

Location of Thalamic Neurons Mediating Vestibulo-Cortical Pathways in Cats

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This study was aimed at examining vestibulo-thalamo-cortical pathways in anesthetized cats. Thirty-six neurons, which were activated by pitch rotation and contralateral labyrinth stimulation, were recorded in the following areas: the ventral posterolateral nucleus, the ventral posteromedial nucleus, the lateroposterior nucleus and the magnocellular nucleus of the medial geniculate body (MGmc) of the thalamus. Thirteen of these neurons were antidromically activated from the anterior suprasylvian sulcus or postcruciate dimple of the cortex. These results suggest that the ventrobasal complex and MGmc convey inputs from the vestibular apparatus to the vestibular cortex in cats.

Key words: anterior suprasylvian sulcus; cat; postcruciate dimple; posterior semicircular canal; thalamus

Many studies have revealed the projection of neurons in the vestibular nucleus to the thalamus (Landgren et al., 1967; Sans et al., 1970; Ödkvist et al., 1975). Anatomical studies have shown that thalamic projections to the anterior suprasylvian sulcus (ASSS) and the postcruciate dimple (PCD) of the cortex originate from the ventrobasal complex or magnocellular nucleus of the medial geniculate body (MGmc) (Liedgren et al., 1976; Mergner et al., 1981). The ASSS and PCD have been identified as receiving vestibular inputs with contralateral dominance in cats using the evoked potential technique (Landgren et al., 1967; Sans et al., 1970; Ödkvist et al., 1975). The ASSS also receives inputs from muscle spindles and the PCD receives inputs from joint receptors (Landgren et al., 1967; Sans et al., 1970; Ödkvist et al., 1975). Thus, the common feature of these cortical areas is the convergence of vestibular inputs and signals from deep somatic receptors (Landgren et al., 1967; Sans et al., 1970; Ödkvist et al., 1975; Liedgren et al., 1976; Mergner et al., 1981).

We have reported that axons of posterior canal (PC)-activated secondary excitatory ves-

tibular neurons project to the oculomotor nucleus, and give off axon collaterals to the thalamus, particularly to the ventrobasal complex in cats (Matsuo et al., 1994). However, the physiological feature of the connection between the PC neurons and the thalamus has been practically unknown. That is, it is uncertain whether axons of the PC neurons make excitatory synapses with the thalamic neurons or are only passing fibers in the thalami. Furthermore, no firing pattern or precise location of the thalamic neurons mediating the vestibulo-cortical pathways could be found. In the present study, we investigated the locations of the thalamic neurons which receive inputs from the vestibular apparatus, particularly from the posterior semicircular canals, and further examined the projections of the thalamic neurons to the ASSS or PCD using anesthetized cats. We hypothesized that the thalamic neurons receiving input from PC neurons could be located in the ventrobasal complex and MGmc and could contribute to the vestibulocortical pathways by making monosynaptic or polysynaptic connections with neurons in the ASSS or PCD.

Abbreviations: ASSS, anterior suprasylvian sulcus; MGmc, magnocellular nucleus of the medial geniculate body; PC, posterior canal; PCD, postcruciate dimple

Materials and Methods

Experiments were performed on 14 adult cats. All procedures used in this study were reviewed and fulfilled the requirements given in "Guidelines for animal experimentation" of the Faculty of Medicine, Tottori University and conformed

to standards set forth by the National Institute of Health's "Guide for the care and use of animals." The animals were anesthetized with sodium pentobarbital or alpha-chloralose (an initial dose of 40 mg/kg, with a subsequent dose of 5 mg/kg/h intraperitoneally). They were mounted in a stereotaxic apparatus which could be sinusoidally rotated in pitch. Ag-AgCl elec-

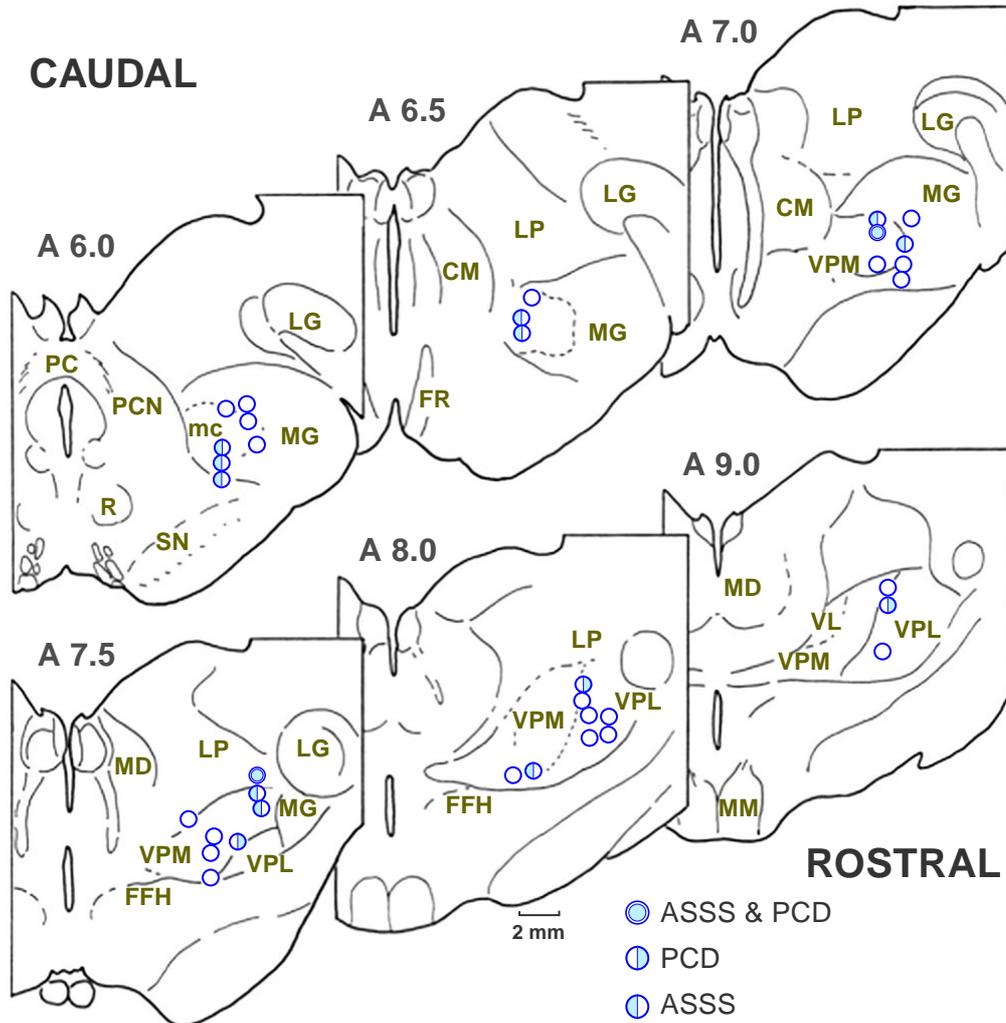


Fig. 1. Frontal plane projection of the brain stem showing distribution of 36 thalamic neurons. Drawings are of cross-sections of the mesodiencephalon on A 6.0, A 6.5, A 7.0, A 7.5, A 8.0 and A 9.0 Horsely-Clarke planes. Each symbol indicates the sites where different projections of thalamic neurons were recorded. The effective sites for antidromic activation of thalamic neurons are indicated by symbols shown at the lower right of the schema. ASSS, anterior suprasylvian sulcus; CG, central gray; CM, centromedian nucleus; FFH, Forel's field H; FR, fasciculus retroflexus; LG, lateral geniculate nucleus; LP, lateral posterior nucleus; mc, magnocellular nucleus; MD, medial dorsal nucleus; MG, medial geniculate body; MM, medial mamillary nucleus; PC, posterior commissure; PCD, postcruciate dimple; PCN, posterior commissure nucleus; R, red nucleus; SN, substantia nigra; VL, ventral lateral nucleus; VPL, ventral posterolateral nucleus; VPM, ventral posteromedial nucleus.

trodes were placed on the left round and oval windows to stimulate the vestibular nerve (Shimazu and Precht, 1965). Then, 2 arrays of 8 concentric stimulating electrodes were positioned in the gray matter of the right PCD and the ASSS to test projections of single thalamic neurons to these regions. The electrode tips were 1.0–1.5 mm deep from the cortical surface. Procedures for implantation were described in our previous paper (Matsuo et al., 1994, 1995). Stimulus intensity was confined to less than 200 μ A. A glass micropipette filled with 2 mol/L NaCl solution, saturated with fast green FCF, was employed for recording extracellular spikes of PC-activated thalamic neurons on the right side. Recorded extracellular spikes were considered to originate from the soma if they fulfilled the following criteria: i) the spike is biphasic negative-positive or predominantly negative with a clearly visible initial segment-soma dendrite break and ii) the spike can be detected sequentially in spite of any movement of the recording electrode over 100 μ m. At the end of each experiment, the recording and stimulating sites were histologically verified in Nissl-stained serial sections of the brain for later reconstruction (Thomas and Wilson, 1965).

Results

We examined the cell locations of PC-activated thalamic neurons and their projections to the ASSS and PCD. Thirty-six neurons were identified as posterior-canal activated thalamic neurons when they were activated by the stimulation of the contralateral vestibular nerve and by nose-up head rotation in the dark. The identified neurons increased the firing frequency of the spikes during nose-up pitch rotation. When the contralateral vestibular nerve was stimulated, the neurons were synaptically activated. These latencies ranged from 2.1 to 11.5 ms. Out of the 36 neurons, 8 neurons were antidromically activated only from the ASSS, 3 neurons from the PCD, and 2 neurons from both the ASSS and PCD. The effective sites for antidromic activation of the thalamic neurons were mainly in the lateral part of the PCD and

the anterior part of the ASSS. The remaining 23 neurons did not induce any antidromic spikes following stimulation of the ASSS and PCD.

Histological examination showed that most of them were located in the ventral posterolateral and -medial nuclei and the lateral posterior nucleus. A smaller number of such neurons were also found in the magnocellular nucleus of the medial geniculate body (MGmc), as shown in Fig. 1.

Discussion

Cortical areas which receive input from the vestibular nerve are located in the PCD and ASSS in cats (Landgren et al., 1967; Sans et al., 1970; Ödkvist et al., 1975; Liedgren et al., 1976; Mergner et al., 1981). These areas receive convergent inputs from proprioceptive, somatosensory and vestibular afferents via thalamic neurons, and were thereby postulated to contribute to conscious spatial orientation (Sans et al., 1970; Schwarz and Fredrikson, 1971). Thalamo-cortical neurons were studied by retrograde transport of horseradish peroxidase injected into the PCD and ASSS in cats (Liedgren et al., 1976; Blum et al., 1979; Mergner et al., 1981). The main location of these neurons are reported to be in the ventral posterolateral nucleus, posterior margin of the ventrobasal complex, and MGmc. Similarly, as we observed in the present study, thalamic neurons which were activated by nose-up head rotation and by contralateral vestibular nerve stimulation were recorded mainly in the ventral posterolateral and -medial nuclei, and some neurons were located in the MGmc, suggesting that the neurons in these areas receive input from the posterior semicircular canal. Thirteen of these thalamic neurons were antidromically activated from the ASSS and/or PCD of the cortex. Latencies of spikes of the identified thalamic neurons followed by contralateral vestibular nerve stimulation ranged from 2.1 ms to 11.5 ms. The shortest latencies of less than 2.9 ms may be regarded as within the disynaptic range, since latencies of monosynaptic activation of vestibular nucleus neurons followed by ves-

tibular nerve stimulation are less than 1.4 ms (Uchino et al., 1982) and the latency of the negative averaged potentials in the ventral posterolateral nucleus ranged from 0.8 ms to 1.5 ms, as shown in the previous studies (Matsuo et al., 1994,1995). Thus, the thalamic neurons which were activated from the contralateral vestibular nerve with the shortest latencies probably received direct inputs from the PC-related secondary vestibular nucleus neurons. These results suggest that the thalamic neurons projected to the ASSS and/or PCD in this study contribute, at least in part, to the primary vestibulo-cortical pathways.

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