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The Lacertidian Reticular Thalamic Nucleus Projects Topographically Upon the Dorsal Thalamus: Experimental Study in *Gallotia galloti*

CARMEN DÍAZ, CARMEN YANES, CARMEN-MARÍA TRUJILLO, AND LUIS PUELLES
Department of Cell Biology, University of La Laguna, La Laguna, Tenerife (Canary Islands), 38205, Spain (C.D.,C.Y.,C.-M.T.), and Department of Morphological Sciences, University of Murcia, Murcia, 30100, Spain (L.P)

ABSTRACT

The projection pattern of the ventral thalamic reticular nucleus onto the dorsal thalamus was studied in the lizard *Gallotia galloti* using in vitro horseradish peroxidase and fluorescent carbocyanine labelling techniques. Localized label deposits at three dorsoventrally spaced sites in the dorsal thalamus elicited retrograde transport into separate, though partly overlapping, medial, dorsolateral and ventrolateral sectors within an extended cytoarchitectonic complex which may be globally identifiable as the reticular nucleus. Neurons found in the dorsolateral and ventrolateral sectors mainly corresponded to the cell group named nucleus ventromedialis (or nucleus of the dorsal supraoptic decussation) in the literature, whereas neurons labelled in the medial sector corresponded to the so-called dorsal hypothalamic nucleus. Sparser cells appear labelled in the superficially placed nucleus suprapeduncularis. Thalamotelencephalic fibers arising from the injected dorsal thalamic nuclei also project to the corresponding retrogradely labeled sectors within the reticular nucleus.

These findings reveal a rough topographic organization in the connections of the extended reticular nucleus complex with the whole dorsal thalamus. This supports the hypothesis of hodological homology between this ventral thalamic formation in *Gallotia* and the mammalian thalamic reticular nucleus.

Key words: ventral thalamus, in vitro labelling, HRP, fluorescent carbocyanines, comparative neuroanatomy

The mammalian thalamic reticular nucleus is a ventral thalamic neuronal population which plays an important role in the modulation of thalamocortical pathways (Scheibel and Scheibel, 1967; Singer, 1977; Sherman and Koch, 1986) and thalamic rhythmic neuronal activity (Steriade and Deschênes, 1984). This nucleus projects to most dorsal thalamic nuclei (Ramón y Cajal, 1909–11; Scheibel and Scheibel, 1966; Jones, 1975, Steriade et al., 1984) and receives axonal collaterals from corticothalamic and thalamocortical fibers (Jones, 1975; Cesaro et al., 1985; Harris, 1987). A slightly overlapping, topographically ordered projection of the reticular nucleus on the dorsal thalamic nuclei has been described in several mammals (Jones, 1975; Steriade et al., 1984; Jiménez-Castellanos and Reinoso-Suárez, 1985; Crabtree, 1992a,b).

A poorly delimited "nucleus of the dorsal supraoptic decussation" (Huber and Crosby, 1926, in *Alligator*) or "nucleus suprapeduncularis" (Papez, 1935, in several reptiles) was proposed to be a possible reptilian homologue of the mammalian thalamic reticular nucleus on the basis of its topography. Recently, this cell group was straightforwardly named "nucleus reticularis" in *Caiman* (Pritz and Stritzel, 1990). Other authors have named the same neuronal group "ventromedial (thalamic) nucleus" (Butler and Northcutt, 1973, in *Iguana iguana;* Cruce, 1974, in *Tupinambis nigropunctatus;* Smeets et al., 1986, in *Gekko gecko*). A general anatomical likeness (e.g., position in the ventral thalamus, in close relation to the dorsal peduncle of the lateral forebrain bundle, and reticular aspect) between this reptilian neuronal population and the reticular nucleus of mammals is easily noticed. However, it is not clear whether its cells extend in an arc from near the ventricle to a rather superficial locus near the ventral geniculate complex, as in mammals. Moreover, few experimental studies in reptiles

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Address reprint requests to Luis Puelles, Dept. of Morphological Sciences, Faculty of Medicine, University of Murcia, 30100 Murcia, Spain.

are relevant to corroborate this homology. Only Pritz and Stritzel (1990) specifically addressed this issue. They found some evidence of ordered projections from this nucleus to the dorsal thalamus in *Caiman*, but could not corroborate the presumption of a prevalent GABAergic nature of its neurons (a typical characteristic of the mammalian reticular nucleus), suggesting some important functional differences with the presumed mammalian homologue.

Hoogland (1982), Belekhova et al. (1985) and Gonzalez et al. (1990) provided partial data suggesting that changing patterns of retrogradely labelled neurons in the reptilian reticular nucleus depend on the portion of the dorsal thalamus that was injected with horseradish peroxidase. However, they did not address this issue specifically.

This report reexamines the complete reticular nucleus neuronal population of the lizard *Gallotia galloti*, determining whether the topographic organization of its projections upon the dorsal thalamus is comparable to the mammalian pattern. To this end, we performed transventricular in vitro labelling with horseradish peroxidase (HRP) or with the fluorescent carbocyanines DiI or DiO (DiI,1-1′-dioctadecyl-3,3,3′,3′-tetramethylindocarbocyanine perchlorate; DiO,3,3′-dioctadecyloxacarbocyanine perchlorate) at three dorsal thalamic loci (nucleus rotundus, nucleus medialis posterior and the dorsomedialis/dorsolateralis nuclear complex) in young specimens of the lizard *Gallotia galloti*. The first two areas project to the dorsal striatal ridge, whereas the third projects to the cortex. On the whole, these areas represent the three dorsoventral tiers in which the dorsal thalamus may be subdivided.

MATERIALS AND METHODS

Experimental procedures

Twenty-five young lizards (*Gallotia galloti*) were used. In a first series of experiments, the tracer, horseradish peroxidase (HRP), was injected in vitro into several dorsal thalamic areas according to the in vitro technique reported previously (Díaz and Puelles, 1992). Animals were anaesthetized with ethyl ether and perfused transcardially with Tyrode solution. The brains were removed and sectioned midsagittally (n = 36 brain halves). HRP was recrystallized on the tip of fine glass micropipettes and then applied through the ventricular lining into three dorsal thalamic areas: dorsomedialis/dorsolateralis complex (n = 14), nucleus rotundus (n = 14) and nucleus medialis posterior (n = 8). Injected brains were placed in culture at room temperature in Minimal Essential Medium (Gibco) supplemented with penicillin and continuously bubbled with a gas mixture (95% O_2, 5% CO_2). After 24–48 hours (the range of diffusion and intensity of HRP was better after the longest periods), they were fixed in 2% glutaraldehyde-1% paraformaldehyde in 0.1 M, pH 7.2 phosphate buffer for 4 hours, and then soaked overnight in cold 20–30% phosphate-buffered sucrose. The pieces were sectioned on a freezing microtome or a cryostat (50–60 μm thick), obtaining either cross-sections or sagittal sections (see Table 1). Sections were mounted on gelatinized slides and treated with nickel-cobalt-diaminobenzidine or nickel-diaminobenzidine, with the addition of one drop of dimethylsulfoxide to each 100 ml of incubation medium. All sections were counterstained with acetate-buffered cresyl violet.

Graphical reconstructions in the topological transverse plane of the observed retrograde labelling patterns in the reticular nucleus were prepared from the sagittally sectioned specimens (see legend to Fig. 10).

Additionally, a series of double labelling experiments were performed by using the two fluorescent carbocyanine dyes DiI and DiO (Molecular Probes, Oregon). The brains of seven young specimens were used (n = 14 brain halves). Animals were anaesthetized with ethyl ether and perfused first with Tyrode solution and subsequently with 4% paraformaldehyde in 0.1 M phosphate buffer (pH 7.2). The brains were removed and cut midsagittaly after postfixation in the same fixer for 1–2 hours. In each experiment, DiI and DiO were inserted into two different dorsal thalamic nuclei (see Table 2) to determine the relative spatial location of the two labelled sectors in n. reticularis and the eventual presence of overlapping. A small crystal of either tracer was inserted in the choosen places with fine glass micropipettes or tungsten needles. The brains were then kept in buffered 4% paraformaldehyde in darkness at room temperature during

Abbreviations

ai	area intercalata
Alh	area lateralis hypothalami
At	area triangularis
cp	cellular plate
D	dorsal
Dl	nucleus dorsolateralis thalami
Dlh	nucleus dorsolateralis hypothalami
Dlm	nucleus dorsolateralis thalami, pars magnocellularis
Dlp	nucleus dorsolateralis thalami, pars parvocellularis
Dm	nucleus dorsomedialis thalami
D-T	dorsal thalamus
fb	forebrain bundle
fr	fasciculus retroflexus
Gld	nucleus geniculatus lateralis, pars doralis
Glv	nucleus geniculatus lateralis, pars ventralis
Habl	nucleus lateralis habenulae
Habm	nucleus medialis habenulae
L	lateral
Lfb	lateral forebrain bundle
Lfbd	lateral forebrain bundle, dorsal peduncle
ln	lateral neuropile
M	medial
Mp	nucleus medialis posterior
Mt	nucleus medialis thalami
O	nucleus ovalis
oc	optic chiasma
ot	optic tract
pc	posterior commissure
Ph	nucleus periventricularis hypothalami
pR	perirotundal belt
PRETEC	pretectum
R	nucleus rotundus
Re	nucleus reticularis
SHab	nucleus subhabenularis
sm	stria medullaris
Sp	nucleus suprapeduncularis
Sph	nucleus sphericus
T	tectum mesencephali
tsh	tractus septohypothalamicus
V	ventral
Vh	nucleus ventromedialis hypothalami
Vl	nucleus ventrolateralis thalami
Vlcp	nucleus ventrolateralis cellular plate
Vm	nucleus ventromedialis thalami
Vmd	nucleus ventromedialis thalami, pars dorsalis
Vmv	nucleus ventromedialis thalami, pars ventralis
V-T	ventral thalamus
yc	yuxtaoptic commissures
zl	tract of the interthalamic zone limitans

TABLE 1. Number of Brain Halves Studied With the In Vitro HRP Technique, Indicating the Injection Site and the Section Plane

Injection site	Section plane	
	Sagittal	Transverse
Dm-Dl complex	10	4
n. rotundus	12	2
n. medialis posterior	6	2

TABLE 2. Number of Brain Halves Injected With the Fluorescent Dyes DiI and DiO[1]

Injection place			Section plane	
DiI	+	DiO	Sagittal	Transverse
R	+	Dm-Dl[2]		2
Dm-Dl	+	R		1
Mp	+	Dm-Dl		3
Dm-Dl	+	Mp		2
R	+	Mp	3	
Mp	+	R	3	

[1]Dm/Dl, dorsomedialis/dorsolateralis complex; Mp, nucleus medialis posterior; R, nucleus rotundus.

30–40 days, or at 38°C for 7–11 days. Given that DiO transport is slower than DiI transport, we labelled the pairs of dorsal thalamic regions with DiI and DiO in an alternating pattern (see Table 2). These brains were sectioned with a vibratome (40–60 μm thick) in the transverse or sagittal planes (see Table 2) and mounted on gelatinized slides with buffered 65% glycerol-1% paraformaldehyde. The sections were observed through a Leitz epifluorescence microscope equipped with green (DiI) or blue (DiI-DiO) excitation filters.

Cytoarchitectonic data

Morphological cross-correlation was possible by utilizing the HRP-processed tissue that was counterstained with cresyl violet. A collection of *Gallotia* brains sectioned in different planes and stained with cresyl violet or Klüver-Barrera techniques was used as well. We followed Smeets et al. (1986) in terminology.

RESULTS

In the present study, we deal only with the experimental results in relation to the connectivity between three dorsoventral tiers of the dorsal thalamic region and the ventral thalamus in the brain of the lizard *Gallotia galloti*. All our label deposits labelled periventricular cell populations plus a substantial portion of the more laterally placed thalamic neurons.

Morphological background

Cytoarchitectural analysis of the labelled ventral thalamus region shows a mediolateral band of neuronal groups that extends around and across the region where the dorsal and ventral peduncles of the lateral forebrain bundle collect in front of the dorsal thalamus (Figs. 1–5). Medially there appears the so-called n.dorsolateralis hypothalami (Dlh), a rather compact mass of small cells which are rostroventrally continuous with the stratum cellulare internum of the hypothalamus (Dlh; Ph; Figs. 1–5). Lateral to Dlh lies the n.ventromedialis thalami (Vm), formed by medium-sized neurons that are loosely arranged in the midst of the dorsal peduncle of the lateral forebrain bundle. The nuclei Dlh and Vm are separated from the dorsal thalamus by a cell-poor space, termed by us, area intercalata (ai; Figs. 1–5). Lateral to Vm, disperse large fusiform cells form the n.suprapeduncularis (Sp); this separates the cell plate of n.ventrolateralis from the lateral forebrain bundle (Sp; Vlcp; lfb; Figs. 1, 2).

All these populations show some differences in cell size and density along the dorsoventral direction, as observed most clearly in sagittal sections (Figs. 7, 8). We interpret the dorsoventral axis as parallel to the fasciculus retroflexus and to the interthalamic zona limitans boundary (see Fig. 7); both are considered to mark the position of transverse intersegmental boundaries (Puelles et al., 1987, 1991; Medina et al., 1993). Nucleus ventromedialis has slightly smaller and more compact cells in its ventral part, compared to its dorsal part (Vmv; Vmd; Fig. 7). The lateral forebrain bundle limits rostrally both these dorsal and ventral sectors as it bends dorsally into the telencephalic stalk (Figs. 7–9). The transverse line of inflexion coincides with the rostral boundary of the anterior parencephalic segment of the diencephalon (Puelles et al., 1987, 1991; Medina et al., 1993).

The cell plates of n.ventrolateralis and n.geniculatus ventralis are dorsolateral to Vm and Sp (Figs. 1–5). The area triangularis (which is confusingly rather rounded in sagittal sections) is located dorsal to the dorsal sector of n.ventromedialis (At; Figs. 1c,d; 2c,d; 7; 8). The cell-poor area intercalata (ai) belongs also to the ventral thalamus. It is enlarged ventrally and separates the other ventral thalamic grisea from the interthalamic boundary and the dorsal thalamus (ai; Figs. 1–5; 7–9). It has been postulated that this area in sauropsids may be homologous to the mammalian zona incerta (Ingvar, 1923).

Experimental results

Both the HRP- and DiI/DiO-labelled series of results showed a markedly ordered connection pattern. Retrogradely and anterogradely transported label appears located in distinct domains of the Dlh-Vm-Sp complex of the ventral thalamus, depending on the region of the dorsal thalamus injected.

In vitro HRP experiments

We deposited HRP separately into three dorsoventral regions of the dorsal thalamus, identified by the main nucleus labelled: (1) nucleus rotundus, (2) nucleus medialis posterior, and (3) nucleus dorsomedialis/dorsolateralis. A given region of the ventral thalamus always becomes labelled anterogradely and retrogradely. The same region is crossed by a labelled fiber bundle of the dorsal peduncle of the lateral forebrain bundle (Fig. 9). Many of these labelled fibers course to the dorsal striatal ridge or the cortex.

Injections in the nucleus rotundus thalami. In these cases, a substantial group of retrogradely labelled neurons was found in the reticular nucleus region. Most of them lie within the nucleus ventromedialis thalami, laterally to the nucleus dorsolateralis hypothalami (Figs. 1, 2). However, the Vm nucleus is not totally labelled. Its ventral zone appears almost unlabelled (Vmv; Figs. 1a,b; 2a,b; 6a; 8a,b). Cross-sections and sagittal sections show the most dense retrogradely labelled region situated close to the unlabelled area triangularis, corresponding to the dorsal zone of Vm (Vmd; Figs. 1b–d; 2b–d; 6a; 8a,b). An intensely stained neuropil is superposed in the same locus. Superficially to the Vmd nucleus, nucleus suprapeduncularis contains some retrogradely labelled large cells and some anterogradely

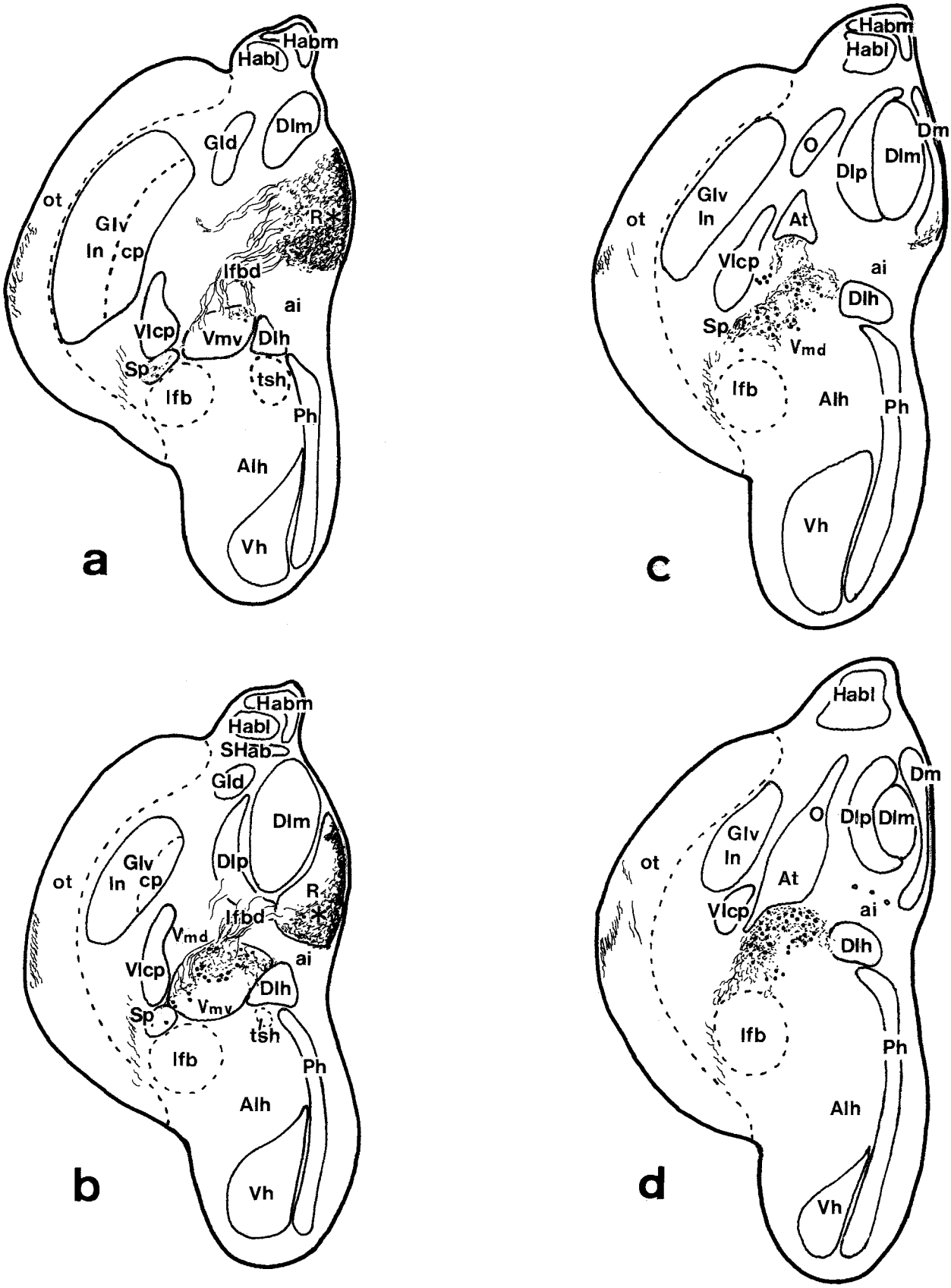


Fig. 1. **a–d:** Drawings of representative cross-sections from a *Gallotia* brain that received a horseradish peroxidase (HRP) injection in n.rotundus (asterisks in a,b). The section levels are arranged from caudoventral (a) to rostrodorsal (d; see section plane in Fig. 7a). Large black dots represent retrogradely labelled cells, thin lines are labelled fibers and small black dots indicate terminal arborizations. HRP labelling is restricted to the dorsal part of the Vm nucleus and some cells in the Sp nucleus. No label was found in Dlh or in the ventral part of the Vm nucleus.

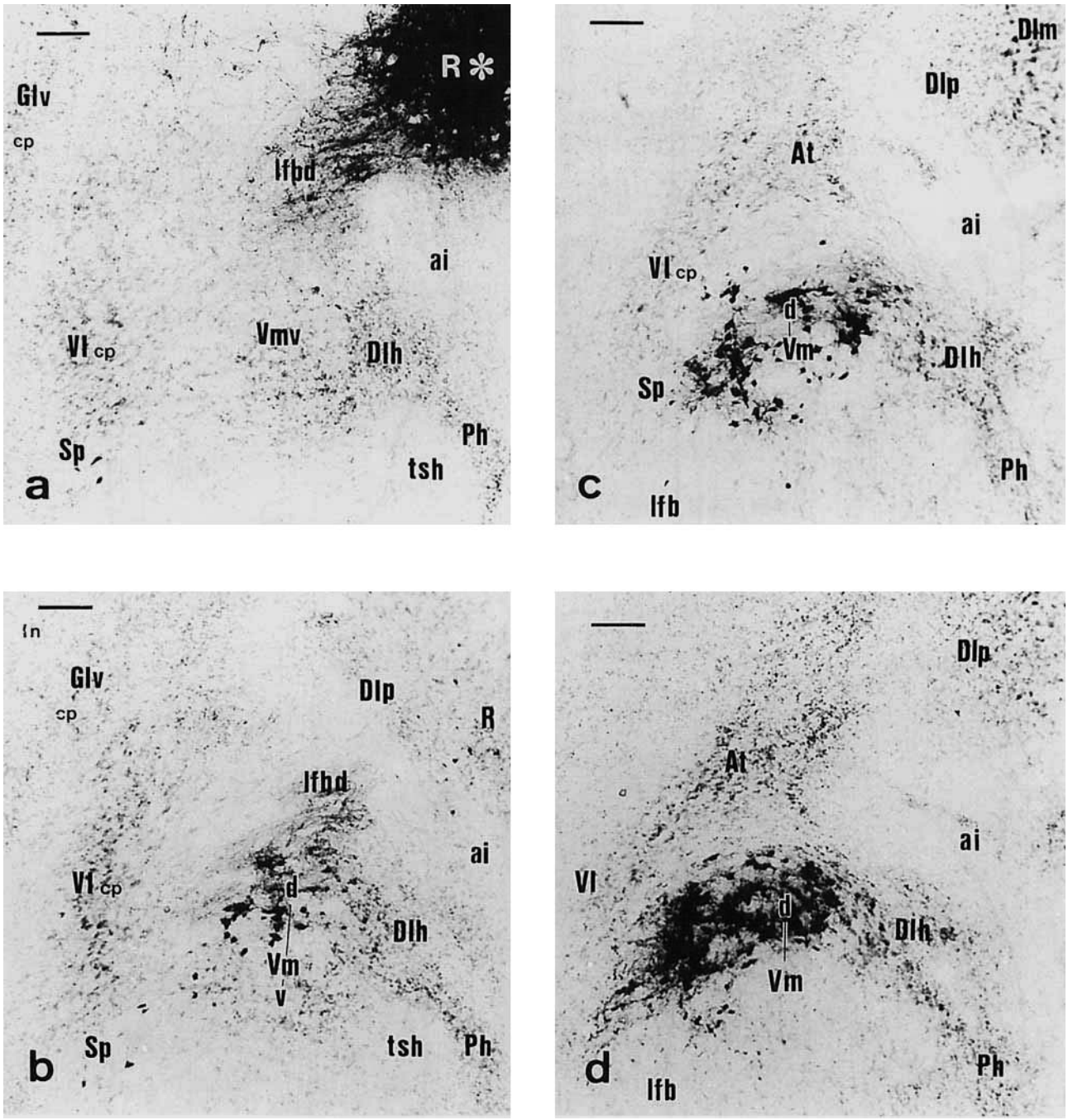


Fig. 2. **a–d:** Injection in n.rotundus. Photomicrographs corresponding to details of the labelled regions in the four cross-sections shown in Figure 1 (same order and orientation). The sections are counterstained to show cytoarchitectural divisions. Note details of labelling in the Dlh-Vm-Sp complex of the ventral thalamus. Asterisk, injection site in n.rotundus. Scale bars = 100 μm.

labelled terminals (Sp; Figs. 1a–c; 2a–c). Fibers of the dorsal peduncle of the lateral forebrain bundle are also labelled. Most of these fibers cross the Vm nucleus and then enter the lateral forebrain bundle (Figs. 1d; 8a,b). Many of them produce fine axonal collaterals within Vmd. Labelled fibers were traced to subcortical areas (lateral and rostrolateral portions of the striatum and rostrolateral portion of the anterior dorsal ventricular ridge; not shown). They represent the well-known rotundostriatal projection.

Injections in the nucleus medialis posterior thalami. In all these cases, many labelled neurons and a dense anterogradely labelled plexus were found also in the Vm nucleus (Figs. 3; 4; 6b; 8c,d). However, the dorsal part of the Vm nucleus showed practically no retrograde transport and the labelled cells and axonal arborizations were concentrated in the ventral part of the nucleus (Vmd; Vmv; Figs. 3; 4; 6b; 8c,d). Labelled thalamotelencephalic fibers coursed through the dorsal peduncle of the lateral forebrain bundle.

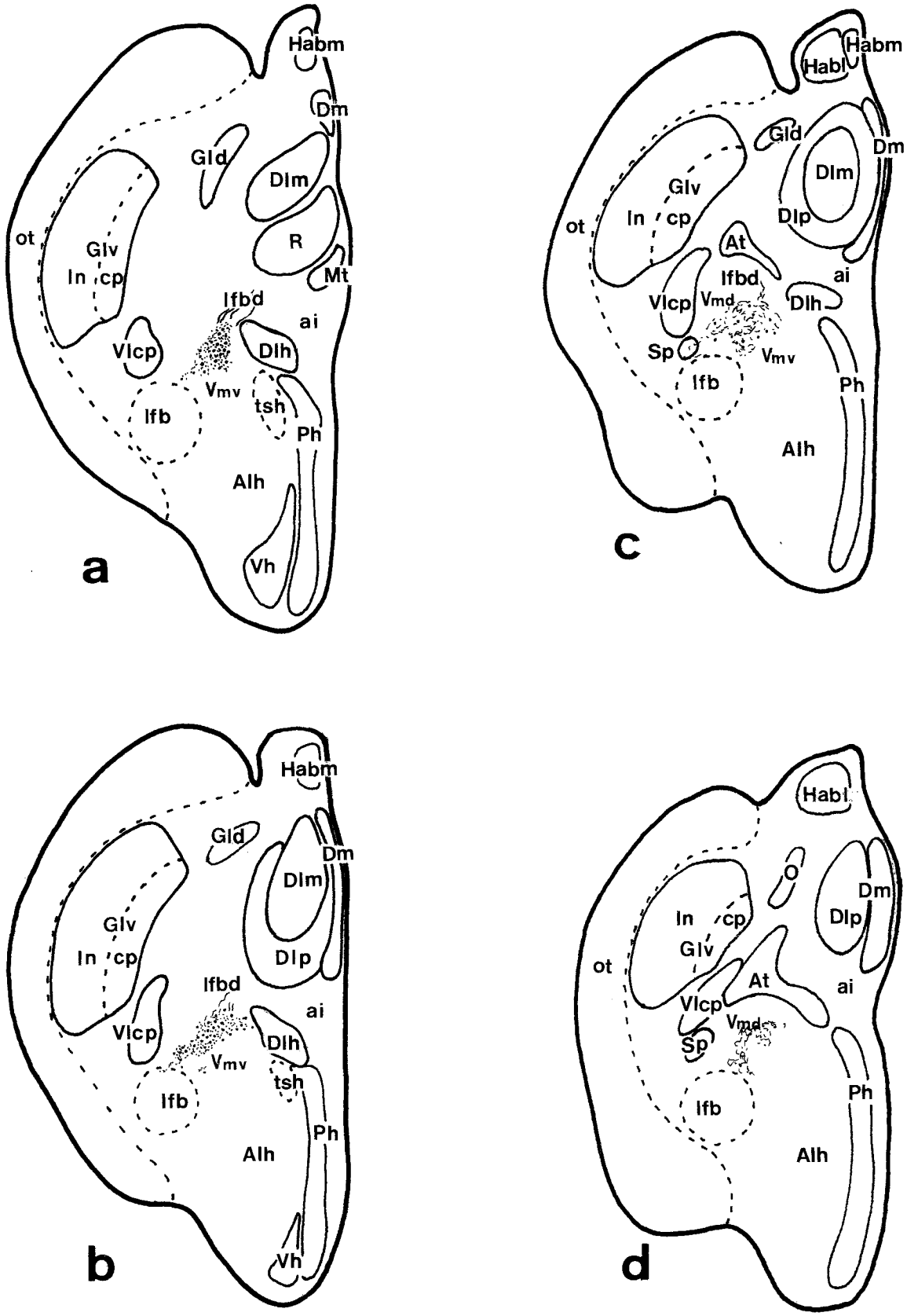


Fig. 3. **a–d:** Drawings of representative cross-sections of a *Gallotia* brain after HRP injection in n.medialis posterior (injection site not shown), mapping transported label in the ventral thalamus. The section levels are arranged from caudoventral (a) to rostrodorsal (d; see section plane in Fig. 7a). The injection site appears caudal to a. Large black dots represent retrogradely labelled cells, thin lines are labelled fibers and small black dots represent terminal arborizations.

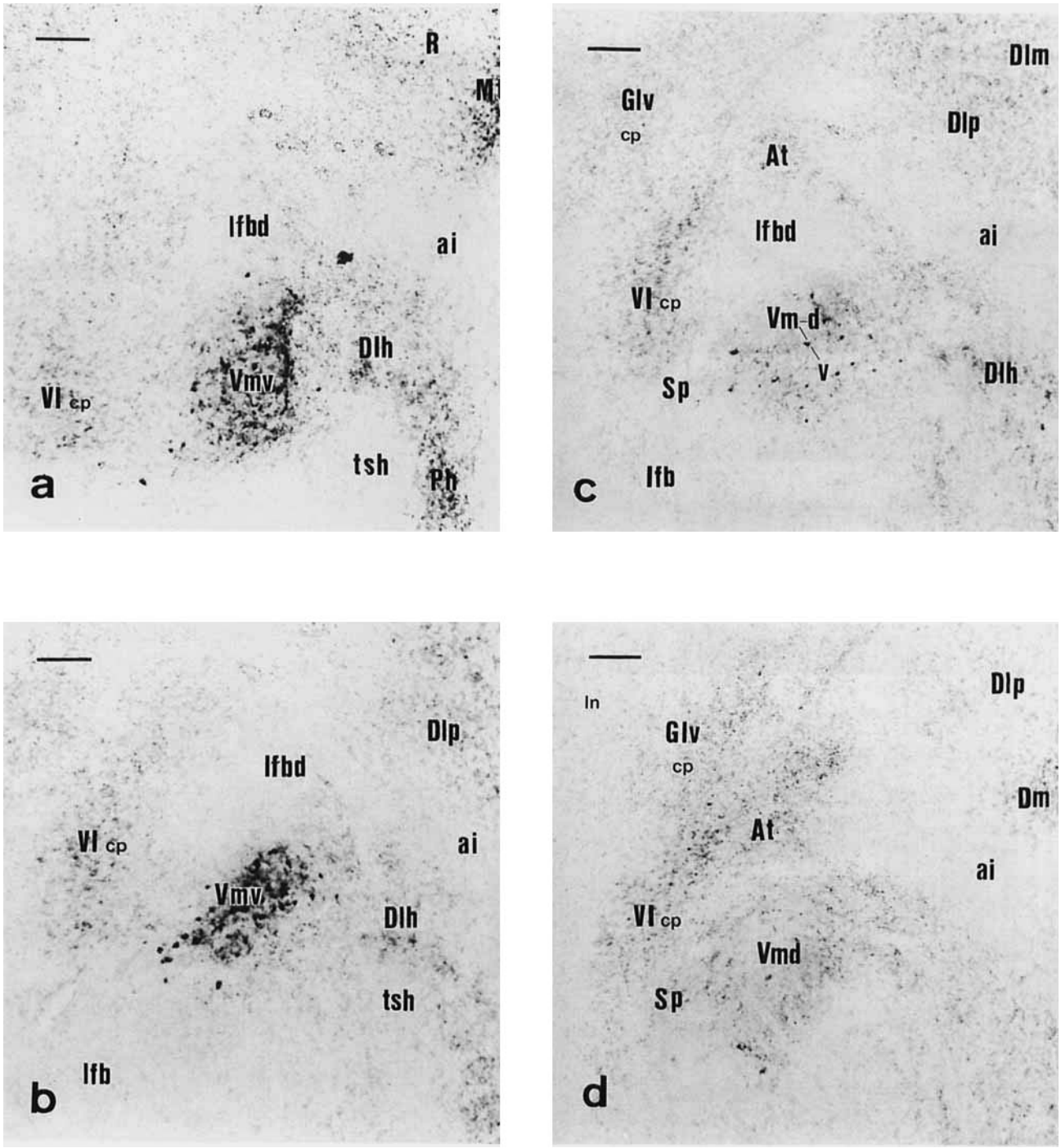


Fig. 4. **a–d:** Injection in n.medialis posterior. Photomicrographs showing details of HRP labelling in the Dlh-Vm-Sp complex of the ventral thalamus on the four counterstained sections mapped in Figure 3 (same order and orientation). Many labelled cells are located in the ventral part of the Vm nucleus. The Dlh nucleus, the dorsal part of the Vm nucleus and the Sp nucleus do not show any label. Scale bar = 100 μm.

Most of these fibers crossed the labelled ventral portion of the Vm nucleus (Figs. 8c,d), then they turned dorsally and followed the lateral forebrain bundle into the telencephalon. Nucleus medialis posterior projects to subcortical areas (striatoamygdaloid area, striatum and caudomedial portion of the anterior dorsal ventricular ridge).

The different HRP localization within the Vm nucleus after injections in nucleus rotundus and nucleus medialis posterior is compared in Figures 6, 8 and 10.

Injections in the nuclei dorsomedialis and dorsolateralis. In these cases, the nucleus dorsomedialis was labelled together with varying amounts of the nucleus dorsolatera-

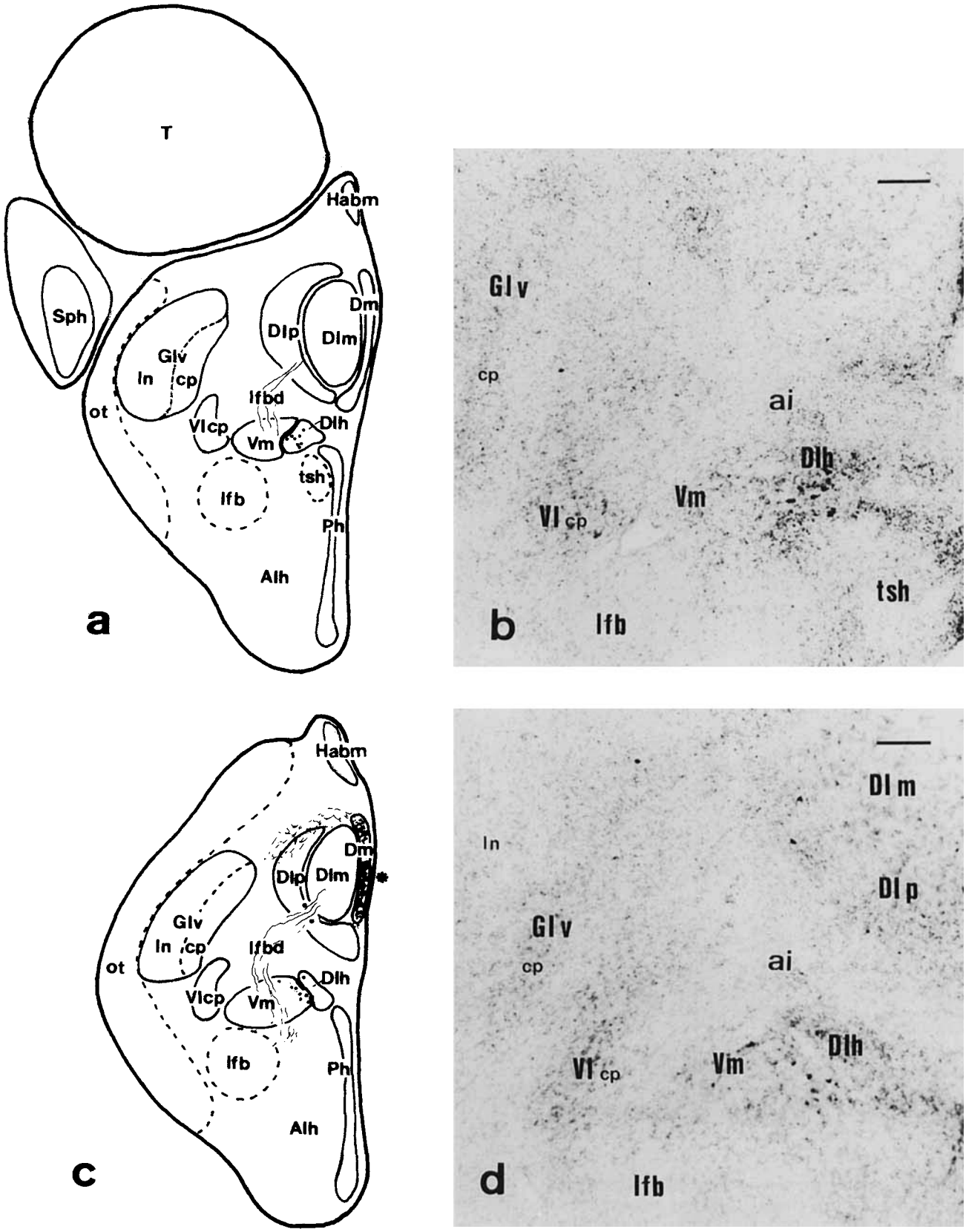


Fig. 5. Injection in the dorsomedial/dorsolateral complex. Drawings and corresponding photographs of two counterstained cross-sections from a *Gallotia* brain, mapping label in the ventral thalamus. **a** is caudoventral relative to **c.** Photomicrographs in **b** and **d** are details of the regions mapped in the drawings a and c, respectively. The injection site (asterisk) is seen only partially in c; it is more extensive in more dorsal sections. Black dots represent retrogradely labelled cells; thin lines indicate labelled fibers. Retrogradely labelled small neurons are shown in the Dlh nucleus and scarce medium-sized neurons appear in the Vm nucleus. Scale bars = 100 μm.

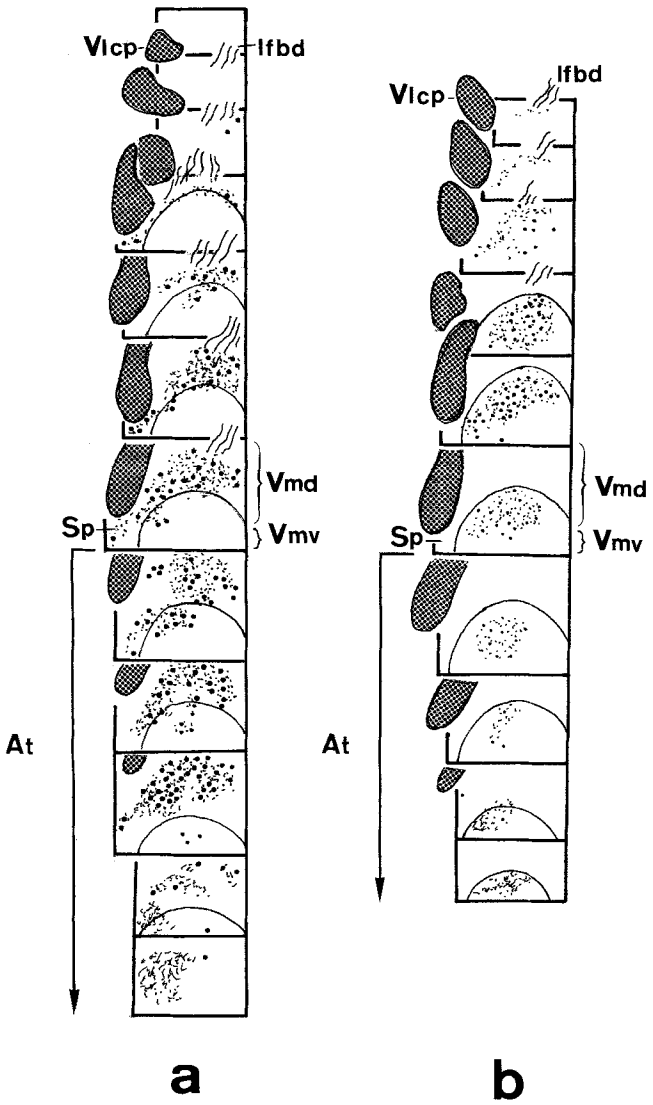


Fig. 6. Schematic comparison of the labelling pattern in the Vm-Sp complex after HRP deposits in the n.rotundus (**a**) and the n.medialis posterior (**b**), including additional serially mapped sections from the experiments shown in Figures 1 and 2, and 3 and 4, respectively. The two series of sections had been cut in the same plane and were matched by using the cell plate of nucleus ventrolateralis (Vlcp, crosshatched), ventrally, and the level of appearance of the area triangularis (At), dorsally. The ventralmost section is represented at the top and the dorsalmost one at the bottom for each series. The rectangles represent the Vm-Sp area in each section, subdivided in dorsal and ventral parts by a curved line. a: Most neurons projecting to n.rotundus are located in the dorsal part of the Vm nucleus, although superficially, a few cells appear in the Sp nucleus. b: Neurons labelled from the n.medialis posterior injection are restricted to the ventral part of the Vm nucleus. The Sp nucleus is unlabelled. Large black dots represent retrogradely labelled cells, thin lines are labelled fibers, and small black dots represent terminal arborizations.

lis, because the HRP was applied through the ventricular lining. Anterograde and retrograde label appears located in these cases in the small-celled periventricular nucleus that is identified in the literature as nucleus dorsolateralis hypothalami; this lies near the unlabelled septohypothalamic tract (Fig. 5a,b; see Smeets et al., 1986). A few larger cells are also labelled in the dorsal part of nucleus ventromedialis thalami, just lateral to the former cell group (Vm; Fig. 5c,d).

Abundant labelled fibers of the dorsal peduncle of the lateral forebrain bundle are observed. They surround the nucleus rotundus laterally and rostrally upon leaving the dorsomedialis/dorsolateralis complex. After traversing the dorsal thalamus and the area intercalata of the ventral thalamus, these fibers cross the ventromedial nucleus region, giving a few very thin collaterals. These course medially to arborize around the periventricular labelled cell population (not shown). After this, the main tract of labelled fibers turns sharply dorsally, almost at a right angle, into the medial and lateral forebrain bundles and proceeds into the telencephalon.

In vitro fluorescent double labelling experiments

Insights into the ordered connections between the reticular nucleus and the dorsal thalamus were provided by the in vitro HRP experiments detailed above. We tested this spatial pattern with double labelling experiments in which different fluorescent carbocyanine tracers (DiI and DiO) were injected into two regions of the dorsal thalamus. Table 2 summarizes these experiments, indicating the corresponding injection sites. The results corroborated systematically the previous HRP findings. One representative case is illustrated in Figure 9, corresponding to a brain in which DiI was placed in nucleus rotundus tier and DiO was located in the subjacent nucleus medialis posterior tier. The sagittal section shows two strongly labelled ovoid populations inside nucleus ventromedialis, rostral to the two injected dorsal thalamic nuclei. A dorsal, dense cell group with abundant DiI-labelled arborizations is distinguishable from a ventral DiO-labelled cell group. However, a precise boundary cannot be established between both cell groups. Scattered DiI-labelled cells are found within the neighboring DiO-labelled ventral group. It should be noted that the small overlap between these dorsal and ventral labelled sectors of n.ventromedialis may be due to partial overlap of the injection sites in R and Mp. Double-labeled neurons were not observed.

DISCUSSION

The lacertidian reticular nucleus as a cytoarchitectonic complex

In vitro experiments labelling collectively a large expanse of the dorsal thalamus showed numerous retrogradely labelled cells in the anterior part of the ventral thalamus. These neurons were mostly interstitial within the dorsal peduncle of the lateral forebrain bundle and formed a wide and continuous mediolateral band extending from periventricular to rather superficial levels in a rostral part of the ventral thalamus. This band is separated from the interthalamic limit by the cell-poor area intercalata (ai; Fig. 9). The band of retrogradely labelled cells encompasses the whole Dlh-Vm-Sp complex. The fact that injections limited within nucleus rotundus or within Dm/Dl each label a continuous cell group bridging, respectively, the ventromedial/suprapeduncular or the Dlh/Vm cytoarchitectonic boundaries supports the conclusion that we deal here with a single, continuous cell population, which may be postulated to be, on the whole, hodologically and topographically homologous to the mammalian reticular nucleus.

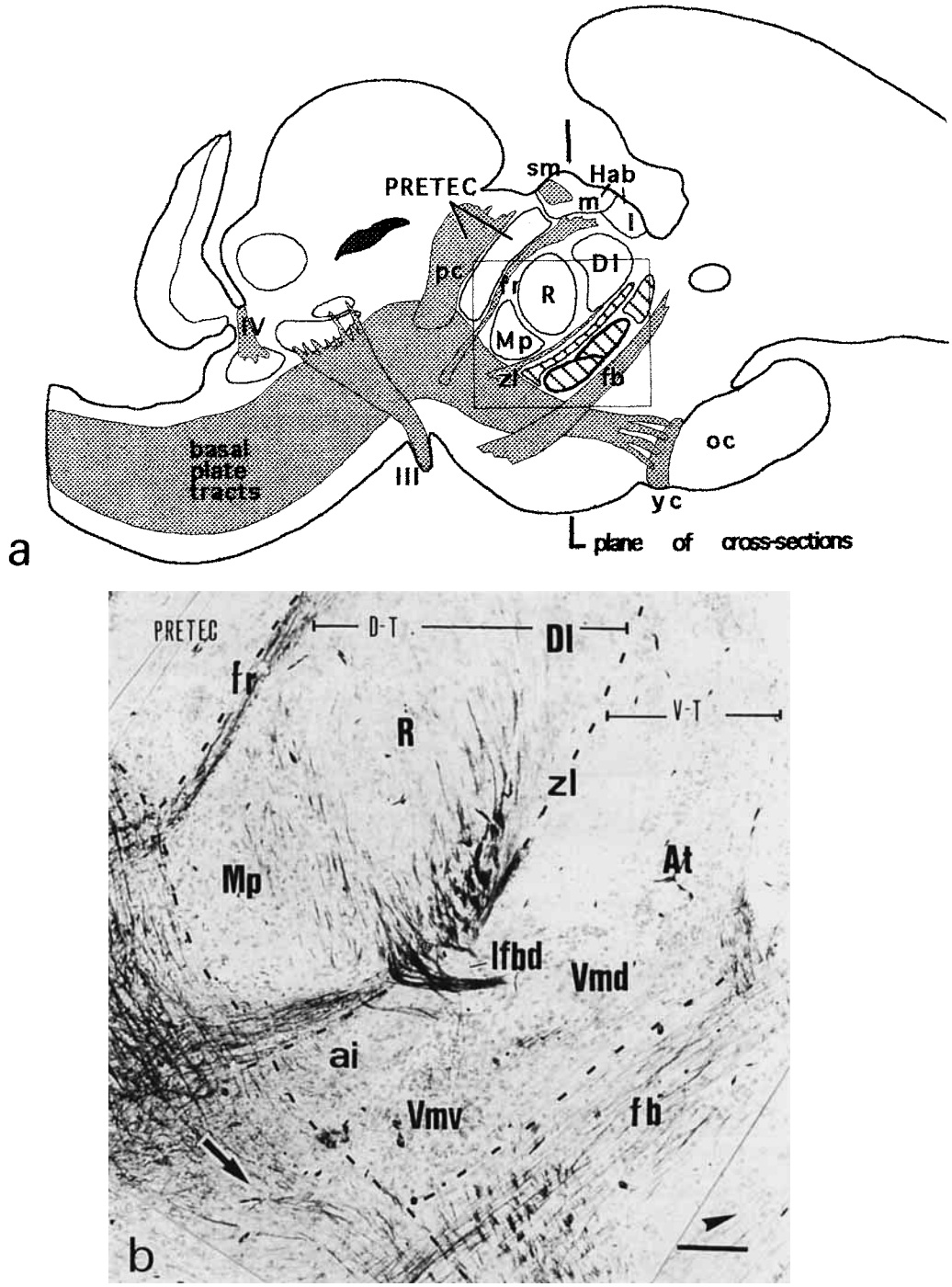


Fig. 7. **a:** Line drawing showing overall diencephalic topography in a Klüver/Barrera-stained sagittal section through the forebrain of *Gallotia*, as well as the boxed area illustrated in b. The main groups of stained myelinated fiber tracts as well as the trochlear (IV) and oculomotor (III) nerves are indicated in stippling. The posterior commissure (pc), the fasciculus retroflexus (fr), the tract limiting the dorsal and ventral thalami (tractus of the zona limitans; zl) and the forebrain bundle (fb) are orthogonal to the longitudinal basal tracts and mark the dorsoventral direction in this part of the brain. The relative position of the dorsal thalamus (D-T) is therefore conceived as caudal to the ventral thalamus (V-T) and rostral to the pretectum (PRETEC), in agreement with a segmental Bauplan (Puelles et al., 1987, 1991; Medina et al., 1993). The three dorsal thalamic nuclear tiers are identified. Ventral thalamic grisea are overlaid with oblique stripes (see identification in b). The two parts of the ventromedial nucleus are drawn with a thicker trace. The approximate section plane of the cross-sections in Figures 1–6 is indicated. **b:** Higher magnification photomicrograph of the area boxed in a shows fiber tracts serving as transverse landmarks and the typical cytoarchitectural subdivisions within the dorsal and ventral thalamus, as well as the interconnecting fibers of the dorsal peduncle of the lateral forebrain bundle (lfbd). The arrow shows the orientation of basal fiber tracts which course rostrad parallel to the longitudinal brain axis (compare with a). Nucleus rotundus lies strictly dorsal to nucleus Mp and ventral to Dl. In this section plane, the ventral thalamus contains the Vmv, Vmd, At and ai subdivisions. The dotted lines mark the caudal and rostral boundaries of the ventral thalamus (D-T) and the dorsal thalamus (V-T). The arrowhead points to the telencephalon. Scale bar = 100 μm.

This "reticular nucleus" population shows an overall mediolateral gradient of increasing cell size. Described cytoarchitectural differences between the subdivisions partly justify the previous classifications into diverse entities recorded in the literature (see Table 3). However, a part of these differences may be only apparent, being perhaps caused by the massive thalamotelencephalic fiber tracts crossing the region (for example, the distinction between Vmv and Vmd). Other differential aspects of the various sectors (notably the changing cell size) may be related to peculiarities of the diverse dorsal thalamic regions upon which they project. The ratio between number (or volume) of reticular cells versus terminal neuropile volume seems different in Vmv and Vmd (Fig. 9), or between Dlh and Vm, though appropriate quantitative studies would be required to establish this point.

It may be asked whether any other studies reached a similar conclusion on the hodological similarity of Dlh, Vm and Sp. Hoogland (1982) described cells labelled in the ventral thalamus of *Varanus exanthematicus* after HRP injections in n.dorsomedialis or n.dorsolateralis as "n.periventricularis hypothalami," "area triangularis" and "n.entopeduncularis anterior." These may perhaps correspond to our Dlh and Vmd nuclei and some cells in n.suprapeduncularis. Reported HRP labelling results in *Gekko qecko* also showed bidirectional connections between the ventromedial and suprapeduncular nuclei and the dorsal thalamus (González et al., 1990; their Figs. 12, 13). In fact, their illustrations suggest that the authors included the Dlh cell group in the area labelled as ventromedial nucleus. A similar analysis by Pritz and Stritzel (1990) in *Caiman crocodilus* did not detect a cell group equivalent to Dlh, but their injection sites seem to have been restricted to rotundic and subrotundic tiers of the dorsal thalamus.

Sectors of the reticular nucleus and connectional topography

Injection sites placed in rotundic, suprarotundic (Dm/Dl) and subrotundic (Mp) parts of the dorsal thalamus ellicited retrograde label transport into different, though partially overlapping, domains of the reticular nucleus. We called them medial, dorsolateral and ventrolateral sectors according to their relative locations. They are respectively traversed and/or projected upon by the thalamotelencephalic fiber bundles originating from the same suprarotundic, rotundic and subrotundic tiers of the dorsal thalamus (Fig. 10e). Table 3 summarizes the terminology previously used for these sectors in several reptilian species.

Dorsolateral and ventrolateral reticular nucleus sectors were labelled after injections in nucleus rotundus and nucleus medialis posterior, respectively (Fig. 10c,d). They correspond to the loosely arranged, medium-sized cells of the ventromedial nucleus that are intercalated between the bundles of the dorsal peduncle of the lateral forebrain bundle. The dorsolateral population always appeared more dispersed than the ventrolateral sector, possibly because of the larger number of fibers crossing it. This gave it a reticular appearance in sagittal and transverse sections. The scattered cells of the suprapeduncular nucleus may perhaps be conceived as a laterally displaced accessory component of the dorsolateral Vm sector. The slight cytoarchitectonic differences between the dorsolateral and ventrolateral sectors may explain why they have occasionally been regarded as two separate entities (e.g., nucleus entopeduncularis and nucleus ventromedialis, by Cruce, 1974; see Table 3). Baker-Cohen (1968) also distinguished histochemically both Vm sectors in sagittal and transverse sections, naming them "dorsal" and "caudal" nuclei of the dorsal supraoptic decussation.

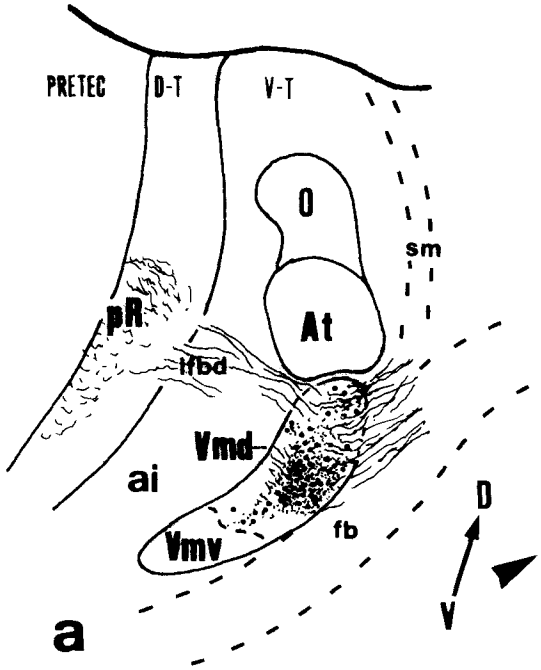
Belekhova et al. (1985) performed HRP injections in n.reuniens of the turtle (rostral subrotundic tier) and apparently obtained retrograde labelling of cells in the ventrolateral reticular sector (p. 137, "density [of retrogradely labelled fibers and cells] was greatest . . . under n.rotundus and more caudally") together with a number of n.suprapeduncularis neurons. González et al. (1990) described HRP injections in n.rotundus and n.medialis as eliciting retrograde transport into the suprapeduncular nucleus. Since they seem to have applied the name "ventromedial nucleus" mainly to the cells surrounding the septohypothalamic tract, termed by us "Dlh" in accordance with Smeets et al. (1986), it is possible that their suprapeduncular nucleus mainly represented our ventromedial nucleus. This appears clearly so in their Figure 12A.

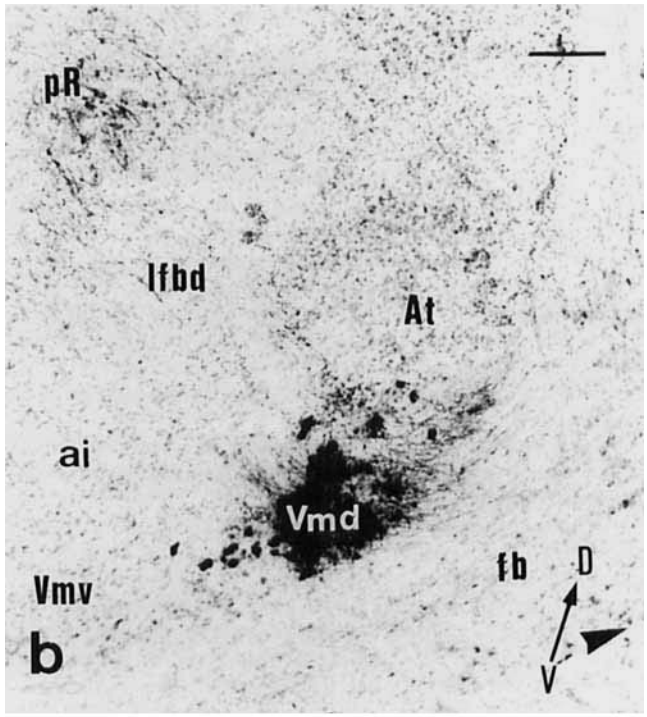
Observations on n.rotundus injections by Pritz and Stritzel (1990) suggest that in *Caiman* the Vm-Sp cell groups may be further displaced laterally than in *Gekko* or *Gallotia*. These authors indicate that location of labelled reticular nucleus cells varied depending on the portion of the dorsal thalamus injected. We think that their injection into the medialis complex produced cells in a more ventral sector of the reticular nucleus than their injection in n.rotundus. This would agree with our results on the dorsolateral and ventrolateral reticular nucleus sectors, but results from our own interpretation of their figures, whose rostrocaudal order (in fact dorsoventral order; compare our Fig. 7) seems to us to have unwittingly been mixed up (the correct "rostrocaudal" sequence according to us would be: Figs. 1B3-1B1-2B3-2B1 [Pritz and Stritzel, 1990]).

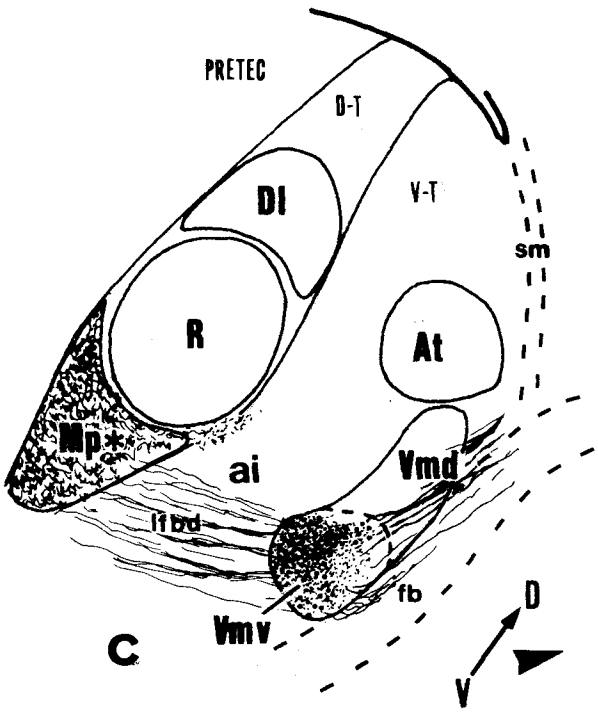
The medial sector of the reticular nucleus in *Gallotia* was labelled specifically when the tracers were injected into the n.dorsomedialis/n.dorsolateralis complex. This densely packed medial cell group has small and basophilic neurons and apparently corresponds to nucleus dorsolateralis hypothalami (or n.microcellularis of Huber and Crosby, 1926; see Table 3). González et al. (1990) illustrated at least two other cases of injection in the *Gekko* dorsomedial nucleus (their Figs. 12E and 13I) with retrograde transport into their "ventromedial nucleus," which corresponds to our Dlh.

These cells have a conflicting position at the border between ventral thalamus and hypothalamus. Several influential authors have included this cell group within the hypothalamus (Butler and Northcutt, 1973 in *Iguana iguana;* Cruce, 1974 in *Tupinambis nigropunctatus;* Smeets et al., 1986 in *Gekko gecko*). However, it is located just medial (deep) to the ventromedial nucleus and both are traversed by common radial glial processes (unpublished observations). This, together with additional observations on embryonic specimens of *Gallotia* inclines us to regard it as a ventral thalamic component.

It would thus seem that the hodological data presently available on reticular nucleus connections in various reptiles are roughly consistent, notwithstanding the terminological and spatial orientation problems cited above. This suggests the existence of a common reptilian pattern. In distinction to the earlier data of Hoogland (1982), Belekhova et al. (1985), González et al. (1990), and Pritz and Stritzel (1990), which were obtained in experiments that were not primarily designed to analyse the connection pattern of the reticular nucleus, our present results were produced with this specific aim in mind. We found that the







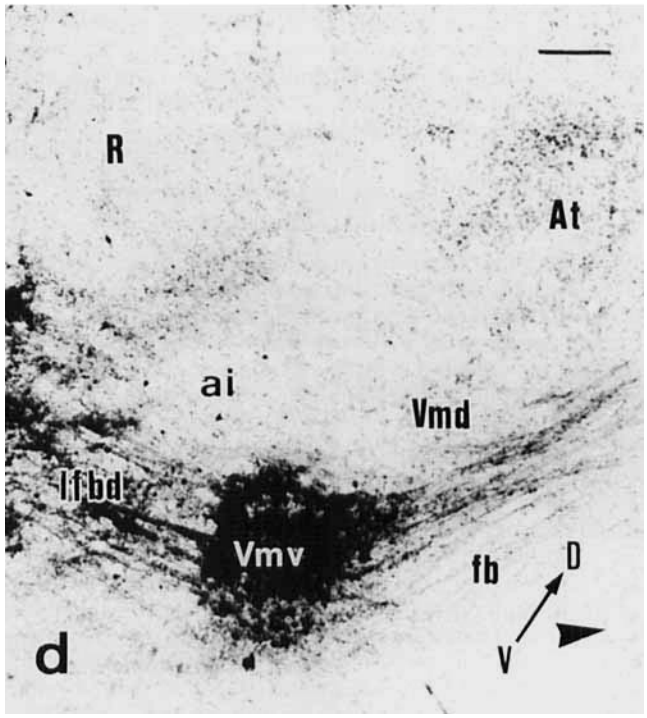


Fig. 8. Drawings (**a,c**) and matched photomicrographs (**b,d**) of sagittal sections through two specimens of *Gallotia*, mapping different domains labelled in nucleus ventromedialis after in vitro HRP injections in n.rotundus (a,b) or in n.medialis posterior (c,d). Note the different spatial location (dorsal versus ventral) of retrogradely labelled neurons in the Vm nucleus and labelled fibers in the dorsal peduncle of the lateral forebrain bundle (lfbd). The unlabelled area triangularis (At) lies above the dorsal sector of the Vm nucleus. Asterisk in c = injection site. Arrowheads point to the basal telencephalon. Arrows point dorsally. Scale bars = 100 μm.

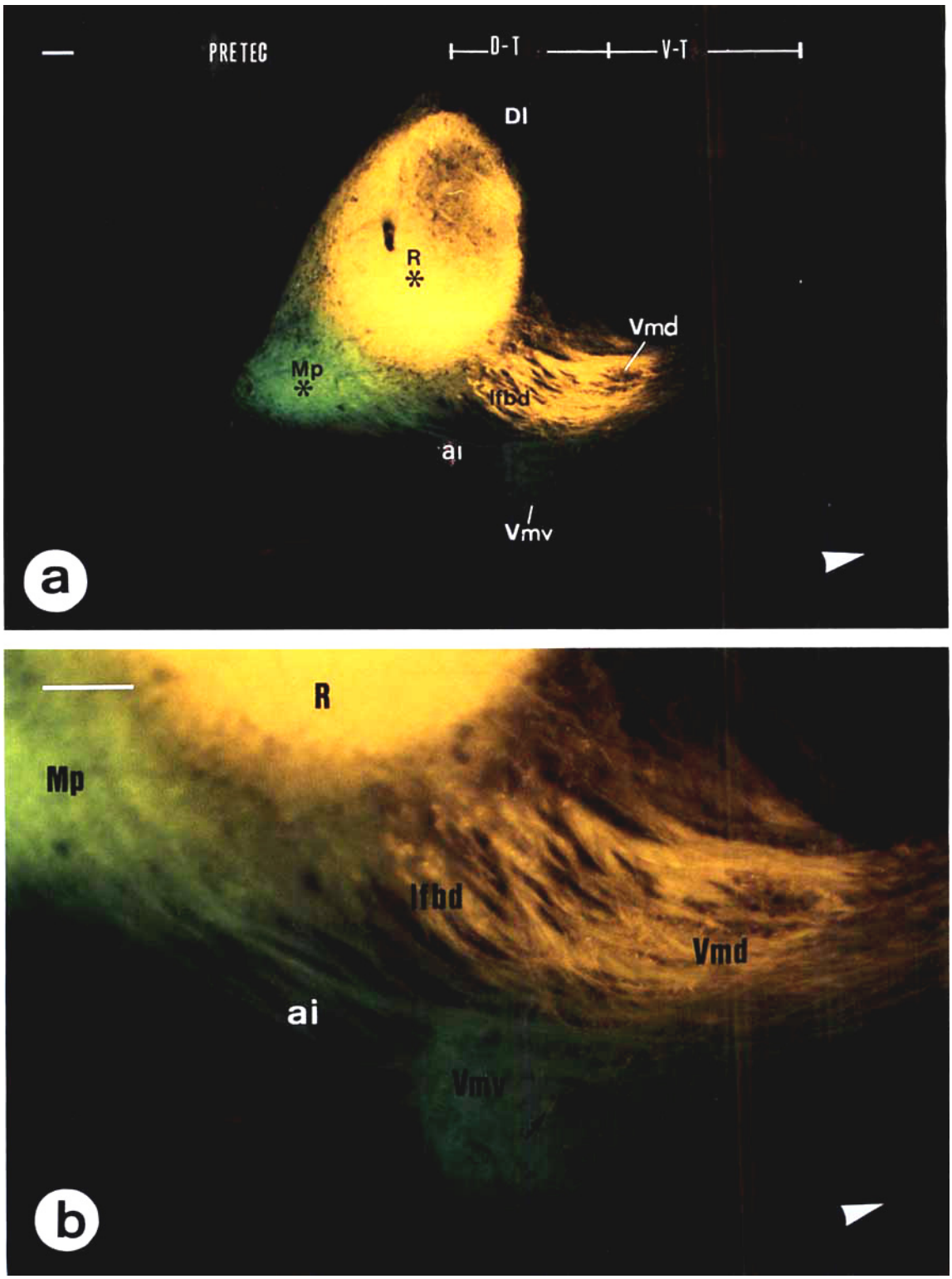
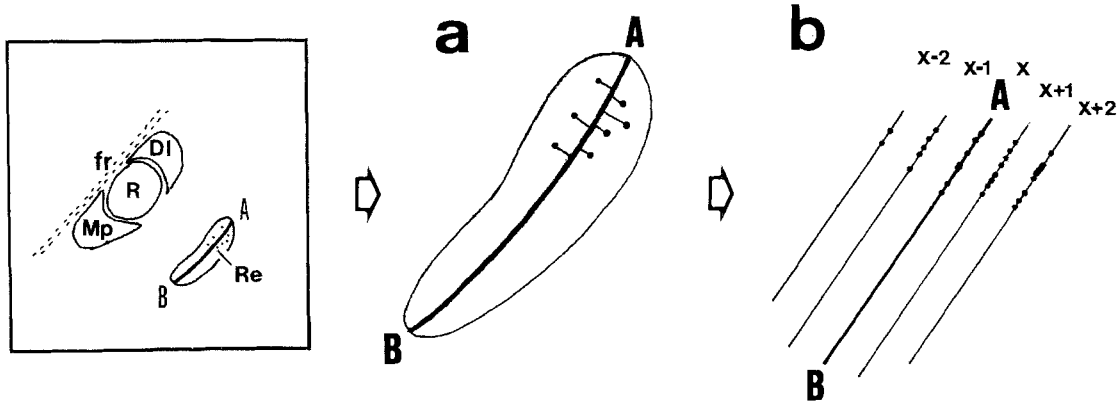


Fig. 9. **a:** Fluorescence photomicrograph of a sagittal section through the thalamus of *Gallotia* showing relative position of two labelled domains in the Vm nucleus after simultaneous in vitro DiI injection in n.rotundus (orange) and DiO injection in n.medialis posterior (green). Subdivision into correlated dorsal (orange) and ventral (green) dorsal thalamic tiers and Vm sectors is demonstrated. Location of the labelled area in front of the dorsal thalamus is directly comparable to that observed in Figures 7 and 8. **b:** Higher magnification of a. Note the presence of a few orange-labelled cells (arrows) within the ventral Vm sector labelled in green. Arrowheads point to the telencephalon. Asterisks, injection sites. Scale bars = 100 μm.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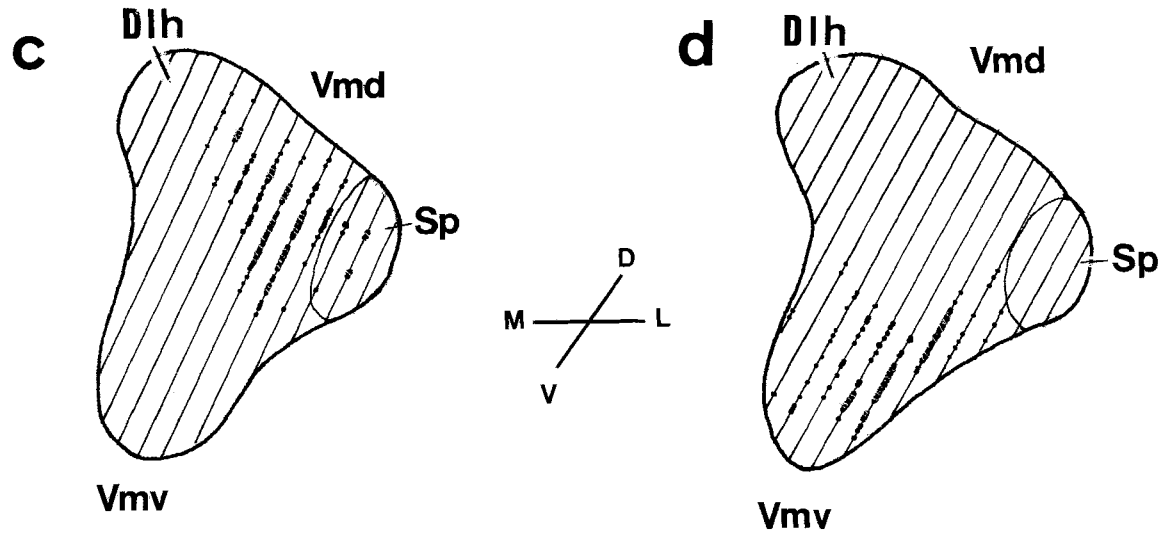
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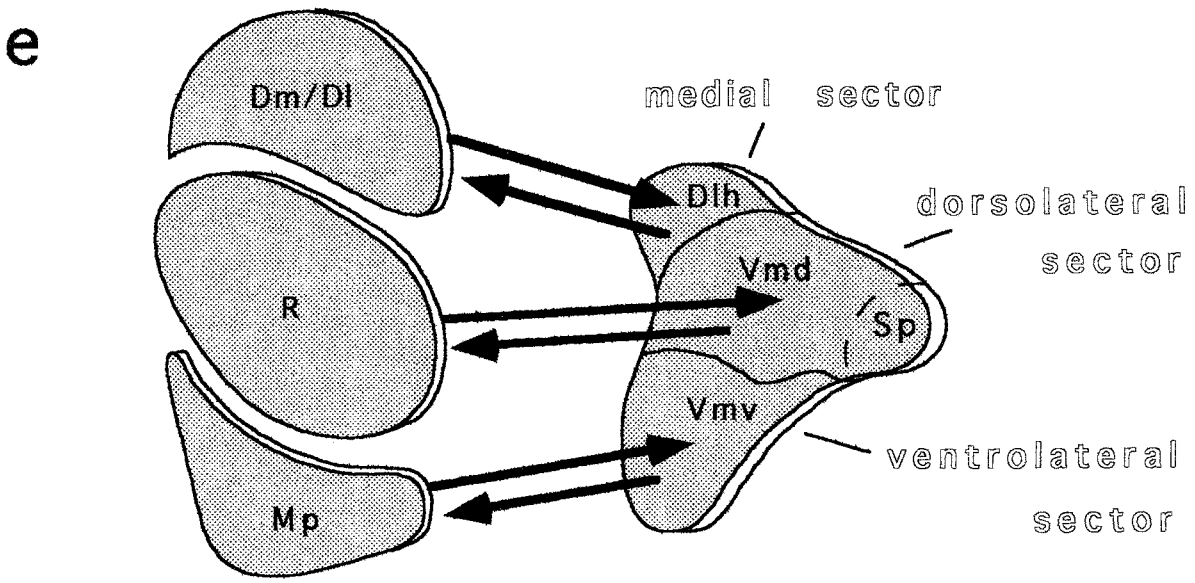
e
Dm/Dl
R
Mp
Dlh
Vmd
Sp
Vmv
medial sector
dorsolateral sector
ventrolateral sector
DORSAL THALAMUS
RETICULAR NUCLEUS

Figure 10

TABLE 3. Nomenclature Used for the Reticular Nucleus Sectors in Reptiles

Diaz et al. (1994) Gallotia galloti	Reticular n. dorsolateral sector	Reticular n. ventrolateral sector	Reticular n. medial sector
Huber and Crosby (1926). *Alligator mississippiensis*	interstitial n. of the olfactory projection tract (part of)	n. of the dorsal supraoptic decussation	n.microcellularis + a.ventromed.?
Frederikse (1931) *Lacerta vivipara*	n.suprapeduncularis	n. suprapeduncularis	n.juxtapeduncularis
Papez (1935) (several species)	n.suprapeduncularis	n.suprapeduncularis	n.suprapeduncularis (medial part)
Baker-Cohen (1968) (several species)	rostral n. of dorsal supraoptic decussation	caudal n. of dorsal supraopt. decussation	—
Butler and Northcutt (1973) *Iguana iguana*	n. entopeduncularis + part of n. ventromedialis	caudal part of n. ventromedialis	n.periventricularis (dorsal part)
Cruce (1974) *Tupinambis nigropunctatus*	n. entopeduncularis + part of n. ventromedialis	caudal part of n. ventromedialis	dorsal hypothalamic area
Smeets et al. (1986) *Gekko gecko*	n. ventromedialis + n. suprapeduncularis	n. ventromedialis + unlabeled mass in Figures 6,7	n.dorsolateralis hypothalami
Pritz and Stritzel (1990) *Caiman crocodilus*	n.reticularis	n.reticularis	—

sagittal sections, which have been employed only by us, are particularly informative in this respect.

It is remarkable that the ventrodorsal set of dorsal thalamic injection sites (Mp - R -Dm/Dl) seems to map anterogradely and retrogradely upon the three sectors of the reticular nucleus in a roughly conserved spatial pattern (Fig. 10c–e): the medial sector is interconnected with the suprarotundic tier of the dorsal thalamus; the dorsolateral sector occupies an intermediate, more lateral position extending superficially into the suprapeduncular nucleus and relates to the rotundic tier; the ventrolateral sector constitutes the ventralmost part of the ventromedial nucleus and is connected with the ventralmost, subrotundic tier. The dorsoventrally arranged dorsal thalamic tiers thus interconnect with a *mediolateroventral* ordered sequence of reticular nucleus sectors. We did not attempt an assessment of topographical order in other dimensions (Crabtree, 1992a,b).

This topographic arrangement in *Gallotia* is globally comparable to the dorsoventrally and mediolaterally ordered reticulothalamic connections described for the mammalian reticular nucleus (Jones, 1975; Steriade et al., 1984; Ohara and Lieberman, 1985; Crabtree and Killackey, 1989). Uncertainties about the homology of specific reptilian dorsal thalamic nuclei with the mammalian ones preclude at this stage a more detailed comparison. On topographical and hodologic grounds, the name *reticular nucleus* may nevertheless be applied to the whole set of Dlh-Vm-Sp neurons, since this joint population coincides at least in those two aspects with the whole mammalian n.reticularis. We thus agree with the recently proposed use of this term in *Caiman* (Pritz and Stritzel, 1990) and with the previous speculations of Papez (1935) and Baker-Cohen (1968).

An analogously placed "reticular nucleus," subdivided into dorsal and ventral parts, is distinguished in birds as well (Benowitz and Karten, 1976). These authors reported a varying pattern of labelled cells in the two subnuclei depending on the dorsal thalamic region injected with HRP. Other reports also give account of various nuclei of the avian dorsal thalamus receiving a projection from this reticular nucleus or from a cell group in that location (Nixdorf and Bischoff, 1982; Gamlin and Cohen, 1986; Wild, 1989a,b; Necker, 1989; Bottjer et al., 1989; Korzeniewska and Güntürkün, 1990).

In the reptilian reticular nucleus, and in the avian and mammalian homologues, the diverse sectors partially overlap one another. In our fluorescent double labelling experiments, cells incorporating one flourescent dye partially invaded the neighboring sector of the reticular nucleus, which was labelled with the other dye. It is difficult to assess to what extent this may have been due to an overlapping of the injection sites. However, Golgi observations in mammals (Scheibel and Scheibel, 1966) indicate that the axon of a single reticular cell may ramify widely within the dorsal thalamus and give collaterals to several dorsal thalamic nuclei, in some cases reaching the mesencephalon. Other observations from our laboratory suggest that massive tectal implants of HRP crystals also produce some retrogradely labelled cells in the thalamic reticular nucleus of *Gallotia* (Pérez-Santana, 1993).

Another interesting similarity is found in the projection of the rostral dorsal cortex of *Gekko* upon the nucleus dorsolateralis hypothalami and the ventromedial nucleus, jointly with a projection upon the dorsomedial thalamic nucleus (Hoogland and Vermeulen-Vanderzee, 1989). This apparently reproduces partially the corticoreticular and corticothalamic projections in mammals (Jones, 1985). Finally, Russchen and Jonker (1988) described, also in *Gekko,* projections from the globus pallidus upon the rostral part of the suprapeduncular nucleus and from the ventral pallidus upon the ventromedial nucleus. They expressed doubts that these connections can be interpreted as homologous to the pallidothalamic pathway in mammals, which projects upon ventral tier nuclei of the dorsal thalamus (Jones, 1985). On the other hand, the mammalian globus pallidus and ventral pallidus have been shown to project upon the reticular nucleus and mediodorsal dorsal thalamus (Haber et al., 1985; Heimer et al., 1985), thus providing a more convincing homologue of that connection.

Nevertheless, Pritz and Stritzel (1990) introduced a note of caution in the drawing of homology between the reptilian reticular nucleus and the mammalian one, at least with respect to *Caiman crocodilus,* since the reticular nucleus neurons projecting to the dorsal thalamus in this species were, in their majority, not glutamic acid decarboxylase-immunoreactive and thus apparently not GABAergic. They thus sharply differed from the mammalian thalamic reticular neurons in this aspect (Houser et al., 1980; Oertel et al.,

Fig. 10. Graphical transverse planar reconstruction of labelling in the reticular nucleus. The open arrows in a and b signify successive steps in the topological transformation of labelled structures in sagittal sections into a planar reconstruction of the reticular nucleus. The boxed **inset** shows the parallel dorsoventral disposition of the retroflex tract and the reticular nucleus, as seen in any given sagittal section ("X" in a; rostral oriented to the right). **a:** Retrogradely labelled neurons in the reticular nucleus section (dots in the inset) were projected orthogonally on the line A–B that links the dorsal and ventral ends of the nucleus. The line A–B is a one-dimensional model of labelling in this section. **b:** Similar lines representing labelled cells in succesive medial ("x − 1," "x − 2" . . .) or more lateral ("x + 1," "x + 2," . . .) sagittal sections were ordered correlatively at intervals proportional to the section thickness × magnification, giving the mapped planar reconstruction. **c,d:** Bidimensional reconstructions of the "flattened" reticular nucleus and the labelled cell distribution in experiments with HRP deposits in n.rotundus (c) and in n.medialis posterior (d). **e:** Schematic representation of the continuous and partially overlapping ordered pattern of connections between the three dorsal thalamic tiers and the corresponding sectors of the reticular nucleus.

1983). Since a few immunoreactive neurons were nevertheless found within this area (Pritz and Stritzel, 1990) and there is evidence that the avian reticular nucleus does contain many GABA-immunoreactive neurons (Domenici et al., 1988; Granda and Crossland, 1989), it may be necessary to reexamine this issue in other reptiles.

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