

## LIMITATIONS TO GENETIC COMPARISON OF POPULATIONS

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In this Symposium we are to discuss biological and social aspects of race. This is, of course, a tender topic, in dealing with which I feel strongly that we must all take especial care to express our ignorance when we are ignorant. Especially is this so in the most sensitive area of the topic, the question whether or not differences between racial groups in so-called mental abilities have an innate genetic component or not. I hope to convince you that nobody knows the answer to this question, and that in present circumstances it is impossible to know or even to foresee with certainty that it will ever be possible to know. Hence, whoever speaks as if he knows that such a racial difference is genetic, or whoever speaks as if he knows that such a racial difference is not genetic, is showing a bias that cannot be justified by the facts. Both they who say the differences are genetic and they who say they are environmental or cultural are equally prejudiced.

Of course, races differ genetically in some respects. This is what race means, though zoologists use the word rather little, preferring to use the more precise term sub-species when appropriate, and the less precise term local population when appropriate. Either of these can mean what I take it race means to anthropologists: a race is a population of a species originally living in a different region and recognizably different from other populations of that species, and it is implicit that some of the differences will be genetic. Further, the more clearly the differences are genetic, the more they are used as diagnostic criteria of race.

That races differ genetically, then, is not the controversial question. Controversy arises when people believe and act as if, because races differ genetically, they may assume that all racial differences are necessarily genetic. The most controversial area, of course, involves observed differences in performance at psychological 'ability' tests.

What we must concern ourselves with, therefore, is the criteria by which it may be possible to test whether, for example, a particular observed IQ difference between two human populations belonging to two ethnic groups is genetic or part genetic or purely environmental or cultural in origin.

Now the criteria needed to assess the genetic differences between two populations differ according to the particular variables we are interested in. First and most critical is the question whether the character we are dealing with varies

discontinuously or continuously within each population. IQ varies continuously. Second is the question whether heritability is 100% or less in each population. The heritability of IQ (that is the proportion of IQ variance that arises from genetic variety) is less than 100%. Thirdly when heritability is less than 100%, that is to say when part of the variation within the population is not genetic but environmental in causation, we have the vital question, is the environmental variation in whole or part culturally caused, and if part is culturally caused, is the culture socially inherited? Part of IQ variation is culturally caused and we need have little doubt that part of the cultural variation is socially inherited.

### **Discontinuous variables**

There is little or no difficulty in assessing the degree to which a race difference in a straightforward\* discontinuous variable has genetic causes. For such differences we are in a position, if the alternative kinds of individual are frequent enough, to say exactly how the relevant biological inheritance works and to say that this individual has these genes and that individual those genes. We may then determine the gene and genotype frequencies of different populations and describe the genetic differences distinguishing them quite precisely. This has been widely done with blood groups and various other biological differences, and different populations and different races have been shown to differ in gene frequencies.

Such characters, then, present us with little difficulty and enable us to make unequivocal statements about differences between races. These statements, however, should be understood properly. They are not usually of the kind that this race has such and such a gene and that race some allelic (alternative) gene. They are of the kind, the frequency of this gene in this population is higher than in that population. They make, therefore, no statement which we can apply to individuals: we cannot say without specific investigation that this white man differs in blood group from that American Indian. We should bear this in mind when thinking about less easily handled characters especially when they involve people's emotive attitudes. We do not deal in real life with racial types. The concept is a dangerous one in this field, it involves abstractions that have no reality. Populations of a species do not differ absolutely, but in the relative frequency of differing genotypes.

### **Continuous variables**

While discontinuous variables such as blood groups present us with little difficulty, continuous variables such as IQ are a different matter, for it is not possible with these to identify specific genotypes and it is therefore not possible to determine gene

\* I am leaving out of consideration threshold phenomena, important though they are, where an underlying continuity can give rise to an observed discontinuity as, for example, with many kinds of disease resistance where the discontinuity is imposed at the environmental level. Such characters involve the same problems as continuous variables.

frequencies. Furthermore, there are always environmental as well as genetic causes of variation. We may measure the relative importance of environmental and genetic causes of variation or heritability within a population, and if the heritabilities are very high, that is the variation is almost entirely a consequence of genetic variety, we may know more than if they are low. But even if they are high, as with fingerprint ridge counts, we are already in difficulties with population comparisons, for *there is no warrant for equating within group heritabilities and between group heritabilities.*

Since this is the core of my argument, I propose to consider it in a little detail, to indicate how the experimental biologist solves the problem with non-human, that is experimentally tractable, material, tell you what kinds of results he may get, and show why the techniques used cannot be used for races of man.

### **Transplant experiments**

The sort of problem we are confronted with is a commonplace in plant ecology. The populations of the same species of a plant that are to be found in different environments are often different. For example, Coxfoot grass plants growing in shady habitats often have broader leaves than those growing in open habitats. There is a well-recognized shade form. The question the ecogeneticist has to ask is whether the shade form is a consequence of development in the shady environment or whether it is a result of the evolution of a different genotype specially adapted to the shady environment. Now the only way he can answer this question is to transplant seeds, plants or cuttings from both habitats to some common environment, say in his experimental garden, and grow them together so as to compare them in a common environment.

Turesson did this with the shade and open habitat forms of Coxfoot. The results depended upon the geographical origin of the shade form used. Shade forms from some areas preserved their shade form in the experimental plots: these shade forms were genetically different from the open habitat form. Shade forms from other habitats lost their shade form in the experimental plots so that there was no evidence that they differed genetically from the open habitat populations. We shall, however, see later that this lack of evidence that there is a genetic difference cannot be taken as evidence that there is not a genetic difference.

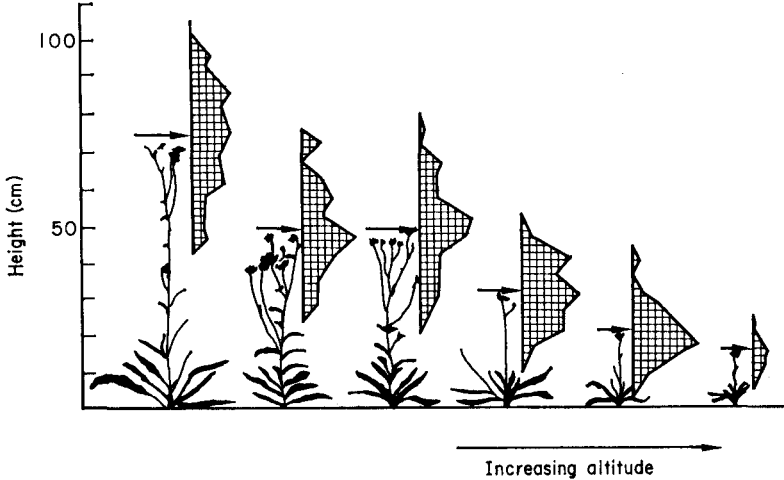
Now this experiment has lessons for us. The same apparent difference between shade form and open habitat form can sometimes have purely environmental causes and sometimes purely genetic causes, and only transplant experiments will tell us which is the cause in any particular case.

Another plant experiment is equally revealing. Populations of golden rod to be found in different places differ from one another. The plants in southern Sweden in shaded habitats are taller than those to be found in exposed habitats in northern Norway. These have been transplanted to experimental environment chambers and grown in high or low light intensities with the results given in Table 1.

**Table 1.** *Solidago virgaurea*—height of plant

Natural habitat of plants	Environment of test (light intensity)	
	Low	High
Exposed, northern Norway	Dwarf	Medium
Shaded, southern Sweden	Tall	Medium

Here we see that the different populations from the different habitats differ genetically, but that the environment has profound effects also, the different genotypes reacting in opposite ways to the environmental variable. We also see a trap we might readily fall into. Grown in high light intensity the two genotypes look alike so that we get no evidence that they differ genetically. As I pointed out above, this is not evidence that they are genetically alike. In fact their reaction to low light intensity shows them to be different. If they had only been grown in the high light intensity we might have reached the erroneous conclusion that they were genetically alike and that their differences in the wild were purely environmental. The lessons of this result are, I think, obvious.



TEXT-FIG. 1. The figure shows an average plant and the range of the distribution of heights in samples of plants taken from each of several populations from different altitudes and raised together in a common environment. The distinct populations are clearly genetically different yet the range in each is such that there is considerable overlap. Transplanting non-random samples could clearly have either exaggerated or negated the real genetic difference between the populations. (After J. Clausen *et al.*, *Experimental Studies on the Nature of Species*. Carnegie Institute of Washington, Publ. 520, 1940. Washington, D.C.)

My final lesson from plants is illustrated in Text-fig. 1 which shows some of the results of the classic work of Clausen, Keck and Hiesey in California. This concerns not only the average results for a population but its variability in transplant experiments and underlines that, for results to be interpretable, we must transplant random samples of the variety of genotypes from each population, a difficult thing to do with, for example, social classes in man.

### **Correlation of genetic and social inheritance in man**

Now let us turn to man. The sort of environmental differences we were concerned with in these plant examples are to be paralleled in man by the climatic differences in which different human populations grow. But with human populations we have an additional problem: part of the environmental component is cultural, and cultural differences may transplant with the people so that in a human transplant experiment we transplant in part environmental as well as genetic differences. Furthermore, cultural differences are in part socially inherited so that a transplanted population may preserve some of its environmental differences over the generations.

We should, in this connection, remember that we have no warrant for supposing that cultural inheritance is any more labile than biological inheritance. In fact the available evidence suggests that sometimes cultural inheritance can be very conservative. Gini (1954) studied five-century-old Albanian settlements in Southern Italy which still preserve 'their language, their traditional costumes, and other cultural characteristics', and less ancient Italian settlements in Sardinia. He concluded that 'In contrast with the current opinions of students of anthropological sciences and perhaps also of students of social sciences, the cultural tradition may be more tenacious and persistent than the physical heredity'. Social inheritance as a cause of persistent differences between peoples has to be taken seriously, and the problem of distinguishing between genetic and social inheritance as causes of any observed difference is very real.

To put the point another way: the social determination and inheritance of cultural differences are correlated with genetic relationship and therefore environmental and genetic variation are confounded. When we are comparing human groups, therefore, whether social classes or ethnic groups, it is problematic whether we can separate genetic and environmental components completely. This is why, of course, twin studies play so profound a part in human genetics. But twin studies are mostly within family studies and can only give us within family estimates of genetic variance and heritability.

When we are interested in social classes, twins reared apart are transplant experiments and can allow us to make some comparisons of within family genetic variance and between family environmental variance. Also adoption and orphanage studies are useful transplant studies, provided we know enough about the natural

parents as well as the foster parents, and there is some hope also, with the same prerequisite of knowledge of the parents, that social mobility may provide us with revealing transplant experiments that will enable us to assess the relative importance of the environmental and genetic components of class differences. The progeny of artificial insemination would also help, given adequate knowledge of the real father.

When, however, we are comparing races we are stuck completely. You cannot transplant individuals from one race to another without transplanting at least some of the environmental-cultural condition membership of race implies, and racial hybrids are both different genotypes and are presented with a special environment. Hence it follows that no-one can make any meaningful statement about the extent to which a racial difference is cultural or environmental unless they can actually determine the frequencies of relevant genes. And we know nothing about the specific genes that mediate the genetic component of IQ variance or any other component of human ability that shows continuous variance.

The only objectively honest answer anyone can give to such a question as 'Are Negroes innately inferior to Whites in IQ?' has therefore two components. First, 'Individual Negroes are not inferior to Whites in IQ. Their mean as a population is, however, lower.' Second, 'Having shown that the average of a particular Negro population is lower than that of a particular White population, nobody can say whether the population difference is all genetic, all cultural, or something in between, or even whether the genetic average of the population with the lower phenotypic average may not be the higher of the two.'

In these circumstances, we need not find it surprising that the conclusions that workers reach about this question vary not so much according to their experimental data but according to the social factors affecting themselves, as Sherwood & Nataupsky (1968) have recently demonstrated by showing that birth order, whether grandparents were American born or no, level of parents' education, rural or urban childhood, and undergraduate scholastic standing, are all variables correlated with the conclusion the workers reached. I say that this is not surprising for it is I hope obvious from what I have said that the conclusions cannot have been scientific conclusions since no scientific conclusions can be reached. The conclusions, however much dressed up as if they were scientific conclusions related to experimental data, must in fact be mere opinions, and mere opinions are to be expected to relate to social factors in the individual experimenter's background.

With these considerations in mind I now want to look at one or two examples of the data about race and IQ so that we can see a little of what it tells us and what it does not tell us.

Firstly, ever since the original findings on recruits to the army in the 1914-18 war, US Negro populations have scored on the average lower than US White populations in IQ tests. This is not at issue: the point at issue is the extent to which the difference is innate or cultural in origin. I have made it clear that at present we

cannot know so that I only wish to make one further comment. This concerns the unfortunate way in which some workers express their findings quantitatively (see for example McGurk, 1967). These workers express the difference in terms of what they call overlap. By this they mean the proportion of Negroes who are above the average IQ of the White population with which they compare them, a measure which may easily lead us to forget that 50% of Whites are below the White average! I am reminded of the story of the Member of Parliament who tabled a question for the Minister of Education, 'Was the Minister aware that 50% of our population are below average intelligence and what was he going to do about it?'

Overlap figures given by McGurk (1967) range from 13 to 30%. Let us look at a different way of expressing these findings. A normal distribution curve includes 34% within one and 47½% within two standard deviations of the mean on any one side. If two populations differ in mean by one standard deviation the overlap computed according to McGurk's criteria is about 15%. But the real overlap is more like 95%. The emotive possibilities of the difference between the two measures of overlap are striking. The proper way of expressing this difference is as follows: if we were to try to classify people into Negroes and Whites according to IQ alone we should only be right 5% more often than if we classified them by chance. Such data should not be represented in such an emotively biased way. To represent a difference as 15% overlap rather than 95% overlap is asking for misinterpretation.

I also wish to refer to the findings of McGurk concerning Negro-White differences of IQ in relation to socio-economic status. This work comes from Alabama and some people might be inclined to ignore it simply because of this, but I believe it is only proper to look at it as objectively as we can, for it does purport to be a serious-minded attempt to test the culture hypothesis of the racial difference of IQ mean. McGurk reports the following findings which he regards as failing to support the culture hypothesis as an explanation of Negro-White differences in psychological test performance. They include:

1. When Negroes and Whites are paired for similarity of socio-economic background the difference in IQ mean persists.
2. The difference was greater among pairs of high socio-economic status than among those of low socio-economic status.
3. The difference between Negroes and Whites was less for those components of the test battery regarded as having high cultural loading than for those components regarded as having low cultural loading.

Now I am not competent to judge the validity of these findings, for this involves, among other things, assessment of the validity of the division of test questions according to cultural loading, and the validity of the criteria of socio-economic status. Further, some of the arguments McGurk uses are wide open to question: for example, one of the assumptions which he does not make explicit, related to

findings I have not quoted, is that the socio-economic status of Negroes in the United States has not only improved over the last 50 years but has improved *relative* to that of Whites. However, it does seem to me that the kind of comparisons McGurk has made are the right kind of comparison, and should be made on a wider scale by sociologists as well as psychologists.

Supposing, however, that such investigations were made and supposing McGurk's findings were supported. Would they tell us anything about the degree to which Negro-White IQ mean differences are biological or social in origin? I submit they would not. They are open to interpretation on either of two hypotheses or any mixture of the two. The first hypothesis is that the difference is genetic, the second that the difference arises from socially inherited differences in racial culture, so that we are left almost where we started. Not quite, however, for the second hypothesis would now concern differences in racial culture, whether autonomous or involving racial interaction. This type of experiment would, in other words, help to disentangle racial from class differences, whether the race differences and the class differences involve genetic differences or not.

We already have strong evidence that these two must not be confused in the findings that Vandenberg (1968) very briefly showed us at the last symposium (Fig. 3 of his published paper). Again the data cannot distinguish between biological differences and differences of racial social heredity. But that the differences between races in mean IQ profile (as distinct from IQ mean) cannot be explained by differences in the distribution of the races among the social classes is clear, for it is evidently independent of social class. If the differences originate from cultural variation we must distinguish between class and race differences in culture, an obvious point perhaps, but one not always given sufficient weight.

Now I have tried to show you that it is at present logically impossible to determine whether or no a difference in IQ mean (among other continuous variables) distinguishing two ethnic groups has a genetic component or not.

In doing so I may have given the impression that such characters in man are totally intractable. I do not think this is in fact so, and since I consider that variation in human ability factors is the most important topic that we can study, I wish to point out in outline what we can do if we do it carefully enough. This requires that we distinguish carefully between at least four questions:

1. What is the genetic component of the within sibship variance?
2. What is the genetic component of the between sibship variance within a population?
3. What is the genetic component of any particular between population variance?
4. Do any two particular populations differ in genes or gene frequencies affecting the character in question?

I wish to stress that questions 3 and 4 are totally different questions. Answering



question 3 positively (if this were possible) would imply a positive answer to question 4. But a positive answer to question 4 would tell us absolutely nothing about the answer to question 3.

Question 1, what is the genetic component of within sibship variance, is answerable from comparisons of fraternal and identical twin pairs. Ideally we should have the four way comparison, between identical twin pairs thought by their family to be identical, identicals thought to be fraternal, fraternal thought to be identical and fraternal thought to be fraternal, so that we can assess the effect of family attitude on twin similarity. However, whatever its weaknesses, the equation  $\bar{V}_F - \bar{V}_I = \bar{V}_{GS}^*$  gives us our only estimate of within sibship genetic variance, and  $\bar{V}_I$  gives us the within family, sex and birthdate environmental variances (together with the more complex genetic components of variance, which I enumerate to avoid expert criticism as, the variance arising from genetic dominance, gene interaction and genotype environment interaction). Given  $\bar{V}_{GS}$  we can then partition the within sibship phenotypic variance into additive genetic variance and birth order, sex ratio, etc., components if we wish to do so, thus providing considerable information on all sibship sizes greater than one. Only children, of course, can only contribute to between family variance.

Question 2 can now be tackled, but is much more difficult because different families have different cultural and physical environments. Here the environmentalist's approach would be to classify the families according to socio-cultural and other environmental factors and see whether the classification is associated with differences in mean IQ, taking due account, of course, of the within family variables such as birth order, etc. But this is clearly illegitimate unless it be assumed *a priori* that the socio-cultural factors that differentiate the classes of family are in no way a consequence of genetic differences. We cannot assume that if so-called deprived families have lower average IQs that the low IQ is a consequence rather than a cause of the deprivation for this is to beg the whole question at issue.

The geneticist, on the other hand, tends to take mid parent-offspring mean regressions as estimates of population heritability, but this is also illegitimate because the genetic component so isolated will include the environmental parent-offspring correlation.

In these circumstances, our only legitimate approach is through theoretical population genetics. Knowledge of the within sibship genetic variance allows us to predict, *assuming random mating*, the between sibship within population genetic variance for in these circumstances since the theoretical genetic correlation between sibs is  $\frac{1}{2}$ , half the population genetic variance is between sibships. Departure from random mating at the phenotypic level is in the direction of positive assortative mating for IQ and many other human metrics, and positive assortative mating at the genetic level will *increase* the between, relative to the

\* The average variance within fraternal twin pairs (of like sex) minus the average variance within identical twin pairs equals the average genetic variance within sib-pairs.

within, sibship genetic variance. Unless we suppose that the positive phenotypic correlation between mates conceals a negative genetic correlation, then the assumption of random mating will give us a minimum estimate of population genetic variance. The phenotypic variance less this will therefore give us a maximum estimate of environmental variance, and hence a maximum estimate of the cultural component of variation. We may go further because the mid parent-offspring mean regression gives us an estimate of the total phenotypic variance attributable to heredity (biological *and* social) so that we can estimate the heritable variance and subtract the genetic variance, thus estimating the proportion of variance attributable to 'heritable' cultural or environmental differences.

Now we must turn to our third question, the heritability of group differences. This is not only the most emotive, but also scientifically the least tractable question, for in so far as group differences such as class or race differences have genetic components these must necessarily be correlated with environmental differences, and we can make no extrapolation of our estimates of within group heritabilities to between group differences, for we may not extrapolate from within to between population genetic variances.

As I have said, only transplant experiments could solve this problem. The equivalent of transplant experiments for man are twins reared apart, orphanages, or mobility between social classes. Given knowledge of the within sibship genetic variance obtained as I have described above, such experiments can tell us something of the relationship between the within sibship and within group environmental variance. There are, however, well-known difficulties of determining whether the 'transplanted' individuals are a random sample of the group from which they came, and of assessing the extent of the differences between the two environments involved so that at present we can make no satisfactory assessment of between group genetic differences, and in consequence no satisfactory assessment even between social classes where transplant experiments in principle are possible. We should however press on in our attempts to do so.

Question 3 is, however, different when we concern ourselves with mean IQ differences between races or ethnic groups, that is genetically more or less isolated populations having different environments. I hope I have made it clear that we cannot know and that, unless we can get at gene frequencies, we will never know whether these different ethnic groups differ in mean IQ for genetic or cultural reasons. It is impossible to transplant people between racial groups and only such transplants could give us estimates of between ethnic group heritability. We are therefore restricted to *describing* differences between ethnic groups and should not attempt to allocate them to genetic or environmental causes.

Question 4, however, is in principle answerable by a technique which has not, as far as I am aware, been used, that could, even where ethnic groups are involved, in principle provide answers to the question 'Do two groups or populations differ genetically?'

Assuming approximately additive gene action, if two populations differ genetically, either in gene frequency or in fixed genes, the mean genetic variance of the progeny of hybrids will be greater than the mean of the two genetic variances within the populations. Now we have a means of assessing within sib-pair genetic variance from comparisons of fraternal and identical twins reared together. If therefore we can show whether  $\bar{V}_F - \bar{V}_I$  for  $F_2$  hybrids is greater than the average of its value for the two parent populations then we can obtain evidence that the populations are genetically different that is not confounded with environmental factors.

It must be stressed, however, that, valuable though such evidence might be, it will *not* provide an answer to question 3, for evidence that two populations, living in different environments, differ genetically is in no sense evidence that the difference between their means has a genetic component. This can be seen easily if we consider the extreme example of a genetically 'superior' population in an 'inferior' environment, with a lower mean than a genetically 'inferior' population in a 'superior' environment. The test could show they were genetically different, but the environment not the genetic difference would be the cause of the lower population mean. Thus the test could give positive evidence that the populations differed genetically even if the genetic difference was of the opposite sign to the phenotypic difference. It could also give positive results even if there were no phenotypic difference, or for that matter no difference of 'genetic mean'.

### Conclusions

Our question 3 is therefore difficult. So difficult in fact that we cannot at present answer the question whether there is any genetic component of social class or race differences in mean IQ. And if we cannot do this, equally we cannot answer the question whether there is any environmental cause of these differences for the two questions are in fact the same.

In this situation, there is no reason why people should be permitted to assume the answer to either of these questions, especially when those people are supposed to be qualified to pronounce on the matter. Hence the paramount need for sociologists and geneticists to preserve an open mind as far as the nature-nurture problem is concerned. This of course in no way precludes the search for environmental factors that will raise IQ, or even environmental conditions that will specifically improve Negro performance (see Katz, Henchy & Allen, 1968). It is merely that closed minds on the nature-nurture problem are unjustifiable and, whichever kind they are, lend weapons to those who need to rationalize their prejudices.

### References

- GINI, C. (1954) The physical assimilation of foreign settlements in Italy. *Atti del IX Congresso Internazionali de Genetica Caryologia*, Vol. VI, Suppl., p. 246.

- KATZ, I., HENCHY, T. & ALLEN, H. (1968) Effects of race of tester, approval-disapproval and need on Negro children learning. *Personal. soc. Psychol.* **8**, 38.
- MCGURK, F.C.J. (1967) The culture hypothesis and psychological tests. In *Race and Modern Science*. Ed. R.E. Kuttner. Social Science Press, New York.
- SHERWOOD, J.J. & NATAUPSKY, M. (1968) Predicting the conclusions of negro-white intelligence research from biographical characteristics of the investigator. *Personal. soc. Psychol.* **8**, 53.
- VANDENBERG, S.G. (1968) Primary mental abilities or general intelligence? Evidence from twin studies. In *Genetic and Environmental Influences on Behaviour*. Ed. J.M. Thoday & A.S. Parkes. Oliver & Boyd, Edinburgh.