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Functional Subdivisions in the Auditory Cortex of the Guinea Pig

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ABSTRACT

The auditory fields in the cortex of the guinea pig were investigated with microelectrode mapping techniques. Pure tones of varying frequencies and amplitudes were used as acoustic stimuli. Mainly, multiunit activity was recorded.

A large tonotopic area is found in the anterior half of the auditory cortex. This area is named the anterior field (field A). Frequency tuning curves of multiunits in field A are generally narrow. Responses to tone stimuli are strong, and latencies are short. Low best frequencies are represented rostrally, high best frequencies caudally. The tonotopy is continuous and quite regular. Field A is narrow dorsally and becomes gradually broader ventrally. Correspondingly, the isofrequency lines slightly diverge from dorsal to ventral.

Caudal to the first field, there is a second, smaller tonotopic area. It lies in the dorsal half of the posterior auditory cortex and is therefore named the dorsocaudal field (field DC). The frequency specificity of the cell clusters in this area is as strong as in field A, but the tonotopy is discontinuous: In the dorsal half of field DC, high best frequencies (16–32 kHz) are represented rostrally; the low frequencies (0.5–2.8 kHz) are represented immediately caudal to the high frequencies, while the intermediate frequencies are missing. Ventrally in field DC, the frequency representation is more complete. Except for this discontinuous map, we did not notice any differences between fields A and DC. A third tonotopic field was found rostral to field A. This field extends over a surface of less than 1 mm^2 and was named the small field (field S). It contains a complete representation of the frequency range; high best frequencies are located rostrally, low frequencies caudally. The response latencies are slightly longer in field S than in fields A or DC, and the tuning curves are broader.

A broad strip of nontonotopic cortex (auditory belt) surrounds fields A and DC caudally. We subdivided this area into the dorsocaudal and the ventrocaudal belt region. In both areas, tuning curves are often broad, and response latencies are longer than in the tonotopic cortex. In the dorsocaudal belt, most multiunits react with a phasic on-response to pure tones; in the ventrocaudal belt, tonic responses occur more frequently. Another nontonotopic region is located in the anterior auditory cortex, rostral to the tonotopic fields, and was therefore named the rostral belt. Tuning curves in this area are broad, latencies are short, and reponse thresholds are often high.

In the discussion, the guinea pig is compared with other mammalian species. Species-specific features in the organization of the tonotopic cortex of the guinea pig are revealed.

Key words: tonotopy, cortical fields, comparative physiology

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An important organization principle of the auditory cortex is tonotopy. A cell's best frequency (BF) is the frequency to which the cell has the lowest response threshold. Tonotopy means that cells are arranged in an orderly way according to their BF. For example, in the primary auditory cortex (AI) of the cat, cells with high BFs are situated anteriorly and cells with low BFs are located posteriorly (for review see Woolsey, '60; Merzenich et al., '79).

Tonotopic organization has been used as a criterion to define functional subunits in the auditory cortex or other parts of the auditory system. It is generally assumed that a complete representation of frequency range in the cortex corresponds to an auditory field; in the cat, there are at least four representations of the frequency range, and they are interpreted as four different functional areas. In other parts of the auditory cortex, a frequency-dependent organization does not exist or is difficult to demonstrate (Merzenich et al., '79; Reale and Imig, '80).

Most of the work on the functional subdivisions of the auditory cortex has been carried out in cats, primates, and bats (for review see Imig and Morel, '83; Creutzfeldt, '83; Brugge and Reale, '85). Detailed reports about other mammalian species are less common, but it is necessary to obtain precise information about other species if one wants to know which traits of auditory cortex organization are part of a general mammalian pattern and which are species specific.

In the present study, the organization of the auditory cortex of the guinea pig *Cavia porcellus* was investigated with microelectrode mapping techniques. The guinea pig is an inexpensive and easily available laboratory animal with good audition (and has therefore been extensively used in research on the peripheral auditory system). It has a lissencephalic cortex, which is an obvious advantage for studies of tonotopy, since the tonotopic structures are not distorted by the uneven course of a gyrus or hidden in the banks of a sulcus, as occurs in gyrencephalic species such as cats or advanced primates.

There are two previous reports of functional fields in the guinea pig's auditory cortex: Kayser and Legouix ('63) recorded extracortical potentials evoked by tones of three different frequencies and defined two tonotopic fields in the guinea pig's auditory cortex. In an anterior area, low frequencies are represented rostrally and high frequencies caudally. In a posterior field, the tonotopic gradient is reversed. Hellweg et al. ('77) confirmed these results and in addition discovered a cortical zone with strong over-representation of 12.5–15.5-kHz tones, which was interposed dorsally between the two tonotopic areas.

The work begun by the authors cited above leaves several questions open, and some of these are addressed in the present paper:

1. Are there other, not-yet-discovered auditory fields in the guinea pig cortex? What are the neuronal response characteristics (frequency specificity, response latencies, etc.) of the tonotopic fields in the guinea pig cortex? Is the "12.5–15.5-kHz area" described by Hellweg et al. a functional unit in its own or is it part of the anterior and/or posterior field?
2. Which traits of the auditory cortex of the guinea pig are shared by other species? Is it reasonable to postulate functional analogies between the auditory fields of the guinea pig and of other species?

Some of the data presented in this paper have been published in preliminary form (Redies et al., '86). The thalamic afferents to the different fields of the auditory cortex in the guinea pig are described in a companion paper (Redies et al., '88).

MATERIALS AND METHODS

Surgery and anesthetics

Young adult guinea pigs (body weight 450–650 g) of either sex were used. The animals were initially anesthetized with a combination of the neuroleptanalgesic drug *Hypnorm* (1.2 ml/kg i.p., i.e., 0.24 mg/kg fentanyl base and 12 mg/kg fluanisone) and the tranquilizer *Valium* (diazepam, 0.4 mg/kg i.m.) (Green, '75). In addition, *Atropin-Pos* (atropine sulfate, 0.1 mg/kg, s.c.) was given to inhibit tracheal secretion and *Solu-Decortin* (10 mg/kg s.c., prednisolone-21-hemisuccinat-natrium) to prevent brain edema.

After introducing a catheter into the saphenous vein and cannulating the trachea, the cranium over the auditory cortex was removed and the dura was carefully resected. The exposed cortex was covered with a warm 3% suspension of *Agar-Agar* dissolved in Ringer's solution. The animal's head was fixed rigidly in a head holder appropriate for auditory experiments (Kaplan et al., '83).

The animal was paralysed with an initial dose of 10 mg/kg *Flaxedil* (gallamine triethiodide, 2% solution in Ringer) and artificially respirated with a rodent respirator (rate: 75–90 cpm, tidal volume: 2–3 ml). The end-expiratory CO_2 level was monitored and adjusted to 3.5–4%. During the experiment, a solution containing 0.02 mg/kg/hour fentanyl base, 8 mg/kg/hour gallamine triethiodide, and 10 mg/kg/hour sucrose dissolved in Ringer was continuously administered. A local anesthetic (xylocaine) was applied onto the surgical wounds at intervals of 2–3 hours. Body temperature was maintained at 37°C.

Acoustic stimuli

Pure tones were used as acoustic stimuli. The tones were generated in a real-time table-lookup procedure by a PDP-11/73 computer extended with a TZQ-11 signal coprocessor. The tones were 100 ms long, trapezoideally shaped, and had a rise/fall time of 8 ms. The experiments were conducted in a sound-shielded room.

Electroacoustical transduction was mediated by a ½" Brüel and Kjaer condenser microphone polarized with 250 V DC and driven at signal amplitudes below 30 V rms. Quadratic distortions were not compensated. The signals were transmitted from the microphone to the animal through a small plastic pipe sealed into the external auditory meatus. Before each experiment, for all stimulation frequencies, the ratio between the electrical signal and the sound pressure inside the small plastic pipe was measured by a Brüel and Kjaer ¼" condenser microphone. During stimulation, signal amplitude was adjusted according to these values, to assure equal intensities for all frequencies.

Mapping techniques

Electrodes were broken glass pipettes filled with 3 M KCl; the impedance was 1–3 MΩ tested at 1,000 Hz. The electrode signal was band-pass filtered (1–5 kHz), conventionally amplified, and displayed on an oscilloscope. Neuronal action potentials (multiunits) were discriminated from noise by appropriately adjusting the level of a Schmitt-trigger. Detected spikes were fed on-line into a laboratory computer (PDP 11/73).

Abbreviations

A	anterior field (guinea pig)
AAF	anterior auditory field
AI	primary auditory field
AII	secondary auditory field
BF	best frequency
DC	dorsocaudal field (guinea pig)
DCB	dorsocaudal belt (guinea pig)
Fiss. sylv	sylvian fissure
IFS	isofrequency strip
MG	Medial geniculate body
MGv	Ventral nucleus of MG
PSTH	peristimulus time histogram
RB	rostral belt (guinea pig)
S	small field (guinea pig)
VCB	ventrocaudal belt (guinea pig)

The electrode was introduced into the cortex with a hydraulic microdrive on an axis approximately perpendicular to the cortical surface. While the electrode was advanced into the tissue, tones of various frequencies and clicks were presented to the animal. When stimulus-evoked activity was found, a tuning curve was recorded (see below); then the electrode was withdrawn and introduced into the next cortical site. Distances between penetrations varied from 0.1 to 1 mm but were about 0.5 mm in most cases.

We found it difficult to make recordings for a period longer than 6–12 hours. After that time, the cortical activity diminished or sometimes became epileptiform, and obviously physiological conditions were no longer normal. Similar problems with small lissencephalic animals have been described in the literature (see, e.g., Dräger, '75). The guinea pig is reported to be a particularly sensitive animal, because of the lability of its cardiovascular system (Green, '75; Evans, '79).

In order to construct reliable maps of the auditory fields, we had to record from as many loci as possible (25–60, see Results) in a relatively short time period. Therefore, no time-consuming single-cell recording was attempted. Instead, we recorded multiunit activity. (For a discussion of mapping techniques in the cerebral cortex see Kaas, '82.)

Because of the above-mentioned time restrictions, it was impossible to map the whole auditory cortex within a single experiment in sufficient detail; therefore, we did two experiments to obtain overview maps with relatively low spatial resolution (Fig. 1a,b) and then proceeded by carefully mapping smaller areas and superimposing these on the overview maps.

Tuning curves and BF determination

Frequency tuning curves were recorded by running a computer program that simultaneously controlled stimulus generation, data acquisition, and data storage and displayed an on-line tuning curve (similar to those shown in Figs. 2, 4, 6, 8) on a graphic screen. Off-line, peristimulus time histograms (PSTHs) and dot displays were routinely generated. The tuning curves obtained during the experiment could be further processed by using appropriate time windows, which were normally centered around the cell's on-response.

In most cases, in order to obtain a tuning curve, tones of 13 different frequencies ranging from 0.5 to 32 kHz and with interfrequency intervals of 0.5 octaves were used, but the set of frequencies could be varied. The number and dynamic range of stimulus intensity levels were also variable. Typically, seven to nine different amplitudes, ranging from 0–20 to 80 dB SPL, were chosen (see Figs. 2, 4, 6, 8). The sequence of the different frequencies and amplitudes was randomized. Each tone was repeated three times, with an interval of 560 ms between consecutive stimuli. For example, to record a tuning curve with 13 frequencies and seven amplitudes,

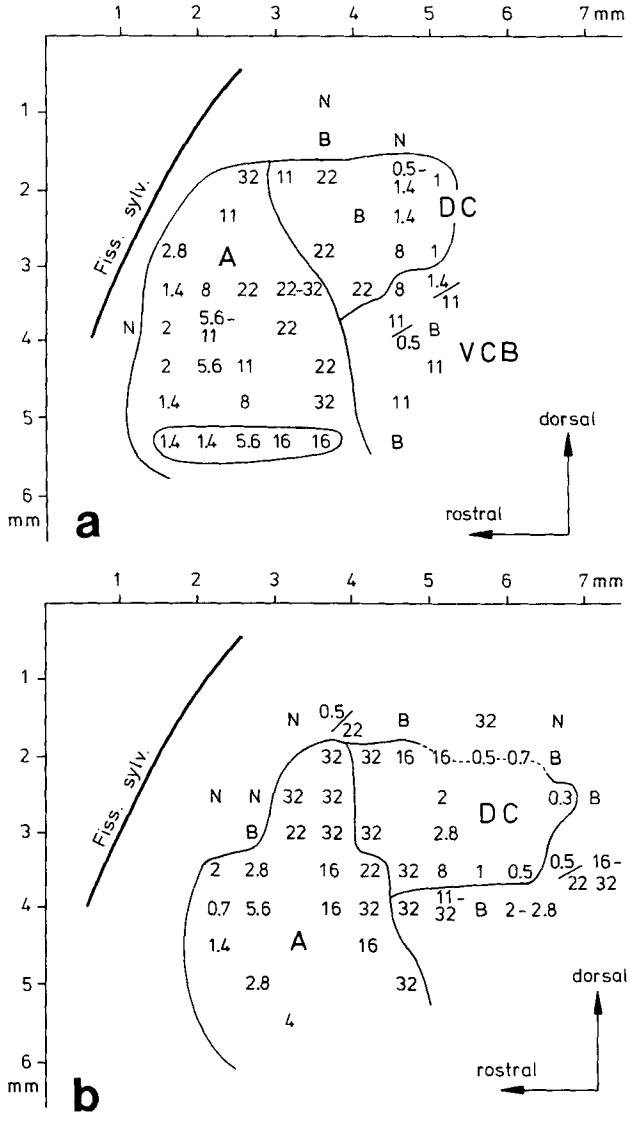

Fig. 1. **a:** A view of the surface of the auditory cortex with a BF map (animal MSE039). For orientation, the sylvian fissure is indicated. Each recording site is represented by a number or a letter. The numbers mean BFs in kHz. Two numbers separated by a slash (e.g., 0.5/22) represent double-peaked tuning curves with two "BFs." Numbers separated by a hyphen (e.g., 16–32) indicate that the cells had a BF range rather than a single BF. The letter B stands for broad tuning curves; i.e., a BF could not be determined. The letter N means no response to pure tones. In this experiment, fields A and DC were mapped with relatively large distances between penetrations (overview map). A part of the VCB is also apparent. As an example of a comparatively irregular frequency progression, the most ventral array of recording sites in field A is circled (1.4, 1.4, 5.6, 16, 16 kHz). For further explanations see text. **b:** Another overview map of the auditory cortex (animal MSE041). Fields A, DC, and parts of the belt region surrounding field DC are visible. The dorsal border of field DC cannot be unequivocally determined in this animal and is therefore represented by a broken line.

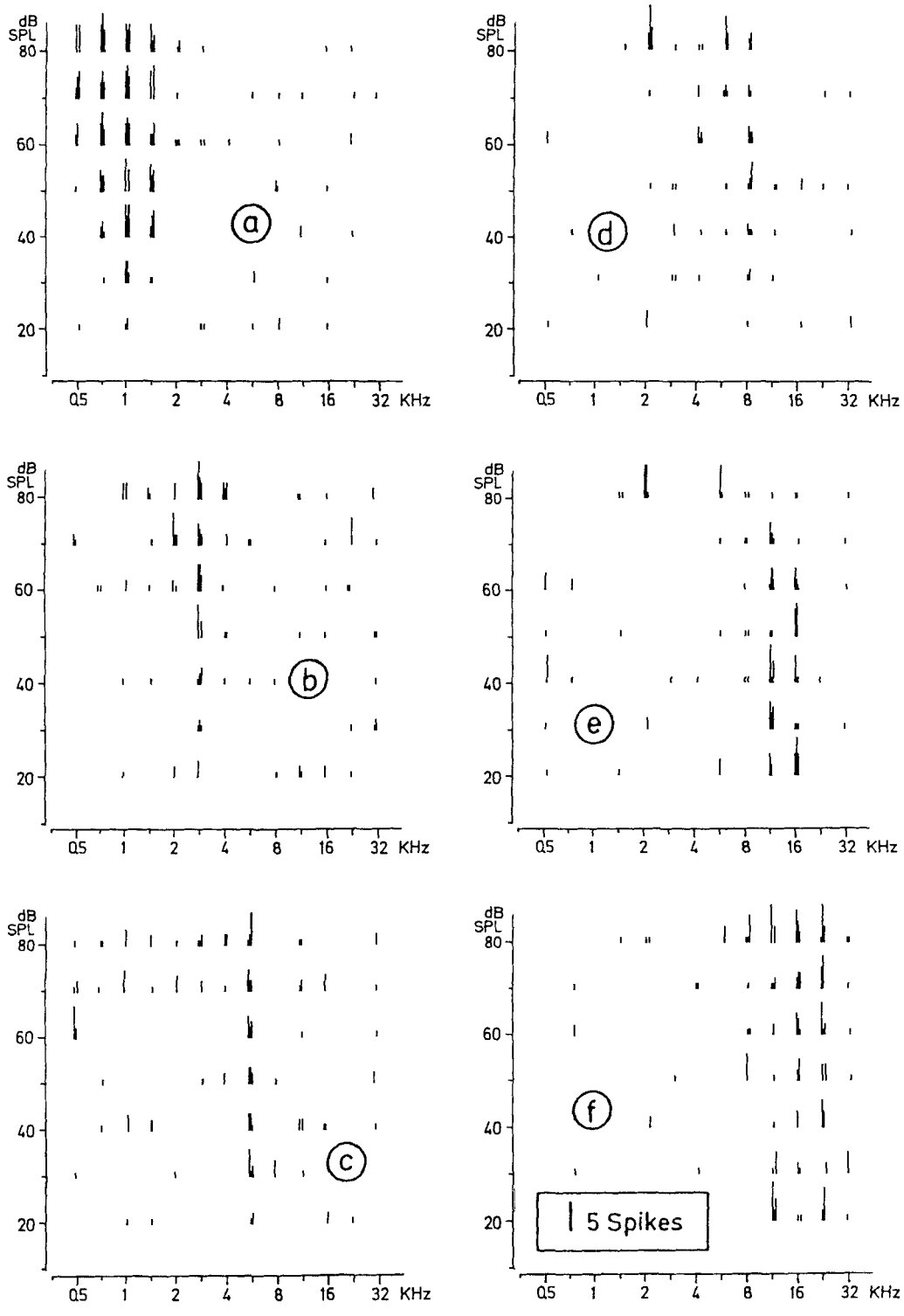

Fig. 2. A representative array of frequency tuning curves from field A (animal MSE032). For each tone of a given frequency (x-axis) and amplitude (y-axis), the number of spikes recorded in an appropriate time window is represented by a vertical bar in the corresponding coordinates. Since each tone was repeated three times, there are three vertical bars or less (points where the cells did not respond were left blank) for each possible frequency-amplitude combination. The **inset** in f shows the scaling for all graphs. See Materials and Methods for further explanations. These tuning curves were recorded in a row from rostral to caudal, with distances of 0.5 mm between penetrations: a is from the most rostral, f from the most caudal position. The six recording sites are bordered by a line in the map of this animal, which is shown in Figure 3a. The BFs and the time windows over which spikes were counted are (**a**) 1 kHz, 8–25 ms; (**b**) 2.8 kHz, 8–25 ms; (**c**) 5.6 kHz, 8–30 ms; (**d**) 8 kHz, 8–25 ms; (**e**) 11–16 kHz, 10–40 ms; (**f**) 22 kHz, 10–30 ms.

$13 \times 7 \times 3 = 273$ tones were emitted in about 3 minutes. Best frequencies were determined by visual inspection of the tuning curves and dot displays.

The tuning curves of some multiunits exhibited response maxima at two frequencies. These were labeled "double-peaked." When a cell group had more than two peaks or responded with equal intensity to a wide frequency range, it was classified as "broad." A further classification of tuning characteristics was not attempted. The reader should be aware that the terms double-peaked and broad are used here to describe multiunit activity and not the responses of single cells. Thus, we cannot decide whether, for example, the tuning curve of a cell cluster is broad because each cell is broadly tuned or because there are several cells with well-defined, but different BFs in the cluster.

Response latency determination

The response latency is defined here as the time elapsed between the stimulus onset and the maximum of the neuronal on-response (peak latency). A PSTH (bin width: 1 ms) was composed from the spikes recorded in response to all frequencies and amplitudes tested by the tuning curve program (see above). The PSTH was smoothed with a weighted window (five bins wide) prior to analysis. In most cases, a clear on-response could be identified. The latency was then calculated by finding the time difference between the beginning of the stimulus and the moment of occurrence of the peak. In cases where no on-response could be identified on the PSTH—for example, if a cell exhibited only a tonic response or an off-response—determination of latency was not done.

Peak response latency as defined above is different from minimum response latency, which corresponds to the time between stimulus onset and the moment of occurrence of the first spike. The latter measure can yield biased results if cells fire spontaneously shortly after stimulus onset. This is more probable in multiunit recordings than in single-cell recordings, and therefore the minimum latency measure was judged inappropriate for our purpose.

RESULTS

Results are reported from 23 successful experiments. Altogether, tuning curves were recorded from about 830 different cortical locations (25–60 sites per animal). Mainly, we recorded from cell clusters 500–1,000 μm below the pial surface, as responses to pure tones were strongest at this depth (Hellweg et al., '77).

In two experiments, overview maps of the auditory cortex were obtained (see Materials and Methods), which revealed the rough features of the structure of the guinea pig's auditory cortex (Fig. 1a,b). It is obvious from these maps that there are at least two tonotopic fields—namely, an anterior field (field A) and a dorsocaudal field (field DC). In addition, rostral to field A, we discovered a third, very small tonotopic area (field S) which was not apparent in the overview maps (but see Fig. 7a–c). These tonotopic areas are surrounded by auditory regions without tonotopic organization, the so-called "auditory belt" (Fig. 1a,b). This paper deals mainly with the tonotopic regions. The surrounding areas were less thoroughly investigated and will be only briefly described.

The tonotopic fields were identified and distinguished from each other mainly by their tonotopic gradient. The delimitation between the tonotopic areas and the surrounding belt region was based on the lack of tonotopy in the belt and on differences in response latencies, frequency specificity, and/or responsiveness to pure tones.

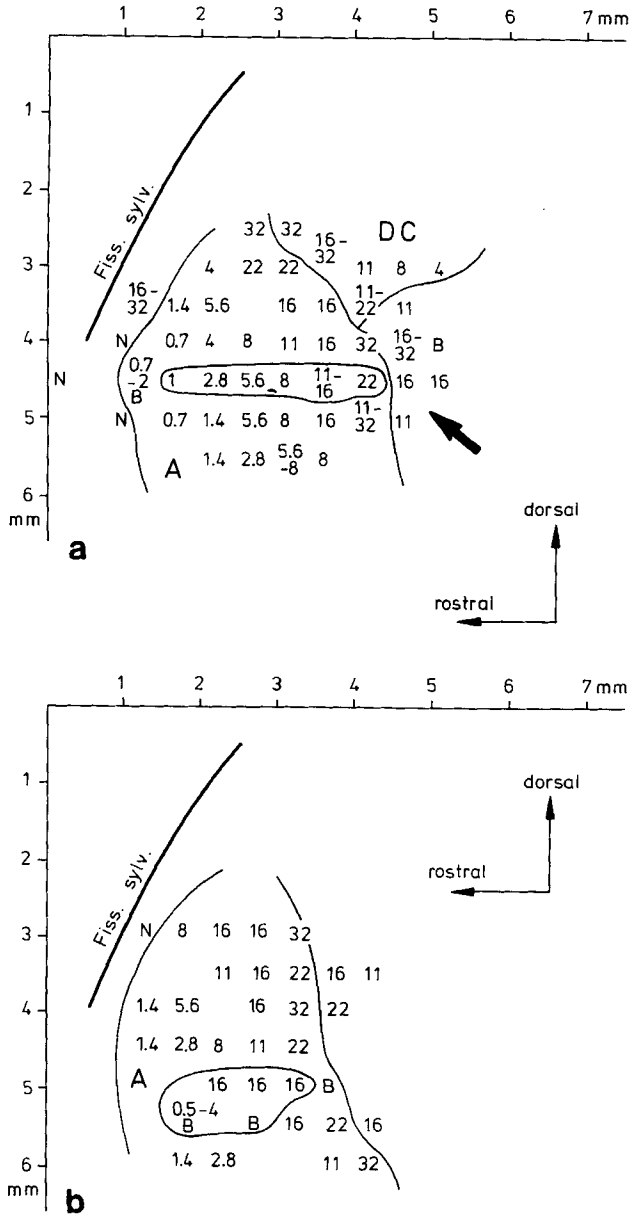

Fig. 3. **a:** Map of the auditory cortex (animal MSE032). Field A is almost completely mapped. The tuning curves corresponding to the circled set of BFs are shown in detail in Figure 2. The arrow points to some recording sites with high BFs (11 and 16 kHz) immediately caudal to field A, which seem to constitute a transition between field A and the VCB (not mapped in this experiment), as explained in the text. See Figure 1a for further specifications. **b:** Another map of field A (animal MSE033). The circled area is an extreme example of irregularities in the tonotopy of field A. See text and Figure 1a for further details.

It was not always possible to define the exact borderlines between neighbouring fields. This is mainly due to the limited resolution of the maps and sometimes to BF scatter (see next section). Of course, it is also possible that exact borderlines do not (always) exist between neighbouring fields: there might be zones of transition instead. Consequently,

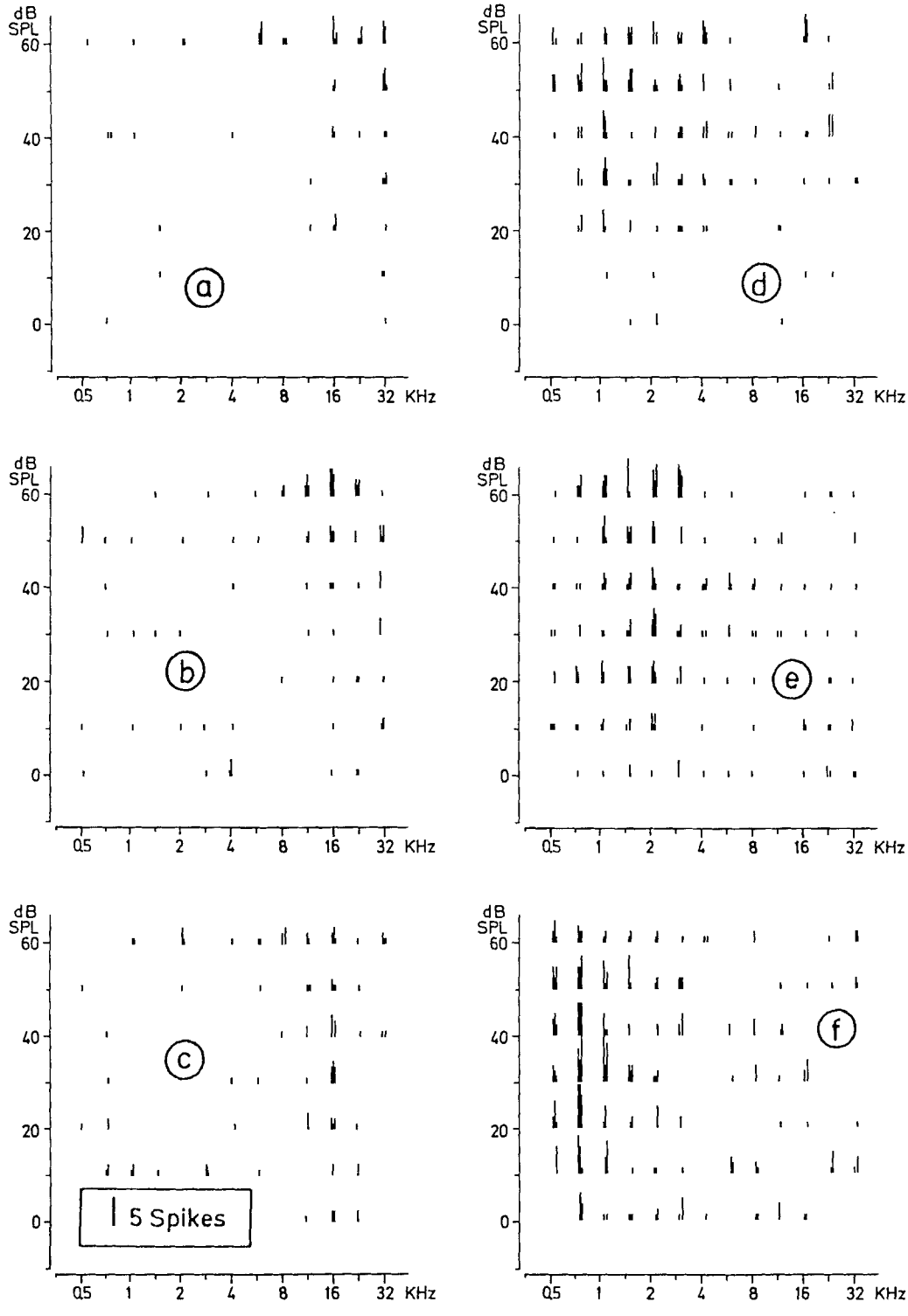

Fig. 4. A representative array of frequency tuning curves from field DC (animal MSE034). These tuning curves were recorded in a row from rostral to caudal, with distances of 0.5 mm between penetrations: a is from the most rostral, f from the most caudal position. The tuning curves correspond to the six recording sites circled in the map of MSE034, Figure 5a. BFs and time windows used are (**a**) 16–32 kHz, 10–30 ms; (**b**) 16 kHz, 10–30 ms; (**c**) 16 kHz, 10–30 ms; (**d**) 1/2.8 kHz, 10–30 ms; (**e**) 2 kHz, 8–25 ms; (**f**) 0.7 kHz, 10–110 ms. Further details as in Figure 2.

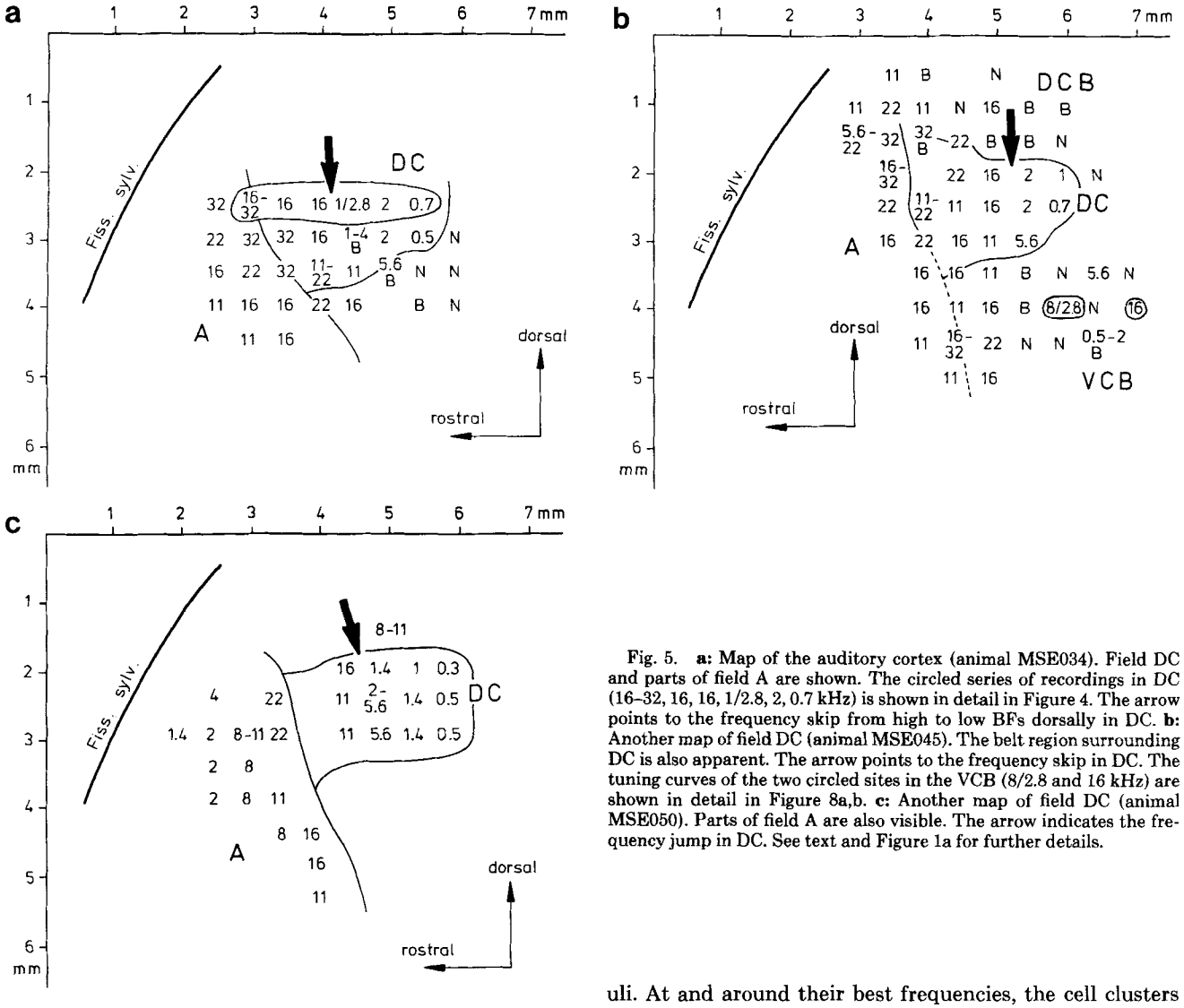

Fig. 5. **a:** Map of the auditory cortex (animal MSE034). Field DC and parts of field A are shown. The circled series of recordings in DC (16–32, 16, 16, 1/2.8, 2, 0.7 kHz) is shown in detail in Figure 4. The arrow points to the frequency skip from high to low BFs dorsally in DC. **b:** Another map of field DC (animal MSE045). The belt region surrounding DC is also apparent. The arrow points to the frequency skip in DC. The tuning curves of the two circled sites in the VCB (8/2.8 and 16 kHz) are shown in detail in Figure 8a,b. **c:** Another map of field DC (animal MSE050). Parts of field A are also visible. The arrow indicates the frequency jump in DC. See text and Figure 1a for further details.

the borders indicated in the maps (Figs. 1, 3, 5, 7) are to a certain extent arbitrary. The description of the multiunit response characteristics typical for each field based exclusively on recording sites unambigously located within that field. For example, the numerous recordings from the high-frequency border between fields A and DC (see below) were discarded from the analysis of response characteristics in these fields.

The anterior field (field A)

A large tonotopic area is situated in the anterior half of the temporal cortex, immediately posterior to the sylvian fissure. Because of its position, this area is labeled "the anterior field" (field A). Field A is relatively narrow dorsally and becomes increasingly broader ventrally. At its largest extent, it measures about 3–4 mm from rostral to caudal and about 5–6 mm from dorsal to ventral, but there are some differences between individuals.

Responses to pure tones, frequency specificity. In general, the neurons encountered 500–1,000 μm below the pial surface were found to respond vigorously to tone stimuli. At and around their best frequencies, the cell clusters typically exhibited an on-response. This was often followed by an inhibition or a tonic response during the tone. In addition, after the tone, off-responses were frequently observed. Reactions without an on-component—for example, pure tonic activation or pure off-responses—occurred only rarely.

Most of the tuning curves in field A showed a clear frequency specificity, and it was easy to determine a BF. A representative example of a series of recordings from field A is shown in Figure 2. The six tuning curves were taken in a row from rostral to caudal. The distance between consecutive recording sites was 0.5 mm.

Tonotopy. Field A is tonotopically organized. Low BFs are represented rostrally, medium BFs medially, and high BFs caudally. This gradient is clearly visible in the two overview maps (Fig. 1a,b) and in the more detailed maps (examples in Fig. 3a,b) of field A. The frequency gradient also appears in the series of tuning curves shown in Figure 2: the BF of the most rostral recording site is 1 kHz; proceeding further caudally, BFs of 2.8 kHz, 5.6 kHz, etc., were encountered.

The tonotopy in field A is rather regular. The scatter of BFs is so small that most of the BF series recorded from ros-

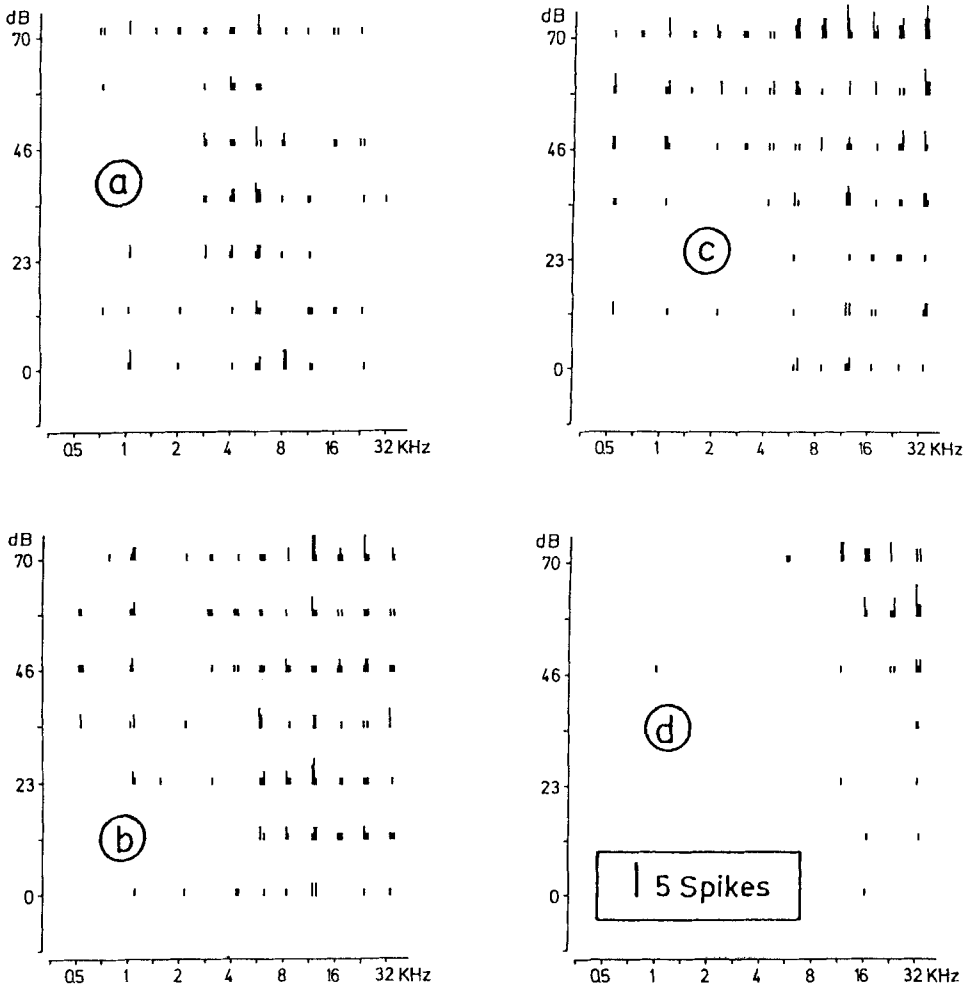

Fig. 6. A representative array of frequency tuning curves from field S (animal MSE044). These tuning curves were recorded in a row from rostral to caudal, with distances of 200–400 μm between penetrations: a is from the most caudal, d from the most rostral position. The map is shown in Figure 7b. The BFs are (a) 5.6 kHz; (b) 11 kHz; (c) 11–32 kHz; (d) 32 kHz. Time window was always 8–30 ms. Further details as in Figure 2.

tral to caudal (with distances of 0.5 mm between penetrations) can be characterized as "strictly monotonic ascending": the BF measured caudally is always higher than the BF of the nearest rostral neighbour. However, in some maps, irregularities were also apparent. For example, the ventral BF series in the map shown in Figure 1a (bordered by a continuous line) is 1.4, 1.4, 5.6, 16, and 16 kHz. This series is not "strictly monotonic," and the sudden jumps from 1.4 to 5.6 or from 5.6 to 16 kHz are atypical for the ventral part of A. Dorsally, the field is smaller, and the frequency differences between neighbouring recording sites tend to be greater.

Cells with similar BFs are arranged in isofrequency lines. These run from dorsal to ventral and are slightly curved. A slight divergence of the isofrequency lines, corresponding to the increase in size of field A, can be seen when proceeding from dorsal to ventral (see schematical drawing in Fig. 10). In the dorsal quarter of A, intermediate and high frequencies predominate. Recording sites with BFs below 4 kHz were found dorsally in two animals only, and in both cases, it is uncertain whether these sites are part of field A or of the adjoining rostral belt region (see below). We therefore conclude that, as a rule, the low isofrequency strips do not extend as far dorsal as the high BFs. The 32-kHz strip, which runs without interruption from the dorsal to the ventral end of the tonotopic cortex, constitutes the border between field A and field DC.

Latencies. The mean response latency to pure tone of multiunits in field A was 14.8 ms (Table 1).

The dorsocaudal field (field DC)

A second tonotopic field is situated caudal to field A. Since this region occupies the dorsal half of the caudal auditory cortex, it is named "the dorsocaudal field" (field DC). It

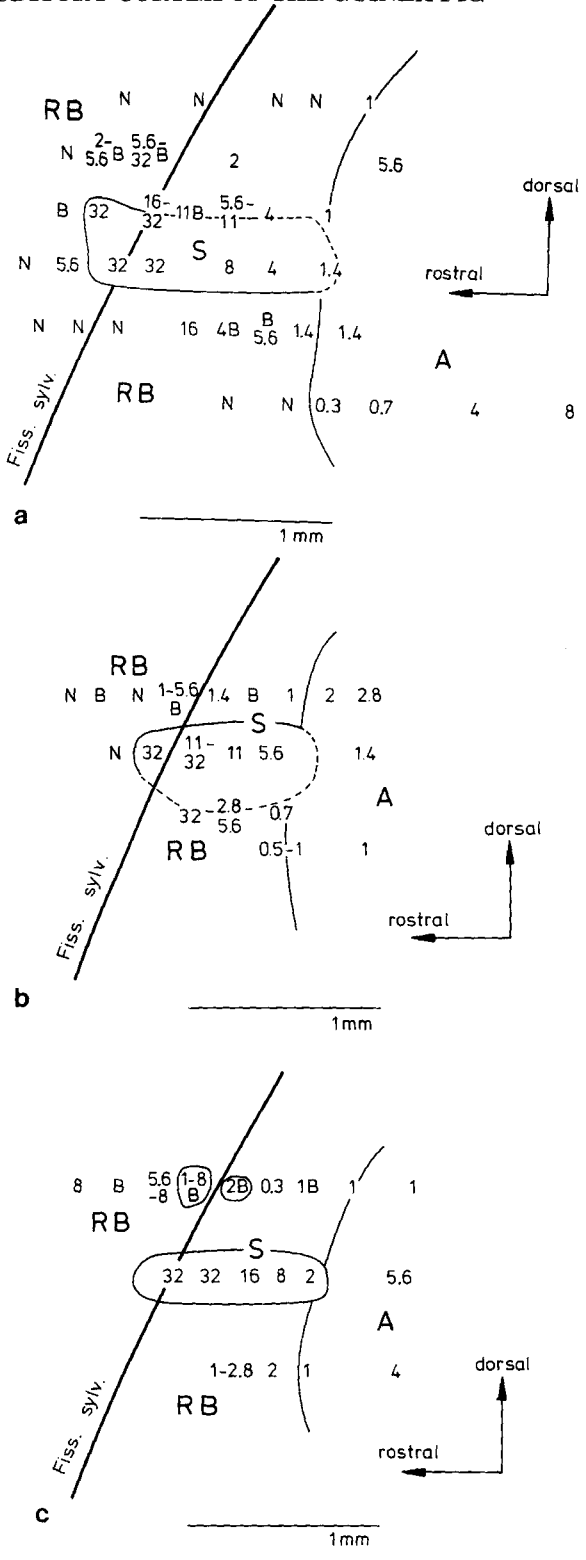

Fig. 7. **a** Map of animal MSE049. Field S, the RB, and parts of field A are apparent. The dorsocaudal borderline of S is difficult to define in this animal and therefore represented by a broken line. **b:** Another map of field S and parts of the RB and of field A (experiment MSE044). The four tuning curves in field S are shown in detail in Figure 6. The ventrocaudal border of field S is represented by a broken line since the map is not detailed enough to clearly define it. **c:** Map of animal MSE043. Field S and parts of field A and RB were mapped. The tuning curves of the two circled recording sites in the rostral belt are shown in Figure 8c,d. Note that the scaling in this figure is different from the maps shown in Figures 1, 3, 5. See text and Figure 1a for further details.

TABLE 1. Latencies in the Auditory Fields (in Ms)

Field	N	Median	Mean	Standard deviation
A	239	14	14.8	3.3
DC	101	15	14.9	2.9
S	42	16	15.6	2.1
VCB	11	23	23.6	5.7
DCB	22	17	20.3	7.1
RB	27	14	14.4	2.9

extends about 2.5–3 mm from rostral to caudal and at least 2 mm from dorsal to ventral. We obtained five complete maps (examples in Fig. 5a–c) and several partial maps (e.g., Fig. 1a,b) of this region. Field DC begins immediately caudal to field A. The fields have a common high-frequency (32-kHz) border. A region of overrepresentation of the 12.5–15.5-kHz frequency range dorsally between the two fields, as described by Hellweg et al. ('77), was not observed. Moreover, field DC occupies only part of the posterior auditory cortex. The rest of it consists, according to the present results, of nontonotopic regions (see below).

Responses to pure tones, frequency specificity. As in field A, nearly all cell groups in field DC responded to pure tones with an on-response, which was often followed by a tonic response or an inhibition during the tone. In many cases, after the tone ended, an off-response occurred. The responses to pure tones were vigorous and highly frequency selective. In Figure 4, a representative series of tuning curves, recorded in a row from rostral to caudal, is shown. Differences in the form of the tuning curves between fields A and DC were not noted.[1]

Tonotopy. To a first approximation, it seems that the tonotopy in field DC is mirror symmetric to the tonotopy in field A, since high frequencies are situated rostrally and low frequencies caudally. But a more detailed analysis reveals that a continuous tonotopic representation does not exist in field DC. In the dorsal half of DC, high BFs (16–32 kHz) were found rostrally; the low BFs (0.5–2.8 kHz) are located immediately caudally, while the intermediate frequencies (11–4 kHz) are missing. This sudden jump from high to low frequencies can be seen in all complete maps of field DC (arrows in Fig. 5a–c; see also Fig. 1b). It is also apparent in the series of recordings shown in Figure 4: tuning curves (c) with a BF of 16 kHz and (d) with a BF of 1–2.8 kHz were recorded only 0.5 mm apart. Further ventrally in DC, the tonotopy becomes more regular: the intermediate frequencies now appear and replace the low frequencies at least partially.

In field DC also, the high and low BFs are represented in dorsoventrally oriented isofrequency strips. For the intermediate BFs, it might be more appropriate to talk of isofrequency points or patches, since these BFs were found only ventrally in field DC and are confined to a very limited area. Consequently the general arrangement of the isofrequency contours differs from the fanlike pattern found in field A.

[1]A quantitative comparison of Q_{10} values or similar measures of the neuronal filter properties in fields A and DC was, however, not possible. The frequency resolution of our tuning curve recording procedure is relatively low, since neighbouring frequencies are separated by 0.5 octaves. The Q_{10} value is defined as the ratio of the BF to the bandwidth of the tuning curve 10 dB above threshold. But often, cells in fields A and DC do not respond to frequencies half an octave higher or lower than the BF at 10 (or even 20) dB above threshold. In many other cases, the threshold or the outlines of the tuning curve cannot be unequivocally determined.

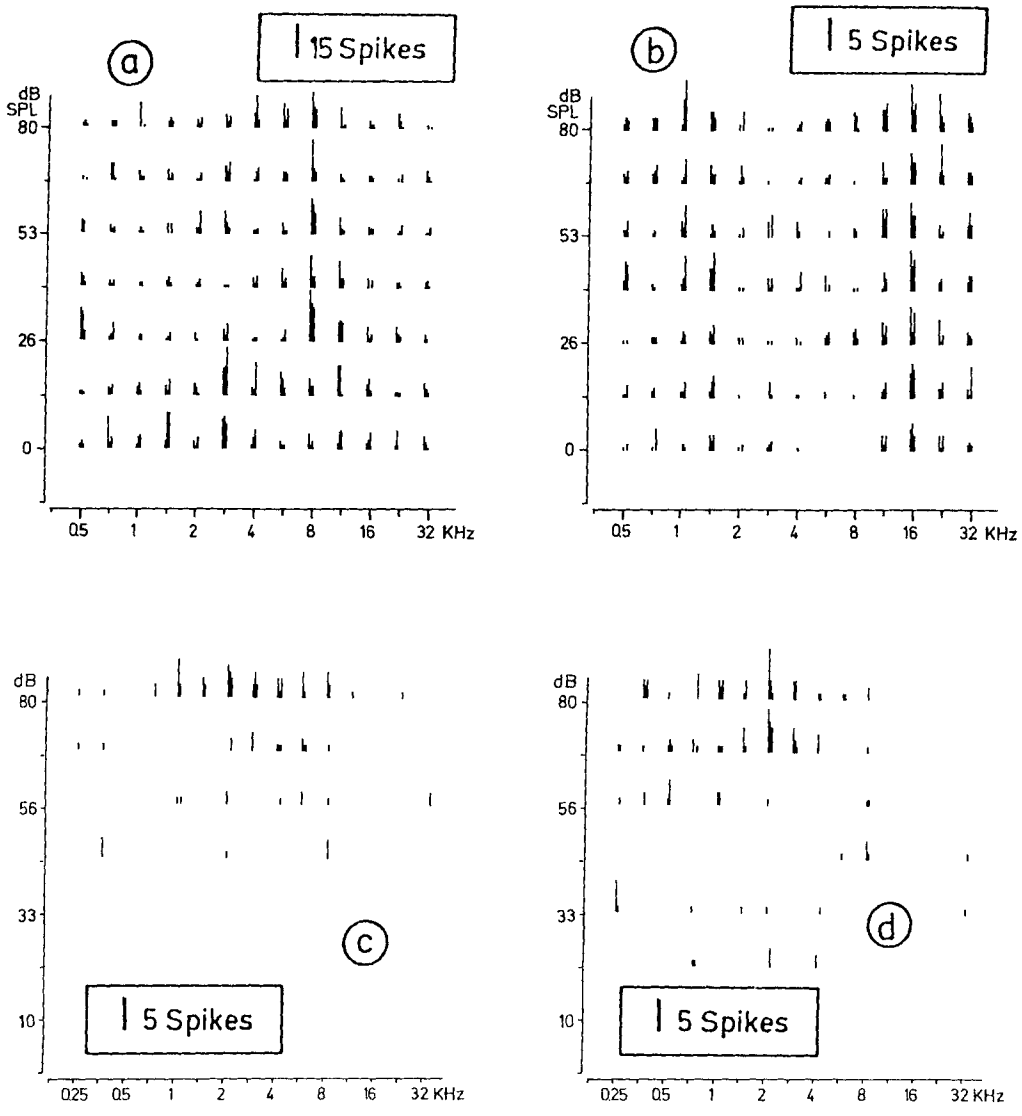

Fig. 8. Representative frequency tuning curves from the nontonotopic cortex. **a:** A tuning curve from the VCB, experiment MSE045 (time window 5–150 ms). The recording site is the left one of the two circled sites in Figure 5b. The threshold is minimum at 2.8 kHz, but the neuronal response is strongest at 8 kHz; it was classified as double-peaked, with BFs at 2.8/8 kHz. **b:** A tuning curve from the VCB, experiment MSE045 (time window 5–150 ms). The recording site is the right one of the two circled sites in Figure 5b. The BF is 16 kHz, but a significant activation also occurs at frequencies below 2 kHz. **c** and **d:** Tuning curves from the rostral belt (experiment MSE043, time window 8–30 ms). The recording sites are circled in Figure 7c; the left site is c and the right site is d. See text for further explanations.

A more complex layout, schematically illustrated in Figure 10, emerges. It should be stressed that despite some differences between individuals, the general features of tonotopy in field DC were similar in all animals investigated.

In some animals, a tonotopic representation of high frequencies (11–22 kHz) was found immediately caudal to field A and ventral to field DC. The tonotopic gradient seemed to be continuous with the high-frequency region of field DC and constitutes the transition between field A and a strip of nontonotopic cortex situated more caudally (see, e.g., Fig. 3a, arrow).

Latencies. The mean response latency of multiunits in field DC was 14.9 ms (Table 1). The difference between fields A and DC is not significant (Mann-Whitney U-test, two-sided, $P < .38$, Siegel, '76).

The small field (field S)

A third tonotopic area was found rostral to field A. This field is only about 1–1.3 mm long (from rostral to caudal) and ca. 0.5 mm wide (from dorsal to ventral). It was therefore labeled "the small field" (field S). Field S extends into the sylvian fissure, which is only a shallow furrow in the guinea pig. The mapping experiments were difficult, since the sylvian fissure is densely covered by blood vessels. We obtained 6 maps of the small field (examples in Fig. 7a–c). Distances between penetrations were normally 100–300 μm, but sometimes, larger intervals were chosen to avoid blood vessels.

Responses to pure tones, frequency specificity. The multiunits in field S responded vigorously to pure

tones. In most recording sites, a BF could be determined. A representative series of frequency tuning curves, recorded in a row from caudal to rostral, is shown in Figure 6. The tuning curves tend to be slightly broader than in area A or DC, but the multiunit response types (on-response, often followed by an inhibition or a tonic response and by an off-response after ending of the tone) were similar.

Tonotopy. In all six maps of field S, a tonotopic organization could be recognized. BFs increase from caudal to rostral (Fig. 7; see also Fig. 6). Thus, the tonotopic gradient is mirror symmetric to field A, but strongly compressed. The frequency range is represented in a continuous manner; i.e., sudden skips (like in the dorsal half of DC) were not observed. However, the high frequencies (>8kHz) seem to occupy a relatively large portion of area S.

Latencies. Mean latency in field S was 15.6 ms, which is slightly longer than in field A or DC (Table 1). The difference between the latencies in S and those in A and DC was statistically significant (Mann-Whitney U-test, two-sided, $P < .005$ for S vs. A and $P < .01$ for S vs. DC, Siegel, '76).

Other auditory regions

Rostrally and caudally, the tonotopic fields (i.e., A, DC, and S) are surrounded by auditory areas without tonotopic organization. The nontonotopic cortex will also be called the belt region in the following (Diamond, '79).

The belt region could be distinguished from the tonotopic fields not only by the absence of tonotopy but also by differences in neuronal response latencies, frequency tuning characteristics, and the responsiveness of the multiunits to pure tones, etc. It can be subdivided into a ventrocaudal belt (VCB), a dorsocaudal belt (DCB), and a rostral belt (RB).

The ventrocaudal belt. A broad strip of nontonotopic cortex is situated caudal to field A and ventral to field DC. It extends for at least 2 mm from rostral to caudal and from dorsal to ventral (Figs. 1a,5b). This region, named "the ventrocaudal belt" (VCB), was mapped in five animals.[2] It was more difficult to evoke neuronal responses to tonal stimuli in VCB than in the tonotopic fields. In many instances, the neurons did not respond to pure tones at all (symbols "N" in the map in Fig. 5b). Sometimes, clicks proved to be more effective. Complex acoustic stimuli—as, for example, amplitude- or frequency-modulated signals—are probably more appropriate to study this area.

Altogether, tuning curves were obtained from 32 recording sites. About half of the tuning curves were classified as broad or double-peaked. For the others, a BF could be determined at least approximately, i.e., with a precision of 1 or 2 octaves. Figure 8a,b shows two typical tuning curves. The BFs seem to be randomly distributed (see maps in Figs. 1a, 5b) over the cortex, but the percentage of high BFs is relatively large.

Only 11 of the 32 recorded multiunits showed a clear on-response to pure tones. The other cells had tonic responses and/or off-responses. This is a further difference between the VCB and the tonotopic fields, where nearly all multiunits exhibited on-responses. Response latencies were determined only for the multiunits with an on-response (see Materials and Methods). The mean latency was 23.6 ms (Table 1).

The dorsocaudal belt. A further nontonotopic region was found dorsally and dorsocaudally of the tonotopic field DC (Fig. 5b) and was, therefore, labeled "the dorsocaudal belt" (DCB). This region was mapped in four experiments. In addition, data from two preliminary experiments were included for determination of mean latency and response types (see footnote 2). As in VCB, the frequency tuning curves in DCB were often broad. Also, in many recording sites, neurons did not respond to pure tones.

Nearly all multiunits which reacted to tone stimuli had an on-response (22 out of 24 cells) that was often followed by a tonic response and/or an off-response. The high percentage of on-responses indicates a functional difference between DCB and VCB, where only about 30% on-responses were observed. The mean response latency in DCB was 20.3 ms (Table 1). This is less than in VCB, but the difference is not significant statistically ($P < .17$, Mann-Whitney U-test, two-sided, Siegel, '76).

The rostral belt. Dorsally, rostrally, and ventrally, the small tonotopic field S is surrounded by a narrow strip of nontonotopic cortex which we named "the rostral belt" (RB) (Fig. 7a–c). In five experiments, 30 neurons or neuron clusters were recorded from this region.

RB is characterized by neurons with broad tuning curves (Fig. 8c,d) and short response latencies (mean 14.4 ms, see Table 1). The differences in latency between RB and VCB and between RB and DCB are statistically significant (RB vs. VCB: $P < .001$; RB vs. DCB: $P < .005$, Mann-Whitney U-test, two-sided, Siegel, '76). In most recording sites, cells responsive to pure tones were found, but normally, the response thresholds were exceptionally high (50–70 dB SPL). Usually, neurons react with an on-response to tonal stimuli. The broad tuning curves and the higher thresholds made it easy to distinguish the rostral belt from the small tonotopic field S.

DISCUSSION

In this paper, the results of microelectrode mapping studies of the guinea pig's auditory cortex are presented. Our findings partly confirm previous work (see the beginning of this paper), but there are also some important discrepancies. New information is provided about response characteristics (frequency specificity, latencies) and the detailed layout of tonotopy in the two auditory fields described by Kayser and Legouix ('63) and Hellweg et al. ('77). Moreover, a third tonotopic area is described, and a brief account of nontonotopic auditory areas is given.

The anterior field (field A)

A large tonotopic area with a rostrocaudal gradient from low to high BFs is situated in the anterior auditory cortex (Fig. 9a,b). This is in agreement with previous work (see the beginning of this paper). Cells in field A exhibit strong responses to pure tones and have high frequency specificity and short latencies.

The isofrequency strips (IFS) in field A do not run straight and parallel to each other as described in the cat's field AI by Merzenich et al. ('75). They diverge progressively in the dorsoventral direction: dorsally, field A is narrow, and the strips are "squeezed together"; ventrally, the field becomes larger, and the isofrequency strips slightly fan out

[2] In addition, data from two preliminary experiments were included for determination of the mean response latency and the neuronal response types, but not for the analysis of BFs and tonotopy. The preliminary experiments differed from the main experiments in the acoustic stimulation system, which was not calibrated in the preliminary experiments (see Materials and Methods). It is unlikely that this influenced latencies or response types.

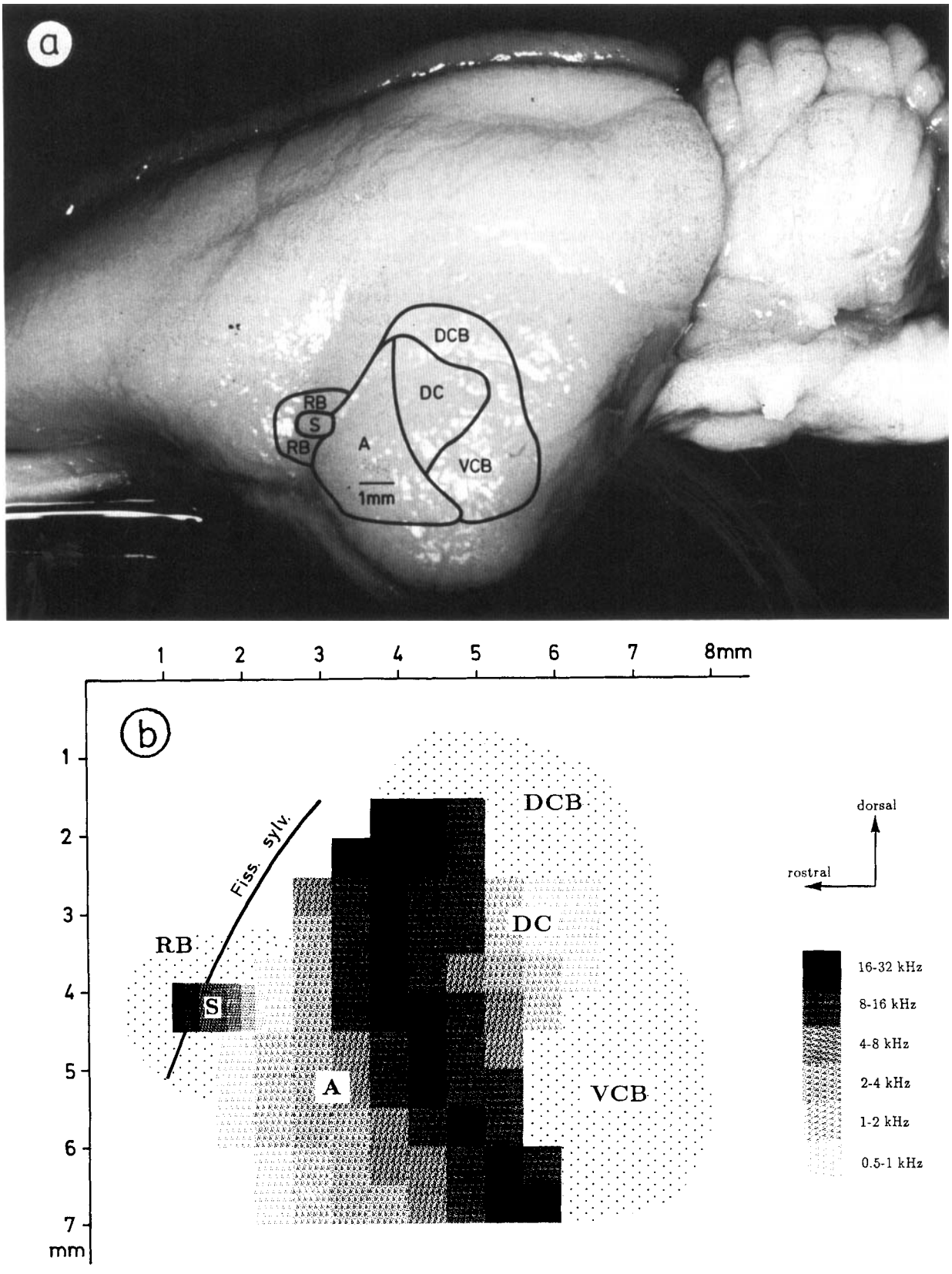

Fig. 9. Functional subdivisions in the auditory cortex of the guinea pig. **a:** Photograph of the lateral surface of a guinea pig brain. The outlines of the auditory fields are indicated. **b:** Schematic representation. The BFs in the tonotopic fields are represented by gray levels; light gray stands for low BFs and dark gray or black for high BFs (see gray-level scale to the right of the figure). The approximate outlines of the nontonotopic areas are indicated by stippling.

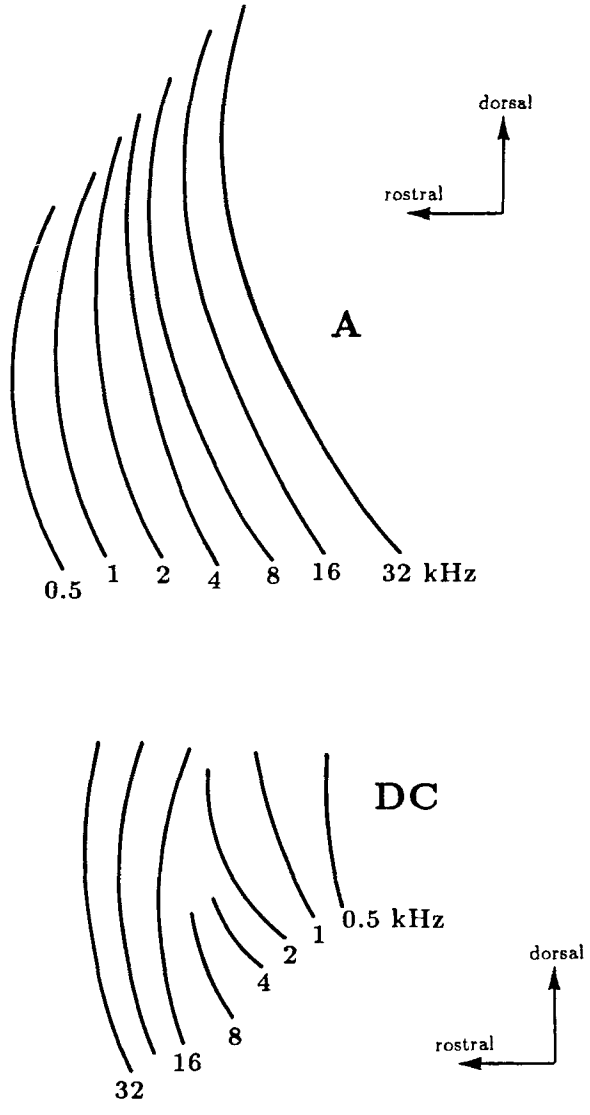

Fig. 10. **Above:** Schematic representation of the layout of the isofrequency lines in field A. The field becomes broader from dorsal to ventral, and correspondingly, the isofrequency lines slightly diverge. Note that the isofrequency lines in the "real" maps are less regular and that there is some variation between individuals. **Below:** Schematic representation of the isofrequency lines in field DC.

(Fig. 10). Such an arrangement has also been observed by Scheich et al. ('86) of the gerbil's auditory cortex. A nonparallel, fanlike layout of isofrequency lines might therefore be a common phenomenon, and not an exception, at least in rodents. Interestingly, in the primary auditory cortex of the marmoset *Callithrix jacchus*, a divergence of IFS was observed as well. But this divergence is much more pronounced than in the guinea pig, and it is oriented in another direction, i.e., the IFS diverge from ventrocaudal to dorsorostral (Aitkin et al., '86).

Any comments on the significance of this divergence must be speculative as long as the functional role of the IFS remains unknown. One might nevertheless hypothesize that the divergence of the IFS is the morphological correlate of a "magnification factor": the stimulus attributes processed along the IFS (for example signal amplitude, see Tunturi, '52; Suga and Manabe, '82) might be represented by a systematic gradient. Some stimuli, with more relevant properties, would then be represented in greater detail than others with less relevant features.

Dorsally between the two tonotopic fields, Hellweg et al. ('77) described an area where tones of 12.5–15.5 kHz were overrepresented. We could not identify such a region. Instead, between the two fields, we found the high-frequency strip (22–32 kHz) that separates fields A and DC (see Figs. 9b, 10).

The dorsocaudal field (field DC)

In the posterior part of the guinea pig's auditory cortex, Hellweg et al. ('77) described a single tonotopic field. The present study shows that this part of the cortex can be divided into a tonotopic and a nontonotopic area. The tonotopic field (i.e., area DC) lies in the dorsal half of the posterior auditory cortex (Fig. 9a,b). A broad strip of auditory belt region surrounds it.

Most multiunits in field DC react to pure tones with a strong on-response. The latencies are short and the frequency specificity is high. Differences between the multiunit response characteristics of fields A and DC were not noted; other work from our laboratory shows that the similarity between fields A and DC extends to fiber connections: Both fields receive afferents from the same subnuclei of the medial geniculate body (MG). A strong and topographically ordered projection originates in the ventral part of the MG (MGv), and a weaker projection arises from the magnocellular part of this nucleus (Redies and Creutzfeldt, '86; Redies et al., '88). It is, however, possible that functional differences between the fields would become apparent if single cell data were compared or if acoustic stimuli other than pure tones were used.

A major finding of the present study is that *the tonotopy in field DC is discontinuous.* In the dorsal half of the field, cells with medium BFs (4–11 kHz) were not found. It should be stressed that this discontinuity was observed in all nine animals where the dorsal part of DC was mapped. Ventrally, the tonotopy becomes more regular, but, altogether, the space occupied by the medium frequencies is very small (schematically shown in Figs. 9b, 10).

It is theoretically possible that the medium frequencies in the dorsal half of field DC are not completely missing but are only compressed into a very narrow space. The impression of a sudden frequency jump might then be caused by the (relatively large) distance of 0.5 mm between penetrations. But this alternative is unlikely. The frequency jump was observed in all cases in which the dorsal half of field DC was mapped. If neurons with medium BFs do exist in the dorsal half of DC, we should have encountered such cells at least occasionally. At any rate, the existence of a few cells with medium BFs would possibly be of little functional significance, since there would still be a pronounced imbalance in favour of high and low best frequencies.

We are not aware of any report in the literature of similar systematic discontinuities in an auditory cortical field with an otherwise continuous tonotopy. Frequency jumps between neighbouring cortical sites have been described in auditory fields that are not strictly tonotopically organized—as, for example, in the secondary auditory field, AII, of the cat (Schreiner and Cynader, '84). But these jumps are very variable between individuals and are apparently due to BF scatter in a field with a weak (or without) tonotopic organization. This is clearly not the case in field DC, where we

found a strict tonotopic organization with a frequency skip at the same place in different animals.

Often, sudden discontinuities in the cortical representation of a sensory surface indicate a transition between two different fields. This does not appear to be the case here: first, the frequency skip is only observed dorsally in DC, while ventrally, the gradient is continuous. Second, the direction of the gradient is the same in the high- and low-frequency parts of the dorsal half of DC; i.e., BFs decrease from rostral to caudal. Third, any differences in functional characteristics (frequency selectivity or latencies) were not observed.

The small field (field S)

We found a third tonotopic field rostral to field A. It occupies a cortical surface of less than 1 mm^2 and was named the small field. High frequencies are located rostrally, low frequencies caudally. This field was not described in the previous publications about the guinea pig's auditory cortex by Kayser and Legouix ('63) and Hellweg et al. ('77).

The frequency tuning curves are broader than in field A or DC. It cannot be excluded that this impression is due to the multiunit recording method: In field S, cells with different best frequencies are less distant from each other than in fields A or DC. Consequently, the multiunit recordings might "integrate" over a larger frequency range, and the tuning curves appear broader, although the individual neurons are as sharply tuned. The response latencies in field S are slightly longer than in field A or DC. The thalamic afferents are different as well: fields A and DC receive their principal input from the MGv; field S is mainly innervated by the rostromedial nucleus of the MG, a region that lies medial to the MGv in the rostral third of the MG (Redies, '87; Redies et al., '88).

The nontonotopic fields

The nontonotopic cortex was less thoroughly investigated than the tonotopic fields. Pure tones, the acoustic stimuli used in this project, are probably not optimal for a study of the physiology of the belt region. Nevertheless, a brief account of the neuronal response properties in the auditory belt was given, since this region has not yet been described in the guinea pig.

The belt region is not a homogeneous area. Probably, there are at least three different functional fields. In the ventrocaudal belt and the dorsocaudal belt, response latencies are longer than in the tonotopic areas. Many tuning curves are broad, and the cell clusters often were not driven by pure tones at all. The percentage of multiunits reacting with an on-response to tone stimuli was much higher in DCB than in VCB. This suggests that both region are different functional fields. Still, additional evidence would be required to confirm this point. The rostral belt differs from the two caudal areas in high response thresholds, short latencies, and, in a certain sense, in better responsiveness to pure tones: In most recording sites in RB, responsive neurons were found, though high stimulus intensities were necessary to drive these cells.

The guinea pig compared with other species

In the cat, the species in which the auditory cortex is most thoroughly investigated, there are at least four tonotopically organized fields (Reale and Imig, '80). Two of these, the primary auditory field, AI, and the anterior auditory field, AAF, exhibit a great similarity to the guinea pig's areas A and DC in several respects: the neurons in AI and AAF respond vigorously to pure tones; they exhibit short latencies and are highly frequency specific (Merzenich et al., '75; Knight, '77; Reale and Imig, '80; Phillips and Irvine, '81, '82). These response attributes—briefly designated as "primarylike"—are typical also for multiunit activity in these areas (Reale and Imig, '80; Schreiner and Urbas, '86; Redies et al., in preparation), which facilitates comparison with the present results. Moreover, AI and AAF have similar thalamic afferents to those of fields A and DC in the guinea pig, i.e., a strong projection from the tonotopic part of the MG and a weaker projection from a magnocellular nucleus (see Andersen et al., '80, for cat).

Tonotopic fields with primarylike response characteristics have also been found in other mammalian species—for example, in the rhesus monkey (Merzenich and Brugge, '73), the owl monkey (Imig et al., '77), the rabbit (Galli et al., '71; McMullen and Glaser, '82), the house mouse (Stiebler, '87), and the gerbil (Scheich et al., '86).

However, there is less similarity between species when the details of the primary fields[3] are considered. Topographically, the fields AAF and AI of the cat correspond to the guinea pig's fields A and DC, respectively. While the fields AAF (cat) and A (guinea pig) are well matched, there are some notable differences between AI (cat) and DC (guinea pig). The frequency representation is continuous in AI (Merzenich et al., '75) but partly discontinuous in DC. Furthermore, in AI, high BFs are represented in greater detail than medium BFs, and medium BFs in greater detail than low BFs (Merzenich et al., '75). In contrast to this, in DC there is a strong imbalance in favour of the high and the low frequencies, while the representation of the medium BFs is scarce. (Compare Fig. 10 in this paper with Merzenich et al., '75, Fig. 10. See Redies et al., '88, for differences in the afferent organization of these fields in cat and guinea pig.)

Other differences become obvious when "nonprimary" auditory fields are compared between both species: In the cat, two more tonotopic areas, named the posterior and the ventroposterior fields, with response characteristics different from AI and AAF, are located caudoventral to the primary fields, in the banks of the posterior ectosylvian sulcus (Reale and Imig, '80). We did not find similar tonotopic areas in the guinea pig. On the other hand, an equivalent to the guinea pig's field S may not exist in the cat. One might argue that such a small area is easily overlooked; however, the cortex rostral and ventral to the low-frequency representation of AAF (corresponding in location to field S) has been investigated and was found to be nontonotopic (Knight, '77; Reale and Imig, '80). Moreover, a thalamic nucleus similar to the guinea pig's rostromedial MG, which provides the main thalamic input to field S (Redies et al., '88), has not been described in the cat.

Differences also exist between the guinea pig and the grey squirrel *Sciurus carolinensis*. In the latter species, only one tonotopic area with primarylike response characteristics (named AI) has been described. Low frequencies are represented anteriorly and high frequencies posteriorly in AI, as in the guinea pig field A (Merzenich et al., '75; Luethke et al., '88). Rostral to AI, a second large tonotopic field with a frequency gradient mirror symmetric to AI was described in the grey squirrel (thus, the two fields have a common low-

[3]By primary fields, we mean fields with primarylike response characteristics, that receive their main input from the tonotopic part of the MG, e.g., fields AI and AAF in the cat, fields A and DC in the guinea pig, etc.

frequency border), but the response characteristics in this field are different than those in AI, i.e., the multiunits often have broader tuning curves and respond less reliably to pure tones. Caudal to AI, in a topographical position roughly corresponding to field DC in the guinea pig, cells do not respond to tones or clicks; however, this region receives afferents from the tonotopic cortex and may therefore be part of the auditory belt (Luethke et al., '88).

Two tonotopic areas with a common high-frequency border have been revealed by means of the 2-deoxyglucose method in the gerbil *Meriones unguiculatus* (Scheich et al., '86), but, as opposed to the guinea pig (see Fig. 9), the gerbil's anterior field (named AAF) is much smaller than the posterior field (named AI). Thus, it is uncertain whether AAF (gerbil) corresponds to A (guinea pig) and AI (gerbil) to DC (guinea pig) or whether, for example, the large fields (i.e., AI in the gerbil and A in the guinea pig) are equivalent, whereas the smaller fields are nonequivalent, species-specific structures. Precise knowledge about the thalamocortical connections of the tonotopic cortex in the gerbil would be a great help to answer this question. A recent microelectrode mapping study in the gerbil describes two additional tonotopic areas caudal to AI. In one of these fields, isofrequency lines are arranged concentrically, with high frequencies in the center and low frequencies in the periphery (Thomas et al., '87), similar to the tonotopic pattern described by Suga and Jen ('76) in the auditory cortex of the bat *Pteronotus parnellii rubiginosus*.

In conclusion, it seems reasonable to assume that one or two areas with primarylike response characteristics exist in all mammals, since they have been found in species belonging to very different branches of Mammalia. However, the number of these fields (one or two), the layout of tonotopy, etc., are variable, and far-reaching functional analogy is sometimes questionable—for example, between fields AI (cat) and DC (guinea pig). More important differences become apparent when nonprimary fields are compared, and no safe conclusion of equivalence can at present be drawn here. Thus, common traits of auditory cortex organization in mammals coexist with species-specific features that have been independently acquired during evolution. The present paper has revealed the existence of species-specific features in the auditory cortex in the guinea pig.

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