国家自然科学基金重大项目

视觉信息加工研究

（一九八八年十月——一九九二年十月）

论文集

上 册

项目学术领导小组

一九九二年十月

前　言

国家自然科学基金重大项目《视觉信息加工研究》经过全体参加者四年的努力，已经按计划并超额完成，取得了一系列基础理论成果和一些有实际应用前景的成果．据初步统计，在此项基金的支持下，在国内外学术刊物和学术会议上共发表／撰写研究论文 267 篇．获中国科学院自然科学二等奖二项、三等奖一项、省级自然科学一等奖二项及本单位奖多项、获国家专利二项．另有待申报国家自然科学成果奖二项、院级奖一项及国家专利二项．这批成果达到了国际水平或为国际领先，为了解视觉信息加工的神经基础和理论描述提供了丰富的资料，受到国内外同行的高度评价和重视．

本研究工作总结包括四部分内容分五册出版．第一部分在简述本项目研究的主要成绩之后，依次说明各个子课题研究所取得的进展，并列出研究论文目录；第二部分是 176篇论文的摘要，它们是我们研究工作的缩影；第三部分是获奖成果简介；第四部分是分上、下二册出版的论文集．承担此项研究的全体同事谨以此献给予我们以有力支持的国家自然科学基金委员会及其生命科学部，献给各位参与评审的专家和所有关心、支持我们的同事和朋友．

项目学术领导小组

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一九九二年十月

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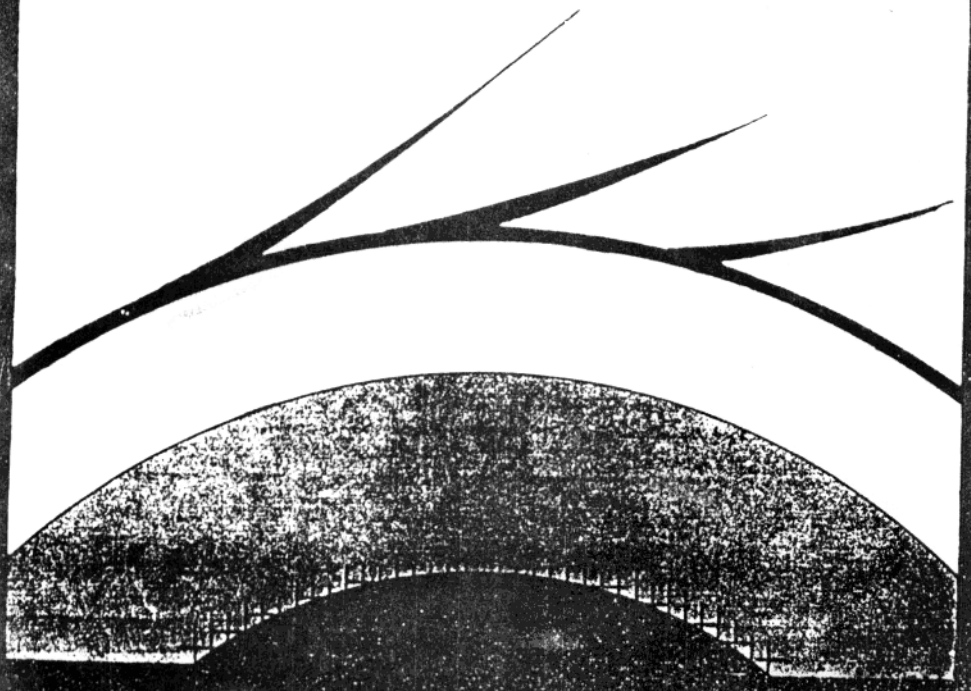

THE NUCLEUS ISTHMUS IS A VISUAL CENTER: NEUROANATOMY AND ELECTROPHYSIOLOGY

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INTRODUCTION

The nucleus isthmus (NI) found as a paired nucleus in the midbrain of all classes of vertebrate except cyclostomes and mammals (77) is first described in anuran amphibians by Gaupp as the ganglion isthmi (39) and then considered to correspond to the secondary visceral nucleus (SVN) of fishes (76). This confusion of NI with SVN arises from such anatomical relationship that they are closely clowded together, and in fishes the large size of SVN overshadows small NI, while in reptiles NI is a prominent structure and SVN is comparatively small. Later, these two nuclei are clearly distinguished from each other in teleosts (35), amphibians (87,88), and reptiles (61,116). Furthermore, Golgi preparations do not show any fiber connections between the nuclei (88). It is suggested that NI of amphibians is equivalent to that of the same name in reptiles and birds (77). In all these classes of vertebrate, the intimate relationship of NI with the lateral lemniscus leads to the supposition that NI is homologous to the mammalian medial geniculate nucleus. However, Le Gros clark (90) believes that NI is not an analogue of the medial geniculate body: the former is a mesencephalic element, while the latter is a diencephalic element; the relation of these two structures to the lateral lemniscus is different. He further proposes a homology between NI of submammals and the parabigeminal nucleus (PBN) of mammals.

It has long been suggested that PBN (100) and NI (89) are the midbrain representatives of the auditory projecting system. Nevertheless, neither auditory nor visual responses are recorded from the frog NI (104), leading to the notion that NI is one of the most obscure structures in the vertebrate brain, although auditory responses are found in the avian NI using larger electrodes (26,54). On the other hand, considerable effort has been made to describe the main primay visual center, the optic tectum (OT); as a further step in studying visual information processing of submammals, in the past decade several laboratories have been interested in NI which has close relation to the tectum. Therefore, from a comparative viewpoint, we have made extensive studies on NI in anuran amphibians, reptiles and brids using neuroanatomical, electrophysiological and histochemical

methods. Taken together with the results from others, it is suggested that NI is a secondary visual center. This review will describe neuroanatomy and electrophysiology, as well as developmental and behavioral aspects of NI and PBN of vertebrates in the evolutionary steps from fishes to mammals.

NEUROANATOMICAL ORGANIZATION

Organization and Fiber Connections

The nucleus isthmi first appears in fishes (77), located in the dorsolateral part of the caudal tegmentum. It is somewhat kidney-shaped (35,73,74), consisting of an outer cell-dense area or cortex and an inner cell-free area or medulla. The cortex covers the rostral, dorsal and ventral parts of NI, and its cell bodies are oval. The medulla contains the dendrites of cells and myelinated fibers of two kinds: thick fibers (7-9 μm diameter) and thin fibers (2-4 μm). The somata, dendrites and the initial segment of axons bear some spines (73).

Degeneration and horseradish peroxidase (HRP) tracing methods show that teleostean NI receives an extensive projection from OT ipsilaterally (24,73,74,95,111,115,122) and from the nucleus pretectalis (NPT) (73,74); it projects back to the ipsilateral OT (73,74,111) as well as to the cerebellum in the carp (95). The cell body of tectal pyriform neurons located in the upper part of the stratum periventriculare gives off one long and thick apical dendrite, which goes up through the stratum album centrale, stratum griseum centrale, stratum fibrosum et griseum superficiale, and ramifies in the stratum opticum. Just above the lower boundary of the stratum fibrosum et griseum superficiale the thick dendrite shaft sprouts an axon, which bifurcates perpendicularly after a short distance. Axons running upward could be traced to the stratum opticum. Axons going downward run medially and caudally through the stratum album centrale and stratum griseum periventriculare. These thin fibers converge into the dorsolateral tegmental area and enter NI dorsolaterally as several fiber bundles, terminating in the core or cortex. Both the core and shell receive thick input fibers from the ipsilateral NPT of Schnitzlein (114). These fibers originate from 100-120 large (25 x 35 um) multipolar neurons of NPT (Fig. 1). They gather to make up a fiber tract, the tractus pretectoisthmicus (74), which travels dorsomedially first and then caudally. It descends along the tractus mesencephalocerebellaris anterior behind the commissura posterior. At the level of decussation of the trochlear nerve, the fibers reach NI at its ventrocaudal pole (73,74). No isthmo-pretectal pathway has ever been reported. Cells in NI are labeled following HRP injections made in the corpus cerebelli in the carp (95). However, the isthmic cells are labeled by tectal injections (111) and never by cerebellar injections in some teleost species (72). Grover and Sharma (48) reported in goldfish retinal and tectal afferents to NPT, which projects to the tectum and cerebellum. NPT in teleosts Adioryx, Myripristis, Sebastiscus and Navodon does not receive retinal input and project to the cerebellum, but receives tectal efferent and projects to NI (72-74,111). It appears that NPT of Grover and Sharma

is not equivalent to NI of Schnitzlein (114), but corresponds to the pretectal cell group P2 (48), which is considered to be equivalent to the nucleus of the basal optic root (31).

The nucleus isthmi is well developed in anuran amphibians. Larsell (88) described in detail this nucleus in three species of anurans (Hyla regilla, Rana pipiens, Acris gryllus). It is located in the caudal tegmentum between the cerebellum and tectum, forming a fragiform body, the smaller end of which is directed medially and somewhat dorsally, and the larger end is rounded and extends caudally and laterally. The nucleus is a paired midbrain structure, although its caudal portion crowds the subcerebellar region. A particularly striking characteristic of this nucleus is its subdivision into a cell-dense cortex and a cell-sparse medulla (Fig. 2). The cortex appears as a row of cell bodies, two or three cells deep, enclosing the nucleus except for a hilus at the rostro-lateral margin. The hilus extends from ventral to dorsal margins of the nucleus (53). At this hilus the medulla is continuous with the structures outside the nucleus. There is a prominent cell-free band (neuropil) internal to the medioventral cortex in frogs Rana nigromaculata (144,145), R. pipiens (47), but it is absent in toads Bufo bufo gargarizans (146). The dimensions measured by using histological sections of the nucleus in Rana nigromaculata are 310 μm rostrocaudal, 560 μm dorsoventral and 630 μm mediolateral (without shrinking correction), slightly smaller than those values measured by three-dimensional computer reconstruction technique (94), but larger than those in R. esculenta (81). Using Abercrombie's correction method (1), the average number of cells in the nucleus in frogs is obtained as 8,000 ranging from 7,200 to 9,200 (53,145). The nucleus in toads is comparatively smaller in size being 260 μm rostrocaudal, 470 μm dorsoventral and 500 μm mediolateral, with cell counts of 4,800 (146), about a half of those in frogs.

In Golgi preparations of the frog NI (81,88), two types of the cortical cells could be distinguished. One of them has a spherical perikaryon with 1-2 short and thick dendrites pointing towards the medulla, where they give rise to several branches and some branches bear dendritic appendages. The second type of neurons possesses small pyriform perikaryon with dendrites arborizing either in the neuropil or among the medullary cells, in some cases, only a few spines and appendages occur on dendritic branches. The majority of medullary neurons are similar to those in the cortex. However, other two types of neurons could be differentiated. One of them has a large irregular perikaryon, from which more than two thick dendrites with some branches originate. The other type of the medullary cells has a medium-sized fusiform perikaryon, the two poles of which give off the dendrites. The dendrites of the isthmic cells do not extend beyond the limits of the nucleus, and usually their axons could not be reliably identified. In some cases, the axons of these cells are also impregnated, but could only be traced for a short distance.

We used HRP tracing and Golgi-Cox impregnation techniques to study the morphology of the isthmic cells and anatomical relationship between the amphibian NI and OT (150). Here, the morphological description of the isthmic cells is mainly based on HRP-labeled

materials. The majority of neurons has a large perikaryon, a wide dendritic field, and dendrites trending to spread out dorsolaterally. According to the number and distribution of the primary dendrites, these cells may be grouped into three types: (i) multipolar neurons having more than three primary dendrites, including those with radial dendrites; those with dendrites spreading in the opposite directions, or in a single direction; (ii) bipolar cells having two primary dendrites, including those with dendrites in one direction or in the opposite directions; and (iii) monopolar cells, including those without dendritic arborization, those with finer branches on the tapered or basal parts of the dendritic shaft. Almost all dendrites of HRP-labeled isthmic neurons following tectal injections are restricted within the limits of the nucleus. In few cases, axon-like processes are seen to travel dorsolaterally. In comparison with HRP-labeled materials, Golgi-Cox impregnated neurons have numerous spines on both dendritic shafts and finer branches, and their dendrites seem to be thicker. The differences in neuronal appearance between HRP-labeling and Golgi-Cox impregnation might be explained by electron-microscopic observations that HRP molecules are only restricted to the cytoplasmic vesicles (9), whereas Golgi black precipitate can fill cells and their processes, or selectively stay in extracellular spaces. In Golgi-Cox sections, a few cortical cells have their dendrites partly in the peri-isthmic area probably being the secondary visceral nucleus or the posterodorsal tegmental nucleus. On the other hand, the dendrites of a few peri-isthmic neurons terminate within NI or pass through its cortex. It appears that these connections are so weak that they are not of functional significance.

In an early detailed study, Larsell (88) pointed out using Golgi methods that the fiber tracts which are connected with NI include the lateral lemniscus, tractus tecto-isthmi, tractus quadrigemino-isthmi, tractus isthmo-tectalis, tractus isthmo-thalamicus, tractus commissura transversa, and a commissura isthmi. From these connections and relationships, NI seems to correspond to the medial geniculate body of mammals. However, many recent studies using HRP tracing, autoradiographic and degeneration techniques indicate that the ipsilateral tectum is the only input to NI (52,150), which projects back to the tecta bilaterally (47,52,53). Therefore, NI is conclusively connected with the tectum. The tecto-isthmic pathway originates from the deeper layers of the tectum (39,52,88,150), leaving the caudal tectum via layer 7 and going directly to the nucleus alongside its dorsolateral circumference including the hilus to enter the medulla. These large-caliber fibers (3-5 um diameter) then break up within NI into terminal branches (53,81,88). The fibers projecting from NI to the ipsilateral tectum exit via the hilus and then form a tract oriented rostro-laterally, immediately mediodorsal to the lateral optic tract. On entering the tectum these small-caliber fibers (1-3 um diameter) travel within the tectum by way of layer 7 and layer 6. They then turn toward the tectal surface and arborize into terminal bushes (47,52,53,150). Moreover, rostral tectal HRP injections label small volumes in the nucleus, whereas caudal injections label larger volumes including areas of the nucleus labeled with rostral injections. This implies that some isthmo-tectal fibers traverse the tectum caudorostrally (53). These ipsilateral isthmotectal fibers end in the superficial layers in register with the

retinotectal terminals. The contralateral isthmo-tectal fibers collect at the lateral tegmentum, contiguous with the lateral optic tract, and run forward. They cross the midline in the supraoptic decussation (postoptic commissure) of the anterior diencephalon, and travel back caudally in association with the optic tract to the tectum, where they terminate in layer A and layer 8 (47,52,53).

In the reptilian midbrain, NI forms a macroscopic swelling and lies at the edge of the anterior medullary velum immediately in front of the superficial origin of the trochlear nerve. It consists of two parts: dorsolaterally placed the nucleus isthmi pars magnocellularis (Imc) and the nucleus isthmi pars parvocellularis (Ipc) located medioventrally. In Sphenodon punctatum, Imc is composed of large, well-stained multipolar cells scattered rather evenly through the medulla, while the cortex contains only a few scattered cells. Ipc contains smaller, rounded, well-stained, closely packed cells (61). The central portion of Imc in Chameleon vulgaris is nearly free of cells. The cortical cells are flattened and darkly stained, while medullary cells are of two kinds: large multipolar cells which are lightly stained and have very large round nucleus, and other cells multipolar but smaller and very darkly stained (116). In our Golgi-Cox preparations, there are a variety of cells in morphology in both subdivisions of the isthmic complex in Gekko gekko. They could be grouped into 3 types according to their dendritic patterns: (i) monopolar cells with pyriform somata giving off one unbranched or branched dendrite; (ii) bipolar cells having polygonal or fusiform somata with two primary dendrites spreading out in the opposite directions or at certain angles; (iii) multipolar cells possessing polygonal or spherical somata with dendrites in a radiation fashion or distributed in two main directions. Imc cells are obviously different from Ipc cells in their morphology: Imc cells are characterized by somatic size of 9-18 μm, thicker primary dendrites with numerous branches, and dendrites having tendency to spread out laterally; whereas Ipc cells have somata of 6-12 μm in diameter and thinner primary dendrites sparsely branched. In all cases, no neuronal processes are seen entering Imc from its surrounding structures including Ipc. Only two Imc cells are found to send part of their dendrites into Ipc or the adjacent tegmentum (158).

The previous studies (61,65,116) show that the reptilian NI receives its input from the tectum, the lateral lemniscus and the nucleus profundus mesencephali (NPM); it is also connected with the contralateral NI via the pars dorsalis of the ventral supraoptic commissure. The nucleus projects to the tectum. Nevertheless, no reports specify which of the two parts of NI has these connections. Among these connections, the recent studies only confirm bidirectional connections between Imc and the ipsilateral tectum, as well as NPM-Imc projection (33,86,147), and newly found indirect pathways connecting Imc and tectum by way of NPM (147). Tectal HRP injections in Gekko gekko and Shinisaurus crocodilurus produce labelings in the ipsilateral Imc and, in some cases, in the ipsilateral NPM. There is one case in which tectal injection leads to labelings in bilateral Imc. Following all isthmic injections, cell bodies in the ipsilateral NPM and tectum are simultaneously labeled. An NPM injection stereotaxically made in Gekko labels some cells in both tectum and Imc

ipsilaterally. However, these tectal cells might be those whose fibers participate in the tectobulbar pathway and terminate in NPM (33), or pass through this nucleus in the tecto-isthmic tract (116), whereas isthmic cells labeled following NPM injection might be those whose fibers pass through NPM to the tectum (116). It appears that there exist at least two neuronal pathways from tectum to Imc: a direct tecto-Imc and an indirect tecto-NPM-Imc pathway (47) (Fig. 3). There are no indications of fibers or terminations in Ipc following tectal HRP injections or tectal lesions in Iguana iguana, Gekko gekko and Shinisaurus crocodilurus (33,147). It is indicated that Ipc in the turtle Pseudemys scripta receives a few tectal fibers and afferents from the ipsilateral Imc, and gives rise to a bilateral tectal projection (86).

The nucleus isthmi of birds is a complex of several nuclear masses, usually including the nucleus isthmo-opticus (ION), the nucleus isthmi pars parvocellularis (Ipc), the nucleus isthmi pars magnocellularis (Imc) and the nucleus semilunaris (SLu) (102). Some authors (26, 121) exclude ION as a component of the isthmic complex. Degeneration studies on chickens show that neuronal connections of the isthmic complex include the lemnisco-isthmic, the tectoisthmic, the isthmotectal, the isthmoisthmic, the isthmocerebellar, the isthmo-oculomotor, and the isthmostriatal pathways, supporting its homology with scattered reticular cells along the lateral lemniscus rather than with the medial geniculate nucleus in mammals (121). Injections of tritiated amino acids with the pigeon's tectum indicate that densely-labeled fibers terminate in the ipsilateral Ipc and SLu. Although terminal labeling appears within Imc, but termination of tectal axons within Imc is to some extent obscured by the passage of brachial fibers through the nucleus. Ipc and SLu project back upon corresponding portions of the tectal cortex (68,69). These are in agreement with earlier findings by Hart (152) that both Ipc and Imc receive a topographically organized input from the tectum. In guinea hen and chicken Imc consists of medium- and large-sized, deeply stained multipolar neurons, whereas Ipc is composed of small multipolar cells. These cells are more closely packed than those in Imc. The cells of SLu are similar to those in Ipc (121).

In mammals, PBN or the corpus parabigeminum has long been suggested to be analogous to NI in submammalian vertebrates (90). This nucleus is located in the lateral margin of the midbrain, just ventral to the brachium of the inferior colliculus and lateral to the lateral lemniscus, forming a small bulge on the lateral wall of the midbrain. The neuroanatomy of PBN has extensively been studied in rat (40,71,86,93,125,151) and in cat (3,25,44,46,79,109,119) as well as in opossum (96), mouse (21), golden hamster (75), gray squirrel (63), rabbit (64), tree shrew (12,56), bushbaby (42) and monkey (55), using a variety of experimental techniques. Tokunaga and Otani (129) first, based on Kluver-Barrera staining, subdivided the rat's PBN into three portions, the dorsal (PBNd), middle (PBNm) and ventral (PBNv) subgroups. PBNm is mainly composed of large- and medium-sized round or polygonal cells stained deeply. Smaller neurons mainly with fusiform bodies form PBNd and PBNv. On the other hand, multipolar cells appear throughout the whole nucleus. It may be doubtful that the multipolar cell is a proper PBN neuron. The parabigeminal

neurons impregnated with Golgi-Cox method are found to be of four cell types, according to the whole profile, orientation and width of the dendritic field. Neurons with the pyramidal dendritic field are found in PBNm and their axons emerge medially toward the mesencephalic reticular formation, presumably being projection cells. Neurons having the hemispherical dendritic field are common in PBNd and PBNv. Several studies (75,93,129,151) indicate that PBN receives strictly ipsilatral projection from the superior colliculus (SC), mainly, if not exclusively, from the superficial layers consisting of the stratum zonale, stratum griseum superficiale and stratum opticum. The statement that the rodent's PBN receives substantially ipsilateral collicular projection is also supported by using transneuronal marker studies (21,40,71,75,86). Intravitreous injections of wheat germ agglutinin-conjugated horseradish peroxidase (WGA-HRP) lead to labelings in all known primary visual pathways, and in addition, in rat the parabigeminal, oculomotor, thalamic reticular and visual cortical areas are also labeled. Anterograde and retrograde tracings show that the three subgroups of PBN receive collicular projections (Fig. 4). Particularly speaking, PBNm receives its input from the rostral SC only, PBNd and PBNv receive their input throughout the SC extent except the extreme rostal pole of SC (93,151). Injections of retrograde tracers into the rostral two-thirds of the superficial layers of SC label cells in the ipsilateral PBNd and PBNv, and the contralateral PBNm. In the cases where the tracers are injected into the caudal third of the SC superficial layers, the labeled cells are only found in the ipsilateral PBNd and PBNv (86,93,151). These PBNm-SC projections might be arranged in the "anteroposterior" direction, e.g., the anterior part of PBN sends fibers to anterior projected areas of SC, and the posterior part to posterior projected area (151). In order to examine the crossed pathway from PBNm to the contralateral SC, Watanabe and Kawana (151) make electrolytic lesions of the supraoptic commissure in the hypothalamus at the level of the suprachiasmatic nucleus immediately after collicular injections of a large amount of HRP. These produce no labeling of cells in the contralateral PBNm, but labeling of cells in the ipsilateral PBNd and PBNv. It is indicated that the parabigeminofugal fibers from PBNm travel via the supraoptic commissure to the contralateral SC (93,151). These connections between PBN and SC are confirmed in golden hamster by Jen et al. (75). The hamster PBN, like that in rat, can also be divided into three subgroups. Connections of SC with each of the three subgroups are similar to those found in rat.

Apart from the above-mentioned connections, Golgi-Cox studies on the rat PBN show that few dendrites of neurons in the lateral reticular formation, the brachium of the inferior colliculus and the lateral lemniscus invade PBN. Also, few PBN cells send their dendrites into the surrounding structure. It is shown that some collicular fibers to PBN intermingle with the colliculo-reticular fibers. Therefore, there is a probability that some reticular neurons which receive colliculo-reticular fibers migrate in PBN (129). HRP injected into the pretectal area, lateral geniculate body, suprachiasmatic nucleus and lateral hypothalamic area, with damage by injection micropipette to axons in the optic tract and supraoptic commissure, labels neurons in the contralateral PBNm or bilateral PBNm; Without damage to these two pathways, no HRP-labeled cells can

be observed in PBN (151). HRP injections into various visual thalamic nuclei result in little labeling in PBN, and the patterns of labeling are different from those obtained following injection into SC (75). In normal rats, there is no pathway from PBN to the contralateral dorsal lateral geniculate nucleus (LGNd). Autoradiographic and HRP tracing studies indicate that this projection is found in adult pigmented rats which had been bilaterally enucleated at birth (125).

The cat PBN has similar localization in the midbrain to that in rats, but no subdivisions which could be differentiated histologically. This nucleus receives substantially ipsilateral projection from SC (3,25,44-46,119). As in rats, the colliculo-parabigeminal projection mainly originates in the superficial layers (3,44,46), particularly in the stratum griseum superficiale of SC (44). A HRP retrograde transport study reveals that injections of PBN label neurons throughout the superficial, intermediate and deep layers, with significantly more numerous in the deep layers (60%) than in the intermediate (30%) or superficial layers (10%). No HRP-positive cells are found in SC contralateral to the injection (3). The discrepancy between opposite results could be explained by the suggestion that HRP injections into PBN involve the lemniscal fibers immediately adjoining tegmentum known to receive afferent fibers from the stratum griseum profundum and griseum intermedium. A puzzling argument is that the injection is strictly specific to PBN, without involving the tegmental areas (3). The colliculoparabigeminal fibers descend through the stratum opticum and stratum griseum intermediate to gather in the stratum album intermediate, where they travel laterally and then descend medially to the nucleus of the brachium of the inferior colliculus to get to the ipsilateral PBN (44). PBN in cats projects back bilaterally to SC (3,46,109,119). There are three striking differences between the ipsilateral and contralateral projections. First, the ipsilateral parabigeminocollicular fibers reach SC by a direct dorsomedial approach, whereas fibers of the contralateral component follow the optic tract forward, cross the midline through the supraoptic commissure and then return with the contralateral optic tract to enter the rostral pole of SC (46,109). Second, comparison of size of the labeled cells in both PBN after one collicular HRP injection shows that most of cells labeled in the ipsilateral PBN are small, while large cells are commonly labeled in the contralateral PBN (119). Third, PBN returns a projection to the caudal two-thirds on the ipsilateral side and to the rostral two-thirds on the contralateral side. The input to the rostral colliculus from the ipsilateral PBN is almost absent and the input from the contralateral PBN is strong, but diffuse and apparently not mapped (46,119).

It is suggested that the colliculoparabigeminal circuit is apparently isolated from other regions of the brain. PBN receives strong input from SC, some input from periaqueductal gray matter and the reticular formation. The output of PBN is almost entirely restricted to SC. There are some studies showing that PBN seems to have connectivity with other structures. It is indicated that some of the parabigeminofugal fibers terminate in the most ventral C-laminae of the dorsal lateral geniculate body (46). Autoradiographic techniques show afferent to PBN from the nucleus cuneiformis in the