Behavior Genetics and Evolution

Lee Ehrman

Peter A. Parsons

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Lee Ehrman
State University of New York, Purchase

Peter A. Parsons
LaTrobe University
Bundoora, Australia

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Preface

Preface to *The Genetics of Behavior*

"The time seems ripe for a modern statement of the division of knowledge we have called 'behavior genetics' . . . not presented as a definitive work, because that would be impossible in a field of study which is in a dynamic stage of growth." The time was May 1960 and the writers, John L. Fuller and W. Robert Thompson, were coauthors of the very first book devoted to this hybrid subject (*Behavior Genetics,* Wiley, New York). Indeed, behavior genetics may be said to have begun in 1869 with the publication of another book, F. Galton's *Hereditary Genius* (followed by his *English Men of Science: Their Nature and Nurture* [1874] and *Inquiry into Human Faculty* [1883], Macmillan, London).

To us and those who advise us (some listed below), the time now seems ripe, one and a half decades later, for the appearance of an advanced textbook devoted to behavior genetics, although the field continues in its dynamic stage of growth. This being so, the present text is again ". . . not presented as a definitive work," a task that even now would still be impossible. Our textbook is directed to those undergraduate- or graduate-level students who already possess a basic background in general genetics. These could be students in biology or psychology or in what now often appears in colleges and universities as programs and majors in psychobiology, itself an increasingly fertile hybrid as can be seen by the rapid development of areas of studies in the behavioral sciences.

Because behavior genetics taught as a formal course is a recent innovation, it is our hope that this book will be useful for those already trained in a variety of ways for a multitude of careers. Professional geneticists, animal biologists, and psychologists come to mind first, but the aspects of behavior genetics covered here also increasingly enter into the work of physicians, veterinarians, animal breeders, sociologists, and educators generally, as should become clear from the examples and the organisms discussed. Thoughts about some major political controversies of our day may also be clarified by an understanding of behavior genetics of human beings and of other organisms as well.

We shall consider as behavior any and all activities performed by the holistic entity, the organism, in relation to this organism's surroundings, its environment. We do so according to the recommendation of Ethel Tobach (1972), but we confine ourselves to those aspects of an organism's muscular, glandular, and neural responses that have been demonstrated, albeit with varying degrees of firmness, to have an underlying hereditary basis—one transmitted via germinal tissues from generation to generation.

The examples we have chosen are necessarily selective, meant to illustrate various aspects of behavior genetics. Omission of some excellent studies is inevitable, just as inclusion of some studies has occurred by virtue of our familiarity with them. Even so, because of the need to be selective, it is our hope that we have managed to provide a relatively advanced and comprehensive text in behavior genetics. We apologize to those who may feel that their work has been neglected, and we would be grateful if our readers draw our attention to matters of this sort that they feel strongly about. Indeed, any comments will be most welcome.

Besides our patient spouses to whom this book is dedicated, we were aided in manifold ways by our students and staff. At the State University of New York at Purchase, they were Geoffrey Ahern, Roslyn Black, Luba Burrows, Dan Cannizzo, Lila Ehrenbard, Toni Faucher, Alena Leff, Max Kirsch, Eileen O'Hara, Dr. Anita Pruzan, Jodi Rucquoi, and Gary Rosenfeld. Bertha Inocencio bore an especially heavy burden. In addition to reading the entire manuscript, she typed parts of it and tended files, phones, and so on, while we wrote and rewrote. Bless her!

At LaTrobe University in Australia, aides were Jeff Cummins, Dr. David Hay, Michele Jones, Lon McCauley, Glenda Wilson, and Cheryl Wynd.

A special mention must be made of Dr. Nikki Erlenmeyer-Kimling, who improved the entire manuscript with her kind and perceptive criticism.

Preface to *Behavior Genetics and Evolution*

Some five years span the appearances of our two books, *The Genetics of Behavior* (1976) and *Behavior Genetics and Evolution* (1981), and they have been hectic ones for behavior geneticists of assorted morphs including ourselves. We coauthors now have so much more primary literature with which to deal that we deem it imperative to state this time that our approach will lean toward the biological side of our topics with special reference to evolutionary matters. The title change for this essentially revised edition follows from this change in emphasis. This simply means we will be assuming some elementary background in genetics and in developmental biology though we review and bolster such preparations using behavioral examples in our rewritten, expanded initial five chapters as well as elsewhere. Even so, as of this writing, more of the active members of the Behavior Genetics Association are trained in psychology and in closely related areas than in genetics specifically such as ourselves. But most important are those few recent graduates trained as behavior geneticists as a result of courses being taught and interdisciplinary graduate programs being newly developed. It is our belief that at various levels graduates with such training will increase rapidly in number; it is our hope that this new book will assist them.

This book incorporates more mechanical details of genetic concerns, such as those of transmission and enzymes, together with the expected incorporation of an updated and enhanced body of literature. Topics previously hardly mentioned now given greater consideration include behavioral changes associated with domestication, cultural versus biological inheritance, plus a discussion of evolutionary strategies involved in habitat selection. Additionally, by way of stressing the evolutionary bias of our book we discuss the behavior genetics of a far greater diversity of organisms than in our antecedent book.

Most importantly, we put even more stress upon what we regard as the unique emphasis that the behavior geneticist must appreciate: In studying the behavioral phenotype of any but the simplest of characters, the precise study of environmental determinants is just as important as the study of genetic determinants. In many ways, this is the justification for writing a book specifically devoted to behavior genetics.

In the last chapter of our initial effort we made predictions concerning future trends in behavior genetics. Some still remain future trends, but information on all has accumulated over the past 5 years. Our previous edition was completed before the widespread discussions of sociobiology, at a time when the heredity-IQ debate was omnipresent. So just as we then attempted to position our discussion of this heredity-IQ debate into perspective within a text on behavior genetics, in this edition we try the same for sociobiology in very brief terms, simply because we regard behavior genetics as the major scientific discipline underlying sociobiology. Finally, we try to develop the role of behavior genetics as a discipline of vital importance in the study of evolutionary biology, including speculation itself.

This book is organized into four main sections:

- Chapters 2 through 5 provide an introduction to genetics as applied to behavior, proceeding from behaviors under the control of single genes and chromosomes to those controlled by many genes. Chapter 2 is a brief introduction to genetics using behavioral examples. Its object is to show that the principles of genetics can be studied while relying upon behavioral examples. Anyone with a scant knowledge of genetics should read Chapter 2 in conjunction with an elementary genetics text, a selection of which is listed at the end of that chapter.

• Chapters 6 and 7 provide the theoretical bases of analyses of traits controlled by many genes in experimental animals and in human beings.

• Chapters 8 through 12 look at behavior phylogenetically, considering bacteria, protozoa, invertebrates (especially *Drosophila*), rodents, *Homo sapiens*, and various other animals on which behavior-genetics studies have been or may be undertaken. Discussion of the heredity-IQ controversy occurs in Chapter 12.

• Chapter 13 discusses the role of behavior in evolution. In this sense it stresses the integration of the material of the preceding chapters. Chapter 14, the concluding chapter, presents a final discussion of the place of behavior genetics in evolutionary biology. Some specific areas where behavior genetics has been uniquely successful are discussed, with comments on likely future trends. In some cases behavior genetics studies are beginning to contribute to other areas of genetics. The point is made that the behavior geneticist of the future must look beyond questions of how heredity and environment, considered discretely, control behavior. At this stage it should have become clear why progress in our understanding of sociobiology will occur, but not rapidly.

Once again we invite corrections, suggestions, reprints, and preprints. We do so as part of the affirmation that scientific advances will make another edition imperative. We also wish to thank all those persons, many unmentioned, who have presented us with helpful comments and indicated errors in our first edition, and we welcome openly a similar response for this edition.

We specifically thank Drs. John McKenzie and Neville White for access to unpublished data and for helpful discussions and Dr. David Hay and Joan Probber for help with literature, interpretations, and helpful discussions. Mrs. Marlene Forrester typed most of a draft and so with Bertha Inocencio simply made this second book possible. And we copiously thank our patient editor, Toni Faucher.

Lee Ehrman
Peter A. Parsons

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1

Introduction

The literature of the earlier part of this century shows clearly that the study of behavior and the study of genetics proceeded independently of each other, with few exceptions. The geneticist, preoccupied with the study of easily defined, mainly morphological or anatomical genetic types, tended to ignore possible genetic components of behavioral traits. No doubt one reason for this was the greater difficulty of measuring behavioral traits as compared with morphological ones; a second reason was that few geneticists had any training in psychology. And when one looks at the psychological literature of the period, it is apparent that experimental and certainly clinical psychologists took little note of genetic components of behavior. Beach (1950), in a rather lighthearted but scientifically serious article, "The Snark Was a Boojum," discussed why genetic variability was largely ignored by psychologists. Nonhuman behavioral work was and still is largely conducted on the Norway rat, *Rattus norvegicus*. A relatively constant genetic makeup was and still is sometimes assumed. This one type is then surveyed for a series of behaviors, so that the behaviors themselves are the variables of study. A geneticist, on the other hand, primarily manipulates genetic types, genotypes, in order to see how traits vary according to the genetic type.

The theoretical and empirical observations necessary for combining the genetic and psychological approaches have been embedded in the literature for a long time. For example, in *Drosophila melanogaster,* the fruit fly commonly used in genetic experiments, differences in male sexual vigor in different strains were reported by Sturtevant as early as 1915. This is all the more remarkable since research on this species began only about five years earlier (by T. H. Morgan and his colleagues in the famous Columbia University *Drosophila* room). These early experiments in *Drosophila* behavior, however, were mainly byproducts of genetic or evolutionary investigations having other objectives. The 1940s did produce a number of pertinent investigations, principally by Dobzhansky, Mayr, and their associates, into sexual isolation among many of the then newly discovered races and species of *Drosophila* (for references see Parsons, 1973). Similarly, during this early period there were reports of behavioral differences among different genetic types in some rodents, principally in house mice and to a lesser extent in rats. These are ably summarized in Fuller and Thompson's (1960) classic, *Behavior Genetics,* a thorough account of behavior genetics literature up to the end of the 1950s. In human beings, despite a few early reports mainly concerning twins (e.g., Newman, Freeman, and Holzinger, 1937), the development of a recognizable behavior-genetics approach is relatively recent. Studies carried out by psychologists dealt mainly with traits of social significance in which measurements are difficult, as are precise genetic interpretations.

In the vast majority of organisms, however, the study of behavior genetics is very recent. Much of the work follows the approach of identifying and studying mutations which alter the nervous systems of protozoans, nematodes, crickets, and other organisms, in addition to those mentioned above—a new field known as *neurogenetics* (Ward, 1977; Quinn and Gould, 1979). Just as recent is the start of a behavior genetics of bacteria, mainly utilizing mutants that manifest different levels of attraction to chemicals (Adler, 1976). The behaviors studied are therefore many and varied, but they are constrained by the organism under study. This facet of behavior genetics is attracting considerable attention, with an ever-increasing literature, but as yet little of it relates to evolutionary processes so it will not be considered in detail here.

With this restriction in mind, what then are the factors that differentiate behavior from other traits, such as morphological ones, that a geneticist may use? Although this question cannot be answered in any absolute sense, the study of behavior genetics does have emphases differing from those of other areas of genetics. As such it must be regarded as a true discipline, but one certainly interacting with other subdivisions of genetics such as developmental, population, and evolutionary genetics, and with other subdivisions of behavioral studies. Three main factors suggest themselves as being of greater concern to the behavior geneticist than to other geneticists; the third is essentially unique to behavior genetics:

1 *Difficulty of environmental control.* In unicellular organisms and invertebrates such as *D. melanogaster,* the environment can be controlled relatively precisely. This means that the effects of environmental variations can be as-

sessed and quantified successfully, given appropriate experimental designs. In rodents this is normally possible, especially if electronic devices are used to monitor behavior. However, with vertebrates complications begin to appear, since variations in early experiences may affect later behavior, an observation true even for *Drosophila* under certain definable circumstances. For example, whether mice are brought up together or separately may influence fighting behavior within a given strain. Often these environmental influences on behavior (by no means restricted to work with rodents) are difficult to assess, or worse, may occur without our being aware of them; differences in results between laboratories could be caused by factors of this sort. With *Homo sapiens* we are dealing with a species in which there is great difficulty in defining early experiences or in using controlled environments. This stress on the need for environmental control and its study was not always considered important by classic geneticists, but it is no less than imperative for the behavior geneticist.

2 *Difficulty of objective measurement*. For an accurate assessment of the relative importance of genetic influences, environmental influences, and interactions between them, a trait must by definition be measured completely objectively, that is, without any bias from the person carrying out the measurements. Clearly, in *Drosophila*, objectivity is normally possible for traits such as mating speed (the time elapsed from meeting to mating), duration of copulation, or phototaxis as measured in a maze. In rodents, objective measurement may be somewhat more difficult. However, for traits such as activity, measured by using automatic counters in activity wheels or photoelectric cells that count the number of times the animal passes a certain defined spot, high objectivity is possible. Objective measurements of mating rituals, social behavior, and territoriality present greater difficulties, though such measurements have indeed been achieved in well-designed experiments. In human beings, except for relatively simple sensory perception traits such as color blindness, objective measurement is a difficult problem. For traits such as intelligence and personality, which are so frequently assessed, it is difficult to avoid the conclusion that some subjectivity is likely to occur in measurement. The problem is that once an element of subjectivity appears, it becomes difficult to assess the relative importance of heredity and environment. In our own species we must cope with the greatest difficulties of all. This element of subjectivity, which should be minimal for biochemical, physiological, or morphological traits, is therefore a factor that partly differentiates the work of the behavior geneticist from the work of other geneticists.

3 *Learning and reasoning*. Behavior geneticists are concerned with learning and reasoning; other geneticists generally are not. These concerns should be regarded as essentially unique to behavior genetics, when viewed as a branch of genetics. Learning may well be of minor significance in *Drosophila*, since most behaviors surveyed are apparently innate (i.e., a direct property of the nervous system) as opposed to acquired behaviors including learning. As an evolutionary biologist, Mayr (1974) finds difficulties in using the terminological dichotomy of innate versus acquired. *Innate* refers to the genotype, and indeed the term has been restricted to functions at the reflex level and to lower animals. *Acquired* refers to the phenotype, so that neither term is the opposite of the other. Mayr essentially has resolved this problem by relating behavior to the concept of a *genetic program*—a concept derived from an interaction of

molecular biology and information theory. Those behaviors based on genetic programs not allowing for appreciable modifications during the process of translation into the phenotype are called *closed programs*. Other genetic programs are modified during translation into the phenotype—by input occurring during the life span of the owner. They thus have an acquired component and are referred to as *open programs*. Closed programs are widespread in organisms with a short life span, which to date must include *Drosophila*, while open programs are more likely in organisms with longer life spans which include parental care. Even so, learned behavior in *Drosophila* occurs in species-recognition patterns, but few other reports of learning exist, and they need further substantiation at this stage. In rodents, there is ample evidence that early experience affects later behavior patterns (see Erlenmeyer-Kimling, 1972; for review). Patterns and rates of learning also are found to vary among different strains. Therefore, both heredity and environment are involved in learning, as are interactions between heredity and environment. In human beings, in whom learning and reasoning are developed to the highest level, we have less hope of environmental control and generally we do not have known behavioral phenotypes. It is here that genetic programs are likely to be the most open of all.

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2

Requisite Genetics

The object of this chapter is to review such basic principles of genetics as are necessary for an understanding of the chapters to follow. A single chapter provides too little space to propound the complete principles of genetics. Any reader who finds this brief survey insufficient should employ a general genetics text to augment the information given here. A list of appropriate texts is given at the end of this chapter.

2-1 MENDELIAN GENETICS

If we observe differences in eye or hair color and find that these differences tend to run in families, it is clearly insufficient to say that such traits are inherited. We wish to find out *how* traits are inherited. This is one of the main objects of study in the science of genetics. Thus we must turn to the transmission of observed traits from one generation to the next to see what rules can be formulated.

The appearance of an organism is referred to as its *phenotype*. Although the phenotype conventionally refers to the outward appearance of an individual, its definition can be extended to include the totality of physiological, anatomical, and behavioral components of that individual. In this book we concentrate on