Representation of signal periodicity in the auditory cortex

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Abstact

Responses of neurons in the primary auditory cortex (AI) of adult male Mongolian gerbils to tones and amplitude modulated tones (AM) were investigated. It is shown that AM signals with low modulation frequencies (f_m) up to about 100 Hz, i.e. those that evoke a temporal percept (rhythm and roughness), are represented by a temporal (synchrony) code, whereas AM with high f_m between about 200 to 3000 Hz, i.e. those that evoke the (spatial) percept of periodicity pitch, are represented by a spatial (rate-place) code. Hence there seems to be a direct correlate between neuronal auditory cortical activity and the acoustic percept. Furthermore, concerning the rate-place code, evidence is presented that AI neurons receive information from wide spectral ranges to extract the periodicity information from the signal. A model is presented that speculates that the observed spectral integration takes place in the auditory midbrain and that contrast enhancing mechanisms, which operate on the output of this integration, are realized in the auditory cortex.

Introduction

Many animal species, especially among higher vertebrates, have developed highly complex acoustic communication, culminating in human speech. A common characteristic of the voiced parts of both animal communication sounds and human speech is their marked envelope periodicity. The perceptual quality associated with this signal periodicity varies as a function of amplitude modulation frequency (f_m) of the envelope: Signals of low f_m, up to about 100 Hz, evoke percepts with a temporal quality (rhythm and roughness; Terhardt, 1968), at higher f_m percepts have a spatial quality (periodicity pitch; Ritsma, 1962). A recent study has provided evidence that these two different perceptual qualities might be based on different cortical codes for stimulus periodicity, one that is temporal and codes low f_m (synchrony code) and one that is spatial and codes high f_m (rate-place code) (Schulze and Langner, 1997a). Furthermore, it could be demonstrated that auditory cortical neurons integrate over wide spectral ranges to extract periodicity information from the signal. Here, we shortly review these data on periodicity coding in the auditory cortex and present a model which proposes that the observed spectral integration takes place in the auditory midbrain and that contrast enhancing mechanisms, which operate on the output of this integration, are realized in the auditory cortex.

Material and Methods

Neuronal responses from single and multi-units to pure tones and 100% sinusoidally amplitude modulated tones (AM) were recorded extracellularly from the left primary auditory cortex (AI) of anaesthetized (n=6) and unanaesthetized (n=7) adult male Mongolian gerbils (*Meriones unguiculatus*). Pure tones were used to determine frequency response functions (FRF = a plot of spike rate over tone frequency). From the FRF the frequency response range (FRR = range of tone frequencies that increased spike rate) and best frequency (BF = maximum of FRF) were determined. AM-experiments were carried out where (1) the carrier frequency of the AM (f_c) was set to the BF of the unit, and (2) where high f_cs were used so that the AM spectrum was completely above the unit's FRR. f_m ranged from 5 Hz to 5kHz. Responses to AM were quantified using rate modulation transfer functions (rate-MTF = a plot of spike rate over f_m) or synchronization MTFs (sync-MTF = a plot of vector strength (VS, cf. Greenwood and Durand, 1955) over f_m) VS values were tested for statistical significance using the Raleigh test of uniformity (Mardia, 1972). Absolute MTF-maxima are referred to as best modulation frequency (BMF). Q_{3dB} factors (=BF or BMF devided by the bandwidth of the corresponding FRF or MTF 3dB below the maximum, respectively) were used to measure sharpness of tuning.

Results

During stimulation with AM with a f_c equal to the BF of the unit under investigation, 17% of the units in AI responded with discharges phase-locked to the f_m. In some cases significant phase-locking ($P < 0.01$) was observed up to 100 Hz, but for 85% of the units that showed significant phase-locking at all phase-locking was confined to $f_m \leq 50$ Hz. The highest sync-BMF found was 45 Hz (cf. Fig. 2A). VS ranged from 0.15 to 0.81. One example for such a unit is shown in Fig. 1A to D. The tone response of the unit is given as response plane (A, cf. Gerstein et al., 1968) and FRF (C). Its BF of 1 kHz was used as the f_c in the AM experiment shown in B and D (sync-MTF). The unit showed significant phase locking up to 80 Hz f_m ($P < 0.01$) with a sync-BMF of 10 Hz. Phase locking in anaesthetized animals

was generally weaker (VS ranging from 0.15 to 0.53) and confined to even lower f_m, up to 65 Hz only. A systematic topographic representation of sync-BMFs within AI was not found, neither in anaesthetized nor in unanaesthetized animals.

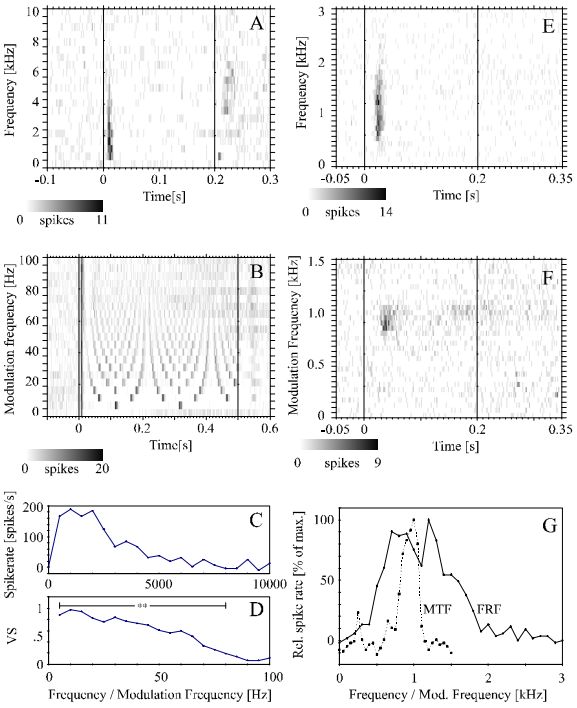

Figure 1. Responses of two units (left and right column) to tones (top panels) and AM (middle panels). Corresponding FRFs (C; G, solid line) and MTFs (D; G, dotted line) are given below. The unit on the left showed phase-locking to AM with low f_m and a f_c equal to its BF (B). The unit on the right discharged to AM with a spectrum completely outside its FRR (fc = 7 kHz), with a phasic-tonic response tuned to a certain range of high f_m (F). Vertical lines in response planes (A, B, E, F) indicate begin and end of stimulation.

In contrast, a systematic representation of rate-BMFs (periodotopy) within the low frequency region of AI (up to about 3 kHz BF) was found using AM with a spectrum completely above a unit's FRR. Within this AI region over 70% of the units (n=232) responded to such AM in both anaesthetized and unanaesthetized animals with discharges tuned to a certain range of f_m. Fig. 1E to G shows responses of such a unit. The responses to tones (E) and to AM (F) and the corresponding FRFs and rate-MTFs (G) are shown. The unit responded to pure tones between 0.5 and 2 kHz. In Fig. 1F AM stimuli were presented with f_m ranging from 0 to 1.5 kHz and a f_c of 7 kHz. Although none of these AM was spectrally within its FRR, the unit responded with discharges tuned to f_m ranging from 800 to 1050 Hz. The AM response showed a longer latency (25.4 ms) and was more sharply tuned (Q_{3dB}=6.9) than the tone response (latency=18.6 ms; Q_{3dB}=1.6). These latter two observations were typical for the population of units tested. BF and BMF of a given unit could differ by more than 2 octaves. A comparison of this rate-place code with the synchrony code described above showed that they covered almost distinct f_m ranges: The distributions of sync-BMFs (up to 45 Hz) and rate-BMFs (50 Hz to about 3 kHz) showed no overlap (Fig. 2A,B). Furthermore, whereas the synchrony code showed no topographic organization, the rate-place code showed a clear periodotopic gradient oriented roughly orthogonal to the tonotopic gradient (Fig. 2C).

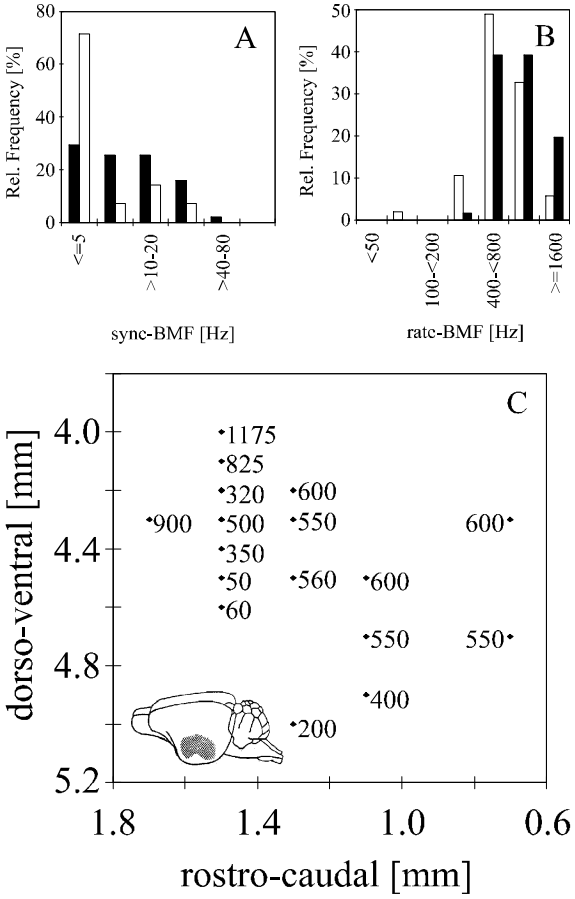

Figure 2. Frequency distribution of sync-BMFs (A) and rate-BMFs (B). Filled and open bars show data for unanaesthetized and anaesthetized animals, respectively. C shows the topographic distribution of rate-BMFs (periodotopy) in one animal: Whereas the tonotopic gradient in AI runs from a caudal representation of low BFs to a rostral representation of high BFs the periodotopic gradient runs from a ventral representation of low BMFs to a dorsal representation of high BMFs. The inset shows the location of the left auditory cortex in the temporal lobe of the forebrain of the gerbil.

Discussion

The data presented show that two separate codes for stimulus periodicity are realized in AI: One that is temporal (synchrony code) and codes for periodicities that create a temporal percept (rhythm) and one that is spatial (rate-place code) and codes for periodicities that create a percept with a spatial quality (pitch). Hence, there is *a potential correlate between neuronal auditory cortical activity and the acoustic percept*.

Considering the rate-place code for periodicity pitch, it is unlikely that distortion products in the cochlea can account for the responses shown, because units can be tuned to high f_m but low tone frequencies (for an example see Schulze et al., 1999) and because the periodotopic gradient is roughly orthogonal to the tonotopic gradient (cf. Fig. 2C). Therefore, and because units responded to AM with spectra far above their FRR (cf. Fig. 1F), it is more likely that *AI units receive information from wide spectral ranges*. If so, one main question arises: Which neuronal connections could explain these responses and where in the auditory pathway could the observed spectral integration take place? In the final section of this paper we present a model of neuronal connectivity between the inferior colliculus and the thalamo-cortical system (Fig. 3) which can explain our results.

The model is based on our data and current knowledge of the anatomy and the morphology of the central nucleus of the inferior colliculus (ICC) and its connections with the thalamo-cortical system as well as of physiological results (for the cat cf. Rockel & Jones, 1973; Oliver, 1984; Oliver & Morest, 1984; Herrera et al., 1988; Oliver et al., 1991; Schreiner & Langner, 1997; for an overview see Oliver & Huerta, 1991; for the marmoset cf. Garey & Webster, 1989; for the chinchilla: Biebel & Langner, 1996; for the gerbil: Ryan et al, 1982).

The ICC is organized into discrete isofrequency laminae where neurons of each lamina share similar BFs covering about 1/4 of an octave (Schreiner & Langner, 1997). Laminae with low BFs are located dorsally, those with high BFs ventrally. Each lamina exhibits a functional fine structure in that neurons that share identical BFs are arranged along isofrequency contours and neurons that share identical BMFs along isoperiodicity contours. Isofrequency and isoperiodicity contours are oriented roughly orthogonal to each other (Langner et al., 1992). Two main cell types, disc-shaped cells and stellate cells are distinguished within the ICC (Oliver, 1984; Oliver & Morest, 1984; Herrera et al., 1988; Oliver et al., 1991; Oliver & Huerta, 1991). Whereas the disc-shaped cells have highly oriented dendritic trees aligned in parallel with the orientation of the isofrequency laminae, the stellate cells are characterized by their oval or spherical dendritic fields crossing the isofrequency laminae. In Fig. 3 this structure of the ICC is sketched as a stack of five isofrequency laminae. The black disks numbered from 1 to 5 represent disc-shaped cells located in different laminae, the shaded disks labeled A to C stellate cells. The orientation (not the dimension) of the dendritic fields of these cells is indicated by the orientation of the wiggled lines. Here only those cells of both types are of interest which project to neurons of the medial geniculate body (MGB) of the thalamus which in turn project to neurons in the auditory cortex (black disks I to III). For the purpose of this model we consider the MGB as a simple relay station. Projections of both ICC cell types are tonotopically arranged, thus connecting units with similar BFs and maintaining the tonotopic organization in each structure.

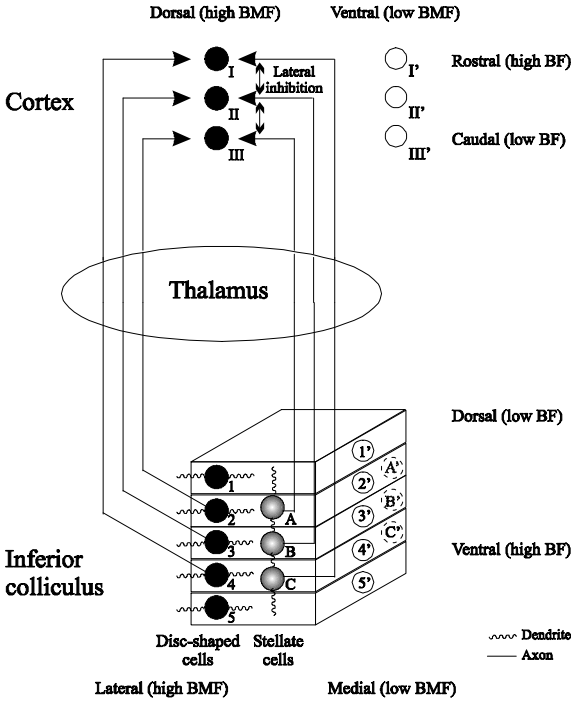

Figure 3. Model of the connectivity between the inferior colliculus and the thalamo-cortical system that can explain the observed wide spectral integration. The model is based on the assumption that stellate cells in the central nucleus of the inferior colliculus (ICC) would receive local projections from disc-shaped cells of different isofrequency laminae thereby integrating over more or less wide spectral ranges. For further explanations refer to the text.

In the model, neurons that are located above each other in different ICC laminae (disc-shaped cells 1 to 5 in Fig. 3) possess the same BMFs but different BFs, that is, they are tuned to signals with the same periodicity but with different spectral content. Stellate cells (neurons A to C in Fig. 3) which are in close register with these units (1 to 5) receive local projections on their dendritic trees crossing the isofrequency laminae. Consequently, they integrate over more or less wide spectral ranges (cf. Meddis, 1996), thereby extracting the time structure of the signal. Those disc-shaped cells that project onto the distal parts of a dendrite of a given stellate cell would activate the cell to a lesser degree than those

cells that project to more proximal parts of the dendrite or to the soma. Different sets of such neurons in the ICC (1' to 5', A' to C' in Fig. 3) not only process different frequency ranges, but also different temporal structures and would be connected to different sets of cortical units (I' to III' in Fig. 3), thereby providing the basis for a tonotopic and a periodotopic organization (cf. Schreiner & Langner, 1988; Schulze and Langner, 1997a).

In the following we will describe how this model could explain the results presented in this study. First, we consider the case of a low-frequency pure tone close to the BF of the disc-shaped cell 2 activating the auditory system. The disc-shaped cell 2 in the ICC would respond to this stimulus with a phasic or combined phasic-tonic response. Furthermore, such a tone would activate the stellate cell A, either via a common input with neuron 2 or by a local projection from neuron 2. Both cells would then activate (via the thalamus) cortical units at a location where frequencies corresponding to their BFs are represented (e.g. unit III in Fig. 3).

Now we consider the case of an activation by an AM tone with high carrier frequencies as used in this study. In analogy to our experiments we select a case where the carrier frequency is equal to the BF of neuron 4. The AM stimulus activates neuron 4 and also neurons 3 and 5, but the modulation frequency is not high enough for the lower sideband to activate neuron 2. In such a case the projections from neurons 3 to 5 would directly activate units in the high frequency area of the thalamus and subsequently in the high frequency area of the cortex, i.e. units I and II. In addition to this spectral activation of the high frequency area of the cortex the pathway to the low frequency area of the cortex could also be activated by such a stimulus: We assume that neurons 3 to 5 also project locally to the distal parts of dendrites of stellate cells in the low frequency region of the ICC (i.e. unit A in Fig. 3). The resulting EPSPs on the dendrite of neuron A could be *summed spatially* which may result in a stronger depolarization than in the case of a (high-frequency) pure tone activation. In other words, in contrast to an activation by pure tones, stimulation with a complex signal (AM) may give rise to a depolarization strong enough to reach the soma of neuron A with an amplitude sufficient to cause neuron A to fire. Under such conditions neuron A would respond to stimuli with a spectrum above its FRR, and would be tuned to a BMF equal to the BMFs of neurons 3 to 5.

Furthermore, we can consider another set of high-BF units (3' to 5') which are tuned to low modulation frequencies and which are projecting to the dendrite of another low-BF stellate cell A'. If we would activate the system with an AM with a carrier frequency equal to the BF of neuron 4' and with the appropriate low modulation frequency, unit 4' would respond with discharges phase-locked to the modulation frequency whereas neurons 3' and 5' would not respond. The resulting EPSPs evoked by the phase-locked spike trains reaching the dendrite of neuron A' could now be *temporally summed* resulting in a strong depolarization sufficient to activate neuron A'. Neuron A' would then in turn activate the cortical unit III' via the thalamic relay station. Neuron III' would therefore be tuned to low modulation frequencies and neuron III would be tuned to high modulation frequencies leading to a periodotopic gradient in the auditory cortex (as shown for the primary auditory cortex of the gerbil in Schulze and Langner, 1997a; for the cat auditory cortex: Langner et al., 1997a; for the human auditory cortex: Langner et al., 1997b).

So far we have discussed our finding that units in the auditory cortex may respond to complex stimuli with a spectrum outside their FRR and we have asked for the underlying neuronal connectivity. In this paragraph we will discuss an observation that the response range to modulation frequencies of AI neurons could be broadened under the influence of BIC, while the pure tone tuning properties were not significantly affected (Schulze and Langner, 1997b). Several studies report GABAergic neurons in the auditory cortex (Winer & Laure, 1989; Winer et al., 1995; Hendry & Jones, 1991; Prieto et al., 1994a,b). The finding that the AM tuning properties were influenced by the application of BIC is in line with the assumption of Prieto et al. (1994a,b) that the receptive field size in the auditory cortex might be modulated by intracortical GABAergic circuits. From the fact that the pure tone tuning properties were not influenced by BIC we infer that there must exist a $GABA_A$-mediated lateral inhibiton (cf. Winer & Laure, 1989) in the cortex that sharpens the cortical AM-responses, possibly by influencing the projections originating at the ICC-stellate cells. According to the model, the $GABA_A$-mediated lateral inhibiton could not influence the projections originating at the ICC-disc-shaped cells, because otherwise the tuning to pure tones should also have been influenced by the application of BIC. We propose, that sharpening of the responses to pure tones is mediated by another inhibitory receptor for GABA, e.g. $GABA_B$.

The integration model is able to explain also some other details of our results. First, we observed a difference in response latency between responses to pure tones and AMs (cf. also Schulze and Langner, 1997a): The mean latency of the response to AM was about 10 ms longer than the mean latency of the response to pure tones. The model would predict a longer latency for the response to AM for two reasons: Stellate cells in ICC should integrate over several local projections from disc-shaped cells in ICC including one additional relay station for AM compared to pure tone activation. In addition, the integration of EPSPs evoked by AM stimuli on the distal portions of the dendrites of stellate cells would result in longer response latencies (as measured here at cortical cells) due to the time required for the EPSPs to spread to the spike initiation zone. Dendritic conductance velocity is in the range

between 0.3 and 0.45 ms^{-1} for thick dendrites of cortical pyramidal neurons (Stuart & Sakmann, 1994; Stuart et al., 1997) and should be even less for thinner dendrites. Therefore, the dendritic conductance time of dendrites of stellate cells that cross several isofrequency-laminae of the ICC should be in the range of some milliseconds.

Second, it was shown that the latency as well as the strength of the responses to AMs varies as a function of carrier frequency, i.e. of spectral content of the AMs (cf. Schulze and Langner, 1997a): There seemed to be an optimal spectral distance of the AM from the FRR, that is, out of the range of f_cs of the AM tested, the AM with one particular f_c elicited the strongest responses with the shortest latencies. The integration would predict that a given stellate cell should exhibit the shortest latencies and strongest responses to inputs originating from those disc-shaped cells closest to its soma. Also the observation that the responses to AMs under the influence of BIC for AMs with carrier frequencies that were not effective under normal conditions had a longer mean response latency than those under normal conditions, i.e. those with lower carrier frequencies (cf. Schulze and Langner, 1997b), is in line with this consideration: AMs with very high carrier frequencies should activate projections to very distal portions of the dendrites of the target stellate cells causing longer dendritic conductance times for the EPSPs evoked by these projections compared to AMs of lower carrier frequencies.

The model may also explain the observations of other studies showing that a tone presented outside the frequency receptive field of a unit can facilitate the response to a simultaneously presented tone within the frequency receptive field (Oonishi & Katsuki, 1965; Ehret & Merzenich, 1988; Nelken et al., 1994). According to the model, a pure tone that would excite a high-BF neuron in the ICC (disc-shaped cell 4 or 5 in Fig. 3) would elicit an EPSP in stellate cell A with a subthreshold amplitude. But if neuron A was already excited by a second tone driving disc-shaped cell 2, than the pure tone could cause a stronger, facilitated response of neuron A. The assumption of Oonishi & Katsuki (1965) that the facilitatory effects they observed were based on intra-cortical integrative mechanisms were already disproved by Abeles & Goldstein (1972).

In conclusion, we presented evidence that the psychoacoustic percepts evoked by AM have a direct correlate in the neuronal auditory cortical activity elicited by the same stimuli: The temporal percept (rhythm and roughness) is reflected in the temporally structured neuronal activity (synchrony code) whereas pitch, the percept with a spatial quality, is represented via a spatial (rate-place) code. Furthermore we could demonstrate that this latter code is based on wide spectral integration and presented a model that proposes that this integration takes place in the auditory midbrain, but that contrast enhancing mechanisms (lateral inhibition), which operate on the output of this integration, are realized in the auditory cortex.

Acknowledgements

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