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In Memoriam

Herbert Henri Jasper 1906–1999

An Appreciation and Tribute to a Founder of Modern Neuroscience

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Herbert Jasper died on March 11, 1999, just a few days before his 93rd birthday, after a coronary artery thrombosis. He remained in full control of his remarkable intellectual powers until the end, and his interest in the working of the brain remained undimmed over the decades. He was born in La Grande, Oregon, in 1906. His father was a Protestant minister and a philosophical, religious, and social scholar. After service as a messenger boy in an army camp during World War I, he entered Willamette University in Salem, Oregon then transferred to Reed College, where he graduated. His first interest was in philosophy, and he was particularly attracted to the Bergsonian view of creative evolution. He majored in philosophy and experimental psychology, and decided to devote his life to studies of brain, mind, and behavior.

Through a friend, the daughter of the superintendent of a mental hospital and lived on the grounds, and through contact with the patients there, Jasper developed an awareness of psychiatric disorders. He was, as he said, "astounded by the strange distortions in thought and behavior we encountered in patients for whom there seemed to be little or no treatment, only good custodial care." "Only a thin line separated them from what might pass as normal or only slightly odd. What disturbances in brain function could underlie such tragic derangements in mental activity and behavior, was a question that has haunted me all my life."

The late 1920s and early 1930s were a particularly fertile and exciting period in the development of neuroscience. During this period, Joseph Erlanger and Herbert Gasser at Washington University first used the cathode ray oscilloscope to visualize the precise form of nerve action potentials. Hans Berger published a series of papers on the electroencephalogram of humans, later confirmed by Lord Adrian at Cambridge. Henry Dale and Otto Loewi's work on chemical transmission of nerve impulses at synapses (the so-called "soup school") appeared, as did the electrical school ("sparks") led by John Eccles, then of Oxford. Hodgkin and Huxley demonstrated the ionic mechanism of transmission of impulses in nerve fibers, and Francis X. Schmitt and his brother Otto studied the molecular structure of nerve membranes.

Jasper became aware of these developments and chose to devote his life to brain research. His father "was somewhat dismayed, for he wondered how I was going to make a living, because I was neither interested in studying medicine to become a doctor, nor in becoming a university professor!" After graduation from Reed College, he worked during his holidays as a unionized meat cutter and organized a landscape gardening company. He was then admitted to Reed College for postgraduate studies and produced his first paper on "Optimism and Pessimism in College Environments," published in the *American Journal of Sociology* in 1929. He enrolled in a Master's degree program in experimental psychology at the University of Oregon in Eugene. His thesis was entitled "Perservation and its Relation to Depression and Introversion."

In graduate school, Jasper met his first wife, Connie Cleaver. They had a daughter, Marilyn, and later in life he had a good relationship with his grandchildren. He had applied for graduate fellowships at several midwestern universities and was accepted by all. He was advised to choose the one that paid the lowest stipend, because it was likely that the best program could attract many good students for less. At the University of Iowa, Jasper studied the effects of hemispheric cerebral dominance on bilateral coordination of movements in normal individuals and in those with severe stuttering. An account of this work was published in *Psychological Monographs* in 1932. Exposure to faculty members in medicine, physiology, and psychiatry, and awareness of the work on electrical stimulation of nerve and muscle (*chronaxie,* as developed by Lapicque and Bourguignon in France) further broadened his horizons.

At a meeting of the American Physiological Society, he met Alexandre and Andree Monnier, who invited him to work with them at the Sorbonne. With the support of the Rockefeller Foundation, he was able to join the Department of Physiology chaired by Lapicque in 1931, and

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FIG. 1. Jasper and the Fellows at the Neurophysiology Laboratory of the MNI in 1952. Front row: Annie Courtois (France and Canada), Doros Oeconomos (Greece), William Feindel (Canada). Middle row: Stoll (U.S.A.), Herbert Jasper (Canada), Cosimo Ajmone Marsan (Italy). Top row: Guy Courtois (Canada), Pierre Gloor (Switzerland), Hunter (Australia), Kenan Tukel (Turkey), David Ingvar (Sweden), Maida Tukel (Turkey), Jake Hanbery (U.S.A.).

worked on mathematical aspects of nerve excitability. During his stay in Paris, he met Alfred Fessard, J. Z. Young, E. D. Adrian, Frederick Bremer, Ragnar Granit, John Fulton, Charles Sherrington, and John Eccles. He also became an enthusiastic sailor, a hobby he pursued throughout his life.

In 1932, Jasper was invited to establish a research laboratory at the Bradley Hospital in East Providence, Rhode Island, adjacent to the Brown University campus. From a German psychiatrist, William Malamud, he learned of the publications of Hans Berger on "Das Elektrenkephalogram" and, excited by the potential of this discovery, set out to repeat some of this work. An apparatus suitable for recording the EEG was built by Howard Andrews, an electronics engineer, with Leonard Carmichael, one of Jasper's colleagues. They were "successful in obtaining very good records with this splendid apparatus that Howard had created." They found that both "he and Carmichael had an excellent alpha rhythm," which made it possible to confirm many of Berger's findings. The first North American paper on the EEG was published by Jasper and Carmichael in 1935.

During his years at Brown, Jasper finished his doctoral thesis, which he presented at the University of Paris and which was composed of two parts: "Recherches sur l'excitabilité et les caractères de la reponse dans le systeme musculaire des crustacés. Influence des centres ganglionaires" and "Electroencéphalographie chez l'homme." All the members of the examining committee were enthusiastic about the second subject of the thesis,

FIG. 2. Herbert Jasper assisted by Mary Roach, who had been Dr. Penfield's nurse anaesthetist: The beginnings of electromyography.

which was to be the basis of Jasper's work for the following three decades.

In the meantime, Hallowell Davis, Alexander Forbes, Erna and Fred Gibbs, William Lennox, Donald Lindsley, and Bill Derbyshire were developing EEG technology and clinical applications in the Harvard laboratories. Albert Grass was their electronics engineer. This pioneering work led to the later development of two schools of electroencephalography with differing emphasis and perspectives.

The political turmoil of the 1930s was not ignored. Jasper wrote about Hans Berger's persecution by the Nazis, a preamble to Berger's later suicide, and about the dilemma of Martha, the daughter of Cecile and Oscar Vogt, whom he advised to leave Germany and for whom he helped obtain a fellowship in Britain. During these years, Jasper met and was influenced by Cajal, Pavlov, Grey-Walter, Denis Hill, William Cobb, and, above all, by Sir Charles Sherrington.

While at Brown University, Jasper and his colleagues had heard of Wilder Penfield's observations on the exposed cortex of patients being treated surgically for control of their focal epilepsy. They invited Penfield to come Brown to give a seminar in the Psychology Department, and he then visited the EEG laboratory in the basement of Bradley Hospital. Although skeptical at first, Penfield agreed to operate on patients Jasper had studied, and, in the first two, found lesions underlying the area where abnormalities had been localized by electroencephalography. There is some controversy whether Jasper's subsequent working visits to the Montreal Neurological Institute (MNI) took place during the week or on weekends. He loaded the equipment into the trunk of his car and on arrival at the MNI studied Penfield's patients, returning later in the week to Brown to continue his work. Considerable determination and fortitude were required to travel over the icy Green Mountain roads from Providence to Montreal and back. Penfield's enthusiasm was fired, and he invited Jasper to join him at the MNI, where he was to work for the next three decades.

Of this period in Montreal, Herbert Jasper wrote, "My time with Wilder Penfield and his family, in which I became an adopted member, working with his splendid enthusiastic staff and hundreds of colleagues and students from all over the world who worked with us, was certainly the most pleasant and productive 27 years of my life." During this period, epilepsy was their great teacher. Delighted by this environment and on Penfield's

urging, he enrolled as a medical student at McGill and completed the abbreviated wartime curriculum in 3 years. He also did experimental work on antibiotics for the treatment of open head injury, peripheral nerve injuries, and studies of blackout in pilots.

Previously divorced, Herbert fell in love and married Margaret Goldie, a nurse at the MNI and a valued collaborator in EEG and neurophysiology, who also worked with Dr. Penfield's patients on the wards. Goldie, as she was affectionately known, helped him through medical school, and they had two children, Stephen and Joan, now living in the United Kingdom. He was devoted to her during her terminal illness and missed her greatly.

After the War, the new laboratory enjoyed a period of extraordinary flowering, attracting bright young men and women from all parts of the globe. The Jasper school of EEG was to flourish during his years of association with Wilder Penfield at the MNI, investigating patients with intractable focal epilepsy being considered for surgical treatment.

Jasper always insisted that recording one's own brain waves was essential for training in EEG. It led to proper interpretation and was, in particular, a deterrent to overreading.

Jasper was energetic, tireless, enthusiastic, and demanding of his fellows. He was at the same time unfailingly kind to me and, particularly, to my wife Eva who, as a graduate student, shared an office with his daughter Joan, whom he visited frequently. In his later years, he always had a kind word for the new generation of epilepsy fellows at the MNI whose eyes lit up when they were introduced to him.

In 1996 Jasper wrote, "It was Penfield's dream to create a multidisciplinary neuroscience institute in which the basic scientists worked closely with clinicians and the laboratories of radiology, neuropathology, neurochemistry, neuroanatomy, neuropsychology, and, of course, with electroencephalography and neurophysiology, in a fusion of clinical and basic research. This was a forerunner of what soon became what we now know as neuroscience. I was delighted to take part in the realization of Penfield's dream, which soon became my own as well; it became for me an international as well as an interdisciplinary dream." In the post-War period, the Institute attracted a great number of highly accomplished and imaginative young men and women who continued to pursue distinguished careers in neurophysiology, neurosurgery, neurology, and neuropsychology. Jan Drooglever Fortuyn, Jerzy Olszewski, Cosimo Ajmone-Marsan, David Hubel, Peter Gloor, Brenda Milner, Costas Stefanis, Guy Courtois, John Hunter, and Kenan Tukel were members of that group. The scientific output was prodigious and culminated in Wilder Penfield's and Herbert Jasper's masterpiece, *Epilepsy and the Functional Anatomy of the Human Brain,* published in 1954 and still, half a century later, an invaluable reference in our search for the understanding of focal epilepsy.

During this peroid, the staff of the Institute expanded, and the need for molecular understanding of the mechanisms of epileptogenesis led to the recruitment of K.A.C.

FIG. 3. Jasper and Penfield at the time of the publication of *Epilepsy and the Functional Anatomy of the Human Brain.*

(Allan) Elliot, a brain chemist who established the first neurochemistry unit endowed by the Donner Canadian foundation. Jasper's interest turned more and more to the investigation of single nerve cell discharges studied by depth electrode recording, in conjunction with Allan Elliot's neurochemical studies. Ernst and Elizabeth Florey were invited to come to the MNI to study Substance I, an inhibitory factor they had isolated from brain extracts. This was subsequently found to be γ-aminobutyric acid (GABA), the major inhibitory transmitter in brain. Jasper relinquished his activities in electroencephalography to his successor, the brilliant encephalographer and neurophysiologist Peter Gloor. He devoted his activities to the study of excitatory amino acids and GABA and their receptors, an area that continues to be a primary focus of activity at the MNI.

In 1960 Jasper became the executive director of the newly formed International Brain Research Organization, incorporated by the Canadian parliament on the proposal of Herbert Jasper, Wilder Penfield, and the professor of physiology at McGill, Hank MacIntosh. He moved to Paris for 1 year to launch its activities and devoted a great deal of time and energy to it for the next 4 years. Jasper then decided to concentrate on experimental neurophysiology by combined neurochemical and microelectrode techniques and joined the newly formed Centre de Recherches en Sciences Neurologiques at the Université de Montreal, led by the late Jean-Pierre Cordeau, who had been Jasper's disciple at the MNI. There, with Tomas Reader, Jacques de Champlain, and Laurent Descarries, he did important work on catecholaminergic mechanisms in the cerebral cortex and became a key figure in the development of that department.

Jasper summarized some of the work in the field of neurotransmitters and cortical function at the time of his 80th birthday celebration in 1986 at a symposium organized in his honor by Massimo Avoli and Peter Gloor of the MNI, and Tomas Reader and Bob Dykes of the University of Montreal.

I quote a few excerpts:

Significance of cortical neurotransmitters:

> The contributors to the present symposium have provided many fascinating and important highlights of recent research on the many neurotransmitters or modulators which have played a leading role in the remarkable advances being made during recent years in our understanding of chemical and molecular mechanisms involved in the organization of cortical function. We shall attempt to present some of our impressions of the overall importance of these developments with an emphasis on the subtitle of this book, *From Molecules to Mind.*

Amino Acids:

> It would seem that the only good candidates for the chemical synaptic mediation of the rapid transient transmission

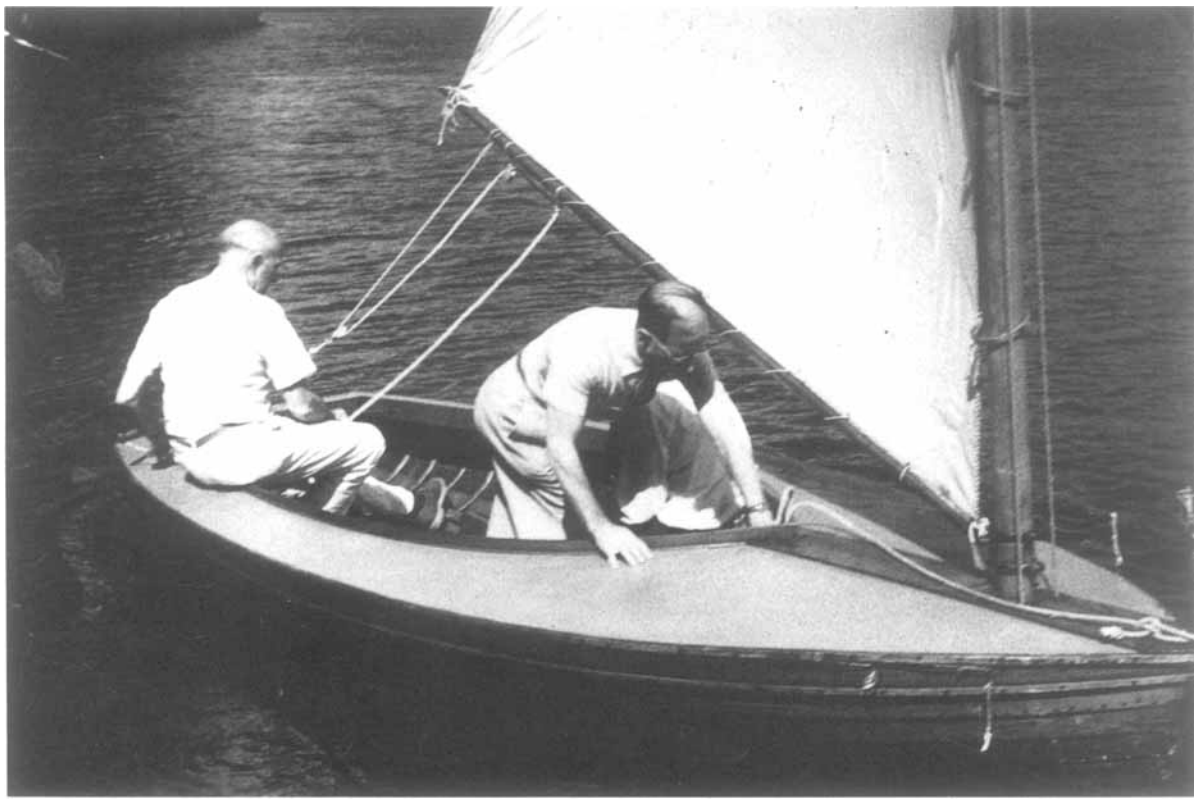

FIG. 4. 1954: sailing with Wilder Penfield on Lake Memphremagog in the Astrocyte.

of excitatory and inhibitory actions on specific information processing, cognitive, and specific motor functions of cerebral cortex are amino acids (glutamic and aspartic acids), which are universally excitatory, while GABA is the major, if not the only, generally active inhibitory substance in cerebral cortex. All of the other neuroactive substances in cerebral cortex have slower and longer lasting effects, modulating excitability and the action of other neurotransmitters. Some may be "cotransmitters" as shown by Jones with his immunocytochemical studies of glutamic acid decarboxylase (GAD, the enzyme for GABA synthesis from glutamate) and certain peptides.

It would seem to be of considerable importance that metabolism of glutamate and GABA are so closely interrelated, GABA being produced by the decarboxylation of glutamate by means of a specific enzyme, GAD, together with the coenzyme pyridoxine phosphate (vitamin B_6). Rate-limiting steps in the synthesis of both GABA and glutamate are also closely related, as shown by Szerb.

The fact that the most important excitatory substance can be the immediate precursor of the most important inhibitory substance suggests that these interrelationships may be relevant to the maintenance of a balance in excitatory and inhibitory controls in synaptic mechanisms involved both in information processing as well as in integrative motor control. Defects in GABA-mediated inhibitory controls may lead to epileptic discharge as described by Avoli, and may abolish pattern discrimination in cells of visual cortex, as shown by Sillito and Murphy. Dykes et al. have shown that blocking of GABA action by bicuculline enlarges and blurs receptive fields of single cells in somatosensory cortex.

Thus, GABA may play a leading role in all higher integrative functions of cerebral cortex in which patterns of excitation are being molded by inhibition.

The specific ionic channels mediating the excitatory properties of glutamate and aspartate have not been clearly elucidated, but they probably involve both Na and Ca conductances. The ionic mechanism of inhibition by GABA involves Cl channels. GABA receptors are very closely related and coupled to benzodiazepine receptor sites as described by Lambert et al. The barbiturates may also act, in part, via the GABA system, further increasing the importance of GABA in such physiological phenomena and pointing to its importance in neuropharmacology.

These prolonged excerpts illustrate admirably Jasper's extraordinary talent for summarizing the highlights of prolonged and complicated scientific meetings, an ability that I admired as a neophyte at the meetings of the American Epilepsy Society, and which I continued to admire since.

Not surprisingly, many honors and awards were bestowed on him. He became a Fellow of the Royal Society of Canada, and received the following: Ralph Gerard Prize of the Society of Neuroscience; Officer of the Order of Canada; the McLaughlin Medal of the Royal Society of Canada; the F.N.G. Starr Award of the Canadian Medical Association; elected into the Canadian Medical Hall of Fame; the Albert Einstein World Science Award of the World Cultural Council; and Grand Officier de l'Ordre National du Quebec, June 1996.

In the introduction to his autobiography, published in the *History of Neuroscience,* edited by Larry Squire, his long and fruitful scientific life is summarized:

"Herbert Henri Jasper dedicated his life to studies of the brain in relation to the mind and behaviour. He pioneered the establishment of the electroencephalogram (EEG) for the study of the electrical activity of the brain in relation to states of consciousness, learning, and epileptic dis-

FIG. 5. In the Laurentians at one of the yearly EEG-Ski Meetings of the Eastern EEG Society.

charge. He proceeded to use microelectrodes to record from single brain cells and synapses combined with studies of neurochemical mechanisms involved in the control of brain activity."

More recently, Jasper found happiness and companionship in his new marriage to Mary Lou McDougall Jasper, an administrator at McGill University.

Despite his life-long preoccupation with brain, mind, and behavior, he never discussed these from the philosophical perspective, at least not in my hearing. This was in contrast to the inclination of other elder neurological statesmen such as Penfield and Eccles, who indulged in neurophilosophy in the autumn of their careers.

Jasper thought that scientific investigation and brain research

> might be an excellent channel for the promotion of better international relations because so many of these problems are based on malignant mental attitudes that might respond to scientific studies of brain function as a detriment of social behavior. I feel strongly that modern neuroscience with all its advances during recent years should be used to apply knowledge and techniques to the understanding and prevention of such malignant mental attitudes that form the basis for so much conflict.

FIG. 6. Laden with honors: Jasper in his later years.

He propounded these principles during his extensive travels and remained idealistic but perhaps also somewhat overoptimistic in his expectations for change in the attitudes of entrenched political regimes.

As Peter Gloor, in a tribute to Herbert Jasper wrote,

> We are now standing on an exciting threshold of scientific history, where we can hope that at least some aspects of how the human mind works can be understood, not necessarily in the traditional terms of biophysics and biochemistry—because such a hope would betray a too naively reductionist point of view—but in terms of mechanisms that involve organizational levels of which biophysical and biochemical processes are the indispensable building blocks. In this sense, fundamental biophysical and biochemical principles can be brought to bear on the study of the mind. If the topics of the present symposium seem to be related more to the basic molecular aspects of these problems, to the building blocks, rather than to the study of the mind as such, it is because at the present time we are still only able to make precise scientific measurements at that level. The higher organizational principles which emerge when these mechanisms act in a complex information-handling system such as the brain are yet to be studied. How far this quest can lead us and whether we will ever reach the point where we really can fully account for the functioning of the human mind is of course impossible to say at this juncture. I believe we all secretly hope that this point will never be reached, for when what else would there be left to be investigated scientifically?

Herber Jasper's life work was a giant step in our understanding of these building blocks, and more than any other neuroscientist of this century, he was able to bring together clinical and basic neurophysiology with psychology, anatomy, chemistry, teaching, scientific writing, editing, and public service in science. He was indeed a founder of neuroscience in the 20th century.

Selected Publications of Herbert Jasper, chosen by the author from *The History of Neuroscience in Autobiography,* vol 1, edited by Larry R. Squire, with permission

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