Book Reviews

The Chemical Senses

Taste, Olfaction, and the Central Nervous System. A Festschrift in Honor of Carl Pfaffmann. DONALD W. PFAFF, Ed. Rockefeller University Press, New York, 1985. 346 pp., illus. $29.95. From a symposium, New York.

My own experience with sensory neuroscience began in an undergraduate physiological psychology course in 1971. Our first reading assignment for the course was a review of the neurophysiology of afferent taste coding written by Carl Pfaffmann. In the review Pfaffmann defined the major questions in gustatory psychophysiology to be addressed through the use of current physiological techniques, reviewed the relevant results, and advanced an explanation of how neural signals in single gustatory afferent fibers might be interpreted by the brain. This short review riveted my attention to the "visceral senses" at a tender age. I suspect that this festschrift in honor of Pfaffmann may have much the same effect on advanced undergraduate and graduate physiological psychology students for some time to come.

Donald Pfaff has selected 14 papers that cover many topics currently of interest in gustatory and olfactory physiology. In the first chapter, Pfaffmann presents a brief overview of the history of investigation into the basis of taste sensation. He then launches into a typically enthusiastic discussion of his current researches, in this case on the biophysical basis of electrical taste. He concludes with a thoughtful attempt to resolve an issue concerning the chemical senses that has a history of being controversial—whether the perception of taste is based on the activation of chemospecific "labeled lines" or on the interpretation by the nervous system of parallel taste fiber activity in an "across-population" manner. Pfaffmann speculates that the chemical recognition process of the gustatory system is similar to that of the immune system as it is described by his colleague at Rockefeller, Gerald Edelman. Thus, in either system primary receptors may be just different enough from one another that a single receptor may be activated by only a very narrow range of chemical stimuli. Additionally, however, it may be possible to identify groups of these receptors with properties that are similar enough to allow each group to respond to a similar class of stimuli in a practically identical manner. Such an arrangement (termed "degenerate" by Edelman and, now, Pfaffmann) would afford either system both specificity and range in the recognition of chemical stimuli.

The debate concerning coding in the gustatory system is continued in chapters by two principal, opposing champions: Marion Frank presents a convincing argument for the existence of highly specific labeled lines in the peripheral gustatory nerves, and Robert Erickson argues that taste-specific neural channels may exist more in the mind of the investigator than in reality. These two antithetical positions are resolved to a considerable degree in the lucid discussion by David Smith of his group's multivariate statistical analysis of the response properties of pontine gustatory neurons in the hamster. Smith makes the convincing argument that, though across-population patterns of gustatory responsiveness are dominated by single neuron "types," more than one neuron type must contribute to the total gustatory neural population response to produce the distinct patterns evoked by dissimilar stimuli.

Though the study of neurophysiological coding of taste information has received substantial attention, other issues concerning the chemical senses are being examined as well, and many of them are discussed in this book. Lloyd Beidler and Keiichi Tonosaki and William Jakinovich discuss biophysical, electrophysiological, and biochemical evidence for multiple "sweet" gustatory receptor types. Bruce Oakley has updated his earlier work on neurally mediated regeneration and maintenance of taste receptor function. He concludes that the structure and function of mammalian taste buds are trophically maintained, only in gustatory epithelium, by processes requiring axonal transport in gustatory nerves. In a section devoted to the mechanisms underlying taste perception and behavioral decisions made in response to taste perception, Bruce Halpern discusses the temporal features of the decision to ingest or not to ingest the source of a particular taste stimulus. He observes that, though rats can make accept-reject taste preference decisions in less than 200 milliseconds, humans require over 500 milliseconds to react behaviorally to a taste stimulus. Halpern proves that this latency difference between rats and humans is not explained by either differences in first-order neural pathlength or "sluggish" first-order gustatory responses in humans. Rather, neural mechanisms that protect the tongue or a more complex (and slower) taste evaluation machinery may be responsible for slower human taste reaction times.

Linda Bartoshuk and J. F. Gent take on the difficult task of correlating the psychophysical phenomena resulting from the application of taste mixtures with the known anatomy of gustatory projections in the brain. These authors make the point that a good deal of the confusion and apparent inconsistency of results obtained when mixtures of different tastes are applied to the tongue may be based on essential anatomical and neurophysiological differences in the relationships between central neurons carrying taste information from different parts of the tongue. Regarding projections of gustatory afferents in the brain, Ralph Norgren describes the pathways and loci responsible for the processing of taste afferent signals and reviews the evidence that indicates that the brainstem contains the essential circuitry necessary for the production of taste preference behavior as well as of satiety and ingestion in response to metabolic deficits.

Though Pfaffmann's career has been dedicated principally to studies of the gustatory sense, he has also made major contributions to the study of olfaction. Likewise, though this festschrift deals principally with taste, the final four chapters provide a good review of several important olfactory issues. Maxwell Mozell and David Hornung discuss the peripheral mechanisms of the olfactory transduction process. They conclude from their earlier, elegant "reverse-flow" data that the olfactory mucosa acts much like a small gas chromatograph, imparting differential olfactory mucosal retention to different odorant stimuli. Additionally, olfactory receptors with differential chemospecificity may be arrayed on the olfactory mucosa to take advantage of this differential odorant retention.

John Scott continues with a discussion of the anatomical organization of the central olfactory projections, emphasizing the detailed anatomy of individual cell types in the olfactory bulb. Gordon Shepherd follows with a demonstration that central olfactory processing by the olfactory bulb is not as diffusely organized as was first thought. Indeed, he has, with the aid of electrophysiological and 2-deoxyglucose histological methods, identified a subset of olfactory bulb glomeruli that may represent the labeled line responsible for detecting nipple odor cues that direct infant suckling behavior. The book concludes with an interesting comparison by Robert Johnston of the function of the olfactory and vomeronasal chemosensory systems.

All of the chapters in this collection are well written, and together they form a fitting tribute to a remarkable career in chemosensory science.

RICHARD C. ROGERS
Department of Physiology, University of Nevada School of Medicine, Reno 89557

Three-Manifold Topology

The Smith Conjecture. JOHN W. MORGAN and HYMAN BASS, Eds. Academic Press, Orlando, Fla., 1984. xvi, 245 pp., illus. $49.50. Pure and Applied Mathematics, 112. From a symposium, New York, 1979.

What is the nature of the fixed point set of a periodic diffeomorphism of the three-dimensional sphere? Or, more specifically, can the fixed point set be a knotted circle? This is not a question likely to stir familiar and vivid images in the minds of most people or to cause public debate and conjecture. Nevertheless, it is a question that has had a tremendous influence on mathematics and that has for several years engaged some of the best research mathematicians in an attempt to find an answer.

Now, nearly 40 years after it was first clearly posed, the question has been answered. The answering of the question has gone far beyond the resolving of a fundamental question in the topology of manifolds. It is the result of a beautiful confluence of technique and knowledge from diverse areas of mathematics, and it has had a profound influence on the methods of analyzing three-dimensional manifolds. Since the publication of the seminal work that played a major role in answering the question, it is possible to find articles in popular magazines describing the study of three-dimensional manifolds. These articles attract considerable interest, particularly if they provide a metaphorical relation to the shape of the universe. Recently molecular chemists have become concerned with the symmetries of the three-dimensional sphere that leave knotted circles invariant (fixed with respect to set rather than with respect to point), and they speak of molecular graphs in the language of three-manifold topology.

At the turn of the century and into the 1920's, mathematicians were formalizing the basic concepts of topology and beginning a topological study of several mathematical objects. From the point of view of topology it is natural to study the transformations and symmetries of mathematical objects, and so it was natural to study periodic transformations that deform an object. These deformations may be arbitrary, but they never cut, tear, or puncture the object. Preceding this work by several years and using both analytical and geometrical methods, a systematic study and classification of surfaces had been carried out. Surfaces fit into the scheme of topology now called manifold topology, in which they represent two-dimensional manifolds. And so there was interest in a study of periodic diffeomorphisms of surfaces. Most relevant to this review is the study of periodic diffeomorphisms of the two-sphere.

An understanding of periodic diffeomorphisms of the two-sphere followed the work of L. E. J. Brouwer and B. Kerekjarto done in the 1920's (although there were gaps that were filled by S. Eilenberg in 1934). Brouwer and Kerekjarto's work showed that an orientation-preserving, periodic diffeomorphism of the two-sphere is equivalent to a rotation about an axis. In other words, any orientation-preserving, periodic diffeomorphism of the two-sphere is precisely as one would imagine it to be.

In a sense, the study of three-manifolds, as well as of all higher-dimensional manifolds, can be thought of as a generalization of the study of two-manifolds. It was in this context that P. A. Smith wrote a series of papers in the 1930's and 1940's in which he examined periodic homeomorphisms of the n-dimensional sphere. He discovered that certain topological invariants of the fixed point set of a periodic diffeomorphism of an n-sphere were the same as those of a lower-dimensional sphere. Interpreted in the special case of a nontrivial, orientation-preserving, periodic diffeomorphism of the three-sphere, the work of Smith means that a nonempty fixed point set is precisely a circle. (The word "circle" is used in the general sense here, as a space topologically equivalent to a round circle in the plane.) For every positive integer $n > 1$ there are orientation-preserving diffeomorphisms of the three-sphere, periodic with period n and having as a fixed point set an unknotted circle. A circle in the three-sphere is considered unknotted if there is a self-diffeomorphism of the three-sphere taking the given circle onto a round circle determined by the intersection of the three-sphere and a two-dimensional linear subspace of Euclidean four-space. Smith then asked if there are knotted circles that arise as fixed point sets of orientation-preserving, periodic diffeomorphisms. The negative answer to this question became known as the Smith conjecture.

In the fall of 1978, the Smith conjecture was proved to be correct. In the spring of 1979, a symposium was held at Columbia University on the solution of the Smith conjecture. It was an exciting time. The principal participants in arriving at the solution presented the various pieces of the proof. There was an electricity in the air, for it was recognized that this was the beginning of a new era in three-dimensional topology. The proof, as its beauty finally emerged, represented ideas and techniques from several areas of mathematics, including classical three-manifold topology, hyperbolic geometry, Kleinian groups, the algebra of matrixes, and minimal surface theory. The symposium was also an occasion for a tribute to Smith, who had spent most of his mathematical life at Columbia University and lived in retirement in the neighborhood.

The volume edited by Morgan and Bass contains written versions of the presentations given at the symposium. In addition, there are two papers containing generalizations of the methods used in the proof of the Smith conjecture, as well as one presenting a discussion of the situation in higher dimensions.

The history of the Smith conjecture and the outline of its proof, explaining, with a "flow diagram," how the various pieces of the proof fit together, provide a spectacular example of the powerful techniques employed in the proof and of the relation among the various areas of mathematics. This subject is capably dealt with in the book by Morgan.

The general theme of proof is credited to W. Thurston. However, several other individuals were involved in creating the final solution, and at least three new and major contributions to the theory were introduced. These new contributions, combined with recent discoveries from classical three-manifold topology, provided the pieces necessary for an answer.

The proof begins with the assumption that one has a nontrivial, orientation-preserving, periodic diffeomorphism of the three-sphere that has prime power