9.

The Genetics of Behavior

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Six years after the inauguration of modern experimental psychology by Gustav Theodor Fechner, Gregor Johann Mendel founded the science of genetics by executing a brilliantly designed series of studies on the garden pea. It is a curious fact that these two life sciences which grew up in the same period of history have rarely worked closely together. Genetics has concerned itself almost exclusively with morphology; it has paid scant attention to behavior. Psychology, on the other hand, although it has taken a lively interest in heredity, has too often attempted to investigate the relation of behavior to genetic constitution by methods of pre-Mendelian vintage.

A real genetics of behavior promises to emerge, however, as psychologists continue to adopt the procedures of modern genetics, and as geneticists turn their attention more systematically to behavior. This encouraging trend will ultimately give status and stature to an interdisciplinary science of *psychogenetics*. The psychogeneticist of the future will presumably be trained in the methods and techniques of both genetics and psychology.

A survey of the present accomplishments of this hybrid discipline is the task of this chapter. It reviews the methods of genetics and their application to the investigation of the genetic basis for psychological traits, and it recounts some of the initial attempts to establish a genetics of behavior. It is not primarily concerned with the nature-nurture argument, nor does it attempt to evaluate investigations of human heredity. In the writer's opinion, the genetics of behavior must be worked out on species that can be subjected to controlled breeding. At the present time this precludes human subjects.

The main objectives of psychogenetics are four in number: (1) to discover whether a given behavior pattern is transmitted from generation to generation, (2) to determine the number and nature of the genetic factors involved in the trait, (3) to locate the gene or genes on the chromosomes, and (4) to determine the manner in which the genes act to produce the trait.

HEREDITY AND BEHAVIOR

The first objective, to find out whether heredity plays a part in the determination of a psychological characteristic, may be realized best by the method of selective breeding and by the method of comparison of different strains, breeds, or species. The method of selective breeding is the more arduous of the two. The comparison of strains already established, e.g. wild versus tame strains of rodents, is relatively simple.

Selective Breeding

Selective breeding consists of mating animals that display the desired trait and of selecting for breeding from among their offspring those that express the trait. If the trait is regulated by heredity, continued selection for a number of generations in a uniform environment will result in a strain that breeds more or less true for the character under study. Selection for more than one value of the trait may be made. In a trait that expresses itself alternately, e.g. susceptible or not susceptible to audiogenic seizures, two strains, susceptible and resistant, may be established concurrently by selective breeding. If the trait is one that expresses itself in degree on a continuum, e.g. maze learning, selection of a number of different values of the trait may be made. In practice, selection for a "quantitative" trait is usually limited to the extremes of the distribution, e.g. fast and slow maze learners.

Maze learning. Tryon (1940, 1942) was able to prove, by selective breeding, that maze-learning ability in the rat is inherited. Tryon describes his experiment as follows:

> An experiment was begun in 1927 that had as its purpose the establishment by selective breeding of a pure line of maze-bright and a pure line of maze-dull rats. Each animal was run nineteen trials through a seventeen-blind T maze. His score was the total number of entrances into blind alleys. The breeding schedule consisted in mating together the brightest rat within each of the brightest litters, the dullest within each of the dullest. Rigorous environmental controls were effected (1) by instituting standard procedure of animal care and of breeding, (2) by using an automatic mechanical device for delivering the animals into the maze without handling, and (3) by employing an electric recorder for the scoring of each rat's maze run. These controls have remained constant for eleven years. Selective breeding has continued for eighteen generations. [1940, p. 112.]

Tryon's parental generation consisted of an unselected, heterogeneous population of 142 rats. The distribution of their scores appears on the top line of Fig. 1. As Tryon states, "the breeding schedule consisted in mating together the brightest rats within each of the brightest litters, the dullest within each of the dullest." These F_1 rats were run on the maze, and the resultant distribution of scores appears on the next line of Fig. 1. The same breeding procedure was followed for each successive generation.

TABLE 1

A STATISTICAL SUMMARY OF TWELVE GENERATIONS OF TWO STRAINS OF RATS SELECTIVELY BRED FOR ACTIVITY AND INACTIVITY (RUNDQUIST)

(Revolutions in thousands for 15 days)

Parental Generation

Males			Females		
No.	Mean	S.D.	No.	Mean	S.D.
24	21	10	24	28	22

Generation	Active Strain Males			Inactive Strain Males				Active Strain Females			Inactive Strain Females			
	No.	Mean	S.D.	No.	Mean	S.D.	C.R.*	No.	Mean	S.D.	No.	Mean	S.D.	C.R.*
F_1	17	141	78	14	72	89	2.27	10	115	65	9	104	83	0.33
F_2	10	138	72	15	84	65	1.89	9	142	39	18	90	48	3.02
F_3	7	153	92	13	65	66	2.24	7	200	67	7	129	65	2.01
F_4	24	143	96	25	129	104	0.49	31	181	122	20	173	89	0.27
F_5	19	141	96	16	31	27	4.77	22	198	61	20	60	52	7.90
F_6	30	178	90	23	22	25	9.04	23	255	69	25	68	55	10.28
F_7	28	131	80	18	10	17	7.77	27	205	97	28	50	45	7.55
F_8	29	136	70	11	15	19	8.57	29	234	70	19	39	49	11.30
F_9	32	168	41	21	22	45	11.38	20	237	53	25	46	47	12.62
F_{10}	26	150	75	25	4	5	10.12	26	257	77	23	24	34	14.02
F_{11}	26	151	66	21	6	9	11.02	25	267	104	29	23	28	11.45
F_{12}	26	123	53	29	6	5	11.23	23	172	66	23	20	24	10.29

* Critical ratio.

Gradually the two groups, maze-bright and maze-dull, pulled apart, and in F_7 there was practically no overlapping between them.

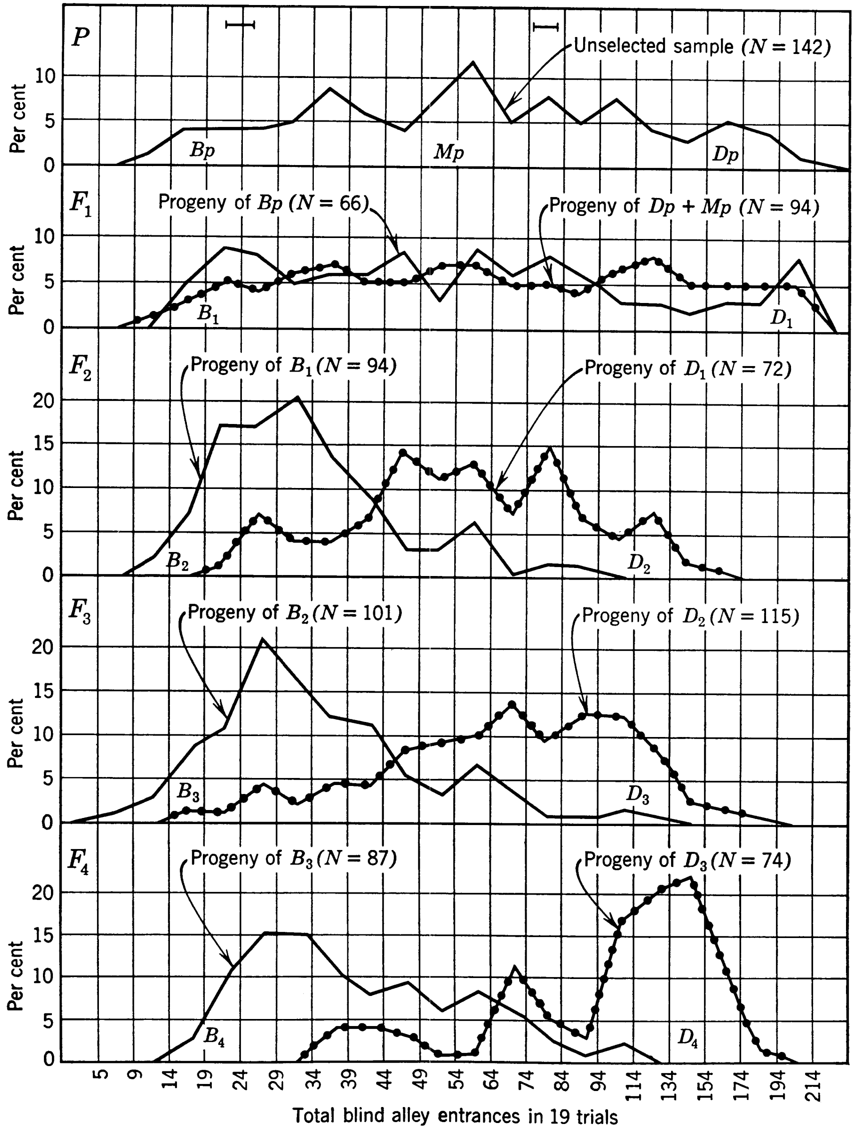

FIG. 1. Selective breeding for maze-learning ability in rats. (Tryon, 1942.)

Tryon writes, "There appears to be a law of diminishing returns, for after the F_7 negligible effects of selective breeding are noted" (1940, p. 114).

Tryon's experiment has been repeated by Heron (1935) with similar results.

Voluntary activity. Rundquist (1933) used the method of selective breeding to investigate the role of heredity in voluntary activity of the rat. Voluntary activity is defined as the number of revolutions turned by the rat in a revolving drum. Rundquist selected for high activity and for low activity and was able to establish two strains that displayed some consistency, from generation to generation, in the two extreme manifestations of the trait (Table 1). It is interesting to note that during the first four generations selection within each strain was not practiced. Instead Rundquist mated together the most active rats even though

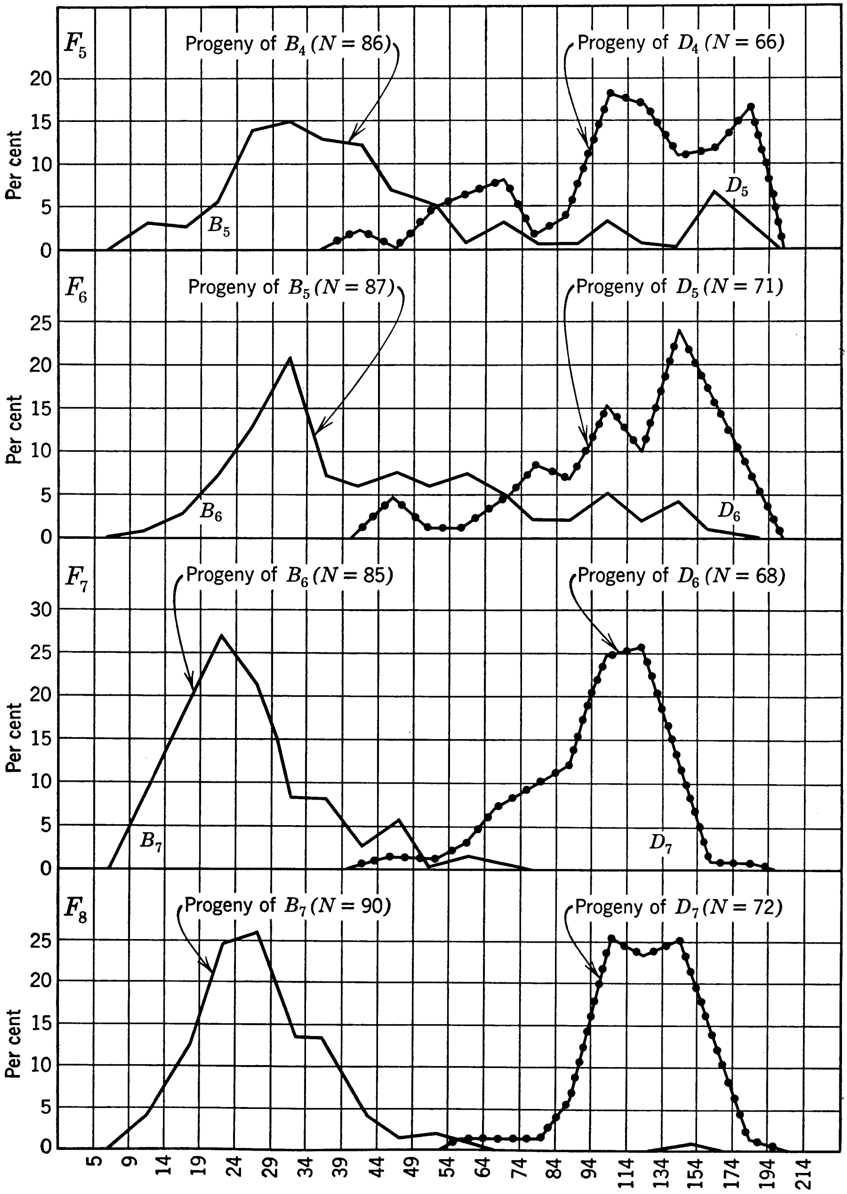

FIG. 1 (*continued*).

they might have had inactive parents, and the most inactive rats even though they might have had active parents. As a consequence of selection regardless of ancestry, no differentiation between the groups occurred from F_1 through F_4. If selection is to be effective in producing strains that breed true, it is necessary to continue breeding within the family lines that have been initially selected from the parental population.

Emotionality. A third example of selective breeding for a psychological trait is the investigation of emotionality in the rat by Hall (1938). Hall established that defecation and urination in a strange situation are valid measures of emotionality (1934). The procedure consists of placing a single animal in a brightly lighted circular enclosure 7 feet in diameter, for 2 minutes a day for 12 days. A record of urination and defecation on each trial is kept. The range of scores varies from 0 (no instance of either urination or defecation) to 12 (the rat defecates or urinates during every trial in the field). The parental generation, consisting of 145 rats, was a heterogeneous group. The high-scoring rats were mated together to start the emotional strain, and the low-scoring animals were bred *inter se* to initiate a nonemotional strain. In succeeding generations the highest scoring animals of the emotional strain were interbred and the lowest scoring animals of the nonemotional strain were interbred. The results appear in Table 2. The emotional strain becomes, on the average, more emotional until the ninth generation, when the mean becomes stabilized at approximately 10 and the standard deviation at a little over 2. Selection for nonemotionality yields less systematic results. The averages and variabilities fluctuate in a random fashion within rather narrow limits. It is significant that the maximum effects of selection for nonemotionality are realized in the first generation, whereas it takes nine generations for the emotional strain to become stabilized. Further comment upon this point will be reserved for a later section.

TABLE 2

A STATISTICAL SUMMARY OF TWELVE GENERATIONS OF TWO STRAINS OF RATS SELECTIVELY BRED FOR EMOTIONALITY AND NONEMOTIONALITY (HALL, UNPUBLISHED MATERIAL)

No. of Days of Defecation or Urination
Parental Generation

No.	Mean	S.D.
145	3.86	3.54

	Emotional Strain			Nonemotional Strain			
	No. of Days of Defecation or Urination			No. of Days of Defecation or Urination			
	No.	Mean	S.D.	No.	Mean	S.D.	C.R.
F_1	40	3.07	3.36	35	0.46	0.77	4.74
F_2	18	4.72	4.12	18	1.94	2.28	2.50
F_3	65	3.92	3.64	50	1.02	1.30	6.00
F_4	84	4.69	3.89	52	1.40	1.43	7.00
F_5	75	4.96	3.85	59	0.41	1.18	8.44
F_6	48	6.87	3.28	51	0.51	1.13	12.72
F_7	72	7.82	3.18	53	0.17	0.47	20.40
F_8	77	8.37	2.94	40	1.07	2.46	14.29
F_9	85	10.31	2.09	32	1.68	3.25	14.15
F_{10}	66	10.41	2.08	22	1.45	3.13	12.45
F_{11}	57	10.11	2.39	42	1.05	2.01	20.11
F_{12}	47	10.40	2.18	31	1.65	2.53	15.91

The consistency within some litters of the emotional and nonemotional strains may be illustrated by two examples of parent-child resemblances. Two F_9 rats with scores of 10 and 12 had a litter of nine whose scores were 12, 12, 12, 12, 12, 12, 11, 11, and 10. Two nonemotional F_9 rats with scores of 0 and 0 had a litter of six whose scores were 0, 0, 0, 0, 1, and 1.

To the investigator planning a selective breeding experiment the following suggestions and cautions may prove useful. (1) Since an experiment of this nature usually requires many years and many dollars, the investigation of psychological traits of primary importance should be given priority. (2) The investigator should make certain that the measure or measures employed are reliable and valid. Tryon (1942) has discussed this point thoroughly. (3) Uniform procedures for raising, handling, and testing the animals are essential, since variations in procedure may distort conclusions. Temperature, feeding schedules, the type of food, the amount and kind of handling, litter, size, the type of living cages, the age at which the animals are tested, and numerous other details must remain constant from generation to generation. The animals should also be kept free of parasites, for, as Russell (1941) reminds us,

> . . . some differences that have been attributed to genetic causes may be due to parasites. Because of the limited number of parents, there is a relatively high probability that an inbred line will become uniformly infected, particularly with parasitic organisms that are transmitted from mother to offspring. [P. 347.]

(4) The health and vigor of the strains should be maintained at a constant level. Selection for uniform vigor as well as for the trait under study will help to insure the maintenance of the strains. (5) Fertility is another important requisite. Obviously the loss of a strain through sterility must be avoided. Fertility must be maintained even at the risk of the confusion that would be introduced into the genetic picture if the trait investigated should turn out to be correlated closely with fertility. However, the danger of such confusion is probably not great, for Wright (1922) has shown that variations in fertility and vigor are determined largely by environment. In practice only fertile animals should be selected for breeding. (6) The transmission of a trait from generation to generation may appear to be genetic, whereas in reality it is due to an extragenetic factor. The mode of transmission may be some prenatal or postnatal influence of the mother on the young. The prenatal influence can be determined by transplanting the fertilized egg to a host mother of a different strain. The postnatal influence can be investigated by placing the neonates with a foster mother.

In sum, the psychogeneticist must always remember that in studying trait inheritance he puts himself in the difficult position of trying to prove a negative: that the trait in question is *not* due to extragenetic factors. He adds to the plausibility of his conclusions in direct measure as he controls the effects of all extraneous influences.

Strain Differences

A strain is defined as a group of individuals of a species that have a common lineage resulting from either natural or artificial selection and inbreeding. The extent of common ancestry determines the degree to which the strain is inbred. Close inbreeding, viz., brother-sister matings, for a number of generations eventually produces a pure strain. The animals of a pure strain are genetically identical except for the segregation of sex chromosomes. A pure strain will breed true for genetically determined traits, unless mutations occur. The animals of a strain that is not homozygous (pure), but in which some inbreeding has occurred, will tend to possess certain common characteristics that differentiate them from animals of other strains. Hence, by comparing the behavior of different strains, whether pure or not, we gain some information regarding the influence of heredity on behavior.

Wild and tame strains. Wild and tame strains of certain species, such as the dog, have been in existence since the Stone Age. The domesticated type differs markedly from the wild form in temperament. In rodents the viciousness of the wild animal stands out in sharp contrast to the docility of the tame form. Yerkes (1913), Coburn (1922), Stone (1932), and Dawson (1932) have made quantitative measurements of the difference in wildness and savageness of wild and tame rats and mice, and their results corroborate those evident to casual observation. Since the two strains breed true for wildness and tameness, it is evident that this difference has a hereditary basis.

Audiogenic seizures. Differential susceptibility of various strains of rats and mice to convulsions produced by auditory stimulation has been noted by a number of investigators. Farris and Yeakel (1943) found that wild gray Norway rats, descendants of a captive wild strain maintained by King, reacted with greater frequency and severity to an air blast than did a sample of the inbred Wistar albino strain. Griffiths (1944), however, reports that not one animal out of 141 trapped wild Norway and Alexandrine rats displayed either hyperactivity or convulsions when stimulated by an air blast, key jingling, or a Galton whistle. Most of the rats were tested within a few days after they were trapped. Instead of displaying fear, they attacked the metal nozzle of the air hose. Griffiths suggests that the difference between his newly trapped nonsusceptible wild rats and the highly susceptible King wild strain which had bred in captivity for from 46 to 49 generations may be due to conditions peculiar to domestication; for example, dietary deficiencies produced by laboratory stock diets, confinement in small cages, lack of practice in meeting new situations, and endocrine changes occurring during captivity. He also suggests that the King strain may have been selectively bred for sensitivity to sounds of high frequency. The contradictory findings of these two investigations are in need of further elucidation.*

Maier (1943) found a difference between two strains of rats in his colony. In one strain 79 per cent of 116 animals tested reacted to the jingling of keys, whereas in the other only 29 per cent of 130 rats were susceptible. Martin and Hall (1941) obtained differences in susceptibility to audiogenic seizures between two strains of rats, one that had been selectively bred for emotionality, the other for nonemotionality. More frequent and more serious seizures were displayed by the rats of the nonemotional strain.

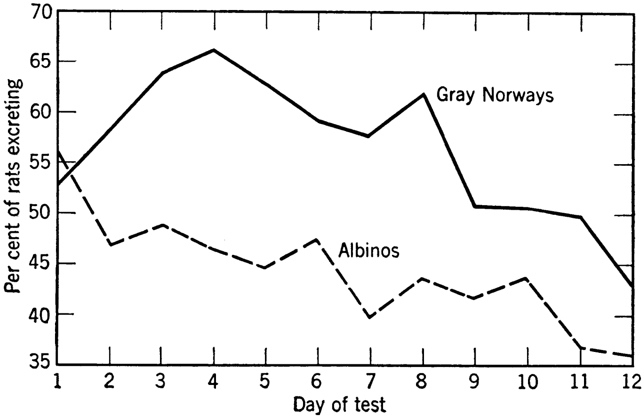

FIG. 2. A comparison of emotional defecation and urination in Norway and albino strains of rats. (Farris and Yeakel, 1945.)

In the foregoing investigations it is not at all clear just how inbred were the strains compared. One study (Hall, 1947) has been reported comparing two *pure* strains of mice maintained at the Jackson Memorial Laboratory. Mice of the Little *dba* strain (line 1) manifested many more audiogenic seizures and with greater severity than did mice of the Little *C57* black strain (line 6).

Emotionality. Gray Norway rats, descendants of the forty-third generation of the

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* Another hypothesis (Patton, 1947) is that a necessary, though perhaps not sufficient, condition for audiogenic seizures in rats is middle-ear infection (Editor).

King captive wild strain, proved to be more emotional than Wistar albino rats (Farris and Yeakel, 1945). The test of emotionality used was defecation or urination during a 2-minute period on each of 12 days in a circular enclosed field (Fig. 2).

Tryon has reported briefly (1942) that there are personality differences between his two strains of rats. The rats of the maze-bright strain are more emotionally disturbed in nonmaze situations than are the maze-dull animals, whereas just the opposite is true in the maze proper, where the dull animals display more emotional upset.

These two studies confirm the finding that emotionality (or nonemotionality) is an inheritable trait in the rat.

Aggressiveness. It is fashionable to reject an instinct of pugnacity in favor of a frustration-aggression hypothesis. Social scientists are prone to assert that men fight for economic or political or social reasons or because they were taught to fight as children, not because there is anything inherent in man's nature that makes him aggressive. The Freudian theory that aggressiveness has its roots in the constitutional impulse has not been widely accepted outside psychoanalytic circles.

That aggressiveness (fighting) has a genetic basis is supported by three studies. Hall and Klein (1942) compared two strains of rats for aggressiveness. One strain had been selectively bred for emotionality (fearfulness), the other for nonemotionality (fearlessness). Two rats were placed together in a cage for 5 minutes, and they were rated for aggressiveness according to the following scale:

THE KLEIN-HALL SCALE OF AGGRESSIVENESS

0 No interest in each other except occasional slight nosing.

1 Frequent vigorous nosing. No blocking, shoving, crowding, or any other display of hostility.

2 Occasional blocking, shoving, or crowding.

3 Frequent blocking, shoving, or crowding of opponent. The aggressor keeps after the other animal throughout the period.

4 Slight wrestling and/or assuming a dancing position in which the rats clasp each other while standing nose to nose.

5 Fierce wrestling. They jump, roll, and turn all over the cage very rapidly.

6 Fierce wrestling. A rat bites the other hard enough to draw blood.

Three groups of male rats, 10 in a group, were tested. Each rat was paired with every rat in its group *twice,* once in its own living cage and once as a visitor to the other rat's home cage. The 15 nonemotional rats initiated 326 attacks as against 68 initiated by the 15 emotional rats. The severity of the attacks by the nonemotional rats was, on the average, twice that of the emotional animals. The investigators concluded that the basic determiner of fighting is a genetic one.

Scott (1942) observed differences in aggressiveness among three *pure* strains of mice maintained at the Jackson Memorial Laboratory. Observations were made under the following conditions: A strange male mouse was introduced into the home cage of the mouse to be tested, and behavior was recorded for a 10-minute period. As soon as a fight started, the visitor was removed in order to avoid fatal injuries. The visiting mouse was selected from a pure stock (Bagg albino), and a new mouse was used for each observation.

Scott, in lieu of quantitative data, presents the following impressionistic descriptions of the behavior of the three strains selected for study.

> The *C57* blacks (subline 10) always showed immediate interest in the intruding male and made many contacts, at times apparently licking and cleaning him. There was no evidence of aggressive behavior, although they fought back when attacked. The *A* albino males made very little preliminary contact with the intruders and usually at-

tacked them within a couple of minutes. Finally, the *C3H* agouti males tended to sniff briefly at the intruder and then to keep to the opposite side of the pen for several minutes. During this time the fur fluffed up and the animals breathed in a labored fashion. If the intruder had not attacked in the meantime the *C3H* males eventually started a fight, usually preceded by a series of feints and withdrawals. [Pp. 12–13.]

A quantified study of the aggressiveness of three of the Jackson Laboratory inbred strains of house mice was performed by Ginsburg and Allee (1942). Each mouse was paired with every other experimental mouse, and the winner of each bout was recorded. The *C57* black mice won the greatest number of fights, followed by the *C3H* agoutis, and the *C* albinos proved to be the most inferior in fighting ability. In order to control for the possible influence of the mother on the aggressiveness of her offspring, litters born by black and by albino females on the same day were split shortly after birth, so that each dam reared both black and albino offspring together. This did not produce a difference in fighting ability; the black mice reared by an albino foster mother were still superior, and the albino mice reared by a black foster mother were still inferior.

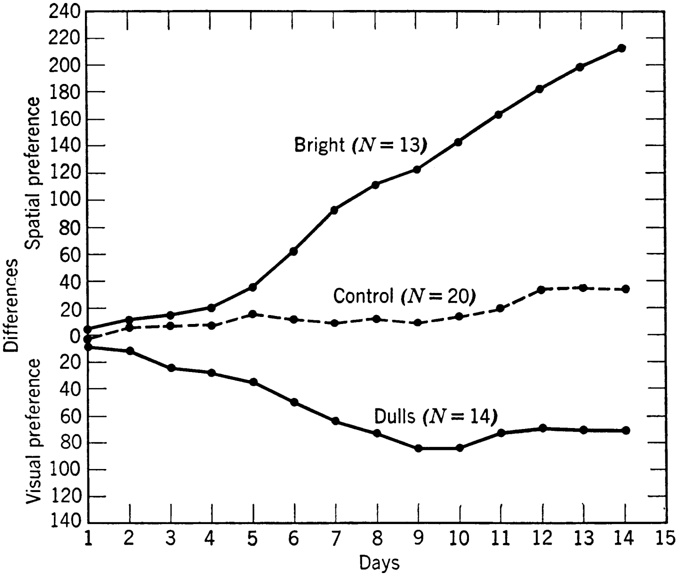

FIG. 3. A comparison of the types of "hypotheses" displayed in a multiple discrimination box by strains of rats selectively bred for brightness and dullness in maze-learning ability. (Krechevsky, 1933.)

In the light of these findings, continued insistence upon the acquired nature of aggressiveness and the exclusion of the genetic contribution is unwarranted.

"Hypotheses." Krechevsky (1932) has conclusively proved that during the presolution period in discrimination learning the rat displays systematic rather than random choices among the alternatives offered it. He has termed this systematic behavior an "hypothesis." In order to discover whether genetic factors play a part in the type of hypothesis selected, Krechevsky (1933) ran groups of Tryon's F_7 maze-bright and maze-dull strains in a multiple-discrimination box. He also tested a group of heterogeneous ani-

mals. The problem set the animal had no solution, since the correct pathway through the box was varied at random from trial to trial. It was possible for the animal to have eight different "hypotheses," four of which were visual and four spatial. The results are depicted graphically in Fig. 3. Krechevsky concludes,

> . . . there is a definite indication that the "bright" strain of animals, when placed in a difficult (non-solvable) situation, attempt spatial "hypotheses" in trying to solve the problem, the "dull" animals attempt non-spatial (visual) "hypotheses," and a non-selected group try about as many spatial as visual "hypotheses." In other words the kind of "hypotheses" which an animal can bring with him to a problem situation is to some extent hereditarily determined. [Pp. 108–109.]

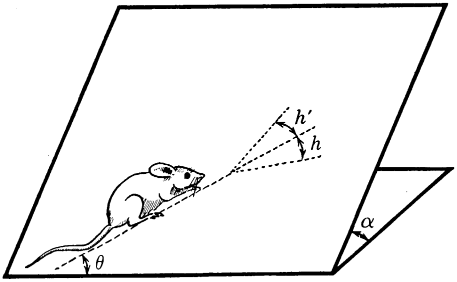

FIG. 4. Illustrating the definition of the angles θ and α in geotropic orientation in young rats. (Crozier and Hoagland, 1934.)

Geotropism. Young rats are negatively geotropic; i.e. they will crawl up an inclined plane (Crozier and Hoagland, 1934). The rat's path up the plane forms an angle with the horizontal which is a function of the angle of inclination (Fig. 4) and is described by the formula,

$$\cos\theta = a - b\sin\alpha$$

where a and b are constants. Three different strains of rats, A, B, and K, each of genetic uniformity, were tested for the form of the functional relations. The form of the function is the same in the three strains, but the numerical values of the constants are characteristic for each strain. Figure 5 shows that the intercept constants and the slope factor are clearly different for the two races, A and K, although the form of the function is the same. The slope factor is the same for strains A and B, but the threshold intercept is higher. The three strains differ in two respects, namely, slope and intercept constants.

Temperature preferences. If a mouse is presented with a wide range of cage floor temperatures from which to choose, he will select after some trials a particular temperature in which to rest and sleep. This temperature is referred to as his "thermotactic optimum." Herter (1936) found differences between the temperatures preferred by wild and albino strains of mice. The thermotactic optimum of the albino strain is 34.36 ± 0.12, and that of the wild strain is 37.36 ± 0.12 degrees C.

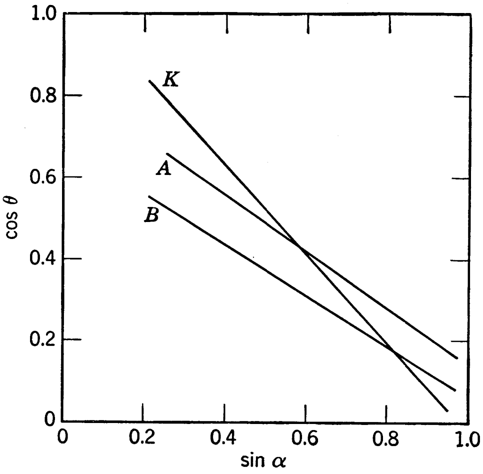

FIG. 5. Data from several series of observations with young rats of three strains, K, A, and B, which illustrate strain differences in geotropism. (Crozier and Hoagland, 1934.)

Speed of reaction. Utsurikawa (1917) invented a simple device for measuring the rat's speed of reaction. One end of a small box rests on legs; the other is suspended from a spring. Movements of the rat in the box move the spring, and these vertical displacements are recorded on a kymograph. A bell was used as the stimulus, and the speed and intensity of reaction were measured. Utsurikawa tested two strains of rats, one inbred and the other outbred, and found that the inbred rats reacted more quickly and with greater intensity than the outbred animals. Vicari (1929) measures speed of running in a simple two-unit maze. Different strains of mice differed in the average speed with which they traversed the pathway.

This summary of experiments involving selective breeding and strain comparisons is intended to be illustrative rather than complete. Heredity is pervasive. The major dimensions of temperament, viz. emotionality, activity, aggressiveness, reactivity, have their source in the germ plasm. Intelligence as measured by maze learning and by the use of "hypotheses" has a genetic basis. The fact that temperature preference is inherited suggests that 'interests' and 'values' may be originally determined by genetic constitution.

It is likely, on theoretical grounds, that heredity is a factor in all psychological traits. The justification for this broad generalization rests upon the organismic or holistic viewpoint which has gained prominence in recent years. According to this doctrine, as applied to behavior, any act is an expression of the whole organism. Since the chromosomes are constituents of the organism — indeed, they are the principal differentiated structures of the primary organism, the fertilized egg, as well as of each cell in the multicellular individual — they must be of extensive organismic significance. Genetics has proved this to be true for morphology and some physiological functions. It has yet to be fully documented for psychological characteristics.

It needs to be reiterated that the building of a science of psychogenetics does not deny the role of modifiability, which is itself an inborn property of living organisms. Is there anyone who doubts that profound alterations can be made in the structure, function, and behavior of living organisms? With each addition to his knowledge, man gains an increment of power to change the world and himself. The genes themselves are subject to alteration by external forces, e.g. X-rays, radium rays, ultraviolet light, and heat rays. It should be emphasized, however, that, if a change is to be instituted through education, therapy, or stimulation by various forms of energy, the effectiveness and precision of the alteration will depend primarily upon our knowing the nature of the raw material that is to be altered. Psychogenetics is the study of this raw material.

GENETIC ANALYSIS OF BEHAVIOR

In order to have a genetics of behavior it is not sufficient merely to show that psychological traits, like morphological features, have a genetic foundation. Genetic analysis is also required. The number of gene pairs that contribute to the expression of the trait and the presence or absence of dominance in each pair should be identified. A slight beginning in this direction has been made; more rapid strides will follow as investigators make increased use of highly inbred strains — strains that have reached maximum homozygosity. Calvin Stone (1947) has observed,

> To many of us who have worked for a long time in the field of comparative psychology it is a matter of shame and regret that only an amateurish beginning has yet been made by psychologists in the utilization of pure lines of animals in fundamental research in the nature-nurture area. [P. 344.]

Geneticists assert that in order to work out the genetics of quantitative traits, such as maze learning, highly purified and genetically homogeneous strains are essential. Since quantitative traits are the ones that most interest the psychologist, let us consider more at length the method of obtaining these essential pure strains (see also the excellent account by Russell, 1941).

Inbreeding

The objective of inbreeding is to produce a homozygous strain, one in which all the animals are identical genotypes except for the segregation of the X and Y chromosomes. The rate at which homozygosity is reached varies with the closeness of inbreeding. Self-fertilization, which is possible only in certain plants, results in virtual homozygosity after eight generations. Brother-sister matings produce approximate homozygosity in about thirty generations, and double first cousins in about forty-five generations (Fig. 6). When the inbreeding is as far removed as second cousins, the percentage of homozygotes does not materially increase from generation to generation.

Inbred strains of laboratory mammals have been produced almost exclusively by brother-sister mating. Under this system *there are only two parents for each generation and these parents are always brother and sister.* When a pure line has been established, complete relaxation of inbreeding should be avoided: it will tend to perpetuate any heterozygosis that may be introduced by mutation. However, in order to make available a large number of homozygous animals, inbreeding in an isogenic line may be temporarily halted; but it is always advisable occasionally to bring the inbred line back to a single pair of parents by discarding for breeding purposes all but a single brother-sister pair.

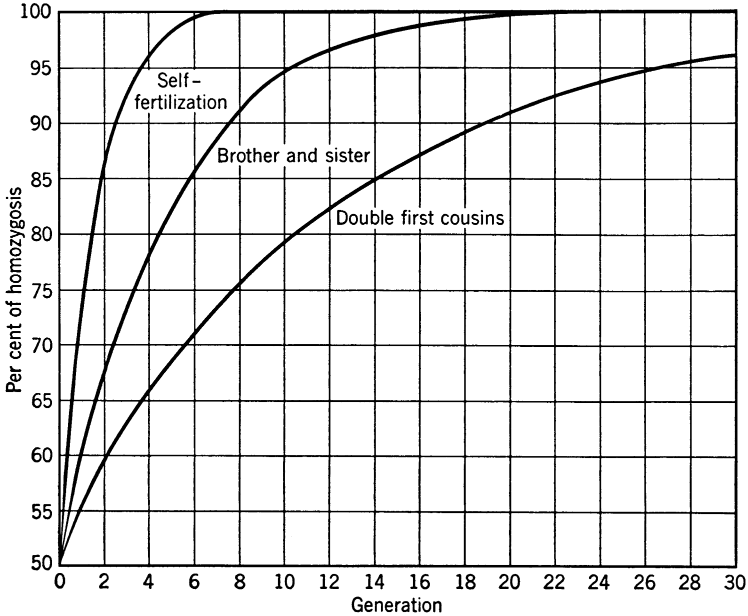

FIG. 6. The percentage of homozygosis in successive generations under three systems of inbreeding. (Russell, 1941.)

Russell (1941) has issued a warning regarding the risk of an accidental outcross of an inbred line.

> Since a high degree of homozygosis is obtained only after many generations of inbreeding, a single unfortunate outcross may undo years of work. In a mouse colony in which different lines are maintained, an accidental outcross may occur as a result of

> faulty pens, into which stray animals can enter, or the returning of animals to the wrong pen after removal for any purpose. Risk of the latter can be reduced to a minimum by handling different lines and sublines at different times and by keeping them in separate parts of the laboratory or cage rack, certainly not in adjacent sections of wooden boxes. When several inbred lines are to be started it is desirable to mark them with different coat colors or other genetic characteristics, contamination of which will be readily recognized. [Pp. 344–345.]

Selection for a particular characteristic is often combined with inbreeding. In selective inbreeding it is desirable to start with a parental generation of maximum heterogeneity in order that all the alleles (genes occupying corresponding loci on homologous chromosomes) of all factors that influence the trait may be represented. Furthermore it is a wise practice to start a number of sublines from the parental generation, since the expression of the trait in some animals may be nongenetically controlled. If two animals, i.e. a brother and sister, in which the trait is nongenetic should be selected, the desired genetic factors would be lost, and the investigator would have to begin all over again with a heterozygous population. If he starts with a number of sublines, he can discard those that do not produce offspring like themselves. Selection and brother-sister matings within each subline should be rigorously followed and crosses between sublines studiously avoided if complete homozygosity is desired. One subline may not be genetically identical with another subline, since it is probable that different genetic patterns become fixed within each subline. Starting a number of sublines from the original parental generation helps also to insure against the strain's dying out. When genetic uniformity has been attained in the several sublines, it is then possible to retain one line and discard the others.

In order to work out the genetics of a psychological trait it is necessary to obtain two or more pure strains that differ in their expression of the trait. These strains may be secured by selective breeding, or they may be obtained by finding differences in a trait between strains that have been inbred for other purposes or in which there has been natural inbreeding. Since many inbred strains of mice have been developed and are now available, particularly from the Jackson Laboratory at Bar Harbor, Maine, it would be fruitful to investigate other psychological traits in these strains already at hand.

Another advantage of employing pure lines is that the occurrence of a mutation that might influence a behavior trait is more easily noticed. If the mutant form differs in behavior from the pure strain, we are informed of the additional fact that the trait is controlled by a single pair of genes.

Unit Characters

A trait conditioned by a single pair of alleles is called a unit character. It is sometimes assumed that, because psychological characteristics are predominantly quantitative in their expression and are distributed normally, they must be determined by many genetic factors rather than by one or two pairs. On the other hand, several unit characters of distinct psychological significance have been discovered. Other unit characters will doubtless be identified as progress is made in psychogenetics.

A unit character is identified by making various types of crosses and comparing the results with those that would be theoretically expected if a single pair of genes were operating. If two pure strains, *A* and *B*, display a dichotomy in behavior, *M* and *N*, the first step is to hybridize the two strains. If the trait is a unit character, the hybrids can behave in only one of three possible ways: *M*, *N*, or intermediate between *M* and *N*. If they all manifest behavior *M*, resembling thereby the parent strain *A*, the allele conditioning *M* is dominant over the allele conditioning *N*. If the F_1's resemble the other parent strain *B*, the allele for *N* is dominant over the one for M. Finally, if the hybrids are intermediate in behavior between M and N, the pair of genes are said to blend; that is to say, they contribute equally to the trait and no dominance exists.

The second step is to mate the F_1's *inter se* to obtain the F_2's. If dominance exists, a ratio of three animals resembling the dominant strain to one animal resembling the recessive strain is expected among the F_2's. Two backcross matings, F_1 with the dominant strain and F_1 with the recessive strain, will yield ratios of 1:0 and 1:1 respectively, for a unit character.

Russell (1941) observes that even when these ratios are obtained they are not critical criteria for the presence of a single pair of genes.

> There is a common belief that a character occurring only in alternate categories (as opposed to the other extreme: a continuous distribution) must be due to alternate genes in the same way that agouti and black coat color are. This has sometimes led to a hunt for a single major gene difference as the cause of a character difference that shows no, or little, overlap in two inbred strains. . . . Such a hunt is all right if it is critical. It can only be critical if cognizance is paid to the fact that, owing to the common occurrence of biological thresholds, of all-or-none processes in development, many characters are necessarily alternate in expression. Many genes may be involved, the effects of some combinations falling below the threshold, while the effects of the others fall above. If this fact is realized it will be appreciated that apparent dominance in the F_1 of a cross between strains, a 3:1 ratio in the F_2, and a 1:1 ratio in the backcross, are not critical criteria of the presence of a single major pair of genes. Many genes may be involved and the above generations happen to be cut by a threshold of effect into approximately the above proportions. . . . *The critical experiment is to test the genetic nature of the types apparently segregating in the backcross or F_2 by breeding them with the "recessive" stock.* [P. 346, italics Hall's.]

Several examples of unit behavior characters will be presented.

Audiogenic seizures. Two pure strains of house mice which differed greatly in the number and severity of audiogenic seizures were crossbred according to the steps outlined above, including the crucial test suggested by Russell (Witt and Hall, 1949). The results of the several types of matings are summarized in Table 3. The observed percentages conform closely, except for the critical backcross (the last cross in Table 3), to those that would be expected if audiogenic seizures are a unit character. The divergence of the critical backcross suggests that there may be some modifying factors. If there are such modifying factors, they are of minor importance since the other crosses yield progeny who react as though audiogenic seizures were inherited as a *single dominant gene.*

The genetics of audiogenic seizures has been investigated in the genus *Peromyscus,* which includes the deer mouse and other white-footed mice of North America. The genetic analysis differs from that found by Witt and Hall for the common house mouse of the genus *Mus musculus.* Dice (1935) and Watson (1939) conclude from their investigations that epilepsy, as they label the behavior that is conventionally called "audiogenic seizure," is a recessive character. Dice's conclusion is based upon meager data. Epileptic males mated with normal females yielded 15 offspring, all of whom behaved normally when they were exposed to jingling keys. The backcross of the F_1's to epileptic males produced 48 offspring, 12 epileptic and 36 normal. This obtained ratio of 1:3 diverges greatly from the expected ratio of 1:1, were the trait a recessive one.

Watson used many more mice in her investigation. A summary of the most pertinent results appear in Table 4. The 12 mice of the Palouse River stock who should have reacted, but did not, Watson terms "normal overlaps." A normal overlap is a mouse who is genotypically epileptic but pheno-

TABLE 3

GENETIC ANALYSIS OF AUDIOGENIC (*As*) * SEIZURES IN HOUSE MICE (*Mus musculus*) (WITT AND HALL, 1949)

	No.	Percentage	Percentage Expected	Genetic Formula
Inbred *C57* strain				
Susceptible	2	5 ± 3.5	0	
Resistant	36	95 ± 3.5	100	*as as*
Inbred *dba* strain				
Susceptible	31	94 ± 4.1	100	*As As*
Resistant	2	6 ± 4.1	0	
F_1 (*C57* × *dba*)				
Susceptible	72	91 ± 3.2	100	*As as*
Resistant	7	9 ± 3.2	0	
F_2 (F_1 × F_1)				
Susceptible	54	76 ± 5.1	75	*As As* + *As as*
Resistant	17	24 ± 5.1	25	*as as*
Backcross (*F1* × *C57*)				
Susceptible	38	54 ± 5.9	50	*As as*
Resistant	32	46 ± 5.9	50	*as as*
Backcross (F_1 × *dba*)				
Susceptible	20	91 ± 6.1	100	*As As* + *As as*
Resistant	2	9 ± 6.1	0	
Backcross [resistant (F_1 × *C57*) × *C57*]				
Susceptible	12	25 ± 6.2	0	
Resistant	36	75 ± 6.2	100	*as as*

* The symbol *As* has been chosen to designate the dominant gene for audiogenic seizures; *as* represents the recessive gene.

TABLE 4

INHERITANCE OF EPILEPSY (*p*) IN *Peromyscus maniculatus artemisiae* COLLECTED FROM PALOUSE RIVER, WASHINGTON (AFTER WATSON, 1939)

	No.	Percentage	Percentage Expected	Percentage Expected, Corrected for Normal Overlap	Genetic Formula
Palouse River stock (*PRS*)					
Susceptible	184	93.9 ± 1.7	100	93.9	*pp*
Resistant	12	6.1 ± 1.7	0	6.1	
Backcross (F_1 × *PRS*)					
Susceptible	97	41.6 ± 3.2	50	43.9	*pp*
Resistant	136	58.4 ± 3.2	50	56.1	*Pp*
F_2 (F_1 × F_1)					
Susceptible	86	20.6 ± 2.0	25	18.9	*pp*
Resistant	331	79.4 ± 2.0	75	81.1	*PP* + *Pp*

typically resistant to auditory stimulation. By correcting the backcross and F_2 progeny for the percentage of normal overlaps (6.1), the obtained percentages conform very closely to those that would be expected on the assumption that audiogenic seizure (epilepsy) is inherited as a *single recessive gene* in *Peromyscus maniculatus artemisiae.*

The contrasting results obtained for *Mus musculus* and *Peromyscus maniculatus artemisiae* demonstrate that for two genera the genetic constitution underlying the same type of behavior may be different. In the former genus the gene for audiogenic seizures is a dominant; in the latter it is a recessive. Modifying factors may, of course, be present in both.

Investigations of the genetics of audiogenic seizures in rats have yielded contradictory results. Maier and Glaser (1940) found that their data, obtained from crossing (1) susceptible with susceptible, (2) susceptible with resistant, and (3) resistant with resistant, fitted the assumption that the trait was a dominant one. The percentages of offspring reacting with seizures from the three types of crosses were 74, 52 and 0, respectively. However, Maier (1943), in a later investigation, did not confirm the Maier and Glaser findings. He concluded that the genetics of audiogenic seizures is complex rather than simple. However, since in neither study were uniform strains used, the results are necessarily ambiguous. The same criticism applies to Griffith's (1942) attempt to unravel the genetics of audiogenic seizures in rats. He divided his animals into an *H* group which reacted on 50 per cent or more of their 60 standard preliminary trials and an *L* group which reacted on less than 50 per cent of the trails. The results of $H \times H$, $H \times L$, and $L \times L$ crosses suggests, according to Griffiths, two pairs of genetic factors.

Finger's (1943) experiment does not help to elucidate the genetics of audiogenic seizures in the rat. He made various crosses and obtained the results shown. He observes that "it appears very doubtful that the tendency (to react with a seizure) is inherited as a simple Mendelian dominant."

	No.	Percentage Susceptible
Susceptible × susceptible	58	66
Susceptible × resistant	63	73
Resistant × resistant	22	68

As a result of using impure strains of rats, three different types of genetic constitution have been postulated for audiogenic seizures: a simple dominant (Maier and Glaser), two pairs of genes (Griffiths, 1942), and multiple factors (Maier, Finger). It should be clear, from this example, that a genetics of behavior cannot be developed by utilizing strains of unknown genetic constitution.

Thermotactic optimum. As previously mentioned, different strains of mice may prefer different temperatures. A cross between a wild strain whose average thermotactic optimum was 37.36 degrees C and an albino strain whose preferred temperature averaged 34.36 degrees C resulted in an F_1 whose preference, 34.76 degrees C, resembled that of the albino strain. Other crosses were made. A summary of all the results is presented in Table 5.

These findings, according to Herter (1936, 1938*a*, *b*), indicate that the thermotactic optimum is dependent upon a single pair of genes, the gene causing the lower optimum being dominant over its allelomorph causing the higher optimum. The small number of animals observed is a weakness of this study. However, should this finding be corroborated, it would suggest that other preferential or choice behavior might have a simple genetic basis.

Mutations in Inbred Strains

The value of maintaining and systematically observing inbred strains is enhanced by the fact that any mutation that occurs will be more readily noticed in a uniform stock than in a heterogeneous one. In support of this statement, the important findings of King and Donaldson (1929), King (1939),

TABLE 5

Crosses between Strains of Mice with Different Temperature Preferences (after Grüneberg)

	No. of Individuals Obtained	No. of Individuals Expected	No. of Determinations	Average Thermotactic Optimum in Degrees C	Range of Averages for Individual Mice
Wild strain	19	19	1048	37.36 ± 0.12	36.34–37.92
Albino strain	16	16	1300	34.63 ± 0.12	33.88–35.60
Wild × Albino (F_1)	17	17	850	34.76 ± 0.12	34.20–35.78
$F_1 \times F_1$ (F_2)					
Type 1 (dominant)	12	14.25	600	34.62 ± 0.11	34.06–34.96
Type 2 (recessive)	7	4.75	350	37.16 ± 0.15	36.94–37.54
F_1 × albino	28	28	1400	34.93 ± 0.10	34.24–35.76
F_1 × wild					
Type 1 (dominant)	16	14	800	34.80 ± 0.19	34.28–35.42
Type 2 (recessive)	12	14	600	37.32 ± 0.12	36.74–37.80

and Keeler and King (1942) of the Wistar Institute may be cited. Wild gray Norway rats were trapped, and they constituted the parental generation from which numerous filial generations were bred. Many mutations, expressed in coat colors, occurred during the maintenance of this uniform, although not entirely purified, strain. In 1942 Keeler and King published an account of the differences in behavior of these mutant strains. The following character sketches were formulated from independent descriptions made by five observers who were familiar with the strains.

Mutant albino. When not tamed they are as wild and vicious as the original gray Norway rats. When tamed they resemble the tamed Norway in their tendency to bite when handled.

Cinnamon (*brown pigment*). They are easier to tame than grays, but they may revert to their original wildness. They are ordinarily more peaceful than grays, but, when they do fight, they fight as well as the grays.

Curly. They are difficult to catch even after they are tamed. They ordinarily do not bite when held, but they can never be entirely trusted.

Stub. These animals are always fighting one another. They do not mind their own business as do the gray rats, but throw themselves against the cage when anyone approaches.

Albino waltzers. They are easier to tame than mutant albinos from which they were derived. When tamed they rarely bite their handler.

Black. The black strain does not have to be tamed, since they are tame by nature. If very excited they may click their teeth, but they are not apt to bite.

Although these descriptions are impressionistic, one of these mutant strains, the black, is unique in comparison with the others. This difference in behavior of the wild and savage gray Norway rat and the tame and docile black rat is ascribed by Keeler and King to the mutation of a single gene in the original Norway strain. They write:

> A survey of eighteen stocks shows that most of the naturally tame strains of albino rats now employed in American scientific laboratories were tamed principally by the black gene or by the black and piebald genes combined, the coat color effects of which genes are masked by albinism as we have stated above. Most of the stocks not bearing the black gene are probably tamed principally by other mendelian genes such as pink-eyed yellow, red-eyed yellow, hairless,

> and ruby-eyed dilute, because strains containing these genes singly are, in our experience, invariably tame. [1942, p. 249.]

This is a dramatic finding. The popular theory of domestication asserts that tame strains of animals came into existence as a consequence of the accumulation of a host of gene mutations, each mutation contributing an almost imperceptible amount to the final result of the domesticated strain. According to Keeler and King, a single mutation transforms a wild form into a domesticated one. A major evolutionary step is mediated by a minor gene-change. They state, *"It is also clear that the basis of temperament and behavior is inherited in gene controlled patterns, the effects of a single gene being distributed irregularly throughout the whole field of response, like dabs of a particular color in a polychrome print"* (1942, p. 246).

It should be borne in mind that this discovery was made possible by having available for observation over a number of generations a relatively homozygous line.

A number of mutations that express themselves in bizarre neuromuscular disorders have been found in inbred strains of house mice. The mutant forms, all of which are recessive, the genetic symbol, and a brief description of the behavior of each form follow.

Waltzing: (*v* for *valse*, French). As described by Yerkes in 1907, the behavior consists of "(1) movement in circles with all the feet close together under the body, (2) movement in circles, which vary in diameter from 5 to 30 cm., with the feet spread widely, and (3) movements now to the right, now to the left, in figure eights." Exclusive circling in one direction does not occur, although preference for right or left turning does appear.

Shaker 1: (*sh*-1). The salient feature is a nervous head movement which consists of rapid, successive, upward jerks of the head.

Shaker 2: (*sh*-2). This form is phenotypically indistinguishable from shaker 1. That the genes for shakers 1 and 2 are different has been established by crossing *sh*-1 with *sh*-2. If they were the same recessive gene, all F_1's should express choreic head movements. Actually, all F_1's are quite normal.

Jerker: (*je*). This mutant is also indistinguishable from both shakers, but that it is a different gene has been confirmed by appropriate crosses.

Pirouetting: (*pi*). As first described by Woolley and Dickie (1945), the behavior is that of rapid whirling in circles of small diameter.

> The mouse swings its head sharply to one side, places the inner forefoot back toward the rear foot, toes turned out, and seems to place the opposite forefoot in such a position that it aids in pushing the mouse into a small diameter rotation. The mice whirl incessantly for long periods of time. [Pp. 282–283.]

It is regrettable that comparative psychologists have not had or availed themselves of the opportunity to make routine behavior measurements of inbred strains of rodents. Such strains have been in existence in this country and in Europe for some years and have provided the biogeneticist with some of his best material. Numerous gene mutations, affecting principally such morphological characters as coat color, hair texture, size and body form, and diverse skeletal features, have been described by Grüneberg for the mouse. In his 412-page book, fewer than four pages are devoted to behavior.

Multiple Factors

When several sets of genes contribute to the determination of the same character, they are called multiple factors. Formerly it was assumed that multiple factors have equal and cumulative effects on the character, but it is now well established that dominance may also be present. The existence of multiple factors is indicated when the F_1's are uniform and intermediate between the two parental strains in behavior and the F_2's are extremely variable.

Tryon (1942) believes that a theory of multiple factors explains the fact that a continuous unimodal distribution is usually found when a population is measured for a psychological trait. He writes:

> We shall describe this theory by showing how it may account for individual differences in maze-learning ability. It is assumed that there is a large number, *k*, of genes determining this ability. First, consider one of these genes, A, which exists in two degrees of expression, *A* and *a*. An individual of homozygous constitution, *AA*, is brighter than one of *aa* constitution, and a heterozygous individual, *Aa*, lies between the two. No dominance is assumed. But there are *k* such genes, A, B, C, D, ···, each possessing the same properties as those described for A. Thus an individual of constitution *AABBCCDD* ··· would be the brightest possible in maze ability; *aabbccdd* ··· the dullest; and *AaBbCcDd* ··· would be average. All degrees of ability would be possible: *aABBCCDD* ··· next to brightest, *aaBBCCDD* ··· next, *aabBCCDD* ··· next, and so on. Thus the continuity of individual differences is adequately explained. Under random mating, the types of individual that could exist and the frequency of each can be found from the product of $(A+a)^2$ $(B+b)^2$ $(C+c)^2$ $(D+d)^2$ $\cdots$. In the resulting series the terms show the various genotypes, and their coefficients the frequency of their occurrence. The result is a *normal distribution curve,* if *k* is large enough. Hence, the wide, continuous, and unimodal dispersion of individuals in the *P* generation . . . [see Fig. 1] whose parents were randomly mated is adequately accounted for.
>
> According to this theory, the effects of selective breeding result simply from the gradual sorting into one race of all the large-lettered genes for brightness, and into the other, all the small-lettered genes for dullness. In a final bright pure line, *all* individuals would be *AABBCCDD* ···, and their progeny would be exactly like them; analogously, in the dull pure line, all would be *aabbccdd* ··· and would breed true for dullness. [P. 349.]

Although Tryon has made a plausible case for the importance of multiple factors in the genetics of behavior, as yet his view can be supported by very little concrete evidence. To date, more unit characters than multiple factor traits have been isolated. Tryon's own investigation of the inheritance of maze-learning ability has produced equivocal results. Those of Brody (1942) and of Hall (unpublished material) are equally inconclusive. These three studies contain inherent weaknesses which will be brought out in the following discussion.

Maze learning. Tryon crossed his 'bright' and 'dull' strains to produce an F_1 and intermated the F_1's to secure an F_2. If the lines were pure at the time of hybridizing, the F_1 generation would show uniform maze performance and the F_2 generation would display wide variability in maze learning. The F_1 progeny were not uniform; they were just as variable as the F_2 rats (Fig. 7). These results mean that the strains were not pure at the time they were crossed. This is to be expected because of the type of inbreeding Tryon followed. Instead of a single line of brother-sister matings, each strain actually consists of a number of sublines. It is not likely that different sublines will be genetically identical; different hereditary patterns will ordinarily become fixed within each subline. Accordingly, if a heterogeneous sample of rats from several bright sublines are mated with an equally heterogeneous sample from various dull sublines, the F_1 progeny obviously will vary widely in maze performance. Moreover, if Tryon had permitted a certain amount of crossbreeding between sublines while he was developing the two strains, genetic homozygosity within each strain would not have been achieved. Close inbreeding within a single line is essential for the establishment of pure lines.

Voluntary activity. The ambiguity that results from crossing strains that are not homozygous for the trait being studied is revealed by Brody's study (1942) using Rundquist's active and inactive strains of rats. Brody crossed active F_{21} females with inactive F_{21} males and inactive F_{21} females with active F_{21} males. Since the offspring of these reciprocal crosses did not differ significantly in their activity, they may be lumped together. The F_1 progeny were bred together to obtain an F_2. The F_1 rats were also backcrossed to (1) rats of the active strain and (2) rats of the inactive strain. The same breeding program was carried out with a sample of the F_{22} generation. The results of these several crosses for the two generations are presented in Table 6. Only one systematic trend appears in the results for both generations. F_1 backcrossed to the active strain produces offspring that resemble the active parent strain, whereas the progeny of $F_1 \times$ inactive strain resemble the inactive parent strain. This suggests that more of the contributing genes are dominant for higher activity level. Other than this, the data are inconclusive. By some legerdemain I am unable to follow, Brody concludes that ". . . the two strains differ with respect to a single gene rather than with respect to multiple factors . . . . The gene apparently behaves as a dominant

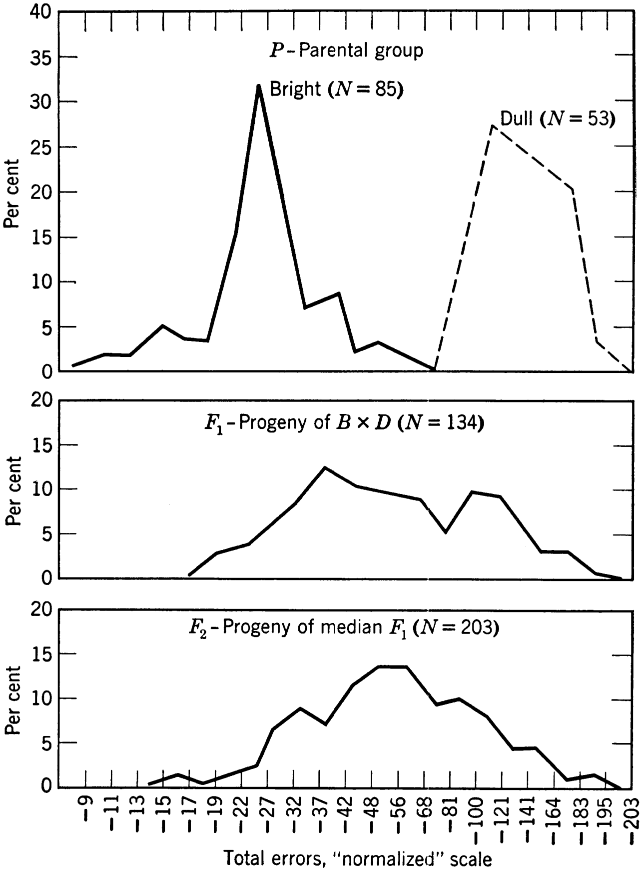

FIG. 7. The results of crossing two strains of rats selectively bred for brightness and dullness in maze-learning ability. (Tryon, 1940.)

TABLE 6

A Summary of Results Obtained from Crosses between Active and Inactive Strains of Rats (after Brody, 1942)

(Revolutions in thousands for 15 days)

	Mean	S.D.		Mean	S.D.
F_{21}	Active females		×	Inactive males	
	125	37		10	14
F_{21}	Inactive females		×	Active males	
	14	20		140	54
	Females			Males	
F_1	116	56		75	43
F_2	69	66		33	44
F_1 × active	129	69		55	57
F_1 × inactive	41	67		2	4
F_{22}	Active females		×	Inactive males	
	169	54		11	19
F_{22}	Inactive females		×	Active males	
	17	24		110	51
	Females			Males	
F_1	81	60		22	28
F_2	143	80		42	47
F_1 × active	182	43		95	61
F_1 × inactive	53	52		11	13

in the males and as a recessive in the females" (1942, p. 23). This type of gene, which is dominant in males and recessive in females, is called a *sex-influenced* factor.* An example of sex-influenced characters, which are quite uncommon, is baldness in man. Brody's findings do not seem to justify the conclusion that the difference between the Rundquist strains results from a single sex-influenced gene pair. That there is a genetics of activity cannot be questioned, but until strains homozygous for activity and inactivity are available the genetics of this important trait will remain unknown.

Emotionality. Hall (unpublished data) made three crosses for the F_{10}, F_{11}, and F_{12} generations of his emotional and nonemotional strains of rats. The results are presented in Table 7. Had the two strains been pure, the variability of the hybrids would have been smaller than that found. These results duplicate those of Tryon, since the means and standard deviations closely resemble the heterogeneous parental population, whose mean and standard deviation was 3.86 and 3.54, respectively. It was deemed unfruitful to make further crosses with impure strains. The most that can be inferred is that the alleles for nonemotionality are dominant over those for emotionality. The dominance of the nonemotional factors would explain (1) the skewness of the distribution of scores for the parental generation; i.e. there was an overbalance of low-scoring animals; (2) the rapid effects of selection in the nonemotional strain (Table 2); (3) the slower effects of selection for emotionality (Table 2); and (4) the greater resemblance of the scores of the hybrids to the nonemotional animals than to the emotional rats.

TABLE 7

A Summary of the Results Obtained from Crosses between Emotional and Nonemotional Strains

Generation Emotional × nonemotional	No. of Offspring	Defecation-Urination Scores Mean	S.D.
$F_{10} \times F_{10}$	32	4.53	3.84
$F_{11} \times F_{11}$	22	2.81	2.15
$F_{12} \times F_{12}$	27	3.00	2.55

In view of the negative results obtained by Tryon, Brody, and Hall, the multiple-factor theory as applied to the genetics of behavior traits remains unproved. Since the negative results were obtained by faulty methods, it is probably only a matter of time before evidence for the theory will be provided. It is certainly the most plausible theory by which to explain the genetics of traits that conform to the normal probability curve.

THE MAPPING OF CHROMOSOMES

In view of the embryonic state of psychogenetics any extensive discussion of this topic at this time would appear to be premature. With the exception of some of the neuro-

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* A sex-influenced factor should not be confused with either a *sex-linked* or a *sex-limited* factor. A sex-linked factor is one that is carried in the sex chromosomes and may be either dominant or recessive. A sex-limited factor is one that is capable of expression in one sex but not in the other.

muscular disorders, e.g. waltzing, shaker, and pirouetting, there is no information regarding the location of the genes on the chromosomes for behavior characters. Consequently this objective of psychogenetics will be discussed only in general terms.

When two or more factors are located on the same chromosome, they are said to be *linked.* The evidence for linkage is provided by the way in which characters hang together. Thus in the house mouse, the two characters, waltzing and jittery, appear together, whereas waltzing and shaker 1 do not. The factors for waltzing and jittery are assigned to the same chromosome (No. 10) whereas waltzing and shaker 1 are assigned to different chromosomes (Nos. 10 and 1, respectively). However, linked factors do not invariably stay together, and because of this it is assumed that there is an exchange of homologous parts between the chromosome pairs early in the maturation of germ cells. This is called *crossing over.* The amount of crossing over provides the basis for locating the genes more or less accurately on the chromosomes. A large amount of crossing over implies that the two genes are far apart on the chromosome; a small amount implies that they are close together on the chromosome.

Snell (1945, for example, found that there was 26 per cent crossing over in an F_2 population bred from an F_1 generation heterozygous for waltzing and jittery. This is a high value for crossing over and suggests that the two genes are widely separated on the same chromosome. Their location as given on a chromosome map of the mouse is at the two ends of chromosome 10 (Staff, Jackson Laboratory, 1945).

Aside from shaker 1, shaker 2, waltzing, and jittery, no other genes for behavior characteristics in the mouse have been mapped.

HOW GENES PRODUCE BEHAVIOR TRAITS

"Between the presence of the genes in the chromosomes and the appearance of the developed characters in the individual organism there exists a gap which is not yet thoroughly understood" (Snyder, 1940, p. 356). This is Snyder's opening sentence in his chapter on *How Genes Act.* In the same chapter he summarizes the known genetic effects in development:

> . . . a complete complement of chromosomes as well as a normal environment is necessary for development; early differentiation is probably effected primarily by gradients imposed from without upon a cytoplasm already under the control of genes; later differentiation takes place through interactions of genic substances in differential gradients, the whole process being a continuous one of reciprocal reactions between genes and cytoplasm in progressively differing gradient fields; and finally the action of the genes may take the form of enzyme production, elaboration of reactive chemical substances, or modification of the plane or frequency of cell division in localized areas. [Pp. 364–365.]

It is not within the scope of the present chapter to weigh and evaluate the conflicting hypotheses regarding the action of the genes. The exact nature of gene action will be worked out by the cooperative efforts of geneticists, cytologists, and embryologists.

It is within the province of psychogenetics to inquire about the bodily structures and functions which regulate behavior and which are in turn regulated by the genes. For it should be apparent that the genes cannot control directly a psychological trait, e.g. maze-learning ability; they can only exert an influence through the mediation of physical structures.

Few clear-cut studies correlating genetic constitution, bodily structures, and behavior have been reported. Herter's (1938) investigation of the thermotactic optimum is a model in this respect. Having discovered that the temperature preference of the mouse is dependent upon a single pair of genes, he then sought an answer to the question: upon what physical feature does this preference rest? He found that body temperature as taken rectally was not the factor, since the wild strain, which preferred the higher temperature, had approximately the same body temperature (37.39 degrees C) as the albino strain (37.68 degrees C), which chose the lower temperature. Also, the temperature of the belly differed only slightly: 32.93 degrees C for the wild mice and 31.14 degrees C for the albino mice. Herter then examined the skin and fur of the belly and ascertained that the density of the fur and the thickness of the epidermis differed in the two strains. The wild mice had about 70 hairs per unit square as compared with about 46 hairs for the albino mice. The skin of the wild mice was markedly thinner than that of the albino animals. The F_1 progeny obtained from crossing wild × albino resembled the albinos in thermotactic optimum, hair density (51.66 hairs per unit square), and thickness of epidermis. In a backcross of F_1 mice to the wild strain, 12 mice with a preferred temperature of 34.56 degrees C had an average hair density of 52.75, and 8 mice with a thermotactic optimum of 37.10 degrees C had a density of fur of 70.94. Undoubtedly the preferred temperature is controlled by the density of the belly fur and the thickness of the belly skin, and it is these features that are determined by the genes.

Many differences in behavior are probably mediated principally by neurohumeral mechanisms. Yeakel and Rhoades compared the weights of several endocrine glands, viz. adrenal, thyroid, and pituitary, of the emotional and nonemotional strains of rats selectively bred by Hall. Significant differences both for absolute weight of the glands and relative weight, i.e. gland weight divided by body weight, were obtained. The emotional males had heavier adrenals and thyroids than the nonemotional males. There was no appreciable difference in the weight of the pituitary for the males of the two strains. The emotional females had heavier thyroids and pituitaries than the nonemotional females, but the difference for the adrenals did not reach the criterion of significance. If it is assumed that heavy glands produce more hormones than light glands, then it may be surmised that the emotional rats are emotional because they are primed by their blood chemistry to react emotionally. Their chemique produces a lower threshold for the evocation of fear as compared with the threshold of the nonemotional rats. Such speculations are interesting, but only a more intensive and critical search for the precise *modus operandi* of the genes upon emotionality, similar to that performed by Herter on thermotactic preference, will provide exact knowledge.

Rundquist and Bellis (1933) compared the respiratory metabolism of the F_{15} generation of active and inactive strains of rats using the Ebeling-Corey method for determining metabolism. The average number of calories per gram body weight per hour for the two strains by sex are given in the table. The differences between the means are statistically significant. The higher metabolic rate of the active strain is to be expected and suggests that the inherited structural feature upon which voluntary activity is based is the thyroid.

	No.	Active Strain	No.	Inactive Strain
Males	29	8.25	16	6.28
Females	20	8.70	22	6.45

No difference in the brain weights of maze-bright and maze-dull rats was found by Silverman, Shapiro, and Heron (1940).

Lashley (1947) has recently surveyed the available knowledge of the inheritance of structure in the nervous system in relation to behavior. Actually very little is known about this subject. It has been established that "the brain is extremely variable in every character that has been subjected to measurement" and "some of the more conspicuous structural differences have been shown to be hereditary" (p. 333). These inherited differences include brain size, fissurization, absence of corpus callosum, and the irregular twisted fibers of the corpus striatum in athetosis. Although the relation of these macroscopic features either to behavior or to genetic constitution has not been clearly revealed, Lashley feels that the structural variations must have functional significance.

> It is not conceivable that the inferior frontal convolutions of two brains would function in the same way or with equal effectiveness when one contains only half as many cells as the other; that two parietal association areas should be identical in function when the cells of one are mostly minute granules and of the other large pyramids; that the presence of Betz cells in the prefrontal region is without influence on behavior. [P. 333.]

CONCLUDING REMARKS

The foregoing sections have presented a brief review of the nature and potentialities of the interdisciplinary science of *psychogenetics*. As an organized and dependable body of knowledge of the inheritance of psychological traits, psychogenetics is as yet more a promise than an actuality. The experimental work in this area is fragmentary, and what has been done has sometimes failed to utilize the proper methods of genetic analysis. Specifically, psychologists have not always realized the importance of employing pure strains of animals in their investigations of quantitatively expressed traits. This is an oversight that can easily be rectified since pure strains of some mammals, notably mice, are available.

As the science matures we may confidently expect it to free itself of distracting excursions into pseudo-problems, chief of which has been the heredity-environment issue. This issue is one of the legacies inherited by psychology from philosophy, and it has plagued experimental psychology for nearly a hundred years. Nativism versus empiricism, McDougall's instinct psychology, Watson's adoption of a strict Lockean viewpoint, the anti-instinct polemics of the 1920's, the nature-nurture controversy of the 1930's, culminating in the publication of *The Thirty-Ninth Yearbook* of the National Society for the Study of Education (1940), are but a few manifestations of this age-old debate. Although hindsight is always easy, it now appears that if the energy, not to mention the money, that has been expended in casuistry and the collection of amphibolous data had been devoted to carefully designed psychogenetic investigations, we might now have a substantial body of knowledge about the genetics of behavior. If such knowledge were in existence, it would then be possible to evaluate by experimental methods the role of modifiability in altering innate constitution.

The writer has attempted, **in this chapter,** to avoid speculation and argument from analogy. For instance, the whole question of sex differences has been omitted because its discussion would have to be largely inferential. There is no doubt that innate sex differences in psychological traits exist: the aggressiveness of the male rat versus the pacificism of the female, contrasting courtship and copulatory patterns, and maternal behavior, to mention a few. These disparities have been traced to the action of gonadal hormones: androgen, estrogen, and progesterone. It is now well established that the male secretes some female sex hormone and the female secretes some male sex hormone, which fact precludes a sharp dichotomy between the sexes. All this information is extremely valuable, but it does not belong in a chapter on the genetics of behavior. One might infer that these established sex differences were controlled, primordially, by the sex chromosomes, but this inference has yet to be confirmed.

In order to have a science of psychogenetics it is not sufficient to determine merely that certain behavior traits are genetically transmitted. This is the first step. Genetic analysis, the mapping of chromosomes, and the specification of the *modus operandi* of the genes are also necessary functions of the psychogeneticist. In short, psychogenetics must imitate biogenetics.

One might ask, what will psychogenetics contribute to our understanding of the individual? The answer is that it may well be of tremendous value in clarifying the dynamics of behavior. The individual is a purposive, striving, selective, adjusting, animated organism. He does not spring to life just because stimuli from the outside world fall upon him. Nor does he lapse back into passivity and desuetude at their termination. There are inner forces that regulate, control, and precipitate his responses to the world. Psychologically these forces are called motives, intentions, values, interests, attitudes, and sentiments. Physiologically they are hormones, neural impulses, and chemical states. Genetically they are forces residing within the chromosomes. These genetic forces must be extremely important in shaping the psychological destiny of the individual. Any structures that can produce such varied forms as the flea and the elephant, the starfish and the kangaroo, the shark and the rabbit, must be potent causes of individuality within a species. Accordingly, an understanding of psychogenetics is a prerequisite for the development of a dynamic psychology.

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