HERITABILITY

A technical term in quantitative genetics and behavioral genetics, signified by h^2, heritability has a very precise quantitative meaning. It does not refer simply to the fact that genetic factors are involved in the development of a given characteristic or trait (physical or behavioral) in an individual. Rather, h^2 is a statistical estimate of the proportion of population *variance* in a given phenotypic (i.e., objectively observable or measurable) characteristic attributable to genetic factors (i.e., variance in genotypes, the particular genetic "blueprint," encoded in the DNA, for the development of a given characteristic). Heritability can also be thought of as the squared correlation between the phenotypic and genotypic values on a trait in the population. The heritability of a trait cannot be estimated from study of an individual, because h^2 expresses a proportion of the total variance in some phenotype, and variance depends upon differences among individuals. (Variance, denoted as V, is the mean of the squared deviations of individuals from the arithmetic mean of the group.) Because h^2 is estimated in a sample of the population, it is subject, like any other sample statistic, to sampling error, the magnitude of which is inversely related to the square root of the sample size. Estimates of h^2 are also influenced by the amounts of genetic and environmental variability in the population sampled, and by the nature and reliability of the trait measurements. Thus h^2 for a given trait is clearly not a constant like π or the speed of light. It is more akin to a population statistic like say, the infant mortality rate in a given population, at a given time and in a given place, under a given criterion for tabulating infant deaths.

Heritability can be most clearly understood in terms of the components of variance making up the total phenotypic variance of the trait in question. The total phenotypic variance V_p can be expressed as the sum of the following components of variance:

$$V_p = V_G + V_E + V_{GE} + 2\text{Cov}GE + V_e,$$

where V_G = genetic variance
V_E = environmental variance
V_{GE} = statistical interaction of genetic and environmental factors
CovGE = covariance of genetic and environmental factors
V_e = error variance due to unreliability of measurements.

The genetic variance, V_G, can itself be divided into four components:

$$V_G = V_A + V_D + V_{Ep} + V_{AM},$$

where V_A = additive genetic variance,
V_D = nonadditive genetic variance due to dominance (interaction of alleles at the same chromosomal loci),
V_{Ep} = nonadditive genetic variance due to interaction among genes at different loci, termed *epistasis*, and
V_{AM} = genetic variance due to assortative mating, that is, the increment in genetic variance attributable to the degree of genetic resemblance between mates on the characteristic in question.

Given all the above components of variance, one can precisely define heritability. There are two definitions, narrow and broad heritability, signified h_N^2 and h_B^2, respectively:

$$h_N^2 = V_A/V_p \quad \text{and} \quad h_B^2 = V_G/V_p.$$

Estimates of h_B^2 sometimes include other components in the numerator:

$$h_B^2 = (V_G + V_{GE} + 2\text{Cov}GE)/V_p.$$

In quantitative genetics, h^2 without subscript usually means heritability in the narrow sense, h_N^2; in behavioral genetics it usually means heritability in the broad sense, h_B^2.

The heritability (h_N^2 or h_B^2) of a trait is estimated from various kinship correlations (monozygotic and dizygotic twins, siblings, parent–child, etc.), from which the various components of phenotypic variance can be estimated. For example, the correlation between monozygotic twins separated at birth and reared apart in uncorrelated environments is itself an estimate of h_B^2. The regression of single offspring on midparent (the average of both parents), is an estimate of h_N^2 only, provided the offsprings and parents have not shared a common environment. (Hence the importance of adoption studies for the estimation of heritability.) The use of other kinship correlations involves much more complex formulas for estimating variance components and heritability, and are explicated in most textbooks of quantitative and behavioral genetics (Falconer, 1960; Plomin, DeFries, & McClearn, 1980).

Heritability is an important theoretical concept for understanding the sources of individual differences in behavioral traits: abilities, personality factors, and mental illness. However, three popular misconceptions about heritability should be dispelled: (1) it does not refer to the absolute amount or value of a trait or characteristic in an individual, but to the proportion of *variance* in the trait conditioned by genetic factors; (2) there is no necessary relationship between the heritability of a trait and its psychological or social importance; and (3) there is no necessary or absolute relationship between the heritability of a trait and its mutability in potential response to all possible environmental factors. That is to say, the proportion of trait variance attributable to nongenetic or environment factors (i.e., $1 - h_B^2$) refers only to variation in the environmental factors that are actually contributing to phenotypic variance in the population at the time h^2 is estimated. Such an estimate does not, and logically cannot, take into account the possible effects of environmental factors (or novel combinations of factors) that are not currently present in the population.

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HERITABILITY OF PERSONALITY

Heritability of personality traits is one of the oldest, as well as one of the most hotly debated, topics of modern psychology. The roots of such theorizing can probably be traced back several thousand years to Plato, whose famous "myth of metals" in *The Republic* presupposed genetic determinants of ability:

> You, citizens, are all brothers, but the God who created you has put different metals into your composition—gold into those who are fit to be rulers, silver into those who are to act as their executives, and in those whose task it will be to cultivate the soil or manufacture goods he has mixed iron or brass. Most children resemble their parents. Yet occasionally a golden parent may beget a silver child or a silver parent a child of gold; indeed, any kind of parent may at times give birth to any kind of child.

It was the ardent belief during the eighteenth and nineteenth centuries that people were born as "blank slates" (tabula rasa) on which the environment inscribed the elaborate and detailed architectural plans for the developing personality. The human psyche, untampered by the tendrils of evil, would blossom in kindness, virtuosity, and reason. The myth of the tabula rasa was epitomized by the charge of John Stuart Mill that "of all the vulgar modes of escaping from the consideration of the effect of social and moral influence on the human mind, the most vulgar is that of attributing the diversities of conduct and character to inherent natural differences."

The twentieth century witnessed the stark realities of the human propensity to turpitude. Perhaps one of the derivatives of the tumultuous sociopolitical and cultural changes during the early decades of the twentieth century was a need to look "inward" for answers to the baffling riddles of human behavior. The change in attitude toward genetics is reflected in a quip by