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Cats can detect repeated noise stimuli

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Abstract

We assessed the ability of cats to detect repeated noise (RN), a stimulus generated by seamlessly presenting short segments of white noise in a continuous loop, in a modified go-nogo task. A recent study of the gerbil suggested that animals might have an extremely limited ability to detect RN compared to human subjects. We find that cats can discriminate RN from continuous noise with reasonable accuracy until the period length of the RN sequence reaches 450–500 ms. This is slightly longer than the maximum detectable RN period length found in gerbils, but falls far short of human performance.
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Sensory information is held in memory for short time periods in order to permit further processing. In the auditory system, the short-term retention of sound in memory may be critical for higher order auditory functions, including language processing.

White noise, a stimulus that contains a broad range of frequencies presented in random phase relation, would seem at first to be an unlikely tool with which to explore auditory memory. Humans perceive white noise as a featureless sound completely described by its loudness. However, when we take a short sequence of white noise and present it seamlessly in a continuous, repeated loop it is perceived quite differently [2,5,7] (see also http://www.periodic-noise.de). Humans can readily discriminate so-called repeated noise (RN) with period lengths of up to several seconds from continuous white noise [5,7,16]. This is taken as evidence for a storage system that can retain non-categorical auditory information. Consistent with this hypothesis is evidence that early cortical processing stages appear to be active during discrimination of RN [8].

Recently, the ability to detect RN has been tested in the rodent [9]. Mongolian gerbils can discriminate RN sequences of up to 360 ms. This dramatic difference between the performance of gerbils and humans is surprising. Gerbils appear to have a sophisticated auditory

system, and can discriminate basic acoustic features such as frequency modulation [12,18,19] and even complex stimuli such as vowels [11]. The poor performance of gerbils in the RN discrimination task could be taken to suggest that humans posses a specialization in their auditory system that affords them a qualitative advantage over other animals.

Here we explore this hypothesis and test the ability to discriminate RN in other animals. Studies involving a broad range of stimuli [1,3,10] including speech sounds [14] and tests of higher cortical function [13,15] suggest that the cat auditory system is in many ways comparable to our own [4]. Thus, we sought to determine whether the cat's performance in the RN task is comparable to the performance of gerbils or closer to human performance.

Data were obtained from two adult female cats. One cat (M) had previously received surgery to implant microelectrodes. This surgery was confined to primary visual cortex and would not be expected to affect auditory processing. All experiments were performed in accordance with NIH principles of laboratory animal care and the Swiss regulations of the Protection of Animals.

Stimuli are generated using methods described by Kaernbach [6]. Pseudo-random numbers with a Gaussian distribution are converted to an acoustic stimulus (so-called white noise) at a sample rate of 22 kHz. This stimulus is presented continuously (continuous noise, CN) during testing under free-field conditions at a sound level of 55

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dB SPL. At 10–15 s intervals, the CN stimulus is replaced by the RN stimulus. A single presentation of the RN stimulus lasts ≥ 1.5 s, and contains at least ten repetitions of the repeated sequence. For a given day of testing the maximum period length is reported. Three different random sequences were used in a given training session to avoid long-term memory effects. Note that due to the random nature of the white noise stimulus, there is no discernable acoustic artifact at the transition between the CN and RN stimuli. Furthermore, the comparatively low sample frequency of 22 kHz does not limit the significance of our data. In humans, the detection of periodicity is not restricted to repeated broadband noise. It will also occur if the RN is low- or high-pass filtered [5] and even in repeated band-pass filtered noises [17].

We adopted a 'go-nogo' experimental design. Cats were trained to press a lever upon presentation of the RN stimulus. On each day of testing, the cat was placed in a standard operand box measuring $80 \times 30 \times 35$ cm. Stimuli were delivered through two laterally placed speakers. A light in front of the cat was illuminated immediately following a correct response, concomitant with a food reward.

Cats took approximately 20 days to learn to perform the auditory go-nogo task. They were first adapted to the laboratory environment and trained to perform a purely visual go-nogo discrimination task using light stimuli placed on either side of the operand box. Training progressed to a cross-modal cueing paradigm, when CN was presented, interspersed at random intervals with the RN stimulus (primary discriminative stimulus), concomitant with the light stimulus (secondary discriminative stimulus). Then, the RN stimulus was presented at relatively higher volume than the CN stimulus to make it more salient. During the final few days of training, the light stimulus was removed and the volume of the RN stimulus was matched to the CN stimulus.

All of the analysis was based on the lever-press responses made during the go-nogo discrimination task. Three classes of response are possible: a Hit, where the cat presses the response bar within the allotted reaction time of the RN stimulus, a Miss, where the cat fails to press the bar within this time, and a False Alarm, corresponding to all lever presses outside this time window.

A conservative estimate of the accuracy of detection performance, P, can be obtained by $P = (H - FA)/(H + M)$ where H is the number of hits, M is the number of misses, and FA is the number of false alarms. Note that pressing the lever at random times will result in more false alarms than hits. Hence values of $P \geq 0$ indicate performance better than chance, while perfect performance will yield $P = 1$.

We estimated the maximum RN period length that the cat could discriminate and the rate at which each cat's performance progressed. When discrimination performance reached 65% on three consecutive days, the RN period length was incremented by 10% (rounded to one significant

digit). For the analysis of learning speed over short timescales, we calculated mean improvement in performance in the days following an increment in RN period length. As RN period length is fixed until performance reaches the criterion level, any day-to-day improvement in performance during this period will reflect the impact of experience and/or learning. When analyzing long-term changes in performance, we must consider the dependency between performance and RN period length, which was varied by the experimenter according to fixed accuracy criteria. Strictly speaking, RN period length is not a dependant variable but is related to task performance indirectly via the criteria governing its incrementation. We developed a method to estimate the (equivalent) RN period length corresponding to a fixed level of accuracy in the task. It was based on the assumption that accuracy would improve at a constant rate during the time between successive increments in RN period length. We then measured the change of performance (ΔP) as a function of the change in RN period length (ΔPL). The coefficient, $\Delta PL/\Delta P$, can be used to back-transform the series of accuracy measurements to obtain a series of estimates of the equivalent threshold period time (ETP): $ETP(t) = PL(t) + (P(t) - \varnothing P_{PL})^* \Delta PL/\Delta P$, where P is the performance on a given day and $\varnothing P_{PL}$ is the average performance during the time in which the actual RN period length, PL, was fixed. At an intuitive level, this formula treats RN period length as a dependent variable, and makes performance, P, the independent variable.

Testing progressed over a period of 78 days for cat C and 76 days for cat M. On average, cat C performed 58 trials per day while cat M performed 55. Average performance was 72.9% for cat C and 68.0% for cat M, with a standard deviation of approximately 13% in each case. Note that chance performance corresponds to a value of less than 0. During the course of the study the period length of the RN was successively increased. The maximum RN period length that the cats were able to discriminate was 500 ms in the case of cat C and 450 ms for cat M. A linear regression of the cat's performance revealed no significant correlation between performance and duration of training ($r^2 < 0.01$, $r^2 < 0.27$ for cats C and M, respectively, Fig. 1, lower trace). This confirms that throughout the whole testing period cats maintained a stable ability to detect RN sequences.

As a next step, we investigated how performance decays once the apparent maximal period length is exceeded. Two extremes can be envisaged, ranging from a sharp threshold-like collapse in performance to a more gradual decline, as period length is further increased. Cat C's accuracy with a RN period length of 500 ms was 78%. When the period length was increased to 520 ms performance fell sharply and several days of training did not restore it to criterion levels. Cat M failed to reach the 65% criterion level when RN period length exceeded 450 ms. Thus, it appears that performance decays relatively suddenly beyond a certain
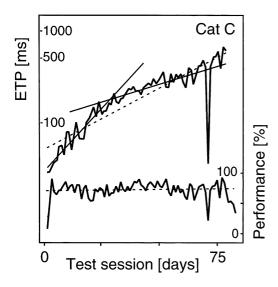
Fig. 1. (bottom, right scale) Daily accuracy values for cat C (solid line) measured over the testing period. Linear regression reveals no significant correlation between performance and the duration of training (solid straight line). (top, left scale) Estimate of the RN period length (equivalent threshold period, ETP) at which cat C could perform the task with 65% accuracy calculated for each day of training, based on the daily accuracy measures. Single linear regression (thin, dotted line) and piecewise linear fit (bold, dotted lines) are shown.

RN period length and that this value is in the region of 500 ms.

We assessed the change of performance between successive increments in RN period length. On average, an improvement in performance accuracy of 7.5% is seen during the 3–6 day period between successive increments. Another way of viewing this result is to say that a 10% increase in RN period length results in a 7.5% reduction in accuracy of performance. We calculated an ongoing estimate of the equivalent RN period length at a fixed performance (ETP). We then used this estimate to examine the rate at which each cat learned to discriminate successively longer period lengths over the entire testing period (Fig. 1, upper trace). ETP increases gradually throughout the testing phase. A single linear regression reveals an adequate fit to the data (thin, dotted line). However, it is apparent that ETP rises more steeply during the initial weeks of testing than at subsequent stages. A heavyside optimization procedure was used to explore whether the progression in the values of ETP could be divided into distinct early and late phases. The bold, discontinuous lines indicate the results of this analysis. The fits provide a surprisingly good approximation of the data, with χ^2 values of 2.10 (68 d.f.) and 3.49 (66 d.f.) for cat C and cat M, respectively. This does not rule out that it is possible to bit the data to a nonlinear function describing the whole range. Nevertheless, it shows that in the initial stages of training involving short RN period lengths, the optimal linear regression indicates a rate of learning of 6.9% and 9.7% per session for cat C and cat M, respectively. During

the later, more gradual phase of learning, the slope was estimated to be 1.9% (cat C) and 4.5% (cat M) per session. The intersection of the two linear regressions takes place at day 26 (cat C) and day 19 (cat M), corresponding to RN lengths of 150 and 50 ms, respectively. Thus, the rate estimates during the early and late phases of training differ by a factor of between 2 and 3.

Our findings suggest that cats can discriminate RN from CN with a reasonable degree of accuracy until the period length of the RN sequence reaches approximately 500 ms. The progression in the cat's discrimination performance over time appears to be divided into two distinct phases. Cats learn to discriminate period lengths of up to 50–150 ms in as little as 19 days, while their ability to discriminate RN stimuli at successively longer period lengths develops over a more prolonged time period.

The cat's ability to discriminate RN is slightly higher than the performance found in gerbils, but falls short of human performance by a large margin. Which performance could have been expected in these different species? We may take the size of the brain as a crude estimate for its processing capabilities. Clearly, the differences in body size must be taken into account, and we assume that the brain size of related species varies with the power of 2/3 of the body weight. When taking the body and brain weights of cats (3000 and 40 g, respectively) and gerbils (70 and 1.04 g, respectively; Ingo Stürmer & Holger Schulz, pers. commun.) into account, the scaled brain of a cat is on a log scale about half-way between gerbil and human scaled brain size (62000 and 1250 g, average female body and brain weight, respectively). Relating this result on a log-log scale to human performance in the RN task, a performance of cats of about 1800 ms maximal period length of RN could be expected, which is much more than the 500 ms observed. Thus, the ability of cats to discriminate RN stimuli falls short of human performance even when taking into account different brain sizes.

Furthermore, we found evidence that the cat may rely on two distinct systems to discriminate short and long duration RN sequences. When we analyzed the rate at which performance in the RN task progressed towards the final limit, we found evidence that learning progressed at two distinct rates. Up to period lengths of approximately 150 ms, learning progressed relatively quickly, but then slowed by more than a factor of two as the animal attempted to discriminate still longer period lengths. To understand this aspect better we need to discuss the way the brain stores auditory inputs. Cowan [2] reviewed a large number of studies of human auditory memory and concluded that humans have at least two types of sensory (non-categorical) auditory store. Inputs of less than about 200 ms duration appear to be held in a so-called short auditory store. Retention of inputs of longer duration is achieved using the so-called long auditory store. However, use of the long auditory store appears to require greater effort and training. The results of the study by Kaernbach and Schulze [9]

suggest that the capacity of the sensory store in the gerbil would just exceed the limits of the human short auditory store. Although the maximal detectable RN period length of cats is only slightly larger than that of gerbils, it is significantly beyond the range of 200 ms and shows different learning dynamics. This supports the view that a long auditory store for non-categorical information is not limited to the human species.

Acknowledgements

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