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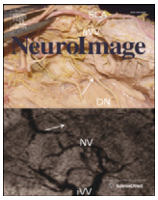

Reduced visual processing capacity in sleep deprived persons

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A B S T R A C T

Multiple experiments have found sleep deprivation to lower task-related parietal and extrastriate visual activation, suggesting a reduction of visual processing capacity in this state. The perceptual load theory of attention (Lavie, 1995) predicts that our capacity to process unattended distractors will be reduced by increasing perceptual difficulty of task-relevant stimuli. Here, we evaluated the effects of sleep deprivation and perceptual load on visual processing capacity by measuring neural repetition-suppression to unattended scenes while healthy volunteers attended to faces embedded in face–scene pictures. Perceptual load did not affect repetition suppression after a normal night of sleep. Sleep deprivation reduced repetition suppression in the parahippocampal place area (PPA) in the high but not low perceptual load condition. Additionally, the extent to which task-related fusiform face area (FFA) activation was reduced after sleep deprivation correlated with behavioral performance and lowered repetition suppression in the PPA. The findings concerning correct responses indicate that a portion of stimulus related activation following a normal night of sleep contributes to potentially useful visual processing capacity that is attenuated following sleep deprivation. Finally, when unattended stimuli are not highly intrusive, sleep deprivation does not appear to increase distractibility.

Introduction

Deficits in attention are an important contributor to cognitive performance degradation after a night of sustained wakefulness (Lim and Dinges, 2010). This reduced ability to focus limited mental resources on salient information and tasks at a given moment can take several forms, specifically the impairment of sustained (Chee et al., 2008; Doran et al., 2001; Tomasi et al., 2009), selective (Chee et al., 2010; Horowitz et al., 2003; Lim et al., 2010; Mander et al., 2008) and divided attention (Drummond et al., 2001).

Across different imaging experiments assessing changes in attention in sleep deprived persons, reduced task-related activation has been found to correlate with behavioral impairment. Interestingly, attenuation of brain activation at different task loads (Chuah and Chee, 2008) or levels of perceptual difficulty (Chee and Tan, 2010) has been observed even with correct trials, suggesting that a portion of the higher task-related activation observed after a normal night of sleep might correspond to spare information processing capacity. Supporting this hypothesis, maintained or increased task-related activation during SD often corresponds with less compromised or maintained task performance (Chee and Tan, 2010; Chee and Choo, 2004a; Drummond et al., 2005).

The implied spare processing capacity associated with relatively higher task-related activation in the rested state could have utility in processing unattended but consequential stimuli. For example, while driving in the rain and focused on difficult road conditions, it would be helpful to retain the capacity to detect important but unattended road signs.

The perceptual load theory of attention (Lavie, 1995) provides a useful framework for evaluating SD-induced change in visual information processing. According to this model, focusing attention on a task-relevant stimulus inhibits the processing of task-irrelevant distractors to the extent that available perceptual processing capacity is engaged in processing the task-relevant stimulus. Conversely, if the task-relevant stimulus places low demands on the perceptual system, spare capacity becomes available to perceive the unattended distractors (Forster and Lavie, 2007; Pessoa et al., 2005; Rees et al., 1997).

Unattended distractor processing can be inferred from the magnitude of fMRI signal suppression related to distractor repetition as the latter scales with the extent to which these are perceived (Yi et al., 2004). Critically, when faces are task-relevant and background scenes are distractors, the spatial dissociation of brain regions maximally activated by the two types of images permits activation associated with the distracting scenes to be evaluated relatively free from being confounded by face stimulus-related signal. Examining how perceptual load interacts with state to modulate repetition suppression can thus be used to determine how SD affects visual processing capacity.

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To test the hypothesis that SD reduces visual processing capacity, participants were instructed to detect repeated faces in successive composite pictures comprising face photographs at the center of a larger background scene (Yi et al., 2004). Perceptual load was manipulated by altering the clarity of the central faces. To assess repetition suppression, the accompanying background scenes were either novel or repeated and MR signal in the PPA was measured. We expected to find preserved repetition suppression for distractor scenes irrespective of load during rested wakefulness (RW) but reduced repetition suppression for the high perceptual load condition in SD.

Materials and methods

Participants

Eighteen healthy right-handed participants (mean age 22.1 ± 2.0 years) were selected from respondents to a web-based questionnaire who fulfilled the following criteria: (1) have habitual good sleeping habits (sleep no less than 6.5 h/night), (2) not be of extreme morning or evening chronotype (score no greater than 22 on a modified Morningness–Eveningness scale (Horne and Ostberg, 1976), (3) not be on any long-term medications, (4) have no symptoms associated with sleep disorders, and (5) have no history of any psychiatric or neurologic disorders.

The sleeping pattern of each participant was monitored and only those whose actigraphy data indicated habitual good sleep (i.e., sleeping no later than 1:00 AM and waking no later than 9:00 AM) entered the study after giving informed consent. All participants indicated that they did not smoke, consume any medications, stimulants, caffeine or alcohol for at least 24 h prior to scanning.

Experimental design and stimuli

The experiment investigated how SD and perceptual load influence the magnitude of repetition suppression associated with unattended scenes while volunteers attended to faces in face-scene composite pictures (Fig. 1A). To uncover repetition effects, scenes were either completely unique in successive frames or repeated in alternating frames. To manipulate perceptual load, the central faces were either undistorted (low-load trials) or visually degraded (high-load trials) by the addition of 25% salt and pepper noise. A within-subject design was used so each participant underwent both RW and SD sessions as described below.

Within each session, participants completed 5 runs of the task, each lasting 432 s. Each run consisted of 12 high-load and 12 low-load trials. Each trial comprised a series of 6 emotionally neutral grayscale faces (2.8°×2.8°) that occluded the center of a larger outdoor scene (9.8°×9.8°). Each face-scene frame was shown for 500 ms, followed by a 500 ms checkerboard mask. To ensure attention to the central faces, participants were asked to detect whether the face was repeated within the trial. They responded at the end of the trial when a blank screen was presented for 3000 ms. Within each run, only 4 out of 24 trials contained repeated faces. These repeated faces occurred in a random position within the trial and with equal frequency in trials involving repeated and non-repeated scenes. A fixation cross was shown for 9000 ms before the next trial began.

Participants viewed task stimuli using MR-compatible LCD goggles (Resonance Technology, Los Angeles, CA, USA) and responded with a button box held in the right hand. An eye-camera was used to continuously monitor eyelid closures. Participants were prompted through the intercom system whenever they failed to respond to two consecutive trials.

Study procedure

Participants visited the lab three times, approximately once a week. The first visit was a briefing session during which they were informed about the study procedure and requirements. They also practiced two runs of the task. At the end of this session, the participants were given a wrist actigraph (Actiwatch, Philips Respironics, USA) to wear throughout the study. Participants were scanned twice, once during RW and once following SD. The order of the scans was counterbalanced across participants.

RW scans took place at 8:00 AM. For the SD session, participants were monitored in the laboratory from 6:00 PM onwards, and scanning took place at 6:00 AM the next day. Participants were allowed to engage in non-strenuous activities such as reading, watching videos and conversing. Every hour throughout the study night, they performed a short battery of psychometric tests.

Imaging procedure

Images were acquired on a 3-Tesla Tim Trio system (Siemens, Erlangen, Germany). A gradient echo-planar imaging sequence with TR 2000 ms, TE 30 ms, FA 75°, FOV 192×192 mm and a 64×64 pixel matrix was used to acquire functional images. Thirty-six oblique axial slices (3 mm thick with a 0.3 mm inter-slice gap) parallel to the AC–PC line were acquired. High-resolution coplanar T1-weighted anatomical images were also obtained for image registration. For the purpose of image display in Talairach space, an additional high-resolution anatomical reference image was acquired by using an MPRAGE sequence (TR 2300 ms, TI 900 ms, flip angle 9°, BW 240 Hz/pixel, FOV 256×240 mm, 256×256 matrix; resulting voxel dimensions: 1.0×1.0×1.0 mm).

Functional localizer scans were conducted at the end of the last run to identify the PPA and FFA for each individual participant (Epstein et al., 2003; Epstein and Kanwisher, 1998). This comprised four runs, each of which consisted of 24 alternating scene and face blocks interleaved with fixation. Six face or scene images were shown in each block, each appearing for 800 ms followed by a 200 ms checkerboard mask. Stimuli used in the localizer runs had identical dimensions as those used in the main experiment, except that a scene stimulus consisted of a scene occluded by a checkerboard instead of a face, and a face stimulus consisted of a face surrounded by a checkerboard instead of a scene (Fig. 1B).

Image analysis

The functional images were processed using Brain Voyager QX version 1.10. (Brain Innovation, Maastricht, The Netherlands). All functional images were realigned using rigid-body transformation to the first image of the functional run that was acquired immediately before the coplanar T1-weighted image. Inter-slice timing differences attributable to slice acquisition order were adjusted using trilinear and sinc interpolation. Gaussian filtering was applied in the spatial domain by using a smoothing kernel of 4-mm FWHM for individual level activation maps. The T1-weighted images were used to register the functional data set and the resulting aligned images were transformed into Talairach space.

The functional imaging data was analyzed by using a general linear model with four predictors, one for each condition (low-load non-repeated background, low-load repeated background, high-load non-repeated background and high-load repeated background), in both states. Incorrect and missed trials, if any, were modeled using a separate predictor. Each predictor was created by convolving relevant trials (each 6 s duration) with a canonical double gamma hemodynamic response function.

The PPA was defined in each individual using the contrast of scene versus face blocks in the functional localizer scans. The resulting

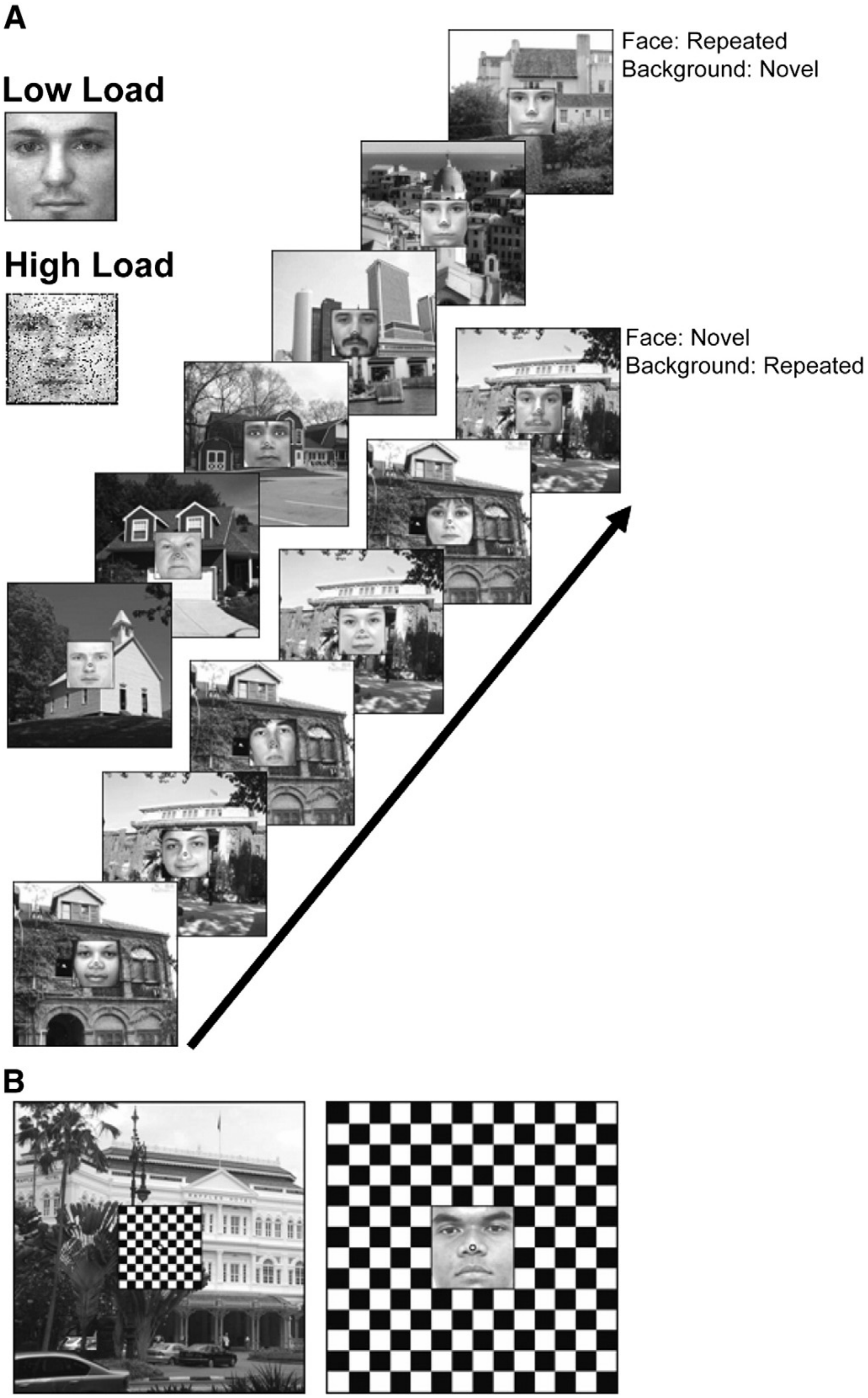

Fig. 1. Schematic of the experimental task. (A) Each trial consisted of a series of six scene–face composite pictures, each shown for 500 ms, followed by a 500 ms checkerboard mask (not shown in figure). Faces were either undistorted (low-load condition) or degraded with salt and pepper noise (high-load condition). Surrounding each face were either alternately repeated (lower series) or completely non-repeated background scenes (upper series). After all frames had been presented, participants were given 3000 ms to indicate whether any face was repeated (upper series). A fixation cross was shown for 9000 ms before the next trial began. (B) Examples of scene and face stimuli used in the functional localizer task. The stimuli had the same dimensions as those used in the primary task.

contrast maps were thresholded at $p<0.05$ (Bonferroni corrected) to derive a mask for the subsequent ROI analysis. Within this masked region, the 15 functional voxels ($3\times3\times3$ mm each) that showed the highest parameter estimates (PE) across state ($PE_{RW}+PE_{SD}$) in the low-load, non-repeating background images were used for the determination of repetition suppression effects in an unbiased fashion. This procedure was repeated using a 10 voxel cut-off to verify that the result would be robust to changing thresholds (Park et al., 2004). An identical procedure was used to identify the FFA.

To assess the magnitude of repetition suppression at these functionally determined ROI, normalized repetition suppression indices: $(PE_{\text{Non-repeat}} - PE_{\text{Repeat}})/PE_{\text{Non-repeat}}$ were computed for each load and state and further analyzed using 2-way repeated-measures ANOVA. Only correctly responded trials were analyzed.

Results

Behavioral results

Sleep deprivation was associated with fewer correct detections of face repetition ($F_{1,\ 17} = 13.68$, $p < 0.001$; Fig. 2), more false alarms ($F_{1,17} = 6.17$, $p < 0.05$) and more non-responses ($t_{17} = -4.42$, $p < 0.01$).

There was a main effect of load ($F_{1,\ 17} = 13.30$, $p < 0.001$) on accuracy. Participants detected the face repetition better in the low-load condition relative to the high-load condition in both states (RW: $t_{17} = 4.52$, $p < 0.001$; SD: $t_{17} = 1.83$, $p < 0.05$; Fig. 2).

Imaging findings

Repetition suppression within the PPA, an indication of residual capacity to process unattended stimuli, was the primary measure of visual processing capacity. There was a main effect of load ($F_{1,\ 17} = 5.94$, $p < 0.05$) but not state ($F_{1,\ 17} = 0.70$, n.s.) on the repetition suppression index. Critically, there was a significant interaction between load and state ($F_{1,\ 17} = 7.31$, $p < 0.01$, Fig. 3B). Post-hoc t-tests showed that repetition suppression was significantly greater than zero in both RW conditions (low-load: $t_{17} > 3.67$, $p < 0.01$; high-load: $t_{17} > 3.43$, $p < 0.01$) and SD low-load condition ($t_{17} > 6.09$, $p < 0.01$), but not in SD high-load condition ($t_{17} > -0.27$, n.s.). Similarly significant results were obtained with 15 functional voxel and 10 functional voxel PPA masks. These data support the main hypothesis that SD reduces visual processing capacity.

Additionally, attenuation of repetition suppression correlated with change in FFA activation across state ($r = 0.50$, $p < 0.05$; Fig. 4B). The reduction in response to faces in the FFA ($F_{1,\ 17} = 53.65$, $p < 0.0001$) was a second, albeit indirect marker of reduced visual processing capacity during SD, as suggested by the positive correlation between SD-related attenuation of FFA activation and reduction in performance accuracy across state ($r = 0.44$, $p < 0.05$; Fig. 4A).

Additionally, the SD-related drop in FFA activation correlated with an altered differential in PPA activation across load during SD ($r = 0.47$, $p < 0.05$; Suppl. Fig. 1B). Lower PPA activation in the high-load relative to low-load conditions during SD might correspond to the expected reduction in residual processing resources available for unattended house processing with increased perceptual load and sleep deprivation. (Note that as PPA signal is largely inconsequential to the detection of face repetition it did not correlate with behavior.)

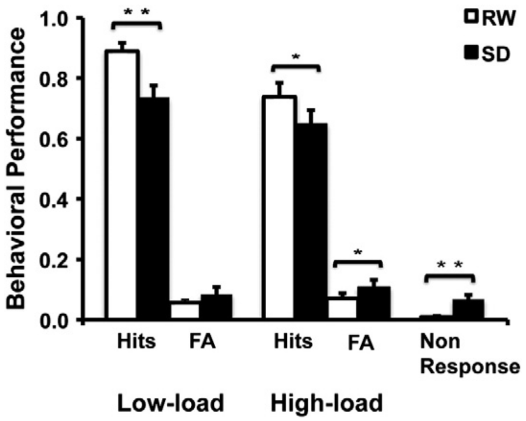

Fig. 2. Behavioral results. Face repetition detection performance as measured by hit and false alarm (FA) rates during RW and SD in both low-load and high-load conditions. Error bars indicate standard error. (*, $p < 0.05$; **, $p < 0.01$).

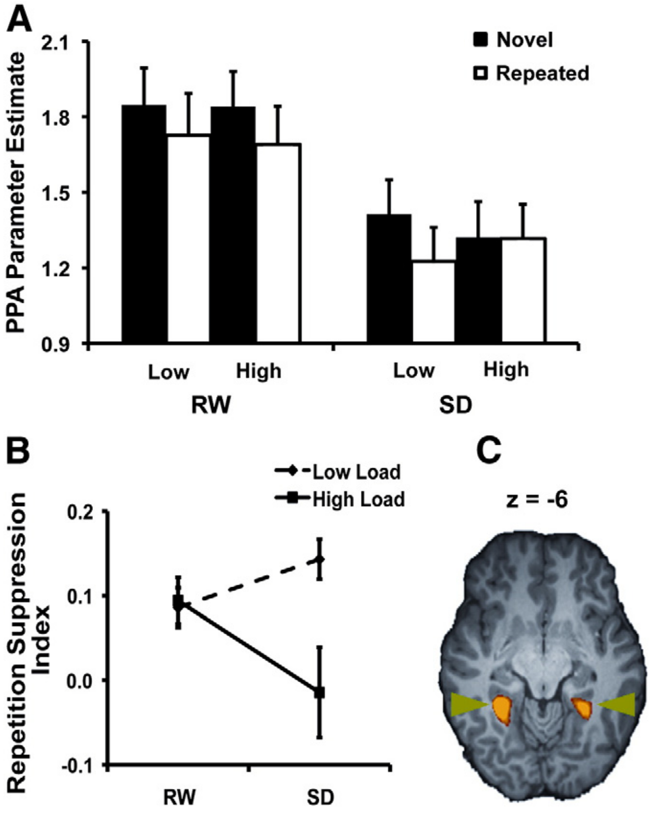

Fig. 3. Activation and repetition suppression effects in PPA. (A) Activation in the PPA corresponding to the different task conditions in each of the two states (*, $p < 0.05$; **, $p < 0.01$). (B) Repetition suppression index during RW and SD in the PPA as a function of perceptual load. Significant state by load interactions were present ($F_{1,\ 17} = 7.31$, $p < 0.01$). (C) Group activation map showing the PPA ($p < 0.05$, Bonferroni corrected; Averaged Talairach Coordinates, left PPA: −29 −50 −11; right PPA: 26 −47 −7). Note that the figure is primarily for illustrative purposes as repetition suppression was determined from individual ROIs.

To determine the robustness of the aforesaid state effects in ventral visual cortex activation, we examined the functional localizer data obtained in both RW and SD conditions. Significant decrement in both PPA ($t_{17} > 3.99$, $p < 0.0001$) and FFA activation was observed ($t_{17} > 4.59$, $p < 0.0001$) (Suppl. Fig. 2A). There was also significant correlation between reduced repetition suppression across state and the attenuation of FFA activation ($r = 0.62$, $p < 0.01$; Suppl. Fig. 2B).

To identify potentially important effects not evident in the ROI-based analyses within higher-order visual cortex, we conducted a whole brain voxel level ANOVA. Task-related activation was observed in all 4 conditions within brain regions that comprise the task-positive network (inclusive of bilateral prefrontal regions, bilateral intra parietal sulcus (IPS) and the medial frontal region; Suppl. Fig. 3B). During RW, increase in perceptual load was associated with higher activation in the bilateral frontal eye fields (FEF) ($t_{17} > 2.50$, $p < 0.05$) and bilateral IPS ($t_{17} > 1.98$, $p < 0.05$). There was an effect of state in bilateral FEF ($t_{17} > 3.15$, $p < 0.01$) and IPS ($t_{17} > 2.9$, $p < 0.01$) (Suppl. Fig. 3A). No area showed an interaction of state and perceptual load.

Discussion

We found evidence for reduced visual perceptual processing capacity in sleep deprived young adults in the form of attenuated

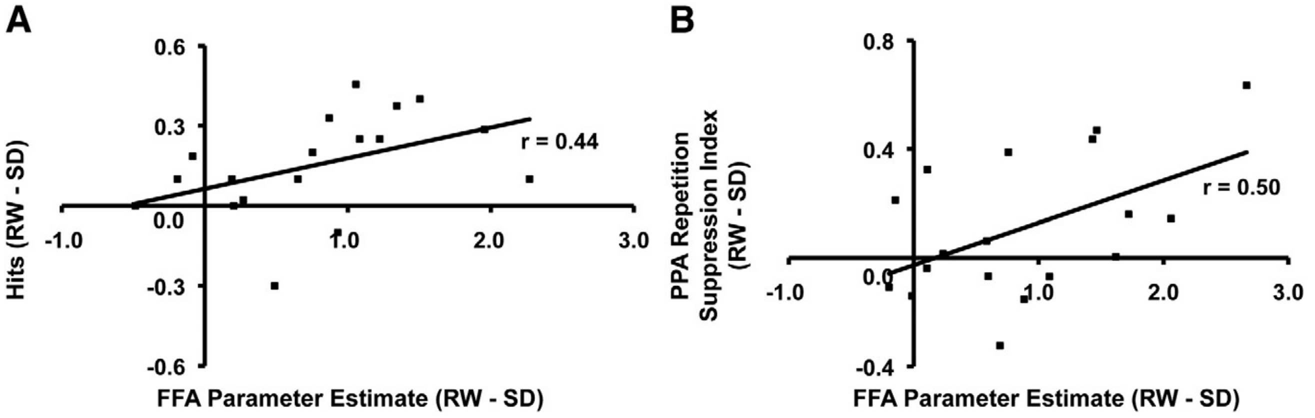

Fig. 4. Correlations between FFA activation, behavioral performance and PPA activation. (A) Significant positive correlation ($r = 0.44$; $p < 0.05$) between SD-related reduction in FFA (Averaged Talairach Coordinates, left FFA: −43 −56 −13; right FFA: 38 −54 −14) activation during the main task and the magnitude of performance impairment across states. (B) Significant correlation between state-related reduction in FFA activation and PPA repetition suppression index following SD ($r = 0.05$; $p < 0.05$).

repetition suppression to unattended place scenes when the perceptual load associated with attended faces was high. Additionally, we found that reduction in FFA activation following sleep deprivation may be a secondary marker of lowered processing capacity as it was correlated with behavioral performance (face repetition detection) as well as attenuated repetition suppression.

Sleep deprivation reduces capacity to process task-irrelevant distractors

As predicted by the perceptual load model of attention (Lavie, 1995; Lavie et al., 2004) we found that perceptual difficulty and sleep deprivation interact to attenuate the limited visual processing capacity available for the unattended pictures. This conclusion is indirect and founded on the premise that the magnitude of repetition suppression indexes 'meaningful' information processing. Prior functional imaging studies have shown that higher repetition suppression to be related to memory strength (Turk-Browne et al., 2006) and superior navigational ability (Epstein et al., 2003; Epstein et al., 2005).

As the magnitude of activation and repetition suppression are often positively correlated (Chee and Tan, 2007), lower repetition suppression in the SD condition could potentially be due to reduced ventral visual cortex activation. However, this is unlikely here as the repetition suppression index used was normalized to take into account varied levels of activation to non-repeated place scenes across individuals and state. Perhaps more significantly, repetition suppression in the low-load condition following SD resembled that in RW, indicating that lower activation does not obligate reduced repetition suppression (Turk-Browne et al., 2007).

The significant associations between state-related decline in FFA activation, performance accuracy and repetition suppression in the PPA suggest that state-related change in FFA can also index perceptual processing capacity in SD. Interestingly, although the effect of increasing perceptual load was evident from reduced face repetition detection accuracy and higher fronto-parietal activation during RW, it was not evident in the FFA in either state. The perceptual load theory (Lavie, 1995; Lavie et al., 2004) predicts that under conditions of higher perceptual load, there would be stronger responses to target stimuli and weaker responses to distractors. This has been demonstrated in an ERP study (Rorden et al., 2008). However, the current findings replicate previous results using the same experimental design (Yi et al., 2004) and are likely the consequence of the opposing effects of stimulus visibility, which lowers visual cortex activation (Gläscher et al., 2007; Rose et al., 2005; Turk-Browne et al., 2007) and increase exercise of top-down control when stimuli are more difficult to perceive (Marois et al., 2004).

Distractors did not interfere with performance of central task

Optimal task performance requires us to maintain selective attention. Conversely, increased distractibility compromises performance. Such failure to inhibit task-irrelevant distractors has been shown to contribute to performance degradation in healthy elderly persons (Clapp et al., 2010; Gazzaley et al., 2005, 2008).

Although we and others have drawn parallels between the negative cognitive impact of sleep deprivation and cognitive aging (Chee and Choo, 2004b; Habeck et al., 2004; Harrison et al., 2000), increased distractibility of the type observed in previous experiments on healthy elderly was not apparent here. Had it been, we would have observed increased rather than decreased repetition suppression in the SD conditions. Additionally, had processing resources been diverted to the unattended scenes, reduced FFA activation during SD would have been accompanied by either preserved or elevated PPA activation and/or intact repetition suppression in the high-load condition. Neither was observed here.

A critical caveat is that in the current experiment we evaluated how execution of a central task would affect the processing of unattended distractors instead of examining how distractors *interfere* with task performance. The placement of task-relevant faces at the center and task-irrelevant scenes in the periphery would be expected to make the latter less of a distraction than had faces and scenes completely overlapped (O'Craven et al., 1999). The ability or failure to suppress distractors in the context of SD remains to be further evaluated in future experiments.

Functional utility of 'superfluous' task-related activation

Across several studies, SD-vulnerable individuals have been found to show greater decline in task-related activation when sleep deprived (Chee and Tan, 2010; Chuah and Chee, 2008; Lim et al., 2007). As only correct responses were analyzed in these experiments, trials in which reduced activation could be attributed to volunteers falling asleep were excluded. While mindful of the neural efficiency model which suggests that efficient brains activate *less* to successfully accomplish a given task (Rypma and Prabhakaran, 2009), we hypothesized that the relatively higher mean task-related activation during RW has functional value (Chuah et al., 2009). A crucial point in our argument is that the relevant comparison concerns activation elicited by the same person performing the identical task but under two different states.

Reduced activation during SD may indicate that neurons or circuits functional during RW go 'off-line' during SD. While not affecting the ability to respond correctly for the given trial, there are nevertheless consequences. Support for this hypothesis comes in the form of an observation that better learners in a perceptual learning task showed higher initial activation within the extrastriate visual cortex and fronto-parietal areas of the attentional network (Mukai et al., 2007). In the current experiment, participants showing a greater decrement in FFA activation following SD were those showing larger declines in performance accuracy and loss of repetition suppression in the PPA under conditions of high perceptual load, providing the most direct evidence of the functional significance of higher task activation in the RW state.

The current findings also provide a parsimonious re-interpretation of prior data that suggested persons with higher task-related activation during RW were more resistant to SD (Chee et al., 2006; Mu et al., 2005). This conclusion was not replicated when volunteers were re-studied (Lim et al., 2007). However, re-examination of these studies and others that have followed (Chee and Tan, 2010; Chee et al., 2010; Chuah and Chee, 2008) indicate that it is not the higher level of activation in RW that is critical but the fall in activation following SD that is critical.

Conclusion

Sleep deprivation can impair cognitive performance by reducing visual processing capacity. This was indexed by the attenuation of repetition suppression to unattended stimuli as well as the change in task-related activation to attended stimuli across state. When the unattended stimulus is not particularly intrusive, sleep deprivation does not appear to increase the effect of such distractors.

Supplementary data to this article can be found online at doi: 10.1016/j.neuroimage.2010.12.057.

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