

THALAMIC RETICULAR NUCLEUS IN *CAIMAN CROCODILUS*: RELATIONSHIP WITH THE DORSAL THALAMUS

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Abstract—The thalamic reticular nucleus was investigated in one group of crocodylians, *Caiman crocodilus*. This neuronal aggregate is composed of two parts: a compact portion and a diffuse region made up of scattered cells within the forebrain bundles. In *Caiman*, both the lateral and medial forebrain bundles project to the telencephalon and the thalamic reticular nucleus is associated with each fiber tract. In the lateral forebrain bundle, the compact area is termed the nucleus of the dorsal peduncle (dorsal peduncular nucleus) while the diffuse part is called the perireticular area. In the medial forebrain bundle, the interstitial nucleus comprises one part of the compact area while another region without a specific neuronal label is also present. Similar to the perireticular cells of the lateral forebrain bundle, scattered cells are also present in the medial forebrain bundle. Morphological features of the thalamic reticular nucleus are revealed with stains for the following: fibers; cells; succinic acid dehydrogenase; and acetylcholinesterase. Regardless of which dorsal thalamic nucleus was injected, a localized region of the thalamic reticular nucleus contained retrogradely labeled cells and anterogradely labeled axons and terminals. This grouping was termed clusters and was felt to represent the densest interconnection between the dorsal thalamus and the reticular nucleus. Using clusters as an index of interconnections, the reticular nucleus was divided into sectors, each of which was associated with a specific dorsal thalamic nucleus. An organization similar to that found in *Caiman* is present in other sauropsids as well as in mammals. These data suggest that a thalamic reticular nucleus is present in all amniotes and

has morphological properties similar to those described in this analysis. Lastly, a hypothesis is presented to explain how the external shape of the reticular nucleus in *Caiman* might be transformed into the homologous area in a representative bird and mammal. © 2016 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: dorsal thalamus, evolution, lateral forebrain bundle, medial forebrain bundle, reptiles, thalamic reticular nucleus.

INTRODUCTION

In all mammals, the thalamic reticular nucleus occupies a strategic position lying within the fiber bundle that interconnects the dorsal thalamus and the telencephalon (Jones, 2007). Although this neuronal aggregate exhibits a number of characteristics, its most consistent and, perhaps, its most distinguishing feature is its relationship with the dorsal thalamus (Jones, 2007). The mammalian thalamic reticular nucleus is segregated into specific sectors that are related to individual dorsal thalamic nuclei (Crabtree, 1999; Guillery and Harting, 2003; Jones, 2007). Using this latter character as an identifier, a thalamic reticular nucleus has been identified experimentally in both reptiles (Belekhova et al., 1985; Pritz and Stritzel, 1990; Díaz et al., 1994; Kenigfest et al., 2005) and birds (Benowitz and Karten, 1976; Deng and Rogers, 1998) after injection of retrograde tracers into certain dorsal thalamic nuclei. Like mammals, this neuronal aggregate in sauropsids is located in a similar topographic position associated with the forebrain bundles, the major fiber tract connecting the thalamus with the telencephalon.

Using the approach described above, a thalamic reticular nucleus was identified in one group of crocodylians, *Caiman crocodilus*, after injection of a retrograde tracer into one of two dorsal thalamic nuclei, either nucleus rotundus or the medialis complex posterior. Retrogradely labeled neurons were found in an area associated with the lateral forebrain bundle. This nucleus was termed the nucleus of the dorsal peduncle of the lateral forebrain bundle (Pritz and Stritzel, 1990) or dorsal peduncular nucleus. Extending the logic used in the identification of this nucleus in mammals, this area in *Caiman* was considered to be the crocodylian counterpart of at least a portion of the mammalian thalamic reticular nucleus (Pritz and Stritzel, 1990).

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Abbreviations: AChE, acetylcholinesterase; AvI, area ventrolateralis; BnH, bed nucleus of the hippocampus; c, caudal; d, dorsal; D, nucleus diagonalis; Dla, nucleus dorsolateralis anterior; Dma, nucleus dorsomedialis anterior; dp, nucleus of the dorsal peduncle of the lateral forebrain bundle; DT, dorsal thalamus; FB, forebrain bundles; Gv, ventral geniculate nucleus; H, hypothalamus; Hb, habenula; HRP, horseradish peroxidase; ic, internal capsule; IIIv, third ventricle; iN, interstitial nucleus; l, lateral; LFB, lateral forebrain bundle; LM, nucleus lentiformis mesencephali; LV, lateral ventricle; m, medial; MCA, medialis complex anterior; MCP, medialis complex posterior; MFB, medial forebrain bundle; MFBc, contralateral medial forebrain bundle; MFBi, ipsilateral medial forebrain bundle; OT, optic tract; PC, nucleus postero-centralis; r, rostral; Rc, nucleus reuniens pars centralis; Rd, nucleus reuniens pars diffusa; Rt, nucleus rotundus; SDH, succinic acid dehydrogenase; SM, stria medullaris; TRT, tecto-reuniens tract.

While these initial observations examined two nuclei of the dorsal thalamus, nine additional neuronal aggregates have been identified in the dorsal thalamus in *Caiman* (Pritz, 2014). How these other dorsal thalamic nuclei relate to prior observations on this previously described reptilian thalamic reticular nucleus is unknown.

In *Caiman*, nucleus rotundus and the medialis complex posterior share a number of properties (Pritz and Stritzel, 1994; Pritz, 2014, 2015). However, other identified dorsal thalamic nuclei in *Caiman* differ from rotundus and the medialis complex posterior in their site of termination in the telencephalon as well as in the fiber tract in which their respective axons travel (Pritz, 2014, 2015). While the majority of dorsal thalamic nuclei in *Caiman* utilize the lateral forebrain bundle, nucleus dorso-lateralis anterior projects bilaterally to general cortex (Pritz and Stritzel, 1987) and utilizes the medial forebrain bundle (Pritz, 2014). In addition, while most dorsal thalamic nuclei whose telencephalic connections are known use the lateral forebrain bundle to terminate in the dorsal ventricular ridge (dorsolateral area of Crosby, 1917), the medialis complex anterior seemingly ends in the basal ganglia (ventrolateral area of Crosby, 1917) (Pritz, 2014).

To determine the relationship between specific dorsal thalamic nuclei and the thalamic reticular nucleus as well the latter's morphology in *Caiman*, two types of experiments were analyzed. One involved tracer placements into other dorsal thalamic nuclei as well as additional injections into nucleus rotundus and the medialis complex posterior. The distribution and location of retrogradely labeled neurons in the thalamic reticular nucleus were then determined as was the relationship between retrogradely labeled neurons and anterogradely

labeled boutons and fibers. The other examined the overall morphology of this thalamic reticular nucleus as revealed by fiber, Cresyl Violet, and histochemical staining. On the basis of these results and a comparison with other amniotes, an explanation is presented that might account for the diverse morphological appearance of the thalamic reticular nucleus between *Caiman* and pigeon and mouse.

EXPERIMENTAL PROCEDURES

Experiments described in this report were approved by the Animal Care Committee of the institution in which they were performed. These protocols conformed to the National Institutes of Health guidelines. All line drawings and photos are presented as right-sided figures. For all figures that showed transverse sections (Figs. 1–12), medial is to the left and ventral is down.

Descriptive morphology

Caiman brains were examined in the transverse plane where they were blocked in a standard fashion (Pritz, 1974a) or aligned to achieve a similar transverse orientation. Details of Cresyl Violet 0.5% concentration (Pritz, 1974a) and histochemical staining for succinic acid dehydrogenase (SDH) and acetylcholinesterase (AChE) (Northcutt, 1974) are available elsewhere. The fiber stain used followed a protocol described by others (Schneider, 1969; reference and note 31). Pertinent details are as follows. Briefly, after euthanasia and transcardiac perfusion with 10% formalin, brains were blocked in a standard transverse plane (Pritz, 1974a), postfixed in 10% formalin,

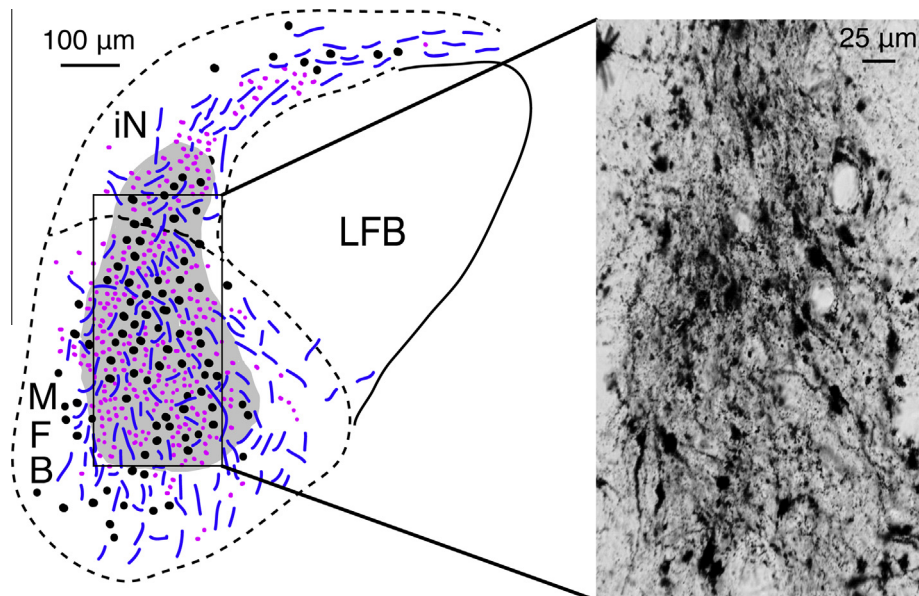


Fig. 1. Clusters in the thalamic reticular nucleus. Camera lucida drawing (see Fig. 12G, right panel, for section location) showing the distribution of cells (large dots), terminals (small dots), and fibers (line segments) seen after tracer injection (injection site is shown in Fig. 12A–E). Clusters (denoted by gray shading in the left-sided panel) are those areas marked by the presence of retrogradely labeled cells and anterogradely labeled fibers and boutons. Photomicrograph of the enclosed area in the drawing to the left is shown in the photo to the right. Medial is to the left and ventral down.

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