THE SENSES: A COMPREHENSIVE REFERENCE

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Volume 4
OLFACTION AND TASTE

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Introduction to Volume 4

This volume of the *The Senses: A Comprehensive Reference* provides a current review of the chemical senses of taste and smell. Historically, these were considered the minor senses. Descriptions of them were often combined in textbooks both because the natural stimuli are chemicals and because not much was known about them compared with vision and audition. Presumably, they were less studied since it did not seem so bad if humans lost their ability to smell or taste; blindness and deafness were much more serious concerns. However, one might justifiably argue that if all animal life were considered, these are the most important senses. Taste is devoted to a single overwhelmingly important function: it insures that an organism takes in appropriate nutrients and avoids poison. The sense of smell has more varied functions. It too is involved with recognizing food and motivating its intake but it also plays a critical role in monitoring the environment for danger and, perhaps most importantly, in regulating social and sexual activities. Thus, without these two senses most animals would neither eat nor mate! For humans, we have been learning more about the crucial roles taste and smell play in regulating food choice and intake, modulating social interactions, surveying the chemical environment, and providing pleasure. Loss or alteration of smell and taste are not trivial afflictions.

Fortunately, research in the chemical senses is no longer neglected. Indeed, the remarkable rate of progress may, at first blush, even make the idea of a handbook seem absurd. By the time you read these chapters there will be tens of new publications not covered in this book. But in fact it is all those papers that make a compendium like this useful, even if necessarily incomplete. Not long ago one could start out in the fields of olfaction or taste and come up to speed in the literature quite easily. Indeed, for some of us that was one of the attractions of the field. The advent of new techniques, their successful application to questions in chemical sensing, the attraction of investigators from other fields, suddenly transformed the chemical senses from the most mysterious to the most investigated of the sensory systems. Now it is critical to be able to read papers in molecular biology, anatomy, physiology, imaging, psychophysics, genetics, bioinformatics, genomics. . .

So the value of a handbook is as a quick but inclusive reference that will bring even senior investigators rapidly up to speed in an unfamiliar area. In this respect, the contributors to this volume have done an admirable job. Chapters cover all of the above topics in the context of specific systems in olfaction and taste, they cover historical literature (now anything published before 1995 it seems), and provide the kind of background that will facilitate appreciation of the up-to-date advances that appear monthly, if not weekly, in our dynamic field.

This handbook will also, we hope, serve new entrants in the field, especially students and postdoctoral fellows. Each chapter has extensive citations that are an excellent guide to the current literature, and will remain so for many years. The authors have endeavored not only to review the current state of the field, but also to identify important questions and remaining mysteries. Although there have been amazing advances in the past decade and a half, there are even more questions, and more interesting questions, than there were when the last edition of this Handbook appeared.

So, how about the next edition? What will it contain? Will it appear in print or only electromagnetically? What are the advances that will be chronicled in that edition? Who will the chapter authors be? This is a remarkable era in the chemical senses. Our bet is that it is only beginning. We thank the authors for their work to chronicle its current progress and to set the stage for future discoveries.

Gary K. Beauchamp

Dedication

David V. Smith (1943–2006)

David Smith was prominent among a cohort of taste physiologists born in the 1940s on three continents, who have collectively defined – or trained those who defined – gustatory activity in the central nervous system. They learned from the founders of our discipline: Yngve Zotterman, Carl Pfaffmann, Lloyd Beidler, and Masayasu Sato. Equipped with self-styled microelectrodes, they extended recordings from peripheral axons to the small, medial neurons of this ancient sense and taught us how taste selects from a perilous chemical environment to compose a healthy body.

Even as David made his way from his boyhood home in Memphis to study psychology in Knoxville forces were aligning in a competition that was to become the central motif of his career: labeled-line versus patterning. It was a binary that always concerned David, but never consumed him, as it did others of his era. It was our primary topic of professional conversation when David and I explored the South Pacific for a month in the early 1970s, and still the focus of a chapter we wrote three decades later. However voluminous the data, however sophisticated the analyses, they have never been sufficient to seal a victory, and now the issue, still unresolved if indeed a resolution exists, lies exhausted at the periphery of the field (see Chapter 4.17 A Perspective on Chemosensory Quality Coding by M. Frank)

David was always respectful of the coding arguments from both sides, as he was of those who made them. However, he could never divorce his thinking from the central discovery of gustatory electrophysiology – that taste cells are broadly tuned – and permit himself to favor a labeled-line strategy that would seem poorly suited to that finding. Thus, David remained an advocate of patterning even as he vowed unsuccessfully, three times in my presence, never to entertain the topic again.

David trained with Don McBurney in psychophysics, then with Pfaffmann in the electrophysiological techniques that became central to his life's work. He experimented on blowflies, frogs, mice, rats, rabbits, cats, and humans, but David's primary focus was on the hamster hindbrain. Over 30 years, David generated a body of data from the hamster that complemented each component that others had revealed in rats: anatomical connections, membrane qualities, coding principles, neurotransmitters, and centrifugal influences (see Chapter 4.12

Neurotransmitters in the Taste Pathway by R. Bradley). David's thinking was creative and original; his techniques precise; his analyses sophisticated and unbiased. He did not work in large groups – across all his publications David has a mean of fewer than 1.5 co-authors – but over time he worked with scores of colleagues, learning their techniques, sharing his, and always pressing for deeper understanding (see Chapter 4.15 Central Neural Processing of Taste Information by D. Smith and S. Travers).

His objective pursuit of information absent personal agendas made David a trusted colleague and leader. The Association for Chemoreception Sciences (AChemS; Minneapolis) elected him Executive Chairperson (now 'President') in 1985. David directed the neuroscience program at the University of Wyoming in the 1970s and 1980s, the Taste and Smell Center at Cincinnati in the 1980s and 1990s, served as Vice-Chair of Anatomy and Neurobiology at the University of Maryland School of Medicine in the 1990s and 2000s, then completed his life cycle, returning to Memphis as endowed Department Chair of Anatomy and Neurobiology at the Tennessee Health Science Center. In each role, David was fair, collegial, yet demanding, as he was as Executive Editor of *Chemical Senses*.

David was in the fullness of his personal and professional life, living in the city that had called him home, surrounded by appreciative colleagues and by his wife Michiko, whose devotion David requited. In my last chat with the healthy David in 2005, he expressed as much satisfaction with his life as his modesty would permit. It was all too brief.

Thomas R. Scott