

IN MEMORIAM

George Oster

UC Berkeley

1940 – 2018

George Oster, professor of Cell and Developmental Biology at University of California, Berkeley, died on April 15th, 2018. His death is a true loss for the biophysics, mathematical biology, and applied mathematics communities. A pioneer of these fields, George fostered our understanding of biological molecules, cells, and tissues as mechanical machines.

After finishing high school on Long Island, NY in 1957, George attended the U.S. Merchant Marine Academy at Kings Point, NY and spent a year at sea. In 1961, he continued his studies at Columbia's graduate school and received a Ph.D. in nuclear engineering. At the end of his Ph.D., George realized that science attracted him more than engineering and pursued another degree in biophysics. Shortly after that, he met Aharon Katchalsky, a pioneering Israeli scientist, who saw George's talent and persuaded him to work together on the thermodynamics of biological networks. With Katchalsky, George did his postdoctoral work at Weizmann Institute in Israel and also at University of California, Berkeley. George fell in love with the vibrant political and scientific scene of the Berkeley campus in the late 1960s but also with the natural beauty of the Bay Area. He stayed at Berkeley as a faculty member for the rest of his life, changing departments as his insatiable curiosity drove him from one biological problem to another.

George was very fortunate to be a part of a great generation of scientists who had the audacity and freedom to move between disciplines. Early in his career, he worked on pathbreaking mathematical models of population dynamics and developed the first detailed theories of caste evolution among social insects (with Edward Wilson) and theories of bifurcations to a hierarchy of periodic oscillations and chaos in simple ecological models (with Robert May).

At some point in life, every great scientist discovers a unique point of view that reveals a hidden natural order that was previously unknown. George made his discovery in the late 1970s – early 1980s, when he realized that biological molecules, cells, and tissues can be seen as peculiar mechanochemical machines, in which mechanical forces, chemical reactions, and stochastic Brownian movements are intimately coupled. For the next 35 years of his remarkable career, George unraveled the laws of this mechanochemical coupling, which led to an understanding of the physics of the cell.

With Garrett Odell, James Murray, and others, George pioneered mechanical models of morphogenesis. These models revealed how forces and deformations of the cell cytoskeleton integrate with chemical and genetic signals to shape tissues in the development of organisms. With Alan Perelson, George proposed that the swelling of the cytoskeletal gel can drive protrusions at the cell front, laying the foundation for quantitative studies of cell motility. From populations, to tissues, to individual cells — George did not stop there. Next, he looked at molecular motors – peculiar and fundamentally important proteins moving on polar cytoskeletal fibers and exerting forces on a pico-Newton scale. George realized that these biological machines operate in a realm that is dominated by thermal fluctuations, and that nature found a way of turning thermal noise into a uni-directional, ratcheted Brownian motion through physical-

chemical reactions which generate forces and movements. This discovery led to a dramatic breakthrough in our understanding of how energy transduction occurs in all living organisms.

In the 1990s, George together with Charlie Peskin and his students, postdocs, and experimental collaborators, made another breakthrough: he discovered how to go from abstract ratchet models to mechanochemical models by using structural, biochemical, and genetic analyses of molecular motors. During this decade, George established an important shift from conceptual to detailed and predictive mathematical models of biological systems. This new way of modeling is best exemplified through two Nature papers about the reverse-engineering of ATP synthase. In this work, George, together with Hongyun Wang and Tim Elston, integrate mathematical models with biophysical data to account for minute details of the motor's behavior. Luckily, this theoretical work coincided with a revolution in the experimental field brought about by usage of optical traps — many of their theoretical predictions were tested and inspired new experiments. It would not be an exaggeration to say that George, more than any other physicist or mathematician, inspired our current knowledge of molecular motors.

George was one of the first biophysicists who 'married' experiments and theory by developing computational models of a bewildering variety of molecular machines – kinesin motor, flagellar rotary motor, RNA polymerase and protein translocation motors, 'one-shot' actin polymerization motor, and 'snot-gun' motor of bacterial gliding. He wrote influential papers on cell membrane mechanics, neural pattern formation, endocytosis, and actin-based protrusions, which have set the high standards of theoretical biology that we take for granted today. George taught us how to choose which biological systems are ripe for modeling. He also showed us how to pry open the secrets of molecular and cellular machines by combining experimental observations with physical intuition, engineering principles, and mathematical tools. He established the now common approach to solving biological puzzles through iterative cycles of modeling and experimentation and not by holding onto a model in the face of 'inconvenient' experimental data.

George received international recognition as one of the most profound and original scientific leaders. He was a Guggenheim and MacArthur Fellow; he was awarded Weldon Memorial Prize by Oxford University, Winfree Prize by the Society for Mathematical Biology and Sackler International Prize in Biophysics. He was elected to the National Academy of Sciences in 2004.

George often said that people are what is most important in science. He inspired so many with his brilliance, enthusiasm, and passion for science and life. Generations of students, friends, and colleagues will never forget the fountains of ideas gushing out of him in the Brewed Awakening café on Euclid Avenue at the edge of Berkeley campus, where George held informal group meetings almost every morning. I will never forget his quiet, intense, and artfully modulated voice when George, an incomparable storyteller, described his great idea of the day.

George was a warm man who radiated the joy of doing science. He was at the peak of his powers in research and teaching when Lewy-Body Parkinson's disease overcame him. It has been heart-breaking to see such a brilliant mind fade away. He will be sorely missed by the scientific community and by his many friends who have been lucky to bask in the light of George's mind.