ESSENTIALS OF BEHAVIOUR GENETICS

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Preface

This text introduces behaviour genetics to the advanced student in genetics or psychology. Twelve years of teaching these two groups of students at La Trobe has revealed their different expectations of behaviour genetics. Psychology students want an approach to behaviour genetics which adds to knowledge of the behaviours and concepts discussed in their other psychology courses. But the same does not apply in genetics. Contemporary concepts of molecular and population genetics are often far removed from the very simple level of genetic analysis currently needed for most behaviour genetic studies and except in the area of quantitative genetics, there is only a very limited role for behavioural examples. Instead genetics students can be presented with behaviour genetics as a different way of viewing genetic analysis. Behaviour is often much more difficult to measure than the characteristics to which genetics students are accustomed and they need to appreciate that a small procedural manipulation can totally alter the results of a behaviour genetic analysis. Particularly in human behaviour genetics, the student has to think beyond the results of any genetic analyses to their potential significance for society.

This text is structured around the diverse needs of these two student groups. Psychology students will find many examples where the behaviour genetic approach provides a different view of material presented in courses on abnormal, cognitive, developmental, educational and experimental psychology. For genetics students there is an introduction to the problems of behavioural measurement to alert them to the unique difficulties of behaviour genetic analysis. While a discussion of basic genetics is mandatory in any behaviour genetics text, it is presented here in terms of the role of genetics in mental retardation, so that students already having a grounding in genetics will find something new to maintain their interest.

Behaviour genetics may be a relatively new discipline, but it has already had more than its share of controversy. There is controversy among behaviour geneticists over the best approaches to particular problems and over the best methods of analysis. There are also critics of behaviour genetics who find fault with all the available data and question the motives behind those researching in the field of behaviour genetics. These disputes can only confuse the student and make him or her unclear whom to believe. Rather than ignoring these questions which simply delays the problem until the student consults the original references, they are introduced in what I hope is a fairly unbiased manner and are often returned to in the discussion questions which conclude each chapter. To more accurately capture the original ideas of the contributors to such disputes, extensive use has been made of quotations, especially in Chapter 8 which deals with contentious social and racial issues.

The introduction to every recent behaviour genetics text has included the disclaimer that the authors have had to be selective and that people should not be offended if their favourite experiment is omitted. The present text is no exception. To keep this text to a length which does not daunt the student, it has been necessary to pick representative examples from different areas rather than trying for a comprehensive coverage. Also for the needs of a student, a limited list of references at the end of each chapter replaces a full bibliography. While not ideal in many ways, it seems better to direct the student to a few key references than to leave him or her alone in a veritable sea of information.

Many people have contributed to this book although I must take responsibility for the final form. I should like to acknowledge: Professor Peter Parsons of La Trobe University who gave the initial impetus to this text and Robert Campbell and Mark Robertson of Blackwell's whose advice and patience helped see it through to fruition; Pauline O'Brien and Marena Ross who kept my research projects functioning while I was occupied with the task of writing; Lindon Eaves (Medical College of Virginia), Lynn Feingold (Oxford University), Norman Henderson (Oberlin College), and Glayde Whitney (Florida State University) for helpful discussions and useful comments about a draft of this manuscript; Professor Walter Nance and the Medical College of Virginia where I held an A. D. Williams Distinguished Visiting Professorship while completing Chapters 6-8; graduate students, past and present, particularly Jeffrey Cummins, Karen Lavery and Grant Singleton, but also Richard Rosewarne, Tommy Solopotias and Theresa Theobald, who provided advice from their particular fields of expertise; Judi Bolton, Marianne de Ryk, Debra Duckworth, Marlene Forrester, Toni McElhenny and Ann Monkman for their efforts in typing the text and preparing the diagrams; Sally Collett, Carol Johnston and Lesley Tan for their help in checking references and preparing the index; Wayne Singleton whose cartoons enliven the text; the many former students whose reactions to the examples and to the discussion questions have shaped the text — perhaps I learned more from them than they did from me.

May 1984

David A. Hay

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Contents

1 The development and scope of behaviour genetics

Topics of this chapter

1 The interrelationships between genetics, psychology and behaviour genetics and the concept of a 'genetically aware psychology'.
2 'Garbage in, garbage out' — the importance of adequate behavioural measures in any behaviour genetic analysis.
3 The history of behaviour genetics and the reasons why its development has been so recent.
4 Distinctions between behaviour genetics, sociobiology and other approaches to the determinants of behaviour.

What does behaviour genetics involve?

Behaviour genetics is a new area of science growing out of two disciplines, genetics and psychology, which themselves are both products of the twentieth century. It is only since 1960 and the first behaviour genetics text (Fuller and Thompson 1960) that the area of behaviour genetics has come to be recognized as a distinct entity.

Many people associate behaviour genetics only with the well-publicized controversies over the genetics of differences in human intelligence within and between racial groups and the social and educational consequences which may follow. It is easy to see how such a misconception arose since many recent discussions of behaviour genetics (Kamin 1974; Taylor 1980; Vernon 1979) do deal solely with intelligence test performance.

Although the intelligence debate may have much relevance to our society, the approach in this text is that the whole issue of genetics and behaviour is best understood by examining the inheritance of many different behaviours in organisms ranging from bacteria to man. We shall see that some behaviours are largely inherited, while others even in the same species are influenced mainly by environmental factors.

In the case of human behaviour genetics where the analytic methods are much in dispute, this diversity of results is important. While the outcome of genetic analysis of intelligence test scores is often dismissed by postulating defects and biases in the methods of analysis, it is a lot more difficult to explain away the fact that similar analyses of other behaviours yield quite different outcomes.The strength of the methods is that they do produce different results when applied to different behaviours and do not reflect biases towards consistently finding behavioural variation to be largely inherited.In the case of experimental animals the study of different behaviours and their differing degrees of inheritance is a valuable means of understanding the organization and evolution of behaviour.

The variety of species becomes important because it is obviously much easier to carry out unambiguous genetic analyses in laboratory organisms whose breeding and environment can be rigorously controlled.If we can find parallels between the results of animal and human research, we can then put more reliance on the human data with all their imperfections.

The study of behaviours in a diversity of species leads to a better appreciation of the genetic analysis of intelligence or any other single characteristic than does an exclusive concentration on that one behaviour.

The organization of the text

Chapter 1 introduces behaviour genetics, its relationship to genetics and psychology and the reasons why behaviour genetics is such a recent discipline.

Chapter 2 presents the prerequisite genetic knowledge, by discussing the ways in which genetic factors may contribute to mental retardation and the use to which genetic knowledge may be put in helping retarded individuals and their families.

Chapter 3 describes the genetic techniques for analysing the behaviour of experimental animals and the importance of considering genetic variation in all research on animal behaviour, not just that directed specifically towards genetics.

Chapter 4 may seem far removed from human behaviour since it involves research solely on invertebrates. But techniques are available with invertebrates which provide unique information on how genes influence behaviour and on how evolution and ecology can shape behaviour.

Chapter 5 discusses results obtained with behaviour genetic analyses of nonhuman vertebrates, mainly mice and rats, where genetic diversity is an important means of analysing different components of behaviour, their relationship with biochemical variables and the effects of environmental manipulation.

Chapter 6 outlines the controversies surrounding the twin, adoption and family study methods of human behaviour genetics and introduces several newer methods which avoid some of the pitfalls. Intelligence test data provide a common example to illustrate all the methods.

Chapter 7 applies the same methods to other areas of human behaviour, particularly to the mental illnesses and to an understanding of the components of intelligence and personality and how these change during development.

Chapter 8 ventures into a discussion of the significance of genetic differences within and between human racial groups and dismisses several conventional myths such as the idea that genetics is the antithesis of social change.

A text of this length cannot discuss every aspect of behaviour genetics but can only provide illustrations of the different methods and controversies. Apart from one other introductory text (Plomin *et al* 1980), lengthier texts are available with a bias towards the student of psychology (Fuller and Thompson 1978) or of genetics (Ehrman and Parsons 1981). This text places more emphasis on the understanding of behaviour than on genetics while still stressing that we can learn much from developments in genetics. To understand why such distinctions between the 'behaviour' and the 'genetics' in 'behaviour genetics' exist, we must consider the ways in which behaviour genetics has grown from the two parental disciplines.

Behaviour genetics — part of genetics or of psychology?

Until about 1975 it was unnecessary even to ask this question. Most research in behaviour genetics was directed to providing the first unambiguous evidence that genes could influence behaviour. This required the application of conventional genetic techniques to conventional measures of behaviour, with both parent disciplines contributing more or less equally. It was possible for geneticists at that time to view behaviour as something to be analysed in the same way as any measurable physical or biochemical characteristic — usually referred to as the 'phenotype' — of animals or even plants.

My purpose is to examine the experimental and analytical consequences of accepting the premise that behaviour, like any other property of an organism, is a phenotype, determined jointly by inherent causes (usually referred to as nature or genotype) and external agencies (nurture or environment). (J. L. Jinks (1965) *Bulletin of the British Psychological Society* **18**, 25.)

At the same time, experimental psychologists were realizing that all organisms were not identical in behaviour and that individual differences could be studied systematically by genetic techniques.

It was then while overcome by feelings of disenchantment (obviously without laws, behavior study could never be science) that I embraced genetics. There was true science. My passion became even more intense when I realized that, like thermodynamics, genetics has three laws: segregation, independent assortment and the Hardy-Weinberg law of population equilibria. What a foundation they provided for my beloved individual differences. (J. Hirsch (1970) *Seminars in Psychiatry* **2**, 89)

Geneticists and psychologists worked together to accumulate a sizeable store of information on the nature and extent of genetic determination of behaviour. There was also growing cooperation with other disciplines concerning anatomical, biochemical and physiological factors underlying behavioural differences. But science cannot proceed by the simple cataloguing of more and more examples of the inheritance of behaviour. Geneticists became critical of behavioural traits, where the difficulty of adequate measurement and the apparently very complex interplay of genetic and environmental influences made behaviour a very poor choice when it came to trying to learn more about genetics. For example,

> There has not been, and in the present state of developmental and neural biology cannot be, any attempt to analyze cellular and developmental mechanisms of gene action in influencing cognitive traits. Nor can it be maintained that work on the biometrical genetics of intelligence has somehow led to progress in biometrical genetics as a general approach. On the contrary, because of the impossibility of control and manipulation of human environments and mating, man is among the worst choices of experimental organisms for testing the methods of quantitative genetics. (R. C. Lewontin (1975) *Annual Review of Genetics* **9**, 401.)

While this viewpoint may hold for some geneticists, psychology and society as a whole have placed so much emphasis on intelligence, its determinants and consequences that it seems shortsighted to dismiss research on this area just because it does not lead to a greater understanding of genetics.

The dilemma facing behaviour genetics in the early 1970s is best summarized by Vale, who wrote,

> Two basically different concepts of behavior genetics derive from the question of how close its formal ties to the goals and methods of genetics should be. On the one hand, behavior genetics may be seen as a genetics of behaviors, that is, a subspecies of genetics whose primary concern is the extension of the range of traits examined with the methods of genetics from morphological and physiological to behavioral. On the other hand, it may be seen as a genetically aware psychology, whose primary *raison d'etre* is the further understanding of behavior, and which therefore seeks the best use of genotype in behavioral analysis. This difference is crucial not only at the conceptual level, but, perhaps more importantly, at the operational level, because of differences in the kinds of techniques employed and information generated. A genetics of behaviors studies the functioning of genes through the use of genetic tests applied to behavior. A genetically aware psychology seeks to augment the study of behavior through the manipulation of genotype. In the first case the experimental situation is so structured as to provide the maximal genetic information, while in the second it is structured so as to provide the maximal information about behavior. (J. R. Vale (1973) *American Psychologist* **28**, 872.)

This text is directed towards the latter option, Vale's 'genetically aware psychology', explaining how both animal and human behavioural research can be aided by the consideration of genetic variation. The mere demonstration that a particular behaviour has a genetic determinant should not be seen as the final aim of research, but only the beginning, the stage from which more detailed analyses of the ramifications of genetic differences can proceed. For example, rodent strains differing in alcohol preference differ also in many other aspects of biochemistry, physiology, behaviour, reaction to other addictive drugs and the incidence of diseases related to alcohol consumption. In this way we learn far more about alcohol and its effects than just that alcohol preference is partly inherited. The same applies to human behaviour. The evidence in Chapter 7 that different intellectual skills vary in the extent to which they are inherited may be of little interest to the geneticist, but provides uniquely important information about a longstanding debate in psychology over the structure of human abilities and has possible implications for educational practice.

The approach we adopt is one where genetics is a means to an end and not an end in itself. But while psychologists can claim this approach to behaviour genetics as part of their discipline, two recent developments in genetics show that the interest of geneticists in behaviour genetics is not dead but has merely changed direction. Both these developments may also direct behaviour genetics away from what has always been a major complaint about psychology, namely the limited range of behaviours studied and the limited number of species in which these are studied. Such criticisms of psychology are more frequent nowadays (Lockard 1971; Wilcock 1972), but are not new. Figure 1.1 is from a 1950 article bemoaning the narrowness of psychology at that time.

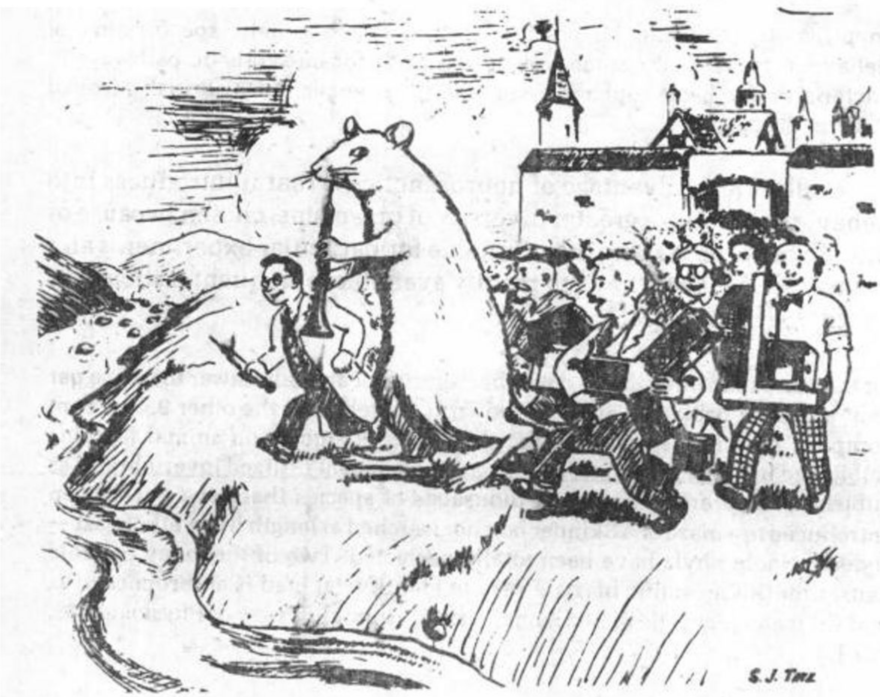

FIG. 1.1 Beach's prediction of the future of experimental psychology. 'Unless they escape the spell that *Rattus norwegicus* is casting over them, experimentalists are in danger of extinction.' (From F. A. Beach (1950) *American Psychologist* **5**, 115.)

Neurogenetics or 'molecular ethology'

This topic discussed in Chapter 4 concerns the use of behavioural changes to indicate genetic alterations at the level of the molecules which encode genetic information. Geneticists are using behaviour as a tool in studying gene action, because altered behaviour can sometimes be a more convenient indicator of genetic changes than either altered anatomy or physiology. Now that the molecular bases of genetics are fairly well understood, some geneticists feel behaviour provides the next challenge, not

The problem of gene structure and coding was exciting while it lasted. The story of the past two eventful decades, including my own contributions, has been well told, and need not be repeated here. But molecular genetics, pursued to ever lower levels of organization, inevitably does away with itself: the gap between genetics and biochemistry disappears. More recently, a number of molecular biologists have turned their sights in the opposite direction, i.e. up to higher integrative levels, to explore the relatively distant horizons of development, the nervous system, and behavior. The problem of tracing the emergence of multidimensional behavior from the genes is a challenge that may not become obsolete so soon. (S. Benzer (1971) *Journal of the American Medical Association* **218**, 1015.)

and one to which the same methods can be applied

In principle, it should be possible to dissect the genetic specification of behaviour much in the same way as was done for biosynthetic pathways in bacteria or for bacteriophage assembly. (S. Brenner (1973) *British Medical Bulletin* **29**, 269.)

A subsidiary advantage of neurogenetics is that it introduces into behaviour genetics a greater diversity of organisms, chosen because of unique features making them suitable for particular experiments and not merely because they are readily available, a frequent criticism of psychology in general.

Of the more than one million described species of animals, fewer than five per cent possess a backbone and are known as vertebrates; the other 95 per cent comprise the invertebrates. Of the thousands of studies on animal learning published in the past decade, only some five per cent utilized invertebrates as subjects. There are hundreds of thousands of species that have never been introduced to a maze or a Skinner box nor watched at length by an ethologist — indeed, whole phyla have been totally neglected. Two of the many possible causes for this scientific bias are easy to identify: (a) man is anthropocentric, and (b) man is lazy. (J. V. McConnell (1966) *Annual Review of Physiology* **28**, 107.)

Ecological and evolutionary influences on behaviour

This approach is outlined in Chapters 4 and 5 and is emphasized in one recent text (Ehrman and Parsons 1981). While we normally think of genes influencing behaviour through a sequence of chemical and physical pathways, the questions of ecology and evolution remind us that behaviour can also influence genes or at least the extent to which particular genetic types are represented in particular populations. Genetically determined differences in behavioural responses to environmental stresses or in migration or mating propensity are all factors which influence how a population evolves and its genetic structure. Consideration of genetics and evolution can influence which behaviours are measured and in which organisms. Psychology has only recently come to appreciate that animals are biologically adapted and have evolved so that some behaviours are more likely than others to occur in given situations, a concept termed 'biological preparedness' by Seligman (1970).

A simple example of this would be the response of an animal experiencing an electric shock or some other painful stimulus. In this situation, it is much easier to 'condition', that is to train the animal to avoid the shock by jumping out of the apparatus or running down an alleyway than by running in an activity wheel or a shuttle box. In a shuttle box an animal shocked in one side of the box moves to the other side of the box. When shocked here, the animal shuttles back again and the cycle is repeated. In real life no animal would return to where it had just been hurt as in the shuttle box or put in the effort in a running-wheel which restrains it in the environment where the pain was administered. Hence the animal is contraprepared to learn in these two situations.

Another example is that many animals in the wild adopt a 'win-shift' strategy, moving on to look for food elsewhere once they have found it in a particular spot. But this strategy is the opposite of that favoured in the maze-learning experiments of traditional animal psychology where the animal is trained to return to the same spot.

Unfortunately behaviour genetics lags behind such developments in psychology. Among the experiments on rodent behaviour discussed in Chapter 5, apparatus such as the shuttle box and the maze feature widely despite their inadequacies. The same can be said for many of the measures of human behaviour described in Chapters 6 and 7.

Beyond the specific neurological and ecological genetic approaches, there is an even more fundamental reason why behaviour genetics should not become divorced from advances in genetics. It is not too harsh to say that behaviour genetics at the present time has ignored most developments in genetics since the early 1950s when the main methods for analysing complex phenotypes became established in plant and animal breeding. That is, a geneticist of that time would find few new genetic concepts in present day behaviour genetics but just some new characteristics to which his methods are applied and some extension of the methods to human data.

Since then there has been an explosion of interest in molecular genetics, in studying the biochemical means by which genetic information is stored and passed onto subsequent generations. Certainly, this knowledge has meant that we no longer think of genes for behaviour as such. Rather genes code for specific proteins which go on to determine anatomical, biochemical and physiological characteristics in association with the internal and external environment. The outcome of all these processes may include some effect on behaviour.

In one of the first symposia on behaviour genetics (Hirsch 1967), Caspari indicated some potential applications to behaviour of this knowledge. Eleven years later Fuller and Thompson (1978) did the same, suggesting that this information has had very little influence on the majority of behaviour-genetic research. For example, behaviour genetics has largely ignored the possibility that genes can be 'regulatory' rather than 'structural', and regulate the function of other genes instead of directly influencing a pathway to behaviour. The situation now arises where the expression of an individual's genetic endowment is not necessarily obvious at birth but may alter with the internal (e.g. hormonal) or external environment.

Medical genetics illustrates the significance of such a possibility. Haemoglobin in the fetus binds oxygen so strongly that there is a flow of oxygen from the mother to fetus. Postnatally this tight binding could deprive tissues of oxygen and so the production of fetal haemoglobin is diminished and genes determining the production of the adult form become active. The existence of this mechanism is confirmed by disorders that involve a persistence of the fetal form, that is, where its genes are not 'switched off'. While behavioural parallels have not yet been described, Chapter 7 provides examples from human intellectual development that may be explained by regulatory genes acting at the time of puberty.

Some potential applications of molecular techniques to mental retardation and to mental illness are discussed in Chapters 2 and 7 respectively, but one fundamental difficulty remains before behaviour genetics can fully utilize such recent advances in genetics. We must be able to measure the behaviour of interest with a sufficient degree of precision, unconfounded by other variables. As the next section illustrates, this is not as easy as it might seem.

'Garbage in, garbage out' — the need for adequate behavioural measurement

The dictum 'garbage in, garbage out' can be applied to many areas of behavioural science, and is directly relevant to behaviour genetics. It means that no matter how sophisticated and expert our genetic analysis, the results of our study will be worthless unless we have been able to measure behaviour adequately in the first place. Apart from the question of *validity* and whether a measure actually measures what it is supposed to, there are two criteria of particular relevance to behaviour genetics.

The first, *reliability*, examines whether the measure of behaviour is consistent or if the result varies when the measure is repeated or made by someone else. When we measure a behaviour which reflects underlying and constant genetic influences, we would expect the result always to be the same. If our measurement techniques are inadequate and results fluctuate, then we are more likely to conclude that the behaviour is determined largely by the environment and that this explains the variation from one test to another.

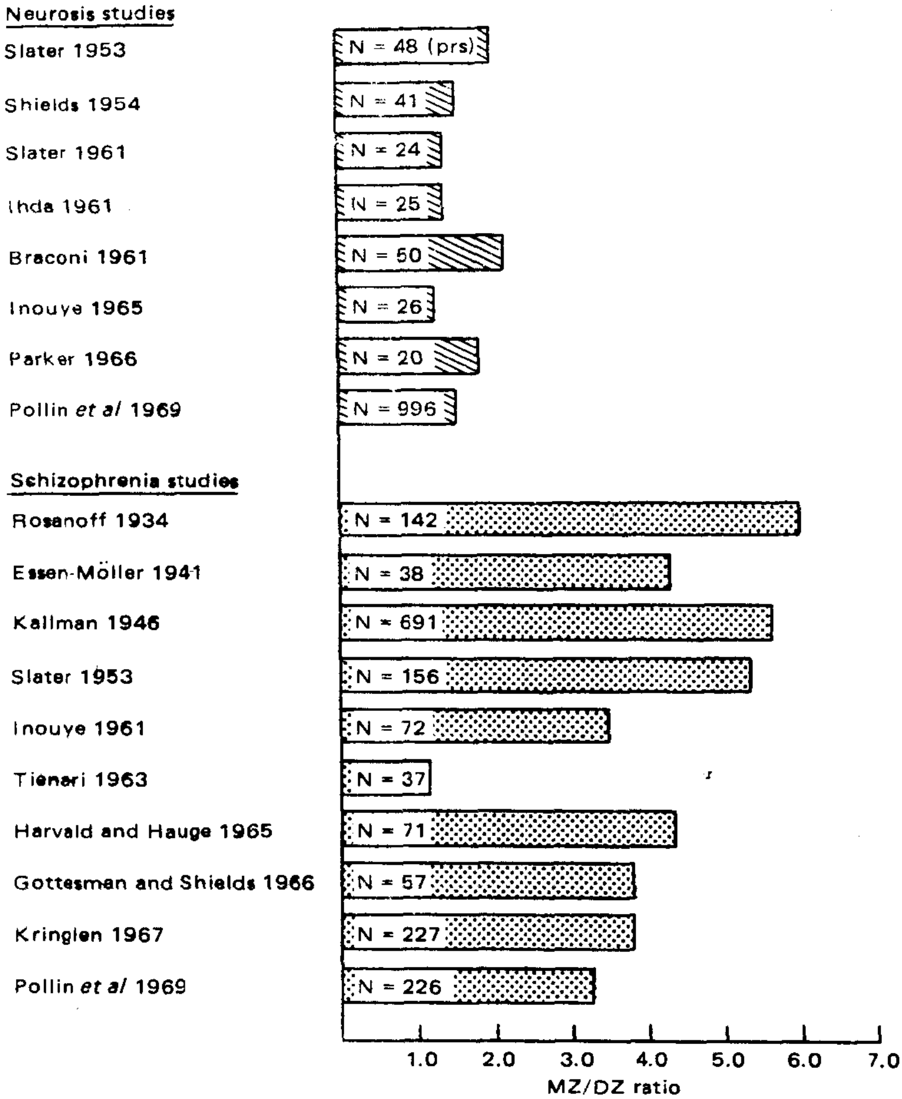

FIG. 1.2 The similarity of MZ (identical) relative to DZ (non-identical) twins in studies of neurosis and schizophrenia. An MZ/DZ ratio of 1 means they are equally similar and greater than 1 that MZ are more similar than DZ. (From W. Pollin (1976) in *Human Behavior Genetics*, Kaplan A. R. (ed.) p. 279, Thomas, Springfield, Ill.)

Figure 1.2 is an example from the area of mental health of how the reliability of measurement sets an upper limit on how much of the variation in a behaviour is seen to be determined by inheritance. The twin method is discussed in Chapter 6 but basically involves comparing the similarities between identical twins (monozygotic (MZ) twins who are genetically identical) with those between fraternal (dizygotic (DZ) twins who genetically are only as alike as any two brothers or sisters). If genetic factors are involved, the identical twins will be much more similar, as seen for the data on schizophrenia in Fig. 1.2. If it is mainly the environment that matters, the two types of twins will show the same degree of similarity, as seen for the neurosis data in Fig. 1.2.

But do these results mean that schizophrenia is necessarily more of a genetic disorder than neurosis? Schizophrenia is a much more severe disorder and there is a higher degree of consistency between psychiatrists in its diagnosis. Neurosis is a much milder disorder covering a wide range of symptoms and overlapping with the behavioural differences seen among the normal, non-mentally ill population and varying more with society's tolerance of people who are in some way 'different'. Thus reliability of diagnosis is potentially much lower.

To make things even more difficult, Fig. 1.2 is a compilation of twin data from studies in many different countries and there are international differences in diagnostic categories. United States psychiatrists have in the past had a far wider definition of schizophrenia so that no less than 50% of the schizophrenics classified in New York hospitals during the US–UK Cross National Project were later diagnosed by the project staff as having some other psychiatric disorder. With the more precise British classification, agreement between psychiatrists on schizophrenia can be as high as 92%. The situation is changing with the introduction in 1980 by the American Psychiatric Association of a new *Diagnostic and Statistical Manual of Mental Disorders*, abbreviated to DSM-III. While this has resulted in a much more rigorous definition of many disorders, especially schizophrenia, it has created an additional problem for geneticists who compile data on individuals diagnosed over a period of time, some under the old DSM-II, others under DSM-III.

If the psychiatric diagnosis of an individual is subject to so many variables, then what hope is there of accurately comparing twins or other relatives for the purpose of genetic analysis? We are left with a situation where the apparent differences in inheritance between schizophrenia and neurosis may be real, or may just be due to differences in the reliability of diagnoses. A satisfactory answer depends not so much on better genetic analyses, but more on improved methods of diagnosis in the first place.

The second criterion is *ease and speed of measurement*. Ever since the first genetic experiments carried out by Mendel on peas over a century ago (Chapter 2), it has been clear that any breeding experiment involves the scoring of many individuals. The laws of genetics are based on probability and accurate estimates of probabilities require large samples. Behaviour genetic analysis is no exception and imposes additional constraints. Behaviour may have to be measured in individuals of the same age to eliminate developmental differences and at the same time of day to avoid diurnal rhythm effects. In organisms such as the vinegar fly, *Drosophila*, widely used in genetics because of its short generation time, the total lifespan of 2–3 weeks may leave only a very short period during which behavioural measures can be made. The same problems do not arise with humans, but since people usually volunteer for research, the tests must again often be short as well as being limited in other ways for ethical reasons.

The dilemma imposed by the need for fast, reliable measurement is summarized below:

There can be no doubt that these requirements have influenced the choice of behavioural characters used in such studies. It has got to be something easily and quickly measured, and if measurement can be automated so much the better. The number of squares entered in an open field and faecal boli deposited there (rats), time taken to emerge from a small box, revolutions of a running wheel or speed of acquisition of a conditioned avoidance response (mice), scores of preening, walking or standing still in response to a mechanical stimulus (*Drosophila*) — these are typical measures employed.

Most ethologists would have grave doubts about the relevance of such measures to the behaviour of the animals in their natural habitats. This is not to say that behaviour genetics must always satisfy ethological criteria, but it does make arguments on the evolution of behaviour derived from some quantitative studies much more hazardous. Further, some measures, however easy to make in the laboratory, are subject to all the problems of validating behavioural units touched on earlier. (A. Manning (1975) in *Function and Evolution in Behaviour* Baerends G., Beer C. and Manning A. (eds), Clarendon, Oxford, p.77.)

Much of behaviour genetics is a compromise between what Manning sees as the approach of ethologists, namely the detailed observation of behaviour often in the field rather than the laboratory, and the limitations imposed by the numbers needed for genetic analysis. It might seem extreme to say that behaviour geneticists often do not know what they are measuring, except that whatever it is, they are measuring it quickly and reliably. The following three examples, one each from *Drosophila*, rodents and humans all deal with behaviours that have been the subject of extensive genetic analyses and suggest that this criticism is not without foundation.

Taxes in Drosophila

In 1959, Hirsch introduced a method for 'reliable mass screening of individual differences' in geotaxis (the attraction to and from gravity). *Drosophila* are introduced into the start of a vertically placed multiple-choice maze (Fig. 1.3). At each choice-point they can either go up against gravity (negative geotaxis) or go down (positive geotaxis). Their sequence of choice is reflected in the tube they reach at the end of the maze. Flies with a consistently negative geotaxis will be in the top tube (−5), those with a positive geotaxis in the bottom tube (+5). A system of one-way cones prevents the flies from turning back in the maze.

The system can be adapted to study phototaxis (the attraction to and from light) by covering a horizontally placed maze with a screen, which only allows light to reach one side of each choice-point. Positively phototactic flies turn towards the light, while negatively phototactic flies turn away.