Spontaneous and Driven Responses of Semicircular Canal Primary Afferents in the Unanesthetized Pigeon

T. J. ANASTASIO, M. J. CORREIA, AND A. A. PERACHIO

Departments of Physiology and Biophysics and Otolaryngology,
The University of Texas Medical Branch, Galveston, Texas 77550-2778

SUMMARY AND CONCLUSIONS

1. Spontaneous activity from 120 vestibular semicircular canal (SC) primary afferents and driven responses from 20 SC primary afferents to 2.3-decade bandwidth (0.029-6.152 Hz) sum of sinusoidal angular rotations were characterized in 10 unanesthetized pigeons. The results were compared with those previously gathered from barbiturate anesthetized pigeons.

2. The average spontaneous mean firing rate (MFR) of SC primary afferents in unanesthetized pigeons was found to be 168 impulses per second (I/s), \( \mu = 120 \), and is \( \sim 80\% \) higher than that for SC primary afferents in anesthetized pigeons [93 I/s, \( \mu = 149 \) (Ref. 9) and 92 I/s, \( \mu = 124 \) (Ref. 22)].

3. The spontaneous discharge of SC primary afferents from unanesthetized pigeons was classified according to the coefficient of variation (CV) of 512-1,024 interspike intervals (ISIs) into regular (CV < 0.1), intermediate (0.1 \( \leq \) CV < 0.4), and irregular (0.4 \( \leq \) CV) categories. The percentages of SC primary afferents falling within each CV category were similar for unanesthetized and anesthetized pigeons (22).

4. The relation between the spontaneous mean ISI and its standard deviation (SD) for SC primary afferents in the unanesthetized pigeon was found to be 168 impulses per second (I/s), \( n = 120 \), and is \( \sim 80\% \) higher than that for SC primary afferents in anesthetized pigeons [93 I/s, \( n = 149 \) (Ref. 9) and 92 I/s, \( n = 124 \) (Ref. 22)].

5. The spontaneous ISIs of individual SC primary afferents in the unanesthetized pigeon were found to be distributed either normally, log-normally, or according to the first passage time of the Wiener-Levy (WL) process.

6. The gain of anterior SC primary afferents at 0.25 Hz is similar for anesthetized (2.93 I \( \cdot \) s\(^{-1}\) \cdot deg\(^{-1}\) \cdot s\(^{-1}\), \( n = 14 \)) (11) and for unanesthetized (3.01 I \( \cdot \) s\(^{-1}\) \cdot deg\(^{-1}\) \cdot s\(^{-1}\), \( n = 14 \)) pigeons. Bode plots constructed from the responses to sum of sinusoidal angular accelerations reveal that SC primary afferents in unanesthetized pigeons display a phase lead and gain enhancement at frequencies between 0.6 and 6 Hz. Also, the time constant (\( r_L \)) of a first-order transfer function relating SC primary afferent firing rate to head velocity is similar for anesthetized (mean = 10.24 s, range 4.45 s to 18.61 s) (21) and for unanesthetized (mean = 7.66 s, range 4.76 s to 14.18 s) pigeons. However, the degree of adaptation, expressed here as a fractional exponent of s (31), appears to be greater in anesthetized (mean = 0.24, range 0.02 to 0.58) (21) than in unanesthetized (mean = 0.09, range 0.00 to 0.16) pigeons.

INRODUCTION

Single-unit neural responses of vestibular first order neurons have been studied in both unanesthetized and anesthetized mammals. Spontaneous and driven activity of vestibular semicircular canal (SC) primary afferent neurons have been studied in the unanesthetized rhesus monkey (8, 20, 23, 25), in the barbiturate anesthetized rhesus monkey (20), and in the barbiturate anesthetized squirrel mon-
key (14, 16, 17). In these studies, generally no difference in either the spontaneous or driven activity was reported between unanesthetized and anesthetized monkeys. The spontaneous activity of SC and otolith primary afferents, and the driven activity of SC primary afferents, have been studied in the unanesthetized cat (4) and in the unanesthetized-decerebrate cat (13). In the barbiturate-anesthetized cat, the spontaneous and driven activity of SC primary afferents (2, 12, 32, 34) and of SC and otolith primary afferents (1) have been studied. In these studies, the spontaneous mean firing rate (MFR) of SC primary afferents was generally higher in the unanesthetized cat. No difference in driven activity between unanesthetized and anesthetized cats seems to exist. In a study that compared the spontaneous discharge and tilt responses of vestibular primary afferents in anesthetized and unanesthetized-decerebrate gerbils (28), the average spontaneous MFR for pooled SC primary afferents in unanesthetized-decerebrate gerbils was significantly \( P < 0.001 \) higher than the average spontaneous MFR that was reported for an approximately equal number of SC primary afferents in the anesthetized (ketamine and urethan) gerbil.

Spontaneous activity (9, 10, 22) and electrical (22) and rotatory (21) driven activity of SC primary afferents have been studied in the barbiturate-anesthetized pigeon. Preliminary data (Correia, unpublished observations) indicated that the MFR of SC primary afferents in the unanesthetized bilateral destriate pigeon was elevated compared with that obtained from barbiturate-anesthetized pigeons (9, 10, 22). The purpose of the present study was to characterize the spontaneous and driven activity of SC primary afferents in pigeons with intact brains but free of central nervous system depressants (barbiturates). The results of the present study are compared with past studies that we (9, 10, 21) and others (22) have performed on barbiturate-anesthetized pigeons and form a basis for comparison to data we will obtain from central vestibular neurons in the unanesthetized pigeon. Additionally, the present study was designed to extend the response analyses of SC primary afferents in the anesthetized pigeon (21, 22) by using a larger bandwidth of rotation and by studying the responses of horizontal as well as anterior SC primary afferents.

**METHODS**

Ten chronically prepared, unanesthetized white king pigeons (*Columba livia*) provided useful results. Spontaneous activity was recorded from 120 SC primary afferents, and 20 canal afferents (14 anterior, 6 horizontal) were tested with angular rotation. Both the spontaneous activity and driven discharges of SC primary afferents were recorded from four pigeons. Spontaneous activity only was recorded from another four pigeons, and driven discharges only were recorded from two pigeons. During testing each animal was blindfolded and restrained in a gimballed test apparatus. Part of this apparatus was the U-frame of a stereotaxic holder (Fig. 1, lower). The bird's head was coupled to the frame by an L-shaped bracket, which was fastened to one arm of the stereotaxic U-frame by way of a stereotaxic carrier base and to the bird by clamping onto a stud that was chronically implanted into the bird's head (Fig. 1, upper). The stud was implanted while the bird's head was held with ear and beak bars, in such a manner that the horizontal SCs were in the stereotaxic horizontal plane, and the bird's mid sagittal head plane was coplanar with the mid sagittal vertical plane of the stereotaxic U-frame. Prior anatomic studies on a series of 10 pigeon cadavers revealed that the major plane of the pigeon's exposed horizontal canal was parallel with the stereotaxic horizontal plane when the pigeon's beak was tilted down 10 deg. The stud was attached to the bird's head by the following surgical procedure. Under deep barbiturate anesthesia, slots were cut in the skull behind the eyes and two stainless steel screws (no. 2-56, \( \frac{1}{4}" \)), whose heads had been machined flat, were inverted and inserted in the slots between the dura and the cranium and secured with nylon nuts. Near the front of the skull and at the base of the beak, a third stainless steel screw (no. 2-56, \( \frac{3}{4}" \)) was tapped into a naturally occurring triangular pocket of bone. These three screws were attached to the head stud using dental acrylic. Two holes (4 mm in diam) were trephined in the skull at stereotaxic coordinates that were known to correspond to the entry point of a microelectrode tipped 10 deg forward (off the transverse head plane), which intersected the vestibular nerve in its medial course between Scarpa's ganglion and the vestibular nuclei. Premachined nylon tubes were placed over the holes in the cranium and secured to the head stud and anchoring screws using dental acrylic. It was determined empirically that the microelectrode had to track through the brain at a 10 deg-forward angle to miss an intracranial artery laying between the ventral surface...
of the cerebral hemisphere and the vestibular nerve. The nylon tubes were sealed between recording sessions. Following surgery, all pigeons recuperated for a period of at least 2 wk prior to their first recording session.

Single-unit recordings were made using slender (0.2-mm shaft diam) glass micropipettes (27) carried inside a stainless steel guide tube (26 gauge). The guide tube, with the micropipette inside, was lowered to a position 2 mm above the vestibular nerve, and the micropipette was advanced toward the nerve with a hydraulic microdrive. The micropipettes, filled with either 2 or 3 M NaCl, routinely had tip diameters between 1 and 2 μm and impedance values at 1 kHz between 6 and 12 MΩ.

The gimballed superstructure that held the pigeon was mounted on the platform of a Contraves-Goertz model no. 823 rate table. In the "standard position," the pigeon's horizontal SCs were coplanar with the earth's horizontal plane and the plane of rotation. The animal could be statically tilted to any angle between ±90° in either pitch or roll. To test the horizontal SCs, the animal was held in the standard position and rotated about an earth-vertical axis. To test the vertical SCs, the animal was rolled 90 deg, placing the sagittal head plane in the plane of rotation, and rotated about an earth-vertical axis.

Stimuli included two bandwidths of sum of sinusoidal rotations. The low and high bandwidth sum of sinusoidal rotational stimuli were each composed of five frequencies ranging from 0.029 to 0.615 Hz and from 0.293 to 6.152 Hz, respectively. Two series of low and high bandwidth sum of sines were used. In one series, the five frequencies in each bandwidth were odd, prime multiples (3, 7, 13, 31, and 61) of a base frequency chosen to minimize intermodulation of responses. In early experiments, a different series consisted of five odd multiples (3, 7, 15, 31, and 63) of a base frequency; although two of the five multiples in
this series were not prime, no two frequencies were related by any harmonic lower than the fifth. The reference signals for these rotational stimuli were produced by a programmable ROM function generator. Tachometer output served as the rotational stimulus reference signal with which the responses of the SC primary afferents were compared. The function generator held reference signal amplitude constant for each frequency in a sum of sinusoidal stimulus. Peak velocity was 13.52 deg/s ± 0.47 (SEM) for each frequency component in the low bandwidth and 9.55 deg/s ± 0.19 (SEM) for each frequency component in the high bandwidth sum of sinusoidal rotational stimuli. The variability in the stimulus peak velocities represents a slight variability in rotator response at different frequencies (maximum error < 3% at 6 Hz) but primarily a deliberate shift of stimulus peak velocity to lower values in several experiments in order to decrease microelectrode movement during recording. To determine phase errors between the pigeon’s head and the rotator introduced by the dynamics of the gimbaled superstructure, a linear accelerometer (Entran EGC-240-SD) was mounted on the superstructure (off center) at the level of the head holder and tests were made of the phase error of the tachometer signal with regard to the tangential linear acceleration signal. Phase errors ranged from 3.98-deg phase lead at 0.029 Hz to −1.38-deg phase lag at 6.15 Hz. Data were not corrected for these small phase discrepancies.

Receptor of origin of individual SC primary afferents was determined by a series of manual yaw, pitch, and roll rotations and tilts (3, 12, 28). Spontaneous activity was gathered from horizontal canal units with the animal in the standard position. Spontaneous activity was gathered from vertical canal units with the animal in the standard position or rolled 90 deg (right ear down). Spontaneous activity is defined here as the neural discharge of a SC primary afferent recorded with the animal held in either of the above mentioned orientations but in the absence of any angular accelerative stimulation. Neural activity was amplified by conventional electronics and tape recorded for off-line analysis. The bandwidth of the amplification and recording system was 300 Hz–10 kHz. All data were analyzed off-line using a DEC PDP 11/20 minicomputer.

Mean interspike interval, $ISI = 1/n \sum_{i=1}^{n} ISI_i$, mean firing rate, $MRF = ISI^{-1}$, SD = $M_2^{1/2}$, coefficients of variation, $CV = SD/ISI$, skewness, $\beta_1 = M_3/M_2^{3/2}$, kurtosis, $\beta_2 = M_4/M_2^2$, and excess, $\beta_2 - 3$ (26) were calculated for $n = 1,024$ or 512 interspike intervals (ISIs) (measured with a resolution of 10 μs) from segments of the spontaneous activity of individual SC primary afferents. In the above equations (see Ref. 26)

$$M_k = 1/n \sum_{i=1}^{n} (ISI_i - \bar{ISI})^k \quad (K = 2, 3, 4 \cdots)$$

Cycle histograms of binned impulse frequency were constructed from the responses to sum of sinusoidal rotational stimulation. The bin width was fixed at 100 ms for the slow sum of sines and 10 ms for the fast sum of sines. The amplitude, phase shift, and DC level of the response was determined by fitting a sum of sinusoids of known frequencies through the cycle histogram using a nonlinear least-squares algorithm. The frequencies of the sum of sinusoidal fits were identical to those of the sum of sinusoidal stimuli. Complete sums of sinusoids were fit to the positive part of the rectified responses as though the rectified data were continuous with negative values of discharge frequency (24). Phase relations and amplitude ratios (ARs) were calculated between the various frequency components of the digitized tachometer signal and the corresponding frequency components of the best-fit curve to the cycle histogram response.

Each of the two bandwidths of sum of sinusoidal stimuli were composed of five frequencies that spanned ~1.3 decades. The driven-discharge analysis program was restricted to 1,024 bins per sum of sinusoidal data segment. One consequence of this bin number restriction was that the higher frequencies in each segment of sum of sinusoidal data was sampled with less than optimal resolution, resulting in a constant phase error that depended on the frequency of the data. By analyzing an electronically generated pulse train that was modulated by the sum of sinusoidal stimulus signals, phase errors due to bin resolution restrictions were found to range from 0.48-deg phase lead at 0.029 Hz to 11.55-deg phase lead at 6.15 Hz. Data were corrected for phase errors due to bin resolution restrictions. Transfer functions were fit to AR and phase values by using a nonlinear least-squares method (6). Statistics and parameters describing the spontaneous activity and driven discharge, respectively, of SC primary afferents in the unanesthetized pigeon were compared with one another and with those from the anesthetized pigeon. All statistical comparisons were made using the two-tailed t test unless otherwise indicated, and statistically insignificant differences are assumed when $P > 0.05$.

**RESULTS**

Analysis of spontaneous discharge was performed on 120 SC primary afferent neurons from eight unanesthetized pigeons. This sample consisted of 31 horizontal, 82 anterior, and 7 posterior afferents. No significant difference was observed when comparisons were...
made between the average spontaneous MFRs of the following SC primary afferent combinations: anterior versus horizontal, anterior versus posterior, and horizontal versus posterior. For 61 of the 82 anterior afferents, spontaneous discharge was gathered while the animal was in the standard position, and for 21 of the 82 anterior afferents, spontaneous discharge was gathered after the animal was maintained in a 90-deg roll position for 30 s. The average spontaneous MFR of the anterior afferents tested in the standard position was 166 I/s ± 12 (SEM), and the average spontaneous MFR of the anterior afferents tested in the 90-deg roll position was 184 I/s ± 12 (SEM). No significant difference in MFR was noted for spontaneous activity of anterior afferents in the standard position when compared with those in the 90-deg roll position. Although tilt did not significantly affect the MFR of anterior afferents on the average, tilt did affect the spontaneous discharge rate of individual SC primary afferents in the unanesthetized pigeon. During static tilts of 10 deg either pitch up or pitch down, the spontaneous discharge rate was changed (i.e., either increased or decreased) by 10% or more in 53% (8/15) of the SC primary afferents tested in three unanesthetized pigeons. Because, on the average, MFR was not significantly different for the comparisons listed above, tilted anterior afferent spontaneous data were pooled with those gathered in the standard position. These pooled data were then combined with those gathered from horizontal and posterior afferents, and a histogram of this pooled distribution is presented in Fig. 2A. The overall average MFR was determined to be 168 I/s ± 7 (SEM), the median MFR was 161 I/s, and individual values varied from 8 to 396 I/s. For comparison, also presented in Fig. 2A is a distribution of spontaneous MFRs from a sample of 149 anterior SC primary afferents from barbiturate-anesthetized pigeons (9). These spontaneous discharge data were gathered while the anesthetized pigeons were rolled 90 deg from the standard position. The average spontaneous MFR for the anesthetized preparation was 93 I/s ± 5 (SEM). The average spontaneous MFR of the 21 anterior afferents tested in the 90-deg roll position in the unanesthetized pigeon was significantly faster than the average spontaneous MFR of the anesthetized sample (one-tailed t test, P < 0.001). Also, the overall average spontaneous MFR for the unanesthetized preparation was significantly faster than the average mean for the anesthetized preparation (one-tailed t test, P < 0.001).

The CV of the spontaneous ISI has been shown to correlate with the dynamic response properties of SC primary afferents (17). Figure 2B presents the distribution of CVs of the spontaneous ISIs of SC primary afferents in unanesthetized pigeons. The CVs ranged from 0.06 to 1.40. Arrows indicate arbitrary divisions of the distribution into three categories of “regularity” of firing. Afferents were grouped into regular (CV < 0.1), intermediate (0.1 ≤ CV < 0.4), and irregular (0.4 ≤ CV) classes. Using this division, 35/120 (29%) SC primary afferents were classified as regular; 48/120 (40%) were classified as intermediate; and 37/120 (31%) were classified as irregular. Lifschitz (22) determined the CV distribution (also shown in Fig. 2B) of 122 horizontal SC primary afferents from the barbiturate-anesthetized pigeon preparation: 36/122 (29%) were regular; 46/122 (38%) were intermediate; and 40/122 (33%) were irregular using the CV classifications enumerated above. No significant difference was found between the unanesthetized and anesthetized CV distributions (χ² test, P > 0.05). In the unanesthetized pigeon, the average spontaneous MFRs for the three CV categories were: regular, 194 I/s ± 9 (SEM); intermediate, 198 I/s ± 12 (SEM); and irregular, 103 I/s ± 10 (SEM). No significant difference in the spontaneous MFR was found between regular and intermediate afferent categories. However, irregular afferents had a significantly slower MFR than did either regular or intermediate afferents: regular versus irregular (one-tailed t test, P < 0.001); intermediate versus irregular (one-tailed t test, P < 0.001).

Because the distribution of CVs was not significantly different, but the ISI was significantly smaller in unanesthetized as compared with anesthetized pigeons, we studied the relation between ISI and SD for SC primary afferents in unanesthetized pigeons. A scatterplot of spontaneous ISI against the SD for 120 neurons is plotted in Fig. 2C. Also presented in the figure is the best-fit power
function and 99% tolerance limits (33). A best-fit power function provided a significantly better fit to these data than did a best-fit straight line ($P < 0.001$), as determined by using the Williams and Kloot test (19). The equation (exponent $\pm$ SE of the estimate) and correlation coefficient ($r$) for the power function was

$$SD = 0.049(ISI)^{1.769 \pm 0.005}, \quad r = 0.86 \quad (1)$$

Correia and Landolt (10) regressed spontaneous ISI against SD for 51 anterior afferents in the anesthetized pigeon. The equation for the best-fit power function that described those data was

$$SD = 0.072(ISI)^{1.827 \pm 0.157}, \quad r = 0.81 \quad (2)$$

The slopes and intercepts of the best-fit lines to the log-log transformation of Eqs. 1 and 2 were compared. Although the parameters in Eqs. 1 and 2 are similar and the log transforms of the coefficients were not significantly different, the log transforms of the exponents were significantly different ($P < 0.05$).

Pearson and Hartley (26) have shown that univariate probability density functions (pdfs) can be characterized by coordinates corresponding to the coefficients of skewness and excess. Because currently there are no data
regarding synaptic events in the SC neuroepithelium in warm-blooded animals, we (10) have used the pdfs of ISI histograms to make inferences about events related to the origin of spontaneous discharge in the anesthetized pigeon (see DISCUSSION). A similar analysis for the unanesthetized pigeon is presented in Fig. 2D, which is a scatterplot of the coefficient of skewness ($\beta_1$) versus the coefficient of excess ($\beta_2-3$) of the spontaneous ISIs of 118 SC primary afferents. The best-fit straight line relating $\beta_1$ and $\beta_2-3$ for the entire population (120 SC primary afferents) is presented below

$$\beta_1 = 0.75(\beta_2-3) - 0.16, \quad r = 0.999 \quad (3)$$

The points that comprise this plot (Fig. 2D) appear to fall along the lines representing the gamma and the WL families of distributions. However, the slope of the best-fit line relating $\beta_1$ and $\beta_2-3$ of the ISI histograms is significantly different from the slopes of both the gamma line (slope = 0.66, $P < 0.001$) (26) and the WL line (slope = 0.60, $P < 0.001$).

Because the dominant distribution describing ISI histograms could not be determined unequivocally by a linear-regression analysis of $\beta_1$ and $\beta_2-3$ coefficients, individual pdfs were fit to the ISI distributions of representative SC primary afferents. Twenty-five percent of the points (30/120) fell within a box whose ($\beta_1$, $\beta_2-3$) coordinates were $\pm 0.1$ about (0,0) (coordinates for the normal distribution). Forty-five percent of the points (54/120) fell within a box whose ($\beta_1$, $\beta_2-3$) coordinates were $\pm 0.5$ about (0,0). By using methods described previously (5, 7, 10), best-fit pdfs were determined for all of the ISI histograms whose ($\beta_1$, $\beta_2-3$) statistics fell within the $\pm 0.1$ box. Candidate pdfs tested were: normal, log-normal, WL, and gamma. Also tested were seven ISI histograms whose ($\beta_1$, $\beta_2-3$) coordinates fell along with the best-fit line described by Eq. 3. Mean-square error (MSE) was used as a measure of goodness of fit. The normal distribution produced the best-fit in 14/30 (47%) of the ISI histograms whose skewness and excess coefficients fell in the $\pm 0.1$ box. The log-normal produced the best-fit in 9/30 (30%), and the normal produced the best-fit in 7/30 (23%). Excluding the distributions whose skewness and excess coefficients were near the origin, 7/7 of the remaining ISI histograms whose coefficients were along the best-fit straight line were best-fit by the pdf for the first passage time of the WL process. This distribution provided a statistically significant better fit than the second best-fitting distribution (log-normal) in 3/7 cases ($P < 0.01$), as determined by using the Williams and Kloot test (19).

There is a highly significant correlation between ($\beta_2-3$) and $\beta_1$ ($r = 0.999, P \leq 0.001$). Also there is a significant correlation between CV and ($\beta_2-3$) ($r = 0.286, P < 0.01$) and between CV and $\beta_1$ ($r = 0.2767, P < 0.01$). However, no significant correlation exists between ISI and either ($\beta_2-3$) or $\beta_1$ or between SD and either ($\beta_2-3$) or $\beta_1$.

Figure 3, A–C, represent Bode plots of the driven responses from 5 regular, 10 intermediate, and 5 irregular SC primary afferents from the unanesthetized pigeon. For the purpose of fitting transfer functions, gain data for each afferent were translated so the log gain values at 0.303 Hz (low-bandwidth sum of sines) and at 0.293 Hz (high-bandwidth sum of sines) were set equal to one. Due to the translation of gain data, the numerical value of the gain parameters in the best-fit transfer functions are meaningless and are therefore represented only as “G.” Phase values were not translated. Gain and phase data were averaged at each frequency. Transfer functions for the driven responses of SC primary afferents in unanesthetized pigeons were fit to the following generalized equation

$$H(s) = G s^{r_1} (r_2 s + 1)^{r_3} (r_4 s + 1) \quad (4)$$

Each term in this equation has been associated with a different aspect of the mechanoelectric transduction process: $r_1$, the viscoelastic (long) time constant of the cupula-endolymph system (14); $r_2$, a time constant governing cupular velocity sensitivity at high frequencies (14); $s^k$, an operator describing neuronal adaptation (11, 21, 30, 31); and $G$, the gain. Best-fit transfer functions based on the data in Fig. 3, A–C, and associated MSEs are

reg.—$H(s) = G s^{1.1} (7.6 s + 1)^{-1}, \quad \text{MSE} = 0.23 \quad (5)$

int.—$H(s) = G s^{1.14} (9.9 s + 1)^{-1} \times (0.01 s + 1), \quad \text{MSE} = 0.11 \quad (6)$

irr.—$H(s) = G s^{1.10} (9.2 s + 1)^{-1} \times (0.02 s + 1), \quad \text{MSE} = 0.12 \quad (7)$
The best-fit transfer function for 14 anterior canal afferents in the barbiturate-anesthetized pigeon across CV classes was found to be (21)

\[ H(s) = C s^{1.24} (10.2 s + 1)^{-1} \]

This transfer function described frequency response data over the bandwidth from 0.01 to 2.0 Hz.

Individual transfer functions were fit to the gain and phase data of 10 SC primary afferents in the unanesthetized pigeon (3 regular, 5 intermediate, and 2 irregular afferents). Individual values of \( \tau_L \) ranged from 4.76 to 14.18 s in the unanesthetized driven sample. Individual values of \( k \) from 14 SC primary afferents in the barbiturate-anesthetized pigeon ranged from 0.00 to 0.16 in the unanesthetized driven sample and from 0.02 to 0.58 in the anesthetized driven sample (21). A significant difference was found between \( k \) values from the unanesthetized as compared with the anesthetized pigeon (Mann-Whitney U statistic, \( P < 0.05 \)).

Again enhancement in the frequency range from 3 to 6 Hz and phase advance in the
frequency range from 0.6 to 6 Hz is apparent in the Bode plots for the intermediate (Fig. 3B) and irregular (Fig. 3C) SC primary afferents in the unanesthetized pigeon. The time constant of the velocity-sensitive operator (τ_v) for the intermediate afferents is 0.01 s (Eq. 6), whereas that for the irregular afferents is 0.02 s (Eq. 7). No velocity-sensitive operator was necessary to fit the Bode plot data for regular afferents, (Eq. 5 and Fig. 3A) because no gain enhancement or phase advance was evident for the regular afferents in the frequency range from 0.6 to 6 Hz.

In the present study, lateral canal afferents were stimulated in the standard position, whereas anterior canal afferents were stimulated after rolling the pigeon 90 deg from the level standard position. This procedure did not place the anterior canals in the horizontal plane of rotation. Instead, this anterior canal orientation was chosen because it matched that used to study the responses of anterior canal afferents in the anesthetized pigeon (21). Neither anesthetized nor unanesthetized average sensitivity values were corrected for the fact that the 90-deg roll position is not optimal for stimulation of the anterior canal. For the unanesthetized pigeon, the average sensitivity was 3.01 I s⁻¹ deg⁻¹ ± 0.36 (SEM) for 14 anterior canal afferents and 4.60 I s⁻¹ deg⁻¹ ± 0.81 (SEM) for 4 lateral canal afferents at 0.293 Hz. The difference in gain between anterior and lateral SC primary afferents in the unanesthetized pigeon is not statistically significant. For the anesthetized pigeon, the average sensitivity for 14 anterior canal afferents at 0.25 Hz was 2.93 I s⁻¹ deg⁻¹ (11). The sensitivities of anterior canal afferents in the unanesthetized and the anesthetized pigeon are very similar.

**DISCUSSION**

Our data indicate that barbiturate anesthesia significantly lowers the SC primary afferent average spontaneous MFR in pigeons. In contrast, Keller (20) compared the spontaneous activity of horizontal canal afferents from unanesthetized and anesthetized rhesus monkeys and found that barbiturate anesthesia did not affect the spontaneous discharge rate of horizontal SC primary afferents; the average spontaneous MFR was 106 I/s for a sample of 33 horizontal afferents from the unanesthetized rhesus monkey and 100 I/s for a sample of 9 horizontal canal afferents from the barbiturate-anesthetized rhesus monkey. The average spontaneous MFR for a sample of 448 SC primary afferents from the barbiturate-anesthetized squirrel monkey was 91 I/s (16). This value is similar to the average spontaneous MFR values determined for SC primary afferents from unanesthetized rhesus monkeys. For a sample of 43 horizontal canal afferents from the unanesthetized rhesus monkey, the average spontaneous MFR was 105 I/s (23); for samples of 121 horizontal and 102 vertical canal afferents from the unanesthetized rhesus monkey the average spontaneous MFR was 102 I/s (8). In a study that compared the spontaneous discharge and tilt responses of vestibular primary afferents in anesthetized and decerebrate unanesthetized gerbils (28), the average spontaneous MFR for 91 horizontal and anterior afferents in the unanesthetized rhesus monkey was 88 I/s. This value was significantly higher than the average spontaneous MFR of 66 I/s that was reported for 84 horizontal and anterior afferents in the anesthetized (ketamine and urethan) gerbil. The average spontaneous MFR for 55 horizontal canal afferents in the unanesthetized cat is 59 I/s (4). This value is the same as that reported for 78 horizontal canal afferents in the decerebrate unanesthetized cat (13). The average spontaneous MFR for SC primary afferents from anesthetized cats is much lower than this: 37 I/s, n = 130 horizontal canal afferents (12); 44 I/s, n = 102, pooled SC primary afferents (32); 32 I/s, n = 177 horizontal canal afferents (34). In one study carried out on anesthetized cats, the average spontaneous MFR for an unreported number of horizontal canal afferents was 67 I/s (1), and the authors suggest that this higher value could have resulted from a sampling bias. Thus it appears that anesthetics lower the average spontaneous MFR in pigeons, gerbils, and cats but not in monkeys.

The increase in the spontaneous activity of SC primary afferents in unanesthetized pigeons as compared with barbiturate-anes-
theanesthetized pigeons may be due to increased activity of the vestibular efferent system, because barbiturate anesthesia is known to reduce or abolish efferent impulses in the frog (15, 29). In the barbiturate-anesthetized monkey, stimulation of the vestibular efferent system did indeed result in an increase in the firing rate of vestibular primary afferents (18). However, there was no difference in average spontaneous MFR between unanesthetized and anesthetized monkeys (20). This may be because the vestibular efferent system in monkeys is not blocked by barbiturate anesthesia, because it is not tonically active, or because of a sampling bias (nine units comprised the anesthetized rhesus monkey sample). It is possible that barbiturates could directly affect the SC primary afferents in the barbiturate-anesthetized pigeon and account for their decreased average spontaneous MFR as compared with the unanesthetized pigeon. However, barbiturate anesthesia does not seem to affect the discharge rate of SC primary afferents in monkeys at all (20), whether directly or via the vestibular efferent system. Therefore the increased spontaneous activity of SC primary afferents in the unanesthetized pigeon as compared with the anesthetized pigeon could possibly be due to an unmasking of the effects of a tonic, excitatory vestibular efferent system in the unanesthetized birds.

In Fig. 2C and Eqs. 1 and 2, a power function relationship is shown between the spontaneous ISI and its SD. In general, for the unanesthetized as for the anesthetized pigeon, as firing rate increases, the variability decreases. A similar general finding was reported for the anesthetized squirrel monkey (17), both among afferents in a sample of SC primary afferents, and for the same afferent when it was driven to various discharge rates by constant angular accelerative rotational stimuli. Because the spontaneous MFR of irregular afferents in the unanesthetized pigeon is slower than that of regular and intermediate afferents, Fig. 2C and Eq. 1 predict that the CV of irregular afferents would be affected more by an increase in MFR than would the CV of regular and intermediate afferents. Goldberg and Fernández (17) also reported that the decrease in variability with increased discharge rate of a driven SC primary afferent was more pronounced for irregular than for regular afferents.

Figure 2B shows that the CV distribution of SC primary afferents is the same for the unanesthetized pigeon sample as it is for the anesthetized pigeon sample of Lifschitz (22). This similarity of the CV distributions from anesthetized and unanesthetized pigeons could be explained if the observed increase in the average spontaneous MFR of unanesthetized pigeons was accompanied by a decrease in the SD of the spontaneous ISIs of individual SC primary afferents in the unanesthetized birds. Indeed a decrease in SD with a decrease in ISI would be expected from the relationship between spontaneous ISI and SD that is given in Fig. 2C and described by Eq. 1. Equation 1 indicates that the CV would be equal to 0.049 $\text{ISI}^{0.769}$.

Although the regression line relating $\beta_1$ and $\beta_2-3$ (Fig. 2D) had a slope that was significantly different from that of the lines representing the gamma and WL families of distributions, 43% of 30 SC primary afferents tested had ISI histograms that were best-fit by the pdf of the WL process. This process has been used to describe the activity of a particle undergoing Brownian motion before it passes through an absorbant barrier. Correia and Landolt (10) generalized this model to describe events in the vestibular neuroepithelium related to spontaneous activity. They suggested that the WL process could be used to describe the postspike recovery period of a randomly firing postsynaptic neuron (vestibular afferent) that receives converging graded inputs from randomly firing excitatory and/or inhibitory presynaptic neurons. A direct test of this model by measuring synaptic events in the avian vestibular neuroepithelium remains to be done.

A comparison of the parameters of transfer functions of the form of Eq. 4 that were fit to the frequency response data of SC primary afferents in unanesthetized and anesthetized pigeons revealed that $\tau_1$ is similar for unanesthetized as compared with anesthetized pigeons, but that the fractional part of the exponent of s, i.e., $k$, which has been related to adaptation (11, 21, 30, 31), is higher in anesthetized than in unanesthetized pigeons. Keller (20) found no difference in the dynamics of horizontal canal afferents between unanesthetized (33 units) and anesthetized (9 units) rhesus monkeys over the frequency range from 0.25 to 4.0 Hz. Also, Louie and Kimm (23) found the general dynamics of
horizontal canal afferents in the unanesthetized rhesus monkey over the frequency range from 0.1 to 4.0 Hz to be similar to those found for the anesthetized squirrel monkey (14). Using step angular accelerative stimuli in the dark, Büttner and Waespe (8) reported that \( \tau_L \) for the horizontal canal afferents in the unanesthetized rhesus monkey was between 5 and 6 s. This is in agreement with estimates of \( \tau_L \) in the anesthetized squirrel monkey, which were derived from both step and sinusoidal stimuli and were 5.41 and 5.73 s, respectively (14). Similarly, in the unanesthetized decerebrate cat, \( \tau_L \) was determined from the responses of horizontal canal afferents to both steps of rotational acceleration and sinusoidal rotational stimuli to be 4.1 s (13). This value of \( \tau_L \) is in close agreement with those that were determined for SC primary afferents in the anesthetized cat [3.9 s (2); 4.7 s (1); 4.9 s (32)].

The velocity sensitive operator was first proposed by Fernández and Goldberg (14) to describe a gain enhancement and phase advance in the high-frequency (to 8.0 Hz) response of SC primary afferents in the barbiturate-anesthetized squirrel monkey (\( \tau_V = 0.049 \) s). This gain enhancement and phase advance is also apparent in the Bode plots and transfer functions of the intermediate (Fig. 3B and Eq. 6) and irregular (Fig. 3C and Eq. 7) SC primary afferents in the unanesthetized pigeon. The irregular afferents are more velocity sensitive than the intermediate afferents, as indicated by their time constants and their Bode diagrams (Fig. 3B and C). The Bode plot and transfer function for the regular afferents (Fig. 3A and Eq. 5) indicate that regular SC primary afferents from the unanesthetized pigeon show little or no velocity sensitivity. There appears to be a continuum with regard to velocity sensitivity among SC primary afferents in unanesthetized pigeons, where regular afferents are the least velocity sensitive and irregular afferents are the most velocity sensitive (Fig. 3D). Goldberg and Fernández (17) reported that irregular SC primary afferents showed more velocity sensitivity than regular SC primary afferents in the anesthetized squirrel monkey (irregular, \( \tau_V = 0.080 \) s; regular, \( \tau_V = 0.017 \) s). The same relationship between variability of afferent spontaneous discharge and velocity sensitivity at high frequencies is found for SC primary afferents from the unanesthetized pigeon (Fig. 3D). Additionally, Goldberg and Fernández (17) reported that, in the anesthetized squirrel monkey, irregular SC primary afferents showed more adaptation than regular SC primary afferents, and they expressed adaptation in terms of a pole-zero type of adaptation operator, which describes adaptation at low frequencies only. Likewise in the anesthetized (ketamine and urethan) gerbil, Schneider and Anderson (30) reported that irregular SC primary afferents showed more adaptation than regular SC primary afferents, and these authors expressed adaptation in terms of the \( s^k \) operator (11, 21, 30, 31), which describes adaptation at all frequencies. In contrast to these studies done in mammals, there does not appear to be a relationship between variability and adaptation in the unanesthetized pigeon. The \( s^k \) operator, which describes neural adaptation in this study, indicates by its value of \( k \) that the adaptation is similar for regular, intermediate, and irregular afferents in the unanesthetized pigeon.

The sensitivities of anterior canal afferents in the unanesthetized and the anesthetized pigeon are very similar, and it appears that anesthesia does not affect SC primary afferent sensitivity in the pigeon. Apparently, this finding is also true for the monkey. Keller (20) showed that the sensitivity of horizontal canal afferents to sinusoidal rotational stimuli at 0.5 Hz were the same whether the monkeys were anesthetized or unanesthetized. Büttner and Waespe (8) reported that the sensitivities of horizontal canal afferents to steps of angular acceleration in the unanesthetized rhesus monkey were similar to the sensitivities of SC primary afferents to steps of angular acceleration in the anesthetized squirrel monkey (16). Miles and Braitman (25) reported that the average gain of horizontal SC primary afferents in the unanesthetized rhesus monkey was 0.63 I·s⁻¹·deg⁻¹·s⁻¹, as determined from their responses to sinusoidal oscillation at 0.2 Hz, ±20 deg. This value falls within the range of values reported for the gains of pooled SC primary afferents in the anesthetized squirrel monkey, which was determined from their responses to 0.25 Hz, 80 deg·s⁻¹·s⁻¹ oscillation (Ref. 14, Fig. 9). In the unanesthetized cat, the sensitivity of SC primary afferents during 0.25-Hz sinusoidal rotation is 0.275 I·s⁻¹·deg⁻¹·s⁻² (4). This value is in close agreement with the
sensitivity value of 0.389 $1\cdot s^{-1}\cdot deg^{-1}\cdot s^{-2}$, which was determined during 0.25-Hz rotational stimulation from anesthetized cats (1).

In conclusion, it seems that the average spontaneous mean firing rate is increased, and the SD is decreased, for SC primary afferents in unanesthetized as compared with anesthetized pigeons. Also, adaptation to angular accelerative stimuli may be greater for SC primary afferents from unanesthetized than from anesthetized pigeons, but the so-called cupula $\tau_c$ is the same. The CV and the sensitivity to rotational stimuli of SC 77550 USA* called cupula 7L is the same. The CV and adaptation to an- cessional stimulation from anesthetized cats (1).

The CV and spontaneous mean firing rate is increased, and the SD is decreased, for SC primary afferents in unanesthetized as compared with anesthetized pigeons. Also, adaptation to angular accelerative stimuli may be greater for SC primary afferents from anesthetized than from unanesthetized pigeons, but the so-called cupula $\tau_c$ is the same. The CV and the sensitivity to rotational stimuli of SC primary afferents appear to be the same for unanesthetized as for anesthetized pigeons.

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Address reprint requests to: Prof. M. J. Correia, Unit 9-A OJSH (F-03), Univ. Texas Med. Br., Galveston, TX 77550 USA.

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