

A Special Issue Honoring Alan Peters



This issue of *The Journal of Comparative Neurology* celebrates the person and career of Alan Peters, Waterhouse Professor and Chairman of the Department of Anatomy and Neurobiology at Boston University Medical School. Alan is well known for his numerous and elegant contributions to neurocytology and to our understanding of the texture of the central nervous system. The idea for this issue was proposed about two years ago by Alan's former students and postdoctoral trainees as an expression of their gratitude for his contributions to science and to their professional lives. We hope that this issue will be a source of pride for Alan, as he recognizes that many of those who trained with him have become successful and independent scientists and teachers. Alan's influence has touched many. When colleagues learn that we have trained with him, they tell us that they would take the latest edition of *The Fine Structure of the Nervous System* into the darkroom while they prepared electron micrographs and would try to match the quality of their pictures with those in the book. This example is just one indication of the esteem that Alan's work commands in the neuroscience community. His students learned to strive for the level of excellence that he set for himself and practiced. We hope that his work will continue to inspire and encourage succeeding generations of neuroscientists. We thank Janet Harry, Alan Peters's Administrative Assistant at Boston University for providing information and Terri Segneri, at the M.S. Hershey Medical Center, for secretarial assistance.

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A Memoir in Appreciation of Alan Peters on his Sixty-Fifth Birthday

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Alan Peters first came to the United States in 1963 as a Visiting Lecturer in Anatomy at the Harvard Medical School. He had received his university education at the University of Bristol, including his doctorate nine years earlier, and he had been a Research Fellow and Lecturer at Edinburgh University in Scotland. I first met him at a meeting of the Anatomical Society of Great Britain and Ireland near the end of 1961, and I visited him in Edinburgh a few months later. He struck me even then as an energetic, enterprising young scientist, well on his way to a successful scientific career and likely to make significant contributions to our knowledge of the structure and function of the nervous system. My favorable impression of him at that time was shared by the officers of the Anatomical Society, who awarded him the Symington Memorial Prize in 1962. He had already published articles on silver staining, including electron microscopy, and he had examined the structure and development of myelin sheaths in both the central and peripheral nervous systems. He was one of the first to show that myelin in the central nervous system has a spiral architecture, just as in peripheral nerves. In the process he had discovered a radial component in central myelin, the significance of which would not be elucidated until nearly two decades later. At Harvard, in 1963 and 1964, he analyzed the synaptic architecture of the lateral geniculate body of the cat in a pioneering electron microscopic study of thalamic glomeruli. These early investigations established the major themes for the rest of his scientific career: the fine structure of neurons and the neuroglia, the structure and development of myelin sheaths, the architecture and organization of the visual system, especially the visual cortex, and the aging brain. At the end of his Visiting Lectureship he returned to Edinburgh and continued his work on the myelin of nonamniote vertebrates.

In 1965, when Arnold Relman, the chairman of a committee to select the next Waterhouse Professor and Chairman of the Department of Anatomy at Boston University, came to me with a request for my opinion of several candidates on his short list, I had no hesitation in commending to him the name of Alan Peters. The excellence of Alan's accomplishments and his energetic pursuit of neurocytological questions supported the nomination, and in 1966 he returned to Boston to create one of the most vibrant departments of anatomy in the country. His commitment to teaching has been demonstrated not only in his lectures to generations of medical and dental students, but also in his training of 16 graduate students and 14 postdoctoral fellows during the 29 years of his tenure as head of the department.

It is difficult now to imagine the state of neurocytology when Alan began his work in electron microscopy. Although the structure of nerve cells, axons and dendrites,

and the chemical synapse had been clarified, there was still a great deal of controversy about the identification of neuroglial cells, the structure of the membranes in the myelin sheath, the relation between oligodendroglia and myelin in the central nervous system, and the relation of microtubules and neurofilaments to the argyrophilia of nerve fibers. Our understanding of the organizational structure of the central nervous system had hardly progressed beyond the monumental work of Ramón y Cajal at the beginning of the twentieth century. Neuroscientists still imaged the nerve cells as suspended in a great sea of extracellular space, black silhouettes connected to one another by permanent, genetically predetermined wiring. Although early in this century, Ramón y Cajal had espoused a much more dynamic vision, this static view of the nervous system prevailed and was reinforced by the schematic renditions of Golgi-impregnated nerve cells given in commonly used textbooks.

As the techniques for electron microscopy rapidly improved during the late 1950s and 1960s, this rigid view of the nervous system gave way to the current concept of a plastic, morphologically and functionally dynamic system. I do not mean to suggest that electron microscopy was alone, or even mainly, responsible for this change in attitude, but it was influential. It showed that nerve cells contained the same intracellular structures as cells in other tissues. It showed that nerve cells and neuroglial cells, like cells in other epithelia, occupied almost all the space in their organs, leaving only a very small proportion for extracellular space. It called attention to the intercellular relationships. Alan Peters contributed significantly to all of these developments. He provided direct evidence of the continuity of oligodendrocyte processes to the myelin sheath and examined the node of Ranvier in the central nervous system. He characterized astrocytes in the developing optic nerve and recognized the unique morphological features of the axon hillock and initial segment in cells of the cerebral cortex. Together with James Vaughn, then his postdoctoral fellow, he discerned a variety of neuroglial cell that appeared to be a precursor to the classical macro- and microglia or a reserve stem cell. He began studies on the small pyramidal cells of the cerebral cortex with Ita Kaiserman-Abramof, which later blossomed into a detailed examination of the architectural patterns and connections of the cerebral cortex.

Toward the end of his first sojourn in Boston in 1964, Alan had proposed that we should prepare a book explain-

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ing the discoveries of the first decade of successful electron microscopy of the nervous system. I counseled delay until the field had advanced further, as there were still many problems that would probably be resolved while the book would be in press. On his return to Boston, after he had settled in his department, Alan brought up the question again. Now it appeared that the time was ripe. A number of beautiful atlases of electron micrographs of cells and tissue had already appeared, notably two by Porter and Bonneville (1963 and 1968) and by Fawcett (1966), but for all their merits these books were essentially illustrations with extended figure legends. The intricate morphology of the nervous system required a more ample discussion, an illustrated text rather than an atlas. The Paul Hoeber Company, which had a list of neuroscience books, was interested in producing it. After enlisting the collaboration of Henry deF. Webster, we set about writing the text and selecting electron micrographs for illustrations.

At the end of the summer of 1968, *The Fine Structure of the Nervous System, The Cells and Their Processes*, was ready for the publisher. But in the two years that it had taken us to complete the book the publisher had been swallowed by Harper & Row and now had different goals. Not trusting the ordinary mail, Alan and I packed up the typescript with the figures mounted on boards and took the Eastern Shuttle from Boston to New York. We found the editorial office in serious disarray. Hardly anyone whom we had previously dealt with was still on the staff. They received our packages with courtesy but without enthusiasm. It was an inauspicious beginning. Nevertheless they agreed to provide us with sample copies of the illustrations for our approval before going ahead with the press run. In due course we received full-page reproductions of four or five figures by the letterpress method. Although their quality was rather good, we offered some suggestions for improvement, especially to increase the contrast. The printers, a company in Forge Village, Massachusetts, promptly decided that we were too demanding and withdrew from their contract. Hoeber/Harper found another printer, in Princeton, New Jersey, but they were primarily color printers, and they proposed to reproduce the illustrations by offset, a method with which we were then unfamiliar. With some trepidation, we accepted these changes, and the publication slowly went forward. In the end, the illustrations were acceptable, and the book came out in 1970 under the imprint of the Hoeber Medical Division of Harper & Row. Although the publisher announced the book only once and never advertised it, the entire print run of some 5000 copies sold out. By 1973, the book was out of print, the field had made enormous advances as neuroscience rapidly expanded, and numerous colleagues urged us to prepare a new edition. When we approached the publishers, Harper & Row, they told us that they were not interested in small volume printings, but that they would sell us the right to take the book to another publisher for \$500. Fortunately, when we signed the original contract, our attorney had insisted that one of us, Alan, should hold the copyright. Thus, Alan was able to inform Harper and Row, politely, that we owned the copyright and would seek another publisher without paying them anything.

After considering various publishing houses, we settled on Saunders, partly because of their excellent production and promotion of the several editions of Bloom and Fawcett's *Textbook of Histology* and Fawcett's electron microscope atlas, *The Cell*, and because the editor, John Dusseau,

promised to see the production of the book through to the end. The preparation of the second edition was a much more onerous undertaking than the first. The pertinent literature had increased by more than a thousand references; new techniques, such as freeze fracture, scanning electron microscopy, and tract-tracing with radioactive amino acids and horseradish peroxidase had come into use, and many new findings had deepened our insight into the structure and function of the nervous system. We retained only 30 of the micrographs from the original edition and inserted 88 new plates. When the second edition appeared in 1976, with a slightly altered subtitle, it was a new book almost three times as large as the first.

Still, it had its share of misfortunes. Mr. Dusseau ordered 9000 copies to be printed, but when the first set were to be bound the binders at Saunders were on strike. As the labor dispute lingered for weeks, Mr. Dusseau became concerned that our book would be delayed. He contracted with another company to bind 3000 copies of the book. With great pride he rushed off the first copies to us. Unfortunately, the binders had not received accurate instructions and had trimmed the pages incorrectly, leaving white margins on the top or bottom and cutting off labels that were close to the right edge. We never learned how the publishers disposed of the defective copies.

The second edition also succeeded with a large audience, and by the early 1980s it, too, was out of print. When we began to prepare a new edition in 1987, we learned that Saunders (which had meanwhile been swallowed up by a large conglomerate) was not interested in small press runs and would release us from the contract. The success of the book, however, attracted a number of less commercially minded publishers, and after much deliberation we settled on the Oxford University Press (which we thought was not likely to be bought up by some giant corporation during our lifetime). The persistence of Jeffrey House, editor at Oxford, also had a great influence on our decision. The third edition was ready for the annual meeting of the Society for Neuroscience in November 1990 and came out with the date of 1991. This revision was thoroughly rewritten and was illustrated with 137 figures, 51 of them new. The Oxford Press did a superb job of reproducing the electron micrographs and many of them were better than in the previous editions. Upon publication the book was selected by the Science Book Club for its members.

The Fine Structure of the Nervous System has had an enormous influence on the field of neurocytology and has instructed generations of neuroscientists in the structure of the nervous system as well as set the standard for successful electron microscopy in morphological research on these difficult tissues. As the principal author of the book in all of its editions, Alan deserves the major credit for this achievement. A measure of its influence is seen in the identification of the book as a Citation Classic in *Current Contents, Life Sciences*, June 3, 1991. At that time the first two editions had been cited in more than 1,585 publications, an unusually strong showing for a book.

As mentioned above, Alan showed an early interest in exploring the architecture of the cerebral cortex, especially the primary visual cortex in rats and monkeys. The work began with a series of electron microscope studies of pyramidal and nonpyramidal cells in the sensorimotor cortex of rats in the late 1960s and early 1970s with his colleagues, Ita Kaiserman-Abramof, C. Proskauer, Mary T. Walsh, Deborah Vaughan, and Martin Feldman. These

studies provided preliminary generic descriptions of pyramidal cells and stellate cells in the cortex. In the course of this work Alan discovered the pattern of dendritic bundling in the cortex, at about the same time as Fleischhauer and his colleagues in Germany.

The analysis of the cortex was given considerable impetus by the development of an efficient method for combining the Golgi impregnation method with electron microscopy. This method, developed by Alfonso Fairén while working in Alan's laboratory (1975–1977), involves the replacement of the usual silver chromate precipitate within neurons by gold toning. This method has the advantage of marking impregnated neurons with fine particles of gold while preserving their intracellular organelles fairly well. Thus, a cell identified in the light microscope by its size, shape, and cytology can be recognized in an electron microscope section through the same region by the identifying gold particles in its cytoplasm. Using this method, Alan and his coworkers carefully examined the large and small pyramidal cells, codified some eight or nine classes of nonpyramidal cells, described the kinds and distributions of afferent fibers ending on the surfaces of different neurons, and correlated some of these cell types with immunocytochemical markers for neurotransmitters and peptides. The application of antibodies to microtubule associated protein 2, which detect the microtubules of dendrites and perikarya, provided an important marker for the analysis of the cellular organization of the cortex.

These studies culminated in the elaboration of a comprehensive organizational plan for the cerebral cortex, consisting of unitary, vertical columns of pyramidal cells and their apical dendrites, the pyramidal cell modules. This plan was a distant descendant of Mountcastle's 1978 proposal that the cortex is composed of minimal vertical clusters of cells, called minicolumns. The Peters plan demonstrated the composition of the columns, their center-to-center spacing, and their relationship to the cytochrome oxidase blobs in layer II/III, and the honeycomb pattern of cytochrome oxidase in layer IVA. Because these are correlated with the distribution of color sensitivity, ocular dominance, and direction selectivity in the visual cortex, the neurons in any one pyramidal cell column probably mediate a common physiological response. Individual and neighboring modules could be connectionally assembled into larger units, such as ocular dominance columns. Thus the pyramidal cell modules can be conceived of as the basic architectural and functional units of the cerebral cortex. This concept provides an important scaffold for our thinking about how the cortex operates and how it is modified from place to place to perform the specific functions peculiar to its different topographic regions. The elaboration of this organizational principle reflects sustained, careful, precise, and insightful meditation upon the problem, together with meticulous morphological and experimental observation, characteristics that have distinguished Alan's work throughout his career. For his significant contributions to the understanding of cortical architecture, Alan was invited to give a Special Lecture to the Society for Neuroscience at its annual meeting in Phoenix in 1989 and the 22nd annual Pinckney Harman Lecture to the Cajal Club at its annual meeting in Philadelphia in 1990. In 1991 the Cajal Club presented him with the Krieg Cortical Discoverer Award in honor of his achievements.

In the early 1980s, Alan joined with Edward G. Jones in the production of a series of multiauthored volumes on the

cerebral cortex, published by Plenum Press of New York. Originally, the publication was conceived of as a treatise "reviewing the present state of knowledge of the structure and function of the cerebral cortex" to consist of perhaps six or seven volumes covering cellular and regional morphology, physiology, evolution, development, and experimental and natural pathology. They recruited a large roster of the world's experts to write authoritative and highly informative chapters. Both Alan and Ted wrote numerous chapters themselves or with the aid of colleagues. The treatise expanded to nine volumes and then to ten. The first volume appeared in 1984 and the series is still going on. The books provide a highly useful, authoritative, and current account of the cortex. They have proved to be an indispensable reference for all students of cortical structure and function.

Alan's activities over the years have not been limited to his research work and his teaching or administrative duties. He has served as a member of the Anatomy Test Committee for the National Board of Examiners, setting anatomical questions for the National Board Examinations (1972–1975). He was a member of the Neurology B Study Section of the National Institute for Neurological Diseases and Stroke from 1975 to 1979, serving as chairman during the last year of his membership. He was President of the American Association of Anatomy Chairmen for the year 1976–1977. He served the Cajal Club as a member of its Krieg Kudos Committee (1986–1990), and he was on the Executive Committee of the American Association of Anatomists (1986–1990), of which he was elected President for the academic year 1992–1993. He has also worked on many other committees, both in this country and abroad. Most important for the readers and editors of this journal, he has been a member of the Editorial Board of *The Journal of Comparative Neurology* since January 1981. He was also a member of the editorial boards of the *Journal of Neurocytology* (1972–1990 and again beginning in 1993), the *Anatomical Record* (1972–1981), *Anatomy and Embryology* (1988–1992), and, currently, *Cerebral Cortex* (since its founding in 1990). Among other honors, he was given a Senator Javits Neuroscience Investigator Award from the National Institutes of Health in 1986.

As a colleague and a friend, Alan remains thoughtful, considerate, and objective. His students regard him as supportive and compassionate in his dealing with them as well as critical, direct, and honest. His staff members know that he is demanding, yet understanding of human fallibility. In his private life, he carries on much the same, with a certain gruff tenderness, perhaps expressing his English heritage. With his wife Verona (Rona), and his three daughters, he enjoys the comforts of a warm and loving family. When he scrapes up some free time, he indulges his fondness for playing the piano, building model sailing ships, and gardening, or he goes to his summer cottage in Ashburnham. He has been known to play a competitive game of squash, but recently in deference to Rona's wish for companionable exercise, he has taken up ballroom dancing. As in everything that he does, he enjoys himself. Long may he continue to do so!

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