Animal Hormones

A COMPARATIVE SURVEY

Part I - Kinetic and Metabolic Hormones

P. M. JENKIN

ANIMAL HORMONES

A comparative survey

Part I—Kinetic and Metabolic Hormones

PENELOPE M. JENKIN
M.A., D.Sc.
Senior Lecturer in Zoology, Bristol University
Associate of Newnham College, Cambridge

with a foreword by

JOHN E. HARRIS, C.B.E., M.A., Ph.D., F.R.S.
Professor of Zoology in the University of Bristol

PERGAMON PRESS
NEW YORK · OXFORD · LONDON · PARIS
1962

PERGAMON PRESS INC.
122 East 55th Street, New York 22, N.Y.
1404 New York Avenue N.W., Washington 5, D.C.

PERGAMON PRESS LTD.
Headington Hill Hall, Oxford
4 & 5 Fitzroy Square, London, W.1

PERGAMON PRESS S.A.R.L.
24 Rue des Ecoles, Paris V^e

PERGAMON PRESS G.m.b.H.
Kaiserstrasse 75, Frankfurt-am-Main

Library of Congress Card Number 60-8977

Set in Imprint 10/11pt and Printed in Great Britain by Cox and Wyman Ltd., London, Reading and Fakenham

ACKNOWLEDGEMENTS

I ACKNOWLEDGE with gratitude the help and stimulus that I have received from many friends and experts, with whom I have discussed different sections of this book. Among these I would mention particularly Professor B. Hanström, who read the whole of chapter 3; Professor M. Thomsen and Dr. Ellen Thomsen who discussed the general plan with me; Professor H. E. Heller who read § 5.3 on electrolyte and water balance; Dr. J. A. Kitching, who read §§ 4.1 and 5 and Sir Francis Knowles and Dr. D. B. Carlisle who gave me much information on crustacean hormones and discussed the nomenclature which has been adopted here and, in part, in their own recent book. Professor J. E. Harris went far beyond the duties of an Editor in encouraging me in every way and not least in his penetrating discussion of fundamental problems of hormone action. Though all these have saved the book from many errors, I must accept sole responsibility for any that remain, as I do for the selection, interpretation and presentation of the material.

I am particularly indebted to Sir Francis Knowles for allowing me to reproduce some of his beautiful coloured photographs of chromatophores in *Leander* and to the publishers of *Endeavour* for supplying copies of the blocks for these. My warm thanks for permission to reproduce or adapt their figures are also due to Dr. E. Thomsen and Dr. S. P. Carlson, who provided photographs for Figures 2-3 and 3-19; to Dr. W. Junk of the Hague, for the block of Figure 5-6, and to all the other authors and publishers indicated in the legends and references, as well as to the following publishers and sponsors of journals:

Academic Press Inc. (Figs. 2-10, 4-10, 4-11, 5-10).
American Institute of Biological Sciences, Washington (Fig. 3-23).
American Physiological Society (Figs. 3-7, 4-2, 4-3, 4-4, 4-5, 5-9, 5-22).

Chas. J. Branford, Co. (Fig. 3-3).
Butterworths Scientific Publications (Figs. 5-14, 5-23).
Cambridge University Press (Figs. 3-1, 3-5, 3-6, 3-14, 3-16, 3-20, 3-21, 3-22, 3-24, 5-1, 5-2, 5-3, 5-12, 5-13, 5-16, 5-20, 5-24, 5-25, 5-26).
Professor I. Chester Jones (Figs. 5-12, 5-13, 5-20, 5-24).
Colston Research Society (Figs. 5-14, 5-23).
Company of Biologists (Figs. 2-1d, 2-4, 5-1, 5-2).
Council of the Marine Biological Association of the United Kingdom (Figs. 3-1, 5-3, 5-26).
D. C. Heath & Co. (Fig. 5-8).
Koninklijke Vlaamsche Academie voor wetenschappen, Brussels (Fig. 5-11).
Marine Biological Laboratory, Wood's Hole, Massachusetts (Figs. 2-1c, 2-5, 2-7, 2-9b, 3-2, 3-12, 3-15, 5-4, 5-7).
Masson et Cie. (Figs. 2-1e, 2-9a).
Oxford University Press (Figs. 2-1d, 2-4).
Springer Verlag (Figs. 2-1b, c, g, 2-2, 3-9, 3-10, 3-11, 5-18, 5-19).
Stazione Zoologica, Naples (Fig. 2-6).
Charles C. Thomas (Figs. 2-14c, 2-15).
University of Chicago Press (Figs. 5-5, 5-17).
Verlag Birkhäuser (Fig. 2-3).
Wistar Institute of Anatomy and Biology, Philadelphia (Figs. 3-13, 3-17).

I am most grateful for the skill and understanding co-operation of Mr. W. R. B. Buchanan and his staff in redrawing many of these figures and interpreting my sketches; and for the clear photographs of my drawings, taken by Mr. Ken Wood, for Figs. 2-1 (*a–f*) and 2-14. I also wish to thank Miss J. McKinney for her help in completing the indices and not least Mrs. P. M. Richards for her unstinted help and encouragement in the preparation of the typescript and the main part of the indices, and in correction of the proofs. Finally it is a pleasure to acknowledge my indebtedness for the many facilities afforded me by the Director and Library staff of the Marine Biological Laboratory, Plymouth, as well as by the staff of the Zoological Department at Bristol.

FOREWORD

A foreword, like an aperitif, should whet the appetite without dulling the critical appreciation of what is to follow. Many wise people therefore avoid them. Nevertheless, it is a personal pleasure for me to be asked to provide one to this volume, for the initiation of which I was, at least in part, responsible.

Specialized scientific publications in these days may be broadly, and thus inaccurately, divided into scientific papers summarizing experiments, reviews summarizing scientific papers, and books summarizing reviews. Among the multitude of these last, the really interesting book is all too rare—one with a broad but scholarly treatment, which stimulates the reader to think about the subject, to produce his own ideas and to design his own experiments. Such a book must provide a sufficiently clear account of the experimental techniques for the student to appreciate the methods of study and their limitations; it must establish a theoretical background which gives coherence to the subject as a whole; finally it must tread sufficiently near to the frontiers of knowledge to provide a glimpse of what may lie beyond.

Such a stimulus has already reached several generations of Bristol students through Dr. Jenkin's lectures on hormones; I hope that in its present form her book will successfully challenge a wider audience.

JOHN E. HARRIS

PREFACE

The idea of writing this book arose from lecturing on hormones to second and third year students of zoology, for whom the subject formed part of a course in comparative physiology. It was found that no introductory book covered the whole subject equally; even Hanström's admirable *Hormones in Invertebrates* (1939) dealt with only a part of the field and was already out of date in 1956, when he assured me that he would not be rewriting it and encouraged me to attempt this general survey.

To do so necessitated evolving a scheme within which to consider and select suitable examples from the mass of available material. This resulted in a comparative arrangement, which should be of general application, since it is based on the actions of hormones, rather than on their sources or on their phyletic distribution.

The actions of hormones were then seen to fall into three well-defined groups, the *kinetic*, the *metabolic* and the *morphogenetic*, although these had not all been named nor clearly defined at that time. Subdividing these groups brought together examples acting upon similar effectors, such as muscles, chromatophores or glands, or having similar metabolic actions, such as increasing water excretion, blood-sugar or respiration. Still further subdivision brought together the hormones that stimulate a given action or facilitate a given process and separated them from those having the opposite effects. When consistently adhered to, this approach helped to give a clear picture of hormone actions, to emphasize cases where antagonistic hormones were known and to draw attention to apparent gaps in recorded knowledge.

In writing the book, invertebrates and vertebrates were placed side by side to show the extent to which both are now known to have hormones with similar actions. Describing the invertebrate examples before those from vertebrates was a deliberate attempt to emphasize this fact. To have given pride of place to the vertebrates might have given a more clear-cut picture, and could certainly have provided more abundant and detailed examples; but it would have thrown the intended comparison out of perspective. The search for good examples among invertebrates proved unexpectedly successful. It has been decided, therefore, to publish the book in two parts instead of one; but the unified plan of relatively simple presentation is being maintained.

The present part of the book covers only the kinetic and metabolic hormones, their sources, actions and the ways in which their secretion is controlled. The second part* will contain a similar treatment of the morphogenetic hormones, namely those concerned with growth, differentiation and reproduction; it will also discuss such topics as the relation of the chemical constitution of hormones to the sources from which they are derived and their type of action. A consideration of the distribution of hormones in the animal kingdom may also throw some light on the possible evolution of these chemical activators, as well as suggesting problems for investigation.

Many of these problems must be apparent to anyone who surveys the field of hormone research; yet it is permissible to assume that few research workers have time to undertake such a survey, as their own work becomes more and more specialized and results in the publication of books that are confined to single classes of animals or single endocrine organs. It is therefore hoped that the present work may be useful to some specialists as well as to the teachers and students for whom it is primarily intended.

It has clearly not been possible for the writer to review the whole literature of so rapidly expanding a subject; but the main original papers on the kinetic and metabolic hormones of invertebrates have been covered up to the summer of 1958, while the vertebrate examples have been checked by recent reviews and reports of symposia. The references at the end of each chapter show the sources used, but make no pretence to being complete, though they should provide a useful starting point for anyone wishing to go further.

* *Animal Hormones*, a comparative survey. Part II. *Morphogenetic Hormones*, in preparation.

It is much to be regretted that these references are not more nearly up to date; but publication has been delayed by various unforeseeable causes, including the printing industry's national dispute during 1959 and the writer's serious illness.

Finally a word of explanation about some of the things which have not been included in the book. Examples in which extracts of one kind of animal have been tested upon another kind have been avoided, on the grounds that they are apt to lead to unsound physiological deductions. Details of standard techniques are omitted, since the reader can refer to any physiological textbook for an account of such methods as recording muscle contractions by means of levers that mark a revolving smoked drum (e.g. Figs. 3-1 and 3-3). The use of commercial hormone preparations and methods of quantitative estimation of hormones by biological assay are also omitted, as being primarily of clinical interest. Since the book is intended for zoologists and comparative physiologists, the mammalian examples have been chosen from species other than man, while reference to pathological and clinical material has been omitted, as being outside their chosen field. Such material is easily accessible elsewhere, and should not be difficult to fit into the present framework, if the reader so desires.

Bristol. P. M. J.

CORRIGENDA

Figure 2–14 should be inserted facing page 48, as indexed, instead of at page 23 as at present.

Figure 5–8 (page 194) caption, line 6, should read "a coenzyme" instead of "an enzyme".

References to Chapter 5 (page 264) should include:

OWEN, J. A. and ENGEL, F. L. (1957) *Endocrinology*, **60**: 698–704.

Animal Hormones: a comparative survey. Part 1—Kinetic and Metabolic Hormones.

CONTENTS

LIST OF TABLES

CHAPTER 1

INTRODUCTION

1.1 Discovery of hormones

The discovery of hormones was a late-comer in the study of physiology; the circulation of the blood was demonstrated in the seventeenth century by Harvey (1628), but it was more than two centuries before it was realized that chemical messengers could be carried in that circulation. The first hint of this was when Berthold (1849)* showed conclusively that the morphogenetic effects of transplanting the testes of cockerels must be transmitted by some factor in the blood. It was even longer before Oliver and Schäfer (1895) found that a chemical extract of the adrenal medulla, if injected into the circulation, could induce a pronounced rise in blood pressure. In 1901 the active substance in this extract was isolated, identified and called adrenaline. The general term "Hormone" is derived from the Greek ὁρμάω, meaning "I arouse", and indicates the stimulating action of such chemicals; it was first used by Starling (1905) for secretin, that had been discovered in 1902 and shown to induce the flow of alkali from the pancreas. Two hormones concerned with the cure of human disease, insulin for the control of diabetes mellitus, and thyroxine for cretinism, were among the more spectacular discoveries of the early twentieth century, and led to an intensive search for more hormones in man and other mammals. This resulted in the gradual discovery of some thirty kinds of endocrine cells and glands that can produce minute quantities of chemical substances which are carried in the blood, to stimulate or inhibit various specific effectors, or to control different aspects of metabolism and morphogenesis.

* See Harris (1955) for a translated account of his experiments.

The first indication of any hormone in an invertebrate was that postulated by Kopeć (1922) as carrying the brain stimulus for moulting in *Lymantria*. Then Koller (1927) found a blood-borne factor controlling the colour changes of certain shrimps, and Perkins (1928) located its source in the eyestalk. The discovery of other hormones has followed, mainly in crustaceans and insects, where they have almost as many actions as those carried out by the better-known hormones of vertebrates.

1.2 Chemical activators

During this period, when hormones were being discovered in ever-increasing numbers, different kinds of chemical activators were being found in other fields of biology. Substances akin to hormones were found in plants; nerve transmission in vertebrates and some invertebrates was found in many unrelated species to be due to release of either acetylcholine or adrenaline, at the point of contact between one neuron and the next, or between the motor axon and its effector. The control of the pattern of development in early embryos of Amphibia was found to be due to the diffusion from cell to cell of particular chemical substances or organizers; these substances were not specific in that they were capable of producing similar effects in a wide range of genera (Spemann and Mangold, 1924).

Some order was brought into the variety and diversity of these and other chemical activators by Huxley (1935) in an important scheme of classification. Its main weakness was that it did not include neurosecretory cells derived from nerve cells and capable of yielding hormones. These cells had been recognized histologically in vertebrates by Dahlgren (1914), and in some invertebrates by Hanström (1931); but their action in releasing hormone-like substances into the blood was first established by the Scharrers (1937). They are now well known in Annelida, Arthropoda and some other invertebrates as well as in vertebrates.

Huxley's (1935) classification of chemical activators may therefore be modified as follows, to include neurosecretion:

A. Para-Activators. By-products of normal and pathological metabolism with effects on correlation or differentiation, e.g. carbon dioxide in its effect on the respiratory centre.

B. TRUE ACTIVATORS. Chemical substances produced by the organism and exerting specific functions in regard to correlation or differentiation:

1. *Local activators*, with effects on the same cell, or cells, within which they are produced.
   - (a) *Intracellular activators* ("intracellular hormones" of Goldschmidt), acting in each cell singly and being the direct expression of *gene* activity, in relation to regional differentiation.
   - (b) *Regional activators*, responsible for the *chemodifferentiation* of specific regions in embryos and for *growth gradients*.
2. *Distance activators*, with effects on cells other than those in which they are produced.
   - (a) *Diffusion activators*, distributed by diffusion through the tissues.
     - (i) Direction of transport restricted by structural organization. *Growth hormones* in *plants*.
     - (ii) Diffusion restricted to tissues in direct contact. *Organizers* in embryos and "*organisines*" in animals without a circulatory system. It is possible that the cortical releasing factor, *CRF*, from the brain of vertebrates should also be included here (§ 4.323).
     - (iii) Diffusion restricted mainly by chemical means. *Neurohumoral secretions* at nerve- and neurosecretory cell-endings ("neurohormones" of Welsh, 1955).
     - (iv) Diffusion unrestricted, the substances passing out of the tissues and into the surrounding medium to act on other individuals, usually of opposite sex. These include "*gamones*" and "*ectohormones*".
   - (b) *Circulatory activators* or *vascular hormones*, distributed to all parts of the body in the blood circulation, so that their actions must be limited by the sensitivity or competence of the tissues which they reach. They may be secreted by:
     - (i) *Isolated cells* such as those of unknown origin in the gut mucosa of vertebrates (§ 2.21).