

# Prioritized attentional processing: Acute stress, memory and stimulus emotionality facilitate attentional disengagement

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## ABSTRACT

Rapid attentional orienting toward relevant stimuli and efficient disengagement from irrelevant stimuli are critical for survival. Here, we examined the roles of memory processes, emotional arousal and acute stress in attentional disengagement. To this end, 64 healthy participants encoded negative and neutral facial expressions and, after being exposed to a stress or control manipulation, performed an attention task in which they had to disengage from these previously encoded as well as novel face stimuli. During the attention task, electroencephalography (EEG) and pupillometry data were recorded. Our results showed overall faster reaction times after acute stress and when participants had to disengage from emotionally negative or old facial expressions. Further, pupil dilations were larger in response to neutral faces. During disengagement, our EEG data revealed a reduced N2pc amplitude when participants disengaged from neutral compared to negative facial expressions when these were not presented before, as well as earlier onset latencies for the N400f (for disengagement from negative and old faces), the N2pc, and the LPP (for disengagement from negative faces). In addition, early visual processing of negative faces, as reflected in the P1 amplitude, was enhanced specifically in stressed participants. Our findings indicate that attentional disengagement is improved for negative and familiar stimuli and that stress facilitates not only attentional disengagement but also emotional processing in general. Together, these processes may represent important mechanisms enabling efficient performance and rapid threat detection.

## 1. Introduction

Attention is a crucial cognitive ability, allowing us to select, process and respond to relevant information in the environment. Two processes appear to be particularly relevant for efficient attentional processing: orienting and disengagement. Attentional orienting involves voluntary visual selection, a process that depends on intraparietal and superior frontal cortices, as well as rapid detection of relevant stimuli, which activates the right temporoparietal and inferior frontal cortices (Corbetta et al., 2000; Corbetta and Shulman, 2002). In contrast, attentional disengagement refers to the ability to redirect attention away from a specific stimulus. Lesion studies identified the parietal lobe as a crucial brain structure involved in attentional disengagement (Posner et al., 1984; Posner and Petersen, 1990). In addition, prefrontal brain regions may play a role in task goal dependent disengagement, involving controlled, top-down processes (Eimer and Kiss, 2010; Petersen and Posner, 2012). Factors that are known to guide our attentional orienting and that are strongly interacting with each other are the emotional state of the individual, as well as the emotionality of and prior experience

with the stimuli themselves. Specifically, the processing of emotional stimuli, especially under stress, as well as the processing of previously encountered stimuli that are stored in our memory, is prioritized (for examples see Öhman et al., 2001; Weymar et al., 2012; Goldfarb et al., 2016). Yet, it is to our knowledge still unknown whether and how this prioritized processing affects attentional disengagement away from these stimuli.

The prioritized processing of emotional stimuli is evident by their rapid detection in the environment, a highly preserved mechanism that has been shown for evolutionary relevant threatening stimuli (Öhman et al., 2001) as well as for socially relevant stimuli such as emotional faces (Bradley et al., 1997). This attentional bias toward emotional stimuli is driven by exogenous, bottom-up processes that occur automatically (Öhman et al., 2001). Time-sensitive electroencephalography (EEG) recordings suggest that enhanced attentional orienting toward salient stimuli can occur within the first 100 ms of stimulus presentation (Carretie et al., 2004; Carretie, 2014). Functional magnetic resonance imaging (fMRI) studies further suggest that the amygdala is a crucial brain region that directly - or indirectly via prefrontal cortex regions -

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enhances attentional processing of emotional stimuli (Vuilleumier et al., 2004; Vuilleumier, 2005; Pourtois et al., 2013). These modulatory influences of the amygdala are likely driven by rapid noradrenergic mechanisms (van Stegeren et al., 2005). A delay in attentional disengagement from emotional stimuli has mainly been observed in high trait-anxious participants (Fox et al., 2002) and in individuals suffering from anxiety disorders (Cisler and Koster, 2010) and disorders such as depression or posttraumatic stress disorder (PTSD; Disner et al., 2011; El Khoury-Malhame et al., 2011; Koster et al., 2011; but see Carlson and Reinke, 2014). Due to facilitated processing of emotional stimuli, as indicated by enhanced early event-related potentials (ERPs; Carretie, 2014), we expect more efficient disengagement from emotional stimuli in our sample of healthy participants.

Similar to emotional stimuli, also the processing of previously encountered stimuli that are stored in our memory is prioritized. Specifically, successful retrieval of previously learned stimulus locations has been shown to facilitate attentional orienting. This effect was mediated by the hippocampus and attention-related frontoparietal brain regions, which may act as a control network to optimize perceptual processing (Summerfield et al., 2006; Stokes et al., 2012). The influence of memory on attentional orienting has been shown across different tasks and memory systems (Hutchinson and Turk-Browne, 2012; Rosen et al., 2016). For instance, in a modified visual search task, both cognitive, hippocampus-dependent and habitual, striatum-dependent memory systems were shown to facilitate attention (Goldfarb et al., 2016). Whereas previous research focused mainly on the role of memory in attentional orienting, its influence on attentional disengagement remains unclear. Given that memories can rapidly optimize perceptual processing, an effect that is comparable to the effects of emotional stimuli, we hypothesize that disengagement from previously seen stimuli is enhanced. However, since the underlying neural mechanisms likely differ from these observed for emotional stimuli (Hutchinson et al., 2009; Hutchinson and Turk-Browne, 2012), we expect that memory, compared to stimulus emotionality, has a more pronounced effect when attentional mechanisms become synchronized with other networks, such as memory networks (e.g. at the time of the N400f; Kutas and Federmeier, 2011).

In addition to characteristics of the attended stimuli, being in a stressful state promotes the prioritized processing of emotional stimuli. Stress is known to induce changes in cognition, including altered learning and memory processes (Lupien et al., 2009; Joels et al., 2011; Schwabe et al., 2012; Wirz et al., 2018), as well as impaired higher cognitive functions, including cognitive inhibition, working memory and cognitive flexibility (Arnsten, 2009, 2015). Accordingly, stress has been shown to disrupt top-down guided attentional control (Liston et al., 2009; Sanger et al., 2014). In contrast, attention toward and processing of emotional stimuli is thought to be facilitated under stress, which is directly linked to the preferential recruitment of the salience network, a network that includes the amygdala and the ventral attention network (Hermans et al., 2011, 2014). Stress was shown to amplify sensory processing of emotional faces in early visual cortex and face-sensitive brain regions (van Marle et al., 2009). In addition, stress was associated with an extended period of heightened attentional vigilance (van Marle et al., 2010) and was shown to facilitate attention to rapidly presented stimuli (Schwabe and Wolf, 2010). In line with these findings, an EEG study revealed stress-induced increases in the late positive potential (LPP) in response to emotional pictures (Weymar et al., 2012). Because previous research supports the notion that the LPP reflects more elaborate perceptual processing of motivationally salient stimuli (Cuthbert et al., 2000), these results suggest greater motivational attention allocation toward emotional stimuli under stress. Previous studies also revealed a positive association between the magnitude of the LPP in response to negative pictures and later memory performance (Palomba et al., 1997; Dolcos and Cabeza, 2002; Weymar et al., 2012). The LPP may therefore also be involved in retrieving information from memory, thereby influencing subsequent motivational attention

processes. Similar to the effects of stimulus emotionality and memory, it is currently not known how stress influences attentional disengagement. Given that stress promotes attentional vigilance (Hermans et al., 2014), we hypothesize that attentional disengagement is facilitated in response to stress.

The primary goal of the present experiment was to investigate the influence of prior exposure to (and thus memory for) emotional and neutral stimuli on attentional disengagement and how this disengagement may be modulated by acute stress. For this purpose, participants were asked to memorize negative (angry and fearful) and neutral facial expressions. After being exposed to a control condition or an experimental stressor, participants performed an attention task that probed disengagement from the previously learned compared to new facial expressions. Due to its excellent temporal resolution, EEG is ideally suited to investigate temporal differences in the influence of emotionality and prior exposure on disengagement and is a highly valuable addition to reaction time (RT) data. Therefore, EEG data were recorded while participants performed the attention task. Since the pupillary response is controlled by the locus coeruleus-noradrenaline system, which is critical for attentional control processes and reflects attentional effort (Kahneman, 1973; Gilzenrat et al., 2010; Goldinger and Papesh, 2012), we additionally measured pupil dilation. Although this study focused primarily on attentional disengagement, we were also interested in the effects of stress, stimulus emotionality and prior exposure on early visual processing.

Since emotional stimuli and stress activate regions of the salience network, which promotes attentional vigilance, we expect enhanced attentional orienting toward and processing of emotional stimuli, especially under stress. Due to this enhanced processing, we further expect more efficient disengagement from emotional stimuli, in particular after participants experienced a stressful event. Similar to emotional stimuli, processing of familiar stimuli is prioritized and expected to facilitate attentional disengagement. In contrast to the effects of stress and stimulus emotionality, we expect the neural effects underlying enhanced disengagement from familiar stimuli to be most prominent when attention networks synchronize with memory networks (N400f).

## 2. Materials and methods

### 2.1. Participants and experimental design

A total of 74 healthy, young, normal-weight Caucasian volunteers from European ancestry participated in this experiment (mean age = 24.62 years, SD = 3.28 years; mean body-mass index [BMI] = 22.41 kg/m<sup>2</sup>, SD = 1.92). Exclusion criteria were assessed in a standardized interview and included medication or drug intake and any past or current neurological or psychiatric disorders. To control for factors influencing the responsivity of the hypothalamus-pituitary-adrenal (HPA) axis to stress as well as the glucocorticoid metabolism, smokers and participants with a BMI < 18 kg/m<sup>2</sup> or > 25 kg/m<sup>2</sup>, as well as women taking hormonal contraceptives, were excluded and women were only tested outside their menstrual cycle phase (Kirschbaum et al., 1999; Rohleder and Kirschbaum, 2006; Rutters et al., 2010; Herbison et al., 2016). Participants gave written informed consent and received a moderate monetary compensation of 35 € for their participation. The study was approved by the ethical review board of the University of Hamburg and was performed in accordance with the Declaration of Helsinki.

In order to examine the influence of memory and emotionality of facial stimuli on attention and its modulation by stress, we used a 2 × 2 mixed design with the between-subjects factor treatment (control vs. stress) and the within-subject factors prior exposure (old vs. new face) and emotionality (negative vs. neutral face). Participants were randomly assigned to the stress or control condition and all testing took place in the afternoon in order to control for the diurnal rhythm of cortisol. Ten

participants had to be excluded from the analyses because of poor performance ( $N = 3$ ; one participant with 58% false alarms and two participants with 43% and 53% misses, respectively, in the recognition task) or too much noise in the EEG data ( $N = 7$ ), leaving a total of 64 participants for the analyses (control group: 15 men, 16 women; stress group: 18 men, 15 women).

## 2.2. Stress and control manipulation

In the stress condition, participants underwent the Socially Evaluated Cold Pressor Test (SECPT; Schwabe et al., 2008a), a commonly used laboratory stressor that reliably leads to increases in subjective stress levels, as well as autonomic nervous system and HPA axis activity (Schwabe and Schachinger, 2018). During the SECPT, participants were asked to immerse their non-dominant hand for 3 min into ice water ( $0-2^{\circ}$ ), while being videotaped and evaluated by a non-reinforcing experimenter. In the control condition, the water was lukewarm ( $35-37^{\circ}\text{C}$ ) and participants were neither videotaped nor evaluated.

To assess the effectiveness of the stress induction, subjective and physiological stress measures were taken at several time points throughout the experiment. Subjective changes in mood were evaluated by means of a German mood questionnaire (MDBF; subscales: depressed vs. elevated, restless vs. calm, sleepy vs. awake; high scores indicate elevated mood, calmness and wakefulness; Steyer et al., 1994) and a questionnaire in which participants rated how difficult, unpleasant, stressful and painful they had experienced the SECPT or control manipulation on a scale from 0 ('not at all') to 100 ('very much'). Blood pressure and pulse were measured using a Dinamap system (Critikon, Tampa, USA) before ( $-45$  min,  $-20$  min), during (0 min) and after ( $+15$  min,  $+30$  min,  $+45$  min,  $+60$  min,  $+75$  min,  $+90$  min) the experimental manipulation. Furthermore, saliva samples were collected before ( $-45$  min,  $-20$  min) and after ( $+15$  min,  $+30$  min,  $+45$  min,  $+60$  min,  $+75$  min,  $+90$  min) the stress or control manipulation using Salivette® collection devices (Sarstedt, Nümbrecht, Germany). Saliva samples were stored at  $-18^{\circ}\text{C}$  until the free fraction of cortisol was determined using a commercially available luminescence immunoassay (IBL, Hamburg, Germany).

## 2.3. Experimental tasks

### 2.3.1. Stimulus material

A total of 240 stimuli of Caucasian faces with negative and neutral expressions were taken from the Chicago Face Database (CFD; Ma et al., 2015), the Radboud Face Database (RaFD; Langner et al., 2010) and the Karolinska Directed Emotional Faces database (KDEF; Lundqvist et al., 1998). Face stimuli were counter-balanced for sex and negative facial expressions consisted of an equal number of fearful and angry faces, since these show similar valence and arousal ratings and are known to elicit similar attentional biases (Vuilleumier, 2002; Mogg et al., 2007). Importantly, only one expression from each of the 200 faces was used. In addition, we only selected faces depicted from the front and that had no facial accessories or hair, which may obscure the internal features of the face. Face stimuli were scaled uniformly and aligned with roughly the same position of the eyes and nose. At the beginning of the experiment, it was randomly decided which negative and neutral facial expression was used for the face memorization, recognition and line orientation tasks. In all tasks, facial expressions were presented in greyscale and edited in Matlab (version R2015a, MathWorks, Natick, USA) to achieve the same average luminance and presented in the middle of the screen against a grey background that was equiluminant to the average of all stimuli.

### 2.3.2. Face encoding task

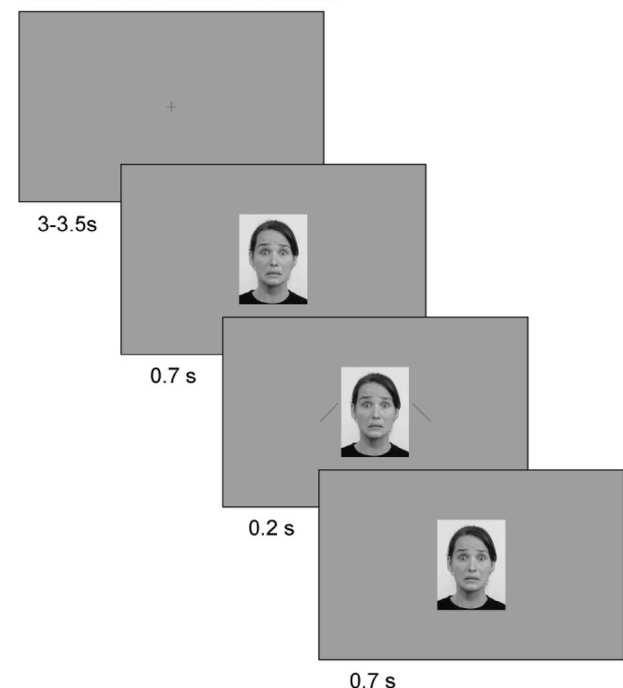
In order to investigate how memory and emotionality of facial expressions may modulate attention, participants first viewed 40 negative and 40 neutral facial expressions and were explicitly instructed to memorize them for a subsequent memory test. Each face stimulus was

shown two times for 4 s each, distributed over two runs. During the first run, participants were asked to rate the valence of the face stimuli ("negative", "rather negative", "rather neutral", or "neutral"), whereas during the second run, participants passively viewed them. As expected, the majority of face stimuli was rated in accordance with their category (92% of negative facial expressions were rated as negative or rather negative, 88% of neutral facial expressions as neutral or rather neutral). Memory for the facial expressions was assessed by means of a forced choice recognition test, in which participants viewed all 80 old, as well as 40 new (20 negative, 20 neutral) faces and indicated by button press whether they thought it was an old or a new face. Memory for the encoded faces was tested in a recognition test 60 min after encoding.

### 2.3.3. Line orientation task

In order to investigate attentional disengagement from emotional and old or new stimuli, participants performed 2 blocks of 80 trials of the line orientation task (LOT, Fig. 1), a frequently employed target-distractor task (Carrette, 2014). In this task, participants viewed either a previously memorized or a new face (in total 80 old and 80 new faces, with 40 negative and 40 neutral faces per category) for 700 ms. Then a line on both sides of the face was added for 200 ms, after which participants viewed only the face again for another 700 ms. In addition, each block contained another 20 trials (10 negative, 10 neutral faces) in which no lines were presented, with the purpose of preventing an overly strong readiness potential in the EEG which may overshadow our ERPs of interest. Between trials there were jittered fixation periods of 3–3.5 s, resulting in a total task duration of 16 min. Participants were instructed to indicate by button press as fast as possible whether the two lines that appeared next to the face had the same or a different orientation. They were also asked to look at the fixation cross between trials and to keep their eyes fixated during stimulus presentation. RT was measured as a behavioral index of exogenous attention to the distracting faces, showing the extent of disruption in the ongoing task. Matlab and the

## Line orientation task



**Fig. 1.** Line orientation task (LOT). Participants were presented with a neutral or negative facial expression that had either been presented during an encoding task before ("old") or not ("new"). Two lines appeared next to the face and participants had to indicate as fast as possible whether these lines have the same or a different orientation.

Psychophysics Toolbox (version 3.0.12; Brainard, 1997; Pelli, 1997) were used for stimulus presentation and response recordings. Stimuli were presented on a Dell U2412M 24" screen with a resolution of 1920 × 1200 px and a refresh rate of 60 Hz. Participants were seated 60 cm from the screen, the facial stimuli were 567 × 425 px large (visual angle of 14.44 × 10.95°) and the lines appeared with a distance of 19 px from the face tilted by 45° (113 × 6.99 px large, visual angle of 3.82 × 0.17°).

## 2.4. Experimental procedure

After participants had given written informed consent, they performed the face encoding task. Next, the EEG and eye tracker recordings were prepared and participants read the instructions for the LOT. Sixty minutes after the face encoding task, memory for the encoded faces was assessed by means of a forced choice recognition test, in which participants had to indicate for each face stimulus whether it had been presented before or not. Participants then underwent the stress or control manipulation. Approximately 20 min after the onset of the stress or control manipulation, participants performed the LOT.

## 2.5. Behavioral and physiological data analyses

Physiological and subjective stress parameters, as well as picture ratings and recognition performance were analyzed using mixed-design analyses of variance (ANOVAs) with treatment (stress vs. control) as between-subjects factor and stimulus emotionality (negative vs. neutral) as within-subject factor. RT data of the LOT were analyzed with prior exposure to the faces (old vs. new) as an additional within-subject factor. Our memory analyses focused on hits and false alarms and we additionally calculated the sensitivity index  $d'$ , using hits and false alarms according to signal detection theory (Wickens, 2002), because this measure corrects for individual response biases. Differences in memory performance for negative and neutral faces were investigated by means of paired-samples  $t$ -tests.

All statistical analyses were performed using SPSS Statistics software (version 22; IBM, USA). All reported  $p$ -values are two-tailed and either Cohen's  $d$  or partial eta squared are reported as indicators of the effect size. In case of violation of the sphericity assumption, Greenhouse-Geisser correction was applied. For all analyses of our behavioral and physiological data, statistical significance was defined by an alpha of  $p < .05$  and a large effect size (Cohen's  $d \geq 0.6$ , partial eta squared  $\geq 0.06$ ). Effects at trend level were defined by  $p < .10$  and a medium effect size (Cohen's  $d \geq 0.4$ , partial eta squared  $\geq 0.05$ ).

## 2.6. EEG acquisition and analyses

EEG was recorded from 64 active electrodes arranged according to the international 10–20 system. Four facial electrodes recorded electrooculograms (EOGs) generated by blinks and eye movements. A Biosemi Active-Two amplifier system was used with a sampling rate of 2048 Hz (Biosemi, Amsterdam, The Netherlands). Common mode sense and driven right leg electrodes served as recording reference and ground, respectively. EEG data were preprocessed offline using the Brain Vision Analyzer software (Brain Products, Gilching, Germany). After the EEG signal was downsampled to 512 Hz, the data were high-pass filtered at 0.01 Hz. To remove artifacts from electrical lines, a 50 Hz notch filter was applied. We then visually inspected the EEG data to discard any extreme artifacts, e.g. caused by movement. Bad channels were replaced by means of topographic interpolation. Blinks and eye movements were removed with the method developed by Gratton et al. (1983). In case ocular artifacts were not satisfactorily removed, an independent component based approach was used instead. EEG data were then re-referenced to the average of all electrodes and segmented into epochs from –200 to 1.600 ms with respect to face onset. Subsequently, epochs were baseline corrected relative to the 200 ms preceding the face stimulus. Trials were rejected if there was a voltage step higher than 50

$\mu\text{V}$  between sample points, or a voltage difference of more than 100  $\mu\text{V}$  or a signal lower than 0.1  $\mu\text{V}$  within a trial was detected. Trials for each stimulus combination (old negative, old neutral, new negative, new neutral) were then averaged.

Event-related potentials (ERPs) are highly useful to investigate distinct processing stages. Since our main goal was to investigate disengagement, we were particularly interested in attention-related ERPs in response to the presentation of the lines next to the face stimulus. Specifically, we were interested in the N2pc, an ERP component which is known to capture attentional shifting and which represents the time course of attentional orienting (Eimer, 1996; Brosch et al., 2011; Luck, 2012). The N2pc was calculated as the mean amplitude in the time window between 200 and 400 ms post line onset at parietal electrodes (P9, P10), where the N2pc was most pronounced. Another ERP component of interest was the N400f, which is associated with face recognition and that arises at frontal electrode sites at a time when exogenous attention becomes synchronized with a broader and multimodal network (Kutas and Federmeier, 2011). The N400f was calculated as the mean amplitude in the time window between 300 and 500 ms post line onset at fronto-central electrodes (Fz, FCz, F1, F2, FC1, FC2). Another highly relevant ERP component is the LPP, which reflects sustained endogenous attention and is known to increase during processing of emotional stimuli (MacNamara and Hajcak, 2009; Weinberg and Hajcak, 2011; Carretie et al., 2013). The LPP was calculated as the mean amplitude in the time window between 400 and 900 ms post line onset at centro-parietal electrodes (Pz, CPz, P1, P2, CP1, CP2).

Since the processing of emotional stimuli – especially under stress – and the processing of information stored in memory is prioritized, these factors likely influence the time it takes for distinct attentional processing stages to be initiated. In order to investigate the timing of distinct processing stages and when attention may differentiate between our stimulus conditions and experimental groups, it is crucial to investigate onset latencies of our ERPs of interest. For this purpose, we used a jackknife approach and measured fractional area latency, a combination which has been shown to yield the best results when measuring and statistically comparing ERP latencies (Kiesel et al., 2008). Due to the jackknife approach, the signal-to noise ratio is much higher, which is particularly important for complex factorial designs such as the present, in which the number of trials is naturally restricted (e.g. participants can only memorize a certain number of faces). While this approach increases statistical power, it has also been shown to yield appropriate Type I error rates (Ulrich and Miller, 2001). Since onset latency measures are easily distorted by high-frequency noise, a low-pass filter with a half-amplitude cutoff of 10 Hz and a slope of 24 dB/octave was applied to our averaged EEG data (Luck, 2014). As recommended by Ulrich and Miller (2001), we calculated the grand averages for each stimulus combination (old negative, old neutral, new negative, new neutral), separately for the stress and control groups, each time omitting one participant from the respective group. The jackknifed averages were then imported into ERPLAB (version 7.0.0; Lopez-Calderon and Luck, 2014) as part of the Matlab-based EEGLAB toolbox (version 14.1.2; Delorme and Makeig, 2004), where we then calculated the 50% area latency, the most reliable fraction for measuring area latency (Luck, 2014). Estimates of the latencies of the individual participants were then retrieved as described by Smulders (2010). The advantage of this approach is that no additional adjustments are required when computing the statistical tests.

Since we were also interested in the neural correlates of facial processing, we performed explorative analyses of ERP components in response to the faces. We were particularly interested in early visual processing components, namely the P1 and the face-sensitive N170, which have been associated with automatic attention and that have been shown to increase during processing of emotional stimuli (Carretie, 2014; Hinojosa et al., 2015). The P1 was calculated as the mean amplitude in the time window between 50 and 120 ms post face onset at occipito-parietal electrodes (O1, O2, PO7, PO8), the N170 as the mean



amplitude in the time window between 120 and 200 ms post face onset at parietal electrodes (P9, P10). In addition, we investigated the N400f (mean amplitude in the time window between 300 and 500 ms post face onset at fronto-central electrodes [Fz, FCz, F1, F2, FC1, FC2]), which has received increasing attention with respect to facial recognition (Kutas and Federmeier, 2011).

For all statistical analyses, mixed-design ANOVAs with treatment (stress vs. control) as between-subjects factor and stimulus emotionality (negative vs. neutral), prior exposure (old vs. new) and electrode site as within-subject factors were used to investigate modulatory effects by stimulus condition and/or experimental group.

## 2.7. Eye tracking acquisition and analyses

An EyeLink 1000 Plus (SR Research, Ottawa, Canada) eye tracker with desktop mount was used to monitor the pupil size of the right eye and to ensure that participants' gaze remained fixated on the middle of the screen during the LOT. To reduce EEG noise and to guarantee a constant distance between the participants' eyes and the screen, a chin rest was used. All eye tracker operations were integrated and executed in Matlab and data were acquired with a sampling rate of 1000 Hz. Before the LOT and between the two blocks, the eye tracker was calibrated using a 9-point calibration and validation procedure. Pupil data were preprocessed as described by Urai et al. (2017). Missing data detected by the EyeLink software (version 5.12) were linearly interpolated. Through deconvolution, effects of blinks and saccades on the pupil response were estimated and removed using linear regression. The residual pupil time series were z-scored per run. Trials were then epoched and baseline-corrected by subtracting the mean pupil size in the 2 s before stimulus onset. Pupil responses were defined as the mean pupil size during 1–3 s post face onset, a time window which takes into account the delay of the pupil response (de Gee et al., 2014). A mixed-design ANOVA with treatment (stress vs. control) as between-subjects factor and stimulus emotionality (negative vs. neutral) and prior exposure (old vs. new) as within-subject factors was used to investigate stimulus effects on pupil dilation.

## 3. Results

### 3.1. Memory performance

Participants performed very well on the forced-choice recognition test 60 min after picture encoding and recognized on average  $90 \pm 7\%$  of all facial stimuli. The sensitivity index  $d'$  was larger for neutral compared to negative faces (Table 1;  $t_{(1, 63)} = 5.006$ ,  $p < .001$ , Cohens  $d = 0.626$ ), owing to a significantly larger false alarm rate for negative (mean = 25, SD = 14) compared to neutral faces (mean = 17, SD = 13;  $t_{(1, 63)} = 5.131$ ,  $p < .001$ , Cohens  $d = 0.641$ ), likely because the enhanced subjective feeling of recollection for negative facial expression impedes memory accuracy (Sharot et al., 2004). Although participants had not been exposed to the control or stress manipulation yet, false alarm rates for neutral faces tended to be larger for participants who later underwent the stress manipulation ( $t_{(1, 62)} = 1.992$ ,  $p = .051$ ,

**Table 1**  
Memory performance in the recognition test 60 min after encoding.

|              | Control       |               | Stress        |                              |
|--------------|---------------|---------------|---------------|------------------------------|
|              | Neutral       | Negative      | Neutral       | Negative                     |
| Hits         | 36.097 ± .585 | 35.968 ± .535 | 35.939 ± .567 | 36.000 ± .519                |
| False alarms | 2.774 ± .442  | 4.484 ± .504  | 4.000 ± .428  | 5.636 ± .488*** <sup>#</sup> |

Data represent mean percentages ± SEM.

Emotionality (Neutral vs. Negative) \*\*\* $P < .001$ .

Treatment (Control vs. Stress) <sup>#</sup> $P = .051$ .

Cohens  $d = 0.499$ ).

### 3.2. Subjective, autonomic and endocrine stress response

The successful stress induction by the SECPT was verified by changes in subjective mood, blood pressure and salivary cortisol. Compared to the control procedure, the SECPT was rated as significantly more difficult, unpleasant, painful, and stressful (all  $F_{(1, 62)} \geq 47.657$ ,  $p < .001$ ,  $\eta_p^2 \geq 0.435$ ). Participants' mood decreased and they became increasingly restless after the stressor compared to the control condition (time × treatment: both  $F_{(4, 57)} \geq 2.521$ ,  $p \leq .051$ ,  $\eta_p^2 \geq 0.150$ ). Independent of treatment, participants became increasingly tired during the experiment (time:  $F_{(4, 57)} = 25.663$ ,  $p < .001$ ,  $\eta_p^2 = 0.643$ ).

In response to the SECPT, compared to the control procedure, activity of the autonomic nervous system rapidly increased, as indicated by a significant rise in systolic and diastolic blood pressure, and pulse (Fig. 2A–C; time × treatment: all  $F_{(8, 54)} \geq 6.167$ ,  $p < .001$ ,  $\eta_p^2 \geq 0.477$ ). Finally, exposure to the SECPT, as opposed to the control procedure, led to significant increases in salivary cortisol concentrations, providing evidence for a stress-induced activation of the HPA-axis (time × treatment:  $F_{(7, 56)} = 5.787$ ,  $p < .001$ ,  $\eta_p^2 = 0.420$ ). As shown in Fig. 2D, peak cortisol concentrations were reached approximately 25 min after the SECPT, when participants performed the LOT.

### 3.3. Faster attentional disengagement from old and negative stimuli

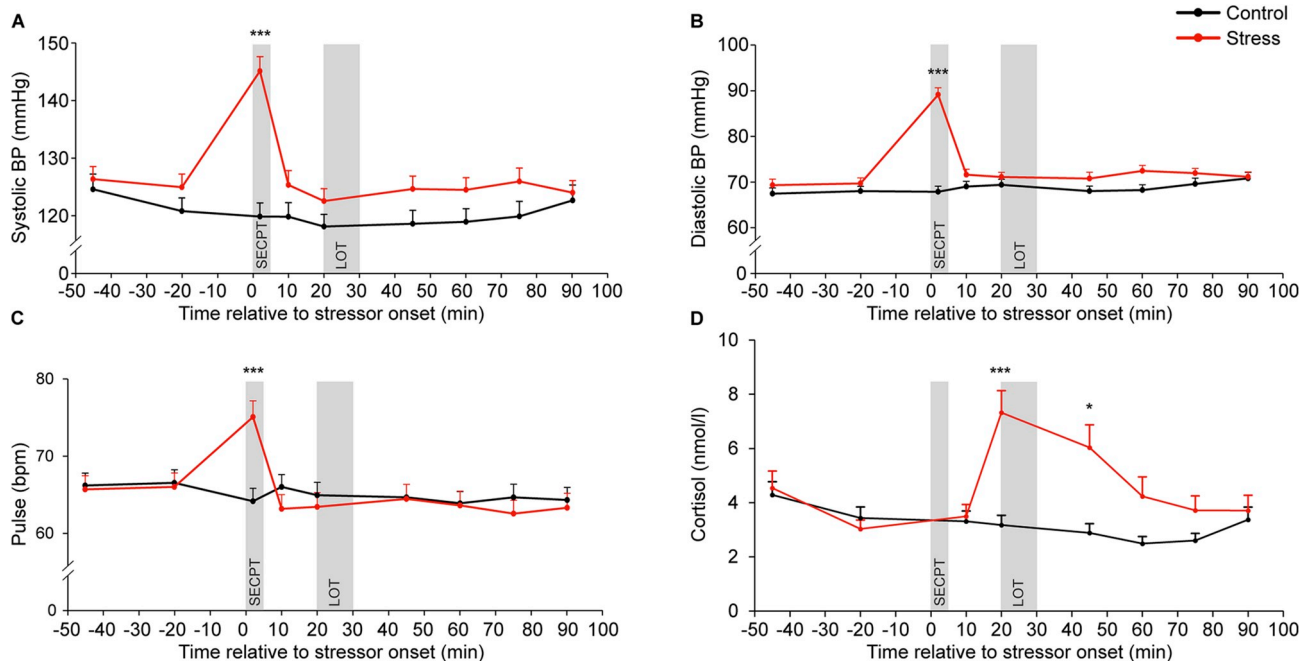
#### 3.3.1. Reaction times

In line with an emotional modulation of attention, RTs in the LOT significantly differed depending on the emotionality of the facial expressions (Table 2;  $F_{(1, 62)} = 332.703$ ,  $p < .001$ ,  $\eta_p^2 = 0.843$ ). Specifically, when participants had to respond to lines which appeared next to negative facial expressions, RTs – indicators for the disengagement from these stimuli – were about 40 ms faster than when the lines appeared next to neutral facial expressions. RTs also tended to be faster when lines appeared next to faces that had been presented before (Table 2;  $F_{(1, 62)} = 3.940$ ,  $p = .052$ ,  $\eta_p^2 = 0.060$ ). This finding suggests faster disengagement from old faces and is in accordance with more efficient and effortless processing of previously seen stimuli (Natu and O'Toole, 2011). When controlling for memory performance by entering  $d'$  as a covariate, this effect was no longer significant (time:  $F_{(1, 61)} = 0.041$ ,  $p = .840$ ,  $\eta_p^2 = 0.001$ ; time × memory:  $F_{(1, 61)} = 0.490$ ,  $p = .486$ ,  $\eta_p^2 = 0.008$ ; memory:  $F_{(1, 61)} < 0.001$ ,  $p = .997$ ,  $\eta_p^2 < 0.001$ ), suggesting that this effect was indeed driven by the memory for the previously encoded stimuli. Importantly, however, the effect of emotionality on RT was unaffected by this covariate and remained significant ( $F_{(1, 61)} = 9.888$ ,  $p = .003$ ,  $\eta_p^2 = 0.139$ ; time × memory:  $F_{(1, 61)} = 1.744$ ,  $p = .192$ ,  $\eta_p^2 = 0.028$ ), suggesting that stimulus emotionality and memory had separable effects on attentional disengagement.

Overall, stress tended to accelerate RTs (Table 2;  $F_{(1, 62)} = 3.625$ ,  $p = .062$ ,  $\eta_p^2 = 0.055$ ), irrespective of whether the presented faces were negative or neutral, old or new (all  $F_{(1, 62)} \leq 1.244$ , all  $p \geq .269$ , all  $\eta_p^2 \leq 0.020$ ). This finding is in line with stress-induced improvements in selective attention and increases in processing efficiency (Schwabe and Wolf, 2010; Cornelisse et al., 2011). Although stress-induced cortisol increases did not correlate with RT ( $r = 0.021$ ,  $p = .907$ ), correlations between RT and autonomic stress parameters indicated negative associations for systolic and diastolic blood pressure, measured as the area under the curve with respect to the ground (Pruessner et al., 2003; RT and systolic blood pressure:  $r = -0.434$ ,  $p = .013$ ; RT and diastolic blood pressure:  $r = -0.455$ ,  $p = .009$ ; Fig. 3). These negative correlations suggest that stronger autonomic stress responses were associated with faster responses in the LOT.

#### 3.3.2. Event-related potential amplitudes and onset latencies

In order to gain insights into distinct attentional processing stages and to investigate the neural correlates of our RT findings, we measured



**Fig. 2.** Physiological response to the stress and control manipulation. Compared to the control manipulation, exposure to the Socially Evaluated Cold Pressor Test (SECPT) led to significant increases in (A) systolic blood pressure (BP), (B) diastolic BP, (C) pulse, and (D) salivary cortisol concentrations. LOT line orientation task \*\*\* $p < .001$  \*  $p < .05$ , error bars represent SEM.

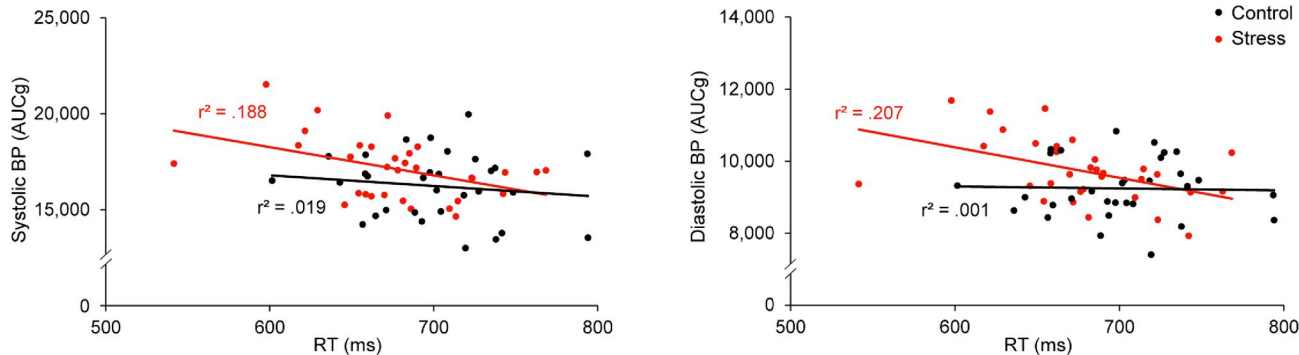
**Table 2**  
Reaction times in the line orientation task.

|     | Control         |                 | Stress          |                           |
|-----|-----------------|-----------------|-----------------|---------------------------|
|     | Neutral         | Negative        | Neutral         | Negative                  |
| New | 722.319 ± 8.883 | 685.408 ± 8.843 | 697.422 ± 8.609 | 662.430 ± 8.571           |
| Old | 718.249 ± 8.549 | 676.785 ± 8.010 | 699.708 ± 8.286 | 656.583 ± 7.764***<br># + |

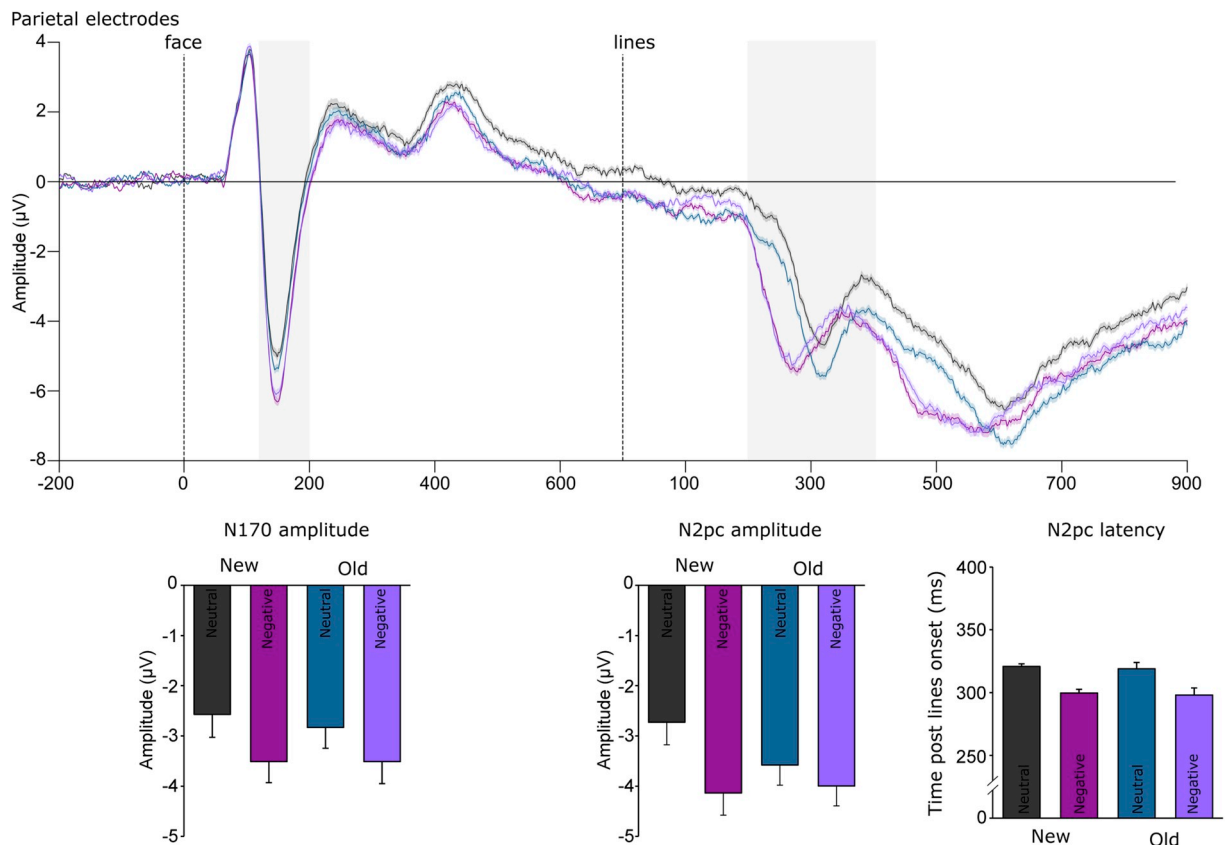
Data represent mean percentages ± SEM.  
Emotionality (Neutral vs. Negative) \*\*\* $p < .001$ .  
Prior exposure (New vs. Old) #  $P = .052$ .  
Treatment (Stress vs. Control)+ $P = .062$ .

the mean amplitude and fractional onset latency of relevant ERP components during the LOT and investigated how these neural measures were affected by stimulus emotionality, memory, and stress. In line with the importance of attentional shifting in disengagement and a faster RT in response to lines presented next to negative faces, the amplitude of the N2pc was significantly enhanced when lines appeared next to

negative compared to neutral faces ( $F_{(1, 62)} = 19.767, p < .001, \eta_p^2 = 0.242$ ). In addition, an emotionality  $\times$  prior exposure interaction ( $F_{(1, 62)} = 5.924, p = .018, \eta_p^2 = 0.087$ ) suggested that this influence of face emotionality was significant for new ( $F_{(1, 62)} = 24.243, p < .001, \eta_p^2 = 0.281$ ) but not for old faces ( $F_{(1, 62)} = 2.048, p = .157, \eta_p^2 = 0.032$ ; Fig. 4), possibly because attentional disengagement is already more efficient for both negative and neutral faces when they are old, as suggested by our RT data. Stress, however, had no influence on the N2pc amplitude, neither alone, nor in interaction with stimulus emotionality or prior exposure to the faces (all  $F_{(1, 62)} \leq 2.258$ , all  $p \geq .138$ , all  $\eta_p^2 \leq 0.035$ ). In accordance with the importance of ERP onset latency as a means to measure when attention differentiates between stimulus conditions, our data revealed significant differences in fractional onset latencies. Specifically, 50% area latency data for the N2pc showed that the N2pc was initiated significantly earlier when attention was disengaged from negative compared to neutral faces ( $F_{(1, 62)} = 34.224, p < .001, \eta_p^2 = 0.356$ ; Fig. 4). Whereas no differences in the amplitudes of the N400f or LPP were observed (all  $F_{(1, 62)} \leq 2.048, p \geq .157, \eta_p^2 \leq 0.032$ ), earlier onset latencies for negative compared to neutral faces were also shown for the N400f ( $F_{(1, 62)} = 97.199, p < .001, \eta_p^2 = 0.611$ ; Fig. 5) and the LPP



**Fig. 3.** Correlation between reaction times (RT) in the line orientation task and blood pressure (BP). Increases in systolic and diastolic BP were negatively correlated with RT, indicating that larger increases in blood pressure were associated with faster behavioral responses.



**Fig. 4.** Electroencephalographic (EEG) data at parietal electrodes. Amplitude of the N2pc was significantly enhanced when participants disengaged from negative compared to neutral facial expressions, especially when these were old. In addition, onset latency of the N2pc was significantly earlier when participants disengaged from negative compared to neutral faces. Amplitude of the face-sensitive N170 was larger for negative vs. neutral facial expressions. Shaded error bars represent SEM.

( $F_{(1, 62)} = 27.113, p < .001, \eta_p^2 = 0.304$ ; Fig. 5). This suggests that faster disengagement from negative facial expressions also facilitates later attentional processes that are presumably under top-down control. In addition, onset latency of the N400f was significantly earlier for old compared to new faces ( $F_{(1, 62)} = 4.430, p = .039, \eta_p^2 = 0.067$ ; Fig. 5), likely because attentional shifting is facilitated when faces are familiar, an effect that is again in line with our RT findings. Exposure to stress had no influence on these ERP latencies (all  $F_{(1, 62)} \leq 2.890$ , all  $p \geq .094$ , all  $\eta_p^2 \leq 0.045$ ), although an emotionality  $\times$  treatment interaction at trend level ( $F_{(1, 62)} = 3.835, p = .055, \eta_p^2 = 0.058$ ) suggested such an influence for the N400f. However, post-hoc comparisons revealed significantly earlier latencies for negative compared to neutral facial expressions in both the control ( $F_{(1, 30)} = 109.108, p < .001, \eta_p^2 = 0.784$ ) and stress condition ( $F_{(1, 32)} = 23.763, p < .001, \eta_p^2 = 0.426$ ). RT and LPP onset latency were positively correlated, independent of stimulus emotionality (RT and LOT onset latency neutral face:  $r = .304, p = .015$ ; RT and LOT onset latency negative face:  $r = 0.472, p < .001$ ; RT neutral face and LOT onset latency negative face:  $r = 0.419, p = .001$ ; RT negative face and LOT onset latency neutral face:  $r = 0.325, p = .009$ ). Thus, longer RTs were associated with a later onset of the LPP ( $r = 0.419, p = .001$ ; Fig. 6), an ERP component which evolves around the time when participants made their response (mean LPP onset latency = 635 ms, mean RT = 690 ms).

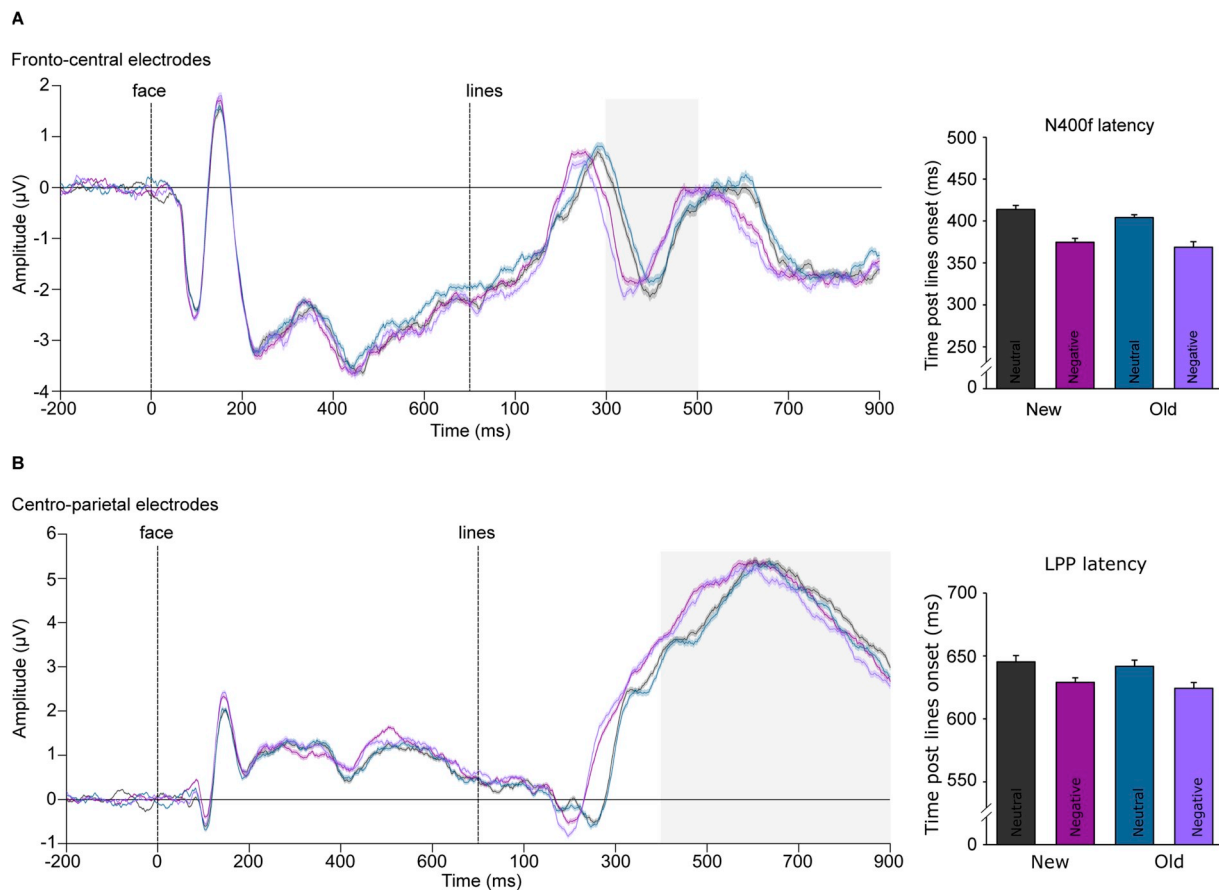
In line with our RT and electrophysiological data, which showed facilitated disengagement from negative faces, pupil dilation was enhanced in response to neutral faces ( $F_{(1, 62)} = 3.962, p = .051, \eta_p^2 = 0.060$ ; Fig. 7), which might suggest enhanced attentional effort that is required to disengage from neutral facial expressions. Stress exposure, in contrast, did neither alone, nor in interaction with stimulus emotionality, influence pupil dilation (all  $F_{(1, 62)} \leq 3.096$ , all  $p \geq .083$ , all  $\eta_p^2 \leq 0.043$ ).

### 3.4. Early visual processing of faces is modulated by stimulus emotionality and stress

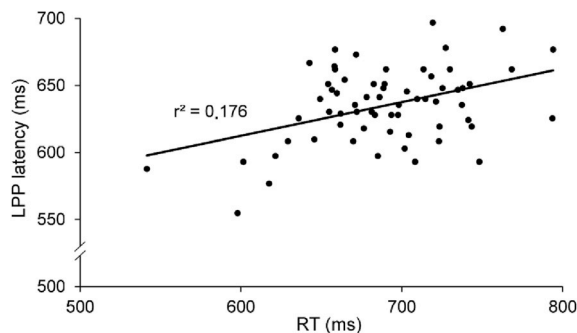
In addition to the influence of stimulus emotionality and stress on attentional disengagement from facial expressions, we were interested in the actual processing of neutral vs. negative faces before the lines appeared. Corroborating research showing rapid responding to emotional faces (Vuilleumier et al., 2001), amplitudes of early ERP components were significantly increased for negative compared to neutral facial expressions. Specifically, this was shown for the P1 ( $F_{(1, 62)} = 4.478, p = .038, \eta_p^2 = 0.067$ ; Fig. 8) and the face-sensitive N170 ERP components ( $F_{(1, 62)} = 45.985, p < .001, \eta_p^2 = 0.426$ ; Fig. 4). This very early modulation supports the notion that detection of facial expression – whether it is negative or neutral – does not depend on the identification of the face (Eimer and Holmes, 2002). Even more interestingly, an emotionality  $\times$  treatment interaction ( $F_{(1, 62)} = 5.641, p = .021, \eta_p^2 = 0.083$ ) showed that an enhanced P1 amplitude for negative vs. neutral faces was only observed in stressed participants ( $F_{(1, 32)} = 9.485, p = .004, \eta_p^2 = 0.229$ ; Fig. 8) but not in the control condition ( $F_{(1, 30)} = 0.036, p = .850, \eta_p^2 = 0.001$ ), suggesting enhanced early visual processing of negative facial expressions under stress. Prior exposure to the faces neither had an effect on early ERP components (P1 and N170: both  $F_{(1, 62)} \leq 0.922, p = .341, \eta_p^2 = 0.015$ ), nor on the N400f component ( $F_{(1, 62)} = 0.832, p = .365, \eta_p^2 = 0.013$ ), which has been associated with facial recognition (Kutas and Federmeier, 2011).

## 4. Discussion

The capacity of our attentional resources is limited and it is therefore crucial to efficiently select which information to attend to and which to ignore. In the present experiment, we investigated how prior exposure to



**Fig. 5.** Electroencephalographic (EEG) data at fronto-central electrodes. Onset latencies of the (A) N400f as well as the (B) LPP were significantly earlier when participants disengaged from negative compared to neutral faces. Shaded error bars represent SEM.



**Fig. 6.** Correlation between reaction time (RT) in the line orientation task and latency of the late positive potential (LPP) at centro-parietal electrodes. A positive correlation indicates that a longer LPP latency is associated with a slower response.

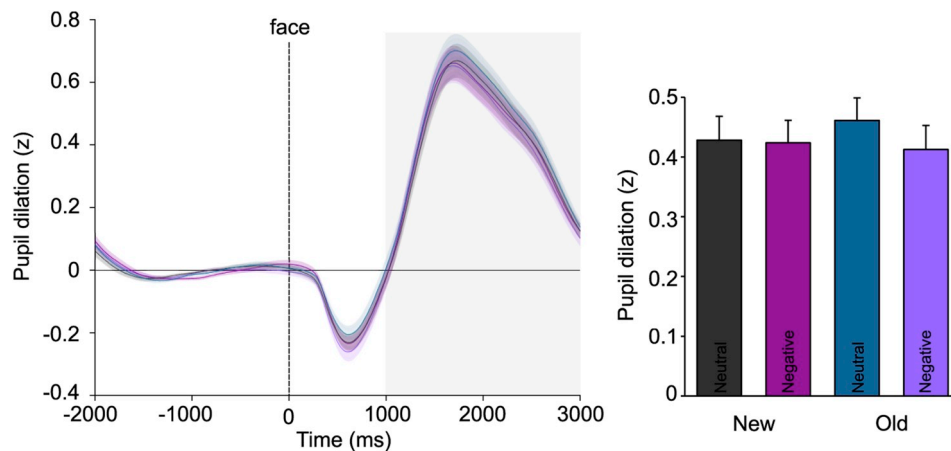
emotional and neutral information affects attentional disengagement, and whether putative emotion and memory effects on attentional disengagement are modulated by acute stress. Our results show facilitated attentional disengagement from negative (vs. neutral) and previously seen (vs. new) stimuli, which may be due to more efficient perceptual processing, allowing faster reorientation toward the task. In addition, stress was associated with faster attentional disengagement and overall enhanced early visual processing of negative stimuli, mechanisms which may be highly relevant under acute threat. These results are in line with research showing that stress as well as memory and stimulus emotionality influence attention toward and processing of visual stimuli (Vuilleumier, 2005; Yiend, 2010; Hutchinson and

Turk-Browne, 2012; Hermans et al., 2014).

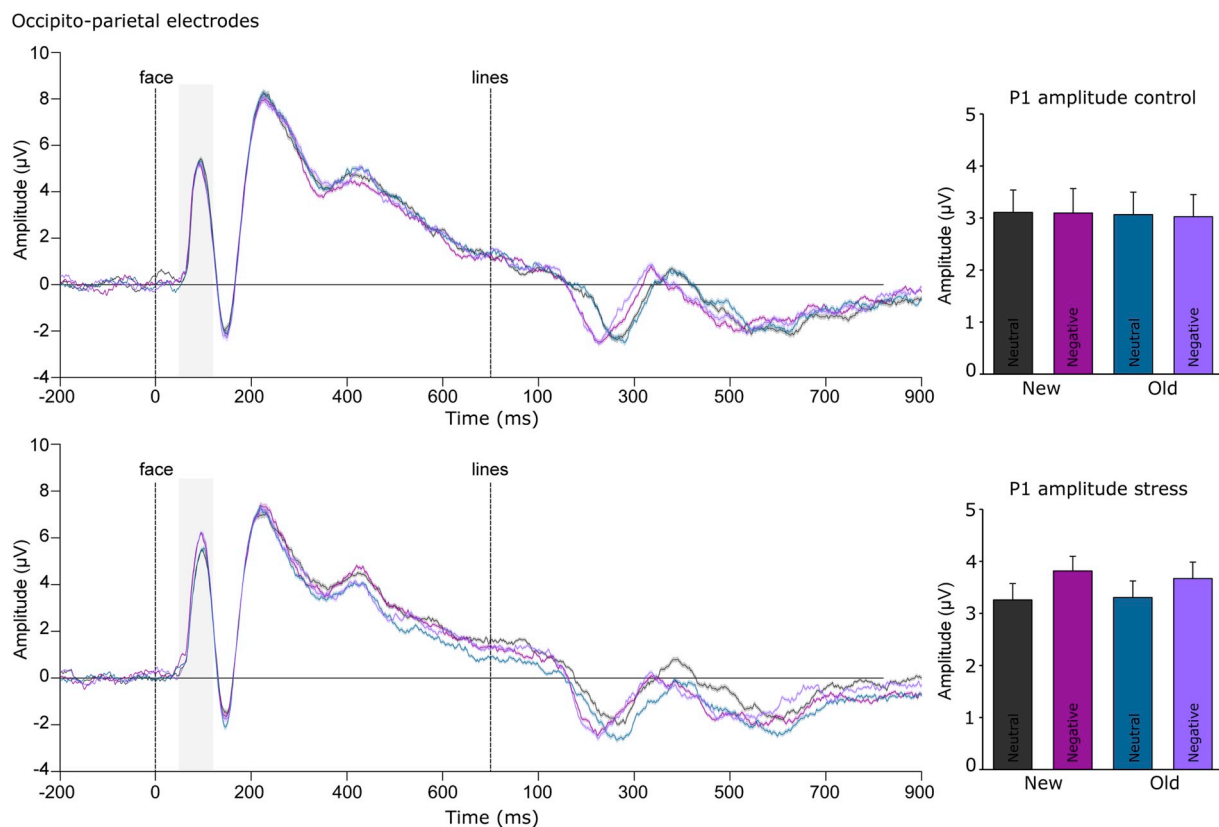
Whereas recent research has made progress regarding the role of memory in attentional orienting (Hutchinson and Turk-Browne, 2012), whether and how prior stimulus exposure may affect attentional disengagement from these stimuli has not yet been investigated. Our behavioral and neural data are the first to suggest that disengagement from facial expressions is facilitated when participants were previously exposed to the faces. RT tended to be faster when participants had to disengage from old faces and our EEG data revealed an earlier onset latency of the N400f. The N400f has been associated with familiarity of faces (Eimer, 2000; Curran and Hancock, 2007) and occurred about 386 ms after the lines appeared next to an old face, approximately 302 ms before a response was made. No effects of prior stimulus exposure were observed for the onset latency of earlier (N2pc) or later (LPP) components, supporting the notion that the N400f is specialized for face familiarity and that this ERP may not only be relevant for orienting toward but also for the disengagement from familiar faces. Interestingly, we did not observe an N400f effect during facial processing (before the lines appeared). This is in line with an earlier study (Caharel et al., 2002), in which faces were only passively viewed. In contrast, N400f effects did occur in experiments that required active evaluation of the faces (e.g. detection of face identification or profession; Bentin and Deouell, 2000; Eimer, 2000). This suggests that an active task may be required for this ERP component to occur and in our experiment in particular it suggests that the N400f may be a relevant indicator of the active disengagement from familiar facial expressions.

The neural mechanisms of memory-guided attention are not clear yet and two different routes have been proposed: an indirect route through which memory systems influence attention networks and a route through which memories directly influence perceptual representations,





**Fig. 7.** Pupil dilation in response to facial expressions. Neutral compared to negative facial expressions led to larger dilation of the pupil, possibly indicating enhanced cognitive effort that is needed for attentional disengagement. Shaded error bars represent SD.



**Fig. 8.** Electroencephalographic (EEG) data at occipito-parietal electrodes. Amplitude of the P1 was enhanced in response to negative vs. neutral facial expressions, especially in stressed participants. Shaded error bars represent SEM.

thereby changing their competition for attention (Hutchinson and Turk-Browne, 2012). It has been shown that memory-guided attention involves interactions between memory-related brain regions such as the hippocampus and a frontoparietal network involved in visual orienting (Summerfield et al., 2006). Another study showed a modulation of long-term memories on preparatory activity in the visual cortex in addition to activations in the hippocampus and a dorsal frontoparietal attention network (Stokes et al., 2012), suggesting that memories may influence both perceptual as well as attentional mechanisms. Although we did not find evidence for an influence of prior exposure to the faces on their perceptual representations (before the lines were presented), we observed an earlier onset of the N400f when participants had to

disengage from old faces, pointing to an interactive communication between memory and attention networks.

In addition to the role of memory in attentional disengagement, we also obtained evidence for facilitated attentional disengagement from negative compared to neutral facial expressions. In addition to faster RTs, we observed enhanced N2pc amplitudes as well as earlier N2pc onset latencies. The N2pc seems to be a valuable marker of early disengagement processes, because of its essential role in rapid attentional shifting (Brosch et al., 2011; Luck, 2012). In addition, both attentional disengagement and the N2pc have been argued to involve top-down as well as bottom-up processes (Eimer and Kiss, 2010). Therefore, these results suggest faster attentional disengagement from

negative compared to neutral stimuli. Interestingly, the emotion-induced increase in N2pc amplitude was only observed when the presented facial expression was unknown to participants. In contrast, both negative and neutral facial expressions led to comparable N2pc amplitudes when the face had been presented before. This early interaction between stimulus emotionality and prior exposure was neither observed for the onset latency of the N2pc, nor in our RT data or for later ERP components (N400f, LPP). Similar to the interpretation of stronger activations in fMRI experiments (Poldrack, 2015), an enhanced amplitude of the N2pc component may reflect either more or less cognitive effort that is required for attentional disengagement. Thus, an augmented N2pc amplitude for new faces with a neutral expression likely reflects more cognitive effort that is required for attentional disengagement. This is further supported by our pupillometry data, which showed larger pupil dilation in response to neutral compared to negative facial expressions, an indication for more effortful attentional control that is required to disengage from these faces (van der Wel and van Steenbergen, 2018). Although the disengagement from both negative and old facial expressions appears to require less effort, the time course of the modulatory influences of emotion and memory seem to differ. Attentional disengagement was modulated by emotionality as early as 278 ms (N2pc) after stimulus presentation, but its modulation by prior exposure did not occur before around 372 ms (N400f) post stimulus onset. These temporal differences of around 100 ms seem very plausible, because although attentional orienting effects seem generally similar for salient stimuli and stimuli retrieved from episodic memory, different brain regions are involved in these modulatory influences (Hutchinson et al., 2009). The additional time is likely required for attention and memory networks to synchronize (Kutas and Federmeier, 2011).

An earlier onset latency of the LPP when participants had to disengage from negative faces further supports the enhanced efficiency of processing negative compared to neutral faces at a later, more cognitive stage of processing. It is also in line with the notion that the LPP reflects sustained motivational attention allocation (Cuthbert et al., 2000), since the participant's goal is to redirect attention toward the task, which they manage to do more efficiently when they have to disengage from a negative face, as is shown in our RT data. Importantly, this is supported by a positive association between RT and the LPP onset latency. Since processing of negative faces seems to be more efficient, participants may be able to more effectively reallocate their attention toward the task based on their motivation to make a quick response. Since the LPP reflects a long-lasting and highly integrated cascade of different cognitive processes, we cannot disentangle the exact cognitive process that is influenced by the emotionality of the face. However, our findings do suggest more efficient, likely motivationally driven, sustained attention allocation toward the task when participants had to disengage from negative faces.

Several studies have suggested that only rapid, bottom-up attentional processes are influenced by stimulus emotionality and that top-down inhibition processes take place when these stimuli are not relevant for task goals (Holmes et al., 2006; Eimer and Holmes, 2007; Eimer et al., 2009). We showed here that when participants had some time to explore the faces (700 ms) before the actual task (responding to the orientation of the lines), emotionality of and prior exposure to the faces did influence and actually facilitate attentional disengagement. The majority of studies investigating the effects of emotional distractors on attentional disengagement showed a delay in disengagement that was explained by their enhanced ability to automatically capture attention (Carretie, 2014). Our study suggests that attentional disengagement is facilitated rather than impaired when distractors have a negative valence. One possibility may be that the processing of the lines, which appeared very close to the faces, was actually enhanced. Support for this view comes from a study which showed that discrimination of the orientation of a bar was improved when the bar replaced a fearful compared to a neutral face (Pourtois et al., 2004). The most likely

explanation for these apparent contradictory results, however, concerns differences in the stimulus onset asynchrony (SOA) of the targets and distractors. Specifically, whereas previous studies showed target and distractor stimuli at the same time (visual search tasks; Fox et al., 2002; Carretie et al., 2013) or with a relatively short SOA (Posner cuing task, e. g. 133 ms; Carlson and Reinke, 2014), we used an SOA of 700 ms due to our experimental demands (participants needed time to be able to recollect the old faces). This issue has also directly been addressed in a visual search task (Theeuwes et al., 2000; Theeuwes, 2010). Specifically, the authors argued that when the distractor is presented some time before the search display, top-down control can ensure that attention is directed toward the target and disengagement should not be delayed. They tested different SOAs (from 50 to 300 ms) and their results suggest that the distractor only interfered with target search for the early SOAs (<100 ms). Our data suggest that at even longer SOAs, disengagement may be facilitated. Therefore, whereas emotional stimuli automatically and rapidly capture attention, their fast and efficient processing (Vuilleumier, 2005) can also be beneficial and actually facilitate attentional disengagement.

Evidence for prioritized processing of emotional information was provided by larger P1 and N170 amplitudes in response to negative compared to neutral facial expressions, which is thought to reflect early processing in visual cortices and face processing areas (Carretie et al., 2013). Interestingly, although stress did not interact with stimulus emotionality or prior exposure effects on attentional disengagement, an enhanced P1 amplitude in response to negative facial expressions was only observed in stressed participants. This finding fits very well with research showing increased stress-induced activation of the salience network, including the amygdala, leading to enhanced attentional vigilance (van Marle et al., 2010; Hermans et al., 2011). Interestingly, this reconfiguration of neural networks seemed to depend on noradrenaline, because only beta-adrenergic receptor blockade but not cortisol synthesis inhibition reduced this effect (Hermans et al., 2011). The amygdala receives early visual inputs (LeDoux, 2000) and interacts with attention-related brain regions (Vuilleumier, 2002). Stress and salient emotional stimuli both increase noradrenergic activation of the amygdala, thereby facilitating rapid attention toward and processing of these stimuli (van Stegeren et al., 2005; Hermans et al., 2014). The effect of enhanced early visual processing (P1) in response to stress for negative but not for neutral faces is in line with stress effects on other cognitive domains, such as memory. Specifically, several studies have shown memory-enhancing effects of stress only for emotionally arousing but not for neutral material (Quirarte et al., 1997; Elzinga et al., 2005; Payne et al., 2007; Roozendaal et al., 2007; Schwabe et al., 2008b). Noradrenergic activation may also be a driving force leading to generally faster disengagement in stressed participants; a first hint at this possibility is provided by the negative correlations between RT and systolic as well as diastolic blood pressure increases. This finding is also in line with a study suggesting a stress-induced enhancement of attentional processing in the attentional blink paradigm (Schwabe and Wolf, 2010). Similarly to the present results, stress did also not interact with stimulus emotionality in this study.

To conclude, our results show that memories may not only guide attentional orienting but also facilitate attentional disengagement. Further, we show that emotionally arousing stimuli may aid attentional disengagement, which might be owing to enhanced processing efficiency. Moreover, acute stress facilitated attentional disengagement in general and enhanced the prioritized processing of negative facial expressions. Both rapid attentional orienting toward and efficient disengagement from emotionally salient and previously seen but irrelevant information are highly relevant for survival, in particular during stressful encounters. Deficits in these attentional processes have been linked to several psychiatric disorders and several therapeutic interventions have been developed to modify specifically biases in attentional processes (Hakamata et al., 2010; Browning et al., 2012; Kuckertz et al., 2014; Mogg and Bradley, 2016). Rapid attentional orienting

promotes threat detection, whereas disengagement from irrelevant information aids efficient processing of relevant information. Our study provides first evidence that these processes may be facilitated under acute stress as well as for emotionally arousing and familiar stimuli.

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Both authors report no conflicts of interest.

## CRediT authorship contribution statement

**Lisa Wirz:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing - original draft. **Lars Schwabe:** Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Validation, Writing - review & editing.

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## References

- Arnsten, A.F., 2009. Stress signalling pathways that impair prefrontal cortex structure and function. *Nat. Rev. Neurosci.* 10, 410–422. <https://doi.org/10.1038/nrn2648>.
- Arnsten, A.F., 2015. Stress weakens prefrontal networks: molecular insults to higher cognition. *Nat. Neurosci.* 18, 1376–1385. <https://doi.org/10.1038/nn.4087>.
- Bentin, S., Deouell, L.Y., 2000. Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cogn. Neuropsychol.* 17, 35–55. <https://doi.org/10.1080/026432900380472>.
- Bradley, B.P., Mogg, K., Millar, N., Bonham-Carter, C., Fergusson, E., Jenkins, J., Parr, M., 1997. Attentional biases for emotional faces. *Cognit. Emot.* 11, 25–42. <https://doi.org/10.1080/026999397380014>.
- Brainard, D.H., 1997. The psychophysics toolbox. *Spat. Vis.* 10, 433–436. <https://doi.org/10.1163/156856897X00357>.
- Brosch, T., Pourtois, G., Sander, D., Vuilleumier, P., 2011. Additive effects of emotional, endogenous, and exogenous attention: behavioral and electrophysiological evidence. *Neuropsychologia* 49, 1779–1787. <https://doi.org/10.1016/j.neuropsychologia.2011.02.056>.
- Browning, M., Holmes, E.A., Charles, M., Cowen, P.J., Harmer, C.J., 2012. Using attentional bias modification as a cognitive vaccine against depression. *Biol. Psychiatry* 72, 572–579. <https://doi.org/10.1016/j.biopsych.2012.04.014>.
- Caharel, S., Poiroux, S., Bernard, C., Thibaut, F., Lalonde, R., Rebai, M., 2002. ERPs associated with familiarity and degree of familiarity during face recognition. *Int. J. Neurosci.* 112, 1499–1512. <https://doi.org/10.1080/00207450290158368>.
- Carlson, J.M., Reinke, K.S., 2014. Attending to the fear in your eyes: facilitated orienting and delayed disengagement. *Cognit. Emot.* 28, 1398–1406. <https://doi.org/10.1080/02699931.2014.885410>.
- Carrette, L., 2014. Exogenous (automatic) attention to emotional stimuli: a review. *Cognit. Affect Behav. Neurosci.* 14, 1228–1258. <https://doi.org/10.3758/s13415-014-0270-2>.
- Carrette, L., Hinojosa, J.A., Martin-Loeches, M., Mercado, F., Tapia, M., 2004. Automatic attention to emotional stimuli: neural correlates. *Hum. Brain Mapp.* 22, 290–299. <https://doi.org/10.1002/hbm.20037>.
- Carrette, L., Kessel, D., Carboni, A., Lopez-Martin, S., Albert, J., Tapia, M., Mercado, F., Capilla, A., Hinojosa, J.A., 2013. Exogenous attention to facial vs non-facial emotional visual stimuli. *Soc. Cogn. Affect. Neurosci.* 8, 764–773. <https://doi.org/10.1093/scan/nss068>.
- Cisler, J.M., Koster, E.H., 2010. Mechanisms of attentional biases towards threat in anxiety disorders: an integrative review. *Clin. Psychol. Rev.* 30, 203–216. <https://doi.org/10.1016/j.cpr.2009.11.003>.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215. <https://doi.org/10.1038/nrn755>.
- Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P., Shulman, G.L., 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat. Neurosci.* 3, 292–297. <https://doi.org/10.1038/73009>.
- Cornelisse, S., Joels, M., Smeets, T., 2011. A randomized trial on mineralocorticoid receptor blockade in men: effects on stress responses, selective attention, and memory. *Neuropsychopharmacology* 36, 2720–2728. <https://doi.org/10.1038/npp.2011.162>.
- Curran, T., Hancock, J., 2007. The FN400 indexes familiarity-based recognition of faces. *Neuroimage* 36, 464–471. <https://doi.org/10.1016/j.neuroimage.2006.12.016>.
- Cuthbert, B.N., Schupp, H.T., Bradley, M.M., Birbaumer, N., Lang, P.J., 2000. Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. *Biol. Psychol.* 52, 95–111.
- de Gee, J.W., Knäpen, T., Donner, T.H., 2014. Decision-related pupil dilation reflects upcoming choice and individual bias. *Proc. Natl. Acad. Sci. U. S. A.* 111, E618–E625. <https://doi.org/10.1073/pnas.1317557111>.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134, 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>.
- Disner, S.G., Beevers, C.G., Haigh, E.A., Beck, A.T., 2011. Neural mechanisms of the cognitive model of depression. *Nat. Rev. Neurosci.* 12, 467–477. <https://doi.org/10.1038/nrn3027>.
- Dolcos, F., Cabeza, R., 2002. Event-related potentials of emotional memory: encoding pleasant, unpleasant, and neutral pictures. *Cognit. Affect Behav. Neurosci.* 2, 252–263.
- Eimer, M., 1996. The N2pc component as an indicator of attentional selectivity. *Electroencephalogr. Clin. Neurophysiol.* 99, 225–234. [https://doi.org/10.1016/0013-4694\(96\)95711-9](https://doi.org/10.1016/0013-4694(96)95711-9).
- Eimer, M., 2000. Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clin. Neurophysiol.* 111, 694–705. [https://doi.org/10.1016/S1388-2457\(99\)00285-0](https://doi.org/10.1016/S1388-2457(99)00285-0).
- Eimer, M., Holmes, A., 2002. An ERP study on the time course of emotional face processing. *Neuroreport* 13, 427–431. <https://doi.org/10.1097/00001756-200203250-00013>.
- Eimer, M., Holmes, A., 2007. Event-related brain potential correlates of emotional face processing. *Neuropsychologia* 45, 15–31. <https://doi.org/10.1016/j.neuropsychologia.2006.04.022>.
- Eimer, M., Kiss, M., 2010. The top-down control of visual selection and how it is linked to the N2pc component. *Acta Psychol.* 135, 100–102. <https://doi.org/10.1016/j.actpsy.2010.04.010> discussion 133–109.
- Eimer, M., Kiss, M., Press, C., Sauter, D., 2009. The roles of feature-specific task set and bottom-up salience in attentional capture: an ERP study. *J. Exp. Psychol. Hum. Percept. Perform.* 35, 1316–1328. <https://doi.org/10.1037/a0015872>.
- El Khoury-Malhame, M., Reynaud, E., Soriano, A., Michael, K., Salgado-Pineda, P., Zendjidian, X., Gellato, C., Eric, F., Lefebvre, M.-N., Rouby, F., Samuelian, J.-C., Anton, J.-L., Blin, O., Khalfa, S., 2011. Amygdala activity correlates with attentional bias in PTSD. *Neuropsychologia* 49, 1969–1973. <https://doi.org/10.1016/j.neuropsychologia.2011.03.025>.
- Elzinga, B.M., Bakker, A., Bremner, J.D., 2005. Stress-induced cortisol elevations are associated with impaired delayed, but not immediate recall. *Psychiatry Res.* 134, 211–223. <https://doi.org/10.1016/j.psychres.2004.11.007>.
- Fox, E., Russo, R., Dutton, K., 2002. Attentional bias for threat: evidence for delayed disengagement from emotional faces. *Cognit. Emot.* 16, 355–379. <https://doi.org/10.1080/02699930143000527>.
- Gilzenrat, M.S., Nieuwenhuis, S., Jepma, M., Cohen, J.D., 2010. Pupil diameter tracks changes in control state predicted by the adaptive gain theory of locus coeruleus function. *Cognit. Affect Behav. Neurosci.* 10, 252–269. <https://doi.org/10.3758/CABN.10.2.252>.
- Goldfarb, E.V., Chun, M.M., Phelps, E.A., 2016. Memory-guided attention: independent contributions of the Hippocampus and striatum. *Neuron* 89, 317–324. <https://doi.org/10.1016/j.neuron.2015.12.014>.
- Golinger, S.D., Pappas, M.H., 2012. Pupil dilation reflects the creation and retrieval of memories. *Curr. Dir. Psychol. Sci.* 21, 90–95. <https://doi.org/10.1177/0963721412436811>.
- Gratton, G., Coles, M.G.H., Donchin, E., 1983. A new method for off-line removal of ocular artifact. *Electroencephalogr. Clin. Neurophysiol.* 55, 468–484. [https://doi.org/10.1016/0013-4694\(83\)90135-9](https://doi.org/10.1016/0013-4694(83)90135-9).
- Hakamata, Y., Lissek, S., Bar-Haim, Y., Britton, J.C., Fox, N.A., Leibenluft, E., Ernst, M., Pine, D.S., 2010. Attention bias modification treatment: a meta-analysis toward the establishment of novel treatment for anxiety. *Biol. Psychiatry* 68, 982–990. <https://doi.org/10.1016/j.biopsych.2010.07.021>.
- Herbison, C.E., Henley, D., Marsh, J., Atkinson, H., Newnham, J.P., Matthews, S.G., Lye, S.J., Pennell, C.E., 2016. Characterisation and novel analyses of acute stress response patterns in a population based cohort of young adults: influence of gender, smoking and BMI. *Stressforskningsrapport* 19, 139–150.
- Hermans, E.J., Hendkens, M.J., Joels, M., Fernandez, G., 2014. Dynamic adaptation of large-scale brain networks in response to acute stressors. *Trends Neurosci.* 37, 304–314. <https://doi.org/10.1016/j.tins.2014.03.006>.
- Hermans, E.J., van Marle, H.J., Ossewaarde, L., Hendkens, M.J., Qin, S., TvK, M., Schoots, V.C., Cousijn, H., Rijpkema, M., Oostenveld, R., Fernández, G., 2011. Stress-related noradrenergic activity prompts large-scale neural network reconfiguration. *Science* 334, 1151–1153. <https://doi.org/10.1126/science.1209603>.
- Hinojosa, J.A., Mercado, F., Carrette, L., 2015. N170 sensitivity to facial expression: a meta-analysis. *Neurosci. Biobehav. Rev.* 55, 498–509. <https://doi.org/10.1016/j.neubiorev.2015.06.002>.
- Holmes, A., Kiss, M., Eimer, M., 2006. Attention modulates the processing of emotional expression triggered by foveal faces. *Neurosci. Lett.* 394, 48–52. <https://doi.org/10.1016/j.neulet.2005.10.002>.
- Hutchinson, J.B., Turk-Browne, N.B., 2012. Memory-guided attention: control from multiple memory systems. *Trends Cogn. Sci.* 16, 576–579. <https://doi.org/10.1016/j.tics.2012.10.003>.
- Hutchinson, J.B., Uncapher, M.R., Wagner, A.D., 2009. Posterior parietal cortex and episodic retrieval: convergent and divergent effects of attention and memory. *Learn. Mem.* 16, 343–356. <https://doi.org/10.1101/lm.919109>.
- Joels, M., Fernandez, G., Roozendaal, B., 2011. Stress and emotional memory: a matter of timing. *Trends Cogn. Sci.* 15, 280–288. <https://doi.org/10.1016/j.tics.2011.04.004>.



- Kahneman, D., 1973. Toward a theory of mental effort. In: *Attention and Effort*. Prentice-Hall Inc, Englewood Cliffs, NJ, pp. 13–27.
- Kiesel, A., Miller, J., Jolicœur, P., Brisson, B., 2008. Measurement of ERP latency differences: a comparison of single-participant and jackknife-based scoring methods. *Psychophysiology* 45, 250–274. <https://doi.org/10.1111/j.1469-8986.2007.00618.x>.
- Kirschbaum, C., Kudielka, B.M., Gaab, J., Schommer, N.C., Hellhammer, D.H., 1999. Impact of gender, menstrual cycle phase, and oral contraceptives on the activity of the hypothalamic-pituitary-adrenal axis. *Psychosom. Med.* 61, 154–162. <https://doi.org/10.1097/00006842-199903000-00006>.
- Koster, E.H., De Lissnyder, E., Derakshan, N., De Raedt, R., 2011. Understanding depressive rumination from a cognitive science perspective: the impaired disengagement hypothesis. *Clin. Psychol. Rev.* 31, 138–145. <https://doi.org/10.1016/j.cpr.2010.08.005>.
- Kuckertz, J.M., Amir, N., Boffa, J.W., Warren, C.K., Rindt, S.E., Norman, S., Ram, V., Ziajko, L., Webb-Murphy, J., McLay, R., 2014. The effectiveness of an attention bias modification program as an adjunctive treatment for Post-Traumatic Stress Disorder. *Behav. Res. Ther.* 63, 25–35. <https://doi.org/10.1016/j.brat.2014.09.002>.
- Kutas, M., Federmeier, K.D., 2011. Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annu. Rev. Psychol.* 62, 621–647. <https://doi.org/10.1146/annurev.psych.093008.131123>.
- Langner, O., Dotsch, R., Bijlstra, G., Wigboldus, D.H.J., Hawk, S.T., van Knippenberg, A., 2010. Presentation and validation of the Radboud faces database. *Cognit. Emot.* 24, 1377–1388. <https://doi.org/10.1080/02699930903485076>.
- LeDoux, J.E., 2000. Emotion circuits in the brain. *Annu. Rev. Neurosci.* 23, 155–184.
- Liston, C., McEwen, B.S., Casey, B.J., 2009. Psychosocial stress reversibly disrupts prefrontal processing and attentional control. *Proc. Natl. Acad. Sci. U. S. A.* 106, 912–917. <https://doi.org/10.1073/pnas.0807041106>.
- Lopez-Calderon, J., Luck, S.J., 2014. ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Front. Hum. Neurosci.* 8, 1–14. <https://doi.org/10.3389/fnhum.2014.00213>.
- Luck, S.J., 2012. Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related ERP components. In: Luck, S.J., Kappenman, E.S. (Eds.), *The Oxford Handbook of Event-Related Potential Components*. Oxford University Press, New York, pp. 329–360.
- Luck, S.J., 2014. Quantifying ERP amplitudes and latencies. In: *An Introduction to the Event-Related Potential Technique*, 2 Edition. MIT Press, Cambridge, pp. 299–302.
- Lundqvist, D., Flykt, A., Öhman, A., 1998. The Karolinska directed emotional faces - KDEF, CD ROM from department of clinical neuroscience, psychology section, 91. Karolinska Institutet, 630-7164-9.
- Lupien, S.J., McEwen, B.S., Gunnar, M.R., Heim, C., 2009. Effects of stress throughout the lifespan on the brain, behaviour and cognition. *Nat. Rev. Neurosci.* 10, 434–445. <https://doi.org/10.1038/nrn2639>.
- Ma, D.S., Correll, J., Wittenbrink, B., 2015. The Chicago face database: a free stimulus set of faces and norming data. *Behav. Res.* 47, 1122–1135. <https://doi.org/10.3758/s13428-014-0532-5>.
- MacNamara, A., Hajcak, G., 2009. Anxiety and spatial attention moderate the electrocortical response to aversive pictures. *Neuropsychologia* 47, 2975–2980. <https://doi.org/10.1016/j.neuropsychologia.2009.06.026>.
- Mogg, K., Bradley, B.P., 2016. Anxiety and attention to threat: cognitive mechanisms and treatment with attention bias modification. *Behav. Res. Ther.* 87, 76–108. <https://doi.org/10.1016/j.brat.2016.08.001>.
- Mogg, K., Garner, M., Bradley, B.P., 2007. Anxiety and orienting of gaze to angry and fearful faces. *Biol. Psychol.* 76, 163–169. <https://doi.org/10.1016/j.biopsycho.2007.07.005>.
- Natu, V., O'Toole, A.J., 2011. The neural processing of familiar and unfamiliar faces: a review and synopsis. *Br. J. Psychol.* 102, 726–747. <https://doi.org/10.1111/j.2044-8295.2011.02053.x>.
- Öhman, A., Flykt, A., Esteves, F., 2001. Emotion drives attention: detecting the snake in the grass. *J. Exp. Psychol. Gen.* 130, 466–478. <https://doi.org/10.1037/0096-3445.130.3.466>.
- Palomba, D., Angrilli, A., Mini, A., 1997. Visual evoked potentials, heart rate responses and memory to emotional pictorial stimuli. *Int. J. Psychophysiol.* 27, 55–67.
- Payne, J.D., Jackson, E.D., Hoshcoid, S., Ryan, L., Jacobs, W.J., Nadel, L., 2007. Stress administered prior to encoding impairs neutral but enhances emotional long-term episodic memories. *Learn. Mem.* 14, 861–868. <https://doi.org/10.1101/lm.743507>.
- Pelli, D.G., 1997. The Video Toolbox software for visual psychophysics: transforming numbers into movies. *Spat. Vis.* 10, 437–442. <https://doi.org/10.1163/156856897X00366>.
- Petersen, S.E., Posner, M.I., 2012. The attention system of the human brain: 20 years after. *Annu. Rev. Neurosci.* 35, 73–89. <https://doi.org/10.1146/annurev-neuro-062111-150525>.
- Poldrack, R.A., 2015. Is "efficiency" a useful concept in cognitive neuroscience? *Dev. Cogn. Neurosci.* 11, 12–17. <https://doi.org/10.1016/j.dcn.2014.06.001>.
- Posner, M.I., Petersen, S.E., 1990. The attention system of the human brain. *Annu. Rev. Neurosci.* 13, 25–42. <https://doi.org/10.1146/annurev.ne.13.030190.000325>.
- Posner, M.I., Walker, J.A., Friedrich, F.J., Rafael, R.D., 1984. Effects of parietal injury on covert orienting of attention. *J. Neurosci.* 4, 1863–1874. <https://doi.org/10.1523/JNEUROSCI.04-07-01863.1984>.
- Pourtois, G., Schettino, A., Vuilleumier, P., 2013. Brain mechanisms for emotional influences on perception and attention: what is magic and what is not. *Biol. Psychol.* 92, 492–512. <https://doi.org/10.1016/j.biopsycho.2012.02.007>.
- Pourtois, G., Grandjean, D., Sander, D., Vuilleumier, P., 2004. Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebr. Cortex* 14, 619–633. <https://doi.org/10.1093/cercor/bbh023>.
- Pruessner, J.C., Kirschbaum, C., Meinlschmid, G., Hellhammer, D.H., 2003. Two formulas for computation of the area under the curve represent measures of total hormone concentration versus time-dependent change. *Psychoneuroendocrinology* 28, 916–931. [https://doi.org/10.1016/s0306-4530\(02\)00108-7](https://doi.org/10.1016/s0306-4530(02)00108-7).
- Quirarte, G.L., Roozendaal, B., McGaugh, J.L., 1997. Glucocorticoid enhancement of memory storage involves noradrenergic activation in the basolateral amygdala. *Proc. Natl. Acad. Sci. U. S. A.* 94, 14048–14053. <https://doi.org/10.1073/pnas.94.25.14048>.
- Rohleder, N., Kirschbaum, C., 2006. The hypothalamic-pituitary-adrenal (HPA) axis in habitual smokers. *Int. J. Psychophysiol.* 59, 236–243. <https://doi.org/10.1016/j.ijpsycho.2005.10.012>.
- Roozendaal, B., Barseganyan, A., Lee, S., 2007. Adrenal stress hormones, amygdala activation, and memory for emotionally arousing experiences, 167, 79–97. [https://doi.org/10.1016/s0079-6123\(07\)67006-x](https://doi.org/10.1016/s0079-6123(07)67006-x).
- Rosen, M.L., Stern, C.E., Michalka, S.W., Devaney, K.J., Somers, D.C., 2016. Cognitive control network contributions to memory-guided visual attention. *Cerebr. Cortex* 26, 2059–2073. <https://doi.org/10.1093/cercor/bhv028>.
- Rutters, F., Nieuwenhuizen, A.G., Lemmens, S.G., Born, J.M., Westerterp-Plantenga, M. S., 2010. Hypothalamic-pituitary-adrenal (HPA) axis functioning in relation to body fat distribution. *Clin. Endocrinol.* 72, 738–743. <https://doi.org/10.1111/j.1365-2265.2009.03712.x>.
- Sänger, J., Bechtold, L., Schoofs, D., Blaszkewicz, M., Wascher, E., 2014. The influence of acute stress on attention mechanisms and its electrophysiological correlates. *Front. Behav. Neurosci.* 8, 353. <https://doi.org/10.3389/fnbeh.2014.00353>.
- Schwabe, L., Wolf, O.T., 2010. Emotional modulation of the attentional blink: is there an effect of stress? *Emotion* 10, 283–288. <https://doi.org/10.1037/a0017751>.
- Schwabe, L., Schachinger, H., 2018. Ten years of research with the socially evaluated cold pressor test: data from the past and guidelines for the future. *Psychoneuroendocrinology* 92, 155–161. <https://doi.org/10.1016/j.psyneuen.2018.03.010>.
- Schwabe, L., Haddad, L., Schachinger, H., 2008a. HPA axis activation by a socially evaluated cold-pressor test. *Psychoneuroendocrinology* 33, 890–895. <https://doi.org/10.1016/j.psyneuen.2008.03.001>.
- Schwabe, L., Bohringer, A., Chatterjee, M., Schachinger, H., 2008b. Effects of pre-learning stress on memory for neutral, positive and negative words: different roles of cortisol and autonomic arousal. *Neurobiol. Learn. Mem.* 90, 44–53. <https://doi.org/10.1016/j.nlm.2008.02.002>.
- Schwabe, L., Joels, M., Roozendaal, B., Wolf, O.T., Oitzl, M.S., 2012. Stress effects on memory: an update and integration. *Neurosci. Biobehav. Rev.* 36, 1740–1749. <https://doi.org/10.1016/j.neubiorev.2011.07.002>.
- Sharot, T., Delgado, M.R., Phelps, E.A., 2004. How emotion enhances the feeling of remembering. *Nat. Neurosci.* 7, 1376–1380. <https://doi.org/10.1038/nn1353>.
- Smulders, F.T., 2010. Simplifying jackknifing of ERPs and getting more out of it: retrieving estimates of participants' latencies. *Psychophysiology* 47, 387–392. <https://doi.org/10.1111/j.1469-8986.2009.00934.x>.
- Steyer, R., Schwenkmezger, P., Notz, P., Eid, M., 1994. Theoretical analysis of a multidimensional mood questionnaire (MDBF). *Diagnostica* 40, 320–328.
- Stokes, M.G., Atherton, K., Patai, E.Z., Nobre, A.C., 2012. Long-term memory prepares neural activity for perception. *Proc. Natl. Acad. Sci. U. S. A.* 109, E360–E367. <https://doi.org/10.1073/pnas.1108555108>.
- Summerfield, J.J., Lepsien, J., Gitelman, D.R., Mesulam, M.M., Nobre, A.C., 2006. Orienting attention based on long-term memory experience. *Neuron* 49, 905–916. <https://doi.org/10.1016/j.neuron.2006.01.021>.
- Theeuwes, J., 2010. Top-down and bottom-up control of visual selection. *Acta Psychol.* 135, 77–99. <https://doi.org/10.1016/j.actpsy.2010.02.006>.
- Theeuwes, J., Atchley, P., Kramer, A.F., 2000. On the time course of top-down and bottom-up control of visual attention. In: Monsell, S., Driver, J. (Eds.), *Control of Cognitive Processes*. MIT Press, Cambridge, pp. 104–124.
- Ulrich, R., Miller, J., 2001. Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. *Psychophysiology* 38, 816–827. <https://doi.org/10.1111/1469-8986.3850816>.
- Urai, A.E., Braun, A., Donner, T.H., 2017. Pupil-linked arousal is driven by decision uncertainty and alters serial choice bias. *Nat. Commun.* 8, 14637. <https://doi.org/10.1038/ncomms14637>.
- van der Wel, P., van Steenbergen, H., 2018. Pupil dilation as an index of effort in cognitive control tasks: a review. *Psychon. Bull. Rev.* 25, 2005–2015. <https://doi.org/10.3758/s13423-018-1432-y>.
- van Marle, H.J., Hermans, E.J., Qin, S., Fernandez, G., 2009. From specificity to sensitivity: how acute stress affects amygdala processing of biologically salient stimuli. *Biol. Psychiatry* 66, 649–655. <https://doi.org/10.1016/j.biopsycho.2009.05.014>.
- van Marle, H.J.F., Hermans, E.J., Qin, S., Fernández, G., 2010. Enhanced resting-state connectivity of amygdala in the immediate aftermath of acute psychological stress. *Neuroimage* 53, 348–354. <https://doi.org/10.1016/j.neuroimage.2010.05.070>.
- van Stegeren, A.H., Goekoop, R., Everaerd, W., Scheltens, P., Barkhof, F., Kuijter, J.P., Rombouts, S.A., 2005. Noradrenaline mediates amygdala activation in men and women during encoding of emotional material. *Neuroimage* 24, 898–909. <https://doi.org/10.1016/j.neuroimage.2004.09.011>.
- Vuilleumier, P., 2002. Facial expression and selective attention. *Curr. Opin. Psychiatr.* 15, 291–300. <https://doi.org/10.1097/00001504-200205000-00011>.
- Vuilleumier, P., 2005. How brains beware: neural mechanisms of emotional attention. *Trends Cogn. Sci.* 9, 585–594. <https://doi.org/10.1016/j.tics.2005.10.011>.
- Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron* 30, 829–841. [https://doi.org/10.1016/S0896-6273\(01\)00328-2](https://doi.org/10.1016/S0896-6273(01)00328-2).



- Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., Dolan, R.J., 2004. Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nat. Neurosci.* 7, 1271–1278. <https://doi.org/10.1038/nn1341>.
- Weinberg, A., Hajcak, G., 2011. The late positive potential predicts subsequent interference with target processing. *J. Cogn. Neurosci.* 23, 2994–3007. <https://doi.org/10.1162/jocn.2011.21630>.
- Weymar, M., Schwabe, L., Löw, A., Hamm, A.O., 2012. Stress sensitized the brain: increased processing of unpleasant pictures after exposure to acute stress. *J. Cogn. Neurosci.* 24, 1511–1518. [https://doi.org/10.1162/jocn\\_a\\_00174](https://doi.org/10.1162/jocn_a_00174).
- Wickens, T.D., 2002. *Elementary Signal Detection Theory*. Oxford University Press, New York, pp. 1–38.
- Wirz, L., Bogdanov, M., Schwabe, L., 2018. Habits under stress: mechanistic insights across different types of learning. *Current Opinion in Behavioral Sciences* 20, 9–16. <https://doi.org/10.1016/j.cobeha.2017.08.009>.
- Yiend, J., 2010. The effects of emotion on attention: a review of attentional processing of emotional information. *Cognit. Emot.* 24, 3–47. <https://doi.org/10.1080/02699930903205698>.