BEHAVIOR GENETICS[1]

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A chapter on behavior genetics is new to the *Annual Review of Psychology*. This creates certain problems with respect to the time span which should be covered. Some papers in this area have previously been reviewed in chapters dealing with comparative or experimental psychology. The nearest approach to a treatment of behavior genetics was Kallman & Baroff's (64) review of behavior abnormalities in 1955, which emphasized the inheritance of mental disorder.

An article in the *Annual Review*, whatever the time span it covers, should fairly represent contemporary interest as distinguished from historical trends. The year 1954 has been selected as a starting point, because, in a relatively small area such as behavior genetics, a five-year period permits a representative sampling of present-day interests. Furthermore, this choice of date allows the inclusion of a major summarizing volume, *Genetics and the Inheritance of Integrated Neurological and Psychiatric Patterns* (57).

Books

As yet there is no book which systematically covers the field of behavior genetics. During the past five years a number of volumes have appeared, however, which have more than routine significance for this area. Perhaps the most important is the previously mentioned volume, which was the outcome of an annual conference of the Association for Research in Nervous and Mental Disease. A number of individual contributions to this symposium are referred to in more detail later in this chapter. The volume as a whole, however, gives a fairly comprehensive account of various approaches to the physiological genetics of behavior. Many of the authors are concerned with the pathways through which genes produce behavioral variation. Errors of metabolism, such as phenylketonuria, and anatomical defects find a prominent place, although some attention is given to the inheritance of intelligence (Thompson), the functional psychoses (Kallman), and genetics and adaptibility (Glass). Another group of chapters deals with problems of behavior development, the area usually called genetic psychology. It is good to find such papers in juxtaposition to papers on heredity, for the fields of psychological genetics and genetic psychology have sometimes seemed to pull in opposite directions.

Two books come to grips with the problem of heredity and behavior as part of a treatment of the general subject of individual differences. Tyler's *The Psychology of Human Differences* (122) devotes a brief chapter to the hereditary basis of individual differences. Although the results of twin studies

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[1] The survey of the literature pertaining to this review was completed in April, 1959.

are criticized on technical grounds, Tyler believes that the consistency of the evidence on similarities of identical twins is proof that genetics plays an important part in the production of individual differences in human behavior. The environment of both members of one-egg twin pairs is undoubtedly more similar than that of the members of two-egg pairs, but this does not seem large enough to account for the observed greater similarities of the one-egg pairs. Anastasi (5) has published a third edition of the well-known *Differential Psychology*. This book contains no separate chapter on heredity, but two long and comprehensive chapters deal with heredity and environment interactions. Anastasi gives an excellent account of the types of confusion which have centered about the nature-nurture issue. Students exposed to this text should be more sophisticated than some of their predecessors. In the earlier editions, this text might have been classified as slightly environmentalist. The present edition, though still highly critical of naive hereditarian views, strikes a very sound middle ground. It is perhaps one of the best sources for critical consideration of methodological problems.

The relationships of genetics to behavior are considered from the viewpoint of a biologist in Scott's *Animal Behavior* (104). Emphasis is placed on experimental evidence from animals, and sex differences in behavior are taken as a model of the inheritance of psychological characteristics. Adaptiveness of behavior is viewed as an outcome of selection operating on genetic mechanisms. The biologists' viewpoint complements, rather than conflicts with, that of the psychologist.

Two other books should also be mentioned here. One, *Behavior and Evolution* (94), is the result of two conferences sponsored jointly by the American Psychological Association and the Society for the Study of Evolution. Although genetics is possibly the biological science currently most concerned with the dynamics of evolution, most of the chapters in this book deal with the classical method of comparisons between phyletic groups, the end results of the evolutionary process. Some of the contributors (Caspari, Harlow, Pitendrigh), however, have dealt with the problem of the interactions between behavioral variation and selection pressures which could lead to progressive modification of behavior patterns. The second volume is the report of the Milbank Conference on *The Nature and Transmission of the Genetic and Cultural Characteristics of Human Populations* (80). In contrast with the Association for Research in Nervous and Mental Disease contributors, the Milbank authors show less concern with the mechanisms by which genes influence behavior and place more emphasis on heredity as a source of psychological differences within and between populations.

Finally, in this introduction it is interesting to compare the emphasis placed upon behavioral genetics in different scientific disciplines by counting the number of contributed papers in this category in three recent International Congresses, the First International Congress of Human Genetics (Copenhagen) (38), the Fifteenth International Congress of Psychology (Brussels) (37), and the Tenth International Congress of Genetics (Montreal)

(117). The Human Genetics Congress produced 21 papers in the field, 5 on endogenous psychoses, 5 on mental deficiency, and 11 on normal and abnormal behavior patterns. Some of the latter, however, would not be included in the stricter definitions of the field of behavior genetics. The Psychological Congress and the Genetics Congress produced two papers each. It may be concluded that activity in behavior genetics is still predominantly directed at practical human problems. Nevertheless, a steady output of experimental papers continues.

THEORY AND METHODS

Dobzhansky (30) has dealt exhaustively with the relationship between genes and behavioral characters. Nature is not fatalistic, but, in a sense, our bodies and hence our phenotypes are by-products of the self-copying of genes. In this sense all characters might be considered as 100 per cent hereditary [cf. (47) for a similar view]. Genes must determine characters such as intelligence, since different genotypes develop differently in the same environment. But the intelligence of two individuals of different genotypes might be exactly the same provided their environments were different. Dobzhansky believes that human development is unique since it is determined by three factors instead of the usual two—environment, heredity, and culture. To this reviewer, it seems more parsimonious to consider culture as a unique form of environment which shows progressive evolutionary modification. It is interesting to contrast Dobzhansky's view of the uniqueness of man with Harlow's (51a) espousal of a very close physical relationship between man and other primates. We are not yet rid of arguments on the continuity or discontinuity of man and beast, though the area of disagreement has shifted from biology to psychology.

In a presidential address, Anastasi (6) has gone somewhat beyond her textbook in outlining a program for research in the nature-nurture area. Historically, the first question asked in this field was, "Which determines a particular trait?" Later interest shifted to "How much does each contribute to a trait?" but the focus should go on to "How does a trait develop?" One can agree with much of this analysis without conceding that the question "How much?" is obsolete. The kinds of questions one can ask about nature and nurture with respect to individuals are different from those one can ask with respect to populations. For an individual, the question "How much?" has no significance, since all traits may be logically considered as completely hereditary or completely environmental. In dealing with populations, however, the contribution of heredity to total variance is still a useful object of inquiry, though with increased sophisitication we have come to see that the answer to "How much?" is not a universal constant.

Two papers have dealt with the contribution of factor analytic theory to the definition of traits which might be useful for genetic analysis. Royce (100) has pointed out a similarity between the multiple factor theory of psychology and the multiple factor theory of genetics. In the diagrams which accompany his article, separate groups of genes are assigned to each factor of intelligence, such as, for example, the ability to perceive spatial relationships and memory. Such isomorphism of genetic and psychological elements has not been proved and seems unlikely on neurological principles. Thompson (119) in dealing with this problem has gone back to the genetic meaning of correlations. Two phenotypic characters may be correlated because they are dependent upon a common gene, upon two genes present in the same chromosome, upon genes which happen to be present in the same populations or because of mutual dependence upon an environmental factor which has no genetic significance. Without incorporating some test of genetic meaning it is logically impossible for factor analysis to lead directly to biological factors which are genetically simple. Thompson suggests that Eysenck's "Criterion Analysis" might prove a useful technique, though it has not been adequately tested. The problem of defining behavioral phenotypes in a form best suited to genetic analysis deserves more attention. Most investigators adopt measures which intuitively seem to have meaning for them.

The use of split-litter technique in psychological research has been critically reviewed by Ross, Ginsburg & Denenberg (98). They warn against the facile assumption that this method is a good control for genetic variability. Whether it is or not will depend upon the breeding structure of the population sampled. In actual practice, split-litter technique is probably more useful for the control of environmental factors common to litters than for the control of genetic variability. The evidence from such areas as endocrinology and pharmacology (78) indicates that efficiency of bioassay is markedly improved by use of littermate control.

A technical advance particularly suitable for behavior genetic studies with small organisms, such as fruit flies, has been described by Hirsch & Tryon (56). Their procedure of mass screening reliably classifies every individual's behavior without handling or observing it individually. Such a method is particularly useful in selection experiments in which large numbers of individuals should be tested in order to proceed efficiently. Another technique new to behavior genetics is the manipulation of chromosomes which can be identified reliably by marker genes (54). This permits evaluation of the effect of a specific chromosome upon variability of a specific behavior measure. Techniques of this sort bring behavior genetics close to the model of ordinary experimental psychology, in which the chromosomes are independent variables under the control of the experimenter. Unfortunately, they are better adapted to drosophila than to mammals, in whose behavior there is greater interest.

BEHAVIOR GENETICS OF INVERTEBRATES

Hereditary mechanisms are, of course, similar in vertebrates and invertebrates. The advantage of invertebrates for behavior genetics lies in a more rapid succession of generations. The behavior of invertebrates appears stereotyped, and it seems reasonable to assume that the correlation between genotype and behavioral phenotypes may be higher than in most vertebrates. Arguments for the use of the rich genetic variability available in the fruit flies have been summarized by Hirsch (54).

A small, but varied, group of papers have utilized the fruit flies and a scattering of other insect species. Other classes and phyla are still neglected. Habitat preference has been studied in a series of strains of *Drosophila melanogaster* (126). Differences with respect to light, temperature, and humidity optima were established. Since the strains differed at loci other than the one which gave them their name, it is probable that habitat choice is affected by a polygenic system. Courtship and mating of fruit flies have continued to attract attention, since selective mating based on behavioral differences must have evolutionary significance. Earlier studies in this area proved that selective mating existed, but did not determine its behavioral basis. In a yellow strain of *D. melanogaster*, the reduction of "sex drive" in males can apparently be attributed to the *y* gene itself (8, 9). No such effect was demonstrated in females. Indeed, females of well-established *y* bearing stocks were found to be unusually receptive, probably because highly receptive females will be positively selected when only low-drive males are available. In another species, *Drosophila subobscura*, the side-to-side courtship movements of the female probably confer selective advantage on more vigorous males (111). These active movements interfere with copulation, and hence discriminate against the less athletic males. Both of these studies emphasize the important role of male vigor, and de-emphasize discriminative choice by either sex. However, there is evidence that under some circumstances female drosophilae do discriminate genetically different males, and that assortative mating results from this (116).

Experiments on genetic selection for behavioral traits were not common during the half-decade considered in this review, and two of these employed *D. melanogaster*. Apparently scientists today are in too much of a hurry to carry out selection studies with the slower breeding laboratory mammals. Hirsch & Boudreau (55) developed strains of flies showing strong and weak phototaxis. Both phototaxis and geotaxis in different races of *D. melanogaster* were observed by Dürrwachter (32). He reared subjects in both darkness and light, and claims to have demonstrated progressive changes in the strength of the phototactic response.

Crickets, moths, and honeybees have also served as subjects for behavior genetics. The heritability of specialized courtship and mating behavior patterns has been demonstrated by von Hörmann (58) in crosses between two closely related European crickets. The separate parts of the pattern follow different patterns of inheritance in the hybrids. The results indicate that the components are not dependent upon a single central mechansim, but that each has its own set of genetic determiners. Similar independence of the genetic control of components of complex behavior has been shown by two other workers. Food plant selection and cocoon structure were studied in the hybrid larvae of two moths, *Callosamia promethea* and *C. angulifera*, by

Haskins & Haskins (52). Food preferences of the F_1 hybrids were almost completely those of the *C. angulifera* parent, but the cocoon structures were mostly intermediate with a scattering of both parental types.

A particularly interesting study of honeybees also disclosed the genetic separation of two components of a well-integrated pattern. One of the mechanisms by which this species resists the disease, American foul brood, is the opening by the workers of the cells containing a diseased larva and its removal from the hive. This has been called "hygienic behavior" by Rothenbuhler (99). This investigator crossed a strain which showed the behavior with a disease-susceptible strain which did not. In the F_1 hybrids no hygienic behavior was evident, but backcrosses to the hygienic strain produced equal numbers of workers who (*a*) showed the complete pattern, (*b*) opened cells, but did not remove larvae, (*c*) removed larvae only after the cell was artificially uncapped, and (*d*) neither uncapped cells nor removed larvae. These findings suggest that uncapping and removal behavior are inherited as monogenic recessive characters.

BEHAVIOR GENETICS OF VERTEBRATES

Sexual Behavior.—The inheritance of sexual behavior has been studied from several aspects. Clark, Aronson & Gordon (25) hybridized platyfish and swordtails, which apparently do not interbreed in nature although they do so readily in aquaria. The courtship patterns of the males were special objects of interest and it was shown that the F_1, F_2, and backcross generations behaved in a manner predictable from their genetic origin. The inheritance of the special courtship movements did not follow simple Mendelian ratios, however, and the genetic mechanisms must be complex. In the F_2, segregation of genes affecting structure gave rise to individuals who phenotypically resembled either swordtail or platyfish grandparents, but the morphological characteristics were not correlated with behavior. In a similar fashion, the courtship patterns of interspecific hybrids of birds, greenfinch, goldfinch, and canary have been studied by Hinde (53). Patterns normally appearing in only one parent species appear less intensely in the F_1; patterns which are somewhat similar in both parent species appear in intermediate form; and similar patterns which only vary in frequency in the parents appear in the hybrids at an intermediate frequency. Hinde argues that the evidence favors a homology of the genetic determinants of behavior in the three species. If the similar phenotypes were based on different genotypes, the behavioral development of the hybrids would probably be disrupted, since the two systems would not mesh smoothly.

A series of studies on sexual behavior in guinea pigs has been carried out at the University of Kansas under the general direction of Young. In these experiments the complex interaction of genes, hormones, and experiential factors has been thoroughly investigated. Such research is based on the concept that behavior development is an interaction between a genotype and a specific environment, and that one task of behavior genetics is the quantitative evaluation of the effect of various combinations of factors. The basic studies (49, 123) showed that inbred strains and genetically heterogeneous strains differed significantly with respect to strength of "sex drive." As in yellow strain *Drosophila*, an inverse relationship was found in the sex scores of males and females in the same strain (49). The oxygen consumption of males of the more sexually vigorous strain is high compared with less vigorous strains, but within strains the correlation of sexual activity and metabolism rate is insignificant (91). This observation suggests that energy output places an upper limit upon sexual activity, but does not determine it directly. Type of rearing has considerable influence upon later sexual activity; males with a minimum of contact with other animals generally have low sex behavior scores as adults (50, 124). The critical period for acquiring contactual experience lies between 10 and 25 days for heterogeneous strains, but is later than 25 days for the inbred strains. The depressing effects of isolation are confined to the period in which sexual response patterns are being organized. These authors follow Beach's hypothesis of dual components of mating behavior. The capacity for sexual performance, a matter of response organization, is primarily dependent upon social experience. The second component, sexual excitability, seems unrelated to social experience and more directly under genetic control. Just as the effects of experience upon sexual behavior differs with genotypes, so do the effects of hormones. Strains with low sex drive are not raised to a high level by large doses of androgen (92).

The family intercorrelation method has been used to study genetic effects upon the sex drive of cockerels (130). By using a number of sire families with each sire mated to several dams, it is possible to obtain measurements of the contribution of both dam and sire to performance. In this study, differences between sire families were significant, but those between dams (within a sire family) were not. Some evidence was found that the sex behavior differences were in this case positively correlated with androgen production as measured by comb height. Crosses using high-libido and low-libido males also gave evidence for the heritability of sexual activity (129).

Sexual selection, and indirectly sexual behavior, has been studied in mice by a method somewhat analogous to that reported in fruit flies (74, 81). Strain ST males, competing with CBA males for receptive females, sired six times as many litters as their competitors. These results are attributed to the dominance hierarchy setup between males, not to choice on the part of the female.

Other specialized behavior patterns.—Several studies have dealt with the heritability of rather specialized behavior patterns which show considerable individual variation. Curtis (28) made quantitative measurements of circling behavior in inbred strains selected for this characteristic. Circling and waltzing mice are well-known, but as a rule this behavior is found to depend upon specific genes which affect the vestibular system at one or more levels.

Circling in Curtis's strains is possibly under polygenic control, though the genetic analysis was not conclusive. Although the circling is clearly affected by genotype, the phenotypic expression of the trait is strongly modified by the conditions of testing.

The eating behavior of a rather remarkable mutant mouse characterized by extreme obesity has received some attention. The condition is inherited as a monogenic recessive. Fuller & Jacoby (44) found that both normal and obese mice responded similarly to changes in the palatability of food, and that, in general, obese mice were not characterized by a higher hunger drive. However, over a period of days, normal mice adjusted to unpalatable or to palatable and high-caloric diets on the basis of caloric need, while obese mice made such adjustments less effectively. The authors concluded that a central hunger-control mechanism was defective in their obese subjects. These results are consistent with the feeding cycles which Anliker & Mayer (7) demonstrated in a bar-pressing apparatus. A 24-hour cycling is evident in normal mice, but the genetically obese animals eat periodically throughout the day and do not show typical satiation. Rather remotely allied to these experiments on genetic factors and ingestive behavior is a study of free alcohol intake in successive generations of mice (82). The experiment does not really test a genetic hypothesis, but it has been offered as evidence for Williams' (128) genetotrophic theory of alcoholism.

A series of studies by Stamm (113, 115) has dealt with strain differences and heritability of hoarding in rats. Black-hooded, brown-hooded, and Irish rats showed significant differences in the time of onset of hoarding and the number of pellets transported. F_1 hybrids hoarded about as much as the high-hoarding black-hooded parents, and backcrosses of the F_1 to Irish parents were intermediate. Stamm reported that his results were consistent with a single gene difference between the strains, but the genetic experiment is not extensive enough to really prove this. The F_1s were used in a test of the hypothesis that hoarding is positively correlated with dominance, but the predicted association was not found (114).

Temperament.—Strain differences in emotionality continue to be of considerable interest in behavior genetics. Broadhurst has utilized the familiar Hall defecation test for emotionality in the rat. After considering situational factors (13) and experiential factors (14) affecting the results, Broadhurst concluded that the test could be used with considerable reliability in behavior genetics. Significant differences were found between a number of inbred rat strains, some of which were the same as those used by Stamm in his study of hoarding (15). Broadhurst (16) has also developed by selection strains of emotionally reactive and nonreactive subjects. These stocks were used to test a prediction that the emotional subjects should show less alternation behavior than nonemotional because of a greater tolerance of reactive inhibition (109), but the hypothesis was not confirmed.

Various activity measures have been the most commonly used tests of temperament. Wild and domesticated Norway rats were compared in spontaneous activity by Richter & Rice (89), who found that fasting increased the activity of wild rats much more than domestic. Richter & Uhlenhuth (90) found the activity of wild rats less affected by gonadectomy. The generality of behavior-physiology correlations obtained in experiments with domesticated laboratory animals is certainly questionable. Laboratory strains of mice and rats have also been compared on many types of activity tests. Kish & Antonitis (70) found that C57BL/6 mice have a significantly higher operant rate of platform depression than BALB/c's. McClearn (76) observed six mouse strains on four tests, each test measuring some aspect of exploratory behavior. Strain differences on all tests were significant, and the concordance between them was high enough to indicate that some common factor was measured. F_1 crosses were made between two of the most different strains and tests were repeated on the hybrids. The results suggested to McClearn that so-called exploratory behavior is made up of at least two subcharacters which behave differently in the hybrids. This is an interesting hypothesis. It should be noted, however, that the tests in which the hybrids were intermediate involve sampling of behavior over a period of time; the tests which showed "dominance" involved a single major output of activity. The difference in phenotypic ratios may be a function of the tests rather than of internalized subcharacters within the organism. Physiologically, the hybrids may be intermediate with respect to a single activity factor, but the expression of this factor will differ on tests which give an essentially continuous distribution of scores and on those which require that the subject exceed a threshold in order to receive a score.

Inbred strains of rats from the University of Miami stocks were subjects in another study of exploratory behavior (20). Hooded rats explored more than either Albino-Fischer or Blacks. There was a slight indication that the Blacks were more likely to choose three successive unlike arms in the test Y-maze, which might indicate more rapid satiation of an "exploratory drive."

Breed differences in the activity of dogs during routine weekly weighing were reported by Scott & Charles (105). This paper is particularly interesting because of its theoretical formulations. Each breed follows a characteristic developmental path, a process which may be called canalization. Training tends to fix responses, but the direction of the canalization appears to be a function of heredity. By the interaction of training and genetic determinants, the authors claim that a relatively small inherited initial difference can be magnified, as development once started along divergent courses leads to extremely different end products. These views have also been applied to a wider sampling of forms of behavior (106). Somewhat similar heredity-environment interactions on complex behavior were reported by Freedman (41, 42). Subjects from four breeds were reared by either "indulgent" or "disciplinary" methods. The effects of his differential procedures were tested by a "conscience" test, in which subjects who had been punished by the experimenter for attempting to eat were observed through a window after the experimenter left the room. In two breeds, Shetland sheepdogs and basenjis, method of rearing had no significant effect upon the test. Indulged beagles and wire-haired terriers refrained from eating for a longer period than did their disciplined sibs. Freedman's work was undertaken with the avowed intent of testing the effects of different systems of child rearing. He emphasizes a point made in other studies, that developmental laws apply to particular organisms and that genetic differences play a major role even within a single species.

The study of temperamental differences between dog breeds extended beyond the laboratory in the work of Mahut (77), who observed her subjects in the homes of their owners. Timidity was rated in a test for irrational fears when dogs were suddenly presented with such objects as a mechanical snake, a musical top, and a Hallowe'en mask placed on the owner. Breed differences were highly significant and the author believes she has demonstrated an important hereditary effect upon emotional behavior which overrides the fact that her subjects must have had quite different life experiences. She believes it unlikely that her results can be explained by the hypothesis that particular kinds of owners select particular breeds and impose their own stereotype of appropriate dog behavior upon their canine cohabitants. This reviewer, who has owned several breeds of dogs, is inclined to agree.

Psychological literature on audiogenic seizures has decreased in volume as the problem seems to have become one of physiology and biochemistry. Frings, Frings & Hamilton (43) reported on convulsion responses in animals selected for both low and high susceptibility. Their results indicated that the F_1 hybrid between the two selected stocks was quite variable and most of the individuals could be classified in the high- or low-susceptibility classes, while relatively few were intermediate. They suggest that there are two stable developmental equilibria, a concept reminiscent of the threshold hypothesis of Scott & Charles (105). Audiogenic seizures were also used as a test of emotionality as related to free-choice alcohol consumption (29). This experiment was designed as a partial test of Williams' genetotrophic theory of alcoholism. It was reasoned that susceptibility to audiogenic seizures might be related to the same kinds of genetic biochemical blocks which Williams postulates as etiological factors in alcoholism. As predicted, rats with high seizure susceptibility were also the heavy alcohol imbibers.

The inheritance of aggression has been reviewed by Scott (103), who places considerable emphasis upon physiological factors, particularly male sex hormones. Experimental studies have been conducted predominantly with inbred strains of mice. Fredericson & Birnbaum (39) found that BALB/c mice tended to share a single piece of food while C57BL mice would fight vigorously over it. When, however, the normally passive BALBs were paired with the aggressive C57BLs, a vigorous battle broke out. In a later study (40), it was found that trained C57BLs fought much less after a female mouse was introduced into the fighting arena. BALB/c males were less distractable and continued to fight vigorously in the presence of the opposite sex. These authors interpret the results in terms of differential strength of sexual and aggressive motivation. The same two strains were used by Bauer (10) in a study of the effect of types of rearing, social or isolated, upon attacking behavior in later life. The C57BLs were, as in other investigations, more aggressive, but the mode of rearing had little effect upon fighting behavior.

Somewhat similar in concept was the study of King & Eleftheriou (68) on the effects of early handling upon adult behavior in two subspecies of deermice, *Peromyscus maniculatus*. These workers specifically hypothesized that handling, in their experiment accomplished by a mechanical device, would be more effective with the more docile subspecies, *Peromyscus gracilis*, than with the wilder *Peromyscus bairdii*. This hypothesis was not completely confirmed but they did find a highly significant subspecific treatment interaction, and concluded that the effects of early handling and other special experiences do vary according to the genotype of the animal so exposed.

Perhaps the most important conclusion from this whole set of diverse papers is that investigators are not now studying so much the inheritance of emotional characters as the effects of the genotype upon developmental history of emotional behavior. Such a rephrasing of the problem eliminates a host of semantic and interpretive problems. It is probable that strain differences can be demonstrated in almost any measure of emotionality which is systematically investigated. Such results by themselves are not of great significance, since the point has already been adequately confirmed. Strain differences are merely a starting point for detailed studies of behavioral development and as sources of biochemical, anatomical, and physiological variations, which can be correlated with behavior.

Social behavior.—In a broad sense, sexual and aggressive behavior are considered social, since they involve more than one organism. In the more limited definition of this section, however, social behavior is considered to be an attribute of groups rather than individuals. A group does not have a single genotype, but its organization is affected by the genotypes of its members. The three studies cited here were carried out at the Roscoe B. Jackson Memorial Laboratory. In a comparative study of dog breeds, King (66) found that basenjis formed more rigidly organized social hierarchies than cocker spaniels, and that their organized groups were less open to strangers. These results are in agreement with those of Pawlowski & Scott (85), who reported that the proportion of complete dominance relationships was higher in basenjis and wirehaired terriers than in beagles and cocker spaniels. In the latter breeds, dominance tests frequently gave inconclusive results. The breed differences were largely due to the strong dominance of males over females in the basenjis and terriers.

The stability of social groups in inbred mouse strains was considered by Calhoun (19) to reflect the physiological homeostasis of individuals who make up the population. In his experiments, artificial communities of DBA/2 mice were much less stable than those of C57BL/10 mice. Calhoun's hypothesis is that physiological instability in the DBA results in emotional arousal, failure to make the fine discriminations needed for social adjustment, and the eventual breakdown of social organization. The case for DBA instability rested largely upon their high susceptibility to audiogenic seizures.

Intelligence and learning.—Thompson (118), in summarizing three-quarters of a century's work on the inheritance of intelligence, stated that, as a result of it all, perhaps two conclusions were justifiable: (*a*) intelligence is heritable to a degree and (*b*) depriving an organism of stimulation during early life has permanent deleterious effects on its development. Five years of additional work have not changed the situation greatly, but there is perhaps an indication in recent research that the interaction between genotype and the nature of early experience as well as other factors affecting intelligence has not previously been fully appreciated.

The bright and dull rat strains developed at McGill (118) have been used in a number of studies which attempt to characterize their differences in performance in a more precise form. On a test of exploratory activity in a Y-maze, bright rats showed a faster decline of activity within trials and explored in a more orderly manner (120). They also seemed to discriminate better between two different mazes and explored less in one which had been previously investigated. The author explained the effects in terms of differential susceptibility to retroactive inhibition. These strains, transferred to the University of Manitoba, have also been used to retest the controversial glutamic-acid-effect on the development of intelligence. Large doses of glutamic acid failed to improve the performance of bright rats on a Hebb-Williams maze, but produced significant improvement in dull rats (61). The effect is considered by these authors to be relatively permanent (62) on the basis of a finding that treated rats were still superior on retests 30 and 60 days after drug administration. However, the difference between the groups fell progressively, and, in terms of improvement from trial to trial, control animals were superior on the retests. The experiment should be repeated with additional control groups. In a later experiment (60) glutamic acid enhancement was not obtained for reasons which are still obscure. Perhaps the most interesting of this group of papers is a study of the effects of enriched and restricted early environment on the performance of these strains in the Hebb-Williams maze (27). In an enriched environment, bright and dull rats both made few errors; in a restricted environment, both made many errors. In neither case were the strain differences significant. Under normal laboratory rearing conditions, the expected gross difference in performance was obtained. The results suggest a sort of threshold effect. Dull rats do not have a lower potentiality, but they do require more stimulation to attain a high level of performance. Both bright and dull rats appear to have the same ceiling.

Somewhat similar in concept to the Cooper & Zubek experiment was a study of the effect of the conflict situation on learning ability in two strains of inbred mice (69). Two strains of mice were compared in avoidance performance in a shuttle box after half of each genetic group had been put under severe stress by shocking them whenever they drank. The control C57BL subjects performed significantly better than BALB/cs, but the two strains behaved similarly after stress. Here, too, there is evidence that the same treatment has unlike effects on the learning of different genotypes. An abstract by McClearn (75) describes strain differences between inbred mouse strains in performance on an elevated Lashley III maze. Presumably this will be used as a basis for additional genetic analysis. Differences in learning ability of dog breeds have been described by Fuller & Scott (45). It appears that heredity affects performance on almost any test which an experimenter may select.

BEHAVIOR GENETICS OF MAN

Laterality.—The phenomena of handedness and eye dominance have long been favorite subjects for behavioral genetics. Handedness itself, as a trait, may not be of major social importance, although various ills have been attributed to forcefully changing "innate handedness"; however, study of the trait does provide a testing ground for ideas on the nature-nurture interaction. An extensive analysis of three older studies on the familial occurrence of left-handedness was carried out by Trankell (121). He applied the classical methods of population genetics to the problem, with a correction for the fact that there is a strong environmental pressure against the manifestation of left-handedness. Using this model, he showed that the older studies of Ramaley, Chamberlin, and Rife were in substantial agreement with a monogenic recessive determination of left-handedness. Estimates for the frequency of the gene in all three populations were just over 0.40. Trankell's method, the calculus of penetrance, is presented as a general technique for population genetic analysis of behavioral traits.

Two other papers dealing with the handedness problem include new data. Merrell (79) compared eye and hand dominance in his subjects and their families. Although heritability of both types of laterality was shown, the association between the two was not significant, and Merrell concluded that they must have developed independently. Merrell supports Rife's theory that left-handedness is a monogenic recessive and that all homozygous (rr) individuals are left-handed. Heterozygotes (Rr) are developmentally labile and are equally likely to go in either direction. The model is quite different from Trankell's, but we have no critical test between them. Falek (36) was more concerned with the details of the nature-nurture interaction in the development of handedness than in genetic models. His study was based on a sample of parental matings of the types right-handed × right-handed, right-handed × left-handed, and left-handed × left-handed. The interesting feature of Falek's results was that the heritability of left-handedness was a function of the sex of the left-handed parent and the occupational status of the parent. Left-handed fathers who were skilled laborers have fewer left-handed children than might be expected. From the results of personal interviews, Falek attributed this to the fact that these parents find left-handedness a disadvantage in their daily work and strongly train their children against it. The fact that some children in the sample persisted in left-handedness despite strong contravening measures was taken to indicate the importance of genetic factors, as was the higher proportion of left-handedness in the relatives of the left-handed index cases.

Two studies on the development of handedness were not, strictly speaking, concerned with heredity, but do point up problems involved in studying heritability of a trait whose overt expression becomes more pronounced with practice. Cole (26) studied paw preference in cats and rejected the hypothesis that laterality preference is the result of feeding habits. He was able to reverse handedness by small lesions in the contralateral motor cortex and suggested that an anatomical asymmetry might lie at the base of lateral preferences. Warren (127) further investigated the development of paw preferences in cats and monkeys, finding that the degree of laterality increased with practice and was more pronounced on tasks requiring finer coordination. He concluded that learning is more important in the higher mammalian orders such as primates, and criticized Cole, not so much for his being wrong as for his naïveté. However, Warren's own explanation overlooked the differences in developmental rates between the various species of mammals. By the time a human infant is born, it is already older chronologically than a cat which may have developed a clear-cut handedness. The longer ambilaterality of the primates may reflect nothing more than a slower biological development. Warren characterizes the nature-nurture issue as a "pseudoproblem," which is fair enough insofar as a single individual is concerned. One's handedness cannot be divided up into inherited and acquired parts. But the differences between individuals in handedness may result solely from one class of factor or the other. This point still needs attention.

Personality.—The popularity of the Pogo cartoons indicates a public acceptance of a relationship between animal traits and human personality. In scientific psychology the areas seem rather far apart. Animal temperament is defined for behavior genetics according to activity or aggression scores; human personality is defined in terms of introversion-extraversion and cyclothymia. Perhaps their chief common element is the fact that both are heritable to a degree.

The classical method of comparing monozygotic and dizygotic twins continues to be used in personality studies. Monozygotic twins reared apart appear to be commoner than previously believed (63). Shields (107) found that the risk of psychiatric disorder in twins is approximately the same as in the general population. He found strongest evidence for genetic effects in psychosomatic disorders, but claimed that genetic factors cannot be ruled out for neurotic symptoms. In a later study (108) he reported on a fairly large sample of monozygotic twin pairs reared apart. These were compared with a control sample of twins reared together. Correlations between members of pairs on an extraversion-introversion test were .60 and on a neuroticism test .52. Shields concluded from these tests and from clinical judgments of personality that twins reared apart are about as much alike as twins reared together. "Our material shows that uniovular twins can be alike without the operation of subtle intrafamilial or intertwin relationships. If nothing else, it goes some way toward vindicating some of the pre-suppositions of twin research." In another comprehensive twin study, Eysenck (35) compared the two types of twins with respect to similarity on intelligence factors, an extraversion-introversion factor, and an autonomic factor. Though intercorrelations between the three factors were nonsignificant, monozygotic twins were significantly more alike on all three. Together with earlier research from the Maudsley group, these papers represent an attempt to describe personality in terms of a group of independent heritable factors. The factor analytic approach to trait definition was also used in a series of studies by Cattell and co-workers (21, 22) at the University of Illinois. The personality factors employed for phenotypic description are derived from personality tests designed by Cattell himself. In contrast to the standard twin method, the Illinois group works with personality correlations within families of different types, for example, monozygotic twin pairs, dizygotic twin pairs, unrelated children reared together, related children reared apart, and the like. The variance equations contain terms for the between- and within-family hereditary factors, the between- and within-family environmental factors, and their intercorrelations. The equations are not uniquely solvable, but solutions may be developed on the basis of certain psychological assumptions and the internal consistency of the data. Applying these methods, it has been found that certain factors have particularly high genetic determination in a sample of middle western male children 9 to 14 years of age. These factors are general intelligence, comention, and cyclothymia. Particularly low heritability was found for an assertiveness factor and immediate overresponsiveness. As might have been predicted from Thompson's (119) theoretical analysis, factors, in general, showed a combination of environmental and genetic determination. It is highly doubtful that the method can lead directly to personality factors which are completely determined by heredity and, hence, represent basic biological nature. Nevertheless, the method is powerful and might well be used on a larger scale.

In contrast to the highly structured approach to personality through factor analysis is the more naturalistic type of appraisal which was started over 20 years ago by Gottschaldt (48). Twins from many German cities were brought together in a summer camp, and longitudinal studies have been conducted on many of them. The "endothymic" traits of personality are considered to have remained stable and are strongly heritable. Intellectual interests have been modified by life experiences.

Intelligence and learning.—Turning to the studies on the genetics of intelligence in man, we find that conflicting views are still expressed at the end of three-quarters of a century's investigation. Twin investigations continue to show that monozygotic twins are much more alike than dizygotic pairs on both general intelligence and on tests purporting to measure primary mental abilities (12). Vandenberg (125) has published preliminary results of the

University of Michigan twin study which employed many psychological and physiological tests. In general, the computed heritability of intelligence was less than that of body measurements, but a little greater than that of personality tests or of many physiological and biochemical measures. This may be explained by the fact that intelligence is a more stable characteristic of an organism than is urinary excretion or specific metabolites. Burt (18) has presented a rather thorough summary of his extensive researches on the inheritance of intelligence in the London school system. With Howard (18a), he has proposed a multifactorial theory for the inheritance of intelligence within the normal range. Single Mendelian factors seem to be involved primarily in the determination of mental defect. Burt believes that the hypothesis of intelligence as a general ability is more valid than the assumption of the existence of discrete independent mental factors. His balance sheet for the partition of the variance of intelligence scores gives greater weight to genetic factors than does any other with which this investigator is acquainted. The computations are based upon test scores which were adjusted by consideration of teachers' records on individual students. In this allocation, the fixable genetic component is stated to be 47.92 per cent; nonfixable genetic, 21.73 per cent; assortive mating, 17.1 per cent; systematic environmental, 1.43 per cent; random environmental, 5.77 per cent; and unreliability, 5.24 per cent. These results, as Burt states, apply only to the specific population studied. They stand in marked contrast to views such as those expressed by Sarason & Gladwin (101), who state, "Although at the present time practically all responsible workers in the field recognize that conclusive proof of the heritability of mental ability is still lacking, where no organic or metabolic pathology is involved, the assumption that subnormality has a genetic basis continues to crop up in scientific studies." Unfortunately, much of the evidence against which Sarason & Gladwin train their guns is based on intelligence-test differences between racial groups. These are no more satisfying to geneticists than to psychologists. This same paper states that most psychologists "recoil in alarm over the implication that the IQ be taken as a measure of inherent as against learned mental capacity, yet this presumption must be made if the IQ is to be considered genotypic." This statement betrays confusion over a fundamental distinction of genetics, the distinction between genotype and phenotype. Intelligence has never been considered genotypic, and an extremely complex network of events lies between an IQ score and a set of genes. The striking fact is that this complex network is orderly, and predictable relationships can be found between genes and complex phenotypes such as intelligence.

It is, of course, true that intelligence does not spring full-formed from a set of genes but is stimulated by many subtle factors. One of these, family size, has been studied over a number of years by Nisbet (84). There was little change from 1949 to 1956 in the significant negative correlation between number of siblings and intelligence test scores. Nisbet's hypothesis is that children in larger families receive inadequate verbal stimulation and hence do less well on the standard intelligence tests. Allen (2, 3) has provided effective summaries of the genetic approach to problems of mental disorder, particularly mental deficiency. He deals with one rather subtle argument that the persistence of mental disease in the face of negative natural selection proves its nongenetic etiology. This argument holds that the lowered fertility of the defective individual should, over the course of generations, eliminate the responsible gene. The weakness of the criticism lies in the fact that selection acts upon phenotypes and not genotypes. The responsible gene may not be exposed to natural selection, for it may appear late in life after the reproductive age, or be rarely expressed except in industrial societies. Since industrial society is a new phenomenon, this means that selection has had very few generations to operate. Allen's most interesting suggestion is that many genes which produce deleterious effects under certain circumstances may be paying their way by some other action which is positively selected. This view is possibly borne out by the recent report that psychoses are more common in persons with blood type "O" than in the general population (17). Although many forms of feeblemindedness are associated with specific Mendelian units, it is still true that common high-grade familial mental deficiency is best accounted for in genetic terms as a cumulative effect of multiple genes. A particular genotype should not be considered, however, to set a ceiling on intellectual capacity. For each person, heredity fixes an IQ corresponding to every possible environment to which he might be exposed. As medical and educational techniques improve, the development of the familial mental defective may well be changed for the better. Like the Cooper & Zubek dull rats, the moron may simply be an individual who must have a highly stimulating environment to develop average intelligence.

Behavior deviations.—Psychiatric genetics will not be discussed here in detail, but a few papers will be cited to illustrate some of the current activities. The extensive genetic and clinical study of enuresis reported by Hallgren (51) is a model for family investigations. The investigation was based upon cases referred to pediatric clinics and all were followed up by the author. This study includes detailed investigations of the clinical history of the index cases, and the role of environmental factors in etiology is thoroughly discussed. Following this analysis, Hallgren concludes that there is probably a "nuclear" group of enuretics whose condition is attributable primarily to genetic factors. The data do not permit distinguishing between the hypothesis that susceptibility depends on a dominant of incomplete penetrance and one based upon a polygenic system which determines a threshold of susceptibility to environmental factors.

The heritability of psychoses, particularly schizophrenia, was reviewed by Kallman (63a). The case for genetic factors is strong, but agreement has not been reached on the nature of the genetic system. Slater (110) has made computations to test Bööks' hypothesis that schizophrenia has a monogenic basis, and that it is manifested in all homozygotes and in one-fifth of heterozygotes. The expectation of schizophrenia, s, is then given by the equation $s = 2mp(1-p)+p^2$, where m is the manifestation rate in the heterozygotes and p is the frequency of the essential gene. For each and every value of p and m, it is possible to calculate theoretical expectations for the occurrence of schizophrenia in various classes of relatives of affected individuals. Slater has carried out these computations and matched the results against the empirical data of a number of investigators from different countries of Western Europe. He believes that the statistical evidence agrees with the theory, and that the best values in the series of samples are $m = 0.26$; $p = 0.015$. Mitsuda (83) has utilized genetic techniques to analyze the relationships between schizophrenia, manic-depression, and epilepsy. The "atypical" schizophrenias seem to be related to other psychoses, while "typical" schizophrenia stands by itself.

A general discussion of the application of genetic expectancies to the study of human behavior disorders has been presented by Pearson & Kley (86). These writers advocate the use of empirical family morbidities for empirical prognosis regardless of their genetic or environmental causation. They also have the opinion that extremely low and high individuals on any psychological scale may represent genetic deviates of unique genes, not merely the low or high accumulation of polygenes. Even genius might, in their opinion, be a single factor, as has been proved to be the case for many types of feeblemindedness. This view, of course, contrasts with the more conventional belief that the high deviates in intelligence can be accounted for completely within the normal curve. From the practical point of view, Pearson & Kley advocate more use of special populations for the psychological study of development of behavior disorders. Research on a sample of children with schizophrenic relatives, for example, would yield more information per unit of effort on the etiological factors in this disease than the study of a random sample from the general population.

PHYSIOLOGICAL NATURE OF GENETIC EFFECTS

It is commonly agreed that genes act primarily upon metabolic processes and that their most immediate effects are to be found in the variations of enzyme systems or in the production of specific antigenic substances. It is the enzymes which have attracted the attention of some behavior geneticists. Ginsburg (46) reported on the effects of a large number of metabolically active compounds upon susceptibility of various mouse strains to audiogenic seizures. Substances which increased the occurrence of seizures in one strain did not necessarily do so in another. This was interpreted as an indication that different metabolic deficiencies may be responsible for similar nervous instability of the two strains. A given behavioral phenotype may arise from a variety of genetic causes. Thus the C57BL/6 and C57BL/10 mice are behaviorally indistinguishable with respect to audiogenic seizure susceptibility, but breeding experiments prove that the genetic basis is not the same in the two strains. The experiments of Abood & Gerard (1) showed that mice, during their age-period of susceptibility, were deficient in brain enzymes. At least some cases of strain differences in seizure resistance could be accounted for by differences in amount of the enzyme, ATPase, and in the rates of active phosphorylation. Interestingly, the more susceptible strains, which emit most energy when stimulated, are those showing a deficiency of energy releasing systems in the brain.

Ginsburg (47) in a later theoretical and summarizing paper proposed that genetically produced enzymatic variations be used as natural units in behavior genetics. He suggests that the effects of such disorders as phenylketonuria, tyrosinosis, and alcaptonuria be studied in a series of related organisms. The behaviors affected would, in his opinion, be homologous since they would be related to the same biochemical structures. The use of genetic strains to study the effects of metabolic variation upon behavior is certainly one of the important contributions of behavior genetics. One may question, however, Ginsburg's statement that a series of genotypes, each leading in its own way to a behavioral phenotype that represents a deviation from the normal, provides a natural dissection of the nervous system. Phenylketonuria may be genetically and biochemically simple, but it does not disturb a single neurological or psychological unit. Instead, it is associated with a syndrome, a group of diverse behavioral effects which are mutually affected by a disorganization of metabolism. Despite the importance of genetic psychochemistry, it should not become a sort of biochemical phrenology. Biochemistry can assist in locating carriers of recessive genes which are responsible for disorders such as phenylketonuria (71), but the natural units of behavior must be defined at a behavioral level, not in terms of genetics, chemistry, or neurology.

Another series of experiments relating behavior genetics to enzymes has been carried out at the University of California (72, 73, 95, 97). These investigators, employing descendants of Tryon's maze-bright and maze-dull rats, have reported a correlation between cholinesterase concentration in the brain and adaptive behavior as tested in the Krech hypothesis apparatus. The early papers stated that high brain cholinesterase was related to visual preference in the Krech apparatus, but later it was found that the strains differed in a more complex manner which was brought out when the visual or spatial stimuli were made progressively more and more reliable cues to the maze pattern. The concentration of brain cholinesterase obviously differs between strains and changes characteristically for each during the life cycle. Experiments by Roderick (93) showed that it was possible by selection to produce rat strains with either high or low brain cholinesterase, but the animals' behavior in hypothesis apparatus did not agree with the earlier findings. Animals of the low cholinesterase strain proved to be more spatial and more adaptive. Chow & John (24) found that spatial and visual preferences of the two rat strains were not modified by intracerebral injection of anticholinesterase drugs, even with dosages which produced gross disturbances such as ataxia and convulsions. On this basis, the authors criticize the hypothesis that adjustive behavior is correlated with brain cholinesterase, but their criticism has been challenged (96). Whether or not the cholinesterase hypothesis is confirmed by other workers, it is obvious that the relationship between the brain enzyme and complex adaptive responses is indirect and may vary from one strain to another. Cholinesterase variations can be demonstrated in natural populations as well as in laboratory strains and the possibility exists that these have adaptive value (33). Obviously, much more research is needed in this area.

A few papers have dealt with hormone activity and neurological factors as pathways through which genetic variation is reflected in behavioral differences. Relatively aggressive and nonaggressive strains of mice castrated and given equal doses of testosterone, androsterone, and dehydroisoandrosterone continued to behave in fighting tests in a manner compatible with their status as intact animals (11). These results greatly resemble those of the Kansas group on the hormonal control of sexual behavior. A somatic difference in response to hormones, rather than a difference in hormone production, seems to be the source of the strain difference in behavior. Such results may be particularly characteristic of the steroid hormones. Thyroid activity in mice has been shown to be under genetic control and the generalized activity of the strains seems to be positively correlated with the rate of thyroid metabolism (4, 23). It would be interesting to test for the existence of a somatic response factor to thyroid hormones, using activity as an index.

Only one paper was found relating neurological findings to strain differences in emotionality. King (65) placed electrolytic lesions in the septum of highly reactive Lashley hooded rats and in more passive Wistar albino rats. Both strains became more aggressive, but the relative position of the strains on a rating scale was not abolished by the operation. Again, the evidence favors a pervasive somatic factor which is not localized in a particular brain area nor referrable to a specific hormone.

EVOLUTION OF BEHAVIOR

Three papers, presented in a symposium on mammalian genetics, have utilized the process of domestication as a model of evolution (88, 102, 112). This, it will be remembered, was a fundamental part of Darwin's original evolutionary arguments. Richter believes that the behavioral changes in rats seen under domestication are largely a manifestation of endocrine differences. Selection for docility has brought about a reduction in the importance of the adrenal glands and a corresponding increase in the significance of the gonads and pituitary. Such changes are a concomitant of selection for fertility and successful rearing of offspring under laboratory conditions. Scott has compared the behavior of dogs with wolves and considers that no new patterns have appeared under domestication. Rather, the frequency and intensity of some components have been altered. Snyder's paper is concerned with the effects of selection in man upon changes in intelligence. He does not believe there is any real danger of a drop in intelligence because of differential fertility associated with scores on intelligence tests. Whether natural selection continues to operate in modern man has been considered by Dobzhansky & Allen (31). Essentially their answer is "Yes," but the genotypes which possess highest Darwinian fitness in the environments created by man are not the ones most favored by selection in the past. In the Darwinian sense, fitness is measured by the survival of one's genes, which is equivalent to the number of one's offspring. Dobzhansky & Allen suggest, however, that the cultural bridge of human society is such that the number of one's grandchildren may be a more adequate measure of fitness. Like Snyder, they hold a reasonably optimistic view of man's genetic future, but they do make a plea for continuous attention to the human gene pool. Man must be prepared to take over controls for conservation of genes if this is necessary to correct the deficiencies of natural selection. Insofar as the genetic mechanisms of behavioral evolution are concerned, mankind offers a fertile field for speculation, but the changes from the Pleistocene to the Atomic Age are probably explained better by cultural historians than by geneticists. The evolutionary process can, however, lead to behavioral divergence in species who have only the most rudimentary, if any, aspects of culture. Physiological variation among geographical or ecological races of a single species is well documented (87). In many instances, the physiological differences are manifested also in behavior. In the previously cited Roe & Simpson volume (94), Mayr, Spieth & Pitendrigh concern themselves with such problems as the conflict between selection for a fixed mode of response which is optimum under average conditions, and a plastic response system which adapts itself to the particular conditions to which it is exposed. Both systems are equally under genetic control and both are highly successful in appropriate circumstances.

The plastic adaptive response system is one which effectively carries out the function known to psychologists as learning. The evolution of this capacity has been discussed by Harlow (51a), who has made important contributions in this area. He states that "the study of animals under laboratory conditions reveals many learning capabilities whose existence is hard to understand in terms of survival value." In contrast with such writers as Etkin (34) and Dobzhansky (30), Harlow minimizes the basic psychological gap between phylogenetic levels and, particularly, between other primates and man. If one accepts his view that organisms are more intelligent than is demanded by the ordinary conditions of life, one is forced to de-emphasize the importance of natural selection. A point which Harlow does not consider, however, is that the nervous system may be more efficient when working under less than full load. The unrealized capacities may simply be inevitable by-products of natural selection operating to produce a brain which will be highly efficient at ordinary operating levels. In engineering terms, natural selection may operate to produce a margin of safety in the design of the brain.

King (67) has tried to relate behavioral differences between subspecies of *Peromyscus maniculatus* to rates of biological development. Specifically, he attempts to show a positive correlation of slow maturation with tameness. It would be desirable to extend these observations to a larger sample of subspecies to determine their generality.

In summary, students of behavior and evolution have given serious thought to the pathways between genes and behavior and the ways in which selection might lead to a change in gene frequencies. At this level, population genetics and physiological genetics both join hands with psychology. There is perhaps a place for additional selection experiments in the laboratory in which the objective will not be so much the production of divergent strains to be used as experimental subjects, but rather an understanding of the evolutionary process. Fossil behavior is not available to the psychologist, so that it is unlikely that he can reconstruct the past as accurately as the paleontologist. Laboratory science can make a contribution to evolutionary theory, however, through the testing of simple models involving behaviors of known heritability.

SUMMARY

Behavior genetics is currently undergoing reactivation, though certain types of studies, notably selection experiments with mammals, are not sharing in this upswing. Strain comparisons and twin studies (which are equivalent to strain comparisons) are becoming oriented toward considering genotype as an independent variable and behavior as a dependent variable. This point of view is replacing the effort to identify the genes for activity, wildness, or hoarding. This type of investigation appears to pay off only with insects and fishes. In accordance with the available stocks and with the genetic skills of the investigator, it is possible to manipulate single genes, chromosomes, or whole genotypes. For the most part, psychologists have dealt with genotypes as a whole. With *Drosophila* and even to an extent with mice, it is now possible to observe the effects of smaller genetic units.

Another active area in behavior genetics is the manipulation of chemical and physiological characteristics of the organism through selection and inbreeding. Such material has great potential value for physiological psychology, and it is not being exploited adequately. Eventually all behavior genetics may reduce to the determination of the heritability of organic traits, and the study of the effects of such characters upon behavior. The prospect appears remote at this time.

It is neither necessary nor desirable that there be a mass conversion of psychologists from the investigation of environmental variables to the study of genetic variables. The number of studies, however, which have shown significant interaction between genotype and treatment indicates that psychologists have often generalized too broadly from the Wistar albino rat. Early handling, rearing in isolation, glutamic acid, testosterone, and septal lesions, for example, can change behavior but their effects are not unrelated to the genetic substrate of the organism to which they are applied. The moral is obvious: experimenters must restrict their generalizations or test them on a wider variety of organisms. On the one hand, the experimenter can control heredity and carry out his tests on a wide variety of genotypes. On the other hand, he may work with genetically uncontrolled and heterogeneous material to insure that some of his subjects will be susceptible to the agent being tested. In the latter case he will be unable to separate interaction and experimental error, but he will be less likely to confuse the peculiarities of a single genotype with a general law. Adequate consideration of genetic factors may help to eliminate some current disagreements in the literature.

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