Contents

Introduction VII
Foreword VIII
Prologue XI

Chapter 1
Introduction into the Comparative Physiology of Sleep . 1
The Subject and the Aims of the Investigation 1
Comparative and Evolutionary Aspects of the Study of Sleep
(Review of the Literature) 5
Fish 7
Amphibians 8
Reptiles . 9
Birds 15
Mammals . 19

Chapter 2
Evolution of the Circadian Biorhythmcity of Sleep and Wakefulness 24
Species-Specific and Seasonal Characteristics of Circadian Biorhythmcity of
Wakefulness and Sleep in Fish, Amphibians and Reptiles 25
Data Obtained on the Catfish (Ictalurus nebulosus) 28
Data Obtained on the Brown Frog (Rana temporaria) . 33
Species Characteristics of the Circadian Periodicity of Wakefulness and Rest in Some
Fish of the Black Sea Basin 40
Characteristics of Circadian Periodicity of Wakefulness and Rest in the Lake Frog
(Rana ridibunda) 47
Circadian Periodicity of Wakefulness and Rest in the Pond Turtle 48
Species-Specific Characteristics of the Circadian Periodicity of the Wakefulness-Sleep
Cycle in Day-and Night-Time Birds 53
Data Obtained on Hens . 53
Data Obtained on Owls . 55
Conclusions 60

Chapter 3
On the Comparative-Physiological A nalysis of the Nature and Regulation of the States
of Wakefulness, Rest and Sleep 66
Reptiles 80
Birds 81
Introduction

It is with a great deal of pleasure that I follow the suggestion and wish of both the author and publisher to introduce this book with a few words of appreciation and thanks.

Among the many topics on sleep that have been written about during the last forty years, its evolutionary aspects - aside from a few single articles - have been all but neglected. Still, studies on the evolution of this important second state of our existence - even if they consider the vertebrates only - are bound to yield many important and novel data that can greatly enrich our insight into, and our understanding of, sleep; in particular its functional significance, its ‘purpose’, as well as its controlling mechanisms. Professor Karmanova, together with her dedicated collaborators, has produced a host of such new information, only a small part of which has found its way into the literature of the West. So we learned only very late about her important concept of primary sleep-, the evolutionary forerunner of the sleep as we know it in our (mainly mammalian) laboratory animals. With this book we have, for the first time, an opportunity to get acquainted with Professor Karmanova’s extensive work along these lines. This book also cites a number of other contributions from Eastern countries which would
have otherwise been lost for us in the West and we would have been deprived of some very important information about a special and - as mentioned above - very significant area of sleep research.

I had an opportunity to read, and was asked to judge, the manuscript of this book - a translation from a Russian original. Admittedly, it proved to be necessary to correct many linguistic deficiencies and - at times - also the style of presentation. Still on many occasions I preferred to leave the text as it stood, in order not to alter the ‘Eastern’ flavor of the writing style, not rarely going parallel with the ‘Eastern’ style of doing research which, as we all know, often differs from our own attitude but, nonetheless, is not to be regarded to be any worse than our way of doing things.

With this book, Ida Gavrilovna Karmanova has done an excellent service to all sleep researchers.

Werner P. Koella
+
Foreword

The question about the essence of sleep, of this everyday and wellknown state characterized by changes in the entire behavior and especially by changes in brain activity, of the state vital both for man and animals for the maintenance of normal life activity, has been attracting close attention by researchers for many decades. However, science is still far from having a clear and exhaustive answer to the question of what sleep is from neurophysiological, metabolic, biochemical, psychological and many other points of view. We cannot as yet answer the question as to what sleep is necessary for in detail, although we subjectively can comprehend a state which is expressed by the words ‘I want to sleep’; and another one which we all experience with a feeling of being rested; i.e. the restoration of mental and physical capacities even after short-time period sleep.

An intensive study of the events connected with the state of sleep has revealed that, as judged by the physiological mechanisms regulating sleep, by the neurophysiological patterns of the processes observed in brain, and by a number of other functional shifts in the organism accompanying it, sleep is a far more complex phenomenon than it has been thought before. The establishment of the fact that sleep in normal man consists of two different phases which were termed slow wave sleep (SWS) and rapid or paradoxical sleep (PS) appeared to be a turning point in the study of sleep. Their physiological characteristics were found to be opposites in many aspects. Dreams turned out to be connected with the PS phase. The experiments in various laboratory animals have revealed that sleep in many infrahuman species also consists of these two different phases; however,
their relative proportion is quite variable in the various species. SWS and PS underwent further electrophysiological investigation which showed that both sleep phases possess complex multilink organizations. One of the problems, of interest from the evolutionary point of view, lies in the question as to which one of the two phases would be the more ancient one. A number of data in fact give evidence that PS seems to be the phylogenetically more ancient one; however, there are arguments in favor of the opposite point of view.

Foreword IX

It always was assumed that if sleep is a period of rest, relaxation and restoration, then metabolism during this state should be reduced; namely circulatory activity be slowed down etc. However, many investigations have revealed that brain blood flow increases already with the transition from quiet wakefulness to SWS and sharply rises again with the appearance of PS. Investigations neither of the O2 consumption in brain nor of the CO2 dynamics suggest a decrease in energy processes during sleep.

As has been stated above, numerous cardinal problems remain unsolved in spite of a great number of investigations. Every researcher in the field of natural sciences must always bear in mind that no phenomenon can be understood unless the history of its origin and of its development is clarified. Thus, the problem of sleep should also be approached from the point of view of evolutionary physiology. The essence of Prof Karmanova's monograph lies in the fact that it is pointedly aimed at the clarification of the problem of sleep and sleep-like states seen in the light of evolutionary processes. Here though it should be mentioned that even before Prof Karmanova started her numerous and purposeful investigations on the evolution of sleep, there had been many pieces of research devoted to the comparative-physiological study of the process of sleep and other related forms of rest performed on various vertebrates - mammals, birds as well as poikilothermic species. Many of those works resulted in quite interesting facts.

When studying problems of the evolution of sleep. Prof Karmanova touched upon an extremely wide range of questions. First, the evolutionary approach demanded a well thought-out choice of experimental animals among various classes of vertebrates. Second, this work called for taking into all-embracing consideration of the animals' ecological peculiarities and of various forms of sleep and wakefulness in all the organisms studied in connection with their terrestrial or aquatic mode of life. For these investigations, the author proceeded from her earlier work devoted to the analysis of the phenomenon of 'photogenic catalepsy' [cf Karmanova, 1964].
Prof Karmanova began her investigations from the analysis of the evolution of circadian biorhythms of wakefulness and rest in poikilotherms. Numerous forms of wakefulness, sleep and sleep-like states were subjected to electrophysiological analysis and problems concerning the central control of the functions of sleep in the representatives of various classes have been investigated. Based on those investigations, an attempt was made to classify the forms of sleep in vertebrates. This work revealed an urgent need for a thorough study of sleep in the course of ontogenesis of various vertebrate species and also of an intensification of complex researches of sleep during its evolution by physiologists and biochemists.

The data stemming from the study of behavioral and electrophysiological aspects of sleep, rest and wakefulness in poikilotherms with all their variations in ecology and life rhythms are of particular interest in the present context. The author has introduced the concept of 'primary sleep' for fish and amphibians and that of 'intermediate sleep' for reptiles. The study of the evolution of sleep in the course of phylogensis of vertebrates reveals the universality of the recurrence of spontaneously arising activation of various brain systems proceeding against the background of sleep and sleeplike states. The author develops her notions on the departure of the paradoxical phase of sleep from more primitive forms of activation arising in poikilotherms against the background of their primary sleep. Of course, as always, observations and facts presented in a given book call for further investigation. However, there is no doubt that this monograph by Prof Karmanova is a valuable contribution to the literature on the study of sleep and it is the first work devoted in its entirety to research on the grounds of evolutionary theory.

E.M. Kreps

Prologue

A certain language barrier existing between the physiologists of East and West hampers swift spreading of scientific ideas. Therefore, I cherish some hopes that the English edition of this book will be helpful for all those who work on sleep, in learning about some - as it seems, important aspects of hypnology that are being worked on in our part of the world. The English edition of the present book contains many observations which have been obtained at our laboratory during the years after the publication
of this book in Russian. In particular, the stages of evolution of the diurnal organization of the states of 'wakefulness-sleep' cycle in vertebrates from fish to mammals are defined more accurately. This book also presents data confirming the divergent nature of evolution of the ancient forms of rest, i.e. immobility of the catalepsy, catatony and cataplexy type which we consolidated into the one concept of 'primary sleep'. One of the major theses set forth in the present treatise is the hypothesis about the existence of the evolutionary succession between these forms of rest and the states of 'wakefulness-sleep' cycle in higher vertebrates.

It is my hope that this book might be useful not only to physiologists but to geneticists and clinical neurologists as well. So, pathological forms of sleep revealing manifestations of catalepsy, catatony and cataplexy, which are well known to physicians, have first been identified by us in fish and amphibians as natural states constituting their primary sleep. This allows approaching the characterization of disturbed forms of sleep in man in a new way, basing on the theory of the evolution and dissolution of sleep.

I want to express deep gratitude to all my co-workers who rendered invaluable help during the work on the elaboration of the theory of the evolution of sleep; their names appear in many of the references added to this book. I also feel most indebted to Prof. N.N. Demin, a neurochemist, and to Prof A.I. Vein, a neuropathologist, for their fruitful scientific cooperation. I am also thankful to Prof Olga Petre-Quadens and to Prof Werner P. Koella who visited our laboratory and stimulated and supported our research through their penetrating suggestions into the 'logic' of the present investigation.

Ida Gavrilovna Karmanova