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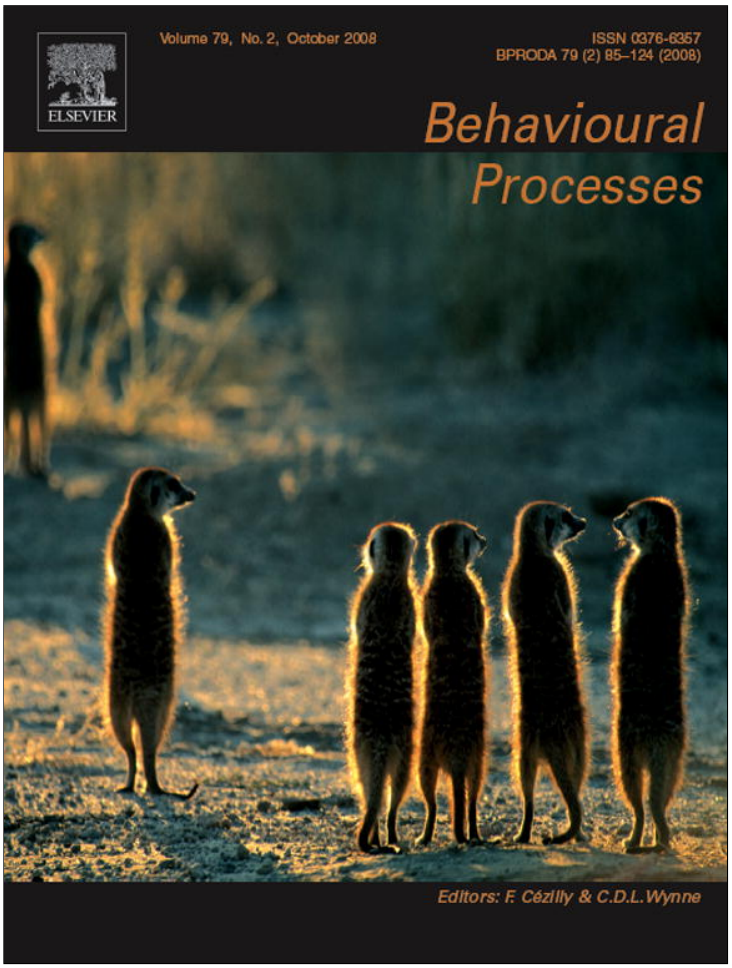

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Echoic memory in pigeons

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ABSTRACT

It is unknown whether birds are able to retain the memory of purely sensory auditory information such as white noise over an extended period of time. In a Pavlovian heart rate conditioning paradigm, four pigeons were trained to associate a mild electric shock with periodic random waveforms, and no shock with aperiodic noise. Periodic waveform detection requires echoic memory, i.e., the online retention of a waveform pattern over a limited time. Starting with 40 ms, the waveform period was increased after successful learning until no significant stimulus discrimination could be found. Significant discrimination was achieved at periods of up to 2560 ms. This is the first demonstration that echoic memory performance in birds is clearly superior to cats and gerbils, and comparable to naive human performance.

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1. Introduction

Due to the absence of any cortical organisation of the avian brain, it was traditionally assumed that birds lack complex cognitive faculties, and that their behaviour is entirely instinctive. Recently, this view has dramatically changed, since the Avian Brain Nomenclature Consortium has highlighted the homology of the avian and the mammalian pallium, paving the way for a completely new vision of the neural structure and the cognitive capacities of birds (Reiner et al., 2004). Behavioural studies make it indeed clear that birds have cognitive capacities that were thought to be the privilege of primates (Emery and Clayton, 2004).

Memory is arguably the most important human cognitive capacity. In the search for the neural mechanisms of memory, mammals are usually preferred to birds as model systems, due to their closer evolutionary relation to humans. However, the recent developments make it important to compare the behavioural and neural memory mechanisms of birds and mammals in a much more detailed way. The most sophisticated studies on avian learning and memory are conducted within the realm of the song system. Songbirds are extreme auditory and vocal specialists and share with humans the capacity for vocal learning. Birdsong learning is considered to be the closest animal equivalent to human speech acquisition and the avian vocal learning system is a highly evolutionary derived set of interconnected structures that is about as unique within the class of aves as is the human speech system for mammals (Bolhuis and Gahr, 2006). Experimental studies of short-term auditory memory persistence of tonal signals have consequently been conducted with songbird species and have revealed a remarkable capacity of these animals (Zokoll et al., 2007).

Since humans are highly specialized for language learning, their speech system can hardly be used as a model to study general principles of vocal learning in the class of mammals. Similarly, generalizations from song birds and their auditory capabilities to birds in general may not be feasible. What is needed instead are studies with avian generalists using an auditory memory paradigm for which comparable data are available with various mammalian species. Generalists are more representative for their class than individuals with highly specialized and accomplished cognitive and sensory capacities. Generalists are known for their ability to survive in many kinds of habitats and forage for a wide variety of food. Within the class of aves several well-studied generalists are known like silvereyes, goshawks, and pigeons (Scott et al., 2003; Rutz and Bijlsma, 2006).

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[1] This is the location where the experiment was carried out.

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Here, we trained pigeons in a complex auditory memory task, requiring them to discriminate between periodic and aperiodic waveforms. Periodic white noise consists of a seamless repetition of a piece of frozen white noise. If a sample of white noise of, say, 40 ms duration is repeated over and over again it can be discriminated from continuous random noise.

The capacity to discriminate periodic from aperiodic waveforms requires the ability to temporally store and integrate the waveforms' acoustic properties over time. The retention and comparison of acoustic features is therefore referred to as echoic memory (cf. Kaernbach, 2004; for review, see Cowan, 1984). The longer the periodic waveform sample, the less discernable it is from continuous random noise. Thus, at the limit, a repeated long finite sample of noise and continuous random noise will be indiscriminable. The length of a sample that is discriminable depends on the lifetime of the auditory memory of the animal tested.

Cowan (1984) proposed two types of auditory sensory memory: a short-lasting auditory trace with memory spans not exceeding several hundreds of milliseconds, and a longer retention of auditory information lasting up to several seconds. Periodic random waveforms (Guttman and Julesz, 1963) have proven to be a good probe to test the longer auditory store in humans and non-human animals (Cowan, 1984; Kaernbach, 2004) because subjects can succesfully discriminate between stimuli even when waveforms lengths exceed the lifetime of the short-lasting auditory trace. For a demonstration of the stimulus see www.periodic-noise.de.

2. Methods

2.1. Subjects

Four naïve pigeons (*Columba livia*) were trained in an echoic memory task. They were obtained from local breeders and raised in the institute's own aviary, and, during the time of training and testing, housed in a cage (40 cm × 40 cm × 40 cm) in a colony room with a 12-h dark:12-h light cycle with lights on at 8 a.m. The animals had access to food and water ad libitum in their homecage at all times. All subjects were kept and treated according to the German guidelines for the care and use of animals in neuroscience, and the European Communities Council Directive of 24 November 1986 (86/609/EEC). The research was approved by the Ethics Committee of the State of Nordrhein Westfalen, Germany.

2.2. Procedure

In contrast to the other species tested up to now in echoic memory tasks, auditory discrimination in pigeons using food rewards is often slow and arduous (see Jenkins and Harrison, 1960; Delius and Emmerton, 1978). We therefore opted to use a simple Pavlovian heart rate conditioning discrimination procedure with a mild electric shock as the unconditioned stimulus. In short, the animals learned to anticipate an electric shock (unconditioned stimulus, US) administered after exposure to periodic white noise (positive conditioned stimulus, CS+). No shock was administered after aperiodic noise (negative conditioned stimulus, CS−). We measured the animals' heart rate increase during noise presentation with electrocardiogram (ECG). A significant difference in the heart rate increase between stimulus conditions was considered indicative of successful stimulus discrimination (cf. Bräucker, 1986).

In detail, pigeons were trained in an aperiodic-noise/periodic-noise (AN/PN) discrimination task with increasing period lengths for the PN stimuli. The CS− was never associated with an electric shock, the CS+ contained a PN phase and was always associated with a shock. The stimuli were generated online with Matlab (see below for details). Both the CS− and the CS+ stimuli consisted basically of several tens of seconds of white noise. This noise was ramped on and off over 500 ms, and was followed by a silent interstimulus interval of 2 s.

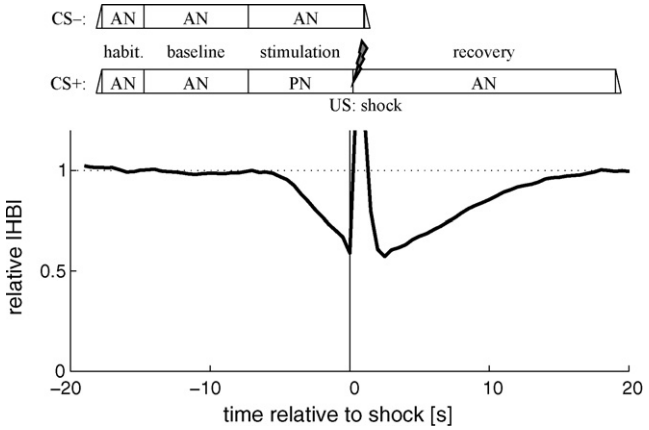

Fig. 1. Illustration of stimulus composition for CS− and CS+ (diagram on top), and exemplary time course of relative IHBI during CS+ stimulus, relative to the time of the shock (diagram on bottom). The upper graph shows a CS− trial and a CS+ trial (AN: aperiodic noise; PN: periodic noise). (Lower graph) The relative IHBI has been averaged across all 40 CS+ trials of one session for one pigeon. This example is of session 20, with a period length of 480 ms. The CS+ stimulus was periodic during the last 10 s before the shock. Average relative IHBI are calculated every 0.5 s for 1 s bins. A reduction in relative IHBI corresponds to an increase of the heart rate. Immediately following the shock no heart beats are detected due to crosstalk between the electrodes. This results in an artificial increase of the IHBI.

CS+ stimuli started with 4 s of AN in order to get the pigeon habituated to the noise. This habituation phase was followed seamlessly by another 10 s of AN of the same type serving as baseline to establish the momentary heart rate. These 14 s of homogenous AN were followed seamlessly by 10 s of PN, the stimulation phase. At the end of the stimulation phase a 50 Hz shock was delivered for 100 ms. The stimulation phase was followed seamlessly by 26 s of AN that served to get the heart rate back to normal. The total duration of the CS+ stimulus was 50 s without ramps.

CS− stimuli lasted 25 s without ramps, i.e., one second longer than CS+ stimuli up to the shock. No periodicity was embedded in CS− stimuli. Nevertheless, they were divided virtually into habituation phase, baseline phase, and stimulation phase to allow for proper statistical comparison with CS+ effects. An illustration of the composition of the stimuli can be found in Fig. 1 (upper panel).

These parameters of the CS+ and CS− stimuli were valid as long as period lengths were short. To compensate for the small number of periodic phases at long period lengths, from 640 ms on upwards the duration of both the baseline phase and the stimulation phase was set to 15 s. The total duration of the CS+ stimuli was then 60 s without ramps. The duration of the CS− stimulus was increased to 35 s.

Each session began with a succession of two CS− trials, followed by a randomised sequence of 40 CS+ trials and 40 CS− trials. With the longer stimuli for period lengths beyond 640 ms, only 30 CS+ trials and 30 CS− trials were performed in a single session. Total session duration was between 50 and 60 min.

In the first session of the experiment, the period length of the white noise in CS+ trials was 40 ms. In general, the period length did not change between sessions as long as neither of the two following criteria was reached. Once a pigeon reached the criterion of two successive sessions of successful discrimination performance (see below for the quantification of discrimination performance), the period length was increased in the upcoming session. Once a pigeon failed in two successive sessions, the period length was decreased

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in the following session in order to test whether the drop of performance was a function of period length, of habituation or of fatigue. The schedule of period lengths was 40, 60, 80, 120, 160, 240, 320, 480, 640, 960, 1280, 1920, 2560 ms.

2.3. Apparatus, electric stimulation and white noise generation

The pigeons were restrained by a loose cloth bag and placed in a shielded, sound-attenuated aluminum box (35 cm × 85 cm × 35 cm). The cloth bag restricted them from making body and wing movements, but did not cover their head or neck, so that hearing was undisturbed. Two speakers, one at each side of the box, were used to apply the acoustic stimuli. The electrodes were connected to the recording system/shock application device by a plug that was attached to the socket on the pigeons back. During training and testing, the box was closed and illuminated by a houselight. The electric shock was generated by a custom-made standard laboratory dc power supply. The dc signal was converted into a 50 Hz pulse by a Matlab routine, and was delivered for 100 ms. The US consisted of a series of electric shock pulses of 3 mA intensity in a range from 4 to 12 V. The actual shock intensity used in each session was individually adjusted for every animal so that the shock was just large enough to elevate the heart rate above baseline level, as determined in a baseline session prior to each testing session. For every animal, the current intensity was repeatedly adjusted during the course of the experiment to account for slow changes in the electrode impedance. The ECG signal was amplified and filtered online with a low-noise amplifier (npi electronics, Germany, DPA 2F amplifier), digitised at a sampling rate of 20 kHz, and then stored on computer using standard CED AD converters, and Spike2 software (Cambridge Electronic Design, UK, 1401 plus system).

White noise was generated using a uniform random generator. The amplitude of the digital samples spanned 45% of the total possible range. Periodic noise was generated by iterating the same sequence of random numbers as long as required. The period of the periodic noise was determined by iterating the appropriate number of random numbers, i.e., the duration of the period times the sampling frequency. The digital noise was converted by a sound card (Creative Technology ES1373). The sampling frequency was 44,100 Hz. The sound produced by the card deviated less then 1 db over the relevant frequency range (10 Hz to 22.05 kHz). This noise was then presented with commercially available loudspeakers (Juster AirWave 221). Sound volume was kept at 70 dB SPL.

2.4. Surgery and electrocardiogram recordings

For surgery, pigeons were anaesthetized with a mixture of ketamine (Ketavet, Pharmacia & Upjohn, Germany; 35–45 mg/kg, i.m.) and xylazine (Rompun, Bayer, Germany; 5–15 mg/kg, i.m.). Four silver plated copper-electrodes (Ø 0.4 mm) were implanted for ECG recording and shock application. Two electrodes were bilaterally positioned under the pigeons scapula bones, the other two electrodes were bilaterally positioned under the pubic spines. For each electrode, the protruding ends were soldered together, insulated with shrinkable tubing, and connected and fixed with dental acrylic to a socket that was loosely attached to the pigeons back. This configuration allowed the pigeon to move freely and undisturbed without damaging the electrodes and socket-connections. The ECG-difference signal was measured between the left scapula and the left pubis electrode, the electric shock was applied via the right pubis electrode, and the right scapula electrode served as common ground for both ECG recording and shock application. Pigeons were allowed to fully recover from surgery before training and testing.

2.5. Data analysis

ECG data were pre-processed using the peak-detection routines in the Spike2 software package (Cambridge Electronic Design, UK). Every heartbeat produced two positive, and two negative peaks in the filtered ECG signal. Generally, the first positive peak was used as the event-time marker. In a few cases, the first peak was too weak to be consistently detected by the routine. In these cases, the second positive peak was used as the event marker. Within a given session, either the first or the second peak was consistently used for event-time marking, but never both peaks. Heartbeat times, stimulus on- and offsets, and electric shock on- and offsets were then exported and further processed by Matlab routines.

We computed the relative inter-heart-beat interval (IHBI) as a measure of heart rate. For the calculations of the IHBIs, each single IHBI of a certain trial was divided by the mean IHBI during the baseline phase of the same trial. Fig. 1 (bottom panel) shows a typical time course of the relative IHBI in case of a CS+ stimulus. The IHBI was reduced during the last 5 s before the shock, and for about 15 s after the shock. This reduction in IHBI corresponded to an accelerated heart rate, in anticipation of and in reaction to the shock. The increase of the IHBI shortly after the shock was artificial and due to the de-calibration of the recording system as a result of the high electric input.

A significant reduction in the IHBI during the presentation of the PN in CS+ trials relative to the IHBI in CS− trials was considered a successful discrimination between CS+ and CS− trials. To test for significant differences, the average across all CS+ stimuli of the relative IHBI in the final second of the PN stimulation phase of a given session was compared to the corresponding average across all CS− stimuli of the same session. If the difference was larger than 1.96 times the expected standard deviation of this difference (calculated on the basis of the variances of the relative IHBI for CS+ and CS− stimuli during this session), this session's performance was deemed to demonstrate significant discrimination. Note that this criterion corresponds to a two-sided 95% confidence interval. Thus, we would expect a 5% error rate, scoring significant differences when no real difference exists 5% of the time (i.e., 5% in both directions, 2.5% in the expected direction).

Moreover, we also tested for significant differences on the group level. The relative IHBIs of all pigeons were sampled in steps of 500 ms after CS onset. We then computed an analysis of variance (ANOVA) for repeated measures for each period length condition, with the within-subject factors 'stimulus-type' and 'time after CS onset'. Because pigeons need to sample several waveform repetitions to be able to discriminate between CS+ and CS−, we expected that they would not discriminate between stimuli right after CS-onset, but only after some time has elapsed. Hence, we hypothesised a significant interaction between time and stimulus-type.

3. Results

All pigeons showed an anticipatory increase in heart rate during periodic, but not aperiodic noise, and thus significantly discriminated between CS+ and CS− stimuli. Fig. 2 shows a comparison of IHBI of CS+ with CS− trials in an exemplar session. The graph displays the IHBI relative to baseline during the stimulation phase, averaged across all trials (30 CS+ trials and 30 CS− trials per animal) and animals ($N = 4$, mean and standard error of the mean) in a session with period length of 960 ms. The figure clearly shows a decrease in IHBI across the CS+ stimulation (black line) interval with respect to CS− stimulation (grey line), suggesting a significant

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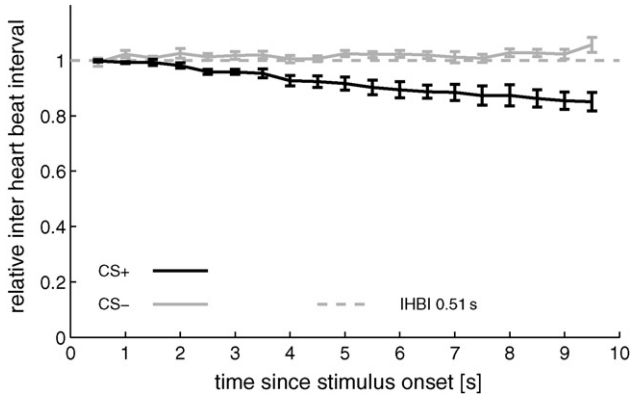

Fig. 2. Example of successful noise discrimination. The figure shows the IHBIs relative to baseline (dashed horizontal line, corresponding to an IHBI of 0.51 s) during the stimulation interval for CS+ and CS− trials. Data are taken from one exemplar session with stimuli of 960 ms period length, and are averaged across all trials (30 CS+ trials and 30 CS− trials per animal) and animals ($N = 4$, mean and S.E.M.).

increase in heart rate, and hence successful discrimination between periodic and aperiodic noise.

Table 1 lists the number of sessions with and without significant AN/PN discrimination per pigeon as a function of period length. With pigeon 1, the period length was in some cases increased even when only one session had demonstrated significant discrimination performance. While it reached a maximum period of 1920 ms with significant performance once, it did not show significant performance again until back to 640 ms. A possible reason for this fall-back might have been an instability of the electrodes of this animal at the end of the experiment. Pigeon 2 and 3 showed significant discrimination performance in several sessions with a 1280 ms period, and pigeon 2 once with a 1920 ms period. Pigeon 4 demonstrated significant discrimination performance with a very small effect size in two sessions with 2560 ms periods.

The ANOVA revealed a significant interaction effect between time after CS onset and relative IHBI in all period length conditions (all $F > 5.8$, all $p < 0.001$), suggesting that pigeons significantly discriminated between CS+ and CS− in all conditions (note that, due to our strict inclusion criterion, not all pigeons performed all period length conditions). Table 2 lists the statistical parameters for all period lengths, and it also contains the first occurrence when the IBHI significantly differed between CS+ and CS− trials. Because a given number of waveform repetitions takes longer with long than short period lengths, pigeons needed progressively more time with increasing period lengths to discriminate between stimuli.

4. Discussion

Pigeons performed amazingly well in an AN/PN discrimination task that required echoic memory. This is particularly remarkable in light of the performance of other species. Humans are vocal learners and can discriminate between periodic noise (PN) and aperiodic noise (AN) up to period lengths of 10 or 20 s (Warren et al., 2001; Kaernbach, 2004). Non-vocal learning mammals are able to learn an echoic memory task but their ability for periodic noise detection has up to now not been demonstrated for periods longer than 500 ms. Naive Mongolian gerbils showed difficulties discriminating 100 ms PN from AN, and highly trained animals (156 days, 9360 trials) showed significant performance up to 360 ms, but could not proceed to 400 ms (Kaernbach and Schulze, 2002). Cats showed a slightly better performance: Within 75 days (4240 trials) they learned to discriminate PN with periods of 450–500 ms from AN (Frey et al., 2003). While the performance of these two species clearly demonstrates the ability of animals to retain sensory information for a fraction of a second, they fall short of human performance. The pigeons tested in the present experiment were the first species besides humans where retention of auditory sensory memory beyond one second has been demonstrated. Considering the difficulties in mimicing human discrimination performance in animal experiments, it could be said that the performance of pigeons comes almost close to that of humans. Hence, we have developed a behavioural paradigm and animal model for testing auditory memory that we believe to be superior to previously used tasks and animal models.

Our study did not only differ from previous ones with respect to the animal model but also with respect to the reinforcer in use. While previous experiments have used appetitive paradigms, we conducted a shock-conditioning procedure. This was motivated by studies which made it likely that pigeons have learning constraints to associate tones with appetitive rewards (Jenkins and Harrison, 1960; Delius and Emmerton, 1978). It is therefore in principle possible that our pigeons were considerably more successful than cats due to the higher level of motivation created by the shock-association paradigm. Although it is impossible to rule out this explanation, we have reasons to believe that this is not likely: learning phenomena tested with various reinforcers including shock often display similar qualitative results, although acquisition speed can differ (Weiss, 1976; Cohn and Weiss, 2007). In some cases, high-value aversive stimuli like electric shocks even delay learning performance because stress probably interferes with contingency acquisition (Zhao et al., 2004). Thus, we cannot discard the possibility that our decision to use a shock-association experiment increased learning speed, but believe it less likely that the final performance baseline was increased to a significant extent by the procedure in use.

Table 1
Number of sessions with and without significant discrimination performance as a function of period length for the four pigeons

Pigeon	Period length (ms)							
	40	60	80–480	640	960	1280	1920	2560
1	3/2	3/0	2/0	3/1	1/3	1/3	1/3	0/0
2	3/2	3/0	2/0	2/0	2/0	3/1	1/3	0/0
3	2/3	2/1	2/0	2/0	2/0	4/3	0/3	0/0
4	1/4	3/0	2/0	2/0	2/0	4/0	4/1	2/1

Table 2
Reapeted measures ANOVA for differences in relative IHBI between CS+ and CS− trials for each period length (only interaction effects between stimulus condition and time after CS onset are shown)

Period length	ANOVA	First significant difference between CS+ and CS− (s) ($p < 0.05$)
40	$F(18,342) = 11.66$, $p < 0.001$	2.5
60	$F(18,198) = 28.43$, $p < 0.001$	2.5
80	$F(18,126) = 15.91$, $p < 0.001$	2.5
120	$F(18,126) = 34.89$, $p < 0.001$	3.0
160	$F(18,126) = 36.07$, $p < 0.001$	3.5
240	$F(18,126) = 70.92$, $p < 0.001$	3.0
320	$F(18,126) = 39.58$, $p < 0.001$	4.0
480	$F(18,126) = 40.61$, $p < 0.001$	4.5
640	$F(18,162) = 21.33$, $p < 0.001$	6.0
960	$F(18,162) = 6.34$, $p < 0.001$	7.0
1280	$F(18,324) = 5.84$, $p < 0.001$	6.5
1920	$F(18,420) = 10.3$, $p < 0.001$	8.5
2560	$F(18,36) = 7.74$, $p < 0.001$	5.5[a]

The table shows that the pigeons significantly discriminated between CS+ and CS− trials in all conditions. The third column gives the timepoint of the first occurrence of a significant difference in IHBI (resolution 500 ms). Pigeons discriminated between stimuli progressively later with increasing period lengths.

[a] Not consistenly significant afterwards.

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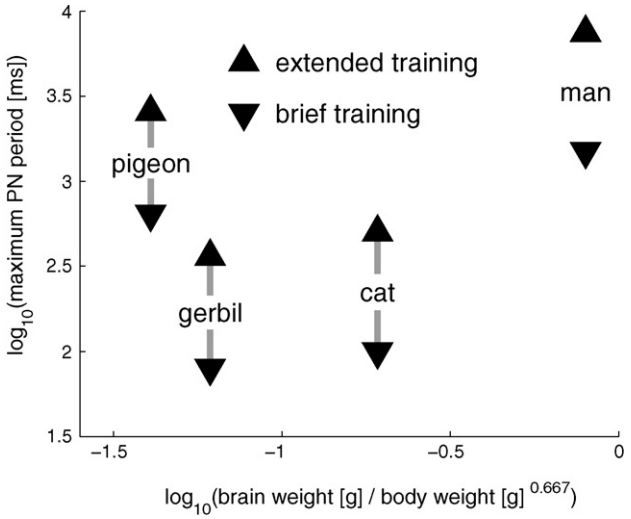

Fig. 3. Allometric comparison of maximum PN period as a function of relative brain size. Relative brain size was calculated by dividing the brain weight by the body weight to the power of 2 over 3. This exponent corresponds to the regression coefficient of brain weight and body weight if plotting these parameter for hundreds of species in a log–log plot.

Fig. 3 shows an allometric comparison of sensory retention as a function of relative brain weight. From this comparison it becomes obvious that the lifetime of sensory information in the long auditory store is not a function of relative brain weight. Instead, long sensory retention seems to depend on an algorithm that is present in humans and pigeons but is less developed in gerbils and cats.

What are the neural algorithms underlying echoic memory? Presently, we can only speculate what these mechanisms might be. In order to detect waveform repetition, the animals must be able to temporarily store at least some sequences of frequencies for the duration of a waveform length, and then compare the currently perceived sequence with the memorised one. The nidopallium caudolaterale (NCL), the avian prefrontal cortex (Mogensen and Divac, 1982, 1993; Durstewitz et al., 1998; Güntürkün, 2005) is a likely candidate to perform this operation: Single NCL neurons have been repeatedly shown to play a role in the temporary retention and manipulation of sensory information (Kalt et al., 1999; Diekamp et al., 2002b; Kalenscher et al., 2005a,b), and pharmacological interventions with NCL functioning and lesions of NCL impair an animals' ability to maintain and work with stored sensory information (Diekamp et al., 2000, 2002a; Lissek et al., 2003; Lissek and Güntürkün, 2003, 2004, 2005). In order to detect waveform repetition, the animal must be able to compare waveforms of only a few milliseconds duration. Because the NCL is known to perform similar operations, it is a straightforward guess to hypothesise its involvement in the present task. But it is equally possible that the computations are processed at subforebrain level (Wagner et al., 2005). The final behavioural output could then result from the interaction of brainstem auditory structures and the NCL.

As a concluding note, advances at various fronts of neuroscience have recently accumulated to a paradigm shift in our understanding of vertebrate brain evolution (Reiner et al., 2004; Jarvis et al., 2005). New evidence not only show that birds have a large pallium with comparable 'cortical' organizational features (Reiner et al., 2004), but also account for the fact that the avian forebrain developed more recently than the mammalian cortex (Jarvis et al., 2005). Our evidence that echoic memory in pigeons surpasses that of some mammals with higher brain weight underlines the notion of this paradigm shift and opens the door to future electrophysiological studies on echoic memory, aimed at identifying the neural structures and mechanisms involved in this type of auditory memory.

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References

Bolhuis, J.J., Gahr, M., 2006. Neural mechanisms of birdsong memory. Nat. Rev. Neurosci. 7, 347–357.
Bräucker, R., 1986. Die Herzfrequenzkonditionierung als Methode zur Messung psychophysischer Wahrnehmungs- und Unterscheidungsschwellen an Vögeln. Heart-rate Conditioning as a Method to Measure Psychophysical Perceptual and Sensory Discrimination Thresholds in Birds. Doctoral Thesis at the Ruhr-Universität Bochum. Bochum.
Cohn, S.I., Weiss, S.J., 2007. Stimulus control and compounding with ambient odor as a discriminative stimulus on a free-operant baseline. J. Exp. Anal. Behav. 87, 261–273.
Cowan, N., 1984. On short and long auditory stores. Psychol. Bull. 96, 341–370.
Delius, J.D., Emmerton, J., 1978. Stimulus-dependent asymmetry in classical and instrumental discrimination learning by pigeons. Psychol. Rec. 28, 425–434.
Diekamp, B., Kalt, T., Ruhm, A., Koch, M., Güntürkün, O., 2000. Impairment in a discrimination reversal task after D1-receptor blockade in the pigeon "prefrontal cortex". Behav. Neurosci. 114, 1145–1155.
Diekamp, B., Gagliardo, A., Güntürkün, O., 2002a. Nonspatial and subdivision-specific working memory deficits after selective lesions of the avian prefrontal cortex. J. Neurosci. 22, 9573–9580.
Diekamp, B., Kalt, T., Güntürkün, O., 2002b. Working memory neurons in pigeons. J. Neurosci. 22, RC210.
Durstewitz, D., Kröner, S., Hemmings Jr., H.C., Güntürkün, O., 1998. The dopaminergic innervation of the pigeon telencephalon: distribution of DARPP-32 and coocurrence with glutamate decarboxylase and tyrosine hydroxylase. Neuroscience 83, 763–779.
Emery, N.J., Clayton, N.S., 2004. The mentality of crows: convergent evolution of intelligence in corvids and crows. Science 306, 1903–1907.
Frey, H.P., Kaernbach, C., König, P., 2003. Cats can detect repeated noise stimuli. Neurosci. Lett. 346, 45–48.
Güntürkün, O., 2005. The avian 'prefrontal cortex' and cognition. Curr. Opin. Neurobiol. 15, 686–693.
Guttman, N., Julesz, B., 1963. Lower limits of auditory periodicity analysis. J. Acoust. Soc. Am. 35, 610.
Jarvis, E.D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., Paxinos, G., Perkel, D.J., Shimizu, T., Striedter, G., Wild, J.M., Ball, G.F., Dugas-Ford, J., Durand, S.E., Hough, G.E., Husband, S., Kubikova, L., Lee, D.W., Mello, C.V., Powers, A., Siang, C., Smulders, T.V., Wada, K., White, S.A., Yamamoto, K., Yu, J., Reiner, A., Butler, A.B., 2005. Avian brains and a new understanding of vertebrate brain evolution. Nat. Rev. Neurosci. 6, 151–159.
Jenkins, H.M., Harrison, R.H., 1960. Effect of discrimination training on auditory generalization. J. Exp. Psychol. 59, 246–253.
Kaernbach, C., 2004. The memory of noise. Exp. Psychol. 51, 240–248.
Kaernbach, C., Schulze, H., 2002. Auditory sensory memory for random waveforms in the Mongolian gerbil. Neurosci. Lett. 329, 37–40.
Kalenscher, T., Güntürkün, O., Calabrese, P., Gehlen, W., Kalt, T., Diekamp, B., 2005a. Neural correlates of a default response in a delayed Go/No-Go task. J. Exp. Anal. Behav. 84, 521–535.
Kalenscher, T., Windmann, S., Diekamp, B., Rose, J., Güntürkün, O., Colombo, M., 2005b. Single units in the pigeon brain integrate reward amount and time-to-reward in an impulsive choice task. Curr. Biol. 15, 594–602.
Kalt, T., Diekamp, B., Güntürkün, O., 1999. Single unit activity during a Go/NoGo task in the "prefrontal cortex" of pigeons. Brain Res. 839, 263–278.
Lissek, S., Güntürkün, O., 2003. Dissociation of extinction and behavioral disinhibition: the role of NMDA receptors in the pigeon associative forebrain during extinction. J. Neurosci. 23, 8119–8124.
Lissek, S., Güntürkün, O., 2004. Maintenance in working memory or response selection? Functions of NMDA receptors in the pigeon "prefrontal cortex". Behav. Brain Res. 153, 497–506.
Lissek, S., Güntürkün, O., 2005. Out of context: NMDA receptor antagonism in the avian 'prefrontal cortex' impairs context processing in a conditional discrimination task. Behav. Neurosci. 119, 797–805.
Lissek, S., Diekamp, B., Güntürkün, O., 2003. Impaired learning of a color reversal task after NMDA receptor blockade in the pigeon (*Columba livia*) associative forebrain (neostriatum caudolaterale). Behav. Neurosci. 116, 523–529.
Mogensen, J., Divac, I., 1982. The prefrontal 'cortex' in the pigeon. Behavioral evidence. Brain Behav. Evol. 21, 60–66.
Mogensen, J., Divac, I., 1993. Behavioural effects of ablation of the pigeon-equivalent of the mammalian prefrontal cortex. Behav. Brain Res. 55, 101–107.

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Reiner, A., Perkel, D.J., Bruce, L., Butler, A., Csillag, A., Kuenzel, W., Medina, L., Paxinos, G., Shimizu, T., Striedter, G., Wild, M., Ball, G.F., Durand, S., Güntürkün, O., Lee, D.W., Mello, C.V., Powers, A., White, S.A., Hough, G., Kubikova, L., Smulders, T.V., Wada, K., Dugas-Ford, J., Husband, S., Yamamoto, K., Yu, J., Siang, C., Jarvis, E.D., 2004. Revised nomenclature for avian telencephalon and some related brainstem nuclei. J. Comp. Neurol. 473, 377–414.

Rutz, C., Bijlsma, R.E., 2006. Food-limitation in a generalist predator. Proc. R. Soc. Lond. B 273, 2069–2076.

Scott, S.N., Clegg, S.M., Blomberg, S.P., Kikkawa, J., Owens, I.P.F., 2003. Morphological shifts in island-dwelling birds: the roles of generalist foraging and niche expansion. Evolution 57, 2147–2156.

Wagner, H., Brill, S., Kempter, R., Carr, C.E., 2005. Microsecond precision of phase delay in the auditory system of the barn owl. J. Neurophysiol. 94, 1655–1658.

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

Weiss, S.J., 1976. Stimulus control of free operant avoidance: the contribution of response rate and incentive relations between multiple schedule components. Learn. Motiv. 7, 477–516.

Zhao, H., Bucci, D.J., Weltzin, M., Drew, K.L., 2004. Effects of aversive stimuli on learning and memory in Arctic ground squirrels. Behav. Brain Res. 151, 219–224.

Zokoll, M.A., Klump, G.M., Langemann, U., 2007. Auditory short-term memory persistence for tonal signals in a songbird. J. Acoust. Soc. Am. 121, 2842–2851.