
Handbook of Olfaction and Gustation

Second Edition
Revised and Expanded

edited by
Richard L. Doty

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Richard L. Doty

*University of Pennsylvania
Philadelphia, Pennsylvania, U.S.A.*



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Foreword

In the rise of modern neuroscience during the last century, the great sensory systems—vision above all, but also the somatosensory systems and audition—played the leading roles in the elucidation of principles underlying the neural mechanisms of perception. Work on the senses of taste and smell lagged behind, hampered by the difficulties of controlling the stimuli in precise ways and by the belief that these senses were of minor importance to humans.

No more! That era of chemosensory darkness ended during the past two decades because of illumination from new studies at many levels of these systems. Gene families that express receptors for chemical stimuli have been identified. Membrane mechanisms of stimulus transduction and second messenger signaling have been revealed. Topographic patterns of the convergence of axons from the sensory cells onto higher levels in the sensory pathways have been mapped. A variety of methods have revealed that different odors elicit different activity patterns, which constitute virtual “odor images.” In the olfactory system, as in the other great sensory systems, stimulus space (in this case, the multidimensional space of odor molecules) has now been mapped into two-dimensional neural space.

The synaptic microcircuits in the olfactory bulb have attracted a new generation of electrophysiologists from other fields. Using patch recordings, calcium imaging and advanced microscopy, they are analyzing the dendritic and synaptic properties of the microcircuits that process the odor images as the basis for perception. In addition to this revitalization of electrophysiological studies of the chemical senses, the neuroscience community has been attracted to the extraordinary plasticity of these systems, evidenced, in part, by the ongoing turnover of taste and olfactory cells, and the constant generation of new interneurons from the anterior migratory stream at the base

of the brain. These systems are therefore on the cutting edge of current research on stem cells and neurogenesis in the brain.

New psychophysical studies challenge the traditional view of human olfaction as weak, and suggest instead that our ability to perceive low levels of odorants may be as good or better than that of macrosomats such as rodents and carnivores. Moreover, such studies have expanded our understanding of the complexity of the chemical senses, and, along with a plethora of basic science studies, have demonstrated that these senses are intimately involved in a wide range of medical disorders. Indeed, the olfactory system may provide early indicators for disease states such as neurodegeneration and schizophrenia. We now have a better understanding of the significance of the olfactory and gustatory systems for such critical human behaviors as infant nutrition, the prevalence of obesity in developed countries, and the strong links between the chemical senses and emotion and memory.

All of these developments and many more are covered in the second edition of this widely recognized book, the largest compendium of data on the chemical senses published to date. Richard Doty’s introduction provides a masterly overview of the rapidly evolving events in these fields, and the ensuing chapters provide a wealth of information on topics ranging from basic anatomy, physiology, and clinical disorders of the chemical senses to advances in functional imaging, molecular neurobiology, human and animal psychophysics, and even olfactory system cybernetics.

As the fields of gustation and olfaction continue their strong growth, there will be an increasing need for a source to which one can go for orientation to the broad range of research involved and critical assessments of progress, problems, and opportunities. This new edition fills those needs

superlatively for a wide range of readers: neuroscientists, organic chemists, toxicologists, biomedical engineers, psychologists, and a variety of clinicians, as well as the interested layperson.

*Gordon M. Shepherd, M.D., D. Phil.
Professor of Neuroscience
Yale University
New Haven, Connecticut, U.S.A.*

Preface

Since the publication of the first edition of the *Handbook of Olfaction and Gustation* in 1995, advances in chemosensory science have been staggering. Indeed, during this period the chemical senses have become a central element of the field of modern neuroscience, largely because of their regenerative capacities, integral association with stem cell research, and unique transduction processes. As a consequence of the proliferation of commercially available olfactory tests, olfaction is now routinely and quantitatively evaluated in most major medical centers, as well as within the food, beverage, cosmetic, and energy (e.g., gas works) industries. Of particular relevance to the physician is the fact that decreased smell function is likely the first clinical manifestation of Alzheimer's disease (AD) and idiopathic Parkinson's disease (PD). Indeed, accurate assessment of olfaction can aid in the "preclinical" identification of individuals at risk for these disorders. Such assessment can also aid in differential diagnosis, since diseases often misdiagnosed as AD or PD (e.g., major affective disorder, progressive supranuclear palsy) are unaccompanied by meaningful olfactory loss.

The second edition of the *Handbook* represents the largest collection of basic, clinical, and applied knowledge on the chemical senses ever compiled in one volume, with contributions from over 80 of the world's leading researchers. The material in this up-to-date treatise has been tailored to be of value to a wide range of medical specialists, as well as to basic scientists working in academics, industry, and government. Because the information is presented in a straightforward manner, this volume can serve as a textbook for graduate students, medical students, and

postdoctoral fellows from numerous disciplines. The chapters are conveniently arranged into three major sections corresponding to olfaction, gustation, and other chemosensory systems and, with the exception of the last section, are subdivided into (A) anatomy and neurobiology, (B) functional measurement, ontogeny, and genetics, and (C) clinical applications and perspectives. Unlike the first edition, this edition contains an author index that makes it possible for researchers and others to quickly find references and sections based on individual contributions. As in the first edition, historical perspective and clinical relevance have been emphasized, but not at the expense of basic science. The book has been expanded from 38 to 48 chapters, so as to take into account major growth in a number of fields, including neuroscience, functional imaging, cybernetics, toxicology, structure-activity assessment, molecular biology, and animal behavior.

I am grateful to the contributors, who have been a model of objectivity and scholarship in the development of their chapters, and who have graciously taken into consideration my often extensive editorial suggestions and criticisms. I am also indebted to the staff of Marcel Dekker, Inc., particularly Jinnie Kim, Assistant Acquisitions Editor, and Ann Pulido, Production Editor, who have patiently and painstakingly worked with me to ensure a volume of the highest quality. Without the support of the following grants from the National Institutes of Health, this work would have never been accomplished: PO1 DC 00161, RO1 DC 04278, RO1 DC 02974, and RO1 AG 27496.

Richard L. Doty

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Contributors

Steven E. Arnold, M.D. Smell and Taste Center and Departments of Psychiatry and Neurology, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.

Harriet Baker, Ph.D. Department of Neurology and Neuroscience, The Burke Medical Research Institute, Weill Medical College, Cornell University, White Plains, New York, U.S.A.

Michael A. Barry, Ph.D. Division of Neurosciences, Department of Oral Diagnosis, School of Dental Medicine, University of Connecticut Health Center, Farmington, Connecticut, U.S.A.

Lloyd M. Beidler, Ph.D. Department of Biological Science, Florida State University, Tallahassee, Florida, U.S.A.

Ottorino Belluzzi, Ph.D. Department of Biology, University of Ferrara, Ferrara, Italy

Ilene L. Bernstein, Ph.D. Department of Psychology, University of Washington, Seattle, Washington, U.S.A.

Robert M. Bradley, M.D.S., Ph.D. Department of Biologic and Materials Science, School of Dentistry, University of Michigan, Ann Arbor, Michigan, U.S.A.

Peter A. Brennan, Ph.D. Department of Animal Behaviour, University of Cambridge, Cambridge, United Kingdom

Steven M. Bromley, M.D. Smell and Taste Center, University of Pennsylvania, and Department of Neurology, Thomas Jefferson University, Philadelphia, Pennsylvania, U.S.A.

Kathleen C. Chambers, Ph.D. Department of Psychology, University of Southern California, Los Angeles, California, U.S.A.

Meng Inn Chuah, Ph.D. Department of Anatomy and Physiology, University of Tasmania, Hobart, Australia

Thomas A. Cleland, Ph.D. Department of Neurobiology and Behavior, Cornell University, Ithaca, New York, U.S.A.

Dean M. Clerico, M.D. Valley ENT, Forty Fort, Pennsylvania, U.S.A.

J. Enrique Cometto-Muñiz, Ph.D. Chemosensory Perception Laboratory, Department of Surgery (Otolaryngology), University of California, San Diego, La Jolla, California, U.S.A.

Richard M. Costanzo, Ph.D. Department of Physiology, Virginia Commonwealth University, Richmond, Virginia, U.S.A.

Alan R. Dahl, Ph.D. Battelle Memorial Institute, Columbus, Ohio, U.S.A.

Laurence J. DiNardo, M.D. Department of Otolaryngology Head and Neck Surgery, Virginia Commonwealth University, Richmond, Virginia, U.S.A.

Xinxin Ding, Ph.D. Wadsworth Center, New York State Department of Health, and School of Public Health, State University of New York at Albany, Albany, New York, U.S.A.

Richard L. Doty, Ph.D. Smell and Taste Center and Department of Otorhinolaryngology: Head and Neck Surgery, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.

Adam Drewnowski, Ph.D. Nutritional Sciences Program, School of Public Health and Community Medicine, University of Washington, Seattle, Washington, U.S.A.

Heather J. Duncan, Ph.D. Department of Internal Medicine, University of Cincinnati College of Medicine, Cincinnati, Ohio, U.S.A.

Howard Eichenbaum, Ph.D. Department of Psychology, Boston University, Boston, Massachusetts, U.S.A.

Albert I. Farbman, D.M.D., Ph.D. Department of Neurobiology and Physiology, Northwestern University, Evanston, Illinois, U.S.A.

Marion E. Frank, Ph.D. Division of Neurosciences, Department of Oral Diagnosis, School of Dental Medicine, University of Connecticut Health Center, Farmington, Connecticut, U.S.A.

Richard E. Frye, M.D., Ph.D. Department of Neurology, Children's Hospital, Boston, Massachusetts, U.S.A.

Judith R. Ganchrow, Ph.D. Institute of Dental Sciences, The Hebrew University–Hadassah School of Dental Medicine Founded by the Alpha Omega Fraternity, Jerusalem, Israel

Janneane F. Gent, Ph.D. Department of Epidemiology and Public Health, Yale University, New Haven, Connecticut, U.S.A.

Mary Beth Genter, Ph.D. Department of Environmental Health, University of Cincinnati, Cincinnati, Ohio, U.S.A.

Timothy A. Gilbertson, Ph.D. Department of Biology, Utah State University, Logan, Utah, U.S.A.

Lloyd Hastings, Ph.D. Smell and Taste Center and Department of Otorhinolaryngology: Head and Neck Surgery, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.

Thomas P. Hettinger, Ph.D. Division of Neurosciences, Department of Oral Diagnosis, School of Dental Medicine, University of Connecticut Health Center, Farmington, Connecticut, U.S.A.

David L. Hill, Ph.D. Department of Psychology, University of Virginia, Charlottesville, Virginia, U.S.A.

Bradley N. Johnson, M.D. Department of Bioengineering, University of California, Berkeley, California, U.S.A.

David W. Kennedy, M.D. Department of Otorhinolaryngology: Head and Neck Surgery, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.

Eric B. Keverne, M.A., Ph.D., D.Sc., F.R.S. Department of Animal Behaviour, University of Cambridge, Cambridge, United Kingdom

Gerd Kobal, M.D., Ph.D. Department of Pharmacology and Toxicology, University of Erlangen, Erlangen, Germany

Igor L. Kratskin, M.D., Ph.D. Smell and Taste Center and Department of Otorhinolaryngology: Head and Neck Surgery, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.

David G. Laing, Ph.D. Centre for Advanced Food Research, University of Western Sydney, Sydney, Australia

Donald C. Lanza, M.D. Department of Otolaryngology and Communicative Disorders, The Cleveland Clinic Foundation, Cleveland, Ohio, U.S.A.

Cheng Li, M.D. Smell and Taste Center, and Department of Otorhinolaryngology, Head and Neck Surgery, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.

Christiane Linster, Ph.D. Department of Neurobiology and Behavior, Cornell University, Ithaca, New York, U.S.A.

Alan Mackay-Sim, Ph.D. Centre for Molecular Neurobiology, Griffith University, Brisbane, Queensland, Australia

Joel Mainland, Ph.D. Wills Neuroscience Institute and Department of Psychology, University of California, Berkeley, California, U.S.A.

Robert F. Margolskee, M.D., Ph.D. Department of Physiology and Biophysics, Howard Hughes Medical Institute, The Mount Sinai School of Medicine, New York, New York, U.S.A.

Joel Maruniak, Ph.D. Department of Biological Sciences, University of Missouri, Columbia, Missouri, U.S.A.

Richard D. Mattes, Ph.D., R.D. Department of Foods and Nutrition, Purdue University, West Lafayette, Indiana, U.S.A.

Bert Ph. M. Menco, Ph.D. Department of Neurobiology and Physiology, Northwestern University, Evanston, Illinois, U.S.A.

Julie A. Mennella, Ph.D. Monell Chemical Senses Center, Philadelphia, Pennsylvania, U.S.A.

Claudia S. Miller, M.D. Department of Family Practice and Community Medicine, University of Texas Health Science Center, San Antonio, Texas, U.S.A.

Inglis J. Miller, Jr., Ph.D. Department of Neurobiology and Anatomy, Wake Forest University School of Medicine, Winston-Salem, North Carolina, U.S.A.

Marian L. Miller, Ph.D. Department of Environmental Health, University of Cincinnati College of Medicine, Cincinnati, Ohio, U.S.A.

Charlotte M. Mistretta, Ph.D. Department of Biological and Materials Sciences, School of Dentistry, University of Michigan, Ann Arbor, Michigan, U.S.A.

Cheil Moon, Ph.D. The Johns Hopkins University School of Medicine, Baltimore, Maryland, U.S.A.

Edward E. Morrison, Ph.D. Department of Anatomy, Physiology, and Pharmacology, Auburn University, Auburn, Alabama, U.S.A.

Claire Murphy, Ph.D. Department of Psychology, San Diego State University, and Department of Surgery (Otolaryngology), University of California, San Diego, School of Medicine, San Diego, California, U.S.A.

Krishna C. Persaud, Ph.D. Department of Instrumentation and Analytical Science, University of Manchester Institute of Science and Technology, Manchester, United Kingdom

Aras Petrusis, Ph.D. Department of Psychology, Georgia State University, Atlanta, Georgia, U.S.A.

Donald W. Pfaff, Ph.D. Laboratory of Neurobiology and Behavior, The Rockefeller University, New York, New York, U.S.A.

Richard H. Porter, Ph.D. Laboratoire de Comportement Animal, Unité de Physiologie de la Reproduction et des Comportements, Institut National de la Recherche Agronomique/Centre National de la Recherche Scientifique, Nouzilly, France

Evan R. Reiter, M.D. Department of Otolaryngology–Head and Neck Surgery, Virginia Commonwealth University, Richmond, Virginia, U.S.A.

Klaus Reutter, Ph.D. Anatomical Institute, University of Tübingen, Tübingen, Germany

Edmund T. Rolls, D. Phil., D.Sc. Department of Experimental Psychology, University of Oxford, Oxford, United Kingdom

Gabriele V. Ronnett, M.D., Ph.D. Department of Neuroscience, The Johns Hopkins University School of Medicine, Baltimore, Maryland, U.S.A.

Benoist Schaal, Ph.D. Centre Européen des Sciences du Goût, Dijon, France

Hendrik N. J. Schifferstein, Ph.D. Department of Industrial Design, Delft University of Technology, Delft, The Netherlands

Marlene Schwanzel-Fukuda, Ph.D. Laboratory of Neurobiology and Behavior, The Rockefeller University, New York, New York, U.S.A.

James E. Schwob, M.D., Ph.D. Department of Anatomy and Cellular Biology, Tufts University School of Medicine, Boston, Massachusetts, U.S.A.

Thomas R. Scott, Ph.D. College of Sciences, San Diego State University, San Diego, California, U.S.A.

Nancy L. Segal, Ph.D. Department of Psychology, California State University, Fullerton, California, U.S.A.

David V. Smith, Ph.D. Department of Anatomy and Neurobiology, University of Tennessee Health Science Center, Memphis, Tennessee, U.S.A.

Gregory S. Smutzer, Ph.D. Smell and Taste Center and Department of Otorhinolaryngology, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.

Noam Sobel, Ph.D. Wills Neuroscience Institute and Department of Psychology, University of California, Berkeley, California, U.S.A.

Alan C. Spector, Ph.D. Department of Psychology, University of Florida, Gainesville, Florida, U.S.A.

Regina M. Sullivan, Ph.D. Department of Zoology, University of Oklahoma, Norman, Oklahoma, U.S.A.

Wyatt C. To, M.D. Department of Otolaryngology and Communicative Disorders, The Cleveland Clinic Foundation, Cleveland, Ohio, U.S.A.

Tari D. Topolski, Ph.D. Department of Health Services, University of Washington, Seattle, Washington, U.S.A.

John Q. Trojanowski, M.D., Ph.D. Smell and Taste Center, Center for Neurodegenerative Disease Research, Department of Pathology and Laboratory Medicine, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.

Luca Turin, Ph.D. Department of Physiology, University College, London, United Kingdom

Donald A. Wilson, Ph.D. Department of Zoology, University of Oklahoma, Norman, Oklahoma, U.S.A.

Martin Witt, M.D., Ph.D. Department of Anatomy, University of Technology Dresden, Dresden, Germany

Fumiko Yoshii, Ph.D. Graduate School of Science and Technology, Niigata University, Niigata, Japan

David M. Yousem, M.D. Department of Radiology, The Johns Hopkins University School of Medicine, Baltimore, Maryland, U.S.A.