

Connections of the Tectum of the Rattlesnake *Crotalus viridis*: An HRP Study

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ABSTRACT We have studied the connections of the tectum of the rattlesnake by tectal application of horseradish peroxidase. The tectum receives bilateral input from nucleus lentiformis mesencephali, posterolateral tegmental nuclei, anterior tegmental nuclei and periventricular nuclei; ipsilateral input from nucleus geniculatus pretectalis, and lateral geniculate nucleus pars dorsalis; and contralateral input from dorso-lateral posterior tegmental nucleus and the previously undescribed nucleus reticularis caloris (RC). RC is located on the ventro-lateral surface of the medulla and consists of large cells 25-45 μ m in diameter. Efferent projections from the tectum can be traced to the ipsilateral nucleus lentiformis mesencephali, the ipsilateral lateral geniculate region, anterior tegmental region and a wide bilateral area of the neuropil of the ventral tegmentum and ventral medulla. We have not found any direct tectal projections from the sensory trigeminal nuclei including the nucleus of the lateral descending trigeminal tract (LTDD). We suggest that in the rattlesnake, RC is the intermediate link connecting LTDD to the tectum.

Snakes of the subfamily *Crotalinae* (fam. *Viperidae*) and of the family *Boidae* possess infrared-sensitive pit organs which are innervated by branches of the trigeminal nerve (Lynn, '31). These primary fibers project to a nucleus of the bulbar trigeminal sensory complex. This nucleus is called the nucleus of the lateral descending trigeminal tract and designated LTDD by Molenaar ('74, '77). Schroeder and Loop referred to the same nucleus as the nucleus descendens lateralis nervi trigemini, designating it DLV; they provided the first experimental evidence that this nucleus is involved in the infrared sensory system by tracing cobalt, iontophoresed into the superficial maxillary branch and part of the mandibular branch of the trigeminal nerve (Loop and Schroeder, '75; Schroeder and Loop, '76).

Infrared-sensitive units, driven by the ipsilateral pit organs, have been recorded in the region of LTDD or its tract in both crotalids (Terashima and Goris, '77; Stanford and Hartline, '78) and boids (Molenaar, '78b). Stanford and Hartline verified histologically that their recording electrodes were within

the nucleus LTDD, not the tract; they also demonstrated that they were recording from post-synaptic neurons. It is thus known that LTDD processes infrared information from the pit organs.

Infrared-driven neural responses have also been recorded from intermediate layers of the optic tectum (crotalines: Hartline, '72, '74; Goris and Terashima, '73; Kass et al., '78; boids: Haseltine et al., '77; Haseltine, '78). These infrared-responsive units have been localized predominantly in the stratum griseum centrale of the tectum (crotalines: Kass et al., '78; boids: Haseltine, '78).

We have presumed that the infrared input to the tectum comes by way of the LTDD; a direct projection from LTDD to the tectum in pythons was recently proposed by Molenaar and Fizaan-Oostveen ('78), and in crotalines by Auen ('78). We recognized the need for a thorough investigation of the LTDD-to-tectum pathway in the rattlesnake. Accordingly, we have examined tectal connections in *Crotalus* using horseradish peroxidase. We report here an important finding of our study: the

absence of a direct projection from LTDD to tectum, at least in the crotaline species we used. At the same time, we describe a nucleus with a tectal projection that is a strong candidate as an infrared system intermediate between LTDD and tectum. We also describe other efferent and afferent connections of the rattlesnake tectum.

MATERIALS AND METHODS

We used adult southern Pacific rattlesnakes, *Crotalus viridis*. Animals were between 40 cm and 120 cm in length.

Morphology of brain

For cytoarchitectonic observations we prepared stained brains with either a modification of the Davenport et al. Bodian protein silver method (Gray, '75) or with cresyl violet. The brains were embedded in paraffin and cut at 15 μ m in the transverse plane.

Tectal HRP iontophoresis

Preliminary experiments revealed that horseradish peroxidase introduced into the tectum by either hydraulic injection or by application of soaked pledgets would be accumulated by retrograde transport in several extratectal nuclei. In order to make more circumscribed injections, we then used an iontophoretic method previously described (Gruberg and Udin, '78).

Seven animals were anesthetized with metofane, their tecta exposed and the dura and arachnoid removed. Tapered glass capillary tubes with tip diameter of 15-20 μ m were filled with a freshly prepared 25% solution of HRP (Sigma Type VI) in 0.05 M Tris buffer at pH 8.6. The capillary tubes were connected to a pulse generator which was adjusted to pass 1 μ A at 5 Hz (square waves with 50% duty cycle). The tips of the HRP-filled electrodes were positioned 200-600 μ m below the tectal surface by a micromanipulator. Deeper depths were used for more lateral penetrations. Three to four widely separated unilateral tectal injections were made in each animal. Current was passed for five to ten minutes at each site. Following survival times and temperatures ranging from two days at 22°C to nine days at 29°C, the animals were again anesthetized and perfused first with saline and then with 2.5% glutaraldehyde and 2% paraformaldehyde in pH 7.4 phosphate buffer. Their brains were removed from the cranium, fixed an additional three hours and placed overnight in

a phosphate buffer with 10% sucrose. On the following day, the brains were frozen and cut at 40 μ m in a cryostat at -10°C. Sections were collected on subbed slides and thoroughly dried. They were then treated by the blue benzidine/sodium nitroferricyanide method (Mesulam, '76).

RESULTS

Wherever possible, we have followed the nomenclature used in cytoarchitectonic studies of previous authors (Warner, '35, '47; Halpern and Frumin, '73; Northcutt and Butler, '74; Molenaar, '77). However, a comprehensive description of the rattlesnake brain has not been made. We have therefore, relied on the terminology used for other reptiles (Northcutt and Butler, '74) and used our best judgment in naming several cell groups.

Figure 1 summarizes the major cell groups of the rattlesnake brain. It shows a series of transverse hemisections stained with cresyl-violet. The cell groups in these sections are labelled on the right.

The results of the tectal HRP injection studies are summarized in figure 2, which shows in diagrammatic form the fiber tracts, cells and injection sites stained with HRP reaction product. The injection sites were approximately 400-500 μ m in diameter (fig. 3). All injections were restricted to the tectum and were centered in the intermediate tectal layers with substantial spread into more superficial layers (figs. 2G,H; 3).

Medulla projections

The result of most immediate interest to us was that HRP activity was absent in the cells of the LTDD in all our animals. Thus we find no evidence for a direct projection from the LTDD to the tectum in the rattlesnake. In fact, we consistently found that only one circumscribed nucleus in the medulla contralateral to the injection sites contained stained cells (figs. 2J-L, 4, 6). This nucleus had not been described in snakes by previous authors. We suggest here that it be named "nucleus reticularis caloris" (RC). RC is made up of large cells approximately 25-45 μ m in diameter (fig. 4). The nucleus is a superficial structure that runs rostrally from a level immediately posterior to the fifth nerve root and ends caudally posterior to the closure of the fourth ventricle (fig. 2, inset). The RC is located on the ventrolateral surface and is ventral and separated from the lateral descending trigeminal

tract (lttd). The lttd in *Crotalus* (figs. 1J-L, 5) closely matches the location and extent of the lttd of boids as described by Molenaar ('78a,b). The lttd shares its rostral boundary with RC and runs parallel to RC for most of its extent. The LTTD, the nucleus of the lttd, overlaps the caudal end of RC and extends into the upper levels of the spinal cord (figs. 1K-M). The LTTD in rattlesnakes is thus more caudal than in boids.

In Bodian-stained material the RC stands out clearly as a collection of transversely planar multipolar cells which are interleaved by large, longitudinally oriented axons of approximately 5 μ m diameter (fig. 5). Immediately surrounding the nucleus are more densely packed tracts of smaller caliber fibers longitudinally oriented. This has the effect of highlighting the region of the RC as a light area on a darker surround. The lttd has a similar light appearance in transverse sections, although it is made up of smaller caliber axons. The LTTD itself, at the caudal end of the medulla and in the uppermost extent of the spinal cord, contains large cells enmeshed in a more densely stained background.

We found HRP-labelled cells throughout almost the entire length of the RC contralateral to the injected tectal lobe. We saw no stained cells in the ipsilateral RC. All brains showed stained cells in the contralateral RC except for the shortest survival time (2 days at 22°C). Longer survival times, seven and nine days, gave denser staining than the shorter times.

The pathway from RC to tectum is clearly demarcated in our HRP material. Fibers exit the nucleus medially and pass near or through the tbsd, crossing the midline in a tope-shaped bump (figs. 2I,J, 6). They then form a longitudinally oriented tract near the ventral surface about one-third the distance lateral from the midline. The tract proceeds rostrally into the caudal tegmentum where it courses dorsally to the tectum along the lateral surface of the brain.

The only other HRP-stained cells in the medulla were scattered in and near the ipsilateral division of the RC-tectal tract (fig. 2J). These scattered, stained cells are clearly medial of the RC.

Other afferent tectal projections

1. Postero-lateral tegmental nucleus (PLT)

A group of HRP-stained cells lies in a narrow dorsoventral band near the lateral edge

of the caudal tegmentum (figs. 1H, 2G). These cells are bilaterally distributed. The contralateral stained cells are more ventrally located than the ipsilateral cells of this nucleus. We can trace a pathway backward from the injected tectum exiting caudal of the third nerve nucleus, running ventrad down the lateral edge of the tegmentum to the ipsilateral postero-lateral tegmental nucleus (fig. 2G). In the longer surviving animals, other fibers in this group course forward in the tegmentum, traverse the diencephalon, cross the supraoptic decussation (fig. 2B), turn caudally and run back to the contralateral tegmentum (fig. 2G). These fibers appear to originate from the cells of the contralateral PLT, although there may exist additional pathways to the tectum that are less prominent by our HRP technique. The location, the bilateral connection of the PLT to the tectum, and the presence of significant acetylcholinesterase activity (Newman, Gruberg, Hartline, in preparation) suggest that this cell group may be part of the nucleus isthmi (Gruberg and Udin, '78).

2. Antero-lateral tegmental nucleus (ALT)

A bilaterally stained cell group lies in the rostral tegmentum (fig. 2F). It is on the same dorso-ventral level as the cells of the postero-lateral tegmental nucleus described above but is not continuous with that cell group and does not show any discernible acetylcholinesterase activity.

3. Dorso-lateral posterior tegmental nucleus (DLT)

Another group of stained cells, contralateral to the injected tectal lobe, lies at the extreme caudal level of the dorsal tegmentum (fig. 2H).

4. Pretectal complex

A set of cells of nucleus lentiformis mesencephali (LM) (fig. 2E) is labelled bilaterally in the pretectal area immediately rostro-ventral of the tectum. Labelled cells are also seen in the ipsilateral nucleus geniculatus pretectalis. The labelled cells of the LM surround an area of dense noncellular staining which we attribute to anterograde filling of the terminals of tecto-pretectal fibers (figs. 2E, 8). We did not see labelled cells in the nucleus posterodorsalis.

5. Lateral geniculate

An ipsilateral group of cells is labelled in

Abbreviations

AC, anterior commissure	on, optic nerve
ALT, antero-lateral tegmental nucleus	OS, superior olive
Ch, cerebellum	ot, optic tract
CD, dorsal horn	P, nucleus paraventricularis
CM, nucleus cochlearis magnocellularis	PD, nucleus geniculatus lateralis pars dorsalis
D, dorsal cortex of telencephalon	PDM, nucleus geniculatus lateralis pars dorsomedialis
DL, nucleus dorsolateralis hypothalami	PE, nucleus lentiformis thalami pars extensa
DLT, dorso-lateral posterior tegmental nucleus	PH, nucleus periventricularis hypothalami
DM, nucleus dorsomedialis	PLT, postero-lateral tegmental nucleus
ds, tract of supraoptic decussation	PO, nucleus preopticus
DVR, dorsal ventricular ridge	PR, nucleus parvocellularis reticularis superior medialis
GC, griseum centrale	RC, nucleus reticularis caloris
GP, nucleus geniculatus pretectalis	RI, inferior lateral reticular nucleus
HbM, medial habenular nucleus	RM, nucleus reticularis medius lateralis
HbL, lateral habenular nucleus	Ru, nucleus ruber
HC, habenular commissure	S, septal region
IPM, nucleus interstitialis pars medialis	SCN, suprachiasmatic nucleus
L, lateral cortex of telencephalon	soc, supraoptic commissure
lfb, lateral forebrain bundle	SON, supraoptic nucleus
LL, nucleus of lateral lemniscus	ST, nucleus of solitary tract
LM, nucleus lentiformis mesencephali	tbd, uncrossed dorsal tecto-bulbo-spinal tract
lttd, tractus descendens lateralis n. trigemini	tbsd, crossed dorsal tecto-bulbo-spinal tract
LTTD, nucleus descendens lateralis n. trigemini	tbtv, uncrossed ventral tecto-bulbo-spinal tract
M, medial cortex of telencephalon	TeO, optic tectum
mfb, medial forebrain bundle	ttd, tractus descendens n. trigemini
MR, nucleus magnocellularis reticularis superior lateralis	VA, nucleus vago-accessorius
ND, Deiters nucleus	VH, nucleus ventralis hypothalami
NH, nucleus of hippocampal commissure	VL, nucleus ventrolateralis
NDs, nucleus descendens n. trigemini	VM, nucleus ventromedialis
NPD, nucleus posterodorsalis	III, third nerve root
NS, nucleus sphericus	VM, motor nucleus of trigeminal
NIII, oculomotor nucleus	VIII, eighth nerve root
NIV, nucleus nervi trochlearis	XMD, nucleus motorius dorsalis nervi vagi

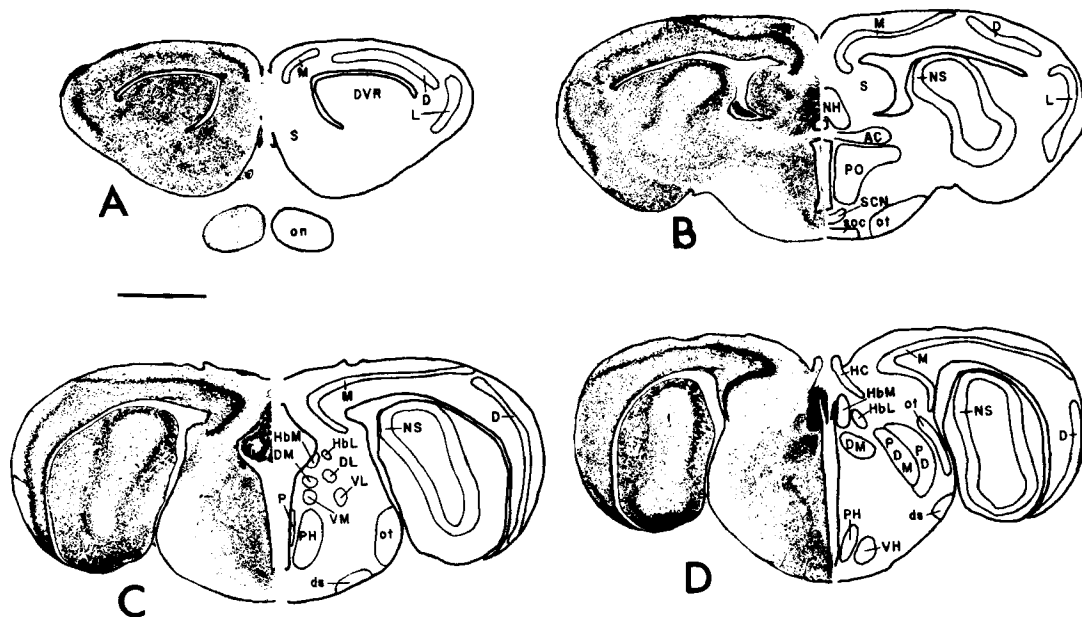


Fig. 1 Cresyl violet stained transverse hemisections of rattlesnake brain on the left. Anatomical subdivisions are shown on right. A is most rostral, N is most caudal. Scale 1 mm. The level at which these sections were made is shown in the inset in figure 2.

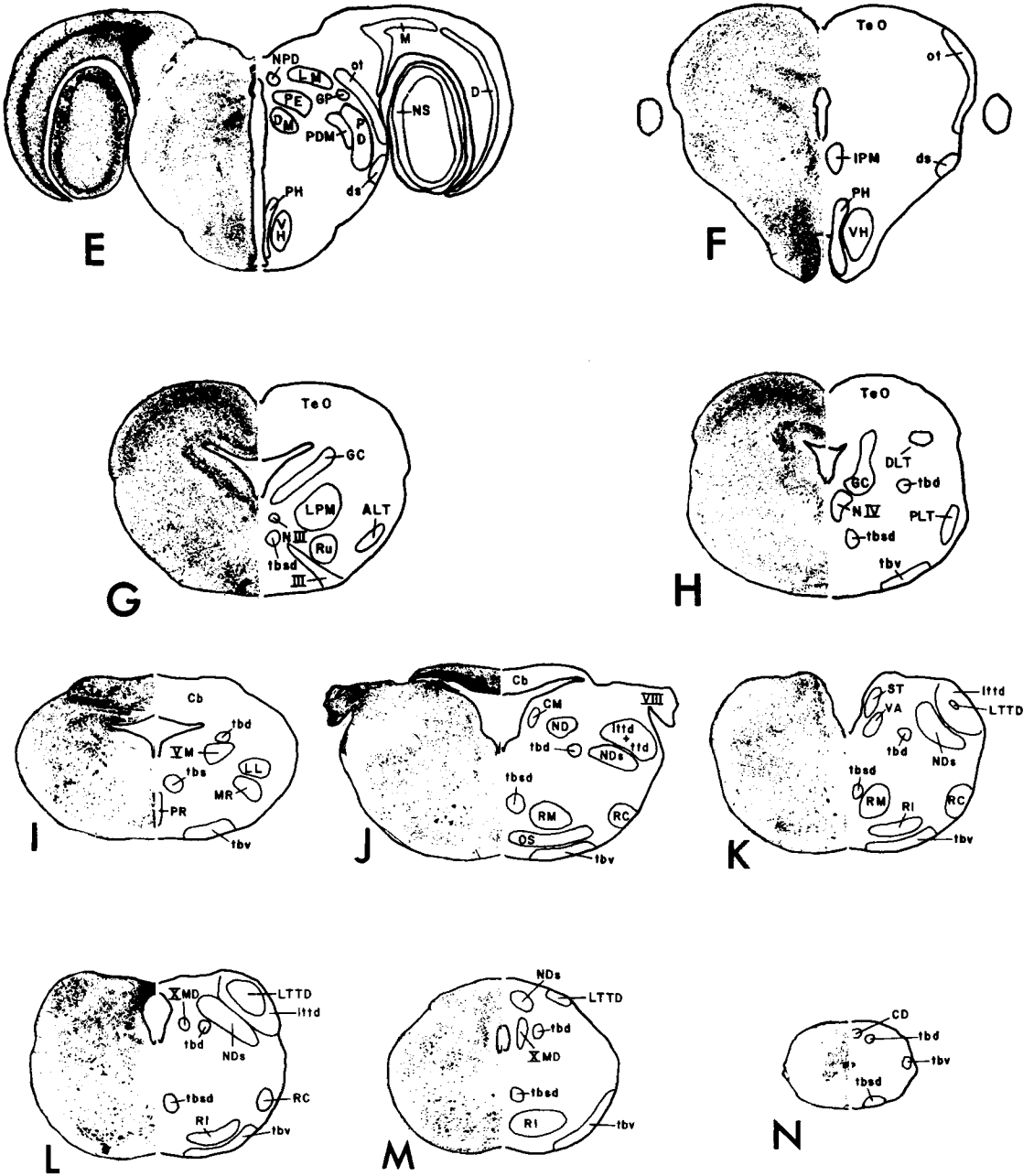


Figure 1

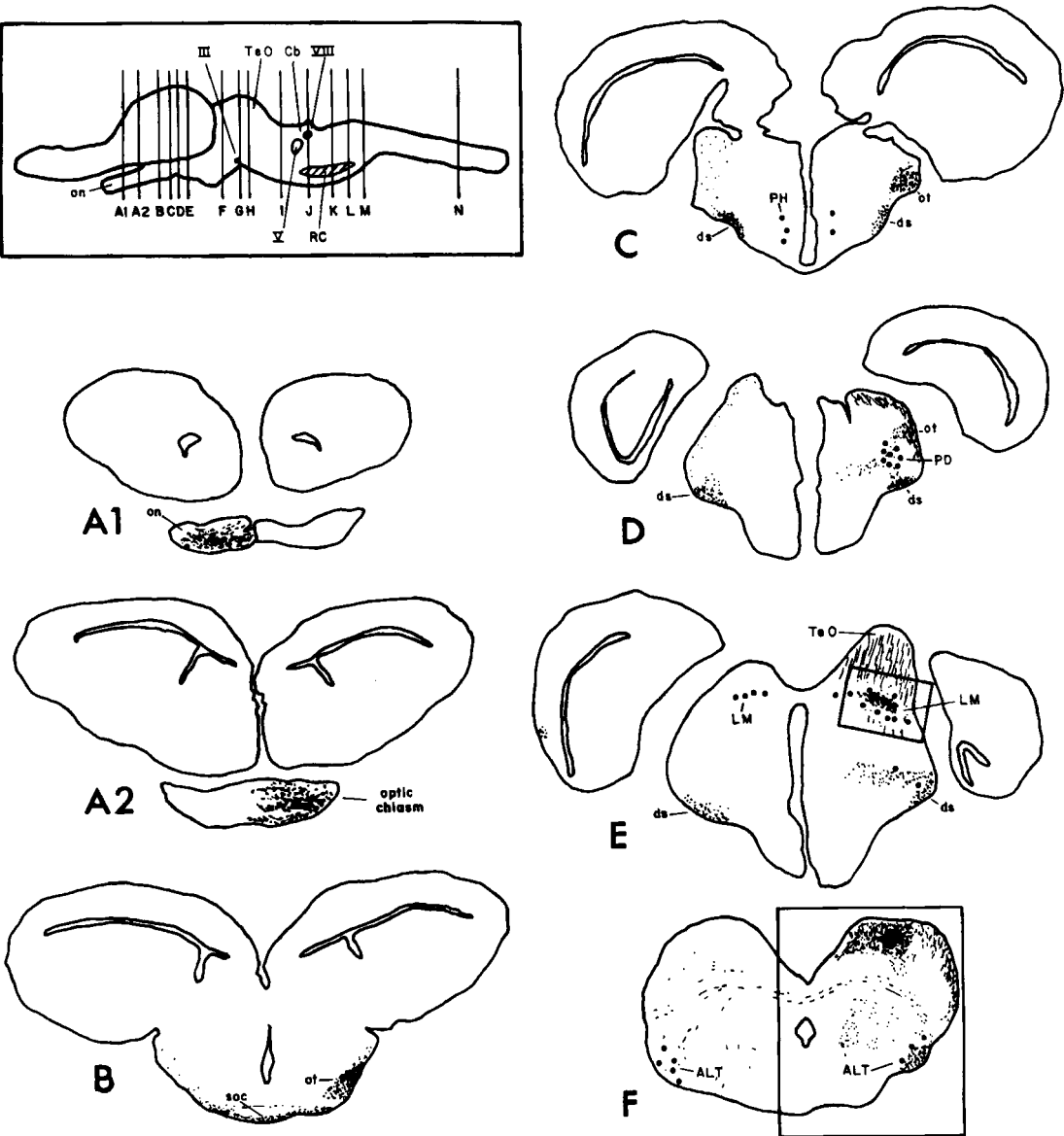


Fig. 2 Camera lucida summary diagrams of distribution of HRP-stained material after tectal injection. Dots and dashes represent stained fibers, filled circles represent stained cells. Sections E, K and L are taken from a 7-day survival animal, all other sections are from a 9-day survival animal. Sections approximately matched with those shown in figure 1 of same alphabetical letter. Section A of figure 1 is between sections A1 and A2 of figure 2.

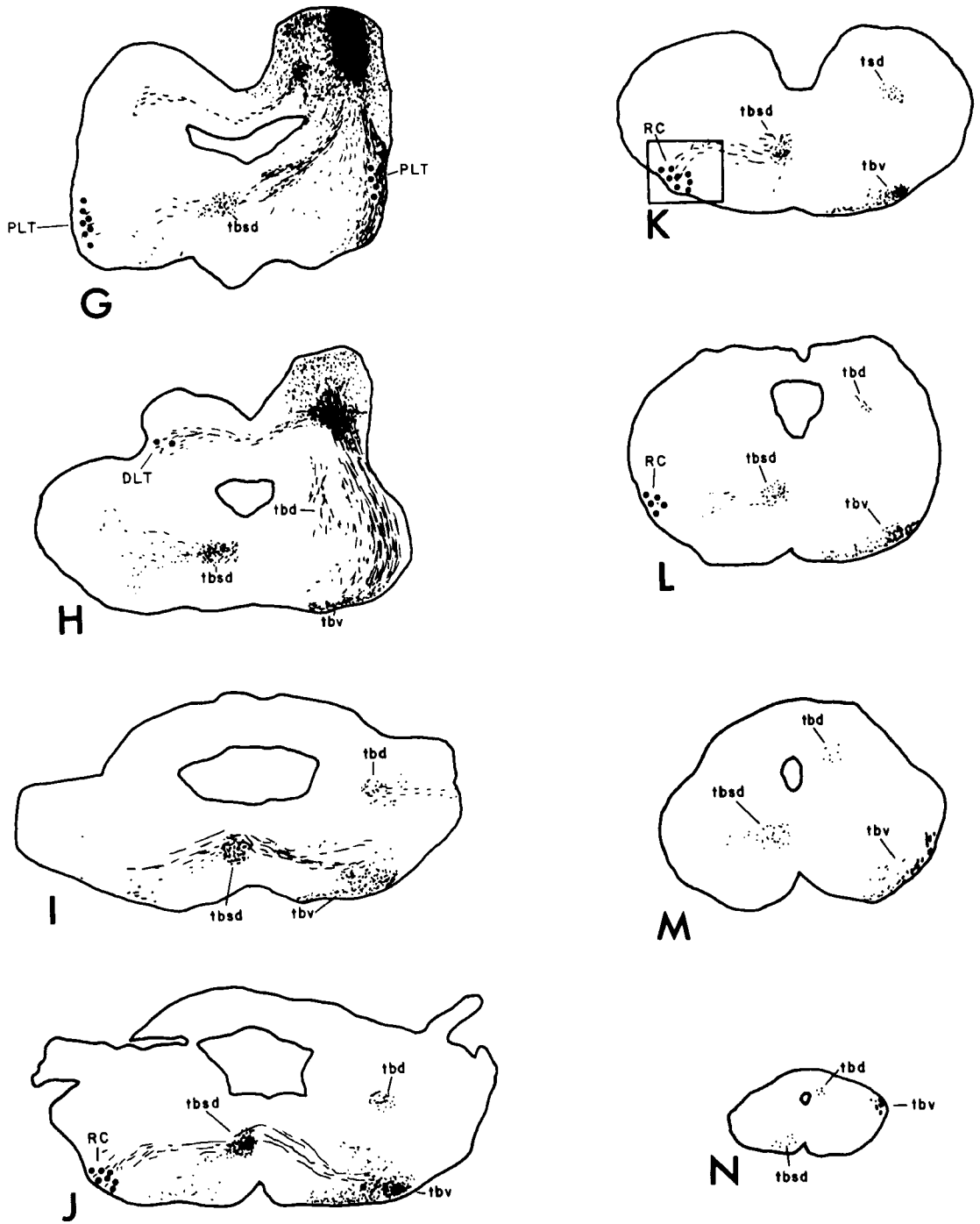


Figure 2

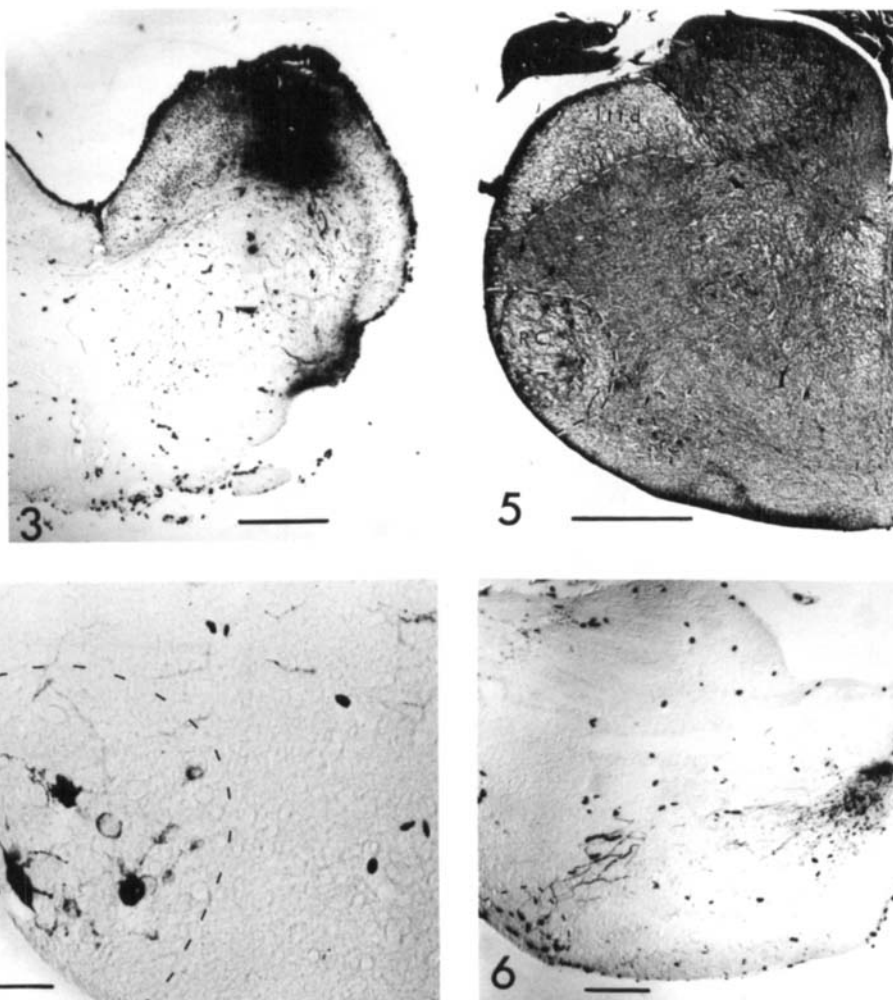


Fig. 3 Typical HRP injection site in the optic tectum (boxed area of fig. 2F). Scale: 250 microns.

Fig. 4 HRP-stained cells of RC contralateral to injection site (boxed area of fig. 2K). Scale: 100 microns.

Fig. 5 Bodian-stained hemisection just caudal to the VIII nerve root. Regions of the ltt and the RC (dashed areas) stand out as lighter areas on darker surround. Several large cells can be seen in RC. Scale: 500 microns.

Fig. 6 HRP-stained RC fibers decussating through crossed tecto-bulbar-spinal tract. Section at approximately level of figure 2J. Scale: 250 microns.

the midthalamus. Following Halpern and Frumin ('73; fig. 1D), we have identified this group as the lateral geniculate nucleus pars dorsalis (PD) (figs. 2D,E). In the dorsal region of this nucleus there is noncellular staining due to anterograde filling of tecto-PD terminals. Other stained fibers run diffusely through an area medial and ventral to the PD.

6. Hypothalamus

Labelled cells are distributed bilaterally in

the periventricular nucleus of the hypothalamus (PH) (fig. 2C).

Other fiber projections

1. Optic nerve fibers exit at the rostral end of the tectum and traverse the diencephalon in a superficial dorso-lateral tract. Further rostrally, the tract sweeps ventrad and joins the optic chiasm. The tract runs separately from the tract of the supra-optic decussation (fig. 2B). In our preparations we find stained

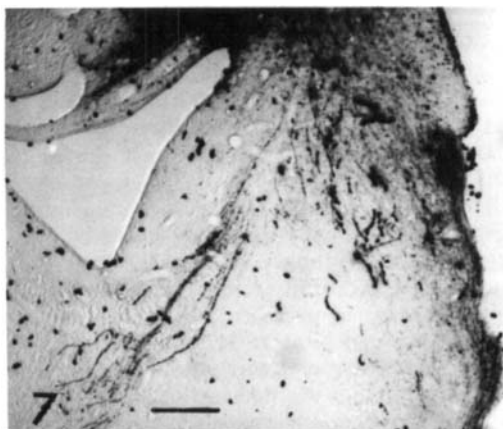


Fig. 7 HRP stain of efferent radiations of tectum at approximately the level of fig. 2G. Scale: 250 microns.

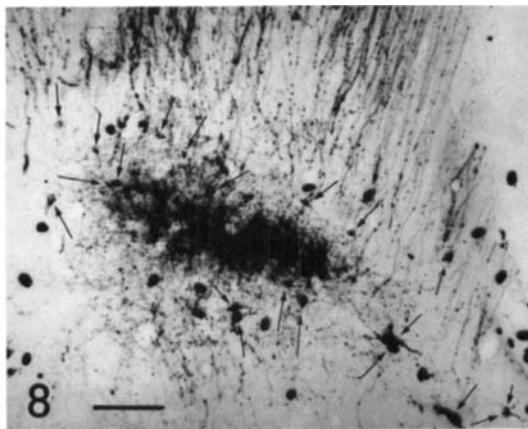


Fig. 8 Pretectal area showing HRP-labelled cells (arrows) and dense fiber staining of tecto-pretectal terminal field (boxed area of fig. 2E). Scale: 100 microns.

fibers only in the optic nerve contralateral to the HRP tectal injection.

2. Tectal commissure fibers are sparsely distributed in the intermediate layers of the contralateral tectum (figs. 2F,G). Some of these fibers can be followed through the contralateral tectum laterally and ventrally to the anterior tegmental field.

3. The main descending projections from the tectum exit from an intermediate tectal layer and course ventrally at approximately the level of the third nerve nucleus. Fibers can be distinguished in three tracts. One set of fibers collects on the ipsilateral ventral surface of the tegmentum (tbv). Another set of uncrossed fibers maintains a more dorsal location (tbd). The third set of fibers (tbsd), which seems comparable to the radiations of Meynert in mammals (Kappers et al., '36), crosses and collects in a deep medial tract of the contralateral tegmentum (figs. 2G, 7). The three tracts can be traced the entire length of the medulla in the same relative locations in transverse sections (figs. 2G-M). Some fibers from tbv and tbsd terminate in a wide area of the neuropil of the ventral tegmentum and ventral medulla. In the spinal cord the tbsd assumes a superficial ventro-medial position (fig. 2N). The tbv shifts to a superficial lateral position. The tbd maintains its relative position. For the survival times we used, we saw no stained cells in the spinal cord.

DISCUSSION

In our preparations, the main cell groups

that project to the optic tectum are: the pretectal complex bilaterally; postero-lateral tegmental nuclei bilaterally; lateral geniculate par dorsalis ipsilaterally; anterior tegmental complex bilaterally; dorso-lateral posterior tegmental nucleus contralaterally; periven-tricular nucleus bilaterally; and the nucleus reticularis caloris contralaterally.

Stanford and Schroeder ('79), using Fink-Heimer degeneration staining after electrolytic lesions, have demonstrated a direct projection from LTTD to the ipsilateral RC in rattlesnakes. They did not find a direct projection from LTTD to the tectum nor to any other cell group that projects directly to the tectum. Our findings, combined with these degeneration results, suggest that RC is the intermediate link connecting the LTTD to the tectum.

It is not clear whether there are structures homologous to RC in other vertebrate species. The RC is closely related to the trigeminal complex given its input from ipsilateral LTTD. It is generally agreed that the primary trigeminal complex in the medulla oblongata of higher vertebrates is divided into two parts — the main (principal) trigeminal nucleus and an elongated descending (spinal) division. The descending division has in turn been divided into three nuclei which are, in rostro-caudal order, the nucleus oralis, the nucleus interpolaris and the nucleus caudalis (Olszewski, '50).

The LTTD in rattlesnakes is located in the caudal end of the medulla and in the rostral spinal cord. This location suggests that the

LTTD is related to, and perhaps is a subdivision of the nucleus caudalis seen in mammals (Olszewski, '50). This is supported by an electron microscope study of the closely related pit viper, *Aghistrodon* (Meszler, '75), which shows that the cellular and synaptic architecture of the LTTD most closely resembles that of the nucleus caudalis.

The nucleus caudalis has been shown to project to the ipsilateral reticular formation in a number of mammals (Carpenter and Hanna, '61; Stewart and King, '63; Dunn and Matzke, '68; Kawamura, '71; Roberts and Matzke, '71; Tiwara and King, '74). Additionally, Tiwara and King found a small projection from the lateral reticular formation to the contralateral tectum. However, their lesions in the reticular formation were adjacent to the nucleus caudalis and not more rostral where the bulk of the nucleus caudalis-to-reticular formation projection lies (Darian-Smith, '73; Carpenter and Hanna, '61; Stewart and King, '63). Thus in mammals no direct projections have been found from the primary trigeminal nuclei to the tectum. There exists, however, an area of the reticular formation which receives trigeminal input and in turn projects to the contralateral tectum. This suggests that the LTTD-RC-tectal pathway of the rattlesnake may be homologous to the trigeminal-reticular formation-tectal pathway of other species.

On the other hand, Molenaar, in a Fink-Heimer study of the python, describes a direct projection from LTTD to the contralateral tectum. The conflict between Molenaar's finding and our own work on the rattlesnake, where we find no such direct projection, could be due to species differences. The python and rattlesnake belong to two distantly related families of snakes. Thus in the python, the cells of RC, instead of forming a separate nucleus, may be intermingled with the cells of the LTTD. This is in keeping with the observations of Molenaar and Fizaan-Oostveen ('78) who, in a Fink-Heimer study, described an elaborate intranuclear projection within the LTTD.

Auen ('78) recently reported that HRP injections in the tectum of the rattlesnake lead to retrograde filling of cells in the contralateral LTTD (called "LTD" by Auen). We cannot account for the difference between our work and his. We consistently filled cells of RC and not LTTD. We are puzzled by his results, because the location of his HRP-stained

cells in the LTD are shown to be at the level of the VIII nerve root (his fig. 1D). This location is much forward of where we find the LTTD in a similar rattlesnake species, but is on a level with the RC. However, his drawing shows filled cells in a location distinctly dorsal to where we find the RC.

The tectal afferent groups we have found agree significantly with those found by Wilczynski and Northcutt ('77) in the frog. Following HRP tectal injections, they found that cell groups in the pretectal area of the lateral nucleus stained bilaterally, and that cells in the dorsal posterior nucleus and large-celled pretectal nucleus stained ipsilaterally. In the tegmentum the anterodorsal, posterodorsal and posteroventral fields had HRP-stained cells ipsilaterally; the ventral preoptic nucleus and suprapeduncular nucleus were stained bilaterally, and the nucleus isthmi was stained ipsilaterally. In the frog, Gruberg and Udin ('78) found bilateral input to the tectum from the nucleus isthmi.

Ulinski ('77) used degeneration staining to study tectal efferent connections in the banded water snake. He found bilateral projections to the brainstem reticular formation, the nucleus lentiformis mesencephali, lateral habenular nuclei and posterodorsal nuclei and the dorsal lateral geniculate nucleus (densely). He found ipsilateral projections to the ventral lateral geniculate, the suprapeduncular nucleus, the caudal thalamus (diffusely throughout its central part) and the basal optic nucleus. In addition he found fibers in the contralateral tectum.

There is thus substantial similarity between well-known connections of cold-blooded vertebrate tecta and connections that we have demonstrated in rattlesnake. In addition, we have found a nucleus in the medulla, the RC, which is a strong candidate for the link that relays infrared information from the LTTD to the intermediate layers of the optic tectum. Possible parallels of this trigemino-tectal pathway exist in mammals. It now remains to be determined whether the RC in rattlesnakes contains infrared-sensitive neurons and whether its mammalian counterpart, if it exists, is involved in thermoreception.

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