

behavior mechanisms in monkeys

heinrich klüver

With an introduction by K. S. Lashley

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BEHAVIOR MECHANISMS IN MONKEYS

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K. S. LASHLEY

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PREFACE (1957)

It seems paradoxical that an age which has suddenly discovered something called "behavioral sciences" appears, in general, less thorough, less subtle, and less mature in its experimental and theoretical analyses of behavior than an age which had not yet officially taken cognizance of Behavioral Sciences. As far as primates other than man, and particularly monkeys, are concerned, there is no denying that recent years have brought an awakening of interest in their behavior, although not necessarily in the underlying behavioral mechanisms. Behavioral aspects in monkeys have become of interest in laboratories as different as those at the School of Aviation Medicine, Randolph Field, Texas, and at the Virus Research Institute in Entebbe, Uganda. The great interest in simian or primate behavior is even evident in recent treatises dealing chiefly with morphological and anatomical aspects, such as the series of comprehensive monographs on *Primates* by W. C. Osman Hill and the handbook of primatology, *Primatologia*, now being edited by H. Hofer, A. H. Schultz, and D. Starck. In view of these developments, it seems unfortunate that the present monograph, *Behavior Mechanisms in Monkeys*, has been out of print for many years. It has proved to be and apparently continues to be of some interest to neuropsychologists, psychologists, physiologists, psychiatrists, neurologists, endocrinologists, zoologists—in fact, to biologists in general as well as to sociologists and anthropologists. While it is true that at least some of the behavior data presented here have been adequately summarized in Earnest Hooton's popular book, *Man's Poor Relations*, it is also true that an ever increasing number of investigators in fields ranging from radiobiology to psychopharmacology are at present more interested in the methods and techniques for obtaining such data than in the behavior data themselves. Since the University of Chicago Press has decided to reissue this monograph, such investigators will again have easy access to the original description of the methods and techniques I devised for analyzing the behavior of non-human primates and to the detailed accounts of the application of these methods to various problems. It deserves special mention that at least some of the methods presented in this monograph (which have even found their way into books on methodology, such as T. G. Andrews' *Methods of Psychology*) have been subsequently used with success by other investigators in studying primates as well as non-primates; some of these methods, however, which were found to be equally, if not more, fruitful in neurophysiological, pharmacopsychological, and other lines of investigation have so far been employed only in my own researches. At this point attention should be called to certain techniques which I developed during the years following the publication of this monograph and which at the present time may be of great assistance to investigators in various sci-

ences who wish to obtain behavior data on non-human primates (and other animal forms). The chief of these techniques involves the use of vacuum-tube amplification in conjunction with the various "pulling-in techniques" or with certain testing devices which I subsequently developed (cf. references 1-3). How fruitful these techniques have proved to be may be judged from various studies in which they have been extensively employed (6, 7, 9, 10). The range of their applicability is wide, since they have been found to be of value in studying interrelations of neural and behavioral mechanisms, aspects of social behavior, responses to the discriminable or isolable aspects of the external environment, as well as other forms of learned or unlearned behavior. The attention of investigators should also be called to the "formboard" technique (which in one form or another has in the meantime been used by numerous students of animal behavior) and to the "hemianoptic testing board" (5).

It is now almost a third of a century ago that I developed the "method of equivalent and non-equivalent stimuli." The work reported in this monograph probably still represents the most sustained effort at coping with facts of "equivalence." In recent years psychologists have again become interested in "generalization" (and even "generalization gradients") and in various forms of behavioral "invariance," although they have been fairly successful in completely ignoring the troublesome problems centered around facts of equivalence. It is of interest that my critical analysis of Pavlovian "generalization" and "differentiation" (cf. p. 344) appeared at about the same time as the penetrating critiques of Pavlovian concepts by Erwin Straus and P. Ranschburg, that is, approximately twenty-five years ago. There is a great deal of evidence that Pavlov, as well as almost all investigators since then who have been concerned with facts of "generalization" on the behavioral level, was unaware of the implications and the significance of the facts of equivalence and non-equivalence. Thus we encounter equivalence in the field of logic (for instance, the "equivalence" and "L-equivalence" of Carnap) and again when studying the organism along physiological, biochemical, anatomical, and pathological lines. Since many of the behavior data in the present volume have been obtained by employing the method of equivalent and non-equivalent stimuli, investigators may be interested in some of the studies in which in the course of the years I have again and again returned to the general problem of equivalence (4, 7, 8, 9).

In 1933, when introducing the Bibliography of this monograph (cf. p. 368), I called attention to the more than eleven hundred references in Stephen Polyak's *The Main Afferent Fiber Systems of the Cerebral Cortex in Primates*. In the meantime, death has terminated the activities of this outstanding investigator, and it has been my lot, during the last two years, to see his last monumental work, *The Vertebrate Visual System*, through the press. I should like to call attention to the fact that a large number of the

approximately ten thousand references in the Bibliography of this book (published by the University of Chicago Press) deal with the behavior of non-human primates and should therefore be of great interest to all investigators in this field.

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HEINRICH KLÜVER

CULVER HALL
UNIVERSITY OF CHICAGO

INTRODUCTION

K. S. LASHLEY

For the rapid development of comparative and physiological psychology, studies of the lower primates offer what is in many ways the most promising material. The monkeys represent an important stage in the transition to anthropoid behavior. They are similar enough to man to justify homologies and at the same time are sufficiently primitive and diverse in behavior to provide contrasts which will be helpful in analyzing the more complex traits common to them and to the anthropoids. The Macaques have been used extensively in physiological and medical studies, and the data accumulated in these fields provide an important background for investigations of behavior. The nervous anatomy of these forms is more completely known than that of other primates; so they provide unusual opportunities for correlations of structure and behavior.

Our knowledge of the psychology of the monkeys is still very limited. There have been casual studies of simple sensitivity and a few tests of the solving of puzzles involving, no one knows what, psychological processes; but no intensive, systematic investigation of any phase of their behavior has been carried out. Only the barest outline of the evolution of mind has been sketched, and the task of discovering the rudiments and tracing the development of mental traits remains to be performed.

Dr. Klüver's monograph sets a new standard for analytic studies of behavior. He has proposed the question, Just what properties in complex sensory situations are significant for the animal's reactions? and has carried out the investigation with unique thoroughness. As a result, he presents for the first time something approaching a complete picture of the perceptual world of an animal. This perceptual organization is surprisingly like that of man. Not only are the animals sensitive to the same physical stimuli but for them also the relational properties of the situations are the same. As with man, reactions are but little dependent upon the simple physical properties of the stimulus but rather upon abstract relations which may subsist in physically unlike situations. The processes of abstraction and generalization involved in the perception of similarity and difference seem as efficient in the Macaques as in man and not fundamentally different.

In what ways then do the limitations in capacity in the lower primates appear? The study suggests the nature of some of the limitations but serves rather to define the problem than to answer it adequately. What is more important for future work is the provision of a method for studying the higher mental processes which is applicable to a wide range of animal forms and

which may be extended to cover the most abstract logical processes. "Preference tests" have been used before as controls in studies of sensory physiology and for demonstrating transposition in unidimensional series of stimuli, but Dr. Klüver shows here in his "method of equivalent stimuli" the far wider usefulness of such tests. They permit, in brief, the rapid determination of those aspects with respect to which two situations are alike or differ for the animal, and any desired degree of abstractness may be introduced into the relations involved. For a study of the development of intellectual functions the method seems superior to any other available, for it is relatively independent of the sensorimotor equipment of the animal and is as applicable to the most primitive mammal as to primates, with only minor changes which need not affect the essential relations involved in the situations.

The most immediate value of the study is in laying a foundation for investigations of the neurophysiology of behavior. Clinical evidence is far from adequate to settle the major problems of nervous integration and of the organic mental disorders and must be supplemented by experimental studies. But experimental neurology has made little progress toward an understanding of the mechanisms of thinking for lack of an adequate knowledge of the normal behavior of the animals studied and of means of detecting any but the grossest disorders of behavior. The data and methods, here made available, open the way for an experimental attack upon many of the problems of sensory agnosia and the organic disturbances of thinking.

In brief space it is impossible even to mention many other problems of psychology upon which the data accumulated by Dr. Klüver have significant bearing. In his own interpretation of the material he has maintained a wise conservatism. His discussion of the principles of interpretation in psychological studies seems to me one of the most important recent contributions to theoretical psychology. He is skeptical of formulas, whether they be the schemata of behaviorism, the field properties of the configurationists, or the images and ideas of structuralism, and justifies an experimental and phenomenological approach to the problems. In the infancy of a science generalizations are rarely true beyond narrow and too often undefined limits. The important contributions to psychology are not the classifications which confuse the issues, the explanations which overlook the problems, and the neologisms which disguise our ignorance but the tracing of relations through the intricate web of dependent processes which is mind. Always the question, How? punctures the bubble of theory, and the answer is to be sought in analysis and ever more analysis.

AUTHOR'S PREFACE

Investigators who for some reason or other are interested in the study of sub-human primates, and especially in methods and techniques for analyzing their behavior, will find the core of this monograph in Chapters IV and V. These chapters contain the description of our experiments. In this description theoretical matters so far as possible have been excluded. There is no doubt, however, that the course of research in the field of animal behavior has been and still is strongly influenced by hypotheses and concepts taken from human psychology and human physiology. In formulating problems and in interpreting results it becomes necessary, therefore, to take into account a number of theories and facts gleaned from investigations with human material (cf. especially Chaps. I, III, and VII).

While the study of behavior is approached here from a biological point of view, it is difficult to say whether we can draw a sharp line of demarcation between a "biological" and a "sociological" approach to the study of behavior. By way of introduction we shall briefly indicate our stand in this matter.

It is easily seen that in many instances we cannot point to any biological differentiae when considering forms of behavior differing widely in social significance. The motor reactions performed in tearing up a piece of scrap paper may be the "same" as performed in destroying a document of great legal or historical importance. Many of the reactions which from the biological point of view are similar or alike are utterly different in social respect. In many instances widely different forms of social behavior are "biologically neutral." Whether or not certain forms of behavior are "antisocial" cannot be determined by analyzing single reactions or by studying tendencies to certain reactions. What is "antisocial" varies to a great extent with the norms of the penal codification which, again, vary from epoch to epoch and from one social group to the other. These norms can be understood only by reference to certain scales of *values*. The genesis of various forms of evaluation represents, of course, a question which can be scientifically studied. We can also study the possibilities of influencing various forms of evaluation. But that is all, and it does not alter the fact that the distinction, for instance, between "antisocial" and "social" is a distinction which is drawn, not on the basis of scientific criteria, but, at least to a remarkable extent, on irrational grounds and which is, therefore, of no special help to the scientist, not to mention to the man who wants to *control* human behavior.

A somewhat different picture presents itself if we confine ourselves to *one* system of evaluation and neglect other systems. If we confine ourselves to *one* system, a system expressing itself in a number of definite norms and

laws, and study human behavior from the biological point of view we find certain characteristic reaction tendencies and find, furthermore, that some reaction tendencies manifest themselves in the presence of widely different stimuli. There is evidence to show that the *form* of reacting may remain the same although the material reacted to may vary from visual stimuli consisting of nonsensical configurations of lines to socially significant stimuli. Someone who is interested and trained in judging human behavior in the light of particular norms and laws will easily recognize that certain forms of reacting are socially far more significant than others while still others are "socially neutral"; he naturally wishes to see research done on forms of reacting which are of greatest significance from the social point of view. This does not mean that research of this kind is bound to yield definite or valuable results simply because the experimenter employs "socially significant" situations. The socially significant situations are frequently impossible of scientific control with the methods of study available. To recognize the social significance of certain forms of reacting is one thing; to formulate methods for the analysis of such forms is another thing. Whether sociological, psychological, physiological, biochemical, or other lines of inquiry are most likely to be fruitful is very difficult to predict.

Theoretically we may perhaps expect no difficulties in attempting an evaluation of various forms of behavior in terms of any *single* set of norms or laws. But even in such a case, workers in the fields of psychiatry, criminology, and criminal pathology have frequently discovered that biologically similar forms of behavior are markedly different from the sociological point of view. Forms which on the basis of clinical criteria are etiologically closely related may not belong together from the standpoint, let us say, of criminal pathology (139).

In reality the situation is even more distressing. What is "antisocial" today may not be "antisocial" tomorrow; furthermore, the existence of biologically fundamental reaction tendencies represents only one of the factors which must be taken into account when formulating norms of social behavior or of penal codification. In view of this situation it may seem wise to leave aside sociological considerations entirely and to confine ourselves to a study of reaction mechanisms from a biological point of view. Unfortunately, studies of biologically fundamental tendencies often reveal a great discrepancy between socially existing norms or systems of evaluation and what might be called biological norms. It is clear, however, that it is not the task of the biologist or of the psychologist to worry about the relation of his findings to problems of social value. Zuckerman, in his book *The Social Life of Monkeys and Apes* (309), reaches, for instance, the conclusion that "social behaviour—the inter-relation of individuals within a group—is determined primarily by the mechanisms of reproductive physiology." Granted that facts of reproductive physiology are of "fundamental importance to the interpretation of the mechanisms of social behaviour": the evaluation of

this result in terms of sociological criteria is not the business of the biologist. Some of the more intricate questions which arise when both biological and sociological factors are considered have been discussed in previous publications (138, 139). In this volume we shall limit ourselves to a discussion of the problems arising when the study of behavior is approached from the biological angle only.

In view of the fact that in this work we have been interested not only in behavior mechanisms *per se* but also in obtaining behavior data which may be of use in connection with neurophysiological and related problems, it is easily understood why we have chosen the monkey as a subject. Says Poliak (227): "The brain of the lower primates is . . . in its essential features and in its finer structure a simplified replica of the human brain. . . . Certainly a systematic experimental investigation of all the chief anatomical, physiological, and psychological problems of the brain on a large scale and with a broad view, according to a prearranged plan, using primates, would give results amply compensating the labor, the time, and the expense involved."

It is apparent that the experiments reported in Chapters IV and V suggest at every point the necessity for and the possibility of further work. The data do not permit of any final conclusions; nevertheless, as a result of our work many problems have received a more precise formulation. No doubt, an immense amount of work still remains to be done before there is some agreement as to what "functions" or "mechanisms" are truly "fundamental" or "basic" in behavior.

For help and encouragement throughout this research I am deeply indebted to Dr. K. S. Lashley. I can but inadequately express my sincere appreciation and gratitude for his constant interest in the various problems under investigation.

Practically all the work reported here was done under the Behavior Research Fund at the Institute for Juvenile Research, Chicago. For providing me with some animals for preliminary study, grateful acknowledgment should be made to the Graduate School of the University of Minnesota. These preliminary experiments, conducted in 1925-26, led to the first systematic application of what I have called the "method of equivalent stimuli."

Especial thanks are due to Dr. Herman M. Adler and to Dr. Paul Schroeder, Dr. Adler's successor, for providing me with facilities and for making it possible for me to carry on my work at the Institute. It would not have been possible for me to collect such a mass of experimental data in the time at my disposal had it not been for the valuable assistance and splendid co-operation of Mr. John C. Weigel, administrator of the Institute and the Behavior Research Fund.

I am indebted to Dr. E. W. Burgess for helpful suggestions and to many members of the staff of the Institute for assisting me in various phases of my work, particularly to Mrs. Lillian Davis for editorial assistance, to

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Some of the data on reactions to sudden changes have previously been published in the Commemorative Volume for William Stern under the title "Zur Psychologie der Veränderungsauffassung bei niederen Affen" (*Zsch. f. angew. Psychol.*, 1931, Beiheft 59, pp. 132-56). I desire to acknowledge my indebtedness to the publishers (Johann Ambrosius Barth, Leipzig) for allowing me to make use of this material.

H. K.

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