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MONOAURAL AND BINAURAL PATHWAYS IN THE ASCENDING
AUDITORY SYSTEM OF THE PIGEON

by

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Abstract

Monaural and Binaural Pathways in the Ascending Auditory System of the Pigeon
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The organization of ascending auditory projections to the midbrain and thalamus of the pigeon was examined with the Fink-Heimer (1967) method for tracing axonal and terminal degeneration and the horseradish peroxidase technique of retrograde transport.

In the first experiment, the organization and afferent connections of n. mesencephalicus lateralis, pars dorsalis (MLd), the avian inferior colliculus, were studied. In the pigeon the cochlear-lagenar division of the eighth nerve terminates in the cochlear nuclei, n. angularis and n. magnocellularis; the latter nucleus projects bilaterally to an adjacent cell group, n. laminaris. These three rhombencephalic nuclei project to the contralateral MLd by a direct pathway as well as an indirect route (via the superior olive and the lateral lemniscal nuclei).

One major finding of this study was that n. laminaris, the avian homologue of the mammalian medial superior olive, projects upon a restricted zone in MLd, the rostro-medial division. On the other hand, of the brainstem nuclei receiving primary, monaural auditory input, n. angularis projects topographically onto MLd, and n. magnocellularis terminates very sparsely in MLd, if at all.

Afferents to MLd from regions caudal to the trapezoid body (n. angularis, n. laminaris, and the superior olive) are predominantly contralateral. More rostrally, one of the ventral nuclei of the lateral lemniscus projects ipsilaterally to MLd; the dorsal lateral lemniscal afferents (n. ventralis lemnisci lateralis, pars anterior -- VLVa) are entirely contralateral.

In addition, a somatosensory projection was found from the dorsal column nuclei to the external nucleus of the torus semicircularis, a compact group of cells located just ventral to MLd.

The second experiment investigated the afferentation of n. ovoidalis, the avian thalamic auditory relay. All parts of MLd were found to project to n. ovoidalis. Furthermore, the rostro-medial division of MLd terminates homotopically in a restricted zone of n. ovoidalis on both sides of the brain.

It is concluded that auditory information is comprised of distinct channels which remain segregated in the brainstem, the midbrain, and probably the thalamus as well. Binaural input from n. laminaris and monaural information from n. angularis, are represented in distinct subnuclei
of MLD. The tonotopic representation of auditory space in n. angularis (Konishi, 1970) is maintained in MLD. Furthermore, the organization of MLD is conserved in the thalamus by the topographic projection of that nucleus upon n. ovoidalis.

These results suggest strong parallels between the organization of avian and mammalian auditory systems. The significance of these findings is also discussed in relation to physiological studies of the avian and mammalian auditory systems.

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Introduction

In the pigeon, auditory information is relayed from the Organ of Corti to the brainstem via the cochlear-lagenar nerve. Upon its entry into the brainstem, this nerve bifurcates and projects ipsilaterally to two dorsal rhombencephalic cell groups — the cochlear nuclei. The lateral branch of the cochlear-lagenar nerve projects upon n. angularis (NA), a heterogeneous cell group which extends rostrally and dorsolaterally into the lateral cerebellar peduncle (Fig. 1a). The medial branch terminates in n. magnocellularis (NM), a nucleus containing large, spherical cells (Cajal, 1908, 1909-1911; Boord and Rasmussen, 1963; Boord, 1969; Rubel and Parks, in press). The representation of auditory information within both NA and NM has been shown to be organized tonotopically (Konishi, 1970; Rubel and Parks, in press).

A third cell group of the dorsal brainstem, n. laminaris (NL) (Fig. 1a) contains a second order, tonotopically organized binaural representation of auditory information (Boord, 1969; Rubel and Parks, in press). The dorso-medial dendrites of the NL neurons are projected upon by cells in the ipsilateral NM, while the ventrolateral dendrites receive projections from the contralateral NM via the dorsal acoustic striae (Boord and Rasmussen, 1963; Parks and Rubel, in press; Leibler, unpublished data).

The connections of n. laminaris are similar to those of the mammalian medial superior olive, a fact which has led to the conclusion that these two cell groups are homologous (Cajal, 1909-1911; Boord, 1969). Likewise, both of these nuclei are specialized for processing information about interaural time differences (Parks and Rubel, in press; Moushegian et al., 1964; Goldberg and Brown, 1968).
The rhombencephalic auditory nuclei in turn project upon a
distinct ovoid region in the caudal midbrain, which has been designated
n. mesencephalicus lateralis pars dorsalis (MLd). This group of medium
and small cells is located centrally within the torus semicircularis,
below the tectal ventricle (Boord, 1968). The fibers which arise from
nucleus angularis and n. laminaris and perhaps n. magnocellularis as well
form the trapezoid body. Some trapezoid fibers terminate in the ipsilateral
superior olive, while others decussate and continue rostrally in the
contralateral lateral lemniscus. Axons of this pathway terminate in
the ventral nuclei of the lateral lemniscus and in MLd. The connections
(Boord, 1968; Karten, 1967) and electrophysiological response properties
(Biederman-Thorson, 1967) of MLd have led to the conclusion that it is
the homologue of the mammalian inferior colliculus.

As in the mammalian auditory system, the mesencephalic auditory
relay of birds, MLd, sends a massive ascending projection to a particular
cell group in the thalamus (Karten, 1967), nucleus ovoidalis, a
distinct encapsulated group of ovoid cells lying medial to the nucleus
rotundus and separated from the third ventricle by a thin periventricular
zone (Fig. 1b). Fibers from MLd travel through a crescent-shaped
nucleus ventral to n. ovoidalis, n. semilunar is parovoidalis, where some
termination also occurs (Karten, 1967). N. ovoidalis in turn projects
to a well defined region of the telencephalon, designated Field L of
the neostriatum caudale (Karten, 1968). Studies of single unit responses
to auditory stimuli in these nuclei (Biederman-Thorson, 1970; Leppelsack,
1974) as well as the pattern of connections between them (Karten, 1967;
1968), indicate that n. ovoidalis and Field L are homologous with the mammalian medial geniculate body, pars ventralis (Morest, 1964), and the thalamic recipient neurons of auditory cortex, respectively.

In the present group of studies, the detailed organization of the ascending auditory system of birds at the mesencephalic and diencephalic levels is examined, with the hope of providing some understanding of the anatomical bases of avian auditory function. The auditory system of some birds has been found to play a crucial role in the development and normal functioning of their behavior. For example, some songbirds will not learn their characteristic song if deprived of a conspecific auditory model (Nottebohm, 1970). In other birds, sound localization is extremely important and sophisticated, and nucleus laminaris is correspondingly enlarged (Schwartzkopff, 1968), apparently because of its important role in processing interaural phase differences (Parks and Rubel, in press).

In this paper, I shall present the results of two experiments on auditory pathways in the pigeon. The first deals with the afferentation of MLD; the second concerns the projection from MLD to the thalamic auditory relay, n. ovoidalis. In these studies, both anterograde degeneration methods and retrograde transport techniques have been employed in order to provide a precise delineation of interneuronal associations in the auditory system.

One of my particular interests has been to determine whether auditory information is segregated at midbrain and thalamic levels into discrete anatomical channels related to the different rhombencephalic auditory nuclei (NA, NM, and NL). In particular, n. laminaris is
specialized for processing information about interaural time differences (Parks and Rubel, in press). However, the way in which this information is represented at higher levels in the avian brain has not been delineated. Resolution of this question may likewise shed light on the organization of the mammalian auditory system, where a comparable situation is found.

A second objective of my work has been to clarify the nature of bilateral recombinations in the avian auditory system. The only binaural convergence rostral to the dorsal rhombencephalon occurs in n. ovoidalis, which receives a bilateral projection from MLD (Karten, 1967; Boord, 1969).

I have therefore tried to identify all pathways that might lead to the binaural recombination of auditory input as well as the cell groups in which such bilateral connections originate.

Finally, an attempt was made to establish whether the topographic, and hence tonotopic maps in NA, NM and NL (Boord, 1969; Konishi, 1970; Rubel and Parks, in press) are preserved by topographic ascending projections to the mesencephalon and diencephalon.

These connections were studied in the pigeon because much of the information available to date about non-mammalian auditory systems has been collected in that animal (Boord, 1969). Furthermore, the availability of a very accurate stereotaxic atlas of the pigeon brain (Karten and Hodos, 1967) has facilitated the placement of lesions and injections.
General Method

For both experiments, male and female White Carneaux pigeons (Columba livia), ranging in age from 3 months to 4 years and weighing 400 to 600 grams, were obtained from Hillside Pigeon Farm, Clarksburg, Maryland and Palmetto Pigeon Plant, Sumter, South Carolina. Each pigeon was anaesthetized with Equithesin (Jensen-Salsbery Laboratories; 0.26 ml/100 g body weight) prior to surgery and its head placed in a stereotaxic headholder (Karten and Hodos, 1967).

Experiment 1: Ascending Projections to n. mesencephalicus lateralis pars dorsalis (MLd)

Methods

Anterograde degeneration studies

Unilateral stereotaxic lesions were made in the cochlear nuclei (n. magnocellularis and n. angularis) and in nucleus laminaris of 15 animals. In each case, the calvarium was removed, the cerebellum exposed and the electrode lowered stereotaxically to its target. A radiofrequency or direct current lesion was made, using an insect pin coated with insulation except at the tip. Control animals included pigeons with lesions in the cerebellum, the vestibular nuclei, the vestibular nerve, the reticular formation, and the cochlea.

Two to eight days following surgery the animals were anaesthetized and perfused through the heart with 0.9% saline followed by 10% formalin in saline. The calvarium was removed, and the brain blocked stereotaxically in the frontal or sagittal plane (Karten and Hodos, 1967). The brain was post-fixed for 3-7 days in formol-saline and 4-10 days in 10% formalin with 30% sucrose (Ebbesson, 1970). It was then rinsed in distilled water,
embedded in albumin-gelatin (Ebbingon, 1970; Snodgress and Dorsey, 1963), and sectioned on a freezing microtome at a thickness of 25 μm. Every eighth section was stained by the Fink-Heimer I method (1967) for degenerating axons and boutons. In some cases additional sections were stained with the Fink-Heimer I method and adjacent sections with cresylecht-violet. The extent of the lesion and the pattern of fiber and terminal degeneration were recorded on enlarged tracings of individual sections.

Retrograde transport studies of projections to MLD

Horseradish peroxidase (HRP) (Sigma Chemical Co., Type VI) was injected iontophoretically or hydraulically (Graybiel and Devor, 1974) into nucleus mesencephalicus lateralis pars dorsalis (MLD) of thirteen pigeons. In three cases (PPE1, PPE3, and PPE9) the HRP-filled pipette was lowered stereotaxically through the overlying forebrain to MLD. This approach proved to be difficult in many cases, as the calvarium curves under the caudal surface of the forebrain and over the tectum; therefore in the remaining ten cases part of the caudal forebrain was removed by suction to reveal the obstructing bone, which was removed, exposing the surface of the tectum, from which the pipette was lowered stereotaxically into MLD.

For the hydraulic injections, HRP was dissolved in 3-4 times its weight of distilled water and drawn into the tip of a Vycor glass micropipette measuring 30-75 microns in diameter at the tip. The flow of HRP was controlled by a microdrive system connected to the pipette by means of polyethylene tubing filled with oil or water. Air bubbles were excluded from the drive system except at the interface between the HRP solution
and the driving fluid. Single or multiple injections were made, ranging from 0.05 microliters to 0.70 microliters of HRP solution.

For iontophoretic injections 2 mg of HRP were dissolved in 15 microliters of tris buffer (pH 8.6) (Sigma Chemical Co., St. Louis). Glass micropipettes were drawn on a Kopf vertical pipette puller and the tip beveled to a 30° angle against a glass slide. The resulting micropipettes measured 12-25 microns (internal diameter) at the tip; they were filled under microscopic view using the hydraulic system described above.

One to three days after the operation, the pigeons were sacrificed by perfusion through the heart with 0.9% saline followed by a weak Karnovsky fixative (1.5% paraformaldehyde, 2.0% gluteraldehyde buffered in 0.1 M phosphate, pH 7.2-7.4, with 5% sucrose). The brain was blocked stereotaxically in the frontal plane and removed from the head. In most cases, the brain was post-fixed for a few hours in cold fixative and washed overnight in cold 0.1M phosphate buffer, pH 7.4 with 10% sucrose. It was then cut on a freezing microtome in 50 micron thick sections which were collected in 0.1M phosphate buffer pH 7.4 with 5% sucrose. In some cases the brain was sectioned immediately after removal from the calvarium. This variation in procedure did not appear to affect the results.

Sections were preincubated in 3-3' diaminobenzidine tetra HCl (Sigma Chemical Co.) for 15-30 minutes, reacted for another 15-30 minutes by adding 10 ml of 0.06% H₂O₂ to each 250 ml of DAB solution (LaVail and LaVail, 1972; Graybiel and Hartwig, 1974) and then washed in three changes of phosphate buffer to stop the reaction. Sections were mounted
on chrome alum-gelatinized slides (Heimer, 1970). After drying they were defatted for half an hour in an equal mixture of chloroform and absolute alcohol. The tissue was lightly counterstained with thionin or cresylechtviolet; in several cases alternate sections were left unstained.

The reaction product appears as a deep brown stain at the injection site. Retrogradely transported horseradish peroxidase appears as fine brown dots in the cell bodies of neurons which project to the injection site (LaVail and LaVail, 1974; Nauta et al, 1974). Sections were examined under dark field illumination for cells containing the reaction product; labelled cells were charted on enlarged drawings of individual sections.
Results

Anterograde degeneration studies

Large lesions of the rhombencephalon involved parts of n. angularis, n. magnocellularis and n. laminaris. After these lesions, degeneration was found in the contralateral n. laminaris, the ipsilateral superior olive, the contralateral and ipsilateral lateral lemniscal nuclei, and the contralateral MLD. Many of the lesions also damaged structures within the cerebellar peduncle, parts of the vestibular nuclear complex and the vestibular nerve itself; degeneration was often seen in the oculomotor nuclei, n. ruber, n. intercollicularis, and parts of the vestibular nuclear complex. These areas contained degeneration in the control cases as well, where no degeneration was found in MLD or other auditory system nuclei. Consequently, this report will not consider further these non-auditory structures.

In order to understand the pattern of projections from brainstem auditory nuclei to the lateral lemniscal nuclei and the pattern of lemniscal nuclear afferents to MLD, the reader should keep in mind that these nuclei are actually a heterogeneous collection of cell groups. They are best depicted in sagittal section (Fig. 1c). Nucleus lemnisci lateralis pars ventralis (LLv) consists mostly of small spherical cells, densely packed in clusters interstitial to the lateral lemniscal fibers. A group of uniformly large ovoid cells called nucleus ventralis lemnisci lateralis (VLV) is located at the rostral end of LLv (Karten and Hodos, 1967). A third nucleus, caudal to VLV and similar to it in cytoarchitecture as well as position in the brainstem but differing in its connections, has also been called VLV (Karten and Hodos, 1967). This nucleus will therefore be referred to as VLV pars posterior (VLVp) whereas the more rostral nucleus
will be called VLV pars anterior (VLVa).

Although large lesions caused degeneration in all parts of the auditory system caudal to and including MLD, restricted lesions involving either n. laminaris or n. angularis resulted in strikingly different patterns of degeneration.

**Projections of n. laminaris (NL)** In cases with lesions involving nucleus laminaris but sparing n. angularis (NA) degeneration was found to be moderate in the ipsilateral superior olive, minimal in the contralateral lateral lemniscal nuclei, and heavy in the rostro-medial portion of the contralateral MLD.

**Animal PA33** (survival 4 days) was typical of NL lesioned cases (Fig. 2). The lesion (Fig. 2a-c) spared NA but destroyed most of NL and the rostral part of n. magnocellularis; it also involved n. vestibularis lateralis and the brachium conjunctivum. Degeneration in the dorsal brainstem contralateral to the lesion was confined to the rostro-ventral aspect of n. laminaris (Fig. 2a-c). No degeneration was seen in n. angularis on either side or in n. magnocellularis contralaterally.

In this and several other cases, more rostral lesions of n. magnocellularis resulted in rostrally located degeneration in the contralateral n. laminaris, and more caudal lesions in degeneration of the caudal part of the contralateral NL. Thus, in the pigeon as in chick (Parks and Rubel, in press), the projection from n. magnocellularis to n. laminaris appears to be topographically organized.

In case PA33, the trapezoid body emerges as a bundle of fibers ventral to n. laminaris which penetrates the medial aspect of the entering vestibular nerve and then courses laterally towards the ipsilateral
superior olive. Some fibers from n. laminaris show evidence of termination in the superior olive, mostly dorso-medially (Fig. 2d). The rest of the trapezoid fibers continue rostrally, decussate, and ascend in the lateral lemniscus. Some lateral fibers of the lateral lemniscus terminate sparsely in LLv and others more heavily in VLVa, but none terminate in VLVp (Fig. 2e-f).

From VLVa, the degenerating lateral lemniscal fibers can be followed rostrally, laterally and dorsally. Ventrolateral to MLD, these fibers turn medially, and course towards that nucleus, where they terminate (Fig. 2g-i). A few fibers appear to enter adjacent portions of the torus semicircularis.

The results of this and several other cases involving lesions of n. laminaris suggest strongly that the projection arising from n. laminaris is restricted exclusively to the rostro-medial portion of MLD (Fig. 2g-i). This topographic restriction is even more strikingly evident, in cases cut in the sagittal plane. In case PA3, the degeneration in MLD after a lesion of n. laminaris (animal PA3) (Fig. 3) is confined entirely to a rostral cap of small spherical cells.

Projections of n. angularis (NA) The pattern of degeneration in MLD and in the nuclei of the lateral lemniscus after lesions of nucleus angularis stands in sharp contrast to the more limited pattern of termination seen after lesions of n. laminaris. In cases with damage to n. angularis, degeneration was found in the superior olive ipsilaterally and was extensive in LLv and VLVa contralaterally, and in VLVp bilaterally. Whereas n. laminaris lesions resulted in degeneration in the contralateral MLD restricted to
the rostro-medial pole, degeneration after lesions of n. angularis was found primarily in the caudal part of the nucleus.

A typical case was PA38 (survival 6 days). The lesion (Fig. 4a-c) involved the rostral part of NA, the lateral cerebellar peduncle, the vestibular nerve and the lateral, dorsolateral, and superior vestibular nuclei. Both n. magnocellularis and n. laminaris were free of degenerating bilaterally, as was the contralateral nucleus angularis.

Degenerating trapezoid body fibers are seen to collect ventrolateral and rostral to the lesion site (Fig. 4d). Some of these fibers turn caudally and terminate in the superior olive, in this case mostly laterally (Fig. 4c). However, after other lesions involving a greater extent of n. angularis, heavy degeneration extended more medially in the olive, indicating that this projection may be topographically organized.

The degenerating trapezoid body fibers from n. angularis course rostrally and decussate at the level of VLVa (Fig. 4f), somewhat rostral to the point where fibers from n. laminaris cross. The contralateral ascending fibers terminate in all three nuclei of the lateral lemniscus -- LLv, VLVp and VLVa (Fig. 4e-f); some also terminate in VLVp ipsilateral to the lesion (Fig. 4e). These fibers of the lateral lemniscus course dorsally, rostrally and laterally; they enter Mld from its lateral margin and can be followed to an area of relatively sparse terminal degeneration in the caudal part of the nucleus (Figs. 4g-i). Only a few degenerating fibers are found in rostral parts of Mld.
In addition, degeneration was found primarily on the ipsilateral side in n. paraprincipalis lateralis (PPL), a cell group situated ventral to n. sensorius principalis nervi trigemini. This finding was also observed in other cases with lesions of n. angularis. However, lateral lemniscal projections to PPL have not been previously reported; furthermore, the data in this study do not exclude the possibility that some other area damaged by NA lesions (e.g. the vestibular nuclei) projects upon PPL. This question will be investigated in future experiments.

Several conclusions can be drawn from tracing anterograde degeneration following lesions of n. angularis and n. laminaris. These data demonstrate that MLD is the major midbrain auditory relay in the pigeon. Partial lesions of either n. angularis or n. laminaris result in restricted degeneration in the superior olive and MLD, and indicate that the afferentation of the superior olive may be topographically organized. Unfortunately, the extent of projections from n. magnocellularis to the superior olive and MLD cannot be assessed from the anterograde data, because lesions of n. magnocellularis also damaged nucleus laminaris. Finally, fibers from both nuclei are mixed together as they ascend within the lateral lemniscus even though nucleus angularis projects more heavily than n. laminaris to the lateral lemniscal nuclei.

Other afferents to the region of MLD. One non-auditory area in the caudal hindbrain was found to project to a cytoarchitecturally distinct zone of the torus semicircularis external to MLD. In pigeon PX77 (survival 6 days) a unilateral lesion was
made which destroyed parts of n. cuneatus, n. gracilis, n. solitarius, the dorsal motor nucleus of the vagus, n. intermedius, and n. hypoglossi (Fig. 5a). Some degenerating fibers were observed to ascend rostrally in the contralateral ventral hindbrain to the level of VLVa, where they turn dorsally to join the lateral lemniscus (Fig. 5b-c). These fibers enter the torus semicircularis and terminate ventral to MLd at caudal levels, lateral and dorsal to MLd at more rostral levels (Fig. 5d-e; Fig. 6). The region of termination consists mostly of small, densely packed cells; it will henceforth be referred to as the external nucleus of the torus semicircularis. A smaller number of degenerating fibers were found to terminate ipsilaterally in the external nucleus.

Retrograde transport experiments

The retrograde transport of horseradish peroxidase (HRP) was used in order to determine the precise cells which give rise to the various ascending projections to MLd. HRP was injected into MLd in 13 pigeons. The extent of the deep brown reaction product at the injection site varied from 200 microns to several millimeters in diameter. The size of the fields of labeled cells did not always vary accordingly, and in one case no labeled cells at all were seen after an iontophoretic injection of HRP into MLd.

The results of the thirteen retrograde experiments are summarized in Table 1. After injections of MLd, cells containing the retrogradely transported enzyme were seen ipsilaterally in LLv, and contralaterally in MLd, VLVa, the superior olive, n. angularis, n. laminaris, cells interstitial to the radix of the cochlear-lagenar nerve, and the dorsal column nuclei. Occasionally a few cells were seen ipsilaterally in the
superior olive, NA, NL, and the dorsal column nuclei. No cells were ever seen in VLVP of either side.

One case -- PPE52 (survival 1 day) -- having three hydraulic injections centered in ventral parts of MLd and affecting most of the ascending projections to that nucleus will serve to delineate the full extent of input to MLd from the dorsal rhombencephalic auditory nuclei (NA, NM, and NL). In this animal, the injected enzyme also spread to the tectum, n. intercollicularis, n. semilunaris, the isthmic nuclei and VLVa. Labeled cells were found in all parts of nucleus angularis and nucleus laminaris (Fig. 7). Every neuron appeared to be labeled in n. laminaris, but only about one half of n. angularis' cells contained a visible label. The heavy labeling of n. laminaris in case PPE52 confirms our conclusion from anterograde material that this cell group projects primarily to MLd. However, in animals with more restricted injections of MLd, labeled cells were rarely found in the rostral part of n. laminaris, a fact which suggests that this region of NL may project more sparsely to MLd than do the more intermediate and caudal parts. Alternatively, the rostral part of n. laminaris may have been labeled by the spread of HRP to areas in the vicinity of MLd.

In contrast to the extensive retrograde labeling of n. angularis and n. laminaris, only a few cells were labeled in the contralateral n. magnocellularis in case PPE52. These labeled cells were found in the lateral and ventrolateral divisions of the cell group, but not in the rostral and medial parts. Nor were labeled cells found in n. magno-cellularis in any other case. These observations suggest either that n. magnocellularis projects very sparsely to MLd or that it projects instead to a nearby area.
Other labeled cells were seen contralateral to the injection in several areas; they were found dorsomedial and ventral to n. laminaris, in the region between NA and NL, and interstitial to the cochlear nerve. With the exception of the latter, these areas, along with the ventrolateral division of NM, receive projections from the macula lagena, an organ of as yet undetermined function, rather than from the auditory ganglion (Boord and Karten, 1974); their projection to the midbrain may convey input other than sound information to MLD (see discussion below).

Because the retrogradely transported HRP concentrates only weakly inside neuronal perikarya, the spread of label from the injection site in both the tissue and the ventricular system to the dorsal parts of the ipsilateral LLv and the contralateral MLD obscured labeled neurons in these areas. In fact, this problem was common to all cases with large injections and prevented a complete assessment of the extent of projections from the contralateral MLD. In addition, the mediocre perfusion in PPE52 results in poor preservation of many cores structures in that brain; as a result, the labeling in the superior olive, in particular, was obscured.

Other auditory areas labeled in PPE52 were the contralateral VLVa and ventral parts of the ipsilateral LLv. Labeled cells were also found in the dorsal column nuclei. Other areas with cells containing the reaction product included the dorsal and ventral divisions of the ipsilateral intermediate archistriatum, the ipsilateral n. ventralis thalami, and a cell group in the ipsilateral ventro-medial hypothalamus. These areas were never labeled after injections limited to MLD; they were probably labeled in this case because of spread of the enzyme to areas surrounding MLD (e.g., the tectum or n. intercollicularis).
In animals with smaller injections restricted to different parts of Mld, the location of cells labeled with HRP varied according to the placement of the injection. The results of these cases confirm the finding in the anterograde degeneration experiment that n. laminaris and n. angularis have separate representations within Mld. They also have indicated that NA projects topographically to Mld. Furthermore, they demonstrate that all parts of Mld and VLVa project to the contralateral Mld.

Case PPE1 (survival 2 days) best demonstrates the projection from nucleus laminaris to the rostro-medial division of Mld. In this animal the HRP was injected hydraulically (0.1 microliters of 7% HRP in saline). and was concentrated in a roughly straight track extending ventrally from the dorsal surface of the rostral Mld along its medial border with n. intercollicularis pars anterior (Fig. 8b-c). Labeled cells were seen in the contralateral nucleus laminaris, mostly at caudal levels, and in the region surrounding n. laminaris dorsally and ventrally (Fig. 8d).

The latter region extended to the borders of n. angularis, but few cells were labeled within NA proper. Some labeled cells were seen in the rostro-medial part of the contralateral Mld (Fig. 8b). No HRP was found in other auditory nuclei or in the dorsal column nuclei.

Nucleus intercollicularis is known to receive projections from the archistriatum (Nottebohm et al., in preparation; Zeier and Karten, 1971), where a few labeled cells were indeed found (Fig. 8a). In any given section there were only a few labeled cells; however, these neurons were confined to a similarly located restricted region in all the sections. Although this brain could not be precisely reconstructed in order to determine the longitudinal continuity of the labeled cells, this result
suggests that the archistriatum may contain longitudinally organized fields of cells projecting to restricted parts of n. intercollicularis.

Case PPE8 (survival 2 days) illustrates the topographic projection of n. angularis upon MLD and the contralateral projection to that cell group from a lateral lemniscal nucleus -- VLVa. This animal received a hydraulic injection of HRP (0.05 microliters, 20% HRP in water) in the caudolateral part of MLD (Fig. 9a-b). Labeled cells were found in the contralateral VLVa (Fig. 9c), and the contralateral n. angularis. Except for a few cells in the contralateral MLD, other auditory nuclei were not labeled. Labeled cells were confined to the dorsolateral part of n. angularis throughout its rostro-caudal extent (Fig. 9d).

In animal PPE9 (survival 1 day) other auditory afferents to MLD are revealed from the lateral lemniscal nuclei, the superior olive and n. angularis, as well as a somatosensory projection to the torus semicircularis. The HRP injection in this case was iontophoretic (2 microamps, 13 minutes pulsed current) and was centered in the caudal and medial region of MLD, extending to the caudal, medial, and ventral borders of the nucleus (Fig. 10a-b). Heavily labeled cells were found in the contralateral MLD, the ipsilateral LLv (Fig. 10c) and the superior olive. The contralateral VLVa was not labeled. Most of the labeled superior olivary neurons were located contralaterally, although a few ipsilateral cells were found (Fig. 10d).

Labeled neurons were seen contralaterally in the medial part of nucleus angularis, in the caudal n. laminaris and in the region between these two nuclei (Fig. 10e). The ipsilateral n. angularis, the rostral
contralateral n. laminaris and the contralateral locus coeruleus each contained one labeled cell. Four heavily labeled cells were also seen in the ipsilateral paleostriatum primitivum.

In the caudal hindbrain, labeled cells were found in the dorsal column nuclei (Figs. 10f, 11), mostly contralaterally. These were the only cell groups in the caudal hindbrain which contained labeled neurons after MLD injections, regardless of the size of the injection. Cells were never labeled in the dorsal column nuclei after restricted dorsal and rostral injections. On the basis of this result as well as the anterograde findings it appears that the external nucleus of the torus semicircularis receives a predominantly contralateral projection from the dorsal column nuclei.

A comparison of cases with small injections in MLD reveals much about the organization of afferents to MLD (Table 1).

In two cases, cells of origin for projections to MLD were seen either in n. laminaris (PPE1) or in n. angularis (PPE8), but not in both. Thus the retrograde data confirm the conclusion that inputs from these rhombencephalic auditory nuclei are segregated within MLD. In other animals of this series, cells in both cell groups accumulated the enzyme, probably because the injection affected more than one zone in MLD or incoming lemniscal fibers en route to other regions of MLD.

The results of five cases with restricted HRP injections in MLD (Table 1) show that the projection of nucleus angularis upon MLD is topographically organized. The dorsolateral part of n. angularis projects laterally in MLD, and the ventro-medial part of NA projects medially.
Cells were labeled contralaterally in MLD in 9 cases, sometimes in the region corresponding to the injection. In PPE1, for example, an injection in the rostro-medial MLD resulted in a labeling of neurons in the rostro-medial portion of the contralateral MLD (Fig. 8b). In PPE9 the injection was more caudal, and cells were found in the caudal and central parts of MLD as well as rostrally (Fig.10 a-b). The appearance of this projection seemed particularly sensitive to the quality of the perfusion. After large injections labeled cells were also obscured by spread of the label into the ventricular space (Table 1). Therefore the percentage of cells in MLD which have commissural connections could not be assessed.

In the lateral lemniscus, labeled cells were found ipsilaterally in LLv and contralaterally in VLVa after MLD injections. The former was labeled after more medial injections (e.g., PPE9), the latter after more lateral injections (e.g., PPE8 and PPE19); however, this distinction was not absolute. No projection to MLD was found from the 'dorsal nucleus of the lateral lemniscus' (LLd -- Karten and Hodos, 1967). This nucleus does not seem to be related to the lateral lemniscus at all, for it received no projections from the cochlear nuclei and n. laminaris in the anterograde material.

The data above suggest that the superior olive may have topographically organized connections with the dorsal rhombencephalic auditory nuclei and with MLD. Lesions of the rostral part of n. angularis gave rise to restricted degeneration in the ipsilateral superior olive. Partial injections in medial parts of MLD resulted in the labeling of restricted parts of the olive (Fig.10d, PPE9); larger injections caused a larger field
of cells to be labeled. Unfortunately, the case with the most complete injection (PPE52) was poorly perfused and cells in the superior olive were consequently obscured. Thus the full extent of superior olivary projections to MLD could not be determined. In some cases (e.g., PPE9 -- Fig.10d), a few superior olivary cells were found to project ipsilaterally to MLD. However, the predominance of contralateral input to MLD from the superior olive was not as great as it was from NL and NA.
Experiment II: Ascending Auditory Projection to n. Ovoidalis

Method

In order to determine the precise interrelationships of neurons in MLD and the thalamic nucleus n. ovoidalis, both anterograde degeneration and retrograde transport techniques were once again employed.

Anterograde degeneration experiments

Stereotaxic radio frequency lesions were made unilaterally in MLD and n. intercollicularis in four pigeons, using a dorsal surgical approach. Invariably the electrode penetration damaged the tectum and the caudal forebrain as well. Three of the animals were allowed to survive four days; the fourth was sacrificed after six days. The brains were prepared for staining with the Fink-Heimer I method (1967), as described above.

Control cases included animals with lesions of the cochlea, the cochlear nuclei, n. laminaris, the reticular formation, the cerebellum, the vestibular nuclei, the optic tectum and the dorsal column nuclei.

Retrograde experiments

Horseradish peroxidase (HRP)(Sigma Chemical Co., Type VI) was injected into n. ovoidalis of seven pigeons. The procedure for making and filling pipettes was the same as in Experiment I.

Six pigeons received iontophoretic injections of HRP. A hole 2-3 mm. in diameter was drilled in the calvarium. The forebrain was exposed and part of it suctioned off to reveal the thalamic surface. The pipette was then advanced stereotaxically to its target, where
HRP was electrophoresed continuously for 20-30 minutes (2 microamps, pipette polarity positive). The pipette was withdrawn, the ablated tissue replaced with gelfoam, and the head sealed with Autoclips (Clay-Adams) or Collodion. One day later the animals were sacrificed and their brains prepared for histology as described in Experiment I.

In the seventh animal, the injection was made hydraulically (0.1 microliters, 20% HRP in water) without ablating the overlying forebrain.

**Results**

In both the anterograde and the retrograde experiments, all parts of MLD, including the rostro-medial division, were found to project bilaterally to n. ovoidalis. These data also provide evidence that the projection from MLD upon n. ovoidalis is topographically organized.

**Anterograde degeneration experiments**

Lesions of MLD were made at the rostro-medial pole (2 cases), the caudal and lateral area (1 case), and the rostral and lateral part (1 case). These lesions were very large (1-2 mm diameter) and caused damage to surrounding structures, including parts of n. intercollicularis the central grey, the optic tectum, the mesencephalic reticular formation and parts of the overlying neostriatum caudale. No degeneration was seen in n. ovoidalis after the control lesions. On the other hand, after these large MLD lesions, extensive degeneration was found ipsilaterally in non-auditory areas of the thalamus, the isthmo-optic nucleus, and the midbrain tegmentum, bilaterally in the septum and the anterior commissure, and contralaterally in the paramedian nucleus. The origin of this degeneration
is either unknown or is non-auditory; consequently the analysis of data will be restricted to the degeneration in n. ovoidalis, which is known to receive auditory projections from MLD (Karten, 1967).

**Animal PA40** (survival 6 days) had a lesion which damaged MLD, the rostral part of n. intercollicularis, and the overlying tectum and forebrain. Within MLD, the lesion was confined mostly to the rostro-medial division (Fig. 12a). However, the degeneration in the contralateral MLD was located rostrally and laterally.

At the lesion site, a fiber bundle the brachium of MLD, emerged ventral to MLD and medial to n. isthmi parvocellularis (Fig. 12a). The brachium of MLD ascends dorsolateral to the ectomammillary nucleus (Fig. 12b) and bifurcates at the level of n. ovoidalis (Fig. 12c). One component of the brachium turns dorsally and enters the ipsilateral tractus ovoidalis; it terminates heavily in the ventral part of n. ovoidalis. The second component runs rostrally from the point of bifurcation and crosses to the contralateral diencephalon in the dorsal supraoptic decussation (Fig. 12d). The crossed component descends in the brachium of MLD; it enters the tractus ovoidalis contralateral to the lesion and terminates ventrally in n. ovoidalis (Fig. 12c). Sparse degeneration was also found on both sides in n. semilunaris parovoidalis (Fig. 12c). Thus, MLD appears to project bilaterally to homotopic zones in n. ovoidalis.

In three other cases, the pattern of degeneration in n. ovoidalis differed somewhat, but there was some overlap in the projections of different parts of MLD. In PA41 (4 day survival), the degeneration pattern was similar to PA40. The lesion was located more rostrally and ventrally than in PA40, but the terminal degeneration was restricted to caudal levels.
of n. ovoidalis. In PA42 (4 day survival) and PA43 (4 day survival) the lesions were in the rostro-lateral and caudo-lateral parts of Mld, respectively. In both cases the degeneration in n. ovoidalis was located mostly caudally and was entirely absent only dorso-medially. In these two cases, degeneration in the contralateral n. ovoidalis was considerably weaker than degeneration found ipsilaterally.

Details of the topography of projections from Mld to n. ovoidalis cannot be determined from these anterograde data because the exact trajectory of efferent fibers from Mld, and therefore the origin of the efferent fibers destroyed by the lesions, is unknown. However, it is clear that the binaural, rostro-medial division of Mld projects bilaterally to a restricted zone of n. ovoidalis. The fact that the contralateral projection to n. ovoidalis was weak in some cases but heavy in others remains unexplained by the data; different parts of Mld may project in different degrees to the contralateral side.

Similarly, little can be concluded from the anterograde data about the extent of commissural connections between the nuclei Mld of both sides. In only one case (PA40) was any degeneration seen in the opposite Mld, and that projection was not to the homotopic area (Fig. 11c).

Retrograde transport studies

Seven pigeons received HRP injections in various parts of n. ovoidalis. In all of these cases, labeled cells were found bilaterally in Mld. The location and extent of these neurons were dependent on the location and size of the injection in n. ovoidalis. In no case were labeled cells seen in the contralateral n. ovoidalis.
Animal PPE7 received the largest injection (hydraulically
(0.1 microliters), 20% HRP) (Fig.13a). The center of the injection was
located caudally and dorsally in n. ovoidalis, but label spread throughout
the entire extent of the nucleus, and tractus ovoidalis fibers were
heavily labeled as well. The pipette cut a wide track through structures
dorsal to n. ovoidalis, and HRP undoubtedly leaked into those areas.
As a result, cells were labeled not only in MLD, but also in the ipsilateral
archistriatum, n. commisuralis septi, the paleostriatum, and the deep tectal
layers. The nucleus reticularis superior of the thalamus was labeled
in both its dorsal and ventral subdivisions.

Labeled cells were found in MLD both ipsilaterally and contralaterally,
but the labeling was heaviest in the rostro-medial division on both sides
of MLD (Figs. 13b, 14). It was weaker laterally and at intermediate
levels of MLD, becoming heavier again at more caudal levels. The external
nucleus of the torus semicircularis was also heavily labeled. No
difference was found in the degree or extent of labeling between the
ipsilateral and contralateral sides, except for the external nucleus
of the torus semicircularis, where labeling was heavier ipsilaterally.

Some neurons in the most rostral and dorsal part of the ipsilateral
LLv were lightly labeled, and heavily labeled cells were found on both
sides in an adjacent laterally located parvocellular nucleus (not
previously described in the literature). However, no lateral lemniscal
neurons were labeled after restricted HRP injections of n. ovoidalis.

In one animal with a lesion extending from the lateral lemniscus
to n. sensorius principalis nervi trigemini (PX57, 6 days survival),
some degeneration was found in n. semilunaris parvooidalis. However, further
experimentation is needed to definitively establish both the origin of
the projection to n. semilunaris paraventralis and the thalamic target
of projections from the region of the lateral lemniscus.

In six other cases, iontophoretic injections of HRP were made
in restricted parts of n. ovoidalis.

In PPE43 (1 day survival) the injection was located ventrally
and caudally in n. ovoidalis and extended ventrally to n. semilunaris
paraventralis and n. subrotundus (Fig. 15b). Cells labeled in MLD were
confined to the rostro-medial division (Fig. 15c). No difference was
seen in labeling between the ipsilateral and the contralateral
sides, and the external nucleus was not labeled on either side. This
result agrees with the anterograde degeneration data from lesions restricted
to the rostro-medial pole of MLD (case PA40; Fig. 11).

Some cells were also labeled in the ipsilateral n. reticularis
superior pars dorsalis (RSd) (Fig. 15a).

In PPE47 (1 day survival) the injection was confined to the
dorsal region of n. ovoidalis (Fig. 16a). Labeled cells were located
caudally in MLD (Fig. 16b); slightly more cells were labeled ipsilaterally
than contralaterally.

A comparison of these two cases suggests that the rostro-medial
division of MLD is represented ventrally, whereas more caudal levels
of MLD are represented more dorsally in n. ovoidalis.

The results of cases with HRP injections in n. ovoidalis are
summarized in Table II. They confirm the finding that MLD projects
topographically upon n. ovoidalis. However, these data provide little
further information about the details of this topography, because
restricted injections of the lateral parts of n. ovoidalis and of n. semilunaris par.ovoidalis were not made. Furthermore, adequate anterograde data are lacking about the course and distribution within n. ovoidalis of tractus ovoidalis fibers from different parts of MLD. The results of HRP injections in n. ovoidalis may therefore be complicated by a fiber of passage problem within n. ovoidalis which can obscure existing topographic relationships.

**Summary of Results**

The ascending projections of the avian auditory system are summarized schematically in Figure 17. The cochlear-lagenar nerve enters the dorsal rhombencephalon and projects topographically upon the ipsilateral nucleus angularis (NA) and nucleus magnocellularis (NM) (Boord and Rasmussen, 1963). A third dorsal rhombencephalic structure, n. laminaris (NL) receives bilateral secondary projections from n. magnocellularis and is also tonotopically organized (Rubel and Parks, in press). N. angularis and n. laminaris (and perhaps n. magnocellularis) project to the ipsilateral superior olive. The data also indicate that n. angularis may project topographically upon the superior olive.

N. angularis and n. laminaris differ in their ascending projections beyond the superior olive. NL projects via the contralateral lateral lemniscus to terminate heavily in the rostro-medial, parvocellular division of the contralateral MLD, the avian homologue of the mammalian inferior colliculus; NA projects via a similar route to the remainder of MLD. Among the lateral lemniscal nuclei, only VLV pars anterior (VLVa) receives a heavy projection from NL. In contrast, NA
projects heavily upon the nuclei of the lateral lemniscus -- bilaterally in the posterior VLV (VLVp), and contralaterally in LLv and VLVa.

Retrograde studies of afferents to MLD confirm the finding of the anterograde degeneration studies that binaural inputs (from NL) and monaural inputs (from NA) are represented in distinct subnuclei of MLD. They also show that the projection of NA upon MLD is topographic, and indicate that the superior olive may also project topographically upon MLD. Afferents to MLD from regions caudal to the trapezoid body (n. angularis, n. laminaris, and superior olive) are predominately contralateral. More rostrally, LLv projects ipsilaterally to MLD, VLVa contralaterally, and VLVp apparently not at all.

A further input to the torus semicircularis originates in the dorsal column nuclei of the somatosensory system. These nuclei project to the external nucleus of the torus semicircularis, a cytoarchitecturally distinct region which surrounds MLD.

Further experiments using both anterograde and retrograde methods have shown that MLD projects bilaterally and topographically upon n. ovoidalis, the avian thalamic auditory relay. The binaural, dorso-medial division of MLD projects to a restricted zone in the ventral part of n. ovoidalis. The monaural division of MLD also projects to n. ovoidalis; however the existence of a topography in this connection could not be determined from the data. In addition, the external nucleus of the torus semicircularis also projects to the dorsal or ventro-dorsal thalamus.

Other afferents to n. ovoidalis originate in n. reticularis superior pars dorsalis of the thalamus.
Discussion

The foregoing results have shown the ascending auditory system of the pigeon to be comprised of several discrete channels originating in different dorsal rhombencephalic auditory nuclei. These channels remain anatomically segregated at the mesencephalic level and probably at the diencephalic level as well. Binaural cells in n. laminaris and monaural cells in n. angularis send parallel ascending projections which terminate in distinct subnuclei of the contralateral MLD; both subnuclei project in turn to n. ovoidalis, the thalamic auditory relay. The projection from MLD to n. ovoidalis is topographic and apparently preserves the segregation of information present both at rhombencephalic and mesencephalic levels.

A third channel of input to the region of MLD originates in the dorsal column nuclei and is represented separately in the contralateral external nucleus of the torus semicircularis. This somatosensory nucleus also sends projections to the thalamus.

Other, more indirect auditory system connections to MLD arise from the ipsilateral superior olive, the ipsilateral ventral nucleus of the lateral lemniscus (LLv) and the contralateral nucleus ventralis lemnisci lateralis pars anterior (VLVa), the most dorsal nucleus of the lateral lemniscus. All of these nuclei receive input from NA and NL (and perhaps NM). Additional afferents to n. ovoidalis were noted from the thalamic nucleus reticularis superior pars dorsalis.

The existence of a tonotopic organization appears to be a consistent feature at all levels of the auditory system. Electrophysiological experiments by Konishi (1970) and Rubel and Parks (in press) as well as anatomical experiments (Boord and Rasmussen, 1963; Parks and Rubel, in press) have
shown that n. magnocellularis, n. laminaris and n. angularis each contains a tonotopic representation. The auditory area of the forebrain (Field L of the neostriatum caudale) contains a tonotopic map (Konishi and Zaretsky, personal communication), and one might therefore expect a similar kind of frequency representation at the level of MLD and n. ovoidalis. The results of the present study demonstrate that the projection of n. angularis upon MLD does indeed preserve the tonotopic map of NA; because some topographic organization was found in the projection of MLD upon n. ovoidalis, it is likely that the latter nucleus also contains such a representation. Nucleus laminaris is also tonotopically organized, and it seems possible that the binaural channel which originates in this nucleus may be organized in a similar fashion. The fact that small HRP injections in MLD often resulted in a localized pattern of retrogradely labeled neurons in n. laminaris supports this hypothesis.

Cells in the caudalmost part of n. laminaris and in the area between n. angularis and caudal NL accumulate NRP after injection of the enzyme in the contralateral rostro-medial division of MLD (Fig. 7d). These regions receive projections from the macula lagenae rather than from the Organ of Corti (Boord and Karten, 1974). Rubel and Parks (in press) could not find any units responsive to sound in the 0.1 - 5.0 kHz range in this zone and in the ventro-lateral division of n. magnocellularis, which also receives lagenar projections (Boord and Karten, 1974). They suggest that these areas be re-named "n. lagena ris". In contrast to other parts of this region which project heavily to MLD, the ventro-lateral division of n. magnocellularis projects only very lightly upon MLD, if at all as is the case for (auditory) lateral division of NM.
At the present time, the function of the lagena is unknown. On the basis of its primary projections in the brainstem, the lagena has been said to be both auditory and vestibular in function (Schwartzkopff, 1968). The "auditory" lagernar region of the brainstem lies adjacent to the parts of n. laminaris and n. angularis which receive low frequency input; it projects in turn to a region in MLD receiving input from the caudal, low frequency region of NL. Thus the "auditory" lagernar system may be concerned with extremely low frequency sound. The functional significance of this type of perception is underscored by the fact that Kreithen (personal communication) has been able to condition homing pigeons to respond to infrasound stimuli with frequencies as low as 0.25 Hz; the conditioned response is eliminated after removal of the cochlea and the lagena.

The fact that MLD receives almost entirely contralateral projections from structures caudal to the lateral lemniscus and ipsilaterally from LLv excludes these structures from playing a major role in the bilateral convergence of auditory information. The commissural connection between the nuclei MLD provides one route for binaural convergence at the level of MLD. VLWa, which receives projections from the contralateral dorsal rhombencephalic auditory nuclei, projects to the contralateral MLD and may contribute to binaural convergence at the level of MLD. Further bilateral convergence occurs in n. ovoidalis as a result of its bilateral afferentation from MLD. The functional significance of these convergences and re-convergences is not known; further electrophysiological data are needed to establish the nature of the bilateral influences on neurons in MLD and n. ovoidalis.
The pattern of connections to and from the nuclei of the lateral lemniscus is particularly complex. One nucleus, n. VLV pars posterior, receives bilateral projections from n. angularis; yet it does not project to MLD. The largest nucleus of the group, LLv, receives projections from the contralateral n. angularis and projects ipsilaterally to MLD. However, the most rostral and dorsal of these nuclei, VLV pars anterior, receives projections from both NA and NL of the contralateral side and projects in turn to the contralateral MLD. A fourth nucleus, the "dorsal nucleus of the lateral lemniscus" (LLd of Karten and Hodos, 1967 and Boord, 1968) receives no projections from brainstem auditory nuclei and does not project rostrally upon MLD; no other connections of this nucleus are known. Therefore, LLd is probably not an auditory nucleus at all.

VLVa and VLVP are distinct both in their location and their connections and should thus be considered as separate cell groups. The latter is probably a part of the ventral lateral lemniscus (or the trapezoid complex). The former, rather than LLd, should be considered the true dorsal nucleus of the lateral lemniscus, for like its mammalian counterpart, it is located dorsally in the lemniscal complex and has contralateral projections to the inferior colliculus (Stötler, 1953; Goldberg and Moore, 1967).

In addition to its afferentation from MLD, nucleus ovoidalis also receives projections from the nucleus reticularis superior thalami. Reticularis superior (RS) lies in the anterior lateral diencephalon within the fasciculus prosencephali lateralis. Benowitz and Karten (in press) have shown that the dorsal nucleus, RSd, projects upon n. rotundus, the major thalamic target of visual efferents from the tectum, whereas
RSv projects to thalamic structures dorsal to the sulcus of Herrick. The data in this study confirm Benowitz and Karten's conclusion that RSd projects only to thalamic structures ventral to the sulcus of Herrick. The projection from RS to specific thalamic nuclei may represent a feedback mechanism for biasing the response properties of thalamic populations, as has been argued for similar projections described in mammals (Scheibel and Scheibel, 1966; 1967).

Validity and interpretation of results

The investigation of the avian auditory system by both anterograde and retrograde methods has allowed some comparison of the relative sensitivity of these two techniques. The HRP technique proved, on the whole, to be sensitive even to nuances of projections that seemed to be sparse in the Fink-Heimer material. An example of this is the projection from nucleus angularis to MLD, which is known from HRP material to be highly organized topographically, but which appeared to be sparse in anterograde degeneration cases.

However, the data of these HRP studies suggest that the effective injection site is generally smaller than the total area of tissue colored deep brown with the reaction product. For example, in one case, the entire mesencephalon was brown with reaction product, yet the dorso-lateral part of n. angularis, known from more restricted injections to project to MLD, failed to be labeled. On the other hand, a more localized injection, carefully placed at different locations within lemniscal fibers entering MLD, succeeded in labeling all parts of NA. Thus, in interpreting data from HRP experiments, one must be careful not to overestimate the effective injection site. These facts do not, however, exclude the
possibility that axons of other neuronal systems might transport HRP from areas containing the enzyme which are not immediately adjacent to the location of the pipette tip.

Functional correlates of anatomical organization in the avian auditory system

The results of this study demonstrate that the major organizational features present at lower levels of the auditory system are preserved at mesencephalic and diencephalic levels. In addition, studies of single unit responses in the telencephalic projection zone, Field L, suggest that at least some of these properties are preserved there as well. Information from binaural (NL) and monaural (NA) brainstem structures continues to be segregated into separate subnuclei of MLd and may be similarly segregated within n. ovoidalis. Furthermore, nuclei at all levels of the auditory system apparently are organized tonotopically.

The electrophysiological responses of neurons in the binaural channel have been studied in detail only at the rhombencephalic level. In a study of single unit responses in nucleus laminaris of the chick, Rubel and Parks (in press) found that most units were excited equally by either ear and often responded in phase with the auditory stimulus. Parks and Rubel (in press) further propose that for a given characteristic stimulus frequency NL neurons respond best to an optimal interaural time difference based on their position along the medial-lateral axis of n. laminaris. The results reported above suggest that some units at higher levels of the auditory system may preserve information based on interaural time differences and may be further specialized for other kinds of information based on binaural convergence.
The importance of this function in birds is underscored by the fact that several species are specialized for the binaural localization of sound. The oilbird (*Steatornis caripensis*) and the swiftlet of bird's nest soup (*genus Collocalia*) (Griffin, 1958) find their way in total darkness by echolocation. Some owls (e.g., *Tyto alba*) can strike a mouse in total darkness (Payne, 1962) and have asymmetrical external ears which can accentuate interaural time differences (Schwartzkopff, 1968; Erulkar, 1972). The enlargement of NL in such species (Schwartzkopff, 1968; Leibler, unpublished observation) probably reflects the increased importance of processing interaural time differences. It would be interesting to note whether the area of MLD which receives direct projections from NL is also correspondingly enlarged.

The representation of different auditory channels in distinct subnuclei of MLD and probably n. ovoidalis as well is similar to the situation found in the tecto-fugal visual system (Benowitz and Karten, in press). Cells lying at different depths in the stratum griseum centrale of the optic tectum project upon distinct divisions of nucleus rotundus thalami. The continuing segregation of different information processing channels at higher levels of the brain may be a feature common to at least parts of all sensory systems in vertebrates.

Some features of the processing of frequency-encoded information are preserved at higher levels, whereas others show evidence of "re-processing". Information about stimulus frequency is represented topographically in NA (Konishi, 1970), NM (Konishi, 1970; Rubel and Parks, in press), NL (Rubel and Parks, in press), MLD (this study) and Field L (Konishi and Zaretzky, personal communication). However, the nature of the information
represented by these tonotopic maps increases in complexity at higher levels. Although neurons in NA respond readily to pure tone stimuli, most Field L units fail to respond to pure tones and prefer more complex stimuli (Biederman-Thorson, 1970; Leppelsack, 1974). This fact suggests that at each level of the auditory system frequency-encoded information is subjected to a process of integration and recombination whose end result is a complex representation of auditory stimuli.

The ability of birds to extract complex auditory information from incoming signals is apparently a necessary condition for normal behavioral development in some species. Young chaffinches and other songbirds are unable to develop their normal song if they have been deafened or isolated from other individuals of their species (Nottebohm, 1970; Nottebohm and Nottebohm, 1971); a conspecific model is required for proper song development (Nottebohm, 1972). Unfortunately, the anatomical pathways by which auditory input affects the development of bird song have yet to be examined, even though the anatomical pathways underlying both auditory function and song production have been studied in detail (Nottebohm et al., in preparation).

Comparisons with the mammalian auditory system

In mammals, as in birds, nuclei at all levels of the auditory system are involved in the processing of cues for auditory localization and are organized tonotopically.

Electrophysiological experiments have shown that units responding preferentially to interaural time or intensity differences can be found at all levels of the auditory system from the superior olive onwards (Goldberg and Brown, 1969; Boudreau and Tsuchitani, 1968; Rose et al.,
1966; Brugge et al., 1970; Aitkin and Webster, 1972; Brugge et al.,
1969; Brugge and Merzenich, 1973). One study (Brugge and Merzenich,
1973) even suggested that columns of cells exist in the cortex, each
column of which is sensitive to one interaural time difference.

In these studies, auditory frequency differences were found to be
represented tonotopically at all levels of the auditory system.
Neurons sensitive to interaural phase differences generally respond best
to low frequency sounds (Guinan et al., 1972); neurons sensitive to
interaural time differences respond best to higher frequencies. Because
of the tonotopic organization of auditory nuclei, neurons sensitive to
interaural phase differences tend to be segregated into the low frequency
region of a nucleus; thus, for example, these neurons are present only
in the dorso-medial tip of the inferior colliculus (Rose et al., 1966).
The medial superior olive (MSO) which is specialized for detecting
interaural time differences has a preponderance of low frequency neurons;
the lateral superior olive contains a high proportion of high frequency
neurons.

Behavioral studies of animals with selected lesions show that
structures at all levels of the mammalian auditory system are involved
in the processing of cues for sound localization. In cats, localization
disorders, including the animal's inability to respond to interaural
time difference cues, result from destruction of the lateral lemniscus
(Masterton, Jane and Diamond, 1967), the inferior colliculus and its
brachium (Masterton, Jane and Diamond, 1968; Erulkar, 1972) and the
auditory cortex (Masterton and Diamond, 1965; Neff et al., 1956).
Suga (1969a) has shown that bilateral ablation of the inferior colliculus
in blinded Yuma bats abolishes the bats' ability to avoid obstacles by echolocation; however this behavior is not systematically eliminated in this species after bilateral ablation of the auditory cortex (Suga, 1969b).

Similar behavioral and physiological data are generally not available for birds; however, several parallels are apparent in the anatomical organization of mammalian and avian auditory systems (Table III). The medial superior olive (MSO), the homologue of NL (Cajal, 1908), receives a heavy projection on its medial aspect from the contralateral spherical cell region of the anteroventral cochlear nucleus (AVCN) (homologous to NM) and from the ipsilateral AVCN on its corresponding lateral aspect (Warr, 1966). The MSO projects heavily to the inferior colliculus (Stotler, 1953), as do parts of the cochlear nuclei (Osen, 1972; Warr, 1969; 1972). Both ipsilateral and contralateral projections exist from the lateral lemniscal nuclei to the inferior colliculus (Goldberg and Moore, 1967); the dorsal nucleus of the lateral lemniscus (like VLVa in birds) projects contralaterally to the inferior colliculus via the commissure of Probst (Stotler, 1953; Goldberg and Moore, 1967). Two zones of the inferior colliculus contain somatosensory representations: the intercollicular region (input from the spinal cord — Mehler, 1969) and the external nucleus (input from the dorsal column nuclei — Jane and Schroeder, 1971).

Although further anatomical details are not available, the mammalian and avian auditory systems seem more notable for their similarities than for their differences. Both classes of animals have parallel patterns of auditory projections, and auditory nuclei in both mammalian and avian
auditory systems are tonotopically organized. The finding that n. laminaris projects heavily to a restricted part of MLd, which in turn projects to a limited part of n. ovoidalis suggests yet another parallel -- that units in the midbrain and thalamus of birds may respond to optimal interaural time differences, as do units in the inferior colliculus and the medial geniculate body of mammals (Rose et al., 1966; Aitkin and Webster, 1972).

Conversely, the similarities between the auditory systems of birds and mammals suggest that the ascending auditory pathways of mammals may likewise be organized into discrete and parallel anatomical channels. These pathways may originate in rhombencephalic auditory nuclei which process different kinds of auditory information. Electrophysiological data have already indicated that one such channel, originating in the MSO and specialized for processing interaural time differences, is anatomically segregated in the dorso-medial part of the inferior colliculus of the cat (Rose et al., 1966; Guinan et al., 1972).

In conclusion, the organization of neural information into parallel ascending channels may be a general feature of the vertebrate auditory system. This hypothesis has already been demonstrated for the avian auditory system (this study); it is also valid for the tectofugal visual system of birds (Benowitz and Karten, in press). Future anatomical studies may likewise demonstrate that some sensory systems in other classes of vertebrates, including mammals, are also organized into anatomically discrete parallel ascending channels, each of which conveys a different aspect of sensory information.
References


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TABLES

Table I. HRP injections in MLd in 13 cases and the resulting pattern of retrograde labeling of neurons. Abbreviations: hyd = hydraulic, ion = iontophoretic injection; C = contralateral, I = ipsilateral labeling; *** = heaviest labeling, ( ) = a very small number of labeled neurons, \( \chi \) = amount of labeling could not be determined due to poor perfusion or spread of label. Other abbreviations are as in Table 4.

Table II. HRP injections in n. ovoidalis in 7 cases and the resulting pattern of retrograde labeling. Abbreviations as in Table 1.

Table III. Avian auditory nuclei and their mammalian homologues.

Table IV. List of abbreviations.
<table>
<thead>
<tr>
<th>INJECTION SITE</th>
<th>DESCRIPTION</th>
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<tr>
<td>PPE52 large, multiple hyd</td>
<td></td>
</tr>
<tr>
<td>PPE50 very large, 7 injections hyd</td>
<td></td>
</tr>
<tr>
<td>X*** C**** XI*** XI** C* C*</td>
<td></td>
</tr>
<tr>
<td>X*** C*** XI*** XI** C* C*</td>
<td></td>
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<tr>
<td>X* * C** C** C** C**</td>
<td></td>
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<tr>
<td>X* * C** C** C** C**</td>
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<tr>
<td>X* * C** C** C** C**</td>
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<tr>
<td>X* * C** C** C** C**</td>
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<tr>
<td>X* * C** C** C** C**</td>
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<tr>
<td>(I)</td>
<td>A31, 2</td>
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<tr>
<td>(I)</td>
<td>A32</td>
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TABLE II.

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<th>LLv</th>
<th>ToS</th>
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<td></td>
<td></td>
<td></td>
<td>dorsal</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>ventral</td>
<td></td>
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<tr>
<td>PPE7</td>
<td>large in Ov; dorsal thalamus; habenula</td>
<td>hyd</td>
<td>***</td>
<td>**</td>
<td>C***</td>
<td>C**</td>
<td>I*</td>
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<tr>
<td>PPE38</td>
<td>ventral and lateral, poor perfusion</td>
<td>ion</td>
<td></td>
<td></td>
<td>C*</td>
<td>I*</td>
<td>(C)</td>
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<td>PPE43</td>
<td>ventral in Ov; SPO; SRT</td>
<td>ion</td>
<td>**</td>
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<tr>
<td>PPE47</td>
<td>dorsal and medial</td>
<td>ion</td>
<td>( )</td>
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<td>PPE48</td>
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<td>PPE54</td>
<td>dorso-medial</td>
<td>ion</td>
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**TABLE III.**

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<td></td>
<td>and dorsal cochlear nucleus</td>
<td>Cajal, 1908</td>
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<td>n. magnocellularis (NM)</td>
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<td>pars medialis and pars lateralis</td>
<td>anteroventral cochlear nucleus</td>
<td>Boord, 1968</td>
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<td>pars ventrolateralis</td>
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<td>n. laminaris (NL)</td>
<td>medial superior olive</td>
<td>Cajal, 1908</td>
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<tr>
<td>Superior olive (OS)</td>
<td>lateral superior olive (?)</td>
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<td>n. lemnisci lateralis, pars ventralis (LLv)</td>
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<tr>
<td>pars posterior (VLVp)</td>
<td>ventral n. of the lateral lemniscus (?)</td>
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<tr>
<td>pars anterior (VLVa)</td>
<td>dorsal n. of the lateral lemniscus</td>
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<td>inferior colliculus (central nucleus)</td>
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<td>pars dorsalis (MLd)</td>
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<td>this study</td>
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<tr>
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<td>(and n. intercollicularis [?])</td>
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<td>n. ovoidalis (Ov)</td>
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<td>Karten, 1967</td>
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<td>Field L</td>
<td>auditory I cortex, layer 4</td>
<td>Karten, 1968</td>
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<td>Abbreviation</td>
<td>Description</td>
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<tr>
<td>Ad</td>
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<td>Commissure of Probst</td>
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<tr>
<td>CT</td>
<td>Commissura tectalis</td>
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<td>CTz</td>
<td>Trapezoid body</td>
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<td>DSV</td>
<td>Decussatio supraoptica ventralis</td>
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<td>EM</td>
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<td>GC</td>
<td>Nuclei gracilis et cuneatus (dorsal column nuclei)</td>
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<td>Hyperstriatum ventrale</td>
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<td>Ov</td>
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<td>PA</td>
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<td>PP</td>
<td>Paleostriatum primitivum</td>
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<tr>
<td>PrV</td>
<td>Nucleus sensorius principalis nervi trigemini</td>
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<td>Substantia grisea et fibrosa periventricularis</td>
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<td>Nucleus subrotundus</td>
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<td>TOv</td>
<td>Tractus ovoidalis</td>
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<td>Nucleus tegmenti pedunculo-pontis, pars compacta</td>
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<td>TTD</td>
<td>Nucleus et tractus descendens nervi trigemini</td>
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<td>VeL</td>
<td>Nucleus vestibularis lateralis</td>
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<td>VeS</td>
<td>Nucleus vestibularis superior</td>
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<td>Nucleus ventralis lemnisci lateralis, pars anterior</td>
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<td>VLVP</td>
<td>Nucleus ventralis lemnisci lateralis, pars posterior</td>
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FIGURE LEGENDS

Fig. 1. Low power photomicrographs of auditory nuclei in the pigeon.
Nissl stain. Dashed lines in insets enclose area shown in photos.
Bar: 200μ

a. Nucleus angularis (NA), n. laminaris (NL) and n. magnocellularis
(NM), shown in transverse section.
b. Transverse section through n. ovoidalis. Ov = n. ovoidalis;
SPo = n. semilunar is parvoaudalis; SRT = n. subrotundus.
c. Sagittal section through the lateral lemniscal nuclei.
LLv = n. lemnisci lateralis pars ventralis; PrV = n. sensorius
principalis nervi trigemini; VLVa = n. ventralis lemnisci lateralis,
pars anterior; VLVP = n. ventralis lemnisci lateralis, pars posterior.

Fig. 2. Transverse sections of lesion of n. laminaris in case PA33
and resulting degeneration in auditory nuclei. See text for
description of case. Not shown: degeneration in the contralateral
n. ruber and n. nervi oculomotorii, pars ventralis. In this figure
and those which follow fiber degeneration is represented by lines,
terminal degeneration by dots. Triangles= fiber degeneration
coursing perpendicular to the plane of section.

Fig. 3. Degeneration in MLD following lesions of n. laminaris is confined
to the rostro-medial division of MLD (Fink-Heimer I stain).
a. Low power photomicrograph of transverse section showing
degeneration in the rostro-medial division of MLD (case PA14).
Area enclosed in dashed lines on inset is shown in photo. Bar: 200μ
b. High power view (40X objective) of degeneration in a. Bar: 20μ
c. Medium power view (20X objective) of sagittal section of MLD (case PA3). Degeneration is confined to the area on the left, located rostrally in MLD (see inset). Bar: 50μ

Fig. 4. Transverse sections of lesion of n. angularis and subsequent degeneration in auditory nuclei (case PA38). See text for description of case. Not shown: degeneration in the contralateral n. nervi oculomotorii, pars dorsalis, bilaterally (albeit mostly ipsilaterally) in n. parapincipalis lateralis. In this figure and subsequent ones, the lateral border of the rostro-medial division of MLD is indicated at rostral levels by a dashed line. Bar: 1 mm.

Fig. 5. Transverse sections of a lesion of the caudal hindbrain, and subsequent degeneration in the midbrain in case PX77. See text for a description of the case. Degeneration ascending to the thalamus is not shown. Bar: 1 mm.

Fig. 6. Medium power photomicrograph of degeneration in Fig. 5d. Arrows indicate the border of the external nucleus of the torus semicircularis, where the degeneration is found. MLD, however, is free of degeneration. (Fink-Heimer I stain). Area enclosed by dashed lines in inset is shown in photo. Bar: 50μ

Fig. 7. Dark field photomicrograph showing cells labeled in n. angularis and n. laminaris after a large HRP injection into MLD (case PPE52). Bar 1 mm.
Fig. 8. In case PPE1, an HRP injection in the rostro-medial division of MLd (indicated by arrow in b) resulted in labeling of cells in the contralateral n. laminaris (d -- filled circles). Cells in the ipsilateral archistriatum (a) and the contralateral MLd (b) are also labeled. Bar: 1 mm.

Fig. 9. Injection of HRP into the caudo-lateral part of MLd (case PPE8) results in labeling of neurons in the contralateral VLVa and n. angularis. Bar: 1 mm.

Fig. 10. Injection of the caudal and medial MLd with HRP and subsequent labeling of neurons (case PPE9). See text for description of case. Bar: 1 mm.

Fig. 11. Labeled cells in the contralateral dorsal column nuclei in case PPE9. Medium power photomicrograph (0.0 X objective) taken from the same section as Fig. 10f. Bar: 80μ

Fig. 12. Transverse sections of a lesion of MLd and subsequent degeneration in the thalamus (case PA40). See text for a description of the case. Not shown are a projection to the septum and a descending projection. Bar: 1 mm.

Fig. 13. Transverse sections showing a large HRP injection into n. ovoidalis (animal PPE7) which resulted in bilateral labeling of cells in MLd and the external nucleus of the torus semicircularis (compare with Fig. 5d). Bar: 1 mm.
Fig. 14. Dark field photomicrograph of labeled cells in the rostro-medial division of MLd after injection of the contralateral n. ovoidalis (case PPE7). The labeling pattern was similar in MLd ipsilateral to the injection. Bar: 80μ.

Fig. 15. Labeling in MLd (c) and RSd (a) following an HRP injection in n. ovoidalis (restricted to the ventral division) and in n. semilunaris parovoidalis (b) (Case PPE43). See text for further description. Bar: 1 mm.

Fig. 16. A dorsally placed HRP injection of n. ovoidalis results in cells being labeled in caudal parts of MLd (case PPE47). Bar: 1 mm.

Fig. 17. The avian auditory system — hindbrain, midbrain, and thalamus. The view is a 'shadowcast' reconstruction projected onto a dorsal surface view of the pigeon brain, with the cerebellum and forebrain removed. Ascending auditory pathways are indicated schematically. (See text for detailed explanation.)
Fig. 1 (c)
Fig. 8
Fig. 16