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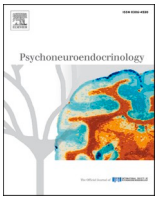

Rapid and delayed stress effects on recognition of female and male faces

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ABSTRACT

Stress and the stress hormone cortisol typically impair memory recognition, especially for emotional words, scenes or objects. However, prior research almost exclusively focused on rapid non-genomic cortisol effects. Additionally, findings for stress hormone effects on face stimuli are contradictory and rare, although very relevant for everyday life. In this preregistered study, we investigated the rapid and delayed stress effects on memory recognition for faces. In a two-day design, 52 healthy men first encoded pictures of male and female faces with distinct emotional expressions. One day later, participants were exposed to a psychophysiological stress (Socially Evaluated Cold-Pressor Test) or a (warm water) control procedure. Memory for the faces was tested at two time points: 25 min after stress onset at the peak of the cortisol increase for stressed participants (rapid non-genomic cortisol effects, which presumably operate within minutes through membrane bound receptors), as well as 90 min after stress onset when cortisol concentrations were back to baseline (delayed genomic cortisol effects, which describe an altered gene transcription resulting in modified neural functions, acting supposedly via intracellular receptors). Rapid stress effects led to enhanced memory recognition for female faces selectively, whereas delayed stress effects led to enhanced memory recognition across male and female faces. Altogether, we observed a beneficial rather than detrimental impact of stress on face recognition with a differential impact on recognition of male and female faces over time. It remains to be determined if this beneficial stress effect relies on the interaction of participants' sex and the sex of facial stimuli. Future research should also more closely look at the underlying mechanisms of how stress exactly influences face recognition, which is for example critically relevant for testimonies.

1. Introduction

Gatherings can be joyful, but also unpleasant when you are confronted with a person you have met before but do not remember. Not or wrongly recognizing a person can result in awkward situations. Moreover, in the context of eyewitness testimonies it can have a substantial impact on somebody's life. Several studies emphasised that stress impairs retrieval of certain words or pictures (Shields et al., 2017). However, face stimuli in that context have only rarely been investigated and the few studies investigating faces led to heterogenous findings (Li et al., 2014, 2013; Marr et al., 2021b).

When we experience a stressful situation, our body initiates a cascade of responses to prevent us from potential hazards, simultaneously maintaining homeostasis (McEwen, 2004). Our body activates the sympathetic nervous system (SNS) and the hypothalamus-pituitary-adrenocortical (HPA) axis (de Kloet et al., 2005). The initiation of the SNS results in an immediate secretion of the catecholamines norepinephrine and epinephrine. The HPA axis triggers a succession of hormonal secretions leading to a release of glucocorticoids like cortisol peaking around 20–30 min after stressor onset (Dickerson and Kemeny, 2004). Stress predominantly reduces memory retrieval as observed in free recall and recognition tasks (Shields et al., 2017). However, mixed results occurred in particular for recognition, such that stress sometimes did not reduce recognition (Li et al., 2014; Marr et al., 2021b) or even enhanced recognition (Hupbach and Fieman, 2012; Schwabe et al., 2009).

One important factor influencing results comprises the timing of the stressor. Directly after the stressor, when cortisol levels are still quite low, most studies did not find a stress effect on memory retrieval (Schwabe and Wolf, 2014). However, retrieval is affected when taking place during the time frame of rapid non-genomic as well as delayed genomic cortisol effects (Joëls et al., 2013; Schwabe and Wolf, 2014). The stress hormone cortisol binds to glucocorticoid (GRs) as well as mineralocorticoid receptors (MRs), which are differently distributed in

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the brain and differ in their affinities for cortisol. While MRs are particularly distributed in limbic regions, GRs are expressed more far-reaching and cumulative. Additionally, MRs have a higher affinity for cortisol, entailing an active state when cortisol levels are rather low, while GRs are operative rather under high cortisol concentrations. Furthermore, rapid non-genomic cortisol effects are presumably mediated via membrane bound MRs and GRs, while delayed genomic cortisol effects seem to be liable to intracellular MRs and GRs. Based on these influencing factors, genomic and non-genomic effects of the stress hormone cortisol elicit distinct response patterns to stress (de Kloet and Joëls, 2023; Hermans et al., 2014; Joëls et al., 2013).

Non-genomic cortisol effects influence neural functioning shortly after stressor onset. During the very early stress response, cortisol interacts with increased levels of catecholamines activating the basolateral amygdala, enhancing hippocampal plasticity and impairing prefrontal functioning (Gagnon and Wagner, 2016). This might result in a fast acting "memory formation mode" facilitating emotional memory encoding and consolidation of stressor related information while suppressing the competing process of retrieving unrelated material (Gagnon and Wagner, 2016; Shields et al., 2017; Wolf, 2017).

Genomic cortisol effects start to emerge around 60 min after stressor onset when both catecholaminergic activity and cortisol levels are often decreased again (Hermans et al., 2014; Joëls et al., 2013). During this time frame, intracellular restructuring results in a reduction of hippocampal plasticity or increased interaction between amygdala and prefrontal cortex (Gagnon and Wagner, 2016), initiating a "memory storage mode" which allows for consolidation of already encoded memory contents (Wolf, 2017). This in turn leads to a suppression of both, encoding and retrieval of unrelated information (Gagnon and Wagner, 2016; Wolf, 2017). Only one study so far (Schwabe and Wolf, 2014) investigated both non-genomic and genomic cortisol effects on memory recognition. Impairments in memory performance were found 25 min as well as, even stronger, 90 min after stress onset, which were independent of stimulus valence. However, several other studies showed that stress mostly impaired recognition of emotional material (Shields et al., 2017; Wolf, 2017).

Not only stimulus valence but also stimulus type might influence the outcome of memory performance (Galli and Otten, 2011). Surprisingly, only very few previous stress studies included face stimuli. In a first study by Li and colleagues (2013), stress significantly impaired memory recognition for faces independently of emotional valence. In a second study, the authors found stress to recruit medial temporal and frontal brain areas during recognition: stress had an enhancing impact on processing emotional in comparison to neutral faces, but no differences in memory performance emerged (Li et al., 2014). Another study likewise did not observe any stress effects on the recognition of face stimuli (Marr et al., 2021b).

Are faces indeed special? Multiple studies showed that faces might be more holistically processed than other types of visual stimuli due to face sensitive brain areas such as the fusiform face area (Kanwisher and Yovel, 2006). Does that imply that faces might be differently affected by stress than other stimulus types? This question was diversely answered by memory experts and eyewitness experts in a recent survey of Marr and colleagues (2021a). Among eyewitness experts the answers were quite balanced, with a slightly more percentage agreeing with this statement, while most memory experts had no answer to that question.

Other influencing factors like the influence of sex on face memory have not been sufficiently investigated yet. Additionally, a varying influence of recollection and familiarity on memory processes has been reported. Since recollection predominantly relies on the hippocampus (Yonelinas, 2002), stress could exert an impact especially on recollection processes (Wiemers et al., 2013). Including these influencing factors, we aimed to investigate whether stress has different effects on recognition of female and male faces, either 25 or 90 min after stressor onset. We expected memory recognition to be impaired especially in the stress group (versus the control group) and for emotional stimuli (versus neutral stimuli). Furthermore, we assumed memory performance to be impaired not only 25 min after stressor onset, but especially at 90 min after stress induction. When comparing familiarity-based memory and recollection-based memory, we expected recollection to be impaired more strongly in the stress relative to the control group.

2. Material and methods

The present study was preregistered at the Open Science Framework (https://osf.io/6jgst/?view_only=6f5ea7f16f7f479ba51f0f966f4bbba8).

2.1. Participants

Power analysis with G*power 3.1.9.4 (Faul et al., 2009) using a 1-$\beta \geq 0.85$ power to detect a medium effect size of $f = -0.245$ or $d = -0.49$ (see meta-analysis by Het et al., 2005) at $\alpha \leq 0.05$ with a correlation of $r = 0.30$ and a non-sphericity correction of $\mathcal{E} = 0.80$ revealed a target sample of 52 participants.

Fifty-four men were recruited via advertisements on the internet or the campus of the Ruhr University Bochum. Two participants had to be excluded, one due to missing data and one due to arbitrary rating behaviour or non-understanding of the memory task (see data analysis), leaving the required number of 52 participants for the analysis. To rule out sex hormone levels as a potentially confounding factor (Jentsch et al., 2022), only men were tested. All of them were right-handed, healthy, between 18 and 35 years old and had a body mass index between 18.2 and 29 kg/m^2. Participants were only tested if they were non-smokers, without regular drug, alcohol or medication intake and if they did not donate blood, experienced a time shift of more than 5 h or an extraordinary stressful situation in their everyday life within the last two weeks or obtained a vaccination within the last four weeks before the testing days (Strahler et al., 2017). Participants were also excluded if they worked in night work or shiftwork within four weeks before the testing. Furthermore, participants were instructed not to eat or drink anything else except water and not to do any demanding sports within one hour before the experiments. For their participation they received 30€ or course credits.

Data collection procedure was approved by the ethics committee of the Faculty of Psychology, Ruhr University Bochum (registration number: 18–6448) and followed the guidelines of the Declaration of Helsinki.

2.2. Stimuli and randomization

For the memory recognition task, 120 Caucasian frontal view face images were taken from the Radboud Face Database (Langner et al., 2010) and the Chicago Face Database (Ma et al., 2015). Applying the shine toolbox (Willenbockel et al., 2010) and the image editing program GIMP (GNU Image Manipulation Program 2.10.8.), stimuli were matched in their brightness, quality and alignment. All faces were displayed on a white background and presented on a black screen.

Stimuli were rated by 24 independent participants (10 men and 14 women; mean age=25.5 years, *SD*=4.39) regarding their arousal, valence and authenticity beforehand and equally divided into two different sets (set A=60 stimuli and set B=60 stimuli) regarding their valence ratings (on a 9-point Likert scale ranging from very negative to very positive; negative *M*=2.58, *SD*=0.21; neutral *M*=4.94, *SD*=0.31; positive *M*=7.17, *SD*=0.45). Negatively rated pictures included angry, neutral pictures neutral and positive pictures happy facial expressions. The valence ratings during the experiment confirmed this assignment (see results).

In each case, stimuli were randomly collected from one of the two sets (A or B) for the 'old' stimuli shown during encoding, leaving the second set for the additional 'new' stimuli shown during recognition. Stimuli during encoding as well as the two recognition phases were

presented using block randomization. Each phase comprised 60 stimuli in total: Encoding was divided into two blocks of 30 faces, composed of 10 angry, 10 happy and 10 neutral faces, of which 5 were represented by men and 5 by women each. On no account more than two faces of the same valence were presented consecutively.

Half of the previously encoded faces (30) and 30 additional faces were presented in the first recognition phase, while the other half (30) as well as 30 additional faces were presented in the second recognition phase. Likewise, stimuli were presented in two blocks, sharing the same number and randomization of emotional facial expressions and male/female faces as during encoding.

2.3. Memory paradigm

The memory paradigm with one encoding and two recognition phases (see Fig. 1) was presented via MATLAB (version 2018b) using the Psychophysics Toolbox (Kleiner et al., 2007) and the OTBR Toolbox (Rose et al., 2008). Each of the phases lasted about 16 min and participants were instructed about their task orally and in written form. In preparation for each phase a test run consisting of four additional stimuli was conducted.

Prior to the encoding phase, a short story was presented, in which participants were instructed to imagine joining a party. During this fictional party they were asked to try to memorize the faces of the people they are confronted with to be able to distinguish them from additional new faces at a different party which was planned for the second experimental session. Additionally, participants were asked to rate the perceived valence of each presented face on a 7-point Likert scale ranging from 1 (very negative) to 7 (very positive).

In two separate recognition phases, each presenting different stimulus sets, participants were again introduced to the party context. They were asked to rate each face depending on if they think they had seen the face before as well as on how sure they were about their decision on a 6-point Likert scale (1 - very sure new, 2 - fairly sure new, 3 - slightly sure new, 4 - slightly sure old, 5 - fairly sure old, 6 - very sure old). Participants were instructed to adjust their rating during each memory phase using the arrow keys on the keyboard.

2.4. Stress induction

On day two before recognition, 52 participants were randomly exposed either to the Socially Evaluated Cold-Pressor Test (SECPT; Schwabe et al., 2008) or the respective control procedure (each group consisted of 26 participants). Over the course of the SECPT, participants were required to immerse their hand in ice-cold water with a temperature of about 0–2 °C, while being videotaped and observed by an unknown woman for three minutes. They were further led to believe that their facial expressions will be subsequently analyzed (which was not the case). In the control procedure, the water had a temperature of about 37 °C and participants were neither observed nor videotaped.

The immediate reaction of the SNS was measured via pulse, systolic and diastolic blood pressure three times within three minutes respectively, right before, during and after the stress or control procedure, using an Omron m700 Intelli IT (HEM-7322 T-D; OMRON Healthcare Co. Ltd.). For statistical analyses, the mean of the three measurements was used at each time point. Directly after the stress or control procedure, a post-treatment evaluation enquiring the perceived difficulty, unpleasantness, stressfulness and painfulness of the previous situation was surveyed on an 11-point Likert scale ranging from 0 (not at all) to 100 (very much; Schwabe et al., 2008).

To measure the neuroendocrine stress response as well as subjective momentary affect, saliva samples using Salivette collection devices with a synthetic swap (Sarstedt, Nuembrecht, Germany) and affect ratings using the German version of the Positive and Negative Affect Schedule (PANAS; Breyer and Bluemke, 2016) were collected at eight different time points on both days. Measures were taken on day one: a) right before and b) right after encoding, as well as on day two: c) before (baseline) and d) right after the stress/control procedure (+3), e) before (+25) and f) after recognition one (+43), as well as g) before (+90) and h) after recognition two (+108; cf. Fig. 1).

Saliva samples were stored at − 20 °C and salivary cortisol and alpha amylase (sAA) concentrations were subsequently processed in the local biochemical laboratory. Salivary cortisol was analyzed on a Synergy2 plate reader (Biotek, USA) using a commercial enzyme-linked immunosorbent assay (ELISA; IBL International GmbH, Hamburg, Germany) according to the manufacturer's instructions. Intra- and inter-assay variability were less than 10%. sAA was analyzed via a colorimetric test using 2-chloro-4-nitrophenyl-α-maltrotriosoide (CNP-G3) as a substrate reagent compliant as described before (Lorentz et al., 1999). All intra- and inter-assay variabilities were below 8%.

2.5. Procedure

Experimental sessions were conducted on two consecutive days

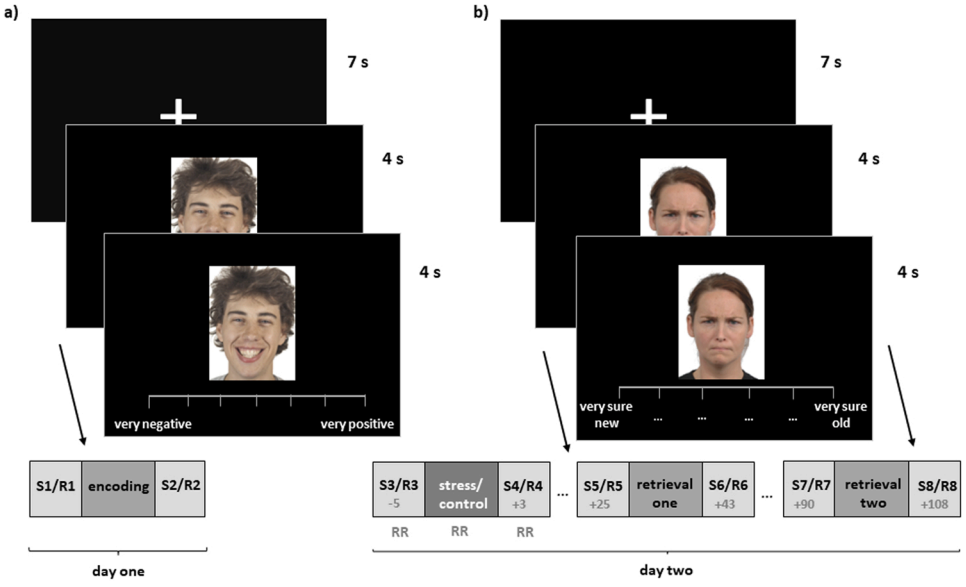

Fig. 1. Memory paradigm for a) encoding on day one and b) the two recognition phases on day two. During each phase, first, the stimulus was presented alone (4 s), then, the rating scale was additionally displayed (4 s), followed by a light-matched, jittered fixation cross (7 s, jittered in 0.192 s steps within 2.5 s). The recognition scale is depicted in simplified terms; in reality, all levels of the scale are formulated in words (see section memory paradigm in the main text). Only saliva measures (S), affect ratings (R), pulse and blood pressure measures (RR), memory phases and the stress and control procedure (stress/control) are depicted. Time (in minutes) is represented in relation to the onset of the stress or control procedure.

between 12.30 and 6 p.m. to control for diurnal cortisol fluctuations (Kudielka et al., 2009). On day one, participants first received detailed information about the study and provided their informed consent as well as their personal data. Afterwards participants read the encoding instructions, passed through a test run and provided the first saliva sample (S1) as well as the first affect rating (R1) before the encoding phase started, followed by the second saliva sample (S2) and affect rating (R2; cf. Fig. 1).

The experimental session on day two always started about 24 h (± 1 h) later. Here, participants provided their first saliva sample (S3) and affect rating (R3) approximately five minutes after arrival followed by the cardiovascular baseline measure and a subsequent information about their group allocation. Participants in the stress group were required to give their informed consent to take part in the subsequent SECPT procedure. After that, they either underwent the SECPT or the warm water control procedure, having their pulse and blood pressure simultaneously monitored. Directly afterwards, the second saliva sample (S4) and affect rating (R4) were provided and participants completed the post-treatment questionnaire. Five additional minutes later, pulse and blood pressure were measured for one last time.

During a short break, participants first filled out two questionnaires, the Stait-Trait Anxiety Inventory (STAI-T, Spielberger et al., 1983) and the Brief Symptom Inventory (BSI; Derogatis and Melisaratos, 1983). They were afterwards instructed to watch emotionally neutral instruction and documentation videos. Videos were used to bridge the time between the different phases on day two. All videos were prepared in a way that voices, faces and emotional scenes were cut out and the original sound was mostly replaced by calm music.

Before providing the next saliva sample (S5) and affect rating (R5) exactly 25 min after onset of the stress or control procedure, participants were instructed for the recognition phase and underwent a test run. Immediately afterwards (27 min after stress/control onset), participants performed recognition one and subsequently provided the next saliva sample (S6) and affect rating (R6). During a second break, participants continued watching the video clips. At the end of the second break, participants were asked to rate their feeling of valence and arousal about the video clips on two different 9-point Likert scales (valence: 1 (very negative) to 9 (very positive); arousal: 1 (emotionally calm) to 9 (emotionally arousing)). Ratings did not differ between the groups (all $p > .53$), video clips were rated as rather emotionally calm (M=2.46, SD=1.62) and positive (M=6.8, SD=1.63).

Before providing the next saliva sample (S7) and affect rating (R7) exactly 90 min after onset of the stress or the control procedure, the second test run was performed. Finally, recognition two started 92 min after stress or control onset. After that, a last saliva sample (S8) and affect rating (R8) were provided, participants were debriefed, compensated and dismissed.

2.6. Data analyses

Data was analysed using R version 4.1.3 (2022–03–10) and MATLAB R2020b (Natick, Massachusetts: The MathWorks Inc.). If normal distribution or homoscedasticity was not given as examined using the Kolmogorov-Smirnoff test, the WRS (Wilcox, 2012) and the WRS2 package (Mair and Wilcox, 2020) were applied to conduct robust analyses, based on sample trimmed means. The standard $p < .05$ criterion was used for significance testing.

Success of the stress induction was investigated using separately conducted robust repeated measures ANOVA for the physiological stress response (salivary cortisol and sAA) and the subjective momentary affective state (positive and negative affect) for day one and two respectively, including the within-subjects factor Time (day one: before vs. after encoding; day two: baseline, +3, +25, +43, +90 vs. +108) and the between-subjects factor Group (stress vs. control). Similarly, cardiovascular data (pulse, systolic and diastolic blood pressure) was analyzed, including the factors Time (before, during vs. after the stress/control procedure) and Group. To analyze the post-treatment evaluation, individual Yuen-Welch tests for independent samples were applied for each category to detect group differences.

Exploratory robust three-way mixed ANOVAs served to investigate differences in ratings of valence and sex of the stimuli on day one, including the within-subjects factors Valence (happy vs. angry vs. neutral faces) and Sex (female vs. male faces) as well as the between-subjects factor Group.

General recognition performance was analyzed using the sensitivity index (d′) and the bias index (C), according to the signal detection model (Snodgrass and Corwin, 1988). Furthermore, the two memory component processes recollection (r0) and familiarity (dF) were computed according to the dual-process signal detection model (Yonelinas, 2002) using the receiver operating characteristics (ROC)–Toolbox (Koen et al., 2017). To investigate the influence of stress on memory recognition, robust repeated measures ANOVA were conducted separately for recognition one (+25) and two (+90) including the within-subjects factors Valence and Sex as well as the between-subjects factor Group.

All analyses were performed on the entire sample. However, we additionally calculated memory data for cortisol responders and non-responders separately, using a fixed threshold classification criteria of 15.5% baseline-to-peak cortisol increase (Miller et al., 2013) as preregistered.

Two participants did not rate the valence of the stimuli during encoding as instructed (one of them in the stress and one in the control group). However, since both did not show any noticeable problems during the recognition phases, we suggested that they simply did not understand the rating procedure of the encoding task. Consequently, they were only excluded from the encoding analyses, but not from the recognition analyses. Exclusion of these two participants yielded the same results for memory performance. Additionally, if ROC curves could not be created, participants were excluded from the ROC analyses but not from other memory analyses.

When data was missing due to technical difficulties or specific saliva samples could not be analyzed, the concerning participant was only excluded from the respective analysis of the dependent variable in the particular phase. For one participant however, memory data was missing due to technical difficulties. As a result, this participant had to be excluded from the whole analysis. Another participant showed rating behavior at chance level, leading to the suggestion that the participant did not understand or did not conscientiously fulfill the task. Admittedly, we did not preregister proceedings for this issue, but we decided to also exclude this participant. Both excluded participants were replaced by new participants to stay within the required sample size of 52 participants.

3. Results

3.1. Participants

There were no significant differences between groups for age ($Y_{t\ (30)}$= 0.483, p = .633) and body mass index ($Y_{t\ (22.46)}$= 0.834, p = .413; see Table 1).

3.2. Physiological stress response

On day one, no significant main or interaction effects occurred for salivary cortisol (all $p > .14$). On day two, a significant main effect Time ($F_{(5,22.15)}$= 15.28, $p < .001$) and a Group*Time interaction ($F_{(5,22.15)}$= 7.14, $p < .001$) was observed. Post-hoc tests revealed significantly higher cortisol concentrations in the stress group (versus the control group) directly before ($p < .005$) as well directly after recognition one ($p < .005$) only, but not at baseline or any other sample, in particular before or after recognition two (all $p > .28$; see Fig. 2).

On day one, sAA levels were slightly higher in the stress (M=234.12, SD=146.36) compared to the control group (M=191.81, SD=181.69;

Table 1
Mean (± SEM) age, body mass index as well as alpha amylase levels, blood pressure, pulse and stress rating data separately for the stress and control group. *P*-values of independent-sample Yuen-Welch tests for trimmed means are given for comparisons between the stress and control group.

	control	stress	*p*-values
demographics			
age	25.35 ± 4.34	25.46 ± 4.19	0.633
body mass index (kg/m^2)	24.36 ± 2.19	23.81 ± 2.10	0.413
alpha amylase (U/l) day 1			
before encoding	196.64 ± 146.18	249.57 ± 157.35	0.120
after encoding	187.35 ± 212.13	218.67 ± 135.81	0.113
alpha amylase (U/l) day 2			
baseline	186.38 ± 143.91	220.42 ± 135.50	0.115
+ 3 min	203.53 ± 184.36	228.25 ± 130.65	0.161
+ 25 min	179.67 ± 174.62	239.73 ± 215.85	0.099
+ 43 min	175.77 ± 150.65	238.80 ± 197.53	0.107
+ 90 min	205.05 ± 230.32	210.29 ± 159.58	0.282
+ 108 min	207.42 ± 187.68	265.55 ± 245.20	0.271
pulse (bpm)			
baseline	74.87 ± 14.26	67.85 ± 8.92	0.091
during hand immersion	73.95 ± 13.91	75.22 ± 12.40	0.886
5 min after stress/control	73.06 ± 13.38	65.22 ± 7.51	0.039
systolic blood pressure (mmHg)			
baseline	123.68 ± 13.05	121.13 ± 10.79	0.224
during hand immersion	121.97 ± 11.52	137.19 ± 11.17	< 0.001
5 min after stress/control	118.26 ± 11.91	118.26 ± 9.06	0.977
diastolic blood pressure (mmHg)			
baseline	69.38 ± 9.39	69.10 ± 8.36	0.822
during hand immersion	68.76 ± 7.99	84.23 ± 10.51	< 0.001
5 min after stress/control	66.21 ± 8.25	69.71 ± 9.06	0.307
stress ratings after stress/control procedure			
difficulty	1.60 ± 4.73	62.69 ± 30.67	< 0.001
unpleasantness	4.00 ± 7.07	63.85 ± 27.87	< 0.001
stressfulness	2.40 ± 4.36	54.23 ± 29.82	< 0.001
painfulness	0.80 ± 2.77	65.00 ± 26.42	< 0.001

main effect Group; $F_{(1,27.93)}= 7.53$, $p < .05$). No further main or interaction effects were found for sAA on day one or two.

Results for pulse, systolic and diastolic blood pressure showed a main effect Time (pulse: $F_{(2,22.73)}= 10.34$, $p < .001$; systolic: $F_{(2,24.61)}= 64.31$, $p < .001$; diastolic: $F_{(2,20.64)}= 27.13$, $p < .001$), a main effect Group (diastolic: $F_{(1,29.61)}= 4.77$, $p < .05$) and a Group*Time interaction (pulse: $F_{(2,22.73)}= 9.50$, $p = .001$; systolic: $F_{(2,24.61)}= 39.48$, $p < .001$; diastolic: $F_{(2,20.64)}= 27.24$, $p < .001$). Post-hoc tests revealed significantly higher systolic and diastolic blood pressure during stress compared to the control procedure (systolic: $p < .001$; diastolic: $p < .001$), while pulse was significantly lower after the stress compared to the control procedure ($p < .05$; see Table 1).

3.3. Subjective response of stress and momentary affect

For positive as well as negative affect, robust repeated measures ANOVA revealed no main or interaction effects on day one (all $p > .09$).

On day two, a significant main effect Time could be observed for positive affect ($F_{(5,21.83)}= 17.25$, $p < .001$), but post-hoc tests could not further track significant differences between time points. For negative affect, a significant main effect Group ($F_{(1,17.87)}= 6.81$, $p < .05$), Time ($F_{(5,18.12)}= 3.43$, $p < .05$) as well as a Time*Group interaction ($F_{(5,18.12)}= 3.60$, $p < .05$) were found. Post-hoc tests confirmed that negative affect ratings were significantly higher for the stress (M=1.57, SD=0.67) versus the control group (M=1.05, SD=0.12), directly after the SECPT only ($p < .001$).

For the stress ratings, separate Yuen-Welch tests revealed significantly higher ratings directly after the SECPT compared to the control procedure for difficulty, unpleasantness, stressfulness and painfulness ($p < .001$; see Table 1).

3.4. Memory encoding

Valence ratings during encoding differed significantly from each other (main effect Valence; $F_{(2,24.43)}= 216.32$, $p < .001$). Positive faces (M=5.71, SD=0.82) were rated as significantly more positive than negative (M=2.12; SD=0.64) and neutral faces (M=3.75; SD=0.66). Additionally, neutral faces were rated as significantly more positive than negative faces ($p < .001$). No further main or interaction effects occurred.

3.5. Influence of stress on memory recognition

3.5.1. Sensitivity measure (d′)

Results for d′ showed a significant Group*Sex interaction ($F_{(1,89.79)}= 8.07$, $p < .01$) for recognition one (+25). Subsequent robust post-hoc tests revealed that stress improved memory recognition for female ($p < .001$) but not for male faces ($p = .382$). For recognition two (+90), a main effect Group ($F_{(1,85.85}$ =9.25, $p < .005$) indicated that stress facilitated memory recognition overall (see Fig. 3A). No further main or interaction effects emerged.

3.5.2. Bias index (C)

For the bias index (C) no significant results for recognition one (+25) were found. For recognition two (+90), a main effect Valence ($F_{(2,61.55)}= 6.69$, $p < .005$) emerged indicating an overall significantly lower bias level for negative compared to neutral faces ($p < .005$; see Fig. 3B). Thus, negative faces were more likely rated as old than neutral

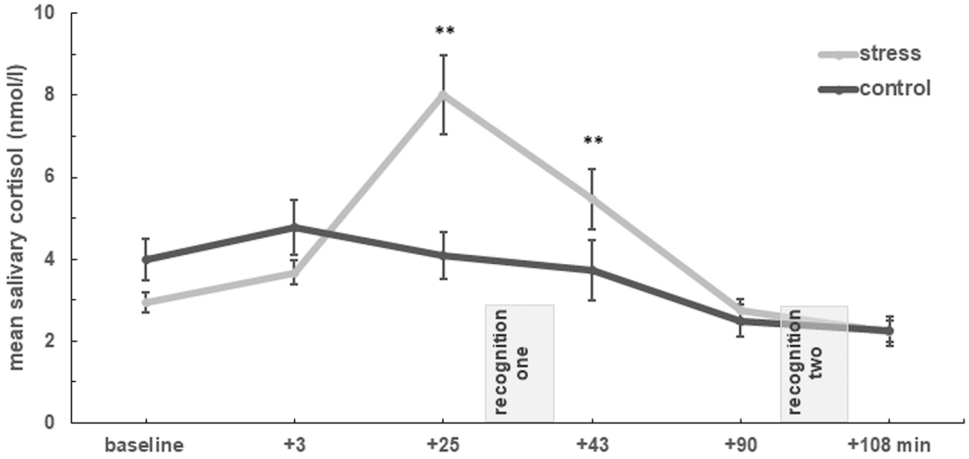

Fig. 2. Mean salivary cortisol concentrations depicted at distinct time points at day two. Stress induction successfully elevated cortisol concentrations immediately before and after recognition one, whereas cortisol concentrations were no longer different between the stress and control group before and after recognition two. Error bars represent standard errors of the mean. ** $p < .005$.

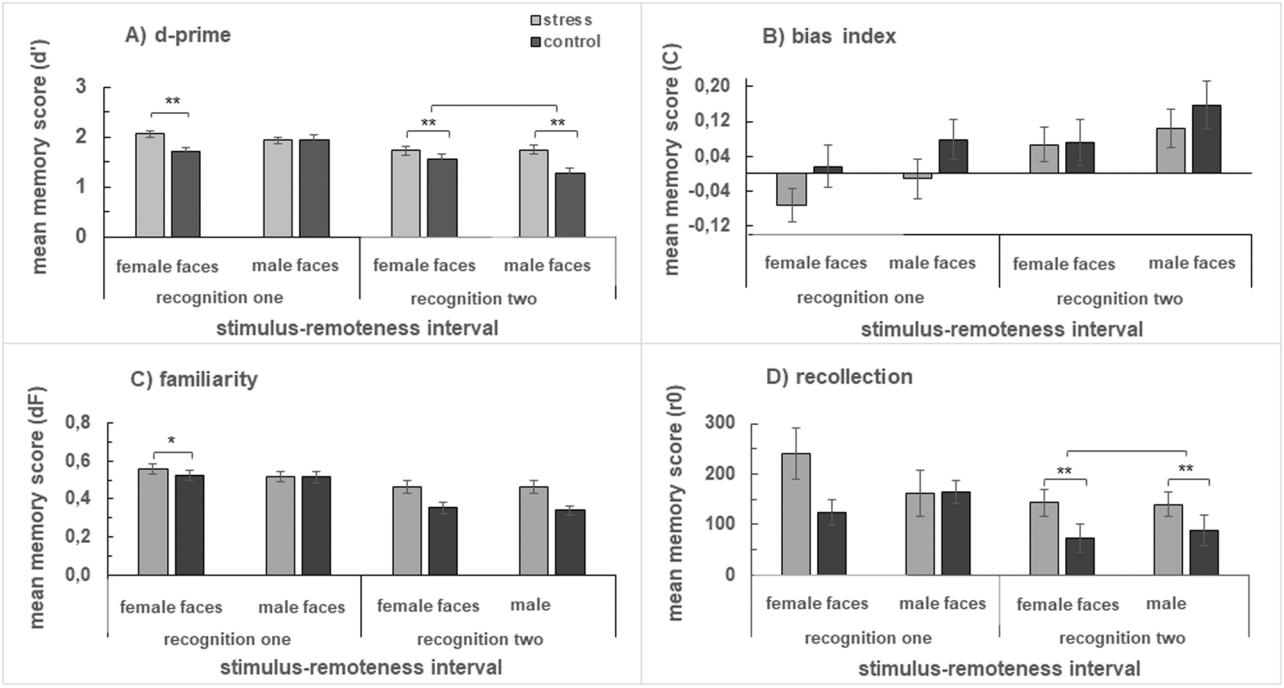

Fig. 3. Mean memory performance scores, divided into D-prime d′ (A), bias index C (B), familiarity dF (C) and recollection r0 (D) scores. All memory scores are depicted separately for female and male faces and both recognition phases (one: +25 min, rapid non-genomic cortisol effects; two: +90 min, delayed genomic cortisol effects). D-prime (A) as well as familiarity dF (C) scores during recognition one were higher in the stress group for female faces only, whereas during recognition two, both D-prime (A) and recollection (D) where higher in the stress group than in the control group, regardless of stimulus sex. Error bars are standard errors of the mean. * $p < .05$, * * $p < .005$.

faces. No further main or interaction effects occurred.

3.5.3. Familiarity (dF)

For recognition one (+25), a significant Group*Sex interaction ($F_{(1,92.95)}= 6.42$, $p < .05$) emerged for familiarity (dF), showing female faces to be rated as more familiar in the stress compared to the control group ($p < .05$). No further main or interaction effects emerged (see Fig. 3C).

3.5.4. Recollection (r0)

Analysis of recognition one (+25) did not show any significant effects. For recognition two (+90), a significant main effect Group ($F_{(1,91.12)}= 9.62$, $p < .005$) was observed, revealing that the stress group overall showed a significantly better recollection performance than the control group (see Fig. 3D). No further effects were found (see Fig. 3D).

3.5.5. Responder analyses

Analyses of memory data for cortisol responders in the stress group (24/26 participants) and non-responders in the control group (19/26 participants), using a fixed threshold classification criteria of 15.5% baseline-to-peak increase were conducted. Responder analyses confirmed prior analyses for all memory measures. Thus, D-prime and familiarity data revealed significantly better recognition performance for female faces only in the stress versus the control group during recognition one (+25; all $p < .05$). During recognition two (+90) D-prime and recollection data of the stress group (versus the control group) depicted better recognition performance irrespective of stimulus sex (all $p < .005$). Additionally responder analysis resulted in a main effect Group for D-prime ratings during recognition one (+25; $F_{(1,76.29)}= 7.70$, $p < .01$). Post-hoc tests confirmed that faces were better recognized in the stress versus the control group independent of stimulus sex. Furthermore, the former non-significant main effect Group for familiarity ratings during recognition two (+90) turned significant ($F_{(1,71.48)}= 8.54$, $p < .005$).

4. Discussion

In the current study, stress increased recognition of female and male faces. This effect was especially observed for female faces during recognition one (+25) with elevated cortisol levels in the stress group. For recognition two (+90), when cortisol levels in the stress group were low again, stress improved recognition performance regardless of stimulus sex. Analyses investigating cortisol responders and non-responders confirmed and even extended these findings, strengthening the idea that cortisol might constitute a major driving force for the observed effects.

Previous studies primarily showed that stress hormones impair memory retrieval (Shields et al., 2017; Wolf, 2017). Still, a few other experiments found either no effect (Marr et al., 2021b) or even enhancing stress hormone effects on memory retrieval (Hupbach and Fieman, 2012; Schilling et al., 2013; Schwabe et al., 2009). These heterogenous findings might be explained by several accounts, as for example the type of memory testing. Studies on the influence of stress on recognition memory are not entirely unambiguous (Marr et al., 2021b; Schwabe and Wolf, 2014), while many of the studies showing an impairing effect were based on free recall (de Quervain et al., 2000; Kuhlmann et al., 2005). Most importantly, while several types of stimuli have been previously investigated in the context of stress (Kuhlmann et al., 2005; Schönfeld et al., 2014; Wiemers et al., 2013), research on face stimuli is very sparse. The few studies investigating stress effects on recognition of face stimuli have sometimes found negative effects (Li et al., 2013), but sometimes also no significant effects (Li et al., 2014; Marr et al., 2021b).

Faces might be differently, more holistically, processed than other types of stimuli (Kanwisher and Yovel, 2006), relying for example on contributions of the prefrontal cortex, hippocampus and amygdala (Prince et al., 2009), areas strongly influenced by stress (Gagnon and Wagner, 2016). Moreover, faces contain a broad spectrum of social information like mood, intention or identity. Faces are likely the most

prominent and important stimuli in our everyday lives, which makes it easier for us to recognize familiar faces in comparison to other stimuli. However, the recognition of unfamiliar faces still seems challenging (Bruce and Young, 1986; Kanwisher and Yovel, 2006).

Not only the stimuli in the present study were highly social, but also the contextual embedding of the memory task. Participants' task was to imagine being on a party and to remember faces to be able to distinguish them from additional faces on another party on the second day. This task description could have placed the participants in a social everyday-life situation and could thus have influenced learning and memory performance. It is possible that the present memory results might not result from the well-known "fight-or-flight" (Cannon, 1915), or else "freeze" response (Roelofs, 2017), but rather from a more social mechanism. The "tend and befriend" theory describes an increased prosocial tendency of individuals after being exposed to stress (Taylor, 2006; von Dawans et al., 2012). A seeking for social support after the stressful situation, resulting in increased attention and consequently enhanced recognition memory for faces, might be adaptive in this situation. Hence, the social context embedded in the present study presumably elicited prosocial behavior.

Additionally, another crucial influencing factor for inconsistent results on this topic might be the severity of the stressor or the level of cortisol concentrations. The general stress-induced increase in cortisol in this study (delta mean: 5.08 nmol/l) is comparable to other studies using the SECPT, but it is still a moderate increase (Li et al., 2014; Schwabe and Wolf, 2014). In previous studies, different doses of cortisol affected memory retrieval in an inverted U-function. More precisely, a moderate cortisol increase led to enhanced memory retrieval, while very high or low cortisol increases did not (Schilling et al., 2013). Relatedly, in other studies showing beneficial effects of stress hormones on memory retrieval, the delta cortisol increase was quite similar to the current results (Hupbach and Fieman, 2012; Schwabe et al., 2009; cortisol responders in Zoladz et al., 2014) leading to the speculation that the exact cortisol increase might play an important role for memory retrieval. Furthermore, each of the studies showing enhanced effects of stress on memory retrieval, which did not use a pharmacological manipulation, used a physiological stressor, either the SECPT (Schwabe et al., 2009 and our study) or the CPT (Hupbach & Fiemann, 2012 and Zoladz et al., 2014 (in the latter only cortisol responders (comparable to the cortisol increase in our study) showed enhanced retrieval performance).

Moreover, stress especially increased recognition of female faces for recognition one (+25). Importantly, a woman conducted the SECPT and thus functioned as a stressor. Previously, glucocorticoids like cortisol led to selective attention towards potentially hazardous stimuli (Hermans et al., 2014). Furthermore, salience for threatful stimuli seems to be mediated especially at an early processing stage via MRs, which are particularly activated by cortisol under low levels and are very important for fast processing of relevant information (Taylor et al., 2011). Since participants in the stress group showed a significant but rather moderate increase of cortisol, this might have increased vigilance to stressor related stimuli via MRs. Speculatively, female faces might have been subconsciously classified as a potential threat or otherwise relevant information and directed attention to female stimuli after being exposed to a woman conducting the SECPT.

Interestingly, results regarding the genomic and non-genomic cortisol effects are consistent with the study by Schwabe and colleagues (2014) albeit showing opposite directions. In both studies genomic and non-genomic effects resulted in comparable, either enhanced or decreased effects, at least on the behavioral level. This aspect indicates that the stress hormone cortisol acts beyond the non-genomic effects in a longer time window. It must be noted that the term "non-genomic" as well as "genomic" in this context is restricted to cortisol related processes. In addition to the glucocorticoid effects, acute stress also triggers a redistribution of immune cells, which leads to enhanced immune function (Dhabhar et al., 2012). While genomic cortisol effects are presumably already in action 90 min post-stressor, immunologic cytokine effects are presumably still in a non-genomic state (Rohleder et al., 2006). It is therefore important to distinguish between different response levels. Accordingly, to measure genomic effects of the immune response, a longer time window would be necessary.

We further investigated the distinction between recollection and familiarity, since familiarity might mainly rely on perirhinal areas, and recollection might be primarily determined by the hippocampus (Wiemers et al., 2013; Yonelinas, 2002). Descriptive analyses of both memory measures strengthened the assumption that stress has an improving influence on memory recognition likewise for recollection and familiarity. However, results indicate that the effects of stimulus sex during recognition one (+25) were mainly driven by a feeling of familiarity, while the general stress effects during recognition two (+90) were more subject to hippocampus-based recollection processes. These results might serve as a first hint for future studies to disentangle possible differential effects of recollection and familiarity measure in memory for faces.

Importantly, it must be noted that the study sample was restricted to male participants in order to rule out possible hormonal influences. Yet, it is very important to examine sex hormone-specific effects more closely, since sex hormone levels (Merz and Wolf, 2017) or especially oral contraceptives might influence stress effects on memory retrieval (Jentsch et al., 2022). Furthermore, not only participants' sex should be further investigated, but also the interaction with the sex of the stimuli. Especially, whether similar results occur in male participants with a male stressor, or with female participants in combination with a female or male stressor should be considered in the future. Also, there were no cut-offs for emotion recognition as this would have limited the number of stimuli available for analysis. Future studies with more stimuli should look at the results focusing on those stimuli whose emotions were correctly recognized.

In sum, stress enhanced memory recognition of female faces 25 min as well as of female and male faces 90 min later. Thus, stress does not seem to always reduce memory recognition as often postulated. Rather, various influences such as stimulus material, the intensity of the stress (hormone) reaction or the context can lead to memory recognition being positively influenced by stress. Investigation of the underlying neural mechanisms could shed light especially on the distinction between genomic and non-genomic cortisol effects, the contribution of different brain regions involved in recollection and familiarity processes as well as the influence of stimulus material. Since faces are highly relevant stimuli, it is crucial that future studies focus on this rather underexplored type of stimuli in the context of stress with implications regarding fairness in the legal system and in particular the questioning of eyewitnesses (Deffenbacher et al., 2004).

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Author contributions

Lisa Pötzl: Formal analysis, Investigation, Data curation, Writing – original draft, Visualization; **Oliver T. Wolf:** Conceptualization, Methodology, Writing – review & editing; **Christian J. Merz:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declarations of interest

None.

Data Availiability

The data that were used in this study are openly available in the homepage of the Open Science Framework (OSF) and can be accessed via the following link: https://osf.io/fwbh3/?view_only=9c10023d2c2943da8f047e080889d5f6.

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