Auditory sensory memory for random waveforms in the Mongolian gerbil

Christian Kaernbach[a], Holger Schulze[b],*

[a]*Institut für Allgemeine Psychologie, Universität Leipzig, Seeburgstrasse 14–20, 04 103 Leipzig, Germany*
[b]*Leibniz-Institut für Neurobiologie, Brenneckestrasse 6, 39118 Magdeburg, Germany*

Abstract

Mongolian gerbils ($N = 21$) were trained to discriminate between continuous and repeated auditory white noise. While for periods up to 40 ms of the repeated noise spectral effects make this a perceptual task, longer periods require auditory sensory memory to solve the task. Short periods (20 ms) could easily be discriminated by naive gerbils (discrimination performance, i.e. hit rate minus false alarm rate >80% after 8 days of training). Discrimination was more difficult for longer periods (100 ms: discrimination performance $\approx$ 50% after 18 days of training). By long-term training (156 days) using an optimized training paradigm two further gerbils learned to discriminate up to a period length of 360 ms but could not proceed at 400 ms. While this falls short of human performance, it demonstrates for the first time sensory memory for random waveforms in animals. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Mongolian gerbil; Repeated noise; Periodic noise; Periodic random waveforms; Auditory memory; Auditory sensory memory; Preattentive memory

Auditory white noise is perceived by human listeners as a homogenous, featureless stimulus, completely described by its loudness. This changes dramatically if the otherwise random waveform of the noise starts to repeat itself after a second or less [8]. This 'periodic' or 'repeated noise' (RN) elicits distinct percepts that are highly specific for the repeating noise segment, tend to be stable across presentations, and correlate to a certain degree between listeners [9] (for a demonstration see www.periodic-noise.de).

The percepts elicited by RN are considered evidence for a preattentive auditory storage system in humans that can retain non-categorical sensory information [2,4,5,12]. With only a few minutes of training human listeners can detect periodicities of several seconds – some as long as 20 s [12,18]. Following the terminology of Cowan [4], this classifies human RN perception as a phenomenon of the 'long auditory store'. Thus, the study of the perception of RN leads beyond purely perceptual issues to topics in memory research. With sensory memory, where trace refresh by mental rehearsal does not play a role [6], the comparison of human and animal performance is of special interest (see e.g. ref. [3]). In a first approach to address the perception of RN in a non-human model, the present study investigates the ability of Mongolian gerbils (*Meriones unguiculatus*) to discriminate between RN and non-repeated noise (NRN; i.e. normal white noise).

In Experiment 1 we assessed the learning speed and the final performance for five groups of naive gerbils that had to discriminate RN from NRN for five different cycle lengths. A total of 21 adult Mongolian gerbils (*M. unguiculatus*) from our own breeding colony were housed in a temperature-controlled room (23 ± 1°C) under 12 h light/12 h dark cycle. Rodent food pellets, sunflower seeds and water was given ad lib.

The noise stimuli were produced by means of a Gaussian random number algorithm [9]. These numbers were then converted at 44.1 kHz and presented free field at about 60 dB sound pressure level via two speakers located above the animals head. Different noise samples were generated for each trial. The length of the stimuli was 8 s. For RN, cycle lengths of 20, 40, 60, 80, or 100 ms were used. For instance, if the cycle length was 100 ms, the algorithm was used to calculate 4410 consecutive amplitude values which were concatenated 80 times to produce 8 s of RN. The stimuli were ramped with linear on- and offset ramps of 10 ms length.

* Corresponding author. Tel.: +49-391-626-3322; fax: +49-391-626-3328.

E-mail addresses: christian@kaernbach.de (C. Kaernbach), holger.schulze@ifn-magdeburg.de (H. Schulze).

Animals were trained to discriminate RN and NRN stimuli in a footshock avoidance procedure. A shuttle-box with two compartments ($18 \times 16 \times 22$ cm) separated by a 3 cm high hurdle was used. Five groups of naive gerbils were trained to discriminate RN with periods of 20 ms ($n = 4$), 40 ms ($n = 4$), 60 ms ($n = 4$), 80 ms ($n = 4$) and 100 ms ($n = 5$) from NRN.

Animals were given a stimulation-free habituation period of 3 min before each session started. During the session, RN samples served as CS + (reinforced conditioned stimulus: reaction [crossing of hurdle] required) and NRN samples as CS − (non-reinforced CS). As soon as the animal crossed the hurdle, the stimulus stopped. If the animal did not cross the hurdle within 4 s after the onset of the CS + of a given trial, an unconditioned stimulus (mild, 150–300 μA, electrodermal stimulation) was applied via a floor grid and this application and the CS + presentation continued until the gerbil crossed the hurdle, but maximally for another 4 s. In order to control for false alarms, the same unconditioned stimulus was applied for 0.5 s upon crossing of the hurdle to CS − . Daily training sessions with 60 trials each (randomized presentations of 30 different CS + and CS − ; cf. ref. [7]) were carried out with each animal. Inter-trial intervals (start to start) were 16 ± 4 s. Training was continued until a stable discrimination performance (see below) was reached.

Numbers of hurdle crossings (conditioned responses; CR + and CR − , respectively) were counted in each session and converted to normalized CR + and CR − rates. Discrimination performance for each training session was defined as the difference between the conditioned response rates (CR + − CR −). Behavioral data were quantified separately for each individual animal by measures of how fast and how well gerbils learned to discriminate between CS + and CS − . The first session in which the CR + value was significantly different from the CR − on the 1% level (fourfold table χ^2-test) for at least two consecutive sessions served as an index of learning speed. If this criterion was fulfilled for at least three subsequent consecutive sessions the discrimination performance was considered 'stable'. The maximum discrimination performance that was reached by each individual gerbil served as the measure of how well gerbils learned to solve the task.

As a main result of this experiment it became apparent that Mongolian gerbils are able to discriminate RN from NRN. Apparently, longer periods need more training time and are less easy to discriminate. Fig. 1 shows the course of discrimination learning for five groups of naive gerbils that were trained to discriminate RN with different periods from NRN. The figure shows the discrimination performance (CR + − CR −) for each of the five groups as a function of training session. With increasing RN period the slopes of these functions become smaller, indicating slower learning of the discrimination task, and the maximum discrimination performance reached decreased.

In the inlay in Fig. 1 we plotted a measure of how well (maximum discrimination performance) against how fast
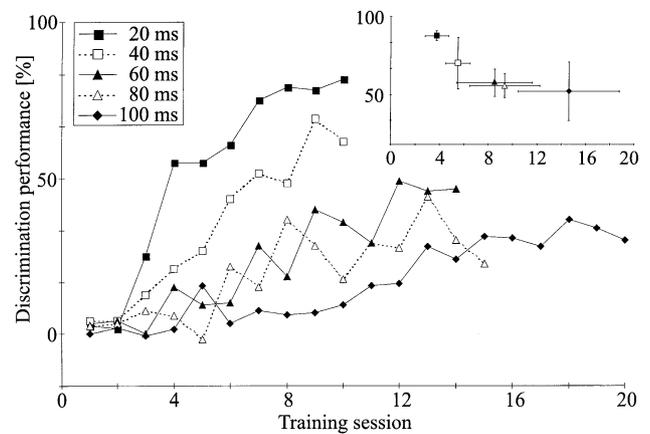
Fig. 1. Discrimination performance (CR + − CR −) for each of the five groups as a function of training session. The inlay shows the maximum discrimination performance plotted against first session with significant discrimination (= a measure of how fast gerbils learned to discriminate RN from NRN). Given are group mean values and standard deviations. The data point for RN periods of 80 ms is calculated for $n = 3$, as one animal did not reach significant RN/NRN discrimination.

(index of first session with significant discrimination) gerbils learned to discriminate between RN and NRN. Given are group mean values and standard deviations. Again, it is obvious that learning speed and discrimination performance decreased with increasing period of RN. The nullhypothesis (identical mean values) was rejected by an analysis of variance performed separately for both these parameters ($P < 0.001$ and $P < 0.01$, respectively). A post-hoc Scheffé-test revealed significant differences in learning speed between groups 20 and 100 ms RN ($P < 0.01$) and between groups 40 and 100 ms RN ($P < 0.01$) as well as a significant difference in discrimination performance between groups 20 and 100 ms RN ($P < 0.05$).

While Experiment 1 served as a proof of principle, demonstrating RN/NRN discrimination performance in naive gerbils, the training procedure was possibly not ideal for demonstrating good discrimination performance at long RN periods. Periods of 100 ms prove a difficult task for the gerbil. For longer periods, it seems advisable to start with an easy version (i.e. short periods) and then to successively increase the period.

In Experiment 2, we trained two additional animals with increasing periods. The cycle length was increased whenever the gerbil reached stable discrimination performance (same criterion as in Experiment 1). In contrast to Experiment 1, the RN sample did not change from trial to trial: only one RN sample had to be discriminated from varying NRN samples. When elongating the stimulus cycle, its beginning was left unchanged. This modified procedure allows a discrimination strategy making use of a longterm memory representation of the RN segment which should facilitate performance within sessions and possibly also across sessions. The cycle length was elongated by 20 or

40 ms, and training continued until again a stable discrimination performance was reached, but at least for 5 days. This procedure was repeated until RN/NRN discrimination ceased.

Fig. 2 shows the data for both gerbils. Triangles on the abscissa indicate in which session the RN cycle length was increased. Bars above the panels indicate for each session whether CR + differed significantly from CR − on the 1% level. Training started with a constant RN sample with 80 ms period. Deviating from the above described rule, this sample was replaced in the 16th training session by another 80-ms sample to test whether due to long-term memory interactions such a change would result in a significant drop of performance. This was not the case in neither animal. In the 21st session we switched back to the first RN sample and increased the cycle length to 100 ms. Training then continued as described above. Across consecutive sessions both animals showed considerable variability of discrimination performance sometimes yielding values below statistical significance. Nevertheless, both animals reached stable discrimination for RN samples up to 360 ms period. For cycle lengths of 400 ms performance dropped below significance for most sessions. Although animals still showed significant discrimination in some sessions, they could not restore stable discrimination performance within 31 days of further training. The mean discrimination performance over all sessions of both animals drops sharply from 54% for 360 ms (50% for 80–360 ms) to 18% for 400 ms. Whether the coincidence of this drop in

both animals at the same period length is evidence for a kind of threshold or not, remains to be seen.

The major result of the present study is that gerbils can discriminate RN with periods up to 360 ms from NRN. While for periods as short as 20 ms it is likely that the discrimination performance is based on the spectral resolvability of the first few harmonics, RN/NRN discrimination for periods as long as 100 or 360 ms can not be explained by spectral differences between RN and NRN stimuli: spectral components are no longer resolvable by the gerbil cochlea if their spacing is closer than about 25 Hz (i.e. if the period is longer than 40 ms) [14]. The discrimination performance at these period lengths clearly represents evidence for sensory memory for random waveforms, which has not been demonstrated in animals up to now.

While in Experiment 1 naive gerbils had considerable difficulty to discriminate 100 ms RN from NRN, the continual progression of cycle lengths in Experiment 2 helped the gerbils to maintain a good performance up to cycle lengths of nearly 400 ms. A second procedural difference was that in Experiment 2 the noise segment was not changed from trial to trial. It is difficult to evaluate the share of this measure in the improvement of the discrimination performance. It may, however, be speculated that it did not contribute much: While in humans sensory representations have a lifetime of several seconds [4,12,18] and could thus bridge between trials, the breakdown at about 400 ms for gerbils indicates that it is not very plausible that the memory representation could endure across trials. Moreover, a comparison of the data for Experiment 2 with those of the 80-ms group of Experiment 1 does not reveal an advantage for those animals that are trained with a single frozen noise segment.

It is remarkable that the maximum performance (360 ms) found in Experiment 2 is much less than the maximum cycle lengths observed in humans. It could be speculated that this difference is due to different processing of auditory noise. However, auditory processing seems to be highly evolved in gerbils. They are able to discriminate basic features such as amplitude modulations [17] and frequency modulations [16,19,20] as well as ecologically irrelevant higher order features such as vowels [15]. Therefore it has not necessarily to be expected that the basic processing of auditory noise is so much different as to explain their inability to detect RN with long periods. In humans, RN perception seems to involve mainly early auditory processing [13], with probably an important contribution of the primary auditory cortex [11]. It is unlikely that early auditory processing should operate qualitatively different in gerbils than in higher evolved species. It might be speculated that quantitative differences are at the origin of the different RN perception in gerbils: The gerbil cortex may be capable to handle only a smaller number of features compared to primate cortices. However, the detection of periodicity in humans is not restricted to repeated broadband noise but will also occur in reduced stimuli that provide a smaller number of features such as repeated bandpass filtered noises
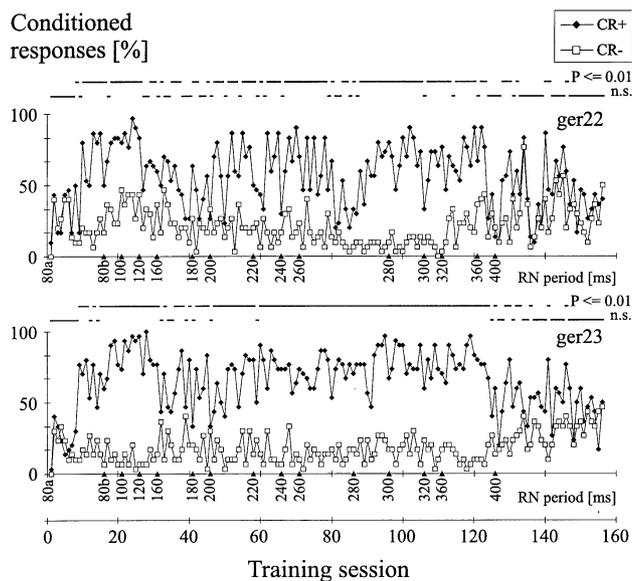
Fig. 2. Course of RN/NRN discrimination learning for two gerbils (ger22 and ger23, respectively) in a long-term training paradigm with constant RN which was successively prolonged. Bars above the panels indicate for each training session whether or not CR + differed significantly from CR − on the 1% level (fourfold table χ^2-test). Triangles on the abscissa indicate sessions RN samples have been changed. RN periods in ms are given below the triangles.

[1] or RN stimuli with only small portions of the period kept constant [10]. The reason for the difference between human and gerbil performance remains unclear.

Human RN/NRN discrimination for periods up to 20 s is attributed to *long* auditory storage, characterized by time constants around 10 s. It is remarkable that other auditory storage phenomena in humans are related to the so-called *short* auditory storage [3], with time constants around 200 ms, i.e. close to gerbil RN/NRN discrimination performance. It seems, however, futile to speculate whether the memory system that gerbil RN/NRN discrimination is based upon is more comparable to a scaled-down version of human long auditory storage, or to human short auditory storage.

Gerbils can discriminate periodic random waveforms with periods of several hundred ms from non-periodic waveforms. Therefore, they represent an interesting model that should allow the study of basic mechanisms involved in sensory memory. However, the performance of highly trained gerbils falls short of the performance of naive human listeners. In order to fully understand human sensory memory and the reasons for the limited maximum period length for gerbil RN perception it might therefore prove necessary to study other species as well that demonstrate RN/NRN discrimination at a level closer to human performance.

[1] Bashford, J.A. and Warren, R.M., Pattern recognition within spectrally isolated regions of broadband complex sound, J. Acoust. Soc. Am., 87 (1990) S24.

[2] Berti, S., Schröger, E. and Mecklinger, A., Attentive and preattentive periodicity analysis in the auditory system: an event-related potential study, NeuroReport, 11 (2000) 1883–1887.

[3] Brown, C.H. and Maloney, C.G., Temporal integration in two species of old world monkeys: blue monkeys (*Cercopithecus mitis*) and gray-cheeked mangabeys (*Cercocebus albigena*), J. Acoust. Soc. Am., 79 (1986) 1058–1064.

[4] Cowan, N., On short an long auditory stores, Psychol. Bull., 96 (1984) 341370.

[5] Cowan, N., Attention and Memory: An Integrated Framework, Oxford University Press, Oxford, 1995.

[6] Demany, L., Clément, S. and Semal, C., Does auditory memory depend on attention? In D.J. Breebaart, A.J.M. Houtsma, A. Kohlrausch, V.F. Prijs and R. Schoonhoven (Eds.), Physiological and Psychophysical Bases of Auditory Function, Shaker Publishing BV, Maastricht, 2001, pp. 461–467.

[7] Gellerman, L.W., Chance orders of alternating stimuli in visual discrimination experiments, J. Genet. Psychol., 42 (1933) 206–208.

[8] Guttman, N. and Julesz, B., Lower limits of auditory periodicity analysis, J. Acoust. Soc. Am., 35 (1963) 610.

[9] Kaernbach, C., On the consistency of tapping to repeated noise, J. Acoust. Soc. Am., 92 (1992) 788–793.

[10] Kaernbach, C., Temporal and spectral basis of the features perceived in repeated noise, J. Acoust. Soc. Am., 94 (1993) 91–97.

[11] Kaernbach, C., Early auditory feature coding, In A. Schick, M. Meis and C. Reckhardt (Eds.), Contributions to Psychological Acoustics: Results of the 8th Oldenburg Symposium on Psychological Acoustics, University of Oldenburg, Oldenburg, 2000, pp. 295–307.

[12] Kaernbach, C., Sensory memory and short-term memory, In C. Kaernbach, E. Schröger and H. Müller (Eds.), Psychophysics beyond Sensation: Laws and Invariants of Human Cognition, Erlbaum, Mahwah NJ, 2003.

[13] Kaernbach, C., Schröger, E. and Gunter, T.C., Human event-related brain potentials to auditory periodic noise stimuli, Neurosci. Lett., 242 (1998) 17–20.

[14] Kittel, M., Wagner, E. and Klump, G.M., An estimate of the auditory-filter bandwidth in the Mongolian gerbil, Hearing Res., 164 (2002) 69–76.

[15] Ohl, F.W. and Scheich, H., Orderly cortical representation of vowels based on formant interaction, Proc. Natl. Acad. Sci. USA, 94 (1997) 9440–9444.

[16] Ohl, F.W., Wetzel, W., Wagner, T., Rech, A. and Scheich, H., Bilateral ablation of auditory cortex in Mongolian gerbil affects discrimination of frequency modulated tones but not of pure tones, Learn. Mem., 6 (1999) 347–362.

[17] Schulze, H. and Scheich, H., Discrimination learning of amplitude modulated tones in Mongolian gerbils, Neurosci. Lett., 261 (1999) 13–16.

[18] Warren, R.M., Bashford, J.A., Cooley, J.M. and Brubaker, B.S., Detection of acoustic repetition for very long stochastic patterns, Percept. Psychophys., 63 (2001) 175–182.

[19] Wetzel, W., Ohl, F.W., Wagner, T. and Scheich, H., Right auditory cortex lesion in Mongolian gerbils impairs discrimination of rising and falling frequency-modulated tones, Neurosci. Lett., 252 (1998) 115–118.

[20] Wetzel, W., Wagner, T., Ohl, F.W. and Scheich, H., Categorical discrimination of direction in frequency-modulated tones by Mongolian gerbils, Behav. Brain Res., 91 (1998) 29–39.