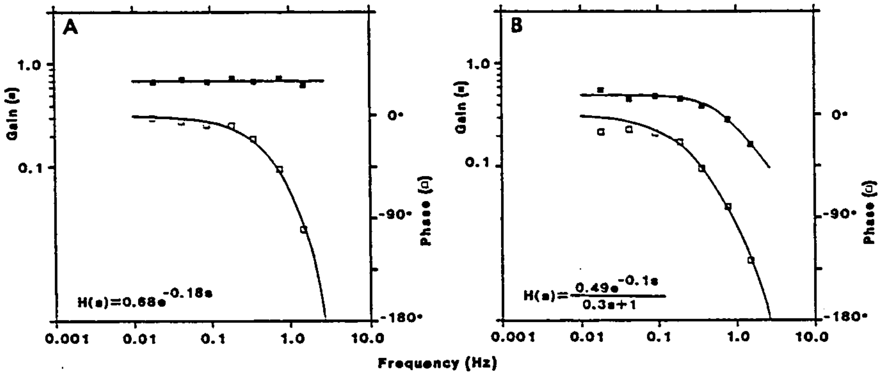

Figure 3

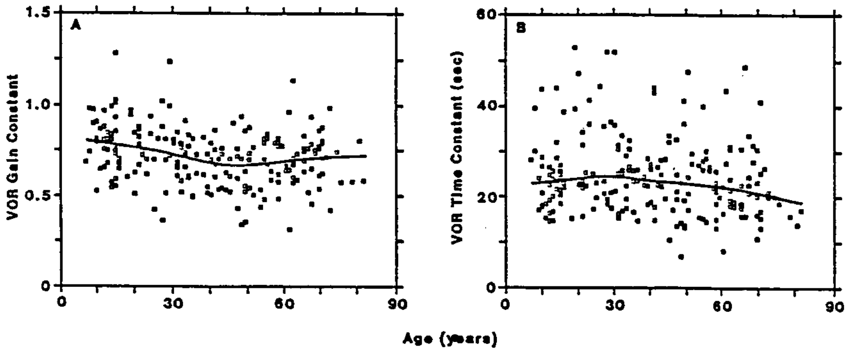

Figure 4

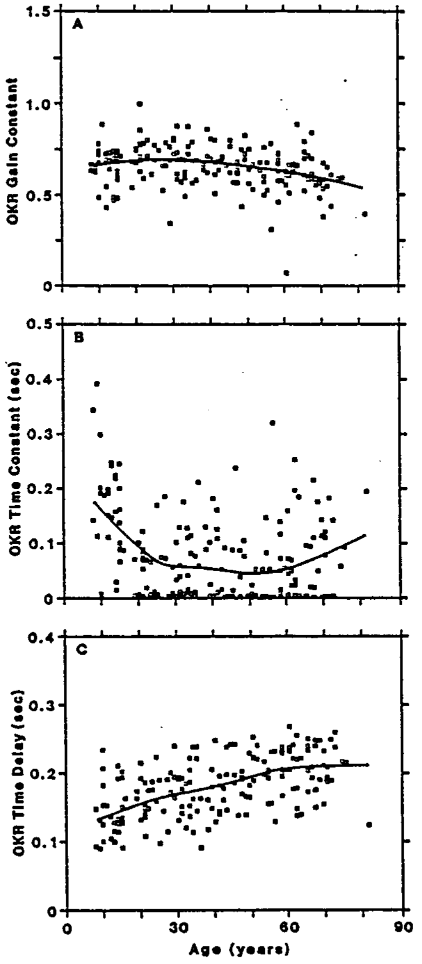

Figure 5