Roger W. Sperry 1914 – 1994



Roger W. Sperry, the Board of Trustees Professor of Psychobiology, Emeritus, died April 17, 1994, of complications associated with lateral sclerosis. He had been a member of the Caltech faculty since 1954, for most of that time the Hixon Professor of Psychobiology, and in 1981 won the Nobel Prize for his discoveries concerning the functional specialization of the two hemispheres of the brain. John M. Allman, the current Hixon Professor, chaired a memorial observance June 3 in the Beckman Institute Auditorium, during which several people who had known Sperry well spoke of the importance of his scientific work and his impact on his students, on his colleagues, and on society.

Norman Horowitz Professor of Biology, Emeritus

I was Roger Sperry's oldest friend on the Caltech faculty. I first met him in 1951, when we were both on the program of a symposium that was held at Smith College in Northampton, Massachusetts. Roger's talk, which I can still remember, was truly brilliant, dazzling. I'm a geneticist; I'm not a neuroscientist, or a behavioral biologist, or a psychobiologist, but I could recognize a master at work. I would not have been surprised if someone had told me then that Roger would be one of the principal shapers of the modern view of how the brain works. In his talk, Roger demonstrated the capacity to design experiments that gave clean answers to interesting questions in one of the most difficult areas of



Roger Sperry at Caltech in 1954.

biology. His surgical skill and his imagination in designing tests of brain function were enormously impressive to me. He proved beyond a reasonable doubt in that paper that the many individual nerve fibers that make up the regenerating optic nerve in amphibians have separate chemical identities that determine where they make their connections as they grow back into the brain. He showed this by logical inference from his biological results, without performing any actual chemistry.

The second thing that struck me about Roger's lecture was its conclusion. Here he displayed a comprehension of the broader biological issues that made him almost unique for that time. I want to read the last two sentences of that paper. They may surprise some people who came to know Roger only in his later years. "Finally, to return to our original theme, it would seem that with the foregoing picture of the developmental processes, almost no behavior pattern need be considered too refined or too complicated for its detailed organization to be significantly influenced by genetic factors. The extent to which our individual motor skills, sensory capacities, talents, temperaments, mannerisms, intelligence, and other behavioral traits may be products of inheritance would seem to be much greater on these terms than many of us had formerly believed possible."

When I got back to Caltech I knew what I had to do. At that time we were searching for the first Hixon Professor of Psychobiology. I spoke to George Beadle, who was then division chairman, and to Anthonie Van Harreveld, who was chairman of the Hixon search committee, and suggested that Roger be invited for some lectures. Roger was invited; he came, he conquered, and the rest is history.

Ronald Meyer

Professor of Developmental and Cell Biology University of California, Irvine

(Meyer came to Caltech as a graduate student in psychobiology, earning his PhD in 1974. In his memorial talk he described some of his experiences in Sperry's diverse lab and traced the development of Sperry's theory of chemoaffinity—work that began in the 1930s and 1940s. Although it had been postulated earlier that growing nerve fibers used chemical clues to find their way, no one had been able to discover any evidence to support that idea, and current studies were leading in the opposite direction. At the University of Chicago, Paul Weiss concluded that all nerve fibers was unimportant, and that the pattern of nerve connections was unimportant, and that the important thing in innervation was learning. Sperry was Weiss's graduate student at Chicago and set out to test this idea.)

Initially he was interested in its functional aspects, so one of the first experiments he did was to cross some of a rat's nerves so that they innervated the wrong muscles. Then he looked at the behavior of those rats very carefully; it hadn't been done all that carefully before. He observed that the basic reflex behavior of these animals was always abnormal; the rat could learn to adapt to this screwed-up leg, much as you might be able to walk with a cast, but the function was really abnormal. What he concluded from this was that specific nerves did mediate certain responses, and that connection was important.

Around this time a number of reports appeared showing that in lower vertebrates, such as frogs and salamanders, you could cut the optic nerve and it would grow back. The folks who did this interpreted the results along the lines Paul Weiss had championed at the time-that the animals were simply learning to adapt to abnormal connections. Then Roger did what was perhaps his most famous experiment: he rotated a frog's eye 180°, then cut the optic nerve and let it grow back. (This was not particularly easy. I tried it a few times as a graduate student and gave up.) Now, normally you can tell what the frog sees by using a little wire with a fly on the end. If you put it in front of the frog, the frog will try to eat it; if you put it in back of the frog, the frog turns around and then tries to eat it. The frog has very good visual localization. What

Roger found when he turned the eye upside down was that, when you put the lure behind the frog, the frog would try to eat it. And if you put the lure in front of it, the frog would turn around. It saw the world completely turned around by 180°. Fortunately frogs are very stupid. They never learned how to adapt to this; if you didn't feed them forcibly, he found, they would simply starve to death.

The conclusion Roger drew from this experiment was that nerve fibers from the eye must have grown back to specific locations within the brain, in an area called the tectum. These regenerating fibers were reestablishing the map from the retina onto the tectum. In spite of the fact that they had started out upside down, they managed to straighten themselves up and go back to their original targets. He theorized that during development a position-dependent differentiation occurred in the retina so that different nerve fibers from different regions acquired specific properties. In the tectum, nerve fibers in different regions also acquired specific properties, and there was some way in which the nerve fibers growing from the retina could then locate those particular regions in the tectum and find the right place. This is the heart of chemoaffinity.

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He wrote 16 or so papers extending this finding to a number of different nerve systems. His work evidently made quite an impression at the University of Chicago, and they duly acknowledged it by denying him tenure. If there is a top-ten list of the worst tenure decisions in the world, Roger must be on it.

But Chicago's loss was Caltech's gain. When he came here he performed what was probably one of his next most important experiments. Together with Domenica Attardi, he developed a method for visualizing optic fibers while they were growing into the brain of a goldfish. He found that if he removed part of the eye, fibers from the remaining part of the retina would grow into the tectum; they would even grow past the wrong regions and selectively terminate in the correct regions. Furthermore, en route to the tectum they would take specific paths to lead up to the correct angle to approach the tectum. On the basis of this work, in the early 1960s Roger published an elaborated version of his chemoaffinity hypothesis, spelling it out with particular reference to the visual system: that during development, retinal cells acquire a positiondependent differentiation, probably in a gradient fashion; that the tectum acquires a similar gradient distribution of molecules; and that fibers from the retina or elsewhere could selectively navigate through this myriad of cues in a selective fashion and innervate the particular targets.

Some of us kept on with this work, but Roger's interest shifted toward the higher-order functions in the brain, such as consciousness and perception. Why, you might wonder, didn't he go after the molecules to prove that his chemoaffinity hypothesis was correct? He felt that this was a waste of time, that he had already solved the problem. And, really, from his perspective he had. He had asked the question: does the specificity of nerve connections determine function? And he had shown that it does. How do they do it? By a developmentally regulated process that gives them labels. He wasn't interested in going after the molecules, and, since no one has yet definitely proven what they are in the visual system, I'd say that was a wise career decision on his part. He was interested in how nerve structure determines behavior and function, and he went on to examine issues at the higher end. How does nerve structure determine perception in the cortex? How much is that wired in? What was the basis of consciousness? It didn't really represent that much of a change of interest.

(Meyer went on to describe some of the arguments and skepticism about Sperry's chemoaffinity hypothesis that arose during the 1970s and 1980s, and speculated that they might have been responsible for his not receiving the Nobel Prize for this work. Meyer made a distinction between what he called Sperry's special theory of chemoaffinity, based on the expanded research into the visual system, which Meyer called 90 percent correct, and the general theory of chemoaffinity-the big picture of how the formation of nerve connections is regulated. There is no serious questioning of the general theory today, and it's accepted as a theory nearly in the same way that evolution is just a "theory." Meyer concluded with the observation that, since the theory is now so generally accepted, it's easy to forget that there was ever even a question of whether nerves had specific identities and that we have Roger Sperry to thank for telling us that they do.)

Brenda Milner

Dorothy J. Killam Professor of Psychology Montreal Neurological Institute, McGill University

(Milner, according to Allman, is one of the great figures in the field of neuropsychology, known for her classical studies of the role of the medial temporal lobe structures, including the hippocampus, in memory. These studies have had enormous influence on modern neurobiology. She spoke of Sperry's contributions to the study of human cognition, beginning with some personal reminiscences, recounting a time in 1972 when they

both happened to be in Cambridge, England, where Sperry was receiving an honorary degree; Milner described the ceremony.)

The Cambridge orator, who had to give an

account of everything in Latin, had a lot of trouble with the frogs and the motor connections because apparently the Romans had the same word for nerve and muscle. So he had a little difficulty making this distinction in elegant Latin; fortunately we also had a translation. He began by pointing out that this is a person with many careers; that it is given to very few scientists to make major contributions in more than one field-contributions that will have enormous impact on the work of future scientists in those fields. If you want to explore complex issues and problems, you have to ask yourself the right questions. And Roger was so good at asking the right questions, the important ones, and he had little use for what he thought were trivial questions. He could be very impatient about things he thought were really no longer issues and always wanted to look ahead at some big question that was waiting to be tackled. How did he do it? He did it, first of all, not by expensive equipment, but by very simple means with very elegant methods. And, the orator added, he did it with dexterous hands, with skilled hands-this is the meticulous surgeon, the meticulous scientist. And above all, he did it with a mind that was dedicated to looking for natural causes, with the inquiring mind and the investigative look. The orator concluded by saying that if you have this approach and these qualities, then you can open up a "broad path into a closed field." And I think the broad path into the closed field is what we saw in the results and consequences of Roger's work on the split brain.

How did the field look before this work, and what difference did Roger make? For years there had been a number of neurologists and psychologists in different countries who had been gathering compelling evidence of the important contributions of the right, nondominant hemisphere to intellectual, cognitive tasks. These contributions particularly involved visuo-spatial skills, the representation of visual patterns, and so on. Here there was real evidence that the right hemisphere was not merely competent, but that it was more competent than the left, language-dominant, side. Most of this evidence came from the study of patients with circumscribed brain lesions. This is evidence by subtraction—the richness and the capacity of the person's intellect was in some way diminished by reduction of language, memory loss, loss in visuo-spatial perceptual abilities,

or by some change in personality. There's a diminution of an entity.

Commissurotomies (cutting the corpus callosum, which connects the two hemispheres) had been done before, but no one had discovered that anything was wrong. What was new with Roger's approach was that he told us how to examine these patients, how to address questions to each of the separated hemispheres. We wonder now how others could have missed something so glaring. Roger believed very strongly that you learn good lessons from behavioral studies in animals. He had learned from all his work on commissurotomies in monkeys and cats that the two sides of the brain can function amazingly independently in carrying out various tasks. He took the next logical step and asked whether this occurs in humans. And of course, the logical, commonsense answer was, why not? Illogically, however, the feeling was that, no, consciousness is one, a human brain can be diminished by a lesion but it can't be split. But Roger followed the path of science and applied to humans the methods he had applied to other species. (It's much more difficult when you can't just cut the optic tract; he had to develop methods for channeling information into one hemisphere and out from the same hemisphere.) Then he presented the world with this notion of two minds in one head, two organizations of neurons capable of thinking. Of course, they have the brain stem in common, exerting some general unifying influence on the two halves, but cognitively they remain distinct. The right hemisphere doesn't talk, or talks very little, but it thinks for itself. Roger demonstrated that by addressing the question directly to one side of the brain, he could elicit one kind of behavior, and a contrasting behavior when the same question or task was addressed to the other side. Encountering patients who exhibited these two consciousnesses coexisting gave us a fresh understanding of the logical consequences of separating two equally complex organizations of nerve cells and pathways.

Roger characterized the right side as being more holistic, the left as more analytic. Perhaps the popular press took this over too wholeheartedly and talked about "educating the right hemisphere," and so forth. In the person with intact hemispheres, I think, you can only educate an organism, the whole person, but the demonstration of the coexistence of two entities, two thinking minds, in the patients with divided commissures was incredibly compelling. It gave a great boost to our field. This field, now fashionably called cognitive neuroscience, owes an enormous debt to these insights of Roger Sperry.

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Sperry in his lab in 1974.

Dr. Joseph Bogen Clinical Professor of Neurological Surgery, University of Southern California Adjunct Professor of Behavioral Neuroscience, University of California, Los Angeles

(Bogen, who was stimulated by Sperry's experiments to propose severing the corpus callosum to limit epileptic seizures in humans, worked with Sperry over several decades in studying these split-brain patients. He contributed a few anecdotes that he hoped would "reflect my impression of Roger's genius, his style, and his demeanor." He also referred again to the elegance and simplicity of Sperry's early experiments with frogs' leg muscles and rotated eyes—in the latter the demonstration of the frog's vision using a fly on the end of a stick or wire. "That took real genius—to think of this really simple way.")

The first time that I saw Roger was over 40 years ago, when he gave his famous Sigma Xi lecture in the Athenaeum. He lucidly explained and astoundingly illustrated the discriminative ability of cats that had various alterations of their visual cortices. I was not in a position at that time to arrive at an informed evaluation of that talk, but perhaps I can convey to you how I felt by referring to a time when I was trying to educate my elder daughter about wine-how to tell good wine from not-so-good. I gave her some wine to try; she swirled it and sniffed it and rolled some around in her mouth and swallowed it. Then she said, "Nobody has to tell me that's good." That's how I felt about Roger's talk that day, and that's the way I've felt about

Roger Sperry for the ensuing 40 years.

In 1955 I came to Caltech as a graduate research assistant to Anthonie Van Harreveld. Van Harreveld's lab and office were on the third floor of Kerckhoff, just down the hall from Roger's. I spent quite a bit of time down at Roger's end of the hall, because those split-brain cats were mind-boggling. They made a profound impression on everybody who saw them. It was the most influential experiment that I ever saw or ever knew about or heard about before or since. It set the course of my life.

Three years later I came back to Van Harreveld as a postdoc, and during that time Roger and I became better acquainted. It was necessary for me to go up and down the hall several times a day, and usually when I would go by Roger's office the door would be open and he would be sitting there reading or maybe doodling on a pad. Sometimes he'd just be leaning back in his chair with his feet on the desk, staring into space. Then one day he disappeared, into the lab. Not long after that we had a biology seminar, at which Sperry and Attardi presented their work on optic nerve regeneration. The slides were sections of goldfish brain that were stained a deep bluishblack, except for the regenerating fibers. These fibers, sneaking their way through the jungle of the optic chiasm, up around the optic lobe and then abruptly diving into their intended destinations, were stained a brilliant pink. It was spectacular. It has always seemed regrettable to me that when this work was finally published in the Journal of Experimental Neurology, the pictures were reproduced in black and white. That was in 1963, five years after the abstract first appeared in the Anatomical Record in 1958. Such a long delay was not unusual for Roger. He could keep a paper on his desk for a long time for a variety of reasons. One of them was that he liked to see how the follow-up experiments were going to turn out. The idea was that when you went back and wrote the final form of the first paper, the discussion would have some sensible things to say. It seemed to me he thought of everything. I hung on his every word, of which there were not very many. . . .

Around 1960, when I was working at County Hospital, I wrote an essay about epilepsy, entitled "A Rationale for Splitting the Human Brain." I brought it up to Roger, and he had a number of recommendations, the first of which was, "Maybe you should change the title." Also, he told me to look up some papers by Akelaitis, which I did, and it turned out that the callosal surgery performed by Van Wagenen 20 years before had actually turned out better than was then, in

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Roger Sperry receives his Nobel Prize from Sweden's King Carl Gustav in Stockholm on December 10, 1981.

1960, the prevailing medical opinion. This suggestion led to a joint effort of nearly 30 years.

At about the same time, one of my projects involved some behavioral experiments with rats, the results of which I really didn't understand. I thought that if anybody could explain it, it would be Roger. So I brought my data up to Caltech. He had some helpful comments to make, and then he said, "If you keep working with that, you might very well come up with something dramatic." Roger Sperry's facility for coming up with something dramatic time after time in a variety of contexts was not simply because he kept in mind the value of a decisive counterintuitive result. And it was not just because he was a highly creative and self-disciplined presenter, and not just because he was an expert experimentalist. Essential, I believe, was the fact that Roger was among the deepest, the most profound neurothinkers of our time.

Theodore Voneida Department of Neurobiology Northeastern Ohio Universities College of Medicine

(Voneida met Sperry as a visiting graduate student in 1958, working with split brain cats in Sperry's lab, and returned to Caltech as a postdoc in the early sixties. "This was a rich and exciting time for me, and it really established the pattern of my research, which has continued in the same vein for over 30 years. . . . I never failed to be impressed with his tremendous insight into questions of research. One could spend an hour discussing an idea with Roger and leave the discussion knowing whether or not it was worth pursuing." Voneida remembered fondly Sperry's sense of humor and the Sperrys' great parties, where Roger served his famous punch, "one glass of which would strip away at least 200,000 dendritic spines.")

I do not intend to review all or even a few of Roger's major contributions. Others have done that. Rather, I will restrict my comments to the area of his most recent interest, namely the concept of mind, or consciousness, as an emergent property of brain function. Like most emergent properties the mind is a unique entity, and as such in no way resembles the structures from which it arises, namely the hundreds of millions of neurons constituting the central nervous system. An important point, however, is that while the mind is not the same as the central nervous system, it is dependent for its existence on the central nervous system. This may appear obvious, but Roger always emphasized that this concept of the mind should not be construed in any way as supportive of dualism. A second point, and one that may not at first be obvious, is that the mind continuously feeds back onto the central nervous system and this feedback results in a constantly changing nervous system. The feedback aspect is very important and often is not recognized. The cognitive revolution, according to Roger, from an ethical standpoint might equally well have been called a values revolution, through which "the old value-free, strictly objective, mindless, quantitative, atomistic descriptions of materialist science are being replaced by accounts that recognize the rich, irreducible, varied, and valued emergent macro and holistic properties and qualities in both human and nonhuman nature."

He goes on to tell us that "subjective human values become the most critically powerful force shaping today's civilized world, the underlying answer to current global ills and the key to world change." In short, the cognitive revolution, in Sperry's view, represents a possible last hope for survival, through which two powerful groupsscience and religion-might find a common ground for cooperation in dealing with problems such as increasing population pressures, ecological destruction, and global warming. This concept of the mind as a single unifying force was generated in great part during his retirement years, and may prove to be one of his most significant contributions, though it is difficult to say that about a person who has made so many significant contributions.

In an article entitled "Science and the Problem of Values," written in 1972, he wrote, "The



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prime hope for tomorrow's world lies not in outer space or improved technology, but rather in a change in the kind of value belief systems we live and govern by. The more strategic way to remedy global conditions such as poverty, population explosion, energy and pollution, is to go after the social-value priorities directly in advance, rather than waiting for the value changes to be forced by worsening conditions. Trends toward disaster in today's world stem mainly from the fact that, while man has been acquiring new, almost godlike, powers of control over nature, he has continued to wield these same powers with a relatively shortsighted, most ungodlike, set of values, rooted on the one hand in outdated biological hangovers from evolution in the Stone Age, and on the other in various mythologies and technologies based on little more than faith, fantasy, and intuition." He concludes that the human brain is today the dominant control force on our planet: what moves and directs the brain of man will, in turn, largely determine the future from here on.

(Voneida noted Sperry's discussions of his ideas with Nobel (physiology or medicine) Laureate Rita Levi-Montalcini, who proposed an international meeting at Trieste. This grew into two international meetings, one in December 1992 and the other in November 1993, at which a 12-point Declaration of Human Duties with the subtitle "A Code of Ethics of Shared Responsibility"—was drafted. When approved and signed, it will be delivered to the United Nations, where it will serve as a corollary document to the Declaration of Human Rights. Voneida presented Sperry's work at these conferences and is also active in an ongoing series of conferences in Japan that are working toward establishing the Network University of the Green World, in which students worldwide will communicate on topics related to human values.)

This has been a necessarily brief overview of some of the impact and the promise that Roger's recent ideas have had. They continue to be heard, and there is no question that they will continue to have an enormous impact on our thinking about mind, consciousness, and values well into the 21st century and beyond.

From my own point of view I'd like to say that my own life was very greatly enriched by having known and having worked with this quiet, reserved man with a grand, wry sense of humor. To me he was a superb teacher, a wonderful and generous colleague, and a dear friend. I owe him more than I'm able to say. And the best I can do is to continue studying and disseminating what I have learned from him to the widest possible audience, with the hope that humankind will open its collective mind to a new way of thinking and a new set of values before it's too late.

Seymour Benzer

James G. Boswell Professor of Neuroscience, Emeritus Crafoord Laureate

Roger Sperry, as well as having influence on the world as a whole, also had a great influence on me and my career of the last almost 30 years. It's a well-kept secret that I spent two years in Roger's laboratory here at Caltech from 1965 to 1967. We never worked together and we never published together, so there's no fossil record of those events. I came to Caltech for a change of career, switching from molecular biology to an interest in neurobiology. I had done that once before, many years earlier, when I switched from physics to molecular biology by coming and working in Max Delbrück's laboratory. Delbrück's laboratory and Sperry's laboratory had a great deal in common; not only were they headed by towering intellectual figures, but each lab was what is now referred to in industry as an "incubator"-an institution that forms a sort of protective cover over young entrepreneurs who are trying to establish their own businesses. A dozen of them are put together in the same building so they can share facilities and learn from each other the ropes of making a career in the business world. So in both Delbrück's and Sperry's labs there was a motley crew of characters working on many different things and, in both cases, many of Roger and Norma Sperry collected fossil ammonites, some of which were exhibited, along with some of Sperry's artwork, at the memorial service. This 70-million-yearold specimen, however, displayed in their living room in 1987, was too large to move. The Sperrys found it in the Mexican Rio Grande.



the people who emerged have had very distinguished careers.

I had been at Purdue working on the structure of the gene and how genetic information gets transcribed and translated in bacteria. It struck me that if people have different genes, then their nervous systems might not develop in exactly the same way. That might account for their different behavior, which was beginning to puzzle me, especially with respect to my two children, who, from day one, behaved very differently. On looking into the literature, I encountered Roger Sperry's ideas and experiments on chemospecificity of neurons and its role in wiring up the nervous system, and his idea that genetics was behind the mechanism. Since I still had a fond attachment to Caltech from the Delbrück experience, I asked Max whether Sperry's lab would be a good place to go. His response was, "You could do worse." When I approached Sperry with the idea, he apparently also asked Max about me, and I suspect he got the same answer.

Last night, I dug out some of the original correspondence with Sperry in 1965. It goes as follows:

Dear Dr. Sperry: Thanks for making my visit to your group such a pleasant and informative one. It seems silly for me to look any further for the best place to learn the brain business. Would you permit me to spend my sabbatical in your laboratory starting in September? Best regards.

Dear Dr. Benzer: Yes, we'd all be happy indeed to have you spend your sabbatical here. I should probably warn you that you may find our Caltech group rather small and lacking in much of the exciting diversity you might see in a larger setting. This might be compensated in part by visiting connections with UCLA, which has become much closer to Caltech in recent years through new freeway developments. I'm not sure what you'd like to do, if anything, in the way of actual experimentation that might involve research space and facilities. I assume you mainly want a kind of home base from which to read, think, watch, talk, and learn, rather than a place to engage in specific projects. But mainly we should probably be sure you don't wish to use a special brand of computerized bevatron that we don't have. Others here, including Max Delbrück and Jean Weigle, are equally enthusiastic about the idea.

Dear Dr. Sperry: Thank you for your yes. Please rest assured that I've little interest in either computers or bevatrons, let alone their combination. Nor do I intend to spend a year on the freeway, which to me is a foretaste of hell. My ambition is to work seriously with you on a specific problem. While a solution to the memory riddle in one year may be too much to ask [I was pretty naive], I do hope for an opportunity to obtain a working knowledge of brain splitting, psychological testing, and the associated arts.

Dear Dr. Benzer: OK, fine. We'll count on solving the biochemical basis of memory in the fall and there'll be plenty of time meanwhile to decide what to look at next. All best wishes and we'll be looking forward to your arrival.

(Benzer described some of the personalities and the work going on in the incubator of Sperry's lab, which he called "a real zoo, both in animal terms and intellectual terms.")

All the activities in the lab had one thing in common: none of them had anything to do with genes. To me this was the wide open field through which one could build a big road. So I went around the corner to Ed Lewis [who is now the Thomas Hunt Morgan Professor of Biology, Emeritus] and got some fruit flies and some test tubes, which were not to be found in Sperry's lab, and went to work. And I've been doing that ever since. So Roger's contribution was not unlike Delbrück's: a role model for creative thinking; an attitude of skepticism, which served as a goad to do something that would make an impression; but at the same time the generosity to provide a supportive environment in which each of us could learn from the other weirdoes in the lab, try out crazy ideas, and develop our own thing. For that I will always be indebted to, and will always remember, Roger Sperry.

OK, fine. We'll count on solving the biochemical basis of memory in the fall and there'll be plenty of time meanwhile to decide what to look at next.