

SEYMOUR BENZER
1921 – 2007


Seymour Benzer, the Boswell Professor of Neuroscience, Emeritus, a founder of modern genetics, and one of the giants of 20th-century science, died from a stroke on November 30, 2007, in Pasadena. He was 86.

In a series of elegant experiments, Benzer made groundbreaking discoveries about the structure of genes, finding that they were not indivisible units of inheritance, as many scientists had believed. He also pioneered the field of behavioral genetics, in which he probed the connection between genes and behavior.

Benzer was born to Polish immigrants in New York City, growing up on a street nestled between Jewish and Italian neighborhoods in Brooklyn. During the Depression, his parents, who worked in the garment district, managed to shield him and his three sisters from most of the era's hardships. To make ends meet, Benzer's parents brought clothes home to work on late into the night.

Benzer had an interest in

science from an early age. During summer trips to the Catskill Mountains in upstate New York, he caught and dissected frogs. A whole new world opened up when his brother-in-law bought him a microscope for his 13th birthday, he said in his oral history. He looked at everything he could find, and did experiments in his basement laboratory—such as making frog legs twitch with electric wires. Although never a religious person, Benzer said he respected his parents' faith, and followed his father to synagogue on holy days. There, he would slip a physics book on top of the Torah; his father looked the other way while he read.

Benzer was the first in his family to go to college, enrolling in Brooklyn College in 1938. Although he was interested in biology, he eschewed the introductory classes and instead graduated with a physics degree in 1942. He went on to earn his PhD at Purdue University, developing a special type of germanium

crystal for a secret military project. His work led to the first transistor and a Nobel Prize for William Shockley (BS '32), John Bardeen, and Walter Brattain in 1956. The researchers who developed the transistor came to him and told him, "You should have done this," he recalled. He said, "It escaped me, and it was under my nose."

By then, however, he was an assistant professor in physics at Purdue with a renewed interest in biology. Inspired by Erwin Schrödinger's book *What is Life?*, Benzer attended a summer course in 1948 on bacteriophages, viruses that attack bacteria, at Cold Spring Harbor—organized by Caltech biology professor Max Delbrück. "Three weeks of that, and I was converted," Benzer said. He continued studying bacteriophages during a year at Oak Ridge National Laboratory in Tennessee before joining Delbrück's lab at Caltech for two years as a postdoc. He then went to the Pasteur Institute in Paris for a year, before returning to Purdue. Back in Indiana, he started what would become some of his most well-known work on the structure of the gene.

At the time, molecular biology was in its embryonic stage. James Watson and Francis Crick had just discovered the double-helix structure of DNA in 1953. But until Benzer's experiments, the physical nature of the gene was a mystery.

He worked with mutant strains of a bacteriophage that infected *Escherichia coli*. When two strains of the virus

infected *E. coli*, their offspring contained new genes that combined elements of the same gene from both progenitors. Benzer analyzed tens of thousands of these so-called recombination events, in which portions of the gene called *rII* swapped places. By comparing the length of these portions, he mapped *rII*'s fine structure, showing that it was not an indivisible unit of heredity, but many smaller units strung together. His map was on a scale large enough, in fact, to see changes the size of a single nucleotide—the letters that make up the DNA code and formed the double helix. This work bridged the gap between classical genetics and molecular biology.

As molecular biology exploded in popularity, Benzer went in a different direction. In the 1960s, partly inspired by the divergent personalities of his daughters, he became interested in behavior and the "nature-versus-nurture" debate. He began experiments with the fruit fly *Drosophila melanogaster* while on sabbatical from 1965 to 1966 in the lab of Roger Sperry, Caltech's Hixon Professor of Psychobiology, and stayed on to become a professor of biology in 1967. At Caltech, Benzer developed a novel device that allowed him to separate flies according to behavior and isolate mutant strains. Benzer treated the flies as if they were particles, bits of statistical data from hundreds of individuals that he could collect in minutes, rather than taking weeks to prepare a handful of rats.

His lab first studied the flies' response to light, creating strains that failed to go toward a light, as normal flies do. Benzer, his students, and his postdocs also developed strains that slept and woke at random intervals, flies that died early, and mutant females that brushed away males. By finding these kinds of mutants, they identified the genes responsible for the flies' circadian rhythms—the natural biological clocks of organisms—and other genes responsible for courtship, memory, and learning.

His research was controversial at the time, as many scientists were skeptical as to whether the small and simple fruit fly could be used to dissect the complexities of behavior. His first seminar in Sperry's lab outlining some of his initial fly research was met with a divided reaction. "They were pretty much split down the middle between those who thought that this was great stuff and others who thought this was pure crap," he recalled. "They were really screaming at each other."

Nevertheless, Benzer was highly respected, and he pursued his interests with freedom. His work with fruit flies grew into the new field of neurogenetics, showing that much of behavior is hardwired and not the result of one's environment.

He became Caltech's Boswell Professor in 1975 and officially retired in 1992, although he remained an active researcher afterward. In the late 1990s, Benzer and colleagues identified the

famous "Methuselah" gene in fruit flies. Named after the Biblical character who supposedly lived 969 years, the gene is key to longevity. The mutants lived 35 percent longer, tolerated higher temperatures, survived longer without food, and were more resistant to poison than normal flies.

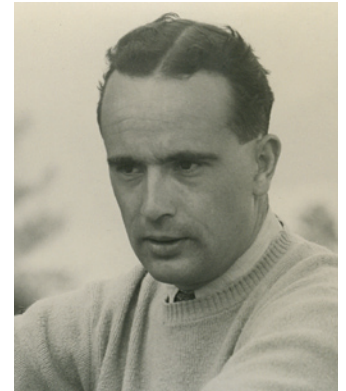
Over his career, Benzer accumulated more than 40 honors, including membership in the National Academy of Sciences, the Royal Society, and the American Academy of Arts and Sciences. He won the National Medal of Science, the Wolf Prize in Medicine from Israel, the Crafoord Prize of the Royal Swedish Academy of Sciences, the International Prize for Biology from Japan, the Albert Lasker Award for Basic Medical Research, and the Albany Medical Center Prize. He also won the Gairdner International Award twice. In 2000 he became the subject of the book *Time, Love, Memory: A Great Biologist and His Quest for the Origins of Behavior*, by Jonathan Weiner. Although many colleagues said his work deserved a Nobel Prize, the award eluded him. "My mother always regarded me as a failure because I didn't get the Nobel Prize," he remarked.

Benzer savored gastronomic experiences, whether it was discovering sushi in Japan or, upon encountering a dearth of good restaurants in Cambridge, England, forming a gourmet club with friends to prepare their own meals. Colleagues in his lab recalled him offering them bizarre food

such as rotten fish or chocolate-coated grubs.

His enthusiasm for trying diverse cuisine paralleled his passion for reaching across scientific disciplines, having gone from physics to molecular biology to neurogenetics. Colleagues remembered him as a visionary and scientific maverick, following wherever his curiosity took him. But his science was more than mere interest—it was an extension of who he was. Often waking up just before noon, he would work deep into the early morning hours, prompting colleagues to wonder if his own biological clock was the inspiration behind his research on circadian rhythms. He relished starting afresh in a new field in which he was ignorant and could ask basic questions. "Ask stupid questions," he said, "and you often get amazing answers."

Benzer is survived by his wife, Carol Miller; two daughters, Barbara Freidin and Martha Goldberg; a son, Alexander Benzer; two stepsons, Renny and Douglas Feldman; and four grandchildren. His first wife, Dorothy Vlosky, died in 1978. □—MW



David C. Elliot, professor of history, emeritus, died on November 21. He was 90.

Born in Larkhall, Scotland, Elliot was the son of a minister. He attended the University of St. Andrews, where in 1938 he met Nancy Haskins, an exchange student from Chattanooga, Tennessee. The next year, they decided to get married.

India was then under British colonial rule. Elliot joined the Indian Civil Service, of which only about 1,000 members governed the country at a given time. In 1940, he was sent to the Punjab region at what today is the northern border of India and Pakistan. At 23, he governed an area larger than Scotland, and he spent much of his time traveling the countryside on horseback. He would return to India in 1997 for the 50th anniversary of the nation's independence.

In order for Haskins to join Elliot in India, she had to be a British citizen—or at least married to one. She went to South Carolina, which recognized common law marriage, and married Elliot by proxy.

She spent the next six years trying to join him in India, finally succeeding in 1945. They had a second wedding in Lahore.

The couple left India in 1947 and went to the United States, where Elliot studied history at Harvard. He earned a master's degree in 1948 and his PhD in 1951. He later earned a second master's from Oxford in 1956. Immediately after Harvard, he ventured out west to Caltech, became an assistant professor, and was appointed a full professor in 1960. He served as secretary of the faculty from 1973 to 1985, before retiring in 1986.

Elliot's research interests included the Liberal Party in Scotland, the English Restoration, arms control, and national defense. A consultant for RAND, NASA, and the Ford Foundation, he served as a trustee and honorary trustee of the Institute of Current World Affairs, and he spent 30 years on the board of trustees of Westridge School in Pasadena. He was chairman of Caltech's 75th anniversary celebration and, in 1977, Caltech students voted him the most popular professor. On his own time, Elliot was an avid golfer and bridge player.

Predeceased by his son, John, in 1991 and his wife in 1994, he is survived by his daughters, Nan Elliot Hale and Enid Elliot, a son-in-law, Richard Kool; and four grandchildren and two great-grandchildren. □—MW

HERBERT B. KELLER 1925 – 2008



Herbert B. Keller, professor of applied mathematics, emeritus, and a leader in numerical analysis and scientific computing, died in his Pasadena home on January 26, after his routine morning bicycle ride. He was 82.

The son of a bartender who loved numbers and puzzles, Keller was born in Paterson, New Jersey. He studied electronics at Georgia Tech and joined the Naval Reserve Officers Training Corps. During World War II, he became a fire-control officer in charge of the guns on the USS *Mississippi*, where he trained future president Jimmy Carter to be a gunnery officer.

Keller later went to New York University and received his PhD in mathematics in 1954. He eventually became a professor of applied mathematics at the Courant Institute of Mathematical Sciences at NYU. In 1965, he came to Caltech as a visiting professor and returned as a full professor two years later, joining the newly formed applied-mathematics group. He later became the executive officer for applied mathematics and director of Caltech's branch of the Center for Research on Parallel Computation.

Keller made significant contributions toward techniques for solving complex problems with a computer. He was known for developing methods to solve two-point boundary-value problems, which arise in many areas of physics and engineering, from fluid flow to stellar structure. He also made strides in bifurcation theory, which looks at how changes in parameter values influence a system. One simple example is the problem of how changing the number of fishing licenses given out each year affects fish population dynamics. He remained an active researcher even after his retirement in 2000.

Colleagues described him as a mathematician with chutzpah, unafraid to speak his mind and to go after whatever problem interested him—advice that he doled out through the years as an influential mentor to dozens of students and postdocs. His fearless approach to research mirrored his other passion in life: cycling.

His brother recalled a cycling trip they took in the south of France in 1948, when they inadvertently joined the Tour de France after riding through roads lined with cheering spectators. Keller rediscovered the sport in the early 1980s, and despite suffering countless accidents—many with serious injuries—never stopped riding. In one of his most oft-told stories, he said a collision he had with a pile of lumber in Germany fixed his nearsightedness. Typically biking 100 to 150 miles a week, Keller didn't allow age to slow him down—he finished a 1,250-mile European tour when he was 68. He completed several centuries

and double centuries, which are rides stretching 100 or 200 miles; he said he rode his last double century when he was 72.

In addition to serving on numerous committees and councils, he was a fellow of the American Academy of Arts and Sciences, the American Association for the Advancement of Science, and the Guggenheim Foundation. He was the president of the Society of Industrial and Applied Mathematics, and later won their von Kármán Prize. With Eugene Isaacson, he coauthored a textbook that became a classic in numerical analysis.

His brother, Joseph, a retired professor of mathematics and mechanical engineering at Stanford University; his son, Steve; his daughter, Debra; and four grandchildren survive him. □—MW