THE JOURNAL OF COMPARATIVE NEUROLOGY 269:523-534 (1988)

Distribution of Catecholamine Fibers in the Cochlear Nucleus of Horseshoe Bats and Mustache Bats

M. KÖSSL, M. VATER, AND H. SCHWEIZER
Zoologisches Institut der Universität München, 8000 München 2, Federal Republic of Germany

ABSTRACT

The glyoxylic-acid-induced fluorescence technique was applied to demonstrate patterns of catecholaminergic innervation within the auditory brainstem of echolocating bats and the house mouse. In the cochlear nucleus of the rufous horseshoe bat (*Rhinolophus rouxi*) and the mustache bat (*Pteronotus parnellii*), species-specific catecholaminergic innervation patterns are found that contrast with the relatively homogeneous innervation in the rodent.

In both bats the subnuclei of the cochlear nucleus receive a differentially dense supply of catecholaminergic fibers, and within the subnuclei, the catecholamine innervation densities can be correlated with the tonotopic frequency representation. The areas devoted to the high-frequency echolocation calls are less densely innervated than those regions which are responsive to lower frequencies.

Apart from this common scheme, there are noteworthy distinctions between the two bats which correlate with specialized cytoarchitectural features of the cochlear nucleus. The marginal cell group, located medially to the anteroventral cochlear nucleus of Pteronotus, receives the densest supply of catecholaminergic fibers of all auditory nuclei. This plexus is formed by a morphologically distinct population of catecholaminergic fibers.

Key words: histofluorescence, auditory system, echolocation

Sensory processing is known to be modulated by catecholamines (CA) (Foote et al., '75; Pettigrew and Kasamatsu, '78; Rogawski and Aghajanian, '80; Waterhouse et al., '80). For the auditory system, Foote et al. ('75) report an improvement of the signal-to-noise ratio of cortical auditory neurons during noradrenaline (NA) injection. Noradrenergic input appears to influence auditory neuronal responses already at the cochlear nucleus (CN), the first central synaptic station of the ascending auditory pathway. During electrical stimulation of the locus ceruleus (LC), the site of origin of noradrenergic fibers (Levitt and Moore, '79), the activity of auditory neurons in the CN is inhibited (Chikamori et al., '80). A behavioral study of Pickles ('76) showed that local application of NA onto the surface of the CN increased both absolute and masked tone thresholds. The anatomical basis for these actions is the relatively dense innervation of the CN by catecholaminergic fibers (Kromer and Moore, '76: rat).

The present study investigates and compares the distribution of catecholaminergic fibers in the CN of two bat species and the house mouse. The CN of echolocating bats represents a promising model for studying the mode and degree of catecholaminergic influence on the peripheral auditory system. In horseshoe bats and mustache bats parts of the CN are hypertrophied, and the functional organization of the CN reveals adaptations for processing the echolocation calls (Suga et al., '75); Neuweiler and Vater, '77; Schweizer, '81; Zook and Casseday, '82; Feng and Vater, '85). Both bats use multiharmonic orientation calls consisting of a long constant frequency (CF) component followed by a frequency-modulated component, and the auditory system is sharply tuned to the CF frequency of the second harmonic (Pollak et al., '72; Suga et al., '75; Neuweiler et al., '80). Despite this convergent evolution, the cytoarchitectural substructure of the CN shows some remarkably different features. The dorsal CN (DCN) is divided into a laminated and nonlaminated part in *Rhinolophus* (Schweizer, '78, '81; Feng and Vater, '85), whereas in *Pteronotus* it is only weakly laminated as a whole (Zook and Casseday, '82). Significantly, the CN of *Pteronotus* contains

Accepted October 13, 1987.

a group of large multipolar neurons, the marginal cells (Zook and Casseday, '82), which is not found in other mammals. In both species the tonotopic arrangement in the three subnuclei is known and found to be biased toward an overrepresentation of the frequency range of the CF frequency of the dominant second harmonic of the orientation call (Feng and Vater, '85; Kössl, '87). With this background, the question can be addressed of whether the innervation by a modulatory neuronal system like the catecholaminergic system is related to cytoarchitectural areas involved in processing of biologically relevant frequency information. We report that both the degree and pattern of the catecholaminergic innervation in the CN of bats differ significantly from the house mouse and are related to the frequency representation. Furthermore, the marginal cells of *Pteronotus* receive the densest supply of Ca fibers within the auditory system.

MATERIALS AND METHODS

Four individuals of *Rhinolophus rouxi* from Sri Lanka, four *Pteronotus parnellii* from Jamaica, and three house mice (*Mus musculus*) were used. The animals were decapitated under deep nembutal anaesthesia (5 mg/100 g body weight). The brains were quickly removed and then processed according to a slightly modified protocol of de la Torre and Surgeon ('76) and de la Torre ('80). Brain tissue slabs 5–10 mm thick containing the brainstem and the cerebellum were cut and immediately placed onto the object-holder of the precooled cryostat that maintained a temperature of −28° to −30°C. Sections 30 μm thick were cut, attached to a glass slide, and immediately dipped three times into the glyoxylic acid solution (1% glyoxylic acid monohydrate, 6.8% sucrose). The sections were air dried, covered with paraffin oil, and then kept for 3.5 minutes in an oven prewarmed to 94–97°C. Coverslips were applied and the slides were ready for examination with a Reichert-Jung epifluorescence microscope (excitation filter 390–450 nm, barrier filter 475 nm). With this method NA and dopamine (DA) were indistinguishable since they emit similar blue/green fluorescence, but both were easily differentiated from the yellow, fast-fading serotonin reaction product.

Since the cutting plane cannot be accurately controlled with this procedure, the transverse sections of different brains are oriented in slightly different angles (see Fig. 9). Transverse sections were cut in a plane roughly perpendicular to the dorsal surface of the cortex, and the dorsoventral axis in the figures refers to this plane. Since the brainstem of bats is flexed in relation to the cortex surface, the anterior part of the anteroventral CN is shifted dorsally and the DCN ventrally. This is due to the cutting plane and does not reflect a principle difference to other mammals. To verify CA distribution differences found on different transverse sections, additional brains were cut parasagittally. The sections were analyzed at 250 times and 1,000 times magnification and representative drawings were made of all detectable fibers and terminals with a camera lucida. After examination for fluorescence the sections were stained with cresyl violet for cytoarchitectural analysis. Cytoarchitectural borderlines were defined by superimposing the stained sections and the drawings, using brain outlines, small holes, and blood vessels as reference. Additional slices from different brains were processed for acetylcholinesterase with a modified Koelle-Friedenwald thiocholine method according to Hardy et al. ('76). The cytoarchitectural division of the CN is on the basis of the work of Zook and Casseday ('82) for *Pteronotus* and Feng and Vater ('85) for *Rhinolophus*. For the house mouse the nomenclature of Willard and Ryugo ('83) was used. On the basis of the pattern of CA innervation and results on the auditory frequency representation in the CN of *Pteronotus* (Kössl, '87), the marginal cell group was further divided into a lateral and medial part.

Abbreviations

an	auditory nerve
AV	anteroventral cochlear nucleus
AVa	anterior part of AV
AVp	posterior part of AV
CA	catecholamine
CF	constant-frequency component of echolocation calls
CN	cochlear nucleus
DA	dopamine
das	dorsal acoustic stria
DCN	dorsal cochlear nucleus
DCd	dorsal part of DCN
DCv	ventral part of DCN
dt	dorsal tegmental nucleus (von Gudden)
f	facial nerve
fn	facial nucleus
gr	granular cells
ias	intermediate acoustic stria
IC	inferior colliculus
icp	inferior cerebellar peduncle
io	inferior olivary complex
LC	locus ceruleus
LNTB	lateral nucleus of the trapezoid body
LSO	lateral superior olivary nucleus
LT	lateral tegmentum
MA	marginal cell group
MAl	lateral part of MA
MAm	medial part of MA
mcp	middle cerebellar peduncle
MNTB	medial nucleus of the trapezoid body
MSO	medial superior olivary nucleus
NA	noradrenaline
PV	posteroventral cochlear nucleus
PVd	dorsal part of PV
PVv	ventral part of PV
PVl	lateral part of PV
PVm	medial part of PV
rm	raphe magnus
scp	superior cerebellar peduncle
st	spinal tract of trigeminal nerve
tb	trapezoid body
tm	motor nucleus of the trigeminal nerve
ts	principal sensory nucleus of the trigeminal nerve
VNTB	ventral nucleus of the trapezoid body
vg	vestibular ganglion

RESULTS

Catecholaminergic fibers are readily detected by their intense blue/green fluorescence. Fluorescent fibers in the CN are approximately 0.5–2 μm in diameter (Figs. 2, 6) and show characteristic varicosities separated by intervaricose segments. The varicosities represent the typical terminal specializations of CA fibers as sites of transmitter release (Moore and Card, '84).

The fiber distribution within the CN is species specific. In the house mouse all the subnuclei of the CN receive a rather homogeneous innervation by CA fibers (Fig. 1), and the fiber distribution is similar to that in the rat (Kromer and Moore, '76). There are only minor variations in density. In the posteroventral CN (PV) the density is slightly higher than in the anteroventral CN (AV), and within the DCN, the molecular layer receives a low fiber supply. In contrast, both bats show clear regional differences in the CA inner-

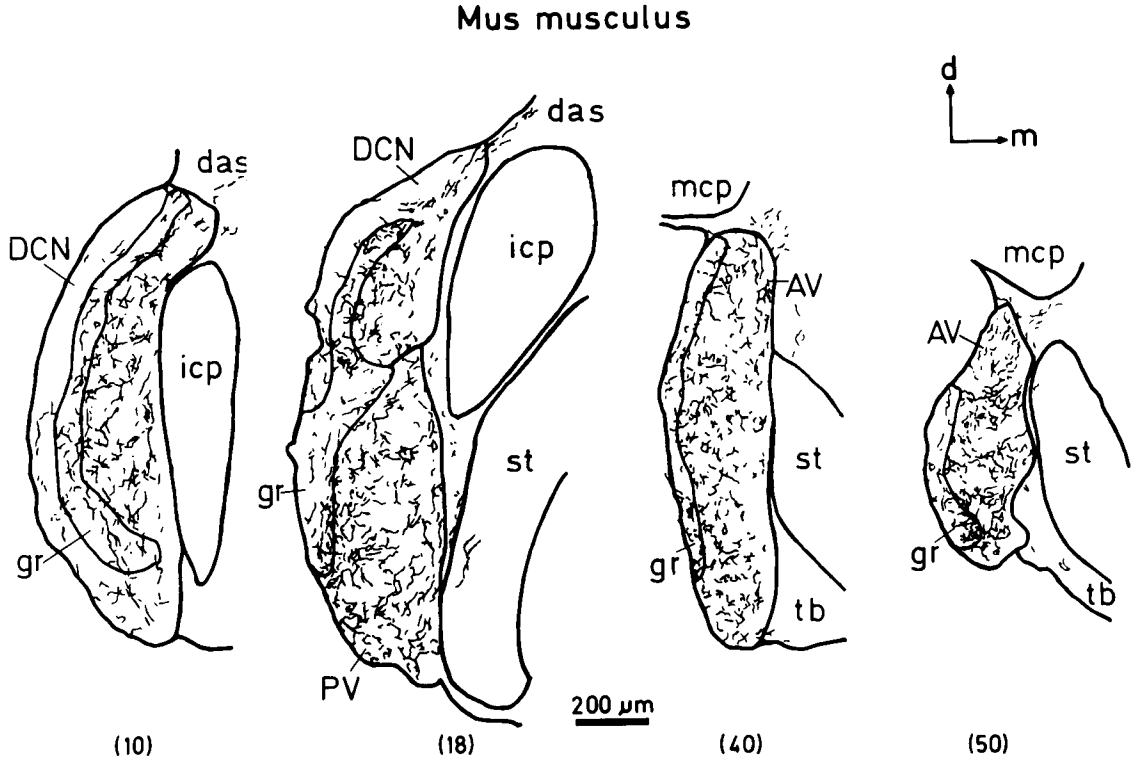

Fig. 1. Camera lucida drawings of catecholaminergic fibers (glyoxylic-acid-induced histofluorescence) in the cochlear nucleus of the house mouse (transverse sections). The fibers are relatively homogeneously distributed with a slightly denser innervation in the PV. They enter the CN with the das and between the mcp and st. As in Figures 3 and 4; section numbers starting from the most caudal CN section are given in parentheses.

vation pattern of the CN. Moreover, the areas of highest fiber density are different between the two bat species (Figs. 2–4).

In *Rhinolophus* the DCN is most heavily innervated with CA fibers (Figs. 2, 3, 5). This subnucleus is composed of a laminated ventral part (DCv), similar to the DCN of other nonprimate mammals, and a dorsal part (DCd) lacking lamination (Feng and Vater, '85). The ventral DCN, where low frequencies are processed, exhibits a particularly prominent network of CA fibers (Fig. 2a). This plexus is densest at the location of granular cells, which form a caplike structure extending from the DCN to the laterocaudal AV and PV (Figs. 3, 5). The dorsal DCN is less densely innervated than the ventral DCN (see Fig. 5). The dense innervation of the granular cells in *Rhinolophus* is in clear contrast to the house mouse, where granular cell areas are innervated by fibers of similar density as in the rest of the CN (Fig. 1).

The ventral CN of *Rhinolophus* has a significantly lower innervation density than the DCN. In particular the caudal part of the AV, where high frequencies are represented (Feng and Vater, '85), is only sparsely innervated. The innervation density increases toward more rostral sections of the AV, where low frequencies are represented (Feng and Vater, '85). This is especially evident in the sagittal series of Figure 5. Judging from cytoarchitecture the AV can be separated into an anterior part (AVa) with densely packed small spherical cells, and a posterior part (AVp) of lower cell density, which additionally contains large multipolar or globular cells (Feng and Vater, '85). This cytoarchitectural separation does not exactly match the CA innervation pattern since the rostral parts of both anterior and posterior AV are more densely innervated, but in general the anterior AV has higher CA density.

The PV is divided into a dorsal part (PVd) of low cell density containing large multipolar or stellate cells and a ventral part (PVv) which is densely populated by small cells. The CA innervation is sparse throughout PV. A slightly higher fiber density in the rostral and ventral parts of the PV roughly coincides with the PVd/PVv distinction.

The cytoarchitecture and the CA innervation pattern of the CN of *Pteronotus* are in some aspects clearly different from *Rhinolophus* (Figs. 2, 4, 5).

The DCN of *Pteronotus* is not divided into two cytoarchitectural regions as in *Rhinolophus*, and the degree of lamination is low (Zook and Casseday, '82). The CA innervation density is comparable to the dorsal DCN of *Rhinolophus* and is generally higher than in the adjacent AV or PV but lower than in the ventral DCN of *Rhinolophus*. The granular cell cap also receives a dense CA innervation but is in its extension not as prominent as in *Rhinolophus*. The innervation of the AV is higher in rostral than in caudal regions and thus comparable to *Rhinolophus*. In the PV the CA innervation is less homogeneous than in *Rhinolophus* since the medial PV (PVm, homologous to the *Rhinolophus* PVv) clearly receives a denser CA fiber supply than the lateral PV (PVl, homologous to PVd) (Figs. 4, 5).

The highest CA innervation density of the whole CN complex of *Pteronotus* is found in the marginal cell (MA)

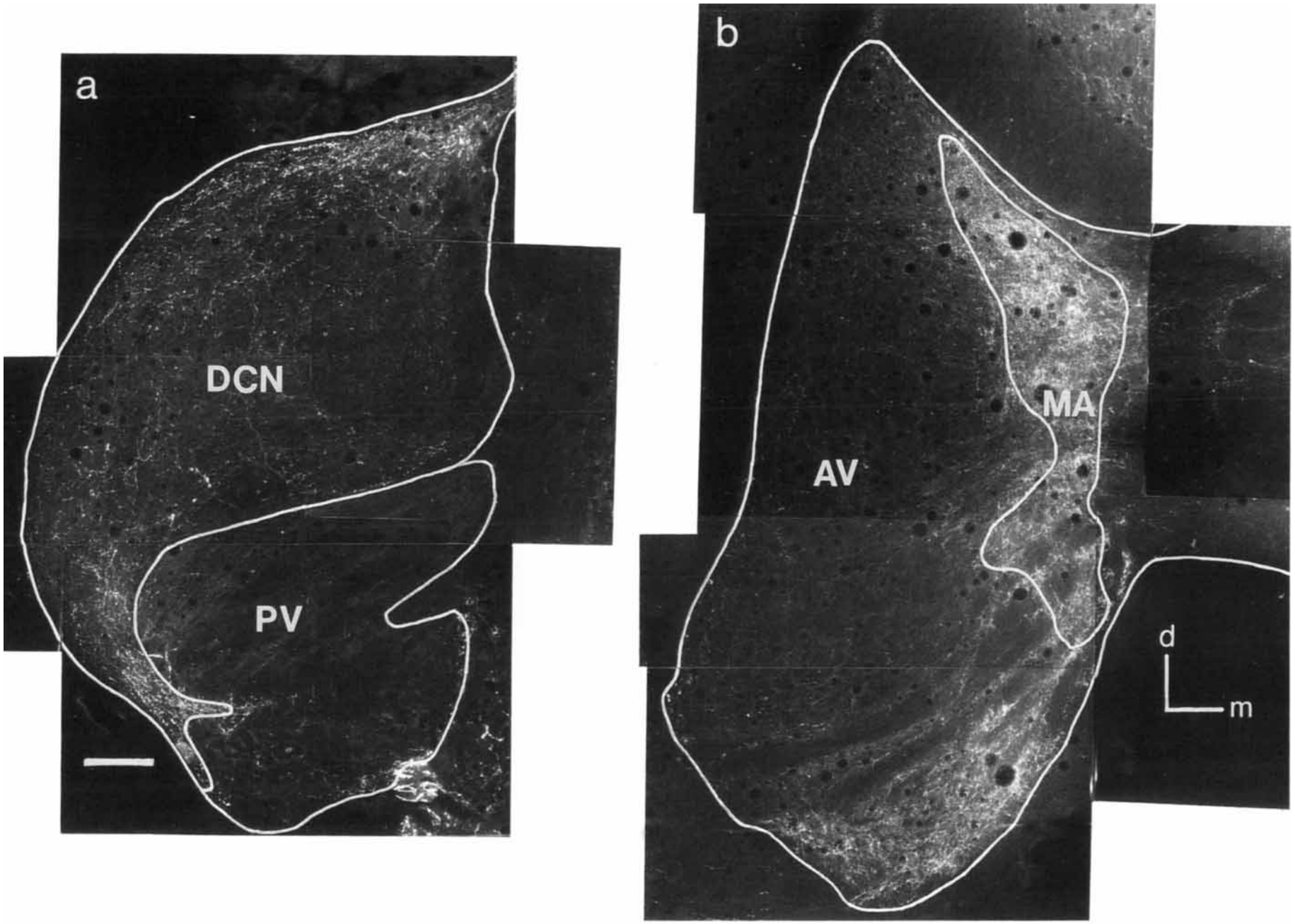

Fig. 2. Photomicrographs of catecholaminergic fibers in the cochlear nucleus of the two bat species. **a:** DCN and PV of *Rhinolophus*. Note that the DCN has a much denser CA innervation than the PV. **b:** MA cells and AV of *Pteronatus*. Note the very dense innervation of the MA cell group and of the ventral part of the AV. Transverse sections, calibration bar represents 100 μm.

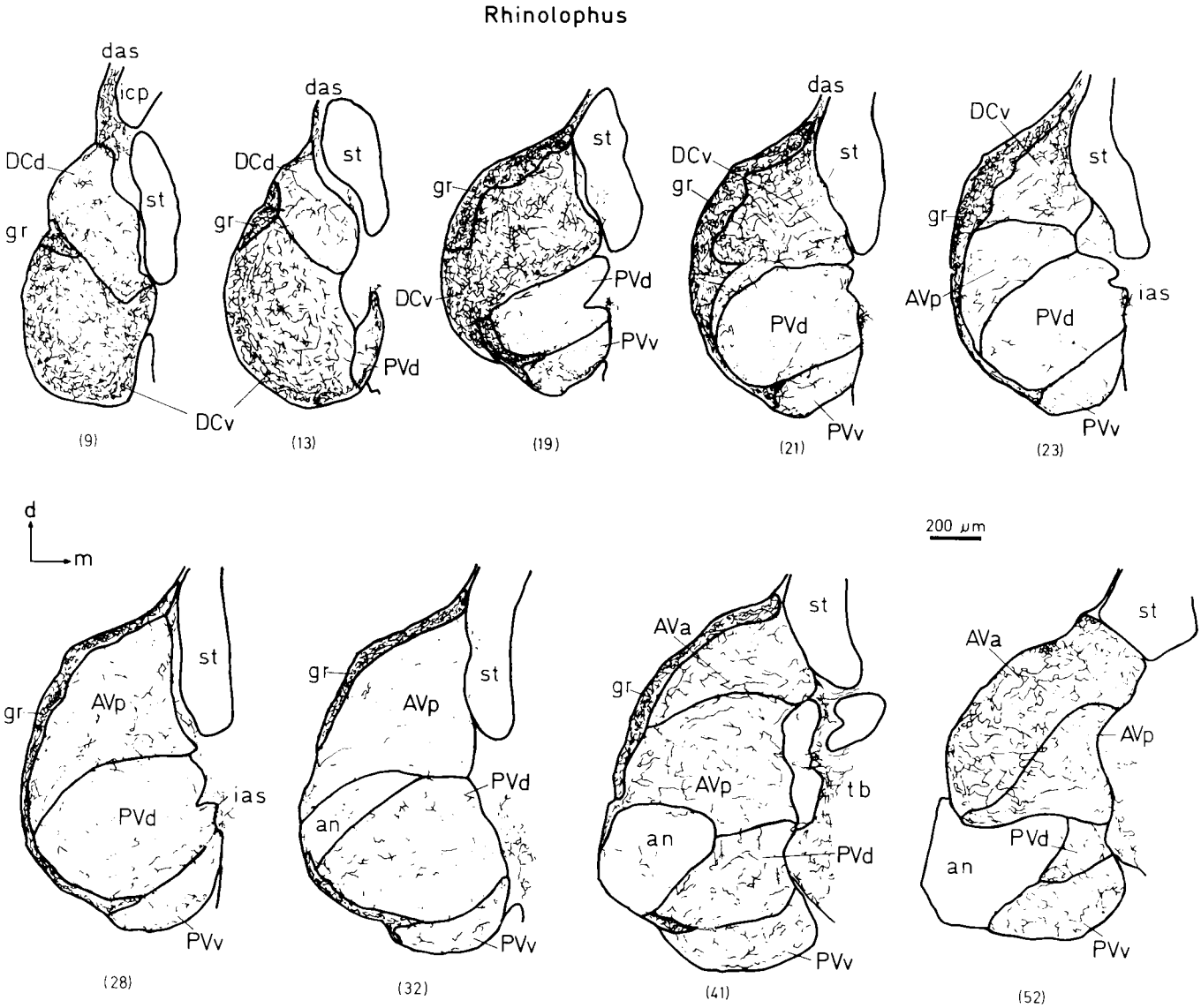

Fig. 3. Camera lucida drawings of the catecholaminergic innervation of the cochlear nucleus of *Rhinolophus* (transverse sections). Note the areas of densest innervation in the ventral part of DCN (DCv) and the granular cell cap of AV and PV (gr). The rostral parts of AV and PV also show higher innervation density than the caudal parts. The fibers enter through the das, ias, and the tb.

area and in the rostral AV (Figs. 2b, 4). The MA group contains large multipolar cells darkly staining with cresyl violet and is a species characteristic feature of *Pteronotus* (Zook and Casseday, '82). These cells are located either medially to AV and PV (here defined as medial subdivision of MA: MAm) or between DCN and PV (lateral subdivision: MAl). The dense CA fiber network is restricted to the medial MA group and to adjacent parts of the ventral and rostral AV (both AVa and AVp) (Figs 4, 5). The dense fiber network does not extend into the lateral MA group where the fiber density is not higher than in the surrounding PVl and DCN (Figs. 4, 5). As demonstrated in Figure 7, which shows the relation of the CA fibers to Nissl-stained cell bodies, the medial MA cells are covered by a very dense carpet of fibers that also fills up the neuropil. The fibers in this area are even denser than in *Rhinolophus* DCN (compare Fig. 6a with 6b, Fig. 7) and appear to be finer (Fig. 6). They show many varicosities that are on the average smaller than in the rest of the CN complex of both bats, and the difference between varicosities and intervaricose segments is less distinct. Because of the numerous varicosities and the high degree of arborization these fibers most probably constitute a terminal field and are not fibers of passage. Such passing fibers are seen in the trapezoid body and are straighter and thicker and show less varicosities. The CA fiber network of the medial MA represents the most densely CA-innervated area of the auditory system.

In addition to the CA innervation the medial group also receives a rather dense and distinct network of fibers staining positively in acetylcholinesterase histochemistry (Fig. 8). The area of dense acetylcholinesterase stain is restricted to the medial MA group, does not cover the lateral MA

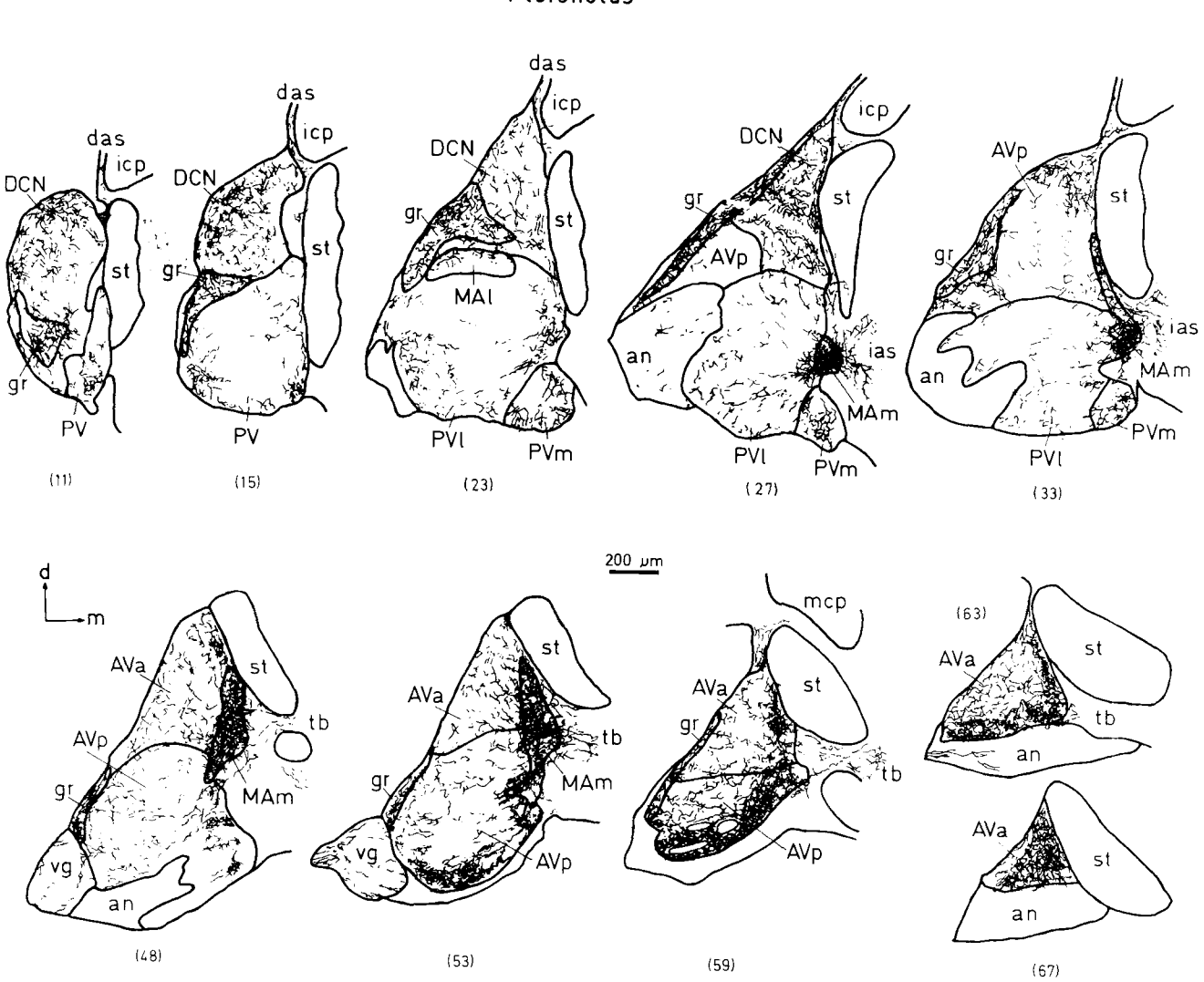

Fig. 4. Camera lucida drawings of the catecholaminergic innervation of the cochlear nucleus of *Pteronotus* (transverse sections). The DCN shows only slightly denser innervation than AV and PV. Maximal CA density is found in the granular layers (gr) and especially in the medial MA group (MAm) and adjacent ventral AV.

region, and unlike the CA fibers also does not extend into the most anterior AV. In both bats the DCN represents the only other CN region with high acetylcholinesterase content.

The CA fibers enter the CN complex within different pathways. One prominent entry is along the dorsal acoustic stria (das). These fibers presumably supply the DCN and the granular cells. Additionally there are fibers entering the AV through the trapezoid body (tb), and also some fibers enter within the intermediate acoustic stria (ias). Since the fibers cannot be traced unambiguously over a long distance, their origin is unclear. In the brainstem catecholaminergic cell bodies are located in the LC and in the lateral tegmentum (LT) (Fig. 9), which are probably homologous to rat A5 or A7 cell groups (Moore and Card, '84). In *Pteronotus* prominent bundles of CA fibers are travelling ventrally at the rostrocaudal level of the locus ceruleus and lateral tegmentum (Fig. 9) and are candidates for supplying the medial MA terminal field via the trapezoid body.

DISCUSSION

In contrast to the homogeneous distribution of CA fibers in the CN of the house mouse, the CN of bats exhibits a regionally differentiated pattern of supply. There are differences of innervation density within the subnuclei which can be correlated with the tonotopic frequency representation. Furthermore, cytoarchitectural differences between horseshoe bats and mustache bats are reflected by differences in the innervation by CA fibers, which is especially evident for the MA group of *Pteronotus* and will be discussed first.

The catecholaminergic innervation of the marginal cell group

The CA innervation of the CN in *Pteronotus* shows unusual features correlating with a unique cytoarchitectural specialization, the MA group. In the CN of rats the CA innervation seems to be exclusively noradrenergic (Kromer

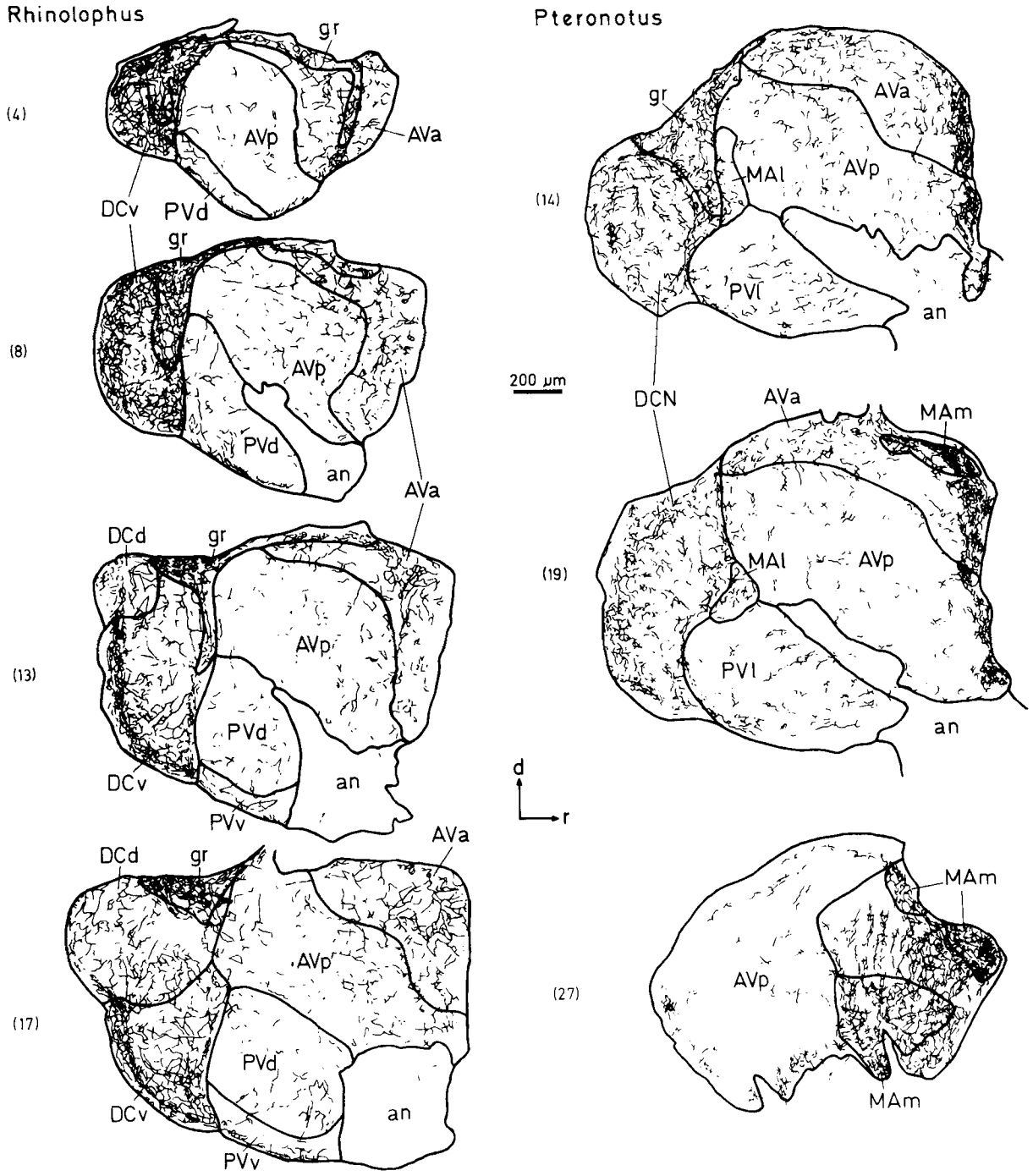

Fig. 5. Camera lucida drawings of the distribution of catecholaminergic fibers (parasagittal sections) in the CN of *Rhinolophus* (left) and *Pteronotus* (right). In *Rhinolophus* the DCv, granular cells, and rostral AV are most densely innervated. In *Pteronotus* the medial MA group and the most rostral AV receive the highest density of supply with CA fibers. Section numbers starting from the most lateral CN section are given in brackets.

and Moore, '76; Levitt and Moore, '79). Its origin is most probably the LC because the biochemically measurable NA content of the CN disappears after bilateral lesions of the LC (Levitt and Moore, '79). In the rat the NA fibers of the LC are characterized by regularly shaped varicosities of intensive fluorescence and very thin intervaricose segments (Lindvall and Björklund, '74a,b; Moore, '78; Levitt and Moore, '79). Ca fibers of similar morphology innervate the CN of *Rhinolophus* and most parts of the CN of *Pteronotus* and therefore most probably are noradrenergic. A different type of CA fibers is observed in the medial MA group. These fibers are finer and denser and the varicosities are smaller (Fig. 6). Their distinct morphology suggests the possibility that their site of origin is different from the LC.

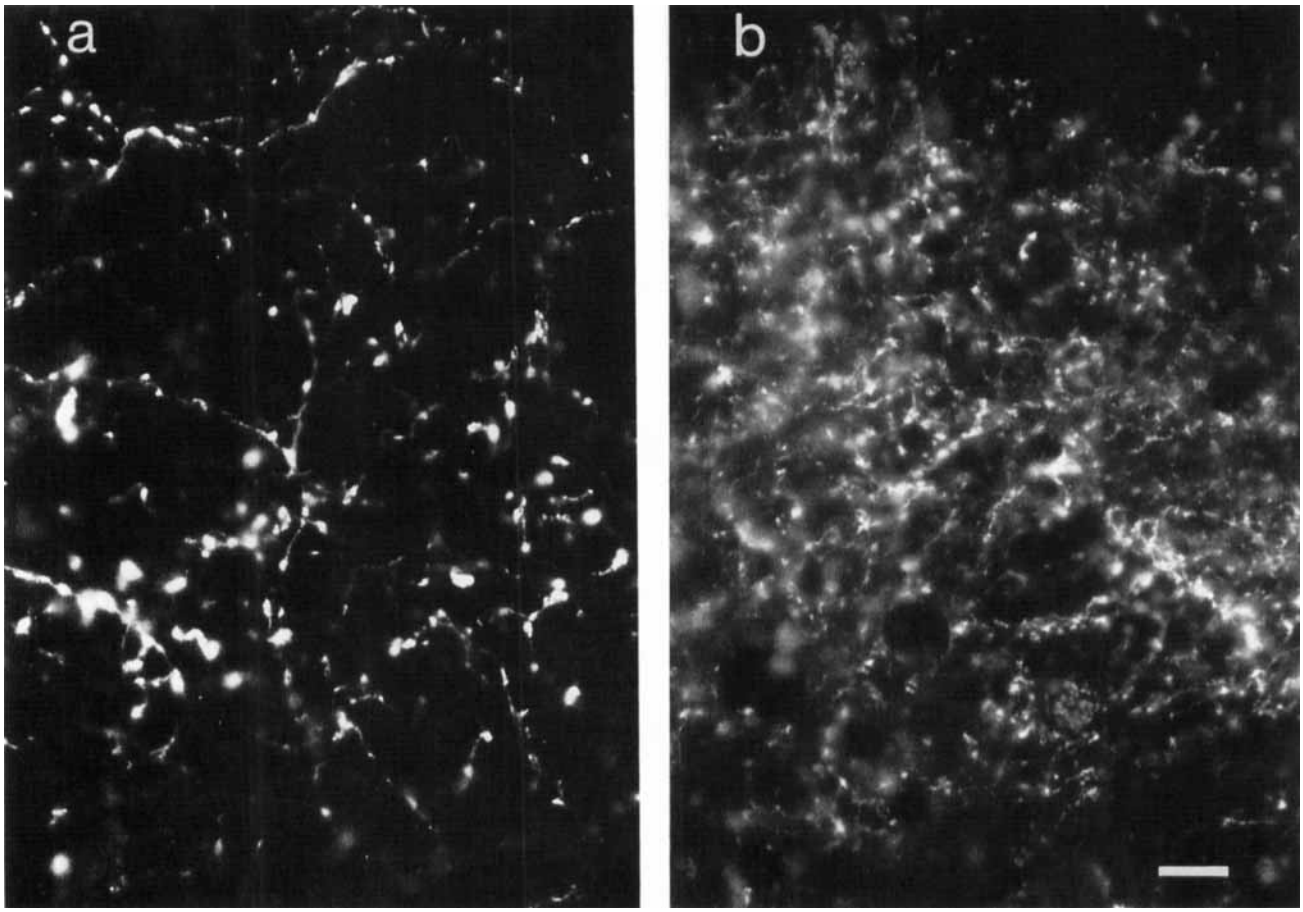

Fig. 6. Photomicrographs of catecholaminergic fibers in the DCN of *Rhinolophus* (**a**) and the medial MA group of *Pteronotus* (**b**). Note that in the medial MA group the fibers are denser and the varicosities are on the average smaller than in the DCN. Calibration bar represents 10 μm.

The fibers could come either from DA cells of the ventral and medial tegmentum, which give rise to terminal fibers of very dense and fine appearance (Lindvall and Björklund, '74a; Björklund and Lindvall, '84), or they might originate in the lateral tegmental NA cells, whose fibers are more heterogeneous than the LC fibers (Lindvall and Björklund, '74a,b). However, dopaminergic innervation of the CN or noradrenergic innervation from sources other than the LC has not been reported in other animals. The precise nature of the CA innervation of the MAm region is presently being studied more closely with pharmacological tools. In this context, it is of considerable interest that both catecholaminergic and acetylcholinergic systems establish dense fiber networks in the medial MA region. This indicates a functional relationship of the two transmitter systems. Complex modulatory interactions with acetylcholine are reported both for DA (Giorguieff et al., '76; Puro, '83; Yeh et al., '84), and for NA (Löffelholz, '79; Muscholl, '79; Waterhouse et al., '80).

Relation between CA innervation and frequency representation

In the CN of the house mouse there is no obvious gradient of CA fiber innervation: all parts of the subnuclei show similar fiber densities. Therefore neurons tuned to different tone frequencies are most probably affected in a similar degree by the presumed catecholaminergic modulation.

In the anteroventral CN of both *Rhinolophus* and *Pteronotus*, there is a clear increase of CA density from caudal to rostral. The tonotopic arrangement in the AV is such that neurons processing similar tone frequencies are arranged in transverse slabs. Slabs of increasing frequencies are organized in a rostrocaudal direction (Feng and Vater, '85, for *Rhinolophus*; Kössl, '87, for *Pteronotus*). This implies that neurons located rostrally and processing low frequencies receive a denser innervation than the caudally located high-frequency areas. The regions processing the dominant second harmonic (*Rhinolophus*) and second and

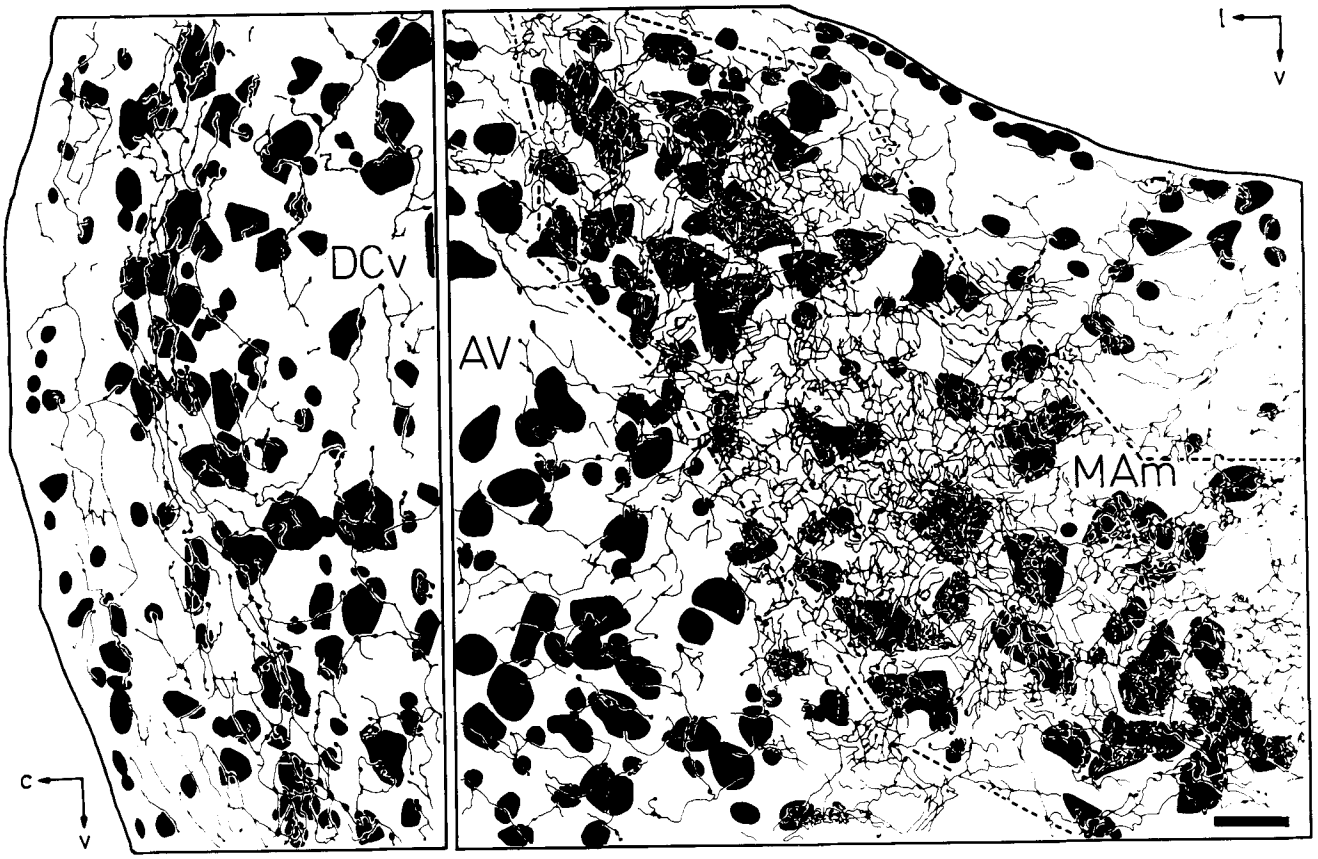

Fig. 7. Camera lucida drawings of the distribution of catecholaminergic fibers in relation to the cell bodies superimposed from pictures drawn prior to and after counterstaining the individual section. **Left**: Parasagittal sections of the DCN of *Rhinolophus*; most fibers are located in the fusiform cell layer. **Right**: transverse sections of the AV and the medial MA group of *Pteronotus*. Despite similar cell density, the medial MA neurons receive much denser innervation. Calibration bar represents 25 μm.

third harmonics (*Pteronotus*) of the echolocation calls (i.e., CF frequencies of 78 kHz for *Rhinolophus* and both 61 and 92 kHz for *Pteronotus*) underlie less catecholaminergic influence than the areas dealing with the less intense first harmonic of echolocation calls and with low-frequency communication calls. The same relationship holds true for the DCN of *Rhinolophus* where the less densely innervated dorsal part processes the frequencies of the second harmonic component, whereas the more strongly innervated ventral part is devoted to lower frequencies. The medial subdivision of the PV of *Pteronotus* representing low frequencies is also more densely innervated than the lateral subdivision, which processes high frequencies. In the PV of *Rhinolophus* and the DCN of *Pteronotus* such gradients are less obvious or absent. To summarize, in all the subnuclei of the CN of both bats where there is a significantly inhomogeneous CA innervation, low-frequency regions receive denser innervation than the high-frequency regions processing the dominant echolocation frequencies. Most interesting is the high innervation density in the medial MA group in *Pteronotus*, which contains a frequency representation biased for frequencies between 24 and 30 kHz (i.e., the range of the first harmonic of the echolocation calls; Kössl, '87).

At present, we can only speculate about the functional implications of the observed pattern since it remains to be demonstrated if the presumed modulatory effects of CA system are inhibitory (Hoffer et al., '71, '73; Siggins et al., '71) or more complex and also facilitatory as implied by a number of reports (Moises et al., '79; Waterhouse et al., '80, '82; Waterhouse and Woodward, '80). The regional differences in CA supply could imply that signal processing in the high-frequency areas devoted to the main echolocation frequencies is rather stereotyped and less susceptible to CA modulation.

The dense CA innervation of the low-frequency range might nevertheless be important for echolocation more indirectly by enabling the animal to focus on specific features of the acoustic signals:

(1) If the Ca modulation of the CN were mostly inhibitory as in other species (Pickles, '76; Chikamori et al., '80), its

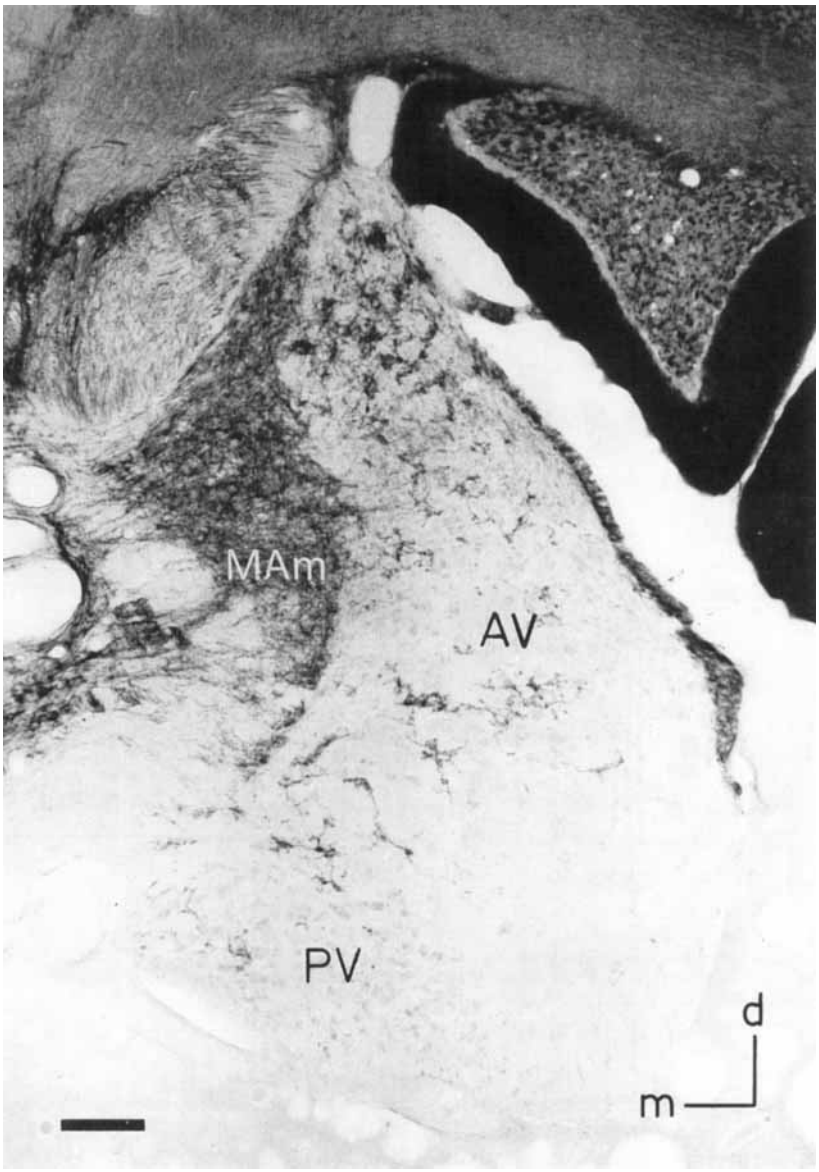

Fig. 8. Photomicrograph of an acetylcholinesterase-stained section of the CN of *Pteronotus*. Note that the staining is distinctly restricted to the medial MA group. Calibration bar represents 100 μm.

activity would lead to a selective inhibition of the low frequencies, possibly improving detection of the high-frequency echolocation sounds in noise.

(2) In the central auditory system of *Pteronotus* the weak first harmonic (24–30 kHz) of the multiharmonic calls is an necessary trigger for delay-sensitive neurons. These neurons respond to the high frequencies of the dominant second or the third harmonic (60 and 90 kHz) only if those have a certain delay to a first harmonic pulse (Suga et al., '78, O'Neill and Suga, '79, '82; Suga, '84). Under the assumption that the first harmonic pulse derives from the emitted call and the second high-frequency sound from the returning echo, these neurons are able to code the distance between bat and prey. The distinct CA innervation of the medial MA group and the rostral AV which are responsive to the frequency range of the first harmonic might play a role within this functional context. A selective control of the first harmonic gating mechanism could then be achieved already at the level of the CN.

ACKNOWLEDGMENTS

This work was supported by the SFB 204 "Gehör." We thank G. Neuweiler and R. Roverud for critically reading an earlier version of this manuscript.

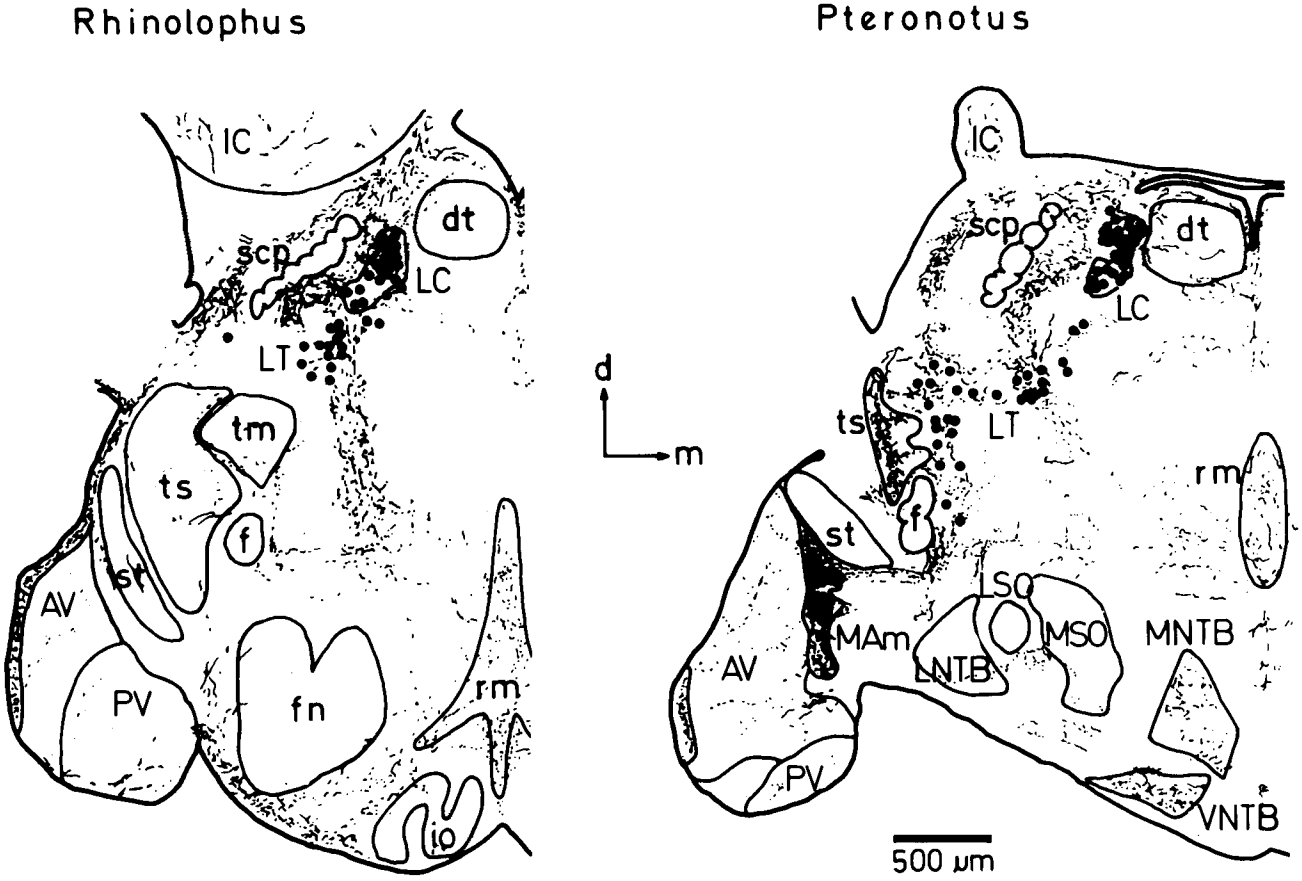

Fig. 9. Camera lucida drawings of transverse sections through the brainstem of *Rhinolophus* (**left**) and *Pteronotus* (**right**) showing the location of noradrenergic cell bodies in the locus ceruleus (LC) and in the lateral tegmentum (LT). Rostrocaudal position is not quite comparable because of differences in the cutting plane. For further explanation see text.

LITERATURE CITED

Björklund, A., and O. Lindvall (1984) Dopamine-containing systems in the CNS. In A. Björklund and T. Hökfelt (eds): Handbook of Chemical Neuroanatomy. Vol. 2: Classical Transmitters in the CNS, Part 1. Amsterdam: Elsevier Science Publishers B.V., pp. 55–122.

Chikamori, Y., M. Sasa, S. Fujimoto, S. Takaori, and I. Matsuoka (1980) Locus coeruleus—induced inhibition of dorsal cochlear nucleus neurons in comparison with lateral vestibular nucleus neurons. Brain Res. *194:*53–63.

de la Torre, J.C., and J.W. Surgeon (1976) A methodological approach to a rapid and sensitive monoamine histofluorescence using a modified glyoxylic acid technique: The SPG method. Histochemistry *49:*81–93.

de la Torre, J.C. (1980) An improved approach to histofluorescence using the SPG method for tissue monoamines. J. Neurosci. Methods *3:*1–5.

Feng, A.S., and M. Vater (1985) Functional organization of the cochlear nucleus of Rufous Horseshoe bats (*Rhinolophus rouxi*: Frequencies and internal connections are arranged in slabs. J. Comp. Neurol. *235:*529–553.

Foote, S.L., R. Freedman, and A.P. Oliver (1975) Effects of putative neurotransmitters on neuronal activity in monkey auditory cortex. Brain Res. *86:*229–242.

Giorguieff, M.F., M.L. Le Floch, T.C. Westfall, J. Glowinski, and M.J. Besson (1976) Nicotinic effect of acetylcholine on the release of newly synthesized [^{3}H]dopamine in rat striatal slices and cat caudate nucleus. Brain Res. *106:*117–131.

Hardy, H., L. Heimer, R. Switzer, and D. Watkins (1976) Simultaneous demonstration of horseradish peroxidase and acetylcholinesterase. Neurosci. Lett. *3:*1–5.

Hoffer, B.J., G.R. Siggins, and F.E. Bloom (1971) Studies on norepinephrine containing afferents to Purkinje cells of rat cerebellum: II. Sensitivity of Purkinje cells to norepinephrine and related substances administered by microiontophoresis. Brain Res. *25:*523–534.

Hoffer, B.J., G.R. Siggins, A.-P. Oliver, and F.E. Bloom (1973) Activation of the pathway from locus coeruleus to rat cerebellar Purkinje neurons: Pharmacological evidence of noradrenergic central inhibition. J. Pharmacol. Exp. Ther. *184:*553–569.

Kössl, M. (1987) Frequenzrepräsentation und Frequenzverarbeitung in der Cochlea und im Nucleus Cochlearis der Schnurrbartfledermaus *Pteronotus parnellii*. Doctoral thesis, Munich.

Kromer, L.F., and R.Y. Moore (1976) Cochlear nucleus innervation by central norepinephrine neurons in the rat. Brain Res. *118:*531–537.

Levitt, P., and R.Y. Moore (1979) Origin and organization of brainstem catecholamine innervation in the rat. J. Comp. Neurol. *186:*505–528.

Lindvall, O., and A. Björklund (1974a) The organization of the ascending catecholamine neuron systems in the rat brain as revealed by the glyoxylic acid fluorescence method. Acta Physiol. Scand. [Suppl.] *412:*1–48.

Lindvall, O., and A. Björklund (1974b) The glyoxylic acid fluorescence method: A detailed account of the methodology for the visualization of central catecholamine neurons. Histochemistry *39:*97–127.

Löffelholz, K. (1979) Release induced by nicotinic agonists. In D.M. Paton (ed): The release of catecholamines from adrenergic neurons. Oxford: Pergamon Press, pp. 275–302.

Moises, H.C., D.J. Woodward, B.J. Hoffer, and R. Freedman (1979) Interactions of norepinephrine with Purkinje cell responses to putative amino acid neurotransmitters applied by microiontophoresis. Exp. Neurol. *64:*493–515.

Moore, R.Y. (1978) Catecholamine innervation of the basal forebrain. I. The septal area. J. Comp. Neurol. *177:*665–684.

Moore, R.Y., and J.P. Card (1984) Noradrenaline-containing neuron systems. In A. Björklund and T. Hökfelt (eds): Handbook of Chemical Neuroanatomy. Vol. 2: Classical Transmitters in the CNS, Part 1. Amsterdam: Elsevier Science Publishers B.V., pp 55–122.

Muscholl, E. (1979) Presynaptic muscarinic receptors and inhibition of release. In D.M. Paton (ed): The release of catecholamines from adrenergic neurons. Oxford: Pergamon Press, pp. 275–302.

Neuweiler, G., and M. Vater (1977) Response patterns to pure tones of cochlear nucleus units in the CF-FM bat, *Rhinolophus ferrumequinum*. J. Comp. Physiol. *115:*119–133.

Neuweiler, G. V. Bruns, and G. Schuller (1980) Ears adapted for the detection of motion, or how echolocating bats have exploited the mammalian auditory system. J. Acoust. Soc. Am. *68:*741–753.

O'Neill, W.E., and N. Suga (1979) Target range-sensitive neurons in the auditory cortex of mustache bats. Science *203:*69–73.

O'Neill, W.E., and N. Suga (1982) Encoding of target range and its representation in the auditory cortex of the mustached bat. J. Neurosci. *2:*17–31.

Pettigrew, J.D., and T. Kasamatsu (1978) Local perfusion of noradrenaline maintains visual cortical plasticity. Nature *271:*761–763.

Pickles, J.O. (1976) The noradrenaline-containing innervation of the cochlear nucleus and the detection of signals in noise. Brain Res. *105:*591–596.

Pollak, G., O.W. Henson, Jr., and A. Novick (1972) Cochlear microphonic audiograms of the 'pure tone' bat *Chilonycteris parnellii parnellii*. Science *176:*66–68.

Puro, D.G. (1983) Cholinergic transmission by embryonic retinal neurons in culture: Inhibition by dopamine. Dev. Brain Res. *9:*79–86.

Rogawski, M.A., and G.K. Aghajanian (1980) Norepinephrine and serotonin: Opposite effects on the activity of lateral geniculate neurons evoked by optic pathway stimulation. Exp. Neurol. *69:*678–694.

Schweizer, H. (1978) Struktur und Verschaltung des Colliculus Inferior der Grossen Hufeisennase (*Rhinolophus ferrumequinum*). Doctoral thesis, Frankfurt.

Schweizer H. (1981) The connections of the inferior colliculus and the organization of the brainstem auditory system in the Greater Horseshoe bat (*Rhinolophus ferrumequinum*) J. Comp. Neurol. *201:*25–49.

Siggins, G.R., B.J. Hoffer, A.P. Oliver, and F.E. Bloom (1971) Activation of a central noradrenergic projection to cerebellum. Nature *233:*481–483.

Suga, N. (1984) Neural mechanisms of complex-sound processing for echolocation. Trends Neurosci. *7:*20–27.

Suga, N., J.R. Simmons, and P.H.-S. Jen (1975) Peripheral specializations for fine analysis of Doppler shifted echoes. J. Exp. Biol. *63:*161–192.

Suga, N., W.E. O'Neill, and T. Watanabe (1978) Cortical neurons sensitive to combinations of information-bearing elements of bisonar signals in the mustache bat (1978). Science *200:*778–781.

Waterhouse, B.J., and D.J. Woodward (1980) Interaction of norepinephrine with cerebrocortical activity evoked by stimulation of somatosensory afferent pathways in the rat. Exp. Neurol. *67:*11–34.

Waterhouse, B.D., H.C. Moises, and D.J. Woodward (1980) Noradrenergic modulation of somatosensory cortical neuronal responses to iontophoretically applied putative neurotransmitters. Exp. Neurol. *69:*30–49.

Waterhouse, B.D., H.C. Moises, H.H. Yeh, and D.J. Woodward (1982) Norepinephrine enhancement of inhibitory synaptic mechanisms in cerebellum and cerebral cortex: Mediation by beta adrenergic receptors. J. Pharmacol. Exp. Ther. *221:*496–506.

Willard, F.H., and D.K. Ryugo (1983) Anatomy of the central auditory system. In J.F. Willot (ed), The Auditory Psychobiology of the Mouse. Springfield, Illinois: Clark C. Thomas Publishers, pp. 201–304.

Yeh, H.H., B.-A. Battelle, and D.G. Puro (1984) Dopamine regulates synaptic transmission mediated by cholinergic neurons of the rat retina. Neuroscience *13:*901–909.

Zook, J.M., and J.H. Casseday (1982) Cytoarchitecture of auditory system in lower brainstem of the mustache bat, *Pteronotus parnellii*. J. Comp. Neurol. *207:*1–13.