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Distribution of histaminergic neuronal cluster in the rat and mouse hypothalamus

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ABSTRACT

Histidine decarboxylase (HDC) catalyzes the biosynthesis of histamine from l-histidine and is expressed throughout the mammalian nervous system by histaminergic neurons. Histaminergic neurons arise in the posterior mesencephalon during the early embryonic period and gradually develop into two histaminergic substreams around the lateral area of the posterior hypothalamus and the more anterior peri-cerebral aqueduct area before finally forming an adult-like pattern comprising five neuronal clusters, E1, E2, E3, E4, and E5, at the postnatal stage. This distribution of histaminergic neuronal clusters in the rat hypothalamus appears to be a consequence of neuronal development and reflects the functional differentiation within each neuronal cluster. However, the close linkage between the locations of histaminergic neuronal clusters and their physiological functions has yet to be fully elucidated because of the sparse information regarding the location and orientation of each histaminergic neuronal clusters in the hypothalamus of rats and mice. To clarify the distribution of the five-histaminergic neuronal clusters more clearly, we performed an immunohistochemical study using the anti-HDC antibody on serial sections of the rat hypothalamus according to the brain maps of rat and mouse. Our results confirmed that the HDC-immunoreactive (HDCi) neuronal clusters in the hypothalamus of rats and mice are observed in the ventrolateral part of the most posterior hypothalamus (E1), ventrolateral part of the posterior hypothalamus (E2), ventromedial part from the medial to the posterior hypothalamus (E3), periventricular part from the anterior to the medial hypothalamus (E4), and diffusely extended part of the more dorsal and almost entire hypothalamus (E5). The stereological estimation of the total number of HDCi neurons of each clusters revealed the larger amount of the rat than the mouse. The characterization of histaminergic neuronal clusters in the hypothalamus of rats and mice may provide useful information for further investigations.
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Abbreviations: 3V, 3rd ventricle; Arc, arcuate hypothalamic nucleus; ArcD, arcuate hypothalamic nucleus, dorsal part; ArcL, arcuate hypothalamic nucleus, lateral part; ArcM, arcuate hypothalamic nucleus, medial part; ArcMP, arcuate hypothalamic nucleus, medial posterior part; ArcLP, arcuate hypothalamic nucleus, lateroposterior part; DM, dorsomedial hypothalamic nucleus; DMC, dorsomedial hypothalamic nucleus, compact part; DMD, dorsomedial hypothalamic nucleus, dorsal part; DMV, dorsomedial hypothalamic nucleus, ventral part; DTM, dorsal tuberomammillary nucleus; f, fornix; fr, fasciculus retroflexus; LH, lateral hypothalamic area; MRe, mammillary recess of the 3rd ventricle; mp, mammillary peduncle; mt, mammillothalamic tract; PBP, parabrachial pigmented nucleus of the VTA; Pe, periventricular hypothalamic nucleus; PH, posterior hypothalamic nucleus; PHA, posterior hypothalamic area; PLH, peduncular part of the lateral hypothalamus; pm, principal mammillary tract; PMD, premammillary nucleus, dorsal part; PMV, premammillary nucleus, ventral part; SNCD, dorsal tier of the compact part of substantia nigra; SNR, reticular part of substantia nigra; Spa, subparaventricular zone of the hypothalamus; TuLH, tuberal region of lateral hypothalamus; VTA, ventral tegmental area; VTAR, rostral part of ventral tegmental area; VTM, ventral tuberomammillary nucleus; ZI, zona incerta; ZID, zona incerta, dorsal part; ZIV, zona incerta, ventral part.

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1. Introduction

Neuronal histamine in the mammalian hypothalamus is synthesized from l-histidine by histidine decarboxylase (HDC) in the histaminergic neurons (Haas et al., 2008; Panula et al., 2014) consists of HDC-containing nerve cells with multitudinous varicose dendrites and axons, and is involved in various cerebral functions such as the circadian rhythms, wakefulness, feeding behavior, thermogenesis, neuroendocrine regulation, mood, memory, learning, and cognitive performance (Dere et al., 2003; Haas et al., 2008; Parmentier et al., 2002; Provensi et al., 2014; Sakata et al., 2003; Wada et al., 1991; Yoshimatsu et al., 2002; Yu et al., 2014). The development of histaminergic neurons is characterized as follows; histamine-immunoreactive neurons are detected first at the border of the mesencephalon and the metencephalon at embryonic day 13; on both sides of the midline on the ventral side of the cerebral aqueduct; and on the caudal side of the pons at embryonic day 16, and they were observed in the caudal, tuberal, and postmammillary caudal nuclei in the posterior hypothalamus at embryonic day 20, while the histaminergic neurons in the mesencephalon and myelencephalon completely disappear by this embryonic day (Auvinen and Panula, 1988; Vanhala et al., 1994). On the first postnatal day, histamine-immunoreactive neurons appear in all three magnocellular subnuclei, namely the caudal, tuberal, and postmammillary caudal magnocellular nuclei and around the ventromedial and dorsomedial hypothalamic nuclei. The distribution of histamine-immunoreactive neurons in these nuclei attains an adult-like appearance at postnatal day 20 (Auvinen and Panula, 1988). In particular, histamine-immunoreactive neurons developed from the border area between mesencephalon and metencephalon, showed two streams of the lateral area of the posterior hypothalamus and peri-cerebral aqueduct area (Panula et al., 1988). These two substreams of histamine-immunoreactive neurons appeared to develop into several subclusters comprising the histaminergic nervous system of adult vertebrates (Haas et al., 2008; Molina-Hernandez et al., 2012). The adult rat exhibits five subgroups of HDC-immunoreactive neuronal clusters in the hypothalamus, namely E1, E2, and E3 in the posterior hypothalamic area; E4 in the ventromedial hypothalamic area; and E5 in more dorsal part of the hypothalamus in a diffusely scattered pattern (Inagaki et al., 1990). In the rodent hypothalamus, histaminergic neuronal clusters are grouped in five clusters, E1–E5, each of which sends overlapping projections throughout the neuroaxis with a low level of topographical organization, and are bridged by scattered neurons (Ericson et al., 1987; Inagaki et al., 1990). The former three subclusters E1–E3 appear to develop from the border area between mesencephalon and metencephalon, and the latter two subclusters E4–E5 develop from the peri-cerebral aqueduct area of the diencephalon (Auvinen and Panula, 1988; Haas et al., 2008; Molina-Hernandez et al., 2012; Vanhala et al., 1994; Watanabe et al., 1984). The manner of the histaminergic neuron development in rats and mice shares a high degree of similarity despite a relatively short developmental period in mice (Nissinen et al., 1995; Nissinen and Panula, 1995). Understanding this distribution of histaminergic clustering in the hypothalamus is likely to be important for further physiological studies of the histaminergic nervous system of mammals (Blandina et al., 2012). However, there is an urgent need to compare the hypothalamic distribution of the five-histaminergic neuronal clusters in rats and mice because of the scarcity of data with respect to precise depictions by common rodent brain maps. The intractable nature of hypothalamic histaminergic neuronal cluster nomenclature has further complicated histaminergic research and hindered our ability to contextualize research findings, particularly from studies involving mice (Inagaki et al., 1990; Karlstedt et al., 2001; Michelsen and Panula, 2002; Miklos and Kovacs, 2003; Puelles et al., 2012; Sunkin et al., 2013; Umehara et al., 2010, 2011, 2012).

In the present study, we conducted an immunohistochemical investigation to examine the hypothalamic orientations of five histaminergic neuronal clusters of rats and mice in an aim to contribute to further research in the relationship between physiological regulation and the distribution of histaminergic neuronal clusters in the mammalian hypothalamus.

2. Materials and methods

2.1. Animals

In this study, 10 male Wistar rats and 10 male 57Bl/6 mice with initial weights of approximately 290 g and 26–30 g about 10 weeks according to previous reports (Table 1), respectively, were used. Four animals were housed per cage in a soundproof room under a 12-h/12-h light/dark cycle (lights on at 07:00) and fed a standard laboratory diet and tap water ad libitum. All procedures were performed in accordance with the Oita University Guide for the Care and Use of Laboratory Animals, which is based on the National Institutes of Health guidelines, and were approved by the Animal Care Committee of Oita University.

2.2. Chemicals

For light microscopic immunohistochemistry, a rabbit polyclonal antibody to full length histidine decarboxylase without cross-reactivity to DOPA decarboxylase of rat and mouse (HDC; 1/2000, PROGEN Inc., Heidelberg, Germany) (Dartsch et al., 1999), a rabbit IgG (Santa Cruz Biotechnology, Inc., Dallas, USA), the EnVision System (antirabbit IgG-HRP conjugated, Dako Inc., Copenhagen, Denmark), bovine serum albumin (BSA; Sigma Aldrich Chem., St. Louis, USA), and 3,3′-diaminobenzidine 4HCl (DAB; Wako Pure Chemical Industries, Ltd, Osaka, Japan) were used.

2.3. Experimental procedures

All animals were anesthetized at 10:00 with pentobarbital sodium (150 mg/kg i.p.) and perfused through the left ventricle with ice-cold saline followed by 4% paraformaldehyde in 0.05 M Cacodylate buffer (pH 7.4). Brains were removed, placed in fixative overnight, and then dehydrated with ethyl alcohol series before embedding in paraffin. Frontal serial sections were cut at a thickness of 10 μm and fixed to MAS-coated glass slides (Matsunami Glass Ind. Ltd., Osaka, Japan). Sections

Table 1
Determination of histaminergic neuronal clusters of HDC-positive neurons.

Inagaki et al. (1990)	Ericson et al. (1987)	Köhler et al. (1985)	Staines et al. (1987)	Bleier et al. (1979)
Wistar, m	SD, m	SD, m	SD, m	HA, f
E1	TMVc	TMv	Ps	CMc
E2	TMVr	TMv	Ls	CMr
E3	TMMv	TMv	Vs	N.D.
E4	TMMd	TMdm	Ts	TM
E5	TMdiff	TMdif	Is	N.D.

The first row represents corresponding author in classification; the second row: rat name and gender; and the third to seventh row: subgroup names for each study. Wistar: represents Wistar rats; SD: Sprague–Dawley rats; HA: Höltzman albino rats; m: male, and f: female: TMVc and TMVr: caudal and rostral parts of ventral subgroup of the TM, respectively: TMMv and the TMMd; ventral and dorsal part of medial subgroup of TM, TMdiff: the diffuse part of the TM, respectively: TMv, TMdm, and TMdif: ventral, dorsomedial, and diffuse parts of the TM, respectively: Ps: posterior subdivision of postmammillary caudal magnocellular nucleus: Ls: the lateral subdivision of the caudal magnocellular nucleus: Vs: the ventral subdivision of a cell group at the base of the hypothalamus between the arcuate nucleus (Arc) and the premammillary nucleus, which continues caudally within the peripheral borders of the mammillary body: Ts: the subdivision of a tightly gathered cluster near to the third ventricle, rostrally, or the mammillary recess, caudally: Is: the interstitial subdivision of a field of dispersed cells found at anterior levels of the tuberomammillary nucleus: CMc: the caudal part of the caudal magnocellular nucleus: CMr: the rostral part of the caudal magnocellular nucleus: TM: the tuberal magnocellular nucleus: N.D.: not determined.

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