ANIMAL BEHAVIOR

Neurophysiological and Ethological Approaches

Edited by
Kiyoshi Aoki,
Susumu Ishii, and
Hiromichi Morita



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Foreword

This volume is the research results of the special project on "The Mechanisms of Animal Behavior" supported by a Grant-in-Aid for Special Project from the Ministry of Education, Science and Culture of Japan from 1979 to 1982. The purpose of the project was to promote an interdisciplinary approach to the study of behavioral mechanisms giving particular impetus to the area of animal behavior. The value of research on the latter subject is increasing because of the growing interaction between biologists, neurophysiologists and molecular biologists, and a single volume which includes original reviews of recent research progress on behavior in both lower and higher animals is of great significance. It is hoped that these articles will stimulate researchers in neuroethology as the subject has been defined by Drs. G. Hoyle and J.-P. Ewert, and will introduce the field to young scientists who are interested in animal behavior. It is my sincere hope that the volume will be of great benefit to both researchers and students in this interesting area of science.

> Masutaro Kuwabara National Institute for Basic Biology

Preface

The special grant-in-aid "The Mechanisms of Animal Behavior" was the first large biological research project in Japan and involved about 100 researchers from such different fields as zoology, ethology, neurophysiology, neurochemistry, neuroanatomy, and genetics. The project had two objectives, both applicable to vertebrates and invertebrates: one was to gain a greater understanding of the neurophysiological bases of animal behavior, especially instinctive behavior; the other was to provide impetus to the growing significance of electrophysiological, neuroanatomical, quantitative, and ethological studies of animal behavior. The seven subject areas into which the project was divided were: 1) behavior of unicellular organisms, 2) genetics and developmental analysis of animal behavior, 3) hormonal control of animal behavior, 4) analysis of releasers in animal behavior, 5) neural mechanisms of key stimulus detection, 6) neural command systems in animal behavior, and 7) mechanisms of rhythmic behavior and motivation.

The papers in this volume were presented at five symposia organized by the general committee of the project from 1979 to 1982. Dr. J.-P. Ewert and Dr. W. Heiligenberg were among those attending the final

symposium held at Sophia University in December, 1982 and presented special lectures on various approaches to vertebrate neuroethology from their area of study. Dr. F. Huber who attended the symposium on "Neurons and Behavior" held in Kyoto in August, 1980, has contributed speculative reviews of insect behavior of somewhat greater scope. Dr. R. Wyman who attended the symposium on "Genetic and Developmental Analysis of Insects" held in Tokyo in 1981 has also contributed a review highlighting his research. Japanese contributors have provided a collection of papers representing a variety of approaches to the study of animal behavior, including multidisciplinary research in neurophysiology, ethology, neurochemistry, and endocrinology. This book is intended to point out some of the major questions about animal behavior and instinctive behavior and to demonstrate some of the ways by which answers to these questions are being sought. Through the presentation of these ideas and methods young researchers and students are introduced to ways of developing their own studies. A special intention of this book is to promote interdisciplinary research among scientists from such diverse fields as biology, medicine, psychology and agriculture.

The editors would like to dedicate this book to Dr. Masutaro Kuwabara, a promoter of the field of neurobiology in Japan. For many years he realized the great need for research on animal behavior in this country and his efforts were rewarded when this special interdisciplinary research project was initiated. We honor him for his stimulating contributions to this field.

We are particularly grateful to Dr. F. Huber, Dr. R. Wyman, Dr. J.-P. Ewert and W. Heiligenberg for their contributions and are also grateful to our companions of the project. We would also like to thank Ms. Akiko Sakai for her help in the preparation of the book.

We would like to express our deep gratitude to the Ministry of Education, Science and Culture of Japan for its substantial financial support towards the publication of this volume.

July 1983 Editors

Introduction

The aim of this book is to introduce research workers and graduate students of biology to a developing area of knowledge uniting studies on behavior and neurobiology in Japan. Reports are presented by foreign neurobiologists and Japanese research workers whose intention is to contribute to the current state of knowledge on the mechanism of animal behavior.

Historically speaking, ethology is still a young research area with no overall framework. It is only recently that the descipline has become generally accepted as a branch of the natural sciences. The main emphasis of early ethological research initially dealt with "The Study of Instinct" in 1951 by N. Tinbergen. Written in German, the 1952 translation into English opened wide-ranging interpretive discussions of animal behavior among ethologists, behaviorists and comparative physiologists. Tinbergen illustrated that K. Lorenz proposed a synthesis which forms the basis of ethology and the main subject of his study was the innate motor pattern underlying instinctive movements, a physiological event overlooked by the physiologist of classical reflex. From his analysis of innate behavior patterns, Lorenz found the key stimuli that release a specific behavior, and discovered from his own observation, an inborn disposition to learn in the phenomenon of im-

printing as a basis for induction. Tinbergen provided many suggestions for later studies by dominant and subordinate instincts, in his schema of the "hierarchy of instincts" based on his studies of the reproductive behavior of sticklebacks. New concepts of innate and acquired releasing mechanisms, imprinting, drive intensity and central nervous hierarchies for sensory and motor functional processes of fixed action patterns were born from the study of ethology. Von Frish, Lorenz and Tinbergen were awarded the 1973 Nobel Prize for their foundation of comparative behavior. Tinbergen wrote "Our next task after the study of the sensory stimulus and the hormones involved would have to be a study of what happens in the nervous system." Since that time the order of functional organization within the central nervous system has been described.

The major development in neurophysiology, meanwhile, has been a much greater understanding of the structure and function of the nervous system as a result of the progress of electrophysiology and the electron microscope. The characteristic action of this system is clarified by electrophysiological analysis in three broad categories of electrical events:

- 1) Compound potential waves due to the synchronized activity of many neurons; these are recorded from the surface of the brain or scalp.
- 2) Unitary action potential recorded from a single neuron of fiber by fine electrode.
- 3) Local graded potentials generated in the dendrites, soma axon and pre- and postsynapse of nerve cells; these can be obtained by intracellular recording.

This kind of information can help the observer to understand the involvement of neurons in the correlation of animal behavior with neural events or specific stimuli. However, the nervous system is so intricate and nerve elements so numerous that it often proves difficult to decide whether or not they are related to any given behavioral phenomenon. Therefore, it becomes necessary to ask questions about the kinds of deductions which are regarded as meaningful with reference to the special problems of behavior and neural events. Researchers of

INTRODUCTION

behavior seek the entities which underlie observable behavioral phenomena and which offer broad generalized explanations for those phenomena. Some of their answers may have a neural basis and neuroethology is concerned with the way in which the release and control mechanisms of behavior depend on the action of cellular elements of the nervous system.

The reports in this book were presented at five symposia held in conjunction with a Special Grant-in-Aid Project "The Mechanisms of Animal Behavior" from 1979 through 1982. They deal with implications of the mechanisms of animal behavior from diverse aspects, such as ethology, neuroethology, neuroanatomy, neurophysiology, endocrinology and neurogenetics. Contained is information gained in experimental exploration on such questions as:

- 1) How are signals detected in the brain?
- 2) What are the means of detecting, recognizing and recalling information in the central nervous system?
- 3) How can genetical behavior be related to neuronal mechanism?
- 4) What is the endocrinological basis for the motivation of behavior?

Selected among studies which have made a contribution to neuroethology in the research of the animal behavior, the main chapter topics provide facts on the neural bases of behavior of both invertebrates and vertebrates. General emphasis by chapter is:

- 1) How do research strategies differ between invertebrate neuroethology and vertebrate ethology?
- 2) How are ontogenetic developments and genetics related to neuronal mechanisms?
- 3) How are signals recognized in insects? How is a motor pattern coordinated and controlled in invertebrates?
- 4) What is the neuronal mechanism of stimulus in vertebrates? How are sensory decisions made and transformed into an efferent motor in vertebrates?
- 5) What are the bases for motivation of behavior from hormonal events?

6) What are the bases for rhythmical behavior?

It is hoped that the researcher of animal behavior will find interest in this neuroethological study of behavior and that the topics covered will provide many fruitful suggestions for further study on this subject.

August 1983

Kiyoshi Аокт Sophia University

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