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Hearing Research 206 (2005) 12–27
HEARING RESEARCH
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An atlas of the inferior colliculus of the gerbil in three dimensions

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Received 18 November 2004; accepted 10 February 2005
Available online 28 April 2005

Abstract

An atlas of the inferior colliculus of the gerbil is presented in three dimensions. Sections were cut in the transverse (coronal), horizontal or saggital planes and fit to a common cartesian coordinate grid. The sections used for the atlas were reacted for cytochrome oxidase activity, a functional marker that can be used to distinguish different areas in the brainstem. The atlas can be used for representation, comparison and correlation of neuroanatomical, neurophysiological, neurochemical and other data that can be spatially mapped in the inferior colliculus.

Keywords: Auditory system; Brain atlas; Gerbil; Inferior colliculus; Neuroanatomy

1. Introduction

The inferior colliculus (IC) occupies a pivotal position in the auditory pathways (see reviews by Ehret, 1997; Casseday et al., 2002). Projections from all of the major brainstem auditory nuclei as well as from several non-auditory nuclei terminate in the IC (e.g., Adams, 1979, 1980), and it is, in turn, the major source of auditory projections to the forebrain (e.g., Aitkin and Phillips, 1984). In addition, the IC receives substantial inputs from the auditory cortex and gives rise to descending projections that may play an important role in the organization of motor responses to auditory stimuli (Huffman and Henson, 1990; Casseday and Covey, 1996; Casseday et al., 2002). Because of the complexity of its afferent and efferent connections as well as the existence of an extensive and highly organized intrinsic and commissural circuitry (e.g., Morest and Oliver, 1984; Saldaña and Merchán, 1992), a detailed knowledge of the neuroanatomical organization of the IC is fundamental for understanding auditory function.

Studies of the basic termination patterns of the major inputs to the IC have established that the distribution of terminal arbors from the various sources is not homogeneous (reviewed by Irvine, 1986). Rather, it appears that inputs from different sources may overlap completely, partially, or not at all (e.g., Roth et al., 1978; Brunso-Bechtold et al., 1981; Kudo, 1981; Ryugo et al., 1981; Henkel and Spangler, 1983; Oliver, 1984, 1987; Aitkin and Schuck, 1985; Coleman and Clerici, 1987; Maffi and Aitkin, 1987; Saldaña et al., 1996; Shneiderman

Abbreviations: amv, anterior medullary velum; APT, anterior pretectal nucleus; Aq, cerebral aqueduct; BF, basal forebrain; BIC, brachium of the inferior colliculus; BICn, nucleus of the BIC; Ca, caudate nucleus; CBM, cerebellum; CO, cytochrome oxidase; Co, commissure of the inferior colliculus; Ctx, cortex; DCN, dorsal cochlear nucleus; DThal, dorsal thalamus; f, fornix; HC, hippocampus; HThal, hypothalamus; IC, inferior colliculus; IO, inferior olivary complex; LL, lateral lemniscus; ml, medial lemniscus; ot, optic tract; PAG, periaqueductal gray matter; PG, pontine gray nuclei; RN, thalamic reticular nucleus; SCs, superficial gray layer of the superior colliculus; SCi, intermediate gray layer of the superior colliculus; SCd, deep gray layer of the superior colliculus; scp, superior cerebellar peduncle; SN, substantia nigra; SOC, superior olivary complex; TEG, mesencephalic tegmentum; Vmot, motor nucleus of the fifth nerve; VIIm, motor nucleus of the seventh nerve; VIIn, seventh motor nerve root; VN, vestibular nuclei; x, fiducial hole in superior colliculus; IV, fourth ventricle; 4n, fourth nerve root

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doi:10.1016/j.heares.2005.02.014

and Henkel, 1987; Ross and Pollak, 1989; Oliver et al., 1997; Loftus et al., 2004). Even when inputs from several sources appear to converge in one part of the IC, it is possible that they form synaptic connections with different sets of neurons. Indeed, recent physiological studies support the idea that specificity of connections extends to the level of individual cells (Davis et al., 1999; Ramachandran et al., 1999; Davis, 2002). Therefore, the connectivity of the IC must ultimately be studied at the level of the organization of inputs to single neurons (cf. Oliver, 2000). To provide guidance for systematic studies of the neuroanatomy at this level of analysis, it is desirable to establish the distribution patterns of the terminal arbors from each of the major sources of IC input with a high degree of resolution (cf. Oliver et al., 1997).

In our laboratory, we have undertaken a series of studies of the gerbil IC designed to evaluate the three-dimensional organization of its major inputs (including those from the cochlear nuclei, superior olivary complex, nuclei of the lateral lemniscus, contralateral IC, and auditory cortex) at the light microscopic level. As a first step, we have developed a detailed three-dimensional atlas in order to provide a standard framework for representation of data both from our own experimental neuroanatomical cases and also from other types of studies (e.g., physiological, immunocytochemical, developmental and aging studies). We chose cytochrome oxidase histochemistry as the histological procedure to visualize the IC because it is easily performed, is compatible with standard histological fixation procedures, and gives reliable and consistent results. A further advantage of the method is that the observed differential distribution of CO activity within the IC may have functional significance (see Section 4). In subsequent reports, the atlas will be used as a framework for describing the organization of the projections to the gerbil IC from both the brainstem and the forebrain.

2. Materials and methods

Female gerbils were obtained from Charles River Laboratories. The three gerbil brains used for the atlas described in this report were chosen from an extensive collection of normal and experimental brains. Some or all of the sections in many of these cases were reacted for cytochrome oxidase (CO) histochemistry. The criteria for selecting the particular brains used are discussed below. All procedures in our laboratory involving animals are approved by the Duke University Institutional Animal Care and Use Committee and are in accord with NIH guidelines.

2.1. Cytochrome oxidase histochemistry

Animals were given an overdose of Nembutal (>70 mg/kg) and allowed to become areflexic. Just when respiration ceased, the chest was opened and the animals were perfused through the heart with a rinse of 0.1 M phosphate buffer (pH 7.6) followed by 4% paraformaldehyde in the same buffer. The brains were removed the following day and kept in buffered 30% sucrose overnight. They were then frozen in powdered dry ice and sections 40 μm thick were cut on a sliding microtome (American Optical). The sections were incubated the same day in the following solution at room temperature (based on Wong-Riley, 1979): 50 mg diaminobenzidine (DAB) in 75 ml distilled water, 25 ml 0.4 M phosphate buffer (added after the DAB had dissolved), 25 mg cytochrome *c* from horse heart (Sigma #C7752), and 4 g sucrose. When the gray and white matter in the brainstem appeared well-differentiated, usually after about 4 h, the sections were rinsed in buffer, mounted on glass slides, allowed to dry, dehydrated in a series of alcohols, cleared in xylenes, and sealed under coverslips with Permount.

2.2. Choice of representative brains

It is our experience that every gerbil IC reacted for cytochrome oxidase activity has essentially the same appearance, so we did not choose the brains used because they seemed especially similar to one another. Rather, our assumption going into the project was that it would be feasible to match any three brains to the same coordinate grid if they were cut at right angles to one another and also symmetrically (i.e., each slice cut through exactly the same structures on both sides of the brain). The brains used for the atlas were chosen because they fit these criteria as well as, or considerably better, than any others in our collection. (The brains used were not perfect in some other respects. A few sections are missing, and some sections show evidence of damage during processing.)

All three gerbils were obtained at a reported age of 8 weeks. One brain (case #02-554) was cut in the transverse plane (i.e., transverse to the long axis of the brain stem; also referred to as the frontal or coronal plane; see Fig. 1 for orientation). The second brain (case #02-556) was cut in the horizontal plane (Fig. 1), and the third (case #04-649) was cut in the sagittal plane. The gerbils used for the transverse, horizontal and saggital series were killed at approximately 10, 8 and 9 weeks of age, respectively. In all three cases, every other section through the IC was reacted for CO. (The alternate sets of sections were processed in other ways.)

2.3. Acquisition of images

A Zeiss AxioCam HRc digital camera attached to a Zeiss AxioSkop 2 compound microscope was used to acquire images of every CO-reacted section through the IC