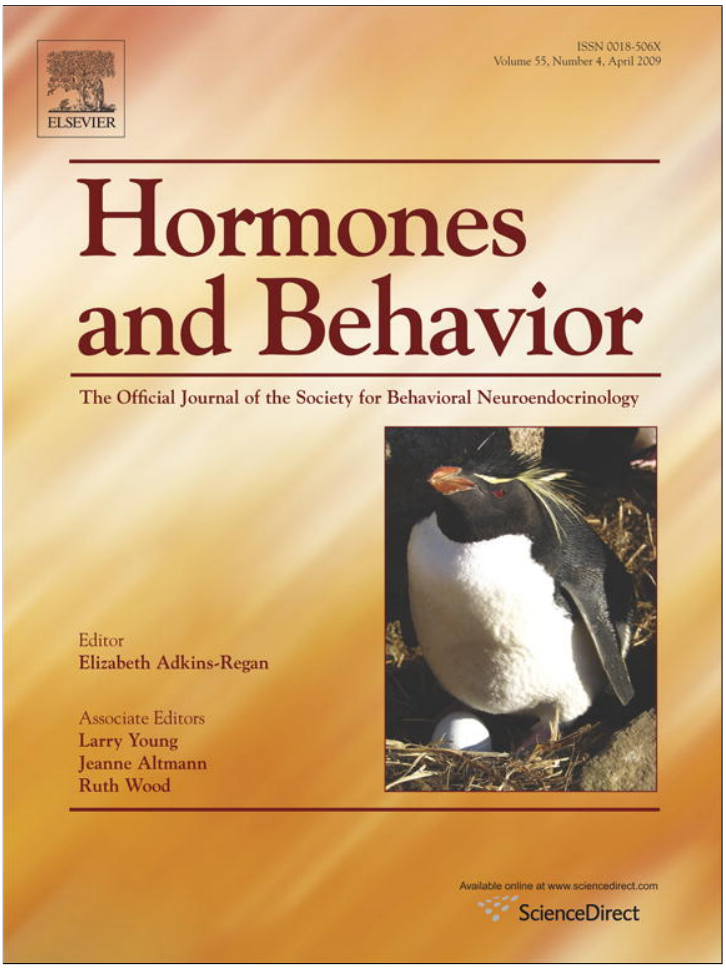

Hormones and Behavior 55 (2009) 507–513

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Social cognition under stress: Differential effects of stress-induced cortisol elevations in healthy young men and women

Tom Smeets [a,*], Isabel Dziobek [b], Oliver T. Wolf [c]

[a] Faculty of Psychology and Neuroscience, Maastricht University, P.O. Box 616, 6200 MD Maastricht, The Netherlands
[b] Neurocognition of Decision Making, Max-Planck-Institute for Human Development, Germany
[c] Department of Cognitive Psychology, Ruhr-Universität Bochum, Germany

ARTICLE INFO

Article history:
Received 15 December 2008
Revised 28 January 2009
Accepted 30 January 2009
Available online 7 February 2009

Keywords:
Social cognition
Sex differences
Trier Social Stress Test (TSST)
Cortisol (CORT)
Tend-and-befriend

ABSTRACT

Humans as social beings often have to perform complex social cognitive tasks while under stress (e.g., during a social conflict). Previous research has established that the brain regions responsible for social cognitive tasks are target regions for stress hormones. However, little experimental research has been done testing the acute effects of stress on social cognition. Here, we investigated whether stress exposure and the ensuing glucocorticoid (i.e., cortisol) elevations affect social cognition. Thirty-two men and 32 women were exposed to either a psychosocial stress or a non-stressful control test before assessing their social cognition using the Reading the Mind in the Eyes Test (RMET) and the Movie for the Assessment of Social Cognition (MASC). Results showed differential effects of stress-induced cortisol responses among men and women for the MASC, but not the RMET. Among men, high cortisol responders displayed elevated MASC scores compared with low cortisol responders. Moreover, for stressed men a positive association between the magnitude of the cortisol responses to the stressor and MASC scores emerged. Among women, enhanced MASC scores were found for low cortisol responders relative to high cortisol responders and non-stressed controls. A strong negative association between cortisol reactivity and MASC scores was found among women. These results imply sex specific effects of glucocorticoids on social cognition and partially support the idea of sex differences in biobehavioral stress responses, with men engaging in fight-or-flight responses while women may react to stress with tending and befriending behavior.

Introduction

The ability to form enduring social relationships permeates human society and in large part is dependent on individuals' social cognition. Social cognition refers to the mental operations that underlie social interactions and includes the ability to attribute mental states (e.g., emotions, thoughts, intentions) to oneself and others. A key brain structure implicated in successful social cognition is the prefrontal cortex (PFC) (for review, see Gallagher and Frith, 2003; Olsson and Ochsner, 2008; Singer, 2006). Aside from being implicated in social cognition, the PFC is also concerned with the feedback regulation of the stress responsive hypothalamic-pituitary-adrenal (HPA) axis (e.g., de Kloet et al., 1998). Of course, there is abundant evidence that the secretion of glucocorticoid (GC) stress hormones (e.g., cortisol; CORT) may modulate memory functioning (e.g., de Kloet et al., 1999; McGaugh and Roozendaal, 2002; Wolf, 2008). However, despite vigorous research of the past decades, only very few studies have focused on social aspects of information processing.

Meanwhile, there is considerable evidence suggesting that the effects of stress-induced CORT elevations on memory performance may be moderated by sex differences (e.g., Andreano and Cahill, 2006; Wolf et al., 2001). For example, Wolf et al. (2001) found that within a group of young adults exposed to the Trier Social Stress Test (TSST; Kirschbaum et al., 1993), CORT increases displayed a strong and negative correlation with memory retrieval performance in men, while no such correlation was found among women. Similarly, Andreano and Cahill (2006) demonstrated that low, but not high, CORT responses to stress enhanced memory consolidation and that this effect was restricted to male participants. In line with the results of Andreano and Cahill (2006), a number of studies (e.g., Buchanan and Tranel, 2008; Nater et al., 2007) have shown that memory modulation following stress exposure may depend on the magnitude of the CORT response.

In relation to this, it has been proposed that the biobehavioral response to stress differs between men and women (Taylor et al., 2000). Traditionally, the primary human stress response has been characterized as a "fight-or-flight" response. According to Taylor and colleagues, men and women share this fight-or-flight response on the physiological level, yet they differ in their behavioral stress response. Specifically, Taylor et al. (2000) suggest that, depending on the nature of the stressor, men either fight or flee. Women, on the other hand,

* Corresponding author. Fax: +31 43 3884196.
E-mail address: tom.smeets@psychology.unimaas.nl (T. Smeets).

0018-506X/$ – see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.yhbeh.2009.01.011

engage in a so-called "tend-and-befriend" behavioral stress response. Here, tending refers to nurturing activities that are adaptive when the offspring is nearby, while befriending refers to the construction and maintenance of social relationships to alleviate stress. This latter issue points to the distinct possibility that in times of stress, women might show enhanced social cognition.

With this in mind, the current study was set out to determine whether stress-induced CORT elevations would yield sex-specific effects on one of the most important types of human social cognition, namely the ability to attribute internal states to oneself or others based on external cues (e.g., facial expressions, speech).

Materials and methods

Participants

Thirty-two male and 32 female undergraduates with a mean age of 25.89 years (SD=4.33) participated in the current study. Suffering from cardiovascular diseases, severe physical illnesses (e.g., fibromyalgia), hypertension, endocrine disorders, substance abuse, heavy smoking (>10 cigarettes/day) or being on any kind of medication served as exclusion criteria. Women using oral contraceptives were also excluded from participation. Test protocols were approved by the national ethic committee of the German Psychology Association (DGPs). All participants signed a written informed consent and were given a small financial compensation (20€; approximately 30$) in return for their participation.

Materials

Autism Spectrum Quotient (AQ)

The Autism Spectrum Quotient (Baron-Cohen et al., 2001a) is a self-report questionnaire measuring the degree to which an adult of normal IQ possesses traits related to the autistic spectrum. Scores range from 0 to 50, with higher scores indicating more autistic traits. In the present study, the AQ served to evaluate potential group differences in subclinical autistic symptomatology that may affect social cognition.

Negative affect

Negative affective experiences following the stress or control task were measured using the Positive and Negative Affect Schedule state version (PANAS; Watson et al., 1988). The PANAS is a sound psychometric tool (Watson et al., 1988; see also Crawford and Henry, 2004) consisting of two subscales that quantify positive affect (PA) and negative affect (NA). The NA subscale comprises 10 items for which respondents indicate on a 5-point scale (anchors: 1=very slightly or not at all; 5=extremely) the extent to which certain feelings and emotions apply to them. Higher scores are indicative of higher levels of experienced negative affect. In the current study, the NA subscale was administered at baseline and immediately after the TSST or control task.

Reading the Mind in the Eyes Test — Revised (RMET-R)

The Reading the Mind in the Eyes Test — Revised version (Baron-Cohen et al., 2001b) measures the performance of inferring mental states of individuals using only the information conveyed in those individuals' eyes. For each of the 36 sets of eyes that were shown, participants were instructed to choose one out of four mental state descriptors. To control for general deficits in face recognition, participants were also asked to indicate the sex of the individual in the picture.

Movie for the Assessment of Social Cognition — Multiple Choice version (MASC-MC)

To assess social cognitive competence the Movie for the Assessment of Social Cognition (MASC; Dziobek et al., 2006a) was used. The MASC is a computerized test for the assessment of mindreading abilities that approximates the demands of everyday life. It involves watching a 15 min film about four characters getting together for a dinner party and it requires subjects to make inferences about the featured characters' mental states. The film is stopped at 45 points during the plot and questions referring to the characters' feelings, thoughts, and intentions are asked (e.g., "What is Betty feeling?", "What is Cliff thinking?"). Participants' correct responses are scored as one point and added to an overall score. In addition, the MASC allows separate quantification of the extent to which emotional mental states (EMS; e.g., anger, disappointment) and non-emotional mental states (non-EMS; e.g., thoughts, action plans) are inferred correctly (Dziobek et al., 2006b). Moreover, it allows separate quantification of individuals' tendency (*i*) to make overly complex inferences based on social cues that result in errors (OCI_{error}), i.e., to over-interpret social signs, (*ii*) to make overly simplistic inferences (OSI_{error}), i.e., to under-interpret social signals, and (*iii*) to not make any inferences at all from social cues (NI_{error}). We used the multiple-choice version of the MASC that offers four options for each query (MASC-MC; Fleck et al., 2006). The MASC is a reliable instrument that has proven sensitive in detecting even subtle mindreading difficulties in individuals of normal IQ (Dziobek et al., 2006a).

Stress manipulation

The Trier Social Stress Test (Kirschbaum et al., 1993) is a psychosocial challenge test consisting of a preparation period, a free speech, and a mental arithmetic task in front of an audience while being videotaped. The TSST is a valid and reliable procedure to induce physiological stress responses in children and young as well as elderly adults (e.g., Kirschbaum et al., 1992; Kudielka et al., 2004a,b). The TSST was found to provoke the most robust CORT stress responses relative to various other laboratory stress tasks (Dickerson and Kemeny, 2004).

Design and procedure

A 2 (Group: stress vs. control)×2 (Sex: men vs. women) between-subject design was employed. Specifically, the 32 male and 32 female participants were randomly assigned to a psychosocial stress or a no-stress control group. Participants were tested in sessions run between 09 h and 11 h. To allow for controlled saliva collection participants were asked not to brush their teeth and were deprived of food, drinks, and heavy exercise at least 1 h prior to the test phase. During the first 35 min after arrival in the laboratory, participants were informed about the TSST and social cognition tests, gave written informed consent, and completed the AQ and PANAS NA. The stress group was subsequently exposed to the TSST (cf. supra) while the no-stress control group completed a non-stressful control task of equal duration (i.e., delivering a speech and performing an undemanding counting task by themselves in an otherwise empty room; see Kuhlmann et al., 2005; Schoofs et al., 2008). Immediately following TSST or control task, participants completed the PANAS NA a second time and were subsequently exposed to the RMET-R and MASC-MC. Finally, participants were debriefed, paid, and thanked for their participation. Fig. 1 summarizes the timeline of the experimental protocol.

Saliva sampling and biochemical analyses

CORT was measured in response to the TSST as a measure of activity of the stress-responsive HPA-axis. CORT data were obtained with cotton Salivette (Sarstedt®, Etten-Leur, the Netherlands) devices over a 65 min period at four assessment points: $t-5$ (baseline), $t+20$, $t+30$ and $t+60$ min with reference to the start of the stressor. The saliva samples were stored at −20 °C immediately on collection. Free CORT levels were determined by a commercially available

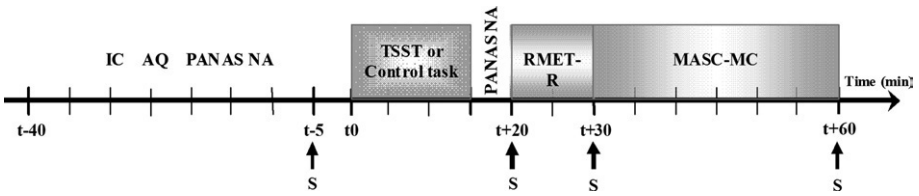

Fig. 1. Sequence of completing questionnaires, performing stress or control task, completing tests of social cognition, and salivary cortisol measurements; IC = Informed Consent; AQ = Autism Spectrum Quotient; PANAS NA = Negative Affect; TSST = Trier Social Stress Test; RMET-R = Reading the Mind in the Eyes Test, Revised; MASC-MC = Movie for the Assessment of Social Cognition, Multiple Choice version; S = Salivette device for cortisol sampling.

luminescence-assay (LIA; IBL, Hamburg, Germany) with high sensitivity (lower detection limit: 0.15 ng/ml). Mean intra- and inter-assay coefficients of variation both were 7%.

Data analysis

Potential group differences in background characteristics (age, BMI, and AQ) were evaluated using 2 (Group: stress vs. control)×2 (Sex: men vs. women) Analysis of Variance (ANOVA). Negative affect following TSST/control task was evaluated with a 2 (Group: stress vs. control)×2 (Sex: men vs. women)×2 (Time: pre-stress vs. post-stress) ANOVA. Shapiro–Wilk tests of normality showed skewness of CORT data and, therefore, these data were log-transformed before use in subsequent analyses. Because our primary interest was the effect of stress-induced CORT elevations on social cognition, the stress group was split into low and high CORT responders on a post-hoc median split basis for men and women separately. This resulted in a group of 16 low CORT responders (8 men and 8 women) and 16 high CORT responders (8 men and 8 women). CORT responses were evaluated using a 3 (ResponderGroup: controls vs. low CORT responders vs. high CORT responders)×2 (Sex: men vs. women)×4 (Time: $t-5$ vs. $t+20$ vs. $t+30$ vs. $t+60$) ANOVA. Δ CORT responses were defined as the highest CORT level following TSST or control task minus the baseline measurement and evaluated with a 3 (ResponderGroup: controls vs. low CORT responders vs. high CORT responders)×2 (Sex: men vs. women) ANOVA. Social cognition data were scored as follows. First, the control task of the RMET showed that none of the participants experienced difficulties in judging the sex of the depicted faces and, therefore, these data will not be addressed further. RMET performance was quantified as the proportion correct answers of the 36 reading the mind in the eyes stimuli. Second, similar to the RMET, MASC-MC performance was assessed by computing the proportion correct answers of the 45 individual items. RMET and MASC-MC scores were subsequently analyzed using 3 (ResponderGroup: controls vs. low CORT responders vs. high CORT responders)×2 (Sex: men vs. women) ANOVAs. Within the stress group, Pearson correlations were computed between RMET and MASC-MC scores and Δ CORT responses to the TSST for each sex separately. When sphericity assumptions were violated, Greenhouse–Geisser corrected p-values are reported. Alpha was set at 0.05 and adjusted (Bonferroni) for multiple comparisons where necessary.

Results

Background characteristics

With regard to age and AQ scores, there were neither main effects of Group or Sex, nor a Group×Sex interaction (all $ps>0.10$). Men had higher BMI scores than women ($p<0.01$).

Negative affect following TSST/control task

ANOVA revealed significant Group×Time [$F(1,60)=15.26$; $p<0.001$] and Sex×Time [$F(1,60)=5.75$; $p=0.020$] interactions. Therefore, ANOVAs were run for men and women separately. For men, the ANOVA showed a main effect of Time [$F(1,30)=4.32$; $p=0.046$] and a Group×Time interaction [$F(1,30)=9.23$; $p=0.005$], but no main effect of Group. Follow-up t-tests indicated that the control group displayed a decrease in NA over time while the stress group increased in NA (both $ps<0.05$). For women, a main effect of Group [$F(1,30)=7.28$; $p=0.011$] and a Group×Time interaction [$F(1,30)=7.55$; $p=0.010$] emerged, but no main effect of Time. Similar to men, NA decreased over time for women in the control group, but increased in the stress group (both $ps<0.05$).

CORT stress responses

Fig. 2 shows CORT responses for men and women in the control group, and low and high CORT responders in the stress group. As the ResponderGroup×Sex×Time interaction reached significance [$F(6,168)=2.31$; $p=0.05$], ANOVAs were run for men and women separately. For men, significant effects of Time [$F(3,84)=8.65$; $p<0.001$] and ResponderGroup×Time [$F(6,84)=16.25$; $p<0.001$] were obtained while the main effect of ResponderGroup approached significance ($p=0.06$). Follow-up tests for men showed that (1) the 3 groups did not differ at baseline, (2) high CORT responders displayed higher CORT levels at $t+20$, $t+30$, and $t+60$ when compared with controls (all $ps<0.01$), and (3) low CORT responders differed from controls only at $t+60$ ($p<0.05$). Similarly, for women ANOVA yielded significant effects of Time [$F(3,84)=9.53$; $p<0.001$], ResponderGroup [$F(2,28)=11.61$; $p<0.001$], and ResponderGroup×Time [$F(6,84)=34.67$; $p<0.001$]. Follow-up tests for women showed that (1) groups had similar CORT levels at baseline, (2) high CORT responders displayed higher CORT levels at $t+20$, $t+30$, and $t+60$ when compared with controls (all $ps<0.01$) and at $t+20$ as well as $t+60$ when compared with low CORT responders ($p<0.05$), and (3) low CORT responders differed from controls at $t+30$ and $t+60$ ($p<0.01$).

Mean (untransformed) Δ CORT responses for male controls, low CORT responders, and high CORT responders were −1.25 nmol/l (±0.81), 5.10 nmol/l (±2.10), and 13.33 nmol/l (±2.58), respectively. For women, mean (untransformed) Δ CORT responses for controls, low CORT responders, and high CORT responders were −2.48 nmol/l (±0.51), 5.40 nmol/l (±1.07), and 14.86 nmol/l (±2.23), respectively. ANOVA showed a main effect of ResponderGroup [$F(2,56)=147.83$; $p<0.001$], but no main effect of Sex or a ResponderGroup×Sex interaction. As to be expected, controls had significantly smaller Δ CORT responses to the control task than low and high CORT responders did to the TSST (both $ps<0.001$). Likewise, low CORT responders had smaller Δ CORT responses to the TSST than did high CORT responders ($p<0.001$).

Reading the Mind in the Eyes Test

Mean RMET scores for male controls, low CORT responders, and high CORT responders were 0.79 (±0.03), 0.83 (±0.04), and 0.80 (±0.03). For women, mean scores were 0.79 (±0.03), 0.84 (±0.04), and

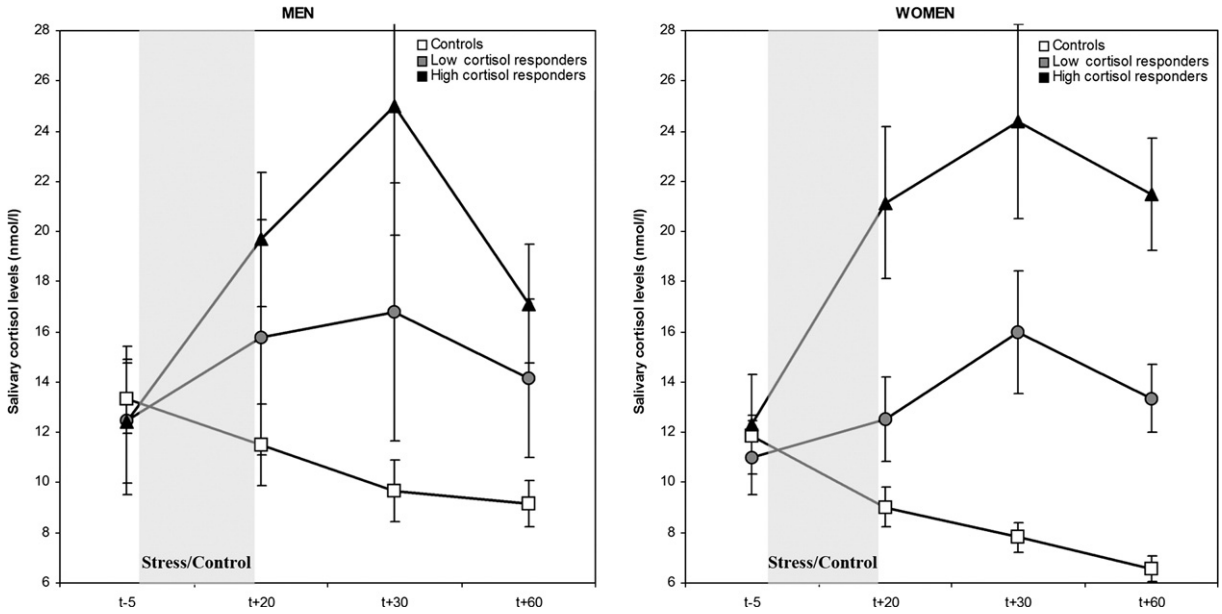

Fig. 2. Mean salivary cortisol concentrations (nmol/l) of male and female no-stress controls and low and high cortisol responders in the stress group. Data points indicate cortisol concentrations throughout the session. Error bars represent standard error of mean (S.E.).

0.71 (±0.02). ANOVA showed no effects of ResponderGroup, Sex, or the ResponderGroup×Sex interaction.

Movie for the Assessment of Social Cognition

Fig. 3 shows MASC-MC scores for male and female controls, low CORT responders, and high CORT responders. ANOVA revealed a significant ResponderGroup×Sex interaction [$F(2,58)=10.22$; $p<0.001$] in the absence of main effects of ResponderGroup or Sex. Further exploring this interaction, univariate ANOVAs on MASC-MC scores were run for men and women separately. ANOVA showed that the effect of ResponderGroup was significant for both men [$F(2,29)=4.00$; $p=0.029$] and women [$F(2,29)=6.33$; $p=0.005$]. Follow-up tests among men showed that male high CORT responders had a higher proportion correct score compared with male low CORT responders ($p<0.01$), but not when compared with male controls. Male controls also did not differ from male low CORT responders. Similarly, follow-up tests among women showed that compared with female low CORT responders, both female controls ($p<0.05$) as well as female high CORT responders ($p<0.01$) displayed a lower proportion correct score. Female controls did not differ from female high CORT responders.

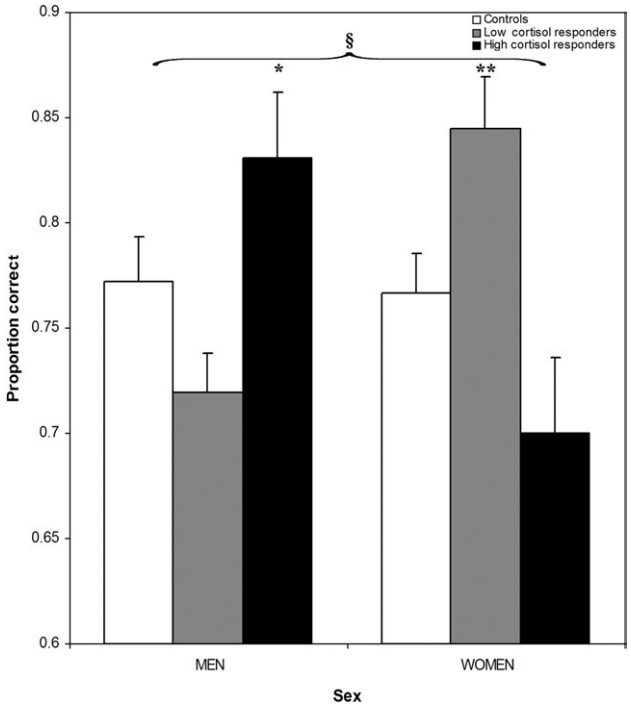

Fig. 3. Mean proportion correct answers on the Movie for the Assessment of Social Cognition test of male and female no-stress controls and low and high cortisol responders in the stress group. Error bars represent the standard error of mean (SE). §$p<0.001$ for the ResponderGroup×Sex interaction term; *$p<0.01$ when compared with male low cortisol responders; **$p<0.05$ when compared with female controls and $p<0.01$ when compared with female high cortisol responders.

To identify which aspects of social cognition were enhanced in male high CORT responders and in female low CORT responders, ResponderGroup ANOVAs followed by post-hoc contrasts (LSD) were run for men and women separately on the MASC-MC subscales emotional mental states (EMS) and non-emotional mental states (non-EMS), as well as the amount of errors due to making overly complex inferences (OCI_{error}), the amount of errors due to making overly simplistic inferences (OSI_{error}), and the amount of errors due to not making any inferences from social cues (NI_{error}) (see Table 1). For men, OCI_{error} were less frequent among high CORT responders than among non-stressed controls and low CORT responders (both $ps<0.05$). Alternatively, high CORT responding women had lower EMS scores than non-stressed controls ($p<0.05$) and low CORT responding women ($p<0.01$). In addition, high CORT responding women had higher OCI_{error} rates than non-stressed controls and low CORT responding women (both $ps<0.01$).

Associations between Δ CORT responses and social cognition

To further evaluate the role of stress-induced CORT elevations in influencing social cognition, correlations between RMET and MASC-MC scores and Δ CORT responses within the stress group were computed. A significant and positive association was found between Δ CORT responses and MASC-MC scores for stressed men ($r=.54$; $p=0.03$). Among stressed women, a strong negative association between Δ CORT responses and MASC-MC scores was obtained

Table 1
Movie for the Assessment of Social Cognition scores for the dimensions emotional mental states (EMS) versus non-emotional mental states (non-EMS), errors due to making overly complex inferences (OCI_{error}), errors due to making overly simplistic inferences (OSI_{error}), and errors due to not making any inferences from social cues (NI_{error}) of non-stressed men and women in the control group and low and high cortisol responding men and women in the stress group

	Men			Women		
	Non-stressed controls	Low cortisol responders	High cortisol responders	Non-stressed controls	Low cortisol responders	High cortisol responders
EMS	0.75±0.04	0.68±0.05	0.84±0.05	0.79±0.03	0.87±0.04	0.69±0.04**/***
Non-EMS	0.79±0.03	0.78±0.04	0.85±0.03	0.77±0.03	0.82±0.05	0.75±0.05
OCI_{error}	0.13±0.01	0.15±0.03	0.08±0.01*	0.10±0.01	0.08±0.01	0.16±0.02****
OSI_{error}	0.06±0.01	0.08±0.01	0.06±0.02	0.09±0.01	0.08±0.01	0.09±0.02
NI_{error}	0.03±0.01	0.04±0.01	0.03±0.01	0.05±0.01	0.03±0.02	0.04±0.01

Values represent mean proportion scores (range: 0–1.00)±standard error of mean.
* $p<0.05$ when compared with controls and low cortisol responders.
** $p<0.05$ when compared with controls.
*** $p<0.01$ when compared with high cortisol responders.
**** $p<0.01$ when compared with controls and low cortisol responders.

($r=-.56$; $p=0.02$). These correlations differ significantly from each other (Fisher's $Z=3.15$; $p<0.01$). No significant associations were found with regard to RMET scores.

Discussion

The current study investigated whether stress-induced CORT elevations would yield sex-specific effects on social cognition. Results from this study can be summarized as follows. First, no differences in RMET scores were found between low CORT responders, high CORT responders, and non-stressed controls. However, on the more ecologically valid and complex and, thus, more sensitive video-based MASC measure (e.g., Dziobek et al., 2006a,b), we obtained evidence for sex specific effects of stress-induced CORT responses. Specifically, male high CORT responders scored higher on the MASC compared with low CORT responders, an effect attributable to their reduced tendency to make overly complex inferences. In contrast, among women higher MASC scores were evident for low CORT responders relative to high CORT responders and non-stressed controls. This effect was primarily driven by the fact that low CORT responding women were better in correctly inferring emotional mental states and that they made less errors due to overly complex inference making. Second, while a positive correlation between the magnitude of the CORT responses and MASC scores was observed among men, a strong and negative association between CORT reactivity and MASC performance was found among women.

The current study for the first time showed that stress-induced CORT reactivity may yield opposing effects on social cognition in men and women. This study thereby ties in nicely with human (e.g., Stark et al., 2006; Zorawski et al., 2006) and especially animal (e.g., Conrad et al., 2004; Luine, 2002; Wood et al., 2001) studies suggesting that sex differences influence the effects of stress/GCs on cognitive performance. The current results thus highlight the importance of paying close attention to participants' sex when investigating the effects of stress and/or CORT levels on cognitive performance and of systematically further exploring whether it is men or women that are more prone to these effects.

Perhaps, then, the observed differential effect of stress-induced CORT elevations on social cognition among men and women relates to the idea that the biobehavioral response to stress is sex specific (Taylor et al., 2000). Taylor et al. suggest that whereas men react with the well-known fight-or-flight stress response, women engage in a tend-and-befriend behavioral stress response. In the tend-and-befriend response, befriending signifies the active construction and maintenance of social relationships in order to effectively deal with the stressful situation. Furthermore, Taylor et al. state that oxytocin and endogenous opioid mechanisms may be at the core of the tend-and-befriend response. It is crucial to note here that oxytocin, a neuropeptide secreted by the anterior pituitary, is strongly involved in the regulation of HPA stress responses. That is, in times of stress the release of oxytocin has anxiolytic and stress-buffering effects (Grewen et al., 2005; Heinrichs et al., 2003; Light et al., 2005). Moreover, the release of oxytocin under stressful conditions appears to be larger in women than in men (e.g., Carter, 2007; Jezova et al., 1996). Collectively, this suggests that in the current study, low CORT responding women may have had higher oxytocin levels following stress exposure compared with high CORT responding women and women in the control group, as wells as compared with the male participants. This is especially relevant given that oxytocin is known to improve social cognition in healthy (Domes et al., 2007) and autistic (Hollander et al., 2007) people. Thus, the fact that low CORT responding women displayed higher levels of social cognition might be explained by their higher oxytocin levels following stress exposure. Alternatively, high levels of CORT may have blocked any positive effects of oxytocin among high CORT responding women. We acknowledge, though, that these interpretations are speculative and thus remain open to empirical testing.

Notice that as young offspring might not yet be able to have complex thoughts and may not be able to verbally communicate their emotions, it would be highly adaptive for stressed women to engage in tend-and-befriend behavior. Our data indeed showed that the low CORT responding women who purportedly tend-and-befriend become particularly good in reading emotions. That is, low CORT responding women were better in correctly inferring emotional mental states than their high CORT responding counterparts. Moreover, from inspecting the error patterns it also became evident that low CORT responding women did not make fewer errors per se, but that they specifically made fewer errors due to overly complex inference making.

The current data also showed that among men, high CORT responders displayed enhanced social cognition compared with low CORT responders and non-stressed controls. As it well known that there is a dense expression of GC receptors in the PFC and that GC receptors become exceedingly saturated at high levels of CORT, this might suggest that high stress levels resulted in reduced PFC capacity. This reduced PFC capacity, in turn, might have rendered high CORT responding men less cognitive and more emotional, thereby benefitting their social cognitive skills. Note however that social cognition is not exclusively subserved by the PFC, but also depends on brain regions like the amygdala, the superior temporal sulcus, and the temporal–parietal junction (e.g., Olsson and Ochsner, 2008), and that the effects of stress hormones on some of these regions has yet to be explored. An inspection of the error patterns indicated that enhanced social cognition among high CORT responding men was not attributable to a general lowering of the amount of errors. Rather, enhanced social cognition among high CORT responding men was specifically associated with a reduced tendency to make overly complex inferences, again implying that

highly stressed men become less complex in interpreting social cues and more emotional.

In addition, heightened stress levels may be associated with decreased levels of testosterone (e.g., Elman et al., 2002; Fernandez-Garcia et al., 2002; but see Chichinadze and Chichinadze, 2008), while conversely it is also known that testosterone may inhibit stress-induced HPA responses (e.g., Viau and Meany, 1996, 2004). It has also been established that high levels of testosterone reduce the incidence of empathic behaviors as well as the ability to correctly recognize facial emotions (e.g., Baron-Cohen, 2002; Hermans et al., 2006; van Honk and Schutter, 2007). Possibly, the fact that high CORT responding men showed enhanced social cognition relative to low CORT responders and non-stressed controls may have been related to decreases in testosterone levels among high CORT responding men. Note in passing that the influence of sex steroids on social cognition is not restricted to men. There is abundant evidence that among women ovarian hormone status and associated levels of estradiol and progesterone can influence facial emotion recognition (e.g., Derntl et al., 2008a,b). Whatever the case may be, these data suggest that in addition to the impact of gonadal steroids, adrenal steroids also appear to modulate social cognition. Future studies could profit from measuring stress-induced alterations in sex steroid levels and relating them to GC-induced modulation of social cognition.

In sum, the present study showed sex specific effects of stress-induced CORT responses on social cognition assessed with a video-based test with high sensitivity and ecological validity. We found that both high CORT responding men and low CORT responding women showed improved social cognitive skills in attributing mental states to others based on perceptual and language cues, and that these effects were strongly associated with the magnitude of the stress-induced CORT response. To some extent, these results are supportive of the idea that when women are confronted with moderately stressful circumstances, they respond with tending and befriending behavior that may ultimately give rise to improved social cognition. In any case, the present study confirms previous work showing that GC stress responses, depending on their magnitude and individuals' sex, can enhance or impair cognitive performance in healthy young adults.

Acknowledgments

This research was supported by grants from the Netherlands Organization for Scientific Research (NWO) to Dr. Tom Smeets (446-07-014) and a German Research Foundation (DFG) Grant DFG WO 733/7-1 to Prof. Dr. Oliver T. Wolf.

References

Andreano, J.M., Cahill, L., 2006. Glucocorticoid release and memory consolidation in men and women. Psychol. Sci. 17, 466–470.
Baron-Cohen, S., 2002. The extreme male brain theory of autism. Trends Cogn. Sci. 6, 248–254.
Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., Plumb, I., 2001a. The "Reading the mind in the eyes" Test revised version: a study with normal adults, and adults with Asperger syndrome or high-functioning autism. J. Child Psychol. Psyc. 42, 241–251.
Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., Clubley, E., 2001b. The Autism-Spectrum Quotient (AQ): evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. J. Autism Dev. Disord. 31, 5–17.
Buchanan, T.W., Tranel, D., 2008. Stress and emotional memory retrieval: effects of sex and cortisol response. Neurobiol. Learn. Mem. 89, 134–141.
Carter, C.S., 2007. Sex differences in oxytocin and vasopressin: implications for autism spectrum disorders? Behav. Brain Res. 176, 170–186.
Chichinadze, K., Chichinadze, N., 2008. Stress-induced increase of testosterone: contributions of social status and sympathetic reactivity. Physiol. Behav. 94, 595–603.
Conrad, C.D., Jackson, J.L., Wieczorek, L., Baran, S.E., Harman, J.S., Wright, R.L., et al., 2004. Acute stress impairs spatial memory in male but not female rats: influence of estrous cycle. Pharmacol. Biochem. Be. 78, 569–579.
Crawford, J.R., Henry, J.D., 2004. The Positive and Negative Affect Schedule (PANAS): construct validity, measurement properties and normative data in a large non-clinical sample. Brit. J. Clin. Psychol. 43, 245–265.
de Kloet, E.R., Vreugdenhil, E., Oitzl, M.S., Joels, M., 1998. Brain corticosteroid receptor balance in health and disease. Endocr. Rev. 19, 269–301.
de Kloet, E.R., Oitzl, M.S., Joels, M., 1999. Stress and cognition: are corticosteroids good or bad guys? Trends Neurosci. 22, 422–426.
Derntl, B., Kryspin-Exner, I., Fernbach, E., Moser, E., Habel, U., 2008a. Emotion recognition accuracy in healthy young females is associated with cycle phase. Horm. Behav. 53, 90–95.
Derntl, B., Windischberger, C., Robinson, S., Lamplmayr, E., Kryspin-Exner, I., Gur, R.C., et al., 2008b. Facial emotion recognition and amygdala activation are associated with menstrual cycle phase. Psychoneuroendocrinology 33, 1031–1040.
Dickerson, S.S., Kemeny, M.E., 2004. Acute stressors and cortisol responses: a theoretical integration and synthesis of laboratory research. Psychol. Bull. 130, 355–391.
Domes, G., Heinrichs, M., Michel, A., Berger, C., Herpertz, S.C., 2007. Oxytocin improves "mind-reading" in humans. Biol. Psychiat. 61, 731–733.
Dziobek, I., Fleck, S., Kalbe, E., Rogers, K., Hassenstab, J., Brand, M., et al., 2006a. Introducing MASC: a Movie for the Assessment of Social Cognition. J. Autism Dev. Disord. 36, 623–636.
Dziobek, I., Fleck, S., Rogers, K., Wolf, O.T., Convit, A., 2006b. The "amygdala theory of autism" revisited: linking structure to behavior. Neuropsychologia 44, 1891–1899.
Elman, I., Goldstein, D.S., Adler, C.M., Shoaf, S.E., Breier, A., 2002. Inverse relationship between plasma epinephrine and testosterone levels during acute glucoprivation in healthy men. Life Sci. 68, 1889–1898.
Fernandez-Garcia, B., Lucia, A., Hoyos, J., Chicharro, J.L., Rodriguez-Alonso, M., Bandres, F., et al., 2002. The response of sexual and stress hormones of male pro-cyclists during continuous intense competition. Int. J. Sports Med. 23, 555–560.
Fleck, S., Dziobek, I., Rogers, K., Mielke, R., Kalbe, E., Kessler, J., et al., 2006. Der MASC-MC, ein neues filmisches Verfahren zur Erfassung der "Theory of Mind". Zeigen Patienten mit Asperger-Syndrom ein spezifisches Antwortmuster? Der Nervenarzt 77, S343.
Gallagher, H.L., Frith, C.D., 2003. Functional imaging of "theory of mind". Trends Cogn. Sci. 7, 77–83.
Grewen, K.M., Girdler, S.S., Amico, J., Light, K.C., 2005. Effects of partner support on resting oxytocin, cortisol, norepinephrine, and blood pressure before and after warm partner contact. Psychosom. Med. 67, 531–538.
Heinrichs, M., Baumgartner, T., Kirschbaum, C., Ehlert, U., 2003. Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. Biol. Psychiat. 54, 1389–1398.
Hermans, E.J., Putman, P., van Honk, J., 2006. Testosterone administration reduces empathetic behavior: a facial mimicry study. Psychoneuroendocrinology 31, 859–866.
Hollander, E., Bartz, J., Chaplin, W., Phillips, A., Sumner, J., Soorya, L., et al., 2007. Oxytocin increases retention of social cognition in autism. Biol. Psychiat. 61, 498–503.
Jezova, D., Jurankova, E., Mosnarova, A., Kriska, M., Skultetyova, I., 1996. Neuroendocrine response during stress with relation to gender differences. Acta Neurobiol. Exp. 56, 779–785.
Kirschbaum, C., Wüst, S., Hellhammer, D., 1992. Consistent sex differences in cortisol responses to psychological stress. Psychosom. Med. 54, 648–657.
Kirschbaum, C., Pirke, K.-M., Hellhammer, D.H., 1993. The 'Trier Social Stress Test': a tool for investigating psychobiological stress responses in a laboratory setting. Neuropsychobiology 28, 76–81.
Kudielka, B.M., Buske-Kirschbaum, A., Hellhammer, D.H., Kirschbaum, C., 2004a. HPA axis responses to laboratory psychosocial stress in healthy adults, younger adults, and children: impact of age and gender. Psychoneuroendocrinology 29, 83–98.
Kudielka, B.M., Schommer, N.C., Hellhammer, D.H., Kirschbaum, C., 2004b. Acute HPA axis responses, heart rate, and mood changes to psychosocial stress (TSST) in humans at different times of day. Psychoneuroendocrinology 29, 983–992.
Kuhlmann, S., Piel, M., Wolf, O.T., 2005. Impaired memory retrieval after psychosocial stress in healthy young men. J. Neurosci., 25, 2977–2982.
Light, K.C., Grewen, K.M., Amico, J., 2005. More frequent partner hugs and higher oxytocin levels are linked to lower blood pressure and heart rate in premenopausal women. Biol. Psychol. 69, 5–21.
Luine, V.N., 2002. Sex differences in chronic stress effects on memory in rats. Stress 5, 205–216.
McGaugh, J.L., Roozendaal, B., 2002. Role of adrenal stress hormones in forming lasting memories in the brain. Curr. Opin. Neurobiol. 12, 205–210.
Nater, U.M., Moor, C., Okere, U., Stallkamp, R., Martin, M., Ehlert, U., et al., 2007. Performance on a declarative memory task is better in high than low cortisol responders to psychosocial stress. Psychoneuroendocrinology 32, 758–763.
Olsson, A., Ochsner, K.N., 2008. The role of social cognition in emotion. Trends Cogn. Sci. 12, 65–71.
Schoofs, D., Preuss, D., Wolf, O.T., 2008. Psychosocial stress induces working memory impairments in an n-back paradigm. Psychoneuroendocrinology 33, 643–653.
Singer, T., 2006. The neuronal basis and ontogeny of empathy and mind reading: review of literature and implications for future research. Neurosci. Biobehav. Rev. 30, 855–863.
Stark, R., Wolf, O.T., Tabbert, K., Kagerer, S., Zimmermann, M., Kirsch, P., Schienle, A., Vaitl, D., 2006. Influence of the stress hormone cortisol on fear conditioning in humans: evidence for sex differences in the response of the prefrontal cortex. Neuroimage 32, 1290–1298.
Taylor, S.E., Klein, L.C., Lewis, B.P., Gruenewald, T.L., Gurung, R.A., Updegraff, J.A., 2000. Biobehavioral responses to stress in females: tend-and-befriend, not fight-or-flight. Psychol. Rev. 107, 411–429.

van Honk, J., Schutter, D.J.L.G., 2007. Testosterone reduces conscious detection of signals serving social correction: implications for antisocial behavior. Psychol. Sci. 18, 663–667.
Viau, V., Meaney, M.J., 1996. The inhibitory effect of testosterone on hypothalamic-pituitary-adrenal responses to stress is mediated by the medial preoptic area. J. Neurosci. 16, 1866–1876.
Viau, V., Meaney, M.J., 2004. Testosterone-dependent variations in plasma and intrapituitary corticosteroid binding globulin and stress HPA activity in the male rat. J. Endocr. 181, 223–231.
Watson, D., Clark, L.A., Tellegen, A., 1988. Development and validation of brief measures of positive and negative affect: the PANAS scales. J. Pers. Soc. Psychol. 54, 1063–1070.
Wolf, O.T., 2008. The influence of stress hormones on emotional memory: relevance for psychopathology. Acta Psychol. 127, 513–531.
Wolf, O.T., Schommer, N.C., Hellhammer, D.H., McEwen, B.S., Kirschbaum, C., 2001. The relationship between stress induced cortisol levels and memory differs between men and women. Psychoneuroendocrinology 26, 711–720.
Wood, G.E., Beylin, A.V., Shors, T.J., 2001. The contribution of adrenal and reproductive hormones to the opposing effects of stress on trace conditioning in males versus females. Behav. Neurosci. 115, 175–187.
Zorawski, M., Blanding, N.Q., Kuhn, C.M., LaBar, K.S., 2006. Effects of stress and sex on acquisition and consolidation of human fear conditioning. Learn. Mem. 13, 441–450.