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Gene–culture coevolution of complex social behavior: Human altruism and mate choice

(behavior genetics/developmental psychology/epigenetic rules/gene–culture transmission/sociobiology)

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ABSTRACT **The hypothesis is examined that genes bias the development of complex social behavior in one direction over alternatives. Studies of altruism and political attitudes in twins estimate that ≈50% of the variance is associated with direct genetic inheritance, virtually 0% with the twin's common family environment, and the remainder with each twin's specific environment. Studies of human marriages show that spouses choose each other on the basis of similarity, assorting on the most genetically influenced of a set of homogeneous attributes. These data imply a genetic canalization of social influences such that, within the constraints allowed by the total spectrum of cultural alternatives, people create environments maximally compatible with their genotypes.**

Increasing efforts are being made to understand the relationship between human cultural and genetic transmission. As Lumsden and Wilson (1) argued when presenting the theory of gene–culture coevolution, neither purely genetic nor purely cultural modes of transmission are likely to be evolutionarily stable. Instead, they provided a model to integrate genetic and environmental influences into a reciprocating circuit such that epigenetic rules guide individual development in one direction over alternatives (termed gene–culture transmission). Innate biases to learn one pattern of cultural information over another provide a particularly likely mechanism by which dual inheritance can occur.

Most if not all of the components of cognitive development examined to date have supported the gene–culture model of transmission (1–7). Corresponding data on personality and social development have been attended to far less. Here we review research in support of the hypothesis that epigenetic rules bias the development of complex social behavior, choosing as illustrative examples, altruism and mate choice. In so doing, we contrast Lumsden and coworkers' (1–7) approach with models of cultural transmission hypothesized by Cavalli-Sforza, Feldman, and their colleagues (8–10). While the latter authors incorporated the phrase "gene-culture coevolution" in a study of the transmission of altruism (10), they have generally failed to adopt the concomitant prescription that epigenetic rules bias individual development. As a result, much of their perspective is discordant with knowledge about social learning in families. By contrast, gene–culture coevolutionary formulations, in the sense originally intended by Lumsden and Wilson (1), appear to be highly compatible with these same facts.

Epigenetic Rules in Social Development

Extensive theorizing in both the evolutionary and social sciences errs in not taking into account that social learning is dependent upon the innate capacities and biases of the learner (e.g., refs. 8, 9, and 11). For example, most models of cultural transmission within the family (i.e., vertical, from parent to child, and horizontal, from sibling to sibling) imply that siblings will resemble each other, over and above shared genes, as a result of a common family environment. Gene–culture theory, in contrast, leads to the expectation that siblings will differ from each other in part because their nonshared genes incline them to acquire patterns of behavior best fitting their particular genotype (gene–culture transmission). While it may seem intuitively correct to assume that common family environment shapes individual development, consideration of data reveals quite a different set of relationships.

Behavior genetic model fitting techniques provide increasingly powerful tests of alternative hypotheses about the genetic and social influences on family resemblances (12–15). One useful design involves the comparison of monozygotic and dizygotic twins reared together. While critics have argued that the twin method is invalid, detailed empirical work demonstrates the critiques to be of limited importance (16, 17). In a twin study, the raw data are the between- and within-pairs variances and covariances. The between-pairs mean squares reflect both pair resemblances and pair differences, and the within-pairs mean squares, pair differences. The genetic models are fitted to these mean squares. The total phenotypic variance can be partitioned into the following three sources: $V(G)$, additive genetic effects; $V(CE)$, common environmental influences that affect both twins equally; and $V(SE)$, specific environmental influences that affect each twin individually. This latter is a residual term that is comprised of many sources, including measurement error and certain kinds of interaction between genotypes and environments. Thus, the total phenotypic variance is partitioned as $V(G) + V(CE) + V(SE)$.

Using such a design with 573 adult monozygotic and dizygotic twin pairs, Rushton *et al.* (18) examined the cultural and genetic inheritance of individual differences in altruism and aggression. Components of these traits were measured by paper and pencil questionnaires in which the 1146 respondents endorsed items measuring their self-reported altruistic behavior, empathy, nurturance, aggressiveness, and assertiveness. Maximum-likelihood model-fitting estimation procedures revealed ≈50% of the variance on each scale to be associated with genetic effects, virtually 0% with the twin's common environment, and the remaining 50% with each twin's specific environment and/or error associated with the test. Correcting for the unreliability in the tests raised the heritabilities to ≈60% and reduced the specific environment variance to 40%. A summary of the results is presented in Table 1.

These data not only signify a strong association of genetic factors with the characteristics in question but also indicate a negligible influence of the twin's shared environment. Rather, the distinct experiences of the individual account for almost all the environmental variance. Approaches such as

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Table 1. Estimates of variance components and estimates corrected for unreliability from a biometrical analysis of altruism, empathy, nurturance, aggressiveness, and assertiveness questionnaires from 573 adult twin pairs

	Additive genetic variance		Common environmental variance		Specific environmental variance	
Trait	%E	%EC	%E	%EC	%E	%EC
Altruism	51	60	2	2	47	38
Empathy	51	65	0	0	49	35
Nurturance	43	60	1	1	56	39
Aggressiveness	39	54	0	0	61	46
Assertiveness	53	69	0	0	47	31

%E, variance component; %EC, estimates corrected for unreliability. Data has been adapted from Rushton *et al.*, ref. 18.

those by Cavalli-Sforza and Feldman (8, 9) imply a substantial effect for common environment. Clearly, this assumption is incompatible with the empirical data reported in Table 1. The account provided by a mechanism of gene–culture transmission, on the other hand, predicting that social development will be guided by epigenetic rules that incline individuals to particular learning experiences is directly compatible with the large specific environment term shown.

The discovery that common family environment plays a very limited role in social development (even for traits that parents are expected to socialize heavily such as altruism and aggression) runs counter to prevailing theories of personality development that assume that the important environmental variance is between families, not within. Yet the observation that the environmental factors that influence development are those that are specific to each sibling, rather than common, is robust, having been replicated using samples of four different types: twins reared together, twins reared apart, adoptive parents and their offspring, and adoptive siblings (19–24). Regardless of whether one considers the transmission of socially undesirable traits such as crime, obesity, and schizophrenia, or more normative personality characteristics such as vocational interests and value systems, the evidence reveals that whereas genetic influences have an important role to play, the common family environment alone has little apparent effect. For example, a study of 14,427 children separated from parents at birth found that children were at risk for criminal conviction if their biological parents had been so convicted, but not if their adopting parents had been (20). Moreover, siblings and half-siblings adopted separately into different homes tended to be concordant for convictions. That siblings raised apart for many years in complex environments grow to be significantly similar to each other and that their degree of similarity is predicted by the number of genes they share, implies the presence of genetically based stabilizing systems that channel development. The manner in which people create environments maximally compatible with their genotypes has become a central issue to some psychologists (25–27).

A compelling test of alternative models of transmission has been made in the context of social attitudes (Cavalli-Sforza *et al.*, ref. 9; Martin *et al.*, ref. 24). Since attitudes are more flexible than personality, purely cultural models of transmission might be considered especially likely, with at least some vertical transmission occurring from parent to child. Cavalli-Sforza *et al.* (9) attempted to illustrate this with data on beliefs, interests, and attitudes from a sample of nuclear families. Unfortunately, as the authors acknowledged, their design conflated the different types of transmission that may have been occurring (e.g., genetic with cultural). Martin *et al.* (24), on the other hand, provided strong evidence that vertical cultural transmission of the type proposed by Cavalli-Sforza *et al.* (9) fails to influence social attitudes. They received questionnaires measuring attitudes toward such issues as the death penalty from 4600 pairs of adult twins. Other sources provided estimates of assortative mating. Path analysis indicated a very poor fit when the genetic contribution to the observed variation was set to zero. On the other hand, models deleting vertical cultural inheritance gave an extremely good fit when allowances were made for assortative mating. The cogency of the estimation techniques, sample sizes, and questionnaire validities employed were such that the authors were able to predict the correlations that would be expected in other relationships: e.g., 0.00 between foster parent and adult foster child; 0.52 between parents and children; and 0.62 for separated monozygotic twins. The results led the authors to conclude that: ". . . geneticists and social scientists [might] have misconceived the role of cultual inheritance and that individuals acquire little from their social environment that is incompatible with their genotype" (ref. 24, p. 4368).

One feature of developmental research highlighted by a gene–culture coevolutionary perspective, but underexamined to date, is the role epigenetic rules play in modulating human life-history phenomena. Familial concordances show that genetic mechanisms sequence such trajectories as growth rates in height and mental development; age of onset of puberty, menopause, and first sexual experience; family size; fecundity; a variety of health-related phenomena including degenerative diseases associated with aging; and longevity itself (28, 29). Chronogenetics may also influence changes in personality and attitudes. Rushton *et al.* (18) found altruism increased over the age span from 19 to 60 years old, whereas aggressiveness decreased. Other studies suggest a correlation between age and political conservatism (24). It was hypothesized that epigenetic rules underlie age changes in creativity (30). Longitudinal behavior genetic studies will be required to ascertain more precisely the influence of innate biases in the human life cycle.

Assortative Mating and Gene–Culture Coevolution

So far the discussion has been limited to individual social development. From the perspective of gene–culture coevolution, however, the potential of epigenetic rules to bias behavior and affect society goes well beyond ontogeny. Via cognitive phenotypes and group action, altruistic inclinations may be amplified into charities and hospitals, creative and educative dispositions into academies of learning, and martial tempers into institutes of war. Such macrocultural innovations can be expected to influence the genetic composition of future generations, thus completing a reciprocal circuit.

Consider the role of mating systems in this respect. Mate choice may be one of the most important decisions individuals make affecting their social environment. The tendency is for marriage partners to choose individuals who are similar. In the previously mentioned study on social attitudes, for example, the interspouse correlations for political conservatism that were used ranged from +0.40 to +0.67 (24). While these are among the highest correlations between spouses reported to date, equalled only by similarity on age, socioeconomic status, religion, and ethnic background, the literature is clear that, on average, spouses resemble each other in almost every feature (31, 32). A review of the world literature on IQ (intelligence quotient), for example, shows an average correlation between spouses of +0.37 (33). Assortment for personality attributes (such as altruism) tends to be positive, but lower (*rs*, +0.02 to +0.29 with a mean of about +0.15; ref. 34). Spouses also show resemblances on a variety of anthropometric variables (e.g., neck circumference) with coefficients of the order of +0.10 to +0.20 (35). Since heritabilities have been found for all of these characteristics, it follows that spouses are genetically more similar to each other than to random members of the population.

Genetic similarity between spouses is likely to affect gene–culture coevolution. While not necessarily changing the population mean of the attribute in question (unless there is directional dominance of the genes involved), positive assortative mating will increase variability and thereby have a substantial influence on the genetic structure of the population. While these effects may be small for any single generation, the cumulative effects over many generations may be considerable. For example, given a mean IQ of 100 and a standard deviation of 15, Jensen (34) estimates that if the present level of assortative mating for intelligence has existed for several generations, it may account for over half the present frequency of persons with IQs above 130 and 80% of those with IQs over 145 and that there are approximately 20 times as many persons above an IQ of 160 as would be expected from random mating. Consequently, IQ-based stratification systems may emerge and society become more differentiated (the nature of current Western IQ-based educational and occupational hierarchies have been discussed by Gottfredson, ref. 36; Hunter and Hunter, ref. 37). In turn, changes in the complexity of society are likely to alter the prescribed mating system and individual mate choice.

Mate choice, therefore, provides another testing ground for theories of gene–culture coevolution. The epigenetic rules that bias spouses to choose each other on the basis of similarity may be particularly fine tuned, inclining individuals to assort most on the more genetically influenced of a set of homogeneous attributes. Positive correlations between assortative mating coefficients and heritability estimates have been observed for a variety of anthropometric, cognitive, and personological characteristics (38, 39). These data were predicted by genetic similarity theory, a formulation that extends the idea of kin selection by postulating that organisms have a tendency to favor any individual of similar genotype, regardless of whether or not they are "kin" (Rushton *et al.*, refs. 27 and 40). The phenomenon of assortative mating can be explained in this way. Advantages thought to accrue to choosing optimal genetic similarity in mates include increased marital stability, greater fecundity, increased relatedness to offspring, and increased within-family altruism (31, 40).

Discussion

The evidence presented here supports the conclusion that ontogeny in the domains of personality, attitudes, and their associated behaviors depends upon gene–culture transmission through the activity of epigenetic rules biasing individuals in one direction instead of another. This evidence joins the extensive data set already assembled indicating a pervasive role for gene–culture transmission in human development (1–3). While open to continuing empirical test and to theoretical modification, the concept of combined gene–culture transmission has provided a useful heuristic (4–7, 10, 30, 41, 42). At present it would appear that models assigning principal roles to genetically unbiased transmission of cultural information, or to entirely genetically determined behavior, are not compatible with the large body of available evidence. In contrast, consistent endorsement has been implied for the hypothesis that epigenetic rules bias individuals to preferentially use culture traits in accord with their particular genotype to shape their social development. As such, the data support a biased transmission and hence a tight correlation between genetic and cultural evolution, as proposed by Lumsden and Wilson (1). At a more general level, continued assertions that diverse gene–culture models can all be treated by population biologists as equally likely on intuitive grounds (Maynard Smith and Warren, ref. 43) is an especially unproductive fallacy. The substance of behavior genetics and developmental psychology can provide improved criteria for eliminating any number of dual inheritance formulations that otherwise might be thought intuitively plausible.

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