



## Research paper

# Monaural spectral processing differs between the lateral superior olive and the inferior colliculus: Physiological evidence for an acoustic chiasm

Nathaniel T. Greene<sup>a,b</sup>, Oleg Lomakin<sup>a,b</sup>, Kevin A. Davis<sup>a,b,\*</sup>

<sup>a</sup>Departments of Biomedical Engineering and Neurobiology and Anatomy, University of Rochester, Rochester, NY 14642, USA

<sup>b</sup>Center for Navigation and Communication Sciences, University of Rochester, Rochester, NY 14642, USA

## ARTICLE INFO

## Article history:

Received 19 May 2010

Received in revised form

21 June 2010

Accepted 22 June 2010

Available online 30 June 2010

## ABSTRACT

Evidence suggests that the lateral superior olive (LSO) initiates an excitatory pathway specialized to process interaural level differences (ILDs), the primary cues used by mammals to localize high-frequency sounds in the horizontal plane. Type I units in the central nucleus of the inferior colliculus (ICC) of decerebrate cats exhibit monaural and binaural response properties qualitatively similar to those of LSO units, and are thus supposed to be the midbrain component of the ILD pathway. Studies have shown, however, that the responses of ICC cells do not often reflect simply the output of any single source of excitatory inputs. The goal of this study was to compare directly the monaural, spectral response properties of LSO and type I units measured in unanesthetized decerebrate cats. Compared to LSO units, type I units have narrower V-shaped excitatory tuning curves, higher spontaneous rates, lower maximum stimulus-evoked firing rates and more nonmonotonic rate-level curves for tones and noise. In addition, low-frequency type I units have lower thresholds to tones than corresponding LSO units. Taken together, these results suggest that the excitatory ILD pathway from LSO to ICC is mostly a high-frequency channel, and that additional inputs transform LSO influences in the ICC.

© 2010 Elsevier B.V. All rights reserved.

## 1. Introduction

Interaural level differences (ILDs) are the primary cues that animals use to localize high-frequency sounds in the horizontal plane (Erulkar, 1972; Mills, 1972). An excitatory pathway specialized to process these cues is initiated by the lateral superior olive (LSO), where coded sound intensities at the two ears are compared to each other on a frequency-by-frequency basis (Boudreau and Tsuchitani, 1968; Brownell et al., 1979; Caird and Klinke, 1983; Guinan et al., 1972a,b; Tollin and Yin, 2002a,b). The frequency-specific ILD

sensitivity of an LSO cell is derived largely from the pattern of its afferent inputs. LSO cells receive excitatory inputs from spherical bushy cells in the ipsilateral cochlear nucleus (CN) and inhibitory inputs from globular bushy cells in the contralateral CN via a synapse in the medial nucleus of the trapezoid body (for review, Schwartz, 1992). Thus, LSO cells show tuned excitatory responses to stimulation of one ear, and inhibitory responses to stimulation of the other ear. In response to changing ILDs, the firing rates of LSO cells decrease as ILDs shift to favoring the inhibitory ear. Information from the LSO is conveyed bilaterally to the central nucleus of the inferior colliculus (ICC). The contralateral projection to the ICC originates predominantly from LSO cells sensitive to high frequencies and is mostly excitatory in nature, whereas the ipsilateral projection is mainly from low-frequency LSO cells and largely inhibitory (Brunso-Bechtold et al., 1981; Glendenning et al., 1992).

Single units in the ICC of unanesthetized decerebrate cats can be grouped into three major response types based on the patterns of excitation and inhibition observed in contralateral pure-tone frequency response maps (Ramachandran et al., 1999). The response maps of type I units show a narrow I-shaped area of excitation at frequencies around best frequency (BF), with flanking regions of inhibition. Type V units produce frequency response maps that exhibit a broad V-shaped excitatory area with no signs of

*Abbreviations:* 7 N, seventh cranial nerve; ANF, auditory nerve fiber; BF, best frequency; CN, cochlear nucleus; DLPO, dorsolateral periolivary nucleus; DNLL, dorsal nucleus of the lateral lemniscus; EXC, excitatory inputs; GABA,  $\gamma$ -amino butyric acid; IC, inferior colliculus; ICC, central nucleus of the inferior colliculus; ILD, interaural level difference; im, intramuscular; INH, inhibitory inputs; ITD, interaural time difference; iv, intravenous; LNTB, lateral nucleus of the trapezoid body; LSO, lateral superior olive; MNTB, medial nucleus of the trapezoid body; MSO, medial superior olive; Q, quality factor; SOC, superior olivary complex; VNLL, ventral nucleus of the lateral lemniscus.

\* Corresponding author. Department of Neurobiology and Anatomy, University of Rochester, 601 Elmwood Ave., Box 603, Rochester, NY 14642, USA. Tel.: +1 585 273 4844 (work); fax: +1 585 756 5334.

E-mail address: [kevin\\_davis@urmc.rochester.edu](mailto:kevin_davis@urmc.rochester.edu) (K.A. Davis).

inhibition, and type O units have maps that are dominated by inhibition except for an O-shaped island of excitation at low stimulus levels. Units that produce type I and type O maps have BFs that span the cat's range of audible frequencies, whereas type V units typically have low BFs. When tested with dichotic stimuli, type I units show binaural excitatory/inhibitory interactions, type V units show facilitation and type O units show only weak binaural interactions (Davis et al., 1999). Based on the close resemblance of their monaural and binaural response properties with those of LSO units, it has been conjectured that type I units, at all BFs, receive their dominant excitatory inputs from the LSO and thus represent the midbrain component of the ILD pathway.

Several lines of evidence suggest, however, that the response properties of ICC type I units are not likely to reflect simply the output of the LSO. First, *in vivo* recordings show that most ICC neurons receive synaptic inputs from inhibitory as well as excitatory sources (Covey et al., 1996; Kuwada et al., 1997). Second, pharmacological studies reveal that inhibitory inputs shape the frequency tuning and ILD sensitivity of many ICC units (e.g. Burger and Pollak, 2001; Faingold et al., 1993; Klug et al., 1995; LeBeau et al., 2001; Li and Kelly, 1992a,b; Vater et al., 1992; Yang et al., 1992). In particular, blockade of these inputs can result in ICC response maps showing broader excitatory tuning curves, and some ICC units losing altogether their sensitivity to ILD. Finally, studies in Mexican free-tailed bats have shown that ILD processing differs quantitatively in the LSO and ICC (Park, 1998; Park et al., 2004).

The goal of the present set of studies was to compare directly the monaural and binaural response properties of units in the LSO and the ICC of unanesthetized decerebrate cats; here, we report on differences in their monaural spectral response characteristics. Standard extracellular recording techniques were used to obtain single-unit data from the LSO. Comparable data from ICC type I units were available (Ramachandran et al., 1999) but were collected anew to reduce any methodological differences. The main result of this study is that the response properties of LSO and ICC type I units are qualitatively similar, but quantitatively different in many respects. Most notably, ICC type I units have lower thresholds to tones at low BFs and narrower tuning curves at all frequencies than corresponding LSO units. The former result suggests that, contrary to expectations, the LSO is not a suitable source of dominant excitatory inputs for most low-BF type I units. Thus, the excitatory ILD pathway from LSO to contralateral ICC is primarily a high-frequency channel, consistent with prior anatomical and pharmacological observations. The latter result indicates that hierarchical transformations (in the form of additional excitatory and inhibitory inputs) sharpen the high-level frequency selectivity of type I units thereby enhancing the analysis of complex sounds.

## 2. Methods

Experiments were performed on 23 adult male cats (3–4 kg) (10 LSO; 13 ICC) with clean external ears and clear tympanic membranes. All procedures were approved by the University Committee on Animal Resources at the University of Rochester.

### 2.1. Surgical procedures

Cats were anesthetized with intramuscular (im) injections of ketamine (40 mg/kg im) and xylazine (0.5 mg/kg im), and given atropine (0.05 mg/kg im) to minimize respiratory secretions and dexamethasone (2 mg/kg im) to reduce cerebral edema. Thereafter, body temperature was maintained at  $39 \pm 0.5$  °C using a regulated heating blanket, and respiration and heart rates were monitored. The cephalic vein was cannulated to allow intravenous (iv) infusions of fluids, and a tracheotomy was performed to facilitate quiet

breathing. Supplemental doses of ketamine (20 mg/kg im) and xylazine (0.25 mg/kg im) were administered as needed (e.g. a heart rate over 180 beats/min) to maintain areflexia until the decerebration procedure was complete.

A midline incision was made over the skull and the temporalis muscles reflected to visualize the top of the skull and the ear canals. A craniotomy was performed over the left parietal cortex, and cats were made decerebrate by aspirating under visual control the brainstem between the superior colliculus and the thalamus. No further anesthesia was given.

Both ear canals were transected near the tympanic membrane to accept hollow ear bars for delivering closed-field acoustic stimuli. The animal's head was then fixed in the recording position, 30° and 0° nose-down with respect to stereotaxic horizontal coordinates for the LSO and the ICC, respectively, using a headpiece and two ear bars. The left LSO was accessed by removing the skull along the midline at the nuchal ridge, and aspirating the cerebellum overlying and bordering the floor of the fourth ventricle. The left IC was exposed by performing a craniotomy just rostral to the bony tentorium, aspirating the underlying cortical tissue and removing a small semicircular section of the tentorium. Surgery was usually confined to a single target nucleus within an experiment to minimize trauma to the nervous system.

Cats were euthanized at the end of each experiment with an overdose of sodium pentobarbital (100 mg/kg iv). Four cats used in LSO experiments were perfused intracardially with 0.9% saline followed by fixative (3% paraformaldehyde and 0.1% glutaraldehyde in 0.1 M phosphate buffer; pH 7.4) and two sucrose solutions (10 and 30%). The brains of these cats were removed from the skull and immersed in a 30% sucrose solution until they sank. Frontal sections (40 µm thick) of frozen brain were cut on a sliding microtome and stained with cresyl violet. The location of electrode tracks and recording sites within the LSO were verified from patterns of gliosis and electrolytic lesions. Images of sections were acquired using a MicroFire digital camera mounted on an Olympus AX70 microscope and Image-Pro software.

### 2.2. Data collection and analysis

Experiments were conducted inside a double-walled sound-attenuating chamber (IAC). Acoustic stimuli were delivered bilaterally via electrostatic speakers (TDT or STAX) that were coupled to hollow ear bars. The frequency response of each closed system was calibrated at the start of an experiment by inserting a probe tube microphone into the ear bar near the tympanic membrane. Responses of the TDT systems decreased monotonically from 110 dB SPL at 800 Hz to 90 dB SPL at 48 kHz; responses of the STAX systems were flat at 100 dB SPL ( $\pm 5$  dB) at frequencies from 40 Hz to 25 kHz and decreased by 20dB/oct for frequencies above 25 kHz. Interaural crosstalk was at least 30 dB (and typically > 50 dB) down at all frequencies in the ear opposite to the sound source (Davis, 2005; Gibson, 1982), which is well below the maximum ILD used during binaural testing (used here to aid unit identification).

All test stimuli, including tones and broadband noise, were digitally created with TDT System 3 hardware. Frequency response maps were constructed from responses to tone bursts that were 50 ms in duration and presented at a rate of 4 bursts/s; rate-level (and rate-ILD) curves were generated from responses to stimuli that were 200 ms long presented at a rate of 1 burst/s. All stimuli were gated on and off with 10 ms rise/fall times. Analog signals were created by playing the waveforms through a 16-bit D/A converter at a sampling rate of 100 kHz. Tones were attenuated relative to the acoustic ceiling at each frequency to achieve a desired input sound pressure level in dB SPL. Noise stimuli were flat at the tympanic membrane (i.e., corrected for non-flat

Download English Version:

<https://daneshyari.com/en/article/4355654>

Download Persian Version:

<https://daneshyari.com/article/4355654>

[Daneshyari.com](https://daneshyari.com)