Behavior of the lower organisms

Jennings H S
Columbia University Biological Series

EDITED BY
HENRY FAIRFIELD OSBORN
AND
EDMUND B. WILSON

I. FROM THE GREEKS TO DARWIN
   By Henry Fairfield Osborn

II. AMPHIOXUS AND THE ANCESTRY OF THE VERTEBRATES
    By Arthur W. Willard

III. FISHES, LIVING AND FOSSIL. An Introductory Study
    By Bashford Dean

IV. THE CELL IN DEVELOPMENT AND INHERITANCE
    By Edmund B. Wilson

V. THE FOUNDATIONS OF ZOOLOGY
    By W. K. Brooks

VI. THE PROTOZOA
    By Gary N. Calkins

VII. REGENERATION
    By T. H. Morgan

VIII. THE DYNAMICS OF LIVING MATTER
    By Jacques Loeb

IX. STRUCTURE AND HABITS OF ANTS. (In preparation)
    By W. M. Wheeler

X. BEHAVIOR OF THE LOWER ORGANISMS.
    By H. S. Jennings
BEHAVIOR OF THE LOWER ORGANISMS
BEHAVIOR OF THE LOWER ORGANISMS

BY

H. S. JENNINGS

ASSISTANT PROFESSOR OF ZOOLOGY IN THE UNIVERSITY OF PENNSYLVANIA

New York
THE COLUMBIA UNIVERSITY PRESS
THE MACMILLAN COMPANY, AGENTS
LONDON: MACMILLAN & CO., LTD.
1906

All rights reserved
PREFACE

The objective processes exhibited in the behavior of the lower organisms, particularly the lower animals, form the subject of the present volume. The conscious aspect of behavior is undoubtedly most interesting. But we are unable to deal directly with this by the methods of observation and experiment which form the basis for the present work. Assertions regarding consciousness in animals, whether affirmative or negative, are not susceptible of verification. This does not deprive the subject of consciousness of its interest, but renders it expedient to separate carefully this matter from those which can be controlled by observation and experiment. For those primarily interested in the conscious aspects of behavior, a presentation of the objective facts is a necessary preliminary to an intelligent discussion of the matter.

But apart from their relation to the problem of consciousness and its development, the objective processes in behavior are of the highest interest in themselves. By behavior we mean the general bodily movements of organisms. These are not sharply distinguishable from the internal physiological processes; this will come forth clearly in the present work. But behavior is a collective name for the most striking and evident of the activities performed by organisms. Its treatment as subsidiary to the problems of consciousness has tended to obscure the fact that in behavior we have the most marked and in some respects the most easily studied of the organic processes. Such treatment has made us inclined to look upon these processes as something totally different from the remainder of those taking place in organisms. In behavior we are dealing with actual objective processes (whether accompanied by consciousness or not), and we need a knowledge of the laws controlling them, of the same sort as our knowledge of the laws of metabolism. In many respects behavior presents an exceptionally favorable field for the study of some of the chief problems of life. The processes of behavior are regulatory in a high degree. Owing to their striking character, the way in which regulation occurs becomes more evident than in most other fields, so that they present a most favorable opportunity for study of this matter. To
the regulatory aspect of behavior special attention is paid in the following pages.

The modifiability of the characteristics of organisms has always been a subject of the greatest importance in biological science. In most fields the study of this matter is beset with great difficulties, for the modifications require long periods and their progress is not easily detectible. In the processes of behavior we have characteristics that are modifiable with absolute ease. In the ordinary course of behavior variations of action are continually occurring, as a result of many internal and external causes. We see quickly and in the gross the changes produced by the environment, so that we have the best possible opportunity for the study of the principles according to which such changes occur. Permanent modifications of the methods of action are easily produced in the behavior of many organisms. When we limit ourselves to the subjective aspect of these, thinking only of memory, or the like, we tend to obscure the general problem involved. This problem is: What lasting changes are producible in organisms by the environment or otherwise, and what are the principles governing such modifications? Perhaps in no other field do we have so favorable an opportunity for the study of this problem, fundamental for all biology, as in behavior. There seems to be no a priori reason for supposing the laws of modification to be different in this field from those found elsewhere. The matter needs to be dealt with from an objective standpoint, keeping the general problem in mind.

A study of behavior from the objective standpoint will help us to realize that the activities with which we deal in other fields of physiology are occurring in a substance that is capable of all the processes of behavior, including thought and reason. This may aid us to be on our guard against superficial explanations of physiological processes.

But the chief interest of the subject of the behavior of animals undoubtedly lies, for most, in its relation to the development of psychic behavior, as shown by man. The behavior of the lowest organisms must form a fundamental part of comparative psychology.

In the special field of the behavior of the lowest organisms the foundations of our knowledge were laid by Verworn, in 1889, in his "Psycho-physiologische Protistenstudien." Binet, in his "Psychic Life of Micro-organisms" (1889), gave a most readable essay on the subject, presenting it frankly from the psychical standpoint. Lukas, in his "Psychologie der niedersten Tiere" (1905), has recently again dealt with the questions of consciousness in lower animals, the treatment of objective processes being subsidiary to this matter.

The present work was designed primarily as an objective descrip-
tion of the known facts of behavior in lower organisms, that might be used, not only by the general reader, but also as a companion in actual laboratory experimentation. This description, comprising Parts I and II of the present work, on the Protozoa and lower Metazoa, respectively, was made as far as possible independent of any theoretical views held by the writer; his ideal was indeed to present an account that would include the facts required for a refutation of any of his own general views, if such refutation is possible. These designs have involved a fuller statement of details, with sometimes their repetition under new experimental conditions, than would have been necessary if the theoretical discussion had been made primary, and only such facts adduced as would serve to illustrate the views advanced. But the scientific advantages of the former method were held to outweigh the literary advantages of the latter.

As originally written, this descriptive portion of the work was more extensive, including, besides the behavior of the Protozoa and Coelenterata, systematic accounts of behavior in Echinoderms, Rotifera, and the lower worms, together with a general chapter on the behavior of other invertebrates. The work was planned to serve as a reference manual for the behavior of the groups treated. But the exigencies of space compelled the substitution of a chapter on some important features of behavior in other invertebrates for the systematic accounts of the three groups last mentioned. The accounts of the Protozoa and of the Coelenterata as representative of the lowest Metazoa remain essentially as originally written.

After this objective description was prepared, the need was felt for an analysis of the facts, such as would bring out the general relations involved. Part III is the result. Thus the conclusions set forth in Part III are the result of a deliberate analysis of the facts presented in a description which had been made before the conclusions had been drawn. The selection of facts set forth in the descriptive parts of the work has therefore been comparatively little affected by the general theories held by the writer. The loss of unity toward which this fact tends has perhaps its compensation in the impartiality which it helps to give the descriptions.

The writer is conscious of the necessarily provisional nature of most general conclusions at the present stage of our knowledge, and the analysis given in Part III is presented with this provisional character fully in mind. The reader should approach it in a similar attitude.

Since the book is written primarily from a zoological standpoint, it would be appropriate in some respects to entitle it "Behavior of the Lower Animals." But the broader title seems on the whole best, since the treatment of unicellular forms involves consideration of
many organisms that are more nearly related to plants than to animals.

The figures have been drawn for the present work by my wife. Figures not credited to other authors are either new or taken from my own previous works.

The author is much indebted to the Carnegie Institution of Washington for making possible a year of uninterrupted research, devoted largely to studies preliminary to the preparation of this work and to its actual composition. He is further indebted for the use of a number of figures first published by the Carnegie Institution.

University of Pennsylvania,
December 11, 1905.
# CONTENTS

## PART I

**BEHAVIOR OF UNICELLULAR ORGANISMS**

### CHAPTER I

**Behavior of Amoeba**

<table>
<thead>
<tr>
<th>1. Structure and Movements of Amoeba</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>2. Reactions of Amoeba to Stimuli</td>
<td></td>
</tr>
<tr>
<td>A. Reaction to Contact with Solids</td>
<td>6</td>
</tr>
<tr>
<td>B. Reactions to Chemicals, Heat, Light, and Electricity</td>
<td>9</td>
</tr>
<tr>
<td>C. How Amoeba gets Food</td>
<td>12</td>
</tr>
<tr>
<td>3. Features of General Significance in the Behavior of Amoeba</td>
<td>19</td>
</tr>
<tr>
<td>Literature</td>
<td>25</td>
</tr>
</tbody>
</table>

### CHAPTER II

**Behavior of Bacteria**

<table>
<thead>
<tr>
<th>1. Structure and Movements</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>2. Reactions to Stimuli</td>
<td>26</td>
</tr>
<tr>
<td>3. General Features in the Behavior of Bacteria</td>
<td>27</td>
</tr>
<tr>
<td>Literature</td>
<td>37</td>
</tr>
</tbody>
</table>

### CHAPTER III

**Behavior of Infusoria; Paramecium**

*Structure; Movements; Method of Reaction to Stimuli*

<table>
<thead>
<tr>
<th>Introductory</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Behavior of Paramecium; Structure</td>
<td>41</td>
</tr>
<tr>
<td>2. Movements</td>
<td>41</td>
</tr>
<tr>
<td>3. Adaptiveness of the Movements</td>
<td>44</td>
</tr>
<tr>
<td>4. Reactions to Stimuli</td>
<td>45</td>
</tr>
<tr>
<td>5. “Positive Reactions”</td>
<td>47</td>
</tr>
<tr>
<td>Literature</td>
<td>54</td>
</tr>
</tbody>
</table>

### CHAPTER IV

**Behavior of Paramecium (Continued)**

*Special Features of the Reactions to a Number of Different Classes of Stimuli*

<table>
<thead>
<tr>
<th>1. Reaction to Mechanical Stimuli</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>2. Reactions to Chemical Stimuli</td>
<td>59</td>
</tr>
</tbody>
</table>

ix
CONTENTS

3. Reactions to Heat and Cold .......................... 70
4. Reaction to Light ........................................ 72
5. Orienting Reactions, to Water Currents, to Gravity, and to Centrifugal Force
   A. Reactions to Water Currents ......................... 73
   B. Reactions to Gravity ................................. 75
   C. Reaction to Centrifugal Force .................... 78
6. Relation of the Orientation Reactions to Other Reactions ......................... 78
Literature .................................................. 79

CHAPTER V

BEHAVIOR OF PARAMECIUM (CONTINUED)

Reactions to Electricity and Special Reactions

1. Reactions to Electricity .................................... 80
   A. Reaction to Induction Shocks ......................... 81
   B. Reaction to the Constant Current .................. 83
2. Other Methods of Reaction in Paramecium ................... 89
Literature .................................................. 91

CHAPTER VI

BEHAVIOR OF PARAMECIUM (CONTINUED)

Behavior under Two or More Stimuli; Variability of Behavior; Fission and Conjugation; Daily Life; General Features of the Behavior

1. Behavior under Two or More Stimuli ....................... 92
2. Variability and Modifiability of Reactions ................ 98
3. Behavior in Fission and Conjugation ..................... 102
4. The Daily Life of Paramecium ............................ 104
5. Features of General Significance in the Behavior of Paramecium
   A. The Action System ................................... 107
   B. Causes of the Reactions, and Effects produced by them ....................... 108
Literature .................................................. 109

CHAPTER VII

BEHAVIOR OF OTHER INFUSORIA

Action Systems. Reactions to Contact, to Chemicals, to Heat and Cold

1. The Action System ..................................... 110
   A. Flagellata ........................................... 111
   B. Ciliata .............................................. 113
2. Reaction to Mechanical Stimuli .......................... 117
3. Reaction to Chemicals ................................... 120
4. Reaction to Heat and Cold ................................ 124
Literature .................................................. 127