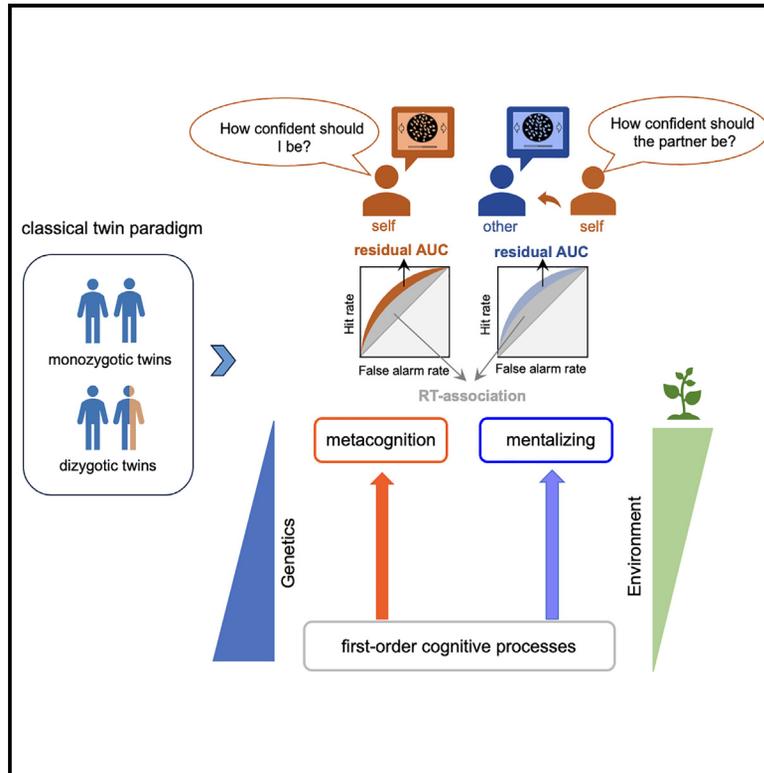


Distinct genetic and environmental origins of hierarchical cognitive abilities in adult humans

Graphical abstract



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In brief

Jiang et al. employ the classical twin paradigm to compare the genetic and environmental contributions to human cognitive abilities. They reveal that the first-order cognitive abilities are primarily influenced by genetic factors, but the second-order cognitive abilities of metacognition and mentalizing are more influenced by shared environmental factors.

Highlights

- Human cognitive abilities can be categorized into a two-order hierarchy
- First-order cognitive abilities are primarily influenced by genetic factors
- Second-order cognitive abilities are more influenced by environmental factors
- Multiple family factors contribute to second-order cognitive abilities



Article

Distinct genetic and environmental origins of hierarchical cognitive abilities in adult humans

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Human cognitive abilities ranging from basic perceptions to complex social behaviors exhibit substantial variation in individual differences. These cognitive functions can be categorized into a two-order hierarchy based on the levels of cognitive processes. Second-order cognition including metacognition and mentalizing monitors and regulates first-order cognitive processes. These two-order hierarchical cognitive functions exhibit distinct abilities. However, it remains unclear whether individual differences in these cognitive abilities have distinct origins. We employ the classical twin paradigm to compare the genetic and environmental contributions to the two-order cognitive abilities in the same tasks from the same population. The results reveal that individual differences in first-order cognitive abilities were primarily influenced by genetic factors. Conversely, the second-order cognitive abilities have a stronger influence from shared environmental factors. These findings suggest that the abilities of metacognition and mentalizing in adults are profoundly shaped by their environmental experiences and less determined by their biological nature.

INTRODUCTION

The origins of individual differences in human abilities, particularly within the realm of cognition, have been a topic of long-standing interest.^{1,2} Human cognitive functions can be conceptualized as a hierarchical structure comprising two levels of cognitive processes. At the first-order level, cognitive processes involve basic functions, such as perception, decision-making, and memory. At the second-order level, cognitive processes are responsible for monitoring and regulating the first-order processes; that is, cognition about cognition.^{3–5} Notably, the abilities associated with these two levels of cognitive functions are distinct from each other. For example, the capacity to accurately monitor one's own decisions, known as metacognition, demonstrates significant variation even when first-order performance accuracies in the decision-making tasks are matched across individuals.^{6,7} However, it currently remains unknown whether the genetic and environmental factors that contribute to individual differences in these two levels of hierarchical cognitive abilities are distinct. Cognitive abilities are not solely determined by biological nature. Environmental factors, such as nutrition, education, and socioeconomic status (SES), also play a crucial role in molding these cognitive abilities.

Classical twin studies are a valuable method for investigating the underlying biological and environmental factors that contribute to individual differences in human cognitive abilities.^{8,9} Monozygotic (MZ) twins share identical genetic material, while dizygotic (DZ) twins, on average, share approximately half of their genes. Additionally, both MZ and DZ twins are commonly raised in similar family environments.² As a result, a greater resemblance in a cognitive ability between MZ twins compared with DZ twins suggests a stronger influence of genetic factors, while a similar resemblance between MZ and DZ twins indicates the presence of shared environmental factors.⁸ Decades of extensive research utilizing the classical twin paradigm have consistently demonstrated the heritability of nearly all first-order cognitive abilities.¹⁰ It has been estimated that approximately 50% of the variability in individual differences in first-order cognitive abilities among twins can be attributed to shared genes.^{9,11} Furthermore, individuals who excel in one cognitive task tend to demonstrate high performance across other tasks, suggesting a common underlying factor referred to as “g” or IQ (intelligence quotient). Research suggests that general intelligence has a heritability ranging from 50% to 80%.^{9,11,12}

However, general intelligence alone is insufficient to account for second-order cognitive abilities despite both of them making



Table 1. The MZ and DZ twins' demographics and socioeconomic status (SES)

| | MZ | DZ | χ^2/T | p Value |
|--------------------------------------|--------------|--------------|------------------|-----------|
| <i>n</i> (pairs) | 57 | 48 | – | – |
| Girls (%) | 48 | 58 | 1.0 | 0.31 |
| Age range | ~20–30 | 20–29 | – | – |
| Mean age (SD) | 25.1 (2.4) | 23.4 (2.8) | 1.5 ¹ | 0.14 |
| Self education in years ² | 16 | 16 | 3.8 | 0.22 |
| Father's education ² | 12 | 12 | 2.5 | 0.37 |
| Mother's education ² | 12 | 12 | 1.4 | 0.26 |
| Self-income per month ² | ~5,000–7,000 | ~5,000–7,000 | 2.9 | 0.42 |
| Father's income ² | ~3,000–5,000 | ~3,000–5,000 | 8.6 | 0.10 |
| Mother's income ² | ~3,000–5,000 | ~3,000–5,000 | 8.8 | 0.13 |
| Father's occupation ² | 3 | 3 | 3.8 | 0.43 |
| Mother's occupation ² | 3 | 3 | 0.5 | 0.49 |

¹T value.

²The median.

significant contributions to human daily performance.¹³ The second-order cognitive functions here are referred to as metacognition and mentalizing. Metacognition involves cognitive processes that monitor one's own first-order cognitive processes by introspecting internal mental states. On the other hand, mentalizing focuses on comprehending the internal mental states of others, utilizing social cue associations and theory of mind (ToM) to infer mental states of others.¹⁴ Hence, there exists a notable distinction in the representation of mental states between these two second-order cognitive functions.¹⁵

While extensive research has focused on exploring the psychological and neurobiological mechanisms underlying metacognition and mentalizing,^{16–19} the genetic and environmental origins of individual differences in these cognitive abilities still remain largely unclear. Given evidence demonstrating that both metacognition and mentalizing are observed even in preverbal infants,^{20,21} it is conceivable that these second-order cognitive abilities may also have a genetic basis. However, there is ongoing debate regarding the extent of genetic influence on mentalizing.^{22–25} In the case of metacognition, twin studies are currently lacking, likely due to the challenges associated with obtaining reliable confidence ratings from children.²⁶ To address these challenges, the present study simultaneously assessed both first-order and second-order cognitive abilities in the same tasks for a population of adult participants. We utilized the classical twin paradigm to discern the relative contributions of genetic and environmental factors to these two levels of cognitive abilities.

RESULTS

Experimental paradigms and task setting

We recruited a total of 57 pairs of adult MZ twins and 48 pairs of adult DZ twins from the BeTwiSt twin database (Table 1; Figure S1) to participate in our experiment. On each occasion,

there were two twin pairs coming together. For each pair of randomly paired participants, one participant performed the metacognition task, while the other concurrently completed the mentalizing task, with the former participant serving as the observed partner. In the metacognition task, the partner made a decision regarding the direction of the random dot kinematogram (RDK) stimulus and rated a confidence level (Figure 1B, top). The task difficulty was titrated individually by adjusting the coherence level, ensuring that each participant's accuracy remained around 0.5 (chance level: 0.25). In the mentalizing task, the observer concurrently viewed the partner's performance on the metacognition task and assigned a confidence level to the partner. If the observer concurrently held his/her own confidence on the similar stimulus, he/she tended to use the self's confidence as a proxy of the partner's confidence (Figure S2). Importantly, to exclude such potential confounding, that the observer would use his/her own confidence to estimate the partner's confidence, we designed the mentalizing task with the stimuli that were presented to the observer to be different from those presented to the partner. Specifically, only the dots moving coherently were kept in motion, while the remaining dots remained stationary in the mentalizing task (Figure 1B, bottom). Subsequently, the observer was presented with a progress bar indicating the response time (RT) of the partner when making a choice. However, the partner's choice and confidence rating were not revealed to the observer. Hence, the mentalizing process merely used the external social cue (RT) but was independent of the observer's metacognitive process. Notably, the partner in the task could be either the participant's sibling or a participant from another twin pair. Thus, each participant completed both the metacognition and mentalizing tasks twice, with the task order counterbalanced. To ensure anonymity of the partner in the mentalizing task, we used board panels to physically separate the two pairs of participants. Furthermore, a network connection using the TCP/IP (transmission control protocol/internet protocol) protocol via an ethernet cable synchronized the concurrent metacognition and mentalizing tasks (Figure 1C).

Distinct origins of two-order hierarchical cognitive abilities in the metacognition task

The first-order and second-order behavioral metrics associated with the metacognition task demonstrated little correlation, except for the relationship between metacognitive abilities and performance accuracies in both MZ and DZ twins (Figure S3A). No significant differences were observed between MZ and DZ twins in either the first-order or second-order behavioral metrics related to the metacognition task (Figure S4). To assess the reliability of these behavioral metrics, we evaluated the test-retest correlations as each participant performed the metacognition task twice. Apart from the RDK stimulus coherence, which remained the same across the two runs for each participant (Figure S4H), the first-order behavioral metrics in the RDK task (accuracy, median RT, and RT variance) and mean confidence demonstrated high reliability across the two runs (Pearson's $r = \sim 0.68$ – 0.95 , bootstrapped Cronbach's α ranging from 0.78 to 0.95; Figures S4A–S4D). Meanwhile, the second-order behavioral metrics (RT-confidence correlation, Goodman and

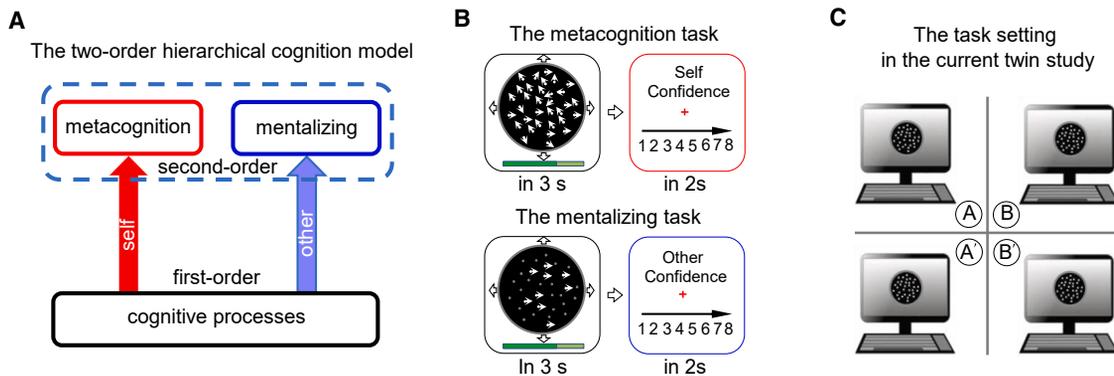


Figure 1. Experimental paradigms and task setting

(A) The two-order hierarchical structure of human cognition. Both metacognition and mentalizing are second-order cognitive processes, where individuals monitor their own and others' first-order cognitive processes, respectively.

(B) Experimental paradigms. In the metacognition task, the participant perceived and judged the net direction of an RDK stimulus within 3 s (the elapsed time was displayed as a progress bar under the stimulus) and then reported the confidence rating. In the mentalizing task, the participant perceived noiseless moving dots in that the originally randomly-moving dots in the metacognition task remained stationary. Concurrently, the participant perceived the elapsed time that the partner used to make a choice. Afterward, the participant reported the estimate of the partner's confidence rating.

(C) On each time, two pairs of twins (A-A' and B-B', either MZ or DZ) participated in the experiment and conducted both the metacognition task and the mentalizing task twice. They were paired randomly, with one participant conducting the metacognition task while another participant concurrently conducted the mentalizing task. Participants were physically separated by board panels, and their computers were, if necessary, synchronized via network connection following the TCP/IP protocol.

Kruskal's gamma correlation [γ] between confidence and actual decision correctness, raw AUC (area under the receiver operating characteristic curve), and residual AUC; STAR Methods) exhibited moderate reliability ($r = \sim 0.50\text{--}0.72$, bootstrapped Cronbach's α ranging from 0.50 to 0.80; Figures S4E–S4G). These behavioral metrics related to metacognitive abilities also demonstrated high consistency among themselves (Cronbach's α : $\sim 0.65\text{--}0.80$ in MZ and DZ twins; Figure S4I). Notably, there were no significant differences in the reliability of these behavioral metrics between MZ and DZ twins.

We then calculated the intraclass correlation coefficients (ICCs) to compare the resemblance between the pairs from the same twin pairs (within-twins) and those from different twin pairs (cross-twins). In the metacognition task, the within-twins ICCs for both MZ and DZ consistently exhibited higher values compared with the corresponding cross-twin ICCs (gray histograms represent random pairs crossing MZ and DZ twins, respectively; Figure S5), suggesting significant contributions from shared genetic and/or shared environmental factors to individual differences. Notably, the ICCs for all first-order behavioral metrics within MZ twins consistently exceeded those within DZ twins (coherence: MZ, 0.41 ± 0.11 [mean \pm 95% confidence interval], DZ, 0.13 ± 0.18 ; median RT: MZ, 0.31 ± 0.09 , DZ, 0.05 ± 0.10 ; mean confidence: MZ, 0.33 ± 0.06 , DZ, 0.11 ± 0.07 ; for variance RT, there was no significant difference: MZ, 0.29 ± 0.11 , DZ, 0.24 ± 0.14 ; Figures S5A–S5D). This suggests considerable genetic contributions to these first-order metrics. In contrast, the ICCs for the second-order behavioral metrics in metacognition did not exhibit significant differences between MZ and DZ twins (RT-confidence correlation: MZ, 0.20 ± 0.14 , DZ, 0.19 ± 0.17 ; γ : MZ, 0.18 ± 0.19 , DZ, 0.15 ± 0.18 ; raw AUC: MZ, 0.32 ± 0.13 , DZ, 0.30 ± 0.14 ; Figures S5E–S5G), or, in some cases, the ICCs for DZ twins were even numerically larger

than those for MZ twins (residual AUC: MZ, 0.11 ± 0.18 , DZ, 0.21 ± 0.17 ; Figure S5H), indicating negligible genetic contributions to these second-order behavioral metrics.

To quantify the genetic and environmental contributions, we utilized maximum likelihood to compare various potential structural equation models (SEMs) that decomposed the covariance of each behavioral phenotype among the MZ and DZ twins. These models incorporated different components associated with latent factors such as additive genetic (A), shared environmental (C), non-additive genetic (D), and non-shared environmental (E) factors, which encompass measurement errors, commonly known as the ACE or ADE models (Equations 2 and 3; STAR Methods). These models also took into account the other correlated behavioral variables as confounding variances in the SEMs (Figure S3A). Using Akaike's information criteria (AIC), we selected the most parsimonious model with the lowest AIC value as the best-fitting model to explain individual variances in each behavioral phenotype.

The metrics associated with first-order cognitive abilities (coherence, median RT, RT variance, and mean confidence, while accuracy was controlled) were best explained by AE or DE models (Table S1), with genetic contributions ranging from 0.36 to 0.41 in individual differences among MZ and DZ twins. In contrast, the behavioral metrics related to second-order cognitive abilities (RT-confidence correlation, Goodman and Kruskal's γ , raw AUC, and residual AUC) were best accounted for by the CE model, with shared environmental contributions ranging from 0.17 to 0.40. To validate the reliability of these model comparison results, we conducted 100,000 iterations by randomly sampling three-quarters of the MZ and DZ twins and replicating the same analysis approach (bootstrapping procedure). The dominant models remained as AE/DE for first-order cognitive abilities and CE for second-order cognitive abilities (Figure 2). The

the partner's decision and confidence. Consequently, the estimated confidence demonstrated a strong correlation with the partner's self-reported confidence (Figure S6A) and was also indicative of the partner's decision correctness. To assess the consistency between the participant's estimated confidence and the partner's decision correctness, we calculated the Goodman and Kruskal's γ and AUC (Figures S6B and S6C). There were no notable systematic differences observed in the behavioral metrics between MZ and DZ, and these metrics of mentalizing abilities displayed high internal consistency (Cronbach's α ranging from 0.46 to 0.70 through bootstrapping; Figure S6D). However, after removing the RT-associated component from the estimated confidence, the residuals did not show any significant correlation with the decision confidence reported by the partner (Figure S6E). Accordingly, the Goodman and Kruskal's γ and residual AUC calculated from the residuals approached the chance levels (0 and 0.5, respectively; Figures S6F and S6G). These observations indicate that participants efficiently used the RT-confidence association to estimate the partner's decision confidence. However, the behavioral metrics of the mentalizing abilities calculated by the residuals (residual AUCs) might represent participants' internal mentalizing abilities that are independent of the RT associations but are noise. These residuals have consistently exhibited correlations with the neural activities in the dorsomedial prefrontal cortex (dmPFC) during mentalizing, indicating allocentric mental state representations.^{19,28} In fact, the residual AUCs demonstrated a consistent pattern among each other, with a Cronbach's α range of 0.30–0.70 upon bootstrapping (Figure S6H). Furthermore, the within-twin ICCs of residual AUCs for both MZ and DZ twins were significantly larger than the random-pairing cross-twin ICCs (Figure S7). Notably, the mentalizing abilities were not correlated with participants' metacognitive abilities in either MZ or DZ twins (Figure S3B), as the corresponding metacognitive process was deliberately excluded during performance of the mentalizing task.

The ICCs of most behavioral metrics within MZ and DZ twins were significantly higher than the corresponding cross-twin ICCs (Figure S7), indicating a stronger resemblance of mentalizing abilities among twins who share both genes and the family environment. The ICCs for all first-order behavioral metrics consistently demonstrated higher values within MZ twins compared with DZ twins (RT weight – MZ: 0.35 ± 0.09 , DZ: -0.02 ± 0.12 ; γ – MZ: 0.33 ± 0.07 , DZ: 0.17 ± 0.09 ; raw AUC – MZ: 0.45 ± 0.06 , DZ: 0.22 ± 0.08). This suggests considerable genetic contributions to these first-order behavioral metrics. In contrast, the ICCs for the second-order behavioral metrics (residual AUCs) did not exhibit significant differences between MZ and DZ twins (MZ, 0.23 ± 0.08 , DZ, 0.24 ± 0.08 ; Fig. S7), indicating a negligible genetic contribution to the second-order behavioral metrics in mentalizing.

To qualify the genetic and environmental contributions, we also conducted model comparisons for the behavioral metrics in the mentalizing task. The first-order behavioral metrics were primarily accounted for by the AE/DE model, with genetic contributions ranging from 0.31 to 0.46 and negligible shared environmental contributions (Table S2). In contrast, the residual

AUCs were best explained by the CE model (Figure 3), indicating a shared environmental contribution of approximately 0.23 (Table S2). The bootstrapping procedure confirmed these findings (Figure 3), and the results obtained from the full ACE model were consistent with the best-reduced model (Table S2). Therefore, the first-order cognitive abilities of mentalizing based on the RT-confidence association were predominantly influenced by genetic factors, while the second-order cognitive ability of mentalizing beyond the RT-confidence association (namely, the core ability of ToM) was instead influenced by shared environmental factors.

Multiple family environmental factors contributed to individual differences in the metacognition and mentalizing abilities

To assess the specific shared family environmental factors that contribute to influences on second-order cognitive abilities in metacognition and mentalizing, we conducted further analysis. MZ and DZ twins were divided into two subgroups using a median split based on their ages, family incomes, and parental education levels, respectively. Using the ACE/ADE models, we reanalyzed each subgroup within MZ and DZ twins, comparing the differences in contributions from shared family environmental factors. The results consistently demonstrated that older age and higher familial SES (family income or parental education) were associated with more reliable shared environmental contributions to both second-order cognitive abilities in metacognition and mentalizing. Notably, the ratios of contributions (c^2) between the subgroups did not exhibit systematic differences (Figure 4). These findings highlight the importance of age and familial SES in shaping the shared environmental influences on second-order cognitive abilities.

Reliability of the environmental contribution biases to the second-order cognitive abilities

The assumptions that the shared environmental factor and the non-additive or dominant genetic factor are alternately effective in the ACE and ADE models may not hold true, as both factors can simultaneously influence behavioral phenotypes.²⁹ Ignoring the non-additive or dominant genetic factor in the ACE model can result in underestimating the shared environmental effect.³⁰ Additionally, potential confounding factors, such as gene-by-environment interactions, assortative mating, and sibling interactions can be mistakenly attributed to the shared environmental factor, potentially leading to its overestimation. To address these biases in the ACE and ADE models, we collapsed the additive and non-additive genetic factors into a single genetic factor (G) and employed a q -GCE model (Equations 5 and 6; STAR Methods). This allowed us to assess the reliability of the genetic factor or the shared environmental factor contributing to each behavioral phenotype by varying the weight of the genetic factor (q) in DZ twins relative to MZ twins.²⁹ Across a wide range of q values, the dominance of the genetic factor or the shared environmental factor remained stable in its contribution to each behavioral phenotype in both tasks (Figure 5). Crucially, the shared environmental contributions to the residual AUC and the RT-confidence association in the metacognition task (Figure 5A), as well as the residual AUC in the mentalizing task

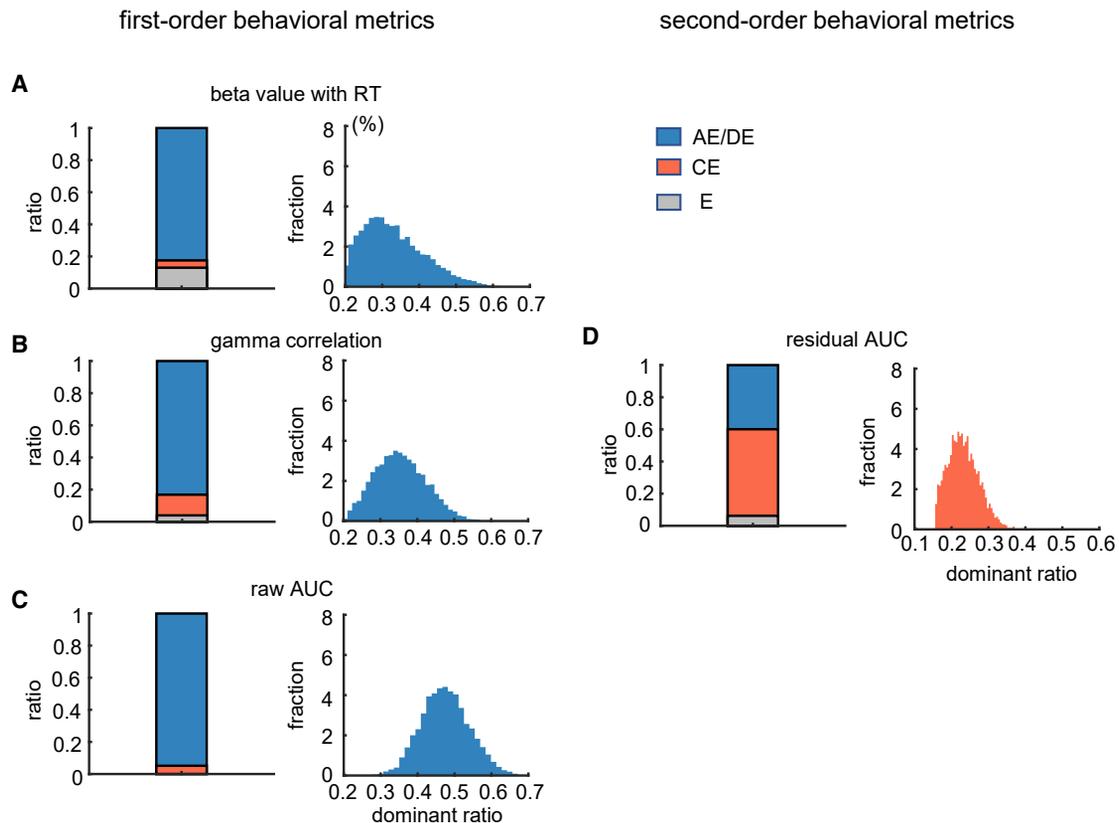


Figure 3. Distinct origins of first-order and second-order cognitive abilities in the mentalizing task

(A) Beta value of regression between estimated confidence and the partner's RTs.
(B) Goodman and Kruskal's γ between estimated confidence and other's correctness.
(C) Raw AUC.
(D) Residual AUC.

Shown are fraction ratios of the selected best models from 100,000 bootstrapping iterations (left) and the dominant ratios of shared genetic or environmental contributions (right) to behavioral metrics in the mentalizing task. The left two columns denote first-order cognitive abilities, while the right two columns correspond to second-order cognitive abilities (MZ, 57 pairs; DZ, 48 pairs).

(Figure 5B) remained consistent as the q values varied. Therefore, the distinct biases in genetic contributions to first-order cognitive abilities and shared environmental contributions to second-order cognitive abilities should be valid across a reasonable range of model spaces.

To further evaluate the reliability of our findings, we conducted post hoc power analyses using simulated data that shared the same covariance structure for MZ and DZ twins, obtained from the conventional ACE model for each behavioral phenotype. These analyses were performed using the OpenMx module. First, we calculated selectivity indices of contributions from the genetic and shared environmental factors ($\frac{a^2 - c^2}{a^2 + c^2}$) based on the simulated data (100,000 times). Positive values of selectivity indices indicate genetic biases, while negative values indicate environmental biases. The results revealed systematic biases between the two-order hierarchical cognitive abilities: prominent genetic biases in the first-order cognitive abilities but environmental biases in the second-order cognitive abilities (Figure 6A). Comparisons of the relative importance of genetic and shared environmental contributions

to the two-order hierarchical cognitive abilities showed significant differences in both the metacognition task ($p = 0.021$ between the four first-order behavioral metrics and the four second-order behavioral metrics) and the mentalizing tasks ($p = 0.043$ between the three first-order behavioral metrics and residual AUC; Figure 6A).

Furthermore, we also assessed the statistical power to discern the relative importance of genetic and shared environmental factors in contributing to the first-order and second-order cognitive abilities in the metacognition and mentalizing tasks, respectively. The post hoc power analysis using the sample size employed in our study revealed a power of 0.58 (effect size: Cohen's $d = 0.21$) for distinguishing the four first-order behavioral metrics from the raw AUC in the metacognition task. Additionally, the power was 0.51 (effect size: Cohen's $d = 0.20$) for distinguishing the four first-order behavioral metrics from the residual AUC in the metacognition task. In the mentalizing task, the power was 0.46 (RT weight vs. residual AUC, effect size: Cohen's $d = 0.18$) (Figure 6B). Thus, the distinct biases observed in the genetic and shared environmental contributions to the two-order

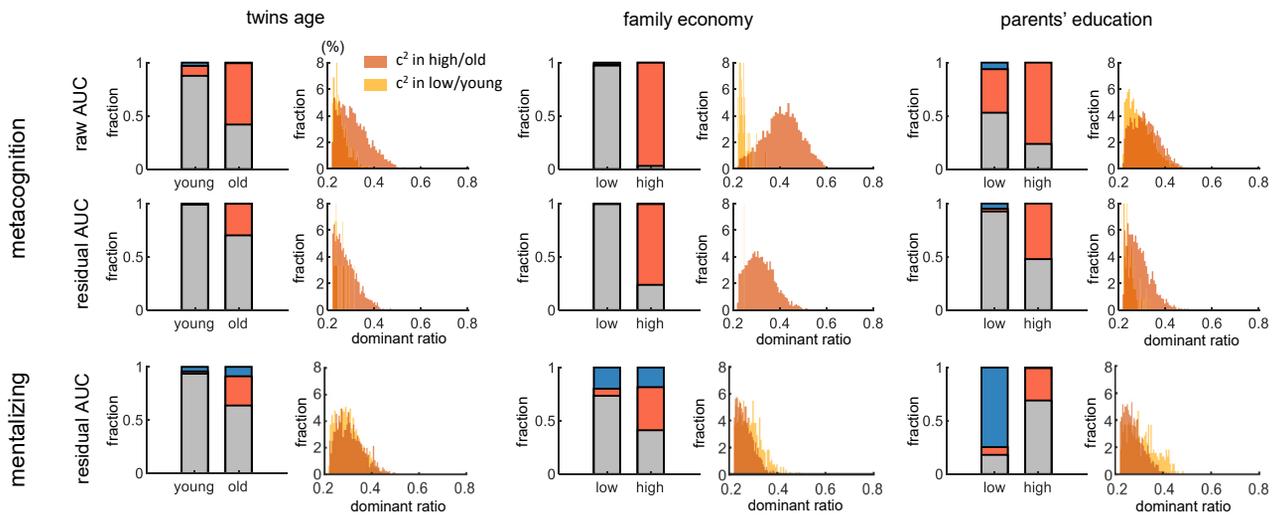


Figure 4. The shared family environmental factors contributing to second-order cognitive abilities in metacognition and mentalizing
The MZ and DZ twins were median split according to their age, family economy, and parent's highest education (MZ, 57 pairs; DZ, 48 pairs).

hierarchical cognitive abilities, based on our current sample size, were reasonably reliable.

DISCUSSION

The present study enforces the existing literature on human cognitive abilities, where genetic effects are typically prominent.^{9,10} However, it sheds light on a unique finding: that genetic factors might exert less influence on the second-order cognitive abilities of metacognition and mentalizing in adults compared with shared environmental factors. This distinctive selectivity demonstrated remarkable consistency and robustness in multiple aspects of the findings in the current study. First, the assessments of the two-order cognitive abilities in the same tasks within the same population helped to minimize covariance and enhance the distinction between genetic and environmental contributions. Second, if genetic effects remained stable in cognitive abilities, then we would expect higher heritability in adults compared with children due to potential gene-environment interactions during cognitive development.^{31,32} Genetic effects typically amplify under favorable environmental opportunities, which are often influenced by SES. Notably, there were no systematic differences in SES between the identical (MZ) and fraternal (DZ) twins in our study (Table 1; Figure S1). Third, the stable contributions of shared environmental factors to second-order cognitive abilities across variational *q*-GCE models supported the robustness of our findings. Fourth, our results replicated previous findings of biased environmental influence on mentalizing abilities in false-belief tasks, including studies with large samples of participants.^{22,25} Fifth, and remarkably, the genetic and environmental influence on cognitive abilities associated with the metacognition and mentalizing tasks distinctly aligns with the two-order hierarchy; while genetic factors predominantly influence first-order cognitive abilities, shared environmental factors primarily shape second-order cognitive

abilities. This distinct contribution of genetic and shared environmental factors in the two-order hierarchical cognitive abilities carries profound implications for comprehending the interplay between nature and nurture in the development of human cognitive abilities.

While the metacognition bias (mean confidence) has been shown to have a heritable component,³³ the metacognition sensitivity does not exhibit heritability. Notably, these two behavioral metrics are independent from each other. It is common for individuals to have a tendency to overestimate their performance, which is known as the Dunning-Kruger effect,³⁴ even after receiving explicit feedback based on actual outcomes.³⁵ In contrast, the metacognition sensitivity, which refers to the ability to accurately discriminate confidence levels in relation to actual decision accuracy, can improve through extensive learning from personal experience and guidance from others. It is important to highlight that the explicit meta-cognitive competence of reporting confidence is not present in infants; rather, it gradually develops during childhood and approaches maturity around 8–9 years of age, reaching an ability similar to that observed in adults.³⁶ However, even preverbal infants show implicit metacognition competence in automatically monitoring decision uncertainty.²¹

The mentalizing process examined in the current study can be broken down into two distinct components: the association with an external cue (RT)^{37,38} and an internal modeling process independent of the external cue.^{19,28} The association with the external cue represents a crucial first-order cognitive ability that contributes significantly to mind reading.^{37,38} In contrast, although the internal modeling component alone cannot accurately predict the true mental states of others, cue-independent residuals derived from neural activities in social brain regions, particularly the dmPFC,^{19,28,39} may reflect individual variation in internal mentalizing ability by virtue of their unique internal models. These internal models allow individuals to simulate general internal mental states of others, even when interacting with

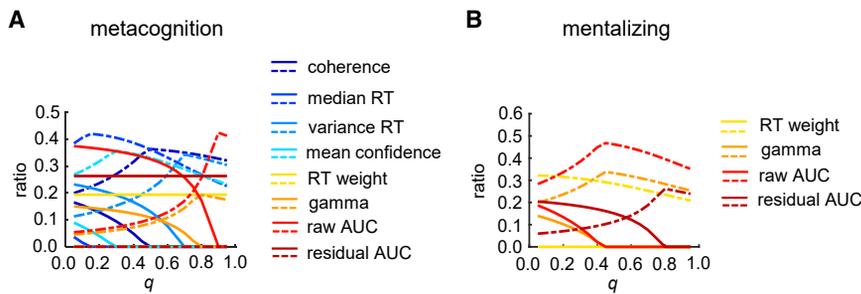


Figure 5. The contribution ratios of genetic factors and shared environmental factors changed with the q values in the q -GCE model

(A) Contribution ratios of genetic factors (broken lines) and shared environmental factors (solid lines) varied with q values in the metacognition task. The contribution ratio was always larger from genetic factors than shared environmental factors in each behavioral phenotype of the first-order cognitive abilities across the entire range of q values [0.05, 0.95]. Instead, the contribution ratio

was larger from shared environmental factors than genetic factors in the behavioral metrics of the second-order cognitive abilities across a broader q value range. (B) Contribution ratios of genetic factors (broken lines) and shared environmental factors (solid lines) varied with q values in the mentalizing task (MZ, 57 pairs; DZ, 48 pairs).

an anonymous partner, constituting a form of ToM.^{37,38,40} While the association with the external cue was influenced by heritable factors, the internal mentalizing ability was not genetically determined. Our findings suggest that the development of the internal models about others' minds for mentalizing should be significantly molded by participants' shared family experiences and cultural influence.⁴¹

The first-order cognitive functions primarily involve processing external information from the physical world that is similar across individuals and generations. As a result, the anatomical structures in the brain areas associated with these first-order cognitive processes are both evolutionarily and developmentally stable.^{42,43} The intrinsic functional connectivity across

these brain regions also remains stable from infancy to adulthood within and across individuals.^{44,45} In contrast, the second-order cognitive functions, metacognition and mentalizing, specifically deal with internal information from the mental world. These functions are characterized by subjectivity, volatility, and idiosyncrasy.^{41,46} Metacognition is predominantly associated with the frontoparietal control network,^{18,19,28} while mentalizing is associated with the dedicated social brain network.^{17,19} The anatomical structures in these two brain networks, in contrast, have undergone significant evolutionary and developmental expansion.^{42,43} Moreover, their intrinsic functional connectivity displays considerable diversity from infancy to adulthood within and across individuals.^{44,45}

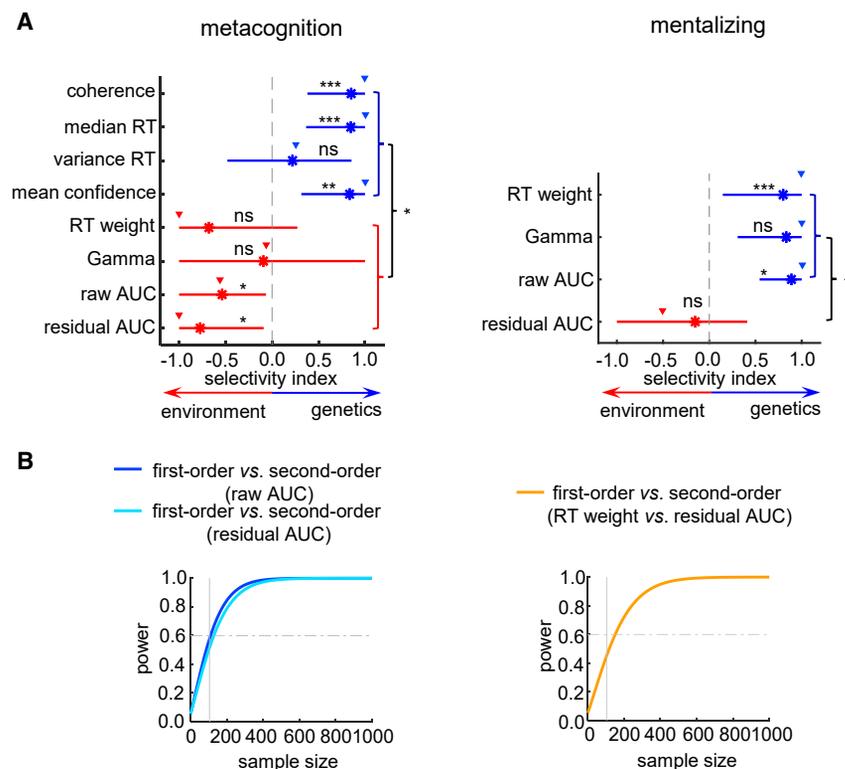


Figure 6. The post hoc power analyses

(A) Selectivity index ($\frac{e^2 - c^2}{e^2 + c^2}$) of contributions from genetic factors or shared environmental factors in 100,000 simulations with the same sample size as used in the present study. Blue asterisks represent the mean, and bars represent the 95% confidence interval (CI). Triangles indicate the selectivity index of the empirical data. Statistical signs above each bar indicates the significance level compared with zero. ns, no significance; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

(B) Power variation with sample size, including both MZ and DZ twins. Vertical gray lines indicate the same sample size as used in the present study, and the horizontal broken lines indicate a power of 0.6.

Predictability of decision accuracy through metacognition and mentalizing requires substantial experiences. Instructions received from caregivers, such as parents and teachers, are presumed to be an important influencing factor during cognitive development.^{3,47} Cultural learning,^{3,41,46,48} including maternal discussions about children's minds,⁴⁹ may play a crucial role in guiding children to understand their own and their caregiver's mental states. Our findings suggest that higher family SES exerts more reliable influence on the second-order cognitive abilities of metacognition and mentalizing. Therefore, shared family environmental factors, such as parental nurturing and the transmission of cultural values,^{3,41,46,48} likely play a significant role in shaping the mental state representations in metacognition and mentalizing.

Limitations of the study

The present study possesses several limitations that merit consideration. Firstly, it remains uncertain whether the second-order cognitive abilities evaluated by the tasks utilized in this study are indicative of individuals' overall metacognition and mentalizing capabilities. Both metacognition and mentalizing encompass complex features across diverse task domains.^{4,50} There are ongoing debates concerning whether metacognitive abilities are domain general or domain specific.^{51–55} Furthermore, assessing individual differences in conventional mentalizing tasks, such as the false-belief task, is not applicable to healthy adults.^{23,50} Although the current version of the mentalizing task aimed to dissociate cue association from the mentalizing process to successfully capture individual differences even in healthy adults, it must be noted that the employed mentalizing task was still relatively new, despite its prior use in other studies.^{19,27} Therefore, further investigations employing alternative tasks involving metacognition and mentalizing are warranted. Second, while the effect sizes and post-hoc powers observed in this study were reasonable in distinguishing the relative contributions of genetic and shared environmental factors to the two-order hierarchical cognitive abilities (post-hoc power around 0.5), the reliabilities of the behavioral metrics associated with internal mentalizing abilities were moderate, with mean Cronbach's α coefficients of 0.45 (DZ) and 0.58 (MZ). Thus, future twin studies with larger sample sizes are warranted to validate the current findings. Third, although the classical twin paradigm enables the quantification of genetic contributions to behavioral phenotypes, it does not identify specific genes. Therefore, future research should incorporate genome sequencing and genome-wide association studies (GWASs) in twin populations. These endeavors will be vital in identifying the precise genetic factors linked to individual differences in first-order cognitive abilities, offering valuable insights into the genetic foundations of cognitive functions.

In conclusion, the present study, utilizing the classical twin paradigm, provides empirical evidence suggesting that the dissociable first-order and second-order cognitive functions may have distinct sources. First-order cognitive abilities are primarily influenced by genetic factors, whereas second-order cognitive abilities have an environmental origin, possibly shaped by shared family experiences and cultural influences during cognitive development. Thus, the metacognition and mentalizing abilities in adults are likely to be more influenced by their shared environments, with a lesser degree of pre-determination from their biological nature.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.celrep.2024.114060>.

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AUTHOR CONTRIBUTIONS

S.J. and F.S. conducted the experiments. S.J. and X.W. analyzed the data. P.Y. assisted with data collection. Y.J. and X.W. designed the experiments, wrote the manuscript, and supervised the project.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|----------------------------|------------|-------------------------------------------------------------------------------------------------------------------------------|
| Software and algorithms | | |
| MATLAB R2019a | MathWorks | https://www.mathworks.com/products/MATLAB.html ; RRID:SCR_001622 |
| R (version: 3.5.3) | Rstudio | https://cran.r-project.org/ ; RRID:SCR_001905 |
| Psychophysics toolbox PTB3 | N/A | http://psychtoolbox.org |
| OpenMx(version: 2.12.2) | N/A | https://openmx.ssri.psu.edu/openmx-features |
| Other | | |
| Data and Code | this paper | https://zenodo.org/doi/10.5281/zenodo.10793598 |

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Xiaohong Wan (xhwan@bnu.edu.cn).

Materials availability

No reagents were generated in the study.

Data and code availability

- The data reported in this study have been deposited at Github and are publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- All custom code has been deposited at Github and is publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this work paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Participants

A total of 251 right-handed healthy participants took part in the study, including 65 pairs of MZ twins and 55 pairs of DZ twins of the same gender (24.2 ± 2.6 years old, 118 females). The twins were recruited from the BeTwiSt twin database at the Institute of Psychology, Chinese Academy of Sciences. In addition, 25 righted-handed healthy participants (22.2 ± 2.3 years old, 14 females) were recruited to separately take part in a task with concurrent metacognition and mentalizing. All participants provided informed consent, and the study was conducted in accordance with a protocol approved by the institutional review board, following the principles set forth in the 1964 Helsinki declaration and its later amendments, or comparable ethical standards. Based on performance criteria (see [Training](#)), eight pairs of MZ twins and seven pairs of DZ twins were excluded from the analyses. The sample size was determined through post-hoc power analyses.

METHOD DETAILS

Socioeconomic status

We gathered the education levels of each participant and their parents, categorized as 1. Middle school, 2. High school, 3. College, and 4. Postgraduate. We also collected data on monthly income for each participant and their parents, divided into categories as follows: 1. $\leq 1,000$ Yuan, 2. 1,000–3,000 Yuan, 3. 3,000–5,000 Yuan, 4. 5,000–7,000 Yuan, 5. 7,000–10,000 Yuan, and 6. $\geq 10,000$ Yuan. Additionally, we recorded the occupations of the participants' parents, classified as 1. Unemployed and retired, 2. Partly skilled, 3. Skilled, 4. Professional and technical, and 5. Governmental and managerial. The distributions of these various SES variables were shown in [Table 1](#) and [Figure S1](#).

Experimental procedures

During the experiment, two pairs of twins (either MZ or DZ) participated together for approximately one and a half hours. Each participant completed both the metacognition task and the mentalizing task twice. In the mentalizing task, each participant was randomly partnered with either his/her sibling or a participant from another pair of twins who concurrently performed the metacognition task. Participants were physically separated by board panels (Figure 1C). A network connection, following the TCP/IP protocol through an Ethernet cable, was used to synchronize the concurrent metacognition and mentalizing tasks. Each task consisted of ninety trials and lasted for 10 min.

Stimuli

In the metacognition task, the random-dot-kinematogram (RDK) stimuli⁵⁶ were presented within an aperture with a radius of 3° (visual angle); a total of three hundred white dots (radius: 0.08° , density: 2.0%) moved in various directions at a speed of 8.0° per second on a black background. The lifetime of each dot lasted for three frames. A fraction of the dots moved toward the same direction (one of the four directions: left, down, right, and up), while the rest moved in various random directions.

Metacognition task

This task was designed to evaluate each participant's metacognitive ability in monitoring his/her own decisions. During each trial, a participant was presented with an RDK stimulus and required to judge its net moving direction within 3 s. The elapsed time since the onset of the stimulus was simultaneously displayed at the bottom of the screen using colors: green, yellow, and red representing 1, 2, and 3 s, respectively. Afterward, the participant rated his/her confidence in the correctness of the decision within 2 s. Confidence ratings were measured on a scale of 1–8, where 1 indicated the highest level of uncertainty and 8 indicated complete certainty. Feedback regarding the correctness of the decision was not provided (Figure 1B). The coherence of the RDK stimulus remained constant across all trials and was individually titrated by a staircase procedure before the main experiment to ensure a convergence of accuracy rate at 0.5 for each participant. However, there were variations in actual accuracy among participants. MZ twins demonstrated actual accuracies of 0.47 ± 0.12 [mean \pm standard deviation (S.D.)], while DZ twins had actual accuracies of 0.48 ± 0.12 (Figure S4B).

Mentalizing task

This task was designed to contrastingly assess each participant's mentalizing ability to monitor a partner's trial-by-trial decision confidence. A participant observed a partner's behavioral performance on the metacognition task, and then reported the estimate of the partner's confidence within 2 s (Figure 1B). To ensure that the participant did not rely on his/her own decision confidence on the same RDK stimulus perceived by the partner, a distinct stimulus was presented to the participant. This stimulus only contained the coherently moving dots, while the rest remained stationary. Critically, this setup allowed for a fair evaluation of a participant's mentalizing ability without interference from his/her own metacognition ability. Simultaneously, the participant observed the elapsed time taken by the partner to make a choice. However, the partner's choice and confidence rating were not disclosed to the participant. Hence, the only available information concerning the partner's task performance was the response time (RT), as the RDK stimulus coherence remained constant.

To demonstrate that a participant's own concurrent metacognitive states might interfere the evaluation of the partner's confidence during mentalizing, we separately conducted a task in which a participant concurrently reported his/her own confidence and the partner's confidence (Figure S2A).

Training

In our previous studies, we have observed that participants' first-order and second-order behavioral performance in the metacognition task tends to improve and stabilize with sufficient practice. Thereby, each participant underwent a 40-min training session before proceeding to the main experiment. The task difficulty was dynamically adjusted on a trial-by-trial basis using a staircase procedure based on Levitt's method.⁵⁷ Following this procedure, the RDK stimulus coherence was increased by one level after two consecutive correct trials, decreased by one level after two consecutive incorrect trials, and kept unchanged otherwise. The initial coherence level of the RDK stimulus was set to be 50% and gradually decreased to reach a stable level. By the end of the practice session, participants' accuracy rate approached 0.5. However, we excluded eight pairs of MZ twins and seven pairs of DZ twins, as at least one of their coherences of the RDK stimulus required to achieve an accuracy of 0.5 was above 20% (three S.D. outside of the remaining participants with 11.5 ± 2.9).

QUANTIFICATION AND STATISTICAL ANALYSIS

Statistical tests

Statistical analyses of the data were conducted using the MATLAB statistical toolbox (MATLAB2019, Mathworks, USA). To determine whether there were significant differences in behavioral metrics between MZ and DZ twins, as well as within-twins and cross-twins, two-sample t-tests or z-tests were employed. Additionally, populations were compared using two-sample Kolmogorov-Smirnov (K-S) tests through bootstrapping with a significance level set at $\alpha = 0.05$.

Individual metacognition and mentalizing abilities

To assess each participant's metacognition and mentalizing abilities, nonparametric approaches were employed. First, a receiver operating characteristic (ROC) curve was constructed by using different confidence ratings as judgment criteria to characterize correct probabilities. The area under the ROC curve (AUC) was then calculated to assess the participant's abilities in predicting decision correctness. A larger AUC indicates a higher level of metacognition or mentalizing ability. In both metacognition and mentalizing, the RTs were the only external information that could be used to predict the estimated confidence. Thereby, we also assessed the internal metacognition and mentalizing abilities by calculating the residual AUCs using the residuals of the estimated confidence after the RT-associated component was regressed out, respectively. By this means, we could separately assess the two components of metacognitive and mentalizing processes, respectively. Furthermore, we also computed the Goodman and Kruskal's gamma correlation⁵⁸ (γ) to examine the association between the reported confidence and the actual decision correctness.

Behavioral metrics

In the metacognition task, we assessed both first-order and second-order cognitive abilities separately for each participant. The first-order cognitive abilities were evaluated using several behavioral metrics, including stimulus coherence, accuracy, median response time (RT), RT variance, and mean confidence. The second-order cognitive abilities, which involved quantifying the consistency between the reported confidence and actual first-order performance, were evaluated using the correlation between RT and confidence, Goodman and Kruskal's gamma correlation between confidence and decision correctness, raw AUC, and residual AUC.

In the mentalizing task, participants utilized the RT information to estimate the partner's decision confidence. We calculated the correlation between the estimated confidence and RTs, the correlation between the participant's estimated confidence and the partner's reported confidence, Goodman and Kruskal's gamma correlation between the estimated confidence and the partner's actual decision correctness, as well as the raw AUC between the estimated confidence and the partner's actual decision correctness. As expected, these behavioral metrics were primarily influenced by their association with RTs, thereby they were classified as first-order cognitive abilities. To isolate the second-order ability of mentalizing from these first-order cognitive abilities, we regressed out the RT-associated component from the estimated confidence and calculated the residual AUC as a proxy of the internal mentalizing ability, that is, the core ability of ToM (see [discussion](#)).

Intraclass correlation coefficients (ICCs)

To assess the familial resemblance of behavioral metrics within twin pairs, we employed a one-way analysis of variance (ANOVA) random-effect model to calculate intraclass correlation coefficients (ICCs). This was done separately for MZ and DZ twins, accounting for the source of variance among twin pairs while disregarding the order of twins within each pair.⁵⁹ That is

$$ICC = \frac{MS_b - MS_w}{MS_b + (k - 1)MS_w} \quad (\text{Equation 1})$$

where MS_b and MS_w are mean square of variances between and within twins. k is specific to 2 in the twin study. Hence, the ICC value is expected to be higher if the variances between twins are significantly greater than those within twins, and vice versa. We combined the data of the two runs in each task for analyses. As baselines, we also calculated the ICCs of the random pairs among the MZ and DZ twins (cross-twins, see [Bootstrapping](#)).

Modeling

To quantify the genetic and environmental influences on each first-order and second-order cognitive ability related to the two tasks, we applied structural equation models (SEMs) to analyze the variance-covariance matrix between MZ and DZ twins.^{29,60} By examining the differences in covariance between MZ and DZ twins, we identified the SEM parameters that enabled us to compare the covariances along the observed variable as follows

$$CV_{MZ} = V_A + V_{NA} + pV_C + V_E \quad (\text{Equation 2})$$

$$CV_{DZ} = \frac{1}{2}V_A + rV_{NA} + pV_C + V_E \quad (\text{Equation 3})$$

where CV_{MZ} is the covariance between the MZ twins, CV_{DZ} is the covariance between the DZ twins, V_A is the additive variance, and r is a coefficient for the non-additive variance (V_{NA}), which is set to 1/4 or 0, p is a binary coefficient (0 or 1) for the common environmental variance (V_C), and V_E is the error variance including unshared environmental variance. If the resemblance between MZ twins is greater than twice the resemblance between DZ twins, then V_{NA} (or dominant genetic effect, D) is considered, but V_C is then disregarded. That is, r is 1/4 and p is 0, and this model is referred to as the ADE model. Otherwise, r is 0 and p is 1, and this model is referred to as the ACE model.

To identify which model that best accounted for each behavioral phenotype, we used two model-selection statistics. The first was the chi-square goodness-of-fit statistic. Higher statistical values (χ^2) indicate poor model fit to the observed covariance. When dealing with nested models (i.e., identical except for constraints placed on the sub-model), the difference in their fits can be evaluated

with the chi-square difference ($\Delta\chi^2$). If the chi-square difference is not statistically significant, the more parsimonious model is selected, as this test indicates that the constrained model fits the data equally well. The second model-selection statistic used was the Akaike information criterion (AIC), which is calculated as follows:

$$\text{AIC} = -2 * \text{LL} + 2 * n \quad (\text{Equation 4})$$

where LL represents the log likelihood of the model on the estimated dataset, and n denotes the number of parameters in the model. The data was analyzed using maximum-likelihood (ML) methods implemented by the OpenMx module⁶⁰ (version: 2.12.2) in R (version: 3.5.3).

However, it is likely that the behavioral phenotypes are influenced by a combination of common environmental, additive, and non-additive genetic factors.²⁹ For instance, in the ACE model, neglecting to consider V_{NA} could result in an underestimation of V_C . To address potential biases in the traditional ACE and ADE models, we collapsed the additive and non-additive genetic factors into a single genetic factor ($V_G = V_A + V_{NA}$). Consequently, the SEM is modified to a q -GCE model as follows:

$$CV_{MZ} = V_G + V_C + V_E \quad (\text{Equation 5})$$

$$CV_{DZ} = qV_G + V_C + V_E \quad (\text{Equation 6})$$

where

$$q = r_A V_A / V_G + r_{NA} V_{NA} / V_G \quad (\text{Equation 7})$$

represents the ratio of the genetic factors in the DZ twins in reference to the MZ twins, r_A and r_{NA} represent the ratios of additive and non-additive genetic factors, respectively. For example, the phenomenon of assortative mating, where individuals with similarities are more likely to marry, can contribute to overestimating the common environmental factor. In such cases, the assortative mating effect can be accounted for by incorporating it into the genetic factor, with a value of r_A greater than 1/2. In the conventional ACE model, the value of q is typically set at 1/2. However, when considering additional non-genetic effects besides the shared environmental effect, the value of q can surpass 1/2. In order to systematically evaluate the reliability and tolerance of genetic or shared environmental effects on each behavioral phenotype, we compared their contributions while progressively adjusting the value of q across a range from 0.05 to 0.95 (Figure 5). This range allowed us to assess the effects under various scenarios and determine the potential impact of different genetic and shared environmental factors.

Bootstrapping

To assess the reliabilities of the behavioral metrics, we performed 100,000 iterations of random sampling involving three-quarters of all MZ and DZ twins. This allowed us to measure Pearson's correlation and Cronbach's alpha on test-retest observations in the meta-cognition task (Figure S4). Additionally, to examine the reliability of familial resemblance, we conducted 100,000 iterations of random sampling involving the same group of twins and random pairs among the MZ and DZ twins (cross-twins). This enabled us to calculate the respective distributions of intraclass correlation coefficients (ICCs) within the MZ and DZ twins and cross-twins using a similar bootstrap procedure (Figure S5; Figure S7).

To evaluate the reliabilities of the selected model and its parameters, we conducted 100,000 iterations of random sampling involving three-quarters of the MZ and DZ twins. This allowed us to compare SEM models that offered the best fit to the observed data, utilizing a similar bootstrap procedure (Figure 2; Figure 3).

Furthermore, to gain further insights into the specific types of family environmental factors that may influence second-order cognitive abilities, we divided the MZ and DZ twins into two sub-groups based on whether their ages, family economic income (including parental income), or the highest parental education exceeded the median. For each sub-group, we performed 10,000 iterations of random sampling involving three-quarters of the MZ and DZ twins. This allowed us to compare the SEM models that best fit the observations within each sub-group across both MZ and DZ twins, using a similar bootstrap procedure (Figure 4).

Power analyses

To evaluate the replicability of our conclusions based on the empirical data, we conducted post-hoc power analyses. We utilized the OpenMx module (version: 2.12.2) in R (version: 3.5.3), which is specifically designed for power analysis in twin studies.^{8,60} The analyses were performed assuming that the same covariance matrices of MZ and DZ twins were acquired through random sampling using the selected sample size.

To examine the relative importance of the genetic and environmental factors in contributing to each behavioral phenotype, we conducted 100,000 iterations for each behavioral phenotype and assessed the selectivity indices of contributions ($\frac{a^2 - c^2}{a^2 + c^2}$, where a^2 represents the contribution of the genetic factor and c^2 represents the contribution of the environmental factor in the ACE model) (Figure 6A).

Additionally, we estimated the post-hoc power for various sample sizes, assuming constant covariance matrices of MZ and DZ twins. We specifically computed the power to distinguish the relative importance of genetic and environmental factors in the overall contribution to first-order and second-order cognitive abilities in the metacognition and mentalizing tasks, respectively.

To calculate post-hoc power, we determined the log likelihood difference between the AE (additive genetic and non-shared environmental) model and the CE (common environmental) model for each behavioral phenotype. In the metacognition task, where the first-order behavioral metrics were independent but the second-order metrics highly correlated, we subtracted the log likelihood of either the raw AUC or the residual AUC from the sum of log-likelihoods of the four first-order behavioral phenotypes. In the mentalizing task, we subtracted the log likelihood of the residual AUC from the log likelihood of the RT weight. These differential log-likelihoods were then treated as the χ^2 values based on the current sample size, and post-hoc power was calculated accordingly. We also extended this calculation to estimate the powers with the same effect sizes across various sample sizes ([Figure 6B](#)).