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Sound localization cues in the marmoset monkey

Sean J. Slee *, Eric D. Young

Biomedical Engineering Dept., Johns Hopkins University, 505 Traylor Research Building, 720 Rutland Avenue, Baltimore, MD 21205, USA

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ABSTRACT

The most important acoustic cues available to the brain for sound localization are produced by the interaction of sound with the animal's head and external ears. As a first step in understanding the relation between these cues and their neural representation in a vocal new-world primate, we measured head-related transfer functions (HRTFs) across frequency for a wide range of sound locations in three anesthetized marmoset monkeys. The HRTF magnitude spectrum has a broad resonance peak at 6–12 kHz that coincides with the frequency range of the major call types of this species. A prominent first spectral notch (FN) in the HRTF magnitude above this resonance was observed at most source locations. The center frequency of the FN increased monotonically from ~12 to 26 kHz with increases in elevation in the lateral field. In the frontal field FN frequency changed in a less orderly fashion with source position. From the HRTFs we derived interaural time (ITDs) and level differences (ILDs). ITDs and ILDs (below 12 kHz) varied as a function of azimuth between ±250 μs and ±20 dB, respectively. A reflexive orienting behavioral paradigm was used to confirm that marmosets can orient to sound sources.

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1. Introduction

The sound localization cues available to the brain are produced by the interaction of sound waves with the head and external ears. Previous studies have shown that the most important cues are interaural level difference (ILD), interaural time difference (ITD), and spectral shape (SS) provided by directionally-dependent filtering of the pinnae. When these cues are imposed on broadband sounds and presented with earphones, they provide sufficient information to reproduce the perception of the direction of an auditory event (Wightman and Kistler, 1989; Middlebrooks and Green, 1991; Middlebrooks, 1999).

Sound localization cues have been measured in several species including human (Harrison and Downey, 1970; Shaw, 1982; Middlebrooks et al., 1989; Wightman and Kistler, 1989; Middlebrooks and Green, 1990), macaque monkey (Spezio et al., 2000), cat (Roth et al., 1980; Musicant et al., 1990; Rice et al., 1992; Tollin and Koka, 2009), marmoset monkey (Aitkin and Park, 1993), ferret (Carlile, 1990; Schnupp et al., 2003), tamar wallaby (Coles and Guppy, 1986), several species of bat (Jen and Chen, 1988; Obrist et al., 1993; Wotton et al., 1995; Fuzessery, 1996; Firzlaff and Schuller, 2003; Aytekin et al., 2004), rat (Koka et al., 2008), gerbil (Maki and Furukawa, 2005), guinea pig (Carlile and Pettigrew, 1987; Sterbing et al., 2003), mouse (Chen et al., 1995), and barn owl (Moiseff, 1989; Keller et al., 1998). Here, we present additional measurements of sound localization cues in the common marmoset (callithrix jacchus), a vocal new-world primate. The marmoset is gaining popularity as a model system for unanesthetized studies in the auditory pathway including the inferior colliculus (Nelson et al., 2009), thalamus (Bartlett and Wang, 2007), and cortex (Lu et al., 2001a,b; Bendor and Wang, 2006; Wang, 2007).

The general characteristics of marmoset head-related transfer functions (HRTFs) are similar to those seen in other animals. Specifically, the greatest variation in both ILD and ITD occur with azimuth and the spectral shape of the HRTF magnitude is directionally dependent. The frequency of the first spectral notch (local minimum) in the HRTF magnitude changes with both source azimuth and elevation. The most orderly variation in the frequency of the first spectral notch occurs with changes in the elevation of lateral source positions.

Because there are no reports of sound localization behavior in marmosets, we measured reflexive orienting movements to sounds varying in azimuth and elevation. The tests were informal using untrained animals and were designed only to verify that marmosets orient to sounds. The behavioral responses suggest that marmosets can perceive the location of sound sources.

Abbreviations: HRTF, head-related transfer function; DTF, directional transfer function; AZ, azimuth; EL, elevation; ITD, interaural time difference; ILD, interaural level difference; FN, first-notch; HF, high frequency; dB, decibel; SS, spectral shape; TM, tympanic membrane; EKG, electrocardiogram; s, second; h, hour; mg, milligram; kg, kilogram; cm, centimeter; mm, millimeter; *L*, length; *W*, width; *r*, radius; Fig., figure; ml, milliliter; kHz, kilohertz; ms, millisecond; A/D, analog to digital

* Corresponding author. Tel.: +1 443 287 6186.
E-mail address: sslee1@jhmi.edu (S.J. Slee).

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2. Methods

2.1. Sound source and stimulus presentation

All experiments were conducted in a double-walled, acoustically-isolated sound chamber (internal dimensions 2.5 m × 2.6 m × 2 m) with 7 cm thick sound absorbing foam (Pinta Acoustics) covering the walls, ceiling, and floor. Sound was presented over a dual speaker system with a high-frequency tweeter (Fostex, model FT28D) and a mid range woofer (Morel, model CAW 428) enclosed in a custom built wooden box (21 × 20 × 10 cm). The speakers were connected by a 4th order Linkwitz-Riley crossover network (crossover frequency = 2 kHz, −24 dB/octave, Dayton Audio model 260–140) that provided a wideband stimulus over the 0.2–40 kHz range of the marmoset's audiogram. The source was attached to an arc-shaped stand that placed the speakers 1 m from the monkey's head. The tweeter was centered along the arc while the woofer was laterally offset by 8.6°.

The arc was first aligned vertically (relative to the floor) using a level and then bolted to the ceiling of the chamber. A bob on a string was used to align the tweeter at 90° EL, the position of the center of the animal's head, and the center of rotation of the rotary table holding the animal. The center of the tweeter at 0° EL and the position of the eardrum were aligned in the horizontal plane by measuring their heights above the floor with a tape measure and level. At the end of this procedure it was verified that the position corresponding to the center of the animal's head was the same distance from the face of the tweeter at all elevations. During the experiment the animal's head was aligned in the median plane (yaw) visually relative to the speaker arc.

Source locations were in reference to a single-pole coordinate system centered at the monkey's head. Azimuthal (AZ) angles of ±90° correspond to the source position directly lateral to the right/left ear and 0° corresponds to the source position directly in front. Angles of elevation (EL) below the horizontal plane are negative and those above are positive. An EL of 90° corresponds to the source position directly overhead. To change the AZ, the monkey was turned on a rotary table connected to a computer-controlled stepper motor with a resolution 0.01°. The EL of the source was adjusted by manually moving the speakers along the arc. The stimuli were presented from 150° (ipsilateral to the right ear) to −150° AZ in steps of 7.5° or 15°. ELs ranged from −30° to 90° in 17 steps of 7.5°.

The acoustic stimulus was a pair of 8192-point Golay codes (Zhou et al., 1992), sampled at 97.656 kHz, and converted to analog with 12 bit resolution (Tucker-Davis Technologies RP2.1). Experimental stimulus blocks consisted of the 84 ms Golay stimulus repeated 20 times. The Golay stimulus has a spectrum that varies less than 1 dB from 0 to 48 kHz.

2.2. Recording system and signal processing

The pressure waveforms near both tympanic membranes (TMs) were transduced into an electrical signal using hearing aid microphones (Knowles Electronics model FG-23329-C05). In two animals (77T and 9N) each microphone was coupled to the ear through a stainless steel probe tube (1 mm outer diameter, 18 mm length). This probe tube adds to the measurements a first order low-pass frequency response and a peak at around 3 kHz. In the third animal (67S) the microphones were not coupled to probe tubes, but were placed directly in the ear canal. The frequency responses of the microphones in this case were first order low pass at frequencies above ~15 kHz. (See Section 2.3 for details of the microphone placement.) The microphone signal was amplified (34 dB with a custom built amplifier), filtered (0.2–40 kHz, −24 dB/octave with a Krohn-Hite model 3100 filter), and digitized (12 bits at a 97.656 kHz sampling rate using a TDT model RP2.1).

"Free-field" measurements (no monkey, with the microphone at the position of the animal's ear) were made in about half the source positions to allow the properties of the speaker, microphone, probe tube (if present), and room to be eliminated from the HRTF. The spectrum of the free-field signal, computed as described in the next paragraph, is shown in Fig. 1C by the gray line. It shows a roll off at low frequencies (<0.15 kHz, not shown) and at

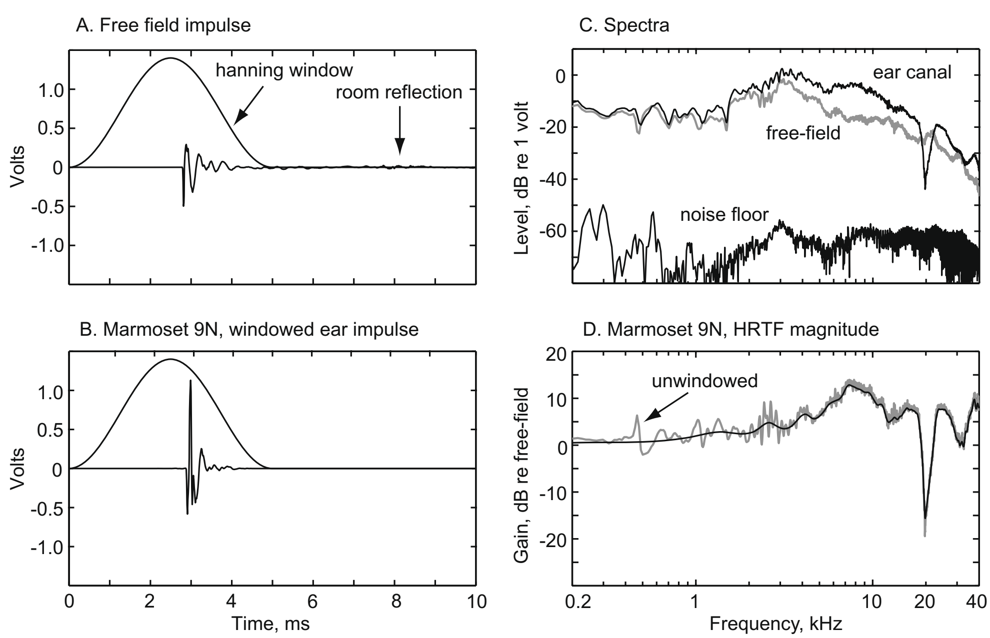

Fig. 1. Signal processing steps to compute the HRTF. (A) Impulse response computed using the Golay method of a speaker located at 0° AZ and 0° EL in free field. The microphone and probe tube were placed at approximately the same position in the room as if in the ear canal, but no animal was present. Reflections from the wall are evident. The Hanning window used to smooth the signals is shown. (B) Impulse response for the same speaker and microphone placement, except recorded in the ear canal. The impulse response is shown after the window was applied. (C) Spectra of the un-windowed impulse responses in the ear canal and free field, as the magnitude of the Fourier transforms of the signals. The dB scale is arbitrary, with 0 dB at the peak amplitude. The noise floor was measured with the probe tube filled with modeling clay. (D) Magnitude of the HRTF for the signals in C un-windowed (gray line) and windowed (black line).