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The Relationship of Conduction Velocity to Other Physiological Properties of the Cat's Horizontal Canal Neurons

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Summary. The conduction velocity and other physiological characteristics of the first order horizontal canal afferents were studied in 24 anesthetized cats. From their spontaneous discharge patterns, neurons were classified into three groups: regular, intermediate and irregular. The irregular units tended to have a low resting rate, high sensitivity to angular acceleration, frequently exhibited adaptation during prolonged acceleration, and showed a short latency from the time of electric stimulation of the labyrinth to recording the action potential near Scarpa's ganglion. The regular units tended to have a high resting discharge rate, low sensitivity, were mostly non-adapting, and showed longer latency to electric stimulation. The intermediate neurons had a mixed character of regular and irregular units.

Based on the very short conduction times (mean 0.34 msec) and the work of Moxon (1971), we conclude the locus of activation of electrical stimulation is neural rather than the receptor cells.

Since the latency is due predominantly to conduction in the first order axon, and since there is a direct linear relation between conduction velocity and fiber diameter in the medullated nerve fibers, it is possible to speculate that the regular cells have thin fibers which innervate the slope of the crista, the irregular neurons have thick fibers which innervate the summit of the crista, and the intermediate units have medium caliber fibers which innervate both the slope and summit of the crista ampullaris.

Key words: Vestibular – Labyrinth – Conduction velocity

Introduction

To the present there has been little correlation, especially in mammals, between the functional characteristics of first order vestibular canal afferents (Estes et al., 1975; Blanks et al., 1975; Walsh et al., 1972; Goldberg and Fernández, 1971a; Goldberg and Fernández, 1971b; Fernández and Goldberg, 1971; Lifschitz, 1973) and their morphological substrates (Wersäll, 1956; Ades and Engström,

1965; Lindeman, 1969; Lim, 1971, 1975). Significant exceptions are the investigations of O'Leary and his colleagues (O'Leary et al., 1976; Dunn and O'Leary, 1976) in the isolated labyrinth of the guitarfish, who demonstrated a clear relation between primary afferent fiber size and adapting characteristics and sensitivity to angular acceleration. Goldberg and Fernández (1977) correlated regularity of spontaneous firing with antidromic conduction times in the vestibular nerve of squirrel monkey. In another important contribution, Walsh et al. (1972) showed cat primary vestibular afferents having regular spontaneous resting discharges tended to be found to those parts of the vestibular nerve with smaller fibers and irregular units from regions with larger axons.

In the present study in cat primary horizontal canal afferents, we compared the functional characteristics, particularly regularity of spontaneous firing and sensitivity to angular acceleration, to the time delay between electrical labyrinthine stimulation and recording from the afferents near Scarpa's ganglion.

Methods

Twenty-four cats weighing 1.5–3.5 kg were used in this study. The animals received pentobarbital sodium (40 mg/kg) intraperitoneally and following a tracheotomy were placed in a stereotaxic frame.

To expose the primary neurons for recording, a right parieto-occipital craniotomy was performed and portions of the paraflocculus and the flocculus were aspirated. Using an operating microscope, the vestibular nerve was exposed by removing the roof of the internal auditory meatus with a small cutting burr. During the experiment the exposed nerve was covered with warm Ringer's solution. In order to stimulate the vestibular nerve, silver wire electrodes, insulated except for tips, were placed on the oval and round windows and cemented in place (see Fig. 1). The cats were then moved to a gimbal-turntable (Estes et al., 1972). The body temperature of the animals was maintained at 37–38° C by an infrared lamp.

Extracellular activity from single horizontal canal neurons was recorded in the area of Scarpa's ganglion of the superior vestibular nerve, approximately 1.5 mm lateral to the bony margin of the internal auditory canal, using glass microelectrodes filled with 2M NaCl (DC resistance 4–6 MΩ). The electrode was coupled to an MPA-6 unity gain amplifier and then to a 100 gain 741 operational amplifier, both on the turntable. The frequency response of the recording system was flat DC to 10 KHz. The resting discharge of the neurons and the latency to the electric stimulation were photographed with a Grass Kymograph C-4 camera from an oscilloscope. The spike activity was also led to a comparator circuit which allowed conversion of the spike firing frequency to a DC voltage. The latter was led to a strip chart recorder. Interspike intervals were measured from motion picture film taken at 50 mm/sec and enlarged such that 1 msec equaled 2 mm on the enlargement. From 80–1000 (usually 250) interspike intervals were measured to determine the resting rate of each unit or each trial.

Rectangular pulses from a WPI interval and pulse generator were led through an isolation unit to the stimulating electrodes in the oval and round windows. Positive pulses of 0.1 msec duration, 1/sec and intensity of 0.5–3.0 volts were delivered to the electrode on the round window with the one in the oval window being the reference electrode. Latency measurements were made from photogaphs taken of 8–10 superimposed sweeps at 0.5 msec/cm and then enlarged 7.5 times. The latencies were measured from the beginning of the stimulation artifact to the foot of the response.

Conduction velocities were calculated from the conduction distance and adjusted conduction time. The conduction distance was determined from measurements made from the center of the horizontal canal ampulla to the recording site in four vestibular nerves carefully exposed in two cats weighing 2.5 kg, with typical head shapes for those used in the present experiment. The average

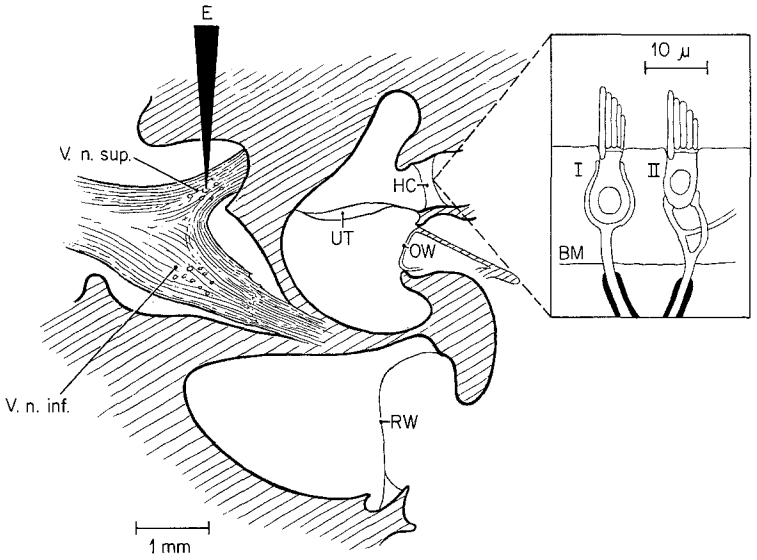

Fig. 1. A tracing of key portions of the right labyrinth from a histological section made in the stereotaxic frontal plane. Top of the figure is dorsal and lateral is to the right. A recording microelectrode (E) has been drawn in with the tip in the region of Scarpa's ganglion in the superior vestibular nerve (V. N. sup.). Large stimulating electrodes were inserted into the oval window (OW) after the head and both crura of the stapes had been removed, and into the round window (RW). The insert shows a portion of the sensory epithelium from the horizontal canal (HC) crista with Type I and II hair cells, unmyelinated nerve fibers, basement membrane (BM), and beginning of myelinated nerves. The drawing is to scale, using averages of dimensions measured from EM photographs from Ades and Engström (1965), Wersäll (1956) and Smith and Tanaka (1975)

distance was 3.2 mm (range 3.1–3.3). The site of electrical activation was assumed to be the nerve at or near the beginning of myelination, about 10 μ below the hair cells (see Discussion). The time for spike generation (setting-up time) was estimated to be 0.1 msec (see Discussion), and this value was subtracted from the actual conduction time to give the adjusted conduction time.

The cat's head was positioned 22° nose down and 6° right ear down, bringing the right horizontal canal as closely as possible into the plane of the turntable (Blanks et al., 1972). The technique for functional identification of horizontal canal neurons is covered in Estes et al. (1975). Only horizontal canal afferent units were examined in this study.

The acceleration profiles consisted of constant angular acceleration over a range of values from 2.5–19.0 deg/sec^2 lasting from 11–80 sec. This was followed by a constant velocity phase of 200 deg/sec for 60 sec. Deceleration was accomplished in 50 sec at 4 deg/sec^2. Sixty seconds were allowed between each profile. Four to six profiles were usually carried out on each unit.

Sensitivity, the number of spikes per second per degree of acceleration, defines the unitary activity at a given moment in time for a neuron responding to constant angular acceleration. When the unitary response increased, as during ipsilateral angular acceleration, the sensitivity was termed incremental sensitivity (S_i). When the unitary response decreased, it was termed decremental sensitivity (S_d). Individual sensitivities for a unit were determined from the strip chart recording by dividing the maximal frequency response in a given profile by the acceleration. Each unit was tested with 2–8 profiles at different accelerations and the results for the unit averaged or plotted on linear coordinates (see Fig. 4, Blanks, Estes and Markham, 1975).

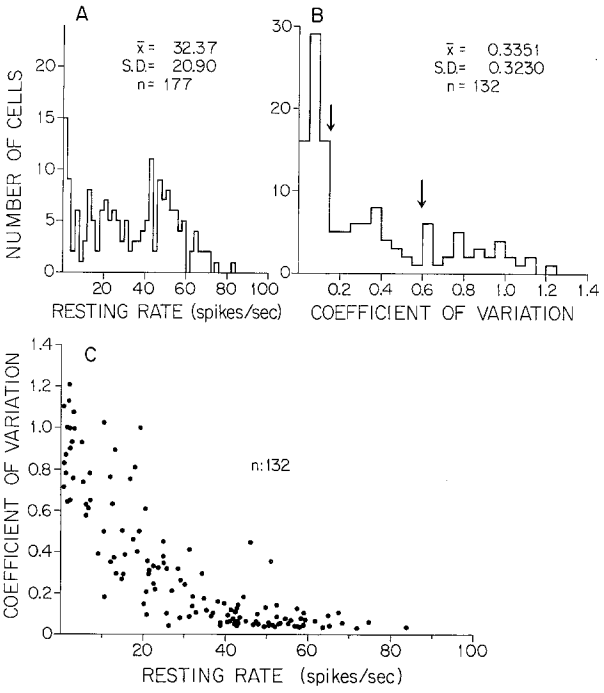

Fig. 2. Resting activity of first order horizontal canal neurons. **A** Histogram of the resting discharge rate. **B** Histogram of the coefficient of variation of the resting discharge. Arrows divide population into regular, intermediate and irregular groups. **C** Coefficient of variation as a function of resting rate

Results

Resting Activity

First order vestibular neurons of the horizontal canal had an average resting rate of 32.4 spikes/sec with a standard deviation of 20.9 and a range of 0 to 84 (n = 177). See Figure 2A. In the population sampled, 8 neurons showed no resting discharge, but did respond to horizontal rotation, were maintained for 5–25 min, and did not appear injured. The regularity of the units was determined by using the coefficient of variation (CV), defined as the standard deviation of the interspike intervals divided by mean interval. In a previous study (Estes et al., 1975) under the same conditions used here, regularity was characterized by both CV and the moment coefficient of skewness (Walsh et al., 1972). Since we demonstrated a high degree of correlation, we have used only CV in the present investigation. The average CV for the horizontal canal neurons was 0.335 with a standard deviation of 0.323 and a range of 0.033 to 1.212. See Figure 2B. From the values of CV, the neurons were classified into three groups: the regular firing units, CV $<$ 0.15, the intermediate units, 0.15 $\leq$ CV $\leq$ 0.60 and the

irregular firing units CV > 0.60. The mean CV's of the regular, intermediate and irregular groups were 0.0763, 0.3311 and 0.8465, respectively. Of the 132 units measured, 46% were regular, 31% were intermediate and 23% were irregular.

The relationship between the CV and the mean rate of resting discharge for each neuron can be seen in Figure 2C. It is clear that the higher resting rate neurons showed greater regularity in their resting discharge and the low resting rate neurons fired in a more irregular pattern. The average resting rates of regular, intermediate and irregular units were 48.7 ± 12.7 (n = 61), 24.5 ± 11.7 (n = 40) and 6.4 ± 6.0 (n = 31) spikes/sec, respectively. These groups were from different populations ($P < 0.001$). The significance level here and elsewhere in this paper was determined using the two-tailed *t*-test.

Response to Angular Acceleration

The sensitivity of horizontal canal neurons to constant angular acceleration was examined. The average S_i of total 122 units tested in the acceleration range of 4 to 6 deg/sec^2 was 2.10 ± 1.29 spikes/sec/deg/sec^2. The mean S_i of regular, intermediate and irregular units at same acceleration range was 1.55 ± 0.83 (n = 54), 2.51 ± 1.12 (n = 40) and 2.53 ± 1.82 (n = 28), respectively. The left side of Figure 3 shows the S_i of the 122 units, grouped according to their resting discharge rate into regular (A_1), intermediate (B_1) and irregular (C_1). The right side of Figure 3 shows the responses of typical neurons from each group. The mean S_1 of the regular firing units was low when compared to intermediate ($P < 0.001$) and irregular ($P < 0.005$) units. However, the irregular unit group contained the units with the lowest sensitivity (0.2 spikes/sec/deg/sec^2) and the highest sensitivity (7.3 spikes/sec/deg/sec^2) of the total population. Five units with zero resting rate had extremely low S_i (mean 0.3 spikes/sec/deg/sec^2) at acceleration level of 4 to 6 deg/sec^2.

There were two main types of neuronal responses to prolonged angular acceleration: adapting and non-adapting. Adapting cells (AD) were characterized by a response decline during the course of constant angular acceleration, and by an "undershoot" or secondary response at the end of acceleration. See page 1251 and Figures 1, 3 and 4 in Blanks et al. (1975). Non-adapting cells (NA) responded to constant acceleration with an initial, approximately exponential increase in firing rate, leveled off to a maximum rate which was maintained to the end of acceleration, and at the end of acceleration fell to the prestimulus level without undershoot or overshoot. Of the 122 neurons used in the study, 73 were found to be of the non-adapting type, 28 were classified as adapting types and 21 units could not be classified. The ratio of non-adapting to adapting neurons was 46/3 for regular units and 6/15 for irregular cells.

The relation between stimulus magnitude and unitary response was also examined by comparing firing rates induced by several magnitudes of acceleration. Forty-seven cells were studied in this manner. Each was tested with a minimum of five different acceleration profiles which ranged from 2.8 to

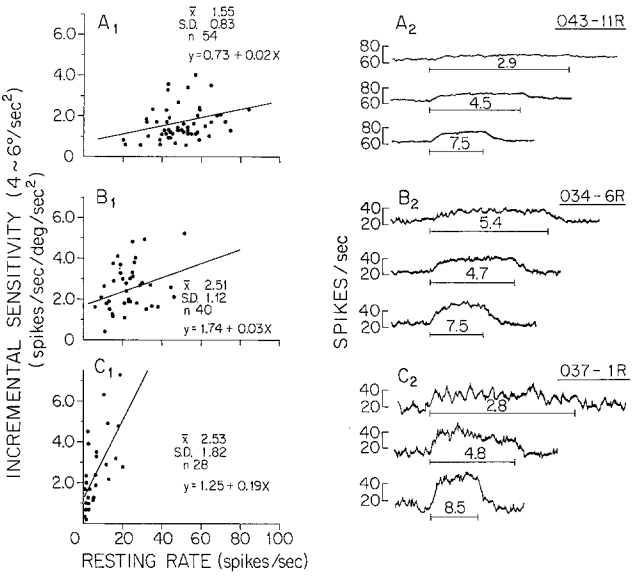

Fig. 3. Incremental sensitivity to acceleration as a function of resting rate (left column) for 122 neurons, divided on the basis of spontaneous firing into regular (A_1), intermediate (B_1) and irregular (C_1) groups. The straight lines in each of these subfigures are regression lines. The right column (A_2, B_2, C_2) shows unitary activity of three typical neurons to three levels of acceleration, the magnitude and duration being given below each tracing. A_2 shows a regular unit (CV = 0.0567) with a high resting rate (64.0 spikes/sec) and low S_i (1.9 spikes/sec/deg/sec^2). C_2 shows an irregular unit (CV = 1.0247) with a low resting rate (10.4 spikes/sec) and high S_i (5.8 spikes/sec/deg/sec^2). B_2 shows an intermediate neuron (CV = 0.4438) with a resting rate of 22.6 spikes/sec and S_i of 3.8 spikes/sec/deg/sec^2

18.7 deg/sec^2. At each acceleration trial, the extra spikes/sec were determined at 1, 2, 4, 8, 12 and 16 sec after the onset of acceleration. When the frequency increases were plotted for each level of acceleration, two types of response were evident. Those neurons which showed an approximately linear increase in firing rate at different elapsed times from the beginning of acceleration and to several levels of acceleration were termed linear. Others which tended to have an asymptotic response to increased acceleration were termed logarithmic. See Figures 2Aa and 2Ba from Shinoda and Yoshida (1974). Thirty-one cells responded in an approximately linear fashion over this range of acceleration. The remaining sixteen cells showed an approximately logarithmic relationship. Both types of responses were seen in the same animal. The ratio of linearly responding neurons to logarithmic type responses in regular, intermediate and irregular groups was 12/3, 4/3 and 9/1 (linear neurons/logarithmic neurons).

Latencies on Electrical Stimulation of the Ipsilateral Labyrinth

One hundred and twenty-four units were functionally characterized as described in the previous sections, and the latency to single shocks to the ipsilateral

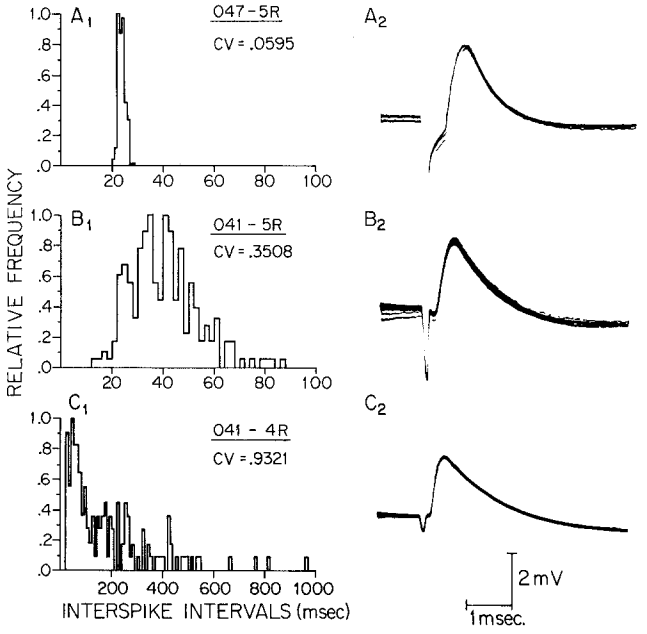

Fig. 4. Interspike interval histograms of resting discharges in three horizontal canal afferents (A_1, B_1, C_1) and their responses to electric stimulation (A_2, B_2, C_2). **A** shows a regular, **B** an intermediate and **C** an irregular unit. The photographs represents the superimposition of 10 sweeps

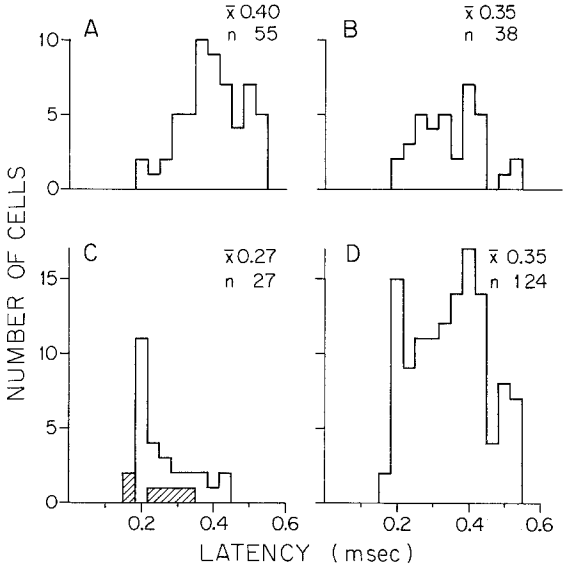

Fig. 5. Histograms of response latencies to electric stimulation. The histograms indicate the population of **A** regular, **B** intermediate, **C** irregular and **D** all the units. Shaded areas in **C** represent the units which were silent at rest

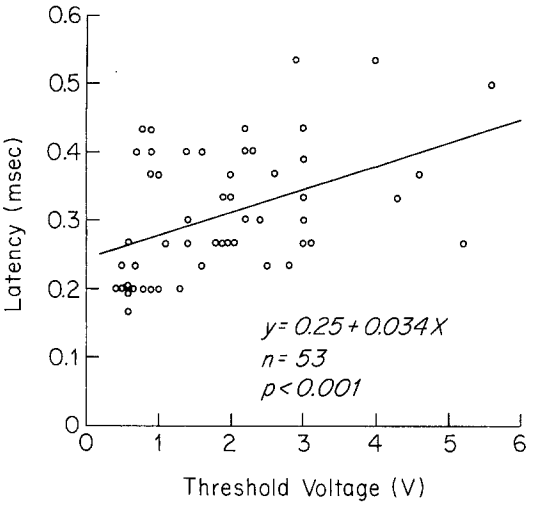

Fig. 6. In 53 adequately identified horizontal canal primary afferents, conduction time (latency of evoked response to electrical stimulation) is compared to voltage threshold. Sloping line is calculated regression line

labyrinth determined. Electrical stimulation at 1.5–2.0 times threshold resulted in a consistent shortening of latency of 20–60 microseconds from values obtained at threshold. There was no further shortening at moderately higher intensities. Using stimulus intensities of 1.5 to 2 times threshold, the average response latency was 0.35 ± 0.10 msec with a range of 0.17 to 0.53 msec. The evoked responses and interspike interval histograms of typical examples of regular, intermediate and irregular units are shown in Figure 4.

The histograms in Figure 5 show the relationship between regularity (CV) and latency. Figure 5A illustrates the latencies of the regular, 5B the intermediate and 5C the irregular firing units, and 5D the total population. The mean latencies of the regular and irregular groups are 0.4 msec and 0.27 msec; these are significantly different ($P < 0.001$). It should be noted the zero resting rate units, shown shaded in Figure 4C, had mean latencies of 0.24 msec with two of them having the shortest latencies of the total population, 0.17 msec.

A clear positive correlation was observed between response latency and threshold voltage, i.e. units which responded with shorter latency exhibited lower thresholds and units which responded with longer latency showed higher thresholds ($P < 0.001$), $n = 53$ (see Fig. 6).

The conduction velocities of the neurons can be estimated as follows. The average distance from the crista of the horizontal canal to the recording site was 3.2 mm. Assuming the point of electrical stimulation is the nerve endings of the horizontal canal crista, assuming we are stimulating myelinated fibers of constant diameter, and assuming a setting-up time for spike generation of 0.1 msec to be subtracted from the actual conduction time, we can conclude the average conduction velocities range from 7.4 to 46 m/sec (mean 12.8 m/sec). See Discussion for justification for these assumptions.

Discussion

The relation of the precisely formed and complex anatomical structure of the semicircular canal sensory epithelium to the neural activity recorded in the vestibular nerve has long intrigued us. Our decision to re-examine the question was based on several factors. Earlier work in cats suggested a bimodal distribution in resting rate of identified canal vestibular first order afferents (Fig. 3 in Estes et al., 1975). In the same study there was a highly skewed unimodal or multimodal distribution of regularity as measured by the coefficient of variation. Other work in the guitarfish (O'Leary et al., 1976; Dunn and O'Leary, 1976) showed a strong correlation of fiber size and location in the crista to physiological characteristics. And more recently, Goldberg and Fernández (1977) in the squirrel monkey showed an inverse correlation between antidromically determined conduction times in the proximal axon of vestibular nerves and regularity of resting discharge. Thus, we set about comparing nerve conduction velocity to function and then relating these findings to the fine structure of the crista.

The main functional characteristics of horizontal canal neurons identified by natural stimulation are not unlike prior results in the cat. The mean resting rate was 32.4 spikes/sec (range 0 to 84), comparable to other studies with 36 spikes/sec (range 0.5 to 114) (Estes et al., 1975), and to ranges of 3 to 125 spikes/sec (Rupert et al., 1962) and from less than 10 to 110 (Walsh et al., 1972). Regularity of spontaneous firing rate, which turned out to be a decisive functional criterion, allowed neurons to be divided into regular, intermediate and irregular groups on the basis of the coefficient of variation in the present and one past study (Estes et al., 1975). Walsh et al. (1972) found regularity determined in terms of skewness to be correlated with electrode position in the vestibular nerve.

Using regularity of spontaneous firing as a starting point, units were categorized as regular, intermediate, or irregular. The regular units in this study tended to have a high resting rate, low sensitivity and were mostly non-adapting. The irregular units usually had low resting rates, high sensitivity and showed adaptation. These findings are similar to those found in the guitarfish (O'Leary et al., 1976), pigeon (Lifschitz, 1973), cats (Estes et al., 1975; Blanks et al., 1975), and gerbils (Schneider and Anderson, 1976). In the squirrel monkey resting rates and sensitivity were similarly inversely correlated, but no clear relationship was established between resting rate and regularity (Goldberg and Fernández, 1971b).

Electrical stimulation may excite the nerve via the receptor cells. Or it may act on one of several neural elements. In the lateral line organ of Necturus maculosus, Sand et al. (1975) found that the electrical stimulation is more effective when delivered near the hair cells than when delivered deeper in the region of the nerve terminals. These workers also showed that afferent nerve terminals were relatively insensitive to intracellular injection of current as compared to intracellular injection in hair cells and concluded electrical stimulation in their preparation acted via the receptors. Strelioff and Honrubia (1974) and Dodson et al. (1974) showed in the lateral line organ of Xenopus laevis that anoxia caused a very similar depletion of response to transepithelial

application of electric current and to mechanical stimulation, and suggested that these two forms of stimulation acted on the same sensory substrate. On the other hand, Murray (1956) passed current from lateral line nerve through the epidermis containing the sensory organ and vice versa, and concluded that impulses recorded in the nerve were initiated subterminally in the nerve, possibly at the first node.

In the cat the situation seems clearer. Moxon (1971) compared click and electrical stimulation applied near the round window and found that electrical stimulation induced, in single cochlear nerve fibers, a consistently earlier response, usually at a lower threshold which was little altered by histological damage to hair cells by Kanamycin. Moxon concluded that electrical stimulation acted directly on neural elements. In the present study, the latencies of the response averaged 0.34 msec, with the shortest being 0.17 msec. This is too short to go via the chemical synaptic mechanism of the receptor cells. Based on this and Moxon's work, we are persuaded that in the cat electrical stimulation delivered between the oval and the round windows acts directly on the nerve.

Assuming this to be the case, the electrical stimulation might act on the actual nerve terminals; on the short (possibly averaging 10 μ) segments of unmyelinated nerves; at the first node of Ranvier, usually just below the basement membrane; or more proximally on the nerve. The usual assumption is that the point where the myelin begins is electrically excitable (Flock, 1971), but there is no proof that either naturally occurring or electrically generated spikes begin here. On the contrary, in the Pacinian corpuscle the unmyelinated portion appears to be the site of action for both electrically induced antidromic and mechanical stimuli (Ozeki and Sato, 1953) and can conduct both antidromic and orthodromic impulses (Hunt and Takeuchi, 1962). In the present experiment, we avoid this point and make the assumption that the electrically generated action potentials begin in the region immediately below the hair cells.

The time from electrical stimulation between the oval and round windows until an evoked action potential is picked up from the axon of a canal vestibular neuron near Scarpa's ganglion is largely determined by three elements: 1. The time it takes the current to reach the neural site of electrical excitation, just below the receptor cells. This depends on the spread of current in a volume conductor and is practically instantaneous. 2. The time of spike generation or "setting-up" time. At threshold this time is longer and more variable than at stimulus values distinctly above threshold when values of 0.06 to 0.1 msec have been measured in the frog (Erlanger and Gasser, p. 83, 1937; Blair and Erlanger, 1935–1936). We have used the value of 0.1 msec which Hunt and Kuffler (1951) used in the cat. At stimulus values of 1.5–2.0 times threshold there is little fluctuation in the response time as may be seen in the close superimposition of 10 spikes in Figure 3, A_2, B_2 and C_2. 3. The time of conduction in the primary afferent nerve. Here we make the assumption the conduction time is little altered whether or not the site of initiation of the action potential is in the unmyelinated portion(s) or at the first node of Ranvier. This is based on the very short length of the unmyelinated fibers and on not dissimilar conduction velocities of small myelinated and unmyelinated fibers (Paintal, 1967).

The most significant variable in conduction times among myelinated nerve fibers is almost surely fiber size. Differences of fiber diameter, including myelinated sheath, have been well described in the entire vestibular nerve of the cat (Gacek and Rasmussen, 1961; Walsh et al., 1972), as well as in the pigeon (Landoldt et al., 1973), guinea pig (Gacek and Rasmussen, 1961), monkey (Gacek and Rasmussen, 1961), and man (Rasmussen, 1940; Engström and Rexed, 1940). In the cat the diameter ranges from 1 to 10 μ with the majority being from 2 to 4 μ (Gacek and Rasmussen, 1961) or a little larger (Walsh et al., 1972).

Taking the range of conduction times in the present experiment from 0.17 to 0.53 msec (mean 0.35), and subtracting 0.1 msec from setting-up time (see above), and using a conduction distance of 3.2 mm, the conduction velocities are calculated to range from 7.4 to 46 meters/sec (mean 12.8). If the conduction velocity is in 6:1 proportion to the fiber diameter including the myelin sheath as determined by Hursh (1939) in the peripheral nerves of cats and kittens and accepted by Rushton (1951), one might conclude the fiber diameters range from 1.2 to 7.6 μ (mean 2.1). Since we did not find conduction times less than 0.17 msec and since the stimulation artifact in the present experiment would not impede measurement of even shorter latencies, it may indicate very large diameter fast-conducting fibers are uncommon in neurons serving the horizontal canal. In fact, histograms from Gacek and Rasmussen (1961) and from Walsh et al. (1972) indicate fibers over 8 μ in diameter constitute less than 5% of the total vestibular nerve population in the cat.

In the present experiment there is a strong correlation between threshold to electrical stimulation and conduction time (see Fig. 6), similar to the finding of Brown and Hayden (1971). Fernández and Goldberg (1977) did not find such a relation, possibly because the site of excitation of the vestibular axons traversing the root entry zone in the brain stem in their experiment did not have the same properties to electrical stimulation as did the subterminal neural elements in our work.

Using the conduction velocities determined in the present experiment, we can correlate low conduction velocities (and by inference, small diameter axons) with high electrical stimulation thresholds, high resting discharge rate, regular discharge, low sensitivity to constant angular acceleration and infrequent adaptation. High conduction velocities (and by inference, large axons) correlate with lower stimulation thresholds, low resting rate, irregular firing, higher sensitivity and frequent adaptation.

Turning now to fine structure of the sensory epithelium, some of the variables are: 1. In mammals and birds there are two types of receptors, a flask-shaped Type I cell whose base is surrounded by a large cup-shaped nerve ending and a columnar-shaped Type II with many bouton terminations from the primary afferents (Wersäll, 1956; Ades and Engström, 1965; Lindeman, 1969). Frogs and other lower vertebrates have only Type II receptors (Gleisner et al., 1973; Wersäll and Bagger-Sjöbäck, 1974).

2. Wersäll (1956) found the population density of Type I hair cells in the guinea pig was greatest in the central portion of the crista and decreased in number toward the peripheral zone, whereas Type II cells were distributed over

the greater part of the sensory epithelium, tending to concentrate in the periphery. However, Lindeman (1969) found, also in guinea pigs, a ratio of about 60:40 for Type I's to II's in both the central and peripheral portions of the crista.

3. Wersäll (1956) found in the guinea pig the thickest nerve fibers (6–9 μ in diameter) go to the sensory epithelium on the summit of the crista where they divide into 3–4 branches, each of which goes to a Type I receptor. Fine afferent fibers (1–2 μ) form a highly ramified plexus on the slope of the crista and innervate many Type II cells, often at a great distance from each other. Medium diameter nerve fibers (3–5 μ) are found throughout the crista, supplying either Type I or Type II or occasionally both (Ades and Engström, 1965).

Thicker fibers go to the summit of the crista in the guinea pig (Wersäll, 1956) and guitarfish (Dunn and O'Leary, 1976); and thinner fibers to the sides of the crista. It is probable the same distribution is true for the cat. Since the physiological characteristics in the guitarfish (O'Leary et al., 1975) are much the same as in the cat, and since the guitarfish has only Type II receptor cells, it strongly suggests the size and ramification of fibers in the crista are more important than the mixture of Type I and Type II receptors found in mammals.

Based on these aspects of the sensory epithelium, we conclude that the properties of lower resting rate, greater sensitivity to angular acceleration and more frequent adaptation are associated with the complex of receptor cells and subterminal neural elements on the crest of the crista and on larger diameter axons; and the inverse physiological characteristics are associated with the receptor-neural apparatus on the sides of the crista. Among several possibilities, we may speculate the lower resting discharge is related to larger neurons (Henneman et al., 1965a, 1965b; Carpenter and Henneman, 1966) or larger axons (Katsuki and Yoshino, 1952); and greater adaptation to less viscoelastic coupling between shorter hairs and the cupula on the crest of the crista (Lim, 1971, 1975) as compared to the long hairs on the side of the crista which curve up into and have more contact with the cupula (see Discussion in Blanks et al., 1975).

Sensitivity, the relation between extra spikes/sec and the applied stimulus angular acceleration, is also greater for the fast conducting neurons presumably serving the crest of the crista, and less for the slower conducting ones going to the sides of the crista. Sensitivity does vary between canals (Blanks et al., 1975; Curthoys et al., 1977) and between species, possibly due to geometric properties of the canals, particularly the radius of the curvature of the canals (Blanks et al., 1975). However, this would not explain the wide range of sensitivities, from 0.3 to 7.4 spikes/sec/deg/sec^2, found among first order neurons from one canal (Blanks et al., 1975). Here the explanation must lie in the receptor-nerve relations or in fiber size differences on the sides versus the crest of the cristae.

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