

Vestibular, Auditory, and Somatic Input to the Posterior Thalamus of the Cat*

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Summary. The responses of 157 neural units in the magnocellular (mc) and parvocellular (pc) components of the medial geniculate nucleus (MG) and other nuclei of the posterior (PO) thalamic group were recorded and analyzed. Units were tested for a response to electrical stimulation of the vestibular nerve, natural auditory and electrical cochlear nerve stimulation, and natural stimulation of joint, muscle, and cutaneous receptors of the limbs, trunk, and neck (somatic stimulation). Only 45% of the units responded to these stimuli. Twenty-four percent of the responsive units were multimodal, responding to more than one stimulus. All multimodal units were activated by auditory stimuli. More units responding to vestibular stimulation were found in mcMG than in pcMG or other components of the PO group. Potentials evoked by vestibular nerve stimulation were recorded in all 3 regions with latencies of 5–25 msec. No evidence was found for a thalamic relay from vestibular nerve to cortex in the area investigated, since the recorded latency for activity from vestibular nerve stimulation was longer than the latency of responses recorded in the cortex. This region of the thalamus appears to be important for reception of auditory information and integration with vestibular and somatic modalities.

Key words: Medial geniculate body – Posterior thalamic nuclei – Ascending vestibular pathway – Sensory convergence.

Ascending vestibular projections in the cat and monkey reach portions of the posterior (PO) thalamus, including the magnocellular (mc) and parvocellular (pc) components of the medial geniculate (MG) nucleus and other nuclei of this

* This investigation was supported in part by USPHS Grant NS 11307

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group (Gernandt, 1950; Spiegel et al., 1965; Copack et al., 1972; Liedgren et al., 1976a, b). There is evidence suggesting that these nuclei relay vestibular activity directly to the cerebral cortex. First, lesions of the posterior thalamus that destroy medial geniculate, suprageniculate, and medial PO nuclei reduce severely the amplitudes of the cerebral cortical potentials evoked by vestibular stimulation (Spiegel et al., 1965; Potegal et al., 1971). Second, anatomical studies employing retrograde neuronal tracing with the enzyme horseradish peroxidase have suggested that neurons in PO provide the thalamic input to the vestibular projections region in the anterior suprasylvian area of the cerebral cortex (Liedgren et al., 1976a). Third, evoked potentials in the cat (Spiegel et al., 1965; Copack et al., 1972) and unit potentials in the monkey (Liedgren et al., 1976b) occur in MG at short latencies (2–4) msec) after electrical stimulation of the vestibular nerve. These latencies are shorter than those recorded in the cerebral cortex in response to vestibular nerve stimulation (Andersson and Gernandt, 1954; Fredrickson et al., 1966a; Sans et al., 1970; Copack et al., 1972; Ödkvist et al., 1975a; Roucoux-Hanus and Boisacq-Schepens, 1974).

Despite this evidence, there are reasons to question the view that neurons in the posterior thalamus relay vestibular information to cortex. Studies of relay nuclei that depend upon the results of lesions present the problem that a lesion may interrupt an incoming axonal pathway rather than the relay neurons. Second, investigations by Day et al. (1976) using the retrograde transport of horseradish peroxidase from cerebral cortex to thalamus have not supported the conclusion of Liedgren et al. (1976a) that neurons in the PO group of nuclei provide the major thalamic input to the anterior suprasylvian area of the cerebral cortex in the cat. Third, studies of the ascending vestibular projections employing evoked potential techniques have given misleading information (cf. Deecke et al., 1973, 1974; Liedgren et al., 1976b).

The present investigation was undertaken to use single unit recording techniques and electrical stimulation of the peripheral branches of the vestibular nerve to explore the possibility that the posterior nuclei of the cat relay vestibular activity to the cerebral cortex. If a relay is located in this region, the units should respond to stimulation of the vestibular nerve at shorter latencies than responses recorded in the cerebral cortex. Also, thalamic vestibular neurons should respond to both vestibular and proprioceptive stimulation, because of the convergence of these modalities on single neural units in the vestibular nuclei (Fredrickson et al., 1966b). Convergence of other somatosensory inputs with vestibular activity upon single units also would be expected since it has been reported previously in the thalamus (Liedgren et al., 1976a) and cerebral cortex (Boisacq-Schepens and Hanus, 1972; Ödkvist et al., 1975b).

Methods

Adult cats weighing 2.0 and 3.5 kg were anesthetized with alpha-chloralose, 60 mg/kg. Cannulae were placed in the trachea and in a femoral vein and femoral artery. The blood pressure was

maintained above 100 mg Hg with dextran if necessary and the body temperature was held above 37° C with a thermostatically controlled heating pad. The animals were paralyzed with Flaxedil and respired artificially during recording.

Microdissection was performed through the right bulla to expose the cochlear nerve and the utricular and superior canal branches of the vestibular nerve (Andersson and Gernandt, 1954; Landgren et al., 1967). A stainless steel bipolar electrode (Rhodes SNEX-200) was positioned on the vestibular nerve and an identical electrode on the cochlear nerve. The bulla then was filled with petroleum jelly and the electrodes were cemented to the cut edge of the bulla. To monitor spread of current during electrical stimulation of these nerves, insulated bipolar concentric electrodes were placed stereotaxically in the ipsilateral lateral vestibular and dorsal cochlear nuclei of the brainstem with reference to the atlas of Snider and Niemer (1961). Vestibular nerve stimulus intensity was determined using a stimulus voltage level which at first yielded an averaged evoked response in both the vestibular and the cochlear nuclei. The voltage then was lowered progressively until there was a response in the vestibular nucleus and no response in the cochlear nucleus. An analogous procedure was followed to determine the intensity of cochlear nerve stimulation that would provide an optimal amplitude cochlear nucleus response with no response in the vestibular nucleus. Control recordings from these sites were made at regular intervals throughout each experiment and stimulus intensities were adjusted as necessary to prevent spread of current.

Natural stimulation was used to assess unit responsiveness to stimulation of joint, muscle, and cutaneous receptors of the limbs and trunk and receptors of the cochlea. Flexion and extension of all four limbs and the vertebral column were used for joint and muscle stimulation. Blowing and light brushing across the fur of the limbs, face, and trunk were used for cutaneous stimulation. Hand clapping and clicks were used for auditory stimulation.

Unit activity was recorded in the thalamus with glass microelectrodes filled with 4% pontamine blue in 5% NaCl using standard amplification and display techniques. Evoked potential recordings were alternated with unit recordings in the electrode tracks by adjusting the electrical filters and averaging the responses to 128 trials of vestibular stimulation at 0.3 Hz using a Fabritek 1072 computer. To ensure that neural units responsive to vestibular stimulation would be found, the vestibular nerve was stimulated at 0.3 Hz as the electrode slowly approached the MG. Units responsive to this stimulus and those showing activity without overt stimulation (spontaneous activity) were recorded and analyzed. Each unit was tested with the following stimuli: vestibular nerve electrical stimulation at 0.3 Hz and 30 Hz; cochlear nerve electrical stimulation at 0.3 Hz; natural auditory stimulation; and somatic stimulation (joint, muscle, and cutaneous). Units were considered responsive to a particular stimulus if a stimulus-locked response was identified in a post-stimulus time histogram or dot raster display or if continuous stimulation (30 Hz vestibular nerve stimulation or natural somatic stimulation) caused a change in ongoing activity. A change in ongoing activity was defined in the following manner. One minute of activity was recorded first without stimulation and then with stimulation. The distributions of spikes during these time intervals were compared with a non-parametric test (the Mann-Whitney *U* Test). The convergence of inputs from several sensory modalities onto single neural units was detected by testing each unit independently with each modality of stimulation. Upon completion of each electrode penetration, small pontamine blue marks were made at the bottom and top of the electrode track by passing 5–10 μ A of current for 5–10 min (Godfraind et al., 1972). The site of recording of each unit and evoked potential was determined by histological examination of the tissue and the recorded stereotaxic parameters.

Results

1. Single Unit Data. The activity of 50 neural units was recorded within mcMG, 50 in pcMG, and 57 in other components of the posterior thalamic group. All units but one had spontaneous discharge. The spontaneous activity showed three patterns of discharge, single spike activity (23%); burst activity (clusters of 3 to 6 spikes with approximately 1–2 msec between spikes, 69%); and a combination of the two (8%). The discharge rate was measured for 1–3 min and

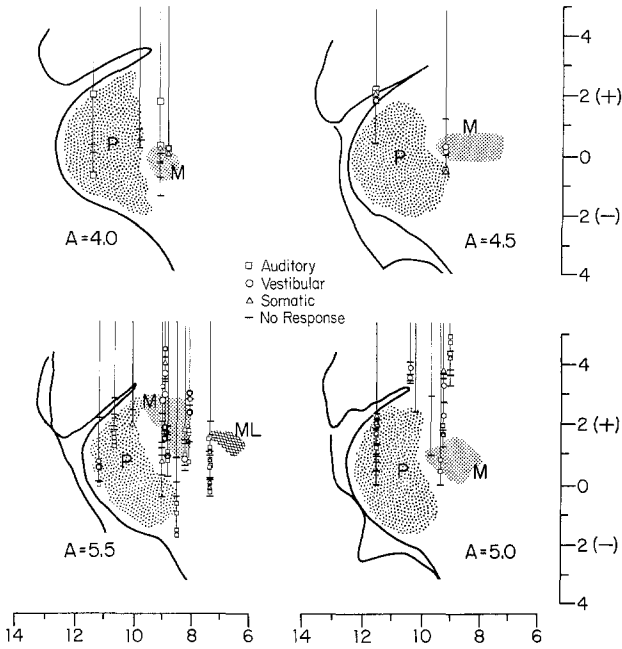


Fig. 1. Drawings of cross-sections through the diencephalon at four positions measured anterior to the inter-aural line. Symbols represent the locations of 157 units recorded. P = Parvocellular medial geniculate body, M = Magnocellular medial geniculate body, ML = Medial lemniscus

the mean was categorized as fast (>10 Hz, 18% of units), medium (2–10 Hz, 30% of units), or slow (<2 Hz, 52% of units). There was a relationship between rate and pattern of spontaneous discharge; 83% of units with slow spontaneous activity had burst-type discharge and 66% of units with fast activity had single spike discharge.

Only 45% (71 of 157) of all units tested responded to any of the stimuli presented. Responsive units did not differ from unresponsive units in location (Fig. 1) or in pattern or rate of spontaneous discharge. Auditory stimuli, electrical and natural, activated 80% of responsive units and were the most effective of all stimuli presented. Fifty-two percent of the units activated by auditory stimulation responded only to natural stimulation, 24% responded only to electrical stimulation of cochlear nerve, and 24% responded to both electrical and natural stimuli. The latency to onset of activation following electrical stimulation of the cochlear nerve ranged from 4–20 msec.

Vestibular nerve stimulation activated 21% (15) of the responsive units. Six units of the 15 had a stimulus-locked response when stimuli were applied to the vestibular nerve at 0.3 Hz. The remaining 9 units showed no stimulus-locked response but all developed an overall increase in discharge rate during stimulation of the vestibular nerve at 30 Hz. The units with a stimulus-locked response showed a latency to onset of response ranging between 10 and 40

msec. During successive applications of vestibular stimuli at 0.3 Hz, all six of the units showed variations of latency of ± 5 msec and there were frequent trials in which a stimulus-locked response failed to occur. One unit showed a higher failure rate, sometimes exceeding 50%. Typical patterns of neuronal activity for units showing stimulus-locked responses are presented in Figure 2a, b. Units activated by vestibular stimulation were found dorsal to and within the mcMG (Fig. 1). A higher proportion of units in mcMG (9 of 22) was affected by vestibular stimulation than units in pcMG (2 of 20) and in other areas of the posterior thalamus (4 of 29).

Twenty-three percent of responsive units also reacted to somatic stimulation. These units were not confined to a single anatomical region but were found clustered near the borders of both mcMG and pcMG (Fig. 1).

2. Convergence of Sensory Input. Twenty-four percent of the responsive units were activated by more than one modality and each of these units was activated by auditory stimulation. There was no difference between mcMG, pcMG, and other regions in the degree of convergence found (Table 1). No units responded only to vestibular and somatic stimulation, although two units did respond to vestibular, auditory, and somatic stimulation.

3. Vestibular Evoked Potentials. Averaged potentials evoked by vestibular nerve stimulation were employed to locate responsive regions in and around MG. Evoked responses with latencies of 5–25 msec were found throughout the recording region (Fig. 3), and responses were seen more consistently in the rostral portions of mcMG than elsewhere. In many sites an evoked potential could be recorded but unit activity in the same site was unaffected by vestibular stimulation. Conversely, many sites containing units responsive to vestibular stimulation showed no evoked potential. Consequently, the presence of an evoked potential did not predict the effect of vestibular stimulation on single unit activity when the unit and the evoked potential recordings occurred in the same location in a single animal.

Table 1. Response of each unit to sensory stimulation classified by type of response and anatomical location on unit

Effective Stimulus Modalities	Cell Locations			Totals
	mcMG	pcMG	Other Areas	
Vestibular	4	0	2	6
Auditory	9	15	18	42
Somatic	2	2	2	6
Vestibular and Auditory	4	2	1	7
Vestibular and Somatic	0	0	0	0
Auditory and Somatic	2	1	5	8
Vestibular, Auditory, and Somatic	1	0	1	2
Totals	22	20	29	71

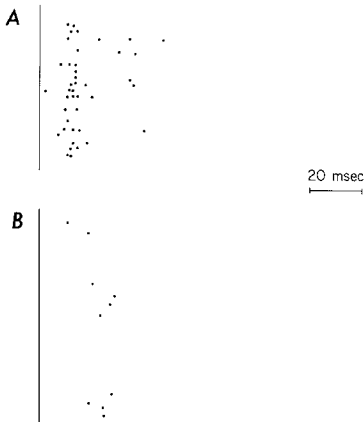


Fig. 2. Responses of two units from mcMG to 0.3 Hz vestibular nerve stimulation. Raster display represents a single spike as a dot and stores repetitive trials one below the other

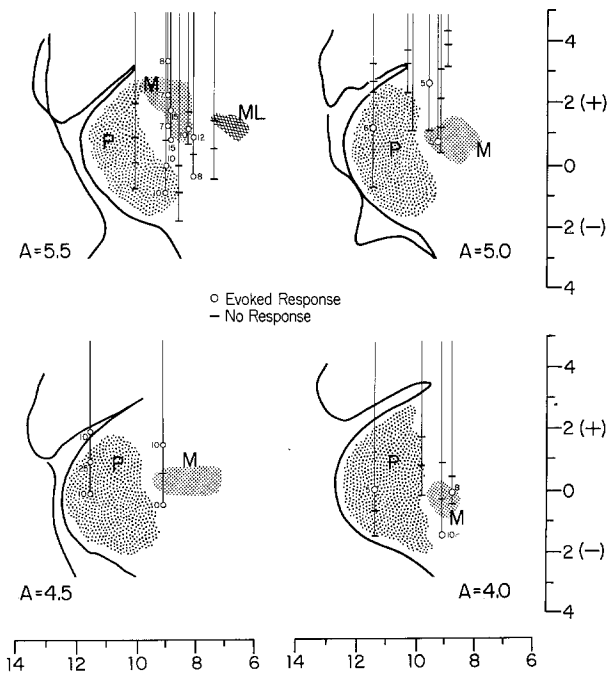


Fig. 3. Drawings of cross-sections through the diencephalon at four positions measured anterior to the inter-aural line. Symbols represent positions investigated for vestibular nerve evoked potentials. Numbers refer to msec latency of evoked potential. Remaining labels as in Figure 1

Discussion

The present findings confirm the existence of a vestibular input to the medial geniculate nucleus and other nuclei of the posterior group, as reported previously in studies with evoked potentials in cat (Spiegel et al., 1965; Copack et al., 1972) and monkey (Deecke et al., 1973; Liedgren and Schwarz, 1976) and with unit recordings in cat (Wepsic, 1966) and monkey (Liedgren et al., 1976b). About 20% of units in the PO group responsive to sensory stimuli were activated by vestibular nerve stimulation. In contrast to the small percentage of neural units affected by vestibular stimuli in the posterior group, 80% of the responsive units were affected by auditory stimuli in all three segments of the posterior nuclei investigated. Natural auditory stimulation altered neural unit activity more strongly than electrical stimulation.

The latencies to the onset of a response to vestibular stimulation of the units in the present study differed from those reported previously. Liedgren et al. (1976b) in the squirrel monkey and Wepsic (1966) in the cat found that units in the posterior nuclei had short latencies (2–4 msec) to the onset of a response to vestibular stimulation. We found that the shortest latency responses after vestibular nerve stimulation was 10 msec. There are several possible explanations of the differences in latencies between studies. In Wepsic's (1966) investigation, electrical stimulation of the vestibular nucleus was used to test the response of a thalamic neuron to vestibular stimulation. Electrical stimulation of the vestibular nucleus presents two problems: ascending systems other than vestibular can be activated inadvertently, since the vestibular nucleus of the cat receives fibers mediating somatosensory inputs (Fredrickson et al., 1966b; Wilson et al., 1966), and there is the additional hazard of stimulus spread to adjacent brainstem structures. The discrepancy between the results of the present study and those reported by Liedgren et al. (1976b) in the monkey are more difficult to reconcile. There may be differences between species in the vestibular projections to the posterior nuclear group that account for the presence of short-latency responses in the monkey and the absence of such responses in the cat. It is also possible that the posterior group of the cat contains a very small percentage of short latency vestibular-activated neurons and these units were undetected in the present study. The methods of applying electrical stimulation to the vestibular nerve in the two studies, however, may best explain the differences in results. In the present investigation, vestibular nerve stimulation was purposefully conservative. It is possible, as a consequence of this methodology, that the fastest conducting ascending vestibular pathway was not activated in its entirety. There is no doubt, however, that this method of stimulation activates at least a segment of the fast conducting pathway to cortex, since potentials appear in both the pericruciate and the anterior suprasylvian regions of the cerebral cortex at latencies of 4–6 msec with this technique of stimulation (Copack et al., 1972; Abraham et al., 1977).

Based on our findings that 1. neurons in the PO group are activated by vestibular stimulation at long and not at short latencies and 2. neurons in the PO group do not show convergence of vestibular with proprioceptive inputs as a prominent feature of unit responses, we consider it unlikely that neurons in the

posterior group of nuclei investigated in this study provide an important relay of vestibular activity to the cerebral cortex in the cat. Our findings indicate that neurons in the posterior portions of the thalamus receive vestibular input mediated by a slow or multisynaptic pathway. There is strong evidence of a potent auditory input to neurons in this region, including neurons responsive to vestibular and somatosensory inputs. Accordingly, this area appears to be important for the integration of auditory with vestibular and somatosensory stimuli.

Acknowledgement. The authors are indebted to Ms. T. Genningsen for histological preparations of tissues and Mr. J. Friedman for assistance in data analysis.

References

- Abraham, L., Copack, P., Gilman, S.: Brainstem pathways for vestibular projections to cerebral cortex in the cat. *Exp. Neurol.* **55**, 436–448 (1977)
- Andersson, S., Gernandt, B.E.: Cortical projection of the vestibular nerve in cat. *Acta Oto-Laryng. (Stockh.) Suppl.* **116**, 10–18 (1954)
- Boisacq-Schepens, N., Hanus, M.: Motor cortex vestibular responses in the chloralosed cat. *Exp. Brain Res.* **14**, 539–549 (1972)
- Copack, P., Dafny, N., Gilman, S.: Neurophysiological evidence of vestibular projections to thalamus, basal ganglia, and cerebral cortex. In: *Corticothalamic Projections and Sensorimotor Activities* (eds. T.C. Frigyesi, E. Rinvik and M. Yahr), pp. 309–339. New York: Raven Press 1972
- Day, M., Blum, P., Carpenter, M.B., Gilman, S.: Thalamic components of ascending vestibular projections. *Neurosci. Abstr.* **2**, 1058 (1976)
- Deecke, L., Schwarz, D.W.F., Fredrickson, J.M.: The vestibular thalamus in the rhesus monkey. *Adv. Oto-Rhino-Laryng.* **19**, 210–219 (1973)
- Deecke, L., Schwarz, D.W.F., Fredrickson, J.M.: Nucleus ventroposterior inferior (VPI) as the vestibular thalamic relay in the rhesus monkey. *Exp. Brain Res.* **20**, 88–100 (1974)
- Fredrickson, J.M., Figge, U., Scheid, P., Kornhuber, H.H.: Vestibular nerve projection to the cerebral cortex of the rhesus monkey. *Exp. Brain Res.* **2**, 318–327 (1966a)
- Fredrickson, J.M., Schwarz, D., Kornhuber, H.H.: Convergence and interaction of vestibular and deep somatic afferents upon neurons in the vestibular nuclei of the cat. *Acta Oto-Laryng. (Stockh.)* **61**, 168–188 (1966b)
- Gernandt, B.: Midbrain activity in response to vestibular stimulation. *Acta Physiol. Scand.* **21**, 73–81 (1950)
- Godfraind, J.M., Meulders, M., Veraart, C.: Visual properties of neurons in pulvinar, nucleus lateralis posterior, and nucleus suprageniculatus thalami in the cat. I. Quantitative investigation. *Brain Res.* **44**, 503–526 (1972)
- Landgren, S., Silfvenius, H., Wölsk, D.: Vestibular, cochlear and trigeminal projections to the cortex in the anterior suprasylvian sulcus of the cat. *J. Physiol. (Lond.)* **191**, 561–573 (1967)
- Liedgren, S.R.C., Kristensson, K., Larsby, B., Ödkvist, L.M.: Projection of thalamic neurons to cat primary vestibular cortical fields studied by means of retrograde axonal transport of horseradish peroxidase. *Exp. Brain Res.* **24**, 237–243 (1976a)
- Liedgren, S.R.C., Milne, A.C., Rubin, A.M., Schwarz, D.W.F., Tomlinson, R.D.: Representation of vestibular afferents in somatosensory thalamic nuclei of the squirrel monkey (*Saimiri sciureus*). *J. Neurophysiol.* **39**, 601–612 (1976b)
- Ödkvist, L., Larsby, B., Fredrickson, J.M.: Projection of the vestibular nerve to the SI arm field in the cerebral cortex of the cat. *Acta Oto-Laryng. (Stockh.)* **79**, 88–95 (1975a)
- Ödkvist, L.M., Liedgren, S.R.C., Larsby, B., Jerlvall, L.: Vestibular and somatosensory inflow to the vestibular projection area in the post cruciate dimple region of the cat cerebral cortex. *Exp. Brain Res.* **22**, 185–196 (1975b)

- Potegal, M., Copack, P., deJong, J.M.B.V., Krauthamer, G., Gilman, S.: Vestibular input to caudate nucleus. *Exp. Neurol.* **32**, 448–465 (1971)
- Roucoux-Hanus, M., Boisacq-Schepens, N.: Projections vestibulaires au niveau des aires corticales suprasylviennes et postcruciées chez le chat anesthésié au chloralose, *Arch. Ital. Biol.* **112**, 60–76 (1974)
- Sans, A., Raymond, J., Marty, R.: Réponses thalamiques et corticales à la stimulation électrique du nerf vestibulaire chez le chat. *Exp. Brain Res.* **10**, 265–275 (1970)
- Snider, R.S., Niemer, W.T.: A stereotaxic atlas of the cat brain. Chicago: University of Chicago Press 1961
- Spiegel, E.A., Szekely, E.G., Gildenberg, P.L.: Vestibular responses in midbrain, thalamus, and basal ganglia. *Arch. Neurol. (Chic.)* **12**, 258–269 (1965)
- Wepsic, J.G.: Multimodal sensory activation of cells in the magnocellular medial geniculate nucleus. *Exp. Neurol.* **15**, 299–318 (1966)
- Wilson, V.J., Kato, M., Thomas, R.C., Peterson, B.W.: Excitation of lateral vestibular neurons by peripheral afferent fibers. *J. Neurophysiol.* **29**, 508–529 (1966)

Received August 19, 1977