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Cortisol awakening response and testosterone jointly affect adolescents' theory of mind

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ABSTRACT

Adolescence is a critical period for the maturation of neurobiological processes and hormone secretion. Recent studies on the dual-hormone hypothesis have indicated that basal cortisol and testosterone jointly affect dominant and aggressive behavior among adolescents and adults. Whether this hypothesis applies to prosocial-related understanding of others' mental states remains unclear. The present study investigated associations between basal testosterone, basal cortisol (and cortisol awakening response [CAR]), and the cognitive/affective theory of mind (ToM) in 243 adolescents (67.9 % male, aged 14 to 17 years, M_{age} = 16.09, standard deviation = 0.62). Cognitive ToM (cToM) and affective ToM (aToM) were assessed with a cartoon story reasoning task: In the cToM condition, participants viewed a comic strip story and needed to predict what would happen based on a character's intentions, and in the aToM condition, they viewed a comic strip of two characters interacting and needed to think about what would make the protagonist feel better. The results showed that basal testosterone and basal cortisol did not interact with each other to affect the performance of ToM, either in terms of ToM accuracy or response speed. However, under the condition of low CAR, testosterone is associated with the fast performance of cToM, although the interaction of testosterone and CAR occurred only in female adolescents. Overall, our data provide new evidence for the dual-hormone hypothesis and further extend the hypothesis to social understanding.

1. Introduction

Humans are inherently social, and the ability to infer the unobservable mental states of others is crucial for successful social interaction. Fundamental deficits in the social understanding of others' mental states are associated with several mental disorders, including antisocial personality disorder (Mokros et al., 2015), psychopathy (Hare and Neumann, 2008), autism spectrum disorders (O'Nions et al., 2014), and some personality traits related to aggressive and violent behaviors, including alexithymia (Demers and Koven, 2015; Winter et al., 2017) and callous-unemotional traits (Aoki et al., 2014). The capacity to make inferences regarding other people's mental states, including knowledge, needs, and intentions, was first called the theory of mind (ToM) in 1978 (Premack and Woodruff, 1978). Subsequently, a distinction was made between "affective" and "cognitive" ToM (Brothers and Ring, 1992; Frith and Frith, 1999, 2006; Schurz et al., 2014; Schurz et al., 2021; Shamay-Tsoory et al., 2010). Cognitive ToM (cToM) requires an understanding of others' thoughts, intentions, and beliefs, while affective ToM (aToM) concerns understanding how others feel; the latter is sometimes referred to cognitive empathy (reasoning about others' affective states) (Coundouris et al., 2020; Schurz et al., 2021; Völlm et al., 2006).

Studies have found that the first milestone in this ability appears around the age of four, and it is accompanied by the maturation of core belief processing regions (temporoparietal regions, precuneus, and medial prefrontal cortex) and their connection to the prefrontal cortex (Grosse Wiesmann et al., 2017; Wiesmann et al., 2020). The second milestone is the onset of puberty, which typically begins between 9 and 12 years of age (usually 1–2 years earlier in girls than in boys) (Baron-Cohen et al., 1999; Crone and Dahl, 2012), with evidence that hormone

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levels and neural circuitry mutually influence each other during adolescence (Blakemore, 2008a, b; Blakemore et al., 2007; Burnett et al., 2009; Sebastian et al., 2012). Given the importance of neuro-developmental and hormone levels during adolescence, we are interested in the testosterone and cortisol interaction during this period, as it provides an extraordinary opportunity to advance our understanding of cognitive functions and social-emotional behavior.

The so-called dual-hormone hypothesis is that cortisol might moderate the impact of testosterone on status-relevant behavior. Specifically, testosterone is positively related to status-seeking behaviors only when cortisol concentrations are low. When cortisol concentrations are high, testosterone's impact on status-seeking behaviors is attenuated (Mehta and Josephs, 2010; Mehta and Prasad, 2015). Recently, a context-dependent dual hormone hypothesis extends prior hypothesis and makes a distinction between two types of status motives (status-seeking and status-loss avoidance) (Knight et al., 2022). According to the context-dependent dual-hormone hypothesis, for those low-cortisol individuals, high testosterone is expected to promote status-seeking behavior as they are accompanied with a higher approach motivation to earn higher social rank. But for those high-cortisol individuals, high testosterone is expected to induce status-loss avoidance as they are accompanied with a higher avoidance motivation to avoid competing against high-status opponents (Knight et al., 2022). But in general, high testosterone consistently anticipated higher status motivation, both for status-seeking and status-loss avoidance.

Achieving high social-status is a complex process involving a variety of factors. Research has identified three major routes to status: a dominance route (Cheng et al., 2010; Maner and Case, 2016), achieved by unempathic and ruthless behaviors to coerce and intimidate, a competence route, based on demonstrations of high quality skills, knowledge and wisdom that earn respect (Cheng et al., 2010; Maner and Case, 2016), and a virtue route, based on demonstrations of moral virtue by garnering admiration from others (Bai, 2017). In recent years, an increasing number of studies have found the dual-hormone effect in adults' prosocial behavior (Sollberger et al., 2016), emotion recognition ability (Lausen et al., 2020), and self-reported empathy and empathic accuracy (Nitschke and Bartz, 2020; Zilioli et al., 2015). Prosocial behavior and empathic ability are endorsed to achieve status when the status is defined by generosity, respect, or admiration. Critically, an individual with higher social skills (theory of mind) can convey advice and transmit knowledge to achieve social prestige and maintain respect on the one hand. On the other hand, the ability of understanding of others' thoughts, beliefs, and feeling can help individuals attract more peers by conforming to followers (Cheng et al., 2010). Some researches have linked emotion recognition and empathy to high social status and leadership (Kellett et al., 2006; Rubin et al., 2005). So far, however, relatively limited research has investigated the interaction between testosterone and cortisol on social skills such as the theory of mind,

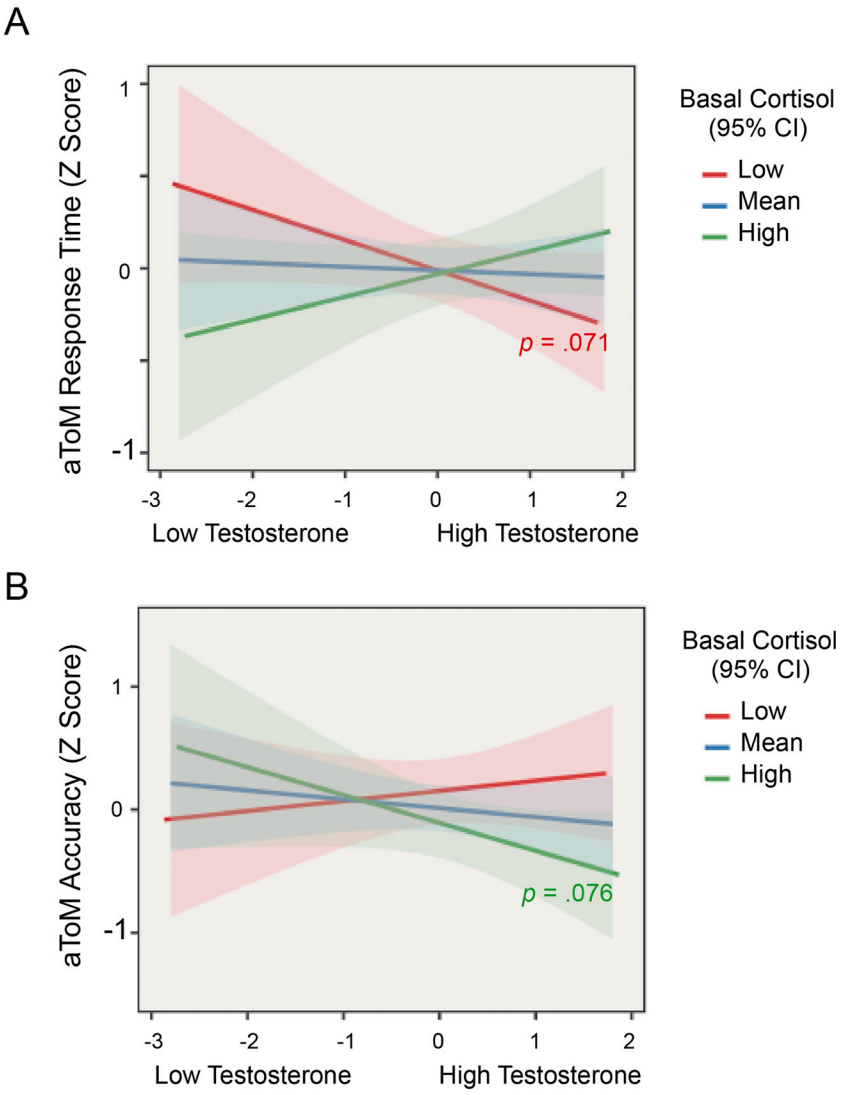

Fig. 1. Examples of stimuli from the four conditions. Physical 1 and Physical 2 are the controls for the cognitive theory of mind (cToM) and affective theory of mind (aToM), respectively. Each block began with an introductory question for 6 s that indicated the required type of inference (cToM condition: "What will the main character do next?"; aToM condition: "What will make the main character feel better?"; Physical 1 and Physical 2 conditions: "What is most likely to happen next?"). Each cartoon strip was presented for 6 s, and then another two cartoons showing the possible outcome were imposed on the bottom of the screen for 4.5 s. Participants were required to choose between the two possible outcomes of the stories by pressing the button as soon as possible. The red box represents the correct answer (derived from Völlm et al., 2006).

especially on the adolescents. Popma et al. (2007) found an interaction between cortisol and testosterone in relation to overt aggression in male adolescents (Popma et al., 2007). Duell et al. (2021) also found that high testosterone with low cortisol was associated with greater conformity with highly prosocial peers (Duell et al., 2021). However, few studies focused on the interaction between the testosterone and cortisol of adolescents in their social understanding ability.

To address these questions, we test cToM and aToM in adolescents using a validated experimental paradigm (see Fig. 1) (Völlm et al., 2006). In the cToM condition, participants view a comic strip story and need to predict what would happen next based on a character's intentions (the control condition is to view a cartoon story and predict what would happen based on physical causality). In the aToM condition, they view a comic strip of two characters interacting and need to think about what would make the protagonist feel better (in the control condition, they view a cartoon story showing two persons in neutral everyday situations and predict what would happen next based on physical causality).

Additionally, besides basal cortisol, we test another index of the hypothalamus-pituitary-adrenal (HPA) axis function, the cortisol awakening response (CAR) (Schmidt-Reinwald et al., 1999). Within the circadian rhythm of cortisol secretion, the CAR is initiated by morning awakening that involves a burst of cortisol secretion of 70–150 % within 60 min upon awakening from a night's sleep (Pruessner et al., 2003; Schmidt-Reinwald et al., 1999; Wilhelm et al., 2007). The CAR is specifically regulated by several neuroendocrine and psychological processes, it is considered an indication of the body mobilizing energy to meet the anticipated demands of the upcoming day, and unlike the general cortisol circadian rhythm, it mainly reflects phasic psychophysiological processes specific to the morning awakening (Elder et al., 2014; Fries et al., 2009; Wilhelm et al., 2007). It is often regarded as a trait measure of the basal HPA-axis reactivity and flexibility and often used as a stronger prospective predictor of stress-related mental illnesses. CAR was positively related to general life stress, major depressive disorder, and peritraumatic dissociation while negatively related to fatigue and burnout (Adam et al., 2010; Chida and Steptoe, 2009; Hardeveld et al., 2014; Wager, 2011). In a recent review, the researchers reviewed 100 original research articles related to disease risk (such as mental health, cardiovascular health, cancer, diabetes, obesity, pulmonary health, sleep, and fitness). They found that the accentuated CAR and a steeper circadian rhythm were both associated with positive health outcomes (Caulfield and Cavigelli, 2020). Another meta-analysis focused on the first-episode psychosis (FEP) and psychosis risk states, the results showed that the CAR level was attenuated in FEP but not in psychosis risk states (Misiak et al., 2021). Research indicates that the CAR rank-order between individuals remains moderately stable during adolescence (Kuhlman et al., 2019; Platje et al., 2013b; Wang et al., 2014) and can be regarded as a stable biological marker of basal HPA axis activity (Kennis et al., 2020) with a heritability of approximately 40 % (Wüst et al., 2000). The extent to which cortisol influences different functions can get through both rapid non-genomic (independent of alterations in gene expression) and slow, genomic (mediated by alterations in gene expression) effects (Joëls et al., 2006). Furthermore, these rapid and slow effects of cortisol have been shown to have different consequences (Shields et al., 2015). Previous studies have manipulated the slow genomic changes by exogenous cortisol or an isolated sampling point during the day, we focus on a more stable cortisol (CAR) that is secreted naturally instead of exogenous cortisol administration. Moreover, CAR itself has been found to have a direct or indirect relationship with empathy (Baliyan et al., 2021; Yu et al., 2019). Therefore, it is interesting and meaningful to study the joint effect of CAR and testosterone on ToM.

Taken together, it remains unclear whether there is a dual-hormone effect on social and affective understanding in adolescence. Therefore, we aim to test whether social understanding is affected by (1) testosterone, basal cortisol, or their interaction, and (2) testosterone, CAR, or their interaction. In addition, some studies have found no significant sex-related differences in ToM development (Andrews et al., 2021), while others found that girls performed significantly higher on the ToM than boys (Calero et al., 2013; Gao et al., 2019). Thus, in view of the differences between previous studies on the impact of sex on ToM, we also explore (3) whether the dual-hormone effect differs between sexes. Consistent with the dual-hormone hypothesis, we hypothesize that testosterone will decrease the ability of ToM only on the low basal cortisol or low CAR condition. In addition, we assume that there may be sex-related differences in the dual-hormone hypothesis of ToM.

2. Methods

2.1. Participants

Participants were 243 children (32.1 % female, 67.9 % male), aged 14 to 17 years (M_{age} = 16.09; standard deviation [SD] = 0.62). They were recruited at a state-run high school in Hebei Province of China, and informed parental consent was obtained for all participants. After excluding subjects who forgot to do saliva collection at home, required unreasonable sampling time, missed more than three sampling points, or forgot to bring the sampling test tube to the laboratory, the final sample included 223 participants (30.9 % female, 69.1 % male) with a mean age of 16.11 years (SD = 0.36, range: 14–17). None of the participants had any history of neurological or psychiatric disorders. All protocols were approved by the institutional review board of Beijing Normal University.

2.2. Experimental procedure

This study took place on two successive weekdays. On the first day, after completing self-report questionnaires (including the self-reported State-Trait Anxiety Inventory) (Spielberger et al., 1983), the participants were instructed on how to collect saliva samples using Salivette collection devices (Sarstedt, Nümbrecht, Germany), both verbally and through a pack containing a written version of the instructions. They were required to collect five saliva samples: one at pre-bedtime at night (S0); the remaining four samples were collected immediately upon awakening the following morning (S1), and then 15 min (S2), 30 min (S3), and 60 min (S4) later. They also had to record the sampling time to obtain reliable salivary data as outlined in previous studies (Stalder et al., 2016; Wu et al., 2015). No food, drink, or tooth brushing were allowed at least 60 min before sampling. All participants went to bed before 11:30 pm and awakened after 5:00 am the next morning, with an average sleep duration of 7.5 h. Participants were asked to keep the five saliva samples in the refrigerator or freezer, and to send them to school on the second day. After collecting the saliva samples of all children, we transported them to the external laboratory in dry ice for testing.

On the second day, the participants finished a battery of behavioral tasks including the “ToM task” in the morning at school. The order of these tasks is as follows: Trust Game, Dictator Game, Ultimatum Game, the Balloon Analogue Risk Task, and ToM task. The tasks lasted approximately 2 h, and none of them included feedback about performance or monetary payoffs. To standardize hormonal measurements among participants, we did not randomize the order of the behavioral tasks, similar to previous studies (Zethraeus et al., 2009). Only the “ToM task” is reported in this paper.

2.3. Salivary cortisol and testosterone collection and analysis

The salivary samples were taken to the laboratory where they were kept frozen (at −80 °C) until the assay. Samples from participants who reported any sickness (i.e., periodontitis, fever, or endocrine diseases), related medication regimen (especially hormone medicines) within the last two weeks, close menstrual cycle (for girls), or failure to adhere to sampling time were not analyzed further. After freeze-thawing, the samples were centrifuged at 3500 rpm for 5 min. The concentrations of

salivary cortisol were analyzed using electrochemiluminescence immunoassay (Cobas e 601, Roche Diagnostics, Nümbrecht, Germany), and those of testosterone were analyzed using an enzyme-linked immunoassay kit developed for saliva (Salimetrics, State College, PA) with sensitivity of 0.500 nmol/L (lower limit). The standard range in the assay was 0.5–1750 nmol/L for cortisol and testosterone. The intra- and inter-assay coefficient variations for cortisol were below 10 %, and we did not test the precision of testosterone because there was not enough saliva.

Cortisol was assayed from all five samples. The incidence of missing data of cortisol were 4.5 %, 1.3 %, 0.9 %, 0.9 %, and 1.8 % for basal cortisol and S1, S2, S3, and S4 separately. The cortisol was interpolated by mean value at each sampling point. Then, we calculated the CAR through the area under the curve (AUC) for four points in the morning, with respect to the first sample synchronized with the moment of awakening (Clow et al., 2010), as follows:

$$AUCi\ (morning) = (S1 + S2) \times 0.25/2 + (S2 + S3) \times 0.25/2 + (S3 + S4) \times 0.5/2 - S1 \times (0.25 + 0.25 + 0.5)]$$

Basal testosterone and basal cortisol were assayed from the pre-bedtime sample, because studies showed that humans' testosterone also has a circadian rhythm that reaches the peak level after waking and declines over the day to an evening nadir (Bremner et al., 1983; Kuzawa et al., 2016). Therefore, we believe that the pre-bedtime testosterone level is relatively stable and reliable as an indicator of baseline testosterone.

After mean imputation, both basal testosterone and basal cortisol showed a right-biased distribution while CAR level was normally distributed, so basal testosterone and basal cortisol were log-transformed (see Table S1). Before analyzing data formally, we did an independent sample *t*-test to detect whether there were sex differences in cortisol and testosterone. We found that boys had significantly greater testosterone concentrations than girls while girls had significantly greater CAR levels than boys. Therefore, CAR and testosterone were z-transformed in the two sexes respectively. Basal cortisol did not differ by sex, thus it was z-transformed directly in the overall (see Table S2).

2.4. ToM and empathic accuracy task

The task derived from Völlm et al. (2006) consists of four categories of stories:

1. cToM,
2. aToM,
3. Physical causality, one character (Physical 1), and
4. Physical causality, two characters (Physical 2).

A total of 40 comic strips were presented in eight blocks, with five different comic strips depicting a short story in each block. The sequences of the blocks and the comic strips in each block were counterbalanced. Each block began with an introductory question for 6 s to engage the corresponding mental construct in the participant (cToM condition: “What will the main character do next?”; aToM condition: “What will make the main character feel better?”; Physical 1 and Physical 2 conditions: “What is most likely to happen next?”). Then, a cartoon strip was presented for 6 s on the upper half of the screen, and two other cartoons showing the possible outcomes were imposed on the bottom of the screen for 4.5 s. Participants were required to choose between the two possible outcomes of the stories by pressing the button as soon as possible. Accuracy and response times were recorded for all cartoons. A score of 1 indicated a correct answer, while a score of 0 indicated an error.

The cToM condition required the participants to infer the character's intention, and no social interactions or emotional situations were depicted in the cToM condition. The two physical conditions relied only on the comprehension of physical causalities. The stories of cToM and Physical 1 described only one character, while aToM and Physical 2 described two characters. Therefore, Physical 1 and Physical 2 are the controls for cToM and aToM, respectively. Fig. 1 shows examples of the stimuli for each condition.

2.5. Data analysis

Statistical analyses were performed using SPSS (version 25, Chicago, IL, USA) and R (version 4.1.0). The alpha was set at 0.05 and post-hoc pairwise comparisons following significant regression analyses were corrected for multiple comparisons using a Bonferroni-corrected threshold of α’ = alpha level divided by the number of tests. The cToM (cToM-Physical 1) and aToM (aToM-Physical 2) were separately regressed on adolescent cortisol (log-transformed basal cortisol and CAR) and log-transformed testosterone and their interaction term (mean-centered)(Mehta et al., 2015). CAR varies by sex (Oskis et al., 2009; Wright and Bukowski, 2021) and has a complex relationship with age (Elder et al., 2014; Heaney et al., 2010; Knoops et al., 2010; T. Yu et al., 2020). Age and sex also play important roles in determining interindividual differences in testosterone (Barry et al., 2011; González-Sales et al., 2016; Handelsman et al., 2018). Our data show that the sex differences in testosterone concentrations are mainly in higher age groups (see Table S13 and Fig. S1), therefore, biological sex (coded as male = 1; female = 0) and age were included as covariates. Simple slope analyses were performed following statistically significant interactions at relatively low (−1 SD) and relatively high (+1 SD) levels of basal cortisol/CAR (Chafkin et al., 2021; Mehta et al., 2015). To conduct a further exploratory test for whether sex moderated the relationship between testosterone and cortisol, we added sex, the two-way interactions of cortisol × sex and testosterone × sex, and the three-way interaction of cortisol × testosterone × sex to the multiple regression models.

3. Results

3.1. Participants' psychological and endocrinal measures

Cortisol levels as a function of sampling time points (i.e., S0, S1, S2, S3, and S4) are shown in Fig. 2 and Table S1. Participants' cortisol responses prominently increased from pre-bedtime (S0, basal cortisol) to immediate awakening in the morning (S1), and they peaked around 15–30-min later (S2 and S3), followed by a rapid decline at 60 min after awakening (S4) in both sexes. Repeated-measures analyses of variance with sampling time as a within-subject factor, sex as a between-subject factor, and age as a covariate for cortisol data demonstrated a significant interaction effect of time × sex [$F(4,880) = 6.319$, $p < 0.001$, partial $\eta^2 = 0.028$] and a significant main effect of sex [$F(1,220) = 17.563$, $p < 0.001$, partial $\eta^2 = 0.074$]. Further post-hoc analyses revealed that the pre-bedtime cortisol level was significantly lower than cortisol levels at all other four points the following morning for both sexes ($p < 0.001$ for all other four points, Bonferroni corrected). No significant correlation was found between the basal cortisol and CAR ($r = -0.059$, $p = 0.383$). Independent-sample *t*-tests were also conducted to examine potential differences in CAR at the five sampling time points of cortisol and the basal testosterone between the sexes. These analyses revealed no significant differences between the sexes in their cortisol levels at pre-bedtime (S0, basal cortisol) and immediate awakening (S1; $p > 0.08$; Table S1). However, male adolescents compared with female ones showed lower morning cortisol increases [CAR, S2, S3, and S4; Fig. 2B and Table S1; $t_{CAR}(221) = -2.389$, $p < 0.05$, Cohen's d = −0.346; $t_{S2}(221) = -2.821$, $p < 0.01$, Cohen's d = −0.428; $t_{S3}(221) = -3.524$, $p < 0.001$, Cohen's d = −0.565; $t_{S4}(221) = -3.760$, $p < 0.001$, Cohen's d = −0.612]. This is consistent with previous results (Hollanders et al., 2017). Moreover, these results indicate the prominent diurnal dynamics of the HPA-axis system in adolescents, with lower basal cortisol levels

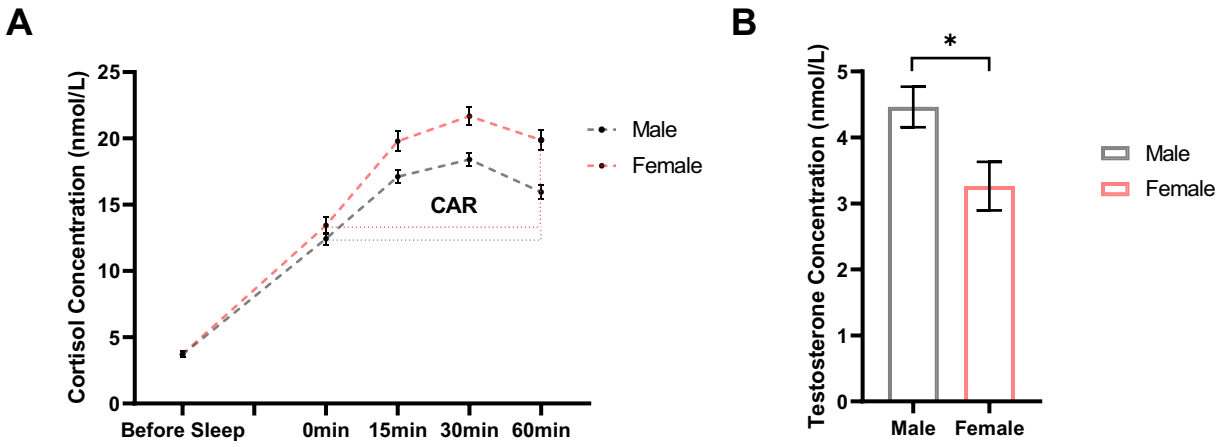

Fig. 2. Salivary cortisol and basal testosterone levels. (A) Averaged cortisol levels as a function of sampling time points between subjects of different sexes. The x-axis represents the five time points of saliva sampling at pre-bedtime during the night; within the first hour in the following morning immediately after awakening (0 min); and 15 min, 30 min, 60 min after that. The y-axis represents salivary cortisol concentration (nmol/L). Areas enclosed by the dotted line represent the cortisol awakening response (CAR) and the area under the curve of four points in the morning with respect to the first sample synchronized with the moment of awakening. The results showed that males have lower morning cortisol increases compared to females. (B) Testosterone concentration differences between male and female adolescents. Note: Error bars represent the standard error of the mean.

before sleep (i.e., S0) and elevated CAR in the morning for both sexes, especially female adolescents. We also found that the basal testosterone concentration of males was significantly higher than that of females [Fig. 2B; t (221) = 2.503, $p < 0.05$, Cohen's d = 0.334]. No significant correlation was found between basal cortisol and CAR ($r = -0.059$, $p = 0.383$).

3.2. Relationship between testosterone and ToM moderated by basal cortisol

First, we found significant correlations between aToM, cToM, Physical 1, and Physical 2 (Table S3) in both accuracy and response time. Based on previous work, we defined the cToM condition relative to the Physical 1 condition as an index of "cToM" (cToM-Physical 1, for accuracy/response time), and the aToM condition relative to the Physical 2 condition as an index of "aToM" (aToM-Physical 2, for accuracy/response time) (Borbás et al., 2021; Gao et al., 2019; Sebastian et al., 2012; Völlm et al., 2006).

Then, we created a simple descriptive statistic and found no significant sex-related differences between aToM and cToM (all $p > 0.082$), indicating that boys and girls are evenly matched in their ability of ToM. To test the classical dual-hormone effect among cToM and aToM, we developed several multiple regression models. The Benjamini–Hochberg false discovery rate (FDR) method (calculated using the p.adjust function in R) was used for multiple comparisons. These analyses revealed a significant testosterone × basal cortisol interaction for aToM response time [age and sex as covariates: B = 0.140, F (1,217) = 4.534, $p_{uncorrected}$ = 0.032, partial η^2 = 0.020, $p_{corrected}$ = 0.193; remove covariates: B = 0.144, F (1,217) = 4.775, $p_{uncorrected}$ = 0.027, partial η^2 = 0.021, $p_{corrected}$ = 0.112]. Tests of simple slopes revealed that, at low (−1 SD) levels of basal cortisol, testosterone was not associated with aToM response time [B = −0.17, F (1,217) = 3.283, $p = 0.071$, partial $\eta^2 = 0.015$]. Testosterone was also unrelated to the aToM response time at high (+1 SD) and average (mean) levels of basal cortisol [B = 0.113, F (1,217) = 1.475, $p = 0.226$, partial $\eta^2 = 0.007$, and B = −0.027, F (1,217) = 0.176, $p = 0.675$, partial $\eta^2 = 0.001$, respectively]. A graphical representation of this interaction is included in Fig. 3A. There was no significant dual-hormone effect for cToM (Tables S4 and S5).

Next, we conducted several exploratory analyses to incorporate sex into the regression model: we added sex, two-way interactions of sex × testosterone and sex × basal cortisol, and the three-way interaction of sex × testosterone × basal cortisol. The result also showed a significant testosterone × basal cortisol interaction [B = 0.183, F (1,214) = 6.457, $p_{uncorrected}$ = 0.012, partial η^2 = 0.029, $p_{corrected}$ = 0.139] for aToM response time, while the interaction of testosterone × basal cortisol was not significant [B = −0.194, F (1,214) = 3.304, $p_{uncorrected}$ = 0.159, partial η^2 = 0.015, $p_{corrected}$ = 0.477] for aToM accuracy (Tables S6). Subsequently, simple slopes revealed that, at low (−1 SD) and average (mean) levels of basal cortisol, testosterone was unrelated to aToM accuracy [B = 0.130, F (1,214) = 0.759, $p = 0.385$, partial $\eta^2 = 0.004$ and B = −0.063, F (1,214) = 0.393, $p = 0.531$, partial $\eta^2 = 0.002$, respectively]. In contrast, testosterone was negatively associated with aToM accuracy at high (+1 SD) levels of basal cortisol, although with marginal significance (B = −0.257, F (1,214) = 3.177, $p = 0.076$, partial η^2 = 0.015). A graphical representation of this interaction is provided in Fig. 3B.

We did not find significant testosterone × basal cortisol × sex interactions and the two-way interactions of testosterone × sex and basal cortisol × sex for aToM. Similarly, for cToM (accuracy and response time), we found no significant main effects of testosterone or basal cortisol, and there were non-significant interactions of testosterone × basal cortisol and testosterone × basal cortisol × sex (Table S6).

3.3. Relationship between testosterone and ToM moderated by CAR

Second, we conducted several multiple regression models to test whether testosterone and CAR jointly influence cToM and aToM. The results revealed no significant effect of testosterone, CAR, and testosterone × CAR interactions (Tables S7 and S8). Next, we did an exploratory analysis to incorporate sex into the regression model: we added sex, two-way interactions of sex × testosterone and sex × CAR, and the three-way interaction of sex × testosterone × CAR. The result showed a significant sex × testosterone × CAR interaction [B = −0.317, F (1,214) = 6.110, $p_{uncorrected} = 0.012$, partial $\eta^2 = 0.028$, $p_{corrected} = 0.055$] and a significant testosterone × CAR interaction [B = 0.258, F (1,214) = 6.327, $p_{uncorrected}$ = 0.011, partial η^2 = 0.029, $p_{corrected}$ = 0.055] for cToM response time (Table S9). We further characterized the interaction of testosterone and CAR in each sex for cToM response time. The results revealed a significant interaction of testosterone × CAR in only female adolescents [B = 0.26, F (1,65) = 5.859, $p = 0.018$, partial $\eta^2 = 0.083$ for girls, and B = −0.061, F (1,149) = −0.641, $p = 0.425$, partial $\eta^2 = 0.004$ for boys]. Subsequent simple slope analysis in girls showed that at low (−1 SD) levels of CAR, testosterone was associated with the cToM performance (faster response speed) [B = −0.30, F (1,65) = 4.221, p =

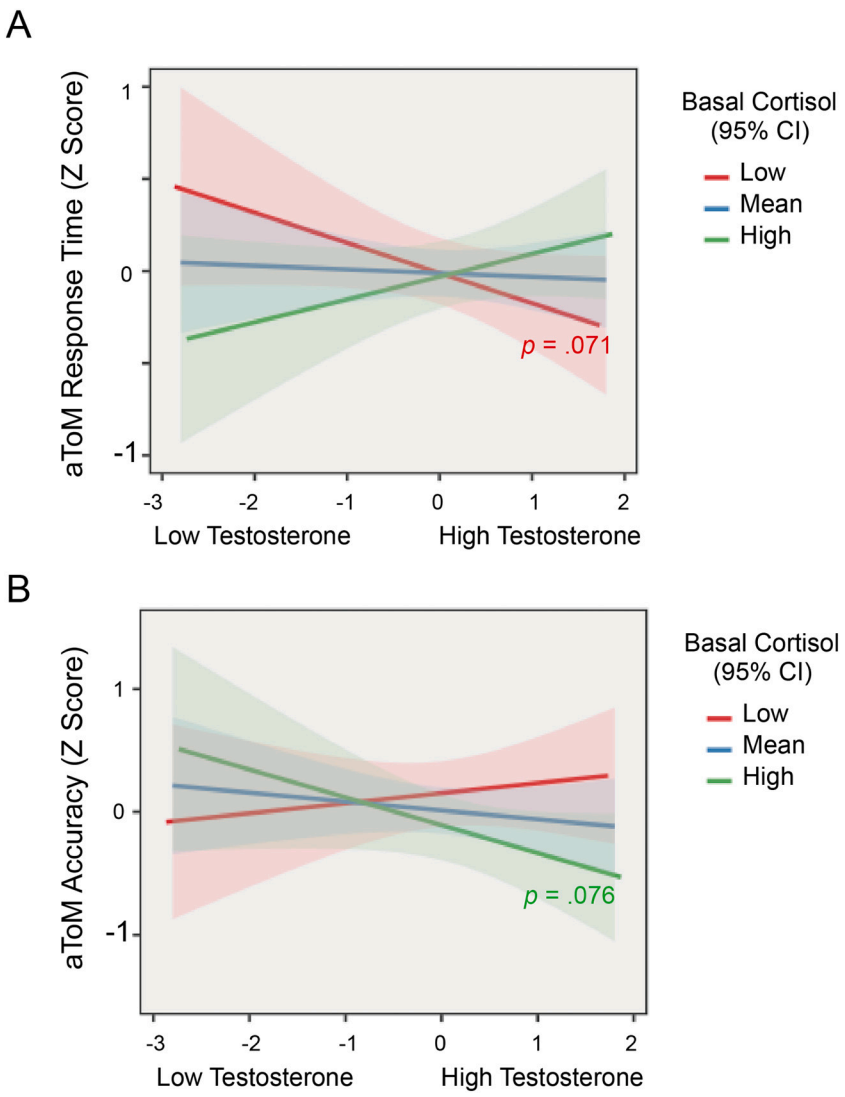

Fig. 3. Interaction of basal cortisol and testosterone in the correlation of the affective theory of mind (aToM) response time and accuracy. At low (−1 standard deviation [SD]) and high (+1 SD) levels of basal cortisol, the correlation between testosterone and aToM (both for response speed and accuracy) was insignificant. Note: Plotted points represent conditional low and high values (±1 SDs) of testosterone (standardized within each sex and cortisol log-transformed) and cortisol.

0.044, partial $\eta^2 = 0.061$]. In contrast, testosterone was unrelated to cToM performance at high (+1 SD) and average (mean) levels of CAR [B = 0.183, F (1,65) = 1.730, $p = 0.193$, partial $\eta^2 = 0.026$, and B = −0.059, F (1,65) = 0.337, $p = 0.563$, partial $\eta^2 = 0.005$, respectively]. A graphical representation of this interaction is included in Fig. 4A and B. For cToM accuracy and aToM (accuracy and response time), our results showed no significant main effects of testosterone or CAR, and we found a non-significant two-way interaction of testosterone × CAR and a three-way interaction of testosterone × CAR × sex (Tables S9).

4. Discussion

This study is the first to test the roles of testosterone and cortisol (basal cortisol and CAR) in the ToM, which is a phenomenon that lies within the realm of social cognition and is defined as the capacity to make inferences regarding other people's mental states (Premack and Woodruff, 1978). We focus on the two aspects of ToM—"affective" and "cognitive" ToM, The former refers to understanding what another is feeling, while the latter mainly emphasizes the understanding of another's thoughts, intentions, and beliefs (Burnett et al., 2009; Coundouris et al., 2020; Shamay-Tsoory et al., 2007, 2010).

First, regarding cortisol and testosterone, we found that the basal testosterone concentration of boys was significantly higher than that of girls, which has been confirmed in a large number of studies (Kyriakopoulou et al., 2013; Maestripieri et al., 2010; Ostatníková et al., 2002; Shirtcliff et al., 2002). In addition, our results found no apparent sex differences in basal cortisol on immediate awakening; however, male adolescents, compared with females, showed lower morning cortisol increase (CAR). This is consistent with the results in previous meta-analyses, which show that girls have higher CAR than boys, although the evidence is not unequivocal (Hollanders et al., 2017; Kunz-Ebrecht et al., 2004; Van der Voorn et al., 2017). We found no significant correlation between basal cortisol and CAR, which is also consistent with previous studies (Quintana, 2019). Second, we found no significant difference between boys and girls in both aToM and cToM abilities. So far, there is no unified consensus on whether sex plays an important role in the ToM ability of adolescents. Some results show that girls' cToM and aToM are better than those of boys (Arango-Tobón et al., 2020; Calero et al., 2013; Ibanez et al., 2013; Mestre et al., 2009), and others show that men's cToM is better than that of women (Gao et al., 2019). Studies have also found no sex difference in aToM or cToM (Andrews et al., 2021; Di Tella et al., 2020). This may be attributed to different ToM task paradigms and indicators, as well as the controlling of other influencing factors, such as age and intelligence (Di Tella et al., 2020). Therefore, we

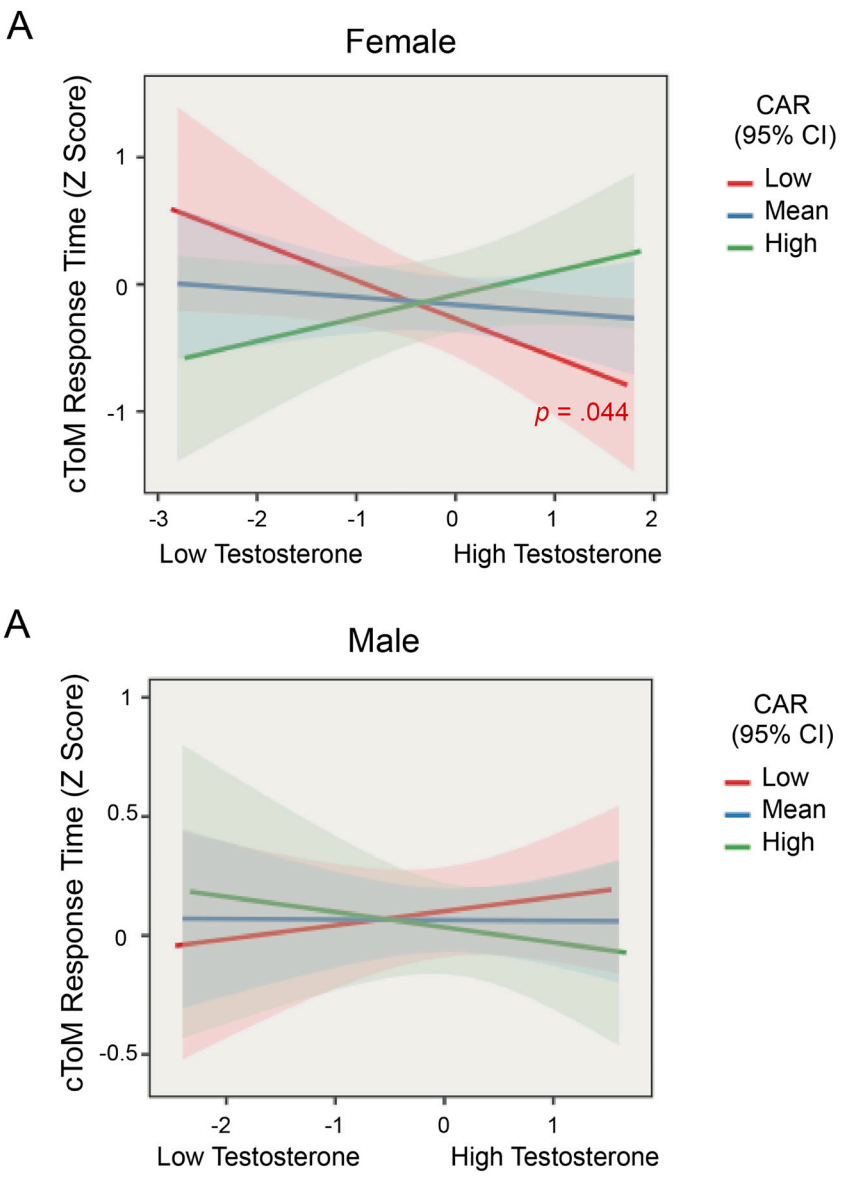

Fig. 4. Interaction of testosterone × cortisol awakening response (CAR) in the cognitive theory of mind (cToM) response time moderated by sex. (A) Testosterone was negatively associated with cToM response time in female adolescents with low CAR (−1 standard deviation), and (B) there was no interaction of testosterone × CAR in male adolescents. Note: Plotted points represent conditional low and high values (±1 SDs) of testosterone (standardized within each sex and cortisol log-transformed) and CAR.

encourage future research to use a multi-method approach to test the sex-related effect of ToM.

In light of previous results showing that cortisol regulates the relationship between testosterone and status-related behaviors, a theory known as the dual-hormone hypothesis (Mehta and Prasad, 2015; Mehta et al., 2015), the first aim of the present study was to test whether the dual-hormone hypothesis can be successfully applied to measures of the ability of ToM. Endogenous testosterone has been linked to diminished social cognitive function, and studies have found that higher levels of endogenous testosterone are negatively correlated with people's accuracy in inferring other people's thoughts and feelings (Nitschke and Bartz, 2020; Ronay and Carney, 2013). To date, much of the research has also found a link between exogenous testosterone and ToM. Exogenous testosterone impairs the ability to accurately infer motivation, attention, thoughts, and emotions from the eye area of another person's face (Van Honk et al., 2013). Use of anabolic androgenic steroids reduces aToM and cToM capacity (Vaskinn et al., 2020). Studies have found that the reduced cognitive empathy caused by exogenous testosterone is similar to the neural mechanism of autism during the "reading the mind in the eyes" test (Bos et al., 2016). Exogenous testosterone administration in men has been shown to weaken affective and cognitive empathy accuracy (Heany et al., 2020; Nadler et al., 2019; Nitschke and Bartz, 2020; Ronay and Carney, 2013; Zilioli et al., 2015). More importantly, recent studies have reported that the negative relationship between testosterone and empathy accuracy occurs only in low cortisol conditions, which is a significant dual-hormone effect (Nitschke and Bartz, 2020). However, some opposite results have been reported, for example, a study found that high T was associated with higher ToM accuracy only when cortisol levels were low (Lausen et al., 2020). Unexpectedly, our results do not provide evidence for the classical dual-hormone hypothesis, given that our results showed that basal testosterone and basal cortisol did not interact with each other to affect ToM performance, either in terms of ToM accuracy or response speed.

The second aim of the present study was to test whether the relationship between testosterone and ToM can also be moderated by CAR. CAR is described as the "tipping point" of the day—it reflects the reactivity or flexibility of the HPA axis, as it occurs within a short period when the brain switches from night-time sleep to daytime consciousness (Clow et al., 2010; Clow and Smyth, 2020; Elder et al., 2014). Moreover, because it is synchronized with the daily rhythm, CAR is stable for the long term compared with basic cortisol (Kuhlman et al., 2019; Wang et al., 2014). CAR was also shown to reflect the anticipatory

mobilization of the endocrine system for the environmental challenges of the upcoming day, as well as reflect the previous day's life stress events (Chida and Steptoe, 2009; Fries et al., 2009; Law et al., 2020; Wu et al., 2015; Xiong et al., 2021). Our results found an interaction between testosterone and CAR, although this only happened for girls. We found that testosterone increases girls' cToM response speed at low levels of CAR. In contrast, testosterone was unrelated to cToM performance speed at high and average (mean) levels of CAR. Given the maturation of the nervous system and the development of executive function and reaction speed that accompanied by children and adolescents, reaction time can be taken as evidence for spontaneous mentalizing (Blakemore, 2008a, b; Blakemore and Mills, 2014). In addition to response accuracy, response speed has been used as an indicator of ToM capability in many studies (Apperly et al., 2011; de la Osa et al., 2016; Lausen et al., 2020; Nijhof et al., 2017). Previous studies on brain and behavior also demonstrated the specificity between aToM and cToM, with most studies showing that sex influences the neural correlates of cToM (Gabriel et al., 2021; Gao et al., 2019) but not aToM. It is worth noting that we did not find the interaction of testosterone and CAR in male adolescents. Therefore, it is still unclear whether this is just a sex-specific effect, or if it is an overall effect that applies to boys and girls, because there is a relatively large sample size difference between males and females in our study. Future research should consider a more balanced sample and verify this result for multiple ToM indicators, such as false belief attribution tests or reading the mind in the eyes task tests (Schurz et al., 2014).

Notably, our results appear to be contrary to our hypothesis, as we assume that testosterone decreases ToM performance under low cortisol conditions, whereas our results suggest that testosterone increases the response speed of cToM. A similar result was found in a previous study where high testosterone was associated with higher response accuracy when cortisol levels were low (Lausen et al., 2020). Although endogenous testosterone has often been associated with weaker social cognitive functioning in previous studies, such as higher levels of endogenous testosterone are negatively correlated with people's accuracy in inferring other people's thoughts and feelings (Nitschke and Bartz, 2020; Ronay and Carney, 2013). It is worth noting that these results have often been found to differ by gender. For example, studies have found that testosterone in young men can significantly negatively predict the performance of ToM, however, it is not observed in women (Grainger et al., 2021; Lausen et al., 2020). In addition, previous studies have paid little attention to ToM response speed indicators, which makes it difficult to directly compare our results with others' studies, and we recommend that researchers may pay attention to response time, because the social cognitive speed of children and adolescents is in a continuous developmental stage, and if they already perform well in terms of ToM response accuracy (above 80 % for both boys and girls in our study), then the examination of response speed becomes important. Although our results are inconsistent with the hypothesis regarding the relationship between testosterone and ToM, the results are consistent with the direction of the dual-hormone hypothesis that testosterone is associated with ToM performance only under low cortisol (CAR) conditions. Cortisol can suppress the effects of basal testosterone's link to status-related behavior both in by a slow genomic way (Knight et al., 2022; Mehta et al., 2017) and a rapid non-genomic way (Prasad et al., 2019a; Prasad et al., 2017). Previous research tested the slow-moving genomic changes through one time point accompanied by the behavior (Mehta et al., 2017) or 240 min after receiving a 10 mg hydrocortisone (Henckens et al., 2011), consistent with slow genomic mechanisms, our measurement of cortisol (CAR) was a regular and naturally secreted cortisol, the sampling time is independent and ahead of the behavioral measurements. As a pattern of secretion of cortisol, the CAR has been shown to exert a slow genomic effect on brain functional of hippocampal-prefrontal coupling (Xiong et al., 2021) and the functional connectivity of the medial prefrontal cortex (mPFC) and other brain areas, including the angular gyrus, and middle temporal gyrus (Wu et al., 2015), which are considered as parts of the social brain (Blakemore, 2008a, b). A possible molecular mechanism for cortisol's suppressive effects on basal testosterone's link to status-related behavior is the “functional cross-talk” between the hypothalamic-pituitary-adrenal (HPA) and hypothalamic-pituitary-gonadal (HPG) axes (Viau, 2002). The cross-talk means that each axis mutually inhibits the other, for example, cortisol may affect the secretion of the gonadotrophins through the secretion of GnRH or the feedback actions of gonadal hormones (Tilbrook, 2000). The cross-talk also occurs at the receptor level, for instance, the suppression of androgen receptors accompanying by HPA axis reactivity (Handa and Weiser, 2014; Phumsatitpong et al., 2021). Therefore, given the possible functional cross-talk between the HPA axis and the HPG axis, the dual hormone effect applies not only to the status-related behaviors, and it is likely that cortisol consistently suppresses other behaviors that are closely related to testosterone, such as empathy or theory of mind.

This study has some limitations. First, the CAR data were obtained from saliva sampled on one day only. Although previous studies reported that CAR shows relatively high stability across days (Edwards et al., 2001), recent research has increasingly recommended that CAR data should be assessed over two or more sampling days to achieve reliable trait data on CAR (Hellhammer et al., 2007; Stalder et al., 2016). Second, although we took all possible precautions in the sampling procedure, including being passively awakened by an alarm clock and self-report of exact sampling times, it is still difficult to obtain an absolutely unbiased CAR estimate at a home environment (Stalder et al., 2016). In the current study, the participants were instructed to place saliva samples in their home freezer immediately after finishing the collection and to return them to the lab as soon as possible, while the potential effects of short-term thawing during transport were inevitable. We provided cortisol metrics at all sampling time points (including total post-awakening cortisol levels, e.g., AUCG) in the supplementary material, which could further be explored by interested researchers. Third, although enzyme immunoassays are widely used to measure salivary testosterone in preadolescent children and adolescents (Grotzinger et al., 2018; Ostatníková et al., 2002), recent studies have proved that this method is not stable enough, especially for lower testosterone concentrations (Prasad et al., 2019b; Welker et al., 2016). We encourage future researchers to measure salivary testosterone by more reliable and accurate methods such as liquid chromatography tandem mass spectrometry, which has been confirmed to reliably and accurately measure testosterone concentrations in both adults' and adolescents' saliva samples (Büttler et al., 2016; Keevil et al., 2014). Finally, there are many regressors in our multiple regression models, and the *p*-values for significance cutoffs were not significant after multiple comparisons. Therefore, we recommend that future researchers conduct a preregistration to address the flexibility of analytical methods and improve reproducibility. Besides, our research found associations between hormone concentrations and social understanding, but we cannot draw causal conclusions. Pharmacology experiments that manipulate hormone concentrations are needed to confirm causality. For example, previous research found that amplified CAR is associated with extensive psychological and physical conditions, including depression and chronic stress (Chida and Steptoe, 2009). Blunted CAR has been found to be related to fatigue, burnout, and posttraumatic stress disorder (Boehringer et al., 2015; Law and Clow, 2020; Rauch et al., 2020). Further, recent evidence has indicated a close link between blunted CAR and antisocial behavior, such as conduct problems during childhood (Owens, 2017), aggressive behavior in adults (Böhnke et al., 2010), and aggression perpetration and rule-breaking in male adolescents (Platje et al., 2013a, c; Richards et al., 2018; Yu et al., 2016). Additional research has also found that individuals with alexithymia and callous-unemotional traits have lower CAR (Alkan Härtwig et al., 2013; Von Polier et al., 2013). Therefore, future research can seek pharmacological methods to increase or decrease CAR on the one hand and, on the other, also focus on patients who experience changes in CAR and cortisol.

In addition to the aforementioned limitation, we should note that the meta-analysis showed that the effect size of the interaction between testosterone and cortisol on status-relevant behavior was small (Dekkers et al., 2019). Other conclusions did not support the dual hormone hypothesis (Glenn et al., 2011; Grebe et al., 2019; Pfattheicher, 2016), and some studies found that the relationship between testosterone and status-relevant behavior under a higher cortisol condition (Singh, 2021; Welker et al., 2014). Therefore, future studies are needed to better define different patterns of the dual hormone hypothesis, such as exploring the regulation of testosterone on cortisol-behavior relationship or exploring other possible mediators, or exploring the direction of the regulation of two hormones.

5. Conclusions

Our study provides evidence for demonstrating that under the condition of low CAR, testosterone predicts the performance of ToM (faster response speed), although the interaction of testosterone and CAR was found only in female adolescents. Overall, our data provide new evidence for the dual-hormone hypothesis and further extend the hypothesis to social understanding.

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CRediT authorship contribution statement

Huagen Wang: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft. **Sihui Zhang:** Conceptualization, Data curation. **Simeng Wu:** Conceptualization, Data curation. **Shaozheng Qin:** Supervision, Funding acquisition. **Chao Liu:** Supervision, Funding acquisition, Project administration.

Declaration of competing interest

The authors declare no competing financial interests.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.yhbeh.2022.105258.

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