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Research paper

A behavioral audiogram of the red fox (*Vulpes vulpes*)

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ABSTRACT

We determined the absolute hearing sensitivity of the red fox (*Vulpes vulpes*) using an adapted standard psychoacoustic procedure. The animals were tested in a reward-based go/no-go procedure in a semi-anechoic chamber. At 60 dB sound pressure level (SPL) (re 20 μPa) red foxes perceive pure tones between 51 Hz and 48 kHz, spanning 9.84 octaves with a single peak sensitivity of −15 dB at 4 kHz. The red foxes' high-frequency cutoff is comparable to that of the domestic dog while the low-frequency cutoff is comparable to that of the domestic cat and the absolute sensitivity is between both species. The maximal absolute sensitivity of the red fox is among the best found to date in any mammal. The procedure used here allows for assessment of animal auditory thresholds using positive reinforcement outside the laboratory.

1. Introduction

The red fox (*Vulpes vulpes*) has the most widespread natural distribution of all carnivores, ranging across Europe and Asia to North America, parts of North Africa and including an introduced population in Australia (Larivière and Pasitschniak-Arts, 1996). Despite of its high abundance (involving also the ever-increasing reports of urban foxes), its popularity and proverbial keen senses, little is known about its sensory biology. As a crepuscular and nocturnal hunter, the red fox is reported to rely predominantly on its sense of hearing (Österholm, 1964). Voles constitute a large proportion of the red fox diet (Hockman and Chapman, 1983), which foxes often attack from a distance by taking a large leap, the so called mousing jump, through which they pin the unsuspecting prey to the ground (Nowak, 1999). Because the prey is often hidden in dense grass, below leaves or snow, preventing the use of visual cues to guide prey capture, the fox apparently locates prey based on acoustical cues. This is indicated by the stereotypic approach behavior before a mousing jump during which the fox cocks its ears and carefully positions and repositions the head to facilitate sound localization (Červený et al., 2011). The sound localization ability of red foxes is highly accurate (resolution down to approximately 4°) and frequency dependent (Isley and Gysel, 1975; Österholm, 1964). Isley and Gysel (1975) concluded that the latter results from a switch between reliance on phase differences at low frequencies and intensity differences at high frequencies. On the other hand the authors acknowledged that, since no audiogram was available to them, the observed differences in the localization of pure tones of different frequencies could simply be a consequence of the auditory sensitivity.

Only one study to date has investigated the hearing sensitivity of the red fox. Peterson et al. (1969) used cochlear microphonic potentials to estimate the auditory sensitivity in twelve species of fissiped carnivores. They concluded that the red fox belongs to a group of carnivores with an inefficient mode of sound reception, but also admitted that cochlear microphonics might not be sufficiently accurate to allow valid interspecific comparisons.

Psychoacoustics is the only means to comprehensively assess the properties of animal auditory perception by taking into account the various stages of signal processing from the primary receptors to the higher order cognitive centers (Long, 1994). A fundamental property of a sensory system is the minimum energy level needed to detect a stimulus. For the auditory system this translates into the audiogram, a characterization of the distribution of perceived auditory frequencies and the minimum detection intensities at each frequency. In contrast to studies on humans, establishing an accurate behavioral audiogram in animals is time consuming.

Abbreviations: IR, infrared; LED, light-emitting diode; SPL, sound pressure level

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Within the framework of operant conditioning, animals must be trained to report the presence or absence of the stimulus in order to receive a reward or to avoid an electric shock (Heffner and Heffner, 1995). The chosen method mainly depends on the species to be investigated (Fay, 1992). Standardization of methodologies and techniques have over the years yielded comparable results providing a reliable and comprehensive database of vertebrate audiograms (confer Fay, 1988). However, despite the relatively long history of animal psychoacoustics, still only 1.2% of all mammalian species have been adequately tested for auditory sensitivity (Heffner et al., 2014).

Here, we present the audiogram of the red fox, *Vulpes vulpes*, obtained through a reward-based psychoacoustic procedure with a go/no-go task. In contrast to many other studies requiring the capture and transport of subjects to laboratory environments, a transportable setup for assessing the audiogram was designed and brought to the animals, reducing stress and handling time prior to auditory experiments.

2. Methods

2.1. Subjects

Three young (3–8 month old) red foxes (*Vulpes vulpes*, two males and one female) were tested. The experiments were performed in an empty horse stable in a rural area of the Bohemian Forest, Czech Republic (49°9′10.28″N, 13°20′56.45″E). The animals were kept in cages outdoors or within the stable by foresters as pets with permits of the local veterinary and Nature and Animal Protection authorities. The daily acoustic environment of the animals consisted mainly of natural environmental sounds and some occasional noise of cars infrequently passing by on a nearby small road. The foxes were fed on dry canine diet and were given access to water *ad libitum*. They received at least 80% of their daily food ration during the training and test sessions. Regular monitoring ensured the good health of the animals. One animal (female) was trained and tested in 2012, two other animals in 2013.

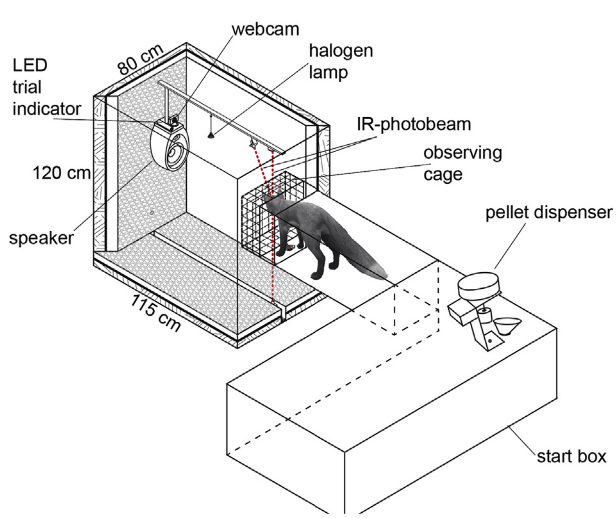

Fig. 1. Setup used to establish the red fox behavioral audiogram. A transportable semi-anechoic chamber was either connected to a wooden start box or placed in front of the cage of the animals. The foxes were trained to wait in the observing position for the presentation of a pure tone upon which they should leave the observing cage to obtain a food reward from an automatic pellet dispenser. False alarms were punished with timeouts. Stimulus presentation, subject control through infrared-photobeams, and reward/punishment allocation were fully computerized.

2.2. Behavioral testing apparatus

A custom-designed semi-anechoic chamber (115 × 80 × 120 cm) was employed to attenuate environmental noise, to house the speaker and other equipment, and to ensure a fixed position of the foxes' head within the sound field during test sessions (Fig. 1). The walls of the chamber were constructed of 80 mm thick PE-compound panels which were covered on the inside by a 40 mm layer of heavy weight compound-foam, followed by a 2 mm layer of bitumen paper and an inner layer of acoustical foam. Except for a single opening (25 × 25 cm) through which the animals entered the observing cage, the chamber was tightly sealed. The animals were transferred into a wooden start box from which they had free entry to the observing cage. For the female no start box was used, but instead we placed the whole system in front of the home cage so that the fox was free to enter and start trials voluntarily during the sessions. Compound-foam padding (40 mm thickness) below the chamber reduced the transmission of environmental low frequency vibrations into the chamber.

Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.heares.2014.12.001.

The observing cage was constructed of brass bars (<5 mm diameter) and prevented the subjects from climbing into the chamber. Two infrared (IR) sensors detected the entrance of the subject, started a trial and ensured the correct observing position during the trial as well as the response after tone presentation, all of which was automatically controlled (see 2.4). A 12 V halogen lamp hanging from the chamber ceiling illuminated the chamber. Closed-circuit video observation via an IR-sensitive webcam equipped with IR-light emitting diodes (LED) mounted above the speaker allowed visual control during the test sessions. An ongoing trial was indicated by blue flashing LEDs mounted on top of the speaker.

2.3. Stimulus control

Pure tones of 500 ms duration were generated, amplified, and attenuated by means of an RZ6 Multi-I/O processor unit (Tucker–Davis Technologies (TDT)) with a maximal sampling rate of 200 kHz. A software-controlled cosine gate (RPvdsEx V. 74, TDT) created rise and fall times of 25 ms (50 ms for frequencies below 125 Hz). Stimuli with frequencies higher than 63 Hz were transmitted through a dual concentric loudspeaker (Arena Satellite, Tannoy, UK; 80 Hz–54 kHz frequency response), for frequencies lower than 80 Hz we used a 12″ (30 cm) subwoofer (Punch HE, Rockford Fosgate, USA, 28–200 Hz frequency response). The loudspeaker was mounted at 0° elevation and at a distance of 60 cm in front of the animal. The subwoofer was placed on the foam-covered floor of the chamber facing away from the animal.

Sound intensity at the head position was calibrated for each frequency at 80 dB sound pressure level (SPL) (re 20 μPa) with a precision sound level meter (Brüel & Kjær (B&K) 2231) equipped with a 1/4″ free field microphone (B&K 4939, 4 Hz–100 kHz; corrected for free field response with protection grid on). A flexible extension rod (B&K UA 0196) minimized the risk of measuring reflections from the case of the sound level meter. A 1/3-octave filterset (B&K 1625) was used to measure sound pressure levels between 50 Hz and 20 kHz, higher frequencies were measured with the high pass (>12.5 kHz) filter of an infra- and ultrasound filter set (B&K 1627). The sound field was measured in the area in which an animal might hold its head (confer supplementary video 1) and found to vary by no more than ± 3 dB. To check the sound stimuli for harmonics and distortion we connected the output of the sound level meter to a digital USB oscilloscope (PicoScope 4224, Pico Technology Ltd.)