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CARL PFAFFMAN

1913—1994

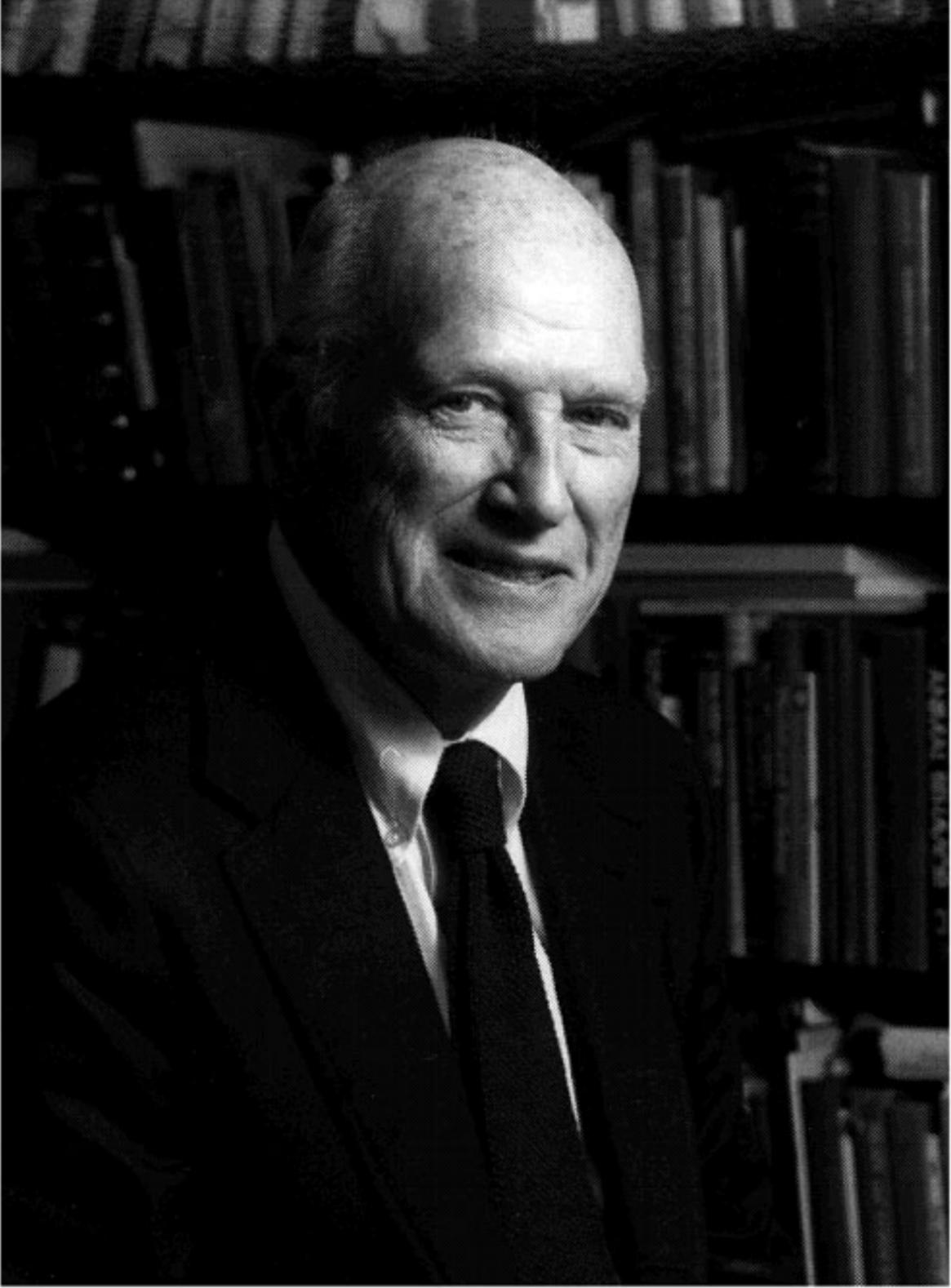
A Biographical Memoir by

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Biographical Memoir

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May 27, 1913–April 16, 1994

BY LORRIN A. RIGGS

A RHODES SCHOLAR is chosen for scholastic abilities, for such qualities as truthfulness, courage, kindness, and devotion to duty; for moral force of character and instincts to lead and to take an interest in others; and for physical vigor and sportsmanship. Carl Pfaffmann was awarded a Rhodes scholarship while he was a graduate student at Brown University. Already he had shown the qualities listed above. He had graduated from Brown *magna cum laude*, with honors in psychology; he had played saxophone in orchestras and dance bands; he had been involved with the swimming team; and his scholarship had earned him the respect of Leonard Carmichael, then chairman of the psychology department, who had invited him to join the teaching and research activities of the laboratory. From this beginning Carl went on to a career in which his all-around talents took him to a position of world leadership in his chosen academic field of the chemical senses of taste and smell.

Carl Pfaffmann was born in Brooklyn, New York, on May 27, 1913. All four of his grandparents had emigrated from Germany and lived in New York City as their families grew up. Carl's parents, Charles and Anna Pfaffmann, had to work hard and never went to high school. By the time Carl

was born they had achieved sufficient success to purchase a home on Long Island and to give him the opportunity to attain the education they never had. Carl, in turn, did well enough in school to qualify for rapid advancement and to graduate from high school with honor grades at the age of sixteen.

Next came college at Brown. As a freshman Carl undertook an ambitious schedule of earning tuition money, participating in sports and concert tours, and working hard at his studies. During his sophomore year he discovered the academic field that was to dominate his whole future career. This came about because of a young and enthusiastic professor, who in Carl's words (1989) "had been recruited from Princeton to head and modernize the development of a psychology department at Brown." Listening to lectures and observing experiments performed by Carmichael persuaded Carl that here was an exciting new field for his own future career. Furthermore, on consultation with Carmichael, he found that a good opportunity to get personally involved was to enroll in the honors program. Carmichael suggested, in fact, that Carl do experiments and write an honors thesis on the subject of human taste sensitivity. This subject was selected because relatively little was known about it in comparison, say, with vision or hearing. It appealed to Carl's pioneering spirit that he could open up new findings in an uncharted field.

On graduating from Brown, Carl considered various options for continuing work on the chemical senses. He chose to stay at Brown because Carmichael had been successful in building up a graduate program and had offered him a teaching assistantship. Furthermore, he could go with a research assistantship to the nearby laboratory of Herbert Jasper, who was doing pioneering work with the recording of human brain waves. Jasper's electrophysiological record-

ing equipment provided Carl with the opportunity to record nerve impulses in animals in response to tactile stimuli and chemical solutions. This research was reported in a 1935 publication with Jasper. Carmichael, who was also working with Jasper at the time, was so impressed by Carl's research that he urged him to apply for a Rhodes scholarship. The Rhodes award was made in 1935, and Carl spent the next two years at Oxford University. By this time he had convinced himself that a necessary part of his career goal was to do research on the neurophysiology of taste; but because he had no formal training in physiology, he devoted the two years at Oxford to the achievement of a B.A. degree in that subject.

Carl's third and fourth years of the Rhodes program were devoted to research for a Ph.D. degree from Cambridge University. This was in the famous physiological laboratory of Lord Adrian, and the only degree requirement was for an original thesis. Carl set for himself the ambitious goal of recording the responses of taste nerve fibers in the cat. The aim was to "crack the code" of how different types of taste quality were mediated by the receptors and afferent nerve fibers from the tongue.

Going into this program of research, Carl was familiar with the psychologists' current classification of basic taste components as sweet, sour, salty, and bitter. He thus anticipated that, if he could successfully isolate individual sensory fibers from the cat's tongue, each fiber would be found to respond differentially to sugar, acid, salt, or quinine; but his initial attempts to isolate single taste fibers were unsuccessful. The lingual nerve of the cat was made up primarily of nontaste-sensitive fibers whose responses "drowned out" those that responded to chemical stimuli; but persistent efforts at dissection, together with a judicious use of newly developed recording techniques, finally resulted in the iso-

lation of responses in single units responsive to chemical stimulation. Then came the surprising result: every fiber responded to acid; some of them to acid plus salt, some to acid plus quinine, and some to acid alone. No response to sugar was ever found. The conclusion Carl drew from this pioneering work was that the coding for taste discrimination must be based, not on sensory units (each of which is tuned to a particular type of stimulus) but on an across-fiber pattern of response that the brain uses to identify specific tastes. Thus, acid would be identified by the cat if all of its taste fibers were active: bitter, if only the fibers sensitive to acid and bitter were involved; salt would be signaled by the acid-salt fibers. The absence of a sweet-sensitive system was later shown to be characteristic of the cat; some taste fibers in monkeys and other animals, presumably including humans, are strongly affected by sweet substances. Furthermore, responses to sugar have been shown to be more prevalent in the glosso-pharyngeal and petrosal nerves than in the chorda tympani, from which the original recordings were made.

Carl submitted his dissertation on taste nerve responses to his mentor at Cambridge, but Adrian declined to read it, saying that Carl should first give it to the examining committee and defend it himself against possible criticisms. Adrian, it seems, was insistent that the dissertation be judged as the original work of the candidate, not modified by any ideas of the thesis adviser. Is this too lofty an ideal to be maintained in our present-day evaluations of a dissertation?

The clouds of World War II were gathering in Europe as Carl completed his work at Cambridge. At this point an opportunity for postdoctoral research became available to him back in the States. This was at the Johnson Foundation for Medical Physics at the University of Pennsylvania. The invitation to Carl was from Detlev Bronk, who had estab-

lished the foundation after doing research at Cambridge with Adrian. The year of 1939-40 in Bronk's laboratory gave Carl additional experience in the recording of nerve impulses from single fibers. Carl was the third psychologist to have been at the Johnson Foundation, the earlier ones having been Clarence Graham and Lorrin Riggs.

In 1939 Carl married Hortense Louise Brooks, whom he had met at Oxford. They had three children, Ellen Anne, Charles Brooks, and William Sage.

In 1940 Carl received an appointment to the faculty of Brown University. By this time Walter Hunter had succeeded Leonard Carmichael as head of the psychology department. Hunter's goal was to build up a center for physiological and experimental psychology, and other appointments went to Graham, Lindsley, and Riggs. World War II intervened, and all of us, including Hunter, had to devote our efforts to various military causes. Carl was commissioned an officer of the U.S. Naval Reserve, advancing to the rank of Commander in 1945. His service included experiments on visual factors related to aircraft landings.

At the war's end Carl was able to embark on a professional career of research, teaching, and administration. First at Brown University (1945-65) and then at Rockefeller University (1965-94) he pursued the problem he had uncovered during his graduate study: how can we identify and discriminate the basic taste components of sweet, sour, salty, and bitter given that each of the individual sensory units responds to more than one type of stimulus? The answer gradually emerged from a prodigious amount of research by Carl and his teams of co-workers, as well as by colleagues working in this field throughout the world.

When Carl returned to Brown after the war he found it to be a stimulating environment. Hunter, who had been a leader among the psychologists working on military prob-

lems, had now turned his efforts to securing grant funds, laboratory facilities, and professional staff for the Department of Psychology. Realizing that the department was relatively small, and housed in old frame houses, he aimed to concentrate its efforts on sensory and physiological psychology. Thus, Carl was given a generous allotment of space for his research on the chemical senses.

On the teaching side, also, the mood at Brown was one of enthusiasm and expansion. Students returning from military service were unusually mature and dedicated to academic achievement. Supported by grants for their tuition under the G.I. Bill, they enrolled in record numbers. This in turn had the effect that the faculty and staff could be expanded. Graduate students could be supported by teaching and research assistantships. Faculty members were solicited by national agencies, notably the Office of Naval Research, for the purpose of underwriting projects of their own choosing in the areas of sensory and physiological psychology. This support meant that faculty members could build up their laboratory facilities, hire secretarial help, pay their assistants, and avail themselves of funds for travel to professional meetings. Under these favorable conditions research teams were formed with members of the faculty, graduate students, postdoctorals, and scientists from other institutions.

Carl found that he could design an effective experimental program at Brown, making use of these favorable surroundings. During the twenty-one years of his tenure at Brown he published thirty-eight research articles, seven chapters in books, fourteen abstracts of reports at meetings, four articles on the methodology of teaching, five articles for encyclopedias, and three biographical articles. His research, much of it conducted jointly with colleagues, graduate students, and postdoctoral fellows, involved a variety of

methodologies employed in the study of taste. These included neurophysiological recordings from gustatory nerves and observations of the feeding behavior of experimental animals. Human subjects made psychophysical determinations of sensitivity and qualities of experiences of taste and smell.

Among his research collaborators at various times were Abbott, Bare, Bartoshuk, Benjamin, Carpenter, Erickson, Frank, Frommer, Hagstrom, Halpern, Hockman, Johnston, MacLeod, Matthews, McBurney, McCutcheon, Morrison, Mozell, Nord, Oakley, and Pierrel. Most of them lived on or near the Brown campus, as did the Pfaffmanns. Carl and his wife Louise were active in campus activities. Every year they hosted a Christmas party, mainly for the psychology department.

These were happy years for all of us. First Walter Hunter (1946-56) and then Harold Schlosberg (1956-66) were benevolent chairmen of the department, making sure that each member could attain his own goals without competition with the others. Neither Carl nor I was pressured into becoming the department chairman. One sad time was when we heard that the Pfaffmann's first son Charles had died in an aircraft accident.

A major expansion of our facilities at Brown occurred in 1957-58 with the construction of the Hunter Laboratory of Psychology. Carl was able to move his experiments into specially designed basement rooms, where he and his team of co-workers could be together and share their equipment and plans. In another portion of the basement a vision research unit was established under my leadership. The two of us worked together harmoniously; vision was a field more highly developed while the study of the chemical senses was more of a pioneering effort in which new findings could be uncovered by a relatively small number of workers.

During his years at Brown, Carl first turned his attention to neurophysiological experiments in which he and his colleagues explored the roles of taste fibers they found in portions of the seventh, ninth, and tenth cranial nerves. Their single-fiber recording from the chorda tympani, for example, gave beautiful records in which the impulse frequency increased progressively in response to higher and higher concentrations of the stimulating solution. Thus, the neural coding for stimulus magnitude was shown to be similar to that which had been established for the senses of vision, hearing, and touch. The coding for taste quality, however, turned out to be much more complex. Each single fiber did respond most vigorously to stimulation of the tongue by a particular chemical substance, but the same fiber might respond, albeit less vigorously, to other substances as well. Some fibers had a high sensitivity for two or more types of stimuli. These results on the rat confirmed and extended the findings in Carl's original thesis on the cat. Detailed studies by Beidler and others showed that even individual sensory cells exhibited this multiple sensitivity. Thus, it was concluded that an animal's ability to distinguish the various types of chemical solution must depend on the brain. The brain centers must be able to analyze out the separate taste qualities from the barrage of lingual nerve impulses. This is the theory that Carl called the "across-fiber patterning" hypothesis.

Further experiments by Carl and his students revealed that certain chemical substances had similar abilities to arouse taste nerve responses. This generalization resembled the stimulus similarity reported by human tasters for certain classes of chemical substances. This resulted in an adaptation in which the neural responses to that substance were diminished or eliminated. Related substances then showed a "cross-adaptation" in which there was also a diminished

response. This type of generalization occurs also in vision and other senses with human and animal subjects. Carl's student Erickson developed a quantitative analysis of the combinations of neural response that led to judgments of taste quality.

Stimulus deprivation experiments also were conducted by Carl, initially with his student Bare. They found that, while cravings exist for salt or sugar in animals deprived of these substances, there is no evidence that this results from any diminution of taste sensitivity. More generally, it can be said that food preferences depend on central as well as receptor factors. Experiments have been performed in which lesions in the hypothalamus and other regions have altered the feeding behavior of animals. Human food intake is facilitated by "taste enhancers" and other aspects of the environment. Genetic factors are shown dramatically in the case of "taste-blind" subjects, who lack the ability possessed by most individuals to experience bitterness of a test substance, phenyl thiocarbamide.

Further psychophysical experiments revealed a spatial summation on the tongue, such that small areas required strong solutions for their arousal. Moreover, good taste discriminations required that large tongue areas be covered by the stimulating solutions. Saliva played a role also; in some cases a prior rinse with distilled water rendered the tongue much more sensitive.

With all this enterprise devoted to the sense of taste, Carl was not unmindful of the importance of smell. He always included olfaction in his writings on the chemical senses, and he did conduct some experiments in olfaction with colleagues and students at Brown. For practical reasons, however, he devoted a major part of his research to the taste experiments, leaving to others the task of analyzing the principal facts and interpretations of olfaction. His ex-

expertise in the evaluations of taste and smell led to his occasional involvement in setting up panels of tasters for the food industry. One of Carl's most important articles, "The Pleasures of Sensation" (1960), brought out the predominant role of the chemical senses in the hedonic side of human experience.

Brown University has always been an institution where undergraduate teaching is considered a duty and an art. Carl entered enthusiastically into a seminar program that President Wriston had introduced under the heading of "The Identification and Criticism of Ideas." To quote from Carl's own account (1984):

I agreed to handle the second semester, which began with reading Freud's original lectures on psychoanalysis (in English edition, 1952), followed by the modern behavioral extensions and reinterpretations thereof. This meant that I personally had a great deal of new reading and preparation to do, both ahead of time and during the second semester.

Carl also undertook, with his colleague Harold Schlosberg, development of an undergraduate teaching laboratory in which students obtained firsthand practice in the methods of experimental psychology. They were also taken on visits to nearby mental hospitals and clinics. The success of the whole enterprise led to an expansion of the faculty and graduate teaching assistantships during the 1950s.

By the end of the 1950s Carl's reputation had spread far beyond his own university. He was elected in 1959 to the National Academy of Sciences¹ and soon became chairman of its Assembly of Behavioral and Social Sciences. He became a delegate to the Academy's counterpart societies and laboratories in the Soviet Union. He was elected President of the Eastern Psychological Association and of the Division of Experimental Psychology of the American Psychological Association. In 1959, together with Lloyd Beidler

and Yngve Zotterman, he founded the International Symposium of Olfaction and Taste, which still meets every three years with the International Congress of Physiology.

In 1965 Carl was chosen by President Bronk to become a vice-president and professor of the Rockefeller Institute for Medical Research. Carl was given the challenge to build up the biobehavioral sciences. This move was part of a plan to broaden the institute, with a view to attaining the status of a university. Bronk's other moves in that direction included new appointments in physics, mathematics, and philosophy.

Responding to the challenge, Carl first persuaded Neal Miller to leave his very prestigious chair at Yale and join the faculty at Rockefeller. Next he recruited two other distinguished psychologists, William Estes from Stanford and George Miller from Harvard. At the same time a joint program of the New York Zoological Society enabled the Rockefeller Institute to attract Donald Griffin from Cornell and Peter Marler from Berkeley to establish a program of research in animal behavior. The official name change to Rockefeller University occurred in 1967, and the biobehavior group continued to thrive after the retirement of Bronk and the subsequent (1968-78) administration of Frederick Seitz as president.

Neal Miller extended his research and training activities to include a unit of the New York City Hospital on Roosevelt Island. He and his students and colleagues demonstrated the success of behavioral training techniques for the rehabilitation of patients with neurological disorders. Griffin and Marler established a field station for animal behavior research on property given to the university in Milbrook, New York. There they pursued basic research on genetic and learned influences on patterns of singing behavior in birds.

Carl's own laboratory at Rockefeller became a world-class

center for research on the chemical senses. Despite his administrative duties Carl devoted much of his time to working with postdoctoral students and junior faculty members. Among these were Bernard, Coutreras, Costanzo, Frank, Grill, Herness, Leonard, Meredith, Norgren, Nowliss, Pfaff, Ralls, Scott, Singer, Smith, and J. and S. Travers. He was called on also to contribute many articles and summary chapters, and he gave lectures at international meetings.

Coding of taste quality continued to be a major concern in Carl's Laboratory of Physiological Psychology. Work on the specificity of monkey taste neurons by one of his students, Marion Frank, led him to reevaluate the across-fiber patterning hypothesis. The monkey experiments revealed that each taste neuron was typically activated most strongly by one particular stimulus. Other stimuli might also be effective but to a lesser degree. This led Carl to conclude that the test stimulus gave a "clue to their labeled-line significance, that is, their primary quality." He felt that this view of the neurophysiological data could be seen as consistent with the psychophysical finding of primary taste qualities.

Carl's earlier interest in the hedonic importance of the chemical senses was given substantial foundation in new discoveries of taste fiber projections into the limbic system. These studies were accompanied by behavioral measures of feeding behavior and sexual activity that were conditioned by specific taste and smell stimuli in the same experimental animals.

Experiments with human subjects made use of taste sensations elicited by electrical or chemical stimulation of spots on the tongue. Other studies involved individual differences among normal subjects and subjects with a specific taste disorder.

Carl experienced a considerable disappointment after the retirement of President Seitz in 1978 and before his own

retirement in 1983. Administrative support for his program was cut back. As a result, Estes left Rockefeller in 1979 to go to Harvard, and George Miller left the same year to go to Princeton. Neal Miller stayed on for two more years until his retirement, and Carl himself retired two years after that.

Carl's successor as head of the laboratory was Donald Pfaff, who had been a member of Carl's group for many years. Under a new name, Laboratory of Neurobiology and Behavior, the group continued to study the biological bases for behavior; but, in line with national and international trends in this field, they identified themselves with the newly expanding organizations of neuroscience, rather than the traditional ones in physiological and comparative psychology.

Carl's autobiography, written after his retirement, gives a retrospective view of his accomplishments. He gave enthusiastic credit to his early mentors and later colleagues who had an influence on his career. Among these were Carmichael, Adrian, Bronk, Zotterman, Bujas, and Beidler. He expressed particular satisfaction in his "family" of graduate students and postdoctorals in the laboratories at Brown and Rockefeller. They gathered to celebrate his seventieth birthday at the annual meeting of the Association of Chemoreception Sciences in 1983. He gave approval to a new program for clinical taste and smell research centers organized with advice from his former students Bruce Halpern and Max Mozell. One of these centers was cofounded by one of his former students, Linda Bartoshuk, and is now directed by another, Marion Frank. Another center, emphasizing research in olfaction, is operated by Max Mozell. Carl never became caught up in any theoretical framework for his accomplishments. He was satisfied with the empirical discovery of new facts, and a good part of his life was devoted to the estab-

lishment and administration of research facilities for that purpose.

The last few years of Carl's life were spent at his home in Killingworth, Connecticut. In his late seventies he suffered irritating and sometimes painful skin ailments. He was also afflicted with a rare condition called Ramsey-Hunt syndrome in which there is a deterioration of some of the cranial nerves. One aspect of his own symptoms was particularly intriguing to Carl: Ramsey-Hunt was known to affect taste nerves. He therefore called upon his former student and co-worker Linda Bartoshuk to make a psychophysical study of these effects. Shortly after this he suffered a stroke that ended his life.

In looking back over Carl's career I am reminded again of the attributes of a Rhodes scholar. His superb scholarship was accompanied by an ability to inspire and direct the activities of his students, and he was warmly respected by his colleagues. He was a devoted husband to Louise throughout their marriage of fifty-five years and a loving father to their children. The discoveries and writings based on his pioneering dissertation at Cambridge blossomed into the present huge corpus of literature on the chemical senses.

IT WAS A PRIVILEGE to be associated with Carl at Brown University, where our laboratories were adjacent to one another from 1945 to 1965. In describing earlier and later events of his career I have relied heavily on his 1989 autobiography. I am particularly indebted to his former student and colleague Linda Bartoshuk for supplying me with publications and for helpful comments on the present memoir.

NOTE

1. It is remarkable that membership in the National Academy of Sciences was attained by ten out of the relatively small group of psychologists at Brown during the Pfaffmann years.

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