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The Efferent Projections of the Central Nucleus and the Pericentral Nucleus of the Inferior Colliculus in the Cat

RICHARD A. ANDERSEN, G. LINN ROTH, LINDSAY M. AITKIN, AND MICHAEL M. MERZENICH
Departments of Physiology and Otolaryngology, Coleman Laboratory-863 HSE, University of California, San Francisco, California 94143

ABSTRACT The efferent projections of the central nucleus of the inferior colliculus (ICC) and the pericentral nucleus of the inferior colliculus (ICP) were examined by placing restricted injections of anterograde tracers at electrophysiologically defined loci in the inferior colliculus (IC) of the cat.

It was found that single loci in the ICC projected bilaterally onto the ventral division of the medial geniculate body (MGB) in the form of caudorostrally oriented sheets of terminals. The ICC loci also projected bilaterally onto the MGB in the form of caudorostrally oriented columns of terminals; these columns had their caudal aspects located in the medial division and their rostral aspects located in the deep dorsal nucleus of the dorsal division. The caudal aspect of the sheets of terminals in the ventral division was folded and passed through both pars lateralis and pars ovoidea of the ventral division. Every component of the ICC-to-MGB projection was cochleotopically ordered. Periodic discontinuities of two types were noted in the projections of the ICC onto pars lateralis (Vl) of the ventral division. The one type of periodic discontinuity sometimes approximated bands oriented caudorostrally in the caudal aspect of Vl. The second type of discontinuity was of very thin parallel columns of more intense labeling oriented roughly dorsoventrally and oblique or normal to the first type of discontinuity.

Injections in the ICP produced autoradiographic labeling in the caudal dorsal nucleus (Dc) of the dorsal division of the MGB. Thus the ICC-to-MGB and ICP-to-MGB projections are segregated.

The efferent connections of the IC with other brainstem auditory structures were noted.

There is now a substantial body of knowledge concerning the details of the thalamocortical and corticothalamic connections of the auditory system. Numerous anatomical investigations in the cat and tree shrew have indicated that there are parallel systems of connections between the various auditory cortical fields and the auditory thalamus (Rose and Woolsey, '58; Diamond et al., '58; Morest, '65a, b; Casseday et al., '76; Graybiel, '72, '73; Winer et al., '77; Oliver and Hall, '78b; Andersen, '79; Andersen et al., '80). Recent findings indicate that repeating subunits in the first auditory cortical field (AI) receive and give thalamocortical and corticothalamic connections from and to repeating parallel bands in the morphologically laminated parts of the ventral division of the medial geniculate body (MGB) of the cat (Andersen et al., '80).

The findings of parallel systems of connections and periodic discontinuities of connections between the MGB and cortex raise questions about the organization of projection of the inferior colliculus onto the MGB. How do the spatial distributions of the parallel tectothalamic terminal fields within the MGB relate to the spatial distributions of the MGB neurons of the parallel thalamocortical systems? What is the relation of the pattern of

Send correspondence to: Richard A. Andersen, Department of Physiology, The Johns Hopkins University, School of Medicine, 725 N. Wolfe St., Baltimore, Md. 21205.

Dr. Roth's present address is Department of Neurophysiology, University of Wisconsin, Madison, WI

Dr. Aitkin was on leave from the Department of Physiology, Monash University, Clayton, Australia.

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the ascending collicular projections to the repeating bands of the MGB-AI connections?

To answer these and other questions, it is important to know the fine details of the projection of the inferior colliculus (IC) onto the MGB. It has been shown both anatomically (Berman, '68; Geniec and Morest, '71; Rockel, '71; Rockel and Jones, '73a, '73b) and physiologically (Aitkin et al., '75, '78; Merzenich and Reid, '74; Rose et al., '63; Roth et al., '78) that the IC is composed of several subdivisions differing in their afferent connections and functional properties. However, previous studies in the cat provide little information about the detailed form and systematic topography of the projections of these various IC divisions onto the MGB (Woollard and Harpman, '40; Moore and Goldberg, '63; Powell and Hatton, '69; Van Noort, '69; Jones and Powell, '71; Kudo and Niimi, '78).

In order to study these projections in more detail, we have made small injections of anterograde tracers into the IC (Cowan et al., '72), and thus eliminated problems such as damage to fibers of passage inherent in the previously employed anterograde degeneration techniques. All injection sites in the central nucleus of the inferior colliculus were identified electrophysiologically in terms of the cochleotopic organization of the nucleus. Thus, it was also possible to study the systematic topography of the ICC-to-MGB projection as a function of the tonotopic organization of the central nucleus.

METHODS

Anterograde (and retrograde) tracing experiments were performed in 19 animals. The methods used in these experiments have been published in detail elsewhere (Roth et al., '78; Andersen et al., '80). Briefly, adult cats were anesthetized with sodium pentobarbital (40 mg/kg). The IC was exposed by removing the occipital cortex and bony tentorium cerebelli. Limited microelectrode recording maps were made of the tonotopic organizations of the pericentral (ICP) and central nuclei (ICC) of the inferior colliculus. After a sufficient map was obtained, a Hamilton microsyringe with a varnished 28-gauge needle was lowered into the IC. Evoked multiunit activity was recorded from the unvarnished tip of the needle. A good correlation was generally found between the best-frequency representational site previously determined by the microelectrode recording technique for a particular depth in the IC and the best frequency recorded at that depth through the syringe needle. Injections of .1 to .5 μl solutions of combined tracers, 3H-1-leucine (10 μC/μl), and horseradish peroxidase (HRP) (40%) dissolved in sterile saline were made only at tonotopically defined loci. The needle was left in position for 15 to 30 minutes after injection.

After 24 to 48 hours, the cats were perfused transcardially with heparinized saline followed by cold .2 M phosphate buffered (pH 7.6) 2% paraformaldehyde. Frontal sections were cut on a freezing microtome in repeating 90-30-30 μm series. The 90 μm sections were incubated for 10 to 20 minutes in a .07% solution of 3,3′ diaminobenzidine in Trisma buffer (pH 7.6) with hydrogen peroxide (Graham and Karnovsky, '66; LaVail et al., '73; Ralston and Sharp, '73). One set of 30 μm sections was processed for autoradiography (ARG) (Cowan et al., '72). The other set of 30 μm sections was processed for both autoradiography and HRP (Colwell, '75). Exposure times for the autoradiograms were 3 to 4 months.

The size and position of the injection sites were reconstructed from the examination of Nissl-counterstained frontal sections under the microscope with dark-field and bright-field illumination and from the examination of photomicrographs of these sections. The drawings in Figure 1 were traced from dark-field photomicrographs of slides containing the injection sites that were processed for autoradiography. An example of a dark-field photomicrograph through the center of a .25 μl injection site is shown in Figure 7. Typically the total diameter of an injection site assessed in this manner was 1 to 2 mm, although there is reason to believe that the diameter of neural tissue that actually transported label was much smaller (see Cowan et al., '72; Andersen et al., '80a, '80b).

Some of the results of the HRP labeling from these cases have been presented in an earlier report (Roth et al., '78).

The method of parcellation of the MGB used in this report has been described in detail elsewhere (Andersen et al., '80a). Briefly, the MGB was divided into the classical ventral (V), medial (M), and dorsal (D) divisions as described by Ramon y Cajal ('55) and Morest ('64; '65a). The ventral division was divided into pars lateralis (Vl), pars ovoidea (Vo), a "transitional zone" (Vt), and ventral lateral nucleus (VL) (Morest, '64, '65a). The dorsal division was divided into the deep dorsal nucleus (Dd) (Morest, '64) and the caudal dorsal

nucleus (Dc) (Morest, '64; Winer et al., '77). Comparison of these subdivisions with those made on the basis of Nissl cytoarchitecture (Rioch, '29; Rose, '49; Moore and Goldberg, '63) indicated that pars principalis includes all subdivisions of the ventral division of MGB, as well as the caudal dorsal nucleus and the most dorsolateral aspect of the deep dorsal nucleus. Pars magnocellularis includes the medial division and, more rostrally, most of the deep dorsal nucleus. These correlations are in general agreement with those made by Morest ('64).

RESULTS

Ascending projections of the ICC to the auditory thalamus

As described by others, the projection of the CC onto the thalamus was always bilateral nd was of similar pattern on the two sides; nowever, the contralateral projection was always significantly lighter than the ipsilateral projection. Given the bilateral symmetry of the ICC to auditory thalamus projection, only the ipsilateral pattern will be described.

Injections of 3H-l-leucine in the ICC produced two distinct and continuous components of terminal label in the rostral two-thirds of the MGB. The medially located component was in the form of a column oriented rostrocaudally in the nucleus. Caudally this column of label passed through the medial division (M) of the MGB (Fig. 4), and more rostrally it passed through the deep dorsal nucleus (Dd) of the MGB (Figs. 2 and 5). This column was generally 1.5 to 2.0 mm long.

The lateral component of terminal label was in the form of a continuous sheet that passed caudorostrally through the ventral division of the MGB. This sheet of label was folded caudally and had a nearly vertical orientation more rostrally (Figs. 2 and 3).

The caudal folded aspect of the sheet of label passed continuously through three subdivisions of the ventral division: pars lateralis (Vl), pars ovoidea (Vo), and the "transitional zone" (Vt) (Fig. 2). Although some of the label in Vo and Vt may have included labeled fibers within the brachium of the inferior colliculus, much of it was a result of labeled terminals. It was apparent that this autoradiographic labeling was of terminals because in many cases no labeling was seen in the brachium of the inferior colliculus caudal to the MGB, while labeling was present in the Vo and Vt subdivisions of the medial geniculate.

Rostral to the folded sheet configuration a laminar configuration of autoradiographic label was observed in pars lateralis of the ventral division (Fig. 2). There was a transitional stage between these two configurations of autoradiographic label. Going rostrally from the caudal folded sheet configuration, the label in Vo and Vl united into a single lamina that paralleled the surface of the MGB. This lam-

Abbreviations

AI	First auditory field
AII	Second auditory field
ARG	Autoradiography
BIC	Brachium of the inferior colliculus
D	Dorsal division of the MGB
Dc	Caudal dorsal nucleus of the MGB
Dd	Deep dorsal nucleus of the MGB
EE	Ipsilateral and contralateral ear stimulation are both excitatory
EI	Contralateral ear excites and ipsilateral ear stimulation inhibits this excitation
HRP	Horseradish peroxidase
IC	Inferior colliculus
ICC	Central nucleus of the IC
ICP	Pericentral nucleus of IC
ICX	External nucleus of the IC
M	Medial division of the MGB
MGB	Medial geniculate body
MPO	Medial preolivary nucleus
POl	Lateral division of the posterior group of the thalamus
V	Ventral division of the MGB
Vl	Pars lateralis of the ventral division of the MGB
VL	Ventral lateral nucleus of the ventral division of the MGB
Vo	Pars ovoidea of the ventral division of the MGB
Vt	Transitional zone of the ventral division of the MGB

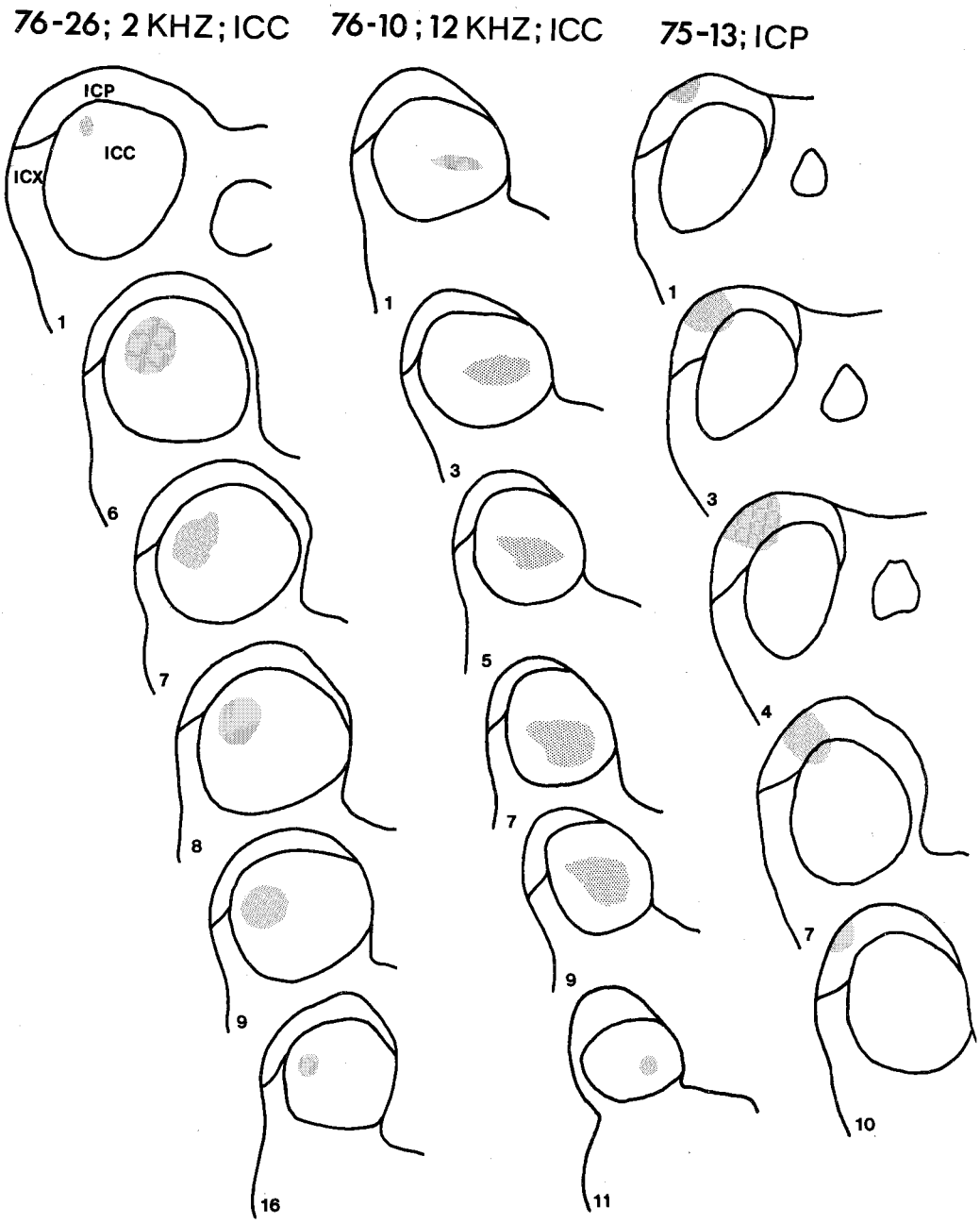

Fig. 1. Reconstruction of three injection sites. The drawings are of 30 μm frontal sections through the inferior colliculus that have been processed for autoradiography and have been Nissl counterstained. The row of sections on the left are from an experiment (76-26) in which the injection was centered at a 2 kHz representational site in the central nucleus of the inferior colliculus; the central row is from another experiment (76-10) in which the injection was centered at a 12 kHz representational site in the central nucleus; the row on the right is from an experiment (75-13) in which an injection was centered in the pericentral nucleus of the inferior colliculus. Each section number represents a 120-μm step, with the lower numbered sections located more rostrally. Autoradiographic labeling at the injection sites is indicated by the stippling. The extent of each injection site was accessed from dark-field photomicrographs of each section (like the photomicrograph in Figure 7) and by visual inspection of the sections under the microscope using both dark-field and bright-field illumination.

ina was flanked medially by a focus of label in Vt which in turn was located lateral to the autoradiographic label of the more medial column (Fig. 5). As described in more detail in a later section, there were often discontinuities in the autoradiographic labeling of the ventral division (Figs. 2, 4, and 5).

The autoradiographic label in Vl and Dd in the rostral third of the MGB merged rostrally with terminal-field labeling in the lateral division of the posterior group of the thalamus (POl).

The general pattern of autoradiographic label in the MGB and POl seen after single ICC injections was of the same form as the pattern of autoradiographic or HRP label seen in the auditory thalamus after single injections of anterograde or retrograde tracers in the AI cortical field (Colwell and Merzenich, '80; Andersen et al., '80a). Thus the colliculogeniculate projection of single loci in the central nucleus terminates in the MGB in the same basic form as the arrays of cells in the MGB that project to single loci in AI. Likewise the general form of the colliculogeniculate terminal fields in the MGB is the same as the general form of the AI corticogeniculate terminal fields in the MGB.

Systematic topography of the ICC-to-MGB projection

There is a systematic, and probably cochleotopic, organization of the projections of the ICC onto the MGB. Injections at higher frequency representational sites in the ICC produced folded sheets of autoradiographic label in the caudal aspect of the ventral division which were located more medially, rostrally, and dorsally than injections at lower frequency representational sites (see Fig. 3, top section). The vertical sheets of autoradiographic labeling in the rostral aspects of the ventral division were also located more medially with higher frequency representational site injections (see Fig. 3, bottom section).

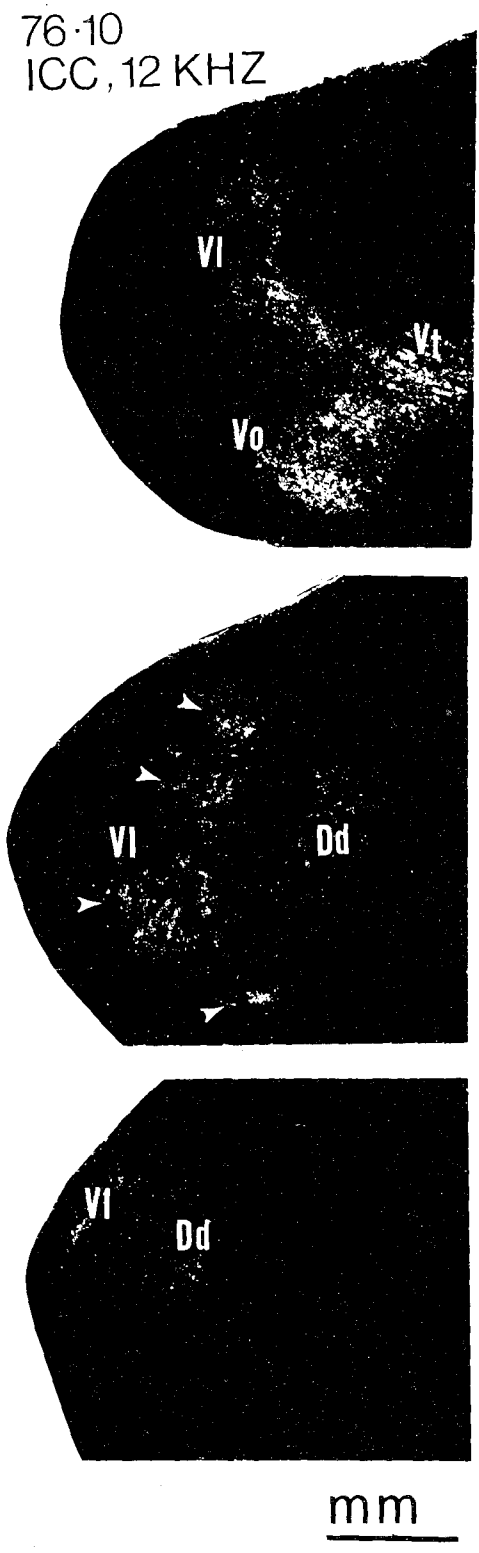

Fig. 2. Labeling in the auditory thalamus after a .25 μl injection of 3H-l-leucine at a 12 kHz representational locus in the ICC (injection site shown in Figures 1 and 7). The dark-field photomicrographs are of frontal sections taken from various levels of the ipsilateral MGB; the upper section is taken from the middle third of the MGB; the middle section is from the caudal aspect of the rostral third of the MGB, and the bottom section is from the rostral aspect of the rostral third of the MGB. The arrows on the middle section indicate discontinuities in the projection onto Vl.

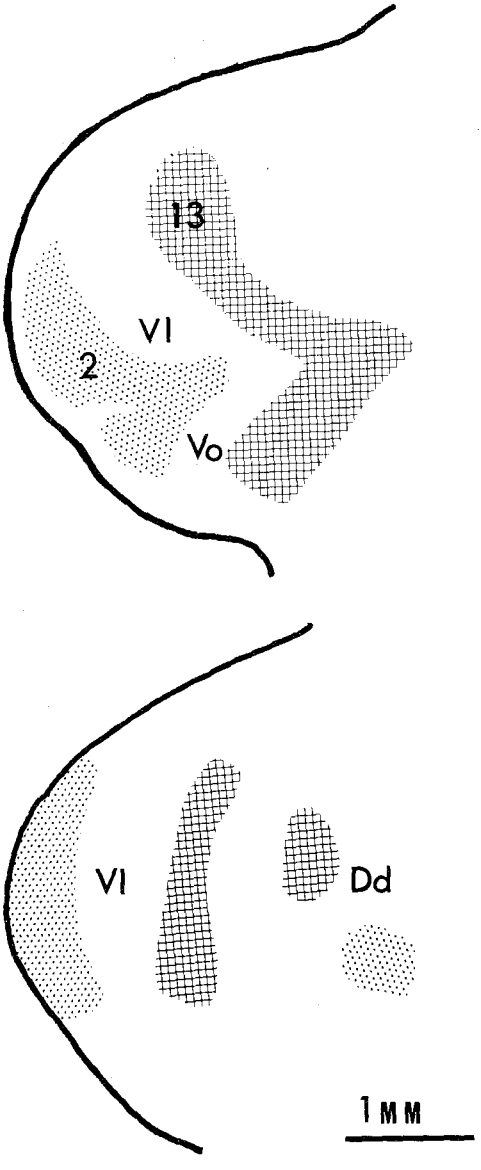

Fig. 3. Demonstration of the topographic organization of the ICC to MGB projection with respect to the tonotopic organization of the ICC. Single medium-sized injections (.2 μl) of anterograde tracer were made in two different experiments at 2 and 13 kHz representational loci in the ICC. Autoradiographic labeling from the ipsilateral middle third of the MGB (upper section) and ipsilateral rostral third of the MGB (lower section) has been transposed onto single frontal sections. Above background labeling resulting from the 13 kHz representational locus injection is crosshatched. Labeling resulting from the 2 kHz representational locus injection is dotted.

In the caudal region of the ventral division, injections at lower frequency representational sites in the ICC produced labeled sheets in Vo and Vl that were folded closer together than those produced with higher frequency site injections (see Fig. 3, top section). With the lowest-frequency injections, the two labeled regions sometimes appeared to merge (Fig. 4). Thus, although all loci in the ICC projected along continuous laminae which passed through Vl, Vt, and Vo, the increased folding with progressively lower frequency injections resulted in the lowest-frequency representational sites of the ICC appearing to project along the lateral aspect of the mutual border of Vl and Vo.

Injections at successively higher frequency representational sites produced medial columns of label through M and Dd that were located successively more dorsolaterally and rostrally (see Fig. 3). With very high-frequency ICC locus injections, the label in Vl and Dd came into close apposition. This result suggests a topographic reversal between Dd and Vl with the highest-frequency representational sites in the ICC projecting along their mutual border.

This systematic topography of the ICC to MGB projection as a function of the tonotopic organization of the ICC was the same as the systematic topography of the reciprocal connections of AI with the MGB as a function of the tonotopic organization of AI (Colwell and Merzenich, '80; Andersen, '79; Andersen et al., '80a).

Discontinuities in the projection from ICC to the ventral division

The ventral division component of the projection of single loci in the ICC onto the MGB has been described in general terms as forming a sheet of terminal label in three dimensions. However, there were always discontinuities in the pattern of autoradiographic labeling within this general sheet form. There were two types of discontinuities recorded in this material.

The one type of discontinuity was the periodic light and heavy labeling that often occurred within the ventral division (see Fig. 2 and 4). These periodic patches of label were commonly 300 to 500 microns in diameter with small (.25 μl) injections. They were most prominent in the caudal, folded-sheet region of the ventral division projection. In the rostral regions of the MGB, where there is a transi-

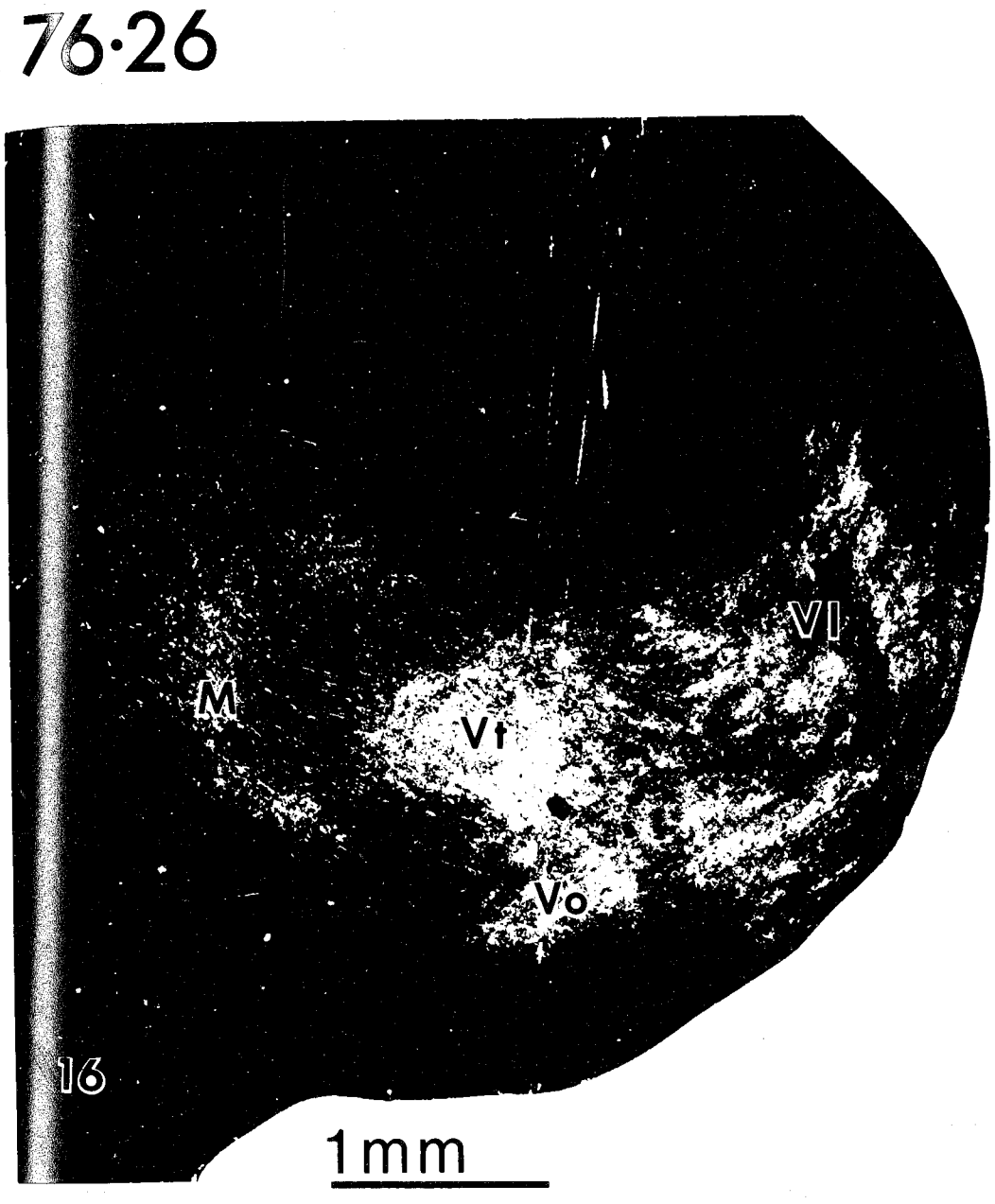

Fig. 4. Demonstration of discontinuous labeling in Vl. A single large injection (.5 μl) of 3H-l-leucine was made at a 2 kHz representational locus in the ICC. This dark-field photomicrograph is of a frontal section from the ipsilateral middle third of the MGB. A reconstruction of the injection site is shown in Figure 1.

Fig. 5. Finger-like discontinuities of label in V1, which parallel the surface of the MSP. The

tion in the ventral division label to a single vertical sheet in Vl, these patches often became indistinct. With larger injections of anterograde tracer in the ICC, they became wider in the frontal plane along an axis oblique or normal to the surface of the MGB and the described orientation of the morphological laminae (Morest, '65a) and the isofrequency contours (Aitkin and Webster, '72; Merzenich et al., '77; see Fig. 4). With small injections, these discontinuities sometimes approximated, in three dimensions, parallel columns that were oriented caudorostrally. These columns were commonly 1 mm in length.

The discontinuity in the ICC to ventral division projection described above was somewhat similar to the periodic, discontinuous pattern of HRP and autoradiographic labeling seen in the ventral division after small injections of retrograde and anterograde tracers in AI auditory cortex. (Andersen, '79; Andersen et al., '80a). However, these discontinuities were much less uniform than those seen after AI injections.

The second type of discontinuous label seen in Vl took the form of many very thin bands of heavier autoradiographic labeling that were oriented parallel to each other and to the surface of the MGB (see Figs. 4 and 5). They also appeared to parallel the described preferred orientations of the cell processes (Morest, '64) and isofrequency contours (Aitkin and Webster, '72) of Vl. These periodic thin bands were, on the average, about 100-μm wide. They were oriented oblique or normal to the larger first type of periodic discontinuity (see Fig. 4). This second type of discontinuity was not seen in studies of the thalamocortical or corticothalamic connections of Vl with AI.

ICP projection to the MGB

Injections into the pericentral nucleus of the inferior colliculus produced a focus of terminal label in the caudal aspect of the dorsal division (Dc); an example is illustrated in Figure 6. Label in Dc was noted only in the ipsilateral MGB. There was also light autoradiographic label in the ventromedial quadrant of the caudal aspect of the MGB (Fig. 6). However, it was not clear whether this label was of projecting fibers or whether it represented a terminal field. The injections of anterograde tracer in the ICP always resulted in some spread of tracer into the ICC (the ICP is under 1-mm thick). Thus, we could not determine if the ICP also projected to subdivisions of the MGB described earlier as receiving input from the ICC. However, when injections were made in the aspect of the ICP which overlies the ICC dorsally, the other labeled areas of the MGB excluding the Dc were of the same pattern as the labeled areas recorded after low-frequency ICC injections. Since low frequencies are represented dorsally in the ICC, this suggests that the ICP projects exclusively to the caudal MGB. The region in Dc to which the ICP projects is connected reciprocally and exclusively with the AII and "temporal" cortical fields (Rose and Woolsey, '58; Diamond et al., '58; Andersen et al., '80a).

Extrathalamic projections of the ICC

There were efferent projections from the ICC to several other auditory centers besides the auditory thalamus. There appeared to be a projection to the ipsilateral external nucleus of the inferior colliculus (ICX) (see Fig. 7). Fibers left the injection site and coursed horizontally and laterally to the ICX. Whether there was terminal labeling in this region was difficult to discern unequivocally, since labeled fibers continued ventrally from this site and coursed near the lateral surface of the midbrain just lateral to the lateral lemniscus (the tectopontine tract; see Woollard and Harpman, '40; Rasmussen, '64). However, it appeared that labeling in this region was of terminals as well as fibers since autoradiographic labeling in ICX was much more intense than was the labeling of fiber paths entering and leaving this region.

The ventrally directed efferent fiber path from the IC traveled very near the surface of the midbrain. A portion of this fiber tract can be followed into the ipsilateral dorsolateral pontine nucleus where there was very light terminal labeling. This is the same region that receives descending auditory cortical projections (Andersen et al., '80b). There was very strong terminal label in the medial preolivary nucleus (MPO) after ICC injections of tritiated amino acids. This projection was precisely reciprocal since the sections which were processed for both HRP and autoradiography always showed a group of HRP-labeled cells in MPO directly overlaid by autoradiographic grains. There was very light label noted in one case in the ipsilateral dorsal cochlear nucleus. The other lower brainstem auditory nuclei which contained HRP-labeled neurons after these injections (including bilaterally the lateral superior olives, the dorsal nuclei of the lateral lemnisci, and the three major divisions of the cochlear nuclei; ipsilaterally the

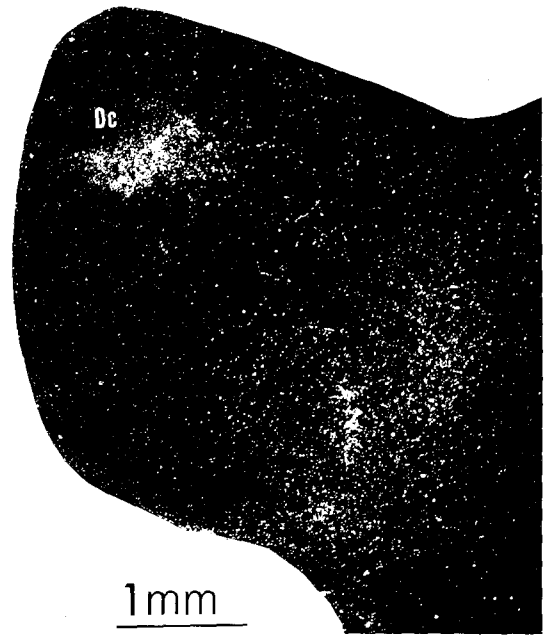

Fig. 6. Demonstration of the ICP to MGB projection. An injection of anterograde tracer was centered in the ICP. The dark-field photomicrograph is of a frontal section taken through the caudal third of the MGB. The apparent terminal labeling in the upper left corner of the section is in the caudal dorsal nucleus (Dc). The more medially placed label in the lower right aspect of the section is over the brachium of the inferior colliculus and the medial division (it is unclear if these are labeled terminals or fibers of passage).

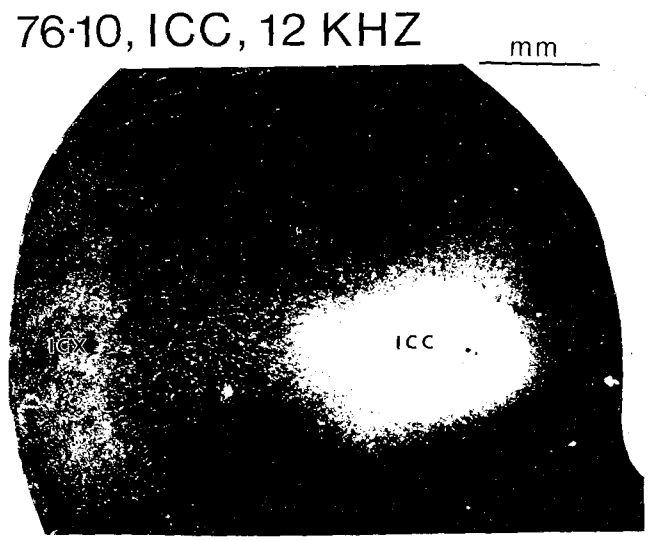

Fig. 7. Representative demonstration of a probable ICC to ICX projection. In this experiment, a .25 μl injection of 3H-l-leucine was made at a 12 kHz locus in the ICC. This dark-field photomicrograph of a frontal section through the IC shows the injection site on the right. Fibers were followed from the injection site to a region of heavier autoradiographic labeling in the ICX on the left.

medial superior olive and the ventral nucleus of the lateral lemniscus) were not autoradiographically labeled.

Injections of HRP in the ICC never produced HRP-labeled neurons in the MGB.

DISCUSSION

Relation to previous studies—ICC-to-MGB projection

These experiments indicate that the ICC projects bilaterally to the laminated portion of the ventral division (Morest, '65a), the medial division, the deep dorsal nucleus, and the lateral division of the posterior group.

In other investigations in the cat, several different schemata for the parcellation of the MGB have been used. However, the patterns of connection reported in these studies are, in general, consistent with the present results in terms of the corresponding positions of the label in the MGB (Morest, '65a; Andersen et al., '80a). Thus, a bilateral projection from the IC to the ventral and lateral aspect of the MGB has been observed, using anterograde degeneration techniques (Woollard and Harpman, '40; Moore and Goldberg, '63; Powell and Hatton, '69; Van Noort, '69; Jones and Powell, '71), which corresponds to the ventral division projection described here. Anterograde degeneration experiments (Moore and Goldberg, '63; Powell and Hatton, '69; Van Noort, '69; Jones and Powell, '71) also revealed a bilateral medial projection in the MGB, which corresponds to the medial and deep dorsal projections recorded in our material. Anterograde degeneration experiments have indicated a projection to POl (Moore and Goldberg, '63). Injections of tritiated amino acids in the ICC have been reported to produce label in the ventral and medial divisions (Kudo and Niimi, '78).

Relation to previous studies—ICP-to-MGB projection

The present experiments indicate that the ICP projects ipsilaterally to the caudal aspect of the MGB in the caudal dorsal nucleus (Dc). In previous investigations lesions of the inferior colliculus produced very sparse degeneration in this region (Moore and Goldberg, '63; Powell and Hatton, '69; Van Noort, '69). Kudo and Niimi ('78) have reported that injections of tritiated leucine in the dorsal aspect of the IC produced label in the dorsal division (as well as in other regions of the MGB), and that HRP injections in the dorsal division of the MGB produced label centered in more dorsal aspects of the ipsilateral IC, including the ICP. A projection from the ICP to the caudal aspect of the MGB has been noted in the tree shrew (Casseday et al., '76).

Two-systems hypothesis

The important anatomical studies of Rose and Woolsey ('58), Diamond et al. ('58), Casseday et al. ('76), Winer et al. ('77), Graybiel ('72, '73), and Sousa-Pinto ('73) have demonstrated that there are multiple parallel pathways between the auditory thalamus and auditory cortex. Some of these investigators have categorized these multiple pathways according to two general systems of connections (Rose and Woolsey, '58; Casseday et al., '76; Winer et al., '77; Graybiel, '73). These two-system schemes have in common a major pathway between the ventral division and AI auditory cortex (as defined by Woolsey and Walzl, '42) and a second major pathway between areas of the auditory thalamus surrounding the ventral division and auditory cortex surrounding AI.

We have recently examined the connections of the auditory cortex in combined microelectrode mapping and axonal transport-anatomical tracing experiments and have confirmed the existence of two largely segregated systems of connections (Andersen, '79; Andersen et al., '80a). The use of more refined techniques in these studies than were used in previous investigations allowed for an extensive elaboration of the properties of the two systems of connections. These elaborations include: 1) the observation that both systems of connections involve several auditory cortical fields. Previous investigations suggested that one of the systems involved only the single auditory field AI. 2) The two systems of connections correspond to two functionally distinct types of auditory cortical fields. The *cochleotopic system* connects only cortical fields whose functional organization is cochleotopic. The neurons of the cortical regions that receive input from this projection system are relatively sharply tuned; that is, they receive a convergent input from relatively limited sectors of the cochlear sensory epithelium. The *diffuse system* projects to cortical fields which are functionally organized in complex ways that may not be cochleotopic. The neurons of these cortical fields are relatively broadly tuned. The term diffuse refers to the high degree of convergence that these neurons receive from across the cochlear sensory epithelium; this extensive convergence is indicated by the

broad tuning of these neurons. 3) The anatomical organization of the thalamocortical projections to each cortical field of the cochleotopic system appears to be cochleotopically organized and thus provides a structural basis for the functional cochleotopic organization of these cortical fields. The connections of the diffuse system do not appear to be cochleotopic. 4) The use of a combined microelectrode mapping-anatomical tracing paradigm has placed the two systems of connections within the context of the current maps of the auditory cortex. Previous anatomical studies in the cat were based on the classical evoked-potential maps of the auditory cortex (Woolsey and Walzl, '42; Woolsey '60). These maps have since been extensively revised by the use of the microelectrode recording techniques, and these revisions have included the addition of newly discovered auditory cortical fields as well as the rearrangement of the boundaries of previously described fields (Merzenich et al., '77; Reale and Imig, '77; Knight, '77; Merzenich et al., '75).

The results of the present study are consistent with the idea that the two largely segregated thalamocortical projection systems derive their input from different inferior colliculus subdivisions. Single loci in the ICC project with the same basic form and systematic topography onto the MGB (and POl) as the arrays of neurons in the MGB (and POl) that project onto single loci in at least three of the four known cochleotopically organized cortical fields (Andersen et al., '80a). Thus the ascending ICC projections are relayed via the ventral division, medial division, deep dorsal nucleus of the dorsal division of the medial geniculate, and the lateral division of the posterior group to the auditory cortical fields of the cochleotopic system. The diffuse system's principal thalamic unit, the caudal dorsal nucleus of the dorsal division of the MGB, receives its midbrain auditory input from the ICP.

Parallel systems of projection from the IC to the MGB have been noted in previous anatomical studies in the cat (Morest, '65b; Kudo and Niimi, '78) and in the tree shrew (Casseday et al., '76; Oliver and Hall, '78a). In particular, the heavy projection from the central nucleus of the inferior colliculus to the ventral division has been included in the definition of the ascending projection system that terminates in AI auditory cortex (Casseday et al., '76; Winer et al., '77). A projection from the ICP to the posterior aspect of the MGB has been noted in the cat (Kudo and Niimi, '78) and tree shrew (Casseday et al., '76). Parallel projections from the deeper layers of the superior colliculus (Casseday et al., '76; Oliver and Hall, '78a) and the lateral tegmentum (Morest, '65b; Casseday et al., '76; Oliver and Hall, '78a) onto the MGB have also been noted; however, it is not known if these projections are conveying auditory information.

This work and the studies cited above point to two systems of projection that begin at least at the level of the inferior colliculus and pass largely in parallel and in a segregated fashion to the auditory cortex. Moreover, these two systems of connections may be even more extensive, passing in parallel from the cochlear nuclei or cochlea to the auditory cortex. It is obviously important to determine the differences in the projections of the lower brainstem auditory nuclei onto the ICC and ICP. It has long been appreciated that the ICC receives projections from a remarkable number of lower brainstem auditory nuclei (see Roth et al., '78 for review). To our knowledge, there is no report in the literature of the sources of ascending input to the ICP. The fact that the tuning curves of neurons in the ICP are much broader than those of the ICC (Aitkin et al., '75) suggests that they at least receive a wider degree of topographic convergence in projection from the cochleotopically organized lower brainstem auditory nuclei.

Discontinuities in the projection of the ICC onto Vl

The periodic discontinuities in the pattern of projection of the ICC onto Vl sometimes take the form, in three dimensions, of roughly parallel columns oriented caudorostrally. Thus, they share some similarities with the form of the periodic discontinuities observed in studies of the reciprocal connections of AI with Vl. One functional possibility is that the periodic discontinuities in the Vl connectional pattern with the cortex may reflect a segregation of binaural response properties in Vl into EE (contralateral and ipsilateral ear stimulation excite the neurons) and EI (contralateral excites and is inhibited by ipsilateral stimulation) regions (Andersen et al., '80a). If this is the case, then this alternating periodic segregation of EE and EI regions in the MGB, which is also present in AI cortex (Imig and Adrian '77; Middlebrooks et al., '78), would first be formed by the projection of the ICC onto the MGB. Further electrophysiological studies must be conducted to determine whether there are in fact segregated EE and

EI dominant regions in Vl.

There were also discontinuities in the density of projection which formed thin fingers of autoradiographic label in Vl that paralleled the described orientation of the morphological laminations in that nucleus (Morest, '65a). The regions of dense labeling are 4 to 5 times wider than the width of the morphological laminae of Vl (Morest, '65a). Since these finger-like discontinuites occur bilaterally, the less densely labeled regions of the ipsilateral Vl may receive dense projections from the contralateral ICC. Thus, it is possible that they are spatially representative of some form of processing that is accomplished in the projection of the two ICC's onto Vl.

Topography of projection

There is a systematic topography of connections between the ICC and all component nuclei of the MGB to which the ICC projects. The topography of the connection with Vl is similar to that reported by Kudo and Niimi ('78). This topography of connections appears to be in register with the cochleotopic organizations of both the central nucleus of the inferior colliculus and the nuclei of the MGB in which microelectrode mapping experiments have been performed (Vl of cat, Aitkin and Webster, '72; Dd of squirrel monkey, Gross et al., '74). Thus, only cochleotopically homotypic regions of the ICC and MGB appear to be connected.

In summary, these experiments indicate that there are two parallel systems of projection from the inferior colliculus to the medial geniculate which provide separate inputs to two general auditory thalamocortical systems. The projection of the central nucleus of the inferior colliculus onto the ventral division of the medial geniculate exhibits two types of periodic discontinuities. Finally, all the components of the projections of the central nucleus of the inferior colliculus onto the medial geniculate appear to be cochleotopically organized.

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