

Response of Cat Semicircular Canal Afferents to Sinusoidal Polarizing Currents: Implications for Input-Output Properties of Second-Order Neurons

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SUMMARY AND CONCLUSIONS

1. We studied the response of cat vestibular afferents, most likely innervating the semicircular canals, to sinusoidal polarizing currents applied to an electrode implanted near the horizontal ampulla.

2. Electrode implantation abolished responses to natural stimulation and reduced the level of resting activity compared to a population of afferents from unimplanted animals. The distribution of coefficients of variation of resting activity was, however, similar to that seen when the labyrinth is intact.

3. Many fibers were modulated sinusoidally by polarizing currents in the frequency range 0.175–4 Hz. Phase was mainly constant and typically led stimulus negativity by approximately 14° , although about half the regular fibers had a phase lead that increased with frequency. Mean sensitivity (spikes \cdot $s^{-1} \cdot \mu A^{-1}$) of regular and irregular fibers increased by a factor of about 1.5 over the frequency studied. Absolute sensitivity was about 7 times higher for irregular than for regular fibers. The overall behavior of the afferents could be well described by a transfer function in the form, s^k , with $0 < k < 1$.

4. We compared the response of afferent fibers to sinusoidal current with the response of second-order neurons studied under similar conditions in earlier experiments (15, 23). While the slopes of the sensitivities were similar, second-order neurons developed a phase advance over afferents at frequencies around 1 Hz. This difference in dynamics can be described by a transfer function in the form $\tau s + 1$, with $\tau = 12$ ms. This predicts

that second-order neurons can develop a phase lead of about 25° with respect to afferents at 6 Hz, a frequency still in the physiological range. It remains to be determined whether this applies to a particular subset of second-order neurons contributing to vestibulocollic reflexes.

INTRODUCTION

Sinusoidal polarization of cat ampullary nerves with electrodes implanted near the ampulla (19) evokes a vestibulocollic reflex (VCR) whose central processing closely resembles that of the VCR evoked by natural stimulation (1, 23). The behavior of second-order vestibular neurons to sinusoidal polarization has also been described (15, 23). When horizontal sinusoidal rotation is used as a stimulus, the behavior of low-order central vestibular neurons in different animals and types of preparations often appears to reflect closely that of the incoming vestibular signal (for review see Ref. 22, p. 155); it seemed likely that the same was true with sinusoidal polarization as the stimulus (23).

Goldberg, Smith, and Fernandez (8; J. M. Goldberg, personal communication) have shown recently that in the monkey the response of vestibular afferents to sinusoidal galvanic stimulation is typically characterized by a Bode plot of flat phase and small gain increases at frequencies between 0.01 and 4 Hz. Because second-order neurons show increasing gain and phase advance in the same frequency range (23), this suggests that they may transform and not just reflect the incoming signal. In the experiments of Goldberg, Smith, and Fernandez (8), how-

ever, the stimulating electrode was in the perilymphatic vestibule at some distance from the ampulla. We have now studied the response of cat vestibular afferents to sinusoidal polarization with an electrode implanted near the ampulla near the horizontal canal nerve so as to compare, under similar stimulating conditions, the behavior of afferents with that of second-order neurons studied in our earlier experiments.

METHODS

Animal preparation

Experiments were performed on 11 cats prepared under halothane-nitrous oxide anesthesia and later decerebrated at the precollicular or intercollicular level. Blood pressure was monitored from the femoral artery and, where necessary, was maintained above 100 mm Hg by intravenous infusion of a solution of 80 $\mu\text{g/ml}$ metaraminol bitartrate (Aramine, Merck, Sharp & Dohme) in physiological saline. Rectal temperature was maintained between 36 and 38°C by a heating pad and infrared lamp. When muscle recording was completed (see below), the animals were paralyzed by injection of gallamine triethiodide (Flaxedil, Davis-Geck), pneumothorax was performed, and artificial respiration begun. Expired CO_2 was then monitored and maintained at 3–4%.

To expose primary afferents for recording, a parietooccipital craniotomy was performed and lateral portions of the cerebellum were aspirated. The roof of the internal auditory canal was removed with a dental drill to expose the area of Scarpa's ganglion and visualize the superior division of the vestibular nerve.

Electrode implantation and stimulation

In eight cats a bipolar stimulating electrode made of 40- μm stainless steel wires was implanted near the horizontal ampulla (19). The success of implantation was tested while the animal was under gas by observing the eye movements induced by trains of stimulus pulses. It was usually possible to obtain pure horizontal eye movements with such stimuli at intensities of <100 μA . When the effects of sinusoidal polarization (see below) were tested before paralysis, eye movements often had a vertical as well as a horizontal component and the responses of dorsal neck muscles were not always reciprocal. Even when movements appeared purely horizontal, we must assume that our stimuli may have activated some anterior as well as horizontal canal afferents.

In three cats, electrodes made of 60- μm stainless steel wires were implanted into the perilymphatic space through a hole made in the bone between the round and oval windows (8).

Sinusoidal stimulating currents were applied monopolarly against a distant ground to one of the two wires of the implanted electrode alternately depolarizing and hyperpolarizing the tissue, as described in detail previously (23). The stimulus waveforms were generated by a Digital Equipment Corp. PDP 11-45 computer and consisted of either single sinusoids or a compound waveform made up of 10 superimposed sine waves of different frequencies, usually 0.175–4.047 Hz, that were relatively prime harmonics of a common base frequency (15, 23). Almost all the data were obtained in response to compound waveforms. Throughout this paper, stimulus intensity will be expressed as the amplitude of the individual components of the compound waveform; maximal amplitude of the compound waveform was approximately 8 times this intensity.

Natural stimulation in yaw was provided by manual rotation of the table on which the preparation was mounted. The cat's head was inclined approximately 30° to place the horizontal canal in the plane of rotation.

Recording and data analysis

In some experiments compound electromyogram (EMG) activity of the splenius muscle was recorded bilaterally with intramuscular bipolar electrodes. EMG was differentially amplified, full wave rectified, and low pass filtered with a 1 ms time constant.

The activity of primary afferents was recorded from the rostral portion of the superior vestibular division with glass micropipettes filled with 3 M KCl (resistance, 7–15 M Ω). Resting rate and coefficient of variation were usually calculated from 1,000 interspike intervals; in cases of very slow discharge, 500 or fewer intervals were used. Measurements were often repeated several times between periods of stimulation with superimposed sine waves.

The computer program that produced superimposed sine waves converted EMG and spike data into 64-point cycle averages or histograms, each synchronized with one of the stimulus frequencies (23). A least-squares procedure was then used to fit these data with the first and second harmonics of the stimulus frequency plus a DC term. The remaining variation of the data after this fitting represented the noise in the signal. A signal-to-noise (S/N) ratio was obtained from the ratio of the first-harmonic amplitude to the root mean square value of this remaining noise. The ratio of the second harmonic to the first gave a measure of harmonic distortion that could arise, for example, if the system acted like a rectifier. Data points were discarded if they were heavily distorted (nonsinusoidal) or showed no evidence of modulation. This typically occurred with signal-to-noise ratios less than 0.6 or harmonic dis-

tortion greater than 50%. Similar procedures were followed with the responses to single sinusoids.

RESULTS

Static properties of afferent fibers

We recorded from 103 fibers in eight experiments in which an electrode had been implanted near the horizontal ampulla. Even though efforts were made not to damage the membranous labyrinth during implantation, almost no afferents responded to horizontal rotation. Considering the recording location (5), the population can be assumed to consist of a mixture of horizontal and anterior canal afferents although the possibility exists that some utricular afferents are included in the sample. Action potentials were always positive and typically 1–5 mV in amplitude. The frequency of spontaneous activity ranged from less than 10 to almost 90 impulses/s (Fig. 1A), with a mean of 33 ± 19 (SD). In three experiments in which the stimulating electrode was implanted in the perilymphatic space between the round and oval windows, 16/36 afferents did respond to horizontal rotation, as described earlier by Goldberg,

Smith, and Fernandez (8) and the mean firing rate was 42 ± 29 ($n = 46$). Ninety-one afferents recorded in experiments with no electrode implantation (unpublished observations from another series of experiments on similar preparations) had a mean firing rate of 49 ± 21 , significantly higher (t test, $P < 0.02$) than the rate in cats with implanted ampullae and comparable to the rates of 44 impulses/s recently measured in cats by Tomko et al. (21).

While electrode implantation near the ampulla lowers resting discharge, it has no obvious effect on the coefficient of variation (CV). The latter was distributed as in cats with intact labyrinth (compare Fig. 1B with Fig. 2B in Ref. 24) and was inversely related to the resting rate. Firing was classified as regular, intermediate, and irregular (6), using the same criteria as those of Tomko et al. (21): regular, $CV \leq 0.1$; intermediate, $0.1 < CV \leq 0.3$; irregular, $CV > 0.3$. In a modest number of afferents CV continued to change for some time after penetration. It was our experience that firing classified as regular or irregular always remained in the same category, while firing initially classified as inter-

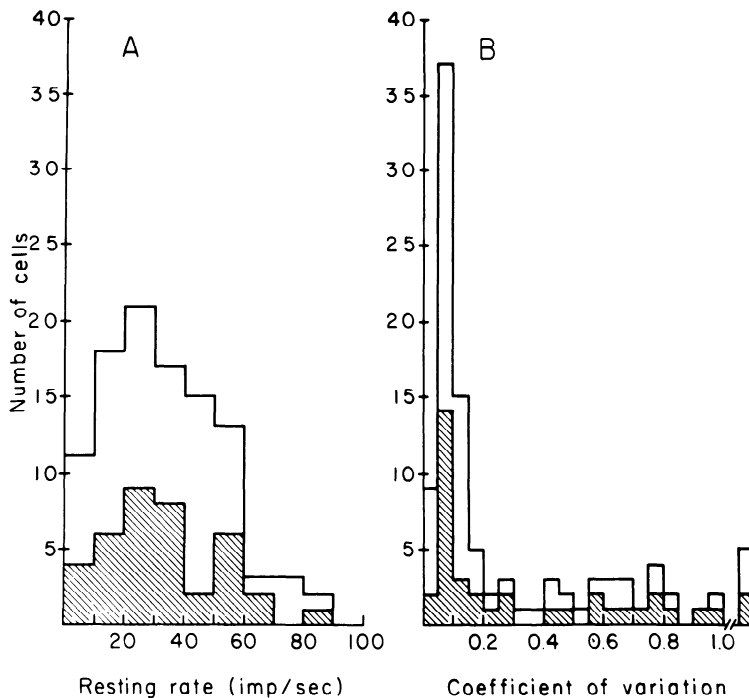


FIG. 1. Distribution of resting rate (A) and coefficient of variation (B) for 103 afferents. Shaded histograms indicate the population of 38 fibers whose dynamics were studied.

mediate sometimes became regular if studied long enough. Because some fibers were lost before the CV could be measured more than once, there is some uncertainty about the intermediate category and the description that follows is restricted to regular and irregular fibers.

Response to sinusoidal stimulation of ampullary nerves

The firing of primary afferents was increased by stimulus negativity and decreased by stimulus positivity. We used single-frequency (stimulus intensity, 0.5–10 μA) and superimposed (intensity, 0.6–3.3 μA) sine waves to study the responses of 38 fibers that responded to the stimulus and were held long enough for systematic study. The population consisted of 16 (42%) regular fibers, 8 (21%) intermediate fibers, and 14 (37%) irregular fibers; this distribution is similar to that of Tomko et al. (21). As might be expected from the behavior of neck muscles and second-order neurons (15, 23), the behavior of afferent fibers was sufficiently linear in the frequency range studied for sinusoidal analysis:

sensitivity ($\text{impulses} \cdot \text{s}^{-1} \cdot \mu\text{A}^{-1}$) or phase of a given afferent was approximately the same whether measured in response to a single sine wave or to the same frequency component of a multiple sine wave and changed little with stimulus intensity.

IRREGULAR AFFERENTS. The responses of 14 individual afferents are shown in the Bode plot of Fig. 2A, while their mean behavior is illustrated in Fig. 4 (open triangles). Phase was usually flat, with a mean lead with respect to stimulus negativity of about 14° ; only 2/14 fibers had a phase lead that increased with frequency. Gain routinely increased with frequency: mean sensitivity at 0.175 Hz was 6.9 ± 5.9 (SD) $\text{impulses} \cdot \text{s}^{-1} \cdot \mu\text{A}^{-1}$ and it was typically 1.5 times higher at 4 Hz.

REGULAR AFFERENTS. Figure 2B illustrates the responses of 16 regular fibers whose mean behavior is shown in Fig. 4 (open circles). In some respects the responses of regular and irregular fibers were similar: gain of regular fibers also increased with frequency by approximately 1.5 times, and the phase of the

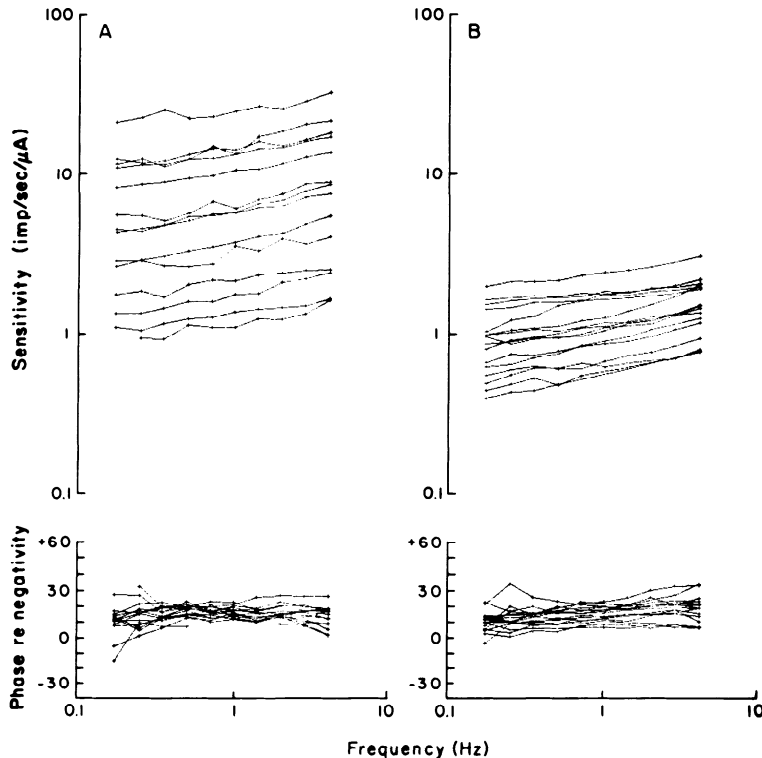


FIG. 2. Bode plots of irregular (A) ($n = 14$) and regular (B) ($n = 16$) afferents.

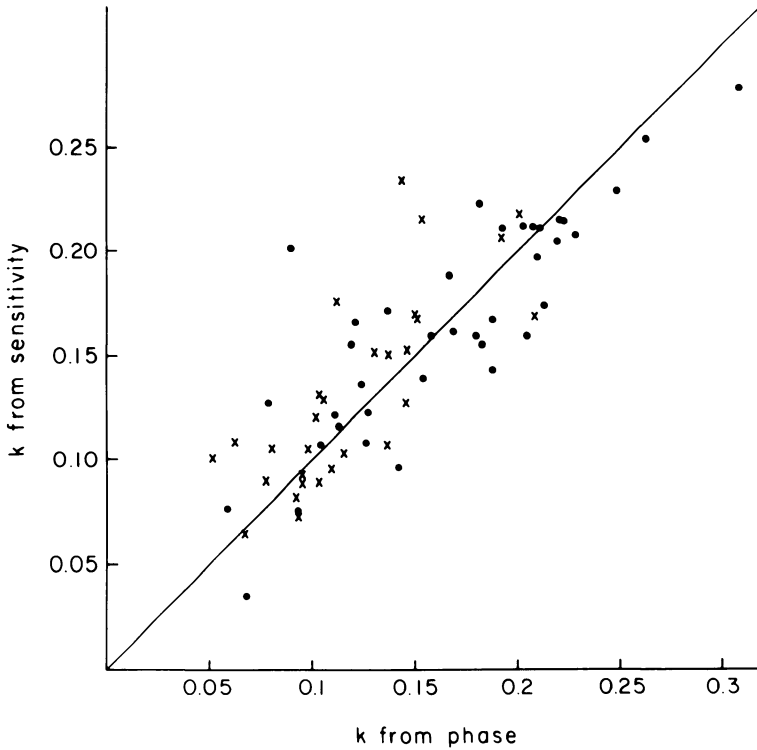


FIG. 3. Graph of k values for afferents modulated with an electrode near the ampulla (●) and in the more distant perilymphatic space (×). Straight line has a slope of 1. For further details, see text.

response led the stimulus over the whole frequency range. There were two differences, however. First the sensitivity of regular afferents was only 1 ± 0.5 impulses \cdot s $^{-1} \cdot$ μ A $^{-1}$ at 0.175 Hz, one-seventh the sensitivity of irregular fibers (8). As a reflection of this difference in sensitivity, in order to produce modulation with an acceptable S/N ratio, stronger stimuli were often needed for regular than for irregular fibers. An illustration of this is that the mean stimulus used for regular fibers was 2.3 μ A, while it was only 1.3 μ A for irregular fibers. Second, while the mean phase of regular afferents does not differ significantly from that of irregular fibers, 9/16 had increasing phase advances with increasing frequency: advances between 0.175 and 4 Hz were 7–24° (mean 13°). The phase lead of these nine fibers was 12–31° at 4 Hz.

TRANSFER FUNCTION. If we neglect the relatively small phase advance frequently seen in regular fibers, the behavior of afferents can be described as follows: phase exhibits a constant lead of about 14° over the frequency

range employed and gain increases with a constant slope (Figs. 2 and 4) where slope is less than 1 with log-log coordinates. These characteristics can be well described by a fractional transfer function $T(s) = As^k$ (A = sensitivity factor and $0 < k < 1$), where k , the slope of the log-log gain curve, is also related to the constant phase lead (θ)

$$k = \frac{\theta}{90^\circ} = \frac{\Delta \log \text{ sensitivity}}{\Delta \log \text{ frequency}}$$

We calculated the k values of individual afferent fibers separately from the best-fit straight line of log gain versus log frequency and from the estimated mean phase. Figure 3 shows that the k values calculated in these two ways are similar and fall close to a line with a slope of 1.

Response to sinusoidal stimulation in more distant perilymphatic space

An electrode inserted into the perilymph between the round and oval windows was used to study the responses of 31 afferents (16 regular, 15 irregular). Mean sensitivity

was much lower than with ampullary stimulation: at 0.175 Hz it was 0.9 ± 0.5 impulse \cdot $s^{-1} \cdot \mu A^{-1}$ for irregular fibers, 0.2 ± 0.1 for regular fibers. Gain still increased with frequency by a factor of about 1.5 for both irregular and regular fibers over the span from 0.175 to 4 Hz. The response of both fiber types led the stimulus by $10\text{--}12^\circ$ over most of the frequency range, with a tendency for a decrease in the lead above 2 Hz. The increasing phase lead seen in many regular fibers with ampullary stimulation was seen in only 1/16 regular fibers and 2/15 irregular fibers with perilymphatic stimulation.

As can be seen from Fig. 3, the transfer function $T(s) = As^k$ also describes the response of afferents to modulation with the more distant electrode. The k values are smaller because of the somewhat smaller slope of the sensitivity curve and somewhat smaller phase lead seen in response to this stimulus.

Response of neck muscles

Behavior of splenius muscle in response to sinusoidal stimulation studied at the beginning of five experiments before paralysis of the animal was identical to that described earlier in this laboratory (15, 23). Amplitude of sine-wave stimuli required to produce typical modulation ranged from 1.9 to 4.7 μA .

DISCUSSION

Placement of an electrode near an ampullary nerve has obvious consequences on the behavior of canal afferent fibers: there is no response to natural stimulation and a decrease in the level of spontaneous activity. However, many fibers are active and the wide spectrum of CV is similar to that seen in intact preparations, as is the proportion of regular, intermediate, and irregular fibers. Furthermore, the behavior of the afferents in response to sinusoidal stimulation is similar whether the electrode is placed near the nerve or further away in the perilymphatic space. For all of these reasons, we assume that the afferents are in satisfactory condition.

Response of afferent fibers to sinusoidal polarization

There are many similarities between our results and those of Goldberg et al. (8; J. M. Goldberg, personal communication). First, the sensitivity of irregular fibers to polariza-

tion is much greater than that of regular fibers. The mean difference, in our case 7 to 1, is greater than the difference in sensitivity of the two types of afferents to natural stimulation, typically reported as about 1.6 to 1 (2, 6, 21, 24). Second, in our frequency range, gain in their experiments increased by a factor of 1–1.6; most of our afferents were characterized by a 1.5 increase in gain. Third, there is a relatively constant phase lead of the response with respect to stimulus negativity over the whole frequency range studied. We do find some difference between regular and irregular fibers with regard to phase. Irregular fibers typically have a flat phase advance with respect to the stimulus over the whole frequency range. In contrast, about half of the regular fibers have a phase lead that increases somewhat with frequency. This is not seen when the electrode is placed more distantly and probably is a function of electrode location. It would seem that the basic response of cat vestibular afferents to polarizing sine waves in the frequency range we studied is well described by the transfer function $T(s) = As^k$, i.e., flat phase and increasing gain. Proximity of the electrode to the afferents causes an increase in the absolute value of the sensitivity and minor variation in the slope of the sensitivity and of the phase; there is a tendency for more interfiber difference in the phase of the regular fibers.

In their analysis of the response of vestibular afferents to natural stimulation several authors have modeled the deviation from the first-order lag system expected from the torsion pendulum model by the introduction of fractional exponents (12, 17, 21). If we assume that polarizing currents delivered into the perilymphatic space either near the ampullary nerve or at a greater distance act mainly on the nerve terminals (10, 13), then it follows that some of the processes described by the fractional power transfer function are related to impulse initiation by the current, one of the possibilities suggested earlier by Schneider and Anderson (17; see also Ref. 20). In any case, our results show that these processes reside, at least in part, central to mechanical transduction.

Comparison of afferent fibers and second-order neurons

For this comparison we have assembled from previous experiments on decerebrate,

decerebellate cats (15, 23) a population of 32 second-order neurons that were activated by sinusoidal polarization of the horizontal and/or anterior canal. Of 24 neurons with known location, 18 were in Deiters' and 4 in the descending nuclei; some neurons were tested and identified as projecting in the vestibulospinal tracts (VSTs). The mean behavior of this population in response to sinusoidal polarization is shown in the Bode plot of Fig. 4. Goldberg, Fernandez, and Highstein (7) have shown in the monkey that second-order neurons may receive three kinds of input: predominantly from regular or irregular fibers or mixed. We must keep this in mind when comparing the dynamics of afferents with those of second-order neurons. Whether we make the comparison with the mean be-

havior of regular or irregular afferents or with the mean behavior of the whole population of afferents including intermediate fibers, it is evident from Fig. 4 that while the slope of the gains is the same, second-order neurons display a phase advance over the afferents that appears below 1 Hz and reaches approximately 18° at 4 Hz. The difference between the mean phases and the normalized gains of second-order neurons and of the whole population of afferents can be modeled by a transfer function of the form $\tau s + 1$. Figure 5 shows the excellent fit between the data and the curve calculated with $\tau = 12$ ms using a least-squares fit. The transfer function predicts phase advances of 25° at 6 Hz. If such predictions apply to responses to natural stimulation, they have physiological sig-

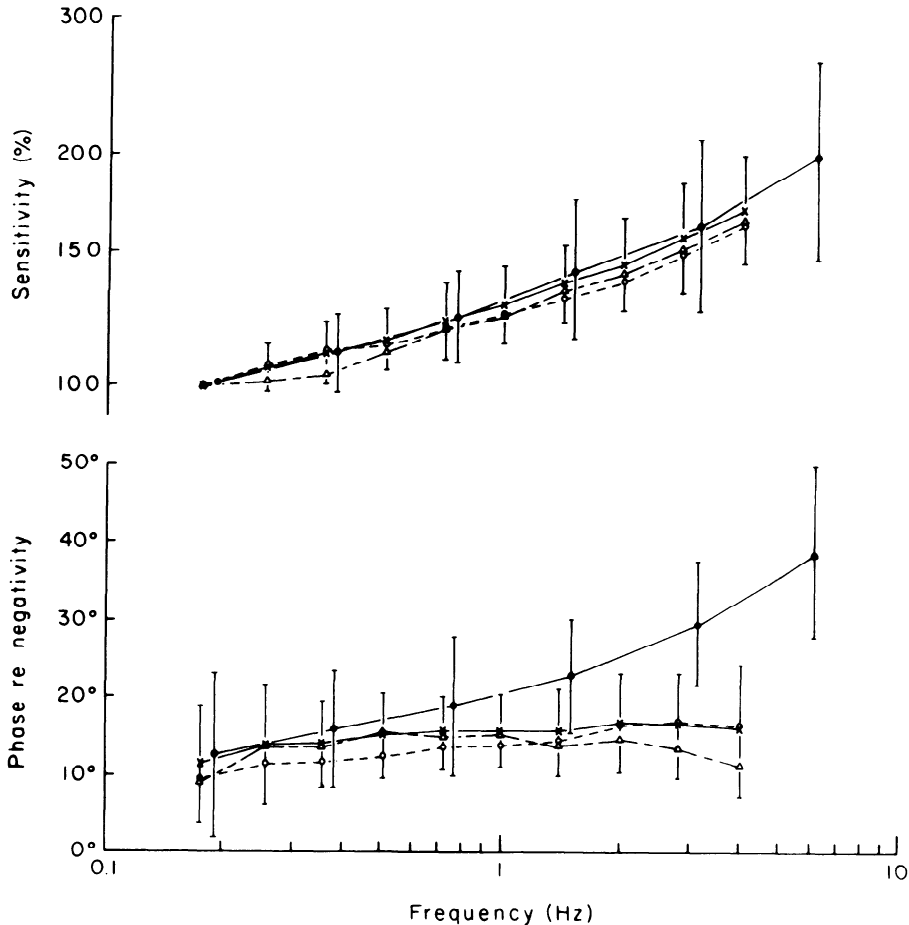


FIG. 4. Bode plots of mean gain and phase for regular afferents (\circ), irregular afferents (Δ), all afferents (\times), and second-order neurons (\bullet , from data of Refs. 15 and 23). For the second-order neurons, phase was derived from 32 neurons, gain from 26. Error bars show standard deviation for second-order neurons and for population of all afferents. Sensitivity normalized at 0.175 Hz for afferents, 0.19 Hz for second-order neurons.

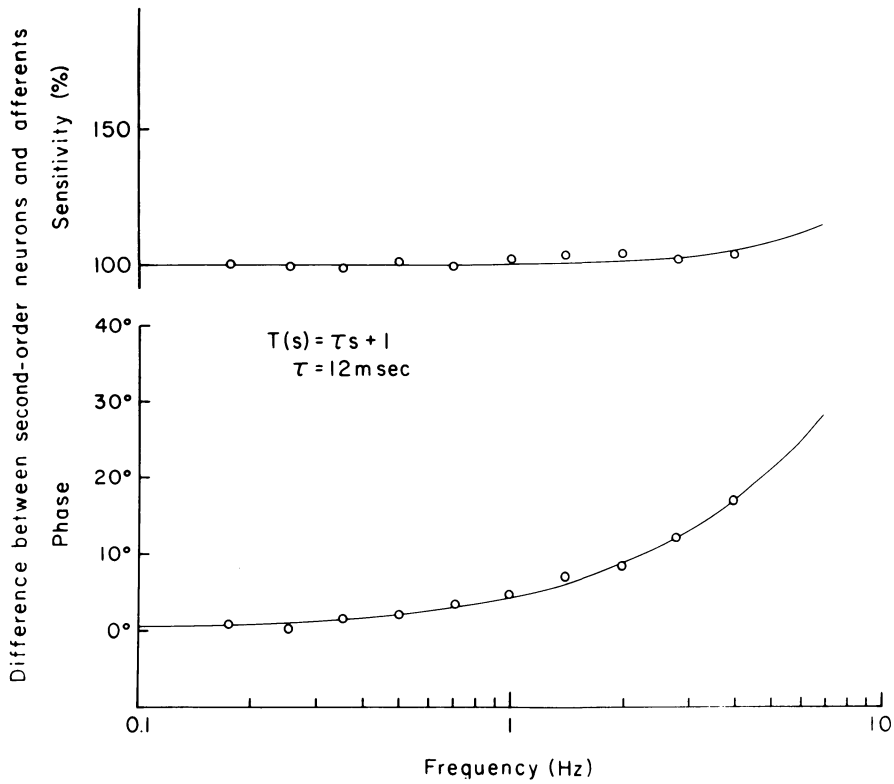


FIG. 5. Bode plot of differences in phase and gain between second-order neurons and the population of all afferents. Solid line calculated from transfer function, circles from experimental data. Differences were calculated from interpolated values for the second-order neurons (Fig. 4) at points corresponding to frequencies used to study afferents.

nificance because frequencies up to 6 Hz and even higher are an important component of head movement in the cat (3, 9).

We suggest that the high-frequency phase advance is not a function of the type of stimulus used to activate the afferent fibers. From the viewpoint of second-order neurons, the main difference between activity evoked by movement and by electrical polarization is probably in the mixture of regular, intermediate, and irregular fibers recruited by the stimulus. This may be of little consequence, at least for those neurons excited primarily by regular or irregular fibers. If this is so, a phase advance of second-order over first-order neurons would be expected with natural stimulation. Most studies of the frequency response of central (horizontal) vestibular neurons have *a*) used frequencies of 1 Hz or less and *b*) recorded from type I rather than identified second-order neurons. These populations included but almost surely did not consist entirely of second-order neurons (16).

Furthermore, with natural stimulation the dynamics of afferents with different CV vary widely. Therefore, it can be difficult to determine input-output relations of second-order neurons when the nature of the specific input (e.g., regular or irregular afferents) is not known. Within these limitations, horizontal type I neurons in cat and monkey usually reflect the behavior of the average incoming signal without evidence of a phase lead (11, 14, 18). The same result was obtained in gerbils by Schneider and Anderson (17) who used frequencies up to 4 Hz but anesthetized their animals with ketamine. On the other hand, Fuchs and Kimm (4) working with alert monkeys noted that some type I "vestibular only" neurons lagged input acceleration by less than 50° at 0.93 Hz and, therefore, seemed to lead even irregular afferents (6). Similarly, G. Bilotto, J. Goldberg, and B. W. Peterson (personal communication) have recently observed second-order neurons in the decerebrate cat with high-fre-

quency phase advances equal to or greater than that of the most phase-advanced irregular fiber illustrated by Tomko et al. (21).

The functional meaning of the high-frequency phase advance of second- over first-order neurons would be clear if it were the property of a subset of vestibulospinal neurons contributing to the VCR: the reflex develops a considerable phase advance with respect to the stimulus at higher frequencies when evoked by sinusoidal polarization (23) and, unlike the vestibuloocular reflex (VOR), also develops a considerable phase advance when evoked by natural stimulation (1). Whether the phase advance is a property of a subset of neurons remains to be determined. The question cannot be answered from our sample, which consists almost entirely of Deiters' and descending nucleus neurons, some identified as, and most others presumably, VST neurons. Some phase-advanced neurons studied by Fuchs and Kimm (4) were in Deiters' nucleus and in the medial nucleus and were, therefore, possible contributors to the VSTs. Further experiments should be performed on vestibular neurons identified as projecting to different locations; for example, to the proximity of neck or extraocular motoneurons.

Afferent fibers and vestibulocollic reflexes

Because both the VCR and irregular afferent fibers display a considerable phase ad-

vance at higher frequencies of natural stimulation, it has recently been suggested that irregular afferents make a particularly important contribution to this reflex (1). With some forms of galvanic stimulation, irregular afferents have a lower threshold than regular fibers (8), and it is therefore conceivable that the polarization-evoked VCR is due to stimuli that modulate mainly or only irregular afferents, which may then project to a special population of VST neurons. Our results bear only on the second of these points. In earlier experiments, typical VCRs were evoked at stimulus strengths of 2–4 μA (15, 23); in the present series, stimuli of 1.9–4.7 μA were required. Therefore, while the contribution of regular and irregular fibers to the pathways producing the VCR remains unknown, our results show that both irregular and regular fibers are modulated at the stimulus strengths required to produce the reflex.

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