ORIGINAL PAPER

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Distribution of dopamine-immunoreactive neurons in the brain of the male native Thai chicken

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Abstract

Introduction. Dopamine (DA) is a neurotransmitter/neuromodulator found in both central and peripheral nervous systems. It plays several physiological functions in some mammalian and avian species. DA has been indicated to be associated with the neuroendocrine regulation of the reproductive cycle and maternal behaviors in the female native Thai chickens. Indeed, male birds express parental behaviors as well. To date, there are no data describing the functional aspects of the DAergic system in the male native Thai chickens. Thus, the objective of this study was to elucidate the localization of tyrosine hydroxylase (TH; a DA marker) neuronal groups in the brain of the roosters.

Material and methods. The distributions of TH immunoreactivity in the brain were detected utilizing the immunohistochemical technique.

Results. TH immunoreactivity was located throughout the brain and extensively in the diencephalon and mesencephalon. The highest density of TH-immunoreactive (-ir) neurons and fibers was found within the nucleus intramedialis (nI) and nucleus mamillaris lateralis (ML). The numbers of TH-ir neurons within the nucleus anterior medialis hypothalami (AM), nucleus paraventricularis magnocellularis (PVN), nI, and ML were then compared and revealed that the numbers of TH-ir neurons within the nI and ML were significantly higher than those of the AM and PVN.

Conclusions. These present findings suggest that the DAergic neurons within the nI and ML might play an important role in the reproductive activities of the native Thai roosters. Interestingly, the DAergic system in the nI might be involved in male reproductive activities and/or parental behaviors in this equatorial species. *(Folia Histochemica et Cytobiologica 2022, Vol. 60, No. 1, 1–12)*

Key words: birds; brain; dopamine; hypothalamus; male; thyroxine hydroxylase

Introduction

Dopamine (DA) is a neurotransmitter/neuromodulator found in both central and peripheral nervous systems in many vertebrate and invertebrate species [1–3]. It has several important physiological functions involved in a wide variety of behaviors and reproduction. In mammals, DA is well known to be involved in the onset and maintenance of maternal care and male sexual behaviors [4]. In birds, it has been well established that DA controls two major neuroendocrine systems that play a pivotal role in avian reproduction; the gonadotropin-releasing hormone/follicle-stimulating hormone-luteinizing hormone (GnRH/FSH-LH) and vasoactive intestinal peptide/prolactin (VIP/PRL) systems [5]. Numerous studies have reported that DA neurons are distributed within several regions of the avian brain, especially in the hypothalamus, and have been shown to be immunoreactive for VIP, the avian PRL releasing factor [6–7]. Activation of DA

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neurons is linked to the activation of GnRH-I and VIP neurons and subsequent secretion of LH and PRL [8]. To date, there are numerous reports regarding the physiological roles of DA and its receptors in birds such as food intake [9], food reward [10], cognitive performance [11], feather pecking [12], singing behavior [13–16], song learning [17], social activity [18], aggressive behavior [19], mate competition [20], courtship motivation [21], egg production [22], incubation [23], reproductive cycle [24], and male sexual behaviors [25]. More importantly, DA is involved in the regulation of the reproductive cycle and maternal behaviors (incubating and rearing behaviors) in the female native Thai chicken, a non-seasonally breeding species [26–29].

The anatomical distributions of DA neurons and fibers have been mapped in several avian species and there are distributed in several regions of the brain such as the area praeoptica (POA), nucleus preopticus medialis (POM), nucleus ventrolateralis thalami, suprachiasmatic nucleus, nucleus anterior medialis hypothalami (AM), regio lateralis hypothalami (LHy), nucleus paraventricularis magnocellularis (PVN), nucleus ventromedialis hypothalami, nucleus dorsomedialis hypothalami, nucleus intramedialis (nI), nucleus premamillaris (PMM), nucleus mamillaris medialis (MM), nucleus mamillaris lateralis (ML), area ventralis (AVT), nucleus tegmenti pedunculo-pontinus, pars compacta (substantia nigra; TPc), locus ceruleus (LoC), brachium conjunctivum ascendens (BCA), brachium conjunctivum descendens (BCD), cerebellum (Cb), lateral septum, pons, and medulla oblongata [6, 30–35]. DA fibers are extensively distributed within the external layer of the eminentia mediana (median eminence; ME) [30–32]. Similarly, in the female native Thai chickens, tyrosine hydroxylase (TH; a DA marker)-immunoreactive (-ir) neurons and fibers are extensively distributed throughout the brain, especially in the diencephalic and mesencephalic regions and changes in the numbers of TH-ir neurons within the nI are associated with the reproductive stages. The number of TH-ir neurons within the nI is lowest in the non-egg laying stage, then markedly increases in the egg-laying, reaches the highest density in incubating (INC) hens, and decreases in the rearing chicks (R) hens [26]. Disruption of incubation behavior by nest deprivation decreases the numbers of TH-ir neurons within the nI and ML [27]. In addition, the number of TH-ir neurons within the nI decreases in non-rearing hens (NR) when compared with that of R hens [28]. Recently, it has been reported that the presence of eggs or chicks is associated with the decreased numbers of TH-ir neurons within the nI and ML, and the increased numbers of mesotocin (MT)-ir neurons within the nucleus supraopticus; pars ventralis (SOv),

POM, and PVN during the transition from incubating to rearing behavior [29].

Native Thai chicken (*Gallus domesticus*), an equatorial, tropical, non-seasonally breeding species, has been domesticated without genetic selection. It expresses strong maternal behaviors which are inherited from the ancestor, the wild jungle fowl in Southeast Asia [36–39]. It is well documented that the neuroendocrine regulation of reproductive cycle and maternal behaviors are associated with GnRH, VIP, DA, PRL, MT, and neuropeptide Y in the female native Thai chickens [5, 29, 40–43]. Presently, the neuroendocrine regulation of reproductive behaviors has been extensively studied in female native Thai chickens. However, there are limited data regarding the neuroendocrine regulation of reproductive activities in males. It has been reported that changes in the numbers of VIP-ir neurons within the nucleus inferioris hypothalami (IH) and nucleus infundibuli hypothalami (IN) are observed across the reproductive stages and mirrored directly with circulating PRL and testosterone levels in the male native Thai chickens [44]. The distributions of MT-ir neurons and fibers have also been reported, suggesting that MT-ir neurons within the SOv and POM might be involved in the reproductive activities and/or parental behaviors in the native Thai roosters [45]. Interestingly, it has been documented that male birds exhibit parental behaviors such as nest building, brooding, protection, and feeding of the young in many species [5, 46]. To date, there has been no report regarding the physiological role(s) of the DAergic system in the male native Thai chicken. Thus, the objective of this study was to investigate the localization of the DA neuronal groups in the brain of the male native Thai chickens, enabling further studies of neuroendocrinology related to behavior. The findings of the distributions of TH-ir neurons and fibers might be related to the regulation of reproductive activities and/or paternal behaviors in the male native Thai chickens.

Materials and methods

Experimental animals. Male native Thai chickens, 12 months of age, were used. They were reared and housed together with mature females (1 male: 8 females) in floor pens equipped with basket nests under natural light (approximately 12 h of light and 12 h of darkness; 12L: 12D) with free access to feed and water (*ad libitum*). The animal protocols used adhered to the guidelines approved by the Suranaree University of Technology Animal Care and Use Committee.

Experimental design. To determine the distributions of TH-ir neurons and fibers in the brain of the male native

Thai chicken, 6 mature males (12 months of age) were used. The brains of the roosters were fixed by pressure perfusion with a freshly prepared 4% paraformaldehyde (Code No. 416780010, Lot No. A0331790, Acros Organics, Inc., New Jersey, USA) in 650 ml of 0.1 M phosphate-buffered saline (PBS; pH 7.4). Tissue sectioning was performed in the coronal plane at a thickness of 16 μm utilizing a cryostat and further processing by immunohistochemistry (IHC) technique according to a previously described method [28]. In this study, the primary and secondary antibodies used for detecting TH immunoreactivity were primary mouse monoclonal antibodies raised directly against TH (Catalog No. 22941, Lot No. 1602001, ImmunoStar, Inc., Hudson, WI, USA), TH antibody diluted 1:1000 with PBS (pH 7.4), containing 1% bovine serum albumin (Catalog No. 268130100, Lot No. A0324472, Acros Organics, Inc.) and 0.3% Triton-X 100 (Catalog No. 215680010, Acros Organics, Inc.) and Cy™3-conjugated AffiniPure donkey anti-mouse immunoglobulin G (Code No. 715-165-150, Lot No. 137771, Jackson ImmunoResearch Laboratories, Inc., West Grove, PA, USA) at 1:500 dilution with PBS, respectively. TH immunoreactivity using these antibodies has been previously described [26–28, 42].

Image analysis. Microscopic images of the brain sections were visualized under a fluorescence microscope (Nikon ECLIPSE 80i, Tokyo, Japan) fitted with a cooled digital color camera (Nikon DS-Fi1, Tokyo, Japan). The images were captured and stored by NIS-Elements Documentation software (Nikon, Tokyo, Japan). TH-ir neurons and fibers in each individual area of the brain were visualized and analyzed. The numbers of TH-ir neurons of six adjacent sections for each rooster (6 roosters per area) were counted manually to determine changes in the numbers of TH-ir neurons within the individual hypothalamic areas (AM, PVN, nI, and ML). To avoid double-counting neurons with cell bodies that appeared on two adjacent sections, sections were viewed under 400× magnification, and only ir neurons with detectable nuclei or showing the appropriate shape (round and smooth edged) were included in the analysis. The mean values were compared across the hypothalamic areas [47]. The mean values were then compared across the hypothalamic areas [28]. Atlas of the chick brain [48] and the chicken hypothalamus [49] were used for the identification of specific brain regions of TH immunoreactivity.

Statistical analysis. Significant differences among the numbers of TH-ir neurons within the AM, PVN, nI, and ML (mean ± SEM) were compared employing a one-way analysis of variance (ANOVA). Significant differences between each individual hypothalamic area were computed utilizing the Tukey's HSD test. $P < 0.05$ was considered statistically significant. All statistical tests were analyzed using SPSS for Windows software (version 17.0, SPSS Inc., Chicago, IL, USA).

Results

The results of this study revealed that TH-ir neurons and fibers were located throughout the brain of the native Thai rooster including the telencephalon, diencephalon, mesencephalon, and rhombencephalon. The distributions of TH-ir neurons and fibers were predominantly located within the diencephalon and mesencephalon. TH-ir fibers were extensively distributed in the diencephalon and very dense fibers were observed in the internal and external layers of the ME (Fig. 1).

The majority of TH-ir neurons and fibers were distributed in the diencephalon and mesencephalon. The densest TH-ir neurons and fibers were distributed in a discrete region lying close to the ventriculus tertius (third ventricle; V III) through the hypothalamus (Figs. 2, 3, and 4). The greatest density of TH-ir neurons and fibers was located within the nI (Fig. 2A) and ML (Fig. 2B) in the diencephalon. A modest density of TH-ir neurons and fibers was observed within the nucleus septalis lateralis (SL; Fig. 3A) and nucleus septalis medialis (SM; Fig. 3B) in the telencephalon. The distributions of TH-ir neurons and fibers were moderately within the AM (Fig. 3C), LHy (Fig. 3D), PVN (Fig. 3E), and organum paraventriculare (PVO; Fig. 3F) in the diencephalon. Scattered TH-ir neurons and fibers were also found within the AVT, adjacent to the nervus oculomotorius (Fig. 4A), TPc (Fig. 4B), LoC (Fig. 4C and D), BCA (Fig. 4D and E), and BCD (Fig. 4D and F) in the mesencephalon. Small numbers of TH-ir neurons and fibers were found within the tractus quintofrontalis (QF; Fig. 5A), tractus septomesencephalicus (TSM; Fig. 5B), nucleus preopticus periventricularis (POP; Fig. 5C), nucleus suprachiasmaticus, pars medialis (SCNm; Fig. 5D), tractus occipitomesencephalicus (OM; Fig. 5E), substantia grisea centralis (GCt; Fig. 5F), tractus infundibularis (IF; Fig. 5G), and PMM (Fig. 5H). Moreover, TH-ir neurons were also found lining the cortex layer of the Cb (Fig. 5I) and nucleus mesencephalicus nervi trigemini (nVm; Fig. 5J) in the rhombencephalon. The numbers of TH-ir neurons in four hypothalamic areas including the AM, PVN, nI, and ML were then compared (Fig. 6) and revealed that the numbers of TH-ir neurons were significantly higher ($P < 0.05$) within the nI (35.00 ± 3.75 cells) and ML (28.25 ± 1.56 cells) when compared with those of the AM (18.83 ± 2.05 cells) and PVN (18.33 ± 2.24 cells).
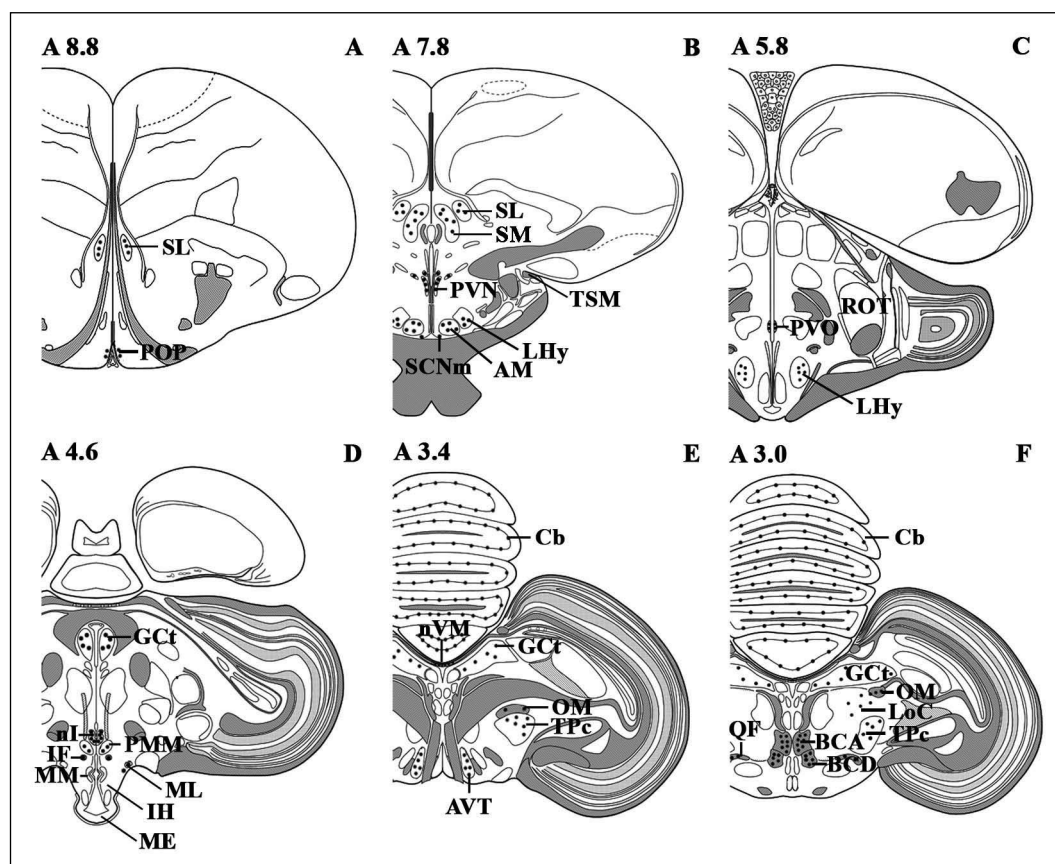
Figure 1. Schematic diagrams of coronal sections illustrate the areas of the chick brain showing the distributions of TH-ir neurons (black dots) and fibers throughout the brain of the male native Thai chicken. Coronal illustrations were redrawn from the stereotaxic atlas of the chick brain [47]. The following abbreviations are used in the figure legends: AM — nucleus anterior medialis hypothalami; AVT — area ventralis; BCA — brachium conjunctivum ascendens; BCD — brachium conjunctivum descendens; Cb — cerebellum; GCt — substantia grisea centrlis; IF — tractus infundibularis; IH — nucleus inferioris hypothalami; LHy — regio lateralis hypothalami (lateral hypothalamic area); LoC — locus ceruleus; ME — eminentia mediana (median eminence); ML — nucleus mamillaris lateralis; MM — nucleus mamillaris medialis; nI — nucleus intramedialis; nVm — nucleus mesencephalicus nervi trigemini; OM — tractus occipitomesencephalicus; PMM — nucleus premamillaris; POP — nucleus preopticus periventricularis; PVN — nucleus paraventricularis magnocellularis; PVO — organum paraventriculare; QF — tractus quintofrontalis; ROT — nucleus rotundus; SCNm — nucleus suprachiasmaticus, pars medialis; SL — nucleus septalis lateralis; SM — nucleus septalis medialis; TPc — nucleus tegmenti pedunculo-pontinus, pars compacta (substantia nigra); TSM — tractus septomesencephalicus.

Dense clusters of TH-ir fibers were innervated in the diencephalon. TH-ir fibers were extensively distributed within the nucleus rotundus (ROT; Fig. 7A), IH (Fig. 7B), MM (Fig. 7C), and very dense fibers were observed in the internal and external layers of ME (Fig. 7D).

Discussion

The results from the present study demonstrate the distributions of TH-ir neurons and its fibers in the brain of the male native Thai chickens. TH-ir neurons and fibers were extensively located throughout the brain. There was a dense accumulation of TH-ir fibers in the diencephalon. The distributions of TH-ir

neurons and fibers were predominantly located within the nI and ML. The numbers of TH-ir neurons within the nI and ML were significantly higher than those of the AM and PVN. The present findings suggest that the DAergic system within the nI and ML might be associated with the physiological function(s) of reproductive activities in the male native Thai chickens.

The anatomical distributions of TH-ir neurons and fibers in this present study are in accordance with previous studies in the avian brain including Japanese quails [31, 50–52], pigeons [30, 53–55], zebra finches [56–58], chickens [32, 59, 60], budgerigars [61], turkeys [6, 62], collared doves [34], canaries [63], and female native Thai chickens [26–29]. The present findings demonstrate that the majority of TH-ir neurons and
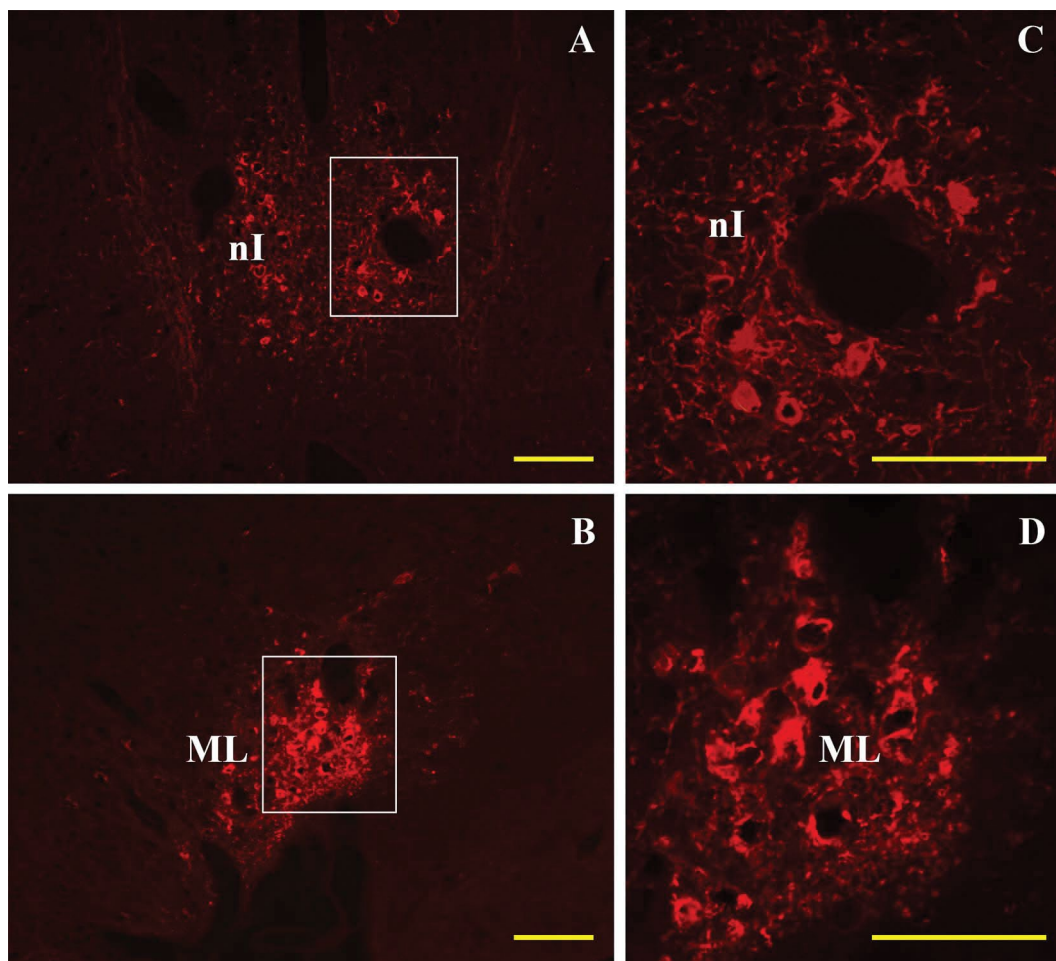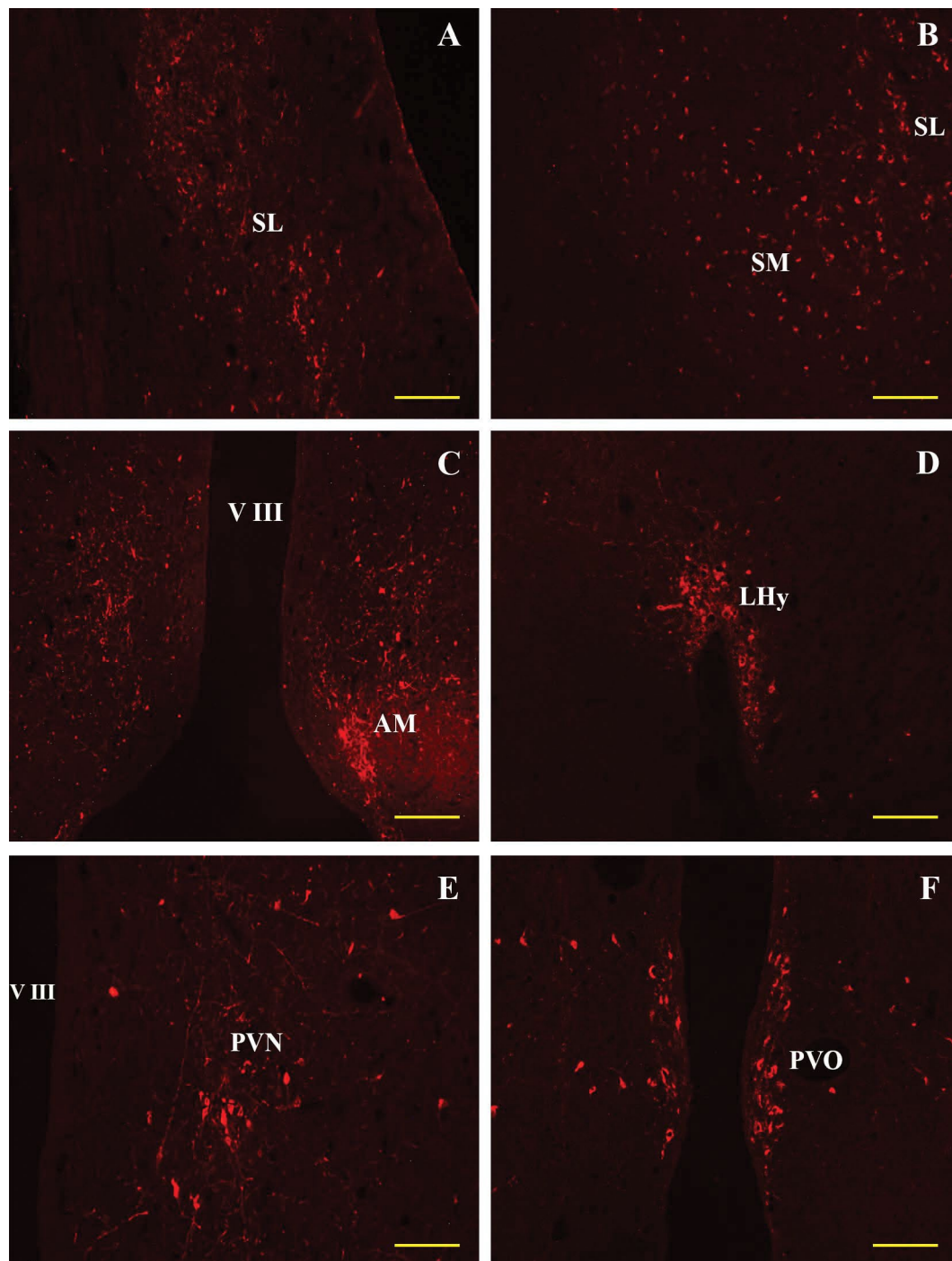
Figure 2. The distributions of TH-ir neurons and fibers within the (**A**) nI and (**B**) ML of the male native Thai chicken. Rectangles indicate areas from which higher magnification photomicrographs were taken in the (**C**) nI and (**D**) ML; A, B, scale bar = 100 μm; C, D, Scale bar = 50 μm. See Fig. 1 for a description of the abbreviations.

fibers was distributed in the diencephalon and are consistent with previous reports in Japanese quails [31, 52], pigeons [30, 53], zebra finches [57], and female native Thai chickens [26–29]. In addition, TH-ir neurons and fibers were widely located in the mesencephalon. These results are in good agreement with previous reports in the female native Thai chickens [26]. Thus, there are no differences in TH-ir neuron distribution between male and female brains.

The present results illustrate that the distributions of TH-ir neurons and fibers were located in a discrete region lying close to the V III from the level of POA. The distributions of TH-ir neurons and fibers were found abundance within the nI and ML. These results correspond with the previous reports in females [26–29]. Similarly, in other avian species, TH-ir neurons are extensively distributed along the V III in canaries and pigeons [30, 63]. Moreover, TH-ir neurons and fibers were moderately observed within the SL and SM in the telencephalon and found within

the AM, LHy, PVN, and PVO in the diencephalon as in females [26, 28]. Indeed, the distribution of TH-ir neurons is scattered within the SL, SM, AM, PVN, and PVO in Japanese quails, collared doves, and canaries [34, 52, 63]. Like in females, a modest density of TH-ir neurons and fibers was observed within the AVT, TPc, LoC, BCA, and BCD in the mesencephalon [26], and these distributions are also reported in chickens and pigeons [30, 32]. The major groups of TH-ir neurons and fibers are detected in the AVT (A10), TPc, and LoC in collared doves and canaries as well [34, 63]. In the present study, small numbers of TH-ir neurons and fibers were found within the QF, TSM, POP, SCNm, OM, GCt, IF, and PMM. In addition, TH-ir neurons were also found lining the cortex layer of the Cb and nVm as reported in the females by Sartsoongnoen et al. [26]. Similarly, the distributions of TH-ir neurons and fibers in this present study are in accordance with previous studies in Japanese quails [52], pigeons [30], chickens [32], and canaries [63].
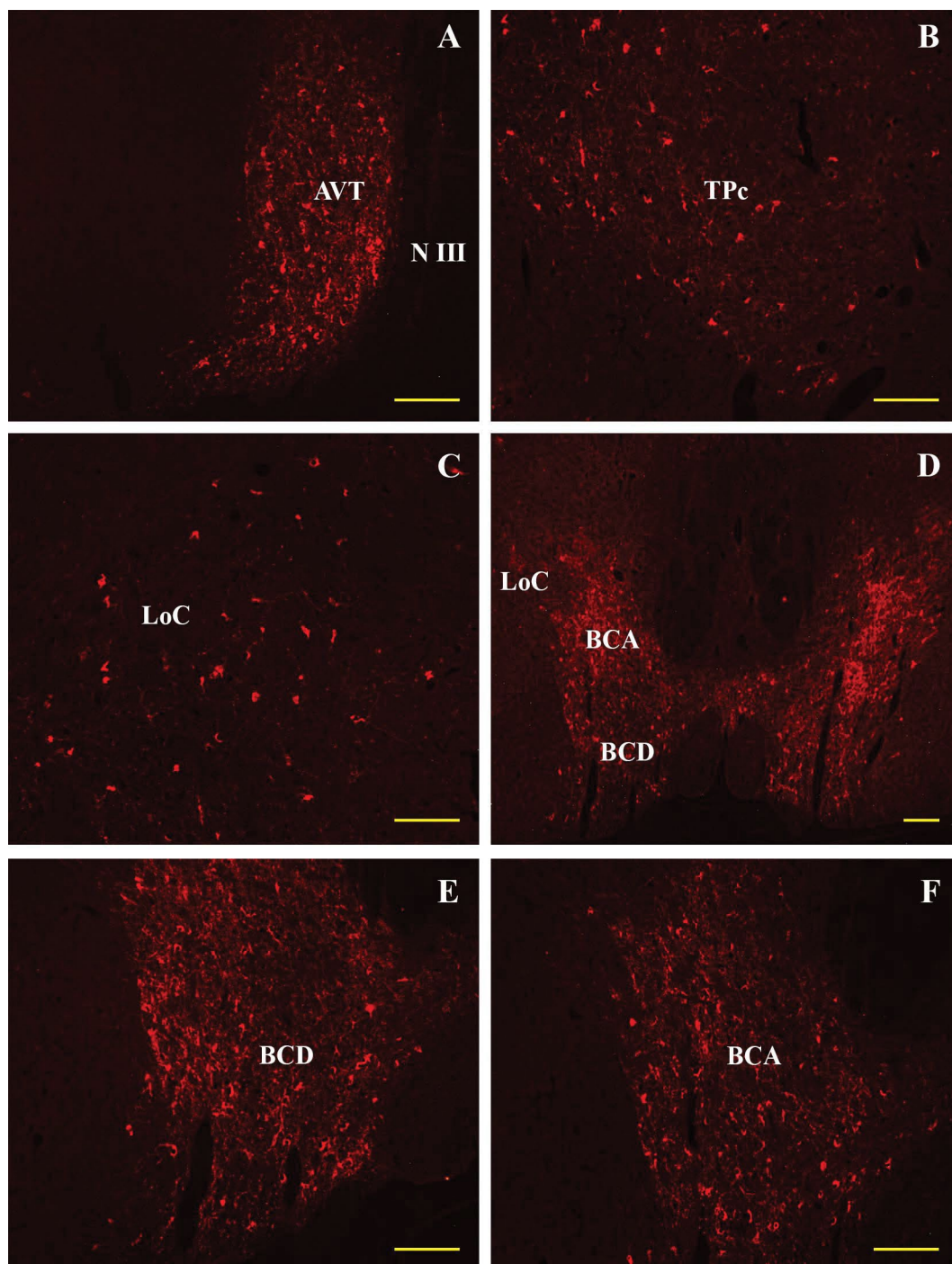
Figure 3. Photomicrographs illustrating the distributions of TH-ir neurons and fibers within the (**A**) SL, (**B**) SL, SM, (**C**) AM, (**D**) LHy, (**E**) PVN, and (**F**) PVO. V III, ventriculus tertius (third ventricle). Scale bar = 100 μm. See Fig. 1 for a description of the abbreviations.

The numbers of TH-ir neurons in four hypothalamic areas revealed that the highest accumulation of TH-ir neurons was observed within the nI and ML when compared with those of the AM and PVN. These results are consistent with previous findings in the female native Thai chickens [27–29]. In fe- males, previous studies report that the numbers of TH-ir neurons within the nI is associated with the reproductive stages, with the numbers of TH-ir neurons in this nucleus and plasma PRL levels increase significantly in the INC hens, and decrease in the R hens [26]. Disruption of incubation behavior by nest

Figure 4. Photomicrographs illustrating a modest density of TH-ir neurons and fibers within the (**A**) AVT, adjacent to the nervus oculomotorius (NIII), (**B**) TPc, (**C**) LoC, (**D**) LoC, BCA, BCD, (**E**) BCD, and (**F**) BCA. D, scale bar = 200 μm; A–C, E, F, Scale bar = 100 μm. See Fig. 1 for a description of the abbreviations.

deprivation causes the numbers of VIP-ir neurons within the IH-IN and TH-ir neurons within the nI and ML to decrease [27]. The numbers of TH-ir neurons within the nI is significantly higher in the R hens when compared with that of the NR hens, while plasma PRL levels are directly mirrored with changes in the number of TH-ir neurons in the nI, indicating that DA neurons in this nucleus and plasma PRL levels are enhanced to initiate and maintain the rearing behavior than for egg incubation [28]. Recently, the numbers of TH-ir neurons within the nI and ML and plasma PRL levels decrease in the replaced-eggs-with-chicks
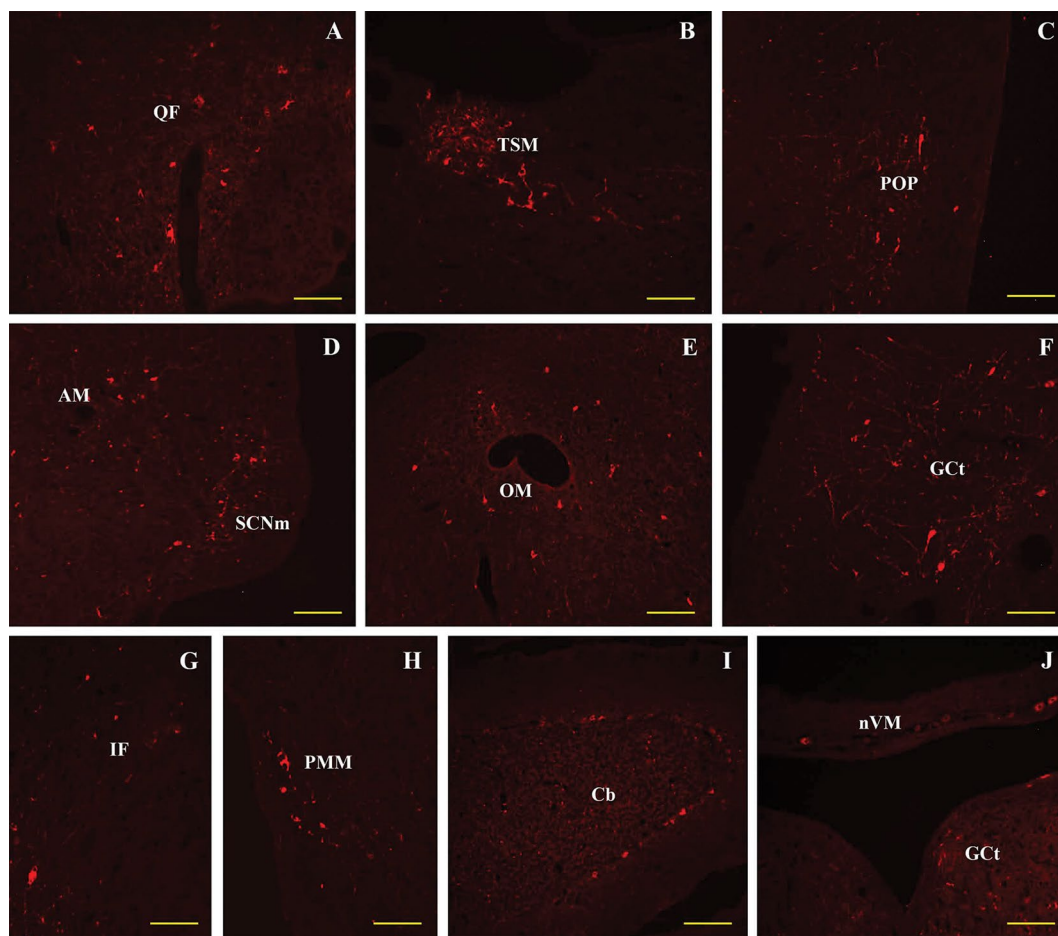
Figure 5. Photomicrographs of coronal sections showing small numbers of TH-ir neurons and fibers within the (**A**) QF, (**B**) TSM, (**C**) POP, (**D**) AM, SCNm, (**E**) OM, (**F**) GCt, (**G**) IF, (**H**) PMM, (**I**) Cb, and (**J**) nVM. Scale bar = 100 μm. See Fig. 1 for a description of the abbreviations.
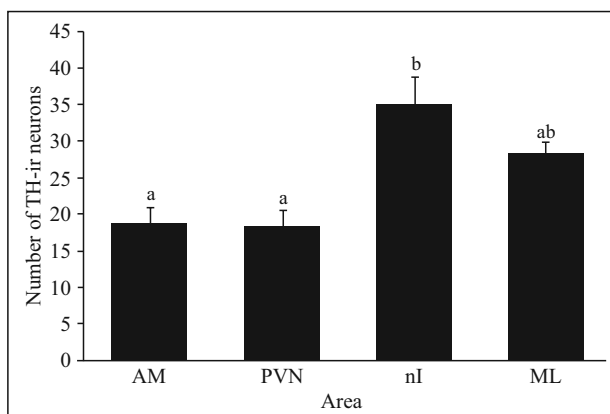
Figure 6. The number of TH-ir neurons in the individual hypothalamic areas (AM, PVN, nI, and ML) of the male native Thai chicken. Significant differences between values (mean ± SEM) in each hypothalamic area are indicated by different letters ($P < 0.05$).

(REC) hens when compared with that of the INC hens [29]. Moreover, it has been reported that the activation of the DA neurons in the ML is associated with the stimulation of GnRH-I and VIP neurons and the subsequent release of LH and PRL [8]. Taken together, these results demonstrate that the DAergic system within the nI and ML might play a regulatory//pivotal role in year-round reproductive activities and//or parental behaviors in this equatorial species.

In the present study, TH-ir fibers were found in abundance within the ROT, IH, MM, and very dense fibers were observed in the internal and external layers of the ME. These findings correspond with the previous results in the females [26, 28]. A previous study in chickens suggests that L-DOPA-ir and DA-ir neurons are distributed within the ROT, IH, MM, and ME [32]. The presence of DAergic fibers within the ME has been reported in the turkeys [6], pigeons [30], Japanese quails [31], and chickens [32]. It has been reported that DA inhibits GnRH release via presynaptic inputs at the ME in the chickens [59, 64], which has been suggested that these areas are involved in the regulation of PRL secretion. PRL
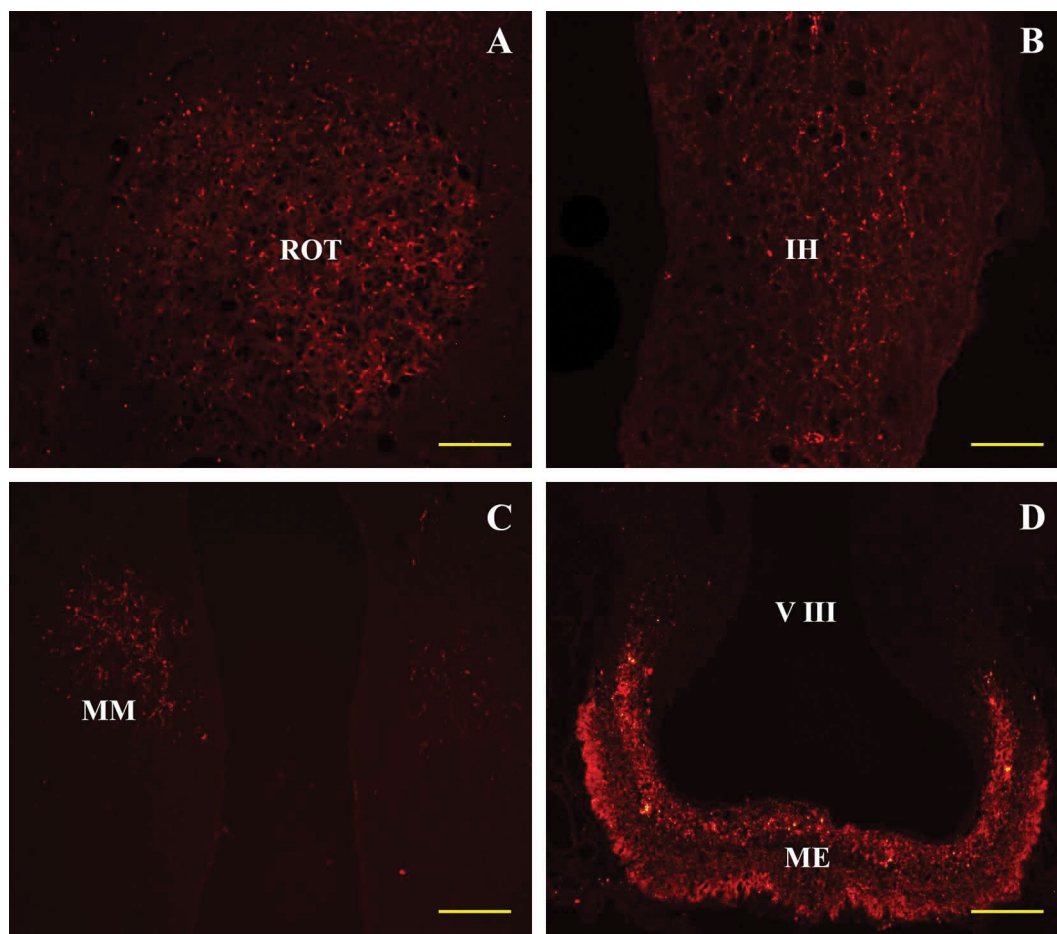
Figure 7. Photomicrographs of coronal sections showing TH-ir fibers within the (**A**) ROT, (**B**) IH, (**C**) MM, and (**D**) ME. V III, ventriculus tertius (third ventricle). Scale bar = 100 μm. See Fig. 1 for a description of the abbreviations.

secretion is regulated by the inhibitory control of the tuberoinfundibular DAergic neurons residing in the infundibular nuclear complex [2, 65], which release DA that acts directly upon the D_2 DA receptors located on pituitary lactotrophs [66]. Thus, it is possible that the discovery of a large population of DA immunoreactivity in the hypothalamus whose axons and fibers project to the ME may be involved with reproductive activities, probably paternal behaviors in the male native Thai roosters.

In conclusion, this study illustrates the distribution of TH immunoreactivity throughout the brain of male native Thai chickens. The greatest density of TH-ir neurons and fibers was found within the nI and ML, suggesting that the DAergic neurons in these nuclei may be involved with the physiological function(s) of reproductive activities in the male chickens. Moreover, the number of TH-ir neurons in the nI was high in the male brain, implicating that the DAergic system in this nucleus might play an important role in the male reproductive activities and/or parental behavior in this equatorial species.

Acknowledgments

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