BRAIN RESEARCH 1220 (2008) 33–46

available at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

ELSEVIER

BRAIN RESEARCH

Research Report

Auditory memory: A comparison between humans and starlings

Melanie A. Zokoll[a], *Nicole Naue*[b], *Christoph S. Herrmann*[b], *Ulrike Langemann*[a,*]

[a] *Zoophysiology and Behaviour Group, Institute for Biology and Environmental Science, Carl von Ossietzky University Oldenburg, Germany*
[b] *Biological Psychology, Institute of Psychology, Otto-von-Guericke-University Magdeburg, Germany*

ARTICLE INFO

Article history:
Accepted 7 January 2008
Available online 30 January 2008

Keywords:
Sturnus vulgaris
Delayed non-matching-to-sample
DNMTS
Sensory memory
Auditory short-term memory

ABSTRACT

In this study, we compare the processing of acoustic signals in European starlings (*Sturnus vulgaris*) and in human listeners by observing the decay of short-term auditory memory in delayed non-matching-to-sample experiments. A series of identical "sample" stimuli and a final "test" stimulus were separated by variable delays (1 to 180.1 s). Subjects had to classify sample and test stimuli as being either the same or different. Test stimuli were pure tones that differed in a single signal feature, i.e., frequency, and song motifs that differed in multiple signal characteristics. We have tested several predictions concerning the memory performance of starlings and humans and we obtained the following outcome: (1) In contrast to our expectation, signal complexity had no effect. The overall analysis of the starling data did not show differences in memory performance for signals differing in single or multiple signal features. (2) Starling and human data supported the hypothesis that auditory memory impairs with increasing delay. This was also seen when interfering noise was added to the delay periods in an additional series with human subjects. (3) The starling data showed that the repetition of sample stimuli improved memory performance, compared to only a single presentation. Human memory performance, however, was similar for a single and for the repeated presentation of signals. (4) Differences in salience between sample and test stimuli were positively related to memory performance only for tonal stimuli but not for song motifs. Results are discussed with respect to a model based on signal detection theory and to requirements for the analysis of natural communication signals.

1. Introduction

The structure of vocal signals in songbirds has striking parallels to that of human speech, and both song and speech are acquired by vocal learning (e.g., Doupe and Kuhl, 1999). Like speech, birdsong consists of a sequence of sounds. The smallest unit of song is termed an element that may be analogous to the phoneme, the smallest unit of speech (Doupe and Kuhl, 1999). Song elements form syllables (units of sound separated by silent intervals) which in turn form song types or "motifs" (e.g., Adret-Hausberger and Jenkins 1988; Eens et al., 1989, 1991b; Gentner and Hulse, 2000). The timing and succession of syllables and motifs follow species-specific rules (song syntax; Doupe and Kuhl, 1999). The evaluation of complex sequences of communication signals demands storing signal elements or signal characteristics in the auditory memory. In this study, we investigate whether the starling (*Sturnus vulgaris*) is a suitable animal model for the perception and processing of acoustic signals in humans. We test whether humans and songbirds have comparable memory performance and memory persistence times when tested under similar experimental conditions.

---

* *Corresponding author*. Carl von Ossietzky Universität Oldenburg, IBU, Fak. 5, AG Zoophysiologie and Verhalten, Postfach 2503, 26111Oldenburg, Germany. Fax: +49 441 7985615.
E-mail address: Ulrike.Langemann@uni-oldenburg.de (U. Langemann).

0006-8993/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.brainres.2008.01.049

A signal feature for which both species are most sensitive in detecting a change is the frequency. The just noticeable difference for frequency is better than for other signal characteristics like duration or rate of amplitude modulation (e.g., Fay, 1988). We employed pure tones as physically simple signals that provide frequency information and that only differed in a single signal characteristics (i.e., a change in frequency). To probe the effect of signal complexity on auditory memory, we decided to employ starling song motifs that exhibit differences in multiple signal characteristics (e.g., peak frequency, amplitude and frequency modulations). The song motifs presented to the subjects were chosen to have salient differences in peak frequencies. Multiple signal characteristics would provide more acoustical cues than a single signal feature. Thus we tested the hypothesis that memory performance for complex signals is superior to performance for simple signals in all experimental conditions (signal complexity hypothesis).

Similar to two previous studies (Zokoll et al., 2007, in press) memory performance was evaluated in a delayed non-matching-to-sample (DNMTS) paradigm. The subjects' task was to compare sample and test stimuli separated by delays of various duration and to decide whether sample and test were matching or non-matching. Our hypothesis was that auditory memory should fade significantly with increasing delay (delay hypothesis). Auditory memory persistence times were estimated on the basis of forgetting functions, i.e., functions that describe the decay in report accuracy as a function of increasing delays (e.g., Cowan, 1984, 1997; White, 2001). Since, at least in starlings, song motifs are repeated during song bouts, we tested the hypothesis that the repetition of sample stimuli improves memory performance, compared to only a single presentation (sample repetition hypothesis). Finally we tested the hypothesis that differences in salience between sample and test stimuli are positively related to memory performance (salience hypothesis).

2. Results

In order to test whether the starling is a suitable model for the processing of acoustic signals in humans, we are comparing starling and human auditory memory for spectral characteristics of song motifs and tonal signals. Subjects were presented with 1, 3, or 5 identical sample stimuli and a final test stimulus within each experimental trial. In half of the trials, the test stimulus was matching the sample stimulus. In the other half of the trials, test and sample stimuli were non-matching. To assess auditory memory, we varied the delay between the last sample stimulus and the test stimulus, the number of sample stimulus presentations within a trial and the differences in salience between non-matching sample and test stimuli. Differences in salience between sample and test stimuli were assessed either by the size of the difference in frequency of pure tones or by the size of the difference in peak frequency between song motifs. Human listeners received an additional series with starling song motifs where the delay between sample and test stimuli was filled with interfering noise.

In the following, we present the data obtained in both experimental series with starlings and with humans in separate sections and we evaluate the results according to the hypotheses given in the introduction. Note that the data were analysed in two different ways. In most cases the data were transformed to the sensitivity measure d' (see Green and Swets, 1966, for signal detection theory) that was calculated based on responses from both matching and non-matching trials (see Eq. (4) in Experimental procedures). Whenever the difference in salience between sample and test stimuli is involved in an analysis, we report the hit rates because differences in salience were evaluated from non-matching trials only.

2.1. *Starlings*

We first tested the signal complexity hypothesis, i.e, we investigated whether memory performance for complex signals was superior to performance for simple signals in all experimental conditions. A general linear mixed model (GLMM) analysis of variance (ANOVA) was applied to evaluate the overall effect of the different experimental factors on the starlings' hit rate. Factor was the experimental series (song motifs, tones). The delay (1.0, 1.6, 2.6, 4.1, 6.6, 10.5, 16.8, and 26.8 s), the number of sample presentations within trials (1, 3, and 5), and differences in salience between sample and test stimuli were included as covariates. Differences in salience were related either to peak frequency (song motifs) or to carrier frequency (tonal stimuli) and were expressed as the number of steps (1 to 5) in Weber fraction. For song motifs one, two, three, four, and five steps corresponded to an average peak frequency ratio of 1.24, 1.57, 1.98, 2.40, and 2.88, respectively. For tonal signals one, two, three, four, and five steps corresponded to a frequency ratio of 1.26, 1.59, 2.00, 2.52, and 3.17, respectively. Bird identity was the random variable. The GLMM analysis revealed a significant decrease in the hit rate with increasing delay [$F(1,987)=6.968$, $p<0.05$], with decreasing number of sample presentations [$F(1,987)=6.075$, $p<0.05$] and with decreasing difference in salience [$F(1,987)=5.896$, $p<0.05$]. There was, however, no significant effect for the different experimental series [$F(1,988)=3.540$, n.s.], hence the overall analysis of the starling data did not support the signal complexity hypothesis. We additionally found a significant interaction between the differences in salience and the experimental series [$F(1,987)=5.822$, $p<0.05$]. The salience x series interaction may be mainly explained by the fact that for the different steps in Weber fraction, the hit rate of the starlings changed more for tonal signals (i.e., from 75 to 93% hit rate) than for motifs (data varied between 87 and 92% hit rate).

2.1.1. *Effect of delay*

We performed one way repeated measures (RM) ANOVAs to test the hypothesis that auditory memory performance would decrease with increasing delay. For song motif stimuli (1440 trials per bird) as well as for tonal stimuli (480 trials per bird) there was a significant effect of delay on performance expressed as d' [$F_{\text{motifs}}(7,32)=12.151$, $p<0.001$, $F_{\text{tones}}(7,24)=15.400$, $p<0.001$], supporting the delay hypothesis. For song motifs, d' values for delays longer than 4.1 s were significantly worse than d' values for the shortest delays of 1.0 and 1.6 s (Tukey tests, all $p<0.05$). The d' values generally decreased with increasing delay from d' values of about 2.5 to d' values just below 1.0 (Fig. 1). For tonal signals, d' was significantly different for the two longest delays (16.8 and 26.8 s) compared to all other delays (1.0 to 10.5 s; Tukey tests, all $p<0.05$, with one exception of 6.6 vs. 16.8 s, $p=0.074$). The d' values decreased with increasing delay from about 2.5 to