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Tonotopic organization of the auditory forebrain in a songbird, the European starling*

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Summary. The auditory area in the caudomedial forebrain of birds is explored by microelectrode recordings in a songbird. Multi-unit recordings reveal a clear tonotopic representation of stimulus frequency (Figs. 1, 2a, 3) with a mainly dorsoventral gradient (low frequencies dorsal). Frequency tuning is lost only in peripheral parts of the nucleus where wideband responses prevail. The functional structure is related to neuroanatomical landmarks of the forebrain by means of a 3-dimensional reconstruction from cell- and fibre-stained brain sections (Figs. 3, 4). For instance, a core region of high spontaneous and evoked activity (Figs. 5, 6b) is related to the input region (field L2) of the area. Additional single unit recordings support the multi-unit data (Fig. 6). The tonotopic organization found in the starling is compared with the organization of the caudomedial forebrain reported for other bird families.

Introduction

Song birds have complex vocal repertoires which partly are innate and partly consist of learned song elements. As these songs contribute to the territorial and reproductive behaviour, the auditory system expectedly reflects adaptations to biological relevant sound parameters (Scheich et al. 1983). Thus, song birds lend themselves to the study of the processing of auditory stimuli in higher brain centres. Investigations aiming at functional subdivisions depend on the knowledge of the exact spatial organization of the nuclei involved. Comparable studies in mammals have led to the subdivision of the auditory cortex into functionally different zones with repetitive tonotopic organizations (Suga et al. 1983; Reale and Imig 1980). In contrast, the telencephalic auditory projection areas of birds do not show a cortical organization. Efferent connections from the nucleus ovoidalis thalami (the diencephalic nucleus of the auditory pathway) terminate in a coherent region formed by caudal parts of the neostriatum and hyperstriatum ventrale (Karten 1968; B.A. Bonke et al. 1979). Unlike other auditory nuclei, these sensory telencephalic areas can not easily be deliminated or distinguished by morphological criteria.

Using the 2-Deoxyglucose (2DG) technique, Scheich et al. (1979) demonstrated stimulus specific labelling first in the caudal neostriatum of gallinaceous birds. These neurohistological results were found to be congruent with neurophysiological recordings from the same region (D. Bonke et al. 1979; Theurich et al. 1984). On this basis the authors subdivided the nucleus into three layers (L1, L2, L3) thereby referring to the original cytoarchitectonic nomenclature of Rose (1914), who introduced the term Feld L for the caudomedial neostriatum. The three areas show a common tonotopic organization.

In song birds the 2DG method also reveals a tonotopic organization of the forebrain (Müller and Scheich 1985). Thus it is plausible to expect a congruent neurophysiological organization here as well. Nevertheless, the rare electrophysiological data corroborating this finding are often incomplete, if not contradictory. For the zebra finch, Zaretzky and Konishi (1976) have described an orderly tonotopic arrangement in the horizontal plane, differing from the mainly dorsoventral frequency gradient found by Müller and Leppelsack

Abbreviations: *cer* cerebellum; *fpl* fasciculus prosencephali lateralis; *lh* lamina hyperstriatica; *lmd* lamina medullaris dorsalis; *ven* ventricle; *2DG* 2-Deoxyglucose

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(1985) in parasagittal planes for the European starling. In any case, the spatial extension and the three-dimensional tonotopic organization of this auditory processing area cannot be inferred from these data.

In this paper we present data on the three-dimensional organization of the auditory telencephalon in the European starling. The tonotopic organization found is used as guidelines in a current study which aims at refining the functional subdivision of the auditory areas, on the basis of more complex test stimuli.

Methods

The experiments were performed on 13 starlings, *Sturnus vulgaris* (8 males and 5 females).

Two days before the first recording session the animals were anaesthetized with Halothane and placed in an animal holder. The head was fixed by ear bars with the bill inclined by 40° below the horizontal plane. A ring-shaped stainless steel chamber was mounted with dental cement on top of the skull. The centre of the horizontally oriented chamber was between 1.0 mm and 2.5 mm lateral to the midsagittal plane and between 1.5 mm and 3.0 mm in front of the ear bars. In the recording sessions, this ring-shaped chamber served as an aid for a rigid and reproducible fixation of the head during the recording sessions and for a precise adjustment of the electrode position.

During the experiments the animals were conscious, and were constrained by being wrapped in a piece of cloth and fixed in a head holder. Before the first session, some contour data of the head were measured in the experimental setup relative to a reference point on the head holder (topview of the midline of the bill, sideview of the bill, eye position). Comparison of these data with histological data from previous experiments improved the pre-experimental information about the three-dimensional position of the brain within the skull. On the basis of this information a single hole was drilled in the skull through which all electrode penetrations were performed. Electrodes were moved vertically by a step-motor microdrive (2 μm steps), and different locations in the forebrain were reached by tilting the animal on its platform around the rostrocaudal and/or mediolateral axis. Both forebrain hemispheres were tested in this study, making up to 25 electrode penetrations in a single animal. The location of best frequencies were accumulated in stereotaxic maps for further analysis, and for comparison with brain sections obtained later on from the same subject.

Stimulus generation and on-line control of the experiment as well as the on-line and off-line data analyses were performed by a laboratory computer (PDP 12, Digital Equipment). The acoustic stimuli (pure tones and bandpass noise, duration 256 ms, on/off-slope 12 ms) were given with a repetition rate of 1/s at intensities between 60 and 40 dB SPL.

By digital filtering of wideband noise, nine bandpass signals were generated (Dörrscheidt and Rübsamen, submitted) that completely covered the hearing range of the starling from 150 Hz–8.5 kHz (Kuhn et al. 1982). Rounded values for cut-off and centre frequencies of the stimuli are indicated in Table 1. The absolute bandwidth increased linearly from 320 Hz in band No. 1 up to 1,560 Hz in band No. 9. The relative bandwidth decreased from 1 in band No. 1 to 0.2 in band No. 9. This follows the tendency of sharper tuning in auditory neurons towards higher frequencies (Manley 1980). The sum of all nine bandpass signals forming a wideband noise pulse served as a tenth stimulus.

Multi-unit recordings were made with low impedance micropipettes (0.5–1 MΩ) filled with 3 *M* KCL. During the course of penetration, activity was measured every 100 μm. The best response to the set of 10 stimuli was gathered from stimulus-related dot-displays and from a statistical on-line classification (Dörrscheidt and Rübsamen, submitted). It was also possible to quantify the spontaneous background activity, the degree of stimulus induced activation or inhibition and to describe the discharge pattern. Stereotaxic maps were drawn illustrating the variation of best frequencies in the dorsoventral, rostrocaudal and mediolateral direction.

Later on, single-unit recordings with high impedance micropipettes (5–12 MΩ) were made in preselected areas of the auditory forebrain. In the given context they served for verifying the inferences drawn from the multi-unit recordings. The results will be analyzed in detail in a subsequent paper.

Finally, eight constant-current lesions (4 in depths of 4,000 μm and in 2,000 μm each) were made at four tilting angles enclosing the recording sites. After the recording sessions the animals were fatally anaesthetized by an overdose of Nembutal (50 mg/100 g body weight), and following an initial flushing with Ringer solution, the brains were fixed by transcardial perfusion of 500 ml Formalin (10%). The brain was kept in the same fixative for several days, after which the skull was removed and the brain kept for 36 h in distilled water with 30% sucrose serving as a cryoprotective. The brain together with marker needles for serial reconstruction was then embedded in egg yolk fixed by glutaraldehyde in a small embedding chamber. Alternating frozen sections (62 μm) were collected in two series. One passed through cresyl violet cell staining, and the other through a fibre staining (either a Haematoxilin staining after Spielmayer-Benda (Romeis 1948) or a silver impregnation after Gallyas 1979).

Drawings of serial sections were arranged to their true spatial configuration using the marker holes as guides. The lesions allowed the calculation of the shrinking of the sections caused by the histological procedure, and to relate the stereotaxic maps to distinct brain areas. Thus physiological and morphological data from the same preparation could be directly compared.

Before pooling the data gathered from different preparations, differences in brain size and in shrinking caused by the histological procedure were normalized in the following way: An imaginary cube, having an edge length of half the brain width, was fitted to the hemispheres recorded from, in such a way that one of its surfaces became tangent to the midsagittal plane, and the two other perpendicular surfaces touched the forebrain hemisphere one at the caudal pole and the other at the most dorsal point. The dorsal surface was adjusted perpendicularly to the zero penetration (no tilting of the animal in both directions, see Fig. 3). With the edge length of the cube set to one, the coordinates of the recording sites (two tilting angles and depth) were then converted into relative Cartesian coordinates. With the frequency specific classification of the recording site added, these coordinates formed the basis for the computer evaluation of the tonotopic organization.

Results

Multi-unit recordings aiming at the three-dimensional tonotopic organization of the auditory forebrain centre in the starling were performed on 13 animals.

Electrode penetrations in a dorsoventral orientation (Fig. 1) revealed an onset of acoustic excit-

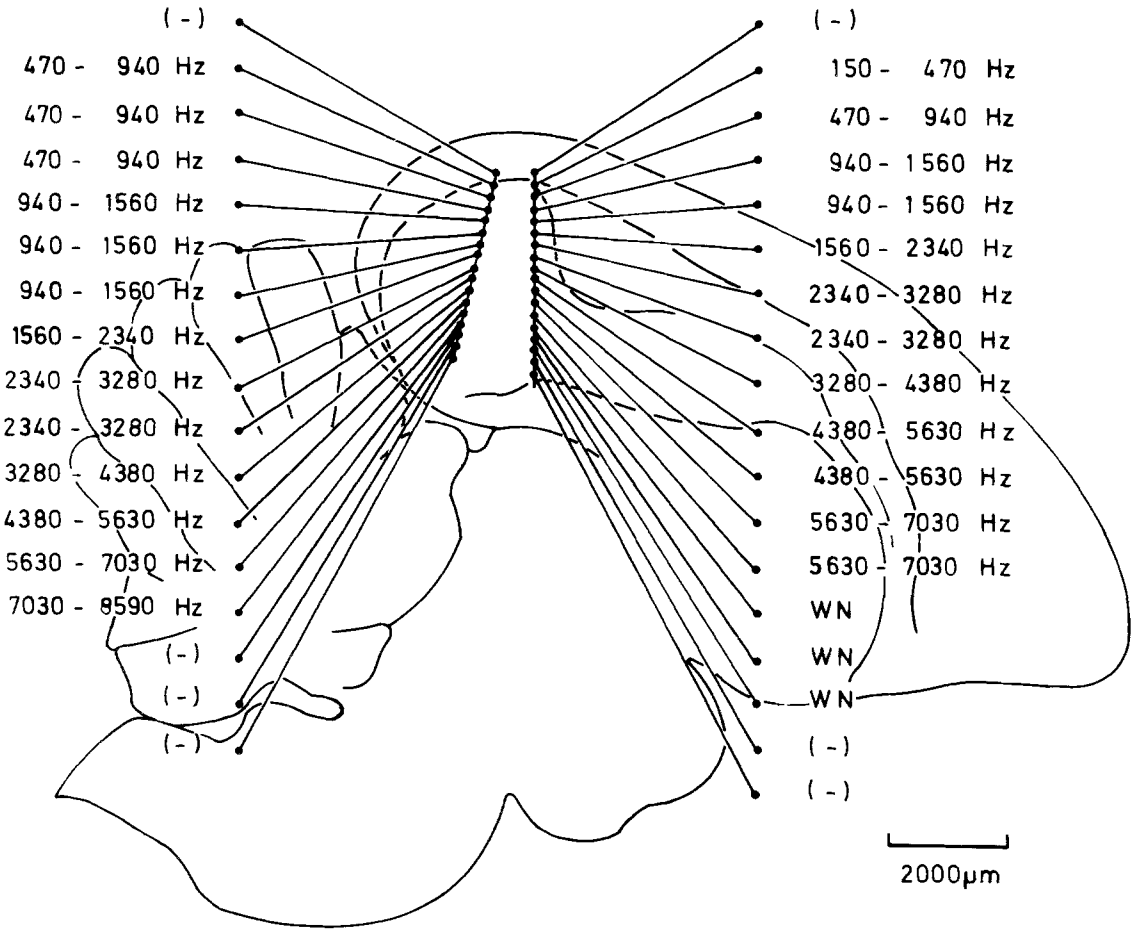

Fig. 1. Two multi-unit electrode penetrations through the caudomedial forebrain of the starling. Parasagittal plane, penetration (tilting) angles 0° and 10° caudally. Brain contours from the corresponding sections are related to stereotaxic coordinates of the penetrations as described under Methods. Frequency values specify the best frequency range determined by bandpass noise stimulation (see Table 1). *WN* best response to white noise, (−) no response. Note the clear dorsoventral gradient of best frequencies

ability in a depth of about 1,000–1,800 µm depending on the position of the electrode along the rostrocaudal brain axis. The best frequencies then increased systematically with depth over a distance of 2,000–2,500 µm, starting with initial values ranging between 150–1,560 Hz. In single penetrations through the centre part of the auditory nucleus, the best frequency found covered the whole frequency range tested in our experiments (150 Hz up to 8,500 Hz). Sometimes broad tuning or best activation by wideband noise defined the ventral border of the acoustic area. Activation by wideband stimuli could also be seen in some penetrations near the rostral and caudal margins.

Tonotopic organization of the forebrain was found in all 13 starlings tested. Following the normalization of recording coordinates (see Methods), data from all individuals were subjected to a joint computer analysis. This allowed to locate recording sites of specified functional characteristics and to display them in stereotaxic maps. Figure 2 gives an example covering four animals.

Figure 3 summarizes the analysis performed under the aspect of best-frequency distribution for all 13 animals. It shows that recording sites with identical best frequencies can be related to coherent slabs covering the mediocaudal neostriatum and parts of the hyperstriatum ventrale. Acoustic excitability was prominent immediately after passing the dorsal ventricle. In the lateral view of Fig. 3 the iso-frequency slabs show a parallel arrangement in the caudomedial region of the auditory area, oriented perpendicularly to the dorsoventral brain axis. At the rostrolateral margin the isofrequency slabs bend dorsally and cross the lamina hyperstriatica (lh). A corresponding fibre arrangement could be shown in silver-impregnated brain sections (Fig. 4b). The main fibre bundle enters the auditory telencephalon from a ventrolateral position as a part of the fasciculus prosencephali

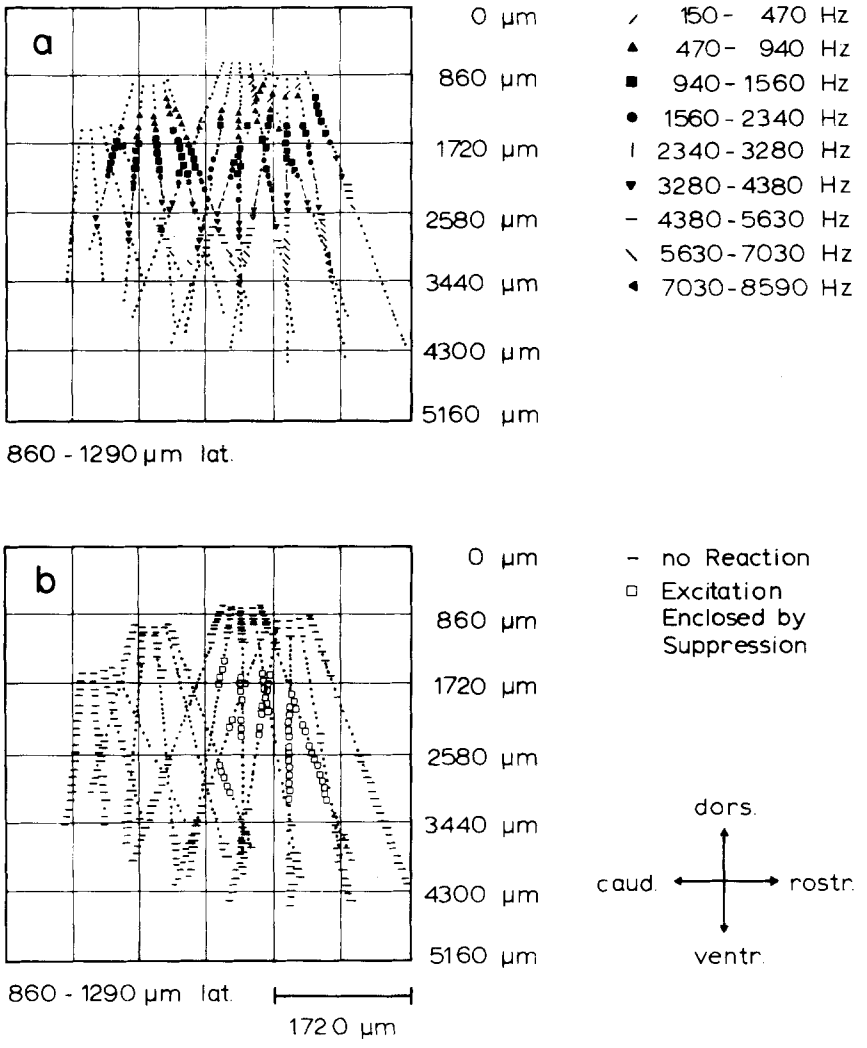

Fig. 2a, b. Functional differentiation of the auditory nucleus in a lateral view. Data from 4 animals are compiled in normalized coordinates (see also Fig. 3). The computer analysis covers about 1/7 of the mediolateral extent of the nucleus near its centre: Dots mark recording sites. **a** Distribution of best frequency bands. **b** Spatial limits of sensitivity to bandpass stimuli and distribution of a response type assumed to be characteristic of neurons from the input region of the nucleus: (–) recording sites lacking acoustic excitability; (□) strong acoustic excitability in the input layer

lateralis (fpl) and ascends dorsomedially. Parallel fibres can be followed which leave the bundle in a rostrodorsal direction and cross the lamina hyperstriatica perpendicularly. These fibres run parallel to the isofrequency slabs. Whether some of them originate in the field L could not be verified in the fibre-stained material. The main input fibre bundle disperses into the caudal parts of field L giving off thin fibres that run further caudally, again arranged in parallel to the isofrequency contours. Those fibres which take a caudal course are additionally crossed by ascending fibres bifurcating from the main input bundle near the lmd to run dorsocaudally, aiming at the hvc.

Inspection of Fig. 3 also discloses that in a frontal view the isofrequency layers are inclined towards the lateral margin. Near the midline of the brain best frequencies exclusively fall into the upper frequency range, while near the lateral border only low best frequencies are found.

The tonotopically organized region extends dorsoventrally from the ventricle (ven) down to the lamina medullaris dorsalis (lmd) and caudorostrally from the caudomedial pole of the neostriatum to about 500–1,000 µm beyond the lamina hyperstriatica (lh). The lamina hyperstriatica, itself a prominent fibre tract which separates the neostriatum and the hyperstriatum (Fig. 4) does not constitute a border for the auditory areas, nor for the continuous frequency representation. Over the mediolateral extent, tonotopic organization could be demonstrated from a midsagittal plane, where the neostriatal areas of both hemispheres are separated only by the lamina zonalis, to a parasagittal plane of about 2,500 µm to 2,800 µm from the midline.

While the medial, caudomedial and dorsal borders of the auditory forebrain nucleus are clearly determined by the extent and the course of the ventricle, the rostral and the lateral boundaries were found more difficult to identify. Towards the rostral boundary, the tonotopic arrange-

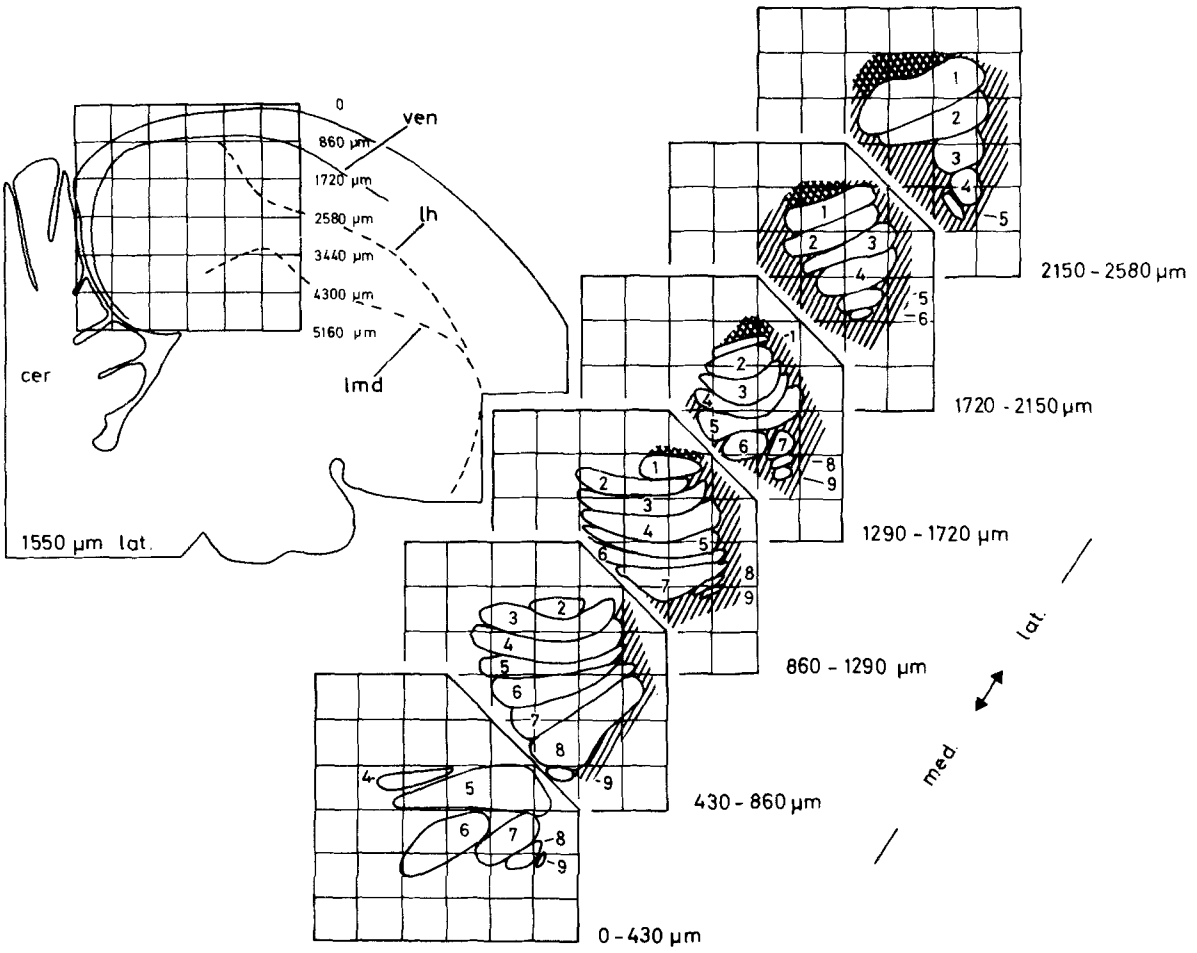

Fig. 3. Spatial reconstruction of isofrequency slabs covering all 13 preparations. Right: Contours of isofrequency slabs were drawn on the basis of computer analyses as shown in Fig. 2, performed for each band separately. Numbers 1...9 specify the best band (1: 150–470 Hz, 2: 470–940 Hz, 3: 940–1,560 Hz, 4: 1,560–2,340 Hz, 5: 2,340–3,280 Hz, 6: 3,280–4,380 Hz, 7: 4,380–5,630 Hz, 8: 5,630–7,030 Hz, 9: 7,030–8,590 Hz). Hatched: wideband responses. In the cross-hatched dorsolateral region responses could not be classified on the basis of multi-unit recordings. Left: Superposition of the coordinate grid over a parasagittal section in the plane containing the caudal pole of the forebrain which is used as zero point of the rostrocaudal axis in the reconstructions (see Methods); *cer* cerebellum; *lh* lamina hyperstriatica; *lmd* lamina medullaris dorsalis; *ven* ventricle

Table 1. Frequency bands used for stimulation

Band no	Frequency limits	Centre
1	150– 470 Hz	320 Hz
2	470– 940 Hz	700 Hz
3	940–1,560 Hz	1,250 Hz
4	1,560–2,340 Hz	1,950 Hz
5	2,340–3,280 Hz	2,810 Hz
6	3,280–4,380 Hz	3,830 Hz
7	4,380–5,630 Hz	5,000 Hz
8	5,630–7,030 Hz	6,330 Hz
9	7,030–8,590 Hz	7,810 Hz
10	150–8,590 Hz	WB

ment becomes progressively blurred in the hyperstriatum ventrale, the tuning changes into a weak wideband sensitivity and then fades away. Caudolaterally, the auditory nucleus does not reach the ventricle. Here the tonotopic region is bordered by an area where spontaneous activity is suppressed within a wide range of stimulus frequencies. Towards the lateral margin, where low frequencies are represented, activity successively diminishes beyond the parasagittal plane at 2,800 µm.

Within the auditory processing area the spontaneous background activity as well as the activation strength (number of spikes/stim) changed with the position of the recording electrode. A clearly defined elongated region, between 2,000 µm and 3,500 µm in depth, caudoventrally to and partly parallelling the lamina hyperstriatica, was characterized by its high spontaneous activity. In this area strong tonic discharges in excitatory frequency bands could be recorded. Excitatory areas were enclosed by inhibitory sidebands (Fig. 2b). In brain sections this area is characterized by a dense

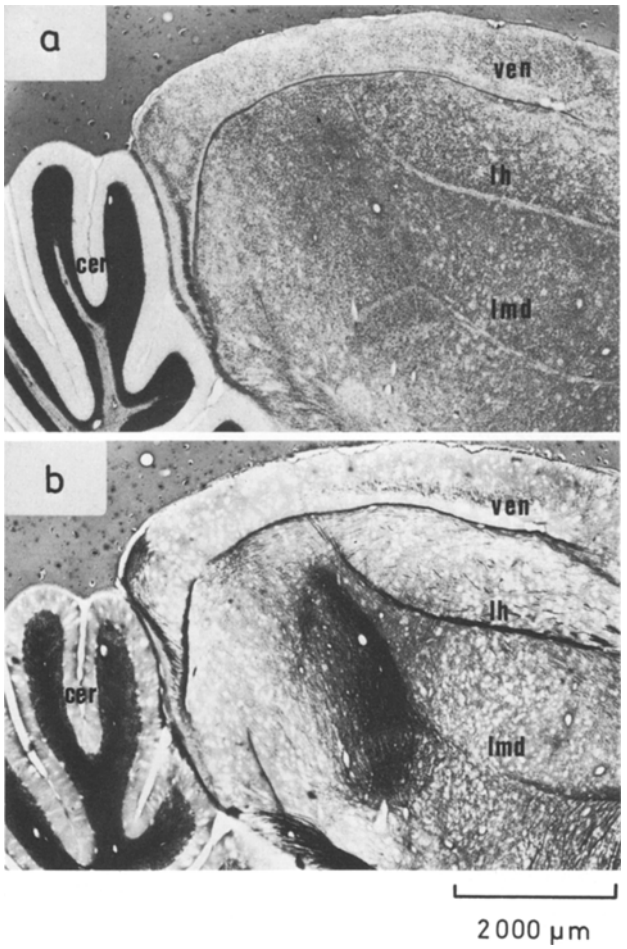

Fig. 4a, b. Parasagittal section (1,600 µm from the midline) through the mediocaudal telencephalon in the auditory projection area (*cer* cerebellum; *lh* lamina hyperstriatica; *lmd* lamina medullaris dorsalis; *ven* ventricle). **a** Cell staining, **b** Fibre staining

tangle of myelinated fibres (Fig. 4b). In neighbouring regions spontaneous activity was lower, pure tone stimulation evoked a more phasic activity pattern, and sideband inhibition was less prominent.

Subsequent single-unit recordings confirmed these results. While in other areas of the forebrain the rate of spontaneous activity rarely exceeded 20/s, the spike rate could reach 100/s in this core region (Fig. 5). The change of spontaneous activity and of stimulus induced response properties (frequency dependent activation and suppression) is demonstrated within a single electrode penetration by the dot-displays of three single-units recorded (Fig. 6).

Discussion

By multi-unit recordings it was possible to determine the absolute size and intrinsic organization of the telencephalic auditory area in the starling. The auditory processing area encloses the entire caudomedial neostriatum including the field L of Rose (1914) and integrates parts of the hyperstriatum ventrale.

It was shown that the frequency representation is organized in best-frequency slabs mainly arranged dorsoventrally with frequency values increasing ventrally. These slabs are tilted laterally with the result that low best frequencies dominate in dorsolateral positions and high frequencies ventromedially. A core region of the auditory telencephalon can be defined by physiological criteria: high spontaneous activity of the units and high stimulus induced tonic activation in the best frequency band enclosed by inhibitory sidebands. This characterization agrees both with the functional description given by D. Bonke et al. (1979) for the input zone L2 in the Guinea fowl, and that of single units in the afferent diencephalic nucleus (the nucleus ovoidalis), in the starling (Bigalke et al., in prep.). Morphologically, the centre of the auditory telencephalon is accentuated by a dense tangle of myelinated fibres. It contains an accumulation of small cells, termed intercalated cells in

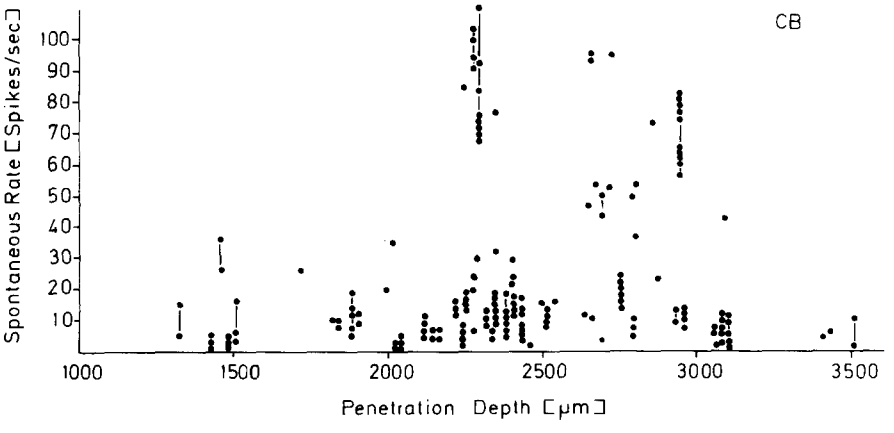

Fig. 5. Spontaneous rate of the single units found in different depths of a single penetration in preparation CB. Lines connect rates recorded from the same unit at different times. Note the higher rates in the core region

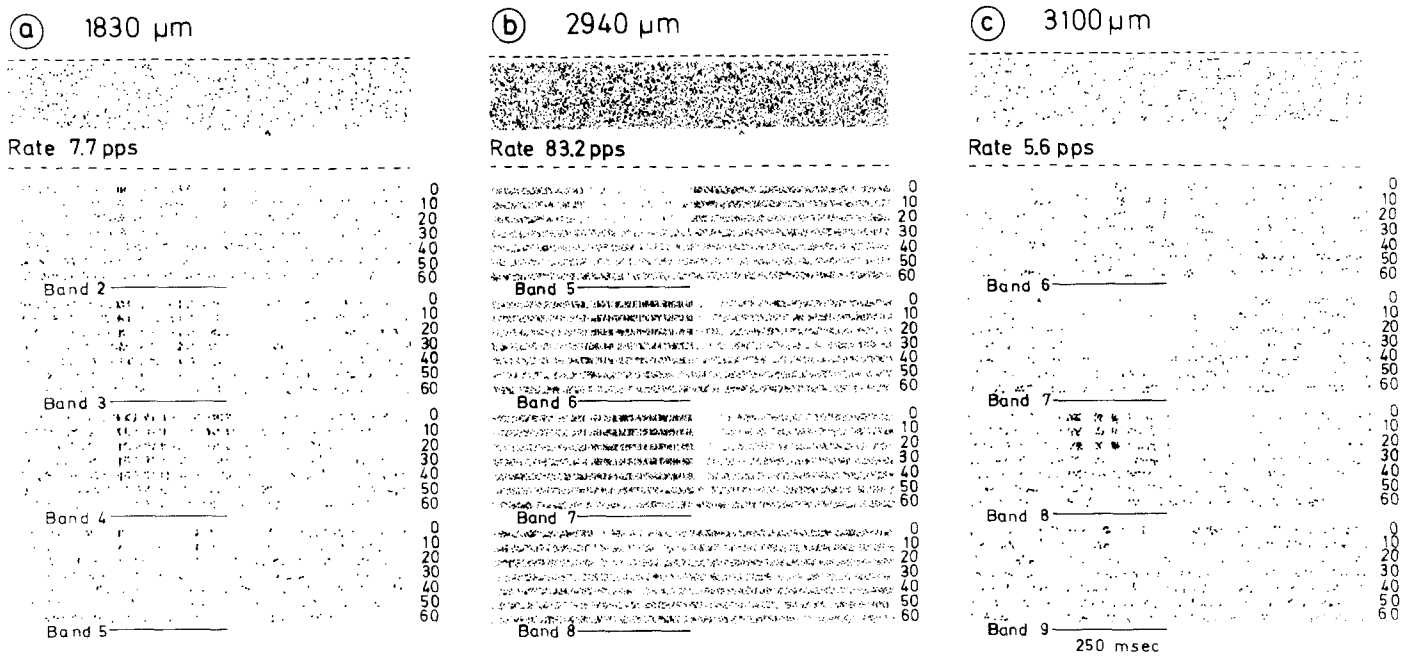

Fig. 6a–c. Activity of 3 neurons recorded at different depths within a single penetration illustrated by dot-displays of their spontaneous activity (top) and of their responses to bandpass noise stimuli (below). Stimulus evoked discharges are shown around the band of best response (frequency values of the numbered test bands: 2: 470–940 Hz, 3: 940–1,560 Hz, 4: 1,560–2,340 Hz, 5: 2,340–3,280 Hz, 6: 3,280–4,380 Hz, 7: 4,380–5,630 Hz, 8: 5,630–7,030 Hz, 9: 7,030–8,590 Hz; stimulus bar 250 ms). Notice that the best frequency increases with increasing depth (from left to right). Every stimulus was presented at 7 intensity levels (0–60 dB attenuation listed to the right of the dot-displays, corresponding to 70–10 dB SPL) with 5 repetitions at each level. Display duration = stimulus repetition period = 1 s

the pigeon (Karten 1968), or microneurons in the starling (Saini and Leppelsack 1981). In our recordings, the high-rate activities of the type described are restricted to this region. For these reasons we equate the core region with L2. A difference between the starling and the gallinaceous birds, with regard to spontaneous activity in L2 (as considered by Müller and Leppelsack 1985) is not supported by our data.

In continuation with the core region the isofrequency slabs expand dorsorostrally and caudally. In both directions they are paralleled by fibres. This arrangement of isofrequency slabs, which extends over three morphologically and physiologically differentiated layers, hampers an appropriate comparison between the tonotopic organization in the forebrain and the frequency map found in the cochlea (Ryals and Rubel 1982). Müller and Leppelsack (1985) attempted such a comparison with arbitrarily located dorsoventral electrode penetrations and obtained contradictory results in one and the same preparation. Heil and Scheich (1985), on the other hand, who restricted their neuromorphological reconstruction based on 2DG data to L2, have shown that the frequency map is not even uniform in this homogeneous input layer.

The maximum dimensions of the auditory telencephalic nucleus are 2,500 µm in the rostrocaudal, 2,800 µm in the mediolateral and about 3,000 µm in the dorsoventral extension. This appears surprisingly large compared with the absolute size of the nucleus ovoidalis, which has a maximum diameter of about 600 to 800 µm in the same species (Bigalke et al., in prep.). This might be due to the fact that parts of the above described auditory area receive additional inputs from other sensory modalities. Necker and Rehkämper (1982), for instance, have reported integration of auditory and somatosensory excitability in caudal parts of the hyperstriatum ventrale of the pigeon.

In designing the frequency range of our test signals (about 150–8,500 Hz, Table 1) we had referred to the behavioural audiograms of the starling (Kuhn et al. 1982). Our experiments showed that the tonotopic map contains best frequencies from the complete test spectrum. The ventromedial location of the high-frequency area near to the lmd, which forms the ventral border of the auditory neostriatum, supports the suggestion that 8.5 kHz (the upper limit of our test frequencies) is near the upper limit of hearing sensitivity. Whether 150 Hz, the lowest frequency tested, really corresponds to the low frequency limit remains questionable. These frequencies are located in the

dorsolateral area of the auditory neostriatum, the extent of which could not be defined by morphological criteria.

The three-dimensional tonotopic arrangement and the absolute size of the auditory forebrain described here are congruent with the results reported by Müller and Scheich (1985) for the starling employing the 2-deoxyglucose technique. These authors additionally investigated species belonging to other bird families thereby demonstrating systematic relations between varying morphological features (Rose 1914) and the orientation of the auditory forebrain. On the basis of this analysis, it is also possible to compare the tonotopic arrangement of the auditory forebrain in song birds with that of gallinaceous birds (Scheich et al. 1979; Müller and Scheich 1985). In general, the internal arrangement of the auditory forebrain (fields L1, L2, L3) appears the same in both birds. The three-layered structure in one bird family can be transformed into the other by tilting it around a virtual axis running from ventromedial to dorsolateral. In the chicken, the three layers are mainly oriented from dorsomedial to ventrolateral, and are therefore best seen in a frontal view. In song birds, the auditory input-layer L2 is best recognized in a lateral view with L1 oriented rostrodorsally and L3 ventrocaudally. Apart from this fact and from the wider frequency range represented in song birds, our results show considerable similarities between the physiological organization of the auditory forebrain of the starling and that of gallinaceous birds.

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