

RESPONSE PATTERNS OF PRIMARY VESTIBULAR NEURONS TO THERMAL AND ROTATIONAL STIMULI

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SUMMARY

The neural responses of vestibular ganglion cells to quantified thermal and rotational stimulation were studied in anesthetized squirrel monkeys. All cells exhibited a spontaneous discharge rate with the average being 72 ± 27.8 spikes/sec. The observed increases and decreases in discharge rates during sinusoidal angular rotation were consistent with the morphological polarization patterns of the hair cells. Likewise, the ganglion cell responses resulting from thermal stimulation by a controlled temperature air stream directed on the lateral portion of the horizontal canal were in agreement with those expected on the basis of Barany's convective current theory and the polarization pattern of the hair cells.

In an attempt to determine the relationship between thermal and rotational stimuli, the sensitivities of individual cells to both types of stimuli were determined. Those cells most sensitive to angular rotation were also most sensitive to caloric stimulation. An equivalency value for the two types of stimuli was defined and found to be $1.84 \text{ }^\circ\text{C/radian} \cdot \text{sec}^{-1}$.

The global response characteristics of the vestibular endorgan were studied by simultaneous thermal and rotational stimuli. The thermal stimulus was used to bias the cupula at a new equilibrium position while a rotational stimulus was used to determine the differential sensitivity at that cupular position. For the cells with a more regular spontaneous discharge rate, the differential sensitivity was observed to be a function of the instantaneous discharge rate. No such relationship was observed for the more irregular cells.

INTRODUCTION

Although angular and linear acceleration of the head are the physiological

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stimuli for the vestibular endorgans, thermal stimuli are commonly used in clinical and research settings to assess vestibular function. The fact that thermal stimuli could elicit labyrinthine symptoms was known in 1853, but it was not until 1906 that Barany¹ introduced caloric testing as a clinical test. Since that time various theories concerning the origin of the caloric response have been postulated, but Barany's theory suggesting that the caloric reaction results from endolymphatic density changes due to imposed temperature gradients across the lateral semicircular canal is almost universally accepted today⁹. Even though Barany's theory is widely accepted, little quantitative neurophysiology has been added since Gernandt's study in 1949 (see ref. 5). Data are needed concerning the effect of thermal stimuli on the various ampullae and maculae, the equivalency between thermal and rotational stimuli and the feasibility of using caloric stimuli to obtain quantitative neurophysiological data. The present study was undertaken in an attempt to provide insight into these various questions.

Recent developments in neurophysiological techniques^{2,3,7,8} have permitted the recording of single cell neural responses from Scarpa's ganglion in mammals. The recording of these responses during a combination of controlled thermal and rotational stimulations offers an excellent opportunity for analyzing response properties of the peripheral vestibular system. Barany's classical theory of caloric stimulation can be examined in detail by directing a controlled temperature air stream on the lateral portion of the horizontal semicircular canal while recording from neurons innervating the various ampullae and maculae. Use of both rotational and thermal stimuli not only provide new information about the receptor, but permit a quantified comparison of the thermal and rotational responses of individual cells.

METHODS

Single cell recordings from the vestibular ganglion were obtained from 7 squirrel monkeys (*Saimiri sciureus*). All animals were given an initial 20-mg dose of ketamine hydrochloride (Ketalar) intramuscularly followed by a 2-mg dose of pentobarbital sodium (Nembutal) injected intraperitoneally. Supplementary doses of Ketalar were administered as required throughout the experiment. The surgical exposure of the VIIIth cranial nerve was essentially that of Rose *et al.*¹⁴. A circular opening in the skull, approximately 15 mm in diameter, was made over the internal auditory meatus, the dura reflected and the cerebral cortex aspirated. Following removal of the cerebellar tentorium the anterolateral portion of the cerebellum was also aspirated, thereby exposing the VIIIth cranial nerve as it emerges from the internal auditory canal. A cylindrical plastic chamber was cemented to the skull and warm mineral oil used to fill the chamber and cavity above the nerve. A microdrive was attached to the plastic chamber, thereby hydraulically sealing the cavity and permitting stable recordings from single cells during rotation. In addition, the lateral portion of the horizontal semicircular canal was exposed by a postauricular approach.

Following these operative procedures, the animal was placed on a gimbaled platform mounted on a rate table. This equipment allowed positioning of individual semicircular canals with respect to the plane of rotation and the gravitational field.

In order to permit simultaneous caloric and rotational stimulation, the animal was tilted back approximately 15° so that the plane of the horizontal semicircular canal was orientated at 45° to both the plane of rotation and accelerative gravity vector. All recordings were obtained with the animal in this position.

Neural recording was accomplished by means of glass pipette microelectrodes filled with 3 M NaCl and having impedances between 5 and 15 M Ω . These electrodes were directed into Scarpa's ganglion with the aid of an operating microscope. Signals from the electrode were amplified by a capacity-compensated AC amplifier (Grass P-15) which was positioned on the rate table and set with a gain of 100 and a bandpass from 300 to 3000 Hz. The signal passed from amplifier output, through slip rings, to a dual beam oscilloscope (Tektronix 565). One trace of the scope was used to discriminate unitary cell discharges with the unblanking signal from this trace serving as input to one channel of a KW-12 timer associated with a PDP-12 computer (Digital Equipment Corp.) for storage on digital tape and generation of on-line poststimulus histograms. The second trace of the oscilloscope was observed at a slower sweep rate and provided a general indication of the response of the cell and the effectiveness of the discrimination by the trigger circuit of the first trace. All responses were monitored audibly and stored in analog form on a direct record channel of an instrumentation tape recorder (Hewlett Packard, model 3960C).

Caloric stimuli consisted of a controlled temperature air stream directed on the exposed portion of the horizontal semicircular canal. An air flow rate of 4 l/min was delivered to the canal through a polyethylene tube (0.085 in. I.D.). Mounted at the end of the tube and in the center of the air stream was an iron-constantan thermocouple. The temperature measured by this thermocouple was continuously recorded on a Grass polygraph (model 5) and used as a measure of the thermal stimulus. Temperatures from 2 to 10 $^\circ\text{C}$ above and below the animal's rectal temperature were used. Control of the air stream temperature was by a thermoelectric device⁴.

Rotational stimuli were delivered by a rate table with velocity feedback control (Inland model TT-5742A). The power supply for the motor (Inland Controls 60-ICM-600) was programmable and in conjunction with a function generator (Hewlett Packard model 3310A) was capable of driving the motor through sinusoidal angular velocity profiles of variable frequency and amplitude. Rotational stimuli used in this study were sinusoids with periods of 2 sec and amplitudes varying from 32 to 96 $^\circ$ /sec. In addition to a voice commentary, the tachometer signal and synchronization signals from the function generator were recorded on FM channels of the analog tape recorder.

The digital data which were stored on computer-compatible magnetic tapes were later used to generate poststimulus, interspike-interval and period histograms of the responses. Rotational single cell responses were analyzed by computation of the Fourier coefficients (computed on the basis of 20 bins/cycle of the stimulus) for the period histograms. For this computation, aperture error resulting from a finite number of bins was insignificant.

RESULTS

General response characteristics

Positioning of the animal with respect to the plane of rotation and the gravitational vector not only provided a canal orientation suitable for simultaneous caloric and rotational stimulation, but also made possible classification of a cell as to the endorgan it innervated. To permit simultaneous caloric and rotational stimulation of the horizontal semicircular canal, the animal was positioned so that the plane of the horizontal semicircular canal formed a 45° angle with the gravitational vector and with the plane of rotation. With the horizontal canal in this position, the plane of the posterior canal also formed an approximate 45° angle with the gravitational vector and plane of rotation. The plane of the superior canal was approximately vertical. For those cells responding to horizontal rotation when the animal was positioned as described above, the difference in functional polarization of the hair cells in the horizontal and posterior ampullae permitted identification of the ampulla a cell innervated. Units exhibiting an increase in discharge rate during ipsilateral rotation (utriclelopetal cupular deflection) were identified as originating from the horizontal canal, while units which decreased their discharge rate upon ipsilateral rotation were considered to be posterior canal units. Those cells not responding to horizontal rotation might innervate either the superior canal or the otoliths.

Of the 37 cells quantitatively analyzed, all had a non-zero spontaneous discharge rate with the average being 72 ± 27.8 spikes/sec (mean \pm S.D.) and fit into one of the above classifications. No neurons were observed which responded with an increased or decreased discharge rate to both ipsilateral and contralateral rotation. Twenty-seven of the total 37 cells used in the study were from the horizontal canal, 5 from the poste-

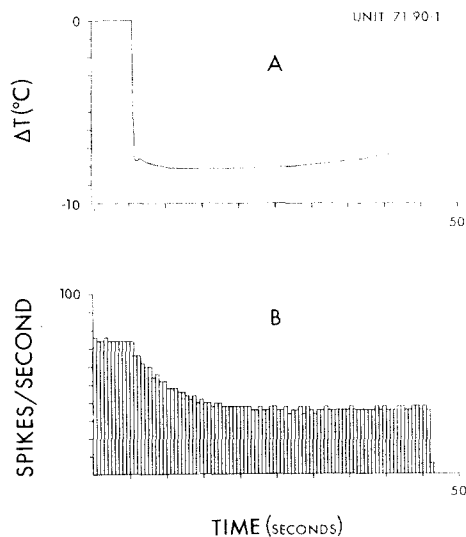


Fig. 1. Caloric response of a cell innervating the horizontal canal. A: temperature change of the air stream directed on the lateral portion of the horizontal semicircular canal. B: poststimulus histogram of the neural response (bin width = 0.5 sec).

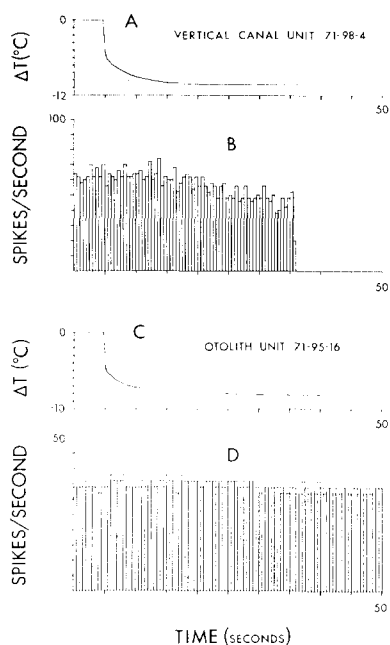


Fig. 2. Caloric responses of posterior canal and otolith neurons. A and B: stimulus and neural response of a posterior canal cell, respectively. C and D: stimulus and neural response of an otolith cell, respectively.

rior canal and 5 did not respond to horizontal rotation. The proportion of cells in each group by no means reflects the population of the nerve since many vertical canal and otolith neurons were observed but no attempt was made to study the majority of these cells—only a small proportion were studied to determine if temperature changes were affecting the nerve directly.

A typical response exhibited by the horizontal canal neurons to caloric stimulation is shown in Fig. 1. During cold thermal stimulation, the discharge rate of this particular cell decreased from its spontaneous discharge rate of 76 spikes/sec to a constant rate of 36 spikes/sec. All horizontal canal units showed this type of decrease in discharge rate during stimulation with cold air and showed an increase in rate during warm caloric stimulation.

The effects of thermal stimuli on ganglion cells innervating vestibular endorgans other than the horizontal canal are shown in Fig. 2. The caloric responses of posterior canal units were of the same direction as horizontal canal units; however, effects were small and developed slowly due to greater temperature conduction time (compare Figs. 1B and 2B). Fig. 2D demonstrates the caloric response of a unit which did not respond to rotation but did respond to tilting about the mid-sagittal axis. This cell had a maintained firing level of 32 spikes/sec with the head level, but when the contralateral ear was tilted down 8° , the discharge rate increased to 42 spikes/sec. Upon return to a level head position, the discharge rate returned to 32 spikes/sec. This cell

and all other cells not responding to horizontal rotation did not respond to caloric stimulation.

Response of horizontal canal cells

The discharge level of the 27 horizontal canal units studied decreased during cold caloric stimuli, increased during warm stimuli and returned to the spontaneous level following cessation of the caloric stimulus. Depending on the sensitivity of the cell and its spontaneous rate, a cold thermal stimulus could be applied which completely inhibited the discharge of the cell. On the other hand, no maximum discharge rate was observed during warm caloric stimulation but no temperature changes above 10 °C were applied to the horizontal canal in order to avoid damage to the preparation.

Although vestibular adaptation, as measured by nystagmus and subjective sensation, is well known, only recently has peripheral adaptation to a natural stimulus been demonstrated. Goldberg and Fernandez⁶ reported that a portion of the cells they studied exhibited adaptation to constant angular acceleration. The caloric stimulus corresponding to a constant angular acceleration is a stimulus which maintains a constant pressure difference across the cupula. This constant pressure condition should be approximated by the maintenance of a constant temperature at the lateral portion of the horizontal canal. As is shown in Fig. 1, the discharge rate of a cell could be maintained at a constant non-spontaneous discharge level by an approximately constant air stream temperature. For the units studied, no large adaptive effects were observed during maintenance of a reasonably constant temperature for 20 sec to over 3 min in some cases. The majority of the units studied had a very regular spontaneous discharge pattern and according to Goldberg and Fernandez⁷ no large adaptive effects would be expected for these regular units.

In order to provide a quantitative measure of the transient response to a thermal stimulus, 12 units were studied with respect to their time response to a step decrease in temperature. Following application of this step decrease, the discharge rate approached a new firing level in an exponential fashion with an average time constant of 4.9 ± 0.9 sec.

One of the major objectives of this study was to determine the relative sensitivity of the horizontal semicircular canal to both thermal and rotational stimuli by analyzing the responses of individual ganglion cells to the two types of stimuli. The sensitivity of 18 units to caloric stimulation was studied by defining caloric sensitivity as the change in discharge rate per degree change in temperature of the stimulating air stream. If a caloric stimulus inhibited the discharge of a cell completely, no value of sensitivity was determined. Sensitivity values varied from 3.8 to 13.4 spikes/sec/°C with an average of 7.7 ± 2.8 . It should be reemphasized that these values were obtained with the plane of the horizontal canal at 45° with respect to the gravitational vector.

Twenty-six horizontal canal units were also studied to determine their sensitivity to rotation. All rotational sensitivities were determined by analyzing the response of the cell to sinusoidal angular velocity profiles of 0.5 Hz. Rotational sensitivity was defined as the ratio of the response amplitude to the maximum angular velocity of the rate table. The amplitude of the response was determined by the fundamental compo-

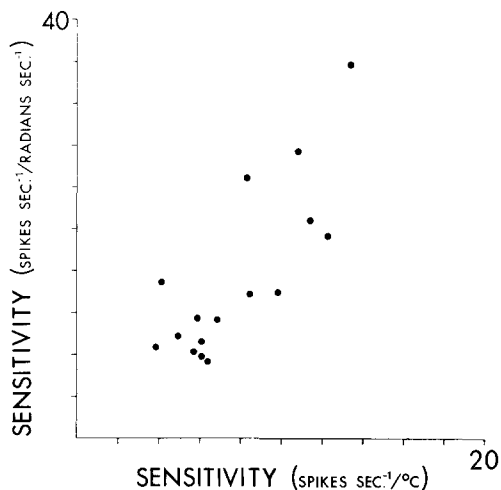


Fig. 3. Relationship between caloric sensitivity (abscissa) and rotational sensitivity (ordinate) for 16 horizontal canal cells. See text for definitions of thermal and rotational sensitivity.

ment of the Fourier series expansion of the period histogram response. These values ranged from 7.4 to 36.0 spikes/radian with an average of 18.4 ± 10.4 . The average phase lead with respect to velocity at 0.5 Hz was $16.8^\circ \pm 7.9$.

A comparison of the rotational and caloric sensitivity of 16 cells is shown in Fig. 3, where the abscissa is caloric sensitivity and the ordinate is rotational sensitivity. Each datum point represents the caloric and rotational sensitivity of an individual cell. A trend can be seen in that the cells most sensitive to rotation were also most sensitive to caloric stimulation.

Nonlinearities

As a result of its general applicability and relatively simple techniques, linear system analysis (for example, Bode plot analysis) has become a common tool in the study of some biological systems. Although a biological system may respond linearly over a limited range, nonlinear analysis is probably appropriate when studying system responses to large inputs. In view of the nonlinearities in neural responses from the semicircular canals^{2,11,12} it was deemed desirable to investigate the linearity of ganglion cell responses resulting from stimuli of larger magnitude.

Simultaneous caloric and rotational stimulations provided an effective means for examining the response of the peripheral vestibular system to these large stimuli. Caloric stimuli were used to bias the cupula at a nonequilibrium position and thereby mechanically biasing the ganglion cells at a firing level which differed from their spontaneous value. A small sinusoidal rotational stimulus was then given to determine the differential sensitivity of the cells at this nonequilibrium cupular position and new discharge rate. This scheme of stimulation is shown in Fig. 4 for a cell with a spontaneous discharge level of 100 spikes/sec. Following an approximately 5 °C cold caloric stimulus, the discharge rate decreased to 30 spikes/sec, at which time a sinusoidal rotational stimulus was given and the response noted, thus permitting determination

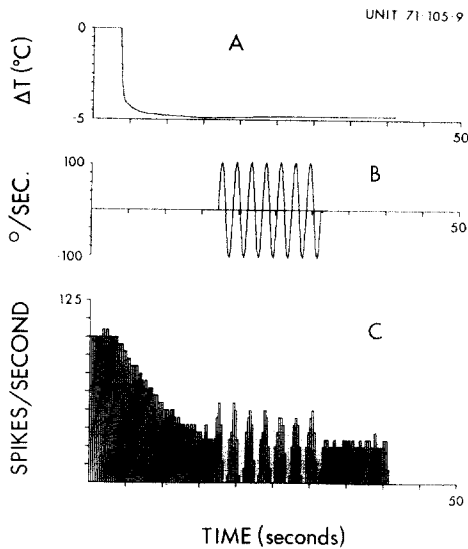


Fig. 4. Scheme used for analysis of nonlinearities. A: a caloric stimulus was used to bias the ganglion cell at a discharge rate differing from its spontaneous rate. B: a rotational stimulus was then given to determine the differential sensitivity at the biased discharge rate. C: poststimulus histogram showing the response to the simultaneous thermal and rotational stimuli.

of the differential sensitivity of the cell to rotation when it was biased at a discharge rate of 30 spikes/sec.

Fig. 5 shows the results from one neuron for a series of rotational stimulations at different bias levels. This particular cell (unit 71-90-1) had a spontaneous discharge rate of 76 spikes/sec and exhibited a response to rotation as shown in Fig. 5C when no caloric stimulus was present. A cold caloric stimulus was then administered causing utriculofugal deflection of the cupula and a decrease in the ganglion cell discharge rate to 36 spikes/sec, at which time the rotational stimulus was again delivered and the resulting response is shown in Fig. 5E. The stimulus temperature was then increased and the differential sensitivity determined at a discharge rate of 53 spikes/sec (Fig. 5D). Using warm thermal stimuli, the cupula was utriculopetally deflected and the differential sensitivity measured at bias levels 22 and 42 spikes/sec above the spontaneous level (Figs. 5B and 5A respectively). Fig. 5 illustrates how the differential sensitivity of unit 71-90-1 changes as a function of its biased discharge rate. The greater the discharge rate, the greater the differential sensitivity to rotation.

The type of response described above was not representative of all units since some did not show this type of change in sensitivity during caloric biasing and rotation. For our sample, dependence of sensitivity upon bias level was correlated with regularity of firing and average sensitivity to rotation. The neurons exhibiting changes in differential sensitivity showed a lower average sensitivity and a much more regular discharge pattern than the cells not showing these changes in sensitivity.

The above mentioned differences between regular and irregular units are illustrated in Fig. 6 where differential sensitivity to rotation is plotted *versus* discharge level

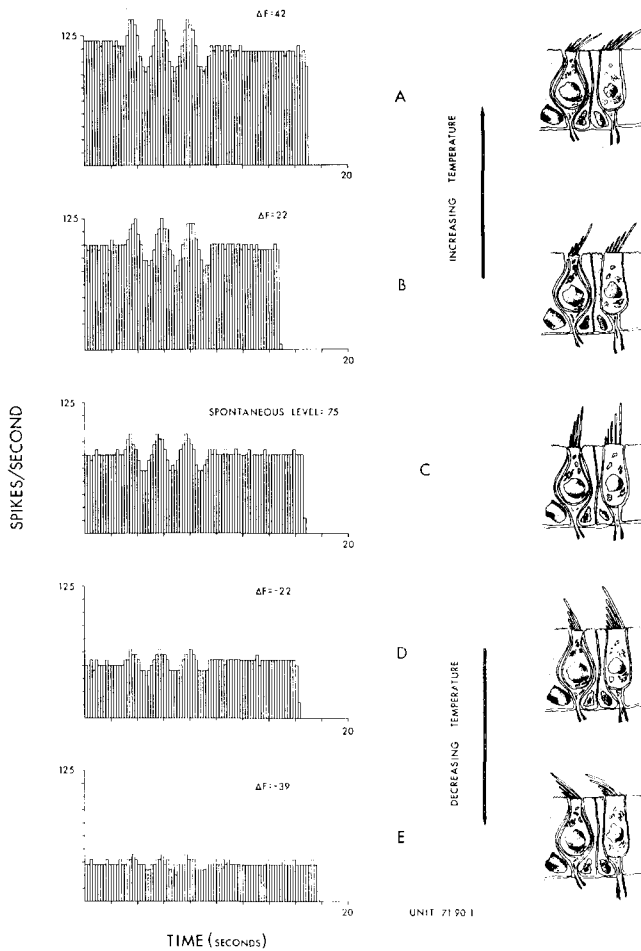


Fig. 5. Effect of thermal biasing on rotational sensitivity of a neuron with a regular discharge. Shown is the temperature change used to bias the cell, and a schematic representation of assumed hair cell position. A: rotational response when the cell is biased 42 spikes/sec above the spontaneous level ($\Delta f=42$). B: $\Delta f=22$. C: $\Delta f=0$, rotational sensitivity at the spontaneous discharge rate. D: $\Delta f=22$. E: $\Delta f= -39$.

for 3 regular units (Fig. 6A) and two irregular units (Fig. 6B). Also shown are representative interspike-interval histograms for these two groups. (Units were considered to have a 'regular' spontaneous discharge if the coefficient of variation for the interspike interval was less than 0.2 and the unit was classified as 'irregular' if the coefficient of variation was greater than 0.2 (see refs. 7 and 15).) The regular units show an approximately linear relationship between sensitivity and discharge level for rates from 20 to approximately 120 spikes/sec, whereas above 120 spikes/sec, data from only one unit is shown (unit 71-95-3) and a non-increasing relationship is indicated. This type of response above 120 spikes/sec was observed for other regular units. Differences in sensitivity scales between Figs. 6A and 6B should also be noted.

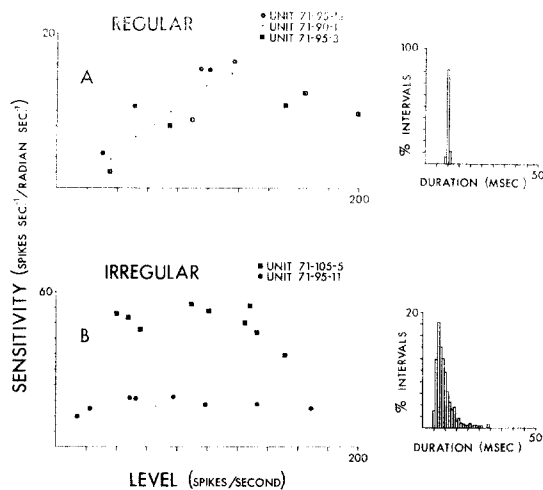


Fig. 6. Comparison of the effect of thermal biasing on the differential sensitivity to rotation for regular and irregular neurons. A: rotational sensitivity is plotted as a function of the discharge level for 3 regular units. The regularity of the spontaneous discharge is illustrated by the interspike-interval histogram to the right. B: same as A but data from irregular units.

The data from Fig. 6A suggest that the differential sensitivity of regular units is a function of the discharge rate of the cell, for example, unit 71-90-1 has a spontaneous rate of 76 spikes/sec whereas unit 71-95-12 has a spontaneous level of 105, but when biased to the same discharge rate they show approximately the same differential sensitivity to rotation. To investigate this in more detail, differential sensitivity *versus* discharge level is plotted in Fig. 7 for 15 regular units. Also shown in this figure is the straight line calculated from the data by linear regression analysis.

With this nonlinearity in mind, it was deemed desirable to reexamine the relationship between caloric and rotational sensitivity. To account for this change in sensitivity, rotational sensitivity was defined as the average of the sensitivity at the spontaneous discharge rate and the sensitivity at the discharge rate at which the caloric sensitivity was determined. This correction was applied to 13 of the neurons shown in Fig. 3, and the resulting equivalency between temperature changes and angular velocity averaged: 1 radian/sec = 1.84 °C.

DISCUSSION

Spontaneous activity

One of the striking features of the neural activity in Scarpa's ganglion of the squirrel monkey is the high spontaneous discharge rate observed during these experiments. These rates are especially high in comparison to the resting discharge observed by Precht *et al.*¹³ in the vestibular nerve of the frog and by Groen *et al.*⁸ in the elasmobranch. The majority of neurons observed in the frog had either no detectable resting discharge or a spontaneous rate below 15 spikes/sec, and in the elasmobranch, the average rate was approximately 20 spikes/sec.

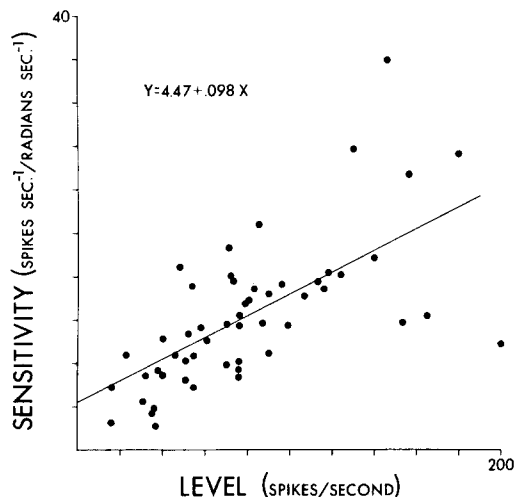


Fig. 7. Differential sensitivity to rotation *versus* discharge level for 15 regular neurons. Shown is the straight line resulting from linear regression analysis of the data.

Lowenstein and Sand¹⁰ hypothesized that this spontaneous activity provided a means for bidirectional coding of angular rotations, in which case the spontaneous rate could be thought of as a carrier of pulses subject to frequency modulation by rotational stimuli. The degree of bidirectional coding at the first order neuron has important implications for clinical testing methods. During bithermal stimulation, one labyrinth must code bidirectional cupular displacements if nystagmus responses of equal magnitude to 44 °C and 30 °C water are to result. If the spontaneous rate in the nerve was low one would not expect caloric responses of equal magnitude to result from bithermal testing.

Not only did the frequency of spontaneous discharge vary from cell to cell in Scarpa's ganglion, but the pattern of firing also varied. The regularity of spontaneous activity can also be correlated with other parameters of the response of the cell, such as sensitivity and adaptation⁷. The relationship between spontaneous activity and differential sensitivity will be discussed later. Undoubtedly once the origin and mechanism of the spontaneous discharge is elucidated, the significance and relationship of this discharge to various response parameters will be better understood.

General response characteristics

For all units studied, the responses to thermal and rotational stimuli could be explained on the basis of the convective current theory of Barany¹ and cupular-endolymphatic displacement. With the horizontal and posterior canals at 45° with respect to the horizontal plane and the gravitational field, the ampulla of the horizontal canal is up whereas the ampulla of the posterior canal is down. Therefore, ipsilateral rotation causes utriculopetal cupular deflection and contralateral rotation causes utriculofugal deflection in the horizontal ampulla. Assuming that the sensory hair cells

of the lateral canal are depolarized by utriculopetal cupular movements and hyperpolarized by utriculofugal deflections, one would expect ipsilateral rotation and warm caloric stimulation to result in an increase in the discharge rate of the ganglion cells and contralateral and cold thermal stimuli to cause decreases in the firing level. These response patterns were observed in all 27 horizontal canal neurons studied.

Recalling the functional polarization of the posterior canal sensory cells, one would expect contralateral rotations and warm thermal stimuli to increase the discharge rate of the ganglion cells and ipsilateral rotation and cold stimuli to decrease the rate. Again, all posterior canal units showed the expected response patterns.

The question of the effect of caloric stimulation on the otoliths has not been thoroughly investigated but the very limited data presented here indicate absence of otolith response to caloric stimulation when the animal is positioned as previously described. However, the present data do not rule out the possibility that in a clinical testing position (horizontal canal in the vertical plane), thermal stimuli might stimulate the otoliths.

One of the major objectives of this study was to determine if the response of a neuron to caloric stimulation of the horizontal canal provided predictive information concerning the cell's response to rotation and if so, what the relationship between the two types of stimuli is. As was shown in Fig. 7, a somewhat linear relationship between thermal and rotational sensitivity was found, thereby implying that thermal stimulation provides an indication of the response of a cell to the physiological stimulus, angular rotation. An equivalency between thermal and rotational stimuli was determined, but it should be emphasized that this particular relationship has been shown to hold only at the ganglion cell level and may change at various levels within the central nervous system.

Following a step change in temperature at the lateral portion of the horizontal canal, the average response time constant portion of canal units was 4.9 sec. This time constant should represent the combined effects of any thermal time constants and the long time constant (π/Δ) of the horizontal canal. Although we are presently unable to determine the thermal time constant, we are able to state that π/Δ , as measured by thermal stimuli, is approximately 4.9 sec or less.

Goldberg and Fernandez⁸ reported an average value of 5.7 sec for π/Δ by observing responses of individual ganglion cells in the squirrel monkey during constant angular acceleration. Therefore, we can probably assume that the thermal time constant in our experiments was small compared to π/Δ , and that the response time constant of 4.9 sec reflects π/Δ .

Analysis of nonlinearity

One of the requirements of a linear system is that the superposition principle be satisfied. In the context of this study, superposition predicts that the differential response to a rotational stimulus is independent of the biased discharge level established by thermal stimulation. This was generally the case for the neurons with a more irregular spontaneous discharge, whereas the regular neurons exhibited changes in sensitivity during thermal biasing. Many questions arise as to the origin and signif-

icance of this nonlinearity exhibited in the neural response of the more regular cells. Is this nonlinearity of mechanical or neural origin? Is this nonlinearity the same as that described by Fernandez and Goldberg²?

Two experimental observations seem significant when discussing the origin of the nonlinearity resulting from changes in differential sensitivity to rotation. The first is the fact that not all neurons exhibited the nonlinearity which would seem to argue against the hypothesis that the nonlinearity results from mechanical properties of the cupular-endolymphatic system only, but one could argue that various hair cells are mechanically coupled to the cupula differently. Since the sensory cells are distributed along the slopes of the crista, as well as on the top of the crista, the possibility for different modes of coupling between the cupula and hair cells certainly exists, but our present concepts of cupular mechanics do not yield theoretical grounds for differences in coupling. In view of the second observation—the fact that the nonlinearity was correlated with the pattern of spontaneous discharge—an alternative explanation is that the sensitivity changes probably reflect the physiology of the hair cells and/or the afferent terminal.

On the basis of the differential sensitivity changes exhibited by the more regular units, one would expect the excitatory response from these cells to be larger than the inhibitory response. This type of response asymmetry has been observed not only for the regular units but also for the more irregular units³. For the more irregular cells, they also observed that adaptation to inhibitory stimuli was greater than adaptation to excitatory stimuli thereby providing a possible explanation for the asymmetry between the excitatory and inhibitory responses of the irregular cells. Since the more regular cells do not show much adaptation, the observed response asymmetry exhibited by regular units may be the result of differential sensitivity changes.

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