Available online at www.sciencedirect.com

ScienceDirect

Is stress affecting our ability to tune into others? Evidence for gender differences in the effects of stress on self-other distinction

L. Tomova [a,b], B. von Dawans [c], M. Heinrichs [c,d], G. Silani [e], C. Lamm [a,b,*]

[a] Social, Cognitive and Affective Neuroscience Unit, Department of Basic Psychological Research and Research Methods, Faculty of Psychology, University of Vienna, Vienna, Austria
[b] Cognitive Science Research Platform, University of Vienna, Austria
[c] Department of Psychology, Laboratory for Biological and Personality Psychology, University of Freiburg, Germany
[d] Freiburg Brain Imaging Center, University Medical Center, University of Freiburg, Germany
[e] Cognitive Neuroscience Sector, International School for Advanced Studies, SISSA-ISAS, Trieste, Italy

Summary Stress is a ubiquitous challenge in society as we consistently interact with others under the influence of stress. Distinguishing self- from other-related mental representations plays an important role for social interactions, and is a prerequisite for crucial social skills such as action understanding, empathy, and mentalizing. Little is known, however, about the effects of stress on self-other distinction. We assessed how acute stress impacts self-other distinction in the perceptual-motor, the affective, and the cognitive domain, in a male and female sample. In all domains, the results show opposing effects of stress on the two genders: while women showed increases in self-other distinction, men showed decreases. Our findings suggest that women flexibly disambiguate self and other under stress, enabling accurate social responses, while men respond with increased egocentricity and less adaptive regulation. This has crucial implications for explaining gender differences in social skills such as empathy and prosociality.
© 2014 Elsevier Ltd. All rights reserved.

* Corresponding author at: Social, Cognitive and Affective Neuroscience Unit, Department of Basic Psychological Research and Research Methods, Faculty of Psychology, University of Vienna, Liebiggasse 5, 1010 Vienna, Austria. Tel.: +43 1427747130.
E-mail address: claus.lamm@univie.ac.at (C. Lamm).

Our daily lives are fraught with various stressors and we often need to interact with others while under the influence of stress — both at the workplace and in our private lives. Various cognitive processes — such as strategic reasoning, feedback processing, and reward sensitivity are affected by stressful situations (e.g., Starcke and Brand, 2012), and this presumably also affects social cognition and behaviour. Self-other distinction — the ability to distinguish self- from other-related mental representations — is a particularly important socio-cognitive skill, in a variety of domains. In the perception-action domain, self-other distinction is required to control automatic imitative tendencies, to enable smooth and flexibly regulated cooperative interactions (Wang and Hamilton, 2012). In the domain of empathy, failing to maintain the boundaries between one's own and another's emotions can result in personal distress. This self-centred response prevents other-oriented empathic responding and negatively affects prosocial behaviours (Batson, 1987; Eisenberg et al., 1989; Singer and Lamm, 2009). Self-other distinction is also crucial in more high-level cognitive processes such as perspective taking — as perceiving the world in another's stead requires to be able to disentangle one's own views and intentions from those of the other (Epley et al., 2004).

Surprisingly little, though, is known about how stress affects self-other distinction and our ability to understand others. Stress is an essential psychobiological mechanism in which additional resources are recruited by the human organism to react to demanding circumstances (Dickerson and Kemeny, 2004). From this observation, different predictions on how stress might affect self-other distinction can be made. For one, as stress is known to result in a fallback on processes and behaviours that are less resource demanding (Starcke and Brand, 2012), stressed individuals may default to more self-related or "egocentric" processes, which is less resource demanding than also taking into account the mental states of others (e.g., Epley et al., 2004). In this case, self-other distinction would be decreased under stress. On the other hand, concepts such as the "tend-and-befriend" hypothesis posit that stress leads to increases in prosocial and affiliative behaviour (Taylor et al., 2000). Stress might therefore motivate us to act in a more other-oriented manner, using social support as a stress coping strategy. Such a strategy would predict improvements in self-other distinction, as this would facilitate understanding of others and increase accurate social responding and behaviour.

While there is no specific experimental evidence on how stress modulates self-other distinction, prior evidence on the effects of stress on social cognition and emotion has been rather inconsistent. For instance, social cognitive abilities have been shown to either improve or decrease under stress, and that this depends on an individual's magnitude of their cortisol response. Notably, these effects were also modulated by gender (Smeets et al., 2009). From attention research, though, there is evidence that perceptual self-other distinction is reduced under threat (Ma and Han, 2010). In contrast, the tend-and-befriend hypothesis suggests that prosocial and affiliative behaviour increases in stressful situations (Taylor et al., 2000). Originally only stated for women, a more recent finding by our group indicates that men also show stress responses that can be interpreted in line with a tend-and-befriend pattern (von Dawans et al., 2012). In the domain of social emotion research, experimen-

tal evidence is very scarce — with only one recent study showing that higher anxiety is associated with reduced empathic abilities (Negd et al., 2011).

To close that gap of knowledge, we therefore used a standardized laboratory stressor task to assess how acutely induced psychosocial stress affects self-other distinction (Trier Social Stress Test for Groups (TSST-G); von Dawans et al., 2011). Self-other distinction was investigated using tailored experimental tasks tapping into this ability on three different levels. These levels ranged from low-level perceptual-motor processes as the control of imitative response tendencies, to higher-level cognitive perspective taking. To tap into self-other distinction in the affective domain, we used a task recently developed by our group which enabled us to measure overcoming emotional egocentricity bias during empathic judgments. The choice of these tasks built up on recent developments in social cognitive neuroscience, pinpointing a common mechanism subserved by neural networks at the interface of the right inferior parietal and posterior superior temporal cortex enabling self-other discrimination in these different domains (e.g., Decety and Lamm, 2007; Santiesteban et al., 2012; Silani et al., 2013). Because of previously documented gender differences in response to social stressors (Smeets et al., 2009; Seidel et al., 2013), we explored the effects of stress on self-other distinction in a male and a female subsample, which had been matched for socio-cognitive skills. Based on prior research showing that higher anxiety is associated with reduced empathic abilities (Negd et al., 2011), we hypothesized that stress would lead to decreased self-other distinction in participants.

Furthermore, based on a lack of direct comparisons of genders in previous research in the same task paradigm (including in our own work; (von Dawans et al., 2012)), we aimed to explore whether men and women would show differences in the effects of stress on self-other distinction.

1. Methods

1.1. Participants

80 healthy participants (40 females) between 18 and 40 years were included in the study. Screening questionnaires were used to exclude participants who reported acute or chronic psychiatric illness, high social anxiety, taking prescription medication, abuse psychoactive drugs or alcohol, or smoked on a daily basis. Socio-cognitive abilities were determined, using the perspective taking scale and the empathic concern scale from the Interpersonal Reactivity Index (IRI; Davis, 1983), the Emotion Contagion Scale (EC; Doherty, 1997), and the Reading the Mind in the Eyes Test (RMET; Baron-Cohen et al., 2001). In order to assure similar basic socio-cognitive abilities in the sample, participants who showed scores above or below two standard deviations from the group mean in any of those assessments were excluded from participation. We chose the strict exclusion criterion of two standard deviations, in order to guarantee that participant' socio-cognitive abilities were closely matched. The Trier Inventory for the Assessment of Chronic Stress (TICS; Schulz and Schlotz, 1999) was used to control for individual differences in chronic stress as a possible confound. Female participants were not using hormonal contraceptives and participated in the experiment during their luteal phase of the menstrual cycle, as it has been shown that cortisol responses

during this phase are most comparable to those of men (Kirschbaum et al., 1999). Menstrual cycle phase was determined by self-reports of usual menstrual cycle duration and onset of last menstrual period. The study was approved by the ethics commission of the University of Vienna and subjects were treated according to the Declaration of Helsinki (1964) regarding the treatment of human research participants. Written informed consent was obtained. All participants received 20 € for participation in the experiment.

1.2. Self-other distinction paradigms

Three well-established paradigms were implemented in order to assess self-other distinction on the perceptual-motor, the affective, and the cognitive level. Crucially, all tasks required online control of co-activated self and other representations.

1.2.1. Imitation-inhibition task

This paradigm enables assessment of self-other distinction on a basic perceptual-motor level. It requires participants to lift their index or middle finger in response to a visually presented cue, which coincides with congruent or incongruent finger movements of a hand of another person shown on the screen (Brass et al., 2005). Perceiving these movements activates automatic imitation tendencies (Brass et al., 2005, 2009), which in the case of incongruent movements interfere with the instructed movement execution and therefore need to be inhibited. Thus, participants had to maintain the focus on their own movement intentions, and to inhibit the tendency to imitate the incongruent movement of the other hand. As established by previous investigations (Brass et al., 2009), self-other distinction was assessed by means of the interference effect, which was computed by subtraction of response times and error rates, respectively, of congruent from incongruent trials. Higher interference indicated reduced self-other distinction.

1.2.2. Emotional egocentricity task

This task enables assessment of self-other distinction in the emotional domain by measuring emotional egocentricity bias (Silani et al., 2013). This is achieved by simultaneous visuo-tactile stimulation of the participant's and another person's hand, with stimulation resulting in either pleasant or unpleasant emotions. Crucially, the valence of stimulation between participant and other person was either congruent or incongruent, and participants were required to empathize with the feelings of the other person. Previous research (Silani et al., 2013) has shown that empathic judgments are shifted (i.e. egocentrically biased) towards the participant's own emotional state under incongruent conditions. This emotional egocentricity bias therefore served as a measure of emotional self-other distinction, and was computed by subtracting ratings in incongruent trials from those in congruent trials. A higher bias indicated higher egocentricity, and therefore reduced self-other distinction.

1.2.3. Perspective-taking task

Self-other distinction in the cognitive domain was investigated by using a perspective taking paradigm (Keysar et al., 2000; Santiesteban et al., 2012). Participants had to move objects on a shelf according to the instructions of a "director". In experimental trials, the task required participants to disentangle their own visual perspective from the one of the director, as there were differences in the objects he could see in comparison to what participants saw from their own perspective. Self-other distinction was assessed by the number of errors and response times in experimental trials. Slower responses and more errors indicated reduced self-other distinction. The paradigm also included control trials which did not require disentangling the different perspectives. These trials were used to ensure that the results for the self-other distinction paradigms could not be explained by general effects of stress on cognitive load or other "non-social" processes.

1.3. Procedure

24 h prior to the experiment, participants were instructed to abstain from drinking alcohol, smoking, and taking medication. On the day of the experiment, participants were told to abstain from consuming caffeine. Experimental sessions took place between 14 h and 18 h in order to control for diurnal cortisol variation. Participants were not allowed to communicate with each other during the experiment. Psychosocial stress was induced by the group version of the Trier Social Stress Task (TSST; von Dawans et al., 2011) which includes public speaking (vs. group reading in the control condition) and mental arithmetic (vs. easy counting in the control condition) as stress inducing elements. In the remainder of this text, the term "stress" is used synonymous with psychosocial stress (as this is what our design induced), unless noted otherwise. Participants were assigned randomly to the stress or to the control condition. Following a preparation phase, in which baseline cortisol was measured and subjects had received instructions for the self-other distinction tasks, participants were provided with instructions for the TSST-G stress or control task and had 10 min to prepare for the public speaking/group reading. Fig. 1 shows the timeline for the experimental procedures. The order of the self-other
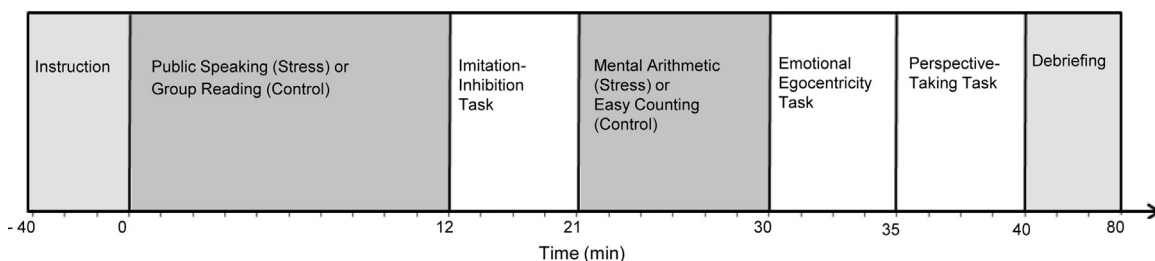

| Instruction | Public Speaking (Stress) or Group Reading (Control) | Imitation-Inhibition Task | Mental Arithmetic (Stress) or Easy Counting (Control) | Emotional Egocentricity Task | Perspective-Taking Task | Debriefing |

-40   0   12   21   30   35   40   80
Time (min)

Figure 1 Timeline of experimental procedures. Time point zero indicates onset of TSST-G or TSST-G control.

distinction paradigms was fixed across participants, as we expected carry-over effects from the individual self-other distinction tasks. We chose this order based on the rationale that a lower level task (i.e., imitation-inhibition task) might interfere less with a higher level task (i.e., perspective-taking task) than vice versa, due to the stronger engagement of meta-cognitive processes in the latter. After the experiment, participants stayed in the laboratory until the last saliva sample was taken (80 min after onset of stressor) and were debriefed. Finally, participants received their payment of 20 €.

1.4. Stress measures and non-responder/outlier exclusion

Autonomic stress levels were assessed by recording of heart rate using a wireless chest transmitter and a wrist monitor recorder (Polar RS800CX, Polar Electro Oy, Kempele, Finland). We recorded continuous beat-to-beat intervals (aggregated to mean levels per minute) and translated them to beats per minute. The heart rate of four participants was not recorded reliably due to technical problems. For cortisol measures, we collected saliva samples at eight time points using Salivette collection devices (Sarstedt, Wr. Neudorf, Austria). Time points for saliva sampling were: baseline (−40 min; i.e. before instruction for the stress task), 10 min before stressor onset (−10 min; i.e. after instruction for the stress task), directly at stressor onset (0 min), after public speaking/group reading (+12 min), after mental arithmetic/easy counting (+30 min), after the perspective taking task (+40 min), and then after another 20 and 40 min to cover the cortisol response recovery phase (+60 min and +80 min). After each experimental session, samples were stored at −20 °C. Salivary cortisol concentrations were determined by a commercially available chemiluminescence-immunoassay kit with high sensitivity (IBL, Hamburg, Germany). Inter- and intra-assay coefficients of variation were below 10%. All biochemical analyses were conducted at the biopsychology laboratory of Technical University of Dresden (head: C. Kirschbaum, http://biopsychologie.tu-dresden.de). Subjective stress levels were measured by means of a visual analogue scale. At each time point of saliva sampling (i.e. eight times throughout the experiment), participants used a visual analogue scale (ranging from 0 to 100) to indicate their subjective stress level. For cortisol levels, heart rate and subjective stress measures, the areas under the individual response curves with respect to ground (AUC_G) were calculated with the trapezoid formula (Pruessner et al., 2003). By this, an aggregated measure of physiological changes over time is provided (see supplemental material for analysis of areas under the curve with respect to increase, AUC_I). In order to assure that our experimental manipulation of stress induction was successful on an individual basis, we assessed cortisol response curves of each participant individually (see Foley and Kirschbaum, 2010 for evidence on predictability of cortisol for psychosocial stress). This enabled us to detect non-responders in the stress group and participants with cortisol responses in the control group — who presumably experienced the sole participation in an experiment as stressful. We excluded six non-responders from the stress group and five responders from the control group (see

supplemental material for exclusion procedure). Four additional participants were excluded due to incorrect task understanding or lack of compliance with abstinence criteria. Additionally, one participant had to be excluded because he showed extremely high cortisol levels in baseline and all other time points (>3 SDs of mean cortisol levels of stress group), indicating abnormal HPA axis functioning. Inclusion of this participant does not significantly change the results of any reported analyses. After outlier exclusion, our final sample consisted of 64 participants (32 stress group (15 female), 32 control group (17 female)). For heart rate data, analyses were conducted for 60 participants (31 stress group (14 female), 29 control group (16 female)). Note though that analyses with the full sample showed that outlier exclusion only increased sensitivity but left the basic pattern of results unaffected (see Section 2.4).

1.5. Statistical analyses

In order to assure that stress and control group did not differ in variables such as age, socio-cognitive abilities, social anxiety and chronic stress, we computed two-way ANOVAs for each measure, with the factors *group* (stress vs. control) and *gender*. The effectiveness of the stress induction was tested with repeated measures ANOVAs with the within subject factor *time* (8 repeated measures for cortisol and subjective stress ratings, 35 for heart rate) and the between subject factors *group* and *gender*. Behavioural data of the self-other distinction paradigms were analyzed in a repeated measures ANOVA with the within subject factor *task* (imitation-inhibition, emotional egocentricity and perspective taking) and the between subject factors *group* and *gender*. In order to be able to compare the data of the three different self-other distinction tasks in a repeated measures ANOVA, scales were standardized using z-score transformation for each individual and each task. For the imitation-inhibition and the perspective-taking task, we used reaction times as dependent variables in the z-transformed rmANOVA. Note that the purpose of z-transformation was to enable comparison of the three tasks on one common scale. Hence, for individual ANOVAs, results with raw data and z-transformed data were identical as the latter were simply a linear transformation of the former. Greenhouse—Geisser corrections were used when homogeneity of covariances was violated (as determined by Mauchly test of sphericity). Bonferroni corrected post hoc comparisons were used to examine interactions and omnibus main effects. Associations between cortisol levels, heart rate, and subjective stress were assessed by correlating AUC_G (see supplemental material for analyses of AUC_I) of the respective measures using Pearson correlations. Additionally, stress response measures were correlated with behavioural data from the self-other distinction paradigms. All data were analyzed using SPSS (v.20) and the significance threshold was set to $p < 0.05$. Effect sizes are reported as η_p^2.

2. Results

Stress and control group did not differ in age, social anxiety, chronic stress, and any of the trait socio-cognitive abilities measures (all p-values > 0.16). Furthermore, there was no effect of gender on any of these measures (all p-values > 0.14).

2.1. Stress manipulation

Cortisol showed significant main effects of time ($F(2.59,155.08) = 18.797$, $p < 0.001$, $\eta_p^2 = 0.70$) and group ($F(1,60) = 35.710$, $p < 0.001$, $\eta_p^2 = 0.37$), and a significant interaction time × group ($F(2.59,155.08) = 25.573$, $p < 0.001$, $\eta_p^2 = 0.30$; see Fig. 2a). Gender and its interactions were not significant (all *p*-values > 0.16).

Heart rate showed significant main effects of time ($F(6.13,343.44) = 59.396$, $p < 0.001$, $\eta_p^2 = 0.97$) and group ($F(1,56) = 5.280$, $p = 0.025$, $\eta_p^2 = 0.09$), and a significant interaction time × group ($F(6.13,343.44) = 3.927$, $p = 0.001$, $\eta_p^2 = 0.07$; see Fig. 2c). Gender and its interactions were not significant (all *p*-values > 0.15).

Subjective stress showed a significant main effect of time ($F(4.60,276.01) = 29.231$, $p < 0.001$, $\eta_p^2 = 0.68$), a trend significance for group ($F(1,60) = 3.817$, $p = 0.055$, $\eta_p^2 = 0.06$), and a significant interaction time × group ($F(4.60,276.01) = 3.175$, $p = 0.010$, $\eta_p^2 = 0.05$; see Fig. 2b). Gender and its interactions were not significant (all *p*-values > 0.19).

2.2. Correlations between stress measures

Aggregated stress measures (AUC_G) correlated significantly for heart rate and cortisol ($r = 0.267$, $p = 0.040$), and on a trend level for heart rate and subjective stress ($r = 0.255$, $p = 0.053$). Cortisol and subjective stress were not correlated ($r = 0.156$, $p = 0.227$). Correlations with AUC_I measures are reported in the supplemental material.

2.3. Self-other distinction paradigms

The repeated measures ANOVA showed a significant group × gender interaction ($F(1,60) = 15.526$, $p < 0.001$, $\eta_p^2 = 0.20$) but no main effect of group, gender, or task, nor any significant interactions (all *p*-values > 0.39). Bonferroni
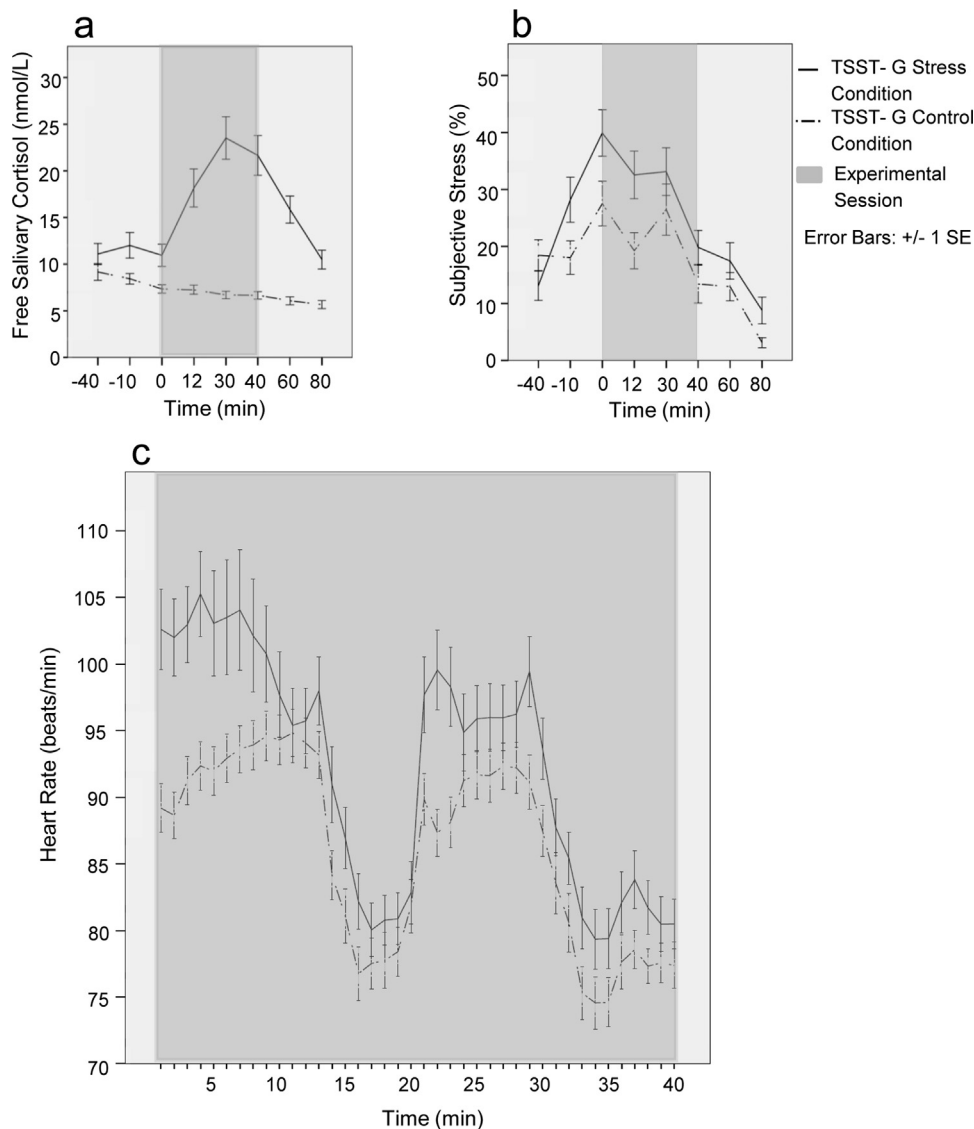

Figure 2 Stress levels of stress and control group assessed by (a) free salivary cortisol, (b) subjective stress and (c) heart rate. Grey marking indicates time of experimental session. Error bars indicate standard error of the mean. Time point zero indicates onset of TSST-G.

corrected pairwise comparisons showed that men in the stress group showed significantly *lower* self-other distinction ($p = 0.009$) than men in the control group (mean difference $\pm$ SEM = -0.564 ± 0.209) while women in the stress group showed significantly *higher* self-other distinction ($p = 0.008$) than women in the control group (mean difference $\pm$ SEM = 0.576 ± 0.209). Although the factor task or its interactions were not significant, indicating that the gender $\times$ group interaction was comparable across all tasks, we nevertheless computed separate two-way ANOVAs for each task in order to assess whether the group $\times$ gender interaction was significant for each task as well.

2.3.1. Imitation-inhibition task
The two-way ANOVA showed a significant group $\times$ gender interaction for the interference effect in response times ($F(1,60) = 6.925$, $p = 0.011$, $\eta_p^2 = 0.10$), but no main effect of group or gender (all p-values > 0.16). Error rates showed no significant effects (all p-values > 0.19). Fig. 3a illustrates that stressed women showed a decrease of interference (i.e. better self-other distinction) compared to non-stressed women, whereas men showed the opposite pattern (i.e. higher interference and thus reduced self-other distinction when stressed). Bonferroni corrected post hoc comparisons of the group $\times$ gender interaction for the interference effect in response times showed a significant difference ($p = 0.006$)

between men and women in the control group with women showing higher interference effects than men (mean difference $\pm$ SEM = 50.32 ± 17.60 ms). Men and women did not differ significantly in the stress group ($p = 0.392$).

2.3.2. Emotional egocentricity task
The two-way ANOVA showed a significant group $\times$ gender interaction for emotional egocentricity bias ($F(1,60) = 5.041$, $p = 0.028$, $\eta_p^2 = 0.08$), but no main effect of group or gender (all p-values > 0.66). Fig. 3b illustrates that stressed women exhibited a reduction in egocentricity (i.e. better self-other distinction) compared to non-stressed women, whereas men showed the opposite pattern. Bonferroni corrected post hoc comparisons showed no significant difference ($p = 0.206$) between men and women in the control group or between men and women in the stress group ($p = 0.063$).

2.3.3. Perspective-taking task
The two-way ANOVA for response times on experimental trials showed a significant group $\times$ gender interaction ($F(1,60) = 4.408$, $p = 0.040$, $\eta_p^2 = 0.07$), but no main effect of group or gender (all p-values > 0.45). No significant effects were observed for error rates (all p-values > 0.44). Fig. 3c illustrates that stressed women showed lower response times (i.e. better self-other distinction) compared
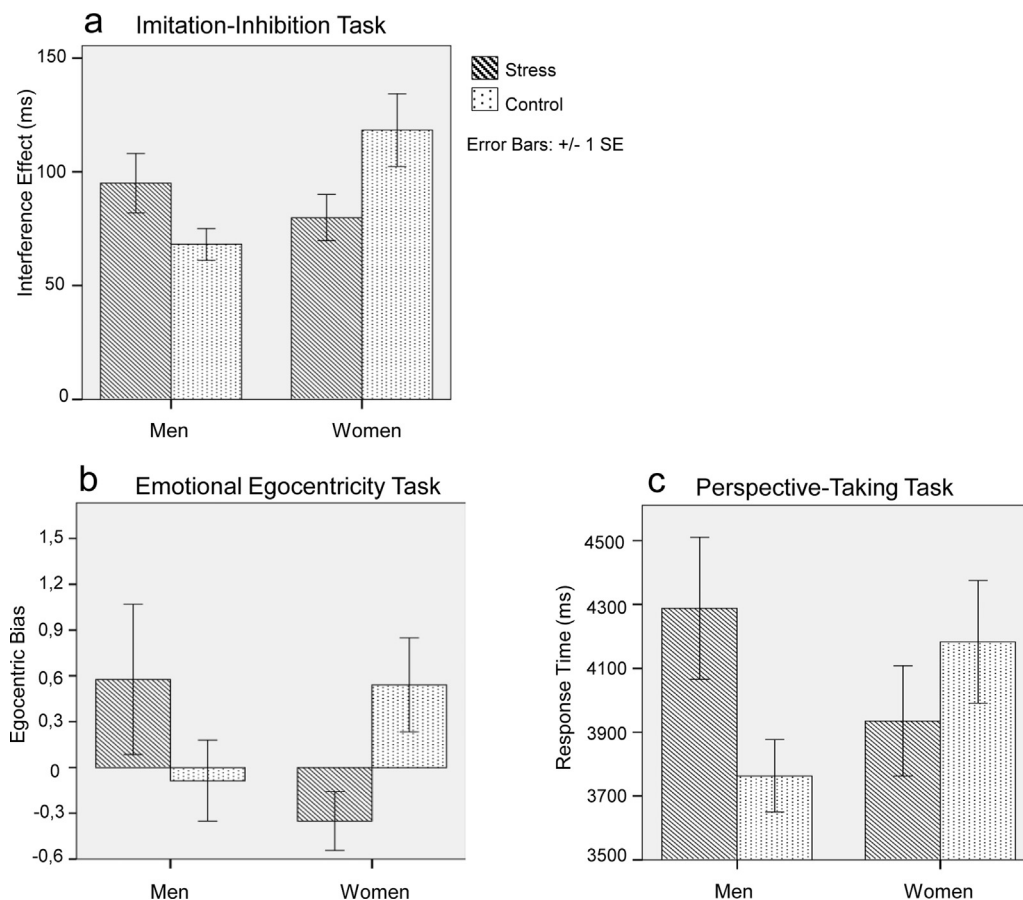

Figure 3 Mean scores as a function of conditions for (a) interference effect of imitation-inhibition task, (b) egocentric bias of the emotional egocentricity task and (c) response times of experimental trials in the perspective taking task. Error bars indicate standard error of the mean. The figure displays the raw values instead of z-scores for ease of interpretation.

to non-stressed women, while men showed the opposite pattern. Bonferroni corrected post hoc comparisons of the group × gender interaction in response times of the experimental trials showed no significant difference ($p = 0.112$) between men and women in the control group or between men and women in the stress group ($p = 0.180$).

Assessment of control trials of the perspective-taking task showed no significant main effects or interactions, for both response times and error rates (all p-values > 0.28).

2.3.4. Correlations between stress measures and self-other distinction paradigms

We did not find any significant correlations between stress measures and self-other distinction tasks (all p-values > 0.07).

2.4. Self-other distinction paradigms — full sample analysis

In order to demonstrate that outlier exclusion only increased sensitivity of our measures but left the basic pattern of results unaffected, we here also report the results of the data analysis without outlier exclusion. Effectiveness of stress induction showed similar results for cortisol data, heart rate and subjective stress level as in the reduced sample after outlier exclusion (data not shown, but available on request). From the full sample of 80 participants, three participants showed a basic misunderstanding of the instructions for the emotional egocentricity task (i.e. they believed they had to rate their own emotions during the task instead of rating the emotions of their assigned partner). We therefore excluded these participants and report results from a sample of 77 participants (39 stress group (20 female), 38 control group (20 female)). The repeated measures ANOVA showed a significant group × gender interaction ($F(1,73) = 10.157$, $p = 0.002$, $\eta_p^2 = 0.12$) but no main effect of group, gender, or task or any interactions (all p-values > 0.35). Bonferroni corrected pairwise comparisons showed that men in the stress group showed significantly lower self-other distinction ($p = 0.047$) than men in the stress group (mean difference ± SEM = -0.394 ± 0.195) while women in the stress group showed significantly higher self-other distinction ($p = 0.015$) than women in the control group (mean difference ± SEM = 0.467 ± 0.187). Again, the factor task did not reach significance, indicating that these effects were comparable across all tasks. Separate two-way ANOVAs for each task separately showed very similar results as in the reduced sample after outlier exclusion (data shown in supplemental material). Taken together, the results of the full sample suggest that outlier exclusion only increased sensitivity, but left the basic pattern of results unaffected.

3. Discussion

The present study assessed the effects of acute psychosocial stress on the ability to distinguish self- from other-related representations, across three different levels. We consistently found the same general response pattern: while stressed women showed higher self-other distinction than women in the non-stressful control condition, men showed the converse pattern. More specifically, stressed women showed reduced emotional egocentricity bias, enabling them

to judge the emotions of the other person in a way that was less influenced by their own emotional state. Moreover, their response times in the cognitive perspective-taking task decreased under stress, documenting that they were able to regulate the mismatch between their own and the "director's" perspective faster under stress. Finally, stressed women showed a reduction of automatic imitative tendencies in the imitation-inhibition task, indicating that they were able to overcome low-level social signals interfering with their own movement intentions. Note that the latter finding is crucial. It highlights that women did not simply show an increase in other-related responses under stress — as this would have resulted in increased interference from automatic imitation. Instead, they were able to flexibly increase either self- or other-related representations, depending on the task demands which either required overcoming egocentric biases, or overcoming social interference. The tend-and-befriend hypothesis by Taylor and colleagues suggests that women show increased affiliative behaviour when stressed (Taylor et al., 2000). However, experimental evidence on the effects of stress on social interaction skills is scarce. We are aware of only one study experimentally assessing social cognitive abilities after psychosocial stress exposure (Smeets et al., 2009). Here, the authors found that social cognition improved in men and women, although this effect was modulated by the magnitude of the cortisol response. However, social cognition was improved by fewer errors due to overly complex interference making. Thus, this finding might also be explained by cognitive rather than social mechanisms. In the present study, however, we controlled for effects of stress on general cognitive load and thus can rule out that our effects are due to fewer cognitive resources under stress.

As appropriate self-other distinction is a prerequisite for crucial social interaction skills such as empathy (Singer and Lamm, 2009), perspective taking (Epley et al., 2004), and control of mimicry (Wang and Hamilton, 2012), our findings show experimental evidence that social interaction skills improve in women under stress and thus, crucially extend the tend-and-befriend hypothesis. Notably, the finding that women under stress showed an increase in their ability to overcome egocentricity in empathic responding is of particular relevance. Because empathy is directly linked to prosocial behaviour (Batson, 2010), more accurate empathic responding might represent a possible mechanism for how stress enables increases in prosocial behaviour in women.

In contrast, men exposed to acute stress showed diminished self-other distinction on all three levels. Their emotional egocentricity bias increased, they needed more time to disentangle their own from the "director's" perspective, and their ability to overcome automatic imitation tendencies was reduced. Therefore, in line with a protective "fight-or-flight" stress response, it seems that men respond to stress by defaulting to less resource demanding and more automatic processing strategies. As representing the feelings and intentions of others is resource-demanding, they display a fall back towards more self-related or "egocentric" processes, when having to judge emotions or the perspective of others. Since imitation represents a more automatic tendency than its inhibitory control, they show an increase of imitation tendencies in the imitation-inhibition task.

Seemingly controversial, however, a recent study by our group investigating a male sample only showed increased prosocial behaviour under stress (von Dawans et al., 2012). However, a crucial aspect differentiating this study from the present one was that prosocial behaviour was measured by economic exchange games. As social contact has been shown to induce stress-buffering effects (Heinrichs et al., 2003), the prosocial behaviour shown in that study might have been a strategy to decrease stress-related negative emotions. Notably, such a "stress-buffering strategy" could not be applied in our experiment, since our tasks only targeted self-other distinction and did not involve direct social interaction or behaviour.

Importantly, we did not find gender differences in physiological and subjective stress responses. This allows us to rule out that gender differences in stress reactivity can account for the differences in self-other distinction. Furthermore, neither gender nor group showed a significant main effect or any interaction in the control trials of the perspective-taking task. As these trials represented a measure of general cognitive load, this suggests that unspecific effects of stress on cognitive processing do not account for the differences in self-other distinction. What are the putative variables leading to stressed women being better in self-other distinction, while stressed men become worse? One explanation is that women, in general, might show better social skills, and hence will also show better social skills when under stress. However, what speaks against this interpretation is that we had matched trait socio-cognitive and — affective abilities of men and women in our sample. Therefore, differences in trait socio-cognitive abilities (i.e. differences also present without putting participants under stress) can be ruled out as an explanation for our results. Alternatively, it has been proposed that women are more prone to seek social support in general (Tamres et al., 2002). Thus, they might have learned by experience that they receive more support when they are able to relate more accurately to others, which in turn might explain their better ability for self-other distinction under stress. A putative candidate to explain the gender differences on a physiological level is the oxytocin system (Heinrichs et al., 2009; Meyer-Lindenberg et al., 2011), because there is some evidence that women might show higher oxytocin release under stress than men (Sanders et al., 1990; Ježová et al., 1996; Carter, 2007). Furthermore, oxytocin has been shown to improve mind reading (Domes et al., 2007) and enhance emotional empathy (Hurlemann et al., 2010). Most importantly, a recent study found that administration of oxytocin leads to sharpened self-other perception (Colonnello et al., 2013). Thus, the gender differences in self-other distinction under stress might be related to gender differences in oxytocin release, and its positive effects on coping with stress (Heinrichs and Domes, 2008). One limitation of this study is the fixed order of the self-other distinction paradigms, which was chosen based on the rationale that lower-level tasks should interfere less with higher-level tasks. This approach however precluded to control for carry-over or order effects. Future replication studies should therefore consider randomized task ordering. Furthermore, the stress procedures were also implemented in a fixed order. The ordering of the public speaking and mental arithmetic parts of the TSST-G was based on an established procedure in earlier work of our group (von Dawans et al., 2012). We did not include a third stress procedure before the perspective-taking task based on the reasoning, that a third stress part might suffer from habituation effects. However, as documented in Fig. 2, stress levels were increased throughout the time span of our self-other distinction paradigms, showing that all tasks were run while participants experienced high levels of stress. Direct comparisons of men and women in each group (i.e. stress and control) separately, showed that directly compared men and women in each group did not differ in their responses in most of our measures. Thus, our findings are limited to draw conclusions about differences between stressed and non-stressed men and differences between stressed- and non-stressed women. We only found a significant difference of men and women in the interference effect of the imitation-inhibition task in the control group. This finding is in line with prior mimicry studies showing that women tend to show higher mimicry than men (Dimberg and Lundquist, 1990; Hermans et al., 2006; Cheng et al., 2008). Apparently this effect was diminished by the stress induction in our study, probably by enhancing self-other distinction abilities and regulatory mechanisms in women and resulting in an interference effect that did not differ between men and women in the stress group. Future studies might assess whether this effect of stress induced reduction of mimicry in women is restricted to our imitation-inhibition paradigm, or is also present in other measures of mimicry, such as facial mimicry. Possible a priori gender differences in socio-cognitive abilities can be ruled out in our study, as we matched participants for socio-cognitive abilities. However, future studies might assess in non-matched samples how a priori differences in social cognition might affect the effects of stress on self-other distinction. The present study's design is limited in scope to the effects of psychosocial stress. However, it might be that some of the observed effects would also be caused by non-social stressors. Future work should therefore test the specificity of our findings by investigating the effects of non-social stressors as well.

Taken together our results suggest that under stress men and women differ in social cognitions and emotions although they might display similar prosocial behaviours (Taylor et al., 2000; von Dawans et al., 2012). These differences should be considered in future research linking mental representations to social behaviours. They also highlight the importance of studying both genders in stress research. Additionally, taking into account gender differences in socio-cognitive and — affective responses may contribute to more tailored psychological interventions and therapies. This seems particularly relevant for social conflicts in environments where stressful situations often arise — such as the workplace, or in private conflicts.

Role of the funding source

Conflict of interest statement

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.psyneuen.2014.02.006.

References

Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., Plumb, I., 2001. The reading the mind in the eyes test revised version: a study with normal adults, and adults with Asperger syndrome or high-functioning autism. Journal of Child Psychology and Psychiatry and Allied Disciplines 42, 241—251.

Batson, C.D., 1987. Prosocial motivation: is it ever truly altruistic? Advances in Experimental Social Psychology 20, 65—122.

Batson, C.D., 2010. Empathy-induced altruistic motivation. In: Mikulincer, M., Shaver, P.R. (Eds.), Prosocial Motives, Emotions, and Behavior. American Psychological Association, Washington, DC.

Brass, M., Derrfuss, J., Von Cramon, D.Y., 2005. The inhibition of imitative and overlearned responses: a functional double dissociation. Neuropsychologia 43, 89—98.

Brass, M., Ruby, P., Spengler, S., 2009. Inhibition of imitative behaviour and social cognition. Philosophical Transactions of the Royal Society B: Biological Sciences 364, 2359—2367.

Carter, C.S., 2007. Sex differences in oxytocin and vasopressin: implications for autism spectrum disorders? Behavioural Brain Research 176, 170—186.

Cheng, Y., Lee, P.L., Yang, C.Y., Lin, C.P., Hung, D., Decety, J., 2008. Gender differences in the mu rhythm of the human mirror-neuron system. PLoS ONE 3 .

Colonnello, V., Chen, F.S., Panksepp, J., Heinrichs, M., 2013. Oxytocin sharpens self-other perceptual boundary. Psychoneuroendocrinology 38, 2996—3002.

Davis, M.H., 1983. Measuring individual differences in empathy: evidence for a multidimensional approach. Journal of Personality and Social Psychology 44, 113—126.

Decety, J., Lamm, C., 2007. The role of the right temporo-parietal junction in social interaction: how low-level computational processes contribute to meta-cognition. Neuroscientist 13, 580—593.

Dickerson, S.S., Kemeny, M.E., 2004. Acute stressors and cortisol responses: a theoretical integration and synthesis of laboratory research. Psychological Bulletin 130, 355—391.

Dimberg, U., Lundquist, L.O., 1990. Gender differences in facial reactions to facial expressions. Biological Psychology 30, 151—159.

Doherty, R.W., 1997. The emotional contagion scale: a measure of individual differences. Journal of Nonverbal Behavior 21, 131—154.

Domes, G., Heinrichs, M., Michel, A., Berger, C., Herpertz, S.C., 2007. Oxytocin improves mind-reading in humans. Biological Psychiatry 61, 731—733.

Eisenberg, N., Fabes, R.A., Miller, P.A., Fultz, J., Shell, R., Mathy, R.M., Reno, R.R., 1989. Relation of sympathy and personal distress to prosocial behavior: a multimethod study. Journal of Personality and Social Psychology 57, 55—66.

Epley, N., Keysar, B., Van Boven, L., Gilovich, T., 2004. Perspective taking as egocentric anchoring and adjustment. Journal of Personality and Social Psychology 87, 327—339.

Foley, P., Kirschbaum, C., 2010. Human hypothalamus-pituitary-adrenal axis responses to acute psychosocial stress in laboratory settings. Neuroscience and Biobehavioral Reviews 35, 91—96.

Heinrichs, M., Baumgartner, T., Kirschbaum, C., Ehlert, U., 2003. Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. Biological Psychiatry 54, 1389—1398.

Heinrichs, M., Domes, G., 2008. Neuropeptides and social behaviour: effects of oxytocin and vasopressin in humans. Progress in Brain Research 170, 337—350.

Heinrichs, M., von Dawans, B., Domes, G., 2009. Oxytocin, vasopressin, and human social behavior. Frontiers in Neuroendocrinology 30, 548—557.

Hermans, E.J., Putman, P., van Honk, J., 2006. Testosterone administration reduces empathetic behavior: a facial mimicry study. Psychoneuroendocrinology 31, 859—866.

Hurlemann, R., Patin, A., Onur, O.A., Cohen, M.X., Baumgartner, T., Metzler, S., Dziobek, I., Gallinat, J., Wagner, M., Maier, W., Kendrick, K.M., 2010. Oxytocin enhances amygdala-dependent, socially reinforced learning and emotional empathy in humans. Journal of Neuroscience 30, 4999—5007.

Ježová, D., Juránková, E., Mosnárová, A., Kriška, M., Škultétyová, I., 1996. Neuroendocrine response during stress with relation to gender differences. Acta Neurobiologiae Experimentalis 56, 779—785.

Keysar, B., Barr, D.J., Balin, J.A., Brauner, J.S., 2000. Taking perspective in conversation: the role of mutual knowledge in comprehension. Psychological Science 11, 32—38.

Kirschbaum, C., Kudielka, B.M., Gaab, J., Schommer, N.C., Hellhammer, D.H., 1999. Impact of gender, menstrual cycle phase, and oral contraceptives on the activity of the hypothalamus-pituitary-adrenal axis. Psychosomatic Medicine 61, 154—162.

Ma, Y., Han, S., 2010. Why we respond faster to the self than to others? An implicit positive association theory of self-advantage during implicit face recognition. Journal of Experimental Psychology: Human Perception and Performance 36, 619—633.

Meyer-Lindenberg, A., Domes, G., Kirsch, P., Heinrichs, M., 2011. Oxytocin and vasopressin in the human brain: social neuropeptides for translational medicine. Nature Reviews Neuroscience 12, 524—538.

Negd, M., Mallan, K.M., Lipp, O.V., 2011. The role of anxiety and perspective-taking strategy on affective empathic responses. Behaviour Research and Therapy 49, 852—857.

Pruessner, J.C., Kirschbaum, C., Meinlschmid, G., Hellhammer, D.H., 2003. Two formulas for computation of the area under the curve represent measures of total hormone concentration versus time-dependent change. Psychoneuroendocrinology 28, 916—931.

Sanders, G., Freilicher, J., Lightman, S.L., 1990. Psychological stress of exposure to uncontrollable noise increases plasma oxytocin in high emotionality women. Psychoneuroendocrinology 15, 47—58.

Santiesteban, I., Banissy, M.J., Catmur, C., Bird, G., 2012. Enhancing social ability by stimulating right temporoparietal junction. Current Biology 22, 2274—2277.

Schulz, P., Schlotz, W., 1999. The Trier Inventory for the Assessment of Chronic Stress (TICS): Scale construction, statistical testing, and validation of the scale work overload.(Trierer Inventar zur Erfassung von chronischem Streß (TICS): Skalenkonstruktion,

teststatistische Überprüfung und Validierung der Skala Arbeitsüberlastung). Diagnostica 45, 8—19.

Seidel, E.M., Silani, G., Metzler, H., Thaler, H., Lamm, C., Gur, R.C., Kryspin-Exner, I., Habel, U., Derntl, B., 2013. The impact of social exclusion vs. inclusion on subjective and hormonal reactions in females and males. Psychoneuroendocrinology 38, 2925—2932.

Silani, G., Lamm, C., Ruff, C.C., Singer, T., 2013. Right supramarginal gyrus is crucial to overcome emotional egocentricity bias in social judgments. Journal of Neuroscience 33, 15466—15476.

Singer, T., Lamm, C., 2009. The social neuroscience of empathy. Annals of the New York Academy of Sciences 1156, 81—96.

Smeets, T., Dziobek, I., Wolf, O.T., 2009. Social cognition under stress: differential effects of stress-induced cortisol elevations in healthy young men and women. Hormones and Behavior 55, 507—513.

Starcke, K., Brand, M., 2012. Decision making under stress: a selective review. Neuroscience and Biobehavioral Reviews 36, 1228—1248.

Tamres, L.K., Janicki, D., Helgeson, V.S., 2002. Sex differences in coping behavior: a meta-analytic review and an examination of relative coping. Personality and Social Psychology Review 6, 2—30.

Taylor, S.E., Klein, L.C., Lewis, B.P., Gruenewald, T.L., Gurung, R.A.R., Updegraff, J.A., 2000. Biobehavioral responses to stress in females: tend-and-befriend, not fight-or-flight. Psychological Review 107, 411—429.

von Dawans, B., Fischbacher, U., Kirschbaum, C., Fehr, E., Heinrichs, M., 2012. The social dimension of stress reactivity: acute stress increases prosocial behavior in humans. Psychological Science 23, 651—660.

von Dawans, B., Kirschbaum, C., Heinrichs, M., 2011. The Trier Social Stress Test for Groups (TSST-G): a new research tool for controlled simultaneous social stress exposure in a group format. Psychoneuroendocrinology 36, 514—522.

Wang, Y., Hamilton, A., 2012. Social top-down response modulation (STORM): a model of the control of mimicry in social interaction. Frontiers in Human Neuroscience 6, 1—10.