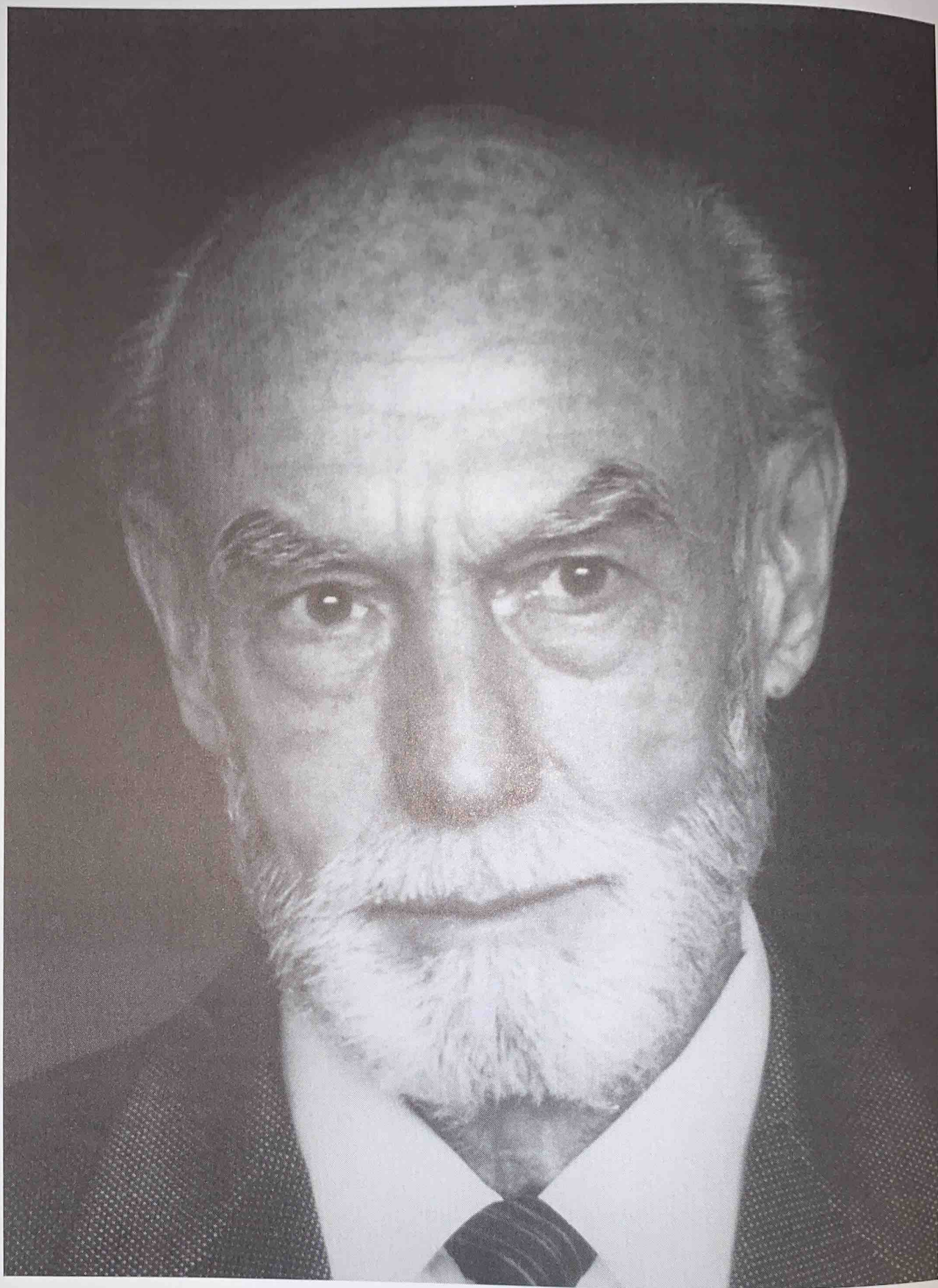


ROGER WOLCOTT SPERRY

20 August 1913–17 April 1994

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Roger Sperry

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20 August 1913–17 April 1994

Elected For.Mem.R.S. 1976

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'Where does behaviour come from? What is the purpose of consciousness?' Questions such as these, which appeared on the first page of Sperry's class notes in a freshman psychology course at Oberlin College, represent an accurate preview of a career that included major contributions to fundamental issues in neurobiology, psychology and philosophy. Indeed, his first paper, published in the *Journal of General Psychology* in 1939, entitled 'Action current study in movement coordination' (1)*, begins: 'The objective psychologist, hoping to get at the physiological side of behavior, is apt to plunge immediately into neurology trying to correlate brain activity with modes of experience', and continues, setting the stage for much that was to follow: 'The result in many cases only accentuates the gap between the total experience as studied by the psychologist and neural activity as analyzed by the neurologist.'

Roger Sperry was born in Hartford, Connecticut, and spent his early years on a nearby farm, where he developed a lifelong interest in nature. After the death of his father, the family moved to West Hartford, where he attended high school and established an all-state record in the javelin event. Sperry was accepted to Oberlin College under a full academic scholarship, earning his board by waiting tables. He maintained an active interest in sports and was elected captain of the varsity basketball team, as well as receiving varsity letters in baseball and track. As an undergraduate he attended R.H. Stetson's course, 'Introduction to psychology'. It was during a lecture by Stetson in this course that Sperry got the idea for a paper he published some 20 years later entitled 'On the neural basis of the conditioned response' (5). This short paper carries powerful theoretical implications for those interested in central nervous pathways in conditioned learning. Sperry remained at Oberlin College, in Stetson's laboratory,

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through 1937, when he received his M.A. in psychology.

Sperry took his Ph.D. in Zoology from the University of Chicago in 1941, under the tutelage of the renowned neuroscientist Paul Weiss. During that period, in addition to developing highly skilled neurosurgical techniques, he made the first of what was to become a number of successful challenges to existing concepts related to neuronal specificity and brain circuitry. In a series of carefully controlled and clearly written publications between 1941 and 1946, Sperry conclusively demonstrated that the rat's motor system was 'hard wired' and unmodifiable (following transplants) by training. This work clearly established that the basic circuitry of the mammalian central nervous system is largely hard wired for specific functions and seriously challenged Weiss's 'resonance principle' and 'impulse specificity theory'.

These studies were to have an impact on human neurosurgery as well. From 1942 to 1945, during his military service with the Office of Scientific Research and Development, Nerve Injury Project, Sperry's work, along with that of Weiss and others, resulted in a major change in the surgical management of nerve-damaged soldiers. It was common practice until that time to surgically transplant nerves to antagonistic muscle groups and then to subject the recipient to intense retraining, with the goal of regaining normal function. The demonstration that the basic structure of the mammalian central nervous system is hard wired, and unmodifiable by training, resulted in significant modifications of treatment protocols.

During Sperry's postdoctoral years with Karl S. Lashley at Harvard and at the Yerkes Laboratories of Primate Biology in Orange Park, Florida, he continued the work on neuronal specificity that he had begun as a doctoral student and initiated a new series of studies on the role of electrical fields in neocortical functioning. It was also during this period that he performed a series of brilliant experiments involving the rotation of eyes in amphibians. The optic nerves were sectioned and the eyes rotated through 180°. The question was whether vision would be normal after regeneration or would the animal forever view the world as 'upside down' and right-left reversed. Should the latter prove to be the case, it would mean that the nerves were somehow 'guided' back to their original sites of termination. Restoration of normal vision (i.e. 'seeing' the world in a 'right-side-up' orientation) would mean that the regenerating nerves had terminated in new sites, quite different from the original ones. The answer was unequivocal. The animals reacted as though the world was upside down and reversed from right to left. Furthermore, no amount of training could change the response. These studies, which provided strong evidence for nerve guidance by 'intricate chemical codes under genetic control' (7), culminated in Sperry's chemo-affinity theory (3).

Sperry later confirmed anatomically his behavioural studies with amphibia in a series of papers published between 1952 and 1964, on nerve-muscle and retino-tectal regeneration in fish. These experiments laid the foundation for many of our present-day views about neuronal specificity in brain development. Although a number of recent studies have challenged the chemoaffinity theory, it still stands as 'one of the most profound insights in developmental neurobiology'. Thus, through an ingenious combination of behavioural and anatomic approaches, Sperry related the functional interconnection of neuronal elements to developmental principles of differentiation, cellular interaction, cytochemistry and genetics. It was primarily this work, begun as a pre-doctoral student in 1938 and pursued through the early 1960s, that led to his election to the National Academy of Sciences in 1960.

Sperry's reason for choosing Lashley as a postdoctoral mentor is not entirely clear, but reflects his interest in Lashley's principle of equipotentiality. Sperry was uncomfortable with

the idea that electrical fields or waves acting in a volume conductor were critical for neocortical processing. His first study to challenge this concept was published in 1947 (2). Here he demonstrated that motor coordination in monkeys remained virtually unaffected after multiple transections of sensorimotor cortex. Later, in a series of papers with Miner, Myers and Zartman, he confirmed this point by demonstrating that neither subpial slicing, the insertion of numerous short-circuiting tantalum wires or insulating mica plates into the cortex had any adverse effect on cortical function. These studies demonstrated that perception depends on vertically oriented afferent and efferent cortical axons, predating Mountcastle's discovery of vertically oriented cortical columns. Sperry's premise was based on his keen understanding of neuroanatomy and neurophysiology, including the work of Santiago Ramon y Cajal and Lorente de Nó, both of whom had demonstrated the importance of radial cortical connections to cortical function. In these few carefully conducted experiments, Sperry once again upset two major theories of brain function—the gestalt electric field theory of perception and the reduplicated interference pattern hypothesis. Indeed, when the renowned neuroembryologist Viktor Hamburger presented Sperry with the Ralph Gerard Award from the Society of Neuroscience in 1979, he proclaimed: 'I know of nobody else who has disposed of cherished ideas of both his doctoral and his postdoctoral sponsor, both at that time the acknowledged leaders in their fields.'

It was during this postdoctoral period that Sperry began thinking about the functions of the corpus callosum. The function of this 'great cerebral commissure', which represents the major set of connections between the two cerebral hemispheres, had remained a mystery to neurobiologists. Some even joked about it, possibly out of embarrassment, for very little was known of its function at the time. Lashley, for example, is said to have remarked that its major function may be to mediate epileptic seizure activity from one hemisphere to the other; Warren McCulloch quipped that it may simply be there to keep the two hemispheres from falling into each other. The mystery of the corpus callosum continued to absorb Sperry, and shortly after moving to the Department of Anatomy at the University of Chicago in 1946, he began to examine this problem.

Sperry remained at Chicago through 1953, during which time several momentous events took place in his life. On 28 December 1949 he and Norma Deupree were married in Wichita, Kansas. Norma was to become his lifelong collaborator and mother of two children, Glenn Tad and Jan Hope.

In 1949 Sperry contracted tuberculosis from a monkey he had been dissecting to obtain tissues for nerve transplants. The diagnosis was made during a routine physical examination, the initial results of which declared him in excellent health (Norma Sperry, personal communication, 1995). Chest X-rays and further tests, however, confirmed the diagnosis, and the Sperrys began a sabbatical leave at Saranac Lake in upstate New York, for a period of rest and recovery. Norma relates that while there was very little rest, there was a great deal of fishing, swimming, hiking and writing. In six months Sperry was given a clean bill of health, and he and Norma spent the remainder of his sabbatical year at the Marine Biology Laboratory in Coral Gables, Florida.

Sperry returned to Chicago and became Associate Professor of Psychology in 1952, a position he held concurrently with his position as Section Chief of Neurological Diseases and Blindness at the National Institutes of Health. The first published description of his studies on callosal function appeared as an abstract in 1953, in collaboration with his doctoral student, Ronald Myers (4). Plans to move to Bethesda, Maryland, were postponed by a delay in building construction at N.I.H., during which time Sperry was offered the prestigious Hixon Professorship of

Psychobiology at the California Institute of Technology, a position he began in 1954.

During the next four decades, a large number of students and visiting scholars were to study in Sperry's laboratory. I first met Roger during the summer of 1958, when I spent several months with him as a visiting graduate student from Professor Marcus Singer's laboratory at Cornell. Singer and Sperry generously shared the cost of my visit, and I was able to take my wife and young daughter along for a summer that was to have a profound effect on my career. Sperry was, among other things, an outstanding neuroanatomist, and we hit it off immediately. My work on central nervous substrates of conditioned learning began during the summer of 1958 and continued in his laboratory through September 1962. My work continues to this day and remains strongly influenced by the impact of Sperry's thinking.

Sperry was a great teacher, but not in the conventional method of lecturing to students about factual material. His style involved one-to-one discussions, exchanging ideas and providing insightful critiques of proposals. He once told me, during a discussion about a research idea, that I should 'write it up, as if you have completed the study'. I was rather surprised by this, but he went on to explain that by writing the Introduction, I would be forced to not only critically review the literature but also consolidate my ideas. Materials and methods would tell me exactly what I would need to carry it out, and 'you pretty well know that the results will turn out one way or another, so you should write it up both ways'. 'Finally', he said 'the Discussion section will assist you in critiquing your results, whatever they are. By the time you get that done, you will know whether its worthwhile to embark upon the study'. Then he said with a broad grin: 'And you will already have the paper written'.

Sperry's laboratory in the Division of Biology at Caltech also became a centre for many new studies on nerve regeneration in fish and amphibia, reinforcing his earlier work on chemoaffinity and genetic control as major factors in neural development. His interests in learning began to take full form during the early years of this period, and in 1955 he published a short provocative paper on the nature of the conditioned response (5) in which he emphasized the role of transitory facilitatory motor sets and 'perceptual expectancy' that continues to have a profound effect on work in this area. It was also at Caltech where Sperry began to develop, along with a growing number of graduate students, postdoctoral fellows and visiting scientists, his 'split-brain' experiments, in which the two brain halves are separated by midline section of forebrain and midbrain commissures. These studies elegantly elucidated some of the major functions of the corpus callosum in interhemispheric memory transfer and eye-hand coordination. Restriction of sensory input to one brain half in commissurotomed animals was shown to limit the learning of various tasks to that hemisphere; the opposite side was capable of learning but remained naive to those tasks until trained. Learning curves for each hemisphere were virtually identical; it was as if two separate brains were housed within a single cranial vault. A large number of experiments were carried out by Sperry and his students during the late 1950s and early 1960s, all based on the possibilities suggested by the split-brain preparation. Sperry was very generous about sharing authorship. He insisted on being second or third author on much of the work published with his students. When I once suggested that he should be first author on a study that we had worked on together, he said he would prefer that I be sole author, but if I felt that it might help to have his name on the paper, he would be second author. I remained sole author on most of the work I performed in his laboratory because Sperry felt that it would help my own career more that way. This was very typical of his attitude toward authorship when he felt that another had done the bulk of the work in the area, even though he had made important contributions to it. He was a fair and

generous person in all of his interactions with others.

In 1960 Dr Joseph Bogen, who had been doing research in the Biology Division at Caltech, suggested that the split-brain work might be extended to humans because earlier studies by Van Wagenen, Akelitis and others had suggested that commissurotomy was efficacious in the treatment of epilepsy. Commissurotomy was known to have little effect on general levels of intelligence and motor coordination, and it was felt that this operation might not only reduce seizures but also prevent their propagation, with little or no severe side effects. The opportunity arose in 1962, when a Second World War veteran with progressively worsening seizures (up to 20 per day) underwent a callosalectomy by Drs Philip Vogel and Joseph Bogen. The operation was successful, and there was a dramatic reduction in the number and severity of the patient's seizures.

Sperry, along with Bogen and Sperry's graduate students, Colwyn Trevarthen and Michael Gazzaniga, then began a series of tests directed at understanding the effects of commissurotomy on human perception, speech and motor control. The work on humans allowed investigators to compare cognitive abilities between the two separated brain halves, demonstrating differences theretofore unrecognized. The left brain half, for example, was found to be superior to the right in tasks involving analytical, sequential and linguistic processing; the right performed better in wholistic, parallel, and spatial abilities.

For the next 20 years the work of Sperry and his collaborators revolutionized our understanding of brain function. They elucidated the unique capabilities of each hemisphere and demonstrated that the combined effect of bihemispheric activity amounted to more than the simple additive effects of the two separate hemispheres. Sperry's brilliant studies on the functional specialization of the cerebral hemispheres won him a share of the 1981 Nobel prize for physiology or medicine (20).

Far from resting on his laurels, Sperry left others to continue the examination of right-hemisphere/left-hemisphere functions and moved forward to explore the emergence of consciousness from the unified brain. His first major paper on the topic of the mind and consciousness appeared in 1965 (8) and was only the beginning of many more to follow over the next 30 years. He had actually broached this issue as early as 1959 as part of a discussion at a Josiah Macy conference on the central nervous system and behaviour (6), where he stated:

I have never been entirely satisfied with the materialistic or behaviouristic thesis that a complete explanation of brain function is possible in purely objective terms with no reference whatever to subjective experience; i.e., that in scientific analysis we can confidently and advantageously disregard the subjective properties of the brain process. I do not mean we should abandon the objective approach or repeat the errors of the earlier introspective era. It is just that I find it difficult to believe that the sensations and other subjective experiences *per se* serve no function, have no operational value and no place in our working models of the brain.

In his 1965 paper entitled 'Mind, brain and humanist values' (8), Sperry proposed that subjective experience plays a principal role in brain function. He posited that behaviourism and reductionism must both be replaced by a new concept of consciousness, based on the ideas of emergence and downward causation. The concept of emergence, according to Sperry, 'occurs whenever the interaction between 2 or more entities, be they subparticles, atoms or molecules, creates a new entity with new laws and properties formerly nonexistent in the universe'. He notes the parallel with quantum physics in which 'interactions among subatomic particles result in emergent properties which in no way resemble the particles from which they arose'. It is important to emphasize that Sperry did not see this as dualism, which treats the

mind as a separate entity outside the brain that is capable of existing independently of it. Nor did he accept the term 'psychophysical interaction', 1980, suggested by Popper and Eccles in 1977. Sperry pointed out in 'Holding course amid shifting paradigms' (12) that the erroneous classification of this conception is probably based on an earlier terminology in which 'mentalism' was equated with dualism. He describes his reasons for retaining the term mentalism in preference to Bunge's (1977, 1980) 'emergent materialism' or Natsoulas's (1987) 'physical monism', emphasizing that this new form of mentalism must be viewed as a 'quite different intermediate position which is monistic, not dualistic'.

Thus, consciousness, in Sperry's view, while generated by and dependent on neural activity, is nonetheless separate from it. Consciousness emerges from the activity of cerebral networks as an independent entity. This newly emerged property, which we call 'mind' or 'consciousness', continually feeds back to the central nervous system, resulting in a highly dynamic process of emergence, feedback (downward causation), newly emergent states, further feedback, and so forth. Reducing consciousness to its separate components obliterates the emergent phenomenon of 'mind' with all its great power and uniqueness.

Sperry elevated this concept of emergence from the individual to the global level, stating that the 'new paradigm affirms that the world we live in is driven not solely by mindless physical forces but, more crucially, by subjective human values. Human values become the underlying key to world change' (9). He contended that this view, integrating macro- and microdeterminism with the causal reality of mental states is a more valid foundation for all science, not just psychology, with 'endless humanistic implications for philosophy, religion and human values' (11). By introducing the issue of human values, Sperry moved beyond the specifics of mind and consciousness to urge that these very unique and powerful forces be directed toward improving and preserving the quality of life on our planet, rather than the reverse. He made a strong appeal, especially to his scientific colleagues, to turn their efforts toward these goals. His message began, finally, to be heard by the scientific community. In response, and under the able leadership of his long-term friend and colleague, Dr Rita Levi-Montalcini, an international conference was convened at the University of Trieste in November 1992 to discuss these ideas in greater detail. The plan was to work toward the creation of a strong statement of human duties, generated by the scientific community, but speaking to every 'mind' willing to listen. This might represent a corollary to the United Nations's Declaration of Human Rights. The first meeting of the group, which, unfortunately, Sperry was not able to attend, included 10 Nobel laureates and numerous others, representing such widespread disciplines as neurobiology, chemistry, physics, economics and theology. After much discussion, a draft version of 'The Magna Carta of human duties' was generated, with an agreement to continue discussion the following year. In November 1993 a near-final draft was completed, and after circulation to all participating members for ratification, the final version, entitled, 'A Declaration of Human Duties', was agreed on in 1994. The document was forwarded to the United Nations, where it is presently under review and consideration.

A second series of conferences inspired by Sperry's ideas on the mind and human values was organized by Professor Kaoro Yamaguchi. The long-term goal of these conferences (there have been four to date), held on the island of Awaji, is to work toward establishing an International Network University of the Green World, dedicated to the continuing study of human values.

Sperry's thinking about subjective experience, consciousness, the mind and human values

makes a powerful plea for a new scientific examination of ethics in the workings of consciousness. These ideas were crystallized in his paper 'The impact and promise of the cognitive revolution' (11), which I had the honour of delivering for him at the centennial meeting of the American Psychological Association. It was his great hope and sincere belief that if we humans could simply be persuaded to put our collective minds together and use the enormous emergent powers that they are capable of generating, we would not merely improve the quality of life on the planet, we would ensure our very survival.

Finally, on a personal note, Roger and I remained close friends and correspondents from the time I left Caltech until his death in 1994. My wife and I were frequent recipients of the Sperry's warm hospitality, and I last visited him in October 1993. Roger, Norma and I enjoyed an evening and breakfast together at Sperry's home in Pasadena, discussing the forthcoming Trieste and Japan conferences on human values. During the many years of our friendship, I came to appreciate his quiet, thoughtful manner and to respect his insightful comments, high ethical standards, deep love of science and wry sense of humour. Though a rather private person, preferring the quiet beauty of remote places to large crowds, he was known during the early 1960s for his delightful parties, with good conversation, dancing and his special 'split-brain' punch. His interests were seemingly unlimited. Along with Norma and his two children, he searched for giant ammonites and dinosaur bones in the South-West. The family also shared numerous adventures in Baja California, camping on remote beaches and fishing from a 12-foot rubber boat with homemade lures. On one occasion he hooked a 14-foot marlin, which towed the boat for a considerable distance. He instructed Norma to 'just keep snapping pictures'. She did and took a prize-quality photo of the entire fish in mid-air, with foaming water flying in all directions. I asked him later what happened to the fish. 'I cut it loose, of course', he said quietly, looking straight into my eyes. 'What in the world would I have ever done with a 14-foot marlin?' My wife and I recently purchased the Sperry's 1986 camper truck with extra-wide tyres and plan similar trips to Baja. We continue to discover ingenious little space-saving devices in the camper, ranging from refrigerator doorguards to fold-out shelves; wonderful reminders of the quiet, practical man who installed them. Roger was also a highly talented sculptor, artist and ceramicist. The Sperry home is filled with busts of his family, paintings and other items attesting to Rogers combined artistic and scientific creativity.

This brief review is inadequate to describe Roger Wolcott Sperry's multiple talents and inspired contributions to science, art and philosophy. I have tried to provide a few examples of the far-reaching, global effects that emerged from the synaptic interactions, transmitters and circuitry of his brain. No doubt these were quite similar to most other brains. But the *mind* that emerged from those interactions was truly unique, for it not only stimulated and inspired his students, colleagues and friends, it has stirred as well the minds of thousands of others and will continue to excite and inspire new thinking from generations of minds yet to emerge.

Scientist, teacher, philosopher, humanist—Roger Sperry has left us a rich legacy of ideas and a challenge to foster the emergence of new understandings of human capabilities and responsibilities.

ACKNOWLEDGEMENT

I want to thank Norma Sperry, not only for her help in providing personal information about Roger, but also for reading and commenting on drafts of this Memoir.

The frontispiece photograph by Lois MacBird was taken in 1979, and is reproduced with the permission of the California Institute of Technology.

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NOTE ON THE TEXT

1. Harris, W.A. and Holt, C.E. 1995 From tags to rags: chemoaffinity finally has receptors and ligands. *Neuron* **15**, 241–44. For a review of work on neuronal specificity from the post-Sperry era to the present, see Holt, C.E. and Harris, W.A. 1993 Position, guidance, and mapping in the developing visual system. *J. Neurobiol.* **24**, 1400–1422.

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