THE JOURNAL OF COMPARATIVE NEUROLOGY 204:268-279 (1982)

Axon Morphology of Mesencephalic Trigeminal Neurons in a Snake, *Thamnophis sirtalis*

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ABSTRACT

The morphology of single axons of mesencephalic trigeminal neurons (Mes V) was studied in the eastern garter snake *(Thamnophis sirtalis)* by solid filling them with an extracellular horseradish peroxidase technique. Each Mes V axon can be divided into central, peripheral, and descending branches. The *central* branch descends from its soma of origin in the midbrain to the dorsal aspect of the motor nucleus of the trigeminal (Motor V) and the motor root, where it splits into peripheral and descending branches. The *descending* branch travels caudally from Motor V to the brainstem-spinal cord junction. The *peripheral* branch passes dorsal to motor V and joins the motor root of V to exit the brainstem. All three branches issue a massive collateral system that distributes terminal swellings within the nuclear boundaries of Motor V. Single Mes V axons diverge to sparsely contact a large number of motoneurons throughout the nucleus, suggesting that single motoneurons receive a convergent input from many Mes V neurons. Since Motor V contains multiple, highly overlapping motor pools, single afferents are positioned to contact different motor pools. The descending branch is situated medial and adjacent to the spinal sensory nucleus of the trigeminal (Sensory V). It issues a collateral field to the entire length of Sensory V. The terminal swellings of these collaterals form rostrocaudally aligned sheets, flattened in the horizontal plane. Single terminal sheets have a divergent projection to a large field of sensory cells and single, fusiform sensory cells are positioned to receive a convergent projection from many terminal sheets.

The results provide the first detailed description of Mes V axon morphology. The overall pattern of these axons closely resembles that recently described for spinal Ia afferent fibers in cat. There is evidence in both cases for divergence of single afferent terminal fields to a set of spatially overlapping motor pools and a convergence of input to single motoneurons from a large population of afferents. This anatomical pattern is consistent with the recently proposed role of sensory feedback in the activity of single motoneurons.

The trigeminal mesencephalic nucleus (Mes V) is a group of large, oval neurons present in the midbrain roof of all jawed vertebrates (reviews: Weinberg, '28; Woodburne, '36). Early comparative anatomists proposed that these are primary sensory neurons equivalent to neurons in the dorsal root ganglia, but located within the central nervous system (May and Horsely, '10; Herrick, '14; Allen, '19; Thelander, '24; Sheinin, '30, '33). Later anatomical and physiological studies confirmed the primary sensory nature of Mes V, showing that the majority of Mes V neurons innervate jaw muscle spindle organs and directly contact the motoneurons serving these muscles (Corbin, '40; Corbin and Harrison, '40; Harrison and Corbin, '41; Szentágothai, '48; Pearson, '49; Jerge, '63; Cody et al., '72). However, these studies could not determine the morphology of the central processes of Mes V neurons or establish their relationship to neurons in the trigeminal motor nucleus (Motor V). Thus, an overall concept of the structural organization of Mes V does not exist and there is no anatomical basis for hypotheses about its functional organization.

Accepted October 14, 1981.

0021-9967/82/2043-0268$03.50 © 1982 ALAN R. LISS, INC.

It was noticed in the course of studies of the optic tectum in the eastern garter snake *(Thamnophis sirtalis)* that horseradish peroxidase injections into the region of Mes V produced a complete, Golgi-like filling of single Mes V axons and their terminal collaterals. This material was used to study the Mes V system. The results provide the first detailed description of the Mes V axon system in any species. Since the trigeminal motor nucleus in snakes forms a single, encapsulated group of neurons, it was possible to study the spatial organization of Mes V terminals within the entire motor complex and effect a comparison between spinal muscle afferents and the Mes V system.

MATERIALS AND METHODS

The morphology of the Mes V axon system was studied in three garter snakes *(Thamnophis sirtalis)*. Horseradish peroxidase HRP (Sigma type VI) was iontophoretically injected into the optic tectum by means of the technique of Graybiel and Devor ('74) as modified by Balaban ('79). A concentrated solution of HRP in Tris buffer (pH 8.6) was placed in a micropipette broken to a 30-μm tip opening. Injections were made after stereotaxic placement of the pipette, by passing positive current (2–15 μamp) for several minutes. After a 3-day survival time, animals were perfused through the heart with buffered, normal saline followed by a buffered solution of 3% glutaraldehyde and 1% formaldehyde. Brains were removed, soaked in 30% sucrose overnight, embedded in gelatin, and immediately sectioned on a freezing microtome at 80 or 100 μm. Sections were treated according to the cobalt-enhanced diaminobenzidine (DAB) protocol of Adams ('77).

Nissl-stained material was derived from two brains embedded in celloidon, sectioned at 25 μm in either the horizontal or coronal plane, and stained with cresyl violet.

RESULTS

The following sections first describe the general course of the Mes V axon system in *Thamnophis* and then consider the morphology and organization of the terminal collateral systems in the motor and sensory nucleus.

General organization of the Mes V system

Mes V consists of spherical and darkly stained neurons, 15–25 μm in diameter, embedded in the periventricular gray layer of the optic tectum (Fig. 1). Although single Mes V neurons are scattered through much of this region, they tend to be more numerous in the caudal half of the tectal midline, where they form large clusters of apposed somata (Fig. 1b).

Processes of Mes V cells could be visualized following tectal injections of HRP. An example of such an injection site is shown schematically in Figures 2 and 3H. All injections were confined to the caudal half of a single tectal lobe and all labeled Mes V axons remained ipsilateral to the injection. The results are derived from a total of ten, completely filled axons in three snakes. No single axon could be unequivocally followed through serial sections, and a complete single axon reconstruction was thus not possible. However, the morphology and distribution were identical for all the labeled axons, suggesting a characteristic pattern for the Mes V system.

Other tectal efferent systems were labeled by these injections. However, the axons of Mes V cells could be distinguished from those of tectal origin by their large diameter, the characteristic deep brown color of the HRP reaction product that filled these axons, their unique position in the trigeminal mesencephalic and motor roots, and by a terminal field in the trigeminal motor nucleus (Weinberg '28). Tectal HRP injections that did not encroach upon the periventricular Mes V cells produced no such labeling, and no tectal efferent fibers were found to travel in the Mes V root or its terminal fields (unpublished observations), thus confirming the observations of others (e.g., Goldstein and Jacobs, '69, Harting, '77, Ebbesson, '81).

The parent or central branch of each Mes V axon initially follows a tortuous path near its soma. It then turns laterally to run along the border of the periventricular gray and the central fiber layer of the tectum. At the caudal pole of the tectum, the periventricular gray is continuous with the brainstem periaqueductal gray (Pag) and Mes V axons turn in a caudal and ventral direction to follow the lateral border of the Pag (Fig. 3H). This course is followed until the axons reach a rostral pole of motor V (Fig. 3F). They then make a sharp, lateral turn to join the dorsal aspect of the motor root of the trigeminal. The approximate diameter of the central branch is 3 μm; it is heavily myelinated.

The central branch (Fig. 4A,B) splits into a peripheral and a descending branch as it passes above the motor nucleus. The peripheral branch continues laterally in the motor root of V to exit the brainstem. The descending branch arises at right angles to the peripheral branch and courses caudally into the brainstem. It follows a straight course in a cell-poor region medial and adjacent to the spinal sensory nucleus of the trigeminal (sensory V; Fig. 2A–C). Single axons could be traced along this descending pathway in serial sections from the level of Motor V to the brainstem-spinal cord junction. Both the peripheral and the descending branches maintain a diameter approximately that of the central branch and are also myelinated.

At the rostrodorsal aspect of the motor nucleus, the central, descending, and peripheral branches of the Mes V axon issue a massive collateral system that descends into the motor nucleus and is confined to its nuclear borders (Fig. 4A). Collaterals originate from the nodes of Ranvier as single, primary branches (Fig. 5). Each primary collateral is smooth and approximately 1 μm thick. It passes ventrally, directly into the motor nucleus, and gives off several secondary branches of finer caliber that bear large, bulbous swellings along their entire length. Secondary

Abbreviations

Cer	Cerebellum
IP	Interpeduncular nucleus
Mes V	Mesencephalic nucleus of the trigeminal
MN V	Motor nucleus of the trigeminal
Mr V	Mesencephalic root of the trigeminal
OT	Optic tectum
PC	Posterior colliculus
pd	Predorsal bundle
SR	Superior raphé
SN V	Sensory nucleus of the trigeminal
Sp V	Spinal tract of the trigeminal
tb	Ipsilateral tectobulbar tract
Ve N	Vestibular nuclei
3	Oculomotor complex
VIII	Eighth nerve

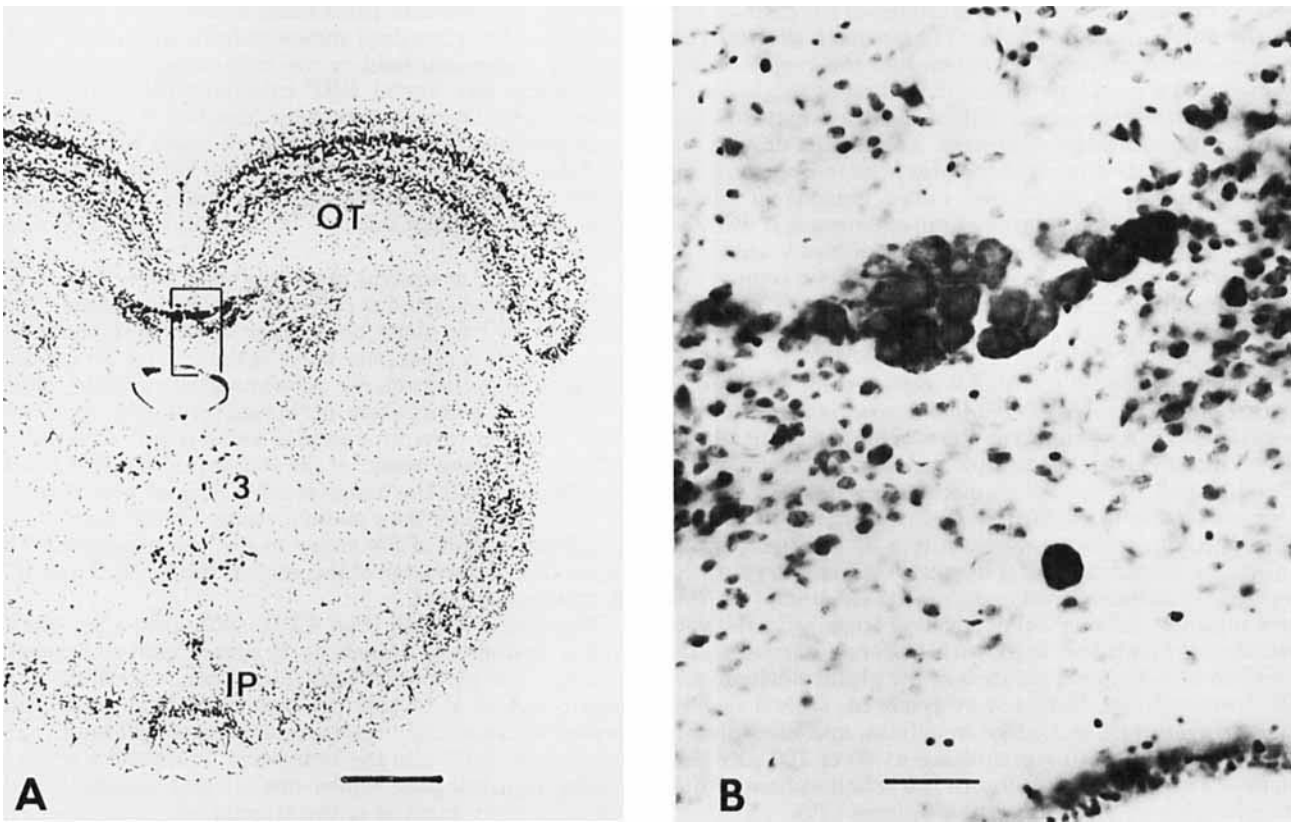


Fig. 1. Appearance of Mes V in Nissl material. A. Caudal midbrain. Mes V cells are embedded in the tectal periventricular gray, close to the midline. B. At higher magnification (boxed in area in *A*), they are large, densely stained cells that frequently form large clusters of apposed somata. Scale bar in A = 200 μm; B = 30 μm.

collaterals are sparsely branched, but are spread throughout much of the rostrocaudal and mediolateral extent of Motor V.

Single collateral branches arise from the nodes of Ranvier of the descending Mes V axons at regular intervals of 50 to 80 μm and project laterally into the sensory nucleus (Fig. 2A,B). Sensory V can be distinguished as a column of small, spindle-shaped neurons, lying just medial to the spinal tract of V. It extends to spinal levels where it is continuous with the dorsal horn. Like the Motor V projection, the primary Sensory V collaterals are initially smooth and about 1 μm in diameter. This smooth portion varies in length, depending on the distance of the parent axon from the cellular border of Sensory V. Upon entering Sensory V, collaterals bear large swellings, like those seen on the terminal collaterals in Motor V, and may remain unbranched or branch sparsely. The branching pattern differs from that seen in Motor V in that a single primary collateral and its branches do not spread out sparsely and diffusely, but form a terminal field that runs in a straight line across the mediolateral extent of Sensory V and is flattened in the horizontal plane (Figs. 6, 7).

Organization of collaterals in Motor V

Primary collaterals arising from Mes V axons above the motor nucleus are smooth and about 1 μm in diameter. They branch sparsely and are studded with bulbous swellings upon entering Motor V (Figs. 4a, 5). A few tertiary branchlets, of much finer caliber, arise from secondary branches (Fig. 4C). The size of the swellings on these twigs, though, is as large as those on the thicker collaterals. These conspicuous masses correspond to the classic *boutons terminaux* of Ramón y Cajal ('11), observed initially on many central axon terminals with the Golgi technique and more recently with anterograde and intracellular HRP techniques (e.g., Vanegas et al., '78; Bowling and Michael, '80). Electron microscopic studies demonstrate that these terminal swellings are indeed the source of synaptic contacts and are reliably identifiable at the light microscopic level (Peters and Proskauer, '80).

The distribution of these putative terminals was confined to the nuclear borders of Motor V (Figs. 3a, 4a). Terminal swellings appeared associated with the neuropil in proximity to neuronal somata in sections counterstained for Nissl. However, no swellings appeared to contact the large somata of motoneurons, suggesting that synaptic contacts are made principally on the proximal dendritic shafts of motoneurons. This agrees with the probable distribution of Mes V terminals in the Motor V nucleus observed electron microscopically in another snake *(Agkistrodon)* by Moody and Meszler ('80). In addition, similar terminal morphology and distribution have been seen in the Motor V nucleus in the oppossum, *Didelphis marsupialis* (Hamos and King, '80).

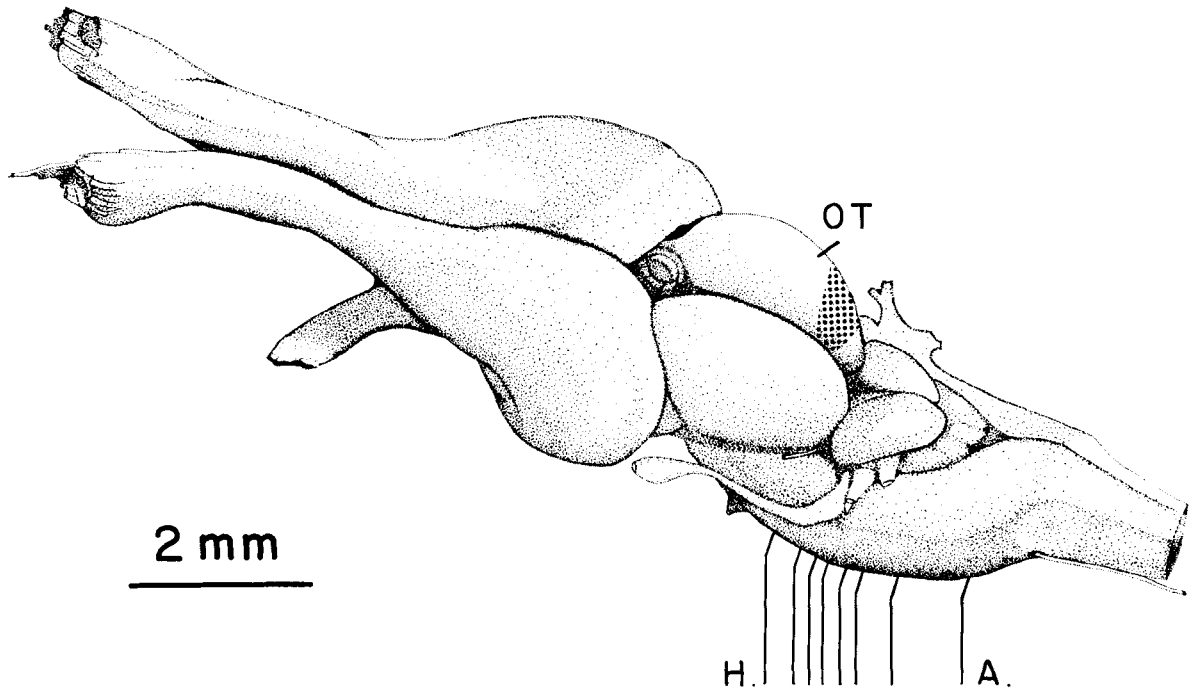


Fig. 2. Dorsolateral view of the brain of *Thamnophis*. HRP injection site in the optic tectum is marked by the heavy stipple. Approximate locations of the sections in Figure 3 are shown by the lines labeled A through H.

Since the distribution of all collateral fields was widespread and highly overlapping, the actual terminal distribution of a small number of collaterals could not be readily appreciated from tracings such as that shown in Figure 5. To gain this information, the positions of terminal boutons from three parent Mes V axons were plotted in serial sections through the rostrocaudal extent of the motor nucleus (Fig. 8). Only three Mes V axons were labeled in this case and, as in the other cases, their terminal fields completely overlapped. The great majority of motoneurons visible are closely approximated by at least one terminal. The bouton distribution suggests that the terminal fields of single axons are not spatially segregated from each other or within any portion of the motor nucleus. Instead, each terminal field is spread throughout much of the rostrocaudal and mediolateral extent of Motor V.

Organization of collaterals in sensory V

The descending branch of the Mes V axon courses through the brainstem in close association with the spinal sensory column. Primary collaterals originate from nodes of Ranvier at regular intervals and course laterally into Sensory V. It was not possible to distinguish unequivocally whether every node gives rise to a collateral, although this appeared to be the case. As in the Motor V collateral system, primary collaterals are smooth and unbranched. They branch sparsely upon entering the cell column and become studded with large terminal swellings. The terminal field of a single collateral branch, however, has a characteristic distribution different from that in Motor V. Each collateral enters Sensory V at right angles to the parent axon and forms beaded, straight extensions that pass through the mediolateral extent of the sensory cell column. The secondary collateral branches do not spread out or radiate diffusely into Sensory V, but are restricted in the horizontal plane (Fig. 7). Since the descending branch issues collaterals at regular intervals at all rostrocaudal levels of Sensory V, the distribution of all the collaterals from a single stem axon forms a thin, horizontally elongate sheet that runs the entire length of the nucleus, but that is limited to one dorsoventral plane. In consequence, when the terminal sheets of many single Mes V axons are solidly filled they stack up in overlapping layers along the dorsoventral axis of Sensory V.

From the present material it could not be determined to what degree terminal sheets overlap, but the laminar organization of this collateral system is clear. Neurons in the terminal fields of these axons are fusiform in the dorsoventral plane (unpublished observations). Thus, single cells along the length of the sensory column may receive contacts from many Mes V axons and this input could be distributed in an organized way along the length of the radiating dendrites of Sensory V cells. Because of this spatial relation, it is probable that Mes V input to Sensory V is divergent and that each Sensory V neuron receives convergent input from many Mes V axons.

DISCUSSION

The concept of the morphology of Mes V axons that results from this study is summarized in Figure 9. Each Mes V axon has a massive collateral projection to Motor V and to Sensory V. Several primary collaterals arise near the bifurcation point of the parent axon and terminate diffusely throughout Motor V. The descending branch of the parent axon issues a series of collaterals to the entire length of Sensory V. The Discussion will focus on the organization of the Mes V projections to these structures and conclude by comparing the Mes V axons to the spinal Ia afferent system.

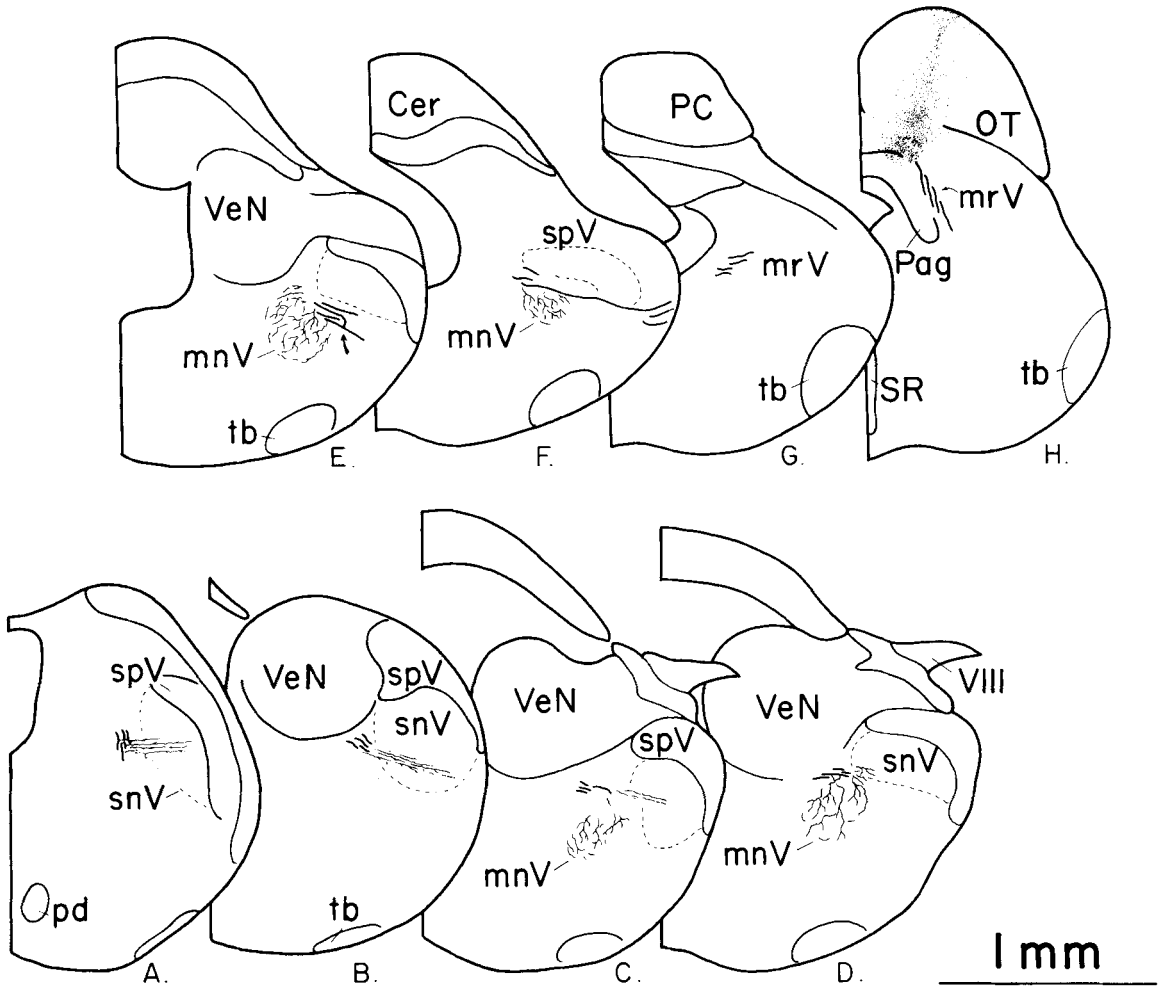


Fig. 3. An overview of the course and terminal distribution of Mes V axons. In this case four axons were solid filled. HRP injection site is depicted as a fine stippling in *H*. The parent Mes V axons are traced as thick lines and their terminal collaterals as finer lines. Axons travel caudally in the mesencephalic root (MrV) and bifurcate at the level of the motor nucleus (MNV; arrow in E), into a peripheral branch that exits the brainstem (E) and a descending branch that passes through the medulla along the lateral margin of the sensory nucleus of V (SNV). Terminal collaterals distribute to MNV and SNV.

Origin of the descending pathway

A descending pathway of Mes V origin was first suggested in 1899 by Probst (cf. Corbin, '42), and early studies with the Marchi method raised the possibility of a bifurcating axon as the origin of this pathway (Thelander, '24). The presence of a descending pathway was confirmed by degeneration studies in cats (Corbin, '40; Szentágothai, '48), in the lizard *Lacerta viridis* (Goldstein and Jacobs, '69), and the frog *Rana pipiens* (Rubinson, '70). More recently the descending pathway was observed in the rhesus monkey with the aid of the autoradiographic tracing technique (Harting, '77), and Mes V neurons were retrogradely labeled after spinal injection of HRP in cats (Matsushita et al., '81). In the frog *Rana esculenta* (Matesz and Szekely, '78) and in rats (Matesz, '81), cobalt filling of Mes V axons demonstrated that the descending pathway originates as a bifurcation of the parent axon, in agreement with the present findings in *Thamnophis*. Thus the descending branch is part of the parent axon and input from each Mes V axon is distributed to both Motor V and, in *Thamnophis*, Sensory V.

Relation to Motor V

The collateral projection to Motor V was first observed with the Golgi technique (Ramón y Cajal, '11) and with the Marchi degeneration method (May and Horsely, '10; Allen, '19; Thelander, '24). Later evoked potential (Corbin and Harrison, '40; Harrison and Corbin, '41) and degeneration studies (Szentágothai, '48) confirmed the direct projection from Mes V to Motor V. Since that time, there have been no studies of the anatomical organization of the Mes V collateral system in Motor V. The present results show that multiple collaterals from single Mes V axons produce a massive terminal arborization in Motor V. Terminal swellings are diffusely or sparsely scattered throughout the nucleus so that the number of contacts from any single Mes V axon to a single motoneuron is very small in comparison with the total number of terminals per axon. This results in an overall divergent/convergent

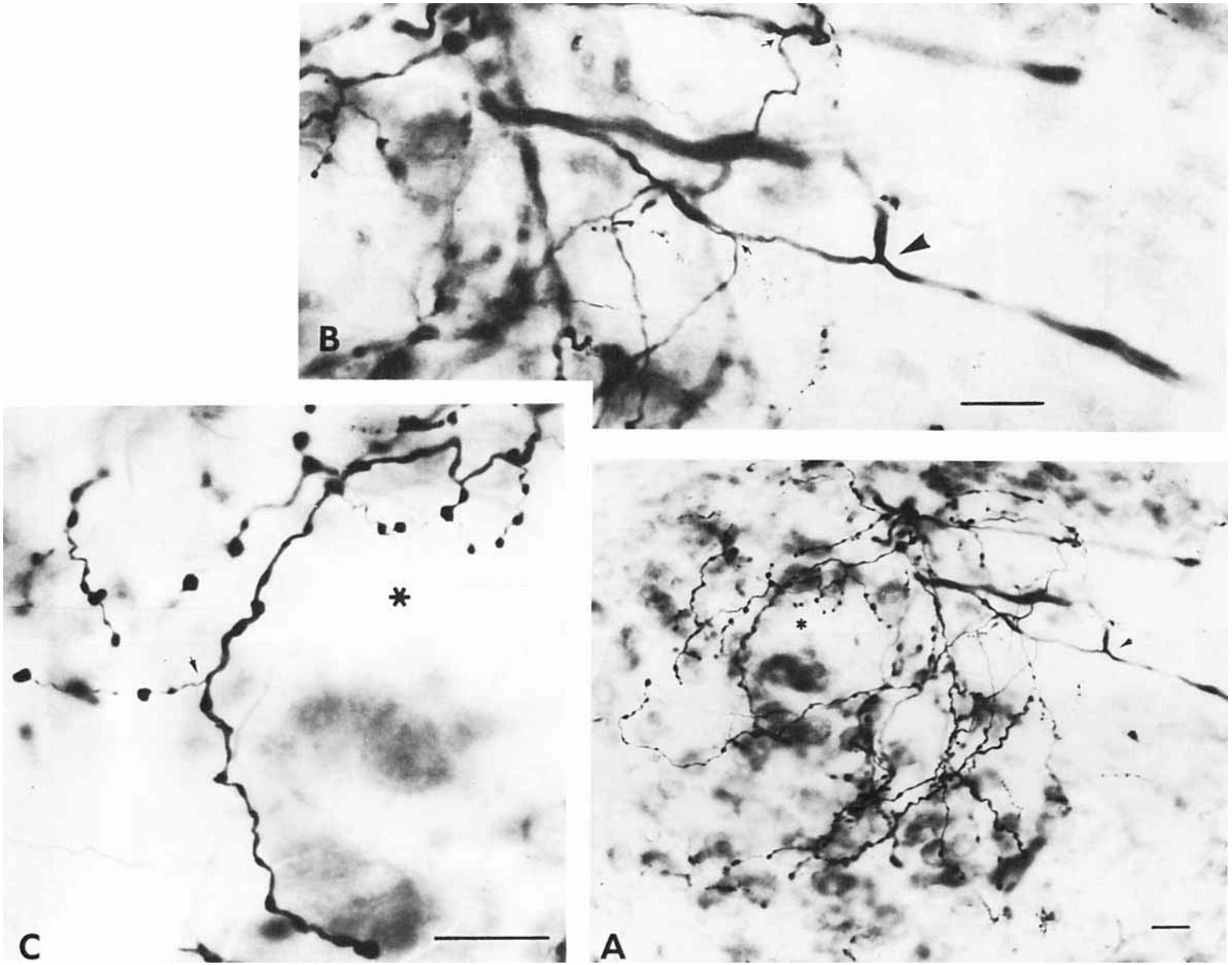


Fig. 4. Morphology of Mes V collaterals in the motor nucleus of V. A. Single axons issue multiple, primary collaterals that spread throughout the motor nucleus but are confined to its nuclear borders. B. Thick arrow in *A* shows the corresponding point in *B* at high magnification and points to the primary bifurcation of a single Mes V axon. Thinner arrows point to the origin of primary collaterals from the descending branch. C. Corresponding points in *A* and *C* are related by the asterisk. Secondary collaterals bear large swellings along their length and occasionally issue fine tertiary branchlets (arrow). Scale bar = 30 μm.

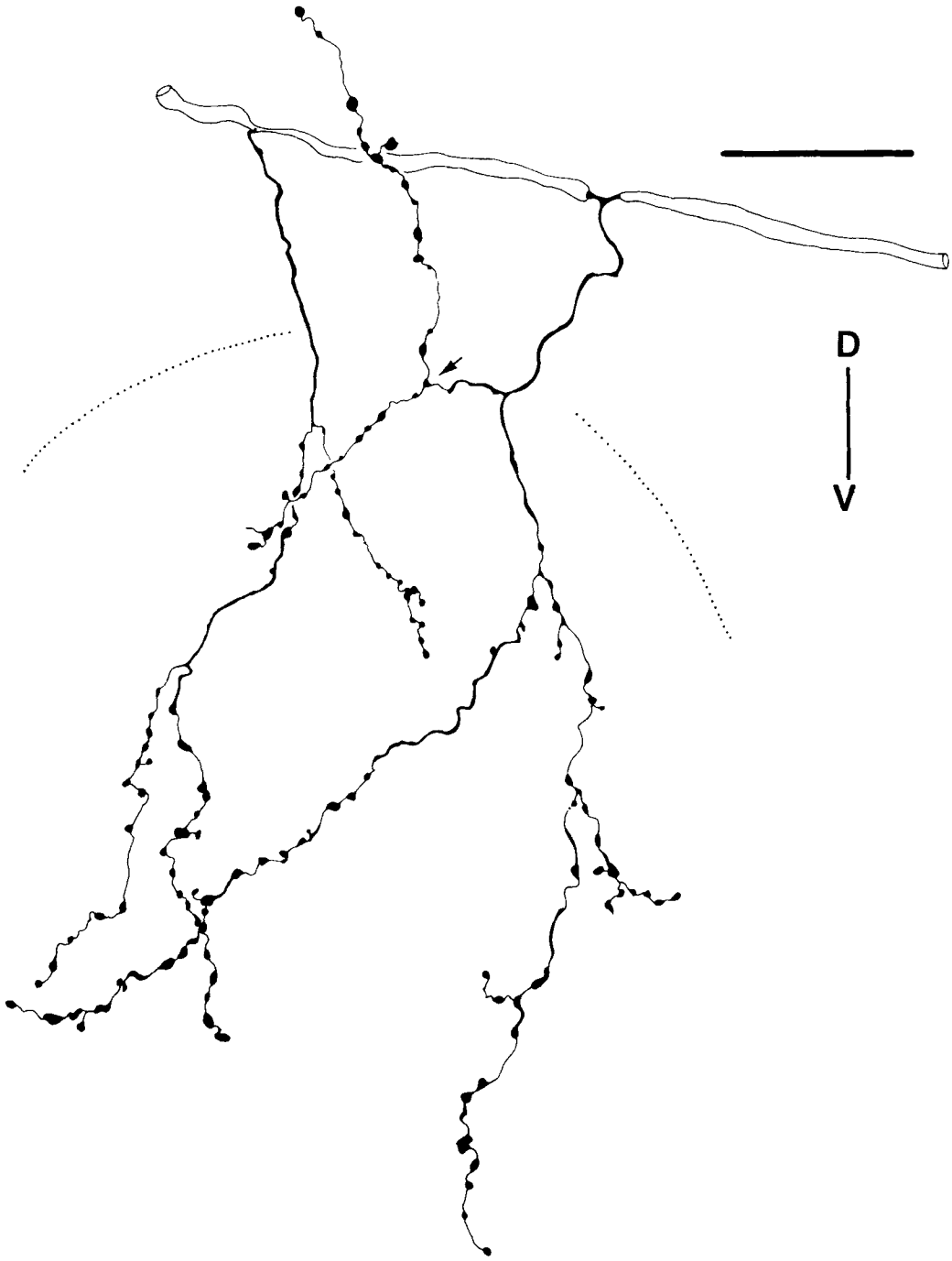
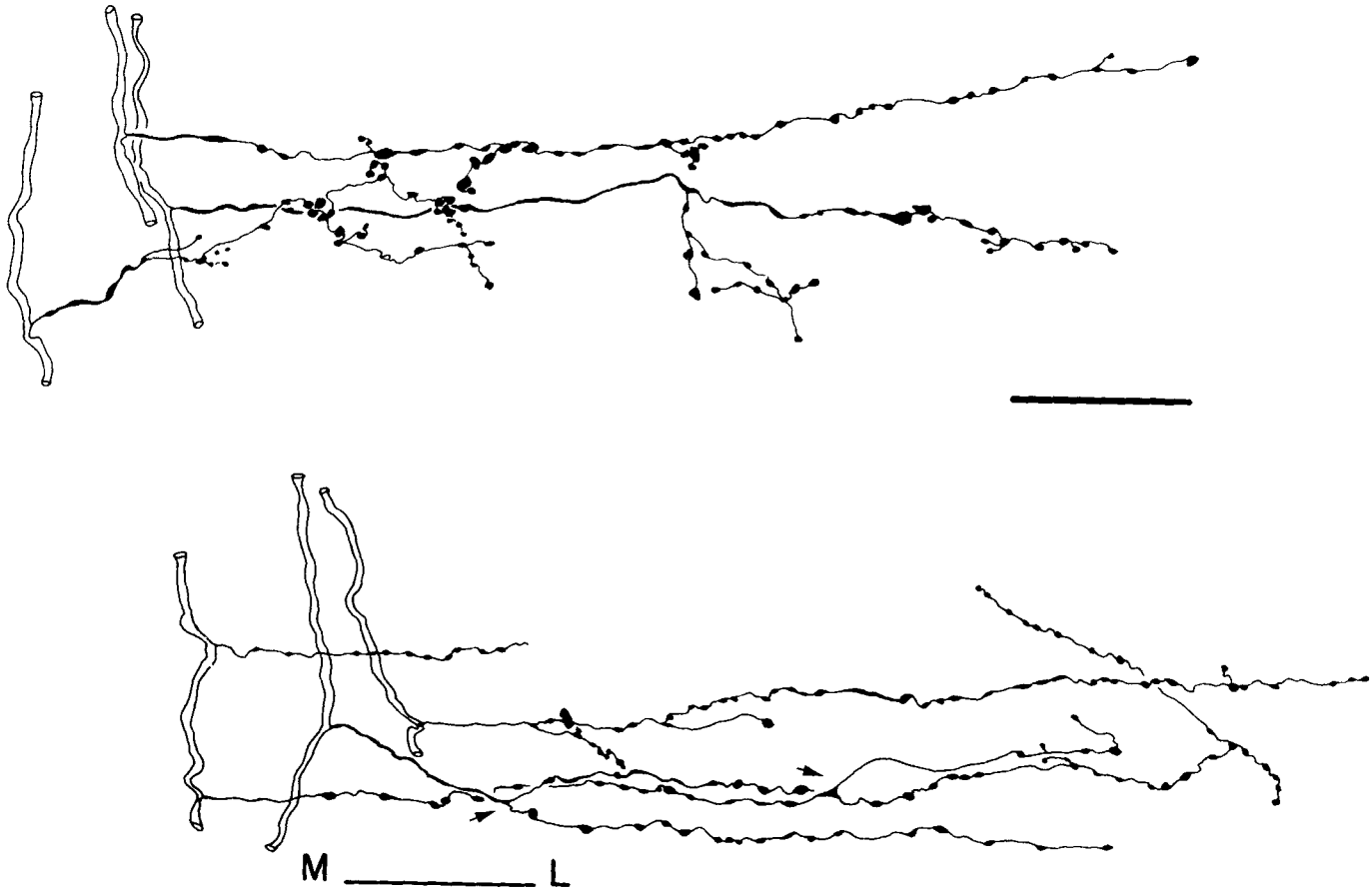
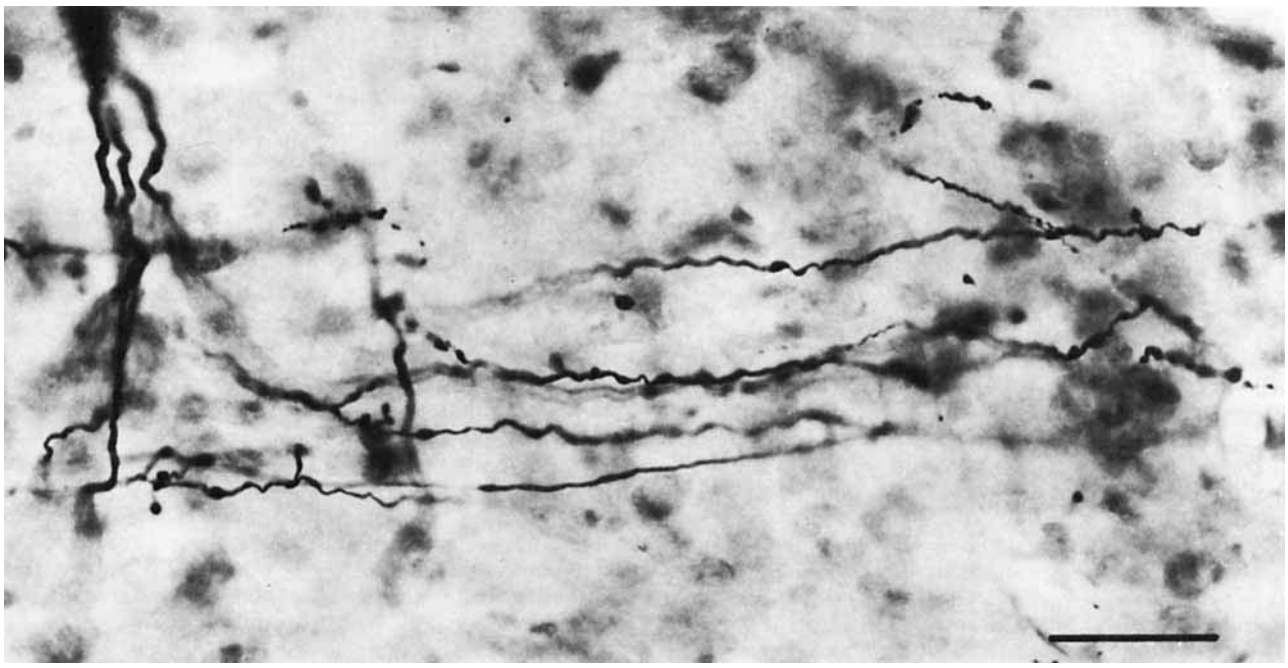


Fig. 5. Terminal collaterals in the motor nucleus. This camera lucida tracing shows a segment of Mes V axon that sends two primary collaterals into the motor nucleus. They branch sparsely and bear terminal swellings upon entering the nuclear borders of Motor V (marked with a dotted line). One secondary collateral recurves dorsally to enter the rostral pole of the sensory nucleus of V (arrow). D-V, dorsal-ventral. Scale bar = 50 μm.





Figs. 6, 7. Collaterals in the sensory nucleus. Figure 6 shows camera lucida tracing of collaterals in the sensory nucleus of V. Figure 7 is a photomicrograph of the lower tracing in Figure 6. Primary collaterals extend in straight lines from the parent axon into the sensory cell column. Like Motor V collaterals they are beaded. Secondary collaterals tend to stay in the plane of the primaries (arrows) and tertiary branchlets are short. M-L, medial-lateral. Scale bar = 50 μm.

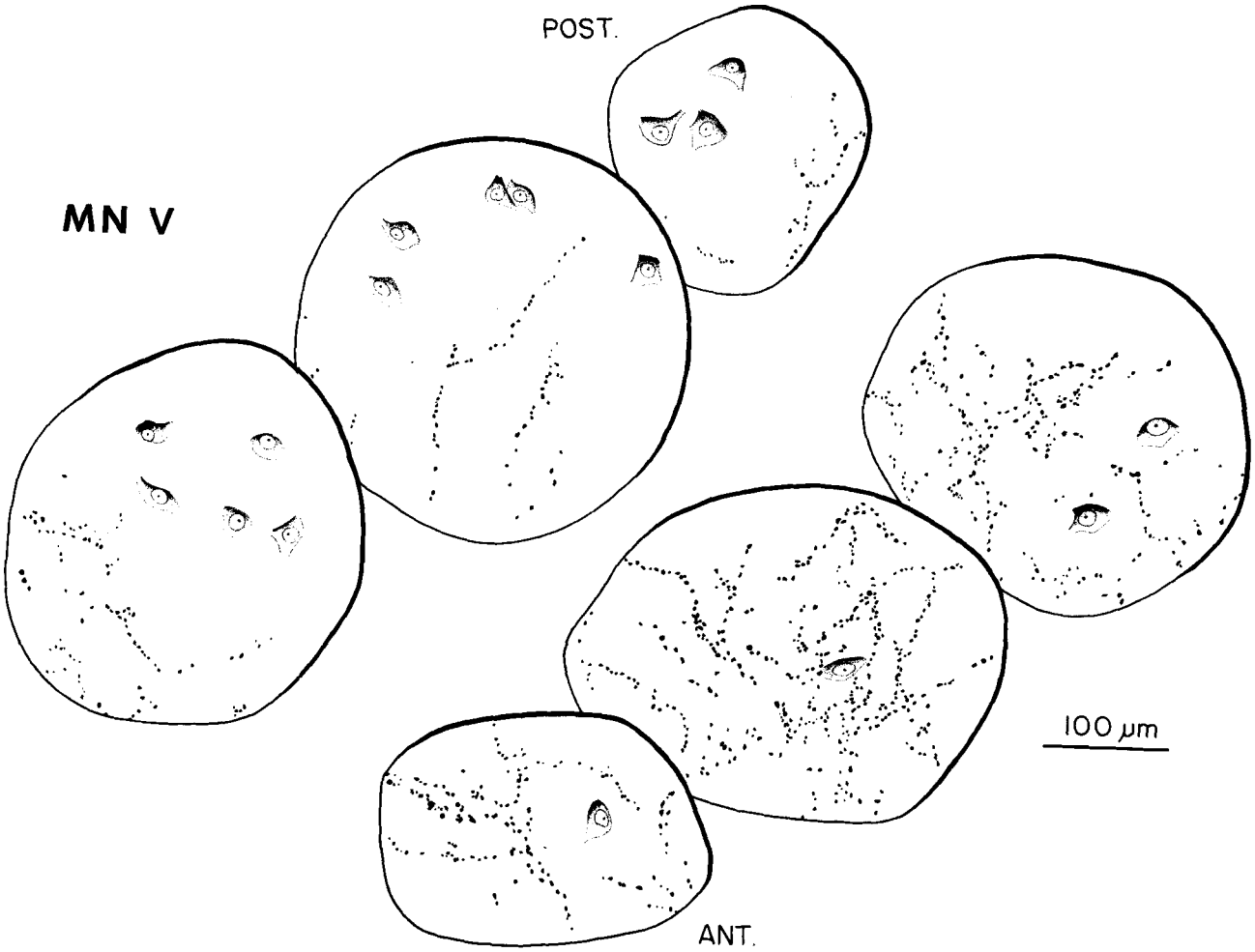


Fig. 8. Distribution of Mes V axon terminals in the motor nucleus of V. In this figure the terminal swellings of three overlapping Mes V axons are shown in serial, 80-μm-thick sections through the motor nucleus. Each dot is a tracing of a single collateral swelling. A few motoneurons (traced from a Nissl counterstain) are depicted. Motoneurons are large (40 μm) relative to the size of the nucleus. Mes V terminals are large (3–5 μm) and have a widespread distribution through the motor nucleus.

pattern of organization: Single Mes V axons have a divergent projection to a large number of motoneurons, single motoneurons receive a convergent projection from a large number of Mes V cells. (A quantitative verification of this impression necessitates a detailed reconstruction of single, identified axons and their terminals at the light and electron microscopic level.) This pattern of organization has functional implications if the subnuclear organization of the motor nucleus is considered.

The spatial organization of motor pools for the jaw muscles has been mapped recently in another snake, the cottonmouth moccasin *(Agkistrodon mokassin)*, using the retrograde HRP technique (Moody and Meszler, '80). Motor pools are highly overlapped and form columns through the rostrocaudal extent of the large, egg-shaped nucleus. The topography of motor pools has been studied with the same techniques in the pigeon (Wild and Ziegler, '80) and several mammals (e.g., Mizuno et al., '75; Batini et al., '76; Limwongse and DeSantis, '77). These studies show a similar basic organization, but with variation in the degree to which motor pools are spatially segregated. The pigeon has the most discrete motor pools of the systems studied thus far, while *Agkistrodon* has the most overlapped. The cytology of Motor V in *Thamnophis,* when compared to *Agkistrodon,* shows even less nuclear subdivision, suggesting that the motor pool interdigitation may even be greater in this animal. Given the widespread distribution of single Mes V afferents and the spatially coextensive motor pools, it appears that motoneurons from all the motor pools represented might receive a quantitatively and qualitatively similar afferent sensory barrage from the entire trigeminal muscle group.

This anatomical scheme is consistent with physiological and behavioral findings in other systems (e.g., Székély et al., '69; Williamson and Roberts, '81), showing that the elimination of sensory feedback from muscles does not affect the basic temporal pattern of motoneuron output, bur rather affects its excitation threshold. Thus, the role

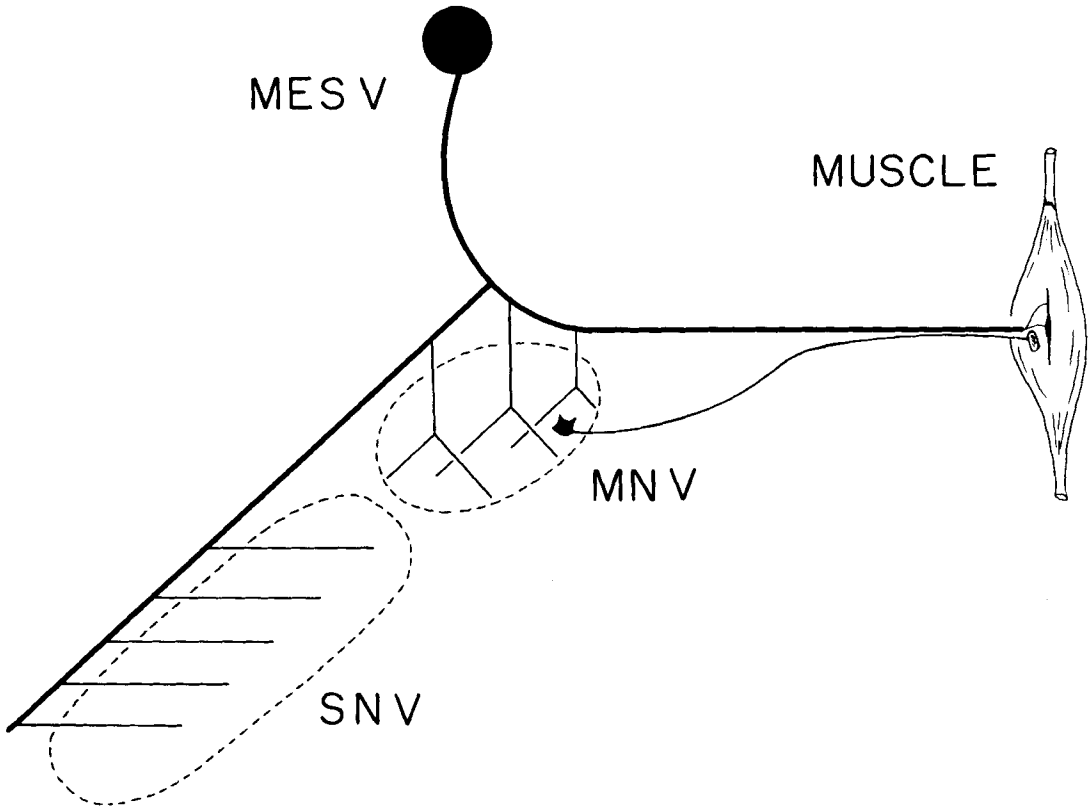


Fig. 9. Summary of the Mes V axon system in *Thamnophis*. Unipolar Mes V cells have a central branch that extends from the soma to the motor nucleus of V (MNV), where it splits into descending and peripheral branches. The peripheral branch exits the brainstem to contact muscle spindle organs. At the point of bifurcation multiple collaterals fill the motor nucleus. The descending branch issues a terminal sheet to the sensory nucleus of V (SNV).

of sensory feedback from muscles during a natural movement sequence could be to bias or adjust the threshold state of the entire motoneuron population without affecting the temporal program of motoneuron output.

Relation to Sensory V

A few other studies have considered the possible targets of the descending pathway. In mammals, projections to the facial (VII), hypoglossal (XII), and the dorsal motor nucleus of the vagus (DMX) have been described (Corbin, '40; Matesz, '81, Szentágothai, '48; Pearson, '49), suggesting that the descending branch is a route by which these other cranial motor nuclei could participate in masticatory reflexes. Projections into and around Sensory V have recently been observed in rats by cobalt filling of Mes V axons (Matesz, '81). Goldstein and Jacobs ('69) and Ebbesson ('81) studied the Mes V pathways in lizards with silver degeneration techniques and observed projections to Sensory V as well as Motor VII, DMX, and the nucleus of the solitary tract. Cobalt filling of Mes V axons in *Rana* demonstrated a similar pattern, with an additional projection to the midbrain periventricular gray (Matesz and Szekely, '78).

In *Thamnophis*, solid filled Mes V axons send a collateral terminal field only to the sensory trigeminal cell column. No projections were seen to cranial nerve motor nuclei. This result may derive from either a sampling problem (since a relatively small number of Mes V axons were solid filled) or from real species differences in Mes V connections. The lack of a projection to the XII, for example, is not surprising since, in snakes, the tongue is highly modified and is specialized for chemoreception; it is completely retracted in a sheath during food ingestion.

There have been no previous studies of the anatomical organization of the descending Mes V projection. The present results suggest that, in *Thamnophis* at least, collaterals of single axons form horizontally flattened sheets that pass rostrocaudally through the Sensory V cell column. The collateral fields of many axons would then presumably stack up in laminae along the dorsoventral axis of the nucleus. One possible consequence of this projection pattern is that information from single afferents is not preserved, but is highly convergent onto single cells. This mode of organization is reinforced by neurons in Sensory V that are spindle-shaped in the dorsoventral axis (personal observation). Thus, their radial dendrites are positioned to pass through the terminal sheets of many axons. Since the terminal fields of single axons pass through the entire cell column, input is also highly divergent onto a large number of sensory cells. This kind of spatial organ-

ization is consistent with the lack of muscle-specific representation in the Mes V nucleus. Indeed, clusters of Mes V cells (as shown in Fig. 2) are coupled by gap junctions (Hinrichsen and Larramendi, '68) and many different muscles are represented within a cell cluster (Alvarado-Mallart et al., '75).

The projection of Mes V to Sensory V raises the question of the relation of proprioceptive to somatic sensory afferents. The central projection of the trigeminal nerve has been studied recently in a boid snake, *Python reticulatus* (Molenaar, '78). The distribution of the three nerve branches in the tract and nucleus follow the common vertebrate plan: The ophthalmic branch is situated dorsally, the mandibular is ventral, and the maxillary is in an intermediate position. Primary fibers bifurcate to ascend and descend in the spinal tract, issuing collaterals to all subdivisions of Sensory V. Thus, somatotopic organization is preserved from dorsal to ventral in Sensory V, but a peripheral point may be represented as a lamella or rostrocaudally extended sheet through the nucleus (Kruger and Michel, '62; Kerr et. al., '68). Although it is not known how the Mes V afferents are related to this "point to line" topographic arrangement, it is interesting that the horizontally flattened sheets formed by Mes V collaterals follow a mode of organization similar to that of the somatic input. Given the distribution of somatic fibers to all parts of the Sensory V, it is unlikely that proprioceptive input is somehow segregated within the nucleus. On the contrary, the widespread distribution of single Mes V afferents raises the possibility that they may be distributed in register with somatotopic domains. The effect that proprioceptive input have on the activity of neurons in the sensory nucleus is unknown.

Comparison to spinal muscle afferents

The intracellular injection of HRP has recently been used to study the morphology of physiologically identified Ia afferents to the lumbar spinal cord in cats (Brown and Fyffe, '78; Burke et. al., '77; Ishizuka et al., '79). Ia fibers are characterized by a long ascending stem axon that gives off a massive collateral system along its course to the dorsal and ventral horn. Collaterals arise at regularly spaced intervals and project to a longitudinal sensory column at the base of the dorsal horn and a motor column in the ventral horn. Collaterals of single axons branch sparsely to contact the proximal dendrites and somata of motoneurons along the entire extent of a motor column that is 10 mm long and represents several overlapping motor pools (Burke et al., '77). The number of contacts per motoneuron is sparse (mean of 3.3) compared to the total number of terminal boutons for a single Ia afferent (mean of 2,160; Ishikuza et al., '79). A similar divergent/convergent pattern of organization was found in the sensory cell column. Thus, at least for some of the large hindlimb muscles of the cat, the terminals of single Ia afferents contact large numbers of motoneurons in multiple, overlapping motor pools. However, the number of contacts on single motoneurons is comparatively very low. These results agree with and extend Golgi (Cajal, '11; Szentágothai, '67; Scheibel and Scheibel, '69) and physiological studies of motoneurons recorded intracellularly during stimulation of single (Mendell and Henneman, '71) or multiple (Eccles et al., '57; Eccles and Lundberg, '58) Ia afferents.

There is strong evidence that Mes V afferents to Motor V arise only from muscle spindles (Jerge, '63; Cody et al., '72) and represent the primary Ia afferent population for the head. In *Thamnophis,* solid filled Mes V axons are myelinated and similar in caliber to their spinal counterparts. For Mes V, the peripheral branch is extended (since the somata of origin are in the CNS) and may also contribute collaterals to motoneurons. Basically, however, the distribution of terminals in the motor and sensory columns closely matches the pattern observed for spinal Ia's studied thus far. Moreover, the divergent projections of single axons to multiple motor pools, coupled with a sparse distribution of terminals to single motoneurons, form the same type of divergent/convergent organization in both cases. Whether this pattern provides a general picture of the relation of proprioceptive afferents to motor pools awaits detailed study of afferent organization in other, defined motoneuron populations.

ACKNOWLEDGMENTS

I am especially grateful to my adviser, Dr. P.S. Ulinski, for guidance during all phases of this project. This study was supported by PHS grant NS12518. Shirley Aumiller provided photographic assistance and Debra Randall typed the manuscript.

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