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RESEARCH ARTICLE

Impact of total sleep deprivation on behavioural neural processing of emotionally expressive faces

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Abstract Sleep deprivation impacts subjective mood states, but very little research has examined the impact on processing emotional information. In the current study, we investigated the impact of total sleep deprivation on neural responses to emotional facial expressions as well as the accuracy and speed with which these faces were categorized. Forty-nine participants completed two tasks in which they were asked to categorize emotional facial expressions as Happy, Sad, Angry, or Fearful. They were shown the 'full' expression of the emotions in one task and more subtle expressions in a second task in which expressions were 'morphed' with neutral faces so that the intensity of emotion varied. It was expected that sleep deprivation would lead to greater reactivity (indexed by larger amplitude N170 event-related potentials), particularly for negative and more subtle facial expressions. In the full face task, sleep-deprived (SD) participants were significantly less accurate than controls (C) at identifying Sad faces and slower to identify all emotional expressions. P1 was smaller and N170 was larger for the SD compared to C group, but for all emotions, indicating generalized impairment in low-level visual processing. In the more difficult morphed face task, SD participants were less accurate than C participants for Sad faces; as well, the group difference in reaction time was greatest for Sad faces. For the SD group, N170 increased in amplitude with increasing perceptual difficulty for the Fearful and Angry faces, but decreased in amplitude with increasing difficulty for Sad faces. These data illustrate that sleep deprivation led to greater neural reactivity for the threat-related negative emotions as they became more subtle; however, there was a failure to engage these perceptual resources for the processing of Sad faces. Sleep loss preferentially impacted the processing of Sad faces; this has widespread implications for sleep-deprived groups.

Keywords Sleep deprivation · Emotion · Face processing · Event-related potentials · P1 · N170

Introduction

The deleterious effect of sleep deprivation on subjective mood is a long-standing and robust experimental finding (Patrick and Gilbert 1896; Pilcher and Huffcutt 1996); however, little systematic research has examined the influence of sleep loss on processing emotional information. Given the widespread problem of sleeplessness in our society—due to shift work, lifestyle, ageing, and sleep/medical disorders—it is important to understand the impact of sleep loss on brain function related to emotion regulation and behaviour. Given that deprivation has been reported to impact functioning of the frontal brain region in particular (Goel et al. 2009; Harrison and Horne 2000), and emotion processing also involves frontal regions (Adolphs 2002), one would expect emotion processing to be disrupted by sleep loss. We therefore examined the impact of total sleep deprivation on behavioural and neural sensitivity to facial displays of emotion using event-related potentials (ERPs).

There have been reports of behavioural difficulties in rating emotional pictures following sleep deprivation, such as reduced accuracy and slower speed for recognizing cartoon expressions (Pallesen et al. 2004), impaired accuracy identifying emotional expression in faces (Huck et al. 2008), and a tendency to judge neutral pictures as more negative

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(Tempesta et al. 2010). In one particular study, van der Helm et al. (2010) investigated the impact of one night of sleep deprivation on rating emotional intensity in faces that varied in the intensity of expression. A male model's face was morphed at 10 different intensity levels (from neutral to 100 % expressive) and delivered at random within separate blocks for Happy, Sad, and Angry expressions, respectively. Participants provided ratings for each face, from 1 (neutral) to 4 (most expressive). The emotional intensity ratings were lower following the sleep-deprived condition compared to the rested control condition for Angry and Happy (but not Sad) faces. These effects were apparent only at the moderate levels of intensity and were more robust for women. The lower ratings were interpreted as a reduced ability to accurately identify emotional expressions or 'emotional blunting' as a result of sleep loss. Interpreting behavioural data alone can be misleading, however, since accuracy and reaction time (RT) are generally impaired on a variety of tasks following sleep deprivation (for review, see: Goel et al. 2009).

Psychophysiological measures provide more insight into the mechanisms that underlie sleep-loss-related impairments in emotion processing. Imaging studies have demonstrated 'reactivity' in specific brain regions when processing both negative and positive visual stimuli. Specifically, one study showed that sleep deprivation led to greater amygdala activation when viewing negative picture scenes (Yoo et al. 2007), as well as a lack of connectivity between the prefrontal cortex (PFC) and limbic regions. A subsequent study showed greater activity in brain regions associated with reward when viewing positive picture scenes (Gujar et al. 2011), and reduced connectivity between the PFC and the medial and orbitofrontal regions. Behaviourally, sleep-deprived participants in this study showed a bias towards rating stimuli as more positive. In a recent fMRI study, enhanced reactivity to threatening visual stimuli followed selective REM sleep deprivation, but not an equivalent interruption to non-REM sleep (Rosales-Lagarde et al. 2012), indicating that REM sleep may play a specific role in emotion processing. Although imaging techniques provide information about specific brain regions affected by sleep loss, they lack the temporal resolution to measure the timing of cognitive processes. One study used pupillography as a measure of autonomic nervous system reactivity when viewing positive, negative, and neutral pictures (Franzen et al. 2009). Following sleep deprivation, a larger pupil response or reactivity was found to negative pictures in particular. Although pupil diameter was measured following each stimulus presentation, stimuli were delivered in blocks of five pictures from the same valence category. Researchers reported an anticipatory pupil response in the pre-stimulus period for negative pictures in the sleep-deprived group; this suggests that presenting stimuli in blocks of the same valence may lead to a general change in mood state or arousal. An event-related design, where visual stimuli of different valence types are presented at random, allows for assessment of the physiological response that is time-locked to the stimulus.

Event-related potentials (ERPs) provide a temporally sensitive measure of central nervous system (CNS) activity associated with immediate perception of stimuli and are ideal for investigation of the impact of sleep loss on brain information processing (for review, see Colrain and Campbell 2007) and for the processing of discrete emotional expressions in particular. Visual stimuli evoke two prominent ERP waveforms, P1 and N170. The earliest component that is thought to reflect differential processing of face-like stimuli is the N170 (Rossion and Caharel 2011). Peaking around 150–200 ms post-stimulus onset, the N170 is larger to faces than most other stimuli and reflects the perception of a face (Bentin and Golland 2002; George et al. 2005; Mondloch et al. 2013), rather than low-level stimulus characteristics (Rossion and Caharel 2011). The N170 is maximal at lateral occipito-temporal right-hemisphere sites and is enhanced or delayed by manipulations that make face detection more difficult (e.g. inversion, reviewed in Rossion and Jacques 2012). The N170 is also modulated by identity (at least in some priming tasks; see Rossion and Jacques for a review) and by variation in individual face characteristics (Zheng et al. 2011). In contrast, the earlier visual component (the P1) is maximal at lateral occipital sites and is influenced by low-level stimulus characteristics, rather than the perception of a face per se (reviewed in Rossion and Jacques 2012). While some propose that facial affect is not processed until later stages of information processing and that N170 indexes only structural encoding of the face (Eimer 2000), others maintain that facial emotion is processed rapidly and various studies have shown N170 is sensitive to the emotional expression in the face (e.g. Batty and Taylor 2003; Blau et al. 2007; Meaux et al. 2013).

In the present study, we investigated the impact of one night of total sleep deprivation on categorization of emotionally expressive faces and the neural correlates in young adults. Accuracy and RT, as well as the amplitude of P1 and N170 ERPs, were measured during the performance of two face processing tasks. The full face (FF) task required participants to categorize facial expressions as Happy, Sad, Angry, or Fearful in picture stimuli where models depicted their full expression of the emotion. In the morphed face (MF) task, these expressions were 'morphed' with the model's neutral face (e.g. 30 % Sad and 70 % neutral) to systematically alter the subtlety of each expression (i.e. to increase perceptual difficulty). Based on the previous studies that showed behavioural impairment in rating the intensity of emotional faces (van der Helm et al. 2010), and evidence for central (Yoo et al. 2007; Gujar et al. 2011) and peripheral (Franzen et al. 2009) nervous system reactivity to emotional picture stimuli following sleep deprivation, it was hypothesized that sleep deprivation would impair accurate categorization of emotional expressions and lead to a larger amplitude N170 ERP (reflecting reactivity), particularly for the negative and more subtle facial expressions.

Method

Participants

Participants were recruited from a university campus through poster advertisements, classroom presentations, and an online recruitment tool. To be eligible, all individuals had to be 18–30 years old, healthy, good sleepers (i.e. with a consistent sleeping pattern from approximately 11 p.m./midnight–7/8 a.m.), non-smokers, right-handed, fluent in English, free of medications, and free of psychiatric and neurological conditions. The final sample consisted of 49 participants, which included 24 men (Control Group: $n = 13$; $M_{\text{age}} = 19.23$; SD = 1.48; Sleep-Deprived Group: $n = 11$; $M_{\text{age}} = 20.55$; SD = 2.21) and 25 women (Control Group: $n = 12$; $M_{\text{age}} = 19.25$; SD = 1.29; Sleep-Deprived Group: $n = 13$; $M_{\text{age}} = 19.15$, SD = 1.57).

Materials

Face processing tasks

In the FF task, participants were presented with Happy, Sad, Angry, and Fearful faces that depicted the model's expression of the emotion at 100 % intensity. A total of 360 faces were presented (18 models showing four expressions, each repeated five times); the duration of the task was approximately 15 min and included one break. In the MF task, participants were presented with the expressions of Happy, Sad, Angry, and Fearful faces that were manipulated to be more subtle. Specifically, using Norrkross MorphX software (http://www.norrkross.com), each model's emotional expression was morphed with their own neutral facial expression such that the level of intensity of the emotion was either 30, 40, or 50 %. This procedure effectively provided a systematic manipulation of the subtlety of the facial expression of the emotion, wherein the 30 % condition was most perceptually difficult. In the MF task, a total of 576 faces were presented (eight models showing four expressions at three morph levels, each repeated 6 times); the task took approximately 25 min to complete and included five breaks. For both tasks, stimuli were black-and-white images (12 cm high) from the NIMSTIM database (Tottenham et al. 2009), which were cropped to eliminate features such as hair and clothing; half of the models were women. Face stimuli were presented at random in the centre of a black computer screen (duration = 500 ms; inter-stimulus interval = 1–3 s). Participants were asked to respond once the face disappeared using a 4-button response box to indicate whether the expression was Happy, Sad, Angry, or Fearful.

Procedures

Additional details on participant screening and the full performance assessment battery may be found in the previous publications (Cote et al. 2013; Renn and Cote 2013). Following standard overnight polysomnography (PSG) and questionnaire screening, eligible participants spent two consecutive nights and 1 day in the Sleep Research Laboratory. The first night was a baseline recording of sleep from 2300 to 0700 h in all participants, following which participants were randomly assigned to sleep or to stay awake on the second night in the laboratory. The SD group was continually supervised by the research assistants; they spent the night watching movies and playing card/board games. They received three 100-calorie snacks throughout the night (at 1 a.m., 3 a.m., and 5 a.m.) and were not permitted any caffeinated or sugar beverages. The two face processing tasks were administered at 14:30 h (i.e. after 31.5 h awake for the SD group and 7.5 h awake for the C group) within a larger battery of tasks. Waking EEG was recorded at 1,000 Hz sampling rate during the tasks from 64 scalp sites using Neuroscan Synamps II amplifiers, Quikcap electrode caps, and version 4.5 SCAN software (Compumedics Neuroscan, Inc., El Paso). Scalp electrodes were referenced to FPz with the ground at AFz for online recording; an offline reference for EEG sites was created prior to the data analysis by averaging the right and left mastoid sites (A1 and A2). Bipolar recordings included vertical and horizontal electrooculography (EOG), submental electromyography (EMG), and electrocardiography (EKG).

Data analysis

Accuracy was calculated for the categorization of emotional faces in each task. Valid response times (RT) to correct categorizations of faces were those between 500 ms (duration of stimulus presentation) and 3,000 ms. For the FF task, accuracy and RT were analysed using group (SD and C)-by-emotion (Happy, Sad, Angry, Fearful) mixed-model ANOVAs. For the MF task, accuracy and RT were analysed using group-by-emotion-by-morph-level (30, 40, 50 %) ANOVAs. Analyses were also carried out to examine response patterns when participants made errors identifying the emotional expression of the face. Independent *t* tests were conducted to examine whether groups differed on the proportion of responses for each emotion type when making an error on negatively valenced faces (there were too few errors at identifying Happy faces to examine a response pattern).

Using Neuroscan software, EEG data were epoched by stimulus category within each task from −100 to 900 ms (and baseline corrected using a pre-stimulus interval from −100 to 0 ms). Eye regression procedures were done using Neuroscan software to correct EEG for eye blink artefact. All trials were visually inspected for additional artefact. In order to retain a sufficient number of trials for reliable ERP averaging, only parietal–occipital channels were included in the analysis, where ERPs related to face processing, P1 and N170, are maximum. Because it is important to have a comparable number of ERP trials between conditions and groups, only participants with a target number of artefact-free trials in all conditions were included in the analysis. The first 40 artefact-free trials per emotional expression per subject were included for the FF task; the average number of trials per condition for the MF task is listed in the "Results" section. Sample size also varied by site because some participants had missing data due to poor-quality recordings at specific sites. The individual subject ERP averages were FIR filtered with a bandpass of 1–30 Hz 6 dB for measurement and display. P1 and N170 peaks were picked in the individual averages for each emotional expression (and morph level in the MF task) in both groups, at six right-hemisphere parietal–occipital sites (P4, P6, P8, PO4, PO6, and PO8) where the peaks appeared largest in the grand averages. Left-hemisphere sites were investigated, but are not reported here because there were no robust effects.

For the FF task, P1 and N170 amplitudes were analysed using group (C and SD)-by-emotion (Happy, Sad, Angry, and Fearful) mixed-model ANOVAs at each site separately. For the MF task, P1 and N170 amplitudes were analysed using group-by-emotion-by-morph-level (30, 40, 50 %) mixed-model ANOVAs at each site. In line with the hypotheses, interactions were predicted between group and emotion (and morph level in the MF task) for N170 specifically. The earlier P1 was investigated to determine whether sleep deprivation impacted low-level visual processing because effects at the timing of P1 could carry-over and influence the N170 component of interest. EEG scalp site was not investigated as a factor in the ANOVA because no interactions with site were hypothesized. Effects were expected to be widespread over the right-hemisphere parietal–occipital regions; therefore, ANOVAs were carried out separately at the six scalp sites. Gender was initially investigated as a factor in the ANOVAs because of the findings reported by van der Helm et al. (2010), but was omitted from the results for the clarity of presentation because there were no significant effects. For all analyses, significant interactions were followed-up with two- and one-way ANOVAs and Bonferroni planned comparisons or *t* tests as appropriate. Prior to all statistical analysis, data were inspected for outliers and normality; cases that were more than three standard deviations from the mean were removed. Violations to sphericity were corrected using the Greenhouse-Geisser.

Results

Behavioural data

Full face (FF) task

Behavioural data were missing for two SD participants in the FF task. There was no significant group-by-emotion interaction for accuracy, $p = 0.13$. However, there was a main effect for group, $F(1,45) = 5.10$, $p = 0.029$, $\eta^2 = 0.10$. As shown in Fig. 1a, the SD group was significantly less accurate ($M = 80.91$, SE $= 1.20$) than the C group ($M = 84.63$, SE $= 1.13$). There was also a main effect for emotion, $F(3,135) = 37.29$, $p < 0.001$, $\eta^2 = 0.45$. Bonferroni tests showed that all of the faces were significantly different from one another (ps < 0.01),

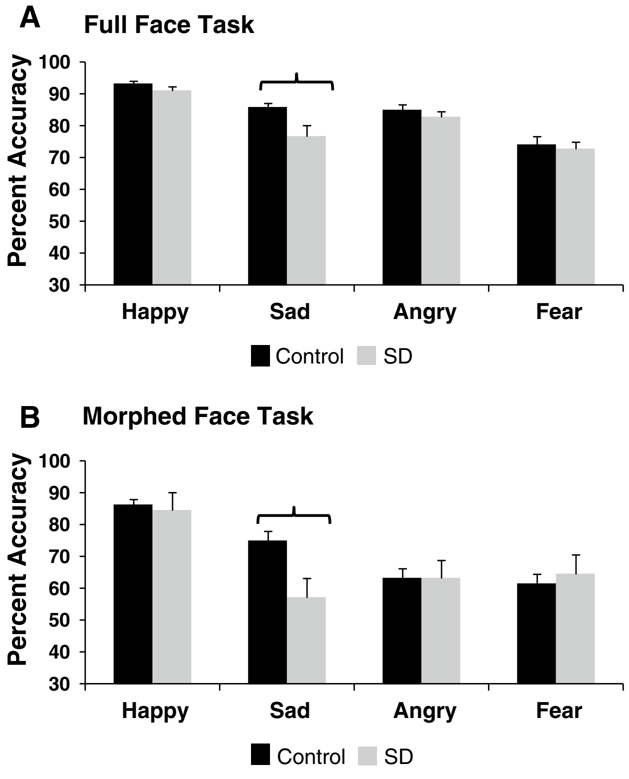


Fig. 1 Percent accuracy by group and emotion in the **a** full face (*upper*), and **b** morphed face (*lower*) tasks. *Note Error bars* are standard error. Conditions that differ between groups are denoted with the *bracket*

except for Sad versus Angry. Accuracy was highest for Happy ($M = 92.29$ %, SE = 0.68), comparable for Sad ($M = 81.37$ %, SE = 1.72) and Angry ($M = 84.02$ %, SE = 1.05), and lowest for Fearful faces ($M = 73.41$ %, SE = 1.75). Although there was not a statistically robust interaction, inspection of the means indicated that groups differed on Sad faces more than the other emotions. Hence, *t* tests were run to explore the hypothesized group differences on each expression separately; this was done to test the consistency of effects seen in the MF task. SD participants were significantly less accurate than C participants to Sad faces, $t(45) = 2.62$, $p = 0.017$, $d = 0.794$, but not Happy ($p = 0.092$), Angry ($p = 0.286$), or Fearful ($p = 0.714$) faces.

There was no significant group-by-emotion interaction for RT in the FF task. However, there was a main effect of group, $F(1,45) = 8.03$, $p = 0.007$, $\eta^2 = 0.15$; the SD group was significantly slower ($M = 603.8$, SE = 33.17) than the C group ($M = 474.92$, SE = 31.11) in categorizing facial emotions. There was also an emotion main effect, $F(3,135) = 83.54$, $p < 0.001$, $\eta^2 = 0.65$. Bonferroni tests indicated that RT differed between all emotions (*p*s < 0.001), except for Sad versus Angry. RT was fastest for Happy ($M = 382.63$ ms, SE = 20.73), comparable for Sad ($M = 546.18$ ms, SE = 29.36) and Angry ($M = 550.52$ ms, SE = 24.56), and slowest for Fearful faces ($M = 678.11$ ms, SE = 26.45).

When making errors in response to negatively valenced expressions, the C group was more likely to choose another negatively valenced emotion, whereas the SD group was more likely to choose Happy. Specifically, when making a mistake on Sad face trials, C participants were more likely than SD participants to choose Fear ($M_C = 61.77$ %, $SD_C = 25.50$, $M_{SD} = 41.89$ %, $SD_{SD} = 25.22$, $t(45) = 2.68$, $p = 0.010$, $d = 0.784$), while SD participants were more likely than C participants to choose Happy ($M_C = 15.52$ %, $SD_C = 17.52$, $M_{SD} = 31.14$ %, $SD_{SD} = 27.87$, $t(45) = -2.33$, $p = 0.024$, $d = 0.688$). Likewise, when making a mistake on Fear face trials, C participants were more likely than SD participants to choose Sad ($M_C = 71.76$ %, $SD_C = 16.14$, $M_{SD} = 56.09$ %, $SD_{SD} = 21.84$, $t(45) = 2.82$, $p = 0.007$, $d = 0.825$), while SD participants were more likely than C participants to choose Happy ($M_C = 7.74$ %, $SD_C = 7.67$, $M_{SD} = 19.13$ %, $SD_{SD} = 14.80$, $t(45) = -3.25$, $p = 0.003$, $d = 1.015$). SD participants were also more likely than C participants to choose Happy when making a mistake on Angry trials ($M_C = 8.09$ %, $SD_C = 9.32$, $M_{SD} = 20.13$ %, $SD_{SD} = 19.71$, $t(45) = -2.62$, $p = 0.014$, $d = 0.829$).

Morphed face (MF) task

Behavioural data were missing for two SD participants in the MF task. There was a significant group-by-emotion interaction for accuracy in the MF task, $F(3,135) = 7.28$, $p < 0.001$, $\eta^2 = 0.14$. Follow-up independent *t* tests were run to compare accuracy between groups for all emotion types (collapsed across morph level). The SD group was less accurate than the C group for Sad faces, $t(45) = 4.42$, $p < 0.001$, $d = 1.302$; groups did not differ on any other emotional expression. See Fig. 1b for the illustration of accuracy data in the MF task.

There was also a significant emotion-by-morph-level interaction for accuracy, $F(6,270) = 17.79$, $p < 0.001$, $\eta^2 = 0.28$. Follow-up one-way ANOVAs on morph level for each emotion showed significant morph-level main effects for all four expressions (*p*s < 0.001). Bonferroni comparisons indicated that, for all expressions, accuracy was significantly lower for each increasing level of difficulty or morph level (*p*s = 0.024–0.001). This was confirmed by a significant morph level main effect, $F(2,90) = 508.26$, $p < 0.001$, $\eta^2 = 0.92$, which demonstrated that accuracy varied systematically with each morph level ($M_{30} = 57.62$ %, $SE_{30} = 1.25$; $M_{40} = 71.41$ %, $SE_{40} = 1.31$; $M_{50} = 79.31$ %, $SE_{50} = 1.08$). To further examine the nature of the emotion-by-morph-level interaction, one-way ANOVAs on emotion were also run separately at each morph level. Bonferroni comparisons indicated that, for the 40 and 50 % morph levels, participants were more accurate on Happy faces than all others (*p*s < 0.001), with no differences in accuracy between any of the negative emotions, whereas for the most difficult 30 % morph level condition, participants were more accurate on Happy faces than all others (*p*s < 0.001), but they were also more accurate on Sad compared to both Angry ($p = 0.048$) and Fearful faces ($p = 0.003$).

There was a significant group-by-emotion interaction for RT in the MF task, $F(3,135) = 2.97$, $p = 0.034$, $\eta^2 = 0.06$. Follow-up independent *t* tests were run to compare RT between groups for all expressions (collapsed across morph level). RT was slower for SD compared to C participants for Happy ($M_C = 488.45$, $SD_C = 130.58$; $M_{SD} = 576.64$, $SD_{SD} = 158.26$; $t(45) = -2.09$, $p < 0.05$, $d = 0.611$), Sad ($M_C = 589.50$, $SD_C = 152.88$; $M_{SD} = 761.28$, $SD_{SD} = 206.70$; $t(45) = -3.25$, $p < 0.01$, $d = 0.955$), and Angry ($M_C = 592.86$, $SD_C = 160.92$; $M_{SD} = 712.98$, $SD_{SD} = 175.44$; $t(45) = -2.45$, $p < 0.05$, $d = 0.714$) faces, with only a marginal difference for Fearful faces ($M_C = 643.89$, $SD_C = 169.15$; $M_{SD} = 738.65$, $SD_{SD} = 173.19$; $t(45) = -1.90$, $p = 0.064$, $d = 0.554$); as for accuracy, the group difference in RT was largest for Sad faces.

There was also a significant emotion-by-morph-level interaction for RT, $F(6,270) = 3.41$, $p = 0.006$, $\eta^2 = 0.07$. Follow-up one-way ANOVAs on morph level for each emotion showed significant morph-level main effects for Happy, $F(2,92) = 58.22$, $p < 0.001$, $\eta^2 = 0.56$, Angry, $F(2,92) = 10.03$, $p < 0.001$, $\eta^2 = 0.18$), and Fear faces,

$F(2,92) = 25.15$, $p < 0.001$, $\eta^2 = 0.35$, with a marginal effect for Sad, $F(2,92) = 3.09$, $p = 0.050$, $\eta^2 = 0.06$. For Happy faces, Bonferroni comparisons indicated that RT was slower in the most difficult 30 % morph level compared to both the 40 % ($p < 0.001$) and 50 % ($p < 0.001$) levels, and slower in the 40 % compared to the 50 % level ($p < 0.001$). Similarly, for Fearful faces, RT was slower in the most difficult 30 % morph level compared to both the 40 % ($p < 0.001$) and 50 % ($p < 0.001$) levels, and slower in the 40 % compared 50 % level ($p < 0.05$). For Angry faces, RT was slower in the 30 % ($p < 0.001$) and 40 % ($p < 0.01$) levels than the 50 % level, although there was no difference in RT between 30 and 40 % levels ($p = 0.216$). RT did not vary significantly across morph levels for Sad faces. A significant morph-level main effect, $F(2,90) = 51.21$, $p < 0.001$, $\eta^2 = 0.53$, also showed that RT slowed systematically with increasing morph level or perceptual difficulty ($M_{30} = 690.20$ ms, $\mathrm{SE}_{30} = 24.61$; $M_{40} = 632.90$ ms, $\mathrm{SE}_{40} = 23.41$; $M_{50} = 590.99$ ms, $\mathrm{SE}_{50} = 21.16$).

Groups were also compared on the pattern of response choices when making errors on the negatively valenced expressions in the MF task, collapsed across morph levels. There were no group differences in the pattern of errors made in response to Sad faces. When making a mistake on Angry face trials, SD participants were more likely than C participants to choose Happy ($M_{\mathrm{C}} = 15.62$ %, $\mathrm{SD}_{\mathrm{C}} = 12.12$, $M_{\mathrm{SD}} = 23.76$ %, $\mathrm{SD}_{\mathrm{SD}} = 13.76$, $t(45) = -2.15$, $p = 0.037$, $d = 0.629$), more likely than C participants to choose Fear ($M_{\mathrm{C}} = 12.19$ %, $\mathrm{SD}_{\mathrm{C}} = 9.58$, $M_{\mathrm{SD}} = 23.82$ %, $\mathrm{SD}_{\mathrm{SD}} = 14.76$, $t(45) = -3.19$, $p = 0.003$, $d = 0.956$), and less likely than C participants to choose Sad ($\mathrm{M}_{\mathrm{C}} = 72.19$ %, $\mathrm{SD}_{\mathrm{C}} = 13.86$, $\mathrm{M}_{\mathrm{SD}} = 52.42$ %, $\mathrm{SD}_{\mathrm{SD}} = 20.99$, $t(45) = 3.79$, $p < 0.001$, $d = 1.135$). When making a mistake on Fearful face trials, SD participants were more likely than C participants to choose Happy ($M_{\mathrm{C}} = 9.90$ %, $\mathrm{SD}_{\mathrm{C}} = 8.39$, $M_{\mathrm{SD}} = 18.55$ %, $\mathrm{SD}_{\mathrm{SD}} = 8.70$, $t(45) = -3.47$, $p < 0.001$, $d = 1.021$), more likely than C participants to choose Angry ($\mathrm{M}_{\mathrm{C}} = 18.87$ %, $\mathrm{SD}_{\mathrm{C}} = 13.98$, $\mathrm{M}_{\mathrm{SD}} = 28.51$ %, $\mathrm{SD}_{\mathrm{SD}} = 17.12$, $t(45) = -2.12$, $p < 0.05$, $d = 0.620$), and less likely than C participants to choose Sad ($M_{\mathrm{C}} = 71.23$ %, $\mathrm{SD}_{\mathrm{C}} = 15.32$, $M_{\mathrm{SD}} = 52.94$ %, $\mathrm{SD}_{\mathrm{SD}} = 14.70$, $t(45) = 4.18$, $p < 0.001$, $d = 1.219$).

ERP data

Full face (FF) task

Means and standard deviations for P1 and N170 amplitude data are presented in Table 1 for the FF task. Forty-three participants (22 C and 21 SD) had a sufficient amount of artefact-free ERP data for the analysis in the FF task; two additional control participants were excluded from all analyses because they were outliers at most sites. There were no emotion main effects or group-by-emotion interactions for P1 or N170 in the FF task. There was a significant group main effect for P1 amplitude at four right-hemisphere sites; SD participants had significantly smaller P1 amplitudes than C participants at P4, $F(1,39) = 5.50$, $p = 0.024$, $\eta^2 = 0.12$, P6, $F(1,36) = 7.87$, $p = 0.008$, $\eta^2 = 0.18$, P8, $F(1,35) = 6.50$, $p = 0.015$, $\eta^2 = 0.16$, and P06, $F(1,38) = 5.46$, $p = 0.025$, $\eta^2 = 0.13$ sites. There was also a significant group main effect for N170 amplitude; it was larger for the SD than the C group at P8, $F(1,36) = 7.92$, $p = 0.008$, $\eta^2 = 0.18$, and P06, $F(1,38) = 6.05$, $p = 0.019$, $\eta^2 = 0.14$, with trends in the same direction noted at neighbouring sites, P6, $F(1,37) = 3.39$, $p = 0.074$, $\eta^2 = 0.08$, PO4, $F(1,39) = 3.15$, $p = 0.084$, $\eta^2 = 0.08$, and P08, $F(1,38) = 3.38$, $p = 0.074$, $\eta^2 = 0.08$. In order to confirm that the group differences in N170 were independent of differences in the earlier P1 component, a follow-up ANCOVA was run at the sites where group differences in N170 amplitude were apparent, controlling for P1 amplitude; data were collapsed across expressions. P1 was not a significant covariate for the group difference observed in N170 at P8 and P06 (nor for the sites where trends for group differences were observed). ERPs at parietal–occipital sites are illustrated in Fig. 2.

Morphed face (MF) task

Means and standard deviations for P1 and N170 amplitude data are presented in Table 2 for the MF task. Twenty-nine participants (14 C and 15 SD) had a sufficient amount of artefact-free ERP data in each condition (i.e. all four expressions at three morph levels) for the analysis in the MF task. ANOVAs on P1 amplitude revealed a group-by-morph-level interaction at P8, $F(2,42) = 4.45$, $p = 0.018$, $\eta^2 = 0.18$; the SD group had a significantly smaller P1 amplitude than C group at the 50 % morph level, $t(21) = 2.33$, $p = 0.03$, $d = 1.032$, but not for the 30 and 40 % levels (i.e. the SD group produced a P1 equivalent in amplitude to that of the C group in the more challenging conditions). Significant main effects of morph level for P1 amplitude were apparent at P8, $F(2,42) = 4.38$, $p = 0.031$, $\eta^2 = 0.17$ and PO8, $F(2,44) = 3.73$, $p = 0.032$, $\eta^2 = 0.15$. Bonferroni tests indicated that P1 amplitude was marginally larger in the 30 % morph level relative to the 50 % level, for both groups and all expressions combined at P8 ($p = 0.075$) and PO8 ($p = 0.096$) (i.e. P1 amplitude was modulated by the perceptual difficulty of processing the face). There were no other significant main effects or interactions for P1 amplitude in the MF task.

ANOVAs on N170 amplitude revealed a significant group-by-emotion-by-morph-level interaction at site P6, $F(6,138) = 2.42$, $p = 0.030$, $\eta^2 = 0.10$, as well as trends for 3-way interactions at adjacent sites, PO4, $F(6,162) = 1.96$,

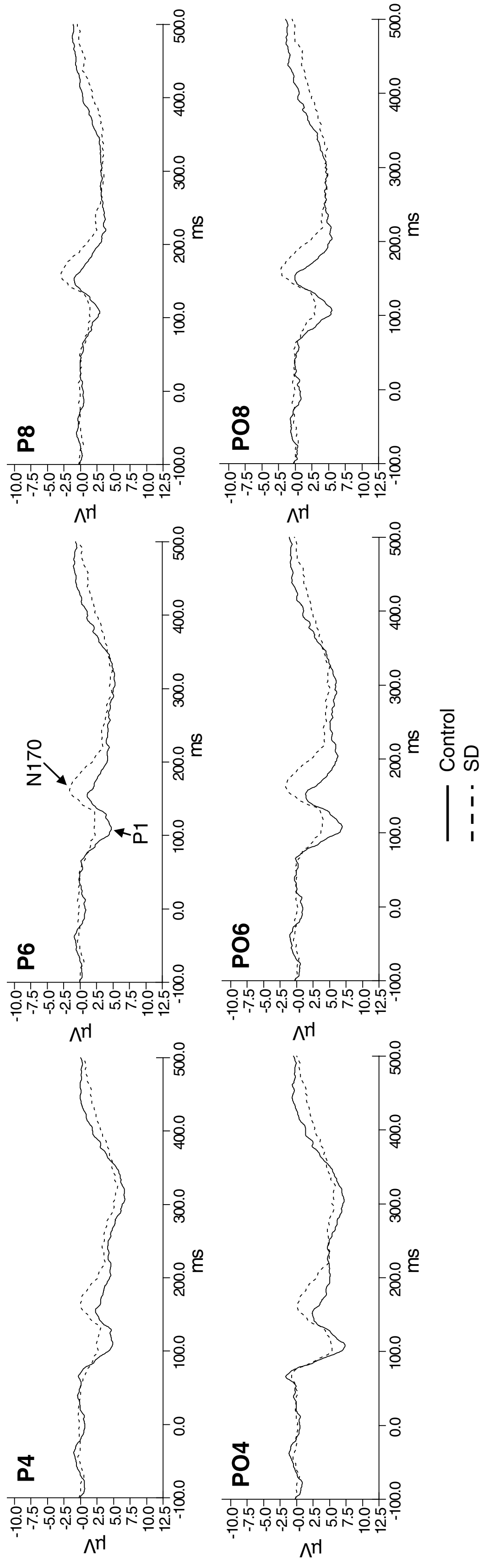
Table 1 Means and standard deviations for P1 and N170 amplitude data for full face (FF) task

Peak	Site	*n*	Group	Group mean	Happy	Sad	Angry	Fearful
P1	P4	20	C	7.51 (0.58)*	7.41 (2.71)	7.52 (2.87)	7.27 (2.63)	7.83 (3.37)
		21	SD	5.62 (0.56)	5.10 (3.45)	5.91 (2.60)	5.73 (3.63)	5.73 (3.63)
			Emotion		6.26 (0.49)	6.71 (0.43)	6.50 (0.50)	6.78 (0.55)
	P6	19	C	6.62 (0.47)**	6.05 (4.76)	6.86 (3.02)	6.47 (2.71)	7.11 (3.34)
		19	SD	4.77 (0.47)	4.53 (2.91)	4.96 (2.48)	4.79 (2.19)	4.79 (2.19)
			Emotion		5.29 (0.64)	5.91 (0.45)	5.63 (0.40)	5.95 (0.46)
	P8	20	C	4.35 (0.38)*	4.63 (2.36)	4.24 (2.42)	4.34 (2.27)	4.19 (2.74)
		17	SD	2.93 (0.41)	2.65 (2.66)	3.21 (2.15)	2.94 (1.81)	2.94 (1.81)
			Emotion		3.64 (0.41)	3.73 (0.38)	3.64 (0.34)	3.56 (0.39)
	PO4	20	C	8.54 (0.68)	8.93 (3.08)	8.63 (2.54)	8.10 (2.40)	8.49 (3.39)
		21	SD	7.99 (0.66)	7.96 (4.18)	8.52 (3.86)	7.74 (3.84)	7.74 (3.84)
			Emotion		8.45 (0.58)	8.57 (0.51)	7.92 (0.50)	8.11 (0.57)
	PO6	20	C	8.80 (0.62)*	9.05 (3.11)	8.86 (3.38)	8.35 (3.66)	8.94 (3.90)
		20	SD	6.77 (0.62)	6.87 (3.75)	6.93 (2.74)	6.63 (3.40)	6.63 (3.40)
			Emotion		7.96 (0.54)	7.90 (0.49)	7.49 (0.56)	7.79 (0.58)
	PO8	20	C	7.03 (0.55)	7.47 (2.33)	6.95 (2.56)	6.62 (3.11)	7.09 (2.95)
		20	SD	6.07 (0.55)	6.15 (3.48)	5.87 (2.87)	6.13 (3.19)	6.13 (3.19)
			Emotion		6.81 (0.47)	6.41 (0.43)	6.38 (0.50)	6.61 (0.49)
N170	P4	20	C	0.38 (0.62)	0.29 (3.04)	0.80 (3.19)	0.37 (3.48)	0.07 (3.32)
		21	SD	−0.87 (0.60)	−1.53 (2.99)	−0.75 (3.19)	−0.60 (3.45)	−0.60 (3.45)
			Emotion		−0.62 (0.47)	0.02 (0.50)	−0.12 (0.54)	−0.27 (0.53)
	P6	19	C	−0.53 (0.61)$^{+}$	−0.38 (3.09)	−0.14 (2.90)	−1.50 (4.00)	−0.12 (4.14)
		20	SD	−2.10 (0.59)	−2.86 (2.27)	−2.23 (3.16)	−1.66 (3.98)	−1.66 (3.98)
			Emotion		−1.62 (0.43)	−1.18 (0.49)	−1.58 (0.64)	−0.89 (0.65)
	P8	20	C	−1.97 (0.51)**	−1.99 (2.03)	−1.79 (2.05)	−2.10 (2.47)	−1.98 (2.32)
		18	SD	−4.05 (0.54)	−4.46 (2.81)	−3.63 (2.58)	−4.06 (3.16)	−4.06 (3.16)
			Emotion		−3.23 (0.40)	−2.71 (0.38)	−3.08 (0.46)	−3.02 (0.45)
	PO4	20	C	0.65 (0.75)$^{+}$	0.50 (3.90)	0.91 (3.82)	0.46 (3.64)	0.72 (3.69)
		21	SD	−1.22 (0.73)	−1.69 (3.84)	−0.39 (3.92)	−1.39 (3.64)	−1.39 (3.64)
			Emotion		−0.60 (0.60)	0.26 (0.60)	−0.47 (0.57)	−0.33 (0.57)
	PO6	20	C	−0.20 (0.81)*	−0.25 (3.78)	0.05 (3.96)	−0.29 (3.88)	−0.31 (3.64)
		20	SD	−3.03 (0.81)	−3.37 (4.01)	−2.52 (4.44)	−3.12 (4.02)	−3.12 (4.02)
			Emotion		−1.81 (0.62)	−1.24 (0.67)	−1.71 (0.63)	−1.72 (0.61)
	PO8	20	C	−1.44 (0.75)$^{+}$	−1.40 (3.15)	−1.36 (2.97)	−1.43 (2.97)	−1.58 (3.27)
		20	SD	−3.39 (0.75)	−4.00 (4.40)	−3.20 (4.34)	−3.18 (3.93)	−3.18 (3.93)
			Emotion		−2.70 (0.61)	−2.28 (0.59)	−2.31 (0.55)	−2.38 (0.57)

Marginal means and standard error are given for the group and emotion factors. Units are microvolts

Significance at $p < 0.05$ is indicated by * and $p < 0.01$ by **; trends are indicated by $^{+}$

$p = 0.074$, $\eta^2 = 0.07$, PO6, $F(6,132) = 1.85$, $p = 0.093$, $\eta^2 = 0.08$, and PO8, $F(6,138) = 1.80$, $p = 0.10$, $\eta^2 = 0.07$. To follow-up, emotion-by-morph-level ANOVAs were run in each group separately for the four right-hemisphere posterior lateral sites above. There were significant emotion-by-morph-level interactions in the SD, but not C group, at P6, $F(6,66) = 2.32$, $p = 0.043$, $\eta^2 = 0.17$, and PO4, $F(6,84) = 3.33$, $p = 0.005$, $\eta^2 = 0.19$. To follow-up on the 2-way interactions in the SD group, one-way ANOVAs were run to examine N170 amplitude across morph levels in each expression separately; linear polynomial contrasts were inspected to test the hypothesis that N170 changed systematically with increasing morph level. For Sad faces, there were significant linear effects at both P6, $F(1,11) = 5.31$, $p = 0.042$, $\eta^2 = 0.33$ and PO4, $F(1,13) = 5.37$, $p = 0.037$, $\eta^2 = 0.29$; N170 amplitude was smaller as perceptual difficulty level increased. In contrast, for Fear faces, a linear effect at P6, $F(1,11) = 5.49$, $p = 0.039$, $\eta^2 = 0.33$ and a trend at PO4, $F(1,14) = 3.23$, $p = 0.094$, $\eta^2 = 0.19$ illustrated that N170 amplitude became larger as perceptual difficulty level increased. Similarly, Bonferroni tests following the main effects of morph level for Anger at PO4, $F(2,28) = 7.91$, $p = 0.002$, $\eta^2 = 0.36$ showed that N170 amplitude was



◀**Fig. 2** Event-related potentials (ERPs) at right-hemisphere parietal–occipital sites for Happy faces by group in the full face (FF) task. *Solid line* control (C) group; *Dashed line* sleep-deprived (SD) group

significantly larger for 30 % level compared to the 40 % level ($p = 0.006$). N170 amplitude at PO4 was stable across morph levels for Happy faces at both sites. See means plot of emotion-by-morph-level interaction at site P6 in Fig. 3 and ERPs for the SD group in Fig. 4.

Group main effects for N170 amplitude were widespread at sites P4, $F(1,23) = 4.69$, $p = 0.041$, $\eta^2 = 0.17$, P6, $F(1,23) = 7.08$, $p = 0.014$, $\eta^2 = 0.24$, P8, $F(1,21) = 5.73$, $p = 0.026$, $\eta^2 = 0.21$, and PO8, $F(1,23) = 4.50$, $p = 0.045$, $\eta^2 = 0.16$; N170 was larger in the SDs compared to Cs. There were no significant main effects for emotion nor group-by-emotion interactions for N170 in the MF task.

Discussion

The present study investigated the impact of one night of total sleep deprivation on processing emotionally expressive faces in young adults. Sleep deprivation was expected to disrupt accurate categorization of emotional expressions and lead to a larger amplitude N170 ERP (reflecting reactivity), particularly for the negative and more subtle facial expressions. Behavioural and neurophysiological data converged to show that sleep deprivation led to impairment in categorizing and processing Sad emotional expressions in particular. On both tasks, the SD group was less accurate than the C group for Sad faces. Moreover, while RT was generally slower in the SD compared to the C group, the difference in RT was largest for Sad faces in the MF task. Neural reactivity was evident in the N170 marker of face processing for the SD group in both tasks; however, differential processing for the various emotional expressions was apparent for the SD group when faces were morphed to be perceptually more difficult. Specifically, while N170 increased in amplitude with perceptual difficulty level for Fearful faces, and to some extent for Angry faces, N170 decreased in amplitude with perceptual difficulty level for Sad faces. Thus, sleep deprivation led to greater neural reactivity as hypothesized for the threat-related negative emotions as they became more subtle; however, there was a failure to engage these perceptual resources for the processing of Sad faces.

The behavioural data indicated that our task was valid. Specifically, accuracy and RT varied across emotional expression in the FF task in a manner consistent with prior literature (Ekman et al. 1971; Russell 1994); accuracy was highest and RT fastest for Happy compared to the negatively valenced emotions, while accuracy was lowest and RT slowest for Fearful faces. Accuracy and RT also

Table 2 Means and standard deviations for P1 and N170 amplitude data for morphed face (MF) task

	Site	*n*	Group	Group mean	Happy			Sad			Angry			Fear			Morph level
					30 %	40 %	50 %	30 %	40 %	50 %	30 %	40 %	50 %	30 %	40 %	50 %	(30, 40, 50)
P1	P4	14	C	7.48 (0.61)	7.16 (2.81)	7.39 (3.31)	7.40 (2.46)	7.60 (3.03)	7.97 (2.74)	7.46 (2.86)	7.51 (2.67)	6.53 (2.73)	7.45 (2.97)	8.22 (2.86)	6.72 (3.49)	8.32 (3.03)	6.96 (0.38)
		13	SD	6.09 (0.63)	6.41 (2.25)	6.15 (2.57)	5.70 (3.66)	6.51 (2.78)	5.80 (3.53)	6.33 (3.90)	5.42 (3.45)	6.63 (3.00)	5.20 (3.91)	6.83 (2.37)	5.82 (3.99)	6.24 (2.32)	6.63 (0.53)
			Emotion		6.70 (0.46)			6.94 (0.50)			6.46 (0.49)			7.02 (0.49)			6.76 (0.52)
	P6	13	C	7.13 (0.68)	6.88 (3.16)	7.04 (2.97)	6.92 (2.63)	7.05 (3.10)	7.45 (2.81)	7.70 (2.88)	6.84 (3.29)	6.49 (2.97)	6.70 (3.59)	8.22 (2.76)	6.46 (3.58)	7.85 (3.10)	6.47 (0.49)
		12	SD	5.40 (0.71)	5.70 (2.54)	4.93 (2.39)	5.31 (3.51)	6.63 (3.05)	5.56 (3.53)	5.21 (3.61)	4.85 (3.11)	5.81 (2.97)	4.57 (3.52)	5.58 (2.55)	5.54 (3.15)	5.11 (2.22)	6.16 (0.53)
			Emotion		6.13 (0.50)			6.60 (0.52)			5.88 (0.55)			6.46 (0.51)			6.17 (0.53)
	P8	14	C	5.00 (0.51)	4.68 (2.86)	4.65 (2.24)	4.65 (2.27)	5.27 (2.71)	5.21 (2.09)	5.65 (2.28)	4.98 (2.45)	5.06 (2.26)	5.00 (2.99)	5.22 (2.56)	4.32 (2.97)	5.25 (2.42)	4.92 (0.47)
		9	SD	3.96 (0.64)	4.61 (2.13)	3.82 (1.95)	3.99 (2.47)	5.37 (2.45)	4.06 (2.32)	3.21 (1.05)	5.19 (2.90)	3.92 (2.71)	3.18 (2.32)	4.06 (1.65)	3.05 (2.76)	3.04 (2.37)	4.26 (0.45)
			Emotion		4.40 (0.44)			4.80 (0.38)			4.56 (0.47)			4.16 (0.46)			4.25 (0.38)
	PO4	14	C	9.04 (0.66)	8.61 (2.54)	8.53 (2.92)	8.82 (2.46)	9.72 (3.06)	9.65 (1.43)	8.97 (2.37)	8.61 (2.71)	8.58 (2.44)	9.23 (3.03)	9.76 (2.91)	8.72 (3.25)	9.34 (3.30)	8.54 (0.47)
		15	SD	7.85 (0.64)	7.52 (3.44)	7.31 (3.49)	7.57 (3.51)	7.74 (3.11)	7.66 (4.17)	8.20 (3.62)	8.01 (4.11)	8.43 (3.64)	7.57 (3.54)	8.33 (3.02)	7.60 (3.86)	8.21 (2.91)	8.31 (0.50)
			Emotion		8.06 (0.51)			8.66 (0.48)			8.40 (0.54)			8.66 (0.50)			8.49 (0.50)
	PO6	13	C	9.56 (0.74)	9.09 (4.04)	8.98 (3.04)	9.01 (2.61)	9.69 (3.82)	10.36 (2.40)	9.88 (2.35)	9.83 (3.17)	8.71 (3.26)	9.56 (4.01)	10.65 (3.39)	8.94 (3.59)	9.99 (3.32)	9.01 (0.61)
		11	SD	7.98 (0.80)	8.29 (3.53)	7.37 (2.30)	7.96 (3.67)	8.10 (4.06)	8.66 (4.10)	8.29 (2.70)	7.95 (3.93)	8.08 (3.84)	7.39 (3.56)	8.45 (3.24)	7.79 (3.53)	7.38 (2.73)	8.61 (0.57)
			Emotion		8.45 (0.59)			9.16 (0.54)			8.59 (0.65)			8.87 (0.59)			8.68 (0.55)
	PO8	12	C	8.45 (0.63)	8.52 (2.74)	7.93 (2.26)	7.77 (2.35)	8.81 (3.63)	9.15 (2.12)	8.96 (2.14)	8.59 (2.93)	7.94 (2.76)	8.48 (3.33)	8.99 (2.64)	7.78 (2.95)	8.50 (2.71)	7.89 (0.52)
		12	SD	6.62 (0.63)	7.35 (3.12)	6.38 (2.53)	6.50 (3.08)	6.69 (3.20)	6.87 (3.35)	6.41 (2.12)	7.59 (3.12)	7.01 (2.70)	5.70 (3.10)	6.63 (2.35)	6.75 (2.77)	5.50 (1.90)	7.48 (0.46)
			Emotion		7.41 (0.47)			7.82 (0.46)			7.55 (0.54)			7.36 (0.47)			7.23 (0.42)
N170	P4	14	C	0.24 (0.65)	0.58 (2.80)	0.37 (3.17)	0.34 (3.45)	0.48 (2.85)	0.97 (3.05)	−0.70 (2.78)	0.15 (3.31)	0.18 (2.78)	0.17 (2.46)	0.07 (2.81)	0.00 (2.85)	0.20 (3.14)	−0.89 (0.51)
		11	SD	−1.90 (0.74)	−2.36 (1.88)	−1.65 (2.43)	−1.80 (1.99)	−0.96 (3.78)	−2.17 (3.03)	−2.53 (4.27)	−2.87 (3.29)	−0.98 (3.31)	−1.88 (3.47)	−2.21 (2.63)	−2.17 (2.88)	−1.22 (3.03)	−0.68 (0.50)
			Emotion		−0.75 (0.51)			−0.82 (0.59)			−0.87 (0.53)			−0.89 (0.47)			−0.93 (0.53)
	P6	13	C	−0.69 (0.64)	−0.67 (2.98)	0.23 (3.02)	0.05 (3.08)	−0.74 (2.23)	−0.02 (3.01)	−1.26 (2.44)	−0.67 (3.39)	−1.47 (2.89)	−0.95 (2.33)	−0.95 (3.06)	−0.99 (3.09)	−0.81 (3.34)	−1.97 (0.48)
		12	SD	−3.14 (0.67)	−3.15 (2.35)	−2.83 (2.96)	−3.21 (2.20)	−1.80 (3.70)	−3.55 (2.61)	−3.78 (3.16)	−4.03 (2.61)	−2.20 (3.08)	−3.45 (3.12)	−3.74 (2.20)	−3.81 (2.84)	−2.14 (3.60)	−1.83 (0.50)
			Emotion		−1.60 (0.48)			−1.86 (0.50)			−2.13 (0.50)			−2.07 (0.52)			−1.94 (0.47)
	P8	14	C	−1.80 (0.48)	−1.71 (2.34)	−1.38 (2.74)	−1.69 (2.47)	−1.87 (1.95)	−1.48 (2.35)	−2.19 (2.19)	−1.54 (2.91)	−2.37 (2.90)	−1.34 (1.64)	−1.89 (2.64)	−2.33 (2.41)	−1.81 (2.61)	−2.49 (0.40)
		9	SD	−3.62 (0.59)	−3.40 (1.62)	−4.26 (1.59)	−3.32 (1.07)	−3.31 (1.07)	−3.98 (1.57)	−3.83 (2.05)	−2.81 (2.36)	−3.20 (1.80)	−4.38 (2.17)	−3.47 (1.97)	−4.50 (1.94)	−3.00 (1.72)	−2.94 (0.41)
			Emotion		−2.63 (0.43)			−2.77 (0.41)			−2.61 (0.40)			−2.83 (0.42)			−2.70 (0.38)
	PO4	14	C	0.98 (0.78)	1.07 (2.97)	1.04 (3.41)	0.87 (3.61)	1.69 (2.95)	1.94 (3.09)	0.00 (3.20)	0.62 (3.42)	0.82 (3.65)	0.80 (3.35)	1.00 (3.53)	0.90 (3.20)	0.97 (3.59)	0.07 (0.53)
		15	SD	−0.82 (0.76)	−0.73 (3.55)	−0.67 (3.51)	−1.42 (3.51)	0.15 (3.66)	−1.63 (3.55)	−1.60 (4.13)	−1.56 (3.48)	0.87 (3.72)	−0.52 (3.93)	−1.65 (3.25)	−0.82 (3.71)	−0.20 (3.43)	0.31 (0.59)
			Emotion		0.03 (0.57)			0.09 (0.58)			0.17 (0.61)			0.32 (0.55)			−0.14 (0.58)
	PO6	13	C	−0.42 (0.94)	−0.44 (3.54)	−0.09 (3.20)	−0.14 (4.30)	−0.30 (2.75)	0.76 (3.64)	−0.86 (3.37)	−0.27 (3.42)	−1.22 (3.94)	−0.80 (3.59)	−0.44 (4.62)	−1.03 (3.18)	−0.18 (3.91)	−1.69 (0.67)
		11	SD	−2.60 (1.03)	−2.77 (4.22)	−2.42 (3.77)	−3.17 (3.59)	−2.14 (3.95)	−271 (4.12)	−2.66 (4.49)	−2.85 (3.21)	−1.16 (4.54)	−1.49 (4.54)	−4.30 (3.88)	−2.97 (4.48)	−2.52 (4.08)	−1.35 (0.73)
			Emotion		−1.50 (0.74)			−1.32 (0.71)			−1.30 (0.73)			−1.91 (0.72)			−1.48 (0.75)
	PO8	13	C	−1.47 (0.84)	−1.78 (3.23)	−0.70 (2.84)	−1.46 (3.65)	−1.55 (2.65)	−0.49 (3.08)	−1.77 (3.13)	−1.44 (3.11)	−2.13 (3.54)	−1.10 (2.81)	−1.47 (4.20)	−2.25 (2.41)	−1.46 (3.26)	−2.80 (0.61)
		12	SD	−4.05 (0.88)	−3.36 (4.41)	−4.23 (3.65)	−4.52 (3.39)	−4.35 (3.32)	−4.47 (3.48)	−4.08 (3.82)	−3.42 (3.84)	−2.90 (4.32)	−3.76 (4.81)	−5.01 (3.00)	−4.38 (4.99)	−4.05 (3.67)	−2.70 (0.66)
			Emotion		−2.68 (0.67)			−2.78 (0.60)			−2.46 (0.65)			−3.11 (0.62)			−2.78 (0.64)

Table 2 continued

Site	*n*	Group	Group mean	Happy			Sad			Angry			Fear			Morph level
				30 %	40 %	50 %	30 %	40 %	50 %	30 %	40 %	50 %	30 %	40 %	50 %	(30, 40, 50)
No. trials		C		19.53	19.87	19.80	17.53	19.33	19.27	16.07	18.60	19.33	14.93	17.33	19.13	
		SD		18.13	19.80	19.60	16.27	15.87	17.07	14.40	16.80	19.07	14.07	17.80	18.60	

Marginal means and standard error are given for the group, emotion, and morph-level factors. Units are microvolts. 'No. trials' is the average number of trials per participant for each condition

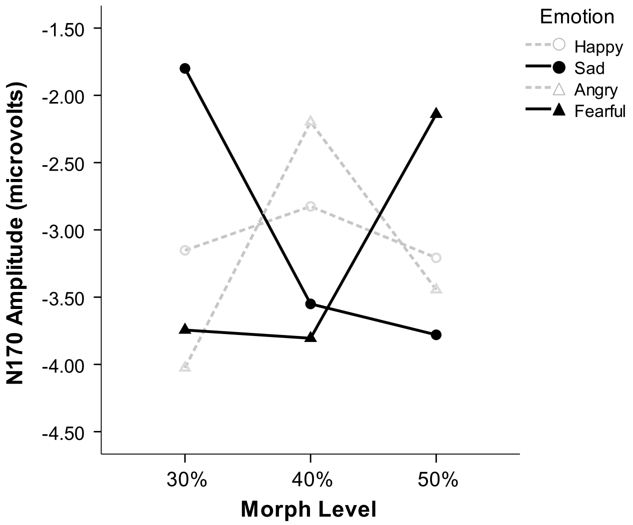


Fig. 3 N170 amplitude at the P6 site across morph levels for the different emotion types in the sleep deprivation (SD) group. *Note* 30 % is the most difficult level (i.e. 30 % emotion morphed with 70 % neutral expression). *Note Grey dashed line with open circles* Happy, *Grey dashed line with open triangles* Angry, *Black solid line with filled circles* Sad, *Black solid line with filled triangles* Fearful. N170 gets larger (more negative) with increasing perceptual difficulty for Fearful faces, while N170 gets smaller (less negative) with increasing perceptual difficulty for Sad faces

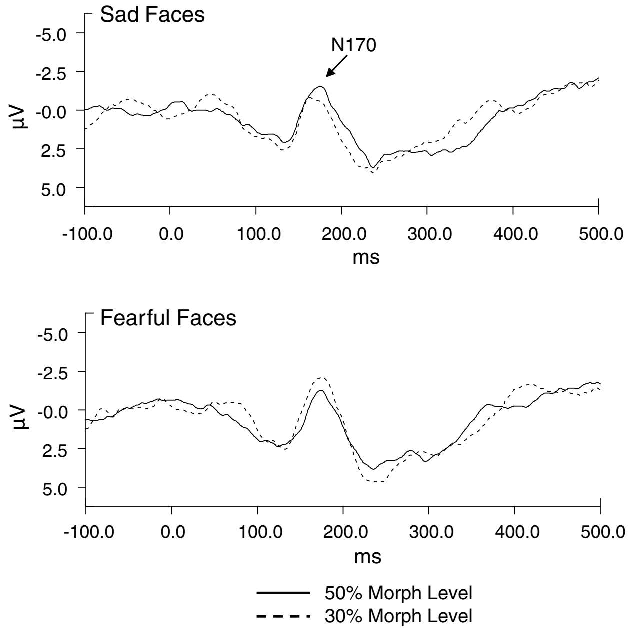


Fig. 4 Event-related potentials (ERPs) for Sad and Fearful faces at P6 in the MF task for SD group. *Solid black line* 50 % morph level; *Dashed black line* 30 % morph level (most difficult condition)

changed systematically as expressions became more subtle for both groups in the MF task, confirming the stimuli varied in perceptual difficulty as intended.

Based on the behavioural data, there was support for the hypothesis that sleep deprivation impairs perception of emotional expressions, and evidence for differential processing of the emotionally expressive faces in both tasks. In the FF task, the SD group made more errors and had longer response times overall compared to the C group. This group difference in accuracy in the FF task was most robust for the Sad faces, a finding confirmed in the more difficult MF task for which sleep deprivation impaired both accuracy and RT for Sad faces in particular. The behavioural data are in contrast to those of van der Helm et al. (2010) who reported that sleep deprivation reduced accuracy for Happy and Angry, but not Sad faces. While both studies showed a behavioural impairment in detecting emotion in faces, there were a number of methodological differences that could explain the different pattern results, such as stimulus characteristics (e.g. the specific emotions studied, and the number of models and levels of morphed faces investigated), response type (ratings of emotional intensity vs. categorization), number of trials administered, and most notably the block design implemented by van der helm et al. (presumably to be compatible with MRI), versus the rapid, random stimulus presentation in the present study with the aim to measure ERPs. Viewing blocks of faces of the same expression (e.g. viewing and rating all Angry faces) may influence arousal or affective state, whereas ERPs tap brain information processing time-locked to the perception of the stimulus qualities itself. Also, in the van der Helm et al. study, participants were asked to rate the intensity of a 'known' emotional expression (due to the fact that it occurred in a block), rather than categorize the type of expression, so that study did not address the question of whether or not sleepy participants experienced more difficulty detecting Sad faces.

In addition to impacting accuracy and RT, sleep deprivation influenced the pattern of errors when participants made incorrect responses to negatively valenced expressions. Specifically, in the FF task, the SD group was more likely than the C group to choose Happy, whereas the C group was more likely than the SD group to choose another negatively valenced emotion (e.g. to select Fear on a Sad face trial). In the MF task, the SD group was again more likely than the C group to choose Happy, but also more likely to mix up Anger and Fear, and less likely to choose Sad compared to the C group. It seems that the SD participants were less likely than C participants to choose Sad overall, regardless of accuracy, which converges with other findings in the current study pointing to an exceptionality about processing Sad faces when sleep deprived. The tendency for SD participants to choose Happy more often was consistent across the two tasks. A positive ratings bias in sleep-deprived participants has also been reported by Gujar et al. (2011) when viewing positive compared to neutral picture scenes. It is possible that SD participants choose Happy more often because of a 'rose-coloured glasses' outlook due to an affective imbalance in the sleep-deprived state (i.e. an actual misperception of the negative emotional expressions as being positive). Alternatively, the response bias may simply have been due to a tendency to select the first button of the response pad when sleep-deprived participants either 'do not know' or 'do not care'. However, it is unlikely that the ease of pressing the first button on the response pad explains this finding because in the more difficult MF task, SD participants were also more likely than C participants to choose Fear and Angry and less likely to choose Sad. Our findings suggest that following sleep deprivation, participants have a bias towards positively valenced (Happy) and high arousal (Fear, Angry, and Happy) responses. Nonetheless, counterbalancing response options across participants in future studies will clarify the reasons for the response bias on error trials.

ERP data provided a window into the impact of sleep deprivation on neural processing of faces that paralleled behavioural changes in performance. In the FF task, there were generalized impairments in visual processing that were apparent for all emotions, as seen in the smaller P1 and larger N170 amplitudes in the SD compared to C group; the analysis of covariance confirmed that the larger N170 amplitude was independent of the smaller P1 amplitudes. In the MF task, P1 was smaller in the SD group compared to C group in the 50 % morph level, but P1 increased in the SD group to the level of the C group for the more difficult 40 and 30 % conditions. More specific effects for N170 were observed for the SD group in the MF task when the expressions were more subtle. The pattern was not uniform across emotional expressions; N170 amplitude increased with perceptual difficulty level for Fearful faces and to some extent for Angry faces, but decreased with difficulty level for Sad faces.

The P1 peak is thought to index low-level visual processing (Rossion and Jacques 2008; Rousselet et al. 2008). Sleep deprivation did affect the amplitude of P1 in the FF task and in the 50 % morph level of the MF task; low-level visual processing may have been disrupted as a result of the extreme degree of sleep deprivation. In the MF task, it is possible that effort or compensation for the more difficult perceptual levels may have ameliorated these impairments in low-level visual processing. Nonetheless, the P1 effects did not vary across emotional expressions in either task and likely do not reflect face-specific processing.

In contrast, the N170 is a marker of perceptual expertise and is thought to reflect face-specific processing. There is a debate in the literature about the extent to which the N170 is sensitive to facial expressions of emotion. Several studies have shown that the N170 can be modulated by emotion (e.g. Batty and Taylor 2003; Blau et al. 2007; Meaux et al.

2013); however, some argue that such changes at the time of N170 are not due to differences in emotion per se (e.g. Eimer 2000). In the FF task of the current study, N170 was larger for the SD compared to the C participants as hypothesized; however, again these were general effects and not specific to any one facial expression. The lack of a group-by-emotion interaction in the FF task likely reflects the ease with which these intense expressions were identified (73 % for Fearful faces and > 80 % correct for all other emotions). Data from the more difficult MF task does support the hypothesis that sleep deprivation differentially impacted processing of emotional faces. When the task was made more difficult by morphing expressive faces with a neutral version of the same identity, N170 amplitude was larger in SD participants than controls, as seen in the FF task, but the interaction of emotion-by-morph level was significant only for SD participants. Specifically, in the SD group, N170 amplitude increased as the perceptual difficulty of the emotional expression increased for Angry and Fearful faces, but decreased with difficulty level for the Sad faces. Increased N170 amplitude in response to increased task difficulty is reminiscent of the finding that inverting faces in face detection tasks (another manipulation that increases task difficulty) consistently increases the latency of the N170, and in many, but not all cases, increases its amplitude (Itier and Taylor 2004; Rossion et al. 2000; reviewed in Macchi Cassia et al. 2006), despite the ability of adults to detect that the inverted stimulus is a face. These effects have been attributed to increased task difficulty increasing the activation of face-specific networks or to more widespread neural recruitment (e.g. the involvement of object areas; Sadeh and Yovel 2010). The larger N170 observed in response to Angry and Fearful faces following sleep deprivation likely reflects a similar increase in reactivity and/or that additional cortical resources were being engaged. The opposite was observed for Sad faces; N170 decreased as the perceptual difficulty of the emotional expression increased. Thus, the ERP data, consistent with the behavioural data, illustrate that greater brain resources were engaged in order to accurately identify the threat-related faces, but such compensation was not realized for the Sad faces. These differential patterns do not likely reflect differences in task difficulty across emotional expressions because accuracy was lowest for Fearful expressions, yet it was Sad expressions that were especially impaired by sleep deprivation. Further, accuracy and RT were similar for Angry and Sad expressions and yet the relationship between task difficulty and N170 amplitude was similar for Angry and Fear (the least well-recognized expression) and opposite for Sad.

Data from the current study show that sleep deprivation differentially impacts the processing of emotionally expressive faces at early stages of information processing, but what remains unknown is the exact process captured by the N170. The N170 may reflect emotion perception per se; alternatively, it may reflect a precursor to emotion perception such as detection of featural cues (e.g. furrowed brows, raised lips). There is a similar debate about whether the N170 peak indexes structural encoding of the facial features (e.g. eye size) that help us to discriminate faces (Eimer 2000; Zheng et al. 2011) or facial identity per se (Jacques et al. 2007; see Zheng et al. 2012 for evidence that identity perception is first reflected in the N250). Further research is needed to address this important question, perhaps by including neutral faces for comparison and examining later stages of information processing (e.g. P300).

What is so special about Sad faces? There are a number of things that are unique about Sad faces relative to other types of emotional expressions that may shed light on why sleep deprivation preferentially impacted the processing of Sad faces. From an evolutionary perspective, Sad faces are relatively less salient or important for one's own survival and well-being than the threat-related Angry and Fearful faces, and thus Sad faces may simply be allocated less attention when cognitive resources are limited by a challenge like sleep deprivation. A psychological view may be that because sleep deprivation impacts subjective mood, one's internal mood state may impact how emotional information is processed, i.e. that information processing may mirror the subjective state (van der Helm et al. 2010). Further, as a highly self-relevant emotion, Sad may be more difficult to recognize in others and that difficulty may be exacerbated by sleep loss. In a similar vein, sleep deprivation may reduce the ability to empathize; it may be better to focus on oneself for survival than to waste energy being concerned with others. From a cognitive perspective, Sad faces may be more vulnerable to sleep deprivation because they require more effortful or controlled processing, as opposed to the threat-related faces that are processed more automatically. Research shows that sleep deprivation tends to affect top-down control of attention and vigilance (e.g. Goel et al. 2009; Harrison and Horne 2000; Humphrey et al. 1994; Killgore 2010). From a neurocognitive perspective, Sad faces may be processed differently because they are associated with lower autonomic and CNS arousal (Adolphs 2002) relative to the other common emotional expressions. The circumplex model (e.g. Bullock and Russell 1984) places emotions on gradients along dimensions of arousal and valence. Anger and Fear are both high arousal, negatively valenced emotions, whereas Sad is unique in the quadrant representing low arousal and negative valence. As a low arousal, negatively valenced emotion, Sad facial expressions might be particularly vulnerable during sleep deprivation because arousal systems are so profoundly impacted during extended wakefulness. Indeed, the brain areas involved in face processing (e.g. fusiform gyrus, occipital, and temporal cortices; Haxby et al. 2002), and emotion recognition (e.g. amygdala, basal ganglia, orbitofrontal, occipital, and parietal regions; Adolphs 2002), are widespread and overlapping with areas controlling arousal.

Despite a long history of research demonstrating mood instability as a result of sleep loss, few studies have examined physiological response to emotional stimuli. Future research in this area should measure both autonomic and CNS measures of reactivity to emotional facial expressions, as well as other modalities of emotional information (e.g. words, pictures, and music). Examining varying levels of sleep loss is important to demonstrate the role of sleep in emotion processing; however, less extreme degrees of sleep disruption may influence the N170 ERP differently when low-level visual processing is not disrupted (as seen with the P1 ERP in the present study). The extent to which sleep deprivation disrupts processing of emotion per se can be studied further by including neutral faces and images for comparison, and by examining the effects on later stages of information (e.g. by using target detection tasks where specific emotional expressions must be identified in a series or array of other expressions). Further, given the recent findings of Rosales-Lagarde et al. (2012), it would be of interest to examine the contributions of REM sleep to emotion regulation and processing. Lastly, an important avenue for research will be to examine the role of personality and emotional style in the sleep-loss-related changes in emotion processing.

Accurate processing of emotion in faces is important for social interaction and survival, and thus, sleep-loss-related impairment in processing emotion in faces has significant consequences for many groups that are acutely or chronically sleep deprived. In the current study, behavioural and neurophysiological data converged to show that processing of Sad faces in particular was disrupted following total sleep deprivation. Impairment in processing Sad faces as a result of sleepiness may contribute to a lack of empathy that has been described in specific professions such as medical, military, or policing. These findings have widespread implications for understanding the impact of sleep loss on brain function related to emotion and behaviour, and may be particularly important for groups where there is a sleep and affective component, such as children, adolescents, or psychiatric populations.

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