Please cite this article in press as: Zhu et al., Heritability of the Specific Cognitive Ability of Face Perception, Current Biology (2009), doi:10.1016/j.cub.2009.11.067

Current Biology *20*, 1–6, January 26, 2010 ©2010 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2009.11.067

Report

Heritability of the Specific Cognitive Ability of Face Perception

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Summary

What makes one person socially insightful but mathematically challenged, and another musically gifted yet devoid of a sense of direction? Individual differences in general cognitive ability are thought to be mediated by "generalist genes" that affect many cognitive abilities similarly without specific genetic influences on particular cognitive abilities [1]. In contrast, we present here evidence for cognitive "specialist genes": monozygotic twins are more similar than dizygotic twins in the specific cognitive ability of face perception. Each of three measures of face-specific processing was heritable, i.e., more correlated in monozygotic than dizygotic twins: face-specific recognition ability, the face-inversion effect [2], and the composite-face effect [3]. Crucially, this effect is due to the heritability of face processing in particular, not to a more general aspect of cognition such as IQ or global attention. Thus, individual differences in at least one specific mental talent are independently heritable. This finding raises the question of what other specific cognitive abilities are independently heritable and may elucidate the mechanisms by which heritable disorders like dyslexia and autism can have highly uneven cognitive profiles in which some mental processes can be selectively impaired while others remain unaffected or even selectively enhanced.

Results and Discussion

To isolate face-specific processing, unconfounded from more general cognitive functions such as attention and decision making, we devised three behavioral measures, each of which contrasts face processing with processing of a matched non-face stimulus. These difference measures were chosen as phenotypic variables because absolute measures of accuracy on face perception tasks are likely to dilute the cognitive process of interest (i.e., face-specific perceptual processing) with other domain-general processes (e.g., low-level vision, attention, decision making, etc.), whereas in the difference measures the domain-general functions are subtracted out. One hundred and seventy-three twin pairs (102 monozygotic [MZ] and 71 dizygotic [DZ], age 7–19) were tested on these three measures of face-specific processing (Table 1). Because MZ twins share 100% of their genes and DZ twins share 50%, if genes account for the variation between individuals in face recognition ability then MZ twins should be more similar to each other on these measures than DZ twins.

First, each twin performed an immediate old/new recognition memory task on faces or houses (Figure 1A); our measure of face-specific recognition ability (FRA) was the difference in accuracy between face and house recognition (see Experimental Procedures). Intraclass correlation analysis showed that FRA was significantly more similar in MZ twins than in DZ twins (Fisher's z test, two-tailed, $z = 2.17$, $p < 0.05$), indicating significant heritability of face-specific recognition (Table 2). Standard maximum-likelihood model-fitting analyses were performed to estimate heritability, i.e., the proportion of total phenotypic variance attributable to genetic variance [4]. Heritability of FRA was 38.9% (95% confidence intervals: 20.1% to 54.2%) (estimated by an ADE model that is a genetic model for twin studies including dominance genetic effects, chi-square goodness-of-fit test, $\chi^2(4) = 2.29$, $p = 0.68$) (Figure 2A). The genetic influence specific to recognizing faces was not due to a larger number of MZ twins or to the inclusion of opposite-sex DZ twins in the DZ group, because correlations were nearly identical when the number of twin pairs was matched, and opposite-sex DZ twins were excluded (see Figure S1 available online).

The heritability of face-specific recognition suggests that it is face recognition in particular that is heritable, not some more-general aspect of visual information processing. However, face and house stimuli differ in many respects, any of which could underlie the difference in heritability. Therefore, we next revisited the question of face specificity using a classic set of control stimuli that share virtually all visual properties of faces yet are not processed as faces [2, 5]: inverted faces. Specifically, we measured the heritability of the face-inversion effect (FIE), that is, the difference in perceptual discrimination performance (on a successive same-different matching task) on upright versus inverted faces. The FIE was significantly more correlated between MZ than DZ twins ($z = 2.17$, $p < 0.05$) (Figure 1B). Heritability was estimated at 24.8% (5.9% to 41.6%) for the FIE ($\chi^2(4) = 2.17$, $p = 0.70$) (Figure 2A). Thus, it is not low-level visual processing but rather the mental processes specifically engaged during face perception that are heritable.

What exactly are those face-specific processes? Extensive behavioral and neural investigations have shown that the key difference in the way that faces are processed, compared to other stimuli, is that faces are represented as integrated wholes, rather than as sets of independent components. The classic test of holistic face perception is the composite-face effect (CFE), in which subjects find it harder to identify one half of a combination face (e.g., the top half of George Bush with the bottom half of Tony Blair; see Figure 1C) if the inconsistent other half-face is aligned with the target half rather than if it is misaligned [3]. (Another measure is the whole-part effect [6]; see Figure S2.) Using a perceptual version of the composite-face test (same-different matching on successively presented composite faces), we found a significantly greater correlation in the CFE for MZ than DZ twins ($z = 2.72$,

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Table 1. Means, Standard Deviations, and Correlations with Age and Gender for Each of the Component Tests

Cognitive Test	Mean (SD)	Correlation	
		Age	Gender
1. Old/new			
Face	0.73 (0.10)	0.32**	0.15*
House	0.79 (0.10)	0.19**	0.06
FRA	−0.04 (0.08)**	0.13	0.08
2. Face inversion			
Upright	0.83 (0.09)	0.31**	0.14
Inverted	0.68 (0.10)	0.31**	0.20**
FIE	0.10 (0.07)**	−0.06	−0.10
3. Composite face			
Align	0.67 (0.12)	0.46**	0.10
Misalign	0.70 (0.12)	0.47**	0.11
CFE	0.11 (0.14)**	−0.20**	−0.02
4. Global-local			
Consistent	0.45 (0.15)	−0.52**	−0.05
Inconsistent	0.49 (0.16)	−0.53**	−0.08
GLI	0.02 (0.05)**	−0.10	0.05

The test battery included the old/new recognition task, where the difference in accuracy between face and house recognition served as the phenotypic variance of FRA. Other tests were selected to sample across diverse specific face recognition ability types, including FIE ($t(343) = 29.01$, $p < 0.001$), CFE ($F(1,340) = 239.03$, $p < 0.001$), and GLI ($F(1,338) = 26.84$, $p < 0.001$). The means and standard deviations indicate a wide range of variability for each of the tests, consistent with previous observation [42–44], and the split-half reliability analysis shows that our tests are quite reliable (Table S1). For the raw scores of all tests, all correlations with age were significant (p values < 0.01), with older subjects performing better, whereas the above-mentioned effects associated with the development of face perception either stayed unchanged or slightly decreased with age [12]. The effect of gender differences proved to be minimal, though girls performed slightly better in the old/new and face-inversion tasks. *$p < 0.01$; **$p < 0.001$.

$p < 0.01$) (Figure 1C); heritability was estimated to be 31.0% (10.6% to 48.2%) ($\chi^2(4) = 7.69$, $p = 0.10$) (Figure 2A).

Evidence presented so far strongly suggests that the perceptual mechanisms that are engaged specifically in the holistic processing of faces are heritable. Before this conclusion can be accepted, however, we must consider whether the heritability of these apparently face-specific mechanisms might instead be attributed to more domain-general cognitive mechanisms. One such possibility is global processing of visual stimuli, which has been linked to holistic face perception [7]. We therefore measured global-to-local interference (GLI) in a variant of the Navon task [8], which reflects the tendency for global visual information to be privileged attentionally over local information. Although GLI was significant overall (Table 1), it was not heritable: the correlation for MZ twins was not greater than the correlation for DZ twins ($z = -1.37$, $p = 0.17$) (Figure 1D). The lack of genetic influence on the global processing of nonface objects is not simply attributable to the use of reaction time (RT) as a phenotypic variable. Instead, RT in both consistent and inconsistent conditions was more similar between MZ twins than DZ twins (Table 2), and heritability was 37.7% (19.4% to 52.8%) for average RT in this global-local task ($\chi^2(4) = 2.7$, $p = 0.61$) (Figure 2A). These results replicate the previously demonstrated heritability of reaction time [9] and show that the heritability for face perception is not due to a more general heritability of global visual processing.

A second, quintessentially domain-general factor is IQ. Previous studies have shown that performance on tests of many specific cognitive abilities, such as verbal ability, spatial ability, memory, and perceptual speed, is both correlated with IQ [10, 11] and heritable, and multivariate analyses indicate that the same generalist genes underlie the heritability of each of these abilities [1]. Might the heritability of face-specific processing also derive from a correlation of face processing and IQ? This hypothesis was rejected in tests on a new population of singleton subjects, which found no positive correlation between the FIE or CFE and IQ (measured by Raven's advanced progressive matrices), yet found a correlation between the FIE and CFE ($r = 0.11$, $p < 0.05$) (Figure 2B), showing that these two measures tap a common underlying face-specific mechanism. The lack of a correlation of FIE or CFE with IQ is not a result of insufficient power, because the correlations were in fact significantly negative in both cases (FIE: $r = -0.17$, $p < 0.005$; CFE: $r = -0.24$, $p < 0.001$). This negative correlation reflects the fact that the correlation between IQ and perception of upright faces was weak (FIE task, $r = 0.13$, $p < 0.05$) or nonexistent (CFE task, $r = 0.03$, $p = 0.60$), whereas the correlation was significant between IQ and perception of both inverted ($r = 0.25$, $p < 0.001$) and misaligned ($r = 0.23$, $p < 0.001$) faces, perhaps because the ability to devise strategies for processing novel stimuli (inverted and misaligned faces) is related to IQ. Thus, the heritability of face-specific processing demonstrated here does not derive from either GLI or IQ, ruling out two of the most plausible domain-general accounts for our effects.

The environment parameter (errors of measurement and nonshared environmental influences) estimated from the ADE model, or twins' resemblance not explained by heritability, accounts for 61.1%, 75.2%, and 69.0% of the variance for FRA, FIE, and CFE, respectively (Figure 2A). Therefore, although genetic factors play a significant role in face recognition, our data also suggest substantial environmental influence. This result is consistent with well-established experiential effects on face perception [12] such as the other-race effect [13, 14] and perceptual narrowing effects [15, 16]. Interestingly, genetic factors explained substantially more of the variance among older (13–19 years of age) than younger (7–12 years of age) children (see Figure 2C), as reported for other cognitive traits [17], perhaps indicating that experiential factors exert a stronger influence on the time course of development than on the level of performance ultimately achieved.

In sum, our findings demonstrate the heritability of a very specific cognitive process: the ability to perceive and recognize faces. This finding goes beyond prior work on the heritability of cognition in several respects. First, face perception is a more cognitive, high-level process than the sensory phenomena previously shown to be heritable, such as visual acuity [18] and pitch perception [19]. Second, although some studies have demonstrated that some aspects of language processing are heritable independent of IQ [20, 21], consistent with our claim of cognitive specialist genes, these studies have not specified which aspect of language processing is heritable. What distinguishes our work from most other studies on the heritability of cognition is our use of measures that isolate a very specific cognitive process, face recognition, unconfounded from more general perceptual and cognitive abilities. Specifically, we found heritability of face-specific processing measured in three different paired tasks that contrast performance on faces with (1) other meaningful visual object categories (houses) and (2) two classes of stimuli that are visually

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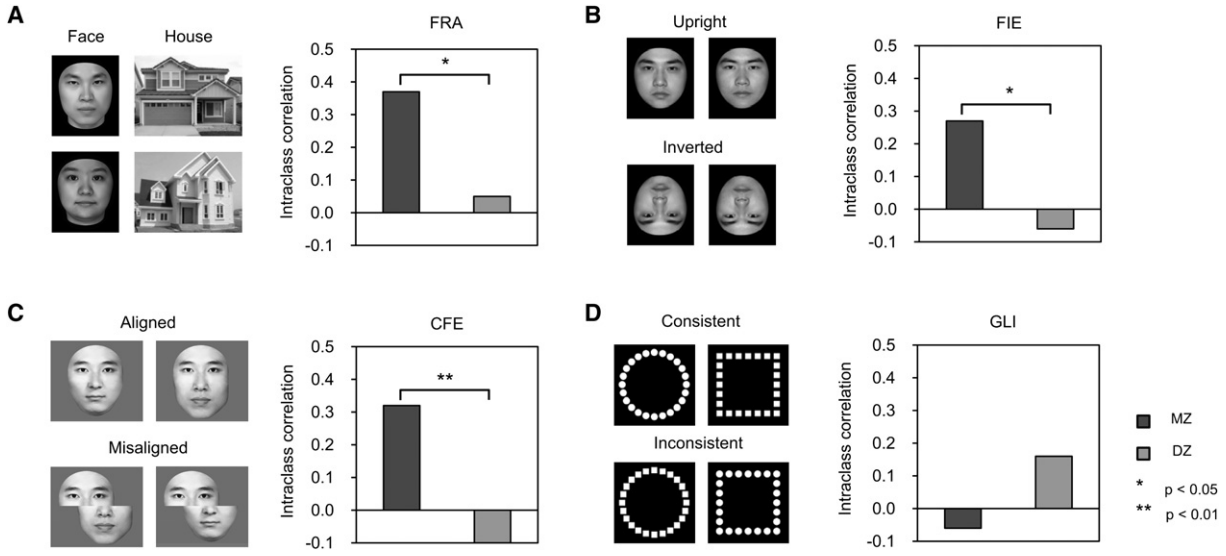

Figure 1. Intraclass Correlations for Monozygotic and Dizygotic Twins

(A) The old/new recognition task. The y axis shows the intraclass correlations (r) in face-specific recognition ability (FRA) for monozygotic (MZ) and dizygotic (DZ) twins.

(B) Face-inversion effect (FIE).

(C) Composite-face effect (CFE).

(D) Global-to-local interference (GLI).

similar to faces but processed differently (inverted faces and misaligned faces). Further, the heritability we find for face-specific processing does not result from more domain-general phenomena such as perceptual speed, global attention, or IQ. Thus, our data provide some of the first evidence for cognitive specialist genes that affect a specific domain of cognition. Note that our findings do not argue against the existence of generalist genes, they simply show that not all genetic influences on cognition are general.

Our evidence for heritability of face-specific processing fits well with two other recent lines of evidence indicating that genes influence face perception. First, a congenital disorder in face recognition runs in families [22, 23]. Second, Polk et al. [24] found that the spatial distribution of fMRI responses across the ventral pathway to faces (but not chairs or words) is more similar between monozygotic than dizygotic twins, although face perception was not tested in that study. However, these findings do not tell us which genes are involved or by what causal pathways they affect face perception, from increasing social interest (and hence experience with face perception) to directly wiring up the neural circuits for face perception. Evidence that genes may be largely responsible for wiring up much of the face system comes from recent reports indicating that impressive face discrimination abilities are present in human newborns [25] and in baby monkeys reared without ever seeing faces [16].

Our results connect to three long-running debates in cognitive science. First, our finding that face-specific perceptual processing is not positively correlated with IQ adds to prior evidence for the cognitive and neural specificity of the face-processing system [5, 26] in supporting the modularity of mind [27, 28], that is, the idea that certain special domains of cognition are functionally distinct from each other and from more general-purpose cognitive machinery. Second, the question of whether such cognitively and neurally specific modules of mind and brain are also shaped by cognitively specific genes has been fiercely debated for decades, with some proposing innately specified organs of the mind [27, 29–31] and others arguing that genes do not produce cognitively specific effects [1, 32]. Note that cognitively specific brain regions do not in themselves imply cognitively specific genes: the visual word form area is a functionally specific brain region that must be wired up largely by experience, because it responds very specifically to words and letter strings only in an orthography the subject knows [33]. Thus, our finding that face-specific processing is heritable is not a foregone conclusion from the known functional specificity of the face system. Finally, the existence of cognitive specialist genes helps

Table 2. Intraclass Correlations and Their 95% Confidence Intervals for Monozygotic and Dizygotic Twins for Each of the Component Tests

	Intraclass Correlation	
Cognitive Test	Monozygotic	Dizygotic
1. Old/new		
Face	0.44 (0.27–0.58)	0.38 (0.16–0.56)
House	0.16 (−0.04–0.34)	0.17 (−0.06–0.39)
FRA	0.37 (0.19–0.52)	0.05 (−0.19–0.28)
2. Face inversion		
Upright	0.32 (0.13–0.48)	0.24 (0.01–0.45)
Inverted	0.18 (−0.02–0.36)	0.16 (−0.07–0.38)
FIE	0.27 (0.08–0.44)	−0.06 (−0.29–0.17)
3. Composite face		
Align	0.27 (0.08–0.44)	−0.01 (−0.24–0.22)
Misalign	0.22 (0.03–0.40)	0.21 (−0.03–0.42)
CFE	0.32 (0.13–0.48)	−0.10 (−0.32–0.14)
4. Global-local		
Consistent	0.35 (0.17–0.51)	0.12 (−0.11–0.35)
Inconsistent	0.37 (0.19–0.53)	0.08 (−0.16–0.31)
GLI	−0.06 (−0.25–0.14)	0.16 (−0.08–0.38)

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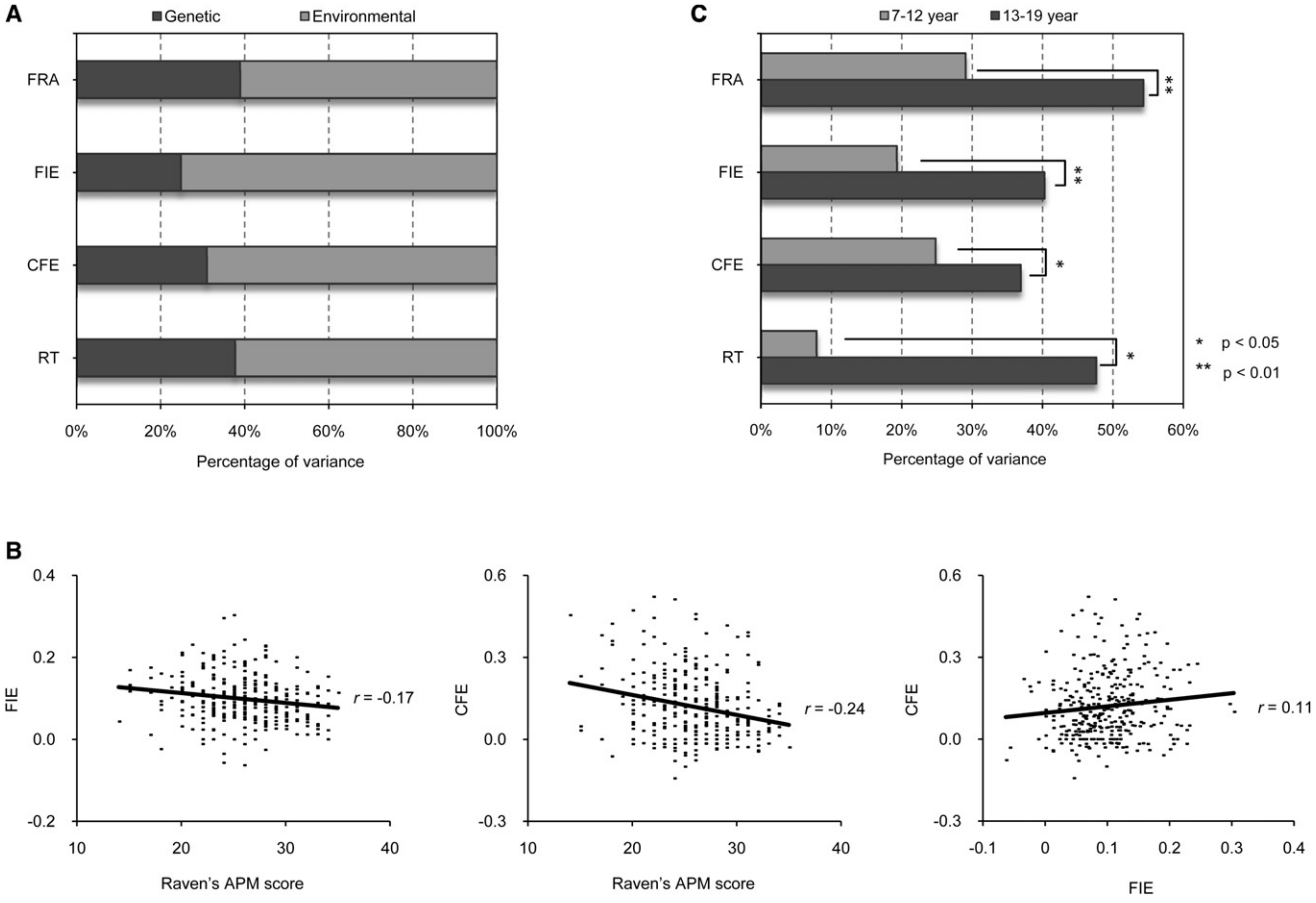

Figure 2. Heritability of Face Processing and Its Relation to General Cognitive Ability

(A) Estimates of proportions of variance due to genetic and environmental influences, as derived from maximum-likelihood model-fitting analyses of twins. For each measure, the full model fit well, suggested by both chi squares (FRA: 2.29; FIE: 2.17; CFE: 7.69; reaction time [RT]: 2.70) and Akaike fit indices (FRA: −3.71; FIE: −3.83; CFE: 1.69; RT: −3.30). For each measure, the best-fitting model was one that included only nonadditive genetic and nonshared environment parameters, with the following chi squares with four degrees of freedom: 2.29, 2.17, 7.69, and 2.70, respectively. In other words, dropping the additive genetic component of variance from the full model did not significantly reduce the fit of the model ($\Delta\chi^2(1) = 0$). In contrast, dropping either the nonadditive genetic parameter (E model, likelihood-ratio test, FRA: $\Delta\chi^2(1) = 14.71$, $p < 0.001$; FIE: $\Delta\chi^2(1) = 6.57$, $p < 0.01$; CFE: $\Delta\chi^2(1) = 8.58$, $p < 0.005$; RT: $\Delta\chi^2(1) = 14.66$, $p < 0.001$) or nonshared environment parameter (D model, p values < 0.0001) from the model significantly worsened the fit.

(B) Correlation between IQ (assessed by Raven's advanced progressive matrices [APM]) (36 items, mean raw score = 25.8, standard deviation [SD] = 4.03) and face perception ability measured by the face-inversion effect (FIE) (left) and the composite-face effect (CFE) (middle). Correlation between FIE and CFE is shown (right).

(C) Genetic influence on face recognition increases with age. The data from the childhood group (age 7–12, age mean = 10.8, SD = 1.23) and the adolescence group (age 13–19, age mean = 14.9, SD = 1.63) were simultaneously analyzed in one model with different parameter estimates for the two age groups. The genetic effects were significantly larger for the adolescence group than for the childhood group, because forcing parameter estimates to be equal for the two age groups significantly worsened the fit of the model (FRA: $\Delta\chi^2(2) = 11.83$, $p < 0.005$; FIE: $\Delta\chi^2(2) = 12.19$, $p < 0.005$; CFE: $\Delta\chi^2(2) = 6.25$, $p < 0.05$; and RT: $\Delta\chi^2(2) = 8.81$, $p < 0.05$).

explain how some cognitive functions can be impaired while others are preserved or even enhanced in heritable disorders such as autism, dyslexia, developmental language impairments [34], and Williams syndrome [35].

The specific heritability of face perception demonstrated here invites a broader investigation of whether other cognitively and neurally specialized mental processes (such as navigation, language [20, 21], and understanding number) are also heritable and whether the heritability of such domain-specific components of cognition are dissociable from each other and from domain-general aspects of cognition such as IQ [36]. This work may ultimately elucidate the mechanisms by which genes interact with experience to produce distinct components of the human mind and brain.

Experimental Procedures

Subjects

One hundred and eighty-nine pairs of twins (age 7–19, mean = 12.7, standard deviation [SD] = 2.48) were recruited from elementary and middle schools in Beijing, China. The zygosity of the twins was determined by a questionnaire about physical twin resemblance, which has over 95% accuracy in predicting blood-typed zygosity of twins and was validated by the number of placenta where necessary [4]. Sixteen pairs were excluded because of a history of neurological illness, uncertain zygosity, failure to finish the test, or failure to follow the instructions. Outliers more than a 3.5 standard deviation away from the mean were excluded from further analysis, separately for each of the tests. This resulted in exclusion of one DZ pair, one MZ pair, two MZ pairs, and three pairs (1 MZ and 2 DZ) from the old/new task, the face-inversion task, the composite-face task, and the global-local task, respectively. In addition, 321 college students (age 18–23, mean = 20.8, SD = 0.90) participated in an experiment assessing

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both intelligence (by Raven's advanced progressive matrices) and face perception ability. The study was approved by the institutional review board of Beijing Normal University. Prior to testing, written informed consent was obtained from the subjects and/or from their parents or guardians.

Behavioral Test and Analysis

The participants were tested individually at their schools by trained experimenters with a computer-based test battery that consisted of tasks widely used in previous studies on different aspects of face recognition ability (see Supplemental Experimental Procedures). FRA, FIE, CFE, and GLI were calculated as follows: FRA = (face − house)/(face + house); FIE = (upright − inverted)/(upright + inverted); CFE = (aligned [different − same] − misaligned [different − same])/(aligned [different + same] + misaligned [different + same]); GLI = (consistent [global − local] − inconsistent [global − local])/(consistent [global + local] + inconsistent [global + local]).

Genetic Analysis

Both age and gender accounted for some amount of the variance in performance on all tests for the individuals aged 7 to 19 years (Table 1). Because these effects inflate resemblance for twins, all scores were adjusted for age and gender with a multiple-regression procedure [37] before they were submitted to intraclass correlation and model-fitting genetic analyses.

Intraclass correlation was used to calculate the strength and direction of resemblance between pairs of twins [38], and Fisher's z test was used to test whether the resemblance between MZ twins was significantly larger than that between DZ twins [39, 40]. Maximum-likelihood model-fitting analyses were performed via Mx [41] to estimate genetic and environmental components of variance and to test the significance of their contribution. Because the DZ correlation was less than half the MZ correlation in all tests, the univariate ADE model was chosen to estimate additive genetic (A), nonadditive genetic (D), and nonshared environmental (E) contributions to variance in face recognition.

To compare the genetic influences between the two age groups, we tested whether parameter estimates (i.e., A, D, and E) in the two age groups were the same. Specifically, for each of the component tests with significant genetic influences, the data from the two age groups were first simultaneously analyzed in one model with different parameter estimates for the two age groups (i.e., unconstrained). Next, the parameter estimates for the two age groups were treated as being equal (i.e., constrained). Testing of quantitative differences in fit between the two models was done by means of likelihood-ratio tests, by subtracting the negative log likelihood for the more restricted model from that for the more general model.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, one table, and two figures and can be found with this article online at doi:10.1016/j.cub.2009.11.067.

Acknowledgments

We thank D. Dilks, R. Saxe, G. Yovel, W. Johnson, and C. Jennings for comments on the manuscript; R. Xu, J. Zhang, Y. Luo, Y. Huang, Y. Tong, M. Xu, Q. Xu, C. Li, F. Ma, and Y. Qian for data collection; R. Xu and Y. Luo for programming and testing the battery; and S. Qiao, W. Liang, and T. Li for help with registering twins. This study is funded by the National Natural Science Foundation of China, the Chinese Academy of Sciences, the Ministry of Science and Technology of China, the Ministry of Education of China, the National Eye Institute, the National Center for Research Resources, and the Mental Illness and Neuroscience Discovery Institute.

Received: August 24, 2009
Revised: October 20, 2009
Accepted: November 9, 2009
Published online: January 7, 2010

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Please cite this article in press as: Zhu et al., Heritability of the Specific Cognitive Ability of Face Perception, Current Biology (2009), doi:10.1016/j.cub.2009.11.067

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