Racker, Efraim (*b*. Neu Sandez, Poland, 28 June 1913; *d*. Ithaca, New York, 9 September 1991), e*nzymology; energy metabolism* [OR *bioenergetics*]*; biomembranes*.

Efraim Racker — 'Ef' to his friends and colleagues — contributed significantly to the study of enzymes and energy in the cell in the mid-twentieth century. He developed methods for reconstituting proteins in biological membranes, fundamental to studying their individual effects. Using these methods, he helped assemble artificial vessicles that demonstrated conclusively the chemiosmotic theory as proposed by Peter Mitchell (who subsequently earned a Nobel Prize for his ideas).

Racker also earns credit for many important particular discoveries: F_o, a major component of the enzyme that generates adenosine triphosphate (ATP), the basic molecule of energy in the cell; CF_1, the central component of ATPase in plant chloroplasts; the mechanism of energy transfer to ATP in glycolysis; the first energy-rich thioester; and transketolase and (in parallel with other labs) the pentose phosphate cycle. These reflect Racker's remarkable experimental skills in tinkering with and coaxing unfamiliar cellular enzyme systems into relief. Racker was equally important institutionally, mediating debate, writing advanced textbooks, promoting basic research and a strong work ethic, and buoying the high-stakes field of bioenergetics with good humor. He also became involved in two episodes of misconduct. One gained wide renown and eventually became a canonical case of fraud in science, although Racker's role is widely misreported. His legacy also includes a series of aphorisms that wittily express experimental know-how, such as "don't waste clean thinking on dirty enzymes."

Early Life: Pathway to Basic Research

Racker was born in a large town in southern Poland. In his infancy the family moved to Vienna, where they lived in a poor neighborhood and experienced the anti-semitism of the era. Young Efraim did not respond well to the formalisms of school. He enjoyed competitive sports and chess. He also liked to draw and paint. Inspired by the work of Viennese native Egon Scheile, and with the encouragement of painter and art educator Victor Löwenfeld, Efraim decided to pursue a career as a painter. At age eighteen he gained admission to the highly selective Vienna Academy of Art. Again, he became disillusioned with the formal training style, left, and enrolled at the University of Vienna School of Medicine. He passed Freud's home on his daily walk to school and, with his older brother Heinrich, shared a fascination with psychiatry and psychoanalysis. He graduated in 1838 when, as Racker described it, "a mass psychosis invaded Vienna." As Naziism advanced, he left via Denmark for England.

After reading a 1936 paper on "Biochemistry and Mental Disorder," Racker sought work with its author, J. Hirsh Quastel, in Cardiff, Wales. He studied the psychotic effects of amines on brain metabolism, yet began to realize that knowledge of normal metabolism was then too limited to understand the pathology. When Great Britain entered World War II, Racker became classified as an enemy alien. He emigrated to the United States in 1941, ultimately to the University of Minnesota. Capitalizing on funds available from the March of Dimes, Racker began research (for a salary of "12,000 dimes a year", he noted) on how the polio virus altered metabolism in the brain. Again, he faced problems due to lack of foundational knowledge about

glycolysis, the breakdown of sugar in cells. He later called it a turning point, which led him into basic research on carbohydrate and energy metabolism. Later in his career, in 1979, Racker defended the value of basic research in a book aimed at political critics and began by citing this experience.

Glycolysis

Following two years as a physician at Harlem Hospital, Racker joined the Microbiology Department at New York University Medical School, where he enjoyed support from Severo Ochoa and Colin MacLeod. Racker continued his research on viral inhibition of glycolysis, but soon found that his samples had been contaminated with iron. Undeterred, he traced how the iron inhibited the enzyme glyceraldehyde-3-phosphate (GAP) dehydrogenase, and then how glutathione reversed the effect. Glutathione was a known co-factor for another enzyme, glyoxalase, and Racker was led to interpret its role as an intermediate in energy transfer. Although glyoxalase itself was relatively obscure, Racker had identified for the first time how energy could be transferred biologically though an energy-rich thioester (sulfur-containing) bond. His 1951 discovery became an important precedent for interpreting this widely occurring energy-transfer mechanism. Racker would also later instruct his students that "Troubles Are Good for You", profiling how, as in this case, a skilled investigator can turn ostensively disastrous results to an advantage.

Continuing his work with his technician Isidore Krimsky, Racker returned to the glycolysis enzyme that helped break down and capture energy from GAP. There, he found, GAP reacted with an enzyme-bound sulfhydryl group. This, in turn, produced an energy-rich thioester bond (as in the case of glyoxalase), which was handed off, along with its energy, to phosphate. The energy-rich phosphate was transferred again to adenosine triphosphate, or ATP, the basic molecule of energy in the cell. Racker's findings upset the then widely accepted claims by renowned biochemist Otto Warburg. More importantly, however, Racker had documented the first mechanism for how ATP is generated in cells. This 1952 discovery also set an important precedent, but one that, ironically, helped misguide biochemists for the next two decades, as described below.

Pentose Phosphate Pathway

In 1952 Racker accepted a position at Yale University, where he shifted his metabolic investigations to a reaction pathway that branches off glycolysis: the hexomonophosphate shunt. Energy is derived from a six-carbon sugar, which is then broken down into a series of five-carbon sugars, or pentose phosphates. Some of these become important components in synthesizing other molecules, such as the units of DNA. Racker's lab discovered a new enzyme, transketolase, that breaks down the five-carbon sugars further (coincidentally, into GAP as a product). In 1954, Racker returned to New York City, now at the Public Health Research Institute. As he continued work, the successively recrystallized enzyme lost its specific activity. Racker traced the problem to the presence of a second enzyme, an epimerase, which had been extracted along with the first and partly accounted for the reactions they had been observing. Racker sorted out which enzyme reacted with which pentose, correcting what he and several labs had concluded earlier. Racker found a lasting lesson in his experience, which he later preached to his students: "Don't think, purify first." And: "Don't waste clean thinking on dirty enzymes."

In further work, Racker recognized a chemical analogy that prompted him to test

transketolase on another molecule in the pentose phosphate reaction pathway. It worked there, as well. The enzyme functioned twice. This helped Racker (aided by students Paul Srere, Hans Kornberg, Dan Couri and June Fessenden) to reconstruct the whole system. The "pathway" ultimately recreated the initial hexose: it was a cycle, a conclusion also reached in other labs, notably by Bernard Horecker at the National Institute of Health. Racker's transketolase experiment had further significance, as well. Melvin Calvin had been working to elucidate the steps of photosynthesis, whereby plants fix carbon dioxide from the air, then synthesize glucose. Many of the enzymes and intermediate compounds were shared with the pentose pathway. While having dinner with Calvin in New York in 1954, Racker mentioned his experiments revealing the second function of transketolase, which transformed a six-carbon molecule into a four-carbon molecule. "I see it all know," Calvin replied cryptically. He then explained to Racker that he had just provided him the clue for linking his own photosynthetic reactions into a cycle — an achievement that earned Calvin the 1961 Nobel Prize in Chemistry

ATPase

Racker's new institutional surroundings in New York proved exceptionally fruitful. Maynard Pullman arrived shortly after him and they decided to tackle another major metabolic system, oxidative phosphorylation, or ox phos. These reactions in the mitochondria use the oxygen we breathe to transform the energy from the citric acid cycle (breaking down the food we eat) to the energy-rich adenosine triphosphate, or ATP (by adding the final phosphate). Racker believed that to solve complex problems, such as psychoses of the mind or multienzyme systems of the cell, one needed to resolve them into their parts and reassemble them functionally. Racker apparently exhibited his strategy early in life: at age six he took apart a broken clock and tried (unsuccessfully) to fix it. They now applied this strategy to ox phos.

Racker noted later that reconstituting systems successfully required three things. First, one needed cheap labor. Pullman's skilled new student Harvey Penefsky provided that. Second, one needed large quantities of stable material. David Green had pioneered how to prepare mitochondria from beef heart. He invited the team to the University of Wisconsin where they learned his techniques. Finally, one needed "new ideas." Here, that meant a new machine for shaking the cells and proteins apart. Centrifugation then sedimented out "submitochondrial particles" and the team tested re-adding various soluble fractions to identify functional factors. The first, named F_1, was the main part of the enzyme, ATPase, where ATP was formed. Later, Yasuo Kagawa helped confirm that F_1 units could be seen in electron micrographs as small knobs on the inside of the mitochondrial membrane. Kagawa and Racker then isolated the segment of ATPase, embedded in the membrane, where F_1 attached. It was named F_o for re-establishing a known function: inhibition by oligomycin. Racker tried many other methods of destroying and separating the mitochondria, yielding an array of particle types. More supplemental factors emerged: two factors that held F_1 to F_o (F_6 and part of F_4, later renamed OSCP) and F_2 (also Factor B), all whose regulatory function was elucidated much later. (F_3, F_4, and F_5 were later reclassified or abandoned as contaminated extracts.)

As progress stalled, Racker looked for a more easily resolvable system, targeting the ATPase in photosynthesis. Using less foul-smelling spinach, he and Vida Vambutas isolated the chloroplast's analog to F_1: CF_1. Their work helped underscore the strong similarities between ox phos and photophosphorylation (how plants generate ATP from light). Racker summarized his work and the state of the field in an advanced textbook in 1965. The following year his

professional contributions were recognized by election to the National Academy of Science.

Reconstituting Membrane-Bound Enzymes

In the mid-1960s, research on ox phos became notoriously frustrating. The system was located in the mitohondrial membrane. Membranes are primarily lipids, chemically more like oil than water, and no one could extract membrane-bound proteins that still functioned. Peter Mitchell suggested a possible reason. He contended that energy did not flow through a succession of energy-rich bonds, as modeled in Racker's 1952 account of glycolysis. Mitchell proposed instead a "chemiosmotic" mechanism, whereby ox phos generated an electrochemical proton gradient across the membrane. Any system would thus require an intact closed vesicle. The membrane was itself viewed as a functional barrier. Racker met with Mitchell in New York City in 1965 and discussed his ideas, but he did not deem them supported by the available evidence.

Racker accepted an opportunity to lead a new department at Cornell University and moved to Ithaca, New York in 1966. His investigative focus also shifted. Whether influenced primarily by Mitchell or by experimental exigencies, he began examining the role of the membrane more fully. He showed first how proteins functioned differently on each side of the membrane, and then how they were positioned asymmetrically (or allotopically, as he called it). Eventually, the membrane became part of his reconstitution strategy. Racker's lab recombined the isolated proteins with lipids and a detergent, then gradually removed the excess by either dialysis or dilution. In 1971, with Peter Hinkle leading as a chemiosmotic advocate, they reconstituted cytochrome oxidase, the last component of the electron transport chain, in the first functional vesicle. The reaction rate was controlled by the concentration of protons and Racker, while observing the instrument readings in the lab, seemed to concede that Mitchell was correct, at least about the proton gradient. Successful reconstitution of a proton-pumping ATPase soon followed, guided by Yasuo Kagawa. These liposome vesicles lost function when the membranes "leaked," persuading Racker fully of the need for closed compartments and thereby completing his acceptance of chemiosmotic principles.

Adopting the new theoretical framework, Racker soon consolidated his lab's findings in a dramatic capstone experiment. In 1973, Dieter Oesterfelt and Walther Stoeckenius had isolated a new photosynthetic pigment, bacteriorhodopsin, from halobacteria and shown that it transported protons across the membrane when exposed to light, in accord with chemiosmotic mechanisms. In 1974 Racker collaborated with Stoeckenius to create a thoroughly unnatural vesicle. Introducing sonication as yet another method of reconstitution, they recombined membrane lipids from soybeans, bacteriorhodopson from halobacteria, and ATPase from beef mitochondria. Although mixing elements from cells from three kingdoms, the artificial vesicles produced ATP in light. That "unphysiological" chimera epitomized reconstitution for Racker: it integrated the separate parts *functionally*. The chimeric vesicles were also an important benchmark in demonstrating chemiosmotic mechanisms for ox phos and photophosphorylation to a wide community of biochemists. By 1975 all the components of ox phos had been isolated and analyzed separately. Racker again summarized the status in the field in a new advanced textbook in 1976. Racker shared the Warren Triennial Prize with Mitchell in 1974 and received the National Medal of Science in 1976.

Late Work

Racker's methods of lipsome reconstitution opened wide the investigation of membane-bound proteins. He helped train a whole new generation in membrane biology, including Günter Hauska, Peter Hinkle, Richard Huganir, Baruch Kanner, Ladislav Kovác, Richard McCarty, Chris Miller, Maurice Montal, Nathan Nelson, Michael Newman, Jan Rydstrøm, Dennis Stone, Bernie Trumpower and Charles Yoccum. Having demonstrated that protons were indeed transferred across membranes, Racker turned to study the mechanisms of transport. He considered many ion pumps for clues. In so doing, he reconstituted the first Ca^{2+}-ATPase pump from muscle cells and (with Richard Huganir) the acetylcholine receptor of nerve cells. He showed how the later functioned through conformational changes, opening a channel for the passage of ions which initiate the nerve impulse. In parallel work, however, he failed with the lactate transporter and with the Na^{+}-K^{+}-ATPase in tumor cells. Racker once called the erratic behavior of membrane proteins "molecular psychology". In 1985 Racker wrote one last text, detailing the strategies and methods of reconstitution.

During his career Racker's interest in pathological states never waned. Much of his late work, far less fruitful than his earlier achievements, was oriented to cancer. A series of minor contributions, tallied over several decades, was accompanied by many stymied efforts, ironically illustrating his own views about the primacy of basic research. Racker never considered his investigations complete. Even at age 73 he was retooling, learning the new techniques of recombinant DNA. He even modified his old adage about proteins, "Don't think, purify first," to "Don't think, don't purify: clone!".

Professional Leadership

Racker's stature derived in part from his professional leadership. He served on the editorial board of the *Journal of Membrane Biology* from its founding in 1969 until his death. Racker's posture towards resolving disagreement was especially significant, notably during the highly contentious debates over ox phos. For example, after a disagreement about sequence of elements in the electron transport chain with Britton Chance, Racker and his student went to his lab, where additional tests clarified the results. Racker expressed the "moral" for students:

> When you find something that disagrees with a paper or review, . . . get in touch with the person with whom you disagree. If the issue is indeed important to you, straighten it out by collaborative experiments rather than by polemics.

His early-life experience with politics in Europe seemed to shape his later actions. Racker tried to find the middle ground in theoretical debates on chemiosmotic ideas. He offered one conceptual hybrid, he admitted, as "a gentleman's political compromise. From my early childhood, I had wanted to live in a peaceful world. Although I have always enjoyed friendly controversy and arguments, I have been most uncomfortable during the bitter polemics in our field in the last decade". Racker endeavored to quell the ox phos tempest. In March 1974, he circulated a letter to ten leading biochemists, appealing for unity and proposing to publish a joint statement that, he hoped, would help stabilize the field and improve its negative image among other scientists and funding agencies. After two and a half years of correspondence, and of alliances severed and mended, and Racker personally coaxing Mitchell to rejoin the project on at least two occasions, six researchers published a multi-authored review which, while hardly free of residual conflicts, was nonetheless widely interpreted as resolving the decades-old controversy. The following year, Peter Mitchell received the Nobel Prize in Chemistry. Given

Racker's important work on reconstitution and the chimeric vessicles that helped secure the status for chemiosmotic theory, many colleagues were surprised that the honor did not include him also. His recognitions continued, however, with a Gairdner Award in 1980.

Episodes of Research Misconduct

Racker became involved in two episodes of scientific misconduct. In one case, he was leading critic; in the other, primary victim. The case in Racker's own lab gained wide notoreity and remains an oft-cited example of scientific fraud. However, both cases are needed to understand Racker's own conduct fully. They are striking complements, yet each illustrates Racker's professional leadership. His responses were considered exemplary by most colleagues.

The first episode occurred during the heyday of conventional chemical approaches to ox phos. George Webster, a graduate student working in David Green's lab, had published a series of papers (1962-1965) proposing a high-energy interemediate in the reaction series: Reduced Cytochrome *c* Coupling Factor, or RCCF. Racker tried to replicate the findings, hoping to resolve discrepancies with his own findings. At first, he noticed only errors in the methods for measuring ATP. Eventually, Racker went with two colleagues to Green's lab at the University of Wisconsin, where experiments again failed, using Webster's methods on samples they had prepared themselves. Racker asked to consult Webster's laboratory notebooks (which did not exist), and Webster acknowledged having fabricated his data. In this episode, Racker was credited for actively pursuing the false claims and for establishing definitive results with his strong experimental skills.

In the second episode, fraudulent data was fabricated in Racker's own lab. Initially, in 1980, Mark Spector was considered a brilliant Ph.D. student with exceptional technical aptitude and promise. At the time, Racker was shifting his research to cancer cells, as he returned to puzzles about rates of glycolysis that he had set aside for several decades. Spector was set the task of purifying the membrane-bound ATPase from tumor cells, where it exhibited reduced activity. Spector's quick success seemed to confirm the strong recommendations that had accompanied his graduate school application. His remarkable work seemed to continue as he reportedly isolated, in turn, a series of enzymes that sequentially triggered inefficient ATP-dependent membrane transport of sodium (leading further to excess glycolysis). Finally, he announced that the first component in the "kinase cascade" was similar to a protein produced by the Rous sarcoma virus. The events that led to viral cancer seemed solved! The model generated much excitement when first presented to the Tumor Virus Group in May, 1981. Racker and Spector published the scheme in *Science* on July 17. Just one week later, one of Spector's collaborators at Cornell, Volker Vogt, approached Racker. He and his student had earlier encountered problems generating Spector's results. Now he had discovered that Spector's electrophoretic gels, supposed to be labeled with radioactive phosphorus, instead contained radioactive iodine. The original gels were the primary clue to doctored results. The developed images (autoradiograms), used in data analysis, would have carried no trace of any manipulation. Racker and Vogt confronted Spector. Racker personally supervised the next set of experimental replications. Some of the original results seemed partly confirmed, others not. By September, Racker had dismissed Spector. The co-authors, led by Racker, retracted all the suspect papers. Racker even offered to resign from his various committees and editorial boards until the issue was fully resolved. At the first indication of fraud, Racker acted promptly and decisively. Consequences continued, however. Earlier that spring, U.S. Congressional hearings had stirred

up public concerns about scientific misconduct. In addition, the case served as grist for Nicholas Wade, a science journalist for *Nature*, who was actively reporting fraud. Exposure to the Spector episode was thus greatly amplified. Still, colleagues respected Racker for investigating and acknowledging the errors himself, thereby modeling how to manage such problems responsibly. The affair certainly did not discourage the American Society of Biological Chemistry from awarding Racker their prestigious Sober Memorial Lectureship the following year. Many years later, in 1989, Racker reflected on his experience, publishing his views on misconduct in science in *Nature*.

Personality in Professional Context

Racker exuded good humor and a dry wit, enriching even his scientific discourse. He made light of the many obstacles that faced chemists working on cell metabolism in the 1960s. For example, "'Nature may be difficult, but she is never malicious'" he quoted Einstein as saying. Einstein, he then commented, "obviously had never worked on oxidative phosphorylation". At a 1963 conference, Racker remarked slyly that "anyone who is not thoroughly confused just does not understand the situation." He reviewed the complex reactions, then concluded: "I shall not show you a scheme of the topography of the various factors in mitochondria because I promised to keep this presentation simple. But I carry a picture of it in my wallet, together with photos of my wife and daughter and I'll be glad to show all three of them to anyone who cares to see them." The comment, which appeared in the published paper, was not entirely gratuitous. It conveyed in a light-hearted way, the complexity that so deeply and repeatedly frustrated the "family" of biochemists working on the problem. Such comments helped counterbalance the prevailing mood of debate at the time, characterized by other researchers as "contentious and often rancorous", even "vitriolic".

In a similar spirit, Racker's issued his entering graduate students at Cornell University "Twelve Rules," styled tongue-in-cheek after the Biblical commandments. For example: "When thou usest isotopes, thou shalt remember that 'not everything that counteth counteth.'". Such pithy lessons also appeared in his advanced textbooks. For example: "A clean experiment is worth more than a few hundred dirty calculations." Or: "It doesn't matter if you fall down as long as you pick up something from the floor while you get up." Many such witticisms, typically encoding bits of professional wisdom, became stock sayings echoed throughout the field.

Racker was an avid artist. He began painting at age thirteen when he received a box of oil paints for his birthday. Later he likened reconstituting liposomes to drawing a portrait: each was a functional, but distorted representation. Colleagues recognized how Racker embodied a fruitful combination of creative thinking and rigorous experimental analysis. Racker's paintings included landscapes and seascapes, in an austere, semi-abstracted modern style and sombe hues. For one colleague, they reflected the darker, and also private, side of Racker's thoughts. He sold many paintings to support scholarships for students. Posthumous sale of others funded an annual lecture in his memory. Racker's artistic interests also extended to music. He played cello with "enthusiasm," although he was also apparently "incompetent".

Racker also modeled the spirit of investigation. "We need to know more," he once said, "about ion fluxes, neurotransmitters, mental diseases, love, hate, crime, and mass psychology. I believe they are all related". He enjoyed "the game of intellectual domination" as a tool to delve deeper into arguments. He was not afraid to be wrong, however, and extolled the virtues of learning from error. While sometimes "egocentric, insensitive, even overbearing", Racker was

also known to friends and colleagues for his warmth and openness. Racker was, above all, a tireless worker. He kept long days in the lab, working on Saturdays — and expecting his students and research associates to do likewise. In one of his Rules, he instructed students: "Every week hath seven days. Six days shalt thou labor for twelve hours of the day. But on the seventh day thou canst stop ONE HOUR EARLIER. And in that hour thou shalt clean thy bench." The humor was balanced by Racker's own dedication to his labors. Indeed, he died at age seventy-eight, two days after a stroke, which had followed a full Saturday of work in the lab.

DOUGLAS ALLCHIN

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