CHAPTER 4

The Inheritance of Behavior

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TO ILLUSTRATE A POINT concerning the inheritance of gestures, Darwin (1872) quoted an interesting case which had been brought to his attention by Galton.

> A gentleman of considerable position was found by his wife to have the curious trick, when he lay fast asleep on his back in bed, of raising his right arm slowly in front of his face, up to his forehead, and then dropping it with a jerk so that the wrist fell heavily on the bridge of his nose. The trick did not occur every night, but occasionally. . . .

Nevertheless, the gentleman's nose suffered considerable damage, and it was necessary to remove the buttons from his nightgown cuff in order to minimize the hazard.

> Many years after his death, his son married a lady who had never heard of the family incident. She, however, observed precisely the same peculiarity in her husband; but his nose, from not being particularly prominent, has never as yet suffered from the blows. . . . One of his children, a girl, has inherited the same trick [pp. 33*f*.].

Probably everyone could cite some examples, perhaps less dramatic than Mr. Galton's, where some peculiarity of gait, violence of temper, degree of talent, or similar trait is characteristic of a family, and such phrases as "a chip off the old block," "like father, like son," and "it runs in the family" give ample evidence of the general acceptance of the no-

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tion that behavior traits may be inherited in the same manner as physical ones. The central purpose of this chapter is to consider the history of scientific inquiry into these matters.

Behavioral genetics may be informally defined as that discipline concerned with elucidating the degree and nature of genetic determination of similarities and differences in the behavior of individuals. Progress in this endeavor has necessarily depended upon prior progress of genetics as well as of psychology. It will also be necessary, therefore, to examine, in a modest way, the growth and development of the field of genetics.

Ancient Concepts

It is usually extremely difficult, if not impossible, to pinpoint the earliest expression of a view concerning any subject matter. The present topic is no exception, but as a matter of general interest, we may note that its origins must be very remote indeed.

The concept that "like begets like" has had great practical importance in the development of domesticated animals, which have been bred as surely for behavioral as for physical characteristics. By extrapolation, it might be suggested that a glimpse of the notion of inheritance, including inheritance of behavior traits, may have appeared in human thought as early as 8000 B.C., to which date the domestication of the dog has been traced.

The workings of inheritance have been of great interest to men all throughout recorded history, and many interesting conjectures were made (Zirkle, 1951). Most of these notions have little direct continuity with the present topic, however, and we may turn shortly to the nineteenth century, pausing only to mention briefly some examples of early Greek thought on the subject.

One of the most familiar of the early statements is that of Theognis (Roper, 1913, p. 32), in the sixth century B.C., who commented on contemporary mores:

> We seek well-bred rams and sheep and horses and one wishes to breed from these. Yet a good man is willing to marry an evil wife, if she bring him wealth: nor does a woman refuse to marry an evil husband who is rich. For men reverence money, and the good marry the evil, and the evil the good. Wealth has confounded the race.

By implication, at least, Theognis believed that such marriages with "evil" spouses would not generate "well-bred" offspring.

The Spartans, as is well known, took direct and positive action to eliminate those who were not "well-bred," by the practice of infant exposure. This infanticide was designed to eliminate those of unsound soul as well as those of defective body, for as Roper (1913, p. 19) points

out, "To the Greeks, believing only in the beauty of the spirit when reflected in the beauty of the flesh, the good body was the necessary correlation of the good soul."

In *The Republic* (Davis, 1849, p. 144), Plato suggested a course of action whereby the principles of inheritance of behavior could be used to develop a more ideal society:

> It necessarily follows . . . from what has been acknowledged, that the best men should as often as possible form alliances with the best women, and the most depraved men, on the contrary, with the most depraved women; and the offspring of the former is to be educated, but not of the latter, if the flock is to be of the most perfect kind. . . . As for those youths, who distinguish themselves, either in war or other pursuits, they ought to have rewards and prizes given them, and the most ample liberty of lying with women, that so, under this pretext, the greatest number of children may spring from such parentage.

The age of parents was also seen as an important factor, and Plato suggested that men should procreate when thirty to fifty-five years of age, while women should bear children when between the ages of twenty and forty. If, by chance, children should be conceived past the prime periods, they should be exposed at birth.

Aristotle offered less counsel on these matters than did Plato, but he had some definite ideas concerning the proper age of parents and the optimal season of the year for procreation. Eighteen and thirty-seven were the recommended ages, for women and men respectively, to begin reproduction.

> It is extremely bad for the children when the father is too young; for in all animals whatsoever the parts of the young are imperfect, and are more likely to be productive of females than males, and diminutive also in size; the same thing of course necessarily holds true in men; as a proof of this you may see in those cities where the men and women usually marry very young, the people in general are very small and ill framed . . . And thus much for the time which is proper for marriage; but moreover a proper season of the year should be observed, as many persons do now, and appropriate the winter for this business. [Ellis, 1912, pp. 233–4.]

Thus we see that both Plato and Aristotle, who contributed so much to subsequent philosophical thought, attached great importance to the circumstances surrounding mating, including the nature of the parents themselves.

ADVANCES IN BIOLOGY

BIOLOGICAL THOUGHT during the ensuing centuries was dominated by Aristotle's pronouncements on natural history, and by the

teachings of the Roman, Galen, concerning anatomy. Progress in understanding biological phenomena was virtually halted during the general stagnation of nontheological intellectual pursuits which typified the Middle Ages. Then came the Renaissance. For biology, the Renaissance may well be described as beginning with Vesalius's brilliant work on anatomy in 1543 which, in contrast to the earlier work, was based on actual painstaking dissection of the human body. Harvey's momentous discovery of the circulation of the blood followed after a considerable interval, in 1628. This finding was of far-reaching importance, for it opened the way to the mechanistic as opposed to the vitalistic viewpoint, and thus to empirical research on phenomena of life.

The pace of biological research quickened, and many fundamental developments in technique and in theory ensued in the following century. One of the cornerstones of biology was laid by Linnaeus in 1735, when in *Systema Naturae* he described over 4,000 species of animals and plants. Subsequent work in taxonomy, showing at the same time the great diversity of life and the extent to which many groups appeared to be variants of a common theme, suggested to some that various types of organisms had developed or evolved from other types.

One of the dominant figures of this period was Lamarck, who argued that the deliberate efforts of an animal could result in modifications of the body parts involved, and that the modifications so acquired could be transmitted to the animal's offspring. For example:

> . . . we perceive that the shore bird, which does not care to swim, but which, however, is obliged (*a besoin*) to approach the water to obtain its prey, will be continually in danger of sinking in the mud, but wishing to act so that its body shall not fall into the liquid, it will contract the habit of extending and lengthening its feet. Hence it will result in the generations of these birds which continue to live in this manner, that the individuals will find themselves raised as if on stilts, on long naked feet; namely, denuded of feathers up to and often above the thighs [Packard, 1901, p. 234].

For various reasons, Lamarck's and similar theories concerning evolution were unsuccessful. However, the cumulative thought set the stage for the most fundamental contribution to biological science yet made—the evolutionary theory of Charles Darwin.

The Era of Darwin and Galton

Darwin's Theory of Evolution

Natural selection. It was in 1859 that Charles Darwin yielded to the persuasions of friends and published his monumental *The Origin of Species by Natural Selection* as an "abstract" of his theory of evolu-

tion. The essence of this theory was that species and genera had been differentiated as a consequence of the "struggle for life."

> Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive [Darwin, 1869, p. 61].

This principle was called Natural Selection, and it is clear that Darwin considered that behavioral characteristics are just as subject to natural selection as are physical traits. In *The Origin of Species* an entire chapter is devoted to a discussion of instinctive behavior patterns, and in the later *The Descent of Man and Selection in Relation to Sex*, detailed consideration is given to comparisons of mental powers and moral senses of animals and man, and to the development of intellectual and moral faculties in man. In these discussions Darwin was satisfied that he had demonstrated that the difference between the mind of man and the mind of animals "is certainly one of degree and not of kind" (Darwin, 1873, p. 101)—an essential point, since one of the strongest objections to the theory of evolution was the qualitative gulf which was supposed to exist between the mental capacities of man and of lower animals. All the behavior traits cited in support of this idea must be, by implication, inherited, since, for Darwin, it is only the inheritable traits which have long-range evolutionary significance.

In an explicit summary statement, based largely on observations of "family resemblance," Darwin said:

> So in regard to mental qualities, their transmission is manifest in our dogs, horses, and other domestic animals. Besides special tastes and habits, general intelligence, courage, bad and good temper, etc., are certainly transmitted. With man we see similar facts in almost every family; and we now know through the admirable labors of Mr. Galton that genius, which implies a wonderfully complex combination of high faculties, tends to be inherited; and, on the other hand, it is too certain that insanity and deteriorated mental powers likewise run in the same families [1873, Vol. I, pp. 106*f*.].

SOURCES OF VARIABILITY. It was most crucial for the evolutionary theory that heritable variation be present in each generation, or evolution could not continue. But, by the commonly accepted principle that characteristics merged or blended in offspring, it was apparent that variability of a trait would be roughly halved in each generation, and would rapidly diminish to a trivial level, were it not replenished in

some manner. Darwin devoted much attention to the causes of variability (Darwin, 1868) and concluded that changes in the conditions of life in some way altered the reproductive systems of animals in such a manner that their offspring were more variable than they would have been in stable conditions. Ordinarily, this enhanced variability would be random—natural selection would then preserve those deviants which by chance happened to be the better adapted as a consequence of their deviation. Sometimes, however, particularly if continued for a number of generations, an environmental condition might induce *systematic* change—the environment directly inducing changes making organisms more adapted to it.

Another source of variability was presumed to be the effects of use and of disuse:

> Increased use adds to the size of a muscle, together with the blood-vessels, nerves, ligaments, the crests of bone to which these are attached, the whole bone and other connected bones. So it is with various glands. Increased functional activity strengthens the sense-organs. Increased and intermittent pressure thickens the epidermis; and a change in the nature of the food sometimes modifies the coats of the stomach, and increases or decreases the length of the intestines. Continued disuse, on the other hand, weakens and diminishes all parts of the organisation. Animals which during many generations have taken but little exercise, have their lungs reduced in size, and as a consequence the bony fabric of the chest, and the whole form of the body, become modified [1868, Vol. II, p. 423].

Likewise, with respect to behavioral characteristics, ". . . some intelligent actions . . . after being performed during many generations, become converted into instincts, and are inherited" (1873, Vol. I, p. 36) and "It is not improbable that virtuous tendencies may through long practice be inherited" (1873, Vol. II, p. 377).

It should be noted that Darwin was not completely satisfied with the doctrine that characters acquired by use, disuse, or environmental modification could be transmitted to subsequent generations (see Fisher, 1958, pp. 607). Yet such a mechanism seemed to be necessary to explain some of the facts. As we shall see, a vigorous controversy has persisted over this theory, which is generally described as Lamarckian.

Galton's Contribution

The *Origin of Species* caused a violent reaction. Fierce denunciation came from those whose sensibilities were shocked by this contradiction of the Biblical account of creation. There was opposition, too, from other scientists, whose favorite theories were challenged by the new conceptions. There were, however, some scholars to whom the argu-

ments were immediately compelling. Among this latter group was Francis Galton, Darwin's half-cousin.

The *Origin* directed Galton's immense curiosity and talents to biological phenomena, and he soon developed what was to be a central and abiding interest: the inheritance of mental characteristics.

HEREDITARY GENIUS. In 1865 two articles by Galton, jointly entitled "Hereditary Talent and Character," were published in *Macmillan's Magazine*. Four years later a greatly expanded discussion was published with the title, *Hereditary Genius: An Inquiry into its Laws and Consequences.*

The general argument presented in this work is that among the relatives of persons endowed with high mental ability is to be found a greater number of other extremely able individuals than would be expected by chance; furthermore, the closer the family relationship, the higher the incidence of such superior individuals.

Applying Quetelet's "law of deviation from an average," at the time a fairly recent development, but later to become familiar as the normal curve, Galton distinguished fourteen levels of human ability, ranging from idiocy through mediocrity to genius.

No satisfactory way of quantifying natural ability was available, so Galton had to rely upon reputation as an index. By "reputation" he did not mean notoriety from a single act, nor mere social or official position, but "the reputation of a leader of opinion, of an originator, of a man to whom the world deliberately acknowledges itself largely indebted" (1869, p. 37). The designation "eminent" was applied to those individuals who comprised the upper 250 millionths of the population (i.e., one in 4,000 persons would attain such a rank), and it was with such men that the discussion was concerned. Indeed, the majority of individuals presented in evidence were, in Galton's estimation, the cream of this elite group, and were termed "illustrious." These were men whose talents ranked them one in a million.

On the basis of biographies, published accounts, and direct inquiry, Galton evaluated the accomplishments of eminent judges, statesmen, peers, military commanders, literary men, scientists, poets, musicians, painters, Protestant religious leaders and Cambridge scholars, and their relatives. (Oarsmen and wrestlers of note were also examined to extend the range of inquiry from brain to brawn.) In all, nearly 1,000 eminent men were identified in the 300 families examined. With the over-all incidence of eminence only 1 in 4,000, this result clearly illustrated the tendency for eminence to be a family trait.

Taking the most eminent man in each family as the reference point, the other individuals who attained eminence (in the same or in some other field of endeavor) were tabulated with respect to closeness of family relationship. Table 1, in which each entry is expressed in per-

centage form, gives the principal results. These data give a uniform picture of decreasing likelihood of eminence as the degree of relationship becomes more remote.

Galton recognized the possible objection that relatives of eminent men would share social, educational, and financial advantages, and that the results of his investigation might be interpreted as showing the effectiveness of such environmental factors. To demonstrate that reputation is an indication of *natural* ability, and not the product of environmental advantages, three arguments were presented. First, Galton stressed the fact that many men had risen to high rank from humble family backgrounds. Second, it was noted that the proportion of eminent writers, philosophers, and artists in England was not less than that in the United States, where education of the middle and lower socioeconomic classes was more advanced. The educational advantages in America had spread culture more widely, but had not produced more persons of eminence. Finally, a comparison was made between the success of adopted kinsmen of Roman Catholic Popes, who were given great social advantages, and the sons of eminent men, and the latter were judged to be the more distinguished group.

TABLE 1

INCIDENCE OF EMINENCE IN RELATIVES OF EMINENT MEN *

NATURE OF KINSHIP	Judges	Statesmen	Commanders	Literary	Scientific	Poets	Artists	Divines	All Classes
Father	26	33	47	48	26	20	32	28	31
Brother	35	39	50	42	47	40	50	36	41
Son	36	49	31	51	60	45	89	40	48
Grandfather	15	28	16	24	14	5	7	20	17
Uncle	18	18	8	24	16	5	14	40	18
Nephew	19	18	35	24	23	50	18	4	22
Grandson	19	10	12	9	14	5	18	16	14
Great-grandfather	2	8	8	3	0	0	0	4	3
Great-uncle	4	5	8	6	5	5	7	4	5
First cousin	11	21	20	18	16	0	1	8	13
Great-nephew	17	5	8	6	16	10	0	0	10
Great-grandson	6	0	0	3	7	0	0	0	3
All more remote	14	37	44	15	23	5	18	16	31

*These figures express the incidence of eminence per 100 families. From Francis Galton, *Hereditary Genius*, p. 317. Published in 1869 by MacMillan of London, and used with their permission.

In Galton's view, men of mediocre talents might be supressed by environmental obstacles, but inherited genius will out, regardless of adversity, and no amount of social or educational advantage can serve to raise a man to eminence unless he possesses inherited natural ability.

POLITICAL AND SOCIAL IMPLICATIONS OF THE INHERITANCE OF EMINENCE. Galton was keenly aware of the powerful implications of his arguments. In introducing *Hereditary Genius*, he announced:

> I propose to show in this book that a man's natural abilities are derived by inheritance, under exactly the same limitations as are the form and physical features of the whole organic world. Consequently, as it is easy, notwithstanding those limitations, to obtain by careful selection a permanent breed of dogs or horses gifted with peculiar powers of running, or of doing anything else, so it would be quite practicable to produce a highly-gifted race of men by judicious marriages during several consecutive generations [1869, p. 1].

Improvement of mankind in this way, by the application of principles of heredity, was given the name "Eugenics" (Galton, 1883, p. 24) and the furtherance of eugenic goals became the underlying theme around which most of Galton's work was oriented.

PIONEERING RESEARCH IN PSYCHOLOGY AND STATISTICS. To be sure, the "highly gifted race" Galton envisaged would need to be physically sound, and much attention was given to measurements of health and physique; but Galton was primarily concerned with the sound mind, and focused his efforts on the problems of assessing mental characteristics. In a prodigious program of research, he developed apparatus and procedures for measuring auditory thresholds, visual acuity, color vision, touch, smell, judgment of the vertical, judgment of length, weight discrimination, reaction time, and memory span. In addition, a questionnaire technique was employed to investigate mental imagery, and association of ideas was studied by introspection. One particularly intriguing, although not especially successful, investigation involved the use of composite portraiture, whereby the photographs of a number of individuals could be superimposed to yield their common features. These composite photographs were then used in an effort to determine what relationship, if any, existed between the facial characteristics of certain groups and various attributes of their intelligence, personality, morality, and health.

The problems of properly expressing and evaluating the data obtained from such researches were formidable, and Galton also turned his remarkable energies to statistics, pioneering in the development of the concepts of the median, percentiles, and correlation.

It was, of course, desirable to have data from large numbers of in-

dividuals, and various stratagems were employed to this end. For example, Galton arranged for an "Anthropometric Laboratory for the measurement in various ways of Human Form and Faculty" to be located at an International Health Exhibition. Some 9,337 people paid fourpence each for the privilege of being measured for various bodily and sensory characteristics! On another occasion a contest was sponsored in which awards of £7 were given to those submitting the most careful and complete "Extracts from their own Family Records." Thus did Galton obtain a large number of pedigrees which he could examine for evidence of human inheritance.

TWINS AND THE NATURE-NURTURE PROBLEM. Of special relevance to the present topic is Galton's introduction (Galton, 1883) of the twin-study method to assess the effectiveness of *nature* (inheritance) and *nurture* (environment). The essential question in this examination of twins was whether twins who were alike at birth became more dissimilar as a consequence of any dissimilarities in their nurture, and conversely, whether twins unlike at birth became more similar as a consequence of similar nurture. Galton acknowledged two types of twins: those arising from separate eggs, and those arising from separate germinal spots on the same egg, yet he did not distinguish between the two types in his discussion, except as they fell into his "alike at birth" or "unlike at birth" categories. Gathering his evidence from answers to questionnaires and biographical and autobiographical material, Galton observed that, in thirty-five cases of twins who had been very much alike at birth, and who had been reared under highly similar conditions, the similarities persisted after they had grown to adulthood and gone more or less separate ways.

In twenty cases of originally dissimilar twins, there was no compelling evidence that they had become more alike through being exposed to similar environments.

> There is no escape from the conclusion that nature prevails enormously over nurture when the differences of nurture do not exceed what is commonly to be found among persons of the same rank of society and in the same country. My fear is, that my evidence may seem to prove too much, and be discredited on that account, as it appears contrary to all experience that nurture should go for so little [1883, p. 241].

GALTON'S WORK IN PERSPECTIVE. The ten years between *Origin of Species* and *Hereditary Genius* had not been sufficient for the idea of man as an animal to be digested. For many of those who accepted Darwin, of course, Galton was a natural and logical extension: man differs from animals most strikingly in mental powers; man has evolved as have other animals; evolution works by inheritance; mental traits are inheritable.

For those whose faith in the special creation of man remained firm, Galton was unacceptable, atheistic, and reprehensible.

Even among those not arguing primarily on theological grounds, there were wide differences of opinion as to the proper frame of reference for the study of man. In psychiatric theorizing, for example, some views were based upon the concept that human behavior is determined by biological processes, and that no adequate theory of mental functioning or malfunctioning could disregard man's fundamentally animal nature. On the other hand, there were those who chose to regard the "psyche" as capable of investigation in and of itself, with organic processes ignored as irrelevant (see White, 1948).

There were also scholars whose inquiries stemmed, not from interest in psychiatric problems, but from a general desire to understand "mind." The philosophical approach was dominated by the British philosophers, whose emphasis was clearly on experience and thus on "nurture," having been inspired by Locke's seventeenth-century *tabula rasa* dictum that ideas are not inborn, but come from experience. The role of experience was also emphasized by experimental psychology, which is usually dated from Wundt's establishment of the *Psychologisches Institut* in 1879, just prior to Galton's major works. In spite of the fact that Wundt had come to psychology from physiology, his approach was not biological in the same sense as Galton's, and the goal at Wundt's institute was the identification, through introspection, of components of consciousness. Individual differences, which formed the very heart of Galton's investigations, were nuisances in this search for principles which had general application to all. One notable exception to this general trend was provided by an American named J. McK. Cattell, who, as a student of Wundt, insisted on studying individual differences. After Cattell left Leipzig, he worked for a while with Galton, and had his belief in the importance of individual differences strengthened and confirmed. Cattell had an important influence on the development of American psychology, and, as we shall see later, inspired some of the earliest experimental work in behavioral genetics.

From the foregoing it may be seen that Galton's work was neither completely in step nor completely out of step with the times. As it happened, Galton lived in the greatest period of intellectual turmoil which had occurred in biology. His work was both a product and a causal factor of the advances made. Galton was not the first to insist upon the importance of heredity in traits of behavior. We have seen explicit statements on this matter by the ancient Greeks. Nor was Galton the first to place his conclusions in an evolutionary context. Spencer had introduced an "evolutionary associationism" in 1855 (Boring, 1950, p. 240). But it was Galton who championed the idea of inheritance of behavior, who vigorously consolidated and extended it, and who gave it

a substance and direction it had hitherto lacked. If it ever becomes of moment to designate the "father" of behavioral genetics, Galton will have no real competition for the title.

Theories of Inheritance

For Darwin and Galton the transmission of characteristics from generation to generation was an essential concept. There was substantial evidence of the importance of heredity, but its laws had proved extremely resistant to analysis. In particular, a vast amount of data had been accumulated from plant and animal breeding. Offspring frequently resembled one of the parents, or were perhaps intermediate to both parents. But two offspring from the very same parents could be quite unlike. As Lush described the situation even considerably later, the first rule of breeding was that "like produces like," while the second rule was that "like does not always produce like" (Lush, 1951, p. 496).

PANGENESIS. The theory of heredity most successful in explaining the confusion of facts at the time was the "provisional hypothesis of pangenesis" as described by Darwin. On this view, the cells of the body,

> . . . besides having the power, as is generally admitted, of growing by self-division, throw off free and minute atoms of their contents, that is gemmules. These multiply and aggregate themselves into buds and the sexual elements; . . . [1868, p. 481].

Gemmules were presumably thrown off by each cell throughout its course of development. With the uniting of gemmules from the male and female parents, gemmules of the various developmental periods would come into play at the proper times, and thus direct the development of a new organ like that from which they had arisen.

If a body part were modified by use or disuse, the gemmules cast off by the cells of the body part would also be modified, and thus acquired characteristics could be transmitted to the offspring. Of specific interest to our present topic, we may note Darwin's statement:

> With respect to mental habits or instincts, we are so profoundly ignorant on the relation between the brain and the power of thought that we do not know whether an inveterate habit or trick induces any change in the nervous system; but when any habit or other mental attribute, or insanity, is inherited, we must believe that some actual modification is transmitted; and this implies, according to our hypothesis, that gemmules derived from modified nerve-cells are transmitted to the offspring [1868, p. 472*f*.].

Galton took issue with some of the features of pangenesis, and performed a long-range study which was a direct attempt to determine if

gemmules from one breed of rabbit would affect the progeny of another breed when transfused in the blood. This experiment, which, incidentally, was performed in collaboration with Darwin, had a quite negative outcome. Galton also doubted the inheritance of acquired characteristics. A substantial, but on the whole friendly, disagreement grew up between Darwin and Galton on these issues, with the latter publishing extensively on a revised theory. Galton's revision foresaw many of the later developments, but to Gregor Mendel must go the credit for providing the basic answer to the riddle of inheritance.

MENDEL'S EXPERIMENT AND THEORY. Mendel was an Augustinian monk who conducted his critical researches on pea plants in the garden of a monastery at Brunn, Moravia.

Much of the information concerning heredity available at the time had been based on experiments on "plant hybridization" involving the crossing of plants of different species. Among the difficulties of this approach, two of the most important were that the offspring were frequently sterile or semi-sterile, so that succeeding generations were difficult or impossible to obtain, and that the features which had been investigated were generally too complex for clear analysis. Mendel's success can be attributed in large part to his method of dealing with these problems. By crossing different varieties within the same species, Mendel got viable and fertile offspring, and thus was able to proceed to hybrids of the second generation. By concentrating his attention on simple dichotomous characters, he was able to make a thorough analysis, uncluttered by problems of measurement or distinction of categories. Curiously, Mendel's greatest innovation was evidently his insistence on *counting* all the progeny, and not being content with an attempt at a verbal summary of the typical result. This was, of course, made convenient by dealing with dichotomous characteristics.

In all, some seven morphological characters were investigated, and uniform results were obtained with respect to all. In the first-generation hybrid offspring (later named the F_1 or first filial generation) between plants differing with respect to any one of the characters, all plants were uniform, and like one of the parents. That parental character which appeared in the F_1 was called dominant; the parental character which was not expressed was called recessive. When the F_1 plants were allowed to self-pollinate, plants showing the dominant trait and plants showing the recessive trait were found among the offspring (the F_2, or second filial generation) in a definite 3:1 ratio, but no plants were found which were intermediate. Furthermore, it was found that the recessive plants "bred true"—their offspring always showed the recessive character. One third of the dominant plants also bred true, but two thirds yielded both types of progeny.

To account for these results, Mendel postulated that each parent possessed two elements which determined the particular trait. Each parent would transmit one of its elements to its offspring. In the case where the parents differed in respect to a characteristic, an element contributed by the one parent might be dominant over that contributed by the other parent, and the offspring would resemble the former. Nonetheless, the recessive element would not be contaminated in any way by its association with the dominant element. When the individual offspring in turn had offspring, it would pass on the element which it had received from each of its own parents to one half of its progeny—and the nature of the recessive element passed on would not differ in any way from its nature when transmitted from the original parent. Thus, the gametes (sex cells) were regarded as pure and essentially inviolable. Now, when such a hybrid offspring (F_1) is self-pollinated (or more generally, when two such hybrids are mated), the male and female germ cells (gametes) will each contain one of the elements only. The gametes will unite at random. Thus if *A* represents the dominant element and *a* the recessive, each hybrid is *Aa*, but each gamete produced by the hybrid will be either *A* or *a*. When two hybrids are crossed, yielding an F_2 generation, the following combinations can occur: *AA*, *Aa*, and *aa*, and these will occur in a 1:2:1 ratio. Because of dominance, the *AA* will not be distinguishable from the *Aa*, except by examination of their offspring, so that the observable character will be displayed in a 3:1 ratio. This was Mendel's first law, the "law of segregation." Figure 16 shows the relationships graphically.

The second major law was the law of independent assortment. This principle was discovered when parents differing in two or more characteristics were crossed. For example, a pea plant having yellow, round seeds was crossed with one having green, wrinkled seeds. The first generation hybrid plants uniformly had yellow, round seeds, since these elements are dominant. In the generation resulting from the self-pollination of these plants, the characteristics were combined at random. The elements for yellow and round were not bound together simply because they were associated in that combination in the "grandparents." The elements, indeed, were sorted out at random, hence the name "independent assortment." A schematic illustration of this feature of Mendel's theory is shown in Figure 17.

Development of Modern Genetics

Mendel's results and theory were read to the Brunn Society of Natural Science in 1865, and were later published in the proceedings of the Society. The crucial experiments had therefore been done and reported prior to Darwin's most complete statement of pangenesis, and

The "big" parent is characterized by the two *A* elements. The "small" parent has two *a* elements.

Each gamete formed can contain only one element, and, in this case, each parent can form only one kind of gamete.

The gametes unite to form F_1 individuals. Because of dominance of *A* over *a*, the F_1 individuals are all like their "big" parent.

The F_1 individuals can each produce two kinds of gamete, *A* or *a*, and these will be formed in equal numbers.

If mating occurs between two F_1 individuals, the gametes will combine at random to form several combinations.
Three kinds of zygote occur in the F_2, in the ratio 1:2:1. Because of dominance, however, *AA* cannot be distinguished from *Aa*, and the ratio actually observed will be 3:1.

The "small" and one third of the "big" individuals can produce only one kind of gamete. The other two thirds of the "big" individuals can produce two kinds of gamete, as was true of the F_1. An *a* gamete from one of the latter will not be different from the *a* gamete from the "small" individual of the F_2.

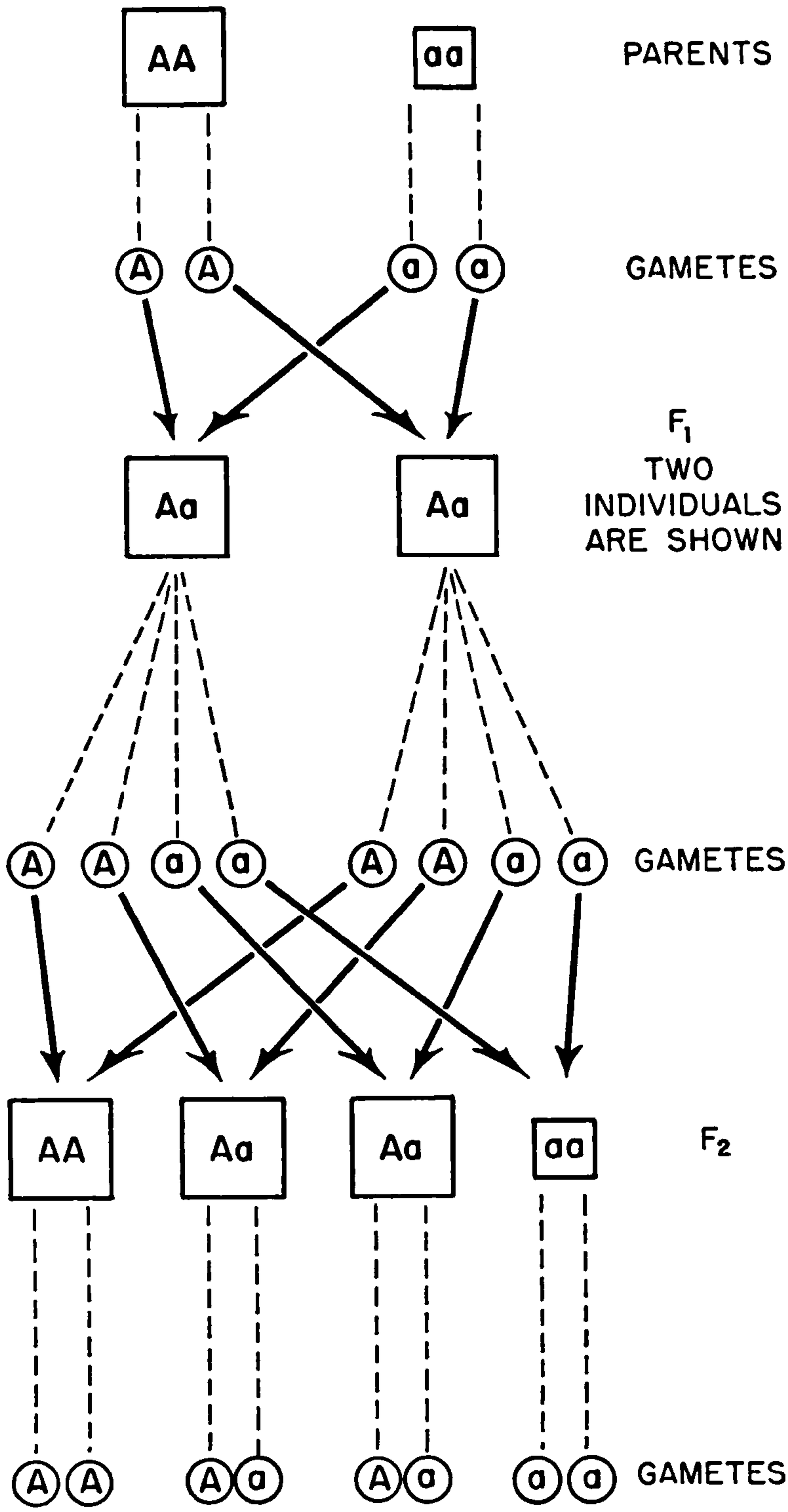

FIGURE 16. A schematic illustration of the Law of Segregation when one element is dominant. The hypothetical character is indicated by the size of the squares. Gametes are shown as small circles.

The *AA* combination results in a "big" individual, and the *aa* combination results in a "small" individual. *BB* results in a "square," and *bb* results in a "diamond." *A* is dominant over *a*, and *B* is dominant over *b*.

With regard to these characters, each parent can produce only one kind of gamete.

F_1 individuals are all alike: "big" and "square."

Each F_1 individual can form four kinds of gamete with regard to these characters.

This diagram shows the result of random combination of the gametes of a female and of a male F_1 individual. All possible combinations of "big," "small," "square," and "diamond" appear. The grandparental combinations of *AABB* and *aabb* occur no more often than expected by chance.

Note that the ratio of F_2 phenotypes is:

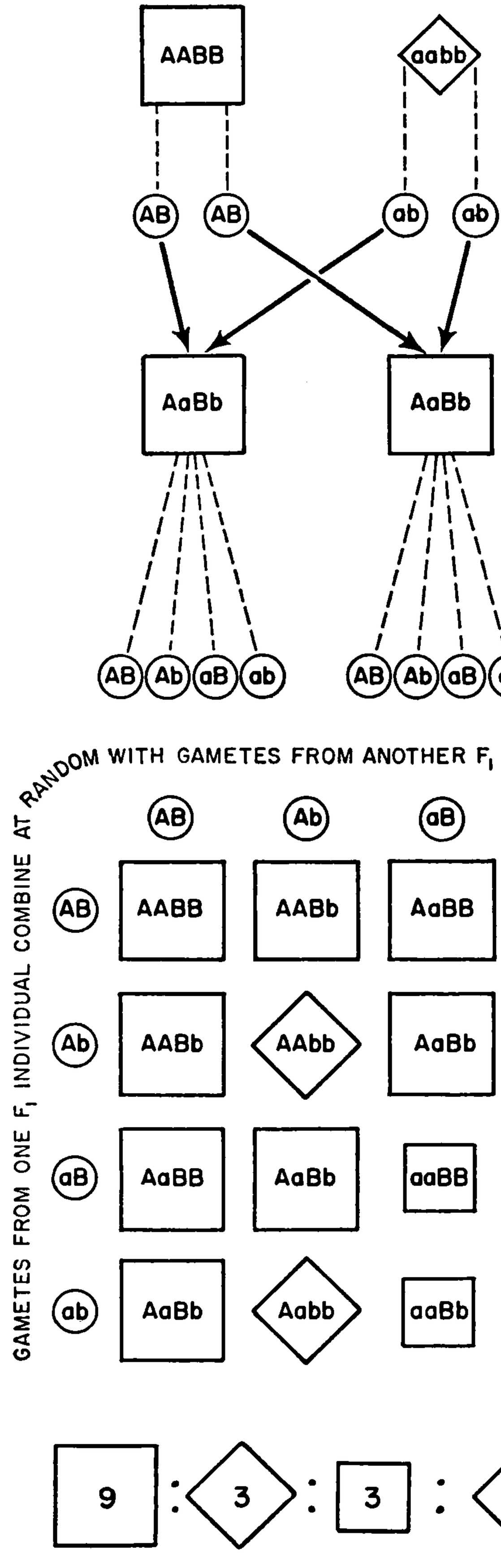

FIGURE 17. A schematic illustration of the Law of Independent Assortment. Two hypothetical characters are considered, each of which acts in a dominant fashion.

before *Hereditary Genius*. But Darwin and Galton were not alone in overlooking Mendel's ideas. For thirty-four years, the "Versuche über Pflanzen-Hybriden" (Mendel, 1865) remained almost completely unheeded. Then, in 1900, three investigators—Correns, de Vries, and von Tschermak—almost simultaneously "rediscovered" Mendel's work, and a period of intensive research was inaugurated in which the Mendelian results were confirmed and extended. Some modifications ensued. Not all factors displayed dominance; there were cases in which the hybrid offspring were intermediate to the parents. Nonetheless, the factors emerged from the hybrid unchanged. The "purity of gametes" held in spite of the superficial appearance of blending. Furthermore, it was found that the law of independent assortment did not hold absolutely. Sometimes assortment was not at random, but factors tended to stick together in the gametes produced by an individual in the same relationship as in the gametes which produced the individual.

The vigorously developing area of research came to be known as genetics in 1909, and the name "gene" was proposed for the Mendelian factors. At the same time, a fundamental distinction was made by Johannsen between the *genotype*, which is the genetic composition of the individual, and the *phenotype*, the apparent, visible, measurable characteristic. The importance of this distinction is that it makes clear that the observable trait is not a perfect index of the individual's genetic properties. Given a number of individuals of the same genotype, one might nonetheless expect differences among them—differences caused by environmental agencies. Thus, two beans might be from the same "pure line," and have identical genotypes with respect to size, yet one might be larger than the other because of differences in "nurture." Nevertheless, their genotypes would remain unaffected, and the beans of the plants grown from these two beans would be of the same average size. The inheritance of "acquired" characters obviously has no place in this scheme.

THE PHYSICAL BASIS OF HEREDITY. Mendel was convinced that his "elements" were material units located in the gametes, but with the state of knowledge of cytology at the time, it was not possible for him to specify their physical nature in any greater detail. It was fortunate that, for the purposes of establishing the basic Mendelian laws, the "elements" or "genes" could be treated as hypothetical constructs, and no precise knowledge of their location or structure was necessary. There was, naturally, considerable speculation, but the real breakthrough in understanding the physical nature of the determiners of heredity awaited critical developments in the field of cytology.

CYTOLOGICAL DISCOVERIES. The study of the cell and its contents had progressed rapidly since the general acceptance, in the mid-

nineteenth century, of the doctrine that cells are the structural and functional units of living organisms. Aided in no small degree by advances in the chemistry of dyes, cytologists were able to develop means of staining the contents of cells to render them more visible for study. It was soon found that a portion of the cell, the *nucleus*, contains a number of small rod-shaped bodies which are called *chromosomes* (colored bodies) because of their capacity to be stained by particular dyes. The number of chromosomes, with some exceptions that need not concern us now, are the same in all somatic cells of an organism, and all individuals of a species have the same number. The number of chromosomes, however, varies greatly from species to species. It was known that in the process of growth the cells divide into two "daughter cells," each of which then later divides into two more, and so forth. Study of the chromosomes revealed that a remarkable series of changes takes place during this process of cell division, or *mitosis*. Prior to the splitting of the cell, the chromosomal material doubles, and during the cell division, half of the material goes into one daughter cell, half into the other. The chromosomes are somewhat distinctive in shape and size, so that it was possible to determine that each daughter cell receives an equivalent chromosomal complement. This distinctiveness of chromosomes also permitted the observation that chromosomes are present in pairs, and that the chromosomal material in a cell could be viewed as consisting of two comparable or *homologous* sets.

Quite independently of knowledge of the Mendelian laws, evidence was obtained that the chromosomes are, in some way, concerned with heredity, and it was concluded that one *set* of chromosomes is contributed by each parent. The process by which this is accomplished (meiosis) consists essentially of the splitting of a cell into two without the prior doubling of chromosomal material which is found in mitosis. One member of each pair of chromosomes is drawn into each daughter cell before the division is complete. The set included in any one gamete, however, is not necessarily the complete set which the individual had received from its mother or from its father. A reshuffling takes place, so that an individual transmits to its offspring some of the chromosomes it received from its own mother along with some received from its own father.

Chromosomes and genes. This interesting behavior of the chromosomes was seen to parallel the behavior of Mendel's "elements": two elements, paired chromosomes; one element in each gamete, one of each pair of chromosomes in each gamete. On this, and other evidence, it was suggested that the genes are in fact particulate physical bodies residing at specific *loci* on the chromosomes.

The advances in understanding of the chromosomal basis of hered-

ity also allowed explanation of the exceptions to the law of independent assortment which had been noted (see p. 160). It was evident that there are more genes than there are chromosomes, and that therefore each chromosome must contain a number of genes. If two characteristics under study are determined by genes on the same chromosome, it is clear that these genes cannot assort independently. Such *linkage* was experimentally demonstrated, but it was also discovered that linkage is not a permanent, unbreakable bond. During one stage of gamete formation, the chromosomes line up pair by pair. Each member of each pair separates into two. The adjacent members of this *tetrad* frequently come into contact and exchange parts. This mutual exchange is usually done with such precision that equivalent sections are traded—each of the members participating in the exchange receiving the same loci that it gives.

Figure 18 is a diagrammatic illustration of this process for one pair of chromosomes only. It should be remembered that the same events may be occurring at the same time for all other chromosome pairs. In Figure 18A are shown the two members of the chromosome pair. The maternal chromosome, carrying the genes *A*, *b*, and *C*, is shown as white, and the paternal chromosome with the genes *a*, *B*, and *c* is shown as gray. At one stage in meiosis each of the chromosomes can be seen to be duplicate, as shown in Figure 18B. In Figure 18C the adjacent members are shown as crossed over one another. During this stage the chromosomes may break and rejoin, yielding the configuration of Figure 18D. Each one of these four members will be transmitted to one gamete. Consider only the *A*-*a* and *B*-*b* locus for the moment. As shown in Figure 18E, one gamete will carry the genes *A* and *b* as in the grandmother, one will carry *a* and *B* as in the grandfather, and the other two will carry *A* with *B* and *a* with *b*. For these last, recombination has taken place. Crossing over of this kind does not always occur at the same place, and the probability that recombination will occur is a function of the distance between the genes involved. In Figure 18, for example, the crossing over has not affected the relationship between the *A*-*a* and the *C*-*c* loci. All gametes are either *AC* or *ac*, as in the grandparental combinations, since the crossover did not occur between these loci. Crossing over could occur between the *A* and *C* loci, but would be less frequent than between *A* and *B*. Because of this, the crossover gametes frequently occur less often than the non-crossover, and this forms an exception to the law of independent assortment. Genes located on different chromosomes do, of course, assort at random.

Autosomes and sex chromosomes. Detailed examination of the chromosomes revealed that one pair was exceptional, in that the

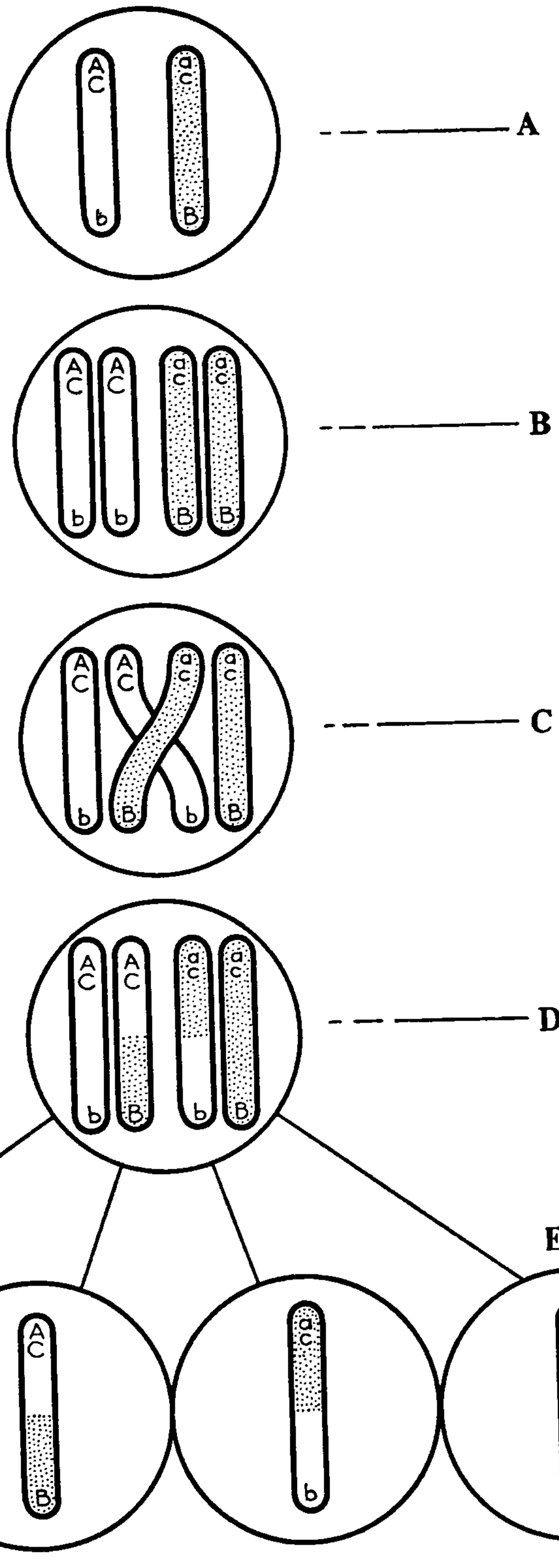

FIGURE 18. Diagrammatic illustration of crossing over—the mutual exchange of material by homologous chromosomes.

members of the pair were of obviously different size and shape. Eventually, it was possible to relate this atypical pair of chromosomes to sex determination. Whereas the situation differs in birds and some insects, the mechanism in mammals, including man, is briefly as follows: Females have two similar-sized chromosomes which are called X. Males have one X and a smaller chromosome called Y. Females obviously can form only X-bearing eggs, but males form both X- and Y-bearing sperm. If an egg is fertilized by a Y-bearing sperm, the zygote will be male; if fertilization is by an X-bearing sperm, the zygote will be female.

Genes located on the sex chromosomes give phenotypic results which differ from the usual Mendelian results of genes carried on autosomes (chromosomes other than sex chromosomes), primarily because the Y chromosome appears to be relatively barren. In humans, for example, color blindness is due to a gene carried on the X chromosome. In females it acts as a recessive, so that a woman will be color-blind only if homozygous. Frequently, the recessive gene will be paired with a dominant, and such a heterozygote will have normal color vision. In males, however, there is no corresponding locus on the Y chromosome, so that a single recessive, present on the X, will be expressed. Thus, color-blindness and other X-linked conditions are much more frequent in men than in women.

CHROMOSOMAL ABNORMALITIES. The delicacy and precision of chromosomal events is marvelous, yet, as appears to be true of all living systems, mishaps sometimes occur. Occasionally, chromosomes which are not members of the same pair will exchange parts, with the result that gametes may be formed which contain an extra allotment of some genes and a lack of others; sometimes a segment of chromosome breaks off and reattaches backward, or is lost, or attaches to the "wrong" chromosome; sometimes gametes are formed in which the whole chromosome set is present in duplicate; occasionally, the division of chromosomal material in meiosis is not exact, and both of a pair of chromosomes will go into one daughter cell, leaving another daughter cell with one chromosome completely missing. This latter phenomenon, which was first described in the fruit fly *Drosophila* (Bridges, 1913), warrants further comment, since we shall have occasion to refer to it later.

If an egg is formed which contains, say, two X chromosomes instead of the usual one, and is fertilized by a Y-bearing sperm, an XXY zygote will result. Likewise, if an egg which has no X chromosome at all is fertilized by a Y-bearing sperm, the resulting zygote will be YO (where O represents absence of a chromosome). In like manner, XXX and XO gametes will be formed if eggs of these respective constitutions are fertilized by X-bearing sperm. In Drosophila, XXX and YO flies

usually die, but XXY are viable, fertile females, and XO are viable but sterile males. These abnormalities of chromosomal distribution can occur with respect to autosomes as well as to sex chromosomes, and occur in male as well as in female gametogenesis.

MODIFIABILITY OF THE GENES. Mendel's conclusion concerning the "purity of the gametes," and Johannsen's demonstration that environmental modification of a phenotype does not alter the genotype, present a view of the genes as being highly stable and well insulated from the effects of environment. There were, however, many observations which showed that the stability of the genes is a relative matter. On occasion, a given gene might undergo a more or less permanent change, called a mutation. The reasons for this alteration in the nature of genes are still incompletely understood, but significant advances have been made since the discovery in 1927 by Muller that irradiation of corn and barley increases the rate of gene mutation. Since this discovery of the *mutagenic* effect of X-rays, other means of experimentally inducing mutations have been discovered, including certain chemical compounds and the application of extreme temperatures, and the mutability of the hereditary material of other species has been demonstrated. Thus, *certain environments* can bring about changes in genotype, but this situation differs greatly from the old notion of inheritance of acquired characters. Under that scheme, the environment was thought capable of bringing about systematic changes, or else the organism, by use or disuse of body parts, caused a change, which made the organism *more adapted to the environment*, and this adaptation could be transmitted to subsequent generations. The mutations, however, induced by X-ray and other mutagenic agents, as well as those occurring "spontaneously," are apparently random—the mutation might affect eye color or wing shape or any of a large number of such characteristics, but the organisms are not made more adapted for example, to an X-ray environment. Actually, the mutations which occur seem much more likely to be deleterious than advantageous to the organism.

The capability of experimentally inducing mutations has proved to be of marked value in genetic research, and has contributed greatly to the elucidation of the molecular structure of genes and of the biochemistry of gene action.

Progress in the understanding of mutations has also been of importance to evolutionary theory. It may be recalled that Darwin took great pains in considering the possible sources of heritable variation, and somewhat reluctantly concluded that Lamarckian mechanisms are among the important factors. Contemporary evolutionary theory views mutation as an important (and perhaps the only) source of the genetic variability upon which natural selection operates.

Mechanism of gene action. At one level, gene action may be described in terms of dominance, recessiveness, or additivity. Further insights into the mechanism of gene action have been obtained by certain experiments with fruit flies. In *Drosophila melanogaster* there are four chromosomes and, of course, each fly has two of each. By proper techniques, however, it is also possible to obtain flies with abnormal numbers of a given chromosome. The effect of varying "dosages" of genes can then be studied. An example of the results of this kind of research is given by the mutant gene "shaven," which reduces the number of abdominal bristles on the fly (see Wagner and Mitchell, 1955). Representing the normal gene by *S* and the "shaven" by *s*, and letting $<$ mean "has fewer bristles than," we may describe the three possible types of normal flies (each possessing two chromosomes) as follows: $ss < Ss < SS$. By adding or subtracting chromosomes containing the *s* gene, the following is obtained:

$$s < ss < sss < Ss < SS$$

An interpretation of these findings is that the mutant gene is working in the same direction as the normal gene, but is simply less effective. This kind of mutant is described as a *hypomorph*. By similar experiments (see Wagner and Mitchell), other types of mutants have been described: *antimorphs*, which have an effect contrary to the normal gene; *hypermorphs*, which have an effect greater than the normal gene; *neomorphs*, which have an effect unrelated to the normal gene; and *amorphs*, which have no effect at all. All of these can be incorporated into an explanatory scheme if one assumes that genes produce some substance, and that it is through the substance produced that they have their effect. The key role of enzymes in biochemistry early led to the notion that genes produce enzymes, and a great amount of research brought forth the "one gene—one enzyme" hypothesis which stated that each gene produces a single enzyme. This is now thought to be an oversimplification, but it is clear that genes confer specificity upon enzymes, although several genes may be involved in determining specificity of a given enzyme (Davis, 1954, p. 29). The enzymes, of course, are centrally involved in the metabolic processes resulting in development and functioning of the sensory, associative, and effector organs, and thus can influence behavior through any or all of these systems. Figure 19 gives a diagrammatic indication of the complexity of the intermediate steps between the initial gene action and the phenotypic expression. Here it may be seen that alteration of any one of a number of different pathways may result in change of a given phenotype, and that, conversely, alteration of any one pathway may have consequences for a number of different phenotypes.

In view of the complexities suggested in Figure 19, it is no sur-

prise that, in numerous cases, "modifier" genes have been described which alter the effect of a major gene upon some character. Indeed, it is clear that describing any gene as "*the*" gene determining a character is only a convenient short-hand expression. All genes exert their influence in the context of the total genetic system, and identifying the gene for "shaven," for example, is simply an expedient way of saying that the gene occupies a particularly strategic location in the network of the genetic factors acting upon the formation of abdominal bristles.

THE COLLABORATION OF GENES AND ENVIRONMENT. One of the most important principles to emerge from genetics research is that a phenotype is the joint product of genetic and environmental factors.

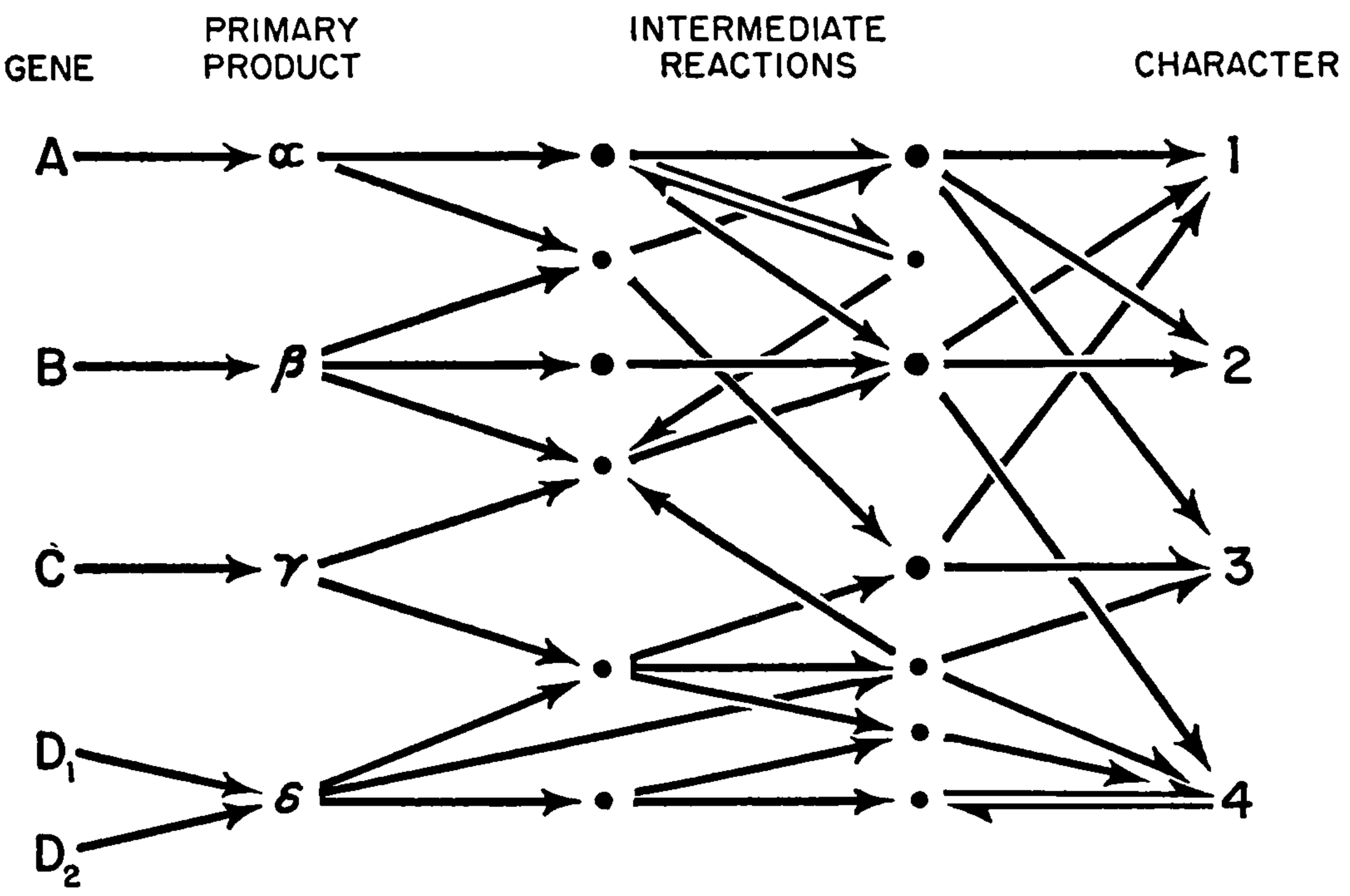

FIGURE 19. Diagrammatic representation of the complexity of gene interaction in the production of a character. (By G. Ledyard Stebbins.)

This is easily made apparent by a *reductio ad absurdum:* if there is no environment, no organism can develop to display any phenotype whatsoever. Likewise, without a genetic constitution, there will be no organism. It is clear that a question asking if a trait is due to heredity or to environment is nonsense. Without both, there would be no trait at all. A meaningful answer, however, may be sought to a question concerning the *relative* contributions of genetic *differences* and environmental *differences* to the *variability* of a characteristic. We must not then seek absolute answers to the question of the importance of heredity or of environment in determining a characteristic. The answer obtained will

depend upon the extent to which relevant genetic variability exists within the group being considered and upon the range of environmental differences to which the individuals are exposed. If genetic variability is eliminated, or reduced drastically, and environment allowed to vary, then environmental agencies will appear important. The average and the variability of the phenotype will depend, however, on the nature of the common genotype. If environment is held constant and genotype allowed to vary, then genotype will be seen as important, but the average and the variability of the phenotype will depend upon the nature of the common environmental conditions. Hogben (1933, pp. 96*f*.) presented a discussion of Krafka's data on eye mutants which succinctly demonstrates these principles. Two different mutants, "low-bar" and "ultra-bar," reduce the number of facets in a fly's eyes. The extent of reduction, however, depends upon temperature. Figure 20 shows this interaction. The distance *AB* represents the phenotypic difference between two stocks of flies, one homozygous for low-bar and the other homozygous for ultra-bar, when the fly larvae developed at 16° C. The distance *CD* represents the phenotypic difference between the same genetically different stocks, when development takes place at 25° C. It is clear that the magnitude of effect of the genetic difference depends upon the environment. The drops from *A* to *C* and from *B* to *D* represent the effect of environmental difference upon phenotype for low-bar animals and ultra-bar animals respectively. Environment has an affect upon both stocks, but the magnitude of the effect varies with the genotype. It may also be seen that, at any one temperature, the role of genetic differences is emphasized, and conversely, for any one stock, the role of environmental differences is stressed.

The extension of Mendelian theory to quantitative characteristics.

Throughout the early period of enthusiastic research following the rediscovery of Mendel's laws, Galton's biometrical approach to problems of the inheritance of continuously varying characteristics had been pursued vigorously, notably by Pearson. Rather than finding mutual support in each other's work, the Mendelians and the biometricians came into acute conflict. It was difficult for the Mendelians to reconcile continuous variation with the type of qualitative, discrete difference, mediated by particulate genes, with which they had worked. The biometricians, on the other hand, supported the blending hypothesis, and were inclined to regard the Mendelian type of inheritance as an unimportant exception to the general rule. With justification, they pointed to the obvious importance of the smoothly continuous, quantitative characteristics, such as height, weight, intelligence, and so on. It was apparent, to the biometricians, at least, that the type of thing investigated by Mendelians—causing qualitative differences, and usually

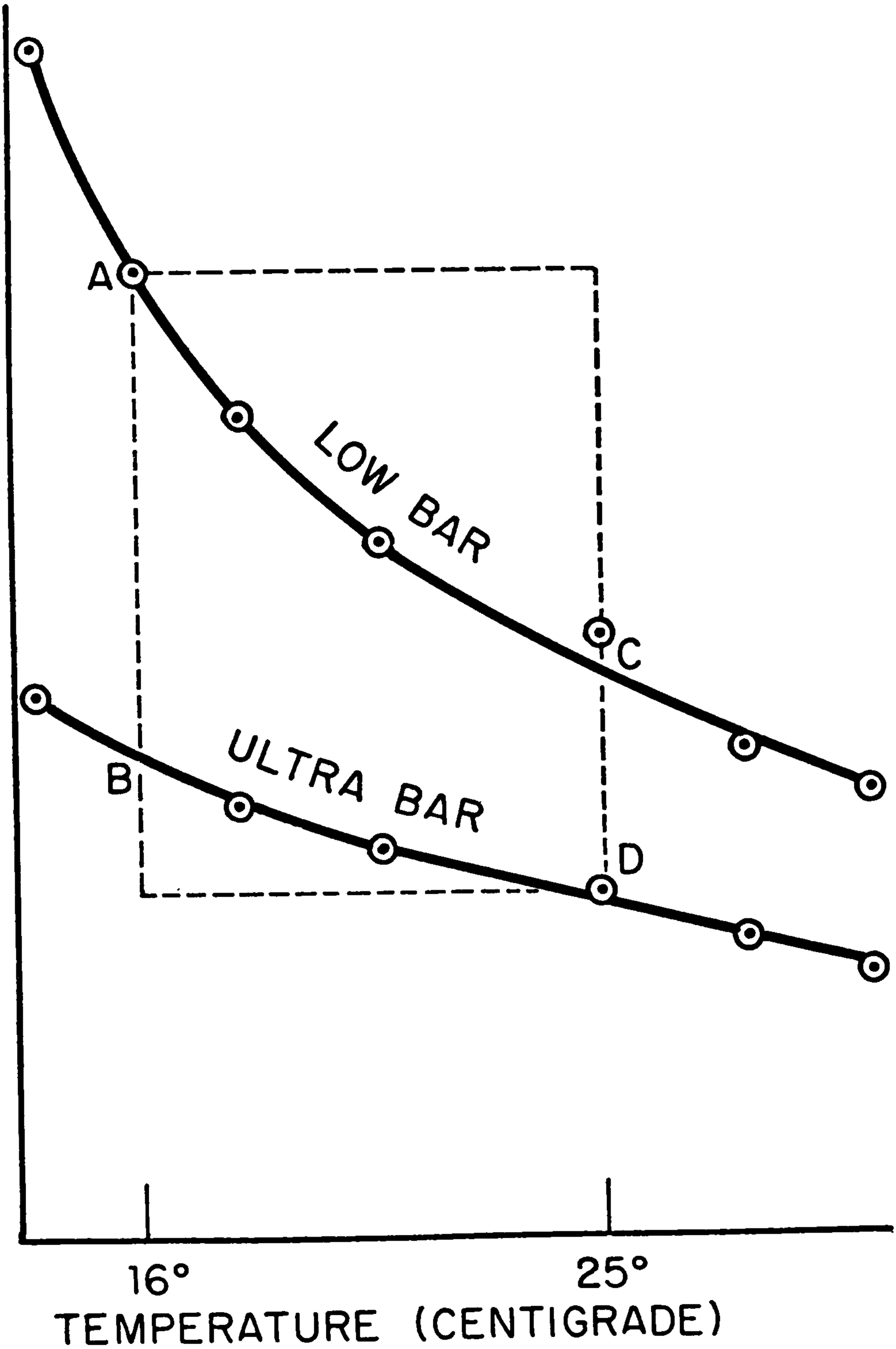

FIGURE 20. Hogben's plot of Krafka's data, showing gene-environment interaction in the production of eye facet number in *Drosophila*. (From L. Hogben, *Nature and Nurture*, Figure 2. Published in 1933 by George Allen & Unwin Ltd., and used with their permission.)

abnormalities—could not possibly account for such continuous distributions.

The multiple factor hypothesis. The groundwork for the resolution of this conflict had been provided, in fact, by Mendel himself, when he suggested that a certain characteristic might be due to two or three elements. General acceptance of this idea, however, was not forthcoming until the work of Nilsson-Ehle (1908) and of East and collaborators (East and Hayes, 1911; Emerson and East, 1913). These researchers showed that if one assumed a *number* of gene pairs, rather than just one pair, each of which exerted a small and cumulative effect upon the same character, and took into consideration also the effects of environment, the final outcome would be an apparently continuous distribution of the characteristic instead of dichotomous categories such as had been featured in the typical Mendelian researches. This was quite different from the blending hypothesis for, in this *multiple factor* hypothesis, the hereditary determiners were not presumed to vary continuously in nature from individual to individual, thus determining a gradation of the characteristic in the population. Rather, the genes were acknowledged to occur in discretely alternative conditions (typically two, sometimes more), but when a number of such discrete units bear upon the same character, the final outcome is a continuous distribution, just as the simultaneous tossing of a number of coins which can each have only one of two "states"—heads or tails—can have a large number of outcomes. Elaborate statistical development of this notion was provided by Fisher (1918) and by Wright (1921), and this work presented convincing demonstrations that the biometrical results in fact follow logically from this multiple factor extension of Mendel's theory. The blending hypothesis was gradually discarded, and as early as 1914 Bateson could remark, "The question is often asked whether there are not also in operation systems of descent quite other than those contemplated by the Mendelian rules . . . none have been demonstrated." [2]

An illustrative model of polygenic inheritance. To illustrate the multiple factor, or, as it is sometimes described, the *polygenic* [3] type of inheritance, we may consider the simple hypothetical example of Table 2. For the moment, we shall disregard any environmental contribution to variability of the trait. We assume that a characteristic is influenced by genes at two loci (in actual cases many more loci

[2] From K. Mather, "The Progress and Prospect of Biometrical Genetics" in L. C. Dunn, ed., *Genetics in the 20th Century*, p. 111. Copyright 1951 by The Macmillan Company, and used with their permission.

[3] There are certain distinctions made between the terms "multiple factor" and "polygenic" in some usages. For present purposes, they may be considered synonymous.

may be involved). Furthermore, we assume that two alleles, or alternative gene states, exist at each locus, i.e., *A* or *a* and *B* or *b*, and that the alleles act additively within a locus and also between loci. If each allele represented by a capital letter adds one unit to the trait, the various gene combinations will yield the phenotypic values shown in Table 2a. Now, suppose an *AABB* individual, with a score of 4, to be mated with an *aabb* individual, with a score of 0. All the offspring will be *AaBb*, and all will have scores of 2. Each such F_1 individual will be able to generate 4 kinds of gamete. The genetic combinations which could result from a mating of two F_1 individuals are shown in Table 2b, where the possible

TABLE 2a

PHENOTYPIC VALUES FOR VARIOUS GENOTYPES ASSUMING ADDITIVE GENE ACTION

(See text for explanation)

GENOTYPE	*AABB*	*AABb*	*AaBB*	*AAbb*	*AaBb*	*aaBB*	*Aabb*	*aaBb*	*aabb*
PHENOTYPIC VALUE	4	3	3	2	2	2	1	1	0

TABLE 2b

GENOTYPES OF OFFSPRING OF MATING OF TWO F_1 INDIVIDUALS
PHENOTYPIC VALUES SHOWN IN PARENTHESES

		GAMETES PRODUCIBLE BY FEMALE F_1 PARENT			
		AB	*Ab*	*aB*	*ab*
GAMETES PRODUCIBLE BY MALE F_1 PARENT	*AB*	*AABB*(4)	*AABb*(3)	*AaBB*(3)	*AaBb*(2)
	Ab	*AABb*(3)	*AAbb*(2)	*AaBb*(2)	*Aabb*(1)
	aB	*AaBB*(3)	*AaBb*(2)	*aaBB*(2)	*aaBb* (1)
	ab	*AaBb*(2)	*Aabb*(1)	*aaBb*(1)	*aabb*(0)

gametes are shown in the margins, and the entries in the body of the table show the genotypes which would result from the random combination of the gametes. It can easily be seen that variability will exist in this F_2 generation. Tables 2c and 2d show the results of *backcrossing* F_1 individuals to the *AABB* parent and to the *aabb* parent, respectively. Under the simple model we have been using, the parents and F_1 have no variability, while the backcross groups have some variability, but less than the F_2. With respect to averages, the F_1 is located halfway be-

tween the parents, the F_2 mean is at the same point, and the backcross means are intermediate between the F_1 value and that of the parent to which the backcross mating was made. Figure 21a compares the different groups with respect to these statistical features.

The very simple situation we have considered may be complicated

TABLE 2c

GENOTYPES OF OFFSPRING OF BACKCROSS OF F_1 TO *AABB* PARENT
PHENOTYPIC VALUES SHOWN IN PARENTHESES

	GAMETES PRODUCIBLE BY F_1 PARENT			
	AB	*Ab*	*aB*	*ab*
GAMETE PRODUCIBLE BY *AB* *AABB* PARENT	*AABB*(4)	*AABb*(3)	*AaBB*(3)	*AaBb*(2)

TABLE 2d

GENOTYPES OF OFFSPRING OF BACKCROSS OF F_1 TO *aabb* PARENT
PHENOTYPIC VALUES SHOWN IN PARENTHESES

	GAMETES PRODUCIBLE BY F_1 PARENT			
	AB	*Ab*	*aB*	*ab*
GAMETE PRODUCIBLE BY *aabb* PARENT — *ab*	*AaBb*(2)	*Aabb*(1)	*aaBb*(1)	*aabb*(0)

TABLE 2e

PHENOTYPIC VALUES FOR VARIOUS GENOTYPES WITH ADDITIVE GENE ACTION AT ONE LOCUS AND DOMINANCE AT THE OTHER LOCUS

GENOTYPE	*AABB*	*AABb*	*AaBB*	*AAbb*	*AaBb*	*aaBB*	*Aabb*	*aaBb*	*aabb*
PHENOTYPIC VALUE	4	3	4	2	3	2	2	1	0

in various ways. Let us consider, for example, what would result if the *B* alleles acted additively, while the *A* alleles displayed dominance. The phenotypic values for the possible genotypes would be as shown in Table 2e. The F_1 of the cross between *AABB* (4) and *aabb* (0) would, of course, be *AaBb*, as before, but under these conditions the phenotypic value of such individuals would be 3 instead of 2. The F_2 and backcross generations would also have the same genotypes as those shown in Table 2b for the first example, but different phenotypic values would result

for many of the genotypes. Figure 21b shows the distribution of the trait in the various generations for the new hypothetical case. The differences in statistical values—means, standard deviations, skewness—under the two conditions are apparent.

Another complicating feature, and one of paramount importance, is that environmental factors will also contribute to the variability of the

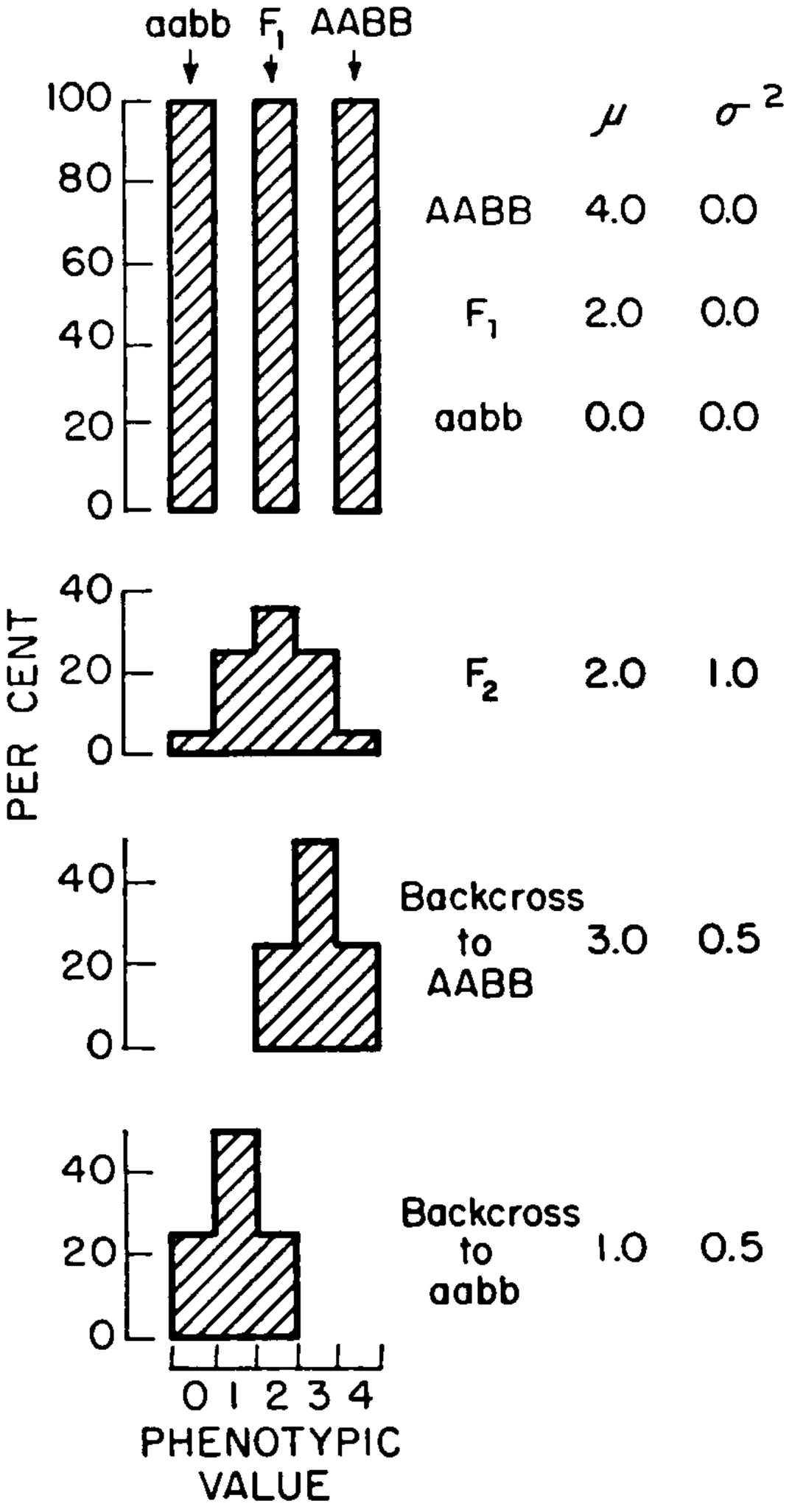

FIGURE 21a. Distributions of *AABB* and *aabb* parents and various derived generations, assuming additive gene action and negligible environmental influence.

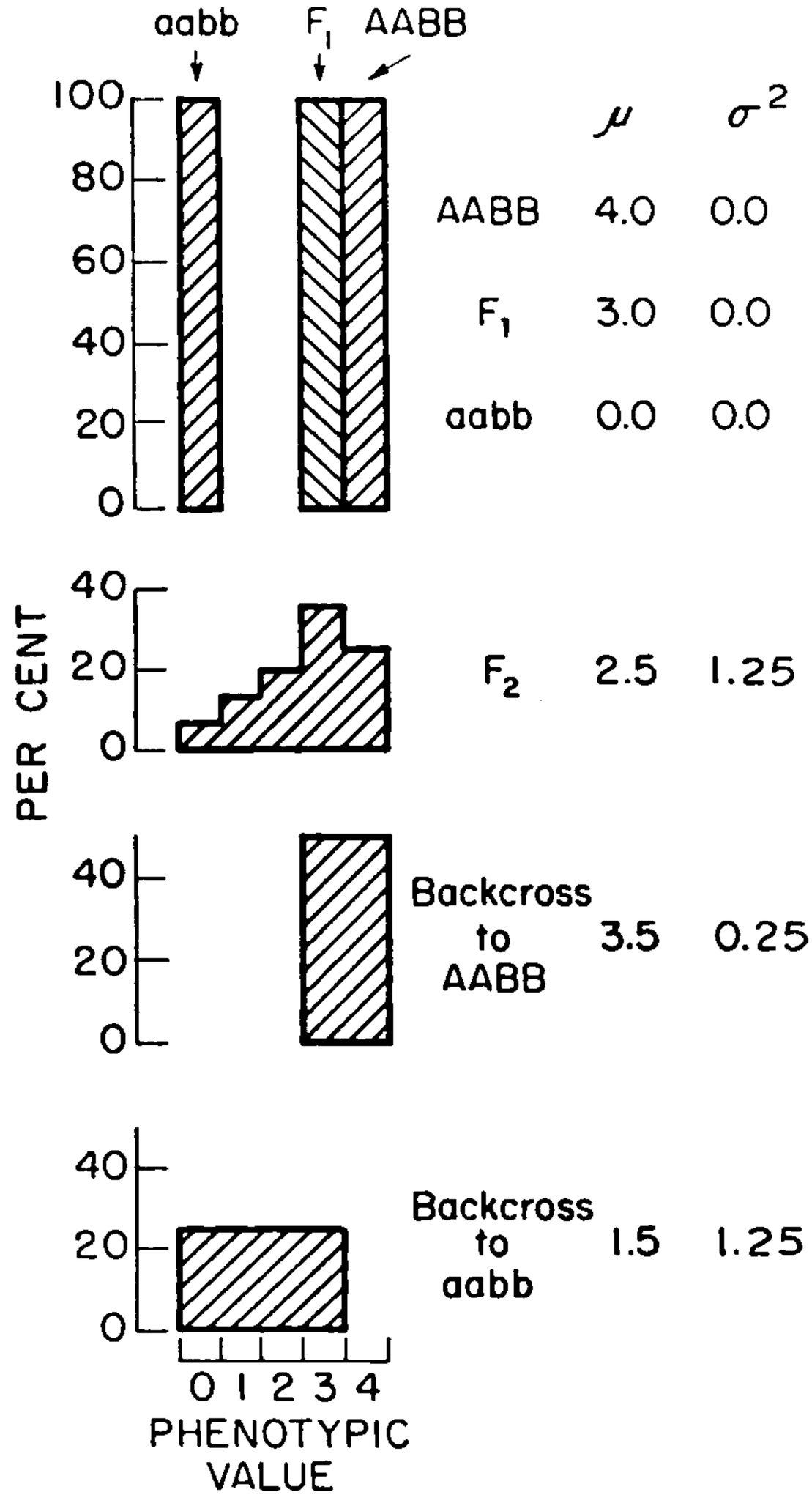

FIGURE 21b. Distribution of *AABB* and *aabb* parents and various derived generations, assuming additive gene action at one locus, and dominance at the other. Environmental influence is assumed to be negligible.

trait. When the environmental contributions are added to, or subtracted from, the value that we would expect on the basis of genotype alone, the result is a blurring of the boundaries between adjacent score values. The distribution of the trait may be less symmetrical, may encompass a greater range, and may in various other ways differ from the diagrammatic neatness of Figures 21a and 21b. The effect of a simple pattern of environmental action on the genotypic situation depicted in Table 2b is shown in Figure 21c. The latter was constructed by assuming a popula-

tion of ninety-six individuals, composed of six representatives of each genotype in Table 2b. It was further assumed that randomly acting environmental forces could affect the scores by ±2.0, ±1.5, ±1.0, ±0.5, or 0 units. Assigning these environmental effects randomly to the ninety-six individuals gave the outline frequency distribution of Figure 21c. For comparison, the shaded frequency distribution shows the result to be expected on genotypic value only. It is easily seen that the environmental effects have blurred the symmetry of the genotypic distribution.

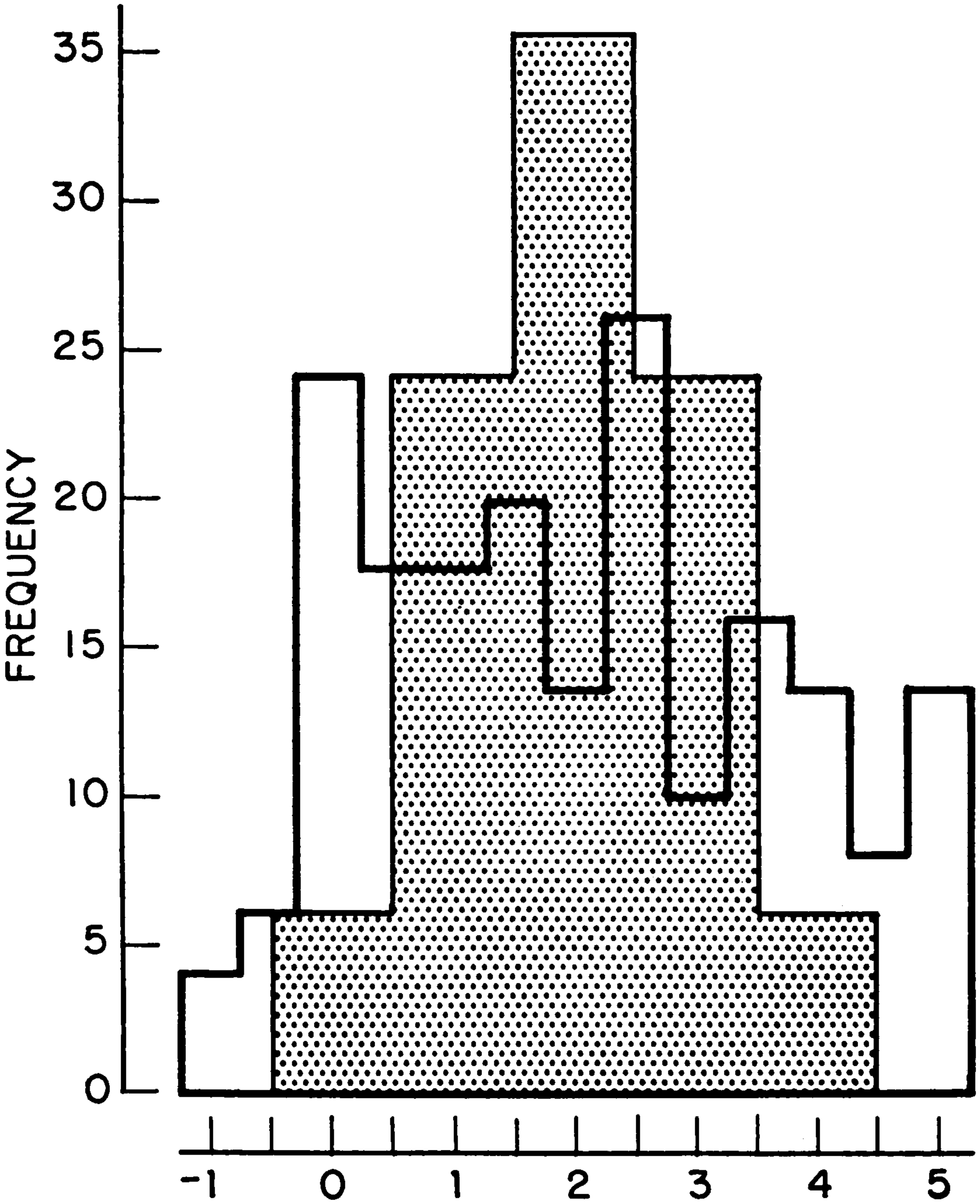

FIGURE 21C. Comparison of distributions of hypothetical F_2 population ignoring environmental effect (shaded distribution), and assuming random environmental effect described in text (outline distribution).

Other complications include the possibility of one locus contributing more to the trait than others, linkage of loci, and *epistasis*, or interaction between loci, in which the effect of an allele at one locus is dependent upon the nature of the alleles at some other locus.

As is readily apparent, the Mendelian procedures for investigating single major genes are inappropriate in analyses of polygenic inheritance. The theoretical developments by Fisher and Wright, and subsequently elaborated by them and by other workers, have made possible a statistical approach to the problem. By the analysis of various statistics, particularly correlations among relatives and variances of groups of different genetic constitution, it is possible to assess the relative contributions of genetic and environmental factors, and the nature of action (additive, dominant, epistatic, etc.) of the genes involved. (For recent statements of the statistical approach to quantitative genetics, see Falconer, 1960; Lerner, 1958; Mather, 1949; and Wright, 1952.)

MAJOR GENES, POLYGENES, AND BEHAVIOR. The success of the polygenic interpretation of quantitative characters is of crucial importance for behavioral genetics. A very large proportion of psychological phenotypes is of the quantitative variety, and with reference to Figure 20, must be regarded as being well over toward the right margin. At least on the level of description and analysis permitted by current knowledge, intelligence and personality characteristics, for example, must surely be resultants of the action of a large number of organ systems, and consequently will be products of the genes influencing the various contributing systems.

Searching for *the* gene of intelligence or temperament, then, is likely to be a fruitless task, although the various subcomponents of such phenotypes may quite possibly be subject to fairly simple genetic determination. This is not to say that single gene effects are never to be expected. Even in phenotypes well established as polygenically determined, it is sometimes found that a single gene pair may have potent influence. In the case of normal variation in human stature, for example, there is little doubt that a number of loci is involved. Yet a single gene is known which causes chondrodystrophic dwarfism (see Stern, 1960, p. 99). The same situation probably obtains in the case of intelligence, with several known conditions of feeble-mindedness (to be discussed in some detail later) providing examples of single genes overriding the polygenic system which determines the "normal" variation in intelligence.

DEVELOPMENT. Any particular trait chosen for study is susceptible to change during the life of the organism. Genetic and environmental forces begin their interaction at conception. The chemical

nature of the cytoplasm of the fertilized egg, and later the adequacy of the placental attachment, for example, play equally indispensable roles, and are just as much part of the environment as the postnatal food the organism eats and the air it breathes.

Analysis of the long-term development of a characteristic may provide insights into the operation of the hereditary and environmental forces which would be unattainable by study at only one selected developmental period.

Salient features of the developmental process have been summarized schematically by Waddington (1957) with reference to tissue development. In Figure 22 an "epigenetic landscape" is presented. The

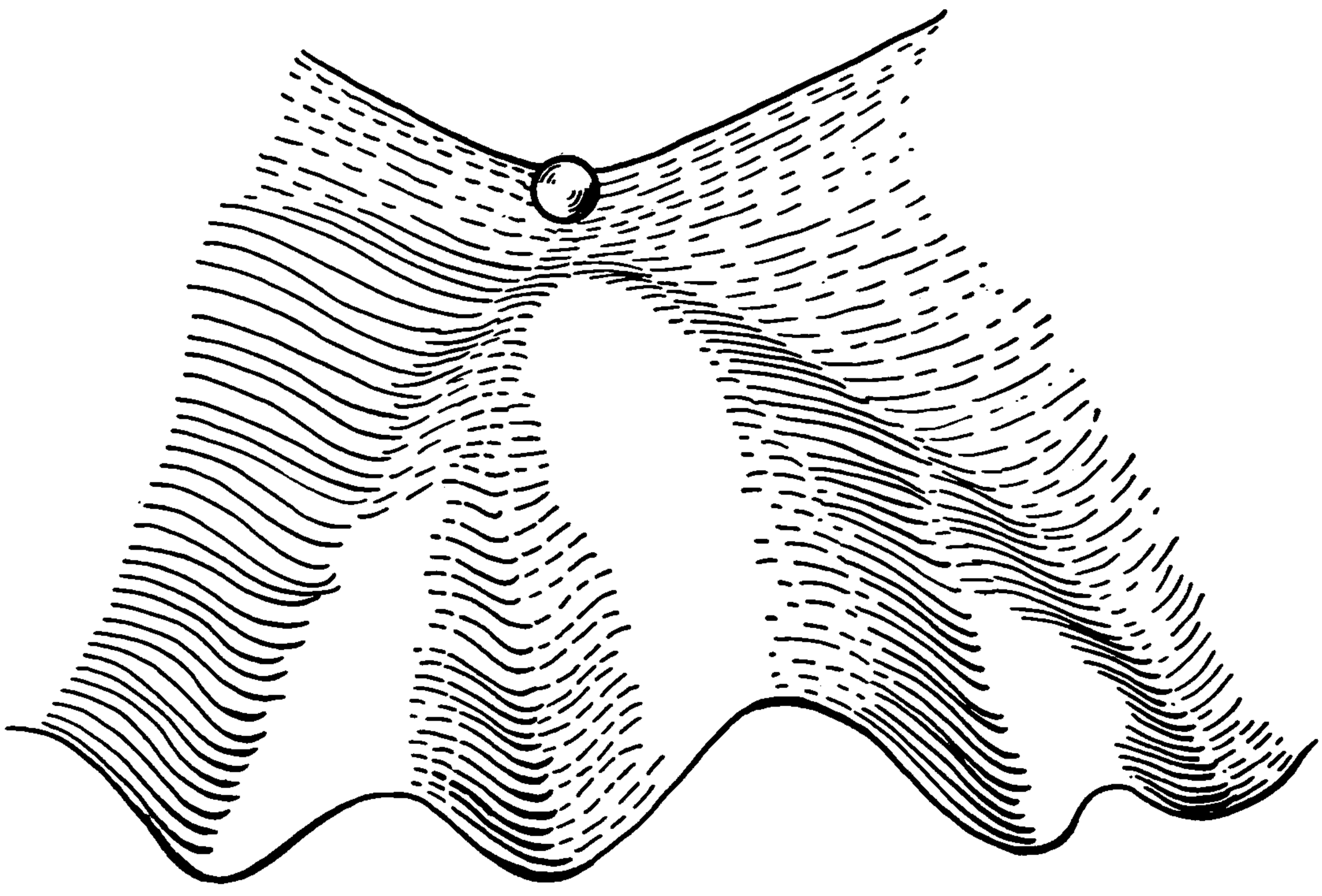

FIGURE 22. Waddington's "epigenetic landscape"—a hypothetical model describing gene-environment interaction in development. For interpretation, see text. (After C. H. Waddington, *The Strategy of the Genes*, Figure 4, p. 29. Published in 1957 by The Macmillan Co. and George Allen & Unwin Ltd., and used with their permission.)

background corresponds to conception and the foreground shows different phenotypic values at some point in development. The path of the ball, as it rolls downhill, represents the development of some particular part of the egg. The landscape is characterized by valleys and hills, and the particular contour of the landscape may be considered to be determined by genotype. Each individual of different genotype may thus have a different contour. Environmental forces act to move the ball laterally, and may thus switch development from one channel to another if applied at a critical juncture.

Concerning this model, Waddington says:

> Although the epigenetic landscape only provides a rough and ready picture of the developing embryo, and cannot be interpreted rigorously, it has certain merits for those who, like myself, find it comforting to have some mental picture, however vague, for what they are trying to think about. For instance, it makes one reflect that there may be regions at upper levels which are almost flat plateaus from which two or three different valleys lead off downwards. These, in fact, correspond to what we know as states of competence, in which embryonic tissues are in a condition in which they can be easily brought to develop in one or other of a number of alternative directions. Again, the model immediately suggests that one ought to consider the degree of canalisation of any particular path of development. Has the valley a flat bottom and gently sloping sides? If so, there will be only a rather slight tendency for a developmental trajectory, when displaced from the valley centre, to find its way back there again; the final adult character will be easily caused to vary by minor fluctuations in the conditions under which development occurs. On the other hand, if the valley bottom is very narrow and the sides steep, it will be more difficult to push the trajectory away from its normal course and it will quickly return there, unless indeed it has been pushed over the brow of a watershed either into another valley or on to a plateau which represents some aberrant conditions intermediate between one organ and another [4] [1957, pp. 30–1].

In addition to its heuristic value, Waddington's model provides an instructive summary, for with this schema in mind, it is difficult to forget the complexity of interactions, among genetic factors and between genetic and environmental factors, which lead to the development of a characteristic.

SUMMARY OF DEVELOPMENTS IN GENETICS. The foregoing account has been necessarily simplified, and vast areas of genetic theory and research have been ignored completely. The attempt has been made to present a reasonably contemporary picture of those aspects of genetic theory that appear to be most salient in relation to phenotypes of behavior.

In the short span of half a century, genetics has metamorphosed from a minor area on the outskirts of biological research to a central area of paramount importance to all the biological and related fields.

We may now turn to a consideration of the import of genetics for psychology. For convenience, the subject matter is divided into human research and research on experimental animals. Within each of these categories, the emphasis will be on the earlier research, from the turn of

[4] From C. H. Waddington, *The Strategy of the Genes*. Published by The Macmillan Company and George Allen & Unwin Ltd. and used by their permission.

the century until about 1930, with a briefer treatment of the subsequent work.

Human Research

Although most of the major advances in genetics resulted from research on plants and lower animals, many studies were made of the inheritance of a wide variety of characteristics in humans. Most of the characteristics studied were abnormalities of one kind or another, and in time, hereditary defects were identified in almost all organ systems (see Gates, 1946). Now, practically any organ or tissue, and particularly components of receptor, effector, and associative systems, may play a role in behavior, so that in a very real sense the discovery of the genetic basis for color-blindness, deaf-mutism, and certain forms of ataxia, for example, have been contributions to behavioral genetics. At present, however, we shall emphasize the developments in respect to those traits that fall within the customary definitions of intelligence, aptitude, mental deficiency, psychosis, neurosis, and personality.

Several general approaches to the problem may be distinguished: pedigree analyses and family histories, correlations among relatives, twin studies and foster-child studies. Some researchers have used combinations of these methods, but insofar as possible, we shall consider the developments within each technique separately.

Studies on Eminent and "Degenerate" Families

Eminent and royal families. Several extensive surveys followed Galton's procedure of investigating the accomplishments of relatives of notable people. Royal families provided particularly convenient source material, owing to the easy availability of their genealogical records (Woods, 1906; Gun, 1930a, 1930b). One disadvantage of this line of inquiry, however, was the sometimes dubious correspondence of legal and biological parentage. For example, Gun (1930b, p. 195) in discussing King James I, remarks, "his characteristics have but little resemblance to those of any of his ancestors. This fact was so obvious that from an early period doubts arose as to his parentage, some considering that he was the son of Mary by David Rizzio, while others contended that he was a changeling." Nevertheless, Gun was convinced that the family histories clearly showed the inheritance of certain traits. Thus the Stewarts were said to be characterized by tactless obstinacy, which "ran like a thread down the direct male line . . ." (1930b, p. 201). The Tudors, on the other hand, were thought to be hereditarily endowed with love of learning.

THE "JUKES" FAMILY. Dugdale, on the other hand, had concerned himself with the other end of the scale of social merit. As a member of the executive committee of the Prison Association of New York, Dugdale was named a committee of one to inspect county jails. In one county he was impressed by finding six of the prisoners to be related. Undertaking an intensive survey of this family, he was able to trace the lineage back to six sisters, to whom he gave the pseudonymous label "Jukes." One of the six had left the country and was not traceable. The remaining five had provided a most striking posterity, characterized by criminality, immorality, pauperism, and feeble-mindedness. Dugdale was primarily a social reformer, and was rather cautious in assigning the causal role in this pedigree of sordidity to nature or to nurture. That there was a social problem was clear enough. Dugdale (1877) estimated the cost to the state, in welfare relief, institutional care, etc., to exceed one million dollars over a seventy-five-year period. In 1911 some of Dugdale's original manuscripts were found, which gave the real name of the Jukes family. Estabrook (1916), acting upon this information, was able to trace the family history over the forty years ensuing since the first study. Estabrook summarized his study as follows:

> For the past 130 years they have increased from 5 sisters to a family which numbers 2,094 people, of whom 1,258 were living in 1915. One half of the Jukes were and are feeble-minded, mentally incapable of responding normally to the expectations of society, brought up under faulty environmental conditions which they consider normal, satisfied with the fulfillment of natural passions and desires, and with no ambition or ideals in life. The other half, perhaps normal mentally and emotionally, has become socially adequate or inadequate, depending on the chance of the individual reaching or failing to reach an environment which would mold and stimulate his inherited social traits. . . . Heredity, whether good or bad, has its complemental factor in environment. The two determine the behavior of the individual [1916, p. 85].

This conclusion was reasonably modest, assigning importance to both heredity and environment, but the findings of the study were enthusiastically endorsed by the more ardent eugenicists, and came to be regarded as proof of "morbid inheritance."

Various criticisms have been leveled at the Jukes study, and at a number of similar studies which followed. Perhaps the most cogent objection raised was that members of the families shared similar environments as well as a common lineage. Thus, while the more or less anecdotal evidence could be accepted as presenting a dismaying picture of human degradation, there was no means of determining the relative contributions of environment and heredity.

The "Kallikaks." In 1912 Goddard published an account of a family which, in his view, provided a clear-cut resolution of the problem of disentangling nature and nurture. This family consisted of two branches, each of which could be traced back to the same man. According to the report, "Martin Kallikak" (again, a pseudonym), while a soldier in the Revolutionary War, had an affair with a feeble-minded girl whom he met in a tavern. When the girl gave birth to a son, she named him "Martin Kallikak, Jr." After the war, Martin, Sr. returned home, married a girl of good family, and began the other branch of the family. Among 480 descendants of the illicit affair, a very "Jukes"-like picture was presented. Among the descendants of the marriage, almost all were normal, good members of society.

These results were taken to demonstrate that feeble-mindedness, which was regarded as the root of all the family difficulties, was inherited. A discussion of Mendelian principles was provided in the report, but judgment was reserved as to whether feeble-mindedness is a unit character, caused by a single gene.

The investigation of the Kallikaks was carried out largely by a field worker interviewing members of the family and people who knew members of the family. In discussing the general methodology, Goddard stated that although the evidence was occasionally ambiguous, and judgment had to be withheld, the field worker could usually decide easily the mentality of the persons interviewed. He also defended the assessment of the intellect of deceased individuals by interview of acquaintances, which was part of the procedures used in the study.

Criticism of family studies. As with the Jukes, the Kallikak findings were widely hailed in some circles, and vigorously criticized in others. In 1942 Goddard wrote a defense of the study, replying to some of the principal critics. To the criticism that assessment by a field worker was unreliable, Goddard replied that the field worker was well trained, and from familiarity with institutionalized cases, could adequately judge mental level. Furthermore, if doubt remained, a case was marked undetermined. To the objection that the evidence that Martin, Sr. was the father of Martin, Jr. was scant, and would not be acceptable in a court case, Goddard simply replied, "A strange statement. Courts have always accepted such evidence and still do. In this case there was not even a doubt" (1942, p. 575).

These answers were not very satisfying, and one of the strongest critics, Scheinfeld (1944), retorted in detail. Particularly, he remained unconvinced that the evidence for Martin, Jr.'s paternity, "a single short sentence, *unaccompanied by any documentation or supporting evidence*" (p. 262), could serve the purposes of a scientific investigation. If this particular point is not adequately demonstrated, of course, the

whole study becomes meaningless. Scheinfeld also remained unimpressed by the unsupported claim of accuracy in diagnosing the mental condition of the living, not to mention the dead, Kallikaks.

But even if the above could all be allowed, there remained another fundamental, and indeed a vitiating, problem. This concerns Goddard's failure to consider seriously the possibility that differences in environment might have been strong factors in creating at least some of the disparity between the two Kallikak branches. "This possibility he dismissed lightly by saying that the bad Kallikaks . . . are not open to this argument," and ". . . that we are dealing with a problem of true heredity no one can doubt" (Scheinfeld, 1944, p. 262). Such a major issue cannot be so easily disposed of, and, in fact, the impossibility of separating genetic and environmental effects renders the whole study pointless.

The objections raised to the studies of eminent and degraded families are telling, and by current standards we must judge that, whatever their worth as sociological documents, these studies merely serve to confuse the problem of determining the relative influence of nature and nurture.

Pedigree Studies on Mental Defects [5]

Aside from the large-scale efforts described above, there were numerous smaller pedigree studies involving the investigation of many families with relatively fewer individuals studied per family. In a review of the literature to 1912, Davenport (1912) was in fact able to present data on musical ability, artistic composition, literary composition, mechanical skill, calculating ability, memory, temperament, handwriting, pauperism, narcotism, criminality, and feeble-mindedness.

Most of these studies are susceptible to the same type of criticism as was applied to the Kallikaks, but in the subsequent research on one of the topics, feeble-mindedness, the pedigree approach achieved its most substantial success as applied to the problems of behavioral genetics.

One of the most influential of the early publications was that of Tredgold (1908). In examining the family histories of some 200 cases of "every grade and variety of amentia," he concluded that there were two basic causal factors: intrinsic (hereditary) and extrinsic (environmental), and he regarded the former to be of "immense importance," accounting for some 80 per cent of the cases. The roles of age of parents and of intoxication at the time of conception were specifically examined and judged to be of trivial importance. Other conditions, however, were thought to be very effective in bringing about deterioration in the

[5] The terms "mental defect," "feeble-mindedness," and "amentia" are employed interchangeably in this discussion.

germ cells. After discussing the Mendelian hypothesis that gametes are unaffected by environment, Tredgold (1908, p. 36) rejected it as being inconsistent with the experiences of physicians.

> With regard to the causation of amentia, I believe that there are certain diseases which bring about a deterioration of the germ plasm. The chief of these are alcoholism and consumption. . . . In consequence, there results a pathological change in that part of the offspring which is at once the most elaborate, the most vulnerable, and of most recent development—namely, the cerebral cortex. This change consists in a diminished control of the higher, and increased excitability of the lower, centres, and is manifested clinically as neurasthenia, hysteria, migraine, and the milder forms of epilepsy. We may say that a neuropath has been created. Should the adverse environment continue, or should such a person marry one similarly tainted, then the nervous instability becomes accentuated in the following generation, and insanity, the graver forms of epilepsy, and early dementia, make their appearance [1908, p. 37].

Thus the various traits mentioned, ranging from neuroses through insanity to profound mental deficiency, were regarded to be all the outcome of successive stages in a hereditary deterioration set in action by some environmental factor.

Two years after his study of the Kallikaks was published, Goddard (1914) presented an extensive collection of pedigrees of mentally defective patients at the Vineland Training School. The Binet-Simon Measuring Scale of Intelligence was administered to a number of the inmates, but the remainder of the pedigrees were primarily studied by field-worker interviews. After studying the pedigrees, Goddard concluded that, of 327 families investigated, the mental defectiveness was inherited in 164, and probably inherited in another 34 cases. The remaining cases were described as due to accident (57), having no determined cause (8), unclassified (27) and neuropathic (37). The latter group was composed of families in which there was little or no history of feeble-mindedness per se (apart from the institutionalized patient), but many other conditions, such as alcoholism, paralysis, suicidal tendency, nervousness, etc., were prevalent. For Tredgold this was the typical picture in inherited mental deficiency. Goddard thought that the feeble-mindedness in these families was probably *not* transmissible, and suggested that some might be due to adverse influences on the mother's "power of nutrition."

In what Goddard called the hereditary cases, he concluded:

> Since our figures agree so closely with Mendelian expectation and since there are few if any cases where the Mendelian formula does not fit the facts, the hypothesis seems to stand: viz. normal-mindedness is, or at least behaves like, a unit character; is dominant and is transmitted in accordance with the Mendelian law of inheritance.

> The writer confesses to being one of those psychologists who find it hard to accept the idea that the intelligence even *acts like a unit character*. But there seems to be no way to escape the conclusion from these figures [1914, p. 556].

In the ensuing years, a number of further pedigree studies were published. Gates reviewed the evidence to 1933, and concluded:

> . . . it may be stated that feeble-mindedness is generally of the inherited, not the induced, type; and that the inheritance is generally recessive. Most often a single recessive gene appears to be involved; but, as with other abnormalities, occasionally the inheritance is of a different type [1933, p. 265].

By this time the Mendelian principles dominated the conceptual approach to the problem, but were still not universally accepted. Tredgold (1937), for example, in a revision of his earlier text, considered some of the evidence that feeble-mindedness was a recessive condition, and acknowledged that this might be the case in certain special types of defect, but maintained that for mental defect in general, it had not been demonstrated.

We also find evidence of the still-lingering Mendelian-biometrician dispute in a 1930 lecture by Pearson (published in 1931):

> Attempts have been made on very inadequate data, most inadequately handled, to fit insanity and feeble-mindedness into the Mendelian theory. Of these attempts I shall hardly find time to say anything in this lecture; in my opinion they fail hopelessly, for they overlook essentially the fact that insanity and feeble-mindedness are far from being simple unit characters. The boundary between sanity and insanity is a perfectly indefinite one. . . . There is no mental test which will separate the normal from the feeble-minded child, the measurements of intelligence show no breaks from one end of the scale to the other [1931, p. 366].

To support the last point, Pearson presented his analysis of Jaederholm's data, which showed that when intelligence test scores of normal children and of children classed as mentally deficient were superimposed, the result was a smooth continuous distribution. There was no gap, no separation into two discrete groups. Pearson saw the problem as even more complicated, for not only was it impossible to separate clearly the feeble-minded from the normally intelligent, but feeble-mindedness was also confounded with other defects. In a conclusion reminiscent of Tredgold, Pearson stated:

> . . . in feeble-minded stocks mental defect is interchangeable with imbecility, insanity, alcoholism, and a whole series of mental (and often physical) anomalies [1931, p. 379].

Here, indeed, is a serious problem. If the different phenotypes cannot be adequately distinguished, how can a pedigree study possibly yield any valuable result?

At about the same time, Crew (1932) reviewed the status of work on the genetics of mental defect, and he, as did Pearson, called attention to the continuous distribution of intelligence.

Pearson had concluded that the Mendelian approach was doomed to failure because of the absence of a clear dichotomy. Crew did not question the applicability of Mendelian theory, but emphasized that there were probably many different genetic types of mental defect, and that genetic analysis would need to consider the various types separately. Furthermore, he stressed that the various types need not be subject to the same type of genetic action—some might be dominant, some recessive, some due to multiple factors.

As a matter of fact, there had been an increasing attention to this possibility with a growing tendency to investigate distinct syndromes, and, especially in those conditions which involved gross nervous system damage, there were encouragingly good "Mendelian" results. (See Gates, 1946; Böök, 1953.)

PHENYLKETONURIA. In 1934 Penrose published an essay the purpose of which was to examine the available methods for the study of human heredity. To illustrate a principle concerning the relatively high frequency of cousin marriages among parents of offspring showing rare recessive conditions, he presented some data which he had collected on an "unspecified type" of mental defect. In the same year Fölling announced (1934) that the urine of some feeble-minded persons contained an abnormally large amount of phenylpyruvic acid. Penrose (1935a) thereupon tested 500 feeble-minded patients and found one case in which phenylpyruvic acid was excreted. This patient had a brother who was also feeble-minded, although not institutionalized. The biochemical peculiarity was also found in this brother, but not in two normal sibs or the parents. Returning to the first family, Penrose (1935b) then tested the urine of the one surviving feeble-minded individual, and found phenylpyruvic acid. By 1937 Jervis (1937) was able to confirm the recessive nature of the condition, as had been suggested by Penrose's data, and numerous studies have since explored one aspect or another of the condition, known variously as Fölling's disease, phenylketonuria, or phenylpyruvic oligophrenia. A number of hypotheses have been put forward to account for the excessive phenylpyruvic acid in the urine and some other related biochemical anomalies (Jervis, 1954). Jervis (1947, 1953) has provided strong evidence that the basic biochemical deficiency is a reduction in the ability to convert phenylala-

nine into tyrosine, due to a loss or deficiency of the enzyme involved in that reaction. The reaction has been localized in the liver (Udenfriend and Cooper, 1952), and the relationship of the reaction to other biochemical substances has been traced (see Neel and Schull, 1954; Wagner and Mitchell, 1955). Recently, there have been several clinical investigations into the effect of reducing the phenylalanine content of the diet of phenylpyruvics (e.g., Bickel, Gerrard, and Hickmans, 1954). These studies have shown a reduction in biochemical defect while the special diet is given, and a recurrence when an ordinary diet is reintroduced. Observations on general behavior and tests of mental age give promising indications that an improvement in intelligence also accompanies the special diet.

Another recent contribution to the understanding of phenylketonuria has been the demonstration (Hsia *et al.*, 1956) that persons of normal intelligence, who must nevertheless be heterozygous for the gene causing phenylketonuria (e.g., parents of an affected child), are distinguishable from homozygotic normals by the chemical constitution of certain body fluids. Apart from practical applications in genetic counselling, this finding illustrates a most important principle, namely, that the mode of gene action may differ at different levels of analysis. At the level of mental defect, phenylketonuria provides a clear example of a recessive condition, yet at a biochemical level, the mode of gene action must be at least partial dominance, for the heterozygotes are discriminable from the normals.

Thus, in phenylketonuria, we find the most complete genetic analysis of a human behavioral phenotype: the mode of gene action is known on the "Mendelian" level (i.e., homozygous recessives show the trait), heterozygotes are identifiable biochemically, the gene action is known to affect an enzyme involved in a specific reaction, the organ in which the crucial reaction occurs has been identified, the relationship to other biochemical processes has been described, and an environmental alteration which modifies the trait has been discovered, offering a reasonable hope that a full cure may some day be found.

In 1954 a review article (Jervis, 1954) listed 312 identified cases. In terms of the reference defective populations, this represents about six-tenths of one per cent.

OTHER TYPES OF MENTAL DEFECT. The great progress in analyzing phenylketonuria has inspired vigorous examination of other varieties of feeble-mindedness, and, while none other has as yet been as well described, a substantial amount of information has been acquired (see Böök, 1953). Jervis (1952), in a review of the literature, discussed some twenty types of mental deficiency concerning which some genetic infor-

mation is available. Some conditions appear to be dominant, some recessive, and for others various irregularities are reported. This same author has also shown that the various syndromes can be classified according to the tissue affected (i.e., cutaneous or osseous) or the type of biochemical deficiency involved (metabolism of lipids, amino acids, carbohydrates, or pigments).

There remains, apart from these delineated conditions, a large number of "undifferentiated" mental defectives. It is likely that refined searches on the biochemical level might identify other unitary conditions with a simple pattern of inheritance. Other conditions (as in the case of Mongolism, to be discussed later) might prove to be due to quite unusual genetic irregularities. There will probably remain a "hereditary" group, below the arbitrary division point in the distribution of intelligence, which resists analysis by the pedigree method. These individuals undoubtedly represent the lower tail of the distribution generated by assortment of the polygenes underlying "normal" intelligence, and should no more be considered abnormal than those whose intelligences are an equal distance above the mean.

Finally, we must not disregard the cases of environmental origin. Unquestionably, a variety of environmental factors acting either postnatally (such as severe head injuries), or prenatally (such as infection of the mother by rubella during pregnancy) can eventuate in mental defect. Advancement in understanding genetic factors in mental defect, as well as in therapeutics and preventive measures, depends upon the study of the "environmental" as well as the "genetic" conditions.

From the vantage point of current knowledge, we may judge that Tredgold was correct in concluding that some cases of mental deficiency were attributable to hereditary factors, and others due principally to environmental factors, but his ideas about the origin of the germ-plasm damage and progressive degeneration must be judged wrong. Goddard was right in that some mental deficiency was a single-locus recessive effect, but wrong in overgeneralizing to all feeble-mindedness, and incorrect in concluding that normal intelligence was necessarily due to a single locus if defective intelligence was. Pearson had a major and valid point in the lack of a discrete gap between normal and abnormal, but was too willing to judge therefrom that Mendelian analysis could not succeed in any degree. Gates assessed well the evidence on hand, but was overoptimistic concerning the likelihood of finding all cases of mental deficiency to be of the Mendelian variety.

Thus, in this brief account of the development of theories concerning inheritance of mental defect, we may see that the progress was not made by a single penetrating discovery or pronouncement, but rather proceeded by increments, with the contributors at various stages frequently being both correct and incorrect in varying degrees.

Correlations Between Relatives

The biometricians concentrated their investigations on quantitatively varying characteristics, and developed and employed the correlation technique for use in their studies. The chief spokesman for this approach was Pearson, who assumed that, since Galton's work, the fact of inheritance of mental characteristics could not be denied. The next step was to determine if heredity is as potent in determining mental as in determining physical characters. Arguing the impossibility of comparing adult moral and mental traits with those of children, Pearson settled upon the measurement of correlation between sibling pairs. Through an appeal in a professional journal, Pearson got the cooperation of a number of teachers in supplying measurements or ratings of sibling pairs with respect to certain physical characteristics—health, eye color, cephalic index, etc., and with respect to certain "psychical" characters—vivacity, assertiveness, introspection, popularity, conscientiousness, temper, and ability. The average correlation for the physical traits was slightly in excess of .50 and the same was true for the psychical traits.

> We are forced absolutely to the conclusion that the degree of resemblance of the physical and mental characters in children is one and the same. It has been suggested that this resemblance in the psychical characters is compounded of two factors, inheritance on the one hand and training or environment on the other. If so, you must admit that inheritance and environment make up the resemblance in the physical characters. Now these two sorts of resemblance being of the same intensity, either the environmental influence is the same in both cases, or it is not. If it is the same, we are forced to the conclusion that it is insensible, for it cannot influence eye colour. If it is not the same, then it would be a most marvellous thing, that with varying degrees of inheritance, some mysterious force always modifies the extent of home influence, until the resemblance of brothers or sisters is brought sensibly up to the same intensity! Occam's razor will enable us at once to cut off such a theory. We are forced, I think literally forced, to the general conclusion that the physical and psychical characters in man are inherited within broad lines in the same manner, and with the same intensity [Pearson, 1904, pp. 155–6].

The logic of this procedure seemed at the time to be clear and straightforward. The correlations between siblings on various mental traits could be compared to the empirical value for physical traits (presumed to be highly hereditary), and with each other, and the relative degrees of hereditary control of the various mental traits could thereby be determined. It was with essentially this orientation that several studies on intelligence were conducted. These represented an improvement over Pearson, in that objective measures of performance were obtained rather than ratings. Starch (1917), for example, measured the

resemblance of siblings on a variety of "mental traits," some of which were presumably directly affected by school work (e.g., reading ability, vocabulary, spelling, arithmethical ability) and some presumably not so affected (e.g., canceling of "A's" in a page, rate of tapping). Large differences in correlation values were obtained for the different tests, but the values for traits supposed to be influenced by direct tuition were not, on the average, higher than those for traits less subject to training. This result was interpreted as support for the hereditary interpretation, "since the resemblance is no greater in those traits which are more directly affected by environment" (Starch, 1917, p. 237). Thorndike likewise used Pearson's value of .50 as a benchmark. Employing data obtained from Institute of Educational Research Tests, applied to ninth through twelfth grade pupils, he concluded that the sibling correlation in the whole population would be about .60.

> If we may accept Pearson's results for the resemblance of siblings in eye color, hair color, and cephalic index (.52, .55, and .49), and regard .52 ± .016 as the resemblance in traits entirely free from environmental influence, we may infer that *the influence upon intelligence of such similarity in environment as is caused by being siblings two to four years apart in age in an American family today is to raise the correlation from .52 to .60* [Thorndike, 1928, pp. 52–3].

Fisher's classic 1918 paper, and various contributions following it, provided a theoretical basis for Pearson's empirically obtained value, for it was shown that, under certain conditions, the assortment of Mendelian factors would generate a value of .50 for parent-offspring as well as for sibling correlations. This would occur when (1) the genes involved acted additively (i.e., heterozygotes were intermediate to homozygotes), (2) mating between parents was random with respect to the trait, and (3) environment had no effect upon the trait.

A substantial number of correlations was subsequently published, and while there were differences from study to study, the values reported tended to cluster around .50. Jones (1928), for example, presented parent-child and sibling correlations of .51 and .49, respectively, on Army Alpha and Stanford-Binet test scores. Roberts (1941) obtained a sibling correlation of .53 in intelligence measures.

It is very tempting to interpret these findings as indicating that the genetic mechanism underlying intelligence is that specified in the assumptions by which the theoretical value of .50 was obtained. Indeed, this is one possible interpretation, but as we shall see, it cannot be rigorously shown to be the correct one.

SOME DIFFICULTIES OF THE CORRELATIONAL APPROACH IN THE STUDY OF HUMANS. Consider first the assumption of additive gene action. If in fact this assumption does not hold, the predicted correlation

is changed, and the amount of change depends upon the degree of dominance, the magnitude of epistatic effects, and the relative frequencies of the alternative alleles in the population. If dominance is complete, and the alleles are equally frequent, for example, and the other assumptions are valid, the predicted parent-offspring correlation (r_{PO}) is .333 and the sibling correlation (r_{OO}) is .416 (see Li, 1955).

Next, consider the assumption of random mating. This demands that the correlation between parents be zero, which has been definitely shown to be incorrect with respect to intelligence. Conrad and Jones (1940) found a husband-wife correlation of .52 with respect to Army Alpha scores, and Willoughby (1928), who administered eleven different tests, found husband-wife correlations ranging from .20 to .65. This positive association between parents will tend to raise both r_{PO} and r_{OO}, and the amount of increment will depend upon the magnitude of the parental correlation.

Finally, we may examine the assumption that environment has no effect upon the trait. Although the empirical evidence on the effects of enriched or impoverished environments is rather ambiguous (see Thompson, 1954, p. 220) it would be rash to argue dogmatically that the assumption is valid for the kind of characteristic we have been considering. If the effective environmental factors are distributed randomly, the correlation will be reduced to an extent dependent upon the magnitude of the environmental effect. But even this assumption that effective environmental factors are randomly distributed throughout the population is an improbable one. From general considerations it seems likely that environmental factors are more similar within families than between families. Furthermore, on objective grounds, it has been found repeatedly that a substantial correlation exists between children's intelligence and various economic and cultural attributes of the home. Burks (1928a) found a correlation of .48 between children's IQ and a rating of the home cultural level. Leahy (1935) found correlations of .51, .52, and .45 between the IQ of the child and a cultural index, an economic index, and the father's occupational level, respectively.

It has been argued that such values demonstrate the efficacy of the environment in determining intellectual level. It is just as defensible to argue that the parents with the better inherent intelligence provide better environments for their children.

Such a correlation between genotype and environment, if it exists, has rather complicated effects upon the correlations among relatives, depending upon the proportion of additively acting genes and the degree of genotype-environment correlation. Generally, r_{PO} and r_{OO} will be raised.

An additional possible complication was pointed out by Gray and Moshinsky (1932–3), who found sister-sister correlations to be higher

than either brother-brother or brother-sister correlations. They suggested that this difference might be attributed to a greater uniformity of early environments of female sibs than of mixed pairs or of pairs of brothers.

There are further pitfalls in the correlational approach, which are not directly related to genetic theory. We may illustrate some of these by again referring to the literature on intelligence.

Thorndike (1928) gave clear expression to one of the difficulties—biased sampling—in his study. In this project, two forms of a test battery were administered, one year apart, to brothers and sisters in school. There was a tendency to eliminate the poorer students from the sample, because data could only be used from those who remained in school during the one-year interval. Any such elimination of extremes will, of course, have an effect on the correlation coefficient by virtue of restriction of the range of scores.

Another biasing effect was due to the fact that only children in high schools were measured, and only the intellectually abler students proceeded that far in their education.

Furthermore, since dull children could fail promotion, and bright children could be accelerated, there would be a tendency for brighter younger brothers and duller older brothers to be included in the survey. This factor would tend to reduce within-family resemblance.

Jones (1928) overcame some of these sampling problems by administering tests to whole families, rather than just to pupils in school. Alert to the possibility that what was found in one population might not apply to another population, Jones's concern was to obtain a representative and homogeneous New England rural population. But selection of a sample of restricted range may, in general, be expected to have a depressing effect on a correlation coefficient. Cattell and Willson (1938) therefore attempted to get a broad sample covering the total range of intelligence. The mid-parent–mid-child correlation thus obtained was .70.

The correlational technique poses other vexing problems of a statistical nature (see Burks, 1928c), and corrections are frequently required. Many of the coefficients discussed earlier were, in fact, corrected for one reason or another. The study of Cattell and Willson provides an illustration of the types of correction used and of their effect upon the final reported value. Beginning with the raw correlation of .70, corrections were made to compensate for age differences, lack of normality of the distribution, range, and attenuation. The final correlation value reported was .91. Obviously, the adequacy of the corrections made in the various studies will have an important effect on their comparability.

The value of .91 is greatly in excess of the general trend of the previously cited results. Cattell and Willson provided other corrected correlations, as follows: one parent–one child, .84; pairs of siblings, .77;

husband-wife, .81. These values are all greater than those previously obtained, and the authors regard them to be nearer to the "correct" values, because of the greater sampling range in their study, and because more adequate corrections were made. Thorndike (1944) tested 409 pairs of brothers at Columbia College, and found a raw correlation of .41. When this value was corrected to estimate correlation in the general population, a value of .73 was obtained. The data of the 1928 study were also re-examined, and a sibling correlation of .69 was obtained. Thorndike concluded, in agreement with Cattell and Willson, that the true value of family correlations is considerably higher than was previously thought to be the case.

The greater part of the research employing correlations of relatives has been directed toward intelligence, but a number of specific apitudes and personality traits have also been investigated. As examples, we may note the studies of May and Hartshorne (1928) and of Crook (1937). May and Hartshorne studied cheating and deception by use of a number of task situations where deception could be detected. Correlations between siblings ranging from .21 to .70 were obtained. Rejecting common environment as the sole factor in determining the similarity in tendency to cheat, the authors concluded that genetic factors are about as important in determining tendency to deceive as they are in determining intelligence.

Crook performed a study on certain personality characteristics, and, drawing his conclusions from his own and previous work, concluded that, with respect to traits of neuroticism, introversion, dominance, and self-sufficiency, the best estimate of parent-offspring correlation was .16, and of sibling correlation, .18. These values were taken to indicate the relatively lesser importance of genotype in determining individual differences in these personality traits than in intelligence.

From the above discussion, it is clear that the interpretation of correlations among relatives is not a simple matter. If an adequate sample is available, and random mating within the population assured, or the extent of husband-wife correlation known; if environmental factors are known to be random, or their relationship to genotype known; and if the test itself has adequate reliability—then empirically obtained correlation coefficients could be used to reach conclusions concerning the nature of the gene action.

Theoretically, these matters are all capable of accomplishment. Practically, however, there are formidable difficulties. One fundamental problem may be singled out for special mention: it is practically impossible to list exhaustively, let alone measure adequately, *all* the *relevant* environmental variables.

As it stands, then, a large number of different conclusions may be deduced from the same obtained correlation values.

Twin Studies

DEVELOPMENT OF TWIN-STUDY LOGIC. Another principal technique which has been utilized in the study of the inheritance of mental characteristics in man has been the investigation of twins, a procedure first introduced by Galton.

The first major study to follow Galton's example was that of Thorndike (1905), who published a paper entitled "Measurements of Twins," several years after taking his doctorate under J. McK. Cattell.

A fairly lengthy discussion of the nature of twinning was presented, and specific attention was given to the suggestion that there are two kinds of twins; those arising from the same egg and always of the same sex ("duplicate twins"), and those arising from separate eggs and either like-sexed or of different sexes ("fraternal twins"). After assessing the evidence, Thorndike rejected this hypothesis, and proposed that all twins are of the same kind, but on a continuous distribution of degree of resemblance. Therefore, in handling the data of this investigation, all the twins were considered together. Fifty pairs of twins were located from the New York public schools, and they were tested on efficiency in arithmetic computations, naming word opposites, finding misspelled words, and crossing out letters. The possibility of assigning quantitative scores to each individual represented an advance over Galton's original work, where anecdotal evidence was relied upon. The logic of this investigation, however, was essentially the same as Galton's; if environment is important to the traits measured, twins should become more alike the longer they are exposed to the same environment. Therefore the correlation between twin pairs should be higher for twins twelve to fifteen years old than for twins nine to twelve years old. Furthermore, the less the difference between the correlation of sibling pairs and the correlation of twin pairs, the greater the effect of environment. Finally, nurture is important to the degree that the correlation between twins in respect to traits judged "subject to home training" exceeds that for traits not so easily subject to training. The results showed the twins to be more similar to each other than were siblings, the older twins being actually somewhat less similar rather than more similar than the younger, and the correlations for traits subject to training were no greater than for traits not susceptible to training. These results

> . . . are easily, simply and completely explained by one simple hypothesis: namely, that the natures of the germ cells—the conditions of conception—cause whatever similarities and differences exist in the original natures of men, that these conditions influence body and mind equally, and that in life the differences in modification of body and mind produced by such differences as obtained between the environ-

ments of present-day New York City public school children are slight . . . [Thorndike, 1905, p. 9].

Thorndike cautioned, however, against confusing

> . . . two totally different things: (1) the power of the environment, —for instance, of schools, laws, books and social ideals,—to produce differences in the relative achievements of men, and (2) the power of the environment to produce differences in absolute achievement. It has been shown that the relative differences in certain mental traits which were found in these one hundred children are due almost entirely to differences in ancestry, not in training; but this does not in the least deny that better methods of training might improve all their achievements fifty per cent, or that the absence of training, say in spelling and arithmetic, might decrease the corresponding achievements to zero [1905, p. 11].

Twin study was then largely neglected for about twenty years, following which a spate of studies was published within a short period.

Merriman, by 1924, was able to employ more refined test procedures than had previously been used, and administered the Stanford-Binet, Army Beta, and National Intelligence Test, in addition to obtaining teachers' estimates of the intellectual capacity of the subjects. Using the same type of comparison as Thorndike, Merriman found that the correlations between twin pairs ten to sixteen years of age were not greater than those between twin pairs five to nine years of age. Moreover, Merriman reopened the question of whether there were two types of twins. After reviewing current biological evidence, and relevant aspects of his own research, he concluded, Thorndike to the contrary notwithstanding, that there are two classes. fraternal and duplicate. From this, a new type of comparison was suggested:

> The fraternal, being of the two-egg origin, should show no greater resemblance than ordinary siblings, since each individual of the pair develops from a wholly independent arrangement of the factors for heredity in the germ cells. . . . The duplicate being of the one-egg origin, should show a very much higher degree of resemblance than the fraternal because each member of the pair develops from substantially the same arrangement of the factors for heredity in the germ cells [Merriman, 1924, p. 3].

Now, a real difficulty was that, while all unlike-sexed twins could be clearly identified as fraternal, some like-sexed twins would be fraternal and some duplicate. But, lacking a clear way of distinguishing the two kinds of like-sexed twins, Merriman accepted the error that was entailed, and compared the like-sexed pairs, consisting of fraternal and duplicate cases, with the unlike-sexed pairs, composed solely of frater-

nals. The correlations for like-sexed pairs were in every case higher than for unlike-sexed pairs, and the latter quite reasonably approximated the value of .50 which Pearson had found to be characteristic of sibling correlations. Clearly, greater intellectual similarity accompanied greater genetic similarity. Indeed, the correlations obtained for like-sexed twins were in the neighborhood of .90, leaving apparently little variability to be explained by environmental differences.

Lauterbach's (1925) study followed almost immediately. The results on a number of intelligence tests confirmed Merriman's findings nicely, in that the correlations between older and younger twins did not differ, and the correlations between like-sexed twins exceeded those between unlike-sexed twins. Wingfield (1928) contributed more evidence confirming Merriman and Lauterbach, and went the further step of separating out a group of like-sexed twins which appeared, to himself and to the subjects' teachers, to be physically identical. These "identicals" were much more similar to each other than were the remaining non-identicals.

In the same year Tallman (1928) presented her results on Stanford-Binet IQ scores of twins. As in the previous studies, like-sexed twins were more similar than unlike-sexed twins. An "identical" group was separated out from all the like-sexed twins, and the comparison of this group with the non-identicals confirmed Wingfield's results.

TWIN DIAGNOSIS. It is obvious that general and subjective impressions of similarity do not provide an adequate criterion for the classification of twins. A refinement was offered by Siemens, who, in 1924, published his *Die Zwillingspathologie*, a book which inaugurated a long series of twin studies on human pathological conditions by German workers. Essentially, Siemens' scheme (see Siemens, 1927) was to determine various characteristics which almost always were the same in identical twins, and only rarely so in fraternal twins. Any new set of twins could then be compared with respect to a list of such traits (e.g., hair, eye, and skin color). The probability that fraternal twins would by chance be alike with respect to all the traits, and thus misclassified as identical twins, was quite small if a sufficiently large list was employed. This, of course, involved a bit of circular reasoning, for it was necessary first to identify a group of identical twins in order to determine in what traits they were alike and to develop criteria for classifying identical twins.

The ideal was to find good "Mendelian" traits, practically unaffected by environmental differences, which were segregating in the family of the twin pair. Then, if the twins were identical with respect to all of these, they would undoubtedly be identical twins; if unlike in any, they would be fraternals.

Unfortunately, most of the human single-locus conditions then known were of rare occurrence and could therefore be used only in exceptional cases. Nevertheless, the criteria of physical similarity which were gradually evolved allowed reasonably unambiguous classification of most twin pairs. (Later, a more definite set of criteria was provided by the discovery of the Mendelian basis for human blood groups, characters which are present in all humans and are essentially unmodifiable by environmental factors.)

One of the major studies to come after the establishment of reasonably adequate criteria for identifying twin types was that of Newman, Freeman, and Holzinger (1937), who were able to apply ten criteria of physical similarity in obtaining a group of fifty pairs of identical twins and another of fifty pairs of fraternal twins. The fraternal pairs selected were all like-sexed, because the identicals are necessarily so, and the authors wanted to avoid any complications due to within-pair sex differences. In addition to physical measurements and various questionnaire data on school history, interest, etc., each twin was tested with an extensive battery of tests, including the Stanford-Binet, Otis Self-Administering Test, Downey Will-Temperament Test, and the Woodworth-Mathews Questionnaire.

Salient features of the conclusions from this large study are as follows:

> In most of the traits measured the identical twins are much more alike than the fraternal twins, as indicated by higher correlations. This is true of physical dimensions, of intelligence, and of educational achievement. The only group of traits in which identical twins are not much more alike consists of those commonly classed under the head of personality. For the rest it is obvious that the twins who have the same inheritance are the more alike. By and large, this indicates, since the environment is similar for both groups, that genetic constitution is a large factor in physical dimensions (as well as appearance and qualitative differences), mental ability, and educational achievement. This conclusion seems clearly warranted.
>
> The difference in resemblance of the two classes of twins, however, is not the same in the different groups of traits. In general, the contrast is greater in physical traits, next in tests of general ability (intelligence), less in achievement tests, and least in tests of personality or temperament.[6]

VALIDITY OF ASSUMPTIONS UNDERLYING TWIN STUDIES. As we found to be the case in the correlational approach, certain shortcomings

[6] From H. H. Newman, F. N. Freeman, and K. J. Holzinger, *Twins: A Study of Heredity and Environment*, p. 352. Copyright 1937 by the University of Chicago. Extracts here and following reprinted by permission of the University of Chicago Press.

of the twin method gradually came to light. In the first place, there was some uneasiness regarding the very fundamental assumption that environment is no more and no less effective in producing differences between fraternal twins than between identical twins. Certainly, for example, it could be argued that parents tended to emphasize the similarities of their identical-twin offspring by having them dress alike, etc., whereas this tendency might be much less marked with respect to fraternal twins. In addition, persons of different genotypes might well seek out different aspects of a common environment.

In 1934 Wilson presented a direct investigation of the assumption of equal environmental effects, by asking twins about the extent to which their home, school, and play activities and preferences were shared by their co-twins. The conclusion was that both types of twins had more similar environments than ordinary siblings, and that the environment of identical twins was much more similar than that of fraternal twins.

The findings of greater similarity of environments for fraternal twins than for siblings were supported by Herrman and Hogben (1932–1933), who found sibling correlation in intelligence measures to equal .32, whereas the like-sexed fraternal value was .47 and the unlike-sexed fraternal value was .51. It appears that the difference between fraternal twin pairs is an inadequate reflection of environmental influence. For that matter, the environmental range to which siblings are usually exposed is relatively restricted, so that comparisons of identical twins and siblings could hardly give an indication of the contribution of environment to intelligence differences *in the population at large.*

Other evidence has since been provided to show that prenatal environment must also be considered in assessing twin data. Both types of twins are exposed to such factors as differences in position *in utero* and site of implantation. Only identical twins, however, are susceptible to a phenomenon called lateral inversion, which is presumably due to differences in the cytoplasmic material received by each twin. (See Price, 1950, for a thorough discussion of this phenomenon.) Fraternal twins, on the other hand, are sometimes affected by mutual circulation when their placentae happen to fuse. Generally, these effects are regarded as making identical twins less alike than would be expected on the basis of the postnatal environments, and fraternal twins more alike than would be expected on the basis of their genetic similarity.

With these complicating features of the role of environment, the apparent ease of weighing the relative effects of nature and nurture by twin study vanishes. A greater disparity observed between fraternals than between identicals may be interpreted as due to heredity or environment or to some indeterminable combination of the two, depending upon the predilections of the person making the interpretation.

TWINS REARED APART. An alternative approach had been developing since 1922, when Popenoe gave an anecdotal account of a pair of female identical twins who had been separated in infancy. Over the years they had visited each other occasionally and had corresponded, but on the whole had been subjected to quite different environments. One, for example, had had scant formal schooling, but the other had completed high school and had done some university work. From the account of one of the twins, they were not only very similar physically, but had also shown remarkable similarities in interests and intellectual abilities. Muller (1925) administered a battery of formal tests to the girls when they were thirty years old. Despite the large difference in education, the twins were remarkably alike on the intelligence tests. On the tests of association and reaction time and on temperament and emotions, however, the twins differed strikingly. Muller urged more research of this kind, but identical twins reared apart are quite rare, and the accumulation of cases was slow. Newman (1930) reported three more cases, in two of which the twins had not even known of each other's existence until adulthood. In two of the cases, intelligence-test scores showed no greater similarity than that of fraternal twins reared together, but temperament and personality were judged to be rather similar. In the third case, the intellectual resemblance was a bit better, but personalities were stated to differ substantially.

By 1937 Newman, Freeman, and Holzinger could report on nineteen cases, including Newman's original three. An extensive battery of tests was employed, consisting of the Stanford-Binet, Otis Self-Administering Test of Mental Ability, Thurstone Psychological Examination, International Test, Stanford Achievement Test, Woodworth-Mathews Personal Data Sheet, Kent-Rosanoff Free Association Test, Pressey Test of the Emotions, and the Downey Will-Temperament Test. A large reference group of fifty identical pairs reared together and fifty fraternal pairs reared together was also tested.

We have already seen (p. 195) the conclusions which stemmed from the comparison of identicals with fraternals. The following was found when the average differences between separated identical pairs were compared with the average differences between identical pairs reared together:

> In one of the physical traits, weight, and in intelligence and school achievement the differences are significantly greater, demonstrating the effect of environment on these traits. In height, head measures, and the score on the Woodworth-Mathews test, on the other hand, no significantly greater difference is found. This is important since it indicates, as does the comparison of identical and fraternal twins, that some characteristics are more susceptible to environmental influences than are others [Newman *et al.*, 1937, p. 356].

This study, therefore, demonstrated that environmental factors could affect performance on intelligence tests. The magnitude of the environmental effect is, however, difficult to assess. One of the major difficulties is that of determining just how large the *relevant* environmental differences between the separated identical twins actually were. This was attempted by ratings of various aspects of the environment by several judges. These ratings proved to be quite reliable, in that inter-judge correlation was high. By the criteria used in these judgments, most of the separated twins were not, in fact, subjected to grossly different environments, so the greater difference obtained between separated and unseparated twins provides a modest estimate of the environment's capabilities—not minimal, perhaps, but certainly not the maximal effect which could be expected from the greatest conceivable environmental differences. On the other hand, in those cases judged to have the greater environmental disparity, the phenotypic differences were greater. As Woodworth (1941, pp. 26*f*.) has pointed out, two of the three authors, when writing elsewhere, have concluded that relatively large differences in environment are required to produce substantial changes in the intelligence quotient.

Perhaps some of the difficulty stems from the basic problem of determining how big is big. For example, the average difference in the Binet IQ scores of all the separated twins was 8.21. For the unseparated twins, this difference was 5.35. The difference between the differences is only 2.86 points, which might be regarded as almost trivial. On the other hand, the Binet-score differences of the separated twins correlated +.79 with the ratings of differences in excellence of educational aspects of the environment, and by most standards this would be regarded as a sizable relationship.

CO-TWIN CONTROL. The difficulty of adequate specification of environmental differences has been directly attacked in the co-twin control method which was introduced by Gesell and Thompson in 1929. In this procedure the identical twins are kept in environments as similar as possible, except for one particular feature which is under the control of the experimenter. Therefore, any differences which are found between the twins can be reasonably attributed to the known, specific environmental difference. In the Gesell and Thompson (1929) study, for example, one twin was given extensive early training in certain motor tasks. The other twin was given a shorter period of training later. The general conclusion was that special training administrered prior to the attainment of a requisite level of maturation did not confer long-term advantages in proficiency. Several other studies have appeared, dealing with memory and motor performance (Hilgard, 1933), perceptual mo-

tor tasks (Luria and Mirenova, 1936), vocabulary learning (Strayer, 1930), and language learning (Price, *et al.*, 1944).

One of the major efforts in co-twin control studies (McGraw, 1935) provides an object lesson in the importance of having adequate techniques for determining whether twins are identical or fraternal. After this study was well under way, it was discovered that the twin pair involved was actually fraternal, thus rendering the study essentially null and void from the point of view of genetic interpretation.

OTHER TWIN STUDIES. It has been convenient to outline the development of the methodology of twin studies with primary reference to studies on intelligence. This should not be taken to indicate that other areas have been neglected.

In personality traits, emotionality, and attitudes, the correlations for both types of twins have been generally found to be lower than those obtained for IQ. Nevertheless, identical twins have been found to resemble each other more closely in personality characteristics than do fraternal twins (Carter, 1933). McNemar (1933) applied the twin technique to a study of motor skills and obtained identical-twin correlations ranging from .73 for card-sorting to .95 for pursuit rotor performance. The fraternal twin-correlations were .50 for both of these tests. Jones and Morgan (1942) showed that the similarity in eye-movement pattern of identicals greatly exceeded that of fraternals. Lennox and co-workers (e.g., Lennox, Gibbs, and Gibbs, 1945; Lennox, 1951) explored the inheritance of epilepsy and brain-wave patterns by the twin method. In EEG pattern, identical-twin and fraternal-twin records were judged identical in 85 per cent and 5 per cent of the cases respectively. In epileptic patients who had twins, both were epileptic in 84 per cent of the identical-twin cases and in 10 per cent of the fraternal-twin cases. Jost and Sontag (1944) found identical twins to resemble each other more than siblings on measures of autonomic nervous-system function such as respiration and skin resistance.

A wide variety of anthropometric, biochemical, and psychological measurements has been taken on twins by Vandenberg and collaborators (Vandenberg, 1956). The importance of the genotype in determining individual differences in each characteristic was assessed by the extent to which the differences between fraternal pairs exceeded the differences between identical pairs. In general the genetic contribution was greater (i.e., the identical twins were relatively more similar) in the anthropometric than in the biochemical or psychological variables. It was also shown that, within each of these general categories, some traits were more "under genetic control" than others.

In this research, contrary to most earlier reports, some measures of

personality (e.g., the Thurstone Temperament Test: Vigorous) showed as large a genetic influence as many of the intellectual measures (e.g., the WISC Vocabulary, the Standard Spelling Test, and Raven's Progressive Matrices).

A particularly large literature has grown up regarding psychoses (see Slater, 1953a and 1953b, for review). One of the most extensive programs has been that of Kallmann, who has used twin comparisons in conjunction with studies of other family members. Some of Kallmann's principal findings with respect to schizophrenia, manic-depressive psychosis, and involutional melancholia are shown in Table 3. These results are in excellent accord with a general hypothesis of genetic determination, but, of course, are not exempt from the difficulties arising

TABLE 3

EXPECTANCY RATES FOR RELATIVES OF AFFECTED INDIVIDUALS *

PSYCHOTIC CONDITION	Half sibs	Full sibs	Fraternal twins	Identical twins
Schizophrenia	7.1	14.2	14.5	86.2
Manic-depressive psychosis	16.7	23.0	26.3	95.7
Involutional psychosis	4.5	6.9	6.9	60.9

* Table entries refer to percentage of relatives of given degree of genetic relationship to affected individuals which also have condition during their lifetimes.

Data taken from Franz J. Kallmann, *Heredity in Health and Mental Disorder*, Fig. 36, p. 124. Published in 1953 by W. W. Norton and used with their permission.

from the confounding of environmental similarities with genetic similarities. Kallmann has made specific interpretations regarding the mode of inheritance of these psychotic conditions. Schizophrenia, for example, is regarded as a single-locus autosomal recessive condition. The evidence for this view is somewhat contradictory, however (see Slater, 1953a), so these simple Mendelian hypotheses must be regarded as tentative. Slater (1953a) has provided another large twin study, based upon case histories, in which various behavioral abnormalities were investigated. Both twins were schizophrenic in 76 per cent of the identical-twin pairs, and in 14 per cent of the fraternal-twin pairs. In a relatively smaller sample of psychopathic and neurotic cases, the percentage of cases in which both twins were affected was low for identical twins, and not appreciably greater than for the fraternal twins. This suggests that environmental forces play a predominant role in the last named conditions. Eysenck and Prell (1951), however, determined the scores of twins on a "neuroticism" factor, extracted from a test battery

by factor analysis, and found the identical-twin correlation to be .85, whereas the fraternal-twin correlation was .22.

This sampling of twin studies is far from complete, but will perhaps serve to illustrate the tremendous effort which has gone into this particular method in the study of human behavioral genetics.

Adopted Children [7]

We may now turn to a consideration of the last general method of study of nature and nurture in humans.

In studying family resemblances of "real" parents and children, the hereditary and environmental factors are complexly interwoven—siblings, for example, share a genetic background and environmental circumstances. An adopted child, however, while sharing environment, has no genetic relationship to its family. Comparing the relative magnitudes of parent-offspring and sibling resemblance with parent-adopted offspring and adopted-sibling resemblances, therefore, offers an apparent means of separating the variables.

Following some early studies, two major investigations appeared simultaneously in 1928. One of these (Freeman *et al.*, 1928) was conducted at the University of Chicago, and the other (Burks, 1928a) at Stanford University.

THE CHICAGO STUDY. The Chicago study used Stanford-Binet and International Group Mental Test scores for children and the Otis Self-Administering Test and a vocabulary test for adults. One group of seventy-four children had been tested prior to adoption and again several years after adoption. The average IQ of the group rose from 91.2 to 93.7, and examination of individual cases showed that those adopted into "better" homes (as judged by the ratings of field workers) gained as much as five IQ points. Children in the less adequate foster homes showed no gain. This result was taken to demonstrate the positive effects of environment.

Another group consisted of 125 pairs of siblings who had been adopted into different foster homes. The sibling correlation obtained was .25 or .34 (depending on the method of computing the correlations)—less than the frequently encountered values of .50 for siblings reared together. Of thirty-eight pairs separated after living together for five years or more, the correlation was .49, while for forty-six pairs separated before either had reached six years of age, the value dropped to .32. Evidently the commonly shared environment had increased the re-

[7] In the literature of this area, "foster-child" and "adopted-child" are frequently treated as synonymous, although contemporary usage would distinguish between full legal adoption and the more temporary fostering arrangement.

semblance of those who had lived together for a substantial period of time.

In thirty homes there was at least one own child and one adopted child. The correlation of adopted children's IQ scores with the own children's scores was .34. There were also seventy-two homes in which unrelated children had been adopted. The correlation between IQ's of these children was .37.

THE STANFORD STUDY. In the study by Burks (1928a), the Stanford-Binet test was given to 214 adopted children and their foster parents, and to a control group of 105 children and their real parents. The control group was closely equated to the adopted group in terms of age of children, educational and occupational level of parents, etc. The children were tested between five and fourteen years of age and, to reduce the effect of pre-adoption environment, only children adopted before the age of twelve months were studied.

The main results are shown in Table 4.

TABLE 4

CORRELATIONS OBTAINED IN BURKS' FOSTER CHILD STUDY

CORRELATION BETWEEN IQ OF CHILDREN AND	Foster children	Control children
Father's mental age	.07	.45
Mother's mental age	.19	.46
Midparent mental age	.20	.52

The control correlations are in accord with the previous parent-child studies and the differences between control and adopted correlations argue for the important influence of hereditary factors.

By applying Wright's mathematical techniques, Burks concluded that "*Home environment contributes about 17 percent of the variance in I.Q. . . . The total contribution of heredity . . . is probably not far from 75 or 80 per cent*" (1928a, p. 308).
As a general summary statement,

> *Home environment in the most favorable circumstances may suffice to bring a child just under the borderline of dullness up over the threshold of normality, and to make a slightly superior child out of a normal one; but it cannot account for the enormous mental differences to be found among human beings* [Burks, 1928a, p. 308].

The disagreement in the general tone of the conclusions, as well as in the specific results of these two studies of adopted children, was

examined by Burks (1928b), and she concluded that the factor of selective placement, whereby adoption agencies strive to place children of "good parentage" in the better homes, can account for at least part of the differences. Other authors (e.g., Anastasi and Foley, 1949, pp. 356*f*.) have also pointed out the subtle ways in which such selection can take place, even when specific knowledge of the child's IQ, or of that of its parents, is unknown.

SUBSEQUENT RESEARCH. Leahy's (1935) study on adopted children was inspired by the discrepancies between the conclusions of Burks and those of Freeman *et al.* The correlations obtained by Leahy for IQ scores were: adopted children–foster fathers, .19; adopted children–foster mothers, .24; true children–true mothers, .51; true children–true fathers, .51. These results on intelligence are in striking accord with Burks'. There is also an agreement that personality and character traits are more influenced by environment than is intellectual level.

Another long-term study of adopted children was conducted by Skodak and Skeels (1949). These investigators concluded that the mean IQ of the adopted children was substantially higher than would be expected in view of the intellectual level of their true parents, and suggested that this represented a beneficial effect of environment. There was, however, a substantial correlation between the adopted child's IQ and that of the true mother. The magnitude of the correlation was found to increase with age, being very low at two years, and rising until, at about six years, the correlation was approximately .35. Honzik (1957) has compared the Skodak and Skeels results on adopted children with her results on "own" children. Figure 23 shows the comparison when educational level is used as an index of the mental ability of the mother or foster mother. The striking feature of these data is that the IQ's of the adopted children correlated as highly with their own mother's education as did the own children's IQ's with their own mother's education, in spite of the fact that the latter had been reared by their own mothers and the former had not. The correlation of the child's IQ with the foster mother's education is seen to be low at all age levels. Honzik concludes:

> The finding that the parent-child resemblance in ability follows the same age changes in the two studies, even though the true parents did not rear the children in the Skodak-Skeels group, suggests that the existing relationship is largely due to genetic factors which tend to become manifest in the child during the later preschool years [1957, p. 227].

POSSIBLE BIASES IN STUDIES OF ADOPTED CHILDREN. In the interpretation of studies of adopted children, many of the reservations dis-

cussed with reference to other methods must be applied. Some specific problems have also been identified.

We may note, for example, a basic difficulty in drawing conclusions on the evidence of gain in IQ after adoption. The circumstances surrounding the pre-adoption intelligence testing might well have a depressing effect on the child's performance. In like manner, the IQ scores of true mothers of adopted children are frequently obtained during the

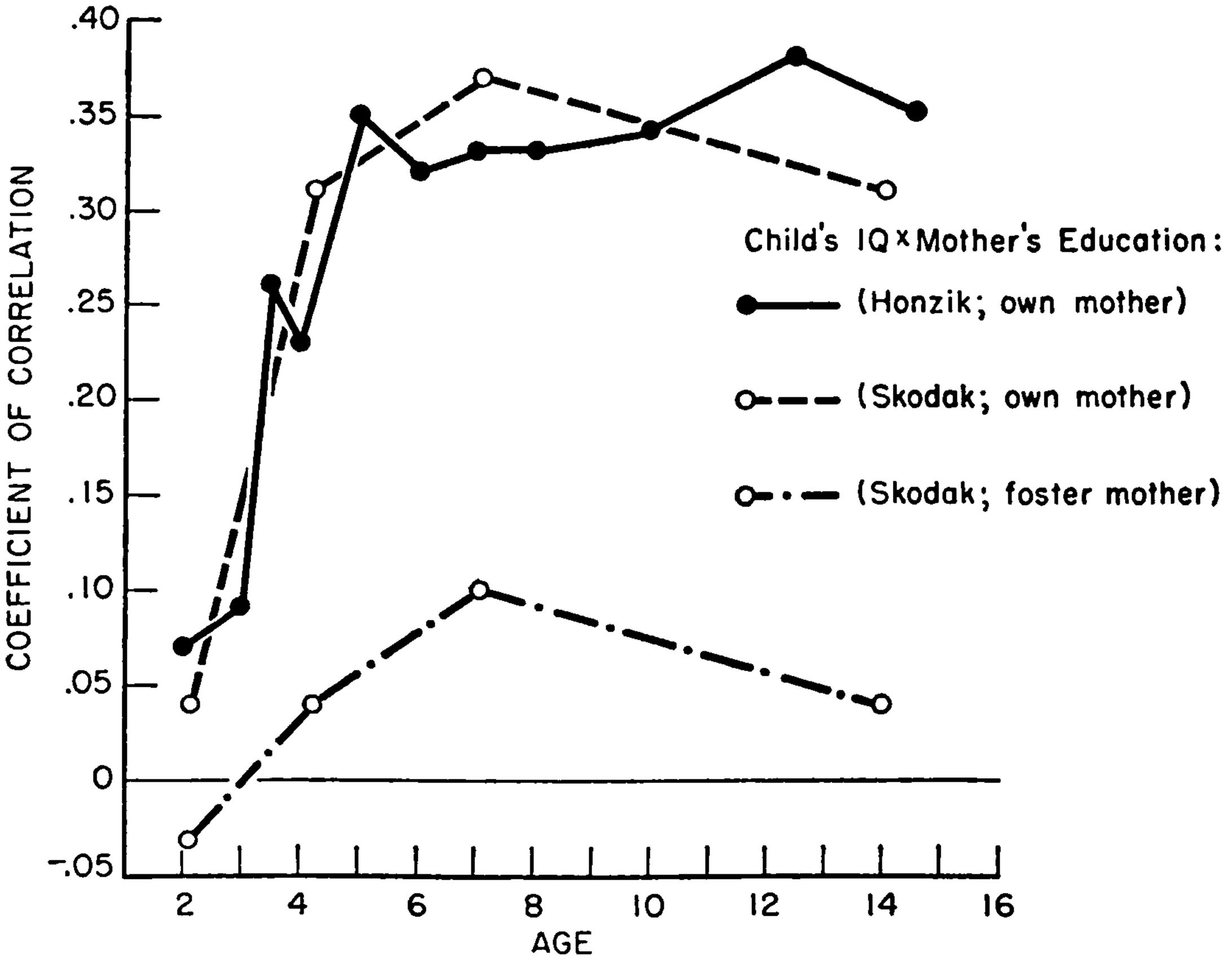

FIGURE 23. Coefficients of correlation at different ages between child's IQ and educational level of own or of foster mother. (After Marjorie P. Honzik, "Developmental studies of Parent-Child Resemblance in Intelligence," *Child Development*, 1957, 28, Figure 2. Used with permission of the Society for Research in Child Development.)

stressful period prior to delivery of an illegitimate child, and may therefore be depressed.

We have already seen the possibility of selective placement, whereby placement agencies may employ whatever information is available in placing children of superior genotype in superior home environments. The degree to which this factor influences the results has been debated, and it is likely that its effect varies from study to study. Insofar as selective placement exists, of course, there is a genotype-environment correlation which makes the accurate assessment of the relative contributions of heredity and environment impossible.

Woodworth has provided the following interesting summary of studies of adopted children:

> We have thought of them as studies of environment, but they are also tests of the foster child's heredity. When we say, as we are apt to do, that children of "poor heredity," placed in good foster homes, turn out fairly well in spite of their heredity, are we not asserting the impossible? No one can achieve anything that is beyond his potentiality. If a child, from whatever parentage, develops superior intelligence, we know for certain that his heredity was good enough to make that achievement possible. We have simply been misjudging his heredity. The low economic and cultural level of his parentage has misled us. We have forgotten that the offspring of any given parents may differ widely in genetic constitution, and we have forgotten that these particular parents because of their own early environmental handicaps are probably functioning below the level of their hereditary potentialities. The more we stress the importance of environment, the less are we justified in inferring a child's heredity from the social status of his parents, and the less are we entitled to speak of a child as having "poor heredity" just because his parents are poor, uneducated, shiftless and immoral. Placement of the child in a good home gives him a chance to show how good his heredity really is. What the foster child studies are doing when seen from this angle, is to check up on the heredity of the offspring of certain classes of parents.[8]

Combined Approaches

In terms of logic and historical development, it is possible to distinguish among the various methods discussed above: pedigree, correlational, twin study, foster-child study, etc. Yet, to a considerable extent, the methods may overlap. Thus, a "foster-child" study may compare the correlation of true mothers and children with that of foster mothers and children; a "twin study" may involve the comparison of sibs, half sibs, and foster children, as well as identical and fraternal twins.

Insofar as each general approach can provide a unique source of information, the advantages of a multiple approach to any particular problem is apparent. Cattell (1953) has proposed a "multiple-variance" method in which the variability of a number of different groups, of differing genetic and environmental similarities, are simultaneously assessed in one analytic framework. For example, the variances of (1) identical twins reared together, (2) fraternal twins reared together, (3) sibs reared together, (4) sibs reared apart, (5) unrelated individuals reared together, and (6) general population, on various personality test factors, were utilized in an analysis of components of variance to de-

[8] From Robert S. Woodworth, *Heredity and Environment*, pp. 68–9. Published in 1941 by the Social Science Research Council, Bulletin 47.

termine relative contributions of heredity and environment (Cattell *et al.*, 1955, 1957). These authors have discussed a number of other groups which would provide relevant information (e.g., half-sibs reared apart) and have considered the assumptions, similar to those already described for correlational studies, twin studies, and foster-child studies, which are essential to multiple-variance analysis.

Chromosome Numbers, Sexual Abnormalities, and Mongolism

MONGOLISM. This section will be chiefly concerned with Mongolism, which is one of the more frequent conditions of feeblemindedness. It has been singled out for separate consideration because of the variety of procedures which have been employed in the attempt to understand its etiology, and also because of the new techniques which have been recently brought to bear in its study. The account of the research on Mongolism also provides a clear demonstration of the interplay among seemingly diverse discoveries in the advancement of science.

A distinctive condition, Mongolism (or Mongolian idiocy), presents a complex of symptoms, in addition to the mental deficiency, of protruding, furrowed tongue, presence of epicanthal fold of the eyes, depressed nose, short stature, and a number of other physical characteristics, including a certain configuration of creases in the palm of the hand. The brain of Mongoloids has been shown (Davidoff, 1928) to be of small size, with relatively fewer cells than normal, and with an "embryonic" convolutional pattern.

The name of the condition derives from a superficially oriental appearance of the affected individuals, and has no racial significance. (Asiatics, in fact, regard them as Caucasian in appearance [Penrose, 1959, p. 99]).[9]

Since the initial description of Mongolism in the middle of the nineteenth century, an enormous effort has been made to determine the genetic and/or environmental causal factors. Twin studies (Jenkins, 1933; Macklin, 1929) have generally shown concordance among identical twins and discordance among fraternals. However, some cases of discordance in putative identicals (e.g., van Beukering and Vervoorn, 1956) complicate the picture. In examinations of the families of Mongoloid individuals, cases have been found (Macklin, 1929; Penrose, 1934) of two, three, and even four affected sibs in the same family. In

[9] The inappropriateness of the terms "Mongolian idiocy" or "Mongolism" has often been mentioned. A proposal has recently been made (Allen *et al.*, communication to *Lancet*, 1961, Vol. 1, p. 775) that "Langdon-Down anomaly," "congenital acromicria," "trisomy 21 anomaly," or some other term be used to replace the older designation.

assessing the over-all evidence on familial incidence, however, Penrose concluded that

> . . . it is difficult to produce convincing evidence that the familial cases are due to familial concentration and not to chance sampling. Moreover, in some of the familial instances the diagnoses are open to doubt. . . . Furthermore, the occurrence of more than one case in a sibship might not be genetical but due to a consistent peculiarity of maternal environment [1949, p. 189].

A number of such maternal environmental factors, many of them rather vague and unspecific, have been proposed: endocrine deficiencies, "reproductive exhaustion," mental or physical strain during pregnancy, etc. (for reviews see Allen, 1958; Gates, 1946; Penrose, 1949). Whatever the relevant variable or variables, it became clear that they must change with the age of the mother, for Penrose (1941, 1949) demonstrated a striking increase in the incidence of Mongolism in the children of older mothers. The risk of a mother forty-five to forty-nine years of age is, in fact, about fifty-five times as great as that of a twenty to twenty-four-year-old mother. The genotype, and therefore the genetic constitution of the gametes produced, is basically set at conception, and does not change with age, whereas any number of environmental factors, such as those mentioned above, could easily be visualized as doing so. This seemed to indicate that environmental factors are responsible. There is some evidence, however, obtained from research on the fruit fly, that the frequency of crossing over does increase with age. Crossing over "releases" new combinations of genes, and in this sense a change in the nature of the gametes that a fly can produce does, in fact, occur with age. This may or may not be true in human beings, so the relevance to Mongolism is not known. Chromosomal abnormalities were also considered. Polyploidy (duplication of chromosomes) is known to be more frequent in some somatic cells with increasing age. It is conceivable that chromosomal alterations may also occur in reproductive cells more frequently with increasing age. Penrose (1941) and Waardenburg (1932) both, in fact, suggested that chromosomal abnormalities might underlie Mongolism.

It is clear from the foregoing that the demonstration of the effect of maternal age in Mongolism does not absolutely rule out hereditary mechanisms as important in the etiology. But the evidence from which conclusions might be drawn has been confusing. There is little consanguinity (mating of related individuals, such as cousins) among the parents of Mongoloids (Penrose, 1949). This is an indication against a recessive gene. On the other hand, the parents of Mongoloids do not themselves show the condition. This observation rules out dominance. Yet a single gene might be transmitted according to a simple Mendelian

system, but not express itself in each person who received the "abnormal" genotype, owing either to environmental factors or to the effects of other genes present. On the other hand, a polygenic system could easily account for the facts.

A most interesting observation was made concerning the patterns of creases and ridges on the palms of the hands of Mongolian idiots. One special pattern, common to Mongoloids, is present only in a small percentage of the population at large. In relatives of Mongoloids, however, the incidence is greatly increased, suggesting that they are heterozygotes, or are homozygotes who by good environmental fortune have failed to develop the more severe symptoms.

KLINEFELTER'S SYNDROME, TURNER'S SYNDROME, AND CYTOLOGY. Before continuing with genetic findings regarding Mongolism, we must turn to some cytological considerations. In 1949 a cytological difference was discovered between the neurons of male and female cats (Barr and Bertram, 1949). This distinction was also found in man, and it proved possible to determine "nuclear sex" by examination of the blood (Davidson and Smith, 1954) and skin (Moore and Barr, 1955). These new techniques were quickly applied to the study of certain human sexual abnormalities which suggested intersexuality. One of these conditions is Turner's syndrome, in which the individuals, always apparent females, show sexual infantilism, dwarfism, and some other anomalies. Suggesting that some failure of sexual development was at fault, Polani *et al.* (1954) tested for nuclear sex of three Turner's individuals, and found them all to have characteristic male cell nuclei. Shortly thereafter Riis *et al.* (1956) examined skin cells of two patients showing Klinefelter's syndrome. This condition occurs in apparent males, who have small testes, failure of spermatogenesis, feminine distribution of fat, and development of the breasts. The two "males" examined showed typical female nuclei. These dramatic findings naturally gave rise to speculation about the sex-chromosome constitution of the affected individuals. With the nuclear-sexing technique it was not possible to examine the chromosomes directly, so the evidence brought forward was genetic. By examining the incidence of color-blindness, a sex-linked recessive condition in affected individuals, it was possible to infer that Turner's "women" actually had a chromosome constitution of XO or XY (Polani *et al.*, 1956), and that Klinefelter's "men" were XX (Polani *et al.*, 1958). Plunkett and Barr (1956) had previously suggested an XX complement in Klinefelter's syndrome, but also mentioned the possibility of XXY.

The direct examination of human chromosomes to test these suggestions was not feasible until the introduction of new and improved techniques by Tjio and Levan in 1956. With the improved procedure it

was shown that the normal number of human chromosomes was forty-six, and not forty-eight, as had long been thought to be the case (Tjio and Levan, 1956; Ford and Hamerton, 1956; see also Ford, Jacobs, and Lajtha, 1958, for a review). Results from Klinefelter's patients showed forty-seven chromosomes, however, and detailed examination showed the Y chromosome to be present, along with an extra chromosome belonging to the size range in which the X chromosome is to be found. In all likelihood, then, some, at least, of Klinefelter's "males" are XXY (Jacobs and Strong, 1959). Ford *et al.* (1959b) and Fraccaro *et al.* (1959) found only forty-five chromosomes in Turner's patients, and provided evidence that the sex-chromosome constitution was XO.

Cytology and Mongolism. Returning now to considerations of Mongolism, it may be remembered that Waardenburg and Penrose had both suggested at one time that a chromosomal abnormality of some kind might underlie the condition. Mittwoch (1952), working before the advent of the improved cytological techniques, examined tissue from a Mongoloid individual, and reported ". . . the chromosomes were not sufficiently distinct from one another to make an exact count possible; nevertheless, the approximate diploid number of 48 chromosomes could be made out in several cells" (p. 37). Penrose (1954), in a review of the literature, accepted this evidence as ruling out gross chromosomal abnormality at least.

After the dramatic findings on abnormalities of sexual development, the issue was reopened by two groups of investigators, Lejeune *et al.* (1959) and Jacobs *et al.* (1959). Nine Mongoloid individuals were examined in these studies, and in each case, forty-seven chromosomes were found. The evidence strongly suggested that the extra chromosome was an autosome.

The crowning confirmation of the whole approach was presented almost immediately by Ford *et al.* (1959a) who found forty-eight chromosomes in the cells of an individual showing both Klinefelter's syndrome and Mongolism—the basic forty-six plus one extra autosome plus one extra sex chromosome.

These fast-breaking developments have not, of course, provided an "explanation" of Mongolism. They do clarify the irregularities and confusions of the preceding genetic data, but still to be explained are the increased incidence in the Mongoloid pattern of palm ridges in relatives, the reason that the non-disjunction which results in the extra autosome occurs more frequently in older mothers, and perhaps most basic of all, the physiological events whereby the extra chromosome, with the surplus genetic material it provides, causes the Mongoloid condition. There can be absolutely no doubt, however, but that the cytological work has opened up many new exploratory avenues, and thus tre-

mendously enhanced the likelihood of an ultimate thorough understanding, which will carry with it the implications of remedial and preventive therapy.

It may be confidently predicted that in the future the cytological approach will be applied vigorously to a great variety of human pathological conditions. Whether the implications for behavioral genetics will be great or small cannot even be guessed at the present time.

Summary of Human Studies

One of the principal problems of human behavioral genetics has been that of definition and measurement of the phenotypes under investigation. It is generally acknowledged that any measurable attribute of an individual is a legitimate phenotype, so there can be no complaint, for example, about studying the rate of crossing out A's on a printed page, or reading comprehension, or ability to deal with verbal analogies. The difficulty arises when a common term is used to describe the trait being assessed by the various tests. Thus, different studies on the inheritance of intelligence, say, may be dealing with quite different phenotypes, and consequently may not be at all comparable. This problem is, of course, a central problem of psychometrics, and, as we have seen, the improvements in test design and standardization have at the same time improved precision of identifying phenotypes for genetic studies. In like manner, improvement in diagnostic criteria and systems of classification have led to greater clarity in research on the inheritance of feeble-mindedness and neurotic and psychotic conditions. It is to be anticipated that further progress in psychometrics and clinical classification will be profitably utilized by students of the genetics of human behavior in the future.

Another likely trend in future investigations is the greater use of factor analysis, in which the factors common to a group of tests, rather than a single test score, can be examined. This approach has been urged recently by Thompson (1957) and R. B. Cattell (1953). The latter author has provided concrete examples of such an approach to the genetics of personality (Cattell *et al.*, 1955, 1957).

These problems are, however, subordinate to the critical difficulty of arriving at clear-cut, unambiguous determinations of the relative influences of genetic differences and environmental differences in determining the individual variability in phenotypes. These difficulties result primarily from the failure of human circumstances to comply with the assumptions of the logic underlying the methodological procedures, and this situation is basically attributable to the fact that man is not an experimental animal. It is not possible to assign various genotypes randomly to various designated environments. Siblings can-

not be separated deliberately and assigned to different types of homes for rearing. Random mating cannot be guaranteed by assigning marriage partners on a random basis.

This is a fundamental consideration. In a discussion of the interpretation of correlation coefficients, Falconer (1960, p. 164) considers the problems introduced by assortative mating and by covariance due to common environments, and says, "For these reasons human correlations cannot easily be used to partition the variation into its components." Neel and Schull have asserted, "In its present context, the twin method has not vindicated the time spent in the collection of such data." [1] Woodworth (1941, pp. 45*f*.) concluded, "On the whole we may expect results of considerable practical value, but of no great scientific precision, from the study of foster children."

These judgments are indeed sobering, and indicate the necessity for methodological advances in the study of the inheritance of human behavior. The only satisfactory way of dealing with the problem would appear to be the precise evaluation of the extent to which the basic assumptions are not met, with proper compensation then being made in interpretation of results. This will require much more extensive knowledge concerning the important social, economic, educational, and cultural determinants than is now available. Progress in understanding the genetic basis of human behavior can occur only with concomitant progress in understanding the environmental bases.

Animal Research

Selection

Selection for learning performance. The animal researcher is able to make use of techniques not available to those working with humans. One of the most important of these is artificial selection.

Selection by natural agencies was, of course, the central theme of Darwin's theory, and "artificial" selection by man, as we have seen, has been a practical art for centuries. The Mendelian discoveries and later developments permitted a more rational approach to the practical aspects of plant and animal breeding, and allowed the development of selection procedures as scientific devices for elucidating genetic mechanisms. If the phenotypic differences shown in a population are determined to any appreciable extent by genotypic differences, a selection program in which animals from one extreme are mated together and animals from the other extreme are likewise mated together, may be expected over a number of generations to result in the establishment of two distinct lines, differing substantially in the characteristic. On the

[1] From J. V. Neel and W. J. Schull, *Human Heredity*, p. 281. Copyright 1954 by the University of Chicago. Used by Permission of The University of Chicago Press.

other hand, as Johanssen had shown with his beans, if the differences in the original population are due solely to environmental differences, such a selection procedure would have no effect. Thus the success of a selective breeding program demonstrates that at least some of the phenotypic variance in the original population was due to genotypic differences.

TOLMAN'S INITIAL STUDY. The application of selective breeding to problems of the inheritance of behavior was reported in 1924 by E. C. Tolman. We may reasonably infer the indirect influence of J. McK. Cattell in this work, since Tolman credited Professor Warner Brown, who had been one of Cattell's doctoral students, with providing the original impetus for the study. It is also of interest that Barbara Burks was involved in the statistical evaluation of the results.

Tolman saw the genetic approach, and selective breeding particularly, as a tool for "dissecting" behavioral characteristics:

> The problem of this investigation might appear to be a matter of concern primarily for the geneticist. Nonetheless, it is also one of very great interest to the psychologist. For could we, as geneticists, discover the complete genetic mechanism of a character such as maze-learning ability—i.e., how many genes it involves, how these segregate, what their linkages are, etc.—we would necessarily, at the same time, be discovering what psychologically, or behavioristically, maze-learning ability may be said to be made up of, what component abilities it contains, whether these vary independently of one another, what their relations are to other measurable abilities, as, say, sensory discrimination, nervousness, etc. The answers to the genetic problem require the answers to the psychological, while at the same time, the answers to the former point the way to those of the latter [1924, p. 1].

As his own contribution toward this end, Tolman began with a diverse group of eighty-two rats, which were assessed for learning ability in an enclosed maze. Using as a criterion for selection "a rough pooling of the results as to errors, time, and number of perfect runs," nine male and nine female "bright" rats were selected and mated with each other. Similarly, nine male and nine female "dull" rats were selected to begin the "dull" line. The offspring of these groups comprised the first selected generation. These animals were then tested in the maze and selection was made of the brightest of the bright and the dullest of the dull. These selected animals were mated brother by sister to provide the second selected generation of "brights" and "dulls."

The results were quite clear in the first generation, with the bright parents having bright progeny, and the dull parents dull progeny. The difference between "brights" and "dulls" decreased, however, in the next generation, primarily because of a drop in efficiency of performance of

the bright strain. These second-generation results were, of course, disappointing, and Tolman examined several possible explanations. In the first place, the particular maze used turned out to be a not particularly reliable measuring instrument. Secondly, it was suggested that the mating of brother with sister might have led to what was known as inbreeding degeneration—a phenomenon quite commonly encountered in genetic work.

To facilitate further investigation, an automatic, self-recording maze was developed by Tolman in collaboration with Jeffress and Tryon (1929). With the new maze, which provided superior control of environmental variables and which proved to be highly reliable, Tryon began the selection procedure again, starting with a large and highly heterogeneous "foundation stock" of rats. The energies of Tolman himself were taken up in the development of his theory of learning, and he did no further actual experimentation on behavioral genetics. Nevertheless, he made a continuing contribution to the field by insisting on the importance of heredity in his well-known H.A.T.E. (Heredity, Age, Training, Endocrine, drug, vitamin conditions) list of individual-difference variables.

TRYON'S AND HERON'S STUDIES. Tryon's (1940) results are shown in Figure 24. It is clear that two different lines were established, one clearly superior to the other in terms of errors made in learning the maze. In fact, by generation 7 there was practically no overlap between the distributions for the two groups. The dullest bright rats were about equal to the brightest dull rats.

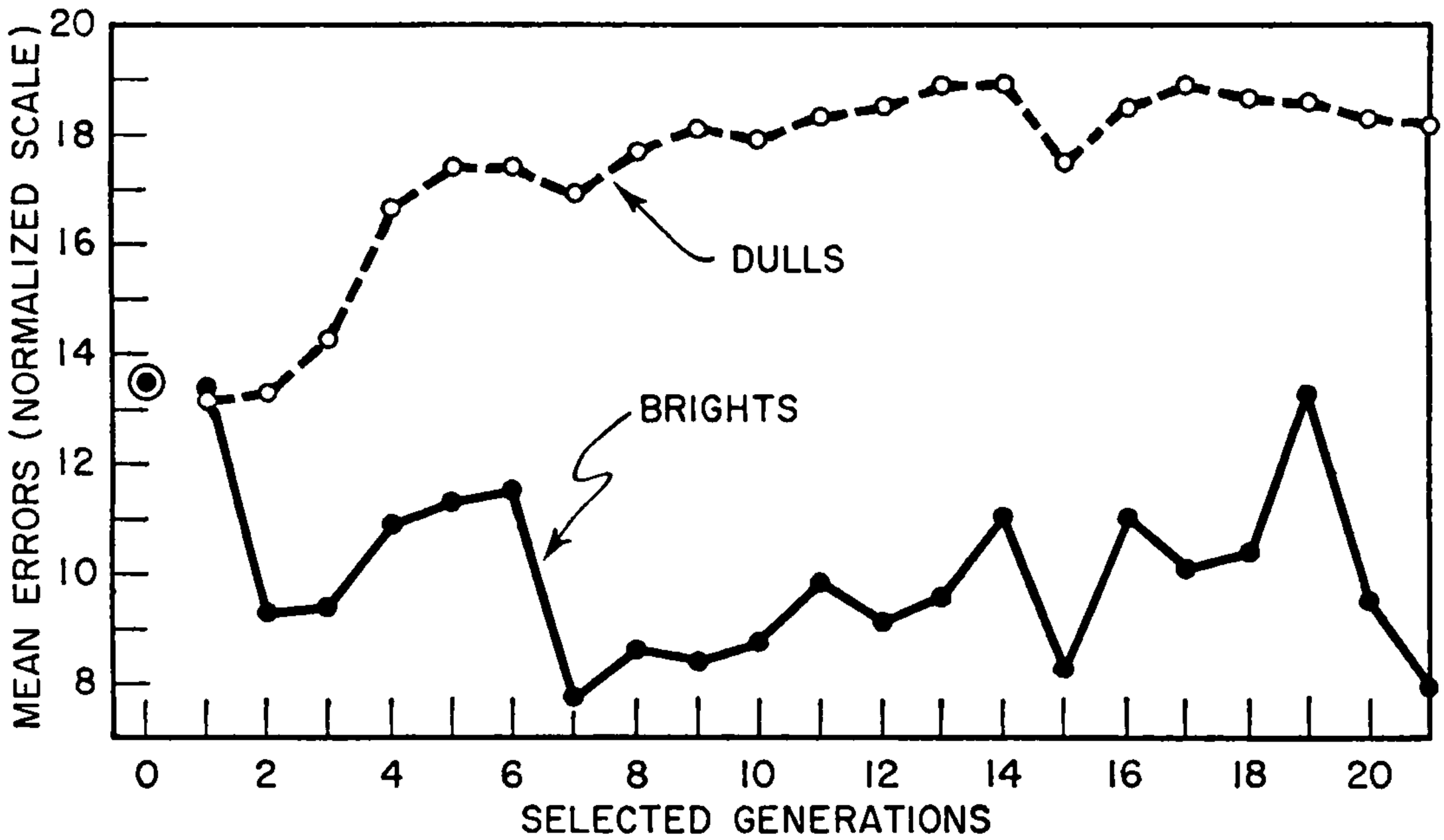

FIGURE 24. The results of Tryon's selective breeding for maze-brightness and maze-dullness. (From data provided through the courtesy of R. C. Tryon.)

Heron (1935, 1941), at about the same time, was also selectively breeding for maze performance, beginning with a different foundation population and using a different (but also automatic) maze. This study also yielded two clearly distinct strains. Yet another successful program of selection for maze ability has been reported by Thompson (1954). In this study the rats were presented with the Hebb-Williams set of tasks, which increase systematically in complexity, thus providing a closer analogue to human intelligence tests than did the previous studies using only one maze pattern.

SELECTION FOR OTHER BEHAVIORAL CHARACTERISTICS. Selection has also been applied to phenotypes other than maze performance. Rundquist (1933) selected for active and inactive strains of rats, using the number of revolutions in a rotating cage as the selection criterion. Hall (1938) used selection to derive an "emotional" and a "nonemotional" strain of rats, where emotionality was defined in terms of defecation and urination in a brightly illuminated open-field test. More recently, Broadhurst (1958a) has reported another successful selection program for these behaviors. Frings and Frings (1953) have successfully developed several strains of mice which differ in susceptibility to sound-induced convulsive seizures and also in the pattern of the seizure, and Nachman (1959) has selectively bred for saccharin preference in rats.

In a different phylum, Hirsch and Boudreau (1958) have developed two strains of Drosophila, characterized by different intensities of light-approaching tendencies.

Further Research on Behaviorally Selected Strains

By their success, the selection studies have demonstrated that hereditary differences were important contributors to the individual differences in behavioral phenotypes displayed in the foundation stocks with which the studies began. By reasonable inference, these conclusions may be extended to heterogeneous populations in general. In addition, the strains which were developed in the course of the breeding programs have proved to be of the greatest importance to subsequent research. Several examples may be taken from work with Tryon's and Heron's animals.

TRYON'S STRAINS. Tryon (1940) bred his "bright" rats with "dull" rats, and the resulting F_1 generation was tested in the maze. These animals were intermediate to the parent strains and, from this and other evidence, Tryon concluded that a multiple factor genetic system determined rat maze-learning ability. Krechevsky (1933) tested

Tryon "brights" and "dulls" in a situation which offered both visual and spatial cues, and found that animals of the bright strain tended to respond to spatial cues, whereas the dull rats responded to visual cues. This outcome is in accord with the fact that the selection measure employed by Tryon was spatial maze performance. The question remained as to whether the "brights" were generally superior, or superior only in this specific type of situation. Searle (1949) examined this point directly by subjecting "brights" and "dulls" to a battery of tests which measured learning under hunger motivation, learning under escape-from-water motivation, activity, and emotionality. The "brights" learned better than the "dulls" in the hunger-motivation problems, whereas the "dulls" were superior to the "brights" in the escape-from-water situations. Furthermore, "brights" were more active in the maze but less active in rotating wheels. Other differences were found with respect to emotionality. "Brights" were more "emotional" in open spaces, while "dulls" displayed emotional behavior with respect to certain of the mechanical features of the maze. The selection program had quite obviously resulted in strains which differed from each other in complex ways—not simply in ability to learn a pattern of responses in the maze. In selective breeding, characteristics other than those deliberately sought may fortuitously become associated in the developing lines. It is not possible, therefore, without further research, to determine which of the constellation of behavior differences between strains are fundamental to the principal behavior difference, and which are only incidental.

GENES, ENZYMES, AND LEARNING. Krech, Rosenzweig, Bennett, and collaborators (Krech *et al.*, 1954, 1956; Rosenzweig *et al.*, 1955, 1958a, 1958b) have systematically investigated the relationship among genes, brain biochemistry, and behavior in descendants of the original Tryon strains, which have been maintained without selection from the twenty-first generation to the present. In a number of learning situations the descendants of the "brights" have proved to be less stereotyped and more flexible in behavior than the "dull" descendants. It has also been shown that the "brights" have a higher level of cholinesterase (ChE) activity in the cerebral cortex. This enzyme, ChE, determines the rate of breakdown of acetylcholine (ACh), which is involved in neural transmission. Krech *et al.* (1956) proposed that the greater ChE activity in the "brights" reflected greater ACh activity, and that this was related to greater efficiency of neural transmission. However, these authors recognized the possibility of fortuitous association, and undertook to determine if in the present case the relationship between the characters was only a matter of chance.

One approach was to mate animals from the separate strains to

obtain an F_1, and then to mate the F_1 animals *inter se* to obtain an F_2. In the F_2 there will be genetic reassortment. If there is no genetic communality underlying the two traits, then the correlation between them should be zero. If the traits have common genetic bases, in whole or in part (or if there is linkage among relevant genes), there should be a correlation in the F_2. With reference to the present problem, there should be a negative correlation between ChE activity and the number of errors made. The actual outcome of this test, however, was a *positive* correlation in F_2—the animals with the greater ChE activity tended to make more errors (Rosenzweig *et al.*, 1958b).

Another approach was to breed selectively for cholinesterase activity, without regard to any behavioral characteristics. Again, the results were contrary to the initial hypothesis. The animals selected for high ChE activity performed more poorly, on the whole, than did those selected for low ChE activity. These results have suggested that

> . . . among strains or individuals the levels of ACh and ChE are determined by independent genetic mechanisms. In this case, raising the level of ChE activity and leaving ACh unaltered may cause too rapid a breakdown of ACh for efficient synaptic transmission. Behavioral selection, as in Tryon's case, may have been made for both ACh and ChE. To be certain about the level of ACh metabolism at the synapse will require measurement of both ACh and ChE in the same subjects [Rosenzweig *et al.*, 1958b].

Recently reported results are congruent with this hypothesis (Rosenzweig *et al.*, 1960).

HERON'S STRAINS. Heron's strains were also subjected to further investigation. Harris, for example (1940), showed that the learning curve of the Heron "dulls" dropped from an initially high error score to about the chance level of 50 per cent correct responses. This was shown to be due to a decreasing tendency to make repeated entries into the same incorrect alley. The "dulls" never did learn to select the correct alley of the two alternatives at each choice point, but simply learned not to repeat errors. The "brights," on the other hand, showed a systematic increase in percentage of correct choices of the proper alleys. The Heron "brights" were also found to show a higher rate of bar-pressing in a Skinner box (Heron and Skinner, 1940), and a faster speed of running the maze than the "dulls" (Harris, 1940).

Comparisons of Strains Not Behaviorally Selected

In addition to the study of strains deliberately selected for behavioral differences, a very substantial number of researches have

taken advantage of the existence of other strains, derived in the most part without regard to their behavioral characteristics. These studies have differed from each other in several ways. Some have consisted solely of comparisons between two, or among several, strains. For such studies, the logic has been as follows. If two strains of animals of different origins have been maintained separately, with no matings between the strains having occurred, one may safely presume that the strains differ genetically. (Indeed, under such circumstances, it would not be possible for the strains to retain genetic identity). Therefore, if the compared strains differ in behavior, and the environmental circumstances are similar, one may presume that the genetic differences account for the behavioral differences. Nothing whatever is revealed concerning the nature of the genetic differences. In other cases, the strains have been mated to provide F_1 and further generations, sometimes with the purpose of determining the presence of segregating Mendelian genes, but more often to examine the means and variances of the derived generations with respect to the parent strains. From the study of derived generations, it is frequently possible to determine something about the nature of the genetic mechanism.

In the earlier work, particularly, it was possible to make only rather vague distinctions between the strains. Thus "tame" laboratory rats were compared to "wild" rats, and many of the mouse strains compared were simply stocks from different pet shops, different laboratories, or even different trapping sites. Gradually, however, the maintenance and breeding of laboratory animals became more systematic. In the case of mice, for example, a vigorous program of selection, largely for tumor characteristics, provided a number of discrete identifiable strains. In many cases, furthermore, the selected strains were subjected to intense inbreeding, which has the effect of greatly reducing genetic variability within the strains. The obtained (relative) genetic uniformity enormously facilitates genetic interpretation of results. The gradual adoption of these inbred strains has been one of the principal advances of methodology in strain-comparison studies.

EARLIER RODENT RESEARCH: RODENT "TEMPERAMENT." One of the earliest studies on strain differences was that of Yerkes (1913), who compared tame and wild rats for savageness, wildness, and timidity. These characteristics were inferred from the observable behaviors of biting, gnashing of teeth, squeaking, jumping, hiding, excited running, urination, defecation, cowering, and trembling, exhibited when the animals were taken from the cage. Rating scales from 0 to 5 were established to describe the degree of the trait exhibited by each rat, and Yerkes claimed high reliability for the observations. The observations were made on wild and tame rats, on the F_1 obtained from mating tame

female with wild male rats, and F_2 descendants. The wild rats received ratings of 3, 4, or 5, indicating high expressions of all three characteristics. The tame rats received ratings of 0 or 1. Most of the F_1 animals obtained high ratings, but there was a moderate spread, with some F_1 animals being found in almost every category. In the F_2, the average rating was lower and the variability was greater than in the F_1. In this study, Mendelian-like categories, such as timid vs. non-timid, or savage vs. non-savage, were not used. The use of rating scales acknowledged the quantitative variation of the traits being investigated, but with the work of Fisher and Wright still some years in the future, Yerkes had to content himself with the assertion, "The results . . . prove conclusively that savageness, wildness, and timidity are heritable behavior-complexes. It is hoped that the further study of these characteristics in the third generation hybrids, and in special matings from the first and second generation hybrids, may yield more definite results concerning the modes of transmission" (1913, p. 296).

A closely related study on mice, undertaken by Coburn (1922) at the suggestion of Yerkes, was completed in 1914, although it was not published for a number of years. Utilizing behavioral indices very much like those used by Yerkes with rats, Coburn examined wildness and savageness of wild mice, tame mice, and the subsequent F_1 and F_2 generations. For both wildness and savageness, the F_2 generation had a greater variability than the F_1. The tame mice all scored 0 on a Yerkes-type scale, and the wild mice all scored 4 or 5. The restriction of each character to 5 grades, which imposes a perhaps artificial upper and lower limit, makes comparison of the parental and F_1 variabilities difficult, but the greater variability of the F_2 generation was taken by Coburn to support a multiple-factor interpretation of the inheritance of both wildness and savageness.

Yerkes, in obtaining his F_1, had mated tame females with wild males, and the possibility existed that the outcome would have been different had wild females been mated with tame males. In the first place, the behavior of the tame mother might have provided quite different environmental stimulation to the young during their development than would a wild mother. In the second place, the relevant genes might be located on the X chromosomes, in which case the male offspring would receive all the determining genes from their mother. Obviously, in this case, the "reciprocal crosses" would be expected to differ. Coburn tested these possibilities in his mice by obtaining F_1's from both crosses: wild males with tame females and tame males with wild females. No differences were found in the behavior of the offspring of these reciprocal crosses. The factors determining wildness, savageness, and tameness thus are evidently not located on the sex chromosomes, and the behavior of the mothers of different strains (or the quality of their

milk, etc.) does not provide environmental stimulation which differentially affects the phenotype.

THE WISTAR RATS. Over a period of years, the Wistar Institute had developed an inbred strain of rats with brains of somewhat less than normal weight, and J. H. Donaldson of the Institute had suggested to J. B. Watson, of Johns Hopkins University, that the strain might be deficient in ability to acquire habits. Watson encouraged Basset to investigate the matter. Two learning problems were used. The first was the Watson circular maze, and the second was a problem box in which a treadle had to be pressed to give access to food. These problems were presented to animals of the low brain weight group, and also to a control group of "normal" brain weight, and it was concluded that the rats with less than normal brain weight were slightly inferior to the normal controls (Basset, 1914).

While Basset's work was in progress, the Wistar Institute also suggested a cooperative research program to R. M. Yerkes of Harvard. Yerkes undertook some preliminary studies, and then turned the problem over to a colleague, Mrs. Yerkes. In a footnote to the paper, R. M. Yerkes describes his interest in the research (and incidentally anticipated the later findings of Searle in regard to the Tryon strains).

> In suggesting to Mrs. Yerkes a comparative study of stock and inbred rats, I expressed especial interest in the attempt to analyze "the temperament" of the animals, for certain previous observations in comparison with those reported by Basset had convinced me that crude measurements of modifiability, if directly compared, might lead to seriously misleading conclusions because of differences in timidity, savageness, aggressiveness, sensibility, etc., in the two groups of organisms under observation [A. W. Yerkes, 1916, p. 267].

The Watson circular maze was again employed, along with the Yerkes brightness discrimination box. On the basis of the small number of animals available, it was concluded that the Wistar animals were somewhat inferior to normal control animals. The former were generally slower than the latter, and this was believed to be due to timidity.

Utsurikawa (1917) at Harvard, presumably under the influence of Yerkes, compared the Wistar rats with a control group, some of which were obtained from a Miss Lathrop, and some of which were from a second Wistar stock. A number of differences were described, with the Wistar animals being less active than the control animals, more prone to bite, more responsive to auditory stimulation, and more "timid," in that they retreated to the back of the cage as the experimenter approached. These results, in general, confirmed the work of A. W. Yerkes, who had used a control group of similar constitution with which to compare her Wistar rats.

In 1929 Crozier and Pincus presented the first of a series of studies on the inheritance of geotropic orientation in rats. It was found that three strains of rats differed in the angle of orientation adopted in climbing an inclined plane. It was shown, furthermore, that the relationship of orientation angle to steepness of the incline differed among the strains. In various F_1 and backcross-generation tests, it was concluded that variability of response, as well as magnitude of response, was inherited (Crozier and Pincus, 1932).

LEARNING BY MICE. Meanwhile, Bagg had made a study of strain differences in learning by mice. The influence of Cattell is acknowledged by Bagg: "In the work here described an attempt has been made to apply the methods of genetics to the study of conduct. Such work was begun by Professor J. McKeen Cattell some fifteen years ago, but the results obtained by him and his students were not published and the problem was given to me" (1916, p. 222). The initial report of this study was made in 1916, and a later report, on an increased number of subjects, was presented in 1920. Albino and colored mice (mainly yellow) were presented with two learning situations, a two-choice position discrimination problem and a multiple-choice problem. A considerable strain difference was found, with the yellow mice being poorer learners. In analyzing the records of mice within the same families, Bagg was unable to find any particular resemblance. However, it was noted that the quick learners exhibited a high degree of flexibility of behavior, as reflected in their quick mastery of the discrimination problem when the situation was reversed, and the formerly incorrect response was made correct. This relatively greater flexibility was later found in "bright" rats, as noted above (p. 215).

It should also be noted that Bagg, in a limited way, had applied some artificial selective breeding in his research. Two exceptionally poor learners of the yellow strain were mated, and their offspring proved to be greatly inferior to the white mice.

Another study on mouse learning was soon presented by Vicari (1921). The maze was an adaptation of the Cattell-designed maze used by Bagg, and two different strains of mice were employed—the Japanese Waltzer and the Bagg albino. Both of these strains had been inbred for nine or more years, and consequently could be expected to be relatively uniform genetically.

Several measures of performance were used—the number of errorless trials, the number of consecutive errorless trials, and the running time. With respect to the first two measures the strains were quite similar, but the Japanese waltzers showed much longer running times than the Bagg albinos.

Turning to the F_1 hybrids, a surprising result is found: 10 percent of the mice in this generation made more perfect trials than any parent in either parent race; some individuals excel all those in the parent races in the number of consecutive perfect trials; and the time averages, instead of being intermediate between those of the parent races, are considerably lower, lower even than the averages for the albinos [Vicari, 1921, p. 132].

Thus, hybrid vigor was identified in a behavioral characteristic.

A subsequent report (Vicari, 1929) gave the results for four highly inbred mouse strains, their F_1's and F_2's. In addition to the Japanese waltzing mice and the Bagg albino strain, this study included a dark brown strain and a brown strain with abnormal eyes (the eye abnormality being due to a mutation experimentally induced by X-rays and involving defects ranging from reduction in size to absence of one or both eyes).

In examining the learning curves for reaction time, Vicari found it possible to identify three types of curves: Type I, a flat curve, e.g., the dark brown animals' curve in Figure 25; Type II, a gradually descending curve, e.g., the Bagg albino curve in Figure 25; and Type III, a descending-ascending curve which was displayed only by the Japanese waltzers. When waltzers were mated with Bagg albinos, the Type II curve characteristic of the albinos was found for the F_1 and F_2. The F_1 animals were faster than either parent, and the F_2 animals were inter-

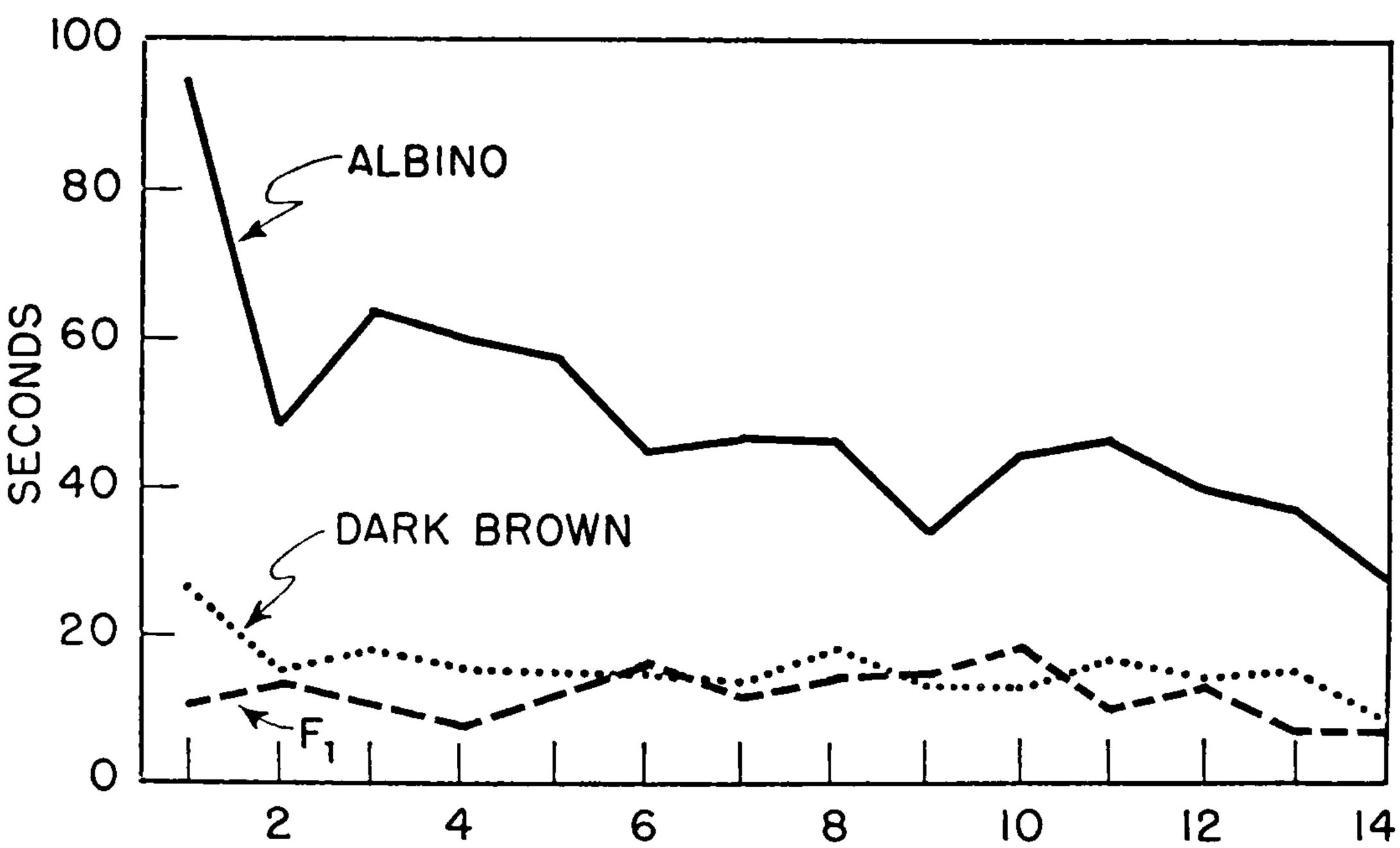

FIGURE 25. Different types of learning curve for running time for two mouse strains and their F_1. (After Vicari, 1929).

mediate to the parents. When albinos were mated with dark brown, the dark browns' Type I curve appeared in F_1. This outcome is shown in Figure 25. The average F_2 curve also resembled a Type I, but was irregular. Closer inspection led to the conclusion that thirty-five F_2 animals showed Type I and eleven showed Type II—very nearly a 3 : 1 Mendelian ratio!

Finally, crossing abnormal-eyed mice, characterized by a Type I curve but with generally high reaction time, with a dark brown, also with a Type I curve but much lower reaction time, gave an F_1 which was faster than either parent during the last half of the testing period —once again Vicari had found hybrid vigor. The F_2 resembled the dark brown parental strain.

In all three crosses the F_1 curve fell closest to the curve of the fastest parent, suggesting dominance of fast reaction time over slow reaction time. The hybrid vigor in the waltzer albino F_1, followed by intermediacy of the F_2, and the greater variance of F_2 relative to F_1, suggested that these two strains differed in respect to multiple factors. For the albino × dark brown cross, where a 35 : 11 F_2 ratio was found, Vicari proposed that the parent strains differed with respect to only one gene.

Generally speaking, the examination of individual family pedigrees gave results in accord with these interpretations.

THE DAWSON STUDY. In 1932 Dawson reported another mouse study, dealing with what was termed wildness and tameness. Two parental strains were obtained: one, the wild strain, consisted of laboratory-reared descendants of wild trapped mice which were easily excited, resisted handling, and were prone to bite. The other, tame stock consisted of relatively placid, easily handled mice obtained from various sources. From these strains, reciprocal F_1, F_2, and backcross generations were obtained.

The behavior measured was the time required for a mouse to traverse an enclosed runway approximately twenty-five feet long. Wild animals ran the runway much more quickly than did the tame animals. No difference was found between reciprocal F_1's, and the F_1 mean speed was nearly equal to that of the wild parents. The F_2 mean speed was slightly less than that of the F_1, but closer to the wild mean than to the tame mean, and F_2 variability was greater than F_1 variability. The backcross of F_1 to wild produced animals which ran as rapidly as the wild parents, and the backcross to tame gave animals which ran almost as slowly as the tame parents.

Dawson concluded from these results that the genes for "wildness" (as defined) were almost completely dominant, and that no maternal effect existed. Examination of the results for the sexes separately gave

no evidence of sex linkage. Two to three gene pairs were estimated to account for the difference between tame and wild.

Dawson also applied selective breeding within strains for four generations. The fastest of the wild were mated, and the slowest of the tame were mated. This selection had no effect on the wild line, but produced progressively slower animals in the tame line. This result amply demonstrates that considerable genetic variability existed in the original tame stock, a fact which renders interpretation of the results somewhat ambiguous.

RECENT MOUSE RESEARCH. Thus far, we have seen the procedure of strain comparison utilized in studies on learning and various attributes of "wildness" of rats and mice. In subsequent years there was a marked increase in the types of behavior pattern investigated and also some improvement in the breadth of coverage of other species. The large number of researches which have been performed makes it impossible to do more than briefly list some representative examples.

AGGRESSIVENESS. Scott (1942) found a strain of mice designated C3H to be more likely to initiate aggression than were C57BL mice. Ginsburg and Allee (1942), however, showed that males of the C57BL strain were superior to C3H in ability to win fights. The role of environment was also considered in this study, and it was found possible to make a given mouse either more or less aggressive by subjecting it to a systematic series of victories or defeats. Fredericson (1952) then showed that foster rearing of C57BL and BALB/c animals did not affect their aggressive behavior. Ecological implications of strain differences in aggressiveness were pointed out by Calhoun (1956), who placed small samples of mice in rooms containing food and a water supply and numerous nesting boxes. C57BL mice were placed in one room and DBA/2 mice in another. The DBA/2 mice were much less successful than the C57BL in reproducing themselves under these conditions. At least part of the difference was attributed to the fact that DBA/2 animals fought more often and more intensely than the C57BL animals. Occasionally, an aggressive DBA/2 was even found to attack a female, something which was never observed in the C57BL colony. Generally, the C57BL's appeared more adaptable to the environment, making quicker use of new food and nesting material, and, in respect to fighting behavior, the C57BL pattern tended to become one of threats and retreats, or relatively mild pushing about. Among the DBA/2's, on the other hand, the dominant male vigorously attacked subordinate males at every opportunity.

The mouse has also been featured in studies on exploratory or locomotor activity. Fredericson (1953) showed that, in an enclosed area,

C57BL mice were more prone than C3H or C Bagg albino mice to leave the area adjacent to the wall and to go to the center of the field. Thompson (1953) tested a number of inbred strains on several behavior traits, including the amount of locomotor activity displayed in an apparatus which contained numerous barriers. C57BL and C57BR sublines were very active, while BALB/c mice and mice of an A strain were very inactive. Other strains were more or less intermediate. The same general ranking of strain activity was later found (Thompson, 1956) in a Y maze, and in several other types of apparatus (McClearn, 1959), showing that the behavioral differences were not an idiosyncratic result due to the peculiarities of any one apparatus situation.

LEARNING. Relatively few of the more recent studies have been concerned with learning in mice. King and Mavromatis (1956) found C57BL mice to condition more rapidly than BALB/c mice in a shock-avoidance situation, but the BALB/c mice relearned more rapidly. Other studies (McClearn, unpublished data) have shown C57BL to be about equal to BALB/c mice in maze and discrimination learning, and both of these strains are superior to C3H animals. Denenberg (1959) has reported a difference between the conditioning rates of two C57 sublines which had been separated for approximately thirty generations. The genetic changes which have occurred during this interval are probably quite small relative to the total genotype, and the results appear to indicate, therefore, that changes in a relatively small number of genetic factors may appreciably influence learning ability.

ALCOHOL PREFERENCE. Strain differences have also been shown in alcohol preference when animals were given a choice between plain water and a 10 per cent alcohol solution (McClearn and Rodgers, 1959). C57BL mice gradually come to drink most of their daily consumption from the alcohol bottle, while animals from the A, DBA, and BALB/c strains almost completely abstain. F_1's between C57BL and the non-preferring strains show a mean preference higher than that of the non-preferring parent strain, but considerably lower than that of the C57BL strain (McClearn and Rodgers, 1961).

AUDIOGENIC SEIZURES. Another area in which mouse studies have made important contributions is that of the genetics of audiogenic seizures. Hall (1947) reported that DBA mice were much more prone to convulsive seizures than were C57BL mice, when presented with a loud auditory stimulus. In analyzing the responses of F_1, F_2, and back-cross animals, derived from these parent strains, Witt and Hall (1949) concluded that susceptibility to seizure was determined by a single

autosomal dominant gene. Ginsburg, Miller, and Zamis (1950) mated a different C57BL subline to DBA and found that the seizure incidence of the F_1 was intermediate. In the F_2, seizure incidence was about three-fourths of that in F_1. These authors took these data to indicate the presence of two or more non-dominant alleles. It was further found that different sublines of DBA had different degrees of susceptibility, and that the F_1's and F_2's derived from crossing these sublines with C57BL mice also differed. Ginsburg (1954) has emphasized, on the basis of differential response to various metabolites, that different genotypes underlie the seizure proneness of several susceptible strains which he has investigated. Fuller, Easler, and Smith (1950) also rejected the single-gene explanation in favor of a multiple-factor hypothesis.

RECENT RAT RESEARCH: HOARDING, ACTIVITY, AND EMOTIONALITY. In an investigation of rats, Stamm (1954) demonstrated large differences among three strains in food-hoarding behavior. The F_1 between a high-hoarding and low-hoarding strain hoarded as much as the high-hoarding parent strain, and a backcross of F_1 to the low-hoarding strain was intermediate between these two groups (Stamm, 1956). Broadhurst (1958b) studied five rat strains, including the three used by Stamm, in respect to locomotor activity and emotionality, as defined by defecation. Clear strain differences were found in both types of behavior, which were not, however, significantly correlated with each other. In comparing the strain characteristics with Stamm's results, a correlation between hoarding tendency and defecation was found.

Carr and Williams (1957) have also reported differences in locomotor (exploratory) behavior in an investigation of three rat strains.

DOMESTICATION, HORMONES, AND BEHAVIOR. A number of studies have compared the inbred Wistar albino rats with wild rats, in attempts to identify endocrine changes associated with the process of domestication. Hatai (1914) showed that wild Norway rats had heavier adrenals and gonads, but smaller hypophyses than the Wistar. No strain differences, however, were found in thyroid weight. King and Donaldson (1929) compared a group of gray rats, which had been in captivity for ten generations, with both wild animals and with the Wistar strain. Behaviorally, the gray line had become somewhat less savage, but were still less tame than the Wistars. Relative to the wild rats, the hypophyses, adrenals, and gonads of the gray rats were heavier, lighter, and equal, respectively. Relative to the Wistar strain animals, these glands were lighter, heavier, and heavier, respectively. In general, the results suggested a change in endocrine pattern of the gray rats toward that of the Wistars. Farris and Yeakel (1945) utilized the criteria of

tendency to defecate and/or urinate in an illuminated field in an effort to objectify the behavioral differences between wild and Wistar rats, and found the latter group to display much less emotional elimination.

Richter (1952) compared a line descendant from the original Wistar strain with rats trapped in the wild, and reported smaller adrenals, larger hypophyses, and more quickly developing gonads in the domesticated animals. Richter regards the changes as due to natural and artificial selection in the laboratory setting, where there is protection against predators, and an advantage given to the more fertile, milder, and "better-adjusted" rats. The argument is extrapolated to man, and evidence of similar changes during human "domestication" is presented (Richter, 1952, p. 283).

The general impression from the above studies is that laboratory selection, acting upon polygenic systems, has gradually altered the endocrinic basis of behavior described as indicating tameness. Keeler and King (1942), however, have summarized "character sketches" of various mutant stocks, and concluded that tameness may be accomplished by a mutant coat-color gene. Reservations concerning this interpretation have been expressed by Scott and Fredericson (1951).

AUDIOGENIC SEIZURES. Rats have also been employed in the study of susceptibility to audiogenic seizure. Strain differences have been found (Farris and Yeakel, 1943; Maier, 1943), and various experiments were oriented toward the problem of determining the number of genes involved. As was true in the case of the mouse research on this topic, the interpretation changed from a simple dominant hypothesis (Maier and Glaser, 1940) to a multiple-factor hypothesis (Maier, 1943; Finger, 1943). Hall (1951), in reviewing these researches, has taken the view that ambiguity in this case was due to the lack of genetic homogeneity within the strains employed.

MYERS' STUDY. We may close the consideration of studies comparing strains of rats with the remarkable investigation of Myers (1959). In this experiment, which dealt with shock-avoidance learning, there were five variables: type of stimulus (CS) (buzzer vs. tone); type of response (pressing a bar vs. rotating a wheel); time of testing (day vs. night); shock condition (floor and three walls shocked vs. floor and all four walls including manipulandum [bar or wheel] shocked); strain of animal (Sprague-Dawley vs. Wistar). When the data were analyzed in terms of the relative increase in responses, above operant level, during the period between CS and shock, a bewildering array of interactions emerged. When the manipulandum was not shocked, Sprague-Dawley rats were superior to Wistar rats when a tone CS was employed, but

were inferior when a buzzer was used. Furthermore, under this condition, both strains performed better during the day testing when tone CS was used, but more poorly when buzzer CS was used. However, when the manipulandum was shocked, differences between day and night testing were greatly reduced. The Wistars' performance to tone CS was better than the Sprague-Dawleys', but for buzzer CS conditions, strain differences were very small. Myers presented an ingenious explanation, based on an assumed strain difference in emotional startle responses to the manipulandum, with the level of such responses increasing at night in both strains. Whether or not this explanation proves ultimately to be correct, the empirical data have provided an admirable demonstration of the subtle ways in which genotypic differences may interact with environmental variables.

RESEARCH ON OTHER SPECIES. Sex drive was found to differ among males of different guinea-pig strains (Valenstein *et al.*, 1954), and it was demonstrated that the administration of sex hormones to previously castrated animals did not eliminate the strain differences (Riss *et al.*, 1955). Furthermore, the effectiveness of various conditions of social experience upon subsequent sexual behavior was found to vary from strain to strain (Valenstein *et al.*, 1955).

In rabbits, strain differences have been reported in nest-building behavior (Sawin and Crary, 1953), and in aggression (Denenberg *et al.*, 1958).

In mice of the genus *Peromyscus*, the study of various species and subspecies has revealed differences in climbing and jumping ability (Horner, 1954), in maternal behavior (King, 1958), in activity on an elevated maze (King and Shea, 1959), and in habitat selection (Harritt, 1952). In some instances the various subspecies or races are interfertile, and F_1 animals can be obtained for study. For example, Harritt (1952) mated *Peromyscus maniculatus bairdi*, which selected an artificial grass environment rather than an artificial tree-trunk environment, with *Peromyscus maniculatus gracilis*, which preferred the tree-trunk habitat. The F_1 results suggested dominance of the genetic factors determining grass preference, for the F_1 showed a strong preference for this type of habitat.

The well-established dog breeds have also provided valuable research material. James (1941) studied the behavior of dogs of a number of breeds in classical Pavlovian conditioning situations. Many animals were found to fall in one of two extreme behavior types: excitable or lethargic. Many others were intermediate. Some breeds were almost exclusively of one behavior type. For example, Basset hounds were all lethargic and German shepherds were all excitable. Five Basset hound-

shepherd F_1's were also studied, and were found to be intermediate. In seven F_2 animals the entire range from one extreme type to the other was displayed.

In other dog studies, breed differences have been shown in the development of dominance hierarchies (Pawlowski and Scott, 1956), response to different modes of rearing (Freedman, 1958), spontaneous activity (Anderson, 1939), "emotional behavior" (Mahut, 1958), trainability (Fuller, 1955), specific behavior characteristics such as trail-barking propensity (Whitney, 1932), and aggression (Fuller, 1953).

Whereas research on mammals has been predominant, some investigations have been made of other taxonomic groups. Hinde (1956), for example, investigated various threat, submission, and courtship behavior patterns in canaries, goldfinches, and green finches, and in F_1's derived from these species. In those instances where both parents possessed the behavior pattern, it was found to be unchanged in the F_1. When only one parent showed the behavior, or when it was shown in different degrees in the two parents, expression was intermediate in the F_1.

Differences in behavior among several Drosophila species have been intensively investigated from the point of view of the reproductive isolation of one species from another (see Spieth, 1958; Santibañez and Waddington, 1958; Manning, 1958). Another example of insect research is provided by Rothenbuhler (1958), who found one inbred line of honey bees which quickly removed diseased brood from the comb, and another line which did not. The F_1 resembled the last-named line, indicating that the "hygienic" behavior pattern is recessive.

The above must be regarded as only a sample of the literature available, but will perhaps serve to illustrate that clear evidence of genetic influence has been obtained in a wide variety of behavior patterns and at various phylogenetic levels.

THE SEARCH FOR SINGLE GENE EFFECTS. In view of the history of genetics it is understandable that in many of the pioneer behavioral studies rather persistent attempts were made to interpret the results in accord with simple Mendelian hypotheses. It is, of course, legitimate, and, indeed, obligatory, to examine any results to determine if they are susceptible to a single-locus interpretation. In the earlier discussion of genetic principles, however, it was pointed out that the dependence of most behavior patterns upon many integrated organ systems makes a polygenic hypothesis *a priori* more likely. In fact, we have seen that many of the simple interpretations had to give way later to polygenic ones. On the other hand, the success of the human researches in establishing the simple genetic basis of some mental-deficiency syndromes provides a reminder that single genes, strategically located in the

causal paths leading to a phenotype, may produce large effects. Similar reminders are available in the mouse literature, particularly in the studies on neurological and labyrinthine disorders.

WALTZING AND OTHER "NEUROLOGICAL MUTANTS." As a matter of fact, some of the very earliest behavioral genetics studies dealt with one of these conditions, which is known as "waltzing." Waltzing is a periodic, extremely rapid whirling movement, and was characteristic of a strain of mice called "Japanese waltzing" or "Japanese dancing" mice. The syndrome also includes head-shaking and deafness.

Von Guaita reported (1898, 1900) that mating waltzers with normal albino mice yielded offspring which did not show the waltzing characteristic. Darbishire (1904) also mated waltzers with normal albinos in a study aimed at determining if coat color and waltzing were inherited in a Mendelian manner. Two hundred and three F_1 offspring were obtained, none of which waltzed. When the F_1 animals were mated to other F_1 animals, the resulting F_2 consisted of 458 non-waltzers and 97 waltzers. Darbishire concluded that, while waltzing was recessive in good Mendelian fashion in the F_1, the F_2 results were too discrepant from the expected 3 : 1 ratio to support the notion of Mendelian segregation. In general, from the waltzing and coat-color data, Darbishire upheld the biometrical insistence on a form of blending inheritance, and denied the "purity of gametes."

In 1907 R. M. Yerkes published a book devoted to a description of the behavior and capabilities of the Japanese waltzing mouse. With respect to waltzing behavior, Yerkes noted that one line of waltzers tended to whirl to the left while another line consisted of left-whirlers, right-whirlers, and mixed-direction whirlers. He suggested that the "pure" waltzer inherited a tendency to whirl to the left, and that this tendency was obscured in the one line because its ancestry included some non-waltzing mice. No attempt was made to relate this suggestion to Mendelian genetics, although Darbishire's results and Bateson's Mendelian interpretation of them had been considered earlier in the book.

Later research (summarized in Grüneberg, 1952) has made it clear that waltzing is a Mendelian recessive condition, and that the discrepancies in F_2 ratio, such as were noted by Darbishire, are due to reduced viability of the homozygous animals, which results in the death of some of this group before they can be classified.

A number of other mutants have been found which give rise to waltzer-like symptoms (e.g., jerker, fidget, shaker), thus illustrating that similar phenotypes can result from the action of different genes.

Other "neurological" conditions, involving, variously, muscular tremor, incoordination, abnormal posture, head-shaking, and deafness

or auditory hypersensitivity have also been described as single-gene effects.

DROSOPHILA MATING. Insect research has provided more examples of single-gene effects. Several studies (e.g., Reed and Reed, 1950; Merrell, 1953) have shown that some conditions determined by a single gene lower mating activity in Drosophila. Bastock's (1956) research provides an illustration of this type of experiment. It had long been known that mutant yellow males were less successful in mating than were normal males. Bastock's aim was to determine if this fact was due to a behavioral difference which resulted from the presence of the yellow gene, which is a sex-linked recessive. Thus it was important to obtain normal and yellow males which were highly similar in other genetic respects. To accomplish this, heterozygous females were mated to yellow brothers. The male offspring of this cross were yellow and normal in equal numbers, and other genetic differences could be expected to be randomly distributed between the two color groups.

The normal courtship pattern of the male Drosophila includes a bout of wing vibration, which evidently provides important stimuli which are detected by the female antennae. It was found that the duration of the wing vibration bouts by yellow males is shorter than normal, and this behavioral difference reduces the effectiveness of the courtship of the yellows.

The Lamarckian Issue

In general, the researches on behavioral genetics have not been particularly involved in the development of concepts within the field of genetics itself. The over-all picture is rather one of the application of already demonstrated principles and techniques to the particular subject matter of behavior. With respect to the question of the inheritance of acquired characteristics, however, the behavioral studies formed an important part of the evidence, and were centrally involved in the controversy which took place. We have seen that the Mendelian theory posited a "purity of the gametes" which was incompatible with the idea that acquired traits could be transmitted. Nonetheless, "Lamarckism" persisted obstinately and was repeatedly put forward in spite of much contradictory evidence. The first negative study in behavior was provided by Yerkes (1907) in his work, *The Dancing Mouse*. One male and one female from each of two lines was taught a black-white discrimination, and they were then mated. From their litters, one male and one female were chosen for training, and were then mated, and so on for a total of four generations. There was no indication that the offspring benefited in learning ability by having parents, grandparents,

and even great-grandparents who had learned the problem. "There is absolutely no evidence of the inheritance of this particular individually acquired form of behavior in the dancer" (p. 283).

Griffith (1922) reported an experiment in which white rats were rotated day and night in revolving cages for several months. When the animals were released from the cages, they showed marked changes in posture and a characteristic circling movement. When these affected animals were mated with normal rats, some offspring were found who displayed disequilibration. Detlefson (1923, 1925) soon reported similar results. A number of defects of these studies were pointed out by later workers, the most compelling of which was the possibility that the animals had contracted a middle ear disease, affecting the labyrinthine mechanism. The accumulation of animal waste during the uninterrupted rotation of the cages would be favorable to the spread of a disease organism. In the matings the infection could be transmitted by parents to offspring, and a superficial appearance of "inheritance" would be given.

In the face of these and other objections (see Munn, 1950, p. 40), the Griffith and Detlefson studies came to be regarded generally as inconclusive.

PAVLOV'S ANNOUNCEMENT. A new round in the controversy was dramatically begun by Pavlov, who stated in 1923 during a lecture tour in the United States:

> The latest experiments (which are not yet finished) show that the conditioned reflexes, *i.e.*, the highest nervous activity, are inherited. At present some experiments on white mice have been completed. Conditioned reflexes to electric bells are formed, so that the animals are trained to run to their feeding place on the ringing of the bell. The following results have been obtained.
>
> The first generation of white mice required 300 lessons. Three hundred times was it necessary to combine the feeding of the mice with the ringing of the bell in order to accustom them to run to the feeding place on hearing the bell ring. The second generation required, for the same result, only 100 lessons. The third generation learned to do it after 30 lessons. The fourth generation required only 10 lessons. The last generation which I saw before leaving Petrograd learned the lesson after 5 repetitions. The sixth generation will be tested after my return. I think it very probable that after some time a new generation of mice will run to the feeding place on hearing the bell with no previous lesson [1923, pp. 360–1].

Thus could conditioned reflexes, through a Lamarckian mechanism, be converted into unconditioned reflexes!

CONTRADICTORY EVIDENCE. Just a few months later, two reports contradictory to Pavlov's results were announced. Vicari (1924), using mice, and MacDowell (1924), using rats, found no evidence that offspring of maze-trained ancestors learned the maze with any more facility than did their ancestors. Another negative report came from Sadovnikova-Koltzova, who examined her data on rats' maze performance and concluded that ". . . we see that the teaching of parents did not increase the abilities of the offspring" (1926, p. 316).

McDougall felt that Darwinian natural selection was not sufficient to account for the evolutionary process, and that the Lamarckian principle had to be invoked. Pavlov's results were a bit too good to be true, so McDougall had attempted to replicate them, with no success. He had therefore written Pavlov concerning the matter, and Pavlov had replied, ". . . briefly stating that he no longer held his deductions from his experiments to be valid" (McDougall, 1927, p. 271). Anrep, who translated Pavlov's works into English, also told McDougall that Pavlov had authorized him to make a retraction in the forthcoming *Conditioned Reflexes*. This was duly made in a footnote as follows:

> Experiments . . . upon hereditary facilitation of the development of some conditioned reflexes in mice have been found to be very complicated, uncertain and moreover extremely difficult to control. They are at present being subjected to further investigation under more stringent conditions. At present the question of hereditary transmission of conditioned reflexes and of the hereditary facilitation of their acquirement must be left entirely open [Pavlov, 1927, p. 285].

Razran (1958) informs us that there is no evidence that Pavlov carried out his announced intention to repeat the experiment, and the whole topic is conspicuously absent from Pavlov's later publications.

MCDOUGALL'S RESEARCH. McDougall persevered, however, and undertook a long-term investigation with Wistar strain rats. The learning situation employed consisted of three parallel alleys in a water tank. The animals were placed in the center alley, and upon swimming its length could choose to turn either right or left into one of the side alleys. Each side alley contained an escape platform and could be illuminated or left dim. The dim alley was the correct path. The platform in the illuminated alley was electrified so that the rat would receive an electric shock if it attempted to escape the water by that route. Each generation was obtained by supposedly random selection from the preceding generation. The principal results were a decrease in the number of errors made in the thirty-four successive generations, and the gradual development of "photophobia." The results were interpreted

as demonstrating the inheritance of characteristics acquired by the experience of the ancestors (McDougall, 1927, 1930, 1938; Rhine and McDougall, 1933).

Criticisms appeared at once (Hazlitt, 1927; Crew, 1930), directed primarily to procedural matters. One of these criticisms suggested that there had been non-deliberate selection of faster learning animals as parents. Furthermore, McDougall had unfortunately failed to maintain an untrained control group from the same initial stock as the trained group, but had relied upon animals newly imported to his laboratory for control observations. McDougall challenged some of the criticisms, and undertook to select for *poorer* learning ability. There was still improvement over a number of generations.

ATTEMPTS TO REPLICATE McDOUGALL'S RESULTS. The issue was of such importance that two repetitions of the costly experiment were attempted. Crew (1936) also began with Wistar strain rats, and used an apparatus similar to McDougall's. In this study, however, a control line was maintained from the outset. Some of the control animals were tested in each generation to provide data for comparison with the trained line, and other control line animals were retained, untrained, to provide the next generation. In the trained line, of course, all animals were trained. Over eighteen generations, Crew (1936) found no convincing evidence of a decrease in errors among the trained line, and they were, in fact, not different from the untrained controls. In both groups there were wide fluctuations from generation to generation.

Agar and collaborators (1948) likewise started with Wistar rats, used an apparatus similar to McDougall's, and maintained a control line. In this experiment a progressive improvement did occur over twenty-eight generations in the trained group, but this was followed by a worsening in performance from the twenty-eighth to the thirty-sixth generation. More important, the results were remarkably paralleled by the control group, in which the parents of each successive generation *had never been trained.*

It is not possible to establish definitely exactly what accounts for McDougall's results, but the failure of Crew's and Agar's attempts to replicate them casts serious doubt on the validity of the Lamarckian explanation, and various alternative explanations have been advanced. The small size of the breeding population, for example, could lead to inbreeding depression, and all the cited researches agree that less vigorous animals learn more quickly in this particular situation. Small breeding populations are also susceptible to genetic drift, so that over a period of time a line could change quite considerably in genetic constitution, even in the absence of any selection. The possibility of gradual

and systematic change in environmental conditions of rearing and testing during the many years involved in such an experiment is another important possibility.

Failures to demonstrate unambiguously the Lamarckian phenomenon, and the great successes of the genetical theory which presupposes absence of Lamarckian effects, have brought Lamarckism into general disrepute in modern genetics. The only notable exception is provided by Russian Lysenkoism. One very recent line of research, moreover, has shown how apparent transmission of acquired characters may be due to subtle selection for modifying genes (Waddington, 1957).

Summary of Animal Research

The general picture presented by animal behavioral genetics is of a discipline which has established a base of operations by the demonstration of genetic influence in a wide variety of behaviors and in diverse animal species. Over and above the establishment of the simple fact of genetic contribution, some progress has been made in determining the mode of gene action. In some cases it has been possible to demonstrate single-gene effects. In some polygenic characters, descriptions of additive effects or of partial average dominance are available. There have also been advances in describing the causal processes between genes and behavioral characters.

In terms of application of current genetic theory and procedure, behavioral genetics lags behind. For example, one of the central concepts of modern genetics is that of *heritability*, which is defined as the ratio of the variance attributable to additive gene effects to the total phenotypic variance. This quantity represents the genetic contribution which is "useful" in the sense that it provides for firm prediction of the outcome of various matings (e.g., in a selection program). Effects due to dominance and epistasis, which are, to be sure, genetic, are dependent upon the vagaries of combinations of genes, and consequently are less predictable. As yet, only a few studies have attempted to estimate heritabilities of behavioral traits (Hirsch and Boudreau, 1958; Broadhurst, 1959). Further development of behavioral genetics will require the precise estimation of the heritabilities of a broad range of behavior patterns.

Again, it is rather remarkable that in animal work, where the technique could be most appropriately applied, there has been so little work on correlations among relatives. Only one study in which correlations were the chief concern (Burlingame and Stone, 1928) has come to the author's attention. Other techniques have also remained untried. For example, a very recent publication by Broadhurst (1959) provides the first example of the use of diallele crossing in studying behavioral

traits. In this procedure F_1's are obtained among a number of inbred strains, and the results provide estimates of heritability and description of the relative contributions of additive, dominance, and epistatic effects.

Another technique only recently introduced to behavioral genetics is that of chromosome analysis in Drosophila (Hirsch, 1961). In this technique specific chromosomes may be combined in desired combinations, and the contributions of each chromosome to a particular type of behavior can be assessed.

It seems reasonable to judge that the foundation of behavioral genetics is now sufficiently stable to permit the future course of research to be more detailed and refined explorations of the dynamics of genetic determination of behavior.

Behavioral Genetics and Psychology

To this point, little has been said of the relationship which studies in behavioral genetics have had to psychology in general. To a considerable extent, of course, developments in behavioral genetics were directed by contemporary trends in psychology. The great concern with the inheritance of learning ability in animals, for example, reflects the dominant role which learning theory has played in psychology. Furthermore, the techniques which could be utilized in the study of the genetics of behavior have depended upon the refinements and improvements in psychological procedures. The Watson circular maze gave way to the multiple T-maze; assessment of intelligence in humans was made ever more precise as new instruments were developed, and so on.

The reciprocal influence, that of behavioral genetics upon developments within psychology as a whole, has been limited by the predominantly environmentalistic orientation which has characterized psychological theory.

From the beginning, there have been vigorous opponents to any suggestion that the composition of a man's chromosomes could have any determining effect upon his intelligence, personality, emotional stability, or any other "mental or moral" characteristic. There ensued an intense debate, which has come to be known as the nature-nurture controversy.

In all controversies of this type, apparently, the motivations of the opposing teams are diverse and various, and this is clearly true of the nature-nurture debate. For some, religious convictions may have played a predominant role in shaping opinions. Political attitudes were also undoubtedly involved. Are not all men created equal? This was a self-evident truth to the signers of the Declaration of Independence. Arguments that some men are inherently wiser than others have appeared to some to be inimical to the democratic ideal, and to imply the rightness of a rule by the elite. The dominant political philosophy of a large part

of Western culture during much of the nature-nurture controversy has insisted, on the contrary, that education and socioeconomic reform can improve the lot of individuals and thereby the stature of a culture. Pastore (1949) has presented a detailed defense of the thesis that sociopolitical allegiances have played a major role in determining opinion on this issue. In the late 1930's and the 1940's, particularly, the horror at the results of the Nazis' perverted application of their pseudogenetics of race differences led to a strong bias against any suggestion of inheritance of mental characteristics.

Another factor which presumably acted to reduce interest in psychological genetics was the dampening of the ardor of eugenicists. As newly discovered genetic principles were brought to bear on the proposals of eugenics, it became clear that some of the early hopes for quick improvement in human welfare through genetic alteration were overly optimistic. Since eugenic considerations had directly or indirectly motivated much of the human research, it was inevitable that the disenchantment would have an adverse effect on the vigor with which studies on behavioral genetics were conducted. (See Scheinfeld, 1958, for a discussion of changing views in eugenics.) Furthermore, as we have seen, there is considerable room for differences in interpretation of the evidence, especially in the case of the human data.

But the most important factor was no doubt the development of the "behavioristic" point of view which assumed a dominating role in the developing discipline of psychology, particularly in America. With J. B. Watson as the prime mover, behaviorism developed as a protest against all forms of introspective psychology. Mental states, consciousness, mind, will, imagery—all became taboo. Stimulus and response were the only acceptable explanatory terms.

The instinct doctrine, which had been brought to its culmination by McDougall (1908), was also attacked by behaviorists as being redundant and circular. Instincts had been thought of as inherited patterns of behavior in contrast to learned behavior, and with the rejection of instincts, the whole notion of heredity influencing behavior was cast into discard. The burden of explaining individual differences fell completely to environmental factors.

> So let us hasten to admit—yes, there are heritable differences in form, in structure . . . These differences are in the germ plasm and are handed down from parent to child. . . . But do not let these undoubted facts of inheritance lead us astray as they have some of the biologists. The mere presence of these structures tells us not one thing about function. . . . Our hereditary structure lies ready to be shaped in a thousand different ways—the same structure—depending on the way in which the child is brought up [Watson, 1930, p. 97].

Objectors will probably say that the behaviorist is flying in the face

of the known facts of eugenics and experimental evolution—that the geneticists have proven that many of the behavior characteristics of the parents are handed down to the offspring. . . . Our reply is that the geneticists are working under the banner of the old "faculty" psychology. One need not give very much weight to any of their present conclusions. We no longer believe in faculties nor in any stereotyped patterns of behavior which go under the names of "talent" and inherited capacities" [p. 99].

Our conclusion, then, is that we have no real evidence of the inheritance of traits. I would feel perfectly confident in the ultimately favorable outcome of careful upbringing of a *healthy, well-formed* baby born of a long line of crooks, murderers and thieves, and prostitutes. Who has any evidence to the contrary? [p. 103].

Then came the familiar and frequently quoted challenge:

> I should like to go one step further now and say, "Give me a dozen healthy infants, well-formed, and my own specified world to bring them up in and I'll guarantee to take any one at random and train him to become any type of specialist I might select—doctor, lawyer, artist, merchant-chief and, yes, even beggar-man and thief, regardless of his talents, penchants, tendencies, abilities, vocations, and race of his ancestors." I am going beyond my facts and I admit it, but so have the advocates of the contrary and they have been doing it for many thousands of years [p. 104].

Woodworth (1948) has pointed out that this extreme environmentalism was not a necessary consequence of the behavioristic philosophical position, and suggests that Watson's stand was taken, in part at least, "to shake people out of their complacent acceptance of traditional views" [2] (1948, p. 92). For whatever reason Watson sought to exorcise genetics from psychology, he succeeded to a remarkable degree, and the position taken in his *Behaviorism* soon became the "traditional view" which was "complacently accepted" by the majority of psychologists.

It is quite apparent from the account given above that this majority view was not without opposition. In fact, since Watson's pronouncement, no single year has passed without publication of some evidence showing it to be wrong. Collectively, these researches have demonstrated the important role of the genotype in many kinds of organism and in many varieties of behavior pattern. From the accumulated evidence, it is obvious that genetic differences are fundamental to individuality, in behavior as well as in physical characteristics.

It would be rash to predict in any detail the effect which the implications of this generalization will have upon psychology in the future. It does appear, however, from a striking increase in the rate of publications

[2] From Robert S. Woodworth, *Contemporary Schools of Psychology*, Revised Edition: Copyright 1948, The Ronald Press Company.

in the past decade, that a growth of interest is under way. The hope might be expressed that this growing interest presages a general understanding of the fallacy of the nature-nurture dichotomy, and an acknowledgment of the mutual, interacting, and co-operative roles played by the genes and by environmental agencies in shaping psychological characteristics.

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