



David H. Hubel

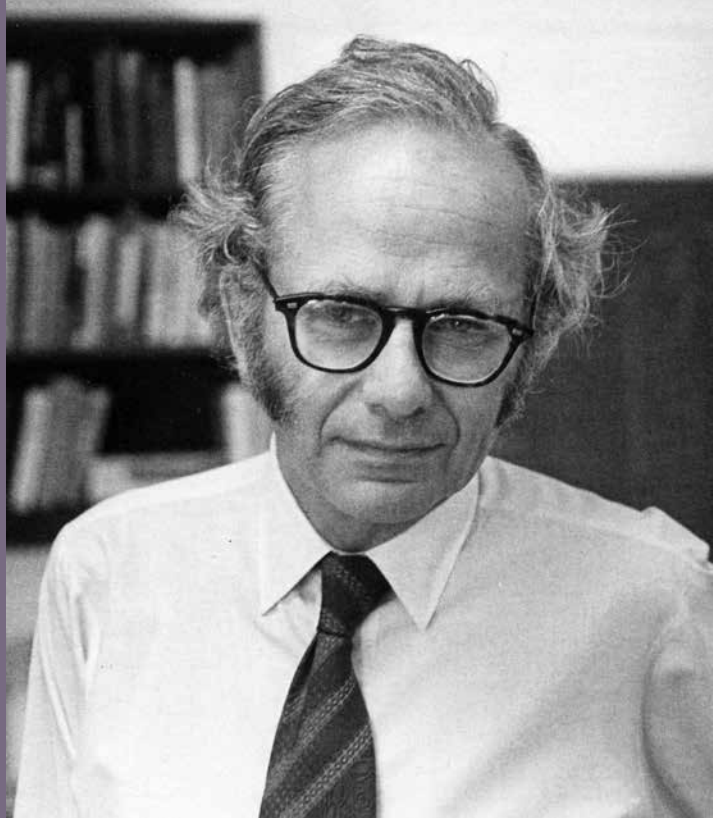
1926–2013

BIOGRAPHICAL

Memoirs

*A Biographical Memoir by
Robert H. Wurtz*

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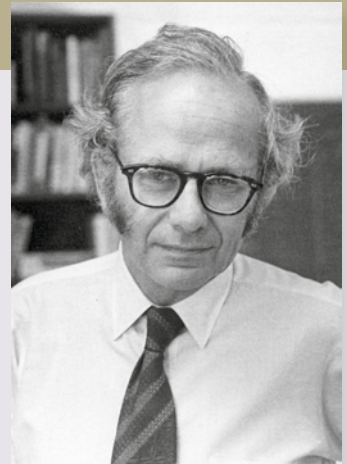
NATIONAL ACADEMY OF SCIENCES

DAVID HUNTER HUBEL

February 27, 1926–September 22, 2013

Elected to the NAS, 1971

David Hunter Hubel was one of the great neuroscientists of the 20th century. His experiments revolutionized our understanding of the brain mechanisms underlying vision. His 25-year collaboration with Torsten N. Wiesel revealed the beautifully ordered activity of single neurons in the visual cortex, how innate and learned factors shape its development, and how these neurons might be assembled to ultimately produce vision. Their work ushered in the current era of analyses of neurons at multiple levels of the cerebral cortex that seek to parse out the functional brain circuits underlying behavior. For these achievements, David H. Hubel and Torsten N. Wiesel, along with Roger W. Sperry, shared the Nobel Prize for Physiology or Medicine in 1981.



A handwritten signature of David Hunter Hubel in black ink, written in a cursive style.

By Robert H. Wurtz

Early life: growing up in Canada

David Hubel was born on February 27 1926 in Windsor Ontario. Both of his parents were American citizens, born and raised in Detroit, but because he was born in Canada, he also held Canadian citizenship. His father was a chemical engineer, and his parents moved to Windsor because his father had a job with the Windsor Salt company. His mother, Elsie Hubel, was independent minded, with an interest in electricity and a regret that she had not attended college to study it. His paternal grandfather had emigrated from Germany to Detroit, where he had invented the first process for the mass production of gelatin pill capsules.

When David was three, his family moved to Montreal. David was fascinated by science very early, with chemistry being a central interest. That interest was probably inspired by his father's work and was further stimulated by the gift of a chemistry set that developed into a small basement laboratory. In his experiments he "perfected" an explosive mixture of potassium chlorate, sugar, and potassium ferricyanide. One test produced an explosion that rocked the neighboring houses, was heard over the Montreal suburb of Outremont, and elicited a visit from the police. A second, less explosive interest was electronics, which

When he decided to go to medical school his future physics advisor opined, “Well, I admire your courage. I wish I could say the same for your judgment!”

led to the successful construction of a one-tube radio and a life-long interest in amateur radio. Another enduring interest in his life was the piano; David started taking lessons before he could read and continued into college.

David went to an English speaking school in Montreal. Learning French was required in schools in the bilingual province of Quebec, but teaching

was mainly for written rather than spoken French. As a result he could not speak French as readily as he could read it. In high school ten subjects were compulsory but one additional could be selected, and he chose Latin. As he recalled, “Mathematics was considered appropriate for future engineers, Latin for future doctors, and biology for dumb students.”

He had an influential teacher who required an essay every week based on ideas, not just facts, which perhaps contributed to the clarity of his writing, a skill for which he was well known later in life. After high school graduation David planned to go to college in the United States and had interviews at MIT, but the onset of World War II disrupted that plan. He stayed in Montreal and went to McGill University. He did honors in math and physics “because these subjects fascinated me and there was almost nothing to memorize.” He graduated in 1947.

Accepted for graduate work in physics at McGill, on a whim he also applied to medical school, though he had never taken a biology course. When he decided to go to medical school his future physics advisor opined, “Well, I admire your courage. I wish I could say the same for your judgment!”

David found medical school to be hard work, and the only course he enjoyed was biochemistry. By the second year he developed a strong interest in the brain. This was a fortunate interest, because the Montreal Neurological Institute, part of McGill, was world famous for its work on epilepsy by the neurosurgeon Wilder Penfield and the neurologist Herbert Jasper. David screwed up his courage and arranged to meet the famous Dr. Penfield. It must have been a successful meeting because Penfield promptly arranged a meeting with Dr. Jasper, who in turn offered David a summer job doing electronics in his physiology laboratory. This critical afternoon was stressful for David. When he got back to his car he found it running, with the keys locked inside. He had to take the streetcar home to get a spare key.

By the time David received his MD degree in 1951, he found that he enjoyed clinical medicine. He continued his training at McGill, doing an internship, a year of neurology residency, and a fellowship year in clinical electroencephalography (EEG) with Jasper. He had worked two summers in Dr. Jasper's laboratory, and during his year-long stay he had become Jasper's assistant for interpreting EEG records. He came to regard Jasper as a major mentor.

David finally had the opportunity to move to the United States to do a second year of neurology residency at Johns Hopkins beginning in 1954. The move also subjected him to the doctor's draft in the United States because of his citizenship. He volunteered for the Army, and successfully sought to be assigned to a laboratory, the Walter Reed Army Institute of Research in Washington, DC. In 1955, close to age 30, David had his first opportunity to do research on his own.

Walter Reed: foray into research

David's mentor at Walter Reed was Michelangelo "Mike" Fuortes, a spinal cord neurophysiologist who collaborated with Karl Frank at the National Institutes of Health (NIH) in Bethesda. David had no experience in animal research or in electrophysiology, and he regarded himself as fortunate to have a mentor as supportive as Mike. David did an initial experiment with Mike that compared the flexor and extensor reflexes in decerebrate cats, which gave him a thorough grounding in electrophysiology. David was then casting about for his own research project when Mike suggested placing wires in the cortex of cats and recording from them while they were awake. The attempt was a failure, but the idea captured David's imagination.

He began developing techniques for recording from animals while awake. He first developed a tough tungsten microelectrode, and then developed an electrode advancer that moved the electrode to record from isolated neurons. Both inventions required multiple versions. The advancer required so many versions that he decided to make new ones himself, so he learned to operate a lathe. David recorded from freely moving cats during sleep and wakefulness and noted that neuronal activity was strongly affected by the level of arousal. He also recorded from primary visual cortex, and was able to confirm the main results that Richard Jung's laboratory in Germany had obtained using full field visual stimulation in anesthetized cats. Many neurons were not activated by full field stimulation (as reported by Jung's group) or by David's flashlight. Some of these unresponsive neurons, however, did respond when he moved his hand in front of the

cat. Some responded to hand movement in one direction but not the other, a preview of what was to be seen later in the analysis of the visual activity of the anesthetized cat.

David was not quite the first person to record from awake, behaving animals. His mentor Herbert Jasper had visited David's laboratory to learn how to make tungsten electrodes. Jasper used them in experiments on classical conditioning in monkeys, which he published in 1958, a year before David published his findings from cats during wakefulness and sleep in 1959. After David joined in collaboration with Torsten Wiesel he was fully occupied with anesthetized animals with eyes paralyzed, permitting the precise mapping of receptive fields. Ed Evarts at the NIH perfected a complete system for use in awake monkeys that became the standard in the field.

David never lost interest in this early work; his visits to Ed's NIH laboratory years later quickly moved to animated comparison of recording devices between the fathers of the field. David had successfully demonstrated restrictive receptive fields in the lateral geniculate nucleus, which he said he found difficult to study "since a waking cat seldom kept its eyes fixed for more than a few minutes." Because a monkey moves its eyes several times per second, before the visual system could be studied in awake monkeys, the awake monkey had to hold its eyes steady long enough to map receptive fields. This problem was solved by developing a behavioral procedure that rewarded the monkey for not moving its eyes. These techniques of restraining the monkeys, recording single neurons and requiring the monkeys to maintain visual fixation have become standards in the field of vision research. While David left awake animal recording in 1959, he left a legacy of innovations that are incorporated into methods that are taken for granted today.

Landmark studies of the visual cortex

While the insights into the nervous system that the collaboration between David Hubel and Torsten Wiesel produced are landmarks in the evolution of neuroscience, the collaboration itself was fortuitous. David and Torsten first met when Torsten visited Walter Reed to learn how to make David's tungsten electrodes. At the time Torsten was in Stephen Kuffler's laboratory in the Wilmer Institute at Johns Hopkins. Kuffler had made major discoveries about the retinas of cats, but had not himself worked on vision for several years. David was planning to join the physiology department at Johns Hopkins at the invitation of Vernon Mountcastle. The snag was that the physiology laboratories at Hopkins were being renovated and would not be available for a year.



Figure 1. David Hubel and Steve Kuffler in the Neurobiology Department Library. (Courtesy of Edward Kravitz and the Photo Archive of the Department of Neurobiology, Harvard Medical School.)

In light of this delay, Kuffler suggested that David spend time in his laboratory collaborating with Torsten, an ingenious solution to the space problem. In 1958 David moved to the Wilmer Institute. After discussions between Kuffler, Torsten and David, they agreed that the best research direction would be to extend the investigations that Kuffler had done on the cat retina to the visual cortex.

It was a particularly farsighted decision and the start of a collaboration that lasted twenty five

years. Throughout the long series of experiments that followed, Kuffler was their major mentor, tough critic, and lifelong friend. When Kuffler moved from the Wilmer Institute at Johns Hopkins to Harvard Medical School in 1959, David and Torsten moved with him and were among the inaugural members of what eventually became the Department of Neurobiology at Harvard. They were thus not only at the forefront of studying the visual system, but did so in one of first departments devoted to studying the nervous system in the emerging field of neuroscience.

When they began their experiments at Johns Hopkins, David and Torsten set up in the laboratory that Kuffler had used to study the cat's retina. They incorporated instruments that were classics as well as ones that were newly developed. They initially used the projection ophthalmoscope that Kuffler had used to stimulate the retina, and for holding the anesthetized cat's head steady, they used the same stereotaxic frame used nearly 20 years earlier by Samuel Talbot and Wade Marshall to map the topography of the cat's primary visual cortex. The tungsten electrode and the electrode advancer that David had developed at Walter Reed were new additions.

The goal of David and Torsten's experiments was to see what changes occurred in visual processing beyond the retina. Individual retinal receptors break the image falling on the retina into hundreds of thousands of individual messages. Each message conveys infor-

mation about one tiny part of the visual field, the visual receptive field of the individual neuron. These messages are transmitted by the optic nerve to a nucleus of the thalamus, the lateral geniculate nucleus, and from there to the primary visual area of the cerebral cortex. The task of the cerebral cortex is to reconstruct these messages so that the brain can “see” the image. At the time of their experiments, there was little idea, much less experimental evidence, about how this reconstruction came about.

What was known about the neuronal mechanisms of the cat retina was largely based on the investigations of Steve Kuffler on the output neurons of the retina, the ganglion cells. Kuffler had shown that these retinal neurons primarily responded not to full field illumination but to light or dark spots in the receptive field of the retinal neuron. At the start of David and Torsten’s experiments, the issue was whether there would be a change in what stimuli neurons at higher levels of the visual pathway required. The answer to that was relatively quick; they had great difficulty activating cortical visual neurons with spots of light.

But persistence enabled a serendipitous finding that changed the course of their experiments. For one neuron, they were able to find only faint responses to spots of light in one part of the visual field, but when they changed the slide in the ophthalmoscope they produced a burst of activity. It was the line produced by the edge of the slide that excited the neuron, as they subsequently verified by using lines instead of spots. This preference for oriented line stimuli revealed a major feature of primary visual cortex: neurons responded to oriented lines better than to the spots of light that were effective in the retina. Subsequent experiments showed that different neurons preferred different orientations, and across a sample of neurons all orientations were represented.

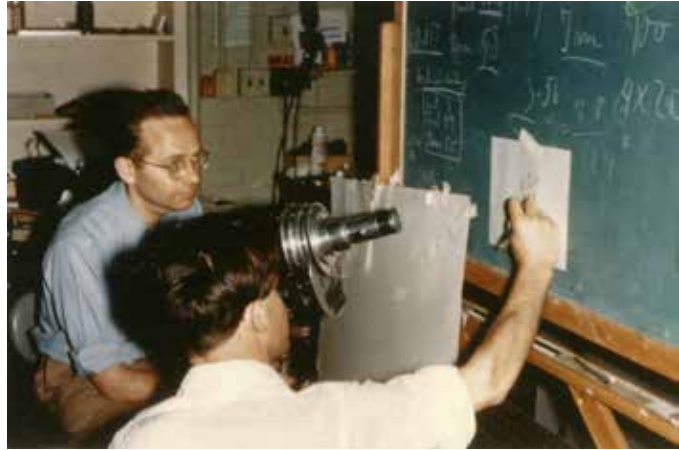


Figure 2. Hubel and Wiesel mapping a receptive field in cat visual cortex using a “crude projector and screen.” (Photo source: Harvard Medical Library in the Francis A. Countway Library of Medicine.)

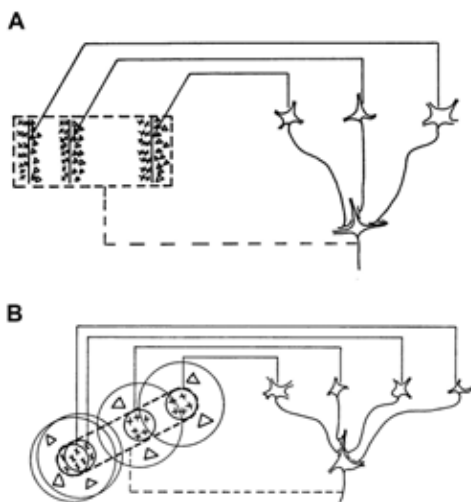


Figure 3. Drawings of the sequence of visual processing in striate cortex proposed by Hubel and Wiesel in 1962. A. The transformation from circular receptive fields of the retina to the elongated fields of a simple cell in primary visual cortex. B. Construction of complex cell receptive fields from inputs from simple cells. (From Hubel and Wiesel, 1962.)

sequential organization of the cells. Cortical simple cells responded to line stimuli as a result of the alignment of the circular receptive fields of their input neurons (Figure 3A). Complex cells that required less precise localization of a line stimulus were driven by inputs from multiple simple cells (Figure 3B). This was a major step: they suggested how activity in one neuron class might result from the input of a previous neuron class in the sequence. This of course raised the possibility that, if the sequence were followed high enough in the visual system, the neuronal activity underlying visual perception might be understood.

Subsequent work in the cat showed a continued modification of receptive field organization in the visual areas just beyond the primary visual cortex, and in at least one visual area beyond those. They then largely switched to studying the monkey, first going

David and Torsten's first publication was in 1959 and reported the orientation selectivity of primary visual cortex. In 1962 they published their first magnum opus in which they differentiated between classes of visual neurons, described the columnar organization of these neurons (an organization previously found by Vernon Mountcastle in the somatosensory cortex), and showed that neurons within a column preferred similar orientations. They also showed that cortical neurons had ocular dominance; they received input from each eye but most had a greater response from one eye than the other.

One of the salient points of the 1962 paper was not the results but the interpretations. David and Torsten suggested that neurons in visual cortex could be categorized by the stimuli that optimally activated them. The first two classes were termed "simple" and "complex" cells.

They went on to suggest there was a

back to the lateral geniculate nucleus and showing that the receptive field center and surrounds had a color opponent organization (stimuli in the center responded best to one color; stimuli in the surround responded to a different color). This was followed by a series of investigations on the monkey visual cortex including the organization of ocular dominance columns and orientation columns and their changes across the topographic map in primary visual cortex. A hypothesis that arose from these observations was the ice cube model of cortical modules in which the ocular dominance and orientation columns ran in orthogonal directions. The series of experiments opened entirely new directions of research on visual mechanisms in the brain that are still being pursued by laboratories throughout the world.

Within three years after beginning the study of the visual cortex in adult cats, David and Torsten also began studying its development. They knew that children with congenital cataracts had substantial visual deficits even when those cataracts were removed. It seemed possible that from their new understanding of the visual processing in cerebral cortex, the nature of the deficit, its location in the visual pathway, and the extent of plasticity in the developing visual system might be determined. This turned out to be the second major direction in their research collaboration.

They first recorded from kittens at successive ages during development. They found that shortly after the kitten's eyes opened many neurons in the primary visual cortex showed orientation selectivity similar to that in adults. They concluded that at least some neurons must have made the proper connections before the eye opened. They then tested to see if the visual responses changed when the kitten was deprived of vision as would be the case with a child with cataracts. In the laboratory they produced this deprivation by sewing the lids of one eye closed in newborn kittens under anesthesia in order to produce monocular deprivation. When they looked after a few months of closure in the lateral geniculate nucleus and primary visual cortex, they found reduced responses and anatomical changes in neurons receiving input from the deprived eye while the neurons receiving input from the open eye appeared normal. Cortical neurons that usually received input from both eyes now usually responded only to input from the normal eye. The monocular deprivation was most severe when started before eye opening, less severe if the eyes were open for a few months and then sutured closed, and normal if the suturing was done in the adult cat.

These experiments established two fundamental points about visual development: the neuronal connections are probably largely present before the eyes open and the visual

system is used, and the organization of these connections deteriorates if deprived of visual input during a critical period after birth. Subsequent experiments established that the critical period was between four and six to eight weeks after eye opening. For treatment of humans with cataracts or disorders of the alignment of the two eyes it is essential to make the corrections before the end of a comparable human critical period. The findings had provided support for both sides of the old controversy between nature and nurture: there were neuronal connections at birth which supported the nature view, but the continued use of the system was required to maintain its function, the nurture point of view.



Figure 4. Torsten Wiesel, Roger Sperry, and David Hubel in Stockholm, 1981. (Photo source: Harvard Medical Library in the Francis A. Countway Library of Medicine.)

A series of experiments followed that explored the effects of deprivation in baby monkeys, a better animal model of human visual function. Here they found that the critical period starts at birth with high sensitivity to lid closure during the first 4- 6 weeks, lower sensitivity for another few months, and no effect after a year. The greater precision in the organization of the monkey cortex and the use of more advanced anatomical techniques produced clear visual evidence for ocular dominance columns and their change with monocular deprivation. These experiments on the plasticity within the visual system also spawned a new field of research, including a search for the synaptic and molecular mechanisms of that plasticity.

The work on the functional structure of the visual system and its developmental plasticity were both cited by the Nobel committee when it awarded David and Torsten the Nobel Prize for Physiology or Medicine in 1981 that they shared with Roger Sperry.

Summing up the collaboration

The collaboration between David Hubel and Torsten Wiesel flourished for 25 years, and is summarized in their 2005 book, *Brain and Visual Perception*. The collaboration is certainly one of the most successful in biological science and one of the longest. The two shared common views about how to go about doing science, what was important and what was not. They asked the right question: how did the system work? Their respect for each other was immense as was their realization that they each brought special abilities to the collaboration, different but complementary.

Over the years of long shared hours Torsten remarked that there was also a bonding between them, and a familiarity with each other's attitudes and habits. David recalled that when an experiment extended late into the night "I knew we should quit when Torsten began to talk in Swedish."

At the memorial service for David, Torsten described the collaboration as the best years of his life. David, during his lifetime, also referred to his time at Harvard collaborating with Torsten as an idyllic period. The collaboration strengthened as their discoveries multiplied; they realized that they had arrived at the visual cortex at just the right time with the right techniques, and been given a golden opportunity. Their success was due to their own insight and diligence, to luck, and to the initial research direction that was the gift of Steve Kuffler. The two repeatedly and gratefully acknowledged the critical advice and guidance provided by Kuffler. They would have been pleased to share the Nobel Prize with Steve, but he died in 1980, the year before they were awarded the prize.

Within a few years of their initial publications, their results attracted widespread attention. Within ten years of the initial publications, they were so well known that they were referred to universally as H & W as if they had become a name brand, which they had.

With the perspective of a half century after the initial reports, it is interesting to review why their research was so riveting. First, they recorded single neurons from among the millions in the visual cortex, in contrast to the EEG, and evoked potential methods that averaged across pools of possibly unrelated neurons. Second, single neuron recording allowed them to compare the change in neuronal response to changes in the visual stimulus, a comparison that many doubted would be useful in a brain with billions of neurons. Third, they proposed a specific sequential organization of individual neurons that over a series of steps offered a mechanistic explanation of why different neurons responded best to different stimuli.

Finally, the proposed transformations across a series of neurons offered the first glimpse of how the sequential connection between neurons might transform the signals responding to spots in the retina into the oriented lines in cortex. This in turn raised the possibility that understanding such a progression might lead to insights into the brain mechanisms underlying visual perception.

In addition, their later experiments on monkeys contributed to shifting the field of visual research to the primate brain. The addition of behavioral techniques to control fixation of the eyes, momentarily stabilizing the visual fields, to David's microelectrodes and advancer, made higher levels of the visual system the prime target for investigating higher brain functions. Thus a substantial fraction of what we know about the cerebral cortex, particularly higher behavioral functions, results from the exploration of the visual system, and the genesis of that work is the observations of Hubel and Wiesel.

David remained at Harvard for the rest of his life as the John Franklin Enders University Professor of Neurobiology. He continued to work on the visual system with a number of collaborators and students, including a ten-year collaboration with Marge Livingston that included identifying the functional correlates of the sub-modalities of vision (such as form, contrast, and color). Torsten moved to Rockefeller University, where he concentrated on the connections within striate cortex with Charles Gilbert.

Beyond the laboratory

In addition to winning the Nobel Prize in 1981, David's contributions were recognized by election to the leading learned societies of the world, including the National Academy of Sciences in 1971, the American Academy of Arts and Sciences in 1965, the American Philosophical Society in 1982, and the Royal Society, as a Foreign Member, in 1982. He was honored by multiple honorary lectures and awards, and received thirteen honorary degrees.

In 1954, David married Ruth Izzard shortly after she graduated from the Department of Psychology at McGill. She went to work as a laboratory technician to supplement David's minimal stipend. Ruth was warm and friendly to anyone who encountered her, and she gave David over their nearly 60-year marriage the support he needed for his life's work.

Ruth and David had three sons, Carl, Eric, and Paul, born in Washington, DC, Baltimore, and Boston respectively. Their sons speak with fond memories of David and their home life growing up. They comment on his devotion to Ruth, and the happy

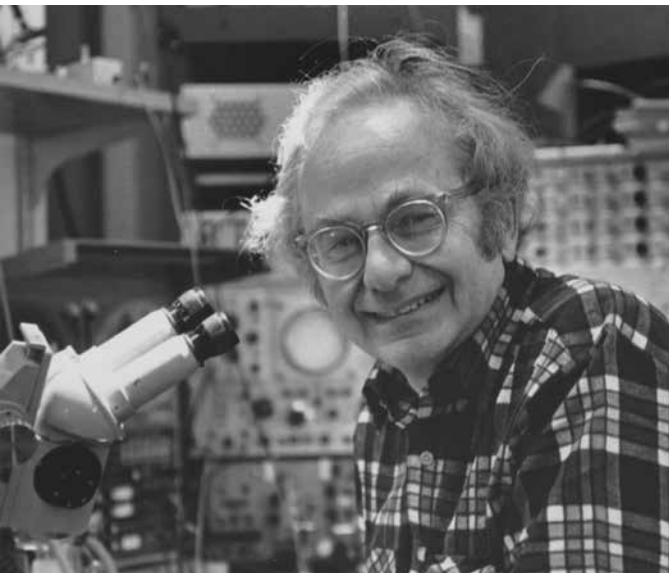


Figure 5. David Hubel at the microscope.

his son Carl, David's interests outside of the lab included piano, flute, and recorder; woodworking and metalsmithing (he made most of the household furniture, lamps, and picture frames); rug and scarf weaving; ham radio and Morse code; languages (French, German, Japanese); astronomy and photography (he had a darkroom in the basement); bicycling, sailing, skiing, and tennis.

During the years when he was engaged in experiments, David did little teaching, but on becoming emeritus he began teaching Harvard freshmen, which both teacher and students enjoyed. Though David and Torsten concentrated on their collaboration and had few students in the lab for many years, David was passionate about engaging students. I directly experienced his enthusiasm after hearing his talk at Woods Hole in 1961 when I was a graduate student. Detecting my more than casual interest, he invited me to visit their laboratory, put me up overnight, and let me watch the day's experiments (long microelectrode penetrations through a cortex). It changed my life, as interactions with David changed the lives of so many others. The case was similar for many of the

dinners of the family on the nights David was home (he and Torsten worked late into night a couple of times per week). They comment on his endless curiosity that stimulated their own curiosity. The challenge in science is always the competing demands between life in the laboratory and life at home. Judging from the comments of his sons, David seems to have achieved an enviable balance.

David had many interests out of the laboratory, and shared a number of them with his sons. Already noted was skill with a lathe that he referred to as "occupational therapy." According

medical and graduate students who were fortunate enough to spend time in Hubel and Wiesel's laboratory.

David had strong opinions on many subjects, which he expressed with conviction. His opposition to animal rights activists became particularly evident when, as President of the Society for Neuroscience, he used his position and prestige to point out the tremendous benefits of animal based research to understanding and treating human diseases. As a Nobel Laureate his views were exceptionally influential.

Perhaps David expressed his strongest views on what he regarded as the best way to do science. He extolled the virtues of small groups of hands-on scientists, and the benefits that come from principal investigators spending time at the bench. He cited his time at Harvard, and particularly his collaboration with Torsten, as a period when their time was largely spent doing their own research that was designed to test their own ideas. Graduate students and postdoctoral fellows in their laboratory had similar liberty. They were part of a Neurobiology Department organized by Steve Kuffler whose style was a model for the ideal laboratory that David envisioned. It was an era of what we might call “mom and pop science,” not a pejorative description but one of nostalgia and envy. It was a different era, in which David and others like him flourished. In David's view, why would we want to stray from such a successful system?

ACKNOWLEDGEMENTS

I am indebted to Torsten Wiesel for reading a draft of this biography. I appreciate the help provided me by Carl Hubel, and I have also incorporated some comments made by Carl, Eric and Paul, particularly those made at the memorial service for David at Harvard on November 16, 2013. Recollections from David's early life are adapted from his 1996 autobiographical chapter published in the collection *The History of Neuroscience in Autobiography*.

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