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THE CYTOARCHITECTURE OF THE INFERIOR COLLICULUS REVISITED: A COMMON ORGANIZATION OF THE LATERAL CORTEX IN RAT AND CAT

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Abstract—The inferior colliculus (IC) is the major component of the auditory midbrain and contains three major subdivisions: a central nucleus, a dorsal cortex, and a lateral cortex (LC). Discrepancies in the nomenclature and parcellation of the LC in the rat and cat seem to imply different, species-specific functions for this region. To establish a comparable parcellation of the LC for both rat and cat, we investigated its histochemistry and inputs. In both species, the deep lateral cortex is marked by a transition between the nicotinamide adenine dinucleotide phosphate-diaphorase (NADPH-d) rich superficial cortex and a cytochrome oxidase (CO) rich central nucleus. In both species, focal injections of anterograde tracers in the cochlear nucleus at sites of known best frequency produced bands of labeled inputs in two different subdivisions of the IC. A medial band of axons terminated in the central nucleus, while shorter bands were located laterally and oriented nearly perpendicularly to the medial bands. In the rat, these lateral bands were located in the third, deepest layer of the lateral (external) cortex. In the cat, the bands were located in a region that was previously ascribed to the central nucleus, but now considered to belong to the third, deepest layer of the LC, the ventrolateral nucleus. In both species, the LC inputs had a tonotopic organization. In view of this parallel organization, we propose a common parcellation of the IC for rat and cat with a new nomenclature. The deep layer of the LC, previously referred to as layer 3 in the rat, is designated as the 'ventrolateral nucleus' of the LC, making it clear that this region is thought to be homologous with the ventrolateral nucleus in the cat. The similar organization of the LC implies that this subdivision of the IC has similar functions in cats and rats. © 2008 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: auditory pathways, external cortex, external nucleus, pericentral nucleus, ventrolateral nucleus.

The lateral cortex (LC) is one of the three subdivisions of the inferior colliculus (IC), that also includes the central nucleus and dorsal cortex, but it is the least understood. Interspecies differences in the cytoarchitecture in the lateral region of the IC (see, for example Morest and Oliver, 1984; Faye-Lund and Osen, 1985; Malmierca et al., 1993) have limited our understanding of the functional role of the lateral IC. Nevertheless, it is clear that the lateral IC has both auditory and somatosensory inputs, and some parts may be involved in multisensory integration (Aitkin et al., 1978, 1981; Jain and Shore, 2006; Zhou and Shore, 2006). Auditory inputs to the deeper parts of the lateral IC arise from the cochlear nucleus and superior olive (Adams, 1979; Brunso-Bechtold et al., 1981; Shneiderman and Henkel, 1987; Shneiderman et al., 1988; Schofield and Cant, 1992, 1996; Oliver et al., 1995, 1997, 1999; Cant and Benson, 2003, 2006, 2008; Loftus et al., 2004a). These same auditory inputs also target the central nucleus and dorsal cortex of the IC. Somatosensory afferents arise from spinal cord, dorsal column nuclei, and spinal trigeminal nuclei (Aitkin et al., 1978, 1981; Robards, 1979; Feldman and Kruger, 1980; Morest and Oliver, 1984; Coleman and Clerici, 1987; Wiberg et al., 1987; Jain and Shore, 2006; Zhou and Shore, 2006). Recent studies of the lateral IC suggest that it may play a unique role in the descending auditory system (Groff and Liberman, 2003; Ota et al., 2004). Despite the potential significance of the LC for both ascending and descending auditory processing, results obtained in different species have been difficult to compare because of perceived differences in its architecture and connections.

Here, we studied the architecture and auditory connections of the lateral IC in both the rat and cat. Architecture was addressed by analyzing the distribution of two chemical markers, cytochrome oxidase (CO) and nicotinamide adenine dinucleotide phosphate-diaphorase (NADPH-d) in the IC. CO is a mitochondrial enzyme associated with oxidative metabolism. NADPH-d is colocalized with nitric oxide synthase that catalyzes the production of the retrograde messenger, nitric oxide. These markers have previously been used to distinguish IC subdivisions (NADPH-d: Druga and Syka, 1993; Coote and Rees, 2008, CO: Cant and Benson, 2005).

Electrophysiological and anatomical approaches were combined in order to identify frequency-specific inputs to the IC. Deposits of anterograde tracers in the cochlear nucleus labeled the terminations of auditory inputs to the IC. Recordings of tone-evoked responses at the injected sites revealed the frequency selectivity of labeled inputs,

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Abbreviations: ABC, avidin biotin complex; BDA, biotinylated dextran amine; BF, best frequency; CNIC, central nucleus of the inferior colliculus; CO, cytochrome oxidase; DC, dorsal cortex of the inferior colliculus; ECIC, external cortex of the inferior colliculus; FD, fluorescein dextran; IC, inferior colliculus; LC, lateral cortex of the inferior colliculus; LN, lateral nucleus; NADPH-d, nicotinamide adenine dinucleotide phosphate-diaphorase; TMR, tetramethylrhodamine dextran; VLN, ventrolateral nucleus.

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and allowed us to determine if LC afferents are organized tonotopically.

In both species, we found that: 1) the deep LC was characterized as a transition zone between the CO rich central nucleus and a NADPH-d rich perimeter; 2) auditory inputs target the deep LC and had a consistent spatial relationship to the inputs to the central nucleus, and 3) auditory inputs to the LC had a tonotopic organization within the LC, separate from that of the central nucleus. These commonalities suggest a homologous structure and function for the lateral IC in the cat and rat. To emphasize these commonalities, we propose a new nomenclature for the LC of the IC that can be applied to both species.

EXPERIMENTAL PROCEDURES

Anatomical tracer experiments were performed on six cats and six rats using procedures and some animals reported earlier (cat: Oliver et al., 1997, rat: Malmierca et al., 2002). In addition, three cats and two rats were used for CO and NADPH-d assays in the IC. All experiments were done in accordance with institutional guidelines at the University of Salamanca, University of Connecticut Health Center, and NIH guidelines for the care and use of laboratory animals. All efforts were made to minimize the number of animals used and their suffering.

Procedures for the anatomical tracer experiments are as follows. Anesthesia was induced in rats with ketamine (57 mg/kg i.m.) and xylazine (8.6 mg/kg i.m) and the animals were maintained in an areflexive state with the same compounds during the surgery and recording. Anesthesia was induced in cats with ketamine (33 mg/kg i.m.) and xylazine (1 mg/kg i.m.). Cats were then intubated and maintained in an areflexive state with isoflurane mixed with oxygen for the duration of the surgery and recording.

All of the procedures described henceforth were the same for both cats and rats. Animals were put into a stereotaxic frame which incorporated hollow ear bars to deliver sound stimuli, appropriately sized for the species. Surgery and sound recording was done in a double-walled sound attenuating chamber (IAC, Bronx, NY, USA). Cochlear nuclei on the right side were exposed by a craniotomy and aspiration of parts of the lateral and floccular cerebellum.

Extracellular recordings and tracer injections were done with glass micropipettes filled with anatomical tracers dissolved in saline. These were advanced into the dorsal cochlear nucleus or anteroventral cochlear nucleus while calibrated tonal stimuli were delivered by speakers coupled to the hollow ear bars of the stereotaxic frame. Stimuli were sequences of pure tone bursts swept through a range of frequencies and delivered at the same, moderate intensity (60–70 dB SPL). For a given intensity, the frequency that elicited the largest single- or multi-unit response was deemed the best frequency (BF) for that recording site. At a selected site, tracer was iontophoresed through the same pipette used for recording. Two types of tracers were used for anterograde transport: i) 10% tetramethylrhodamine dextran (TMR), dissolved in 0.9% saline, and ii) a mixture of 10% biotinylated dextran amine (BDA) and 10% fluorescein dextran (FD), dissolved in 0.9% saline. Iontophoresis parameters varied between 2 and 6 μA for durations of 5–24 min, with a 50% duty cycle (7s on/7s off).

After the survival period of 7–10 days for anterograde transport, animals were deeply anesthetized and then perfused transcardially with 4% paraformaldehyde. Tissue was prepared for light microscopy according to previously described procedures (Oliver et al., 2003; Loftus et al., 2004a; Malmierca et al., 2005). Brains were blocked in the Horsley-Clark plane and transverse sections were cut at a 50 μm thickness. Histology included avidin biotin complex (ABC) histochemistry for visualization and stabilization of BDA-labeled afferents using cobalt and nickel to make a black reaction and immunohistochemistry with antisera for TMR, followed by ABC histochemistry with Nova Red or DAB without cobalt and nickel to visualize the TMR labeled afferents. Every sixth section was Nissl stained and used to outline the cytoarchitectural subdivisions of the IC.

Tissue was analyzed with epifluorescence (for FD and TMR) and light microscopy (for stabilized BDA and TMR). In the latter material, BDA-labeled axons and boutons appear black and TMR-labeled axons and boutons appear red. Data analysis consisted of plotting the axons and boutons in transverse sections of the IC using Neurolucida software (Microbrightfield, Colchester, VT, USA). Closed contours were used to outline the fields of boutons. Comparison of the photographs of the raw data with outlines indicated that contours accurately captured the afferent organization. Digital images of injection sites in the cochlear nucleus and labeled afferents in the IC were acquired with a SPOT camera (Diagnostic Instruments, Inc., Sterling Heights, MI, USA) and contrast, brightness, and color were adjusted with Photoshop software (Adobe Systems, Inc., San Jose, CA, USA).

Methods for the CO and NADPH-d histochemistry were the same for both species. Briefly, deeply anesthetized animals were perfused transcardially with 4% paraformaldehyde. Brains were blocked in the Horsley-Clark plane, cryoprotected overnight in 10% sucrose, and then cut into 50 μm thick sections in the transverse plane. Two of every six sections were sampled for CO and NADPH histochemistry. For CO staining, free floating sections were incubated in a reaction mixture of 0.025% cytochrome C (Sigma C-7752) in 0.12 M phosphate buffer for ~21 h at 37 °C. For NADPH-d staining, sections were incubated in a solution of 0.05% b-NADPH (QBiogene ALX-480-004-M250, Irvine, CA) in 0.12 M phosphate buffer for 44 h at 4 °C followed by 4 h at 37 °C.

The images of the CO- and NADPH-d-stained tissue presented here were processed in Photoshop software in the following manner. Digitized color images were converted to gray scale, the gray level histograms were equalized, and the gray level range was inverted so that areas of more intense staining appear brighter. Images of a CO section and nearest NADPH-d section were aligned using the IC outline and blood vessels as a guide. A pseudo-color image was formed by assigning the CO image to the green channel and the NADPH-d image to the red channel.

RESULTS

Architecture of the LC

The LC can be subdivided into superficial and deep parts in both rats and cats. Fig. 1 shows these regions in Nissl-stained sections along with the names used in previous studies of these species and the new names that we propose. In cats (Fig. 1A), the LC has a superficial portion named the lateral nucleus (LN) with two layers (Fig. 1A, *1, 2*), a fibrous layer one that includes the fibers of the brachium of the IC and a cellular layer 2. The deep portion of the LC is the ventrolateral nucleus (VLN) and contains a mixture of neurons of different sizes including larger ones than in layers 1 and 2. Dorsally, the LN borders the dorsolateral, low frequency part of the central nucleus (Fig. 1A, *CNIC*). Ventrally, the VLN is intercalated between the LN and the lateral margin of the central nucleus.

In rats (Fig. 1B), the LC is better known as the external cortex of the IC (Fig. 1B, *ECIC*). As in the cat, the superficial portion of the rat's LC can be divided into two layers: an outer fibrous layer one and a small cell middle layer 2 (Fig. 1B, *1, 2*). The deeper layer 3 contains larger neurons (Fig. 1B, *3*), and is adjacent to the entire lateral border of

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