Sir Francis Galton, Epigenetic Rules, Genetic Similarity Theory, and Human Life-History Analysis

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ABSTRACT In this article, an evolutionary perspective is applied to individual differences. Among the issues discussed are: (*a*) the seminal contributions of Francis Galton and the subsequent ideological reaction, (*b*) the distal-proximal continuum for understanding levels of explanation in social behavior, (*c*) consistent patterns of group differences in behavior (age, sex, social class, and race), (*d*) the heritability of personality and the role epigenetic rules play in guiding development in one direction over alternatives, (*e*) the genetic similarity theory perspective on friendship and mate choice, and (*f*) the view that personality is part of an r-K reproductive strategy involving a compensatory exchange between the production of gametes and parental care. It is suggested in conclusion that personality traits be considered aspects of a coordinated life cycle deeply embedded in evolutionary history.

The data sets and ideas in this article may be unfamiliar to readers and even strike some as unlikely, so I begin by emphasizing a historical tradition too often left unacknowledged in contemporary research. It is regrettable that the "Galton School" of analyzing individual differences from a biological and evolutionary perspective that began 125 years ago is still so poorly understood. However, a direct line leads from Charles Darwin (1809–1882) and his cousin Francis Galton (1822–

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1911) to contemporary research, and some of my arguments may be better appreciated when placed in this context.

Sir Francis Galton: Establishing the Tradition

The concept of personality stems from the observation of individual differences in human behavior, the scientific study of which may rightfully be thought to begin with Galton. History could of course go back to those ancient Greeks, Galen and Hippocrates, and their four humor-based temperaments for the first typology, but Galton can be considered the originator of modern personality research. His 1865 article "Hereditary Talents and Character" was published 14 years before Wundt "founded" psychology, at a time when Freud was only 9 years old and long before the births of Allport or Murray. A forerunner to *Hereditary Genius* (1869), the article was concerned with the heritability, distribution, and measurement of individual differences in "zeal and industry," as well as intelligence, and appeared 6 years after *The Origin of Species* (Darwin, 1859), and 6 years before *The Descent of Man* (Darwin, 1871). Providing early evidence that individual differences in intelligence were heritable, this article was the first to advocate using twins for proof. Galton was not exclusively hereditarian; he also carried out surveys to assess the other influences that made for genius, and reported that devoted, high-minded mothers and first-born ordinal position were important predictors (Galton, 1874).

Galton not only advocated the use of twins to help disentangle the effects of heredity and environment, but also carried out breeding experiments with plants and animals anticipating later work in behavior genetics. Less known is that Galton (1879) invented the word association test, creating stimulus words and gathering statistical information on their unconscious associations. These were published in *Brain*, and Freud can almost certainly be included among the readers of this issue, although he never referred to Galton's paper nor credited Galton with priority in suggesting the existence of unconscious mental processes (Forrest, 1974).

The different styles of Galton and Freud are worth noting. Galton gathered hard objective data and invented statistical techniques to analyze them. His orientation was to see human psychology as part of natural science, resting on similar techniques of study and making direct contact with what was known about animals and evolutionary biology. Freud, in contrast, used a subjective, unfalsifiable set of procedures which had discontinuity with other sciences. Some have seen it as a poor reflection that Galton is relatively obscure and maligned, while Freud has an exalted reputation (Eysenck, 1985).

Galton (1887) also studied temperament, as in his article "Good and Bad Temper in English Families." He also pioneered work on assortative mating among spouses, and the interrelationships of intelligence, temperament, and physique, arguing that socially desirable traits tend to go together because of mate preferences. Galton (1894) even made a contribution to Volume 1 of the *Psychological Review* in an article entitled "Arithmetic by Smell," in which, in intrepid Victorian fashion, he self-experimented by associating numbers with different smells and then combined the scents to discover that he added and subtracted their number equivalents automatically.

The longest standing contributions of Galton are statistical. He was among the first to apply the normal distribution, deviation scores, and percentiles to psychological characteristics (1869). He invented the concepts of regression and correlation (1888, 1889). He was influential in founding the journal *Biometrika* (1901) which, by promulgating statistical techniques for the study of biological variation (of which psychological characteristics were included) helped begin the psychometric tradition.

When Galton died in 1911, his will endowed Karl Pearson with a Chair of Eugenics at the University of London. Pearson, later Galton's biographer (1914–30), invented the product-moment correlation and the chi square goodness-of-fit statistic, and helped inaugurate the great biometric trajectory that included R. A. Fisher (inventor of the analysis of variance) and Sewall Wright (inventor of path analysis), both of whom are best known for their "modern synthesis" of Darwinian evolution with Mendelian genetics (Fisher, 1930; Wright, 1931). Few personality psychologists are aware of how the statistics they use were originated for the purpose of estimating the transmission of genetic variance.

A rival to Pearson's Department of Eugenics was the University of London's Psychology Department headed by another Galtonian, Charles Spearman. Spearman invented rank order correlations, factor analysis, discovered the *g* factor in tests of intelligence, and investigated the interaction of personality and intelligence, finding, like Galton before him, that "good" traits such as honesty and intelligence went together (Spearman, 1927). Spearman's successor was Sir Cyril Burt, and two of Burt's most famous students, Raymond Cattell (1982) and Hans Eysenck (1981), have promulgated this unique amalgam of evolutionary biology, behavioral genetics, neuroscience, and psychometrics to the present day. So, too, has Jeffrey Gray (1987), Eysenck's post-retirement successor at London's Institute of Psychiatry whose work maps out the cytoarchitecture underlying anxiety and provides a reformulation of the biological basis of temperament.

Arthur Jensen also wears the Galton mantle. It is not well-known that Jensen's early research was concerned with personality factors in educational attainment, a topic he pursued for his doctoral degree at Columbia. Becoming dissatisfied with what he viewed as the relatively unscientific thinking about personality that he found there (Murray and Freud), and while publishing several articles on the Thematic Apperception Test (TAT), Rorschach, and other projective techniques, he moved to London to carry out postdoctoral research with Eysenck, wrote the 1958 chapter on personality for the *Annual Review of Psychology*, learned about the *g* factor in tests of intelligence, and subsequently became a leading psychometrician (1987). So many recent psychologists have been influenced by the new evolutionary thinking arising out of sociobiology (Dawkins, 1976; E. O. Wilson, 1975) that the Galtonian identity may be lost in what is hopefully an emerging paradigm (Buss, 1984; Rushton, 1984).

It may be important to consider why the Galtonian tradition is not better appreciated than it currently is. Many of the earliest psychologists including Freud, Dewey, James, McDougall, and Thorndike embraced Darwinism with enthusiasm, as did other social thinkers including Marx and Spencer. At this time the eugenics movement was also widely supported, as much by socialist reformers as by right-wing traditionalists (Clark, 1984; Kevles, 1985). The mix of political ideology with human biology, however, eventually led to Galton's unpopularity. By the mid-1930s the political right had gained the ascendancy in claiming evolutionary theory to support their arguments while the political left had come to believe that the concept of "survival of the fittest" was incompatible with the notion of equality. Powerful ideologues such as the anthropologist Franz Boas and his student, Margaret Mead, fought against the idea of biological universals. Mead's (1928) *Coming of Age in Samoa* purported to discover a "negative instance" of adolescence being a time of emotional stresses, and its conclusion became a significant component in the increasingly antibiological orthodoxy. (Today Mead's work can be viewed as being of more dubious status than Burt's, not only because of the problematic existence of the data base but also because Mead's conclusions are completely out of line with subsequent data; Freeman, 1983.)

Opposition to the Nazis clearly played a significant role in blunting Galton's impact. From the 1930s onwards scarcely anyone outside Germany and its allies dared to suggest that groups of individuals might be in any biological respect superior to any other (or even, different), lest it should appear that the author was supporting or excusing the Nazi cause. Those who believed in the biological equality of people were free to write what they liked, without fear of contradiction. They made full use of their opportunity in the decades that followed. Especially following the Holocaust the idea of a genetically based core to human nature on which individuals (and social classes, gender orientations, nations, races, and increasingly even ages) might differ has been consistently derogated. Even trait theory became tainted since by its focus on individual differences it directly increased the likelihood that group differences would be perceived (Adelson, 1978; Hogan & Emler, 1978; Kenrick & Dantchik, 1983). Fear of being labeled "elitist," "sexist," or "racist" has chilled numerous lines of enquiry in the study of behavioral development.

From an evolutionary perspective, however, it has to be expected that both individuals and groups will differ, genetically, in the mechanisms underlying their behavior. The existence of genetic variance both within and between populations is the first postulate of Darwinian theory. (The second is that some parts of this genetic variance are more successful at replication than others.) Coming to terms with such an outlook need not, however, disconfirm the democratic ideal. As E. O. Wilson (1978) put it: "We are not compelled to believe in biological uniformity in order to affirm human freedom and dignity" (p. 52). He went on to quote Bressler (1968) that "an ideology that tacitly appeals to biological equality as a condition for human emancipation corrupts the idea of freedom. Moreover, it encourages decent men to tremble at the prospect of 'inconvenient' findings that may emerge in future scientific research."

Distal-Proximal Levels of Explanation

In fact, no necessary conflicts exist between evolutionary and genetic analyses and those from social learning and situational perspectives. Too many errors and unnecessary debates have occurred as a result of

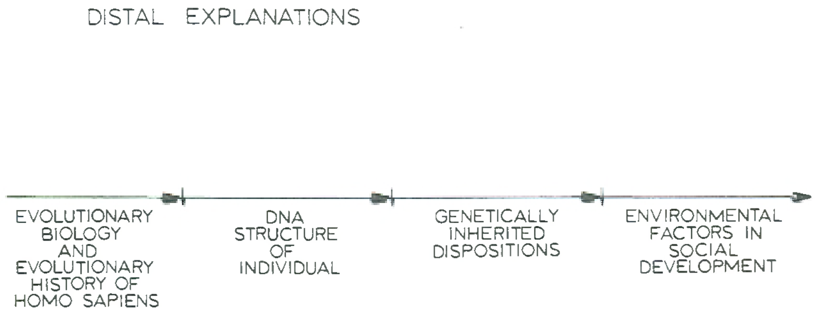


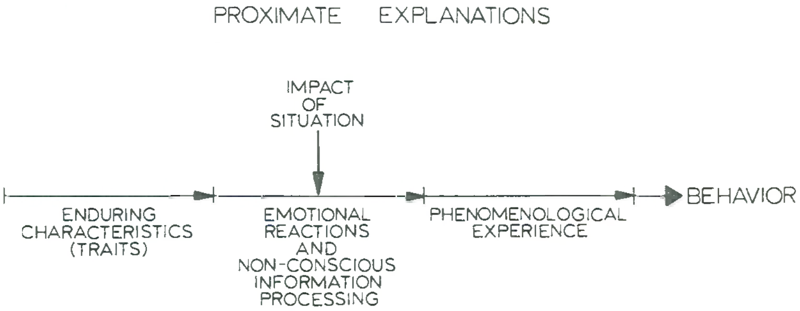
Figure 1
The Distal-Proximal Dimension and the Time Factor in Levels of Explanation for Social Behavior

Note. When explanations move from distal to proximal, controversy does not ensue, whereas the converse is less true. From "Epigenetic Rules in Moral Development: Distal-Proximal Approaches to Altruism and Aggression" by J. P. Rushton, 1988, *Aggressive Behavior*, **14**, p. 36.

confusing distal and proximal levels of reasoning (see Figure 1). Proximate levels emphasize the environmental, cognitive, and physiological mechanisms involved; distal explanations consider the significance of phenomena from perspectives further back in time, ultimately in evolutionary terms of reproductive fitness.

When explanations move from distal to proximal, controversy does not ensue. Evolutionary biologists do not find the heritability of traits problematic, trait theorists accept that dispositions are modified by later learning, and learning theorists believe that the products of early experiences interact with subsequent situations to produce emotional arousal and cognition. Resistance is more likely, however, as explanations move from proximal to distal. Thus some phenomenologists mistrust the reduction that consciousness is partly the result of previous learning. Situationists and learning theorists do not always accept that people's choices and development may be guided by inherited traits. Often behavior geneticists ignore evolutionary history.

Proximal wariness of distal explanation may be due in part to the ideological preferences discussed above. In addition, some have expressed concern about extreme reductionism—for example, that phenomenology is entirely reducible to learning, or that learning is only secondary to genetics. Unfortunately, another reason for dispute arises from lack of knowledge. Most researchers seem devoted to an exclu-



sive orientation. It is rare for cognitive social learning theorists to know much about evolution or genetics; or for social psychologists to understand psychometrics, or for trait theorists to pursue behaviorism. The psychoanalytic and radical behaviorist schisms even create their own journals and professional schools.

Behavior can be analyzed usefully from each of the levels. For example, situations can induce mood changes of happiness and anger which alter people's altruism and aggression. People can also be shown to differ, however, in average mood state. It is at this stage that conceptual problems occur, for some have found it difficult to see how, if people alter their behavior with varying circumstances, they can be said to have enduring characteristics that reliably differentiate them from others. Major reviews of the empirical literature carried out in the 1960s (Mischel, 1968; Vernon, 1964) seemed to show that the trait perspective was limited in its predictive power. Critics pointed to the fact that different indices of the same trait only correlated .20 to .30. Social learning theorists emphasized the modifiability of behavior and intra-individual variation, and deemphasized the focus on interindividual variation.

It is now known that a major error of interpretation was made. The mistake was to use correlations between single items or behavioral events as representative of generalized traits. A more accurate assessment is obtained by using the principle of aggregation, which states that the sum of a set of multiple measurements is a more stable and unbiased estimator than any single measurement from the set. This methodological point applies equally to self-report items, judges' ratings, behavioral measures, and physiological indices, whether assessed in situationally specific or generalized manners (Epstein & O'Brien, 1985; Rushton, Brainerd, & Pressley, 1983). For example, single items on IQ tests only correlate .15; subtests based on four to six items correlate .30 or .40; and batteries of items comprising verbal and performance subscales correlate .80. In a behavioral mode, Eaton (1983) assessed differences in activity level in 3- and 4-year-olds using single versus multiple actometers attached to the children's wrists as predictors, and parents' and teachers' ratings as criteria. Single actometers correlated .33 with the ratings, while scores on multiple actometers correlated .69.

Group Differences in Personality

An often negated topic in personality is group differences (e.g., age, sex, socioeconomic status [SES], race). As with traits generally, the main empirical reason cited for dismissing such effects is the alleged low level of variance accounted for. A necessary prerequisite for adequately examining group differences, however, is reliable measurement, but many studies fail to use aggregate procedures and inadvertently bias the results in favor of the null hypothesis. If there is little reliable variance in dependent variables, then the variance cannot be apportioned sizably to independent variables!

This point is illustrated in an analysis of altruism and aggression questionnaires. For example, males and lower SES groups are found to be significantly more aggressive and less nurturant and empathic than females and higher SES groups. In addition, aggressiveness is found to decrease with age from 20 to 60, while components of altruism increase. These observations would have been missed if the analyses relied on single items, for the variance accounted for by sex differences increases from 1% to 3% to 8% as the number of questionnaire items increases from 1 to 5 to 23. Combining age, sex, and SES in a multiple regression equation, again differentiating a 1- to 23-item scale, increases the multiple R from an average of .18 for single items to .39 for the 23 items (Rushton, 1988a).

Age differences. Psychologists writing on age effects in social behavior often prefer showing how "myths" and "stereotypes" can be dispelled to investigating where genuine changes occur. Age changes in personality, however, have been established. Eysenck (1988) has shown that from ages 16 to 60 scores on his Psychoticism (hostility), Extraversion (sociability), and Neuroticism (anxiety) dimensions all decline while scores on the Lie Scale (prosocial conformity) increase. These parallel the data just mentioned on altruism and aggressiveness, and also many others that have been documented, including those on crime, sexuality, and scientific productivity (Rushton, in press). In accord with common observation it seems as though the affective turbulance of youth is replaced by the relative calm of age. This conclusion is directly supported by data from research on "affect intensity," which is distinctly found to decrease with age (Diener, Sandvik, & Larsen, 1985).

Sex differences. Research on sex differences is particularly at fault for ignoring the principle of aggregation. In a major review of the sex differences literature, Maccoby and Jacklin (1974) concluded that the only sex differences that are fairly well established are that (*a*) girls excel in verbal ability, (*b*) boys excel in visual-spatial ability, (*c*) boys are superior in mathematical ability, and (*d*) males are more aggressive. However, Block (1976) subsequently argued that this review was biased against finding sex differences due to inappropriate methods of combining data. Specifically, Block argued that many of the individual studies reviewed used single-item dependent variables of unknown reliability, and hence they were potentially insensitive to sex differences. To examine this possibility, Block, after specifying the units to be combined, aggregated over studies to determine the proportion favoring males or females in higher mean score on each dimension.

Block's meta-analysis led her to rather different conclusions from Maccoby and Jacklin's (1974). She concluded that males are not only higher on spatial and quantitative abilities and aggressiveness, but also are "better on insight problems requiring restructuring, and more dominant and have a stronger, more potent self-concept, are more curious and exploring, more active, and more impulsive" (1976, p. 307). In addition, she suggested that females not only score higher on tests of verbal ability but also "express more fear, are more susceptible to anxiety, are more lacking in task confidence, seek more help and reassurance, maintain greater proximity to friends, score higher on social desirability, and, at the younger ages at which compliance has been studied, are more compliant with adults" (p. 307).

Meta-analysis alone does not necessarily solve the problem. In a review of empathy, for example, Eisenberg and Lennon (1983) reported that the effect sizes favoring females were minimal or nonexistent on behavioral and physiological measures, moderate on specific self-ratings in specific situations, and largest on self-report questionnaires. On the basis of this evidence, Eisenberg and Lennon (1983) concluded that the widespread belief in sex differences in empathy was probably due to the effects of stereotyping since the behavioral measures were least and the self-report measures most susceptible to this type of influence. An alternative interpretation is that effect sizes depend on the amount of aggregated variability in the dependent variable. To test this hypothesis, Rushton (1988a) examined 7 studies of reflexive crying and 21 studies using questionnaires presented in Eisenberg and Lennon's (1983) review and found that correlations of .69 ($p < .05$) and .73 ($p < .001$) resulted between the size of the effect favoring females and the total number of units possible in the dependent variable. Thus the greater the variability in the dependent variable, the greater the sex difference.

Socioeconomic status. Most psychologists ignore SES differences, leaving them to the province of sociologists (who reciprocate by leaving sex differences to psychologists). This may not have been a wise choice since SES correlates substantially with most of the variables psychologists are interested in, including aggression, crime, educational achievement, family structure, health, intelligence, longevity, sexuality, and social attitudes. Because they are less well-known, let us briefly consider SES differences in health and sexuality.

With respect to health, a major British study has shown that while everyone is living longer, professional classes have gained more years than semiskilled and unskilled workers (Black, 1980). In 1930 people in the lowest social class had a 23% higher chance of dying at every age than people in the highest social class. By 1970, this excess risk had grown to 61%. A decade later, it had jumped to 150%. This *increasing* disparity presents a paradox especially when a national health system has long existed in Britain to minimize inequalities in health-related services (see Rushton, 1987a, for a discussion from an evolutionary perspective).

With respect to sexual behaviors, SES differences were reviewed by Weinrich (1977) who analyzed over 20 studies from the world literature and concluded that the lower the SES, the earlier the age of first coitus, the greater the likelihood of premarital coitus and coitus with prostitutes, the shorter the time before engaging in extramarital affairs, and the less stable the marriage bond. Weinrich (1977) also found that the higher the SES, the more likely the individual was to engage in sexual activities beyond those directly leading to conception, including fellatio, cunnilingus, petting and affection, and coitus during menstruation. Moreover, although lower SES adolescents knew more about birth control devices than upper SES adolescents, they used them less frequently.

Racial group differences. Many scientists have strong negative feelings about the juxtaposition of racial differences in behavior with perspectives from evolutionary biology, even arguing that the concept of "race" is discredited and that the phrase "ethnic" group be substituted, thereby shifting the emphasis away from a "question begging . . . biologistic bias" (Montagu, 1960, p. 697; see also Lewontin, Rose, & Kamin, 1984, pp. 119–129). This neglect, however, leaves much to be desired. We do not know what the evolutionary origins of the races are nor the extent of their similarities and differences, and this ignorance is unlikely to be dispelled by the censorious pronouncements too often made about those who conduct such research. In fact, on a surprisingly large number of variables, the Japanese are similar to the Chinese and Koreans whether assessed in their home countries, Hawaii, or the U.S. mainland, but are different from Russians, Israelis, and Caucasian Americans, who in turn are similar to each other but are different from Kenyans, Nigerians, and African-Americans (Rushton, 1988c; Rushton & Bogaert, 1987). On estimates made of speed of maturation (age to walk alone, age of first intercourse, age of death), personality and temperament (activity level, anxiety, dominance, sociability), sexual restraint (gamete production, intercourse frequencies, size of genitalia), social organization (law abidingness, marital stability, mental health), and brain size and intelligence (brain weight, cranial capacity, test scores), Caucasoids fall consistently *between* Orientals and Africans or African-Americans. The efficient unit of analysis, therefore, is the more encompassing concept of race, within which cluster the different ethnic groups and, ultimately, individuals.

Epigenetic Rules in Social Development

Taking a step or two in the distal direction of Figure 1, consider the genetic origin of individual differences. 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, both twin and adoption designs converge in showing at least moderate effects due to genetic influence (Loehlin, Willerman, & Horn, 1988; Tellegen et al., 1988).

The behavior genetic literature is probably best known in the field of intelligence where, ever since Galton (1869), estimates of genetic influence have been calculated. A major review by Bouchard and McGue (1981) based on 111 studies using 113,942 pairings between various types of biological and adoptive relatives showed a heritability estimate of about .50. Less well-known is that similar results are found with social variables, including those typically considered to be exclusively environmental in origin. Political attitudes, for example, are found to be moderately heritable, including stylistic tendencies such as voicing extreme views, as well as voicing a wide variety of specific opinions (Martin et al., 1986). With respect to crime, Mednick, Gabrielli, and Hutchings (1984) showed in a study of 14,427 children adopted in infancy that a greater risk for criminal convictions existed if biological parents had been convicted than if adoptive parents had been, and that siblings and half-siblings adopted separately into different homes were concordant for convictions with the degree of concordance being dependent upon the number of genes shared.

Genes, of course, do not directly cause behavior. They code for enzymes which, under the influence of the environment, lay down tracts in the brains and nervous systems of individuals, thus differentially affecting people's minds and the choices they make about behavioral alternatives. There are many plausible routes from genes to behavior and collectively these routes may be referred to as epigenetic rules (Lumsden & Wilson, 1981). Arising through the process of evolution, epigenetic rules provide recipes by which development is guided in one direction over alternatives. Their operation is most apparent in embryology in which anatomical and physiological features are constructed. To take a familiar example, the physical development from fertilized egg to neonate follows a preordained course in which development starts in the head region and works its way down the body. By the sixth or seventh month, all major systems have been elaborated, and the fetus may survive if born prematurely. Such a channeling of development requires that constant self-correcting adjustments occur until some targeted end-state is reached. Studies of "catch-up growth" following deficits due to malnutrition or illness are illustrative. Deprived children subsequently develop very rapidly to regain the growth trajectory they would have been on if the diversion hadn't occurred, following which growth slows down and development proceeds at the normal rate (Tanner, 1978).

Epigenetic rules governing complex social behavior also have been identified. For example, canalized end points appear to underlie the evolutionary function of smiling, attachment, and separation responses in infants (Freedman, 1974). Similar interpretations can be advanced for the life-cycle stages documented to occur in ego development, morality, and psychosocial functioning (Rushton, in press). More dramatically, while small fluctuations in one or two molecules might affect ontogeny, studies show that siblings raised apart for many years in complex environments grow to be significantly similar to each other on a variety of traits and that their degree of similarity is predicted by the number of genes they share (Bouchard, 1984; Tellegen et al., 1988). Moreover, identical twins show concordance in age of onset of puberty, timing of first sexual experience, menopause, and death (see Plomin, 1986, for a review). Chronogenetics also affects mental development, as shown in a large sample of twins followed from 3 months to 15 years of age in which the synchronies between lags and spurts were found to average about .90 for identical twins, but only about .50 for fraternal twins (R. S. Wilson, 1983).

One of the less appreciated aspects of behavior genetic studies is the information they also provide about environmental effects. An important discovery is that the primary environmental factors influencing personality are unique to each sibling rather than common. That is, the most important environmental variance turns out to be *within* a family, not *between* families. Such factors as social class, family religion, parental values, and child-rearing styles, for example, are found to have weak or no common effects on siblings. This runs counter to prevailing theories of social development that assume that the important environmental variance is between families and not within them. Yet the observation that the environmental factors influencing development are those specific, rather than common, to each sibling 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 (Plomin & Daniels, 1987; Tellegen et al., 1988).

Such results can be seen in a study of individual differences in altruism and aggression with 573 adult monozygotic and dizygotic twin pairs (Rushton, Fulker, Neale, Nias, & Eysenck, 1986). Components of these traits were measured by questionnaires in which the 1,146 respondents endorsed items measuring their self-reported altruism, empathy, nurturance, aggressiveness, and assertiveness. The raw data were analyzed into between- and within-pair variances and covariances in which the between-pair mean squares reflect both pair resemblances and pair differences, while the within-pair mean squares only reflect pair differences. The total phenotypic variance was partitioned into three sources:

Table 1
Variance Components From an Analysis of Altruism and Aggressiveness Questionnaires From 573 Adult Twin Pairs[a]

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

Note. From "Altruism and aggression: The heritability of individual differences" by J. P. Rushton, D. W. Fulker, M. C. Neale, D. K. B. Nias, and H. J. Eysenck, 1986, *Journal of Personality and Social Psychology*, **6**, p. 1195. Copyright 1986 by the American Psychological Association. Reprinted by permission.

a. Estimates in parentheses corrected for unreliability of questionnaire.

V(G), additive genetic effects; V(CE), common environmental influences that affect both twins equally, and V(SE), the specific nonshared environment, or that portion of the environment that is unique to each twin. This latter is a residual term that is composed of many sources, including measurement error and various kinds of genetic and environmental interactions. Applying a maximum likelihood estimation procedure to this model, about 50% of the variance on each scale was found to be associated with additive genetic effects, virtually none with the twins' common environment, and the remaining 50% with each twin's specific environment. Correcting for the unreliability in the tests raised the heritabilities to 60% and reduced the specific environment variance to 40% (see Table 1).

The concept of epigenetic rule provides an explanation for the important finding that a common family environment plays a very limited role in social development (even for traits such as altruism and aggression, which parents are expected to socialize heavily). It implies that within the same upbringing environment, the more belligerent sibling observationally learns the items from the parents' aggressive repertoire, whereas the more nurturant sibling selects from the parents' altruistic responses. In a study of television effects, for example, Rowe and Herstand (1986) found that although same-sex siblings resembled one another in their exposure to violent programs, it was the more aggressive sibling who identified most with aggressive characters and who viewed the consequences of the aggression as positive. Within-family studies of delinquents find that both IQ and temperament distinguish delinquent siblings from those who are nondelinquent (Hirschi & Hindelang, 1977; Rowe, 1986). It is not difficult to imagine how intellectually and temperamentally different siblings might acquire alternate patterns of social responsibility.

That siblings raised apart for many years 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. Such systems operate within families and make siblings different from one another. As many psychologists have recently suggested, 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 (Rushton, Littlefield, & Lumsden, 1986).

Genetic Similarity Theory

The most distal levels of understanding (Figure 1) derive from knowledge of the evolutionary process. This is where epigenetic rules originate, having arisen from the cumulative selection involved in successfully replicating the genetic material that gave rise to them (Dawkins, 1986). Information from this ultimate point of view can directly inform proximate data.

From an evolutionary perspective, altruism is a means of helping genes to propagate. By being most altruistic to those with whom we share genes we help copies of our own genes to replicate. This makes "altruism" ultimately "selfish" in purpose. Promulgated in the context of animal behavior this idea became known as "kin selection" and provided a conceptual breakthrough by redefining the unit of analysis away from the individual organism to his or her genes, for it is these which survive and are passed on (Hamilton, 1964). Previously it had been unclear how altruism could evolve through Darwinian notions of the fittest individual when such individuals might die in the process of protecting their more selfish conspecifics. This formulation provided a large step forward in founding the discipline of sociobiology (Dawkins, 1976; E. O. Wilson, 1975). Building on this work and on that by others (e.g., Thiessen & Gregg, 1980), and adopting the mechanistic viewpoint of the selfish gene, Rushton, Russell, and Wells (1984) explicitly extended the kin selection theory of altruism to the human case by arguing that if a gene can better ensure its own survival by acting so as to bring about the reproduction of family members with whom it shares copies, then it can also do so by benefiting *any* organism in which copies of itself are to be found. This is the crux of what we referred to as "genetic similarity theory." As such, a new theory of attraction and friendship was constituted.

If humans do detect and prefer those who are genetically similar, it should be possible to demonstrate this within interpersonal relationships. With respect to both friendships and marriages it is widely accepted that partners resemble each other in such characteristics as age, ethnic background, socioeconomic status, physical attractiveness, religion, social attitudes, level of education, family size and structure, IQ, and personality (Buss, 1985; Thiessen & Gregg, 1980). The median assortative mating coefficient for standardized IQ measures, for example, averaged over 16 studies involving 3,817 pairings, is .37 (Bouchard & McGue, 1981). Correlations tend to be higher for opinions, attitudes, and values (.40 to .70) and lower for personality traits and personal habits (.02 to .30). Less well-known is the fact that partners tend to resemble each other on socially undesirable attributes, including criminality, alcoholism, and psychiatric disorders, as well as on a variety of physical features.

Preliminary evidence indicates that social assortment in humans is genetically mediated. Since it is known that the dimensions on which spouses and friends resemble each other are partly inherited, then unless one adopts the implausible idea that humans detecting similarity are responding purely to the environmentally influenced component of a trait, it follows that genetic similarity between partners must occur. More direct evidence is also available using blood tests and differential heritability analyses. Using blood antigens to estimate genetic distance across 10 blood loci using seven polymorphic marker systems (ABO, Rhesus [Rh], P, MNSs, Duffy [Fy], Kidd [Jk], and HLA) over six chromosomes, both male friendship dyads and sexually interacting couples have been found to share more genetic markers than do randomly generated pairs from the same samples (Rushton, 1988b, 1989a). Moreover, among sexually interacting couples involved in cases of disputed paternity, genetic similarity predicted male inclusion: Males not excluded from paternity were significantly more similar to their partners than males who were excluded (Rushton, 1988b).

Other data suggest that genetic influences on social choice are particularly fine-tuned because similarity among marriage partners and best friends is most marked on the more genetically influenced of sets of anthropometric, cognitive, personality, and attitudinal attributes (Rushton, 1989a; Rushton & Nicholson, 1988; Rushton & Russell, 1985; Russell, Wells, & Rushton, 1985). In a study of delinquency in 530 adolescent twins, Rowe and Osgood (1984) found that not only was antisocial behavior about 50% heritable, but that the correlation of .56 between the delinquency in an individual and the delinquency in his friends was mediated genetically. While friends necessarily choose each other on the basis of phenotype (there is no such thing as "genetic ESP"), the important point is that genetically disposed delinquent students were genetically inclined to seek each other out. In a study of 396 adolescent and young adult siblings from both adoptive and nonadoptive homes, Daniels and Plomin (1985) found that genetic influences were implicated in friendship choice because the biological siblings described themselves as having more similar friends to each other than did the adoptive siblings.

Family favoritism has also been studied. It is not often realized that because of assortative mating some children will be genetically more similar to one parent than to the other. This can be demonstrated as follows: If a father provides a child with 50% of his genes, 10% of which overlap with the mother's contribution, and a mother provides the child with 50% of hers, 20% of which overlap the father's contribution, then the child will be 60% similar to the mother and 70% similar to the father. Family members are expected to favor those who are most similar. A test of this prediction was made in a study of bereavement following the death of a child. Both mothers and fathers, irrespective of the sex of child, grieved most for children perceived as resembling their side of the family (Littlefield & Rushton, 1986). Among siblings perceived similarity is correlated with genetic similarity measured by blood tests.

It would appear that people do moderate their behavior in accord with the genetic similarity of others. The implications of these findings may be far-reaching providing, for example, a biological basis for ethnocentrism. Since two individuals within an ethnic group will, on average, be more genetically similar than two from different ethnic groups, people may be expected to prefer their own group over others. Many studies have found that people are more likely to help members of their own race or country than members of other races or foreigners, and other studies have suggested that antagonism between classes and nations may be greater when a racial element is involved (Cunningham, 1981; Rushton, 1989b).

r-K Reproductive Strategies

A comprehensive theory of individual differences was proposed from an evolutionary perspective by Rushton (1985) under the rubric "Differential K Theory." The degree to which an individual had acquired a K rather than an r reproductive strategy was postulated to underlie multifarious aspects of the human life cycle. Originating in the mathematics of population biology, r and K refer to two ends of a continuum of reproductive strategies ranging from maximum egg output and no parental care, to a few offspring intensively nurtured (E. O. Wilson, 1975). Oysters, producing 500 million eggs a year, exemplify the r-strategy, while the great apes, producing only one infant every 5 or 6 years, exemplify the K-strategy. Data from species ranging from dandelions to fish to mice to men indicate that these reproductive strategies are associated with other features of the organism's life history, as summarized in Table 2.

While humans are the most K of all species, some people may be more so than others. Generalizing from the traits listed in Table 2, it is expected that the more K-selected families will space births further apart, produce fewer offspring, show a lower rate of infant mortality, have a more stable family system, and have a better developed system of parental care. The more K-selected person will have a longer gestation period, higher birth weight, more delayed onset of sexual activity, older age at first reproduction, lower sex drive, longer life, more efficient energy system (as in the absence of obesity), higher intelligence, more socially acceptable behavior, and greater altruism.

Evidence for the expected covariation among the K attributes has been found in several studies. For example, Rushton (1987b) contrasted the characteristics of the mothers of dizygotic twins who, because they produce more than one egg at a time, can be considered to represent the r-strategy, with the mothers of singletons representing the K-strategy. The former were found to have a lower age of menarche, a shorter menstrual cycle, a higher number of marriages, a higher rate of coitus, a greater fecundity, more wasted pregnancies, an earlier menopause, and an earlier mortality. In another domain, Ellis (1988) contrasted the characteristics of criminals who, because they are lower in altruism and social organization, can be considered to represent the r-strategy,

Table 2
Some Life History, Social Behavior, and Physiological Differences Between r- and K-Strategists

r-Strategist	K-Strategist
Family characteristics	
Large litter size	Small litter size
Short spacing between births	Long spacing between births
Many offspring	Few offspring
High rate of infant mortality	Low rate of infant mortality
Low degree of parental care	High degree of parental care
Individual characteristics	
Rapid rate of maturation	Slow rate of maturation
Early sexual reproduction	Delayed sexual reproduction
Short life	Long life
Small body size	Large body size
High reproductive effort	Low reproductive effort
High energy utilization	Efficient energy utilization
Low encephalization	High encephalization
Population characteristics	
Opportunistic exploiters of environment	Consistent exploiters of environment
Dispersing colonizers	Stable occupiers of habitat
Variable population size	Stable population size
Competition variable, often lax	Competition keen
Social system characteristics	
Low degree of social organization	High degree of social organization
Low amounts of altruism	High amounts of altruism

with the general population representing the K-strategy. The former were found to have shorter gestation periods (more premature births), a more rapid development to sexual functioning, a greater copulatory rate outside of bonded relationships (or at least a preference for such), less stable bonding, a lower parental investment in offspring (as evidenced by higher rates of child abandonment, neglect, and abuse), and a shorter life expectancy.

Population differences in r-K strategies were also predicted to occur because human groups differ in egg production: namely, lower socioeconomic > higher socioeconomic, and Negroids > Caucasoids > Mongoloids. While the monozygotic twinning rate is nearly constant at about 3.5 per 1,000 in all groups, dizygotic twinning (the r-strategy, caused by a double ovulation) is greater among lower- than among upper-class women in both European and African samples. The rate per 1,000 among Mongoloids is < 4, among Caucasoids = 8, and among Negroids > 16, with some African populations having rates as high as 57 per 1,000 (Bulmer, 1970). Populations adopting an r-strategy approach to egg production would be expected to allocate a larger percentage of bodily resources to other aspects of reproductive effort. To examine this prediction in the context of sexual functioning, Rushton and Bogaert (1987) compiled a review of the literature and carried out novel analyses on data from the Kinsey Institute for Sex Research. The predicted pattern of sexual investment with Negroids > Caucasoids > Mongoloids was consistently observed to occur with measures made of intercourse frequencies (premarital, marital, extramarital), developmental precocity (age of first intercourse, age at first pregnancy, number of pregnancies), primary sexual characteristics (size of penis, vagina, testes, ovaries), secondary sexual characteristics (salient voice, muscularity, buttocks, breasts), and biologic control of behavior (length of menstrual cycle, periodicity of sexual response, predictability of life history from onset of puberty). Concomitant differences were noted in levels of sex hormones and in sexual attitudes. It is possible that racial group differences in brain size and intelligence, law-abidingness, health and longevity, and other attributes may also be ordered by r-K theory (for an exchange of views, see Rushton, 1988c, 1988d; Zuckerman & Brody, 1988).

CONCLUSION

Personality and social behavior may be synthesized more concretely by anchoring them within the context of a life history which has evolved in order to help genes replicate more effectively (Rushton, in press). Thus phenomena such as mate choice and family structure and attributes such as intelligence, altruism, and strength of the sex drive, along with age, sex, socioeconomic, and racial group differences therein, may be considered to be in the service of fertility. Ultimately, by studying the evolution of individual and group differences we may come to appreciate more fully the nature of human diversity as well as the binding commonalities we share with other species (E. O. Wilson, 1984). That, too, would be one of the legacies of the Darwinian (and Galtonian) perspective.

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