Genetic specificity of face recognition

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Specific cognitive abilities in diverse domains are typically found to be highly heritable and substantially correlated with general cognitive ability (g), both phenotypically and genetically. Recent twin studies have found the ability to memorize and recognize faces to be an exception, being similarly heritable but phenotypically substantially uncorrelated both with g and with general object recognition. However, the genetic relationships between face recognition and other abilities (the extent to which they share a common genetic etiology) cannot be determined from phenotypic associations. In this, to our knowledge, first study of the genetic associations between face recognition and other domains, 2,000 18- and 19-year-old United Kingdom twins completed tests assessing their face recognition, object recognition, and general cognitive abilities. Results confirmed the substantial heritability of face recognition (61%), and multivariate genetic analyses found that most of this genetic influence is unique and not shared with other cognitive abilities.

face perception | behavioral genetics | cognitive psychology | twin study

Specific cognitive abilities correlate substantially with general cognitive ability (g). This finding holds true for domains as diverse as literacy (1), spatial reasoning (2), mathematical ability (3), and visual and verbal memory (4). In addition, these diverse specific abilities, and g itself, are typically found to be substantially heritable (5). Genetic correlations between abilities (i.e., the degree to which genetic influences are correlated between them, indicating pleiotropy: common genes influencing multiple traits) tend to be at least as strong as their phenotypic associations (the correlations between task scores or other behavioral measures) (6), and g typically accounts for almost all of the genetic variance in each domain (7). Even though the nature of g itself remains unclear, these phenotypic and genetic intercorrelations among diverse abilities suggest that cognitive domains form a single hierarchy (8). At the apex of this hierarchy is g, explaining on average 40% of the total phenotypic variance in each domain (9) and—via pleiotropic "generalist genes" (10)—almost all of their genetic variance.

Two recent twin studies have suggested that face recognition, the ability to memorize and recognize human faces, may represent an exception to this model. Faces have long been argued to be "special" as a category of visual stimulus, showing both cortical specificity (11) and a wide range of face-specific perceptual effects (12). Whether such effects suggest true domain specificity or merely reflect a highly specialized form of learned expertise (acquired almost universally among typically developing children) has long been the subject of debate (13), with proponents of the former suggesting evolutionary specificity for face recognition (14). In this context, the findings of two recent twin studies (15, 16) are informative. Individual differences in face recognition were found to be substantially heritable: 68% in one study (15) and 39% in the other (16)—the difference perhaps reflecting the different tasks used, or perhaps insufficient power to establish precise point estimates due to the modest sample sizes of these studies (289 and 173 twin pairs, respectively). The ability was also found to be phenotypically largely unrelated either to visual or verbal memory (15) or to g (16).

These findings seem consistent with the argument for evolutionary—and thus genetic—specificity (13), although it should be

noted that the etiology of within-species variation may be unrelated to the evolutionary origins of a trait. However, a low phenotypic correlation between two traits does not inevitably indicate the absence of common genetic influences. Their genetic correlation may be high (even at unity, in principle) when their phenotypic correlation is low, if the heritability of either trait is relatively low (9). Even two highly heritable but phenotypically largely uncorrelated traits could still have a substantial genetic correlation if, for example, a negative environmental correlation counterbalanced a positive genetic correlation. For example, if environmental factors positively influencing the ability to recognize nonface objects (e.g., by promoting interest in activities that provide relevant practice) also tended to have a negative influence on face recognition ability (e.g., by reducing social interaction or attention), then this negative environmental correlation would offset the positive genetic correlation between these traits and confound the interpretation of any study unable to examine their genetic relationship directly.

Unambiguously establishing the architecture of genetic influences on multiple traits is the purpose of multivariate genetic analyses, which have not been reported by any study conducted in this field to date, presumably due to the large samples required for adequate power. The present study administered tests assessing face recognition, general (nonface) object recognition, and g to a large sample of twins to examine directly the degree to which face recognition is genetically distinct from other perceptual and cognitive abilities.

Results

Data. The Twins Early Development Study (TEDS) is a longitudinal cohort study of twins born in England and Wales between 1994 and 1996, with more than 10,000 pairs still enrolled. The recruitment and characteristics of this sample have been described previously (17, 18). Zygosity was assessed at enrollment using a

Significance

Diverse cognitive abilities have typically been found to intercorrelate highly and to be strongly influenced by genetics. Recent twin studies have suggested that the ability to recognize human faces is an exception: it is similarly highly heritable, but largely uncorrelated with other abilities. However, assessing genetic relationships—the degree to which traits are influenced by the same genes—requires very large samples, which have not previously been available. This study, using data from more than 2,000 twins, shows for the first time, to our knowledge, that the genetic influences on face recognition are almost entirely unique. This finding provides strong support for the view that face recognition is "special" and may ultimately illuminate the nature of cognitive abilities in general.

parental questionnaire shown to be more than 95% accurate compared with direct genetic testing (19), with DNA testing conducted where results were unclear. For the present study, a representative subsample was selected from the oldest twins in this cohort (who had passed the age of majority, 18 years of age), and data were obtained from 2,149 participants—924 complete pairs [375 monozygotic (MZ), 549 dizygotic (DZ)]—plus an additional 301 unpaired individuals. Individuals with severe physical or psychological disabilities, or whose mothers had experienced serious medical complications during pregnancy, were excluded. The resulting dataset was 58% female, with a mean age of 19.5 years of age ($\pm$0.3 SD) on completion of the face and object recognition tests.

Face recognition ability was assessed with the widely used Cambridge Face Memory Test (CFMT) (20), requiring participants to memorize a series of unfamiliar faces, from images cropped to exclude cues such as hair and clothing, and then to identify them among distractors in a variety of viewpoints and lighting conditions. General (nonface) object recognition ability was measured using the Cambridge Car Memory Test (CCMT) (21), designed to be matched precisely to the CFMT but using

computer-generated 3D models of cars instead of faces. See Fig. 1 for sample stimuli for both tests. General cognitive ability (g) was assessed during an earlier testing phase for this cohort at age 16, as a verbal/nonverbal composite: the mean of standardized scores from the Mill Hill Vocabulary Scale (22) and Raven's Progressive Matrices (23). See *Methods* for more details on these measures.

Sample sizes and descriptive statistics for these measures are presented in Table 1. The distributions demonstrate a large amount of variability in the sample for these abilities, with face and nonface recognition scores ranging from chance to (in very rare cases) perfect scores, and do not differ significantly from those obtained with the original reference samples (20, 21) for these tests. The face and object recognition tasks were newly administered to the TEDS sample, so care was taken to ensure their reliability. Cronbach's alpha was high for both measures: 0.893 for the CFMT, 0.875 for the CCMT (see *SI Appendix*, Table S1 for more details).

An analysis of variance was performed for each measure to assess the mean effects of sex and zygosity. The only significant mean difference found was a main effect of sex on object

Fig. 1. Sample stimuli. Sample images for the Cambridge Face Memory Test (20), for both the clean (*A*) and degraded (*B*) conditions (see *Methods*), and for the Cambridge Car Memory Test (21), both clean (*C*) and degraded (*D*).

Table 1. Descriptive statistics

	n	Whole sample	Males	Females	MZ	DZss	DZos	Sex	Zyg	Sex × zyg	R^2
Face recognition	1,068	54.10 (9.44)	53.45 (9.62)	54.54 (9.30)	54.04 (9.28)	54.14 (9.55)	54.30 (9.52)	2.78	0.20	0.07	0.00
Object recognition	1,042	50.54 (9.75)	53.84 (10.05)	48.33 (8.90)	50.10 (9.95)	50.81 (9.62)	51.68 (9.52)	85.61**	0.09	1.64	0.07
g	758	0.05 (0.97)	0.08 (1.02)	0.03 (0.93)	−0.03 (0.98)	0.10 (0.95)	0.24 (0.94)	0.39	3.42	0.02	0.01

Mean scores (SDs) for the whole sample, separately by sex, and for monozygotic (MZ) and same-sex (ss) and opposite-sex (os) dizygotic (DZ) twins. n = sample size (sample shown is fully independent, randomly selecting one individual per twin pair). ANOVA was performed on cleaned, normality-transformed data to test effects of sex and zygosity. Results = F statistic. **$P < 0.001$. R^2 = proportion of variance explained by sex, zygosity (Zyg), and their interaction.

recognition (Table 1), explaining 7% of the variance, perhaps relating (as argued by the test's authors) (21) to differential average interest in or experience with cars. Twin analyses are concerned with variances, so a mean sex difference is irrelevant provided (as in our results) the distribution is not restricted. In any case, per standard practice for twin studies (*Methods*), the mean effects of sex were regressed out. All subsequent analyses were conducted using sex- and age-regressed, normality-transformed, standardized data.

Phenotypic Analyses. Phenotypic analyses were conducted using a fully independent sample, randomly selecting one twin per pair. Face recognition ability was moderately correlated with nonface object recognition [$r = 0.29$, 95% confidence interval (CI) 0.23–0.34, $P < 0.001$, $n = 1,042$], and modestly with g ($r = 0.16$, CI 0.09–0.23, $P < 0.001$, $n = 718$). Nonface object recognition and g were similarly modestly correlated ($r = 0.15$, 95% CI 0.08–0.22, $P < 0.001$, $n = 706$). The phenotypic relationship between face recognition and g largely survived controlling for general object recognition (partial correlation, $r = 0.12$, $P < 0.001$, $n = 706$). Similarly, much of the association between face recognition and general object recognition was independent of g (partial correlation, $r = 0.25$, $P < 0.001$, $n = 706$). The smaller samples for those analyses involving g reflect the intersection between the datasets produced at the two testing phases.

Taken together, these results indicate that face recognition is largely, but not wholly, phenotypically independent both from general cognitive ability and from general object recognition. The significant partial correlations suggest that the associations between face recognition and each of these other two measures are largely independent from one another.

Univariate Genetic Analyses. Intraclass twin correlations for monozygotic (MZ) and same- and opposite-sex dizygotic (DZ) twins are presented in Table 2. MZ correlations are consistently significantly higher than those for DZ twins, suggesting genetic influence. From these intraclass correlations, initial estimates may be obtained for heritability (additive genetic influences on the trait), shared environmental influences (environmental factors making twins more similar), and unique (nonshared) environmental influences (the remaining variance, including influences making twins dissimilar, and also any error of measurement)—see

Table 2 for calculation details. These estimates (Table 2) suggest that genetic influence is substantial for all measures.

These initial estimates were tested formally with full-information maximum-likelihood model fitting (accounting for missing data, and using the full dataset including both same-sex and opposite-sex DZ twins) to estimate the variance attributable to additive genetic (A), shared environmental (C), and unique environmental/error (E) components (*Methods*). The results (Fig. 2) confirm substantial genetic influence for all three measures, with heritability estimated at 61% for face recognition, 56% for object recognition, and 48% for g, very similar to the rough estimates (Table 2). Also (similar to the estimates in Table 2), almost no shared environmental influences were detected (i.e., environmental influence was apportioned to E, representing nonshared influences and error of measurement, rather than C). Precise estimates and confidence intervals are presented in *SI Appendix*, Table S2, and fit statistics (*Methods*) in *SI Appendix*, Table S3.

Multivariate Genetic Analyses. The main focus of this study was to examine the genetic relationships between face recognition and other abilities, as indexed by g and general object recognition. This aim may be achieved with twin data using bi- and multivariate model-fitting analyses (*Methods*). Two bivariate correlated factors solution models indicate the genetic, shared, and unique environmental correlations between the traits and (derived from these results) the proportions of the phenotypic correlations (between face recognition and each other variable) attributable to each component (Fig. 3 and *SI Appendix*, Table S4). These phenotypic correlations are substantially genetic in origin: 66% of the correlation with general object recognition and 88% of the correlation with g, the latter being the only component of the correlation with g whose estimate is significant.

However, as the phenotypic correlations are modest, the proportion of the total variance of face recognition ability included in these results is low. However, the genetic correlations with face recognition, which are independent of the phenotypic correlations and heritabilities, are also low (0.31 with object recognition, 0.32 with g; see *SI Appendix*, Table S4), indicating substantial genetic independence. Bivariate Cholesky decomposition analyses (*Methods*) provide another way to quantify these relationships: These analyses indicate the proportion of the heritability of a trait that is due to genetic effects shared with another trait. These analyses

Table 2. Twin correlations and approximated variance components

	Intrapair twin correlations			Variance component estimates			Sample (nos. of pairs)		
	MZ	DZss	DZos	h^2	c^2	e^2	MZ	DZss	DZos
Face recognition	0.60 (0.54–0.66)	0.30 (0.19–0.40)	0.17 (0.05–0.28)	0.60	0.00	0.40	374	289	256
Object recognition	0.58 (0.50–0.64)	0.15 (0.03–0.26)	0.30 (0.18–0.41)	0.58	0.00	0.42	358	276	244
g	0.58 (0.49–0.65)	0.37 (0.25–0.48)	0.28 (0.14–0.42)	0.42	0.16	0.42	285	226	170

Intraclass twin correlations (95% confidence intervals) for monozygotic (MZ) and same-sex (ss) and opposite-sex (os) dizygotic (DZ) twins. Variance component estimates are heritability (h^2, double the difference between the MZ and DZss correlations, constrained not to exceed the former—MZ twins are genetically identical, so heritability cannot exceed their correlation), shared environment (c^2, the MZ correlation minus h^2), and unique environment/error of measurement ($e^2 = 1 - h^2 - c^2$). Sample sizes shown are complete pairs, after exclusions and data cleaning.

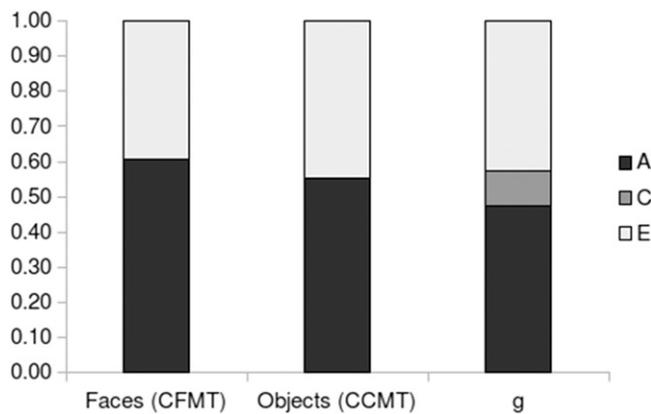PSYCHOLOGICAL AND COGNITIVE SCIENCES

Fig. 2. Model-fitting estimates. Variance due to additive genetic (A), shared environmental (C), and nonshared environmental influences/error (E).

(Fig. 4A and *SI Appendix*, Table S5) show that the genetic effects constituting the heritability of face recognition are largely specific to this trait (~90%), rather than shared either with general object recognition or with *g*. That is, only 10% of the heritability of face recognition, representing 6% of its total variance, is due to genetic effects shared with object recognition. Similarly, 10% of the heritability of face recognition (6% of total variance) is due to genetic effects shared with *g*. Path estimates for these model-fitting analyses are presented in *SI Appendix*, Fig. S1.

However, subjecting the object recognition measure to the same analysis (bivariate Cholesky decomposition, predicted by *g*) reveals a similar pattern to that observed with face recognition. Shared genetic influences between *g* and object recognition account for only 10% of the heritability of the latter (6% of total variance), perhaps suggesting that this *g* composite undercorrects for domain-general processes involved in the face and object recognition tasks (*Discussion*). Details are presented in *SI Appendix*, Table S6 (with fit statistics for all bivariate models in *SI Appendix*, Table S7).

Separate bivariate analyses cannot determine the proportion of influences that might be common to multiple predictor variables. Multivariate extension of the Cholesky decomposition allows the shared and independent components of variance to be estimated sequentially for multiple predictors. Details, fit statistics, and path estimates are presented in *SI Appendix*, Tables S8 and S9 and Fig. S2, respectively, but the main finding (Fig. 4B) is that only 11% of the heritability of face recognition (representing 6% of the total variance in this trait) is accounted for by genetic influences shared both with *g* and with general object recognition. Although the point estimate suggests that an additional 5% of its heritability (3% of total variance) is explained by genetic influences shared only with object recognition, independently from *g*, this estimate is nonsignificant—indicated both by the confidence interval of this estimate intersecting zero (*SI Appendix*, Table S8) and a submodel with this path constrained to zero resulting in no significant deterioration in fit (*Methods* and *SI Appendix*, Table S9). This result suggests that all of the genetic influences shared between face and object recognition are also shared with *g*. However, the large majority of the heritability of face recognition (85% in this model, representing 51% of its total variance) is due to genetic effects that are not shared with either of these other measures.

Since the *g* composite used here is the mean of two standardized test scores (see *Methods*), a more complete multivariate model would incorporate the two scores individually, ensuring that all of the shared variance between these measures is included. An additional model therefore entered the Mill Hill, Raven's, and object recognition scores independently. In this model, the first entered variable (Mill Hill) accounted for 8% of the heritability of face recognition (5% of its total variance). Raven's and object recognition

accounted for no significant additional genetic variance, and again the large majority is unique. Details, fit statistics, and path estimates are provided in *SI Appendix*, Tables S10 and S11 and Fig. S3, respectively.

Race. The "other race" effect, meaning significantly decreased recognition accuracy for faces of less familiar races, has been demonstrated with the CFMT (24). Because the stimuli used here were Caucasian faces, the key analyses were repeated with the sample restricted to Caucasian participants (93% of the sample). The results were virtually identical to those obtained with the full sample, both in test performance (*SI Appendix*, Table S12) and the genetic independence of face perception from other measures (*SI Appendix*, Tables S13 and S14).

Discussion

We show for the first time, to our knowledge, that the substantial heritability of face recognition is due to genetic influences that are mostly specific to this ability, rather than shared either with general object recognition or general intelligence. The phenotypic and univariate genetic analyses broadly supported the findings of the two previous twin studies in this area (15, 16): Face recognition was phenotypically correlated only quite modestly with general object recognition (0.29) and very modestly with *g* (0.16), as indexed by these measures. The substantial heritability of face recognition (61%) is also in line with previous literature. However, one of the main strengths of quantitative genetic methods is their ability to establish the genetic architecture surrounding multiple traits (25). Thus, the main purpose of data collection on this scale from a twin sample was to provide the opportunity to conduct multivariate genetic analyses.

The results of these analyses indicate, first, that face recognition is not wholly distinct genetically either from general object recognition or from *g* and that its phenotypic correlations with each are largely due to shared genetic influences (Fig. 3). It seems that face recognition, as measured here, does after all fall within the traditional cognitive hierarchy to some degree—this result is perhaps unsurprising because the CFMT measure necessarily involves memory, attention, and other cognitive capacities. Most of the substantial heritability of face recognition, however, is due to genetic influences that are not shared either with general object recognition or with *g* (Fig. 4). Since *g* usually accounts for a large proportion of the genetic variance within any specific cognitive domain (7, 10), this finding offers support for the special nature of faces.

However, the CCMT object recognition measure shows similar results: It is genetically largely independent from *g* (*SI Appendix*, Table S6). At first glance, this observation would seem to undermine the argument that face recognition is special, but another
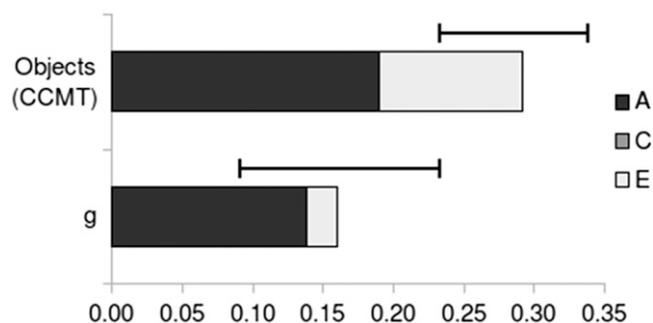

Fig. 3. Decomposition of phenotypic correlations with face recognition. Correlated factor solution analyses, indicating the proportion of the phenotypic correlation between face recognition and each other variable (line length, with 95% confidence intervals) attributable to genetic (A), shared environmental (C), and nonshared environmental influences/error (E).
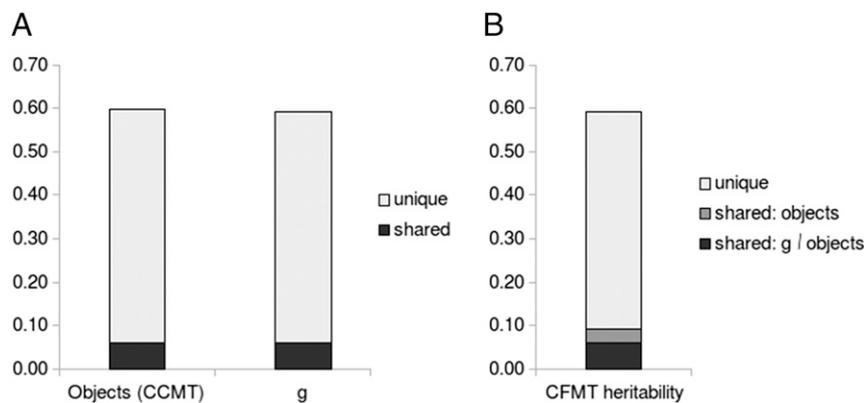
Fig. 4. Decomposition of heritability of face recognition. Cholesky bivariate (*A*) and trivariate (*B*) decomposition analyses, indicating that genetic influences on face recognition ability are largely independent from the genetic influences on general object recognition and *g*.

possible explanation is that the *g* composite used substantially undercorrects for domain-general processes: For example, neither of the component scores in this composite recruit memory. To evaluate this argument, the CCMT measure is the perfect control: The attentional, memory, and other requirements of these tasks are identical, and yet the genetic influences on face recognition, accounting for the majority of its total variance, are almost entirely independent from this measure, too. The multivariate models including both the *g* measure (whether as a composite or its components) and the CCMT show the same pattern: Face perception is almost entirely genetically distinct from both.

An alternative explanation for the CCMT results, of course, is that general object recognition is genuinely genetically dissociable from *g* to the same extent as face recognition. Although there is no reason from the literature to suspect that general object recognition may be special in this way (unlike the case for face recognition), the possibility merits further study, using both additional object recognition measures and also a broader *g* composite including memory performance. Even if it were true, however, the present findings would still be striking: Face recognition is genetically independent both from general object recognition and from all of the general cognitive abilities and processes captured both by this perfectly-matched task and by the *g* composite itself.

Quantitative genetic methods can estimate pleiotropic influences among traits—that is, the degree to which common genes influence multiple traits and drive the observable associations between them—even where the specific genes involved have not yet been identified (25). Among other things, calculating the genetic correlations between traits thus supports both the search for the genes themselves (by predicting the patterns of traits with which they are likely to be associated) and also theorizing about their possible mechanisms and modes of action. Caution is warranted, however: The shared and unique genetic influences on face recognition could reflect the genetic etiology of domain-general and domain-specific cortical development, for example, but equally they could represent influences detectable only as higher level aspects of cognition, behavior, or personality. In any case, our results indicating that face recognition is largely genetically distinct from other cognitive and perceptual domains suggest that identifying genes associated with domain-general cognitive processes (or indeed general cortical development) will be of limited use in understanding face recognition.

It should be emphasized that these results do not rule out the "expertise" hypothesis of face recognition: In principle, the unique genetic influences identified could be unique to the skilled recognition of very highly familiar (i.e., learned from an early age) categories of objects, rather than to faces specifically. Equally, nor do they confirm that those apparently unique influences truly affect

faces alone because it remains possible that they may be shared with abilities or traits not captured adequately by the object recognition or *g* measures used. One possibility in the latter direction is suggested by the various attempts to conceive a broad domain of "social intelligence" (26, 27): Perhaps socially relevant abilities other than face recognition, such as emotion recognition or theory of mind, may be found to share some or all of its genetic etiology.

The very fact that *g* correlates with diverse specific cognitive abilities by only 0.4 on average (9) means that much, and usually most, of the variance in each domain is specific rather than general: All domains are special in this sense. The genetic near-independence of face recognition both from *g* (in contrast to the usual rule) and from a perfectly matched task of general object recognition is striking, however, and lends weight to the view that this ability is more special than most.

Methods

Measures. The Cambridge Face Memory Test (CFMT) (20) instructs participants to memorize six male Caucasian faces, each from three images showing the face in different orientations. Images show the faces with neutral expressions, edited to remove any distinguishing facial blemishes and cropped to remove hair and clothing. Test stimuli present a target face alongside two distractors, and participants make keyboard responses to identify the target. Trials fall into three distinct phases, the first following immediately after the memorization of each face (three trials for each, identifying that face among distractors), the second being a series of 30 trials in which the target can be any of the six memorized faces, and the third a series of 24 trials (again with any target) using impoverished images degraded with Gaussian noise. Correct responses are summed to give a total score out of 72.

The Cambridge Car Memory Test (CCMT) (21), a nonsocial object recognition task, was developed as a matched companion task to the CFMT. The stimuli are computer-generated 3D images of cars, viewed in various orientations. The cars depicted are loosely modeled on contemporary real-world designs, but altered so as not to be identifiable as real cars with which participants may be familiar. The procedure for memorization, testing and scoring is identical to that for the CFMT.

The general cognitive ability (*g*) composite used in this study is the mean of participants' standardized scores on two measures. The first, assessing verbal cognitive ability, is the Mill Hill Vocabulary Scale (22), a multiple-choice test of vocabulary: In each of 33 trials, a target word is presented, and participants select (by clicking on screen) which of six options is closest to it in meaning; correct responses are summed. Nonverbal cognitive ability was assessed using Raven's Progressive Matrices (23): Participants are shown an incomplete pattern and asked each time to select which of eight options completes it; correct responses are summed across 30 trials. Although these measures were administered 3 years earlier than the CFMT and CCMT, this gap is highly unlikely to have influenced the results because the genetic influences on *g* have been found to be highly stable over considerably longer periods (28, 29).

Ethical approval was granted by the relevant ethics committee (Psychiatry, Nursing & Midwifery, at King's College London), and informed consent was obtained. TEDS participants were contacted by post but completed all

measures online via websites developed for the purpose. The *g* battery (administered at age 16) was developed using the Flash browser plugin, and the CFMT and CCMT (administered separately; see *Results, Data*) were developed in Javascript, using the open-source "psy.js" library (https://www.forepsyte.com/resources/public/psy-1.56.js).

Twin Data. Twin studies analyze the intrapair concordances or correlations between monozygotic (MZ) and dizygotic (DZ) twins (9). MZ twins share all their genes whereas DZ twins share (on average) only half of their segregating genes; both share their environments to approximately the same extent. The degree to which the MZ is higher than the DZ correlation thus indicates the degree of genetic influence on a trait, and cross-twin cross-trait correlations allow genetic covariance between traits to be quantified. The twin method relies upon certain assumptions (such as the assumption that MZ and DZ twins share their environments to approximately the same degree), but these assumptions have been widely tested, and other study designs with different assumptions typically replicate results.

Twins are perfectly correlated for age, and MZ and half of DZ twins also for sex. Any effects of age or sex on a trait would thus distort the "true" intrapair correlations and inflate the apparent role of shared environmental influences (30). For this reason, standard practice for twin data is to analyze residuals corrected for any mean effects of age and sex. (This practice does not preclude sex differences being analyzed where appropriate because twin analyses are concerned with variances, which are unaffected by correcting for mean differences.) In addition, for the present data, outliers were removed for each measure beyond three SDs from the mean, random responders were removed (defined as participants with infeasibly low median item response times, under 1.5 SDs below the sample mean), and the dataset was normalized with a van der Waerden transformation (accounting for a slight negative skew present in the raw CFMT and CCMT data).

Model Fitting. Twin analyses were conducted using model-fitting procedures, allowing point estimates and confidence intervals to be established for the variance component estimates, and the goodness of fit of the model to the data to be tested (31). This test may be achieved by comparing the fit statistics of the model to a fully saturated model in which all parameters are allowed to vary, and no particular structure is imposed on the data—if the fit of the constrained model is not significantly worse than that of the saturated model, it may be considered a good fit. A series of maximum-likelihood nested models were applied and fitted to the data (32), based upon the expected genetic and environmental correlations (additive genetic influences correlating 1.0 for MZ twins and 0.5 for DZ twins, and shared environmental influences 1.0 for both). Additive genetic (A), shared environmental (C), and unique environmental (E) influences were estimated, and nested submodels tested which components were required. Any error of measurement was included in the E estimate, deflating A and C equally. All model-fitting was conducted in R, using the structural equation program OpenMx (33).

Multivariate model fitting, based upon cross-twin cross-trait correlations, decomposed phenotypic covariance between traits into genetic and environmental components of covariance. Two algebraically equivalent models with different analytic foci (34) were analyzed in this study. First, a "correlated factors" solution permitted the common A, C, and E influences underpinning multiple traits to be estimated, and thus the phenotypic correlation between them to be decomposed into these components of covariance (as in *SI Appendix*, Table S4). Second, in a manner analogous to a phenotypic stepwise multiple regression, Cholesky decomposition permitted the ACE influences shared between two or more traits to be determined sequentially, estimating at each step the proportion of the A, C, and E components shared with, and independent from, each variable. Thus, in *SI Appendix*, Fig. S1, showing the structure of additive genetic influences (A), path estimates indicate the proportion of genetic influences common to both the predictor variable and to face recognition, and the proportion unique to the latter. *SI Appendix*, Fig. S2 illustrates a trivariate extension, showing the genetic influences common to all three variables (*g*, object recognition, and face recognition), then the influences common to object recognition and face recognition (but not to *g*), then finally the residual influences unique to face recognition. Further extensions may likewise include additional variables (as in *SI Appendix*, Fig. S3).

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