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A New Vestibular Thalamic Area: Electrophysiological Study of the Thalamic Reticular Nucleus and of the Ventral Lateral Geniculate Complex of the Cat

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Summary. Single unit recordings were carried out in the reticularis thalamic nucleus (RT) and the ventral lateral geniculate body (LGv) of chronically prepared alert cats under sinusoidal vestibular stimulation in the horizontal plane. Optokinetic stimulation was also used.

Of the 57 recorded neurons, 12 present vestibular modulation in the dark, analogous to Duensing's and Schaefer's (1958) type I response in the vestibular nuclei. Responses of 26 cells are similar to response of type II vestibular neurons and 14 units have a type III response; the 5 remaining cells were activated by vestibular stimulation in the vertical sagittal plane. The majority of these cells does not present detectable direct visual responses, but 50% can be driven by optokinetic stimulation.

74% of types I, II and III neurons show saccadic responses to vestibular nystagmic saccades in the dark. About 60% present similar saccadic modulations during optokinetic nystagmus and 55% keep this response for spontaneous saccades in the dark or in front of a striped background. The saccadic responses are constant for a given neuron in all cases of stimulation with latencies ranging from 30 msec prior to the beginning of the saccade to 120 msec after its onset.

The histological localization of these units falls on one hand into the caudal part of the RT nucleus (type III neurons) above the dorsal lateral geniculate nucleus and on the other hand within the internal subdivision of the LGv and its rostral limit (all other types).

The significance of this new, saccadic and vestibular focus in the feline thalamus is discussed in relation with the two previously known vestibular thalamic relays in terms of interrelations between the vestibular and the visual systems.

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The ventral nucleus of the lateral geniculate body (LGv) can be divided into an internal and an external sector (Niimi et al., 1963), which cytoarchitecturally show further subdivisions (Jordan and Holländer, 1972).

It receives visual afferents from the retina, the superior colliculus, the pretectum, the striate and peristriate cortex, and the contralateral LGv (for references see Holländer and Sanides, 1976). It also receives fibers from the interpositus and dentate cerebellar nuclei (Walsh and Ebner, 1973; Graybiel, 1974) and from the subthalamo-perirubral continuum (Graybiel, 1974).

Electrophysiological data concerning the visual properties of the LGv in rodents (Montero et al., 1968; Mathers and Mascetti, 1975), and in the cat (Spear et al., 1977) are available and will be discussed later.

In our earlier study in cats (Magnin et al., 1974) strong modulations of neuronal activity during rotation of the head and/or nystagmic saccades were found in neurons of the LGv and RT. This suggested a role in visual-oculo-vestibular coordination. In contrast to our findings in the cat, however, one of us (Magnin and Fuchs, 1977), found in the pregeniculate nucleus of the monkey (generally regarded as homologue of the feline LGv) only intense saccadic effects as described by Büttner and Fuchs (1973), but not vestibular influences.

The purpose of the present experiments has been to elaborate the qualitative and quantitative characteristics of saccadic and vestibular modulations in the LGv and RT areas of the cat and to aim at a more precise anatomical localization of these types of neuronal responses within these structures.

Materials and Methods

Four adult cats were prepared during a surgical session under Nembutal® anaesthesia (35 mg/kg i.p.). Wells to support a micro-electrode drive were positioned stereotaxically at A.P. +7, LAT. 10 and sealed to the skull together with a head fixation device. Silver-silver chloride electrodes were implanted around the orbits to record eye movements in the horizontal and vertical planes. In one case the eye opposite to the recorded side was immobilized by intracranial sectioning of the III, IV and VI nerves (see Berlucchi et al., 1966) to make an accurate search for visual receptive fields.

During recording sessions (started after 5–10 days of recovery), the animals rested in a hammock. Their heads were fixed at the center of a velocity servo-controlled turntable, permitting sinusoidal horizontal stimulation with peak velocities of ±30°/sec or ±60°/sec. The turntable was surrounded by a cylinder with an inbuilt diffuse light source and equipped with black and white bars for optokinetic testing. When the light was off, the animals were in complete darkness. With the light on, optokinetic stimulation was produced by rotating the cylinder at constant speeds of either 12°/sec or 24°/sec. Combined optokinetic and vestibular stimulation could be produced by rotating the turntable in front of the stationary background.

During long sessions, amphetamine sulfate (1–3 mg i.m.) was administered to prevent drowsiness. The drug increased spontaneous saccades, but otherwise caused no gross changes in behaviour or neuronal responses. Unit activity was recorded through Epoxylite insulated tungsten microelectrodes with a 100 Hz–10 kHz bandpass. It was monitored on an oscilloscope, a Grass polygraph and a loud-speaker. Spikes, eye position (bandpass: 0–300 Hz), speed and position of the

table, and photocell signals corresponding to the optokinetic stimulation were stored on FM-tape for subsequent processing.

At the end of selected recording sessions, the electrode position was marked by passing a DC current (20 mA, 15 sec) through the microelectrode, or an iron deposit was produced electrolytically with lower currents (1.5 μA, 10 sec) according to the technique of Merrill (1974). Reconstruction of the electrode tracks was done on enlarged microphotographs from cresyl violet stained 60 μ serial sections, and positive recording sites will be presented on appropriate frontal planes, as conventional stereotaxic atlases lack precision in this particular area.

Sufficient data were obtained from 57 neurons within the RT and the LGv. Each unit was tested during: 1. sinusoidal vestibular stimulation in the dark; 2. sinusoidal vestibular stimulation in light, against the immobile striped cylinder; 3. in the dark and in the light without rotation to determine spontaneous activity and response of the neurons to spontaneous saccades. In 27 neurons effects of optokinetic stimulation were tested in both directions of rotation.

A PDP8I computer was used for data processing. The characteristics of spontaneous neuronal activities were determined by a statistical time series analysis (Pernier and Echallier, 1973). The vestibular, optokinetic and saccadic evoked activities were characterized by appropriate post-stimulus-time histograms (Pernier et al., 1974).

Results

1. Response Characteristics to Vestibular Stimulation in the Dark

52 out of the 57 recorded cells presented responses to horizontal vestibular stimulation in the dark. Three types of responses were found. Figure 1 illustrates an example of each type. The topmost histogram shows sinusoidal modulation of neuronal activity in close relation with the direction of stimulation; this unit increases its firing during rotation towards the recorded side (ipsiversive rotation) and is completely inhibited during contraversive rotation. This response corresponds to type I vestibular neurons of Duensing and Schaefer (1958). It was encountered in 12 units. An opposite mode of response (decrease with ipsiversive rotation and increase in contraversive rotation (second histogram of Fig. 1), similar to the type II vestibular neurons of Duensing and Schaefer, was found in 26 cells. Finally (third histogram of Fig. 1), 14 units were activated either by ipsiversive or contraversive stimulation, matching type III vestibular neuron of Duensing and Schaefer.

The sinusoidal modulation of types I and II responses is in close phase relationship with the velocity of the stimulus. It appears that for all types I and II neurons, the amplitude of the vestibular response is roughly half when the peak velocity values of the stimulus are reduced from ±60°/sec to ±30°/sec. In the two conditions, the responses present a phase-lag of −10° to +30° with respect to the maximum values of velocity and this phase-lag remains constant for a given neuron. The responses of type III neurons are correspondingly delayed by 150 msec to 300 msec when we consider the firing minima with respect to the zero value of velocity.

Five cells, not reacting to horizontal rotation, responded with directional specificity to angular movement of the head in the vertical plane. Figure 2 shows an example in which firing is accelerated each time the head is manually raised in the saggital plane. Our apparatus, however, did not allow quantitative studies of such vertically sensitive units.

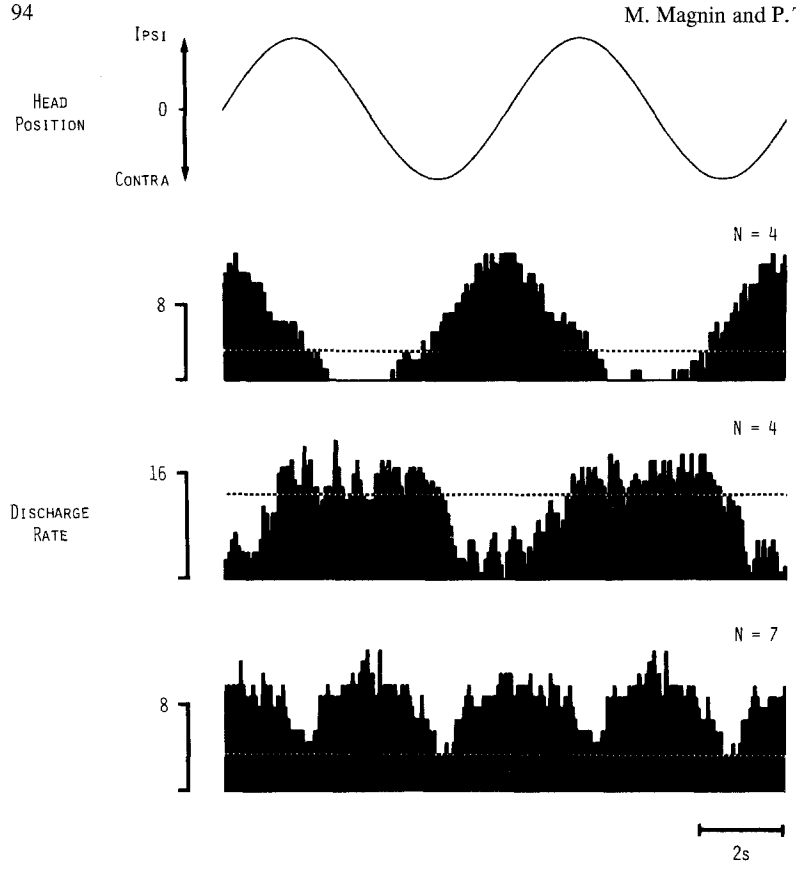

Fig. 1. Three typical examples of horizontal vestibular evoked responses obtained in the dark. From top to bottom are post-stimulus time histograms of activity in type I, type II and type III vestibular neurons. Spikes are summated every 160 msec during 13.5 sec. Discharge rate is characterized by the number of spikes per bin. N is the number of summations. Broken lines represent level of spontaneous activity in the dark.

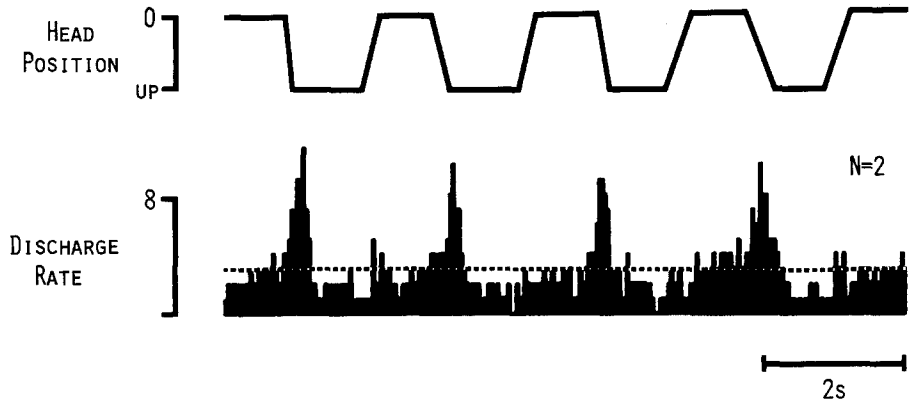

Fig. 2. An example of a vertical vestibular sensitive unit. This cell presents an increase of its activity corresponding to a change of head position (tilting) in the sagittal plane. The amplitude of stimulation is about 30° from the horizontal plane (= O, UP = nose upwards). Spike sampling each 50 msec during 9.5 sec. Number of summations is 2. Spontaneous level of activity in the dark is given by broken line

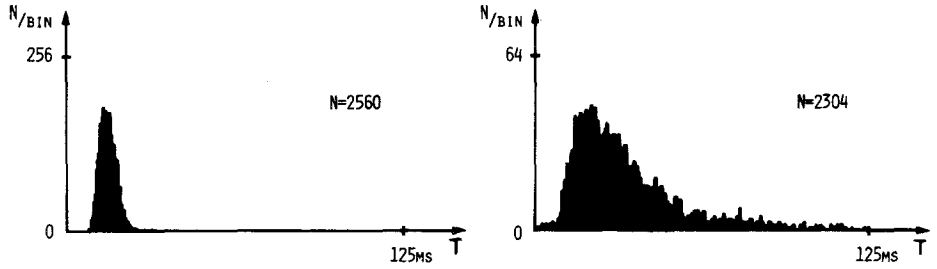

Fig. 3. Spontaneous activity in the dark. Interspike interval time histograms of a type I neuron (group A) on the left and a type III neuron (group B) on the right. N is the number of interspike interval processed. T is the duration of the interspike interval. The time scale is divided into 256 bins. The sharper aspect of the left histogram corresponds to the highly regular spontaneous firing rate observed in neurons of type I and type II (group A)

2. Characteristics of Spontaneous Activity in the Dark

Neurons could be classified into two groups according to their spontaneous activity in the dark: group A neurons (including type I, type II and vertically sensitive neurons) present a characteristic highly regular spontaneous activity and appear fairly independant of the stage of alertness; group B neurons (composed of the type III neurons) show a more irregular pattern of spontaneous activity and are influenced by changes in the animals state of vigilance. However, the mean values of firing rate of groups A and B are not statistically different (group A = 32 ± 13 spikes/sec; group B = 22.5 ± 12.5 spikes/sec). If one considers the interspike interval histograms (Fig. 3) of representatives of the two groups, it can be noted that the most probable time value of interspike interval is the same in both cases (14 msec) and that they are ruled by an identical law of distribution: this is verified by applying a mathematical model (see Pernier and Echallier, 1973) to the histograms. Yet, the mean interspike interval time values are different (group A: 15 msec; group B: 35 msec) with respective variances of 14 $msec^2$ and of 570 $msec^2$. This large difference in the variances and the small dispersion of the group A interspike interval histogram account for an immediate impression of difference between units of the two groups.

3. Response Characteristics to Optokinetic (OK) Stimulation

In only four of the 57 studied neurons, it was possible to detect a clear response to "on-off" light stimulation. These four cells all belong to the type III. The cat with one eye paralyzed allowed a more precise search for eventual structured visual receptive fields, but even in this condition, in none of the cells belonging to type I, type II or type III a visual receptive field could be found. Twenty out of the 38 type I or II neurons, and 7 out of the 14 type III neurons, were tested for horizontal optokinetic (OK) stimulation. Of the type I or II cells, 13/20

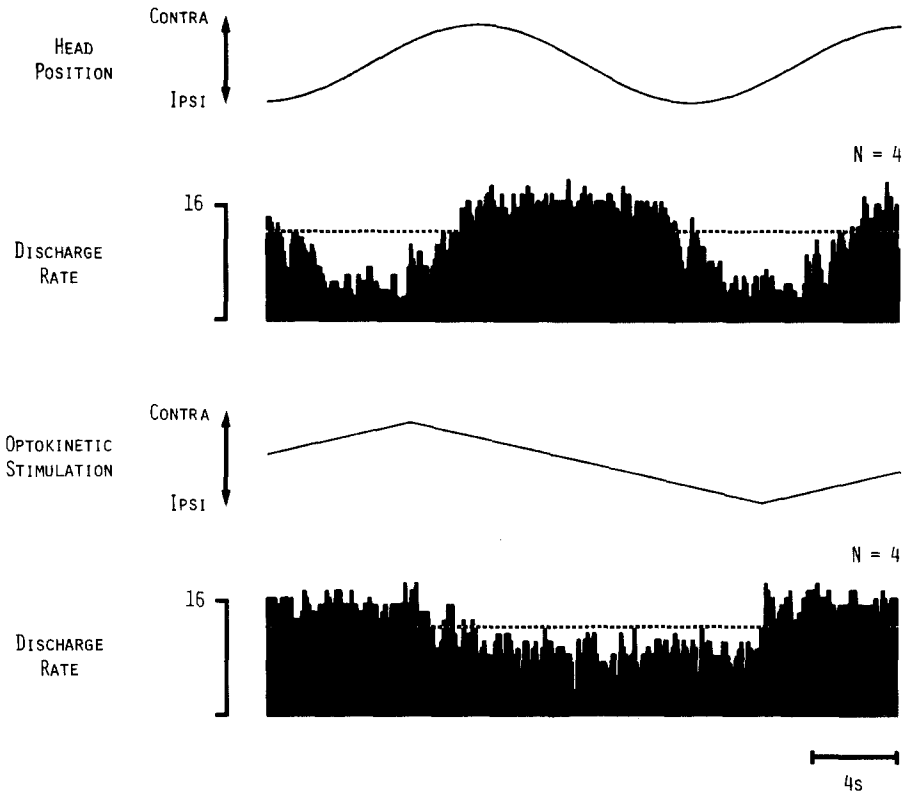

Fig. 4. Optokinetic (OK) response obtained for a type I neuron characterized by its horizontal vestibular stimulation in the dark (upper histogram). The optokinetic modulation is much lower than the vestibular one, and the OK response presents an opposite mode of directional sensitivity. Spike sampling each 160 msec during 29 sec. Number of summations is 4. Broken lines represent spontaneous activity in the dark for the upper histogram, and in diffuse light for the lower. Discharge rate is expressed in spikes per bin

showed modifications of firing in good correlation with the direction of the OK stimulation. The 7/7 tested cells of type III were unresponsive to OK stimulation. These include two neurons which were reactive to "on-off" diffuse light.

An example of OK response from a type I neuron is given in Figure 4. This unit, exhibiting increased activity in response to ipsiversive vestibular stimulation, decreases its firing during ipsiversive OK stimulation, and vice versa. Both type I or type II neurons presented this opposite mode of response for a given direction of vestibular and OK stimulation. In all cases the OK response had a long latency (1 to 3 sec) and the beginning of the tonic modulation was always tied to the beginning of OK nystagmus. We could not observe any relationship between the response amplitude and the two different values of OK stimulation velocity used in our protocol (12°/sec and 24°/sec). In

both situations, the response was an increase or a decrease of roughly 20% of the level of spontaneous activity in diffuse light.

Finally, we tested possible summation of visual and vestibular stimulation by sinusoidal rotation of the animal in front of the stationary illuminated striped pattern. We stimulated 8 cells (6 type II and 2 type I) in such conditions. Slight intensification of the vestibular response obtained in the dark could be observed in 3 units. No change was observed in the five remaining cases.

4. Response Characteristics with Respect to Saccadic Eye Movements

Only saccadic eye movements in the horizontal plane were analyzed. The vertical EOG deviation was used during data processing, only to select pure horizontal eye movements. The following three conditions were studied separately:

A. Vestibular Nystagmic Activity in the Dark. Horizontal saccadic response in both directions was analyzed in 38 cells. Of 28 type I or II neurons, 8 were unresponsive to vestibular horizontal nystagmic eye movements, whereas 20 changed their firing in correlation with the eye movements. This response could be either symmetrical or asymmetrical with respect to the direction of the saccade. It was either an increase or a decrease in firing lasting from 80 msec to 150 msec. The type of change was always the same for a given neuron and for a given direction of the saccade. The latencies ranged from 30 msec prior to the saccade to 50 msec after it. Figure 5A shows a type II neuron during vestibular nystagmus in the dark. Its response is similar for horizontal nystagmic beats directed toward opposite directions, and is characterized by an inhibition starting 30 msec before the saccade and lasting 130 msec. The nystagmic responses observed in 8 of the 10 type III neurons tested were similar to those of types I and II, except for the latency of the response which was systematically greater than 100 msec.

B. Optokinetic Nystagmic Activity. 23 units were studied under this condition: 3 out of 8 type III neurons and 11 of the 15 types I and II cells presented saccadic responses. All the OK saccade responsive cells also responded to vestibular nystagmus in the dark. The reciprocal statement is not true, however; some units responding to vestibular nystagmus were unresponsive to OK saccades. The OK saccadic responses were essentially similar to those obtained with vestibular nystagmus, in the dark, with some changes in the symmetry of the response for saccades of opposite directions. An example of this is shown in Figure 5 (A to be compared with B).

C. Spontaneous Saccades in the Dark and in Front of an Illuminated Striped Screen. Four of the 7 type III neurons and 6 of the 11 type I or II neurons analyzed, responded to spontaneous saccadic horizontal eye movements. This response presented the same characteristics for the two populations. For a given cell the pattern and the type of the response were similar to those obtained with OK stimulation. There was no difference between the response obtained for eye movement in the dark and those performed in front of the striped pattern. These results are illustrated in Figure 5C and 5D for a type II neuron, inhibited by

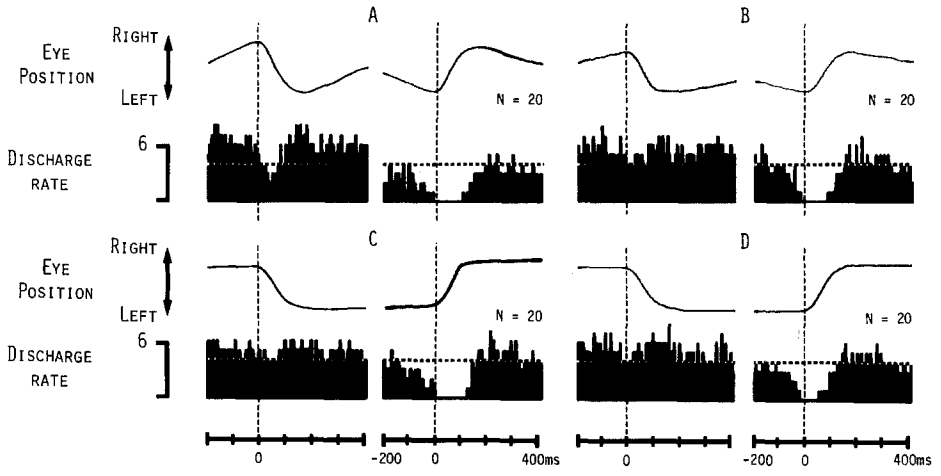

Fig. 5. Horizontal saccadic response of a type I neuron in four different conditions. In **A**, saccadic responses obtained by horizontal vestibular stimulation in the dark. In **B**, optokinetic saccadic response. In **C** and **D**, spontaneous saccadic evoked activity respectively in the dark, and in front of an illuminated stationary striped screen. The results obtained in conditions **B, C, D** are similar. In **A**, however, a clear inhibitory response appears also to vestibular saccadic eye movements to the left, against the raised background of vestibular activation. In the three other conditions, inhibition during saccades to the left is absent or limited to an insignificant trend. For this given cell, the saccadic inhibition starts 30 msec prior to the saccade and lasts 130 msec after. In the case of the vestibular saccadic eye movements to the left, the response is shorter (80 msec) and its latency is delayed to the beginning of the saccade. The histograms are constructed by processing of the neuronal activity 200 msec prior to the saccade and 400 msec after. Saccade onset corresponds to zero on the time axis. Spikes are cumulated every 10 msec, and 20 saccades, which present sufficiently similar characteristics. Broken, horizontal lines correspond to spontaneous level of activity in the dark for conditions **A** and **C**, and in diffuse light for conditions **B** and **D**

saccades to the right. We noted further, that some neurons which exhibited poor saccadic horizontal sensitivity could be influenced more specifically by oblique eye movement. Thus our overall impression was that cells presenting clear saccadic responses tend to be selective for one direction of the saccades.

5. Histological Localization

The histological repartition of this saccadic and vestibular population is divided into two locations, which also reflect a functional subdivision:

1. The majority of the type III neurons are found in the caudal part of RT above the LGd (Fig. 6A and 6B). Two of these touch the lateral dorsal border of the LGd (Fig. 6B) in an area which could correspond to the lateral part of the perigeniculate body (see Szentágothai, 1972) but all the others are distributed more than 300 μm above the LGd within the limits of RT, according to the atlas of Jasper and Ajmone-Marsan (1954).

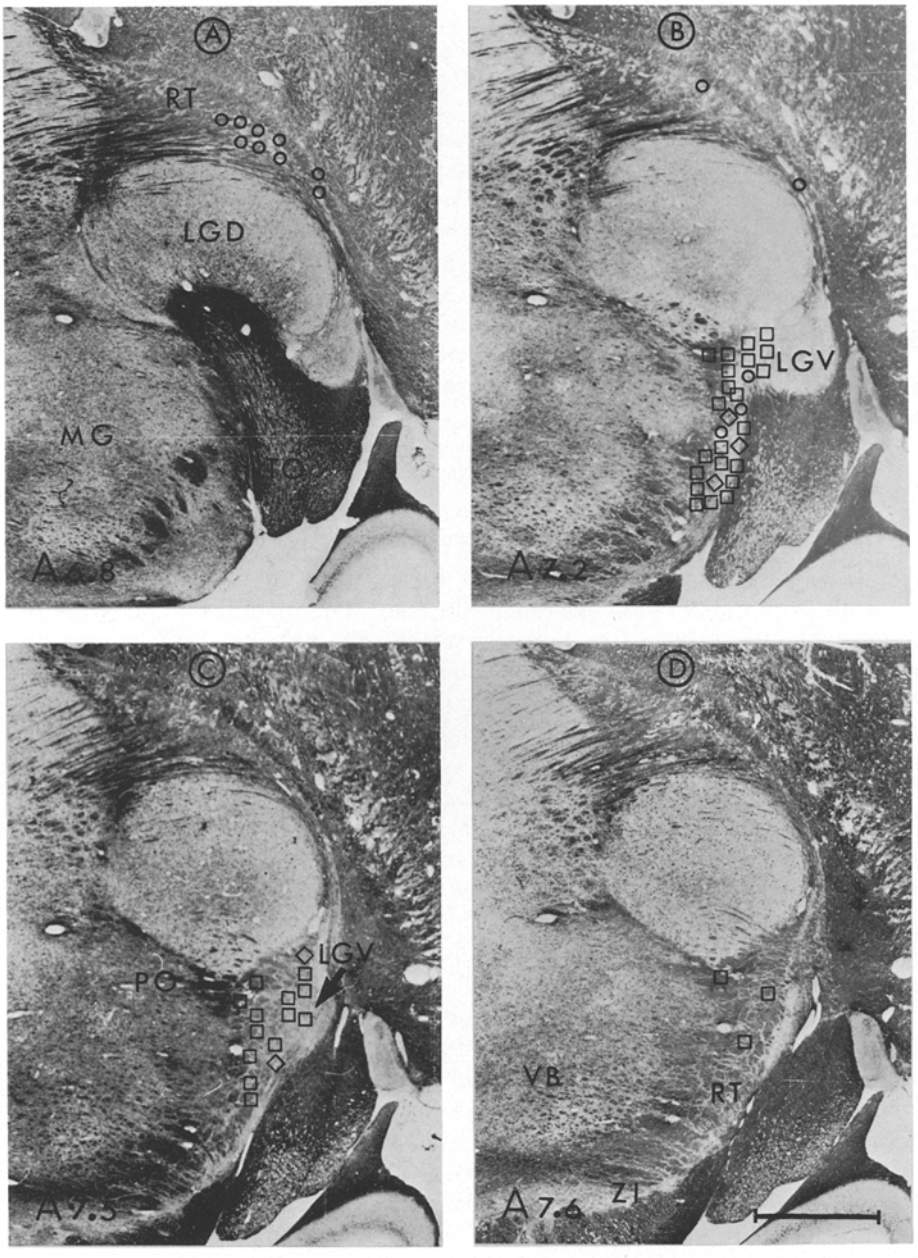

Fig. 6. Histological location of the saccadic vestibular neurons recorded in the cat thalamus. The 57 neurons are represented on four different planes. The stereotaxic plane of reference, given by the Figure 6C, corresponds to plate 7.5 of Berman's atlas. Circle: neurons of type III; square: neurons of types I and II; diamond: vertical vestibular neurons. Note concentration in Figure 6B, within the internal layer of the LGv. *LGD:* dorsal lateral geniculate body; *LGV:* ventral lateral geniculate body; *MG:* medial geniculate body; *PO:* posterior complex; *RT:* reticular thalamic nucleus; *TO:* optic tract; *VB:* ventrobasal complex; *ZI:* zona incerta; Scale: 1.5 mm. Negative tracts or isolated units without saccadic or vestibular modulation are not shown

2. The second cluster (Fig. 6B and Fig. 6C) mainly types I and II neurons, including the vertically sensitive cells, corresponds to the internal division of the LGv (Niimi et al., 1963), a zone described by Jordan and Holländer (1972) as subnuclei a and b of the LGv. The antero-posterior distribution of this neuronal population clearly indicates that the saccadic vestibular area finds its rostral limit in good correlation with the rostral border of the LGv, is more dense in an area overlapping the internal layer of the LGv (Fig. 6B), and caudally extends to a stereotaxic plane where the LGv is no longer in continuity with the RT and the zona incerta (ZI) (intermediate level between Fig. 6A and Fig. 6B).

Discussion

As suggested earlier (Magnin et al., 1974), the thalamic responses obtained in this study by sinusoidal rotation, present a high degree of similarity with responses recorded in the vestibular nuclei of different mammals (Duensing and Schaefer, 1958; Shimazu and Precht, 1965; Kubo et al., 1975; Fuchs and Kimm, 1975):

1. The present responses correspond closely to types I, II and III described by Duensing and Schaefer (1958) in the vestibular nuclei;

2. In accordance with vestibular neurons the relationship between the sinusoidally evoked type I or II responses and the velocity of the stimulation presents a phase-lag of $-10°$ to $+30°$ and shows a good correlation between the intensity of the response and the stimulating velocity. Furthermore, 10% of our cells could be specifically driven by vestibular stimulation in the vertical sagittal plane.

3. Even the type of spontaneous activity conforms with the reports of Matsuoka et al. (1975), and Estes et al. (1975), on the temporal pattern of spontaneous discharge rate in the cat vestibular nuclei.

All these arguments tend to prove the existence of a well structured vestibular thalamic focus, separate from earlier electrophysiologically and histologically described thalamic vestibular relays, located in the magnocellular part of the medial geniculate body (MGmc) (Wepsic, 1966; Liedgren et al., 1976a), and in the ventromedial (VM) and ventroposterolateral (VPL) nuclei of the thalamus (Sans et al., 1970; Raymond et al., 1974; Liedgren et al., 1976b; Büttner and Henn, 1976; Magnin and Fuchs, 1977). Even allowing for a maximal error of ± 200 μm, due to the inherent imprecision in histological reconstruction of the microelectrode tracks, the thalamic vestibular units described in this paper, cannot be confused with the vestibular MGmc neurons, and even less with the vestibular population diffusely distributed within the VPL and VM nuclei. The present recording sites are 5 mm more lateral and 1 mm more rostral than the MGmc (cf. Jasper and Ajmone Marsan's atlas; Wepsic, 1966), and 5.5 mm more lateral and 1 to 1.5 mm more caudal than the vestibular locus of the VM and VPL nuclei (Sans et al., 1970; Raymond et al., 1974; Liedgren et al., 1976a).

Although experimental data for the comparison of the electrophysiological properties of the three different thalamic vestibular populations is largely lacking, the particular point of multimodal sensory activation described by

Wepsic (1966) in the cat and Büttner and Henn (1976), Liedgren et al. (1976b) in the monkey can be discussed. As the LGv belongs to the visual system by its multiple visual afferent connections (for references see Holländer and Sanides, 1976), we tried to find visually driven responses in LGv units chosen on the basis of vestibular or saccadic reactivity. Only four neurons (7%) of type III presented "on" or "off" responses to diffuse light without evidence for a structured visual receptive field. The same cells, when driven by simultaneous vestibular and optokinetic stimulation, did not show any modification with respect to their vestibular response in the dark. On the other hand, 65% of the cells without detectable visual sensitivity could be driven by optokinetic stimulation. We tend to conclude however, that this optokinetic modulation is achieved indirectly via visual stimulation of the vestibular nuclei considering the characteristics of this optokinetic response. Such a visual input to the vestibular nuclei has been demonstrated by Dichgans and Brandt (1972) in the rabbit, Azzena et al. (1974) in the rat, and Henn et al. (1974) in the monkey. Rough testing of other sensory modalities (acoustic and somesthetic stimulations) did not affect our units.

The saccadic responses of the majority of our sample is in contrast with the oculomotor unresponsiveness, reported by Büttner and Henn (1976) and Magnin and Fuchs (1977) in the vestibular neurons of VPLo and VPI nuclei of alert monkeys. Furthermore, our results obtained in four different conditions of saccadic eye movements show similarities with the characteristics of neurons in the monkey vestibular nucleus (Miles, 1974; Fuchs and Kimm, 1975; Keller and Kamath, 1975), although none of these studies reports saccadic modulations for vestibular neurons of type III. However, it should be added that the saccadic properties of our units fit those described for neurons belonging to structures other than vestibular, such as the intermediate layers of the superior colliculus (Straschill and Hoffmann, 1970; Mohler and Wurtz, 1976), which send afferent connections to the LGv, or the thalamic internal medullary lamina of the cat which is connected with the cortical frontal eye field (Orem and Schlag, 1971) and shows saccade related activity in the cat (Schlag et al., 1974). Furthermore, a recent study (Tsumoto and Suzuki, 1976) demonstrates a strong influence of frontal eye field stimulation on neurons of the caudal RT and, perhaps a more discrete modulation in neurons belonging to the LGv. These two locations fit with our positive saccadic recording sites.

It is difficult to compare our results from the LGv with other electrophysiological studies in the same structure (Montero et al., 1968, in the rat; Mathers and Mascetti, 1975, in the rabbit; Spear et al., 1977, in the cat), since these are limited to the visual properties of LGv. Mathers and Mascetti, however, found a significant percentage (24%) of cells presenting complete lack of visual response in neurons confined within the internal part of LGv, where most of our vestibular and saccadic nonvisual neurons are concentrated. Similarly, Spear et al. (1977) found 16.2% of cat LGv units with indefinite visual responses and 22.7% of visually unresponsive cells. Even this may be an underestimate since nonresponsive cells were included in their sample only after the first and before the last visually responsive unit in a penetration through the LGv.

In the pigeon, vestibular input to the LGv has been recently documented by Vollrath and Delius (1976). This may point to a functional similarity between the avian and mammalian LGv. However, the supposed homologue of LGv in the monkey failed to show vestibular responses (Magnin and Fuchs, 1977). Thus, anatomical homology of structure, obviously, does not imply a complete similarity of function in this case.

Physiological and anatomical knowledge of the LGv has multiplied in recent years. Yet, it seems hazardous to formulate any explicite hypothesis on its functional significance. The electrophysiological studies on the LGv have been centered either on the visual or on the vestibular inputs. These would appear to be rather segregated, but it must be admitted that the possibilities of visuo-vestibular integration even within LGv await further analysis. Until more information is available its role in visually guided behaviors "remains, for the most part, a mystery" as stated by Spear et al. (1977).

Although the studies of Edwards et al. (1974) and Swanson et al. (1974) fail to demonstrate a cortical projection of the LGv, it would be tempting to view this zone as a third separate vestibular thalamic relay, related to the visual, or visuomotor system, in the same way as the two better known vestibular relays are related to the somesthetic system.

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