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Most behavior is expressed within social systems, and the genetic analysis of its variance therefore presents theoretical and technical problems that have been sidestepped in most previous research. The dog presents obvious advantages for studying behavioral interactions between genotypes. Two sets of data are summarized that indicate that the magnitude of genetic differences is related to the differentiation of social roles in a competitive situation, whereas similarity of genotypes is an advantage in a situation demanding coordinated activity. Issues concerning the use of correlational techniques to study social behavior are raised.

KEY WORDS: social behavior, genetics of; dog; social genetics; cooperation; dominance.

INTRODUCTION

I am going to begin this article with two general propositions, following which I shall examine their implications for the science of behavior genetics. The first of these, which needs no justification, is that *our major human practical problems are social in nature*—war, crime, poverty, overpopulation, mental health, degradation of the environment—all these are social problems.

The second proposition is one that ought to be equally obvious but is frequently overlooked and as often deliberately avoided: that *almost all behavior that is exhibited by the members of highly social species such as man is expressed within social relationships*. What little solitary behavior

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remains is expressed within social contexts derived from these relationships. This means that, as far as behavior is concerned, *the concept of the independent individual is a myth.* A member of a highly social species always acts as a part of a social relationship, which is the only unit of behavioral measurement that has a large degree of independence.

This has obvious consequences with respect to the study of behavior genetics. One of the first is that it conflicts with the genetic principle of independent assortment. While the chromosomes and the genes carried by them assort independently, the behavior determined (or rather partially determined) by genetic action can be expressed only in connection with the behavior of other individuals that is, in most cases, affected by a different set of genes. It should therefore be no surprise to find that breeding experiments concerned with behavior rarely give results that are clearly consistent with the principle of independent assortment. However, before we can discuss the implications of this proposition in detail, we must consider the nature of social relationships.

THE NATURE OF SOCIAL RELATIONSHIPS

A social relationship is defined as predictable behavior between two or more members of the same species. It can be best understood in its simplest form, the dyad, or relationship between two individuals. This is the most common form of social relationships and also that which has been studied in greatest detail in both human and nonhuman species. It is the least common denominator of social systems, and as a system it has the following characteristics.

Feedback

If we designate the two members of the dyad A and B, the behavior of A affects B, who responds in ways that affect A, who in turn responds again in a somewhat different fashion. Theoretically, this feedback can go on indefinitely, and indeed it does in many cases. Therefore, feedback is one of the dimensions of a social relationship that can be affected by genetics. It can vary both in kind and in duration. In passing, it may be said that there are some human relationships, such as those between television performers and their audiences, in which little or no feedback is involved.

Mutual Adaptation

One of the factors that brings feedback to an end is the process of adaptation. Animals tend to act in ways that conserve energy, and the result is that relationships tend to become more and more efficient sorts of interaction.

Stabilization Through Habit Formation

Once a relationship has been reduced to an efficient form, it will tend to be repeated more or less exactly. The process of habit formation will therefore fix it and stabilize it at this level, with the result that any long-term social relationship tends to be very consistent. Such invariant behavior has often been mistakenly attributed to genetics by instinct theorists who were not acquainted with genetic phenomena.

Unequal Reciprocal Effects

One of the obvious characteristics of the social relationship and one that is especially apparent in dominance–subordination relationships is the fact that individual A may affect B to a greater degree than B affects A. I have called this phenomenon *prostasia* in order to provide a general term that will apply to any relationship, irrespective of whether dominance is involved. It is a measure of relative power, and theoretically the power of one individual could vary from 0% to 100%.

Differentiation of Behavior

The phenomenon of prostasia implies that the behavior of A and B will become different as they develop a relationship. The associated phenomenon of habit formation will then cause behavior to become consistently different. It terms of human social psychology, the members of a dyadic relationship come to play different social roles. The degree of differentiation is an obvious way in which genetics can affect a relationship, and there is sound experimental evidence to support this view as will be seen later.

Change

By their nature, social relationships are dynamic rather than static. They change and develop over time, which implies that any effects of genetics on the relationship might also change with time, even though the genotypes of the individuals must remain constant.

Thus the social organization involved in even a simple social relationship will modify the expression of behavior. This has certain obvious consequences for behavior genetics analysis.

CONSEQUENCES FOR THE GENETIC ANALYSIS OF BEHAVIOR

The most obvious effect of the organization of behavior into relationships is that social interaction may introduce a large new element of variation based on interaction (in the true sense of mutual modification) between the behavior of individuals possessing different genotypes. If the behavior of only one individual is measured, it should reflect not only the effects of his own genes but also those of the other individual involved in the relationship (Scott and Fuller, 1965). Further, the expression of genetic differences will depend on the development of relationships; that is, genetic effects will depend upon time. Obviously, the most important period in development for measuring relationships will be after the relationship has stabilized, but it should be always remembered that relationships are never completely stable.

Most importantly, the true unit of analysis is not the individual but the relationship. As we have stated above, the concept of an individual reacting in a truly independent fashion is a myth. How then are we to adapt techniques of genetic analysis to this major phenomenon?

TECHNIQUES FOR SOLVING THE PROBLEM

My first reaction to this problem when I began to study social behavior, particularly that involved with fighting mice, was to avoid it, and this can be illustrated by the history of this research (Fuller and Hahn, 1976).

Standardizing the behavior of one individual in a relationship has been done in a variety of ways. I first introduced the technique of dangling, in which a mouse held by the tail was forced to act in a standardized fashion toward another mouse (Scott and Marston, 1953). Another technique devised later was to utilize the effects of previous experience (Cairns and Nakelski, 1970; Ebert, 1972). A group-reared mouse is almost always slower to attack than an isolated one, hence at the outset of such a relationship the isolated mouse almost always attacks first. Related to this method is that of studying only the onset of the relationship, i.e., the latency to the first fight, without ever measuring the final relationship (Fredericson, 1951). All of these techniques, while they may facilitate genetic analysis, apply to highly artificial situations which have little relevance to real life.

Still another technique is to use mice of the same genetic strain; thus identical genotypes interact within each dyad. In such a case, the developed relationships should be identical. Fuller and Hahn (1976) have termed this the *homogeneous sets* design. Again, this technique has little relevance for real-life situations, except perhaps in the interactions between human identical twins.

Fuller and Hahn (1976) also describe a technique which they label "the panel of testers." As carried out in most experiments, this involves a round-robin series of encounters between one individual and all members of a group, which usually includes representatives of the same and different strains or breeds. The effects vary according to the capacities for social organization present in a given species. In laboratory mice, the result of a fight determines that the winner will thereafter attack all other mice (at least until he loses) and that the loser will thereafter avoid all other mice. In groups of dogs that develop dominance orders based on individual dominance–subordination relationships between each pair, the result is to determine the relative rank of a particular individual, a rank that is presumably based in part on genetically determined differences and capacities. In the mice, the result will be to determine a rank order of fighting ability between strains. As we have shown earlier, such a rank order can be easily modified by defining the conditions of conflict. If the conflict is brief, one strain may win, whereas if it is prolonged the other strain may win.

All of these experiments with agonistic behavior in mice employ techniques that involve individuals that have no previous social relationships to each other. A major and rather devastating conclusion from this is that almost all of the hundreds of experiments that have been done with fighting mice have relevance only to the effects of social disorganization (Scott, 1975). We must therefore begin to meet the problem head on and to study the interaction of behavior between different and similar genotypes as they are expressed in social relationships.

RESULTS OF EXPERIMENTS WITH GENETICS AND SOCIAL RELATIONSHIPS IN DOGS

The dog is a highly social animal and normally forms relationships with both other dogs and people. It shows the highest degree of genetic variation of any known mammalian species, even exceeding that of man. The dog is thus an ideal species in which to study social genetics. In fact, it is almost impossible to study any behavior of the dog without considering the social relationships that are involved. In our Bar Harbor experiments with different breeds (Scott and Fuller, 1965), we generally followed the techniques listed above, with emphasis on the technique of the standard tester.

Effects of Standardizing Human Behavior

Because many experimenters were involved and because the experiment lasted some 13 years, we tried to standardize the behavior of the experimenters as they worked with the dogs. In practice, this meant that no matter what the dogs did, the experimenters responded in the same way. The effect, of course, was to set up one-way relationships with no feedback. The dogs learned that our behavior would affect them but that their behavior would have little effect on us. The general result, which would be difficult for us to substantiate in any objective fashion because we had not anticipated it, was that the resulting dog–human relationship was a very shallow one compared to the deep relationships that are frequently developed between pet dogs and the members of a family, and between working dogs and their masters (Fuller, 1976).

While they were treated with uniform kindness, our dogs reacted to human beings with nervous and often meaningless activity (presumably because they did not know what to expect next) but with little of the close attentiveness and warm responsiveness of the typical pet dog. More important, our impression was that these dogs never developed the complete capacities that are possible in a long association with an attentive and responsive trainer.

Effects of Individual Testing

In our experiments concerned with performance, we designed the tests so that in most cases the observers were outside the room in which the puppy was tested. Even so, in many cases we had to have an experimenter in the room in order to keep the puppy from reacting strongly and emotionally to the absence of company. As we discovered, puppies as well as older dogs react strongly to the absence of companionship in strange places (Pettijohn *et al.*, 1977).

In general, we found that those dog breeds that have been used and presumably selected for individual performance in the hunting field did much better on these tests than did representatives of a working breed, i.e., dogs that are normally used under direction. In fact, individual Shetland sheep dogs often gave the impression that they were standing around waiting for someone to tell them what to do. Consequently, this breed never exhibited the remarkable capacities for learning complex activities under direction of which they are capable (Table IV).

Results with Dog–Dog Relationships

There was no way in which we could either standardize behavior or isolate individuals in such dog–dog relationships, and all that we could do was to standardize rearing conditions and the type of experience which the group received. We particularly studied the development of dominance–subordination relationships in a food-competition situation. Each litter received regular experience with bones, and at 5, 11, 15, and 52 weeks we individually tested each pair combination in the litter. Dominance–subordination is, of course, a measure of prostasia and role differentiation. We chiefly measured this along one dimension, that of complete dominance, i.e., the ability of one member of the pair to control the possession of the bone at all times.

Our initial results were astonishing. We knew that breeds such as the wire haired fox terrier and basenji were much more likely to show violent fighting behavior than cocker spaniels, beagles, and shelties; yet the data seemed to show that there were few differences with respect to dominance. Then we examined the relationships classified according to the sex of the participants and discovered that in male–female relationships there were clear-cut breed differences, but not in the cases of relationships in which two individuals were of the same sex (Pawlowski and Scott, 1956). What we had done, of course, was to unintentionally test the theory that genetic differences between individuals should lead to role differentiation, whereas genetic similarity should not result in such differentiation.

Once we had become aware of this theory, it was possible to test it independently by comparing the differentiation of dominance–subordination relationships in litters of animals in which no genetic segregation was taking place (pure breeds and F_1's) against those generations in which segregation did take place (backcrosses and F_2's) and thus where there was a greater opportunity for genetic differences between individuals to occur. In every sex combination (Table I), there were significantly more cases of complete dominance in the segregating generations (Scott and Fuller, 1965). As far as I am aware, this was the first experimental test of the theory that genetic differences in behavior produce increasing differentiation of individuals within a social relationship. I have no doubt that other more sophisticated experiments can be done along these lines, but they should lead to the same general result.

In addition, an interesting lead came out of the general analysis of the results of all tests. It came from the fact that the Mendelian experiment was designed with reciprocal crosses between cockers and basenjis, with each purebred mother in the cross producing both F_1 and backcross litters and therefore providing a similar early maternal environment to both, whereas the F_2's had maternal environments provided by F_1 mothers from reciprocal crosses. When the reciprocal crosses were analyzed, there were 20 tests in which the two reciprocal F_1 populations were significantly different, but this number decreased to six between the F_2 populations from the same source.

Table I. Percentages of Complete Dominance at 15 Weeks in Nonsegregating and Segregating Generations

	Nonsegregating	Segregating
Female–female	24	42[a]
Male–male	37	66[b]
Male–female	45	66[b]

[a] $p < 0.05$.
[b] $p < 0.01$.

There are various possible explanations of this effect, but one suggestion was, contrary to our results with dominance tests, that some sorts of breed differences can be augmented as the result of puppies interacting with genotypes similar to their own. This led to the following experiment.

EXPERIMENT ON COOPERATION

In this experiment, we[3] took puppies of three contrasting breeds—Shetland sheep dogs, beagles, and basenjis—and raised them as twins; that is, we weaned them at 4 weeks and thereafter reared them in pairs (see also Scott *et al.*, 1968). When two litters from different breeds were born on the same day or within 1 week of each other, we reared them in a normal fashion with their mothers up to 4 weeks. In an ideal litter of four, one pair was placed in a different room while each member of the other pair was placed in separate rooms with a member of the other breed. Thus we had in each experiment two homogeneous pairs and two heterogeneous pairs. It was as if we had taken two groups of monozygotic quadruplets and raised them as either monozygotic or dyzygotic twins (Table II). Of course, the dog breeds are not actually genetically homozygous, which means that there was some degree of genetic variation between littermates, but the analogy is still a good one.

As a further refinement, at 20 weeks we combined the homogeneous and heterogeneous pairs into groups of four. Thus the homogeneous pairs that had no previous experience with any other breed were now introduced to strangers, whereas the heterogeneous pairs having no experience with their own breed, except prior to 4 weeks, were now reintroduced to them. How would such animals adjust to each other on the basis of their limited social experience?

The experiment was originally designed for three repetitions in each of

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[3] I am particularly indebted to Dr. Frank Bronson and Ms. Alice Trattner for carrying out this experiment, as well as to others who helped collect the data.

the three possible combinations of breeds, but this plan was completed only in the case of the sheltie–beagle combination ($n = 24$), with one repetition each in the other two combinations ($n = 8$ each). Each pair of puppies was subjected to a regular regimen of training and experience involving various sorts of social interaction with each other and human experimenters, with the latter acting in the roles of parents or teachers. Thus the experimenter played with the puppies regularly and later gave them simple obedience training, including sit training and leash training. They were also given the opportunity to compete with each other in regular bone–dominance tests, but perhaps the most interesting test was one of forced cooperation. We had shown before in tests involving competition that genetic differences between pairs had the effect of producing differentiation of behavior. What would happen if we gave the puppies a test that forced them to cooperate?

As part of their early training, the puppies had been taught to run down an alleyway singly and in pairs for a reward of human contact and interaction. Now they were placed in a similar but longer alleyway (Fig. 1), but this time each puppy wore a harness which was connected to that of the other by a chain 18 inches long. The puppies had to run together if they were to get anywhere and, as a matter of fact, usually had relatively little difficulty in doing this. In one interesting exception, a sheltie and basenji were coupled together. The usual effect of restraint on a basenji is to make it struggle, whereas restraint usually causes a sheltie to inhibit whatever it is doing. In this pair, whenever the basenji jerked on the chain, the sheltie would lie down, at which the basenji would jerk frantically, the interaction producing an effect very much like an irresistible force and an immovable obstacle. After some time of futile struggle, the basenji finally came back to the sheltie and barked at it until it got up and they could move together.

In order to make cooperation even more essential, we introduced barriers into the alleyway, starting with one and increasing the number until the puppies had to pass through something that looked very much like a

Table II. Experimental Design

Homogeneous pairs		Heterogeneous pairs	
Sheltie–sheltie	Beagle–beagle	Sheltie–beagle	Sheltie–beagle
Sheltie (S) Sheltie (S) Beagle (B) Beagle (B)		Sheltie (B) Sheltie (B) Beagle (S) Beagle (S)	

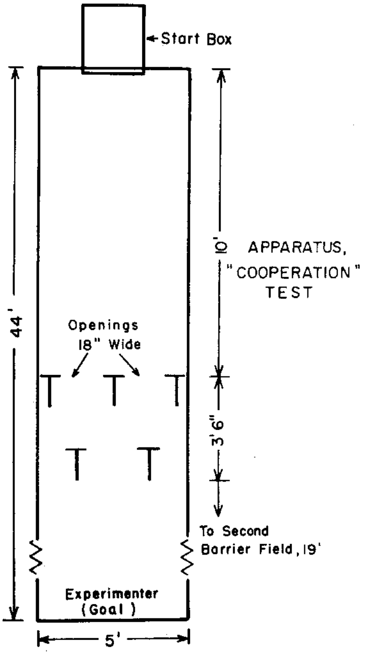

Fig. 1. Apparatus for "cooperation" test in dogs.

tank trap. If the pair tried to go on two sides of one of the barriers, they got hung up. Also, the openings were narrow enough so that it was easier if one puppy led the other. Each pair received four trials on 2 successive days at each of six levels of difficulty (1,2,3,5,8, and 10 barriers), for a total of 24 trials.

The best measure of performance on this test was the number of failures out of a possible 24. At 15 weeks of age, the three top scorers with no failures were Shetland sheep dog pairs. The next two were beagle pairs, with one and three failures, respectively. The worst score was that of a sheltie–beagle combination, with 21 failures (Table III). Applying the Mann–Whitney test, the homogeneous pairs definitely gave superior performances ($p < 0.03$).

The numbers are small, there being only six pairs in each group. However, the same tendency is seen in the two additional experiments involving basenjis, where the two basenji pairs were at the top of the list. Combining all populations, the homogeneous pairs are still superior ($p < 0.02$). Dogs with similar genotypes appear to cooperate better than ones with dissimilar genetic backgrounds, at least at this age and with these breeds.

At 31 weeks, after the puppies had been living in groups of four for more than 10 weeks, we gave them two trials on a single test with only six barriers. The idea was to find out what had been carried over from previous experience, which presumably would be best expressed in the first stages of mutual adjustment. Our only hypothesis was that animals having experience with their own kind would do better with strange animals of a similar breed than those puppies which had only had experience with a different breed not their own, and *vice versa*. This hypothesis was not upheld, there being no significant differences with any of these comparisons.

In a detailed analysis of the data, two things came through clearly. First, the homogeneous pairs were still better than the heterogeneous ones ($p < 0.001$), in spite of the fact that some of the original homogeneous pairs did worse than before. Second, when we examined the two populations as wholes, those whose first experience had been with similar animals compared with those whose first experience was with a different breed, the difference in performance was highly significant ($p < 0.002$), favoring the animals that had early experience with unlike phenotypes.

These conclusions have obvious limitations. The results are based on

Table III. Cooperation Test Failure Scores

Number of failures	Homogeneous pairs		Heterogeneous pairs
	Sheltie	Beagle	Sheltie–beagle
0	I, III, IV		
1		IV	
2			
3		I	
4			
5			
6			III, IV
7			IV
8			
9			I
10			
11			
12			
13			
14			
15			
16		III	III
17			
18			
19			
20			
21			I

only a small number of animals and concern the interaction of only two canine personality types. Nevertheless, we are justified in stating two hypotheses that have important implications. The first is that, in a social interaction demanding similarity of roles, individuals with similar genotypes perform better than those with contrasting genotypes. This is the obverse of our hypothesis derived from experiments with a competitive situation: that dissimilar genotypes lead to role differentiation. The second is that early experience with individuals representing different genotypes is beneficial for later performance involving cooperation with strange individuals with either the same or different genotypes. Translated into human terms, this would mean that identical twins should, on the average, be less well socially adjusted than fraternal twins; or, if one wishes to broaden the hypothesis, the greater the variety of individuals with whom one has early experience, the better the chances of developing good cooperative relationships with a variety of individuals in later life.

SOCIAL GENETICS AND BEHAVIOR GENETICS

As one of the early promoters of the field of behavior genetics, I am sometimes asked what lies ahead. I have usually given an equivocal answer, not caring to predict the unpredictable. Now, however, I am prepared to say where I think our science *should* go: we should directly face the problems of social genetics, and, as we do, we shall not only blaze new pathways but also clear the conceptual brambles out of some old ones.

Intelligence and the IQ

I have long espoused the viewpoint that intelligence, defined as the capacity to respond adaptively to new situations, is not a general unitary capacity. Human beings may solve problems with or without the use of verbal symbols, and there is not only no reason to posit a close correlation between the two processes, but considerable evidence to the contrary. Furthermore, our results with performance tests in dogs indicated that the capacity to solve a particular problem rapidly and easily was associated with a variety of capacities, many of them motivational and emotional, that were inherited independently (Table IV).

Now, what has intelligence to do with social genetics? It is obvious that performance capacities, whether in dogs or people, are not developed in a social vacuum. This is particularly true of the kind of intelligence that is measured by academic intelligence tests. These capacities should be most reliably expressed within the social relationship in which they are developed, namely, the teacher–pupil relationship. It should therefore come as no sur-

Table IV. Rank Order of Breeds in Independent Problem-Solving Tests

	Barrier	Manipulation	Maze	Discrimination	Delayed response	Spatial orientation	Mean rank
Basenji	1	1	4	4	4	3	2.8
Beagle	3	3	1	1	3	2	2.2
Cocker	4	5	2	3	1	1	2.7
Sheltie	5	4	5	5	5	5	4.8
Fox terrier	2	2	3	2	2	4	2.5

prise that various measures of intelligence are less reliable before school age, that they become increasingly reliable with years of schooling, and that they tend to become unreliable again as people either leave school or begin to experience a much more varied intellectual environment than the more or less standardized teacher–pupil relationships of early grammer school.

To what extent is the teacher–pupil relationship standardized? Teachers in training are often advised to treat all their pupils in the same fashion. If they did, we would predict that they would get the same result that we did with our dogs, namely, that the pupils would meet socially unresponsive persons and therefore the development of their intelligence would be impeded. Similarly, if the teacher gives no feedback at all, as is true in many large college classes, the same inhibition of development would be apparent.

This suggests an additional hypothesis to explain the currently observed decline in SAT scores, which Zajonc (1976) attributes to a change in intellectual environment associated with birth orders. Social genetics theory would predict a decline in intellectual development correlated with large classes and large schools. Indeed, even in a family circle, each additional child dilutes the feedback that the parents can give.

Considered from the social genetics viewpoint, the grading system is primarily a formalized attempt to give individual feedback. It is obvious that it is a very limited and inadequate device of this sort, and unless it is intelligently used it can result in encouragement and hence superior development in only a very limited group of individuals.

It is also obvious that if parents are either teachers themselves or act toward their children in the role of teachers, a child will enter school with an enormous advantage over those children who have not had this previous experience.

The teacher–pupil relationship should be a cooperative one, albeit one that has many aspects of forced cooperation. However, individual teachers and pupils differ enormously, as a result of both genetic variation and differences in age and experience. Is the most effective teacher for any particular child one that is similar or different? Our dog experiment, limited as it is, suggests that, while similar individuals initially cooperate more readily with each other than do dissimilar ones, experience with a variety of dissimilar individuals leads to better adjustment in future cooperative attempts with strangers. Beyond this, we know that certain teacher–pupil relationships result in lifelong effects, with very important results, but we have no idea what produces such effects, which in the present state of our knowledge consequently seem almost like miracles.

Correlations Between Relatives

Of necessity, human genetics cannot be experimental. Consequently, three indirect methods of analysis have been developed.

The first of these is pedigree analysis combined with the analysis of gene frequencies. The pedigree provides the theory, and genetic frequency in a population (assuming random mating) provides the test of the theory. However, the method is essentially limited to cases of single genes having 100% determination of phenotypes and hence is rarely used in behavior genetics, although certain analyses of sensory abilities could be considered behavioral, and there is, of course, the well-known case of Huntington's chorea.

A second method has become enormously profitable in recent years—the study of the distribution of enzymes in a population. This is based on the now-well-established generalization of a one-to-one relationship between genes and enzymes; that is, if you measure the phenotype, you know the genotype, and no breeding experiment is necessary to establish the fact. This method may well have applications in behavior genetics. The difficulty is that those enzymes that are most likely to have an effect on behavior are probably restricted to the nervous system, and it is difficult to obtain them without destroying tissue.

This leaves the method of correlation between relatives, which has been a major technique for the study of human behavior genetics. What does social relationships theory (a special branch of systems theory) say about such correlations?

First, the behavior of the members of a system *must* be correlated. If there is no correlation between the activities of two individuals composing a dyad, there is no system. In fact, the degree of observed correlation can be used as a measure of the degree of organization of the system.

Second, this correlation can be either positive or negative, depending on the sort of organization that is involved. As we have seen, if the behavior involves differentiation of social roles, the correlation must be a negative one.

Third, the analysis of such correlations cannot make use of the technique of path analysis. This technique was originally developed by Wright (1968) for the genetic analysis of pedigrees and assumes one-way causation, a legitimate assumption with respect to most gene action; but the basic nature of social systems always involves feedback and reciprocal causation. In order to adequately analyze such correlations, we are going to need to develop a new mathematical theory of correlation involving two-way causation. Perhaps this has already been done, but, if so, I have not heard of it. Also, it is obvious that such a theory cannot be usefully applied unless we have some practical or theoretical knowledge of the nature of the reactions which we are measuring.

Correlational Analysis in Intelligence Testing

Correlational analyses between relatives has been most extensively applied to intelligence testing. When we look at such correlations (Erlenmeyer-Kimling and Jarvik, 1963), the first thing that strikes us is that they are much too high. We know that all behavior is affected by the environment as well as by genetics, but here we find correlations between siblings approaching and exceeding 0.5, which is the genetic upper limit. The assumption has always been that such results were caused by something vaguely designated as "common environment" that could be partialed out by studying identical twins raised apart, foster sibs raised together, etc.

From the viewpoint of relationship theory, the basic difficulty with this approach, apart from its vague nature, is that social interaction between phenotypes does not vary directly with the differences between their associated genotypes. As we have found in dogs, part of the differences between breeds results from the fact that dogs are normally reared with other members of the same breed. Social organization can therefore exaggerate genetic differences in some cases or diminish them in others. Variance analysis in the above fashion would still not give a true picture of gene action unless we knew the precise nature of the social interaction involved.

A second difficulty arises from the nature of the statistics themselves. Correlational analysis is based on the assumption of one-way causation. While this assumption is correct with respect to genetic influences, it is incorrect with respect to social interaction, with the result that correlations between relatives reflect a mixture of one-way causation and two-way causation. Furthermore, Klein (1974) has shown that demonstrating a difference in correlations between two populations requires sample sizes far in excess of those in most published data. For example, to demonstrate a *dif-*

ference of 0.20 in a heritability estimate based on correlation requires a sample size of 800 families of four members each.

A third major difficulty lies in the nature of the tests themselves. In retrospect, if the early psychologists had deliberately tried to invent an instrument that would make behavior genetics analysis difficult, they could not have done any worse than to create the usual general intelligence test. The inclusion of so many different capacities and abilities in one score creates a veritable genetic hash whose composition defies analysis. As Mendel discovered but many people today still do not appreciate, heredity is *particulate*. Ginsburg (1976) has used the analogy of the genetic erector set, each part of which can vary independently of the others and may or may not interact with them. If we are going to make progress on the genetic analysis of intellectual abilities, we must break them down into more and more precise special components as Thurstone *et al.* (1953) pointed out many years ago. The fact that so little progress has since been made along these lines may be due to lack of appreciation that the expression and development of such capacities are phenomena of social rather than individual genetics.

What, then, is the value of intelligence testing? It is a measure of general intellectual development of an individual who is growing up in a particular human culture, hence it has considerable practical value. For example, if a child is doing poorly in school and you give him an intelligence test which shows a score of 150, it is obvious that he is not failing because of lack of intellectual development. On the other hand, if he receives a very low score, it may be the result of a great many things, either singly or in combination, and which are not necessarily genetic. For example, the child may simply be from a different culture.

The basic problem that we should be studying in this area is therefore that of the nature of intellectual development, a problem which has hitherto been approached in only a very elementary and general way. Recently, Zajonc (1976) has proposed such a theory (and a very intriguing one) that explains the relationship between intellectual development and birth order, but even he has used only the vague and global concept of "intellectual environment."

What is this "intellectual environment"? It is obviously a matrix of social relationships of which the individual is a part. Hence it is not really the environment, since the individual concerned is a part of the same system. We have got to abandon such simplistic general terms as "environment," and begin to analyze systems. Intellectual development occurs as a result of interactions between parents and offspring, between siblings, and later between children and teachers and between nonrelated peers. How do they interact to promote and inhibit each other's intellectual development?

I suspect that the answer will give a clue to the nature of motivation. The most important source of human motivation is, after all, rooted in social interaction. Most of our acts are designed to please or annoy certain individuals from whom we seek feedback. With respect to intellectual development, siblings can teach each other cooperatively, as Zajonc has postulated, but they can also compete with each other, even to the extent of assigning one sibling to the role of being bright and another to that of being dull, possibly on the basis of an original relatively slight difference in genetically determined capacities. And there may be many more such processes.

CHOICE OF SPECIES

What is the best species for experimental social genetics? The answer is any species that meets the following criteria:

1. It should be highly social, i.e., develop a variety of social relationships and thus show complex social organization.
2. It should have a reasonably short reproductive cycle in order to facilitate breeding experiments.
3. It should show abundant genetic variation, not only in morphological and physiological characteristics but also in behavior. In addition, if we are to make applications to the human condition, it should have a close evolutionary relationship to man.

Why not study man himself? Our species fits all of these criteria except that of the short breeding cycle, which is a major stumbling block that has, in effect, reduced human genetic studies to the technique of comparing correlations between relatives with those between nonrelatives. Further, the application of experimental techniques to human social genetics is greatly limited. We must consider the possibility of using other species.

The above criteria will quickly eliminate most of the species that hitherto have been popular for the study of behavior genetics. The house mouse, while it is our best-known mammal with respect to basic genetics, has a low degree of sociality, with no more than two or three social relationships that are worth studying. Even the widely studied agonistic relationship is not closely comparable to the subtle and complex dominance–subordination relationships developed among human beings. Mice and men are unfortunately quite dissimilar in both behavior and social organization. The common fruit fly, *Drosophila melanogaster*, is worse in both respects. Even the social insects have the defect that their type of social organization (based on castes) is quite different from the interindividual organization that is the foundation for most vertebrate social organization.

We will now consider other possible species. Among birds, domestic chickens are highly social and have a short reproductive cycle, a high reproductive rate, and abundant genetic variation. In fact, almost all domestic mammals and birds share these advantages and are quite suitable from a comparative standpoint. Among them, one species is almost ideal. It is very highly social, and normally develops complex relationships not only within its own species but also with man. Many of its social relationships are closely similar to those developed among humans. Its reproductive cycle is relatively short; individuals reach maturity at approximately 1 year, and young are produced as often as twice a year. Its reproductive rate is relatively high because of multiple births. Genetically, it is more variable than any other species, even including man. By now, you will have guessed that this species is the dog, *Canis familiaris*. If we want to effectively exploit social genetics in any other species than man, the dog is the obvious choice.

CONCLUSION

I might have called this article "Social Behavior Genetics," but I deliberately chose the more general title because of its wider implications and because I feel that geneticists in general, not merely behavior geneticists, should pay more attention to the relationship between heredity and social systems.

As the science of genetics has evolved, its practitioners have related their field to various systems levels and have developed each of these as subdisciplines. Hence we have molecular genetics, chromosomal or classical genetics, physiological genetics, behavior genetics, and population genetics. The systems level between behavior genetics and population genetics—that of social systems—has been largely neglected, perhaps because of the premature and now discredited ideas of the early eugenicists. Nevertheless, it is self-evident that many of the assumptions of population genetics are incorrect if applied to any high social species. For example, the Hardy–Weinberg law concerning the constancy of gene frequency in large populations cannot operate in a species subdivided into small social groups whose members tend to mate with each other according to the effects of social organization rather than at random. Similarly, if the techniques of developmental genetics are applied to the development of behavior, the results of such development are largely directed by and toward the social systems in which development takes place. Evolutionary geneticists frequently neglect the fact that one of the major functions of any social system is to modify the environment and so protect the individuals within it from many pressures, instituting instead a group of powerful pressures from within the system that can be called social selection.

Social genetics is obviously related to sociobiology, the study of animal societies. Sociobiologists, however, have neglected the study of social genetics, paying little attention to genetic variation within species and concentrating their study on the broad aspects of social organization. Some, like Wilson (1975), have concentrated on a special evolutionary problem, the origin of altruism (in the narrow sense of one individual sacrificing his life for a group). Statistically, such events are extremely rare in both human and other societies, except perhaps in the social insects. Altruism in the broad sense of contributing to the welfare of other individuals, however, is found in any species in which there is care for the young, and it presents no evolutionary puzzles.

I suspect that the only group of scientists who can adequately bring the fields of genetics and sociobiology together and synthesize the relation between these systems levels are the behavior geneticists. After all, social organization is always manifested as social behavior.

To return to the basic general concepts of social behavioral genetics, if we subscribe to the proposition that I presented early in this article, that the concept of the individual is a myth, we are also committed to its corollary, that there is no such thing as "the environment." I am not speaking in the semimystical sense of man's unity with nature but of a hard-nosed scientific conceptual scheme—that life consists of a set of nested systems and subsystems whose organization and relationships can and should be studied. Its study is the challenge facing the science of behavior genetics.

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