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Nature and Nurture: A Modern Synthesis

By JOHN L. FULLER
Research Associate
Division of Behavior Studies
R. B. Jackson Memorial Laboratory
Bar Harbor, Maine

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Preface

I guess I've always liked dogs, and I've had many different kinds. In general, I'm a terrier man, and of all terriers, I like Airedales best. They're good-looking and they're good for all sorts of purposes: they're hunting, herding, or watch dogs—and good with the children. They're at home not only in the country but in a city apartment, too. They're not yappy like so many of the smaller dogs; they have the placid, big-dog temperament, yet they're full of terrier spirit. And they're smart; they learn things so readily.

As a psychologist, I'm well aware of individual differences within any single breed, and I know that a lot depends on how the dog is raised and how he's treated. But still, there are basic differences among the breeds. When we organize our thinking and knowledge of pure-bred dogs (or cats or horses) most of us readily acknowledge that not only appearance but also much of temperament and individuality is genetically determined. When we look at man, however, we find the picture confused. Much of the folklore about the inheritance of psychological characteristics seems manifest nonsense. Much is unclear because of the operation of environmental factors as children are reared by their own parents.

Through the years, many psychologists have undertaken research studies trying to establish the contribution of heredity to individual differences in intelligence. Other psychologists have investigated the contribution of environmental factors. That both are important is evident. In the absence of clear understanding of the actual underlying processes, however, many discussions proceed on the basis of the wishes of the individual, his social philosophy often biasing his view of the evidence.

In order to help clarify thinking in this field, it seemed desirable to approach the general problem from the point of view of the known principles of genetics. What materials from the scientific study of the processes of inheritance relate to the appearance of psychological characteristics?

With the trend toward ever-narrowing specialization in the sciences, it has become increasingly difficult to keep up with the developments in cognate fields. Most psychologists and many students of psychology know principles of genetics as established perhaps a generation ago. But all fields have moved ahead.

In the present paper, Dr. John L. Fuller brings us up to date. "Heredity," he writes, "is the capacity to utilize an environment in a particular way." There then is no nature-nurture dichotomy, for every process and every structure in a living organism results from the transaction between genes and environment. In our understanding of the roles of heredity and culture in producing individual differences, we are helped by descriptions of some of the major investigatory approaches and summaries of selected findings. We are introduced to the difference between major genes and polygenes, and learn that "on the basis of a few studies and on theoretical grounds, it may be hypothesized that polygenic inheritance is the rule" in the inheritance of behavior traits. The significance of contemporary thinking of geneticists for the study of intelligence and behavior deviations, of motivation, and of race and class differences is clarified. Psychological findings are given sharper focus in the synthesis Dr. Fuller provides.

Though the nature-nurture controversy is less bitter today, the interrelations of hereditary and environmental forces still need study if there is to be an adequate description of the development of human individuality and delineation of sound social policies in many segments of life. Dr. Fuller has been engaged in research on the inheritance of social behavior for many years and has prosecuted significant researches, many in association with psychologists. The present paper, a summary for psychologists prepared by an outstanding biologist, is a synthesis of emphases which should provide the sound perspective needed for the integration of past findings into present theories, and for the advancement of future work in the behavior sciences.

EUGENE L. HARTLEY
Consulting Editor
Doubleday Publications in Psychology

section one

A Point of View

What Is the Problem?

In this year's freshman class at State University are two sons of illustrious alumni. Sam Jones is the son of Bill Jones, all-American tackle on the unbeaten Grizzly Bears of twenty-five years ago. Sam plays halfback instead of tackle, but like his father he is the outstanding player on the team. Fred Berwick is the son of Arthur Berwick, distinguished author and historical scholar. Fred achieved the highest record in his class on the verbal portion of an aptitude test given to all freshmen. He is a reporter for the Campus News and his story, published in the student literary magazine, was acclaimed by one of the more critical members of the English Department. Sam frankly admits that his objective in college is only to obtain passing grades so that he can concentrate on making a name for himself as an athlete. The reputation which he makes in this way will be, he hopes, the basis of a successful business career. Fred submits to the required physical education courses with whimsical fortitude, which, it may be added, is also the attitude of his athletic instructor toward him.

What has made these boys so unlike in abilities and interests? It is easy to make out a strong case for nurture. Bill Jones gave his boy a football for his first birthday and saw that he received excellent instruction in all sports. The Berwick residence is always cluttered with books. Dinner conversation, even with children present, is apt to revolve around foreign policy or the novels of Henry James. It will scarcely require a scientific analysis to conclude that these young men of exceptional accomplishment owe a great deal to the circumstances of their upbringing. Nurture is essential. Is it sufficient in itself? Was the training of these boys so effective because of innate qualities which made them particularly adept at acquiring certain skills?

An affirmative answer to this question must be based on evidence that nature plays a part in forming the human personality. Nature, when contrasted with nurture, is generally considered to be equivalent to biological heredity. Since each human being has two parents who contribute almost equally to his genetic endowment, we must consider the genetic contributions of Mrs. Jones and Mrs. Berwick to be equally as important as those of their distinguished husbands. Insofar as physical traits are concerned the influence of heredity is clear. Mrs. Jones is a tall, handsome woman and her son looks like her. The Berwick boy is dark like his mother. But when we try to follow the inheritance of personality traits we encounter difficulty in quantitative measurement. Furthermore, one can only partially determine the genetic potentialities of an individual from his own characteristics. A dominant genetic factor will obscure the effects of a recessive factor. But an individual with both types of factors may pass on the recessive type to his offspring. If both parents do this their child may differ completely from either, yet the difference is due to heredity rather than to nurture. Two children of the same parents may have very different heredity. When the system of mating can be controlled, as in laboratory plants and animals, it is possible to achieve a degree of separation of the effects of nature and nurture; but in the case of the Jones and Berwick families it may as well be admitted that we cannot come to a conclusive answer because of the complexity of the factors involved.

Human beings, even under the most rigid despotisms yet contrived, select their mates for love or economic motives or tribal regulations, or because of sheer propinquity, but not to suit the experimental design of a geneticist. And although there may be approved ways of rearing children which are generally accepted in a cultural group, the actual practice will differ from family to family and from decade to decade. Within a single family the environment of the first-born will be very different from that of younger children. As human beings we cherish our freedoms as individuals, and would not wish to set up experiments on human beings to test rigorously the relative importance of nature and nurture.

Nevertheless, the problem is important. It is important in forming judgments on the significance of the differential birth rate between individuals with high and low scores on intelligence tests. It is important in molding our opinions regarding the potentialities of the peoples of undeveloped countries, people whose scientific and technical achievements do not match our own. The problem is involved when we consider the prevention of mental disease and of other behavioral disorders which render an individual incapable of functioning adequately in his society. And finally every parent comes face to face with the nature-nurture problem in planning the guidance of his own children.

Some Methods of Investigation

In view of the difficulties which surround the scientific investigation of this subject, one may legitimately inquire whether it is ever possible to learn anything beyond vague generalities. Fortunately there are three ways in which one can to some extent circumvent the obstacles. None of these methods is wholly satisfactory, but together they support a point of view which can serve as a tentative guide to action and as a basis for further research.

One of the techniques is the comparison of racial, social, economic, or occupational groups. Although there is great individual variation within groups, significant average differences are often found between groups. This method yields results of importance to educators, but the separation of the effects of nature and nurture must be based upon assumption rather than experiment.

A second technique is to make detailed genetic studies in human families. Analysis of pedigrees has been of particular worth in the case of inheritance of disease. Comparative investigations of identical and fraternal twins have been invaluable in eliciting the importance of genetic influences on normal behavior patterns.

Finally one can study the genetics of behavior patterns in subhuman animals, and apply the results to problems of mankind. The genetic mechanism in man and other sexually reproducing forms is essentially the same, and simple learning and emotional responses appear to be similar. Obviously one cannot use animals to study the inheritance of musical genius or mathematical ability.

It is not easy to synthesize the data obtained from these three techniques in a manner which will satisfy everyone. Before attempting to present and justify a composite point of view, it is of interest to consider the range of scientific opinion on the nature-nurture problem. Why should scientists disagree when the same data is available to all of them? It would lead us too far afield to consider the problem of scientific objectivity, but it is certain that the outlook of individuals trained in a particular discipline is bound to reflect the methodology and theoretical development of that discipline. To set the record straight, the reader should be aware that the author of these pages is a biologist whose own research has dealt with animals, particularly with the factors producing individual differences in behavior and physiological functioning.

The Great Controversy

Psychological literature of the 1930's contains many discussions of the relation between the new science of genetics and individual psychological differences. The innateness of motivation (or instincts) was also the subject of debate which occasionally became acrimonious. The *Psychological Review* provided a forum for the contestants, and the books of Jennings[1] and Watson[2] illustrate two quite divergent viewpoints. Genetics and behaviorism even became the basis for a best-seller. Aldous Huxley in *Brave New World* told of the grim fate of men whose lives were completely determined by the universal application of the conditioned reflexology of Pavlov and Watson to genetically uniform incubator babies.

At the end of this decade of research and theorization results were summarized in the 39th *Yearbook* of the National Society for the Study of Education[3]. Many authors discussed the meaning of intelligence and of environment, as well as deviations in intelligence and its physiological basis. Particular attention was given to the relation between intelligence and sex, race, personality, socioeconomic status, and the environment in general. In an excellent review of the heredity-environment problem Anastasi and Foley[4] cite the *Yearbook* and later contributions as evidence that this issue is still very much alive. The solution which these authors propose involves a substitution of dichotomies. They believe that the etiology of individual personality can be studied better in terms of structure versus reactional biography than in terms of nature versus nurture. Heredity is considered to operate at the structural level; modifications of behavior by learning are considered to be functional.

A Modern Orientation

A biologist finds that structure-function is a dichotomy as full of pitfalls as environment-heredity. What appear to be the functional qualities of a nerve or muscle cell are explainable in terms of the structure of the molecules which make up these cells. What might be called the functions of these molecules can in turn be referred to the atomic groupings within the molecule. Better than either of the dichotomies is the concept of levels of organization. For example, low intelligence may be caused by defective structure of an intracellular enzyme, by a gross anatomical defect in the brain, or by restricted opportunities for perceptual experience. These may be referred to as structure at the molecular level, the organism level, and the social level. The closer one gets to the molecular level, the closer will be the relationship to genetics. Care for a defective, and even therapy, may take no account of the level of the disability or its etiology. On the other hand, when the question of possible transmission of a trait to children arises, the contribution of genes to the expression of a trait is more important than the level at which it operates. For the long pull the nature-nurture relationship is of fundamental significance to our society. There are pessimists who believe that the higher birth rate among the less intelligent means the eventual disintegration of civilization. There are optimists who think that we are raising the average intelligence of our citizens through a broadened educational program. And there are those who are confused by these contradictory outlooks.

In fact the person who considers these problems may well be in the position of the author of the Rubaiyat, who states:

> Myself when young did eagerly frequent
> Doctor and Saint, and heard great Argument
> About it and about: but evermore
> Came out by the same door where in I went.

Actually the situation is not this bad. As our concepts in genetics and psychology change, so also do the kinds of questions which we ask of nature. No good answer is possible to the question of whether a particular behavior pattern or trait is hereditary or acquired. Nature and nurture cannot be set off against one another in this way. This is not due to the limitations of experimental method referred to in the discussion of two imaginary freshman boys; it is because development is a continuous transaction between the organism and its surroundings. At the beginning the organism is largely a collection of genes (hereditary factors) plus nutrient material. Under suitable conditions it eventually becomes differentiated into man, mouse, or earthworm; into male or female; into genius or imbecile. Heredity is the capacity to utilize an environment in a particular way. A legitimate question we can ask concerns the relative contribution of variation in genes and variation in life history to variation in characters such as intelligence and personality traits. Another kind of question inquires as to the relationships between a trait such as aggressiveness, kinds of social training, and the physiological response to hormones; or between maze-running ability in rats and size and form of the brain. Ideally we should like to answer both the genetic and physiological questions simultaneously and demonstrate that genes control a particular physiological function, and that this in turn controls a particular pattern of behavior. In anticipation it may be stated that this ideal has not been obtained even for differences in simple behavior patterns. The following two sections discuss the approaches through genetics and through studies of the development of behavior.

section two

The Genetic Approach

Heredity and Constitution

Since the rediscovery and confirmation of Gregor Mendel's work on the inheritance of structure and color in peas, the science of genetics has made tremendous progress. Heredity has been given a physical basis in the form of genes. Although it has not been possible to count genes we know that a man or a mouse possesses perhaps 10,000 to 50,000 of them, arranged in precise order in visible groups which are called chromosomes. Every human being has 24 pairs of chromosomes, every mouse has 20 pairs, and similarly each other species is found to have a characteristic number. In sexually reproducing animals one-half the chromosomes (therefore one-half the genes) come from each parent. In a number of organisms, particularly in the fruit fly, maize, and the mouse, it has been possible to demonstrate that groups of genes producing known effects are inherited together, and therefore are on the same chromosome. The methods employed represent scientific ingenuity at its best, and the reader is referred to biological works for a complete account[5,6].

Genetic principles are best introduced by selecting a simply inherited characteristic such as color. If a strain of colored mice is crossed with a strain of albino mice, all the offspring are colored. If these hybrids are then crossed to each other the second hybrid generation will tend towards a regular proportion of three colored individuals to one noncolored. The chart on the next page represents these facts, as well as the genetic theory which has been developed to explain them.

It is important to note that the three colored mice in the second hybrid generation look alike (same phenotype) but the results of breeding them would be different. The CC animals would breed true for color, while Cc animals would not.

Colored mouse × Albino mouse

(CC) × (cc)

These letters are a genetic formula. C is said to be dominant over c, because the hybrid mouse is fully colored. c is called recessive to C.

In forming germ cells (sperms or ova) the gene pairs are separated.

↓ ↓

C c

They join in fertilization to produce a first generation hybrid with the genetic formula

(Cc)

A colored mouse

Sperms produced by male hybrids may be either: C c

Ova of female hybrids may be either:	C	c
C	CC	cC
c	Cc	cc

There is an equal chance for each of the possible combinations; hence the genetic formulae in the four boxes of the table represent the expected proportions of the second hybrid generation.

This example can serve as a model for many other cases of hereditary effects, but when we try to apply it to the effects of genes upon constitution we encounter many complexities. (Even our example has been simplified. In reality there is another gene which can substitute for either C or c. This gene known as chinchilla c^{ch} is dominant to c, but recessive to C. Colored animals may be CC, Cc^{ch}, or Cc. Chinchilla animals are very pale, but still colored, and may be $c^{ch}c^{ch}$, or $c^{ch}c$. Only cc animals are full albinos. Many such gene series are known.) A dominant gene may vary widely in its regularity and degree of expression. This is easy to demonstrate in the genetics laboratory, where we can control breeding of animals and secure large numbers of offspring. For example, a mouse with a perfectly normal tail may be proved to carry a gene for kinky tail because his offspring develop this peculiarity. In such cases one can understand why geneticists are careful not to say that kinky tails are inherited, but that a gene *Ki* is inherited. Possessing the gene strongly affects the probability that the caudal appendage will develop abnormally, but does not completely determine it. Similar examples are well known in man.

With these reservations in mind, one may apply the simple genetic model of a single-factor character to a number of constitutional diseases which affect behavior. As an example of a dominant trait we may consider Huntington's chorea. This disease strikes young adults in their prime of life. Over the space of a few months the victim's speech thickens, his mental powers degenerate, and at the end death comes as a welcome release from suffering. This example demonstrates that hereditary conditions need not become manifest until late in life. The victim of Huntington's chorea may have founded a family before the disease can be detected. Some carriers of the gene do manage to live out a normal life span without showing its effects, but they can still transmit it to their children and afflict a new generation.

An example of a recessive gene producing mental deficiency is phenylpyruvic amentia, a disorder characterized by a defect of tissue metabolism. Both parents must carry the gene and transmit it to their child if he is to develop this disease. The list of recognized hereditary diseases affecting intelligence could be much extended. Most of these conditions are rare recessives, but the tragedy of their occurrence is none the less great to the family and individual concerned. Although the stringent application of genetic principles to human reproduction could almost eliminate diseases due to dominant genes, the problem of the recessive genes is more complex, since even complete selection against the phenotype of a rare recessive has only slight effects upon the gene frequency.

Nature certainly contributes more than does nurture to the distinctive character of the two conditions described above. They do not occur without the presence of specific genes. Thus far no way of counteracting the gene-produced deficiencies is known, and the outlook for medical control is not hopeful. Whether a disease can be alleviated or not is of course wholly independent of whether or not it is inherited. Diabetes is a hereditary disease, but it can be controlled by insulin; whereas little can be done to help a paralysis produced by a bullet wound. Control of symptoms of diseases with clear-cut inheritance would entail permanent dependence upon therapeutic measures for afflicted descendants. There is no controversy in such well-studied diseases regarding the preeminent role of heredity. But single-factor control of "normal" characteristics of man (or of plants and lower animals for that matter) seems to be somewhat exceptional. David and Snyder[7] list red blood cell type, the direction of hair on the forehead, and the ability to taste phenylthiourea as among the few clear cases of single gene control of "normal" human traits. Yet the numerous physical resemblances between parents and offspring—similarities which are independent of nutrition or conditions of living—are ample proof of the contribution of genes to human variation. Some more complicated forms of heredity must produce the quantitative variation which results in human individuality.

Quantitative Inheritance

Here it will be convenient to introduce terms for two kinds of genes, major genes and polygenes. Major genes are exemplified by those which control coat color in mice or blood groups in man or Huntington's chorea. One gene by itself determines the character. Why does such a gene sometimes fail to show an effect? It may be due to conditions of development, but sometimes it is because the other genes of an individual modify the action of the major gene. This appears to be the case with human eye color. The gene for brown pigment is dominant over the gene for no pigment (blue eyes), but there seem to be accessory genes which affect the distribution and depth of pigment. In the case of polygenes there is no way to isolate genes with major effects. Instead, the situation appears to be that a considerable number of genes all act as modifiers of the character, some with positive, others with negative effects. There is no sharp line of distinction between modifiers of major genes and polygenes. In fact, so-called major genes probably act as polygenes for characters different from their primary observable effects.

Polygenes are rather elusive. One cannot write neat genetic formulae for them and they must by their nature remain anonymous. How can we name them for their effect when we cannot isolate the effects? Nevertheless, polygenic or multiple-factor inheritance is the type which is of greatest significance to our nature-nurture problem. Take body size, for example. A great number of genetically controlled physiological factors contribute to the determination of the final size of an animal. Some of these determine general body size, and others act only on local parts of the body. Thus we have large or small individuals of widely differing body proportions. By selection it is possible to isolate strains of different size and shape. When differing lines are crossed, the general result is that the offspring are intermediate with respect to their parents. This, however, is not "blending inheritance." The genes retain their individuality and in proper recombination can re-create the parental types after further crossing. Our normal structural differences, and the physiological and psychological differences which may depend upon them, are certainly under a quantitatively different sort of genetic control from that of the single-gene mutations which are the most widely cited examples in biology textbooks.

One of the best ways to demonstrate this fact is to study genetically pure lines of animals. By continued inbreeding it is possible to secure animals in which genetic variability is reduced to an absolute minimum. Animals within one of these inbred strains are as much alike in heredity as are identical twins, but with the difference that an individual type can be produced over and over again to the same specifications. Numerous experiments in biology and psychology have employed such inbred lines, and it may be confidently stated that almost any physiological or psychological measure which is applied will detect strain differences. Races of animals vary consistently in number of red blood cells, rate of heart beat, sensitivity to hormones, timidity in a strange place, or ability to solve a maze. In controlled experiments it is possible to reduce the importance of environmental factors as sources of variation, and thus prove that variations in heredity are causes of the variations in traits. Even under the best of experimental conditions it is impossible to eliminate environmental variation. If one looks carefully, the peas in a pod are really not shaped exactly alike, and the hazards of development are not partitioned equally among even the best cared for laboratory rats. The genetic contribution to variance thus tends to be underestimated in such experiments. There is no doubt that genes can influence significant types of behavior.

Detailed studies of the hereditary mechanisms of physiological and behavioral traits are not numerous. On the basis of a few studies and on theoretical grounds, it may be hypothesized that polygenic inheritance is the rule. It is as though each individual receives large numbers of both positive and negative factors. An excess in either direction will modify the trait up or down. For approximate purposes it is convenient to consider the genic effects as equal and additive. That is, if the variation in a character is conditioned by twenty pairs of genes, the maximum positive number of factors would be forty. Twenty positive factors would be the mid-point of the range of genetic variability, and thirty factors would place an individual halfway between the mean and the upper limit. When there are large numbers of genes involved, the individual effect of each is probably small, and the errors in the above assumption are not serious. It is probably a fair model to use in theorizing about the relationship between heredity and behavior.

At least one important exception must be made, however, to the assumption that genetic effects are additive. This is the concept of thresholds. Assume for the sake of argument that heredity determines the ability of an individual to attain distinction in mathematics. Imagine two boys of equal genetic endowment who take a competitive examination for a single vacancy for entrance to an institute of advanced mathematical studies. Tests given at a later time might show a greater difference between the successful and unsuccessful aspirant than between the unsuccessful candidate and individuals of inferior genetic potentiality. In this example an arbitrarily imposed threshold imposes great phenotypic variability upon a uniform genotype. Many biological examples of this type are known. Animals may be bred true for variability rather than for constancy in the number of their toes. An extra digit regularly appears during embryonic development, but in normal animals it fuses with another digit. If a number of "negative" genes are present, this fusion fails to take place and an extra toe is present in the newborn animal. With a critical number of negative genes present, the issue of fusion hangs in balance and is determined by factors acting in a random fashion upon the embryos. The inheritance of susceptibility to physical or behavioral disorders may well be of this type. In individuals with critical balance between genetic factors, environmental conditions would determine whether or not a breakdown would occur. In other individuals, the balance might be so one-sided that no ordinary environmental conditions would overstress the homeostatic regulation of the organism. It is obvious that the nature-or-nurture question can have no general answer.

Research on the Genetics of Behavior

The principles of genetics have been established by using plants and animals which reproduce rapidly, are easily handled in the laboratory, have small chromosome numbers, and show numerous and obvious structural variations. Investigators of the inheritance of behavioral variation in mammals enjoy none of these advantages. Genetic methods may contribute to the behavioral sciences, but the reverse is not likely to be true. Thus psychologists are more strongly motivated to pursue such studies than are geneticists. Research on psychogenetics up to 1949 has been summarized by Hall[8]. The number of studies is small, but enough has been done to demonstrate the productivity of the field.

One of the major methods employed is to selectively breed animals ranking high and low on a test which is given to an original heterogeneous population. Among the characteristics whose variation in rats has been shown by this method to be determined in part by genetics are: maze learning (Tryon), spontaneous activity (Rundquist), and emotionality (Hall) as determined by the tendency to defecation and urination when the animal is in strange surroundings. In each of the experiments it was found that the selected groups were progressively more differentiated during the first seven to ten generations. Further selective breeding did not increase the difference. Selection, of course, adds nothing new to heredity, but it does modify the distribution of genes to individuals.

Another technique is to compare genetically differentiated strains on standardized performance tests. Differences in tameness (Dawson), in audiogenic seizure susceptibility (Hall, Fuller), in aggressiveness (Fredericson), and in thermal preference (Herter) have been clearly shown in rats and mice. Similar differences in social behavior and in the ability to learn standard problems have recently been described for several pure breeds of dogs[9,10]. These findings are not unexpected. The organism is a whole, and its behavior arises out of its physical structure which has been the product of gene-environment co-action. On both theoretical and empirical grounds one can predict that part of the variation in any behavioral character will prove to have a genetic basis.

The details of the hereditary mechanism by which behavioral traits are determined have been studied by crossing pure lines or strains which have been selectively bred. The interpretation of results of these experiments is difficult. Tryon's maze-bright rats crossed with his maze-dull rats produced a hybrid generation approximately intermediate between the parental stocks in terms of their tendency to make errors. The genes for nonemotionality in Hall's rats appeared to be dominant over those for emotionality. In cases of multiple-factor inheritance, theory would generally predict that the hybrid would be intermediate with respect to the primary genetically controlled character. This is not the same as being intermediate with respect to the behavioral character being measured. Geneticists are familiar with many situations in which variations which are apparently due to single dominants as judged by the phenotype of the hybrid are really due to the combined effects of many genes. Fuller and co-workers[11] described an example of this in the inheritance of audiogenic seizure susceptibility in mice.

Mating highly seizure-susceptible mice of strain DBA to highly resistant mice of strain C57BL yielded an F_1 hybrid which was almost as susceptible as the DBA parents. Backcrossing the F_1 to the DBA stock gave 100% susceptible animals, and backcrossing to the C57BL stock gave about 50% of susceptibles. These are the expectations for a single dominant gene controlling susceptibility. However, a more critical genetic test was employed which consisted of repeatedly crossing susceptible animals from the hybrid stock back to the nonsusceptible C57BL strain. Since genes maintain their integrity despite repeated hybridization, this procedure should result in the continuous production of 50% of susceptible animals in successive generations. Instead, the percentage of reacting animals fell very sharply, and the condition was almost eliminated by the fifth generation.

A theoretical explanation of the genetic control of audiogenic seizure susceptibility in these two strains of mice is illustrated in Figure 1. It is assumed that the seizures are the resultant of a deficiency in the nervous system which varies in severity according to the presence or absence of multiple genes, possibly five or six pairs. All of the individuals of the DBA strain have exactly the same hereditary determinants of susceptibility. All C57BL mice are likewise identical in heredity. The F_1 hybrids between the two strains combine a complete set of DBA and C57BL genes and are exactly intermediate in terms of the number of "susceptibility genes." Inheriting genes, however, is not the same as inheriting susceptibility. The genetic endowment simply fixes the modal point of the population. Variation up and down results from non-uniform conditions of development. This variation is shown by the normal distribution curves for each genetic type.

Let us now combine the genetic model with the idea of thresholds. Seizures are an all-or-none phenomenon and individuals will be classified as positive or negative according to their reaction to a particular degree of stress. Such a dichotomization obscures the continuous nature of the susceptibility gradient. In the diagram the threshold has been drawn at a point which almost completely separates the two parental strains, and which divides the F_1 hybrids into a proportion of approximately three susceptibles to one resistant. Thus, it may be accurately stated that the F_1 hybrids have inherited a tendency for variability of response. One would further predict from the diagram that small changes in the amount of stress (which would have the effect of moving the threshold to the right or left) would change the seizure frequency in the F_1 hybrids without having much effect upon the parental strains. This prediction has been verified.

Considerable attention has been given to the genetics of this rather

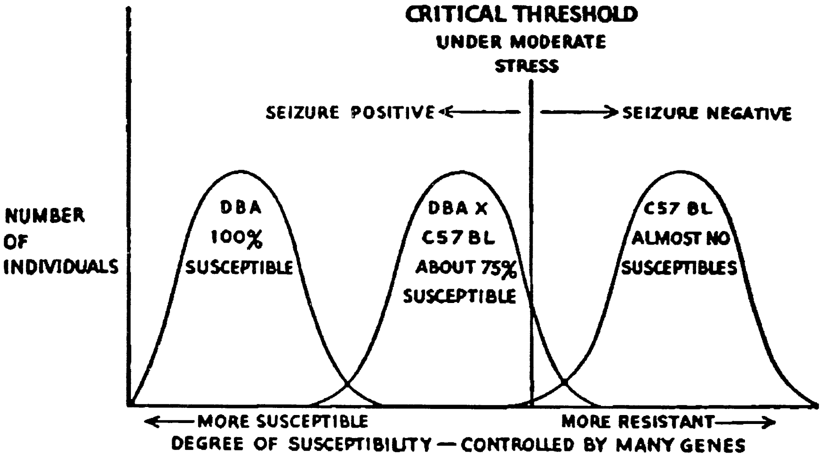

FIG. 1. The multiple factor–critical threshold theory of susceptibility. These idealized curves are based upon research on audiogenic seizures in mice. The DBA and C57BL curves represent the parent populations; the middle curve represents the first generation hybrids between these strains. The model may fit many other stress-induced nervous disorders.

esoteric form of behavior because it may be a model of a kind of hereditary mechanism which is often postulated for human behavior deviations, but which cannot be proved because of the impossibility of performing genetic experiments with man. If the audiogenic seizure be considered a form of behavior analogous to a psychosis or a neurosis, it is evident that both a genetic and an environmental determinant are necessary. Experiments have shown that the DBA stock not only contains more susceptible animals but each individual convulses more readily than do susceptibles from other stocks. If a similar situation is true of human behavior deviations, the amount of environmental stress needed to produce a breakdown of adjustment would be expected to differ for individuals of different constitution. This seems to agree with experience.

A possible application to human genetics lies in suggesting hypotheses for the mode of inheritance of deviant behavior patterns. Without the opportunity for prolonged controlled genetic experimentation the hypothesis of a single dominant gene for audiogenic seizure susceptibility would have adequately fitted the known facts. In human beings such syndromes as schizophrenia and manic-depressive psychoses have been attributed to single recessive or dominant factors. On theoretical grounds, the multiple factor–critical threshold model seems to be more logical and to be more in accord with the somewhat nebulous boundary between abnormal and normal behavior.

Studying Human Inheritance

The belief that intelligence and character are inherited to a very detailed degree is widely accepted in our culture. What parent has not glowed with pride at the splendid biological endowment which enables his child to bring home excellent report cards? Or if the child does not turn out well, who can fail to find the seeds of the difficulty on the spouse's family tree? This tendency to explain personality by genealogy has been amusingly exposed by A. M. Tozzer[(12)] in his essay *Biography and Biology*. Part of this folklore may be an attempt to fill the vacuum due to the scarcity of definitive work on the problem. It is important to have some acquaintance with the methods which must be used by human geneticists in order to study the inheritance of intelligence, deviant behavior, and personality.

An important method is the use of pedigrees of human families. In the country districts of northern Europe, where population has been stable and records have been kept for many years, it has been possible to trace types of feeblemindedness back for more than ten generations. We know how frequently traits determined by dominant genes, by recessive genes, or by sex-linked genes will appear in different types of matings, and theoretical expectancies on each assumption can be tested against pedigree records. When a character is easily diagnosed so that there is no uncertainty regarding proper classification, pedigree studies are very satisfactory. Modern methods of biometry have been developed to such an extent that it is not necessary to have long family histories. The nature of simple genetic mechanisms can be deduced from data on the frequency of a character in individuals of different degrees of relationship. Theory in this field has outstripped data collection, for human genetics lags far behind animal genetics in number of workers and completeness of records.

An important method for the study of quantitative variation is correlation. Individuals close in relationship have more genes in common, on the average, than individuals selected at random. In the case of identical twins the correlation of genotypes is 1.0, since such persons are genetic duplicates. A correlation coefficient measures degree of relationship without reference to the causes of the relationship. Families share not only genes but also a common way of life. In the family, correlations between siblings who share both genetic and environmental factors run higher than correlations between the parents' own children and their adopted children who share only environmental factors. It must be remembered that the genetic similarity of siblings is statistical in nature, and that some sibs may be very unlike in heredity. There is good evidence for some genetic determination of intelligent behavior, but attempts to derive statistically a percentage value for the hereditary and environmental components of the variance of intelligence have limited application, since the relationship between the two variables must be specific for almost every individual.

Both correlation and the mean-difference method have been used in studies of twins. The latter method compares the differences between test scores or other measurements in one-egg twins, two-egg twins of same and of different sex, siblings, and pairs chosen at random. The comparison between one-egg twins and like-sexed two-egg twins is the closest we can get with human material to a controlled experiment on the nature-nurture relationship. The one-egg twins have identical heredity; the two-egg twins are only as much alike genetically as ordinary siblings. In the same household both kinds of twins share common experiences, though parents may tend to keep identical twins in lock step and thus overdetermine the hereditary similarity. Twins are a somewhat special class of people in their development as is shown by a high frequency of birth injuries and lower average intelligence. Since twins are genetically like other people, these defects must be acquired in utero or in birth. Many twins, however, rank high in achievement.

Heredity and Intelligence

Early studies of the inheritance of human intelligence relied upon anecdotes or the estimates of teachers. In recent years standardized tests have become widely available and these provide a reasonably reliable objective instrument for measuring certain human capacities. The intelligence quotient (I.Q.), which is the ratio between an individual's mental age and his chronological age, has become a household term in this country. What intelligence tests measure biologically is not clear. They make use of learned responses, and a high score signifies that the subject has been able to profit from his environment. Motivation is essential to learning, and anything which impairs motivation would hamper the development of intelligence. On a priori grounds a biologist would suspect that intelligence would not be a very good subject for genetic analysis, since it is a complex character depending upon the coordination of many separate processes. Genetics deals most easily with relatively simple characteristics closely related to the primary biochemical action of genes. Whether the so-called factors of intelligence are related to separate gene systems or to different biological substrates is not known. Factors emerge more clearly as education is increased, and thus seem to be a product of training [18]. On the other hand, Halstead[14] has attempted to distinguish biological factors of intelligence related to the integrity of certain brain areas.

Studies of the distribution of I.Q. scores in large, culturally homogeneous populations show that they fit into a normal distribution except for an excess of very low scores below I.Q. 50. The normal distribution is the form expected when a character is determined by the combined action of a large number of randomly assorted minor influences acting together. The excess of very low scores is probably explainable by the fact that certain kinds of defects almost completely disorganize the functions of the higher nervous centers. Many of the very low grade defectives suffer from genetic or traumatic brain injury; others have genetically induced metabolic errors which affect intelligence; in still other cases no physical correlates of the deficiency have been found, nor can experiential factors operating on intelligence be implicated.

A hypothesis which fits the genetic facts would be that over an approximate range of I.Q. 50–200, the development of intelligence is conditional upon biological factors controlled by polygenes. At the low end of the scale, biological factors under single-gene control appear to be significant in some individuals. The question may be raised whether special genetic factors should be postulated for the upper end of the intelligence scale. Is genius biologically determined? No basis for such a hypothesis can be found in the facts. There is a certain arbitrariness about all classifications of genius. Historical accident, fashion, the oblivion which soon surrounds even the most talented who do not happen to achieve fame—all these foster a myth of the uniqueness of genius. Biology probably contributes to genius, but there is no unit factor which will guarantee results.

The parent-offspring correlations of I.Q. scores and correlations between siblings were determined in a rural population by Conrad and Jones[8]. Both correlations were .49, which is approximately the same as other investigators have found for physical traits such as height and weight. No consistent or significant differences were found between correlations of mother-child, father-child, brother-sister, brother-brother, or other pairings in which sex was taken into account. These findings demonstrate the importance of familial determination of intelligence as well as physique. They do not permit partition of the effect into genetic and nongenetic components. If environment were a major factor in producing differences, sibling correlations should be higher than parent-offspring correlations, since age of testing, type of schooling, and the like should be more uniform for the sibling group. This was not found in the Conrad and Jones sample, but other studies have shown such an effect. Anastasi and Foley[15] point out that sibling correlations may be as low as .30 or as high as .70, depending largely upon the range of abilities represented in the sample.

Somewhat more critical tests of the genetic factor in intelligence are possible in twin studies. The correlations between intellectual and physical measurements of identical twins reared together are much higher than for siblings in general. Burks[8] reports values of .95 for I.Q., .96 for height, and .98 for weight. On the other hand, identical twins reared apart may show considerable differences in I.Q. if they have also had considerable differences in schooling and social advantages (15, p. 344). These results are to be expected if heredity determines the detailed structure of the body and this in turn determines the capacity to profit from training. Another conclusion is that the differences in environment must be fairly large in order to have a detectable effect on the measured I.Q. Parents may tend to treat twins more nearly alike than ordinary siblings, but this can never be a perfect equivalence. Furthermore, Anastasi and Foley emphasize the fact that twins tend to develop a specialization of roles which serves as a basis for establishing separate identities, and this should partially compensate for the similarities of development imposed in the family situation.

In summary, familial resemblance in intelligence supports the idea that biological heredity is an important determinant. That the determination operates only within rather broad limitations is shown by the fact that radical changes in environment produce significant effects upon intelligence-test performance. It would be desirable to learn at what level heredity operates, so that a physiological basis for the genetic effects could be presented; but this is asking more than can be shown for many physical characters, and more than we ask for in accepting evidence of learning.

Heredity and Behavior Deviations

The same familial relationships which are found in intelligence are found in mental disease. Kallman[10] has summarized a number of studies of the incidence of schizophrenia in siblings of different degree of relationship to diagnosed index cases. His figures are:

Relationship to a Diagnosed Schizophrene	*Percentage of Individuals Expected to Develop Schizophrenia*	*Percentage of Individuals Having a Schizoid Personality*
One-egg twin (reared with index case)	91.5	8.5
Two-egg co-twin	14.5	23.2
Full sibling	14.2	31.5
Half sibling	7.1	12.5
Step-sibling	1.8	2.7
Parents	9.3	
General population	0.9	

The results are viewed as consistent with the hypothesis that a single pair of recessive genes produce a schizoid type of personality, which breaks down under stress and yields a frank psychosis.

Interpreting these results involves several questions. The diagnostic categories of psychiatry have been criticized for lack of precision. Kallman claims that the familial incidence of schizophrenia is unrelated to the frequency of the other great class of psychoses, the manic-depressive. Certainly he has made a sincere effort to specify the pathognomic criteria for each type, but it is not clear that all diagnoses were made independently of knowledge of the diagnosis of other members of the family group. Kallman believes a specific gene is necessary for an individual to develop a schizophrenic syndrome. If so, no amount or kind of stress could produce schizophrenia in a genetically resistant person, although some other psychological abnormality might result. In a few cases one-egg twins are discordant as to schizophrenia, but in general the histories of such pairs are alike even to details of age of onset and symptomatology. In the discordant cases a positive correlation between physical condition and resistance to the psychosis has been shown.

Culture and Heredity in Mental Disease

Is there an irreconcilable conflict between the genetic theory of psychosis and the theory of social determination of the disease? Psychiatrists and social and clinical psychologists have pointed out the high proportion of psychoses in the lower socioeconomic groups where there is less security, lower educational status, and supposedly greater psychological stress. Separation of cause and effect is not easy. Not all nor even most individuals from poor environments become schizophrenic, nor do the middle and upper socioeconomic groups escape.

Two general points of view can be recognized among the research workers and theorists who have dealt with this problem. These are:

1. The general-constitutional theory. Individuals vary along a continuous scale of resistance to behavioral disintegration. The amount and kind of stress determine what form abnormal behavior will take. Constitution may be determined (*a*) by heredity, (*b*) by previous experience, or (*c*) by an interaction between the two. This view emphasizes the role of cultural factors in channeling behavior deviations.

2. The special-constitutional theory. Individuals differ with respect to the ways in which they will respond to stress. The same set of stimulating conditions will in one case lead to psychosis, in another to an anxiety neurosis, and in a third to stomach ulcers. These specialized forms of response may be determined (*a*) by heredity, (*b*) by previous experience, or (*c*) by an interaction between the two.

Although the notion of general-constitutional weakness was tacitly accepted in many early studies (e.g., the family histories of the Jukes and the Kallikaks), it does not seem to be a good characteristic for genetic investigation. Alcoholism, sexual promiscuity, feeblemindedness, insanity, and criminal records have been lumped together as evidence of genetic behavioral instability. There is no doubt that feebleminded and psychotic persons are socially maladjusted, but social maladjustment is not diagnostic of these conditions. Kallman's data suggests that genetic effects on mental diseases are specific, and this is in accord with our knowledge of how genes operate on development.

An important study of mental health in a specialized cultural group has been reported by Eaton and Weil[17]. The Hutterites are a group of some 8,500 people dwelling in the north-central United States and adjacent Canada. They retain many of the social and religious practices of sixteenth-century European peasants, while they have adopted a sufficient number of modern technical advances so that their physical health is comparable to that of other rural populations in the region. Cardinal principles of the Hutterites are pacifism, adult baptism, communal ownership of all property, and simple living. The history of the group shows no case of murder, arson, severe physical assault, or sex crime. Possibly the absence of such spectacular breaches of the peace has given the Hutterites their reputation of being free of mental illness. The facts are otherwise, for the proportion of psychoses found by intensive survey is as high as or higher than that in other groups studied with equal care to discover all cases. However, the most common type of psychosis among Hutterites is the manic-depressive reaction, which makes up 74% of all cases, in contrast with the almost universal experience that schizophrenia is the most common psychosis. The fact can be explained either by the theory that the manic-depressive gene is unusually prevalent in this isolated population, or by the theory that a rigid, excessively social culture predisposes to depressive disorders rather than to schizophrenia. Possibly a continuing study of the genetics of the group will be able to settle the question.

We may conclude from the Hutterite studies that much antisocial behavior is completely determined culturally. We may suspect that early experiences are most important in forming personality, for in adults the situational determinants of behavioral and psychosomatic disorders do not seem to be all-sufficient. The individual's response depends upon intrinsic rather than extrinsic factors. How heredity and life experiences interact in the development of a mature personality will be discussed in the next section.

section three

The Development of Individuality

Traditionally the study of development starts with origins and considers the changing states of its subject in temporal sequence. This procedure is not possible when we consider the differences in personality among human adults. Instead it is necessary to start with important individual differences, trace these backward to their points of divergence, and try to learn what caused the divergence. Such retrogressive studies can be supplemented by long-term observation of developing children and by experimental treatment of infant animals.

Physiological Diversities

Certain physiological responses are of interest to psychologists because of their intimate association with behavior. These are sensory acuity, the physiological changes accompanying emotion, rate of metabolism, and the relation of physiological needs to motivation. Variations in body form also have a physiological basis and may be considered a more or less static record of an individual's metabolic history.

None of the attempts to explain differences in intelligence or in personality in physiological terms meets rigorous standards of scientific proof. Terman's study of gifted children in California[8] demonstrated that these young people were typically above average in size and health. But no one would seriously try to assess intelligence with a set of scales. We can attribute the correlation to the fact that intelligent parents pass on good genes to their offspring, provide them with a stimulating home environment, and secure adequate nutrition and medical care for them.

There have been recent advances in the method of describing individual physique and function. In the somatotype index of Sheldon[18] each individual is graded on three body components, each evaluated on a seven-point scale. Thus a 3–4–6 somatotype is just below average in endomorphy (fat component), average in mesomorphy (bone and muscle component), and well above average in ectomorphy (linearity component). Similarly the function of the autonomic nervous system has been described in terms of several separate balance mechanisms. Terry[19], for example, identifies factors for skin conductance, heart rate, and blood pressure. The significance of heredity in determining autonomic response patterns was shown by Jost and Sontag[20]. Identical twins were much more alike than other siblings, who were in turn more alike than unrelated matched pairs, on a series of tests of skin conductance, circulatory responses, and salivation.

The psychological significance of somatotype classification is questionable. Sheldon's classification of temperament has not been widely accepted. However, recent experiments on the autonomic nervous system have suggested a possible psychophysiological relationship. Removal of the sympathetic portion of the autonomic system and the use of sympathetic-nerve-blocking drugs have been reported to affect both avoidance conditioning in animals and the alleviation of anxiety symptoms in humans. The hypothesis is that certain autonomic responses become conditioned to "emotionally toned" stimuli. These responses are extinguished with difficulty and operate as a drive leading to avoidance of the conditioned stimulus. Under certain situations this may result in the learning of "neurotic" patterns of behavior. Unfortunately there are unexplained discrepancies between experiments of different workers. In a direct test of the relationship between autonomic factors and results of personality tests, Terry found no significant associations.

Animals, too, have characteristic autonomic reaction profiles which appear to be inherited, since they vary according to breed. Fuller [21] has shown that samples of five dog breeds were significantly different in five physiological measures, as well as in measures of temperament. Before concluding that the physiological and psychological characters are causally connected, it must be shown that they do not segregate independently in cross breeds. A genetic technique can thus aid in testing a psychophysiological hypothesis.

A considerable amount of time has been expended in the search for chemical correlates of personality. It is extremely easy to find biochemical individuality in blood, urine, or saliva. These fluids do not directly affect behavior, but the waste products of the body do reflect the metabolic events which have been occurring in the cells. And the composition of the fluid bathing the nerve cells can depress or facilitate their activity. When the adrenal glands are removed the concentration of blood potassium rises, and the nervous system is profoundly depressed. Death results unless replacement of adrenal hormones is prompt. Sex hormones appear to facilitate specific neural pathways involved in courtship and mating. However, neither normal differences in excitability nor in strength of sex drive have been correlated with quantitative variations in blood chemistry within the ordinary range. Behavior patterns seem to be less responsive to variations in the internal environment than are many other physiological functions, and more sensitive to external events.

One of the most significant series of researches on the physiological determination of drive strength has been performed by W. C. Young and co-workers[22]. Stocks of guinea pigs of high and of low sex drive were obtained by selection. Both strains were almost completely devoid of sexual activity after castration. When male sex hormone was replaced by injection, each stock returned very precisely to its previous level. This was determined, not by the composition of the blood, but by the reaction of the body cells to a particular substance in the blood. It seems likely that studies of biochemical individuality must go inside the cell if they are to prove fruitful for psychology. Behavior itself may be the most sensitive indicator of neuroendocrine interactions.

Genetics and Motivation

There are fundamental differences between species in the physiological basis of motivation. Beach[23] has emphasized the fact that the dependence of sex drive upon hormones becomes progressively less from rodent to carnivore to primate. In primates, the order of mammals which includes man, sex drive becomes released in large measure from hormonal control and becomes a cerebral function responsive to a variety of complex external stimuli and conditioned by the past history of the organism. The whole problem of motivation in animals with complex nervous systems needs more investigation. One view is that there are a few basic needs—food, water, oxygen, elimination of wastes, discharge of the products of the sex glands, and escape from pain. Drives for action correspond to basic needs. Exploratory behavior of rats in mazes or men in scientific laboratories, social reactions of dominance or submission—these are secondary drives derived from primary biological needs. Learning is assumed to be dependent upon the reduction of drive; hence an organism learns to act in a way which will satisfy a biological need. The activity of a scientist, therefore, can be explained as a learned method of meeting these needs. Harlow[24] has recently questioned this generalization, and has shown that monkeys can learn to solve mechanical puzzles when the only apparent reward is the solution of the puzzle. Dominance hierarchies are set up in litters of puppies when there is no biological advantage to the dominant animal (all needs are supplied by the caretakers). If manipulative and social behavior can be demonstrated to be in part independent of the so-called primary needs, we have much greater scope for the effects of heredity upon individual variability. An individual cannot tolerate much variability in his needs for food or water, but variations in exploratory drive or aggressive drive would not be harmful. In fact such variability between individuals might be essential for a smoothly functioning complex social organization. In the beehive a complicated though inflexible social structure has been imposed by the joint action of genetics and larval nutrition. In human societies the social roles in their great diversity are largely learned, but genetic individuality may make it easier for some individuals to learn particular roles.

There are correlations between physical and psychological characteristics in man, but they are low. Furthermore some of the observed relationships may be due to what Anne Anastasi has called the influence of social stereotype. Sam Jones, the hypothetical university freshman of our opening paragraphs, is a tall, handsome boy who looks the way most people think a leader should look. He was elected to several high school offices, enjoyed the experience and today he acts and speaks with a leader's assurance. Heredity has played a part in the development of this ability, but should we conclude that Sam inherited leadership ability? Trainers of animals are well acquainted with other types of constitution-training interaction. Punishment has very different effects upon a puppy of the hereditarily aggressive terrier type and upon the more submissive spaniels. Probably the same is true of children.

A probable reason for the low correlation of physical and psychological characters is that personality is adjusted to the contour of a group of organic factors, not dependent upon the absolute level of one or two. On a priori grounds the diversity of human beings could be attributed to either genetic or nongenetic elements. Both are sufficiently variable. In cultures where child-rearing practices are more homogeneous than in the twentieth-century American city, more uniform personalities might be anticipated. But Eaton and Weil[17] say of the Hutterites:

> Despite this uniformity in the externals of living, Hutterites are not stereotyped personalities. Differences in genetic, organic and psychological factors seem to be sufficiently powerful to produce an infinite variety of behavior, even in a social order as rigid as this one. It appears that the nightmare of uniformity sketched in George Orwell's *Nineteen Eighty-four* is actually unachievable in a living society.

The comparative studies of child-rearing practices in various cultures as related to adult personality in the cultures have certainly demonstrated the tremendous importance of learning. However, a biologist may be somewhat sceptical of the characterization of every individual of a culture as aggressive or sexually repressed. It seems likely that Sioux, Bantu, Samoans, or New Englanders are less stereotyped than some cultural anthropologists and Hollywood script-writers believe. Striking individual differences in behavior are found even among animals of uniform heredity and rearing, and with fewer possibilities of showing differences because of simpler behavior patterns. The experiments of Scott and Fuller[9,10] show that even if we ascribe all the variation *within* a breed of dogs to environmental rather than genetic factors (and this is certainly too extreme) there is a large residue of individual variation ascribable to gene differences. Accepting this possibility for lower mammals and denying it to human beings appears to rest upon the assumption that innate patterns of behavior are less important in man than in lower animals. The deduction is a *non sequitur*. The development of a nervous system which can change its responses with relation to experience is just as much dependent upon genes as the development of a nervous system adapted only for reflex and instinctive acts. In fact the greater complexity of the mechanism affords more scope for variation, and variation is exactly what anatomists find when they look for it. Quantitative differences between individuals in the number of neurons and numbers of connections between neurons may range up to 100% of the average value for the species. This is the sort of difference which theoretical analysis of brain activity predicts would be important for intelligence. Few scientists have been interested in painstaking detailed research on individual variation in brain structure, and the existing studies have not been accompanied by a complete psychological and genetic study of the subjects. This is needed.

Race and Class Differences

One of the most serious questions facing the world today is the matter of relationships between racial groups and socioeconomic classes. Three kinds of explanation have been proposed for the fact that some people are better off, have more privileges, and have more power than other people. The first explanation is that the upper classes have a superior heredity. There are two variations on the theme: (a) a natural aristocracy of birth confers a special fineness or value upon certain races or families, and (*b*) in a competitive society those who have been well endowed with good genes rise to the top and become an aristocracy of achievement. View 1 (a) is favored by members of dominant groups whose parents or grandparents made good; view 1 (*b*) is expounded by self-made men and women. A second major type of explanation places the emphasis upon physical differences in the environment of groups. Here nutrition, climate, and disease are the most important variables. Most children in Africa, Asia, and much of South America suffer from malnutrition, live in an unsanitary environment, and in the tropical regions are subjected to depressing heat. Even in more favored regions, illness and malnutrition plague the poor more than the wealthy, and have a deleterious effect on the intellectual and physical development of many children. A third variety of explanation emphasizes cultural accident for group differences, and cultural stimulation for individual differences within groups. The invention of an alphabet, of ironmongering, of an effective political system, gave the Mediterranean peoples a form of civilization which by a cultural chain reaction has led to the dominant position of the Western nations. Had these cultural accidents occurred in Africa, the Negro race would dominate the earth. The higher I.Q. of children of professional parents, so runs this type of argument, results from the fact that their children grow up in stimulating homes. If maternity hospitals shuffled babies about and dealt them out at random, the social class-I.Q. relationship would be unaffected. Finally, all of these viewpoints recognize the fact that social organization limits the mobility of an individual upwards or downward in the social scale regardless of his individual worth as measured by objective standards. These views of the nature-nurture problem are obviously related to varying political and economic opinions. It is interesting to note that communist and fascist policy, though they are similar in their totalitarian outlook, split widely on the nature-nurture problem. The fascist believes that his race or nation is hereditarily superior to aliens, and has a destiny to rule over inferior peoples. In the communist doctrine environment is supreme, and genetics is only a means of preserving environmentally induced improvements.

Can the scientific study of human races help in evaluating these divergent views, or perhaps lead to a restatement of the problem? If the races of man are like breeds of animals, then we must certainly admit the possibility of biological differences among races which would affect temperament and certain kinds of learning. To test this idea it will first be necessary to define what a biologist means by race. Dobzhansky[28] states: "Races may be defined as populations which differ in the frequencies of some genes. A population is a group of individuals cemented by intermarriage and hence sharing a common treasury of genes."

Races are not static, well-defined entities, but dynamic groups which change as the patterns of human mating change. Races are in a constant process of differentiation and amalgamation, depending upon migration, war, social restrictions, and other factors which affect the flow of genes. Separation by geographical barrier or social barrier or by distance is the prime requisite for the differentiation of a race. Attempts to make rigid classifications of races and speculations upon supposed pure ancestral races are not only biologically unsound but serve to perpetuate "man's most dangerous myth." But though biology cannot recognize any pure races in man, it does make contributions to the nature of the genetic differences between populations by studying differences in gene frequency in various groups.

The argument for innate racial differences in potentialities for developing intelligence is that populations differ in the frequency of genes controlling obvious external characters such as skin color, and in the frequency of genes controlling internal characters such as blood type. Assuming that some genes are responsible for variation in individual intelligence and personality, one might expect a differential distribution of these genes in separate populations. In order to determine the validity of this deduction it will be necessary to consider the processes which produce, maintain, and diminish racial differentiation.

These processes are mutation, selection, genetic drift, and hybridization. We know of no force which is likely to have differentially affected mutation rate in various regions of the world, and can assume that large groups of people over sufficiently long periods of time will have about the same number of mutations. Mutant genes which survive will give distinctive characteristics to the populations which possess them. One of the forces determining whether a mutation will persist is natural selection. Single-gene mutations which cause serious pathological conditions are subject to strong negative selection, particularly if they are dominant or sex-linked. So strong is this selection that it has been mathematically demonstrated that the persistence of conditions like sex-linked hemophilia must be due to recurrent separate mutations. Selection will be less effective against rare recessives unless the heterozygote has some disadvantage, since the pathological type against which selection must operate represents only a minute fraction of the recessive genes. Selection need not be an all or nothing matter. A small difference in fertility will be an effective agent of positive or negative selection over sufficient generations. Since races often live under different physical conditions, it is probable that some differences, such as skin color, may have been selected for their adaptive value. Racial differences in resistance to specific infectious disease have obvious regional adaptive value. It is hard to see how there would be similar differences between regions in the adaptive value of behavioral plasticity which is what we mean by intelligence.

Not all racial characteristics have been maintained through natural selection. When populations are divided into small groups the phenomenon of genetic drift is observed. The laws of genetics are statistical laws which experience has shown to have high predictive value in large populations. When small numbers of individuals are involved, there may be large deviation from the most probable distributions of genes. These few individuals may become the ancestors of a large population, which if it remains reproductively isolated from the original common stock will drift apart in gene frequency. Genetic drift has been shown to be effective on such well-marked genes as those controlling human blood groups[28]. It is unlikely that genetic drift could produce much divergence in polygenic characters, since this would involve correlated drift of numerous positive-acting or negative-acting genes, a practically impossible circumstance. If the idea that genetic influence upon intelligence and temperament is polygenic is correct, it appears impossible that genetic drift would produce races of mankind possessing psychological differences.

Hybridization between races serves to unite gene pools into a new gene pool. In the absence of barriers to free intermarriage in the hybrid population, genes from both sources will continue to circulate through the population. In the absence of selection or mutation, the proportion of genes of different types within a random-mating population remains constant. There are limitations upon random mating in man, but these have never been so strict as in domestic animals. For this reason the races of man are not comparable genetically to animal breeds. Human races might better be compared to regional types of nonpurebred livestock. Animal breeds are roughly analogous to large human kindreds, or even in the case of inbred strains to reduplicated individuals.

The only possibility the geneticist can offer for the development of hereditary differences in psychological capacity between races is that different cultures may put different values upon particular kinds of behavior. In one culture aggressive individuals leave more descendants than peaceful individuals, hence selection for genes causing aggressiveness results. In a different culture aggressiveness might be subjected to negative selection, and peaceful members leave more descendants. Thus genetically diverse races will be formed.

There are two weaknesses to this argument. It assumes a rigid correspondence between a particular genotype and manifestations of an aggressive personality. It is possible that a vigorous individual would do well in either society, though his energies would be culturally channeled in opposite directions. The sociology is oversimplified, for human groups require that their members play divergent roles. Even in the aggressive culture, some must be subordinate; and in the peaceful culture some must lead. Selection may favor diversity within the social group. It is possible to develop animal strains which are so aggressive that normal group organization is impossible, but such breeds persist because man looks after them. Left to themselves they could not survive.

Class Differences in Intelligence and Temperament

All accounts of differential psychology include data on the performance of socioeconomic classes in intelligence tests. One of the best reviews is still that of Jane Loevinger in the 1940 *Yearbook*[8]. Some of the researches summarized there have shown the following facts. There is a consistent upward trend in average I.Q. of groups of children classified in terms of parental occupation from unskilled laborer to professional man. Child intelligence scores correlate better with parental education and intelligence scores than with economic or occupational status of parents. This indicates that the favorable influence upon child intelligence is fairly specific. Environmental influences are more dependent upon intellectual stimulation than upon better living conditions in general. Hereditary transmission of genes producing superior organization of the nervous system is not ruled out, but cannot be proved as a fact. Regardless of the heritability of the factors which lead to socioeconomic hierarchies, it is important to consider the extent to which such social differentiation can lead to biological isolation. People tend to marry within their own social and educational class and to have their children follow in a similar path. In extreme cases, as in India, caste groups approach the definition of a race given above, since rigorous marriage laws limit the exchange of genes among social groups. In the United States social custom and law have partially kept apart the Negro and white races who occupy the same geographical territory.

There can be no doubt that complete reproductive isolation can through genetic drift lead to genetic differentiation of subpopulations of men. That genetic drift could account for any differentiation of socioeconomic classes in the United States appears to be impossible. The populations involved are too large and too imperfectly separated. "Rags to riches" is still possible via the market place or the altar. Once two populations of genes have become mixed up through hybridization, they can be reconstituted as separate populations only by rigorous selection.

There remains the possibility that the division of individuals into socioeconomic classes operates as a continuous selective agent, leading to the concentration of superior genetic endowment within the professional and business classes and inferior genes within the group of unskilled laborers.

This differentiation would be most rapid in a fluid society whose members could rise and fall freely in accordance with their demonstrated ability, and where equal educational opportunities for all individuals insured full expression of genetic factors. Given selective marriage between individuals who land at about the same place in the social order, the eventual product may be something like that of Dr. Tryon's rats, a socially intelligent race of man and a socially dull race. For the short run it makes no difference whether the qualities which put an individual in the upper or lower group are determined by the family genes or the family environment. In the long run it will make a difference, since upper groups typically fail to reproduce themselves. If cultural factors are of preeminent importance, the upper group can be perennially replaced from the lower by simply providing adequate developmental conditions. If biological factors are primary, the decreased frequency of "good genes" could be restored only by radical changes in our marital and family system.

How well does the rat selection model fit the human situation? The society described in the above paragraph has obvious similarities to twentieth-century United States of America. There are also differences. Selection in the laboratory is more precise than in human society, though this is merely a quantitative difference which will retard and diminish but not prevent the genetic separation. There is a more fundamental difference in the basis of selection. A complex human society does not depend upon the ability of each member to run a maze without errors, to excel in linguistics, mathematics, musicianship, or pitching a baseball. Such a society is strong because its members differ in ability. The biological attributes which are of universal value are physical vigor, the ability to modify behavior according to experience, and the ability to extract meaning from more and more complex situations. For social animals in general, and for man in particular, the force of natural selection acts more strongly upon societies than upon individuals. A newborn infant's chance for survival, and hence the survival of his genes, depends less upon his own potentialities for intelligence or even upon the intelligence of his parents, than upon whether he is born in Boston Lying-in Hospital or a Calcutta slum. Yet the gene pool from which the American child draws his individual assortment was, two millennia ago, the gene pool of the barbarians of the Teutonic forest. Not a change in heredity, but a change in social organization has given him a greater chance to survive, marry, and bear children. Against his better chance for individual survival must be balanced a reduced probability of having large numbers of offspring.

All of these arguments must lead to the conclusion that the processes of racial and class differentiation as they currently operate do not in general lead to the separation of genotypes inherently different in their capacity for psychological development. In small, isolated populations genetic drift sometimes may lead to different frequencies of major genes with pronounced behavioral effects, and be reflected in an especially high frequency of deviant behavior. This conclusion does not imply that the individuals within a population are genetically equivalent in their potentialities for psychological development. Biologists find evidence for hereditary determinants of individuality in every body system. Selective breeding of animals for psychological traits has in experiment after experiment demonstrated a genetic factor in the trait variance. One-egg twins have been found more similar than two-egg twins in literally dozens of studies, in characteristics ranging from I.Q. to type of response in the Rorschach inkblot test. Part of the differences between people are the product of genotypic differences. The author considers it possible that genotypic diversity of their members is of benefit to complex human societies, since this may facilitate the adaptation of individuals to various specialized roles.

The dire predictions of some of the older eugenicists regarding the imminent decline of the intellectual capacity of the human species because the less well educated leave more descendants than the well educated does not seem to be borne out, for the short run at least, by the available facts[27]. In fact, some studies show an actual increase in intelligence-test scores. Comparing I.Q. scores from different generations whose educational and home environments are not identical is not a critical test of the hypothesis that the present condition of differential fertility will eventually result in a decreased intellectual capacity. However, this does not appear to be as imminent a danger to human culture as atomic war, crime, starvation, and other social ills. There is nothing in biology to indicate that it could not happen, but the very disorderliness of human society is a protection against rigid selection that might lead to concentration of all favorable genotypes in one class, all unfavorable ones in another. Being "well-born," the literal meaning of the word eugenics, is important, and fortunately the policies which improve the physical surroundings of men contribute to this as much as does genetic selection. Negative eugenics, the elimination of injurious genes, can be highly effective against defects due to dominants, but is much less effective in the elimination of rare recessives. The argument for restriction of reproduction of the grossly unfit through social action rests less upon its effectiveness in eliminating undesirable genes than upon the prevention of human misery. The baby of feebleminded parents has a dismal prospect, even if he be structurally perfect. Married couples in whose families genetic abnormalities have appeared often have problems concerning the risk of defects appearing in their own children. We need more clinics of human heredity to relieve anxiety and give realistic information to people who can base their decisions on facts instead of fears.

In bringing this paper to a close the author is aware of a sense of futility in attempting to summarize the status of the nature-nurture problem in a few terse factual sentences. Many statements which he has made should have been more hedged with qualifications than was possible in a brief account. One caution may be recommended. We need to know more about human heredity, human evolution, and the development of human personality before we go far in consciously guiding human evolution through population policies designed to change the present systems of mate selection.

The nature-nurture "controversy" is less bitter today than two decades ago. Insofar as it still exists, it will be resolved by careful longitudinal studies at the genetic, psychological, and physiological levels and by new theoretical formulations rather than by further gathering and analyzing of statistics. However, prediction from controlled experiments and from mathematical models to actual occurrences in the field is always risky unless there is a vast background of experience to aid the predictor. The history of the human race on this planet is so unique that we do not have this background of experience. History repeats itself very crudely in comparison with the repetitions of phenomena in the laboratory. The scientists of the future will have the opportunity to observe in our descendants the results of the grand scale nature-nurture experiment, and can evaluate the hypotheses of today when the next ice age forces a major crisis in human affairs.

Glossary

audiogenic seizure—A convulsive attack brought on by exposure to intense high frequency sound. Such attacks have been produced in some varieties of rats, mice, and rabbits.

autonomic nervous system—The division of the nervous system concerned with regulation of circulation, digestion, perspiration, and similar "involuntary" activities. It is divided into two portions with generally opposing actions, the sympathetic nervous system (*q.v.*) and the parasympathetic nervous system.

backcross—A mating, or the offspring of a mating, between a pure-line plant or animal and a hybrid descended in part from the same pure line.

C57BL—Standard symbol for a particular pure strain of mice with black coats and high resistance to audiogenic seizures.

chromosomes—Elongated bodies of microscopic size found within the nucleus of cells. The name refers to their strong color reactions with certain dyes.

cotwin—The other member of a twin pair.

DBA—Standard symbol for a pure strain of mice with faded brown coat color and high susceptibility to audiogenic seizures.

dominant—Term applied to a gene which in a single dose can produce an observable effect on an organism. Dominant genes are contrasted with *recessive* genes, which must be present in a double dose (one gene contributed by each parent) in order to produce an observable effect. Actually genes cannot be classified in two wholly discrete groups. Dominance is better considered as a quantitative attribute ranging from 0 in the case of complete recessives to 1 in the case of a gene which in a single dose produces as much effect as in a double dose. In intermediate situations the combination of a dominant plus a recessive is distinguishable from the double dominant.

ectomorphy, endomorphy, mesomorphy—Terms used by Sheldon to denote the components of body structure arising from the three primary layers of the embryo. From ectoderm (outer layer) come the nervous system and outer layers of skin; from endoderm (inner layer) come the lining of the digestive tract and its appendages; from mesoderm (middle layer) come bone, muscle, and connective tissue.

endomorphy—See *ectomorphy.*

F_1—Genetic shorthand for the first filial generation from a mating between two pure strains. Crossing $F_1 \times F_1$ would yield an F_2.

genes—The physical units of heredity. They possess the power of "specific self-duplication"; thus each gene is exactly copied in every cell division. All effects of heredity on organisms depend in final analysis upon gene control of biochemical patterns in cells.

genetic drift—The divergence of originally similar populations with respect to the frequency of certain genes due to the fact that chance determines exactly which genes will be transmitted to succeeding generations. Particularly in small isolated populations chance may lead to wide deviations from the original population. Genetic drift is believed to be an important factor in organic evolution. It should not be confused with changes in gene frequency due to selection.

genotype—The genetic constitution of an individual. See also *phenotype.*

heterozygote—An individual in whom the corresponding members of a gene pair are unlike, for example *Aa*. This may be contrasted with two possible *homozygotes, AA* and *aa*. A heterozygote may transmit either form of gene to his offspring. Pure lines of organisms are homozygous for all or almost all gene pairs.

homeostasis—The maintenance of constant conditions within the body—for example, temperature, and the oxygen content of the blood. Homeostasis does not imply a constant level of activity, but rather a dynamic adjustment of activity to the degree of stress so that body cells are not subjected to unfavorable conditions.

homozygote—See *heterozygote.*

inbreeding—A system of breeding close relatives together. The so-called inbred lines of genetics are established and maintained by unbroken brother-sister matings.

major gene—A single gene producing a large effect on the variability of a trait. Such genes can be readily detected and named. See *polygene.*

manic-depressive psychosis—A functional (no known structual basis) behavioral disorder characterized by emotional and ideational overactivity, alternating with a phase of severe depression and withdrawal.

mesomorphy—See *ectomorphy.*

molecular level—A reference, in this essay, to attempts to explain phenomena in terms of chemistry. The primary effects of genes are molecular, and these in turn affect gross structure and function as studied by the biologist and psychologist.

multiple-factor inheritance—Control of the genetic portion of variability of a trait by the combined action of several pairs of genes. Body size and skin color in man are examples. (Environmentally induced variability is always superimposed upon the genetic components.)

mutation—An abrupt change in the nature of a gene so that it thenceforth reduplicates itself in a new form. A mutation may or may not be observable as a change in phenotype.

phenotype—The description of an organism in terms of its observable qualities. See also *genotype*.

phenylpyruvic amentia—A form of hereditary feeblemindedness characterized by the excretion of phenylpyruvic acid in the urine. The mental symptoms are secondary to a primary gene-controlled deficit in cellular metabolism.

polygene—A gene producing a small quantitative effect on the variability of a trait. Because of their small individual effects polygenes cannot be isolated by genetic techniques. See *major gene*.

psychogenetics—In a broad sense the study of the origin and development of behavioral and mental traits. In a narrower sense it refers to the study of biological inheritance as related to such traits.

schizophrenia—A functional psychosis characterized by withdrawal from reality and a dissociation of emotional expression from accessible thought content. It is generally the most common psychosis and usually becomes manifest in adolescence or young adulthood.

selection—The process by which certain genes or gene combinations change in frequency from generation to generation because of reproductive advantages. Positive selection leads to an increased frequency of the gene; negative selection to a decreased frequency. In man reproductive advantage may be based directly upon fertility and vitality (the ability to survive up to and throughout the reproductive period) or indirectly upon social factors such as mate selection, age of marriage, quality of child care, and voluntary birth control.

sex-linked—Said of genes carried on the chromosomes which determine sex. Red-green colorblindness and hemophilia (bleeder's disease) are well known examples.

single factor inheritance—Control of the genetic portion of variability of a trait predominantly by genes at a single position on a particular chromosome.

somatotype—A classification of body form based upon the development of tissues arising from the three primary layers. See *ectomorphy*.

sympathetic nervous system—A subdivision of the autonomic nervous system whose activity generally increases the energy output of the organism. For example, sympathetic nerve stimulation raises blood pressure, speeds up the heart, increases the sugar content of the blood and causes the sweat glands to secrete. The name "sympathetic" was applied to this division because it becomes increasingly active in emotional states.

twins, one-egg—Twins which arise from the splitting of a single fertilized ovum. Such twins must be of the same sex and have exactly the same genes. Though they are often called "identical," this term does not strictly apply, since environmental differences always produce varying degrees of nonidentity.

twins, two-egg—Twins arising from the contemporary development of two separate fertilized ova. Such twins are on the average only as much alike genetically as ordinary siblings, but may be more alike than ordinary siblings because of a more uniform environment during development.

variance—The average value of the squared deviations from the mean of a distribution of quantitative measurements. In the statistical technique known as analysis of variance the total variance is assigned partly to systematic factors influencing the measurements and partly to experimental error. For example, variability on a test of timidity given to two strains of mice may be shown to be due partly to genetic differences, partly to whether the animals were shocked or not, and partly to unknown factors.

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