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Heritability of the specific cognitive ability of face perception

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Running head: Heritability of face perception

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 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 nonface 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 and 71 dizygotic, 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%) (ADE model, 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 (Figure S1).

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 ($z = 2.72$, $p < 0.01$) (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 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, are 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 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 faces ($r = 0.23$, $p < 0.001$), 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 of 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 children (7 - 12 years of age) (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 i) other meaningful visual object categories (houses) and ii) two classes of stimuli that are visually 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 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 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, as 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 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, 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 pairs) from the old/new task, the face inversion task, the composite face task, and the global-local task, respectively. In addition, three hundred and twenty-one college students (age 18-23, mean = 20.8, SD = 0.90) participated in an experiment assessing both intelligence (by Raven's advanced progressive matrices) and face perception ability. The study was approved by the IRB of Beijing Normal University. Prior to testing, written informed consent was obtained from the subjects and/or from their parents/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 (Supplemental Methods). Face-specific recognition ability (FRA), face inversion effect (FIE), composite face effect (CFE), and global-to-local interference (GLI) were calculated as follows: $FRA = [\text{Face} - \text{House}] / [\text{Face} + \text{House}]$; $FIE = [\text{Upright} - \text{Inverted}] / [\text{Upright} + \text{Inverted}]$; $CFE = [\text{Aligned (Different} - \text{Same)} - \text{Misaligned (Different} - \text{Same)}] / [\text{Aligned (Different} + \text{Same)} + \text{Misaligned (Different} + \text{Same)}]$; $GLI = [\text{Consistent (Global} - \text{Local)} - \text{Inconsistent (Global} - \text{Local)}] / [\text{Consistent (Global} + \text{Local)} + \text{Inconsistent (Global} + \text{Local)}]$.

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 using 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.

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Figure Legends

Figure 1. Intraclass correlations for MZ and DZ twins. (A) The old/new recognition task. The y-axis shows the intraclass correlations (r) in face-specific recognition ability (FRA) for MZ and DZ twins. (B) Face inversion effect (FIE). (C) Composite face effect (CFE). (D) Global-to-local interference (GLI).

Figure 2. (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; 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 4 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, $ps < 0.0001$) 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, 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 (right). (C) Genetic influence on face recognition increases with age. The data from the childhood group (age from 7 to 12, age mean = 10.8, SD = 1.23) and the adolescence group (age from 13 to 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, as 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: $\Delta\chi^2(2) = 8.81$, $p < 0.05$).

Tables

Table 1. Means, standard deviations (SD), 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 |

*: $p < 0.01$; **: $p < 0.001$

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 face-specific recognition ability (FRA). Other tests were selected to sample across diverse specific face recognition ability types, including face inversion effect (FIE, $t(343) = 29.01$, $p < 0.001$), the composite face effect (CFE, $F(1,340) = 239.03$, $p < 0.001$), and the global-to-local interference (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 ($ps < 0.01$) 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.

Table 2. Intraclass correlations and their 95% confidence intervals for MZ and DZ twins for each of the component tests.

| Cognitive test | Intraclass correlation | |
|-------------------|------------------------|-------------------|
| | MZ | DZ |
| 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) |

SUPPLEMENTAL FIGURES

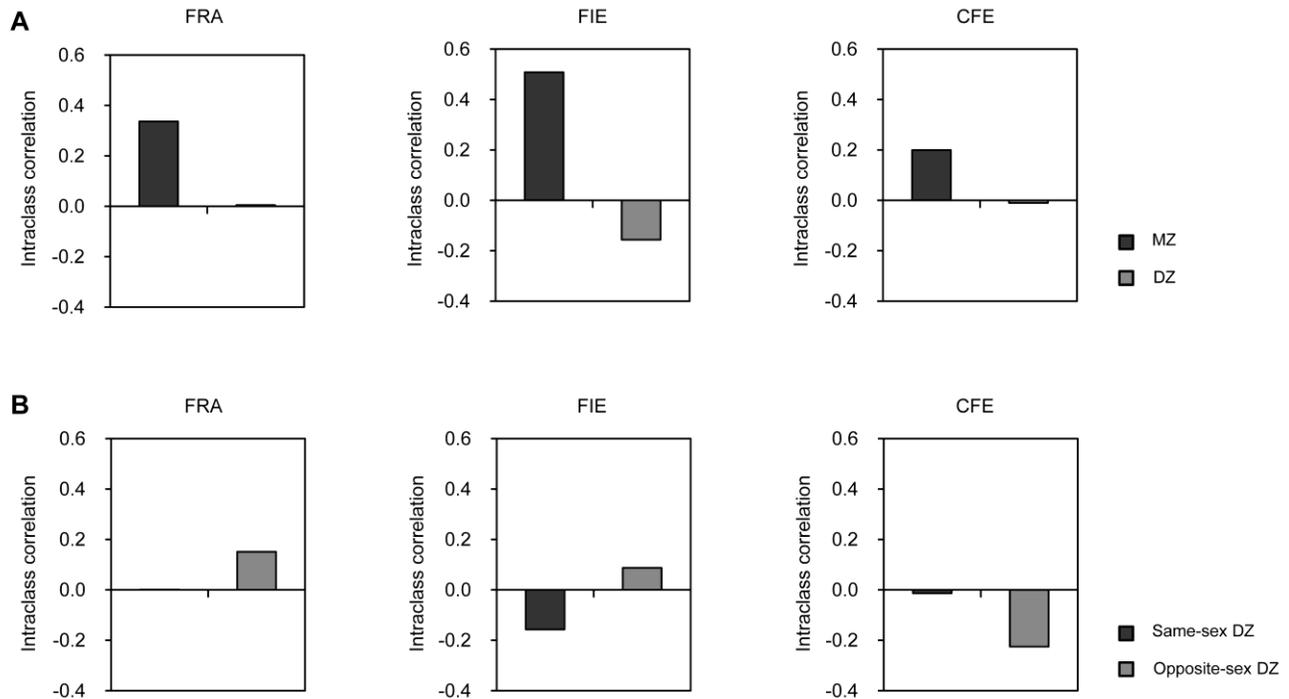


Figure S1. To rule out the possibility that the genetic influences specific for face recognition were due to a relatively large number of twins in the MZ group and/or the inclusion of the opposite-sex DZ twins in the DZ group, intra-class correlations for each of the component tests were calculated when the number of twin pairs was matched and opposite-sex DZ twins were excluded. (A) Intra-class correlations for 40 pairs of MZ twins (age mean = 13, SD = 2.77) versus 43 pairs of same-sex DZ twins (age mean = 12.1, SD = 2.15). The result from the model-fitting analysis shows that the MZ twins were significantly more similar than the DZ twins for all effects ($p < 0.01$), except for the composite face effect ($p = 0.37$), which might be due to the small sample size. (B) Intra-class correlations for same-sex DZ twins (43 pairs) versus opposite-sex DZ twins (28

pairs). No significant differences in intraclass correlations were found between these two groups for all effects (all z s < 1).

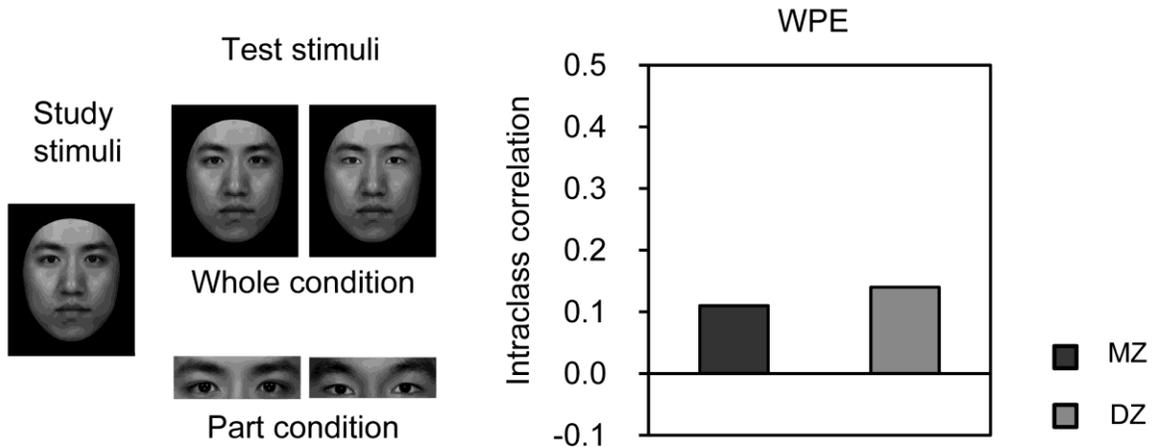


Figure S2. There was no significant effect of zygosity in the whole-part effect (WPE) (MZ: $r = 0.11$; DZ: $r = 0.14$; $z = -0.16$, $p = 0.87$), which refers to a higher accuracy in discriminating a face part in the context of the rest of the face ('whole') than in isolation ('part') (whole: mean accuracy = 0.70; part: mean accuracy = 0.69; WPE: $t(345) = 2.92$, $p < 0.005$). In addition, for both the whole (MZ, $r = 0.20$; DZ, $r = 0.25$) and part (MZ, $r = 0.41$; DZ, $r = 0.32$) conditions, MZ twins correlations were not significantly greater than DZ twins correlations (p s > 0.50). Failure to observe the effect of zygosity in the WPE is possibly due to a small effect size of the WPE ($\eta_p^2 = 0.02$), much smaller than those in the FIE (0.71) and CFE (0.41). Alternatively, the holistic processing involved in the WPE might be different from other aspects of face processing, and this component may be not influenced by genetics.

SUPPLEMENTAL TABLE

Table S1. Split-half reliability for each of the component tests.

| Cognitive test | Reliability |
|-------------------|-------------|
| 1. Old/new | |
| Face | 0.53 |
| House | 0.55 |
| FRA | 0.37 |
| 2. Face Inversion | |
| Upright | 0.68 |
| Inverted | 0.58 |
| FIE | 0.22 |
| 3. Composite Face | |
| Align | 0.62 |
| Misalign | 0.70 |
| CFE | 0.65 |
| 4. Global-local | |
| Consistent | 0.96 |
| Inconsistent | 0.95 |
| GLI | 0.19 |

SUPPLEMENTAL METHODS

One hundred and seventy-three twin pairs comprised 102 MZ (78 males, 126 females; age mean = 13.0; SD = 2.68) and 71 DZ pairs (70 males, 72 females; age mean = 12.2, SD = 2.09). The DZ group had 43 same-sex DZ (42 males, 44 females; age mean = 12.1, SD = 2.15) and 28 opposite-sex DZ (28 males, 28 females; age mean = 12.4, SD = 2.01) pairs.

The whole test battery took about 1.5 hours, and the tests reported here took about 40 min in total. The other tests addressed other cognitive abilities and social traits, which will not be reported here. The accuracy in all experiments was collected, as well as response time in the global-local task. Practice trials with cartoon faces were conducted before each experiment. Only after the experimenters were sure that the subjects understood the task, based on their performance on the practice trials, the experimental trials were begun.

The face stimuli used in these tests were gray-scale adult Chinese faces, with external contour (a roughly oval shape with hair on the top and sides) removed. The face images were selected from an in-house adult Chinese face database, and face images were not repeated in different tests.

Old/New recognition task. In this task, 40 face images and 40 house images were used. There were two blocks in this task: a face block and a house block. Each block consisted of one study and one test segment. In the study segment, 20 images of each object category were shown for 1 sec per image with an interstimulus interval of 0.5 sec, and the 20 images were cycled through twice. In the test segment, 10 studied images were shown twice, randomly intermixed with 20 new images from the same category. On presentation of each image, the subjects were instructed to determine whether the image had been shown in the study segment.

Face inversion task. This task used 25 face images. Pairs of face stimuli were presented sequentially, either both upright or both inverted, in each trial, with trials presented in a pseudorandom order. Each trial started with a blank screen for 1 s, followed by the first face stimulus presented at the center of the screen for 0.5 sec. Then, after an interstimulus interval of 0.5 sec, the second stimulus was presented until a same or different response was made. There were 50 trials for each condition, half of which consisted of face pairs that were identical (same trials), and half of which consisted of face pairs from different individuals (different trials). Same and different trials were randomly intermixed.

Composite face task. Face composites were created from five face images. Composites were created by splitting face images in half horizontally across the middle of the nose, and then recombining the faces using the top and bottom halves of different individuals. The pairs of composite faces were presented sequentially either aligned or misaligned, and aligned- and misaligned-face trials were presented in a pseudorandom order. Each trial started with a blank screen for 1 s, followed by the first composite face presented at the center of the screen for 0.8 sec. Then, after an interstimulus interval of 0.5 sec, the second composite face appeared for 0.8 sec. Subjects were instructed to judge whether the top halves of the composite faces were identical or different. There were 40 trials for each condition, half of which consisted of face pairs that shared the identical top halves (same trials), and half of which consisted of face pairs with different top halves (different trials). On every trial the bottom halves were always different. Same and different trials were intermixed randomly.

Global-local task. The stimuli were four hierarchical shapes of two types: consistent shapes in which the global and the local shapes shared identity, and inconsistent shapes for which the shapes at the two levels had different identities. Subjects identified the shape at either the global or local level in separate blocks. Each block contained 80 trials, preceded by instructions to identify at the local or global level. Each trial started with a

blank screen for 0.5 s, followed by a central fixation cross for 0.7 sec. Then, one of the four possible stimuli appeared for 0.15 sec. Subjects were instructed to indicate a response of disc or square as quickly as possible. In each block there were 40 trials of consistent shapes and 40 trials of inconsistent shapes, which were intermixed randomly.

