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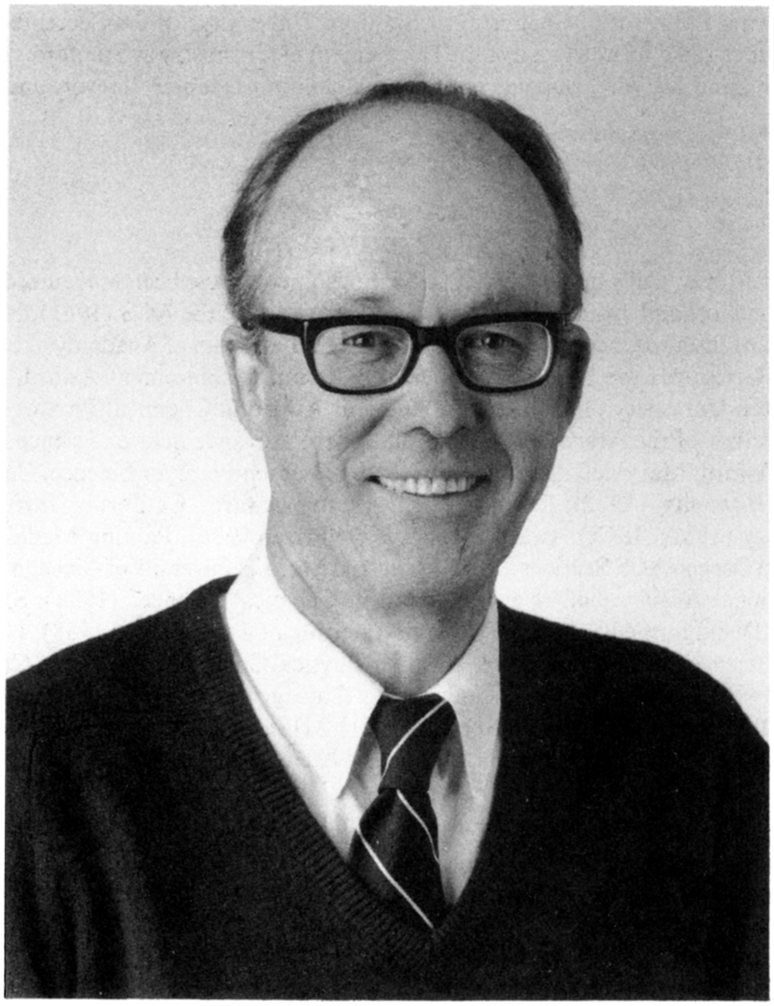

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Harden M. McConnell: A Celebration of His Scientific Achievements

Harden McConnell is a scientist of great imagination and originality. He has made major contributions to theoretical and experimental chemistry for over forty years. On April 4, 1992, to coincide with the American Chemical Society Meeting in San Francisco, approximately 100 of his present and former students, colleagues, and friends held a scientific meeting at Stanford to honor the McConnells on Harden's 65th birthday. As part of the celebration, and with the encouragement of Mostafa El-Sayed, Editor, this issue of *The Journal of Physical Chemistry* was planned. A special issue of the *Biophysical Journal* is being published concurrently to present the more biological work of McConnell's former students and colleagues. These two publications provide a glimpse of the broad scope of activities and careers influenced by Harden McConnell, ranging from molecular quantum mechanics to immunology.

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Biographical Summary

Harden M. McConnell was born on July 18, 1927, in Richmond, VA. He earned a B.S. degree in chemistry from George Washington University in 1947, and his Ph.D. in chemistry from the California Institute of Technology in 1951 with Norman Davidson. After serving for two years as a National Research Fellow in physics at the University of Chicago with Robert S. Mulliken and John Platt, he held a position as research chemist at Shell Development Co. He was recruited by Norman Davidson, Jack Roberts, and Linus Pauling at the California Institute of Technology in 1956 as Assistant Professor of Chemistry. He was promoted to Professor of Chemistry and Physics in 1963, and he moved to Stanford University as a professor in 1964. In 1979 he was named Robert Eckles Swain Professor of Chemistry at Stanford University. From September 1989 to September 1992, he was Head of the Department of Chemistry at Stanford. Harden McConnell and his wife, Sophia, raised three children (Hunter, Trevor, and Jane).

Honors and Awards

Harden McConnell's broad range of accomplishments have been recognized by the following honors and awards: California Section Award of the ACS (1961); National ACS Award in Pure Chemistry (1962); Election to the National Academy of Sciences (1965); Harrison Howe Award, ACS (1968); Alumni Achievement Award, George Washington University (1971); Irving Langmuir Award in Chemical Physics (1971); Elected Fellow of the American Association for the Advancement of Science (1982); Remsen Award, Maryland ACS Section (1982); Dickson Prize for Science, Carnegie-Mellon University (1982); Distinguished Alumni Award, California Institute of Technology (1982); ISCO Award (1984); Wolf Prize (1984); Pauling Medal, Puget Sound and Oregon ACS Sections (1987); Wheland Medal, University of Chicago (1988); U.S. National Academy of Sciences Award in Chemical Sciences (1988); Sherman Fairchild Distinguished Scholar, California Institute of Technology (1988); National Medal of Science (1989); Peter Debye Award in Physical Chemistry, American Chemical Society (1990); Doctor of Science, University of Chicago (honorary) (1991); and Evans Memorial Award, Ohio State University (1991). Harden McConnell has a long and increasing list of honorary lectureships. He has been on the editorial board of several journals and has acted as a consultant for corporations. He is the founder of Molecular Devices Corp. in Palo Alto, CA, and is also the founder of a not-for-profit corporation, the Foundation for Basic Research in Chemistry.

Summary of Research Contributions

Harden McConnell is unusually gifted at dissecting complex phenomena, formulating rigorous but physically illuminating theoretical models, and shaping the key ideas into an intuitively clear framework for experimental investigation. The range of his interests and fundamental contributions is breathtaking. Here we provide a brief overview of his most significant scientific endeavors. Indeed, the sheer abundance of his contributions precludes even mentioning a number of others which are significant in their own right. McConnell is without question one of the most imaginative, stimulating, and productive chemists of this generation. His profound insights and his incisive theories and experiments have provided fertile ground for literally thousands of subsequent investigators.

The Early Days in NMR. In his early work at the Shell Development Co. in Emeryville, CA, and at the California Institute of Technology, Harden McConnell was intimately involved in the development of theoretical models to explain NMR spectra in organic systems. In the 1950s he published a series of 12 papers on the theory and analysis of NMR spectra in *J. Chem. Phys.*[17,19,23–32,35,42,44,49] His paper with McLean and Reilly "Analysis of spin-spin multiplets in nuclear magnetic resonance spectra" introduced group theory for the analysis of high-resolution NMR spectra.[17,26] The paper "Theory of nuclear magnetic shielding in molecules. I. Long-range dipolar shielding of protons"[34] and his work with R. E. Robertson "Isotropic nuclear resonance shifts"[49] are widely cited as important contributions to our understanding of chemical shielding. McConnell showed how the Bloch equations for NMR can be modified to include the treatment of rate processes in his paper "Reaction rates by nuclear magnetic resonance".[42] Other papers in this landmark series contributed to our understanding of nuclear relaxation processes. In short, McConnell played a significant role in establishing NMR as the premiere method for determining molecular structure and dynamics in solution.

EPR Spectroscopy, the Electronic Structures of Free Radicals, and the McConnell Relation. McConnell was a major figure in developing the interpretation of EPR spectra of organic free radicals. His work in this area provided additional important validation of the adequacy of simple molecular orbital theory and valence bond theory. The fundamental paper with D. B. Chesnut on the "Theory of Isotropic Hyperfine Interactions in π-Electron Radicals"[40] led to what has become known as the McConnell relation, $a = Q\rho$, which provides a direct link between the observed proton coupling constant (a) and the unpaired π-electron spin density (ρ) on the adjacent carbon atom. Q is a proportionality factor that is nearly constant for both aromatic and aliphatic free radicals. In a companion paper with J. Strathdee titled "Theory of anisotropic hyperfine interactions in π-Electron Radicals",[57] the theory was extended to the anisotropic component of the nuclear hyperfine interaction, important in free radicals trapped in organic crystals. These two papers became "Citation Classics" (see Literature Citations section). McConnell subsequently published a series of theoretical and experimental studies of the McConnell relation. This relationship has made possible a means of testing theoretical predictions of molecular orbital theory and valence bond theory. Ultimately it has provided a framework for understanding a large literature on the structure of free radicals in organic and biochemical systems.

The recognition and demonstration by McConnell that the spin density on the proton in the "CH fragment" is opposite in sign to that in the $2p\pi$ orbital represent a watershed in the understanding of the electronic structure of hydrocarbon radicals and the concept of spin correlations in molecules. McConnell and his co-workers, C. Heller, T. Cole, and R. W. Fessenden, followed that work with a complete theoretical and experimental description of anisotropic proton hyperfine interaction in the prototypical free radical generated by X-irradiation of a single crystal of malonic acid.[61] McConnell then extended it to the treatment of numerous other free radicals.[62–66,68,77,81,83,84,86]

The use of spin density matrices,[45] β-proton,[65] and carbon-13 hyperfine interactions,[64] the pseudovector hyperfine interaction,[51] the magnetic resonance properties of orbitally degenerate systems,[70,71,84,92,97] charge-transfer complexes,[13,74,95] and zero-field splittings[48,56,91] represent less well-known but equally fundamental investigations of McConnell.

Theories of Triplet Excitons and Ferromagnetism. In several instances, McConnell has developed theoretical concepts many years before it has been possible to verify them experimentally. One interesting case is the theory of triplet excitons. The first prediction of the existence and properties of paramagnetic excitons in organic crystals was made by Sternlicht and McConnell in 1961.[75] Ten years elapsed before the predictions were verified experimentally in elegant work by H. C. Wolf and collaborators in Germany on naphthalene and anthracene. They confirmed the vanishing of proton hyperfine structure and measured the fine structure splittings of excitons. The observed splittings were almost exactly equal to those predicted by Sternlicht and McConnell. Also in 1961, McConnell showed that the remarkable paramagnetic resonance spectra first observed in certain charge-transfer (TCNQ) crystals by Chestnut and Phillips are due to triplet excitons (spin $S = 1$ excitons).[79,82] McConnell predicted that such paramagnetic mobile excitations should be present in other types of organic free radicals, and demonstrated their presence in Wurster's blue perchlorate.[85,88]

Ferromagnetism is another field in which McConnell's theoretical groundwork preceded experiments by many years. In 1963, McConnell published a theory of ferromagnetism in solid free radicals[89] (proposal I). The essence of proposal I is that when aromatic radicals with alternating spin densities are suitably stacked on top of one another, the coupling should be ferromagnetic. McConnell made a second proposal (II) in a discussion following a lecture of Robert S. Mulliken [McConnell, H. M. *Proc. Robert A. Welch Found. Conf. Chem. Res.* **1967**, 144]. McConnell's proposal II invokes the role of orbitally degenerate states in stabilizing ferromagnetism in charge-transfer organic solids. It was not until the 1980s that McConnell's proposal I was demonstrated experimentally by A. Izuoka, S. Murata, T. Sugawara, and H. Iwamura [*J. Am. Chem. Soc.* **1987**, *109*, 2631–2639]. McConnell's proposal II has stimulated synthetic attempts to make organic ferromagnets. Recently McConnell's proposal II has been invoked to explain ferromagnetism in a low-temperature phase of a buckminsterfullerene C_{60} charge-transfer salt [Wudl, F.; Thompson, J. D.; *J. Phys. Chem. Solids* **1992**, *53*, 1449–1455].

ENDOR and ODMR. Not only has McConnell been at the forefront of major theoretical developments in interpreting magnetic resonance spectra, but his theoretical contributions have always been balanced by significant experimental innovations and systematic verification in his laboratory. His numerous contributions to the arsenal of experimental techniques are well-known to many investigators. Less well-known is the fact that two other major developments—electron–nuclear double resonance (ENDOR) of free radicals, and optically detected magnetic resonance (ODMR)—were also suggested by him and pioneered in his laboratory with A. Kwiram. These methods are very active areas of endeavor today.

The Spin Labeling Technique. In 1965 McConnell introduced the concept of utilizing stable free radicals and EPR to detect local environments in biological systems. The first paper with S. Ohnishi utilized the radical ion of chlorpromazine.[98] In a subsequent paper with T. J. Stone, T. Buckman, and P. L. Nordio, employing nitroxide free radicals, he named this approach "spin labeling".[106] Spin labeling has become a powerful tool for probing molecular structure and dynamics. It provides a complementary method to NMR and fluorescence labeling. For more than a decade, McConnell, his students, and colleagues led the development of both theoretical and experimental applications. The range of applications of spin labeling has been substantial. One area has been the dynamics of nonmembrane proteins,[107,110,117] particularly hemoglobin.[111-113,115,118,120,122-124,128] The second area involves applications to membrane model systems and biological membranes. A third area is the application of spin labeling to probing the antibody combining site. Because of their broad impact, McConnell's accomplishments in these latter two fields are discussed separately below.

Discoveries Involving the Structure and Dynamics of Biological Membranes. Harden McConnell has done incisive and innovative research on many aspects of membrane function. He has demonstrated a rare ability to apply combinations of advanced and powerful methods: NMR, EPR, fluorescence, and electron microscopy, often increasing the power of each method by introducing original modifications (e.g., periodic pattern photobleaching recovery[216,247,253,277]), or by advancing the underlying theory. His theoretical contributions are not limited to methods but have advanced our understanding of membrane structure and function at a very basic level. A partial catalog of the discoveries of McConnell and co-workers include the following: (1) An early direct demonstration that the lipids in phospholipid bilayers in living cells are in a liquid state, found in the 1969 paper with W. L. Hubbell, "Motion of steroid spin labels in membranes".[129] (2) Demonstration of the flexibility gradient in fatty acid chains of lipid bilayers and membranes in 1969 with W. L. Hubbell, "Orientation and motion of amphiphilic labels in membranes".[132,134] This work showed that the segmental motion near the polar head group is restricted, whereas near the terminal methyl groups at the center of the bilayer there is high rotational freedom. (3) Measurement of the rate of phospholipid translocation across bilayers (flip-flop) in 1971 with R. D. Kornberg, "Inside-outside transitions of phospholipids in vesicle membranes".[139] This paper established that the rate of phospholipid flip-flop is remarkably low compared to the rate of lateral diffusion of phospholipids in lipid bilayers. (4) Direct evidence for a chain tilt gradient in bilayers in 1971 with B. Gaffney McFarland, "Bent fatty acid chains in lecithin bilayers".[142] (5) Measurements of the rates of lateral diffusion of lipids in model bilayer membranes in 1971 with R. D. Kornberg, "Lateral diffusion of phospholipids in a vesicle membrane",[145] and in 1972 with P. Devaux, "Lateral diffusion in spin-labeled phosphatidylcholine multilayers".[147] (6) Novel methods of determining phase diagrams of phospholipids, and one of the early determinations of phase diagrams of phospholipids in bilayers in 1973 with S. H. Wu, "Lateral phase separations and perpendicular transport in membranes".[171] The papers with C. Linden, K. Wright, and C.F. Fox, "Lateral phase separations in membrane lipids and the mechanism of sugar transport in Escherichia coli",[165] and with E. J. Shimshick, "Lateral phase separations in phospholipid membranes",[166] are fundamental contributions, widely cited in this field. (7) Evidence for the coexistence of two liquid phases in lipid bilayers composed of phosphatidylcholine and cholesterol in 1981 with D. J. Recktenwald, "Phase equilibria in binary mixtures of dimyristolylphosphatidylcholine and cholesterol".[252]

The Nature of the Antibody–Antigen Combining Site. In 1976, Humphries and McConnell found that it is possible to prepare polyclonal rabbit antibodies specifically directed against a nitroxide free radical.[194] In 1982, monoclonal antibodies to a nitroxide lipid hapten were produced.[272] By taking advantage of the broadening of nuclear magnetic resonance spectra by paramagnetic substances such as nitroxide spin labels, the McConnell group showed that NMR difference spectra can be used to observe proton signals from the amino acids in the combining site region of this monoclonal antibody.[286,290,295,298,305,307,317,320,329] It was also shown that the hybridoma producing this antibody can be grown on deuterated amino acids and combinations of amino acids, such that NMR difference spectra can be used to determine the amino acid composition of the combining site region. Further, by varying the spin label hapten concentration, one can vary the distance over which line broadening takes place. Using this information, distances between individual amino acid protons and the spin label hapten in the combining site have been determined. Some 30–35 amino acids in the combining site region have now been identified, along with a number of distances.[335,336,340] Thus, by combining spin labeling and NMR, McConnell succeeded in producing a kind of molecular magnetic resonance imaging of the antibody–antigen combining site in solution, information that is not available by other methods for proteins of this molecular weight.

Molecular Immunology. Reading McConnell's papers and listening to him describe his research provides interesting insights about his successful strategy of approaching problems in the biological sciences. McConnell has selected problems using two criteria—the problems must be significant from a biological point of view, but must also be interesting physical chemistry. His contributions to immunology are an example of this approach.

In the late 1970s, McConnell initiated a series of studies of the immune response utilizing model membranes to discover the structural and dynamical aspects of membranes that are significant in membrane immunochemistry.[189,195,197,198,200,202,204,205,206,211,213,214] One of the major tools used in this work was spin labeling (e.g., spin labeled haptens), and these studies represent a systematic development and use of techniques, including the use of reconstituted lipid membranes. From these and subsequent studies,[218,221,225,226,227,230-233,240-245,255,258,260-262] compelling evidence has been obtained that the physical properties of a lipid membrane can have important effects on antibody-mediated responses to membrane-bound haptens. McConnell and his graduate student, R. Weis, also developed an elegant approach to this problem, using evanescent wave excitation of fluorescently-labeled linker molecules in the membrane–membrane contact region.[267] The method has extraordinary sensitivity for detecting specific biochemical events that are associated with membrane-membrane recognition and is the experimental basis of subsequent experiments in molecular immunology by McConnell and co-workers.

Perhaps the most significant experiment of McConnell in the field of molecular immunology concerns antigen presentation, a process whereby a molecular complex formed between self (major histocompatability complex, MHC, proteins) and foreign antigens, for example viral peptides, on the surface of one membrane, is recognized by a specific receptor on the surface of a T-lymphocyte. McConnell and co-workers, T. Watts and A. A. Brian, in collaboration with J. W. Kappler and P. Marrack, demonstrated that this cell–cell recognition process can be mimicked when one cell membrane is replaced by a reconstituted membrane composed of an MHC–peptide complex incorporated in a lipid bilayer supported on a glass slide.[297] They showed that only two components are required to trigger cultured T-cells, one component being the MHC molecule and the second the antigenic peptide. He followed these studies with a number of papers dealing with this immunological phenomenon, known as "MHC restriction" and "antigen presentation".[302,304,310,312,316,317,322,324]

McConnell combined physical chemistry and molecular immunology in the study of the kinetics of the reaction: MHC + peptide $\rightleftarrows$ complex. He and T. H. Watts showed that the MHC peptide complexes are remarkably long lived, and subsequent experiments have shown that these life times are on the order of days.[323] McConnell followed this initial observation with an extensive study of the kinetics of MHC–peptide reactions.[346,349,351,354,356,360] Their work demonstrated that there is a kinetic intermediate in the reaction of MHC protein and the antigenic peptide,[333] that a protein structural intermediate may be involved in peptide–MHC reactions,[343] and that, surprisingly, each of the two chains (α and β) of the class II MHC can bind antigenic peptide with a long lifetime. Additional new observations were made regarding the binding stoichiometry,[358] the kinetics of peptide binding,[356,359,361,362,369] and cell function.[364,367]

Structures and Phases in Lipid Monolayers at the Air–Water Interface. Physical chemical studies of monolayers date back to the experiments of Irving Langmuir in the 1930s. Much has been learned about the behavior of lipid monolayers by classical techniques. However, since measurements such as pressure–area isotherms and surface potentials are macroscopic, there are limitations on the information that can be inferred from these classical approaches. In 1981, McConnell and von Tscharner constructed a film balance that could be placed on the stage of an epifluorescence microscope, and experimented with phospholipid monolayers doped with a low concentration of fluorescent lipid probe. They discovered that epifluorescence microscopy can be used to visualize lipid monolayers at the air–water interface and that this technique permits the observation of lipid "structures" at the air–water interface.[251] This technique was quickly adapted and advanced by other laboratories. [Of historical interest this work was originally motivated by the desire to transfer monolayers to glass slides in McConnell's studies of the immune response. Previously, McConnell and von Tscharner had succeeded in coating solid supports such as glass microscope slides with lipid monolayers.[256] Using such unique monolayer samples, under water, a number of studies were carried out, including the observation of specific antibody-dependent interactions between macrophages and lipid haptens.[255]]

Using their new technique, McConnell, L. K. Tamm, and R. Weis were among the first to report ordered solid–liquid coexistence at the air–water interface and on solid substrates in their papers "Periodic structures in lipid monolayer phase transitions"[288] and "Two-dimensional chiral crystals of phospholipid".[293] McConnell and his colleagues have since used epifluorescence to make many significant discoveries concerning monolayer structure, domain shapes, dynamics, and lipid phases, including the pronounced effect of cholesterol on domain shape,[300] immiscible liquid phases in monolayers containing cholesterol and phosphatidylcholine,[325] the reversibility of domain shape changes,[308] long-range molecular orientational order in solid lipid domains,[313] and the detection of critical points[325] and critical shape transitions.[341] In parallel with these experimental studies, McConnell has also developed the corresponding theory of domain shapes.[314,326,338,347,355,363,366] This work has advanced not only our current understanding of lipid monolayer behavior, but also the broader theory of domain shapes.[350,365]

The Silicon Microphysiometer Biosensor. Finally, we turn to a field which represents a creative application of modern silicon technology, normally associated with computers, to solve problems in cell biology. McConnell founded Molecular Devices Corp. in 1983, with the idea of interfacing silicon devices directly with biochemical and biological systems. One goal was to invent a device that could rapidly detect changes in metabolism of a small number of cells. In 1983, McConnell and three of his former postdoctoral fellows, J. W. Parce, D. Hafeman, and G. Humphries, discovered the light addressable potentiometric sensor (LAPS).[328,332,339] A spinoff of an illumination scheme for addressing the LAPS, is a 96-well microplate reader with a response time rapid enough to perform kinetic measurements in all 96 wells simultaneously. By 1988, Molecular Devices launched the first LAPS-based instrument Threshold to perform high sensitivity, rapid immunoassays. In 1989, McConnell and the Molecular Devices team, together with K. L. Ross and B. I. Sikic of the Stanford University School of Medicine, published an article in *Science* on "Detection of cell-affecting agents with a silicon biosensor".[345] On the cover is a photograph of living cells retained in an array of 50 μm square wells etched into the surface of the silicon biosensor. The biosensor is called a microphysiometer (the product name is the Cytosensor, introduced in 1992). The microphysiometer repetitively measures the rate of acid production by living cells in a flow chamber. Using the microphysiometer, it is possible to detect chemical substances that affect biological cells such as toxins and drugs, as well as natural substances such as hormones and growth factors. McConnell and his colleagues recently showed that the microphysiometer senses stimulatory effects on metabolism when a wide range of plasma membrane receptors is triggered.[352,357] Recent applications are discussed in the 1992 *Science* article titled "The cytosensor microphysiometer: biological applications of silicon technology".[368]

As this special issue of the *J. Phys. Chem.* goes to press, Harden McConnell and his students and postdoctoral fellows at Stanford University are focusing on three research areas: the antibody combining site structure determination by NMR using spin-labeled haptens, the field of membrane immunology, and the physical chemistry of monomolecular films. At Molecular Devices, McConnell is sharing in the excitement of the development of silicon-based biosensors and the new information they are providing about cellular responses. Over 40 publications in the basic sciences have been contributed by the research staff at Molecular Devices in the short period of time since it was founded by McConnell.

Literature Citations. Another measure of impact is the number of times publications are cited in the literature. Two of McConnell's papers have been selected as Citation Classics. His 1958 paper with D. B. Chesnut, "Theory of isotropic hyperfine interactions in π-electron radicals"[40] was featured in the October 1, 1979, issue of *Current Contents. Physical, Chemical and Earth Sciences* [Vol. 19, No. 40, p 12]. At that time, this paper had been cited 555 times since 1961. By 1990 (the latest data available), the number of citations of this seminal paper had risen to 822. The second Citation Classic is his 1959 paper with J. Strathdee, "Theory of anisotropic hyperfine interactions in π-electron radicals",[57] featured in the April 4, 1988, issue of *Current Contents. Physical, Chemical and Earth Sciences* [Vol. 28, No. 14, p 16. Also in the sister publication *Current Contents. Engineering, Technology and Applied Sciences*, Vol. 19, No. 14, p 16]. By 1990, this paper had been cited 441 times.

Obtaining a complete listing of citations turned out not to be practical (e.g., in the many cases where McConnell was not the first author). However, even a partial list is revealing. Information provided by ISI shows that McConnell has at least *nine additional papers that qualify as Citation Classics*, i.e., that meet ISI's general criteria of 400 or more citations.[23,26,35,42,49,106,134,165,166] Three papers have well over 300 citations[6,21,61] and six papers have between 200 to 299 citations.[24,102,121,132,184] An additional 23 of McConnell's papers have between 100 and 199 citations.[17,33,36,41,43,55,70,74,75,88,95,98,107,109,118,129,137,152,167,168,169,176,191] All of these figures indicate total citations through 1990 and includes some, but not all, of the McConnell articles where someone else is the first author. It would be interesting for completeness to add more recent citations and citations of articles missed in this preliminary search. However, the picture is already clear. McConnell has established a commanding citation record. His large and growing list of citations is a clear indication of the importance of his work and its impact on the scientific community.

Harden McConnell as a Teacher and Mentor

In addition to the impact of his scientific accomplishments, McConnell has launched the careers of a large number of scientists. At the California Institute of Technology and at Stanford University, he has mentored a total of 76 graduate students and 63 postdoctoral fellows to date. An additional number of senior scientists have spent time in his laboratory or worked with him in scientific collaborations (see list below). As part of the April 4, 1992, McConnell Symposium at Stanford, an informal collection of memoirs of Harden McConnell's students and colleagues was put together under the title "The McConnell Book" and distributed at the meeting. The outpouring of goodwill testifies to the strong bond between McConnell and his former students. What shines through in these accounts by his students is that McConnell is someone who rolls up his shirt sleeves and gets intimately involved in the experiments as well as the theory. It is his ability to focus on the essential issues and the sense of partnership which he conveys that has inspired so many of his students. "Enthusiasm for good science", "courage to attempt difficult experiments", "a challenging intellectual atmosphere", "personal energy and intensity", "the lab was bubbling with discussions about everything from biology to relaxation theory", "impatience but with good humor" are typical comments. By transmitting his enthusiasm to his students and demonstrating again and again the importance of focusing on the fundamental questions, McConnell has contributed markedly to his students' success in academic, industrial, and government research and administrative positions throughout the world.

On behalf of all of his students, friends, and colleagues, we wish Harden continued success and enjoyment of his scientific research.

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Publications of Harden M. McConnell

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