A Symposium on

LIGHT
and
LIFE

Edited by
William D. McElroy
and Bentley Glass

A SYMPOSIUM ON

LIGHT AND LIFE

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Edited by

WILLIAM D. McELROY AND BENTLEY GLASS

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PREFACE

A Symposium on "Light and Life" was held at The Johns Hopkins University under the sponsorship of the McCollum-Pratt Institute on March 28-31, 1960. This volume contains the papers and informal discussions presented during the Symposium.

In the planning of the present Symposium we attempted, as in previous symposia, to bring together scientists from a number of different disciplines. Unfortunately time and printing limitations prevented the consideration of a number of interesting photobiological problems.

I would like to acknowledge the active participation of the members of the McCollum-Pratt Institute and of the Department of Biology in the planning of the Symposium. Many of the speakers on the program were helpful in suggesting areas or specific topics that should be discussed. It is also a pleasure to acknowledge the valuable contributions of the following moderators: Dr. Albert Szent-Györgyi, Dr. James Franck, Dr. William Arnold, Dr. C. B. van Niel and Dr. H. K. Hartline.

The support of a limited number of foreign investigators as participants in the Symposium was made possible through the generous aid of the National Science Foundation. Unfortunately, insufficient funds prevented the attendance of a larger number of participants from great distances.

We hope, however, that the published book will be of value to all investigators interested in photobiological processes.

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INTRODUCTION

PHYSICAL MODELS AND LIVING ORGANISMS[1]

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The discussion of the position of living organisms in a general description of physical phenomena has, in the development of science, passed through a number of stages. In Antiquity, the obvious difficulties inherent in a comparison between organisms and primitive machinery deeply influenced the attitude towards mechanical problems and even led to the attribution of vital characteristics to all matter. With the abandonment of these views, at the time of the Renaissance, through the clarification of the principles of classical mechanics, the problem entered into another stage, stimulated by the great anatomical and physiological discoveries at that period.

Recent advances in technology, and especially the development of automatic control of industrial plants and calculation devices, have given rise to a renewed discussion of the extent to which it is possible to construct mechanical and electrical models with properties resembling the behavior of living organisms. Indeed, it may be feasible to design models reacting in any prescribed manner, including their own reproduction, provided that they have access to the necessary materials and energy sources. Still, quite apart from the suggestive value of such comparisons, we must realize that, in the study of models of given structure and functions, we are very far from the situation in which we find ourselves in the investigation of living organisms, where our task is gradually to unravel their constitution and potentialities.

As regards this problem it is essential to realize from the very beginning that in organic life we are dealing with further resources of nature than in the construction of machines. Indeed, for this

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[1] Except for a few small additions the substance of these remarks was presented in a contribution to the symposium on Models in Biology, Bristol, 1959.

purpose we can essentially disregard the atomic constitution of matter and confine ourselves to the account of the mechanical and electrical properties of the materials used and to the application of the simple laws governing the interaction between the parts of the machine. From biological research, however, it is evident that fundamental characteristics of living organisms, and in particular genetic reproduction, depend primarily on processes on the atomic scale, where we are faced with new problems.

On the ground of classical physics, the very question of maintaining a high degree of order of such immensely complicated systems presents serious difficulties. In fact, the incessant encounters between the atoms with a more or less liquid phase like the cytoplasm would lead to rapidly increasing disorder. Doubts have even been expressed about the compatibility of the existence and stability of living organisms with the laws of thermodynamics, but thorough investigation of the exchanges of energy and entropy accompanying the metabolism and movements of the organisms has never disclosed any departure from these laws.

A whole new background has, however, been created by the development of quantum physics, which, at the same time as it has revealed an essential limitation of the deterministic description of classical mechanics, has offered a proper basis for the account of the stability of atomic and molecular structures. As is well known, no picture on classical lines can be given of the electronic constitution of atoms or of the behavior of the electrons responsible for the bindings between atoms in chemical combinations. Owing to the large masses of the atomic nuclei compared with that of the electron, it is possible, however, effectively to retain a pictorial representation of the relative positions of the atoms in accordance with the structure formulae of chemistry, which have proved so adequate even for the highly complicated molecules with which we are concerned in organic metabolism.

In spite of the multifarious enzymatic processes involved in this metabolism, the problem of the stability of the organisms presents a fundamental simplicity, since, in the range of temperatures within which life can be upheld, the thermal fluctuations in the states of vibration and rotation of the molecules are in general far from sufficient to break the chemical bonds. Such fluctuations rather effect the rapid disappearance of correlations between all secondary characters of the states of the reacting systems and permit us to account for the primary features of their constitution merely by a specification of the atoms of which they are composed and the configuration in which these atoms are bound together.

The discoveries in recent years of the specific molecular structures carrying genetic information, and the increasing insight into the processes by which this information is transferred, have opened quite new prospects for the gradual elucidation of biological regularities on the basis of well-established principles of chemical kinetics. In particular, the almost unlimited possibilities of probing our metabolic transformations lend support to the view that the formation and regeneration of the structural constituents of the organisms are to be regarded as processes of not immediately reversible character, which at any step secure the greatest possible stability under the conditions maintained by nutrition and respiration.

Thus, there appears to be no reason to expect any inherent limitation of the application of elementary physical and chemical concepts to the analysis of biological phenomena. Yet, the characteristic properties of living organisms, which have resulted from the whole history of organic evolution, reveal potentialities of immensely complicated material systems, which have no parallel in the comparatively simple phenomena studied under reproducible experimental conditions. It is on this background that notions referring to the behavior of organisms as entities, and apparently contrasting with the account of the properties of inanimate matter, have found fruitful application in biology.

Even though we are here concerned with typical complementary relationships as regards the use of appropriate terminology, it must be stressed that the argumentation differs in essential aspects from that concerning exhaustive objective description in quantum physics. Indeed, the distinction demanded by this description between measuring apparatus and object under investigation, which implies mutual exclusion of the strict application of space-time coordination and energy-momentum conservation laws in the account of individual quantum processes, is already taken into account in the use of chemical kinetics and thermodynamics. Thus, the dual approach in biology does not seem to be conditioned by an interference with the properties of the specific molecular structures, inherently involved in their identification, but is rather required by the practically inexhaustible potentialities of living organisms entailed by the immense complexity of their constitution and functions.

Part I

MOLECULAR STRUCTURE AND EXCITED STATES

INTRODUCTORY COMMENTS

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It is common knowledge that the ultimate source of all our energy and negative entropy is the radiation of the sun. When a photon interacts with a material particle on our globe it lifts one electron from an electron pair to a higher level. This excited state, as a rule, has but a very short lifetime and the electron drops back within 10^{-7} to 10^{-8} seconds to the ground state, giving off its excess energy in one way or another. Life has learned to catch the electron in the excited state, uncouple it from its partner and let it drop back to the ground state through its biological machinery, utilizing its excess energy for life processes.

There is little doubt in my mind that Life was driven, at the beginning, by this electronic energy and must have walked a long and tortuous road perfecting its biological machinery, step by step, by developing the substances fit to deal with the electron. But, however this machinery may have been perfected, it had to retain two major shortcomings: (1) the electron and its energy were linked to the energy-producing machinery and could not be taken out of it; (2) while Life is continuous, radiation is intermittent and the possibilities of storing high-energy electrons are very limited.

The story of the storage and transportation of electronic energy consists of a series of discoveries made by Nature. One of the most important of these was the discovery that it is possible to preserve the electronic free energy by linking two orthophosphate molecules together by an anhydride link, producing pyrophosphate, P-O-P. We meet the P-O-P today in a rather sophisticated form, as part of the ATP molecule. This discovery solved the problem of energy transport and alleviated the problem of energy storage. Energy stored in the form of P-O-P could be transported to different loci, allowing for the development of new organs or processes, and relegating the process of photosynthesis proper to special little factories, chromatophores or chloroplasts. As far as we know, from studies of photosynthetic bacteria, the simplest P-O-P producing system consists of very few components. The excited electron passes in it from chlorophyll to a quinone (Vitamin K or its equivalent), from here to a cytochrome and then back again to chlorophyll to replace its lost electron. All that is left from the electrons circling around a cyclic pathway are the terminal phosphates on ATP. This is a "closed circle" from which nothing leaks out but energy invested into ~P's, (high-energy phosphate bonds).

The next discovery of Nature was that of pyridine nucleotides, TPN, which can take over the excited electrons from chlorophyll, and then send them back to it over riboflavin and cytochromes. This new, somewhat more sophisticated circle is also a "closed" one and may involve oxygen as a catalyst. The energy liberated by the electron dropping down to its ground level again produces ATP only.

The next discovery involved water, the *mater* (mother) and *matrix* of life. The electron, taken over by TPN can be stabilized by binding protons. This means the decomposition of water, the details of which still need clarification. The simplest assumption is to suppose that the chlorophyll regains its lost electrons over a cytochrome from the OH^- ions, left unbalanced after the H^+ was linked to pyridine. The remaining (OH) radicals can then be dismutated into water and O_2.

By introducing ATP and TPN the storage problem was not yet completely solved, for neither of these two substances can be stored by the cell in quantity. The solution was achieved, and the way to higher forms of life was opened, by involving CO_2. Once the cell had ATP and reduced TPN, it could reduce with them CO_2 to carbohydrate. The carbohydrate could further be transformed into fat, substances which could be stored in almost unlimited quantity. To mobilize their energy the process of energy storage had simply to be reversed, the H from carbohydrates and fats being now transferred back onto TPN or DPN. The "closed" circle of photosynthesis was thus opened up by the introduction of the two extraneous substances, H_2O and CO_2. These remarks made no pretence of originality. They are based chiefly on the work emanating from the laboratory of D. Arnon.

Until recently, the classical objects of study in photosynthesis were green leaves or chloroplasts belonging to the highest levels of organization. Only lately were the bacterial chromatophores introduced as material for study. With this, research went back on the phylogen-