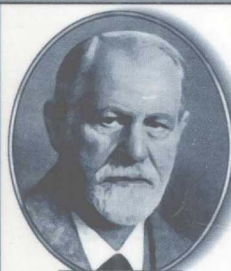


# *Notes on the* ELEMENTS OF BEHAVIORAL SCIENCE



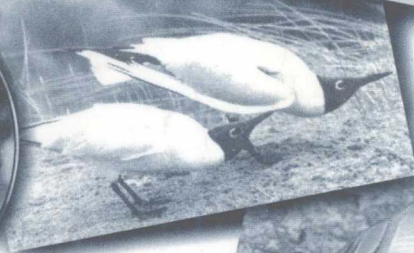
FREUD



MENDEL



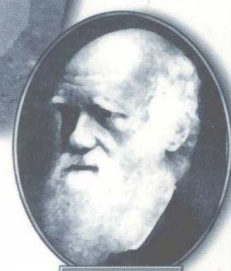
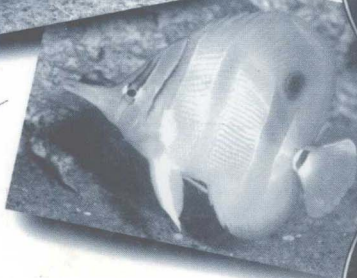
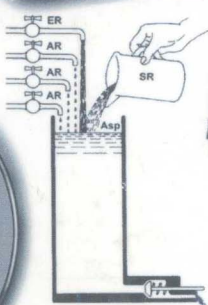
LORENZ



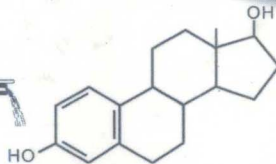
PAVLOV



TINBERGEN



DARWIN



Doris Zumpe and Richard P. Michael

---

*Notes on the*  
**Elements of Behavioral Science**

---

**Doris Zumpe**

and

**Richard P. Michael**

*Emory University School of Medicine  
Atlanta, Georgia*

**Kluwer Academic / Plenum Publishers**

New York Boston Dordrecht London Moscow

Library of Congress Cataloging-in-Publication Data

---

Zumpe, Doris, 1940–

Notes on the elements of behavioral science/Doris Zumpe and Richard P. Michael.

p. cm

Includes bibliographical references and index.

ISBN 0-306-46577-9

1. Psychology. 2. Social sciences. 3. Psychology, Comparative. I. Michael, Richard P. (Richard Phillip) II. Title.

[DNLM: 1. Behavioral Medicine. 2. Behavioral Sciences. WB 103 Z94n 2001]

BF121 .N68 2001

150—dc21

2001020256

---

ISBN: 0-306-46577-9

©2001 Kluwer Academic/Plenum Publishers, New York  
233 Spring Street, New York, New York 10013

<http://www.wkap.nl/>

10 9 8 7 6 5 4 3 2 1

A C.I.P. record for this book is available from the Library of Congress

All rights reserved

No part of this book may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, microfilming, recording, or otherwise, without written permission from the Publisher.

Printed in the United States of America

In fond memory of my parents and of my first great teacher,  
Konrad Lorenz.

D.Z.

To my parents: they found life joyful; and to three of my fine  
teachers, Sir Aubry Lewis, G. W. Harris, and D. W. Winnicott.

R.P.M.

---

# Preface

---

These notes are intended to help undergraduates who need to understand something of behavior both for its intrinsic interest and for their future careers in medicine, biology, psychology, anthropology, veterinary medicine, and nursing. In Emory University's Biology Department, a single-semester course called *Evolutionary Perspectives on Behavior* is given to undergraduates. It amounts to four, not eight months of study, so a great deal of compression is essential. There are several excellent textbooks available that deal with behavioral science from different perspectives, but we have found them too compendious for use in a short course when students are so heavily burdened; it is unsatisfactory to direct them to a chapter here and there in several different books or to this or that review article and original paper. In this volume, we have tried effectively and inexpensively to put in one place what we know is needed. The topics we have selected deal with their subjects in a simple, straightforward way without being too superficial. We could not cover everything and the gaps are not entirely idiosyncratic but reflect what students are given very well in other courses. Thus, there is no mention of the physiology of the axon and synapse; learning, memory, cognition, and basic genetics are hardly touched upon because students know about these matters from elsewhere. This volume particularly emphasizes certain physiological mechanisms when they are known, and it also draws attention to the application of what is known about animal behavior to the human, sometimes even to the clinical situation. The illustrative examples are taken from both the classical behavioral literature and newer work.

It has given us considerable pleasure to write this volume and we trust it will find a useful niche in the education of our students.

## ACKNOWLEDGMENTS

We are grateful to Drs. Andrew Clancy and Darrell Stokes for kindly reading the manuscript and making helpful suggestions. We are also grateful to F. Cawthon and M. Maddox for continuing help and, particularly, to F. Cawthon, who is responsible for all the illustrative material. We also thank several generations of Emory students for stimulating us with their interest and many useful questions.

---

# Contents

---

|          |  |           |
|----------|--|-----------|
| <b>1</b> | <b>The Study of Behavior: History</b>                    | <b>1</b>  |
|          | A Brief History  | 1         |
|          | Classical Ethology                                       | 1         |
|          | Comparative Psychology                                   | 4         |
|          | Emergence of Modern Behavioral Research                  | 5         |
|          | Some Theory and Terminology                              | 6         |
|          | Fitness and Inclusive Fitness                            | 6         |
|          | Benefit–Cost Ratios                                      | 7         |
|          | Optimality Theory  | 7         |
|          | Game Theory  | 8         |
|          | Evolutionarily Stable Strategies                         | 9         |
|          | General Life Strategies: <i>K</i> and <i>r</i> Selection | 10        |
|          | Warnings, Fallacies, and Pitfalls                        | 11        |
|          | Correlational Studies                                    | 11        |
|          | Genes: What They Do and Do Not Do                        | 12        |
|          | Understanding Optimality Theory                          | 12        |
| <br>     |  |           |
| <b>2</b> | <b>Some Ethological Concepts</b>                         | <b>15</b> |
|          | Evolutionary Basis of Behavior                           | 15        |
|          | Ethology’s Objectives                                    | 17        |
|          | General Methods  | 17        |
|          |  | <b>ix</b> |

|   |               |
|---|---------------|
| Fixed Action Patterns (FAPs) .....                                  | 18            |
| Unvarying Form .....  | 18            |
| Coordination of Several Muscle Groups .....                         | 19            |
| Environmental Influences .....                                      | 19            |
| Genetic Factors .....   | 22            |
| Brain Stimulation .....   | 22            |
| Conflict Behaviors .....  | 22            |
| Redirection .....   | 24            |
| Displacement .....  | 25            |
| Intention Movement .....  | 27            |
| Alternation .....   | 27            |
| Ambivalence .....   | 27            |
| Compromise .....  | 28            |
| Conflict in Psychiatry .....  | 28            |
| Vacuum Activity .....   | 30            |
| Ritualization and Displays .....                                    | 30            |
| Stereotypy .....  | 31            |
| Typical Intensity .....   | 31            |
| Association with Conspicuous Morphological Features .....           | 31            |
| Threshold Changes .....   | 32            |
| Motivational Changes .....  | 32            |
| <br><b>3 Some More Ethological Concepts .....</b>                   | <br><b>37</b> |
| Sign Stimuli, Releasers, and Innate Releasing Mechanisms .....      | 37            |
| Perception versus Attention .....                                   | 37            |
| Definitions .....   | 38            |
| Properties of Sign Stimuli and Releasers .....                      | 38            |
| Modifying Influences .....  | 41            |
| Supranormal Stimuli .....   | 43            |
| Advantages and Disadvantages of Innate Releasing Mechanisms .....   | 43            |
| Programmed Learning and Imprinting .....                            | 44            |
| Programmed Learning .....   | 44            |
| Imprinting .....  | 45            |
| Drive or Motivation .....   | 48            |
| Illustrative Model for Thirst .....                                 | 49            |
| Drive Models .....  | 51            |
| <br><b>4 Assessment of Hereditary Influences .....</b>              | <br><b>55</b> |
| Indirect Methods .....  | 57            |
| Presence in Geographically Isolated Populations .....               | 57            |
| Presence in Individuals Raised in Isolation from Conspecifics ..... | 58            |
| Phylogenetic Comparisons: Presence in Closely Related Species ..... | 58            |



|  |           |
|--|-----------|
| Association with Specialized Morphological or Physiological Traits . .   | 58        |
| Studies on Human Twins . . . . .   | 59        |
| Direct Methods . . . . .   | 59        |
| Artificial Selection . . . . .   | 60        |
| Inbreeding . . . . .   | 60        |
| Hybridization . . . . .  | 64        |
| Molecular Changes . . . . .  | 64        |
| <b>5 Behavioral Endocrinology: Gonadal Hormones . . . . .</b>            | <b>67</b> |
| Synthesis and Major Sites of Production . . . . .                        | 69        |
| Estrogens and Progestins . . . . .                                       | 69        |
| Androgens . . . . .  | 70        |
| Transport . . . . .  | 71        |
| Mechanisms of Action . . . . .   | 71        |
| Hormone Receptors . . . . .  | 71        |
| Effects on Tissues . . . . .   | 71        |
| Organizational Effects During Development . . . . .                      | 74        |
| Sexual Differentiation: Somatic Modifications . . . . .                  | 74        |
| Sexual Differentiation: Behavioral Modifications . . . . .               | 75        |
| Sexual Dimorphism in Brain Structures . . . . .                          | 77        |
| Activational Effects in Adults . . . . .                                 | 77        |
| Breeding Seasonality . . . . .   | 78        |
| Activational Effects in the Female . . . . .                             | 78        |
| Activational Effects in the Male . . . . .                               | 83        |
| <b>6 Behavioral Endocrinology: Stress and Adrenal Hormones . . . . .</b> | <b>89</b> |
| Definition . . . . .   | 89        |
| Types of Stress . . . . .  | 89        |
| The Stress Responses of the Body . . . . .                               | 90        |
| The Adrenal Medulla and Sympathetic Arousal . . . . .                    | 91        |
| The Hypothalamus and the Adrenal Cortex . . . . .                        | 91        |
| Corticosteroid Production . . . . .                                      | 92        |
| Corticosteroid Metabolism . . . . .                                      | 93        |
| Habituation to Stress . . . . .  | 95        |
| Functions of Stress . . . . .  | 96        |
| Psychosomatic Medicine . . . . .   | 96        |
| Two Psychiatric Syndromes . . . . .                                      | 97        |
| <b>7 Biological Rhythms . . . . .</b>                                    | <b>99</b> |
| Functions of Biological Rhythms . . . . .                                | 99        |
| Circadian Rhythms (23–26 Hours) . . . . .                                | 101       |

|   |            |
|---|------------|
| Studying Circadian Rhythms .....                    | 102        |
| Location of the Internal Clock .....                | 105        |
| Circadian Rhythms in Humans .....                   | 108        |
| Circatidal Rhythms (12.4 Hours) .....               | 111        |
| Circalunar Rhythms (14.8 Days) .....                | 111        |
| Monthly Rhythms (29.5 Days) .....                   | 112        |
| Circannual Rhythms (365 Days) .....                 | 113        |
| Rhythms in Human Disease .....                      | 113        |
| <br>  |            |
| <b>8 Orientation and Navigation .....</b>           | <b>117</b> |
| Orienting Responses .....                           | 117        |
| Kinesis .....                                       | 118        |
| Taxis .....   | 118        |
| Navigation .....                                    | 121        |
| Navigational Mechanisms .....                       | 121        |
| The Compass Mechanism .....                         | 124        |
| Navigational Cues .....                             | 125        |
| Migration .....                                     | 128        |
| <br>  |            |
| <b>9 Feeding, Foraging, and Predation .....</b>     | <b>131</b> |
| Feeding Behavior .....                              | 132        |
| Social Learning and Facilitation of Feeding .....   | 132        |
| Foraging .....                                      | 134        |
| Optimal Foraging .....                              | 135        |
| Constraints on Optimal Foraging .....               | 138        |
| Coping with Changes in Food Supply .....            | 139        |
| Feeding in Humans .....                             | 144        |
| Some Physiological Aspects of Feeding .....         | 145        |
| Predatory Techniques and Antipredator Defense ..... | 146        |
| Somatic Adaptations .....                           | 146        |
| Predatory Techniques .....                          | 148        |
| Antipredator Defense .....                          | 149        |
| <br>  |            |
| <b>10 Social Behavior .....</b>                     | <b>151</b> |
| Social Systems .....                                | 151        |
| Coelenterate Colonies .....                         | 152        |
| Eusociality in Insects .....                        | 152        |
| Vertebrates .....                                   | 154        |
| Benefits of Sociality .....                         | 155        |
| Reduction in Predator Pressure .....                | 155        |

|  |                |
|--|----------------|
| Improved Foraging and Hunting Efficiency .....   | 156            |
| Improved Defense of Limited Resources .....  | 156            |
| Improved Care of Offspring .....   | 157            |
| Costs of Sociality .....   | 157            |
| Increased Competition between Conspecifics .....   | 157            |
| Increased Risk of Infection .....  | 157            |
| Increased Risk of Mating Interference and Parental Exploitation by<br>Conspecifics ..... | 159            |
| Increased Risk That Offspring Are Killed by Conspecifics .....                           | 159            |
| Philopatry and Dispersal .....   | 159            |
| Dispersal Hypotheses .....   | 160            |
| Evolution of Cooperative Behavior .....  | 162            |
| Cooperation (Mutualism) .....  | 163            |
| Reciprocity (Reciprocal Altruism) .....  | 163            |
| Altruism (Kin Selection) .....   | 164            |
| Mechanisms of Kin Recognition .....  | 165            |
| Location .....   | 165            |
| Familiarity .....  | 165            |
| Phenotype Matching .....   | 166            |
| Allele Recognition .....   | 167            |
| Environmental and Cultural Influences in Primates .....                                  | 167            |
| Nonhuman Primates .....  | 167            |
| Humans .....   | 168            |
| <br><b>11 Communication .....</b>  | <br><b>171</b> |
| Definition .....   | 171            |
| Functions of Communication .....   | 171            |
| “Honesty” and “Deception” in Communication .....   | 172            |
| Communicatory Signals .....  | 174            |
| Sensory Channels of Communication .....  | 176            |
| Visual Communication by Reflected Light .....  | 177            |
| Auditory Communication .....   | 180            |
| Chemical Communication (Olfaction) .....   | 188            |
| Tactile Communication .....  | 195            |
| Electrical Communication .....   | 197            |
| <br><b>12 Agonistic Behavior .....</b>   | <br><b>199</b> |
| Interspecific Agonism .....  | 200            |
| Predatory Aggression .....   | 202            |
| Antipredatory Agonism .....  | 203            |
| Intraspecific Agonism .....  | 203            |
| Individual Distance .....  | 203            |

|  |            |
|--|------------|
| Intraspecific Aggression .....   | 204        |
| Categories of Intraspecific Aggression .....                                   | 206        |
| Intraspecific Submission and Flight .....                                      | 215        |
| Comparisons between Interspecific and Intraspecific Agonism .....              | 216        |
| Human Aggression .....   | 216        |
| <b>13 Sexual Selection .....</b>   | <b>221</b> |
| Asexual and Sexual Reproduction .....  | 221        |
| Sex Determination .....  | 222        |
| Sex Ratio (SR) .....   | 223        |
| Theoretical Considerations .....   | 224        |
| Bateman's Principle .....  | 224        |
| Trivers's Theory of Parental Investment .....                                  | 224        |
| Trivers-Willard Hypothesis .....   | 226        |
| Intrasexual Selection .....  | 227        |
| Competition among Males .....  | 227        |
| Competition among Females .....  | 233        |
| Intersexual (Epigamic) Selection .....   | 233        |
| Desirable Male Qualities .....   | 233        |
| Markers of Male Qualities .....  | 233        |
| Evaluation of Male Qualities .....   | 234        |
| Evolution of Male Traits and Female Preferences for Them .....                 | 234        |
| Mate Choice by Males .....   | 236        |
| <b>14 Courtship and Mating .....</b>   | <b>237</b> |
| Factors Important for the Onset of Courtship and Mating .....                  | 238        |
| Seasonal Factors .....   | 238        |
| Hormonal Stimulation .....   | 238        |
| Social Stimulation .....   | 239        |
| Functions of Courtship .....   | 239        |
| Species (and Strain) Identification .....                                      | 239        |
| Gender Identification .....  | 240        |
| Aggression Reduction between the Male and Female .....                         | 240        |
| Individual Recognition .....   | 241        |
| Behavioral and Physiological Synchronization between the Male and Female ..... | 241        |
| Signaling Competitive and Parental Abilities .....                             | 242        |
| Mating Categories .....  | 243        |
| External and Internal Fertilization .....                                      | 243        |
| Copulatory Patterns in Mammals .....   | 243        |
| Bisexual Behavior .....  | 244        |
| Nonhuman Animals .....   | 244        |
| Humans .....   | 245        |

|  |                |
|--|----------------|
| <b>15 Parental Behavior and Mating Systems</b> | <b>249</b>     |
| Models of the Parent–Offspring Relationship    | 250            |
| The Parental Provision Model                   | 250            |
| The Mutual Benefit (Symbiosis) Model           | 250            |
| The Conflict Model                             | 250            |
| Evolution of Parental Care                     | 252            |
| Sex Differences in Parental Care               | 252            |
| Selection Pressures for Parental Care          | 255            |
| Mating Systems                                 | 258            |
| Definition of Mating Systems                   | 258            |
| Classification of Mating Systems               | 259            |
| <br><b>16 Nonhuman Primates</b>                | <br><b>265</b> |
| Ethology                                       | 265            |
| Fixed Action Patterns (FAPs)                   | 267            |
| Conflict Behaviors                             | 268            |
| Ritualization                                  | 268            |
| Releasers                                      | 269            |
| Sensitive Periods, Imprinting                  | 272            |
| Sociobiology                                   | 273            |
| Social Systems                                 | 273            |
| Mating Systems                                 | 277            |
| Mate Competition and Mate Choice               | 277            |
| Parental Investment                            | 278            |
| Dispersal and Inbreeding Avoidance             | 279            |
| Hormonal and Seasonal Influences               | 282            |
| Language in Apes                               | 286            |
| <br><b>17 Humans</b>                           | <br><b>289</b> |
| Human Ethology                                 | 289            |
| Fixed Action Patterns (FAPs)                   | 290            |
| Conflict Behaviors                             | 291            |
| Ritualization                                  | 292            |
| Releasers                                      | 294            |
| Ethology in Clinical Settings                  | 298            |
| Sensitive Periods, Imprinting                  | 298            |
| Human Sociobiology                             | 299            |
| Mating Systems                                 | 299            |
| Mate Competition and Mate Choice               | 299            |
| Parental Investment                            | 303            |
| Incest Avoidance                               | 305            |
| Hormonal and Seasonal Influences               | 308            |

---

|                     |     |
|---------------------|-----|
| References .....    | 313 |
| Author Index .....  | 323 |
| Subject Index ..... | 327 |

## CHAPTER 1

---

# The Study of Behavior

## *History*

---

### A BRIEF HISTORY

The attempt to understand and classify the behavior of animals, and in particular that of humans, has engaged scholars for many centuries, at least since the time of the Greek philosophers Aristotle and Plato. Ethology developed from zoology, that is, from the study by naturalists of animals in their natural habitat, whereas psychology developed from philosophy. Much of the difference between the theoretical and methodological approaches taken by ethologists and psychologists can be traced to their different origins. The following sections briefly summarize the principal branches of the behavioral sciences, ethology, and comparative psychology, the controversies between them during the 1950s and 1960s, and the subsequent synthesis that has developed into the modern study of animal behavior. This may be the most difficult chapter in the book to master.

### Classical Ethology

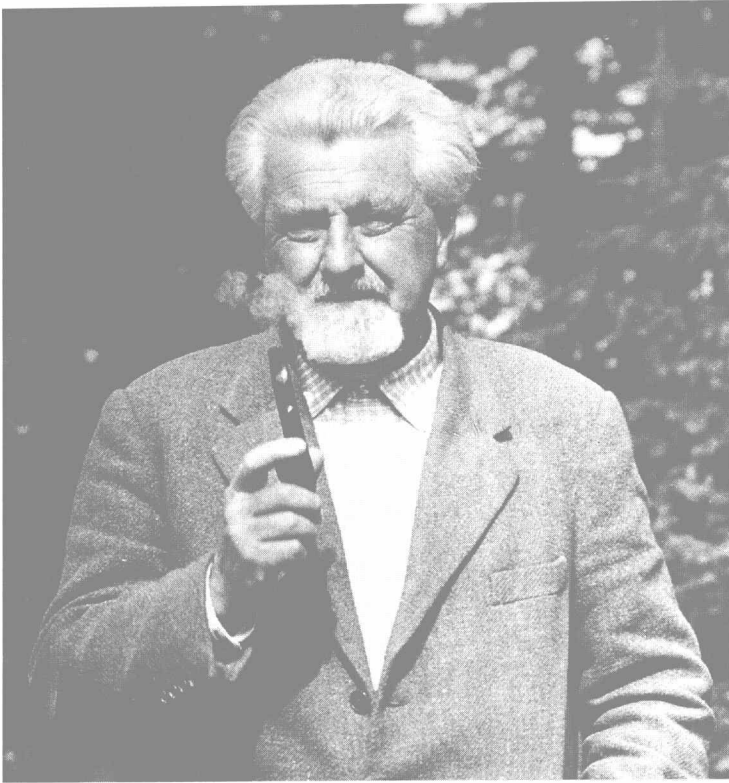
The term ethology comes from the Greek word *ethos*, meaning habit or manner, and was once applied to what we now know as ecology. From the turn of the twentieth century it gradually came to be used to describe the study of the naturalistic behavior of

animals, and has been the generally accepted term for this branch of natural history since 1951.

Ethology received an impetus from scientists who recognized the importance of Charles Darwin's groundbreaking insights into evolution (Darwin, 1859) that, for the first time, linked the behavior of animals with their environment. The basic tenet of ethology is that animals evolve not only morphologically but also behaviorally, due to the selection of traits that allow animals to interact successfully, if not optimally, with their environments to survive and reproduce. Ethologists are therefore concerned with why animals perform certain behaviors in their natural habitats, and seek to understand how animals interact and cope with their environment, that is, how they feed, avoid predation, seek and court a mate, and raise their young. One of the earliest scientists that we would now call an ethologist was Douglas Spalding, a tutor to the family of Bertrand Russell, a twentieth-century philosopher and nuclear disarmament advocate. He conducted experiments with birds, mostly chickens, showing that various adaptive behaviors, those increasing the probability of survival and of producing young, are instinctive (inborn or innate and coded by the genes), although a period of maturation might be necessary for their appearance (Spalding, 1873). At the time, the prevailing view was that an animal or person is born as a *tabula rasa* (a clean slate), and that all behaviors are then learned more or less rapidly during life. The work of Spalding, and others like him, remained unrecognized and mostly forgotten, and some 60 years passed before several European naturalists brought the field of ethology into prominence and eventually into public recognition with the joint award of the 1973 Nobel Prize for Physiology or Medicine to its three main pioneers, Konrad Lorenz, Nikolaas Tinbergen and Karl von Frisch.

Lorenz (Fig. 1-1), generally recognized as the founder of ethology, which he named, was born into the family of a prominent and wealthy Austrian surgeon in 1903. From an early age, he surrounded himself with many different wild animals, especially birds. He obtained a medical degree but soon concentrated on animal studies, and in 1940 took the Chair of Philosophy once held by Emmanuel Kant (psychology was still subsumed under philosophy at that university) at Königsberg University in Germany, until called up as an army doctor in 1941 to serve on the Russian front. He resumed his work in Germany after the war and returned to his ancestral home near Vienna after retirement. Although unaware of Spalding's studies, Lorenz was influenced by the work of earlier naturalists and also that of Sigmund Freud. Lorenz discovered most of the phenomena of ethology on the basis of his keen observational powers, intuitive insights into animal behavior, and inductive reasoning. He relied on studying animals in their natural environments and rarely performed an experiment, although he collaborated with others who did and encouraged his students to do so. The Dutch ethologist Tinbergen, considered the founder of experimental ethology, began his work in Holland with studies on insects and fishes, and with the advent of World War II moved to Oxford University in England, where he remained for the rest of his life working mostly with birds. He shared Lorenz's concern for observing animals in their natural environments, which he combined with elegant experiments conducted mostly in the field. Based on Lorenz's observations and his own experiments, Tinbergen helped to formalize some general principles of ethology, including fixed action patterns, releasers, supranormal stimuli, innate releasing mechanisms, and imprinting. The Austrian zoologist von Frisch





**FIGURE 1-1.** Konrad Lorenz, considered the founder of ethology. (Photo courtesy of Anne Kirchbach)

was primarily an experimentalist, and began his famous, lifelong work on honeybees by wondering why flowers were so colorful, although, at the time, the insects feeding on them were thought to be color blind. He used conditioning techniques that had recently been demonstrated by Pavlov (see below) to show that bees could both discriminate colors from shades of gray and see ultraviolet (UV) light. From this he went on to characterize the sensory world and communicatory systems of honeybees, including the “dance” that signals the location of a food source to bees in the hive.

Ethologists differed from some zoologists (Bierens de Haan, 1940) and psychologists (McDougall, 1936; Tolman, 1932; Russell, 1938), who were called “vitalists” because they postulated inexplicable instincts as the final determinants of behavior, and they differed also from “mechanists,” namely, behaviorists who believed the internal motivational state of an animal to be irrelevant for its behavior (see below). Ethologists held the view that an animal’s behavior is intimately related to its motivational states, and that the physiological mechanisms underlying both could eventually be determined by research.