HISTORY OF THE AMERICAN PHYSIOLOGICAL SOCIETY

The First Century, 1887–1987

EDITED BY

John R. Brobeck Orr E. Reynolds Toby A. Appel

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Foreword

In its hundred and first year the American Physiological Society finds its members concerned about the identity, the nature, and the future of their science. That these concerns are not new a survey of the scientific backgrounds of the Society's first members demonstrates. Of the thirty "original" members listed by Howell (W. H. Howell, The American Physiological Society During Its First Twenty-five Years. Baltimore, MD: Am. Physiol. Soc., 1938, p. 1-89), twenty-one were graduates of medical schools, and of this number nine had been educated in schools that did not have a professor of physiology. Rather their teaching was supervised by a professor of the institutes of medicine. Until he moved to Philadelphia to become professor of medicine at the University of Pennsylvania, William Osler held the chair of the Institutes of Medicine at McGill University (1875–84). His responsibilities included histology and pathology, in addition to physiology. McGill, like Pennsylvania and Jefferson Medical College, had modeled their faculty assignments after Edinburgh, which in turn had adopted them from Leiden. Published in Leiden in 1708, Herman Boerhaave's small textbook, Institutione Medicae, had become the eighteenthcentury guide for teaching of sciences fundamental to instruction in medicine (G. A. Lindeboom, Herman Boerhaave. The Man and His Work. London: Methuen. 1968). From the middle of the nineteenth century, however, the Germanic and French usage, "Physiologie," was assumed by the English and most American medical schools. At least half of the original thirty members of the Society had received a part of their training in Germany, often in Carl Ludwig's laboratory in Leipzig.

The eight original members who earned no medical degree were making their careers in a variety of disciplines—physiological chemistry (Chittenden), embryology/comparative anatomy (Minot), sanitary "engineering" (Sedgwick), experimental neurology (Donaldson), and psychology (Hall and Jastrow), in addition to physiology (Howell and Lee). Many of those holding an M.D. degree were practicing such diverse medical specialties as neurology/psychiatry (Mitchell) and ophthalmology (Ellis), as well as pathology (Welch) and materia medica/therapeutics (Hare, Wood, and possibly Meltzer). We can wonder what a contemporary membership advisory committee would say about the qualifications of such a diversified group of applicants. The only sure conclusion seems to be that if this is physiology, then it is indeed a diffuse kind of science, distributed almost ubiquitously throughout biology and medicine.

In discovering that questions about physiology are longstanding, we do not

immediately solve our own problems concerning nature and future. We can find ourselves reassured, however, as we learn that the questions we ask have remained unanswerable for at least a hundred, if not two hundred, years. Perhaps the vitality of the science depends less on categorization and definition than on the lively imagination and dedicated research effort of coming generations of investigators.

Editorial responsibility for this historical volume became at once lighter and more rewarding when Orr Reynolds agreed to serve as coeditor and when Toby Appel joined the staff as archivist and historian. We are indebted to the editorial staff in the Society's office for the careful attention they gave to publication of the book and to Martin Frank and members of his office for much needed assistance from time to time. As editors, we share also a sense of gratitude to the presidents who served while the volume was in preparation and to the Centennial Committee, particularly to Chairman Alfred Fishman. Finally, and perhaps most important, we thank the presidents and past presidents of the most recent twenty-five years and the authors of the several chapters for their willingness to undertake summaries of material that often required days or weeks of painstaking searching and review, as well as literary composition. We believe that the thoroughness and even elegance with which they have accomplished their assignments will add substantially to the celebration of the centennial. Meanwhile their good-natured spirit of cooperation has made our oversight of this history a pleasant task.

John R. Brobeck

Contents

1	Physiology Flourishes in America Edward F. Adolph	1
2	Founding Toby A. Appel	11
3	First Quarter Century, 1887–1912 Toby A. Appel	31
4	Second Quarter Century, 1913–1937 Toby A. Appel	63
5	Third Quarter Century, 1938–1962 Toby A. Appel	97
6	Presidents, 1888–1962 Toby A. Appel and Orr E. Reynolds	131
7	Presidents, 1963–1987 John R. Brobeck	177
8	Executive Secretary-Treasurers John R. Brobeck	281
9	Membership Joseph F. Saunders and Aubrey E. Taylor	301
10	Spring and Fall Scientific Meetings Michael J. Jackson and Joseph F. Saunders	315
11	Publications Alfred P. Fishman and Stephen R. Geiger	333
12	Educational Programs Arthur J. Vander and Orr E. Reynolds	359
13	Finances Arthur C. Guyton	377

V111	CONTENTS

14	Women in Physiology Toby A. Appel, Marie M. Cassidy, and M. Elizabeth Tidball	381
15	Use and Care of Laboratory Animals Helene C. Cecil and William M. Samuels	391
16	FASEB and the APS John R. Brobeck	407
17	International Physiology Knut Schmidt-Nielsen	413
18	Neuroscience Robert W. Doty	427
19	Sectionalization John S. Cook	435
20	Porter Physiology Development Program A. Clifford Barger	463
21	Perkins Memorial Fund John Pappenheimer	469
22	Awards and Honors Toby A. Appel	473
23	Centennial Celebration Arthur Otis and Martin Frank	479
	Appendix 1	499
	Appendix 2	509
	Appendix 3	513
	Index	515

CHAPTER 1

Physiology Flourishes in America

EDWARD F. ADOLPH+

One hundred years ago, twenty-eight Americans agreed to form the American Physiological Society (APS, the Society). Who were they? Eighteen of them taught physiology to students of medicine; twenty had earned M.D. degrees; ten had Ph.D. degrees (three had both degrees); and sixteen had done experimental research on animals. (For detailed information on the early years of APS, see ref. 16, p. 5, and chapts. 2–6 in this volume.)

The stated object of the Society was to promote the advance of physiology and to facilitate personal intercourse among American physiologists. Persons eligible for membership were those who had conducted research or had promoted physiological research and who resided in North America.

In 1887 the population of the United States plus Canada was sixty-five million. The twenty-eight members of APS thus constituted 0.43 per million inhabitants. In 1984 there were 5,800 members in a population of 265 million, or twenty-two per million inhabitants.

From a precarious employment in 1887 that sustained 0.43 of one physiologist, firm support now exists for twenty-two. Somehow fifty times as many physiologists today justify their economic support by each million citizens. How did this army of physiologists come to deserve its keep?

By what criteria may the worth of physiologists to the population at large be measured? Physiologists contribute to education, to research, to understanding, and to health. Never before have so many citizens profited from, and indirectly paid for, these contributions, and physiology is only one fraction of the sciences that have equally flourished in this twentieth century.

The physiology taught by the twenty-eight original members of APS was repre-

† Edward F. Adolph died on 15 December 1986.

sented in factual textbooks that enumerated the structures of the human body and stated the function of each. But even in 1887 an effort was made to include, among the twenty-eight, a wider representation, namely, a plant physiologist and animal biologists of allied interests. Only a few of the twenty-eight were "full-time" physiologists; medical practice furnished a means of support. In subsequent decades the term physiologist embraced persons of even wider interests (13), some classes of whom will be identified later.

From Europe to America

In classical times, physiology was regarded as a body of knowledge and speculation comparable to anatomy, represented by Aristotle in 340 B.C. (see ref. 2) and by Galen in about A.D. 180 (see ref. 12). The belief that every structure in the animal or human had a use was not rigorously tested until centuries later, when experiments on body organs were gradually devised. Only after 1800 did systematic studies in laboratories reveal specific responses to artificial arousal. Walking, breathing, and digesting were then seen to be controlled processes, each in its particular tissues.

In the early nineteenth century, animal experimentation was practiced in laboratories devoted to it, especially in France (1820–80) by Magendie (see ref. 21) and by Bernard (5), who described his own particular research in which experimental methods were used. The results were so rewarding, in terms of physiological understanding, that practices and techniques of experiment spread. In Germany from 1865 to 1895 Ludwig (23) and others educated a generation of teachers and researchers in laboratories.

Animal experimentation became a refined craft as relevant procedures were discovered. Ether anesthesia was devised in 1847. Aseptic surgery was understood by 1880. However, many studies required neither anesthesia nor surgery. Thus humans and intact animals were subjects for elaborate research on reflex movements, vestibular functions, vision, and tests on blood samples. These methods of study were common in nineteenth-century America, as in Europe. Today these methods are used especially in those countries where domestic animals are not available for students' experiments.

Also in America, research sometimes employed physiological experimentation. Information on the status of physiology among American physicians and medical students in the period up to 1850 resides in the printed theses required of medical students at several schools; the most prominent among these was the University of Pennsylvania. From before 1800 to 1821, 322 theses were printed. Of these, forty-two are now judged to include original experiments (3). Despite this number, it would be difficult to demonstrate that this research appreciably added new understanding of living processes. The chief result, of course, was the educational value of the experiments being performed.

Other modest additions to physiological knowledge came from experiments described by American physicians, as reviewed by Weir Mitchell (20), who was later

a principal founder of APS. As Mitchell pointed out, this research, too, did not appreciably benefit physiology as a science, except for the famous study of gastric digestion by William Beaumont (4).

Permanent laboratories for physiological research and instruction were first established in America in the 1870s. These laboratories copied the European practices. Their principal founders were H. P. Bowditch, H. N. Martin, V. C. Vaughan, and R. H. Chittenden (see ref. 16, p. 1 and 46). The urge to study animals in convenient laboratories was in turn promoted by the organization of APS.

The last half of the nineteenth century saw consistent efforts in research by American physicians and others who were aware of the growth of physiology in Europe.

The New Century

In the first quarter century of the Society, those American biologists who were interested in physiology outside of its bearings on medicine exerted no appreciable influence. Two streams of interest by such persons gradually appeared: 1) the study of animals seen in the wild, and especially at the seashore, and 2) the appraisal of physical and chemical phenomena in living tissues.

Stream 1 arose most sharply among zoologists of the "naturalist" groups about 1888. The U.S. Bureau of Fisheries and the Marine Biological Laboratory established laboratories at Woods Hole, where a unique course in physiology was offered each summer, beginning in 1892 (17). Varied studies of fish, shellfish, insects, and protozoa were recognized as physiological. Jacques Loeb became a member of APS in 1893; G. H. Parker and H. S. Jennings joined the Society in 1900–01 (see ref. 16, p. 179–180). Their research was represented in the Society's journal, but only rarely in its meeting programs.

Stream 2 arose in studies of the physics and chemistry of living animals. At all stages of APS history, models were proposed; an outstanding one was the model of conduction in iron wire immersed in acid, as investigated by R. S. Lillie (18, 19).

Those physiologists who regarded Woods Hole as their home organized the Society of General Physiologists in 1946. Studies of biophysics were not adequately provided for by APS, and a separate society of biophysicists was formed in 1957. By then the definition of physiologist had come to include these and others as subgroups (13).

How did the early part of the new century (1900–40) become the period of reorganization of physiology in America? American scientists still studied in Europe. American medical schools became parts of universities. The Flexner Report on medical education in 1910 (11) led to drastic changes in the quality of physiological teaching and research. The Ph.D.-type of experience on the part of teachers added new foundations to all the sciences. Successful research in specific fields like nerve conduction (7–9) encouraged independent original work in physiology. Federal and state governments took responsibilities for support and practical applications of sciences (e.g., animal husbandry and health). Philanthropists who supported

some types of research efforts appeared. Indeed private philanthropy was directly encouraged to support education and research institutions as a means of avoiding the payment of high income taxes. In short, the economics and the sentiments of the times brought together extended efforts in advanced research and teaching. This recognition of the sciences maintains its momentum in the traditions and actions of the present day.

Changes

What led to the new attitudes toward the sciences? The changes in the material utensils with which scientists worked are easily described and dated. Can the thinking and motivations that elevated physiology from rare experiment to flood of research also be recognized?

Teachers of physiology became professional researchers.³ From 1910 to 1930 research took on the dignity of an occupation. It attracted approval of colleagues and students. It qualified the scientists to teach. The mental processes, as well as the manipulations, produced personal satisfactions. An emotional drive was established. Friendly rivalries among colleagues, among departments, and among institutions led to public appreciation and to enhanced efforts.

These were some of the factors that led to the fiftyfold multiplication of active physiologists during the span of one century. In turn the number of students acquiring doctoral degrees in physiology increased in American universities, from 17 per year in 1925 to 358 per year in 1970 (1). The practical factors that support researchers became available with the internal drives for doing what scientists do.

Instruments of laboratory teaching and research gave scope to practical physiology. In the nineteenth century, progress had depended greatly on the inductorium for activation of excitable tissues and the kymograph for recording of movements. Those two instruments may be compared with the varied manipulations in use today; electrical stimulations now vary in a dozen parameters. Recorded responses can be amplified even from cellular units. There are flow recorders, fluorometers, telemeters, and nuclear magnetic resonances. Recorders now yield not only amplified information but novel types of information. They supply data that no human sense organ can detect without transducers.

The sudden expansion of physiological research after 1940 was a self-acceleration. Demonstrated accomplishments in research and testing emerged during World War II. Graduate students and young physicians were drawn into the expanding laboratories of that period. Traditions of success arose. Federal support for more individuals and for free choices of areas in education, as well as in research, expanded the number and the self-selection of physiologists.

Mixtures of material factors and motivational factors thus favored the multiplication of research efforts. The availability of radioactive isotopes, chromatography, and other methods promoted new specific types of curiosity. Cultural changes justified the existence of all physiology and its importance in the public eye. Similar opportunities for careers in biological sciences had never before existed.

The New Physiologist

The cultural changes of the twentieth century and the deeds of physiologists in the same period elevated the status of life scientists. Particularly in war times, practical efforts became known.

In World War I, aviation subjected pilots to new stresses of low barometric pressures, low oxygen pressures, high centrifugal forces, and low temperatures, all of which required investigation (14). Poison gases suddenly called for study (14). Circulatory shock became a major problem of physiology (6) and continues to be investigated today.

In World War II, extremes of muscular exertion, inanition, dehydration, heat, and ionizing radiation received intensive study (10). In each area the practical approach led to new concepts and to interrelated research in advance of the public interest in these topics.

The growth of physiology in America could easily be divided into the four quarter centuries that APS has celebrated.

The first quarter century (1887–1912) was characterized by the organized effort to advance teaching and research by mutual cooperation. APS was responsible for three outstanding achievements.

- 1. Ten members of APS wrote a comprehensive textbook of physiology (15), with W. H. Howell (1897) as chief editor. After two editions, Howell sponsored the entire book through successive editions.
- 2. The *American Journal of Physiology* was first published (1898), with W. T. Porter as managing editor.
- 3. Apparatus for use in physiological laboratories was manufactured in America (1901) under the supervision of Porter. All three projects required major efforts.

During the second quarter century (1913–36) physiology was established as a profession. Every medical school and many biology departments regarded a full-time physiologist as an important member of the faculty. Both teaching and research by those physiologists became standard and traditional occupations.

In the third quarter century (1937–62) a remarkable expansion of physiology, and especially of research, was evident. Results of research were now expected of every teacher and graduate student. The topics of the research expanded with the new types of equipment that could be applied and afforded. The concepts of animal function that arose in the minds of experimenters brought a new generation of physiologists into being.

In the fourth quarter century (1963–87) deep specialization of concepts and deeds in research and in teaching developed. Instead of designation as a physiologist, an individual was, for example, a neurophysiologist or a vascular physiologist. This development will be further illustrated in subsequent paragraphs.

Social attitudes toward research have undergone a great revolution in the past one hundred years. In 1887 research in physiology or other disciplines was prompted only occasionally, and by the curiosity of individuals. A few saw it as an indistinct path toward improvement of their technical outlook and a contribution to the teaching of their subject. Others were content with book learning.

Today one's accomplishment in research is an entrance to a career, indispensable to the future university professor, government expert, or industrial analyst. More than that, research is recognized as contributing to the national well-being. Hence the support of students and of laboratories is today an obligation of government. Scientists are a national resource. The career scientist cultivating his profession is even accounted an instrument of international policy. What a change in his position from beggar to commander!

As a result of the support of research, teaching has also changed. A large departmental staff allows for variety in methods of student education, more or fewer contacts by faculty in laboratories, more or less initiative by students. Whereas in 1920 a department of physiology usually consisted of three persons (professor, assistant professor, and instructor), in 1987 a department maintains eight to twelve such groups (each group having associate professor, postdoctoral fellow, predoctoral student, and technician). Each group cultivates a specialty.

What social factors led to this specialization of physiologists after 1945? Research accomplishments of the individual gave him recognition as teacher. Once recognized, the associate professor asked for facilities and privileges for himself and his protegés. Teaching hours were generally reduced. Every physiologist was full time. His desirability for "tenure" was enhanced by his research grants, recognition awards, extracurricular activities, and publications. Status crept in where previously the scientist had been self-educated in semi-isolation.

Within APS what has happened in the last quarter century (1963-87)?

Most communications at meetings became "posters." Those who exhibit posters talk one-to-one to help others assess the significance of their data and concepts.

Symposia are more numerous; organizers of symposia vie with one another to report timely advances.

Members and nonmembers join "sections," which tend to gather those with like topics of scientific interest into specialized sessions.

Program subcommittees compete for general attention to their specialties.

Membership in a section confers on the individual a sense of belonging to a manageable portion of physiology (e.g., cell physiology).

Meetings, even fall meetings, are too large to be accommodated on a university campus.

New categories of membership in APS make it easier for more persons to belong.

Voting for officers is by mail, and thus the business sessions are shortened. *The Physiologist* carries reports of Society activities.

Women members have achieved high status in scientific and Society activities, including its presidency.

The face of physiology has changed. In the last quarter century, new techniques and new concepts have been cultivated. Single neurons are studied in situ, cell

components and enzymes can be identified as participants in special processes or actions, whole animals and men go for space walks, and tissues are subjected to zero gravity for long periods.

Not only action potentials are recorded, but also millivolt drifts. There are ion channels, permeability releases, juxtaposed cells, and subcellular compartments. These and many other phenomena are certain to furnish topics of study for decades to come.

It can be said that whereas the past century revealed gross changes in work and concepts of physiologists, even a quarter century is time enough for vast shifts in their outlooks. A single generation of physiologists develops wholly new territories: in turn those fields of endeavor are swallowed as that generation retires. The new generation finds its own areas of interest; it seems intent on superseding in the cherished territory that was the center of effort by predecessors.

New Laboratories

If one of the pioneer physiologists of 1887 were able to return in 1987, he might not recognize the polished rooms as laboratories. What would be notice on coming into a present-day department?

Large number of departmental members

Considerable proportion of women physiologists

Large working space occupied

Rooms set aside for group research

Large number of participants in each research group

Huge, full parking lot

Bright fluorescent lighting

Shining equipment, special to each room

Intercom television

Air conditioning

Bound volumes of departmental research papers

Multiple authorship of each paper

Spacious class laboratory rooms

Cleanliness of animal quarters

Variety of animals living there

Noninvasive techniques

Recording equipment

Computers

Word processors

Along with the revolutions in laboratories are the revolutions in scientists' homes. Ease has been built simultaneously into both laboratories and homes. Fast travel and telephones supplement the new laboratories for electron microscopy and flowmeters, or isotopes and ultracentrifuges, in promoting scholarly work. The efficient use of these conveniences enhances general experience. Still the mind of the researcher, teacher, and student continues to be a limiting factor in his accomplishments.

New Knowledge

The growth in volume of physiological knowledge and understanding is visible to everyone. But the directions and kinds of these "advances" were not predictable. If results of research were measured as information, their kinds appear to arise unforeseen and disconnected. The researcher plans his work as best he can, but the results may appear in an unintended constellation. Workers who adopt a ten-year plan nearly always shift toward brighter prospects as new directions become visible.

Any appraisal of growth in physiology fails if it relies on sheer accumulations of publications or on man-years of employment. In practice there is little agreement on the values of the results reached by research. Eventually some results lead nowhere, whereas others become the bases for brilliant concepts, pathways to future goals.

If future values could be foreseen, more scientists would shift their efforts in preferred directions each year. Though workers search for clear prophecies, most may be better served not to trust them. Perhaps random distributions of efforts produce equal or greater yields for physiology.

The encyclopedic accumulation of physiological knowledge is impressive to the world but frequently is oppressive to students. Students require protection, by learning to pursue their own pathways of search for information.

No one goal in physiological research has come to light as the single aim of this science. Hence each physiologist is entitled to state his private goal in his own way. He is expected to develop the wisdom and the zeal to pursue his aim as he thinks best. He has one lifetime in which to make his contribution.

One minor revolution has occurred in the "planning" of research. A century ago, scientists often tested their ideas in the laboratory before they went to the library to learn what had been done to answer their questions at issue. Today every scientist is compelled, by the need to write a research proposal, to fortify his plans with pertinent knowledge. If the information is in a language other than English, he will wish he could read other languages, as his grandfather scientist could. In any case, his freedom to choose what he does can be defended, since it endows him with maximal power and courage to reach results.

Dependence on libraries adds degrees of freedom to physiologists, often equal to dependence on laboratories. In 1900 the department's subscription to four journals (one volume of each per year) fulfilled most needs. By 1960 the same department would receive twenty or thirty journals. In 1987 even the university's library as a whole cannot subscribe to enough journals (and monographs) to satisfy the needs of all its own physiologists.

Correspondingly, manuscripts for journal publication are usually acceptable only if shorn of details of technical procedures. Even standard methods often are transmitted by interview with workers in a distant laboratory.

Around 1960, interest in the results of scientific work spread to larger populations, "the public." Reporting of experiments and their implications occasionally reached the daily and weekly news. In exceptional research, oral contraceptives were devised as a result of extensive experiments by Gregory Pincus (22) and others; they gave millions of people valued choices in life. In contrast, any one of a hundred other researches that cost equal effort is appreciated only by professional physiologists.

News reporters now visit Woods Hole, Federation meetings, and home laboratories. Scientists appear in television interviews. Prize-winning men and women and their deeds bring to popular attention the sorts of current efforts that were once hidden from laymen's view. Perhaps this attention is part of the feedback through which support for physiologists and for attractive laboratories is now made available.

Summary

The physiologist propelled into 1987 finds himself in a shining world. Instead of gas light and telegraph, he uses fluorescent light and jet travel. Instead of kymograms he preserves magnetic tapes. Instead of synapses he views protein and other chemical receptors. The historical steps by which such methods, results, and concepts were reached, fortunately, are matters of record. By present inference the physiologist can be certain that there is enormously more to be learned by observation and analysis and conceptual thinking. The physiologist of today lives accidentally at one point in a continuum in time that has no visible terminus.

NOTES

- ¹ Experiment as the critical method of physiology gained acceptance in an unforeseen consequence of a special practice in the Paris Academy of Sciences. As early as 1809, after a physiological paper was read to the academy, a committee of referees might be appointed to report on its soundness. Referees sometimes felt obliged to repeat certain of the procedures used by the original author, which meant that they either borrowed or created laboratory arrangements of their own (see ref. 21, p. 66).
- ² The laboratories developed by Vaughan and by Chittenden were for studies of what is now termed biochemistry. But up to 1906 there was no separate society for that discipline. In fact, for nine successive years, Chittenden was president of APS.
- ³ The author (Adolph) entered physiological research as a third-year college student in 1915, early in the second quarter century of APS. Recollection of that time helps him compare how physiologists did and thought, then and now.

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