

The Response of Horizontal Semicircular Canal Afferents to Sinusoidal Rotation in the Cat

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Summary. Dynamic characteristics of primary vestibular afferents innervating the horizontal semicircular canal were studied in decerebrate, unanesthetized cats. Activities of individual afferent fibers were recorded intracranially by glass micropipettes. Frequency of sinusoidal rotation was varied from 0.014 Hz to 0.42 Hz, and phase and gain properties were examined.

All of the fibers recorded fired spontaneously, and their firing rate ranged from 7 to 128 spikes/sec. Regularity of firing, phase lags, and gains were calculated in individual fibers. There was a tendency that the units with high spontaneous firing rates showed regular firing, larger phase lags, and lower gains than the units with low spontaneous firing rates.

The transfer function of the system (firing rate of the primary afferent per angular acceleration of the head) was $\frac{1.98(0.08s + 1)}{4.1s + 1}$. A high frequency phase lead component was needed to account for the data obtained, indicating a slight deviation from the relationship predicted by the torsion pendulum model.

The present phase properties were compared with those of vestibular nucleus neurons reported previously. It was suggested that a group of vestibular nucleus neurons transmits fairly faithfully the phase properties of primary afferents, and that another group of vestibular nucleus neurons receive additional influences from central structures, exhibiting larger phase lags than primary afferents.

Key words: Horizontal canal afferent – Resting activity – Transfer function – Vestibular nucleus neuron.

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Dynamic characteristics of primary afferent activity of the semicircular canal have been analyzed with rotational stimulation in fish (Groen et al., 1952), frog (Precht et al., 1971), cat (Blanks et al., 1975; Estes et al., 1975) and monkey (Goldberg and Fernández, 1971a, b; Fernández and Goldberg, 1971). The dynamics of primary afferents as expressed by the main time constant of the response calculated on the basis of the torsion pendulum hypothesis (Steinhausen, 1933; Egmond et al., 1949) have exhibited a variety of species differences. Precise determination of these dynamic properties in individual species is essential not only for study of receptor mechanisms but also for estimation of transfer characteristics from primary afferents to central structures in various animals. In the cat and monkey, gain and phase properties have been examined in vestibular nucleus neurons (Melvill Jones and Milsum, 1971; Shinoda and Yoshida, 1974; Fuchs and Kimm, 1975), prepositus hypoglossi neurons (Fukushima et al., 1977; Blanks et al., 1977), abducens motoneurons (Skavenski and Robinson, 1973; Shinoda and Yoshida, 1974), forelimb motoneurons (Berthoz and Anderson, 1971a; Anderson et al., 1977) and neck motoneurons (Berthoz and Anderson, 1971b); Ezure and Sasaki, 1978; Ezure et al., 1978).

In a previous study (Shinoda and Yoshida, 1974) dynamics of vestibular nucleus neurons in response to horizontal head rotation were studied with unanesthetized, decerebrate cats. The present study deals with primary afferents of the horizontal semicircular canal in a similar cat preparation to enable a direct comparison of dynamic characteristics between primary afferents and vestibular nucleus neurons. Fundamental properties of primary afferents have been studied with constant angular acceleration in anesthetized cats (Blanks et al., 1975; Estes et al., 1975); we employed the frequency response method with sinusoidal rotation, and did not use anesthesia which might exert some influence on the response obtained in primary afferents.

The present study describes phase and gain properties of primary afferents and provides evidence for the existence of a phase lead element in the high frequency range of sinusoidal rotation, which also exists in monkey (Fernández and Goldberg, 1971) and has so far not been adequately described for cat. The phase properties of primary afferents are an explicit indicator of their dynamics and will be compared with those of vestibular nucleus neurons analyzed previously to characterize the information processing in the vestibular nuclei.

Methods

The experiments were performed on 8 cats, weighing 2.8–3.7 kg. Under ether anesthesia, bipolar silver ball electrodes were placed on the round and oval windows of the left labyrinth by a ventral approach through the bulla. The oval window electrode was close to the stapes which was not removed to avoid possible damage to the end-organ. A portion of the occipital and parietal bone was removed, and the cerebellar vermis and left hemisphere was aspirated. In three animals, the roof of the internal auditory canal was removed by dental burrs, to expose the superior division of the vestibular nerve to Scarpa's ganglion (cf. Gacek, 1969). Following this surgery, the animal was decerebrated precollicularly and ether discontinued. The animal was immobilized with gallamine triethiodide, artificially respired, blood pressure maintained between 90–140 mmHg, and rectal temperature controlled between 36–38°C.

The animal was mounted on a stereotaxic frame fixed to a turntable, with the center of the head on the axis of rotation. The head was inclined 28° nose down so as to optimally isolate the horizontal semicircular canal responses (Estes et al., 1975). The turntable could be sinusoidally rotated from 0.015 Hz to 0.42 Hz with amplitude of 5–50°, peak angular acceleration being kept less than 50 deg/sec².

Single unit activities were recorded with glass microelectrodes from the left vestibular nerve within the brain stem, 6 mm lateral and at the level of the abducens nucleus (Fig. 1A), or in the vicinity of Scarpa's ganglion. The glass micropipettes were filled with 3M KCl, having electrical resistance of 10–15 M Ω . The unfiltered spike waveform was usually positive and monophasic ranging in amplitude from 1–15 mV. Units were classified as vestibular nerve fibers based on their response to electrical stimulation of the ipsilateral labyrinth; units showed minor fluctuation of latency at threshold stimulus intensities, fixed latency with suprathreshold stimulation, and the ability to follow repetitive stimulation of 500–1000/sec. For latency measurement, rectangular negative pulses of 0.1 msec duration and of 0.5–5 V intensity were delivered through the electrode on the round window with the one on the oval window being reference. Units were selected which responded to manual rotation of the turntable in the horizontal plane. These units showed little or no response to small oscillations of the turntable in the vertical plane and thus were presumed to innervate the horizontal semicircular canal. The recording site within the brain stem was marked by the iontophoretic ejection of Fast Green FCF, and the location of the dye mark recovered from serial histological sections.

The train of unitary spikes was digitized and processed on-line (ATAC 501, Nihon Koden; Signal Processor, San-Ei). The coefficient of variation (CV) of interspike interval at rest was calculated from 1000 consecutive intervals. The response of single units to sinusoidal rotation was obtained by averaging the firing rate for 10 to 30 stimulus cycles. The averaged response was traced on a X–Y plotter for the measurement of phase and gain.

In three animals with partial exposure of the vestibular nerve, compound action potentials were recorded from the cut end of a bundle of nerve fibers. The rostral portion of the superior division of the vestibular nerve was teased apart, and was cut at its entrance to the brain stem, care being taken to minimize injury to the nerve or its blood supply. The cut end of the nerve was ligated with a fine silver wire (42 microns in diameter), which served as a recording electrode. The recorded compound action potentials were fullwave rectified, filtered (time constant 10 or 30 msec), and averaged during sinusoidal rotations.

Results

Identification of Primary Afferents and their Spontaneous Activity

Eighty-five units were identified as vestibular nerve fibers innervating the horizontal semicircular canal. Of these, 80 were recorded within the brain stem (Fig. 1A) and five in the vicinity of Scarpa's ganglion.

For the units recorded in the brain stem, electrical stimulation of the ipsilateral labyrinth evoked action potentials at fixed latencies (Fig. 1B). The latency of spikes varied depending on the polarity of stimulating pulses; with the polarity described in Methods (round window cathode, oval window anode), the latency was usually shorter than the reversed polarity by up to 0.2 msec. With intensities of 2 to 3 times threshold for activation of the unit, the latencies ranged from 0.23 to 0.68 msec ($n = 80$). The latency histogram in Figure 1C has a unimodal distribution, with mean and standard deviation of 0.37 ± 0.10 msec.

All the units exhibited spontaneous discharges when the animal was stationary. Stable recordings could be obtained from these fibers for several hours, during which time the spontaneous firing rate remained unchanged. The spontaneous firing rate for 78 units ranged from 7 to 128 spikes/sec, with mean and standard deviation of 59.2 ± 26.7 spikes/sec (Fig. 1D).

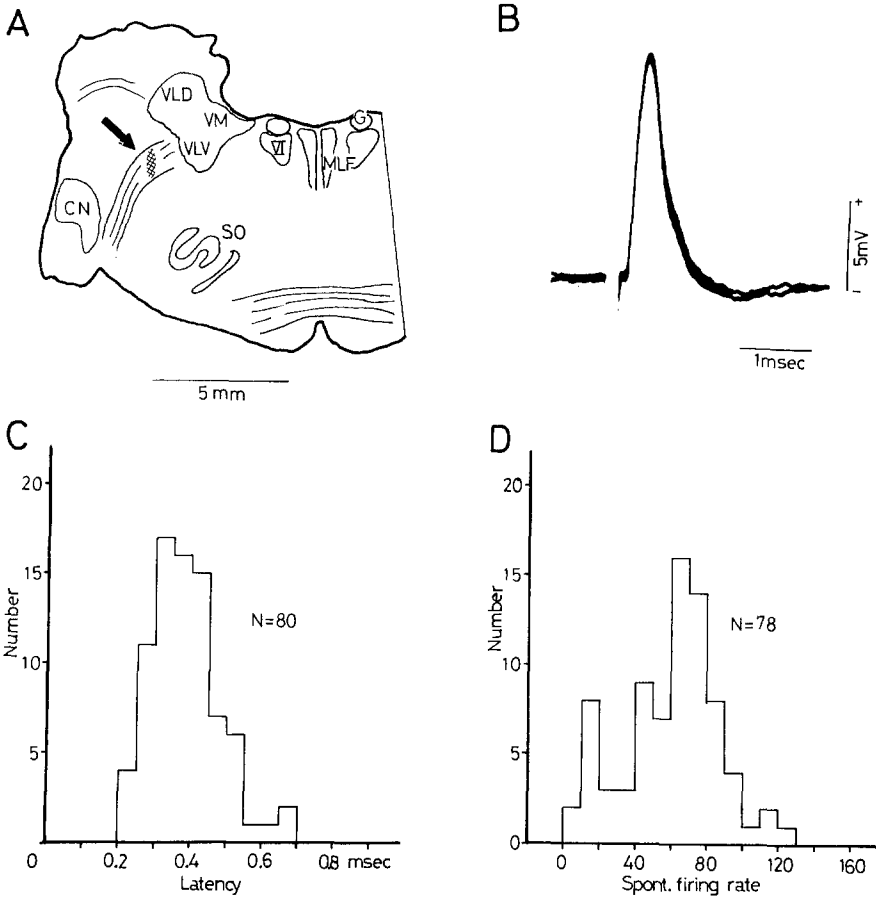


Fig. 1. **A** location of the recording site. Primary afferent fibers innervating the horizontal semicircular canal were recorded from an area 6 mm lateral to the midline (shaded area indicated by arrow). VLD: lateral vestibular nucleus, dorsal division; VLV: lateral vestibular nucleus, ventral division; VM: medial vestibular nucleus; CN: cochlear nucleus; SO: superior olive nucleus; G: genu of facial nerve; VI: abducens nucleus; MLF: medial longitudinal fasciculus. **B** unitary spikes evoked by electrical stimulation of the labyrinth. **C** latency histogram of electrically induced spikes. **D** histogram of the spontaneous firing rates of afferent fibers

The spontaneous firing activity showed a wide range of regularity. Figures 2A and B illustrate examples of interspike interval distributions for two units, one with a regular spacing of spikes (2A), the other irregular (2B). The degree of regularity was quantified by computing the coefficient of variation (CV), defined as the ratio of the standard deviation of the interval distribution to the mean interval. The CVs ranged from 0.025 to 0.97, with a mean of 0.23 ($n = 25$). The majority of the units measured (17/25) had quite regular firing patterns, with CVs less than 0.10 and interspike interval distributions similar to that shown in Figure 2A; the remaining 8 units were fairly irregular, with CVs greater than 0.4, and similar to the unit in Figure 2B. Both the range and mean

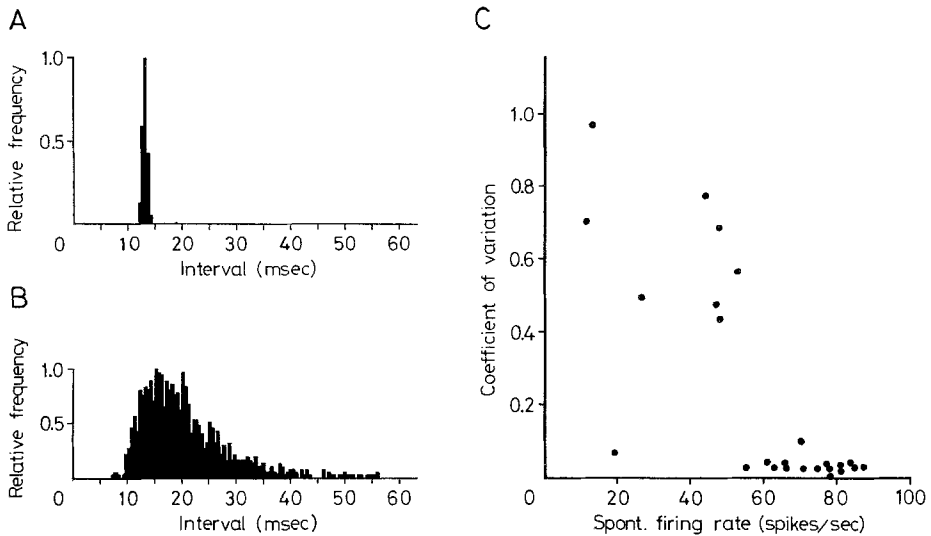


Fig. 2. **A** interspike-interval histogram of regularly firing unit; CV = 0.0347, spontaneous firing rate is 77.5 spikes/sec. **B** interspike-interval histogram of irregularly firing unit; CV = 0.431, spontaneous firing rate is 48.3 spikes/sec. **C** relation between the spontaneous firing rates and CVs for 25 units

of CVs are similar to those found in anesthetized cats (Estes et al., 1975). There was a clear relationship between the mean firing rate and the regularity of the firing. Units having high spontaneous firing rate had small CVs and those having low firing rate tended to have large CVs (Fig. 2C).

Response to Sinusoidal Rotation

Single unit responses to sinusoidal angular acceleration of the head were studied in 62 units. Figure 3A shows the averaged response of a single unit for 10 consecutive stimulus cycles. The firing rate was modulated in a sinusoidal manner about the spontaneous firing level. With the stimulus magnitudes employed, few units exhibited obviously skewed or clipped responses, which were not analyzed in the present study.

The semicircular canal afferents have been reported to behave as an approximately linear system with respect to the gain and phase characteristics of the response (Fernández and Goldberg, 1971). The gain and phase of the unit response relative to the angular acceleration were calculated at various stimulus frequencies. The gain (Γ) was defined as the ratio of the amplitude of the modulated firing frequency to the stimulus amplitude ($\text{spikes} \cdot \text{sec}^{-1}/\text{deg} \cdot \text{sec}^{-2}$) and was represented in dB ($=20 \log \Gamma$); the angular acceleration was computed from the known sinusoidal table position as a function of time (Fig. 3A, top). The phase was measured from the difference between the peak of the firing rate and the peak ipsilateral angular acceleration (in degree). Since all units

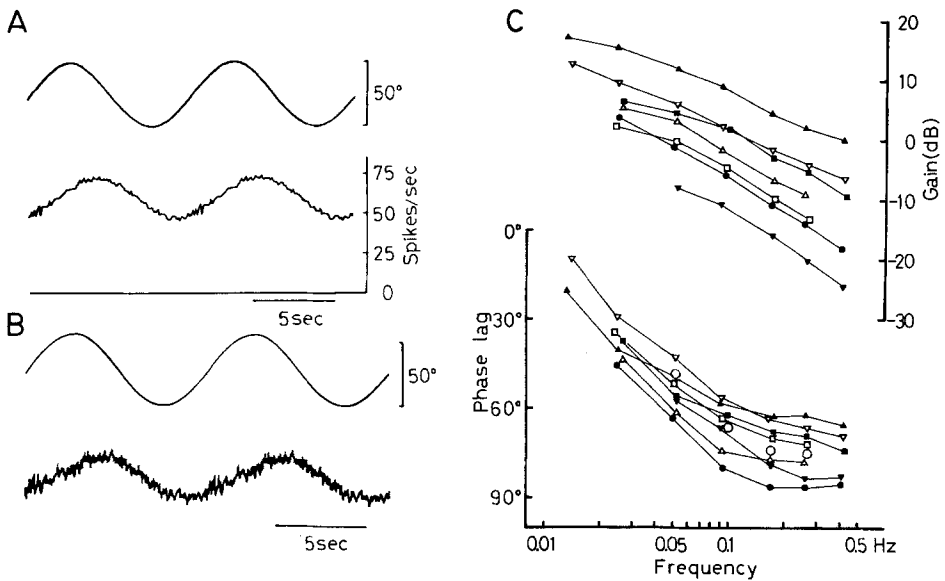


Fig. 3. **A, B** averaged responses of a single unit (**A**) and compound action potentials (**B**), recorded from afferents innervating left horizontal canal. Upper sine curves in **A** and **B** indicate the position of the sinusoidally rotated turntable. Upward movement indicates clockwise (contralateral) rotation; the positive peak corresponds to the peak leftward (ipsilateral) angular acceleration. The averaged data for the cycle are written out twice to aid visual interpretation. **C** Examples of Bode plots for 7 units as indicated by the different symbols. The phase lags and gains relative to ipsilateral head angular acceleration are plotted against the stimulus frequency. Open circles indicate the phase lags obtained from compound action potentials

increased their firing rate with ipsilateral angular acceleration and the peak of the response was later than that of the acceleration, the phase difference was expressed as a phase lag.

The relationship of gain and phase lag to stimulus frequency was represented by Bode plots. Figure 3C shows examples of Bode plots for 7 units, where the gain (in dB) and phase lag are plotted against the logarithm of frequency. The gains of individual units showed a wide variation: at a fixed frequency of 0.1 Hz, the distribution of the gain was found to have a mean and standard deviation of -2.90 ± 6.14 dB ($n = 61$). In spite of such variation, the shapes of the gain curves were generally similar: the gain decreased as the stimulus frequency increased, and the slope was approximately -20 dB per decade of frequency above 0.05 Hz. Coincidentally with the decreasing gain, the phase lag increased with stimulus frequency, from less than 20° (at 0.014 Hz) to about 75° at frequencies above 0.17 Hz, where phase curves became almost flat.

A correlation exists between the spontaneous firing rate and the amount of phase lag of the unit. In Figure 4A, the spontaneous firing rate is plotted against the phase lag at 0.1 Hz for 60 units. As can be seen in this figure, units with low spontaneous firing rate tend to have smaller phase lags. The correlation was statistically highly significant ($r = 0.64$, $P < 0.001$, t -test). Since the regularity of

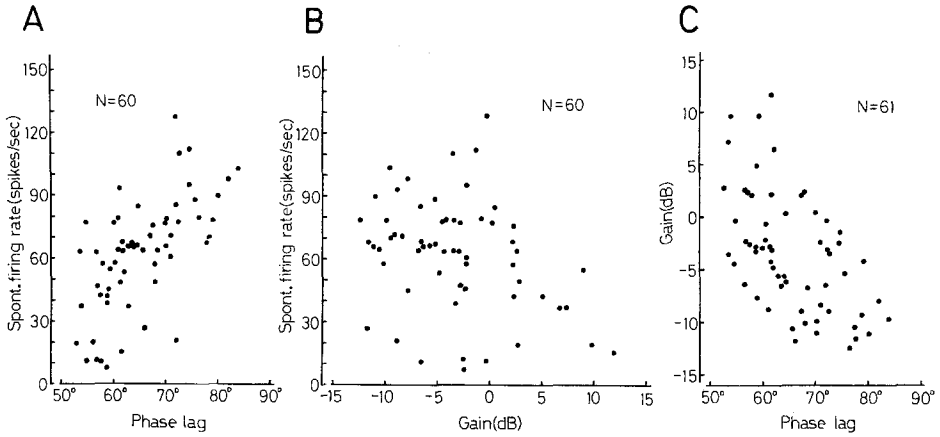


Fig. 4. Relations among spontaneous firing frequencies, phase lags and gains of unit responses at 0.1 Hz. **A** Spontaneous firing rates and phase lags, indicating positive correlation. **B** Spontaneous firing rates and gains. **C** gains and phase lags, indicating negative correlation

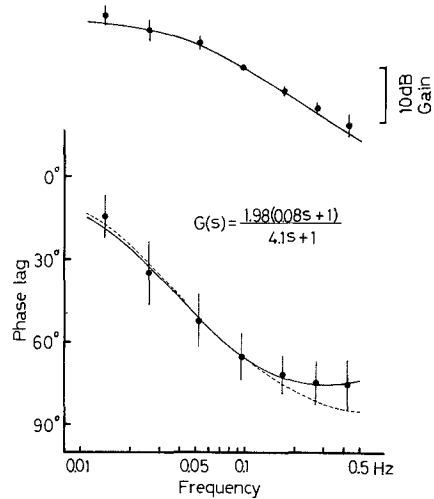


Fig. 5. Determination of transfer function. Filled circles and vertical bars indicate the means and standard deviations of 62 units. Gains are normalized at 0.1 Hz. The best fit curves were estimated by the least squares method. Solid line, the best fit curve expressed by the transfer function $G(s) = \frac{1.98(0.08s + 1)}{4.15s + 1}$ written in the figure. Broken line, the best fit curve approximated by a first order lag system with a time constant of 3.5 sec

the unit was closely related to the spontaneous firing rate (Fig. 2C), a relationship was also found between the CV and the phase lag; the more irregular the unit, the smaller the phase lag ($r = -0.82$, $P < 0.005$, t-test, $n = 10$). The relationship between the spontaneous firing rate and the gain at 0.1 Hz was also examined (Fig. 4B). Although points are scattered widely, there is a slight suggestion of a negative correlation between the variables ($r = -0.32$, $P < 0.02$, Student's t-test, $n = 60$). This weak correlation seems to be attributable to several units with higher gains, which are found among the units with relatively low spontaneous firing rate.

A clear correlation was found between the gain and phase lag of unit response: units with larger gains had smaller phase lags (Fig. 4C). The negative

correlation was statistically highly significant ($r = -0.53$, $P < 0.001$, t -test, $n = 61$).

To form an estimate of the average activity of horizontal semicircular canal afferents as a whole, responses to sinusoidal rotation of the compound action potentials recorded from the cut end of the vestibular nerve were examined (Fig. 3B). The phase lags obtained at 4 different stimulus frequencies in one cat are illustrated by open circles in Figure 3C. They agree quite well with the average phase lags obtained from single unit responses (Fig. 5), the difference at each frequency being less than 5° .

Transfer Function

The transfer function of the system from head angular acceleration to the firing rate of horizontal semicircular canal afferents was estimated from the averaged Bode plots for 62 units (Fig. 5, filled circles). Within the limited frequency range employed, the transfer function based on the torsion pendulum model may be approximated by the first-order lag system represented by the equation.

$$G(s) = \frac{K}{(Ts + 1)} \quad (1)$$

where K is a constant representing the sensitivity ($\text{spikes} \cdot \text{sec}^{-1}/\text{deg} \cdot \text{sec}^{-2}$), T is the time constant of the system in seconds and s is the Laplace transform frequency variable. The time constant T was determined so as to give the best-fit curve for actual phase plots (dotted line in Fig. 5). The estimated value of T was 3.5 sec. For the lower half of the frequency range employed, the first-order lag model gives a good fit to the data, except that a slight phase lead at the lowest frequency may be significant. However, at frequencies above 0.17 Hz, the actual phase lags are less than the values predicted from equation (1). This high frequency deviation from the first-order lag system may be compensated for by introducing an additional high frequency lead component, as was found necessary for the data from the monkey (Fernández and Goldberg, 1971). The new formula for the transfer function becomes

$$G'(s) = \frac{K(T's + 1)}{(Ts + 1)} \quad (2)$$

where T' represents the time constant associated with the high frequency lead element. Note that K and T are not necessarily the same as those in equation (1). The best fit to the observed phase data was obtained with values of T and T' of 4.1 and 0.08 sec, respectively. The corresponding estimate of phase, calculated from equation (2), is shown in Figure 5 by a solid line (lower diagram).

The gain constant K was calculated from the average value of logarithms of unit gains at 0.1 Hz ($n = 61$) and equation (2) with the time constants described above. The value of K thus obtained was $1.98 \text{ spikes} \cdot \text{sec}^{-1}/\text{deg} \cdot \text{sec}^{-2}$. With this value of K , predicted gains at other frequencies agreed well with the observed average values (solid line and filled circles in Fig. 5, upper diagram).

The average time constant of type I neurons in the vestibular nuclei obtained under similar experimental conditions is considerably longer than that of primary afferents observed in this study (5.5 sec using equation (1), Shinoda and Yoshida, 1974). Figure 6 illustrates the distributions of the phase lags at 0.1 Hz for both primary afferent fibers (shaded histogram) and type I vestibular nucleus neurons (blank histogram, from Shinoda and Yoshida, 1974). As compared to the narrow and unimodal distribution of phase lags for primary afferents, phase lags of vestibular nucleus neurons were distributed in a bimodal fashion over a much wider range, exceeding 90° . Based on this, vestibular nucleus neurons were classified into two groups: those with smaller phase lags and those with larger ones, with the boundary being 80° at 0.1 Hz. It appears that the smaller phase lag neurons of Shinoda and Yoshida have phase properties quite similar to those of primary afferents. The averaged time constant for this population of vestibular nucleus neurons, which was calculated from the phase lags at various frequencies by using equation (1), was 3.0 sec and close to the value of 3.5 sec for primary afferents, obtained from the same formula. The response of the remaining vestibular nucleus neurons, having an averaged time constant of 7.2 sec and phase lags exceeding 80° , is distinctly different from that of primary afferents.

Discussion

Extensive studies of the dynamic properties of cat's primary afferents from the horizontal semicircular canal have been made by Blanks et al. (1975), Estes et al. (1975) and Yagi et al. (1977) using the stimulus of step change in angular acceleration. In the present experiments we have employed the frequency response method with sinusoidal rotation. If the system is linear, essentially the same information should be derived from these two methods, though the latter usually provides a more detailed and descriptive information in the actual experimental situation. The time constant T and sensitivity factor K from this study are comparable to those obtained from the responses to an incremental step of acceleration; they are 4.1 sec, $1.98 \text{ spikes} \cdot \text{sec}^{-1}/\text{deg} \cdot \text{sec}^{-2}$ (present study) and 4.0 sec, $1.7 \text{ spikes} \cdot \text{sec}^{-1}/\text{deg} \cdot \text{sec}^{-2}$ (Blanks et al., 1975). The agreement between the values obtained with these two different methods is consistent with the assumption that the system is linear.

Steinhausen (1931) observed the cupula deflection in the ampullae during rotation. The dynamics of cupula deflection caused by the motion of the endolymph have been expressed by the equation for the over-damped oscillation of a torsion pendulum (Steinhausen, 1933; Egmond et al., 1949). The responses of primary afferents to constant angular acceleration tend to exhibit adaptation (Goldberg and Fernández, 1971a; Precht et al., 1971; Blanks et al., 1975). This suggests that the firing frequency of primary afferents is not strictly proportional to the cupula deflection, assuming that the cupula deflection itself obeys the torsion pendulum equation. By introducing Young and Oman's (1969) model for vestibular adaptation based on human psychophysical data and transforming their integral form into a differential

form, the relation between the firing rate of primary afferents (o) and the cupula deflection (ξ) may be formulated as follows:

$$T_a o + o \propto \xi \quad (3)$$

where T_a is a time constant which characterizes the adaptation and is of the order of several tens of seconds (Goldberg and Fernández, 1971a). This modification causes a phase lead at low frequencies from the phase curve expected from the first-order lag system. The phase lead in the low frequency range observed in Figure 4 may be due to such adaptation properties of the primary afferent response.

Previous studies on monkey primary afferents with the frequency response method showed that a high frequency phase lead element is also required to explain the observed deviation of phase and gain from those expected in the first-order lag system (Fernández and Goldberg, 1971; Keller, 1976; Louie and Kimm, 1976). This applies to cat primary afferents as well: the transfer function without the high frequency phase lead element does not fit the data obtained (Fig. 5). The formula of the transfer function is more adequately expressed by equation (2). This suggests that, as described for monkey canal afferents (Fernández and Goldberg, 1971), the response of canal afferents in the cat also has a component which is proportional to the velocity of cupula deflection:

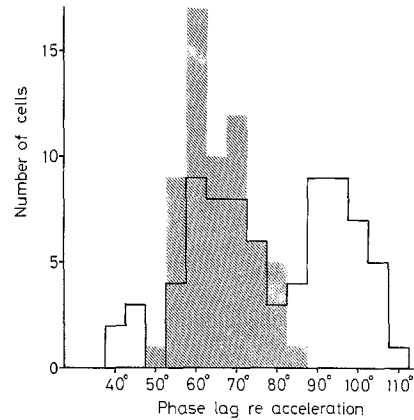
$$o \propto T' \dot{\xi} + \xi \quad (4)$$

where T' is 0.08 sec in the present study.

The present criteria for identification of primary afferents are in principle not appropriate to discriminate afferent fibers from efferent fibers. Most fibers recorded, however, were presumably from afferents, since the phase properties of mass discharges recorded from the cut end of the vestibular nerve exhibited the mean phase value of individual fibers.

The above discussions focus on the average properties of canal afferents. It has been known, on the other hand, that they are not homogeneous in their morphological and physiological properties and can be classified into regular and irregular units on the basis of quantitative analyses of their discharge pattern (Walsh et al., 1972; Estes et al., 1975; Blanks et al., 1975; Yagi et al., 1977 in the cat; Goldberg and Fernández, 1971a, b, 1977; Fernández and Goldberg, 1971 in the monkey). The present results indicate that the irregular units have lower spontaneous firing rates, higher gains and smaller phase lags compared to regular units. These correlations are consistent with the results obtained by previous authors, who in addition demonstrated that the irregular units have faster conduction velocities, more rapid adaptation properties and tend to show a high frequency phase lead. The tendency for larger high frequency phase lead in the irregular units, which also have higher gains, may cause the negative correlation between the phase lag and gain shown in Figure 4C. This negative correlation is in marked contrast to the positive correlation between the phase lag and gain obtained in prepositus hypoglossi neurons (Fukushima et al., 1977) neck motoneurons (Ezure and Sasaki, 1978) and abducens motoneurons (Schor, Shinoda and Yoshida, in prep.).

Fig. 6. Comparison between the phase lags of primary afferents and those of vestibular nucleus neurons. Hatched columns: phase lags of the primary afferents obtained in the present study at 0.1 Hz, N = 61. Open columns: phase lags of vestibular nucleus neurons at 0.1 Hz (from Shinoda and Yoshida, 1974, Fig. 5B), N = 78



Since the vestibular signal is transmitted from hair cells to primary afferents through chemical synapses (Furukawa and Ishii, 1967), general anesthesia might exert some influences on this transmission and thereby on the response pattern of primary afferents. When the present study without anesthesia is compared with the previous studies performed under deep anesthetic conditions (Yagi et al., 1977), spontaneous firing rate seems to be slightly lower in the latter study (7–128 spikes/sec without anesthesia, 0–84 spikes/sec with anesthesia). This difference may be in part due to anesthesia, though effects of exposure of the area near the receptors and the nerve in the previous study could not be excluded. The time constant T and the gain constant K obtained in the present study are in fairly good agreement with those of previous studies (Blanks et al., 1975) and do not seem to be much affected by anesthesia.

Vestibular nucleus neurons in the horizontal canal system have been classified into two groups on the basis of the dynamic characteristics of their response to constant angular acceleration (Shimazu and Precht, 1965) and to sinusoidal rotation (Shinoda and Yoshida, 1974; Keller and Kamath, 1975). The average time constant of the response in each group of neurons was 3.7 and 8.1 sec (Shimazu and Precht, 1965) or 3.0 and 7.2 sec (Shinoda and Yoshida, 1974). The present study, which allows a direct comparison between phase properties of primary afferents and vestibular nucleus neurons in similar preparations (Fig. 6), suggests that a group of vestibular nucleus neurons with shorter time constants (or smaller phase lags) faithfully reflect the phase properties of primary afferents. The other group of vestibular nucleus neurons exhibits distinctly larger phase lags than those of primary afferents. This suggests that these neurons receive additional influences from central nervous structures. Polysynaptic linkage with primary afferents (Precht and Shimazu, 1965), which was found in a group of vestibular nucleus neurons with longer time constants (tonic neurons of Shimazu and Precht, 1965), may be partly responsible for this additional phase lag.

The suggestion that the additional phase lag is centrally formed is based on the lack of primary afferent responses with larger phase lags, exceeding 90°. It is

unlikely that there existed a systematic sampling bias in the present data, since the phase characteristics of mass discharges of the vestibular nerve were consistent with the mean value obtained from individual fibers. There also seem to be no systematic sampling differences between the present study and previous studies (Blanks et al., 1975; Estes et al., 1975; Yagi et al., 1977) based on the similarities of the response characteristics. If, however, there exists a population of extremely thin fibers which have larger phase lags, are hard to isolate for single unit recording, and produce only a minor contribution to the total mass discharges, the above suggestion may need reconsideration.

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