

The Sensory Component of the Facial Nerve of a Reptile (*Lacerta viridis*)

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ABSTRACT The sensory fibers of the facial nerve in *Lacerta viridis* have been studied with a silver impregnation method to follow the course of axonal degeneration. Destruction of the geniculate ganglion demonstrated the degenerated sensory component of the facial nerve adjacent to the anterior vestibular root. Within the lateral vestibular area the facial sensory fibers consist of numerous rootlets separated by vestibular fibers and cells. These rootlets may join to form a main or paired sensory tract that passes through the vestibular nuclei to enter the tractus solitarius and divide into a small ascending prefacial component and a major descending prevagal division. A few fibers continue into the postvagal part of tractus solitarius and extend caudally to terminate in the nucleus commissura infima. Prefacial fibers terminate along the periventricular gray while prevagal fibers terminate within the tractus solitarius on the dendrites of cells of nucleus tractus solitarius and near the periphery of the dorsal motor nucleus of X. There was no noticeable degeneration in the descendens tractus trigemini. Terminal degeneration to descendens nucleus trigemini and motor nucleus of VII followed the tractus solitarius course. Most facial sensory fibers are probably related to taste and other visceral information.

The central nervous system pathway of the sensory components of the facial nerve in reptiles has been little investigated since the description by Kappers et al. ('36) of *Caiman* and *Varanus* and by Barnard ('36) of *Anolis*. They described, in normal brain material stained for axons, a seventh prevagal portion and a ninth postvagal component of the tractus solitarius. Several other investigators have used nonmammals such as carp (Liuten, '75), ducks (Dubbeldam et al., '76), mormyrid fish (Malen et al., '73) and frogs (Matesz and Szekely, '78) to study the central afferent terminations of the seventh nerve. The mammalian nucleus and tractus solitarius have been studied extensively with various anatomic and physiologic methods (Torvik, '56; Cottle, '64; Rhoton, '68; Blomquist and Antem, '65; Martin and Mason, '77) to determine neural connections and to establish functional correlates. This visceral system appears to integrate and regulate respiration, taste, cardiovascular functions and swallowing (Doetsch and Erickson, '70; Calaresu et al.,

'75; Jean et al., '75; Norgren and Pfaffman, '75).

The close proximity of the lizard seventh and eighth nerves extracranially, intracranially and in the vestibular area makes differentiating vestibulo-cochlear and facial sensory nerve degeneration difficult when these nerves are simultaneously involved in a lesion. A similar misinterpretation may occur when the lesion is central and involves vestibular nuclei and the facial nerve. Several investigators (Leake, '74; DeFina and Webster, '74; Foster and Hall, '78) have destroyed parts of the eighth nerve or vestibulo-cochlear nuclei of reptiles to study the axonal degeneration patterns in the brain. There was no mention of the intimate relationship of the seventh nerve to the vestibular roots as the facial nerve passes through the vestibular nuclei.

This report describes the sensory division of the seventh nerve following geniculate ganglion destruction. Its relationship with the eighth nerve, its position in the vestibular re-

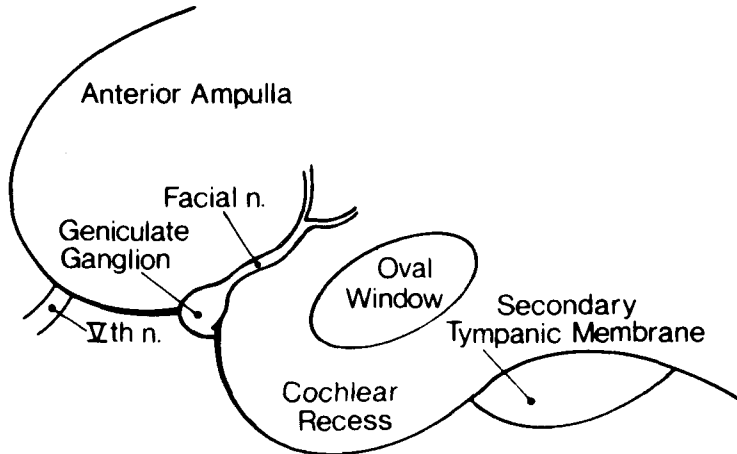


Fig. 1 A diagram of the left medial wall of the reptilian tympanic cavity showing the relationship of the facial nerve and geniculate ganglion to the anterior ampulla and cochlear recess.

gion and its central terminations in nucleus tractus solitarius, descendens nucleus trigemini and facial motor nucleus were assessed, based on silver impregnation of degenerated axons.

MATERIALS AND METHODS

Adult lizards (*Lacerta viridis*) were maintained at about 30°C on mealworms and water for the duration of the experiment. During the surgical procedure all lizards were anesthetized with ether. Using a dissecting microscope, the rostro-ventral margins of the tympanic membrane were incised and reflected to gain access to the middle ear cavity. A dental drill fitted with a fine burr was used to erode the geniculate ganglion and a little of the adjacent bony area in front of the cochlear recess. Extreme caution was taken to avoid damage to the stapedia artery and other major vessels on the medial wall of the middle ear. Following destruction of the geniculate ganglion, the middle ear was loosely packed with particles of Gelfoam. The tympanic membrane was returned to its normal position and covered with adhesive tape. Of the 12 animals operated on, only eight were adequately stained and had lesions that did not involve the surface of the brain.

Postoperatively, the animals were observed for locomotor difficulties and aided with eating if necessary. Survival times ranged from 7-23 days. Each animal was etherized and perfused with 0.65% saline followed by 15 minutes of 10% buffered to neutral formalin so-

lution. Each was decapitated and the brain was exposed for further in situ fixation. After several days the brains were removed from the skull under a dissecting microscope. The brains were cut on a freezing microtome in either sagittal or transverse plane, stained according to the Nauta and Gyax ('54) silver method and mounted serially on slides (Jacobs, '68). A cresyl violet stain was used on normal brain material for cytoarchitectural study. Line drawings of the brainstem and degeneration patterns were made with a camera lucida attachment.

RESULTS

The vascular and neural structures related to the reptilian medial wall of the tympanic cavity were described by Baird ('70). Baird provided me with a *Crotophytus collaris* head in which the dissected middle ear verified the position of the branches of the facial nerve on the medial wall of the tympanic cavity. The branches could be followed toward the angle formed by the anterior ampulla and the cochlear recess where the geniculate ganglion lies (fig. 1). Medial to the geniculate ganglion is the margin of the foramen through which the seventh nerve passes to enter (or leave) the cranial cavity.

Following destruction of the geniculate ganglion, there was a central degeneration of the sensory axons of the facial nerve. The motor axons were spared in the allotted survival period (7-23 days), as long as traumatic changes to the parasympathetic and somatic

Abbreviations

A. Angularis nucleus	IV n. Trochlear nerve
AVR, Anterior vestibular root	IV Vent. Fourth ventricle
Cerebl, Cerebellum	MLF. Medial longitudinal fasciculus
Col, Cochlear nuclei	MM, Magnocellularis medialis nucleus
D, Descendens vestibular nucleus	M. VII. Motor nucleus of facial nerve
DNT, Descendens nucleus trigemini	MTS, Medial nucleus of tractus solitarius
DSCT, Dorsal spinocerebellar tract	PVR, Posterior vestibular root
DTT, Descendens tractus trigemini	TS, Tractus solitarius
DTS, Dorsal nucleus of tractus solitarius	VIII CN. Statoacoustic nerve
FS, Sensory component of facial nerve	VL, Ventrolateral vestibular nucleus
	VM, Ventromedial vestibular nucleus

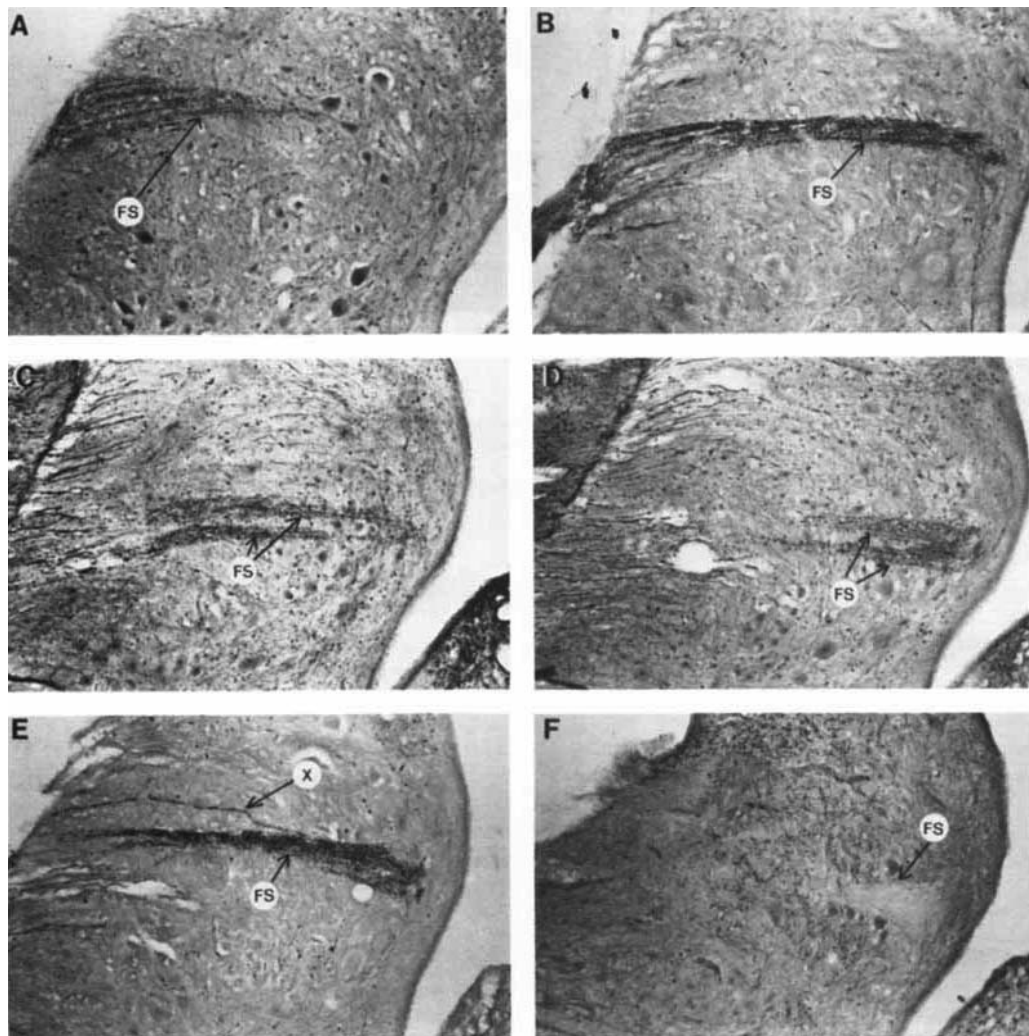


Fig. 2 The left margin of each photomicrograph represents the lateral side of the brain. Photomicrographs A through E are cross sections of the vestibular area showing the degenerated sensory component of the Facial nerve (FS) at the arrows following geniculate ganglion destruction. A and B are adjacent sections from the same animal (23 days survival) showing several small degenerated fascicles that join to form a single dense bundle of degeneration as it passes through the vestibular area. C and D are taken from another animal (18 days survival) in which the FS is split into two separate degenerated bundles that unite near the ventricular wall. E shows a distinct small fascicle (X) of axons in another animal (16 days survival) that joins the main FS bundle. F represents an animal (23 days survival) with an exclusive destruction of the eighth nerve. As a result the FS is unstained and normal in the vestibular region which contains widespread degeneration. $\times 108$.

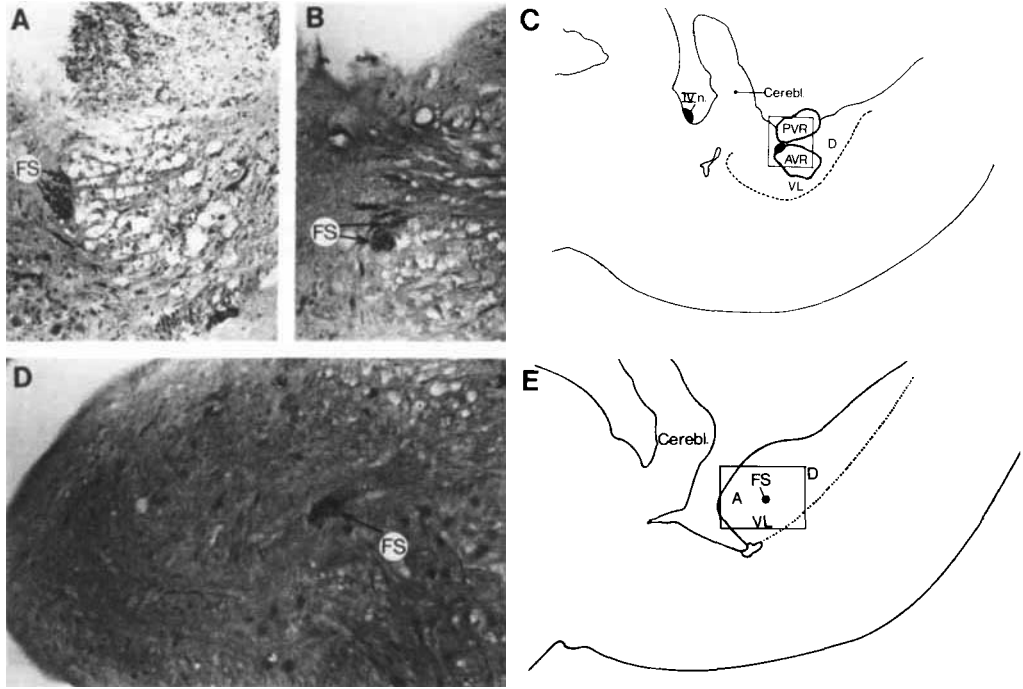


Fig. 3 The photomicrographs of figures A and B were taken from sections as shown in the rectangular area of diagram C. These sagittal views show the relationships of the crosscut FS fascicles to the posterior (PVR) and anterior (AVR) vestibular roots in the lateral part of the vestibular area. Note several separate and distinct FS fascicles near the brain surface (A) and within the lateral part of the vestibular region (B). D was taken from the medial part of the vestibular area as referenced to the blocked area in diagram E. Here the FS is a compact bundle of degenerated axons situated above the ventrolateral vestibular (VL) nucleus. Seven days survival. $\times 108$.

neurons were not severe enough to cause cell death. The silver method thus demonstrated the fragmented sensory axons and terminals of the geniculate ganglion cells but not the efferents of the facial nerve.

Not all lesioned animals showed exclusive geniculate ganglion destruction. In some there was also partial or complete vestibulocochlear involvement. In two lizards, the geniculate ganglion was completely destroyed; in five, both seventh and eighth were partially involved and one animal had a pure eighth nerve lesion. None of the lizards showed involvement of the fifth, ninth or tenth nerves or direct insult to the brain. Brains cut in either sagittal or transverse plane provided a three dimensional view of the course of degenerated axons of the sensory component of the facial nerve (FS) as they traversed the vestibular nuclear complex to form the tractus solitarius (TS).

In sagittally sectioned brains the facial sen-

sory degeneration was immediately anterior and rostral to the anterior vestibular root as the latter entered the vestibular area of the brainstem (fig. 3). The FS separated from the motor component of the facial nerve and passed through the middle of the tangential vestibular nucleus. In the lateral part of the vestibular area, as seen in both sagittal (figs. 3A,B) and transverse sections (fig. 2A), the FS was separated into several (2-6) densely stained degenerated fascicles by the entering vestibular root fibers and cells of the vestibular nuclei. Axonal degeneration consisted predominantly of fine fibrous debris with a few coarse fiber fragments intermingled. Throughout the course of the FS there was no collateral or terminal degeneration in the vestibular nuclei. At the surface of the brainstem no degeneration could be traced from the facial nerve into the descendens tractus trigemini (DTT). This was noted on both sagittal and transverse serially sectioned

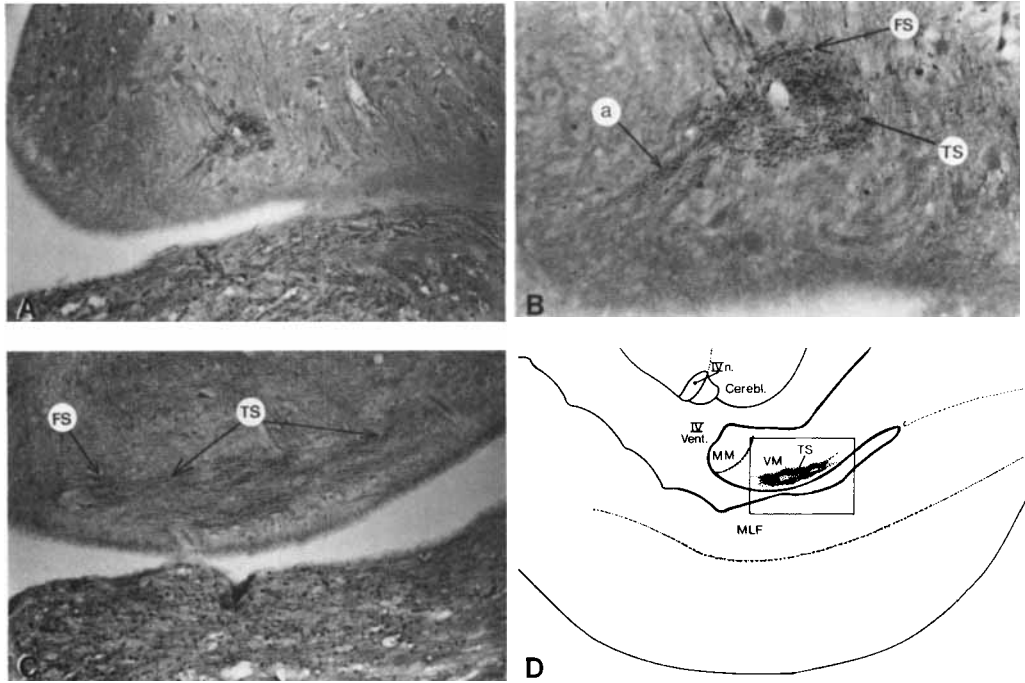


Fig. 4 The tractus solitarius (TS) and its prefacial (a) portion in photomicrograph A are further enlarged in B. Near the ventricular wall the FS divides into the descending TS and the small prefacial component. The prefacial fibers form several small splinters of degeneration that spread rostro-ventrally and terminate in the adjacent central gray of the ventricular wall. In C the sagittally cut prevagal portion of TS was taken from the region outlined in D. Caudal to the FS the TS divides into numerous fascicles along the ventricular wall. Seven days survival. A $\times 108$; B $\times 270$; C $\times 108$.

brains. In one animal not included in this study, there was slight vascular involvement intracranially around the seventh and eighth nerves that showed axon degeneration in the DTT.

Within the lateral vestibular area the FS fascicles were midway between the anterior and posterior vestibular roots. Near the middle of the vestibular nuclear complex, the fascicles of FS usually regrouped into a single degenerated tract (fig. 2B) that continued medially through the vestibular area. In one case, the FS remained subdivided into two distinct fascicles that joined medially at the TS region (figs. 2C,D). In another case a widely separated fascicle joined the main FS near the mid-vestibular region (fig. 2E). The overall course of the FS from its entrance to the ventricular wall was a slight ventromedial curve. One lizard with a pure vestibular nerve lesion showed dense degeneration in the vestibular nuclear area but no degeneration in the FS (fig. 2F). This negative view of a non-degener-

ated FS surrounded by axonal degeneration in the vestibular area helped confirm the path and relationship of the sensory facial fibers through the vestibular area.

Medial to the ventrolateral vestibular nucleus, nearly all the degenerated FS fibers took a "right angle" turn caudally to form the prevagal portion of the TS. A few degenerated fibers passed rostroventrally as the prefacial tractus solitarius. The prefacial fibers assumed a very brief course and ended in the immediate area of the central gray neuropil lateral to the ventricular wall (figs. 4A,B). The prevagal TS descended along the central gray of the ventricle, medial to the vestibular nuclei. In sagittal sections, prevagal degeneration split into several smaller anterior and posterior interconnecting fascicles (fig. 4C). The more anterior degenerating fibers curved ventrally and terminated on adjacent cells of the medial nucleus of the TS (MTS). In transverse section, there was a slight protuberance of the visceral sensory area into the fourth

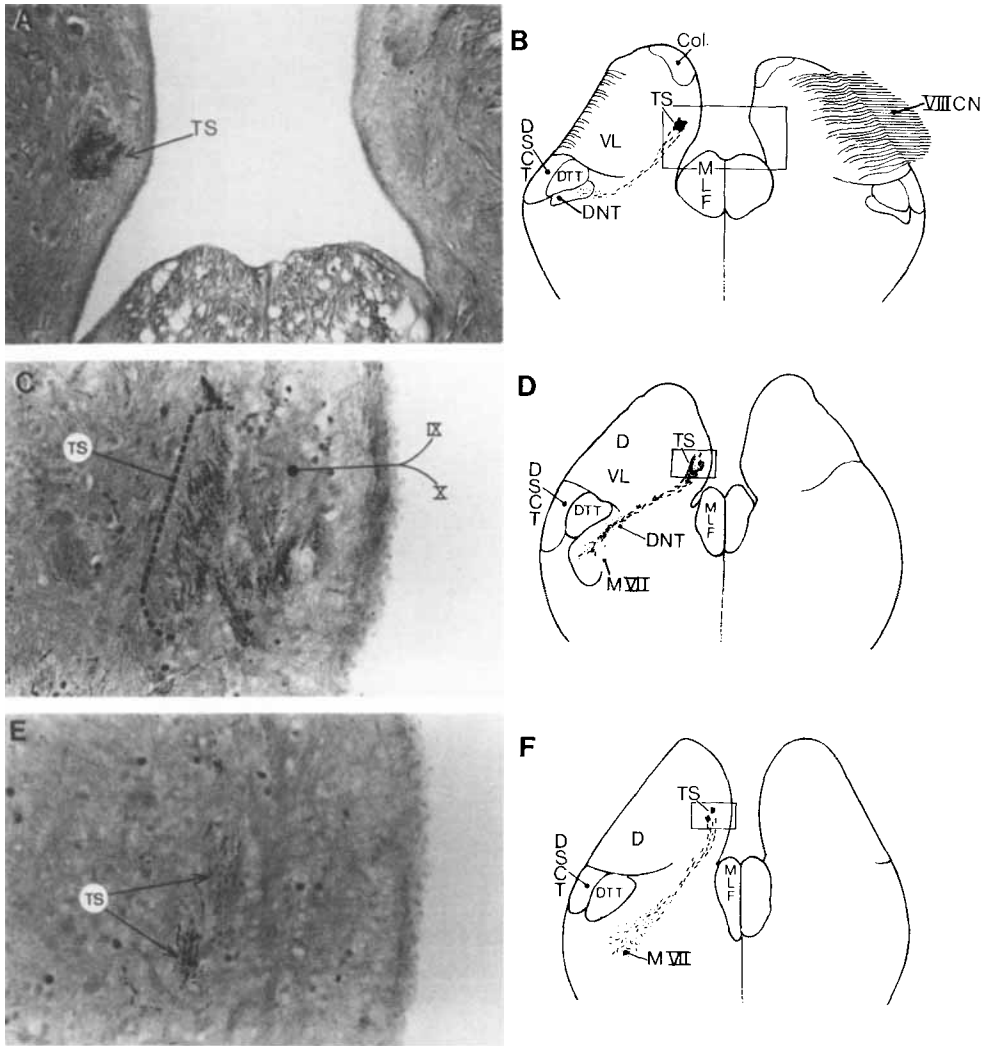


Fig. 5 Photomicrographs A, C, E were taken from the corresponding blocked areas in diagrams B, D, F. In A the dense, compact tractus solitarius (TS) is taken just caudal to the level of entrance of the seventh nerve. In C the normal axons presumably of the ninth and tenth cranial nerves (IX, X) of the TS intermingle with scattered degenerated fascicles derived from the seventh nerve. In E, rostral to the obex, only a few degenerated axons of seventh nerve origin are present. In nearly all levels the descending TS gives off a steady stream of axons that pass to the descendens nucleus trigemini (DNT) or the motor nucleus of the facial nerve (M. VII). Twenty-three days survival. A $\times 108$; C and E $\times 270$.

ventricle that coincided with the TS (fig. 5A). Caudal to the ninth and tenth nerve levels, there were numerous unstained (normal) axons in the TS that are believed to be mainly of glossopharyngeal and vagal nerve origins (fig. 5C).

Along the dorsal and medial margins of TS was the dorsal nucleus of TS (DTS). In Nissl

preparations, the apical dendrites of these cells (fig. 6C) were directed into the TS where, with silver preparations, the fine axonal debris of terminal and preterminal degeneration were visible. Anterior to the TS were alternating cell (MTS) and axon groups oriented vertically with fine terminal degeneration in the neuropil and adjacent cell somas. No de-

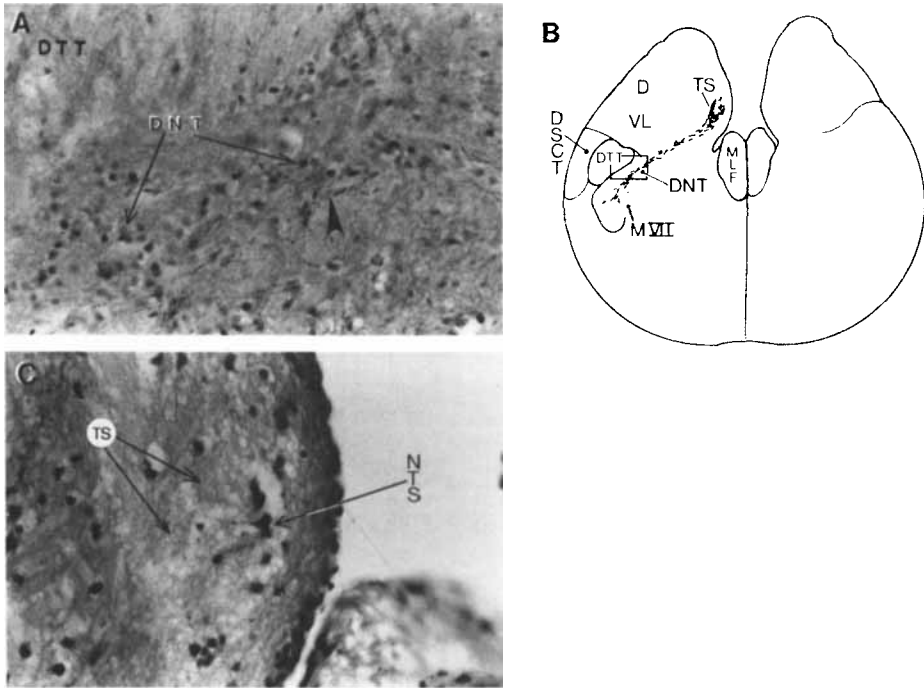


Fig. 6 Photomicrograph A shows the descens tractus trigemini (DTT) dorsal to the descens nucleus trigemini (DNT) with reference to its location in the blocked area in diagram B. Degenerated axons (arrowhead) enter and terminate in a small cell group of the DNT. Photomicrograph C is a cross section of the nucleus tractus solitarius (NTS). The dendrites of the cells project into the tractus solitarius. Twenty-three days survival. A $\times 270$; C $\times 432$.

generation was observed within the dorsal motor nerve of X but some fine, degenerated debris was observed near its limits.

Beyond the vagus nerve level, TS degeneration was considerably reduced, while there were degenerated axons which left the TS and passed to descens nucleus trigemini (DNT) and the motor nucleus of the facial nerve (M. VII). This trickle of axons left the anterior part of TS and, in a sweeping ventrolateral course, passed medial to nucleus vestibularis ventrolateralis and entered the rostral part of DNT (figs. 5B,D,F). Very small cells in the most medial part of the rostral DNT (fig. 6A) received most of the terminal degeneration while only a few fibers entered its more lateral part. Other degeneration continued more ventrally and terminated in the area of the motor nucleus of VII (fig. 5F). At levels rostral to the obex there was no degeneration in the DNT but the M. VII contained fine axonal debris.

At the obex level several degenerated axons remained ipsilaterally and terminated in the

nucleus commissura infima. Throughout the entire extent of the TS there was no crossing or contralateral degeneration in any of the experimental animals.

DISCUSSION

This was the first experimental study on degeneration of the sensory fibers of the facial nerve in a reptile. As previously described on normal reptiles (Kappers et al., '36; Barnard, '36) we selectively demonstrated that the sensory component of the facial nerve (FS) in *Lacerta* enters the brainstem adjacent to the eighth nerve and passes medially through the vestibular region toward the ventricular wall to form the tractus solitarius (TS). There was no evidence of a contribution from the facial nerve to the descens tractus trigemini (DTT) at its entrance into the brainstem as previously reported in the alligator and *Varanus* (Kappers et al., '36). In subreptilian animals a facial component in the DTT has been described (Norris and Buckley, '11;

Maler et al., '73; Matesz and Szekeley, '78) while other reports did not mention these fibers (Fuller, '74; Liuten, '75). The bull frog fifth and seventh nerves form a trigeminal-facial complex or have branches that interconnect the two nerves (Fuller and Ebbesson, '73). In frogs the seventh nerve fibers were traced into the DTT which apparently represented auricular branches supplying a paratympanic cutaneous area (Matesz and Szekeley, '78). Likewise, in the rat only the cutaneous auricular branch of the facial nerve entered the spinal trigeminal tract while there were no contributions to it from the petrosal or chorda tympani nerves or the motor trunk of the facial nerve (Martin and Mason, '77). Following chorda tympani lesions in the duck, axonal degeneration was not reported in the DTT (Dubbeldam et al., '76). It appears that an important consideration is the experimental animal used and the experimental approach to isolating a cranial nerve or one of its branches without damaging the adjacent nerve or brain surface. In this study the absence of facial degeneration in the DTT may be the result of an extracranial rather than intracranial destruction of the seventh nerve. Possibly the auricular cutaneous component of reptiles joins the seventh nerve intracranially and escapes a lesion of the geniculate ganglion. The cutaneous branches may be inconstant in *Lacerta* and may be incorporated in the peripheral branches of the fifth or tenth nerves. Since terminal degeneration appears in the DNT by way of the tractus solitarius, this route may replace the usual pathway seventh nerve fibers take in the DTT to end in the DNT of many of the other animals. However, the critical postoperative survival period for staining the spectrum of degenerated axons in the DTT with silver may not have been attained with the method used and this alone could account for their absence. Further peripheral seventh nerve dissections, other axon degeneration or tracing methods and neurophysiologic studies are required to investigate the facial cutaneous component in lizards.

The numerous fascicles forming the FS and their mode of convergence within the lateral half of the vestibular region would verify the importance of their relationships in experimental investigations on the vestibular system. Numerous FS fascicles are adjacent to large neurons of the ventrolateral vestibular nucleus while others are divided by primary

and secondary vestibular axons. Lesions that destroy certain vestibular nuclei could involve part or all of the FS, due to its variable intramedullary course, and thus simultaneously explain TS degeneration.

The tractus solitarius is divisible into three basic portions: prefacial, prevagal and post-vagal. The prefacial TS is relatively small and consists of short, fine fibers which ramify in the periventricular gray. This closely follows the description for *Anolis* (Barnard, '36) and *Amblystoma* and *Necturus* (Herrick, '14, '30). In the frog most prefacial fibers are derived from the facial nerve while only a few stem from the ninth and tenth (Matesz and Szekeley, '78). The incoming taste and other visceral stimuli following the prefacial fibers could influence the central reticular gray and relay visceral sensory information rostrocaudally to autonomic areas.

Most TS degeneration from the facial nerve terminates rostral to the vagus nerve level in the lizard. Beyond the tenth nerve degenerated fibers are greatly reduced and gradually decrease in number to the level of the obex. This is similar to findings in the rat (Torvik, '56). In the cat, there is apparent lamination of the seventh, ninth and tenth nerves in the TS (Kerr, '62). An overlap of the three nerves in TS and their terminations in NTS were observed in the frog (Matesz and Szekeley, '78). In *Lacerta* there was considerable mixing of the seventh nerve TS fibers with normal axons; the later presumably are derived from the ninth and tenth nerves.

The NTS consists of small cells that rim the dorsal, medial and ventral sides of the TS. Numerous dendrites of these cells project into TS which probably accounts for the gradually decreased degeneration and axon terminations within the tract and for the absence of degeneration outside of the TS. Following ninth and tenth nerve destruction in cats, the remaining 80-85% of non-degenerating axon varicosities of the dorsomedial TS were mainly axodendritic contacts as determined by electron microscopy (Chiba and Doba, '75). It was suggested that these were catecholaminergic nerves for the regulation of cardiovascular reflexes. Whether facial nerve fibers of lizards in this area of TS regulate or influence cardiovascular reflexes needs physiologic verification. Zotterman ('67) has reviewed an enormous number of species and their differences in neural responses to visceral and sapid stimuli. Normal excitable taste stimuli

for either amphibians, reptiles or some mammals do not equally stimulate NTS cells in all of these animals due to the variation and specialization of these cells and their central neural connections.

The trickle of axons from TS to both DNT and motor nerve VII have not been previously reported in reptiles. Throughout the course of these fibers there were no apparent collaterals to the adjacent vestibular or reticular nuclei but rather direct connections were made with motor nerve VII and the DNT. Most fibers were direct to the small celled DNT but a few ramified into its more lateral part. Such connections have been recently described and illustrated in the frog (Matesz and Szekely, '78). It appears that the reptilian counterpart has a much more extensive rostrocaudal distribution and may represent the somatic sensory fibers that do not enter the DTT but instead travel with the FS and TS before terminating on cells of the DNT. The greatly diminished seventh nerve contribution to more caudal portions of the solitary complex in *Lacerta* is not surprising since the postvagal portions of NTS and TS are considered mainly related to the ninth and tenth cranial nerves. In ducks the chorda tympani projections were observed to terminate bilaterally in the caudalmost solitary complex region (Dubbeldam et al., '76). With phylogenetic development of complex laryngeal, respiratory and digestive apparatuses there is a concomitant elaboration of the ninth and tenth cranial nerves and the TS (Barnard, '36). In *Lacerta* as compared to the duck and mammals there are fewer facial sensory fibers in the postvagal solitary complex and these may be minimally related to central reflex mechanisms of taste, swallowing and other visceral functions.

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