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IN MEMORIAM

Peter Georg Debrunner (1931–2024): Pioneer in the Application of Mössbauer Spectroscopy in Biological Physics

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ABSTRACT

Peter Debrunner was one of the emigrants from Europe, in his case Switzerland, who injected vitality and excitement into the Physics Department of the University of Illinois at Urbana–Champaign (UIUC). Peter received his Ph.D. at ETH (Eidgenössische Technische Hochschule) in Zürich and accepted a postdoctoral position in 1960 with Hans Frauenfelder, another Swiss emigrant. During his 40-year career at the UIUC, he achieved the rank of Professor of Physics, with research focused on electron paramagnetic resonance and the Mössbauer effect as applied to heme proteins. Peter was a bright, unassuming physicist with a balanced perspective and was admired and respected by his colleagues for his solid grasp of physics and pioneering work in biological physics, a new field in 1960. We have included here reminiscences/ tributes by several who had worked with him: Robert Austin; Paul Champion; Adam Gilmore; John D. Lipscomb; Eckard Münck.; J. Timothy Sage; Charles Schulz; and Stephen (Steve) Sligar.

Keywords: Biological physics, Mössbauer spectroscopy

INTRODUCTION

We need to celebrate the quiet scientists who have passed amongst us–the ones who do not constantly remind us of how great they are, of their massive achievements, how large their research group is, and of their many grants and honors. Sometimes the best scientists, the influential ones, move quietly and humbly, influencing many lives always in a positive way and building the foundations for the future with solid and deep papers that require careful reading and deep understanding. Yet in his own quiet way, Peter was a pioneer in applying the rather mysterious quantum phenomenon of the Mössbauer effect to the critical heme proteins that play such an enormous role in biology, from photosynthesis to hemoglobin. This work began at the very start of what is now known as biological physics, at a time when pursuing such a direction could make one an outlier and in some places, still does.

In what follows, we present stories of Peter's quiet yet strong influence on many of our lives, both scientific and personal. Let us celebrate the quiet good amongst us.

PERSONAL AND ACADEMIC LIFE

Christian Hans Debrunner
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Personal Life

Peter Debrunner was born on March 11, 1931, in Switzerland, as the sixth of seven children. His mother was Elsie Debrunner, and his father was Rudolf Debrunner. Two years later, the family moved to Seen, a town outside of Winterthur, where Peter's father became the pastor of the Reformed Church. Peter spent the rest of his childhood there. The family lived in a roomy parsonage that had originally been an inn dating back to the 1600s.

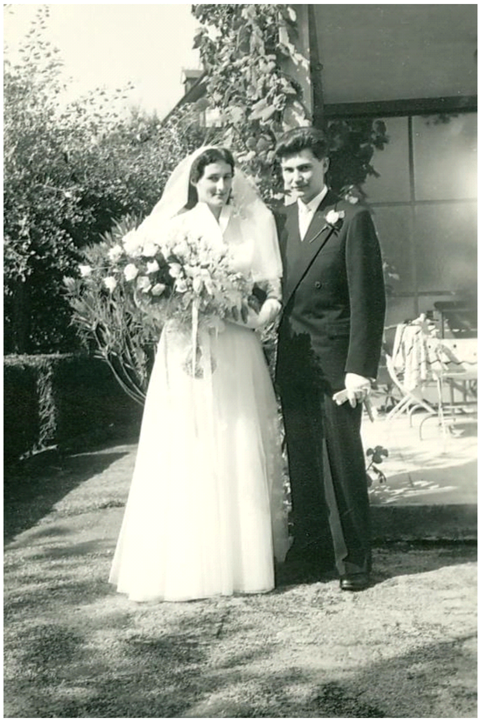

Figure 1. A 1955 photograph of Sigrid and Peter Debrunner right after their wedding; *Source:* Family archives.

In November 1955, Peter married Sigrid, and they moved into an apartment in Winterthur, Switzerland (Figure 1). Sigrid taught piano lessons, and Peter continued his studies at ETH (see below). Their daughter Bettina was born in 1957 (Figure 2), and their son Christian in 1959.

Figure 2. A 1958 photograph of Peter Debrunner holding their first child Bettina. *Source:* Family Archives.

Hobbies

Peter had a lifelong passion for many pursuits, including gardening, reading, tinkering, and traveling. From a very early age, he had his own garden bed to tend, and later he helped his mother maintain a large family garden. Peter sustained his interest in gardening throughout his life.

In September 1960, the family moved to Urbana, Illinois, USA. In the rich Illinois soil, Peter's garden produced prodigious quantities of tomatoes, cucumbers, squash, strawberries, blueberries, raspberries, blackberries, and asparagus, as well as modest amounts of apples, pears, apricots, and peaches. After retiring from the University of Illinois at Urbana–Champaign in 1997 and moving to Conifer, Colorado, he cultivated vegetables suited to the short growing season at an elevation of 8,700 feet, while battling a constant onslaught of deer, rabbits, squirrels, and chipmunks.

Peter was also a prolific reader from early in life. The parsonage where he grew up also served as the local library, which he used extensively. He read not only children's books, but also works on travel, adventure, history, and general literature by Swiss, German, French, English, and Russian authors. After retiring from UIUC in 1997, Peter spent much of his time reading physics and biophysics journals, as well as books on history and fiction.

In addition, Peter had a strong interest in understanding the internal workings of devices of all kinds and in building and repairing them. With guidance from his older brother Hansueli and using his older sister's physics textbooks, he performed many science experiments and built numerous devices, including a bimetal thermometer, a crystal radio, a tube radio, and even a gramophone. As an adult, the skills he had acquired in his youth served him well in furniture building, home electrical installations, and appliance repair projects.

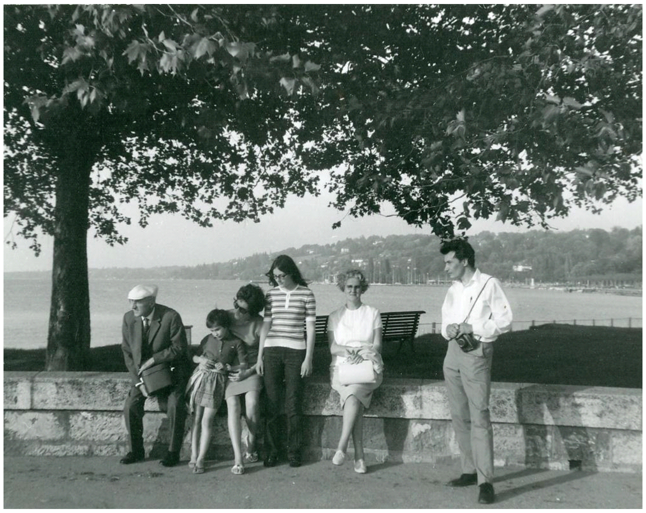

Figure 3. A 1971 photograph of Peter Debrunner's family with Sigrid's parents in Geneva, Switzerland. From left to right: Sigrid's father Theodore Müller, Susan (daughter), Sigrid, Bettina (daughter), Sigrid's mother Anna Müller, and Peter Debrunner. *Source:* Family Archives.

In Switzerland, primary and secondary schools organize annual school trips. These trips, along with the family's annual five-week summer vacations, fascinated Peter and instilled in him a love for travel at an early age. Later in life, while living in the United States, he frequently traveled with his family across much of the country, visiting national parks and friends. The family also returned often to Switzerland to visit in-laws and extended family (see Figure 3 taken during Peter's sabbatical in Geneva).

As Peter's children grew older, the family began taking ski vacations every winter first in Michigan's Upper Peninsula, once in Switzerland, and later in Colorado until his retirement. Peter continued traveling frequently throughout his retirement years until the COVID pandemic and medical issues made travel too complicated.

Academic Studies

In 1946, during his fourth year of secondary school, Peter joined the Humanitas fraternity and remained an active member until 1960, when he completed his PhD at ETH (Eidgenössische Technische Hochschule) in Zürich, Switzerland. Humanitas was unique in that its members abstained from alcohol and often held social exchanges with the Iduna sorority, which was also alcohol-free. It was during one such exchange in 1950 that Peter met Sigrid Müller.

Peter began his university studies at ETH Zürich in the fall of 1949. While he developed an interest in psychology through reading the works of Carl Gustav Jung and Sigmund Freud, he was also deeply interested in physics and ultimately chose it as a more practical field of study. He took Physics I and II from Professor Paul Scherrer, the head of the Physics Department, and was particularly impressed by Scherrer's showmanship during elaborate class demonstrations. He later incorporated many similar demonstrations into his own physics lectures at the University of Illinois at Urbana–Champaign.

At the time, the most well-known physics faculty members at ETH were Wolfgang Pauli and Walter Heitler. Peter greatly enjoyed the lively discussions they initiated at the weekly ETH physics colloquium.

When selecting a research advisor after completing his physics exams, Peter chose Ernst Heer, who studied the angular correlation of gamma-ray emissions. This research required a complex mechanism to vary measurement angles, measure time delays between gamma-ray emissions, and count correlated events (Figure 4 of Peter with others). Heer had implemented this using racks of relays and stepping switches, and Peter's early experience with electronics allowed him to understand and exploit the system effectively. He chose

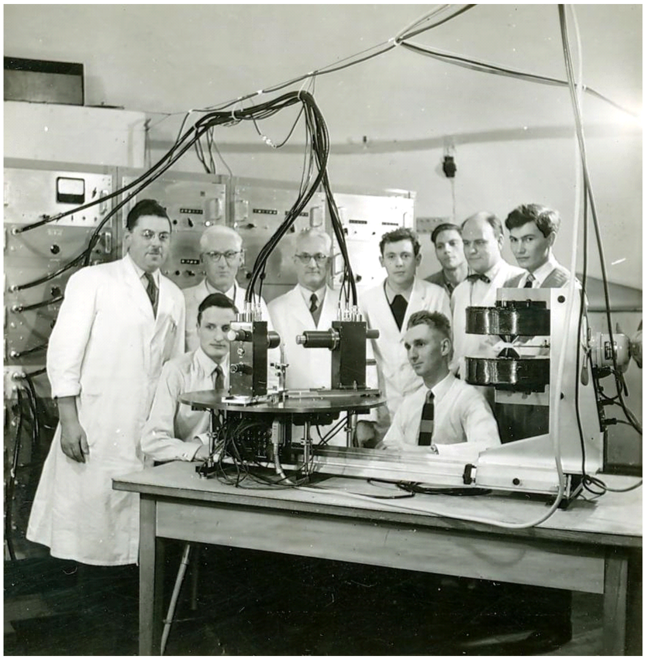

Figure 4. A ~ 1956 photograph of Peter Debrunner (standing on the right) with the *Angular Correlation research group* (Richtungs korrelations gruppe) of Dr. Ernst Heer; the apparatus, used in their research, is on the table in the foreground. *Source:* Family Archives.

the angular correlation of a europium isotope as his thesis topic and completed his PhD in the spring of 1960.

The Years in the USA

After completing his PhD, Peter initially planned to apply for a teaching position at a secondary school in the Swiss mountain town of Schiers. However, Professor Paul Scherrer suggested that he work abroad for a few years. Scherrer contacted a former student at the University of Illinois at Urbana–Champaign, Hans Frauenfelder, who helped arrange a postdoctoral position for Peter.

Although Peter was reluctant to move to the United States, Sigrid was enthusiastic and encouraged him to accept the opportunity. During the summer of 1960, the couple prepared for their move, storing much of their furniture and belongings—including Sigrid's Steinway grand piano at their parents' homes, expecting to return to Switzerland after a few years. Anticipating life in an automobile-dependent country, Peter obtained a driver's license.

With the help of Hansjörg Greber, a colleague from ETH who had taken a postdoctoral position at the University of Illinois shortly before Peter, they found a furnished rental home on Oregon Street in Urbana. On September 12, 1960, the four members of the Debrunner family boarded the *TS Hanseatic* in Le Havre, France, arriving one week later in New York and shortly thereafter in Urbana.

Peter began his postdoctoral work with Hans Frauenfelder, focusing on electron paramagnetic resonance (EPR) and Mössbauer spectroscopy applied to heme proteins. In 1962, Peter and Sigrid's third child, Susan, was born, and the family moved to a larger rental house on Country Squire Drive in Urbana.

After completing his postdoctoral position, Peter accepted an assistant professorship in the Physics Department at UIUC. Although he and Sigrid still expected to return to Switzerland eventually, Peter grew increasingly content with his work in Urbana (Figure 5). Sigrid, however, missed her family and continued to hope for a return.

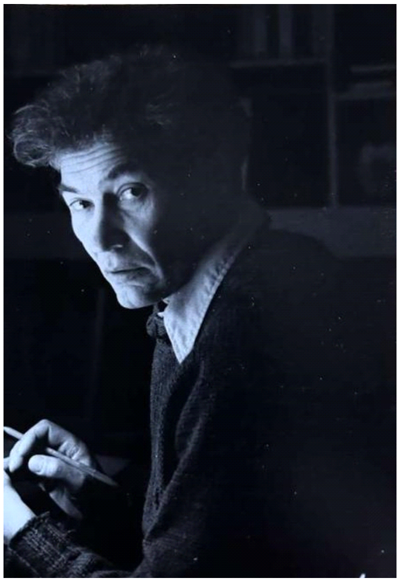

Figure 5. A 1980 portrait of Peter Debrunner in his home in his study. *Source:* Christian (Chris) Debrunner.

Following a memorable snowstorm in the spring of 1967, Peter and Sigrid purchased a home on Eliot Drive in Urbana, where they lived until Peter's retirement in 1997.

Sabbatical in Switzerland

In the spring of 1971, Peter took a sabbatical at CERN (Conseil Européen pour la Recherche Nucléaire) in Geneva, Switzerland. The family lived in a modern fifth-floor apartment on Rue de l'Ancien-Port, just two blocks from Lake Geneva. Sigrid's grand piano was transported from her parents' home in Winterthur to Geneva, much to the dismay of the piano movers, who had to carry it up five flights of stairs.

Although the French schools were challenging for the children, who arrived with little knowledge of French, the city of Geneva and its surrounding countryside offered many opportunities for skiing, hiking, and sightseeing. After the sabbatical, Sigrid noted that Switzerland was not quite as she remembered and became more comfortable with the idea of staying in the United States indefinitely. Later in 1971, she arranged to have her piano and some furniture shipped to the US.

In 1973, the Debrunners purchased a vacation home in Buchen, Switzerland, together with one of Peter's sisters and her husband. The family visited for ski vacations and summer stays throughout the decade. In the 1980s, they sold their share and purchased a ski home in Steamboat Springs, Colorado, where they had been skiing each Christmas since the mid-1970s.

Family and Retirement

In 1983, Peter and Sigrid's eldest daughter Bettina married, and a year and a half later their first grandchild was born. Three more grandchildren followed in 1987, 1989, and 1992. Because Bettina and her family remained in Urbana until nearly Peter's retirement, Peter and Sigrid were able to spend significant time with their grandchildren.

Their youngest daughter Susan married in 1985 and later moved to Texas A&M for graduate studies. She had two sons in 1989 and 1992. Peter and Sigrid's son Chris married in 1997 and moved to Colorado in 1990, as did Susan and her family. Chris and his wife Agnes had three children in 1997, 1999, and 2002.

When Peter retired in 1997, he and Sigrid moved to Colorado to be near Chris and Susan's families, as Bettina and her family had relocated to Connecticut. They purchased a home next door to Chris's in Conifer, Colorado, and enjoyed close relationships with their growing families.

Beginning even before their arrival in Colorado, increasingly severe wildfires affected the Conifer area, causing Sigrid growing concern. In 2013, Peter and Sigrid moved to a home in Morrison, Colorado, at lower wildfire risk. There, they hosted their children and grandchildren every Sunday and on holidays until Peter passed away on April 12, 2024.

THE BROAD INFLUENCE OF PETER DEBRUNNER

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The enzyme cytochrome P450 continues to fascinate biochemists and biophysicists. Among the early leaders in this field (approximately 1965–1972) was the collaborative group at the University of Illinois at Urbana–Champaign (UIUC), consisting of Professors Irwin C. Gunsalus in Biochemistry and Hans Frauenfelder and Peter Debrunner in the Physics Department. Fueled by close friendships and shared enthusiasm including a mutual appreciation for the finest wines of the world this collaboration helped direct the course of P450 investigations worldwide.

Notably, P450 research in Urbana moved directly into biophysics rather than following traditional biochemical approaches. For example, long before a kinetic analysis of substrate turnover had been completed, the detailed spin Hamiltonians describing the P450 heme iron and the iron–sulfur center of the redox transport protein putidaredoxin were elucidated. These insights were obtained through Mössbauer and spin-resonance spectroscopy, efforts led by Peter Debrunner.

The Debrunner–Frauenfelder–Gunsalus collaboration provided an unusually accessible pathway for a physicist such as myself to transition from theoretical astrophysics into biochemistry. Peter was instrumental in facilitating this shift. In 1972, while I was a physics graduate student independently supported by an National Science Foundation (NSF) fellowship and seeking to join this collaboration, Peter characteristically cut to the heart of the matter by asking what precise experiments I intended to conduct on the P450 enzyme system, which already consumed most of the EPR, Mössbauer spectroscopy, and flash photolysis resources of the group.

Having spent the previous summer at Argonne National Laboratory studying fluorescence of dye–DNA complexes, I realized that fluorescence was a tool not yet represented in the Debrunner–Frauenfelder group. I therefore proposed to use intrinsic and labeled fluorescence of the P450 monooxygenase proteins to probe multiprotein interactions and dynamics. Peter quickly pointed out that constructing a homemade fluorimeter was unlikely to advance the field significantly and noted that the world-renowned pioneer of biological fluorescence, Gregorio Weber, was a professor in biochemistry just across the street.

Given that future fluorescence investigations would rely on Weber's instrumentation, Gunsalus (universally known as "Gunny") offered me a desk next to John Lipscomb in the Roger Adams Laboratory. I moved my belongings there, formally completing my transition into biochemistry and related disciplines.

One story illustrates Peter's remarkable attentiveness to his students. In 1973, Gunny suggested that we attend a workshop on the island of Spetses, Greece, following the International Union of Biochemistry meeting in Sweden. This involved flying from Stockholm to Athens and then taking a boat to the island. It never occurred to me that my plane would arrive after the last boat had departed from Piraeus. I had made no plans for lodging or for navigating the transfer. Upon arriving in Greece, I found a message from Peter waiting for me at the airport. He had arranged a hotel reservation, secured a boat ticket, and provided detailed instructions for getting from one to the other. This episode typified Peter's quiet but constant concern for his students' well-being, which extended even to helping us find future employment.

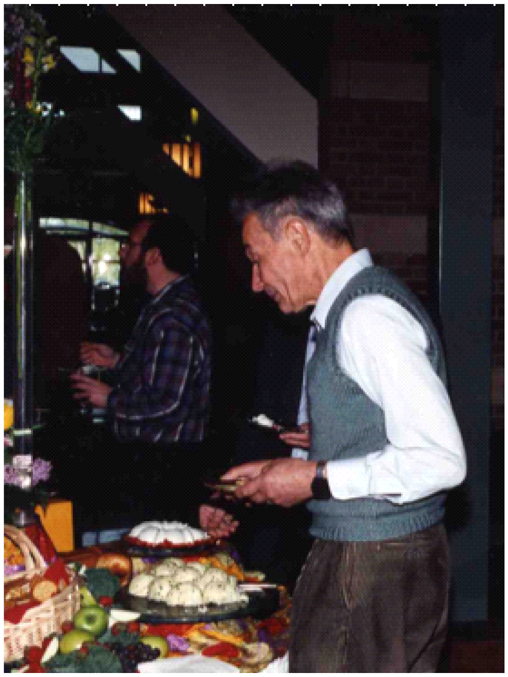

Figure 6. A 1995 photograph of Peter Debrunner at the Beckman Institute, where there was a celebration for the election of Lowell P. Hager (b.1926- d. 2014) to the US National Academy of Sciences. *Source:* Steve Sligar

The scientific and personal guidance provided by Peter Debrunner (Figure 6) was pivotal at this stage of my career (Sligar et al. 1974a, 1974b; Gunsalus et al. 1975) and had a lasting impact on my subsequent scientific accomplishments.

PERSONAL AND PROFESSIONAL REMEMBRANCE OF PROF. PETER DEBRUNNER

Charles Schulz

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My career trajectory and, in many ways, my life have been forever and positively impacted by Professor Peter

Debrunner, as well as by his teammate in the Illinois biophysics group, Professor Hans Frauenfelder. As a mentor, Peter was always calm, supportive, and helpful, allowing me to find my own way through the inevitable roadblocks encountered during a Ph.D. program.

I came to graduate school at the University of Illinois in Urbana-Champaign in 1972, having completed an undergraduate honors project related to Mössbauer spectroscopy. I was therefore excited when Peter offered me the opportunity to work in his group. Students in the Debrunner group pursued a wide range of projects involving metalloproteins and porphyrin model compounds using EPR and Mössbauer spectroscopy techniques.

The first project I worked on with Peter involved the characterization of the iron–sulfur protein rubredoxin in both its native ferrous state and its oxidized ferric state (Debrunner and Schulz, 1976). Later projects included studies of the extensively investigated enzyme cytochrome P450 (Sharrock et al. 1976) and horseradish peroxidase (HRP; Schulz et al. 1979). The HRP work was of particular interest because the enzyme could be frozen in multiple states of its reaction cycle.

Our work on HRP resolved a longstanding puzzle: as no EPR signal was observed for HRP Compound I, despite the clear presence of an unpaired electron. Another topic of special interest to me during my graduate studies was the effect of spin fluctuations on Mössbauer spectra. Peter strongly encouraged my pursuit of this subject, which resulted in several important publications (see, for example, Schulz et al. 1987).

Through Peter's collaboration with Professor W. Robert (Bob) Scheidt of the University of Notre Dame on porphyrin model compounds, I also established my own collaboration with Bob, who remained a valued scientific partner throughout my academic career (see, for example, Scheidt et al. 1992; Schulz et al. 1997; and Bohle et al. 1998). These works addressed topics ranging from spin–spin interactions to EPR and magnetic Mössbauer spectroscopy of compounds related to malaria.

Finally, I owe Peter thanks for what may have been the most important personal event in my life. After I was hired as an Assistant Professor of Physics at Knox College in Galesburg, Illinois, Peter invited me to work in his laboratory during the summer of 1983. During that summer in Urbana, I met my eventual wife, Faye.

Figure 7. A 1984 group photograph in front of the Krannert Center of Performing Arts, University of Illinois at Urbana-Champaign. Left to right: Tim Sage; Mike Hendrich; Hsin Wang; Chuck Schulz; Walt Wise; and Peter Debrunner. *Source:* Chuck Schulz.

I will always be deeply grateful for having known Peter Debrunner and for the many ways in which he had a positive and lasting impact on my life.

I conclude these reminiscences with a photograph of Peter Debrunner (Figure 7) with me and several others at the University of Illinois at Urbana- Champaign.

MY SCIENTIFIC ASSOCIATION WITH PETER DEBRUNNER

John D. Lipscomb
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The structure, molecular mechanism, regulation, and remarkably diverse substrate range of the large family of cytochrome P450 monooxygenase enzymes are now well documented, thanks to research carried out over the past five decades in hundreds of laboratories worldwide. In contrast, during the decade centered on 1970, only three cytochrome P450 enzymes were known: mammalian enzymes from liver and adrenal cortex, and the bacterial enzyme P450cam isolated from *Pseudomonas putida*. While the importance of cytochrome P450 to human health and environmental catabolic cycling was recognized early, the difficulty of obtaining large quantities of pure enzyme from mammalian tissues made the bacterial system especially attractive for kinetic and biophysical studies.

At the University of Illinois at Urbana–Champaign, I. C. Gunsalus ("Gunny") in Biochemistry and Hans Frauenfelder and Peter Debrunner in Physics recognized that understanding cytochrome P450 structure and function required careful evaluation of both the protein framework and the metal-containing active site (Fe–protoporphyrin IX, heme). This necessity demanded effective coordination among the traditionally distinct fields of biochemistry, chemistry, and physics. Remarkably, Gunny, Hans, and Peter achieved nearly daily communication between their research groups over several years, dramatically advancing the field. In this powerful triumvirate, Gunny and Hans provided much of the driving force and motivation, while Peter steadily and quietly ensured that the science remained rigorous and on track. Their coordinated effort represents one of the earliest examples of what is now known as biological inorganic chemistry.

During this period, I was a graduate student in the Gunsalus laboratory. Working with others in the group, I helped develop purification protocols for each of the three protein components of the P450cam system reductase, putidaredoxin, and hydroxylase and scaled these methods to produce gram quantities required for biophysical investigations. The Gunsalus and Debrunner groups had already implemented one of the earliest applications of Mössbauer spectroscopy to biological systems by characterizing the redox protein putidaredoxin (Münck et al. 1972). Mössbauer spectroscopy requires the stable isotope ^{57}Fe, which occurs at only 2% natural abundance. Fortunately, the iron–sulfur cluster of putidaredoxin could be removed and reconstituted with highly enriched ^{57}Fe.

Gunny, Hans, and Peter sought to extend these studies to the hydroxylase component of P450cam, where direct substitution of the heme ^{56}Fe with ^{57}Fe was not possible. Earlier attempts by other groups using unenriched hemoglobin and cytochrome *c* peroxidase had failed to yield sufficiently detailed spin Hamiltonian parameters. After several successful though, in retrospect, ill-advised experiments using radioactive ^{59}Fe, we perfected methods to culture *Pseudomonas putida* strain PpG786 in ^{57}Fe-enriched media. This enabled purification of several grams of hydroxylase containing approximately 90% ^{57}Fe.

Using these preparations, we were able to trap and characterize all known intermediates of the cytochrome P450cam reaction cycle by Mössbauer spectroscopy. This work produced the first detailed characterizations of the oxidized, reduced, substrate-bound, putidaredoxin-bound, and oxygen-bound states of P450cam (Sharrock et al. 1973; Champion et al. 1975a, 1975b; Sharrock et al. 1976).

Peter Debrunner was the guiding force behind each of these studies. The principles established proved applicable not only to all subsequently characterized cytochrome P450 enzymes, but also to many other heme-containing proteins. These investigations were the first to employ a ^{57}Fe-enriched enzyme and demonstrated the immense value of Mössbauer spectroscopy for studying iron-containing biological systems. In the decades since, Mössbauer spectroscopy has provided unique insights into hundreds of enzymes and metalloproteins.

As both an undergraduate and graduate student, I had a strong interest in biophysical methods, but my training in chemistry and biochemistry did not adequately prepare me for the physics underlying these new approaches. Peter was extraordinarily generous with his time, spending many hours with our group and with me personally explaining spin physics and its applications. The collaborative environment fostered by Gunny, Hans, and Peter also led to projects extending beyond Mössbauer spectroscopy, including fluorescence, magnetic susceptibility, electron paramagnetic resonance (EPR), regulatory chemistry, and photolysis (Sligar et al. 1974a, 1974b; Champion et al. 1975). Many of the friendships and scientific collaborations formed during this period continue today, more than fifty years after leaving Urbana.

In my subsequent independent career, I entered the emerging field of non-heme iron enzymology, where Mössbauer spectroscopy and related techniques developed during the P450cam studies found broad application. Meanwhile, Peter continued to provide exceptional cross-disciplinary training for his students. One of these students, Michael Hendrich, advanced both the theory and application of integer-spin EPR for iron-containing proteins and inorganic compounds. At the University of Minnesota, several of us were fortunate to recruit Michael as a postdoctoral fellow, where he applied these methods to landmark studies of the non-heme dinuclear iron site of methane monooxygenase (Hendrich et al. 1990, 1992).

These integer-spin EPR studies were instrumental in driving the development and widespread adoption of the parallel-mode EPR cavity, now standard in most Bruker EPR spectrometers. Peter Debrunner's scientific influence has taken many forms, but his role in fostering new techniques and mentoring the scientists who use them is, in my view, a legacy that will endure for generations.

PETER G. DEBRUNNER (1931–2024): A GLIMPSE OF OUR ASSOCIATION DURING THE 1990s

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We had a wonderful association with Peter Debrunner, former Professor of Physics at the University of Illinois at Urbana–Champaign (UIUC), who passed away on April 12, 2024. Both Peter and one of us (Govindjee) were in a similar age group, and we shared a common interest in biophysics; consequently, we saw each other regularly at seminars. When we became "stuck" in understanding the physics underlying various aspects of photosynthesis, we never hesitated to ask Peter for help, and he always responded generously and insightfully.

At UIUC, Peter taught physics for forty years and published more than fifty papers in professional journals (see Appendix 1 for chronologically arranged references to selected publications). His research focused on measuring and interpreting electron paramagnetic resonance (EPR) and Mössbauer spectra as applied to heme proteins. At the same time, he was deeply committed to applying physics to biological systems, including photosynthesis.

Below, we first describe some of our collaborative research, which included work with a Ph.D. student Hyunsuk Shim (1992). This research involved detailed biochemical and biophysical investigations of the water oxidation complex (WOC) of Photosystem II (PSII). The goal was to dismantle the WOC in a controlled manner and then reconstitute it into its functional form. Shim probed the system using hydroxylamine in salt-treated samples, and the results were interpreted within a "cooperativity" model. It was quantitatively demonstrated that all four manganese atoms in the PSII reaction center are essential for active oxygen evolution. In addition, the critical roles of three extrinsic polypeptides (17, 23, and 33 kDa) were clearly established (Shim et al. 1990).

This work was followed by a study titled *Dependence of Lifetime and Quantum Yield of Chlorophyll a Fluorescence on Light Intensity from Wild-Type and Chlorina Mutants of Barley a(Hordeum vulgare)*. By measuring PSII chlorophyll *a* fluorescence lifetimes from leaves and thylakoids of wild-type and *chlorina* f104 and f2 barley mutants, Gilmore et al. (1996a) elegantly determined the effects of PSII antenna size on the de-excitation of absorbed light energy a study made possible by Peter's guidance.

This was followed by *Comparative Time-Resolved Photosystem II Chlorophyll a Fluorescence Analyses*, which revealed differences between the photoinhibitory reaction-center damage and xanthophyll-cycle-dependent energy dissipation. With Peter's help, Gilmore et al. (1996a) presented a comparative fluorescence lifetime analysis of xanthophyll-cycle- and photoinhibitiondependent changes in PSII chlorophyll *a* fluorescence in wild-type and mutant barley plants. Multifrequency phase and modulation data were analyzed alongside parallel measurements of fluorescence lifetimes and steady-state fluorescence intensities.

Photoinhibition was characterized by a progressive decrease in the main fluorescence lifetime distribution from approximately 2 ns to 0.5 ns after 90 minutes of high-light exposure. These damaging effects were consistent with an increased nonradiative decay pathway for the charge-separated state of the PSII reaction center. In contrast, the ΔpH and xanthophyll cycle exhibited concerted but distinct effects on PSII fluorescence lifetimes and intensities, with the xanthophyll cycle producing the dominant changes (Gilmore et al. 1996b).

Most of the results obtained under Peter's guidance were explained by changes associated with the ΔpH-induced activation step required for binding of de-epoxidized xanthophyll-cycle pigments. A major observation was an increase in the fractional intensity of a short-lifetime distribution at the expense of a longer-lifetime component, suggesting binding of de-epoxidized xanthophylls within the PSII inner antenna. Importantly, photoinhibition and xanthophyll-cycle mechanisms were shown to affect fluorescence lifetimes and intensities in fundamentally different ways.

These newly observed distinctions between xanthophyll-cycle-dependent energy dissipation and photoinhibition mechanisms confirmed and extended the then-available models of PSII exciton dynamics, structure, and function. The underlying physics enabling these advances was, in large part, the contribution of the late Professor Peter G. Debrunner.

PETER DEBRUNNER: REMINISCENCES FROM THE EARLY 1970s

Paul Champion

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As a physics graduate student during turbulent times, I first met Peter Debrunner around 1971, shortly after completing an introductory biochemistry course. I had developed an interest in metalloprotein structure and function and was seeking a thesis advisor. John Wood, the biochemistry course instructor, directed me to the Frauenfelder–Debrunner research group, where I discovered that both Peter and Hans Frauenfelder shared a deep interest in the emerging field of biological physics, with a particular focus on proteins.

At that time, Peter, together with senior research associate Eckard Münck, was deeply engaged in Mössbauer spectroscopy studies of heme proteins. Their primary focus was cytochrome P450cam, pursued through a very active collaboration with biochemists at the University of Illinois at Urbana–Champaign (UIUC), particularly the group led by I. C. Gunsalus.

Soon after I joined Peter's group, new collaborative opportunities arose, and I became involved in studies of several iron-based protein systems in addition to cytochrome P450cam. I am especially indebted to Peter for sending me to the IBM Watson Laboratory to work with Thomas (Tom) Moss on measurements of the magnetic susceptibility of the ferrous form of P450cam. These studies conclusively demonstrated that the ferrous enzyme exists in a pure S = 2 high-spin state (Champion et al. 1975a).

This work led naturally to investigations of other integer-spin, EPR-silent heme systems, for which high-magnetic-field Mössbauer spectroscopy provided iron-specific oxidation-state, spin-state, and ligand-sensitivity information (Champion et al. 1975b, 1975c). As our studies expanded, we also examined both ferric and ferrous states of chloroperoxidase (CPO) in collaboration with Lowell P. Hager and Paul Hollenberg (Champion et al. 1973).

Once again, Peter generously supported my work by arranging a research visit, this time to Bell Laboratories, where I worked with Jack Peisach and William (Bill) Blumberg on the initial EPR studies of CPO. These investigations helped us disentangle the associated Mössbauer hyperfine interactions in ferric CPO. Importantly, the EPR spectra were consistent with our Mössbauer results, demonstrating that the iron environments in CPO and P450cam were remarkably similar.

Later in 1972, when we studied the ferrous states of CPO and its carbon monoxide complex, we observed that both the optical absorption spectra and the Mössbauer spectra closely resembled those of the analogous states of P450cam (Champion et al. 1973). At the time, cysteine was suspected to be the axial heme ligand in P450cam, but the ligation in CPO remained uncertain, as its only sulfhydryl groups were thought to be involved in a disulfide bond. Subsequent work confirmed that a cysteine residue is indeed ligated to the heme iron in both P450cam (Champion et al. 1982) and CPO (Bangcharoenpaurpong et al. 1983).

On a personal level, I always found Peter to be exceptionally generous with his time. Whenever I became "stuck" in the laboratory, he was unfailingly helpful and insightful. I also fondly recall the gatherings that Peter and his wife Sigrid hosted for the combined Debrunner–Frauenfelder research groups. I was continually impressed by their sophistication and warmth when entertaining a group of young physics graduate students who still had many rough edges.

The food was always wonderful, and Sigrid frequently played beautiful music on her grand piano. Those evenings remain vivid memories and are among my most cherished recollections of my time in Urbana.

MY ASSOCIATION WITH PETER DEBRUNNER

Robert Austin
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I was a rather discouraged graduate student in 1969. I was tired of taking courses, although I managed to pass the "notorious" qualifying exam of the Physics Department at the University of Illinois at Urbana–Champaign. At the same time, the United States government was seriously trying to send me overseas to fight what I considered a completely senseless war in the name of "fighting communism" and preserving colonial powers. I knew I was not nearly good enough to be a theorist, high-energy experimental physics at the time looked like stamp collecting (this was pre–Gell-Mann's Eightfold Way), and the solid-state courses at Illinois struck me as deeply uninteresting. Who really needs fourth-order elastic coefficients of ice? I found myself asking: what next?

Rather than going to medical school in Canada, I looked around and was astonished to discover that two Swiss professors trained in nuclear physics–Peter Debrunner and Hans Frauenfelder–were exploring biological physics from neighboring offices. They were investigating the use of the Mössbauer effect in heme-containing proteins. Peter was running a Mössbauer spectrometer equipped with a glass helium cryostat, studying myoglobins at low temperature, while Hans was using flash lamps to study reaction kinetics initiated by light pulses at room temperature.

I became Hans's student, but I also worked closely with Peter on carboxy-myoglobin experiments at 4.2 K. To determine the liquid helium level in the glass Dewar, we used a flashlight to peer inside. Inevitably, some of the light spilled onto the carboxy-myoglobin sample in the cryostat. Peter noticed two remarkable effects upon illumination: first, the Mössbauer spectrum changed from that of the carboxy form to the ferrous state, indicating photodissociation of carbon monoxide; second, the spectrum slowly reverted back to the carboxy-myoglobin form over a period of several days, even at 4.2 K, and notably not with simple exponential kinetics.

This observation was tremendously exciting. It suggested that biological processes in proteins could proceed via quantum mechanical tunneling, and it launched Hans Frauenfelder and his students on a long and productive exploration of protein dynamics and power-law behavior in reaction kinetics.

Working with Peter Debrunner and the excellent high-energy electronics shop at Illinois, we went on to build a special logarithmic time-base transient recorder capable of acquiring data with constant time resolution per decade over eight orders of magnitude in time. This instrument was even patented (Austin et al. 1976).

In a very real sense, it was Peter Debrunner, working together with Hans Frauenfelder, who started me on my research career. Peter was a wonderful scientist and an even more wonderful person: soft-spoken, kind, always with a twinkle in his eye and a quiet laugh. The world is poorer without people like Peter, unfortunately.

REMINISCENCES OF WORKING WITH PETER DEBRUNNER

J. Timothy Sage

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Although I had entered graduate school at the University of Illinois at Urbana-Champaign, with the intention of working in solid state physics, I soon found myself struggling to engage with research which mostly seemed to be applying well-established physics. It was a happy accident that Illinois had three faculty working in biological physics, at a time when this was still a rarity in physics departments. This looked like fresher ground where more interesting questions were being asked, and I was soon working in Peter Debrunner's research group, using Mössbauer spectroscopy to investigate iron sites in proteins.

My Ph.D. research used spin Hamiltonians to model complex Mössbauer spectra of antiferromagnetically coupled two-iron sites, along with other data, and yield structural insights. The strength of the magnetic coupling in these proteins reflects the protonation state of the oxygen atom that bridges the two irons and mediates the magnetic interaction. Enzymes operate by shuttling individual protons and electrons to and from their substrates, and the location of protons is a functionally important detail that is not directly accessible to X-ray diffraction. The work involved collaborations with Professor Don Kurtz (Nocek et al. 1988) on hemerythrin (a nonheme oxygen transport protein) and with Professors Bruce Averill (Averill et al. 1987) and Burt Zerner (Sage et al. 1989) on purple acid phosphatases.

Peter's work was highly collaborative in nature and his extensive research network continued to nourish my career long after leaving his group, in ways that often took years to fully appreciate. After graduating, I undertook postdoctoral training in vibrational spectroscopy of heme proteins with Professor Paul Champion, an earlier student of Peter's, with whom I continued to collaborate for years after. My background in Mössbauer spectroscopy opened further doors near the turn of the century, when the emergence of synchrotron-based techniques for probing the ^{57}Fe resonance provided us with a uniquely specific vibrational probe for active site structure and dynamics in iron-containing proteins. This phase of my career was enhanced by an especially fruitful collaboration with Professor Bob Scheidt at Notre Dame University, who had previously worked with Peter on Mössbauer investigations of porphyrin model compounds. Some of the work from this period is reviewed by Scheidt et al. (2017).

Peter's positive outlook, calm demeanor, and good humor fostered a supportive culture within his research group, and I believe that the influence of his collaborative spirit extended well beyond Illinois. Upon first contact with anyone who had interacted professionally with Peter, simply learning that I was his student never failed to evoke a collegial response. Although he will be missed by many, warm memories of Peter will assuage our sense of loss.

PETER DEBRUNNER: MY FRIEND AND ADVISOR

By Eckard Münck

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In the summer of 1967, I received a letter from Professor Hans Frauenfelder inviting me to come to the University of Illinois at Urbana to study enzymes with Mössbauer spectroscopy. I had just finished my PhD, measuring the magnetic moments of excited nuclear states for a variety of rare earth isotopes using this new technique. Coming to Urbana for two years seemed like a nice adventure for me and my wife, Hilde. Urbana was a little flat for a couple that loved hiking in the Alps, but the place was full of unforgettable characters. I ended up working mostly with Peter Debrunner, and more importantly, he and his wife Sigrid quickly became our best friends. Our friendship lasted for 50 years. Peter introduced me to cytochrome c, and before I knew it, Professor Gunsalus (Gunny) and John Lipscomb were on the scene with putidaredoxin and cytochrome P450cam. Putidaredoxin was a tough cookie, but Peter arranged that I could use a computer in the Coordinated Science Lab. There was no printer for the simulated spectra, but I could view them on a cathode ray tube and take polaroids (>1,000).

A most decisive event for my career occurred in 1971, when Peter went on sabbatical in Switzerland and asked me to run the lab and take care of the graduate students (I said: “Are you kidding, Peter?”). It was rewarding to work with the Urbana students, all smarter than their temporary advisor. During his absence some important seminar speakers came to Urbana, including Bill Orme-Johnson who got our lab into nitrogenase research. It was Gunny who got me together with Bill and two bottles of fine wine.” While we were working on the second bottle, Bill asked Gunny how he can handle his *high-flying Physics colleagues*. He said: “I listen to them, but when I really need to understand something, I ask Peter”. When Peter returned from Switzerland, I had discovered that I might be able to handle an academic career. Yes, I did serve, for many years, as a Professor in the Department of Chemistry at Carnegie Mellon University in Pittsburgh.

After the Debrunners moved to Conifer, Colorado, Hilde and I visited them whenever we headed towards the West. Even better, we visited them many times in Morrison because our son Stefan lives in Golden, 10 miles from Morrison. Once Peter picked us up in Golden, and as we headed towards Morrison on E470, he mentioned that we will be there in 10 minutes “Peter, look at your speedometer, you have to make relativistic corrections”. I have met many wonderful colleagues in my academic career, but Peter had a special place in my heart. During my time in Urbana, we had Tim, a dog pointer, who critically assessed his friendship with people. I am sure about this: when Peter arrived in heaven, Tim was waiting for him at the gate, exuberantly wagging his tail.

CONCLUDING REMARKS

As mentioned in the *News-Gazette* article (on May 11, 2024), Peter Debrunner was described as “a bright, unassuming physicist with a balanced perspective, admired and respected by his colleagues.” Beyond his scientific accomplishments, he truly enjoyed the outdoors and devoted great care to cultivating his beautiful gardens of many kinds of plants making him, in spirit, something of a plant biologist as well.

Figure 8. A 2022 photograph of Peter Debrunner (left) with his son Chris (Christian Hans Debrunner), a coauthor of this paper; place: Denver Botanic Gardens, Denver, Colorado, USA. *Source:* Family Archives

In 1997, Peter and his wife moved to Colorado, where they lived a very happy life surrounded by their children and grandchildren. Figure 8 shows a 2022 photograph of Peter with one of us (Chris). Alongside his love of nature and family life, Peter remained deeply dedicated to physics and to the history of physics throughout the years. His intellectual curiosity and engagement never waned.

Peter Debrunner remains, and will continue to remain, in the hearts of many people around the world especially those of us who had the good fortune to know him personally, including all who participated in writing this tribute. Peter was a wonderful person, remembered fondly for his thoroughness, generosity, and willingness to help others in their scientific pursuits.

In Appendix 1, we provide a list of Peter Debrunner's additional selected key publications. These works should be read by anyone wishing to gain a fuller appreciation of his scientific contributions and the lasting impact he had on physics, biophysics, and the broader scientific community.

ACKNOWLEDGMENTS

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Appendix 1: Chronologically Arranged Selected Additional Publications of Peter G. Debrunner

The publications listed below are presented chronologically to illustrate the breadth and evolution of Peter G. Debrunner's scientific contributions beyond those cited in the main reference list.

1960s

Margulies, S., Debrunner, P. G., & Frauenfelder, H. (1963). Transmission and line broadening in the Mössbauer effect. II. *Nuclear Instruments and Methods, 21*, 217–231.

Morrison, R. J., Atac, M., Debrunner, P. G., & Frauenfelder, H. (1964). Mössbauer scattering of the 155 keV transition of ^{188}Os. *Physics Letters, 12*(1), 36–37.

Atac, M., Debrunner, P. G., & Frauenfelder, H. (1966). Mössbauer scattering in ^{195}Pt. *Physics Letters, 21*(6), 699–702.

1970s

Groves, J. L., Debrunner, P. G., & de Pasquali, G. (1970). Isomer shifts of the 145 keV transition in ^{141}Pr. *Physics Letters A, 33*(1), 51–52.

Potasek, M. J., Münck, E., Groves, J. L., & Debrunner, P. G. (1972). Observation of alignment in a quenched liquid crystal with the Mössbauer effect. *Chemical Physics Letters, 15*(1), 55–58.

Münck, E., Groves, J. L., Tumolillo, T. A., & Debrunner, P. G. (1973). Computer simulations of Mössbauer spectra for an effective spin S = 1/2 Hamiltonian. *Computer Physics Communications, 5*(3), 225–238.

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Winkler, H., Schulz, C. E., & Debrunner, P. G. (1979). Spin fluctuation rates from Mössbauer spectra of high-spin ferrous rubredoxin. *Physics Letters A*, *69*(5), 360–363.

1980s

Boso, B., Debrunner, P. G., Okamura, M. Y., & Feher, G. (1981). Mössbauer spectroscopy studies of photosynthetic reaction centers from *Rhodopseudomonas sphaeroides* R-26. *Biochimica et Biophysica Acta (Bioenergetics), 638*(1), 173–177.

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Boso, B., Debrunner, P. G., Wagner, G. C., & Inubushi, T. (1984). High-field, variable-temperature Mössbauer effect measurements on oxyhemeproteins. *Biochimica et Biophysica Acta*, *791*(2), 244–251.

Hendrich, M. P., & Debrunner, P. G. (1988). EPR spectra of quintet ferrous myoglobin and a model heme compound. *Journal of Magnetic Resonance*, *78*(1), 133–141.

Hendrich, M. P., & Debrunner, P. G. (1989). Integer-spin electron paramagnetic resonance of iron proteins. *Biophysical Journal*, *56*(3), 489–506.

1990s

Osmulski, P. A., Vossbrinck, C. R., Sampath, V., Caughey, W. S., & Debrunner, P. G. (1992). Spectroscopic studies of an insect hemoglobin from the backswimmer *Buenoa margaritacea*. *Biochemical and Biophysical Research Communications, 187*(2), 570–576.

Zhang, J. H., Kurz, D. M., Jr., Xia, Y. M., & Debrunner, P. G. (1992). Conversion of non-functional to functional iron following reconstitution of hemerythrin. *Biochimica et Biophysica Acta, 1122*(3), 293–298.

Vossbrinck, C. A., Osmulski, P. A., & Debrunner, P. G. (1993). Characterization of hemoglobin from the backswimmer *Buenoa margaritacea*. *Insect Biochemistry and Molecular Biology, 23*(3), 421–429.

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2000s

Serth-Guzzo, J. A., Turowska-Tyrk, I., Safo, M. K., Walker, F. A., Debrunner, P. G., & Scheidt, W. R. (2016). Mixed axial ligand iron(III) porphyrinate complexes. *Journal of Porphyrins and Phthalocyanines, 20*, 254–264.