ENVIRONMENTAL PHYSIOLOGY OF ANIMALS

EDITORS

J. BLIGH

J. L. CLOUDSLEY-THOMPSON

A. G. MACDONALD

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J. BLIGH BSc, PhD
Institute of Animal Physiology
Babraham, Cambridge

J. L. CLOUDSLEY-THOMPSON PhD, DSc
Professor of Zoology
Birkbeck College, London

A. G. MACDONALD BSc, PhD
Physiology Department
University of Aberdeen

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Contributors

J.BLIGH, A.R.C. Institute of Animal Physiology, Babraham, Cambridge CB2 4AT

P.J.BUTLER, Department of Zoology, University of Birmingham, P.O. Box 363, Birmingham B15 2TT

A.G.CAIRNS-SMITH, Department of Chemistry, University of Glasgow, Glasgow G12 8QQ

J.L.CLOUDSLEY-THOMPSON, Department of Zoology, Birkbeck College, Malet Street, London WC1E 7HX

P.C.CROGHAN, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ

E.EDNEY, Laboratory of Nuclear Medicine & Radiation Biology, University of California, Los Angeles, California, U.S.A.

LESLEY GOODMAN, Department of Zoology, Queen Mary College, Mile End Road, London E1 4NS

R.D.HARKNESS, Department of Physiology, University College London, Gower Street, London WC1E 6BT

H.E.HINTON, Department of Zoology, University of Bristol, Bristol BS8 1TH

A.G.MACDONALD, Physiology Department, Marischal College, University of Aberdeen, Aberdeen AB9 1AS

C.MONGE, Universidad Peruana Cayetano Heredia, Avenida Honorio Delgado No. 932, Lima, Peru.

K.NAGY, Laboratory of Nuclear Medicine & Radiation Biology, University of California, Los Angeles, California, U.S.A.

J.PATTERSON, Centre for Overseas Pest Research, College House, Wrights Lane, London W8 5SJ

H. POHL, Max-Planck-Institut für Verhaltenphysiologie, 8131 Erling-Andechs, West Germany.

P. TYTLER, School of Biological Sciences, University of Stirling, Stirling FK9 4LA

M. SMITH, A.R.C. Institute of Animal Physiology, Babraham, Cambridge CB2 4AT

M. WHITFIELD, Marine Biological Association, The Laboratory, Citadel Hill, Plymouth PL1 2PB

J. WHITTEMBURY, Universidad Peruana Cayetano Heredia, Avenida Honorio Delgado No. 932, Lima, Peru.

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Introduction

1.1 ENVIRONMENTAL PHYSIOLOGY

The main preoccupation of the physiologist is to study what goes on inside an organism. In the words of the distinguished Argentinian physiologist B. A. Houssay 'Physiology is the science that studies the phenomena occurring in living organisms and endeavours to establish their laws'. An understanding of function brings with it the realization that life is a dynamic system which involves continual interchanges between organism and environment. The Russian physiologist K. Bykov defines our subject thus: 'Physiology of man and animals is the study of function of human and animal organisms in their interaction with the environment'. Bykov's broader definition of physiology makes the title of this book somewhat redundant but, to avoid ambiguity and as a concession to common usage, we have used the term 'environmental physiology'. It is our view that the functions of an organism are only really meaningful when studied in the context of the environment with which the organism is interacting. This book will provide abundant evidence to support that assertion.

1.2 THE COMMON DENOMINATOR

In their cells all organisms share many features. Genetic laws are a good example; indeed, Mendel established the basic rules of heredity, which are applicable to man and fruit-fly alike, by cross-breeding peas in a Moravian monastery garden. Subsequent detailed studies of cellular physiology have amply confirmed that the other functions of living cells, both plant and animal, have a great deal in common particularly in respect of their metabolic and regulatory processes.

At the same time, differences between species depend on differences in the genetic code and these differences are made manifest by the structure and function of individual cells.

1.3 THE BASIS OF EVOLUTIONARY CHANGE

That evolution is based on random changes in the genetic constituents of cells is now well established, and there is no reason to dispute that mutations succeed or fail according to whether the individual which possesses a unique variation in its structure or function is thereby afforded, at some time and in some particular circumstances, marginally improved survival. Only in this way can an organism pass on to future generations improved genetic fitness to live and reproduce *in the particular environmental circumstances in which this fitness has been put to the test.*

If this is substantially the way organisms evolve, then it follows that every variation in form and function must have come about through a long series of natural selections of random changes, each of which gave an individual organism some small advantage in particular environmental circumstances. Thus, it may reasonably be claimed, it is the physical environment, together with biotic factors, that have shaped each species and its particular physiology. It also follows that the forms and functions of organisms are expressions of the relations between these organisms and their environments *at some time* in their evolution. In other words, every variation in form or function has a historical environmental significance, but not necessarily a contemporary environmental significance.

1.4 THE AUTONOMY OF THE CELL AS THE UNIT OF LIFE

Life can be imagined to have started during some phase in the geological history of the Earth as it cooled, which favoured the formation of particular complex molecules or complexes of molecules (Chapter 2). These early transitory unstable structures would have existed dynamically, by constant formation and destruction, and this dynamic feature is still characteristic of living things.

At some relatively late stage their persistence in a changing environment was favoured by the formation of a bounding membrane which protected the molecules from the external environment and provided them with a buffered, local environment. Thus, it may be speculated, a primitive cell membrane constituted an early adaptive structure which protected the 'embryonic chemistry of life' from the harmful effects of environmental changes. By their active processes the membranes of all contemporary cells perform this essential function of sustaining the stability of the intracellular environment despite its difference from, and despite changes in, the extracellular environment.

Life is believed to have existed on earth for approximately 3×10^9 years, but it is quite impossible to say for what part of this period life was exclusively unicellular. What is abundantly clear, however, is that all the basic machinery of cellular life had become established, and largely irrevocably so, before life radiated into the myriad unicellular and multicellular forms that constitute the contemporary array of the fauna and flora.

The great variation in the form and function of unicellular organisms, and the ability of unicellular organisms to become adapted to environmental changes, is ample evidence that all the machinery of genotypic adaptation, and probably also of phenotypic adaptation, is invested in the individual cell. Every cell, whether free-living or a member of a multi-cellular structure, retains a large degree of autonomy within its local environment. The integrative functions of multicellular organisms are to be explained in terms of the interaction of individual cells with their local environments. This, at any rate, is a reasonable reductionist view held by most physiologists. A cell can influence other cells by what it removes from or discharges into a common aqueous medium. A cell may respond to the presence of substances released by other cells (or to other environmental influences). As a consequence of mutations, cells vary in these two properties. Functionally specialized members of a multicellular complex thus contribute blindly to the greater unit of the whole organism.

Consider, for example, a simple neuronally operated reflex response to an externally applied stimulus. A cell, or rather part of the membrane of a cell, is specifically responsive to the particular environmental change (e.g. in light, temperature, pressure or the concentration of a chemical constituent of the environment). This disturbance sets up a change in the ionic permeability of the cell membrane which sweeps across the surface of the axon. When this progressive wave of change in the membrane permeability reaches the end of the nerve axon it causes the discharge of a particular substance into the extracellular environment. This substance acts on a specialized part of another nerve-cell membrane which is specifically sensitive to it. A similar sequence of events is thus activated in the other cell and this has the effect of passing on a message if it is an interneurone, or of responding to the message if it is an effector cell. A functional and apparently purposeful reflex response of the whole organism to an environmental stimulus is thus achieved by a succession of responses of individual cells to changes in their local environments. The ability of millions of cells to act in consonance as a macro-unit of life resides in the differences in the ways in which cells interact with their immediate surroundings. The macro-differences between species are an expression of the micro-differences in the functional specializations of member cells, and of the influences one cell exerts on another as a component of the environment of the other cell.

Thus it is the restraining influences of other cells which 'discipline' the individual cells in acting as integral components of a higher order of unit, the multicellular organism. Each cell, however, remains an entity which lives or dies according to the constitution of the chemical matrix in which it is bathed, and according to its ability to respond to changes in its environment so as to maintain its internal processes of life.

Much the same can be said of the whole multicellular organism. It can only survive as a member of a population. As an individual it is bathed in a fluid matrix which may be aqueous or gaseous. Survival depends on the constitution of its local environment, and on the ability of the organism to maintain the integrity of its internal environment within which its constituent cells are bathed, and on its ability to reproduce its kind.

1.5 TIME SCALES OF ADAPTIVE PROCESSES

Adaptive processes occur on 3 major time scales. The first of these is that of the adaptation of life over a period of 3×10^9 years to the different environments of the earth's crust. This is the time scale of *genotypic adaptations* based on the natural selections of chance mutations.

The second scale concerns the periodic adaptations of animals to the regular (cyclic) environmental changes imposed by the movements of the solar system. This time scale has three sub-divisions: the annual cycle of seasons governed by the movement of the earth round the sun; the monthly cycle governed by the movement of the moon round the earth, and the nychthemeral (or 24-hourly) cycle governed by the rotation of the earth on its axis.

The third major time scale is a very short one, and covers the rapid responses to changes in the immediate environment of an organism such as the presence of a prey or of a predator. This category includes sensory physiology, motor control and the physiology of other effectors.

This book is divided into sections which more or less consider these three time scales of adaptation to the environment. There is no rigid division that makes it easy, or even desirable, to consider only one of these time scales when discussing a representative facet of environmental physiology. Genotypic adaptations of physiological functions, which have been established over the longest time scale, are expressed in the qualitative and quantitative nature of the rapid reflex or slower acclimatory responses. For example, the ability of one species of mammal to sweat and of another to pant during heat stress are genotypic adaptations to particular environmental circumstances. The activation of sweating or panting is a rapid reflex response to heat stress. However, the improvement in the effectiveness of either of these processes that may occur during prolonged heat stress is a phenotypic acclimatory change in the function or capacity of a process and exemplifies what may happen naturally in response to seasonal changes in the climate. Contributors have not, therefore, been asked to limit their treatments to the time scale which the section of the book in which their chapters appear is most concerned.

1.6 CONCLUSION

Because all life depends on the responsiveness of individual cells to their immediate environments, because all the manifestations of life are the consequence of interactions between cells and their environments, and because the whole organism is in a state of continual change in response to environmental changes, it is legitimate to argue that *all physiology is environmental physiology*. On the same premisses some would argue that *all physiology is cellular physiology*. But this view would be unacceptable to many who hold that the physiology of multicellular organisms is to do with the properties which arise from the interactions between specialized component cells and particular environmental changes. To whichever point in the spectrum of reductionist-holistic thinking the reader is inclined, there can be no escaping the validity of Bykov's statement that physiology is the study of organisms in their interactions with the environment. The principal purpose of this book is to amplify that statement.

Progress in the understanding of the functions of living organisms has resulted from countless careful and detailed investigations of particular tissues or systems under controlled laboratory conditions. Thus physiology, like all other sciences, relies in the first instance, on the breaking down of complex concurrent and interacting functions into component parts. The resultant crumbs of biological knowledge are quite useless unless and until they are brought together and used to indicate how a whole organism, or even a whole ecosystem operates. This book is concerned with the overall, dynamic pattern of animal life. Because of the magnitude of the subject it cannot be comprehensive. Instead, considerable selection has been exercised on the items which have been included to illustrate the theme. The contributors and editors have tried to present them in a way which will help the student of biology to synthesize an understanding of the phenomena of life and its absolute dependence on the environment in which it occurs. Unless the student seeks to achieve this wider concept of biology he will fall short of achieving scientific maturity, and become someone who may know everything about his subject except its ultimate significance.

PART II
THE ORIGIN OF LIFE