THE TOPOGRAPHIC REPRESENTATION OF PERIODICITY PITCH IN THE AUDITORY CORTEX

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ABSTRACT

An adaptation of auditory systems important for the processing of speech is that for periodic envelopes. Periodicity is a property not only of signals from vocal chords, but from many physical sound sources. Evidence is accumulating in support of a theory of temporal periodicity analysis as a supplement and refinement of the cochlear frequency analysis. Temporal representations of periodic signals are processed by neurons in the auditory midbrain acting as coincidence detectors and transferring temporal information into rate-place code.

The resulting map for periodicity is arranged orthogonal to the tonotopic map. However, so far little evidence exists for a topographic representation of periodicity information in the mammalian cortex. The present paper compares the results of a neurophysiological study in the Mongolian gerbil and a magnetoencephalographic study of the human auditory cortex which together demonstrate that there might be indeed also periodotopic organizations in the cortex.

1. INTRODUCTION

An important temporal feature of speech is periodicity, because voiced sounds, like vowels, are produced by periodic vibrations of the vocal chords. The fast periodic envelope modulations of such signals are defined by their fundamental frequency and elicit the perception of periodicity pitch. This percept is independent of signal waveform and frequency composition, which may be attributed to the perception of timbre, and remains the same as long as the signal period is the same [1].

When the frequency range of harmonic sounds is sufficiently broad to activate different frequency channels of the auditory system, the neural responses in many frequency channels will be elicited by a superposition of harmonics. Therefore their periodicity will correspond to that of the fundamental or to a multiple of it. By analyzing the periodicity and comparing the result over different frequency channels a neuronal correlation analysis may therefore contribute to auditory binding. This may offer an explanation for the amazing capability of our hearing system to detect speech signals in a noisy environment (cocktail-party effect) [2].

As a result of coincidence detection in the midbrain [3, 4], temporal information is transferred into a rate code. That is, in contrast to the cochlear nucleus [5], units in the midbrain are only weakly synchronized to higher envelope frequencies [2]. Therefore, a transformation into a spatial map might be expected. A well known example of an orderly spatial arrangement of information bearing signal parameters in the nervous system is tonotopy [6]. By providing relative positions and continuous shifts of excitation, such neuronal maps may be useful for processing relations and variations in the corresponding signal space. Correspondingly, periodicity is represented in the inferior colliculus of cat topographically and orthogonal to the tonotopic organization [7, 8]. One implication of orthogonality of frequency and periodicity is that for each range of frequencies there is a ‘complete’ representation of ‘relevant’ fundamental frequencies. Evidence for a topographic representation of periodicity information was also found in the auditory midbrain of guinea fowl, chinchilla, and gerbil [9, 10, 11].

So far little evidence exists for a topographic representation of periodicity information in the mammalian cortex, while in the forebrain of mynah bird envelope periodicity was found to be represented indeed roughly orthogonal to the frequency gradient of the tonotopic map [12].

Therefore, in the present study we used Mongolian gerbils to investigate the cortical representation of envelope periodicities in a mammal. In addition, we used magnetoencephalographic recordings in order to demonstrate that periodicity pitch is arranged orthogonal to frequency in the human auditory cortex- in accordance with the topographic arrangements found in auditory systems of animals.

2. METHODS

2.1 Electrophysiology

Neuronal responses from a total of 231 single- and multi-units to pure and sinusoidally amplitude modulated tones (AM) were recorded from the primary auditory cortex (AI) of 6 anaesthetized gerbils. Experiments were carried out in a sound-attenuated chamber using an electrostatic earspeaker mounted approximately 2 cm in front of the animal’s head.

At each recording site, the unit’s characteristic frequency (CF) and corresponding minimal threshold were determined. Stimuli were presented in random order (10 - 20 repetitions, 30 dB SPL above minimum threshold). Pure tones between 0.05 and 40 kHz were used to determine the unit’s frequency response range (FRR). Modulation transfer function (MTF) and the best modulation frequency (BMF) were measured using AM signals (modulation frequencies up to 5 kHz and carrier frequency either equal or much graeter than CF).

2.2 Magnetoencephalography

Nine subjects with normal hearing participated in the experiments (1 - 5 measurements). Periodicity stimuli were composed of harmonics of 50, 100, 200, and 400 Hz (low cut-off = 400 Hz or 800 Hz; high cut-off = 5000 Hz; duration = 500 ms; rise time = 10 ms; stimulus interval = 1.2 s; 200 repetitions in random order). Spectral differences between the stimuli were small and envelope periodicity (pitch) was the main distinguishing feature. In some experiments each periodicity stimulus was followed by a pure tone with the same pitch. Stimuli were delivered via plastic tubes and earpieces with an output function that increased by about 15 dB/oct. below 1 kHz, was flat between 1 and 2 kHz, and then decreased by 20 dB/oct. Each subject adjusted the amplitudes of the four signals so that all stimuli were of identical subjective loudness (about 60 dB SPL). To focus their attention on the auditory stimuli, subjects were asked to count the number of consecutive signals with the same pitch.

Auditory evoked magnetic fields were recorded in a magnetically shielded room with a 122-channel system covering the whole head [13]. A probe position indicator was attached to the head to provide exact information of the locations and orientations of the sensors with respect to the subject´s head. Fields were recorded with a pass-band of 0.05-100 Hz and the responses to each stimulus were averaged, digitized and stored. After filtering (0-40 Hz), equivalent current dipoles (ECDs, best explaining the measured magnetic field distribution, one in each hemisphere) were computed by a least-squares fit for a spherical volume conductor. The goodness of fit (g) of the model with the measured data was also calculated [14].

3. RESULTS

3.1 Electrophysiology

Units in the auditory cortex (AI) of the gerbil 173 units were tested using AM stimuli with a carrier frequency at their CFs. Each unit was tested 1.) with relatively low modulation frequencies between 5 and 100 Hz and 2.) with high modulation frequencies between 100 Hz and an upper frequency equal to CF, but in any case below 5000 Hz.

From these units only 8% showed significant phase-locking confined to low modulation frequencies up to 65 Hz. For higher modulation frequencies these units exhibited unselective phasic ON-responses like units that exhibited no phase-locking to stimulus envelope at all. Hence only 8% of the units in AI may code

envelopes above 5 Hz in a synchronized way and synchronization is restricted to modulation frequencies up to about 65 Hz.
Many units in AI did respond to AMs with a spectrum located completely outside their FRR, that is, none of the spectral components of the AM alone could activate the unit. From 165 units tested in this way 69% responded selectively to a certain range of modulation frequencies. These units showed enhanced activity in response to a certain periodicity without phase-locking. The filter characteristics of these units (judged by rate) were either band-pass (Fig. 1) or multi-peaked (Fig. 2). Interestingly, the local maxima of the MTF of some of these units with complex filter characteristics were harmonically related. For example the MTF of one unit had four local maxima at the modulation frequencies corresponding to multiples of about 700 Hz (Fig. 2).

Such units with responses to AM signals outside their FRR were confined to the low frequency region of AI up to CFs of about 3000 Hz. BMFs (judged by rate) covered a frequency range from 50 to about 3000 Hz, and therefore six octaves in addition to what has been described so far for synchronization tuning in AI. For almost all units the determined CF differed from the BMF by sometimes more than two octaves. BMFs could be either lower, equal or even higher than the CF of the same unit.

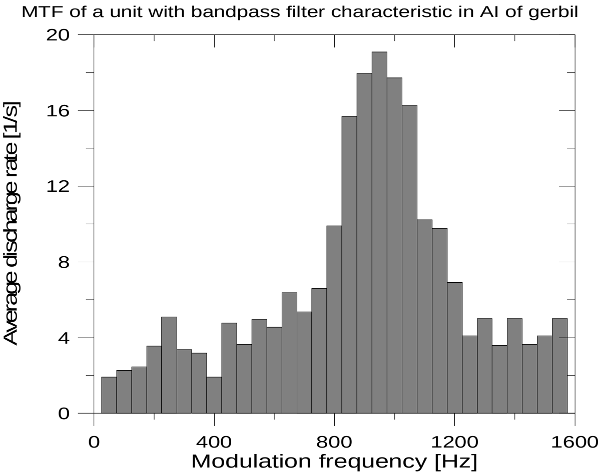

Figure 1. Modulation transfer function of a unit in the auditory cortex (AI) which showed responses to AM stimuli with a spectrum located completely outside the unit's FRR (CF = 600 Hz, carrier = 7000 Hz). The unit had a band-pass filter characteristic with a BMF of 950 Hz.

In some animals evidence was found for a systematic distribution of BMFs (judged by rate). Fig. 3 shows the spatial distribution of BMFs within AI of one animal. There is a periodotopic gradient with low BMF values located ventrally and higher BMFs more dorsally. However, the direction of the periodotopic gradient could not be determined precisely and seems to vary between animals, in contrast to the direction of the tonotopic gradient which was identical in all animals.

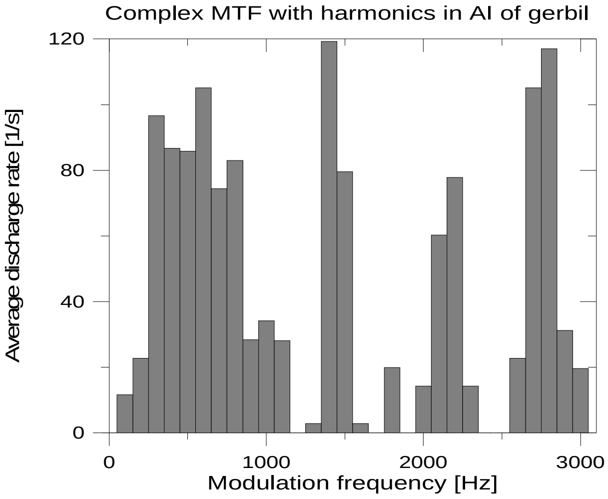

Figure 2. Complex filter characteristic of a unit for AM signals located spectrally outside the unit's FRR (CF = 600 Hz, carrier = 5000 Hz). Local maxima of the MTF are approximately harmonically related.

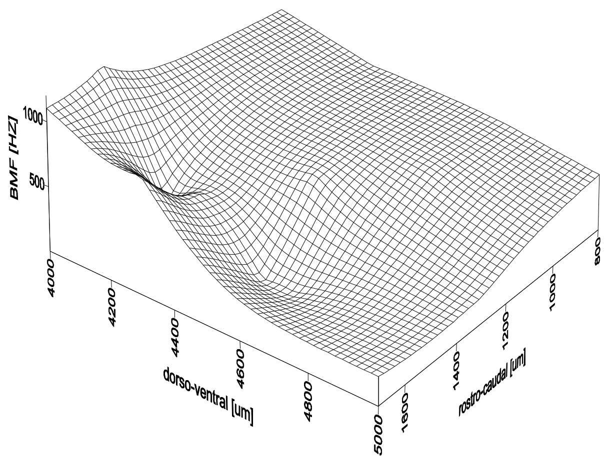

Figure 3. Topographic distribution of BMF (periodotopy) of 17 units in AI of one animal, shown as a three-dimensional plot. In the case

shown the periodotopic gradient is oriented approximately from dorsal to ventral.

3.2. Magnetoencephalography

Magnetic fields evoked in the human auditory cortex by harmonic sounds and pure tones were used to compute the corresponding equivalent current dipoles (ECD) for each hemisphere of the brain. ECD strength was varying in time and space. Figure 4 shows as a result of a stimulation experiment the time course of the ECD strength (Q; in 2-ms intervals) and the corresponding goodness of fit (g) of the dipole model. Around 60, 100 and 200 ms after stimulus onset, and even thereafter, local maxima in the course of both Q and g can be observed. These deflections are referred to as M60, M100, M150, M200 and sustained field (SF). Each local maximum may result from the dominant response of a certain cortical area. The peaks of M60 and M100 are quite sharp. Therefore, it is assumed that for their maxima the spatial position of the ECDs may correspond very well with the positions of their generators in the corresponding auditory areas.

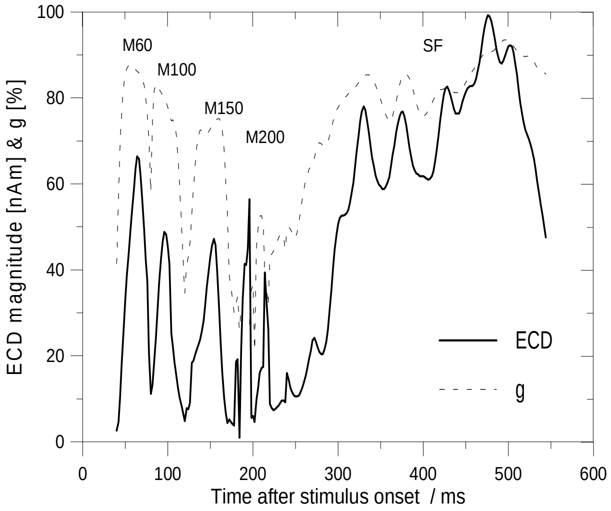

Figure 4 Equivalent current dipole evoked by stimulation with a harmonic sound with a periodicity of 100 Hz.

The most prominent deflection occurred in most cases at about 100 ms after stimulus onset (M100). The latency of the peak of M100 increased with the period of the stimulus. A linear regression analysis revealed a slope close to 1:

$$\text{Latency} = 92\ (\pm 12)\ \text{ms} + 1.17\ (\pm 0.28) * \text{period}$$
$$(r=0.579;\ p < 0.001,\ 5\ \text{subjects}).$$

For a topographic analysis only those time segments of 10 ms around the maxima were evaluated during which the goodness of fit was maximal (about 90%). All calculated locations agree with sources in the supratemporal (auditory) cortex [15]. It was found that the source of M200 is clearly the most anterior as has been described earlier [for review see 16]. Also, the source of the sustained field is slightly more anterior than the source of M100, a result consistent with recent findings [17].

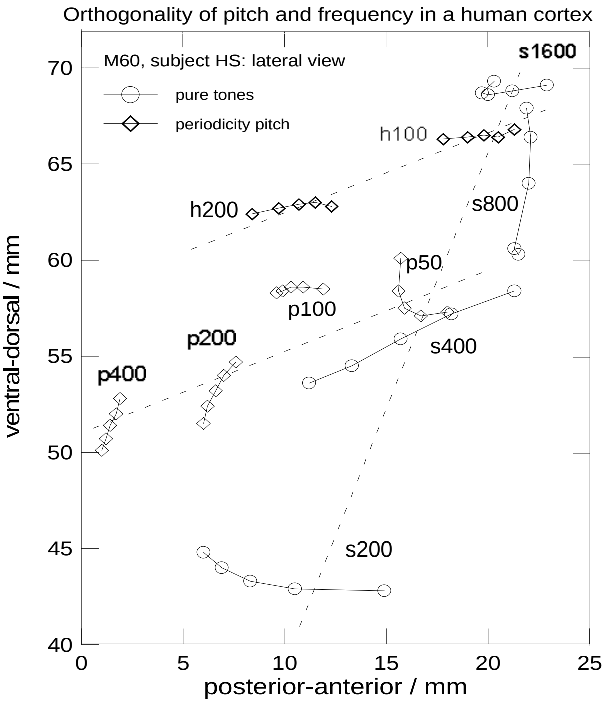

Figure 5 ECD locations of 10-ms intervals (each data point represents 2 ms) were obtained from M60 from the left hemisphere of one subject. Note the grid-like regular spacing of ECDs, especially for harmonic sounds.

In Figure 5 a roughly orthogonal representation of periodicity and frequency in an auditory field related to M60 is demonstrated for the left hemisphere of one subject. As expected, the stimuli with a high cut-off frequency of 800 Hz are displaced in the direction of the tonotopic gradient. Note, that harmonic stimuli with a low cut-off frequency of 400 Hz (p50 - p400) are located near the ECD position for pure tones of 400 Hz, while those with a cut-off frequency of 800 Hz (h100 and h200) are located near the ECD positions for pure tones of 800 Hz.

In addition, the line connecting the ECD positions resulting from *'unmodulated'* pure tones runs along the positions for the ECDs for p50 and h100, the harmonic sounds with the lowest fundamental frequency.

4. DISCUSSION

4.1 Electrophysiology

The most important result of the electrophysiological study is that a high percentage of units in AI respond to AM with a spectrum located completely outside their FRR. One main problem in interpreting these data is that of distortion products: One might argue that the discharges observed after stimulation with such AMs were not elicited by stimulus periodicity but were elicited by difference tones originating in the cochlea and located within the unit's FRR. Concerning the stimulation paradigm used, the most important distortion product here would be the difference tone f2-f1, since the strongest distortion product 2f1-f2 is located outside the FRR. Several lines of evidence indicate that the observed responses are not due to distortion products.

For example, while units responded phasically after pure tone stimulation, they often showed tonic responses after AM stimulation. A distortion product located in the unit's FRR, would probably elicit also a phasic response. Moreover, the fact that the local maxima of the MTF of some units (see Fig. 2) are in almost harmonic relationship is a strong clue that temporal rather than spectral mechanisms are involved in generating these responses.

We conclude from these considerations that the responses to AMs with a spectrum completely outside the unit's FRR reported here indeed code for the time structure of the stimuli and are not responses to distortion products.

Consequently, one has to conclude that cortical units may receive information from frequency regions much wider than what might be expected from their pure tone responses.

In spite of the small dimensions of the auditory cortex of gerbils evidence for a topographic representation of periodicity information was found. Since the gradient of this periodotopy could not be measured exactly and varied between individual animals, it remains to be shown that it is also orthogonal to the well established tonotopic organization**.**

Although the envelope frequency activating certain frequency channels can be a multiple of the fundamental frequency (for example, as a consequence of resonances in a vocal tract) a unit with a BMF higher than its CF was never found at lower auditory levels. For example, for all units in the auditory midbrain BMF was found to be smaller than about CF/4 [4]. The reason for this relationship may be the limited bandwidths of peripheral units which also limit the responses to modulated signals. This restriction seems to be overcome after the transformation from a temporal into a spatial code and spectral integration may be the explanation for units with a BMF higher than CF.

4.2 Magnetoencephalography

Harmonic signals like those used in the magnetoencephalographic study have periodic envelopes and elicit a strong sensation of pitch. Our finding that the M100 peak latency is linearly related to the period of the harmonic stimuli with a slope of about 1 is in line with previous results [18] and suggests a temporal processing of these signals.

The analysis of the location of the ECDs calculated from the responses to the different periodicity pitch stimuli revealed ECD positions that were systematically shifted as a function of the stimulus period. Such systematic shifts were evident around M60, M100, M300 and the sustained field.

Several studies have provided evidence for a tonotopic organization of the human auditory cortex [19, 20, 21]. These studies agree in that the M100 sources for high frequencies are located deeper in the supratemporal cortex than those for lower frequencies which appear to be more superficial. This tonotopic gradient appears to be at variance with the periodotopic gradient proposed in the present study. However, given the interindividual variability, a comparison of results from different studies may yield wrong conclusions. We have therefore conducted experiments in which subjects were exposed to periodicity pitch and to pure tone stimuli of corresponding pitch. Preliminary analysis of the data from these experiments suggests that the sources activated by the two different stimulus classes may indeed be different, unlike the conclusion drawn from previous results [22].

Moreover, results for M60 (Fig. 5) and M100 strongly suggest that periodicity (‘pitch’) and frequency is represented roughly orthogonal to frequency (‘timbre’) in the human auditory cortex. In Fig. 5 the response to the harmonic complex of 400 Hz is located near the proposed 400-Hz iso-frequency line, although the harmonic complexes have broadband spectra and therefore probably activate neurons in the frequency range up to 5000 Hz. One would expect that neurons at this location have BMFs similar to their CF (namely 400 Hz), as found in the gerbil. Like for the cortex of gerbils, spectral integration may offer an explanation.

4. CONCLUSIONS

1. The present results from the auditory cortex of gerbil and man support the assumption that perception of pitch is based on temporal mechanisms.

2. As a result of the temporal analysis periodicity is arranged in the auditory cortex in topographical maps. Recording of magnetic fields revealed periodotopic gradients roughly orthogonal to the tonotopic gradient. This is in line with similar topographic arrangements found at the level of midbrain in several animals.

3. Both, electrophysiological and magnetoencephalographic results suggest that the auditory cortex integrates temporal information over large spectral ranges. Such temporal integration would be needed for pattern recognition in speech processing and for binding of broadband signals.

5. ACKNOWLEDGMENTS

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