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Heritability: uses and abuses

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Abstract

This paper begins with a brief summary of the history of the development of ideas in the field of quantitative genetics. Next there is discussion of the controversy surrounding the contention that IQ tests validly estimate some highly heritable general intelligence factor. The validity of the reasoning supporting this contention is questioned. The theory of correlation between relatives has been of vast importance in plant and animal breeding because it is possible to design and carry out experiments to estimate variance components in expressions for covariances between relatives. However, data on humans is observational and individuals are not randomly assigned to environments, so that estimation of heritability from such data is not on the same firm foundation as it is in plant and animal breeding contexts.

Introduction

There is a massive literature on the inheritance of mental attributes. This literature has been built up by individuals who were extremely fortunate in their 'choice' of parents, their 'choice' of family circumstances, their 'choice' of education, etc. These individuals seemed to me to have no appreciation of their own total background in relation to mental attributes. The methods of data analysis were defective. The logic of data interpretation was defective. It is not surprising that the workers came to invalid conclusions on the nature-nurture problem. The conclusions are based on the use of the notion of heritability. I wrote a long paper on the whole area in *Biometrics* (Kempthorne, 1978), entitled 'Logical, Epistemological, and Statistical Aspects of Nature-Nurture Data Interpretation'. This discussion is essentially a summary of that paper.

Early history

The book *In the Name of Eugenics* by Daniel J. Kevles (1985) gives a long account of the history of eugenics, and provides a good historical background for my topic. This history starts with Francis Galton, born in 1822, who was a half cousin of Charles Darwin. Darwin 'was inclined to agree with Francis Galton that education and environment produce only a small effect on the minds of anyone, and that most of our qualities are innate'. Galton went to Cambridge to read mathematics, tried for an honors degree but could not obtain it, and got a pass degree. Galton's very famous work, 'Hereditary Genius' was based on records of eminent men and drew many very curious conclusions. He found that physical measurements followed the bivariate normal distribution. He coined the term coefficient of reversion, which he renamed the coefficient of regression.

The 1890s and early 1900s

Galton's work on data collection and on correlation and regression was picked up by Karl Pearson. Kevles quotes Karl Pearson as saying 'No training or education can create intelligence'. Galton made a gift to create the Galton Eugenics Professorship, which was given to Pearson. It is clear that Pearson's activities were directed to understanding human characteristics

by accumulating 'tons' of records and calculating correlation coefficients.

Kevles next describes Davenport, who became the director of Cold Spring Harbor, and who developed the study of Mendelian inheritance of eye, hair, and skin color. He became the U.S. leader in human genetics and eugenics. It was, of course, obvious that animal and plant breeding had been going on for centuries. The same ideas held for humans. So it was natural for people to be concerned about the progress of nations with respect to human abilities. It was common for people to agree with R. A. Fisher (1914) who said in 1913, 'The evidence appears to be conclusive that we are breeding more from the worse than the better stocks'.

Eugenics became a matter of political concern from the early 1900s.

Even a superficial reading of the history demonstrates two dominating tendencies: (1) the quantification of the tendency for inheritance of attributes of humans by the use of correlation coefficients, and (2) the use of correlation as a valid measure of causation.

1916 – on

The next step was in the incorporation of ideas of Mendel in a mathematical theory. First steps were made by Udny Yule and Karl Pearson. The big piece of work was by R.A. Fisher (1918) in his paper entitled, 'The Correlation between Relatives on the Supposition of Mendelian Inheritance', with aid from Leonard Darwin, after difficulties with a professor of statistics 'who knew no genetics' and a professor of genetics 'who knew no statistics'.

Fisher used the model in modern terms $P = G + E$ or phenotype = genotypic value plus environmental effect. He assumed, essentially, that the population was in Hardy-Weinberg equilibrium with random mating and that environmental effects were independent of each other and independent of genotype. He was then led to decompose the genotypic effect into 'additive' effects and 'dominance deviations' i.e., $G = A + D$. It was then a consequence that A had variance σ_A^2, and D had variance σ_D^2. Fisher then found that correlation between parent and offspring was one-half of σ_A^2/σ_P^2 and correlation between full sibs was one-half of $(\sigma_A^2 + \frac{1}{2}\sigma_D^2)/\sigma_P^2$. It was natural then to call the ratio σ_A^2/σ_P^2 the heritability.

These results were extended by Cockerham and by Kempthorne in 1954 for an arbitrary number of loci in Hardy-Weinberg equilibrium and random mating. Fisher also tackled the role of assortative mating with an equilibrium argument.

The main bug in Fisher's development and succeeding work was the assumption of the equation $P = G + E$ that the phenotypic value was composed of additive genotypic effects and environmental effects, that environmental effects were independent of genotypic effects and of constant distributions. These assumptions are contained implicitly in the work of Galton (1869), *Hereditary Genius* and in *all* work using the notion of heritability.

Sewall Wright developed a model of quantitative inheritance by his method of path coefficients, though failing to obtain the effects of dominance deviation and epistacy.

During the 20s and 30s there was great development of theory of genetic selection by J.B.S. Haldane, Fisher and Sewall Wright (Provine, 1971). Also, by Fisher, great development of statistical methods for qualitative genetic situations. This was accompanied by discovery of a variety of genetically determined phenotypes. These presented huge dilemmas. Suppose a married couple had given birth to a massively defective child. Should they have another child? What should potential parents of Sardinia do about the prevalence of thalassemia? What about Tay-Sachs disease?

Heritability of I.Q.

It was not surprising that attention was paid to the occurrence of mental defect and more importantly to intelligence. This was given a huge push by Cyril Burt, who became convinced that mental capacities are inherited. Burt obtained (?) data (?) on twins and did analyses that purported to show the I.Q. was very highly heritable (Burt & Howard, 1956). Burt's data and conclusions have been deeply questioned. Burt obtained his ideas from Fisher's 1918 paper, which I have mentioned above.

The methodology of analyzing twin data was examined in detail by Kempthorne and Osborne (1961). The situation is by no means simple. Monozygotic twin pairs have the same genotype, have shared the same fetal and gross prenatal environment, the same neonatal environment, and the same childhood environment. Then there is the strong possibility of homogamy. Under simplifying assumptions one can obtain estimates of genotypic variance divided by phenotypic variance, which may be regarded, perhaps, as