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Responses to Head Tilt in Cat Eighth Nerve Afferents*

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Summary. Responses to head tilt were recorded from eighth nerve axons in barbiturate anesthetized cats. The maximally excitatory head tilt (polarization vector), a zero-force discharge rate, and tilt sensitivity were measured for each cell. In one population of afferents, the maximum discharge frequency was obtained by aligning the saccular plane with gravity. The response properties of these saccular afferents were compared with a second population arising from the utriculus. Both the resting discharge rate and the response sensitivity were lower for saccular than utricular afferents in the cat. The average resting discharge was about 20% lower and the sensitivity about 15% higher in the cat than in the squirrel monkey.

Key words: Maculae – Statoreceptors – Vestibular nerve neurons – Cats

A population of eighth nerve afferents in the squirrel monkey has responses to head tilt which imply that they innervate the sacculus, and respond to shearing forces applied to the receptor haircells. Since these responses can still be recorded after denervation of the utriculus by section of the superior division of the vestibular nerve, it has been concluded that the sacculus functions as an equilibrium organ in that animal (Fernandez et al. 1972; Fernandez and Goldberg 1976a). A similar study in the cat only found tilt-sensitive cells which were concluded to innervate the utriculus (Loe et al. 1973). There is, however, other evidence that the sacculus has an equilibrium function in the cat, because it has been shown to have a role in vestibulo-ocular (e.g., Fluur and Mellstrom 1970; Hwang and Poon 1975; Chan et al. 1977) and vestibulo-collic (Wilson et al. 1977) reflexes. More direct evidence of the ability of the cat sacculus to signal head tilt is that single cells in Deiters' nucleus responded to head tilt after bilateral labyrinthectomy which spared the ipsilateral sacculus (Chan et al. 1979). Vestibular nuclei neurons have also been shown to respond to saccular nerve electrical stimulation when all other portions of the vestibular nerve have been surgically removed (Wilson et al. 1978).

It was the purpose of the present study first, to investigate whether there is in the cat a population of eighth nerve afferents whose response properties are consistent with the known orientation of the saccular plane, and second, to determine the resting discharge and response sensitivity of tilt-sensitive afferents for comparison with similar measures in squirrel monkey peripheral (Fernandez and Goldberg 1976a) and cat vestibular nuclei (Peterson 1970; Schor 1974) neurons. A brief report of these data was already presented (Tomko and Peterka 1977).

Methods

Extracellular single unit recordings were made from 215 cells in 44 penetrations into the right vestibulo-cochlear nerve of 17 barbiturate anesthetized cats using capillary micropipettes. The animal preparation and recording procedures were as described previously (Loe et al. 1973). Briefly, animals were anesthetized with sodium pentobarbital (35 mg/kg, i.p.), the trachea intubated, and a vein catheterized to administer supplemental anesthesia. The roof of the cerebellar fossa was removed on the right side, and the

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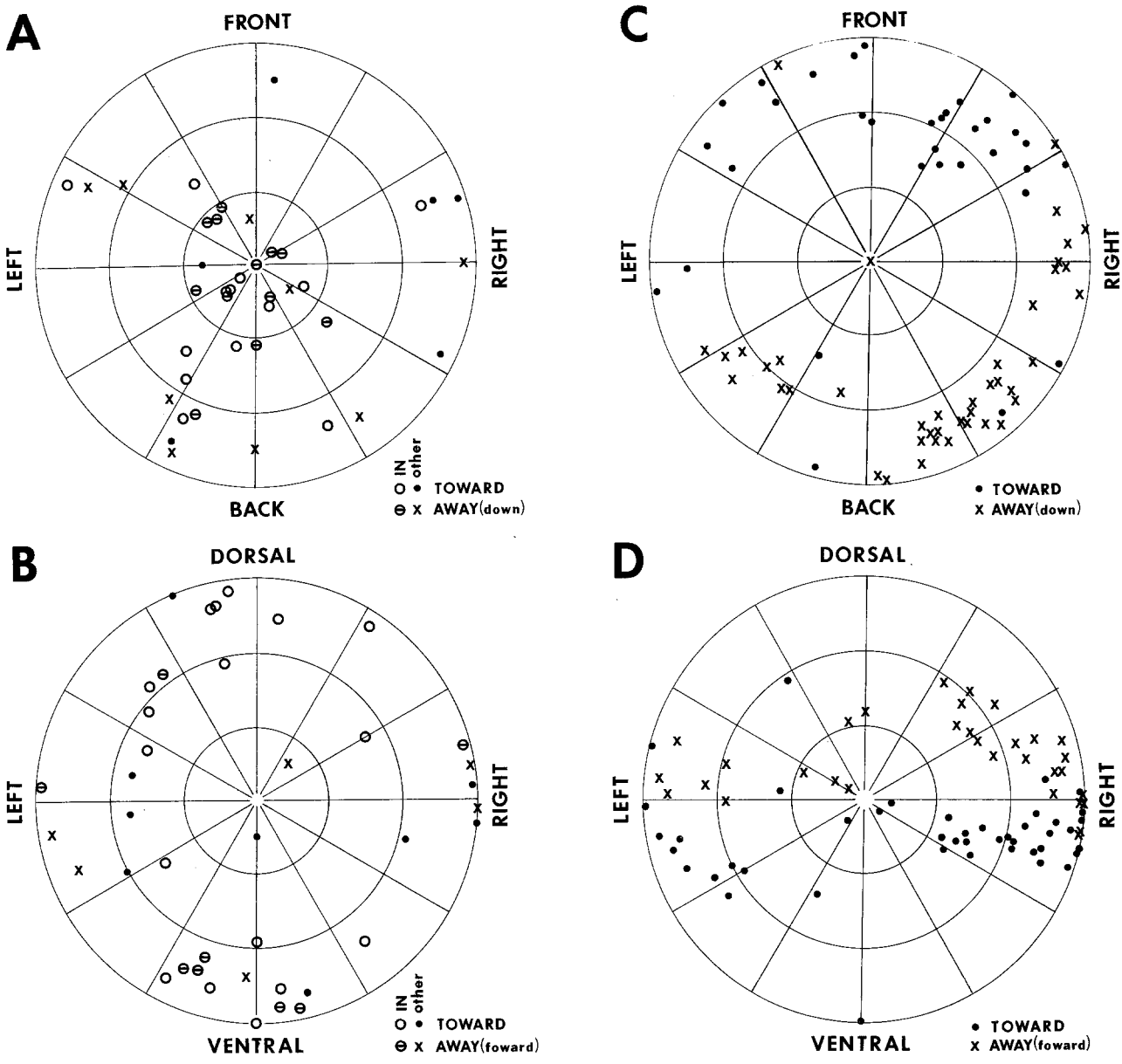

Fig. 1. Functional polarization vectors plotted in polar coordinates of the cat's head. Each graph represents the projections of the 3 dimensional spherical coordinates of the polarization vectors onto 2 dimensional polar coordinates. Since all vectors have equal length, each polar plot provides a complete description of vector locations. For clarity, two different projections are shown for each set of data. **A** and **B** show vectors for 40 cells of the present study viewed respectively from the top and the rear of the head. Vectors pointing toward and away from the reader are as indicated. **C** and **D** show the vectors of 75 of the cells from the previous study (Loe et al. 1973) presumed to be from the utriculus

flocculus and adjacent parts of the cerebellar hemisphere were rapidly aspirated to expose the eighth nerve at its exit from the internal auditory meatus. To insure that the superior and inferior divisions of the nerve were visible for electrode placement, the roof of the internal auditory canal was removed lateral to the internal auditory meatus, until the transverse crest could be visualized separating the two divisions of the nerve. Microelectrode punctures were concentrated in the inferior division of the nerve, posterior to the transverse crest.

A criterion described in previous studies (e.g., Fernandez et al. 1972) was used to determine from which division of the vestibular nerve the recordings were sampled. This criterion uses the fact that axons of cells innervating the anterior and lateral canals, and all utricular afferents lie in the superior branch of the nerve, while only the axons of cells innervating the posterior canal and sacculus lie in the inferior division of the nerve (Gacek 1969). Statoreceptor afferents were assigned to the inferior nerve division (IN cells) if the only other afferents encountered in the microelectrode penetrations were from the posterior canal. Tilt-sensitive afferents recorded in penetrations where only anterior and horizontal canal cells were recorded were presumed for the most part to arise from the utriculus (Other). Statoreceptor cells recorded in

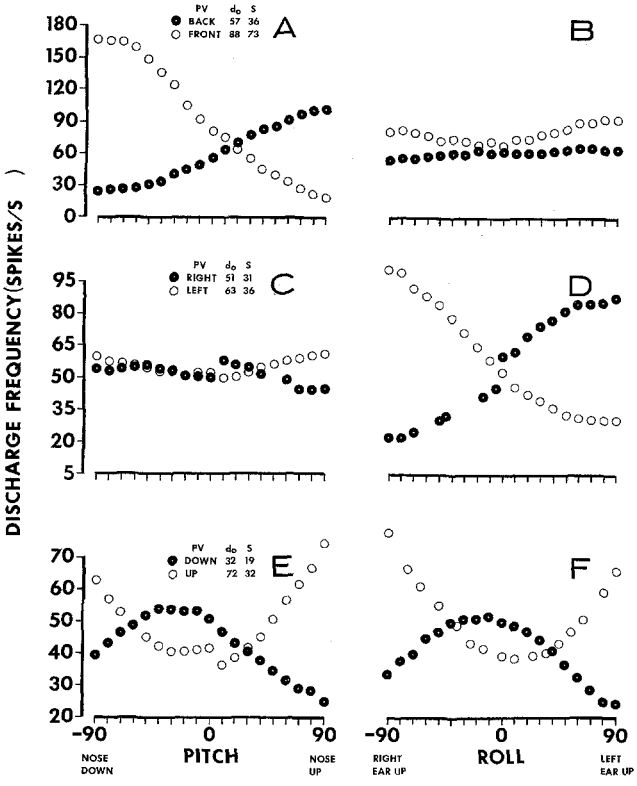

Fig. 2. The response of six neurons to ± 90° of pitch (left) and roll (right) rotations are plotted. On the left graph for each pair of cells are indicated the approximate polarization vector (PV) orientation and the values of d_0 and S

penetrations where there was a mixture of either anterior or horizontal as well as posterior canal afferents could not be assigned to one particular otolith organ. These cells were therefore also assigned to the "other" category. Only cells which had regular discharge patterns (interspike interval coefficient of variation less than 0.10 with the animal horizontal) were included in this study.

The response properties were characterized by applying slow velocity (10 degrees/s) head rotations around the pitch and roll axes, and by recording discharge frequency in various stationary positions (Loe et al. 1973). Stationary positions were in 90° increments, and were maintained for a minimum of 30 s. Adaptation was minimal and the data obtained in stationary head tilts corresponded closely with those of slow velocity rotations. Therefore, the two sets of data were considered to be interchangeable. To characterize the direction and amount of head tilt which would maximally stimulate each afferent, a functional polarization vector was calculated for each cell (Fernandez et al. 1972; Loe et al. 1973). A pair of spherical coordinate angles was used to define the orientation of the polarization vector with respect to the Horsely-Clarke coordinate system. An orientation of the animal in space with the polarization vector of a cell pointing directly downward (i.e. colinear with gravity) would elicit the maximal steady state discharge rate of that cell, while orienting it upward would elicit the minimum. Implicit in the calculations is the assumption that the adequate stimulus is the shearing of the haircell cilia. A zero-force discharge rate, d_0, was calculated to describe the discharge rate in the absence of shearing force (that is, when the polarization vector is oriented perpendicular to the gravity vector), and a sensitivity measure, S, was calculated to specify the response of each cell to a 1 g linear acceleration, as described by Fernandez and Goldberg (1976a). In addition, the standard position zero tilt discharge rate, d_s, was measured with the animal oriented in an upright position, with the Horsely-Clarke horizontal plane parallel to the earth horizontal.

Results

Polarization Vector Orientation

Polarization vector coordinates of 25 IN cells and 15 other cells of the present study are plotted in polar coordinates in Fig. 1A and B. The distribution of these vectors differed markedly from those of an earlier study in the cat (Loe et al. 1973) which were clustered near the horizontal plane (replotted for comparison in Fig. 1C and D). It is clear that vectors of IN cells of the present study were also clustered in a plane, but one which more closely parallels the midsagittal plane of the head and more nearly corresponds to what might be expected from the known orientation of the sacculus (Lindeman 1969).

Figure 2 shows how six cells of the present study responded to ± 90° of roll and pitch head tilt. Cells with polarization vectors oriented toward the nose or the back of the head have a large response to pitch, and almost none to roll tilts (A and B), while those with vectors pointing laterally respond preferentially to roll (C and D). In sharp contrast, cells whose vectors point up or down (E and F) respond symmetrically to head tilts of either pitch or roll. Cells with vectors of intermediate orientation will have responses intermediate between those shown. Since the orientation of the utriculus is near the horizontal plane and the sacculus near the sagittal plane, cells with vectors pointing up or down correspond to the known orientation of the saccular macula, while those pointing toward the ears agree with the known orientation of the utricular macula.

Measures of d_s, d_0 and S

The data of the present study are summarized in the first five rows of Table 1. IN cells had lower discharge rates with the animal in the upright position (d_s), lower zero-force discharge rates (d_0), and lower sensitivity (S) than other cells encountered in these experiments. Only the difference in sensitivity was statistically significant (2 tailed t test, $p < 0.05$). IN cells with upward directed polarization vectors had significantly higher zero-force discharge rates ($p < 0.05$) and greater sensitivity ($p < 0.05$) than IN cells

Table 1. Mean sensitivity (S), zero-force discharge rate (d_0) and zero-tilt discharge rate (d_s), ± 1 standard deviation

	N	Zero-tilt discharge (d_s) (spikes/s)	Zero-force discharge (d_0) (spikes/s)	Sensitivity (S) (spikes/s-g)
IN cells				
(all)	25	43.9 ± 15.9	40.5 ± 22.3	25.1 ± 15.3
(up)	13	37.6 ± 16.1	54.3 ± 27.6	30.6 ± 17.5
(down)	12	50.6 ± 13.1	25.6 ± 12.4	19.2 ± 10.1
Other cells	15	57.3 ± 20.5	50.2 ± 21.6	37.2 ± 17.2
Total	40	47.8 ± 18.2	44.1 ± 22.3	29.7 ± 16.9
Loe et al. data	75	55.0 ± 16.7	55.6 ± 17.9	41.8 ± 13.5
All data	115	52.5 ± 17.5	51.6 ± 20.2	37.6 ± 15.8

with downward pointing vectors. However, when the animal was upright, the discharge rate (d_s) of upward and downward vector cells was similar, as others have found in the squirrel monkey (Fernandez and Goldberg 1976a).

Values of d_s, d_0 and S were also calculated for the data of a previous study (Loe et al. 1973), and are summarized in row six of Table 1. All of the polarization vectors of these cells lay in a single plane, which was close to the Horsely-Clark horizontal. In light of the finding in the present study that there is a second population of statoreceptor afferents with polarization vectors clustered near the sagittal plane, it now seems reasonable to assume that the afferents reported by Loe et al. (1973) arose primarily from recordings from the superior division and represent utricular afferents. The average values of d_s, d_0, and S were 55 spikes/s, 55.6 spikes/s, and 41.8 spikes/s-g, respectively. None of these measures was statistically significantly different from the "other" cell category of the present study, suggesting that these two samples were probably drawn from the same population. There was no difference on any of these measures between cells with rightward and leftward vectors.

A positive correlation between the zero-force discharge and sensitivity was observed for IN ($r = 0.59$) and Other ($r = 0.62$) cells in the present study, as well as in the cells of the previous study ($r = 0.48$; Loe et al. 1973). A similar correlation exists in the squirrel monkey (Fernandez et al. 1972; Fernandez and Goldberg 1976a).

Discussion

The polarization vector orientations of the IN cells of the present study (Fig. 1) are consistent with the conclusion that they innervate receptor cells in the saccular plane. This is direct evidence that in the cat, as in the squirrel monkey, the sacculus functions as an organ of equilibrium. The polarization vector orientation unambiguously describes the response properties of each statoreceptor to any head tilt (e.g. Fernandez et al. 1972; Fig. 5 in Loe et al. 1973). Its use enables one to go beyond the Duensing and Schaeffer (1959) classification scheme, which reduces the three-dimensional vector of a macular afferent to its projection in two directions, transverse, and fore-aft. Furthermore, it permits calculation of the sensitivity to the gravity vector, and allows for comparisons of neural responses between cells in the same animal, between cells in peripheral and central structures, or between species.

Values of sensitivity from the present and previous study (Loe et al. 1973) ranged from 4 to 85 spikes/s-g with a mean of 37.6 ± 15.8. This range is lower than the 14 to 263 spikes/s-g found by Anderson et al. (1978) in the cat. Those authors' method of calculating a cell's sensitivity to gravity assumes that the cell's functional polarization vector lies perpendicular to the roll axis and is in the horizontal plane of the animal's head. Only cells with either of the two polarization vectors which point directly outward toward the ears satisfy these assumptions. The sensitivities of cells with all other polarization vector orientations would be underestimated by this method. Such a methodological difference therefore cannot account for the higher sensitivities found by Anderson et al. (1978). However, two other factors are consistent with this difference in sensitivity between the two studies. First, our sensitivities are essentially steady state ones, whereas theirs (Anderson et al. 1978) were measured with 0.25 Hz sinusoidal oscillations. We would expect our gains to be slightly lower on average than theirs, because the gain of otolith afferents increases as frequency increases, especially for irregularly discharging cells

(Fernandez and Goldberg 1976b). Second, our sample included only regularly discharging afferents, while that of Anderson et al. (1978) included both regularly and irregularly discharging cells; the observation that their highest sensitivity cells were irregularly discharging (Anderson, pers. comm.) is consistent with the observed difference in sensitivity between the two studies.

In the cat, values of d_0 and S of presumed utricular units were about 15% lower and 15% higher, respectively, than regularly discharging cells in the squirrel monkey (Fernandez and Goldberg 1976a). There were larger differences between the values of d_0 of cat and squirrel monkey for IN units (30 to 50% smaller values for cat) but differences in S for the same cells between animals were only 4 to 20% (cat lower). The average zero-tilt discharge rate was about 25% lower in the cat than in the squirrel for IN cells. We have found that in the cat, as in the squirrel monkey (Fernandez and Goldberg 1976a), cells with upward pointing vectors have a greater zero force discharge than those with downward pointing vectors. In the "upright" position, this higher value of d_0 of the upward vector cells keeps their activity biased "on", and equalizes the zero-tilt discharge to that of the downward vector cells.

It would be of interest to compare the sensitivity of peripheral and central neurons to head tilt. In one of the studies on central neurons (Schor 1974) using 15 to 20 deg sinusoidal tilts around the roll axis, it was found that the average sensitivity at a stimulus frequency of 0.1 Hz was between 0.07 and 1.94 spikes/s-deg with most sensitivities of lateral and descending nucleus neurons being around 0.5 spikes/s-deg. The use of such a dynamic stimulus will tend to overestimate the static tilt sensitivity, but probably by not more than a factor of 2. The cells of Schor's study were chosen because they responded preferentially to lateral tilt and therefore presumably had polarization vectors that were oriented primarily toward the ears. Sensitivity was expressed as the change in discharge frequency per degree of roll tilt. These sensitivity measures can be converted to units of spikes/s-g if one assumes that the polarization vectors of all the cells point directly out the ear.[1] For cells with polarization vectors which differ somewhat from this orientation, the assumption results in an overestimation of the effective shear force, and therefore an underestimation of the sensitivity. An additional assumption is that the vestibular nuclei cells have response properties similar to those of peripheral afferents, at least with regard to the polarization vector. Converting Schor's (1974) measures of central neuron sensitivity to spikes/s-g results in a range of values from 4 to 200 spikes/s-g, with a median sensitivity of 37 spikes/s-g for lateral nucleus cells and 111 spikes/s-g for inferior nucleus cells. The sensitivity of inferior nuclei cells is considerably larger on average than that of any group of cells in the present study, while that of lateral nuclei cells is similar to the sensitivity of peripheral statoreceptor afferents.

1 The transverse component of the shear force = $g \cdot \sin(\theta)$, which for small angles of tilt (θ) can be approximated as $g\theta$. Thus multiplying spikes/s-deg by $360/2\pi$ converts the sensitivity to spikes/s-g

Conclusion

The most important results of the present study are *first,* the direct evidence that the sacculus subserves an equilibrium function in cats, as it does in squirrel monkeys, and *second* the measurement of resting discahrge rates and sensitivity of both saccular and utricular afferents in cat. Although the basic morphology of the vestibular endorgan is similar in cats and squirrel monkeys (Lindman 1969), there are functional differences between the two species. In the present study, the most notable difference was that the zero-force discharge and the zero-tilt discharge were 20 to 50% less in the cat than in the squirrel monkey (Fernandez and Goldberg 1976a). These differences in the physiology of the system between species may be associated with the need to encode the particular types of stimuli produced during the animal's normal behavior. The important questions regarding the dynamic operating characteristics of cat statoreceptor afferents, both in the periphery and in the vestibular nuclei, remain to be resolved.

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