
Cooperation and Competition Between Twins: Findings from a Prisoner's Dilemma Game

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Attention to factors influencing cooperation and competition during human social interaction has increased within recent years. This study tested the hypothesis that higher levels of cooperation would be associated with increased genetic relatedness between interactants, and explored questions concerning the expression of cooperative behavior over time. A Prisoner's Dilemma game, in which participants elect to display cooperative, competitive, or exploitative behaviors relative to a partner, was administered to 59 monozygotic and 37 dizygotic twin pairs, between 10.92 and 82.67 years of age. Results from multivariate analysis of variance procedures, cross-lag sequential analyses, and hierarchical linear modeling supported associations between zygosity, and frequency and continuity of cooperation. Mechanisms by which zygosity may affect cooperation were explored by examining relationships between response combinations, and twins' IQ similarity and social closeness. The findings are considered with reference to an evolutionary perspective on behavior that offers a theoretical basis for considering how the relative genetic relatedness of social partners affects their social-interactional processes and outcomes. This report is the first in a series of studies designed to address mechanisms underlying differences in cooperation among pairs who vary in average genetic commonality. © 1999 Elsevier Science Inc.

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Interest in the biological, psychosocial and cultural bases of cooperation, competition and exploitation has increased within recent years. This interest has been explained, in part, by increasing societal concern with the bases of unusual cruelty, indifference, or kindness directed toward some individuals by

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others (Burnstein et al. 1994; Frank 1988; Johnson 1996; McGuire et al. 1994), and with fostering conditions that promote cooperative interactions (Axelrod 1984). The need to apply more varied theoretical and methodological approaches toward understanding behavior in this domain has been emphasized (Bergstrom 1995; Boyd and Richerson 1985; Caporeal et al. 1989; LaFrenière and MacDonald 1996; Rushton 1989; Zahn-Waxler et al. 1992). Proposed research directions include studies of genetic influences on prosocial behavior and reduced reliance on self-report measures in favor of naturalistic studies (Eisenberg and Mussen 1989). Mathematical models describing conditions under which various forms of altruism are likely to evolve also have been developed (Dugatkin et al. 1994).

It is clear that more experimental work is called for as “theoretical arguments have, for the moment, run ahead of the data” (Slater 1994; 222). Eisenberg and Mussen (1989) noted that their own model of prosocial behavior lacks a biological component “because so little information is available” (p. 155). The present study was an attempt to reduce this gap in knowledge about factors influencing the expression and continuity of cooperative behavior. A comparative analysis of social-interactional processes and outcomes expressed by genetically identical (monozygotic [MZ]) and genetically nonidentical (dizygotic [DZ]) twins during a Prisoner’s Dilemma game is presented.

EVOLUTIONARY PERSPECTIVE ON HUMAN BEHAVIOR

Hamilton (1964a, 1964b) developed the modern evolutionary theory of kinship-based altruism, which offers a theoretical basis for considering the relative genetic relatedness between interactants in pursuing cooperative exchanges and in conferring benefits. He reasoned that natural selection will favor alleles predisposing individuals to act in ways that favor the transmission of those alleles into future generations. Alleles that influence individuals to favor others likely to carry replicas of these alleles is an indirect means by which these alleles achieve continued representation. Assisting a close relative with whom one is likely to share genes relevant to altruistic behavior can, therefore, increase one’s *inclusive fitness*. Note, for example, the unique biological relationship between MZ twins and their offspring: Twin aunts/uncles share the same genetic relatedness with nieces/nephews ($r = .50$) as they do with their own children. From an inclusive fitness point of view, cooperation between MZ twins, and between MZ twins and their nieces/nephews, should exceed that between less closely related pairs.

Inclusive fitness may, however, be enhanced (or diminished) only by specific acts or events (as compared with alternative acts or events) that directly affect the organism. Relatives who never meet are unlikely to affect one another in this regard (Dawkins 1989b). Cooperative behavior also may be affected by the age and health status of a potential recipient (Burnstein et al. 1994; Hamilton 1987; Littlefield & Rushton 1986).

Twin Research and Twin Relationships

MZ twins share all their genes, whereas DZ twins share half their genes, on average, by descent. Psychological twin studies typically compare similarity between MZ twins and DZ twins to estimate genetic and environmental contributions to individual differences in behavior. In contrast, the use of a *twins as couples* design facilitates evaluation of social-interactional processes and outcomes associated with the relative genetic relatedness of the interactants. Traditional twin studies have increased in recent years, yet the fruitfulness of the twins as couples approach has been overlooked (Segal 1997a).

A comprehensive review of twin studies on social relatedness, representing diverse theoretical approaches and methods, reveals greater social closeness and cooperation between MZ than DZ co-twins. Greater bereavement response by MZ than DZ twins following the loss of their co-twin provides additional evidence of MZ twins' closer social relationship (Segal 1988, 1997a). It is especially provocative that, following reunion, MZ twins reared apart experience greater feelings of familiarity and anticipated closeness than DZ twins reared apart. Furthermore, both types of reared apart twins experience greater familiarity and closeness toward the co-twin than to the adoptive siblings with whom they were reared (Segal 1999, in press). Such findings pose considerable challenge to more traditional views of human social relationships and direct needed attention toward genetic influences underlying social relations. (These observations also have implications for kin recognition mechanisms, as discussed below). It is additionally compelling that nontwin individuals indicate greater perceptions of close relatedness to hypothetical identical twins than to other kin (Burnstein et al. 1994).

Observations of twins interacting with unfamiliar individuals shed further insight into the nature of their social relations. A study of 6- to 9-month-old infants found that twins interacted as much with their co-twins as with new peers. In contrast, 12-month-old twins favored peers, whereas 2-year-old twins favored their co-twins. Unfortunately, twins in this study were not organized according to twin type (Vandell et al. 1988). A later study found that increased prosocial behavior in 20-month-old MZ twins was associated with reduced empathic response to distressed toddlers, whereas the opposite was found for DZ twins (Zahn-Waxler et al. 1992). Segal et al. (1996) found that 8- to 11-year-old MZ and DZ twins did not differ in their level of cooperation with unfamiliar partners, possibly due to sufficiently diverse social experiences with new individuals.

Debate continues over the extent to which differences in rearing versus differences in biological relatedness explain MZ–DZ differences in social closeness. Difficulties in identifying informative comparison groups for social-psychological (Schaffer 1992) and evolutionary psychological studies also have been underlined (Graves and Byrne 1989; Hartung 1989). It will be argued in the present paper that (1) differences in cooperative behavior associated with the degree of genetic relatedness of the social partners define a domain in which a search for mechanisms can commence, and (2) twins and other kinships (e.g., adopted siblings) offer appropriate

participant groups for testing evolutionary-based hypotheses concerning expressions of cooperative behavior. Interpretation of the findings with reference to competing theoretical perspectives will be presented.

Possible mechanisms underlying social attraction and cooperation between relatives are also considered. In the present paper, IQ similarity and social closeness are explored as possible mechanisms underlying within-pair cooperation. This reports is the first in a series of studies designed to address mechanisms underlying differences in cooperative behavior among pairs who vary in average genetic commonality. Future analyses will examine the effects of physical similarity on cooperation, as assessed by ratings of photographs, and inspection of twins' comments during debriefing sessions in which they described their strategy and their co-twins' strategy during the Prisoner's Dilemma game.

Kin Recognition Mechanisms

Given their genetic identity, MZ twins should display greater cooperation and affiliation than DZ twins and other less closely related individuals. The possibility of selection for "twin-directed altruism" has been dismissed, given the relative infrequency of MZ twinning in human populations (Barash 1979). Indeed, a twin-specific mechanism is *not* proposed here; rather, the well-documented social closeness between MZ twins can be viewed as part of the more general principle that reproductive benefits may derive from directing increased altruism toward close relatives (Segal 1997a). MZ twins' matched physical appearance offers virtual certainty that they share 100% of their genes. It is, however, conceivable that some unrelated individuals share genes for physical features, so a prudent strategy would be to value oneself most highly (Dawkins 1989a).

Sherman and Holmes (1985) have suggested that "kin recognition mechanisms do not reveal relatedness per se; rather, they provide means of assessing social or phenotypic variables that correlate with relatedness" (p. 437). Examples of such mechanisms include spatial distribution (cues based on location) and association (cues based on the timing, rate, and frequency or duration of interactions). Barkow (1989) has identified familiarity and habituation as contributing to recognition of kin. Circumstantial cues, such as familiarity and habituation, could conceivably lead to preferential treatment of kin (Slater 1994). These processes would not, however, explain the social attraction that occurs between many reunited relatives (see above). Recognition alleles (alleles causing the expression of unique traits, recognition of these traits in others, and extension of assistance to individuals who display these traits) also have been considered as a mechanism for enabling discrimination between kin and non-kin. However, Dawkins (1989a) has pointed to the improbability of the trait expression and altruistic tendency being associated with a common gene.

Phenotypic matching (comparison of phenotypes of self and others) have been proposed as another mechanism underlying kin recognition. Specifically, information is learned about one's own phenotypic characteristics or those of relatives. The end product of this learning process is a "learned standard of appearance" (Trivers

1985) against which the phenotype of an unfamiliar individual is assessed.¹ Based on the close social relations of MZ twins, Freedman (1979) suggested that recognizing similar features may foster a “sense of we between ourselves and our fellow tribesmen. Recognition of this sense may trigger a series of emotions whose net effect is tribal unity and the increased chance for altruism” (p. 129). Interestingly, McGuire et al. (1994) have observed associations between different types of recognition (e.g., child or foe) and specific emotions (e.g., pleasure or anger), and between specific biochemical alterations “which in turn trigger a cascade of physiological and psychological events affecting both subsequent signalling and recognition” (pp. 304–305). A mechanism for maintaining selected relationships is, thus, suggested. These exciting findings provide a possible biological analogue to the view of Bowlby (1969) that certain relationships are maintained because they are pleasurable to the participants.

THE PRISONER’S DILEMMA GAME

The Prisoner’s Dilemma game was invented by Merrill Flood and Melvin Dresher, in approximately 1950, and was formalized by A. W. Tucker shortly thereafter (Axelrod 1984). Features of the game derive from the situation of a prisoner confronting the choice of confessing to a crime without knowing if the collaborator will be forthcoming. Points won on each trial, as well as earnings accumulated across trials, are maximized when both players do not confess; otherwise, confession is the best strategy. Choice of strategy reflects the degree of trust that partners invest in each other (Jones and Gerhard 1967). Game theorists have recognized parallels between the Prisoner’s Dilemma and reciprocal altruism (Cosmides and Tooby 1992; Trivers 1985). Reciprocal altruism refers to the exchange between two individuals of altruistic acts that are separated in time. Genetic relatedness may influence altruistic behavior, but is not a necessary requirement for its occurrence. Trivers (1985) has suggested that reciprocity is regulated by an emotional system that includes friendship, moralistic aggression, gratitude and sympathy, guilt and reparative altruism, and a sense of justice.

In the Prisoner’s Dilemma game, two players may achieve mutual gains through cooperation, but the game provides opportunities for an absence of cooperation, as well as exploitation of one partner by another. If both players cooperate they are rewarded for mutual cooperation. If both players exploit the partner, then both are punished. If one player exploits while the other player cooperates, the former gains at the expense of the latter. The central feature of this game is that “there is no

¹A pair of MZ twins separated at birth came into contact due to a chance meeting at the age of 64 years. Their recognition of one another was based solely on physical cues (although each had grown up with the knowledge of having been born a twin). There are also examples of romantic attachments between reared apart relatives who were unaware of their biological relatedness. See, for example, Amery, D. Coupled wed 20 years discover they’re twins. *Sun* December 17, 1985. Also see Gonyo, B. Genetic sexual attraction. *American Adoption Congress “Decree”* Vol 4, 1987, pp. 1, 5.

possibility for 'rational' individual behavior . . . unless the condition for mutual trust exists" (Deutsch 1973: 180).

This study is the first to use the Prisoner's Dilemma game to compare cooperation and competition using a genetically informative research design. Although the effects of participant characteristics, such as age, gender, social class, race (Sampson and Kardush 1965), group status (Brown 1984), friendship status (Mannarino 1976, 1979), and previous social experience with an interactant (Frank 1988) on outcomes from the Prisoner's Dilemma game have been examined, the relative genetic relatedness of the players has never been assessed (see Good 1991 for a review of research in this area).

HYPOTHESES AND QUESTIONS

It was expected that MZ twin pairs would display an increased frequency of cooperative behavior, relative to DZ twin pairs. It also was anticipated that some informative behavioral patterns might emerge. The relationship of responses over time, both within individuals and especially between co-twins, was of interest. Specifically, were MZ twins more highly influenced by their co-twins' behavior than DZ twins? In addition, how would cooperative events unfold over time? Would MZ and DZ twins show differences in the magnitude and direction of cooperative behaviors? This study offered opportunities to explore these interesting issues, and to empirically test several twinship features (e.g., IQ similarity and social closeness) by which genetic factors might influence cooperation.

METHODS

Sample

The sample included 59 MZ twin pairs and 37 DZ same-sex twin pairs who ranged in age from 10.92 to 82.67 years. One young MZ female twin pair was excluded from the analyses due to discordance for a severe congenital physical disability. Mean age and age variance were significantly higher for MZ twin pairs (25.57 years, $SD = 16.88$, range = 10.92–82.67 years) than for DZ twin pairs (19.22 years, $SD = 8.88$, range = 10.92–49.75 years) [$t(91.73) = 2.41, p < .05$; $F(58, 36) = 3.61, p < .001$]. This age difference was due to the presence of four older MZ twin pairs who ranged in age from 60.08 to 82.67 years (Eliminating these pairs from the analyses equalized the age and age variance; however, their removal had a negligible effect on the findings and so they were retained in the sample.) Females were represented among 66% of the MZ twins and 65% of the DZ twins.

Seventy-one of the 96 twin pairs (74%) participated in this study at California State University, Fullerton (CSUF), between 1991 and 1992. Identification of participants was accomplished by newspaper advertising or television news programs (48%), personal referrals (34%), Mothers of Twin Clubs (10%), and other means (8%). It is estimated that 20% of the twin pairs invited to participate were unavail-

able. These twins were initially invited to take part in a study of olfactory perception, thus providing an opportunity to administer the Prisoner's Dilemma game during the visit. Eighty-three twin pairs participated in the CSUF olfactory perception study, but some did not participate in the Prisoner's Dilemma game due to time constraints, and data from opposite-sex pairs were not used in this analysis. The Prisoner's Dilemma game took place toward the end of the session and took approximately 13 minutes. In addition to money the twins might earn from the game, each were offered \$5.00 each for the research visit, which lasted approximately 3 hours.

The remaining 25 twin pairs were identified in Minneapolis/St. Paul through Mothers of Twins Clubs (40%), personal referrals (48%), and contacts with the Minnesota Center for Twin and Adoption Research or chance meetings (12%). These twins participated in a study of twin relationships at the University of Minnesota, between 1988 and 1991 (Segal and Russell 1991, 1992). All twins in this group were adolescents. Three families contacted for participation declined. The Prisoner's Dilemma research protocol was identical for the twin samples from California and from Minnesota.

Zygosity diagnosis. Forty-one twin pairs were assigned as MZ or DZ based upon analysis of blood group systems (ABO, Rh, MNSs, K), serum proteins (Gc, Hp, Bf, PLG, Gm, Km 1), and red cell enzymes (PGM₁, AcP, EsD, GLO). The remaining twin pairs were classified by a physical resemblance questionnaire (Nichols and Bilbro 1966). In the Minnesota study, restricted funding allowed serological analysis to be made available only to twin pairs judged as "difficult to classify." Blood typing was offered to all participants in the CSUF study, although some declined. Agreement between results from blood-typing analyses and the zygosity questionnaire used in the present study is 93% (Nichols and Bilbro 1966).

Procedure

Prisoner's Dilemma game. The Prisoner's Dilemma game can assume various forms, dependent upon motivational orientation, simultaneity of choice, allowable communication, and number of trials. These aspects of the game (with the exception of number of trials) are described to participants prior to the start of the game. Three different motivational orientations are outlined by Deutsch (1973):

1. Cooperative: Players are considered to be partners. "You're interested in your partner's welfare as well as in your own."
2. Individualistic: Players are encouraged to be interested only in their own personal gain. "You simply want to win as much money as you can for yourself, and you don't care what happens to him."
3. Competitive: Players are encouraged to outperform their partners. "You want to make money, rather than lose money, but you also want to come out ahead of the other person."

The individualistic form of the game was used in the present study. This decision was prompted by the view that confirmation of the anticipated twin group dif-

ferences would be more persuasive if participants were directed to work for their own benefit. The payoff matrix is displayed in Figure 1.

The present study did not allow exchange of information between twins in an attempt to permit “tacit coordination” (Jones and Gerhard 1967; Schelling 1960), i.e., the transmission and interpretation of information through events as they unfold during the game. It was reasoned that an absence of explicit communication would most faithfully reveal the nature of twins’ relations.

Co-twins were seated in opposite corners of a testing room facing away from one another. Each twin was provided with two cardboard markers, one red and one blue, measuring approximately 12 inches \times 14 inches. A Prisoner’s Dilemma reference sheet, displaying the various event combinations and outcomes, was available on a wall in front of each participant for access throughout the game.

The following instructions were read:

Each of you will have a chance to win points which you will exchange for money. Each point is worth one penny, but you can win up to five dollars. The person with the most points naturally wins the most amount of money.

It will help you now to look at the chart or reference sheet in front of you. This is what you will do: In front of you are two markers, one blue and one red. On each trial, I will ask you to hold up one of the markers; you can choose either the blue marker or the red marker.

If one of you holds up the blue marker and the other person also holds up the blue marker, then you each will win three points. This is shown on the chart in front of you.

If one of you holds up the red marker and the other person also holds up the red marker, then you both will win only one point. This is shown on the chart in front of you.

If one of you holds up the blue marker, but the other person holds up the red marker, the person holding the blue marker wins nothing, but the person holding the red marker wins five points. This is shown on the chart in front of you.

Similarly, if one of you holds up the red marker, but the other person holds up the blue marker, the person holding the red marker wins five points, but the person holding the blue marker wins nothing. This is shown on the chart in front of you.

FIGURE 1. Payoff matrix used in the Prisoner’s Dilemma game.

		Twin 1	
		Cooperate (blue)	Defect (red)
Twin 2	Cooperate (blue)	3, 3	0, 5
	Defect (red)	5, 0	1, 1

You should feel free to look at the reference sheet at any time during the game. You should not speak at all during the game, and you should not turn around to look at your twin. I will announce each person's choice of blue or red after you make your choices, and I will tell you how many points each of you has won. We will first do ten test trials so that you feel comfortable with the game. *These test trials do not count for points.* You should try to win as many points for yourself as you can. Before we begin, are there any questions?

Questions were resolved following completion of the ten test trials. The game was played for 100 trials, although participants were not informed as to the duration of the game. Trial numbers (e.g., "trial 1," "trial 2") and earnings were, however, continuously announced. There is a folk theorem (based on unrelated players) to the effect that nearly any payoff combination can be achieved when the game is repeated an unknown number of times (Fudenberg and Tirole 1991). We reasoned, however, that obtaining the predicted twin group differences would suggest distinctions between different forms of interaction arising between individuals who vary in genetic relatedness.

It appeared that a genuine incentive to earn points (monetary prize) would more faithfully reveal twin group differences in cooperation and competition than a hypothetical reward. The examiner entered each twins' responses on a scoring sheet, but all sessions were recorded on tape for verification when necessary. Money earned by each twin was awarded at the conclusion of the game. A member of one DZ twin pair (which consistently pursued a competitive strategy during the first 50 trials) grew visibly upset, causing the examiner to halt the game. Both twins (privately) insisted that they would continue to "pick red" to prevent the co-twin from earning points if asked to play 50 additional trials. This information, and the fact that the signed difference in competitive events between the first and second half of the game was -1.95 for DZ twin pairs and -0.85 for all twin pairs, led to the decision to enter their score as 100 competitive events.

IQ testing. The age-appropriate version of the Wechsler IQ test (Wechsler Intelligence Scale for Children-Revised [WISC-R] or the Wechsler Adult Intelligence Scale-Revised [WAIS-R]) was completed by participants (Wechsler 1974, 1981). The correlation between IQ scores from these different versions of the test is .88 (Wechsler 1981). A separate examiner administered the test to each co-twin in a pair in order to avoid biasing effects; this is a recommended procedure in twin research (Segal and Russell 1992). Twins from Minnesota completed the full test, whereas twins from California completed the Information, Vocabulary, Picture Arrangement and Block Design subscales. These subscales comprise a widely used short form of the test and yield composite scores that correlate higher than .90 with the full scale score (Sattler 1989). IQ scores were unavailable for five twins.

Social closeness ratings. Participants from California judged their degree of social closeness on a seven-point scale (1 = Much closer than best friends to 7 = Much less close than casual friends). This measure was included in a packet of personal and medical history questionnaires completed at home prior to arrival at the

laboratory. Parents of twins from Minnesota rated their twins' social closeness on the same scale while the twins participated in research activities in another room. (These data sources are not strictly comparable; however, differences in means and variances, and in the magnitude of correlations with cooperation and competition, were not detected.) Twins from Minnesota also indicated their willingness to share with the co-twin on a four-point scale (1 = Do not like to share 4 = Like to share). Information was unavailable for one twin pair from California.

RESULTS

Data Analysis

Means, standard deviations, and ranges for the four response combinations (Blue-Blue: *Cooperation*, Red-Red: *Competition*, Blue-Red: *Exploitation 1*, Red-Blue: *Exploitation 2*) were calculated for twin pairs, organized by zygosity and sex. (Blue-Red occurred when Twin 1 selected blue and Twin 2 selected red; Red-Blue occurred when Twin 1 selected red and Twin 2 selected blue.) These data are presented in Table 1. The Red-Blue (Exploitation 2) response combination, although presented in the table, was eliminated from the multivariate analyses to avoid singularity of the within cells matrix; this procedure has been used in previous analyses of Prisoner's Dilemma data (Harris 1985). The findings concerning cooperative and competitive choices are of greatest interest and are summarized in Table 2.

The choice of varied data analytic techniques was guided by the hypotheses and questions listed previously. Data analysis was organized into four phases. (1) Multivariate analysis of variance (MANOVA) was used to test for twin group differences in the dependent measures (Cooperation, Competition, and Exploitation 1). Profile analysis was used to examine twin group differences in *level* (total number of events) and *parallelism* (score profile). Analysis of variance (ANOVA) was used to compare the total number of points collectively earned by MZ and DZ twin pairs. Intraclass correlations were computed to compare MZ and DZ co-twin similarity in points earned individually. (2) Time-series analyses were used to assess several relationships between responses across time. Specifically, cross-lag correlations were computed to determine if individual twins' responses across the 100 trials were related. Cross-lag correlations also were examined to determine if the responses of one twin were related to the previous responses of the co-twin, and if the nature and magnitude of this relationship differed for MZ and DZ twin pairs. Time-series modeling was additionally used to assess consistency in the patterning of responses over time. (3) Hierarchical linear modeling (HLM) was used to assess the directionality and magnitude of cooperation as a function of time, zygosity, and sex; in other words, *how* cooperative events unfolded over time. (4) The effects of IQ similarity and social closeness on within-pair cooperation and competition were examined by computing correlations between individual and pair measures of these variables.

1. Multivariate and univariate analyses. Box's M test was significant (for both the MANOVA and profile analysis) suggesting possible violation of the assumption of

Table 1. Means, Standard Deviations, and Ranges for Response Combinations from the Prisoner's Dilemma Game

Zygosity*	(Pairs) <i>n</i>	Response Combinations									
		Blue-Blue**		Red-Red*		Blue-Red		Red-Blue			
		<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>		
MZ	59	12.97	(14.45)	57.83	(24.88)	15.09	(9.62)	14.12	(8.41)	339.48	(86.40)
Range		0-56		4-100		0-42		0-36		200-531	
Male	21	11.48	(14.93)	60.95	(25.41)	16.14	(10.80)	11.43	(7.33)	328.62	(89.15)
Female	38	13.79	(14.32)	56.11	(24.76)	14.50	(9.00)	15.61	(8.70)	345.47	(85.45)
DZ	37	5.84	(8.02)	67.19	(23.44)	13.03	(8.67)	13.95	(9.79)	304.27	(77.29)
Range		0-29		24-100		0-28		0-31		200-451	
Male	13	3.69	(7.53)	77.46	(20.53)	8.77	(6.48)	10.08	(10.49)	271.31	(67.47)
Female	24	7.00	(8.19)	61.63	(24.64)	15.33	(8.94)	16.04	(8.92)	322.13	(77.64)
Sex											
Male	34	8.50	(13.05)	67.26	(24.72)	13.32	(9.96)	10.91	(8.54)	306.71	(85.27)
Female	62	11.16	(12.68)	58.24	(24.20)	14.82	(8.91)	15.77	(8.71)	336.44	(77.29)

*Pair data (sum of points earned by co-twins), based on 100 trials.

Zygosity: * $p < .05$; ** $p < .01$.

Table 2. Proportions of Cooperative (Blue) and Competitive (Red) Choices for MZ and DZ Male and Female Twins

	MZ	DZ	Σ
Male	25.3/74.7	13.1/86.9	19.2/80.8
Female	28.8/71.2	22.7/77.3	25.7/74.3
Σ	27.1/72.9	17.9/82.1	22.5/77.5

homogenous population dispersion. The larger determinant was, however, generally associated with the larger cell size; thus, the probabilities of the F -test values were considered sufficiently accurate for interpretation. Age showed a significant, albeit modest, positive correlation with the cooperative response combination ($r = .22, p < .05$).

A. Multivariate analysis of variance. Zygosity and sex were entered as independent variables, and the three response combinations (Cooperative, Competitive, Exploitation 1) were entered as dependent variables. A significant multivariate effect of zygosity [$F(3, 90) = 3.27, p < .05$] was demonstrated. The effect of sex approached statistical significance [$F(3, 90) = 2.49, p < .07$], whereas the zygosity \times sex interaction was nonsignificant. Univariate tests were significant for both cooperative [$F(1, 92) = 7.11, p < .01$] and competitive behaviors [$F(1, 92) = 4.35, p < .05$]. As expected, the frequencies of cooperative and competitive choices were significantly higher among MZ and DZ twin pairs, respectively. In contrast, the response combination Blue-Red (Exploitation 1) did not differ significantly between twin groups. Despite the significant multivariate and univariate effects obtained, a canonical correlation of .31 indicated that zygosity differences accounted for only 11% of the variability in the discriminant function scores. Proportions of variance in the dependent variables (cooperative and competitive response combinations) explained by zygosity, as assessed by omega-squared, were less than .10.

There was no difference in the relationship between cooperative and competitive events regardless of whether exploitation 1 or exploitation 2 was used in the analysis. The correlation remained the same; thus, the multivariate results are the same. The zygosity main effect stayed significant, the sex main effect stayed marginally significant, and the sex \times zygosity main effect stayed nonsignificant, even though the male-female difference in exploitation 1 and exploitation 2 appeared to differ.

B. Profile analysis. Profile analysis compared MZ and DZ twin pairs with respect to level and patterning of response. (Sex was not used as a grouping variable, given the nonsignificant sex effect and zygosity \times sex interaction in the MANOVA.) The twin group difference in level (total number of events: sum of Cooperative, Competitive, and Exploitative 1 trials) was not significant (MZ: 85.88, $SD = 8.41$; DZ: 86.06, $SD = 9.79$). However, the test for parallelism (Zygosity \times Response Combination) showed a significant difference between MZ and DZ twin pairs [$F(2, 93) = 3.18, p < .05$], indicating that the frequency of events was differentially distributed in the two groups.

The profiles were evaluated in terms of response combinations on which group averages fell outside the 95% confidence intervals of the pooled profile. MZ (12.97) and DZ twins' (5.84) scores for Cooperation fell above and below this interval, respectively (7.62 to 12.81). The Competition score for DZ twins (67.19) exceeded the upper bound of the 95% group interval (56.45 to 66.43), whereas the score for MZ twins (57.83) fell within this interval. Exploitation 1 scores for both MZ (15.09) and DZ twins (13.03) were within the 95% confidence interval for the pooled data. Twin group profiles are, thus, differentiated primarily on the basis of Cooperation and Competition. These findings are consistent with those provided by the MANOVA.

C. Analysis of variance. The number of points earned by MZ and DZ twin pairs across the 100 trials was compared by ANOVA.² Total points collectively earned by MZ twin pairs (sum of co-twins' points) significantly exceeded those earned by DZ twin pairs [$F(1,92) = 4.20, p < .05$]. These findings are consistent with the higher number of cooperative events displayed by MZ twins. The effects of sex and the zygosity \times sex interaction were nonsignificant. These values are displayed in the last column of Table 1.

Intraclass correlations for points earned by each co-twin were computed separately for MZ and DZ twin pairs. Interestingly, the intraclass correlations were *identical* ($r_1 = .66$) for MZ and DZ twin pairs. This finding is *not* inconsistent with the findings presented previously, which support greater cooperation within MZ twinships. Recall that cooperative and competitive interactions award three points or one point, respectively, to each player, which improves the possibility of similar earnings for MZ co-twins and for DZ co-twins. This issue is addressed again in the Time Series Analyses section.

2. Time series analyses. Time series analysis was used to address several interrelated questions concerning the patterning of responses over time (SAS Institute Inc. 1993).

A. Response patterns within individuals. The ARIMA procedure from the SAS ETS module was used to determine if a significant relationship existed among responses across the 100 trials. A significant Chi-square test [$\chi^2(6, N = 192) = 75.87, p < .001$] indicated at least one autoregressive (cross-lag) coefficient. The first [$t = 3.00, SE = .099$] and second autoregressive coefficients [$t = 2.04, SE =$

²Substituting average pair profit or absolute payoff difference for total pair earnings circumvents the problem that some co-twins apparently used an exploitative-like strategy for cooperative purposes, i.e., alternating choices of red and blue. However, calculating the average pair profit involves a linear transformation of the data (i.e., dividing the number of points earned by each pair by 2), so is not informative beyond analyses using total points won. The absolute within-pair payoff difference was smaller for MZ (18.90) than DZ twins (21.89), but did not differ significantly. This is, however, a less informative measure of cooperation than the number of individual or joint cooperative choices, because competitive co-twins who consistently chose red would each gain few points, yielding a small within-pair difference in earnings.

.100] were significant, indicating that responses were correlated between trials separated by one lag (t and $t + 1$) and by two lags (t and $t + 2$), but not by three or more lags. The correlations were $r = .182$ (lag 1) and $r = .264$ (lag 2); the lag 2 correlation was higher, but the difference was slight.

B. Response patterns between co-twins. Cross-lag correlations were calculated separately for MZ and DZ twins. Interestingly, MZ and DZ co-twin correlations were nearly identical between t and time $t + 1$, $t + 2$, $t + 3$, $t + 4$, and $t + 5$, and nearly identical to the within-person cross-lag correlations at lag 1 and lag 2. MZ and DZ correlations were .26 at $t + 1$, and .29 and .27 at $t + 2$, respectively. These findings, although suggesting comparable influence between MZ and DZ interactants, actually mask twin group differences in *magnitude* and *direction* of cooperation or competition. Specifically, correlations within groups could be similar, but the events themselves could be quite different (e.g., repeated simultaneous choices of Red [compete] or Blue [cooperate] would yield identical correlations, but the nature of the interactions would differ). A comparable situation occurred in the analysis of co-twin similarity in individual earnings discussed above.

C. Quality of the data over time. It is possible that 100 trials of a Prisoner's Dilemma game may grow uninteresting, eventuating in atypical responses to "break the boredom." Several twins (both MZ and DZ) admitted that this had happened. Thus, it was important to determine if degradation of the data had occurred across time, a task accomplished by comparison of events during trials 1 and 50 and trials 51 to 100. Autoregressive coefficients were significant for trials 1 to 50 [$r = .37$, $t = 2.79$, $SE = .134$] and trials 51 to 100 [$r = .26$, $t = 1.95$, $SE = .143$] and did not differ in magnitude, thus eliminating concern over degradation of the data.

3. Hierarchical linear modeling. Many behavioral and social science data are naturally organized into nested (or hierarchical) data structures in situations where multiple observations are gathered over time. These multiple observations are "nested" within the individuals participating in the study. Hierarchical linear modeling (HLM) is a recent data analytical technique designed to specifically model nested data structures. With HLM, it is possible to estimate the individual growth trajectories of participants from nested multiple observations. The parameters of the growth trajectories (e.g., linear slope) can then be modeled as a function of other variables, such as zygosity and sex, to see if these variables predict how individuals change across time (Bryk and Raudenbush 1992).

HLM was applied for the purpose of modeling cooperation over time. In the present data set, the 100 observations were nested within each individual. A dependent variable, *Cooperation*, was created by coding "1" if both co-twins chose blue; "0" if one twin chose blue and the twin other chose red;" and "-1" if both co-twins chose red. Using the slope of cooperation on time as the dependent variable, a meaningful relationship was found between the parameter and zygosity [slope = $-.002$, $p < .092$, $t = -1.685$]. Furthermore, evidence existed for slope differences among individuals [heterogeneity among slopes, $\chi^2(93) = 862.28$, $p < .001$]. Thus, due to

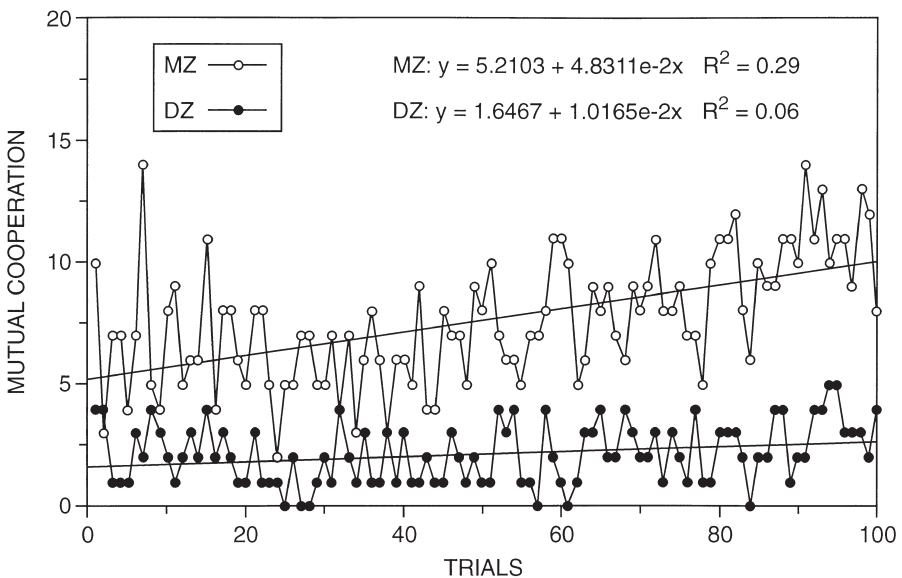
the marginally significant relationship found between cooperation-time slopes and zygosity, it was suspected that these individual differences might be attributable to zygosity group differences, so analyses were conducted separately for MZ and DZ twins. It was found that the slope relating time and cooperation for MZ twins as positive (.0005, $p = .329$), whereas the slope relating time and cooperation for DZ twins was negative ($-.0001$, $p = .296$). Thus, cooperative behavior increased over time for MZ twins, whereas for DZ twins cooperative behavior decreased. Slopes depicting the relationship between the mutual cooperative response combination (blue-blue) and time for MZ and DZ twins separately, across the 100 trials, are displayed in Figure 2.

4. Correlations and summary statistics: IQ similarity, social closeness, and cooperation

A. IQ similarity and cooperation. The mean IQ score for the twin sample was 105.18 ($SD = 14.61$) and ranged between 75 to 150. Mean IQ scores did not differ between MZ (105.80, $SD = 13.79$, $n = 113$) and DZ twins (105.76, $SD = 15.85$, $n = 74$). Mean pair IQ score was significantly associated with two of the three response combinations: cooperative, or blue-blue ($r = .31$, $p < .01$, $n = 93$) and competitive, or red-red ($r = -.27$, $p < .01$, $n = .93$), indicating that pairs scoring higher in IQ were more likely to be mutually cooperative (and less competitive) than pairs scoring lower in IQ.

The within-pair difference in IQ was smaller for MZ (7.93, $SD = 5.94$, $n = 56$) than DZ twins (10.59, $SD = 9.03$, $n = 37$). These values are slightly higher than

FIGURE 2. Cooperative response combination (blue-blue) for monozygotic (MZ) and dizygotic (DZ) twins across trials 1–100.



those of 6.0 and 10.0 that are typically reported for MZ and DZ twin pairs, respectively (Plomin and DeFries 1980). The IQ variance for DZ twins significantly exceeded the variance for MZ twins [$F(36, 55) = 2.31, p < .01$]. Correlations between co-twin differences in IQ score and co-twin differences in individual cooperative choices (i.e., number of “blues”) were negligible for MZ and DZ twin pairs and for the full sample. Age was uncorrelated with the within-pair IQ difference.

B. Social closeness and cooperation. Ratings on the seven-point social closeness scale were provided by twins (California) or by parents (Minnesota). Social closeness ratings were averaged for California twins to obtain a pair measure, whereas the single parental rating for Minnesota twins provided this value. Greater social closeness was indicated for older pairs than for younger pairs ($r = -.32, p < .01, n = 95$), so both uncorrected correlations, and partial correlations in which age was controlled, are provided. The signs of the correlation reflect the assignment of values to the social closeness scale.

Increased social closeness was associated with mutual cooperation ($r = -.25, p < .05, n = 95$) and decreased mutual competition ($r = .23, p = .05, n = 95$). After controlling for age, the correlations decreased to $r = -.18$ and $r = .21$ for mutual cooperation and competition, respectively, but remained statistically significant. The relationship between social closeness and exploitation 1 was negligible.

Mean social closeness ratings did not differ between MZ (2.29, $SD = 1.46$) and DZ twin pairs (2.68, $SD = 1.40$), but the difference was in the expected direction. Among twins from California (in which each twin provided a rating), co-twin differences in social closeness were uncorrelated with co-twin differences in individual cooperative choices. Interestingly, MZ twins were significantly more likely to *agree* about the nature of their social relationship than DZ twins (MZ $r_i = .86, n = 44$ vs. DZ $r_i = .65, n = 26, p < .05$); social closeness ratings were age and sex-corrected prior to calculation of the intraclass correlations, according to procedures described by McGue and Bouchard (1984). This same pattern of findings was reported by Loehlin and Nichols (1976) in a study of 850 twin pairs of high-school age. However, meaningful associations between agreement, and mutual cooperation and competition were not indicated. In contrast, expected relationships between agreement in sharing and mutual cooperation ($r = -.33, n = 25$), and competition ($r = .30, n = 25$) were suggested among twins from Minnesota, i.e., agreement was associated with increased mutual cooperation and reduced competition. Sharing may tap a more specific aspect of social relatedness relevant to the Prisoner’s Dilemma game than social closeness as measured on all twins, a possibility discussed in the next section.

DISCUSSION

Cooperation was displayed more frequently by MZ twin pairs, as evidenced by a significantly higher number of cooperative response combinations, significant MZ-DZ differences in the profile of response combinations (mainly associated with cooperative choices), and increased frequency of cooperation over time. The present

findings, thus, support and extend previous studies in the psychological literature that report associations between genetic relatedness and cooperation.

Both MZ and DZ twins chose to defect more often than to cooperate. This finding is *not* incompatible with the kinship-genetic principles outlined previously. The important point is that the *magnitude* of the discrepancy between cooperative and competitive events was smaller for MZ twins. This pattern suggests a strategy of “greater restraint of selfishness” (Axelrod and Hamilton, 1981; Charlesworth 1996) by MZ co-twins than by DZ co-twins. Similar findings have emerged in other studies using twin children. H. von Bracken (1934) observed a “regulating function” (p. 305) between some MZ co-twins during completion of addition and coding tasks (i.e., the “stronger” co-twin reduced productivity to enable the “weaker” co-twin to catch up). Segal (1984) found that both MZ and DZ twins worked harder for themselves than for their co-twins on a differential productivity task (an activity that shares some features with a Prisoner’s Dilemma game), but that MZ twins worked significantly harder for their co-twins than did DZ twins. Such twin group differences in cooperation may be associated with the differing emotional circumstances of MZ and DZ twinships. This recalls the assertion by Trivers (1985) that various emotions (e.g., sympathy and guilt) may serve regulating functions in social exchanges.

It is curious that zygosity differences accounted for a small proportion of variability in the discriminant scores, and that the proportions of variance in the dependent variables explainable by zygosity differences were small. It is possible that some MZ twins were driven toward within-pair equality in earnings, with less regard for maximization of group gain. Debriefing summaries suggested that some MZ co-twins applied exploitative-like strategies (consistently alternating choices of blue and red) *for the purposes of equalizing points*, rather than for exploiting the co-twin. The possibility of miscalculation of self-interest is thus raised. The difference in twin pair gain from mutual cooperation or blue-blue (600 points in total; 6 points per trial) versus alternating cooperation/defect or blue-red/red-blue (500 points in total; 5 points per trial) may have been too small to have been readily perceived.

The small proportion of variability explained by zygosity differences may come from other sources. Rowe (1989) has suggested that genetically influenced variation in phenotypic similarity detection mechanisms may underlie observed variability in MZ twin relationships. It is also known that some MZ twins show physical and/or behavioral differences associated with prenatal events, such as delayed zygotic splitting or unequal blood supply (Torrey, et al. 1994). These MZ twins may, therefore, be less competent than others in processing cues relevant to assessing relatedness, which may explain the behavioral variability among the MZ twin pairs. (The variance of the cooperative response combination was larger for MZ than DZ twins, as shown in Table 1.) Finally, some older twins declined the monetary award, indicating that it was “not important.” A more meaningful prize may have increased competition between DZ twins.

It is also possible that competitive efforts were inadvertently encouraged by the instructions that established an individualistic orientation (Caporeal et al. 1989). A cooperative orientation, in which twins were encouraged to be concerned for each

other's welfare, may have increased twin group differences in expected directions. Opportunities to communicate may have modified the findings by augmenting cooperation (Deutsch 1973), especially within DZ pairs who showed less mutuality than MZ pairs. It seems unlikely that a single-trial condition versus repeated trials would have altered results substantially. This is partly because response patterns during the first and second half of the game did not differ. Furthermore, Deutsch (1973) observed similar outcomes in one-trial and ten-trial games, such that likelihood and expectation of cooperation did not differ. (In the present study repeating trials revealed a time-related increase in cooperation within MZ pairs.) Varying the conditions of the game in future experiments will be of interest, but the present findings are encouraging and should stimulate further research activity.

The present study explored several mechanisms possibly associated with cooperative behavior. Higher IQ, social closeness, and sharing were associated with increased mutual cooperation and decreased competition. It is reasonable to expect similarity in these measures to enhance attraction, interdependence, and cooperative behavior between MZ twins. However, neither co-twin differences in IQ nor social closeness were associated with co-twin differences in cooperative choices. This was surprising at first, especially because MZ twins showed significantly greater agreement in social closeness ratings than DZ twins. It may be that IQ (general intelligence) and social closeness lack the specificity of a measure such as co-twin consensus in sharing (which was correlated with mutual cooperation and competition) and were, therefore, less sensitive to between-pair differences. Twins who feel close socially may vary in their feelings of trust, loyalty, or willingness to share. More specific social indices (e.g., time spent together, feelings of pride or jealousy) and cognitive measures (e.g., numerical reasoning, perceptual speed) may have yielded the anticipated relationships between phenotypic similarity and cooperative behavior.

Competing Perspectives

Interpretation of the present findings with reference to other theoretical frameworks is instructive. Psychodynamic and psychosocial perspectives lead to similar predictions of differential cooperation within MZ and DZ twinships. This expectation rests on the argument that the similar physical appearance of MZ co-twins encourages similar treatment of pair members, eventuating in behavioral resemblance (Hoffman 1991) and a sense of unity (Siemon 1980). In contrast, DZ co-twins (who are physically dissimilar) would receive more individually tailored treatment. There is, however, negligible empirical evidence of meaningful associations between similarity in twins' treatment and behavior (Bouchard et al. 1990; Hettema et al. 1995; Loehlin and Nichols 1976). Instead, there is growing evidence that the more similar treatment of MZ and DZ twins by others is *elicited* by their more similar behaviors, not the reverse (Lykken et al. 1990). In addition, Segal (1988) found that greater cooperation between MZ and DZ twin children on a puzzle competition task was unrelated to parental judgment of zygosity, membership in a Mothers of Twins Club, perceived physical resemblance by the twins, or self-reported parental encouragement toward similarity or dissimilarity in behavior.

MZ twins are more similar than DZ twins across a wide range of behavioral and physical characteristics (Bouchard et al. 1990). There is also positive assortment (i.e., nonrandom pairing) for intellectual and personality traits among marital partners and friends (Rowe et al. 1994). As such, some might object that the present findings, viewed from an evolutionary perspective, do not advance understanding of kin relations over and beyond what studies of social relatedness can contribute. However, a social-psychological view represents only one level of analysis in our understanding of kin relations, thus eluding some deeper issues.

Environmentally oriented theorists often fail to adequately consider *why* individuals who vary in genetic relatedness may correspondingly vary in the nature of their social interactions. It may be that relative genetic commonality and its correlates (e.g., specific phenotypic similarities, as yet unidentifiable) drive social relationships, resulting in increased frequency of contact and cooperation. This interpretation acknowledges the joint contribution of biological and psychological influences. There is greater evidence that MZ twins who are more alike in personality spend more time together than those who are less alike, as compared with the alternative view that MZ twins who spend more time together *become* more alike in personality than those who spend less time together (Lykken et al. 1990; also see Bouchard 1993). Furthermore, as suggested earlier, the close bonds between many reunited biological relatives seriously challenge theories grounded exclusively in social-psychological effects. The greater social attraction between close genetic relatives than distant relatives may stimulate cooperative exchange and, ultimately, the indirect transmission of shared genes; this process might well provide the psychological mechanism(s) underlying Hamilton's theory of inclusive fitness that we seek. Phenotypic similarities may also explain attraction between spouses and friends, although the phenotypic resemblance is not as pervasive as between close relatives.

Some researchers may argue that MZ twins "intuit" their co-twin's behaviors more successfully than DZ twins, resulting in greater cooperation irrespective of their valuation of each other. This ability could, however, offer a mechanism by which altruistic behavior is expressed. MZ twins' knowledge of their co-twins' behavioral inclinations could conceivably have been exploited for self-interest, but this was not observed in the present study. In other words, knowing a partner's tendencies does not guarantee cooperation.

Research Directions

The finding that zygosity was significantly related to outcomes on the Prisoner's Dilemma game identifies a fruitful domain in which to search further for mechanisms underlying cooperation and competition. Organizing MZ and DZ twin pairs as a function of similarity in physical appearance, specific indices of social closeness, special cognitive abilities, and personality traits should be informative in future studies. Several analyses along these lines are planned. In addition, the work of McGuire et al. (1994) suggests that monitoring associations and changes in biochemical variables as a function of twin recognition, mood following separation and reunion, and emotions expressed during joint activities might highlight factors

related to the seeking out and maintaining of relationships. The implications of genomic imprinting for kinship theory are also becoming increasingly recognized (Trivers 1997).

Emlen (1995) has noted that among nonhuman species, benefits of reproduction are higher for closely related subordinates than for distantly related subordinates when their reproduction is suppressed by dominants. As such, fewer incentives are required for close relatives to remain in the family group. Comparing relations between four twin groups (MZ and DZ twin pairs concordant and discordant for fertility) would offer a convenient test of how reproductive capability may mediate social relatedness among relatives. Especially high cooperation by an infertile MZ co-twin directed toward the fertile twin might be anticipated.

Administering the Prisoner's Dilemma game to ". . . a parent and its offspring or a pair of siblings would be especially promising, and in fact many examples of cooperation or restraint of selfishness are known" (Axelrod and Hamilton 1981: 1394). The inclusion of various pairs of biological and nonbiological relatives and strangers who vary in genetic relatedness, and in past and future opportunities for social interaction, can furnish additional tests of evolutionary-based hypotheses. Informative groups might include unrelated siblings reared together who are the same age (UST-SA); these unique pairs share rearing situations similar to twins, but do not share genes (Segal 1997a, 1997b), triplet sets composed of an MZ twin pair and DZ co-triplet, and MZ and DZ twins reared apart. These siblings are rare, but collaborative efforts may yield sufficiently large samples in the future.

Comparisons between MZ and DZ twins with their co-twins and children would enable simultaneous assessment of genetic and age effects. (Note: DZ twins share exactly 50% of their genes with their children, but 50% on average with their co-twin. DZ co-twin affiliation might, for example, be expected to vary with perceived relatedness to the co-twin and to correspondingly exceed, or be exceeded by, affiliation with a child. MZ twins share exactly 50% of their genes with their children, but 100% with their co-twin. Given that twins are within the reproductive period, greater cooperation between MZ co-twins than between MZ twins and their children might be expected.) LaFrenière (1996) has also suggested that studies of kin relations may illuminate social pressures within pairs of friends.

Hypotheses and questions in the present study were generated by evolutionary psychological reasoning and tested empirically by a twin design. This effort, thus, represents a fusion of two areas (evolutionary psychology and behavioral genetics) that have remained separate for a long time. A number of investigators have commented on the value of combining these disciplines (Bailey 1997; Segal 1993, 1997a). Others are urged to consider joining this fruitful and exciting enterprise.

The present study reported findings that are consistent with associations between genetic relatedness and cooperative behavior. An evolutionary perspective is able to generate new ideas and interpretations of commonly observed, yet highly complex, features of human social behaviors. The present findings are, however, compatible with other theoretical viewpoints, so that multiple perspectives should be considered.

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REFERENCES

- Axelrod, R. *The Evolution of Cooperation*. New York: Basic Books, Inc., 1984.
- Axelrod, R., and Hamilton, W.D. The evolution of cooperation. *Science* 211:1390–1396, 1981.
- Bailey, J.M. Are genetically-based individual differences compatible with species-wide adaptations? In *Uniting Psychology and Biology: Integrative Perspectives on Human Development*, N.L. Segal, G.E. Weisfeld, and C.C. Weisfeld (Eds.). Washington, DC: American Psychological Association Press, 1997, pp. 81–100.
- Barash, D.P. *The Whisperings Within*. New York: Harper & Row, 1979.
- Barkow, J.H. *Darwin, Sex and Status: Biological Approaches to Mind and Culture*. Toronto: University of Toronto Press, 1989.
- Bergstrom, T.C. On the evolution of altruistic ethical rules for siblings. *American Economic Review* 85:58–81, 1995.
- Bouchard, T.J., Jr. Genetic and environmental influences on adult personality: evaluating the evidence. In *Foundations of Personality*, J. Hetteema, and I.J. Deary (Eds.). The Netherlands Kluwer Academic Publishers, 1993, pp. 15–44.
- Bouchard, T.J., Jr., Lykken, D.T., McGue, M., Segal, N.L., and Tellegen, A. Sources of human psychological differences: the Minnesota Study of Twins Reared Apart. *Science* 250:223–228, 1990.
- Bowlby, J. *Attachment*. New York: Basic Books, 1969.
- Boyd, R., and Richerson, P.J. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press, 1985.
- Brown, R.J. The effects of intergroup similarity and cooperative vs. competitive orientation on intergroup discrimination. *British Journal of Social Psychology* 23:21–33, 1984.
- Bryk, A.S., and Raudenbush, S.W. *Hierarchical Linear Models: Applications and Data Analysis Methods*. Newbury Park: Sage Publications, 1992.
- Burnstein, E., Crandall, C., and Kitayama, S. Some neo-Darwinian rules for altruism: weighing cues for inclusive fitness as a function of the biological importance of the decision. *Journal of Personality and Social Psychology* 67:773–789, 1994.
- Caporeale, L.R., Dawes, R.M., Orbell, J.M., and van de Kragt, A.J.C. Selfishness examined: cooperation in the absence of egoistic incentives. *Behavioral and Brain Sciences* 12:683–739, 1989.
- Charlesworth, W.R. Cooperation and competition: contributions to an evolutionary and developmental model. *International Journal of Behavioral Development* 19:25–39, 1996.
- Cosmides, L., Tooby, J. Cognitive adaptations for social exchange. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, J.H. Barkow, L. Cosmides, and J. Tooby (Eds.). New York: Oxford University Press, 1992, pp. 163–228.
- Dawkins, R. *The Selfish Gene*. Oxford: Oxford University Press, 1989a.
- Dawkins, R. *The Extended Phenotype*. Oxford: Oxford University Press, 1989b.
- Deutsch, M. *The Resolution of Conflict: Constructive and Destructive Processes*. New Haven: Yale University Press, 1973.
- Dugatkin, L.A., Wilson, D.S., Farrand III, L., and Wilkens, R.T. Altruism, tit for tat and ‘outlaw’ genes. *Evolutionary Ecology* 8:431–437, 1994.
- Eisenberg, N., and Mussen, P.H. *The Roots of Prosocial Behavior in Children*. Cambridge: Cambridge University Press, 1989.
- Emlen, S.T. An evolutionary theory of the family. *Proceedings of the National Academy of Sciences, USA* 92:8092–8099, 1995.
- Frank, R.H. *Passions Within Reason*. New York: W.W. Norton & Co., 1988.
- Freedman, D.G. *Human Sociobiology: A Holistic Approach*. New York: Free Press, 1979.
- Fudenberg, D., and Tirole, J. *Game Theory*. Cambridge, MA: MIT Press, 1991.
- Good, D.A. Cooperation in a microcosm: lessons from laboratory games. In *Cooperation and Prosocial Behavior*, R.A. Hinde and J. Groebel (Eds.). Cambridge: Cambridge University Press, 1991, pp. 224–237.

- Graves, J., and Byrne, R.W. Mate selection: the wrong control group. *Behavioral and Brain Sciences* 12:527–528, 1989.
- Hamilton, W.D. The genetical evolution of social behavior (I). *Journal of Theoretical Biology* 7:1–16, 1964a.
- Hamilton, W.D. The genetical evolution of social behavior (II). *Journal of Theoretical Biology*, 7:17–52, 1964b.
- Hamilton, W.D. Discriminating nepotism: expectable, common, overlooked. In *Kin Recognition in Animals*, D.J.C. Fletcher and C.D. Michener (Eds.). New York: Wiley, 1987, pp. 417–437.
- Harris, R.J. *A Primer of Multivariate Statistics*, (2nd ed.). New York: Academic Press, Inc., 1985.
- Hartung, J. Testing genetic similarity: out of control. *Behavioral and Brain Sciences* 12:529–530, 1989.
- Hettema, J.M., Neale, M.C., and Kendler, K.S. Physical similarity and the equal-environment assumption in twin studies of psychiatric disorders. *Behavior Genetics* 25:327–335, 1995.
- Hoffman, L.W. The influence of the family environment on personality: accounting for sibling differences. *Psychological Bulletin* 110:187–203, 1991.
- Johnson, R.C. Attributes of Carnegie medalists performing acts of heroism and of the recipients of these acts. *Ethology and Sociobiology* 17:355–362, 1996.
- Jones, E.E., and Gerhard, H.B. *Foundations of Social Psychology*. New York: John Wiley & Sons, Inc., 1967.
- LaFrenière, P.J. Co-operation as a conditional strategy among peers: influence of social ecology and kin relations. *International Journal of Behavioral Development* 19:39–52, 1996.
- LaFrenière, P.J., and MacDonald, K.B. Evolutionary perspectives on children's resource-directed behaviour in peer relationships: an introduction. *International Journal of Behavioral Development* 19:1–5, 1996.
- Littlefield, C.H., and Rushton, J.P. When a child dies: the sociobiology of bereavement. *Journal of Personality and Social Psychology* 51:797–802, 1986.
- Loehlin, J.C., and Nichols, R.C. *Heredity, Environment, and Personality: A Study of 850 Sets of Twins*. Austin: University of Texas Press, 1976.
- Lykken, D.T., McGue, M., Bouchard, T.J., Jr., and Tellegen, A. Does contact lead to similarity or similarity to contact? *Behavior Genetics* 20:547–561, 1990.
- Mannarino, A.P. Friendship patterns and altruistic behavior in preadolescent males. *Development Psychology* 12:555–556, 1976.
- Mannarino, A.P. The relationship between friendship and altruism in preadolescent girls. *Psychiatry* 42:280–284, 1979.
- McGue, M., and Bouchard, T.J. Adjustment of twin data for the effects of age and sex. *Behavior Genetics* 14:325–343, 1984.
- McGuire, M.T., Fawzy, F.I., Spar, J.E., Weigel, R.M., and Troisi, A. Altruism and mental disorders. *Ethology and Sociobiology* 15:299–321, 1994.
- Nichols, R.C., and Bilbro, W.C., Jr. The diagnosis of twin zygosity. *Acta Genetica et Statistica Medica* 16:265–275, 1966.
- Plomin, R., and DeFries, J.C. Genetics and intelligence: recent data. *Intelligence* 4:15–24, 1980.
- Rowe, D.C. Why birds of a feather flock together: genetic similarity? *Behavioral and Brain Sciences* 12:540–541, 1989.
- Rowe, D.C., Woulbroun, E.J., and Gulley, B.L. Peers and friends as nonshared environmental influences. In *Separate Worlds of Siblings: The Impact of Nonshared Environment on Development*, E.M. Hetherington, D. Reiss, and R. Plomin (Eds.). Hillsdale: Lawrence Erlbaum Associates, 1994, pp. 159–173.
- Rushton, J.P. Genetic similarity, human altruism, and group selection. *Behavioral and Brain Sciences* 12:503–518, 1989.
- Sampson, E.E., and Kardush, M. Age, sex, class, and race differences in response to a two-person non-zero-sum game. *Journal of Conflict Resolution* 9:212–227, 1965.
- SAS Institute Inc. *SAS/ETS User's Guide, Version 6* (2nd ed.). Cary, NC: SAS Institute Inc., 1993.
- Sattler, J.M. *Assessment of Children's Intelligence* (2nd ed.). Philadelphia: W.B. Saunders, 1989.
- Schaffer, H.R. Joint involvement episodes as context for development. In *Childhood Social Development: Contemporary Perspectives*, H. McGurk (Ed.). Hillsdale: Lawrence Erlbaum, 1992, pp. 99–129.
- Schelling, T.C. *The Strategy of Conflict*. Cambridge: Harvard University Press, 1960.
- Segal, N.L. Cooperation, competition, and altruism within twin sets: a reappraisal. *Ethology and Sociobiology* 5:163–177, 1984.
- Segal, N.L. Cooperation, competition and altruism in human twinships: a sociobiological approach. In *Sociobiological Perspectives on Human Development*, K.B. MacDonald (Ed.), Springer-Verlag: New York, 1988, pp. 168–206.

- Segal, N.L. Twin, sibling and adoption methods: tests of evolutionary hypotheses. *American Psychologist* 48:943–956, 1993.
- Segal, N.L. Twin research perspective on human development. In *Uniting Psychology and Biology: Integrative Perspectives on Human Development*, N.L. Segal, G.E. Weisfeld, and C.C. Weisfeld (Eds.). Washington, DC: American Psychological Association Press, 1997a, pp. 145–173.
- Segal, N.L. Same-age unrelated siblings: a unique test of within-family environmental influences on IQ similarity. *Journal of Educational Psychology* 89:381–390, 1997b.
- Segal, N.L. *Entwined Lives: Twins and What They Tell Us About Human Behavior*. New York: Dutton, 1999.
- Segal, N.L., Connelly, S.L., and Topoloski, T.D. Twin children with unfamiliar partners: genotypic and gender influences on cooperation. *Journal of Child Psychology and Psychiatry* 37:731–735, 1996.
- Segal, N.L., and Russell, J. IQ similarity in monozygotic and dizygotic twin children: effects of the same versus separate examiners: A research note. *Journal of Child Psychology and Psychiatry* 32:703–708, 1991.
- Segal, N.L., and Russell, J.M. Twins in the classroom: school policy issues and recommendations. *Journal of Educational and Psychological Consultation*, 3:69–84, 1992.
- Sherman, P.W., and Holmes, W.G. Kin recognition: issues and evidence. In *Experimental Behavioral Ecology and Sociobiology. In Memoriam Karl von Frisch 1886–1982*, B. Hölldobler and M. Lindauer (Eds.). Sunderland: Sinauer, 1985, pp. 437–460.
- Siemon, M. The separation-individuation process in adult twins. *American Journal of Psychotherapy* 34:387–400, 1980.
- Slater, P.J.B. Kinship and altruism. In *Behavior and Evolution*, P.K.B. Slater and T.R. Halliday (Eds.). Cambridge: Cambridge University Press, 1994, pp. 193–222.
- Torrey, E.F., Bowler, A.E., Taylor, E.H., and Gottesman, I.I. *Schizophrenia and Manic-Depressive Disorder: The Biological Roots of Mental Illness as Revealed by the Landmark Study of Identical Twins*. New York: Basic Books, 1994.
- Trivers, R.L. *Social Evolution*. Menlo Park: Benjamin/Cummings Publishing Co., 1985.
- Trivers, R.L. Genetic basis of intrapsychic conflict. In *Uniting Psychology and Biology: Integrative Perspectives on Human Development*, N.L. Segal, G.E. Weisfeld, and C.C. Weisfeld (Eds.). Washington, DC: American Psychological Association Press, 1997, pp. 385–395.
- Vandell, D.L., Owen, M.T., Wilson, K.S., and Henderson, V.K. Social development in infant twins: Peer and mother-child relationships. *Child Development* 59:168–177, 1988.
- von Bracken, H. Mutual intimacy in twins. *Character and Personality* 2:293–309, 1934.
- Wechsler, D. *Manual for the Wechsler Intelligence Scale for Children-Revised*. New York: Psychological Corporation, 1974.
- Wechsler, D. *Manual for the Wechsler Adult Intelligence Scale-Revised*. New York: Psychological Corporation, 1981.
- Zahn-Waxler, C., Robinson, J.L., and Emde, R.N. The development of empathy in twins. *Developmental Psychology* 28:1038–1047, 1992.