

THE AHARON KATCHALSKY MEMORIAL LECTURE

“LIFE, FLOW AND DEFORMATION”

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AHARON KATZIR-KATCHALSKY was an outstanding scientist and humanist, whose objective contributions to our knowledge and understanding had long before his tragic death assured him a place in the top rank of this century. The world can ill afford to lose such minds.

Not for this alone, however, is he being missed and mourned. After all, these of his contributions stand and will remain. He is being missed and mourned, by hundreds of people all over the world, for something much more personal and precious, something which each had received from him, at some encounter, at a seminar, at a public lecture, at a private discussion, something of the excitement and wonder of the intellectual pursuit which he could so magically arouse and instil.

There was no occasion which Aharon Katzir failed to improve with his mind and words. Whenever he talked he aroused our intellectual curiosity, stimulated our thoughts, brought forth our interest. Activities which seemed commonplace, subjects apparently banal, he could make engage our minds. He left his audience refreshed, mentally invigorated, newly encouraged in their work, revitalized in their interest.

It is Aharon Katzir who should have delivered the Plenary Lecture he anticipated to give today on biological membranes and biorheology. It is with many sad thoughts and in deep sorrow that I am speaking about his work in his place.

Biorheology, movement and life had always fascinated him and the field stood close to the center of his research interests.

While life is motion, the absence of motion—thermodynamic equilibrium—is death. The further we are from equilibrium, the younger we are, the more alive, the fuller of motion. Living processes should be far from equilibrium, they should override their environment, interact strongly with it, be in command. Biorheology deals with living processes, it deals with the fluid mechanical aspects of life. We could paraphrase biorheology as life, flow and deformation.

In pursuing these aims the biorheologist tends to go in two directions. On the one hand, from a macroscopic point of view, he wants to understand the principles and forces which produce motion; on the other, from the microscopic point of view, he looks for interpretation in the molecular dynamics and structure of the system. This duality of approach was not always realised. The early chemists and biochemists who established the macromolecular, polymeric nature of most biological structural and chemically specific material did not at first see this as a world in motion. They were writing chemical formulas on their paper and for them these structures did not move.

It was left to Werner Kuhn to establish and show that, conformationally, macromolecules

are in turmoil and that mechanical response and motion on the macroscopic scale are the outcome of macromolecular motions acting in unison over structurally related and correlated regions. The changes in length of a striated muscle, for example, are related to dedicated shifts in alignment between macromolecular structures.

Of importance to the biorheologist is not only the fact of moving but the “how”, the biorheological equation of state. This too is governed by macromolecular properties. We interact effectively with our environment not only because of our muscles, but because these are linked to parts of our body, which, due to their macromolecular composition, deform and respond in a suitable fashion.

In this field of molecular biorheology Aharon Katzir's name is very closely linked to that of Werner Kuhn. Together they, for the first time, developed an understanding of the behavior of charged macromolecules, polyelectrolytes [3, 6, 7]. Most biopolymers are indeed polyelectrolytes. In the case of polyelectrolytes, as the electrolytic environment is changed, large conformational transitions occur, and they developed the idea that muscular contraction was due to such interactions. From these beginnings not only the field of polyelectrolyte chemistry [2–5, 8, 9, 14–19, 24, 26, 27, 29, 30, 32–36, 38–41, 43, 45, 46, 48, 50, 51, 57, 59, 61, 62, 65, 69, 73, 74, 76, 95, 99, 102, 111, 112, 114, 121, 133, 138, 147], but the principles of mechanochemistry [17, 47, 49, 56, 58, 80, 105, 107, 110, 137, 139, 142, 146], the direct conversion of chemical energy into mechanical energy, was developed.

The emphasis first placed on polyelectrolytes in relation to muscular contraction was soon dropped since Katchalsky rapidly realised that many other reactions involving the turnover, say, of secondary and covalent bonds could produce conformational changes just as well, if not more effectively, than electrolytic interaction. The response time of such reactions, in particular, was much more in keeping with the rates of muscular contraction than those of the diffusion controlled electrolytic interactions.

And so a new, fundamental question arose. How is the coupling of a chemical reaction and a flow to be described. On the basis of what principles can such a problem be discussed. The field of irreversible thermodynamics seemed to supply the answer, but, at this point, was still very young in its development, its realm of application not fully explored and often misunderstood. Aharon Katzir entered the field and steeped himself in its philosophy. He not only contributed to its fundamental arsenal of formulas, he lifted it out of its abstract inaccessibility, applied it effectively to biological problems and, in particular, to the functioning of biological membranes [71, 82, 87–89, 96–98, 100, 116, 120, 122–128, 131–133, 135, 140, 143, 150, 157].

In its early stages this was a quest for the formalisms into which to cast and then analyse results. To a major extent, however, this was a search for mechanisms, for a specification of the molecular processes, by which directed transport can be achieved out of, *a-priori*, undirected chemical reactions. The idea of a specific macromolecular conformational change following the chemical reaction step suggests itself. This, if binding occurs at sites which are moved, provides the basis of facilitated transport of the so-called macromolecular carrier mitigated transport mechanism so extensively discussed over the last years, unfortunately, so far, with little direct support.

A flaw in approach made its appearance. For the analysis by irreversible thermodynamics to be applicable, the process has to occur close to equilibrium and life processes, as we have already stressed, predominantly occur far away from this condition. For most processes hence the principles of irreversible thermodynamics do not apply and the search for new principles was on, with the disturbing thought that, in this quest, the requirements of ordin-

ary thermodynamics, equilibrium and non-equilibrium, may be of very little help [134, 148–150, 156].

Even the concept of a macroscopic system may have to be modified and re-introduced in such a way as to allow for the obvious heterogeneity of a living system, operating far from equilibrium, incorporating gradients and effecting mechanical and other transport. For this purpose, over the last years, Aharon Katzir began to develop an approach which he called network thermodynamics, or the thermodynamics of flow [136, 149, 150, 152, 157, 159, 163, 164].

In practice, it is an approach borrowed from the electrical engineer, who, by sending electrons to move and oscillate along metallic paths, achieves the purposes of energy conversion and mechanical function. The electrical engineer builds up networks of resistances, capacitors, inductances, each uniform in itself, but making sharp transitions at junctions. Aharon Katzir proposed looking upon chemical and biological systems in a similar way. Reduce large parts of them, according to function, into “uniform” units which, while suppressing much of the structure, retain those elements of it which are relevant to the process under consideration. Between and over such units, which combine into a network, chemical and mechanical transfer takes place.

It is clear that each network description, at the same time, establishes a pattern—characteristic of the situation to be described—and that stationary gradients will be established in this pattern for given fluxes through it. The system is operating in a stationary state superposed on an established structure.

Now we can visualize two cases: (1) We are in the realm of irreversible thermodynamics, close to equilibrium. Under those circumstances the network pattern is that characteristic of equilibrium and, in principle, is uniquely established, since it has to satisfy the thermodynamic criteria of stability. Note the severe restriction implied. Since equilibrium is well defined, the pattern is unique. Major changes in the environment are required to upset it. The living world is much more kaleidoscopic. Our experience teaches us that it is enough to alter the input of energy, sometimes only by slight amounts, in order to upset and change the pattern.

Hence we turn to the second case: (2) We are operating far from equilibrium. New patterns can spontaneously arise. A state of high stability, one pattern, has been gradually pushed to the brink, and the system passes rapidly through a set of unstable states into another state of stability, into a new pattern. These states of high stability are stable stationary states existing far from equilibrium. They are stable since the pattern and the topography of the mechanical and chemical gradients is maintained over a range of energy flux changes without destroying the structure. But not indefinitely so. The pattern can be toppled by going outside the stable range in either way [149].

Model situations can be created in the laboratory which behave in this way, and theoretical models can be derived simulating these properties. The picture is also intuitively acceptable and can be extrapolated to much wider situations. Aharon Katzir, for example, saw in it wide implications for society and social organization in general. Unfortunately very little is known about the systematics of these states, what principles govern their existence, what determines their relative stability under some circumstances and makes them unstable under others.

These are good, but in part philosophical, questions. The network thermodynamics on which Aharon Katzir was working at the time of his death, for example, does not depend on its application on their solution. Building the network already implies acceptance of the

pattern and of the nature of the fluxes. The analysis then tells us how such a system will work and operate, and, by comparison with experiment, whether the description is adequate. The problem here is settling on the pattern, deciding on what network to construct, what to put in and what to leave out. Once this is done the approach gives us an integrated view of a complex system and a powerful tool for its analysis.

This will have wide-ranging implications for biorheologists. We have been concerned, in the past, mainly with characterizing some of the components of a living pattern, those in particular which control, or are subject to, mechanical flow and deformation. The wider questions which have been raised, however, are of no lesser significance. The path pioneered by Aharon Katzir will become of increasing importance to us all.

REFERENCES

- [1] KATCHALSKY, A. and WECHSLER, H. *J. Polymer Sci.* **1**, 229, 1946.
- [2] KATCHALSKY, A. and SPITNIK, P. *J. Polymer Sci.* **2**, 432, 1947.
- [3] KUHN, W., KÜNZLE, O. and KATCHALSKY, A. *Helv. Chim. Acta* **31**, 1994, 1948.
- [4] KATCHALSKY, A. and GILLIS, J. *Rec. Trav. Chim. Pays-Bas* **68**, 879, 1949.
- [5] KATCHALSKY, A. *Experientia* **V/8**, 319, 1949.
- [6] KUHN, W., HARGITAY, B., KATCHALSKY, A. and EISENBERG, H. *Nature, Lond.* **165**, 514, 1950.
- [7] KATCHALSKY, A., KÜNZLE, O. and KUHN, W. *J. Polymer Sci.* **5**, 283, 1950.
- [8] KATCHALSKY, A. and EISENBERG, H. *Nature, Lond.* **166**, 267, 1950.
- [9] KATCHALSKY, A. and EISENBERG, H. *J. Polymer Sci.* **6**, 145, 1951.
- [10] KATCHALSKY, A. and BLAUER, G. *Bull. Res. Council. Israel* **1**, 138, 1951.
- [11] JOEL, C. A., KATCHALSKY, A., KEDEM, O. and STERNBERG, N. (Shavit), *Electrophoretic Measurements of Normal and Pathological Human Spermatozoa*, Vol. 7, *Annali di Ostetricia e Ginecologia*, Milano, 1951.
- [12] KATCHALSKY, A. and STERNBERG, N. *Bull. Res. Council. Israel* **1**, 111, 1951.
- [13] FREI, E. H. and KATCHALSKY, A. *Bull. Res. Council. Israel* **1**, 113, 1951.
- [14] FUOSS, R. M., KATCHALSKY, A. and LIFSON, S. *Proc. Natl. Acad. Sci.* **37**, 579, 1951.
- [15] KATCHALSKY, A., EISENBERG, H. and LIFSON, S. *Bull. Res. Council. Israel* **1**, 116, 1951.
- [16] KATCHALSKY, A. and MILLER, I. R. *J. Phys. Coll. Chem.* **55**, 1182, 1951.
- [17] KATCHALSKY, A. *J. Polymer Sci.* **7**, 393, 1951.
- [18] KATCHALSKY, A., LIFSON, S. and EISENBERG, H. *J. Polymer Sci.* **7**, 571, 1951.
- [19] KATCHALSKY, A., BLAUER, G. *Trans. Faraday Soc.* **47**, 1360, 1951.
- [20] KATCHALSKY, A., EISENBERG, H. and LIFSON, S. *J. Am. Chem. Soc.* **73**, 5889, 1951.
- [21] JOEL, C. A., KATCHALSKY, A., KEDEM, O. and STERNBERG, N. *Experientia* **7**, 274, 1951.
- [22] SALPETER, M., STERNBERG, N. and KATCHALSKY, A. *N.Y. State Dental J.* **18**, 476, 1952.
- [23] KATCHALSKY, A. and SHARON, N. *Bull. Res. Council. Israel* **2**, 317, 1952.
- [24] LIFSON, S. and KATCHALSKY, A. *Bull. Res. Council. Israel* **2**, 302, 1952.
- [25] KATCHALSKY, A. and PAECHT, M. *Bull. Res. Council. Israel* **2**, 312, 1952.
- [26] MILLER, I. R. and KATCHALSKY, A. *Bull. Res. Council. Israel* **2**, 300, 1952.
- [27] KATCHALSKY, A. and SHAVIT, N. (Sternberg) *Bull. Res. Council. Israel* **2**, 298, 1952.
- [28] SHARON, N. and KATCHALSKY, A. *Analyt. Chem.* **24**, 1509, 1952.
- [29] KATCHALSKY, A. and MICHAELI, I. *Bull. Res. Council. Israel* **2**, 295, 1952.
- [30] KATCHALSKY, A. and LIFSON, S. *J. Polymer Sci.* **11**, 409, 1953.
- [31] KATCHALSKY, A. and SHARON, N. *Acta* **10**, 290, 1953.
- [32] KATCHALSKY, A. and SHARON, N. *Interaction of Polymeric Bases with Aldoses*. 13th Int. Cong. IUPAC, Stockholm, 1953.
- [33] KATCHALSKY, A. and STERNBERG, N. *J. Polymer Sci.* **10**, 253, 1953.
- [34] KATCHALSKY, A. *Endeavour* **12**, 46, 1953.
- [35] KUHN, W., KÜNZLE, O. and KATCHALSKY, A. *Bull. Soc. Chim. Begle* **57**, 421, 1948.
- [36] KATCHALSKY, A. *J. Polymer Sci.* **12**, 159, 1954.
- [37] KATCHALSKY, A. and FEITELSON, J. *J. Polymer Sci.* **13**, 385, 1954.
- [38] KATCHALSKY, A., SHAVIT, N. and EISENBERG, H. *J. Polymer Sci.* **13**, 69, 1954.
- [39] KATCHALSKY, A. and MILLER, I. R. *J. Polymer Sci.* **13**, 57, 1954.
- [40] LIFSON, S. and KATCHALSKY, A. *J. Polymer Sci.* **13**, 43, 1954.
- [41] KATCHALSKY, A., COOPER, R. E., UPADHYAY, Y. and WASSERMANN, A. *J. Chem. Soc.* 5198, 1961.
- [42] PAECHT, M. and KATCHALSKY, A. *J. Am. Chem. Soc.* **76**, 6197, 1954.

- [43] KATCHALSKY, A. Polyelectrolyte Gels, *Prog. Biophys. Biophysical Chem.* Vol. 4, p. 1. Pergamon Press, Oxford, 1954.
- [44] KATCHALSKY, A. and PAECHT, M. *J. Am. Chem. Soc.* **76**, 6042, 1954.
- [45] KATCHALSKY, A. and SPITNIK, P. Interactions Entre Polyelectrolytes. Colloques Internationaux du Centre National de la Recherche Scientifique, Vol. 57, Strasbourg, Octobre, 1954.
- [46] SPITNIK, P., NEVO, A. and KATCHALSKY, A. *Bull. Res. Council. Israel* **4**, 318, 1954.
- [47] KATCHALSKY, A. and ZWICK, M. *Bull. Res. Council. Israel* **4**, 319, 1954.
- [48] NEVO, A., DE VRIES, A. and KATCHALSKY, A. *Bull. Res. Council. Israel* **4**, 106, 1954.
- [49] KATCHALSKY, A. and LIFSON, S. *Scientific American* **190**, 72, 1954.
- [50] KATCHALSKY, A. and MICHAELI, I. *J. Polymer Sci.* **15**, 69, 1955.
- [51] NEVO, A., DE VRIES, A. and KATCHALSKY, A. *Biochim. Biophys. Acta* **17**, 536, 1955.
- [52] ELIASSAF, J., SILBERBERG, A. and KATCHALSKY, A. *Nature, Lond.* **176**, 1119, 1955.
- [53] ALTERMAN, Z. and KATCHALSKY, A. *Bull. Res. Council. Israel* **5A**, 46, 1955.
- [54] SILBERBERG, A., ELIASSAF, J. and KATCHALSKY, A. Shear Hardening of Aqueous Polymethacrylic Acid Solutions. *La Ricerca Scientifica* **25**, 2, 1955.
- [55] VOFSI, D. and KATCHALSKY, A. Kinetics of Polymerization of Nitro Ethylene. *La Ricerca Scientifica* **25**, 3, 1955.
- [56] KATCHALSKY, A. and ZWICK, M. *J. Polymer Sci.* **16**, 221, 1955.
- [57] KEDEM, O. and KATCHALSKY, A. *J. Polymer Sci.* **15**, 321, 1955.
- [58] MICHAELI, I., ZWICK, M. and KATCHALSKY, A. *Bull. Res. Council. Israel* **6A**, 172, 1957.
- [59] LOEWENSTEIN, A., MILLER, I. R. and KATCHALSKY, A. *Bull. Res. Council. Israel* **6A**, 173, 1957.
- [60] SILBERBERG, A., ELIASSAF, J. and KATCHALSKY, A. *J. Polymer Sci.* **23**, 259, 1957.
- [61] KATCHALSKY, A., MAZUR, J. and SPITNIK, P. *J. Polymer Sci.* **23**, 513, 1957.
- [62] MICHAELI, I. and KATCHALSKY, A. *J. Polymer Sci.* **23**, 683, 1957.
- [63] KIRSCHMANN, CH., ROSENHECK, K. and ALTERMANN, B. *J. Polymer Sci.* **23**, 955, 1957.
- [64] TOOR, M., KATCHALSKY, A., AGMON, J. and ALLALOUF, D. *Lancet* **1270**, 1957.
- [65] MILLER, I. R. and KATCHALSKY, A. Adsorption of Polyampholytes on Water Surfaces. Gas/Liquid and Liquid/Liquid Interface. Proc. 2nd Int. Cong. of Surface Activity, p. 159. Butterworths, London, 1957.
- [66] VOFSI, D. and KATCHALSKY, A. *J. Polymer Sci.* **26**, 127, 1957.
- [67] DAMIEL, A. and KATCHALSKY, A. *Bull. Res. Council. Israel* **7A**, 90, 1958.
- [68] KATCHALSKY, A. and BREUER, M. *Bull. Res. Council. Israel* **7A**, 114, 1958.
- [69] MILLER, I. R. and KATCHALSKY, A. *Bull. Res. Council. Israel* **7A**, 225, 1958.
- [70] ROSENHECK, K. and KATCHALSKY, A. *J. Polymer Sci.* **32**, 511, 1958.
- [71] KEDEM, O. and KATCHALSKY, A. *Biochim. Biophys. Acta* **27**, 229, 1958.
- [72] ALTERMAN, Z., LITTAUER, U. Z. and KATCHALSKY, A. *Bull. Res. Council. Israel* **7A**, 165, 1958.
- [73] KIRSCHMANN, CH., KATCHALSKY, A. and DE VRIES, A. *Arch. Biochem. Biophys.* **80**, 140, 1959.
- [74] KATCHALSKY, A., DANON, D., NEVO, A. and DE VRIES, A. *Biochim. Biophys. Acta* **33**, 120, 1959.
- [75] BLAUER, G., SHENBLAT, M. and KATCHALSKY, A. *J. Polymer Sci.* **38**, 189, 1959.
- [76] MAZUR, J., SILBERBERG, A. and KATCHALSKY, A. *J. Polymer Sci.* **35**, 43, 1959.
- [77] PAECHT, M. and KATCHALSKY, A. *Nature, Lond.* **184**, 1489, 1959.
- [78] KATCHALSKY, A., ROSENZWEIG, B., AGMON, J. and TOOR, M. *Bull. Res. Council. Israel* **8E**, 18, 1959.
- [79] KLIBANSKY, C., DE VRIES, A. and KATCHALSKY, A. *Pathologie-Biologie* **8**, 2005, 1960.
- [80] KATCHALSKY, A., LIFSON, S., MICHAELI, I. and ZWICK, M. Elementary Mechano-chemical Processes. Contractile Polymers, p.1. Pergamon Press, London, 1960.
- [81] KATCHALSKY, A., KEDEM, O., KLIBANSKY, C. and DE VRIES, A. Rheological Consideration of the Haemolysing Red Blood Cell. *Flow Properties of Blood*, p. 155. Pergamon Press, London, 1960.
- [82] OPLATKA, A., MICHAELI, I. and KATCHALSKY, A. *J. Polymer Sci.* **46**, 365, 1960.
- [83] MICHAELI, I., JESELSON, M. and KATZIR, A. *Bull. Res. Council. Israel* **9A**, 230, 1960.
- [84] TOOR, M., KATCHALSKY, A., AGMON, J. and ALLALOUF, D. *Circulation* **22**, 265, 1960.
- [85] GRODZINSKI, J., KATCHALSKY, A. and VOFSI, D. *Bull. Res. Council. Israel* **9A**, 228, 1960.
- [86] GRODZINSKY, J., KATCHALSKY, A. and VOFSI, D. *Die Makromolekulare Chemie* **44**, 591, 1961.
- [87] KEDEM, O. and KATCHALSKY, A. *J. Gen. Physiology* **45**, 143, 1961.
- [88] KATCHALSKY, A. Membrane Permeability and the Thermodynamics of Irreversible Processes. *Membrane Transport and Metabolism*, p. 69. Prague, 1961.
- [89] KATCHALSKY, A. and KEDEM, O. *Biophys. J.* **2**, 53, 1962.
- [90] SAXL, H., MARIKOVSKY, Y., DANON, D. and KATCHALSKY, A. *Med. exp.* **6**, 54, 1962.
- [91] TOOR, M., KATZIR, A. and AGMON, J. *Dapim Refuim* **21**, 2, 1962.
- [92] TOOR, M., MASSRY, S., KATZ, I., AGMON, J. and KATCHALSKY, A. *Israel J. Exp. Med.* **11**, 64, 1963.
- [93] PAECHT, M. and KATCHALSKY, A. *Israel J. Chem.* **1**, 483, 1963.
- [94] KATZIR, A. *Bull. Res. Council. Israel* **11G**, 180, 1962.
- [95] KATCHALSKY, A. and ALEXANDROWICZ, Z. *J. of Polymer Sci. A-1*, 2093, 1963.
- [96] KEDEM, O. and KATCHALSKY, A. *Trans. Farad. Soc.* **59**, 1918, 1963.

- [97] KEDEM, O. and KATCHALSKY, A. *Trans. Farad. Soc.* **59**, 1931, 1963.
- [98] KEDEM, O. and KATCHALSKY, A. *Trans. Farad. Soc.* **59**, 1941, 1963.
- [99] ALEXANDROWICZ, Z. and KATCHALSKY, A. *J. Polymer Sci. Part A*, **1**, 3231, 1963.
- [100] KATCHALSKY, A. Nonequilibrium Thermodynamics. *International Science and Technology*, p. 43, October, 1963.
- [101] GINZBURG, B. Z. and KATCHALSKY, A. *J. Gen. Physiol.* **47**, 403, 1963.
- [102] KATCHALSKY, A. *Biophys. J.* **4**, 9, 1964.
- [103] PAECHT, M. and KATCHALSKY, A. *Biochim. Biophys. Acta* **90**, 260, 1964.
- [104] KATCHALSKY, A. The Impact of the Scientific Technology in the Development of New States. *Die modernen Wissenschaften und die Aufgaben der Diplomatie*, p. 71, Verlag Styria, Vienna, 1965.
- [105] KATCHALSKY, A. and OPLATKA, A. *Mechanochemistry*. Symposium on Biorheology, Proc. Fourth Int. Cong. on Rheology, Part I (Edited by COPLEY, A. L. and LEE, E. H.) p. 73. Wiley-Interscience, New York, 1965.
- [106] PAECHT, M. and KATCHALSKY, A. The Polymerization of Proline Adenylate. Federation of European Biochemical Societies. Vienna, 1965. A 309.
- [107] YONATH, J., OPLATKA, A. and KATCHALSKY, A. Equilibrium Mechanochemistry of Collagen Fibers. *Structure and Function of Connective and Skeletal Tissue*, p. 381. Butterworths, London, 1965.
- [108] KATCHALSKY, A. and OPLATKA, A. *Israel J. Med. Sci.* **2**, 4, 1966.
- [109] OPLATKA, A. and KATCHALSKY, A. *Makromol. Chem.* **92**, 251, 1966.
- [110] STEINBERG, I. Z., OPLATKA, A. and KATCHALSKY, A. *Nature, Lond.* **210**, 568, 1966.
- [111] MARIKOVSKY, Y., DANON, D. and KATCHALSKY, A. *Biochim. Biophys. Acta* **124**, 154, 1966.
- [112] PERLMANN, G. E., OPLATKA, A. and KATCHALSKY, A. *J. Biol. Chem.* **272**, 5163, 1967.
- [113] RUBIN, M. M. and KATCHALSKY, A. *Biopolymers* **4**, 579, 1966.
- [114] KATCHALSKY, A., ALEXANDROWICZ, Z. and KEDEM, O. Polyelectrolyte Solutions. *Chemical Physics of Ionic Solutions*, p. 295 (Edited by CONWAY, B. E. and BARRADAS, R. G.). Wiley, New York, 1966.
- [115] KATCHALSKY, A., OPLATKA, A. and LITAN, A. The Dynamics of Macromolecular Systems. *Molecular Architecture in Cell Physiology*, p. 295 (Edited by HAYASHI, T.). Prentice-Hall, New Jersey, 1966.
- [116] KATCHALSKY, A. and CURRAN, P. F. *Nonequilibrium Thermodynamics in Biophysics*, Harvard University Press, 1966.
- [117] KATCHALSKY, A. and AILAM, G. *Biochim. Biophys. Acta* **140**, 1, 1967.
- [118] PAECHT-HOROWITZ, M. and KATCHALSKY, A. *Biochim. Biophys. Acta* **140**, 14, 1967.
- [119] LEWINSHON, R., PAECHT-HOROWITZ, M. and KATCHALSKY, A. *Biochim. Biophys. Acta* **140**, 24, 1967.
- [120] KATCHALSKY, A. *Intern. Sci. and Technol.* p. 52, December, 1967.
- [121] MILLER, I. R. and KATCHALSKY, A. The Interaction of Negatively Charged Polyacids with a Positively Charged Mercury Surface at Different Salt Concentration. *Physics and Physical Chemistry of Surface Active Substances* (Edited by OVERBEEK, J. Th. G.), p. 275. Gordon & Breach, N.Y., 1967.
- [122] BLUMENTHAL, R., GINZBURG, B. Z. and KATCHALSKY, A. Thermodynamic and Model Treatment of Active Ion Transport in Erythrocytes. *Hemorheology*, p. 91. Pergamon Press, London, 1967.
- [123] KATCHALSKY, A. Membrane Thermodynamics. *The Neurosciences, A Study Program*, p. 326 (Edited by QUARTON, G. C., MELNECHUK, T. and SCHMITT, F. O.). The Rockefeller Univ. Press, N.Y., 1967.
- [124] KATCHALSKY, A. and SPANGLER, R. *Quart. Rev. Biophysics* **1**, 127, 1968.
- [125] APELBLAT, A. and KATCHALSKY, A. *Int. J. Heat Mass Transfer* **11**, 1053, 1968.
- [126] KATCHALSKY, A. *Pure and appl. Chem.* **16**, 229, 1968.
- [127] REICH, S., KATCHALSKY, A. and OPLATKA, A. *Biopolymers* **6**, 1159, 1968.
- [128] KATCHALSKY, A. Thermodynamic Consideration of Biological Membranes. *Membrane Models and the Formation of Biological Membranes*, p. 318 (Edited by BOLIS, L. and PETHICA, B. A.). North-Holland, Amsterdam, 1968.
- [129] KATCHALSKY, A. Science and the Developing Countries. Proc. 9th Intern. Congr. Life Ass. Med., p. 10, Tel-Aviv 1967. Karger, Basel, 1968.
- [130] KATCHALSKY, A. A Biological Outlook. The Diversity of Cultures as Against the Universality of Science and Technology, UNESCO, 1968.
- [131] BLUMENTHAL, R. and KATCHALSKY, A. *Biochim. Biophys. Acta* **173**, 357, 1969.
- [132] KATCHALSKY, A. Membrane Thermodynamics. Extrait, Editions du Centre National De La Recherche Scientifique, p. 19, Paris, 1969.
- [133] SACHS, S. B., RAZIEL, A., EISENBERG, H. and KATCHALSKY, A. *Trans. Farad. Soc.* **65**, 77, 1969.
- [134] KATCHALSKY, A. Chemical Dynamics of Macromolecules and its Cybernetic Significance. *Biology and the Physical Sciences*, p. 267 (Edited by DEVONS, S.). Columbia Univ. Press, N.Y., 1969.
- [135] KATCHALSKY, A. Non-equilibrium Thermodynamics of Bio-Membrane Processes. *Theoretical Physics and Biology*, p. 188 (Edited by MAROIS, M.) North-Holland, Amsterdam, 1969.
- [136] KATCHALSKY, A. and OSTER, G. Chemo-Diffusional Coupling in Biomembranes. *The Molecular Basis of Membrane Function*, p. 1 (Edited by TOSTESON, D. C.). Prentice-Hall, Engelwood Cliffs, N.J. 1969.
- [137] RUBIN, M. M., PIEZ, K. A. and KATCHALSKY, A. *Biochemistry* **8**, 3628, 1969.

- [138] SHERAGA, H. A., KATCHALSKY, A. and ALTERMAN, Z. *J. Am. Chem. Soc.* **91**, 7242, 1969.
- [139] SUSSMAN, M. V. and KATCHALSKY, A. *Science* **167**, 45, 1970.
- [140] HELFFERICH, F. and KATCHALSKY, A. *J. Phys. Chem.* **74**, 308, 1970.
- [141] SACHS, S. B., KATCHALSKY, A. and SPIEGLER, K. S. *Electrochimica Acta* **15**, 693, 1970.
- [142] KATCHALSKY, A. Demonstration of a Mechanochemical Engine. Proc. IVth Int. Cong. on Pharmacology, Vol. 1, 245, 1970.
- [143] KATCHALSKY, A. A Thermodynamic Consideration of Active Transport. *Permeability and Function of Biological Membranes* p. 20, (Edited by BOLIS, L. *et al.*). North-Holland, Amsterdam, 1970.
- [144] NEUMANN, E. and KATCHALSKY, A. *Berichte der Bunsengesellschaft für Physikalische Chemie* **74**, 868, 1970.
- [145] PAECHT-HOROWITZ, M., BERGER, J. and KATCHALSKY, A. *Nature, Lond.* **228**, 636 (1970).
- [146] KATCHALSKY, A. and OPLATKA, A. Mechano-Chemical Conversion. *Handbook of Sensory Physiology*, Vol. 1, p. 1. Springer, Berlin, Heidelberg, N.Y., 1971.
- [147] KATCHALSKY, A. *Pure and appl. Chem.* **26**, 327, 1971.
- [148] KATCHALSKY, A. Thermodynamics and Life. Proc. of the Int. Union of Physiological Sciences, VIII, 1971.
- [149] KATCHALSKY, A. *Zygon: J. Religion Sci.* **6**, 99, 1971.
- [150] KATCHALSKY, A. *Neurosciences Res. Prog. Bull.* **9**, 397, 1971.
- [151] NEUMANN, E. and KATCHALSKY, A. Hysteretic Conformational Changes in Biopolymers Induced by High Electric Fields—Model for a Physical Record of Biological Memory. Proc. 1st Europ. Biophys. Cong. Vol. 7, 91, 1971.
- [152] OSTER, G., PERELSON, A. and KATCHALSKY, A. *Nature, Lond.* **234**, 393, 1971.
- [153] WINCHELL, H. S., LIN, M. S., SHIPLEY, B., SARGENT, T. and KATCHALSKY, A. *J. Nuclear Med.* **12**, 678, 1971.
- [154] KATCHALSKY, A. and NEUMANN, E. *Int. J. Neuroscience* **3**, 175, 1972.
- [155] NEUMANN, E. and KATCHALSKY, A. *Proc. Nat. Acad. Sci.* **69**, 993, 1972.
- [156] KATCHALSKY, A. *Leonardo* **5**, 249, 1972.
- [157] PERELSON, A. S. and KATCHALSKY, A. *Chem. Eng. Sci.* **27**, 1190, 1972.
- [158] COX, R. A. and KATCHALSKY, A. *Biochem. J.* **126**, 1039, 1972.
- [159] OSTER, G., PERELSON, A. S. and KATCHALSKY, A. Thermodynamics of Biological Networks. *Quart. Rev. Biophys.* **6** (1), 1973.
- [160] KATCHALSKY, A. On the Prebiotic Synthesis of Peptides. Proc. 3rd Int. Conf. from Theoretical Physics to Biology, Versailles 1971. Karger, Basel, 1973 (in press).
- [161] APELBLAT, A., KATCHALSKY, A. and SILBERBERG, A. A Mathematical Analysis of Capillary-Tissue Fluid Exchange. *Biorheology* **11**, (in preparation).
- [162] PAECHT-HOROWITZ, M. and KATCHALSKY, A. Synthesis of Amino Acyladenylates under Prebiotic Conditions. (To be published.)
- [163] ATLAN, H. and KATCHALSKY, A. Tellegen's Theorem for Bond Graphs. Its Relevance to Chemical Networks. (To be published.)
- [164] KATCHALSKY, A. Thermodynamics of Bio-Networks. Lecture at 3rd Int. Conf. From Theoretical Physics to Biology. Versailles, 1971 (in press).

AHARON KATZIR-KATCHALSKY

1913–1972

Born in Lodz, Poland, 1913

M.Sc.—Hebrew University, Jerusalem 1937

Ph.D.—Hebrew University, Jerusalem 1940

Professor and Head of the Department of Polymer Research, Weizmann Institute of Science 1948–1972

Visiting Miller Professor, University of California, Berkeley 1967–1972

Honors

President of the Israel National Academy of Sciences and Humanities

President and then Honorary Vice-President of the International Union of Pure and Applied Biophysics (IUPAB)

Member of the International Council of Scientific Unions
Foreign Member of the National Academy of Sciences
Member of the European Molecular Biology Organization (EMBO)
Member Scientific Council Solvay Laboratories, Universite Libre de Bruxelles
Member Professorial Staff of the Sorbonne

Awards

Weizmann Prize 1954
Israel Prize in Exact Sciences 1961
Honorary Doctorate, Clarkson College of Technology, Potsdam, N.Y. 1965
Doctor Honoris Causa of the Universite Libre de Bruxelles, Belgium 1969
Doctor Honoris Causa of the University of Bern, Switzerland 1969
Rothschild Prize in Chemistry 1972

RESEARCH ACTIVITIES*

Professor Aharon Katzir-Katchalsky

“The physical chemistry of water soluble polymers, and in particular of polyelectrolytes, was seen as the basis for the understanding of the behavior of biopolymers. The thermodynamics, electrochemistry and transport properties of polyelectrolyte solutions and gels were studied, and the interaction of polyelectrolytes with biological systems, and the role of biopolyelectrolytes in cellular organization investigated. During the last couple of years nucleic acids and polynucleotides exhibiting metastable conformational transitions were studied. A remarkable finding was that long-lived transitions can be induced by electrical fields of an intensity comparable to that of a nerve impulse.

Direct conversion of mechanical into chemical energy—underlying the operation of muscle and other biological motile organs—was studied on synthetic models. The laws of mechanochemistry led to the development of the first man-made mechanochemical engines which operate on the principles of biological contractility.

Nonequilibrium thermodynamics have been introduced as a tool for the analysis of biological transport phenomena. Nonequilibrium thermodynamics has been shown to be a valuable tool in the characterization of membrane processes, of metabolic cycles and of flow coupling in cells and tissues. The thermodynamic treatment was extended to nonlinear processes proceeding in inhomogeneous systems, and the network thermodynamics thus developed, is a new approach to the flow of organization in living systems.

The polymerization of peptides under prebiotic conditions was studied. In the presence of clays and minerals, high polypeptides were obtained in aqueous media under physiological conditions.”

* From a report written by him shortly before his death.