PERIODICITY CODING IN THE AUDITORY CORTEX: WHAT CAN WE LEARN FROM LEARNING EXPERIMENTS?

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Many natural sounds are characterized by periodic envelope or amplitude modulation (AM). The perceptual qualities corresponding to this signal characteristic are rhythm for low and pitch for high modulation frequencies (f_m). We demonstrate that f_m ranges corresponding to these two perceptual qualities seem to be represented by different codes in the primary auditory cortex (AI) of the Mongolian gerbil: Low f_m are represented by a synchrony code whereas high f_m are represented by a rate-place code. For the rate-place code we show that in response to AM neurons integrate over spectral ranges much wider than expected on the basis of their classical frequency receptive fields. Furthermore, we present preliminary data from learning experiments where gerbils were trained to discriminate between AM with different f_m. It seems that the different cortical codes used to represent AM with different perceptual qualities are also reflected in the learning curves: learning performance is better for low f_m ranges, where phase-locking is still present, than for high f_m ranges that are encoded by a rate-place code.

1 Introduction

Acoustic communication signals, like human speech and animal vocalizations, are characterized by periodic envelope or amplitude modulation (AM). The perceptual quality associated with this signal periodicity varies as a function of modulation frequency (f_m): AM signals of low f_m, up to about 100 Hz, evoke percepts with a temporal quality (rhythm and roughness) [4], at higher f_m percepts have a spatial quality (periodicity pitch) [2]. 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) [3]. Here we characterize these two cortical codes and propose the hypothesis that there may also be two different learning mechanisms that operate on these different codes. To obtain a first estimate for the validity of this hypothesis we trained gerbils to discriminate between AM of different f_m. Our assumption was that if indeed two different learning mechanisms were realized in the auditory cortex, this might be reflected in the learning performance of the animals.

2 Methods

Neuronal responses from single and multi-units to pure tones and 100% sinusoidally amplitude modulated tones were recorded extracellularly from the left primary auditory cortex (AI) of anaesthetized (n=6) and unanaesthetized (n=7) adult male Mongolian gerbils. Pure tones were used to determine frequency response functions (FRF = a plot of spike 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_c 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) over f_m). 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.

AM discrimination was investigated using a footshock (UCS = unconditioned stimulus) motivated shuttle box avoidance go/no go procedure. Animals were trained to discriminate between two AM of different f_m and a f_c of 2 kHz. Six groups of gerbils, with 3 specimens each, were trained (A to F in Fig. 5). F_m to be discriminated were 10 vs. 20, 20 vs. 40, 40 vs. 80, 80 vs. 160, 160 vs. 320, and 320 vs. 640 Hz. In each group, the AM with the lower f_m served as the CS+ (= conditioned stimulus followed by the UCS), the other AM was the CS- (not followed by the UCS). 15 training sessions with 60 trials each were carried out in each animal. Crossings of the hurdle during a 4 s presentation of the CS+ or CS- (= conditioned responses; CR+ and CR-, respectively) were counted in each session and plotted as a function of training session to quantify learning performance.

3 Results

3.1 *Synchrony code for stimulus periodicity*

For unanaesthetized gerbils 17 % of the units tested (n= 310) responded to AM with a f_c equal to the unit's BF with discharges phase-locked to the f_m. Significant phase locking was observed up to 100 Hz f_m. The highest sync-BMF found was 45 Hz (cf. Fig. 4A); VS ranged from 0.15 to 0.81. An example is shown in Fig. 1. The tone response of the unit is given as response plane [1] (A) 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 ($P < 0.01$, Raleigh test) 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.

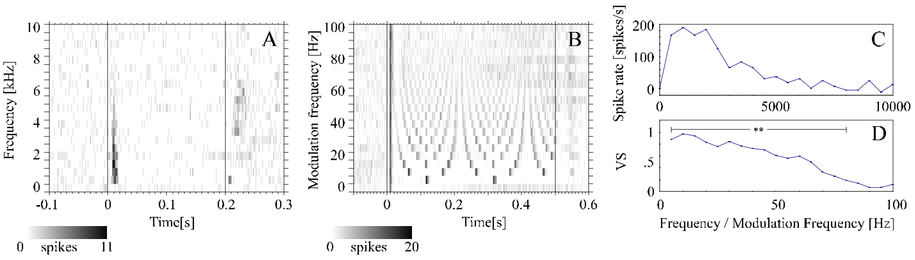

Figure 1. Tone response (A,C) and AM response (B,D) of a unit showing phase locking to f_m of AM. Vertical lines in response planes (A,B) indicate begin and end of stimulation.

3.2 Rate-place code for stimulus periodicity

However, 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. 2 shows responses of two such units (top and bottom row). The responses to tones (left panels) and to AM (middle panels) and the corresponding FRFs and rate-MTFs (right panels) are shown. The unit shown in the upper row responded to pure tones between 0.5 and 2 kHz. Fig. 2B shows the AM response of that unit (f_m = 0 to 1.5 kHz; f_c = 7 kHz). Although none of the 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). The bottom row shows a unit that was tuned to low tone frequencies (0.1 to 0.4 kHz) but to high f_m (0.5 to 1.4 kHz, rate-BMF = 1.25 kHz; f_c=7 kHz). The AM response again showed longer latency (37.1 ms) and sharper tuning (Q_{3dB}=7.4) than the tone response (latency=20.6 ms; Q_{3dB}=2.1). For the population of units the AM response had generally longer latency (Fig. 3B) and sharper tuning (Fig. 3C) than the tone response. BF and rate-BMF of a given unit could differ by more than 2 octaves (Fig. 3A). A comparison of this rate-place code with the synchrony code 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. 4A,B). Furthermore, whereas the synchrony code showed

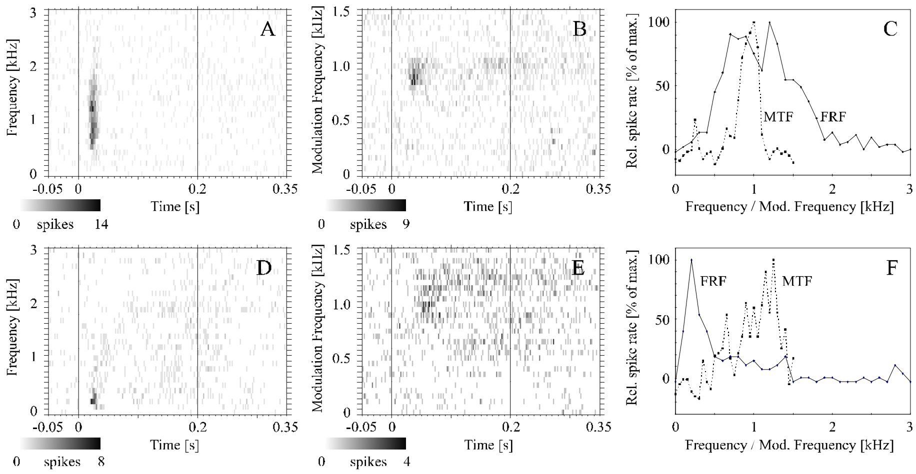

Figure 2. Responses of two units to tones (A,D) and AM with a spectrum completely above the units' FRRs (B,E; fc=7kHz in both cases). C and F show the corresponding FRFs and rate-MTFs. Vertical lines in response planes (A,B,D,E) indicate begin and end of stimulation.

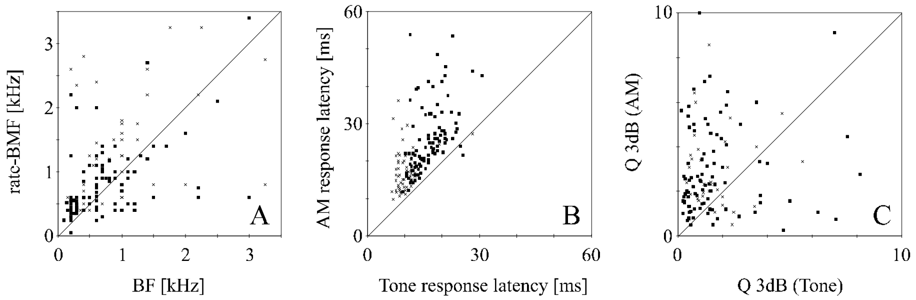

Figure 3. Scatterplots of rate-BMF vs. BF (A), AM response latency vs. tone response latency (B), and Q_{3dB} of AM responses vs. Q_{3dB} of tone responses (C) for the population of units tested. Squares show data from anaesthetized, dots from unanaesthetized animals.

no topographic organization, the rate-place code showed a clear periodotopic gradient oriented roughly orthogonal to the tonotopic gradient (Fig. 4C) [3].

3.3 Behavioral discrimination of stimulus periodicity

To quantify learning performance for AM discrimination we used two measures: A gerbil was considered to discriminate between CS+ and CS- if the CR+ for a given session was at least 3 times as high as the CR-. As a measure of how fast gerbils

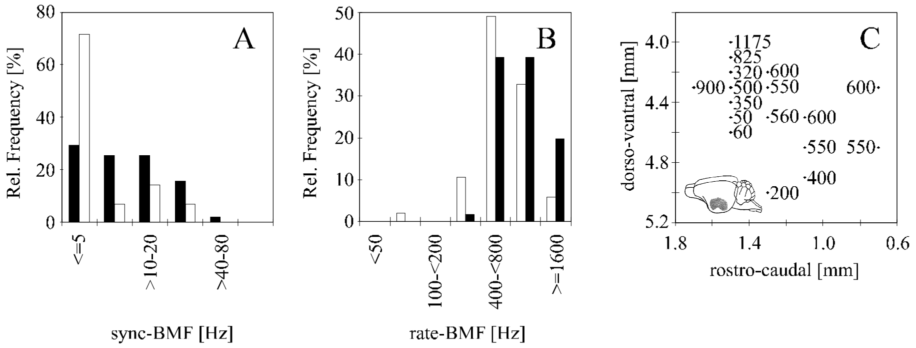

Figure 4. Frequency distribution of sync-BMFs (A) and rate-BMFs (B). Filled and open bars show data for unanaesthetized and anaesthetized animals, respectively. C shows the topographic distribution of rate-BMFs (periodotopy) in one animal. The inset shows the location of the left auditory cortex in the temporal lobe of the forebrain of the gerbil.

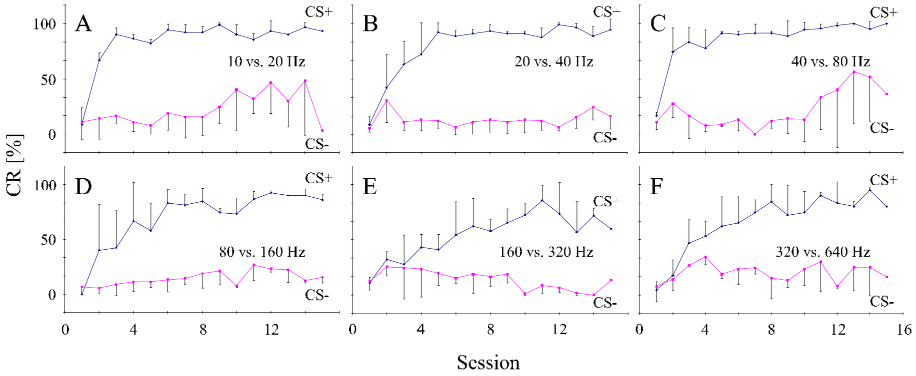

Figure 5. Discrimination of AM tones. Shown are group mean values and standard deviations (n=3 per group) of conditioned responses as a function of training session.

learn to discriminate between CS+ and CS- the first session where this criterion was reached was determined. Furthermore, we determined the maximal difference between CR+ and CR- that was reached for each group to obtain a measure of discrimination performance. Groups A to D reached the criterion for discrimination at session 2 or 3, E and F only around session 6 (Fig. 5). Discrimination performance in A to C was 91 ±1%, in D to F 76 ±2%. So for A to C, when AM is represented by the temporal synchrony code in AI, discrimination learning is fast and discrimination performance is good, whereas when AM is represented by the topographic rate-place code (E and F), learning takes longer and discrimination performance is worse. For the intermediate group D, where an AM that is encoded temporally has to be discriminated from an AM that is encoded spatially, learning is still as fast as in A to C, but discrimination performance is as poor as in E and F.

4 Conclusions

We demonstrated that in AI two codes for stimulus periodicity are realized, one that is temporal and codes for periodicities that create a temporal percept (rhythm) and one that is spatial and codes for periodicities that create a percept with a spatial quality (pitch). Because units can be tuned to high f_m but low tone frequencies (cf. Fig. 2, bottom row) and because the periodotopic gradient is roughly orthogonal to the tonotopic gradient (cf. Fig. 4C) it is unlikely that distortion products in the cochlea can account for the responses shown. Therefore, and because units responded to AM with spectra far above their FRR, it is more likely that AI units integrate information over wide spectral ranges. Finally, on the basis of our behavioral data it seems that the two codes for stimulus periodicity are also reflected in the animals' learning performance: Learning is faster and learning performance is better for periodicities that are encoded temporally than for those that are encoded spatially.

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