THE CENTRAL PROJECTIONS OF THE MESENCEPHALIC ROOT OF THE TRIGEMINUS IN A LIZARD *(LACERTA VIRIDIS)*

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(Accepted February 7th, 1969)

INTRODUCTION

The mesencephalic root of the trigeminus (MRT) has been studied in many vertebrates using both normal and experimental preparations. Since there are extensive reviews of the literature on the anatomy of the MRT[10,27] only the pertinent references will be cited. Prior experimental investigations designed to study this system have employed either the Marchi technique[1,3,15,20,26], the Bielschowsky gross technique[24], or a modified Nauta technique[22].

Collectively these studies have shown that the nucleus of the mesencephalic root of the trigeminus (NMRT) gives rise to the fibers of the MRT, but descriptions of the latter's distribution are at variance. In submammalian forms the cells which constitute this nucleus extend throughout the length of the tectum. In mammals there is an augmentation of the caudal part of the NMRT with its posterior limit found at the level of the motor nucleus of the trigeminus[10,27].

It was previously shown that in some reptilian forms[27,30] the NMRT is located in the tectum with a majority of its cells confined within the limits of the optic tectum (such is the case in *Lacerta viridis*). Because of the unique location of the NMRT in reptiles, as oppossed to mammals, a lesion restricted to the optic tectum would: (1) destroy the majority of the cells of this nucleus and (2) would not involve tegmental structures.

The purpose of this study was to determine the origin and distribution of the mesencephalic root of the trigeminus in *Lacerta viridis* by means of the Nauta silver method, following lesions to the optic tectum. The results of our investigation confirm earlier reports and contribute new information about this proprioceptive system in lizards.

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MATERIALS AND METHODS

Fifteen specimens of *Lacerta viridis* ranging in length from 22 to 26 cm and weighing 24–28 g were used in this study. The animals were anesthetized with ether and with the aid of a dissecting microscope a dorsal approach to the left tectal area was made with a dental burr. The temporalis muscle was retracted, the underlying bone chipped away, the dura mater incised and folded to one side, and a portion of the pia arachnoid covering the left optic lobe was removed. Unilateral tectal lesions were attempted using suction or electrolysis. The wound area was then packed with gelfoam and covered with surgical tape.

The animals were maintained pre- and postoperatively in an environmental temperature of about 27°C. After a survival period of 12–24 days they were sacrificed with an overdose of ether, perfused through the heart with a 0.65% NaCl solution followed by a 10% non-neutral formalin solution. The dorsal portion of the brain was then exposed and the entire head placed in a 10% formalin solution for several days of *in situ* fixation. The brain and the first few segments of the spinal cord were removed *in toto*, freed of their meninges and placed into 10% formalin. The brain was transferred to a 30% sucrose in 10% formalin solution 3–5 days prior to sectioning. Serial frozen sections were then cut at 20 μ, stained by the Nauta method[16] and subsequently placed on slides in a serial arrangement[8].

Normal brains of Lacerta viridis were sectioned in the 3 conventional planes and stained by a cresyl violet method to facilitate identification of the various brain stem nuclei. Cell counts based on the presence of a nucleolus were made of the nucleus of the mesencephalic root of the trigeminus.

OBSERVATIONS

Nature of degeneration

The histological characteristics of degenerated fibers and their terminations in both long (20–24 days) and short (12–14 days) survival groups were found to correspond to those described in reptiles by Kosareva[14] and Jacobs[8]. The term 'terminal degeneration', as used in the present study, has a meaning similar to that given the term by Heimer[6] and denotes degenerated axonal arborizations as well as their synaptic terminal structures.

The nucleus of the mesencephalic root of the trigeminus

The large, ovoid cells which make up this nucleus are found both in a lateral position in the optic lobes and in a medial position above the roof of the aqueduct (Fig. 1). The medial group begins just rostral to the posterior limit of the posterior commissure and extends caudalward through the regions of the optic tectum and torus semicircularis to a point opposite the midportion of the trochlear nucleus (Fig. 2). The lateral group begins just rostral to the anterior limit of the posterior commissure

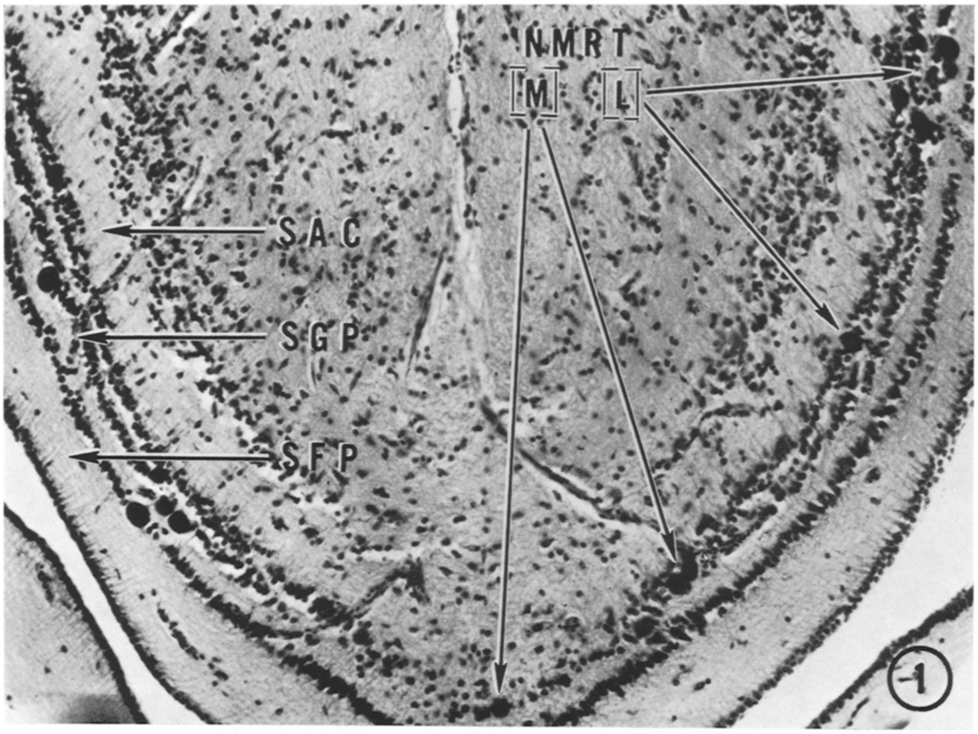


Fig. 1. Photomicrograph of a transverse section through the optic tectum of a lizard, showing the location of the medial (M) and lateral (L) groups of the nucleus of the mesencephalic root of the trigeminus (NMRT) in the stratum griseum periventriculare (SGP). Cresyl violet stain. × 120.
See page 318 for abbreviations in this and following figures.
Fig. 2. Photomicrograph of a transverse section through the torus semicircularis of a lizard, showing the caudal portion of the medial group of the NMRT. Note the absence of the lateral group at this level. Cresyl violet stain. × 120.

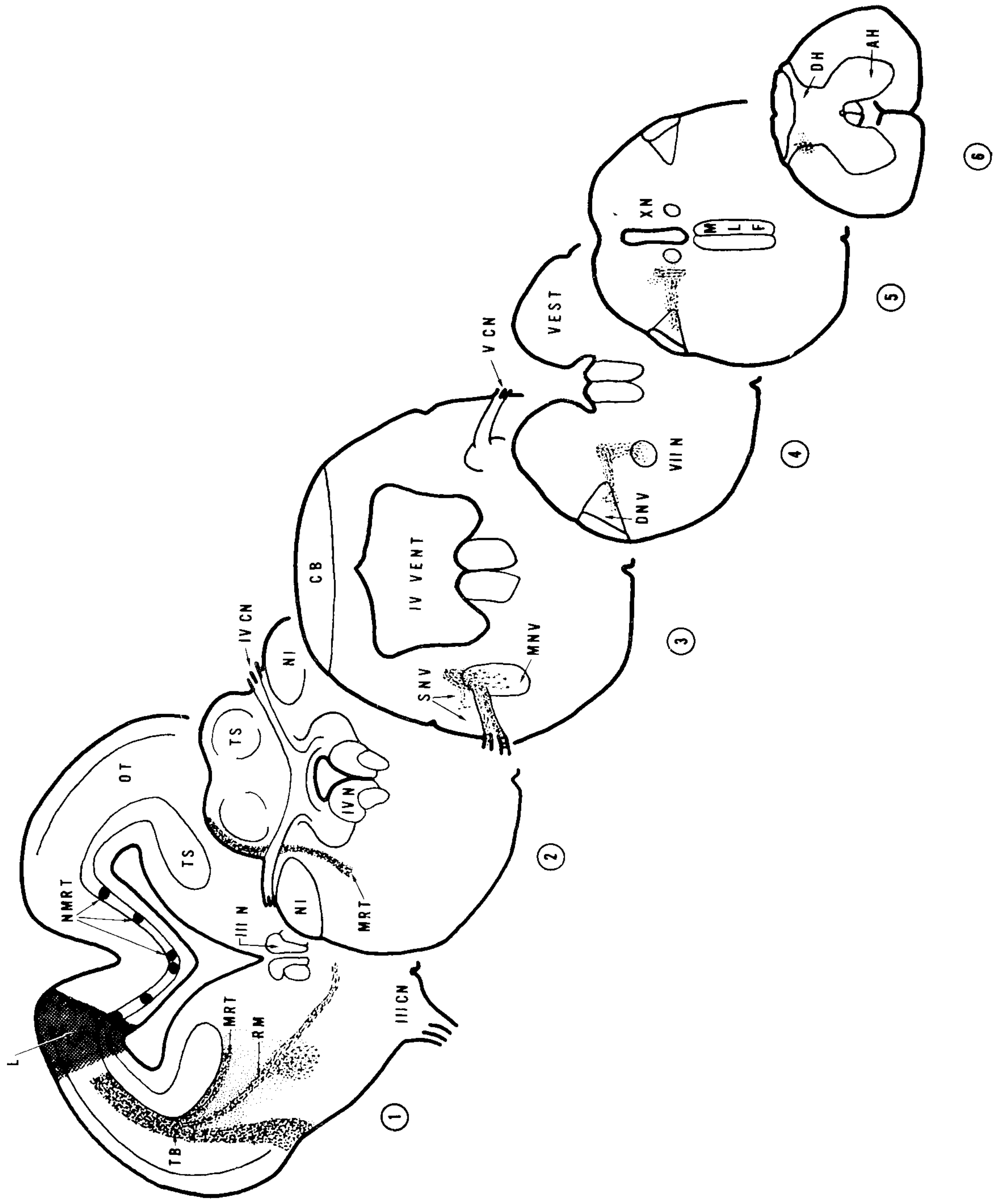
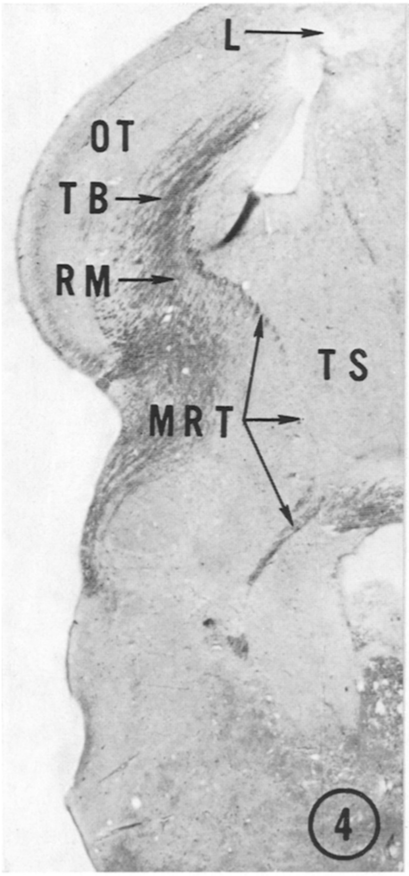


Fig. 3. A series of projection drawings from Nauta-stained brain stem sections of a lizard (LE 35) having a lesion in the optic tectum. Section 1 depicts the relative density of the total degeneration at the midbrain level just caudal to the lesion. Sections 2–6 show only the course and distribution of MRT degeneration through the various brain stem and cervical spinal cord levels.



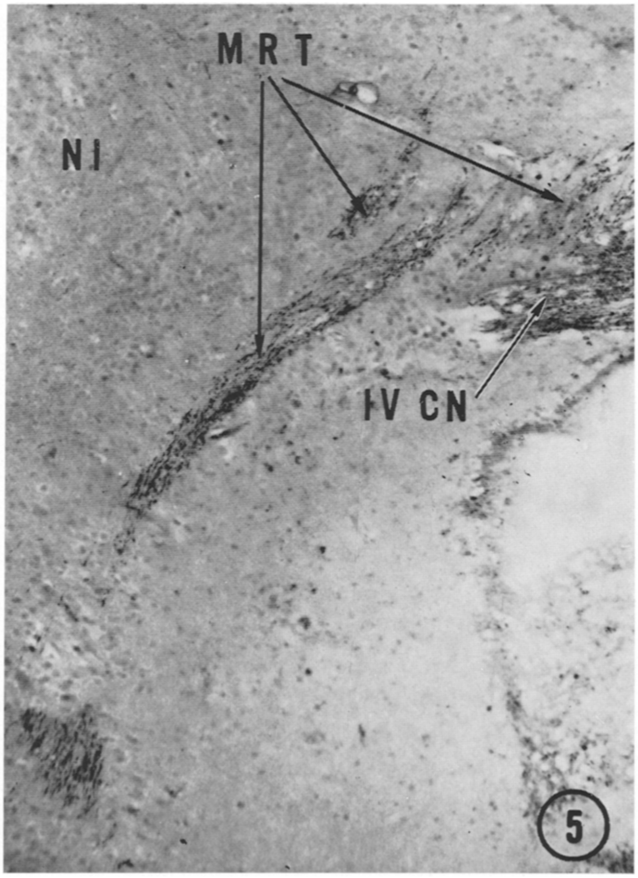


Fig. 4. Photomicrograph of a transverse section through the optic tectum, torus semicircularis and rostral medulla. Note the degenerated fibers of the MRT as they course from the lesion site along with the tecto-bulbar tract and the radiations of Meynert. Nauta stain. × 25.

Fig. 5. Photomicrograph showing degenerated fiber bundles of the MRT passing dorsally and laterally to the ascending root of the trochlear nerve. Detail of Fig. 1 at higher magnification. Nauta stain. × 250, transverse section.

and extends to the caudal limit of the optic tectum (Fig. 1). The cells, symmetrically arranged in both the right and left optic lobes, are confined to the layers of the stratum griseum periventriculare. By cell counts (based on the presence of a nucleolus in the cell) approximately 90% of the NMRT cells are confined to the optic tectum in *Lacerta viridis*, with approximately 60% of this number accumulated in the rostral two-thirds of the nucleus.

Lesions

Microscopic examination reveals that in 12 of the 15 animals used in this study the lesions are confined to some area of the optic tectum (ipsilaterally and bilaterally). In 9 cases the lesions involve all tectal layers, but in 3 animals the lesions are too shallow to involve the stratum album centrale (SAC) which contains the fibers of the mesencephalic root of the trigeminus.

The description of the course of the mesencephalic root of the trigeminus (MRT) is based on the findings in the 9 animals having lesions which involve all tectal layers, and the pattern of degeneration observed in lizard LE 35 is illustrated (Fig. 3). The differences in quantity and patterns of degeneration will be pointed out where necessary. In 3 lizards with restricted lesions superficial to the SAC no evidence of degeneration is seen throughout the distribution of the MRT.

Mesencephalic root of the trigeminus in the midbrain

The mesencephalic root of the trigeminus (MRT) courses ipsilaterally within the stratum album centrale (SAC) of the optic tectum as a broad sheet of small fiber bundles (Fig. 3, 1). In the dorsal portion of the optic lobe the MRT fibers pass with the tecto-bulbar tract and the radiations of Meynert. Near the ventrolateral angle of the tectal ventricular recess the MRT fibers turn ventrally with, and then separate from, the radiations of Meynert by taking a more dorso-medial position within the SAC (Fig. 4). These fiber bundles then fan out over the lateral aspect of the torus semicircularis and are located dorsally, laterally, and ventrally to it as they pass more caudally into the isthmus region. At the level of the anterior medullary velum the degenerated fibers of the MRT run dorsally and laterally to the ascending root of the trochlear nerve. Ventral to the cerebellar commissure the small bundles of degeneration collect in a compact tract which passes obliquely along the medial aspect of the nucleus isthmi (Fig. 3, 2).

The composition of the MRT fascicles is best demonstrated in a cross-section of the isthmus region (Fig. 5). Within each individual bundle there are both large and small degenerated fibers. The debris of axonal degeneration appear as drop-like fragments along the course of the fiber, some of which present large spherical and ovoid swellings interconnected by very fine threads.

MRT at the level of the root exit and motor nucleus of V

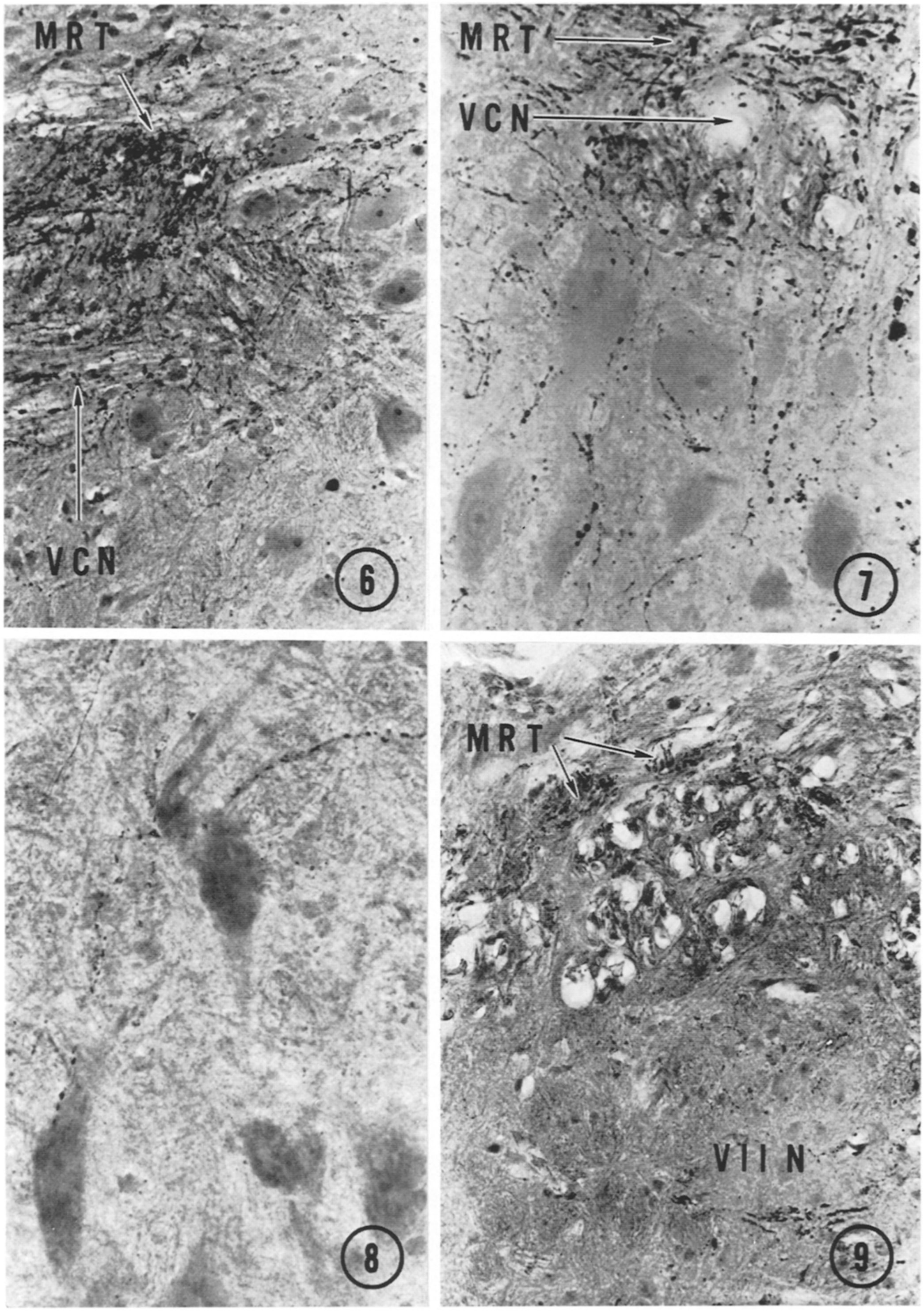
In its ventrocaudal course, the MRT lies adjacent to the lateral recess of the 4th ventricle and medial to the main sensory nucleus of V (Fig. 3, 3). In most cases there

Fig. 6. Photomicrograph showing axonal arborization extending from the MRT into the dorsomedial portion of the MNV. Note the degeneration within this nucleus and other axonal fragments coursing with the trigeminal nerve. Nauta stain. × 250, transverse section.

Fig. 7. Photomicrograph showing terminal distribution of the MRT fibers among the large rostroventral cells of the MNV. Note characteristic bead-like elements near the cell soma. Nauta stain. × 400, parasagittal section.

Fig. 8. Photomicrograph showing a small number of degenerated MRT terminals on the large cells of the caudoventral portion of the MNV. Nauta stain. × 400, transverse section.

Fig. 9. Photomicrograph showing fine beaded axons passing into the dorsal portion of the motor nucleus of VII. Note caudally directed portion of the MRT coursing just above the rootlets of the facial nerve. Nauta stain. × 250, transverse section.


MRT
VCN
6
MRT
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MRT
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are a few degenerated fibers which enter the neuropil of this nucleus. More caudally the MRT fibers pass through the dorso-lateral area of the motor nucleus of V (MNV). At this level numerous degenerated fibers are issued to the MNV. In cross-section (Fig. 6) terminal degeneration surrounding the smaller, more rounded cells of the dorsomedial portion of this nucleus appears as irregular or rounded drop-like fragments near the cell surface. In a sagittal section (Fig. 7) a more uniform distribution of degeneration is demonstrated among the larger more ventrally positioned cells of the MNV. Spreading ventrally from the main MRT bundle terminal degeneration is displayed by characteristic bead-like forms near one side of a cell soma. The rostral half of the MNV appears to receive a larger number of degenerated fibers (both stem fibers and collaterals) from the MRT than are issued to the caudal half of the nucleus (Fig. 8). Opposite the midportion of the MNV the MRT divides into a ventrolateral and a dorsomedial fiber group. The ventrolateral bundle leaves the brain stem as part of the trigeminal nerve, while the dorsomedial group continues caudally within the brain stem (Fig. 3, 2–6). Scattered throughout the trigeminal nerve, remnants of many large axons and a few smaller axons can be distinguished (Fig. 6).

MRT caudal to the V exit

Caudal to the exit of the trigeminal nerve the remainder of the MRT (dorsomedial portion) is composed of several fascicles of degenerated fibers. At this level these fibers lie ventral to vestibular nuclei and dorsal to the motor nucleus of the facial nerve (Fig. 3, 4). A few degenerated fibers enter the most dorsal part of the facial nucleus in the form of very thin strands of beaded fragments (Fig. 9). No degeneration is seen in the peripheral facial nerve or the vestibular region. Throughout the caudal portion of the medulla the MRT descends along the ventromedial aspect of the descending nucleus of V (DNV) (Fig. 3, 4 and 5). Concomitantly there is a reduction in the number of MRT fibers due to the projection of many small fibers into the DNV and surrounding cell groups (Fig. 10).

In the most caudal portion of the medulla the descending fibers deviate from their relatively straight course and follow the pronounced ventral flexure of the medulla. In this caudal course the degenerated fibers of the MRT lie ventrolateral to the solitary fasciculus and lateral to the dorsal motor nucleus of X (Fig. 3, 5) with an

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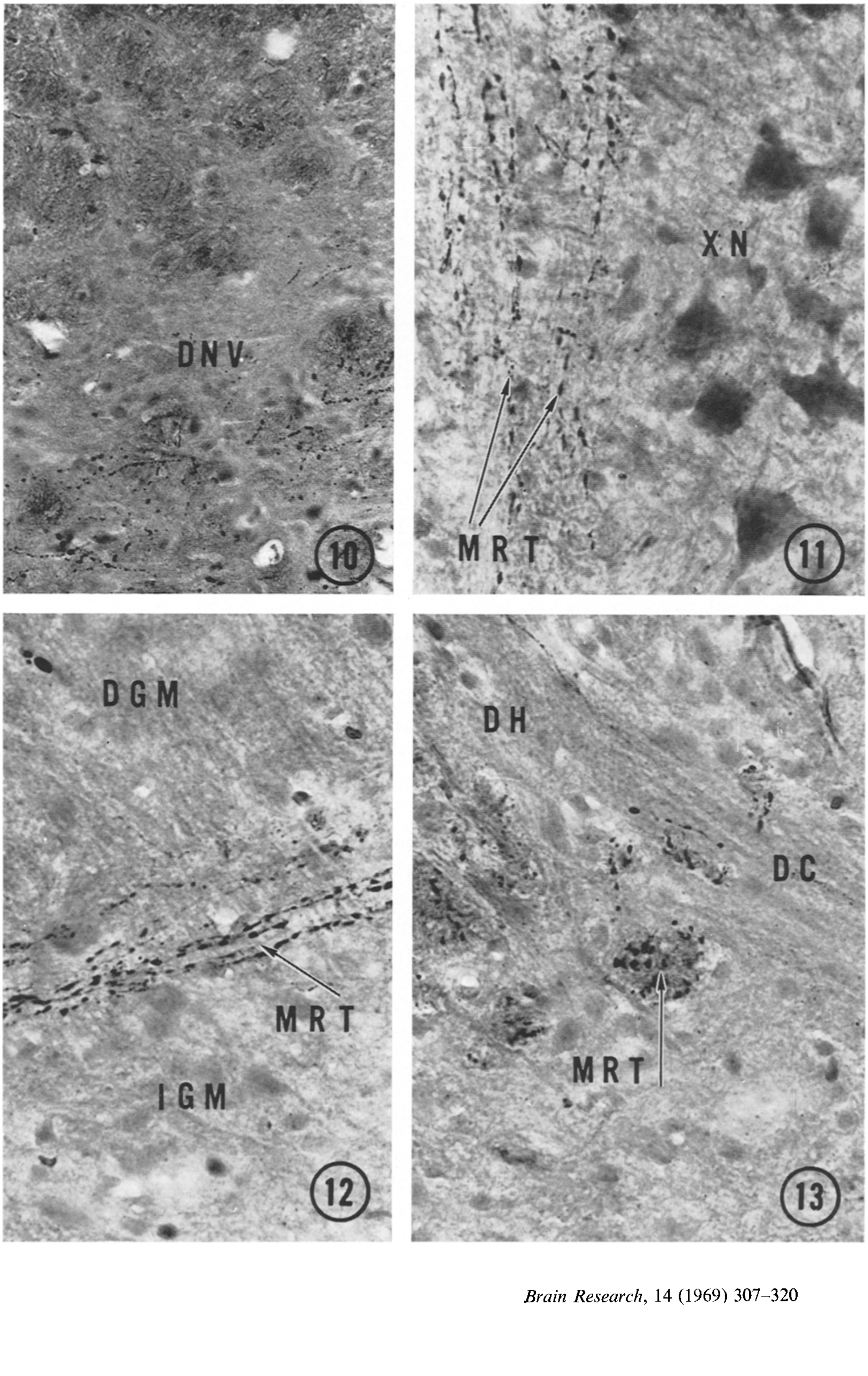
Fig. 10. Photomicrograph showing a few degenerated MRT fibers passing into the descending nucleus of V at the level of the VII nerve. Nauta stain. × 400, transverse section.

Fig. 11. Photomicrograph showing descending MRT fibers passing lateral to the area of the dorsal motor nucleus of X. Very sparse degenerated fragments are seen in this nucleus. Nauta stain. × 400, transverse section.

Fig. 12. Photomicrograph showing degenerated MRT fibers passing through the first cervical segment of the spinal cord. Note that these axonal fragments lie between dorsal and intermediate gray matter. Nauta stain. × 250, parasagittal section.

Fig. 13. Photomicrograph of the first cervical segment of the spinal cord showing degenerated MRT fibers within the fasciculus proprius. Note a few fine degenerated axons passing into the base of the dorsal horn. Nauta stain. × 250, transverse section.


DNV
10
XN
MRT
11
DGM
MRT
IGM
12
DH
DC
MRT
13

occasional terminal fiber entering the neuropil of the latter nucleus (Fig. 11). At the medullo-spinal junction fibers of the MRT enter the cervical spinal cord ventral to the dorsal horn (Fig. 3, 6). These fibers lie within the fasciculus proprius between the lateral funiculus and the dorsal portion of the intermediate region of the gray column (Fig. 12). In the first segment of the cervical cord a few fibers leave the descending tract and terminate among the cells of the dorsal horn (Fig. 13). Terminal degeneration in the dorsal horn appears as spherical or rounded drop-like forms. An occasional degenerated fiber in the dorsal commissure projects toward the midline but in none of the animals is there any evidence of decussation in the spinal cord or any region of the medulla. In this investigation the most caudal extent of the tract was not determined.

DISCUSSION

In the present investigation of the Nauta-stained brain sections, the course and distribution of the mesencephalic root of the trigeminus (MRT) has been determined. Our results, using this improved silver method for axonal degeneration, confirm and add to the prior normal and experimental studies on this system.

Concerning the origin of the MRT there is little disagreement between this study and earlier reports that the nucleus of the mesencephalic root of the trigeminus (NMRT) gives rise to this fiber tract[5,9,10,23,25,27,30]. Some investigators have considered the locus coeruleus as an additional site of origin for the MRT[1,17,26]. In the present study in *Lacerta viridis*, the lesions in the optic tectum did not involve the locus coeruleus, hence, the degeneration of the MRT here described is considered to originate from the NMRT.

Our findings concerning the course of the MRT through the midbrain and isthmus are essentially in accord with earlier descriptions[9,27,30]. Our results, however, have failed to confirm distributions of MRT fibers to: (i) the oculomotor nucleus[19,30], (ii) the oculomotor nerve[25], (iii) the torus semicircularis[23], (iv) the trochlear nucleus[19], or (v) the trochlear decussation[29,30].

A few authors have described in reptiles and mammals direct connections of the MRT that extend into the cerebellum via the anterior medullary velum[4,18,23]. Cupédo[4] referred to this portion of the MRT as a trigeminal midbrain-cerebellar fiber connection. A second midbrain-cerebellar fiber connection, the tractus tecto-cerebellaris, has been demonstrated by Weston[28], and others[5,7,10–12]. There is general agreement among these investigators concerning the course and termination of the midbrain-cerebellar fiber connections but their data concerning the origin of these tracts show discrepancies. The present study in *Lacerta viridis* has produced no evidence of MRT fibers passing into the cerebellum via the anterior medullary velum. Since none of our lesions involved the torus semicircularis (nucleus posterior tecti) we can not confirm Kashiwamura's[11] statement that the fibers of the reptilian tractus tecto-cerebellaris arise chiefly from this nucleus, nor are we able to substantiate the findings of Cupédo[4] who noted that the trigeminal midbrain-cerebellar tract in the rat arises from the caudal cells of the NMRT.

The descending fibers of MRT are distributed largely to the brain stem in relation to the trigeminal complex. The present study has provided new data concerning these projections.

Szentágothai[24] and others[5,21,26,30] have demonstrated in mammals a projection of the MRT to the motor nucleus of V (MNV). In our investigation the lesions were restricted to the optic tectum. This involved the rostral portion of the NMRT which has anatomical connections mainly with the rostral area of the MNV. Since the caudal NMRT was spared so as not to involve the torus semicircularis, it was not possible to conclude whether these cells would project mainly to the more caudal region of the MNV. Such a topographical arrangement may exist.

Our results confirm earlier findings in reptiles[23,27,30] of MRT fibers emerging from the brain stem with the trigeminal nerve. There is no mention in these earlier descriptions, however, of a division of the MRT which extends through the brain stem caudal to the trigeminal roots. In the cat, Probst[20] first outlined this caudal extension of the MRT. A number of authors have confirmed Probst's description in various mammals, and have referred to these fibers as Probst's tract[3,18,25,29] or as a descending portion of the MRT[5,13,22,24,26]. In general these authors agree on the origin of the fiber group but their descriptions of its caudal distribution vary.

In our material the descending portion of the MRT appeared to issue only a few axons to the dorsal portion of the facial motor nucleus, suggesting that this nucleus is not a principal site of MRT termination. Herrick[5], Thelander[26], and Kimmel[13], who reported similar findings in their investigations, mentioned that these fiber connections could possibly constitute a reflex pathway between the trigeminal complex and the facial nucleus.

In contrast to our findings, previous investigations, using normal and Marchi preparations, had revealed no evidence of MRT connections with the descending nucleus of V (DNV). The presence of terminal degeneration within the DNV is a constant finding in the lizard and confirms the observation of Rubinson[22] in the frog. Thelander[26] noted in the cat degenerating MRT fibers passing through the sensory nucleus of V (SNV) to enter the descending spinal tract of V.

In addition to MRT connections to the nuclei of mastication[2,18,25], the Lacerta demonstrated a few axonal terminals in the neuropil of the dorsal motor nucleus of X.

The greatly reduced numbers of degenerated fibers in the ipsilateral portion of the cervical spinal cord suggests that the MRT may not extend caudally beyond the upper cervical segments. Rubinson[22] reported fibers distributed to the contralateral intermediate region of the cervical spinal cord in the frog, but interpreted these as part of the descending tectal system. Szentágothai[24], in cats, described a degenerated fiber group of the MRT extending caudally as far as the ventral horn cells of C1 and C2 after giving off fibers to the caudal cells of the XII nucleus.

In contrast to some reports[5,18,29,30], our investigation has shown no evidence of a decussation in any part of its course.

Lesions which involve all tectal layers undoubtedly destroy many tectal efferent systems. While the tecto-bulbar, tecto-spinal, tecto-reticular, etc. fibers were observed but not reported upon in this paper, our study cannot exclude the possibility that some of these fibers may travel with the mesencephalic root of the trigeminus.

LIST OF ABBREVIATIONS USED IN THE FIGURES

AH	= anterior horn	RM	= radiations of Meynert
CB	= cerebellum	SAC	= stratum album centrale
DC	= dorsal commissure	SFP	= stratum fibrosum periventriculare
DGM	= dorsal gray matter	SGP	= stratum griseum periventriculare
DH	= dorsal horn	SNV	= sensory nucleus of V
DNV	= descending nucleus of V	TB	= tecto-bulbar tract
DTV	= descending tract of V	TS	= torus semicircularis
IGM	= intermediate gray matter	Vest.	= vestibular nuclei
L	= lesion site	III CN	= oculomotor nerve
MLF	= medial longitudinal fasciculus	III N	= oculomotor nucleus
MNV	= motor nucleus of V	IV CN	= trochlear nerve
MRT	= mesencephalic root of the trigeminus	IV N	= trochlear nucleus
		IV Vent	= IVth ventricle
NI	= nucleus isthmi	V CN	= trigeminal nerve
NMRT	= nucleus of the mesencephalic root of the trigeminus	VII N	= facial nucleus
		X N	= dorsal motor nucleus of X
OT	= optic tectum		

SUMMARY AND CONCLUSIONS

A study was made of the descending fiber projections of the mesencephalic root of the trigeminus in *Lacerta viridis*. Twelve lizards with lesions of the optic tectum (unilateral and bilateral) were studied, using the Nauta silver method for identification of degenerated axons. The following results were obtained:

1. The fibers of the mesencephalic root of the trigeminus (MRT) originate from the nucleus of the mesencephalic root of the trigeminus (NMRT) which is located in the stratum griseum periventriculare of the optic tectum. The possibility cannot be excluded that other cells of this layer contribute fibers to the MRT which pass into the caudal medulla and the first few segments of the cervical spinal cord.

2. No evidence was found of direct projections from the rostral part of the NMRT to the (a) oculomotor nucleus, (b) oculomotor nerve, (c) torus semicircularis, (d) trochlear nucleus, (e) trochlear decussation, or (f) cerebellum.

3. Numerous MRT fibers are distributed to the trigeminal motor nucleus, apparently in larger numbers to the rostral than to the caudal parts of the nucleus.

4. Many MRT fibers emerge from the brain stem via the roots of the trigeminal nerve, while other MRT fibers continue caudally and are distributed ipsilaterally to the: (a) descending nucleus of V, (b) motor nucleus of VII, and (c) motor nucleus of X.

5. A few MRT fibers enter the upper segments of the cervical spinal cord in the lateral fasciculus proprius. Some of these fibers appear to terminate among the cells of the dorsal horn.

6. No evidence of decussation was found throughout the descending course of the MRT.

ACKNOWLEDGEMENT

This study was partially supported by Grant AM 06705 from the U.S. Public Health Service.

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