Behavioural Brain Research 418 (2022) 113648

Contents lists available at ScienceDirect

Behavioural Brain Research

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

Improved interhemispheric connectivity after stress during lexical decision making

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ARTICLE INFO

Keywords:
EEG
Stress
Cortisol
Language
Lexical decision task
Interhemispheric connectivity
Asymmetry
Laterality

ABSTRACT

Functional hemispheric asymmetries emerge as the left and the right hemisphere are dominant for different aspects of task processing. However, the hemispheres do not work independent of each other but share information through the corpus callosum. The integration of information across the corpus callosum is dependent on its structural integrity and functionality. Several hormones, like estradiol and progesterone, can influence this function. Since earlier work has demonstrated that long-term changes in stress hormone levels are accompanied by changes in hemispheric asymmetries in several mental disorders, the aim of the current study was to investigate whether acute stress and the associated changes in stress hormone levels also affect information transfer across the corpus callosum. For this purpose, we collected EEG data from 51 participants while completing a lexical decision task and a Poffenberger paradigm twice, once after stress induction with the Trier Social Stress Test and once after a control-condition. While there were no differences in interhemispheric transfer between the stress and the non-stress condition in the Poffenberger paradigm, we observed shorter latencies to stimuli in the left visual field in the left hemisphere at the CP3-CP4 electrode pair after stress. These results suggest that the transfer of lexical material from the right to the left hemisphere was quicker under stress. Stress may increase callosal excitability and lead to more efficient signal transfer across the corpus callosum between language related areas. Future studies using pharmacological intervention are needed to further examine cooperation of the hemispheres under stress in more detail.

1. Introduction

Asymmetry as an organizational principle for the nervous system brings many advantages for the organism [20,21,59]: The allocation of diverse functions to one hemispheres facilitates both faster learning and parallel processing of different tasks [51,60]. While both hemispheres contribute to task processing, each hemisphere shows dominance for specific aspects leading to functional hemispheric asymmetries (FHAs). For example, the left hemisphere shows dominance in semantic processing [15] while the right hemisphere is more proficient in face perception [67].

The corpus callosum plays an integral role in the emergence of FHAs. Its fibers are glutamatergic synapsing on GABAergic interneurons in the contralateral hemisphere [9]. This means that activation of a specific area in the dominant hemisphere leads to inhibition of the homologous area in the non-dominant hemisphere and thus an enhancement of FHAs [45]. However, this inhibitory coupling between hemispheres is not the sole function of the corpus callosum on distribution of task processing; rather it is also essential for information integration between the hemispheres [68]. In this context, the function of the corpus callosum can be influenced by different hormones [23]. It has been proposed that sex steroid hormones like progesterone and estradiol lead to a decoupling of the two hemispheres by interacting with glutamatergic and GABAergic transcallosal signaling [22]. Whereas this would decrease FHAs, it would favor bihemispheric processing and increase interhemispheric integration by strengthening information transfer across the corpus callosum [4].

While the effects of sex steroid hormones on FHAs have been previously investigated [26], the effects of other steroid hormones, such as stress hormones, on FHAs and interhemispheric integration have not

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https://doi.org/10.1016/j.bbr.2021.113648
Received 29 July 2021; Received in revised form 27 September 2021; Accepted 27 October 2021
Available online 30 October 2021

been in the focus of laterality research. This comes as a surprise as stress hormones have played a substantial role in cognitive neuroscience [2,66]. The major stress hormones are adrenaline and noradrenaline, as product of the fast acting sympathetic nervous system, and cortisol which results from activation of the slower acting Hypothalamus–Pituitary–Adrenal (HPA) axis [29]. Corticotrophin-releasing hormone is released from the hypothalamus to stimulate secretion of adrenocorticotropic hormone from the anterior pituitary, which in turn leads to release of cortisol from the adrenal medulla [10].

In a recent review, our group delineated the association between long-term changes in cortisol levels and changes in hemispheric asymmetries in different mental and developmental disorders [6]. Also in the non-clinical context, low birth weight as a marker for intrauterine stress has been associated with changes in asymmetries [11]. These results are corroborated by studies using animal models of asymmetric behavior. For example, prolonged early life stress has been shown to induce atypical leftward turning behavior in rats [44]. This demonstrates that early and prolonged stress can negatively influence the development of asymmetries. However, the effects of acute stress on FHAs are not well understood. In a study recently published by our group, we investigated the influence of acute stress on FHAs on a behavioral level [5]. While there were no changes in FHAs due to stress, there was evidence for an effect of cortisol and sympathetic activity on interhemispheric information integration: under stress, interhemispheric integration of information was improved as evidenced by a positive correlation between these stress markers and the across-field advantage in the Banich-Belger task. Higher levels of cortisol and sympathetic activity indicated by increased alpha amylase levels were associated with better cross-hemispheric integration.

Information transfer could be modified by stress as stress related cortisol release could influence glutamatergic and GABAergic neurotransmission via the corpus callosum [46]. Cortisol increases glutamatergic transmission [3,43] and thus could also change interhemispheric transmission of information.

In that regard, it would be interesting to further investigate the influence of stress and related stress hormones on the neurophysiological level. Since it is not clear how cortisol interacts with information transmission properties of the corpus callosum, EEG could help uncover interhemispheric processing differences under stress. EEG is a widely used and non-invasive tool in neuroscience due to its high temporal resolution [41]. This method lends itself to the investigation of interhemispheric communication as information transfer across the corpus callosum takes less than 20 ms [56]. These timescales are out of reach for slower imaging methods like fMRI.

The aim of the current study was to investigate the influence of stress and stress hormones on interhemispheric transfer of information. For this purpose, participants performed a Poffenberger Paradigm [42,49] as well as a lexical decision task [57] while EEG was recorded after stress induction and a non-stress placebo condition. The Poffenberger Paradigm quantifies the interhemispheric transfer time (ITT) between the two hemispheres. The ITT constitutes a valid marker of transmission properties of the corpus callosum [27]. Latency differences in event related potentials (ERPs) between the left and right hemisphere for stimuli presented to one visual field mark the time it takes for the signal to travel across the corpus callosum to the contralateral homologous area [54]. N1 latencies, a negative component between 80 and 120 ms after stimulus onset, recorded over the contralateral hemisphere are around 10–25 ms faster than over the ipsilateral hemisphere [55]. These latency differences in the N1 between the left and right hemisphere are dependent on corpus callosum structural integrity [63] and are highly reliable measures of interhemispheric transfer [17].

The lexical decision task measures communication between the hemispheres with regard to language stimuli. As the left hemisphere is dominant for language processing [30], word stimuli presented to the right visual field are processed more efficiently, while stimuli presented to the left visual field increase transcallosal connectivity between visual areas [8]. Shorter N1 latencies reflect the higher efficiency of the left hemisphere for language processing [19]. Already in the striate cortex, a latency advantage in the N1 for word stimuli favoring the left hemisphere can be observed [57]. These early latency leads have also been associated with perceptual performance [14]. It has been demonstrated that transfer from the right hemisphere to the left is faster than from the left hemisphere to the right [38,53].

We hypothesize that interhemispheric transfer times will be reduced in the Poffenberger Paradigm in the stress session through the influence of cortisol on the corpus callosum. For this, we will focus on N1 latencies at the O1-O2 electrode pair. Moreover, in the lexical decision task, we hypothesize that information transfer from the left to the right hemisphere will be faster with shorter latencies in the stress condition. Here, we will focus on N1 latencies at the CP3-CP4 electrode pair as these electrodes are situated over the Wernicke area which plays a central role in language comprehension [62] and its right hemispheric homolog.

2. Methods

2.1. Participants

We recorded data from 51 male participants aged between 18 and 39 years (M = 24.5 years, SD = 5.04) at the Ruhr University Bochum, Germany. The sample size was determined using a priori power analysis (G*power 3.1; https://www.gpower.hhu.de/) with an α-error probability of 0.05 and a power of 0.95. Based on the data by Brüne et al. [7] we estimated the effect of stress on hemispheric asymmetries to be small (partial $\eta 2 = 0.07$). Exclusion criteria entailed a history of mental or neurological disorders, intake of medication or drugs, smoking, a body mass index outside the normal range (18.5–25 kg/m^2) as well as performing shiftwork [24,35,37]. All participants were naïve to the stress paradigm.

Handedness was assessed using the Edinburgh Handedness Inventory [47]. Eight participants were left-handed, as categorized by a Lateralization Quotient (LQ) < 0, and 43 were right-handed (M = 64.29, SD = 62.09). Following recent recommendations for neuroscience studies on hemispheric asymmetries [64] we did not exclude left-handers in order to get a more representative sample of the actual distribution of hemispheric asymmetries in the population.

The local ethics committee of the Faculty of Psychology at the Ruhr University Bochum approved the study. All participants were treated in accordance with the Declaration of Helsinki and gave written informed consent. Participants received a compensation of 50€ or course credit. This experiment was part of a larger project investigating the influence of stress on hemispheric asymmetries that consisted of several different studies. Other data from this project will be published in Berretz et al. (In preparation).

2.2. Procedure

Participants were invited for two test sessions which took place between 2 and 6 pm to control for circadian changes in cortisol [37].

After providing written informed consent, participants were setup with the EEG cap. All participants completed baseline subjective stress measurements and the first saliva sample was taken. Subjective stress was assessed with the Subjective Experiences Rating Scale (SERS; [31]) as well as a set of visual analog scales that measure subjective perception of stress (VAS; [36]). Subsequently, participants underwent a stress induction or a control procedure. For this purpose, we utilized the Trier Social Stress Test (TSST, [34]). After a five-minute preparation period, participants had to give a five-minute oral presentation about their positive traits in a mock job interview followed by a mental arithmetic task (subtracting in steps of 17) for a total of 10 min. During the presentation and the arithmetic task, a panel consisting of a woman and a man dressed in lab coats evaluated the participants. The panel refrained from giving any positive feedback. Furthermore, the participant's face

was being videotaped and the video was streamed to a nearby monitor allowing participants to view their own performance. As a control condition, we employed the Placebo-TSST (P-TSST, [25]). The P-TSST also consisted of a preparation period, an oral presentation and an arithmetic task. However, participants were alone during performance and were not videotaped. Moreover, the mental arithmetic task was easy to perform (counting forward in steps of 15). After the preparation period, participants were instructed to talk about their last vacation and when to start counting. For each task, the experimenter left the room. The P-TSST lacks the stressful elements of the TSST like social evaluation and pressure to perform [13] while mimicking its task demands. Therefore, it is a suitable control procedure. The order of TSST and P-TSST sessions was pseudo-randomized. It was planned that half the participants began with the TSST session and the other half with the P-TSST session. As the data collection was cut short due to the Covid-19 pandemic, 9 more participants started with the P-TSST session. Following the stress induction, the second set of stress measurements and a saliva sample was collected followed by 5 min of eye-closed resting state EEG recordings. Following this, participants performed two tasks measuring information transfer across the corpus callosum (see below). Between these tasks, cortisol measurements were collected and with each cortisol assessment, we also assessed the mood of the participants (see Fig. 1).

Salivary samples were collected using Salivette sampling devices (Sarstedt, Nümbrecht, Germany).

2.3. Experimental paradigms

All experiments were administered using Presentation software (Neurobehavioral Systems, Albany, CA, USA). Participants were instructed to rest their chin on a chinrest in 57 cm distance to the computer screen and to focus on the fixation cross at all times. At all times, a central fixation cross with a size of 1° by 1° visual angle was presented and participants were to fixate the fixation cross during the entire session.

2.3.1. Poffenberger EEG paradigm

In the Poffenberger EEG paradigm [17], participants were instructed to press a designated key as fast as possible to visual stimuli presented within each visual half field. Each trial of the task started with a short presentation (0.135 s) of a circular white stimulus (75.02 cd/m^2) on a gray background (20.20 cd/m^2) with a diameter of 1.41°. The outer edge of the stimuli appeared at 5° horizontal and 5° vertical distance from the fixation cross to the lower left or right visual half-field (left visual half-field: LVF; right visual half-field: RVF). The intertrial interval (ITI) was jittered randomly between 1000 and 2000 ms to avoid expectancy effects. The task consisted of two experimental blocks, one for each hand consisting of 25 LVF and 25 RVF trials presented in a randomized order. According to the combination of visual half field (LVF/RVF) and position of electrodes on each hemisphere (LH/RH), this resulted in the conditions RH_LVF, RH_RVF, LH_LVF, and LH_RVF for each hand (left/right).

2.3.2. Lexical decision task

In the Lexical Decision Task (LDT, [57]), participants were asked to identify, if a lexical stimulus presented to them was a word or a non-word. Stimuli consisted of 80 German nouns as well as 80 pronounceable meaningless letter combinations. We used nouns in the word category. Corresponding non-words were created by exchanging two or more letters within the noun. Stimuli were presented horizontally in a randomized order on a 17-inch CRT computer monitor in black against white background with half in the left visual field (LVF) and the other half in the right visual field (RVF). Each stimulus was presented for 160 ms. Stimuli were presented laterally at a distance of 2° visual angle from the fixation cross. To avoid confounding handedness effects, participants were asked to use their dominant hand to indicate on a custom keyboard if the presented item was a word or a non-word. Reaction time was limited to 2000 ms. The ITI was jittered between 150 and 350 ms.

2.4. EEG recording and analysis

EEG data was recorded using a 64 Ag–Ag Cl electrode system (actiCAP ControlBox and QuickAmp 72, Brain Products GmbH, Gilching, Germany), positioned at standard scalp locations according to the International 10–20 system (FCz, FP1, FP2, F7, F3, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, TP9, CP5, CP1, CP2, CP6, TP10, P7, P3, Pz, P4, P8, PO9, O1,Oz, O2, PO10, AF7, AF3, AF4, AF8, F5, F1, F2, F6, FT9, FT7, FC3, FC4, FT8, FT10,C5, C1, C2, C6, TP7, CP3, CPz, CP4, TP8, P5, P1, P2, P6, PO7, PO3, POz, PO4, PO8). Recordings were sampled at 1 kHz. The FCz electrode site was used as reference during recording and impedances were kept under 5 kΩ at the beginning of recording.

Data analysis was performed offline using the Brain Vision Analyzer software (Brain Products GmbH). First, visual data inspection to reject EEG-sections containing technical artifacts and exclusion of faulty or dead channels was performed. After that, a semiautomatic independent component analysis (ICA) with Infomax rotation [12] was applied to

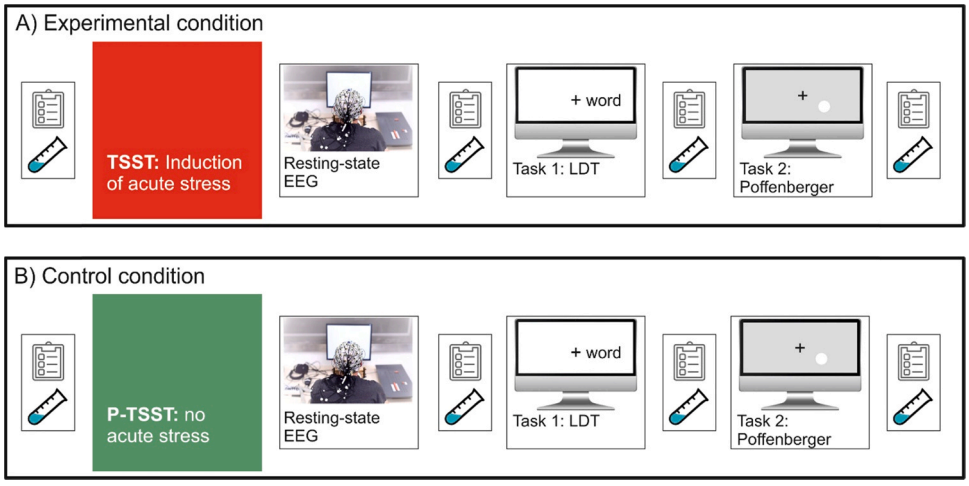

Fig. 1. Experimental design. After TSST or P-TSST, the participant completes a resting state EEG and two experimental tasks; the lexical decision task (LDT) and the Poffenberger paradigm. Before the stress induction and after each section of the experiment, cortisol and subjective stress were assessed. (A) In the stress session, participants undergo the TSST. (B) In the control session, the P-TSST is applied.
Figure adapted from [5].

eliminate reoccurring artifacts like pulse, blinks and eye movements. Next, the FCz and missing or rejected channels were interpolated using topographical interpolation with spherical splines. For the LDT, the data was epoched into 1200 ms segments, extending from 200 ms prior to stimulus onset to 1000 ms post-stimulus onset. In the Poffenberger paradigm, data was epoched into stimulus-locked segments starting 100 ms before and 600 ms after stimulus onset. Subsequently, automatic artifact rejection procedures were applied. We allowed a maximum voltage step of 50 μV/ms, a maximum value difference of 200 μV within a 200 ms interval or amplitudes below 0.1 μV served as artifact rejection parameters. The number of rejected trials was well below 5% of all trials in each condition and for all EEG channels. The FCz was re-referenced with a CSD-transformation [33] that was applied to eliminate the reference potential from the data. After the CSD-transformation, epochs were baseline corrected and N1 amplitudes and latencies were averaged for all conditions for each participant individually. For all further analyses, only correct trials were included in the analysis. The N1 (130–230 ms after stimulus presentation, [41]) amplitudes and latencies were quantified at O1-O2 electrodes for the Poffenberger paradigm and CP3-CP4 electrodes for the Lexical Decision Task.

2.5. Endocrinological measurements

Saliva samples were analyzed in the in-house laboratory of the Departments of Genetic Psychology and Cognitive Psychology at Ruhr University Bochum. To determine cortisol concentrations, a cortisol enzyme-linked immunosorbent assay (Cortisol Saliva ELISA, IBL, Hamburg, Germany) was used with intra-assay coefficients of variance (CV) below 5% and inter-assay CVs below 15%.

Additionally, the enzyme alpha-amylase (sAA) was analyzed from the saliva samples to assess the response of the sympathetic nervous system [52]. A colorimetric test using 2-chloro-4-nitrophenyl-α-maltrotriosoide (CNP-G3) as a substrate reagent was applied to measure sAA concentration [40,65]. Intra- and inter-assay variabilities were below 10%.

2.6. Statistical analysis

We performed a 2 × 5 repeated measures ANOVA with the factors condition (TSST, P-TSST) and time point of measurement (1–5) for cortisol, salivary alpha amylase and affect.

We calculated interhemispheric transfer times (ITT) in the Poffenberger paradigm by subtracting contralateral from ipsilateral latencies:

ITT (LVF) = mean (RH_LVF_right, RH_LVF_left) – mean (LH_LVF_right, LH_LVF_left).

ITT (RVF) = mean (LH_RVF_right, LH_RVF_left) – mean (RH_RVF_right, RH_ RVF_left).

ITT = mean (ITT LVF, ITT RVF).

In later analysis, we only used participants displaying a positive average ITT. As a signal that is presented to the left visual field first enters the right hemisphere and vice versa, it should take longer for the signal to reach the ipsilateral hemisphere. This means that ipsilateral latencies are always slower because of the interhemispheric transfer. This resulted in 43 participants for the Poffenberger paradigm. To determine any differences in ITT between the TSST and P-TSST session, we computed a repeated measures ANOVA with the factors stress (TSST vs P-TSST), visual half field (LVF vs RVF) and electrode (O1 vs O2) as well as a dependent sample *t*-test comparing the total transfer time between sessions. To investigate influences of stress on transfer of lexical information in the LDT, we calculated a repeated measures ANOVA with the factors stress (TSST vs P-TSST), visual field (LVF vs RVF), hemisphere (left vs right) and condition (word vs non-word) for latencies as well as amplitudes. All post-hoc tests were Bonferroni corrected.

3. Results

3.1. Stress induction

The results of the stress induction are identical to the results reported in Berretz et al. (In preparation) as these were the same participants. Only the results from the stress induction overlap in these publications as participants first completed the stress induction followed by several tasks. The results of the tasks presented in this paper have not been published elsewhere.

For cortisol (see Fig. 1A), there was a significant main effect of stress ($F_{(1,50)} = 25.24$, $p < .001$, $\eta_p^2 = .34$) and time ($F_{(4,\ 200)} = 44.87$, $p = .002$, $\eta_p^2 = .10$). There was also a significant interaction effect of both ($F_{(4,\ 200)} = 45.43$, $p < .001$, $\eta_p^2 = .48$). Bonferroni post-hoc tests revealed that cortisol levels were increased in the P-TSST condition ($p < .001$) for the first measurement. During the third, fourth and fifth measurement, cortisol levels were increased in the TSST condition ($ps < 0.001$). Although there was no significant effect of order of test sessions, the higher cortisol levels at the first measurement time point could be due to more participants starting with the P-TSST session. Participants might have been nervous with the new test situation and thus showed an anticipatory cortisol response.

For salivary alpha amylase (see Fig. 1B), there was a significant main effect of time ($F_{(4,\ 200)} = 21.12$ $p < .001$, $\eta_p^2 = .30$). There was also a significant interaction effect of condition and time ($F_{(4,\ 200)} = 18.27$, $p < .001$, $\eta_p^2 = .27$). Bonferroni corrected post-hoc tests revealed that during the first measurement time point, sAA levels were increased in the P-TSST condition ($p = .031$) compared to the TSST condition. During the second measurement time point, sAA levels were increased in the TSST condition ($p < .001$).

For affect measures by the SERS (see Fig. 1C), there was a significant main effect of session ($F_{(4,\ 200)} = 58.44$ $p < .001$, $\eta_p^2 = .54$) indicating that subjective stress levels were higher in the TSST than in the P-TSST condition. There was also a significant interaction effect of condition and time point ($F_{(4,\ 200)} = 23.98$, $p < .001$, $\eta_p^2 = .32$). During the second time point directly after the TSST, subjective stress ratings were increased in the TSST condition ($p < .001$) compared to the P-TSST condition. During the third and fifth measurement time point, subjective stress levels were increased in the P-TSST condition ($ps < 0.049$) (Fig. 2).

3.2. Behavioral data

We did not analyze the behavioral data of the Poffenberger paradigm as they are not reliable [17]. Due to signal transfer through subcortical pathways, behavioral latency differences between left- and right-hand reactions do not reflect latency differences in the cortex [28].

A repeated measures ANOVA for the number of correct responses in the lexical decision task with the factors stress, side of presentation and word condition revealed a significant main effect of word condition ($F_{(1,50)} = 5.79$, $p = .020$, $\eta p^2 = .10$), side of presentation ($F_{(1,50)} = 43.85$, $p < .001$, $\eta_p^2 = .47$) as well as a significant interaction of side and condition ($F_{(1,50)} = 31.00$, $p < .001$, $\eta p^2 = .38$). A Bonferroni corrected post-hoc test revealed more correct responses to stimuli presented on the right side in the word condition and more correct responses to stimuli presented on the left side in the non-word condition.

A repeated measures ANOVA for the number of incorrect responses with the factors stress, side of presentation and word condition revealed a significant main effect of word condition ($F_{(1,50)} = 5.46$, $p = .024$, $\eta p^2 = .10$) and side of presentation ($F_{(1,50)} = 38.80$, $p < .001$, $\eta p^2 = .44$). There was also a significant interaction of side and condition ($F_{(1,50)} = 31.24$, $p < .001$, $\eta p^2 = .39$). A Bonferroni corrected post-hoc test revealed more incorrect responses to stimuli presented on the left side in the word condition and more correct responses to stimuli presented on the right side in the non-word condition.

A repeated measures ANOVA for the number of missed responses

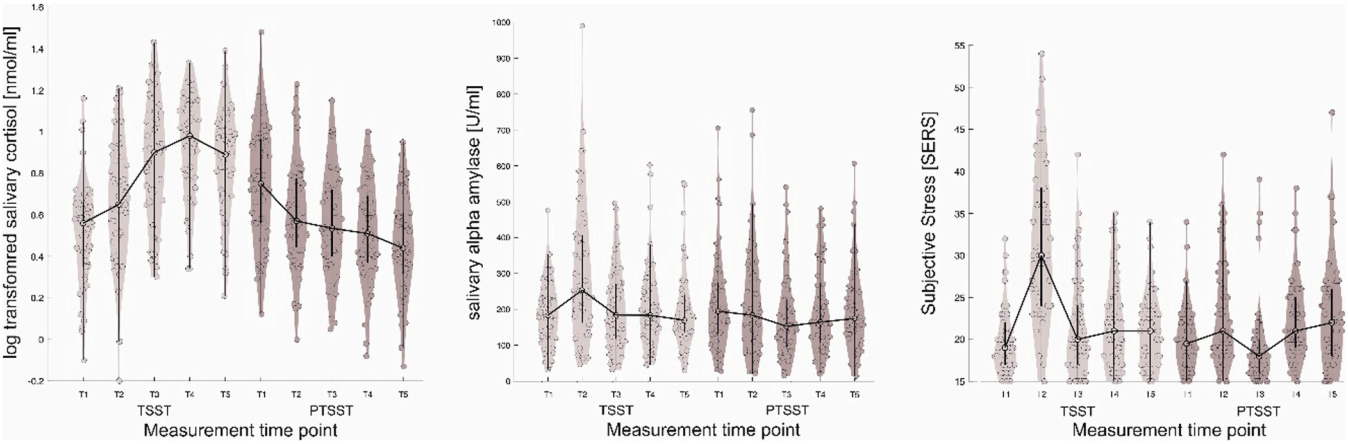

Fig. 2. Physiological and subjective stress response in the TSST and P-TSST sessions. Error bars represent 1 ± SEM from the mean. The first measurement was taken immediately before the TSST or P-TSST preparation period. A) Mean cortisol B) mean salivary alpha amylase and C) mean subjective stress responses measured by SERS for each time point.

with the factors stress, side of presentation and word condition revealed a significant main effect of word condition ($F_{(1,50)} = 7.13$, $p = .010$, $\eta p^2 = .13$) with participants missing more responses to non-words.

A repeated measures ANOVA for reaction times of correct responses with the factors stress, side of presentation and word condition revealed a significant main effect of word condition ($F_{(1,50)} = 47.16$, $p < .001$, $\eta p^2 = .49$), side of presentation ($F_{(1,50)} = 39.14$, $p < .001$, $\eta p^2 = .44$) as well as a significant interaction of side and condition ($F_{(1,50)} = 21.52$, $p < .001$, $\eta p^2 = .30$). A Bonferroni corrected post-hoc test revealed faster responses to stimuli presented on the right side in the word condition.

A repeated measures ANOVA for reaction times of incorrect responses with the factors stress, side of presentation and word condition revealed a significant main effect of word condition ($F_{(1,50)} = 28.79$, $p < .001$, $\eta p^2 = .37$) and side of presentation ($F_{(1,50)} = 8.86$, $p = .004$, $\eta p^2 = .15$). There was also a significant interaction of side and condition ($F_{(1,50)} = 8.74$, $p = .005$, $\eta p^2 = .15$). A Bonferroni corrected post-hoc test revealed faster responses to non-words presented on the right side.

3.3. EEG data

3.3.1. Poffenberger paradigm

The ANOVA for N1 latencies revealed only a significant interaction between electrode and visual field ($F_{(1,42)} = 123.02$ $p < .001$, $\eta_p^2 = .75$). A Bonferroni corrected post-hoc test revealed significantly shorter latencies at the O1 for stimuli presented in the right visual field as well as at the O2 for stimuli presented in the left visual field. The *t*-test revealed no significant differences between total ITIs between the sessions ($t_{(42)} = 0.20$, $p = .846$) on the latencies of the N1 at the O1-O2 electrode pair.

3.3.2. Lexical decision task

The ANOVA for N1 latencies revealed a significant main effect of visual field ($F_{(1,49)} = 4.83$, $p < .05$, $\eta_p^2 = .09$) indicating faster latencies to stimuli in the right visual field. Moreover, the analysis showed a significant interaction between hemisphere and visual field ($F_{(1,49)} = 6.90$, $p < .05$, $\eta_p^2 = .12$) indicating faster latencies to stimuli in the left visual field in the left hemisphere compared to the right hemisphere ($p < .05$). Lastly, the analysis indicated a significant interaction between hemisphere, visual field and stress ($F_{(1,49)} = 4.98$, $p < .05$, $\eta_p^2 = .09$)

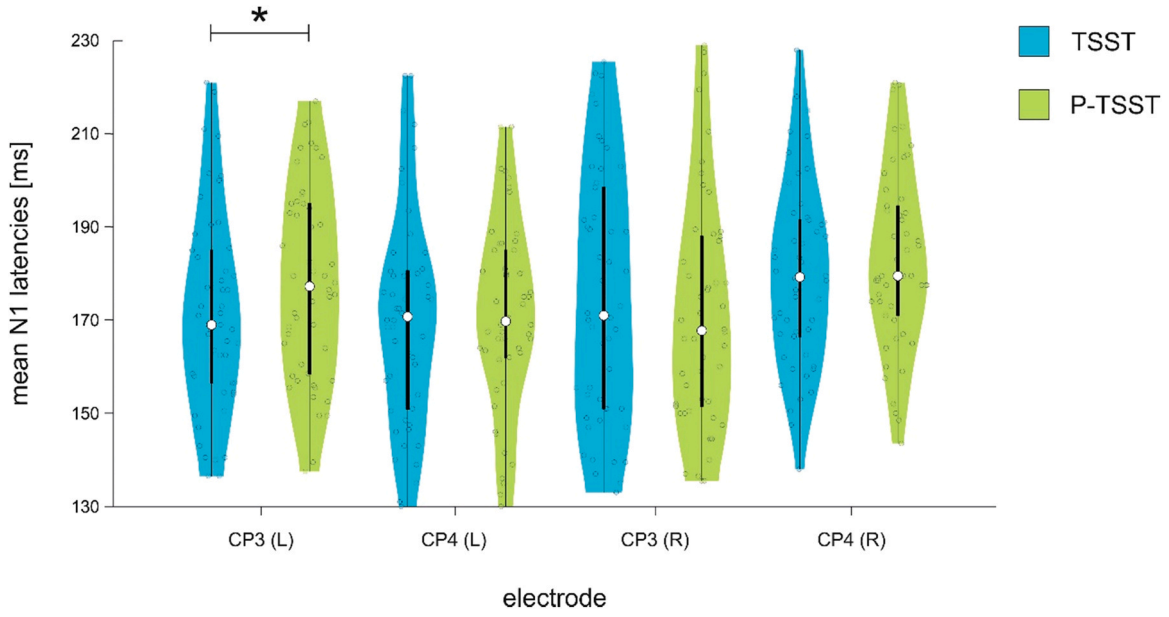

Fig. 3. N1 latencies for electrodes of interest CP3-CP4. L and R refer to left and right side of stimulus presentation.

indicating shorter latencies to stimuli in the left visual field in the left hemisphere during the TSST ($p < .05$) on the latencies of the N1 at the CP3-CP4 electrode pair compared to the P-TSST (see Figs. 3 and 4). This indicated faster information transfer from the right to the left hemisphere during stress.

The ANOVA for amplitudes revealed a significant main effect of hemisphere ($F_{(1,49)} = 22.88$, $p < .001$, $\eta_p^2 = .32$) and a significant main effect of visual field ($F_{(1,49)} = 6.36$, $p < .05$, $\eta_p^2 = .11$) indicating more negative amplitudes over the right hemisphere and for stimuli presented in the left visual field. Moreover, the analysis showed a significant interaction between hemisphere and visual field ($F_{(1,49)} = 8.88$, $p < .05$, $\eta_p^2 = .15$) indicating less negative amplitudes to stimuli in the right visual field in the right hemisphere compared to the left hemisphere ($p < .05$) on the amplitudes of the N1 at the CP3-CP4 electrode pair.

4. Discussion

The current study aimed at investigating the influence of stress on interhemispheric transfer of information. For this, participants completed two tasks, once after stress induction and once after a similar control procedure. Stress induction was successful, which was indicated by an increase in salivary alpha amylase, cortisol and subjective stress ratings after the TSST. In the Poffenberger paradigm, we measured changes in N1 latency differences between the O1 and O2 electrode dependent on stimulus presentation in the ipsilateral or contralateral visual field. We could replicate the classic Poffenberger effect: latencies were shorter at the O1 when stimuli were presented in the right visual field and at the O2 when stimuli were presented in the left visual field. The difference between the latencies at the O1 and O2 constitutes the ITT. There were no differences in ITT between the stress and the non-stress session.

In the lexical decision task, we focused on latency differences at the CP3-CP4 electrode pair. On the behavioral level, we found faster and more accurate reactions to word stimuli in the right visual field. These effects were reflected in the N1 latencies. There were no behavioral differences between the stress and non-stress sessions. However, we observed shorter latencies to stimuli in the left visual field in the left hemisphere during the TSST. This indicates that latencies at the CP3 were shortened in the stress session compared to the non-stress session when stimuli were presented in the ipsilateral visual field.

It is conceivable that stress and the associated stress hormones influence information transmission through the corpus callosum. The corpus callosum is essential for information transfer from one hemisphere to the other [61]: while unilateral processing during simple tasks is increased by transcallosal inhibition, bilateral processing during more complex tasks is furthered by transcallosal excitation. As the LDT requires complex decision-making on the basis of lexical stimuli, it promotes interhemispheric cooperation [32,48]. Karolis et al. showed that communication associated functions display left dominant activation in frontal and temporal areas and that lateralized regions like these exhibit reduced structural connectivity to the corpus callosum [32]. This suggests that functional lateralization is associated with decreased callosal function and thus inter-hemispheric independence. Cortisol has been shown to increase glutamatergic signaling [43]. In the context of the current study, this implies that cortisol could increase callosal excitability and thus more efficient signal transfer across the corpus callosum between language related areas (see Fig. 5A). This interpretation would be in line with previous work by our group demonstrating that stress hormones improved interhemispheric integration in a Banich-Belger task [5]. If this is the case, it needs to be addressed why only latencies in the LDT were affected by stress and no changes were seen in the Poffenberger paradigm. A possible explanation concerns the relationship between functional connectivity and the structure of the corpus callosum. In a recent study, Friedrich et al. [16] could show that higher order functions, to which decision making and language processing belong, are dependent on frontal callosal fibers and lower order perceptive functions, which would be measured via the Poffenberger paradigm, map onto posterior callosal regions. This callosal gradient resembles previous work mapping the diameter and myelination of callosal fibers [1]. Diameter and myelination of fibers have been shown to play a vital role in the fiber's information conduction properties [18]. One might speculate that the influence of stress and stress hormones on interhemispheric communication is tied to the specific function and the fibers it relies on (Fig. 5).

Alternatively, it could be speculated that stress selectively enhances stimulus processing in early visual areas leading to shorter processing latencies in downstream associative areas (Fig. 5B). Acute stress has been hypothesized to shift activation from the executive network to the salience network enhancing detection and integration of sensory information [69]. In this context, the processing of language-related stimuli might be enhanced as well under stress. However, since there was no evidence in the EEG data collected from the Poffenberger paradigm of altered sensory processing in relation to acute stress, this mechanism is less likely to underlie the observed results albeit it could be possible that the lack of an effect in the Poffenberger paradigm could result from the manipulation not being strong enough. As there are different methods of stress induction besides the TSST, it could be worthwhile to investigate this effect after using a different stress induction paradigm like the imaging Maastricht Acute Stress Test (iMAST; [50]) or the ScanSTRESS paradigm [58]. Since neither the iMAST nor the ScanSTRESS require speaking, they could be used to investigate a language-based task like the LDT without possible confounding factors.

4.1. Limitations and outlook

This study used EEG recordings to specifically investigate processing differences after stress and placebo conditions. As language stimuli are processed on a short time scale, the high temporal resolution of the EEG was necessary to discern the dynamics of interhemispheric integration. However, EEG does not allow for making definitive conclusions as to

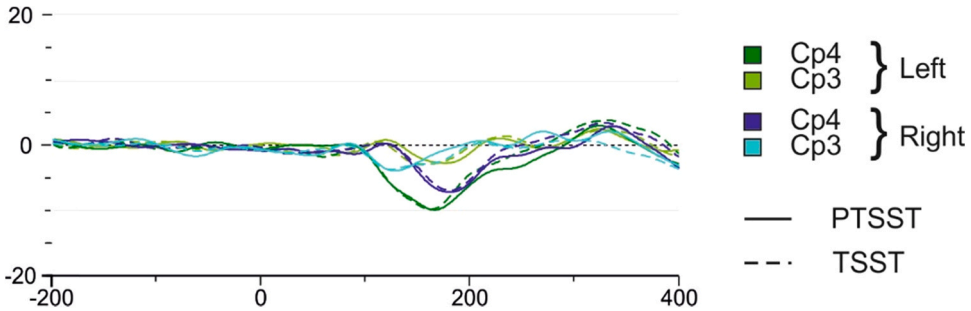

Fig. 4. Time course of ERP components at electrodes CP3 and CP4. Stimulus presentation was at 0 ms. Green lines indicated ERPs in response to stimuli in the left visual field. Blue lines indicated ERPs in response to stimuli in the right visual field. Dotted lines indicate the P-TSST session. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

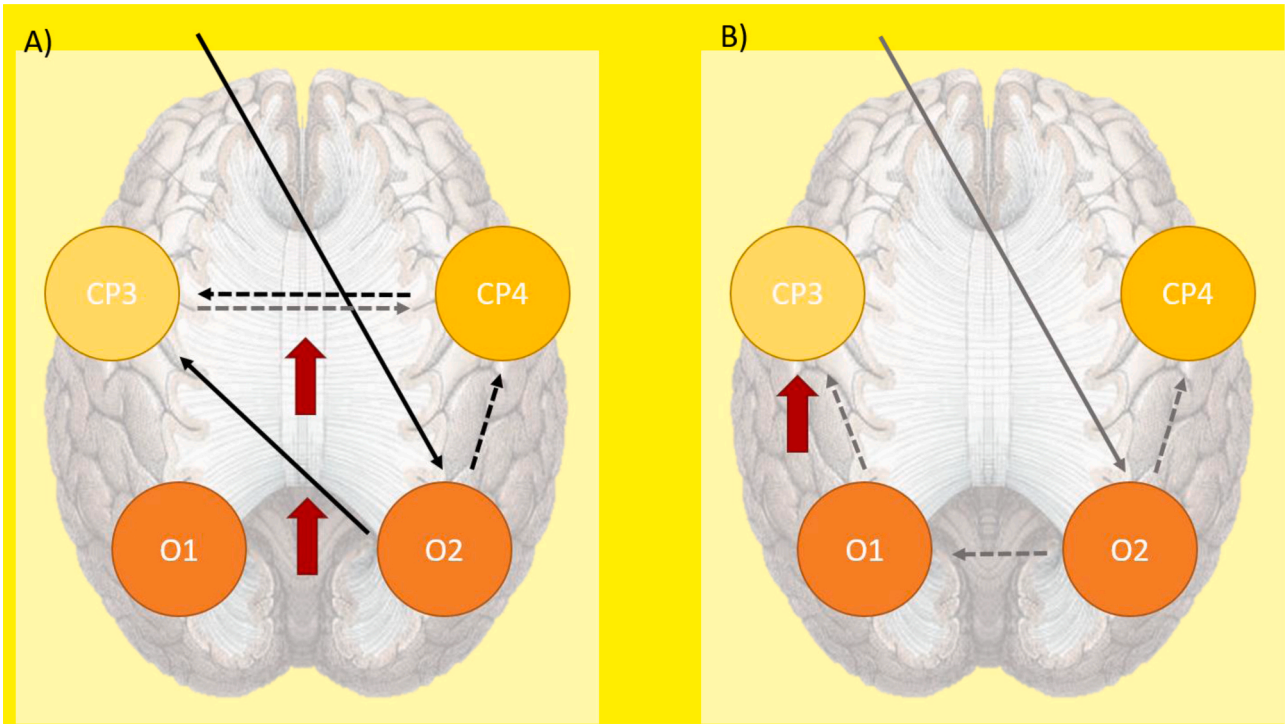

Fig. 5. Possible mechanisms behind shortened latencies at the CP3 in the stress session. A) Information from the left visual field enters the right visual cortex. From there, the information is transmitted to the Wernicke area under the CP3 electrode, either directly or via the right-hemispheric homolog. Stress could influence this transmission by affecting the connecting fibers. B) Information from the left visual field enters the right visual cortex. However, the information is not transmitted to the left hemisphere through involvement of language processing areas. The shortened latencies at the CP3 result from stress affecting the left-hemispheric areas rather than the transmission.

which brain structures were involved as the source regions generating the electrical signal due to its limited spatial resolution. Future studies could use techniques with higher spatial resolutions such as fMRI to pinpoint the activation differences more precisely. Such study designs could further aid in understanding the neural basis of interhemispheric integration.

As participants performed a five-minute resting state EEG after stress induction, it could be conceivable that effects of the stress induction might have slightly decreased over that time. This could have affected the results in a way that subjective stress was lowered after this resting state measure and thus did not affect later tests.

A further limitation concerns the sample composition. Due to the effects of cycling phase-dependent hormones on the stress response and hemispheric asymmetries [22,39], we opted to only test male participants in the scope of our study. Thus, our results might apply to males only. In future studies, the inclusion of female participants and the evaluation of the cycle phase may help to garner stronger generalizability.

5. Conclusion

In the present study, we found no changes in N1 latency or amplitude in the Poffenberger paradigm on occipital electrodes between a stress and a placebo condition. We however found decreased N1 latencies on the CP3 electrode over Wernicke's area to stimuli in the left visual field in the left hemisphere in response to acute stress. This indicates that the transfer of lexical material from the right to the left hemisphere was quicker under stress. Future studies should employ methods with higher spatial resolution to further examine cooperation of the hemispheres under stress.

Funding

This work was supported by the Deutsche Forschungsgemeinschaft project number 400672603, Grant WO733/18-1 and OC127/9-1 and the Research Training Group "Situated Cognition" (GRK 2185/1) as well as the German National Academy for Sciences Leopoldina (LPDS2021-05).

CRediT authorship contribution statement

Gesa Berretz: collected the data, performed the analyses, wrote the manuscript. **Julian Packheiser:** performed the analyses and wrote the manuscript. **Oliver T. Wolf:** designed the study, provided feedback on the manuscript and provided funding. **Sebastian Ocklenburg:** designed the study, helped with statistical analyses, provided feedback on the manuscript and provided funding.

Declaration of conflict of interest

The authors declare no conflict of interest.

Acknowledgments

The authors would like to thank Petunia Reinke for her help in data acquisition.

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