man, M. Kupersmith, E. Estey, M. Goldstein, *Lancet* **1976-II**, 515 (1976); A. Lieberman, T. Miyamoto, A. F. Battista, M. Goldstein, *Neurology* **25**, 459 (1975); A. Lieberman *et al.*, *N. Engl. J. Med.* **295**, 1400 (1976); H. L. Klawans, W. J. Weiner, P. A. Nausieda, P. Volkman, C. Goetz, M. D. Lupton, *Neurology* **27**, 390 (1977).

3. M. O. Thorner, S. M. Ryan, J. A. H. Wass, A. Jones, P. Bouloux, S. Williams, G. M. Besser, *J. Clin. Endocrinol. Metab.* **47**, 372 (1978); L. Lemberger, R. Crabtree, J. Clemens, R. W. Dyke, R. T. Woodburn, *ibid.* **39**, 579 (1974).
4. After the administration of ^{14}C-labeled pergolide, total radiation in plasma reached its peaked concentration at 1 to 2 hours, indicating that the drug was absorbed during this period of pharmacologic activity (A. Rubin *et al.*, unpublished observations).
5. Blood was drawn in heparinized tubes daily at 8:00 a.m. and 9:30 a.m. for the determination of prolactin, LH, FSH, growth hormone, cortisol, and TSH.
6. V. N. Sinha, F. W. Selby, U. J. Lewis, W. P. Vanderlaan, *J. Clin. Endocrinol. Metab.* **36**, 509 (1973). The prolactin standard (V-L-S No. 1) and specific antiserum were kindly provided by the National Pituitary Agency, NIAMDD. Sensitivity of the assay is 0.5 ng/ml, and the coefficient of variation is 6 percent between 8 to 30 ng/ml. A computer program was used for analysis of the counting data. Control serum assayed with each set of samples had an interassay variability of ± 5 percent.
7. R. W. Fuller, J. A. Clemens, E. C. Kornfeld, H. D. Snoddy, E. B. Smalstig, N. J. Bach, *Life Sci.*, in press.

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Genetic Variance in Nonverbal Intelligence: Data from the Kinships of Identical Twins

Abstract. *The multiple relationships within kinships of adult monozygotic twins permit incisive analyses to be made of genetic and environmental effects on behavioral traits. Data from families of 65 monozygotic twin pairs yield evidence of genetic variance on the Block Design Test, a nonverbal measure of general intelligence.*

A comparison of mental ability of foster children with that of their biological and their adoptive parents was first reported in 1924 (*1*), and 1 year later H. J. Muller presented the first case report of intellectual resemblance in monozygotic (MZ) co-twins who had been separated in infancy (*2*). In the succeeding half-century, studies of adopted children and separated identical twins have had a central role in research on genetic and environmental determinants of cognitive abilities. The resultant data have generated a continuing controversy (*3*), and its resolution may require new research designs.

The families of adult identical twins provide a new paradigm of particular promise for behavior-genetic study (*4*). In this report we describe the paradigm and illustrate its application.

In Fig. 1 the multiple parent-offspring relationships found within families of adult identical twins are diagramed. Children in each of the nuclear families derive half their genes from a twin parent, those genes being identical with genes of the parent's twin sister or brother (the children's "twin aunt" or "twin uncle"). Since the children and the twin aunt or uncle do not live in the same households, their relationship is somewhat comparable to that between foster children and their biological mother or father. In this way, studies of children of MZ twins provide a parallel to studies of adopted children, with two important advantages: (i) There is no disruption of the nuclear family milieu; the children are reared by their biological parents in their own homes. (ii) In adoption studies biological fathers are rarely available for study (*5*); the relationship of nephew or niece to twin uncle parallels that of foster children to their biological father.

The environmental covariance of a nephew or niece and the twin aunt or uncle will be markedly less than that of a parent and child living in a common household. It may not be zero, however, because MZ twins may select or create similar postmarital environments. An estimate of such effects can be obtained from the resemblance of nephew or niece to the spouse aunt in kinships of male twins and to the spouse uncle in kinships of female twins. In the absence of assortative mating, the children share neither genes nor a household environment with the spouse aunt or uncle, and any behavioral resemblance would therefore suggest an environmental covariance common to all members of the kinship.

Because their twin parents have identical sets of nuclear genes, children of MZ twins are genetically related to one another as half-siblings; socially, they are reared as cousins in separate homes. Further, in contrast to conventional half-siblings resulting from divorce, death of a parent, or illegitimacy, MZ half-siblings are expected to be of the same age and size. Accordingly, offspring of MZ twins afford a unique human parallel to methods employed in animal genetics, where controlled matings of sires to multiple dams yield estimates of genetic, environmental, and maternal effects from a nested analysis of variance of the full- and half-sib progeny. Better still, half-sib progeny occur with equal frequency among maternal and paternal MZ twins, providing a balanced research paradigm that cannot be achieved in lower animals even with controlled matings. To illustrate the paradigm, we here present a study in which it is applied to the Block Design Subtest of the Wechsler Intelligence Scales.

Wechsler's Block Design Test is an adaptation of one introduced in 1923 by Kohs (*6*), who presented evidence that results from his test correlated highly with results from the Stanford Binet but, unlike the Binet, had only a modest relation to level of education. Research with Wechsler's adaptation supports Kohs's assertion that the block test provides a measure of general intelligence. Across a wide age range, block design is highly related to the general factor common to all Wechsler subtests (*7*); it is the most reliable of the nonverbal subtests, and no

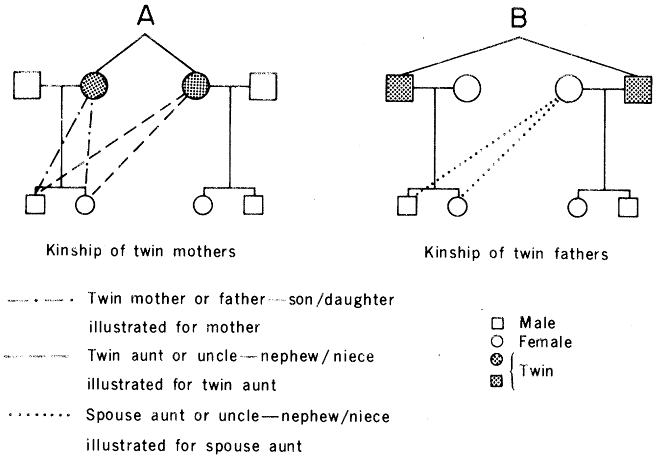

Fig. 1. Parent-offspring relationships in families of identical twins. (A) The offspring of identical twin mothers comprise a maternal half-sibship who genetically relate to their twin aunt as closely as they do to their own mother. (B) In the absence of assortative mating, offspring in a paternal half-sibship share neither common genes nor a common environment with their spouse aunt. In a parallel manner, offspring of identical twin brothers genetically relate to their twin uncle as closely as they do to their own father but offspring in a maternal half-sibship share neither common genes nor a common environment with their spouse uncle.

Table 1. Regression and correlation analyses of Block Design Test scores and fingerprint ridge counts.*

Relationship	Block design scores		Ridge count	
	Coefficient	*N*	Coefficient	*N*
Regressions				
Son or daughter on father or mother	0.28 ± 0.04	572	0.42 ± 0.05	564
Nephew or niece on twin uncle or aunt	0.23 ± 0.06	318	0.37 ± 0.05	310
Nephew or niece on spouse uncle or aunt	−0.01 ± 0.06	241	−0.06 ± 0.07	247
Offspring on midparent	0.54 ± 0.07	254	0.82 ± 0.07	254
Correlations				
Monozygotic twins	0.68 ± 0.06	65	0.96 ± 0.03	60
Full siblings	0.24 ± 0.08	297	0.36 ± 0.08	296
Half-siblings	0.10 ± 0.12	318	0.17 ± 0.12	310
Father-mother	0.06 ± 0.10	102	0.05 ± 0.10	98

*The regressions and correlations for all genetic relationships differ significantly from zero; those for the two nongenetic relationships, the spouse correlation and the regression of nephew or niece on spouse uncle or aunt, do not. Sample sizes for most of the estimates are modest, however, and confidence intervals are quite large.

measure of cognitive ability except vocabulary has lower error variance (*8*). Block design correlates highly with the vocabulary and information subtests, yet in contrast to these verbal tests is but weakly correlated with education (*9*) and, perhaps as a consequence, is not influenced by assortative mating (*10*), again in contrast to the verbal scales.

To serve as a genetic guide for the analysis of block test scores, we have analyzed the fingerprint ridge counts of the study population. Total ridge count is a well-documented example of polygenic inheritance (*11*) that is largely unaffected by postnatal environmental influences, the number of ridges being fixed about the 12th week after conception.

The block test was administered to 550 members of 65 MZ twin kinships (*12*). The regression and correlation results for block design and total ridge count are summarized in Table 1 (*13*). For both traits, familial resemblance appears to be a direct function of shared genes. The parent-offspring regression is comparable in magnitude to that between twin uncle or aunt and nephew or niece (*14*) but in the absence of shared genes neither trait exhibits significant familial aggregation. There is no resemblance between spouse uncle or aunt and nephew or niece nor between husband and wife. Neither environmental covariance nor assortative mating appears to influence either trait.

The parallel pattern of results for block design and for ridge count provides evidence of significant genetic variation in nonverbal intelligence. We emphasize that the evidence is obtained from normal children reared in their natural homes by their biological parents, children who differ in no known way from the larger population to which we wish to draw inferences (*15*). Table 2 presents heritability estimates for both traits that can be derived from the data. The estimates show remarkably close agreement across the multiple genetic relationships contained within each kinship, but the reader is cautioned that they are not statistically independent.

Our analyses suggest that substantial variance in Block Design Test scores is genetic in origin (*16*). An equivalent conclusion, of course, is that substantial variance in those scores is attributable to nongenetic influences, and the twin-family methods which establish genetic variance can also identify systematic sources of environmental influence on nonverbal IQ. Our methodology enables us to assess uniquely one potential source of environmental variation, that of maternal effects. A nested analysis of variance of the offspring data permits a direct comparison of the relative similarity of maternal and paternal half-siblings. In this preliminary sample, we find no evidence of maternal effects in block design data, although such influences are present in verbal IQ scores (*17*). Independently, however, a prenatal environmental influence has been demonstrated by contrasting MZ twins classified into mono- and dichorionic placental types (*18*).

Table 2. Heritability estimates for Block Design Test scores and total ridge counts.*

Relationship	Estimated h^2	
	Block design scores	Total ridge count
Midparent-offspring	.54	.82
Parent-offspring	.56	.84
Twin uncle or aunt–nephew or niece	.46	.74
Full siblings	.48	.72
Half-siblings	.40	.68

*The ratio of additive genetic variance to total phenotypic variation defines the heritability, h^2. From the composition of phenotypic covariances, the regression or correlation of relatives can be expressed as estimates of h^2 (*19*). Interpretation of the estimates should take into account the imprecision of the coefficients on which they are based, the restricted range of variation in our sample, and the fact that possible effects of common environment and dominance variation have been ignored.

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References and Notes

1. S. V. S. Theis, *How Foster Children Turn Out* (State Charities Aid Association, New York, 1924).
2. H. J. Muller, *J. Hered.* **16**, 433 (1925).
3. L. J. Cronbach, *Am. Psychol.* **30**, 1 (1975); L. J. Kamin, *The Science and Politics of IQ* (Erlbaum, Potomac, Md., 1974); H. Munsinger, *Psychol. Bull.* **82**, 623 (1975); L. J. Kamin, *ibid.* **85**, 194 (1978); J. Shields, in *Progress in Clinical and Biological Research: Twin Research*, W. E. Nance, G. Allen, P. Parisi, Eds. (Liss, New York, 1978), p. 79.
4. W. E. Nance and L. A. Corey, *Genetics* **83**, 811 (1976); R. J. Rose, J. Z. Miller, M. Dumont-Driscoll, M. Evans, *Behav. Genet.* **9**, 71 (1979).
5. A serious problem with all published adoption studies is that no data on biological fathers of the adopted children are available. Consequently, the extent of assortative mating by the biological mothers is unknown. Significant assortative mating is likely present [R. Plomin, J. C. DeFries, M. K. Roberts, *Science* **196**, 449 (1977)], and estimates of genetic influence based on present adoption data may be inflated.
6. S. C. Kohs, *Intelligence Measurement: A Psychological and Statistical Study Based upon the Blocks-Design Tests* (Macmillan, New York, 1923).
7. U. Gault, *Aust. J. Psychol.* **6**, 85 (1954); J. Cohen, *J. Consult. Psychol.* **21**, 451 (1957); *ibid.* **23**, 285 (1959); A. J. Kaufman, *J. Consult. Clin. Psychol.* **43**, 135 (1973).
8. D. Wechsler, *Manual for the Wechsler Adult Intelligence Scale* (Psychological Corp., New York, 1955); *Manual for the Wechsler Intelligence Scale for Children—Revised* (Psychological Corp., New York, 1974); National Center for Health Statistics, *Intellectual Development of Youth as Measured by a Short Form of the Wechsler Intelligence Scale* (PHS Publ. 1000-Series 11-No. 129, Government Printing Office, Washington, D.C., 1973).
9. J. E. Birren, K. F. Riegel, D. E. Morrison, *J. Gerontol.* **16**, 363 (1961); D. Wechsler, *The Measurement and Appraisal of Adult Intelligence* (Williams & Wilkins, Baltimore, ed. 4, 1958).
10. T. Williams, *Behav. Genet.* **5**, 405 (1975).
11. S. B. Holt, *Br. Med. Bull.* **17**, 247 (1961).
12. There were 278 males and 272 females, of whom 130 were twin parents, 102 nontwin parents, and 318 offspring. The 232 parents ranged in age from 31 to 64 years [mean = 43; standard deviation (S.D.) = 8.9], their 318 offspring from 6 to 38 years (mean = 15.8; S.D. = 7.1). This is a volunteer, Caucasian sample. Some self-selection, expected in voluntary research, is evident in socioeconomic and educational characteristics of the participants. The IQ data exhibit elevated means and restricted variances: Wechsler scales are standardized on representative national samples with mean = 10 and S.D. = 3; Block Design Test scores of this sample have mean = 11.98 and S.D. = 2.78. Means and variances are homogenous for the twin and nontwin parents, for the children and adults, and for males and females.

   As part of a half-day protocol of medical and behavioral research, the subjects were tested individually by trained examiners, the same team of examiners being assigned to all members of each MZ kinship. Subjects aged 6 through 15 (189 offspring) were given the 1974 revision of the Wechsler Intelligence Scale for Children (WISC); subjects age 16 and over (129 offspring and all parents) were tested with the Wechsler Adult Intelligence Scale (WAIS). The block design subtests of the WISC and WAIS are quite comparable. In samples of 16- to 17-year-old youth, the intertest correlation of block design is as high as its retest reliability on either test alone and exceeds that of any other performance subtest [R. T. Ross and J. Morledge, *J. Consult. Psychol.* **31**, 331 (1967); M. Y. Quereshi and J. M. Miller, *J. Educ. Meas.* **7**, 105 (1970)].

Raw scores from the block design subtest were standardized according to norms in appendices in the Wechsler manuals (*8*) for 30 age-bands from ages 6 to 16 and 7 age-bands from ages 16 to 64.

Usable ridge count data were obtained from 522 members of 60 MZ kinships in the sample. All family members were genotyped with multiple blood markers to confirm monozygosity, for paternity exclusion, and for future linkage analyses.

13. The analysis employed here is identical with that previously reported for plasma cholesterol [J. C. Christian and K. W. Kang, *Am. J. Hum. Genet.* **20**, 462 (1977)]. Regression coefficients are used for their predictive value between generations, and correlation coefficients are used to measure relationships within the same generation. Regression coefficients are the preferred measure of parent-offspring resemblance, because they are less affected by range restriction, assortative mating, and variable sibship size [J. C. DeFries, R. C. Johnson, A. R. Kuse, G. E. McClearn, J. Polovina, S. G. Vandenberg, J. R. Wilson, *Behav. Genet.* **9**, 23 (1979)]. Regression and intraclass correlation coefficients were estimated by the pairwise method [B. Rosner, A. Donner, C. H. Hennekens, *Appl. Stat.* **26**, 179 (1977)]. The regression of offspring on midparent value is included in Table 1, since in the absence of common environmental variance it is a direct estimate of heritability [A. Vetta, *Soc. Biol.* **24**, 166 (1977); J. C. DeFries, G. C. Ashton, R. C. Johnson, A. R. Kuse, G. E. McClearn, M. P. Mi, M. N. Rashad, S. G. Vandenberg, J. R. Wilson, *Behav. Genet.* **8**, 281 (1978)].
14. Normative age-banding may not fully correct for the substantial age differences intrinsic to our measurement of adult-child resemblance. Inadequacies of age standardization and nonequivalence of the two tests would reduce adult-child resemblance relative to that of sibs and half-sibs who are more closely matched in age.
15. We assume that there exist no unique biases in the parental behavior or family structure of MZ twins or the experiences of their children. The assumption is untested, but plausible: personality characteristics of MZ twins cannot be distinguished from those of singletons [J. C. Loehlin and R. C. Nichols, *Heredity, Environment and Personality* (Univ. of Texas Press, Austin, (1976)], and the same is probably true of their parental behavior. The frequency of MZ twinning is equivalent across social and ethnic groups and is not known to be associated with any systematic factors.
16. This analysis is consistent with evidence from a recent adoption study in Minnesota [S. Scarr and R. A. Weinberg, in *Readings About Individual and Group Differences*, L. Willerman and R. G. Turner, Eds. (Freeman, San Francisco, 1979)].
17. R. J. Rose, paper presented at the Second International Congress on Twin Studies, Washington, D.C., 1977.
18. Chorion type is reported to influence similarity of full-scale IQ's in MZ twin children [M. Melnick, N. C. Myrianthopoulos, J. C. Christian, *Am. J. Hum. Genet.* **30**, 425 (1978)], and we are now studying block design performance in a sample of adult MZ co-twins whose placentation was documented at birth; preliminary results (R. J. Rose *et al.*, in preparation) suggest a significant effect of chorion type on within-pair variation.
19. The expected value of parent-offspring regression is $h^2/2$. To estimate heritability, the regression of offspring on single parent is doubled. Since the variance of midparent values is half the variance of individual parent values, the regression of offspring on midparent provides a direct estimate of h^2. If effects of dominance variation and common environments are ignored, the correlation of full siblings also estimates $h^2/2$, that of half siblings $h^2/4$. For details, see references cited in (*13*). The correlations of MZ twins provide upper limit estimates of heritability confounded by their closely shared environments; the estimates are .68 for blocks and .96 for ridge counts.
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The Cheetah: Native American

Abstract. *Two North American fossil species of large felids, hitherto regarded as Late Cenozoic pumas (mountain lion), are in fact closely related to the living cheetah,* Acinonyx, *of Africa and Eurasia. A new subgenus (*Miracinonyx*) is proposed for the American species. Cheetahs and pumas may have had a common ancestor in the Miocene of North America.*

Fossils of *Puma*-like cats are relatively common in the Late Cenozoic of North America (*1*). One species of supposed *Puma*, "*Felis*" *studeri*, from the Pliocene of the Texas panhandle, has long been recognized as distinct from *Puma concolor* because of morphological similarities with Old World cheetahs, but previous work has attributed the similarities to parallel evolution (*1, 2*). Excavations at the Late Pleistocene deposits of Natural Trap Cave, Wyoming (*3*), indicated that another species previously referred to *Puma*, "*Felis*" *trumani* (*4*), also possesses several characters of dentition, skull, and limb architecture that are remarkably "cheetah-like." Again, the similarities were attributed to parallelism, and "*F.*" *trumani* was styled as the "cheetah-like cat" (*3*). Continued excavations at the Wyoming site have yielded hundreds of bones of this felid (*5*), and more recent work (*6*) has revealed numerous shared derived characters that link "*F.*" *studeri* and "*F.*" *trumani* to Old World *Acinonyx*. Other work (*7*) has utilized multivariate comparison of upper and lower tooth rows to group the two American species; evolutionary affinities with Old World cheetahs were also suggested.

Except for size differences and several features which are interpreted as retained primitive characters, the fossils of "*F.*" *studeri* and "*F.*" *trumani* are almost identical with Old World *Acinonyx* species (*6*). The points of similarity are so extensive and of such a complex nature that a hypothesis attributing their origin to other than common genetic descent would require pushing the concept of parallel evolution to an unprecedented extreme.

The systematic paleontology follows:

Family: Felidae
Genus: *Acinonyx*
Miracinonyx subgen. nov.

Derivation of name. From Latin "mirus": surprising, amazing; and *Acinonyx*: Old World cheetah.

Diagnosis. Distinguished from *Puma* and other medium-sized felids by elongation of distal limbs (radius-ulna, tibia-fibula, calcaneum, metapodials); braincase short and expanded; postorbital constriction wide; frontals broad and flat; internal nares enlarged; orbital shelf (zygomatic process of maxilla) short; skull highly arched; coronoid process of ramus weak, slopes noticeably posterior; canines weak; short mandibular diastema; protocone reduced or absent; auditory bulla elongate and flattened anteriorly. The latter character distinguishes *Miracinonyx* from Old World cheetahs (*8*). *Acinonyx studeri* may be distinguished from *A. trumani* by greater overall skull size and elongate, widely spaced occipital condyles (*2*). Old World cheetahs (subgenus *Acinonyx*) are distinguished from the subgenus *Miracinonyx* by a prominent anterior or anterolingual cusp on P^3, inflation of frontal sinus and auditory bullae, and greater development of the medial anteroposterior ridge of the basioccipital.

Geographic distribution. Western United States: Texas (*2*), Nevada (*4*), Wyoming (*3*).

Temporal distribution. Middle Blancan to Late Pleistocene.

Type species. Acinonyx (Miracinonyx) trumani (Orr, 1969) (*4*).

Included species. Type species and *Acinonyx (Miracinonyx) studeri* (Savage, 1960) (*2*).

Description. The skull of *Miracinonyx* is highly arched, with the facial and cranial regions sloping anteriorly and posteriorly from the interorbital area of the frontals. Shortening of the facial region and enlargement of the P^3 have reduced the upper diastema and crowded the P^2 tightly between the P^3 and canine. Both upper and lower canines are reduced, the lower premolars are relatively narrow, and the protocone of the upper carnassial is greatly reduced or absent. The zygomatic process of the maxilla, which in *Puma* forms a distinct shelf in the orbit floor, is reduced. Shortening of the cranial region of the skull gives a bulging appearance to the braincase; the anterior portion of the zygomatic arch is shortened, and the postorbital constriction is widened. The frontals are greatly widened and flat, with the orbits set far apart and high on the face. The postorbital process of the frontals is distinct and of a sharp angular shape; because of frontal sinus inflation the postorbital processes of Old World *Acinonyx* appear more rounded. Dorsally, the skull of *Acinonyx* is readily distinguishable from *Puma*, which has a prominent postorbital con-

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