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LETTER TO THE EDITOR

Genetic Similarity Theory: A Reply to Mealey and New Evidence

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Mealey's criticisms of genetic similarity theory (GST) (Rushton, et al.*, 1984) are rebutted as either based on a misreading of its claims or a failure to grasp the nature of such theorizing. We argue that, if a gene can ensure its own survival by acting so as to bring about the reproduction of any organism in which copies of itself are to be found, then GST is a worthwhile alternative to kin selection theory. The most effective way for this to be accomplished is for organisms to be able to detect copies of its genes in others, and proffer preferential treatment to those most similar. We report novel data congruent with this hypothesis: (a) spouses assort more on the basis of the more genetically influenced of a set of homogeneous traits (i.e., there is a positive correlation between assortative mating coefficients and heritability estimates), and (b) following the death of a child, parental grief intensity is correlated with the child's similarity to the parent.*

KEYWORDS: altruism; assortative mating; bereavement; genetic similarity theory; inclusive fitness; kin-selection; sociobiology.

COMMENTARY AND REJOINDER

Mealey (1985) raised several points in her comment, some of which we agree with, although they are presented as if in refutation of our paper. Other criticisms rest on a misunderstanding of what we and others have said. Mealey argued that (a) there is not much new in genetic similarity

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theory (GST) (Rushton, *et al.,* 1984); (b) what is new is logically flawed; and (c) alternative accounts explain the phenomena better. Her most crucial point is (b), so let us consider it first.

Mealey suggested we failed to understand Hamilton's (1964) theory of inclusive fitness, falling into no less than 5 of the 12 traps that Dawkins (1979) enumerated as fairly common in the literature. She specifies only one of these, but considers it central:

> . . . the main fallacy of GST. This is: it is not the *proportion* of genes shared with another which is relevant for altruistic behavior, it is the *probability* that the two individuals share the "altruism gene." The probability that sibs share such an allele identical by descent (i.b.d.) is .5. This is an exact figure, and is not equivalent to the average 50% proportion of genes that sibs share i.b.d. . . . Altruistic behavior therefore, is contingent solely on the likelihood that another shares this particular allele at a particular locus, not on overall genetic or phenotypic similarity" (p. 572).

Mealey is correct to argue that, to a gene which can detect itself in other bodies, and favor them, the presence or absence of any particular gene at another locus is irrelevant. What matters is whether or not another altruism gene is present at the same locus. Mealey presumes that we do not realize this. This criticism suggests a failure to appreciate the nature of arguments of this sort. No sensible theorist believes that complex behavior such as altruism results quite simply from the presence of one gene. To postulate one is simply a theoretical convenience. Rather, it would be anticipated that the mechanisms would be complex, perhaps involving many genes and supergenes on many chromosomes, as, for example, if large groups of genes became linked and pleiotropic to produce both feature detectors and altruistic behavior, a point which Mealey later acknowledges. Indeed, if it is advantageous for a single gene to work for copies of itself, it should be advantageous for *all* genes to do the same, in which case aggregation effects could clearly be expected. Therefore, it is entirely reasonable to talk of genetic similarity, and not to distinguish between the proportion of shared genes and the probability of a shared altruism gene. It is also worth noting, from the paper which Mealey suggests we should read, that "The distinction between exact and probabilistic coefficients of relationships has yet to be shown to have any importance at all" (Dawkins, 1979, p. 198).

In response to Mealey's criticism that GST is not new, we can only point out that in the article on which she is commenting, several precursors were cited. How fresh or illuminating our way of looking at the facts is depends on how broad-based the alternative accounts are seen to be. At the start of the second of his two key articles, Hamilton (1964) summarizes the first article as follows:

> . . . for a gene to receive positive selection it is not necessarily enough that it should increase the fitness of its bearer above the average if this tends to be done

> at the heavy expense of related individuals, because relatives, on account of their common ancestry, tend to carry replicas of the same gene; and conversely that a gene may receive positive selection even though disadvantageous to its bearers if it causes them to confer sufficiently large advantages on relatives (p. 17).

Note the emphasis on relatives in Hamilton's statement, an emphasis which has persisted throughout sociobiological theorizing. Our theory in contrast makes no mention of degrees of relatedness. Moreover, we were dissatisfied with the various indices concerning degrees of relatedness (e.g., that mothers and offspring are only 50% similar on one metric, yet humans and chimpanzees 98% on another). What seemed to us crucial, and decidedly neglected, was (a) the overall degree of genetic similarity among both "related" and "unrelated" individuals, and (b) the strong tendency of humans to prefer others who are similar. Thus, we made explicit predictions regarding important human relationships including, mate choice, marital satisfaction, family favoritism, same-sex friendship, and ethnic nepotism.

Some of our extrapolations may be controversial. Consider, for example, the issue of ethnic nepotism. We argued that since two individuals within an ethnic group will, on average, be genetically more similar than two from different ethnic groups, the implications for relations among ethnic groups may be far-reaching. Others appear to believe that inclusive fitness theory has no direct implications for racial prejudice or ethnic preference. Dawkins (1981), for example, states "The equating of 'kinship,' in the sense of kin-selection, with 'ties of race' appears to result from an interesting variant of what I have called the fifth misunderstanding of kin selection" (p. 528). We, on the other hand, view GST as providing a biological basis for ethnic nepotism and as having important implications for the social behavior of groups both within and between nations.

NEW EVIDENCE

The ultimate worth of a new theory must be based on more than just a reordering of extant literatures; it must make unique predictions. The strong version of GST is that organisms engage in genetic similarity detection in order to proffer preferential treatment to those most similar. As GST predicts, therefore, individuals will associate with others who are genetically similar and, thus, contrary to alternative formulations (Thiessen and Gregg, 1980), should mate on the basis of the more heritable of a set of homogeneous traits. To test this hypothesis, Russell *et al.* (1985) analyzed data from three publications simultaneously reporting independent estimates of heritability and assortative mating. One study was based on anthropometric variables (Susanne, 1977), a second on cognition (Guttman, 1970), and a third on personality (Hill, 1973). In each

Table I. Estimates of Genetic Influence, Assortative Mating, and Reliability for 54 Personality Variables [After Ahern *et al.* (1982)]

	Estimate of genetic influence			
Personality variable	Parent–offspring regression	Doubled sib–sib intraclass correlation	Assortative mating coefficient	Reliability (alpha coefficient)
Adjective Checklist	(*N* = 669)	(*N* = 1065)	(*N* = 693)	(*N* = 3121)
Number of Adjectives Checked	0.10	0.18	0.09	—
Defensiveness	0.25	0.18	0.14	0.88
Number of Favorable Adjectives Checked	0.26	0.14	0.10	0.95
Number of Unfavorable Adjectives Checked	0.18	0.10	0.07	0.92
Self-Confidence	0.18	0.08	0.02	0.77
Self-Control	0.15	0.06	−0.01	0.73
Lability	0.08	0.14	0.06	0.58
Personal Adjustment	0.18	0.10	0.06	0.75
Need for Achievement	0.14	0.10	0.08	0.83
Need for Dominance	0.16	0.12	0.04	0.82
Need for Endurance	0.08	0.14	0.06	0.79
Need for Order	0.10	0.14	0.05	0.80
Need for Intraception	0.13	0.04	0.06	0.80
Need for Nurturance	0.16	0.08	0.02	0.87
Need for Affiliation	0.18	0.16	0.04	0.89
Need for Heterosexuality	0.12	0.24	−0.03	0.73
Need for Exhibition	0.16	0.04	−0.08	0.74
Need for Autonomy	0.17	0.08	−0.01	0.65
Need for Aggression	0.19	0.04	−0.08	0.83
Need for Change	0.14	0.02	0.03	0.53
Need for Succorance	0.16	0.18	0.04	0.58
Need for Abasement	0.17	0.08	0.03	0.69
Need for Deference	0.17	0.06	−0.06	0.71
Counseling Readiness	−0.03	0.14	−0.01	0.63
Eysenck Personality Inventory	(*N* = 415)	(*N* = 763)	(*N* = 422)	(*N* = 1819)

Introversion vs. Extraversion	−0.10	0.50	0.12	0.67
Emotional Stability vs. Neuroticism	0.19	0.14	0.22	0.82
Lie	0.83	0.76	0.41	0.62
Comrey Personality Scales	(*N* = 117)	(*N* = 174)	(*N* = 117)	(*N* = 453)
Defensiveness vs. Trust	0.12	0.42	0.24	0.78
Lack of Compulsion vs. Orderliness	0.29	0.38	0.18	0.85
Rebelliousness vs. Social Conformity	0.49	0.74	0.33	0.80
Lack of Energy vs. Activity	0.28	0.06	0.25	0.84
Neuroticism vs. Emotional Stability	0.19	0.26	0.19	0.88
Introversion vs. Extraversion	0.44	0.06	0.06	0.91
Femininity vs. Masculinity	0.39	0.28	0.10	0.82
Egocentrism vs. Empathy	0.20	0.22	0.10	0.83
Sixteen Personality Factor Questionnaire	(*N* = 100)	(*N* = 148)	(*N* = 102)	(*N* = 395)
Reserved vs. Outgoing	0.11	0.02	0.04	0.42
Dull vs. Bright	0.26	0.18	0.23	0.51
Affected by Feelings vs. Emotionally Stable	0.21	0.34	0.07	0.60
Submissive vs. Dominant	0.55	0.30	−0.03	0.61
Sober vs. Happy-Go-Lucky	0.22	0.46	0.12	0.70
Expedient vs. Conscientious	0.13	0.34	0.06	0.59
Shy vs. Venturesome	0.24	0.18	0.05	0.79
Tough vs. Tender-Minded	0.23	0.12	0.19	0.61
Trusting vs. Suspicious	0.31	0.32	0.02	0.49
Practical vs. Imaginative	0.42	0.02	0.19	0.24
Forthright vs. Astute	0.26	0.24	0.04	0.31
Placid vs. Apprehensive	0.28	0.02	0.10	0.64
Conservative vs. Radical	0.27	0.18	0.11	0.38
Group Dependent vs. Self-Sufficient	0.24	0.20	−0.10	0.41
Casual vs. Controlled	0.15	0.18	−0.14	0.49
Relaxed vs. Tense	0.11	0.44	−0.04	0.74
Alcohol Questionnaire	(*N* = 183)	(*N* = 259)	(*N* = 185)	(*N* = 708)
Sensation Seeking	0.23	0.12	0.18	0.55
Internal vs. External Locus of Control	0.16	0.24	0.24	0.63
Anomie	0.20	0.02	0.11	0.65

instance, the correlation between the estimate of genetic influence on the trait and the degree of assortative mating was positive ($r = 0.36$, $p < 0.05$, for the 36 anthropometric variables; $r = 0.73$, $p < 0.10$, for the 5 cognitive variables; and $r = 0.44$, $p < 0.01$, for the 11 personality variables).

Similar analyses can be performed on data published by Ahern *et al.* (1982). As can be seen in Table I, we have abstracted from their report two estimates of the magnitude of genetic influence, as well as the assortative mating and alpha coefficients, for each of 54 personality traits. Across the 54 scales, the degree of assortative mating is predicted $r = 0.44$ ($p < 0.001$) by the parent–offspring regression, and $r = .46$ ($p < 0.001$) by the doubled sib–sib intraclass coefficient. While the two estimates of genetic influence only correlated with each other at $r = 0.38$ ($p < 0.001$), a simple arithmetic composite of the two raised the relationship with assortative mating to $r = 0.55$ ($p < 0.001$), a figure not altered when controlling for differential test reliability. While there is substantial fluctuation of predictive power within particular batteries, and the coefficients are based on varying sample sizes, the result from the aggregated analysis accords with prediction.

Others, too, have reported positive correlations between assortative mating and heritability estimates. In a critique of the Hawaii Family Study, Kamin (1978) calculated a 0.79 ($p < 0.001$) correlation for 15 cognitive tests between assortative mating and regression of midchild on midparent. His interpretation of this "interesting but unexplored phenomenon" (p. 277) was nongenetic: He hypothesized that mate selection on similar traits resulted in the passing on of these traits "*by environmental example and reinforcement*" (p. 277). In a reply to Kamin, DeFries *et al.* (1978) carried out a comparable analysis of 13 anthropometric variables (height, nasal breadth, etc.), producing the relevant correlation of 0.62, ($p < 0.001$), a finding not readily attributable to social learning. Finally, Cattell (1982) noted that spouse correlations tend to be lower on the less heritable, more specific cognitive abilities (tests of vocabulary and arithmetic) than on the more heritable general abilities (*g*, from Progressive Matrices). In this case, differential heritabilities have been confirmed via twin and other estimation procedures. It would appear that, as GST predicts, people differentiate genetic from environmentally caused similarity, and mate accordingly.

As discussed in the original paper, one consequence of assortative mating on genetically influenced traits is that children will be genetically more similar to one parent than the other. GST predicts that, all things being equal, parents should favor those children most similar. Support for this prediction was found in a study of familial grief following the death of a child (Littlefield and Rushton, 1985). Both mothers and fathers, irrespective of sex of child, grieved more for children perceived as resembling their side of the family than they did for children perceived as resembling their spouse's side. That perceived similarity may be partially attributable to an increased genetic endowment from one parent or the other, rather than only to environmental causation, is supported by behavior genetic studies of siblings in which there is a positive correlation between perceived similarity and genetic similarity measured by blood tests (Scarr and Grajeck, 1982).

MECHANISMS

Clearly there is no such thing as "genetic ESP." For people to direct altruism to genetically similar others, they must respond to phenotypic cues. In our earlier paper we discussed "strong" and "weak" versions of how this could come about. The strong version suggests that individuals engage in genetic similarity detection in the absence of previous familiarity or other proximal mechanisms. Thus, some phenotypes are inherently more attractive to the organism than are others. The evolutionary origin of such a mechanism could be simple: If like appearance is positively correlated with like genes, any mutation toward preference for like phenotype would tend to proliferate. The weak version states that organisms will evolve to behave such that altruism tends to be directed toward similar others by means other than genetic detection. Phenotype matching based on familiarity with self or kin constitutes one such method. Mealey suggests competitive and selective placement and reciprocal altruism, as additional means. We concur, but note that while placement can be based on similar genes (we know that intelligence, socioeconomic status, values and vocational interests, and so on are genetically linked), the degree to which assortment continues, within already highly selected groups, as demonstrated above, attests to the sensitivity of a genetic detection mechanism. With respect to reciprocal altruism, this is likely to arise more readily to the degree the interactants share genes. If there are evolutionary advantages to be derived from the ability to benefit genetically similar others, many mechanisms may be involved.

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