GENETICS

* *

SECOND OF A SERIES ON

BIOLOGY AND BEHAVIOR

BIOLOGY AND BEHAVIOR

Genetics

Proceedings of a conference under the auspices of
Russell Sage Foundation, the Social Science
Research Council, and The Rockefeller University

David C. Glass, *Editor*

PUBLISHED BY *The Rockefeller University Press*
AND *Russell Sage Foundation* NEW YORK 1968

SECOND PRINTING 1970
LIBRARY OF CONGRESS CATALOG CARD NUMBER 68-24635
PRINTED IN THE UNITED STATES OF AMERICA

Preface

CONTEMPORARY social scientists no longer adhere to a simplistic environmental determinism, just as contemporary biologists no longer embrace a genetic determinism. In both fields there is increasing recognition of the importance of an interaction between the organism and the environment. Neither the genetic parameter nor the environmental parameter alone can account for more than a portion of behavioral variability. With the development of this interactional approach, a revitalized interest in the genetic basis of social behavior has been witnessed. On November 18–19, 1966, Russell Sage Foundation and The Rockefeller University, in collaboration with the Social Science Research Council, sponsored a conference on genetics and behavior in Caspary Auditorium on the Rockefeller campus in New York City. The organization of the meeting was guided by the premise that recent advances in genetics portend serious social, ethical, and legal consequences. It is important that both biological and social scientists study these consequences. Social scientists, in particular, are equipped by training and are implicitly committed to make substantial contributions in this area. However, they often lack the knowledge of behavior genetics necessary for sophisticated analysis of the social consequences of new knowledge resulting from research on genetics. The specialist in genetics, on the other hand, often lacks the interest or skill necessary for examination of the broad implications of this research. The purpose of the conference was to enable participants drawn from both groups of scientists to benefit from exposure to the work of representatives of the other.

The present volume contains a series of fourteen papers delivered at the two-day conference. The papers have been slightly modified to meet the more formal requirements of publication. The topics include discussions of the relationship between genetics and intelligence; behavior genetics research in infrahuman species and its relevance for understanding human social behavior; the role of social competition in natural selection, with particular attention to population control; and biogenetic theories of social structure and process, such as stratification, socialization, deviance, and social change. The major address of the meeting was delivered on the evening of November 18 by Professor Theodosius Dobzhansky of The Rockefeller University. The complete text of his paper, "Genetics and the Social Sciences," is included in this volume.

This volume is the second in a series of three reporting the Biology and Behavior conferences organized by Russell Sage Foundation and The Rockefeller University. The first volume was published in the fall of 1967 and dealt with the topic of neurophysiology and emotion. The third volume will present papers delivered at the conference on environmental influences on behavior, held at the Rockefeller in April, 1967. The ultimate goal of all three volumes is to disseminate information which will foster understanding of behavior through research that rises above the limitations imposed by narrow specializations.

We would like to thank Dr. Orville G. Brim, Jr., President of Russell Sage Foundation, Dr. Detlev W. Bronk, President of The Rockefeller University, and Dr. Pendelton Herring, President of the Social Science Research Council, whose joint efforts and support made the conference possible. We also want to thank Dr. Carl Pfaffmann, Vice-President of The Rockefeller University and Dr. Donald R. Young, Visiting Professor at the Rockefeller and formerly President of Russell Sage Foundation. Both men were instrumental in conceiving and implementing the idea of a conference series on biology and behavior. Our gratitude also goes to members of the Social Science Research Council's Committee on Genetics and Behavior, presently called the Committee on Biological Bases of Social Behavior. Many of its present and former members actually participated in the conference, and all were intimately involved in its planning and execution. Participants from the Committee included its chairman, Gerald E. Mc-

Clearn, Theodosius Dobzhansky, David Rosenthal, James N. Spuhler, and David A. Hamburg. The other Committee members who helped plan the conference were Gardner Lindzey (who is also chairman of the Problems and Policy Committee of the Social Science Research Council), Ernst Caspari, Jerry Hirsch, and Jerome E. Singer, SSRC staff member assigned to the Genetics and Behavior Committee.

Russell Sage Foundation was established in 1907 by Mrs. Russell Sage for the improvement of social and living conditions in the United States. In carrying out its purpose, the Foundation conducts research under the direction of members of the staff or in close collaboration with other institutions, and supports programs designed to develop and demonstrate productive working relations between social scientists and other scientific and professional groups. The program in biology and the social sciences represents one such activity, which was undertaken jointly with The Rockefeller University.

For their assistance and encouragement, I am most grateful to my colleagues at Russell Sage Foundation and The Rockefeller University. As with the previous volume in this series, I would also like to express my gratitude to Mr. William Bayless of The Rockefeller University Press and to Mrs. Betty Davison of Russell Sage Foundation for their assistance in organizing the conferences, publishing the proceedings, and arranging for distribution and advertisement. I would particularly like to thank Mrs. Helene Jordan, of The Rockefeller University Press, who performed invaluable editorial work in bringing the present volume to publication. I would like to join the authors in expressing gratitude for her dedicated assistance.

DAVID C. GLASS
Russell Sage Foundation and
The Rockefeller University

September 16, 1967

Contents

POPULATION SIZE AND SOCIAL BEHAVIOR

GENETICS AND SOCIOLOGICAL RESEARCH

GENETICS

The Nature and Nurture of Intelligence

STEVEN G. VANDENBERG

DISCUSSION

I was prepared to review evidence that genes control part of the variance observed on tests of intelligence and personality. However, two reasons made me decide not to do so, but instead to broaden my presentation to include an overview of some of the many problems that must be solved before we have a reasonably coherent theory of how genes set the limits for behavior in the child and adult. Where possible, I will indicate how some of these problems have been approached, and venture a guess as to how far we have moved.

The first reason for my decision not to limit my paper to a review of the evidence for genetic determination is that Professor Curt Stern reviewed that evidence in an incomparable manner at the recent Third International Congress of Human Genetics.[84] The second reason is that I have attempted to review parts of the evidence, based primarily on twin studies, in three recent papers covering different ground.[97–99] I did not want to repeat myself, and am not ready to integrate all of it into one paper.

STEVEN G. VANDENBERG University of Louisville School of Medicine, Louisville, Kentucky. Present address: Department of Psychology, University of Colorado, Boulder, Colorado

Here I shall address myself to the broad topic, "The nature and nurture of intelligence," using the words nature and nurture in their logical meanings.

THE NATURE OF INTELLIGENCE

What, then, is the nature of intelligence? In past centuries, the term referred to a generic difference between man and animals, or between animals and plants, rather than a graduated concept. The adoption of the term, early in the twentieth century, as an explanatory concept for individual differences in performance has hindered us ever since. Although attempts had been made to devise methods of distinguishing the performance of retarded children from that of normals, the first successful scale was devised by Binet and Simon.[9] It was of momentous consequence that Binet, early in his studies, relinquished the hope of basing his work on a definition of intelligence. Instead, he proceeded in a purely empirical way to find tasks that could be performed by a majority of normal children of a given age. The adoption of age as the single criterion led, of necessity, to a heterogeneous collection of items, although some common threads, such as vocabulary, ran through the scale for all ages.

The almost astonishing success of the method and its rapid adoption in most of the Western world had some unfortunate consequences. It led to a split between experimental psychologists who were bothered by the lack of theory, and the early clinicians and educators who used the method.

Experimental psychology developed, for a time, an overriding interest in learning theory, and in general disregarded the measurement of past learning as embodied in abilities and individual differences. There were notable exceptions. Some statistically inclined psychologists began to study the intercorrelations between different tests, or between items of a test, and developed a whole new branch of psychology. One of their accomplishments was the development of factor analysis, a simplified way of solving a characteristic equation based on correlations among test scores. Unfortunately, by the time they obtained some results, it was too late for them to affect to any great degree the rather well-established traditions of applied testing, which continued to measure a general IQ or attempted to predict single-valued criteria, such as success in college or some type of abnormal behavior.

The studies of these psychologists (Thurstone and Guilford among the most prominent) made it clear that intelligence is multifaceted and so cannot be expected to fit into one definition. It also became clear that the nature of the "general" intelligence measured by a given IQ test depends on the particular mix of items, and can be expected to show considerable differences among babies, children, and average or talented adults. Instead of general intelligence, it may be necessary to measure a number of different abilities, depending on what we wish to diagnose or predict. How many independent abilities there are and how useful each may be for practical purposes remains an unanswerable question. Thurstone[91] put most of his faith in six abilities. Guilford[31] has proposed as many as 120, which he has classified according to three basic characteristics: operations, contents, and products. This produced his well-known intellectual cube, rather than the squares with which we were more familiar. (I go more for circles and spheres.) One problem with Guilford's studies is that until recently they were all based on adults with considerably more than average ability, where one can expect a highly differentiated structure of the intellect. Students of Guilford, such as Dingman, Meyers, Merrifield, and Sister McCartin, recently have studied the applicability of his theories at the primary and secondary school level.

At Least Six Separate Abilities

The available evidence, some of which we will review later, seems to establish the independence, at all levels, of at least six abilities. These are: two verbal, and numerical, spatial, reasoning, and memory abilities.

The *first verbal ability* is size of vocabulary. This depends more or less on the passive recognition of word meanings, and is usually measured by multiple-choice vocabulary tests, although individually administered tests, such as the Binet and Wechsler, call for a definition or explanation of words. The *second verbal ability* is word fluency, and deals with the active recall of words to fit a given demand. These two appear to be independent.

The development of vocabulary, both active and passive, has been extensively studied, benefiting some of the tests, and its importance seems obvious. Many older tests of general intelligence were made up mainly of items measuring these abilities. They still form an important part of newer tests, and they correlate highly with the total score in Binet and Wechsler. Besides their obvious face validity, the predictive validity of verbal tests for success in school or in many jobs is well established.

Numerical ability, or number ability, as it is usually called, simply means facility in basic arithmetic. It is generally measured by seeing how many problems can be solved correctly in a given time limit. The problems may be purely arithmetical or they may be clothed in verbal garb. A classic problem in the latter category is about two carpenters building a house in 12 days. In a joking form the question is: "How many carpenters would it take to build the house in one hour?" The improbable answer is 192. In addition, problems may be increasingly difficult or be of roughly equal difficulty. While such differences tend to lower correlations between tests, all varieties seem to measure the same "general" number ability.

The development of number ability has not received as much attention as has the development of vocabulary or grammar. Piaget[67] has not dealt with the acquisition of specific arithmetical routines, but rather with the development of over-all concepts, such as "more" or "less," that may be necessary for understanding but not for rote memorization of multiplication tables or of additions. It would be interesting to study if the development of number ability in the preschool child can be distinguished from the acquisition of the vocabulary for different numbers, and if learning such additions as $1 + 1 = 2$, or $1 + 2 = 3$ is similar to learning new words. If such is the case, number ability would not appear as a statistically independent factor in analysis of test correlations, at least until it had become well-routinized in an important number of children studied. The validity of number ability or quantitative tests is known, but such ability is, of course, no predictor of success in mathematics, except in numerical analysis.

Spatial ability, or ability to visualize spatial relations, may be for either two- or three-dimensional patterns, which perhaps are partly independent. The existence of this ability has been known for a long time, and it is included in some well-known intelligence tests. However, little information is available about its development in children, and not too much about its value in predicting success in occupations such as biochemistry, engineering, or architecture, which, on the face of it, would seem to require spatial pattern visualization.

Macfarlane Smith[55] has recently reviewed the evidence, and he concludes that, at least in England, tests of this ability are not used sufficiently. He believes that spatial tests may provide better measures of the ability to think abstractly or to form general concepts, than do verbal tests, and feels they may have special merit for selecting research workers in mathematics and the physical sciences. We do not know if this ability can be acquired or if it can be improved by training with moving models and films.

Reasoning ability is definitely independent from number, spatial, and the two verbal abilities. It is less certain that a good measure of "general" reasoning ability can be developed or whether instead there is a whole group of reasoning abilities. Ideally, reasoning should come closest to what early workers believed intelligence to be. Existing reasoning tests usually have considerable verbal or spatial components, and the two types do not correlate highly. Some of the tests were developed by Thurstone and by Guilford, and show only low intercorrelations with verbal and spatial tests. However, their usefulness for occupational selection has not been fully explored. Neither do we know if such an ability can be substantially improved by training in formal logic or other types of reasoning.

Memory is also independent from the other five abilities discussed, but may not be unitary in the same sense as the others. Recent work suggests that there are different mechanisms for short-term and long-term memory storage, as well as separate memory abilities for different types of material. In addition, the measurement of memory does not test a skill acquired in the past, but demands that the subject learn something while taking the test. Motivation thus assumes a much more important role than in the measurement of the other abilities. In fact, some memory tests may be useful in determining a subject's degree of cooperation. I know nothing of the usefulness of memory tests for specific occupations, although I believe that some telephone companies employ a digit memory test in selecting long-distance telephone operators.

USEFULNESS OF THE CONCEPT OF SEPARATE ABILITIES

The basic evidence for the primary nature of all these abilities derives from factor analyses of batteries of tests, in which certain tests group themselves in a way that suggests a common ability in each group. It remains to be seen how useful measures of separate abilities are, compared with a test of general intelligence. Any of the following six criteria might be used: 1) differential prediction of success in various curricula and jobs; 2) stability of the factors over different age ranges; 3) cross-cultural generality of the ability patterns; 4) comparability over different ability levels; 5) differential effects of mental illness or brain damage; 6) different rates of development.

Differential Prediction of Success in Various Curricula and Jobs

Not as much information exists on this criterion as one might like, and what is available is scattered in a variety of journals and books. Only a few representative studies will be mentioned here.

Thorndike and Hagan[90] presented means on five composite scores for 124 occupational groups. The scores were general intellectual, numerical fluency, visual perception, mechanical abilities, and psychomotor abilities. Some occupations showed profiles that seem characteristic for the nature of the work – for instance, architects were high on visual perception tests, accountants and treasurers were high on numerical tests, and the highest composite score of carpenters was on the mechanical composite.

Super and Crites[87] summarized the record on differential prediction of different course grades in college for the Primary Mental Ability (PMA) subtests, and conclude that some correlations in several studies make sense, but that none was higher than .50.

Several French studies have also been published recently. On a battery of 27 tests, Bonnardel[11] compared 1,750 metallurgical workers and 300 office workers between the ages of 20 and 30. He found only modest correspondence between occupation and differential scores. In another study he compared results on 27 tests given to 1,030 men and 410 women grouped into four occupational classes.[12] He found women superior in spelling, clerical speed and accuracy, and manual dexterity, and men in verbal intelligence and concrete intelligence. This obtained at all occupational levels, although there were minor differences. A comparison of factor structures for the data from both studies would be highly informative.

Nguyen-Xuan[61] administered four verbal, four numerical, and four spatial tests to 256 students from the classical and the modern sections of a French *lycée.* Students in the classical section have more instruction in language and history; those in the modern section more in mathematics and science. The correlations between tests and grades in mathematics, science, spelling, essay writing, history, geography, and drawing were in part what one would expect: the verbal tests correlated most with essay-writing grades and the number tests with mathematics grades. The spatial tests did not correlate with science grades, but gave the next highest correlation with those in mathematics.

Several other studies give a total impression that some differential prediction is possible, but success in school or job often seems as well-predicted by multiple regression or by general intelligence scores as by any special ability. In part, this may be because success often does require a combination of several abilities. At least, the evidence is not negative, but further study is needed.

Stability, i.e., the Comparability, of Factors Over Different Age Ranges

Research on this topic has often led to controversy over whether differentiation of abilities or general ability increases with age. The latter would imply that specific abilities decrease in importance as the child becomes an adult.

Reinert, Baltes, and Schmidt[72] reviewed 36 studies dealing with the question of whether increasingly independent abilities emerge during childhood and adolescence, as was suggested by Burt.[15] Only 15 of the studies supported this theory, but in general they were methodologically superior to those that produced negative results. The authors point out that, in most studies, age differences are confounded with differences in ability.

In 1958, Wewetzer proposed a divergence hypothesis, which stated that the factorial structure of subjects with *higher ability* would be more differentiated than would that of subjects with *lower ability*.[103]

Earlier, Burt[15] and Garrett[27] had developed hypotheses which proposed that the factorial structure of *older* subjects would be more differentiated than would those of *younger* subjects. Lienert[50,51] combined the two into one, which he called the developmental divergence hypothesis: the factor structure of children with greater ability should resemble that of older children, and the factor structure of less gifted children should resemble that of a younger age group. Reinert, et al.,[71] proposed calling this model the performance differentiation hypothesis. According to their model, the degree of differentiation of an intelligence factorial structure is dependent on the level of the intellectual test performance. But performance is a function of age and ability combined. (Higher age level can compensate for lower ability, to some extent, and vice versa.) Reinert and his associates performed two related studies to test the new model for the differentiation of intelligence in various abilities. The first study contrasted groups of boys aged 10½ and 12½. The groups were selected so that their intellectual levels, based on age and ability, would be approximately equal; the mean IQs were 106 and 94 respectively. In the second study, two groups of boys of equal mean IQ (99 versus 100) but of a different mean age—and therefore a different level of mean ability—were compared.

In the first study, the investigators predicted the same factor structure; in the second study, they predicted a more differentiated structure for the group with the higher test performance. The results supported their predictions. In a later study of girls by Reinert[71] the first prediction was confirmed, but the second was not. This raises an interesting question about sex differences in development of mental abilities, and might necessitate controlling sex differences in subsequent studies. Many older studies used unequal numbers of male and female subjects, which would make comparison even less promising.

It is difficult to put together findings for the earlier studies because each investigator used different sets of tests. Some studies did produce results different from the reported ones, either because too large or too small a variety of tests was used. Often the results from a group given one set of tests were compared with the results obtained in another study (often conducted by another investigator) with quite a different set of tests. In only a few were the same or similar tests used with subjects of different age ranges. In addition to the early studies of Kelley[45] and the Thurstones,[93] several reports have been published by Meyers, Dingman, and their associates[58,59] on their efforts to compare factor structures in normal children at ages two, four, and six, and retarded children of comparable mental ages. In general, they were able to demonstrate a high congruence across the two samples at all three age levels.

Bonnardel[13] compared 31 test performances of three age groups—17 to 18, 20 to 30, and 30 to 40 years of age. He compared only means and quartiles, but his data would provide a valuable test of comparability across ages in a factor structure.

Cross-cultural Generality of Ability Patterns

Only a few direct tests of cross-cultural generality have been conducted, although a variety of factor analytic studies have been performed in many countries. In general, these arrive at a number of independent factors, which seem rather similar. Vandenberg[94] administered to Chinese students 20 tests from the battery Thurstone used with University of Chicago students, and found a high congruence between the two sets of data for the spatial, verbal, numerical, memory, and perceptual factors. The values for the congruence indexes ranged from .910 to .730. The verbal factor was the only one for which a relationship with acculturation measurements was found.

In a second study, Vandenberg[95] administered the same battery to South American students and compared the factors from their test scores with those from the Chinese students. Congruence indexes between .953 and .780 were found for a native language factor, a verbal ability factor, a memory factor, a spatial visualization factor, a perceptual speed factor, a number ability factor, and a poorly defined reasoning factor.

Irvine, of the University of Bristol, reports the results for several factor analyses of tests administered to students in secondary schools in Kenya, Rhodesia, and Zambia.[41] The results for a group of 442 eighth graders in Zambia are shown in Table 1 (page 13).

In another paper[40] he warns about the difficulties of applying in Africa notions derived from British or American studies without suitable modifications. Yet it seems that the pattern in Table I shows remarkable agreement with what has been reported in the literature on factor analysis of ability test scores of American or European students.

The first factor represents school grades; the second, a spatial and perceptual factor; the third, number ability; the fourth, verbal ability plus spelling; and the fifth, mechanical information. Irvine calls the second factor "g," but while the reasoning test called Mental Alertness has a high loading on it, the vocabulary test does not, nor do the school grades. For this reason, it seems better to consider this second factor a spatial ability with some admixture of reasoning. If more factors had been extracted, these two abilities might have separated.

Some less direct evidence on cross-cultural general ability factors appears in a recent monograph by Lesser, et al.[49] Verbal ability, reasoning, number facility, and space perception were studied in middle- and lower-class families of four cultural groups — Chinese, Jewish, Negro, and Puerto Rican — with 20 boys and 20 girls in each group. The results are shown in Figure 1 (pages 14–15). Interesting differences exist between the author's results for middle- and lower-class performance and different patterns of abilities among the four groups.

Table I

Factor loadings of 10 tests and 12 school grades for 442 eighth-grade students in Zambia

Variable	*School grades*	*Varimax factors*			
		S	*N*	*V*	*Mech.*
Sex	23	–14	16	09	81
AIR* Boxes (3 dimensional)	08	54	15	–20	35
AIR Mechan. Info. 1 + 2	00	48	03	11	63
AIR Mechan. Info. 3	05	26	–05	13	81
AIR Figures (Hidden shapes)	19	63	02	–02	05
Raven Progressive Matrices	–05	77	06	12	03
NB** Mental Alertness (verb. reas.)	11	57	33	35	17
NB Comprehension	17	40	–18	40	05
NB Vocabulary	14	27	09	64	18
NB Spelling	06	–07	32	59	04
NB Computation	05	15	72	11	01
SE English 61	12	–23	–15	50	31
SE Arithmetic 61	12	–04	71	00	14
SE Special test 61	13	57	27	17	05
Grade 6 English 61	44	11	09	52	16
Grade 6 Arithmetic 61	15	13	69	00	09
Grade 6 Geography 61	75	16	13	05	13
Grade 6 History 61	67	–07	11	21	12
Grade 6 Science 61	61	06	05	08	18
Grade 8 English 63	33	25	–02	65	02
Grade 8 Mathematics 63	34	32	58	13	16
Grade 8 Geography 63	68	32	15	18	01
Grade 8 History 63	68	02	18	17	06
Proportion of common variance	.23	.23	.19	.18	.17

* American Institute for Research

** Normal Battery

Of importance in our present context, however, is that in each culture the four separate abilities followed similar patterns in the two socio-economic groups.

Vernon[102] administered to a group of English and a group of West

Indian boys a battery of verbal, memory, perceptual, and performance tests, as well as items based on Piaget's studies on the development of concepts. He reports similar factor structures in the two groups. Because the factor loadings are not reported for the West Indian group, it is not possible to calculate congruence indexes at this time, although it may be possible later.

Earlier, we discussed the controversy between increasing and decreasing differentiation. Another topic that could have been introduced then must be mentioned here. It is one that complicates interpretation of the relevant studies. Probably many advocates of differentiation believe in distinct abilities, and may even believe that they are normative, whether they believe the abilities to be the result of environment (common training) or heredity (innate capacities).

Another view exists—one which has not been forcefully proposed for several years. It has been expressed by Thomson,[89] Ferguson,[24]

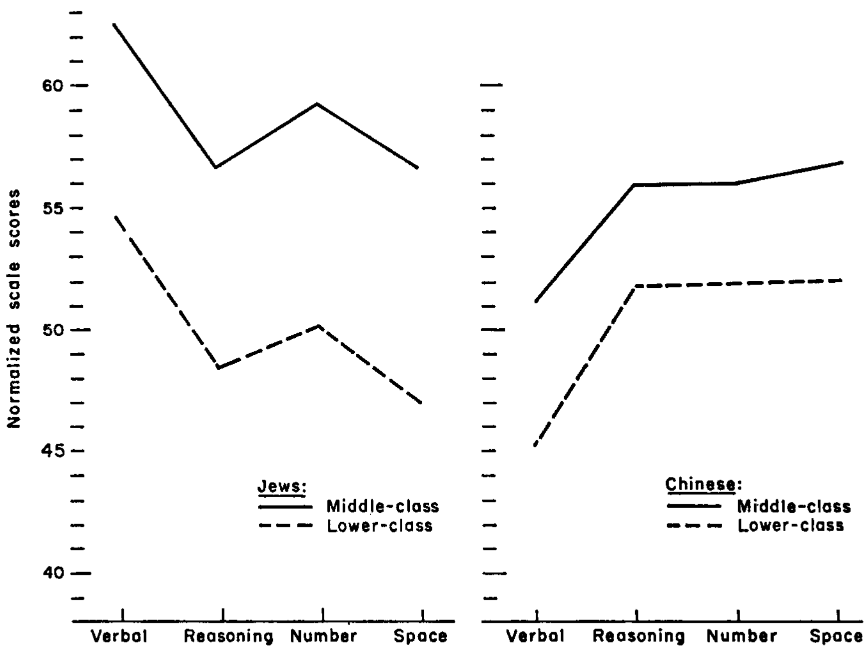

FIGURE 1 Comparison of test performances of children from middle and lower classes for four different cultural groups. (After Lesser, et al., 1965)

and — perhaps less wholeheartedly — by Vernon.[101] According to these views, what seem to be abilities and patterns of abilities (or factors) result from over-learned acquisitions. Accumulation of skills, facts, and so on, may resemble specific abilities, because learning is segmented into specific subject matter. Bonds are formed between temporal neighbors that are learned equally well or equally poorly as a result of such factors as motivation. If this view is correct, one would not expect to find the cross-cultural generality of ability factors referred to above.

Comparability of Factors Over Different Ability Levels

As pointed out by Reinert,[72] one can to some degree trade ability level for age and expect somewhat similar results. What happens to the structure of abilities when one considers not merely low average ability, but actual mental deficiency? Studies by Meyers, Dingman, and associates (mentioned earlier in connection with comparability across age levels) conclude that there is still a good deal of differentiation of abilities.

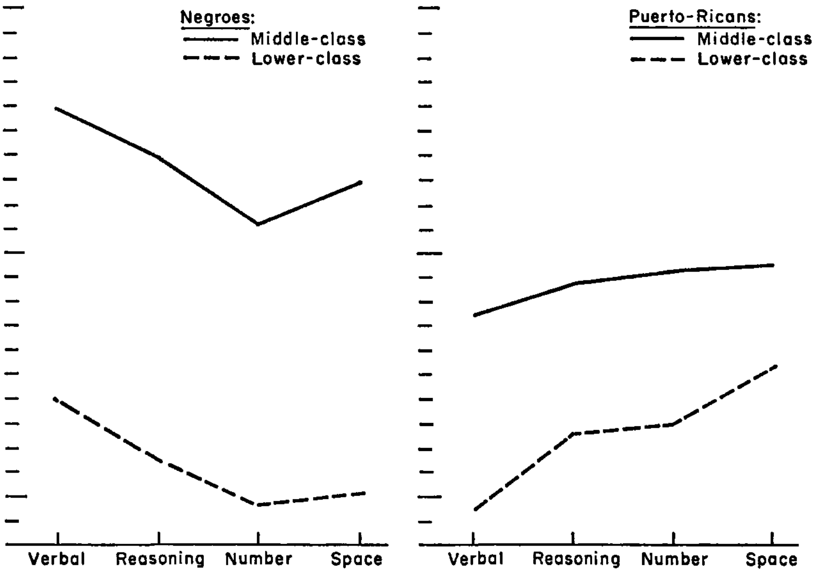

FIGURE 1 *continued*

Similar conclusions were reached by Kebbon[44] in his monograph based on a series of studies on the structure of abilities in retardates in Sweden. Using batteries of 25 and 16 tests with 112 retardates aged 15 to 65, two equal groups of 92 retardates of 15 to 50, and 120 retardates 20 to 34 years old, and comparing the results with those of a group of 92 normals aged 15 to 49, he obtained highly similar factor structures. Congruence indexes ranged from .95 to .97 for four factors — verbal, spatial inductive, numerical, and psychomotor — although part of the time a fifth factor, perhaps perceptual speed, was present. The spatial factor was largely one of shape reproduction rather than one of mentally manipulating a pattern in two- or three-dimensional space. The different factors accounted for different proportions of variance for the several ability groupings, as shown in Figure 2. The

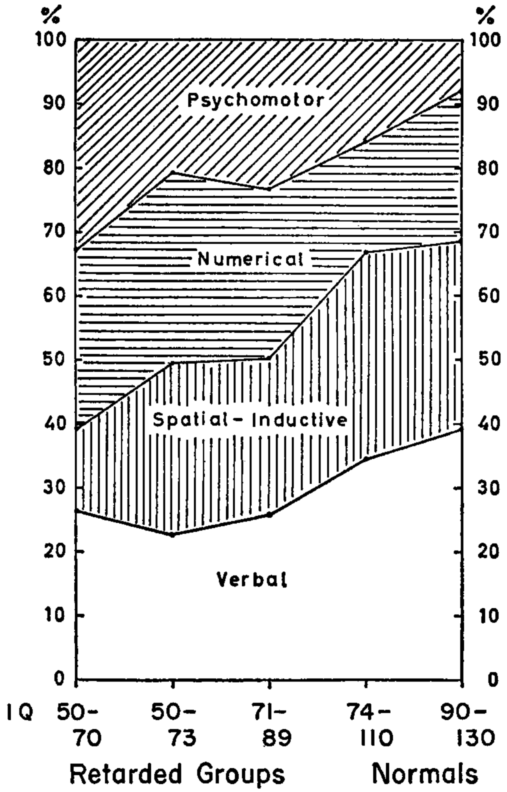

FIGURE 2 Per cent of common variance accounted for by four factors in five different IQ groups. (After Kebbon, 1965)

psychomotor factor, here mainly the speed of writing answers, accounts for more variance and appears to play a much more substantial role in individual differences in test performances of retardates.

Differentiated Effects of Mental Illness or Brain Damage

Such information would be strong support for the idea of separate abilities, because it would show that they are not only behaviorally distinct, but even physiologically separate. I have not had time to search the literature for evidence of differential impairment of primary mental abilities in various types of psychoses and neuroses. However, it is my impression that few such studies exist, because tests of the specific abilities isolated in factor analyses generally have not been used in studies of psychotics or neurotics. Instead, a variety of "clinical" tests have been used, and the exact nature of some of these is not fully understood because they have been used so infrequently with normals that little is known about their psychometric properties. The distinction between concrete and abstract ability has played a large role in this research. Even such a well-known tool as the Wechsler intelligence test has never been administered in a battery that included tests selected as marker variables of well-defined ability factors. Thus, its subtests cannot be specified precisely in terms of the primary abilities studied in normals.

While little work has been done on isolating specific primary mental abilities that are differentially impaired by various functional forms of mental illness, the situation is somewhat different for brain damage.

As the ideas about the nature of mental functions changed, the ideas of relating basic functions to specific brain centers were sure to bounce back and forth. The purely philosophical notions of highly specific "ideas" or "faculties" led to the phrenologists' notion of small areas of localization, which, if well-developed, might even show themselves as bumps on the head.

When intelligence came to be regarded as more unitary in character, the idea of mass action of the brain came to the fore, including the concept of almost complete recovery of function after initial shock, except for general impairment resulting from loss of volume and assuming no primary sensory area had been touched. For many years now, factor analysts have proposed that intelligence is not unitary, but is composed of a number of relatively independent abilities. During this same period there has been a return to the idea that specific areas of the brain are directly related to certain abilities.

There is no perfect correlation, but the two ways of thinking seem to occur in both types of investigation, although perhaps they are somewhat out of phase at times. Present thinking seems to favor the idea of multiple functions, both mental and neurological, while more unitary views are held by some clinicians.

LOCALIZATION OF ABILITIES While the theory of detailed localization of ideas or of small, isolated mental functions has long since been abandoned, assessment of brain injury by Luria,[53] Halstead,[33] Reitan,[73] Zangwill,[106] and others suggests that damage to certain areas results in impairment of some functions and not of others. A thorough review of the psychological effects of brain damage was provided by Meyer in 1961,[57] and briefly by Yates.[105]

Impairment of spatial perception seems to be a disproportionately important tool in the diagnosis of brain damage, whether the test used is the Bender "Gestalt" visual test, the Graham-Kendall test on memory for designs, or the Gottschaldt hidden-figure test. The posterior part of the right parietal lobe and/or the lateral part of the right occipital lobe are often especially implicated when spatial perception is impaired. Often verbal performance is less affected in such cases. Less is known about the other abilities. Impairment of articulate speech occurs when an area near the third frontal convolution of the left cerebral hemisphere is damaged; spelling and grammar may also be impaired. It is unfortunate that no measures of a number of distinctly different abilities have been used in many of the studies.

While Luria[53] holds that factor analytic investigations have been of little help in revealing the basic dimensions of higher mental processes, he believes that some functions can be distinguished by their selective impairment when certain areas in the brain are disturbed. He stresses the social, i.e., learned, origin as well as the cortical basis of all higher mental functions in man. The social origin is really a consequence of the cortical control of nervous functioning, which has reached its ultimate form in man through evolution. Social learning is mediated by what the Russians call the second signaling system. This is not too different from the concept of secondary function, proposed by Gross[30] and by Heymans.[35] This represents the predominant role of past experience, as against the momentary sense impression, in guiding a person's behavior. Gross and, later, Heymans thought of secondary function as one end of a bipolar personality dimension with primary function as the other extreme.

Luria mentions the following more-or-less distinct functions: speech; verbal understanding; fine motor control, as in writing, calculation; and object naming. However, he warns that a focal lesion seldom results in the complete loss of a specific function. He makes the same basic distinction as do others between the left, or dominant, hemisphere and the right, with damage to the former more likely to result in poor word comprehension, writing disorder, and impaired ability to recall words or to name objects. When the visual area is damaged there may be lessening of visual perception, spatial orientation, or ability to calculate.

Different Rates of Development

Zubin[108] has suggested that another way of isolating basic dimensions of abilities is to study the extent to which different skills develop simultaneously or at different rates. Unfortunately, we have virtually no detailed information on this. To secure it, it will be necessary to study — in the *same* subjects — the development over time of several separate abilities, such as verbal comprehension or vocabulary, and compare them with number ability, spatial abilities, etc. Some suggestive evidence is available from cross-sectional material. Thurstone[92] fitted the growth curve of Gompertz[28] to cross-sectional data for scores on seven primary mental abilities: perceptual speed; spatial visualization; reasoning; number ability; memory for paired associates; verbal comprehension; and word fluency.

The results are shown in Figure 3, although results of longitudinal studies eventually may lead to different conclusions. In this graph,

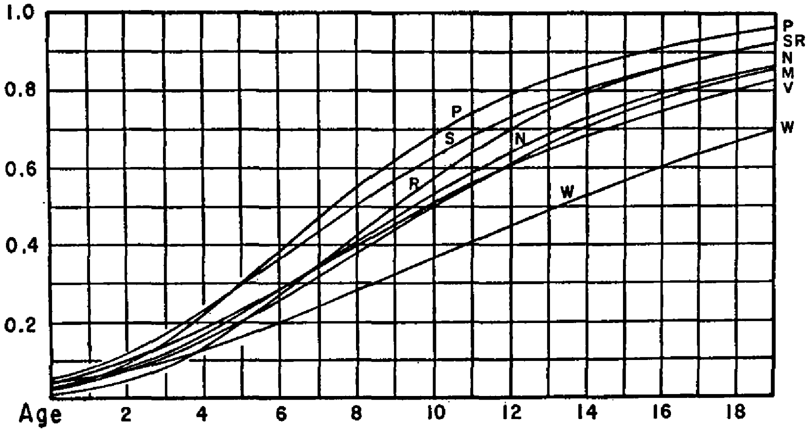

FIGURE 3 Mental growth curves of seven primary abilities. P, perceptual speed; S, spatial visualization; R, reasoning; N, number ability; M, memory for paired associates; V, verbal comprehension; W, word fluency. (Thurstone, 1953)

the upper limit, or asymptote, for each ability has been taken as 100 per cent for ease of comparison.

From the graph it may be seen that the "average" person reaches 80 per cent of the adult performance for perceptual speed at age 12, for spatial visualization and reasoning at age 14, for number ability and memory at age 16, for verbal comprehension at age 18, and for word fluency after age 20. Thurstone also mentions other studies that indicate children reach the adult level on the closure factor at about age 10 or 12.

As Thurstone has cautioned us, these results are based on averages, and individual children may be expected to mature slower or faster in any of these abilities.

As mentioned before, the investigation of abilities has been little influenced by the study of learning, and vice versa, while neither has had enough association with the field of child development. Fortunately, the situation is changing. Many learning studies are being conducted with children, although it is still too early to expect summaries with detailed findings. (Many of the studies are in progress in Russia, and some reports were given at the XVIIIth International Congress of Psychology.)

Stevenson and Odom[85] studied the performance of 354 fourth- or sixth-grade children on five learning tasks: paired associates, concrete discrimination, abstract discrimination, concept formation, and anagrams. The results indicated that different learning tasks require different abilities, and that some kinds of learning are not related to the abilities measured by the California Test of Mental Maturity.

The Educational Testing Service has made several attempts to relate learning to mental abilities. Allison,[1] Stake,[83] Games,[26] and Duncanson[22] all found relationships between ability measures and the parameters of learning curves fitted to the performance of single subjects on individual tasks. Most of the relationships between learning tasks and ability measures occurred when both dealt with material similar in content. Manley[56] did a similar study, concentrating on concept attainment tasks.

NEWER IDEAS ABOUT INTELLIGENCE

With the advent of electronic computing machines, a field of study named *artificial intelligence* has developed. Have we learned anything relevant to our inquiry from these investigations? Without going into much detail, I believe we can answer with a guarded "Yes." First, we can demonstrate how a problem once solved and programed in a "subroutine" can be used as a single instruction; one can then think of a complex operation — for example, matrix inversion — as a single step as easy as adding. This also occurs in the human mind. Thus computer programs provide dramatic illustrations of the way the mind can use shorthand symbols for lengthy and varied tasks and thus enormously condense problem solving and reviewing. We think, "On the way home I will stop at Harry's," but we do not need to go over details of the route while having this thought. If we think, "When preparing that paper this particular point should be emphasized," we do not really think of every word to be used. By the way, subroutines are also a nice illustration of the power of cultural inheritance to multiply any given person's own capability, because they embody many man-hours of work and thought. Now, however, they can be used by others who need only a general idea of what the subroutine does.

Second, computers have helped our theoretical thinking because they present vivid demonstrations that one and the same structure can accommodate an infinite number of states and processes through the variety of the programs that can be temporarily stored in it and the infinite variety of data the programs can be set to work on.

Information theory, so far, has had little impact on the measurement of ability, although two exceptions come to mind: the Problem Solving Instrument (PSI) of John and Miller,[42] and the paper-and-pencil mazes of Elithorn.[18] In both of these, an attempt is made to define the difficulty of a problem in terms of the amount of information (i.e., the number of choices) to be considered. The relation of these tests to conventional ability measures is not known.

One important aspect of intelligent behavior has been seriously neglected. Social intelligence, or the ability to do the "right" thing in interpersonal situations, has not received the same amount of attention as have other aspects of intelligence. One big difficulty is simply to define what is "right." Recently, Guilford has added this area to his sphere of investigations.

After this lengthy presentation of data supporting the view that intelligence is best regarded as a bundle of independent abilities, I turn to my main topic:

ARE THESE ABILITIES DETERMINED IN PART BY GENES?

I am the family face;
Flesh perishes, I live on,
Projecting trait and trace
Through time to finis anon,
And leaping from place to place
Over oblivion.

from "Heredity" by Thomas Hardy

Differences among individuals can be compared with the small part of the iceberg that shows above the water. Behavior geneticists depend on individual differences for their livelihood. As a result, they tend to overlook the enormous amount of common heredity that distinguishes man from dog or horse. It is amusing to speculate, as Clarence

Day has done,[19] what we would be like if we had descended from cats rather than from monkeys. Except for completely stunted individuals, this common heredity includes fingers, toes, heart, and lungs, and the development of abilities such as recall (even in the absence of the original stimuli), foresight, conceptual thought, self-awareness beyond a level present in any other species, and the display of *activities,* which might variously be called "building," "rearranging," "tool-making," or in general "modifying the environment." Expression of this common heredity can be found in any human culture, past or present, technically advanced or primitive.

Estimations of heredity-environment variance ratios take place in the narrow confines of the intersection of a normal environment and a normal genetic make-up. The normal environment includes the unusual conditions found today on the surface of our earth, development in a healthy uterus, and a "normal" psychosocial environment, at least during part of childhood. The permissible variation in genetic make-up is just as small as that for the environmental. A little extra genetic material or even a single mutated gene may be lethal or cause gross abnormality. Figure 4 underlines this point.

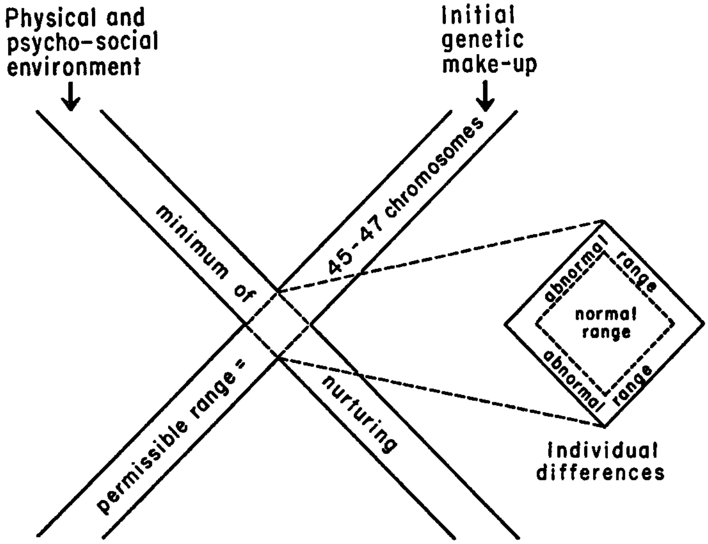

FIGURE 4 Individual differences in the normal range as a function of permissible variation in heredity and environment.

I will not review the story of phenylketonuria, of Down's syndrome, or of sex-chromosomal and other autosomal aneuploids, other than to mention that the psychological tests used in examining such cases should be refined as much as possible if we are to learn the maximum amount from these unfortunate children. Information on such cases should then be collected for reanalysis and perhaps, eventually, linkage studies.

It is known that a number of single gene substitutions cause severe retardation. These probably contribute a large proportion of the retardates in institutions. The higher-grade retarded may, on the other hand, be part of the normal distribution of intelligence controlled by polygenes. This is suggested by data from Roberts,[74] who plotted the IQ distribution of 562 siblings of high-grade and low-grade mental defectives. The mean IQ of the siblings of the low-grade group was about 20 points higher than that of the high-grade group, and was rather similar to that for the general population. The results are shown in Figure 5.

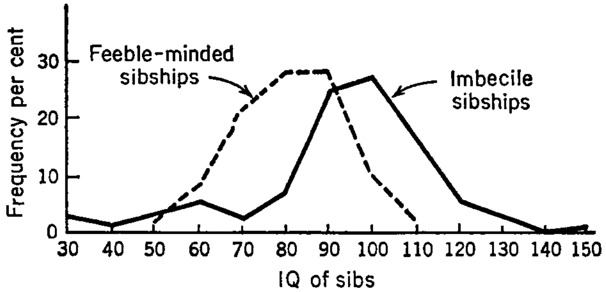

FIGURE 5 Contrasting the distribution of IQ in siblings of high-grade and low-grade retardates. (Roberts, 1952)

A study by Halperin[32] shows that some mentally deficient parents have normal children, and that some of the mentally deficient are born to normal parents. Mentally deficient and normal children born to the same parents, and the parents themselves, were classified. The results are shown in Table II.

Four other methods can supply some answers: family studies, stud-

TABLE II

The percentage of average, inferior, and mentally defective children born to various combinations of parents. The number of cases are shown in brackets

		Children		
Parents	*N*	*% Average or above*	*% Inferior IQ 70–85*	*% Defective IQ 50–70*
Average × average	18	73 (13)	5 (1)	22 (4)
Average × inferior	59	64 (38)	33 (19)	3 (2)
Inferior × inferior	252	28 (70)	57 (144)	15 (38)
Inferior × defective	89	10 (9)	55 (49)	35 (31)
Defective × defective	141	4 (6)	39 (55)	57 (80)

ies of adopted children, twin studies, and studies of the effects of inbreeding.

Family Studies

As far as I know, there is no information on correlations of specific ability scores between relatives. For general intelligence, Erlenmeyer-Kimling and Jarvik[23] have summarized evidence from 52 studies reporting on 99 correlations between paired individuals of degrees of genetic relationship varying from none to complete. The pairs ranged from unrelated through parent-child to identical twins. The results are shown in Figure 6.

Noting that the regular increase in the size of the correlation is good evidence for the importance of heredity in ability, Vandenberg[97] has suggested that the variability of the values may be the result of differences among the mixtures of abilities measured by the tests used in various studies—differences which are related to the degree of genetic determination of these abilities. We will return to this in the section on twin studies.

Studies of Adopted Children

Because similarity among members of a family reflects both common genes and a common environment, one would like to place in

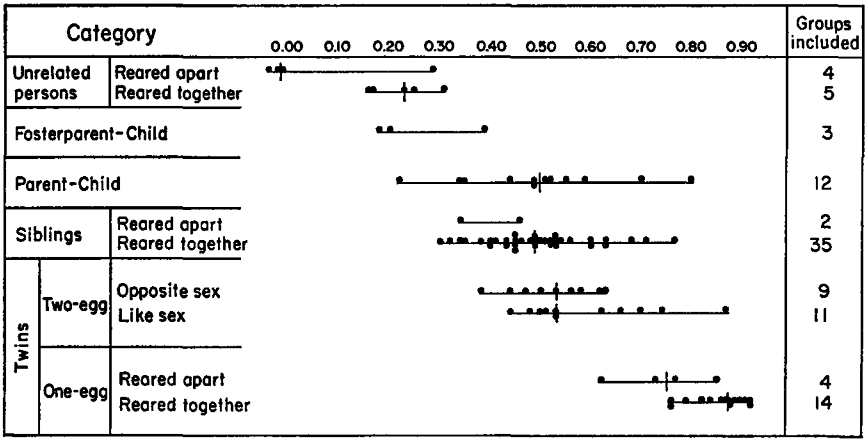

FIGURE 6 Correlations between IQs of paired individuals of genetic relations ranging from none to complete. Dots represent correlations from single studies; lines show range of values; median is shown by short vertical lines. (Erlenmeyer-Kimling and Jarvik, 1963)

carefully selected foster homes certain babies with a high risk for schizophrenia or mental retardation. While this is generally not possible, we do have a limited amount of information on children placed in foster homes at roughly the same very early age. Honzik[37] has summarized results from the study of Skodak and Skeels,[82] and compared them with the results from the California guidance study. The data concern the resemblance of children to their foster parents and to their biological parents. Figure 7 summarizes the results. They show that the children resemble their biological parents more than their foster parents, except for a brief period in the first year of life. This latter finding may in part be caused by the lack of predictive validity in baby tests. As a matter of fact, the babies studied resembled their biological parents just as much as did the California children who grew up with their own parents.

For the detailed description and evaluation of studies on the effect of foster-home rearing on children from retarded mothers, see Stoddard.[86] We will return to this topic briefly when we consider the nurturing of intelligence.

Twin Studies

In discussing the variability of results summarized by Erlenmeyer-Kimling and Jarvik, I suggested that different heritabilities can be expected because the tests might be made up of different mixes of

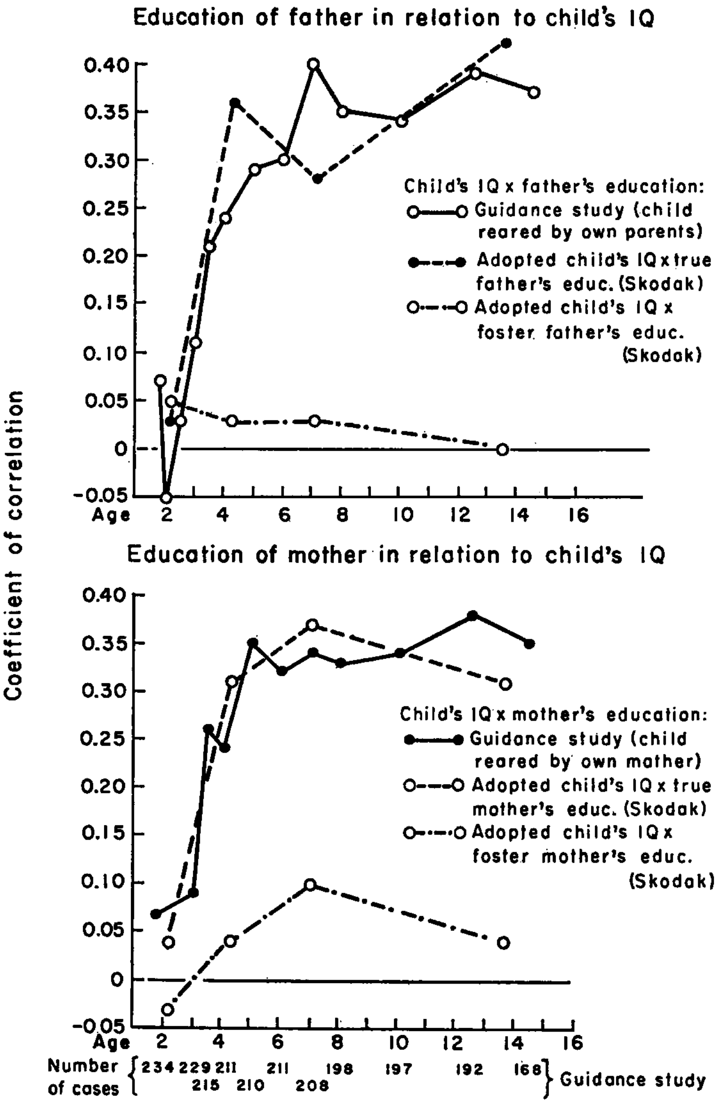

FIGURE 7 IQ resemblance of adopted child to foster and true parents. (After Honzik, 1957)

items that measure various abilities which might differ in their degrees of genetic determination. That there is indeed such a difference between specific abilities was the conclusion of a recent paper.[97] In addition, Nichols[62] has shown that specific abilities may have higher heritabilities than does general ability. His data are based on twins taking the National Merit Scholarship Qualifying Test. Interestingly, even in these talented subjects differential effects were shown. On an English usage test boys showed little effect of hereditary influence; girls did show the effects. The strongest evidence for heredity among the boys was in a test for mathematics usage.

Some criticisms of twin studies may be summarized as follows: they are unrepresentative of the general population; they lack objectivity in classifying twin as MZ (identical) or DZ (fraternal); the environment is not the same for MZ and DZ twins; differences in uterine conditions exist for MZ and DZ twins.

Are Twins Different from the Rest of the Population from Which They Come?

Twins are often said to be slower in their language development, especially before they start school, but studies were generally based on small samples. Better data have come from France[107] and Sweden.[89] When project TALENT analyzes its twin data,[78] we may have information from the United States.

Figures 8 and 9 make clear that there is a consistent difference in favor of single-born children. On the other hand, there are many twins among the National Merit Scholarship contenders and winners.

Twins do not necessarily score lower than do single children on all abilities. This is indicated by data obtained in a study by Koch[46] of 5- to 7-year-old twins, in which the scores on PMA subtests were obtained. The twins were carefully matched with single-born children who had one sibling near to them in age. There were 18 male and 17 female monozygous, 18 male and 18 female like-sexed dizygous, and 17 unlike-sexed dizygous pairs in the study. Dr. Koch graciously permitted me to do a further analysis of her data. The results are shown in Figure 10. The twins did better than the single children on the

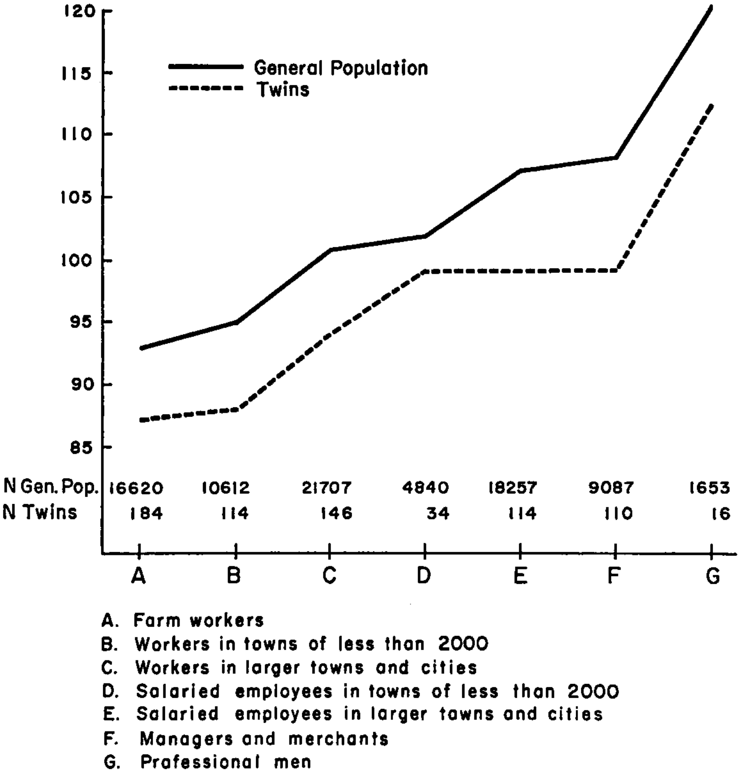

FIGURE 8 Distribution of IQs, by occupation of father, for twins and singletons. (Zazzo, 1960)

perceptual test and not much more poorly than single children on the spatial test.

Are Twins Classified Objectively into MZ and DZ Types?

Most modern twin studies use extensive blood group tests, which make misclassification of an MZ pair as DZ impossible. In addition, such tests err in the classification of truly DZ in only about 5 per cent of the cases, in which the present serological tests fail to detect a difference. Use of fingerprints or anthropometric data generally does not contribute enough information to warrant the trouble, although single items such as a gross difference in height or in color of hair, iris, or skin (for instance, on inside of the arm, which is usually covered)

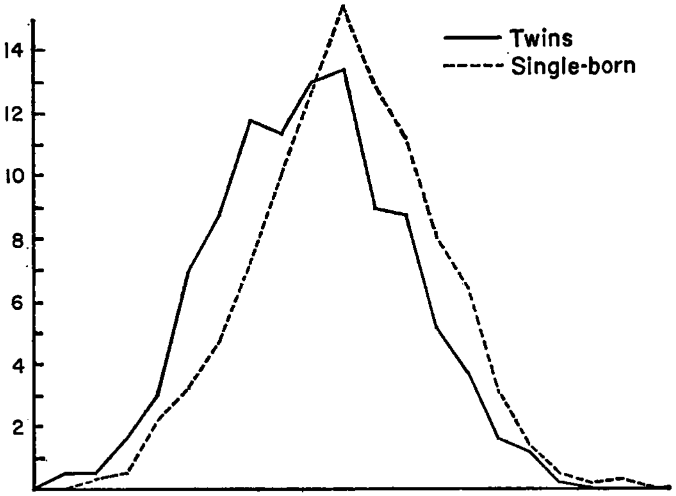

FIGURE 9 Comparison of reading scores of twins and single children (girls). (Husén, 1960)

may occasionally help. It has been shown repeatedly that for large-scale twin studies a few questions about the frequency with which close friends or relatives mistake one twin for the other will provide a sufficiently accurate diagnosis within the limits of the accuracy of the variable under study, whether it be a mental test score or a physical illness. In such a study it is generally desired only to obtain a statistically significant result at a reasonable cost, not to pursue great accuracy at considerable expense.

Is the Environment the Same for MZ and DZ Twins?

Perhaps the question should be: "Is the range of within-pair, environmentally produced differences the same for identical and fraternal twins?" On an intellectual level, this might be answered by a sophistry that goes like this: The greater within-pair differences in parental treatment of fraternal twins compared to identical twins is undoubtedly due in great part to reactions to very early genetic differences and thus may be classified with heredity. But this will not satisfy purists, environmentalists, or hardheaded experimental psychologists.

Nichols[62] reported interclass correlations (concordance) for MZ and

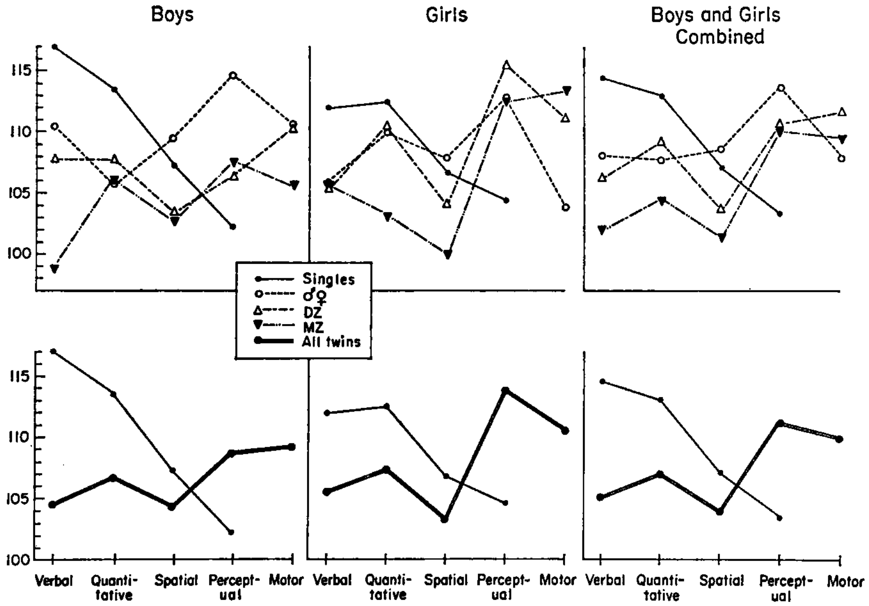

FIGURE 10 Comparison of the scores on five PMA subtests for various types of twins and for single children. (After Koch, 1966)

DZ twins who had been exposed to different experiences and those who had not. The figures are remarkably close. Perhaps even more convincing is the analysis by Vandenberg and Johnson[100] of the IQ differences of separately raised identical twins. When the pairs, whose histories had been collected from the literature, were put in two groups on the basis of whether they had been separated soon after birth or not until after they were two years old, greater within-pair differences were found between pairs separated later. While not too much should be made of this, at least it argues rather strongly against a systematic influence of parental treatment on twin differences. When we discuss the effect of early stimulation we should remember this finding.

Lack of Comparability of Intrauterine Environment

Price[69] has argued convincingly that the prenatal environment of fraternal twins is probably more nearly alike than it is for identical twins. An identical pair reported on by Falkner,[25] in which the uterine conditions led to a great difference, certainly underlines this point. Vascular anastamoses caused one MZ twin to pump blood into the other. This resulted in marked differences at birth, and these disappeared slowly.

Acceptance of Price's arguments leads to a belief that twin studies underestimate the importance of heredity, while belief in the importance of parental influences on twin differences leads to the opposite conclusion.

Results of Twin Studies of Abilities

In earlier papers I attempted to rank-order the various abilities with respect to the importance of heredity as follows: spatial visualization, word fluency, vocabulary tests (especially if they call for more productive answers than multiple choices), number ability, and perhaps some types of reasoning. Perceptual speed or clerical speed and accuracy also seem to have a considerable heredity component. In the memory tests used so far, no effect of hereditary influence could be detected. Tables III, IV, and V summarize the information on which these generalizations were based. (For further discussion, see Reference 97.)

TABLE III

F ratios of dizygous and monozygous twin within-pair variance

Name of PMA subtest	*Blewett*	*Thurstone*	*Vandenberg (Michigan)*	*Vandenberg (Louisville)*
Verbal	3.13**	2.81**	2.65**	1.74*
Space	2.04*	4.19**	1.77*	3.51**
Number	1.07	1.52	2.58**	2.26**
Reasoning	2.78**	1.35	1.40	1.10
Word fluency	2.78**	2.47**	2.57**	2.24**
Memory	not used	1.62	1.26	not used

** $p < .01$
* $p < .05$

Several other studies can be added. First is that of Wictorin,[104] whose results are summarized in Table VI. Here is highly significant

TABLE IV

Two twin studies of the Differential Abilities Tests

	1961	*1965*
Verbal Reasoning	2.29**	2.38**
Numerical Ability	1.39	1.37
Abstract Reasoning	1.47	1.23
Space Relations	1.67	2.19**
Mechanical Reasoning	1.36	1.46
Clerical Speed and Accuracy	2.54**	3.13**
Language Use I: Spelling	3.64**	2.58**
Language Use II: Sentences	3.06**	2.00**
	25 DZ	86 DZ
	47 MZ	109 MZ

** $p < .01$
* $p < .05$

evidence for a hereditary component in two tests of "general" intelligence. I have not seen these tests, so I do not know if they are largely verbal, figural, or a mixture of both. We see further evidence for a considerable hereditary component in number ability and in perceptual speed, and again none in memorizing. Some interesting differences can be seen between the results for boys and girls, but it would take us too long to pursue this here. The interclass correlations are listed in Table VIa.

Table VII summarizes the findings of Husen,[38] who tested twins among Swedish soldiers — probably unselected, and therefore as representative samples as could be found. He used five tests: 1) verbal comprehension and reading speed when following instructions; 2) synonym selection; 3) choosing the mismatched word among a given five words (2 and 3 are both vocabulary tests); 4) Raven's progressive matrixes — a reasoning test that uses figural material (claims have been made that this test measures "general" intelligence); and 5) number series, a numerical reasoning test.

Evidence for a hereditary factor is present for the single verbal comprehension and the two vocabulary tests; it is not as strong, but

TABLE V

F ratios between the within-pair variances of 60 fraternal (DZ) and 60 identical (MZ) twins for the scaled scores of 11 subtests of the WAIS

Subtest	F
1. Information	3.88***
2. Comprehension	2.25**
3. Arithmetic	2.78***
4. Similarities	1.81*
5. Digit Span	1.53*
6. Vocabulary	3.14***
7. Digit Symbol	2.06**
8. Picture Completion	1.50
9. Block Design	2.35**
10. Picture Arrangement	1.74*
11. Object Assembly	1.36
Verbal Score	3.38***
Performance Score	3.41***
Total Score	3.47***

*** $p < .001$ ** $p < .01$ * $p < .05$

still significant, for the figural reasoning, or general intelligence, and the numerical reasoning tests. Results of an analysis Husen made of the school grades of these twins are shown in Table VIII. Note that the highest F value is in arithmetic, but that all values are significant beyond the one per cent level. It is interesting to compare these results with those reported by Nichols[63] for the National Merit Scholarship test results.

Table IX gives separate F values for boys and girls for scores on the five parts of the National Merit Scholarship Corporation qualifying test: English usage, word usage, social studies reading, mathematics usage, and natural science reading. All values but one are significant beyond the one per cent level, and that one is significant at the five per cent level. These test scores are also based on achievement, so are a good confirmation of Husen's findings.

TABLE VI

F ratios between like-sexed fraternal twins (DZ) and identical twins (MZ) within-pair variances for 14 psychological tests, administered to Swedish twins of elementary and high school age

(From Wictorin, 1952)

	Boys	*Girls*	*All cases*
Simplex, a general intelligence test	1.98**	2.84**	2.38**
C-test, a general intelligence test	2.41**	4.35**	3.37**
Verbal Analysis, a verbal comprehension test	1.14	.96	1.12
Form perception, a paper formboard test	1.51*	1.23	1.34*
Picture perception, a perceptual speed test	1.17	1.54*	1.36*
Number perception, a clerical checking test	1.58*	1.91**	1.59**
Number Series, a numerical reasoning test	2.37**	1.70*	2.01**
Number Analysis, a numerical reasoning test	1.61*	1.68*	1.63**
Numerical Classification, a numerical reasoning test	1.47	1.64*	1.57**
Numerical Reasoning, verbal arithmetic problems	2.83**	1.96**	2.18**
Routine simple arithmetic	1.87**	1.51*	1.68**
Memory for 2-digit numbers (Recall)	1.15	1.39	1.24
Memory for 3-digit numbers (Recognition)	.94	1.34	1.17
Paired associates word-number memory	1.32	1.00	1.16
N_{DZ}	66	75	141
N_{MZ}	66	62	128

** $p < .01$ * $p < .05$

Finally, I am able to report some results from a recent study of adult Finnish male twins, thanks to Bruun, et al., who let me read their manuscript.[14] They administered eight tests of five primary mental abilities. The tests were verbal opposites, a vocabulary test;

Table VIa

Intraclass correlations for identical and like-sexed fraternal twins aged 9 to 15 years on 14 psychological tests

	Boys		*Girls*		*All cases*	
	MZ	DZ	MZ	DZ	MZ	DZ
Simplex, a general intelligence test	79	61	91	76	85	70
C-test, a general intelligence test	86	74	92	72	91	73
Verbal Analysis, a verbal comprehension test	64	55	62	59	63	57
Form perception, a paper formboard test	66	41	65	63	65	53
Picture perception, a perceptual speed test	53	64	72	60	64	61
Number perception, a clerical checking test	83	66	83	70	83	69
Number Series, a numerical reasoning test	78	40	74	55	74	49
Number Analysis, a numerical reasoning test	65	53	74	60	69	57
Numerical Classification, a numerical reasoning test	67	44	74	61	70	58
Numerical Reasoning, verbal arithmetic problems	93	72	83	74	87	73
Routine simple arithmetic	83	75	80	70	81	74
Memory for 2-digit numbers (Recall)	60	64	67	52	62	58
Memory for 3-digit numbers (Recognition)	44	50	54	38	49	45
Paired associates word-number memory	35	47	47	56	43	53
N_{DZ}	66		75		141	
N_{MZ}	66		62		128	

a word fluency test; two spatial ability tests—rotated squares and paper formboard: two number ability tests—one of addition and subtraction, and the other "find the longest number" (this also contains a clerical checking factor); and two memory tests (see Table X). All the tests gave highly significant evidence for a hereditary component.

TABLE VII

Ratios between like-sexed fraternal twins (DZ) and identical twins (MZ) within-pair variances for school grades of Swedish twins in 4 subjects (From Husen, 1953)

Nature of the test	*F*	N_{DZ}	N_{MZ}
Following instructions	2.62**	415	215
Finding synonyms	2.09**	532	269
Choosing the odd one from among 5 words	1.77**	532	269
Raven's Progressive Matrices	1.37*	532	269
Number Series	1.54*	117	54

** $p < .01$ * $p < .05$

TABLE VIII

Ratios between like-sexed fraternal twins (DZ) and identical twins (MZ) within-pair variances for school grades of Swedish twins in 4 subjects. (From Husen, 1953)

Subject matter	*F*	N_{DZ}	N_{MZ}
Arithmetic	3.13*	668	352
History	2.82*	624	332
Handwriting	2.45*	668	352
Reading	2.23*	662	350

* $p < .01$

Multivariate Analysis of Twin Differences

With so many different abilities showing hereditary aspects, one may ask whether the genetic component is, perhaps, the same in all tests, with the nongenetic part determining its specific character.

Some idea of this can be obtained by seeing if the twin who does better than his brother on test 1 also does better on test 2. Such information can be secured by correlating the twin differences on the two tests. This was done separately for the identical and fraternal twins with the six subtests of Thurstone's Primary Mental Ability battery, and with the eight Differential Aptitude Tests.

TABLE IX

F ratios between within-pair variances for fraternal and identical twins on five parts of the National Merit Scholarship Qualifying Test. (After Nichols, 1965)*

	Boys	*Girls*
English Usage	1.23**	2.22***
Word Usage	1.72***	2.56***
Social Studies Reading	1.92***	2.27***
Mathematics Usage	2.22***	1.75***
Natural Science Reading	2.86***	1.54***
N_{DZ}	209	273
N_{MZ}	315	372

* These F ratios were estimated from intraclass correlations rather than calculated directly from within-pair variances.

** $p < .05$

*** $p < .01$

TABLE X

Intraclass correlations and F ratios between fraternal and identical within-pair variances for eight ability test scores of Finnish male adult twins. (From Bruun, et al., 1966)

	Intraclass correlation		$F = \frac{\sigma^2 wDZ}{\sigma^2 wMZ}$
	MZ	*DZ*	
V, Verbal opposites	75	51	1.94*
W, Word fluency	81	54	2.28*
S_1, Rotated squares	58	33	1.75*
S_2, Paper formboard	60	39	1.69*
N_1, Addition and subtraction	73	55	1.98*
N_2, Find the longest number	72	45	1.92*
M_1, Memory for names	69	35	2.09*
M_2, Memory II	58	29	1.98*
Number of pairs	157	189	

* $p < .01$

For the PMA, the algebraic average of the correlations was .215 for the identical twins and .373 for the fraternal. For the Differential Aptitude Tests the figures were .157 and .465. The complete tables are shown in Vandenberg.[97] Because the identical twin differences are the results of environment only, and the fraternal twin differences are the results of environment plus heredity, it occurred to me that if we could subtract the first set of correlations from the second, the result would show the correlations between the hereditary ability differences between the fraternal twins. Because such matrixes tend to be non-Gramian, and because heredity and environment are not simply additive, this calculation cannot be made. However, after adjusting for lack of perfect reliability, Loehlin and Vandenberg[52] were able to carry out the analysis, and concluded that a strictly additive model led to a conclusion of a single genetic component common to all six abilities. Because an additive model is probably too simple, it seemed worthwhile to try the other extreme, a multiplicative model. Instead of subtracting, I decided to divide one matrix by the other in a generalization of the F-test. We use $F = \sigma^2{}_{wDZ}/\sigma^2{}_{wMZ}$ or ${}^{\sigma^2}wDZ - F^{\sigma^2}wMZ = 0$ to determine if the excess within-pair variance is statistically significant in fraternal twins. We do so by looking up the value of F for degrees of freedom N_{DZ} and N_{MZ} in an appropriate table.

By the same reasoning, we may ask if the characteristic equation $| C_{DZ} - \Lambda\ C_{MZ} | = 0$ has one or more significant roots.

Earlier, I used a significance test for symmetric matrixes proposed by Bartlett[5] and another one by Anderson.[3] Use of this procedure led to the conclusion that the four significant roots were those interpreted to be similar to, but not identical with, vocabulary knowledge, use of language (as shown in fluency and reasoning), spatial visualization, and number ability. (For details, see Vandenberg[96])

Since then I have learned from Professor Darryl Bock the proper significance test for this asymmetric characteristic equation. It is also by Bartlett.[5a]

If we calculate

$$\left[(N_{MZ} + N_{DZ} - \frac{(N_{DZ} + p + 1)}{2} \right] \sum_{i=1}^{p} \log_e (1 + \frac{N_{DZ}}{N_{MZ}} \lambda_1),$$

this quantity is distributed approximately as chi square. One can calculate this after 1, 2 . . . s of the largest roots are removed by summing from the smallest root up to root s + 1. Bartlett suggests using (p—s) (N_{DZ}—s) degrees of freedom, where p is the rank of the matrix.

Table XI shows the solution of $| C_{DZ} - \Lambda C_{MZ} | = 0$ for the Finnish study, while Table XII shows the results of applying the significance test.

TABLE XI

Solution of $|C_{DZ} - \Lambda C_{MZ}| = O$ *for 8 ability test scores of 157 fraternal (DZ) and 189 identical (MZ) adult male Finnish twins (From Bruun, et al., 1966)*

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
V	330*	421	–470	–029	–210	408	–718	–002
W	518	100	080	–877	461	–054	224	–220
S_1	432	414	152	405	284	272	262	–030
S_2	196	281	347	–032	–233	–633	–029	256
N_1	256	–432	–332	008	–476	259	493	601
N_2	–148	–012	–652	184	322	–521	020	–217
M_1	493	–189	120	129	–380	–056	137	–666
M_2	261	–582	282	122	367	–117	–322	182
λ, size of root	3.556	2.256	1.785	1.682	1.246	1.166	1.132	.974
H	.72	.56	.44	.41	.20	.14	.12	–.03

* Decimals omitted

Use of this new significance test on the earlier PMA results indicates that only three roots are significant in the rather small sample employed, as shown in the top half of Table XII. Applying the same procedure to the data of Bruun, we obtain the results shown in the bottom half of Table XII. Five of the roots are significant beyond the one per cent level of probability and a sixth one beyond the five per cent level. These two sets of results provide partial replication of one another, and indicate that there are several independent hereditary ability components.

Because a multiplicative model for the joint action of heredity and environment is probably more realistic than the earlier model of sim-

TABLE XII

Test of the significance of the next root after extraction of the i-th root

*PMA data from Michigan study**

$N_{DZ} = 37$ $N_{MZ} = 45$ $p = 6$

λ_i	$\log_e(1 + \frac{N_{DZ}}{N_{MZ}} \lambda_i)$	$\sum_{i=1}^{p} \log(\ )$	χ^2	df	p
5.9163	1.768	5.909	351.59	222	.0005
3.3012	1.311	4.141	248.46	180	.001
2.3468	1.072	2.830	171.22	140	.05
1.4812	.798	1.758	107.24	102	.30
.9555	.582	.960	59.04	66	ns
.5652	.378	.378	23.44	32	ns
Finnish data of Bruun, et al. $N_{DZ} = 157$ $N_{MZ} = 189$ $p = 8$					
3.556	1.375	6.844	1799.87	1256	.00001
2.256	1.056	5.469	1438.32	1092	.00001
1.785	.895	4.413	1160.67	930	.0001
1.682	.874	3.518	925.18	770	.0001
1.246	.711	2.644	695.24	612	.01
1.166	.677	1.933	508.38	456	.05
1.132	.663	1.256	330.25	302	ns
.974	.593	.593	155.91	150	ns

---

* I am grateful to Dr. Bock for pointing out the correct significance test. He has recalculated my results and suggested the above, slightly larger values for the roots.

ple additive effects, the weight of the evidence supports the theory that there are at least several abilities, each controlled by different hereditary mechanisms.

Evidence from Inbreeding

Schull and Neel[79] analyzed the score of 2,111 children on a Japanese version of the Wechsler Intelligence scale for children (WISC), constructed by Kodama and Shinagaw.[47] Complete data were avail-

TABLE XIII

The number of boys and girls in the various categories of consanguinity

	Parents Are			
	unrelated	*second cousins*	*1½ cousins*	*first cousins*
Males	538	88	89	249
Females	451	100	102	237
Totals	989	188	191	486

able on 1,854 children in the consanguinity groups shown in Table XIII.

As a first-cousin marriage is between children of siblings, children of first cousins have, on the average, 1 out of 16 pairs of genes by common descent. A marriage of first cousins once removed is between a child of one sibling and a grandchild of another sibling. Children of such unions will have, on the average, one out of 32 pairs of genes by common descent. A marriage between second cousins is between grandchildren of siblings. Children from such marriage will, on the average, have one out of 64 pairs of genes by common descent. When one gene from the father and one from the mother are obtained from a common ancestor, the result is a homozygous pair of genes in half of the cases. The more pairs of genes, or loci, that are homozygous, the more inbreeding. Unrelated individuals are assumed to have no genes in common, so children from such unions are heterozygous for all loci.

The consanguinity groups were carefully compared for differences in socioeconomic status and parental age, and differences were removed statistically. The effects of inbreeding were estimated by multivariate linear regression methods after removing the effects of age and socioeconomic status (SES). The means and standard deviations for age in months and SES are shown in Table XIV. The SES scale used ran from 1 to 20.

Tables XV–XVII show the relative effects of inbreeding compared

TABLE XIV
Means and sigmas for age, socioeconomic status (SES), and inbreeding (F)

	Boys		*Girls*	
Variable	*Mean*	*SD*	*Mean*	*SD*
Age	102.91	17.83	102.23	18.10
SES	20.88	5.26	21.06	5.15
F	1.31	.17	1.41	.17

to a one-month increase in age or a one-point increase in socioeconomic status (on a 20-point scale). While the effect of inbreeding is not too great, it is significant statistically, and the effect on the scores for the Wechsler Intelligence Scale for Children was among the clearest and strongest of all the phenomena studied by Schull and Neel. Other items included physical illnesses, several anthropometric and dental variables, and school grades.

TABLE XV
Comparison of the changes in WISC subtest scores per month of age, per unit of socioeconomic status (SES) and per % inbreeding (F) (From Schull and Neel, 1965)

WISC Subtest	*Age*	*SES*	*F*
Information	.0418	.1230	–.0950
Comprehension	.0271	.0832	–.0742
Arithmetic	.0332	.0844	–.0602
Similarities	.0347	.1449	–.1157
Vocabulary	.0480	.1355	–.1155
Picture completion	.0138	.0817	–.0656
Picture arrangement	.0264	.0708	–.1073
Block design	.0234	.0834	–.0598
Object assembly	.0030	.0717	–.0630
Coding	.0264	.0712	–.0531
Mazes	.0080	.0260	–.0651

TABLE XVI

Effect of inbreeding on intelligence as measured by a Japanese version of the WISC, N = 2,111. (From Schull and Neel, 1965)

WISC subtest	*Mean for outbred** *(offspring of unrelated parents)* *Boys*	*Girls*	*Depression of score as % of increase in F, the inbreeding coefficient*	*Depression as % of mean for the outbred*
Information	11.62	11.21	–.09499	8.1 – 8.5
Comprehension	12.39	12.12	–.07424	6.0 – 6.1
Arithmetic	11.84	12.11	–.06025	5.0 – 5.1
Similarities	11.40	11.91	–.11575	9.7 – 10.2
Vocabulary	10.35	9.86	–.11551	11.2 – 11.7
Picture completion	11.71	10.63	–.06560	5.6 – 6.2
Picture arrangement	11.54	11.27	–.10728	9.3 – 9.5
Block design	11.24	10.99	–.05975	5.3 – 5.4
Object assembly	10.83	9.94	–.06298	5.8 – 6.3
Coding	11.54	12.27	–.05314	4.3 – 4.6
Mazes	12.30	12.09	–.06526	5.3 – 5.4

* Estimated for a child of 120 months of age, a socioeconomic status of 20, and after correcting for the confounding effect of socioeconomic status.

Whatever the size of the effect, inbreeding after correction for socioeconomic status leads to lower WISC scores. That is, perhaps, the most unassailable evidence we have for hereditary control over intelligence, and is certainly suggestive evidence for a multifactorial system, not one controlled by only three to eight loci.

Comparative and Evolutionary Evidence

If abilities are partly controlled by genes, evolutionary processes must have been responsible for their present distribution. Do we have any information from human paleontology and prehistory that is helpful in understanding the origin of the basic dimensions of human abilities? The essentials of man's evolution are thought to have been: walking erect, thus freeing the hands for increased manipulation and tool use; the adoption of permanent tools and their gradual improve-

TABLE XVII

Changes in IQ per month of age, per unit of socioeconomic score, and per % inbreeding (F) for all consanguinity classes

	IQ	*Age*	*Socio-economic status*	*F*
For males	Verbal	0.1687	0.6671	–0.3159
	performance	0.0921	0.4514	–0.2444
For females	Verbal	0.2020	0.4679	–0.5927
	performance	0.0936	0.3036	–0.4280
Both sexes	Verbal	0.1852	0.5740	–0.4418
	performance	0.0930	0.3827	–0.3289

ment through specialized manufacturing; the increased effectiveness of group action through speech; and, above all, the cultural transmission of information as speech evolved into language, writing, and, finally, formal education. Leakey[48] discusses methods probably employed by prehistoric man in producing certain types of stone tools by using bone to split flakes from a piece of flint. Gradually man improved his skill; spatial visualization and mechanical understanding, as well as practice, were required to predict the results of a given blow. Figure 11, taken from Leakey, gives an example of the fine work of which prehistoric man was capable. This particular tool is dated roughly from before the third glaciation (circa 300,000 years ago).

Recent field studies of primates by Goodall,[29] Devore,[20] Schaller,[77] and others have shown that the gap between man and his nearest kin, although they be countless generations apart, is not as great as we once thought.

The rudiments of number concepts may lie in the awareness of both numerosity and patterning. Surely the territoriality so artistically described by Ardrey[4] implies some awareness and memory of spatial arrangements. Studies of a variety of species have demonstrated memory and learning. In fact, current ideas about biochemical fac-

FIGURE 11 Hand ax from the Acheulean period, demonstrating the precision prehistoric man could achieve. (Leakey, 1961)

tors in learning indicate that the basic arrangement for memory storage may have developed with the genetic mechanisms themselves.

Verbal ability is, of course, uniquely human, and is accompanied by a proliferation of problem-solving skills and extremely well-practiced and overlearned subroutines that permit the construction of more complicated abilities. Perhaps these are different to some degree for every person as unique combinations are worked out in individual life histories. I believe so strongly in this uniqueness of the individual and his intelligence that I would like to second, with some modification, a definition of intelligence proposed by Novoselova[64] at the XVIIIth International Congress of Psychology. With minor changes and the italicized addition of some sentences at the end dealing with hereditary variations, the definition is as follows.

Intelligence is a multifaceted, progressively evolving, adaptive activity that undergoes constant reorganization leading to qualitative changes during the lifetime of the individual. It is developed in unity with the capacity to perceive dynamic processes in each person's sphere of activity, and is based on the use by each person of his individual experiences, be they original or imitative, and of social tradition, which to a large extent is laid down in a variety of symbolic forms, which anthropologists call artifacts. It is based on the common human sharing in abilities acquired during evolution. *When the normal genetic endowment is distributed by abnormal genes or abnormal numbers of chromosomes, there may be interference in development, which results in retardation. The hereditary component in the normal variation in intelligence is probably determined by a multiplicity of genes with small cumulative effects. The importance of heredity varies according to the aspect of intelligence under study and the age and sociocultural environment of the subjects.*

In spite of the uniqueness of each person's ability structures, however, there is a good deal of similarity in the grosser structure, which is why a number of separate abilities have been recognized. When we come to the finer details, such as those found in Guilford's studies, one begins to wonder if the results of such studies would hold with subjects from different socioeconomic levels or from different parts or cultures of the world.

Hereditary Factors in Personality

In a recent paper I reviewed hereditary factors in personality.[98] In it is a table that summarizes 15 studies. I concluded that there is consistent evidence for hereditary determination of a trait variously named sociable, extroverted, or its opposite—shy, withdrawn, introverted. This may or may not be related to schizophrenia; the shy person may be heterozygous for the schizophrenia gene(s). Possibly two or three loci are involved. That even a few loci can produce an approximation to a smooth distribution was shown by Lush.[54] Figure 12 illustrates his point. If environment plays some part there might, of course, be an even better fit to a normal distribution.

Although parental influence probably is a factor in schizophrenia, it may be profitable to study in detail the pedigrees of generally extroverted, sociable families with an occasional shy, withdrawn child, to see if such exceptions occur elsewhere in the pedigree in any meaningful pattern.

We also found strong and consistent evidence of a hereditary component in other clusters of personality traits: dominance, assertion,

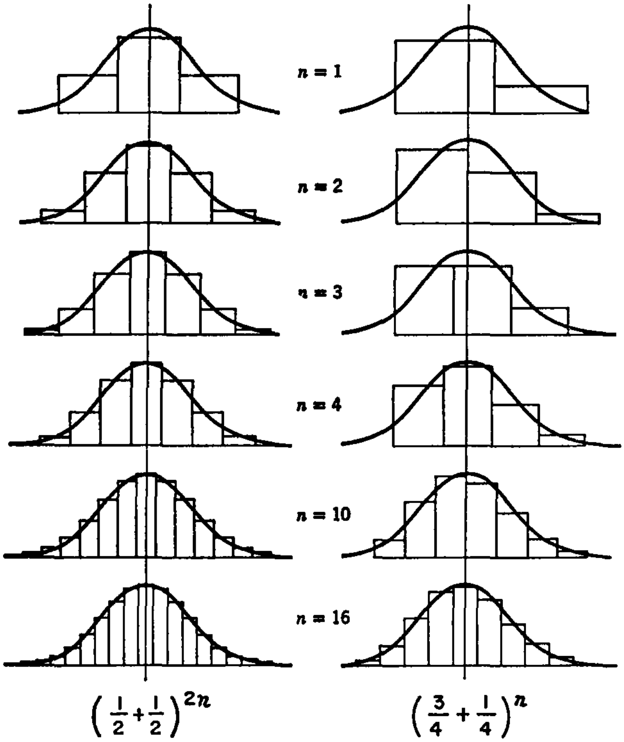

FIGURE 12 Gradual approximation to normal curve of phenotypes controlled by n pairs of genes, where n increases from 1 to 16. Left, no dominance; right, complete dominance for all genes. (After Lush, 1945)

self-confidence; activity, vigor, surgency, energetic conformity, need for achievement, and depression (at the negative end); neuroticism, psychasthenia, psychoneurotic and psychosomatic complaints.

Differences among results of twin studies, even if they used similar psychological tests, are complicated by varying estimates of heritability. This is attributable to three causes: real differences among the heritability of traits in different populations; the degree to which various methods of measuring hereditary components differ on a number of criteria; and the usual limitations of tests — lack of perfect reliability and validity.

The usual considerations of limited validity and reliability must be augmented by some special ones. For instance, two tests of, say, vocabulary that appear to be similar in validity and reliability may give different estimates of the significance of hereditary components. This is because we are dealing with differences between twins and not solely with the scores. Consequently, the results may be unduly affected by varied format or even by the time of day at which the test is administered.

THE NURTURE OF INTELLIGENCE

Do the abilities for which man has acquired genes during his long evolution need special conditions to come to fruition in a particular child? Clinical observations on children without adequate mothering are now backed up by the studies of Harlow,[34] of Scott and Fuller,[80] and others, and indicate that a minimum of social interaction is necessary for normal development in some of the higher mammals, such as monkeys and dogs. Recent work by Krech, Rosenzweig, and Bennett shows that differences in the amount of stimulation leads to differences in brain chemistry, mediating the differences in ability. (For a good summary, see Bennett, Diamond, Krech and Rosenzweig[7])

That the lack of early stimulation has a depressant effect on mental development is generally accepted. To what extent an increase in early stimulation raises the intellectual level has yet to be demonstrated, although the differences in ability between socioeconomic classes are often attributed to such stimulation, in part or in their entirety. To dramatize the distinction we must know if early experience can do something other than *stunting*; if it acts in a manner similar to a *hothouse*, forcing an early bloom which is nevertheless no different from a normal bloom; or if it acts more like *fertilizer*, producing bigger and better yields. To get answers to these questions, perhaps we must try to persuade parents to let us stimulate one twin early and often and leave the other to his own devices. In this way we could stretch the hereditary-environment experiment to its limit.

Stimulation does not have an all-or-none character, but is graduated, according to studies of lower-class whites and Negroes who did or did not move to more favorable environments. Of course, the possibility of selective migration of the more capable cannot be ruled out. Because environmental factors seem of importance, it may even be possible to draw a map of the geographical distribution of ability after controlling statistically for some of the more gross economic factors. Such a map would suggest more detailed studies to see whether, in addition to environmental factors, there are geographic differences in ability that somehow have coalesced into clines, or regions of similar ability. Data from the National Merit Scholarship Corporation and from project TALENT can be used to produce such a map. The unmistakable correlation in Europe between the number of Nobel prize winners and the economic and cultural development of their country of origin might also be a strong argument for the environmental contribution to high ability, especially as countries differing in scientific achievement frequently have similar genetic backgrounds as well as equal educational facilities, although the latter may differ in emphasis.

Studies of the influence of college on students will give more detailed information on the question of how long a stimulation period is needed to influence development. Nichols[63] has reviewed studies performed at NMSC by himself, Holland, and Astin, in which there was little demonstrable effect of college in the *aggregate* on the career plans, intellectual achievement, or personality of talented students in the Merit Scholarship program. The recent report by Coleman, et al.,[16] on equality of educational opportunity in the United States concludes that, of the total variability in intellectual ability and achievement, only between 10 and 20 per cent is associated with differences between schools, while most of the variance is within schools. Differences between schools in the test scores were as large for the first grade as for the twelfth grade, and most differences between schools disappeared when student background factors were controlled.

These findings specifically suggest that in the United States the major source of differences in ability is no longer the quality of schooling, but rather the quality of preschool experience plus innate differences. Of course, this does not mean that full equality in school quality has been reached, because even 10 per cent indicates sizeable differences, but it does indicate the relative importance of the latter two factors.

A similar conclusion seems to have been reached in Sweden.[88] Ninety-four hundred students from different types of schools in Stockholm were compared. No relation was found between type of school and test scores for general ability, reading, writing, mathematics, English, German, history, or chemistry. Neither was there a relation based on contrasting students in the college preparatory course and those in general classes in the fifth, seventh, or ninth grades. A slight tendency toward superior performance was observed in grades six and seven, but not in grades eight and nine, among students who had been placed in college-bound classes at an earlier age.

An English study suggests that ability and social class may interact. In a single community in England, Dockrell[21] tested grammar-school and technical-school children whose fathers were middle class or lower class. He concluded from the patterning of test scores that children from middle-class homes have reached a developmental level in all abilities that makes unimportant (at least from the point of view of their mental development) the type of secondary school they attend. Children of lower-class homes do not have the same level of development, especially in verbal areas, and for them the type of school does make a difference.

I mentioned at the beginning of this paper that we must know more about the influence of education on the various specific abilities. A few promising studies of the effect on spatial test scores of training in late adolescence are suggestive of the kind of data we need. Myers[60] found that United States naval cadets with previous training in mechanical drawing had no better spatial-relation test scores than those without such training. Ranucci[70] found that high school solid geometry did not have an effect on spatial-relation test scores of selected students. On the other hand, Blade and Watson[10] reported three studies in which a college engineering course improved spatial test scores noticeably. However, engineering students may already have a better facility on spatial tests. A more crucial test would be to use unselected high school students for a study of training effects.

Various influences may differ in importance among occupations and types of college specialization. This is suggested by a study of Hilton and Myers[36] in which different background factors predicted, at widely varying levels, the performance of twelfth graders on five criteria. Figure 13 summarizes their findings.

Closer to home, the influence of parental treatment has been investigated by Bayley and Schaefer[6] and by Kagan and Moss.[43] The

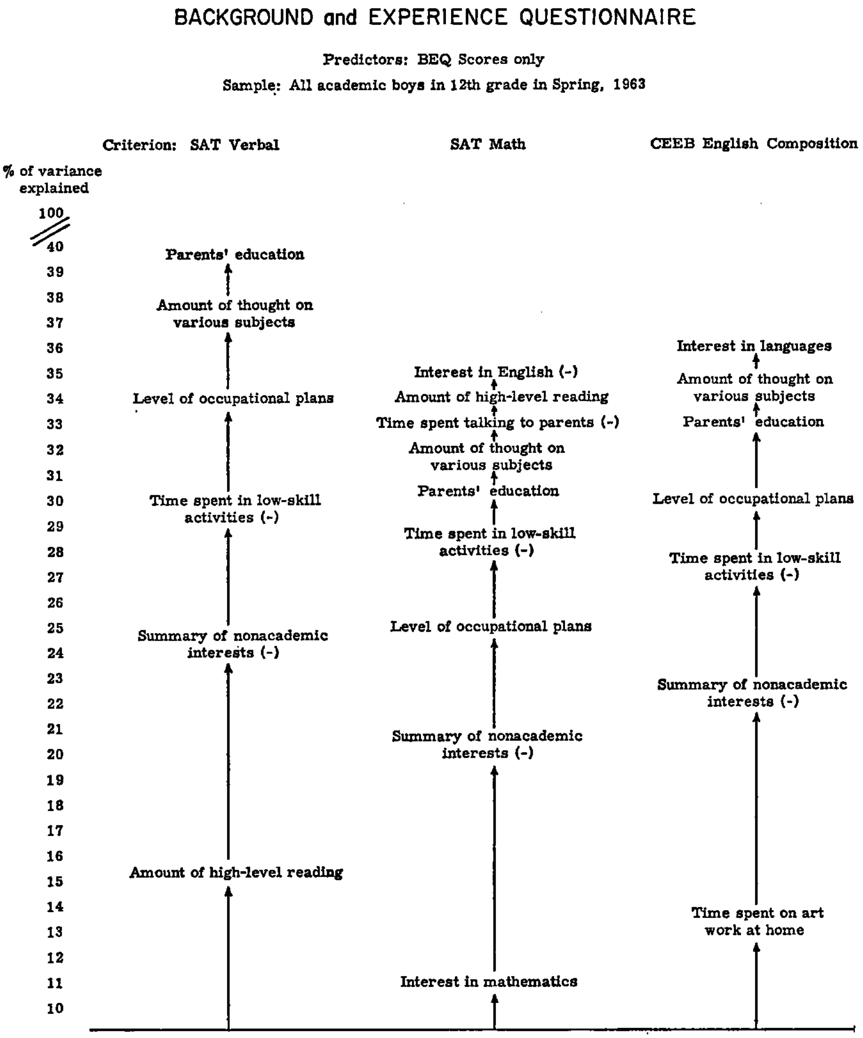

FIGURE 13 A stepwise multiple regression prediction of 12th-grade test scores and rank in class of 1,206 boys, showing the contribution of background variables to be different for different criteria. (Hilton and Myers, 1966)

latter analyzed Fels Institute data for the relation between mother and child behavior and found many significant correlations. They also reported significant correlations between an individual's behavior as a child and as an adult. Especially striking was the consistency between variables relating to achievement in the child and his striving for recognition when adult.

Similarly, Bayley and Schaefer found many correlations between

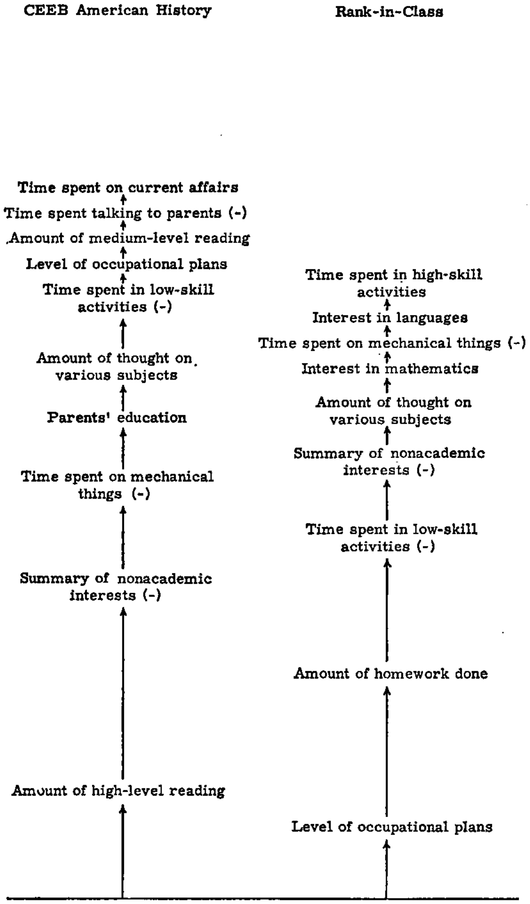

FIGURE 13 *continued*

maternal behavior and the performance of children in the Berkeley Growth Study on intelligence tests during the first year (four age levels), during the period from 13 to 56 months of age (four age levels), and between 5 and 18 years of age (five age levels). They found an interesting sex difference in the patterning of these correlations. Punitive or strict maternal behavior tended to produce positive correlations with IQ during the first year of life for boys, negative correlations for girls. After the first year the picture changed: thereafter these same maternal attitudes produced negative correlations with IQ in the 13- to 54-month and the 5- to 18-year period for boys, but only during the 13- to 54-month period for girls. In fact, for girls 5 to 18 years old the correlations between maternal behavior and intelligence were generally low and not significant; for boys such correlations were quite significant, but negative, except for "positive evaluation" and "equalitarianism" on the part of the mother. Correlations other than intelligence between maternal and child behavior have been reported in Schaefer and Bayley.[76]

The most dramatic claim for the positive effect of early stimulation seems to be that in a recent monograph by Skeels,[81] who studied 25 orphanage children born out of wedlock or taken from their parents for severe neglect. More than 30 years ago, Skeels persuaded authorities to move 13 of these children from the orphanage to an institution for mentally retarded adults. The results appear paradoxical: the children had startling increases in IQ compared with the 12 children who stayed in the orphanage. The explanation is that the orphanage provided little individual attention, while the children who were sent to the mental institution were assigned one or two to a ward, where they were fussed over by patients, attendants, and nurses. Figures 14 and 15 show the changes in IQ for the two groups.

Intelligence tests administered during the first year of life are poor predictors of later IQ, but the consistent increase in the "experimental" group is in marked contrast to the absence of such increases in the "control" group.

Even birth order, which at first sight seems simple, is complex enough to need further study, although some effects are general. Sampson[75] has recently reviewed the effect of ordinal position, and

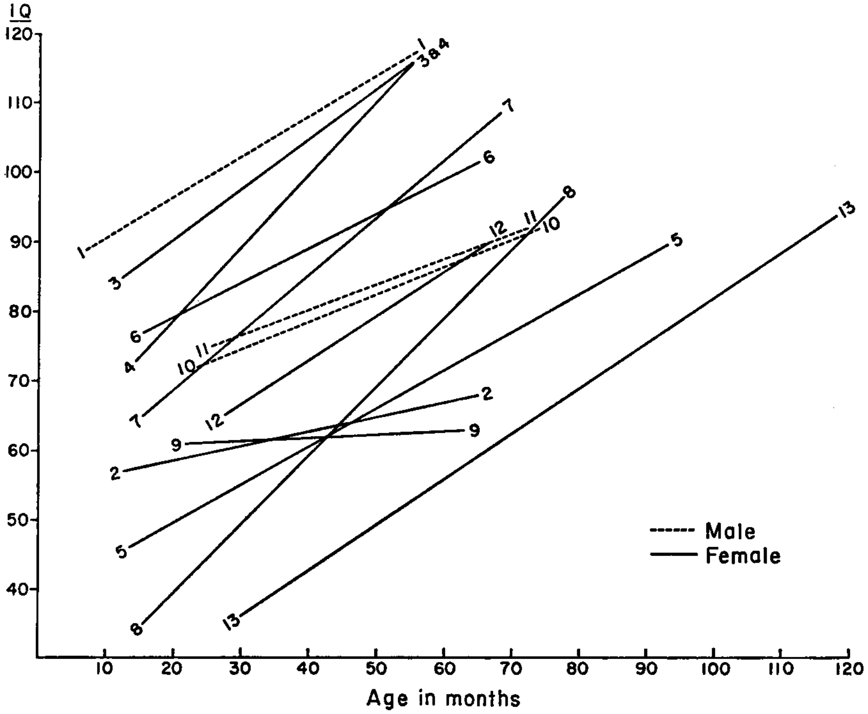

FIGURE 14 Change in IQ scores of thirteen children sent from the Iowa Soldiers' Orphans' Home as "guests" to Glenwood State School for the Retarded. (After Skeels, 1966)

it may be summarized as follows: first-born are more likely to attain intellectual eminence, especially in the sciences; are less likely to express aggressive feelings overtly; are more likely to seek company of others when anxious. Yet they can also be rated as less sociable, less outgoing, less empathetic or sympathetic; to have less self-esteem, perhaps as the result of a shift in the centrality of their family role; and to be more likely to experience conflict over dependence versus independence.

Altus[2] gave further evidence on attainment in first-born children, reviewing, in part, data collected by Nichols at the National Merit Scholarship Corporation. These show that the higher percentage of NMSC finalists are first-born children. Even the month of birth may be of importance. Berglund[8] found no relation between intelligence

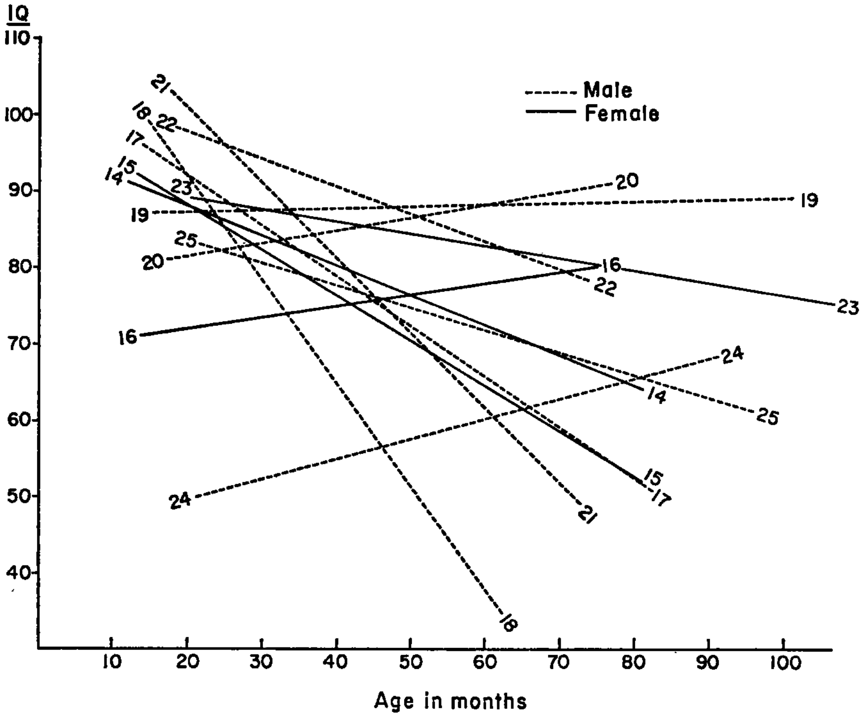

FIGURE 15 Change in IQ scores of twelve children left in Iowa Soldiers' Orphans' Home in the early 1930s. (After Skeels, 1966)

and season of birth in 708 normal children, a slight difference for 237 retarded children with $X^2 = 4.64$. This value of chi square has a 5 to 10 per cent probability of occurring by chance alone. [Medians: December — March 77.6; April — July 78.5, and August — November 79.8]. Pintner and Forlando[68] reported a lower mean IQ for children born between January and March. Orme[65,66] found the highest IQs among 188 retarded adults for those born in summer, and the lowest for those born in the winter. Davies[17] did not find a relation for 300 normal men with an unusually wide age range. So far, the results are contradictory, but suggest the need for a large-scale study. (That prenatal conditions related to atmospheric and climatic conditions may influence ability is further suggested by the work of a South African physician, Professor Ockert Heyns[35a] of the University of Witwatersrand, who for an hour a day put the abdomens of expectant mothers in a device similar to an iron lung to facilitate easy childbirth. He observed higher scores on infant intelligence tests in children of mothers thus treated.)

Ideas about national and racial differences are probably based largely on incorrect stereotypes, but a residue may be the result of differences in educational opportunities. Even when the education is regarded as equal, there may be differences in the systems of education, such as the relatively free choice of courses in the United States versus the more rigid curricula in Europe. Finally, there may be differences in achievement patterns because of national traditions and their different value systems, which determine the skills or intellectual pursuits the children will follow. Modern technologic innovations in machine teaching, including television, may bring new insight on the acquisition of abilities.

Striking a Balance

On the basis of evidence so far presented, it appears that the early environment is more critical than the later. But we still do not know if enrichment of the early environment does as much good as restriction and deprivation do harm.

If stimulation can permanently enhance performance, we might expect some type of multiplicative model to hold for abilities, e.g.:

$\text{Ability} = [C_1 \times \text{genetic anlage}] \times [C_2 \times \text{environmental stimulation}]$

To what extent such a model holds and numerically estimates the specific values of the coefficient C_1 and C_2 for a particular ability can only be determined by co-twin control studies.

Suggestions for Research

I want to make a plea for longitudinal co-twin studies in special schools and summer camps. Such an enterprise would furnish information that cannot be obtained in any other way. My other suggestion is for the inclusion of well-qualified psychologists in cooperative studies of rare genetic anomalies and racial isolates.

THOUGHTS ABOUT THE HUMAN CONDITION

If we believe Leakey's time scale, mankind has not changed drastically in over half a million years, except for his vast improvement in technology. The increase in man's technical ability has not been accompanied with an equal increase in moral and spiritual development.

I would like to end with a poem by that great misanthrope and pessimist, Robinson Jeffers. The title speaks for itself.*

Original Sin

The man-brained and man-handed ground-ape, physically
The most repulsive of all hot-blooded animals
Up to that time of the world: they had dug a pitfall
And caught a mammoth, but how could their sticks and stones
Reach the life in that hide? They danced around the pit, shrieking
With ape excitement, flinging sharp flints in vain, and the stench
 of their bodies
Stained the white air of dawn; but presently one of them
Remembered the yellow dancer, wood-eating fire
That guards the cave-mouth: he ran and fetched him, and others
Gathered sticks at the wood's edge; they made a blaze
And pushed it into the pit, and they fed it high, around the mired
 sides
Of their huge prey. They watched the long hairy trunk
Waver over the stifle-trumpeting pain,
And they were happy.
 Meanwhile the intense color and nobility of sunrise,
Rose and gold and amber, flowed up the sky. Wet rocks were
 shining, a little wind
Stirred the leaves of the forest and the marsh flag-flowers; the
 soft valley between the low hills
Became as beautiful as the sky; while in its midst, hour after
 hour, the happy hunters
Roasted their living meat slowly to death.
 These are the people.
This is the human dawn. As for me, I would rather
Be a worm in a wild apple than a son of man.
But we are what we are, and we might remember
Not to hate any person, for all are vicious;
And not be astonished at any evil, all are deserved;
And not fear death; it is the only way to be cleansed.

---

* From "Selected Poems" by Robinson Jeffers. By permission of Vintage Books, a division of Random House. Copyright, Donnan Jeffers and Garth Jeffers.

Beyond the Fringe–Personality and Psychopathology

IRVING I. GOTTESMAN

It is remarkable that, in this day and age, enlightened students of man's behavior should entertain doubts, if not outright disbelief, about the appreciable genetic contribution to variation in certain human traits. Yet all too often the students of *other* professors — within psychology as well as higher in the pyramid of sciences — have been led to believe that biology and behavior are independent universes. Students from lower in the pyramid are often too zealous in their embrace of "hard data," reluctant to grapple with behavioral traits, and naive about the power of the environment in modifying the behavioral phenotype. The conference at which this paper was given represents another important step on the road to the dissolution of many misunderstandings.

Professor Vandenberg's review has been both scholarly and broad in scope. It is a common belief that survival of a species is furthered by the ritualization of intraspecific aggression. Since our "subspecies" of human behavioral geneticist is so few in number, I would not have it any other way. For the most part, we are concordant in our interpretations of the body of literature bearing on the contributions, both realized and promised, of a genetic and evolutionary framework to the understanding of human behavior.[15,21,22] I am not committed to factor analysis. I agree with some critics that such methods may advance psychology only when used in close relation with the ideas in psychology,[51] and that the entire enterprise suffers from having promised more than it has delivered.[30] One might hope that no further documentation for the importance of genetic variation in individual intelligence is necessary, and that we might move outside the pale of relatively easy measurement — to the fringe and beyond — and deal

---

IRVING I. GOTTESMAN University of Minnesota, Minneapolis, Minnesota

with the fascinating and socially important topics of human personality and psychopathology. Certain facts force me to delay treating these areas. The resurrection, from the graveyard of supposedly dead issues, of the Iowa foster child studies by Skeels[48a] may have surprised Professor Vandenberg as much as it did me. Twenty-six years have done nothing to resolve the controversies,[35,54] and I believe the absence of a suitable schema in the repertoire of genetically naive scientists is responsible — a schema that could lead to an appreciation of the circumstances under which nature and nurture have differential importance.

Let me outline briefly and illustrate such a schema, which I have called the reaction range,[18] and which is termed the norm of reaction by Dobzhansky.[9] Given uniformity of trait-relevant environment, almost all of the observed variance in a trait must stem from variability in the genotype. Given uniformity in that part of the genotype relevant to the trait under consideration, almost all of the observed variance must be associated with environmental factors. Given the heterogeneity that prevails for human genotypes and environments, trait variation must be attributed to some combination of genetic and environmental variances.

The question of how much of intelligence is caused by heredity and how much by environment is meaningless, because neither agent alone can produce the trait. Such phrasing of the question is an important cause of the stalemate that has stifled progress in psychology over the past fifty years. Two answerable questions should be posed in the contemporary concern with the roles played by nature *and* nurture in human behavior. 1) How much of the variability observed within a group of individuals in a *specified* environment on a *particular* trait measure is attributable to hereditary differences among them? 2) How modifiable by systematic environmental manipulations is the phenotypic expression of a trait? A further question is of crucial importance to the basic understanding of human behavior, but it must be deferred until such time as molecular geneticists, developmental biologists, and developmental psychologists are ready to collaborate. That question is: *How* does heredity interact with the environment to produce trait variation (cf. Anastasi[1])? There are no genes *for* behavior or any other phenotypic trait. Genes exert their influence on behavior through their effects at the molecular level of organization. Enzymes, hormones, and neurons may be considered as the sequence of complex path markers between the genes and a behavioral characteristic.[16,50]

Within the reaction range framework, a genotype determines an indefinite, but nonetheless circumscribed, assortment of phenotypes. Each phenotype corresponds to one of the possible environmental regimes to which the genotype could be exposed. Within the broad range of continuous variation in measured IQ, two aspects of the environment, *favorableness* and *commonness,* are important to the concept of reaction range. By this I mean to imply that each genotype has its own more-or-less natural habitat, at least in a society that fosters social mobility* using ability as the sole criterion. In regard to the character intelligence, a natural habitat would include a normal delivery and freedom from organic impairment, an adequate diet, home rearing by both parents or adequate surrogates, exposure to adequate sensory stimulation, and exposure to an adequate system of compulsory education. One of the assumptions underlying the reaction range concept is that marked deviation from the natural habitat occurs with a low probability. It is only when two individuals or two groups come from equally favorable environments that a difference in measured IQ can be interpreted to indicate a difference in genetic potential.

Studies on identical twins reared apart[47] afford us some insight into the effects of differing environments on the same genotype. This information can permit a rough estimate of the reaction range for average individuals under natural conditions. It is probably not more than twelve IQ points in either direction and most probably is less. Thus, IQs from 88 to 112 could indicate the phenotype of equivalent genotypes under the conditions specified.

The Iowa study grew out of a clinical program rather than premeditated research. Their conclusion that the IQs of children of

---

* "Social mobility" here refers to a change either upward or downward in one's adult social status — via education and occupation — as compared to one's father.

feebleminded mothers differed little from that of other foster children[48] is not at all supported by the recent and comprehensive study conducted by Elizabeth and Sheldon Reed in Minnesota.[42] As part of their research into the etiology of mental retardation, they looked at the IQ test results of 1,450 retardates and their 1,951 surviving offspring; both generations had been tested as school children, so that age corrections were unnecessary. Some 43 per cent of the retardates never reproduced. When a retardate in the sample married a spouse who was also retarded, 39 per cent of their offspring were retarded, i.e., had IQs of 69 or less The patently poor intellectual environment provided by these matings did not, however, prevent 24 per cent of their children from obtaining IQs of 90 or above. When a female retardate married a normal spouse, 19 per cent of their children had IQs of 69 or below, 31 per cent ranged from 70 to 89, and 50 per cent were of normal or better intelligence. The Reeds also showed that two parents of normal intelligence, neither of whom had a retarded sibling, had only a 0.53 per cent risk of having a retarded child. However, if either parent had a retarded sibling, the risk rose by a factor of five to 2.5 per cent. The data permit me to conclude that five out of every six retarded individuals, some five million of the six million retardates in the United States, are the offspring of a retarded parent or of a normal parent who has a retarded sibling.

It is also important to note that one of the outcomes of the Minnesota study was the resolution of Cattell's paradox[29]; that is, with the negative correlation of –0.3 between the number of children in a family and their average test intelligence, we should expect the intelligence of succeeding generations to decline — but it hasn't. The explanation is that while some of the retarded produce very large families, most have no children or only one. The individuals at the upper end of the normal curve consistently produce small families of more intelligent children, but virtually *all* reproduce and thus balance the number of children from lower-IQ families.[2]

My next comments apply to topics that could hardly be avoided in the group assembled here. Do observed differences in intelligence between races or social classes have an important genetic component or are they for the most part the result of differences in environmental advantages? We have some scientists who have no doubt that the Negro American is poorly endowed with the genes that lead to intelligent behavior (e.g., George[17]), but most challenge that view (e.g., Gottesman[20]). We also have some genetically knowledgeable social scientists, such as Professor Halsey,[28] who have considerable doubt that current mean differences in intelligence between classes could be innate, and socially knowledgeable geneticists, such as Professor Dobzhansky,[10] who believe that, at present, social stratification is not based on native ability because equality of opportunity has not been in existence long enough for diversifying selection to have taken place.

I can only summarize some of my thoughts on these topics.[23] My evaluation of the literature on race differences has led me to conclude that the differences observed between the mean IQs of Negro Americans and other Americans can be accounted for almost wholly by environmental disadvantages which start in the prenatal period and continue throughout a lifetime. Social classes, like races, can be construed as Mendelian populations or as relatively endogamous breeding groups. In the prehistory of man, a class system probably evolved after food-gathering had been replaced by food-producing, and an efficient practice of agriculture elicited the simple stratification into leaders and laborers. Support for the view that the structure of modern societies is at least in part dependent on biological phenomena rests on the demonstration that stratification is based on ability and, further, that individual differences in ability are partially conditioned genetically. In a truly democratic system, an open-class society[33] permits the formation of differentiated social classes and, most importantly, fosters class change and mobility. Thus, a migration from one class to another, based on presence or absence of ability, is the final essential requirement for a biologically based model of social structure. In contrast to Professor Halsey, Sir Cyril Burt[4,5] estimates that intergenerational social class mobility in the United Kingdom is about 30 per cent.

In comparison to the social structure of Great Britain, the "open class" aspects of democratic society are much more pronounced in the United States. In the mid-1960s, more than 40 per cent of secondary school graduates are enrolling in college. It seems logical to expect that intergenerational mobility in our country is greater than 30 per cent and is moving toward a theoretical maximum of 66.5 per cent. The net result of an open-class system, with equality of opportunity plus assortative mating, makes genetic factors no less important for an understanding of human society than for other mammalian species. "Organic diversity is the adaptive response of living matter to the challenge of the diversity of environments." (Dobzhansky, Reference 10, page 221)

Is it inconsistent to attribute race differences in intelligence tc environmental differences and social class differences to genetic factors? It must be remembered that we are dealing with differences between populations, not between individuals, and that the differences are quantitative, not qualitative. If we estimate that our species, *Homo sapiens,* has been on the face of the earth for the past 500,000 years, detailed knowledge about our existence covers a period of little more than 1 per cent of the total time. It was only after the introduction of agriculture and domestic animals in the Neolithic era, some 12,000 years ago, that two distinctive niches became available. It requires two or more niches, each with its own rate of selection pressure, for a trait such as intelligence eventually to show a divergence in frequency. Only a little more than 300 generations have passed since the introduction of agriculture. I would posit that the essential ingredients of what we call general intelligence are learning ability and problem solving, and that the two niches or habitats did not exert differential selection pressure for intelligence. Some evolutionists—for example, Mayr[36]—maintain that man has not improved biologically for the past 30,000 years.

For some traits, 300 generations have been sufficient time to lead to significant differences. Post[39–41] has examined the literature for population differences in color and acuity deficiencies in vision, and for hearing acuity. He found evidence to support the hypothesis that contemporary hunting and gathering cultures have a much lower prevalence of vision and hearing deficiencies than have populations removed in time and habitat. The observed differences were not accounted for by race per se, but by adaptation to a habitat, followed by selection.

For general intelligence, then, the selection pressures from one geographical race to another either have not been sufficiently different or have not yet been in effect long enough to lead to significant differences in the genetic basis for this character. However, as discussed by Vandenberg, intelligence can be partitioned into many components. Guilford,[27] a psychological authority on the character of intelligence, suggested that there may be as many as 120 factors, or relatively independent components, to general intelligence. We cannot rule out that races may differ in the trait (and gene) frequencies for any number of the *factors* of general intelligence. The possibility has yet to be explored and the appropriate tests have yet to be developed.

Within a race or other Mendelian population that has occupational diversity and provides for social mobility, large differences in general intelligence between noncontiguous strata (e.g., I and III, or II and VI) may have an appreciable genetic component. The continuous gene migration, together with fairly high degrees of assortative mating, yield results somewhat analogous to the high *artificial* selection pressures seen in the improvement of crops and domestic animals. Perhaps you will agree that these speculations about the structure of human society are based on a not-unreasonable interpretation of the available data.

COMMENTS ON GENETICS AND PERSONALITY

In the classical study of twins conducted by Newman, Freeman, and Holzinger,[38] little evidence could be found to support the idea that personality traits are under genetic influence. Since that time, improvements in personality measurement and a new era of psychometric sophistication has led to new tests and a reevaluation of the earlier conclusions. The work of Cattell,[7] Eysenck,[12] Vandenberg,[53] and myself,[19,20,22] among others, on the heritable variation in certain personality traits, suggests that the area is rich for mining but full of crevices and long digressions where one may run out of oxygen. Few researchers have bothered to replicate their studies of personality, and almost all have relied on the twin method alone, so it is hazardous to make many generalizations about which traits have high heritability and which have low. Sex differences in heritability are usually present and difficult to account for. Both sex-role typing and sexual selection may enter into this problem.

My own work leads me to suggest that the traits that should be singled out for research within a behavioral genetics framework are those with possible evolutionary significance and those that existing research shows to have heritabilities greater than 33 per cent in some samples. Among the traits I would nominate are introversion,[46] aggression, anxiety, attention to detail, and social attachment.[15] For those of you who question what a psychologist really thinks a trait is, I refer you to the papers by Cronbach and Meehl[8] on construct validity and by Loevinger[34] on the relationship between objective tests and psychological theory.

COMMENTS ON GENETICS AND SCHIZOPHRENIA

Until a few years ago, no one doubted that the identical twin of a schizophrenic had a high risk of becoming a schizophrenic himself, regardless of whether the cause was thought to be based on genetic factors or on interpersonal and intrapersonal ones. More recently, the results of Tienari[52] in Finland and Kringlen[32] in Norway and their interpretations of their findings have led many former "believers" to have reservations. David Rosenthal[43–45] suggested that the reported concordance rates in the now-familiar studies by Kallmann,[31] Slater,[49] and others were higher than they should be because of an over-representation of severely ill patients and female pairs, and for other errors in method. At the Maudsley Hospital in London, James Shields and I, working in Dr. Slater's Psychiatric Genetics Research Unit, have added another study that gives, with the two above, a new look to research on schizophrenia in twins.[24–26] In summary, we found a concordance rate for hospitalized schizophrenia of 42 per cent in identicals and 9 per cent in same-sex fraternals (without age corrections); our sample came from consecutive admissions over 16 years to a large out-patient department, and so were fresh admissions. We found a striking relationship between severity of schizophrenia and concordance, as had been anticipated by Rosenthal; 75 per cent of the co-twins of severely affected identical probands were themselves schizophrenic, compared to 17 per cent of the co-twins of mildly affected identical probands.

Do findings such as our over-all concordance rates or those reported in the Scandinavian twin samples, together with the rather low rates in siblings (6.8 per cent) and parents (4.5 per cent) reported by Erlenmeyer-Kimling, Rainer, and Kallmann[11] invalidate or attenuate the role of genetic or biological factors in the etiology of the schizophrenias? No. Such a belief would appear to originate from unfamiliarity with at least two facets of human genetics: the relevance and applicability of models from quantitative genetics (e.g., Falconer[13]) to the data in psychiatric genetics, and the progress that has been made in dealing with the genetics of *common* disorders, such as club-foot and pyloric stenosis,[6,14] and diabetes mellitus,[37] which are not inherited in a simple manner.

It has been known that the simple Mendelian ratios are not found in the relatives of schizophrenics. If the etiology of the schizophrenias is heterogeneous, some forms, individually of rare occurrence, might fit Mendelian models. Alternatively and heuristically, we should like to consider the merits of treating schizophrenia as a threshold character with a quasi-continuous distribution.

Let us suppose that the diathesis is polygenically determined and that what is inherited is a constitutional predisposition to schizophrenia — a predisposition that has been named differently by a number of investigators. Polygenic theory, with or without a specific major gene, can go a long way toward giving us the "workable concept of heredity" hoped for by Eugen Bleuler[3] in 1911. The likelihood of manifestation as overt schizophrenia, as well as its form and severity, would depend on how many of the genes in the posited polygenic system were present, the remainder of the genetic background, and the environmental stress factors. Polygenic inheritance could account for the observed irrational, schizoid, and "borderline" personalities in the relatives of schizophrenics. Finally, with this theory we would expect the monozygotic co-twins to be more abnormal than their dizygotic counterparts, especially along personality dimensions supposedly related genetically to schizophrenia. Most instances of the disorder, from the most mild to the most severe, could then be conceptualized as biologically related.

While it is clearly of importance to account for differences within monozygotic pairs, the task is a difficult one. Such environmental reasons as have been given in the literature are insufficient as causes of schizophrenia. Not many underweight babies, or children of constricting, inconsistent mothers, or twins with overly close ties, actually develop schizophrenia. But these very same features, given the diathesis, may determine which twin decompensates or which of two concordant twins is the more severely ill.

Our analysis of the twin studies of schizophrenia leads us to conclude that they are replications of the same experiment, with the heterogeneity of results being more apparent than real, once provision is made for important dimensions.[25] It seems reasonable to continue to postulate that genetic factors, currently indeterminate, are largely responsible for the specific nature of most of the schizophrenias, and that these factors are necessary but not sufficient for the disorders to occur.

The Genetics of Intelligence and Personality

DAVID ROSENTHAL

About a quarter of a century ago, the Committee on Social Adjustment of the Social Science Research Council, one of the three organizations that sponsored the conference on which this volume is based, asked Dr. R. S. Woodworth to prepare a "critical survey of the methods and findings of nature and nurture research." The Committee found Dr. Woodworth's report to be of such "great value in clarifying its own thinking" that it published it in a monograph entitled "Heredity and Environment: A Critical Survey of Recently Published Material on Twins and Foster Children."[7] Many of us have read the report at one time or another, although the details of it may have faded as we have become caught up in our current reflections and investigations. Like Dr. Vandenberg, Dr. Woodworth focused his report on "the influence of hereditary and environmental factors in intelligence and achievement," as the Committee had requested.

It is relevant to our purpose — because there are two such authoritative summaries of the same field, spaced 25 years apart — to inquire about advances made during that time in the genetics of intellectual functioning and personality. Unfortunately, Dr. Vandenberg's report is necessarily truncated because of space limitations, but I am sure he chose to discuss the most important developments concerning intelligence. However, he was able to mention only briefly and generally a few of the findings concerning personality.

A major difference between the two eras lies in "intelligence" itself. In the earlier period, almost all studies of the genetics of this trait equated IQ scores, as determined by Binet-type tests, with intelligence levels. The earlier investigators seem not to have explored seriously the question of whether the IQ represented a unitary trait, probably

---

DAVID ROSENTHAL National Institute of Mental Health, National Institutes of Health, Bethesda, Maryland

because of the prevailing influence of Spearman and his "g" factor. Thurstone's multiple factor analysis began to challenge the Spearman method only toward the end of the earlier era, and the Primary Mental Abilities had just been factored out sufficiently for use in studies of heredity.

By contrast, Dr. Vandenberg devotes about half his paper to the latter issue. He concludes that there are at least six separate intellectual abilities whose usefulness he somewhat favorably assesses according to six criteria, and he is concerned with the relative contribution of heredity and environment to each of these abilities and to performance on various tests which require the abilities in different degrees. The *goal* of clarifying the nature of the trait studied is a clear step forward for our still-maturing discipline. Whether factor analysis is the proper method to achieve this goal is another matter. Luria and others doubt that it is, but at the present time we seem not to have a better one.

If we summarize Dr. Vandenberg's evaluation of separate abilities according to his six criteria, we find the following.

1 The abilities predict success in jobs and curricula about as well as IQ, but not noticeably better.
2 Many studies support the belief that an increase in the number of independent abilities occurs up to adolescence, although many studies do not.
3 The same factors are found in a variety of national groups, but the possibility that specific subject matters may be differentiated and segmented in the course of learning cannot be ruled out as an explanation of this finding.
4 Evidence suggests that the factors are comparable at different levels of ability, but are differently weighted.
5 We do not know if the separate abilities are affected differently by psychoses or neuroses, but the spatial and verbal factors may be associated with specific areas of the brain.
6 We do not know if the separate abilities develop simultaneously or at different times and rates.

Although in such an evaluation there is some reason to be hopeful about the potential heuristic and utilitarian value of the factored abilities, at the present time we hardly have reason to be overwhelmed by feelings of their importance. And what about the genetics of these abilities? Dr. Vandenberg says, "As far as I know there is no information on correlations of specific ability scores between relatives." I found this to be the saddest sentence in the whole chapter. It is a sharp reminder to those of us who would like to point to milestones of progress in the last 25 years.

In any case, I am not clear as to why, if Dr. Vandenberg accepts the separate abilities as so many unitary traits reflecting different genetic components, he continues to concern himself with the concept of a general intelligence. I can see the term "intelligence" being used as a shorthand, convenient term for the sum of an individual's separate abilities, but Dr. Vandenberg's lengthy definition of it goes far beyond that. I would like to know how he plans to study the genetics of an individual's "capacity to perceive dynamic processes in [his] sphere of activity," and what that phrase means. I doubt that adding another definition of intelligence to a long list of predecessors will help to clarify anything. At least one psychologist has defined intelligence as a "chapter-heading in an introductory psychology textbook." It may be hard to improve on that.

One obvious advance over the pre-World War II era has been the increase in statistical sophistication. Dr. Vandenberg does not dwell on this, but his own review and the tables and figures he has presented illustrate the point adequately. Whether the basic experimental designs themselves have advanced during our own generation is another matter. Most of the studies reviewed by Dr. Vandenberg include comparisons of intrapair differences between monozygotic and dizygotic twins. All are versions of Siemens' twin method,[5] which is based on the assumption that intrapair environmental differences are essentially the same for both kinds of twins, and that hereditary and environmental influences are not correlated. Woodworth and several other earlier investigators doubted the validity of these assumptions, but many investigators of our generation have been content to ignore the disagreement or to give it short shrift.

Most work in human behavioral genetics has relied on studies of twins. Either heritabilities are calculated or intrapair differences between MZ and DZ twins are compared. Almost invariably, the intrapair differences are less for the MZ twins. The same finding was true in the earlier era; it occurs with such monotonous regularity that one may sometimes wonder why investigators have kept doing essentially the same thing over the years. Does anyone expect to find traits whose intrapair differences are *greater* for MZ than DZ twins?

I would like to quote from a recent article by Dr. R. C. Nichols[3] in which he discusses his own studies on the genetics of personality traits. "Identical twins were more similar than were fraternal twins on almost all the measures used, but three troublesome findings prevent us from interpreting this to mean that heredity is necessarily an important factor for most dimensions of personality and interest." The three findings were:

1. "The failure to find agreement between the results for boys and those for girls."
2. "The sheer size of the differences in similarity between the two kinds of twins. The many values of HR (the ratio of the hereditary variance to the hereditary plus the common environmental variance) *greater* than 1.0 could not have been produced by the simple additive effects of hereditary factors alone."
3. "The lack of agreement with results obtained by others." The last point refers to Nichols' comparison of his data with Gottesman's, in which he found that Holzinger's h^2 values for 18 CPI (California Personality Inventory) categories correlated –.22 for boys and –.24 for girls.

Nichols concludes that "the twin method may be inapplicable to personality inventories based on self reports" because most of the variance is error. However, he believes error to be equated largely with random events, and explains that such events are probably more common for MZ than for DZ twins. In the broad sense, he is saying that intrapair environmental differences were probably *not* the same for both types of twins.

To exemplify Nichols' belief that most of the variance in his twin data is error, we can look at some of the heritability values he obtained for specific behaviors:

Behaviors

High Heritability	*Low Heritability*
1. Took cough syrup	1. Took a laxative
2. Looked up a word in the dictionary	2. Looked up something in an encyclopedia
3. Rode a roller coaster	3. Rode in a sports car
4. Picked up a hitchhiker	4. Hitchhiked
5. Sang in a glee club or choir	5. Took voice lessons
Occupational Preference	
6. Police judge	6. Judge

Perhaps one can tease out genetic explanations of such findings, but one's confidence in any such attempt would hardly bubble over. And I have selected only a few of these teasers. Anyway, it's a shame that Nichols had to come to such a gloomy conclusion. Think of all the fun we could have explaining why taking cough syrup has such important evolutionary implications, whereas taking a laxative does not.

One statement of Dr. Vandenberg particularly caught my attention. Following his presentation of Schull and Neel's analysis of a Japanese study of IQ in children of consanguineous marriages, he concluded that the study's findings constituted "the most unassailable evidence we have for hereditary control over intelligence. . . ." That he makes this statement after having just presented a large number of twin studies, all of whose findings point to the same conclusion, suggests that he may still have some misgivings about twin studies and the dependability of the conclusions that we can draw from them. He says, with tongue in cheek, "The greater within-pair differences in parental treatment of fraternal twins compared to identical twins is undoubtedly due in great part to reactions to very early genetic differences and thus may be classified with heredity." But if the behavior in question is maintained and directed by parental treatment, it could with equal validity be classified with environment. The largest differences in IQ between twins reared apart usually occur in those pairs whose intellectual environment differs most during their upbringing, a finding that should occasion little surprise.

I do not mean to imply that the twin studies of intelligence may, like Nichols' studies of personality, also be invalidated by lurking error. However, the possibility exists that the assumptions of equal environmental differences for MZ and DZ twins and of negligible correlations between hereditary and environmental influences are not correct, and that heritability values or variance ratios obtained from such studies may be inflated or misleading. To the degree that we have failed to rule out this possibility beyond a reasonable doubt, we have failed the era between the wars and have not advanced beyond it.

The failure may have arisen from human behavioral geneticists having been *too* focused on heredity, if one may say such a thing, just as students of learning have been too focused on environmental parameters, almost to the exclusion of hereditary considerations. For untold years, students in introductory psychology courses have recited the old saw that behavior is a function of the organism interacting with its environment, but many investigators seem to have outgrown this catechismic formulation.

If we are to advance the genetics of common behavioral traits in a full and more exciting sense, we ought to get to the business of studying heredity-environment interaction—or *coaction,* as Woodworth referred to it. To do this, we must first do three things: define the behavior of interest; delineate the genotype under study; specify the environmental variable that is coacting with it.

With respect to intelligence, delineation of the behavior of interest has developed along the lines indicated by factor analytic methods, as Dr. Vandenberg has illustrated in detail today. With respect to other behavioral traits, either relatively specific ones or those more broadly conceived and subsumed under the term "personality," consensus as to their delineation and unitariness is less easy to come by, but factor analysis or some more direct methods may yet prove helpful.

With respect to delineating the genotype under study, human research is not able to employ methods comparable to strain differentiations in the mouse or to experimental selection. Consequently, little has been done. But we are not helpless, and research models that we have hardly exploited are available to us. For example, if we are interested in social introversion, we may begin a study with married couples — let us say those who have just had a baby. The couples are then tested and three groups selected: both parents high on introversion; one parent high and one low; both parents low. The babies are then studied in two ways: we observe parent-child interactions to note differences in parental (especially maternal) behavior and infant response; we program various kinds of stimuli, social and nonsocial, and record the babies' responses. With such a design we could begin to tease out the genetic and interactional components of introversive behavior.

Another possible model is one my colleagues and I are using in our research on schizophrenia. We begin with two groups of parents. In one group, one parent is schizophrenic; in the other, neither parent has any known psychiatric abnormality. The children of both parent groups are given up for adoption at an early age, so that we unconfound the genetic and rearing variables. We study intensively the personality characteristics of both sets of children (now adults). Differences between the two groups of children reflect personality traits contributed by the schizophrenic genotype.

This model can be developed further, in line with the cross-fostering model used in animal work. As before, we start with two groups of parent couples, one with a schizophrenic member, the other without. Children of the schizophrenic parents are given up for adoption to couples who are not known to have any psychiatric illness, or, let us say, who are "normal." In contrast, the children of "normal" parents are given up for adoption to couples each of which has one member known to be schizophrenic. The two groups of children are compared with respect to a wide variety of personality traits, and the relative contributions of genotype and rearing parentage are compared.

The third thing we must do is to specify the environmental variable that interacts with the genotype. I believe that here we have most failed the previous generation. Psychology is now a sophisticated discipline. We have a wealth of basic concepts: conditional and unconditional stimulus and response; reinforcement; the operant; discrimination; stimulus intensity; response amplitude; schedules of reinforcement;

time contingencies between stimulus and response; and many others. However, students of human behavioral genetics have been content to conceptualize environment in broad terms whose specific stimulus parameters are not known. For example, we have often been willing to assume that children of the same social class, or that twins reared in the same home, have the same environment. But we need to know what particular aspect of the environment has stimulus value with respect to the trait in question. Rearing apart is not a meaningful independent variable per se, but specific rearing conditions may be. For instance, a given mother may not constitute the same "environment" to all her children. Rather, it is the specific behaviors in which she engages, contingent upon various behaviors of her children, that bear most directly upon learning or trait development. An illustration of the same mother behaving differently to each of four genetically identical girls may be found in *The Genain Quadruplets.*[4]

I have heard a psychiatrist tell about a son of royalty who was admitted to a mental hospital because he was suspected of being mentally retarded, but it turned out that the prince had been reared under such a sterile, restricted, caretaking regimen that he was really socially and culturally deprived!

The point I am making was actually demonstrated in the pioneering study of foster children reported by Theis as long ago as 1924.[6] The foster homes were classified as "superior" or "mediocre" on the basis of economic, educational, and cultural status. The children reared in the two types of homes did not differ either in practical or scholastic ability. However, the investigators probed further to estimate how well each home cared for its foster child, and found that "some mediocre families showed an unexpected degree of intelligence, understanding, and sympathy in the treatment of their foster children, and some superior homes bungled completely the delicate problem of child training." When the homes were classified according to pattern of child rearing, a fair degree of association was found between the kind of child care and the proportion of children who were judged to be "capable." Unfortunately, even though the study had its faults, the implications of this finding and some others of the pre-World War II era have been largely neglected in our own time.

The behaviorally relevant environmental variable in the Theis study was not social class alone, "but the degree to which the family understood the child and allowed him to follow his own bent, rather than forcing him into their old mould." It is true that social class and many parent behavior variables are correlated, but the correlation is often low enough to obscure one's results if we rely only on the class variable.

However, the behaviorally relevant environmental variable need not always be defined in terms of particular stimulus-response contingencies. For example, in my studies of schizophrenia I am trying to get at heredity-environment interaction in the following way. To begin, we specify two kinds of child-rearing environments. The first is the usual nuclear family pattern of rearing. The second is the communal form of society in Israel called the kibbutz. In this society, children live in houses apart from their parents. Trained caretakers assume many of the rearing functions normally assumed by parents in the nuclear family. There are several other kibbutz-town differences that I won't mention, but they can be specified. We begin the study with kibbutz parents who are known to be schizophrenic and we match them to schizophrenic parents who live in town. To both groups, we match kibbutz and town parents who are not known to have any psychiatric abnormality. In this way we trap two presumed genotypes, one schizophrenic and one normal, and two rearing environments whose major differences can be specified. The children of the four groups of parents are studied on a wide variety of traits. The fourfold table generated by the design lends itself nicely to separating the variance resulting from genotype, that from the rearing environment, and that from interaction between the two. This analysis can be done separately for each trait studied.

Studies of heredity-environment interactions in the very young would be extremely valuable in building our science. Take such a relatively simple trait as smiling. Freedman[1] has studied twin babies and found greater similarity in patterns of smiling behavior among MZ than among DZ twins. On the other hand, Gewirtz[2] has shown that smiling curves for the first 18 months of life differed among babies in four different rearing environments. How fruitful it would be to combine both types of study! We could then learn about the specific environmental influences that can increase the rate of smiling in babies who would otherwise lie so sadly in their cribs, and about the vile influences that reduce smiling rates in babies who would normally be so engaging and lovable in their early months of life.

To conclude, I will summarize the points I have touched on, either implicitly or explicitly. Although the genetics of intelligence and personality has progressed during the past quarter-century, I find the amount of progress disappointing. The basic theoretical issues—and many research strategies—were already well known and had been clearly formulated by Woodworth and the generation whose work he so ably summarized. Most of their suggestions for further research have not been pursued. By contrast, a ferment has developed in animal behavioral genetics, which has become a vital, exciting discipline. Animal behavioral genetics has developed several research models that could have been adapted, in modified form, to work with humans, but we have not exploited them. The greatest progress made, aside from discoveries about gross genetic or chromosomal abnormalities like phenylketonuria and trisomy-21 (Down's syndrome), has been in the study of intelligence. Even here, the basis for the progress has been primarily in the factoring of intelligence into separate primary abilities whose value is not clear, but whose hereditary bases can be studied separately. By far the greatest number of the scientists concerned with the genetics of intelligence and personality have relied on twin studies, to the relative neglect of other methods that must be pursued if this discipline is to flower, fruit, and seed. Twin studies are valuable, of course, but as they are usually conducted they are limited to providing us with heritability values and variance ratios whose significance is not always clear. Everyone agrees that all human behavior is a function of both heredity and environment, but human behavioral geneticists, unlike their counterparts in animal studies, have often been content to conceptualize the environment loosely and broadly, and to pay too little attention to the analysis of heredity-environment interaction.

Genetics and Social Behavior

WILLIAM R. THOMPSON

DISCUSSION

This paper deals with the conjunction of two complex disciplines—"behavior genetics" and "social behavior." If I am to succeed at all in my designated goals of stimulating cross-disciplinary work between these two areas and indicating how the methods and findings of genetics can be useful to the social scientist, there is an onus on me to clarify the manner in which these areas of research are presently understood and how they may be most profitably studied in the same context.

Some workers have proposed that behavior genetics (which includes, of course, the genetics of social behavior) is, in principle, on a par with the genetics of any such phenotype character as eye color, blood group, litter size, and so forth. I do not share this view. To my way of thinking, these traits, unlike behavior, hold for geneticists only a secondary importance as indicators of fundamental, underlying mechanisms whose mode of operation they reflect. This is well demonstrated by the drift of genetics to the study of more and more mo-

---

WILLIAM R. THOMPSON Department of Psychology, Queen's University, Kingston, Ontario, Canada

lecular problems, particularly, of course, the chemical coding of genic material. This is exciting work of tremendous importance. Yet I cannot but regret its apparent remoteness from the study of the whole living organism, which, as a behavioral scientist, is my main concern. Current work on intelligence, personality, and social behavior in mammals seems a very long way from the studies of nucleotides, ribosomes, and *Escherichia coli.* Yet, I must emphasize, it does not seem a long way *behind* such studies — in the sense we might think of the work of the early Mendelians as being behind contemporary genetics — but simply rather different. We do not have people we call, for example, litter-sizeologists or eye-colorologists, but we do have a great number of people we call behavioral scientists, whose primary concern is with this phenotype of behavior. As a result, it is reasonable to regard behavior genetics as a special discipline with its own unique problems that are interesting in their own right and are not necessarily reducible to the more fashionable molecular level. Ernst Caspari stated his agreement with such a position in an address at the XIth International Congress of Genetics at The Hague.[8] In reference to behavior genetics as a special field, he said: "The reason for this particular position of Behavior Genetics seems to me to be twofold. On the one hand, it uses rather special techniques for the analysis of the phenotype with which it deals and is in this way comparable with the field of Immunogenetics. But more important is the fact that the study of behavior has generally been singled out from the biological sciences, because we feel that it offers a certain number of problems of its own which are, at least in degree of complexity, different from other biological descriptions. This is particularly true for human behavior, and accounts for the fact that in all universities human behavior is treated as a separate discipline from the other Life Sciences, namely Psychology."

So genetics, when conjoined with phenotypic behavior, may be a special kind of discipline, facing problems that require unique conceptualization and methodologies, because behavior has fundamental properties that make it interesting to the psychologist. Let me delineate these properties in general and with special reference to social behavior.

To define behavior without tautology is difficult. Most textbook writers adroitly bypass the issue, and I propose to do the same, taking it as such a fundamental part of our experience that its properties need only to be delineated. What are these properties? Without intending them to be exclusive, I would list the three following: behavior is continuous; behavior is complex; behavior is fluid. Let us look at each one of these in turn.

THE NATURE OF BEHAVIOR

Behavior as Continuous

Behavior traits tend to be continuous rather than discrete. Of course, some syndromes, such as severe mental defects, appear to show all-or-none occurrence, but these are relatively rare. Such traits as intelligence, introversion, emotionality, and social behavior in its various aspects vary along a scale from high to low or from strong to weak. This feature of behavior immediately introduces the concepts of sampling and scaling as problems of major concern. We should note in passing that some of the psychiatric classifications that are commonly treated as categorical — schizophrenia, for example — at present make little sense genetically in these terms. That is to say, as Gregory[30] has shown, their incidence in the general population and in different kinship groups does not fit with the predictions of any standard genetic models, although such disease entities clearly seem to be heritable. It is possible that an analysis of them in terms of continuous dimensions might make a great deal more sense and open up problems of a more interesting character than those that have mainly concerned us in the past. The recent and excellent studies of Gottesman and Shields[29] document this point nicely. The fact of the matter is that the explanation of some phenotype in terms of Mendelian models, although perhaps an elegant and satisfying achievement in itself, does not really open up new vistas, nor does it hold much interest for the behavioral scientist. Thus, knowing that phenylketonuria is dependent on a single autosomal recessive — if this is, indeed, the case — does not really tell us what to do next. In point of fact, the ground work laid down by Asbjou Fölling that led to our understanding the biochemistry of this illness—also more complex than is commonly thought—antedated its genetic analysis by Jervis, and could presumably have gone ahead without the latter information.

In any case, most behavioral traits fit mainly polygenic models. And although analyzing the number of genes involved and the kinds of interactions that take place between them may represent a nice exercise in statistical technology, such an enterprise seems to me to have limited usefulness. Where, then, do we look? To answer this question, let us turn to the other two properties of behavior that I have listed.

Behavior as Complex

In 1957, Lee Cronbach, now of Stanford University, suggested that in psychology we have two major methodological orientations, one represented by psychometrics, the other by so-called experimental psychology.[13] The first of these has as its major concern the economical and precise description of behavior traits. Behavior is complex in the sense that any trait can be broken up into an almost unlimited number of components. The psychometric discipline sets itself the task of accomplishing such breaking up in the most logical and meaningful manner. Its primary statistic is the correlation coefficient with its explication in factor analysis, by the use of which, it is hoped, ultimate units of behavior will eventually emerge. Such workers as Eysenck, Cattell, and Vandenberg have attempted to examine the heritability and genetic basis of personality and intelligence. Their major idea is that traits derived from factor analytic procedures would "make more sense" genetically than complex traits measured by factorially impure tests. But while such a notion certainly is intuitively compelling, it is neither logically nor empirically supportable at present. There are many ways of factoring complex traits, and unless we take deliberate steps in our procedures to assure this, there is no reason why particular sets of factors should relate to genotype any more iomorphically than do ordinary tests.

Such steps can, of course, be taken. Examples are the criterion analysis of Eysenck,[19] the selection procedure used both by myself[61] and by Broadhurst,[5,6] the co-variation analysis of Vandenberg,[64] and the factor analytic procedures used by Loehlin.[45] All of these permit a more exact approach to parceling out genetic and environmental factors of personality and intelligence. Table I shows heritability coefficients calculated for pure factors as compared with composite tests. It is clear that they do not differ greatly. Table II illustrates the kinds of results that may be obtained when such a procedure is applied to the phenotypic correlations between morphological variables. It should be remarked that the parceling of phenotypic correlations into genetic and environmental covariance components has been a standard technique in agricultural genetics for some time (cf. Falconer[20]).

TABLE I

Comparison of heritability estimates for composite standard tests, primary factors, and second-order factors

Composite tests (Newman, et al., 1937)		*Primary factors* (Blewett, 1954)		*Second-order factors** (Blewett, 1954)	
Test	h^2	P.M.A. Factor	h^2	Factor	h^2
Stanford-Binet	.73	Verbal	.68	Composite 1	.339
Otis	.79	Space	.51	Composite 2	.594
Stanford Achievement	.61	Number	.07	Composite 3	.549
		Reason	.64		
		Fluency	.64		

* Three types of second-order factors are shown.

TABLE II

Examples of phenotypic, genetic, and environmental correlations

Traits	*Correlations*		
	r_P	$r_{G_A G_B}$	$r_{E_A E_B}$
Milk yield × butterfat yield in cattle	.93	.85	.96
Body length × back-fat thickness in pigs	–.24	–.47	–.01
Fleece weight × body weight in sheep	.36	–.11	1.05
Body weight × egg weight in poultry	.16	.50	–.05

* Environmental correlations also include nonadditive genetic components.

Although such sophisticated techniques are available, most investigators — merely by the nature of their calling — automatically search for better units of analysis and often find them simply by close observation. Indeed, this is ultimately what science is all about, and no amount of sophisticated statistics will replace the keenness of the observers' senses. The history of the ethological movement stands in testimony to this point.

Behavior as Fluid

The third property of behavior is its fluidity or changeability. It is this characteristic with which the other discipline of psychology — the so-called "experimental" — has been mainly concerned. Its standard paradigm is the imposition of some treatment on one group of subjects and the specification of the behavioral changes that ensue by reference to an untreated control group. The term "experimental" signifies, essentially, manipulation to produce change and, in this sense, has a meaning narrower in scope than that given to it by R. A. Fisher, who defined it simply as "planned experience."

Many kinds of behavioral change interest the experimental psychologist. One of the foremost, of course, is that which occurs as the result of learning and memory. Another is the cyclical change in circadian rhythms. Developmental change is yet another type of primary importance in psychology. In all of these, both genotype and environment exert an influence, separately and in interaction. Certainly there is no opposition between genotype and a disposition to change, because the latter is itself determined by genetic factors. As Professor Dobzhansky has stated: "It is, however, a fallacy to think that specific or ordinal traits do not vary or are not subject to genetic modification. Phenotypic plasticity does not preclude genetic variety. There may be variations in degree of plasticity; or some of the functions or roles which exist within a culture may be more congenial, and hence more easily learned than others."[17]

To my mind, the genetic basis of susceptibility (or congeniality) to environmental influence — that is, "buffering" — represents a problem area of great importance to behavior genetics, precisely because the dimension of change is so central a property of behavior. In the standard components of variance equation, $V_P = V_G + V_E + V_{GE}$, this is represented by the contribution of the third or interaction term — the degree to which the phenotypic expression of a given genotype changes from one environment to another. Notice that this term may give a rather different meaning to the notion of heritability. The latter is usually envisioned as a property of populations rather than of individual organisms or of individual traits. To use conventional methods in a search for absolute values that tell us "the extent to which a given trait is inherited" is to follow a will-o-the-wisp. But by using given genotypes tested over a wide range of environments, we could, theoretically, expect to end up with statements about the heritability of a given trait in such genotypes. For example, we might conclude that a trait such as aggression or intelligence in genotype A is "more genetically fixed" or "more inherited" than in genotype B and that, as a consequence, if we wish to manipulate these characters, we may have to take more drastic steps in the one case than in the other. Certainly, the eugenics of today must be more concerned with the manipulation of phenotypes by instituting environmental changes than by dictating breeding patterns in the population. Yet this can be done effectively only if more is known about the genotype-environment interaction, the extent to which different genotypes are affected by different environments, how susceptible each is at different periods of development, and the extent to which an altered phenotype may spontaneously drift back to the path projected by its genotype — what Waddington[67] has called its "creode."

These, then, are the kinds of problems with which behavior genetics should be concerned, and I will attempt to highlight their relevance more clearly by reference to social behavior. Let us first examine the meaning of this datum.

SOCIAL BEHAVIOR

Classification

I have already stated that the term social behavior is complex. Indeed, anyone who surveys the literature purportedly dealing with the subject is likely to find it a catch-all category containing every conceivable kind of animal behavior that does in fact, or could in theory, affect another animal. As a result, it usually takes in all the so-called emotions and drives such as aggression, sexuality, and maternal behavior; characteristics such as leadership, dominance, and territoriality; group attributes such as size and density, division of labor or caste structure; sometimes the relatively simple taxes and kineses; and, of course, the fixed-action patterns studied by the ethologists. Thus, when we attempt to deal with the topic of genetics and social behavior, we are obviously undertaking a great deal.

Because of this diversity of its subject matter, workers in the area have evolved a number of different classification schemes. One of these, by Harlow,[34] deals specifically with what he calls affectional systems, which are divided into five categories according to the age and sex of the animals involved in the relationship. Tinbergen[63] has divided social behavior according to type of behavior involved—mating, care of the young, family and adult group behavior, and fighting behavior. Scott's[53] classification is a combination of both. He lists the following types: contactual, ingestive, eliminative, sexual, epimeletic or care-giving, et-epimeletic or care-soliciting, agonistic or conflict-associative (passive and active), allelomimetic or imitative, and investigative. Notice that not all of these are exclusively social. Investigative behavior, for example, may involve merely an organism-object rather than an organism-organism relation. Harlow's categories, on the other hand, *are* primarily social, although they leave open the problem of designating particular types of behavior.

Clearly, it will be impossible to cover all possible aspects of social behavior that have been studied, even as narrowed down by these various classification systems. Instead, I will try to pick out what I consider the fundamental components of social behavior and deal with some examples.

The Foundations of Social Behavior

Looking over the whole spectrum of animal societies that evolution has produced, we can hardly doubt that genotype must be at the bottom of much social behavior. In some cases, we can broadly trace phylogenetic development within a particular group—for example, the transition from solitary to colonial nesting in the four species of the cuckoo subfamily Crotophaginae has been well described by Davis.[15] *C. guira,* the most primitive anatomically, is a solitary nester. At the intermediate level, *C. major* is a solitary nester, but they unite communally to defend their nesting sites. Finally, *C. ani* and *C. sulcirostris* are communal nesters and defend territory communally. Much the same kind of development applies to bees, in which there appears to be a development from primitive, solitary forms, such as the poppy bee, to those like the various species of Apidae and Meliponidae, which show complex and elaborated forms of social behavior. Again, consider the differences in group behavior between the lowest members of the primate order, such as the lemurs and the tarsiers, and that of the advanced species, such as chimpanzees, baboons, and gorillas, as studied by DeVore, Washburn, Nissen, Goodall, Schaller, and others (cf. DeVore[16]). Here, again, there has been an evolutionary growth toward increased complexity in sociability, group communication, and cooperation.

The central problems we must face in trying to handle these vast trends conceptually are essentially ones to which I have already referred—the location and accurate description of those units of social behavior on which selection must act, and the manner in which genes and environment cooperate to permit and guide such action. In the end, although from the standpoint of population genetics it may be useful to deal with the group as the unit of study, we must return to the individual if we are to trace the paths between genotype and social behavior. The latter may be at least partially accounted for in terms of individual personality and temperament traits, the acuteness of sensory input, and the precision of motor output patterns of each of the two or more organisms involved in a social encounter. Note that consideration of the individual by itself is relevant but not sufficient. The social psychology of lower animals, like that of human beings, must be concerned with organism-organism relations, not merely organism-object relations. To understand the social behavior of a monkey, for example, we must be interested in its temperament as evinced in the presence of a fellow or even of a member of another species. We need not be so much concerned with that temperament in relation to some inanimate, nonresponsive part of his environment. This point has been strongly emphasized, especially by Fritz Heider[37] and Solomon Asch,[2] both of whom have felt that, at least in human social psychology, the one level of discourse is not reducible to the other.

Two sets of traits — affection and aggression — seem basic to any dyadic (two-part) relation that relates to the temperament of the individual. These terms are generally descriptive of all orientations that tend to cement together or to break up the social ties between individuals. For this reason, many thinkers have ascribed to them an epic and almost mystical quality. For example, in one of Sigmund Freud's last major works, *Civilization and its Discontents,* he wrote:[24] "In all that follows, I take up the standpoint that the tendency to aggression is an innate, independent, instinctual disposition in man, and I come back now to the statement that it constitutes the most powerful obstacle to culture. . . . The instinct of aggression is the derivative and main representative of the death instinct we have found alongside of Eros, sharing his rule over the earth. And now it seems to me, the meaning of the evolution of culture is no longer a riddle to us. It must present to us the struggle between Eros and Death, between the instincts of life and the instincts of destruction as it works itself out in the human species."

Freud's sepulchral message may sound remote from the detached rhetoric of experimental science. Yet it may also serve to emphasize dramatically the importance of these two basic postures of social beings — love and hate. They are, in fact, amenable to experimental study, some of the most interesting aspects of which concern their genetic make-up and their plasticity to environmental influence. In presenting some of the available data, I will deal first with affiliative tendencies.

Affiliation

Although a great deal of attention has been paid to sex and reproductive behavior by biologists and psychologists, it is curious that until relatively recently very little has been devoted to the more basic behavioral category of love or affection that must underlie these. I say "more basic" because it is clearly impossible for reproductive activities to run their usual course without some affiliative behavior occurring first. Some indirect indications that the two are separate and distinct are given in the results of recent work on dogs undertaken by Beach and his students at Berkeley.[4]

Apparently unlike females of many other animal species, the female dog cannot easily be classified behaviorally as either receptive or nonreceptive. At the height of estrus, she may mate readily with one male and completely reject another. Furthermore, some males are greatly sought after, others little. The response of males to rebuff also varies; some are patient and persistent, others are easily discouraged.

By careful observation, Beach was able to work out what he labeled a 5-P scale for females, the categories including platonic, provocative, permissive, preventative, and punitive. These types of behavior were recorded for females in response to males in general (yielding what might be called her general affiliative posture) and in response to individual males (yielding her particular social interactive postures). It developed that females differed greatly in their over-all acceptance of males and, in addition, males varied greatly in their over-all acceptability or popularity. I wish to emphasize that the latter was relatively independent of actual sexual competence. Thus, as Beach has remarked,[4] "in the canine world, popularity may be an asset, but it is no guarantee of sexual success." No doubt the same conclusion may apply to other species, including man. At least in the dog, affiliativeness and sexual behavior appear to be distinct, although the second is dependent on the first.

Let us now look more closely at affiliation and its ontogenesis. As Harlow has pointed out,[32] John B. Watson was one of the first academic psychologists to give any real emphasis to the emotion of love conceptualized in a sense broader than mere reproductive activity. But perhaps because of the austerity of Watson's general philosophy, scant attention was paid to this basic emotion, which he believed to be innate in the human infant, together with fear and hunger.

The program initiated by Harlow and his colleagues at Wisconsin represents, to my mind, a major step toward understanding the nature of social behavior in its most basic biological aspects. I have referred closely to his classification system, which is based essentially on the interactions between animals divided according to age and sex. The actual results of his work are now well known. They show that infant rhesus monkeys have a compelling need to affiliate with others of their age group and especially with their mothers. It can hardly be doubted that this desire for what Harlow has called "contact comfort" is rooted in the biological make-up of the organism. Even with an abusive or indifferent mother supplying almost continuous negative reinforcement, infants struggle to find ways of fulfilling this need. Powerful as it is, however, it requires environmental support. Out of the primitive reciprocity that normally occurs between mother and infant emerge the adult forms of social behavior or affectional systems — for example, heterosexual and maternal. Deprivation of contact comfort in early life produces an atrophy of these systems — poor mates, bad mothers, and indifferent companions.

The notion that early affiliative activity is fundamental to many other sectors of social behavior and that its ontogeny is epigenetic (dependent on an environment that permits expression of the genotype underlying this character) has been well-documented in studies of a variety of species. Many of these have been usefully summarized by Rosenblatt in his chapter in *Sex and Behavior,* edited by Beach.[50] Cats, monkeys, guinea pigs, and possibly rats all seem to require some kind of social interactional experience early in life, if adequate sexual performance is to develop. As Rosenblatt says: "As a social bond, sexual behavior grows out of affective relations between the animals, and is rooted in a general background of social responses developed earlier in life."

The conclusion drawn by Rosenblatt also applies to human beings. We have known for some time that social deprivation in early life — through orphanage or foster-home rearing, for example — produces aberrant social behavior and personality difficulties. This has been well-documented by the studies of Bowlby, Spitz, Anna Freud, Goldfarb and others (cf. Thompson[62]). Now we are beginning to obtain more specific information regarding the significance of childhood social interactions as related to adult sexual behavior. Sears,[58] in studies dealing with the acquisition of gender role in children, has been able to identify a number of relevant specific variables of early experience. These include: the father's anxiety about sex; the mother's punitiveness and nonpermissiveness about aggression; physical punishment and ridicule; heavy demands for table manners; and severe weaning and toilet training. Granting that sexuality and general affiliative tendencies are closely interrelated, and that perhaps they lie at the center of much social behavior, we may still ask about their dependence on genotype. It is difficult to answer in precise terms. Certainly the evidence we have indicates that they are part of the biological make-up of most organisms in the sense that they appear without the need for special training, although their emergence may require exposure to a certain kind of environment. It is noteworthy that many animals establish strong affiliative bonds even when they are actively punished for doing so. Fisher[21] has shown that fox terriers which had been severely punished for approaching him would immediately revert to this behavior as soon as punishment stopped. The same appears to hold true in the case of chicks,[38] in young monkeys,[33] and particularly in children. Hebb[36] has made a strong case for the notion that the more complex the brain, the more sophisticated the social behavior, and that in higher species such as dogs, chimpanzees, porpoises, and man, such dimensions of affiliativeness as sympathy, empathy, and altruism begin to emerge. Empathy has even been attributed to the rat. Be this as it may, much social behavior must be referable to the basic make-up of organisms, including, of course, the genotype.

Apart from its universality, this kind of relation might also be expected to show some variability of expression within a species according to the variability of genotypes across individuals, strains, or breeds. Again there is a good deal of evidence to indicate that such variability does exist. It has been documented for dogs by Scott and Fuller,[57] for primates by DeVore, Goodall, Hall, Schaller, and others, and for mice, rats, guinea pigs, and other species by a variety of workers. Thus cocker spaniels and African basenjis, for example, differ strikingly in respect to such variables as incidence and development of tail-wagging, attraction to and following of a handler, retrieving, and emotional reactivity. At least some of these show in breed-cross patterns that are explicable by standard Mendelian models.

In human beings, the same seems to apply. Work by a number of investigators, including especially Vandenberg,[65] Gottesman,[29] and Freedman,[23] indicates heritable variation in respect to what looks like a basic dimension of sociability. We will return to this later.

Aggression

Although inter-individual aggressiveness is construed by many, including Freud, as a trait opposite to affiliation, inasmuch as it tends to produce group dispersion rather than cohesion, it should not be considered as solely disruptive. In fact, it seems to serve a useful function from the standpoint of the whole group. This has been well-documented by Professor Wynne-Edwards[69] in his recent book, *Animal Dispersion*. The various forms of aggressive behavior, such as territorial defense, predation, and dominance hierarchies, can effectively regulate population density and promote an optimal relation between the group and available environmental resources. Viewed in this way, aggressiveness is not the black, destructive force connoted by Freud's death instinct, but rather is as much an integral and positive aspect in social behavior as is affiliation. As Wynne-Edwards said: "One of the characteristics of social relationships is their antithetic combination of cohesion and mutual rivalry."

For this reason, it is not surprising to find aggressive and affiliative tendencies closely interwoven in many behavioral acts at the level of the individual. Mutual grooming in mammals and mutual preening or allopreening in birds are good examples. When two mature mice come together, they usually engage in nudging and sniffing behavior. This, in turn, can often lead directly to fighting. On the other hand, if one of the members of the pair is a female in estrus, courtship and mating behavior will probably ensue.[26] C. J. O. Harrison's recently published study on allopreening in 41 avian families illustrates the same point.[35] The behavior consists in a kind of ritualized "mouthing" or "nibbling" applied by one bird to the plumage of another, particularly that around the crown, nape, and throat, and the feathers near to the eyes. It is often preceded by so-called preening invitation postures on the part of the "preenee." Harrison suggests that allopreening may be a "sublimated" or "inhibited" form of aggressive behavior. It may alternate with or lead directly into overt attack, depending on various factors, such as the dominance relation of the pair involved, the species to which the birds belong, and fortuitous accidents during the actual process of preening.

Aggressive behavior in general has an inherited basis, as is indicated by the great variations shown among species. This has been documented by many workers, including especially Konrad Lorenz,[46] J. P. Scott,[54] and K. Lagerspetz.[44] The same holds true among strains or breeds within a species. Krushinskii[43] has traced through pedigree the transmission in dogs of one form of aggressiveness, which he calls active defense reaction, or the "watch reflex." This is inherited independently of the *passive* defense reaction, although the two occasionally combine to produce an "aggressive-cowardly" animal that alternates aggressive approach with strong avoidance.

Similarly, differences in latency and vigor of aggressive attack in mice have been shown repeatedly by many investigators, including Scott,[52] Scott and Fredericson,[56] Fredericson, et al.,[22] King,[40] and others. Lagerspetz[44] has recently demonstrated that aggressiveness is responsive to artificial selection. Starting with a base population of albino mice, this worker bred an aggressive and a nonaggressive line in seven generations. Significant differences appeared as early as the second generation. Expression of the trait was found to be strongly dependent on environmental factors. Victories in encounters markedly raised the aggressiveness of the high-aggressive mice, although, interestingly enough, this did not hold true for nonaggressive animals.

A trait closely tied in with aggression, or perhaps one aspect of it, is dominance. Much work suggests it also is heritable. Reliable strains and individual differences exist in the characteristic and it is also responsive to artificial selection.[12] Again, environmental experience can strongly influence its expression. One notable attempt to explore the dynamics of dominance has been made by McBride[48] of Queensland University, using chickens. From a tower he took photographs of a flock of chickens foraging in an enclosed pen. Individual birds were identified by numbers on their backs. Plots of the positions they took over time and the directions in which they were facing in relation to each other showed that the animals tended to avoid face-to-face situations when spaced at a certain distance (around 16 to 30 inches). At greater distances they would face each other quite readily but without interaction, and at distances of less than 16 inches they would turn to face each other in offensive or defensive positions. McBride suggests that a kind of force field emanates from any animal, this having fairly precise, specifiable intensity and vector characteristics. The closer the distances, the more head-on the confrontation and the greater the intensity of the field. That intensity is also stronger the more dominant the animal. Submissive chickens tend to keep to the side of or behind more dominant birds. Evidently what Sartre called "the look" in human beings has equal significance in the avian world.

Little is known about the genetic basis of these traits of dominance and aggression in humans. The perennial difficulty of identifying and breaking up the phenotype is not too successfully handled by the various tests available. However, let us look briefly at attempts that have been made. Crook[14] found some time ago with the Bernreuter Test that the dominance scale showed low intrafamily correlation. Carter,[7] using twins, found for the same scale an MZ intercorrelation of 0.71 compared to one of only 0.34 for dizygotics of like sex and 0.18 for dizygotics of unlike sex. This positive result has been substantiated in the more recent work of Gottesman.[27] Using the Cattell High School Personality Questionnaire (HSPQ) he showed that the scale measuring Factor E, submissiveness versus dominance, had a heritability of zero in females and 74 per cent in males. It is not known whether this interesting result represents a real genetic sex difference or, as Gottesman suggests, a difference dependent on the imposition on girls of an environment suppressive of the trait. In females, the MZ correlation of this trait was –0.06, but the DZ correlation was 0.53. About the opposite held for males. It is difficult to know precisely what this means, although we can assume in general terms that it represents the effects of complex genotype-environment interactions. Obviously, this is an area for further exploration.

Let us now consider the manner in which social behavior, as represented by affiliation and aggression, evolves ontogenetically from the interaction of genes and environmental experience.

GENOTYPE, DEVELOPMENT, AND ENVIRONMENT

It is clear that gene expression is monitored by developmental variables. Many components of the final phenotype are absent initially and start to emerge only gradually as the organism gets older. At the cellular level, this emergence perhaps corresponds with so-called chromosome "puffing," which in turn is dependent on operator and regulator genes. Whatever the cause, there is an intimate relation between genetic expression and development. The general relation is indicated by considerable data. For example, a character such as weight in human beings shows a very low hereditary correlation at birth—about 18 per cent. However, the same trait in the adult manifests a hereditary relationship of around 50 per cent or more. The work of Vandenberg and Falkner[66] on increment in height points to the same conclusion. Another example is afforded by Scott's work on the development of barking in five dog breeds.[55] At the age of 11 weeks, the trait shows high hereditary correlations, and two of the breeds differ by a factor of three. At other ages, however, the factor is far smaller. This is not, of course, any guarantee that heritability estimates at these ages are different, but it does indicate that the trait of barking in the dog, measured at different developmental stages, may mean quite different things and may represent the expression of different components of the genotype.

It is also true that many organisms show differential susceptibility to environmental influence at different ages. In general, earlier experiences seem to have a disproportionately greater importance but, even within the early stages of development, limited periods may occur before or after which some function may be resistant to influence. Perhaps the most celebrated example of such "critical" or "sensitive" periods is that postulated with imprinting in various avian species—usually to a member of its own species, sometimes to other animals, objects, or humans, but depending on the kind of exposure to which they have been subjected during the sensitive period.[3] We can only guess whether the approach and following behavior, elicited in a young chick by the presence of a mother or a suitable surrogate, is in any way comparable to the contact-seeking behavior of young monkeys. But certainly it can be regarded as a rudimentary form of social or affiliative behavior. Not only does it contain some minimal sexual components;[1,31] according to some of the evidence, it also seems to influence the choice of mates the animal will make later.

Two points relevant to this discussion may be made. First, it is undoubtedly true that the initiation and closure of a sensitive period is dependent on genetic make-up, inasmuch as this determines the rate of differentiation of input and output capacities that permit recognition of and following some object in the environment.

Obviously, there is wide variation among species in developmental rates. Contrast, for example, such precocial species as some of the gallinaceous birds with such mammalian groups as rodents and primates. Man shows perhaps the longest developmental period in relation to total life span — characters Spuhler has suggested represent a selected response to a cultural environment.[60] Even within a species there are large differences. This has been nicely documented by John A. King[41,42] at Michigan State University for some subspecies of the deermouse *Peromyscus maniculatus. P.m. bairdii* and *P.m. gracilis,* grassland and forest-dwelling subspecies respectively, show differences in developmental rate for many morphological and functional characteristics, including eye lens weight, brain weight, facial and cranial skull size, water-escape learning, and response to electric shock. King suggests[41] that "differences in the types and frequency of responses given by each subspecies during their development apparently provide the basis for differential reinforcement from environmental stimuli. . . . Environmental stimuli may then channel the development of maturing behavioral patterns in the direction most suitable for adaptation to a particular habitat. In nature, the innate responses of *bairdii* may be reinforced more in its native grassland habitat than in other types of habitat, while the forest habitat of *gracilis* would reinforce the development of its innate responses. Ecologic separation of these two subspecies could then depend upon the probability with which the environment reinforces the early behavior of each subspecies." This interesting idea has been put forward more recently by B. F.

Skinner, who speaks of selection for ontogenic contingencies leading particularly to a greater speed of conditioning and the capacity to maintain a larger repertoire (of responses) without confusion.[59] Thus we have a rather complex pathway from genotype to maturational variables, which, in turn, affect the extent and kind of influence environment can exert.

The second point arising from the discussion of the affiliative behavior manifested in imprinting is that the degree to which a particular animal will imprint on *different objects* also appears to be genetically determined. Many of the gallinaceous breeds, such as various chickens, can usually be imprinted on surrogates a good deal different from their real mothers. On the other hand, some of the parasitic birds, such as cuckoos, apparently do not imprint on their foster mother, although they are consistently exposed to her during their early development. In respect to the object with which affiliation comes to be linked, then, we find that different genotypes are differentially buffered. Some are buffered against an inappropriate mating choice, others against an inappropriate territory choice.

Both of the above points indicate that susceptibility to influence by environment — including especially the formation of an affiliative link with some part of it — is ultimately dependent on genetic make-up. Furthermore, it seems likely that if the appropriate environment is not provided at the right time, normal social linkages may not be made.

Here, as I have already indicated, is a rich area for investigation with human beings — one that so far has hardly been touched. Paul Meehl, in his presidential address to the 70th Annual Convention of the American Psychological Association in 1962, pointed research on schizophrenia in this direction.[47] One of the major behavioral features of this illness is a striking deficit in the sphere of social behavior. This is manifested in an interpersonal aversiveness, a fear and distrust of people, and expectation of rejection. Meehl suggests that these and the other symptoms of schizophrenia will always appear in what he calls the schizotaxic person, who carries a genotype for some basic neural integrative defect, provided there is exposure to an unfavorable interpersonal regime and provided, also, that a low capacity for resistance to stress has been inherited. If these conditions are not all fulfilled, the disease will not be present, although the basic personality organization on which it is built may show up in a well-compensated form. This model of the genetics of psychosis is not too different from that put forward by Kallmann[39] a number of years ago, because both postulate the operation of a basic genetic factor, a genetically determined stress-resistance factor, and environmental factors.

At this point, I would like to refer to the work of Raymond Cattell.[9,10] Although not directly concerned with social behavior, the general method of MAVA (multiple abstract variance analysis) developed and applied by him and his students to normal personality characteristics does seem to represent a suitable way of dissecting out the complex genotype-environment interaction of the kind we have just discussed. Essentially, it is an extension of the usual quantitative methods of dividing observed variances into their component parts. For example, the variance between separated identical twins is expressed in terms of a between-family environmental variance plus a within-family environmental variance plus the interaction between these two. The same kind of partitioning is applied to siblings and fraternal twins reared together or reared apart, half-siblings reared together and apart, and so on. Estimates for unknown variances are made by solving a set of simultaneous equations.

An application made by Cattell, Stice and Kristy[11] to personality and intelligence has yielded some interesting and relevant results. First, most of the traits studied showed predominantly environmental determination both within and between families. The major exception was general intelligence — a conclusion in line with most (but not all) of the information we have (cf. Erlenmeyer-Kimling and Jarvik[18]).

Second, variations resulting from within-family environment were less than those caused by environmental differences between families. As the authors put it: "These results favor a psychologist's rather than a sociologist's view of the importance of environment."

Third, there appeared a marked tendency for hereditary deviations to correlate negatively with environmental deviations. This was less marked within families than between families. The result seems to indicate that society in general exerts pressures on individuals to conform, thus reducing phenotypic variation that would ensue if all genotypes in the population were allowed full expression; and that the family social unit is more permissive in this respect than is the whole social group.

The manner in which the family environment can potentiate or attenuate genetic differences can be illustrated by reference to several studies. In 1939, Portenier[49] compared 12 twin pairs with siblings on the various scales of the Bernreuter Personality Inventory. In contrast to the results of an earlier study by Carter,[7] his results for four out of the five scales showed much higher correlations for siblings than for twins. It is true that only two out of his 12 pairs were monozygotic. Consequently, Portenier's study has rather little to do with the heritability of behavioral traits. It does, however, make an interesting commentary on the manner in which family environment operates in fraternal twins as opposed to siblings of different ages. Presumably, when faced with two children who are supposed to be alike because they are twins, some parents feel they must take deliberate steps to make them different; the result is that they show less similarity than that which would be expected from their genotypes. This interesting finding has recently been confirmed by Wilde,[68] who reported that dizygotic twins reared apart in different homes showed more similarity in four out of five trait dimensions tested than did pairs reared together. Oddly enough, he found the opposite held true for monozygotics, which makes any single mode of explanation difficult. At present, Wilde is working at Queen's University on the problem of interpersonal perception and influence in twins, using the Asch-Crutchfield conformity procedure. To date, his findings indicate that members of twin pairs do not show more conformity to each other's overt behavior than do nontwins. Whatever its final outcome, such work represents a good example of how social psychology and behavior genetics can be conjoined.

So far, the developmental dimension has not figured in most of the work done on the genetic basis of human social behavior, but obviously it is a variable that should be considered. The complex nature of the gene-environment interaction in personality traits and social orientation are undoubtedly sorted out relatively early in life.

Such a view has been put forward recently by Gottesman.[28] On several tests administered to twin groups he has shown high and significant heritabilities for the broad traits "social introversion" and "person orientation," as measured by the California Personality Inventory and the Minnesota Multiphasic Personality Inventory. He suggests that these represent a basic posture of sociability that emerges very early in life in the "cuddling" or "contact comfort" behavior of infants, and refers to the interesting work of Schaffer and Emerson,[51] who found that infants may be reliably designated as "cuddlers," "noncuddlers," or intermediates. A propensity in one of these directions is apparently independent of maternal treatment. This was documented recently by the twin studies of Freedman,[23] although maternal treatment may so interact with the behavior of the infant as to produce a healthy or a pathological relationship. It is possible that the interpersonal aversiveness indicated by Meehl as being so salient in the schizophrenic may have its origin here. Again we find the interaction among genotype, environment, and development to be of central importance.

The same general conclusions also appear to apply in aggressiveness. An aggressive breed of dog like the wire-haired fox terrier does not show the behavior to which it is genetically disposed if it is raised in conditions of isolation.[21] In fact, as Scott and Fuller point out,[57] all breed differences tend to disappear under conditions of isolation from humans. Krushinskii[43] has shown that the passive defense reaction (fear of strange persons and places), not carried to a great extent by Airedales and German shepherds when they are reared in conditions of freedom, appears much more strongly when the animals are raised in isolation. This applied more to the shepherds than to the Airedales, suggesting that the latter's natural aggressiveness is apparently less susceptible to environmental manipulation.

The interesting work done by Ginsburg and his colleagues on the socialization of wolves is relevant here. They suggest that, in spite of the similarity of behavioral systems in the dog and wolf,[57] the latter can be tamed to human handlers during a longer period of development than can dogs. Thus, adult wolves can apparently be socialized to some degree, provided that the right procedures are used. These procedures are rather complex, but tend to involve, according to Ginsburg, autonomic habituation to all components of the situation that have specific meaning for the wolf. This attenuates the fear response that otherwise may lead directly to attack behavior. If I interpret Ginsburg's results correctly, it is curious that after such habituation there may appear dominance-aggression patterns that are different from the fear-aggression sequences shown by the completely unsocialized animal. We may well ask whether there are really two distinct kinds of aggression — the one displayed in a context of strangeness and fear, the other in the context of familiarity. We may further wonder how manipulable each is, and if they show genetic interdependence.

CONCLUSION

In conclusion, I would like to re-emphasize the importance of behavioral plasticity and its relation to genotype. Especially in early life, the organism is capable of being altered in various ways, not only in its general temperament — if manipulation is carried out early enough — but also in its social posture towards members of its own and other species. Still later in development, molding of actual behavioral patterns is possible. Together, these three dimensions — basic temperament, affective relations with the world, and instrumental habit patterns — constitute personality. The latter is both situational and transsituational, specific and nonspecific. Whether any given genotype is buffered as a whole or differentially in respect to these dimensions of personality constitutes a question of considerable interest. Fuller's studies of early experience in dogs (cf. Fuller and Clark[25]), particularly the so-called postisolation syndrome, hits at some parts of this general problem. At Queen's, some of my colleagues and I are also engaged in research with both human beings and animals to uncover basic information about buffering and its genetic basis. To my mind, this constitutes, together with the analysis of rational units of behavior, the area of major concern for behavior genetics in general and for the genetic study of social behavior in particular.

Sociocultural and Biological Inheritance in Man

J. N. SPUHLER

In 1935, L. J. Henderson wrote a physiologist's interpretation of Pareto's *General Sociology.* In his book, he divided all knowledge into two classes: the subjects of the first class (including history, literature, economics, sociology, politics, etc.) involved the study of human social interaction, while none of the subjects of the second class (including mathematics, physics, biology, etc.) were so involved.

Henderson pointed to a remarkable difference between the attitudes of workers in the two classes. When adepts of biology or other subjects in the second, nonsocial class disagree ". . . it is a peculiarity of their behavior that they do so most often at the frontiers of knowledge, where growth is taking place; and in the long run a debated question is ordinarily settled by observation, experiment, or some other method they all accept."[8] Although this behavioral activity is true in some subjects concerned with the study of human social interaction, according to Henderson it is not characteristically true in many of the social sciences and humanities.

Our topic, "Genetics and the Study of Social Interaction," cuts across Henderson's two classes. So, by the way, does anthropology. Thus, as an anthropologist interested in human biology, I might be expected both to agree and to disagree with Professor Thompson. Let me first dispose of the disagreements, which are relatively minor.

My main points might be set forth by two slogans: (1) "All testable and verifiable knowledge is valuable," and (2) "De-emphasize Durkheim," or perhaps better, "Integrate Durkheim with behavioral science." It would be wrong to infer that Emile Durkheim himself was "against" biology or psychology (see, for example, his statement

---

J. N. SPUHLER Department of Anthropology, University of Michigan. Present address: Department of Anthropology, University of New Mexico, Albuquerque, New Mexico

to the contrary in the English translation of *The Rules of Sociological Method*, p. 111[3]). Rather, as Bouglé[1] capsulized it: "He believed that a psychology of a special type must be established which will take account of the actions and reactions which individual consciousnesses exercise on each other and of the syntheses which are produced when the consciousnesses are united. Through these syntheses he explained religious beliefs, beliefs which are imperative because collective, the peculiar authority of value judgments, the tendencies of educational systems and the formation not only of moral consciousness but of the categories of reason."

I disagree with Thompson about the "interest" or "usefulness" of knowledge on the formal genetics of behavioral traits. The knowledge that phenylketonuria (PKU) *is* dependent on a gene-controlled enzyme deficiency is of much theoretical and practical importance: it *has* told us a great deal about "what to do next" if we want to prevent the PKU disorder and at the same time to understand the factors responsible for this disorder. I doubt very much that an adequate understanding of the biochemistry of this serious illness could have arrived at the present level without genetic information. But even if Thompson is right about the history of PKU, it is clear that the identification of major genes and of polygenes with known primary gene action is almost certain to be an important step in the development of behavior genetics.

The recent association of specific chromosomal abnormalities with specific behavioral syndromes is of great theoretical and clinical significance in transmission genetics. The demonstration that chromosomal nondisjunction, as well as translocation, results in clinical mongolism or Down's syndrome brought more understanding to the etiology of a serious, relatively widespread, congenital behavioral tragedy that had long defied detailed genetical analysis. Tens of other chromosomal aberrations associated with behavioral differences are now known and hundreds will become known. That seemingly some large-scale chromosomal disturbances are not associated with detectable behavioral consequences in some individuals is a problem of first interest for a deeper understanding of behavior.

If we knew to a fair approximation the number of loci and the kinds of gene action that, interacting in specific environments, give rise to some standard intelligence test scores, we would know much more than we do now about the dynamics of variation and the limits of natural selection. We assume that all testable knowledge relating to behavior genetical theory is interesting and potentially useful. To see if there is any immediate and local interest in estimates of the number of "loci" for polygenic human behavioral traits, let me give you two very rough examples:

Consider an American breeding population with a mean IQ of 100 and a standard deviation of 12. Assume the normal range of IQ is polygenically determined and that it runs from 70 to 130. Assume that, below and above these limits, variation in IQ scores is determined by rare major genes. Now, if persons with an IQ of 70 are homozygous for n loci, their frequency would be $(q^2)^n$, where q is the gene frequency of the minus alleles. Given a normal distribution, the expected frequency of persons with an IQ of 70 (a deviation of 3.5σ below the mean) is about 10^{-4}. Thus, if q at all loci is $\frac{1}{2}$, $(\frac{1}{4})^n = 10^{-4}$, and the number of loci is between six and seven. In this connection, it is of interest to recall Dr. Vandenberg's statement (this volume) that another line of psychometric investigation suggests at least six loci are concerned in intellectual behavior.

A better, but still rough, calculation of n — the minimum number of loci — for performance on intelligence tests may be obtained using a method developed by Wright,[15] who showed:

$$n = R^2/8\sigma_A{}^2$$

where R is the total range (ideally established by selection experiments) and $\sigma_A{}^2$ is the additive genetic variance (estimated from regression or covariance analysis of certain relatives, such as parent-child or sibling-sibling). If we take 60 IQ points as the range and assume[2] that the additive variance is about 48 per cent of the phenotypical variance, then

$$n = 3600/(8 \times 69.12) \cong 6.5.$$

This is of interest, at least to me, because, even though the estimate is a minimum, it is lower than I would have guessed. If we correct for linkage, again using a method developed by Wright,[15] $n \cong 8.7$. On the assumption of a normal range of 80 IQ points and a sigma of

12, the uncorrected and corrected values of n are 11.6 and 22.4 loci.

The above estimates assume there is no dominance and that the differential effects of all pairs of alleles are the same. If complete dominance is assumed, the estimate is increased by 50 per cent. If unequal gene effects are assumed, the estimate can be increased indefinitely.

In some sense, most, if not all, of the many thousands of loci in the human genome are concerned with behavior. Because most chromosomal aberrations found in man have some influence on intelligence, and because translocations of relatively small parts of chromosomes are known to have profound effects, the number of gene loci affecting intelligence must be several times ten. Morton[11] has estimated that, at a minimum, 71 loci are concerned with low-grade mental defects in human populations.

Of course, the above estimates should not be taken too literally, but if they are of the right order (if 10 to 20 are correct, rather than 100 to 200, or 1,000 to 2,000) the prospects are much brighter than commonly supposed that we will be able to identify individual polygenes in man, as Thoday has done in *Drosophila* and Ginsburg and his associates are beginning to do for a behavioral trait in the laboratory mouse. So there is now the possibility that we may one day understand the biological basis of man's ability to symbolize — a fundamental unit in distinctly human behavior.

I fully agree with Thompson that the genetic basis of susceptibility to environmental influences — that is, genotype-environment interaction — is a problem of great importance to behavior genetics. If I understand him correctly (he does not work out his version of the problem in quantitative terms), I disagree with his proposal for giving still another meaning to the concept of "heritability." In principle, as Falconer[4] and others have shown, the problem of genotype-environment interaction (where genotype A may be superior to B in environment X but inferior in Y) can be solved — to the extent that the genotypes and environments can be isolated and controlled — by regarding differing performance in different environments as different characters. Under these conditions, the desired values — for example, the expected performance in an environment different from the one in which selection was experienced — may be estimated in terms of the heritability of the different characters and the genetic correlation between them. The notion of "individual heritability" further muddles a population concept whose name is already used in at least three different ways in biometrical behavior genetics. Besides (again, if I understand what Thompson means), the notions of "penetrance," "expressivity," and "specificity," introduced by Timofeeff-Ressovsky in 1927 provide familiar terms to cover "the heritability of a given trait in a given individual."

With these exceptions, I am in essential agreement with Thompson's viewpoint.

He emphasized that susceptibility to environmental influence is ultimately dependent upon genetic make-up. A general principle in genetics is that genes may control the way an organism reacts to its environment including, in the case of man, the cultural environment. Some of the recent work of David Hamburg[6] and Hamburg and Lunde[7] of Stanford University School of Medicine, among others, on the behavioral genetics of thyroid and adrenocortical hormones is a neat illustration of this point. The work brings together two sets of data:

1 Clinical. For a long time clinicians have known that of 100 people with similar ethnic, social, and economic backgrounds exposed to the "same" stress, about 10 would break down in ways requiring psychiatric help. For some years it has been popular — but not entirely convincing — to explain this 10 per cent in terms of some unfortunate early experience that caused predisposition to the psychosomatic trouble.

2 Physiological, biochemical, and genetical. We now know that the anterior lobe of the pituitary — the master hormone-producing organ — receives polypeptides specific for the production of the several hormones; these chemical messengers are transmitted through the portal vessels from the median eminence of the hypothalamus, which in turn receives messages from the higher cortical centers over the neuronal system.

Compensating mechanisms produced by stress are released by thyrotropic, adrenocorticotropic, and gonadotropic hormones. The blood level of the thyroid, adrenocortical, and gonadal hormones acts as a feedback control to the hypothalamus. Thus, what happens in the higher brain centers may affect hormone production, which, in turn, may affect behavior.

In recent years, biochemical geneticists have recognized some half-dozen mutant genes that control the production or use of thyroid hormones and about a dozen that control synthesis or use of adrenocortical hormones. These latter may cause metabolic blocks that result in defective hydroxylation at C-11 and at C-21, defective hydroxysteroid dehydrogenase, lipoid hyperplasia of the adrenals, defective glucuronic acid conjugation, and Addison's disease. The mutant genes at each of the several loci are usually recessive and in most populations have rather low but variable frequencies. The homozygous recessive condition is a serious handicap for individuals in environments that do not provide hormone therapy.

If we estimate the frequency of individuals who are heterozygous for any one of the several genes, we find this total number — summed over all loci involved in thyroid or adrenocortical hormone production — is about 10 per cent in our population. It is most suggestive that some considerable fraction of the 10 per cent who succumb to stress are heterozygous for a gene which, in the homozygous condition, leads to serious hormonal defect.

In a recent survey of the known mutant genes in man, McKusick[10] lists some 837 autosomal dominants, 531 autosomal recessives, and 119 x-chromosomal-linked genes in man. When he uses more rigid criteria for establishing the mode of inheritance, the estimates are 289 autosomal dominants, 237 autosomal recessives, and 68 x-linked genes. Probably the numbers represent overestimates, as most cases have not been tested adequately for allelism. Nonetheless, the numbers are impressive. Perhaps every mutant gene in man has some differential consequence for some behavior.

Let me summarize my first general point. Hormones are known to affect behavior, especially emotional components of behavior. We have seen that the process of thinking, events that go on in the cerebral cortex, events that may include the very fabric of cultural behavior, can affect hormone production or use. The reverse also holds. Cultures are not composed of neutral actors but of individuals who may differ in the inherited mechanisms underlying the emotional and motivational bases of behavior. There are differences both within and between populations in the frequencies of the genes controlling hormone production and use. Man's capacity to symbolize greatly amplifies the content and even the fundamental nature of his group behavior, but it does not make human social behavior completely autonomous with regard to genetical variations within and between populations.

My second slogan suggested an integration of the Durkheimian point of view in sociology and cultural anthropology with genetic biology to develop a more general behavioral science. Durkheim was concerned that sociology be a legitimate, independent science distinct from biology and psychology and deserving its separate name. Leslie White has the same concern for cultural anthropology; he has renamed one part of the science of culture "culturology." Both correctly assume that large areas of human group behavior can be investigated with good results in an exclusively extrasomatic context. Starting with and since Durkheim, much progress has resulted because scholars adopted this point of view. There still remains an enormous amount of important work to be done by sociologists and culturologists working in the extrasomatic realm without the slightest concern for psychology, genetics, or biology.

Man as a member of a society and a culture can "inherit" and transmit symbols through cognitive and verbal communications, and not solely by biological means. But it does not follow that *all* social science may ignore biology and psychology. Let me quote from a book published in 1966 by Talcott Parsons[12] in order to suggest that many sociologists and cultural anthropologists would consider most of the material mentioned by Thompson as simply irrelevant to the study of human social behavior: "Thus, the *organization* of [social] action systems as a whole is learned, but is based on a set of *generalized* organic facilities, the common availability of which is the most distinctive genetic heritage of human beings. The ways in which they are used—and are built into cultures, social systems, and personalities at the human action level—are independent of *any* genetic particularities of the particular organic stock." Parsons adds: "This is the view of the organic bases of human behavior which modern biological and social science has substituted for the 'instinct' theories that held sway during the early part of this century."

What Konrad Knopp[9] wrote regarding mathematics is also true of social science: "No science rests entirely within itself; each borrows the strength of its ultimate foundations from strata above or below it. . . . Every science must accept *something* as simply given, and on that it may proceed to build. The only question which has to be settled by a criticism of its foundations and logical structure is what shall be assumed as in this sense 'given'; or better, what minimum of initial assumptions will suffice, to serve as a basis for the subsequent development of all the rest."

The British anthropologists Lionel Tiger and Robin Fox,[14] — who believe the overlap between the range of their interests and their names is purely coincidental — point to the phylogenetic basis of such universal human traits as gregariousness, dominance-subordinance, male bonding behavior, smiling response, and greeting. They suggest that independent sociological or culturological explanations probably are not sufficient "to account for even such features of male organisations as group morale, secrecy, female exclusion, hierarchy formation, division of labour, initiations, etc. . . ."

Thompson also pointed out that the infant smile is a phylogenetically determined, species-specific behavior that is the equivalent of social releasers in other animals. The experiments of Spitz[13] demonstrate that the infantile smile is biological, innate, unlearned. Spitz found that smiling could be elicited in infants 2½ to 4 months of age by showing models of the human face; a dummy with the configuration of two eyes, a forehead, and a motion such as nodding or mouth movement is sufficient to release the smile. But it is also important to recognize, as Rosenthal has stated elsewhere in this volume, that there is an environmental component in infantile smiling.

Hamburg[5] said: "Social life is rooted in emotion. . . . Society is not composed of neutral actors but emotional beings — whether we speak of baboons, chimpanzees, or man, emotion lies at the core of the social process." Neurological investigations on nonhuman primates, and only slightly less convincing studies of man, demonstrate there is an innate, species-specific, central nervous system basis for emotional behavior; it is clear that such behavior is not solely the result of social conditioning of a completely plastic infant.

Social facts such as the variable infantile smiling response and the variable place of emotion in social interaction must have some part of their explanation in biology; still other social facts do not alone provide a satisfactory explanation. The biological basis of emotion is variable within the human species; it is not, contrary to the quotation from Talcott Parsons "independent of *any* genetic particularities of the particular organic stock." Durkheim and all social scientists who follow him are simply wrong on this point. Of course, this is not to deny the importance of conventional "ways of acting" that constrain human social behavior in the manner emphasized by Durkheimians. It is, however, to deny that each social fact may be explained fully only by other social facts.

In conclusion, let me emphasize that social facts at large cannot be explained by biology alone or by sociology alone. There is no individually or socially important human behavior independent of culture; there is no human behavior independent of genes. All complex human behavior is a vector outcome of variable human genotypes interacting in a variable nonhuman environment with variable social and cultural things and events. In some areas of human behavior, it is as misleading to assume that all men are identical in genotype and to refer to "the human being," as it is in some aspects of animal behavior to refer to "the rat," "the mouse," or "the monkey." If we are to have a general human behavioral science, we must put considerable effort into the study of connections between man's genetic capacities and his observed social-cultural behavior.

Genotype and Social Behavior

JOHN L. FULLER

First, I shall record agreement with Dr. Thompson's view that the primary *raison d'être* of behavioral genetics is its value to the behavioral sciences. Thus, its phenotypes ordinarily will be chosen with respect to their relevance to problems of behavior, not for convenience of genetic analysis. This may create complications for geneticists, but we must accept it as a fact of life.

I have some suggestions regarding the choice of behavioral phenotypes for genetic analysis, which I shall preface by an account of some recent experiments involving genotype-treatment interaction. These studies are part of a series dealing with the persistent effects of early experiential deprivation upon social, exploratory, and manipulative behavior.

Early deprivation plays a major role in current theories of psychological and social inadequacy. There is an extensive literature dealing with effects of early stimulation or of enrichment of the early environment upon later behavior.[1,5] By exchanging the conventional labels "experimental" and "control," one could reasonably view such experiments as studies of deprivation.

Hypotheses offered to explain postisolation deficits in behavior tend to be of two types. Critical-period theories postulate that the acquisition of social behavior is programed in step with biological maturation.[6] Lack of opportunity to acquire particular forms of behavior during early life produces deficits because they cannot be acquired as well once the sensitive period is past. A contrasting view, which I believe to be more descriptive of our experiments with dogs, emphasizes the stress induced in the experientially naive animal by the postemergence situation.[4]

JOHN L. FULLER The Jackson Laboratory, Bar Harbor, Maine

Deprivation Procedures

In our basic isolation procedure, puppies are removed from their mothers at 21 days of age when, for the first time, they can survive independently without special attention. They are placed in 75 x 60 cm. cages that permit feeding, watering, and removal of wastes without physical or visual contact with a human being. (Further details are given in Fuller and Clark.[4]) Upon this monotonous background, special treatments are superimposed.

Arena Test

The arena test is used for evaluating the effects of modifications of isolation or of postemergence conditions. The puppy is brought to the arena in a transport cage that fits closely into a gate of the arena. The transport cage door is opened and the puppy is free to emerge and interact with the stimuli provided. The test consists of 7½ minutes of observation of the subject's responses to a human, to manipulatable objects, and to another puppy of the same age. These responses are recorded as a series of five-letter words based on a "COde For Observational Description" (COFOD). Observers are instructed to sample the dog's behavior at regular intervals (typically every 6 seconds) and to record these in COFOD. Our primary data from each arena test consists, therefore, of a set of 72 "behavior snapshots" taken under standard conditions.

The first letter of each COFOD word denotes the stimulus to which the subject is attending. The second letter identifies the nature of the response. Location in the testing area is given by the third letter and activity level by the fourth. The fifth letter is reserved for miscellaneous indicators of emotional arousal. Thus the COFOD word COCLN is translated as: a dog is lying quietly in its transport cage facing toward the back of the cage. HMAJT is translated as: a dog is jumping up and down, wagging its tail, and pawing the person or garments of a person seated in the arena.

A useful feature of COFOD is a numerical transformation for letters two and four. Responses (letter 2) are graded from orientation (1) through approach (2), investigation (3), contact (4), and manipulation (5). Adding the numerical values of these letters provides a response index (RI) that is related to the intensity of responses directed toward specified stimuli. Similarly, numerical values of letter four increase from lying down (1) through sitting or standing (2), walking (3), running (4), and jumping (5). Their sum yields an activity index (AI).

GENOTYPE AND VULNERABILITY TO ISOLATION

Procedure

In this experiment, equal numbers of beagles and terriers were compared in the arena after three kinds of treatment administered during weeks 4 through 15. Sixteen animals (groups I and I′) were reared in solitary isolation. Eight were isolated in double-sized cages with a litter-mate companion (group C), and eight were pet-reared (group P). Under laboratory conditions, this meant that group P puppies were caged individually, as were the I and I′ puppies, but they were given the run of the laboratory twice each day while an experimenter serviced the colony. During this period they were treated like household pets. In the opinion of experienced observers, these animals were undistinguishable from home-reared puppies.

Beginning at 15 weeks of age, all subjects were tested in the arena four times per week for five weeks. The arena procedure deviated from our standard practice by having a second puppy continuously present in the arena during the test period. This decoy animal was restrained by a leash within an open transport cage. The test cage and decoy cage faced each other at a distance of about 3½ feet throughout the observations. The purpose of this procedure was to see whether the constant presence of a second animal would facilitate the development of social and manipulative behavior. All pair-isolates (group C) were tested with their cage companion. The solitary isolates (group I) were paired either with another isolate, or (group I′) with a pet-reared animal. All pet-reared subjects were paired with individual isolates.

Outcome

The complete results of the arena test will be published elsewhere. Here I shall concentrate on emergence from the transport cage and the activity and response indexes. A primary difference between isolated and pet-reared dogs is latency of emergence from the transport cage. Isolated dogs seem to encounter a nonphysical barrier at the cage opening; pet-reared puppies of both breeds emerge into the arena and remain there as soon as the door is opened. Isolated beagles remain in their cages longer than do terriers. In both breeds, companion isolates and solitary isolates with pet-reared decoys emerged sooner than isolates with isolate decoys. Once the barriers to emergence are overcome, most subjects rapidly acquire the social and manipulative responses characteristic of their breed and age group. Emergence, then, is essential for achieving a high score on the activity or the directed-response index.

On the activity index, beagles at every stage scored lower than the terriers. In fact, there was no overlap between the activity indexes of beagles and terriers within any of the four treatment groups. The relative performance of isolated and pet-reared subjects was, however, different for beagles and terriers. Beagle isolates were almost completely inactive during the first block of trials, and only gradually did they become more active. Isolate–isolate pairs, in particular, remained low in activity; in a large measure this was because they failed to emerge from the transport cage. By the end of the experiment, activities of isolate and pet-reared groups were about the same, but over-all isolation reduced the activity of beagles. The terrier picture was very different. In the first week the isolated terriers walked, circled, and ran more than they lay down or stood quietly. From the third week on, terriers with an isolation history were more active than pet-reared terriers. Hypokinesis or hyperkinesis are both possible outcomes of rearing in a restricted environment. Genotype and amount of post-emergence experience play major roles in determining which will be manifest.

In contrast with activity, the response scores of pet-reared beagles and terriers did not differ significantly at any stage. Beagles ran and bounced less, but they spent as large a proportion of time investigating and manipulating people, toys, and other dogs. Isolated beagles emitted fewer and less intense directed responses and their deficiency with respect to the pet-reared group was pronounced even after five weeks of arena tests. Again, the terriers with an isolation history differed sharply from beagles treated similarly. By the third block of tests, the three isolated terrier groups were identical to pet-reared subjects on the response index scale. Taking pet-reared animals of the same breed as a standard, isolated terriers were overactive but essentially normal in their responses to social and other stimuli; isolated beagles were underactive and persistently deficient in directed responses.

THREE ORDERS OF PHENOTYPES

We in behavior genetics have been inclined to view an organism as a bundle of traits inferred from a battery of tests given under standard conditions. I believe we should broaden this static concept of a trait to include a second dimension in which our phenotypic units describe differential responses in two or more environments. For mammals, at least, we should look for genetic effects upon a third dimension of the behavioral phenotype—its change over time. The more interesting aspects of the beagle-terrier comparison reside in these second and third dimensions.

This recommendation conflicts with the idea that for genetic analysis we should seek behavioral phenotypes that are invariant over a wide range of situations. If such phenotypes are found, they will be of interest, but to use situational invariance as a criterion of a good behavioral phenotype is to discard the part of behavior genetics most relevant to other behavioral sciences. Of course, most geneticists have faith that one can eventually find invariance if one gets close enough to primary gene action. Unfortunately, we are so far from this in mammalian studies that the matter cannot be tested experimentally.

These suggestions lead to the design of complex experiments with accompanying logistical and analytical difficulties. I do not like this outcome. But our methodology must reflect the conceptual needs of our subject matter — the genetics of social behavior. Behavior geneticists have adopted new and powerful techniques of genetical analysis,[2] but they have not devoted as much thought to the definition of suitable behavioral phenotypes.

GENETICS IN THE SERVICE OF BEHAVIORAL SCIENCE

If, as Dr. Thompson states, behavior genetics exists primarily to serve the behavioral sciences, it should select its problems with reference to important issues in psychology and sociology. In conclusion, therefore, I shall describe three areas in which more information may be needed.

First, we may be sure that the pressure of increased population is not merely a problem of "underdeveloped" countries, but is a global problem. It is relatively certain that social action must eventually be taken to achieve a degree of regulation. The alternative was described some time ago by Malthus. Should such social controls deal with man wholly in quantitative terms, or will man's genotypic differences be utilized in a eugenic program? Most human geneticists now say that knowledge of human genetics is inadequate for a positive eugenics program. Human genetics as a discipline is now much more occupied with chromosomes and proteins than with mild mental retardation and neuropsychiatric disorders. But the contribution of heredity to these latter syndromes is probably of greater social importance. Attaching geneticists to all research programs on the etiology of mental retardation and neuropsychiatric disorders would be a step forward. Increasing population pressure will force decisions of a eugenic nature, whether or not we are prepared with scientific evidence.

Second, we must give physical reality to the concept of genotype-environmental interaction. By the early identification of usually inferior genotypes, we may be able to select a special environment that will enable that genotype to function more adequately than it would normally. The low phenylalanine diets for phenylketonurians are a case in point. The special environments need not be biochemical. Beagles are hurt by isolation during early life. One can make a case that terriers are better adapted to later group life when reared with some isolation. The affiliation of geneticists with longitudinal studies of behavioral development in man and animals might provide useful insights on fitting an environment to an individual.

The third area relates to effects of increasing population density and changing educational status upon the breeding patterns of mankind. Some data of this type are available, but their evolutionary significance should be evaluated.[3] Perhaps for some years animal experiments will provide models that can be extended tentatively to man. However, with animals one cannot introduce the variable of education in genetic principles.

These suggestions are not exhaustive, but I hope they will delineate some ways in which the genetic viewpoint can be integrated more fully into the behavioral sciences.

Breeding Structure and Social Behavior of Mammals: A Servo-Mechanism for the Avoidance of Panmixia

BENSON E. GINSBURG

"Genetics and the Study of Social Interaction," the title of this section, implies a commutative relationship between subject and object, in which it should be considered that not only do genetic variables affect behaviors that provide the potential for a variety of group interactions, but also that these interactions, having various survival values for the group in question, restructure the gene pool of that group, so that social behavior becomes a cause as well as a consequence of evolutionary processes.

From a genetic point of view, one of the most interesting aspects of any population is its breeding structure. Where the early population geneticists preferred to deal with panmictic models, nature seems to

---

BENSON E. GINSBURG Behavior Genetics Laboratory, Chicago, Illinois

have abhorred panmixia, at least so far as many vertebrate groups are concerned, and to have stacked its behavioral cards against it. This makes perfectly good evolutionary sense, as the consequences of random breeding in any fair-sized population under static conditions are genotypic and phenotypic equilibrium, and evolutionary advances depend upon change. Some of this change can be provided by changing environmental conditions, but the frequency, magnitude, and duration of alterations in the physical and biological environment cannot be relied upon. Organisms can only insure that these changes, if not too extreme, can lead to further adaptations by retention of a flexible genotypic repertoire. They can, however, maximize their potential for adaptive change, whatever the environmental conditions, by partitioning the gene pool within an interbreeding population so that sampling variance, inbreeding, and other factors producing genetic nonequivalence over the population's habitat, insure that local phenotypic variations will occur. This is most often accomplished by behavioral means, and such behavior is here viewed as an important aspect of phenotype, having as its major selective value precisely the "purpose" of counteracting the evolutionary stasis that could occur under a panmictic system during eras of relative environmental uniformity.

The work of Schjelderup-Ebbe in the 1920s, followed in this country by that of Allee, Scott, and many others, established that social dominance was a widespread characteristic of vertebrate groups, and that access to mates has a variable and complex relationship to social dominance.[1,15,26,28] For example, Scott has reported that in the sage grouse the dominant cock does most of the mating, and that the genetic contribution of less dominant males on a particular booming ground in a given breeding season is numerically negligible. In consequence, the genes of the dominant cock are distributed widely in the population and "tried out," so to speak, in many combinations with a large number of hens, some of which will be closely related to him—the number depending upon the number of breeding seasons during which he maintains his dominance. This partial inbreeding effect would expose homozygous combinations of deleterious recessives to the direct action of natural selection, thus lowering the frequency of such genes in the population, while at the same time making it possible for favorable combinations and coadapted gene complexes to become established much more quickly than could occur in a large, random breeding group. Allee and his coworkers have shown that social dominance is directly related to success in mating in domestic fowl, and that males at the bottom of the peck order are often psychologically castrated. While more of the higher-ranking males in such a group will mate than do the sage grouse males, especially when there is room for them to space out, success in mating is still highly correlated with social dominance. Similar findings have been reported for a variety of other vertebrates, including a number of mammalian groups.

Over a period of time, a group with this type of breeding structure would achieve slight to moderate consanguinity, and could more easily fix favorable combinations of genes and expose less favorable ones to direct selective influences than would be possible if all members of the species had equal access to members of the opposite sex as mates. If this process were to go on in genetic isolation from other groups of conspecifics, the evolutionary consequence might well be the rapid production of local races, many of which would, by virtue of a small population size, have a limited genetic repertoire and be in danger of extinction and replacement by more successful groups, both within and outside their own species. This is not, however, the breeding structure that is usually achieved by the combined factors of territoriality and social dominance. Instead, the genes are reassorted within the effective mating groups by succession in dominance hierarchies. There is also gene flow between groups, so that such a species forms a reticulum of genetically connected partial isolates, thereby creating a condition favorable for the evolution of the species by providing situations in which genes existing in low frequencies in some groups, and having little opportunity to be "tried out" there, can exist in relatively high proportion in other groups. Where the population size is relatively small, sufficient homozygosis can be achieved through partial inbreeding, so that deleterious recessives and favorably adapted gene complexes will be exposed to the direct effects of selection. Genes not well-represented in a given partial isolate can be introduced from another without swamping the host population and may provide a basis for recombinations with the genetic resources of the other group, as a result of which a new level of adaptation may be achieved. This conforms to the optimum model described by Wright for achieving rapid evolution while maintaining genetic flexibility against the necessity for further evolutionary change.[34]

Returning to the behavioral dynamics of the biological model based on the effects of dominance hierarchies on mating structure just discussed, it should be noted that the simplistic relationship between social dominance and success in mating does not always hold. Our group has been doing a series of comparative studies of canid behavior, one phase of which deals with a captive wolf group, maintained under seminatural conditions, which we have had under observation for nine years. The group was originally composed of the remnants of two litters ($N = 5$) and has since been increased by a number of their offspring. The base population consisted of juveniles that developed the typical social behavior and organization of a wolf pack in the absence of adult animals who might have served as behavioral models.[11,14,24,32] Typically, the dominant female controlled the mating activities of other females by overt attack whenever they were in the proximity of an adult male during the mating season. The dominant female mated each season and effectively prevented some of the lower-ranking females from doing so, thus exercising an effective control on population numbers by behavioral means. On the other hand, the dominant male seldom mated, although females sought him out preferentially. He was highly territorial and controlled the activity of the other males by threat and demeanor. Like the dominant female, he inhibited their mating activity in this way.

During the first few years of observation, most of the mating was done by the beta male. Later, this male became dominant, and concomitantly his mating activities decreased. The effect of the group interactions is a built-in population control, in that not all of the competent adults mate and produce progeny every season. This conforms to the situation observed in the wild.[22] In addition, the mating structure is such that the dominant female has the opportunity to have progeny in each breeding season, and the males have unequal access to females. Evidence suggests that the significant social bonds determining mating preference are formed during the second year of life,[31,32] so that adult females tend to seek out the male who was dominant during that period of their development, whether or not he is still dominant at a later time. During the history of a given pack, a series of preferential mating coteries are formed and are apt to persist. This, coupled with the territoriality of the group, tends to provide a situation analogous in its effects on the partitioning of the gene pool to that resulting from a more direct relationship between social dominance and success in mating. The cohesiveness of wolf packs studied in the wild, including observational evidence that animals from neighboring packs generally mate within their own group, further suggests that a model providing for some inbreeding within groups, as well as for some genetic exchange between them, is applicable to wolf populations in nature.

Woolpy has adduced further evidence for the applicability of comparable models to other mammalian groups, including both nonhuman primates and man.[31] I would here like to focus briefly on the genetic parameters by means of which social behavior provides for the nonrandom structuring of the gene pool with its consequent acceleration of the processes for achieving adaptive fitness. At the same time, I suggest that this is the evolutionary genesis and *raison d'être* for social behavior.

The key components of social behavior in vertebrate groups appear to be the ability to form social bonds, aggressiveness, territoriality, sexuality, play, hunting, and parental behavior. Signal behavior that serves the function of communication is an important ingredient of all of these partially overlapping categories.

The ability of vertebrates to form social bonds varies all the way from built-in automatisms, such as imprintability, to the highly flexible arrangements characteristic of our own species. Much of the work on imprinting in birds has been centered around the identification of a sensitive period during which the bond is formed and the object is labile. Despite the obvious survival value of such a behavioral system, it must evidently be maintained in a population by means of constant selection pressure, because domestic birds show the behavior significantly less often than do their wild counterparts.[18] That the behavior can misfire — that is, become attached to an inappropriate object instead of the normal one during the sensitive period — helps to define the natural phenotype, demonstrates the degrees of freedom that are inherent in the behavioral interaction, and provides a situation in which the behaviors that are essential to the object of the social bond may be identified.

In higher mammals, social bonds are also more easily formed at some times than at others during postnatal development, and the formation of such bonds at the appropriate times appears essential for the development both of normal group behavior among peers and of normal sex and maternal behavior. These behaviors begin with the care of the mother for the young, and are extended and reinforced through play. The details of these interactions and the consequences of disrupting them at particular times have now been elucidated by a number of investigators for a variety of highly social mammals. They include the work of Blauvelt, Collias, and others with sheep and goats; Harlow's work with monkeys; Scott's work with dogs; and Bowlby's work with children.[2–4,17,27]

In our own work in this area, we have paid particular attention to two questions:

1 How and to what extent can one repair the damage resulting from deprived social contacts during the sensitive period?
2 To what extent are the behavioral mechanisms involved dependent on genetic capacities for which there is variability in the species?

Our work with the Alaskan gray wolf, a wild and highly social species, gives one answer to the first question. We have demonstrated that the strong social bond that can be formed between wolf and human — if the former is reared as a pet from an early age — is impermanent unless it continues to be reinforced into adulthood, and also that such social bonds can be initiated with adult animals by methods analogous to behavior therapy.[11,32,33] Several of our extremely tame and affectionate hand-reared wolves were isolated from further human handling after they were six months old and permitted to run with captive wild wolves for periods ranging from 18 to 22 months.

Under these conditions, strong fear responses developed, and the animals were behaviorally indistinguishable from wild adults when they were brought back to the laboratory. Wolves whose socialization with humans extended into the period of sexually mature adulthood did not lose this behavior when they were similarly treated. Wolves socialized with the aid of one of three tranquilizing drugs — librium, reserpine, or chlorpromazine — reverted to a highly fearful behavior typical of the wild animal when the drugs were withdrawn, however gradually. None of our socialized animals (nine to date) has shown the one-mannishness characteristic of many domestic dogs. It is as though an essential condition for the socialization is to bring the subjective affect of fear under control. When this is dulled by drugs or is prevented from occurring by accustoming young animals to human handling from an early age, the behavior reverts to wildness when the fear responses are encountered later. Socialization in older animals, which involves overcoming the fear responses that have already developed, is, by contrast, lasting. Evidence based on observations of free-living wolves indicates that long-term social bonds determining mating preferences and other dyadic relationships are most often formed during the second year of life.[31] Data on the socialization of wolves with each other as well as with man are, therefore, congruent with respect to the finding that the more permanent social preferences and allegiances are formed in early adulthood, and that social bonds that are formed early and not reinforced through the second year of life are probably evanescent.

We have been interested in these fear responses because they appear to us to be highly adaptive for any wild mammal and to be part of our own evolutionary legacy. It is our hypothesis that these responses have been overlain and brought under control by genetic selection for domestication, including the self-domestication of our own species. The behavioral and physiological analyses of genetic wildness may, on this hypothesis, uncover homologies to situations in which these mechanisms have taken over in the human, as in extreme anxiety states.

These responses have a genetic basis and are subject to genetic variability. Selection for domestication would otherwise be impossible to imagine. Comparative studies also demonstrate this. For instance, not all macaques are as difficult to handle as are rhesus monkeys.

In a wild social species, aggressiveness appears to be kept within reasonable bounds because communication behavior associated with threats, dominance, submission, and courtship is highly developed. Schenkel's studies on communication behavior in wolves, buttressed by our own observations, constitute a case in point.[25] The domestic dog, on the other hand, is highly variable in this respect. Many dogs never develop anything like the behavior repertoire used to communicate social intent in even hand-reared wolves. Among dogs that do, or that manifest behavior which appears similar, such as dominance postures and threats, the demeanor is often not an indication of what the dog will actually do. In such cases, the behavior has lost the meaning it had in the wild and has become vestigial.

Regarding aggressive behavior, our own work and that of many others has demonstrated that genetic selection, as well as fortuitous sampling of genetic stocks, reveal a strong genetic effect on aggressive behavior, as measured in a variety of ways in mice, rabbits, guinea pigs, and dogs.[12] Some of the intervening physiological factors have been identified — male sex hormone among them — but, most important for our considerations here, the experimental attacks on the problem are demonstrating that, as with so many other attributes, both physical and behavioral, the phenotypic potential rests on a variety of genetic bases, and these, in turn, show genetically restricted lability in interaction with environmental factors. In a variety of mouse strains reared under identical controlled conditions, aggressiveness — as measured by the latency to fight and the initiation of fights among previously isolated adult males in initial paired encounters — is a function of strain and, therefore, of the genotype.[12,13,15] Moreover, the effects of many environmental manipulations are also, in this sense, genotype-dependent. If representatives of some strains are subjected to environmental stress early in development they become more combative after sexual maturity; in other strains the identical manipulations produce the opposite effect; and in still other strains the experimentals do not differ from the controls as a result of these prior experiences.[9,10,12,13] Where such differences in behavior can be induced by early manipulations, not only are the behavioral outcomes a function of genotype; the sensitive periods during which the experimental manipulations are most effective in altering later behavior are also genotype-specific. These materials are uniquely interesting for the study of the mechanisms by means of which such genotype-environment interactions occur with respect to behavioral potentials. Once these mechanisms have been identified and elucidated, the studies can be extended to other species in which precise genetic control would be more difficult to achieve. Such researches, although not the concern of this volume, constitute a major emphasis in our laboratory.

What emerges from these examples is a picture of a population that, while conforming to the demands of the environment in terms of behavioral phenotypic norms, is nevertheless highly flexible in its behavioral potential so far as its genetic capacities are concerned. A great deal of genetic variability has been assimilated to a normative phenotype, so that selection by nature or man can extract quite different capacities from the same population, even though it is small and apparently uniform, provided that it is genetically much more variable than the phenotypic variability would indicate (i.e., noninbred). A case in point is a population of domestic dogs that has been under long-term investigation.[23] The present population was derived from three females and two males through almost twenty years of breeding as a completely closed population. The original stock all came from a single breed, but consisted of animals unrelated in their immediate ancestry. All had been selected through a number of generations to conform to the phenotypic profile typical of the breed, which included a long back in proportion to shoulder height, and a suspicious, protective temperament. Because of the demands of the situation for which these dogs were to be used — that of leading the blind — a more compact body build and completely different temperament were desirable. This was achieved within the closed population by selection. The normative phenotype, both behavioral and biological, therefore masked a great deal of underlying genetic variability that enabled this extremely small population to respond quickly to the demands of selection for another constellation of characters.

This example and that of the genetic determination of sensitive periods for response to early stress in mice, as well as the demonstration that the behavioral outcomes of such stress-ontogeny intercepts can vary in a polar manner between genotypes, indicate that a population can respond differentially to environmental changes both immediately, because of biologically determined differences in behavioral reactions to similar environments, and over time, through selective effects. In any case, the characterization of the behavioral parameters of a genetically mixed population provides a most inadequate picture from a dynamic point of view, as has been repeatedly emphasized in our laboratory,[12] and especially by McClearn,[21] in the use of inbred strains, and by Hirsch,[19] in studies of individual differences.

Thompson's criticism of my view (page 79), which he represents as the equating of behavior genetics (in principle) with the genetics of any other phenotypic character, involves an oversimplification as well as a genuine argument. Our laboratory has been as much concerned with the study of behavior per se as with its underlying mechanisms and, as the statement implies, vice versa. I view social behavior as having evolved primarily as a means for providing ways of partitioning the gene pool of a species, but this does not in any way place a pejorative value on the descriptive study of social behavior. Neither does it deny that social behavior has come to serve many other functions (such as the regulation of population size, which has also been emphasized by Wynne-Edwards). This is not a quarrel between the approaches of molecular biology and psychology, but rather an argument about how the various levels of organization, from the molecular to the societal, can best be studied and related.

This point and one other, which Professor Thompson has chosen to erect as a straw man to bolster his "so-what" argument in relation to the kind of genetic approach that builds Mendelian models through molecular events to behavior, require further elaboration. I should like to approach both of these through a common example:

some years ago Witt and Hall proposed a monogenic hypothesis for susceptibility to audiogenic seizures in several strains of laboratory mice.[30] This was followed by a polygenic model proposed by Fuller and based on more extensive data, using the same strains.[6] Dr. Dorothea Miller and I found that a two-gene model, which we published some years later, also explained the data.[16] More recently, Schlesinger and others analyzed these models in the light of the accumulated data and reported the interesting fact that F_1, F_2, and backcross data provided an inadequate basis for distinguishing among them. What, then, is the heuristic value of such Mendelian models? Is this a case of how many genes can dance on the head of a pin?

Many recent researches have been directed, not at further model building, but at attempting to find a real existence for some of the proposed genes. Work in our laboratory has clearly demonstrated that one of the loci in the two-gene model is associated with the rate of development and final level of nucleoside triphosphatase activity in the granular cell layer of the dentate fascia of the hippocampus.[5,7,13] This enzymatic activity can be followed independently of the seizures and can be related to the degree of seizure susceptibility in a variety of test situations in which the behavioral scaling (i.e., the seizure incidence) varies with the characteristics of the stimulation. Phenocopy experiments by means of lesions in this area verify its involvement in the seizure syndrome.[7,20] The same anomaly is also involved in other types of stress responses in which a variety of stimuli other than sound may be used. The locus in question is linked with "dilute," a pigment anomaly that has also been associated with seizures. This linkage very probably explains the variable association of the pigment gene with the seizure phenomenon — a possibility that was foreseen by Fuller. Additional work on this anomaly now makes it seem possible that the disturbance in the rate of development of the full enzymatic capacity of the granular cell layer in this region of the brain may be one of the determining factors for setting the sensitive period at which time external stress can be effectively mediated via the hypothalamus-pituitary-adrenal axis.

The second locus in the model is demonstrably associated with glutamic acid metabolism by brain,[7,8] and we have strong preliminary evidence that this comes about through effects upon another enzyme system, glutamic acid decarboxylase, and that the behavioral effect is not restricted to seizures.[29]

Through controlled genetic substitutions at these loci, it has been possible to identify aspects of central nervous system activity associated with a variety of behaviors, thus elucidating a variety of genotype-phenotype relationships. It has also been possible to slough off specious correlations, such as the one occurring through linkage between the locus controlling nucleoside triphosphatase activity and that for dilute pigmentation, and possibilities have been suggested for explaining the differences in timing of sensitive periods associated with the delayed effects of stress. These genes can be manipulated by breeding experiments so they can be dissociated from each other or placed in various combinations on a variety of inbred-strain backgrounds. The background, or interacting genotype, varies the expression of the behavior, thereby implicating other genes, as would be expected. Many other genes are involved in these behaviors, and they rest, in that sense, on a polygenic basis. However, we can hold these constant through the use of inbred-strain backgrounds while we investigate the changes in nature-nurture interactions resulting from a single genetic substitution having behavioral effects. We can then carry these investigations to a two-gene substitution and beyond in a biologically controlled fashion.

Perhaps a higher order of mentality than mine can unravel the complications of behavioral mechanisms without these biological simplifications. But I am sufficiently overawed by the complexities of researches on brain mechanisms and behavior to feel the necessity for such simplification. I wonder, parenthetically, where physics, chemistry, and molecular genetics would be today if kindred simple-minded souls in these fields had not indulged themselves in similar simplistic activities. We may be a long way from understanding the full range of behavioral complexities through such simplified biological models, but we can at least identify and — hopefully — control a few biological correlates of behavior in this manner and, through these, even the behavior itself.

Genetics and the Social Sciences

THEODOSIUS DOBZHANSKY

Many social scientists have, at least since the nineteen-thirties, been sceptical of the relevance of genetics to the understanding of social and cultural processes in human societies. They admit that man is a social animal by virtue of his biological nature, which allows him to be a social animal. But this taken for granted, biologists had better mind their own business and let social scientists mind theirs.

I must concede that social scientists had some valid reasons for their standoffish, and sometimes even hostile, attitude. Certain biologists have taken it upon themselves to make pronouncements, alleged to be scientifically verified truths rather than personal opinions, concerning social and even political problems. Their basic assumption is that man is nothing but an animal and, hence, biologists can understand human societies better than the benighted social scientists ever could. This assumption led to the prostitution of biology on behalf of racisms in Hitler's Germany, in South Africa, and in some quarters closer to home. I certainly do not question the right of these biologists — or of anyone else, for that matter — to express their views on any subject or issue. The opinions uttered by scientists are, however, prone to be utilized by politicians and propagandists for purposes of their own. Is a scientist accountable for misuses of his discoveries and utterances? He ought to be articulate enough at least to disown such misuses.

Some straws in the wind indicate that the attitudes are changing on both sides of the biology-sociology fence. To say that man is an animal is true, but this is only a part of the story. Biologists must

---

THEODOSIUS DOBZHANSKY The Rockefeller University, New York, New York

recognize that man is a great deal more than an animal, or at least that he is a very special kind of animal. And more and more social scientists accept that human nature is not a constant. Instead of a single invariant and unchanging human nature there are about as many different human natures as there are persons living. This does not mean, of course, that what a person is or can become is foreordained by his fixed nature, but neither are the genetic differences so insignificant as to be negligible. What this does mean is that different persons need different environments for their optimal, or socially most useful, development and self-realization. In a roughly uniform environment they will accomplish, or fail to accomplish, different things. The stock argument of some psychologists and sociologists is that since educators and social workers cannot do anything about people's heredity they may as well forget about it. In reality, they can do a lot about it; if they recognize that human natures are not uniform but multiform, they may take steps to provide conditions in which everybody, or as nearly everybody as possible, is able to do his best.

I must at the outset dispose of the evergreen fallacy which stultifies the thinking of many otherwise intelligent and well-informed people. This is that biology has allegedly shown that people are not equal. What biology has shown is that people are genetically diverse; every human being is a genetically unique and unrepeatable individual. It cannot be reiterated too often that equality and inequality are sociological, similarity and diversity are biological, phenomena. A society can grant equality of opportunity to its members, or it can withhold such equality; genetic diversity is biologically given, and could not be stamped out even if this were desirable. Much confusion of thought could be avoided if this simple distinction were kept in mind. And the confusion afflicts not laymen alone but some scientists as well.

Another fallacy to contend with is more subtle because it contains a half-truth. This is that the biological evolution of the human species allegedly terminated when its cultural evolution began. Now, it is correct to say that culture is generally a much more rapid and effective method of adaptation to the environment than genetic change can be. In a nutshell, for a period of perhaps 100,000 years man was adjusting his culture to his genes more often than his genes to his culture. It does not follow, however, that genetic evolutionary changes are no longer taking place. Cultural evolution has not supplanted, it has been superimposed onto, the biological evolution. Culture stands on a biological foundation.

Moreover, this foundation is not a constant quantum but a variable quantity. The more dependent mankind becomes on culture as its chief adaptive instrument, the greater the biological selective pressure to make the biological underpinnings of culture secure, and thus to permit further cultural developments. This is, or at least was during the critical stages of the hominization process, a positive feedback progression. Curiously enough, some of the same authorities who say that biological evolution has completed its course are obsessed with the idea that the biological foundations of culture are in the process of erosion in modern mankind. Regressive evolution is nevertheless evolution. This problem cannot be discussed here in detail, but the inconsistency of the two assertions should be noted.

How much evolutionary change has there been in the genetic endowment of the human species, particularly in the intellectual abilities, during recorded history? Very little, is the answer given rather overconfidently by many authorities, including some biologists. Indeed, the drawings left by Mesolithic artists in the caves of Altamira and Lascaux are not obviously inferior to those of Picasso and perhaps even of Leonardo. A moderately intelligent high school student nowadays knows some important things of which Aristotle was ignorant. It does not quite follow that this high school student is more intelligent than Aristotle was. Even the most outstanding of our contemporaries will, I hope, hesitate to claim an intellectual superiority to Aristotle.

This does not really prove that the level of artistic ability is now lower than it was in Mesolithic times, or that human intelligence is now lower than it was in Greece in the fourth and fifth centuries B.C. Presumably not every inhabitant of Altamira was a painter, as not every contemporary of Leonardo was his worthy rival in the arts. Nor did all the inhabitants of the world in the fifth century B.C.

have intellectual abilities like those of the towering giants of ancient Greece. Biological evolution should not be imagined to be a uniform and gradual change of every member of a species in the same direction. It is, if you wish, a much less orderly process. Mutation generates stores of variant genes; sexual recombination creates countless genetic endowments, genotypes, of individuals. Every individual is a biological experiment in adaptedness. Some genotypes are highly adaptive in some environments, others in other environments, still others in no environment, and probably no genotype is supreme in all environments.

The excellence of some genotypes formed in a population does not preclude formation of inferior genotypes in the same population. Populations, clans, or tribes may be genetically different on the average. In point of fact, it would be a rare coincidence if the averages of two populations or races were identical. However, what must be kept in mind is that the average differences among the populations are probably always smaller than differences among persons in the same population. As the human mobility and the population density increase, the interpopulational differences tend to decrease in relation to the interindividual differences, which increase correspondingly. The interpopulational, racial, differences were probably greater in the past than they are at present.

There is admittedly no incontrovertible evidence either to prove or to refute the hypothesis that mankind has evolved biologically as well as culturally since, let us say, the invention of agriculture and of settled life. The evidence is indirect, but, by analogy with the present situation, suggestive of such changes having occurred. The evolutionary changes which are taking place in the human species at present can be studied, but it is evidently impossible for me to deal here with more than a fraction of the problems that arise in the study of such changes.

The on-going evolution of man is discussed most often from the standpoint of the degenerative changes that are alleged to make the future prospects of our species dark indeed. That such dangers exist, and that they must be watched, is undeniable, although I believe that many writers have greatly exaggerated them. I had an opportunity to discuss this matter elsewhere,[1] and I prefer here to treat of genetic aspects of social mobility. This process has received considerable attention from sociologists, but very little from biologists. In recent years my colleague, B. Spassky, and I have experimented on laboratory models, built with populations obviously not of *Homo sapiens,* but of that lowly yet wonderful insect, the fly *Drosophila pseudoobscura.*

Rigid caste societies tend to do away with all social mobility. The descendants automatically have the same social status, and usually engage in the same occupations, as their parents and other ancestors. By contrast, open-class societies tolerate or even encourage social mobility. In such societies, the division of labor and the ascription of status that goes with it ideally occur on the basis of individual ability and performance, rather than by simply following the status of the parents. If human abilities were not influenced by the individual genetic endowments, the social mobility or the constraints imposed on it would be biologically immaterial. An involvement of genetic variables makes social mobility both a biological and a cultural evolutionary agent of far-from-negligible consequence. Social mobility enhances the fitness of the population groups between which it occurs, and it may lead to the emergence of superior genotypes, which would be less likely to arise without mobility.

The following very brief account of our *Drosophila* experimental models is designed to give you an idea about the possible genetic effects of social mobility in man. I must avoid here going any deeper than absolutely necessary into genetic technicalities, which are discussed elsewhere.[2] Moreover, I hasten to assure you that I do not regard man as a kind of overgrown *Drosophila* fly. Our claim is, we believe, rather more modest: it is that both man and *Drosophila* are sexually reproducing, usually outbreeding, diploid organisms, to which the deductions from the laws of heredity established about a century ago by Gregor Mendel are applicable. Certain insights may thus be gained.

The two traits mainly involved in our *Drosophila* studies are the geotactic and the phototactic behaviors, i.e., the reactions of the flies to gravity and to light. These behavioral traits can be quantified with the aid of classification mazes constructed by Hirsch[5] for geotaxis and by Hadler[3] for phototaxis. As shown in Figures 1 and 2, the mazes are composed of series of funnel-shaped passages, which force the flies to make 15 choices of upward or downward directions (for measuring the geotaxis), or of light or dark channels (for measuring the phototaxis). Depending on the numbers of choices of each kind which the flies make, they enter one of the 16 terminal tubes shown in the figures. The number 16 tubes are reached by choosing 15 times only the downward or the lit passages (positive geo- or phototaxis); number 1 is entered by way of 15 upward or dark passages (negative geo- or phototaxis); numbers 8 and 9 (middle) are reached when the numbers of alternative choices are 7 and 8 respectively (geo- and phototactic neutrality). The reactions of a population may be described by its mean geotactic and phototactic scores and their variances. The Hirsch-Hadler mazes are highly efficient instruments, in that they permit classification of fairly large numbers of individuals without an unduly great amount of labor. In our experiments, we make 300 females and 300 males from each population run through a maze, and select 25 females and 25 males as the progenitors of the following generation.

Most of the populations of *Drosophila pseudoobscura* with which we began our experiments were geotactically and phototactically neutral on the average (mean scores generally between 8 and 9). But this did not mean that these populations were all homozygous for genes guaranteeing geo- and phototactic neutrality. On the contrary, the neutrality was only the average condition, since the populations also contained genetically positive and genetically negative variants. The positive and the negative variants were about equally frequent, so that neutrality emerged as the average behavior. This has been demonstrated by selection in several generations of the individuals which moved to the extreme positive or negative ends of the mazes. Figures 3 and 4 show that the selection was quite effective. We have obtained decidedly geopositive and photopositive and geonegative and photonegative strains. The flies from these strains choose preferentially upward or downward, or light or dark passages. After 15 to 20

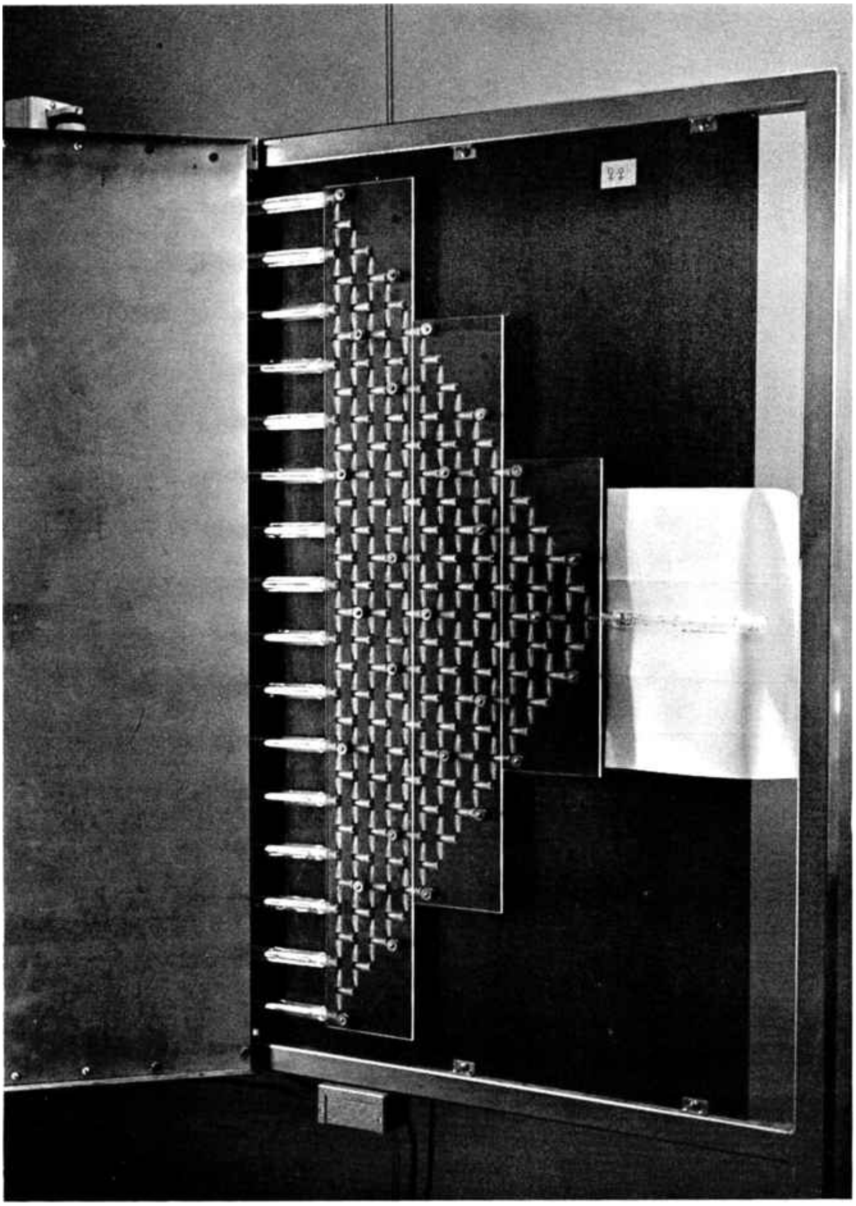

Figure 1 Hirsch's classification maze for geotaxis.

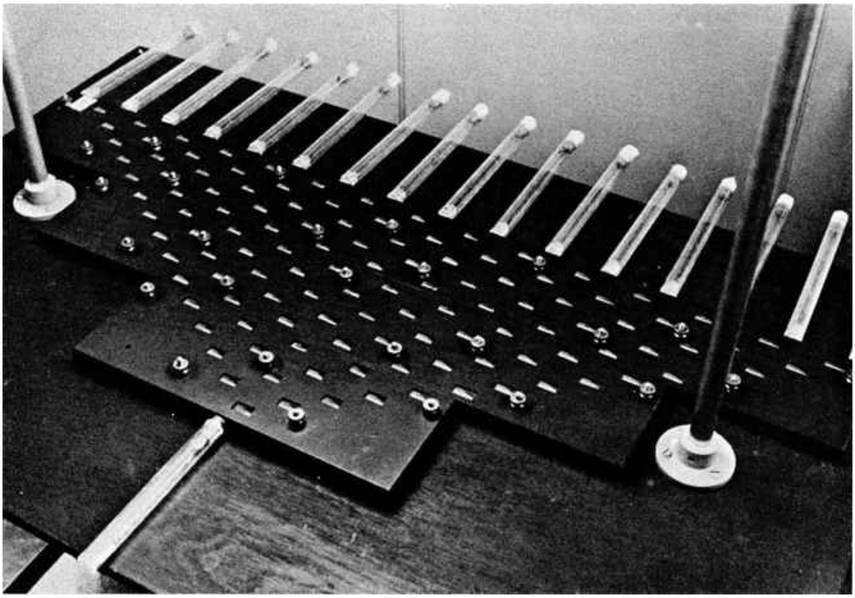

FIGURE 2 Hadler's classification maze for phototaxis.

FIGURES 3 AND 4 Results of maze experiments with *Drosophila*. The ordinates show the phototactic or the geotactic scores, i.e., the averages of the 16 terminal tubes of the mazes into which *Drosophila* distribute themselves. On the geotaxis maze (top), tube number 1 is at the top and number 16 at the bottom. On the phototaxis maze (below) number 1 is reached by 15 choices of light passages and number 16 by 15 choices of dark passages. The selection is made by running 300 females or 300 males through the maze; the 25 most positive or most negative individuals of each sex are selected to be parents of the next generation. On the average, the initial populations were photo- and geotactically neutral. The average scores were between 8 and 9 (an average of 8.5 is exact neutrality). After 19 generations of selection, the positively phototactic line had average scores of 14.4 and 15.0 for females and males respectively, the negatively phototactic line 2.2 and 4.4, the positively geotactic line 12.9 and 12.9, and the negatively geotactic line 4.5 and 4.7. The frequency distributions overlap only slightly in the middle, i.e., only a few flies of the selected strains end up in the terminal tubes.

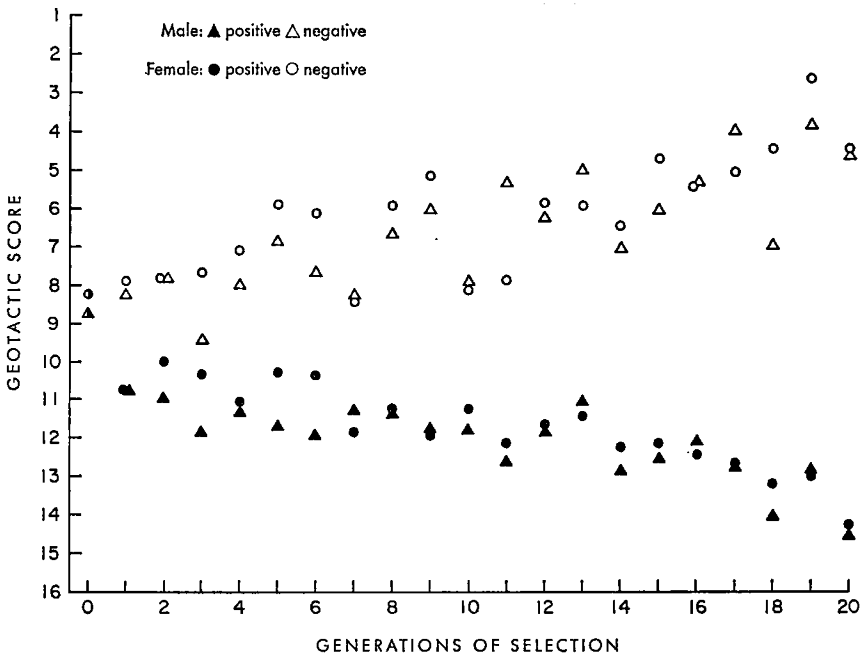

FIGURE 3

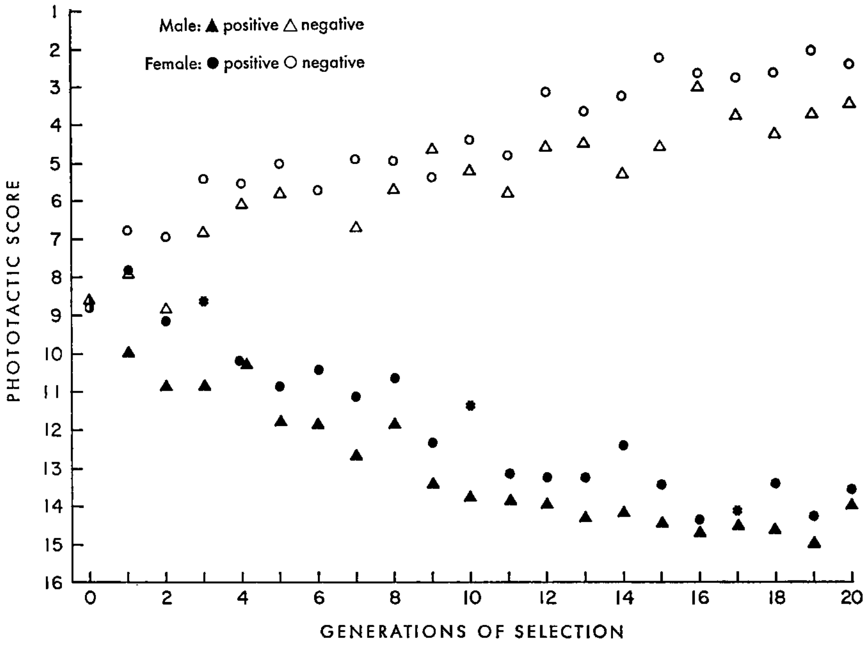

FIGURE 4

generations of selection, only a few flies from the selected strains behave as geo- or photoneutral.

The next problem which arises is the height of the heritability of the geotactic and phototactic behaviors. If I may be permitted to use an oversimplification for the sake of clarity, this is asking how powerful is the hereditary conditioning of these behaviors passed to the offspring, compared to the effects of environments and of pure chance. The heritability may be determined in several ways; Mr. R. Richmond is now working on one of them. We have determined the so-called realized heritability through 15 generations of the selection. This heritability turned out to be very low; only about 3 per cent for the geotactic, and about 10 per cent for the phototactic behavior.

The heritability of IQs in man, estimated by comparisons of identical and fraternal twins; is between 50 and 65 per cent, according to different authors. This is several times greater than the heritability of the geo- and phototactic behavior in our experiments with *Drosophila.* In man, the controversy is still not fully settled, and there are people who question that IQ differences are inherited at all. I submit that the human variation in traits with a heritability as low as that of the geo- and phototaxis in *Drosophila* would almost certainly be regarded as purely environmental. Yet you can see that such traits are by no means devoid of evolutionary significance. A moderate number of generations of selection systematically applied suffice to produce quite appreciable differences in the behavior of the flies.

To test the genetic consequences of social mobility, we have arranged several experimental models. One of these is set as follows. An experimental population of *Drosophila,* kept in the laboratory in a so-called population cage, is being selected generation after generation for positive (or for negative) phototaxis. A certain number of flies are also selected from this population and "migrate" to another experimental population, which is being selected for geotaxis. Vice versa, some flies from a population selected for positive or for negative geotaxis become immigrants to the populations selected for phototaxis. In other words, we work with pairs of experimental populations, which in each generation exchange a fixed number of genetically selected migrants, thus simulating the social mobility in human populations. The question at issue is whether the immigrants derived from a donor population selected for, say, positive phototaxis will exert a genetic influence toward phototactic positivity on the recipient population, which itself is being selected for a different trait — that is, for a certain geotactic behavior. The numbers of the immigrants are, of course, smaller than the numbers of flies selected in the recipient populations themselves (10 and 40 individuals, or 20 per cent immigrants, 80 per cent sedentes).

An intense selection for geo- or phototaxis was practiced on the sedentes in every generation; the 40 "best" individuals were selected among the 600 flies run through the mazes, i.e., the selection intensity was 6.7 per cent. This caused, as anticipated, a rapid improvement of these populations. By "improvement" we mean simply that the populations changed in the directions for which they were being selected. It was also expected that the immigrants would have genetic effects on the receiving populations, and this expectation was realized. However, the experiments also yielded an unexpected and interesting result.

The migrants were always selected in the direction opposite to that in which the sedentes were selected in the donor populations. For example, if a donor population was selected for positive geotaxis, it sent phenotypically negatively geotactic individuals as migrants (for details, see Dobzhansky and Spassky[2]). Will, then, the recipient population change in the direction of negative or of positive geotactic behavior? Because the migrants entering the recipient population are selected for geonegative behavior, one might expect the recipient population to become geonegative with time. On the other hand, the donor population is selected for geopositivity, and it is becoming more and more geopositive. The migrants are, then, the most geonegative individuals coming from a more and more geopositive donor population. In point of fact, the recipient population became more geopositive than it was originally. To put it another way, the phenotypic "rejects" from an "improving" population transfer genotypic improvement rather than deterioration to the recipient population.

What does this result mean? It would be inexplicable if the trait involved had a high heritability. Suppose that individuals having blue eyes, or blood of group O, are selected in some human population to migrate to another population. The heritability of the eye color, and especially of the blood group, is very high. In other words, blood-group O individuals always have genes for that blood group; phenotypically blue-eyed individuals have usually, although not always, genes for blue-eyedness. Their genetic effects on a donor population cannot be other than those expected, owing to introduction of more genes for blood-group O or for blue eyes. The situation is different in our experimental *Drosophila* populations, and it also may well be different with traits of relatively low heritability in human populations.

A low heritability means that the phenotype, the appearance or the observed performance of an individual, does not always reflect accurately his genetic endowment, his genotype. Consider again, for example, a *Drosophila* population being selected for a positive phototaxis, but sending out its negatively phototactic individuals as immigrants to another population. As stated above, the donor population is gradually "improving," meaning by "improvement" a change in the direction in which we are selecting it. The migrants an improving population sends out do not outwardly show this improvement in their phenotype, because the trait involved has a low heritability. The recipient population also slowly but significantly improves, although the immigrants it receives are phenotypically "inferior."

Another experimental genetic model of social mobility may be mentioned here briefly. With this model, the discrepancy between the observed behavior and its genetic base appears even more clearly. Following Halsey's perceptive theoretical analysis[4] of the genetic consequences of social mobility in human populations, we have set up pairs of experimental populations of *Drosophila* flies. One of the populations (called "Aristo," or "elite") in each pair is started in every generation with 50 flies (25 females and 25 males), while the companion population (called "Plebs") is started with 500 flies (250 females and 250 males). In each generation the populations exchange 10 migrants (5 females and 5 males). The migrants, therefore, are 20 per cent of the founders of the small "Aristo" population, and only 2 per cent of the founders of the large "Plebs" population. In each generation both populations are selected for a certain geotactic behavior, positive or negative.

In the small population, which you may liken to some kind of an elite or an aristocracy, the selection is rigorous—40 most positive, or most negative, individuals out of 600. In the large population the selection is very weak, 490 individuals out of 600. Moreover, the large population sends out its 10 best individuals in each generation as migrants to the small population. By "best" we mean, as in the example discussed above, the individuals whose phenotypes conform to the direction in which the selection is being made. The small population sends out 10 "worst" individuals to the large population, "worst" meaning the individuals deviating most in the direction opposite to that in which the selection is being made.

If the trait involved had a high heritability, one would rather confidently predict that the small elite population would change in the direction of the selection. For the large population, the expectation would be little change in either direction, because the weak selection of the sedentes may be frustrated by the immigrants strongly selected in the opposite direction. In reality, both populations change in the same direction, the elite changing more rapidly, but the large population following its lead without, however, quite attaining the elite level. Thus, social mobility may transfer the selectional improvements taking place in an elite population to a much larger nonelite recipient population. With traits of low heritability, such transfer may take place even if the migrants moving out of the elite population are phenotypically minus variants in that population.

The genetic consequences of social mobility, and of the assortative mating to which it leads, are very imperfectly understood. Geneticists have rather neglected this problem, because assortative mating does not of itself change the gene frequencies, and is therefore not in this sense an evolutionary agent. The classical idea is that positive assortative mating (i.e., mating of carriers of like genotypes) leads to an increase of the proportion of homozygotes and a decrease of that of heterozygotes, compared to random mating. At least in human societies, the more interesting consequence is the likelihood of formation of genotypes that would be less likely to arise with random mating. As with the phototactic and the geotactic behavior of *Drosophila* flies, many human traits depend on numerous genes (polygenic traits). Suppose, then, that a certain special ability (for example, musical talent) is the result of simultaneous possession of several genes, each of which has only limited effect separately. The frequencies of each of these genes in the population may be low. If so, under random mating the probability of a genotype arising which carries all such genes may be minute. The situation changes with free social mobility, which brings into a class or a profession the individuals that carry at least some of the genes that qualify these carriers for success in this profession. Positive assortative mating will then be able to produce accumulation of such genes in some individuals, raising their ability level in their special field.

It would be naive to apply the observations on our *Drosophila* populations, and the conclusions drawn from them, directly to the social mobility in human populations. The situation is certainly too complex for such facile extrapolation. Nevertheless, the results obtained in our experimental models are interesting and suggestive of many unexplored processes which may be going on in behavioral traits in human populations. At least, the results show that we need more research on experimental models with animals suitable for this purpose, and more descriptive and statistical studies on the social mobility in human populations.

Population Control and Social Selection in Animals

V. C. WYNNE-EDWARDS

DISCUSSION

My chief purpose is to draw attention to the part that social competition plays in natural selection. It is now well established that vertebrates and arthropods of many kinds are capable of regulating their own numbers (cf. Wynne-Edwards[17]). I may remind you of the wide variety of experiments, performed during the last 50 years, which demonstrate that in confined populations this is so, whether they are of *Tribolium* or other flour- and grain-infesting beetles and moths, of flies such as *Drosophila* and *Lucilia,* of crustaceans such as *Daphnia,* of fish of many kinds, or of laboratory rodents. Parallel studies on wild populations have revealed a widespread ability among animals in most of the great phyla to operate spacing-out mechanisms that effectively resist crowding beyond a certain threshold, and an ability to vary recruitment and mortality according to existing population density and resources.

I shall illustrate these processes in detail at a later stage so that you can appreciate their mode of action. Some of the mechanisms have

---

V. C. WYNNE-EDWARDS University of Aberdeen, Aberdeen, Scotland

long been known, although their functions were not at first understood. They frequently result in expelling whatever population surplus may build up in a locality, and this puts the individuals that have been displaced at greater risk and often results in substantial mortality. Social interaction may affect the admission of recruits to the breeding stock, with the result that some young adults are kept from breeding for a season, or possibly more than one. This means they lose a part, and in some cases the whole, of their chance of contributing anything to posterity.

Social pressures do, in fact, bear unequally on individuals and can condemn a proportion of any given generation to die prematurely without issue. The whole conception of population homeostasis is still comparatively young, and its repercussions on theoretical biology are far from fully explored. Here I would like to give an idea of the scale on which social selection takes place, and try to throw a little light on its possible effects as a process contributing to evolution.

THE BIOLOGICAL FUNCTIONS OF SOCIAL ADAPTATIONS

For a century students of evolution have grown up accepting Darwin's ideas on population ecology, as expressed in Chapter 3 of *The Origin of Species.*[2] "In looking at Nature," he says there, "it is most necessary . . . never to forget that every single organic being may be said to be striving to the utmost to increase in numbers." He had already remarked that all living species must necessarily have the power to multiply in a geometrical ratio, although most of the time they are prevented from doing so by a variety of checks. He went on to emphasize that "The causes which check the natural tendency of each species to increase are most obscure"; but everyday experience and common sense suggested to him that they were likely to fall into four main categories. These are the amount of food, which must give the extreme limit to which each species can increase; the serving as prey to other animals; adverse climatic factors; and the effects of communicable disease, especially on crowded animals.

The capacity for geometric increase, curbed by restraining forces, was of course the basis in Darwin's mind for the struggle for existence, and hence for natural selection. Once it had been generally accepted by biologists, there was no further inclination to question or scrutinize its details or to check it against the results of more recent population experiments and field studies. We are now in the anomalous position of being committed to Darwin's concept that organisms are always striving to increase their numbers, and all that follows from this, and at the same time of finding in actual fact that many animals have efficient adaptations for holding their populations down. Some of these populations are limited to a low ceiling density, and it can be shown that they are rarely, if ever, exposed to Darwin's checks.

Modern studies *have* confirmed the expectation that the factor which ultimately limits the density of animal populations is in most cases the food supply. But it is not usually the executive or proximate factor. The immediate cause of population limitation in any given habitat is generally something completely different, such as an individual space requirement. Nevertheless, it does duty in a rough-and-ready way as a mechanism for limiting the total demand for food.

The necessity for making such a substitution, and for having what amounts to an artificial limiting factor instead of a free-for-all scramble for food, is not difficult to understand. If there were no other checks on population increase except the available stock of food, predatory animals — wolves, for instance — would soon increase to the point at which they would begin to diminish their stocks of prey; the fewer the prey became, the more the survivors would be harried. Research on the red deer (*Cervus elaphus*) inhabiting the Hebridean island of Rhum (where there are no longer any wolves) has shown that, during the time that the herd of about 1,500 head have been experimentally managed for venison production, it has been possible to kill one-sixth of the stock each year without causing any cumulative change in the size of the herd. The cull has been distributed proportionally over both sexes and all age groups except the calves of the year. We can assume that under primeval conditions a similar annual off-take of something like one-sixth would have been available to the wolves, as the natural predators, and that they could not with impunity take very much more. A kill of one-sixth per annum would allow them to take in an average month one deer in every 70, or one in 2,000 on an average day. Killing more than that would probably not be difficult if there were many wolves, but it would lead to the depletion of the stock and diminishing yields in future years.

Similar conditions can apply to any predator, including man. For example, we understand clearly nowadays the folly of overfishing, although we may not always be willing to accept the restrictions required to prevent it. The danger is not even peculiar to predators: overgrazing by herbivores, leading to down-graded pastures and lowered fertility, is equally familiar in human experience. Apart from domestic animals, there have been cases in which deer and moose have multiplied in the wild and damaged their food resources. This tends to happen in localities where the wolves have recently been exterminated by man. The final result is that the deer themselves suffer.

The real state of the balance between supply and demand, when one is dealing with living food resources, is usually hidden, and quite different from what one might expect. I can illustrate this by reference to the beaver. In an hour or less an adult beaver can cut down an aspen tree that will provide bark and twigs to feed its family, perhaps for several days. The tree has taken possibly 20 years to attain a productive and economical size for consumption, so that to get the maximum food-yield from their habitat, beavers should not cut down more than one stem in 7,000 on an average day, if they are to provide for a 20-year rotation. At this rate, their food must always appear to exist in limitless superabundance, even though they are actually consuming the entire annual increment of the poplar forest and there is nothing to spare.

It seems certain that this common need to hold back on the consumption of food is the reason so many animals have become adapted through natural selection to limit their numbers by self-imposed means. To protect such food resources, a ceiling must be put on population density while there is still an apparent abundance of food available. One standing crop must be eked out until the next is ready to be harvested, and demand kept down to the rate at which the supply can be replenished. Such provident ceilings are established by a variety of methods, all of which basically depend on convention. The simplest kind is the subdivision of the habitat and the food it contains into individually held territories. The conventional feature here is that the owner must claim an area big enough to allow him to take all the food he requires without ever running the risk of exceeding its productive capacity.

Through long periods of evolution, many of the density-limiting conventions have grown a great deal more artificial and less direct than this. Gregarious fish, birds, and mammals may hold traditional communal territories, sometimes maintained for many generations, very much like those of primitive human tribes. Within their territories the inhabitants autonomously limit the size of their own flock. In other cases, the feeding grounds are undivided and are shared between social groups. The conventional fabric then depends, for instance, on a pattern of traditional sleeping places, each the property of a different group, or even of a particular individual.

I must make clear that it is by no means necessary to have any overt territorial organization to control population density. For example, guppies in an aquarium, given adequate food, limit their own numbers in relation to the volume of the tank. The mechanism consists simply of eating all the surplus young produced.[1]

Under most kinds of conventional limitation, aggressive behavior intervenes when the acceptable population ceiling is exceeded, and the surplus individuals are driven out. At these times, which ones are to remain within the establishment and which ones are to become outcasts is a question of personal status in a conventional hierarchy, and this is a still more abstract kind of system in the homeostatic machine. Most aggressive competition is itself conventionalized. Hurtful weapons like teeth and claws are often displayed in threat but are seldom used in mortal combat; superiority can be symbolized in far less barbarous ways than by showing savage weapons. Most territorial birds proclaim their ownership by singing. They seldom have any difficulty in dominating intruders of their own species as long as they hold the psychological edge of being on their own ground.

In conventional competition it is rights that are ultimately at stake. The actual contest is always about some substituted, token situation, but a successful encounter secures for the winners the right to belong and live in the habitat, the right to use its resources, especially food, and in many situations the right to reproduce. A male bird without a territory cannot nest; very likely it will be inhibited from maturing sexually, and it may be prevented from feeding in the habitat. The same applies, in most types of gregarious vertebrates, to any low-ranking member of a hierarchy. Rights are accorded only to those that succeed in qualifying themselves either by winning the required kind of conventional property or, in appropriate circumstances, by attaining a personal standing sufficiently high in the social group. These two immediate objectives of competition, the one concrete and the other abstract, are often inseparably combined; property possession can be one of the main symbols of status, and status differences can decide the day between individuals competing for property.

The most unexpected result of my study of homeostatic population control has been realizing that conventional competition could be the basic cause of social evolution. Society appears to be the organization that provides the medium in which conventional competition can take place. Putting it another way, promoting competition under conventional rules for conventional rewards appears to be the central biological function of society. I have developed this theme on a number of occasions elsewhere, and need now remind you of only two points. The first is not to confuse sociability simply with gregariousness; solitary animals like cats or foxes can and do possess elaborate social organizations. The second is to note how accurately the cap fits when we apply it to human social behavior. Wherever we look we see brotherhood and cohesion binding the members of a social group to one another and to their homeland, but they are infiltrated by differences of opinion, the emergence of leaders, the desire for recognition and personal status, and for one's own side to win. Society is inherently competitive, and I believe it can be defined biologically as "an organisation of individuals capable of providing conventional competition between its members" (Reference 17, page 132).

POPULATION HOMEOSTASIS IN THE RED GROUSE

I want to turn now to a practical example of social regulation at work in a natural population, and I have chosen the species on which we have been working longest at Aberdeen, the Scottish red grouse (*Lagopus lagopus scoticus*). This valuable gamebird lives between sea-level and 1,000 meters on open hills and moors covered with a heathy vegetation. The dominant plant is the heather itself, *Calluna vulgaris*, and this is also the staple food of the vegetarian grouse. Much of the year the leaves, buds, flowers, and seeds of heather provide almost 100 per cent of the birds' diet, and at no time less than half of it.

On the better grouse moors, heather appears to cover the ground mile after mile. Measurements show that it actually constitutes between 40 and 75 per cent of the vegetation on the dozen or more areas we have chosen for intensive study during the last 10 years. The grouse themselves are moderately large, noisy birds, easily flushed by men and dogs for counting, and not too difficult to catch and mark with visible colored tabs. Much of our work has depended on studying the behavior of known individuals. There is a visible dimorphism between the sexes, and some recognizable variation in individual plumage, especially in the coloring of the underparts.

At first sight, it is difficult to believe that food could be the ultimate limiting factor, where heather grows in such profusion. The birds seldom exceed a density of 250 per km^2 (one per acre) even under the best summer conditions, and they are often below 50 per km^2 (one to five acres). But it has been clearly shown that population densities are in fact closely correlated with the amount of heather cover, with its nutrient status, and with the type of soil on which it grows. Heather is a low, shrubby evergreen with tiny leaves, and a life-span of up to 35 years. It is far more nutritious when young than when old, and for this reason in the spring grouse moors are customarily burned in small strips and patches, on a rotation of 12 to 15 years. Some older heather is necessary to provide the birds with cover.

Grouse carefully select the parts of the plant they eat, and biochemical studies have shown that what they pick off has a higher nitrogen and phosphorus content than what they leave behind.[14]

Comparing heather of the same age on two adjacent moors, one on a very acid granite soil and the other on more base-rich diorite, it has been found that the nitrogen and phosphorus content of leaves is substantially higher on the richer soil, and the same applies to certain other elements, including cobalt. Although the amount and average age of the heather cover is practically the same on the two moors, over a period of five years the one with the richer mineral status has had, on average, just twice the breeding population of the poorer one.[13,16] A pilot experiment to change the mineral status of 16 hectares of heather by applying nitro-chalk has doubled the grouse-breeding density (from three pairs to six pairs) compared with the initial population and with the untreated control area of 16 hectares alongside, on which there has been no change in numbers.

Direct competition takes place between male grouse for a place to live on the moor. A system of territories held by individual cocks operates most of the year, but in the late summer, when the old birds are molting, the pattern of holdings quietly lapses. Then, within a few fine mornings about the end of September, quite suddenly and surprisingly, a completely new pattern becomes crystallized and remains substantially unaltered for the next 10 to 11 months.

Toward the end of August the young birds are becoming full grown. Family parties of half-a-dozen birds or so are breaking up, and forward young cocks assume a new aggressiveness of behavior. The conventional time for territorial competition begins about dawn. At this season old cocks recovering from the molt may resume their usual positions and indulge in aggressive vocal display for a while. The rest of the population, mostly females and young birds, lies low until the ritual is over, but after that they are all allowed the freedom of the moor for the rest of the day, feeding very much where they please.

But when the critical period arrives, quite suddenly the young males enter the ranks in territorial dawn display. The result is in the nature of a "general post." Usually within one to three days the great annual contest is virtually decided. All the suitable ground is taken up and, as far as the males are concerned, the population finds itself sharply stratified into an establishment of successful territory owners and a residue with lower social status, which can henceforward remain on the moor only on the sufferance of the establishment.

Each morning thereafter, weather permitting, there is an intense display of mutual aggression among the established males, now holding some two to five or more hectares of ground apiece. During this time the exact territorial boundaries are hammered out. It lasts only an hour or two at first, and the noncombatants can still ride it out or keep out of the way until it is over. Freedom to come and go is then restored. Not many weeks later, some of the females become associated with the territory holders and are accepted into the establishment, although pair formation still remains fluid.

The rest of the birds, the subordinates, exhibit social differences among themselves. Some are bolder and less easily scared off, and can be found on the moor at all times. Others resign sooner, and become vagrants, not going far, but spending much of their time away from the heather and only returning for an occasional hour or two to feed. These are eliminated soonest and, in fact, some mortality from expulsion probably begins even before the new territorial pattern has emerged.

All unestablished birds have by now been identified *de facto* as surplus, as far as next spring's breeding stock is concerned. There are likely to be a few casualties in the establishment during the winter months, and these gaps will quickly be filled by the topmost unestablished birds, leaving the existing pattern unchanged. The experiment of shooting established males has been repeated a number of times, and has shown that well into the winter there is still a reserve of potential breeders left to fill their places. However, the mortality among the unestablished birds is extremely heavy, and when the spring finally comes, few or none are left.

In an average year, the August population consists of about 37 per cent old birds (comprising the parental age group, born in earlier years) and 63 per cent young (by this time 10 to 12 weeks old). It is roughly 2½ times the breeding population of the previous April. If the cycle of numbers brings the breeding stock back to the same level a year later, 63 per cent of the August population will have been eliminated again by the end of the following March. Shooting as a source of mortality can be left out of account, because in practice shooting pressure is never high enough to complete the enormous reduction demanded by natural homeostasis, and experiment shows that the grouse do, in fact, bring their population density down to the same final level whether any are shot or not.

It turns out that almost the whole of this mortality results from social causes. Although the details vary, most typically the population is reduced in two large steps, with a long static interval in between. The first drop comes with the establishment of the territorial system in October, which at once stratifies the population and creates a vagrant class. Within the next few weeks the vagrants suffer substantial losses. Nevertheless, some of them manage to adapt to the new regime, and mortality almost ceases again for several months during the winter. But in February or March the territory owners enter a different phase of aggressive behavior. Pair formation is consolidated, and both male and female begin to defend their territory, not merely in the early morning, but all day long. Henceforth trespassers are not tolerated, and within a few weeks almost all the remaining surplus birds have been evicted from the moor.

The mortality peaks are easily detected. Corpses are found, sometimes on the moor and sometimes on marginal ground where there is little or no heather. Postmortems show that some of the dead birds are emaciated, and some of them carry a high burden of parasites, especially the nematode *Trichostrongylus*. Feathers left clinging to the heather show where predators have struck their prey down. Although actual figures are, in the nature of things, difficult to obtain, the available data show that there were proportionally seven times as many predator kills of displaced birds as there were of established birds. The dates when peak numbers of birds of prey were counted on the study areas coincided with the steps in population reduction.[9,10]

Mortality among the established birds is difficult to detect because of the rapidity with which the gaps are filled. The death rate can be estimated only where large numbers of territory owners have been marked with colored tabs and can be individually identified. The best figure available for mortality in the establishment between November and the following August is 18 per cent.

In the red grouse there is practically no long-distance movement; 12,000 birds have been banded, and 95 per cent of the recoveries have been within two kilometers of the place of marking. Except on a local scale, immigration and emigration can therefore be left out of account.

With these data, it is possible to draw up a tentative balance sheet for a standard year, in which it is assumed that the mean population level neither rises nor falls. In practice, grouse numbers do usually fluctuate irregularly from year to year, but this appears to take place without entailing any fundamental differences in the various components that make up the mortality. The figures given in Table I must in any case be regarded as only approximate.

What the model does, I believe for the first time in a wild population, is to distinguish numerically between the mortality which falls on the socially successful — the territory owners and their mates — and that which falls on the subordinate remainder. The ratio is 7:56, or 18 per cent of the former and 100 per cent of the latter. The two

TABLE I

Average recruitment and loss in a red grouse population

August stock	37 old birds	63 recruits
	100	
Autumn territory contest	37 established (all ages)	63 surplus (all ages)
Winter mortality	7 die	56 die
	30 survivors	7 fill gaps
Spring stock	7 substitutes	
	37 breeders	(0 surplus)
August stock	37 old birds	63 recruits
	100	

categories owe their distinction ultimately to social competition, so that for grouse beyond the age of 3 months, one can state that social selection accounts for nearly nine-tenths of all the subsequent mortality. Whether young or old, once a bird's social rights have been stripped away it makes little difference from the standpoint of selection what particular agent happens to deliver the *coup de grace;* the bird has already been rejected by the social machine.

To make the recruitment and loss account as complete as possible, I should add that in the embryonic and adolescent phases of life, before the young complete their growth in August, the over-all mortality averages close to 80 per cent. Much of this is also likely to be socially induced, but as yet we have not enough information to yield any valid analysis.

SOCIAL FITNESS

For the red grouse, therefore, success or failure in social competition is undoubtedly a very important component in deciding the "fitness" of the individual (in the Darwinian sense) because of its influence on survival and reproduction. A bigger surplus is produced in some years than in others, and consequently the pressure of social selection varies, but in our experience of ten seasons on a dozen or more Scottish moors, social competition has emerged as by far the most powerful and consistent selective force. If the environment or food supply suffers a climatic accident, the social organization steps in and influences, at least to some degree, the fate of individuals either as casualties or survivors. If pressure increases from predators or disease, the social status of the individual can influence its relative exposure to risk.

It must be asked whether the red grouse is exceptional in this respect or whether social selection is generally a major phenomenon with far-reaching evolutionary effects.

The beginnings of population homeostasis most probably date to Paleozoic times. There is an immense span of evolutionary development behind it, and in the most advanced animals it has come to depend on an elaborate complex of adaptations. The evidence indicates that a control system depending on social interaction, in general resembling that of the grouse, is an ancient heritage common to all the classes of vertebrates. The principal features of social organization, including competition for real property and personal status, also can be found in the arthropods. They are less universally obvious there than in the vertebrates, but, particularly in the insects and crustaceans, the signs that indicate social homeostasis are not uncommon. They include territoriality, social breeding and roosting, attachment to traditional localities, and communal epideictic displays.[17] I believe the simplest manifestations of all can be traced to about the evolutionary level of the polychaete worms.

Where social homeostasis occurs, social selection automatically becomes a potential factor in deciding the fitness of the individual organism. But it can take effect only at times when there is reproductive power to spare and a surplus of individuals is produced. At all levels in the animal kingdom some populations are likely to appear in which, for one reason or another, surpluses do not arise. As Darwin pointed out, it may be impossible to establish permanent occupation at the edges of the range of some species because of fluctuations in climate. Frontiers must advance and retreat, and the outermost populations tend to subsist as opportunists and pioneers, at densities that seldom build up to a level that calls for homeostatic controls to be brought into action. In other circumstances, there are species subjected to such heavy and continuous predation that for long periods this is the sole factor determining numbers. In the North Sea, where for a long time the fishing fleets of many countries have exerted a heavy pressure, the stocks of all the main commercial fishes are chronically in this state, and their capacity to reproduce and grow appears to be kept at full stretch. Probably few individual fish in these populations are greatly inhibited, or handicapped in fitness, by social pressures because, with the reduction in population density caused by overfishing, mutual competition must have diminished or even ceased to exist.

A few pioneer experiments reveal the enormous reserve of fecundity possessed by some animals, when subjected to extreme predation stress. A. J. Nicholson[16] showed that the populations of the Australian sheep blowfly, *Lucilia cuprina,* were not threatened with extinction even though, in one particular experiment, 99 per cent of all the adults were destroyed each day as soon as they emerged from pupation and before they could reproduce. The one per cent allowed to live was sufficient to keep a thriving population going and to withstand the 99 per cent predation indefinitely. By the time the experimental population had become completely adjusted, compensatory adaptations had roughly doubled the average life-span, increased the daily hatch of larvae per female by 50 per cent, and increased the larval survival by a factor of 38 times. What Nicholson calls the effective coefficient of replacement had thus gone up about 100-fold, and compared with the very much larger control population, they were rearing 5.6 times as many pupae on the same amount of food.

Many studies reveal that the powerful effects exerted by social selection on the red grouse are more or less closely paralleled in other vertebrates. They have been demonstrated in a large number of other birds, in mammals such as primates, rodents, ungulates, and seals, in crocodiles, lizards, and a variety of fish. Although the mortality need not always be equally severe, it seems safe to assume that social selection is a potential force, at least among all the higher animals.

It is important to consider, therefore, the attributes that make for social success or failure in the individual. It can be seen at once that they are not entirely genetic in origin. One of the commonest determinants of status, for example, is the age of the individual. In some species, including many mammals, reptiles, fish, and decapod crustaceans, the males, especially, continue to grow throughout their adult life, so that older adults are automatically stronger than their juniors and enjoy a higher social rank. Alternatively, they may develop progressively finer status symbols in the shape of horns, claws, tusks, manes, crests, and similar adornments. Age differences like these have the function of creating a physical hierarchy in every social group. Often, especially in the male sex, only the senior individuals rank high enough to participate in reproduction. Alternatively, where the qualification for breeding depends on obtaining a property possession, it may be impossible for young contestants to oust the older ones, which have already established themselves in every acceptable site. As I stated earlier, not infrequently this forces young adults to wait, and defers the age at which they first manage to breed, in some cases for several years (cf. Reference 17, Chapter 23).

Age effects are tied up with survivorship, and survivorship in turn depends in part on chance, although generally it must also have a partly genetic basis. Individuals that manage to survive long enough to reach the reproductive class will have better adapted genotypes on average than do those that get weeded out prematurely. In organisms that breed for a succession of years, how long an individual stays alive after entering the reproductive class will again, on average, depend in part on its genotype. It appears to be an advantage to the stock to breed as far as possible from such older individuals, which as a class, by surviving longest, have revealed the hereditary qualities that make for adaptability and resistance to injury.

It is clearly desirable that the socially successful individuals should have the qualities that also enable them to survive the real or ultimate agents of natural selection. In an emergency, especially if it entails a shortage of food, the dominant individuals may soon be the only ones left alive, because the rest of the hierarchy has been eliminated by social competition. It seems safe to assume that, however important conventional structures like horns and plumes may be in social competition, they cannot safely be exaggerated to the point at which they impair the chances of individual survival in an emergency. It will be a very important advantage if social success comes easily to the individuals that are best equipped to resist the hostile forces in the environment, both biotic and physical, which from time to time threaten the stock with extinction.

In daily life, an individual's social status is often closely correlated with his physiological condition at the time, but we must use some caution in trying to distinguish between cause and effect. For example, it is not always easy to say whether an individual is dominant because it is well-nourished, or well-nourished because it is dominant. To give another illustration, subordinate red grouse males are sexually inactive. If in the autumn one of them is implanted experimentally with a pellet of testosterone, he can be stimulated to assert himself and acquire a territory at the expense of established males; consequently he is likely to survive the winter. But once more it is difficult to separate cause and effect, because if an occupied territory is made vacant as a result of the owner being shot in the same season, a similar subordinate male will normally step in, take it over, and become sexually active as a result.

The probability of social success must also depend on whether competition is light or heavy. Where there is a big population surplus, as happens with the lemmings in a peak year, only a minute fraction of dominant individuals will hold their own in the competitive process that commits the vast majority to destruction. In other years there may be no surplus and little or no social competition. Most other kinds of selective forces, including all of those that arise from Darwin's checks, are also variable in their incidence, and there is no reason to think that the varying intensity of social selection nullifies its long-term influence in evolution.

To recapitulate, we have observed that social success can be influenced by the individual's age, by its physiological condition, and by the contemporary intensity of social competition. In human populations another important effect depends on the social status of one's parents, and some trace of a similar prerogative could possibly occur in other species. Assortative mating between individuals of similar appearance has been reported in certain birds (cf. References 8, 11), as well as being normal and commonplace in man. But it seems clear that there is generally a major genetic component, in association with secondary and chance effects, that contributes to the social fitness of the individual, and this hands on the results of social selection to succeeding generations.

In our own species, the ability to succeed depends on the sum of the qualities with which an individual is endowed. The qualities themselves can be endlessly varied and combined; some of them are physical, some temperamental or intellectual. There is no one prescription of qualities that can define the successful man. Instead, innumerable different permutations can be rewarded by roughly the same measure of success as judged by the social yardsticks of wealth, influence, and reputation. It is an anomaly that in civilized races people of higher social standing often have smaller families, and in the long run this is disadvantageous; at the barbarian stage of development and among yet more primitive uncivilized races, social distinction and fitness as measured by family size were strongly and positively correlated (cf. Reference 6, Chapter 11), as they are in other species of animals.

I particularly want to draw attention to this nonspecific attribute of social selection in man, and to its characteristic property of favoring the individual who can impress his fellows and win their respect as a result of having any one among millions of potentially "good" combinations of genes.

It appears probable that social selection has a similar basis in the higher animals generally. Like men, rivals of other species confront one another as whole individuals. The better they are matched, the more likely is the conventional issue between them to be decided on points, rather than by a knock-out from any one genetic difference. It depends not just on the sharpness of the teeth or the color of the scales, but on the total effect, which gives the eye its sparkle and spells confidence in action. Genotypes are a mixed bag, and it may not take many shortcomings in one direction to undo the social chances of an individual well endowed in other respects. In the complexity of their social conventions, other animals differ from man only in degree, and probably there are many combinations of genetic ingredients that predispose their owners to social dominance. Thus, social selection appears not to be narrowly channeled and not strongly inclined to restrict genetic variance or to promote the fixation of particular alleles. No doubt feeble combinations of genes tend to be squeezed out in every generation, and those that are good enough to secure for their owners a respectable rating as individuals come through the social mill.

Time does not allow me to develop these ideas much further, because I have still one other important topic to deal with. It cannot be denied that social selection exists, and that at least in some situations it is a very powerful force. Although social competition relies on a background of real sanctions and the ability to back up postures and threats in actual combat, the artificial symbols of status have become extremely potent weapons. Few hereditary traits appear to be more labile in evolution or more subject to changing fashion than the symbols of personal formidability. In many animals the sexes are dimorphic, and where we have closely related dimorphic species, the most obvious specific differences usually appear in the social insignia of the breeding males. In these cases, population homeostasis and the social organization that promotes it tend to be exclusively male affairs. There is a division of labor, in which the female bears the main burden of reproduction while the male's energies are absorbed in keeping the population density in balance with the available resources; social selection, then, falls more lightly on the female sex. But in the vertebrates it is common to find that, during a long nonbreeding period each year, all adults are effectively neuter in sex, their dimorphism is suppressed, and all are competing socially on common terms.

INTERGROUP SELECTION

I want to conclude by touching on one other major aspect of natural selection. This is the effect that arises over long periods of time from the different fortunes of local stocks or populations as entities in their own right: some of them thrive and spread, like human nations in the course of history, while others decline and fall. It is selection acting at the level of the group.[18]

It arises in part because a social group is much more than merely the sum of its members. Societies have constitutions of their own with regulatory mechanisms, as we have seen, and these elaborate mechanisms can evolve only through a selection that acts directly between homeostatic groups as such. Societies involve a coordination of responses between their members, and their survival is determined by whether they maintain a viable economy. Their efficiency cannot be tested simply by a process of selection acting among their members, any more than the success of a football team can be determined unless the team actually plays against other teams.

As a basis for intergroup selection there must be discrete local populations or groups, each of which is self-perpetuating and capable of maintaining its integrity. No one has done more than Dobzhansky[3,4] to analyze the kind of spatial and temporal organization that typically exists in animal species. Normally there is a small flow of genes from one part of the species range to another, usually close by, but it is so slight that the integrity of each local Mendelian group, each with its own gene pool, is not flooded or violated. This characteristic situation is the same as we normally find among underdeveloped human populations.

From the social standpoint, tradition can be important among animals, just as among men, and local stocks often have long-standing customs — for instance, about places for breeding and sleeping, and territorial boundaries. Perhaps nothing shows the importance attached to maintaining discrete local stocks more clearly than the universal acquisition of precise navigational powers by two-way migrants in all the vertebrate classes and even in some insects. These powers allow them to go far away and yet return surely to resume a previously established citizenship.

Evolutionists generally accept the importance of the local population, or deme, as an evolutionary unit (cf. Reference 12, page 137), and they accept intergroup selection as the process by which can arise, for example, genetic adaptations that affect the group but not the individual. These include the specific number of chromosomes, the frequency of mutations, and the restriction to one sex of crossing-over, as in *Drosophila.* But when it comes to social evolution, doubts have almost always been expressed on the question of selection for self-sacrifice or altruism, which the social code demands. What is best for the social group is often exactly opposite to what is best for the individual. The general conclusion has been, following J. B. S. Haldane,[7] that under natural selection the fitness of the individual is bound to come first: "genes for altruism," to use Haldane's over-simplified concept, have seemed unlikely to spread.

In effect, evolutionists have been side-stepping this issue, because no alternative explanation has been forthcoming. Societies do exist, and the student of social behavior is faced every day with real situations in which individual advantage is quite ruthlessly overridden, apparently for the benefit of the group.

The crux of the matter centers on the social hierarchy. The hierarchy is a group adaptation capable of controlling group size and population density; it identifies the surplus individuals and enables them to be got rid of. In vertebrates, as we know, it often tends to allow older individuals to survive, and expends the younger ones. As I have said, older adults may be stronger and better armed, but in many species there is no material difference, and the advantage of age is solely a moral one. Hierarchies often exist even among members of a single age group.

Their essential feature is that some members are always ready to resign themselves to a subordinate rank and be dominated by others, virtually without protest. Social individuals must actually inherit a kind of switch mechanism, which allows them to assume either the dominant or the subordinate role according to circumstances. When animal strangers meet, their switches can be tipped in opposite directions, sometimes in a few moments, just on the basis of general impressions and without any trial of strength. Their mutual rank may be permanently fixed without more ado, and a not uncommon sequel, as we have seen in the red grouse, is for the subordinate to be made an outcast, condemned to an early death.

The pursuit of individual advantage would encourage the loser not to give up so easily, but to return again and again to the attack: it would be better to die in a reckless bid for success by any means, fair or foul, than meekly to resign one's livelihood without even a struggle. Yet we find no evidence of a selection to maximize ferocity toward rivals in the group, or to eliminate submissiveness, any more than there is an inevitable trend toward higher fecundity, or faster growth, or a longer span of life. Each of these characters varies in a given population over a range of values, which must obviously fit the requirements for survival of the group as a whole. The characters are immune to quick selective changes that could give an antisocial hereditary advantage to the individual, because their physiological control is immensely complex and their genetic basis perhaps even more so. Gene recombination in each new generation stabilizes their frequencies near the pre-existing mean. Polygenes and heterosis can negate any immediate hereditary advantage to the progeny of an individual, and if somehow antisocial self-advantage does make a break-through and increases the fitness of the individual, it will lead sooner or later to the extinction of the group.

No acceptable alternative to intergroup selection has been suggested to explain the evolution of the hierarchic society or of a variety of other more-or-less associated adaptations that characterize the populations of certain species. Most closely related to it is the evolution of castes in the social insects, some of which, being sterile, automatically have no Darwinian fitness at all (cf. Reference 5). Somewhat further removed in function are the sedentary and migratory castes in locusts, aphids, and other insects. There is also the evolution and control of polygamy, uneven sex-ratios, parthenogenesis, and asexual reproduction. The same selective process has presumably intervened to vary the primary reproductive functions of organisms. Some animals and most of the higher plants are hermaphroditic and every mature individual produces progeny; others are bi-sexual, with individuals that contribute either sperms or ova but not both, so that the potential fecundity of the population is effectively only half as great.

In evolving all these adaptations, the relative fitness of particular individuals has clearly been more or less irrelevant. It has been subjugated to the requirements for survival of the group as a whole. The facts demonstrate unequivocally that adaptations have arisen, capable of modifying the fitness of the individual in the overriding interests of group survival. To deny this, it seems to me, is to bury one's head in the sand.

Social Implications of Behavioral Genetics

GERALD E. McCLEARN

The best criterion of the value of a paper must be the chain of thought it initiates in the reader. On this basis, I must score Professor Wynne-Edwards' paper as most valuable, indeed.

I am particularly impressed by Professor Wynne-Edwards' clear demonstration of the role of social structure in determining selective mortality. This seems to be just the required antidote for the idea that, after achieving the status of a "psychosocial" animal, man has somehow become exempted from the process of natural selection. Development of societies has provided environmental circumstances in the context of which different individuals are more or less successful reproductively; these basic rules of the game are not different from the rules for infrahuman primates, or for herbivores, or for carnivores, or for lichens. What seems to distinguish the human social situation is the rate of sustained directional change. It is frequently pointed out that culture has undergone huge changes in 2,000 years, and that the rate of change in the human condition resulting from these cultural changes far exceeds the rate at which alterations in gene frequency could have brought about similar effects. This is undoubtedly true, but Professor Wynne-Edwards' research on grouse illustrates what must also be true, in a general sense, in man. Those adapted to the social structure have an enhanced capacity to survive and reproduce. Those who cannot succeed in the competition for a place within the social structure may have their reproductive potential reduced. This reduction may be for a variety of reasons, but most of them may be an ultimate consequence of the social failure.

As cultures evolved, men were tailored by natural selection to fit them, and as men evolved, they were altering cultures to fit themselves. It is fascinating to consider what the selection pressures were,

---

GERALD E. MCCLEARN Institute of Behavioral Genetics, University of Colorado, Boulder, Colorado

and how they waxed and waned, to bring us to our present state — a patchwork, as it were, of false starts, vestigial behavioral mechanisms no longer of much use, behavioral propensities that counteract other now-disadvantageous behavioral propensities, and, obviously, a number of highly useful, pragmatically successful traits, as well. Along with alterations of teeth, jaw, skull, pelvis, hands, and feet went the corresponding behavioral patterns that led to the basic primate way of life. DeVore[2] believes that a sharp distinction between the human and other primates may be based on the family structure, rules of incest and exogamy, and the practice of hunting and food-sharing at a home base. Furthermore, DeVore points out that for 500,000 years man has been a hunter-gatherer. Surely, much of our basic wiring diagram was set during this time and in accord with that way of life.

It seems generally accepted that, as urbanization occurred, special problems set in — problems related to population density, and thus to our topic for this volume. Inadequate waste disposal, for example, and the diseases that occurred because of the failure to solve that problem, must have exerted an enormous pressure on mechanisms of immunity. The situation was presumably aggravated by the increasing numbers of people and therefore of the frequency of contacts by carriers of disease organisms.[5] The great plagues must have altered gene frequencies considerably. But there was also selection for behavioral patterns. What of territoriality, of personal distance, of tolerance of the ambiguity of not knowing all the members of the community? The changes in the neuroendocrinological basis for the relevant behaviors that accompanied the transition from tribal life to urban life must have been huge. But if that is granted, what can we say of the selection pressures that are being applied today or can be anticipated in the stifling crush of overpopulation we have been warned to expect? For what behavioral characteristics will selection then operate? It seems likely that our species will ultimately either undergo the rigors of selection arising from overcrowding, or we will employ some means of controlling the birth rate. In case of the latter, which would possibly be the more benign outcome, it will be difficult or impossible to design a program that limits the quantity of humans without raising the issue of quality. Even a lottery, it should be noted, would constitute a change from the present reproductive pattern. In any event, we might enter the era of "self-conscious evolution"[3] abruptly, indeed.

It is alarming to think how ill-prepared we are, in terms of concrete information, for either eventuality. To be sure, behavioral genetics, particularly in the past couple of decades, has been accumulating a substantial body of data concerning the genetics of many behavioral traits in animals and man. Of this work, relatively little (but that of good quality—cf. Manning[4]) has been performed with an evolutionary perspective, and our substratum of solid knowledge concerning the relation of human behavioral traits to Darwinian fitness is virtually nonexistent. We may obtain some clues from examining the existing data, however. Roberts[6] has made a most interesting suggestion as to how this might be done. Any trait for which directional selection has been long sustained should have its additive genetic variance largely exhausted. Therefore, a trait that now has a low heritability may have been an important component of fitness in the past. Traits with high heritabilities may have had their additive genetic variance maintained because of selection for intermediate values, which would be important information in itself, or they may not have been conspicuously involved in reproductive fitness in our more-or-less recent evolutionary history.

It is interesting to try these notions on some of the results at hand. One of the most reliable findings in twin or family regression studies is that personality traits have, in general, lower heritabilities than intellectual traits, for which heritabilities appear high indeed. Could this mean that, given some minimum intellectual level, the most important human behavioral traits from the evolutionary point of view were what we nowadays call personality? Aggressiveness, dominance, cooperativeness, sensitivity, surgency, impulsiveness—call them what we will, they have the sound of characteristics that might have been of highest importance to early *Homo sapiens,* and they are not the sorts of things we ordinarily have in mind when we speak of intelligence.

What, indeed, of intelligence, with its apparently high heritability? Scholars considering these problems have a strong tendency to assume that intelligence has been positively related to fitness. Indeed, in some discussions, the implicit assumption appears to be that intelligence *is* fitness. I believe it plausible, however, that stabilizing rather than directional selection has been operating. With individuals of intermediate phenotype, many of whom will be heterozygotes, being favored, additive genetic variance would be maintained in the population, and heritability would remain high. It would follow that, in any population, those near the mean intellectual level would be fittest. It may well have been thus in the past, and it may well be thus today. Within the domain of mental abilities, interesting comparisons can also be made. Vandenberg has reported that two of the six Primary Mental Abilities tests show no evidence of heritability. These two are Reasoning and Memory. It is not impossible to imagine an earlier advantage for these than for the other traits of Number, Verbal, Word Fluency, and Spatial Ability.

But we can go only so far with this kind of consideration. We need more facts gathered in an explicit evolutionary framework. The effort would be much better spent in a coordinated program than in individual forays, because of the complexities that arise because evolution does not operate unidimensionally, and simultaneous consideration must be given to many traits. As the teeth of grazing animals became specialized, their legs became longer, their toes became specialized for running, their distance receptors became more efficient, and so on. This must be analogous with behavioral traits. A certain degree of intelligence may be favorable, if accompanied by so much, but not too much, curiosity; by so much, but not too much, aggressiveness, empathy, sympathy, and so on. In addition, it seems inevitable that a number of permutations of a given set of behaviors would be found to be of high fitness. Society has many niches, and provides rewards for many diverse types of human beings. We may conceive, then, of an n-dimensional set of behavioral coordinates, with reproductive fitness as the criterion variable. There may exist in this n-space a number of separate intersections that will be very fit.[7] These will represent the propitious combinations, between which will be found the less-fortunately endowed. By studying industrialized and nonindustrialized cultures, urban and rural populations, and so on, we might gain some new insights into the selection pressures that made us what we are today and what we may become tomorrow.

The cost of such data would be high, as biological and sociological research projects go, as it would require multiple measurements on many carefully sampled individuals. I might add the desirability of increasing the scope of our instruments. Quite understandably, paper-and-pencil tests have been prominent in research to date. But psychologists other than those using test and measurement methods have been developing techniques for the measurement of behavior. Many of those devised in experimental psychology have high reliability and other attributes desirable from a measurement point of view.

To repeat, the cost will be high. But I agree with Professor Kingsley Davis, who has said elsewhere[1]: "Eventually, regardless of how it comes about, human genetic control seems bound to occur, unless all progress is halted. . . . If and when it does come, the deliberate alteration of the species for sociological purposes will be a more fateful step than any previously taken by mankind." We owe it to our successors, who will probably be the ones to make the crucial decisions, to begin the factual groundwork now. If we are going to tinker with the gene pool of the species — and I think we will — it should be done on the basis of hard information. It is hard to imagine a task with higher priority than that of collecting the necessary data. We can scarcely afford *not* to undertake it.

Social Behavior and Population Dynamics: Evolutionary Relationships

ALEXANDER KESSLER

It is easy to see why Professor Wynne-Edwards' work has evoked so much interest,[11] for he interrelates complex problems of behavior and of evolution with the phenomena of population dynamics. Basically, he considers social behavior and population dynamics in the context of their evolutionary relationships.

I would like to touch briefly on the highlights of Professor Wynne-Edwards' formulation. First, the main function of social behavior or social organization is to maintain optimal relationships between the size of the population and utilization of available food resources. Second, the essence of successfully evolved systems of social behavior is to provide organizational set-ups for social interaction in the form of conventional competition, toward the end of maintaining numbers-resources equilibriums. Conventional competition substitutes, for deadly combat, nonlethal methods of competing for food, shelter, and breeding rights. It includes modes of social interaction that permit the assessment of population numbers and, subsequently, the elimination of recruitment of individuals in accordance with current and prospective supplies of food.

Professor Wynne-Edwards marshals considerable evidence, especially from field studies, that suggests how social interaction can affect processes of natality and mortality even in nonhuman vertebrates, and thereby become an important determinant of population dynamics. Indeed, more and more studies are beginning to document the profound physiological effects that can result when animals, especially vertebrates, interact with members of their own species — with what can be called (in analogy with the physical, nutritional, habitat, and pred-

---

ALEXANDER KESSLER Human Reproduction Unit, W.H.O., Geneva, Switzerland

ator components of environments) the social component of environment. Clearly, social interaction influences not only behavior but almost all other aspects of biology that have been examined — the daily periodicity of many physiological processes; susceptibility to infections and chronic diseases; reactions to drugs; neurophysiological reactivity; as well as rates of growth, sexual maturation, and longevity. Moreover, many attributes of vertebrates can develop normally only in the presence of other organisms of their own kind; they are potentials whose actualization occurs only within the social environment of groups or populations. Age, sex, physiological state, and past experiences — especially past social experiences and the timing and duration of social interaction — appear to be important determinants of the specific ways in which physiology may be modified.

Professor Wynne-Edwards shows how the social ecology of natural populations can act as a prime force to unify populations and govern their dynamics. This viewpoint, as he himself mentions, is not meant to imply that the long-recognized extrinsic factors such as food supply, physical conditions, and predators can never affect populations as primary forces, for "calamitous environmental changes as well as extremely favorable conditions can overcome the stability effects of social structure and can cause local or regional extinction."[1] But these are the extreme situations.

The ways in which such properties of populations as size, density, composition, spatial distribution, birth and death rates, sex ratio, and others are determined in each population by forces generated by social life, and the differences that may arise between populations as a result of their distinct social evolution, are most easily demonstrable in studies of vertebrate populations as carried out in the confines of the laboratory. The ability to control certain environmental variables — to eliminate predators, for example — makes it possible to focus directly on social factors.

This was exactly the basis of my studies at The Rockefeller University on freely growing populations of mice; they were aimed at clarifying relationships among such properties as social organization, numbers, densities, physiology, and genetic changes. I would like to describe one of these briefly, as it clearly illustrates many aspects of

Professor Wynne-Edwards' thesis. In this experiment, three study groups were set up. Two were freely growing populations and one was a control group; all were initiated with equivalent samples of mice of known genetic and environmental background. The control group consisted of a series of randomly mated males and females kept in standard laboratory cages. The three samples of founder mice were the progeny of crosses among four standard inbred strains.

Over the course of a year, the populations grew rapidly to sizes and densities that were several times larger than any previously reported populations of small mammals—between 800 and 1,000 mice in an area of about 13 square feet, or densities of 60 to 80 mice per square foot. Distinctive physiological and behavioral changes accompanied the socio-ecological transformations that took place in these freely growing populations in contrast to the constancy of physiology, behavior, and demographic processes in the control environment. Circadian patterns of activity disappeared, spatial constellations changed, and aggressive behavior, although diminished, became pathological, with attacks by males on young mice and females, even pregnant ones. Aberrations of sexual behavior, including asexuality, and of maternal behavior became more frequent with increasing population density, and there was a transformation of the basic format of mouse social interaction that involved abnormal responsiveness or a total lack of reaction. The behavior of control mice, by contrast, was persistently stereotyped.

Some of the physiological changes that lie at the basis of self-regulation of populations were carefully documented. There were changes of reproductive physiology, such as a high incidence of foetal resorption and inhibition of ovulation, and lower survival of newborns. Behavioral and social abnormalities were causally linked with these changes. It was noteworthy that the cessation of population growth under conditions of extreme crowding occurred in the face of general physical health and with low rates of adult mortality. Chronic adjustment to extremely crowded social environments was compatible with adult life, but took its toll through behavioral and physiological morbidity.

Distinctive differences occurred in the patterns of population dynamics of the two freely growing populations, although they were maintained throughout in identical physical environments. In other studies, variability of growth curves of replicate laboratory populations had been attributed in part to the uncertainties and diversities of the genetic and social backgrounds of the founding mice.[4,9,10] These confounding factors were eliminated in the studies I am describing. The differences in dynamics between the two populations reflected the evolution in each of them of distinctive behavioral, physiological, and social processes. For example, during the early stages, when the absolute rates of population increase in the two populations were almost identical, the relative contribution of birth and death rates differed in the two populations. During the second half of the study the two populations had altogether dissimilar dynamics. Prominent behavioral differences included the greater incidence of cannibalism and of territorial behavior in one population. In such differences, according to Professor Wynne-Edwards' formulations, lie the seeds for group selection, although this is still a completely theoretical construct.

The specificity of the influence of social factors in these populations was further demonstrated by changes that occurred in many of the biological properties of the animals when they were placed in different social environments at the end of a period of study. For example, at the end of a year and a half, animals of one population were given access to a second large, empty, population enclosure. Emigration occurred, and two distinctive subpopulations formed that differed from each other and to varying extents from the original population. Changes were much more marked in the emigrant subpopulation, although both groups showed a decrease in aberrant behavior and an increase in population growth. Social disorganization was greater in the emigrant subpopulation; there was more fighting and higher mortality, but population growth was sixfold greater than in the other subpopulation.

In addition to showing how social organization can affect physiological reactions that are fundamental to population dynamics, one of the important points made in Professor Wynne-Edwards' thesis is that social interaction and competition act differentially on fertility and survival. This is the concept of social selection as one type of natural selection; the crux of social selection, of course, lies in the contributions of social behavior and social organization to Darwinian fitness and evolution.

Actually, little concrete genetic evidence as yet exists to support this reasonable concept. The potential contributions of inheritable behavior to social success have been suggested by studies with inbred strains of animals that demonstrate differences in behaviors relating to the care of young, to sexual activities, to social dominance and fighting, and so on. An experiment described in the literature suggests that certain inbred mouse genotypes survive less well than others in complex social contexts: mice of one inbred strain studied in population cages appeared unable to establish any social organization, and the members of their populations died rapidly. Other inbred strains proved much more capable of socialization.[2]

There are even some specific observations relating social status to reproduction in natural populations, but little is known about the extent to which progeny of socially successful individuals themselves attain social success and, if indeed they do, to what extent they owe their success to genetic endowment.[7,8] For example, one study showed that while still subadults, sons of high-ranking rhesus monkey mothers gained precedence over older, larger, and stronger males. Whether this success was due to genetic factors or was accorded them because of their previous relationship with high-ranking females could not be determined.[5]

Parenthetically, one reason for using mice from a four-way cross between standard strains of inbred mice in the experiment already mentioned was to make it possible to study changes in gene frequencies in relation to population dynamics and social ecology, and to try to determine the associations between genetic factors, social success, and Darwinian fitness. For convenience, changes of allele frequencies at gene loci associated with polymorphic traits were followed; for example, alleles at loci affecting coat color, pigment production, and others.*

---

* Of course, there is no implication here that alleles associated with visible phenotypes should themselves have any selective value. On the other hand, many

In the initial distribution of founder mice to the two experimental populations and the control, care was taken to assure identical frequencies of given alleles. At periodic censuses all mice were classified according to phenotypic traits related to specific alleles, and gene frequencies were estimated. Differences that took place in the patterns of change of gene frequencies between the freely breeding populations and the control group stood out clearly. Although the magnitude of changes in the frequencies of the recessive alleles in the freely growing populations were not large, the consistency of the changes, the similarity of the changes in the two populations, and the lack of change in the control group, all suggested the action of systematic processes.

The important problem revolved about the nature of the associations between recessiveness at the C locus and Darwinian fitness in the sociodemographic context of the freely growing populations and the genetic system available. This proved to be difficult, although certain aspects stood out. Disease played no selective role in these studies; differential adult mortality with respect to the genotypes observed was excluded on the basis of cohort analysis as an explanation for the changes. Social status among males, as judged by a variety of criteria, did not differ among the different male C genotypes. From observations of sexual behavior and measurements of rates of pregnancy and of weights among the recognizable genotypes, no evidence indicated that reproductive processes differed among them, although certainly reproduction was not a random process in the populations. The increases of recessive c alleles in the populations could have been caused by the relative reproductive superiority of heterozygous (Cc) compared with homozygous (CC) dominant animals, but as heterozygous and homozygous dominant mice could not be distinguished, this possibility was not resolvable. Some observations did point to differential survival of homozygous recessive newborns, and this was per-

---

alleles that determine phenotypically recognizable traits have other effects as well, e.g., alleles that determine coat color in rodents and carnivores also appear to affect body size. In addition, the survival of any allele may reflect the selective value of closely linked alleles. Alleles related to easily identifiable phenotypic traits can thus act as convenient markers for more extended, but as yet "silent," chromosomal segments.

haps related to the consistently superior maternal behavior of homozygous recessive females.

Much work still must be done to establish correlations between behavioral attributes and components of Darwinian fitness, especially in different types of population structures and in different phases of population dynamics. One investigator is currently initiating a long-term research project (10 to 15 years) to observe the evolution of different systems of social behavior in relation to different environments — environments structured to induce different possibilities of social interaction and of population dynamics.[3]

It is worth remembering that knowing the adaptiveness of a given genotype in one type of population setting may be of little use in predicting its success in another population context. For example, qualitatively different forms of crowding, such as difference in the age and sex distributions of crowded animals, may have quite dissimilar behavioral and physiological repercussions. In other experiments, when mice of the same genotypes as those used in the freely growing populations were crowded in unisexual groups of the same age, the growth of animals in the population enclosures was not affected by much greater degrees of crowding.

Adaptation to environment certainly is a criterion of successful evolution. Professor Wynne-Edwards' hypothesis presents a rational framework to explain the demographic adaptation of populations of certain species to one aspect of environment — the quantitative aspects of food resources — admittedly an important environmental component. However, I take exception to his important generalization, for he considers only one segment of ecological adaptation and yet attributes to it the main function of social organization. In any species, social organization forms an integrated whole, and the various types of social behavior represent the multiple interadjustments of any species to the demands of their conditions in nature.

It is not easy to measure the adaptive value of populations. A useful concept, suggested in recent years, holds that successful evolution reflects a population's ability to live and reproduce — that is, to adapt to varieties of environments.[6] Success has been achieved in nature in many ways, but the higher the phylogenetic level, the greater the tendency for success to be associated both with increasing capacities to live in heterogeneous environments and, perhaps even more, with the ability to master and gain ascendency over diverse ecological niches.

Looked at this way, population fitness involves much more than demographic adaptation to underutilization of levels of food resources. It requires a wide array of adaptabilities—adaptabilities to select and use new foods as well as to conserve their quantities; to adjust to other populations and to other species; to explore and to investigate new environments; to exploit opportunities as they arise; to acquire knowledge; to anticipate dangers; to develop new skills. All of these serve to extend the species' range and mastery of environments.

Other adaptabilities appear to be integrated with various forms of social organization and interaction that are unrelated to competition and resource preservation. These forms of social organization, to mention only a few, include the complex social structures associated with the prolongation of the period of immaturity; with family ecology; with cooperative pack hunting; with play behavior; with the expression and communication of complex emotions. I believe that an argument could easily be presented to show that the main function served by social organization has been to extend the range of behavioral adaptabilities and thus to maximize the types of relationships that species can make with increasingly diverse types of environments.

As the number of behavioral adaptabilities to diverse environments increases, the intensity of self-regulatory, behavioral demographic adaptations (which seem so obvious in the populations of certain animal species) diminishes. Many of the outstanding examples in Professor Wynne-Edwards' exposition are derived from studies of birds, and doubts can be raised about the importance of similar systems of conventional competition in the social organization of, for example, such higher vertebrates as primates.

What we know about ancestral human populations suggests the existence of social practices that are quite different from those Professor Wynne-Edwards feels are necessary for population homeostasis and intergroup selection. In many hunting and gathering groups, the ability to give rather than to commandeer food supplies is esteemed.

The sharing of food and shelter both within the family group and beyond it are accepted standards of conduct. Sex and mating are associated more with the extension of social alliances than with hierarchical competition; the solitary "have-nots" of birds or of lower mammalian forms have no counterparts in human primitive bands where marriage and family life are universal institutions essential for survival. Territorial relationships among primitive groups are rarely exclusive. Interband social contact is common and is extended by cultural regulations that direct marriage outside the group proper.

Professor Wynne-Edwards' theory is, I believe, part of the increasing attempts by biologists — especially during the past fifteen years — to explain and generalize many of the newly documented, empirical findings of vertebrate social life. A variety of positions, almost of schools, have arisen, each emphasizing a central concept, such as stress, space, or rates of interaction, as the unifying principle. Some of these theoretical constructs touch on questions of genetics and population dynamics, as well as of social ecology.

The variety of such positions, I believe, attests both to the vigor of present-day interest in these problems, and to the lack of any one general theory under which the many empirical findings can be subsumed. Each of these approaches has something to say and has validity as a partial explanation. In a sense, there is little reason to think that there should be universal laws of social organization or population dynamics. Professor Wynne-Edwards' attempt to develop a general theory to explain social organization and population dynamics for the great variety of existing species living under widely different conditions is a comprehensive and bold undertaking.

Sociology, Biology, and Ideology

MARVIN BRESSLER

Sociology relies on a master paradigm, structural-functionalism, which makes extensive use of organismic and homeostatic analogues, but except at this abstract level it now maintains virtually no commerce with biologically based theories of human behavior. Standard treatments of even such seemingly relevant topics as stratification, intelligence, personality, or social deviation ordinarily ignore biogenic explanations and biomeliorative proposals or introduce them in a polemical context to discount their importance. Indeed, no contemporary sociologist has published a major work that sympathetically confronts recent developments in such fields as genetics, ethology, or comparative psychology. Since there are no masters, neither are there any disciples. The typical novice emerges from graduate study equipped with a detailed inventory of the intellectual infirmities of Malthus, Spencer, McDougall, and Lombroso, and with little inclination to consult their distant heirs.

In maintaining the disjunction between social inquiry and other life sciences, sociologists violate the counsel of the founder of their discipline. It seemed apparent to Auguste Comte that the newly established social physics must be "subordinated to the whole of the

---

MARVIN BRESSLER Department of Sociology, Princeton University, Princeton, New Jersey

organic philosophy, which discloses to us the laws of human nature. . . . The whole social evolution of the race must proceed in entire accordance with biological laws; and social phenomena must always be founded on the necessary invariableness of the human organism . . . No sociological view can therefore be admitted, at any stage of the science, or under any appearance of historical induction, that is contrary to the known laws of human nature."[1] These convictions are explicitly incorporated in Comte's methodological precepts. He urged that the general propositions of sociology should be validated not only by the experience of history and by cross-cultural comparison, but also through systematic observation of animal societies.

Contemporary sociologists have failed to heed such advice for reasons that are, in part, attributable to general forces that tend to inhibit interdisciplinary diffusion and borrowing in any science. Both the expansion of knowledge, which makes specialization a necessity, and the aversion to "reductionism," which makes self-sufficiency an ideal, encourage scholarly insularity. But since sociology has assimilated a tolerable measure of wisdom from anthropology, economics, psychology, political science, and social philosophy, its isolation from biology requires further examination.

We may surmise that this alienation persists partly because most of the earlier, and some of the present, biological approaches to the study of man have been demonstrably inadequate as judged by conventional scholarly criteria. The anthropological, statistical, and logical crudities of such as the Comte de Gobineau, Houston Chamberlain, Madison Grant, Lathrop Stoddard, and Harry Laughlin simply do not deserve the attention of serious men. Several generations of academic critics have exposed the more sophisticated pretensions of social Darwinism and the logical frailties of instinctivism. Thus, for example, they have rightly contended that the proof for the existence of instincts often rests on gratuitous teleological assumptions, depends on circular inferences from observed behavior, and is seldom meticulous in distinguishing postulated innate tendencies from learned responses.

The sociological aversion to social biology, however, is based on more than a routine rejection of faulty evidence. It is also fortified by the lingering suspicion that an explanatory sequence that begins with the organism inevitably ends with predatory ethics. This is a plausible expectation; too often in the course of human history social biology has served the purposes of scoundrels. In the very recent past, the early eugenicists, immigration restrictionists, racists, and the leaders of the Third Reich gave us reason to ponder the policy consequences of biologically oriented social thought. Even within the academy, social biologists have typically preferred conservative solutions of social problems, while environmentalism has been the traditional ally of the liberals. Pastore's study in 1949 of twenty-four disputants in the "nature-nurture" controversy revealed that of the "hereditarians" only Lewis B. Terman qualified as a liberal, while John B. Watson was the sole environmentalist proponent of conservative orthodoxy.[2]

Nevertheless, the thesis of this paper is that social biology has been poorly represented by its philosophers, that the moral implications of social biology are more complex and ambiguous than is ordinarily supposed, and that they do not unduly threaten liberal values. This is not an idle exercise; if the ideologically based resistance to biogenic explanations and biomeliorative measures persists as part of the collective unconscious of sociology, it will continue to neglect recent promising developments in a number of areas, particularly ethology and behavior genetics. Accordingly, we shall 1) offer some selected illustrations of the interconnections between these disciplines and the study of human behavior, and 2) examine the ethical consequences of such transactions.

William McDougall and Herbert Spencer are still regularly exhumed by sociologists to symbolize the ideological menace of the "biological approach." In 1908 McDougall identified instinct as "an inherited or innate psycho-physical disposition which determines its possessor to perceive, and pay attention to objects of a certain class (cognitive), to experience excitement of a particular quality upon perceiving such an object (affective) and to act in regard to it in a particular manner or, at least, to experience an impulse to such action (conative)."[3] He specified eleven such instincts—flight, repulsion, curiosity, pugnacity, self-abasement, self-assertion, parental, reproductive, gregarious, acquisitive, constructive — each of which is associated with its own distinctive emotion (e.g., pugnacity-anger; parental-tenderness) and which together form the basis for all complex behavior. In the ensuing two decades, other social psychologists expanded the original list — L. L. Bernard was able to find an astonishing number of instincts that were detected by various authors during this period — and some of these were introduced into other social sciences.[4] Veblen adduced an "instinct for workmanship" as the basis for craftsmanship; Trotter's discussion of war and peace was derived from a "herd instinct"; and Wallas, Parker, Tead, and Patrick relied on instincts to buttress their analyses of economics, politics, and social problems.[5]

To social reformers, the imputation of such instincts as "pugnacity" or "acquisitiveness" seemed calculated to tarnish the image of man and to deny his potentialities. If each successive generation is endowed by its progenitors with immutable Hobbesian traits, then it becomes the hostage of ancestral tyranny. The corruption, avarice, and mendacity of the human beast then become ineluctable expressions of biological destiny. The reformist ethic was moved to dismiss these intimations of intrinsic perversity as an ideological disguise designed to achieve "the prevention of social change through the gloom of a disillusioning fiction."[6]

Social Darwinism had long since acknowledged that this was, in fact, its intention. Nine years before *Origin of Species,* Herbert Spencer had discovered in the metaphor of evolution a convenient rationale for the defense of privilege and the maintenance of hierarchy. He discerned in nature that, even as predators and victims were locked in struggle, they were unwitting accomplices in a compact to secure the perfection of the species. Spencer coined the durable phrase "survival of the fittest" to describe how in both animal and human societies "all vitiation of the race through the multiplication of its inferior samples is prevented; and the maintenance of a constitution completely adapted to surrounding conditions, and therefore most productive of happiness, is insured."[7]

This process, then, was both a natural law and a universal principle of individual and social ethics. The "shoulderings aside of the weak by the strong, which leave so many [the "incapable," the "imprudent," the "idle"] 'in shallows and in miseries,' are the decrees of a large, far-seeing benevolence."[8] Subsequently, the morality of "fitness" as applied to social classes would require only minor tinkering to convert it to racism. "Inferior" races are merely the most highly visible and least competent of all the losers.

Since McDougall and Spencer we have endured all manner of disputation. Amala and Kamala, Donald and Gua, Jimmy and Johnny, Isabelle and Anna, the families of Jonathan Edwards, and the Jukes and the Kallikaks have long since passed in review. During this period W. H. Sheldon devised a new terminology for Kretschmer's body types and Ernest Hooton rediscovered Lombroso. Twins were separated and reunited, the unidimensionality of intelligence was called into question, biochemical theories of personality experienced an increasing vogue, and of course we have experienced the endless polemic on race and "innate" characteristics.

The dialectic seldom varied; the issue was "heredity vs. environment," "instinct vs. learning," "nature vs. nurture," and "beasts vs. men" — and humane scholars felt obliged to choose the second terms of those paired couplets. The typical sociologist warns his classes that the function of biological theories of social behavior is to elevate impulse above reason; to denigrate efforts to achieve peace, brotherhood, and equality by lending scientific respectability to Calvinistic conceptions of ultimate human depravity; to legitimize the existing distribution of rewards and privileges; to subvert the democratic ethos by insisting on the differential contribution of strategic elites and the talentless mass; to absolve society from responsibility for personal and social disorganization; and to withhold compassion from victims, and furnish a rationale for punishment rather than therapy.

This perspective has not been responsive to current developments in comparative ethology and behavior genetics, partly because these disciplines have only recently matured and most sociologists are simply not familiar with their findings. Much has happened since the discovery of biological evolution, and few scholars are now content to follow the late nineteenth-century fashion of seeking the "ultimate intent of nature." The modern era in the study of animal behavior began in the 1920s with Elliot Howard's description of the social organization of birds, Schjelderup-Ebbe's discovery of a pecking order in domestic fowl, and Allee's comprehensive treatment of animal aggregations,[9] and by now ethologists have identified a great variety of social relationships within and between animal groups. A classification scheme devised by J. P. Scott gives some indication of their range: simple aggregations, dominance-subordination, leader-follower, sexual, care-dependency, mutual care, trophellaxes, mutual defense, and territorial. There has also been considerable work in the area of socialization, especially on the problem of "critical periods" in development.[10] The impressive body of literature that has been produced on these topics during the past two decades cannot be absorbed by casual collateral reading.

Recent popular volumes by Konrad Lorenz (*On Aggression*)[11] and Robert Ardrey (*The Territorial Imperative*)[12] — one a distinguished ethologist and the other a gifted amateur — have doubtless served a certain educational function, but since each revives earlier visions of a beak-and-claw universe, we may anticipate that the ideological stance of many social scientists will probably remain frozen. We may confidently expect a modern-day Prince Kropotkin to repeat his famous query, "If we ask nature who are the fittest: those who are continually at war with each other, or those who support one another?, we at once see that those animals which acquire habits of mutual aid are undoubtedly the fittest."[13] According to Lorenz, "human behavior, and particularly human social behavior, far from being determined by reason and cultural tradition alone, is still subject to all the laws prevailing in all phylogenetically adapted instinctive behavior."[14] This assumption permits him to proceed nimbly from the description of animals to sociological analysis. He concludes, for example, that animal aggression is a truly "autonomous" instinct that has both useful and dangerous properties. Intraspecific aggression performs the positive function of assuring the balanced distribution of animals of the same species over the available environment, selection of the strongest by rival fights, and defense of the young,"[15] and under certain circumstances it produces the "blossoms of personal friendship and love."[16] However, he refers also to Steiniger's work on the brown rat, which is gentle and considerate within its own clan and murderously brutal to inadvertent intruders. The human counterpart of this model of intense ethnocentrism is presumably the virulent nationalism that defines other people as enemies and seeks their destruction merely because they are foreigners. Lorenz has no hesitation in concluding that a Martian visitor who was also a knowledgeable ethologist would observe "that man's social organization is very similar to that of rats."[17]

Some of the recent speculations on the direct applications of genetics to human populations appear, at first glance, even more "conservative" than the Lorenz translations from animal behavior. For example, Bruce Eckland's forthcoming essay in the *American Sociological Review* on the integration of genetic and sociological principles — the first such piece ever to appear in this journal — predictably will revive ideological controversy.[18] Eckland notes that social classes are breeding populations," i.e., "aggregates of individuals who are statistically distinct from other aggregates with respect to some gene frequencies as a result of assortative mating." This assertion is supported by modest correlations — in the order of .03 to .06 — in the measured intelligence of spouses. The significance of these considerations lies in the strong positive relationship between test intelligence and various indexes of socio-economic status; the genetic component in IQ is substantial, according to some students accounting for perhaps as high as 70 per cent of the interindividual variance. We may anticipate that the within-class variance in intelligence will contract and the between-class variance will expand.

Given these assumptions, it is reasonable to suppose that the differential birth rate, coupled with a demonstrated inverse association of family size and IQ should result in a declining quality in the population. The reasoning that underlies this expectation is that persons of low ability in the lower social strata will outbreed groups with "superior" endowments. Yet, a number of recent studies in Scotland, England, New Zealand, and the United States fail to reveal any significant intergenerational differences in over-all IQ level.[19] This seeming anomaly may be resolved by noting that "although the least intelligent groups produce more children within marriage, they are the least likely to marry." Any change in the total processes of selection that encourages the fertility of the less gifted without compensatory gains in more able population elements would act to confirm earlier neo-Spencerian prophecies. Eckland's clear implication that demography is, and of right ought to be, both a biological and social science may offend the current *Zeitgeist,* which implies that population quality is a simple function of increasing educational opportunity.

Similarly, Eckland's treatment of social mobility will undoubtedly strike some sociologists as a genetic defense of the *status quo.* Most studies of social mobility measure intergenerational occupational movement. "Perfect mobility" is said to exist when each stratum contributes the identical proportion of sons to any given occupation. Any deviation from this model presumably reflects inequalities of opportunity. However, this assumption is defensible only if we assume that intelligence is equally distributed throughout all strata. If, as Eckland contends, assortative mating and genetic processes account for an appreciable proportion of the variance in intelligence, it "is becoming increasingly unlikely that the same proportions of children from each class have equal capacities to take advantage of their opportunities. The tendency for elites to replace themselves (intergenerationally) is somewhat ensured by the nature of any system in which intelligence is a dynamic factor affecting status placement." It would seem to follow from this analysis that, because the American system of social stratification reflects patterned genotypic variations, it is more rational and equitable than is ordinarily acknowledged by the conventional wisdom of sociology.

A number of behavior geneticists have argued that "psychological groups" may also be treated as Mendelian populations. Recent investigations by Cattell, Blewett, and Belloff, by Vandenberg, and by Gottesman have demonstrated the existence of a genetic component in the observed variation of some personality characteristics.[20] Gottesman, whose studies are the most recent and methodologically sophisticated, concludes that in general "the greater the gene similarity, the greater the personality similarity."[21] These findings likewise suggest that, to the extent that personality is important for achievement and social position, some groups may possess genetic advantages denied to others.

Sociological interpretations of personality, by contrast, typically emphasize uniformities in national character or assume that observed differences are a function of variation in social structure. Differential rates of pathology by ecological area, social class, or educational level are usually attributed to shared features of the environment, while individual propensities toward health or illness are treated as if they were equally distributed throughout the population. Thus, Hollingshead and Redlich's demonstration that the lowest socioeconomic levels have disproportionately high rates of schizophrenia is often wholly explained by the ego deflation that results from public symbolization of low status.[22]

In sum, sociology's traditional antagonism to biogenic theories of social behavior will probably not be assuaged by the sample of recent work in animal behavior and behavior genetics to which they have been exposed. This would be a pity, for there is much to be learned from social biology that involves no hazard to a liberal, humane, and ethical social policy.

Science sets limits beyond which ideologies become mere fantasies. Much of the antipathy to social biology arises from its presumptive threat to the empirical foundations of welfare liberalism. This doctrine, which claims the loyalty of most sociologists, is rather more precise in mood than in substance, but it does not lie outside the range of useful definition. The sources of contemporary liberalism are the political theory of John Stuart Mill, the jurisprudence of Jeremy Bentham, the economics of John Maynard Keynes, the philosophy of John Dewey, the psychology of John B. Watson, and the sociology of Lester F. Ward. It consists of a congeries of values and convictions that includes the "goodness" of man; a sense of compassion and moral concern for people of all nations; the supremacy of rational intelligence in assuring the welfare of mankind; the plasticity of personality; equality of opportunity as a means of improving the lot of the poor, powerless, and oppressed; collective planning to achieve social goals, particularly economic security; the inviolability of dissent; and above all, the desirability, necessity, and inevitability of gradual social change.

This complex of beliefs has traditionally been associated with faith in the omnipotence of the social environment and is allegedly challenged by biogenic and biomeliorative approaches to the human condition. This perception has its source in three general propositions that many, perhaps most, academic liberals have extracted from what they regard as the main tradition of classic and contemporary social biology. These may readily be recapitulated:

1 The social behavior of animals may be extrapolated to human behavior.
2 The characteristics of each are largely genetically "determined" and as such are not markedly responsive to environmental influences. Some of these inherent characteristics are valuable — intelligence, strength, perseverance, for example — and are differentially distributed among social strata and races. Biological superiority thus legitimizes social inequality, race prejudice, and discrimination.
3 Many of these autonomous traits are morally vicious — aggression, greed, sloth — and are universal human properties that negate any possibility of creating and sustaining a rational and compassionate social order.

The argument advanced in the ensuing paragraphs is that these propositions either misrepresent contemporary ethology and behavior genetics, are extraneous to their central findings or derivations, or lend themselves to more benign ideological interpretations than is ordinarily supposed.

THE CURRENT STATUS OF THE POSTULATE OF EXPORTABILITY

Edmund Leach has observed that "Men indeed are animals, but surely they are more than that."[23] The "more" includes what eighteenth-century philosophers called "reason," nineteenth-century anthropologists referred to as "culture," and twentieth-century psychoanalysts are pleased to name "ego" and "superego." Something akin to this is expressed in popular form by a character in Truman Capote's recent crime documentary who tells her brother: "You are a human being with a free will. Which puts you above the animal level."[24] The common idea underlying all these distinctions is that man's sophistication in using tools and manipulating symbols substantially emancipates him from his "animal nature."

B. F. Skinner takes note of the methodological implication of these discontinuities in a passage that merits extended citation:

> [There are] several kinds of pecking orders, differing in their provenances. Some dominant and submissive behaviors are presumably phylogenic stereotypes; the underdog turns on its back to escape further attack, but it does not follow that the vassal prostrating himself before king or priest is behaving for the same reasons. The ontogenic contingencies which shape the organization of a large company or governmental administration show little in common with the phylogenic contingencies responsible for the hierarchy in the poultry yard. Some forms of human society may resemble the anthill or beehive, but not because they exemplify the same behavioral processes.[25]

Ethologists generally concur with Skinner's *caveat* that similar patterns of behavior in men and animals may not arise from similar contingencies. Ardrey's insensitivity to this point reflects the excessive enthusiasm of the newly converted, and Lorenz is a conspicuous deviant among serious scholars. Ardrey, for example, clearly claims too much when he concludes that man is "as much a territorial animal as is a mockingbird singing in the clear California night. We act as we do for reasons of our evolutionary past, not our cultural present . . . if we defend the title to our land or the sovereignty of our country, we do it for reasons no different, no less innate, no less ineradicable than do lower animals."[26] Such magisterial verdicts ignore the most elementary principles of sampling and the rules for establishing generalizations.

What, then, may we learn about ourselves from studying the behavior of animals? At the very least, they furnish us with an incredibly rich source of instructive fables. In an early experiment, Craig deprived the blond ring-dove of female companionship. Within a short time, the bird performed his courtship dance for a white dove, later for a stuffed pigeon, penultimately for a rolled-up cloth, and finally, after two weeks of celibacy, he preened in the privacy of his cage for a nonexistent mistress.[27] Lorenz approvingly quotes Goethe's Mephistopheles: "Having imbibed this potion, you will soon see Helena in every female."[28]

The number of such parables could be endlessly extended, but the literature of animal behavior should not be mistaken for an art form. Facile extensions of animal lore to social behavior are not yet science, but neither are they all demonstrably false. They cannot be verified or rejected until such time as there exist systematic propositional inventories recording the consonant and dissonant behavior patterns of men and other species in their full variety and complexity. The prospects of creating a unified biosocial science are surely not tomorrow's, but it would be a betrayal of a fundamental belief in a coherent universe to dismiss this aspiration as mere fantasy. The insistence on disciplinary isolationism may be the academic version of the territorial imperative.

Paul Cameron's unpublished manuscript on the sources of alienation — feelings of "hostility, distrust, confusion, meaninglessness, apathy, and powerlessness" — represents one effort to integrate ethological and sociological findings.[29] The burden of the author's message is:

1 that we may distinguish four major clusters of "animal values" ("community," "living space," "comprehension," "lack of physical want") that govern men as well as other species, and a like number of "human values" ("status," "freedom," "usefulness," "equality") that have primary reference to *Homo americanus;*
2 the "enduring structural violation" of any of these desiderata will be accompanied by an increase in the incidence of alienation;
3 the congeries of "animal values" constitutes a parsimonious scheme for the analysis of alienation in both the lower phyla and men (e.g., when previously isolated rhesus monkeys or children are introduced into a group, they each exhibit tendencies toward initial partial assimilation and then subsequent withdrawal);
4 all known empirical findings on human alienation may be referred to the system of animal values, including those that are also responsive to "human values" (e.g., leaders who presumably "comprehend" more and exercise greater "freedom" than their followers are correspondingly less alienated) and those that fall outside the range of purely social hypotheses (e.g., the finding that persons who are physically isolated

while at work score high in measures of alienation becomes comprehensible in the context of "living space" values, but not otherwise).

Cameron's specific formulations await further study, but his effort to utilize a simple conceptual scheme to analyze alienation in men and animals is surely a useful exercise in middle-range hypothesis formation. It is possible to think of even more general and abstract propositions. Ardrey has proposed the existence of an "amity-enmity" complex, which he has half-seriously expressed in the formula $A = E + h$: "The amity, in other words, which an animal expresses for others of its kind will be equal to the sum of the forces of enmity and hazard which are arrayed against it."[30] He adds by way of further clarification that "only when defense of what is mutually theirs turns their antagonisms jointly outward may we properly speak of effective amity."[31]

This phenomenon has been observed in numerous animal species and is confirmed by Lorenz even for fish. It appears that families of militant aquarium cichlids will live amicably together so long as they occupy the same tank with more pacific neighbors who serve as congenial targets for their aggression. If the latter are removed, the male cichlid will frequently devour both his spouse and progeny.[32] It is all the more remarkable that Robin Williams' influential inventory of research on intergroup tension contains the following proposition: "The probability of internal group conflict is lowered by the presence of an outside threat which endangers all groups. To find a common dislike is apparently one of the most frequent and gratifying experiences in creating a bond between individuals. It is as though uncomfortable latent hostilities between the two parties are removed by deflection to a third, outside object."[33]

It is noteworthy that Williams discovered the amity-enmity complex without benefit of ethological guidance, which rather suggests that the most parsimonious study of mankind may yet be man. In any event, the detection of resemblances is subject to all the hazards previously cited. Meanwhile, the study of animal behavior will yield no less than suggestive analogues, rich sources of hypotheses, and a wider repertoire of concepts. These are considerable gifts, and they need not be spurned because they sometimes come wrapped in the coarse language of neo-instinctivism.

THE CURRENT STATUS OF THE POSTULATE OF GENETIC DETERMINISM

Few students of animal behavior and virtually no geneticists now speak of "autonomous instincts." Mounting evidence from field and laboratory indicates that some species engage in complex communication, alter their behavior in response to each other, and are influenced by their physical environment. Numerous experiments have demonstrated that environmental stimulation or deprivation can have marked effects on animal learning, perception, emotion, and psychomotor skills.[34] Schaller's summary of the behavior of apes under natural conditions reveals that marked differences can exist even within the same species in different sectors of its own range. For example, chimpanzees in open woodlands sometimes eat monkeys and antelopes and make tools from twigs, while those in the rain forest have never been observed behaving in this fashion.[35]

Human geneticists are even less willing to view the world as a contest between heredity and environment. As J. M. Thoday observes:

> Every character is both genetic and environmental in origin. . . . Genotype determines the potentialities of an organism. Environment determines which or how much of these potentialities shall be realized during development. The doctrine of fixed abilities is nonsense. . . . When asking about the genetic factors or the environmental factors that influence intelligence, or any other characteristic, we are asking about the causes of variety in a population and . . . unless the populations have been artificially produced by special breeding programmes designed to eliminate genetic variety, the causes of variance are *always* both genetic and environmental and the variance can be partitioned into three components, genetic variance, environmental variance and variance arising from genotype-environment interaction.[36]

Even seemingly trivial genetic variance may have meaning, but only in relation to a given population, and its arbitrary character may best be illustrated by referring to deliberately contrived games with fixed values. The difference in performance between two major league baseball players, one reaching base 128 times and the other 112 times in the 400 official times at bat, is expressed in batting averages of .320 and .280 respectively, and is reflected in an annual salary differential that may be as high as one thousand dollars per percentage point. The margin between a national celebrity and a competent journeyman might actually consist of a millisecond advantage in speed that permits the first player to convert poorly stroked balls to the infield into "leg hits" about three times a month.

The significance of genetic variation, then, depends on specific circumstance and must always be interpreted in relation to social expectations, rewards, and sanctions. Indeed, it cannot be assessed at all unless all the actors are operating under the same opportunities and constraints. In a recent address to the National Academy of Science and in a subsequent interview, the Nobel laureate William Shockley failed to heed these fundamental principles, with consequences that have been described as "mischievous" by the entire faculty of genetics at Stanford University. According to Shockley, "the marrow of the city slum problem [is] our uncertainty about its genetic aspects and our fear to admit ignorance and to search openly for relevant facts.... The possibility of significant research is, I believe, materially impeded by the fact that such research will inevitably bear on intelligence distributions of ethnic minorities in general and American Negroes in particular."[37]

In point of fact, there has been considerable research on race differences in intelligence, but the ambiguities are greater than Shockley imagines. One fundamental problem is the difficulty of developing workable definitions of key variables. There are no "pure" races and hence no pure comparisons, and the usual custom of referring to intelligence as if it were an indivisible unitary trait ignores the best substantiated findings about the cognitive domain. The multidimensional character of intelligence is well exemplified by the factorial model of the "structure of intellect" created by J. P. Guilford and his colleagues.[38] A three-way classification scheme specifies the 1) *operations,* "major kinds of intellectual activities or processes" including cognition, memory, divergent production, convergent production, and evaluation; 2) *contents,* "broad classes or types of information discriminable by the organism," including figural, symbolic, semantic, and behavioral; and 3) *products*, "forms that information takes in the organism's processing of it," including units, classes, systems, transformations, and implications. The relationship between these parameters is still moot, and in the important cases of the cognition and retention of knowledge vis-à-vis "divergent production" or "creativity" the association is probably weak, and possibly even negatively correlated.

The subtleties are seldom reflected in the various IQ instruments that are ordinarily employed to measure race differences. On the average, the test performance of Negroes is inferior to whites, but there is, nevertheless, considerable statistical overlap in the distribution of scores. Since the tests are flawed and the two populations differ in learning opportunities and motivation, it is reasonable to suppose that some undetermined proportion of the variance may be attributed to environmental features. However, when selected indexes of social class are held relatively constant, differentials in measured intelligence usually contract, occasionally expand, and sometimes remain unchanged. In the face of so many uncertainties, most social scientists have properly concluded that there is "insufficient evidence to demonstrate intrinsic racial differences in intelligence."

However, it is conceivable that, under optimum testing conditions, whites might indeed prove "superior" to Negroes, the races might be "inherently equal" or, for that matter, Negroes might score higher than whites. The essayist David Cort has cited several bits of data in support of the third alternative. As early as the turn of the century, there were reports that Basutos often surpassed their white counterparts in competitive examinations administered by the British. More recently, the head of the medical school at Natal University has testified that Negro students become superb physicians, and Buckminster Fuller has noted that students at Nkrumah University mastered spherical trigonometry more rapidly than did any of his white classes.[39]

This fragmentary evidence hardly constitutes persuasive proof of the intellectual superiority of Negroes, but, as hypotheses go, it is as reasonable as any. It seems highly arbitrary to assume that intelligence tests and environmental deficits in the United States are so perfectly calibrated as to account for the precise number of IQ points by which Negroes differ from whites. Why dismiss the possibility that the punitive environment to which Negroes are exposed has increased the disparity between their measured and "true" scores by a margin sufficiently great to conceal that they have crossed the white threshold? In the absence of the severe penalties incurred by Negroes, they might not only close the IQ gap as egalitarians maintain, but just as plausibly actually reverse the direction of the point spread.

Although Shockley concedes "that plenty of Negroes . . . are superior to plenty of whites"[40] he does not appear to be in genuine doubt about the ultimate findings of dispassionate inquiry. The Stanford geneticists, who include among their number no less a scientist than Joshua Lederberg, have deplored "his innuendoes about the hereditary basis of the purported intellectual and social deficits of Negroes, and the tone of his entire discussion about 'bad heredity.'" Lederberg and his colleagues agree that Shockley has made "some constructive suggestions — the essentiality of more research in genetic factors in social maladjustment . . . ." but add "the plain fact is that we do not know the answers to his provocative questions, and in our present-day context it falls between mischief and malice to make such a prejudgment in his terms."[41]

But why "mischief" and why "malice"? These are not terms of academic but of ideological outrage. What if all racist allegations were confirmed? Suppose it should turn out that intelligence is 1) a unidimensional trait; 2) adequately measured by test performances; 3) differentially skewed "in favor" of whites over Negroes; 4) eufunctional for all individuals and populations in all historical circumstances, and therefore specifically related to residence in mansions or slums. The Stanford geneticists have formulated a number of appropriate responses for this set of contingencies.

"Howbeit we can be sure of two things: 1) that under any circumstances the rate of the genetic change of the population is very slow compared to the changes in our social institutions, and 2) even if we adopted a totalitarian answer on Shockley's premises, there would be plenty of residual variability to contend with. In these circumstances we can hardly neglect another prescription that Shockley overlooks —

to work out the techniques of medical care, education and industrial and economic organization that can create incentives and useful careers for the whole wonderful variety of human beings."[42]

These are cogent, indeed unanswerable, arguments. Sheltered by this protective logic no militant civil rights advocate need retreat from a single demand for social justice. The potential mischief, then, is presumably psychological. The Stanford geneticists do not say so, but they are apparently troubled that the doctrine of "innate" racial characteristics might further damage the egos of the "inferior" and invite prejudice from the "superior." Expectations of this sort obviously merit the most serious attention. There is no denying that, since all Negroes recognize themselves as such and are so identified by others, any suggestion that taken collectively they are inherently intellectually inferior would also be a blow to their individual self-esteem. The deflation of self-worth among Negroes would be aggravated because of their disproportionate representation in lower socioeconomic strata. The allegation of biological inadequacy would deprive them of the consolation that the social environment is the exclusive determinant of achievement and would remove one of the possible sources of redemption that ease the burden of personal guilt that often accompanies publicly symbolized failure. The psychological injury would be especially painful if the verdict of inherent intellectual inferiority, no matter how qualified, were delivered in the awesome name of science. Such ascriptions could, moreover, be perceived as still another transparent rationale for the consolidation of white power, the maintenance of invidious status distinctions, and the perpetuation of injustice. Any such conviction would result in the development of defensive strategies and increasing militance, which would also disturb the psychological serenity of the white majority.

The imputation of inherent intellectual inferiority would affront all Negroes, but the intensity of their reactions would probably vary according to the strength of their allegiance to one of three classic positions — integration, separatism, pluralism — that define the choices of racial identity and tactics.

The philosophy that animates the struggle for racial integration is that the only definition of equal is "identical." The empirical counterpart of this stance is that all of the apparent differences between Negroes and whites are reducible to something else, usually socioeconomic status. We are asked to be "color-blind," as if the term Negro lacks all descriptive utility and the recognition of difference is an indiscretion. In the name of "full citizenship," Negroes voluntarily offer to become invisible men.

The emergence of black nationalism was a predictable counterreaction of a people who wished to reclaim its identity. It includes all the intellectual trappings of other minority groups in the United States, including their ethnocentrism. According to the mystique of Negritude, to be Negro is to belong not only to a race but to a culture, which, because it has been developed by a people degraded yet ennobled by suffering, is more spontaneous, free, and compassionate—that is to say, superior to white America—in its life styles and in its art. The slogan "black power" is, among other things, one symbol of the Negro's discovery of his distinctiveness and self-worth. It modifies an old verdict to read "separate but morally superior" and signifies that black people do not seek amalgamation but a negotiated peace.

Black chauvinism in its more restrained forms is probably healthy, at least temporarily, in a people that has had to endure for so long so many assaults against its self-esteem. Nevertheless, as Negro freedom and opportunities expand it may be possible for them to achieve a rapprochement between extreme positions. The integrationist says that he is an American and not a Negro; the separatist says that he is a Negro and not an American. The cultural pluralist insists that he is a Negro—and therefore different—and an American—and therefore part of a whole—and that he wishes to be both.

The assertion of white intellectual superiority would be least tolerable to black separatists, who would presumably welcome quite contrary assurances, and very offensive to integrationists, who are made uncomfortable by any evidence of differences, let alone those that are in the wrong direction. Only pluralists could maintain a substantial measure of composure if the statistical distribution of socially valued characteristics were not identical for all groups. Their participation in the broader society would persuade them that none had a monopoly on virtue, vice, or talent. At the same time, pluralists would be confident that each group, out of the totality of its experiences, could make its own *distinctive* contribution to the intricate texture of American life. Some groups might be more heavily represented in the arts, others in the sciences, and still others in equally valuable pursuits. And since every identifiable group is the product of a unique history, which may have included exposure to differential selection processes, it would not be surprising if genetic rather than environmental influences sometimes explained a higher proportion of the variance in observed behavior.

The capacity of any minority to accept serenely the fact of resemblances and differences among people presupposes that the majority will not frustrate their aspirations for full emancipation. There are differences in average IQ scores among white ethnic groups, but the origin and nature of Irish characteristics, for example, are not a matter of public debate or anxious self-scrutiny, precisely because a once-persecuted minority has now been absorbed — despite an unfavorable stereotype — into the mainstream of American society. In this connection, the Stanford geneticists seem to believe that any appearance of scientific support of a doctrine of intrinsic race differences might have unfortunate effects on the attitudes of the white population. It would presumably reduce the fervor of the virtuous, justify the passivity of the uncommitted, and provide moral succor to the bigot. These defensible expectations must be balanced against countervailing considerations. An ideology that tacitly appeals to biological equality as a condition for human emancipation corrupts the idea of freedom. Moreover, it encourages decent men to tremble at the prospect of "inconvenient" findings that may emerge in future scientific research. This unseemly anti-intellectualism is doubly degrading because it is probably unnecessary.

The origins of prejudice are each extraordinarily complex, and the precise nature of their interconnections is by no means clear. The role of rational conviction in sustaining racial bias is especially obscure. The bigot is apparently a man in the thrall of a social generalization. He perceives that members of various socially visible groups share common properties and that these displease him. A case in point is the recent *cause celèbre* of the school-board election in Wayne, New Jersey. The electorate overwhelmingly supported one incumbent who had urged the defeat of his rivals on the explicit grounds that they were Jews and therefore given to lavish spending for educational purposes. Since no one has suggested that extravagance is biologically transmitted, it follows that a cultural explanation, say the vaunted Jewish "learning tradition," will also suffice to support an ominous generalization.

The fact is that any science that confirms the existence of differential *biological* or *social* characteristics runs the risk of furnishing comfort to bigots. Academic liberals who are sensitive to such dangers are confronted by several alternatives: 1) abandon the quest for social generalizations; 2) correct substantive inaccuracies; or 3) educate their constituencies to the fact that they are mostly irrelevant for social policy. The first course would represent the defeat of science and of self-conscious efforts to record the diversity of human experiences, and the second, while sometimes useful, may disarm morality by making it unnecessarily vulnerable to particular facts that are always provisional and sometimes "embarrassing" or true. In Wayne, for example, the political victims could not have truthfully denied the empirical validity of the "indictment" even if they had been so disposed. Both ethics and strategy commend the adoption of the third course. Liberals would do well to inform the citizens of Wayne that fiscal conservatives may quite properly reject a candidate whom they regard as dangerously prodigal, but not because he belongs to a socio-religious subcommunity in which such tendencies are said to be prominent.

From a purely strategic viewpoint, it is always the better part of wisdom to say no more than is necessary to sustain a position. To insist on the "biological equality" of all races is to violate the law of parsimony if the demonstration of statistical overlap will do just as well as a scientific basis for freedom movements. The Negro struggle for equal opportunity does not require proof that identical proportions of Negroes and whites occupy specified points on a curve of intelligence, but only that *some* Negroes are equal or superior to some whites. Since the second of these contentions is virtually tantamount to saying that a Negro is human, it asserts the most basic and incontestable of all scientific facts. And men are not required to submit their biological credentials to earn the freedom to participate in the amenities of a civilized society.

To recapitulate: the preceding discussion has considered a variety of potential consequences of a hypothetical outcome for which there is no demonstrable proof, i.e., that the mean difference in white-Negro IQs depicts the genetic capacities of the races. The over-all conclusions are that, in the doubtful eventuality that such a finding could be sustained, 1) Negroes would experience considerable psychological discomfort, which, however, could be diminished by the antidotes of cultural pluralism and a just society; 2) evidence purporting to show intrinsic racial differences in intelligence imposes no rational restrictions on the struggle for racial justice; and 3) the liberal emphasis on biological equality as the basis for social ethics is misplaced because it unnecessarily rests on empirical generalizations, which are, in principle, subject to verification and therefore vulnerable.

Similar issues arise in relation to the liberal defense of equal opportunity for all social strata. In this connection, we may distinguish three ideal-typical social structures: 1) *caste* systems that prohibit social mobility and are governed by the principle of unequal rewards for equal talent; 2) *meritocracies* with class systems that permit free social movement and offer equal rewards for equal talent; and 3) *egalitarian* systems that provide equal rewards for unequal talent and hence have neither social strata nor mobility. Egalitarian ideologies specifically deny that any moral significance should be attached to superior capacities and skills, so they are, by definition, indifferent to the profile of genotypic variation. Genetic findings are important, if at all, only for competing claims of caste and class.

The theory of meritocracy is, of course, one of the foundations of democratic capitalism, and it survives in suitably amended form as the official creed of virtually all sectors of articulate American social thought. It recognizes that modern economies have highly differentiated occupational requirements and must rely on elaborate social mechanisms to identify, train, distribute, and reward talent. The United States relies primarily on formal education and an open-class system to perform these tasks. In principle, free universal compulsory schooling should furnish quality education to all children; that is, it should train each to the full limit of his capacities. There is increasing consensus that this goal requires the elimination of all impediments to learning, including those which, like the culture of poverty, are external to the school.

The structure of social rewards — the differential distribution of possessions, prestige, privilege, and power — should serve as a major motivational device to bring the hierarchies of trained talent and occupational requirements into proper alignment. Accordingly, eligibility for admission to every stratum should be determined by universalistic criteria and be equally accessible to all. In short, equality of opportunity is not only a principle of democratic justice, but also a functional desideratum of rational social organization.

Liberals and conservatives view the process of social mobility in the United States from rather different perspectives. Liberals identify with the losers, are the theoreticians of lower class failure, and their diagnoses and vocabulary — "initial disadvantages," "trained incapacities," "arbitrary disqualification" — are freely borrowed from sociology. Conservatives celebrate the triumphs of the victors and prefer to speak of "ambition," "dedication," and "superior intelligence" in the manner of the older social biology. Such disputes are ultimately reducible to factual questions about the nature, magnitude, and causes of the disparities between actual and ideal opportunity structures.

It is conceivable that disinterested inquiry might confirm the conservative suspicion that native ability and social position are more consonant than liberals are now willing to concede. However, the principle of equal opportunity itself is quite safe from empirical assault unless we can imagine a series of findings that are contrary to all existing social and genetic knowledge, among them the following:

1 the determinants of social position are identical in all societies and in all historical circumstances;

2 at any given point in time genetic mechanisms account for all of the interstratum variance in such determinants;
3 the genetic characteristics of a stratum are transmitted intact to succeeding generations.

To state these propositions is to perceive them as false. The criteria of "success" obviously have varied according to time, place, and circumstance. The classic polarities of sociology and cultural anthropology — qualities-performances, sacred-secular, production-consumption, wealth-family, Apollonian-Dionysian — are enough to suggest the diversity and instability of the determinants of honor, power, and life chances. Clearly, even such biological categories as age, sex, and race have equivocal social meanings. Jackie Robinson, for example, retired laden with fame and wealth, while Josh Gibson, an even greater Negro ball player, was born too soon, and died in poverty and obscurity.

Emotional stability and intelligence might plausibly be advanced as likely candidates for consideration as universally necessary, if not sufficient, conditions for success, at least in social systems that value achievement, but both have vague and variable meanings. Moderate associations are reported between these characteristics and socioeconomic status, and hereditary may account for some of the interclass variance. The residual variability is, however, clearly substantial, and is at least in part accounted for by inequities and inefficiencies in the mechanisms of manpower allocation.

There is also considerable evidence that one consequence of genetic variability is that both "bright" and "dull" parents produce children who regress to the mean of intelligence of the total adult population. The discrepancy between parent-child abilities may be substantial, and the incidence of poor synchronization is probably greater than observed because environmental factors disguise the superior intelligence of some children and the limited gifts of others.

All of this suggests that American society, the liberal ideology, and the science of genetics have an equal stake in equal opportunity in education, employment, housing, medical care, and so forth. For American society it is, among other things, a necessary condition for the rational allocation of manpower; for liberalism it is a fundamental principle of social ethics; and for genetics it is a methodological requirement for discovering the actual profile of genotypic variation.

THE CURRENT STATUS OF THE POSTULATE OF INCURABLE DEPRAVITY

Opponents of social change have traditionally found it convenient to speak of "human nature" as if it were 1) immutable, 2) manifested in autonomous instincts, 3) deducible from animal behavior, and 4) incurably depraved. These propositions have a certain logical affinity, and having rejected the first three, social biology could hardly accept the last.

The ethological literature is clear that animal behavior exhibits a wide spectrum of characteristics, which by human standards varies from Christian forbearance to extreme brutality, and is amenable to diverse and often contradictory extrapolations. There is in much ethology an unmistakable strain of do-goodism, even tenderness. Lorenz speaks feelingly of the psychic trauma experienced by lonely graylag geese, and compares their plight to the hospitalized children described by René Spitz.[43] It would be odd for an ethology that asserts the fundamental unity of all living organisms to insist too much on the divisions in the kingdom of man. If fish and birds are my kinsmen, then so assuredly is all humanity—the foreigner, the poor, and the dispossessed. The voice of instinct may yet be heard as the spokesman for One World and Brotherhood Week.

Meanwhile, if we are to believe Lorenz, we may note with gratification that the same "parliament of instincts" that decrees that animals, and presumably men, shall be aggressive also determines that they shall be courteous, friendly, and in need of gentle company. The existing data on our nearest evolutionary neighbors, the primates, are especially useful in demonstrating that some animals have congenial personalities and live in egalitarian societies. The recent volume on primate behavior edited by DeVore is instructive:

On aggression: "Langur groups can be characterized as peaceful and relaxed; their members are seldom aggressive and serious fighting is rare. A langur spends most of his life in a relaxed manner, eating, sleeping, and grooming."[44]

On territoriality: "The almost complete overlap of some ranges and observations on peaceful interactions between groups indicate that gorillas have no territory in the sense of an exclusive area defended against others of the same species."[45]

On dominance: "Although there was some evidence of differences in status between individuals, dominance interactions formed a minute fraction of the observed chimpanzee behavior. There was no evidence of a linear hierarchy of dominance among males or females; there were no observations of exclusive rights to receptive females; and there were no permanent leaders of groups."[46]

There are evidently enough models in the animal realm to sustain any number of contrary ideologies, provided only that one is sufficiently selective and avoids contrary instances. But even if some characteristics were demonstrably autonomous, brutish, universal, and transpecific, it does not follow that thoroughgoing sociogenic explanations would offer greater comfort to liberals. This is partly because some "conservative" instincts have surprising extensions. Ardrey, who is fond of twitting liberals for their tender-minded innocence, takes his place with the gentlest of "doves" in at least one phase of current foreign policy discussions. He concludes that escalation in Viet Nam must fail in any ultimate sense because no intruder, whatever his moral pretensions, can overcome the release of energy that is the unique possession of defenders who are moved by the territorial imperative.[47]

An even more pertinent consideration is that the thesis "you can't change human nature" and social reform is therefore futile is actually not much enhanced by appealing to biology. The content of an imputed motive force, its extensiveness in space, or its constancy over time may be just as plausibly affirmed without referring to any presumed "constitutional" base or to the mechanism of heredity. The universality of "aggressiveness" can as readily be declared a functional requisite of social existence, or assumed heuristically. As K. S. Lashley shrewdly observed at the height of the instinct controversy: "The anti-instinct movement was aimed primarily at the postulation of imaginary forces as explanations of behavior. It was incidental that they had been assumed to be constitutional. Somehow the argument got twisted. Heredity was made the scapegoat. . . ."[48]

Aggression becomes no less imperious when we discard the term "instinct" unless we can imagine conditions that might cause it to vanish. The influential social-psychological frustration-aggression hypothesis, for example, offers very few degrees of freedom and even less comfort to anyone who considers frustration an unavoidable feature of social life. An unsought causal sequence, whether social or biological, is equally tyrannical unless, at least in principle, it can be forestalled or controlled.

The eugenics approach is one such effort. It seeks to maximize the probability of creating superior genotypes through both "negative" and "positive" selection. Negative eugenics is more common, and includes such measures as sterilization, abortion, genetic testing, and counseling. Positive eugenics has been less prominent, partly because it violates social codes (e.g., genetic breeding) and also because until recently the basic mechanisms of heredity were regarded as unmoved prime movers that were forever beyond human control. Spectacular developments in molecular biology now promise that it should become increasingly common to correct genetic "errors" at their source. Bonner, for example, has speculated that "it may become possible . . . to cure diabetics by resetting and reactivating the genes responsible for making insulin, which have become repressed through degenerative disease. It is even conceivable that whole genetic programs can be reset to replace tired or damaged organs, or to generate entirely new or additional ones."[49] Similar prophecies have been made about imminent genetic intervention in areas of greater concern to social scientists, including personality and learning.[50]

The most interesting proposal for a program of positive eugenics has been advanced by Muller, who has urged a sweeping program to counteract an anticipated deterioration in the gene pool as a result of culturally mediated selection processes. A sperm bank would be established and, after a period of twenty years to allow better evaluation of the real merits of the donors, superior females would be impregnated through artificial insemination.

As for the female, "means are already known by which the multiple release of mature eggs can be readily affected within the female with the aid of a pituitary hormone. Comparatively little research would be required to develop suitable methods of flushing out these eggs from the female reproductive tract, to be fertilized in vitro with chosen sperm, and then implanted in selected female hosts at the appropriate stage of their reproductive cycle."[51]

The goals to be sought are "genuine warmth of fellow feeling and a cooperative disposition, a depth and breadth of intellectual capacity, moral courage and integrity, an appreciation of nature and of art, and an aptness of expression and of communication." Physically, the aim of positive eugenics would be "to better the genetic foundations of health, vigor, and longevity; to reduce the need for sleep; to bring the induction of sedation and stimulation under more effective voluntary control; and to develop increasing physical tolerances and aptitudes in general."[52]

There are formidable technical problems to be solved in achieving these goals, including the prevention of inbreeding, the identification of carriers of recessive genes, and the prediction of the future adaptiveness of a gene to an unknown environment. Kingsley Davis has recently pointed to the numerous ways in which such schemes conflict with prevailing family values and practices.[53] It is unlikely, therefore, that any extensive program of positive eugenics in the United States is imminent.

Ideologically speaking, specific eugenic procedures are sometimes congenial and sometimes offensive to the liberal conscience. For example, genetic counseling which advises parents of their probability of producing grossly defective children is patently humane. On the other hand, enforced sterilization impresses many as an unwarranted interference with freedom of choice. There is, however, nothing about the eugenic concept as such that is incompatible with liberal ideology. As Davis observes:

> [Those who] attempt to improve mankind can alter the biological capacities and traits of the human organism by artificial selection, or they can reform the culturally transmitted institutions through social movement.... Those who wish to strengthen human health could try a) to institute new health practices and medical services and b) to reduce the reproduction

> rate among carriers of genetically transmitted diseases and susceptibilities. Not only is there no logical conflict between the two principles of human improvement, but the possibility needs to be faced that, in the long run, they are mutually dependent.[54]

Certainly, the eugenics movement in the United States, whatever its past delinquencies, is now wholly within the liberal tradition. Davis, who does not approve of this tendency, describes it as follows:

> Denatured respectability was conferred on the eugenic movement by Frederick Osborn in *Preface to Eugenics* (New York: Harper), first published in 1940 and revised in 1951. As an illustration of how this was done, one can cite (pp. 241–242) the three steps he proposed for the development of a program of positive eugenics:
>
> 1) General improvement of the environment...
>
> 2) Establishment of conditions which will equalize the extent to which all parents are in a position to choose freely how many children they will have...
>
> 3) Finally, the introduction of eugenic measures of a psychological and cultural sort which will tend to encourage births among responsible parents most susceptible to the stimulus of their environment, and to diminish births among those least capable of adjusting themselves to their environment....
>
> In an era when the Nazis in Germany had made genetic control synonymous with racism in the eyes of most intellectuals, Osborn was apparently trying to deflect hostility by borrowing the ideology of 'environmentalism' and conferring it illogically on eugenics. He reached the comforting conclusion that democracy, individualism, and freedom will automatically provide beneficial genetic control. He thus evaded the problem of authority and discipline altogether, but aligned eugenics of the side of liberal dogma, denaturing the movement in the process.[55]

Eugenic procedures, for all their promise, are not now and may never be as significant for human welfare as are measures designed to produce phenotypical changes. It is more immediately relevant that all manner of "depravity"—whatever its putative origins—can be modified after it has appeared by applying appropriate social and/or biological remedies. Lorenz may hold that aggression is instinctive, but he also recognizes that it can be rechanneled to serve desirable human goals. His program includes self-knowledge, sublimation, and cross-national contacts and "the responsible channeling of militant enthusiasm; in other words, helping a younger generation which, on the one hand, is highly critical and even suspicious and, on the other, emotionally starved, to find genuine causes that are worth serving in the modern world."[56] All of this is standard liberal lore and illustrates how alike "instinctivists" and "environmentalists" can sound when they are obliged to deal with the limited alternatives of public policy.

They also share a like tendency to regard biomeliorative measures as peripheral aids in dealing with individual and social pathologies. This is not as curious as it might at first appear. By long tradition each inhabits a cold-war universe, consisting of only two sovereign and antagonistic superpowers in which heredity can be subdued, if at all, by environmental weapons of control. Sin and redemption, despair and hope, stagnation and change thus becomes the philosophical coin in which men make wagers about the ultimate victor. This constricted view of human possibilities cannot deal adequately with either the etiology or treatment of morally condemned or socially disruptive behavior. It has the effect, *inter alia,* of discouraging a more enthusiastic exploration of the entire range of redemptive agents, including biomeliorative procedures.

Schizophrenia, which throughout much of history was regarded as an incurable depravity, is an instructive illustration of one behavior disorder in which biological and environmental elements are intertwined at every stage from cause to symptom to remission. Explanations of schizophrenia are as varied as the schools of psychiatry, but the much-maligned twin studies, as well as clinical evidence, indicate quite clearly that it has both social and genetic causes.[57] The persistence of schizophrenia and other mental illness—and Goldhamer and Marshall show that rates of psychoses have remained remarkably stable since the mid-nineteenth century—is somewhat paradoxical, as genotypes carrying a substantial number of genes associated with schizoid, aggressive, or paranoid personalities are presumably less likely to marry and propagate their kind.[58] Gottesman suggests that only those "genotypes in which a sufficient number of the genes are manifested in the phenotype as pathological will be selected against. Individuals in the continuum of pathological behavior who are below the 'cutting score' established by their culture will then be 'carriers' whose *offspring* may manifest the fullblown illness should there be a suprathreshold accumulation of the associated genes."[59] Some persons who score high on the Minnesota Multiphasic Personality Index schizophrenia scale have been clinically described as "inventive," "creative," "imaginative," and "versatile" and many of these may be salvaged by placing them in a protected environment, or by treating them biochemically in the manner of the niacin therapy practiced by Humphrey Osmond and his colleagues — or preferably both.

The choice of means always involves extra-instrumental considerations. Nazi "eugenic experiments" were unspeakable atrocities. Compare this to the attractive innocence of Haldane's suggestion that the "most efficient method [of reducing the frequency of undesirable recessive conditions] is the introduction of good transport into backward rural areas, thus encouraging outbreeding."[60] Many who regard biochemotherapy as a thoroughly acceptable practice in physical medicine find its extension into the psychic domain repugnant. The possibility of transforming personality from the "outside" without enlisting the will of the patient or relying on his insight recalls to some such heroes of folklore and literature as Pygmalion, the Golem, and the Dybbuk.

Yet these assaults on humanist sensibilities must be balanced against the findings that psychotropic drugs such as chlorpromazine and its successors have already done much to increase the rates of remission in mental hospitals. This is especially encouraging in view of the present inefficiency of the verbal therapies. The drain on resources of time and personnel which they require and their disappointing rates of cure make it doubtful that they can achieve significant reductions in the prevalence of the neuroses and psychoses. Moreover, most environmental psychiatry rests on assumptions that require massive changes in child-rearing practices and the reconstruction of society. As between the realistic prospects of creating a community of saints and developing ever more sophisticated biochemical agents, it seems clear in which direction lies hope.

The fears engendered by the effectiveness of biochemical intervention in mental illness and the prospect of even greater success is part of the larger paradox of social biology, an approach to human behavior that was once genuinely conservative. Sciences which perform the religious function of ministering to the dark anguish of the soul or which confront the mystery of life by bravely deciphering the genetic code cannot be reproached for being overly impressed with the intractability of men or events. It is not possible to predict the scope, magnitude, and direction of biologically induced change in the coming decades. But even now it is abundantly obvious that the "biological approach" can no longer be identified with incurable depravity, limited possibilities, or a static universe.

* *

The ultimate prize to be gained from more sympathetic contact between social biology and sociology is a unified life science that would define the nature and limits of human variability. In the short run, we might clarify a great number of questions to which we are now offering incomplete answers. The fear that greater attentiveness to ethological and genetic findings compromise liberal values is an anachronistic response to a bygone era which both of these disciplines now disavow. The prospects of altering any "awkward" behavior pattern are poor to the extent that it cannot be prevented before it emerges, changed after it appears, or channeled for productive purposes. These conditions obtain or do not, according to the phenomenon being studied, and are not exclusively identified with either the social or the biological approach. By the same token, the selection of therapeutic agents for social or personal reorganization should be selected by such standards as the probability of success, the number of people for whom they are suitable, the least expenditure of resources, and so on. The capacity of biomeliorative or social remedies to satisfy these criteria will likewise vary with circumstances. The contributions of social biology to the understanding of social behavior should be judged by the ordinary criteria of science rather than by the irrelevant standards of outmoded polemic. And if, perchance, greater familiarity with ethology and behavior genetics should impel us to reconsider our most cherished formulations, this change in sociology should not be mistaken for a crisis in the ethical universe.

Biology and Sociology: A Reconciliation

A. H. HALSEY

This conference is exciting because it suggests and even demonstrates the possibility of a unified science of social behavior from the convergence of genetics, psychology, ethology, and sociology. Historians of science might be inclined to scorn our present enthusiasms. They could remind us that great figures of the past, like Freud in psychology or Darwin in biology or (as Professor Bressler points out in his chapter) Auguste Comte in sociology, took it for granted that science is a unity. They might be inclined to add that, having abandoned the nineteenth-century principle of evolution as applied to society in its Spencerian form, our chances of establishing universal biosocial laws are more remote now than ever before.

Certainly we have become more sophisticated. We recognize that there is a long road with many pitfalls between the study of geotactic fruit flies and that of the lumpen proletariat,[4] or from the phenomenon of population control by grouse on the Scottish moors to an explanation of reduced fertility among some of their predators, such as the English upper middle classes in the 1870s.[1,6] Nevertheless, our awareness either of these vast distances or of the oversimplifications of earlier attempts to chart them need not prevent us from recognizing that some intellectual pathways already exist, that some scientific linking principles are known and, above all, that appropriate methods of study have been developed which justify the hope of secure,

---

A. H. HALSEY Department of Social and Administrative Studies, University of Oxford, Oxford, England

if complicated, interconnection between fields of inquiry that too often exist in isolation.

In his most impressive consideration of the area of study occupied by sociologists, Professor Bressler has had to concern himself not simply with isolation but with active hostility. Intriguing as it would be, we need not concern ourselves with the history of the costly divorce proceedings that so quickly followed the brilliant marriage between Spencerian "super-organic" and Darwinian organic evolution. We can accept the melancholy fact that, as Professor Bressler puts it, "Sociology . . . now maintains virtually no commerce with biologically based theories of human behavior." It may be that the story of separation, like Mark Twain's death, has been exaggerated. But no matter: our task is to establish new and durable relationships.

Professor Bressler offers us sufficient reasons for the present state of affairs. They are of three kinds: sociological, scientific, and ideological. The principal sociological reason is that specialization creates vested interests and therefore "trained incapacity" and intellectual narrowness. The resulting barriers between scholars have been justified and reinforced by the main scientific reason, which is that reductionism in general and the instinct theory in particular have been shown to be intellectually unsound. And, finally, the sociological and scientific reasons have been powerfully supported by ideological rejection of social Darwinism and politically reactionary doctrines that have been associated with "the biological approach" to the study of man.

There is nothing logically necessary about the ideological division—nothing that is inherent in science which compels us to adopt conservative or radical political views. We can say, with Professor Bressler, that science is politically and socially neutral. But ideas and ideology are hard to separate in the real world and typically we must ask, as we did of Sweden or Spain in the war, "On which side are you neutral?" Neutrality, as such, is perhaps not our fundamental problem. Certainly it would be difficult to fault Professor Bressler's detached and humane demonstration of the absence of *intrinsic* threat to such social values as freedom and equality in biological theories applied to society. The difficulties stem rather from the passions that guide problem selection in the human sciences. There is no escape from the dilemma that passion is at once both a powerful motive toward and a potential corruptor of scientific work. The dilemma is necessary. Our only protection is in the preservation of the institutions of free scientific inquiry.

Professor Bressler is eloquent and persuasive in his review of some of the problems on which productive collaboration is possible between sociologists and their colleagues in genetics, biology, and ethology. I do not wish to detract from his justifiable enthusiasm, which in any case I share. Nevertheless, we must see to it that our energies are not wasted in swinging a pendulum. Thus I would stress the validity, a specially hard one in sociology, of disciplinary autonomy. There are many far-from-trivial problems in the social sciences to which the importation of genetic ideas is either unnecessary or even positively misleading. The absurdity is obvious in Ardrey's prediction of the necessary failure of American armed force in Vietnam by deduction from the territorial imperative. (By the same reasoning, the European conquest of the continent of America was impossible and the United States does not exist.) Professor Bressler is tempted into the quip that "insistence on disciplinary isolationism may be the academic version of the territorial imperative." Maybe. Analogies can illuminate. But I think we must take more seriously his reminder of "Skinner's caveat that similar patterns of behavior [e.g., pecking orders in chickens and orders of precedence in medieval Europe] in men and animals may not arise from similar contingencies." More telling still are the examples of sociological explanation of population properties that can also perfectly properly be defined genetically. Thus, in recent years we have advanced our understanding of the quality of human populations by temporarily jettisoning the genetic concept of a "pool of ability" and looking at ability as if it were entirely a product of such social forces as economic growth and the expansion of educational provision. This kind of disciplinary autonomy sets limits to the range of soluble problems that can be tackled within the discipline, but within that range the use of extraneous (in this case genetic) ideas actually impede understanding. Nor is it certain that disciplinary autonomy can be only a temporary expedient. I would guess that, for example, the theory of conscious, rational, and organized behavior cannot be constructed from genetic models, but only with models of the cost/benefit type used in economics. In short, there will remain, however successfully we collaborate, many human phenomena which we must approach through Professor Bressler's maxim that "the most parsimonious study of mankind is man."

Above all, these reservations are necessary so that we may insist on the advances open to us through collaboration across the disciplines. The study of social and genetic determinants of intelligence is an outstanding example of exciting possibilities. Professor Bressler has drawn attention to Mr. Eckland's excellent review of the current state of knowledge. I think that there is good ground for hope that, with the extension of work in population genetics on which Professor Dobzhansky reports in this book and the development of more refined models of social stratification and social mobility by sociologists, we may go a long way toward a viable theory of the sociogenetics of human ability.

If we are to use our understanding of past and present isolations in a search for future remedies, we must lay great emphasis on the fact that science is a social organization. Its direction of development is largely determined by the kind of organization it commands. Of course, the chance migration of ideas is historically important, as we all know from the example of Darwinism. "In October, 1838, that is, fifteen months after I had begun my systematic inquiry, I *happened to read for amusement Malthus on Population* [the italics are mine], and being well prepared to appreciate the struggle for existence which everywhere goes on, from long continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved and unfavourable ones to be destroyed. The result would be the formation of new species. Here, then, I had at last got a theory by which to work."[3]

Organization can, however, give structure to a field of probabilities. To take a minor and personal example, my own excursion into the problems of relating genetic to social structures was the direct outcome of the organization of a Center for the Study of Behavioral

Sciences at Palo Alto, California, which brought a lucid and imaginative geneticist like Ernest Caspari into a seminar of social scientists. Again, conferences like this or the symposia recently organized by the Eugenics Society in England[2,5] usefully serve the same purposes. Nevertheless, although formal confrontations of this kind are of obvious value, I am convinced that more permanent arrangements must be made across the boundaries that now typically separate biological from social science faculties in the universities. To this end, there is a movement of great potential utility now in train at Oxford. Encouraged by a successful series of lectures given by geneticists, ethologists, psychologists, geographers, anthropologists, and sociologists, an interfaculty group was formed last year to plan a new first degree in the human sciences, designed to integrate biological and sociological knowledge. Quite apart from its claim to provide an integrated modern education in the sciences and humanities and its promise to supply appropriately educated recruits to many branches of administrative and social service careers, this type of degree is needed to lay a firm foundation for future research. Only the development of such education and training will ensure that adequate numbers of able students are guided towards the research problems that meanwhile lie neglected between the established academic frontiers.

Social Science and Genetics: A Historical Perspective

MARK H. HALLER

In his excellent paper, Professor Bressler has quite rightly argued that the reformist sympathies of today's social scientists have played an important part in their unwillingness to accept biological and hereditarian explanations for human behavior. Indeed, so far have we departed from hereditarian explanations that it would, I think, be difficult for modern biologists and social scientists to imagine the degree to which hereditarian assumptions shaped academic opinion in America during the first third of the twentieth century. As a historian, I would like to sketch the background that led to the close connection between genetics and social science before 1920 and led to their gradual separation after that date.

At the turn of the century, the experts in such fields as the study of feeblemindedness, mental illness, and crime shared a number of beliefs. On the whole, they believed that mental illnesses and aberrations resulted from abnormalities of the brain and nervous system and, being physiological in origin, were rooted largely in heredity. There has, in fact, usually been a close association between an emphasis on the physiological basis of personality and a willingness to accept hereditarian explanations for behavior.

Among those charged with the care and study of the feebleminded, there was no dissent from the proposition that feeblemindedness was almost entirely hereditary and incurable. Psychiatrists, very physiologically oriented in those pre-Freudian days, were generally agreed that "hereditary tendency has more effect, is a more potential agency in the production of insanity, than all other causes put together."[1] While there was, understandably, more disagreement among crimi-

---

MARK H. HALLER Department of History, University of Chicago, Chicago, Illinois

nologists, a large proportion nevertheless believed either that many criminals, as Lombroso claimed, were hereditary criminal types or else that criminality could be explained as hereditary feeblemindedness. At any rate, until World War I the question of heredity virtually dominated discussions of the causes of crime. The study of the Jukes family, published in 1875, and the study of the Kallikaks, published in 1912, were part of a general documentation that social ills, from alcoholism to poverty, from insanity to prostitution, were rooted in heredity.[1]

Another and somewhat separate strand of hereditarian thinking was the pervasive racist and nativist attitude that characterized American thought in the early part of the current century. A standard interpretation of American history by historians was that American democracy represented the flowering of the peculiar genius of the Anglo-Saxon race. Academics and publicists warned that the American system could not long survive if the nation admitted into its borders immigrants from southern and eastern Europe—races characterized by superstition and servility, to say nothing of radicalism and wife-beating. In this enlightened day, it is perhaps well to reflect upon the scientific reception accorded Madison Grant's publication of *The Passing of the Great Race* in 1916. This pro-Nordic and viciously anti-Semitic book, the height of elitist racism, was on the whole received respectfully in the scientific community. The magazine *Science* called the book a "work of solid merit," while the *Journal of Heredity,* official organ of the American Genetic Association, declared, "the book contains little with which specialists are not familiar, but it supplies a readable account of recent work. . . ." and added for good measure: "in the field of anthropology he has followed the latest authorities."[2]

The rediscovery of Mendel's laws and the introduction of the Binet intelligence tests—both shortly after 1900—further reinforced the hereditarian trends. The Mendelian laws of inheritance, with their exciting possibilities for research, increased the interest in heredity among biologists and, furthermore, appeared to provide a simple explanation for the inheritance of many human traits. At the same time, the introduction of Binet tests, which had been developed for the diagnosis of feeblemindedness, produced remarkable and satisfying results. Wherever the tests were used in the early and uncritical days, they appeared to show not only that feeblemindedness was widely distributed through the American population, but also that most criminals, prostitutes, tramps, and other undesirables were hereditary morons. The tests also appeared to provide conclusive proof that, except for Jews, those races that were believed to be inferior were inferior in fact.

The result was a widespread concern with hereditarian reform during the first three decades of the century. The climax of the racist side came in the 1920s, when the U.S. Congress specifically adopted the eugenic argument and enacted immigration laws that restricted immigration, especially of those groups assumed to be racially inferior.[3] There was also a campaign for early diagnosis of the feebleminded, for clinical study of criminals, and for permanent custodial care of those who were feebleminded. By 1931 a successful campaign was waged in some thirty states to pass laws for the sexual sterilization of criminals, the insane, and the feebleminded, even though the laws were seldom enforced.[4] Finally, there was a pervasive concern with what was known as "race suicide"—the high birthrate of the "unfit" and the low birthrate of the "eugenically fit." Many important figures in American academic life lamented the fecundity of the poor and foreign-born and viewed with sorrow the declining birthrate among the successful members of the native-born population. Harvard and Yale men, for instance, were not raising enough sons even to replace themselves, while half the graduates of women's colleges appeared not to be marrying at all.[5]

For many Americans, the hereditarian currents did not necessarily have deep-rooted ideological implications; most Americans were too pragmatic for that. They were quite capable of believing that some persons, whose failures were rooted in heredity, should be prevented from breeding, while other persons, whose failures were rooted in environment, should be reformed by reforming the environment.

Nevertheless, many prestigious biologists, social scientists, and publicists drew specifically "conservative" and elitist conclusions from hereditary interpretations of human behavior. Henry H. Goddard, the psychologist who had introduced the Binet tests into the United States and had written the story of the Kallikak family, seriously argued that "the truest democracy is found in an institution for the feebleminded and it is an aristocracy—a rule by the best." Charles B. Davenport, the nation's most influential human geneticist, went before a national conference of social workers and, with his usual tact, informed them that social reform was futile and that "the only way to secure innate capacity is by breeding it." William McDougall, speaking with authority as the chairman of the department of psychology at Harvard University, specifically called for the replacement of democracy by a caste system based upon biological capacity, with legal restrictions upon breeding by the lower castes and upon intermarriage between the castes.[6] By the 1920s such views appeared to predominate among the scientists and social scientists who were hereditarian in their outlook.

Necessarily, then, the opposition to a hereditarian interpretation of human behavior found much of its motive force in a rejection of the elitist and racist implications of hereditarian attitudes. This was true from the beginning of the academic assault upon hereditarian outlooks. Lester Ward, a distinguished early sociologist with a broad background in science, published the most important early sociological rejection of eugenic elitism. He was, I think, the first prominent thinker in the United States to emphasize the distinction between biological and social inheritance in human evolution and to argue that the progress and dissemination of culture and technology, not biological selection, explained the evolution of human society. Thus he could argue that the lower classes did not differ from the upper classes in biological inheritance, but rather in their unequal access to the social heritage. Franz Boas, the leading graduate teacher of anthropology in this country, vigorously combated racist attitudes and their antireformist implications. His influence, and that of his followers, was important in keeping underground the fairly widespread sympathy with racism among segments of the anthropological profession, especially among physical anthropologists.[7]

Even the rapid acceptance in this country after World War I of such personality theories as behaviorism and Freudianism can be explained, at least in part, by their compatibility with reform ideology. Despite the wide differences in the two movements, they shared some factors in common: both downgraded physiological explanations of human personality; both placed little emphasis upon heredity; and both stressed the malleability of human personality under environmental influences.

The climax of academic rejection of hereditarian thought came, of course, in the 1930s during the period of Nazi consolidation of power in Europe. So concerned were American academics with the rise of Nazism that in the late 'thirties many of the professional associations took official stands against racism and against the scientific validity of Nazi doctrines. In 1938 this was true of the American Association of University Professors, the American Anthropological Association, and the American Psychological Association. In 1939 the International Genetic Congress took a similar stand.[8] By 1940 the climate within academe was quite different from that which had prevailed only ten or twenty years earlier.

Indeed, if one examines the academic rejection of eugenic ideas as a problem in the sociology of knowledge, it is interesting to note that the rejection occurred at the same time the social backgrounds of members of the academic profession underwent change. While I have little statistical evidence to support the generalization, my impression is that universities, before the first World War, were dominated by Americans of native stock. But the 'twenties and, especially, the 'thirties were periods when the proportion with Jewish and other immigrant backgrounds began to rise among students and then faculty. These changing social backgrounds within the academic professions understandably made the professions a good deal less sympathetic with those doctrines that had supported the virulent nativism of the 1920s.

Thus far, I have emphasized my agreement with Professor Bressler concerning the importance of ideology in understanding academic rejection of hereditarian explanations for human behavior. But I have done so in part as a background for explaining the area in which he and I might differ, at least in emphasis. While I agree that ideology is important in explaining the rejection, I believe that expanding knowledge in a variety of fields made the earlier hereditarian explanations of human behavior intellectually untenable. In short, two processes — ideological rejection and intellectual rejection — went on concurrently. It is possible, then, that the continued lack of much reliable information concerning inheritance of *human* social behavior, rather than ideology, may be a major factor in explaining why even today most social scientists find human genetics largely irrelevant to their research interests.

What must be remembered about the period before 1920 is that *if leading scientists were correct in their assertions concerning human heredity,* social scientists could not ignore genetics. Davenport argued that many traits of character had simple Mendelian explanations. He claimed that insanity, feeblemindedness, shyness, love of alcohol, mechanical ability, shiftlessness, and the wandering impulse were recessive; that violent temper and laziness were dominant.[9] Even if social scientists were not sufficiently versed in genetics to be familiar with Davenport's discoveries, they were deeply influenced by McDougall's social psychology based upon instinct theory. McDougall argued that individuals and races differed in the strengths of a variety of instincts and inherited tendencies and that much of social behavior could be understood on such a basis. Furthermore, if psychologists were correct that wide differences in innate intelligence existed among races and social classes, such factors could not be ignored by sociologists and demographers. The major studies of population during the period were therefore centrally concerned with the problems of the eugenic and dysgenic results of population change.[10] If widely accepted racist theories were true, they were crucial in understanding the differences between cultures or between subcultures within the American city. Thus, such studies of American ethnic communities as *The Old World in the New,* by the sociologist Edward A. Ross, were explicitly racist in their assumptions.[11] Finally, if psychologists, criminologists, and experts on feeblemindedness were correct that crime and even poverty were chiefly the result of hereditary feeblemindedness, then heredity was the most important factor in explaining major social problems and had major policy implications.

In the brief space provided here, I can only hint at some of the major ways in which new knowledge undermined old theories. The change was perhaps most obvious and most sudden among those concerned with feeblemindedness. In the two or three years following the first World War, the experts learned that they had exaggerated the hereditary nature of feeblemindedness and had been wrong about the relationship between feeblemindedness and crime. At their annual conventions during the period, the leading alarmists of an earlier period stood up to confess their errors and to call for re-education of the profession.[12] A somewhat analogous development occurred in genetics studies. Before World War I, Davenport had appeared to be, on the whole, in the mainstream of the profession. After the War, particularly in light of developments in genetics resulting from fruit-fly studies by Thomas Hunt Morgan and his colleagues at Columbia, Davenport's brand of genetics seemed increasingly questionable. While he did not substantially moderate his views, the profession changed its view of him. At the same time, changes occurred in the field of psychological testing. As the decade of the 1920s progressed, the cultural factors influencing IQ results became more and more obvious. Increasingly, the members of the profession moderated their claims concerning the degree to which the IQ tests could be said to measure something called "innate intelligence." The factors mentioned above, and many others, undercut the intellectual basis for the former hereditarian emphasis, and many men changed their minds for intellectual, rather than ideological, reasons.[13]

The 1920s also saw important assaults upon the intellectual basis for racism from many directions. One factor, of course, was the declining faith in mental tests. More important, perhaps, were developments in sociology and anthropology. During the 1920s, a remarkable group of urban sociologists at the University of Chicago undertook to study the transportation of Old World culture to the American city. Their impressive and sensitive studies traced immigrant behavior to the social and cultural factors of the urban neighborhoods in which the immigrants lived. Such studies revolutionized the study of immigrant life in America and made racial explanations irrelevant.[14] In the 1920s, the dominant American anthropologists, largely influenced by Boas and already doubtful of racist assumptions, became committed to concepts of cultural relativism: the notion that an anthropologist should not regard cultures as "superior" and "inferior" but rather should study each culture in its own terms. By the late 1920s and early 1930s, the study of culture and personality became a distinct and self-conscious field of anthropology, tracing cultural differences among peoples to the differing ways by which societies socialize the children raised within the society.[15] Finally, geneticists of that period tended increasingly to define "races" in Mendelian terms, recognizing them as populations with characteristic gene frequencies. Such an approach placed greater emphasis upon differences within a racial group, blurred the distinctions between so-called races, and undercut the earlier discussions of "pure races." By the late 1930s, racism no longer commanded intellectual respect in academe.

In short, the intellectual foundations for a hereditarian interpretation of human behavior crumbled at the same time that the hereditarian interpretation came under ideological attack. An explanation for the divorce of behavior genetics and social science during the last thirty-five years lies in part in the *relative* lack of firm and generally accepted evidence concerning the genetic basis for human behavioral characteristics. Indeed, I think that the discontinuity between the present and the past is so great that a person interested today in the genetics of human behavior would find irrelevant almost all work published before 1930.

A major purpose of Professor Bressler's paper is to raise the question: Has research in human behavior genetics during the last few years created a situation in which social scientists must take into account findings in the field of genetics? I am, perhaps, not as optimistic as he concerning the advances that have been made in human behavior genetics.

In this connection, I am pleased that Professor Bressler has warned against the uncritical application of ethological findings to human social behavior. Such authors as Lorenz and Ardrey assume that certain types of social behavior in man have the same biological basis as do certain analogous behavior traits in animals. However, the crucial point — the biological roots of the behavior in human beings — still remains to be demonstrated. Until that is done, the use of an analogy to animal behavior can provide, at best, suggestive hypotheses *to be tested with reference to human behavior;* at worst, it encourages misunderstanding of human social behavior through a failure to appreciate how the learning of symbols and value systems underlies the types of behavior that are of greatest interest to the social scientist.

In short, I fear that a rush to ground sociological theories upon animal behavior might repeat the story of what happened some forty to sixty years ago. It may result in generalizations about human behavior on the basis of unproved assumptions, and thereby again bring into disrepute the relationship between genetics and the social sciences. Geneticists and social scientists now need to begin a dialogue and to map programs for mutually beneficial research. But both should, at the same time, recognize how little is yet known about the genetic basis for the types of behavior that are of primary interest to the social scientist. Indeed, such traits as "leadership," "tolerance," "racial prejudice," "need for achievement," "conservatism," and so forth, may be so indirectly related to any specific biological, and therefore genetic, basis and so directly related to social influences that genetics may never provide explanations that will be helpful to sociologists.

Furthermore, the penetration of biological and genetic knowledge into the social sciences might occur in two phases. The first phase would involve close coordination of psychologists and psychiatrists with geneticists, physiologists, and biochemists to study the biological bases of human behavior. The second step would be the incorporation of such knowledge into the work of sociologists and anthropologists. If this is a sensible way to perceive the manner in which genetic knowledge will eventually become relevant to the sociologist, we might say that the first stage is well under way but that, on the whole, the second stage still lies ahead.

I will conclude by commenting on Professor Bressler's handling of the ideological implications of race differences. He has pointed out that the question of racial equality is irrelevant to the validity of the civil rights movement. *To the extent that the civil rights movement is asking for equal opportunities for Negroes and whites,* he is correct. For a civil rights advocate to argue that Negroes should receive equal opportunity because the total Negro population is innately equal to the white population is, in fact, to accept the major premise of segregationists—that a person's rights depend upon the qualifications of some group to which the individual may be said to belong. On the contrary, civil rights groups should take the position that individuals have a right, as individuals, to receive equal treatment from governmental and other institutions.

To the extent that the civil rights movement has become a drive for compensatory discrimination, however, I am not sure that the question of racial equality is irrelevant. The argument for compensatory discrimination is that current unequal achievement of Negroes is the result of past social discrimination. Justice requires, therefore, that society now discriminate in favor of Negroes, and such discrimination will result in substantially equal achievement by Negroes. Specifically, "Head Start" and other compensatory educational policies will result in equalizing Negro educational achievement. If, as Professor Bressler points out is quite possible, a further study of racial differences in intelligence should indicate that Negroes have a greater genetic potential than whites, it would be a strong inducement for compensatory discrimination. If, on the other hand, further study should suggest that Negroes have a lesser genetic potential for intelligence than whites, the case for compensatory discrimination would be weakened, but not destroyed. It would raise the possibility that the current underachievement of Negroes is partly innate and that compensatory discrimination may not bring equality of achievement.

This is not an argument against the further study of genetic differences between various human populations. However, the question of racial differences is not irrelevant to the question of the validity of some phases of the civil rights movement. We should not be so naive as to believe that findings on racial differences will have no policy implications in the major domestic issue that now faces the United States.

In conclusion, then, I regard Professor Bressler's paper as a highly important and sensitive statement of the mutual relationship that can and ought to exist between the disciplines of sociology and genetics. I would disagree with him only slightly in emphasis. He emphasizes the ideological barriers that lead social scientists to reject hereditarian explanations of human behavior. I would emphasize, in addition, the relative lack of firm scientific information concerning the genetic basis for human behavior. He argues, correctly and convincingly, that a system of humane ethics is compatible with a belief in the genetic basis of human behavior. I would merely add the cautionary note that we must continue to be sensitive to the possible policy implications of theories concerning genetic differences between human populations. The tragic history of the past relationship between genetics and social science shows all too clearly the misuse that can so easily occur.

References

STEVEN G. VANDENBERG. *The Nature and Nurture of Intelligence*

1 ALLISON, R. B. Learning Parameters and Human Abilities, Educational Testing Service, Princeton, N.J., 1960.

2 ALTUS, WILLIAM D. Birth order and its sequelae, *Science,* 1966, Vol. 151, pp. 44–49.

3 ANDERSON, T. W. The asymptotic distribution of the roots of certain determinantal equations, *J. Roy. Stat. Soc.,* Ser. B., 1948, Vol. 10, pp. 132–139.

4 ARDREY, R. The Territorial Imperative, New York, Atheneum, 1966.

5 BARTLETT, M. S. Tests of significance in factor analysis, *Brit. J. Stat. Psychol.,* 1950, Vol. 3, pp. 77–85.

5a BARTLETT, M. S. Multivariate analysis, *Journ. Roy. Stat. Soc.,* Ser. B., 1947, Vol. 9, Suppl. 2, pp. 176–190.

6 BAYLEY, NANCY and E. S. SCHAEFER. Correlations of maternal and child behaviors with the development of mental abilities: data from the Berkeley Growth Study, *Mongr. Soc. Res. Child Develop.,* 1964, Vol. 29, pp. 1–80.

7 BENNETT, E. L., M. C. DIAMOND, D. KRECH, and M. ROSENZWEIG. Chemical and anatomical plasticity of brain, *Science,* 1964, Vol. 146, pp. 610–619.

8 BERGLUND, G. W. Intelligence and season of birth, Report No. 26, Institute of Education, Uppsala University, Sweden, 1966.

9 BINET, A. and T. SIMON. Méthodes nouvelles pour le diagnostic du niveau intellectuel des anormaux, *Année psychol.,* 1905, Vol. 11, pp. 191–244.

10 BLADE, MARY F. and WALTER S. WATSON. Increase in spatial visualization test scores during engineering study, *Psychol. Monogr.,* 1955, Vol. 69, No. 397.

11 BONNARDEL, R. Comparison des capacités de groupes d'adultes de scolarités antérieures de même durée mais d'orientations professionelles différentes, *Trav. Hum.,* 1965, Vol. 28, pp. 311–316.

12 BONNARDEL, R. Comparison à scolarité et à activité professionnelle constante des capacités mentales des adultes des deux sexes, *Trav. Hum.,* 1965, Vol. 28, pp. 331–342.

13 BONNARDEL, R. L'évolution des capacités mentales en fonction de l'age: Étude partant sur des groupes d'ouvriers professionnels, *Trav. Hum.,* 1965, Vol. 28, pp. 91–105.

14 BRUUN, K., T. MARKKANEN, and J. PARTANEN. Inheritance of drinking behavior, a study of adult twins, Helsinki, The Finnish foundation for alcohol research, 1966 (in press).*

---

* Now published. Partanen, J., K. Bruun, and T. Markkanen. Inheritance of Drinking Behavior, Stockholm, Almqvist and Wiksell, 1966.

15 Burt, C. The bearing of the factor theory on the organization of schools and classes, London, Report of the L. C. C. Psychologist, 1919.

16 Coleman, J. S. Equality of opportunity, Office of Education, U.S. Dept. of Health, Education, and Welfare, U.S. Government Printing Office, 1966.

17 Davies, Ann D. M. Season of birth, intelligence and personality measures, *Brit. J. Psychol.,* 1964, Vol. 55, pp. 475–476.

18 Davies, Ann D. M. and M. G. Davies. The difficulty and graded scoring of Elithorn's perceptual maze test, *Brit. J. Psychol.,* 1965, Vol. 56, pp. 295–302.

19 Day, Clarence. This Simian World, New York, Knopf, 1936.

20 DeVore, I. (editor) Primate Behavior, New York, Holt, Rinehart, and Winston, 1965.

21 Dockrell, W. B. Secondary education, social class and the development of abilities, *Brit. J. Educ. Psychol.,* 1966, Vol. 36, pp. 7–14.

22 Duncanson, J. P. Intelligence and the ability to learn, Research Bulletin No. 64–29, Educational Testing Service, Princeton, N.J., 1964.

23 Erlenmeyer-Kimling, L. and Lissy F. Jarvik. Genetics and intelligence: a review, *Science,* 1963, Vol. 142, pp. 1477–1479.

24 Ferguson, George H. On learning and human ability, *Canad. J. Psychol.,* 1954, Vol. 8, pp. 95–112.

25 Falkner, Frank, N. D. Dattabanik, and Richard Westland. Intra-uterine blood transfer between uniovular twins, *Biol. Neonat.,* 1962, Vol. 4, pp. 52–60.

26 Games, Paul A. A factorial analysis of verbal learning tasks, *J. Exp. Psychol.,* 1962, Vol. 63, pp. 1–11.

27 Garrett, H. E. A developmental theory of intelligence, *Amer. Psychol.,* 1946, Vol. 1, pp. 372–378.

28 Gompertz, Benjamin. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies, *Phil. Trans.,* 1825, Vol. 115, pp. 513–585.

29 Goodall, Jane. Chimpanzees of the Gombe stream reserve, *in* Primate Behavior (I. DeVore, editor), New York, Holt, Rinehart, and Winston, 1965, pp. 425–473.

30 Gross, O. Die cerebrale Sekundarunktion, Leipzig, Vogel, 1902.

31 Guilford, J. P. Three faces of intellect, *Amer. Psychol.,* 1959, Vol. 14, pp. 469–479.

32 Halperin, S. L. Clinico-genetical study of mental defect, *Amer. J. Ment. Def.,* 1945, Vol. 50, pp. 8–26.

33 Halstead, Ward C. Some fronto-temporal lobe relationships, *in* Symposium on the temporal lobe, *Arch. Neurol. Psychiat.,* 1955, Vol. 74, p. 567.

34 Harlow, Harry F. The development of affectional patterns in infant monkeys, *in* Determinants of Infant Behavior (B. M. Foss, editor), New York, Wiley, 1961, pp. 75–88.

35 Heymans, Von G. Über einige psychische Korrelationen, *Z. Angew Psychol.,* 1908, Vol. 1, pp. 313–381.

35a Heyns, O. S. Abdominal Decompression, Johannesburg, Witwatersrand Univ. Press, 1963.

36 Hilton, T. L. and A. E. Myers. Personal background, experience and school

achievement: an investigation of the contribution of questionnaire data to academic prediction, *J. Educ. Measurement*, 1967, Vol. 4, pp. 69–80.

37 HONZIK, MARJORIE P. Developmental studies of parent-child resemblance in intelligence, *Child Develop.*, 1957, Vol. 28, pp. 215–228.

38 HUSEN, TORSTEN. Tvillingstudier, Stockholm, Almqvist and Wiksell, 1953.

39 HUSEN, TORSTEN. Abilities of twins, *Scand. J. Psychol.*, 1960, Vol. 1, pp. 125–135.

40 IRVINE, S. H. Towards a rationale for testing attainments and abilities in Africa, *Brit. J. Educ. Psychol.*, 1966, Vol. 36, pp. 24–32.

41 IRVINE, S. H. The factor analysis of African abilities and attainments, constructs across cultures, XVIII International Congress of Psychology, Moscow, 1966. Mimeogr. copy of paper.

42 JOHN, ERWIN ROY and JAMES G. MILLER. The acquisition and application of information in the problem-solving process: an electronically operated logical test, *Behav. Sci.*, 1957, Vol. 2, pp. 291–300.

43 KAGAN, JEROME and HOWARD A. MOSS. Birth to Maturity, New York, Wiley, 1962.

44 KEBBON, LARS. The structure of abilities at lower levels of intelligence, Stockholm, Sweden, Skandinaviska Test Forlaget AB, 1965.

45 KELLEY, T. L. Crossroads in the Mind of Man, Stanford, Stanford Univ. Press, 1928.

46 KOCH, HELEN L. Twins and Twin Relations, Chicago, Univ. of Chicago Press, 1966.

47 KODAMA, H. and F. SHINAGAWA. The WISC Intelligence Test, Tokyo, Nihon Bunka Kagakusha, 1953.

48 LEAKEY, L. S. B. The Progress and Evolution of Man in Africa, London, Oxford Univ. Press, 1961.

49 LESSER, G. S., G. FIFER, and D. H. CLARK. Mental abilities of children from different social class and cultural groups, *Monogr. Soc. Res. Child Develop.*, 1965, Vol. 30, pp. 1–115.

50 LIENERT, G. A. Die Faktorenstruktur der Intelligenz als Funktion des Intelligenzniveaus, *Ber. 22. Kongr. Deutsch. Ges. Psychol.*, Göttingen, Hogrefe, 1960, pp. 138–140.

51 LIENERT, G. A. Überprüfung und genetische Interpretation der Divergenzhypothese von Wewetzer, *Vita Hum.*, 1961, Vol. 4, pp. 112–124.

52 LOEHLIN, J. C. and S. G. VANDENBERG. Genetic and environmental components in the covariation of cognitive abilities: an additive model, *in* Progress in Human Behavior Genetics (S. G. Vandenberg, editor), Baltimore, Johns Hopkins Univ. Press, 1968 (in press).

53 LURIA, ALEXANDER R. Neuropsychological analysis of focal brain lesions, *in* Handbook of Clinical Psychology (B. B. Wolman, editor), New York, McGraw-Hill, 1965.

54 LUSH, J. L. Animal Breeding Plans, Ames, Iowa State College Press, 1945.

55 MACFARLANE SMITH, I. Spatial Ability, Its Educational and Social Significance, San Diego, Knapp, 1964.

56 MANLEY, M. B. A factor analytic study of three types of concept attainment

tasks, Research Bulletin No. 65–31, Educational Testing Service, Princeton, N.J., 1965.

57 Meyer, V. Psychological effects of brain damage, *in* Handbook of Abnormal Psychology (Hans Jurgen Eysenck, editor), New York, Basic Books, 1961.

58 Meyers, C. E., R. E. Orpet, A. A. Atwell, and H. F. Dingman. Primary abilities at mental age six, *Monogr. Soc. Res. Child Develop.*, 1962, Vol. 27, pp. 1–40.

59 Meyers, C. E., H. F. Dingman, R. E. Orpet, E. G. Sitkei, and C. A. Watts. Four ability-factor hypotheses at three preliterate levels in normal and retarded children, *Monogr. Soc. Res. Child Develop.*, 1964, Vol. 29, pp. 1–80.

60 Meyers, C. T. The effects of training in mechanical drawing on spatial relations test scores as predictors of engineering drawing grades, Research Bull. No. 58–69, Educational Testing Service, Princeton, N.J., 1958.

61 Nguyen-Xuan, A. Structure factorielle scolaire et structure factorielle de tests, *Trav. Hum.*, 1965, Vol. 28, pp. 274–292.

62 Nichols, R. C. The inheritance of general and specific ability, Research Reports No. 1, Evanston, Ill., National Merit Scholarship Corporation, 1965.

63 Nichols, R. C. The origin and development of talent, Research Reports Vol. 2, 10, Evanston, Ill., National Merit Scholarship Corporation, 1966.

64 Novoselova, S. L. Specific features of intellectual behavior of primates, *in* Biological and Physiological Problems of Psychology, Vol. 1 of Abstracts of communications, XVIII International Congress of Psychology, Moscow, 1966, pp. 37–38.

65 Orme, J. E. Intelligence and season of birth, *Brit. J. Med. Psychol.*, 1962, Vol. 35, pp. 233–234.

66 Orme, J. E. Intelligence, season of birth and climatic temperature, *Brit. J. Psychol.*, 1963, Vol. 54, pp. 273–276.

67 Piaget, Jean. The Child's Conception of Number, New York, Norton, 1965.

68 Pinter, Rudolf and Georget Forlando. The influence of month of birth on intelligence quotients, *J. Educ. Psychol.*, 1933, Vol. 24, pp. 561–584.

69 Price, Bronson. Primary biases in twin studies, *Amer. J. Hum. Genet.*, 1950, Vol. 2, pp. 293–352.

70 Ranucci, E. Effect of the study of solid geometry on certain aspects of space perception abilities. Unpublished Ph.D. dissertation, Columbia Univ., New York, 1952.

71 Reinert, G. Zur Problematik der faktoriellen Differenzierungshypothese der Intelligenz, *Ber. 24. Kongr. Deutsch. Ges. Psychol.*, Hogrefe, Göttingen, 1965, pp. 167–173.

72 Reinert, G., P. B. Baltes, and L. R. Schmidt. Faktorenanalytische Untersuchungen zur Differenzierungshypothese der Intelligenz: Die Leistungsdifferenzierungshypothese, *Psychol. Forsch.*, 1965, Vol. 28, pp. 246–300.

73 Reitan, Ralph M. Certain differential effects of left and right cerebral lesions in human adults, *J. Comp. Physiol. Psychol.*, 1955, Vol. 48, pp. 474–477.

74 Roberts, J. A. Fraser. The genetics of mental deficiency, *Eugen. Rev.*, 1952, Vol. 44, pp. 71–83.

75 Sampson, E. E. The study of ordinal position: antecedents and outcomes, *in*

Progress in Experimental Personality Research (Brendan A. Maher, editor), Vol. 2, New York, Academic Press, 1964.

76 SCHAEFER, E. S. and NANCY BAYLEY. Maternal behavior, child behavior, and their intercorrelations from infancy through adolescence, *Monogr. Soc. Res. Child Develop.*, 1963, Vol. 28, No. 3, pp. 1–127.

77 SCHALLER, G. B. Year of the Gorilla, Chicago, Univ. of Chicago Press, 1964 (*also* in Ballantine paperback, 1965).

78 SCHOENFELDT, L. F. The project TALENT twin study, a preliminary report, *in* Human Behavior Genetics (S. G. Vandenberg, editor), Proc. Sec. Invitational Conference on Human Behavior Genetics, in preparation.

79 SCHULL, WILLIAM J. and JAMES V. NEEL. The Effects of Inbreeding on Japanese Children, New York, Harper and Row, 1965.

80 SCOTT, JOHN PAUL and JOHN L. FULLER. Genetics and the Social Behavior of the Dog, Chicago, Univ. of Chicago Press, 1965.

81 SKEELS, H. M. Adult status of children with contrasting early life experience, *Monogr. Soc. Res. Child Develop.*, 1966, Vol. 31, Serial No. 105, pp. 1–65.

82 SKODAK, MARIE and H. M. SKEELS. A final follow-up study of one hundred adopted children, *J. Genet. Psychol.*, 1949, Vol. 75, pp. 85–125.

83 STAKE, R. E. Learning parameters, aptitudes and achievements, *Psychometric Monogr.*, 1961, No. 9.

84 STERN, C. Genes and people, public lecture sponsored by the National Foundation, at the IIIrd International Congress of Human Genetics, Chicago, September 9, 1966.

85 STEVENSON, H. W. and R. D. ODOM. Interrelationships in children's learning, *Child Develop.*, 1965, Vol. 36, pp. 7–19.

86 STODDARD, GEORGE D. The Meaning of Intelligence, New York, Macmillan, 1943.

87 SUPER, DONALD E. and JOHN O. CRITES. Appraising Vocational Fitness by Means of Psychological Tests, New York, Harper, 1962.

88 SVENSSON, NILS ERIC. Ability Grouping and Scholastic Achievement, Stockholm, Almqvist and Wiksell, 1962.

89 THOMPSON, GODFREY HILTON. The Factorial Analysis of Human Ability, Boston, Houghton Mifflin, 1951.

90 THORNDIKE, ROBERT L. and ELIZABETH HAGAN. Ten Thousand Careers, New York, Wiley, 1959.

91 THURSTONE, L. L. Primary Mental Abilities, Chicago, Univ. of Chicago Press, 1938.

92 THURSTONE, L. L. The Differential Growth of Mental Abilities, Psychometric Laboratory Report No. 14, Univ. of North Carolina, Chapel Hill, N.C., 1955.

93 THURSTONE, L. L. and THELMA G. THURSTONE. Primary Mental Abilities for Ages 5–7, Chicago, Science Research Associates, 1953.

94 VANDENBERG, STEVEN G. The Primary Mental Abilities of Chinese students: a comparative study of the stability of a factor structure, *Ann. N.Y. Acad. Sci.*, 1959, Vol. 79, No. 9, pp. 257–304.

95 VANDENBERG, S. G. Innate abilities, one or many? A new method and some results, *Acta Genet. Med.* [Roma], 1965, Vol. 14, pp. 41–47.

96 VANDENBERG, S. G. The Primary Mental Abilities of South American students, a second comparative study of the generality of a cognitive factor structure, Research Report No. 9 from the Louisville Twin Study, Univ. of Louisville School of Medicine, 1965.

97 VANDENBERG, S. G. Contributions of twin research to psychology, *Psychol. Bull.,* 1966, Vol. 66, pp. 327–352.

98 VANDENBERG, S. G. Hereditary factors in normal personality traits (as measured by inventories), *in* Recent Advances in Biological Psychiatry (Joseph Wortis, editor), 1960, Grune (*also* Research Report No. 19, Louisville Twin Study, Univ. of Louisville School of Medicine, 1966).

99 VANDENBERG, S. G. Hereditary factors in psychological variables in man, with special emphasis on cognition, *in* Behavioral Consequences of Genetic Differences in Man (J. N. Spuhler, editor), Chicago, Viking Fund, 1966 (c).

100 VANDENBERG, S. G. and R. JOHNSON. Further evidence on the relation between age of separation and similarity in IQ among pairs of separated identical twins, Research Report No. 18, Louisville Twin Study, Univ. of Louisville School of Medicine, 1966.

101 VERNON, PHILIP EWART. The Structure of Human Abilities, London, Univ. of London Press, 1956. (2nd edition, London, Methuen, 1961.)

102 VERNON, R. E. Environmental handicaps and intellectual development, *Brit. J. Educ. Psychol.,* 1965, Vol. 35, pp. 9–20, 117–126.

103 WEWETZER, K. H. Zur Differenz der Leistungsstrukturen bei verschiedenen Intelligenzgraden, *21. Kongr. Deutsch. Ges. Psychol.,* Göttingen, Hogrefe, 1958, pp. 245–246.

104 WICTORIN, M. Bidrag till Räknefärdighetens Psykologi, en Tvillingundersökning, Göteborg, Elanders, 1952.

105 YATES, A. J. Psychological deficit, *Ann. Rev. Psychol.,* 1966, Vol. 17, pp. 111–144.

106. ZANGWILL, OLIVER L. Cerebral Dominance and Its Relation to Psychological Functions, Edinburgh, Oliver and Boyd, 1960.

107 ZAZZO, R. Les Jumeaux, le Couple et la Personne, (2 vols.) Paris, Presses Universitaires de France, 1960.

108 ZUBIN, J. Personal communication, 1960.

ACKNOWLEDGMENT

This work has been supported by National Institutes of Health grants K3–MH 18,382 and HD 00843.

IRVING I. GOTTESMAN. *Beyond the Fringe—Personality and Psychopathology*

1 ANASTASI, ANNE. Heredity, environment and the question "how"? *Psychol. Rev.,* 1958, Vol. 65, pp. 197–208.

2 BAJEMA, CARL JAY. Estimation of the direction and intensity of natural selection in relation to human intelligence by means of the intrinsic rate of natural increase, *Eugen. Quart.,* 1963, Vol. 10, pp. 175–187.

3 BLEULER, EUGEN. Dementia Praecox; or, the Group of Schizophrenias (translated by Joseph Zinkin), New York, Int. Univ. Press, 1950.

4 BURT, CYRIL. Class differences in general intelligence: III, *Brit. J. Statist. Psychol.,* 1959, Vol. 12, pp. 15–33.

5 BURT, C. Intelligence and social mobility, *Brit. J. Statist. Psychol.,* 1961, Vol. 14, pp. 3–24.

6 CARTER, C. O. The inheritance of common congenital malformations, *in* Progress in Medical Genetics, Vol. IV (Arthur G. Steinberg and A. G. Bearn, editors), New York, Grune and Stratton, 1965, pp. 59–84.

7 CATTELL, RAYMOND B. The multiple abstract variance analysis equations and solutions: for nature-nuture research on continuous variables, *Psychol. Rev.,* 1960, Vol. 67, pp. 353–372.

8 CRONBACH, LEE J. and PAUL E. MEEHL. Construct validity in psychological tests, *Psychol. Bull.,* 1955, Vol. 52, pp. 281–302.

9 DOBZHANSKY, THEODOSIUS. Evolution, Genetics, and Man, New York, Wiley, 1955.

10 DOBZHANSKY, THEODOSIUS. Mankind Evolving, New Haven and London, Yale Univ. Press, 1962.

11 ERLENMEYER-KIMLING, L., J. D. RAINER, and F. J. KALLMANN. Current reproductive trends in schizophrenia, *in* Psychopathology of Schizophrenia (P. H. Hoch and J. Zubin, editors), New York, Grune and Stratton, 1966, pp. 252–276.

12 EYSENCK, H. J. The inheritance of extraversion-introversion, *Acta Psychol.* (Amst.), 1956, Vol. 12, pp. 95–110.

13 FALCONER, D. S. Introduction to Quantitative Genetics, New York, Ronald Press, 1960.

14 FALCONER, D. S. The inheritance of liability to certain diseases, estimated from the incidence among relatives, *Ann. Hum. Genet.* (London), 1965, Vol. 29, pp. 51–76.

15 FREEDMAN, D. G., C. B. LORING, and R. M. MARTIN. Emotional behavior and personality development, *in* Infancy and Early Childhood (Yvonne Brackbill, editor), New York, Free Press, 1967, pp. 429–502.

16 FULLER, J. L. The genetic base: pathways between genes and behavioral characteristics, *in* The Nature and Transmission of the Genetic and Cultural Characteristics of Human Populations, New York, Milbank Memorial Fund, 1957, pp. 101–111.

17 GEORGE, WESLEY CRITZ. The Biology of the Race Problem, New York, National Putnam Letters Committee, 1962.

18 GOTTESMAN, IRVING I. Genetic aspects of intelligent behavior, *in* Handbook of Mental Deficiency: Psychological Theory and Research (Norman R. Ellis, editor), New York, McGraw-Hill, 1963, pp. 253–296.

19 GOTTESMAN, I. I. Heritability of personality: a demonstration, *Psychol. Monogr.,* 1963, Vol. 77, No. 9 (whole No. 572), pp. 1–21.

20 GOTTESMAN, IRVING I. Science or propaganda?, *Contemp. Psychol.,* 1963, Vol. 8, pp. 381–382.

21 GOTTESMAN, IRVING I. Personality and natural selection, *in* Methods and Goals in Human Behavior Genetics (Steven G. Vandenberg, editor), New York, Academic Press, 1965, pp. 63–80.

22 GOTTESMAN, IRVING I. Genetic variance in adaptive personality traits, *J. Child Psychol. Psychiat.,* 1966, Vol. 7, pp. 199–208.

23 GOTTESMAN, I. I. Biogenetics of race and class, *in* Race, Social Class and Psychological Development (M. Deutsch and A. R. Jensen, editors), New York, Holt, Rinehart, and Winston, 1967 (in press).

24 GOTTESMAN, IRVING I. and JAMES SHIELDS. Schizophrenia in twins: 16 years' consecutive admissions to a psychiatric clinic, *Brit. J. Psychiat.,* 1966, Vol. 112, pp. 809–818.

25 GOTTESMAN, IRVING I. and JAMES SHIELDS. Contributions of twin studies to perspectives on schizophrenia, *in* Progress in Experimental Personality Research (B. A. Maher, editor), Vol. 3, New York, Academic Press, 1966, pp. 1–84.

26 GOTTESMAN, I. I. and J. SHIELDS. In pursuit of the schizophrenic genotype, *in* Progress in Human Behavior Genetics (S. G. Vandenberg, editor), Baltimore, Johns Hopkins Press (in press).

27 GUILFORD, J. P. Three faces of intellect, *Amer. Psychol.,* 1959, Vol. 14, pp. 469–479.

28 HALSEY, A. H. Genetics, social structure and intelligence, *Brit. J. Socio.,* 1958, Vol. 9, pp. 15–28.

29 HIGGINS, J. V., ELIZABETH W. REED, and S. C. REED. Intelligence and family size: a paradox resolved, *Eugen. Quart.,* 1962, Vol. 9, pp. 84–90.

30 JENKINS, JAMES J. and DAVID T. LYKKEN. Individual differences, *Ann. Rev. Psychol.,* 1957, Vol. 8, pp. 79–112.

31 KALLMANN, F. J. The genetic theory of schizophrenia: an analysis of 691 schizophrenic twin index families, *Amer. J. Psychiat.,* 1946, Vol. 103, pp. 309–322.

32 KRINGLEN, E. Schizophrenia in twins. An epidemiological-clinical study, *Psychiatry,* 1966, Vol. 29, pp. 172–184.

33 LERNER, MAX. America As a Civilization, New York, Simon and Schuster, 1957.

34 LOEVINGER, JANE. Objective tests as instruments of psychological theory, *Psychol. Rep.,* 1957, Vol. 3, pp. 635–694.

35 MCNEMAR, QUINN. A critical examination of the University of Iowa studies of environmental influences upon the IQ, *Psychol. Bull.,* 1940, Vol. 37, pp. 63–92.

36 MAYR, ERNST. Animal Species and Evolution, Cambridge, The Belknap Press of Harvard Univ. Press, 1963.

37 NEEL, JAMES V., STEFAN S. FAJANS, JEROME W. CONN, and RUTH T. DAVIDSON. Diabetes mellitus, *in* Genetics and the Epidemiology of Chronic Diseases (James V. Neel, Margery Shaw, and W. J. Schull, editors), Public Health Service Publication No. 1163, 1965, pp. 105–132.

38 NEWMAN, HORATIO HACKET, FRANK N. FREEMAN, and KARL J. HOLZINGER. Twins: a Study of Heredity and Environment, Chicago, Univ. of Chicago Press, 1937.

39 Post, R. H. Population differences in red and green color vision deficiency: a review and a query on selection relaxation, *Eugen. Quart.*, 1962, Vol. 9, pp. 131–146.

40 Post, R. H. Population differences in vision acuity: a review with speculative notes on selection relaxation, *Eugen. Quart.*, 1962, Vol. 9, pp. 189–212.

41 Post, R. H. Hearing acuity variation among Negroes and whites, *Eugen. Quart.*, 1964, Vol. 11, pp. 65–81.

42 Reed, Elizabeth W. and Sheldon C. Reed. Mental Retardation: A Family Study, Philadelphia, Saunders, 1965.

43 Rosenthal, David. Sex distribution and the severity of illness among samples of schizophrenic twins, *J. Psychiat. Res.*, 1963, Vol. 1, pp. 26–36.

44 Rosenthal, David. Problems of sampling and diagnosis in the major twin studies of schizophrenia, *J. Psychiat. Res.*, 1963, Vol. 1, pp. 116–134.

45 Rosenthal, David (editor) and colleagues. The Genain Quadruplets, New York, Basic Books, 1963.

46 Scarr, Sandra. The origins of individual differences in Adjective Check List scores, *J. Consult. Psychol.*, 1966, Vol. 30, pp. 354–357.

47 Shields, James. Monozygotic Twins: Brought Up Apart and Brought Up Together, London, Oxford Univ. Press, 1962.

48 Skeels, H. M. Some Iowa studies of the mental growth of children in relation to differentials of the environment: a summary. *Yearbook Natl. Soc. Study Educ.*, 1940, Vol. 39 (II), pp. 281–308.

48a Skeels, H. M. Adult status of children with contrasting early life experiences, *Monogr. Soc. Res. Child Develop.*, 1966, Vol. 31, Serial No. 105, pp. 1–65.

49 Slater, Eliot (with the assistance of James Shields). Psychotic and neurotic illnesses in twins, *Med. Res. Counc. Spec. Rep.* (London), No. 278, Her Majesty's Stationery Office, 1953.

50 Thompson, William R. Traits, factors and genes, *Eugen. Quart.*, 1957, Vol. 4, pp. 8–16.

51 Thurstone, L. L. Psychological implications of factor analysis, *Amer. Psychol.*, 1948, Vol. 3, pp. 402–408.

52 Tienari, Pekka. Psychiatric illness in identical twins, *Acta. Psychiat. Scand.*, Suppl. 171, 1963, pp. 9–195.

53 Vandenberg, Steven G. Contributions of twin research to psychology, *Psychol. Bull.*, 1966, Vol. 66, pp. 327–352.

54 Wellman, Beth L., Harold M. Skeels, and Marie Skodak. Review of McNemar's critical examination of Iowa studies, *Psychol. Bull.*, 1940, Vol. 37, pp. 93–111.

ACKNOWLEDGMENT

Preparation of this paper was aided in part by grant MH 11398 from the U.S. Public Health Service.

David Rosenthal. *The Genetics of Intelligence and Personality*

1 Freedman, D. An ethological approach to the genetical study of human be-

havior, *in* Methods and Goals in Human Behavior Genetics (S. G. Vandenberg, editor), New York, Academic Press, 1965.
2 Gewirtz, J. L. The course of infant smiling in four child-rearing environments in Israel, *in* Determinants of Infant Behavior III (B. M. Foss, editor), New York, Wiley, 1965.
3 Nichols, R. C. The resemblance of twins in personality and interests, *National Merit Scholarship Corporation Research Reports,* 1966, Vol. 2, No. 8, pp. 1–23.
4 Rosenthal, David (editor) and colleagues. The Genain Quadruplets, New York, Basic Books, 1963.
5 Siemens, H. W. Die Zwillingspathologie, Berlin, Springer Verlag, 1924.
6 Theis, H. V. How Foster Children Turn Out, N.Y. State Charities Aid Association, 1924.
7 Woodworth, R. S. Heredity and environment: a critical survey of recently published material on twins and foster children, *Soc. Sci. Res. Counc. Bull.,* New York, 1941, Monograph No. 47.

William R. Thompson. *Genetics and Social Behavior*

1 Andrew, R. J. Effect of testosterone on the behavior of the domestic chick, *J. Comp. Physiol. Psychol.,* 1963, Vol. 56, pp. 933–940.
2 Asch, Solomon Elliot. Social Psychology, New York, Prentice-Hall, 1952.
3 Bateson, P. P. G. The characteristics and context of imprinting, *Biol. Rev.,* 1966, Vol. 41, pp. 117–220.
4 Beach, F. A. Problems of classification, description and measurement, Symposium: Evolving Methodology in the Study of Behavior, May, 1965, Michigan State Univ. (Unpublished)
5 Broadhurst, P. L. Experiments in psychogenetics, *in* Experiments in Personality (Hans Jurgen Eysenck, editor), London, Routledge and Kegan Paul, 1960.
6 Broadhurst, P. L. and Seymour Levine. Behavioral consistency in strains of rats selectively bred for emotional elimination, *Brit. J. Psychol.,* 1963, Vol. 54, pp. 121–125.
7 Carter, H. D. Twin similarities in emotional traits, *J. Personality,* 1935, Vol. 4, pp. 61–78.
8 Caspari, E. Perspectives in behavior genetics, *in* Genetics Today (S. J. Geerts, editor), 1963, Vol. 3, pp. 817–821.
9 Cattell, R. B. The multiple abstract variance analysis equations and solutions: for nature-nurture research on continuous variables, *Psychol. Rev.,* 1960, Vol. 67, pp. 353–372.
10 Cattell, Raymond B., Duncan B. Blewett, and John R. Beloff. The inheritance of personality: a multiple variance analysis determination of approximate nature-nurture ratios for primary personality factors in Q-data, *Amer. J. Hum. Genet.,* 1955, Vol. 7, pp. 122–146.
11 Cattell, Raymond B., Glen F. Stice, and Norton F. Kristy. A first approxi-

mation to nature-nurture ratios for eleven primary personality factors in objective tests, *J. Abnorm. Psychol.,* 1957, Vol. 54, pp. 143–159.

12 CRAIG, J. V., L. L. ORTMAN, and A. M. GUHL. Genetic selection for social dominance ability in chickens, *Anim. Behav.,* 1965, Vol. 13, pp. 114–131.

13 CRONBACH, LEE J. The two disciplines of scientific psychology, *Amer. Psychol.,* 1957, Vol. 12, pp. 671–684.

14 CROOK, M. N. Intra-family relationship in personality test performance, *Psychol. Rec.,* 1937, Vol. 1, pp. 479–502.

15 DAVIS, D. E. The phylogeny of social nesting habits in the Crotophaginae, *Quart. Rev. Biol.,* 1942, Vol. 17, pp. 115–134.

16 DEVORE, IRVEN (editor). Primate Behavior, New York, Holt, Rinehart, and Winston, 1965.

17 DOBZHANSKY, THEODOSIUS. Mankind Evolving, New Haven and London, Yale Univ. Press, 1962.

18 ERLENMEYER-KIMLING, L. and LISSY F. JARVIK. Genetics and intelligence: a review, *Science,* 1963, Vol. 142, pp. 1477–1479.

19 EYSENCK, H. J. Criterion analysis — an application of the hypotheticodeductive method to factor analysis, *Psychol. Rev.,* 1950, Vol. 57, pp. 38–53.

20 FALCONER, D. S. Introduction to Quantitative Genetics, New York, Ronald Press, 1960.

21 FISHER, A. E. The effects of differential early treatment on the social and exploratory behavior of puppies. Unpublished Ph.D. dissertation, Penn. State Univ., 1955.

22 FREDERICSON, EMIL, CHARLES D. FINK, and JEAN R. PARKER. Elicitation and inhibition of competitive fighting in food deprived mice, *J. Genet. Psychol.,* 1955, Vol. 86, pp. 131–141.

23 FREEDMAN, DANIEL. An ethological approach to the genetical study of human behavior, *in* Methods and Goals in Human Behavior Genetics (S. Vandenberg, editor), New York, Academic Press, 1965.

24 FREUD, S. Civilization and Its Discontents (translated by Joan Riviere), London, L. and Virginia Woolf at the Hogarth Press, 1930.

25 FULLER, JOHN L. and LINCOLN D. CLARK. Genetic and treatment factors modifying the postisolation syndrome in dogs, *J. Comp. Physiol. Psychol.,* 1966, Vol. 61, pp. 251–257.

26 GINSBURG, BENSON E. Coaction of genetical and nongenetical factors influencing sexual behavior, *in* Sex and Behavior (Frank A. Beach, editor), New York, Wiley, 1965.

27 GOTTESMAN, I. I. Heritability of personality: a demonstration, *Psychol. Monogr.,* 1963, Vol. 77, No. 9 (whole no. 572), pp. 1–21.

28 GOTTESMAN, I. I. Genetic variance in adaptive personality traits, *J. Child Psychol. Psychiat.,* 1967 (in press).

29 GOTTESMAN, IRVING I. and JAMES SHIELDS. Contributions of twin studies to perspectives on schizophrenia, *in* Progress in Experimental Personality Research (B. A. Maher, editor), Vol. 3, New York, Academic Press, 1966, pp. 1–84.

30 GREGORY, IAN. Genetic factors in schizophrenia, *Amer. J. Psychiat.,* 1960, Vol. 116, pp. 961–972.

31 Hamilton, James B. Precocious masculine behavior following administration of synthetic male hormone substance, *Endocrinology,* 1938, Vol. 23, pp. 53–57.

32 Harlow, H. F. The nature of love, *Amer. Psychol.,* 1958, Vol. 13, pp. 673–685.

33 Harlow, H. F., Margaret K. Harlow, and Ernst W. Hansen. The maternal affectional system of rhesus monkeys, *in* Maternal Behavior in Mammals (Harriet L. Rheingold, editor), New York, Wiley, 1963.

34 Harlow, Harry F. Sexual behavior in the rhesus monkey, *in* Sex and Behavior (Frank A. Beach, editor), New York, Wiley, 1965.

35 Harrison, C. J. O. Allopreening as agnostic behavior, *Behaviour,* 1965, Vol. 24, pp. 161–209.

36 Hebb, D. O. and W. R. Thompson. The social significance of animal studies, *in* Handbook of Social Psychology, Vol. I, Theory and Method (Gardner Lindzey, editor), Cambridge, Addison-Wesley, 1954.

37 Heider, F. Social perception and phenomenal causality, *Psychol. Rev.,* 1944, Vol. 51, pp. 358–374.

38 Hess, Eckhard H. Ethology: an approach toward the complete analysis of behavior, *in* New Directions in Psychology, Vol. 1, New York, Holt, 1962, pp. 157–266.

39 Kallmann, Franz Josef. Heredity in Health and Mental Disorder, New York, Norton, 1953.

40 King, John A. Relationships between early social experience and adult aggressive behavior in inbred mice, *J. Genet. Psychol.,* 1957, Vol. 90, pp. 151–166.

41 King, John A. Swimming and reaction to electric shock in two subspecies of deermice (*Peromyscus maniculatus*) during development, *Anim. Behav.,* 1961, Vol. 9, pp. 142–150.

42 King, J. A. Body, brain, and lens weights of *Peromyscus, Zool. J. Anat. Bd.,* 1965, Vol. 82, pp. 177–188.

43 Krushinskii, Leonid Viktorovich. Animal Behavior: Its Normal and Abnormal Development (translated by Basil Haigh), New York, Consultants Bureau, 1962.

44 Lagerspetz, Kirsti. Studies on the aggressive behavior of mice, *Ann. Acad. Sci. Fenn.* [Med.], 1964, Ser. B, Vol. 131, pp. 1–131.

45 Loehlin, John C. A heredity-environment analysis of personality inventory data, *in* Methods and Goals in Human Behavior Genetics (S. Vandenberg, editor), New York, Academic Press, 1965.

46 Lorenz, Konrad. On Aggression (translated by Marjorie Kerr Wilson), New York, Harcourt, Brace, 1966.

47 Meehl, Paul E. Schizotaxia, schizotypy and schizophrenia, *Amer. Psychol.,* 1962, Vol. 17, pp. 827–838.

48 McBride, G. A General Theory of Social Organization and Behavior, Vol. 1, No. 2, Univ. of Queensland Press, St. Lucia, 1964.

49 Portenier, L. Twinning as a factor influencing personality, *J. Educ. Psychol.,* 1939, Vol. 30, pp. 542–547.

50 Rosenblatt, Jay S. Effects of experience on sexual behavior in male cats, *in* Sex and Behavior (Frank A. Beach, editor), New York, Wiley, 1965.

51 Schaefer, H. R. and P. E. Emerson. Patterns of response to physical contact in early human development, *J. Child Psychol. Psychiat.*, 1964, Vol. 5, pp. 1–13.

52 Scott, J. P. Genetic differences in the social behavior of inbred strains of mice, *J. Hered.*, 1942, Vol. 33, pp. 11–15.

53 Scott, J. P. The analysis of social organization in animals, *Ecology*, 1956, Vol. 37, pp. 212–221.

54 Scott, John Paul. Aggression, Chicago, Univ. of Chicago Press, 1958.

55 Scott, J. P. Genetics and the development of social behavior in dogs, *Amer. Zool.*, 1964, Vol. 4, pp. 161–168.

56 Scott, J. P. and Emil Fredericson. The causes of fighting in mice and rats, *Physiol. Zool.*, 1951, Vol. 24, pp. 273–309.

57 Scott, John Paul and John L. Fuller. Genetics and the Social Behavior of the Dog, Chicago, Univ. of Chicago Press, 1965.

58 Sears, Robert R. Development of gender role, *in* Sex and Behavior (Frank A. Beach, editor), New York, Wiley, 1965.

59 Skinner, B. F. The phylogeny and ontogeny of behavior, *Science*, 1966, Vol. 153, pp. 1205–1213.

60 Spuhler, J. N. Somatic paths to culture, *in* The Evolution of Man's Capacity for Culture (arranged by J. N. Spuhler), Detroit, Wayne State Univ. Press, 1959.

61 Thompson, W. R. Inheritance and development of intelligence, *Res. Publ. Assoc. Res. in Nervous Mental Disease*, 1954, Vol. 33, pp. 209–231.

62 Thompson, W. R. Development and the biophysical bases of personality, *in* Handbook of Personality: Theory and Research (Edgar Borgatta and William W. Lambert, editors), Rand McNally, 1967.

63 Tinbergen, N. Social Behavior in Animals, New York, Wiley, 1953. *Also* Methuen, London, 1953.

64 Vandenberg, Steven. Multivariate analysis of twin differences, *in* Methods and Goals in Human Behavior Genetics (Steven Vandenberg, editor), New York, Academic Press, 1965.

65 Vandenberg, S. Hereditary factors in normal personality traits (as measured by inventories), *in* Recent Advances in Biological Psychiatry 1960 (Joseph Wortis, editor), New York, Grune. (*Also* Research Report No. 19, Louisville Twin Study, Univ. of Louisville School of Medicine, 1966.)

66 Vandenberg, Steven G. and Frank Falkner. Hereditary factors in human growth, *Hum. Biol.*, 1965, Vol. 37, pp. 357–365.

67 Waddington, C. H. The Strategy of the Genes, London, Allen and Unwin, 1957.

68 Wilde, G. J. S. Inheritance of personality traits, *Act. Psychol.* [Amst.], 1964, Vol. 22, pp. 37–51.

69 Wynne-Edwards, V. C. Animal Dispersion in Relation to Social Behavior, Edinburgh, Oliver and Boyd, 1962; New York, Hafner.

ACKNOWLEDGMENT

Preparation of this manuscript was aided by grants-in-aid from the National Research Council of Canada and the Arts Research Committee of Queen's University, Kingston, Canada.

J. N. Spuhler. *Sociocultural and Biological Inheritance in Man*

1 Bouglé, C. Durkheim, Émile (1858–1917), Encyclopaedia of the Social Sciences, 1937, Vol. 5, pp. 291–292.
2 Burt, Cyril and Margaret Howard. The multifactorial theory of inheritance and its application to intelligence, *Brit. J. Statist. Psychol.,* 1956, Vol. 9, pp. 95–131.
3 Durkheim, Émile. The Rules of Sociological Method (translated by Sarah A. Solovay and John H. Mueller; edited by George E. G. Catlin), Chicago, Univ. of Chicago Press, 1938.
4 Falconer, D. S. Introduction to Quantitative Genetics, New York, Ronald Press, 1960.
5 Hamburg, David A. Emotions in the perspective of human evolution, *in* Symposium on Expression of the Emotions in Man (Peter H. Knapp, editor), New York, International Universities Press, 1963, p. 316.
6 Hamburg, David A. Genetics of adrenocortical hormone metabolism in relation to psychological stress, *in* Behavior-Genetic Analysis (J. Hirsch, editor), New York, McGraw-Hill, 1967.
7 Hamburg, David A. and Donald T. Lunde. Relation of behavioral, genetic, and neuroendocrine factors to thyroid function, *in* Genetic Diversity and Human Behavior (J. N. Spuhler, editor), Chicago, Aldine, 1967.
8 Henderson, Lawrence J. Pareto's General Sociology, Cambridge, Harvard Univ. Press, 1935, pp. 8, 9.
9 Knopp, Konrad. Theory and Application of Infinite Series (translated from the 2nd German edition by R. C. Young), London, Blackie, 1928, p. 4.
10 McKusick, Victor A. Mendelian Inheritance in Man, Baltimore, Johns Hopkins Press, 1966.
11 Morton, Newton E. The components of genetic variability, *in* The Genetics of Migrant and Isolate Populations (Elisabeth Goldschmidt, editor), New York, Williams and Wilkins, 1963.
12 Parsons, Talcott. Societies, Englewood Cliffs, Prentice-Hall, 1966.
13 Spitz, R. A. The smiling response. A contribution to the ontogenesis of social relations, *Genet. Psychol. Monogr.,* 1946, Vol. 34, pp. 57–125.
14 Tiger, Lionel and Robin Fox. The zoological perspective in social science, *Man,* 1966, Vol. 1, pp. 75–81.
15 Wright, Sewall. The genetics of quantitative variability, *in* Quantitative Inheritance (Eric Cyril Raynold Reeve and C. H. Waddington, editors), London, Her Majesty's Stationery Office, 1952.

John L. Fuller. *Genotype and Social Behavior*

1 Bennett, E. L., M. C. Diamond, D. Krech, and M. R. Rosenzweig. Chemical and anatomical plasticity of brain, *Science,* 1964, Vol. 146, pp. 610–619.

2 Broadhurst, P. L. and J. L. Jinks. Biometrical genetics and behavior: reanalysis of published data, *Psychol. Bull.,* 1961, Vol. 58, pp. 337–362.

3 Crow, J. F. Mechanism and trends in human evolution, *Daedalus,* 1961, Vol. 90, pp. 416–431.

4 Fuller, John L. and Lincoln D. Clark. Genetic and treatment factors modifying the postisolation syndrome in dogs, *J. Comp. Physiol. Psychol.,* 1966, Vol. 61, pp. 251–257.

5 Hunt, Joseph McVicker. Intelligence and Experience, New York, Ronald Press, 1961.

6 Scott, J. P. Critical periods in behavioral development, *Science,* 1962, Vol. 138, pp. 949–958.

Benson E. Ginsburg. *Breeding Structure and Social Behavior of Mammals: A Servo-Mechanism for Avoidance of Panmixia*

1 Allee, W. C. Animal Aggregations: A Study in General Sociology, Chicago, Univ. of Chicago Press, 1931.

2 Blauvelt, H. Neonate-mother relationship in goat and man, *in* Group Processes (Bertram Schaffner, editor), New York, Josiah Macy, Jr. Foundation, 1956, pp. 94–140.

3 Bowlby, J. The nature of the child's tie to his mother, *Int. J. Psycho.-Anal.,* 1958, Vol. 39, pp. 350–373.

4 Collias, Nicholas E. The analysis of socialization in sheep and goats, *Ecology,* 1956, Vol. 37, pp. 228–239.

5 Cowen, J. S. A hippocampal anomaly associated with hereditary susceptibility to sound induced seizures (Master's degree dissertation), Biopsychology, Univ. of Chicago, 1966.

6 Fuller, John L., Clarence Easler, and Mary E. Smith. Inheritance of audiogenic seizure susceptibility in the mouse, *Genetics,* 1950, Vol. 35, pp. 622–632.

7 Ginsburg, B. E. Gene action studies in behavior. (approximate title, manuscript to be submitted to *Science*).

8 Ginsburg, B. E. Genetics and the physiology of the nervous system, *in* Genetics and the Inheritance of Integrated Neurological and Psychiatric Patterns (D. Hooker and C. C. Hare, editors), *Res. Publ. Ass. Res. in Nervous Mental Disease,* 1954, Vol. 33, pp. 39–56.

9 Ginsburg, B. E. Genetics as a tool in the study of behavior, *Perspect. Biol. Med.,* 1958, Vol. 1, pp. 397–424.

10 Ginsburg, B. E. Causal mechanisms in audiogenic seizures, *in* Psychophysiologie, Neuropharmacologie et Biochimie de la Crise Audiogène, Colloques Internationaux du Centre de la Recherche Scientifique, 1963, No. 112, pp. 229–240.

11 GINSBURG, BENSON E. Coaction of genetical and nongenetical factors influencing sexual behavior, *in* Sex and Behavior (Frank A. Beach, editor), New York, Wiley, 1965, pp. 53–75.

12 GINSBURG, B. E. All mice are not created equal: recent findings on genes and behavior, *Soc. Serv. Rev.,* 1966, Vol. 40, pp. 121–134.

13 GINSBURG, B. E. Genetic parameters in behavior research, *in* Behavior-Genetic Analysis (J. Hirsch, editor), New York, McGraw-Hill, 1967.

14 GINSBURG, B. E. Social behavior and social hierarchy in the formation of personality profiles in animals, *in* Comparative Psychopathology, Animal and Human (J. Zubin and H. Hunt, editors), Vol. 22 of the Proceedings of the American Psychopathology Association, 1967.

15 GINSBURG, B. E. and W. C. ALLEE. Some effects of conditioning on social dominance and subordination in inbred strains of mice, *Physiol. Zool.,* 1942, Vol. 15, pp. 485–506.

16 GINSBURG, B. E. and D. S. MILLER. Genetic factors in audiogenic seizures, *in* Psychophysiologie, Neuropharmacologie et Biochimie de la Crise Audiogène, Colloques Internationaux du Centre de la Recherche Scientifique, 1963, No. 112, pp. 217–225.

17 HARLOW, HARRY F. and M. K. HARLOW. The effect of rearing conditions on behavior, *Bull. Menninger Clin.,* 1962, Vol. 26, pp. 213–224.

18 HESS, ECKHARD H. The relationship between imprinting and motivation, Nebraska Symposium on Maturation (Marshall R. Jones, editor), Lincoln, Univ. of Nebraska Press, 1959, pp. 44–77.

19 HIRSCH, JERRY. Individual differences in behavior and their genetic basis, *in* Roots of Behavior (Eugene L. Bliss, editor), New York, Harper, 1962, pp. 3–23.

20 MAXSON, S. C. The effect of genotype on brain mechanisms involved in audiogenic seizure susceptibility. Ph.D. dissertation, Biopsychology, Univ. of Chicago, 1966.

21 McCLEARN, GERALD E. Genotype and mouse behaviour, *Proc. XI Int. Congr. Genet.,* 1963, pp. 795–805. *Also in* Genetics Today (S. J. Geerts, editor), Vol. 3.

22 MECH, L. D. The Ecology of the Timber Wolf (*Canis lupus* Linnaeus) in Isle Royale National Park. Ph.D. dissertation, Department of Agriculture, Forestry and Wildlife, Purdue Univ., 1962. *Also* Dissertation Abstracts, Vol. 22 (1963), pp. 3578–3579.

23 PFAFFENBERGER, C., J. P. SCOTT, B. E. GINSBURG, J. L. FULLER, and S. BIELFELT. A twenty year study of selection and socialization of guide dogs for the blind (approximate title, manuscript in preparation).

24 RABB, G. B., J. H. WOOLPY, and B. E. GINSBURG. Wolf social behavior: a study of the organization of a wolf pack, *Amer. Zool.* (in press).

25 SCHENKEL, R. Ausdrucksstudien an Wölfen, *Behaviour,* 1948, Vol. 1, pp. 81–129.

26 SCHJELDERUP-EBBE, T. Beiträge zur Sozialpsychologie des Haushuhns, *Psychol.,* 1922, Vol. 88, pp. 225–252.

27 SCOTT, J. P. Critical periods in behavioral development, *Science,* 1962, Vol. 138, pp. 949–958.

28 Scott, John W. Mating behavior of the sage grouse, *Auk,* 1942, Vol. 59, pp. 477–498.

29 Sze, Paul. Behavior Genetics Laboratory, Univ. of Chicago. Personal communication.

30 Witt, Governor and Calvin S. Hall. The genetics of audiogenic seizures in the house mouse, *J. Comp. Physiol. Psychol.,* 1949, Vol. 42, pp. 58–63.

31 Woolpy, J. H. Socially controlled systems of mating among gregarious mammals and their implications for the genetics of natural populations (Ph.D. dissertation), Committee on Genetics, Univ. of Chicago, 1967.

32 Woolpy, J. H. Socialization of wolves: formation, consolidation, and retention of social bonds in wolves as a function of age and experience, *in* Science and Psychoanalysis, 1967, Vol. 12 (in press).

33 Woolpy, J. H. and B. E. Ginsburg. Wolf socialization: a study of temperament in a wild social species, *Amer. Zool.,* May, 1967.

34 Wright, Sewall. Statistical Genetics in Relation to Evolution, Paris, Hermann, 1939.

ACKNOWLEDGMENT

The studies on which this paper is based were supported by grant MH-03361 from the National Institute of Mental Health.

Theodosius Dobzhansky. *Genetics and the Social Sciences*

1 Dobzhansky, Theodosius. Changing man, *Science,* 1967, Vol. 155, pp. 409–415.

2 Dobzhansky, Theodosius and Boris Spassky. Effects of selection and migration on the geotactic and phototactic behavior of *Drosophila., I., Proc. Roy. Soc.,* Ser. B., 1967, Vol. 168, pp. 27–47.

3 Hadler, A. M. Heritability and phototaxis in *Drosophila melanogaster, Genetics,* 1964, Vol. 50 (2), pp. 1269–1277.

4 Halsey, A. H. Genetics, social structure and intelligence, *Brit. J. Socio.,* 1958, Vol. 9, pp. 15–28.

5 Hirsch, J. Individual differences in behavior and their genetic basis, *in* Roots of Behavior (E. L. Bliss, editor), New York, P. Hoeberg, 1962.

V. C. Wynne-Edwards.
Population Control and Social Selection in Animals

1 Breder, C. M. and C. W. Coates. A preliminary study of population stability and sex ratio of *Lebistes, Copeia,* 1932, pp. 147–155.

2 Darwin, C. The Origin of Species, London, John Murray, 6th edition, 1872.

3 Dobzhansky, Theodosius. Genetics and the Origin of Species, New York, Columbia Univ. Press, 1938, 1941, 1951.

4 Dobzhansky, Theodosius. A review of some fundamental concepts and problems of population genetics, *Sympos. Quant. Biol.,* 1955, Vol. 20, pp. 1–15.

5 Emerson, Alfred E. Ecology, evolution and society, *Amer. Naturalist,* 1943, Vol. 77, pp. 97–118.

6 Fisher, R. A. The Genetical Theory of Natural Selection, Oxford, Clarendon Press, 1930.

7 Haldane, J. B. S. The Causes of Evolution, London, Longmans, Green, 1932, pp. 207–210.

8 Huxley, J. S. Preferential mating in birds with similar coloration in both sexes, *Brit. Birds,* 1922, Vol. 16, pp. 99–101.

9 Jenkins, David, Adam Watson, and G. R. Miller. Population studies on red grouse, *Lagopus lagopus scoticus* (Lath.) in north-east Scotland, *J. Anim. Ecol.,* 1963, Vol. 32, pp. 317–376.

10 Jenkins, David, Adam Watson, and G. R. Miller. Predation and red grouse populations, *Lagopus lagopus scoticus, J. Appl. Ecol.,* 1964, Vol. 1, pp. 183–195.

11 Manning, T. H. Blue and lesser snow geese on Southampton and Baffin Islands, *Auk,* 1942, Vol. 59, pp. 158–175.

12 Mayr, Ernst. Animal Species and Evolution, Cambridge, Belknap Press of Harvard Univ. Press, 1963.

13 Miller, G. R., D. Jenkins, and A. Watson. Heather performance and red grouse populations, I. Visual estimates of heather performance, *J. Appl. Ecol.,* 1966, Vol. 3, pp. 313–326.

14 Moss, R. Aspects of grouse nutrition. Unpublished Ph.D. thesis, 1966.

15 Nicholson, A. J. Compensatory reactions of populations to stresses, and their evolutionary significance, *Aust. J. Zool.,* 1954, Vol. 2, pp. 1–8.

16 Watson, Adam and David Jenkins. Notes on the behaviour of the red grouse, *Brit. Birds,* 1964, Vol. 57, pp. 137–170.

17 Wynne-Edwards, V. C. Animal Dispersion in Relation to Social Behaviour, Edinburgh, Oliver and Boyd (*also,* New York, Hafner) 1962.

18 Wynne-Edwards, V. C. Intergroup selection in the evolution of social systems, *Nature,* 1963, Vol. 200, pp. 623–626.

GERALD E. McCLEARN. *Social Implications of Behavioral Genetics*

1 Davis, Kingsley. Sociological aspects of genetic control, *in* Genetics and the Future of Man (John Roslansky, editor), New York, Appleton-Century-Crofts, 1966.

2 DeVore, Irven. The evolution of social life, *in* Horizons of Anthropology (Sol Tax, editor), Chicago, Aldine, 1964.

3 Huxley, Julian. The future of man — evolutionary aspects, *in* Man and His Future (Gordon Wolstenholme, editor), A Ciba Foundation Volume, Boston, Little, Brown, 1963.

4 Manning, Aubrey. Evolutionary changes and behaviour genetics, *in* Genet-

ics Today (S. J. Geerts, editor), *Proc. XI Internat. Congr. Genetics,* Vol. 3, The Hague, Oxford, Pergamon Press, 1965.

5 Polgar, Steven. Evolution and the ills of mankind, *in* Horizons of Anthropology (Sol Tax, editor), Chicago, Aldine, 1964.

6 Roberts, R. C. Implications of behavior genetics for genetics, *in* Behavior-Genetic Analysis (J. Hirsch, editor), New York, McGraw-Hill (in press).

7 Wright, Sewall. The roles of mutation, inbreeding, crossbreeding, and selection in evolution, *Proc. VI Internat. Congr. Genetics,* Vol. 1, pp. 356–366, Ithaca, New York, 1932.

Alexander Kessler. *Social Behavior and Population Dynamics: Evolutionary Relationships*

1 Anderson, Paul K. Density, social structure, and nonsocial environment in house-mouse populations and the implications for regulation of numbers, *Trans. N.Y. Acad. Sci.,* Ser. II, 1961, Vol. 23, pp. 447–451.

2 Calhoun, John B. Behavior of house mice with reference to fixed points of orientation, *Ecology,* 1956, Vol. 37, pp. 287–301.

3 Calhoun, John B. Personal communication.

4 Crowcroft, Peter and F. P. Rowe. The growth of confined colonies of the wild house mouse (*Mus musculus*): the effect of dispersal on fecundity, *Proc. Zool. Soc., London,* 1958, Vol. 131, pp. 357–365.

5 Koford, C. B. Rank of mothers and sons in bands of rhesus monkeys, *Science,* 1963, Vol. 141, pp. 356–357.

6 Lewontin, R. C. The adaptations of populations to varying environments, *Sympos. Quant. Biol.,* 1957, Vol. 22, pp. 395–408.

7 Myers, K. and W. E. Poole. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. III, Reproduction. *Aust. J. Zool.,* 1962, Vol. 10, pp. 225–267.

8 Mykytowycz, R. Social behavior of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.). III, Second breeding season, C.S.I.R.O. *Wildlife Res.,* 1960, Vol. 5, pp. 1–20.

9 Southwick, Charles H. The population dynamics of confined house mice supplied with unlimited food, *Ecology,* 1955, Vol. 36, pp. 212–225.

10 Strecker, Robert L. and John T. Emlen, Jr. Regulatory mechanisms in house-mouse populations: the effect of limited food supply on a confined population, *Ecology,* 1953, Vol. 34, pp. 375–385.

11 Wiens, John A. On group selection and Wynne-Edwards' hypothesis, *Amer. Sci.,* 1966, Vol. 54, No. 3, pp. 273–287.

Marvin Bressler. *Sociology, Biology, and Ideology*

1 Comte, Auguste. The Positive Philosophy of Auguste Comte (translated by Harriet Martineau), New York, Blanchord, 1855, p. 487.

2 Pastore, Nicholas. The Nature-Nurture Controversy, New York, King's Crown Press, 1949.

3 McDougall, William. An Introduction to Social Psychology, Boston, John W. Luce, 1918, p. 7. (For a stimulating discussion of the history of the instinct controversy, see the unpublished manuscript by David L. Krantz and David Allen, The Rise and Fall of McDougall's Instinct Doctrine.

4 Bernard, L. L. Instinct: A Study in Social Psychology, New York, Henry Holt, 1924.

5 Parker, C. H. Motives in economic life, *American Economic Review,* Suppl., 1918, Vol. 8, pp. 212–231.

Patrick, George Thomas White. The Psychology of Social Reconstruction, Boston and New York, Houghton Mifflin, 1920.

Tead, Ordway. Instincts in Industry, Boston, Houghton Mifflin, 1918.

Trotter, Wilfred. Instincts of the Herd in Peace and War, London, Unwin, 1917.

Wallas, Graham. The Great Society, New York, Macmillan, 1914.

6 Dunham, Barrows. Man Against Myth, Boston, Little, Brown, 1947, p. 27. (This book contains the single best short critique of racism, social Darwinism, instinctivism, and allied concepts.)

7 Spencer, Herbert. Social Statics, New York, Appleton, 1878, p. 353.

8 *Ibid.,* p. 354.

9 Allee, W. C. Animal Aggregations, Chicago, Univ. of Chicago Press, 1931.

Howard, H. Eliot. Territory in Bird Life, London, Murray, 1920.

Schjelderup-Ebbe, T. Contributions to the social psychology of the domestic fowl, *Z. Psychol.,* 1952, Vol. 88, pp. 225–252.

10 Scott, J. P. The analysis of social organization in animals, *Ecology,* Vol. 37, 1956, pp. 213–221.

11 Lorenz, Konrad. On Aggression, New York, Harcourt, Brace and World, 1966.

12 Ardrey, Robert. The Territorial Imperative, New York, Atheneum, 1966.

13 Kropotkin, Petr A. Mutual Aid; A Factor of Evolution, New York, Knopf, 1917, p. 14.

14 Lorenz, *op. cit.,* p. 237.

15 *Ibid.,* p. 47.

16 *Ibid.,* p. 48.

17 *Ibid.,* p. 237.

18 Eckland, Bruce K. A sociologist's perspective on behavior genetics. (Unpublished)

19 Scottish Council for Research in Education. The Trend of Scottish Intelligence, London, Univ. of London Press, 1949.

Cattell, Raymond B. The fate of national intelligence; test of a thirteen-year prediction, *Eugenics Review,* 1950, Vol. 42, pp. 136–148.

Emmett, W. G. The trend of intelligence in certain districts of England, *Population Studies,* 1950, Vol. 3, pp. 324–337.

Giles-Bernardelli, Betty M. The decline in intelligence in New Zealand, *Population Studies,* 1950, Vol. 4, pp. 200–208.

Tuddenham, Read D. Soldier intelligence in World Wars I and II, *Amer. Psychol.,* 1948, Vol. 3, pp. 54–56.

20 Cattell, Raymond B., Duncan B. Blewett, and John R. Beloff. The inheritance of personality, *Amer. J. Hum. Genet.,* 1955, Vol. 7, pp. 122–146.

Gottesman, Irving I. Heritability of personality, *Psychol. Monogr.,* 1963, Vol. 77, No. 9.

Vandenberg, S. G. The hereditary abilities study: hereditary components in a psychological test battery, *Amer. J. Hum. Genet.,* 1962, Vol. 14, pp. 220–237.

21 Gottesman, *loc. cit.,* p. 20.

22 Hollingshead, August B. and Frederick C. Redlich. Social Class and Mental Illness, New York, Wiley, 1958.

23 Leach, Edmund. Don't say 'boo' to a goose, *New York Review,* VII, 1966, Vol. 10, p. 8.

24 Capote, Truman. In Cold Blood, New York, Signet edition, 1966, p. 165.

25 Skinner, B. F. The phylogeny and ontogeny of behavior, *Science,* 1966, Vol. 153, pp. 1205–1213.

26 Ardrey, *op. cit.,* p. 5.

27 Craig, Wallace. Appetites and aversions as constituents of instincts, *Biol. Bull.,* 1918, Vol. 34, pp. 91–107.

28 Lorenz, *op. cit.,* p. 52.

29 Cameron, Paul. A bio-socio model of alienation. (Unpublished)

30 Ardrey, *op. cit.,* p. 269.

31 *Ibid.,* p. 270.

32 Lorenz, *op. cit.,* p. 54.

33 Williams, Robin M. The Reduction of Intergroup Tensions, New York, Social Science Research Council, 1947, pp. 58–59.

34 For a brief summary of studies dealing with the effects of environmental stimulation on animal behavior, see Robert A. Hinde, Animal Behavior, New York, McGraw-Hill, 1966, pp. 394–395.

35 Schaller, George B. Behavioral comparisons of the apes, *in* Primate Behavior (Irven DeVore, editor), New York, Holt, Rinehart and Winston, 1965, p. 480.

36 Thoday, J. M. Geneticism and environmentalism, *in* Biological Aspects of Social Problems (J. E. Meade and A. S. Parkes, editors), London, Oliver and Boyd (*also* New York, Plenum Press) 1965, p. 95 *et passim.*

37 Shockley, William. Possible Transfer of Metallurgical and Astronomical Approaches to the Problem of Environment versus Ethnic Heredity (speech before National Academy of Sciences), October 15, 1966.

38 For the most recent version of this model, see Guilford, J. P. and Ralph Hoepfner, Current Summary of Structure-of-Intellect and Suggested Tests, Los Angeles, Univ. of Southern California, 1963.

39 Cort, David. The Glossy Rats, New York, Grosset and Dunlap, 1967, pp. 80–81.

40 Shockley, William (Interview with), *U.S. News,* 1965, Vol. 59, pp. 68–71.

41 The Faculty of the Department of Genetics. The issue of bad heredity, *Stanford Medical Bulletin,* January, 1966, p. 41.

42 *Ibid.*

43 Spitz, René. Hospitalism. The Psychoanalytic Study of the Child, Vol. I, New York, International University Press, 1950.

44 Jay, Phyllis. The common langur of north India, *in* Primate Behavior, *op. cit.,* p. 216.

45 Schaller, George B. The behavior of the modern gorilla, *in* Primate Behavior, *op. cit.,* p. 342.

46 Reynolds, Vernon and Frances. Chimpanzees of the Budongo Forest, *in* Primate Behavior, *op. cit.,* p. 415.

47 Ardrey, *op. cit.,* pp. 318–319.

48 Lashley, K. S. Experimental analysis of instinctive behavior, *Psychol. Rev.,* 1938, Vol. 45, pp. 445–472.

49 Lessing, Lawrence. At the controls of the living cell, *Fortune,* 1966, Vol. 73, pp. 154–158.

50 Asimov, Isaac. Pills to help us remember? *N.Y. Times Mag.,* October 9, 1966, p. 38.

51 Muller, Herman J. Should we weaken or strengthen our genetic heritage? (and comments by others), *in Daedalus,* Summer, 1961, pp. 432–476.

52 *Ibid.,* p. 443–448.

53 Davis, Kingsley. Sociological aspects of genetic control *in* Genetics and the Future of Man (John D. Roslansky, editor), Amsterdam, North-Holland (*also* New York, Appleton-Century-Crofts) 1966.

54 *Ibid.,* p. 174.

55 *Ibid.,* pp. 199–200.

56 Lorenz, *op. cit.,* p. 237.

57 Gottesman, Irving I. and James Shields. Schizophrenia in twins: 16 years' consecutive admissions to a psychiatric clinic, *Brit. J. Psychiat.,* 1966, Vol. 112, pp. 809–818.

58 Goldhamer, Herbert and Andrew W. Marshall. Psychosis and Civilization, Glencoe, Ill., The Free Press, 1953.

59 Gottesman, Irving I. Personality and natural selection, *in* Methods and Goals in Human Behavior Genetics (Steven G. Vandenberg, editor), New York, Academic Press, 1965.

60 Haldane, J. B. S. Human evolution: past and future, *in* This is My Philosophy (Whit Burnett, editor), New York, Harper, 1957.

ACKNOWLEDGMENTS

This is a revised version of a paper read at a conference held under the auspices of Russell Sage Foundation, The Rockefeller University, and the Social Science Research Council in November, 1966. Some of the changes were influenced by comments of discussants and other participants at the conference. Few academic meetings have furnished as much stimulation and instruction, and I should like to express my gratitude for both.

A. H. Halsey. *Biology and Sociology — A Reconciliation*

1 Banks, Joseph Ambrose. Prosperity and Parenthood, London, Routledge and Kegan Paul, 1954.

2 Biological Aspects of Social Problems (J. E. Meade and A. S. Parkes, editors), Edinburgh, Oliver and Boyd, 1965. (*Also,* New York, Plenum Press).

3 The Life and Letters of Charles Darwin (Francis Darwin, editor), 1st edition, New York, Appleton, 1888.

4 Dobzhansky, Theodosius and Boris Spassky. Effects of selection and migration on the geotactic and phototactic behaviour of *Drosophila, Proc. Roy. Soc.* [Biol.], 1967, Vol. 168, pp. 27–47. Also his chapter, this volume.

5 Genetic and Environmental Factors in Human Ability (J. E. Meade and A. S. Parkes, editors), Eugenics Society Symposia, Vol. 2, Edinburgh, Oliver and Boyd, 1966. (*Also,* New York, Plenum Press).

6 Wynne-Edwards, V. C. This volume.

Mark H. Haller. *Social Science and Genetics: A Historical Perspective*

1 An overview of hereditarian attitudes will be found in Mark H. Haller, Eugenics: Hereditarian Attitudes in American Thought, New Brunswick, N.J., Rutgers Univ. Press, 1963. For studies of specific areas of hereditarian thought, see Stanley Powell Davies, Social Control of the Mentally Deficient, New York, Crowell, 1930, and Arthur E. Fink, Causes of Crime: Biological Theories in the United States, 1800–1915, Philadelphia, Univ. of Pennsylvania Press, 1938. The quotation is from Isaac Ray in *American Journal of Insanity,* October, 1880, Vol. XXVII, pp. 480–483.

2 Quotations from a book review in *Science,* October 25, 1918, Vol. XLVIII, p. 419; and *Journal of Heredity,* January, 1917, Vol. VIII, p. 34. The best study of American anti-immigrant attitudes is John Higham, Strangers in the Land: Patterns of American Nativism, 1860–1925, New Brunswick, N.J., Rutgers Univ. Press, 1955; for a history of racism, see Thomas F. Gossett, Race: The History of an Idea in America, Dallas, S. Methodist Univ. Press, 1963; for racism within the historical profession, see Edward Norman Saveth, American Historians and European Immigrants, 1875–1925, New York, Columbia Univ. Press, 1948. The most recent study of anti-Negro attitudes of the period is I. A. Newby, Jim Crow's Defense: Anti-Negro Thought in America, 1900–1930, Baton Rouge, La., Louisiana State Univ. Press, 1965. For a review of "scientific" racism, see Haller, Eugenics, *op. cit.,* especially Chapters 4 and 10.

3 Higham, *op. cit.,* especially Chapter 11; also Robert A. Divine, American Immigration Policy, 1924–1952, New Haven, Yale Univ. Press, 1957.

4 Of the many studies of legal sterilization, see especially Abraham Myerson, et al., Eugenical Sterilization: A Reorientation of the Problem, American Neurological Association, New York, Macmillan, 1936; there is also a comprehensive unpublished manuscript by Julius Paul on State Eugenical Sterilization Laws in America, Thought and Practices; see also Haller, Eugenics, *op. cit.,* Chapter 9.

5 A review of the many birth-rate studies will be found in Paul Popenoe and Roswell Hill Johnson, Applied Eugenics, New York, Macmillan, 1918,

pp. 237–279; see, for instance, JOHN C. PHILLIPS, A study of the birth-rate in Harvard and Yale graduates, *Harvard Graduates Magazine,* 1916, Vol. XXII, pp. 25–34.

6 See HENRY H. GODDARD, Psychology of the Normal and Subnormal, New York, Dodd, Mead, 1924, p. 238; CHARLES B. DAVENPORT, Eugenics and charity, *Proceedings of the 39th National Conference of Charities and Corrections,* 1912, p. 281; and WILLIAM McDOUGALL, Is America Safe for Democracy? New York, Scribners, 1921. Two books that popularized the elitist and hereditarian outlook were ALBERT EDWARD WIGGAM, The New Decalogue of Science, Indianapolis, Bobbs-Merrill, 1923, and LOTHROP STODDARD, The Revolt Against Civilization, New York, Scribners, 1922.

7 See especially LESTER F. WARD, Pure Sociology, New York, Macmillan, 1903, pp. 572 ff. and *passim;* and FRANZ BOAS, The Mind of Primitive Man, New York, Macmillan, 1911. For the struggles within the anthropology profession, see an unpublished paper by GEORGE STOCKING, delivered before the Anthropology Colloquium at the University of Chicago in 1966.

8 For the resolutions passed by the associations, see RUTH BENEDICT, Race: Science and Politics, New York, Modern Age Books, 1940, pp. 259–266. This is the same period, of course, during which J. B. S. HALDANE published his Heredity and Politics, New York, Norton, 1938, a brilliant attack on eugenics that had wide influence inside as well as outside the scientific community.

9 C. B. DAVENPORT was a prolific writer, but his major work was Heredity in Relation to Eugenics, New York, Holt, 1911. WILLIAM McDOUGALL's ideas were developed in An Introduction to Social Psychology, Boston, Luce, 1908, which was the standard textbook in the field.

10 For discussion of population from a variety of viewpoints, see EDWARD M. EAST, Mankind at the Crossroads, New York, Scribner, 1923; EDWARD A. ROSS, Standing Room Only? New York, Century, 1927; WARREN S. THOMPSON, Population Problems, New York, McGraw-Hill, 1930; and FRANK LORIMER and FREDERICK OSBORN, Dynamics of Population, New York, 1934.

11 EDWARD A. ROSS, The Old World in the New, New York, Macmillan, 1914.

12 See especially the *Journal of Psycho-Asthenics,* September 1918–June 1919, Vol. XXIII, and 1920–21, Vol. XXVI.

13 For the decline of hereditarian theories, see HALLER, Eugenics, *op. cit.,* especially Chapters 8, 11, 12.

14 A history of the Chicago school will be found in ROBERT E. L. FARIS, Chicago Sociology, 1920–1932, San Francisco, Chandler, 1967; see also MAURICE R. STEIN, The Eclipse of a Community: An Interpretation of American Studies, Princeton, Princeton Univ. Press, 1960, pp. 13–46. For a specific criticism of a hereditarian approach, see FREDERIC M. THRASHER, The Gang, a Study of 1,313 Gangs in Chicago, Chicago Univ. Press, 1927, pp. 400–405.

15 See the writings of such anthropologists as FRANZ BOAS, BRONISLAW MALINOWSKI, ROBERT LOWIE, MARGARET MEAD, and RUTH BENEDICT.

Index

Note: Numbers in italics refer to pages on which figures appear