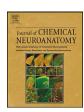
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Medioventral part of the posterior thalamus in the mouse

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ABSTRACT

The posterior thalamus (Po) consists of heterogeneous groups of cells, which have not been clearly defined. In the present study, we focused on a part of the Po in the mouse brain, which is located caudally to the ventral posterior nucleus and rostromedially to the medial geniculate nucleus and shows distinct calretinin immunoreactivity. While we found the region had a considerable unity on the cytoarchitectural and histochemical grounds, it did not correspond to any particular nucleus but partially involved three structures in a widely used brain atlas (Franklin and Paxinos, 2008). Therefore, we tentatively designated the region as the medioventral part of the posterior thalamus (PoMV) and examined its anatomical features with immunohistochemistry and retrograde tract-tracing. The PoMV was appreciated as a reticular structure with prominent calretinin immunoreactivity, especially in horizontal sections, and displayed apparent differences in the cytoarchitecture from its surrounding regions. The PoMV had two divisions: the dorsal division (PoMVd), which contained parvalbuminimmunoreactive fibers, and the ventral division (PoMVv), which lacked these fibers. The tract-tracing studies showed that the somata retrogradely labeled from the injections in the insular cortex and some of the extended amygdalar regions were fairly concentrated within the PoMV, especially in the PoMVd. On the other hand, the labeling from the medial hypothalamus injections was found predominantly within the PoMVv. These findings indicate that the PoMV can be regarded as a distinct structure within the Po, and it may play a role in the emotional aspect of somatosensory processing.

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1. Introduction

In the posterior thalamus (Po), neuronal inputs from different sensory systems intermingle in a complex manner (Moore and Goldberg, 1963; Jones and Powell, 1971; Rockel et al., 1972; LeDoux et al., 1987), and efferents to the association cortex and the

striatum arise from this region (Heath and Jones, 1971). These connections implicate the Po in sensory information processing, although its functional significance remains elusive. This is in contrast to the primary relay nuclei surrounding the Po, namely the ventral posterior nucleus (which consists of medial and lateral parts), the dorsal lateral geniculate nucleus, and the ventral

Abbreviations: AH, anterior hypothalamic area; APT, anterior pretectal nucleus; APTD/V, anterior pretectal nucleus dorsal/ventral part; bic, brachium of the inferior colliculus; bsc, brachium of the superior colliculus; CA3, field CA3 of the hippocampus; CeA, central amygdaloid nucleus; cp, cerebral peduncle; CPu, caudate putamen (striatum); DLG, dorsal lateral geniculate nucleus; EA, extended amygdala (sublenticular part); Ect/TeA, ectorhinal and temporal association cortex; eml, external medullary lamina; Eth, ethmoid thalamic nucleus; F, nucleus of fields of Forel; fr, fasciculus retroflexus; IGL, intergeniculate leaflet; IMA, intermedullary thalamic area; INS, insular cortex (granular and dysgranular); IPAC, interstitial nucleus of the posterior limb of the anterior commisure; LaA, lateral amygdaloid nucleus; LP, lateral posterior thalamic nucleus; LPLC/LR/ MC, lateral posterior thalamic nucleus laterocaudal/laterorostral/mediocaudal part; MG, medial geniculate nucleus; MGD/M/V, medial geniculate nucleus dorsal/medial/ ventral part; ml, medial lemniscus; MPO, medial preoptic nucleus; mRt, mesencephalic reticular formation; MT, medial terminal nucleus; mtg, mammillotegmental tract; opt, optic tract; p1Rt, p1 reticular formation; PaR, pararubral nucleus; PBP, parabrachial pigmented nucleus of the VTA; PF, parafascicular thalamic nucleus; PGMC, pregeniculate nucleus magnocellular part; PIL, posterior intralaminar thalamic nucleus; PLi, posterior limitans thalamic nucleus; Po, posterior thalamus (posterior thalamic nuclear group); PoM, posterior thalamus medial part; PoMVd/v, posterior thalamus medioventral part dorsal/ventral division; PoT, posterior thalamic nuclear group triangular part (posterior triangular thalamic nucleus); PP, peripeduncular nucleus; PR, prerubral field; REth, retroethmoid nucleus; RMC, red nucleus magnocellular part; RPC, red nucleus parvicellular part; scp, superior cerebellar peduncle; SG, suprageniculate thalamic nucleus; SNC/CD/L/R, substantia nigra compact/dorsal tier of compact/ lateral/reticular part; SPF, subparafascicular thalamic nucleus; SPFPC, subparafascicular thalamic nucleus parvicellular part; str, superior thalamic radiation; SubB, subbrachial nucleus; SubG, subgeniculate nucleus of prethalamus (ventrolateral nucleus); VLi, ventral linear nucleus of the thalamus; VMpo, ventromedial thalamic nucleus posterior part; VP, ventral posterior thalamic nucleus; VPL/M, ventral posterolateral/posteromedial thalamic nucleus; VPPC, ventral posterior thalamic nucleus parvicellular part; VTA, ventral tegmental area; ZI, zona incerta; ZIC/D/V, zona incerta caudal/dorsal/ventral part.

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division of the medial geniculate nucleus, all of which receive unimodal sensory inputs and transmit highly resolved information to the primary sensory cortical areas.

The Po has traditionally been subdivided into two (or sometimes into three) divisions based on the distribution of sensory afferents in the cat (Moore and Goldberg, 1963; Jones and Powell, 1971). Accordingly, the area within the Po that receives spinothalamic and trigeminothalamic projections has been named the medial division of the Po (PoM: Jones and Powell, 1971: Jones and Burton, 1974). In the rodent brain, the term "PoM" is frequently used to indicate the region located dorsomedially to the ventral posterior nucleus, although its precise extent has not been determined. Recent investigations in this region of the rat Po (Diamond et al., 1992; Lavelée et al., 2005; Trageser and Keller, 2004; Trageser et al., 2006; Urbain and Deschenês, 2007) have revealed that it has the topographic representation of the body (Diamond et al., 1992), and the neuronal responses in the PoM to vibrissal movements are gated by the inhibitory inputs from the zona incerta, making its neuronal activity dependent on behavioral state (Trageser et al., 2006) or contingent to motion (Urbain and Deschenês, 2007).

On the other hand, in the rodent, the spinothalamic and trigeminothalamic tracts project to an additional target region in the Po, which is located caudally to the ventral posterior nucleus and rostromedially to the medial geniculate nucleus (Lund and Webster, 1967; Gauriau and Bernard, 2004a; Zhang and Giesler, 2005). Some neurons in this region have been shown to receive nociceptive and other somatosensory information and send efferents to the secondary somatosensory cortex, insular cortex, striatum and amygdala (Gauriau and Bernard, 2004b). This region is called the posterior triangular thalamic nucleus (the triangular part of the posterior thalamic nuclear group, PoT; Gauriau and Bernard, 2004a; Zhang and Giesler, 2005; Franklin and Paxinos, 2008). However, to our knowledge, the term PoT has not been applied to the cat or primate thalamus, while most thalamic nuclei in rodents have been designated by terms commonly used in mammals. Such exceptional naming may reflect the scarcity of studies that carefully compare this region among different species. Furthermore, the boundary surrounding the PoT appears ambiguous even in rodents, which may make such investigations difficult, raising the need for some explicit landmark of this region.

In the present study, we investigated the region around the PoT, i.e., the area located caudally to the ventral posterior nucleus, dorsally to the medial lemniscus and rostromedially to the medial geniculate nucleus in mice. In modern neuroscience, more and

more researches use transgenic mice, and thus the details on the wild type mouse brains as the standard are essential to the appropriate interpretation of possible changes observed in such genetically modified mouse brains. We thus used mice in the present study.

By examining the cytoarchitectural and histochemical properties of the mouse Po, we found that a calcium-binding protein, calretinin (CR), is distributed in a restricted region within this area. Although this CR-immunoreactive (ir) area shows a consistent cytoarchitectural feature, this area does not correspond to any particular nucleus. Instead, this region partly involves three nuclei characterized in a widely used brain atlas (Franklin and Paxinos, 2008): the retroethmoid nucleus, the posterior intralaminar nucleus and the PoT. Thus, we tentatively named this CR-ir region the medioventral part of the Po (PoMV), and examined it in detail using immunohistochemistry and retrograde tract-tracing techniques to reveal whether this "PoMV" has any particular neuroanatomical features distinct from its surroundings. The preliminary results of this study have already been reported in abstract form (Motomura and Kosaka, 2007).

2. Materials and methods

All experiments were carried out in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals (NIH Publications No. 80-23, 1996) and the institutional guidance for animal welfare (the Guidelines for Animal Experiment of the Graduate School of Medical Sciences, Kyushu University). All efforts were made to minimize animal suffering and to reduce the number of animals used.

2.1. Animals

Nineteen adult male C57BL/6J mice (22–25 g body weight, 8–11 weeks old and pathogen free; Kyudo Co., Kumamoto, Japan) were used for the immunocytochemistry (9 mice) and the retrograde tract-tracing analyses (10 mice).

2.2. Fluorescent immunohistochemistry

Mice were deeply anesthetized with sodium pentobarbital (100 mg/kg body weight) and transcardially perfused with phosphate-buffered saline (PBS, pH 7.4) followed by a mixture of 4% paraformaldehyde (PFA), 0.1% glutaraldehyde, and 0.2% picric acid in 0.1 M phosphate buffer (PB, pH 7.4). The brains were left in situ for 1 h at room temperature and then removed from the skull. After 24–48 h of postfixation in 4% PFA, the brains were cut coronally into 40-µm-thick serial sections on a vibrating microtome (Leica VT 1000S; Leica Microsystems, Germany). We examined the posterior thalamic region between the level of the posterior commissure and the caudal end of the MG, which approximately corresponds to –2.30 to –3.80 mm posterior from bregma in the atlas of Franklin and Paxinos (2008). Approximately 36 sections from each animal were obtained and grouped into three equidistant series, each of which comprised 12 sections. The sections were incubated for 1 h in 1% BSA in PBS containing 0.3% Triton X-100 and 0.05%

 Table 1

 List of the combinations of primary antibodies, biotin-conjugated or fluorochrome-conjugated secondary antibodies and fluorochrome-conjugated streptavidin used in this study.

Primary antibodies	Biotinylated secondary antibody	Dilution	Fluorochrome conjugated secondary antibody or streptavidin	Dilution	Figures in this paper
Triple labeling for NeuN, CB and CR					
NeuN			FITC-conjugated donkey anti-mouse IgG andibody	1:250	Figs. 2 and 3
CB			Cy5-conjugated donkey anti-rabbit IgG andibody	1:250	
CR			RR-conjugated donkey anti-goat IgG antibody	1:250	
Triple labeling for PV, CB and CR					
PV			FITC-conjugated donkey anti-mouse IgG andibody	1:250	Fig. 4
CB	Biotinylated donkey anti-rabbit IgG antibody	1:200	PB-conjugated streptavidin	1:100	-
CR			RR-conjugated donkey anti-goat IgG antibody	1:250	
Double labeling for FG and CR					
FG	Biotinylated donkey anti-rabbit IgG antibody	1:200	PB-conjugated streptavidin	1:100	Fig. 11
CR			RR-conjugated donkey anti-goat IgG antibody	1:250	

All are obtained from Jackson Immunoresearch Laboratories (West Grove, PA, USA), except for the PB-conjugated streptavidin which was obtained from Molecular Probes (Invitrogen, Carlsbad, CA, USA). FITC, fluorescein isothiocyanate; RR, rhodamine red-X; Cy5, indodicarbocyanine; PB, pacific blue.

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