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Feature extraction and tonotopic organization in the avian auditory forebrain*

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Summary. In a neurophysiological study within the auditory centers of the mediocaudal telencephalon of the starling, 601 neurons were tested for auditory responses. 369 of these units responded to pure tones, noise bands, amplitude modulations (AM), or species-specific sounds. Of all the auditory neurons, 16.8% did not respond to pure tones but only to more complex stimuli (tone-unresponsive-, TU-units). The remaining auditory units were classified as tone-responsive (TR-units). In 44.3% of TR-units (i.e. 36.9% of all auditory units) differing responses to tones versus more complex stimuli were observed. Responses as they occur in TU-units and in the differing responses of TR-units can be explained by neuronal extraction of features in the time (108 out of 198 neurons) and in the spectral domain (82 out of 198 neurons). Responses to species-specific sounds usually can be explained in terms of extraction of these features. Among neurons sensitive to temporal features, exclusive responses to a narrow range of AM frequencies were observed. In those TU-units that represent spectral features some restrict their responses to noise bands with distinct bandwidths centered around a specific midfrequency. These units reject both wider and narrower noise bands. A tonotopic arrangement of auditory units is found in field L, the surrounding neostriatum (NCM), and the Hyperstriatum ventrale (HV). Isofrequency lines run as a continuum through NCM, field L, and the caudal part of HV. TU-units are integrated into the tonotopic gradient according to the midfrequency of effective stimuli (e.g. noise bands or AM). The anatomical position of auditory units is correlated to their response properties. Within one isofrequency contour an increase in response selectivity is seen from field L to the postsynaptic areas in the NCM and the HV. The results are discussed in terms of possible mechanisms of feature extraction in the avian auditory system.

Key words: Auditory system – Forebrain – Feature extraction – Functional organization – Birds

Introduction

A variety of studies have shown that tonotopic organization – i.e. the central nervous representation of the frequency distribution along the sensory epithelium – is a fundamental organizational principle in vertebrate auditory systems (for rev. see: Clopton et al. 1974). Additional central maps have been detected either neurophysiologically or by histological techniques. Functional maps representing auditory space (Knudsen and Konishi 1978), aural interaction (Middlebrooks et al. 1980; Scheich 1983) and features relevant in the echolocation of bats (Suga 1977) have been demonstrated.

So, as in the visual cortex of cats and monkeys, where columnar organizations representing different features of vision have been detected by Hubel and Wiesel (1962; 1968), functional organization principles are also present in the auditory system. However, most of the studies in the auditory system have dealt with features relevant for sound- or object-location and the tonotopic representation of the sensory epithelium. Only little is known about the topographic organization of highly specific units

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which presumably are involved in analyzing complex acoustic signals related to auditory communication. A number of studies investigating the effect of natural and synthetic complex sound stimuli on neuronal responses in a variety of species have revealed units which were unresponsive to pure tones. However, some of these units showed strong responses to a restricted number of complex stimuli (Fuzessery and Feng 1982; Leppelsack 1978; Leppelsack and Vogt 1976; Margoliash 1983; Scheich et al. 1979b; Winter and Funckenstein 1973; Wollberg and Newman 1972). Beside these neurons which respond exclusively to complex sound structures, another group of units has been described in a number of vertebrate species. This group consists of neurons showing different response-types to tones (usually inhibition) and to complex sounds (usually excitation) (Leppelsack 1974; Margoliash 1983; Wollberg and Newman 1972). Little is known about either the physical parameters (features) eliciting these neuronal responses, or about the topography of these units, especially in regard to the tonotopic organization.

Knowledge of the functional organization of higher centers of the auditory pathway can provide us with information about the possible mechanisms of feature extraction, e.g. whether a hierarchical analysis is performed or whether information is processed in parallel pathways. Secondly, knowledge of the physical parameters eliciting selective neuronal responses will give further insight into the mechanisms of information processing within the auditory pathway. Using a variety of artificial and natural sounds, the present study aims to elucidate both the central nervous strategies of information processing as well as the functional topography within the auditory forebrain centers.

Methods

Preparation for single-unit recordings

The experiments were conducted in 5 adult starlings (2 ♂♂, 3 ♀♀) from May through October. To allow constant stereotaxic orientation of the bird's brains over successive experimental sessions, we attached metal chambers (Kirsch et al. 1980) to the dorsal scull under general anesthesia (1–3% Halothane, May and Baker LTD). Semisterile surgery was carried out at least 3 days prior to the first experiment. The chambers were implanted while the animal was fixed in a stereotaxic frame. In 2 animals the chamber was positioned over the right hemisphere, in 3 animals over the left hemisphere. The center of the chamber was oriented 1.5 mm rostral and 1.0 mm lateral to the caudal bifurcation of the sinus sagittalis. The dura mater and the overlying part of the bone were left intact and were only penetrated prior to electrode access.

In between experimental sessions the birds were held in cages following a natural photoperiod.

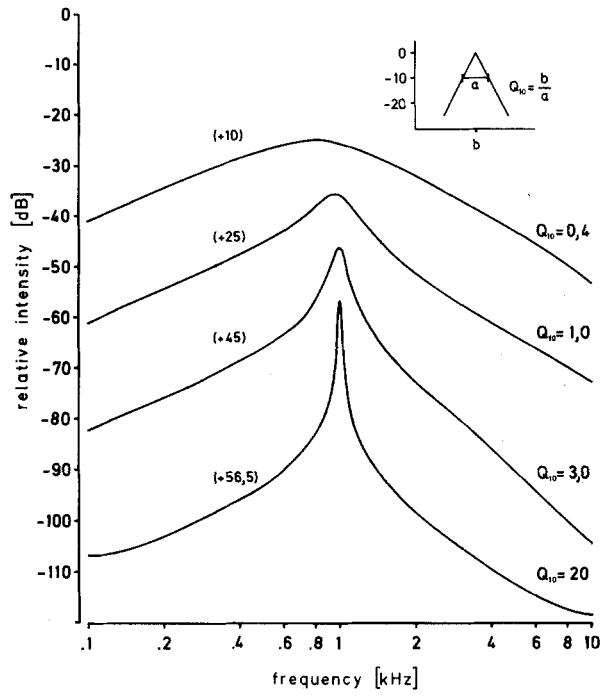

Fig. 1. Filter characteristics of the custom made bandpass-filter at four selected relative bandwidths (Q_{10}). Curves were shifted along the ordinate for better readability by subtracting the values given in brackets. With white noise at the filter input the overall output amplitude is identical for every Q_{10} and midfrequency. The determination of Q_{10} is given in the inset

Unit recording procedure and data analysis

Extracellular single-unit recordings were done in fully awake animals with 3M NaCl-filled glass micropipettes (10–20 MΩ). During experimental sessions the bird's body was restrained by wrapping in a comfortable cloth bag to prevent gross body movements. Conventional neurophysiological equipment was used for amplification and display of neuronal responses. Neuronal discharges, as well as the auditory stimuli, were stored on a multichannel tape recorder (ANALOG 7, Phillips) for off-line analysis. Using a PDP-12 laboratory computer (Digital Equipment Corp.) we made both peri-stimulus-time histograms (PSTH) and series analyses off-line. Series analyses were done by calculating the mean neuronal discharges occuring over the total length (400 ms) of identical stimuli (e.g. noise bands, AM), expressed as counts per stimulus.

Acoustical stimulation

For experimental sessions the animal was placed in an electrically shielded, anechoic chamber that was diffusely illuminated. During electrode advancement, tracking stimuli (White noise, 60 dB SPL, 400 ms duration, 2 ms rise- and decay-time) were presented at a rate of 1/s until single-unit discharges were encountered. Sound stimuli were amplified (CV 60, Dual) and fed over a HP-decade attenuator (350 D) to a midrange speaker (BPSL 100/7, Isophon) placed 70 cm in front of the animal. Intensity measurements of the stimuli were done regularily with a Bruel and Kjaer 1" microphone at the position of the animals head and are given in dB SPL (sound pressure level re 20 $\mu N/m^2$).

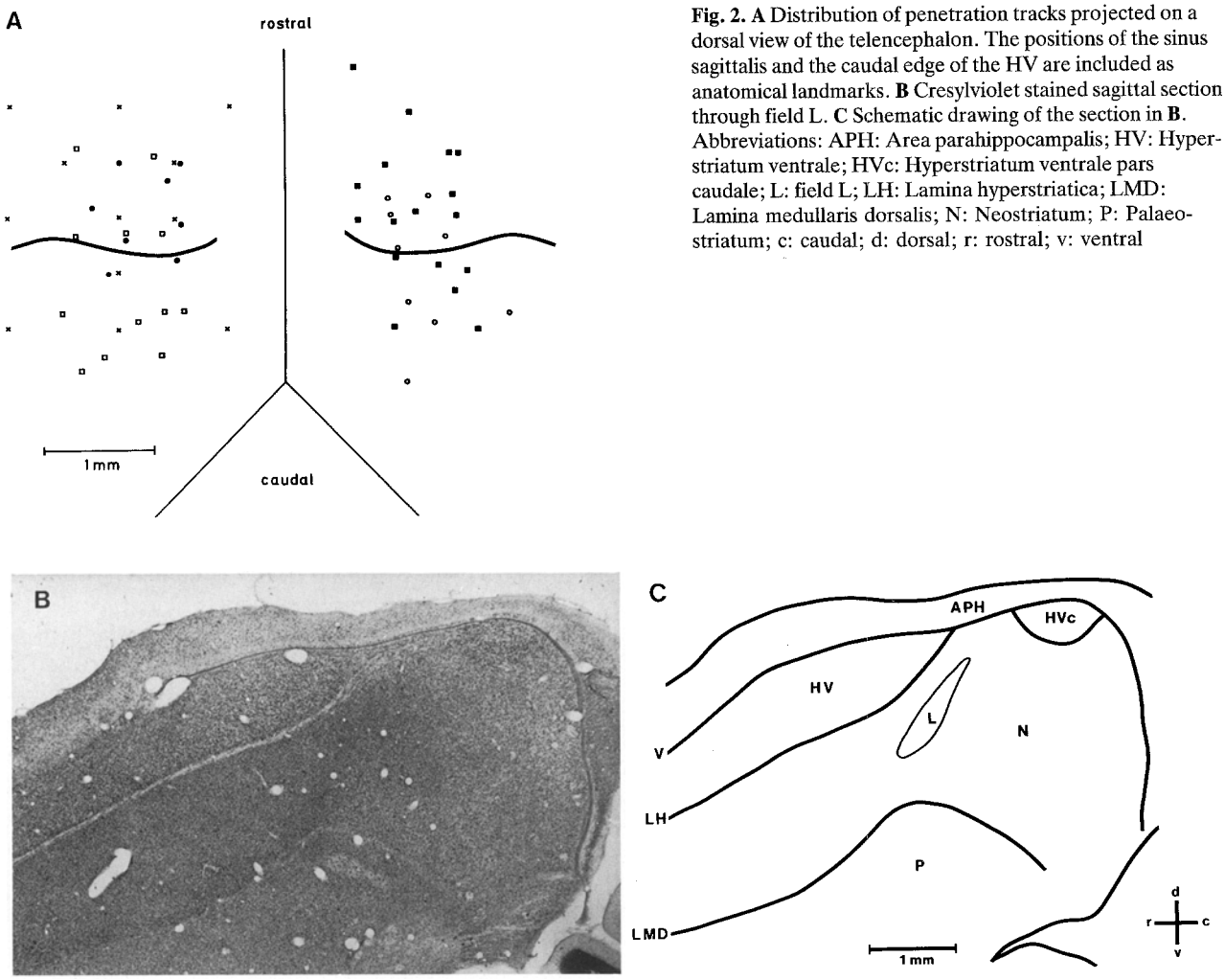

Fig. 2. A Distribution of penetration tracks projected on a dorsal view of the telencephalon. The positions of the sinus sagittalis and the caudal edge of the HV are included as anatomical landmarks. **B** Cresylviolet stained sagittal section through field L. **C** Schematic drawing of the section in **B**. Abbreviations: APH: Area parahippocampalis; HV: Hyperstriatum ventrale; HVc: Hyperstriatum ventrale pars caudale; L: field L; LH: Lamina hyperstriatica; LMD: Lamina medullaris dorsalis; N: Neostriatum; P: Palaeostriatum; c: caudal; d: dorsal; r: rostral; v: ventral

Pure tone stimuli were produced with a sine wave generator (SIT, Rhode and Schwartz), amplitude modulated tones (AM) with a function generator (Wavetek). The modulation depth was usually set to 80%. White noise (30–30.000 Hz) was either presented unfiltered or band-pass filtered. Noise filtering was done with a custom made variable filter of the second order. Center frequencies could be varied in 100 Hz steps from 100 to 11.000 Hz. A total of twelve different relative bandwidths could be selected without affecting the output amplitude of the device. The relative bandwidth (Q_{10}) of the output signal was defined as the center frequency of the signal as a ratio to the bandwidth 10 dB below maximal throughpass (see Fig. 1).

AM-series consisted of stimuli with a constant carrier frequency and the modulation frequencies changed in 10 Hz steps (usually from 10 to 100 Hz) Bandpass-filtered noise was presented in series of stimuli with a constant midfrequency and a successively changed relative bandwidth (Q_{10}).

Beside pure-tone, AM, and noise stimuli, we also presented a series of 80 species-specific vocalizations of the starling which had been used in earlier studies of field L (Leppelsack and Vogt 1976) and cochlear ganglion (Manley 1980) of this species. This sample consisted of both communicative calls and parts of the species' song (Hartby 1969).

Histological verification of electrode penetrations

After termination of the neurophysiological experiments frozen sections of the brains were cut at 40 µm and counterstained with cresylviolet. Figure 2B and C show a sagittal section at the level of field L. Electrode penetrations, as well as the factor of tissue shrinkage were reconstructed from multiple dye markings (6% Alcian Blue in 3M NaCl) injected from the recording electrode at defined depths.

Results

Distribution of auditory units within the medio-caudal telencephalon

In the present study 601 units were investigated during 58 electrode tracks. The distribution of penetrations is given in Fig. 2A. A total of 369 units revealed auditory responses to pure tones and/or to

Table 1. Distribution of units in areas of the mediocaudal telencephalon. Only units for which the exact location was verified histologically (N = 497) are included

	Area of mediocaudal telencephalon:			
	Field L	NCM*	HV	Others
Total of investigated units	41	303	80	73
Auditory units	40 (97.6%)	231 (76.2%)	56 (70.0%)	4 (5.5%)
TU-units	2 (5.0%)	44 (19.1%)	7 (12.5%)	2 (50.0%)

* excluding Field L

complex auditory stimuli. Units were determined to be unresponsive to sounds if:

i. no responses to pure tones or to narrow band noises (Q_{10} = 3.0) – both presented at two intensity levels – with (center-)frequencies varied in third octave steps from 100 to 10.000 Hz could be encountered and

ii. the sample of species-specific vocalizations presented at one intensity level was ineffective in eliciting stimulus coupled responses.

Auditory units could be subdivided into two groups:

i) tone-responsive (TR-) units usually having one defined characteristic frequency (CF), and

ii) tone-unresponsive (TU-) units which showed responses solely to complex auditory stimulation.

The distribution of TU-units as well as all auditory units in the mediocaudal forebrain, for which the location could be determined histologically, is summarized in Table 1. Units whose location in a given structure was ambiguous, i.e. at the border of field L, were excluded. It is obvious that the vast majority of the auditory units is located within the neostriatum and HV, with the highest percentage of auditory units being present in the neostriatal field L. Within this nucleus only one unit was found to be unresponsive to acoustic stimulation. We refer to field L as the morphologically defined nucleus containing small, densely packed somata, as defined by Rose (1914). In the sourrounding neostriatum NCM (which has also been referred to as field L in earlier studies (Scheich et al. 1979b; D. Bonke et al. 1979b)) as well as in the HV, comparable percentages of auditory units are encountered, being less frequent than auditory units within field L.

In regard to the number and distribution of TU-units, field L can again be separated from the other regions. While the number of TU-units in this nucleus is comparably small (5.0% of auditory units), TU-units are more often found within the surrounding NCM (19.1%) and HV (12.5%). Again, similarities are obvious in the latter two areas.

The number and distribution of auditory and TU-units did not differ significantly between the two hemispheres. In addition, no significant differences could be found in males and females.

Only a few auditory units have been encountered in other regions, e.g. palaeostriatum (N = 3) and area parahippocampalis (N = 1), though in the vicinity of the latter evoked potentials to auditory stimulation were recorded routinely.

Tonotopic organization

Penetrations with more than 4 TR-units were tested for the presence of a dependence of unit locations on the CF. Thus, two regression lines were calculated with both a linear and a logarithmic frequency scale over penetration depth. Penetrations were regarded to run through a tonotopically organized structure when at least one regression coefficient could be shown to be significant at the 1% level by the Fisher-t-test (Sachs 1974). Two thirds of the tested penetrations reached this criterion ('tonotopic penetrations'). Of these, one half revealed higher significances for the linear frequency scale, while for the other half the regressions fitted best when a logarithmic frequency scale was applied. No interhemispheric differences could be obtained. Figure 3 shows examples for both types of 'tonotopic penetrations'. CF's typically rise by 2 octaves/mm with increasing depth in most of the 'tonotopic penetrations'. No organizational principle could be defined with respect to the distribution of the two tonotopic sequence types. However, penetrations that did not reach the described criterion for tonotopic organization were preferentially located in lateral and caudal parts of the neostriatum.

Electrode tracks which passed through both the HV and NCM also reflected a tonotopic organization. As shown in Fig. 3B, a continuous rise of CF-values over depth is present in the HV (hatched areas in Fig. 3B) and continues after the electrode penetrates through the lamina hyperstriatica, separating HV and neostriatum (Fig. 2B and C). Hence both anatomically distinct areas share a common functional organizational principle, i.e. tonotopic organization.

Along the rostro-caudal extent of the auditory telencephalon, locations with similar CF's were positioned on a line perpendicular to field L (isofrequency contours). Figure 4 reflects data from one animal. The locations of four frequencies were calculated from regression lines. Isofrequency contours run across the lamina hyperstriatica and continue in HV.

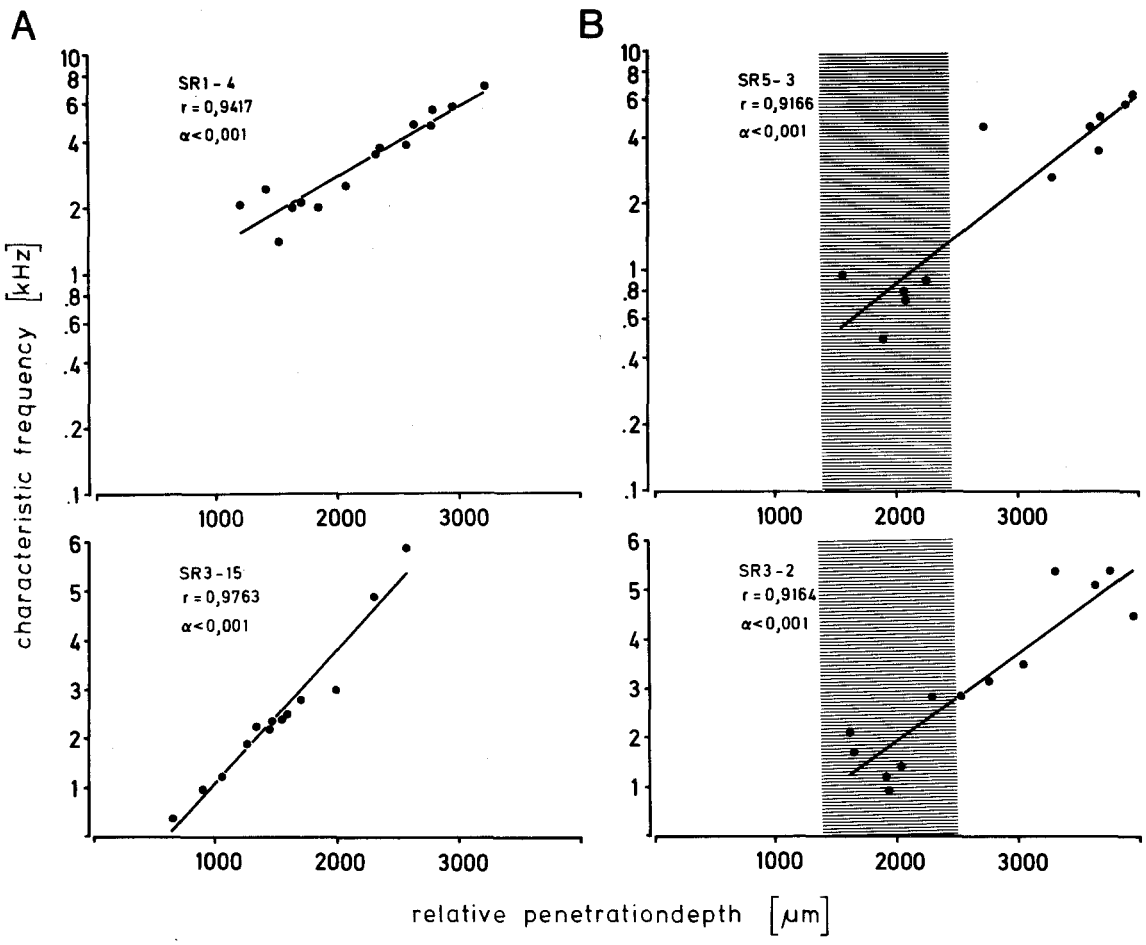

Fig. 3A and B. 'Tonotopic penetrations' through areas of the medio-caudal telencephalon best described by a logrithmic (top) or a linear (bottom) correlation of the frequency with the penetration depth. The correlation coefficient (r) and the error probability (α) of the regression lines are included for each electrode track. **A** Penetrations running through NCM. **B** Penetrations running through both HV (hatched areas) and NCM

In the most rostral electrode tracks penetrating both HV and NCM, only high frequency units (CF ≥ 3 kHz) could be detected.

Differing responses to tones and complex stimuli

A total of 136 units (36.9% of auditory units) revealed differing response-types to either pure tones or complex stimuli. Most of these units (N = 92) showed phasic excitatory responses (mostly with tonic inhibitory components) to pure tone stimulation while complex sounds revealed tonic excitation (Fig. 5). A characteristic of these units was that AM-stimuli were also effective in eliciting a sustained excitatory response (Fig. 5). This indicates that the complexity of the time course of the amplitude is the physical parameter responsible for the differentiation of these neuronal responses. A second subgroup of units (N = 40) showed tonic inhibition to pure tones and tonic excitation to complex stimuli (Fig. 6A). In these units AM-stimuli were ineffective in eliciting any excitatory responses. However, when narrow band noise was presented with a constant midfrequency, a continuous shift of the response characteristic from tonic inhibition (to pure tones) to excitation (to broadband noise) was found as the bandwidth was increased (Fig. 6B).

Response maxima stayed either constant up to white noise stimulation (Fig. 6B) or were restricted to band-filtered noise-stimuli, so that white noise was ineffective or less effective in eliciting a tonic excitation. As AM-stimuli did not reveal an excitatory response but enrichment of the spectral content caused this response, it has to be concluded that spectral parameters are the features represented in this latter group of units.

Only four units with differing responses to tones

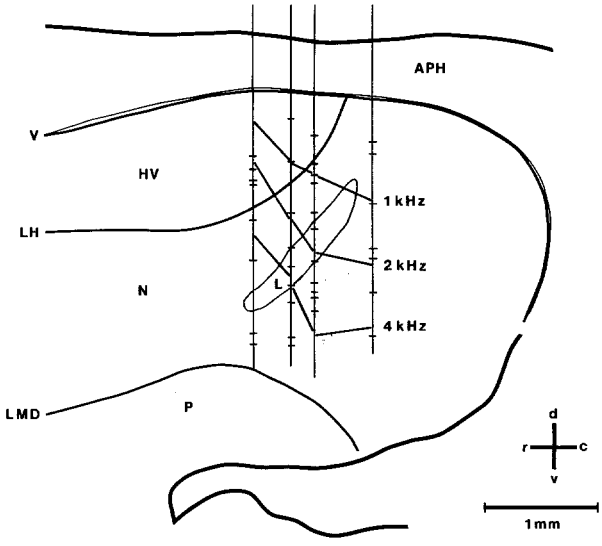

Fig. 4. Orientation of isofrequency contours in the auditory telencephalon. Positions of three frequencies were recalculated from regression lines describing the tonotopy within each penetration. Notice that isofrequency contours lie perpendicular to field L and pass the LH to continue in the HV

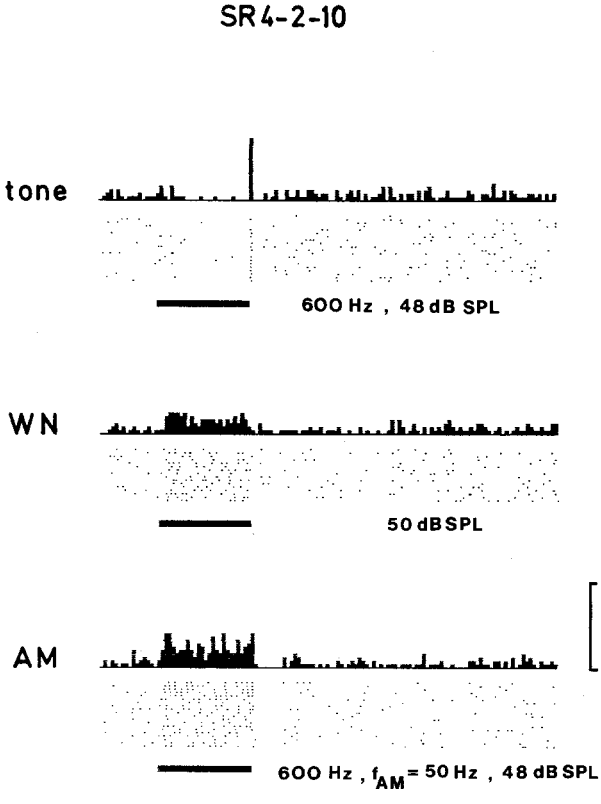

Fig. 5. PST-histograms of differing responses of a TR-unit to a tone burst versus an amplitude modulated tone (AM) and white noise (WN). Modulation depth is 80%. Stimulus durations (400 ms) are indicated by horizontal bars; the vertical bar represents 50 impulses/bin/20 presentations

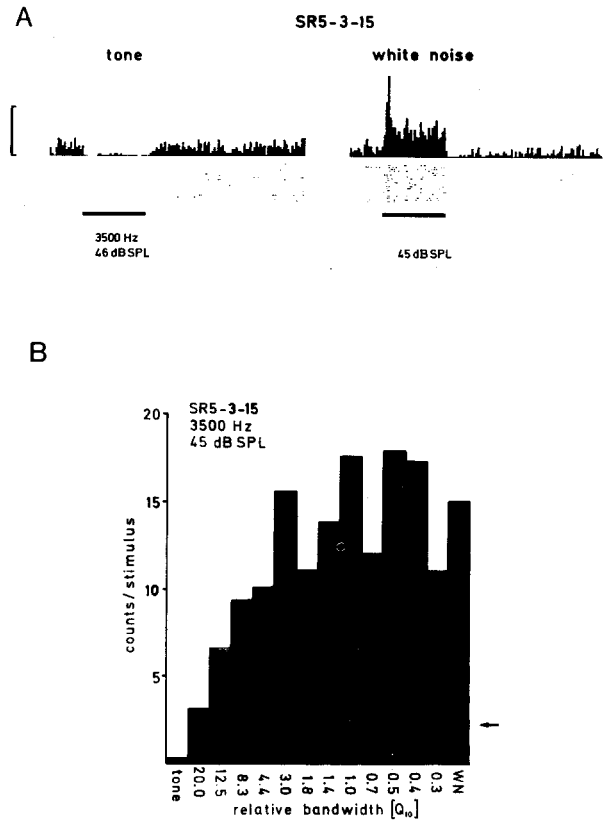

Fig. 6A and B. Dependency of the response on the bandwidth of noise-stimuli in a TR-unit with differing responses. **A** PST-histogram of the differing response to a tone and a white noise stimulus. (Conventions as in Fig. 3). **B** Response strength depending on the relative width of noise-bands with a constant midfrequency (3500 Hz). Notice the continuous shift in response from inhibition (tone) to strong excitation (Q_{10} = 3.0) with widening of the bandwidth. The spontaneous activity level is given by the arrow at the right

and complex stimuli could not be classified in the preceeding two groups. These units showed tonic excitatory responses to tones and inhibitory responses (N = 2) or phasic excitatory responses (N = 2) to complex noise stimulation. All of these units had narrow excitatory tuning curves with wide inhibitory sidebands. Thus even the narrowest noise-bands applied in this study activated both excitatory and inhibitory response areas.

Tone-unresponsive (TU-)units

Beside neurons with clear responses to pure tones, 62 units (16.8% of auditory units) could not be driven with such simple stimuli. However, responses were evident when complex sounds were applied. Likewise TR-units with differing neuronal responses, TU-units can also be divided in two main subgroups; one

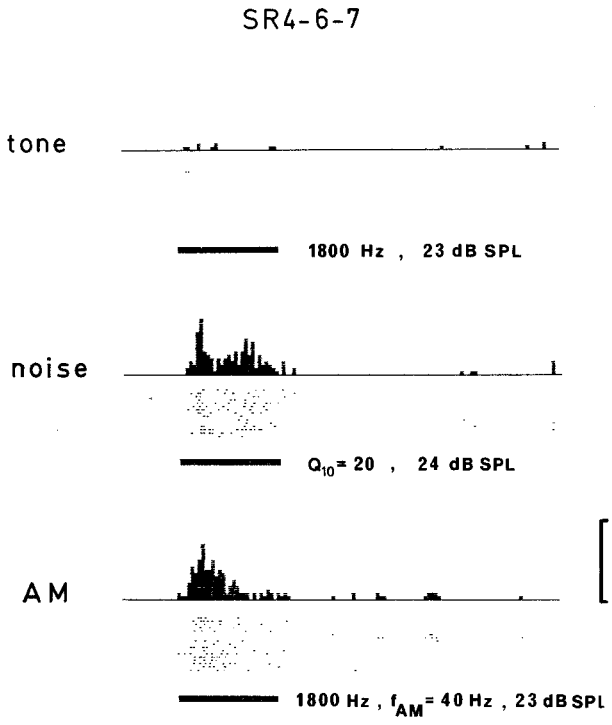

Fig. 7. PST-histograms of the response of a TU-unit to narrow band noise (Q_{10} = 20) and an amplitude modulated tone (modulation depth: 80%). Notice that no response is elicited by tone stimulation. (Conventions as in Fig. 3)

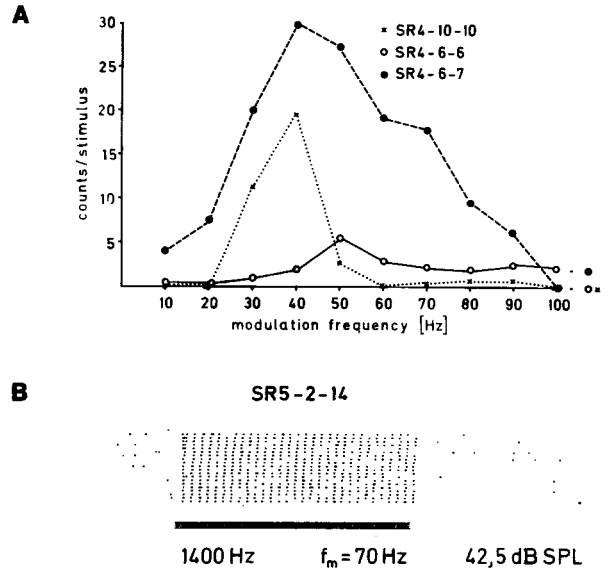

Fig. 8. A Characteristic optimum curves describing the dependency of response strength on the amplitude modulation (AM) frequency in AM-sensitive TU-units. Spontaneous activity levels are given at the right. Modulation depth was 80% in every case. **B** Dot-display of a phase locked response to AM-stimulation (modulation depth: 80%) with a modulation frequency (f_m) of 70 Hz. Stimulus duration (400 ms) is indicated by the horizontal bar

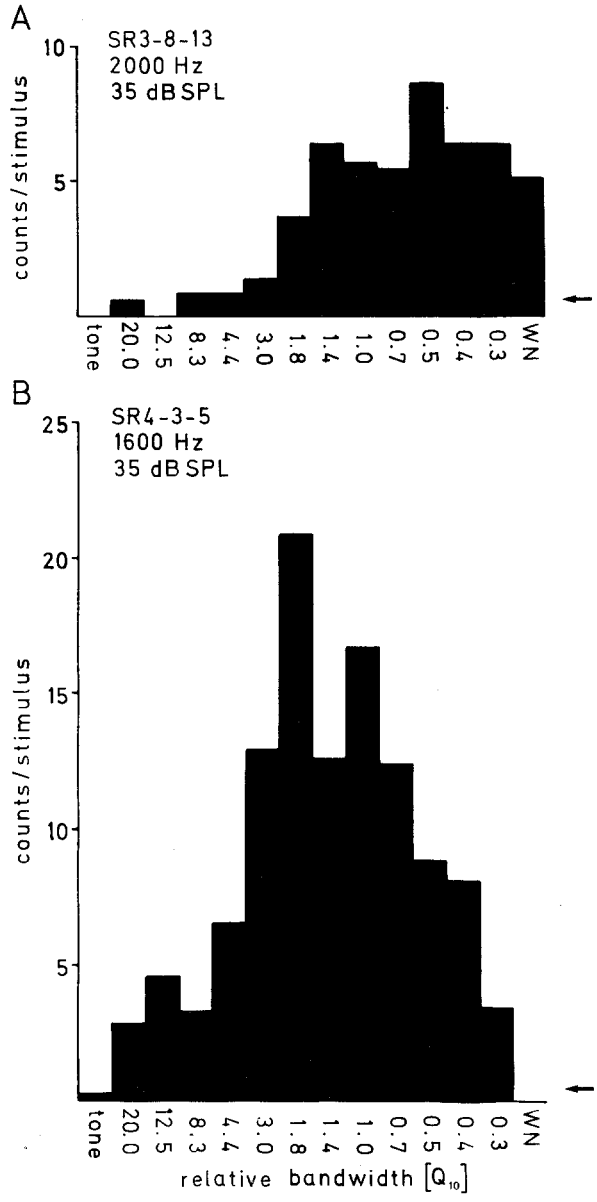

Fig. 9A and B. Different response functions of TU-units in dependence of the bandwidth of noise stimuli. **A** Saturation curve: at a given midfrequency (2000 Hz) all noise bands with a Q_{10} smaller than 1.8 including white noise elicit a constant response strength, while narrow band stimuli ($Q_{10} > 3.0$) are unresponded. **B** Optimum curve: maximum excitation is obtained by medium bandwidths. Widening, as well as narrowing the bandwidth results in reduced response strengths. Tones and white noise are ineffective or might even cause an inhibition. Spontaneous activity levels are indicated at the right

consisting of neurons driven by spectral parameters of a stimulus and others being sensitive to time domain features.

Figure 7 reflects the responses of a unit belonging to the latter group. While tone presentation reveales no stimulus coupled response, both narrowband

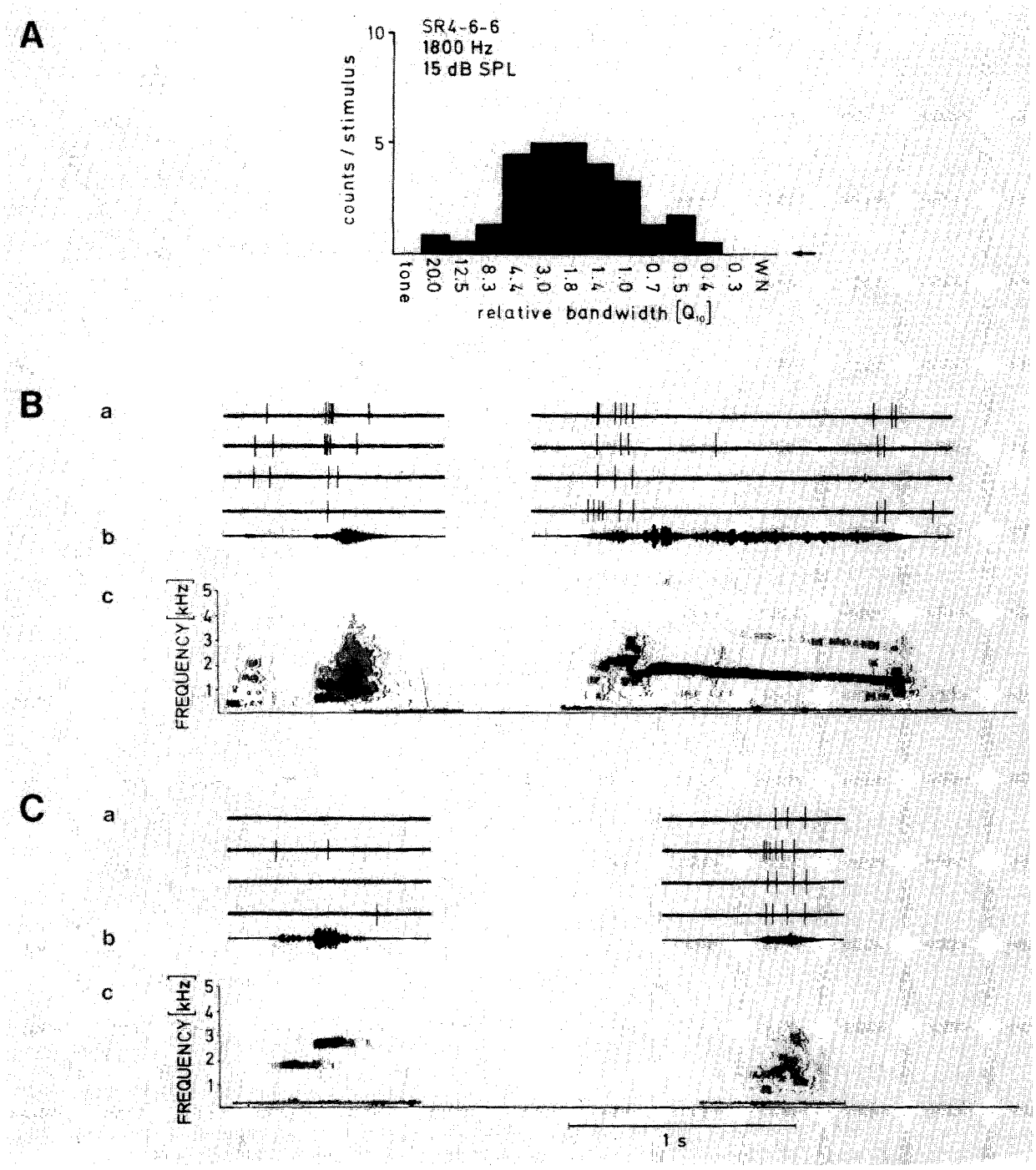

Fig. 10A–C. Responses of a TU-unit to species-specific vocalizations. **A** Optimum function describing the response strength depending on the bandwidth of noise stimuli. Best responses are obtained by medium bandwidths centered around 1800 Hz. **B and C** Original recordings of spiketrains (a) to four presentations of species-specific vocalizations of the starling documented as the oscillogram (b) and sonagram (c). Notice the coincidence of neuronal discharge and the occurence of noise bands in a narrow range around 1800 Hz in the sonagrams

noise (Q_{10} = 20) and AM-stimuli elicit an excitation. A total of 16 units (26%) showed these responses with AM-induced discharge being similar to that elicited by narrow-band noise. This is certainly due to amplitude fluctuations being present especially in band-pass filtered noise of narrow bandwidth.

As shown in Fig. 8A neuronal responses to AM-stimuli could be specifically tuned to certain modulation frequencies. In addition phasecoupling to the modulation frequency has been observed in a number of neurons (see Fig. 8B). This occured not only in TU-units but also in TR-units with phasic

responses to tone-stimulation. None of these units responded to tones of the modulation frequency. The highest modulation frequency being followed in a rigid one-to-one manner was 70 Hz, being near to the upper AM-threshold revealed in behavioral investigations in a bird (Dooling and Searcy 1981).

In the other group of TU-units (N = 42; 68%) neither pure tones nor AM-stimuli were effective in eliciting any response. With the exception of four neurons all of these units could be driven by narrow-band noise and/or WN. Figure 9 gives the response characteristics of two typical examples of TU-units without AM-response. Unit SR3-8-13 (Fig. 9A) was responsive to WN and revealed a response plateau when narrow-band noises centered around 2 kHz were applied. However, when the relative bandwidth exceeded $Q_{10} = 1.8$ no responses were observed.

The unit in Fig. 9B represents 6.2% (N = 23) of all auditory units investigated in the present study. No standard stimulus (tones, WN) nor AM is capable of eliciting a neuronal response. However, strong excitation is observed in response to band-pass filtered noise. In unit SR4-3-5 an increase of response strength is present while widening the relative bandwidth up to 1.8, whereas wider bands of noise were less effective in driving the unit. At higher stimulus intensities, the range of effective bandwidth widened in most of these units. However, pure tones were never effective in eliciting a response even at the highest intensity level of 80 dB SPL.

Three of the four TU-units responding neither to tones, AM, or noise stimuli could be driven by frequency modulated tones. The other one responded only to species-specific vocalizations.

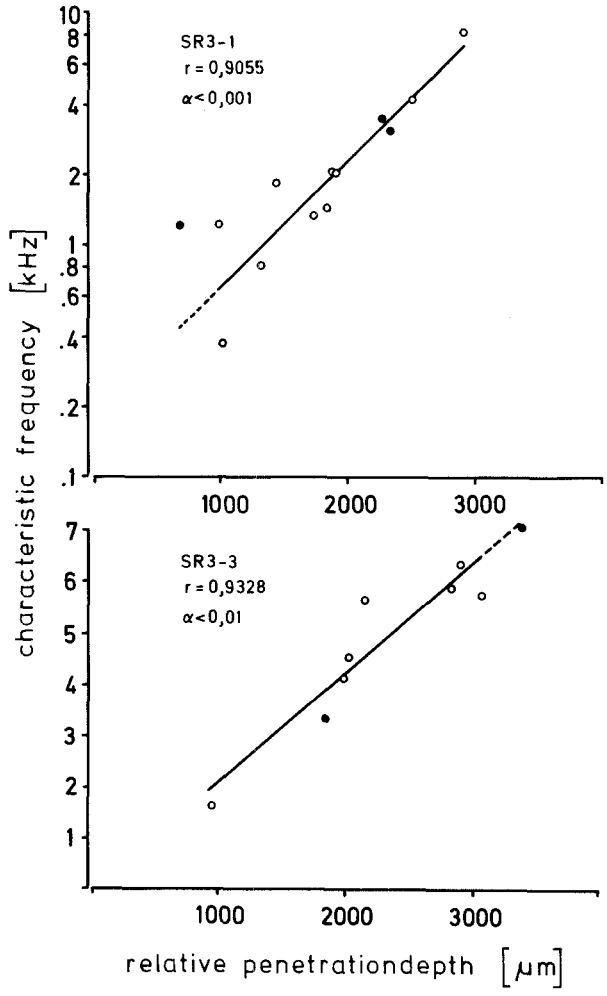

Fig. 11. Localization of TU-units (closed circles) within 'tonotopic penetrations' through NCM. Regression lines are calculated on the basis of TR-units (open circles) within the same track. 'Characteristic frequencies' of TU-units are defined as the center frequency of the most effective noise bands. Conventions are as given in Fig. 2

TU-units; responses to species-specific sounds

When stimulated with species-specific vocalizations, the different subgroups of units introduced above, showed different degrees of selectivity (based on the number of responded sounds out of 80 vocalizations). Those units responding to time domain features usually showed a lower selectivity than those representing spectral features. Units responding only to bandpass filtered noises showed the highest selectivity.

Unit SR4-6-6 responds only to band-pass filtered noise without being excited by tones or WN (Fig. 10A). Only a small number (N = 14) of the 80 presented vocalizations elicited neuronal responses. As with synthetic stimuli, the responses to conspecific sounds are restricted to noisy, narrow-band sounds with a mid-frequency near 1.8 kHz (Fig. 10B and C). Wide band parts of calls, as well as tonal sounds are ineffective (Fig. 10B); the same is true for a third sound composed of two formants (Fig. 10C). Thus, response characteristics revealed by synthetic stimuli hold true for species-specific sound stimulation.

Topography of TU-units in reference to the tonotopic organization

It has been mentioned previously that the percentage of auditory units decreases from field L to NCM and HV (Table 1) while the relative amount of TU-units follows a contrary gradient. Thus TU-units are not homogeneously distributed within one isofrequency contour cutting across the auditory subfields.

The number of TU-units in 'non-tonotopic penetrations' (18% of auditory units) was higher than in 'tonotopic penetrations' (12% of auditory units). As 'non-tonotopic penetrations' were preferentially located outside field L, this corresponds to the functional organization mentioned above. Figure 11 gives the relative location of five TU-units with sole responses to noise bands in two 'tonotopic penetrations'. The TU-units were included by defining the mid-frequency of the effective noisebands as the 'CF'. It is obvious that the mid-frequency of effective stimuli corresponds to the location of TU-units in the tonotopic gradient. The same coherence can be observed for the carrier frequency of units responding preferentially to AM-stimuli. Thus, tonotopic organization can be claimed to be the basic functional organizational principle not only for TR-units but also for TU-units.

Discussion

Functional zones of the auditory medio-caudal telencephalon

Earlier investigations of the NCM proposed the existence of three distinct neostriatal zones. These were distinguished on the basis of spontaneous activity level and the response complexity. The central layer (L_2) was stated to be identical with the field L, as described by Rose (1914). This area was defined neurophysiologically as showing higher spontaneous activity (D. Bonke et al. 1979b) and a lower degree of response selectivity (Langner et al. 1981). In the present paper we could confirm the latter point. However, no obvious increase in spontaneous activity rate was found for units within field L. As discussed by Bonke et al. (1979b) the large recording area of the tungsten-electrodes used in that study might have caused this different result, for field L is characterized cytologically by densely packed small neurons (Rose 1914). High-impedance glass micropipettes, as used in the present study allow reliable isolation of single units, even in areas with high neuronal density.

Two functional zones can be differentiated neurophysiologically in the neostriatum of the starling on the basis of both the amount of acoustically responsive units and of the selectivity of neuronal responses: i. the input layer field L, characterized by a large number of auditory units with a low degree of selectivity, i.e. mainly TR-units, and ii. the surrounding neostriatum with a high percentage of selective units.

Clusters of auditory or TU-units were not detected within this structure or in the auditory responsive area of the HV either in regard to single cell data or the background activity during electrode advancement. Although suggestive, a final statement about the homogeneity of the distribution of auditory and selective units outside field L calls for a systematic sampling procedure. This was incompatible with the use of high-impedance microelectrodes used to guarantee single-cell isolation.

As shown earlier, field L receives its input from the diencephalic nucleus ovoidalis (B. Bonke et al. 1979a; Karten 1968) and sends projections to the surrounding neostriatum (B. Bonke et al. 1979a; Kelley and Nottebohm 1979) and to the HV (B. Bonke et al. 1979a; Bradley and Horn 1979; Saini and Leppelsack 1981). Thus, the increase in response selectivity from field L to the postsynaptic areas supports the view that mechanisms causing increased selectivity are situated within the neostriatum/HV-complex. Recent studies have demonstrated the involvement of intratelencephalic GABAergic inhibition in increasing response selectivity of units within the auditory telencephalon (Müller 1984). These data suggest that information processing within the auditory pathway is based on a hierarchical organization. One structure lying postsynaptically to the auditory neostriatum is the vocal motor nucleus Hyperstriatum ventrale, pars caudale (HVc; Kelley and Nottebohm 1979). As penetrations were biased to locations rostral to HVc in the present study only a few units which did not respond to auditory stimuli were recorded from this nucleus which has been shown to contain highly selective auditory units (Margoliash 1983; McCasland and Konishi 1981). As songspecific unit responses in HVc could not be explained with responses to simple stimuli and noise bands (Margoliash 1983), this nucleus can be viewed as a higher step in this hierarchy.

The present data show clearly that the caudal parts of the HV contain a predominant proportion of auditory units. Both the percentage of auditory units and the selectivity of neuronal responses are comparable to those found in the neostriatum, excluding field L. Mainly on the basis of imprinting experiments with visual stimuli in the chick (Bateson et al. 1978; Horn et al. 1979) it has been stated that HV may be an association center integrating multiple sensory input (Saini and Leppelsack 1981). However, while effects of visual imprinting and visual afferents are predominantly found in a medial proportion of HV (Horn et al. 1979; Bradley and Horn 1978), in the present study auditory responses were restricted to caudal portions of HV adjacent to the lamina hyperstriatica. A similar distribution of auditory

activity within HV has been stated from an autoradiographic study using 2-deoxyglucose (Scheich et al. 1979a). Thus, 'visual' and 'auditory' hyperstriatal regions seem to be separated. It remains unclear whether other sensory modalities are represented in the non-auditory neurons of the caudal HV or, whether even multimodal responses are present within the neurons of the HV which are responding to acoustic stimuli. In view of the close association of different sensory inputs to the HV it seems to be reasonable to assume that this area is acting as a center for sensory integration.

Tonotopic organization

The present data confirm the tonotopic organization of the auditory forebrain nuclei, as described in a gallinaceous bird (D. Bonke et al. 1979b; Scheich et al. 1979b). The axis of the tonotopic gradient lies approximately in dorso-ventral direction, while isofrequency-contours lie perpendicular to the extent of field L. However, the present data are in contrast to earlier investigations in another songbird, the zebra finch (Zaretsky and Konishi 1976) where isofrequency planes were reported to lie in dorso-ventral direction with increasing best-frequencies registered from caudal to rostral. This discrepancy possibly is due to interspecific variability in the orientation of the field L (S. Müller and Scheich 1985). In the starling this area extends from caudo-dorsal to rostro-ventral, whereas the main orientation lies in dorso-ventral direction, being parallel to the lamina hyperstriatica. The same is also true for the guinea fowl (D. Bonke et al. 1979b). Thus, it can be stated that the orientation of the isofrequency planes is critically dependent upon the orientation of the field L, with isofrequency contours lying perpendicular to this anatomical structure.

Beside the neostriatal parts of the auditory forebrain projection of n. ovoidalis, the HV also shows a tonotopic organization. The extension of isofrequency contours into the HV has previously been reported by Scheich et al. (1979a) based on 2-deoxyglucose autoradiographs. The present paper gives the first electrophysiological data concerning both auditory representation and functional organization of the auditory projections within HV.

Positions of maximum basilar membrane displacement (Békésy 1944) and maximum total hair cell loss along the basilar membrane following intense auditory stimulation (Ryals and Rubel 1982) show a dependence on the stimulus frequency, best described by a logarithmic function. The present data on the spatial representation of frequencies within the auditory telencephalon were best described either by a logarithmic or a linear function for each half of the 'tonotopic penetrations'. Similar data have been reported from investigations of auditory cortex in the cat (Clopton et al. 1974). As no clustering of either linear or logarithmic 'tonotopic penetrations' could be observed, it seems likely that the tonotopic gradient follows an intermediate function. However, as most of the datapoints lie within one decade, a clear decision is difficult.

The data of the present study gives strong evidence that the tonotopic organization is the fundamental organizational principle, not only for TR-units, but also for TU-units. Neurones responding only to complex stimuli are integrated into this organization according to the frequency compound of the most effective stimuli.

The fact that the amount of TU-units increases from field L to the postsynaptic areas in NCM and HV indicates a functional hierarchy within one isofrequency contour.

Extracted features and possible mechanisms of feature extraction

With the exception of 4 cells (1% of auditory units) all auditory units could be driven by either tones, AM-stimuli, or noise bands. Stimuli eliciting differing neuronal responses, as well as those eliciting responses in TU-units could be divided into two subgroups: i. stimuli showing complexity in the time course of the amplitude and ii. stimuli with complexity in the spectral composition. In about one quarter (26%) of TU-units with differing neuronal responses AM-stimuli were effective, while about two thirds (68%) could only be driven with stimuli showing spectral complexity.

As amplitude modulation of tones produces additional spectral components in the signal, it seems possible that responses to AM-stimuli also reflect a spectral stimulus feature. However, effective modulation frequencies were usually below 50 Hz in the present study, whereas in the majority of units 10 Hz was already sufficient in eliciting a change of the response-type. It seems unlikely that a stimulus bandwidth covering 20 Hz alone causes the observed changes in neuronal responses. The fact that a number of responses were clearly phase-locked to the modulation frequency supports the idea that the time course of the stimulus is reflected in AM responses. Neurons coding features in the time domain have been reported in the auditory system of bats (Suga 1977; Sullivan 1982) and the auditory midbrain nucleus of the guinea fowl (Langner 1983). Most of

the corresponding unit responses in the present study can be explained by the repetitive occurence of transients in AM- and noise-stimuli. This is in accordance with the phasic response of most of these units to pure tones (Fig. 5).

Whereas responses to time domain features can often be explained by adaptive processes of synaptic transmission of a single input channel, selective neuronal responses to spectral features call for multiple channel convergence. Thus, a simple model for neuronal wiring to explain the response behaviour of neurons with exclusive responses to noise bands is a logical AND-gate. Such a neuronal network can easily be assumed to result from addition of subthreshold excitatory postsynaptic potentials (EPSP's) at the level of the convergence-unit. Subthreshold convergence of different frequency channels has been substantiated in the auditory forebrain of the chicken after blockage of GABAergic inhibition (Müller 1985). To account for units having both a minimal and a maximal bandwidth in response to noise bands (Figs. 8B, 9A) beyond excitatory-excitatory interactions additional inhibitory inputs are necessary. Similar models have been discussed for vowel-discriminating neurons in the mynah bird (Langner et al. 1981). However, most of these units could also be driven by either converging input, which has not been the case in the TU-units of the present study. Neuronal convergence of frequency channels has been validated in the anuran auditory midbrain (Fuzessery and Feng 1982) where both excitatory-excitatory and excitatory-inhibitory interactions were shown. Those units responding solely to combinations of tones described in that study might correspond to the TU-units with sole responses to noise bands of the present investigation.

Two main features extracted from acoustic signals are stated from the present data namely: i. *amplitude modulation* characterizing repetition rates and transients at the beginning and ending of tones as well as within noise stimuli and ii. *spectral composition* of wide- and narrow-band signals as well as harmonic sounds, e.g. formants. Although these two features have been sufficient to explain the responses of all but four TU-units and TR-units with differing responses to tones and complex stimuli it cannot be excluded that additional features are represented in the avian auditory pathway. In fact, a recent investigation of auditory forebrain units in another songbird species has revealed neurons with a high selectivity to single parameters of frequency modulations, e.g. steepness and direction of the sweeps (Leppelsack 1983).

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