

The Mammalian
Cochlear Nuclei
Organization and Function

The Mammalian Cochlear Nuclei

Organization and Function

Edited by

Miguel A. Merchán

University of Salamanca
Salamanca, Spain

José M. Juiz

University of Alicante
Alicante, Spain

Donald A. Godfrey

Medical College of Ohio
Toledo, Ohio

and

Enrico Mugnaini

University of Connecticut
Storrs, Connecticut

Springer Science+Business Media, LLC

Proceedings of a NATO Advanced Research Workshop on
The Mammalian Cochlear Nuclei: Organization and Function,
held September 14–17, 1991,
in Salamanca, Spain

NATO-PCO-DATA BASE

The electronic index to the NATO ASI Series provides full bibliographical references (with keywords and/or abstracts) to more than 30,000 contributions from international scientists published in all sections of the NATO ASI Series. Access to the NATO-PCO-DATA BASE is possible in two ways:

—via online FILE 128 (NATO-PCO-DATA BASE) hosted by ESRIN, Via Galileo Galilei, I-00044 Frascati, Italy

—via CD-ROM "NATO-PCO-DATA BASE" with user-friendly retrieval software in English, French, and German (©WTV GmbH and DATAWARE Technologies, Inc. 1989)

The CD-ROM can be ordered through any member of the Board of Publishers or through NATO-PCO, Overijse, Belgium.

Library of Congress Cataloging-in-Publication Data

The Mammalian cochlear nuclei : organization and function / edited by Miguel A. Merchán ... [et al.].

p. cm. -- (NATO ASI series. Series A, Life sciences : 239)

"Proceedings of a NATO Advanced Research Workshop on the Mammalian Cochlear Nuclei: Organization and Function, held September 14–17, 1991, in Salamanca, Spain"--T.p. verso.

"Published in cooperation with NATO Scientific Affairs Division."

Includes bibliographical references and index.

1. Cochlear nucleus--Congresses. I. Merchán, Miguel A.
II. North Atlantic Treaty Organization. Scientific Affairs
Division. III. NATO Advanced Research Workshop on the Mammalian
Cochlear Nuclei: Organization and Function (1991 : Salamanca, Spain)
IV. Title. V. Series.

[DNLM: 1. Cochlea--anatomy & histology--congresses. 2. Cochlea--
physiology--congresses. 3. Cochlear Nerve--anatomy & histology--
congresses. 4. Cochlear Nerve--physiology--congresses. WV 260
M265 1991]

QP379.M26 1993

599'.01825--dc20

DNLM/DLC

for Library of Congress

92-48455

CIP

ISBN 978-1-4613-6273-9 ISBN 978-1-4615-2932-3 (eBook)
DOI 10.1007/978-1-4615-2932-3

© Springer Science+Business Media New York 1993
Originally published by Plenum Press, New York 1993
Softcover reprint of the hardcover 1st edition 1993

All rights reserved

No part of this book may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, microfilming, recording, or otherwise, without written permission from the Publisher

Preface

The presence of sophisticated auditory processing in mammals has permitted perhaps the most significant evolutionary development in humans: that of language. An understanding of the neural basis of hearing is thus a starting point for elucidating the mechanisms that are essential to human communication. The cochlear nucleus is the first region of the brain to receive input from the inner ear and is therefore the earliest stage in the central nervous system at which auditory signals are processed for distribution to higher centers. Clarifying its role in the central auditory pathway is crucial to our knowledge of how the brain deals with complex stimuli such as speech, and is also essential for understanding the central effects of peripheral sensorineural hearing loss caused by, for example, aging, ototoxic drugs, and noise. Ambitious new developments to assist people with total sensorineural deafness, including both cochlear and cochleus nuclear implants, require a detailed knowledge of the neural signals received by the brainstem and how these are processed. Recently, many new data have been obtained on the structure and function of the cochlear nucleus utilizing combinations of anatomical, physiological, pharmacological and molecular biological procedures. Approaches such as intracellular dye-filling of physiologically identified neurons, localization of classical neurotransmitters, peptides, receptors and special proteins, or gene expression have opened the door to novel morphofunctional correlations.

In order to provide an opportunity for leading scientists working on the cochlear nucleus to present and discuss their recent results, a NATO Advanced Research Workshop was held at the University of Salamanca, Spain, in September, 1991. The resulting volume consolidates the large amount of information presented at this meeting into a book that will be available to the scientific community. The studies presented here reemphasize our knowledge on how parallel channels of information processing are established in the cochlear nucleus and indicate means by which particular cell types in the nucleus are modulated by intrinsic and feed-back mechanisms. We hope that these proceedings will not only help advance further neural network strategies, some of which were discussed at the workshop, but also stimulate the design of mammalian neuroethological approaches, which have so far been promoted almost solely in bats.

The workshop as well as the book were dedicated to the memory of the Spanish neuroscientist, Dr. Rafael Lorente de Nó, (1902-1990). Born in Zaragoza and a follower of the famous neurohistologist Ramón y Cajal, Lorente de Nó produced one of the most extensive early descriptions of the morphology of the cochlear nucleus, a body of work that is still widely referred to by auditory scientists today. During the preparation of the present book, Dr. A. Gallego, one of the contributors to the meeting and a colleague of Lorente de Nó, died in Madrid. Because of his relevant role in the continuity of the Spanish scientific tradition during the last decades, we also wish to extend this dedication to the memory of Dr. Gallego.

Many people were involved in the organization of the meeting and the production of this volume. We gratefully acknowledge the invaluable financial support from the NATO Scientific Affairs Division and the contribution from the Spanish Ministry of Science and Education (MEC-DGICYT), Fondo de Investigaciones Sanitarias de la Seguridad Social (FISS), Town Council of Salamanca, and the Institute of Neuroscience of the University of Alicante. We wish to take this opportunity to acknowledge all the contributors and participants, the Scientific Committee, and the team in Salamanca for their support, advice, and hard work in making this conference and volume a reality. We also wish to extend our thanks to Lisbet Sørensen, who processed the entire text, and to Maria E. Rubio and Adelaida Baso for their help with the tedious work of figure placement.

M. Merchán (Salamanca, Spain)

J. Juiz (Alicante, Spain)

D. Godfrey (Toledo, USA)

E. Mugnaini (Storrs, USA)

In Memory of Rafael Lorente de Nó

The National Institute on Deafness and Other Communication Disorders joins in your salute to Rafael Lorente de Nó. An innovator who successfully translated experimental results into new concepts, Lorente de Nó's significant contributions remain as testimony to his creative genius in central nervous system research. His conceptualization of the organization of the cochlear nuclei provides the foundation for understanding the auditory system.

A scientist who held positions with the Central Institute for the Deaf, Rockefeller University, and the University of California, Los Angeles, Lorente de Nó's interest in the biochemical mechanisms of nerve conduction continued throughout his career. Honored on both sides of the Atlantic for his work, he received the highest scientific accolade the United States can bestow, membership of the National Academy of Sciences. Our thoughts are with you today as you honor the memory of this distinguished scientist, a man whose insight and discoveries form a legacy of knowledge for all investigators of the auditory system.

*James B. Snow, Jr., M.D.
Director of National Institute on Deafness and
Other Communication Disorders
September, 1991*

In Memory of Antonia Gallego

While this book was being prepared for publication, one of its contributors, Prof. A. Gallego, died in Madrid in February 1992, shortly after writing that paper. Antonio Gallego was the most prestigious Spanish neurobiologist of the last 50 years and also a symbol of the scientists that struggled to develop a favorable scientific environment in a country devastated by the material and psychological consequences of a Civil War. Antonio Gallego was born in Madrid in 1915. He obtained his M.D. degree at the University of Madrid and initiated there, still as a medical student, his career in physiology. After a forced interruption during the war and post-war years because of his alignment with the republican side, Gallego travelled to the Rockefeller Institute to work with Rafael Lorente de Nó on electrophysiology of the nerve. Back in Spain in 1950, Antonio Gallego resumed his academic activity and finally became Professor and Chairman of the Department of Physiology at the University of Madrid Medical School in 1960. There, he attracted a whole generation of young Spanish scientists that were impressed by his intellectual independence, his modern scientific views, and his courage to defy established doctrines in politics and science. Most of the present professors of Physiology in Spanish medical schools have been, directly or indirectly, pupils of Antonio Gallego.

His scientific work was mainly dedicated to study the functional structure of the retina. Main findings include the description of a new type of horizontal cell devoid of axon in the external plexiform layer, the report with J. Cruz of retinal association ganglion cells, and the first morphological description of the "interplexiform cell," to which he gave this name.

Antonio Gallego was deeply involved in university politics, directing his enormous energy, intelligence, and brilliant personality to the renovation of medical education and the improvement of research resources at the Spanish university. A whole generation of Spanish scientists owes a debt of gratitude to this man, who sacrificed his time and personal success to obtain a better future for science in his country.

*Carlos Belmonte, M.D., Ph.D.
Director, Institute of Neuroscience
University of Alicante
June, 1992*

Main Authors*

Joe C. Adams

Department of Otolaryngology, Massachusetts
Eye and Ear Infirmary, 243 Charles Street,
Boston, Mass. 02114, USA

Richard A. Altschuler

Kresge Hearing Research Institute, University of
Michigan, Ann Arbor, MI 48109, USA

Albert S. Berrebi

Laboratory of Neuromorphology, Graduate
Degree Program in Biobehavioral Sciences, The
University of Connecticut, Storrs, Connecticut
06269-4154, USA

M. Christian Brown

Harvard Medical School, Eaton-Peabody
Laboratory, Massachusetts Eye & Ear Infirmary,
243 Charles St., Boston, MA 02114, USA

Nell Beatty Cant

Department of Neurobiology Duke University
Medical Center Durham, NC 27710, USA

Donald M. Caspary

Southern Illinois University School of Medicine,
P.O. Box 19230, Springfield, Illinois, 62794-
9230, USA

John H. Casseday

Department of Neurobiology, Duke University
Medical Center, Durham, NC 27710, USA

Ellen Covey

Department of Neurobiology, Duke University,
Medical Center, Durham, NC 27710, USA

Edward F. Evans

Department of Communication and Neuroscience,
Keele University, Keele, Staffs. ST5 5BG, U.K.

Alfonso Fairén

Instituto Cajal, CSIC, Madrid, Spain

Eckhard Friauf

Department of Animal Physiology, University of
Tübingen, Auf der Morgenstelle 28, D-7400
Tübingen 1, Federal Republic of Germany

Antonio Gallego

Department of Physiology, Medical School,
Complutense University, Madrid, Spain

Donald A. Godfrey

Department of Otolaryngology - Head & Neck
Surgery, Medical College of Ohio, Toledo, Ohio
43699-0008, USA

Vicente Honrubia

Division of Head and Neck Surgery, UCLA
School of Medicine, University of California, Los
Angeles, USA

Ricardo Insausti

Department of Anatomy, University of Navarra,
Apdo. 273,
31080 Pamplona, Spain

José M. Juiz

Dpt. of Histology and Institute of Neuroscience,
University of Alicante, Apdo. 374, E-03080
Alicante, Spain

Lawrence Kruger

Brain Research Institute, UCLA Medical Center,
Los Angeles, CA 90024, USA

Patricia A. Leake

Epstein and Coleman Laboratories, Department of
Otolaryngology U499, University of California
San Francisco, San Francisco, CA 94143-0732,
USA

Dolores E. López

Departamento de Biología Celular y Patología,
Facultad de Medicina, Universidad de Salamanca,
E-37007 Salamanca, Spain

*There is an Abstracts Book with a complete list of participants, including contributors to the poster sessions of the workshop. The Abstracts Book also contains the summaries of these poster presentations, some of which are cited in several chapters of this volume.

Paul B. Manis
Department of Otolaryngology-Head and Neck
Surgery, The Johns Hopkins University School of
Medicine, Baltimore, MD 21205, USA

Ray Meddis
Speech and Hearing Laboratory, University of
Technology, Loughborough, UK

D.Kent Morest
Department of Anatomy, The University of
Connecticut Health Center, Farmington, CT
06030, USA

John K. Niparko
Department of Otolaryngology-Head & Neck
Surgery, Johns Hopkins University, Baltimore,
21203 Maryland, USA

Donata Oertel
Department of Neurophysiology, University of
Wisconsin, Madison, Wisconsin, USA

Douglas L. Oliver
Department of Anatomy, University of
Connecticut Health Center, Farmington, CT
06030, USA

Alan R. Palmer
MRC Institute of Hearing Research, University of
Nottingham, University Park, Nottingham NG7
2RD, U.K.

Steven J. Potasznik
Department of Anatomy, University of
Connecticut Health Center, Farmington, CT,
06030, USA

David K. Ruygo
Department of Otolaryngology - Head & Neck
Surgery, Johns Hopkins University School of
Medicine, Baltimore, MD 21205, USA

Murray B. Sachs
Department of Biomedical Engineering and
Center for Hearing Sciences, Johns Hopkins
University, School of Medicine, Baltimore,
Maryland 21205, USA

Enrique Saldaña
Departamento de Biología Celular y Patología,
Facultad de Medicina, Universidad de Salamanca,
E- 37007 Salamanca, Spain

Philip H. Smith
Department of Neurophysiology, University of
Wisconsin, Madison, Wisconsin, USA

Richard L. Saint Marie
Department of Anatomy, University of
Connecticut Health Center, Farmington, 06030
Connecticut, USA

Larry W. Swanson
Department of Biological Sciences, University of
Southern California, Los Angeles, California,
90089-2520, USA

Douglas E. Vetter
Laboratory of Neuromorphology, Graduate
Degree Program in Biobehavioral Sciences,
University of Connecticut, Storrs,
CT 06269-4154, USA

Robert J. Wenthold
Laboratory of Neurochemistry, National Institute
of Deafness and Other Communication Disorders,
NIH, Bethesda, MD 20892, USA

Robert E. Wickesberg
Hearing Research Laboratory, S.U.N.Y. at
Buffalo, Buffalo, New York 14214, USA

Frank H. Willard
Department of Anatomy, University of New
England, Biddeford, Maine, 04005, USA

Thomas A. Woolsey
James L. O'Leary Division of Experimental
Neurology, Department of Neurology and
Neurological Surgery, Washington University
School of Medicine, St. Louis, Missouri 63110,
USA

Eric D. Young
Department of Biomedical Engineering, The
Johns Hopkins University, Baltimore MD, 21205,
USA

John M. Zook
Dept. Zoological & Biomedical Science,
Ohio University, Athens, Ohio, 45701, USA

Contents

The cellular basis for signal processing in the mammalian cochlear nuclei <i>D. Kent Morest</i>	1
I. DEVELOPMENTAL ISSUES	
Cell birth, formation of efferent connections, and establishment of tonotopic order in the rat cochlear nucleus <i>Eckhard Friauf and Karl Kandler</i>	19
Postnatal development of auditory nerve projections to the cochlear nucleus in <i>Monodelphis Domestica</i> <i>Frank H. Willard</i>	29
II. PRIMARY INPUTS	
Anatomical and physiological studies of type I and type II spiral ganglion neurons <i>M. Christian Brown</i>	43
Topographic organization of inner hair cell synapses and cochlear spiral ganglion projections to the ventral cochlear nucleus <i>Patricia A. Leake, Russell L. Snyder and Gary T. Hradek</i>	55
Ultrastructural analysis of synaptic endings of auditory nerve fibers in cats: correlations with spontaneous discharge rate <i>David K. Ryugo, Debora D. Wright, and Tan Pongstaporn</i>	65
III. INTRINSIC CONNECTIONS	
Intrinsic connections in the cochlear nuclear complex studied <i>in vitro</i> and <i>in vivo</i> <i>Robert E. Wickesberg and Donata Oertel</i>	77
The synaptic organization of the ventral cochlear nucleus of the cat: the peripheral cap of small cells <i>Nell Beatty Cant</i>	91
Alterations in the dorsal cochlear nucleus of cerebellar mutant mice <i>Albert S. Berrebi and Enrico Mugnaini</i>	107

IV. DESCENDING PROJECTIONS

Non-cochlear projections to the ventral cochlear nucleus: are they mainly inhibitory? <i>Richard L. Saint Marie, E.-Michael Ostapoff, Christina G. Benson, D. Kent Morest and Steven J. Potashner</i>	121
Non-primary inputs to the cochlear nucleus visualized using immunocytochemistry <i>Joe C. Adams</i>	133
Superior olivary cells with descending projections to the cochlear nucleus <i>John M. Zook and Nobuyuki Kuwabara</i>	143
Descending projections from the inferior colliculus to the cochlear nuclei in mammals <i>Enrique Saldaña</i>	153

V.- NEUROTRANSMITTERS OF THE COCHLEAR NUCLEUS

Localizing putative excitatory endings in the cochlear nucleus by quantitative immunocytochemistry <i>José M. Juiz, Maria E. Rubio, Robert H. Helfert and Richard A. Altschuler</i>	167
Excitatory amino acid receptors in the rat cochlear nucleus <i>Robert J. Wenthold, Chyren Hunter and Ronald S. Petralia</i>	179
Glycine and GABA: transmitter candidates of projections descending to the cochlear nucleus <i>Steven J. Potashner, Christina G. Benson, E.-Michael Ostapoff, Nancy Lindberg and D. Kent Morest</i>	195
Inhibitory amino acid synapses and pathways in the ventral cochlear nucleus <i>Richard A. Altschuler, José M. Juiz, Susan E. Shore, Sanford C. Bledsoe, Robert H. Helfert, and Robert J. Wenthold</i>	211
Glycinergic inhibition in the cochlear nuclei: evidence for tuberculoventral neurons being glycinergic <i>Donata Oertel and Robert E. Wickesberg</i>	225
GABA and glycine inputs control discharge rate within the excitatory response area of primary-like and phase-locked AVCN neurons <i>Donald M. Caspary, Peggy S. Palombi, Patricia M. Backoff, Robert H. Helfert and Paul G. Finlayson</i>	239
Neuropharmacological and neurophysiological dissection of inhibition in the mammalian dorsal cochlear nucleus <i>Edward F. Evans and Wei Zhao</i>	253

Comparison of quantitative and immunohistochemistry for choline acetyltransferase in the rat cochlear nucleus <i>Donald A. Godfrey</i>	267
Choline acetyltransferase in the rat cochlear nuclei: immunolocalization with a monoclonal antibody <i>Douglas E. Vetter, Costantino Cozzari, Boyd K. Hartman and Enrico Mugnaini</i>	279
VI. PROJECTIONS AND RESPONSE PROPERTIES OF COCHLEAR NUCLEUS NEURONS	
The cochlear root neurons in the rat, mouse and gerbil <i>Dolores E. López, Miguel A. Merchán, Victoria M. Bajo and Enrique Saldaña</i>	291
Projections of cochlear nucleus to superior olivary complex in an echolocating bat: relation to function <i>John H. Casseday, John M. Zook and Nobuyuki Kuwabara</i>	303
The monaural nuclei of the lateral lemniscus: parallel pathways from cochlear nucleus to midbrain <i>Ellen Covey</i>	321
Ascending projections from the cochlear nucleus to the inferior colliculus and their interactions with projections from the superior olivary complex <i>Douglas L. Oliver and Gretchen E. Beckius</i>	335
Responses of cochlear nucleus cells and projections of their axons <i>Philip H. Smith, Philip X. Joris, Matthew I. Banks and Tom C.T. Yin</i>	349
Physiology of the dorsal cochlear nucleus molecular layer <i>Paul B. Manis, John C. Scott, and George A. Spirou</i>	361
Coding of the fundamental frequency of voiced speech sounds and harmonic complexes in the cochlear nerve and ventral cochlear nucleus <i>Alan R. Palmer and Ian M. Winter</i>	373
VII. COMPUTER MODELLING OF THE COCHLEAR NUCLEUS	
Computer modelling of the cochlear nucleus <i>Ray Meddis and Michael J. Hewitt</i>	385
Regularity of discharge constrains models of ventral cochlear nucleus bushy cells <i>Eric D. Young, Jason S. Rothman, and Paul B. Manis</i>	395
Cross-correlation analysis and phase-locking in a model of the ventral cochlear nucleus stellate cell <i>Murray B. Sachs, Xiaogin Wang and Scott C. Molitor</i>	411

VIII. APPENDIX: COCHLEAR NUCLEUS PROSTHESES

The development and evaluation of cochlear nucleus prostheses <i>John K. Niparko, David J. Anderson, Kensall D. Wise and Josef M. Miller</i>	421
---	-----

IX. SPECIAL CONTRIBUTIONS IN HONOUR OF R. LORENTE DE NÓ

Lorente de N6's scientific life <i>Antonio Gallego</i>	431
Sensoritopic and topologic organization of the vestibular nerve <i>Vicente Honrubia, Larry F. Hoffman, Anita Newman, Eri Naito, Yasushi Naito and Karl Beykirch</i>	437
Lorente de N6 and the hippocampus: neural modeling in the 1930s <i>Larry W. Swanson</i>	451
The rat entorhinal cortex. Limited cortical input, extended cortical output <i>Ricardo Insausti</i>	457
Axonal patterns of interneurons in the cerebral cortex: in memory of Rafael Lorente de N6 <i>Alfonso Fair6n</i>	467
Glom6rulos, barrels, columns and maps in cortex: an homage to Dr. Rafael Lorente de N6 <i>Thomas A. Woolsey</i>	479
Lorente de N6: the electrophysiological experiments of the latter years <i>Lawrence Kruger</i>	503
INDEX	515