NATIONAL ACADEMY OF SCIENCES

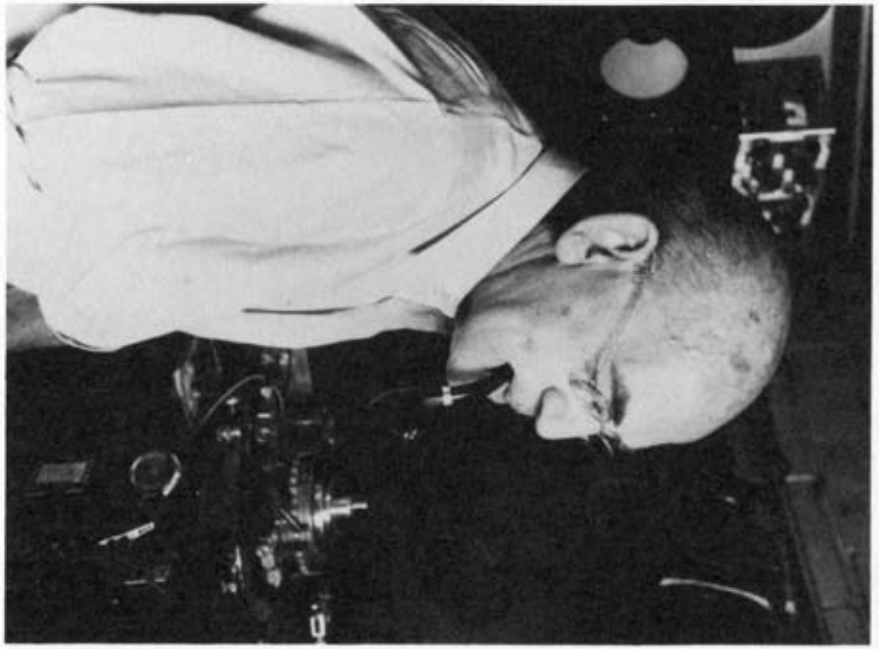
GEORGE HOLMAN BISHOP

1889—1973

A Biographical Memoir by

WILLIAM M. LANDAU

Biographical Memoir



Photograph by Martin Schweig, St. Louis, Mo.

GEORGE HOLMAN BISHOP

June 27, 1889– October 11, 1973

BY WILLIAM M. LANDAU

GEORGE BISHOP was born in Durand, Wisconsin, and grew up in Eau Claire, Wisconsin; Louisiana; and Ann Arbor, Michigan. His parents were graduates of the University of Michigan, and their family life was rich in every way—except financially. From his earliest years, George displayed delight in natural history and an innovative drive to do things in new ways. About the farm his inventions included pumping systems, lathes, homemade skis, equipment for cracking nuts and producing honey—practically anything that could be put together with pocket knife, baling wire, pulleys, and engines. In 1901 he moved with his father to a job with a lumber company in Louisiana, where he first lived with—and abhorred—racial segregation. A series of failed managerial arrangements made him the foreman of the mill before he was sixteen.

His early education had many interruptions, but after the family returned to Michigan the high school principal quickly recognized his initiative, and he advanced rapidly to the highest levels of mathematics, Latin, and English literature. He was a biblical scholar from even earlier days, and St. Paul was his favorite.

In 1908 he entered the Engineering Department at the University of Michigan, but after two years decided to

transfer to the Literary School. Many of the credits earned during the first two years were lost with the change of major. Nevertheless, he completed his work for the B.A. degree in 1912. During the next three years he taught manual training in high schools in Milwaukee, South Dakota, and Seattle. Encouraged by Professor A. S. Pearse at the University of Michigan, he then followed Pearse to the University of Wisconsin.

During World War I his studies were interrupted for service as an enlisted man; he spent the war years as a technician in C. J. Herrick's laboratory at the Army Medical Museum. They maintained friendship and scientific correspondence until Herrick's death; Bishop was deeply influenced by his evolutionary ideas about the nervous system. Herrick, in turn, was appreciative of Bishop's review of the manuscripts of his later career.

He returned to Madison and received his Ph.D. degree in zoology in 1919. His thesis was a cytological study of the fat body of the honey bee, a problem to which he returned with two papers forty years later, utilizing electron microscopy and modern biochemical techniques. It was in Madison that he first met Ethel Ronzoni, a biochemist who later came to the Department of Biochemistry at Washington University and became his wife.

Bishop then spent a year at Northwestern University and another at the University of Tennessee. Joseph Erlanger, impressed with Bishop's engineering background, then brought him to Washington University.

Bishop's description of his beginning in neurophysiology is explicit:

> About the year 1923, in the Department of Physiology at Washington University, I was invited to participate in the research program then well under way on the analysis of the action currents of nerve. . . . Never having taken a course in physiology I did have some repute, having been

raised on the farm, for making workable apparatus out of tin cans and baling wire . . . I had currently been measuring the blood pH of the queen bee (I don't quite remember why) on a drop of fluid in one arm of a four-way stopcock. I accepted with no less trepidation than enthusiasm this generous offer, and transferred my scientific attention forthwith to Biedermann's classical compendium of electrophysiology, and to the effects of electrical currents more or less short of electrocution on the shape of the compound action currents of nerves.

The first product of the triumvirate was the 1924 article entitled "The Compound Nature of the Action Current of Nerve as Disclosed by the Cathode Ray Oscillograph," by Erlanger and Gasser, "with the Collaboration, in Some of the Experiments, of George H. Bishop." Erlanger's Harvey Lecture in 1927, "Analysis of the Action Potential in Nerve," had the subtitle "Based on Experiments Done in Collaboration with H. S. Gasser and G. H. Bishop." Their joint publications continued through 1927.

Bishop then was offended by Erlanger's effort to defer a publication by Bishop's first research fellow, Peter Heinbecker, describing the discovery of the C wave as the physiological manifestation of conduction in unmyelinated nerve fibers. In 1930 Bishop moved to a new laboratory as professor of applied physiology in ophthalmology and began his collaboration with Howard Bartley in the visual cortex. His title was changed to professor of biophysics in 1932. During these several years his collaborations with Heinbecker and O'Leary in peripheral nerve studies proceeded in hot competition with Erlanger and Gasser. This exceptionally productive period for both groups is almost entirely documented in the *American Journal of Physiology* from 1927 to 1935.

With their primitive equipment, all of these workers were tackling, even by modern standards, the most difficult technical problems concerning short latency potential phenome-

na, close to the site of stimulation. Bishop's special forte then was the physics of nerve. Particularly important were "The Form of the Record of the Action Potential of Vertebrate Nerve at the Stimulated Region," (introducing the use of the Wheatstone bridge as a balancing device; *American Journal of Physiology*, 82 [1927]: 462) and "The Reactance of Nerve and the Effect upon it of Electrical Currents" (effect of the sheath; *American Journal of Physiology*, 89 [1929]: 618).

Bishop's early concepts of field potentials from nerve and muscle models underlay his later approach to the electrical potentials of brain structures. With Heinbecker and O'Leary, Wallerian degeneration was used to separate the principal components of cutaneous and motor nerves and study the conducted potentials of the fiber remainders. They first suggested that the small motor fibers to muscle were the source of innervation to muscle spindles. Nerve degeneration was also studied in experimental poliomyelitis. The components of vagus and depressor nerves were worked through. Correlated animal and human experiments, the latter utilizing the investigator's nerves and fresh nerves dissected from executed criminals, led to the establishment of the relationship between nerve fiber sizes and modalities of sensation ("Analysis of Sensation in Terms of the Nerve Impulse," *Archives of Neurology and Psychiatry*, 31 [1934]: 34). Later papers concentrated upon delta and C fiber modalities of pain.

Simultaneously, with Howard Bartley, Bishop began to publish (1932) an epochal series of papers about the rhythmic cortical responses to electrical and photic activation of the optic nerve in the rabbit. O'Leary later joined them in both physiological and correlated neuromorphological analysis of the visual system and functional thalamocortical relations.

Early on, Bishop became dissatisfied with accepted mod-

els of summated axon spikes in the interpretation of brain potentials. An important role for cell bodies, and then dendrites, evolved from studies of evoked responses in optic lobe of the duck and goose and the superior colliculus of the cat where O'Leary's anatomical sophistication proved especially effective.

During much of World War II Bishop had no collaborators or technical aid of any kind. He then turned to investigation of the sensory receptors of skin because he could carry this out upon himself. Self-inflicted skin biopsies established the kinds of sensory endings he had located by mechanical or electrical stimulation. Turpentine injections were used to occasion local inflammation with its attendant aches, itches, and hurts. At one time the area of his body from which skin had been removed is said to have so nearly exceeded that where it mained that there was talk of placing Bishop in hagiology with Bartholomew rather than Paul.

This interest in receptors, particularly those for pain, evolved still later into his concepts of central projections, conditioned by C. J. Herrick: an archaic system that gave off, at the medullary level, a component activated by nonmyelinated peripheral axons and terminated in the midline thalamus, and a neothalamic one for "epicritic" pain, which ended in the ventrobasal complex.

In 1947, when O'Leary became head of neurology, Bishop, without moving his laboratory, became professor of neurophysiology in that department. In the post-war years his major efforts were in the analysis of evoked cortical potentials in the cat, utilizing laminar recording and applied polarization. These evolved to a conclusion, now generally accepted, that dendrites are the primary source (and sink) of the field potentials generated in cerebral cortex and other gray matter.

The writer was an undergraduate in Erlanger's student

laboratory on the exciting day in 1944 when the Nobel Prize to Gasser and Erlanger was announced. His closest friend, O'Leary, recalled that Bishop made no complaint. He finally agreed to accept a share of the prize, proffered by the recipients. He used it only as a laboratory fund.

Of Bishop's science, O'Leary wrote: "A hard-fact physiologist whose voluminous experiences permitted him to speculate shrewdly on his collected data. His grounding in engineering and physics, which he never neglected to improve, provided an ideal background for his work. His power of becoming completely absorbed in what he was doing and the facility with which he subconsciously systematized his data were his biggest assets. After reading a series of his papers in chronological sequence, one soon realized that the speculations never far outran the fact collecting process, and there were always more goods in the warehouse than were displayed in the windows." Bishop's favorite aphorism was a quotation from Mr. Dooley, "Experience is a poor teacher, but the only way a fool can learn."

For Bishop the physiologist's tools were best designed when the simplest for the task in hand. His pocket knife was always as handy as his pipe. He made his own fine dissection instruments with carved handles and bits of razor blades, evolved a Wheatstone bridge device for measuring bronchial air resistance pressure before sensitive strain gauges existed, and wound his own resistors before precision resistors were available. But he was never so bound to his antiques, even his turn-of-the-century typewriter, that he resisted the use of more efficient equipment.

During the Great Depression, Bishop and Ronzoni literally rebuilt an 1820 log house that they discovered in an area that ultimately, to their dismay, became suburbia. Bishop also manufactured walnut furniture and hand wrought copper trays. They had no children, but that home with its

great fireplace was a seat of hospitality to generations of their "adopted" children, students and scientific friends from all over the world. They bequeathed the house to the St. Louis County Park System. Also during the 1930s, Bishop was an aggressive leader on the Board of the St. Louis Civil Liberties Committee, particularly in regard to issues of segregation, free speech, and police brutality.

Neurophysiology was a small club during the 1930s. Bishop was one of the charter active members of a small dinner group who comprised all of American neurophysiology and called themselves the Axonologists. They gathered at the annual meeting of the American Physiological Society. At national meetings, Bishop seldom spoke from the floor, preferring to collar the author of something interesting on the boardwalk or in the bar for extended discussion (the poster presentation had not yet evolved). He quickly spotted pomposity and careless thinking, but with the amusement of a natural historian rather than the anger of a True Believer. Of one such windbag Bishop said, "He's talked about that experiment so much that he has come to believe he did it."

As a teacher, Bishop was superb, but in a very special, individualized manner. His critical thinking got in the way of presenting orthodox dogma, so his formal lectures were never well received. Nor did he ever join the stream of "formal" graduate educators. But for his students, apprentices ranging from visiting and local professors to the lowliest medical student working in an elective period across the hall, the seat next to his desk was always open for discussion wreathed in pipe smoke. He never talked down but rather helped the student work through a more sensible answer by himself. Even when a colleague spilled cement, misplaced instruments, or snitched tools from Bishop's small but well organized workbench, he cleaned up the mess, complained vigorously to the miscreant, but never held a grudge, even

when the offenses were repeated. When a student made persistent technical mistakes, Bishop would patiently go over the lesson again, often humorously putting down the repeated stupidity, but never the student. We reveled in his enjoyment of youthful exuberance and tolerance for error in thought and performance, even as he endeavored to help us grow.

He enjoyed his position as a yankee craftsman who applied his manipulative skills and thinking to science, a tradition going back to Franklin and Jefferson. And he was blessed with the highest of humane gifts, a sense of humor that permitted him to enjoy laughing at himself as in one of his classic poems:

This Bishop's a curious freak,
His methods are clever and chic,
But under the strain of containing the brain,
His tin can can develop a leak.

To fellows and friends confidential,
Was propounded the problem essential,
Which fate is the worse, to be immersed in the source,
Or sunk in the sink of potential?

Now everyone join the refrain,
While the analysts open the drain,
The source of potential is inconsequential,
A brain, is a brain? Is a brain!

During his last decade Bishop was physically handicapped by the poor nutrition and intestinal atony that followed a vagotomy operation for gastric ulcer, ironic because of his extensive investigations of the physiology of the vagus nerve. He also suffered a hip fracture in a fall from a ladder when he was repairing the chimney of his house. He

was delighted that the methacrylate plastic used to fix his hip was the same one he had procured from DuPont to use in his laboratory over the years. Until the end he was quite able to participate actively in laboratory discussions and supervise the care of his severely invalided wife, but he complained of not being able to remember what he read. He died of a stroke; at autopsy it was discovered that he had advanced Alzheimer's disease, an illness that also afflicted his mother.

Bishop received the Lashley Award of the American Physiological Society, the Gold Medal of the St. Louis Medical Society, and an honorary Sc.D. from Washington University. He was present at a symposium in his honor given by the American Electroencephalographic Society and was elected to the National Academy of Sciences in 1967.

THIS MEMOIR INCLUDES material freely cribbed from the recollections and judgments of Bishop's admirers, H. Bartley, H. Jasper, R. King, M. Clare, S. Goldring, S. Kuffler, H. Davis, and especially his brother, Frederick Bishop, and his lifelong colleague, James L. O'Leary.

BIBLIOGRAPHY

1917

An apparatus for gradual dehydration. Trans. Am. Microsc. Soc., 36:27–32.

1920

Fertilization in the honey-bee. I. The male sexual organs; their histological structure and physiological functioning. J. Exp. Zool., 31:225–65.

Fertilization in the honey-bee. II. Disposal of the sexual fluids in the organs of the female. J. Exp. Zool., 31:267–86.

1921

With C. E. Tharaldsen. An apparatus for microdissection. Am. Nat., 55:381–84.

1922

Cell metabolism in the insect fat-body. I. Cytological changes accompanying growth and histolysis of the fat-body of *apis mellifica*. J. Morphol., 36:567–601.

1923

Cell metabolism in the insect fat-body. II. A functional interpretation of the changes in structure in the fat-body cells of the honey-bee. J. Morphol., 37:533–53.

Body fluid of the honey bee larva. I. Osmotic pressure, specific gravity, pH, O_2 capacity, CO_2 capacity, and buffer value, and their changes with larval activity and metamorphosis. J. Biol. Chem., 58:543–65.

Autolysis and insect metamorphosis. J. Biol. Chem., 58:567–82.

1924

With J. Erlanger and H. S. Gasser, with the Collaboration, in Some of the Experiments, of G. H. Bishop. The compound nature of the action current of nerve as disclosed by the cathode ray oscillograph. Am. J. Physiol., 70:624–66.

1925

With E. S. West. The photochemistry of cod liver oil. Science, 62:86–87.

With A. P. Briggs and E. Ronzoni. Body fluids of the honey bee larva. II. Chemical constituents of the blood and their osmotic effects. J. Biol. Chem., 66:77–78.

1926

With J. Erlanger and H. S. Gasser. Experimental analysis of the simple action potential wave in nerve by the cathode ray oscillograph. Am. J. Physiol., 78:537–73.

With J. Erlanger and H. S. Gasser. The action potential waves transmitted between the sciatic nerve and its spinal roots. Am. J. Physiol., 78:574–91.

With J. Erlanger and H. S. Gasser. Distortion of action potentials as recorded from the nerve surface. Am. J. Physiol., 78:592–609.

With J. Erlanger. The effects of polarization upon the activity of vertebrate nerve. Am. J. Physiol., 78:630–57.

1927

With J. Erlanger and H. S. Gasser. The absolutely refractory phase of the Alpha, Beta and Gamma fibers in the sciatic nerve of the frog. Am. J. Physiol., 81:473–74.

With A. S. Gilson. A vibration-free capillary electrometer. J. Opt. Soc. Am. Rev. Sci. Inst., 15:48–52.

The form of the record of the action potential of vertebrate nerve at the stimulated region. Am. J. Physiol., 82:462–77.

With A. S. Gilson. Action potentials accompanying the contractile process in skeletal muscle. Am. J. Physiol., 82:478–95.

The effects of polarization upon the steel wire–nitric acid model of nerve activity. J. Gen. Physiol., 11:159–74.

1928

The relation between the threshold of nerve response and polarization by galvanic current stimuli. Am. J. Physiol., 84:417–36.

With J. McCaughan. Polarizing effects of electrical stimuli upon contraction of skeletal muscle. Am. J. Physiol., 84:437–41.

The effect of nerve reactance on the threshold of nerve during galvanic current flow. Am. J. Physiol., 85:417–31.

With P. Heinbecker. Correlation between threshold and conduction rate in myelinated nerves. Proc. Soc. Exp. Biol. Med., 26:241–43.

With A. I. Kendall. The effects of histamine, formaldehyde and

anaphylaxis upon the response to electrical stimulation of guinea-pig intestinal muscle. I. Agents applied to serous aspect of intestine. Am. J. Physiol., 85:546–60.

With A. I. Kendall. Effects of histamine, formaldehyde and anaphylaxis upon the response to electrical stimulation of guinea-pig intestinal muscle. II. Agents applied to mucosal aspect of intestine. Am. J. Physiol., 85:561–68.

With E. Ronzoni. Carbohydrate metabolism in the honey bee larva. Trans. IV. Intern. Cong. Entomol., 2:361–65.

1929

With A. I. Kendall. Action of formalin and histamine on tension and potential curves of a striated muscle, the retractor penis of the turtle. Am. J. Physiol., 88:77–86.

With A. S. Gilson. Action potentials from skeletal muscle. Am. J. Physiol., 89:135–51.

The reactance of nerve and the effect upon it of electrical currents. Am. J. Physiol., 89:618–39.

With P. Heinbecker. Differentiation between types of fibers in certain components of involuntary nervous system. Proc. Soc. Exp. Biol. Med., 26:645–47.

1930

Condenser technique for measuring glass cell or other potentials in circuits of high resistance. Proc. Soc. Exp. Biol. Med., 27:260–62.

With P. Heinbecker. Differentiation of axon types in visceral nerves by means of the potential record. Am. J. Physiol., 94:170–200.

With E. Ronzoni. Action potentials of muscle treated with iodoacetic acid. Collecting Net, 5:171–72.

1931

With F. Urban and H. L. White. A study of the blocking effect of membranes. J. Phys. Chem., 35:137–43.

With P. Heinbecker. Effects of frequency and intensity in stimulation of cervical sympathetic nerve fibers to eye. Proc. Soc. Exp. Biol. Med., 28:682–83.

With P. Heinbecker. Effect of anoxemia, carbon dioxide and lactic

acid on electrical phenomena of myelinated and unmyelinated fibers of the autonomic nervous system. Am. J. Physiol., 96:613–27.

1932

With P. Heinbecker. A functional analysis of the cervical sympathetic nerve supply to the eye. Am. J. Physiol., 100:519–32.

Certain time-relations of the visual pathway. Proc. Am. Physiol. Soc., 8–9.

With S. H. Bartley. Cortical response to stimulation of the optic nerve. Proc. Soc. Exp. Biol. Med., 29:775–77.

With S. H. Bartley. Electrical activity of the cerebral cortex as compared to the action potential of excised nerve. Proc. Soc. Exp. Biol. Med., 29:698–99.

Action of nerve depressants on potential. J. Cell. Comp. Physiol., 1:177–94.

The relation of nerve polarization to monophasicity of its response. J. Cell. Comp. Physiol., 1:371–86.

With P. Heinbecker and J. L. O'Leary. Nerve degeneration accompanying experimental poliomyelitis. II. A histologic and functional analysis of normal somatic and autonomic nerves of the monkey. Arch. Neurol. Psychiatry, 27:1070–79.

With P. Heinbecker and J. L. O'Leary. Nerve degeneration accompanying experimental poliomyelitis. III. Rate of depression and disappearance of components of conducted action currents in severed nerves; correlation with histologic degeneration in groups of fibers responsible for various components. Arch. Neurol. Psychiatry, 27:1421–35.

With J. L. O'Leary and P. Heinbecker. Nerve degeneration in poliomyelitis. IV. Physiologic and histologic studies in the roots and nerves supplying paralyzed extremities of monkeys during acute poliomyelitis. Arch. Neurol. Psychiatry, 28:272–88.

With S. Gelfan. Action potentials from single muscle fibers. Am. J. Physiol., 101:678–82.

With J. L. O'Leary and P. Heinbecker. Dorsal root fibers which contribute to the tract of Lissauer. Proc. Soc. Exp. Biol. Med., 30:302–3.

With P. Heinbecker and J. L. O'Leary. Allocation of function to specific fiber types in peripheral nerves. Proc. Soc. Exp. Biol. Med., 30:304–5.

1933

With P. Heinbecker and J. L. O'Leary. Nature and source of fibers contributing to saphenous nerve of the cat. Am. J. Physiol., 104:23–55.

With S. Gelfan. Conducted contractures without action potentials in single muscle fibers. Am. J. Physiol., 103:237–43.

With P. Heinbecker and J. L. O'Leary. Pain and touch fibers in peripheral nerves. Arch. Neurol. Psychiatry, 29:771–89.

With S. H. Bartley. The cortical response to stimulation of the optic nerve in the rabbit. Am. J. Physiol., 103:159–72.

With S. H. Bartley. Factors determining the form of the electrical response from the optic cortex of the rabbit. Am. J. Physiol., 103:173–84.

Cyclic changes in excitability of the optic pathway of the rabbit. Am. J. Physiol., 103:213–24.

With P. Heinbecker. Fiber distribution in optic and saphenous nerves. Proc. Soc. Exp. Biol. Med., 30:1312–14.

Fiber groups in the optic nerve. Am. J. Physiol., 106:460–74.

With P. Heinbecker and J. L. O'Leary. The function of the nonmyelinated fibers of the dorsal roots. Am. J. Physiol., 106:647–69.

1934

With P. Heinbecker and J. L. O'Leary. Analysis of sensation in terms of the nerve impulse. Arch. Neurol. Psychiatry, 31:34–53.

With J. L. O'Leary and P. Heinbecker. The fiber constitution of the depressor nerve of the rabbit. Am. J. Physiol., 109:274–85.

With P. Heinbecker and J. L. O'Leary. The significance of frequency, number of impulses and fiber size in vasomotor responses to vagus and depressor nerve stimulation in the rabbit. Am. J. Physiol., 109:409–21.

Electrophysiology of the brain. In: *The Problem of Mental Disorder*, pp. 120–32. New York and London: McGraw-Hill.

With S. H. Bartley. A functional study of the nerve elements of the optic pathway by means of recorded action currents. Am. J. Ophthalmol., 17:995–1007.

The action potentials at normal and depressed regions of nonmy-

elinated fibers with special reference to the "monophasic" lead. J. Cell. Comp. Physiol., 5:151–54.
With P. Heinbecker. On the mechanism of spastic vascular disease. Proc. Soc. Exp. Biol. Med., 32:152–54.
With T. C. Douglass, H. A. Davenport, and P. Heinbecker. Vertebrate nerves: Some correlations between fiber size and action potentials. Am. J. Physiol., 110:165–73.
With P. Heinbecker. The mechanism of painful sensation. Res. Publ. Assoc. Nerv. Ment. Dis., 15:226–38.

1935

With J. L. O'Leary and P. Heinbecker. Analysis of function of a nerve to muscle. Am. J. Physiol., 110:636–58.
With P. Heinbecker. Responses of mammalian nerve to strong shocks. Proc. Soc. Exp. Biol. Med., 32:1278–80.
With P. Heinbecker. The afferent functions of non-myelinated or C fibers. Am. J. Physiol., 114:179–93.
With P. Heinbecker. Studies on the extrinsic and intrinsic nerve mechanisms of the heart. Am. J. Physiol., 114:212–23.
Electrical responses accompanying activity of the optic pathway. Arch. Ophthalmol., 14:992–1019.

1936

With P. Heinbecker and J. L. O'Leary. Functional and histologic studies of somatic and autonomic nerves of man. Arch. Neurol. Psychiatry, 35:1233–55.
With L. A. Julianelle. The formation and development of blood vessels in the sensitized cornea. Am. J. Anat., 58:109–25.
Interpretation of potentials led from the cervical sympathetic ganglion of the rabbit. J. Cell. Comp. Physiol., 8:465–77.
With J. L. O'Leary. Components of the electrical response of the optic cortex of the rabbit. Am. J. Physiol., 117:292–308.
With J. Bronfenbrenner. The site of action of botulinus toxin. Am. J. Physiol., 117:393–404.
The interpretation of cortical potentials. Cold Spring Harbor Symp. Quant. Biol., 4:305–19.

1937

Potentials of the fiber components of the coeliac nerve of the bullfrog. J. Cell. Comp. Physiol., 9:417–28.

With S. H. Bartley and J. L. O'Leary. Modification by strychnine of the response of the optic cortex. Proc. Soc. Exp. Biol. Med., 36:248–50.

With A. S. Gilson. The effect of remote leads upon the form of the recorded electrocardiogram. Am. J. Physiol., 118:743–56.

With S. H. Bartley and J. L. O'Leary. Differentiation by strychnine of the visual from the integrating mechanisms of optic cortex in the rabbit. Am. J. Physiol., 120:604–18.

La Théorie des circuits locaux permet-elle de prévoir la forme du potential d'action? Arch. Int. Physiol., 45:273–97.

With J. L. O'Leary. Limits of the optically active cortex of the rabbit. Proc. Soc. Exp. Biol. Med., 37:539–41.

1938

With J. L. O'Leary. Margins of the optically excitable cortex in the rabbit. Arch. Neurol. Psychiatry, 40:482–99.

With J. L. O'Leary. The optically excitable cortex of the rabbit. J. Comp. Neurol., 68:423–78.

With P. Heinbecker. The mechanism of spastic vascular disease and its treatment. Ann. Surg., 107:270–77.

With J. L. O'Leary. Response of the optic cortex of the cat. Proc. Soc. Exp. Biol. Med., 38:532–35.

With J. L. O'Leary. Potential records from the optic cortex of the cat. J. Neurophysiol., 1:391–404.

With J. L. O'Leary. Pathways through the sympathetic nervous system in the bullfrog. J. Neurophysiol., 1:442–54.

1940

With J. L. O'Leary. Electrical activity of the lateral geniculate of cats following optic nerve stimuli. J. Neurophysiol., 3:308–22.

With S. H. Bartley. Optic nerve response to retinal stimulation in the rabbit. Proc. Soc. Exp. Biol. Med., 44:39–41.

The relation of bioelectric potentials to cell functioning. Annu. Rev. Physiol., 3:1–20.

1941

With J. L. O'Leary. Positive potentials recorded from the superior colliculus. Proc. Soc. Exp. Biol. Med., 46:680–82.

With S. H. Bartley. Activity in the optic system following stimulation by brief flashes of light. Proc. Soc. Exp. Biol. Med., 46:557–58.

1942

With S. H. Bartley. Some features of the optic nerve discharge in the rabbit and cat. J. Cell. Comp. Physiol., 19:79–93.

With J. L. O'Leary. Factors determining the form of the potential record in the vicinity of the synapses of the dorsal nucleus of the lateral geniculate body. J. Cell. Comp. Physiol., 19:315–31.

With J. L. O'Leary. The polarity of potentials recorded from the superior colliculus. J. Cell. Comp. Physiol., 19:289–300.

1943

With J. L. O'Leary. Analysis of potential sources in the optic lobe of duck and goose. J. Cell. Comp. Physiol., 22:73–87.

Responses to electrical stimulation of single sensory units of skin. J. Neurophysiol., 6:361–82.

1944

The peripheral unit for pain. J. Neurophysiol., 7:71–80.

The structural identity of the pain spot in human skin. J. Neurophysiol., 7:185–98.

1945

Regeneration after experimental removal of skin in man. Am. J. Anat., 76:153–81.

1946

Neural mechanisms of cutaneous sense. Physiol. Rev., 26:77–102.

Nerve and synaptic conduction. Annu. Rev. Physiol., 8:355–74.

1948

The skin as an organ of senses with special reference to the itching sensation. J. Invest. Dermatol., 11:143–54.

With M. H. Clare and J. Price. Patterns of tremor in normal and pathological conditions. J. Appl. Physiol., 1:123–47.

1949

Relation of pain sensory threshold to form of mechanical stimulation. J. Neurophysiol., 12:51–57.

With M. H. Clare. Electromyographic analysis of the physiologic components of tremor. Arch. Phys. Med., 30:559–66.

Potential phenomena in thalamus and cortex. Electroencephalogr. Clin. Neurophysiol., 1:421–36.

1950

Critique of Gibbs Law. Electroencephalogr. Clin. Neurophysiol., 2:91–92.

With J. L. O'Leary. The effects of polarizing currents on cell potentials and their significance in the interpretation of central nervous system activity. Electroencephalogr. Clin. Neurophysiol., 2:401–16.

Neurophysiology and behavior. In: *The Biology of Mental Health and Disease*, pp. 159–61. New York: Millbank Foundation.

1951

With J. L. O'Leary. Review of Hill and Parr: EEG, a symposium on its various aspects. Electroencephalogr. Clin. Neurophysiol., 3:116–19.

With M. H. Clare and W. H. Mills. Reflex factors in clonus and tremor. J. Appl. Physiol., 3:714–31.

With J. B. Costen and M. H. Clare. The transmission of pain impulses via the chorda tympani nerve. Ann. Otol. Rhinol. Laryngol., 60:591–609.

With M. H. Clare. Radiation path from geniculate to optic cortex in cat. J. Neurophysiol., 14:497–505.

1952

With M. H. Clare. Sites of origin of electric potentials in striate cortex. J. Neurophysiol., 15:201–20.

With M. H. Clare. The intracortical excitability cycle following stimulation of the optic pathway of the cat. Electroencephalogr. Clin. Neurophysiol., 4:311–20.

With M. H. Clare. Relations between specifically evoked and "spontaneous" activity of optic cortex. Electroencephalogr. Clin. Neurophysiol., 4:321–30.

1953

With M. H. Clare. Responses of cortex to direct electrical stimuli applied at different depths. J. Neurophysiol., 16:1–19.

With W. M. Landau. Pain from dermal, periosteal, and fascial endings and from inflammation. Electrophysiological study employing differential nerve blocks. Arch. Neurol. Psychiatry, 69:490–504.

With M. H. Clare. Sequence of events in optic cortex response to volleys of impulses in the radiation. J. Neurophysiol., 16:490–98.

A simple electronic stimulator suitable for peripheral nerve and skin sensory testing. Electroencephalogr. Clin. Neurophysiol., 5:105–6.

Review: *The Neurophysiological Basis of Mind; the Principles of Neurophysiology* (J. C. Eccles, The Clarendon Press). Electroencephalogr. Clin. Neurophysiol., 5:626–27.

1954

With M. H. Clare. Responses from an association area secondarily activated from optic cortex. J. Neurophysiol., 17:271–77.

1955

With M. H. Clare. Organization and distribution of fibers in the optic tract of the cat. J. Comp. Neurol., 103:269–304.

With M. H. Clare. Properties of dendrites; apical dendrites of the cat cortex. Electroencephalogr. Clin. Neurophysiol., 7:85–98.

With M. H. Clare. Dendritic circuits; the properties of cortical paths involving dendrites. Am. J. Psychiatry, 3:818–25.

With M. H. Clare. Facilitation and recruitment in dendrites. Electroencephalogr. Clin. Neurophysiol., 7:486–89.

1956

Natural history of the nerve impulse. Physiol. Rev., 36:376–99.

With M. H. Clare. Potential wave mechanisms in cat cortex. Electrocencephalogr. Clin. Neurophysiol., 8:583–602.

1957

With M. H. Clare. Action of strychnine on recruiting responses of dendrites of cat cortex. J. Neurophysiol., 20:255–74.

1958

Nuclear and cytoplasmic changes in fat body cells of the queen bee during metamorphosis. J. Exp. Zool., 137:501–25.

With W. M. Landau. Evidence for a double peripheral pathway for pain. Science, 128:712–14.

The dendrite: receptive pole of the neurone. Electroencephalogr. Clin. Neurophysiol., Suppl. No. 10:12–21.

With C. J. Herrick. A comparative survey of the spinal lemniscus systems. In: *Reticular Formation of the Brain*, pp. 353–60. Boston: Little Brown.

The place of cortex in a reticular system. In: *Reticular Formation of the Brain*, pp. 413–21. Boston: Little Brown.

1959

The relation between nerve fiber size and sensory modality: phylogenetic implications of the afferent innervation of cortex. J. Nerv. Ment. Dis., 128:89–114.

With M. Friedkin. Utilization of thymidine-C^{14} by queen bee larvae. J. Exp. Zool., 141:245–56.

Feedback through the environment as an analog of brain functioning. In: *Self-Organizing Systems*, pp. 122–46. Oxford: Pergamon.

1960

The relation of nerve fiber size to modality of sensation. In: *Advances in Biology of Skin*, vol. 1, pp. 88–98. Oxford: Pergamon.

The central paths of the afferent impulses from skin which arouse sensation. In: *Advances in Biology of Skin*, vol. 1, pp. 99–111. Oxford: Pergamon.

With J. L. O'Leary. C. J. Herrick and the founding of comparative neurology. Arch. Neurol., 3:725–31.

Concluding Statement. In: *Inhibitions of the Nervous System and Gamma-Aminobutyric Acid*, pp. 588–91. Oxford: Pergamon.

1961

With M. H. Clare and W. M. Landau. The cortical response to direct stimulation of the corpus callosum in the cat. Electroencephalogr. Clin. Neurophysiol., 13:21–33.

With M. H. Clare and W. M. Landau. The equivalence of recruit-

ing and augmenting phenomena in the visual cortex of the cat. Electroencephalogr. Clin. Neurophysiol., 13:34–42.

With W. M. Landau and M. H. Clare. The interactions of several varieties of evoked response in visual and association cortex of the cat. Electroencephalogr. Clin. Neurophysiol., 13:43–53.

Growth rates of honey bee larva. J. Exp. Zool., 146:11–20.

The organization of cortex with respect to its afferent supply. Ann. N.Y. Acad. Sci., 94:559–69.

The cortex as a sensory analyzer. In: *The Visual System. Neurophysiology and Psychophysics*, pp. 326–33. Berlin: Springer-Verlag.

Review: *The Electrical Activity of the Nervous System* (Mary A. B. Brazier, 2d ed.). Electroencephalogr. Clin. Neurophysiol., 13:831.

Review: *Electrophysiological Methods in Biological Research* (J. Bures, M. Petran and J. Zachar). J. Neurophysiol., 24:552.

1962

Normal and abnormal sensory patterns: Pain. I. Anatomical, physiological, and psychological factors in sensation of pain. In: *The Treatment of Cancer and Allied Disease*, pp. 95–133. New York: Hoeber.

With W. M. Landau and M. H. Clare. Effects of polarizing currents on certain evoked potentials in cerebral cortex. Trans. Am. Neurol. Assoc., 87:72–75.

1964

With J. M. Smith. The sizes of nerve fibers supplying cerebral cortex. Exp. Neurol., 9:483–501.

With M. H. Clare and W. M. Landau. Electrophysiological evidence of a collateral pathway from the pyramidal tract to the thalamus in the cat. Exp. Neurol., 9:262–67.

With W. M. Landau and M. H. Clare. Analysis of the form and distribution of evoked cortical potentials under the influence of polarizing currents. J. Neurophysiol., 27:788–813.

1965

My life among the axons (prefatory chapter). Annu. Rev. Physiol., 27:1–18.

With M. H. Clare and W. M. Landau. The mechanism of pyrami-

dal tract excitation in motor cortex stimulation. Physiologist, 8:135.

With W. M. Landau and M. H. Clare. Site of excitation in stimulation of the motor cortex. J. Neurophysiol., 28:1206–22.

1966

Fiber size and myelinization in afferent systems. In: *Pain*, ed. Knighten and Dumke, pp. 83–89. Boston: Little Brown.

1968

With W. M. Landau and M. H. Clare. Reconstruction of myelinated nerve tract action potentials: an arithmetic method. Exp. Neurol., 22:480–90.

1969

With M. H. Clare and W. M. Landau. Further analysis of fiber groups in the optic tract of the cat. Exp. Neurol., 24:386–99.

With M. H. Clare and W. M. Landau. The relationship of optic nerve fiber groups activated by electrical stimulation to the consequent central postsynaptic events. Exp. Neurol., 24:400–20.

With J. L. O'Leary. C. J. Herrick, scholar and humanist: a memorial essay written for his centenary. Perspect. Biol. Med., 12:492–513.

1971

With M. H. Clare and W. M. Landau. The relation of axon sheath thickness to fiber size in the central nervous system of vertebrates. Intern. J. Neurosci., 2:69–78.