

Functional organization of the auditory cortex in a native Chilean rodent (*Octodon degus*)

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*The tonotopic organization of primary auditory cortex (AI) and surrounding secondary regions has been studied in the **Octodon degus** using standard microelectrode mapping techniques. The results confirm and extend previous observations made in other species. The tonotopic organization of the largest field (AI) apparently covered the hearing range of **O. degus**. Low tonal frequencies were represented rostroventrally and high frequencies caudally, with isofrequency contours orientated dorsoventrally in a ventrocaudal slant. There were additional tonotopic representations adjacent to AI. Rostral to AI, a small field with a tonotopic gradient reversed with respect to that in AI (mirror image representation) was mapped and termed rostral auditory field (R). Best frequencies (BF's) in a range from 0.1-30.0 kHz were found in AI and R, with higher spatial resolution for the representation of lower BF's up to 10.0 kHz. Responses obtained in AI as well as in R were strong, with narrow tuning and short latencies. Caudal to AI, two small additional, tonotopically organized fields, the dorsoposterior field (DP) and the ventroposterior field (VP), could be distinguished. In fields VP and DP, high BF's were situated rostrally, adjacent to the high frequency representation in AI. Low frequency representations were found in caudal part of DP and VP fields. Responses to tone burst within DP and VP were mostly weak, with longer latencies and broader tuning compared to those found in AI and R.*

Key terms: auditory cortex, microelectrode mapping, *Octodon degus*, tonotopic organization

INTRODUCTION

Previous electrophysiological mapping studies have provided evidence that the rodent auditory cortex, like that of other mammals, consists of multiple, topographically organized, cochlear projections. The tonotopy of the auditory cortex in rodents has not been investigated as extensively as that of cats, but several studies are available, e.g., from gerbil (Thomas *et al*, 1993; Scheich & Zuschratter, 1995), Guinea pig (Hellweg *et al*, 1977; Redies *et al*, 1989),

squirrel (Merzenich *et al*, 1976; Luethke *et al*, 1988), mouse (Stiebler, 1987) and rat (Sally & Kelly, 1988; Horikawa *et al*, 1988). In the auditory cortex of each investigated rodent, a large field with a complete and orderly tonotopic organization was found and described as primary auditory cortex (AI), following the definition of AI in the cat (Merzenich *et al*, 1975). As in the cat, responses within this field were sharply tuned and with short latencies.

Differences in AI among rodents are limited to the orientation of the tonotopic

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gradient and the disproportionate representation of certain best frequency (BF) ranges, which are important for certain behaviour, represented in greater detail or occupying a relatively larger area of the cortex. In the squirrel, low frequencies are represented rostrally and high frequencies caudally, while in the gerbil, Guinea pig, mouse and albino rat, a reversed arrangement of BF's was found. With the exception of mapping studies in the albino rat (Sally & Kelly, 1988), a secondary auditory field located rostral to AI could be defined in all rodents. Like the anterior auditory field (AAF) in the cat, BF's are organized as a mirror image of AI. Generally, this rostral field was smaller than AI, but the tone responses obtained were similar to those found in AI. Adjacent to AI, additional areas responsive to acoustic stimulation could be identified in the gerbil, squirrel, Guinea pig, rat and mouse. Altogether, the existence of two tonotopically organized fields with mirror image arrangement of BF's seems to be a general schema for the organization of auditory cortex in rodents. This prompted us to study the organization of the auditory cortex in a Chilean rodent (*Octodon degus*).

METHODS

Twenty adult male and female *O. degus* (weight range 250-300 g) were used for microelectrode mapping studies. Animals were anaesthetized with urethane, 1.4-1.8 g/kg i.p. initially, followed by supplementary doses given as required to maintain light anesthesia during the recording. After removing the skin and temporal muscle, the upper part of the temporal cortex was exposed leaving the dura intact, and covered with an oily erythromycin-cortisone mixture. Lower parts of temporal cortex were kept covered, because one large and many small blood vessels running along the temporal cortex may suffer large haemorrhages and hamper fine grain orthogonal penetrations in a grid type fashions. Electrode penetrations were carried out instead in a dorsal to ventral (tangential) direction, which also gave the

opportunity to obtain reliable 100 μm resolution of measurements along each track. Mapping studies with tangential electrode penetrations had also been carried out in the auditory cortices of the rabbit (McMullen & Glaser, 1982) and the opossum (Gates & Aitkin, 1982). To fix the animal in a stereotaxic frame, an aluminum bar was mounted on the skull by dental cement. As a reference point, we dye marked the bregma onto the cortical surface. Microelectrode penetrations were guided through a nano-stepper 3-D-micromanipulator. In any given experiment, penetrations were parallel to each other.

Tone bursts used for stimulation has durations of 250 or 500 ms, with rise and fall time of 5 ms, followed by pauses of 250 or 500 ms. Sounds were presented free-field to the ear contralateral to the recording side by a speaker (Sennheiser HD-424) and a high frequency speaker, placed about 10 cm from the pinna. A nearly constant sound pressure level (SPL) of 65 ± 5 dB (60-70 dB in the frequency range 0.1-35.0 kHz) was calibrated by a Bruel & Kjaer sound level meter at the position of the animal head. Frequencies were produced by a Rockland synthesizer. Selection of frequencies was in a pseudorandom fashion and with 5 or 10 repetitions by a computer, which displayed spike events as dots on line (Fig 7). Dot displays and their integration in the form of isointensity-frequency histograms were stored. Best frequencies of units were determined from the peak "on" responses in histograms (see Fig 7). Recordings were made with glass-insulated Elgiloy-electrodes (Suzuki & Azuma, 1976) or, for comparison, with 2 M KCl filled glass electrodes with tip exposure for recording small neurons clusters. For later reconstructions, most of the tracks were marked by iron (Elgiloy) depositions (8 μA , 10 s). During the whole experiment body temperature was maintained at 37°C with an electric heating pad. After mapping experiment (prolonged for up to 20 hours), the animals were decapitated and their brains were removed. Frozen sections of 40 μm thickness were made and stained with cresyl violet. To make track marking visible, the Prussian blue method was used.

RESULTS

From the 20 animals studied, 7 fine grain maps were obtained, focussed on different subfields of the auditory cortex and its immediate neighbourhood. Each map was obtained from one animal and shows BF's of 65 dB isointensity responses, obtained from tangential penetrations in the left auditory cortex (Fig 1).

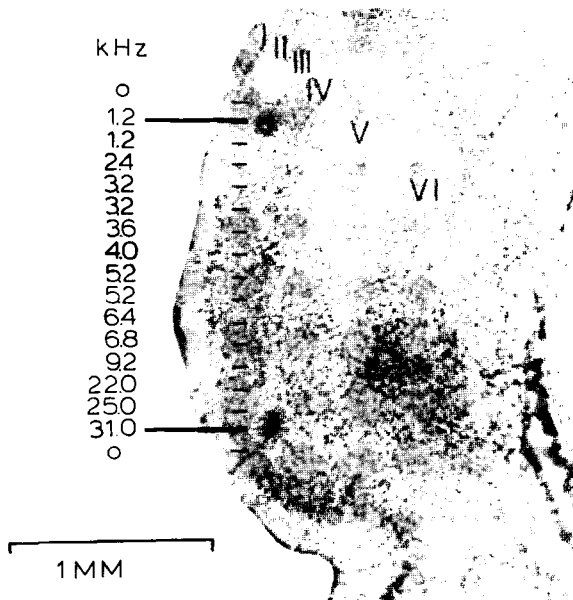


Fig 1. Photomicrograph of 40 µm thick Nissl stained frontal section in rostral (R) auditory field. Determinations of best frequencies (in kHz) made at 100 µm intervals along track indicated by small black bars. Beginning and end of electrode penetration marked by iron deposition, as seen by black dots. Note that this track runs within layers III/IV nearly parallel to cortical surface.

The BF's plots in the charts correspond to cortical sites located within different subfields termed primary auditory (AI), rostral auditory (R), dorsoposterior (DP) and ventroposterior (VP) auditory fields. As described in previous studies (e.g., McMullen & Glaser, 1982; Kass, 1982), boundaries between neighboring fields can be defined on the basis of characteristic changes of BF gradients while progressing from one field to the next. Other criteria, such as response latencies or spontaneous activity, are less suitable, because these parameters may vary with the anaesthesia level of the animals. However, differences

in these response properties between cortical fields were also taken into account for discrimination of subfields. Best frequencies were obtained mostly from neurons and neurons cluster located within superficial and lamina IV cortical layers, where stronger responses were recorded compared to those of other layers. Here, most of the neurons showed "on" and short latency discharges. Due to the curvature of cortex, tracks covered more or less of the dorsoventral extent of the auditory cortex, depending on the tangential depth of penetrations (Fig 1). The variation in the length of isofrequency contours in some of the maps and between different maps may be due to some extent to this bias. Results of the mapping studies are depicted in figures 2 to 6.

Primary auditory field (AI)

The field located in the central position within auditory cortex, with the largest extent among all described auditory field, was called primary (AI) field. It represented a geometrically simple and precisely arranged tonotopic map. Neurons and neuron clusters within this field were characterized by short latency responses (10-25 ms) and narrow tuning, with well defined BF's (Fig 7a). The rostroventral region was characterized by neurons with the lowest BF's (0.1 kHz) (Figs 2, 3, 4), whereas neurons in the caudal region were associated with higher BF's [34.0 kHz (Fig 2) and 35.5 kHz (Fig 5)]. Figures 2, 3 and 5 show the results of three experiments in which AI was mapped in detail. In nearly all tracks, BF's decreased from dorsal to ventral position. Furthermore, tracks located rostrally contained lower BF's than those situated in more caudal regions. Isofrequency contours were interpolated by hand. They roughly took a diagonal course. However, isofrequency contours located in the dorsal region of AI were generally oriented in a dorsoventral direction, while in the ventral part of the auditory field they bent caudoventrally. The longest isofrequency contours were generally found in a range of BF's between 1.0-10.0 kHz, which is not due to a bias of the cortex curvature.

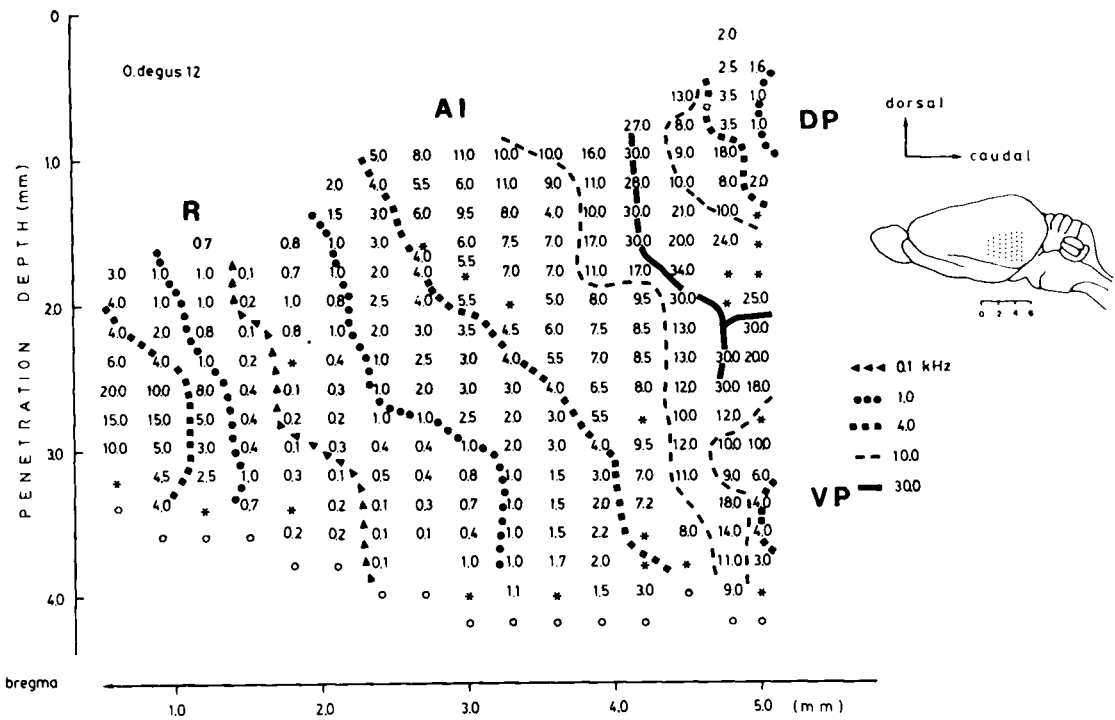


Fig 2. Lateral view of left temporal cortex in one specimen of *O. degus*. Best frequencies (in kHz) from recording sites obtained in tangential (dorsal to ventral) penetrations. Distance between tracks, about 200 μ m. Determinations of BF's carried out each 100 μ m within a track. Orientation of four isofrequency contours indicated by different symbols: 0.1-0.2, 1, 4 and 10 kHz, respectively. Individual variation of course of isofrequency contours among animals made evident by comparing figures 2 and 3. Responses of neurons and neuron clusters where no BF or BF range was obtained, marked by asterisks. Recording sites unresponsive to acoustical stimulation shown by open circles, indicating approximate boundaries of different areas. Bregma used as zero reference for anterior-posterior axis.

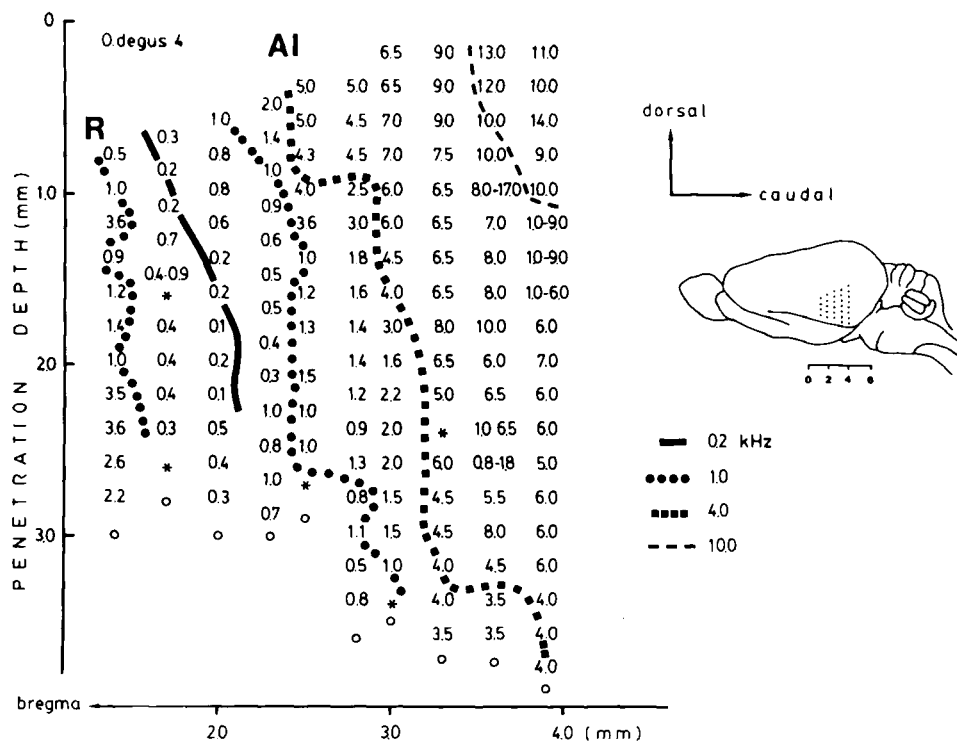


Fig 3. Lateral view of left temporal cortex in another specimen of *O. degus*. Legend as in figure 2.

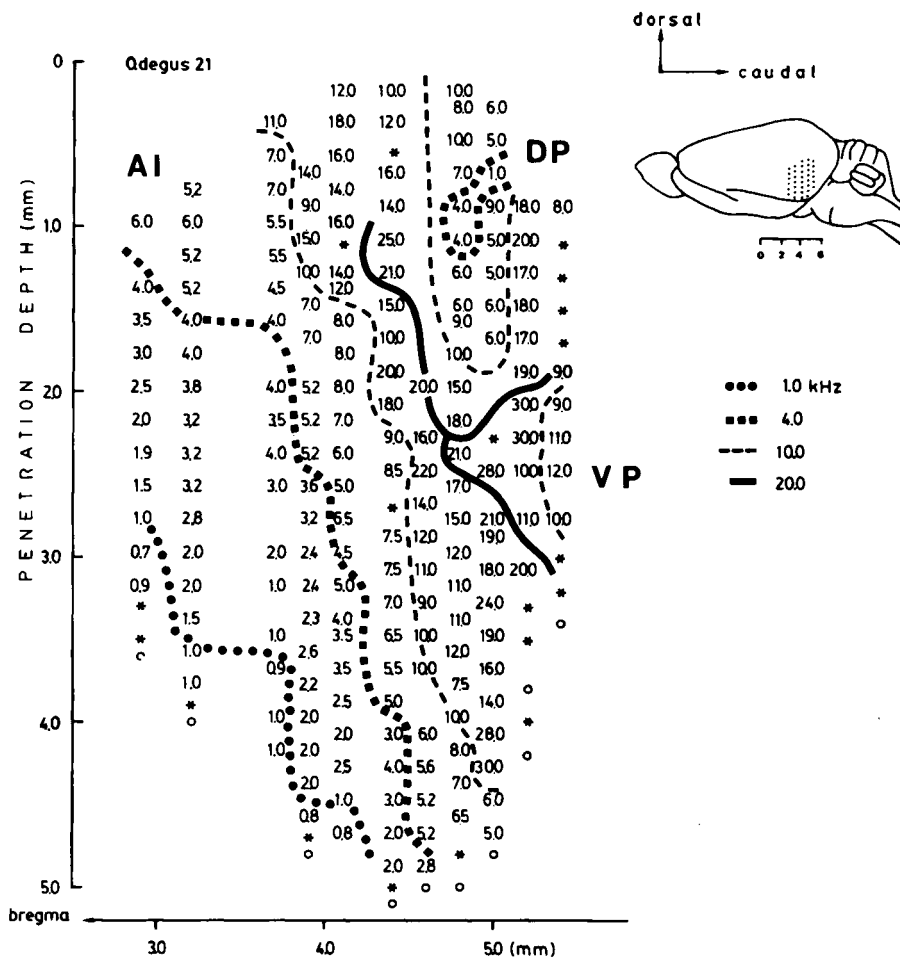


Fig 6. Best frequencies plots for recording sites in fields AI, DP and VP. Boundaries indicated by isofrequency contours for high frequencies (20 kHz) shown by dotted line. Rest of legend as in figure 2.

Rostral (R) auditory field

Recordings in rostral parts of auditory cortex showed reversed BF gradient compared to the frequency organization found in AI. Based on its location with respect to AI, this region was called rostral (R) auditory field. As illustrated in Figures 2 and 4, BF's in tangential penetrations showed decreases in both ventral to dorsal, and rostral to caudal directions. High best frequencies were located rostro-ventrally while low frequencies came to lie near the low frequency representation in AI. Thus, both fields, AI and R, form a mirror image with respect to their frequency representations. Although R has nearly half of the extent of AI, a complete and orderly representation

was recorded from this field, with frequencies ranging from 0.1 to 30.0 kHz. Isofrequency contours were roughly parallel to those found in AI.

Multiunit responses recorded in the transition region between of AI and R were often broadly tuned, with a bandwidth of 4 or 5 octaves, and very short latencies (10.15 ms) (Fig 7b). Responses from other regions of R were comparable to those found in AI.

Dorsoposterior (DP) and ventroposterior (VP) auditory fields.

Caudal to AI, two additional tonotopic representations were identified and termed dorsoposterior (DP) and ventroposterior (VP)

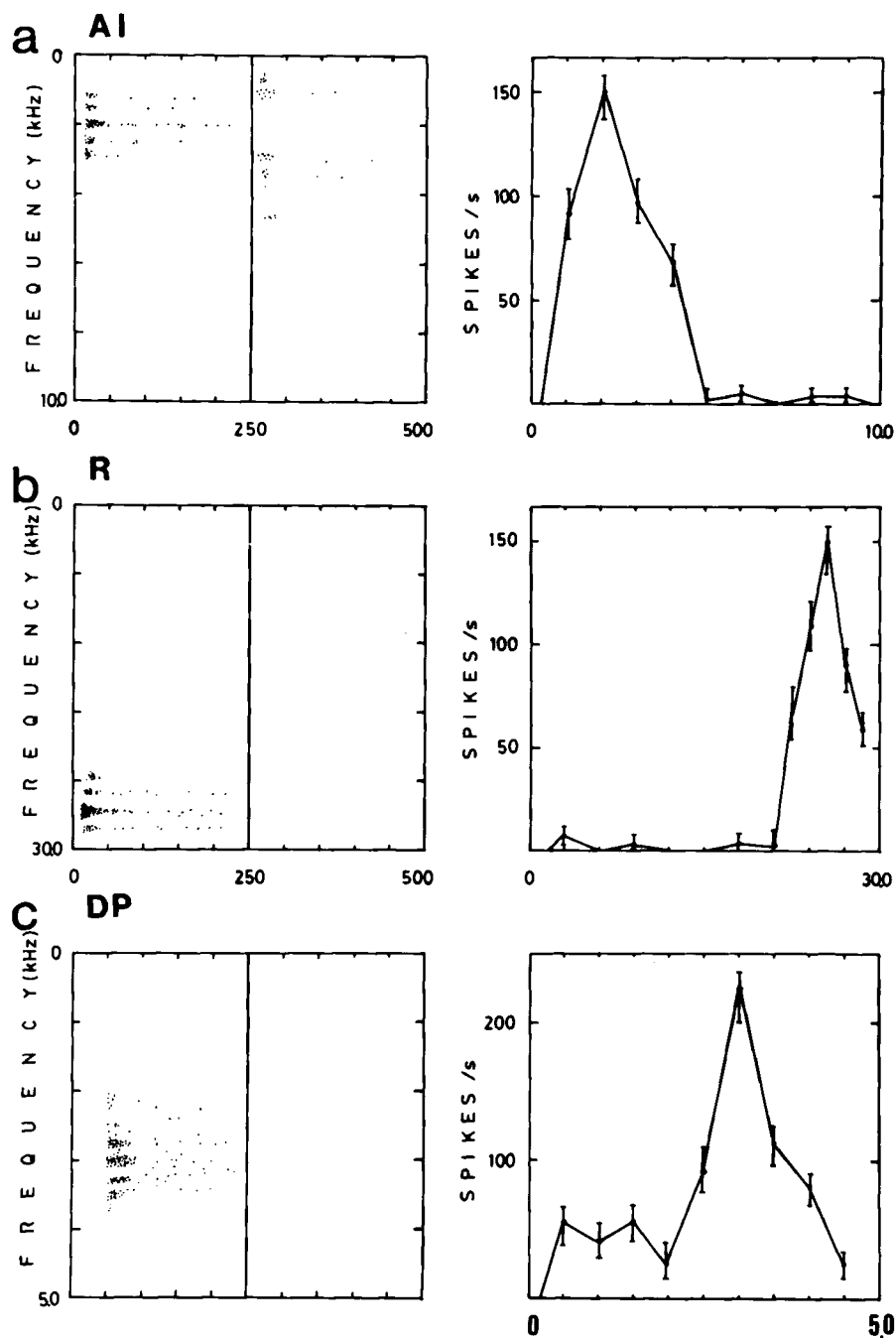


Fig 7. Left column, selection of some typical isointensity responses at 65 ± 5 dB sound pressure level to pure tone stimuli (0 ms tone on, 250 ms tone off) obtained in different fields (AI, R, DP). Ordinates, frequency axes, varying between 0-10 kHz (a), 0-30 kHz (b), and 0-5 kHz (c). Abscissae, time from 0 to 500 ms. Dot displays divided into tone "on" (left) and tone "off" (right). Right column, BF's determined in histograms. Spike events (ordinates) counted for each frequency (abscissae) in a determined time window (depending on response duration) and standardized to 1 s. Vertical bars, standard deviations.

fields (Figs 2, 5, 6), in analogy to the caudal fields reported in the cat (Reale & Imig, 1980). A tonotopic gradient was determined

in both fields. The frequency progression in DP and VP was opposite to that found in AI, *i.e.*, higher BF's were represented rostrally,

and lower BF's in the caudal parts of DP and VP. Best frequencies of between 1.0 and 30.0 kHz could be determined. The borders between the caudal fields, as well as between the caudal fields and AI, were located in the high frequency regions.

Responses to auditory stimuli were more difficult to elicit in the caudal fields than in AI or R, because there was large variability in spontaneous activity and neurons were often characterized by rapid habituation upon exposure to successive stimuli. Furthermore, responses in DP and VP were often weak, with latencies of up to 50 ms (Fig 7c).

DISCUSSION

The present study shows that the auditory cortex in *Octodon degus* is similarly organized in terms of subdivisions and tonotopic representations as in the cat and monkey, species traditionally considered as having a more advanced cortical organization. This leads to a variety of questions with respect to the homology of primary and secondary auditory areas.

The present electrophysiological experiments have provided evidence for the existence of two large and mirror-imaged tonotopically organized auditory fields in *O. degus* cortex. Within a rostral field, high frequencies were found to be located rostrally and low frequencies caudally, while a reversed arrangement of frequencies could be observed in a posterior field. In both fields, isofrequency contours had a roughly dorsal to ventral orientation. Following the nomenclature of auditory fields in the owl monkey (Imig *et al.*, 1977) and squirrel (Luethke *et al.*, 1988), the anterior field was named R and the posterior field AI. On the basis of electrophysiological data, four criteria were used for identification of the primary auditory (AI) cortex: *i*- it is the largest field; *ii*- it represents the complete hearing range; *iii*- it shows the longest dorsoventral isofrequency contours; *iv*- it has the best spatial resolution of the tonotopic gradient.

Primary auditory field AI

The organization of AI in *O. degus* with low BF's located rostrally and high BF's

caudally is comparable to that observed in AI of the squirrel (Merzenich *et al.*, 1976; Luethke *et al.*, 1988) as well as in primates like owl monkey (Imig *et al.*, 1977), macaque monkey (Merzenich & Brugge, 1973) and common marmoset (Aitkin *et al.* 1986b). A reversed organization was found in the cat (Merzenich *et al.*, 1975; Reale & Imig, 1980), gerbil (Thomas *et al.*, 1993; Scheich *et al.*, 1993; Scheich & Zuschratter, 1995), mouse (Stiebler, 1987), rat (Sally & Kelly, 1988; Horikawa *et al.*, 1988) and Guinea pig (Hellweg *et al.*, 1977; Redies *et al.*, 1989) as well as in a marsupial, the Northern native cat (Aitkin *et al.*, 1986a). A tonotopic gradient with high frequencies located dorsally and low frequencies ventrally was described in AI of the rabbit (McMullen & Glaser, 1982), ferret (Kelly *et al.*, 1986; Shamma *et al.*, 1993) tree shrew (Oliver *et al.*, 1976) and galago (Brugge, 1982).

It is notable that one auditory primary field which seems to be homologous-according to several physiological and anatomical criteria- has taken such differential developmental lines. Even, members of same taxonomic order, like rodents (compare *O. degus* to gerbil, mouse and rat) have divergent orientation of the frequency gradient of AI field. This can also be observed comparing carnivores (cat and ferret) and marsupials (opossum and Northern native cat).

Merzenich *et al.* (1976) suggest that the AI field has rotated in different directions along different lines of development. For old world monkeys, one could conceive that the reversed orientation of AI compared to that of the cat might be a consequence of the infolding of the suprasylvian plane during evolution, as described by Hines (1922). Since rotations are found in lissencephalic mammals, this reasoning is not generally applicable and other rationales have to be found.

The isofrequency contours of AI in *O. degus* are orientated in a rostrodorsal to caudoventral fashion, where frequencies up to 10.0 kHz represent longer contours than higher frequencies. This is in contrast to the results found in the cat, Guinea pig and squirrel, where high frequency contours are most expanded. Differences in the course

of isofrequency contours of the same BF's could be seen among animals. In a few animals they run nearly diagonal from dorsal to ventrocaudal (Figs 2, 3), while they were mostly orientated in a dorsal to ventral direction in the upper half and bend in a more diagonal and caudal direction in the ventral half of the contours. In the cat, a large variability in the orientation of isofrequency contours has been reported (Merzenich *et al*, 1975).

Rostral field R

Rostral to AI an additional cochlear representation could be mapped in *O. degus*. Here, high BF's are represented rostrally, while low frequencies form the caudal border. Despite the fact that this field is spatially less extensive than AI, with similar but reversed tonotopy, it has a lot of properties in common with AI. It represents a complete frequency gradient, and the responses to tone bursts show narrow tuning and short latencies. Differences between the two fields are mainly found on the reduced extension of R, which results in shorter isofrequency contours and a lesser frequency resolution. Isofrequency contours in R ran on a slant from rostral to caudal position and in the caudal half from dorsal to ventral direction, parallel to the isofrequency contours found in AI.

A mirror imaged organization of the AI field and an adjoining R field with a common low frequency border has also been reported for the squirrel (Merzenich *et al*, 1976; Luethke *et al*, 1988) and primates (Brugge, 1982). Representations with a common high frequency border, have been found in the cat (Merzenich *et al*, 1975), mouse (Stiebler, 1987), rat (Horikawa *et al*, 1988) and Guinea pig (Redies *et al*, 1989). In the rabbit, a second auditory (AII) field with a mirror image tonotopy was located dorsal to AI (McMullen & Glaser, 1982). This enumeration suggests the existence of two mirror-imaged tonotopically organized fields as a common principle of organization of the auditory cortex. Only one auditory field could be mapped in the opossum, Northern native cat, ferret, tree shrew and marmoset. In the ferret, marmoset and

Northern native cat, evidence for secondary fields, bordering AI has been found, but has not been investigated in detail. For example, anatomical studies concerning connections of marmoset's primary auditory cortex suggested additional secondary auditory fields located rostrally, caudally, and laterally to AI (Aitkin *et al*, 1988). The responsiveness to pure tone stimuli in R is similar and it is difficult to differentiate these two fields in *O. degus* based on their response characteristics. Similar results are reported for the cat, Guinea pig, rat and rabbit, while responses in the secondary field are clearly distinguished from those found in AI in the squirrel, whose responses are weak, with broad tuning and rapid habituation. A small field, located rostral to the anterior field, has been found in the Guinea pig. Within this small rostral field, neuron clusters have longer latencies and broader tuning than in the anterior field A (Redies *et al*, 1989).

Comparing the rostral fields of cat (AAF), gerbil (AAF), *O. degus* (R) and Guinea pig (A) to those of the squirrel (R), a homology appears unlikely. On the other hand, field R of the squirrel corresponds to fields S of the Guinea pig, regarding its response properties. The primary auditory field and the mirror imaged tonotopic organized adjoining field are poorly distinguishable by cytoarchitectonic criteria in *O. degus* (R/AI), gerbil (AAF/AI), Guinea pig (A/DC), squirrel (R/AI) and cat (AAF/AI). These fields are, however, quite different anatomically in the rabbit (Area I/II). Similar physiological properties of two fields do not necessarily include homogenous cytoarchitecture and vice-versa. Concerning the similarity of the auditory "field pair" DC/A in Guinea pig, Redies and Creutzfeldt (1987) discussed these two fields as one functional field having a discontinuous frequency representation. In the rat, Horikawa *et al* (1988) discussed AI/AAF as one area with a concentric frequency representation, where high BF's located in the center were surrounded by lower BF's. The hypothesis of one functional field can also be accepted for AAF/AI in the cat, rat, gerbil and *O. degus*. Due to the similar response characteristics

and anatomical connections of AAF and AI in cat, Phillips and Irvine (1982) assume that parallel processing of auditory information in both fields may be more probable than hierarchical processing. In this way, more information will be available to the auditory cortex in less time. This can give a possible explanation for the differentiation into separately organized tonotopies in advanced mammals, compared to primitive mammals like the opossum.

Caudal fields.

The DP and VP fields are organized with high frequencies represented rostrally and low frequencies caudally. Due to their organization, the caudal fields and AI contain a common high frequency border. Mapping studies in the auditory cortex of the rat (Horikawa *et al*, 1988) indicated the existence of two small organized tonotopic fields located dorsocaudally to AI (PD) and ventrorostrally to AAF (AV). Besides their tonotopy, both fields can be distinguished from AI and AAF by longer latency responses. In DP and VP of *O. degus*, which have similar physiological properties, responses are often weak, with long latencies and broad tuning, and they differ from the responses found in AI and R (Fig 7c). Furthermore, caudal fields appear to be more sensitive to anaesthetic conditions than AI and R. In cat's caudal fields P and VP, most neurons clusters show long latency discharges and can therefore be differentiated from AI and AAF. In the cat, a caudodorsal DP field forming part of a peripheral auditory belt is described, where some neurons are as responsive as in AI, while others are less responsive to tone burst, respond over several octaves or exhibit multiple BF's (Reale & Imig, 1980).

With respect to the different response characteristics of auditory fields in *O. degus*, it must be considered that all data are based on isointensity responses from multiunit clusters. It is probable that more field specific differences in response characteristics, for example tuning and latency, could be obtained by using single unit recordings and BF's determinations at threshold. An increase in sound intensity

above threshold possibly leads to a shift of BF's to higher or lower values, simply expanding substantially the range of frequencies (Aitkin, 1976; Kass, 1982). This might be a significant problem when neurons have different thresholds within or in adjoining fields, and could result in a distortion of tuning and BF's representation. However, the aim of this study was to give an idea of the tonotopic organization rather than to investigate physiological characteristics of each field in detail.

The summary map of Figure 8 shows pooled data from the frequency representations in all the specimens of *O. degus* here studied. Within this map, different extents of auditory fields become clearer. Of the total area responsive to acoustical stimulation (about 14 mm²), the primary auditory field represents approximately nearly one half. This could also be seen in most of the investigated species, where the prominent field occupies about half of the total mapped auditory cortex. To clarify the distribution of different frequencies, four ranges were selected and represented by different symbols. In AI, from where most data were obtained, frequencies between 0.1 and 10.0 kHz occupy about 80% of the mapped surface of AI. A disproportionate representation of frequencies is found in other rodents, like the rat (Sally & Kelly, 1988), where frequencies between 8.0 and 40.0 kHz occupy the main surface of AI, and the Guinea pig (Hellweg *et al*, 1977), for medium frequencies between 12.0 and 15.0 kHz. In the rabbit, the BF's range of 1.0-18.0 kHz, which correlates with the sensitive range of behavioral audiogram, is represented in greater detail in the primary field (McMullen & Glaser, 1982). Further overrepresentations of frequencies are reported in the cat for high frequencies (Merzenich *et al*, 1975) and in primates for middle frequencies (Aitkin, 1976), as well as in bats for ultrasound (Suga, 1982; Radtkeschuller & Schuller, 1995), where a very good correlation between self produced sound emission and frequency overrepresentation could be seen.

The present study shows that the organization of the auditory cortex in *O.*

degus, with its four tonotopic auditory fields, is more complex than that described for other rodents. Merzenich and Kass (1980) discussed the existence of two auditory cortical fields as “ancestral characteristics of lissencephalic mammals”. This is in contrast to the observations performed in *O. degus*, gerbil, mouse, rat and Guinea pig, and leads to the conclusion that parcellation of auditory cortex cannot simply be related to the phylogenetic level of a given species. More detailed information about spatial organization of auditory fields in physiological as well as in anatomical aspects is needed to give a clearer description of the function of different fields. Several approaches have been intended to investigate properties other than frequencies, and for example it has been shown that temporal processing seems to be different in different fields of the cat auditory cortex (Schreiner & Urbas, 1988).

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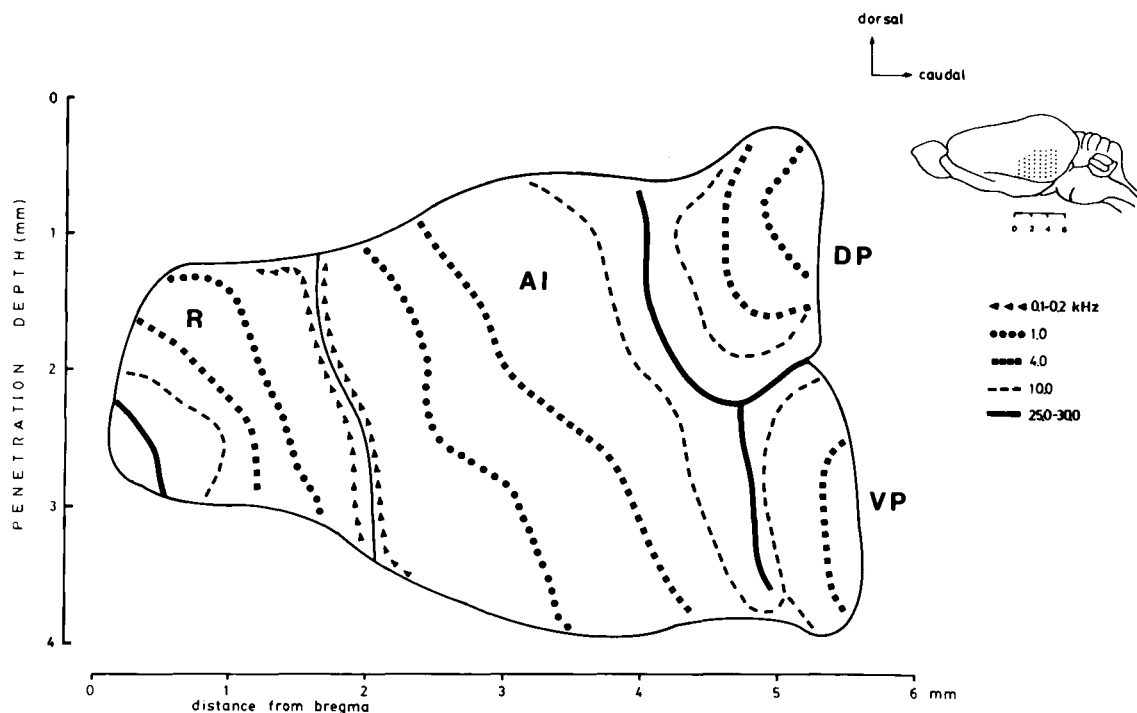


Fig 8. Summarizing schema of frequency organization in left hemisphere of *O. degus* cortex. Map derived by pooling data from individual cases shown in figures 2-6. Boundaries of different physiologically defined fields indicated by continuous lines. Selected isofrequency contours shown to facilitate survey of tonotopic arrangements.

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