BEHAVIORAL GENETICS[1]

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INTRODUCTION

From the viewpoint of the behavioral sciences, behavioral genetics can be regarded as a specialty of differential psychology or of biopsychology. It can also be viewed as a specialty area of genetics distinguished merely by the class of phenotypes investigated. Behavioral phenotypes were among the earliest investigated and, with the research being done by zoologists as well as by psychologists, there seemed no need for a special interdisciplinary label. However, in spite of the accumulating evidence on the inheritance of behavioral traits, psychology (and other behavioral and social sciences) rather abruptly in the mid-1920's embraced an environmentalist philosophy (112). Although research on behavioral genetics never ceased entirely, it has had until recently relatively little influence on the main body of psychological research and theory.

In the 1950's a renascence of interest occurred, and a small number of investigators, some of whom were geneticists and some psychologists, began to present their evidence persistently and insistently to the psychological audience. At first, much of the research did little more than establish the fact of genetic influence on behavior. A simple demonstration of differences among mouse strains in some behavior or other, for example, had probative value at a time when similar evidence in other areas was regarded merely as a starting point for research.

As time went on, confidence grew that behavioral phenotypes were not different in principle from nonbehavioral ones, and increasingly sophisticated behavioral and genetic techniques came to be employed. By this time, after so long a separation and with so many developments in both fields, the curriculum of neither geneticists nor psychologists offered opportunity for adequate training in the other discipline. As a consequence, behavioral genetics is now, of necessity, an interdiscipline. It is having an increasing influence on psychology, and its relevance to other disciplines such as sociology (11, 40, 72) is beginning to be explored.

Recent growth of the pertinent literature has been so robust that this review can only be illustrative, not exhaustive. Comprehensiveness is not

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required in any event, since one manifestation of the field's growth has been the appearance of other reviews, books, and edited volumes (9, 59, 60, 66, 81, 112, 114, 116, 126, 140, 170, 175, 186, 187, 191). My own biases are undoubtedly revealed in the selection of studies cited. Omissions attributable to these biases hopefully will be rectified by reference to these other review works.

Since the field has not previously been surveyed for this series, the present review is a general status report. Those aspects of the field judged most likely to be of interest to geneticists have been selected for presentation, with deemphasis of the behavioral details that might engross a behavioral scientist. Hopefully, however, enough of these behavioral particulars are given to suggest something of the complexity that lurks behind such phenotypic labels as intelligence, personality, learning ability, audiogenic seizure susceptibility, and the like. The purpose in so doing is not to claim that behavioral traits are uniquely more complex than nonbehavioral ones, but only to intimate the wealth of research possibilities within the realm of behavioral phenotypes.

Single Gene Research

In the early years of the century there were many attempts to apply the newly rediscovered Mendelian laws to human behavior. Much of this work was uncritical, if enthusiastic, and the evidence for a simple Mendelian basis for such behavioral characteristics as weakness of will or nomadism is, by modern standards, inadequate both in respect to genetic criteria and measurement of the behavior. Most of these early endeavors are now only of historical interest, inasmuch as they generated no sustained research effort. The literature on color blindness and PTC tasting, of course, provides clear examples of single gene influence on behavioral traits. These phenotypes are too well known to require more than the briefest acknowledgement here. There have also been several attempts to relate human behavioral properties to known single locus conditions. For example, evidence has been found for a slight relationship between 0 bloodtype and manic depressive psychosis (139) but it is not consistent evidence (172). An association between blood group A and relatively high scores for *premsia*, a personality factor that is an index of emotional sensitivity (22), has also been suggested. Most of the recent interest, however, has been focussed on mental retardation and schizophrenia.

Mental retardation.—In the case of mental retardation, there has been a continuing advance, due largely to the identification of phenylketonuria as an etiologically distinct entity (53). With biochemical symptoms permitting reasonably unambiguous classification, it became possible to apply Mendelian procedures effectively, and a demonstration of the single locus autosomal recessive basis for the condition was soon forthcoming (90). The subsequent history of research on PKU with the detection of heterozygotes, the

establishment of dietary therapy, and the more recent complexities introduced by the discovery of hyperphenylalanemia (82, 83) is too well known a part of human genetics to require any further discussion here. The PKU research has served as a model and there have now been described some thirty other types of mental retardation associated with aminoacidurias and presumably having a simple genetic basis (41). Other research, reviewed recently by Anderson (3), has identified mental retardation related to disturbances in metabolism of hormones, carbohydrates and lipids, or to chromosomal anomalies. However, these identified conditions collectively account for only part of the total population of mental retardates. While many of the remaining (or "undifferentiated") may be attributed to birth traumas, disease, accidents, and other environmental sources, many others must necessarily be the lower end of the normal curve generated by polygenic segregation, and for these a quantitative genetic perspective is appropriate. A major problem is the identification of the polygenic segregants within the total population of undifferentiated retardates. The possibility that behavioral measures might be developed to accomplish this is suggested by the work of Frank & Fiedler (54), who showed that multiple discriminant analysis of a number of test scores could discriminate phenylketonuric from Down's syndrome patients, and both of those groups from undifferentiated patients.

Schizophrenia.—In the study of the inheritance of mental illness, attempts to fit simple Mendelian models have been particularly beset by the difficulties of assessing the phenotype. Diagnostic criteria differ from time to time and from place to place and the symptoms vary in severity from individual to individual. See (148, 149), for a detailed discussion of these and other problems.

Kallmann (94), whose monumental study dealt with MZ and DZ twins and other relatives of schizophrenic index cases, concluded that a single-locus autosomal recessive model accounted adequately for the data. Other single locus models have since been proposed, with the most detailed perhaps being that of Slater (165). Other workers have felt that two loci are required to fit the facts (15) and Karlsson (96) proposed a two-locus explanation, based upon detailed pedigree analysis of Icelandic records, that takes explicit account of the allegedly increased incidence of creativity and genius in the families of schizophrenics. Various of the one- and two-gene hypotheses have been reviewed by Gottesman & Shields (70, 163) who themselves recommend a polygenic threshold model.

Animal research.—One of the earliest post-rediscovery attempts to demonstrate the Mendelian phenomena in animals involved a behavioral trait of sorts. Darbishire's (29) data on waltzing mice led him to reject the Mendelian hypothesis (probably because of failure to correct for reduced viability of the homozygous recessive animals). The subsequent research

that established the monogenic basis for the waltzer syndrome as well as the large list of other "neurological" mutants is, of course, well known. These phenotypes would appear to offer particularly valuable material for the researcher concerned with neurophysiological correlates of behavior, but there has not been the volume of work the material merits.

In general, there have been two approaches to simple Mendelian analyses in experimental animals. In one, the phenotype is chosen because of its intrinsic behavioral interest, and appropriate matings are made for a traditional segregation analysis. The other method has been to choose one or more single genes, known by some clearly defined trait, and to compare animals of demonstrable genotypes on various behavioral indices.

The difficulties of the former approach are well illustrated in the history of research on sound-induced seizure susceptibility in mice. An early study (201) of seizure-susceptible (DBA) and nonsusceptible (C57BL) strains and their derived generations provided data clearly in accord with single locus, autosomal dominant determination, with the important exception of a critical back-cross of putative homozygous recessive animals to the presumed homozygous parent strain. Twenty-five percent of the offspring, instead of the expected zero percent, were susceptible to seizures. The literature on audiogenic seizures has since proliferated with polygenic, single gene, and two gene explanations. The latter has proved to be of heuristic value in research on molecular and neuroanatomical correlates of seizure susceptibility (64), which implicates at least two determinant systems. Schlesinger et al (155) used a number of indices and found that some (e.g., lethal seizures at 21 days of age) were consistent with single locus models, whereas others required polygene assumptions. Collins & Fuller (24) have also suggested different sub-processes, with susceptibility on first exposure being determined by a single allelic pair in linkage group VIII, and with risk on subsequent exposures being influenced by other genetic factors. Thus, even in a phenotype that is, at first glance, a fairly clear cut dichotomous one, problems of phenotype definition and assessment arise.

Klein & DeFries (99) faced another situation without obvious dichotomous phenotypic categories in their demonstration of the plausibility of monogenic determination of PTC tasting in mice. This work provides good examples of the methodological problems involved in establishing sensory thresholds and preferences in experimental animals and the methods of analysis when considerable nongenetic variance is present.

A powerful variant of the general approach of searching for single genes within a behavioral domain is the countercurrent distribution technique described by Benzer (7) for phototactic behavior of *D. melanogaster*.

The other general approach, beginning with a known single locus, has become increasingly popular. A review of this literature has been provided by Thiessen et al. (174). In a number of studies using *Drosophila*, loci affecting body color, wings, eyes, and bristles have been found also to have effects on mating success, wing beat frequency, phototaxis, and activity.

Another group of studies, mostly performed since 1964, has been concerned with mouse behavior. Perhaps because of the ease of identifying the homozygous recessive phenotype, the albino locus has been particularly popular. Several studies have shown an influence on learning performance. Winston & Lindzey (199) showed that albino segregants in the F_2 between DBA/8 and A strain mice were poorer in water escape performance than their pigmented littermates. Subsequent studies of similar populations in an electric shock avoidance situation (200) revealed detailed differences in response mode. The albino segregants employed a passive avoidance response almost exclusively, whereas pigmented animals were about equally likely to respond actively or passively. These studies could not, of course, distinguish between a pleiotropic effect of the *c* locus and the effect of some closely linked locus. Two other investigations avoided this interpretational difficulty by making use of single locus mutations on a C57BL/6J background. Fuller (60) found that *cc* animals escaped from water more slowly and made more errors in a water maze that required a differential response to black and to white stimuli than did congenic *Cc* and *CC* animals. Henry & Schlesinger (75), also using C57BL/J6 stock segregating at the *c* locus, showed the albinos to be inferior in shock avoidance learning.

Other observations have been concerned with activity level. Fuller's (60) study, for example, included two measures of activity. The albinos did not differ from the pigmented in rotating drum activity, but were significantly less active in open field activity. The open field results were confirmed by Henry & Schlesinger (75).

DeFries and coworkers (31–33) have been able to assess the effect of the *c* locus in the context of a selective breeding experiment that used the F_2 from C57BL and BALB/c mice as a foundation stock. The effect of the *c* locus was found to account for 12 percent of the additive genetic variance of open field activity, which was the selected trait, 26 percent of the additive genetic variance of the negatively correlated character, defecation during the test session (an index of reactivity or "emotionality") and 21 percent of their additive genetic covariance. Another indication of the role of this locus in determining open field activity is that the percentage of albino animals increased from the 25 percent incidence in the foundation stock to high values in the two replicate low activity lines (about 60 percent in one line and fixation in the other), and to near zero in the two high activity lines.

Thiessen et al. (174) have described a research program in which they are systematically screening 14 alleles, all on C57BL/6J backgrounds, for effects on open field activity, geotaxis, water escape learning, and rotating wheel activity. Preliminary results have revealed the ubiquity of single locus effects; over two-thirds of the alleles tested had some effect on one or more behaviors of the test battery. These findings clearly indicate the potential usefulness of the single locus approach. The objective is not simply to catalog as many such behavioral effects as possible, thus providing increasing assurance that behavioral phenotypes operate under the same rules as nonbehavioral ones,

but it is to provide a solid basis for research into the mechanisms through which gene differences become expressed as behavioral differences. The merits of this strategy have been presented by Merrell (131), Thiessen et al. (174), van Abeelen (1), and others. [See Wilcock (197), however, for a critical view.]

Cytogenetics

Autosomal anomalies.—The rapid developments in human cytogenetics during the past decade have contributed substantially to the body of behavioral genetics knowledge. The discovery with the greatest initial impact for behavioral scientists probably was the aneuploidy associated with mongolism or Down's syndrome (86, 106). This condition is one of the most common types of mental retardation, and had inspired a huge amount of research since its original description [see (88) for a concise summary]. The etiology remained obscure, however, until the presence of extra chromosomal material for autosome 21, either as a trisomy, a translocation, or in mosaic condition, was demonstrated.

The mental defect in Down's syndrome is quite severe. An extensive recent census (91) conducted by the Western Interstate Commission for Higher Education (WICHE) identified 2606 institutionalized cases in the 13 westernmost United States and found their mean IQ to be approximately 29, over 4 standard deviations below the population mean of 100. The identification of the first case of normal/21 trisomy mosaicism came about through the investigation of a child of normal intelligence who displayed some of the physical stigmata of Down's syndrome (23). The possibility that mosaicism could extend to the central nervous system, and that the degree of retardation could be a function of the proportion of trisomic neural cells prompted a number of reports. Rosecrans (147) has reviewed 13 of these, and finds that the cumulative evidence does in fact support that hypothesis; the mean IQ of the 20 reported cases was 65. Johnson & Abelson (91), using the WICHE census materials, located 296 Down's patients for whom karyotype information was available. The mean IQ's for the 238 "classical" trisomics, the 21 translocation cases, and the 18 mosaics were approximately 32, 38, and 29 respectively. The mean of the translocation cases significantly exceeds the other means that do not differ significantly from each other. The IQ level of these mosaic patients is much lower than the value reported by Rosecrans (147). This difference may be due to sampling. The WICHE data dealt only with institutionalized cases, and it is not surprising that institutionalized patients have lower IQs than do those patients kept at home (82, p. 218). The clinical reports summarized by Rosecrans were presumably biased in the opposite direction, being motivated often by an apparently normal or near normal intelligence level accompanying supposed Down's syndrome.

A particularly interesting feature of the comparison of the institutionalized cases is the relative intellectual superiority of the translocation patients. These patients were also found to be significantly higher than the

others in activity, aggressiveness, and incidence of "problem behavior." These results suggest that detailed cytogenetic analysis of the extra chromosome 21 material actually present in a sufficient number of translocation cases might permit chromosomal localization of factors pertinent both to IQ and to the other implicated behavior patterns.

The other autosomal trisomies, involving a group D and a group E autosome, are accompanied by even more serious abnormalities than is 21 trisomy, and the viability of the patients is severely curtailed. Indeed, with their life expectancies being only a few months, detailed study of the nature and severity of their mental retardation is very difficult.

Sex chromosome anomalies.—In the case of the sex chromosome aneuploidies, effects have been found on an assortment of behavioral properties. The monosomic condition XO (and some other anomalies involving the X chromosome) gives rise to Turner's syndrome, which is characterized by gonadal dysgenesis, sexual infantilism, and some characteristic physical stigmata such as short stature and webbed neck. Apart from the psychological problems that arise from failure to mature sexually, Turner's syndrome has behavioral consequences in what appears to be a highly specific cognitive defect. Shaffer (160) found that the mean full scale IQ of 20 Turner's patients, as measured by the Wechsler Intelligence Tests, was only trivially lower than the population mean. This full scale value, however, reflects both a Verbal and a Performance score. The subjects' mean scores were substantially higher than average on the former and lower than average on the latter. Still another mode of analyzing the test results permits computation of "factor" scores, and it was found that the subjects' Perceptual Organization scores were particularly low. This pattern of test performance is similar to that found clinically in certain cases of brain damage (133).

Fifteen of the patients were chromatin negative and presumably XO, while 5 were chromatin positive and presumably XX. In general, about 20 percent of Turner's patients are of the latter variety, with their condition arising from some cause other than aneuploidy. It is interesting to note that the results did not differ for the chromatin positive and the chromatin negative groups. The behavioral deficit is evidently the result of some process commonly initiated by the monosomic XO condition, but capable of elicitation through other causes.

A subsequent description of 38 cases by Money (132) confirmed the earlier findings in all essential details, and still more recent work (134) using a different series of tests (SRA Primary Abilities) specifically designed for assessing different types of intellectual functioning, showed the most serious deficiency of the patients to be in Spatial Abilities. A map-reading test was also administered to test spatial orientation, and the patients were found to be markedly inferior to a control group (133). Some evidence is also presented for a deficiency on the part of Turner's patients in arithmetic operations.

These findings have particular potential for examining the issue of independence of separate components of intelligence.

Klinefelter's syndrome of sexual maldevelopment in males is usually associated with a karyotype involving a Y chromosome and more than one X chromosome. The most frequent finding is of 47,XXY; but 48,XXXY; 49,XXXXY; 48,XXYY; and various other arrangements, including mosaics with as many as 3 cell lines, have been described [see (138) for review]. Early studies reported a degree of mental retardation, with mean full scale IQ values ranging between about 60 and about 90. It is also evident, however, that IQ scores in the normal range can occur with Klinefelter's syndrome (138), and Hsia (82) concludes that only about half of the cases can be regarded as mentally retarded. It does appear that both the likelihood and degree of retardation increase as the number of X chromosomes beyond XY increases. Nielsen et al. (138) have compared chromatin positive (47,XXY) and chromatin negative (46,XY) cases of Klinefelter's syndrome and have found that the former are generally inferior in IQ to the latter. This study was concerned with noninstitutionalized cases, however, and the IQ values of both groups were quite high. In addition to the intellectual deficit that afflicts at least some individuals with 47,XXY, there has been a variety of personality and psychiatric problems reported (138). Sample sizes, possible biases in ascertainment, and similar problems preclude definite conclusions, but the evidence does warrant intensified research effort.

Research on another trisomy involving the sex chromosomes, 47,XYY, is fraught with the same kinds of sampling bias problems and the additional difficulty that preliminary and relatively inexpensive screening by sex chromatin tests is ineffective. Nevertheless, there has been particular attention to this condition because the supposed behavioral correlates involve aggression, and the possibility of "diminished responsibility" under the law for persons with this karyotype has been raised in several highly publicized criminal trials.

The principal data have been obtained from surveys of prison populations, often of those prisoners in special security sections because of their violent behavior. Because the early reports revealed that 47,XYY individuals were significantly taller than average, the surveys have often been also restricted to very tall prisoners. The possibilities for sampling bias are clear, and are discussed in detail by the investigators.

Briefly, most of the surveys have revealed an incidence of from 2 to 12 percent of 47,XYY individuals among tall prisoners (20, 67, 87, 142, 173). This incidence is greatly in excess of the best estimates of the incidence in the population at large, which Court Brown (28) theorizes should be less than 1.3 per thousand of newborns. In empirical studies (27, 28) one 47,XYY was found in a series of 2000 males, and in another random series of 566 newborns, one case was found.

The institutional survey results are supported, by and large, by a number of clinical reports describing one or two patients each. Many of the case

histories feature accounts of aggressive and violent behavior, often beginning while the subject was quite young. Others do not, however, and interpretation is restrained by the possibility that strongly confirmatory or nonconfirmatory cases come more often to attention.

Until large scale population surveys can determine how many 47,XYY men are functioning normally in the society, the assessment of the relationship between the chromosomal anomaly and aggressive, antisocial behavior must be conditional. The evidence at hand is sufficiently suggestive to justify the expensive surveys required.

Quantitative Genetics

Intelligence and aptitudes.—It became apparent early that many of the phenotypes of greatest interest to researchers in behavioral genetics were continuously distributed, and were therefore more appropriately investigated using the theories and methods of quantitative genetics than those pertinent to Mendelian hypotheses. Studies of the correlations of relatives on behavioral properties were among the earliest usages of the correlational technique, and such work as Pearson's (141) pioneering research on the inheritance of "mental and moral characters" in man played a role in the then current controversy between the Biometricans and the Mendelians. The correlational approach became very popular, particularly as applied to the trait of "intelligence" which was just then in the process of being defined and for which adequate measuring devices were being developed. There followed a burst of research that persisted into the 1930's and early 1940's [see for example (21)]. Rather inexplicably, however, enthusiasm for this particular method seemed to wane in the post-war years and twin studies came to predominate. In a recent review of work on the genetics of intelligence, Erlenmeyer-Kimling & Jarvik (47) summarized 52 studies that had reported correlations among relatives of one or another degree, including twins. Of the 12 parent-child correlations reported, the median value was 0.50 with a range from 0.2 to 0.8; of 35 studies of sibling pairs reared together, the range of correlations was from 0.3 to 0.75 with a median value of 0.49. Individually these studies are hardly definitive because of various weaknesses of execution or interpretation, but the combined data are fairly persuasive that intelligence has a substantial genetic component. Indeed, the degree of phenotypic correlation, at least, is as high as is the case for physical traits [as Pearson (141) noted]. These values are so close to those expected in an n locus, additive action, random mating model with absence of environmental effect as to be rather embarrassing, given what is known about the actual degree of assortative mating with respect to intelligence (husband-wife correlation on the order of 0.50), what is at least thought to be known about the influence of environment on intellectual capacity, and the assumed correlation and interaction between genotype and environment for this phenotype.

Twin studies on behavior were initiated in 1883 with Galton's "inquiries into human faculty" (62), and were followed somewhat later by Thorndike's

study (179). This latter research is interesting as an index of the early rapport between genetics and psychology, inasmuch as Thorndike was one of the most influential pioneer psychologists. A long hiatus following Thorndike's paper was terminated by the publication of several twin studies between 1924 and 1928 (see 112). By this time, extraordinary efforts had been devoted by psychologists to the problems of definition of intelligence and of accurate and reliable (repeatable) measurements. The cited twin studies using these highly improved psychometric techniques uniformly found the MZ twins to be very similar and the DZ to be much less so, with the correlation of the latter being of about the same magnitude as that of ordinary siblings. The techniques of the twin method itself were improving during this time, particularly in the area of zygosity determination, and the similarity index approach perhaps reached its highest refinement in the well known research by Newman, Freeman & Holzinger (136). In this study the correlation between MZ twin pairs on the Stanford-Binet IQ measure was found to be 0.91 and the correlation between DZ twin pairs was 0.64. Another way of viewing these data is to note that the mean intrapair difference in IQ score for the MZ twins was 5.9 IQ points, and for the DZ twins it was 9.9 points. The value for the MZ twin pairs is very nearly what one expects as a difference between test and retest on the same individual. This study also presented data on 19 cases of MZ twins separated in infancy and reared apart from each other. Although the merit of this kind of comparison had been propounded previously, this was the largest collection of such cases. The mean difference on the Stanford-Binet IQ measure for the separated MZ twins was 8.2 IQ points, and the correlation between them was 0.67, suggesting that the environmental differences had, indeed, generated IQ differences between the twins reared apart. It is worth recalling that this was the time of the nature-nurture controversy, and the data of this study were a featured attraction of the controversy. Interpretations therefore varied greatly, with some calling attention to the depressed correlation in MZ twins reared apart, others emphasizing the relatively small additional increase in mean differences between them.

Another approach to the problem of determining the extent and nature of the genetic influence on intelligence was to study adopted children. Two major studies appeared at about the same time. These also failed to resolve the controversy in any definitive way, with the work of Freeman et al. (57) supporting the contention that environment was the predominant influence, and the work of Burks (16) and of Leahy (105) suggesting that genotype was of overwhelming importance.

Much of the post World War II research in intelligence has emphasized a finer grained analysis, one that concentrates on the components of intellectual function rather than upon an overall global measure of intelligence. Research into the nature of intelligence, with the identification and description of its various components, has occupied a central position in psychological research for many years. The issue is by no means completely clarified, but

there have been several attempts to characterize the different factors of intellectual function and these have generated a number of highly sophisticated test instruments (184). For example, multivariate analysis of scores on a large number of psychological tests led to Thurstone's (180) definition of Primary Mental Abilities. These comprise *Number*, *Verbal*, *Space*, *Word Fluency*, *Reasoning*, and *Memory* factors. Four genetic studies (including two of his own) making use of these factors have been reviewed by Vandenberg (192). Regarding a significant F ratio of DZ within pair variance to MZ within pair variance as constituting evidence of some degree of heritability, the combined studies clearly show a genetic influence on *Spatial*, *Verbal*, and *Word Fluency*. The results regarding *Number* and *Reasoning* are inconsistent, but there is no evidence at all for a genetic influence on *Memory*. (By way of a caveat, it should be noted that these factor names are used in a technical sense that may or may not be congruous with lay usage). In other research (190) the Differential Aptitude Test battery, measuring a somewhat different set of factors, was employed and evidence for heritability was clear for *Verbal Reasoning*, *Clerical Speed* and *Accuracy*, *Language Use I: Spelling* and *Language Use II: Sentences;* ambiguous for *Space Relations* and absent for *Numerical Ability*, *Abstract Reasoning*, and *Mechanical Reasoning*. Other twin research involving cognitive factors is reviewed in (188, 192).

There has also been a recent return of interest in the study of MZ twins reared apart. Shields (196) located 44 MZ twin pairs who had been reared apart, and found, contrary to Newman, Freeman & Holzinger, that such twins had a correlation ($r = 0.77$) on an IQ measure equal to that of MZ twins reared together ($r = 0.76$). Burt (18) has recently published a plenitude of evidence in this regard, having located 53 cases of MZ twin pairs separated prior to six months of age and subsequently reared separately. Measurements of intelligence, educational achievement, and physical traits were obtained for these subjects and for various other groups of related individuals. Results for one of the intelligence tests, one of the school achievement tests, and two physical measures are presented in Table 1. There it can be seen that the pattern of correlations for IQ closely parallels that for the physical measures, particularly weight. The school achievement measure shows a sharp drop in correlation for MZ twins reared apart, and an elevated correlation for unrelated individuals reared together. These results reinforce the conclusion suggested by previous work that intelligence has a large genetic component and that academic performance is much more subject to environmental influence. It should not be very surprising to learn that there is more than IQ involved in school attainment.

Burt's work has also provided direct evidence concerning an issue that has long plagued this type of research. A high correlation of MZ twins reared apart is not in itself conclusive evidence regarding genetic influence. It is easy to imagine that separated twins are typically placed in similar homes with similar socio-economic levels, and that these environmental factors generate the twin similarity. Examination of occupational status of the two

TABLE 1

CORRELATIONS OF BEHAVIORAL AND PHYSICAL PHENOTYPES

[Data from Burt (18)]

Group	N	Phenotype			
		Stanford-Binet IQ Score	General School Achievement	Height	Weight
MZ reared together	95	.92	.98	.96	.93
MZ reared apart	53	.86	.62	.94	.88
DZ reared together	127	.53	.83	.47	.59
Siblings reared together	264	.50	.80	.50	.57
Siblings reared apart	151	.42	.53	.54	.43
Unrelated reared together	136	.25	.54	−.07	.24

homes in which the members of each separated twin pair were reared showed, contrary to this expectation, that in fact a small negative relationship existed. Selective placement clearly cannot account for the similarity of the twins reared apart.

Another line of evidence implicating the genes in the determination of intelligence has recently appeared. In a study of consanguinity in Japan, a decline in IQ as a function of the degree of inbreeding has been described (157). Confirmatory evidence has been reported by Adams & Neel (2) from observations of children born of incestuous matings. Schreider (156) assembled data of a demographic nature relating the degree of inbreeding for various départments in France to average IQ scores of samples of inhabitants of these same political subdivisions. He found the correlation to be −0.48 for one sample representing 25 départments and −0.52 for a larger sample representing more than 60 départments. These various indications of inbreeding depression in IQ not only constitute evidence of the genetic basis of the trait, but also suggest an average dominance in the direction of higher IQ.

Personality.—In general, the same approaches used in studying intelligence have also been used in the study of normal personality variation. Indeed, many of the studies already mentioned have assessed some personality factors as well as cognitive variables. The typical finding has been that personality indices, on the whole, show lower heritabilities than the inligence measures. As is true for the cognitive realm, it is possible to measure a variety of personality dimensions separately. Gottesman (68), for example, studied twins using the Minnesota Multiphasic Personality Inventory, which assesses such personality dimensions as *Depression*, *Psychopathic deviate*, *Social introversion*, etc. Briefly his conclusion was that neuroses with hypochondriacal and hysterical aspects are mostly environmental in de-

termination, whereas those featuring anxiety, depression, obsession, and schizoid withdrawal have substantial heritabilities. A different way of factoring the realm of personality has been utilized by Vandenberg (189) who found significant F ratios for *Active*, *Vigorous*, *Impulsive*, *Sociable*, but not for *Dominant*, *Stable*, or *Reflective* factors. Eysenck (49) made extensive use of laboratory type personality assessment procedures rather than the paper and pencil variety and found evidence for a substantial hereditary component in the dimensions of extroversion and neuroticism. Shields (162), using a questionnaire type of assessment of these same factors, found that MZ twins reared apart did not show greater intrapair differences than MZ twins reared together.

Eysenck (49) has challenged the notion that personality traits in general are less heritable than intellectual traits. He argues that this impression derives from the simple psychometric fact that the assessment devices for personality have lower reliability (repeatability) than do the tests of intelligence or aptitude, and that this artifactually restrains the heritability estimates of personality phenotypes.

Psychosis.—Another principal focus of research has been on psychoses. Although a variety of psychiatric conditions has been studied, the main effort has been with respect to schizophrenia. It has already been noted that there are proponents of a simple Mendelian interpretation and proponents of a polygenic interpretation of schizophrenia. This is not the only contention, however, and there have been and still are advocates who regard both points of view as irrelevant, claiming an exclusive role for environmental agencies in the causation of schizophrenia and other psychotic conditions.

The pace of research has quickened markedly in the past several years. Studies have involved assessment of morbidity risk in siblings and other relatives, and in offspring of two schizophrenic parents (see review by Shields), but the bulk of the evidence on the heredity of schizophrenia continues to be that derived from research on twins. Slater (166) has summarized the results of six separate studies reported between 1928 and 1961 on European, North American, and Japanese populations. Of the total of 337 MZ twins reported in these studies 65 percent were concordant while only 12 percent of 458 DZ twins were concordant. These earlier studies were to different degrees susceptible to a variety of criticisms, and Rosenthal's series of critical discussions of sampling procedures, diagnostic criteria and so on (148, 149) makes clear the methodological difficulties of this type of research. Of the more recent studies, that of Gottesman & Shields (69, 70) of a British population has provided results comparable to those of the earlier research, with MZ concordance of 42 percent and DZ concordance of 9 percent. Two other studies, one by Tienari (181) on a Finnish population and one by Kringlen (101) on a Norwegian population, have provided much lower estimates of MZ concordance. The reason for these reduced concordance estimates remains unclear. One possibility is that differences in diagnostic

criteria may be responsible. Gottesman & Shields (70) have provided evidence that degree of concordance depends upon the severity of the condition in the proband twin. There are, of course, a number of ways of defining severity of the condition. One criterion defined severe cases as those in which the proband twin has been hospitalized for the condition more than one year, and mild cases as those in which the proband twin has been hospitalized for less than one year. It was found that the concordance rate for MZ twins with severe schizophrenia was 67 percent while that for mild cases was only 20 percent. Eight different criteria of severity, based for example upon percentage of time in hospitals since first admission rather than absolute calendar time, were employed. In all, the severe cases resulted in higher concordance rates than did the mild. The authors believe that these data support their polygenic model.

An important recent development in this area of research has been the reintroduction of the adopted child paradigm in several forms by several investigators. Heston (77) identified 47 children who had been born to schizophrenic mothers but who had been separated from them within a few days of birth. Five of these individuals had themselves become schizophrenic at the time of examination, and psycho-social diabilities were found in about half of the subjects who were not schizophrenic. A control group of subjects also adopted early in life but to nonschizophrenic biological mothers showed no schizophrenia and no remarkable incidence of psycho-social disorders. In a similar study on a Danish population Rosenthal et al. (150) found that biological children of a schizophrenic parent reared in an adopted home showed an increase over control subjects in what was called "schizophrenic spectrum" disorders, which includes borderline cases, schizoid conditions, and so on. Kety et al (97) began with 33 adoptees who had a diagnosis of schizophrenia or schizophrenic spectrum disorder and examined their biological and adoptive families. The incidence of schizophrenic spectrum disorder was much higher in biological relatives than in adoptive relatives.

As Heston (78) has pointed out, these adopted child studies have not only provided direct pertinent data themselves, but they have also served to vindicate the twin method, which, for all its problems, had given similar results.

Selective breeding.—In respect to infrahuman animals, quantitative studies have emphasized selective breeding and crossing of inbred strains. The first major behavioral selective breeding program was reported in 1924 by Tolman (182) for learning ability in rats. Early results were rather disappointing, and it was decided that the maze situation employed was not sufficiently reliable. An improved maze was designed by Tryon and the project continued under his direction to become one of the classical works of behavioral genetics (183). Bidirectional selection resulted in a "maze-bright" and a "maze-dull" line, and after several generations of selection, the distributions of error scores of the two lines were almost nonoverlapping. At

about the same time, Heron (76) was also selectively breeding for learning performance of rats in another type of maze, and Rundquist (152) and Hall (71) both using rats, were respectively successful in selection for activity and for "emotionality" (as measured by defecation tendency in an open field situation). More recently, successful selection (in rats) has been reported again for "emotionality" (12), avoidance learning (8), and for morphine addictability (137). These studies provide unambiguous demonstrations of genetic influence on the phenotypes involved, and they have generated useful research material (see below). In terms of estimating quantitative genetic parameters, their contributions have been rather limited in some cases by use of animals from a single commercial "strain" as foundation stock, and in other cases by deliberate and intensive inbreeding during selection. Indeed, the selection responses achieved have been remarkable in view of these constraints on additive genetic variance.

The mouse has been largely neglected in selective breeding research until recently. Lagerspetz (103) has shown a selection response for aggression. An interesting environmental influence was identified in the effects of victories and defeats on males from the two strains. Defeats markedly decreased aggressiveness of animals from both lines. Victories increased the aggressiveness scores of animals from the aggressive strain but not of animals from the nonaggressive strains.

DeFries & Hegmann (32) have contributed an exemplary study on open field activity, beginning with a segregating population (F_3) derived from a cross between two inbred strains, C57BL/6J and BALB/cJ, demonstrated to be extremely high and low respectively in activity in this situation. Using within litter selection, replicate high lines, low lines, and control lines were derived from this foundation stock. The replicate lines gave very similar results, permitting a pooled estimate of realized heritability of 0.26.

Various *Drosophila* species have also been employed in selection for behavioral phenotypes. Hirsch and coworkers (46, 80) have devised an efficient apparatus for quantitative measurement of geotaxis, and have shown clear selection response in *D. melanogaster*. A variation of the apparatus permits measurement of phototaxis, and Dobzhansky et al (39) have undertaken selection for both of these behaviors in *D. pseudoobscura*. Heritability estimates were low, ranging (for different sexes and directions of selection) from 0.02 to 0.04 for geotaxis and 0.06 to 0.10 for phototaxis. A large divergence was attained in both traits, however, owing to the high selection intensity employed. Upon relaxation of selection, the lines converged about as rapidly as they had diverged under selection. The rate of convergence was not symmetrical, however. Natural selection evidently operates more strongly against both negative phototaxis and negative geotaxis than against the respective positive taxes. Connolly (25) has selected for activity level in *D. melanogaster*. Beginning in generation 94, sublines were established of both the active and inactive lines, and selection was relaxed in these sublines. After 20 consecutive generations of relaxed selection the lines have main-

tained their phenotypic level with no evidence at all of a trend toward the control line.

Manning (122) has investigated mating speed in *D. melanogaster* and found a realized heritability of about 0.30 over the first seven selected generations. Response was asymmetrical, being somewhat more rapid in the slow mating direction. The author notes that the close relationship of the behavior to fitness would be expected to have resulted in nearly maximal mating speed in the foundation population.

Inbred strains.—The earlier animal research made some use of the inbred mouse strains (e.g., Vicari, 193), but their use became particularly widespread in the 1950's. Strain differences were reported in activity (111, 177), aggressiveness (65, 159), alcohol preference (117), audiogenic seizure susceptibility (64, 155, 201), hoarding (125), and learning (10, 19, 198) among other phenotypes. Biometrical analysis has been most complete for various indices of activity. Fuller & Thompson (61) measured activity of F_1, F_2, and backcross generations derived from C57BR/a and A/Jax, which strains are high and low, respectively, in activity in a barrier field apparatus. Comparison of variances yielded an estimate of degree of genetic determination (heritability in the broad sense, 50) of approximately .60. A similar estimate was obtained with different substrains as parents (111). Bruell (14) investigated several different activity measures, and found heterosis to be a common feature.

That considerable nonadditive variance may be present in at least some activity situations, thus accounting for the large estimates of degree of genetic determination, is suggested by the work of DeFries & Hegmann (32). In the same open field apparatus, they obtained estimates using F_1, F_2, and backcross generations derived from C57BL/10J and BALB/cJ mice. In addition they performed parent-offspring regression and half-sib analysis and applied the ultimate test of realized heritability in the selection study described above. The coefficient of genetic determination was 0.63 for males and 0.49 for females. Heritability estimated from regression of offspring on midparent was 0.22, from the intra-class correlation of full sibs 0.37 and from the intra-class correlation of half-sibs 0.14. It will be recalled that realized heritability was 0.26, in close accord with those estimates expected to be free of nonadditive genetic variance. It is well to keep this example in mind when reviewing the generally high estimates of broad sense heritabilities, based only upon F_1, F_2, and backcross generations, in the behavioral literature.

The use of inbred strains has led to clearer understanding of the behavioral phenomena themselves. Bovet et al. (10), for example, have studied the learning performance of DBA/2J and C3H/He mice in detail. In a shock avoidance situation with 200 trial sessions given on 4 successive days, the performance of DBA mice improved continuously, with the performance during the first part of day 2 being superior to the latter trials of day 1, and so on. The C3H/He animals, on the other hand, showed improvement within

each day's session, but the performance at the beginning of days 2, 3, and 4 was almost the same as the beginning of day 1. This outcome, and other supporting results, lend themselves to a two stage theory of memory storage. C3H/He mice are evidently grossly deficient in long term storage capacity.

Once strain differences in a particular phenotype have been described, they have often been utilized explicitly to test hypotheses about necessary relationships among behavioral traits. The same utility is found, of course, in selected lines after a reasonable amount of divergence has been attained. For example, several researches have sought to relate "emotionality" in the rat, as measured by tendency to defecate in an open field test situation, to conditioned avoidance learning, which would appear to involve emotional reactions. Maudsley Reactive rats, selected for high defecation tendency are *less* efficient at conditioned avoidance learning than are the Maudsley Nonreactives (13). The suggestion is that their strong emotional response interferes with learning. The relationship is complex, however, because rats selected for good and poor conditioned avoidance learning were found not to differ in defecation tendency (12). "Emotionality" or "reactivity" might also be expected to be related to other behavioral traits such as activity or agression. In various experiments when both activity and defecation in mice was measured (14, 111, 177, 196) the more active strain defecated less. Observations such as these on a few strains are suggestive of a functional relationship between the two traits but they are not definitive, of course. The critical test is the correlation in a segregating population. DeFries & Hegmann (32) have provided such confirmation by their demonstration that defecation showed a correlated response to selection for activity and that the genetic correlation estimated by the cross covariance of offspring and midparent is a very substantial -0.76.

Lagerspetz (103) found her aggressive strain to exhibit more activity and less defecation in an open field. The necessity of a negative relationship between aggression and "emotionality" is brought into some question by Whitney (196) however.

As a further example, McGaugh et al. (118) have used descendants of Tryon's maze bright and maze dull strains of rat in explorations of the memory mechanism. When learning trials in a maze were presented in rapid sequence (intertrial interval of 30 seconds) a large difference was found between the strains in the expected direction. With intertrial intervals of 5 minutes or longer, however, performance of the maze-dull animals improved to the level of the maze-bright. Evidently the dull rats require a longer memory consolidation time for the effects of a trial than do the bright rats, and if another trial occurs during consolidation the memory process is disturbed.

Rather surprisingly, parent-offspring regression or sibling correlations have not been widely used in animal research. The demonstration of the potential by DeFries & Hegmann (32) can be expected to stimulate further research. Another example is the work of Tyler (185) who fitted a second

degree polynomial to the learning curves of parents and offspring of a genetically heterogeneous stock. Separate estimates of heritability were made of the 3 parameters using two different indices of learning. Values of h^2 ranged from 0.19 to 0.40. Genetic correlation analysis led to the conclusion that many of the genes contributing to individual differences in learning were also involved in the extinction process, which is the elimination of a response when it is no longer rewarded.

Research of the kind described in this section appears to provide a very powerful approach to the resolution and definition of behavioral processes.

Physiological Genetics

The search for anatomical, physiological, and metabolic mechanisms through which genetic effects are expressed began early in the history of behavioral genetics. In the case of phenylketonuria, persistent research has resulted in the most nearly complete description of this causal sequence from gene to behavior. Even here, however, the simple picture of a decade ago has become increasingly complicated by new discoveries and the route must be regarded as far from completely known at the present time. Apart from this classical case of phenylketonuria, and the other amino acidurias that have been studied with PKU as the model, research on physiological mechanisms in behavioral genetics has proceeded rather slowly. Increasing attention has recently been devoted to this topic, however.

In infrahuman research, interest has largely been focused upon the nervous system. Krech, Rosenzweig & Bennett (100, 151), for example, have systematically explored the neurochemistry of maze brightness and maze dullness in rats. Their initial work involved comparison of descendants of the Tryon bright and Tryon dull strains with respect to the brain enzyme acetylcholinesterase (AChE). The bright animals possessed higher levels of this enzyme than did the dulls; the inference being that the differences probably reflected differences in the substrate acetylcholine (ACh), and that levels of ACh, a chemical transmitter, in turn were related to neural efficiency. Subsequently Roderick (146) selectively bred rats for differences in levels of AChE. The resulting high AChE strains were found to be generally *inferior* to the low AChE strains in learning ability. It was next hypothesized that the ratio of ACh to AChE was critical. Newly developed procedures for direct measurement of ACh made possible the testing of this hypothesis and it was found, as predicted, that strains with superior learning ability indeed have relatively more ACh than AChE.

Ginsberg (64) has combined both neuroanatomical and neurochemical approaches in his search for the mechanisms in audiogenic seizure susceptibility. Seizure prone animals are characterized by high activity of adenosine triphosphatase in the granular cell layer of the dentate fascia of the hippocampus. Other research on this phenotype (153, 154) has related seizure susceptibility to various neurochemicals including gamma-aminobutyric acid, norepinephrine, and serotonin.

Lagerspetz et al. (104) have also examined the nervous system in a research for mechanisms underlying aggression. Mice of the aggressive strain were found to have significantly more serotonin in the forebrain and significantly less noradrenaline in the brain stem than do the nonaggressive mice. Serotonin has also been implicated in emotionality of mice (109) and rats (171).

Endocrine glands have been relatively neglected since Richter's (145) discussion of changes in adrenal glands and gonads with domestication in the rat. There are signs of increasing interest currently, however. Feuer & Broadhurst (52) have shown the selectively bred reactive strain of rats to be hypothyroid relative to the nonreactive strain. Shire (164) has suggested a relationship between adrenal function and activity in mice. In addition to the neurochemical differences mentioned earlier, Lagerspetz et al. (104) found that testis weight of the aggressive animals significantly exceeded that of the nonaggressive. In general, these authors conclude that the aggressive animals show physiological signs of higher orthosympathetic activity than do the nonaggressive.

Recently a series of studies has been directed toward elucidation of the role of liver enzyme systems in alcohol preference. McClearn et al. (115) showed a small but significant excess in activity of the liver enzyme alcohol dehydrogenase (ADH) of C57BL (alcohol preferring) mice over that of the DBA/2 (alcohol avoiding) mice. The phenotypic correlation between ethanol consumption and ADH activity was later (113) assayed in a genetically heterogenous stock. A correlation of 0.29 between ethanol consumed and ADH activity in the entire liver suggested that as much as 10 percent of the variance in ethanol intake may be explainable in terms of the ADH system. Subsequent work (161) confirmed the differences in ADH activity between the C57BL and DBA/2 animals and revealed a more substantial difference with respect to the next enzyme in the sequence of metabolism of ethanol; C57BL mice were found to have 300 percent more aldehyde dehydrogenase activity than DBA 2 mice.

In the case of other phenotypes, the physiological or biochemical mechanism has been less well specified than in the foregoing examples, but the data do provide suggestive hints. For example, Kakihana et al. (92) have indirectly implicated the nervous system in determining the differences in sleeping time (narcosis) subsequent to intraperitoneal injection of alcohol in C57BL and BALB/c strains of mice. The level of alcohol was found to be the same in the brains of animals of these strains at different times post injection although the former strain recovers at levels at which the latter are still unconscious. The difference of this behavioral response is not therefore attributable to differences in metabolic rate, but must be related to differences in the sensitivity of the crucial tissue, which is presumably the central nervous system.

That the behavioral effects of albinism in the mouse may be related to the lack of pigment in the visual system has been suggested by several studies.

The difference in locomotor activity between a highly active pigmented strain (C57BL) and an inactive albino (A) strain is reduced when the animals are tested under deep red illumination (110). Subsequently, the activity difference between C57BL and BALB/c animals was shown to be a function of test illumination (35, 120). The visual system is clearly suspect, but the nature of its involvement is unclear. DeFries et al. (33) suggest a fear response to light or photophobia. Van Abeelen (1) has provided some evidence that fear of heights is also characteristic of albino animals.

These examples illustrate the increasing interest in comprehending the mechanisms of gene action in behavior. It is to be expected that this concern will play an increasing role in behavioral genetics research.

Developmental Genetics

It is likely that behavioral genetics will find a rewarding intersection between the flourishing areas of developmental psychology and developmental genetics. Only the bare outlines of this area are visible at present, but the available data promise well. Much of the evidence is in the form of genotype-environment interaction, when the environmental feature is experimentally imposed at some specified developmental stage. Lindzey et al. (108), for example, exposed infant mice to intense sound and measured the effects on their adult behavior. Relative to appropriate within strain control groups, some strains were more affected than others. Similar strain or breed differences in response to longer term rearing conditions have also been described in respect to illumination and activity in mice (36), electrical stimulation or shock and activity (74a), foster rearing and manipulatory behavior in mice (144), handling and avoidance learning in rats (107), and permissiveness of rearing and response to punishment in dogs (55).

Prenatal application of environmental agents has also been investigated. Thompson & Olian (178) showed a differential effect in mice of maternal injection of adrenalin on adult activity. Maternal stress was also found to have an effect on adult activity and on emotional reactivity in mice, but the direction of the effect was different in the two strains investigated (30, 195).

Simply monitoring behavior of various strains at various ages, without environmental manipulation, can also reveal different developmental functions. For example, mouse strains differ in development of learning performance (129) and alcohol preference (93).

Evolutionary and Population Genetics

Among biologists it has been acknowledged, in a general way, that behavior is both a product and an important agent of evolution. Concrete data are now accumulating to support this undoubtedly correct but imprecise generalization.

Mating behavior variation within species and sexual isolation between them provides clear examples of behavioral processes in evolution. *Drosophila* has been the favorite organism in research in this area, and a large

literature has grown since the inceptive work of Dobzhansky and his collaborators (37). Manning (123) has reviewed much of this literature and should be consulted for details. Briefly, it may be noted that courtship behavior of males and receptive behavior of females has been shown to be affected by single loci (6, 130), sexual behavior of both sexes is alterable by selective breeding (122, 124), and mating behavior is related to chromosomal inversions (168). The recent research on low frequency or minority advantage in mating of *Drosophila* (42, 44, 45, 167, 169) is particularly relevant. These studies have shown that mating success of males of a particular genotype, karyotype, or geographical race can often be increased by reducing their frequency relative to other males in a mating chamber. In some manner, at least partly through olfactory stimuli (43), the fact of relative infrequency must be communicated to the flies and through some behavioral mechanism not yet identified, minority male courtship becomes more effective. Although the effect is not universal (4), it is sufficiently prevalent to warrant attention as a possible major factor in population dynamics. There is a clear need for extension of the observations to other taxa.

In mammals, marked mouse strain differences have been described in many components of male sexual behavior (119). By inference, these differences might be related to fitness, but the relationship has not been explored in any detail.

It is apparent that any behavioral difference that alters the probability of two individuals meeting alters the likelihood of their mating. Some pertinent ecological and ethological information on such factors in *Peromyscus* and other mammals has been summarized by King (98).

The importance of social milieu in reproductive success is shown by the work of Wynne-Edwards (202). Grouse have a well developed social structure based upon territorial defense by males. Those males who are unable to defend a territory live on the periphery of the habitat, are more susceptible to starvation, disease, and predation, and in consequence have drastically reduced Darwinian fitness.

Mate selection in some species can also be influenced by the phenomenon of imprinting. An individual of these species shows strong sexual preference for partners that resemble those adults (usually parents) to whom it was exposed during a brief period in its early development. There have been several theoretical explorations (95) of the relationship of imprinting to assortative mating and the effects of absolute and relative imprinting on gene frequencies. Imprinting has been described mostly in birds, and the extent to which it or similar mechanisms operate in other classes remains to be explored.

In man, there have been several behavioral phenotypes whose trends over generations have been of concern. The most durable issue has concerned an anticipated drop in intelligence. Repeated observations that IQ was negatively correlated (on the order of -0.3) with sibship size led to a prediction that the mean IQ of the population would decline from 2 to 4

TABLE 2

REPRODUCTION RATES OF INDIVIDUALS OF DIFFERENT IQ LEVELS

[Data from Higgins, J. V., Reed, E. W., and Reed, S. C. (79)]

IQ range	0–55	56–70	71–85	86–100	101–115	116–130	131+
Number	29	74	208	583	778	269	25
Average no. children	1.4	2.5	2.4	2.2	2.3	2.4	3.0

points per generation (17, 176). However, results from the extensive 1947 Scottish Survey compared to those of the 1932 survey showed no decline (127, 158). Higgins et al. (79) resolved the apparent contradiction with results from a large sample survey study. The distribution of average number of children for parents of different IQ levels was shown to be bimodal with a high peak for those in the 0–55 range (Mean = 4.6) and another somewhat lower peak for those in the 131+ range (Mean = 2.0). To a considerable extent this bimodality could explain the absence of a decline in average IQ. More important, however, is the result obtained when correction is made for the fact that a large percentage of the lower IQ group remains unmarried. When these zero-offspring individuals are included, the relationship is as shown in Table 2. Substantiating results have been reported by Bajema (5) and by Gibson & Young (63). Falconer (51) has addressed theoretical aspects of the problem, pointing out that prediction of change in IQ requires estimation of the additive genetic covariance between intelligence and fitness. The phenotypic correlation provides little information in this regard, because environmental similarities can account for much of the covariance. Using the best estimates available from the data of Higgins et al. and Bajema, Falconer calculated that the rate of genetic change taking place at that time was one to two tenths of an IQ point increase per generation. Change in reproductive habits could change this rate rapidly, of course.

Another issue, not as well resolved as the one just discussed, concerns the maintenance of schizophrenia at a high incidence (nearly one percent) in the population in spite of its selective disadvantage. Huxley et al. (84) have suggested that the high frequency might be maintained through endocrinological and physiological advantage of heterozygotes with respect to disease and stress resistance. Others (102) prefer a more psychological explanation with heterozygotes being less susceptible to pressures of modern life by virtue of a marked ability to "withdraw" behaviorally. Erlenmeyer-Kimling & Jarvik (47) reviewed various of the proffered hypotheses and stated a preference for the view that schizophrenia as a diagnostic category includes a number of genetic entities. Mutation rates of a theoretically acceptable order of magnitude might then maintain the frequency of the individual phenotypes collectively known as schizophrenia.

A longer term evolutionary perspective is apparent in anthropological concern over the behavioral consequences of man's primate ancestry and his

evolutionary development as a hunter-gatherer. Only two examples from this active field will be cited. Hamburg (73), drawing upon the recently prolific primate field studies, has noted the strong selection pressure on wild primates for group membership. He then considers the selective value of emotional processes that facilitate interindividual bonds, and the possibility that contemporary social environment has rendered some of these mechanisms obsolete.

Washburn & Lancaster (194) have pointed out that the hunting mode of life has dominated man's evolution, with the agricultural mode present for only about one percent of the species' history. To the hunting way of life and its attendant selective factors they ascribe cooperativeness, male-male associations, ability to plan, ability to inhibit rage, division of labor between sexes, sharing, curiosity about large geographical area, caring during disease, and, perhaps, handedness.

Although these and similar studies necessarily involve considerable retrospective speculation, they generate testable hypotheses. They are of particular value to behavioral genetics in suggesting phenotypes for investigation and an evolutionary frame of reference in which to interpret them. It can be predicted that this line of endeavor will grow markedly in the years to come (56).

Behavioral Genetics and Society

Probably any phenotype has ultimate relevance to human welfare and social issues. Some behavioral ones are particularly pertinent to immediate matters. The long standing search for the genetic basis of mental illness and mental retardation is of obvious concern, for example. Another illustration is provided by the more recent research on the XYY karyotype. Important questions for our judicial processes have been raised by the argument that such individuals may require special consideration (26, 121, 143). At a more general level, the genetic perspective on variability and individuality has vitally important implications for our educational processes, handicapped as they have been by decades of unmitigated environmentalism (114).

Finally, it may be noted that most of the concern in the controversy over racial differences is with respect to behavioral characteristics. This sensitive issue is too important for the cursory review which is all that would be possible here. The following references are therefore given to provide access to the recent pertinent literature (34, 38, 58, 74, 85, 89, 128, 135).

Summary

Behavioral genetics has shown a striking and accelerating growth since 1950. The research on human beings has largely involved application of quantitative genetic models to continuously varying traits of intelligence and personality, and the favored technique has been one or another version of the twin method. Single locus models have been successfully applied to conditions of metal retardation, and, less compellingly to date, to schizophrenia.

The behavioral correlates of aneuploidy appear variously to involve specific cognitive and personality functions as well as the gross mental retardation that characterizes some conditions.

The research on infrahuman animals has made extensive use of inbred strains (principally mouse) and selected lines (principally rat). Quantitative models have predominated in this research, which has shown hereditary influence in a wide variety of traits, with an emphasis on learning and motivational properties.

Elucidating the physiological and biochemical routes through which the genes are expressed in behavioral traits has become an increasingly popular pursuit. The classical research with phenylketonuria has provided the model. Other conditions of mental retardation involving amino acidurias have been described in man, and a body of knowledge is coalescing concerning enzymes, neurochemicals, and hormones in animals.

Developmental behavioral genetics is just beginning to emerge and almost all of the available information has been obtained from mouse research. Behavioral processes that may be of crucial importance to population genetics have been identified in *Drosophila*, and anthropological considerations are raising exciting new hypotheses for research in man.

The field is thus unevenly developed, but the pace of current research seems to assure that a more balanced situation will quickly emerge.

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