

Discrimination learning of amplitude modulated tones in Mongolian gerbils

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Abstract

Discrimination learning of 100% sinusoidal amplitude modulated tones (AM) was investigated in adult Mongolian gerbils using a footshock motivated shuttle box avoidance go/no go paradigm. AM stimuli to be discriminated had identical carrier frequency (2 kHz) but differed in modulation frequency (f_m) by one octave. Six groups of gerbils were trained to discriminate AM-pairs with f_m ranging from 10 to 640 Hz. Learning proceeded faster and discrimination performance was slightly better for low f_m , up to 80 Hz, than for high f_m , above 80 Hz. These results may be related to cortical AM encoding (Schulze, H. and Langner, G., *J. Comp. Physiol. A*, 181 (1997) 651–663), which is temporal for low f_m (synchrony code) and spatial for high f_m (rate-place code). This may implicate different neuronal learning strategies or distinct behavioral meanings influencing the discrimination training. © 1999 Elsevier Science Ireland Ltd. All rights reserved.

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Periodic envelope or amplitude modulations are characteristic for acoustic communication signals, like voiced speech sounds or animal vocalizations. 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 of rhythm and roughness [8] and those of higher f_m percepts of pitch (periodicity pitch) [6]. A recent study of periodicity coding in the primary auditory cortex (AI) of the gerbil provided evidence that these two different perceptual qualities are paralleled by differences in neuronal responses to low and high stimulus periodicities [7]. In response to AM of low f_m , up to about 100 Hz, neurons in AI showed discharges that were phase-locked to the stimulus envelope. Obviously, such neurons represent the temporal structure of the stimulus (the periodicity) by the timing of their discharges (temporal synchrony code). For this synchrony code, a systematic topographic organization (periodotopy) was not found. In

contrast, in response to high f_m , between 50 and about 3000 Hz, AI units discharged only to stimulus onset or in a sustained fashion without locking of spikes to the envelope fluctuations. In this case neurons with different best f_m were topographically organized (rate-place code). It was concluded in this study that AM with f_m that evoke a percept of a temporal quality (rhythm and roughness) are represented by a temporal (synchrony) code in AI, whereas AM with f_m that evoke a percept of a spatial quality (pitch) are represented by a spatial (rate-place) code.

The fact that these two classes of AM stimuli are represented in a qualitatively distinct manner in auditory cortex theoretically allows for differential influences on performance when animals learn samples of high and low f_m stimuli: one factor whose influence may be experimentally controlled is sensory discriminability. Second, differences in learning performance could result from divergent neuronal mechanisms that might change the neuronal representations of high and low f_m stimuli during learning. Finally, differences could result from distinct behavioral relevance of the high and low f_m stimuli leading to differences in the way animals attribute meaning to stimuli during learning.

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Here we studied the specific question whether discrimination training of AM stimuli taken either from the low or high f_m class develops differently over time.

A footshock (UCS, unconditioned stimulus; 150–300 μ A) motivated shuttle-box avoidance go/no go procedure was used for discrimination training. Adult animals were trained to discriminate between two 100% sinusoidal AM tones of different f_m and always the same carrier frequency of 2 kHz. Stimuli had 400 ms duration with 5 ms rise and fall time (f_m) and were presented repeatedly at 2 Hz. Six groups (A–F) of gerbils, with three specimens each, were trained to discriminate f_m of 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), and the AM with the higher f_m as the CS– (not followed by the UCS). An additional UCS (duration 0.5 s) was applied upon false reaction to the CS–. Animals were given a stimulation-free habituation period of 3 min before each training session. Fifteen daily training sessions with 60 trials each (30 randomized presentations of CS+ and CS– [2]) were carried out with each animal. Intertrial intervals (start to start) were 16 ± 4 s. 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. If the animal did not cross the hurdle within 4 s after the onset of the CS+, the UCS was turned on and the CS+ presentation continued until the gerbil crossed the hurdle, but maximally for 8 s.

Fig. 1 shows the course of discrimination learning for the six groups of gerbils (A–F). For each group, mean values and standard deviations of CR+ and CR– are plotted as a function of sequential training sessions (in the following termed as CR+ or CR– functions, respectively). In those groups which had to discriminate low f_m (below 100 Hz;

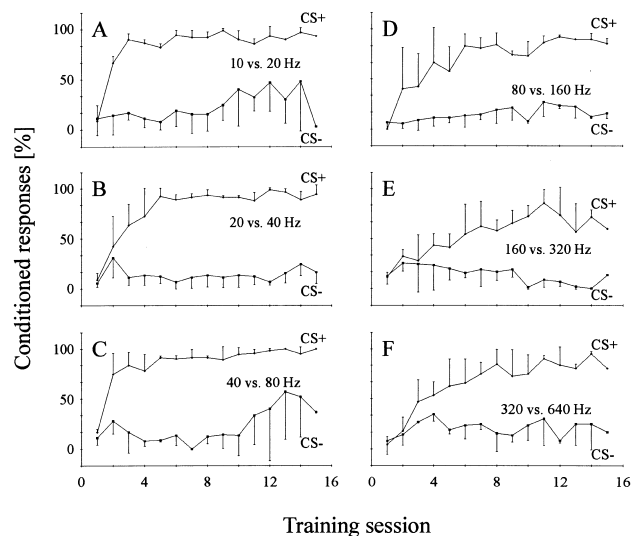


Fig. 1. Discrimination of AM tones by Mongolian gerbils. Shown are group mean values and SDs of conditioned responses as a function of training session for the six groups of gerbils (A–F; $n = 3$ per group). The carrier frequency of the AM to be discriminated was 2 kHz, f_m of CS+ and CS– are given in the panels.

groups A–C) learning was fast (steep slopes at the beginning of the CR+ functions). The maximal performance level (maximal difference between CR+ and CR–) was high. Some animals tended to show conditioned responses to CS– in later training sessions for unknown reasons (beginning around session 11; cf. Fig. 1A,C). In contrast, in groups which had to discriminate f_m above 100 Hz (E,F) learning took longer (shallow slopes of the CR+ functions) and maximal discrimination performance was lower (smaller difference between CR+ and CR–) than in groups A–C. In the group which had to discriminate intermediate f_m (D) the learning performance showed intermediate characteristics. CR– functions generally remained on a low level for all training sessions and all groups (except groups A and C, cf. above).

To quantify these observations we used measures of how fast and how well gerbils learned to discriminate between CS+ and CS–: the first session where the CR+ was significantly different from the CR– on the 1% level (4-fold table χ^2 -test) and where the subsequent session also fulfilled this criterion served as an index of learning speed. The maximal difference between CR+ and CR– that was reached by each individual gerbil served as the measure of discrimination performance.

Fig. 2 shows plots of this discrimination performance over the first session with significant discrimination. The top panel shows the values for each specimen, the bottom panel the group mean values and standard deviations. We encircled data from those animals, which had to discriminate low f_m , i.e. f_m which are represented by the temporal synchrony code in AI (groups A–C), and data from those animals that had to discriminate high f_m , represented by the spatial rate-place code (E,F). Obviously, the areas covered by data of these groupings are distinct from each other and do not overlap. Data from animals in group D, which had to discriminate an f_m of 80 Hz, still likely represented by the rate-place code, fall in between these groupings.

As both panels show, the distribution of values from groups A–C cover regions of the plots that are distinct from those covered by the distribution of values from group E and F. Learning was significantly faster in groups A–C ($n = 9$) compared to groups E and F ($n = 6$) (Mann–Whitney U -test; $P = 0.0004$). Discrimination performance was slightly better in groups A–C (mean values of largest difference between CR+ and CR–: 27.6) compared to groups E and F (23.3), although this difference was not significant (Mann–Whitney U -test; $P = 0.11$). Values of group D fell in between.

These results suggest that the two auditory cortical codes for stimulus periodicity [7] are indeed reflected in the animals' learning performance: learning proceeded faster and discrimination performance was slightly better for those modulation frequencies that are encoded by the temporal synchrony code (groups A–C) than for those that are encoded by the spatial rate-place code (groups E and F).

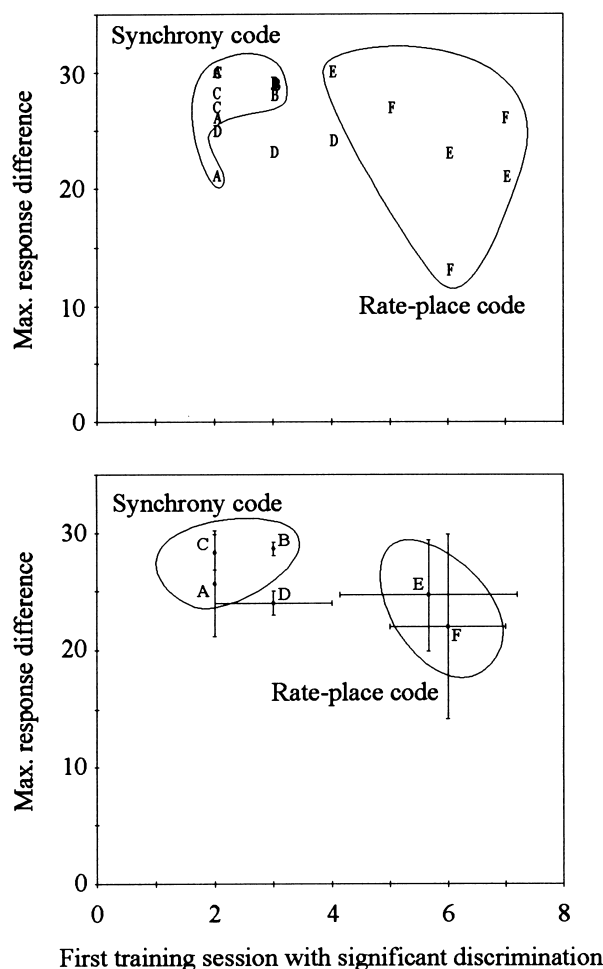


Fig. 2. Plots of the maximal difference between CR+ and CR- (max. response difference = discrimination performance) over the first training session where animals showed significant discrimination between CS+ and CS- (= a measure of how fast gerbils learned to discriminate the AM) for individual data (top) and group data (bottom; means and standard deviations). Letters refer to animal groups (cf. Fig. 1). Groupings within the plots (circles) are made on the basis of electrophysiological data [7] and refer to the cortical code used to represent the AM to be discriminated (synchrony code or rate-place code).

In the intermediate group D, where a temporally encoded f_m had to be discriminated from a spatially encoded f_m , animals also showed intermediate learning performance. Thereby it should be emphasized that the differences in learning performance reflect how many trials were required to consolidate the learned discrimination and not when the discrimination first became salient for the animals. From the stimulus design it seems unlikely that differences in the sensory discriminability of the AM pairs account for the observed differences in learning performance, since the octave distances in f_m between discriminated AM in the present study should all be well above the difference limen for AM discrimination in rodents (cf. [3]). Furthermore, the difference in learning performance develops over several days which makes it also unlikely that stimulus discriminability per se is an important aspect.

As mentioned above this difference in learning performance may be explained by two alternative interpretations: for instance, such differences could be due to the way in which neuronal mechanisms change the neuronal representations during learning. Possibly the learning mechanism is differently effective in changing a temporal representation of the stimuli (synchrony code) or in changing a spatial representation of the stimuli (rate-place code). Spatial learning mechanisms, e.g. changes in topographic representations of stimuli in tonotopic maps in the auditory cortex as a consequence of pure tone discrimination learning, have previously been observed [5]. If however the signals to be discriminated are encoded by the time structure of neuronal responses (e.g. phase-locking), a learning mechanism that is somehow temporally adjusted to influence such discharges might be necessary. It was shown in owl monkeys that AM discrimination learning can lead to more precise timing of the phase-locking of neurons in AI to the AM envelope [1]. Furthermore, the observation during differential tone conditioning that the retuning of pure tone receptive fields is reflected in complex time courses of responses [4] might point to such mechanisms. If there were really two different learning mechanisms for AM discrimination learning, one might speculate that discrimination learning of high f_m takes longer than discrimination learning of low f_m , because changing topographic maps by coherently changing response properties of neurons in the map (as proposed for the spatial learning mechanism for high f_m) may be more demanding than changing temporal response properties of individual, not topographically organized neurons (as proposed for the temporal learning mechanism for low f_m).

Another interpretation for the observed differences in learning performance could be that the different percepts that are evoked by the two classes of AM stimuli (rhythm/roughness vs. pitch) are of different behavioral relevance for the animal: For instance the animal may be more alerted by a 'rough' sounding AM than by sound of a certain pitch. This in turn may be a reason why differential meaning can be attributed faster to AMs with different low f_m than to AMs with different high f_m .

In summary, the present study has shown that the learning performance of gerbils during AM discrimination learning differs as a function of f_m . Future electrophysiological studies on animals trained in the described way will have to decide which interpretation of our data may be correct.

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