



Research paper

Neural sensitivity to novel sounds in the rat's dorsal cortex of the inferior colliculus as revealed by evoked local field potentials

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ABSTRACT

Evoked local field potentials in response to contralaterally presented tone bursts were recorded from the rat's dorsal cortex of the inferior colliculus (ICd). An oddball stimulus paradigm was used to study the sensitivity of ensembles of neurons in the ICd to novel sounds. Our recordings indicate that neuron ensembles in the ICd display stimulus-specific adaptation when a large contrast in both frequency and probability of occurrence exists between the two tone bursts used for generating an oddball paradigm. A local field potential evoked by a tone burst presented as a deviant stimulus has a larger amplitude than that evoked by the same sound presented as a standard stimulus. The difference between the two responses occurs after the initial rising phases of their predominant deflections. The degree of stimulus-specific adaptation increases with the rate of sound presentation up to 8/s, the highest rate used in this study. A comparison between our results and those from previous studies suggests that differences exist between responses to oddball paradigms in the ICd and those in the primary auditory cortex, a major source of projection to the ICd. These differences suggest that local mechanisms exist in the ICd for suppressing neural responses to frequently presented sounds and enhancing responses to rarely presented sounds. Thus, the ICd may serve as an important component of an integrative circuit in the brain for detecting novel sounds in the acoustic environment.

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1. Introduction

The dorsal cortex of the inferior colliculus (ICd) occupies the dorsal and caudal part of the inferior colliculus (IC) and represents one of the three major subdivisions of the mammalian auditory

midbrain (Loftus et al., 2008; Malmierca et al., 1993, 1995b; and 2011; Oliver, 2005). The function of the ICd is not well understood, compared with that of the other two major subdivisions of the auditory midbrain, i.e., the central nucleus and the external cortex of the inferior colliculus (ICc and ICx).

Projections to the ICd are primarily from the layer V of the auditory cortex (AC) (Bajo et al., 2007; Coleman and Clerici, 1987; Druga et al., 1997; Herbert et al., 1991; Herrera et al., 1994; Malmierca and Ryugo, 2010; Saldaña et al., 1996). Other projections to the ICd include those from the ipsilateral ICc and ICx, all the major subdivisions of the contralateral IC, the auditory thalamus, and brainstem auditory structures (Cant and Benson, 2008; Gonzalez-Hernandez et al., 1987; Malmierca et al., 1995a, 2009b; Saldaña and Merchán, 1992; Willard and Martin, 1983; Winer et al., 2002). The ICd projects to the dorsal part of the medial geniculate nucleus (Kudo and Niimi, 1978; Malmierca and Merchán, 2004; Wenstrup et al., 1994). These anatomical findings suggest that the ICd makes a major contribution to the function of a complex neural circuit connecting auditory midbrain and forebrain structures.

Single ICd neurons display stimulus-specific adaptation (SSA) by reducing action potential discharge over repetitive sound presentations and immediately restoring the discharge upon a change in the quality of sound such as the frequency (Aitkin et al., 1994;

Abbreviations: AC, auditory cortex; AMPA, α -amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid; BF, best frequency; CNQX, 6-cyano-7-nitroquinoxaline-2,3-dione; D_N , negative deflection of an evoked local field potential; D_P , positive deflection of an evoked local field potential; f_H , the higher of the two frequencies used for creating an oddball stimulus train; f_L , the lower of the two frequencies used for creating an oddball stimulus train; IC, inferior colliculus; ICc, central nucleus of the inferior colliculus; ICd, dorsal cortex of the inferior colliculus; ICx, external cortex of the inferior colliculus; LFP, local field potential; pStd, probability of presentation of a standard sound; pDev, probability of presentation of a deviant sound; SSA, stimulus-specific adaptation; $SSA_{Am}(fx)$, amplitude-based frequency-specific stimulus-specific adaptation index; $SSA_{Area}(fx)$, area-based frequency-specific stimulus-specific adaptation index; $gSSA_{Am}$, amplitude-based general stimulus-specific adaptation index; $gSSA_{Area}$, area-based general stimulus-specific adaptation index; Train HS-LD, oddball stimulus train with an f_H tone serving as a standard sound and an f_L tone serving as a deviant sound; Train LS-HD, oddball stimulus train with an f_L tone serving as a standard sound and an f_H tone serving as a deviant sound.

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Lumani and Zhang, 2010; Malmierca et al., 2009a; Pérez-González et al., 2005; Syka et al., 2000). These neurons are likely important for detecting novel sounds in the acoustic environment.

SSA has been revealed in sources of projections to the ICd including the AC and the auditory thalamus (Antunes et al., 2010; Malmierca et al., 2009a; Pienkowski and Eggermont, 2009; Szymanski et al., 2009; Taaseh et al., 2011; Ulanovsky et al., 2003, 2004; von der Behrens et al., 2009). Studies of the SSA in the rat's primary AC were conducted by simultaneously recording local field potentials (LFPs) and single- or multi unit action potential discharges (Taaseh et al., 2011; von der Behrens et al., 2009). These studies have revealed that SSA can be reflected in LFPs. A tone burst presented at a lower probability in an oddball paradigm evokes a LFP with a larger peak amplitude than the same sound presented at a high probability. The larger amplitude of response to the deviant sound is at least partially due to the violation of the regularity of sound presentation set by the standard tone, indicating the presence of deviance detection in rat auditory cortex (Taaseh et al., 2011).

It is important to find how SSA is reflected in the activity of neuron ensembles in the ICd. This knowledge is needed for understanding how neurons in the ICd work together in the processing of information related to novel sounds. Furthermore, the knowledge can be used in a comparison with existing results from the AC, leading to an understanding about whether inputs from the AC related to novel sounds are further processed in the ICd. The present study was therefore designed to conduct LFP recordings in the ICd and to use an oddball paradigm to study SSA in ensembles of neurons in this midbrain structure.

2. Methods

2.1. Animal preparation

Experiments were conducted using 26 male adult Wistar albino rats (*Rattus norvegicus*) (250–500 g) obtained from Charles River Canada Inc., St. Constant, Quebec. Anaesthesia was induced by combined injections of ketamine hydrochloride (60 mg/kg, i.m.) and xylazine hydrochloride (10 mg/kg, i.m.) and maintained by supplemental injections of ketamine hydrochloride (20 mg/kg, i.m.) and xylazine hydrochloride (3.3 mg/kg, i.m.) as needed.

A small craniotomy was made on the left side of the skull to permit the placement of an electrode into the ICd. The rat's head was held firmly by using a headbar attached to a stereotaxic instrument (Kopf Instruments, Tujunga, California). The rat was placed inside a single-wall sound-attenuated booth (Eckel Industries, Morrisburg, Ontario) for recordings. All procedures were approved by the University of Windsor Animal Care Committee and were in accordance with the guidelines of the Canadian Council on Animal Care.

2.2. Acoustic stimulation

Acoustic waveforms were generated digitally using a System 3 real-time signal processing system (Tucker-Davis Technologies, Alachua, Florida) controlled by a personal computer running OpenEx software. Sounds were delivered to the right ear using a CF1 closed-field speaker (Tucker-Davis Technologies, Alachua, Florida) connected to a short piece of tygon tubing that was inserted into the rat's external meatus. Sounds used in the present study were brief monaural tone bursts with 2-ms rise/fall times but without a plateau. The sound-generating system was calibrated over a frequency range between 100 and 45,000 Hz using a 7017 condenser microphone (ACO pacific, Belmont, California).

2.3. Recording electrodes

Two types of electrodes were used in the present study. A single-barrel glass micropipette filled with either 3 M NaCl or 3% Neurobiotin (N-(2-aminoethyl) biotinamide hydrochloride) (Vector, Burlingame, CA) in 0.5 M sodium acetate (impedance 300–500 k Ω) was used in experiments in which LFPs were recorded without pharmacological manipulations.

A piggy-back electrode assembly similar to that developed by Havey and Caspary (1980) was used in experiments in which field potentials were recorded while a pharmacological agent was applied. The purpose of conducting pharmacological experiments was to block the glutamatergic neurotransmission at the recording site and to determine whether the field potential signals registered in the present study were of local origin. No attempt was made to determine whether the generation of SSA in the ICd was dependent on local glutamatergic neurotransmission. The electrode assembly was fabricated by using the same single-barrel recording micropipette as described above and an H-configuration five-barrel glass micropipette. The tips of the two pipettes were fixed to each other by cyanoacrylate glue (Viachem Co., Montreal, Quebec) with the pipettes at a 20° angle. Two barrels of the five-barrel pipette were filled with 6-cyano-7-nitroquinoxaline-2, 3-dione (CNQX, 5 mM, pH 9.0, SIGMA), a specific antagonist for the α -amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (AMPA) receptor, in the vehicle of 165 mM NaCl. The remaining three barrels were filled with 165 mM NaCl.

An electrode was driven into the ICd by using a model 2660 micropositioner (Kopf, Tujunga, California). LFPs registered by the single-barrel recording pipette were amplified by a 2400A preamplifier (Dagan, Minneapolis, Minnesota) and monitored audio-visually. Neural responses were sampled at 24.4 kHz using the System 3 real-time signal processing system.

2.4. Recording procedures

The left ICd was approached with an electrode penetrating from a dorso-rostralateral part to a ventro-caudomedial part of the brain. The electrode had a 45° angle relative to the vertical axis and was in an oblique plane that was perpendicular to the horizontal plane and 45° relative to the midsagittal plane. With reference to lambda, the electrode was moved caudally by 0.8–1.2 mm and then within the oblique plane along an axis perpendicular to the electrode by 3.2–3.6 mm. The electrode was lowered into the brain to a depth about 4.2 mm while the response to a tone burst presented to the right ear was monitored audio-visually. Our stereotaxic coordinates resulted in accurate and reliable electrode placement in the ICd (See Fig. 1 for an example).

Trains of tone bursts were used to search for a site where a large auditory response could be elicited. They were also used to determine the best frequency (BF) for generating a response as well as the threshold at BF at this site. Within each train, all tone bursts (typically $n = 7$) had different frequencies. These frequencies were equally spaced on a logarithmic scale. Tone bursts with different frequencies were presented at a randomized order but a fixed level (70 dB SPL for trains used for searching) and a constant rate of 4/s. An auditory response was recognized as a waveform with a relatively small positive deflection (D_p) followed by a large negative deflection (D_N) (See Fig. 2A for an example). The two deflections were in synchronization with sound presentations and about 40 ms in total duration. After a recording site was identified, trains of tone bursts were presented when the sound-pressure level of the composing tone bursts was lowered and the frequency range of the tone bursts was narrowed in comparison to those used in the

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