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Foreword

This Festschrift of *Biophysical Chemistry* was designed to honor and to give pleasure to John Tileston Edsall, one of the founders of physical biochemistry, on the occasion of his 100th birthday. His death in June has cut off the possibility of his reading the contributions of his many students, collaborators and old friends, but not entirely. During his final 3 weeks he received manuscript copies of many of the articles contained in this issue. Reading them was beyond his capacity at this point, but he was aware of the magnitude of the effort on his behalf and of course was delighted to see the names of so many authors who were once close to him. Now, faced with the changed situation after John Edsall died, it surely would not be his liking if we were to convert this Festschrift to a document of sorrow and regret. For this reason, we have decided to leave it intact: it is positive in all its aspects.

The response of the bioscience community to our request for authors for this 'Edsall Issue' was immediate and large. The contributors range through tutees at Harvard, graduate students, postdoctoral fellows, senior visitors to John Edsall's laboratory, life-long friends and declared admirers. Their cumulative comments about him leave no doubt that we are dealing with a man who was truly special. He was a teacher, a researcher, a scientific writer, a creator and editor of journals, a statesman in the science community and its spokesman in critical situations when he felt that it was his personal responsibility to keep society moving along the high road, regardless of personal consequences [1]. This attitude manifested itself early in John Edsall's career: as undergraduate editor of *The Gad-Fly* (a reference to Socrates' characterization of himself as a provocative inquirer), he wrote that ''men in the conduct of their lives often flagrantly belie their professed beliefs, disclosing a profound gulf between their theory and practice'' [2]. He never allowed such a gulf to separate his statements and actions. He adhered to honesty and integrity in his work, modesty and compassion in his dealings with others, and in spite of a native shyness and reticence, he displayed a willingness to speak out publicly when he saw dangers to science or society.

One contribution to this issue puts all others in the shadows. Fortunately, we were given permission to include the personal reminiscences and reflections of the centenarian himself, written 30 years ago when he attained emeritus status [3] (Edsall).[1] We gratefully acknowledge our indebtedness to *Annual Reviews* for allowing us to include this enduring autobiographical chapter as a keystone for the other contributions.

John T. Edsall was born on 3 November, 1902. In this year F. Hofmeister first stated the idea that proteins are amino acids connected by amide-like bonds, the peptide bond. E. Fischer reached the same conclusion, introducing the words dipeptide, tripeptide,… polypeptide, and starting his program of oligopeptide synthesis; he also pointed out that synthetic amino acids are racemic mixtures and that natural amino acids are optically active, except for glycine. In the same year, J. Barcroft and J.S. Haldane quantitatively measured the uptake of O_2 and CO_2 by hemoglobin; 2 years earlier, W.B. Har-

[1] Note that references represented as last names in parentheses, e.g. (Edsall), refer to papers contained in this issue.

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dy had demonstrated that proteins are amphoteric and show characteristic isoelectric points. Tryptophan and proline had just been discovered; there were now 14 known natural amino acids, several of still unknown structure. W. Ostwald, one of the founders of physical chemistry (a field he first defined) did not believe in the existence of macromolecules; the majority shared his view of proteins as amorphous colloids. This was the background in a world that still had not coined the word biochemistry. Things have changed, not the least owing to the life-long ingenuity and hard work of eminent scientists of John Edsall's stature.

One Guest Editor of this Festschrift (RJ) never met John Edsall personally; he did see him once, from a safe distance, lost in stunned admiration for the real author of his favorite references [4,5]. They were unknown to his advisors in 1948, when he started as an undergraduate in botany. However, Hans Kautsky and Hermann Hartmann, the Professors of Inorganic and Physical Chemistry, had mentioned Edsall's name, surprising the freshman with the advice ''Switch to physics or chemistry if you want to ask and answer reasonable biological questions.'' So he switched, and a little later, the first suggested reading for his thesis work 'On the dielectric analog of streaming birefringence' brought him right back to Edsall [6,7]. Fortunately, at this point, biology reentered his life through the backdoor. No doubt, with their capacity to undergo denaturation–renaturation or dissociation–association reactions, biological macromolecules were more attractive than polystyrene or polyvinyl acetate. John Edsall with his talent as a researcher and teacher was the right person to convert a former votary of the *Scientia amabilis*. Considering the publication dates of the above-mentioned references, it is striking that they can still be recommended to undergraduate science majors. Their lifetime must be due to their adherence to the fundamental principles of thermodynamics and basic physics, which are timeless with the ''perfection and dignity of Gothic cathedrals'', to quote Lewis and Randall [8].

Strangely enough, the other Editor (JAS) also started out from dielectrics, in his case as a theoretician. On finishing his thesis in 1951, Walter Kauzmann advised him to learn some biochemistry. So he set off for a post-doctoral stay in the Biochemistry Department at the University of Utah. His only reading in 'biochemistry' had been Schrödinger's 'What is life' and a paper or two by Eyring and Kauzmann. Clearly, more background was desirable, so he bought a copy of Cohn and Edsall's *Proteins, Amino Acids and Peptides* [4], a book that he had seen above Kauzmann's desk. This was assiduously studied for a month or two before his arrival in Utah. When he told the department members about his 'background' in biochemistry, they either looked blank or laughed: biophysical chemistry was unknown or not considered to have anything to do with real biochemical problems. It required a new generation of biochemists, most of them inspired by readings in Cohn and Edsall, to generate the host of important physical studies that prevailed by the end of the 1950s. JAS first saw John Edsall at a Gordon Conference in 1957. As with RJ, he did not *meet* him. At this point of the editors' lives, anyone who had written an authoritative book was a superior being. The situation changed when JAS moved to the University of Oregon. In the early 1960s, the fine Oregon group of biophysicists was yet to arrive. To compensate for the lack of interactions, he asked for, and received, an invitation for a summer stay in the Edsall laboratory. During this rewarding association, Edsall provided the tools and theory for the Raman technique, awoke a budding interest in science history, and introduced him to the larger world of science by putting him in contact with a number of the outstanding scientists in the Harvard–MIT axis. On close contact Edsall was still imposing, but radiated warmth and support. His famous, low-pitched rumblings always seemed to indicate complete agreement with everything said, yet one often departed from conversations with different ideas than those at the start. At home, he and his wife emanated a serene New England charm, which was quite different from the 'Wild West' of Oregon.

Edsall was always ready to listen and advise on scientific and historical matters at meetings and via letters or phone calls. A recent point of consultation had to do with Mortimer L. Anson's studies of the spontaneous folding of hemoglobin in the late 1920s and early 1930s reviewed in [9], a sub-

ject that both editors find interesting and neglected. John at 97 was as sharp as ever. He knew Anson well and provided a great deal of material by phone and by hand-written letters, often composed very late at night. He still had his amazing memory for references.

In trying to give an impression of John Edsall's extraordinary achievements as a researcher, one is immediately struck by the wide range of scientific problems he has tackled in many areas of biochemistry, starting from the physiology of the tortoise, oxygen binding to hemoglobin, muscle proteins, physical chemistry of amino acids, peptides and proteins, plasma fractionation, and ending with the structure–function relation of enzymes and other proteins. Fortunately, we can refer to his own recollections [3,10–12] and to many of the contributors to this Festschrift who generally present his and their own related research topics with more familiarity and authority than we can claim. It may be worthwhile, however, to present a short survey of the topics in one place.

As a prelude we dwell briefly on the path of learning of two exceptional students in the 1920s as compared with the highly organized and regulated curricula of today. Here is the way John Edsall describes how his friend Jeffries Wyman qualified as a graduate student at the age of 21, after 3 years at Harvard College:

> He graduated with highest honours in philosophy, and high honours in biology; his enduring interest in mathematics and physics also developed during those years, and was to influence profoundly the character of his future work in biophysical chemistry. ([11], p.103)

Looking from the other side, the same picture emerges from Jeffries Wyman's letter to John Edsall on the occasion of his 80th birthday:

> The world of our youth…goes back to the days when we were both undergraduates at Harvard. You were studying chemistry with an eye to the Medical School; I was concentrating in Philosophy…but with my mind turning more and more to biology…I remember your enthusiasm at Henderson's course on the history of science…Do you recall the little discussion group which used to meet once or twice a month in one or the other of our rooms?…For each meeting we would invite some glamorous member of the faculty to come and talk to us about his latest interests, and I cannot recall ever being refused. In June 1924 we set out together for Europe. We were to study biochemistry under Hopkins in Cambridge; but, before going there, we had plans to spend the summer in Graz, learning German…Armed with letters from your father, we were well received by Otto Loewi and Professor Pregl, both Nobel laureates, which impressed us greatly…In Cambridge we were enrolled in the course of Biochemistry…before the end of the term I had decided that I wanted to work with A.V. Hill. ([11], p. 191 f)

In those days it was the broad training of the brain and mind that was foremost, and not adherence to strict curricula.

The story of the intertwined careers of these two exceptional scientists and human beings began with their university days and their Wanderjahre and continued for the rest of their long lives. Edsall's two articles on their relationship make rewarding reading [13,11].

After this ''visit to the platonic world of our student days'' (as Jeffries Wyman put it in his letter on the occasion of John Edsall's 80th birthday [11]), we return to the survey of Edsall's scientific achievements. After returning from Cambridge to Harvard, his work started with the biophysical investigation of muscle proteins such as actomyosin, at this time an extremely tedious system owing to the high viscosity and instability of the solutions. Together with Alexander L. von Muralt [6,14], Edsall initiated flow birefringence as a biophysical tool and discovered that actomyosin consisted of very long molecules, thereby demonstrating the existence of a soluble fibrous-protein complex and paving the way for muscle research at the molecular level. Later, this work was extended to fibrin and other fibrous molecules and to related methods of orientation. such as an electric field, as developed by J.L. Oncley, one of Edsall's earliest collaborators. A number of contributions in the present volume give clear evidence that this early work opened a new vista in the study of muscle and the way it works (Gurd & Richards, Rich, Lowey, M. & K. Bárány, Doolittle).

Through the 1930s, John Edsall and Edwin Cohn became deeply involved in studies of the physical and chemical properties of a wide variety of ampholytes, especially amino acids and peptides. Spectroscopic measurements culminated in the pioneer use of Raman spectroscopy to inves-

tigate the ionization properties of amino acids, removing all doubt that neutral amino acids were zwitterions by the direct observation of the state of ionization of the amino and carboxyl groups. Only after the invention of NMR and cloned peptides containing ^{15}N atoms was it possible to study macromolecular systems in the same way. These studies were soon extended to oligopeptides. In summarizing the behavior of these models, it became clear that the interpretation of protein titration curves could be understood from the titration properties of the amino-acid side chains coupled with electrostatic interaction theory of Linderstrøm–Lang [4,15]. This is one of several instances where the physicochemical nature of the building blocks is an essential basis for the understanding of proteins [3,10,16].

In the late 1930s, in close collaboration with George Scatchard and John G. Kirkwood, John Edsall's interest switched to the solvation of ionic, polar and non-polar molecules. It turned out that the hydration of non-polar groups is associated with an anomalously high change in heat capacity, as well as large negative enthalpies and entropies [17]. These are the typical attributes later associated with the hydrophobic interaction by Henry S. Frank [18,19] and Walter Kauzmann [20] (Kyte). Evidently, the time was not yet ripe; if the work had been better known after World War II, our knowledge of the stabilizing forces of proteins would have been significantly accelerated. He returned to the subject later in two reviews, 'Water and its biological significance' [5] and 'The binding of water by proteins' [7]. Both continue to represent not only exemplary expositions of one of the most significant problems in physical biochemistry, but also gems of scientific writing. The hydration problem has not been solved in a quantitative manner to this day (Henn & Kauzmann, Beck et al.).

Fundamental work at Harvard in these early days of physical biochemistry was focused on additivity properties of peptides and proteins, i.e. the question of whether and to what extent proteins reflect the properties of their constituent amino acids. Thermodynamic additivity has come a long way from its origins in simple physical properties, such as volume, heat capacity, etc. For peptides and proteins, it started from the theoretical and experimental work summarized in Cohn and Edsall's monograph [4]; it now extends to advanced group-additivity schemes (Hedwig & Hinz), as well as to the effects of mutations on the free energy of stabilization of proteins (Gassner et al.).

Once enzymes were shown to be proteins that bind specific ligands and catalyze their transformations in consecutive linear or cyclic reaction paths, the question of the structural determinants of ligand binding and the mechanisms which govern their regulation became a central issue in physical biochemistry. Starting from the above protonation–deprotonation work, Edsall developed a long-standing interest in *ligand binding*, especially in the case of hemoglobin and metallo-proteins. In the present Festschrift, a number of contributions deal with aspects of this area of his research, beautifully illustrating the treasures that were hidden in this goldmine (Alberty, Beck et al., Eaton, H. Eisenberg, Fanghänel & Fischer, Henn & Kauzmann, Huang et al., Katchalski-Katzir et al., Klotz, Krem & di Cera, Tanford, Tsai et al., van Holde); he himself contributed to this field as late as his 84th year (Edelstein).

In the 1940s, the pioneering work of Edwin Cohn and John Edsall and their co-workers had resulted in some clear correlations between the solubility and structure of the amino acids, peptides and proteins [4,21]. Having acquired at least the beginnings of a rational basis for the fractionation of proteins in complex mixtures, they had the potential to transform this art into a practical science [4,21]. This became an imperative with the outbreak of World War II, with its anticipated need for the large-scale production of blood-plasma proteins for use in medicine and surgery [3,22,23]. Edwin Cohn reorganized the laboratory ''on what was essentially a war footing'' even before the US entry in 1941, with the result that our Harvard scholar was dislodged from his ivory tower and immersed fully in the war effort. It was Cohn who had the vision and the

> …driving and aggressive energy to get the necessary Government support, to bring together large groups of scientists and clinicians working in a common cause, and to enlist seven major pharmaceutical firms in the industrial produc-

tion of fractionation products by methods worked out in the Pilot Plant at Harvard Medical School. [3]

In addition to Cohn and Edsall, J.L. Oncley, L.E. Strong and W.L. Hughes were central in coordinating and directing these complicated operations [3,22–25]. As part of the war effort, the plasma project had an enormous impact on the welfare of the injured, but it also established a number of techniques for the isolation and study of proteins in their 'authentic native state' that were carried directly into mainstream research after the war.

For some time, basic work on proteins remained closely related to the work on blood plasma, focusing especially on serum albumin, immunoglobulin and lipoproteins (Oncley, Weers et al.). Important issues were the state of association, on the one hand, and effects of charge and ionic strength, on the other. Making use of light scattering as a new method to monitor instantaneously the rates and equilibria of association, the dimerization reaction of mercaptalbumin (with one free sulfhydryl group per molecule) was used as a model for protein association [25,26].

During the last decade of his research activities, until he closed his Harvard laboratory in 1971, John Edsall devoted himself particularly to carbonic anhydrase, that remarkable enzyme in the red blood cell that speeds the uptake of CO_2 into the blood from the tissues, and similarly speeds the discharge of CO_2 from the blood into the lungs; its turnover still holds the world record in terms of its molar activity relative to any known enzyme. In the present volume, R.G. Khalifah in his report on the state of the art confirms John Edsall's conclusion in 1966 [10]:

JTE: after years of hard work…we still have a very long way to go before we understand the function of this enzyme.

RGK: despite enormous progress since Edsall's retirement…the structure–function relationship remains as elusive today as when Edsall first considered these questions.

The same conclusion holds true for most metabolic reactions: for the many thousands of enzymes known today we have no more than a meagerly few mechanisms.

For most scientists, when the 'laboratory is closed', the story ends. Not with John Edsall, because there are other aspects of his life, of no less significance for the scientific community, which are possibly even more important. One facet has already been mentioned: his drive to understand and to describe the physical and chemical fundamentals of biology as an advisor, teacher and scientific writer. Edsall has authored many books and reviews, which have influenced most older and many younger scientists. *Proteins, Amino Acids and Peptides* [4], or 'Cohn and Edsall', as it is usually called, was written mostly by Edsall according to his own statement [3]. It has been a constant companion for many scientists over the years. It is a foundation document for the field of physical biochemistry and a treasury of pre-war investigations. Many of the techniques that are discussed there have had to make room for newer ones: NMR, dynamic light scattering and fluorescence, molecular relaxation and depolarization dynamics, mass spectrometry, circular dichroism, modern chromatography, etc., but the *molecular physics* behind most of these newer methods goes back to the concepts to be found in this book and Edsall's other writings. His other books have general titles, such as *Biophysical Chemistry* [5] and *Biothermodynamics* [27]. By their own account, *Biophysical Chemistry* was the initial stage of learning of biophysical chemistry for many of the authors in this current issue. His long and authoritative reviews include 'Light scattering' [28], 'Some general characteristics of amino acids and peptides' [29], 'Plasma proteins and their fractionation' [23] and 'The size, shape and hydration of protein molecules' [7]. The last of these probably still provides the best initiation for a biochemist into the physics of transport and the rotational properties of large molecules. Equally important in a more general sense are his accounts of the history of biochemistry over the 100 years of his life [3,10,12], especially the story of his and Jeffries Wyman's 'interacting lives' [11]. Fortunately, in this dedicatory volume a number of former students and post-doctoral researchers present lively accounts of John Edsall's devotion and loyalty as a tutor, teacher and mentor (M. and K. Bárány, Eaton, D. Eisenberg, Gurd, Huberman, Karplus,

Katchalski-Katzir, Kay, Khalifah, Lowey, Richards, Rossmann). They speak for themselves and for many others who enthusiastically welcomed the idea of the present Festschrift.

Another aspect of John Edsall's life was his activity as an editor. As Editor-in-Chief of the *Journal of Biological Chemistry* from 1958 to 1968, he guided the journal to its leading position in the field. To quote David Eisenberg [1]:

> …he jacked up standards for authors, reviewers and editors, and read and often revised every letter that went out to authors. His ability to demand and get publications of high quality must have been related both to his colossal diligence and to what Wyman has termed his '*impression of unbounded benevolence*'. This impression stays with everyone who ever dealt with him: his imposing, serious, yet kindly manner somehow conveys that he is seeking the truth and that—within this unvarying principle—he has your best interests at heart. He always paid special attention to rejection letters, and knew how to soften the blow.

Editors, especially of high-impact journals, please take notice. Another favorite of John Edsall's editorial activities was the review series *Advances in Protein Chemistry*. His involvement as a co-editor for close to 50 years was crucial in guaranteeing high standards from the very beginning to this day.

A further area, or perhaps better, arena, in which John Edsall invested energy and time in the second half of his life, was politics. Before Hiroshima and Nagasaki, Edsall's ''…work in science and his concern with politics ran in different channels; after 1945, that was no longer possible'' [3]. His aforementioned *unbounded benevolence*, his proven integrity and his increasing eminence as a scientist permitted him to become the spokesman in a wide range of political issues, mainly connected with scientific freedom and the social responsibility of scientists. He did so with admirable and exemplary courage, especially during the fearful McCarthy era of the mid-1950s. For further details the reader is referred to David Eisenberg's Editorial on the occasion of John Edsalls 90th birthday [1], the personal note of Cyril Kay (Kay), and especially to the contribution at the end of this Festschrift written by Howard Schachman, one of John Edsall's true successors in the domain of scientific ethics and policy (Schachman). A few sentences, taken from a lecture given by John Edsall late in his career [10], suffice to characterize the philosophy behind his life-long endeavors:

> The advances of biochemistry may already have found their way into the kindergartens. Nevertheless, what I think we lack today (*1966*) is perspective on the broader meaning of the discoveries that are being made so fast. Indeed the problem is formidable—the job of digesting the facts is so colossal that the time left for reflecting on them is limited…Certainly the achievements in protein chemistry are immense; 20 years ago I would hardly have believed that such depth of knowledge could be achieved in my lifetime…In an era filled with war, turmoil, and atrocities, the great achievements of modern fundamental science are among the relatively few things in which mankind can take unalloyed pride. However, I cannot stop here. Knowledge translated into action is power, and in our day scientific knowledge is being translated into action with a speed unparalleled in history. The biochemistry of today will be the clinical medicine of tomorrow. Will our clinicians be prepared for the new powers and the new responsibilities that will be in their hands?…The penetration of biochemistry and genetics into a central role in medicine will raise formidable problems of ethics and policy. To meet them adequately will require forethought, which has often been lacking in the past. May the physicians of the future be foresighted in anticipating and facing the powers and responsibilities that the biochemists and geneticists bequeath to them.

Let us take this as a legacy. Finally, we and all those who contributed to this volume know that scientists worldwide join us in commemorating John T. Edsall on his contributions to the biosciences and to the international community of scientists as a scholar, mentor, writer, editor and statesman.

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