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Projections of Auditory Cortex onto the Inferior Colliculus in the Rat

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Summary

The organization of the neocortical projection to the inferior colliculus (IC) was studied in 36 rats using retrograde transport of horseradish peroxidase (HRP) or horseradish peroxidase conjugated with lectin (WGA-HRP). Projection to the external and dorsal cortices originates in the temporal neocortical areas Te 1, Te 2 and Te 3 and in the parietal area Par 2. The corticocollicular projection is predominantly ipsilateral with a weak contralateral contribution. Projection to the rostromedial and rostrolateral part of the external cortex (EC) of the IC arises mainly from the areas Par 2 and Te 1. The participation of the cortical areas Te 2 and Te 3 in this projection is only small. The fibres to the caudobasal part of the external cortex descend from the caudal parts of areas Te 1, Te 2, and Te 3. The corticocollicular projections to the dorsal part of the IC are more numerous than the projections to the EC and originate in all temporal areas, i.e. in area Te 1, Te 2 and Te 3. However, the topographical organization of the corticocollicular projection is more pronounced in the part which projects to the EC. We suggest that the topographical organization of the projections to the EC corresponds with the map of auditory space in the EC. The source of corticocollicular fibres are exclusively neurones of lamina V of all cortical areas sending their fibres to the IC.

Key words
Auditory cortex – Inferior colliculus – Projections – Rat

Introduction

The neocortical projections to the inferior colliculus have been described in mammals as monosynaptic connections, mostly ipsilateral, arising from the primary auditory cortical area and also from the secondary auditory cortical areas (Huffman and Henson 1990). The terminal field of this projection system is located in the peripheral area of the inferior colliculus (Kuypers and Lawrence 1967, Forbes and Moskowitz 1974, Ravizza *et al.* 1976, FitzPatrick and Imig 1978, Casseday *et al.* 1979, Andersen *et al.* 1987, Kelly and Wong 1981, Druga and Syka 1984a, 1984b, Faye-Lund 1985, Coleman and Clerici 1987, Herbert *et al.* 1991, Arnault and Roger 1990, Vaudano *et al.* 1991).

Several tracing methods and approaches have been used to demonstrate that in rodents the neocortical projection to the IC originates in a relatively large cortical area comprising not only the primary auditory cortex but also several areas circumscribing it (Beyerl 1978, Druga and Syka 1984a, 1984b, Faye-Lund 1985, Coleman and Clerici 1987, Gonzalez-Hernandez *et al.* 1987, Druga *et al.* 1988, Arnault and Roger 1990, Herbert *et al.* 1991, Vaudano *et al.* 1991). However, these observations of the cortical areas projecting to the IC indicate that there exist differences which may be caused by several factors.

Neurones sending their axons to the IC in rodents are localized in layer V of the auditory cortex (Beyerl 1978, Druga and Syka 1984a, Gonzalez-Hernandez *et al.* 1987, Druga *et al.* 1988, Herbert *et al.* 1991). Games and Winer (1988) give details of the localization in layer V of area 41 only for rats. Additional data concerning the distribution of corticocollicular neurones in secondary auditory areas are lacking.

The aim of this study was to ascertain the whole neocortical area in the rat where descending fibres to the IC originate. Retrogradely labelled neurones were identified in the cortex after HRP and WGA-HRP injections to the IC and their position were estimated with respect to the cytoarchitectonic maps of the rat temporal cortex (Zilles *et al.* 1980, Zilles and Wree 1985, Zilles 1985). The laminar distribution of corticocollicular neurones in temporal areas Te 1 - Te 3 was visualized after injections of markers had been administered into the external and dorsal cortices of the IC.

Material and Methods

The experiments were performed on 36 albino (Wistar strain) or pigmented (Long Evans strain) rats (20 males and 16 females) weighing 250–300 g. The animals were anaesthetized intraperitoneally with pentobarbital (50 mg/kg body weight) and placed in a stereotaxic instrument. They received a unilateral injection of HRP (Sigma VI, 30 % w/v, 25 animals) or WGA-HRP (Sigma, 2 % w/v, 11 animals) into the inferior colliculus. Tracers, dissolved in distilled water, were injected stereotaxically from the dorsal approach with a micromanipulator-driven Hamilton microliter syringe. The injections consisted of 0.05–0.1 μl of HRP or 0.05–0.1 μl of WGA-HRP. In five animals, small injections of HRP were applied by iontophoresis through a micropipette (2–3 μA, 30 μm tips). The injections were administered over a period of 20–30 min. After completion of the injection, the syringe needle or micropipette was left in place for another 15–20 min.

After a survival time of 48 h, the animals were again anaesthetized and perfused intracardially with saline followed by a mixture of 0.4 % paraformaldehyde and 1.25 % glutaraldehyde with 0.05 mol/l phosphate buffer added (pH 7.4). The brains were immediately removed from the skull and divided into blocks. The blocks were immersed in the same fixative and stored for 12–24 h at 4 °C. They were then placed in a 30 % saccharose solution in phosphate buffer for another 24–48 h, and later cut transversally into sections 40 μm thick. The sections were treated with 3,3-diaminobenzidine according to Warr *et al.* (1981) or with tetramethylbenzidine according to the procedure described by Mesulam (1976). Two series of sections were prepared from each brain. One series was mounted unstained, while the other was counterstained with cresyl violet (DAB) or with alum carmine (TMB). The unstained and stained sections were examined using both bright-field and dark-field microscopy.

The exact positions of the retrogradely labelled cortical neurones were plotted on magnified drawings of the sections with the aid of camera lucida. The boundaries of layer V were depicted in these drawings and layer V was subdivided into two symmetrical sublayers (sublayer a and b) with the aid of a line running parallel to the pial surface. The maps of individual cases were transferred to standard diagrams of a stereotaxic atlas (Zilles 1985). Cytoarchitectonic criteria (Roger and Arnault 1989, Vaudano *et al.* 1991, Zilles *et al.* 1980, Zilles and Wree 1985, Zilles 1985) were used for differentiation of the temporal cortical areas.

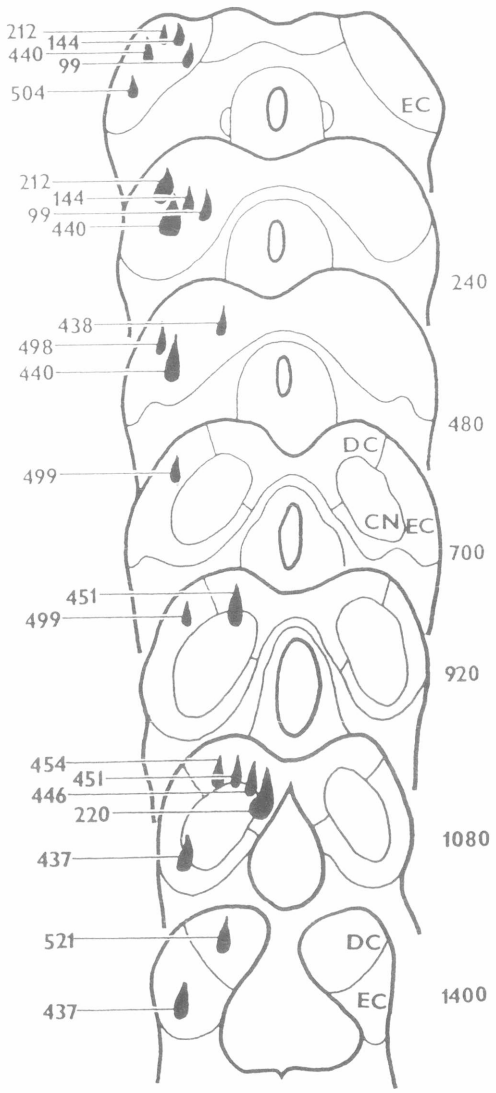

Fig. 1. *Coronal sections showing the HRP or WGA-HRP injection sites in the inferior colliculus. Numerals on the left indicate individual cases. Each depicted injection represents two or three identical or very similar injection sites. Numerals on the right indicate the distance in micrometers from the first section (above).*

The division of the IC into individual parts was based on the criteria given by Faye-Lund and Osen (1985). The extent of the deposit of injected tracers was depicted in the enlarged sections of the brainstem with

the aid of camera lucida. Cytoarchitectonic boundaries of the subdivisions of the IC, assessed in standard Nissl stained sections, were superimposed on the drawings of the injected tracers deposit.

Results

Cortical labelling after injections to the external cortex

WGA-HRP or HRP injections centered rostrolaterally in the EC (R-212, R-410, R-498, R-504, R-440 – Fig. 1) resulted in a moderate number of labelled neurones in Te 1, which were distributed through the whole area Te 1 with a slight dominance in the rostral part. The other two temporal auditory areas Te 3 and Te 2 lacked labelled neurones, or had small clusters of positive neurones in their rostrodorsal parts. A small number of labelled neurones was always present in area Par 2.

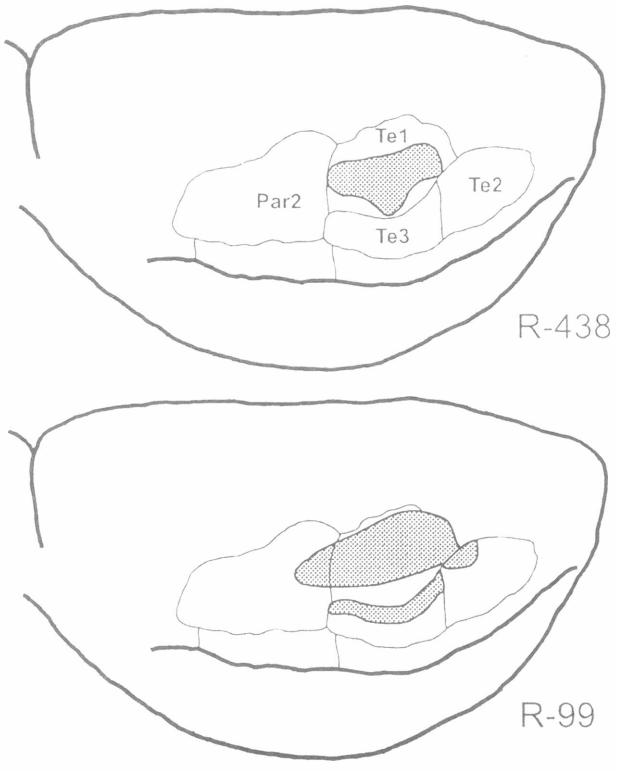

Fig. 2. *A side view of the cortex showing the distribution of labelled neurones (grey areas) after injection of the marker into the rostromedial part of the external cortex.*

Injections of markers in the rostromedial part of the EC (R-99, R-144, R-438 – Fig. 1) led to a similar pattern of retrograde neuronal labelling comparable to the pattern observed in the previous group. Retrogradely labelled neurones prevailed in Te 1, while small numbers of positive neurones were present in restricted parts of Te 3 and Te 2 and in the posterior part of Par 2 (Fig. 2).

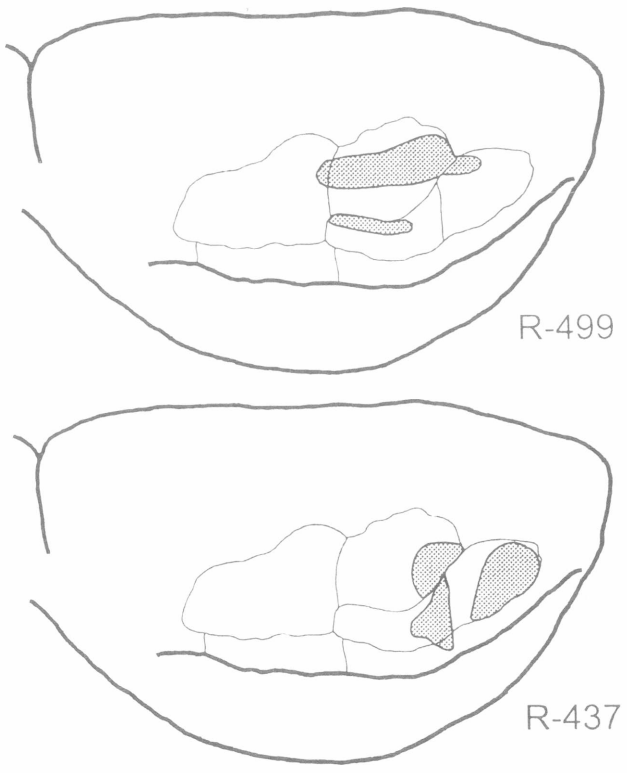

Fig. 3. *A side view of the cortex showing the distribution of labelled neurones after injection of the marker into the middle (R-499) and caudal part (R-437) of the external cortex.*

A very small deposit of WGA-HRP in R-438 led to labelling restricted only to Te 1. Tracer injections into the intermediate part of EC laterally surrounding the central nucleus (R-499) resulted in a pattern of labelling similar to that found with the rostrolateral EC injections. A moderate number of labelled neurones prevailed in Te 1. A smaller number of positive neurones was additionally localized to the dorsal part of Te 3, the caudal part of Par 2 and the anterodorsal half of Te 2 (Fig. 3).

Injections centered into the caudobasal part of the EC (R-437) resulted in a significantly different pattern of cortical labelling. Retrogradely labelled neurones were condensed to caudal parts of all three auditory areas (Fig. 3).

Accidental injections of WGA-HRP or HRP confined to the central nucleus of the IC resulted in no labelling or in entirely insignificant labelling of the auditory cortical areas.

Cortical labelling after injections into the dorsal cortex

Retrograde labelling of cortical neurones after HRP or WGA-HRP injections into the dorsal cortex resulted in a different distribution of labelled neurones than injections into the external cortex of the IC.

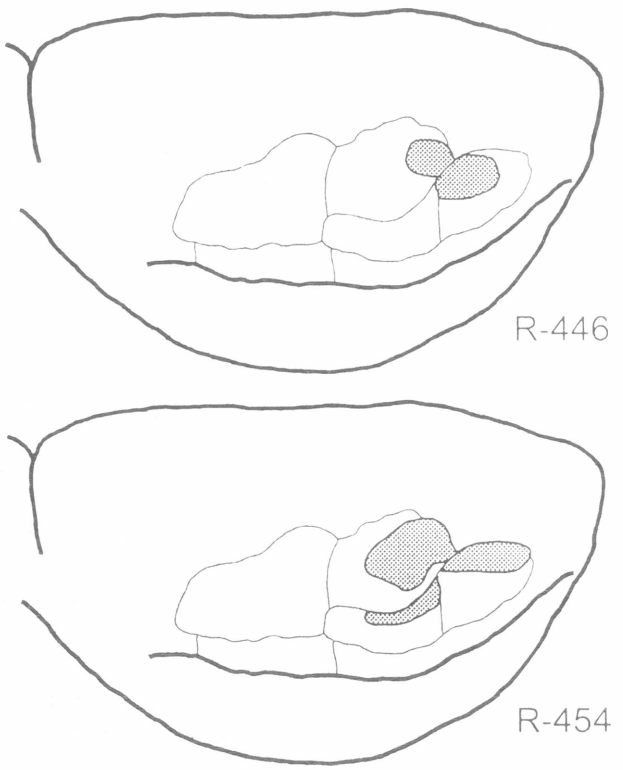

Fig. 4. *A side view of the cortex showing the distribution of labelled neurones (grey area) after injection of the marker into superficial layers of the dorsal cortex.*

In cases where a deposit of the injected marker was placed primarily in superficial layers of the DC (R-451, R-454, R-446 – Fig. 1), retrogradely labelled neurones were present in the dorsal part of area Te 2 and in the caudal half of area Te 1. In some cases, the dorsocaudal part of area Te 3 contained clusters of labelled neurones (Fig. 4).

Involvement of the third layer of the DC or injections of the marker into the most caudal parts of the DC (R-220, R-521,) resulted in massive labelling of large numbers of neurones distributed in the whole anteroposterior extent of the Te 1, Te 3 and Te 2 with the exception of its caudobasal part. Injections infiltrating the mediobasal part of the DC (R-220) led to labelling of neurones located outside the auditory areas, dorsally in area Par 1 and ventrally in area PRh (Fig. 5).

Retrogradely labelled neurones in the contralateral cortex

Retrogradely labelled neurones in the contralateral temporal areas and in the area Par 2 were observed only in cases when the deposit of the marker was present in the dorsomedial part of the EC (R-212, R-144, R-99, R-438 – Fig. 1) and in cases when the deposit reached the caudal part of the DC (R-220, R-446, R-451, R-521 – Fig. 1). In all other cases, no labelled neurones were found in the contralateral cortex. Injections of markers into the rostromedial part of the EC produced labelling in contralateral areas Par 2, Te 1 and Te 3. Injections into the caudal part of the DC led to labelling in the area Te 1 and Te 2. All labelled neurones located in the contralateral cortex were localized in the cortical layer V and their numbers in individual animals never exceeded 1 % of all corticocollicular neurones.

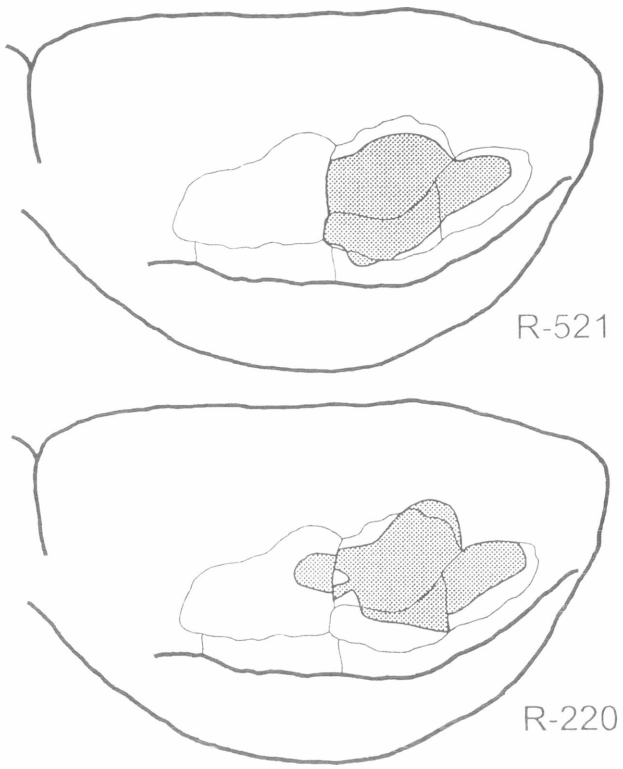

Fig. 5. *A side view of the cortex showing the distribution of labelled neurones after injection of the marker into the deep layers of the dorsal cortex (R-220) and into the caudal part of the dorsal cortex (R-521).*

Laminar distribution and morphological characteristics of corticocollicular neurones

After injections of the marker to the external and dorsal cortex of the IC labelled neurones were always found in layer V of the ipsilateral or contralateral auditory cortex. The analysis of the distribution of labelled neurones in the ipsilateral temporal areas and the area Par 2 showed that there were no labelled neurones in layers I–IV and only a few labelled neurones were present on the boundary between layers V and VI.

In three animals (R-440, R-99, R-438), labelled neurones were counted in sublayers Va and Vb after an HRP injection into the external cortex. Labelled neurones occurred within the area Par 2 in larger numbers in the sublayer Va (58 % of 55 neurones in R-440 and 64 of 62 neurones in rat R-99).

In contrast to this, labelled neurones prevailed in sublayer Vb in the area Te 1 (62 % of 260 neurones in R-440, 67 % of 311 neurones in R-99 and 68 % of 128 neurones in R-438). They were mostly localized near the boundary between sublayers Va and Vb. Only a limited number of neurones could be found in the superficial part of sublayer Va. The localization of neurones in area Te 3 was similar to Par 2: labelled neurones prevailed in sublayer Va (62 % of 76 neurones in R-440, 63 % of 113 neurones in R-99 and 66 % of 62 neurones in R-438). In the area Te 2 only, a few neurones were found after injection of the marker into the external cortex, and these were localized in sublayer Va.

After an HRP injection into the dorsal cortex (animals R-446, R-451, R-521), labelled neurones were found in area Te 1 predominantly in the sublayer Vb (65 % of 965 in R-521, 63 % of 188 neurones in R-446 and 58 % of 261 neurones in R-451), and in the areas Te 2 and Te 3 in sublayer Va (area Te 2: 60 % of 131 neurones in R-521, of 87 neurones in R-446 and 54 % of 98 neurones in R-451; area Te 3: 62 % of 147 neurones in R-521 and 58 % of 43 neurones in R-451).

The perikarya of corticocollicular neurones were pyramidal or triangular in all areas, often with clearly visible apical dendrites and initial parts of basal dendrites. Less frequently oval somas of neurones with an indicated apical dendrite were observed. Other types of somas including inverted pyramids were not found in our material. As far as the size of the neurones is concerned (19–32 times 8–20 μm), the majority of labelled neurones belonged to the category of medium or large pyramidal neurones. The largest neurones were observed in area Te 1 within the sublayer Vb.

We did not observe any essential differences in the parameters of cortical labelling between strains of Wistar and Long-Evans rats.

Discussion

Most studies dealing with the organization of corticocollicular projections use the orthograde approach, which exploits the mechanism of intraaxonal anterograde transport of markers. Several investigators have described corticocollicular projections in the inferior colliculus subdivisions after intracortical injections of HRP or WGA-HRP.

Faye-Lund (1985) introduced the concept of three separate projections originating in the temporal neocortex of the rat: the first partly bilateral projection from area 41 to the deep dorsal cortex of the IC, the second one ipsilateral from area 36 to the superficial dorsal cortex and a third ipsilateral from area 22 to the external cortex. The rostrodorsal part of the auditory cortex thus projects to the external cortex primarily to its rostral part, while the central and the caudoventral parts of the auditory cortex project to the dorsal cortex of the IC.

The results of Coleman and Clerici (1987), who described projections from the rostral part of the auditory cortex (area 39) to the external cortex and from areas 41, 20, 36 to the dorsal cortex, generally agree with the data of Faye-Lund (1985). Arnault and Roger (1990) and Vaudano *et al.* (1991) described weaker projections from auditory cortical areas Te 2 and Te 3 to the external cortex and more massive projections oriented to the medial or ventromedial part of the dorsal cortex without greater relations between the site of cortical injections of the marker and the terminal collicular area. Roger and Arnault (1989) found that injections of WGA-HRP into area Te 1 resulted in anterograde labelling in the dorsal cortex of the IC and to a lesser extent in the external cortex.

Similarly as the results of Herbert *et al.* (1991), our present findings are based on a different approach exploiting the mechanism of retrogradely transported markers. In such studies, injections of markers into subdivisions of the IC reveal precisely the distribution of corticocollicular neurones in the auditory cortical areas and provide more information about the pattern of this projection system than the results of studies using anterograde transport. The results of Herbert *et al.* (1991) are not inconsistent with those of Faye-Lund (1985) and other laboratories, and differences are evident only when injections of WGA-HRP into the rostroventral and rostrodorsal part of the auditory cortex are compared. According to Faye-Lund (1985), the deposit of the marker in the rostrodorsal part of the auditory cortex produces labelling in the external cortex of the IC, while Herbert *et al.* (1991) indicate that only the rostroventral part of the auditory cortex (area Te 3) projects to the external cortex of the IC. Deposits of the marker located in the rostrodorsal part produce labelling in the superficial layers of the dorsal cortex of the IC. On the other hand, Herbert *et al.* (1991) confirmed previous results claiming that the central part of the auditory cortex (area Te 1) and its caudoventral part (area Te 2) preferentially supply the dorsal cortex of the IC. The finding that projections from the middle part of Te 1 (Te 1.m) preferentially supply the third layer of the dorsal cortex led Herbert *et al.* (1991) to a novel subdivision of area Te 1 into three fields (Te 1.a, Te 1.m, Te 1.p).

A comparison of the results of Herbert *et al.* (1991) with our present data indicate some differences in the distribution of corticocollicular neurones. Injection of the marker into the rostrolateral part of the EC resulted in the labelling of neurones in the parietal area Par 2 and in area Te 1. The participation of areas Te 3 and Te 2 was less prominent. In contrast to this, Herbert *et al.* (1991) emphasized the prevalence of labelling in Te 3. Injection of the marker infiltrating the caudal part of EC in our animals led neurones in

the posterior parts of all auditory areas, while Herbert *et al.* (1991) observed more diffuse labelling in these areas with a prevalence in Te 2. Another difference in our results is evident when injections of the marker are localized in superficial layers of the DC. After such injections, Herbert *et al.* (1991) described preferential labelling in the Te 1.a and Te 1.p and rather diffuse labelling of Te 2 and Te 3, while we found labelling in the posterior half of Te 1 and diffuse labelling of Te 2.

Taken together, our results clearly demonstrate that the corticocollicular projection is realized in the rat mostly by ipsilateral fibres with a weaker contralateral component. The ipsilateral component is clearly convergent in character. Projections oriented towards the dorsal cortex are more massive. Although both subsystems of the corticocollicular projections exhibit some level of topographical organization, the topographical organization of the cortical subsystem terminating in the external cortex of the IC is more expressed. The different distribution of retrogradely labelled neurones in the auditory cortex after injections into different parts of the EC could have important functional implications. A topographical representation of auditory space in the external cortex of the IC in the guinea-pig has been described recently (Binns *et al.* 1992). The neuronal responses recorded from the rostral part of the EC revealed a preference for auditory stimuli in the anterior acoustic field, while more caudal neurones preferentially responded to stimuli presented in the posterior acoustic field. This implies that, in addition to the tonotopic organization of different temporal auditory areas, there may also exist a topographical representation of the auditory space in the auditory cortex.

Similarly as our data, the results of Herbert *et al.* (1991) clearly indicate that subpopulations of cortical neurones projecting to the EC and to the DC of the IC are not segregated, but on the contrary overlap. This is one of the characteristic features for this projecting system. It remains to be elucidated if both neuronal subpopulations overlap a third category of neurones giving off axonal collaterals both to the DC and the EC.

The corticocollicular neurones were localized exclusively in layer V of the temporal cortical fields and were never found in the supragranular layers or in layer VI. In the area Te 1, labelled cells prevailed in sublayer Vb regardless of whether the marker was injected into the EC or the DC. After injections of markers into the EC, 62–68 % of labelled neurones were found in area Te 1 in sublayer Vb, whilst after injections into the DC we observed 58–65 % labelled neurones in sublayer Vb. Games and Winer (1988) estimated that within area 41 approximately 60 % of labelled neurones were in sublayer Vb. Likewise, we can confirm the data of Games and Winer (1988) concerning the morphologic and morphometric characteristics of the corticocollicular neurones and the fact that the majority of these neurones are localized in area Te 1 at the boundary of sublayers Va and Vb.

In all other cortical fields (Te 2, Te 3, Par 2) labelled neurones prevailed in the sublayer Va. In these fields a larger scatter of labelled neurones was also evident in layer V. A different intralaminar distribution of corticocollicular neurones in the temporal cortex was described in hamsters by Ravizza *et al.* (1976) and in cats by Kelly and Wong (1981). Corticocollicular neurones prevailed in both species in sublayer Va.

Corticocollicular projections terminating in the EC and DC belong to the glutamatergic system with an excitatory postsynaptic effect (Storm-Mathisen and Ottersen 1988). Subsequent projections from the DC and EC oriented to the central nucleus of the IC (Coleman and Clerici 1987) have not been chemically defined until now. Single-unit recordings indicate approximately the same proportion of excitatory and inhibitory responses in the DC and EC after cortical stimulation (Syka and Popelář 1984, Syka *et al.* 1988). These findings suggest that an intrinsic mechanism located in the inferior colliculus periphery exerts a modulatory effect on the ascending stream of auditory signals processed preferentially in the central nucleus of the IC. Some physiological studies indicate that the auditory cortex enhances the transmission of ascending auditory signals in subcortical relay stations (medial geniculate body, inferior colliculus – see Huffman and Henson 1990).

The recently described chemically defined subpopulations of neurones, such as GABAergic neurones and calbindin and calretinin neurones, may participate in the processing of signals transferred from the cortex *via* IC cortices to the central nucleus of the IC (Celio 1990, Arai *et al.* 1991, Friauf 1994, Gutierrez *et al.* 1994).

The dorsal cortex of the IC is a major recipient of cortical projection. The cortical projection to the EC is less prominent and projections to the central nucleus are insignificant in the rat. The density of cortical projections in inferior colliculus subdivisions is proportional to the density of the NADPH-diaphorase/NOS neurones. Specifically, the high density of such neurones in the DC (Herbert *et al.* 1991, Druga and Syka 1993) suggests their participation in the functional circuits of the IC.

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