Circulation, Respiration, and Metabolism

Current Comparative Approaches

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Edited by R. Gilles

With 190 Figures

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The β-adrenergic pathway.
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The American Society of Zoologists
The Canadian Society of Zoologists
The Japanese Society for General and Comparative Physiology

The Congress has been organized in relation with the 100th Anniversary of the School of Comparative Physiology and Biochemistry of the University of Liège.

The proceedings of the invited lectures to the different symposia of the congress have been gathered in five different volumes published by Springer-Verlag under the following titles:

Circulation, Respiration, and Metabolism
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Edited by R. Gilles (ISBN 3-540-15627-5)

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High Pressure Effects on Selected Biological Systems
Edited by A. J. R. Péqueux and R. Gilles (ISBN 3-540-15630-5)

Foreword

This volume is one of those published from the proceedings of the invited lectures to the First International Congress of Comparative Physiology and Biochemistry I organized at Liège (Belgium) in August 1984 under the auspices of the Section of Comparative Physiology and Biochemistry of the International Union of Biological Sciences. In a general foreword to these different volumes, it seems to me appropriate to consider briefly what may be the comparative approach.

Living organisms, beyond the diversity of their morphological forms, have evolved a widespread range of basic solutions to cope with the different problems, both organismal and environmental with which they are faced. Soon after the turn of the century, some biologists realized that these solutions can be best comprehended in the framework of a comparative approach integrating results of physiological and biochemical studies done at the organismic, cellular and molecular levels. The development of this approach amongst both physiologists and biochemists remained, however, extremely slow until recently. Physiology and biochemistry have indeed long been mainly devoted to the service of medicine, finding scope enough for their activities in the study of a few species, particularly mammals. This has tended to keep many physiologists and biochemists from the comparative approach, which demands either the widest possible survey of animals forms or an integrated knowledge of the specific adaptive features of the species considered. These particular characteristics of the comparative approach have, on the other hand, been very attractive for biologists interested in the mechanisms of evolution and environmental adaptations. This diversity of requirements of the comparative approach, at the conceptual as well as at the technological level, can easily account for the fact that it emerged only slowly amongst the other new, more rapidly growing, disciplines of the biological sciences. Although a few pioneers have been working in the field since the beginning of the century, it only started effectively in the early 1960's. 1960 was the date of the organization of the periodical *Comparative Physiology and Biochemistry* by Kerkut and Scheer and of the publication of the first volumes of the comprehensive treatise *Comparative Biochemistry* edited by Florkin and Mason. These publications can be considered as milestones in the evolution of the comparative approach. They have

been followed by many others which have greatly contributed to giving the field the international status it deserved. Since the 1960's, the comparative approach has been maturing and developing more and more rapidly into the independent discipline it now is, widely recognized by the international communities of physiologists, biochemists, and biologists. It is currently used as an effective tool of great help in the understanding of many research problems: biological as well as clinical, applied as well as fundamental.

The actual development of the field and the interest it arouses in a growing portion of the biological scientific community led some of us to consider the organization of an international structure, bringing together the major representative societies and groups around the world, which would aim at the general advancement and promotion of the comparative approach. This was done in 1979 with the incorporation, within the international Union of Biological Sciences, of a Section of Comparative Physiology and Biochemistry. The first International Congress of CPB I organized in Liège with the help of a few friends and colleagues, is the first activity of this newly founded Section. In 22 symposia it gathered some 146 invited lectures given by internationally renowned scientists on all major current topics and trends in the field. The proceedings of these lectures have been collected in 5 volumes produced by Springer-Verlag, a publisher long associated with the development of CPB. The organization of the CPB Section of IUBS, its first Congress and these proceedings volumes can well be considered as milestones reflecting the international status and the maturity that the comparative approach has gained, as a recognized independent discipline, in the beginning of the 1980's, some 20 years after it was effectively launched.

Finally, I would like to consider that the selection of Liège for this first International Congress has not been simply coincidental. I thus feel that this brief foreword would not be complete without noting the privileged role Liège has played in some events associated with the development of the comparative approach. Liège had a pioneer in comparative physiology already at the end of the last century with Léon Fredericq. With Marcel Florkin, Liège had its first Professor of biochemistry and one of the founding fathers of comparative biochemistry. These two major figureheads of the comparative approach founded and developed what is actually called the Liège School of Comparative Physiology and Biochemistry, which was, at the time of the Congress, celebrating its 100th anniversary. This school provided early support to the European Society for Comparative Physiology and Biochemistry organized by Marcel Florkin and myself some years ago. The society, still headquartered in Liège, was, with the CPB division of the American Society of Zoologists, at the origin of the formation of the CPB Section of IUBS under the auspices of which this first International Congress, specifically devoted to the comparative approach has been

organized. An essential particularity of the Liège school of CPB is that its two founding fathers, scientists interested in general, basic aspects of the organization of living organisms, were also professors at the faculty of medicine. This largely contributed in Liège to avoiding the undesirable structuration of a so-called "zoophysiology" or "zoobiochemistry" independent of the rest of the field. The conditions were thus realized very early in Liège for CPB to play its key role in canalizing the necessary interactions between the general, pre-clinical or clinical and the environmental, ecological or evolutionary tendences of physiology and biochemistry. The possibility of stimulating such interactions has served as a major guide line in the selection of the symposia and invited lectures from which these proceedings have issued.

Liège, Belgium, June 1985 R. GILLES

Preface

Three points of view, or themes, run through this volume of the proceedings of the first congress of the Section of Comparative Physiology and Biochemistry of the International Union of Biological Sciences. On the one hand, as biochemists and physiologists, the contributors are particularly interested in principles of function (at various levels of organization, spanning the range from molecules to whole organisms) which are universally applicable to living systems. The only way to assess the universality of biochemical or physiological functions, of course, is to probe and analyze them across broad sweeps of phylogeny. Thus a second theme running through this volume explores how specific biochemical and physiological functions are put to use in different organisms, or in similar organisms living in different environmental conditions. Not only does this approach assist in identifying truly universal properties of physiology and biochemistry, it also helps to explain the immense diversity of Nature that necessarily and continuously confronts (and sometimes seduces) the comparative biologist. A third theme in this volume, as a kind of blend of the first two and perhaps best characterizing the disciplines of comparative biochemistry and physiology, is *the use of organisms as an experimental parameter per se*. The use of species-specific properties of organisms as experimental parameters in their own right for better illuminating underlying mechanisms and unifying principles is a time-honored research strategy in comparative biochemistry and physiology, going back to the origins of these disciplines. The contributions in this volume beautifully illustrate that this research strategy is as effective today as it was in August Krogh's time and in the subsequent heady days of early comparative biochemistry and physiology. The volume should therefore stand as an important milestone in the field, both in reviewing what has been done and in bringing focus on what should be done next.

P.W. HOCHACHKA

Vancouver, Canada, April 1985

List of Contributors

You will find the addresses at the beginning of the respective contributions

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Symposium I

The Physiology of Exercise: Comparative Approaches

Organizer P.J. BUTLER

Respiratory, Circulatory, and Metabolic Adjustments to Exercise in Fish

C.M. WOOD[1] and S.F. PERRY[2]

1 Oxygen

The increase in muscular work and metabolic rate associated with exercise necessitates both elevated O_2 uptake by the gills ($\dot{M}O_2$) and enhanced O_2 delivery to the tissues. Both of these processes can be considered limiting factors in determining overall exercise performance. The present discussion primarily focuses on the various factors affecting the transfer of O_2 across the gill during exercise. Sections 3 and 4 deal with O_2 delivery to the tissues.

During sustained exercise $\dot{M}O_2$ can increase 12–15 times above the resting rate. Much of this increase can be attributed simply to increased bulk transfer of O_2 as a result of elevated cardiac output and gill ventilation. However, other factors, including changes in gill O_2 diffusive conductance, also contribute to the rise in $\dot{M}O_2$ and maintenance of arterial blood oxygen tensions, especially at higher swimming speeds when blood transit time through the gill vasculature is drastically reduced.

The movement of O_2 across the gill respiratory epithelium can be described by the equation:

$$\dot{M}O_2 = KO_2 \times \frac{A \times \Delta PO_2}{E} \tag{1}$$

where KO_2 = the O_2 permeation coefficient (related to the capacitance and permeability of the respiratory surface to O_2), A = the functional surface area of the gill, E = the thickness of the diffusion barrier and ΔPO_2 = the mean O_2 partial pressure gradient between blood and water ($1/2(P_IO_2 + P_EO_2) - 1/2(P_aO_2 + P_vO_2)$ is a reasonable approximation where P_IO_2 and P_EO_2 = inspired and expired O_2 tensions and P_aO_2 and P_vO_2 = arterial and venous O_2 tensions). A rearrangement of Eq. (1) yields an expression for gill O_2 diffusion conductance (GO_2):

$$GO_2 = \frac{\dot{M}O_2}{\Delta PO_2} = KO_2 \times \frac{A}{E}. \tag{2}$$

Thus, changes in GO_2 due to modifications of KO_2, A, and E as well as changes in ΔPO_2 will affect the overall transfer of O_2 across the gill during exercise. Three factors

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