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Afferent and Efferent Connections of the Octavolateral Cerebellum in the Channel Catfish, Ictalurus Punctatus

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AFFERENT AND EFFERENT CONNECTIONS OF THE OCTAVOLATERAL CEREBELLUM IN THE CHANNEL CATFISH, *ICTALURUS PUNCTATUS*

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LIST OF ABBREVIATIONS

ALLN	anterior lateral line nerve
AN	anterior octaval nucleus
BV	blood vessel
CCMO	corpus of the cerebellum molecular layer
CCG	corpus of the cerebellum granule layer
CON	caudal octavolateralis nucleus
DiI	neuronal tracer indocarbocyanine dye
DCN	dorsal cochlear nucleus
DN	descending octaval nucleus
DON	dorsal octavolateralis nucleus
EG	eminentia granularis of cerebellum
EGl	lateral portion of eminentia granularis
EGla	anterior division of lateral eminentia granularis
EGlp	posterior division of lateral eminentia granularis
EGm	medial portion of eminentia granularis
EGpr	profundus layer of eminentia granularis
ELL	electrosensory lateral line lobe
FL	facial lobe

HRP	neuronal tracer horseradish peroxidase
iDN	inferior descending octaval nucleus
IL	inferior lobe
IO	inferior olivary nucleus
IRF	nucleus of the inferior reticular formation
LC	lobus caudalis
LLN	lateral line nerve
M	medial octavolateralis nucleus
ML	molecular layer
MLF	medial longitudinal fasciculus
MLLN	medial lateral line nerve
MN	magnocellular octaval nucleus
MON	medial octavolateralis nucleus
MZ	molecular zone
nE	nucleus electrosensorius
nMLF	nucleus of the medial longitudinal fasciculus
nPr	nucleus praeeminentialis
ON	octaval (VIIIth) nerve
OT	optic tectum
PLLN	posterior lateral line nerve
PN	posterior octaval nucleus
PV	periventricular nucleus

RF	reticular formation
SGN	secondary gustatory nucleus
TMB	reactant tetramethyl-benzidine
TN	tangential octaval nucleus
TOB	nucleus turn-of-the-bilge
TS	torus semicircularis
V	ventricle
VL	vagal lobe

for Judy and Jessica

CHAPTER I

INTRODUCTION

A Brief Overview of the Octavolateralis System

The octavolateralis system refers to the peripheral and central sensory structures innervated by the VIIIth and the lateral line cranial nerves in vertebrates (for reviews, see Bullock & Heiligenberg, 1986; Atema et al., 1988; Coombs et al., 1989; Webster et al., 1992). The octaval, or VIIIth nerve associated, portion of the octavolateralis system includes auditory (detection of sound) and vestibular (detection of balance, rotational acceleration, and gravity) senses whereas the lateralis, or lateral line nerve associated, components consist of the mechanosensory lateral line (detection of local pressure gradients in aquatic environments) and electroreceptive (detection of weak electric fields) senses. In contrast to the nearly ubiquitous distribution of auditory and vestibular senses among the vertebrates, a mechanosensory lateral line is limited to larval and most adult anamniotes and electrosensory systems are distributed throughout many anamniotic, as well as a few amniotic, taxa.

In anamniotes, each of the octavolateralis senses share organizational similarities from the periphery to central pathways through the hind- and mid-brain. The peripheral receptors for each of the octavolateralis sensory systems are composed, in part, of modified hair cells (for review, see Zakon, 1986; Budelmann, 1988; Platt 1988; Popper et al., 1988; Jørgensen 1989; Münz 1989). Excitation occurs for each of the auditory, vestibular, and mechanosensory lateral line receptor organs, when stimuli deflect an accessory structure that

is attached to the hair cell stereocilia resulting in the opening of mechanically gated ion channels. Electroreceptors, however, are excited when the difference in the electric field potential of an external source and that of the haircell causes the opening of ion channels that are voltage gated. The resultant change in the potential generated in either of these receptor types is then transmitted to fibers of the VIIIth or lateral line nerves via synaptic connections.

Each of the primary octavolateralis nerve fibers are bi-polar neurons that project to the hindbrain ipsilaterally in teleosts (McCormick & Braford, 1988) to nuclei which are rostrally to caudally elongated and lie adjacent to one another in the medulla (McCormick, 1989, 1992). Electrosensory fibers project to the dorsal octavolateralis nucleus (DON) in the case of most electroreceptive anamniotes or to the electrosensory lateral line lobe (ELL) in teleosts. Mechanosensory lateral line medullary nuclei are located medially adjacent to the electrosensory nuclei and are composed of a rostral medial octavolateralis nucleus (MON) and a caudal octavolateralis nucleus (CON). Lastly, octaval nerve fibers carrying auditory and vestibular information project to portions of a series of nuclei, known as the octaval column, that are situated in the most medial divisions of the octavolateralis medulla. In teleosts, these nuclei are known rostrally to caudally as the anterior (AN), magnocellular (MN), tangential (TN), descending (DN), and posterior (PN) nuclei (McCormick & Braford, 1988).

Beyond the level of the hindbrain, ascending lemniscal auditory, lateral line mechanosensory, and electrosensory pathways maintain a parallel yet distinct organization (McCormick & Braford, 1988). Though at each processing level projections are bilateral, the vast majority of fibers project to one side or the other. Medullary projections predominately

decussate to the contralateral midbrain. Higher order midbrain-to-thalamus and thalamus-to-telencephalon connections remain chiefly ipsilateral. Similar to the organization found in the medulla, nuclei processing the various octavolateral sensory information at all subsequent levels are located adjacent to one another with a typical lateral to medial organization of electrosensory, mechanosensory lateral line, and auditory nuclei respectively. The central arrangement of the vestibular projections beyond the level of the medulla differ from other octavolateralis sensory pathways with bilateral projections that both ascend toward the midbrain and descend to the spinal cord (McCormick, 1988).

Based upon the phylogenetic distribution of the auditory, vestibular, and mechanosensory lateral line senses, it is reasonable to presume that each of these octavolateralis sub-systems evolved only once within the vertebrate phyla. Furthermore, because of the similarities in the receptors and central pathways of the VIIIth nerve and mechanosensory lateral line systems, it is likely that these systems share a common ancestry (McCormick & Braford, 1988). In contrast to the auditory, vestibular, and mechanosensory lateral line systems, however, electroreception has been independently evolved along several phylogenetic lines (for reviews, see Bullock & Heiligenberg, 1986). Although the common vertebrate ancestor was electroreceptive and utilized a form of electroreception which may share an ancestry with the other octavolateralis senses, teleosts have lost this sensory system and have re-evolved non-homologous electroreceptive systems in at least two phylogenetically distinct linages. It is therefore parsimonious to suggest, that in teleosts, neither the electroreceptors nor the associated centralized electroreceptive pathways share a common phylogenetic history with the other octavolateralis sub-systems. Rather, the

electrosensory systems found within teleosts are a more recent derivation of the mechanosensory lateral line (Zakon, 1986; Jørgensen, 1989). Though it is outside the scope of this paper, each of the few incidences of electroreception found in the amniotic taxa are also presumed to represent an independent evolutionary occurrence (Bullock, 1982; Bullock et al., 1983; Gregory et al., 1987; Scheich et al., 1986; Gould et al., 1993).

Electroreception in Teleosts

The two major radiations of electrosensory teleosts include taxa from each of the osteoglossomorphan and ostariophysan super-orders (Fink & Fink, 1981; Bass, 1982; Lauder & Liem, 1983). Within Osteoglossomorpha, electroreceptive sub-groups Xenomystidae (African knife fishes) and Mormyridae (African weakly electric fish) are monophyletic whereas Gymnotoidei (South American weakly electric fish) and Siluroidei (catfish) are monophyletic sub-groups of Ostariophysi (Lauder & Liem, 1983). Both xenomystid and silurid fishes have ampullary electroreceptive organs which encode low-frequency electric fields (< 0.1 - 2.0 Hz) whereas the mormyrid and gymnotid fish each have high-frequency tuberous electroreceptors specifically tuned to the frequency of their electric organ discharge (generally around 1 kHz) in addition to the low-frequency ampullary electroreceptors. Because the majority of ostariophysans are not electroreceptive, an analysis of the re-evolution of electroreception in this grouping of animals reveals three levels of octavolateralis organization: (first) ostariophysans other than silurids and gymnotids have a mechanosensory lateral line but lack electroreceptive capabilities whereas (second) siluriforms have low-frequency ampullary receptors in addition to a mechanosensory lateral line and (third)

gymnotids have the highly derived high-frequency tuberous receptors tuned to the discharge of an electric organ as well as ampullary organs and a mechanosensory lateral line. Catfish therefore appear to represent an organizational intermediate between the majority of ostariophysans which do not have an electrosense and the highly derived electroreceptive organization of the gymnotids. A comparison of the catfish electrosensory system with the non-electroreceptive ostariophysans and the weakly electric gymnotids can therefore yield valuable insight into the way sensory systems evolve by demonstrating varying levels of complexity of the same evolutionary path. The results of such an examination may be applicable to the osteoglossomorphan lineage as the similarities in the pattern of octavolateralis organization of the gymnotids and the mormyriforms appears to suggest a similarity in the pattern of electroreceptive evolution in non-homologous systems.

The Catfish Octavolateralis System

Much of the central anatomy of the octavolateralis senses has been determined in catfish and this anatomy is similar to that which has been described for teleosts in general (Knudsen, 1978; Tong, 1982; Tong & Finger, 1983; Finger & Tong, 1984; Finger, 1986; Fritzsch et al., 1990; Striedter, 1991; McCormick & Braford, 1993; New & Singh, 1994). Axons of projection neurons (crest cells) from each of the electrosensory lateral line lobe (ELL), medial octavolateralis nucleus (MON), and descending octaval nucleus (DN) project to segregated divisions of the midbrain torus semicircularis (TS). Collaterals of these neurons divert to an isthmic nucleus known as the nucleus praeeminentialis (nPr). The axons of the nPr neurons that are in synaptic connection to these collaterals form a descending pathway

back to the medullary projection neurons thereby forming a feedback loop (Tong, 1982).

The cerebellum in catfish also plays a role in the processing of octavolateralis information (Bass, 1982; Finger, 1986). The eminentia granularis (EG) is a granular cell region of the catfish cerebellum that is divided into medial (EGm) and lateral (EGl) divisions and the EGl is further subdivided into anterior (EGla) and posterior (EGlp) regions. The EGla receives primary mechanosensory lateral line input whereas electrosensory afferents terminate in the EGlp and primary VIIIth nerve sensory fibers project to the EGm (New & Singh, 1994). Axons of EGl and EGm neurons form a descending parallel fiber system back to the ELL, MON, and DN (Tong & Finger, 1983; Finger, 1986). Other sources of input and output from the EG have not been described though a relationship between the caudal cerebellum and the nPr has been suggested (Finger, 1986).

Research in different animal systems suggest similarities in the anatomical arrangement of descending modulation of sensory information in the medulla. A descending projection from a secondary brainstem nucleus (that is positioned similarly to the nPr) to the granule cell region of the cerebellum has been described in mammalian auditory systems (McDonald & Rasmussen, 1971), and elasmobranch, gymnotid, and mormyrid electrosensory systems (Sas & Maler, 1983, 1987; Schmidt & Bodznick, 1984; Bell & Szabo, 1986; Bastian & Bratton, 1990). It is therefore plausible to assume that a similar descending pathway may occur in siluriforms.

Other conceivable sources of input to the granule cell layer of the cerebellum in catfish may be from a somatosensory relay nucleus in the spinal cord or caudal medulla. Such a pathway has been described for the mammalian auditory system (Itoh et al., 1987; Weinberg

& Rustoni, 1987), and elasmobranch, gymnotid, and mormyrid electrosensory systems (Libouban & Szabo, 1977; Szabo et al., 1979; Sas & Maler, 1987; Schmidt & Bodznick, 1987; Conley & Bodznick, 1989; Szabo et al., 1990, 1991). It is therefore also reasonable to suppose that a similar somatosensory influence occurs in catfish.

Functional Significance of the Catfish Metencephalic Structures

All vertebrates have sensory systems that engage a series of descending or feedback controls from higher brain centers onto lower ones. Such descending pathways are used to regulate and modify ascending sensory information and in so doing, create considerable system flexibility. For example, gain control (increasing or decreasing the sensitivity of the system), filter properties (improving the signal to noise ratio), or selectively increasing the spatial resolution of the system are all features generated through such descending influence. The catfish metencephalic nucleus praeeminentialis (nPr) and eminentiae granularii (EG) are part of a descending octavolateralis control system regulating the medullary processing of ascending sensory information.

It has been shown that stimulation of the dorsal nPr in catfish causes inhibition of ascending electrosensory information as recorded from the contralateral torus semicircularis (TS; Scoma, 1994). Lesioning or anesthetizing the nPr of gymnotid fish has been shown to increase the peripheral sensitivity to electrogenic stimuli as recorded from the electrosensory lateral line lobe (ELL; Bastian, 1986a, b). The dorsal nPr forms a feedback loop onto the ELL and inhibits the responses of this nucleus to incoming stimuli. Neurotransmitter gamma-aminobutyric acid (GABA) is a widespread central nervous system inhibitor (Gottlieb, 1988)

and has been demonstrated to be responsible for inhibiting crest neurons in the ELL of gymnotids (Shumway & Maler, 1989). It is possible that the inhibition of ELL neurons is accomplished when excitatory ascending input to the nPr excites descending inhibitory pathways to the ELL. GABA-ergic neurons have been identified in the catfish nPr (New & Fay, 1993) and are a likely candidate for the source of such inhibition. Furthermore, a finding of descending influences from the nPr onto the regions of the EG (the anterior and posterior lateral EG and the medial EG), may indicate a conservation of octavolateralis organization in the feedback patterns for each of the lateral line and VIIIth nerve systems. It is not known, at the present time, the extent of similarities of descending octavolateralis control mechanisms.

It is the purpose of this project to describe the afferent and efferent anatomical connections to EGl and EGm and to compare these connections to similar vertebrate systems. An additional aim of this thesis is to describe the cellular morphologies and regional placement of nPr neurons involved in these descending control mechanisms. Finally, this thesis provides hypotheses of the way the described central anatomy may allow for such emergent properties as gain control, the filtering of reafference, and spatial resolving capabilities.

CHAPTER II

MATERIALS AND METHODS

Channel catfish, *Ictalurus punctatus,* were obtained from a local commercial distributor and maintained in 24^{0}C freshwater aquaria. Fish ranged from 17-20 cm in total length and from 27-70 g in body weight. All experimental procedures reported in this study were performed under the guidelines approved by the Loyola University Animal Care and Use Committee (IACUC).

Neuronal tracers horseradish peroxidase (HRP, Sigma) and indocarbocyanine dye (DiI, Molecular probes) were used to trace afferent and efferent axonal connections of the octavolateralis cerebellum and descending input to the molecular layer overlying the primary medullary nuclei. Specifically, tracers were injected into the lateral line mechanosensory and electrosensory associated eminentia granularis (EGl) and the VIIIth nerve associated medial eminentia granularis (EGm) as well as the molecular layer overlying the electrosensory lateral line lobe (ELL). Both HRP and DiI are effective for establishing axonal passages through the brain, but utilize different procedures and evaluation techniques. The protocols for each tracing technique are therefore explained separately in the following paragraphs.

Horseradish Peroxidase (HRP) Procedures

A total of 52 specimens of *Ictalurus* were randomly selected for HRP injection.

Individuals were anesthetized in approximately 0.03% tricaine methanesulfonate (MS-222). Proposed injection sites were exposed by using a dental drill to expose the brain while the fish received a continuous flow of water across its gills. Twenty HRP injections were placed into the EGl, 26 were placed into the EGm, and in 6 cases, the tracer was applied to the molecular layer overlying the ELL. In 16 of the 20 EGl cases, HRP partially dissolved in phosphate buffer (.1 *M*, pH 7.4) was applied as a paste on the tip of a #.0000 insect pin with the use of a micro-manipulator. In an additional three EGl cases, HRP completely dissolved in phosphate buffer was applied via iontophoresis. For all iontophoresis cases, a glass micropipet electrode broken to a tip diameter of approximately 40μm was filled with a HRP concentrated solution and positioned in the appropriate location using a micro-manipulator. A fine silver wire electrode was placed inside the glass electrode and another fine wire reference electrode was inserted into the cerebro-spinal fluid surrounding the brain. A Grass SD9 stimulator was used to pass five to ten μamps current as a series of 200 mS , DC step passes. This current was delivered at a frequency of 1.2 pps across the wire electrodes with the HRP electrode as the cathode. Among the 26 cases in which HRP was injected into EGm, sixteen were applied as a paste using an insect pin, six were done by iontophoresis, and in three cases, HRP concentrated in phosphate buffer was pressure injected via a syringe. The six remaining cases of HRP injections were all applied to the molecular layer overlying ELL as a paste on the tip of an insect pin.

Surgical incisions were packed with gelfoam and sealed with dental acrylic and cyanoacrylate adhesive. Following post-surgical survival times of 6-10 days, the specimens were given lethal doses of MS-222 and transcardially perfused with iced phosphate buffer

followed by 4% glutaraldehyde in phosphate buffer. The brains were then wholly removed from the craniums and cryoprotected by immersion in a 4% glutaraldehyde and 20% sucrose (in phosphate buffer) solution for approximately 3-4 hours and subsequently stored, if necessary, in 20% sucrose in phosphate buffer. The brains were then blocked in 20% gelatin (in phosphate buffer) and 20% sucrose and sectioned to a thickness of 36μm on a sliding, freezing microtome.

Series consisting of every sixth section were rinsed with distilled water followed by a rinse of phosphate buffer. A colorimetric reaction was developed using Hanker-Yates (Sigma) reagent as the chromogen to reveal the transported HRP according to the protocols of Hanker et al. (1977). In ten of the EGl cases, and in five of the EGm cases, some of the sections were reacted with 3,3',5,5' tetramethyl-benzidine (TMB, Sigma; Mesulam, 1982) to confirm results determined using the Hanker-Yates protocol. Processed sections were mounted on chrome alum subbed slides, counterstained with cresyl-violet (for Hanker-Yates sections) or neutral-red (for TMB sections), and examined via light microscopy (Olympus BH-2 microscope). Anterograde and retrograde transport of HRP from the injection site was drawn using a camera lucida microscope attachment.

Indocarbocyanine Dye (DiI) Procedures

A total of 10 specimens of *Ictalurus* (5 EGl cases and 5 EGm cases) were randomly selected for DiI injection. For all DiI cases, the specimens were deeply anesthetized with MS-222 and transcardially perfused with phosphate buffer (.1 *M*, pH 7.4) followed by 4% paraformaldehyde in phosphate buffer. Specimens were then decapitated and the dorsal half

of each cranium dissected away exposing all but the most ventral portions of the brain. The heads were then postfixed in a 4% paraformaldehyde solution for 3-4 days in order to sufficiently harden them for subsequent handling. Following this post fix period, each brain was blotted dry and small crystals of DiI were inserted into the EGl or EGm with a fire wire. The head and brain as a unit were then set, but not submerged, in a pool of paraformaldehyde fixative inside a sealed, darkened jar and stored in a 37^{0}C drying oven. Storage times varied as the experiments progressed but were within a range of 15-60 days.

Following sufficient storage times, injected brains were mounted in a 25% gelatin (in phosphate buffer) block and fixed in 25% formalin in phosphate buffer for 48 hours. Sections were cut to a thickness of 50μm using a vibratome and were counterstained by brief immersion in a solution of phenylenediamine (Quinn & Weber, 1988) prior to mounting. The DiI and counterstain were examined using an epifluorescence microscope (Olympus BH-2) and representative cases were drawn using a camera lucida attachment.

CHAPTER III

RESULTS

Afferent and Efferent Connections to the Lateral Eminentia Granularis (EGl)

Axons of the EGl granule cells form a descending parallel fiber network (figs. 1E, 1F, 2A-E). Some of the axons of this network cross the midline of the brain within the caudal cerebellum; the rest remain ipsilateral. The axons on both sides form a portion of the lateral molecular layer (figs. 1F, 2A-E, 3) overlying the electrosensory lateral line lobe (ELL) and the medial octavolateralis nucleus (MON). Ascending EGl projections (fig. 1A-E) travel ipsilaterally along the ventrolateral brainstem to an area immediately ventral and rostral to the metencephalic nucleus praeeminentialis (nPr). Some of these fibers terminate in the ipsilateral nPr though most decussate in a commissure that arches somewhat anteriorly along the ventral boundary of the metencephalon (figs. 1B, 1C, 4). This pathway carrying fibers from the EGl to the nPr also contains fibers traveling in the reverse direction. Both retrogradely filled cell bodies as well as anterogradely labeled terminal processes are seen in portions of the nPr following EGl injections (figs. 1B, 1C, 5).

The bilateral EGl heavily interconnect through a cerebellar commissure arching sharply anteriorly and lying immediately ventral to the cerebellar granule cells (figs. 1C, 1D, 6). The caudal edge of this commissure is at a level corresponding to the middle of EGl in the transverse plane, whereas the rostral end of the arc extends to a level of metencephalon

approximately equal to mid-torus semicircularis (TS). Along the extent of this commissural pathway, neurons were retrogradely labeled with HRP in a nucleus positioned adjacent to the medial longitudinal fasciculus (nMLF; figs. 1A, 7), and one more caudal and close to the IIIrd ventricle, the periventricular nucleus (PV; figs. 1D, 8). Both nMLF and PV neurons utilize this commissural pathway to send descending axons to the EGl (fig. 1A-D).

Retrograde transport of EGl injected HRP resulted in the labeling of neuronal somata in a number of other nuclei that were located in bilateral sensory and basal medullary plates: the inferior (ventrolateral) portions of the dorsal octaval nucleus as described by McCormick and Braford (iDN; figs. 2C, 2D, 10) (1993), the caudal region of the inferior reticular formation (IRF; figs. 2F, 11), and a previously undescribed nucleus, nucleus turn-of-bilge (TOB; figs. 2D, 2E, 11). TOB is positioned on the ventrolateral border of the medulla, dorsolateral and slightly anterior to the inferior olivary (IO), and directly ventral and lateral to the IRF. The axons of these nuclei ascend bilaterally as part of a common tract along the ventrolateral edge of the hindbrain to the caudal cerebellum, the level at which decussation occurs, before terminating within the EGl (figs. 1F, 2A-F, 9). Labeling of IO cells following EGl injections was not observed.

Afferent and Efferent Connections to the Medial Eminentia Granularis (EGm)

Efferent fibers of the EGm decussate and descend bilaterally within the medial molecular layer (figs. 3, 12F, 13A-E) in a manner similar to that described for the EGl. Reciprocal bilateral EGm connections with the nucleus praeeminentialis (nPr) follow a similar organization to the path described for EGl cases (figs. 12C, 12D, 14).

Reciprocal interconnections between the bilateral EGm (fig. 12F) pass though the caudal portion of the cerebellar commissure, but do not arch rostrally as is the case for fibers between the EGls. No labeling of cell bodies was observed in the nucleus of the medial longitudinal fasciculus (nMLF), periventricular nucleus (PV), or similarly positioned metencephalic nuclei.

Caudal medullary input to the EGm arises bilaterally from the inferior olivary (IO; figs. 13F, 15) forming an ascending tract along the ventrolateral hindbrain. This ascending tract is similarly placed to the ventrolateral medullary tract described for EGl injections (figs. 13A-E, 16). However, labeling of other medullary nuclei, such as the descending octaval nucleus (DN), the inferior reticular formation (IRF), and the nucleus turn-of-bilge (TOB) were not observed following EGm injections.

Pathways Associated with Injections into the Molecular Layer

Injections of HRP into the molecular layer overlying the electrosensory lateral line lobe (ELL) labeled pathways corresponding to those described in previous studies(Tong and Finger, 1983; Finger, 1986). Briefly, descending projections arise from the lateral and medial eminentia granularis (EG; fig. 18A, 18B) and from the nucleus praeeminentialis (nPr; fig. 17). Crest cells in each of the ELL, the medial octavolateralis nucleus (MON), and the descending octaval nucleus (DN), have apical dendrites extending into the molecular layer. Their axons ascend bilaterally, but principally contralaterally, to the midbrain torus semicircularis (TS) and to the metencephalic nPr (figs. 19, 20).

Nucleus Praeeminentialis (nPr) Descending Projections to each of the Lateral (EGl) and Medial (EGm) Eminentiae granularii and to the Molecular Layer

A distinct topographic organization of nPr cells descending to the EGl and EGm was observed (figs. 5, 14, 21). The distribution of cells projecting to the EGm begins caudally at the medioventral edge of the nPr and migrates dorsally along the medial border as one progresses rostrally through the nucleus. The number of these labeled cells diminishes at the rostral portions of the nPr. Nucleus praeeminentialis cells projecting to the EGl form two spatially separated groups. One group of EGl labeled neurons is located at the ventral nPr boundary and extends along the mediolateral edge to a point approximately one-half the length of the nucleus. The other EGl associated group is concentrated in the middle portions of the nucleus and extends toward the dorsolateral boundary of the rostral border. Previous physiological studies have demonstrated that the dorsal group of nPr cells is electrosensory and the ventral group is mechanosensory (Tong, 1982).

Nucleus praeeminentialis (nPr) labeled cells projecting to the molecular layer overlying the electrosensory lateral line lobe (ELL) show no similar sort of topographic organization (figs. 17, 21). Rather, these cells are more sparsely distributed and found throughout all of the nPr regions having projections to the lateral and medial EG.

The morphologies of nPr cells projecting to the EGl and EGm are generally similar (figs. 22, 23A, 23B). These are roughly triangular cells, measuring 15 to 20 μm across the somata, and have three equal sized processes. The cells in the nPr which project to the

primary medullary nuclei via the molecular layer have a different morphology. These cells are smaller and more rounded than the cells projecting to the EG, measuring 10 to 15 μm across the somata, and have a small dendritic process and a larger axon which immediately bifurcates into smaller branchlets (figs. 22, 24).

CHAPTER IV

DISCUSSION

Comparisons of the Lateral (EGl) and Medial (EGm) Eminentiae Granularii

A summary of the afferent and efferent connections to the EGl, EGm, and molecular layer overlying the electrosensory lateral line lobe (ELL) in *Ictalurus punctatus* is provided in Table 1; a circuit diagram of the afference and efference to each of the EGl and the EGm is shown in Figure 25. To date, an exhaustive description of the cerebellar octavolateralis connections has been provided for only a few species. Among teleosts, such descriptions are limited to the gymnotid, *Apteronotus leptorhynchus* (Sas & Maler, 1987) and the mormyriform, *Gnathonemus petersii* (Szabo, 1983). Reasons underlying a paucity of similar octavolateralis anatomical descriptions may be technical; the target nuclei are small, obscure, and are often difficult to fill completely with injections of HRP without contaminating adjacent structures or fibers of passage. The spilling of HRP into areas adjacent to the target nuclei causes the obvious possibility of labeling cell bodies that do not project to the area of interest. The solution to this dilemma is to perform a large number of cases in which the target injection site is only partially filled. Upon evaluation, a diagram of the connections may then be constructed by summing the results of several cases while eliminating those cases in which the injection was too large or off target. In these experiments, a sufficient number of cases were performed (see methods) enabling the reconstruction of the vestibulolateral

afference in *Ictalurus.*

Commissures connecting the Bilateral Eminentiae granularii (EG)

Each of the bilateral EGl and EGm are reciprocally connected through cerebellar commissures (figs. 1B-D, 12F, 25). The EGl commissure is large, arches rostrally, and carries axons from cells in the nucleus of the medial longitudinal fasciculus (nMLF; fig. 1A) and the periventricular nucleus (PV; fig. 1B, 1D; both the nMLF and PV are located in the rostral metencephalon). The EGm commissure, on the other hand, is small, does not arch rostrally, and has no additional input. It is possible therefore, that the nMLF and PV do not function in EGm (VIIIth nerve associated) processing.

In Gymnotids, axons of cells in the electrosensory and mechanosensory lateral line portions of the torus semicircularis (TS) have been shown to project to the optic tectum (OT), reticular formation (RF), inferior olivary (IO), nucleus praeeminentialis (nPr), nucleus electrosensorius (nE; affiliated with electrosensory pathways only), and pretectal regions (Carr et al., 1981). Dendritic arborizations from nMLF labeled fibers have also been reported in regions of the rostral mesencephalon (Finger & Tong, 1984). It is possible that the descending toral pathways make synaptic contact with the nMLF dendritic processes in the OT, nE, or pretectal regions, and if this were the case, the anatomy providing for an additional feedback mechanism would be established for the electrosensory and mechanosensory lateral line pathways. That is, a feedback loop would be formed by the following connections: lateral line nerve -> medullary electrosensory lateral line lobe (ELL) and medial octavolateralis nucleus (MON) -> TS -> OT, nE, or pretectal regions -> nMLF

-> EGl -> ELL and MON (fig. 26). Connections of the PV may act as additional modulation to this pathway or serve a role in a separate, but similar, function.

It is reasonable to hypothesize that such a feedback pathway may play a role in the processing of sensory information that necessitates the maintenance of spatial integrity and is therefore not required in the EGm (VIIIth nerve associated) pathways. For instance, both the electrosensory and mechanosensory lateral line systems have receptors distributed across the body surface. The central preservation of information concerning any one receptor position relative to the other receptors is therefore important in determining the exact location of a stimulus source. VIIIth nerve associated processing differs in this regard because these peripheral receptors are clustered in a single location within the cranial cavity.

Pathways between the Eminentiae granularii (EG) and the Nucleus Praeeminentialis (nPr)

Similar reciprocal connections exist for each of the EGl and EGm to the nPr (figs. 1B, 1C, 5, 12B, 12C, 14, 25). Finger (1986) has suggested, that for the catfish electrosensory system, a descending connection from the nPr to the lobus caudalis (LC) of the cerebellum exists. If one defines the LC as the entire caudal portion of the cerebellum, inclusive of both the EGl and EGm, then in a very general sense, Finger's assertion is correct. However, Bass (1982) defines the LC in catfish as including a molecular zone (MZ) and a pars medialis. The pars medialis is equivalent to the EGm and the MZ is a thin dorsoventrally oriented layer of unmyelinated axons that is divergent from the molecular layer overlying the primary medullary nuclei and separates the EGl and EGm granule cell masses. Hence, the LC consists only of

this dorsoventrally oriented molecular sheet and VIIIth nerve associated granule cells and therefore should probably not be considered to receive descending electrosensory fibers from the nPr as these fibers terminate wholly within the EGl.

Eminentiae Granularii (EG) Axons in the Dorsal Molecular Layer (ML)

The molecular layer of the cerebellum is contiguous with the dorsal molecular layer overlying the primary medullary nuclei and is composed of axons arising from the EGl and EGm granule cells (figs. 1F, 2A-E, 3, 13A-E). The medullary dorsal molecular layer lies atop a ventral molecular layer which consists of axons descending from the nucleus praeeminentialis (nPr). Previous reports (Finger, 1986) suggest that fibers of the dorsal molecular layer are not spatially segregated according to the EG (EGl or EGm) source from which they arise; likewise, it was suggested that fibers of the ventral molecular are also not spatially segregated according to the regional placement of originating nPr neurons. The findings in these experiments, however, show that such segregation does exist in the dorsal molecular layer. Axons arising from EGl granule cells are situated lateral to those axons arising from the EGm. These two bundles appear, in transverse sections, to be entirely distinct from one another. Segregation of the axons comprising the ventral molecular layer, based upon the location of originating cell bodies within the nPr, has yet to be fully determined but is unlikely as will be discussed in the section concerning cell distribution and morphology in the nPr.

Ventrolateral Hindbrain Tracts to the Eminentiae Granularii (EG)

Each of the ventrolateral hindbrain pathways ascending bilaterally to the EGl and EGm (figs. 2, 9, 13, 16) share a common course: first, the axons projecting to either the EGl or EGm arise from nuclei located in various regions of the caudal medulla; second, both of these pathways ascend along the ventrolateral border of the hindbrain then divert through portions of the octaval medullary nuclei; last, both tracts decussate in the caudal cerebellum before finally terminating in the EG group that was injected. Differences arise, however, in the location of nuclei accessing these separate pathways (figs. 2B-F, 13F): the pathway leading to the EGl receives input from the inferior reticular formation (IRF), nucleus turn-of-bilge (TOB), and the inferior descending octaval nucleus (iDN); the pathway leading to the EGm receives input only from the inferior olivary nucleus (IO). Comments relating to these differences in medullary connections to the EGl and EGm are given in the following sections.

The Inferior Reticular Formation (IRF) and the Nucleus Turn-of-the-Bilge (TOB)

Nuclei that are located in the basal plate of the caudal medulla and provide afference to the granular cell masses of the caudal cerebellum have been identified in mammals (Itoh et al., 1987; Weinberg & Rustioni, 1987; Young et al., 1993), sharks (Schmidt & Bodznick, 1987; Conley & Bodznick, 1989), gymnotids (Sas & Maler, 1987), and mormyriforms (Szabo et al., 1979; Libouban & Szabo, 1977; Szabo et al., 1990, 1991). These nuclei provide the cerebellum with proprioceptive, corollary discharge, or somatosensory relay type information and their position corresponds (approximately) to the position of the IRF and the TOB, both of which, provide afference to the EGl in catfish (figs. 2D-F, 11, 25). Proprioceptive and

somatosensory input to the EGl may be necessary for the processing of mechanosensory lateral line and electrosensory stimuli. In each of these sensory systems, self generated signals can interfere with the animal's detection of exogenous signals. For instance, a mechanosensory lateral line and electrosensory system may be used to detect the movements and electric fields generated by possible prey. However, the animal's own movements and respiratory activities generate pressure gradients and electric fields that are detectable by its own electrosensory and mechanosensory lateral line receptors. These activities will therefore interfere with the detection of the externally generated stimuli. Proprioceptive and somatosensory input to the cerebellum provides a means whereby the detecting animal has, as part of its octavolateralis processing areas, a measurement of the portion of the sensory signal that comes from self generated stimuli. This self generated portion may them be removed from the overall signal to give the animal a clear description of the external sources of the stimuli.

The Inferior Descending Octaval Nucleus (iDN)

The iDN is anatomically situated to provide an additional source of sensory modulation to the electrosensory and mechanosensory lateral line systems, and possibly, to the general octavolateralis senses as well (figs. 2B, 2C, 10, 25). Crest cell axons of the DN have previously been reported to project to the torus semicircularis (TS) and to the nucleus praeeminentialis (nPr; Finger & Tong, 1984). The DN has also been shown to receive fibers directly from the nucleus of the medial longitudinal fasciculus (nMLF) and, as has been previously discussed, the nMLF dendritic terminations are likely to receive descending toral

input within the optic tectum (OT), nucleus electrosensorius (nE), or the pretectal regions. Both the iDN and the nMLF were revealed in this study to send projections to the EGl. There are, therefore, multiple pathways by which the same originating information may converge upon, and act in conjunction to provide interesting functions for, the EGl. There is a direct pathway (iDN -> EGl), a feedforward pathway (iDN -> TS -> nMLF -> EGl), and a feedback pathway (iDN -> TS -> nMLF -> iDN -> EGl; fig. 26).

The function of these pathways involving the iDN are an area for future research. However, it does appear that any modulatory activity that these pathways may provide does not apply to the VIIIth nerve systems because the EGm is not connected to either the nMLF or the iDN. It is plausible, therefore, that the loops through the iDN act to provide the electrosensory and mechanosensory lateral line systems with additional possibilities for the spatial representation of stimuli, the filtering of unnecessary stimuli, or the heightened (or lessened) sensitivity to particular stimuli.

The Inferior Olivary Nucleus (IO)

In agreement with Tong and Finger (1983), the results of these experiments reveal IO input to the EGm (figs. 13F, 15, 25). Interestingly, Tong and Finger also showed that the electrosensory portion of the torus semi-circularis (TS) sends axons to the IO. Hence, a descending toral pathway to EGm (TS -> IO-> EGm; fig. 26) is provided where one would intuitively suspect the EGl as being the final destination. The EGm, therefore, may play a role in mechanosensory lateral line and electrosensory processing. Establishing that connections exist between the EGm and EGl would be an appropriate next step in determining if EGm

modulation of EGl processing is possible. Such connections were observed in the experiments of this thesis. However, it cannot be said with certainty that these connections actually do occur because the observed labeling in the neighboring EG masses may have been the result of diffusion of the tracer through the cell groups rather than axonal connections.

Cell Distribution and Morphology in the Nucleus Praeeminentialis (nPr)

Upon evaluation of the various nuclei providing afference to each of the EGl and the EGm, it became obvious that there were at least two, and possibly three, distinct nPr cell populations separately associated with the various EG. It was then decided to analyze each of these distributions with respect to the injection site and to compare them with the distribution of nPr cell bodies providing axons as part of the ventral molecular layer overlying the primary medullary nuclei. This comparison was accomplished by making additional injections of HRP which were limited, for two reasons, to the ventral molecular layer of the electrosensory lateral line lobe (ELL): first, this portion of the molecular layer is in a lateral location that is more surgically accessible than the molecular layer overlying the medially adjacent octavolateralis nuclei; second, it was thought that injections limited to an isolated portion of the ventral molecular layer would likely reveal labeling only in isolated portions of the nPr.

Injections to the EGl consistently labeled cells along the lateral edge of the nPr and the distribution of this lateral population is clearly distinct from the more medial distribution of EGm associated cells (figs. 5, 14; for a diagrammatic comparison, see fig. 21). Furthermore, the lateral EGl associated population is likely to be divisible into two separate

sub-groups: a dorsolateral group which is confined to the rostral extent of the nucleus and does not appear to overlap with a caudally situated ventrolateral group. Tong (1982) has provided electrophysiological evidence for the separation of mechanosensory lateral line and electrosensory processing within the nPr. He recorded from cells in the dorsal nPr that corresponded to electrosensory activity in the posterior EGl (EGlp) and from cells in the ventral nPr that corresponded to mechanosensory lateral line activity in the anterior EGl (EGla). These results would suggest that the spatially separated sub-divisions of the lateral population of EGl associated cells in the nPr can be categorized as an anteriorly positioned dorsolateral electrosensory group and a caudally positioned ventrolateral mechanosensory lateral line group. This kind of segregation was not observed in the population of cells giving rise to axons of the ventral molecular layer. These cells were found distributed throughout all of the nPr regions even though the injections were limited to the portion of the ventral molecular layer overlying the ELL (fig. 17). It is therefore probable that the fibers of the ventral molecular layer are not spatially segregated according to a regional placement of nPr neurons. Rather, nPr fibers associated with the different octavolateralis modalities course rostrocaudally together within the ventral molecular layer and make synaptic contact with the medullary octavolateralis nuclei along different lengths; that is, axons traveling from the nPr to the medial octavolateralis nucleus (MON), for example, first course over the ELL before reaching their final destination.

Each of the three nPr cell populations providing afference to the EGl and EGm are distributed in a rostrocaudal manner through the nucleus. It seems likely that within these distributions a topographical mapping of the body surface could be demonstrated as it has

been for the ELL (Finger, 1986) and for the EGl (Finger, 1986; New & Singh, 1994). In systems having a spatial topography, such as the electrosensory and mechanosensory lateral line senses, the preservation of the body surface topography seems necessary at each processing step. Otherwise, feedback mechanisms would act only as general modulators and be meaningless for any particular point along the body surface. This is clearly not the case; feedback mechanisms actually modulate the detected signal at particular regions of space independently and comments relating to this issue will be discussed in the upcoming sections.

Sas and Maler (1983) used Golgi techniques to describe, diagram, and provide photomicrographs for fourteen categories of cell morphologies found within the gymnotid nPr. Of the two catfish nPr cell types revealed in these experiments (figs. 22, 23A, 23B, 24), neither the triangular cells projecting to each of the EGl and EGm, nor the smaller rounded cells projecting to the ventral molecular layer, fit well into any of the categories defined by Sas and Maler. However, the catfish triangular cell type does share some similarities with each of the gymnotid stellate, tufted, and multipolar cells: stellate cells appear in clusters throughout the centralized region of the gymnotid nPr, are approximately 9 - 15 μm across the soma, have 3 - 5 sparse dendrites, and project to the dorsal molecular layer; tufted cells are also distributed throughout the central nPr, have a pear shaped soma that measures approximately 8 x 13 μm, have numerous dendritic tufts arising from the top of the cell, and project to the caudal lobe of the cerebellum; and lastly, multipolar cells are found in infrequent clusters throughout the central region of the nPr, are approximately 23 - 36 μm across the soma, are fairly round, and project to the lobus caudalis (LC). Though the catfish triangular cell type has an appearance, in these findings, that is similar to several of the gymnotid cell

types, it should be noted that the cell morphologies in the catfish were revealed from HRP studies and are therefore only partial representations of the actual cells whereas the Golgi impregnations reveal the entire morphology (soma and processes) clearly. It is quite possible, however, that the catfish triangular cell is of a different cell type than any found in the gymnotid nPr. Such differences in the cellular makeup of the nPr between the two species are likely when one considers the increased complexity of the gymnotid vs. the catfish system: Gymnotids have three tuberous and one ampullary map, each independently topographically organized in the ELL; Catfish have just one ampullary map in their ELL. If, as discussed previously, the topographic distribution of cells is maintained at each processing level, then the gymnotid nPr may necessarily involve more processing that is accomplished entirely different than that in the catfish.

A Comparative Analysis of the Octavolateralis Connections

Comparisons with Weakly Electric Fish

The cerebellar organization in the two taxa of weakly electric fish, the gymnotids (as revealed in *Apteronotus leptorhynchus*)and the Mormyriforms (as revealed in *Gnathonemus petersii*), is essentially the same as it is in catfish (Bass, 1982). The vestibulolateral lobe of the weakly electric fish is comprised of a molecular zone, a Purkinje-like cell layer, a pars medialis, and an eminentia granularis (Bass, 1982). The catfish vestibulolateral lobe likewise has a molecular zone and a Purkinje-like cell layer. In addition, the catfish EGm is equivalent to the weakly electric fish pars medialis, and the lateral eminentia granularis (EGl) in catfish is equivalent to what is simply referred to as the eminentia granularis in weakly electric fish.

Furthermore, the EGl area in each of the weakly electric fish and catfish is divisible into an anterior (mechanosensory lateral line associated) and a posterior (electrosensory associated) sub-group. The axons of the collective cerebellar granule cells in each of these animals form portions of the dorsal molecular layer overlying the primary medullary nuclei. Other similarities in octavolateralis connections include afference to the electrosensory and mechanosensory lateral line granular regions from a number of basal somatosensory nuclei located in the caudal medulla. These nuclei were previously known in weakly electric fish and correspond in position to the nuclei of the inferior reticular formation (IRF) and turn-of bilge (TOB) reported in the findings of these experiments (figs. 2D-F, 11).

The extent of similarities across the taxa concerning connections between the caudal cerebellum and the nPr are currently unknown. In catfish, each of the cerebellar octavolateralis areas form separate reciprocal connections to distinct areas in the nPr. (fig. 21). However, at the present time, only descending connections from the nPr to the electrosensory (posterior) portion of the eminentia granularis has been determined in weakly electric fish and other comparable (mechanosensory lateral line and VIIIth nerve associated) ascending or descending connections are currently unknown.

One important difference arises, between the catfish and the weakly electric fish, in the occurrence of primary afference to the cerebellum. Each of the various EG in catfish have been shown to receive primary afference whereas no primary nerve fibers project to the same groups in weakly electric fish.

Comparisons with Other Vertebrates

The flocculo-nodular lobe is the caudal portion of the amniote cerebellum and is characterized by input directly via the VIIIth nerve as well as indirectly via the vestibular nuclei (Precht, 1978; Kotchabhakdi & Walberg, 1978; Itoh, 1984 as described in Sas & Maler, 1987). Comparisons of the flocculo-nodulus nuclear organization were previously made to the organization of the electrosensory system in weakly electric fish. However, because the EGl in weakly electric fish lacks direct primary fiber input, and because there is no descending input from nuclei in amniotes that parallels the metencephalic nPr in anamniotes, it was suggested that the EGl is a evolutionary specialization and not directly comparable to the flocculo-nodulus (Bass, 1982; Sas & Maler, 1987). The EGm in catfish, however, is certainly a center for auditory or vestibular (or both) processing and has been shown to receive primary (VIIIth nerve) afferents. Though the EGm in catfish has strong reciprocal connections to the nPr (figs. 12B, 14), this feature may be a specialization of the system; a system which is, at a minimum, homoplasic and possibly homologous to the flocculo-nodulus.

The dorsal cochlear nucleus (DCN) of the mammalian auditory system also shares many organizational similarities with the EGl of weakly electric fish (Mugnaini et al., 1980a, b; Mugnaini, 1985): briefly, the cells of each of these nuclei share a similar morphology, receive input from higher brain centers, and send their axons as part of dorsal molecular layer overlying the primary medullary nuclei. However, because these two sensory systems pay attention to entirely different stimuli, and because electroreception has been evolved on (possibly) several occasions, it is most parsimonious to conclude that these systems are non-

homologous. The EGm of catfish, however, also shares the same similarities with the DCN as the EGl and is likely to be involved in auditory processing. Hence, the EGm in catfish provides a well described, and possibly homologous, comparison to the DCN in mammals.

Functional Significance of the Octavolateralis Connections

Gain Control

Bastian (1986) has described a mechanism in the electrosensory system of gymnotid fish whereby sharp increases or decreases in the amplitude of the stimulus are compensated within the central nervous system. Primary electrosensory afferents project to the electrosensory lateral line lobe (ELL) in these fish and make synaptic contact, either directly or through an inhibitory interneuron, with E (excitatory) and I (Inhibitory) cells. The E cells respond to increases in stimulus amplitude with an increase in spike rate whereas the I cells respond to increases in stimulus amplitude with a decrease in spike rate. Recordings have shown that given a sharp increase in the stimulus amplitude, the E cells first respond with a high level of excitation which is followed immediately by modulation of this excitation in a direction back toward the original conditions; that is, the E cells are first taken from a resting rate of spike activity to a high level of activity and then gradually back down to some intermediate level of activity. Recordings have also shown that a similar compensation, but in the opposite direction, occurs for the I cells. Hence, the overall effect is that the excitatory and inhibitory effects of both E and I cells are counterbalanced, through central mechanisms, for sudden changes in the magnitude of stimuli. This phenomenon is termed gain control.

The gain control mechanism of gymnotid fish is accomplished via the feedback

pathways through the nucleus praeeminentialis (nPr) and the EGl. Axons of the electrosensory lateral line lobe E and I cells make excitatory synaptic connections to cells of the nPr. These nPr cells, in turn, send descending projections that make inhibitory connections to the granule cells of the EGl. Finally, the granule cell axons form the dorsal molecular layer overlying the ELL from which excitatory synapses to the apical dendrites of the E and I cells are formed. Hence, increases in stimuli amplitude cause E cell excitation which is transmitted to the nPr and then to the EGl. The inhibitory activity of the EGl removes further descending excitatory signals feeding back onto the ELL and thereby diminish the excitatory influence upon the E cells. As was previously implied, this mechanism works similarly in I cell gain control.

The electrosensory system of teleosts, unlike any of the other octavolateralis systems, lacks efferent projections to the peripheral receptors. The occurrence of electrosensory gain control can therefore only be achieved centrally. Such a centralized mechanism may function in the other octavolateralis systems in addition to the efference to the receptors. This mechanism of gain control may also be applicable to mormyrids; these animals are known to exhibit gain control though the central mechanisms providing this feature are not understood. The results of these experiments indicate that, because of similarities in the anatomy of gymnotids and catfish, gain control is also likely to occur in catfish. Because of the distribution of nPr cells which project to the various EG in catfish (fig. 21), it is also likely that the nPr maintains a rostral to caudal body surface topography that functions in gain control.

Spatial Resolution

When a stimulus moves across the body surface, the gain control mechanism just described generates an enhancement of an animal's spatial resolving capabilities. For every point at which there is stimulus caused receptor excitation or inhibition along the body surface, there is a corresponding burst (or silencing) of activity in the ascending efferent neurons of the electrosensory or mechanosensory lateral line medullary nuclei. This initial response is followed by an immediate modulation of the signal back toward, but not quite arriving at, resting rate. Further, as the stimulus moves from point to point along the body surface, this initial response and subsequent modulation is repeated over and over centrally in a point to point topographic fashion. The consequence of such activity is, if one considers excitatory responses only, the highly excitatory representation on a centralized map of a point in space which is surrounded by areas of diminished excitation. This is called the searchlight hypothesis and is dependent, as demonstrated in other systems, on gamma amino-butyric (GABA) modulation (Crick, 1984). The neurotransmitter GABA has recently been identified in nuclei at all levels of catfish octavolateralis processing except for the EGl and EGm (New & Fay, 1993).

The rostral to caudal elongated distribution of each of the nPr cell groups projecting to the various EG (fig. 21) provides, as has been previously discussed, a possibility for a body mapping topography within the nPr for each of the mechanosensory lateral line and electrosensory systems. Such a topography within the nPr would seem necessary to enable the fine control of these spatial resolution capabilities.

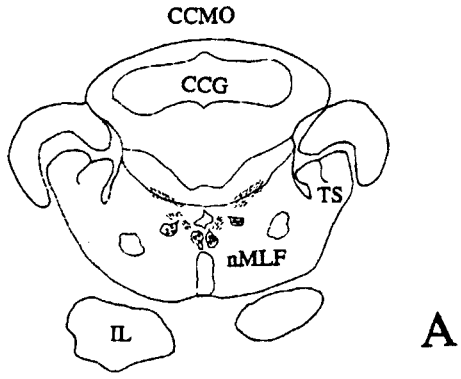
Reafference Filtering

In both the electrosensory and mechanosensory lateral line systems, the filtering out of signals that are detected because of self stimulation, is necessary. For instance, electroreceptive animals can detect the electric fields generated by their own respiratory activities; animals with a mechanosensory lateral line can detect the pressure gradients generated by their own slight positional changes. Because each of these systems utilize peripheral receptors that detect all relevant stimuli regardless of source, centralized mechanisms are necessary in both systems to enable the animal to distinguish self generated from externally generated stimuli. Montgomery and Bodznick (1994) have shown that the granule cells of the EGl play a role in providing the animal with an ability to make such distinctions using both the skate electrosensory and the scorpion fish mechanosensory lateral line systems. In each case, the distinction is made through the use of a mechanism whereby the animal learns to ignore all stimuli presented during a time window that corresponds to the motor activities that are likely to generate conflicting stimuli; that is, the animal learns to ignore any incoming stimuli that is time matched to breathing, moving, or other relevant motor activities. Recordings from the electrosensory lateral line lobe (ELL) and medial octavolateralis nucleus (MON) ascending efferent neurons (the equivalent of the catfish primary medullary crest cells) have shown stimuli presented in a cycle exactly time matched to respiration are initially detected and then gradually, over a time period of approximately 25 minutes, ignored. The hypothesis put forth by Montgomery and Bodznick is that proprioceptive and corollary discharge signals from motor systems impinge upon the cerebellar granule cells and these signals are then transmitted to the dorsal molecular layer

which is in synaptic contact with the ascending efferent neurons. The proprioceptive and corollary discharge signal are equal to a sum total of self generated noise and this noise can then be subtracted, through the use of inhibitory interneurons, from the signal representing all stimuli taking place in the ascending efferent neurons. Furthermore, exogenous stimuli time matched to the animal's respiratory rate is gradually ignored by a mechanism whereby the noise is gradually increased to include this exogenous signal.

In catfish, the observation that nuclei associated with the inferior reticular formation (IRF) and the turn-of-bilge (TOB) provide afference to the electrosensory and mechanosensory lateral line associated EGI provides evidence that is consistent with the reafference filtering model (figs. 2D-F, 11). Nuclei positioned similarly to the IRF and TOB both in sharks and in bony fish have been demonstrated to carry somatosensory reafference and proprioceptive information (Szabo et al., 1979; Libouban & Szabo, 1977; Sas & Maler, 1987; Schmidt & Bodznick, 1987; Conley & Bodznick, 1989; Szabo et al., 1990, 1991).

Figure 1: Afferent and efferent connections to the EGl of the cerebellum in *Ictalurus*. Rostral to caudal (A to F) transverse sections are shown corresponding to levels indicated by the dorsal brain aspect in the top right-hand corner. The injection site is shown as a large blackout in the appropriate section. Fibers of passage are drawn in each section as dashed lines, cell bodies as large circles, and terminal arborizations as small dots. Abbreviations are defined in the *List of Abbreviations.*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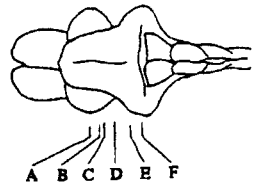
CCG
TS
nMLF
IL

A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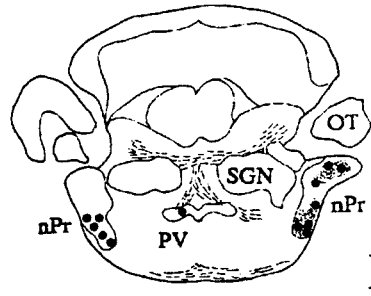
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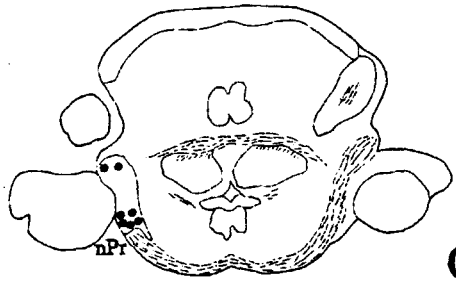
SGN
nPr
nPr
PV

B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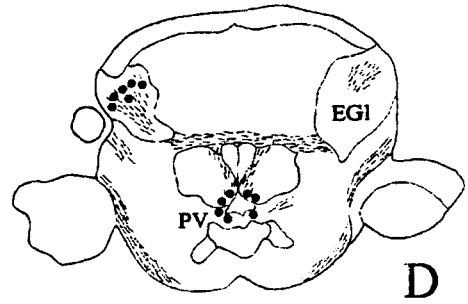
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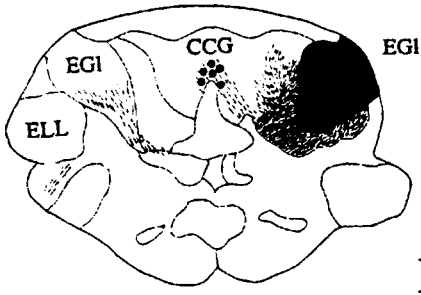
PV

D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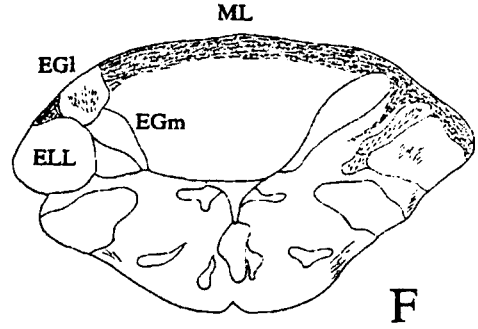
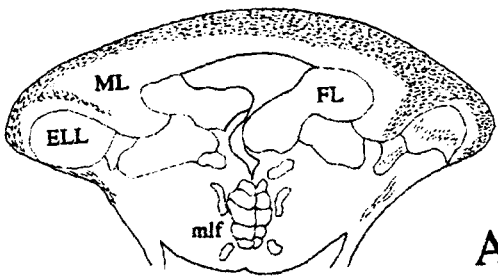
CCG
EGl
ELL

E


ML
EGl
EGm
ELL

F

Figure 2: Afferent and efferent connections to the EGl of the cerebellum in *Ictalurus* caudal to those depicted in Figure 1. Rostral to caudal (A to F) transverse sections are shown corresponding to levels indicated by the dorsal brain aspect in the top right-hand corner. The injection site is shown as a large blackout in Figure 1E. Fibers of passage are drawn in each section as dashed lines, cell bodies as large circles, and terminal arborizations as small dots. Abbreviations are defined in the *List of abbreviations.*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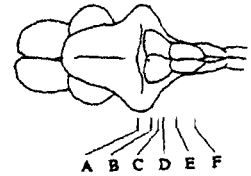
FL
ELL
mlf

A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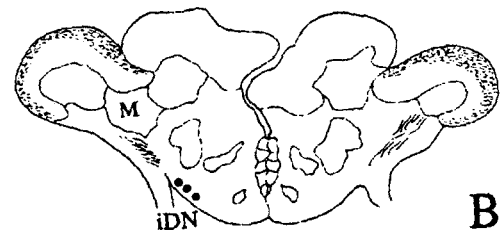
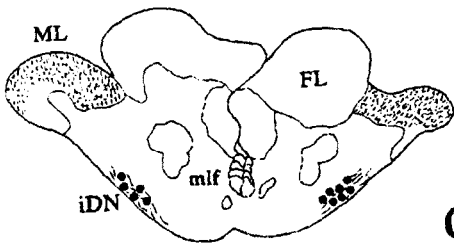
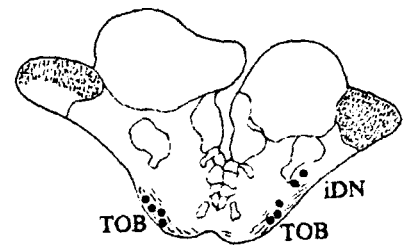

M
iDN

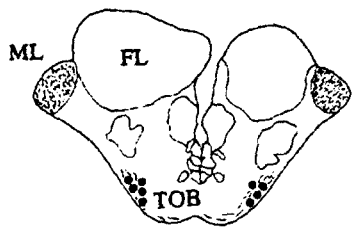
B


ML
FL
mlf
iDN

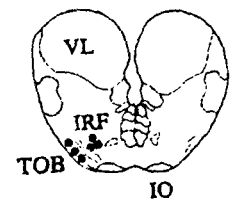
C


iDN
TOB
TOB

D

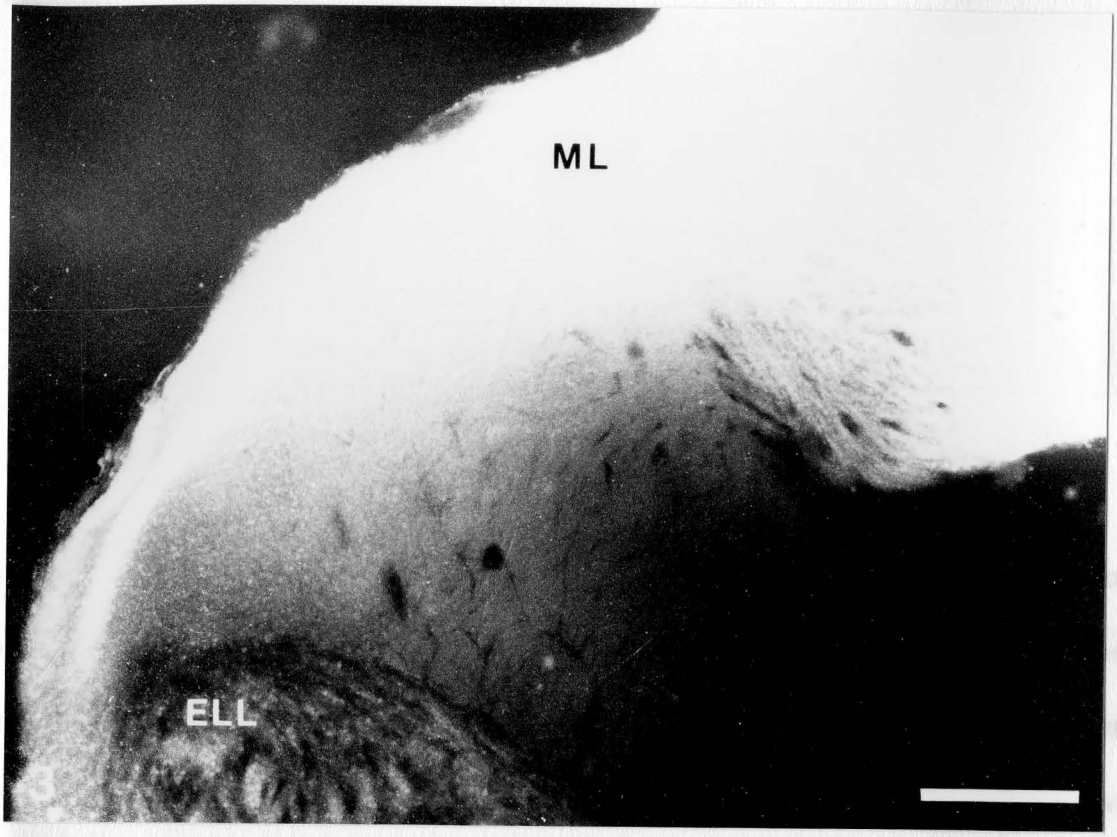

ML
FL
TOB

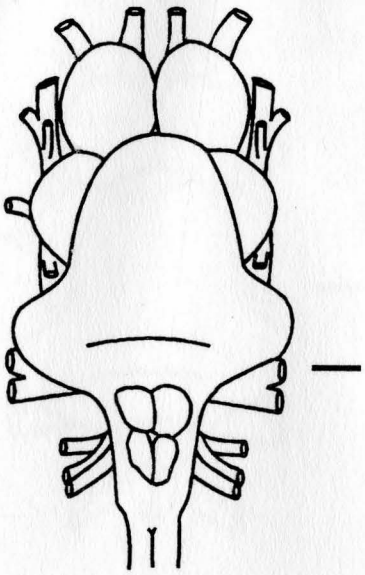
E


VL
IRF
TOB
IO

F

Figure 3: Fluorescent photomicrograph of the molecular layer overlying the primary medullary nuclei. DiI was injected into the molecular layer overlying the right-side ELL. In the photograph, fluorescent fibers are seen throughout the caudal portions of the ML and coursing over the contralateral ELL. A line diagram of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 50 μm. Abbreviations are defined in the *List of Abbreviations.*


ML
ELL



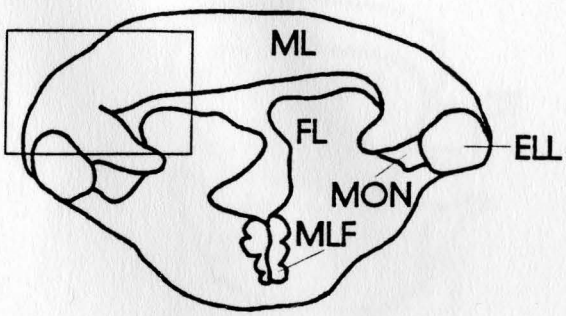
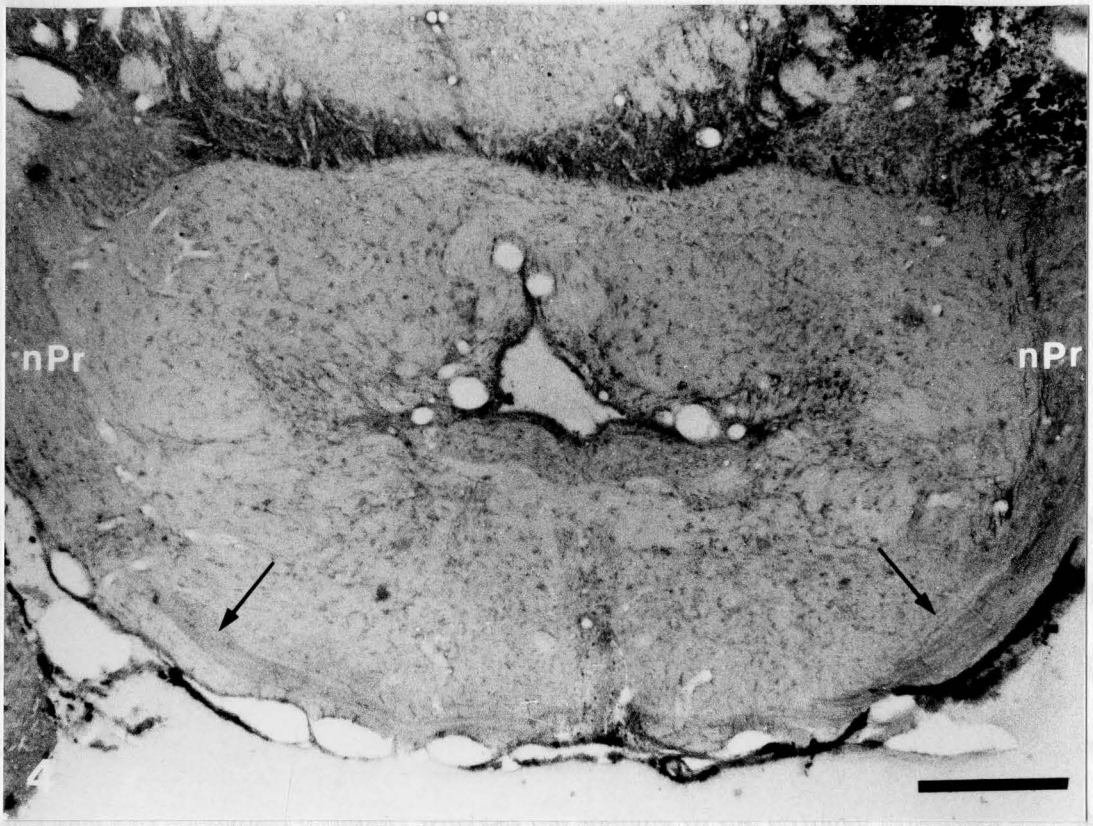
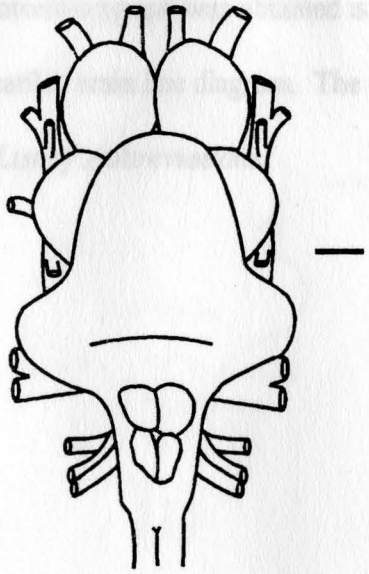

ML
FL
ELL
MON
MLF

Figure 4: Photomicrograph of the commissural pathway that is part of the ascending and descending tract between the bilateral nPr and the various EG. Fibers are shown, at the arrow tips, traveling along the ventrolateral edge of the brain between the bilateral nPr. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 500 μm. Abbreviations are defined in the *List of Abbreviations.*


nPr
nPr



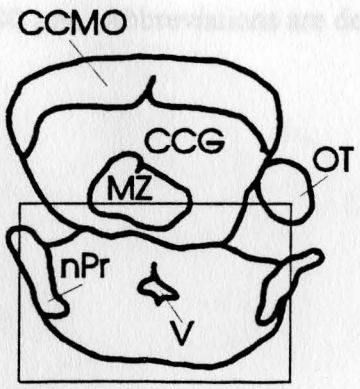
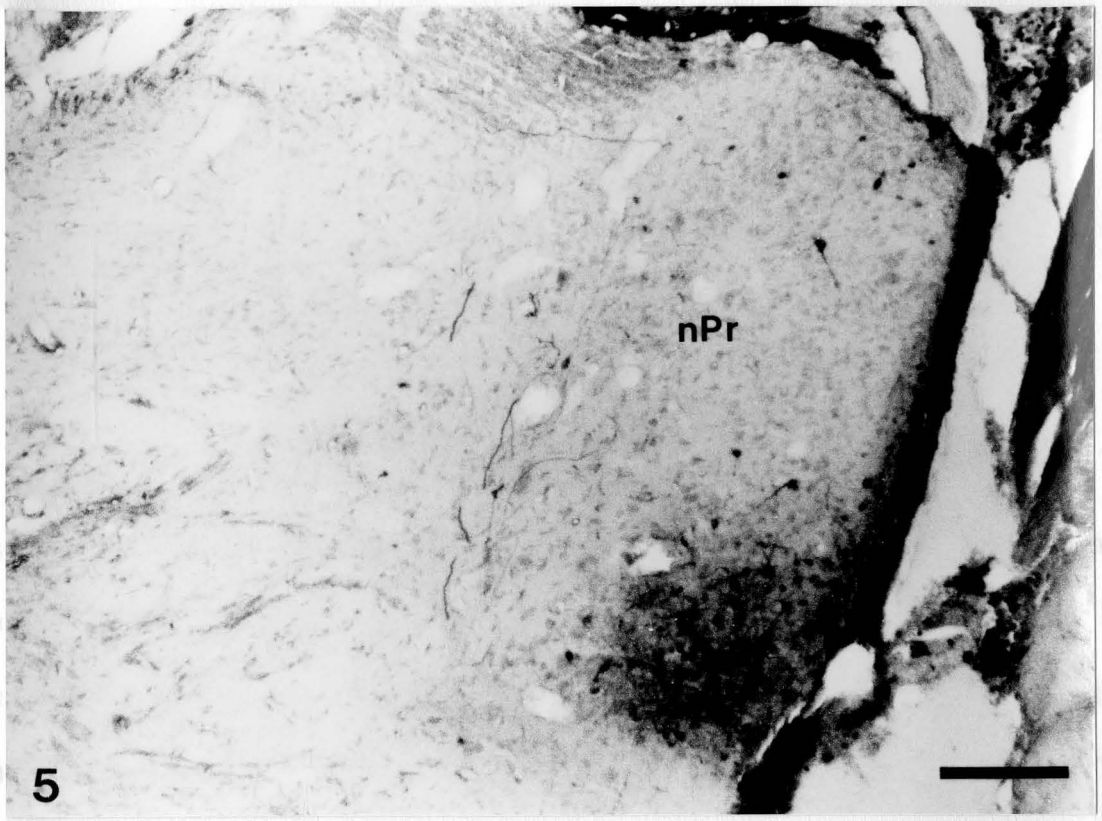
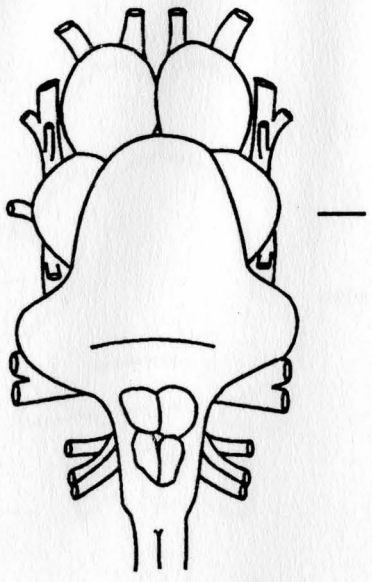

CCMO
CCG
OT
MZ
nPr
V

Figure 5: Photomicrograph of retrograde and anterograde HRP labeling in the ipsilateral metencephalic nPr in *Ictalurus* receiving EGl tracer fills. Labeling is confined to the dorsolateral and ventrolateral regions of the nPr. Both the larger darkly filled cell bodies with processes and the intermixed terminal arborizations can be seen. The staining of the cell bodies indicates retrograde transport whereas the staining of the terminal processes indicates transport in the anterograde direction. A line diagram of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 200 μm. Abbreviations are defined in the *List of Abbreviations.*


nPr
5



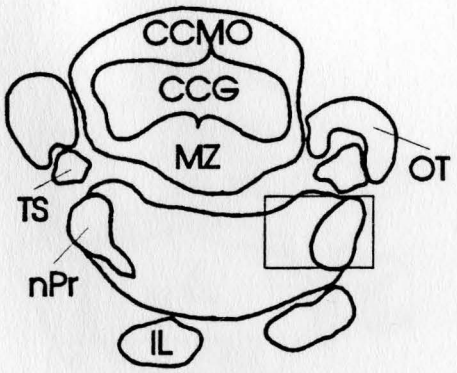
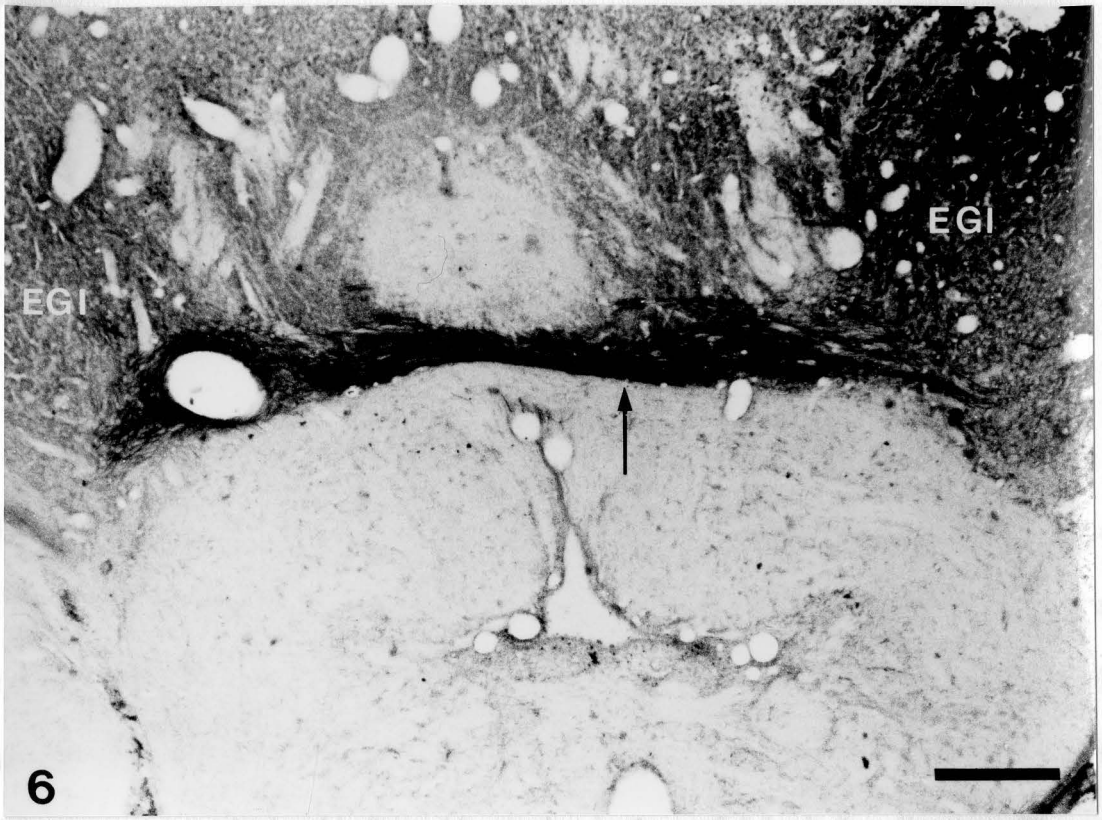
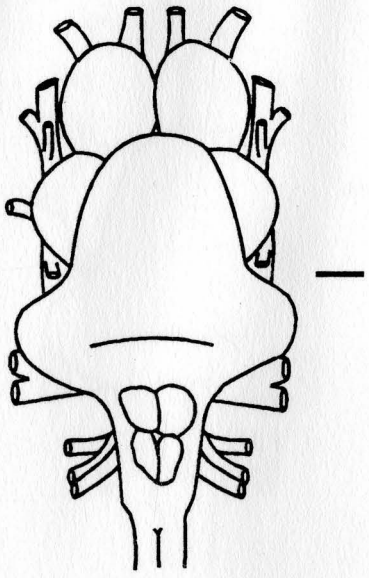

CCMO
CCG
MZ
OT
TS
nPr
IL

Figure 6: Caudal extent of the commissure connecting the bilateral EGl. The densely stained axons forming this commissure are seen in the photomicrograph just above the arrow tip. A line diagram of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 500 μm. Abbreviations are defined in the *List of Abbreviations.*


EGI
EGI
6



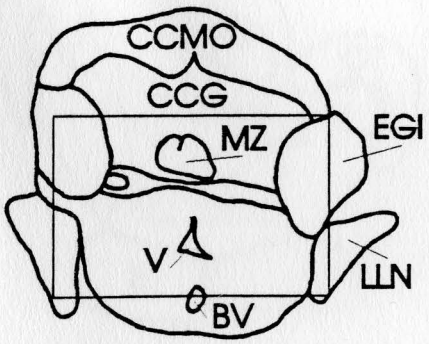
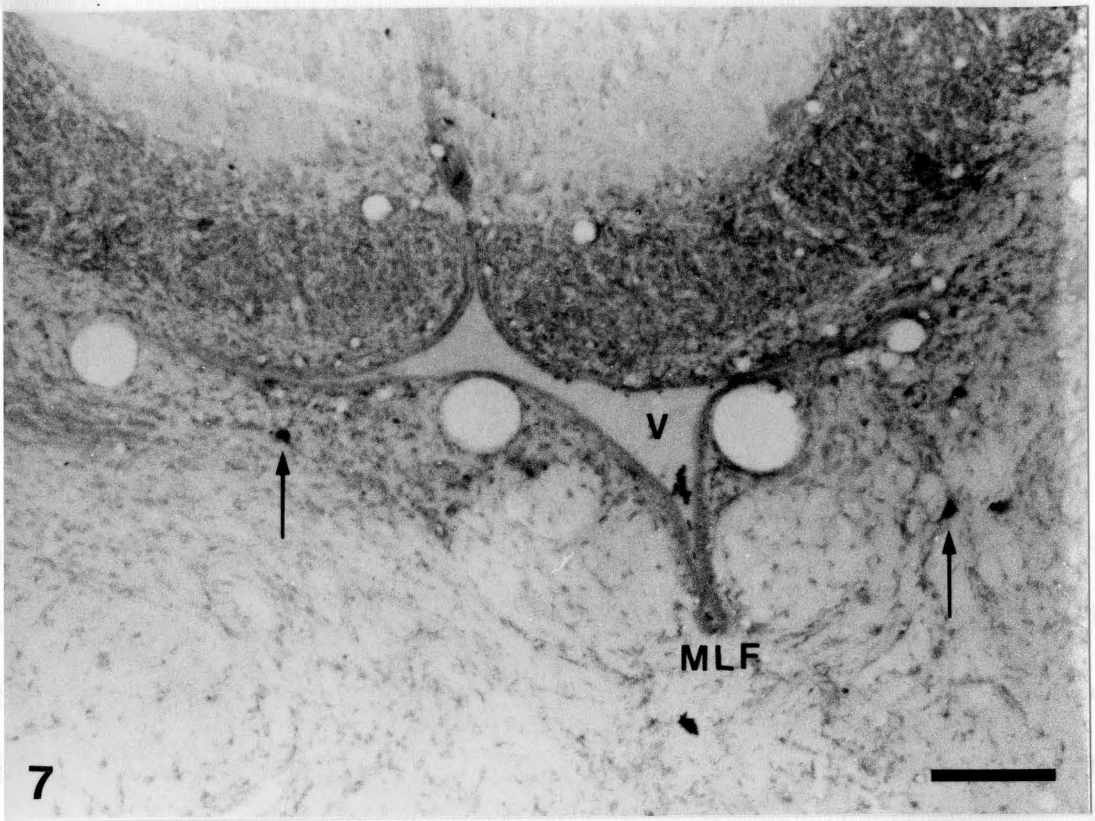
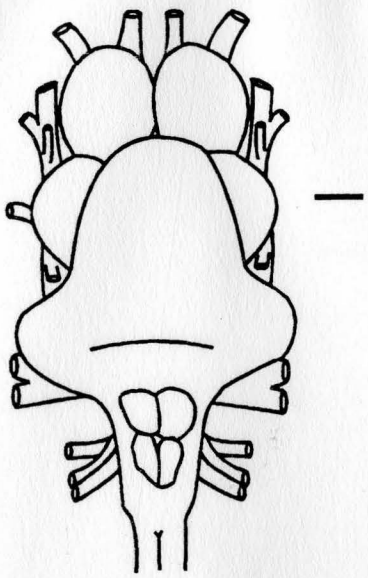

CCMO
CCG
MZ
EGI
V
LLN
BV

Figure 7: Retrograde cell body labeling in the nMLF of *Ictalurus* receiving EGl injections. Cell bodies are seen in the photomicrograph dorsal and lateral to the MLF. Two of the cell bodies have been marked by arrows though additional labeled cell bodies are present. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 200 μm. Abbreviations are defined in the *List of Abbreviations.*


V
MLF
7



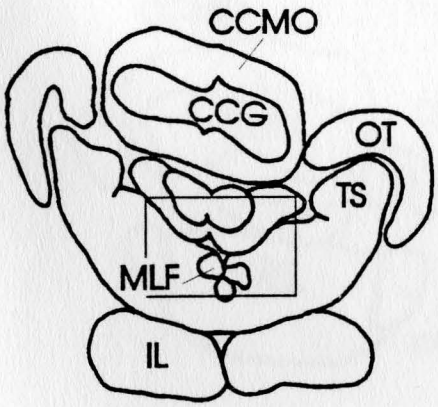
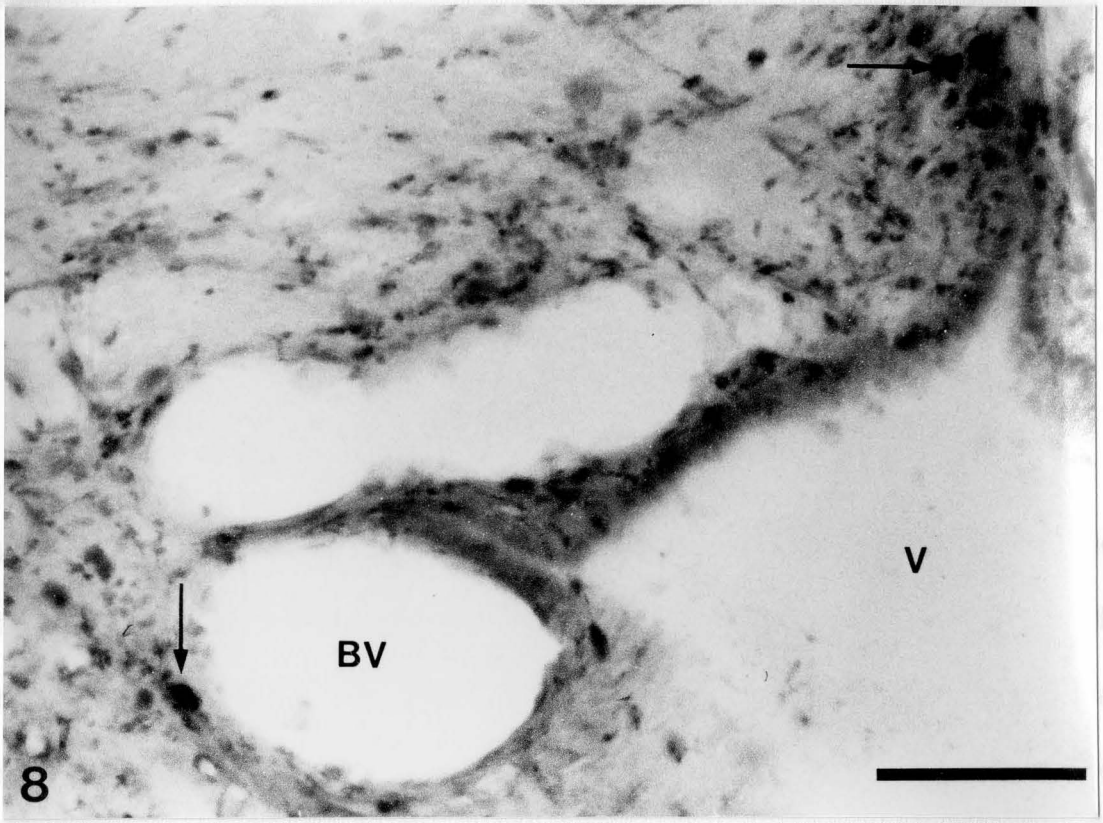
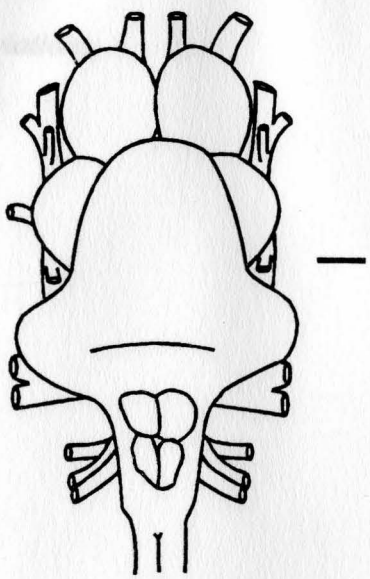

CCMO
CCG
OT
TS
MLF
IL

Figure 8: Retrograde cell body labeling in the PV of *Ictalurus* receiving EGl injections. Labeled cell bodies are seen at each of the arrow tips. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 80 µm. Abbreviations are defined in the *List of Abbreviations.*


V
BV
8



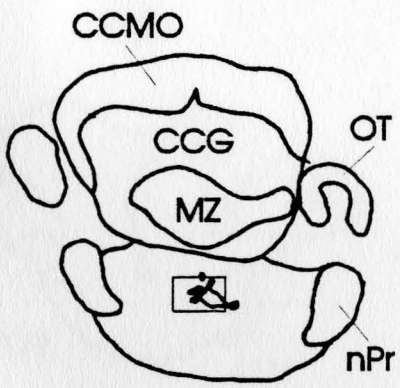
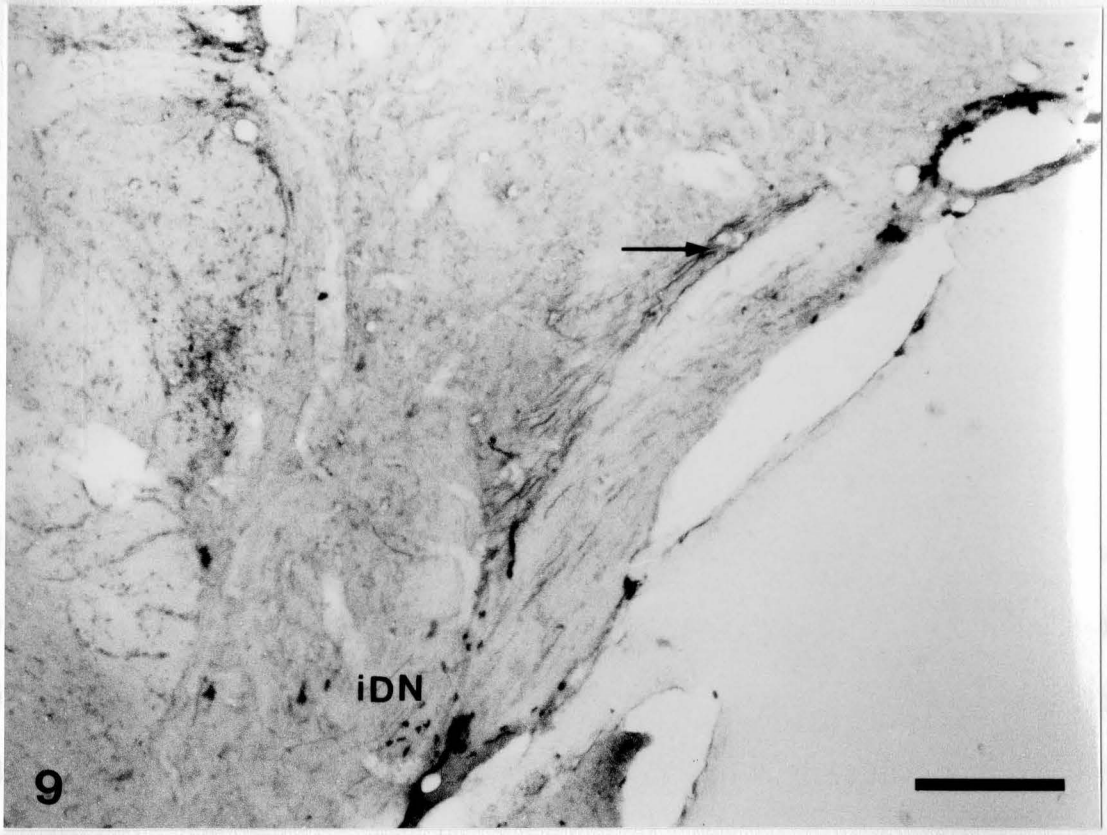

CCMO
CCG
OT
MZ
nPr

Figure 9: Tract ascending along the ventrolateral hindbrain toward the EGl. The fibers seen along the tip of the arrow in the photomicrograph are axons of cells found within the basally located iDN, TOB, and IRF of the caudal medulla. The most anterior portions of the iDN can also be seen. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 400 μm. Abbreviations are defined in the *List of Abbreviations.*


iDN
9

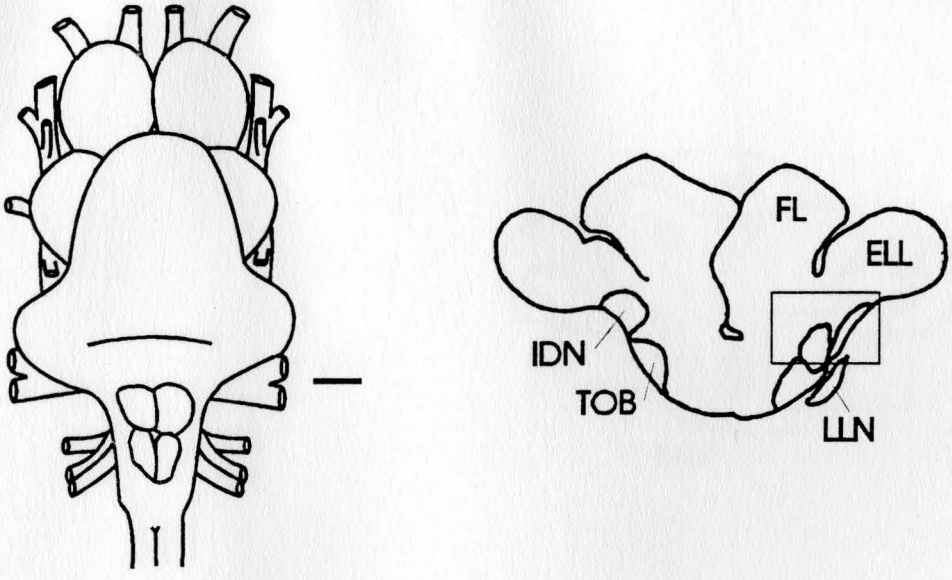
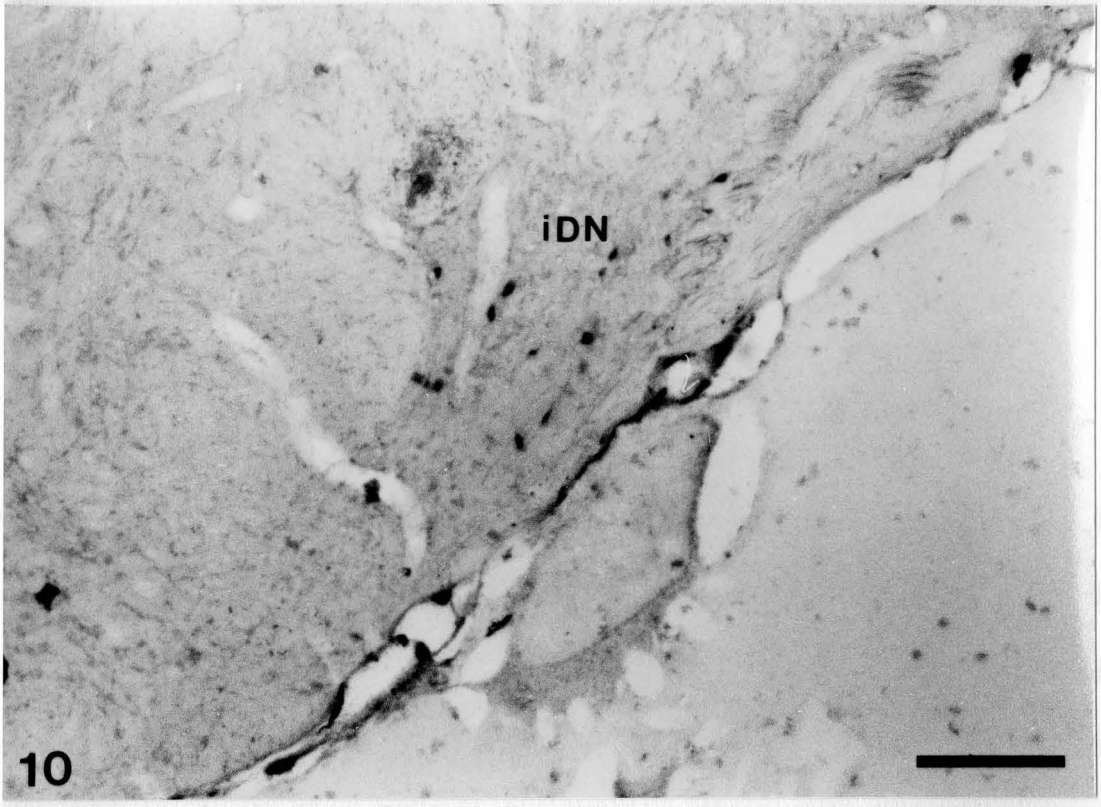

FL
ELL
IDN
TOB
LLN

Figure 10: Retrograde filling of cell bodies in the iDN of *Ictalurus* receiving tracer injections into the EGl. The cell bodies are seen in the photomicrograph as darkly filled circles throughout the iDN area. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 200 μm. Abbreviations are defined in the *List of Abbreviations.*


iDN
10

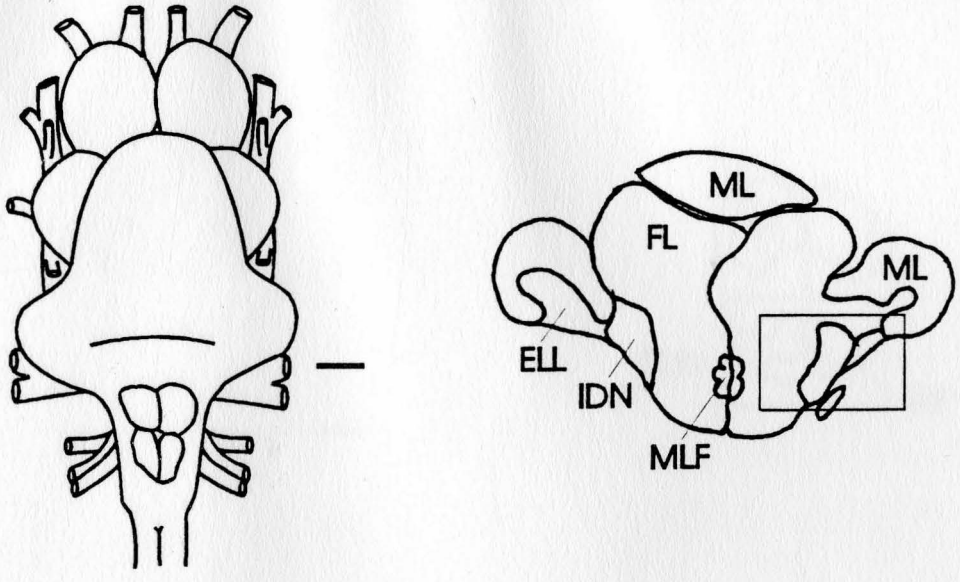
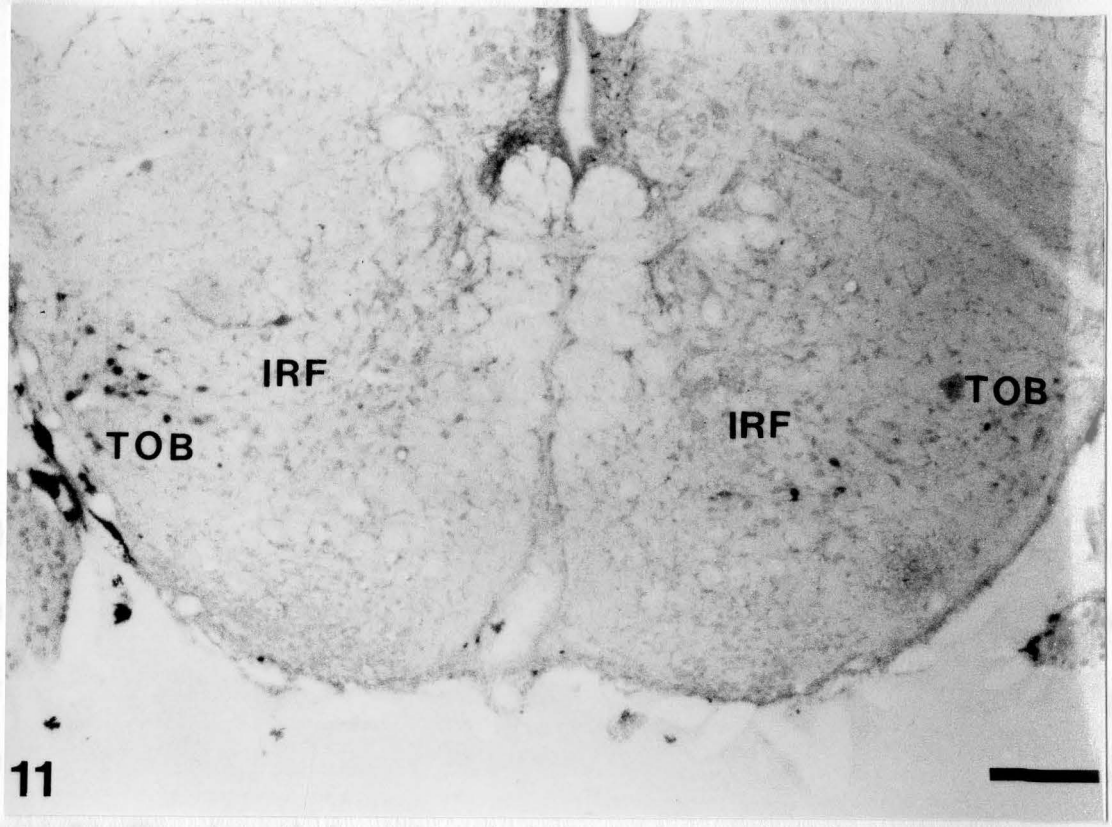
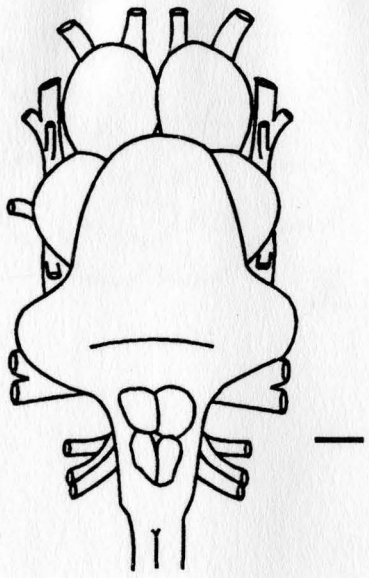

ML
FL
ML
ELL
IDN
MLF

Figure 11: Retrograde cell body labeling in the caudal medullary TOB and IRF. The TOB nucleus is larger and situated slightly ventrolaterally to the nucleus of the IRF. Cell bodies can be seen bilaterally in each of the TOB and IRF. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 200 μm. Abbreviations are defined in the *List of Abbreviations.*


IRF
TOB
IRF
TOB
11



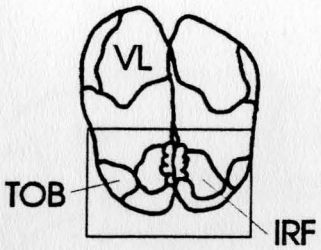
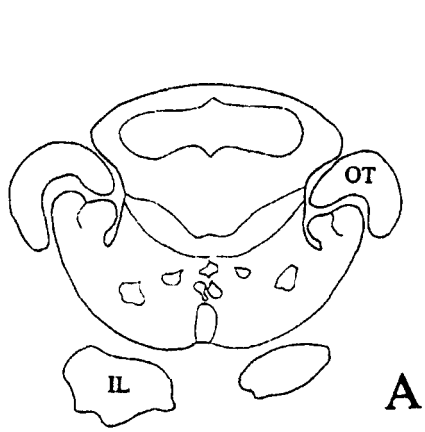
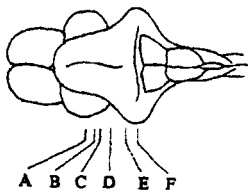
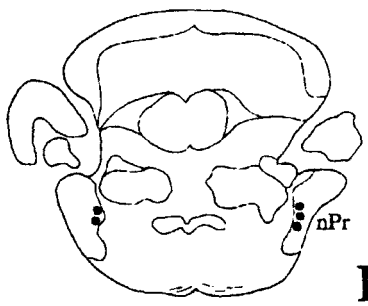

VL
TOB
IRF

Figure 12: Afferent and efferent connections to the EGm of the cerebellum in *Ictalurus*. Rostral to caudal (A to F) transverse sections are shown corresponding to levels indicated by the dorsal brain aspect in the top right-hand corner. The injection site is shown as a large blackout in the appropriate section. Fibers of passage are drawn in each section as dashed lines, cell bodies as large circles, and terminal arborizations as small dots. Abbreviations are defined in the *List of Abbreviations.*

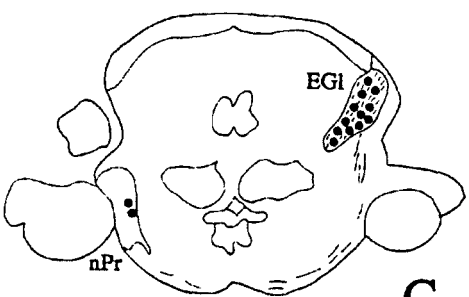


A

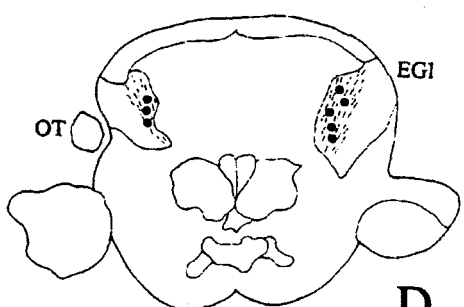




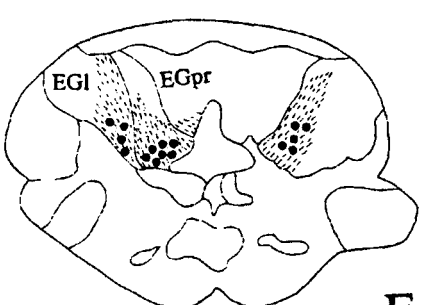
B



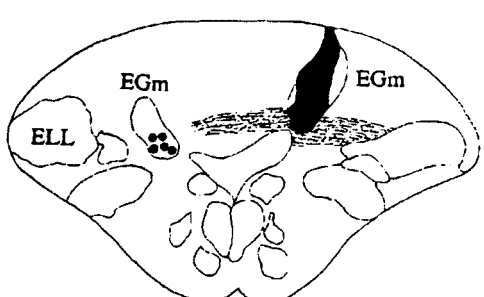
C



D

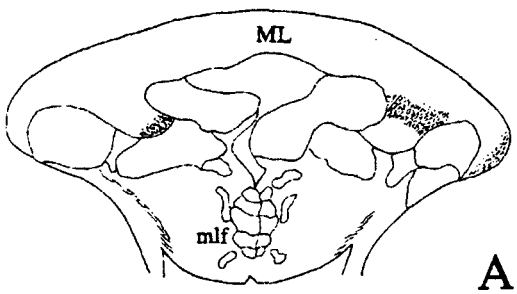


E

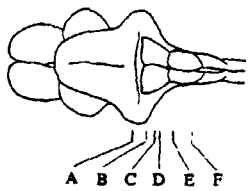


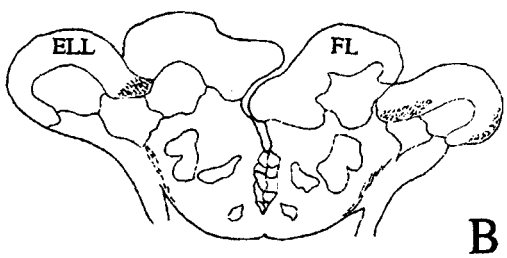
F

Figure 13: Afferent and efferent connections to the EGm of the cerebellum in *Ictalurus* caudal to those depicted in Figure 12. Rostral to caudal (A to F) transverse sections are shown corresponding to levels indicated by the dorsal brain aspect in the top right-hand corner. The injection site is shown as a large blackout in Figure 12F. Fibers of passage are drawn in each section as dashed lines, cell bodies as large circles, and terminal arborizations as small dots. Abbreviations are defined in the *List of Abbreviations.*

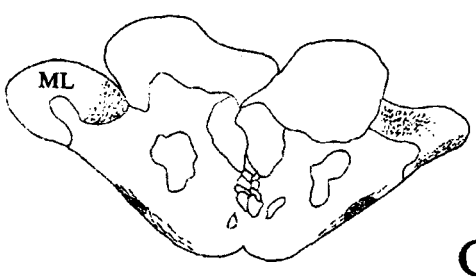


A

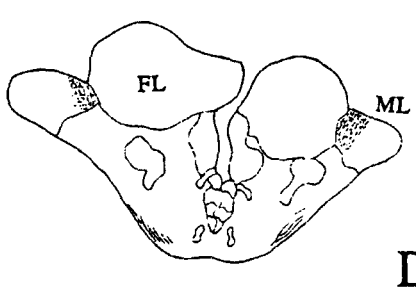




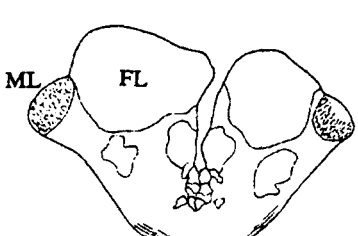
B



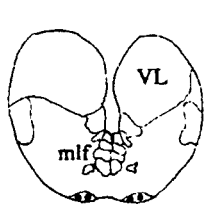
C



D

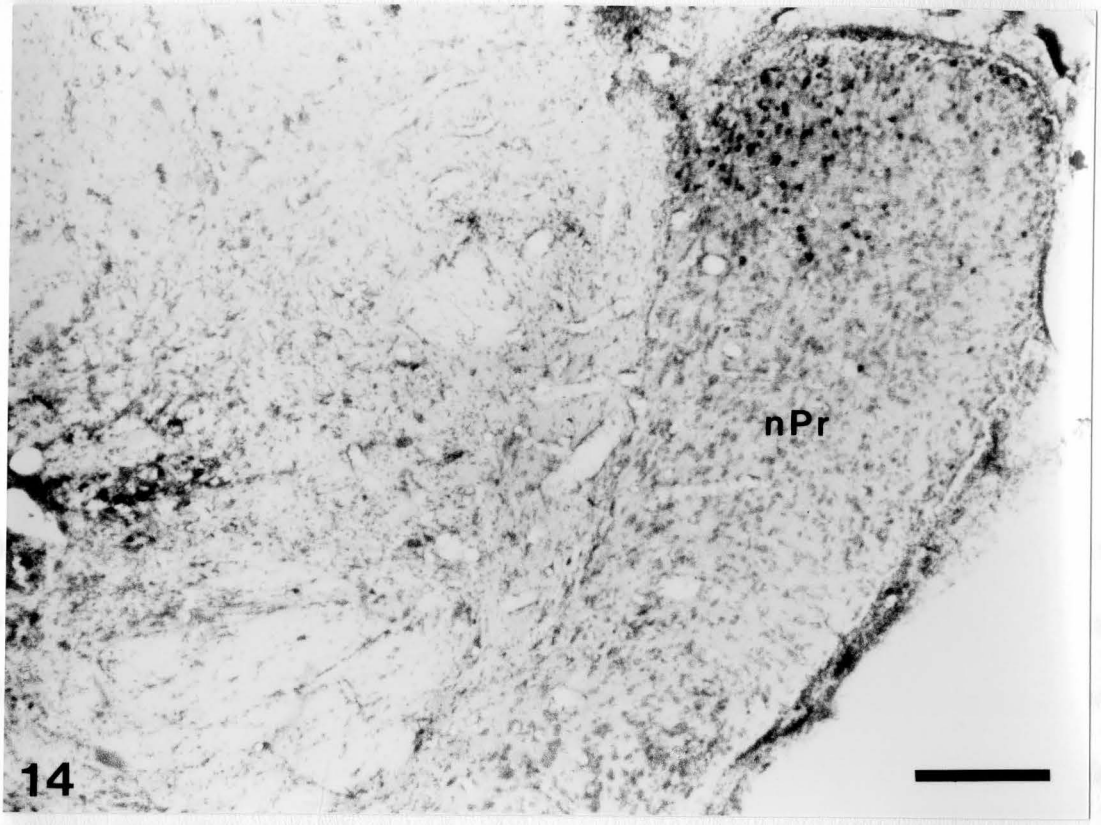


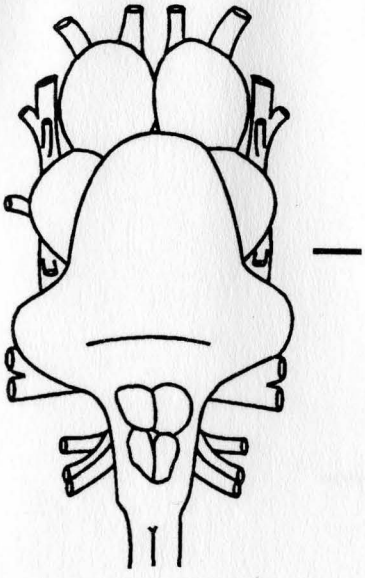
E



F

Figure 14: Photomicrograph of the ipsilateral metencephalic nPr in *Ictalurus* receiving EGm tracer injections. The retrogradely filled cell bodies and intermixed anterogradely labeled terminal processes can be seen confined to the dorsomedial region of the nPr. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 200 μm. Abbreviations are defined in the *List of Abbreviations.*


nPr
14



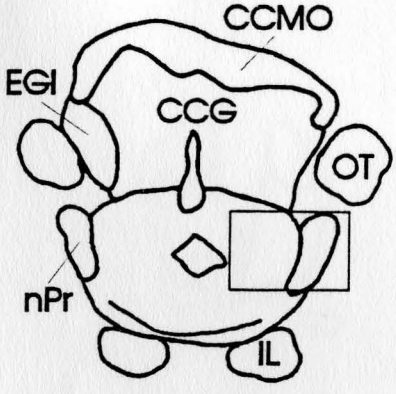
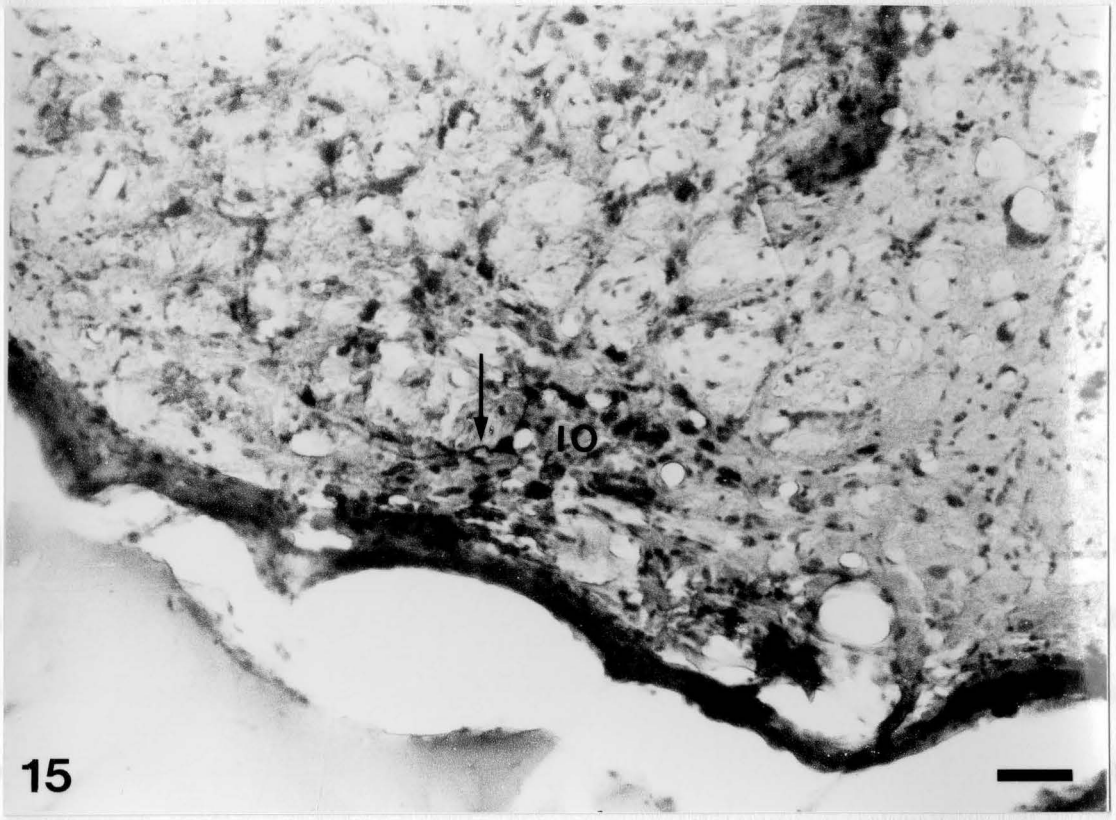
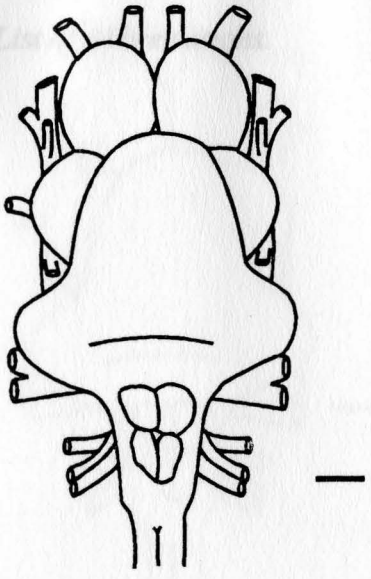

CCMO
EGI
CCG
OT
nPr
IL

Figure 15: Retrograde cell body labeling in the IO of *Ictalurus* receiving tracer injections into the EGm. The arrow in the photomicrograph points to one process of a particularly nicely filled IO cell. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 40 μm. Abbreviations are defined in the *List of Abbreviations.*


IO
15



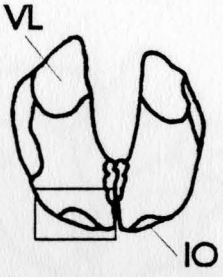
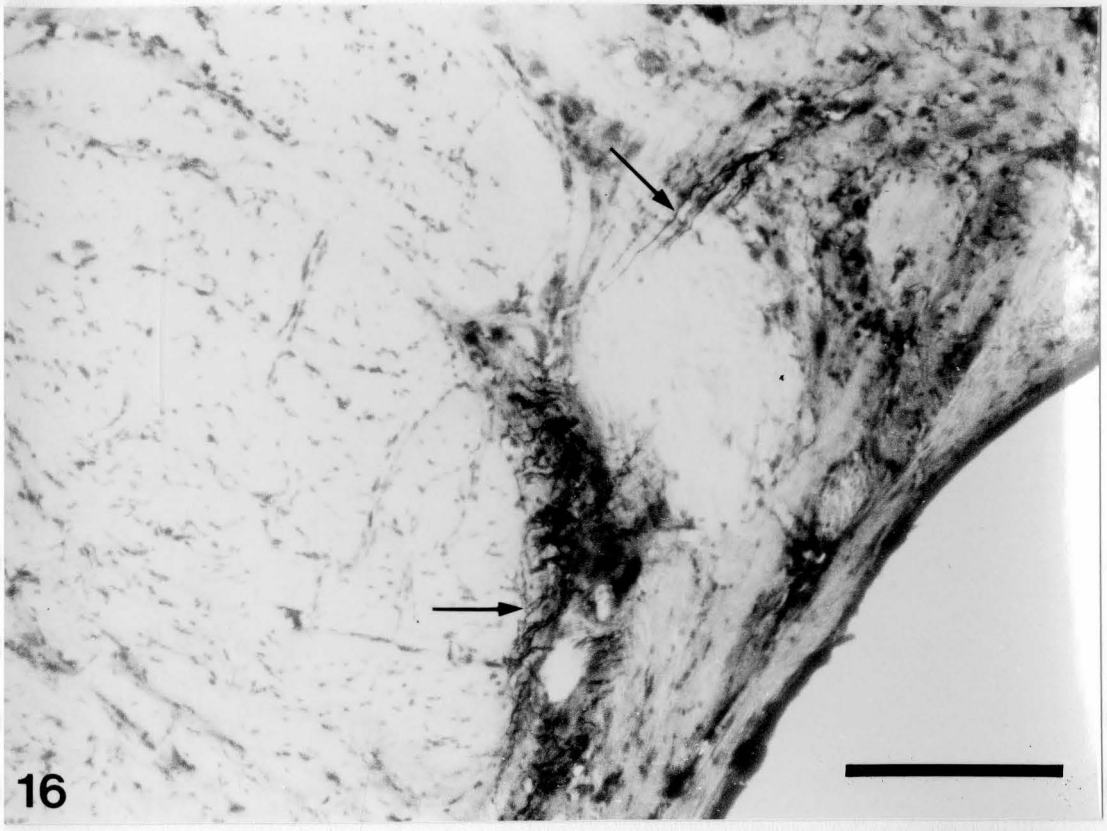

VL
IO

Figure 16: Ascending tract along the ventrolateral hindbrain carrying fibers from the IO to the EGm. The fibers are seen in the photomicrograph in the dark region along the tip of the arrow. These fibers correspond in position to the ascending tract of axons that connect other caudal medullary nuclei to the EGl. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 200 μm. Abbreviations are defined in the *List of Abbreviations.*


16

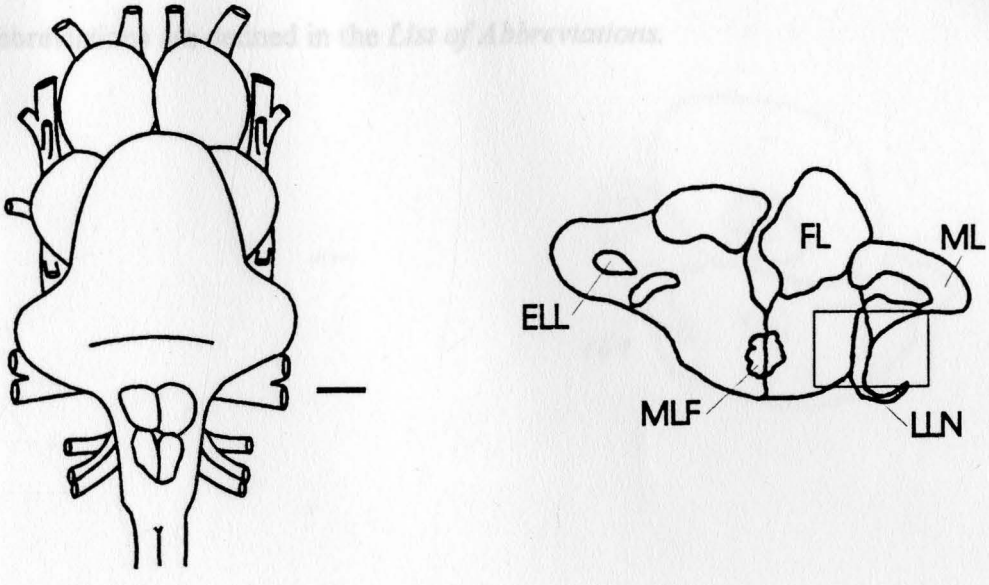
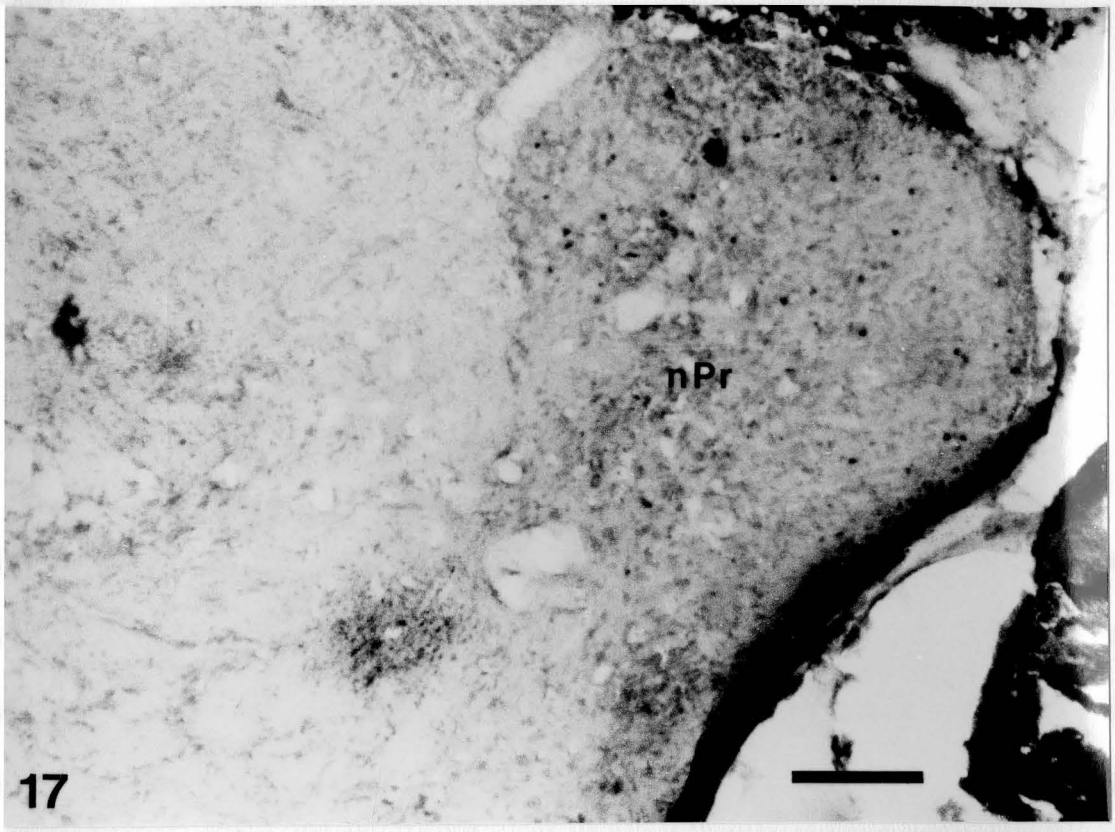
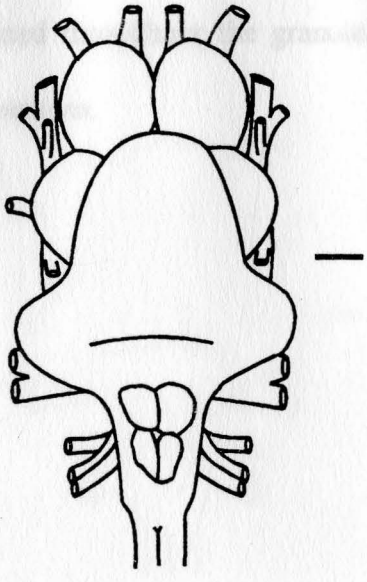

FL
ML
ELL
MLF
LLN

Figure 17: Photomicrograph of the ipsilateral metencephalic nPr in *Ictalurus* receiving injections into the molecular layer overlying the ELL. Retrograde cell body labeling can be seen throughout all portions of the nPr. This distribution of labeled cells is in contrast to the isolated groups of nPr cells providing afference to the various EG. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 200 μm. Abbreviations are defined in the *List of Abbreviations.*


nPr
17



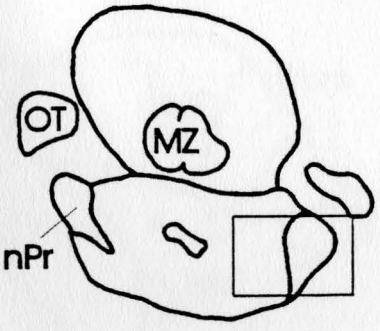
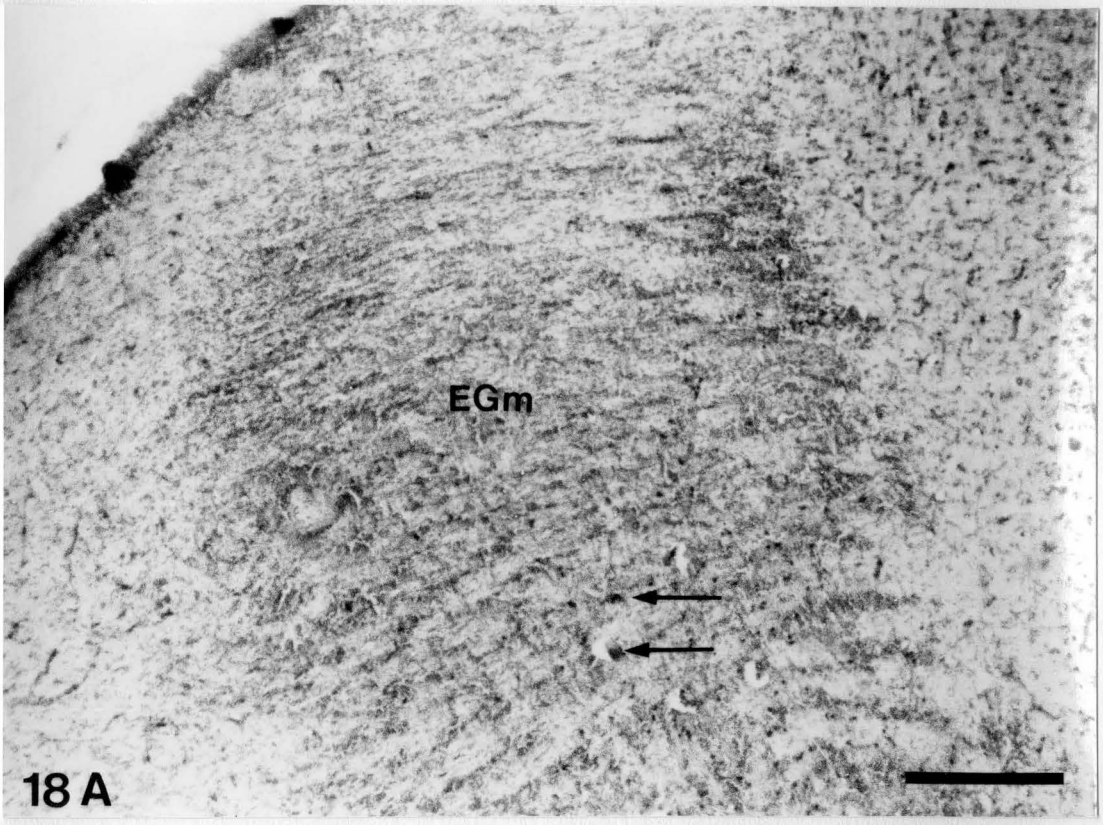
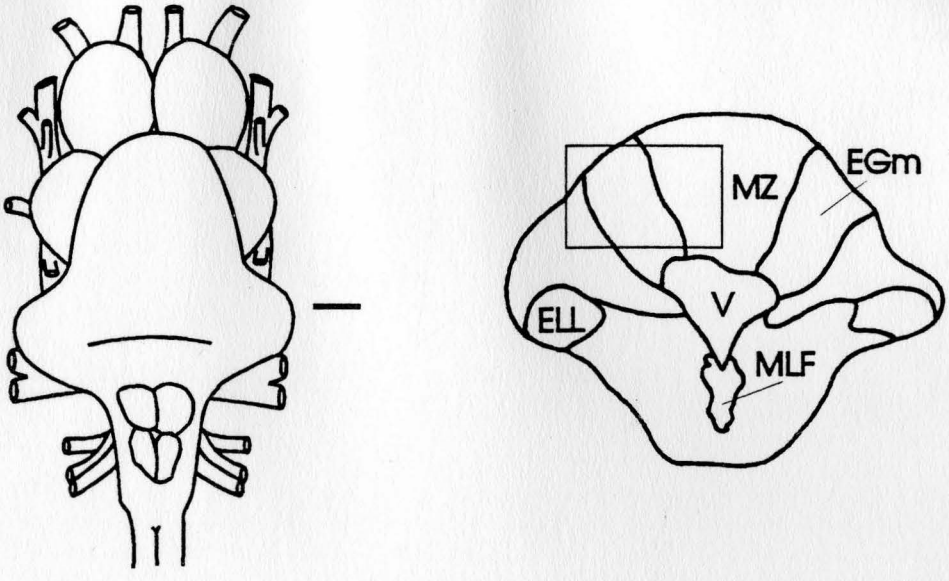

OT
MZ
nPr

Figure 18: A) Photomicrograph of EGm labeled cells in Ictalurus receiving tracer injections into the contralateral ML. Cell bodies can be seen at this magnification (scale bar = 320 μm) along the tips of each of the arrows. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. B) Page 72; Increased magnification (scale bar = 80 μm) of the area in (A) surrounding the arrowheads. Numerous HRP filled cell bodies can be seen distributed throughout the granule cell mass. Abbreviations are defined in the *List of Abbreviations.*


EGm
18 A


MZ
EGm
V
ELL
MLF

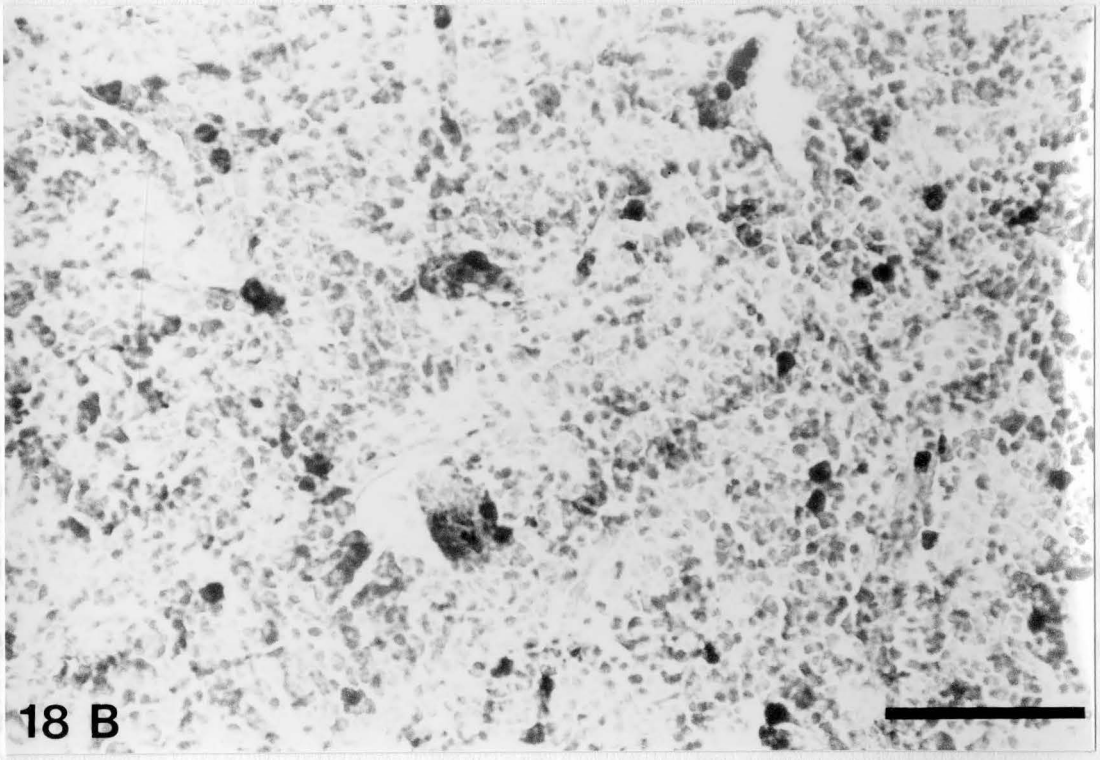
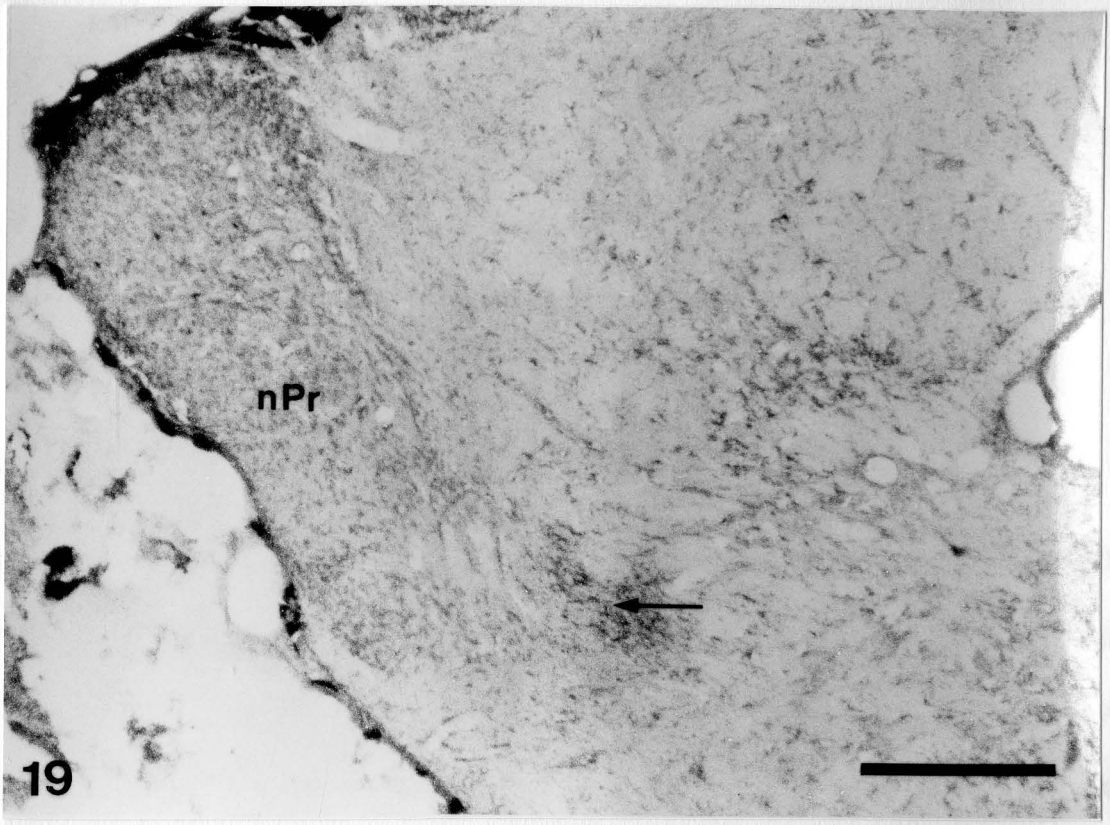
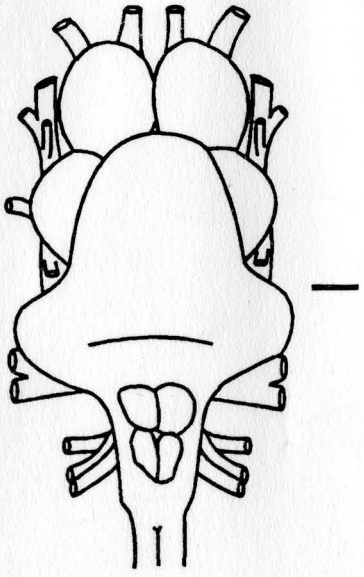

18 B

Figure 19: Ascending primary medullary crest cell axons branching into the contralateral nPr. These fibers can be seen in the darkly stained region surrounding the arrowhead. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 400 μm. Abbreviations are defined in the *List of Abbreviations.*


nPr
19



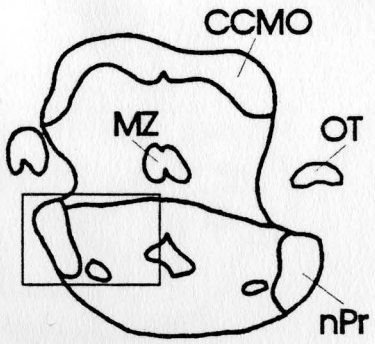
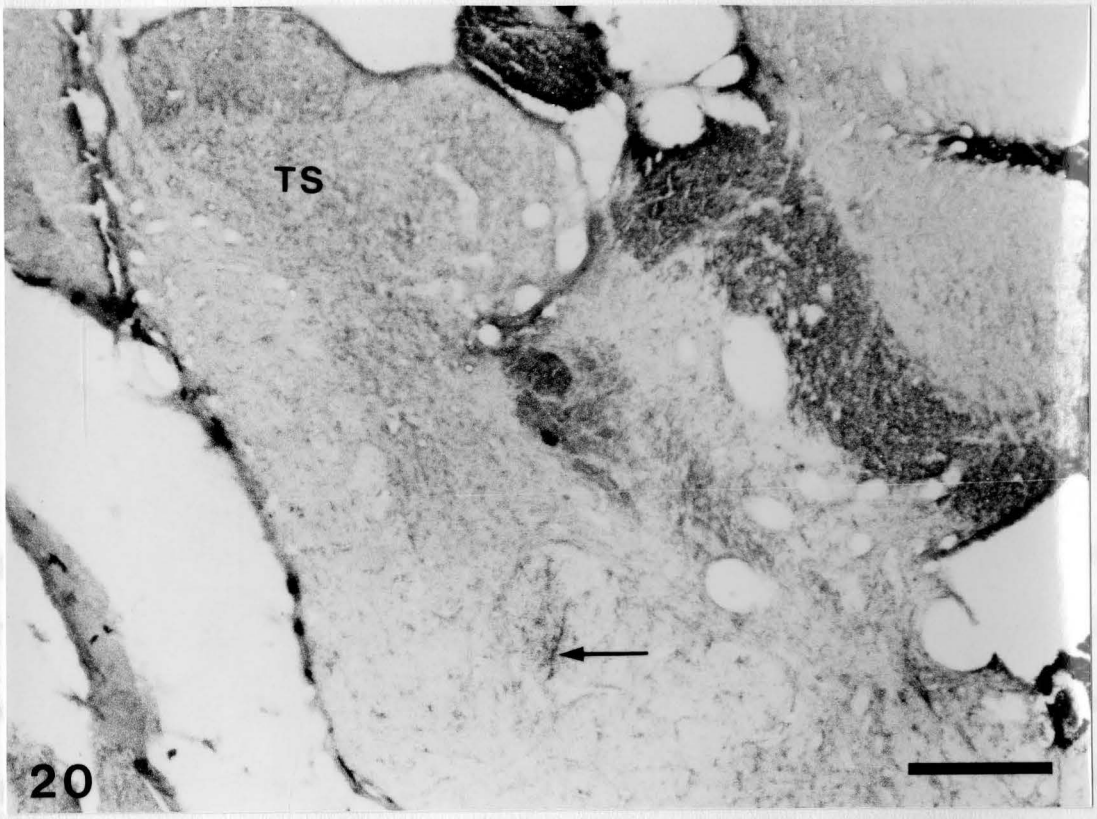

CCMO
MZ
OT
nPr

Figure 20: Ascending primary medullary crest cell axons branching into the contralateral TS. These fibers can be seen along the tip of the arrow. A line drawing of the transverse section from which this photomicrograph was obtained is shown and corresponds to the level indicated by the bar in the catfish brain line diagram. The scale bar is equal to 200 μm. Abbreviations are defined in the *List of Abbreviations.*


TS
20

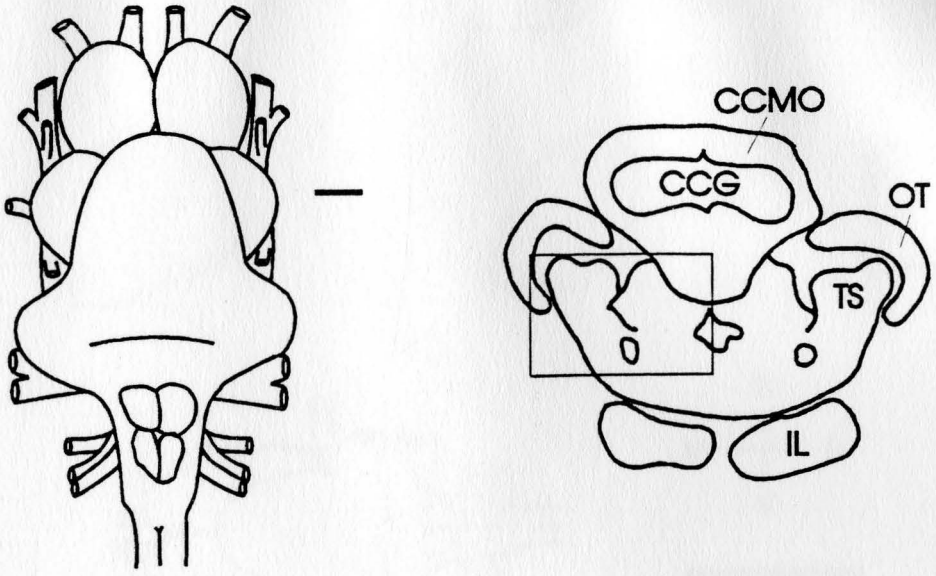

CCMO
CCG
OT
TS
IL

Figure 21: Caudal to rostral nPr transverse sections drawn after tracer injections into each of the ML, EGl, and EGm. The nPr extends along the lateral edge of the metencephalon corresponding to the area between the bars on the dorsal view line diagram of *Ictalurus* brain. Squares on the line drawing indicate various injection sites (see methods). The distribution of cell body and terminal fields in each nPr section are diagrammed as black circles in each of the sections. Section orientation is given in the bottom right-hand corner.

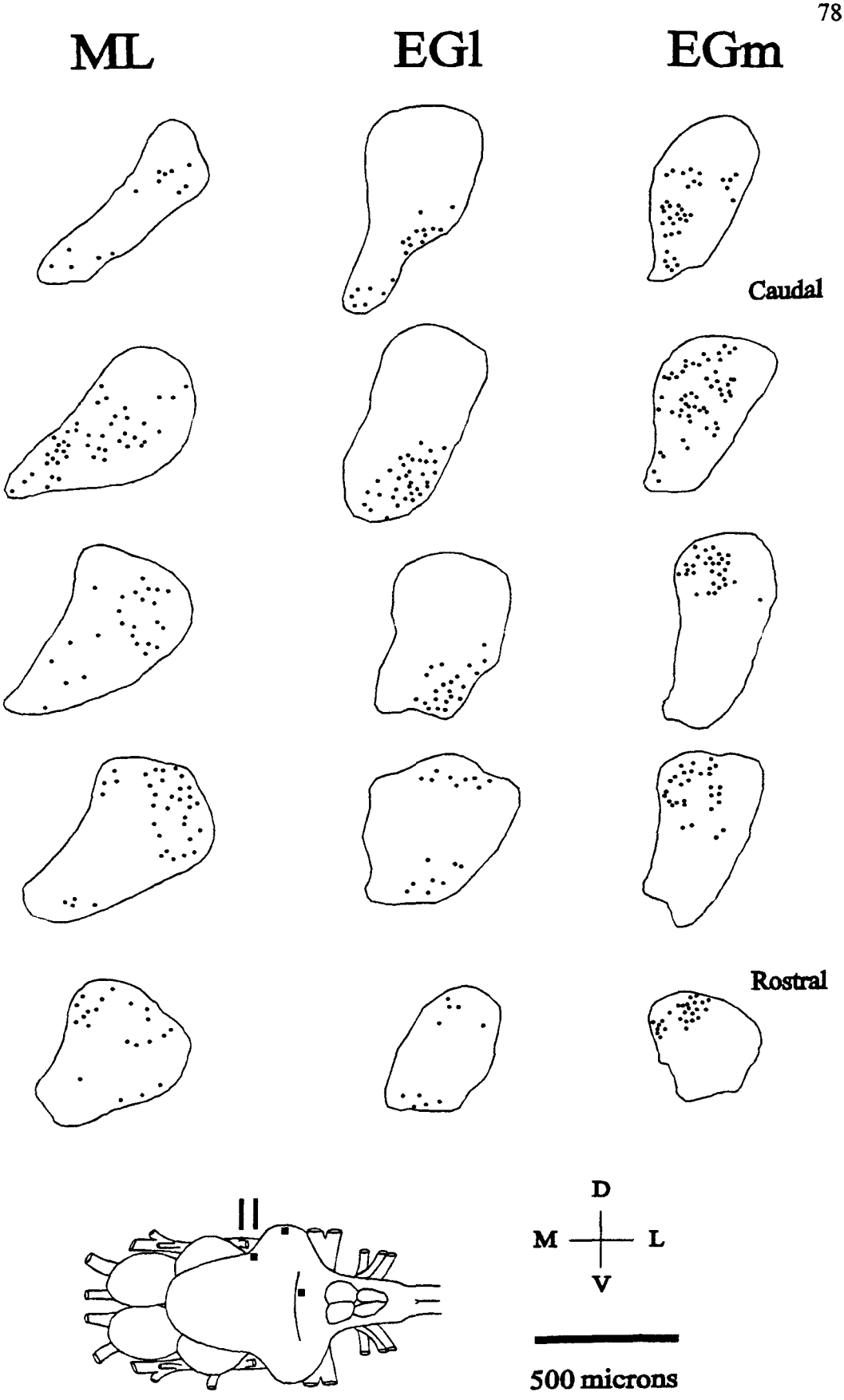
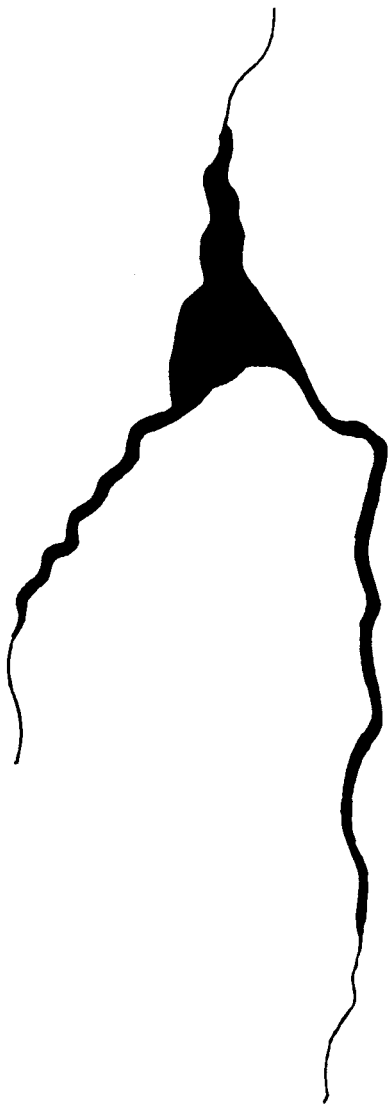

ML
EGl
EGm
Caudal
Rostral
D
M
L
V
500 microns

Figure 22: Drawings of nPr cell morphologies projecting to the EGl and EGm or to the ML. See text for description.

Descending nPr Octavolateralis Cells

To: EGl & EGm



To: ML

Figure 23: A) 100X photomicrograph of a nPr cell projecting to the Egl. B) 100X photomicrograph of a nPr cell projecting to the Egm. The scale bar shown is for each of (A) and (B) and is equal to 20 μm.

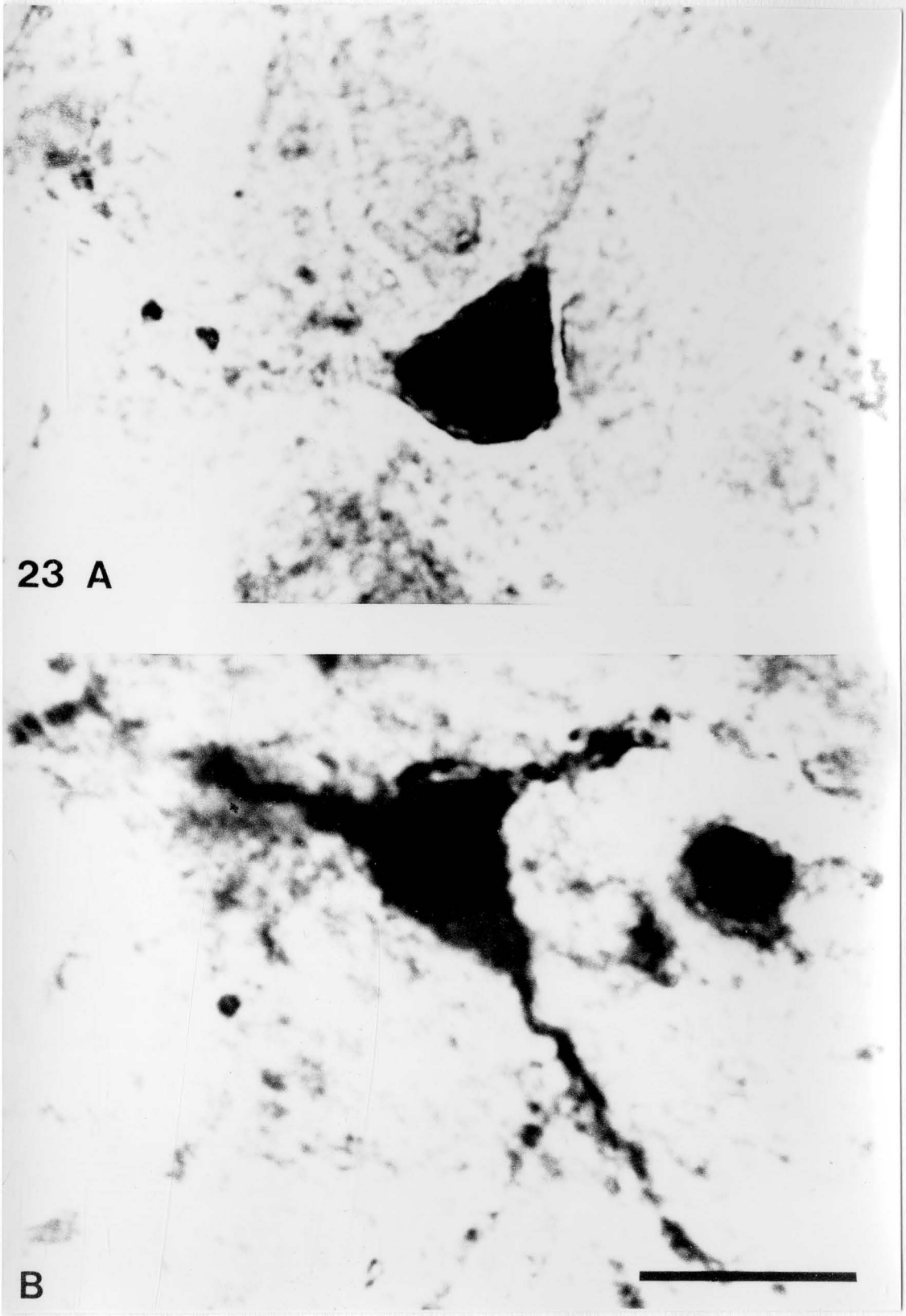

23 A
B

Figure 24: 100X photomicrograph of a nPr cell projecting to the ML. The scale bar is equal to 20 μm.

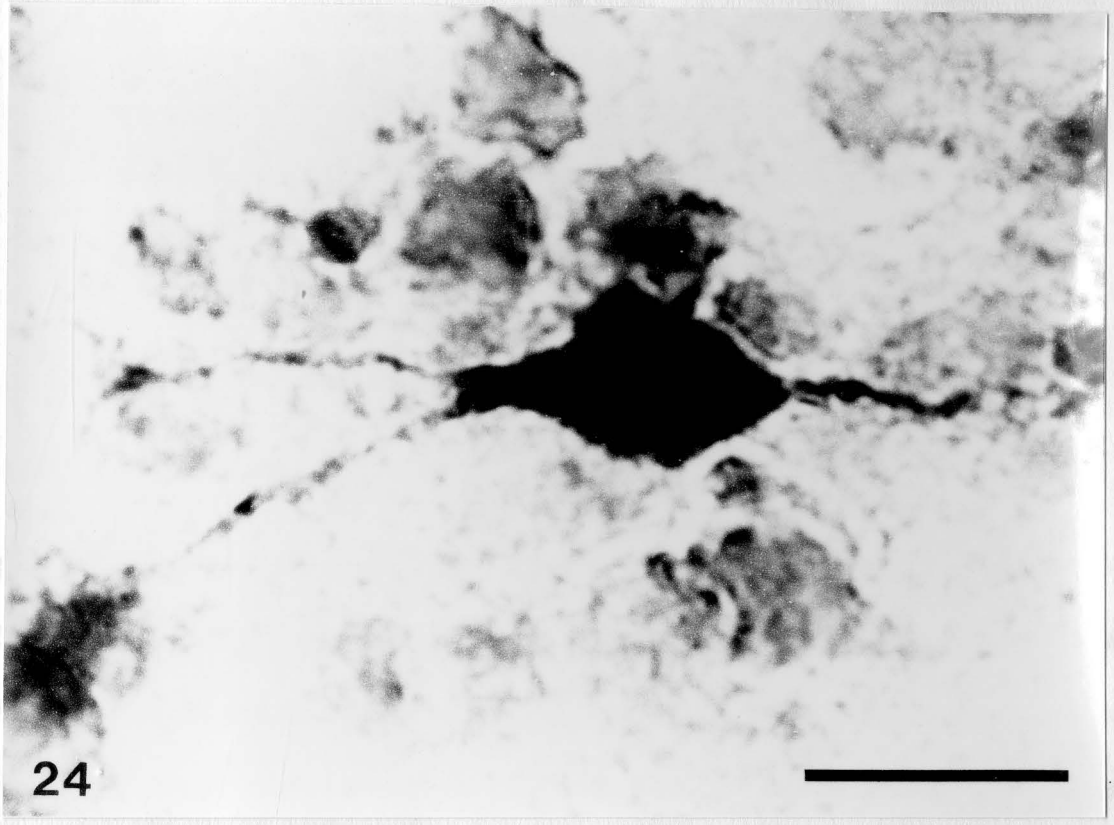

24

Figure 25: A summary circuit diagram of the afferent and efferent connections to the EGl and EGm. Afference to the EGl and EGm is shown on the left side of the bold vertical center-line whereas the diagram on the right side of this line indicates efference. All structures above the horizontal dividing line are metencephalic; all structures below the horizontal dividing line are myelencephalic. All of the connections were firmly established (in catfish) by the experiments of this report except for the afference of the primary nerve fibers to the EGl and efference from the EGl and EGm to the primary medullary nuclei. These particular connections are distinguished as dashed lines and were reported previously (Finger, 1986; New & Singh, 1994). The additional reciprocal connections between the nPr and EGl drawn as dotted lines indicate the possibility of two separate EGl populations (EGla and EGlp) connecting independently to the nPr. Abbreviations are defined in the *List of Abbreviations.*

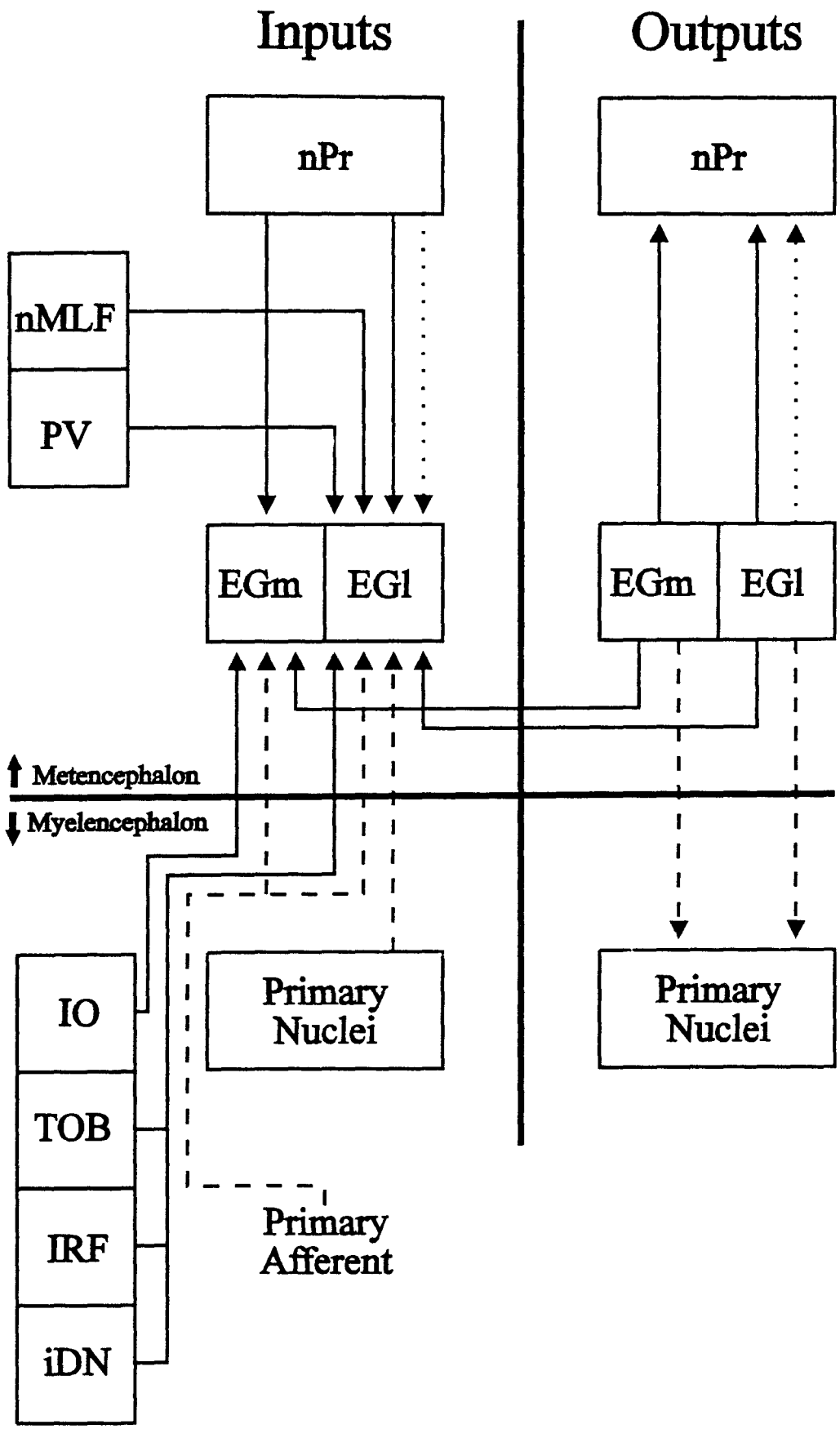

Inputs
Outputs
nPr
nPr
nMLF
PV
EGm
EGl
EGm
EGl
Metencephalon
Myelencephalon
IO
TOB
IRF
iDN
Primary Nuclei
Primary Nuclei
Primary Afferent

Figure 26: A circuit diagram of the various connections providing several feedback and feedforward loops in the processing of octavolateralis signals; see discussion. The connections drawn as filled black lines were established by the experiments of this report. The connections indicated by dashed lines were established previously (Carr et al. 1981; Tong & Finger, 1983; Finger & Tong, 1984, Finger, 1986). The connections shown with a broken line and a question mark have not yet been reported but are possible based upon the locations of reported processes (Carr et al. 1981) of each of these nuclei. Abbreviations are defined in the *List of Abbreviations.*

Feedback

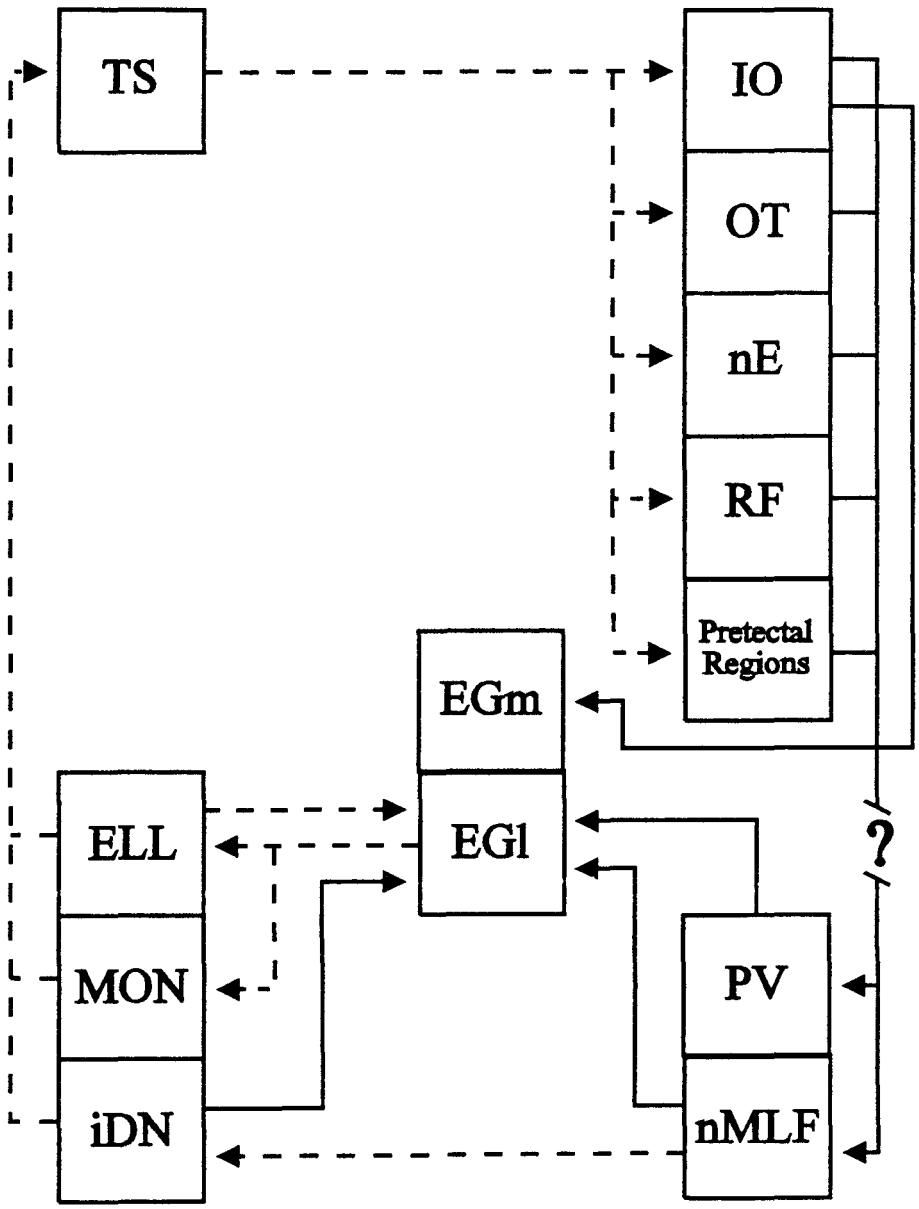


Table 1: A summary table of the nuclei providing afference to each of the EGl, the EGm, and the ML. Abbreviations are defined in the *List of Abbreviations.*

Afference from the:	To the EGl	To the EGm	To the ML
EGl	X	?	X
EGm	?	X	X
nPr	X	X	X
nMLF	X		
PV	X		
IRF	X		
TOB	X		
iDN	X		
IO		X	

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VITA

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APPROVAL SHEET

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The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Science.

12/28/95
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