

## Research Note

# Vestibulo-Thalamic Projection to the Anterior Suprasylvian Cortex of the Cat\*

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**Summary.** Suggestive evidence as to the site of a major thalamic relay of the vestibular projection to the anterior suprasylvian (ASS) cortex in the cat has been obtained using the retrograde axonal transport of horseradish peroxidase. The thalamo-cortical neurons are located in several patches surrounding the posterior margins of the ventro-basal complex (VB). This area also was found to receive vestibulo-thalamic projections. It comprises different nuclear groups known to carry somatic, acoustic, visual or combined information, which possibly have certain functions related to kinaesthesia and body orientation in common.

**Key words:** Cat vestibular cortex – Thalamic relay nuclei – Vestibulo-thalamic projection

The existence of a vestibular field in the anterior suprasylvian (ASS) cortex of cat has been established in several electrophysiological studies (cf. Mergner 1979). Some uncertainty, however, still exists concerning the ascending vestibular pathway and its thalamic relay. Despite some earlier negative results, direct vestibulo-thalamic projections have been demonstrated anatomically (for references, cf. Mergner 1979; also Kotchabhakdi et al. 1980). From these studies it appears that several thalamic nuclei receive afferent projections from the vestibular nuclei. Among these are the ventrobasal complex (VB) together with its posterior border region towards the lateral posterior nucleus (LP), and the magnocellular portion of the medial geniculate body (mcMG). In two recent studies, either one or the other thalamic region has been claimed to represent the main source of afferent fibers to the ASS vestibular field (Blum et

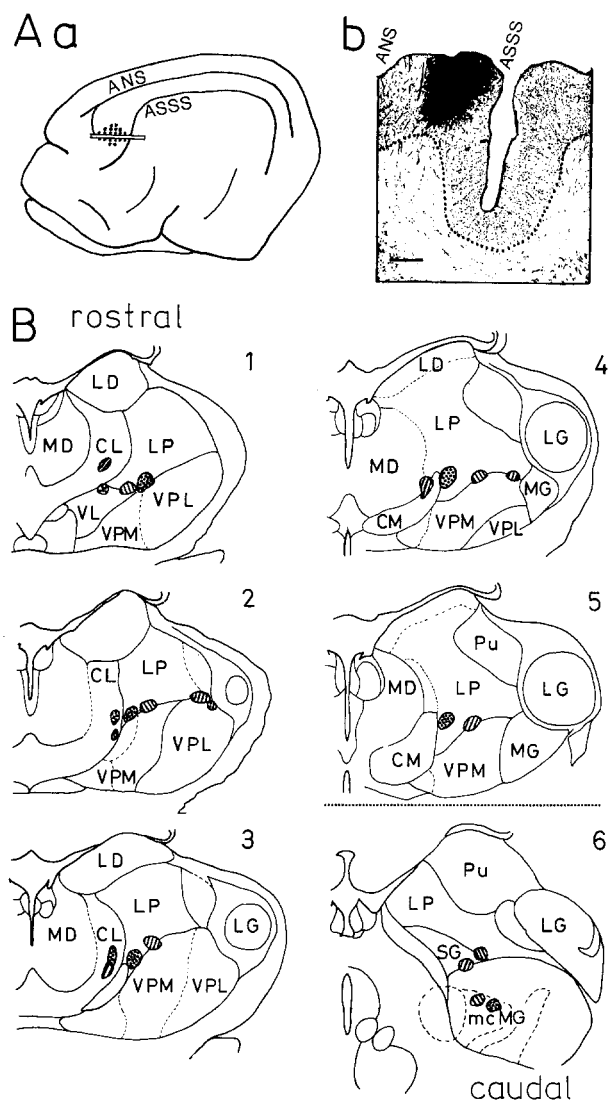
al. 1979; Liedgren et al. 1976). In order to resolve this apparent discrepancy, we reinvestigated this thalamo-cortical projection anatomically. The ASS vestibular field was identified not on grounds of evoked field potentials as in the former studies, but by single neuron responses to natural vestibular stimulation. Furthermore, an attempt was made to demonstrate anatomically vestibulo-thalamic projections to the site of origin of the thalamo-cortical neurons.

## Methods

In two recent studies (Becker et al. 1979; Mergner et al. 1981), we investigated neuronal responses to horizontal rotation in the ASS cortex. In six cats from these electrophysiological experiments and in eight additional ones, horseradish peroxidase (HRP; Sigma VI) was injected at the site of cortical vestibular neurons. Forty-eight hours later the animals were perfused for fixation of the brain under deep anaesthesia. After serial sectioning of the thalamus and enzymatic reaction of the HRP, the thalamic site of neurons labeled by retrograde transport of HRP was identified and plotted on schematic drawings of the thalamus following closely the anatomical description of Jasper and Ajmone-Marsan (1954). Based upon the results from the first animals, the last ten animals after the cortical injection received a further HRP injection on the contralateral side, aiming stereotaxically at the symmetric thalamic sites previously identified as projecting to the ASS vestibular field. In frontal sections of both thalami, the site determined by cortical HRP injection was compared with the thalamic injection site on the opposite side (compare Fig. 2A). The sites were found to be symmetric in five cases. The brainstems of these animals were cut serially and processed, in order to search for retrogradely labeled neurons in the vestibular nuclei.

HRP was injected by pressure (30–50% solution in physiological saline, 0.05–0.2 µl) or by a combined mechanical and iontophoretic method (cf. Mergner et al. 1977). It should be noted that the cortical injections were performed through the intact dura, since previous injections with the dura opened apparently had led to a significant reduction in the number of thalamo-cortical neurons. The fixation procedure and further processing for enzymatic HRP reaction followed the earlier methods of Graham and Karnovsky using 3,3'-diaminobenzidine as chromogen.

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**Fig. 1A, B.** Thalamic projections to the vestibular field in the ASS cortex. **Aa** Location of the vestibular cortical field between tip of ansate sulcus (ANS) and anterior suprasylvian sulcus (ASSS). **Ab** Retouched photograph of sagittal section through this area as indicated in **a**. Black area represents HRP injection site (magnification marker: 1 mm). **B** Schematic drawings of frontal sections through left thalamus showing locations of neurons retrogradely labeled with HRP; superimposed results from three animals. For abbreviations cf. page 458

## Results

### Cortical Injection Site

In the electrophysiological experiments described elsewhere (Becker et al. 1979; Mergner et al. 1981), it was found that vestibular responsive neurons were relatively concentrated in a region between the tip of the ansate sulcus and the anterior suprasylvian sulcus (Fig. 1Aa). HRP injections into the ASS vestibular

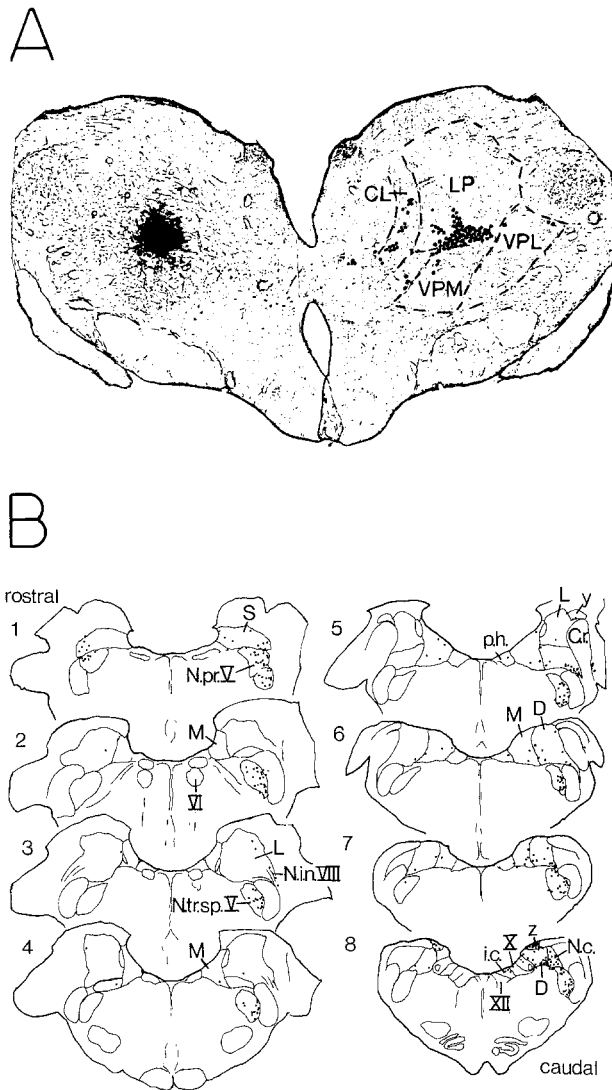
field were considered successful if essentially restricted to the grey matter at this site (Fig. 1Ab). This was the case in the 14 animals reported here.

### Thalamic Locations of Retrogradely Labeled Neurons

The labeled neurons were grouped in several patches surrounding the posterior margins of the VB. The largest and most consistent patches (present in 11 out of the 14 cases) were found in the border region between LP, VL, VB, and CL at rostral levels (Figs. 1B and 2A). Some of these patches reached well into the ventral LP as well as into the posterior VL and VB. Small distinct groups of labeled neurons in CL were arranged in clusters located mainly in middle portions of the nucleus and dispersing in a medio-ventral direction. At more latero-caudal levels, the patches were located in the VB-LP border region (eight cases). Caudal to the VB, patches with less dense packages of labeled neurons were still found. They mostly were located in the SG-LP border region and in the mcMG (five cases). This widespread, but nevertheless characteristic distribution of the relevant thalamic neurons, was even more prominent when superimposing the results obtained with several animals in which the exact locations of the patches showed some variation. An example of three superimposed cases is given in Fig. 1B.

### Vestibulo-thalamic Projection

In five cases, the site of HRP injection in the thalamus on one side corresponded well to the area of patches of labeled thalamo-cortical neurons on the other side. In three animals, both the injection site and the patches with thalamo-cortical neurons were located in the LP-VB border region at a rostral level (cf. example in Fig. 2A). In these animals, some retrogradely labeled neurons were found in all four main vestibular nuclei on both sides. However, there was a clear preponderance in caudal parts of the contralateral descending and medial vestibular nucleus (Fig. 2B). Also, mainly on the contralateral side, labeled neurons were observed in some of the small nuclear regions related to the vestibular nuclear complex; i.e., in the groups y and especially z, also in the interstitial nucleus of the VIIIth nerve, the N. praepositus hypoglossi and the N. intercalatus. Outside the vestibular nuclear complex, a considerable number of labeled neurons were observed in the principal trigeminal nucleus on both sides extending dorsally into the superior vestibular nucleus, as well as in the nucleus of the spinal trigeminal tract and the cuneate nucleus on the contralateral side.



**Fig. 2A, B.** Vestibulo-thalamic projection. **A** Retouched photo of frontal section through rostral thalami. HRP injection site in left thalamus matches location of thalamo-cortical neurons (marked by dots) at posterior margin of right VB. **B** Drawings of frontal sections through brainstem with indicated locations (dots) of neurons retrogradely labeled by HRP injection in **A**

In the two other cases, the thalamic injection site was located more laterocaudally and comprised, apart from the LP-VB border region, also the SG and the mcMG. Retrogradely labeled neurons were observed in the vestibular nuclei essentially with similar locations as above. However, in addition, several of the neurons were found in the reticular formation in close conjunction with the trapezoid body. Three additional animals, which only had received the cortical injection, were used as controls; no labelling of vestibular nuclear neurons was observed in any of these cases.

## Discussion

Considering the vestibulo-thalamic projection first, our results are compatible with those of Kotchabhakdi et al. (1980, for other relevant literature cf. these authors). According to their findings, an ascending projection mainly stemming from caudal parts of the contralateral medial and descending vestibular nuclei and group z reaches the VB and some of its surrounding nuclei (VL, the VB-LP border region resp. their Pom, mcMG; cf. also Mergner 1979). The possible distinct vestibular projection to the CL will not be considered further here.

Certain parts of this thalamic area appear to relay vestibular information to the ASS cortex. Liedgren et al. (1976) injected HRP in the ASS cortex at sites where vestibular nerve stimulation evoked short latency field potentials. They found labeled neurons mainly in the mcMG, but also some in the LP and in the SG-mcMG border region. In a similar study, Blum et al. (1979) observed such labeled neurons mainly in the dorso-lateral VPL and a few in the VPM, LP, VL, and CM. In addition, scattered neurons were found in regions bordering posteriorly the VB including caudally the mcMG. These regions are called the posterior nuclear group (PO; cf. below). The former authors considered the caudal parts of the PO (i.e. the mcMG), the latter the rostral parts of the PO and the VB as the essential thalamic relay. According to our study, the neurons projecting to the ASS cortex are found both in rostral and, to a lesser extent, in caudal parts of the PO, and in the adjacent posterior margins of the VB. The rostral and caudal parts of the PO both were shown to receive projections from the vestibular nuclei; the vestibulo-thalamic neurons being mainly located in the caudal parts of the contralateral MVN and DVN.

It might be interesting to speculate why the thalamic relay neurons projecting to the ASS vestibular field are so dispersed, and what this extended area, which appears to include or overlap several thalamic nuclei, might have in common. According to Diamond and Hall (1969), VB proper phylogenetically represents an only recently demarcated relay for the medial lemniscal system, which emerges from and later is still embedded in older and rather heterogeneous projection systems. In cat, the VB posteriorly and caudally is surrounded by the ventral LP, the SG, and the mcMG. The latter regions or part of them, have been designated the posterior nuclear group, since anatomically as well as electrophysiologically they appear to represent an entity of their own (for literature, cf. Heath and Jones 1971). They not only receive somatic, but also acoustic or combined information, while adjacent

parts of the medial LP might be linked to the (visual) tecto-thalamo-cortical system (cf. Graybiel 1972). Graybiel (1972) puts these thalamic regions into a broader conceptual frame. She considers them to represent "lemniscal adjunct channels" projecting to "proximal association cortices" and basal ganglia. These channels take an intermediate position as to the "lemniscal line systems" to "sensory cortices", on one hand, and pulvinar-nucleus lateralis intermedius projections to "distal association cortices" on the other. She speculates about their functional role as possibly being involved in a "general bodily frame of reference", closely related to effector (motor) mechanisms controlling the orientation of the body axis or the directing of the exteroceptive systems (e.g. gaze, hearing). It appears conceivable that this system comprises a vestibular, or more generally, a kinaesthetic element.

*Abbreviations.* ANS, ansate sulcus; ASSS, anterior suprasylvian sulcus; CM, N. centrum medianum; CL, N. centralis lateralis; C.r., Corpus restiformis; D, N. vestibularis descendens; i.c., N. intercalatus; L, N. vestibularis lateralis; LD, N. lateralis dorsalis; LG, N. geniculatus lateralis; LP, N. lateralis posterior; M, N. vestibularis medialis; MG, N. geniculatus medialis; mcMG, pars magnocellularis of MG; MD, N. medialis dorsalis; N.c., N. cuneatus; N. in. VIII, N. interstitialis of the VIIIth cranial nerve; N. pr. V, principal sensory trigeminal nucleus; N. tr. sp. V, nucleus of the spinal trigeminal tract; p.h., N. praepositus hypoglossi; Pu, pulvinar; S, N. vestibularis superior; SG, N. suprageniculatus; VL, N. ventralis lateralis; VPL, N. ventralis posterolateralis; VPM, N. ventralis posteromedialis; VI, X, XII, motor cranial nerve nuclei; y, z, small cell groups of Brodal and Pompeiano

## References

- Becker W, Deecke L, Mergner T (1979) Neuronal responses to natural vestibular and neck stimulation in the anterior suprasylvian gyrus of the cat. *Brain Res* 165: 139–143
- Blum PS, Day MJ, Carpenter MB, Gilman S (1979) Thalamic components of the ascending vestibular system. *Exp Neurol* 64: 587–603
- Diamond JT, Hall WC (1969) Evolution of neocortex. *Science* 164: 251–262
- Graybiel AM (1972) Some fiber pathways related to the posterior thalamic region in the cat. *Brain Behav Evol* 6: 363–393
- Heath CJ, Jones EG (1971) An experimental study of ascending connections from the posterior group of thalamic nuclei in the cat. *J Comp Neurol* 141: 397–426
- Jasper HH, Ajmone-Marsan C (1954) A stereotaxic atlas of the diencephalon of the cat. National Research Council of Canada, Ottawa
- Kotchabhakdi N, Rinvik E, Walberg F, Yingchareon K (1980) The vestibular projections in the cat studied by retrograde axonal transport of horseradish peroxidase. *Exp Brain Res* 40: 405–418
- Liedgren SRC, Kristensson K, Larsby B, Ödkvist LM (1976) 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
- Mergner T (1979) Vestibular influences on the cat's cerebral cortex. *Prog Brain Res* 50: 565–579
- Mergner T, Pompeiano O, Corvaja N (1977) Vestibular projections to the nucleus intercalatus of Staderini mapped by retrograde transport of horseradish peroxidase. *Neurosci Lett* 5: 309–313
- Mergner T, Anastasopoulos D, Becker W, Deecke L (1981) Comparison of the modes of interaction of labyrinthine and neck afferents in the suprasylvian cortex and vestibular nuclei of the cat. In: Fuchs AF, Becker W (eds) *Progress in oculomotor research*. Elsevier/North Holland, Amsterdam New York Oxford, pp 343–350

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