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Periodicity coding in the primary auditory cortex of the Mongolian gerbil (*Meriones unguiculatus*): two different coding strategies for pitch and rhythm?

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Abstract Periodic envelope or amplitude modulations (AM) with periodicities up to several thousand Hertz are characteristic for many natural sounds. Throughout the auditory pathway, signal periodicity is evident in neuronal discharges phase-locked to the envelope. In contrast to lower levels of the auditory pathway, cortical neurons do not phase-lock to periodicities above about 100 Hz. Therefore, we investigated alternative coding strategies for high envelope periodicities at the cortical level. Neuronal responses in the primary auditory cortex (AI) of gerbils to tones and AM were analysed. Two groups of stimuli were tested: (1) AM with a carrier frequency set to the unit's best frequency evoked phase-locked responses which were confined to low modulation frequencies (fms) up to about 100 Hz, and (2) AM with a spectrum completely outside the unit's frequency-response range evoked completely different responses that never showed phase-locking but a rate-tuning to high fms (50 to about 3000 Hz). In contrast to the phase-locked responses, the best fms determined from these latter responses appeared to be topographically distributed, reflecting a periodotopic organization in the AI. Implications of these results for the cortical representation of the perceptual qualities rhythm, roughness and pitch are discussed.

Key words Amplitude modulation · Envelope periodicity · Periodotopy · Temporal analysis · Timbre

Abbreviations *AI* primary auditory cortex · *AM* amplitude modulation · *BF* best frequency · *BMF* best modulation frequency · *BP* band-pass · *BS* band

suppression · *CF* characteristic frequency · *CX* complex · *EPSP* excitatory postsynaptic potential · *fc* carrier frequency · *fm* modulation frequency · *fm_{max}* highest modulation frequency · *FRF* frequency response function · *FRR* frequency response range · *HP* high-pass · *LP* low-pass · *MTF* modulation transfer function · *NS* non-selective · *SPL* sound pressure level · *VS* vector strength

Introduction

Many natural sounds, particularly voiced speech sounds and animal communication signals, are characterized by periodic envelope or amplitude modulations (AM). The perceptual quality created by such sounds depends on the modulation frequency (fm): for low fms up to about 20 Hz AM signals are associated with the sensation of rhythm (Terhardt 1968), at higher fms a pitch (periodicity pitch) is perceived (e.g. Ritsma 1962). The sensation of pitch occurs within a wide frequency range: For complex harmonic stimuli that contain energy in the fundamental, human subjects can discriminate pitch in the range between 20 Hz and about 20 kHz, although the ability to identify musical intervals deteriorates at periodicities above 5 kHz (cf. Evans 1978). Even if there is no significant energy in the fundamental, the pitch of this "missing fundamental" is still perceived, at least up to envelope frequencies of about 800 Hz (Ritsma 1962).

How such periodic signals are encoded throughout the vertebrate auditory system has been addressed in a large number of studies (for review see Langner 1992). Whereas periodicity coding is well described for lower levels of the auditory pathway, only little is known about the representation of envelope periodicity in the auditory cortex: According to earlier studies in the cat, neurons that respond selectively to a certain range of envelope periodicities only code for a frequency range up to about 100 Hz (Schreiner and Urbas 1988; Eggermont 1994). However, Bieser and Müller-Preuss (1996) recently reported that envelope frequencies up to about

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350 Hz are encoded in the auditory cortex of the squirrel monkey. Nevertheless, this is obviously not sufficient to account for the large range of pitch which may be perceived. In the present study we therefore made an attempt to fill the apparent gap between the demonstrated cortical representation of envelope frequencies and the perceptually relevant range.

Materials and methods

A total of 13 adult male Mongolian gerbils taken from our own breeding colony were used for this study. Experiments were carried out on both anaesthetized and unanaesthetized specimens. We use the term "unanaesthetized" rather than "awake" throughout this paper since it is possible that unanaesthetized animals might have been sleeping during some periods of the experiment.

Surgery

Preparation of animals was performed under deep Halothane (Hoechst) and local anaesthesia. Body temperature was maintained at 37 °C using a feedback-controlled heating blanket.

The skin over the skull and the musculature covering the temporal bone on the recording (left) side were partly removed. The auditory cortex (cf. inset in Fig. 10A) was then exposed by craniotomy; the dura was left intact. During surgery drying up of the dura was prevented by external application of isotonic NaCl solution. A platinum wire reference electrode was implanted between skull and dura over the right parietal cortex.

For acute experiments (anaesthetized animals) a 2.5-cm-long aluminium bar was fixed to the frontal bones with dental acrylic and served as a head anchor for stereotactic fixation during electrophysiological recordings. The animals were then transferred to an anechoic, sound-attenuated chamber. During the course of the experiments anaesthesia was maintained by intraperitoneal application of a mixture of ketamine (Ketavet, 50 mg ml⁻¹), xylazine (Rompun 2%) and isotonic NaCl solution (mixture 9:1:10). The application rate was 0.06 ml h⁻¹. At the end of the recording session (after 20–24 h), animals were killed by intrapulmonary-injected T61 (Hoechst).

For experiments on unanaesthetized animals a chronic preparation was performed. The stability of the head anchor was further improved by inserting insect pins about 0.5 mm into the skull in the shape of a crown and by a small screw that was inserted into the exposed left bulla. A plastic cylinder (inner diameter 6.5 mm) with a screw cap was attached over the trepanation area. Insect pins, bulla anchor, head holder and cylinder were fixed with dental acrylic. The stability of this head-holder enabled us to perform multiple recording sessions over a period of 4–6 weeks on each animal. To minimize animal stress single sessions were limited to a few hours. After the surgery the dura was covered with an antibiotic paste and the plastic cylinder was sealed with the screw cap. The animals were given a period of 2 days to recover. Careful observation showed normal behaviour and no signs of distress or impairment.

Electrophysiological recordings

Neuronal responses of single and multi-units were recorded extracellularly from the left primary auditory cortex (AI) using glass-insulated tungsten microelectrodes (impedance: 0.7–2.5 MΩ at 1 kHz; tip diameter 1–2 μm). The electrode was positioned over the cortex under visual control through an operating microscope. It was then advanced through the dura with a remote-controlled piezo-micromanipulator in a dorsoventral direction. All tracks were aligned tangentially to the temporal cortical surface (cf. Thomas et al. 1993). For acutely prepared animals, positions of

tracks were measured relative to lambda. For chronically prepared animals the position of the first track was marked on a schematic drawing with reference to the surface vasculature as lambda was covered with dental acrylic. All further track positions were measured relative to the position of this first track.

Unit activity was amplified (× 10 000), band-pass filtered (1–3 kHz, 3 dB/octave), and fed into a level discriminator. The filtered electrode signal and the discriminator level were displayed on an oscilloscope. An additional high-resolution oscilloscope with memory function was triggered by discriminated events ("spikes") and used to distinguish visually between single and multi-units. Criteria used were peak and valley amplitudes of triggered spikes as well as spike duration and the time between crossing of trigger level and zero crossing. Multi-units consisted of two to five single units (two to five waveforms were distinguishable). Spikes were displayed on-line as point plots on a computer screen; spike intervals were stored for off-line analysis with 10 μs resolution.

Acoustic stimulation and data analysis

During experiments anaesthetized animals were placed on a heating blanket (37 °C) to maintain body temperature; chronically prepared, unanaesthetized animals sat in a plastic tube. In both cases only their heads were fixed; no further restraints were applied. Acoustic stimuli were delivered free field via an attenuator (HP 350D), an amplifier (STAX SRM-1/MK-2) and an electrostatic speaker (STAX SR lambda professional) which was mounted approximately 2 cm in front of the animal's head. The speaker's output was measured prior to an experiment using a half-inch condenser microphone (Brüel & Kjaer 4134) placed at the position of the animal's head and facing the speaker using a measuring amplifier (Brüel & Kjaer 2610), and a signal analyser (Brüel & Kjaer 2033). For frequencies between 0.3 kHz and 30 kHz the output of the speaker was found to be flat within ± 5 dB and without distortion up to 100 dB sound pressure level (SPL). Stimulus intensities higher than 100 dB SPL were not used.

If possible, at each recording site the unit's characteristic frequency (CF = pure tone frequency with the lowest threshold) and corresponding minimal threshold were determined manually with tone bursts (Wavetek-132 multifunction generator) using audiovisual criteria. The unit's response properties to tones and AM signals (sinusoidally amplitude-modulated pure tones) produced by a computer-controlled multifunction generator (HP 8904A) were studied. Depth of modulation of AM signals was 100% and modulation started at phase zero at stimulus onset. Because of the high spontaneous activity of units in unanaesthetized animals determination of CF and threshold was often difficult. For this reason in unanaesthetized animals all stimuli were therefore presented at a constant intensity of 60 ± 5 dB SPL. For anaesthetized animals, intensity was set 30 dB SPL above a unit's minimal threshold, but not higher than 100 dB SPL (see above).

All stimuli had a duration of 200 ms with 5-ms rise and fall times. Neuronal activity was also recorded during a 50-ms pre-stimulus and a 150-ms post-stimulus period. Stimuli were presented in random order with 10–20 repetitions of each stimulus. Stimuli were randomized separately for each repetition.

Responses to tone bursts were quantified on the basis of average discharge rate during the entire stimulus duration for all repetitions of a given stimulus. This discharge rate was corrected for the spontaneous activity, which was considered as the average discharge rate during all pre-stimulus periods of a given stimulus set.

Pure tone bursts ranging from 50 Hz to 40 kHz were used to determine the unit's frequency response function (FRF = a plot of discharge rate against pure tone frequency) (Fig. 1). As a rule, two sets of tone bursts with equidistant frequency steps were presented: one set covering the whole frequency range tested (see above) and another set covering a small frequency range around the unit's CF. The range of tone frequencies that increased a unit's discharge rate was termed the frequency response range (FRR). The tone frequency that elicited the highest discharge rate (corresponding to the

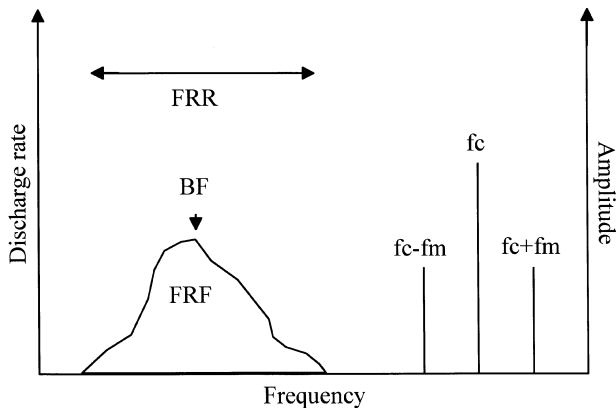


Fig. 1 One of the stimulation paradigms used. Schematic drawing of a pure-tone response of a presumed cortical unit, expressed by its frequency-response function (FRF, left part). *Right*: spectral position of AM stimuli relative to the FRF. The spectrum of an AM consists of three spectral components, the carrier frequency fc and two sidebands $fc-fm$ and $fc+fm$. AM spectra are located completely outside the unit's frequency response range (FRR). *BF* Best frequency; *fm* modulation frequency

maximum of the FRF) is referred to as best frequency (BF) (Fig. 1).

Depending on the pure tone response characteristics encountered at a given recording site two types of AM experiments were performed: first, the carrier frequency (fc) of the AMs presented was set to the unit's BF which implies that at least the central spectral line of the AM was always within the unit's FRR. For this type of experiment usually low fms between 0 Hz (= unmodulated carrier) and 100 Hz were used. In some cases fms up to 5 kHz were tested. In another set of experiments fc and highest fm (fm_{max}) were selected so that the resulting spectra of the AMs (consisting of fc , $fc-fm$, and $fc+fm$) were completely outside the unit's FRR (Fig. 1). As a rule, fms between 0 kHz and 5 kHz were tested in these experiments. In all AM experiments, AM frequency steps were equidistant on a linear scale.

Responses to AMs were quantified according to their discharge rate and their synchronization to the stimulus. A plot of discharge rate, corrected for spontaneous activity, over fm will be referred to as rate modulation transfer function (rate-MTF). To quantify the degree of synchronization of neuronal discharges to the fm vector strength (VS) values were calculated (Greenwood and Durand 1955) and tested for statistical significance using the Raleigh test of uniformity (Mardia 1972). Only synchronization significant at the 1% level was considered. VS plotted over fm will be referred to as synchronization modulation transfer function (sync-MTF). For many units, the onset of AMs of various fms , as well as the unmodulated carrier, evoked similar phasic ON-responses. If such units additionally showed phase-locked responses to the envelope of the AM, the non-AM-specific ON-responses were eliminated for the analysis of VS by choosing appropriate time windows. Maxima of MTFs will be referred to as rate or synchronization best fms (rate- or sync-BMF), respectively. Analogous to FRR, AM response ranges were determined from rate-MTFs.

Q_{3dB} factors were used as a measure of a unit's stimulus selectivity. Q_{3dB} factors were defined as the maximum of the FRF or MTF (=BF or BMF) divided by the bandwidth of the corresponding FRF or MTF 3dB below the maximum, respectively.

Latencies of pure tone and AM responses were determined from point plots. Neuronal filter characteristics of pure tone responses were assigned to several categories on the basis of shapes of FRF. Six categories were distinguished in accordance with Heil et al. (1995) as follows: a FRF was considered band-pass (BP) if the responses (discharge rate) to frequencies higher and lower than the BF were less than 50% of the maximum response. A FRF was assigned to the low-pass (LP) or high-pass (HP) category if only

responses to frequencies higher (for LP) or lower (for HP) than the BF were below 50% of maximum, respectively. If responses to all frequencies tested were above 50% of maximum the FRF was classified as non-selective (NS). A FRF was considered to be complex (CX) if it showed at least two local maxima, and responses between the maxima and on at least one side of the maxima (below the lower one or above the upper one) were less than 50% of maximum. Finally, a FRF was classified as band suppression (BS) if high and low frequencies elicited strong responses, and intermediate frequencies elicited responses below 50% of maximum. Rate- and sync-MTFs were also assigned to these filter categories on the basis of discharge rate or vs respectively.

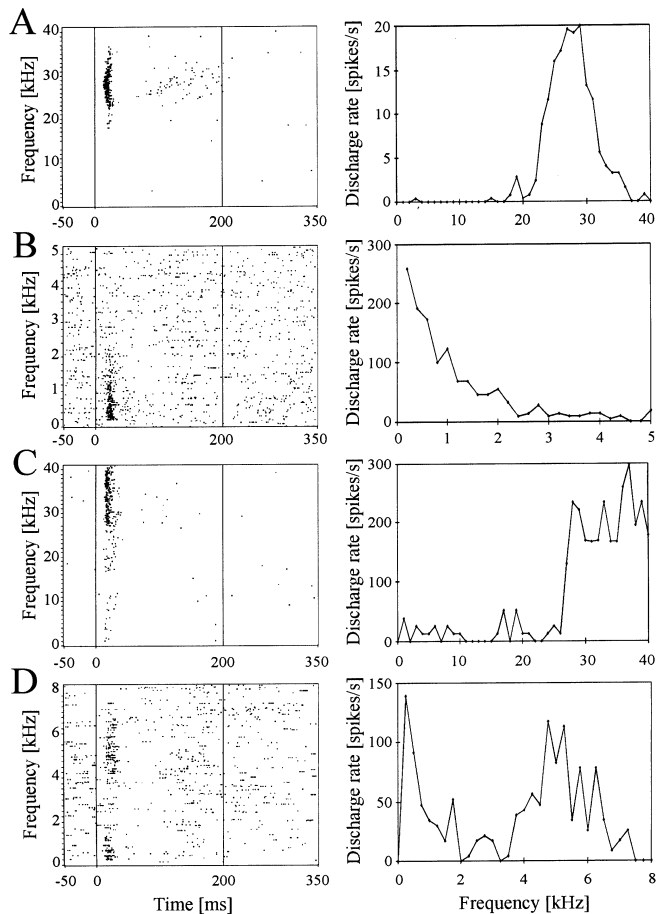
Results

This study is based on electrophysiological recordings from a total of 541 single and multi-units in the left AI of six anaesthetized (231 units) and seven unanaesthetized (310 units) Mongolian gerbils. The results obtained from anaesthetized and unanaesthetized animals were very similar and can therefore be presented together. Differences will be mentioned where necessary.

Neuronal responses to pure tone bursts

In general, neuronal responses to pure tone stimuli were in accordance with results using the anaesthetized Mongolian gerbil (Thomas et al. 1993) and the unanaesthetized Mongolian gerbil presented in Schulze et al. (this volume). Results from pure tone experiments will only be summarized here.

Response characteristics of units in AI were phasic or combined phasic-tonic; for unanaesthetized gerbils they were sometimes also purely tonic. The majority of units showed BP (50%, Fig. 2A) or CX (42%, Fig. 2D) filter characteristics. Only some FRFs were categorized as LP (7%, Fig. 2B) or HP (1%, Fig. 2C). Units showing BS or NS filter characteristics were never observed (cf. Fig. 2). BF and CF covered a frequency range between 0.1 kHz and 40 kHz and were similar for a given unit (linear regression: y -intercept = 0.162, slope = 1.18, $r = 0.89$, $P < 0.001$). BF and CF values were tonotopically organized within the AI with the tonotopic gradient oriented roughly from a representation of low frequencies dorso-caudal to high frequencies rostro-ventral (cf. Thomas et al. 1993). Response latencies were significantly shorter for unanaesthetized animals (ANOVA: $P = 3.4E-11$): For the majority of units the latency in response to pure tones was typically in the range between 10 ms and 25 ms for the anaesthetized animals, and for the unanaesthetized animals between 5 ms and 20 ms (Fig. 3A; the shortest latency measured was 6.9 ms). Neuronal response thresholds also differed significantly for the two groups (ANOVA: $P = 4.8E-23$): for unanaesthetized animals thresholds typically ranged from -10 dB to 30 dB SPL, for anaesthetized animals from 10 dB to 50 dB SPL (Fig. 3B). Sharpness of tuning as expressed by 3-dB ranges varied between 0.3 and 3, similar for both groups of animals (cf. Fig. 9A).



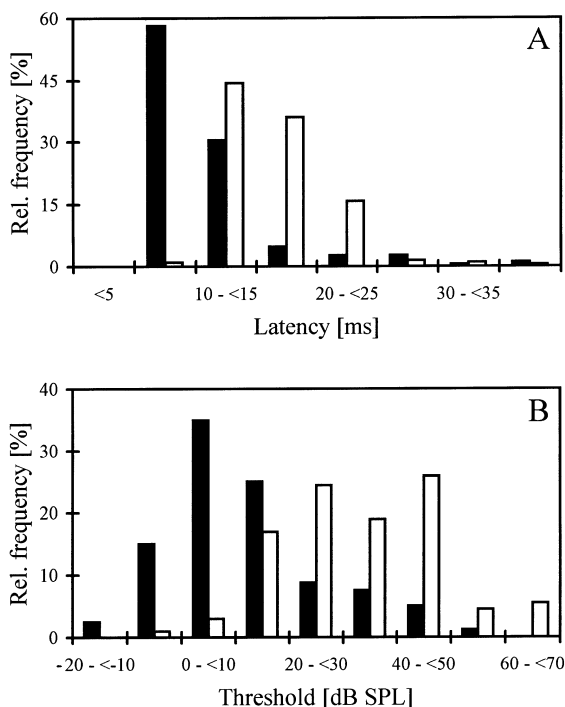
◀ **Fig. 2A–D** Neuronal pure-tone filter characteristics encountered in the AI. Four categories could be distinguished: **A** band-pass (BP), **B** low-pass (LP), **C** high-pass (HP); and **D** complex (CX). Given are point-plots (*left column*: pure-tone frequency is plotted over time; each point represents one triggered neuronal event or “spike”; the *vertical lines* mark beginning and end of the stimuli) and frequency-response functions (FRF, *right column*; discharge rate is plotted over pure tone frequency). For definition of filter categories refer to Materials and methods

Neuronal responses to AM stimuli located within a unit’s spectral receptive field

For the anaesthetized animals, out of all units ($n = 173$) that were tested with AMs with a carrier frequency at the unit’s BF only 8% responded with significant phase locking to the fm. Phase-locking was confined to low fms up to 65 Hz, the highest sync-BMF found was 30 Hz and VS values ranged only between 0.15 and 0.53. One example for such a phase-locked response is given in Fig. 4A (corresponding rate- and sync-MTF are given in Fig. 4C): this unit showed phase-locking to fms between 5 Hz and 25 Hz. Higher fms only elicited short-latency, phasic ON-responses with no tuning to a particular envelope frequency (Fig. 4A, fm above 25 Hz). Units that exhibited no phase-locking to stimulus envelope (Fig. 4B) showed similar unspecific ON-responses to the whole range of fms tested (up to 5 kHz). A preliminary conclusion from these results is that for the anaesthetized gerbil only a small amount of AI units may code for the time structure of acoustic stimuli with frequencies ≥ 5 Hz via a temporal (= synchrony) code, and this type of coding seems to be restricted to low fms up to about 65 Hz. A systematic representation of sync-BMFs within the AI was not found.

Phase locking of neurons in unanaesthetized gerbils was generally better than in anaesthetized gerbils, but still confined to low fms: 17% of the units ($n = 310$) showed phase-locked responses, significant phase locking was observed only for fms up to 100 Hz. The highest sync-BMF found was 45 Hz; VS values ranged between 0.15 and 0.81.

As can be seen in Fig. 4C a rate-code for envelope frequency was also observed using this type of AM stimulation ($f_c = BF$): neurons exhibited an increased discharge rate selectively to a certain range of fms of the AMs. In general, this increased firing rate covered a similar frequency range to the observed phase-locked response. Units that did not show phase-locked responses also failed to code for envelope frequency via a rate code



◀ **Fig. 3A,B** Comparison of pure-tone response parameters for data from anaesthetized (*open bars*) and unanaesthetized (*filled bars*) gerbils. Given are frequency distributions of response latencies (**A**) and neuronal thresholds (**B**) for the two groups of animals: overall response latencies are shorter for the unanaesthetized than the anaesthetized group. Overall neuronal thresholds are lower for the unanaesthetized than for the anaesthetized group. Both differences are highly significant (for statistics see text)

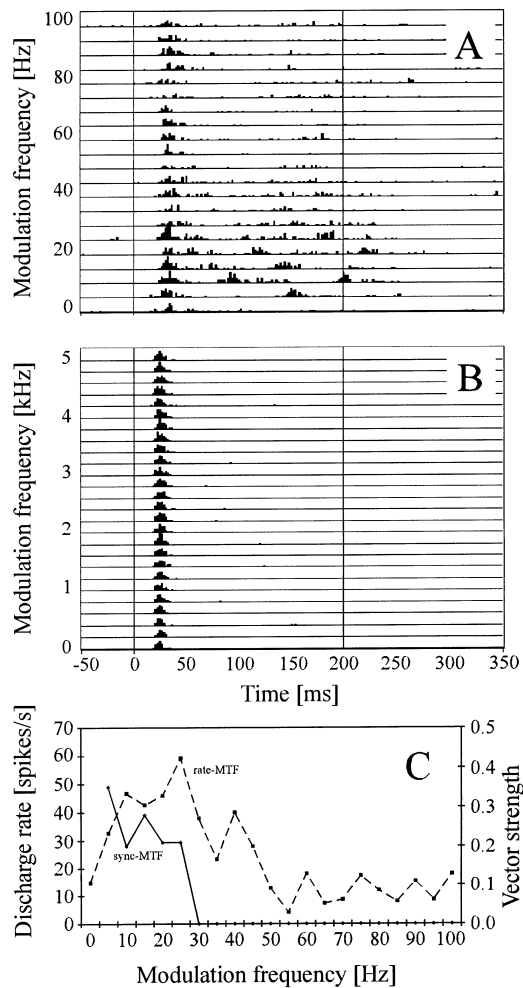


Fig. 4A–C Neuronal responses to AM stimuli with a carrier frequency set to the unit's BF. **A** peristimulus-time histogram (PSTH) of the response of a unit that exhibited discharges phase-locked to the stimulus envelope. In this diagram the fm of the AMs is plotted over time, bandwidth was set to 2 ms. The *vertical lines* mark beginning and end of the stimuli. The BF of this unit was 800 Hz. Rate- and sync-MTF of this response are given in **C**. The sync-MTF was classified as LP with significant phase-locking up to 25 Hz and a sync-BMF of 5 Hz; the rate-MTF was assigned to the BP category with a rate-BMF of 30 Hz. **B** PSTH of a response of a unit that showed no phase locking. BF of this unit was 27 kHz. Recordings of both units shown were made under anaesthesia

(cf. Fig. 4B). Again, although the rate-BMF determined from these responses could differ from the corresponding sync-BMF (Fig. 4C), a topographic organization could not be demonstrated for these rate-BMFs.

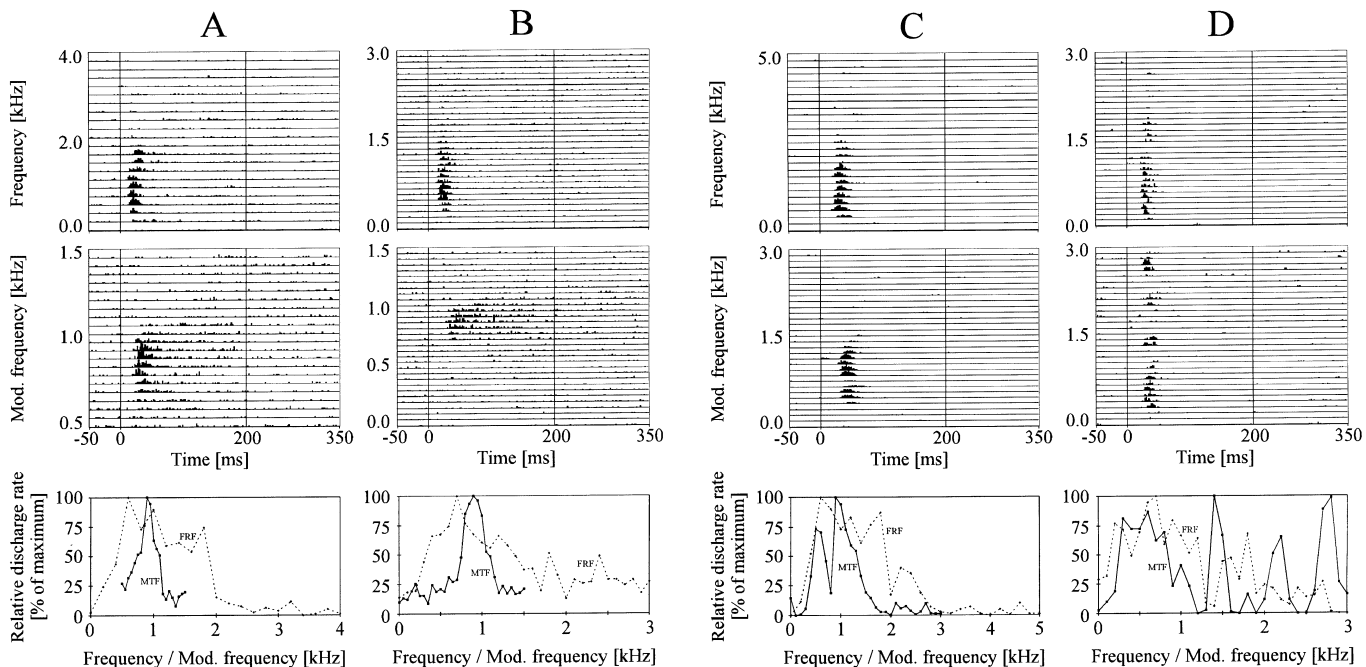
Neuronal responses to AM stimuli located outside a unit's spectral receptive field

In this section we describe responses of units to amplitude modulations with a spectrum completely outside the unit's FRR (cf. Fig. 1), i.e. none of the spectral components of the amplitude modulation alone elicited the unit. This stimulation paradigm was used because of

the following considerations. It is known from psychophysics that complex, periodic sounds like AMs may elicit the perception of “periodicity pitch” (Ritsma 1962). Furthermore, for the harmonic case the perceived pitch only depends on the signal envelope frequency and not on its spectral content. For example, an AM with a fc of 1 kHz and a fm of 100 Hz would elicit the perception of a pitch of 100 Hz, although the frequency of 100 Hz is not part of the spectrum. This perception is known as “pitch of the missing fundamental” (Seebeck 1841; Fletcher 1924; Schouten 1940). It was also demonstrated to exist for a variety of animal species such as the cat (Heffner and Whitfield 1976), the rhesus monkey (Tomlinson and Schwarz 1988) and the starling (Cynx and Shapiro 1986). Obviously, many different signals may elicit the perception of the same pitch, depending mainly on their periodicity and not on their spectral content. A systematic representation of envelope frequency was found in the midbrain of the cat (Langner et al. 1992), in the guinea fowl (Langner et al. 1992), in the auditory cortex analogue (field L) of the mynah bird (Hose et al. 1987), and in the human auditory cortex (Langner et al. 1994; Langner et al., this volume). If one assumes that such a representation is realized in the gerbil auditory cortex, then one possibility would be that stimuli with identical envelope periodicity might be mapped onto the same cortical location independent of their spectral content. Since such a systematic representation of envelope periodicities has not been demonstrated for a non-human auditory cortex using stimuli that simultaneously activate the units spectrally (cf. last section), we attempted to determine whether such an organization could be found using stimuli which do not activate the units spectrally but putatively ‘temporally’, i.e. via inputs activated only by a certain envelope periodicity.

The most important finding of this study was that indeed many units in the AI responded to such AM stimuli. All these units had BFs between 50 Hz and about 3000 Hz and therefore were confined to the low frequency area of the AI. Out of the 232 units tested in this area about 75% responded to the described AMs (anaesthetized group: 74%, unanaesthetized group: 71%). All these units exhibited a rate code for envelope frequency, while phase locking was never observed. Responses were phasic (36%), tonic (34%) or combined phasic-tonic (30%). Only BP (62%) or CX (38%) filter characteristics were observed. Rate-BMFs varied between 50 Hz and about 3000 Hz (cf. Fig. 11B). Tuning sharpness of these AM responses (3-dB ranges varied between 1 and 10) was on average significantly higher than pure-tone frequency sharpness in both anaesthetized and unanaesthetized gerbils (cf. Fig. 9; Table 2).

Figure 5 shows examples of responses of four such units (A–D). In the top panels peri-stimulus-time histograms (PSTH) obtained by pure tone stimulation are given, the middle panels show those obtained by AM stimulation. The lower panels illustrate FRFs (broken lines) and rate-MTFs (solid lines) corresponding to the



AM responses shown in the PSTHs above (top and middle panels, respectively). As summarized above, several response characteristics can be distinguished. The unit in Fig. 5A exhibited a short-latency, phasic ON-response to pure tone frequencies up to 1800 Hz, with a BP filter characteristic and a BF at 600 Hz (Fig. 5A, top and FRF in the bottom panel). The middle panel of Fig. 5A illustrates responses to AMs with a fc of 7 kHz and fms ranging from 500 Hz to 1500 Hz. The lowest spectral component of these AMs ($= fc - fm_{max}$) therefore never fell below 5500 Hz so that all AMs were spectrally clearly above the FRR of the unit. As can be seen, the unit responded to such AM stimuli and the response was tuned to a certain range of fms between about 700 Hz and 1100 Hz. The temporal response pattern was predominantly phasic with an additional weak tonic component. The AM filter characteristic was BP, with a maximum (rate-BMF) at 900 Hz (cf. Fig. 5A, rate-MTF in the bottom panel). The rate-BMF therefore differed from the unit's BF.

A somewhat different response characteristic exhibited the unit shown in Fig. 5B: while its pure tone response was again phasic (top panel), this unit showed a purely tonic discharge pattern after AM stimulation (middle panel). Again, AMs were chosen to be located outside the unit's FRR which covered frequencies between 300 Hz and 1500 Hz: fc of the AMs was set to 7 kHz, fms between 0 Hz (= unmodulated carrier) and 1500 Hz were tested. With changing type of stimuli (pure tone/AM) this unit drastically changed its temporal response behaviour from phasic to tonic. FRF and rate-MTF (lower panel) both showed clear BP filter characteristics. The BF (700 Hz) again differed from the rate-BMF (900 Hz). This latter observation was a common finding for almost all units that responded to AM stimuli spectrally outside the unit's FRR. The dif-

Fig. 5A–D Neuronal responses of four AI units (A–D) to pure-tone (PSTHs, *top panels*) and AM stimuli with a spectrum located completely outside a unit's FRR (PSTHs, *middle panels*). All units were tested with pure tones up to 40 kHz. No discharges were elicited by pure-tone frequencies above the ranges shown in the top panels. The fcs for the four units were 7 kHz (A, B), 8 kHz (C) and 5 kHz (D), respectively. Corresponding FRFs and rate-MTFs are given in the *bottom panels*. Spike rates in these diagrams are expressed as a percentage of the maximum of each function. For details refer to the text

ference between BF and BMF could be more than two octaves (Fig. 6).

The conclusion drawn from these results is that there are units in the AI of the Mongolian gerbil that code for envelope frequency – given by the fm of an AM – via a rate code. Beside the two units presented so far that both had clear BP filter characteristics for envelope frequency, about one-third of the units (see above) exhibited

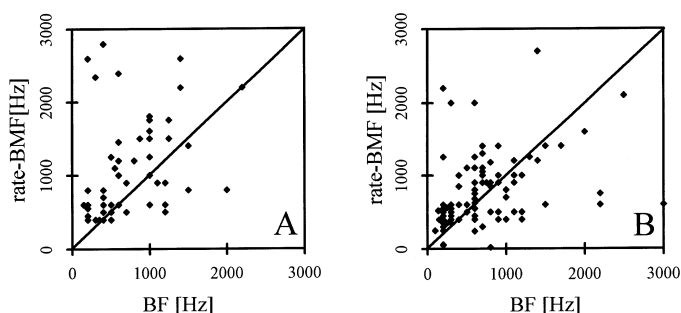


Fig. 6A, B Plots of rate-BMF against BF of units that responded to AM stimuli with a spectrum completely outside their FRR: **A** data of the unanaesthetized group; **B** data of the anaesthetized group. In both groups the rate-BMF of a given unit could be higher, equal or lower than the BF of that unit. The difference between BF and rate-BMF could be more than two octaves

more complex filter characteristics. Examples for such units are given in Fig. 5C, D.

The discharge pattern of the unit in Fig. 5C was purely phasic to both pure tone and AM stimulation, but whereas the pure tone response exhibited a BP filter characteristic ($BF = 600$ Hz), the AM response showed two clearly distinct local maxima in its rate-MTF at 500 Hz and 900 Hz and therefore was assigned to the CX filter type. The FRR of this unit ranged from 400 Hz to about 2600 Hz. The fc of the presented AMs was 8 kHz. The AM response of the unit shown in Fig. 5D was even more complex: the rate-MTF of this unit exhibited four clearly distinguishable local maxima. Interestingly, these local maxima seemed to be in harmonic relationship: the peaks at 600 Hz, 1400 Hz, 2200 Hz and 2800 Hz can all be interpreted as integer multiples of about 700 Hz. As in the unit shown in Fig. 5C all responses were phasic; the fc of the presented AMs was 5 kHz.

There was a highly significant difference between the units' latency after pure tone and AM stimulation (Fig. 7; for statistics refer to Table 1): response latencies after pure tone stimulation were in general shorter than after AM stimulation. For the anaesthetized group la-

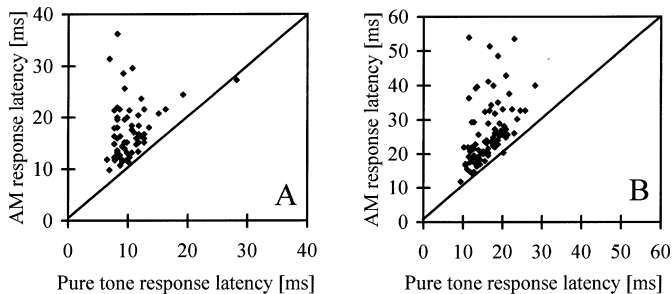


Fig. 7A, B Comparison of response latencies after pure tone and AM stimulation of units that responded to AM stimuli with a spectrum completely outside their FRR: **A** data of the unanaesthetized group; **B** data of the anaesthetized group. In both groups the response latency after AM stimulation was significantly longer than the response latency after pure tone stimulation. For statistics see Table 1

Table 1 Comparison of response latencies after pure-tone and AM stimulation of both anaesthetized and unanaesthetized animals. Given are mean values and standard deviation. In both groups of animals response latencies differ significantly for the two types of stimulation: latencies of pure-tone responses are shorter than those after AM stimulation. See also Fig. 7

	Latency of pure tone responses (ms)	Latency of AM responses (ms)	ANOVA: <i>P</i> Value
Unanaesthetized group	10.4 ± 5.7	17.6 ± 7.0	2.2 E-14
Anaesthetized group	16.7 ± 4.4	26.1 ± 8.8	7.3 E-18

Table 2 Comparison of sharpness of tuning on the basis of Q_{3dB} values after pure tone and AM stimulation of both anaesthetized and unanaesthetized gerbils. Given are mean values and standard deviation. In both groups of animals sharpness of tuning is significantly sharper for AM than for pure tone stimulation (ANOVA)

	Q_{3dB} of pure tone responses	Q_{3dB} of AM responses	ANOVA: <i>P</i> Value
Unanaesthetized group	2.1 ± 2.1	3.4 ± 2.8	0.03
Anaesthetized group	1.9 ± 2.3	3.8 ± 4.5	2.7 E-8

tencies after AM stimulation were on average about 10 ms longer than after pure-tone stimulation. For the unanaesthetized group, as latencies were generally shorter, the absolute difference between onset latencies was less than for the anaesthetized group (about 7 ms), but the relative difference was even more distinct (57% for the anaesthetized gerbils, 70% for the unanaesthetized gerbils).

As a final result of the experiments described in this section we observed a change of BMF, $AM-Q_{3dB}$ range, AM response range and response latency as a function of carrier frequency. One example is given in Fig. 8 which shows BMF values (solid line), $AM-Q_{3dB}$ range (upper and lower limit, dotted lines) and total AM response range (upper and lower limit, broken lines) of a

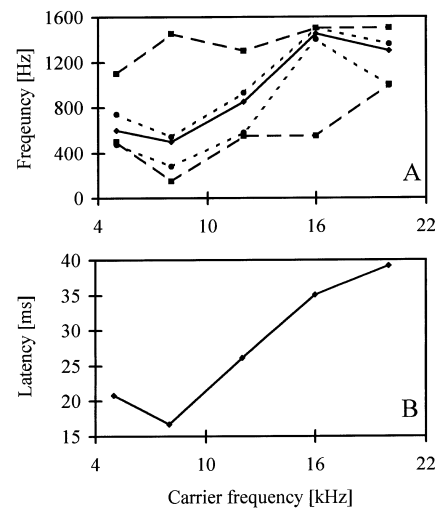


Fig. 8A, B Variation of a unit's AM response properties as a function of the carrier frequency (fc) of the AM. This unit had a best frequency of 300 Hz and a pure tone frequency response range from 100 Hz to 2000 Hz. **A** Shown are the variation of total AM response range (upper and lower limits, broken lines), $AM-Q_{3dB}$ ranges (upper and lower limits, dotted lines) and rate-BMF (solid line) as a function of fc . **B** Variation of AM response latency of the same unit as a function of fc . All AMs presented to this unit were spectrally outside the units FRR

representative unit plotted over carrier frequency (Fig. 8A). All these parameters shifted with increasing carrier frequency, i.e. with increasing spectral distance of the AM from the unit's FRR. The same is obvious for AM response latency (Fig. 8B). No neuronal responses could be evoked by AMs with carrier frequencies increasing above a critical value. For the unit shown this value was 25 kHz. Interestingly, there seemed to be an optimal spectral distance of the AM from the FRR: after stimulation with AMs with a fc of 8 kHz the unit shown exhibited the shortest response latency and the widest response range. A shift in fc in either direction (i.e. closer to the unit's FRR or further away from it) led to both an increase in response latency and a decrease in the width of the AM response range. This behaviour was evident for all units tested with spectrally different sets of AMs.

Topographic organization of periodicity coding

In contrast to sync-BMFs determined from the described phase-locked responses, rate-BMFs determined from responses to AMs spectrally outside a unit's FRR (last section) were found to be systematically distributed within the AI. Figure 10A shows the distribution of

rate-BMF values within the AI of one animal. In Fig. 10B the same data are shown as a three-dimensional plot with the BMFs on the z-axis. As can be seen in this latter plot the periodotopic gradient in this animal runs approximately from a representation of high rate-BMF values dorsal to low values more ventrally. In contrast to the tonotopic gradient which was identical in all animals (low frequencies dorso-caudal, high frequencies rostro-ventral, see above), the direction of the periodotopic gradient could differ (appeared to run in the opposite direction) between animals. Nevertheless, because of the small area where rate-BMFs were encountered (about 1 mm²) and the accordingly small number of recording sites per animal, the exact direction of the periodotopic gradients remains unclear.

Two different coding strategies for envelope periodicity

Considering the results presented so far there seem to be basically two different ways in which auditory cortical

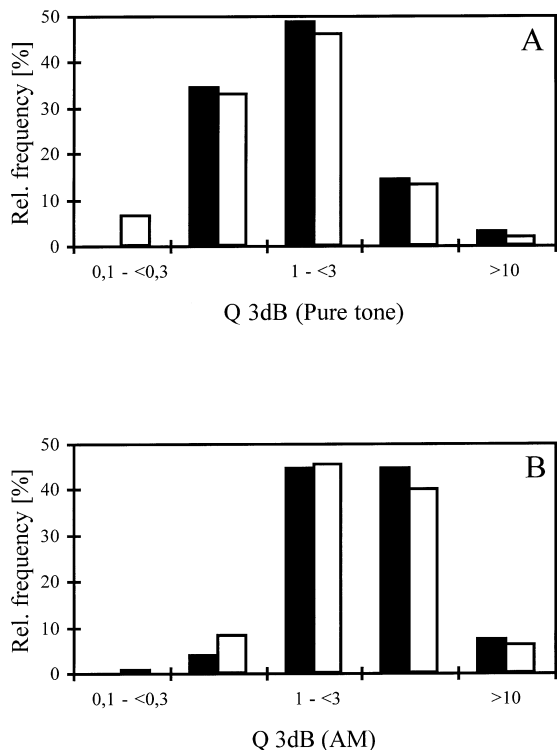


Fig. 9A, B Comparison of Q_{3dB} values between data of the unanaesthetized (filled bars) and anaesthetized (open bars) group. Given are frequency distributions of Q_{3dB} values for pure tone (A) and AM responses (B). For both cases frequency distributions are very similar for the two groups of gerbils. For both groups overall Q_{3dB} values for AM responses are higher than for pure tone responses, that is AM tuning is sharper than pure tone tuning. For statistics see Table 2

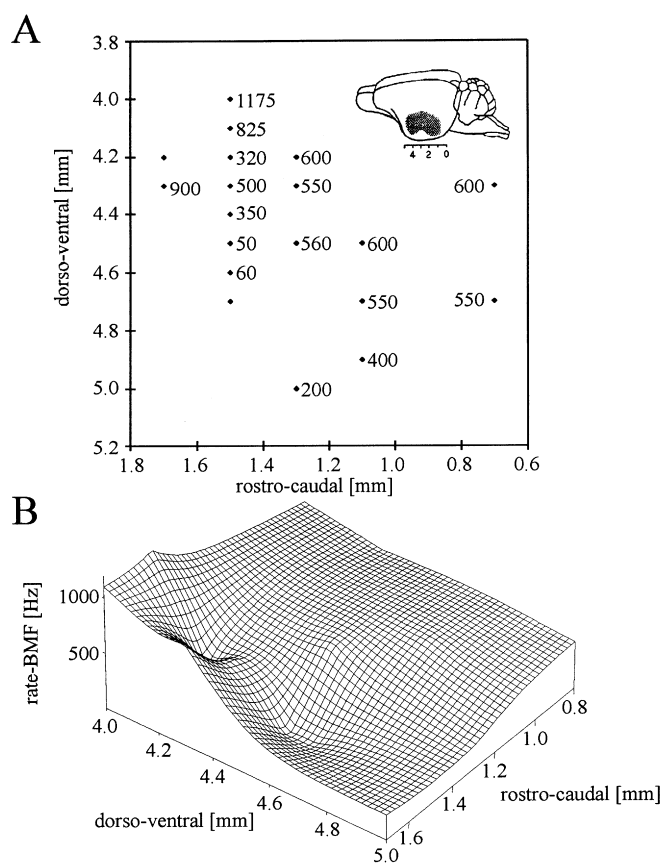


Fig. 10A, B Topographic distribution of rate-BMF values in the AI of one animal, shown as two-dimensional (A, rate-BMFs given as numbers) and three-dimensional plot (B, rate-BMFs on the ordinate). On the spatial coordinate axes distances relative to lambda are given. Rate-BMFs are systematically distributed within the AI, i.e. exhibiting a periodotopic organization. In the case shown the periodotopic gradient runs approximately from a representation of high rate-BMFs dorsal to low rate-BMFs ventral. The inset in A shows the location of the left auditory cortex within the gerbil's brain

neurons code for the envelope periodicity of acoustic stimuli: one possibility is that neurons show temporally structured discharges phase-locked to the stimulus envelope. The other possibility is that neurons code for envelope periodicity via a temporally unstructured, rate-place code. Interestingly, these two codes are used for the representation of almost distinct frequency ranges (Fig. 11). Whereas low envelope frequencies up to about 100 Hz are represented via the temporal code (phase-locking), a higher range of frequencies between 50 Hz and about 3000 Hz is represented via the rate-place code. The intermediate range of frequencies between about 50 Hz and 100 Hz is represented via both types of codes.

Discussion

Methodological considerations

Comparability of single versus multi-unit recordings as well as implications of the tangential alignment of penetration tracks carried out in this study are discussed elsewhere (Schulze et al., this volume). Both issues appear to have minor impact on our conclusions.

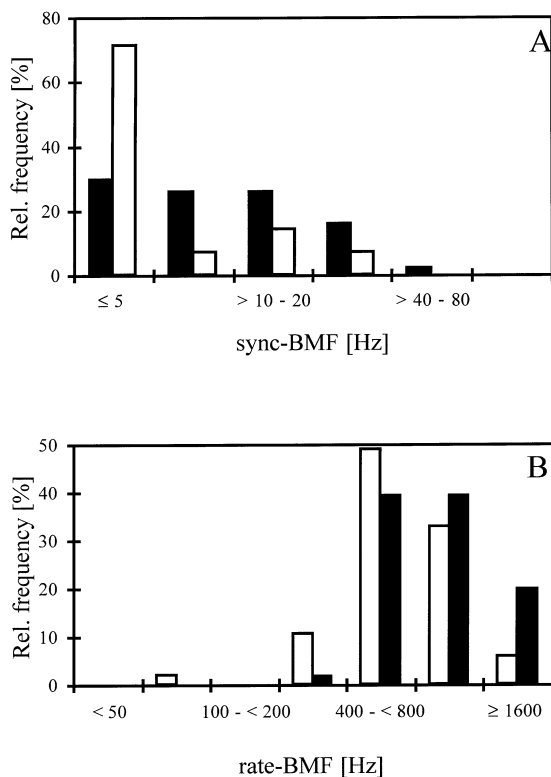


Fig. 11A, B Frequency distributions of sync-BMFs obtained from responses to AMs with the *fc* set to the units' BFs (A) and rate-BMFs obtained from responses to AMs spectrally completely outside the units' FRRs (B). Frequency distributions are similar for unanaesthetized (filled bars) and anaesthetized gerbils (open bars). Note that for both groups sync-BMFs cover only low envelope frequencies and rate-BMFs cover predominantly high envelope frequencies

Comparability between data from anaesthetized and unanaesthetized gerbils

Acoustic stimuli were presented to anaesthetized and unanaesthetized gerbils according to two slightly different stimulation paradigms: whereas unanaesthetized gerbils were stimulated with iso-intensity signals, the anaesthetized gerbils were stimulated with signals of differing intensity, viz. 30 dB SPL above a given unit's threshold. The question arises whether the observed differences in the response characteristics of neurons of the two groups of gerbils could be attributed to this difference in stimulation paradigms. It is known for example that neuronal response latencies decrease with increasing stimulus intensity (Brugge et al. 1969; Phillips et al. 1985), but in fact – because of the high neuronal thresholds of the anaesthetized group in comparison to the unanaesthetized group – the mean intensity of the stimuli presented to the anaesthetized group was somewhat higher than the mean intensity of the stimuli presented to the unanaesthetized group (62 and 57 dB SPL, respectively). The clearly shorter response latencies observed for the unanaesthetized group in comparison to the anaesthetized group cannot therefore be traced back to the difference in stimulation paradigm but can only be a consequence of the physiological state of the animals (anaesthetized/unanaesthetized). All other comparisons between response properties of the two groups of gerbils revealed great conformity. We therefore conclude that the comparability of the data of both groups is high.

Limitation of frequency ranges

Only a distinct number of stimuli out of a limited frequency range could be tested in this study, and some results presented here could be influenced by the selected frequency ranges. One critical parameter is the upper frequency limit for pure-tone stimulation: only tone bursts up to 40 kHz could be tested with the equipment used. The frequency range of tone bursts therefore did not cover the whole audible spectrum of the gerbil which includes frequencies of up to at least 60 kHz (Ryan 1976). The (rare) units with pure-tone filter characteristics classified as HP could therefore in fact be BP filter type units if we had tested the whole audible spectrum of the gerbil.

A more important point is the lower limit for fms tested in this study: envelope frequencies below 5 Hz were never tested which is probably the reason why the portion of AI units with phase-locking abilities was considerably lower (8% and 17% for the anaesthetized and unanaesthetized groups, respectively) than found in other studies where lower envelope frequencies were tested. Tillein (1993) for example used envelope frequencies down to 1 Hz and reported that about 70% of the units in the AI of the gerbil had sync-BMFs below 5 Hz. If we had also used envelope frequencies down to 1 Hz in our study, virtually all units in the AI of the gerbil could be expected to exhibit phase locking.

Possible influence of stimulus waveform on response latencies

In our study response latencies were longer for stimulation with AMs with a spectrum outside the unit's FRR than for pure tone stimulation. However, the observed difference might be a result of different stimulus ramps and merely reflect the time for the stimulus to reach full amplitude. In our experiments all stimuli – pure tones and AMs – had rise and fall times of 5 ms. The waveform of both pure tone and AM reaches its first local maximum after a quarter period ($\pi/2$). The waveform of the stimuli would only have a strong effect on the effective rise time for frequencies below 50 Hz. Above 50 Hz the effective rise time is only determined by the duration of the ramp. As virtually all BF and BMF values as well as the corresponding response ranges of the units of interest here were above 50 Hz (cf. Fig. 7), and the difference in response latency is much bigger than the difference in waveform-dependent rise time, we conclude that the stimulus waveform cannot explain the observed difference in latency between pure-tone and AM responses.

Another possible explanation for the observed long latencies of the AM responses might be that the spectrum of the AMs was above the FRR of the unit. For pure-tone responses it is known that response latency increases as the stimulus frequency moves away from the unit's BF. Since we did not observe any response to single spectral components of these AMs when presented alone, this consideration probably also does not explain the long AM response latencies. In contrast we propose that spectral integration could explain the observed effect (see below).

The problem of distortion products

The most striking result of this study was the observation that about three-quarters of the units in the low frequency region of the AI responded to complex (AM) stimuli with a spectrum located completely outside the unit's FRR. In other words the neurons responded to a combination of spectral components that would not elicit a response when presented alone. However, on the basis of just the (AM) rate responses one can not conclude that these discharges – though confined to a specific range of envelope periodicities – reflect coding of temporal periodicity information. Foremost, the possibility that the responses might be elicited by distortion products has to be ruled out. One might argue that the discharges we observed in response to stimulation with AMs did not code for envelope frequency but were elicited by difference tones originating in the cochlea and located within the unit's FRR. The most important distortion product would be the difference tone f_2-f_1 . (As a consequence of our stimulation paradigm, the strongest distortion product, the cubic difference tone $2f_1-f_2$, only lay inside a given unit's FRR

in the rare case where the distance between the FRR and the f_c fell below twice the f_m ; therefore, it is of no relevance here.)

Several lines of evidence indicate that this interpretation is wrong. First, while the unit shown in Fig. 5B responded with short, phasic discharges on stimulation with pure tones it responded purely tonically to AM stimulation. If the latter response was simply the result of another spectral excitation elicited by distortion products within the unit's FRR, one would not expect that the temporal response characteristics (phasic or tonic discharge pattern) differ. However, as distortion products are less intense than the original signal an intensity effect cannot be totally excluded.

Second, as demonstrated in Fig. 8, several response parameters such as rate-BMF, AM response ranges or response latency shift as a function of carrier frequency. Again, if the AM responses were due to f_2-f_1 there should be no such shift, because the difference tone f_2-f_1 is equal to the f_m and does not change with carrier frequency. Furthermore, the fact that no responses could be elicited when the carrier frequency exceeded a critical value ($f_c = 25$ kHz in Fig. 8) makes it unlikely that a distortion product (not only the difference tone f_2-f_1) can account for the (low carrier) AM response: distortion products also arise from AMs with high carrier frequencies and consequently these stimuli should also elicit a response (cf. Plomp 1965).

Finally, the units shown in Fig. 5D responded to pure tone bursts between 100 Hz and about 1900 Hz, and the rate-MTF of the AM response showed four distinct local maxima at modulation frequencies of 600 Hz, 1400 Hz, 2200 Hz and 2800 Hz. Therefore, the difference tones (f_2-f_1) which could be evoked by AMs with the latter two frequencies (2200 Hz and 2800 Hz) would also be located outside the unit's FRR. Moreover, the almost harmonic relationship of the local maxima of the MTF can be easily explained by temporal but hardly by spectral processing mechanisms.

We conclude that the responses to AMs with a spectrum completely outside a unit's FRR reported here indeed code for the time structure of the stimuli, viz. their periodicity, and cannot be explained by putative distortion products in the cochlea.

Cortical units integrate information over wide spectral ranges

As we have now shown that it is unlikely that the discharges of AI units we observed in response to AMs with a spectrum completely outside the units' FRR are responses to possible distortion products we can now draw another conclusion from the above results. Obviously many units in AI receive information from regions of the cochlea that are much wider than might be expected on the basis of their pure-tone responses (i.e. FRRs). Recall again the responses of the unit shown in Fig. 8. This unit responded to pure

tones only up to frequencies of 2 kHz, but to amplitude modulations with carrier frequencies up to 20 kHz. This particular unit received information from regions of the cochlea covering at least the spectral range below about 20 kHz. Furthermore, preliminary results indicate that under the influence of a micro-iontophoretically applied GABA-blocker (bicuculline) some units in the AI seem to integrate over the whole audible spectrum of the gerbil. Under these conditions neurons were found that responded to AMs with carrier frequencies up to 40 kHz but still exhibited sharply tuned FRRs. Therefore, in contrast to the classical concept of more or less sharply tuned spectral receptive fields we conclude that the majority of AI units integrate information over large spectral ranges.

This mechanism of spectral integration may also explain the observed difference between pure-tone and AM response latencies. The AM stimuli with high *f_c* used here not only activate low-BF neurons in the AI that are tuned to the corresponding envelope frequency but also high-BF neurons (at any level of the auditory pathway) with FRRs corresponding to the spectral content of these stimuli. If such units at a lower level of the auditory pathway project onto the dendritic tree of the spectrally integrating neuron, and if this projection were tonotopically organized, then the longer dendritic conductance times for excitatory postsynaptic potential (EPSP) elicited by stimuli spectrally further away from the integrating unit's BF could explain the longer response latencies of that unit. The details of this proposed mechanism are being studied by H. Schulze and G. Langner (unpublished observations).

Cortical periodicity coding: separate codes for pitch and rhythm

On the basis of this study it is possible to speculate about the functional relevance of the observed responses. As discussed there seem to be two different strategies that units in the AI use to encode envelope periodicities of acoustic stimuli. The first possibility mentioned was the occurrence of temporally structured discharges, locked to a particular phase of the stimulus envelope. Such phase-locked responses were observed by a number of studies and for the auditory cortices of a variety of species. The stimuli used in these studies were at least in part spectrally within the units' FRRs. Nevertheless, in all these studies phase-locked responses are appropriate to encode low envelope frequencies only. In the squirrel monkey, sync-BMFs are described up to about 128 Hz (Bieser and Müller-Preuss 1996). In other species the phase-locking ability of AI units seems to be confined to even lower envelope frequencies. Sync-BMFs of AI units are described in the cat up to 50 Hz (Schreiner and Urbas 1988; Eggermont 1993, 1994; Eggermont and Smith 1995), in the guinea pig up to 20 Hz (Creutzfeldt et al. 1980), in the rat up to

18 Hz (Gaese and Ostwald 1995) and in the big brown bat only up to 10 Hz (Jen et al. 1993). All these studies are in accordance with our findings in the gerbil with sync-BMFs covering only low envelope frequencies up to 45 Hz. Similar results for the gerbil were also reported by Tillein (1993). A systematic topographic representation of these phase-locking units within the AI was never observed.

In addition to this neuronal coding of low envelope periodicities via phase-locked discharges, a second coding strategy, viz. a rate code, was observed. This rate coding of envelope periodicities has already been reported in a number of other studies (e.g. Schreiner and Urbas 1988; Bieser and Müller-Preuss 1996), but in contrast to our results the frequency range covered by the rate-coding abilities of the AI units described in these studies is confined to low envelope frequencies. The highest rate-BMF of 512 Hz was reported for only one neuron by Bieser and Müller-Preuss (1996). A periodotopic organization for this rate code has not yet been observed in a non-human auditory cortex.

For the first time we report here a totally different representation for high modulation frequencies: using complex (AM) stimuli with a spectrum completely outside a given unit's FRR we obtained responses tuned to a certain range of envelope periodicities. Envelope frequencies up to about 3000 Hz were again coded via a rate code. Furthermore, the units were topographically organized within the AI according to their rate-BMFs determined from these responses. Consequently, a rate-place code for envelope frequencies (= a periodotopic organization) seems to be realized in AI of the gerbil.

It is important to distinguish between two different types of rate codes for envelope frequencies. The first is confined to low envelope frequencies and is perhaps not topographically organized, while the other covers high modulation frequencies and shows a periodotopic organization. While the first code for low envelope frequencies is characterized by a synchronized neuronal activity the latter code for high envelope frequencies is characterized by a high average activity. This activity might reflect the conversion of the synchrony code in the peripheral auditory system into the cortical rate-place code for envelope frequencies. A similar topographic organization of envelope periodicities, though for a much smaller frequency range, has so far been found only in a bird (Hose et al. 1987) and in the human auditory cortex using magnetoencephalography (Langner et al. 1994; Langner et al., this volume).

The frequency range of periodicities covered by this rate-place code is distinct from the frequency range covered by the synchrony-code described above. Whereas frequencies up to about 50 Hz are coded mainly by synchronization, the rate-place code was found to cover frequencies between 50 Hz and about 3000 Hz (cf. Fig. 11). Interestingly, the psychophysically known (human) perceptions elicited by envelope

frequencies of these frequency ranges clearly differ. High envelope frequencies elicit the perception of periodicity pitch (Ritsma 1962; Smoorenburg 1970), and low envelope frequencies elicit the perception of rhythm and roughness (Terhardt 1968). Our conclusion is that at the level of the cortex the temporal cue of rhythm is reflected in the temporally structured neuronal activity (synchrony code), whereas pitch, the perception with a spatial quality (represented for example in tone scales), is coded spatially (rate-place code). Finally, within a frequency range in between these two extremes (around 50–100 Hz) some units still respond with phase-locked responses while some other units already code for the periodicity via the rate-place code. This may explain why in this intermediary frequency range a somehow “mixed” perception is evoked (roughness).

The relation between spectral and temporal coding: tonotopy and periodotopy

The direction of the tonotopic gradient was very similar for all animals tested, only differing for a given specimen by some degrees depending on the exact position within the dorso-ventral extent of the AI. In contrast, the direction of the periodotopic gradient – though more difficult to determine because of the small cortical area showing a periodotopic organization – seemed to vary strongly between animals: whereas in some animals the gradient was oriented from ventral to dorsal (cf. Fig. 10), it was oriented in the opposite direction in other animals.

In the midbrain of the cat (Langner et al. 1992) as well as in the human auditory cortex (Langner et al. 1994; Langner et al., this volume) the periodotopic gradients are oriented approximately orthogonally to the tonotopic gradient. Although we cannot conclude from our results that such an orthogonal organization is indeed realized in the AI of the gerbil the data presented in this study are in line with these findings. It should be noted that the periodotopic organization is not simply projected onto the tonotopic organization representing similar pitches on similar cortical locations. On the contrary one has to conclude that the spectral and temporal properties of acoustic signals are represented by two more or less independent topographies producing a large variety of neuronal tuning characteristics within the AI. The resulting combinations of spectral (BF) and temporal (BMF) tuning properties may be important for the coding of complex signals as used in animal communication and speech.

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