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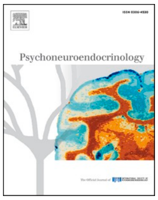

Social high performers under stress behave more prosocially and detect happy emotions better in a male sample

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ABSTRACT

Psychosocial stress is increasing in society, impacting our lives in all social domains. However, the conditions under which stress facilitates (“tend-and-befriend”) or hinders (“fight-or-flight”) social approach remain elusive. We tested whether previous heterogeneous findings might be resolved by accounting for individual differences in social performance under stress. For that purpose, we introduce the novel Trier Social Stress Test (TSST) social performance index that was aggregated across ratings from two independent observers. Moreover, we apply an innovative setup enabling electroencephalographic (EEG) data to be measured inside an electrically-shielded cabin during stress, namely the TSST-EEG. Relying on a sample of 59 healthy male participants, we collected behavioral (i.e., sharing resources with others) and cognitive (i.e., detecting facial emotional expressions) approach patterns while participants experienced either acute psychosocial stress (n = 31) or no stress (control condition; n = 28) and while EEG was being recorded. During stress exposure, high-performing participants behaved more prosocially, and differentiated better between happy and neutral emotions on both behavioral and neurophysiological levels (revealed by intensity differences in a N170-like response). Overall, our findings demonstrate the added value of both the novel TSST social performance index and the novel TSST-EEG setup. By showing that high social performance during the TSST is associated with behavioral, cognitive, and neurophysiological approach patterns, our study offers valuable insights into adaptive or maladaptive psychobiological mechanisms in coping with psychosocial stress. Future stress research should address the role of social performance differences during stress in social interaction to better understand the behavioral consequences of psychosocial stress in humans.

1. Introduction

Psychosocial stress is increasing in society (Salari et al., 2020). However, the effects of stress on our social interactions, which are absolutely essential to our personal health (Holt-Lunstad et al., 2010), remain poorly understood. In this line, even after over a quarter-century of research applying a standardized method to induce psychosocial stress experimentally (i.e., the Trier Social Stress Test, TSST; Kirschbaum et al., 1993), the conditions under which stress facilitates (“tend-and-befriend” hypothesis; Domes and Zimmer, 2019; Margittai et al., 2015; von Dawans et al., 2019, 2012) or hinders (“fight-or-flight” hypothesis; Bendahan et al., 2017; Sollberger et al., 2016; Steinbeis et al., 2015; Vinkers et al., 2013; von Dawans et al., 2018) social approach patterns – or may not even affect them at all (Schweda et al., 2019) - remain elusive. Research has already identified several potential individual and situational variables contributing to heterogeneous findings in the literature (e.g., age and gender, diverging stress induction methods, health-related behaviors, trait characteristics such as social anxiety, timing of the study set-up, variation in the social outcomes studied; von Dawans et al., 2021). However, there is a significant source of

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inter-individual differences which, although obvious, has been largely overlooked so far (Allen et al., 2014): an individual's social performance during the TSST, indexed by approach-oriented nonverbal signaling (e.g., making eye-contact, gesturing frequently, expressing facial emotions) and the quality of one's speech (e.g., modulating one's voice, speaking fluently; Beltzer et al., 2014). By relying on the novel TSST social performance index, in the current study we therefore analyzed whether performance is associated with approach-related patterns under stress across social behavior, social cognition, and underlying neurophysiological activity.

There are three reasons why social performance during the TSST could influence the effects of stress on social approach. *First,* performance is central to the TSST, as participants fear negative evaluation by the panel if they perform poorly (Dickerson and Kemeny, 2004). Correspondingly, qualitative analyses of interviews indicate that the level of experienced stress is highest during a bad performance (Vors et al., 2018). *Second,* expanding upon the appraisal theory of emotions (Lazarus, 1991), the biopsychosocial model of challenge and threat suggests that stress appraisals are crucial in determining responses to stress (Blascovich and Mendes, 2010). Accordingly, if someone perceives that the demands exceed their resources, that triggers threat appraisal; if someone perceives that their resources exceed the demands, that triggers challenge appraisal. This perception is affected by performance during the TSST, because high-performing individuals might find that their resources exceed the demands, while low-performing individuals would find the opposite. Indeed, experimentally inducing challenge appraisals is known to result in more approach-related behavior during stress (Beltzer et al., 2014). *Third,* research has already demonstrated the added value of analyzing social performance during the TSST (Beltzer et al., 2014; Knight and Mehta, 2017). However, their research analyzed performance as a dependent variable, but did not consider its potential role in modulating the effects of stress. Therefore, investigating TSST social performance may yield valuable insight into how stress affects social approach.

Considering the situational moderators of social stress effects, there is another under-researched variable, namely the interaction partner's social group membership. On theoretical grounds, one can argue that "tend-and-befriend" behavior (Taylor, 2006) is more likely when interacting with in-group members, while "fight-or-flight" behavior (Cannon, 1934) is more likely when interacting with out-group members. However, the few studies on this point have yielded inconclusive evidence, and they did not systematically compare approach behavior under stress across positive (i.e., sharing resources with others) and negative outcomes (i.e., taking resources away from others; Schweda et al., 2019; Steinbeis et al., 2015). We therefore investigated whether the behavioral effects of stress are modulated by the interaction partner's social group membership (in-group vs. out-group) as well as outcome valence (positive vs. negative).

In this study, we measured the behavioral (i.e., sharing resources; Schiller et al., 2020) and cognitive (i.e., inferring emotions; von Dawans et al., 2020) approach patterns of 59 healthy male participants while their neurophysiological brain activity was being recorded via electroencephalography (EEG) in a novel TSST-EEG setup. By analyzing the event-related potentials (ERPs) evoked by outcome valuation during the social behavior paradigm and by emotion detection during the social cognition paradigm, we aimed to shed light on the neurophysiological mechanisms underlying the associations between social performance during stress and approach-related behavior and cognition. Half of the participants were subjected to acute psychosocial stress ($n = 31$), the other half to the TSST control condition ($n = 28$). Regarding social behavior, we first checked whether stress effects would differ when analyzing the interaction partner's social group membership and outcome valence. To analyze the stress effects dependent on social performance during the TSST, we created a novel index aggregated across ratings from two independent observers. We assumed that individuals with high social performance would find the TSST to be a more challenging rather than threatening situation (Blascovich and Mendes, 2010) – an appraisal already associated with approach-related emotions and behaviors (Beltzer et al., 2014; Jamieson et al., 2018). We therefore hypothesized that those individuals would tend to reveal behavioral (i.e., more prosocial behavior), cognitive (i.e., better detection of happy emotions) and neurophysiological (i.e., neurophysiological processes associated with more positive evaluations; and better neurophysiological differentiation between happy and neutral emotions) patterns associated with social approach.

2. Methods

2.1. Sample

On the basis of similar research applying standardized stress induction paradigms (von Dawans et al., 2012), we expected a medium effect size of our experimental modulations ($f = 0.25$). 60 participants were needed to detect a significant effect (ANOVA: repeated measures, within-between interaction, G-Power; Faul et al., 2009; F-Tests, ANOVA: Repeated measures, within-between interaction, $f = 0.25$, $\alpha = 0.05$, $\beta = 0.90$, number of groups = 2, number of measurements = 4, correlation among repeated measures = 0, nonsphericity correction = 1). We solicited contact information from students in lecture halls and contacted them by e-mail to inquire about their personal interests in several domains (e.g., arts, politics, soccer). We then recruited participants who were fans of rival soccer clubs or supporters of opposing political parties as indicated by at least medium (= 3) self-reported interest in soccer or politics, on a scale from 1 (very weak) to 5 (very strong; Schiller et al., 2020). Note that allocating rival out-groups was done individually. As there is evidence that intergroup bias is stronger in males (Smith et al., 2022), we focused on a male sample in this study. To account for potential drop-outs, we recruited 64 right-handed participants free of neurological or psychiatric disorders and alcohol, nicotine or drug abuse (Schiller et al., 2022) who had no experience performing the TSST, did not work in shifts, take medication, and who had BMI values under 30. We had to exclude two participants because of corrupted EEG signals (<50% of data were available after artifact correction), two participants due to technical problems during the experiment, and one participant who pressed the button randomly during the social cognition paradigm. Our final analysis sample consisted of 59 participants (stress treatment: $n = 28$; control treatment: $n = 31$; age: $M = 22.25$ y, $SD = 3.05$ y, range: 18–29 y; stress: $M = 21.89$, $SD = 2.73$; control: $M = 22.58$, $SD = 3.32$; $F(1,57)= 0.75$, $p = .392$, $\eta^2 = 0.01$). These participants also demonstrated a strong identification with their favorite social group, as assessed by a modified version of the Sport Spectator Identification Scale (5-point Likert scale; (Wann and Branscombe, 1993); total sample: $M = 3.15$, $SD = 0.56$; stress condition: $M = 3.10$, $SD = 0.49$; control condition; $M = 3.19$, $SD = 0.62$; $F(1,57) = 0.34$, $p = .561$, $\eta^2 = 0.01$). Participants received a show-up fee of 40€ plus additional money earned in the decision-making paradigm ($M = 34.05$, $SD = 4.33$, range: 22.60–41.30). This study was conducted according to the principles expressed in the Declaration of Helsinki and was approved by the Ethics Committee of the University of Freiburg. We carried out all procedures with the adequate understanding and informed consent of all participants.

2.2. Procedure

This experiment involved two appointments. During the *first appointment* in our group laboratory (equipped with 16 PCs), participants played a game-of-chance involving real monetary consequences (Schiller et al., 2020). The group laboratory allows simultaneous data collection from 16 participants and guarantees real interaction with other participants in a social setting before the second appointment in the EEG laboratory, ensuring the credibility of the social decision-making paradigm. We also collected information on trait variables relevant to the stress effects on social interactions in order to control for potential random differences between treatment groups (for details, see Supplementary Table1). The first appointment lasted 1.5 h.

For the *second appointment*, which took place 4–6 weeks after the first one, participants came to our EEG laboratory in individual sessions with the start time varying between 2:00 and 4:00 pm in order to control for diurnal variations in cortisol secretion (Labuschagne et al., 2019). Salivary samples were obtained at several time points during the experiment to analyze endocrinological stress responses, while EEG and ECG were continuously recorded (for details, see Fig. 1). Participants read the instructions and answered control questions on the third-party decision-making paradigm while being prepared for the 128-channel EEG and the ECG measurement in an electrically shielded cabin. The experimenters were blind to the treatment allocation. After the EEG preparation, each participant`s brain activity at rest was recorded for 5 min. Then, participants performed a modified version of the TSST (von Dawans et al., 2019, 2012). After reading the instructions (5 min), participants in the stress treatment prepared for the free speech part of the TSST (5 min). They then performed the free speech (5 min) sitting in the EEG cabin with their head positioned on a headrest (to minimize muscle artifacts) in front of the jury sitting behind an open-able window outside the cabin (see Fig. 2). The TSST jury members who had undergone special training to perform the TSST in the same standard manner could communicate with the participant via microphone while the participant was being recorded by a video camera (those videos were later used for performance ratings). To control for potentially confounding effects of mixing the judges' gender (e.g., Duchesne et al., 2012), we kept them constant, with the active judge always being male and the passive judge always being female. The jury members wore white coats in the stress treatment, while they wore casual clothing in the control treatment and avoided looking at the participants who read an article aloud and performed simple arithmetic (Het et al., 2009). Immediately after the free speech part, the cabin window was closed and participants performed the decision-making paradigm in which they could sacrifice their resources to modulate the game-of-chance outcomes of other in- and outgroup members (ca. 15 min). Participants were aware that the other in- and out-group members had played the game-of-chance knowing that their outcomes would later be modulated by other participants. After the decision-making paradigm, participants performed the mental arithmetic part of the TSST (5 min), and then the social cognition paradigm (15 min; see 2.4). Finally, there was another resting EEG recording period (5 min), before participants completed several subjective ratings (pre/post mood ratings, quality of interaction, current financial situation, socio-economic status, and experience of substance effects), were debriefed about the TSST procedure, and were paid. Applying the Presentation 19.1 (Neurobehavioral Systems, Albany, CA, USA) program, stimuli were presented via projector (placed outside the EEG cabin) on a transparent canvas. The second appointment lasted a total of 2 h, resulting in the entire experiment lasting a total of 3.5 h.

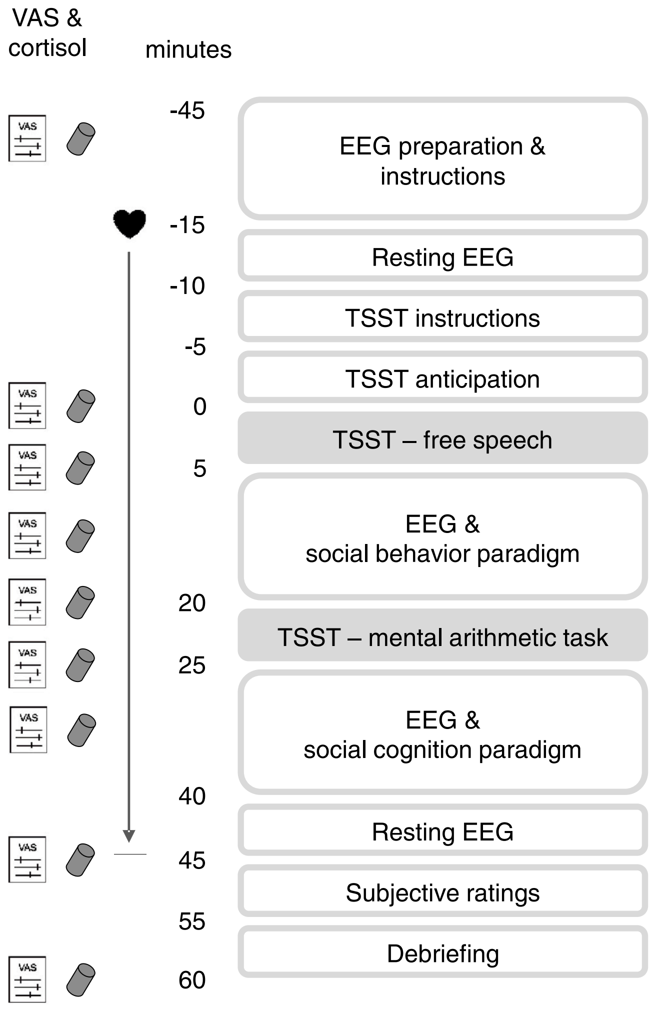


Fig. 1. Timeline and experimental procedure of the main experimental session (second appointment). VAS = visual analogue scale. Minutes are given relative to the start of the TSST free speech part. The heart symbol indicates the time period during which we measured electrocardiological activity. Time points of VAS and cortisol sampling are shown by the respective symbols on the left.

2.3. *Measurement of social behavior*

In the decision-making paradigm, participants could invest their own resources to modulate other players' outcomes, who were either in-group or out-group members. In total, participants took decisions on 84 outcomes (42 for each social group) entailing either gains (+30, +20, +10) or losses (−30,−20,−10; Schiller et al., 2020). Specifically, participants received ten points per trial, each of which they could keep or use to increase or decrease the other person's outcome by three points (exchange rate: 100 points = 1€). All the points they had not used to modulate outcomes were added to their own income. Participants were informed that all decisions would remain anonymous and that persons whose outcome they could modulate could not reciprocate behavior. Therefore, the participants' income depended solely on their own and not the other persons' behavior, making all decisions in which they sacrificed their own resources to modulate other persons' outcomes self-interest free behavior (comparable to studies on third-party behavior, see, e.g. (Baumgartner et al., 2014, 2013; Schiller et al., 2014).

Regarding the procedural details of the decision-making paradigm, participants first saw a fixation cross, followed by the information indicating whether they could modulate the outcomes of an in-group or out-group member. A group symbol displayed the emblem of the other participant's favorite soccer club or political party. Participants saw seven outcomes in a row concerning the same participant from a specific social group. After the group symbol, the outcome was visible. Participants had to make their decision within ten seconds, otherwise they would lose their points in that trial. Via button press, participants had to select one of seven decision options (outcome modulation: +30, +20, +10, 0, −10, −20, −30). Participants took 10–15 min to complete this paradigm on average.

Note that the outcomes affecting in- and out-group members were taken from a game of chance paradigm that all participants had performed, as had additional persons (who only completed the first appointment) and which had been framed within an inter-group context during the first appointment. All participants played the game of chance to raise the credibility of the third-party decision-making paradigm and deepen the emotional involvement of participants. During this game of chance, one had to draw cards (90 trials) from piles on a PC screen triggering randomly distributed gains (+30, +20, +10) and losses (−30,

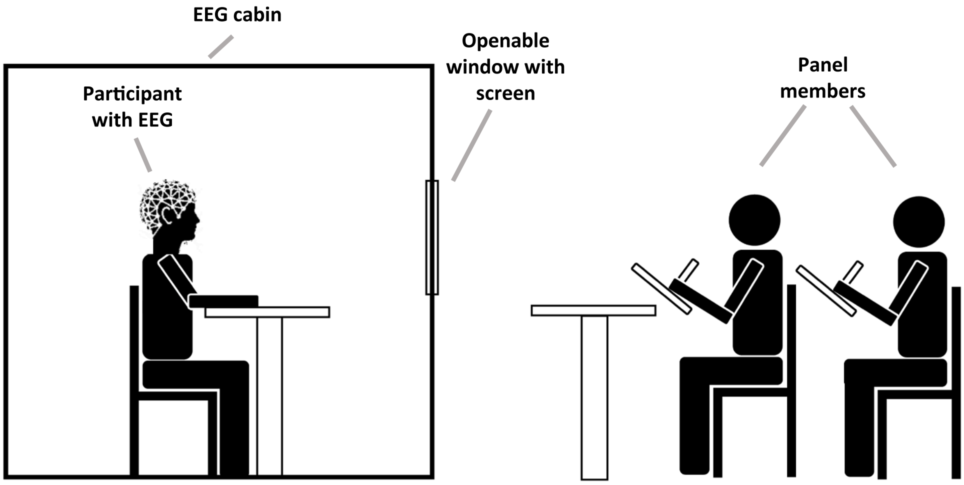


Fig. 2. Experimental set-up of the TSST-EEG. The participant (on the left) sat inside the electrically shielded EEG cabin looking towards the openable window, which also contained the screen where the experimental paradigms were presented. During the TSST, this window was opened and the participant faced the jury consisting of two panel members who sat next to each other behind a table in front of the EEG cabin.

−20, −10). Starting with 1000 points, each outcome had been added to or subtracted from the personal income (exchange rate: 100 points = 1€). The majority of outcomes (84 out of 90 trials) had been predetermined to keep distinct experiences during the lottery from affecting participants' behavior in the third-party decision-making paradigm (a low number of random trials had been added to avoid identical incomes for all participants).

2.4. *Measurement of social cognition*

Participants performed a modulated version of a facial emotion detection task (von Dawans et al., 2020). This task involved detecting emotions (angry and happy) with varying intensity (low and high) from facial stimuli taken from the NIMStim face database (Tottenham et al., 2009). Per block, participants had to decide spontaneously whether a specific emotion was present or not by pressing one of two buttons. Each block comprised 12 stimuli, 6 with specific emotions and 6 neutral, presented in a random order. Each condition was repeated 5 times and presented in a random order, yielding a total of 240 trials. The task lasted 10–15 min.

2.5. *Measurement of TSST performance*

Two individuals with expertise in conducting research in experimental psychology and applying the TSST rated a participant's performance regarding 12 items (six per TSST part) on a scale from 0 (worst performance) to 100 (perfect performance; see Table 1; as there was no performance to be evaluated during the control treatment, this index was only calculated for the stress treatment). In addition, the participant himself rated his general performance on a scale from 0 to 100. To optimize both the reliability and validity of performance ratings, both raters underwent training via video examples of low (e.g., avoiding eye-contact and gestures, and not expressing facial emotions) and high performance (e.g. making eye-contact, gestures, and expressing facial emotions; see also Beltzer et al., 2014) for the respective dimensions, as agreed upon by this paper's authors.

Table 1
TSST Social Performance Score Sheet. Raters should evaluate a participant's performance regarding each item on a scale ranging from 0 (worst performance) to 100 (perfect performance). This rating was done right after the end of each TSST part.

I. Free Speech	II. Mental Arithmetic
Eye-contact	Eye-contact
Gestures	Gestures
Facial expressions	Facial expressions
Intonation	Intonation
Flow of speech	Flow of speech
General impression	General impression

2.6. *EEG analysis*

2.6.1. *EEG recording*

EEGs were recorded using a 64-channel recording system (Brainamp with actiCAP, Brain Products Gmbh, Munich). Scalp impedance was kept below 10 kΩ. FCz served as the reference electrode, AFz as the ground electrode. Horizontal and vertical electrooculographic signals were recorded with two additional electrodes at the left and right outer canthi and one electrode at the left infraorbital. The EEG was online band-pass filtered between 0.1 and 100 Hz, and the data digitized with a sampling rate of 500 Hz.

2.6.2. *EEG preprocessing*

EEG data were preprocessed by using Brain Vision Analyzer (Version 2.0.1.327; Brain Products Gmbh, Munich). Ocular correction was conducted via a semi-automatic Independent Component Analysis (ICA)-based correction process. EEG signals with excessive noise were replaced via a linear interpolation of adjacent electrodes. After an automatic artifact rejection (maximum voltage step: 50 μV; maximum amplitude: ± 100 μV), data were visually examined by two independent raters to eliminate residual artifacts. Data were then band-pass filtered (no additional high-pass, low-pass 30 Hz; Notch filter 50 Hz) and re-derived to average reference.

2.6.3. *EEG second-level analysis*

2.6.3.1. Neurophysiological processes during outcome evaluation (social behavior). We analyzed electrophysiological activity elicited by outcome valuation during a time window from outcome presentation to 500 ms thereafter (Schiller et al., 2020). We averaged artefact-free trials to calculate individual ERPs for each of the four outcome conditions. There was an average 19.94 trials available for averaging (minimum: 12 trials). We then averaged the individual ERPs to calculate the grand-mean ERPs. The individual ERPs were then fed to the RAGU software (version 2020–11–24; Koenig et al., 2011) for an ERP microstates analysis using spatial K-means clustering (Schiller et al., 2023, 2016; Lehmann and Skrandies, 1980) to reveal dominant topographies and a topographic fitting procedure (Michel et al., 1999) to identify the temporal occurrences of each microstate in milliseconds. In line with Schiller et al. (2020), we selected the four cluster solution based on silhouette plot analysis (Rousseeuw, 1987).

2.6.3.2. Neurophysiological processes during emotion detection (social cognition). We analyzed electrophysiological activity elicited by emotion detection during a time window from stimulus presentation to 1000 ms thereafter (reaching well beyond the average response times during the task, $M = 826.52$ ms, $SD = 121.75$ ms). Individual ERPs were averaged into grand means for six conditions ("emotion": angry vs. happy; "intensity": neutral vs. low intensity vs. high intensity). On average, there were 37.37 trials available for averaging (minimum: 17 trials). We again performed microstate analysis on the ERP data using K-Means clustering and then identified the temporal occurrences (in milliseconds) and mean intensities of the resulting functional microstates during emotion detection using topographic fitting. Following the steps described by Habermann et al. (Habermann et al., 2018), we identified the seven cluster solution as the best fitting one.

2.7. Autonomic, endocrine, and subjective stress responses

Cortisol levels were measured by collecting saliva samples via Sali-Caps (IBL, Hamburg, Germany) at various times during the experiment (45 min before the start of the TSST [−45 min], immediately before the TSST [0 min], after the speaking task [+5 min], in the middle of the social behavior measurement [+12 min], after the social behavior measurement/before the arithmetic task [+20 min], after the arithmetic task [+25 min], in the middle of the social cognition measurement [+30 min], 45 min after the TSST [+45 min], 60 min after the TSST [+60 min]). At the same time points, we also measured subjectively perceived stress levels (0–100%). The heart rate was recorded continuously starting five minutes before the TSST and lasting until 45 min after the TSST using three electrodes placed at the outer ends of the left and right shoulder, and at the outer end of the right hip. We preprocessed this heart-rate data via the Brain Vision Analyzer 2 (Version 2.0.1.327; Brain Products, Munich), applying a band-pass filter (high-pass 0.5 Hz, low-pass 30 Hz, Notch filter 50 Hz). R-spikes were detected automatically using the ECG Markers Solution in Brain Vision Analyzer 2 (see above) and then manually corrected in case of artifacts. In the final step and using in-house MATLAB scripts (Matlab 9.12.0, MathWorks, Natick, MA/USA), we applied the time points of R-spikes to calculate inter-beat intervals and mean heart-rate levels per experimental subpart (five minutes of pre-experimental baseline, five minutes of TSST anticipation, five minutes of TSST speaking task, 12 min of social behavior measurement, five minutes of TSST arithmetic task, 12 min of social cognition measurement, five minutes of post-experimental baseline; owing to a temporary breakdown, data from one participant was unavailable during the TSST anticipation and speaking tasks, so that we replaced those values by mean values of participants in the TSST treatment).

2.8. Statistical analyses

2.8.1. Autonomic, endocrine, and subjective stress responses

To run a manipulation check of the novel TSST-EEG setup on the dependent variables cortisol, heart rate, and subjective stress levels, we conducted separate mixed ANOVAs with the within-subjects factor "time" (9 time points for cortisol and subjective stress; 7 time points for heart-rate responses) and the between-subjects factor "treatment" (stress versus control). Significant interaction effects were followed up by ANOVAs with the between-subjects factor "treatment", separately for each time point. For all correlations involving stress responses, we accounted for individual baseline differences by applying difference scores (subtracting the baseline value from the period of interest).

2.8.2. TSST performance

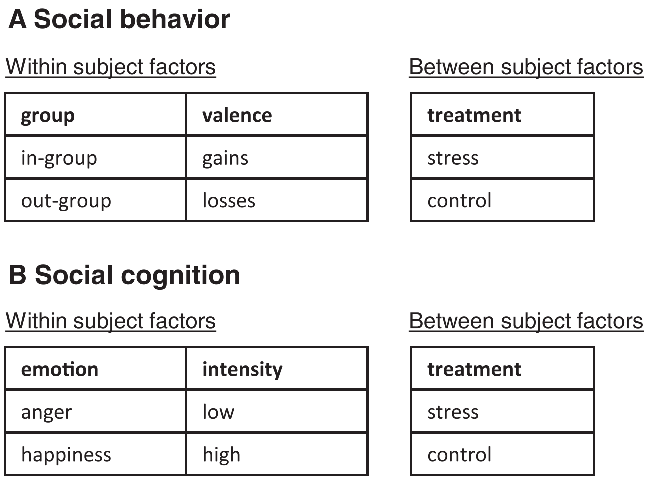
In the first step, we evaluated each judge's intra-rater reliability regarding the values on the 12 items on a participant's performance in the TSST-EEG. For that purpose, we calculated the ICCs (Fisher, 1992; Koo and Li, 2016; two-way mixed effects, absolute agreement). We then averaged values of these items to obtain one z-standardized performance score per rater. In the second step, we evaluated inter-rater reliability across the performance scores of the two raters, calculating ICCs (one-way random effects, absolute agreement). Finally, we averaged both observers' performance scores to obtain the overall performance index that was then used to analyze associations between the TSST performance and other outcome variables (Pearson-coefficients were calculated for normally distributed variables, and Spearman-coefficients otherwise; 2-sided tests, alpha level = 0.05).

2.8.3. Social behavior

For the behavioral analysis, we calculated the effect of a participant's decisions on others' outcomes (before decision-making) for each of the four outcome conditions (net out-group gains, net in-group gains, net out-group losses, net in-group losses). We then conducted an overall ANOVA on the dependent variable "social behavior" (i.e. average points transferred to or subtracted from the other participant) and with the within-subjects factors "social group" (in-group versus out-group) and "valence" (gains versus losses) and the between-subjects factors "treatment" (stress versus control), and "group type" (soccer versus politics; for an overview of the experimental design, see Fig. 3A). To test whether "TSST performance" would modulate stress effects, we added this variable as covariate to the ANOVA and analyzed associations between the TSST performance and behavior (Pearson-coefficients were calculated for normally distributed variables, and Spearman-coefficients otherwise; 2-sided tests, alpha level = 0.05). To control for general associations between an individual's appearance and self-confidence with behavior, we also statistically compared correlations between self-rated performance and behavior between the control and stress treatments (Eid et al., 2013).

2.8.4. Social cognition

Response data was analyzed by applying the signal detection theory (SDT) to measure emotion recognition and response bias (Pessoa et al., 2005; Stanislaw and Todorov, 1999). Emotional face identifications were coded as hits, and misidentifications of neutral faces as emotional



A Social behavior

Within subject factors

group	valence
in-group	gains
out-group	losses

Between subject factors

treatment
stress
control

B Social cognition

Within subject factors

emotion	intensity
anger	low
happiness	high

Between subject factors

treatment
stress
control

Fig. 3. Experimental design for the social behavior task (A) and social cognition task (B), showing within and between subject factors and their levels. Note that while emotion detection sensitivity is calculated within low and high intensity blocks to analyze response behavior in the social cognition task, ERPs are compared across neutral and emotional faces for low intensity blocks to analyze neurophysiological activity (see Fig. 6).

ones were coded as false alarms. Sensitivity index d′, a measure of signal detection performance, was calculated by subtracting the z-transformed average false alarms rate from the z-transformed average hit rate.

Using a mixed measures ANOVA, we analyzed whether there was any treatment (stress vs. control) effect on emotion detection (d′; dependent variable) dependent on the emotion (anger vs. happiness) or its intensity (low vs. high; for an overview of the experimental design, see Fig. 3B). We also performed univariate ANOVAs for each experimental condition. In addition, we added "TSST performance" as covariate to the above-mentioned ANOVA and analyzed associations between performance and emotion detection (Pearson-coefficients were calculated for normally distributed variables, and Spearman-coefficients otherwise; 2-sided tests, alpha level = 0.05). We also compared correlations between self-rated performance and emotion detection between the control and stress treatments.

2.8.5. Neurophysiological activity & social behavior

In the first step, we analyzed the effects of "valence" and "treatment" on the dependent variables temporal occurrences of a microstate associated with positive valuations (red in Fig. 5) and another microstate associated with negative valuations (green in Fig. 5; for details revealing stronger activation in negative valuations-related areas [e.g., insula] during the red microstate as well as stronger activation in positive valuations-related areas [e.g., orbitofrontal cortex] during the green microstate, see Schiller et al., 2020) using randomization statistics (Koenig and Melie-García, 2010). In the next step, we analyzed associations between performance and the relative temporal occurrences of these microstates (Pearson-coefficients were calculated for normally distributed variables, and Spearman-coefficients otherwise; 2-sided tests, alpha level = 0.05) and calculated a mediation analysis (IV: "treatment"; mediator: relative temporal occurrence of microstates; DV: "social behavior"; Hayes, 2013).

2.8.6. Neurophysiological activity & social cognition

To follow up on any behavioral effect of stress on detecting happy emotions of low intensity, we analyzed the effects of "treatment" (stress vs. control) and "intensity" (neutral vs. low) on microstate parameters using randomization statistics. In the next step, we calculated correlation coefficients of performance and those microstate parameters that were modulated by treatment (using difference values of happy faces compared to neutral faces; Pearson-coefficients were calculated for normally distributed variables, and Spearman-coefficients otherwise; 2-sided tests, alpha level = 0.05) and calculated a mediation analysis (IV: "treatment"; mediator: microstate 3′s intensity happy vs. neutral; DV: "emotion detection).

3. Results

3.1. Autonomic, endocrine, and subjective stress responses

To test whether the novel TSST-EEG setup induced robust stress responses over time, we conducted two-way ANOVAs with repeated measures, separately for the dependent variables cortisol, heart rate, and subjective ratings of stress. Regarding cortisol, we observed significant effects of "time" ($F(3.61, 205.89) = 14.07$, $p < .001$, $\eta^2 = 0.20$), "treatment" ($F(1, 57) = 10.63$, $p = .002$, $\eta^2 = 0.16$), and "time x treatment" ($F(3.61, 205.89) = 10.13$, $p < .001$, $\eta^2 = 0.15$). Cortisol levels were higher in the stress than the control condition starting from 10 min after the TSST-EEG (all $p < .032$; see Fig. 4). Regarding subjective stress, we noted significant effects of "time" ($F(4.62, 263.40) = 16.62$, $p < .001$, $\eta^2 = 0.23$), and "time x treatment" ($F(4.62, 263.40) = 12.37$, $p < .001$, $\eta^2 = 0.18$), the effect of "treatment" was not significant ($F(1, 57) = 0.95$, $p = .335$, $\eta^2 = 0.02$). Participants in the stress treatment experienced more stress before ($F(1,57) = 15.53$, $p < .001$, $\eta^2 = 0.21$) and after the speaking task of the TSST-EEG ($F(1,57) = 11.08$, $p = .002$, $\eta^2 = 0.16$) compared to participants in the control treatment; the difference during the arithmetic task was only marginally significant ($F(1,57) = 3.64$, $p = .061$, $\eta^2 = 0.06$; all other $ps >= 0.309$; see Fig. 4). Regarding heart rate, we observed significant effects of "time" ($F(3.10, 176.79) = 135.11$, $p < .001$, $\eta^2 = 0.70$), and "time x treatment" ($F(3.10, 176.79) = 6.11$, $p < .001$, $\eta^2 = 0.10$); the effect of "treatment" was not significant ($F(1, 57) = 0.69$, $p = .409$, $\eta^2 = 0.01$). Descriptively, the mean heart rate was higher under stress throughout the experiment; yet those differences were not (all $ps > 0.121$), or only marginally significant (TSST speaking task: stress: $F(1, 57) = 3.32$, $p = .074$, $\eta^2 = 0.06$; for associations between stress responses and performance, see Supplementary Results). In sum, the TSST-EEG induced robust endocrine and subjective stress responses, while its effects on autonomic responses were modest.

3.2. TSST social performance index: reliability analysis

Intra-rater reliability analyzes yielded ICC values of 0.94 and 0.93, respectively, for each of the two raters. Inter-rater reliability analyzes of the performance indices of both raters (z-standardized and averaged across the distinct items) revealed an ICC value of 0.80. These analyses demonstrate the performance index's good reliability.

3.3. Effects of stress on social behavior

3.3.1. Modulation by situational variables: behavior

Using repeated measures ANOVA, we first analyzed whether stress ("treatment": stress vs. control) modulates social behavior (i.e., average points transferred to or deducted from the other participant; dependent variable) dependent on situational variables such as an outcome's valence (gains vs. losses) or someone's social group membership (in-group vs. out-group). We found no evidence that stress would modulate self-interest free, social behavior in inter-group interactions (all effects including "treatment": $p > .20$; for detailed ANOVA results including all variables and descriptive statistics, see Tables S2 and S3).

3.3.1.1. Modulation by situational variables: neurophysiology. We analyzed neurophysiological brain activity under psychosocial stress elicited by outcome valuation during a time window from outcome presentation to 500 ms thereafter (Schiller et al., 2020). The four cluster maps strongly resembled those detected by Schiller et al., 2020 and explained 92.35% of the variance in our EEG data (compared to 91% in the original study; see Fig. 5). Analyzing valuation-related neurophysiological processing, we first checked whether we could replicate associations between the red microstate with positive valuations and of the green microstate with negative valuations (Schiller et al., 2020). For that purpose, we checked the effect of "valence" on the temporal occurrences of these microstates (dependent variable). As expected, the red microstate occurred when participants were confronted with losses (gains: 0 ms, losses: 352 ms, $p < .001$), while the green microstate occurred when participants were confronted with gains (gains: 322 ms, losses: 0 ms, $p = .019$). No other microstate's temporal occurrence was significantly associated with gain or loss processing (all $ps >= .163$). As in our behavioral findings, we detected no treatment effects (all $ps >= .20$; for detailed results, see Table S4).

3.3.2. Modulation by individual variables: behavior

We next investigated whether stress affects behavior dependent on performance. For that purpose, we added "TSST performance" as covariate to the model above, analyzing participants under stress only (excluding the factor "treatment"). Indeed, there was a significant effect of "TSST performance" on behavior ($F(1,26) = 6.69$, $p = .016$, $\eta^2 = 0.21$), which was not further modulated by "group", "valence", or "group X valence" (all $ps > 0.20$). Correlation analyses confirmed that high-performing individuals behaved more prosocially ($r(26) = 0.420$, $p = .026$; see Fig. 7).

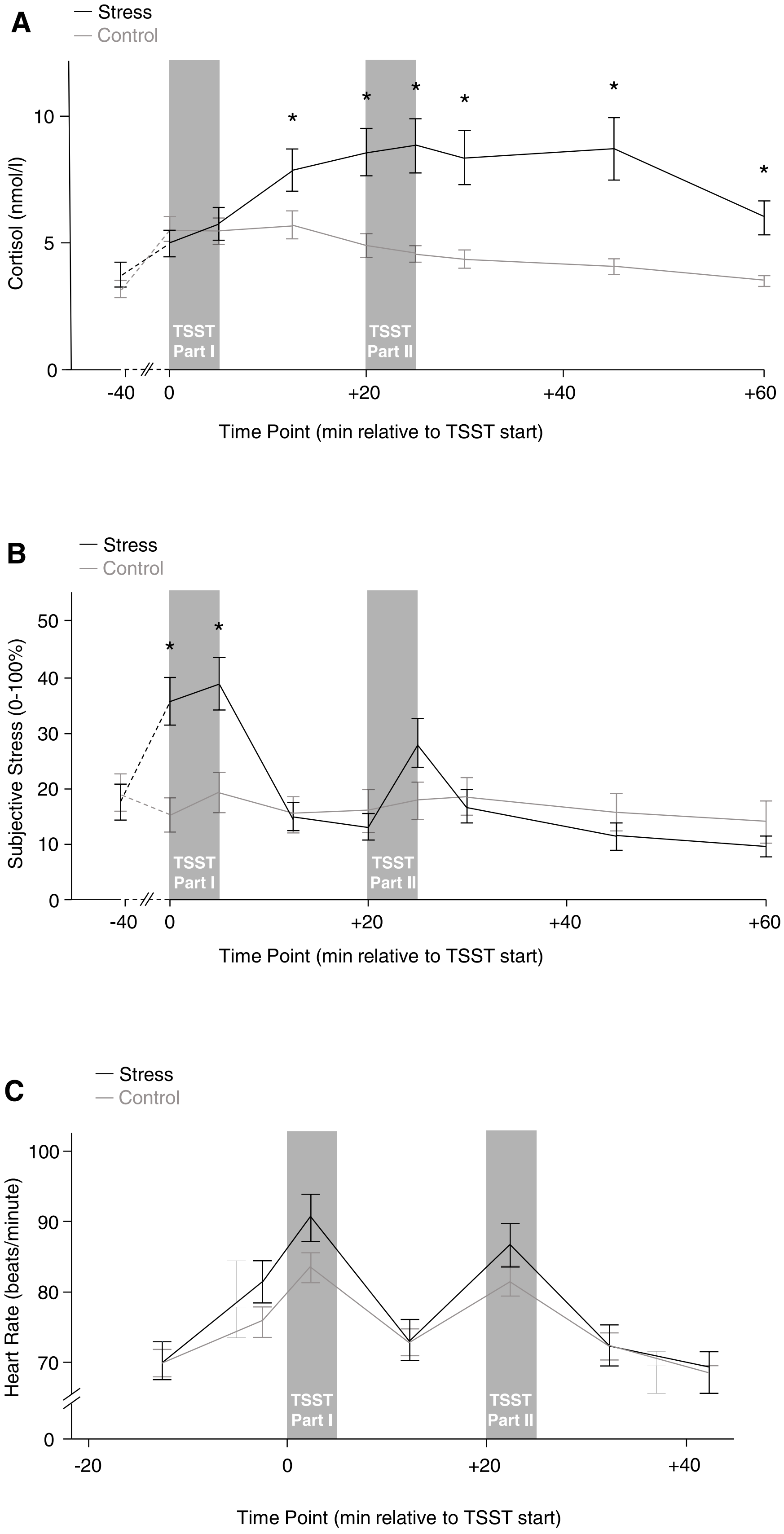


Fig. 4. TSST-EEG effects regarding (A) mean level of free salivary cortisol, (B) mean level of subjective stress, and (C) mean heart rate. Results are shown separately for the stress (in gray) and control (in black) conditions). Time points on the y-axes of (A) and (B) are given relative to the start of the TSST-EEG at time 0. Heart rate levels were averaged across the following time periods: Baseline Pre (−15 to −10 min), TSST anticipation (−5 to 0 min), TSST Part I (0–5 min), Social Behavior (5–20 min), TSST Part II (20–25 min), Social Cognition (25–40 min), Baseline Post (40–45 min). Error bars indicate + /- one standard error of the mean. Asterisks indicate differences between treatment groups significant at $p < .05$.

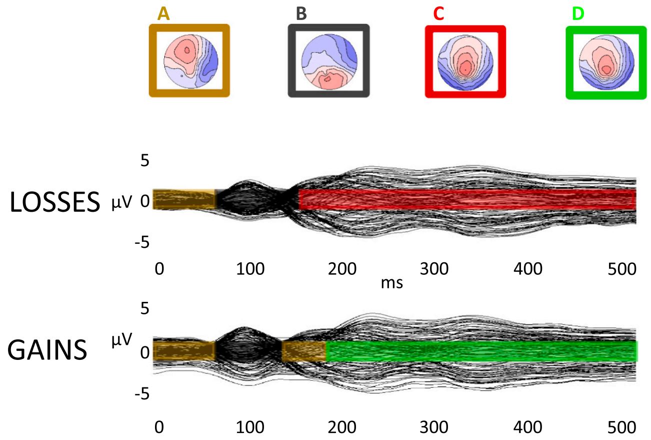


Fig. 5. Neurophysiological processes associated with valuation-related processing revealed from a spatio-temporal ERP microstates analysis (Michel et al., 2009; Schiller et al., 2020; for a review, see (Schiller et al., in press). Briefly, by segmenting electrical activity recorded during outcome valuation into time periods of stable neural network configurations (= stable EEG scalp map topographies) via a clustering approach (Lehmann and Skrandies, 1980) we can identify functional microstates in the brain that represent specific, valuation-related processes. Here, we investigated whether performance would modulate valuations-related processing. Shown is the cluster solution with four distinct maps shown on the top. Head seen from above. Red indicates positive values, blue negative values, referred to average reference. The colored background corresponds to the assignment shown below. These maps are then fitted to the ERPs, resulting in microstates across time (ms) in response to losses (middle) or gains (bottom). The y-axis represents the global field power curve.

Finally, we aimed to control for general associations between an individual's appearance and self-confidence with behavior. Comparing correlations between self-rated social appearance during the TSST and behavior between the control and stress treatments revealed a significant difference ($z = -1.93$, $p = .027$), with a non-significant correlation between performance and behavior in the control treatment ($r_s(29) = -0.132$, $p > .20$), and a significant and positive correlation between appearance and behavior in the stress treatment ($r(26) = 0.379$, $p = .047$). In sum, the association we observed between self-appearance and behavior was specific for the stress condition.

3.3.2.1. Modulation by individual variables: neurophysiology. We next investigated whether performance modulates valuation-related processing. Specifically, we tested whether high-performing participants who behaved more prosocially would display a relatively higher temporal occurrence of the green, positive valuations-related microstate compared to the red, negative valuations-related microstate. However, we found that this association was not significant and only showed a statistical trend ($r(26) = 0.344$, $p = .073$, see Fig. 7; performance X negative valuations-related microstate: $r(26) = -0.315$, $p = .103$; performance X positive valuations-related microstate: $r(26) = 0.291$, $p = .133$).

3.4. Effects of stress on social cognition

3.4.1. Modulation by situational variables: behavior

Using a mixed measures ANOVA, we first analyzed effects of "treatment" (stress vs. control). "emotion" (anger vs. happiness), and "intensity" (low vs. high) on emotion recognition (sensitivity index; dependent variable). None of the effects involving "treatment" were significant (all $ps < .066$; for detailed results and descriptive statistics see Tables S5 and S6). Yet, to inform additional analyses on potential modulatory effects of social performance on emotion recognition, we also conducted explorative post-hoc tests comparing treatment groups separately between distinct conditions (uncorrected for multiple comparisons). These exploratory analyses revealed that stress worsened participants' emotion detection performance towards happy faces of low intensity (stress: d′ happy low = 0.66, $SD = 0.49$; control: d′ happy low = 0.93, $SD = 0.52$; $F(1,57) = 4.00$, $p = .050$, $\eta^2 = .066$; all other $ps > 0.20$).

3.4.2. Modulation by situational variables: neurophysiology

To follow up on this behavioral stress effect as our exploratory analyses had revealed, we analyzed the neurophysiological responses to neutral faces vs. happy faces of low emotional intensity across treatment groups. We identified seven clusters which explained 80.59% of the total variance in our EEG data (see Fig. 6). Fitting these clusters to the ERPs and applying bootstrapping statistics revealed a significant interaction effect of "treatment x emotion" ($p = .016$) regarding the intensity (i.e., mean global field power) of microstate 3 (dependent variable; all other ps involving the factor "treatment" >= .080). While N170-like microstate 3′s intensity was significantly higher in the happy condition compared to the neutral condition in the control condition (Mcontrol/neutral = 1.26 µV, Mcontrol/happy = 1.49 µV, $p < .001$; see Fig. 6), there was no such difference in the stress condition (Mstress/neutral=1.17 µV, Mstress/happy=1.12 µV, $p > .20$). Thus, unlike the participants in the control condition, those in the stress condition revealing impaired detection of low-intensity happy faces failed to differentiate between happy and neutral faces in their N170 response (we observed similar effects conducting single electrode analysis of the amplitude recorded at the P7 electrode, which is commonly analyzed for the N170, Hinojosa et al., 2015; see Supplementary Results and Fig. S1 for details).

3.4.3. Modulation by individual variables: behavior

We next investigated associations between performance and these effects. For that purpose, we added "performance" as covariate to the above model, analyzing participants under stress only (excluding the factor "treatment"). We found significant interaction effects of "performance X emotion" ($F(1,26) = 5.81$, $p = .023$, $\eta^2 = 0.18$) and "performance X emotion X intensity" ($F(1,26) = 8.68$, $p = .007$, $\eta^2 = 0.25$; all other effects involving "performance" showed $ps >= .360$). High-performing individuals proved able to detect happy faces better ($r(26) = .379$, $p = .047$; see Fig. 7), but not angry ones ($r(26) = -.142$, $p > .20$). Following up on the significant three-way interaction, we found that the association between performance and emotion detection was significant only for happy faces of high intensity ($r(26) = 0.434$, $p = .021$; happy low intensity: $r(26) = 0.229$, $p > .20$; angry low intensity: $r(26) = 0.049$, $p > .20$; angry high intensity: $r(26) = -0.216$, $p > .20$).

In line with our behavioral analysis, we finally compared correlations between self-rated social appearance and emotion detection of happy faces between the control and stress treatments. This comparison revealed no significant difference ($z = -0.35$, $p = .362$ with non-significant correlations between self-appearance and cognition in the control condition ($r_s(29) = .056$, $p > .20$), and the stress condition ($r(26) = 0.151$, $p > .20$).

3.4.4. Modulation by individual variables: neurophysiology

We next tested whether the TSST performance would modulate these effects further. Indeed, high-performing individuals showed a stronger differential response to both happy faces in general (i.e., happy vs. neutral; $r(26) = 0.405$, $p = .033$; see Fig. 7), as well as to low-intensity faces specifically (i.e., happy & low intensity vs. neutral; $r(26) = 0.398$, $p = .036$; the association with high-intensity faces was not significant, revealing only a statistical trend: $r(26) = 0.360$, $p = .060$). Further analyses revealed that this positive association between performance and emotion detection was mediated significantly by stronger N170 differentiation between happy and neutral faces ($p < 0.05$, bootstrapping 95% confidence interval of the indirect effect excluded zero: [.01,.19]; direct effect: $t = 1.22$, $p > .20$, indicating full mediation; total effect [direct + indirect]: $F = 4.28$, $p = .025$, for further results, see

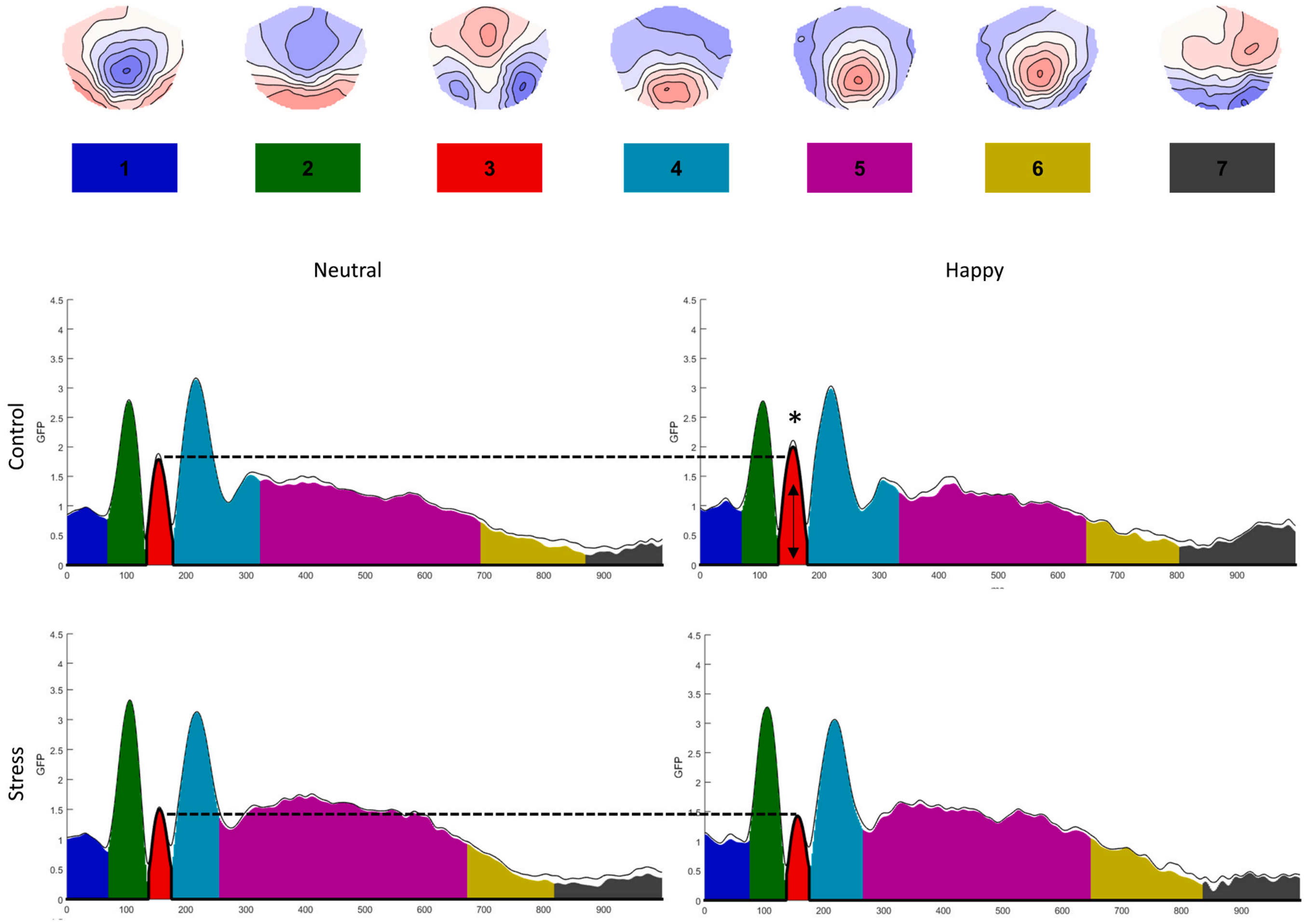


Fig. 6. Neurophysiological processes associated with emotion detection revealed from a spatio-temporal ERP microstates analysis. Top: Solution with seven distinct clusters. Head seen from above. Red indicates positive values, blue negative values, referred to average reference. The colored background corresponds to the assignment shown below. Middle and bottom: These maps are then fitted to the ERPs, resulting in microstates across time (ms) in response to neutral (left) and happy faces (right), separately shown for the control condition (middle) and the stress condition (bottom). The y-axis represents the global field power curve. The dashed line and the asterisk highlight the significant interaction effect of "treatment X emotion" ($p = .016$) regarding N170-like microstate 3′s intensity, driven by a significantly more intense microstate 3 towards happy compared to neutral faces in the control ($p < .001$), but not in the stress condition ($p > .05$).

Supplementary Results).

4. Discussion

By introducing the novel TSST social performance index and the novel TSST-EEG setup, we demonstrate high-performing individuals behaved more prosocially and were more sensitive to happy emotions in both their behavioral and neurophysiological responses. In line with recent review and meta-analytic evidence (Nitschke et al., 2022; von Dawans et al., 2021), our study reveals no consistent general effects of stress on social approach. We also did not find that the interaction partner's group membership or outcome valence modulate the effects of stress on social behavior. However, our study highlights social performance during stress as a significant, but previously overlooked source of individual differences in stress effects, as, across distinct levels of analyses, high-performing individuals demonstrated behavioral, cognitive and neurophysiological responses associated with social approach.

Our findings concur with research evidence on stress appraisals affecting people's responses to stress. According to the biopsychosocial model of challenge and threat (Blascovich and Mendes, 2010), individuals who perceive that their resources exceed the demands they are facing are thought to experience that situation as a challenge and reveal biological responses (e.g., dilatation of the peripheral vasculature) enabling them to mobilize energy and approach others. In contrast, people experience threat when they perceive their resources to be lower than the demands, an appraisal form resulting in biological responses (e.g., constriction of the peripheral vasculature) accompanied by poorer energy mobilization and social avoidance. Empirically, having or inducing a higher level of challenge compared to threat appraisals has been associated with prioritizing the processing of positive stimuli, better health outcomes, and improved behavioral performance – also during the TSST (Beltzer et al., 2014; Jamieson et al., 2018). In the current study, high-performing individuals might find that their resources exceed the demands, enabling them to appraise the TSST more as a challenge than as a threat. Note that these individuals demonstrated approach-related responses on the behavioral, cognitive, and neurophysiological level. Future research might include measures of stress appraisals to solidify the assumption that performance during stress increases social approach via strengthening the challenge compared to threat appraisals.

As an alternative interpretation, it is conceivable that high-performing individuals differ in trait-like characteristics from low-performing ones. Individuals who manage to look good while performing tasks in front of others might possess social skills and/or self-confidence that make them more likely to approach others (Riggio et al., 1990), independent from their social performance during stress. However, additional analyses contradict this alternative interpretation. First, associations between social performance and traits relevant for

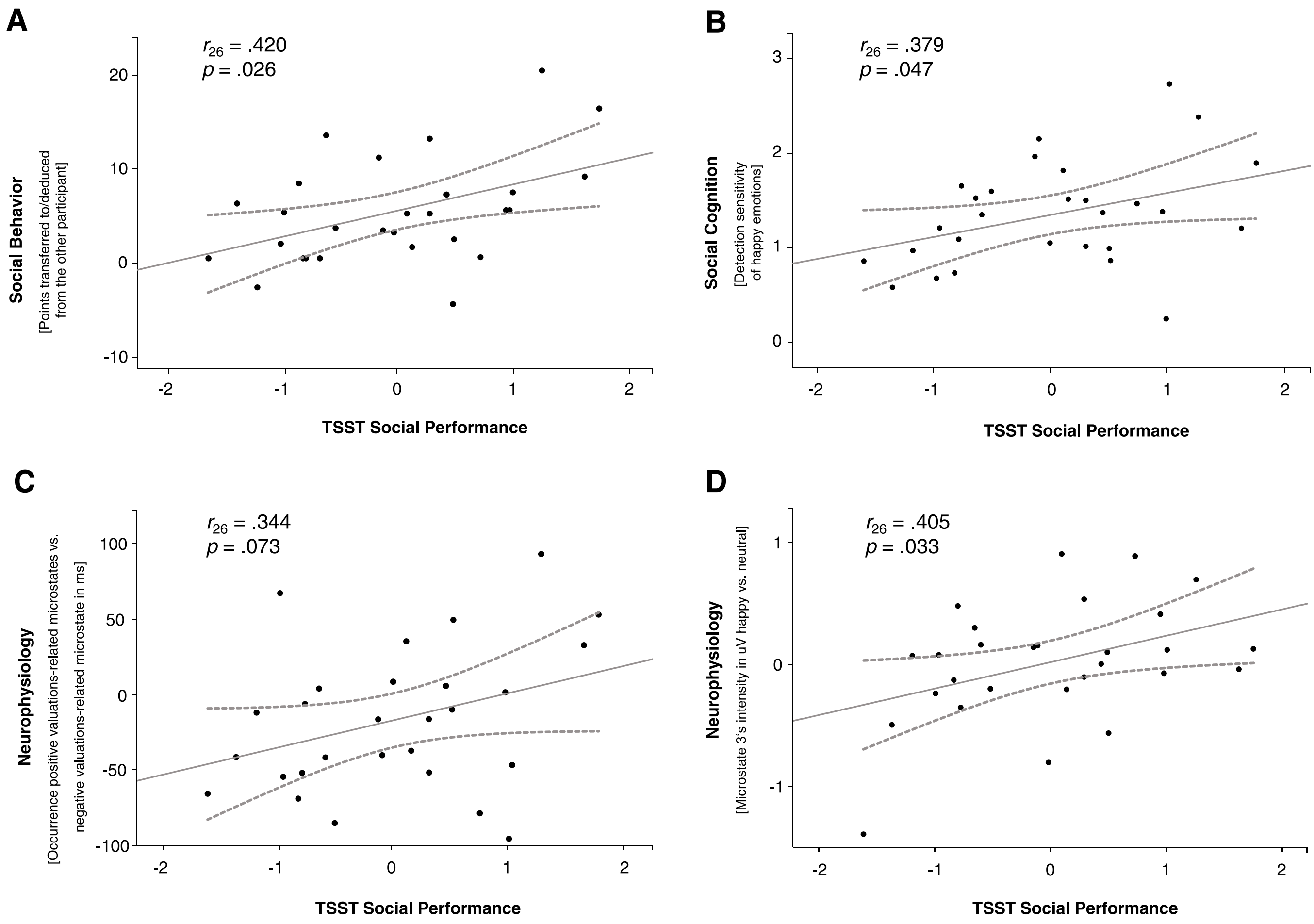


Fig. 7. Associations between TSST social performance and social approach. All scatter plots include regression lines and confidence intervals (95%). **A**: Association between performance and social behavior [points transferred to/deducted from the other participant]. **B**: Association between performance and social cognition, i.e., detection sensitivity for happy faces compared to neutral ones. **C**: Association between performance and valuations-related neurophysiological processing (i.e., temporal occurrence of the positive valuations-related microstate vs. temporal occurrence of the negative valuations-related microstate). **D**: Association between performance and neurophysiological processes during emotion detection (i.e., microstate 3′s intensity in response to happy faces in comparison to neutral ones).

social interactions and stress processing were non-significant (all *ps* <=.203). And second, although self-rated social appearance was positively associated with prosocial behavior under stress, it was neither significantly associated with behavior in the control condition (which would have been the case had we observed a general association between appearance and social approach) nor with emotion detection sensitivity across treatments. Therefore, our findings most likely reflect a direct modulatory effect of social performance on social approach during stress. To solidify this assumption and comprehensively assess social performance in a non-stressed state, future research could include a “friendly” TSST control condition (e.g., Wiemers et al., 2013) during which the jury makes eye-contact with the participants (in contrast to the present study’s TSST control condition during which the jury avoided eye contact with participants, which prevents quantifying the novel TSST social performance index here). This experimental design would enable us to employ a full factorial model (dependent variable: “social approach”; independent variable: “treatment” [stress vs. control]; covariate: “social performance”) which could demonstrate that specifically social performance during stress, but not social performance per se, modulates social approach.

Expanding upon previous research on neurophysiological stress effects (Dierolf et al., 2018; Kamp et al., 2019; Mueller and Pizzagalli, 2016), our study demonstrates modulatory effects of social performance on neurophysiological processes associated with emotion detection. High-performing individuals who were better able to differentiate happy faces from neutral ones exhibited more differentiated neurophysiological responses to those faces as well. Specifically, the better an individual performed socially during stress, the more his N170-like microstate 3′s intensity differed between happy and neutral faces and, in turn, the better he detected this emotion. Given N170′s well-established role in facial emotion processing with more intense responses to emotional compared to neutral faces (Hinojosa et al., 2015; Schindler and Bublatzky, 2020), we could infer that high social performance in the TSST shields against stress-induced impairments in emotion-induced intensity modulations during this early occurring neurophysiological process.

In sum, the present study demonstrates the validity of both the novel TSST social performance index and the novel TSST-EEG setup. While general effects of stress on social approach were absent (regarding social behavior) or modest (regarding social cognition), the TSST social performance index was associated with approach-related patterns across social behavior, social cognition, and underlying neurophysiological activity. Future studies might include specific measures or experimental manipulations of stress appraisals and study larger samples including male and female participants. As approaching others under stress might be considered as an adaptive way to cope with stress by enabling stress-buffering social support and social relationships (Holt-Lunstad et al., 2010), illuminating the modulatory role of social performance on approaching others under stress seems to be an extremely fruitful and societally relevant endeavor for future research in the social and clinical sciences.

CRediT authorship contribution statement

Bastian Schiller, Johanna Brustkern, Bernadette von Dawans, and Markus Heinrichs conceived and designed the study. Bastian Schiller, Johanna Brustkern, Bernadette von Dawans, Marie Habermann, and Marti Pacurar collected data. Bastian Schiller, Johanna Brustkern, Bernadette von Dawans, and Markus Heinrichs analyzed the data and wrote the manuscript. Marti Pacurar, and Marie Habermann commented on the manuscript.

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Declaration of Competing Interest

none.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.psyneuen.2023.106338.

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