A Frequency and Time Domain Study of the Horizontal and Vertical Vestibuloocular Reflex in the Pigeon

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SUMMARY AND CONCLUSIONS

1. The horizontal and vertical vestibuloocular reflex (HVOR and VVOR, respectively) was studied in four chronically instrumented pigeons. Eye movements were measured using the magnetic search-coil technique (56) and were produced by rotation in the dark. During the rotation paradigms, the pigeons were either pharmacologically aroused (using amphetamine) or drug free (normal). The pigeon HVOR and VVOR were tested using step and sinusoidal rotational stimulation. The range of frequencies (0.03-6.0 Hz) and the magnitude of the sinusoidal stimuli were chosen to match those used in a previous study (1) of the responses of semicircular canal primary afferents (SCPAs) in unanesthetized (i.e., normal) pigeons. The pigeon HVOR and VVOR were tested using step and sinusoidal rotational stimulation. The range of frequencies (0.03-6.0 Hz) and the magnitude of the sinusoidal stimuli were chosen to match those used in a previous study (1) of the responses of semicircular canal primary afferents (SCPAs) in unanesthetized (i.e., normal) pigeons.

2. The gain of the HVOR and VVOR in both normal and aroused pigeons was independent of stimulus magnitude (6-30°/s) over the frequency range tested. In aroused pigeons, the frequency independent gain (G) of the HVOR (G = 0.6) and VVOR (G = 0.9) was roughly twice that for normal pigeons. Pigeon VOR phase under all combinations of orientation and arousal level was independent of stimulus magnitude except at the lowest frequency tested (0.03 Hz). At this frequency, phase lead decreased as stimulus magnitude increased for the HVOR and VVOR in both normal and aroused pigeons. At higher frequencies, the pigeon HVOR and VVOR exhibit an increasing phase lag unaccompanied by a gain change —characteristics produced by a pure time delay. The value of this time delay was about 7 ms for both the HVOR and VVOR in both normal and aroused pigeons. The HVOR and VVOR in normal and aroused pigeons lacked the higher frequency lead characteristics present in the frequency responses of most pigeon SCPAs (1).

INTRODUCTION

The function of the vestibuloocular reflex (VOR) is to help stabilize the retinal image during head rotations by producing rotations of the eyes that are nearly equal and opposite to head rotations. The three-neuron arc of the VOR consists of the semicircular canal primary afferents (SCPAs), vestibular nuclear neurons, and extraocular muscle motoneurons (44). The VOR is a feed-forward system that is driven by a head rotational
velocity signal originating in the semicircular canals and transmitted via the SCPAs to the other components of this reflex (61). Since the SCPA signal drives the VOR, certain aspects of VOR operation might be revealed by comparing the transfer characteristics (49) of the SCPAs and of the overall VOR under similar experimental conditions in the same species. For example, the time and frequency domain responses of the SCPAs and of the horizontal VOR (HVOR) have both been studied in squirrel monkeys. It has been determined in these monkeys that the dominant time constant of the responses of horizontal and vertical SCPAs ($\tau_v$) is $\approx 6 \text{ s}$ (22, 26, 27). In comparison, the dominant time constant of the VOR ($\tau_{vor}$) in squirrel monkeys was determined to be $\approx 18 \text{ s}$ for the HVOR (54). These data indicate that $\tau_{vor}$ is longer than $\tau_v$ for the HVOR in this genus. The lengthening of $\tau_v$ to $\tau_{vor}$ may be brought about by means of a centrally located “velocity storage mechanism,” which is thought to comprise part of the neural circuitry of the HVOR in monkeys (55).

From the standpoint of comparative physiology, it is of interest to compare the dynamics of the SCPAs with those of the VOR in other, nonprimate species. Since birds rely more on the vestibulocollic reflex for retinal image stabilization than do monkeys (53), the avian and primate VORs are likely to differ. The frequency response of the SCPAs has been studied in the pigeon. It has been determined that, on the average, $\tau_v$ for the responses of horizontal and vertical SCPAs in both anesthetized and unanesthetized pigeons is $\approx 10 \text{ s}$ (1, 40). Studies of the pigeon HVOR have also been made (50, 53). Mayne (48) analyzed nystagmus latency measures taken by Mower (50) and calculated $\tau_{vor}$ to be $\approx 8 \text{ s}$ for the pigeon HVOR. Outerbridge (53), however, found $\tau_{vor}$ to be $\approx 2 \text{ s}$ based on HVOR frequency response data (phase differences only) in lightly ether-anesthetized pigeons. Outerbridge (53) measured eye movements behind closed eye lids by use of the technique of electrooculography but did not attempt to calibrate the eye movement recordings.

The purpose of the present work was to determine the gain and phase characteristics of both the HVOR and VVOR in the pigeon. The magnetic search-coil technique was used to record and calibrate eye movements. The dynamics of the HVOR and VVOR were studied using sinusoidal rotational stimulation over the same frequency range and in essentially the same chronic unanesthetized pigeon preparation as was used in a previous study of the transfer characteristics of pigeon SCPAs (1). Step rotational stimulation was also used to test the pigeon HVOR and VVOR. The linearity of the pigeon HVOR and VVOR was assessed over the frequency range of interest (0.03–6.0 Hz). Also, since the VOR can be modified by arousal level (16), the HVOR and VVOR were studied in both pharmacologically aroused and in pharmacologically untreated (i.e., normal) pigeons.

**METHODS**

**Experimental preparation**

Four male pigeons (*Columba livia*), weighing $\approx 0.5 \text{ kg}$, provided the results to be reported. Each pigeon was equipped with a surgically implanted headholding device that allowed painless immobilization and precise stereotaxic positioning of the head. The details of pigeon headholder surgery have been described elsewhere (1). Each pigeon also had a scleral search coil implanted in its right eye. The surgical procedure for pigeon search-coil implantation was similar to the one already developed for monkeys (23, 36) with a few notable exceptions. First, pigeons were anesthetized with the drug Equi-Thesin (41, 42), rather than with pentobarbital sodium. Second, the search coils, which were made of Teflon-coated braided silver wire (Cooner Wire #AS632), consisted of only two wraps and had an average diameter of $\approx 1.4 \text{ cm}$. Third, when the search coil was in place, the cut edges of the conjunctiva were approximated and sutured; fine ophthalmic suture (10-O proline) was used for this purpose. About 2 wk postoperatively, all pigeons displayed a pupillary response to light in both eyes and showed no evidence of infection or oculomotor abnormality. No pigeon was tested sooner than 2 wk after search-coil surgery.

**Orientation during testing**

The test apparatus consisted, in part, of a stereotaxic U frame suspended within a gimbaled superstructure. Each pigeon was held within the stereotaxic U frame by use of a halfcylindrical trough that supported its body and a device that coupled the bird’s headholder to the stereotaxic U frame. The headholder was implanted, while the pigeon’s head was centered at stereotaxic coordinates (0, 0, 0) and oriented such that the major
plane of its horizontal semicircular canals was in parallel with the stereotaxic horizontal plane (1). This head position differed from the usual Horsley-Clark stereotaxic position (37) and is referred to as the modified stereotaxic position (MSP). The coupling device, which could be accurately positioned (±0.1 mm) with respect to the stereotaxic apparatus, was used to return the pigeon’s head to the MSP during testing.

In the MSP, the major plane of a pigeon’s horizontal semicircular canals is parallel to the stereotaxic horizontal plane (1), and the pigeon’s beak is tilted down by 40° with reference to the stereotaxic horizontal plane. Also, 40° down from horizontal is the natural angle at which undisturbed pigeons hold their heads. This angle was measured by placing a series (n = 13) of pigeons in a body-restraint device (which allowed freedom of neck and head movement) and positioning them in front of a large wall-mounted protractor in a quiet darkroom. Protractor vertical and earth vertical were aligned using a plumb line. After ~1 min in darkness and quiet, the angle between the line representing earth horizontal (i.e., protractor horizontal) and the imaginary line joining the center of the eye and the tip of the beak was measured to within 5° by sighting the protractor past the pigeon’s head using an infrared imaging device (FJW Industries Find-R-Scope). In the absence of any visual or auditory stimulation, pigeons were found to align their heads so that their beaks were tilted down from earth horizontal by 40° on the average.

In lateral-eyed animals such as the pigeon, horizontal and vertical eye movements are made in the horizontal and coronal planes, respectively. During testing, the entire test apparatus was mounted on the horizontally oriented platform of a servo-driven rotating device (Contraves-Goertz model 823). The gimballed superstructure allowed reorientation of the pigeon and stereotaxic frame with respect to the horizontal plane of rotation of the rotating device. The horizontal and coronal (beak up) stereotaxic planes were placed in the plane of rotation during testing of the HVOR and VVOR, respectively. Since the optic axis of the pigeon is not in parallel with the coronal plane, rotation in this plane may produce a torsional component. No attempt was made to record torsional eye movements in this study.

In both orientations, the axis of rotation passed through the stereotaxic coordinates (0, 0, 0) and so through the center of the bird’s head, preventing any appreciable tangential or centrifugal linear accelerations of the head during rotation. Similarly, in both orientations, the axis of rotation was colinear with the gravity vector during rotation, precluding reorientation of the gravity vector during rotation with consequent alteration of the response characteristics of the VOR (8, 9, 18).

Stimuli

The HVOR and VVOR were tested using single (discrete) sinusoidal rotations at the following eight frequencies: 0.03, 0.06, 0.12, 0.3, 0.6, 1.2, 3.0, and 6.0 Hz. All eight single sine stimuli were delivered at a peak rotational velocity of 12°/s. In addition, stimuli at the frequencies of 0.03, 0.6, and 6.0 Hz were delivered at five different levels of peak rotational velocity: 6, 12, 19, 24, and 30°/s.

The HVOR and VVOR were also tested using impulse rotational accelerations that were delivered at 450°/s². They corresponded to rotational velocity steps of 15.75°/s with a transition time of 35 ms. Steps were delivered in clockwise (CW) and counterclockwise (CCW) directions, and individual stimuli were separated by a 50-s interval to ensure that the response to a step would have dissipated before the presentation of the next stimulus. The rotational acceleration of 450°/s² produced during the step was close to the peak rotational acceleration (452°/s²) produced by 6.0 Hz rotation at 12°/s. Thus the intensities of the step stimuli were comparable to those of the highest single sine stimulus.

Since the VOR response is known to habituate through repeated exposure to the same stimulus (29), the order of presentation of the various combinations of stimulus frequency and magnitude was completely randomized when testing the VOR. Also, since vision can modify the VOR response (35), the VOR was tested in a darkened room with the pigeons enclosed in a light-tight (but ventilated) black bag.

Eye movement recording

Eye movements were recorded using the magnetic search-coil technique (23, 56). The magnetic field generating coils that were used had an inner diameter of 4 in., and each coil pair was separated by 5.25 in. The coils were mounted so that the center of the coil array was coincident with stereotaxic (0, 0, 0). The signal induced in the search coil was amplified (×1,000) on board the test apparatus and subsequently attenuated (~25 dB) after being transmitted through the rotator slip rings. Eye movements were detected by use of a phase-lock amplifier (Princeton Applied Research #5204 Lock in Analyzer) in phase (horizontal eye movements) and in quadrature (vertical eye movements) with reference to the signal induced in a horizontal field reference coil. The polarities of the eye rotational position signals were set according to an established convention (34): leftward and downward eye rotations produced positive voltages, whereas rightward and upward eye rotations produced negative voltages. The rotator
tachometer signal and both eye rotational position signals were monitored on an oscilloscope (Tektronix D12) and stored on FM tape (Hewlett-Packard #3964) at 3.75 in./s for subsequent analysis.

Calibration

The linear range of the magnetic field coil system was determined to be ±30° in both the horizontal and vertical directions. Subsequent tests on pigeons revealed that their maximum eye angular deviations rarely exceeded ±20°, either horizontally or vertically.

The gain and phase of the pigeon HVOR and VVOR are reported relative to head rotational velocity. A calibration factor relating the first derivative of the eye rotational position signal and eye rotational velocity was determined. This was done by fixing each pigeon’s head in space (in both the horizontal and vertical orientations), and then oscillating the coil array about the stationary head at a known frequency (2 Hz) and peak velocity (12°/s). To reduce the occurrence of spontaneous eye movements, the calibrations were done in the dark and the pigeons were lightly anesthetized with 10 mg/kg pentobarbital sodium delivered intramuscularly.

Arousal level

The HVOR and VVOR were tested in pharmacologically normal and in pharmacologically aroused pigeons. To test the VOR in the aroused state, pigeons were given 3 mg/kg im D-amphetamine sulfate. This dose of amphetamine has clearly observable ways without incapacitating the birds (25, 28, 64). The effect of amphetamine administration was monitored by recording the pigeon’s electrocardiogram (EKG) using a differential EKG amplifier and measuring the interbeat intervals using a triggerable digital counter (Tektronix DC 503 Universal Counter). On average, it was found that 3 mg/kg D-amphetamine sulfate raised the pigeon’s heart rate from ~2.5 to ~5 beats/s. The pigeon’s heart rate was monitored during testing in the aroused state, and amphetamine supplements were administered if the heart rate dropped below that observed after administration of the initial dose. The pigeon’s heart rate in the normal state, though not monitored routinely, remained at ~2.5 beats/s throughout the test session.

Eye movement analysis

All sinusoidal VOR eye movement data were analyzed using an eye movement analysis program (51) that was implemented on a DEC PDP 11/20 minicomputer and an array processor (CSP1 MAP 200). Eye rotational position and rotator tachometer signals were low-pass filtered (Krohn-Hite #3342, 35 Hz corner frequency) and digitized at 80 Hz for data at individual frequencies ranging from 0.03 to 1.2 Hz, at 160 Hz for data at 3.0 Hz, and at 214 Hz for data at 6.0 Hz. The program differentiated the eye rotational position record and automatically removed the fast phases of nystagmus. A continuous waveform representing slow-phase eye velocity (with DC offset removed) was then constructed. On average, three or four cycles of the response waveform were analyzed for each frequency and magnitude of stimulus. Amplitude ratio (AR) and phase of slow-phase eye velocity relative to rotator velocity were then computed. The following ratio statistics characterizing slow-phase eye velocity waveform nonlinearities were also computed (19): amplitude asymmetry (AA), skewness (SK), and coefficient of distortion (CD). The statistic AA is peak slow-phase velocity in the CCW direction divided by peak slow-phase velocity in the CW direction. The statistic SK is the time interval for the first quarter cycle divided by the time interval for the second quarter cycle in both the CW and CCW directions. Both AA and SK can be expressed as percents by taking the absolute value of the differences between these ratios and one and multiplying by one-hundred. The statistic CD is derived from Fourier analysis of the slow-phase eye velocity waveform and is the square root of the sum of the amplitudes of the second through tenth harmonic components divided by the amplitude of the first harmonic component. The CD can also be expressed as a percent by multiplying the ratio value itself by one-hundred.

Step responses were analyzed using a modular set of programs (DATS, Prosig) implemented on a DEC PDP 11/73 minicomputer. Each individual step response was analyzed separately. Each step response was digitized at 80 Hz with no prefiltering. The eye rotational position record was digitally differentiated and saccades were edited out. Zero and negative data points were removed, and the remaining slow-phase eye velocity values were transformed to natural logarithm values. The time array was then initialized at the beginning of the response, and a linear regression line was fit to the transformed data.

Transfer functions were fit to VOR frequency response data using a simple grid search program (10) implemented on an Apple II Plus microcomputer. This program fit first-order, pole-zero type transfer functions that incorporated fractional order adaptation and pure time delay terms and provided for the differential weighting of AR and phase. The program gave the transfer function coefficients for which the sum of squares of the deviations of the data points from the calculated fit were a minimum (10). Transfer functions were fit
to the VOR frequency response data of each pigeon and to the averaged VOR frequency response data of all four pigeons for each combination of orientation and arousal level. For the group average VOR fits, AR and phase values were averaged at each separate frequency.

**Statistics**

Statistical tests included the one- and two-tailed *t* tests (parametric), the Mann-Whitney *U* test (nonparametric) and the Wilcoxon signed ranks (WSR) test (nonparametric). For all comparisons, the Mann-Whitney *U* test was used unless other-

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**FIG. 1.** Examples of frequency response tracings (horizontal orientation). *A* and *C*: tachometer tracings produced during sinusoidal rotation at 0.3 Hz (*A*) and 3.0 Hz (*C*). Upward deflections indicate clockwise head rotations. *B* and *D*: horizontal vestibuloocular reflex (HVOR) responses from the same normal pigeon at 0.3 Hz (*B*) and 3.0 Hz (*D*). Upward deflections indicate counterclockwise eye rotations. *E*: detail of saccade circled in *D*; note superimposed oscillation of ~30 Hz in frequency. All traces were low-pass filtered, the cutoff frequencies were 5.5 Hz (*A–D*) and 25 Hz (*E*). Normal pigeon vertical vestibuloocular reflex (VVOR) and aroused pigeon HVOR and VVOR eye movement tracings were qualitatively similar to those of the normal pigeon HVOR shown here.
wise stated, and the comparisons were considered statistically significant when $P < 0.05$. The measures of variability of certain reported values, including the error bars associated with plotted values, represent the standard error of the mean (SE = SD/$\sqrt{n}$). Straight lines were fit by linear regression. Measures of variability associated with parameters estimated from linear regression anal-

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**FIG. 2.** Intensity function plots showing mean data (*) and associated SE values (I) and best-fit straight lines (——) relating peak head rotational velocity ($H$) and peak eye rotational velocity ($E$) at 0.6 Hz for the normal pigeon HVOR (A), normal pigeon VVOR (B), aroused pigeon HVOR (C), and aroused pigeon VVOR (D). See Fig. 1 legend for definitions of abbreviations.
ysis represent the standard error of the estimate (SEE). Goodness of fit of all linear regression analysis is indicated by the coefficient of correlation ($r$) of the data.

RESULTS

Pigeon VOR eye movements were nystagmic whenever the head rotational stimuli...
produced large angular deviations of the eyes (Fig. 1). All pigeon saccadic eye movements, whether occurring spontaneously or as the fast phases of nystagmus, were immediately followed by an oscillation of ~30 Hz in frequency (Fig. 1).

**VOR linearity**

An appraisal of the linearity of the pigeon VOR was made by studying the relationships between single sine stimulus magnitude (peak rotational velocity) and VOR response magnitude (peak slow-phase eye velocity) and phase, and by evaluating the sinusoidal form of the slow-phase eye velocity response. The relationship (intensity function) between single sine stimulus magnitude and VOR response magnitude was determined over a range of stimulus peak rotational velocities extending from ~6 to ~30°/s (CW and CCW) at three separate frequencies (0.03, 0.6, and 6.0 Hz) for both the HVOR and VVOR in both normal and aroused pigeons. Peak slow-phase eye velocity values were determined at each of five different levels of stimulus peak rotational velocity (CW and CCW). Peak slow-phase eye velocity values from all four pigeons were averaged at each level of stimulus magnitude, separately for each combination of stimulus frequency, orientation, and arousal level. Straight lines were then fit to these averaged VOR intensity function data. Averaged intensity function data (points and error bars) and best-fit straight lines for both the HVOR and VVOR in both normal and aroused pigeons at a stimulus frequency of 0.6 Hz are presented in Fig. 2. At all frequencies tested (0.03 and 6.0 Hz intensity function data not shown) the intensity functions indicate that VOR response magnitude is linearly proportional to stimulus magnitude as the latter varies from ~6 to ~30°/s. The coefficients of correlation (r) associated with the best-fit straight lines to the pigeon VOR intensity function data for all combinations of frequency, orientation, and arousal level ranged from 0.987 to 0.999. For eight degrees of freedom, all of the r’s for the intensity functions were significant.

The phase difference between the single sine stimulus and the VOR response was also determined over a range of stimulus peak rotational velocities extending from ~6 to ~30°/s (CW and CCW) at three separate frequencies (0.03, 0.6, and 6.0 Hz) for both the HVOR and VVOR in both normal and aroused pigeons. Peak slow-phase eye velocity values from all four pigeons were averaged at each level of stimulus magnitude, separately for each combination of stimulus frequency, orientation, and arousal level. Straight lines were then fit to these averaged VOR intensity function data. Averaged intensity function data (points and error bars) and best-fit straight lines for both the HVOR and VVOR in both normal and aroused pigeons at a stimulus frequency of 0.6 Hz are presented in Fig. 2. At all frequencies tested (0.03 and 6.0 Hz intensity function data not shown) the intensity functions indicate that VOR response magnitude is linearly proportional to stimulus magnitude as the latter varies from ~6 to ~30°/s. The coefficients of correlation (r) associated with the best-fit straight lines to the pigeon VOR intensity function data for all combinations of frequency, orientation, and arousal level ranged from 0.987 to 0.999. For eight degrees of freedom, all of the r’s for the intensity functions were significant.

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**TABLE 1. Best-fit parameters for frequency and time domain pigeon VOR responses**

<table>
<thead>
<tr>
<th></th>
<th>G</th>
<th>(\tau_{\text{vor}})</th>
<th>k</th>
<th>(\tau_{\text{d}})</th>
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<tbody>
<tr>
<td><strong>A. Pigeon VOR frequency response parameters (fit of mean data)</strong>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Normal HVOR</td>
<td>0.26</td>
<td>4.4</td>
<td>0.11</td>
<td>0.007</td>
</tr>
<tr>
<td>Normal VVOR</td>
<td>0.37</td>
<td>4.3</td>
<td>0.19</td>
<td>0.006</td>
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<tr>
<td>Aroused HVOR</td>
<td>0.56</td>
<td>3.0</td>
<td>0.09</td>
<td>0.007</td>
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<tr>
<td>Aroused VVOR</td>
<td>0.85</td>
<td>3.0</td>
<td>0.18</td>
<td>0.008</td>
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<tr>
<td><strong>B. Pigeon VOR frequency response parameters (mean ± SE of individual fits)</strong></td>
<td></td>
<td></td>
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<tr>
<td>Normal HVOR</td>
<td>0.34 ± 0.12</td>
<td>4.4 ± 0.9</td>
<td>0.10 ± 0.06</td>
<td>0.006 ± 0.003</td>
</tr>
<tr>
<td>Normal VVOR</td>
<td>0.39 ± 0.04</td>
<td>5.2 ± 1.1/</td>
<td>0.18 ± 0.03</td>
<td>0.006 ± 0.002</td>
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<tr>
<td>Aroused HVOR</td>
<td>0.60 ± 0.13</td>
<td>3.5 ± 0.7</td>
<td>0.12 ± 0.05</td>
<td>0.010 ± 0.004</td>
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<tr>
<td>Aroused VVOR</td>
<td>0.89 ± 0.10</td>
<td>3.0 ± 0.6</td>
<td>0.17 ± 0.02</td>
<td>0.008 ± 0.002</td>
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<tr>
<td><strong>C. Pigeon VOR step response parameters (mean ± SE of individual fits)</strong></td>
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<tr>
<td>Normal HVOR</td>
<td>0.56 ± 0.15</td>
<td>3.9 ± 0.4</td>
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<tr>
<td>Normal VVOR</td>
<td>0.88 ± 0.21*</td>
<td>3.2 ± 0.2</td>
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<tr>
<td>Aroused HVOR</td>
<td>0.69 ± 0.18</td>
<td>6.5 ± 0.8</td>
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<td></td>
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<tr>
<td>Aroused VVOR</td>
<td>0.92 ± 0.09</td>
<td>3.4 ± 0.5</td>
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</table>

*G, gain; \(\tau_{\text{vor}}\), dominant time constant for vestibuloocular reflex; k, fractional exponent representing adaptation; \(\tau_{\text{d}}\), pure time delay time constant; HVOR, horizontal vestibuloocular reflex; VVOR, vertical vestibuloocular reflex; VOR, vestibuloocular reflex. *This mean value was strongly influenced by one large gain value (G = 1.5). Exclusion of that value results in a mean ± SE of 0.68 ± 0.04. †These parameters and Eq. 1 describe the curves in Fig. 3.
between the rotational velocity stimulus and slow-phase eye velocity response waveforms were determined at each of five different levels of stimulus magnitude (CW and CCW). Phase values from all four pigeons were averaged at each level of stimulus magnitude, separately for each combination of stimulus direction (CW or CCW), stimulus frequency, orientation, and arousal level. In general, the phase lead of the VOR response at the lowest frequency of rotational stimulation (0.03 Hz) tended to decrease as stimulus magnitude increased. Straight lines were fit to the averaged VOR phase versus stimulus magnitude data, and r was determined. At a stimulus frequency of 0.03 Hz, a negative correlation existed between VOR phase lead and stimulus magnitude for all combinations of stimulus direction, orientation, and arousal level. Under the following conditions and at a stimulus frequency of 0.03 Hz, the negative correlation between VOR phase lead and stimulus magnitude was statistically significant: normal HVOR, CW, and CCW; normal VVOR, CW only; and aroused HVOR, CCW only. The phase lead of the VOR at a stimulus frequency of 0.03 Hz, averaged over all pigeons and all combinations of stimulus direction, orientation, and arousal level, decreased from 72 ± 4° at a stimulus magnitude of ~6°/s to 53 ± 4° at a stimulus magnitude of ~30°/s. By contrast, no consistent trends were observed in the VOR phase lead versus stimulus magnitude data at stimulus frequencies of 0.6 and 6.0 Hz.

An evaluation of the sinusoidal form of the pigeon VOR response to single sine rotational stimulation was made using the ratio statistics: AA, SK, and CD. All three statistics (AA, SK, and CD) were determined for the slow-phase eye velocity response waveforms at each stimulus frequency, magnitude, and direction (SK only), orientation and arousal level employed for testing the pigeon VOR. Expressed as percents, the overall averages of these statistics were: 3% for AA, 6% for SK, and 9% for CD.

**VOR frequency response**

The frequency responses of both the HVOR and VVOR in both normal and aroused pigeons were tested over the stimulus frequency range extending from 0.03 to 6.0 Hz at a constant peak rotational velocity of ~12°/s. AR and phase values of the pigeon VOR frequency response were determined at each of eight discrete values of stimulus frequency. The AR and phase values from each pigeon were averaged at each discrete value of stimulus frequency, separately for each combination of orientation and arousal level. Individual and averaged (n = 4) pigeon VOR frequency response data, for all combinations of orientation and arousal level, were fit with a transfer function (H(s)) of the following general form

\[
H(s) = (G) \frac{\tau_{\text{vor}} \cdot s^{1+k}}{(s \tau_{\text{vor}} + 1)} \cdot e^{-\tau_d s} \quad (J)
\]

where G is the frequency independent gain term, \(\tau_{\text{vor}}\) is the dominant time constant of the VOR, \(k\) is a fractional exponent representing adaptation (17, 19, 62, 65), \(\tau_d\) is a pure time delay time constant (49) and s is the Laplace operator (49). The parameters from the transfer functions that provided the best fit to the averaged VOR frequency response data are given in Table 1A. The averaged frequency response data (points and error bars) are presented for the HVOR and VVOR in both normal and aroused pigeons in Fig. 3. Also shown are transfer functions (smooth curves) based on evaluating Eq. 1 using the parameters in Table 1A.

In general, pigeon VOR frequency response gain increased with stimulus frequency for each combination of orientation and arousal level. The frequency response gain was generally <1 (log AR = 0) for the HVOR and VVOR in both normal and aroused pigeons. The aroused pigeon VVOR (Fig. 3D) was an exception, having frequency response gain values slightly >1 at the four highest frequencies tested (0.6–6.0 Hz).

The parameters of the transfer functions that provided the best fit to the individual pigeon VOR frequency response data were averaged together, and the mean values are given in Table 1B. Statistical comparisons were made between the mean parameters of Table 1B for the different conditions of orientation and arousal level. The frequency independent gain (G) of the VVOR was always greater than that of the HVOR for a given level of arousal, however, this difference was not statistically significant. Also, for a given
FIG. 3. Bode plots representing mean frequency response data (*) and associated SE values (I) and best-fit transfer functions (—) for the normal pigeon HVOR (A), normal pigeon VVOR (B), aroused pigeon HVOR (C), and aroused pigeon VVOR (D). The frequency response gains are presented as the common logarithm of the amplitude ratio (LOG AR). Both gain and phase are reported relative to head rotational velocity (RE VEL). See Fig. 1 legend for definitions of abbreviations.

orientation, G was always greater under the aroused than under the normal condition. This difference was statistically significant for the VVOR but not for the HVOR.

The other mean parameters (\( \tau_{\text{vor}}, k, \) and \( \tau_d \)) presented in Table 1B were also compared for the different conditions of orientation and arousal level. For a given level of
arousal, the values of $\tau_{\text{vor}}$ for the HVOR and VVOR were similar and did not differ significantly. For a given orientation, however, $\tau_{\text{vor}}$ was always shorter in aroused than in normal pigeons, but this difference also was not statistically significant. The value of $k$ was similar and did not differ significantly for aroused and normal pigeons for a given orientation. For both arousal levels, however, $k$ was larger for the VVOR than for the HVOR, and this difference was statistically significant. Finally, the value of $\tau_d$ was $\sim 7$. 
ms for both the HVOR and VVOR in both normal and aroused pigeons.

**VOR step response**

The step responses of the HVOR and VVOR in both normal and aroused pigeons were tested using step rotational velocity stimulation (CW and CCW) with an amplitude and transition time of 15.75°/s and 35 ms, respectively. Typical step responses from two pigeons are presented in Fig. 4. For each combination of orientation and arousal level, each pigeon was subjected to six step rotational stimuli, three CW, and three CCW. Each individual response was analyzed separately. Estimates of $G$ and $\tau_{vor}$ were made by fitting linear regression lines to VOR step response data following semilogarithmic transformation (see METHODS). In analyzing the pigeon VOR step response data, it was assumed for simplicity that the pigeon VOR could be considered as a simple, first-order system with an impulse response $[h(t)]$ relative to rotational acceleration that could be described by the following equation

$$h(t) = (G) \cdot e^{-t/\tau_{vor}}$$  \hspace{1cm} (2)

By making this assumption, no account was taken for the time domain manifestations of VOR adaptation, and so the values of $G$ and $\tau_{vor}$ as estimated from the step-response analysis must be considered as approximations.

Values of $G$ and $\tau_{vor}$ as estimated from the analysis of pigeon VOR step response data were grouped according to step direction (CW or CCW), orientation and arousal level. No significant differences in either $G$ or $\tau_{vor}$ were found when values determined from CW and CCW step rotations were compared, either for the HVOR or VVOR under either normal or aroused conditions. Since $G$ and $\tau_{vor}$ did not differ for CW and CCW step rotations, the values of these parameters as determined from the analysis of the VOR step responses were averaged over all pigeons, trials, and stimulus directions (CW and CCW), separately for each combination of orientation and arousal level. These averaged $G$, and $\tau_{vor}$ step response estimates appear in Table 1C.

![Fig. 4. Examples of step response tracings. Tracings on the left are responses to acceleration (450°/s²) from 0 to 15.75°/s CCW constant velocity rotation. Tracings on the right represent the responses to deceleration (450°/s²) back to 0 after 50 s of constant velocity rotation. A, B, C, and D: HVOR tracings from pigeon 78 for the normal (A and B) and aroused (C and D) conditions. E, F, G, and H: VVOR tracings from pigeon 79 for the normal (E and F) and aroused (G and H) conditions. All tracings were low-pass filtered with a cutoff frequency of 100 Hz. L, left; R, right; D, downward; U, upward. See Fig. 1 legend for definitions of abbreviations.](image-url)
Statistical comparisons were made between the values of G and $\tau_{\text{vor}}$ derived from the analysis of the individual pigeon VOR step responses under the various combinations of orientation and arousal level. For a given level of arousal, step gain was always higher for the VVOR than for the HVOR. Also, for a given orientation, the step gain of the VOR was always higher in aroused than in normal pigeons. However, in neither case were these differences statistically significant. These trends in pigeon VOR step gain with regard to orientation and arousal level generally agree with those already established by the VOR frequency response results. As determined from step responses, $\tau_{\text{vor}}$ was similar for the normal HVOR, normal VVOR, and aroused VVOR. The $\tau_{\text{vor}}$ value, as determined from the HVOR step responses, was longer under the aroused than under the normal condition, and this difference was statistically significant (WSR test).

Despite the approximate nature of the step response estimates, comparisons between G and $\tau_{\text{vor}}$ of the pigeon VOR as determined from either frequency response (Table 1B) or step response (Table 1C) data were made. For any combination of orientation and arousal level, VOR gain was always greater when derived from step rather than from frequency response data, but in no case were the differences statistically significant (WSR test). However, the difference between normal VVOR gain as derived from frequency response data compared with step response data approached significance ($z = 1.83, P = 0.07$). Under the normal condition, $\tau_{\text{vor}}$ was slightly shorter when derived from step rather than from frequency response data. This shortening of the step response estimates of $\tau_{\text{vor}}$ probably was due to the failure to account for adaptation effects in the analysis of the step responses (45, 67). Under the aroused condition, $\tau_{\text{vor}}$ for the HVOR was longer when derived from step rather than from frequency response data. This was true for each of the four pigeons and the mean difference was statistically significant (WSR test).

**DISCUSSION**

Eye movements produced by the HVOR and VVOR in pigeons were nystagmic when large angular deviations of the eyes were involved (Fig. 1). All pigeon saccadic eye movements, whether occurring spontaneously or as the fast phases of vestibular nystagmus, were followed by a brief period (0.1-0.5 s) of oscillation at ~30 Hz in frequency (Fig. 1, D and E). These saccadic oscillations, which have also been observed in the chicken (66) but have not been reported in any mammalian species, appear to be neurally generated. Single-unit recordings from extraocular motoneurons in the pigeon and chicken have revealed that some of these neurons fire bursts at 30 Hz coincident with saccadic oscillations (43).

**VOR response linearity**

The intensity functions relating stimulus magnitude and VOR response magnitude were linear for both the HVOR and VVOR in both normal and aroused pigeons. Thus the gain of the HVOR and VVOR in both normal and aroused pigeons was independent of stimulus magnitude within the ranges of stimulus magnitude (6-30°/s) and frequency (0.03-6.0 Hz) employed. Over restricted ranges of stimulus magnitude, intensity functions were also found to be linear for the aroused macaque monkey HVOR (24) and VVOR (19). Over expanded test ranges (up to ~300°/s), however, intensity function data for the aroused squirrel monkey (54), normal cat (21), and normal rabbit (3) all indicated that HVOR eye rotational velocities in these species saturated at higher levels of stimulus magnitude. It is probable that the eye rotational velocities of the pigeon HVOR and VVOR would also have saturated if tested at higher levels of stimulus magnitude.

Pigeon VOR phase shift was dependent on stimulus magnitude at the lowest frequency tested. A decrease in phase lead as stimulus magnitude was increased from ~6 to ~30°/s (CW and CCW) was observed for the HVOR and VVOR in both normal and aroused pigeons. A similar decrease in phase lead as stimulus magnitude was increased from zero to ~120°/s was observed for the HVOR in aroused squirrel monkeys at a frequency of 0.03 Hz. A similar decrease in phase lead as stimulus magnitude was increased from zero to ~120°/s was observed for the HVOR in aroused squirrel monkeys at a frequency of 0.02 Hz (54) and for the HVOR in normal rabbits at frequencies below 1.0 Hz (3).

For the HVOR and VVOR in normal and aroused pigeons, slow-phase eye velocity waveform nonlinearities were small when quantified using the statistics AA, SK,
When quantified using similar statistics, slow-phase eye velocity waveform nonlinearities were also observed to be small for the aroused squirrel monkey HVOR (54) and aroused macaque monkey VVOR (19); however in both cases a slight skewing of the waveform was noted. In summary, it appears that the VOR in the pigeon produces eye-movement responses that are only modestly nonlinear.

**Transfer characteristics of the VOR**

The frequency response of the VOR has been studied in various species (3, 8, 9, 12, 14, 19, 21, 24, 32, 33, 38, 52–54, 66). Taken together, the frequency response of the VOR of these species has been studied over a range of head rotational frequencies extending from 0.001 to ~7 Hz. Over this frequency range the frequency response characteristics of the VOR in all species tested can be modeled as a first-order lag system with a dominant time constant that has been designated as $\tau_{\text{vor}}$.

**The Dominant Time Constant of the VOR.** By use of step and sinusoidal rotations, we have determined that $\tau_{\text{vor}}$ in the pigeon is ~4 s. In another study (53), $\tau_{\text{vor}}$ was determined to be ~2.5 s from HVOR frequency response data (phase differences only) in lightly ether-anesthetized pigeons. For the II VOR in man, $\tau_{\text{vor}}$ was about 17 (9) and about 19 s (32), as determined from frequency response data. These values for man are quite similar to the $\tau_{\text{vor}}$ values determined from HVOR data in monkeys. The value of $\tau_{\text{vor}}$ for the HVOR as determined from both step and frequency response data was ~18 s in aroused macaque monkeys (14) and ~19 s in aroused squirrel monkeys (54). In aroused macaque monkeys, the value of $\tau_{\text{vor}}$ for the VVOR depends on the type (step or sinusoidal) and direction (CW or CCW, steps only) of the response from which it is estimated. When determined from step responses, the value of $\tau_{\text{vor}}$ was ~17 s for the slow-phase upward VVOR and ~9 s for the slow-phase downward VVOR in aroused macaque monkeys (46). However, when derived from frequency-response data, the value of $\tau_{\text{vor}}$ for the VVOR in aroused macaque monkeys was independent of response direction and was ~6 s (19).

Since the semicircular canals are the transducers that provide head rotational velocity information to the VOR, an important functional aspect of this reflex can be appreciated by comparing $\tau_{\text{vor}}$ with the $\tau_c$ of the vestibular SCPAs in the same species. In both normal (1) and anesthetized (40) pigeons, $\tau_c$ was determined to be ~10 s from the frequency-response data of both horizontal and vertical SCPAs. It is clear that $\tau_{\text{vor}}$ is shorter than $\tau_c$ in the pigeon. In the anesthetized squirrel monkey, $\tau_c$, as determined from both step and frequency response data, was ~6 s (22, 26, 27). Likewise in the normal macaque monkey, $\tau_c$, as determined from SCPA step response data, was also ~6 s (15). It appears that $\tau_{\text{vor}}$ is longer than $\tau_c$ for the HVOR in monkeys, but whether it is greater than or equal to $\tau_c$ for the VVOR is a matter of controversy. In the anesthetized cat, $\tau_c$ as determined from both step (11) and frequency response data (2) was ~4 s. Although not explicitly determined, a lower bound on $\tau_{\text{vor}}$, based on HVOR frequency response data in the cat, has been set at 12 s (60). As for the monkey HVOR, it appears that $\tau_{\text{vor}}$ is also longer than $\tau_c$ for the cat HVOR. These data indicate that, of the species investigated so far, only in the pigeon is the value of $\tau_{\text{vor}}$ shorter than that of $\tau_c$.

It has been suggested that the lengthening of $\tau_c$ to $\tau_{\text{vor}}$ for the HVOR in the monkey is accomplished by means of a centrally located velocity storage mechanism (55). This velocity storage mechanism has been modeled as a neural positive feedback loop (61). Positive feedback of the canal signal would lengthen $\tau_c$ to $\tau_{\text{vor}}$ by an amount proportional to the value of the positive feedback gain. By analogy with the model of Robinson (61), it is proposed here that the shortening of $\tau_c$ to $\tau_{\text{vor}}$ for the HVOR and VVOR in the pigeon is brought about by negative feedback of the canal signal, where the amount of shortening is proportional to the value of the negative feedback gain. The further shortening of $\tau_{\text{vor}}$ for the II VOR and VVOR in aroused compared with normal pigeons could be explained if negative feedback gain was increased under aroused conditions. It is likely that negative feedback gain would be increased under aroused conditions, since the overall gain of the HVOR and VVOR is higher in aroused compared with normal pigeons.
The amount of VOR phase lead in the low-to-middle frequency range is inversely proportional to the value of $\tau_{\text{vor}}$. In the present case for the HVOR and VVOR in both normal and aroused pigeons, and for the HVOR in normal rabbits (3) and aroused squirrel monkeys (54), VOR phase lead at low frequencies decreased as stimulus magnitude increased up to a combined stimulus level of 120°/s peak rotational velocity. Over a similar range of stimulus magnitudes, $\tau_{\text{vor}}$ as determined from the step responses of the HVOR in normal rabbits was shown to increase as stimulus magnitude increased (6). Baloh et al. (6) proposed a model for the mammalian VOR that also incorporated a neural negative feedback loop, which would lengthen $\tau_c$ to $\tau_{\text{vor}}$ by way of a decrease in negative feedback gain. Also, they explained the observed increase in $\tau_{\text{vor}}$ with an increase in stimulus magnitude in the rabbit by postulating that the negative feedback pathway saturates at higher levels of stimulus magnitude (6). Saturation of the neural negative feedback pathway can also explain the low-frequency VOR phase lead nonlinearity described above. If the negative feedback loop saturates at higher stimulus magnitudes, then feedback gain would decrease, $\tau_{\text{vor}}$ would increase, and VOR phase lead at low frequencies would decrease, thus accounting for the observed nonlinear dependency at low frequencies of VOR phase lead on stimulus magnitude in pigeons, rabbits, and monkeys.

An important functional aspect of the VOR in various species is that the dominant time constant of the SCPA head rotational velocity signal is modified before it is actually used to produce compensatory eye movements. Since the direction of this vestibular time constant modification in monkeys and cats is opposite to that in pigeons, it may subserve different teleological roles in mammals compared with birds. The lengthening of $\tau_c$ to $\tau_{\text{vor}}$, as for the HVOR in monkeys and cats, would reduce the amount of phase lead in the HVOR frequency response relative to the SCPA frequency response in the low to middle frequency range. It has been suggested that this reduction in the midrange phase lead effectively extends to lower frequencies the bandwidth over which the mammalian HVOR can produce compensatory eye movements (61). By contrast, the shortening of $\tau_c$ to $\tau_{\text{vor}}$, as for the pigeon HVOR and VVOR, would increase the amount of phase lead in the VOR frequency response relative to the SCPA frequency response in the low to middle frequency range. It is likely that avian retinal image stabilization relies as much on the vestibulocollic reflex (which produces compensatory head movements) as it does on the VOR (53). It has been suggested that the increase in the phase lead of the avian VOR is necessary to offset a phase lag introduced by the avian vestibulocollic reflex in the low to middle frequency range (53).

In cats and monkeys it is possible that the modification of the canal signal (e.g., the lengthening of $\tau_c$) is occurring at the level of the vestibular nuclei, since the time constant of the responses of vestibular nuclear neurons to rotation is close in value to that of $\tau_{\text{vor}}$ for the HVOR in these species. In particular, the time constant of the step and frequency responses of some vestibular nuclear neurons was $\sim 15$ s in normal macaque monkeys (13) and $\sim 7$ s in decerebrated, unanesthetized cats (63). It remains to be tested whether the modification of the canal signal is occurring at the level of the vestibular nuclei in pigeons as well.

VOR RESPONSE ADAPTATION. Adaptation is manifested as a phase lead and gain modification in the frequency response of the VOR. Both lumped and distributed models have been put forth to describe the effects of adaptation. The lumped or pole-zero type adaptation operator accounts for a phase lead and gain attenuation at low frequencies (45, 67) whereas the distributed or fractional order adaptation operator describes a constant phase lead and gradually increasing gain across the entire frequency spectrum (17, 65).

In man and monkey, adaptation in the VOR eye movement frequency response has been described using the pole-zero type adaptation operator \[ s \frac{\tau_a}{s \tau_a + 1}, \] the time constant of which is designated as $\tau_a$ (45, 67). For the human HVOR, $\tau_a$ as determined from frequency response data was $\sim 100$ s (32). For the aroused macaque monkey, $\tau_a$ was $\sim 122$ s for the HVOR (14) and 135 s for the VVOR (19). In the aroused squirrel...
monkey, \( \tau_a \) was \( \sim 80 \) s for the HVOR (54). For comparison, \( \tau_a \) as determined from SCPA frequency response data in the anesthetized squirrel monkey was also \( \sim 80 \) s (22). When described using the pole-zero type adaptation operator, VOR and SCPA adaptation appear to be very similar, and it has been suggested that the adaptive properties of the squirrel monkey VOR merely reflect those of the SCPAs in this species (54).

In normal pigeons (1) and gerbils (62) adaptation in the SCPA response is best described using the fractional order adaptation term \( (s^k; \ 0 < k < 1) \). Fractional order dynamics are exhibited by distributed relaxation processes (65). The normal pigeon SCPA frequency response data of Anastasio et al. (1) was pooled together and refit, and the average \( k \) value was determined to be 0.13. That value was significantly different from the average \( k \) values for the VVOR in both normal and aroused pigeons (Table 1B).

The adaptive properties of the VOR should in part reflect those of the SCPA head rotational velocity signal driving this reflex. However, since the fractional order adaptive properties of the pigeon VVOR differ significantly from those of the SCPAs in this species, it is likely that the dynamics of the overall pigeon VVOR are influenced by another distributed relaxation process such as one involving central pathways or orbital mechanics. Concerning the second possibility, it has been suggested that the orbital suspensory tissues, which exert a passive restraining force on eye movements, are best described as a distributed viscoelastic (i.e., relaxation) process (57, 59).

**Higher Frequency VOR Response.** The VOR has been studied at the higher end of the frequency spectrum (above \( \sim 2 \) Hz) in pigeons and monkeys. The HVOR and VVOR in both normal and aroused pigeons exhibits a phase lag unaccompanied by a gain change observed in the frequency responses of the HVOR and VVOR in both normal and aroused pigeons can be described by a pure time delay term \( (e^{-\pi d}) \). The value of \( \tau_d \) was similar for the frequency responses of the HVOR and VVOR in both normal and aroused pigeons and was between 6 and 10 ms (Table 1B). This value bounds the \( \tau_d \) value of 8 ms that accounted for a component of the phase lag in the higher frequency response of the HVOR in normal macaque monkeys (38).

In the monkey, electrical stimulation of the oculomotor nerve produced eye movements, detected using the magnetic search-coil technique, with a latency of 4–5 ms (58). In the rabbit (30, 31) and cat (4, 5), electrical stimulation of the vestibular nerve produced intracellularly recorded postsynaptic potentials in extraocular muscle motoneurons with a disynaptic latency. If each of the two synapses in the VOR pathway have synaptic delays of \( \sim 1 \) ms, then the time delay values as determined from VOR frequency response data agree well with those measured neurophysiologically.

In various preparations including the normal pigeon (1) and the anesthetized squirrel monkey (22, 26, 27) the higher frequency response of some SCPAs is characterized by a gain enhancement and a phase advance. It has been suggested that this SCPA lead component could compensate for the dynamic loads represented by various vestibular reflex pathways at higher frequencies (22). The higher frequency responses of the HVOR and VVOR in both normal and aroused pigeons exhibit neither the gain enhancement inherent in the SCPA signal nor the gain attenuation expected from the dynamic load of the VOR. This suggests that the SCPA lead component may indeed compensate for the dynamic loads of the pigeon HVOR and VVOR at higher frequencies. In monkeys, it is possible that the gain enhancement attributable to the SCPA lead component may precede in frequency a gain attenuation produced by the dynamic load of the HVOR at higher frequencies, resulting in an apparent gain peak at \( \sim 4 \) Hz (38).

**Arousal effects on the VOR**

As in man (16) and monkey (54), one effect of increased arousal in the pigeon was to increase the gain of the HVOR and VVOR.
The other effect of increased arousal was to lengthen $\tau_{\text{vor}}$ for the aroused pigeon HVOR. The average lengthening of $\tau_{\text{vor}}$ for the aroused pigeon HVOR was 1.7 times that for the other conditions of orientation and arousal level. The reason for this curious finding is unknown.

**Step responses of the VOR**

An analysis of the step responses of the HVOR and VVOR in normal and aroused pigeons revealed that the pigeon VOR was symmetrical in that neither $G$ nor $\tau_{\text{vor}}$ differed as a function of stimulus direction (CW or CCW). In mammals, it is also generally true that the responses of the HVOR and VVOR to step and sinusoidal rotational stimulation are symmetrical, with one notable exception. In response to step rotational velocity stimulation, $\tau_{\text{vor}}$ is longer for the slow-phase upward VVOR than for the slow-phase downward VVOR in normal cats (39), aroused cats (20), aroused macaque monkeys (46, 47), and humans (7). It has been proposed (19) that these asymmetries in the VVOR step response could result from amplitude or frequency dependent nonlinearities produced by large step stimuli. Therefore, in this study the angular acceleration of the step stimuli used to test the time domain responses of the pigeon VOR did not exceed that of the sinusoidal stimuli used to test its frequency domain responses. No asymmetries were observed in either the step or sinusoidal responses of the HVOR or VVOR in either normal or aroused pigeons. It has also been suggested that the velocity storage mechanism, which lengthens $\tau_c$ to $\tau_{\text{vor}}$ for the primate HVOR, is also present for the upward primate VVOR but is weak or absent for the downward primate VVOR (46, 47). It is proposed here that the primate velocity storage mechanism, which has been modeled as a neural positive feedback loop (61), has as its avian counterpart a neural negative feedback loop that shortens $\tau_c$ to $\tau_{\text{vor}}$ in pigeons. The lack of asymmetries in the pigeon time and frequency domain data suggest that this proposed neural negative feedback loop apparently operates symmetrically for both the HVOR and VVOR in normal and aroused pigeons.

For the pigeon HVOR and VVOR under both conditions of arousal, $G$ was always higher for step than for frequency responses, and this difference was always greater under the normal than under the aroused condition. It is likely that sudden step stimuli are inherently more arousing than are continuous sinusoidal stimuli. Therefore, since $G$ depends on arousal level, $G$ would be higher for step than for frequency responses, since the step stimulus is more arousing. It is also likely that the jump in arousal level brought about by a step stimulus is higher under the normal than under the aroused condition, explaining why the difference in $G$ between VOR step and frequency responses is greater under the normal than under the aroused condition.

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