Functional imaging correlates of impaired distractor suppression following sleep deprivation

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ABSTRACT

Sleep deprivation (SD) has been shown to affect selective attention but it is not known how two of its component processes: target enhancement and distractor suppression, are affected. To investigate, young volunteers either attended to houses or were obliged to ignore them (when attending to faces) while viewing superimposed face–house pictures. MR signal enhancement and suppression in the parahippocampal place area (PPA) were determined relative to a passive viewing control condition. Sleep deprivation was associated with lower PPA activation across conditions. Critically SD specifically impaired distractor suppression in selective attention, leaving target enhancement relatively preserved. These findings parallel some observations in cognitive aging. Additionally, following SD, attended houses were not significantly better recognized than ignored houses in a post-experiment test of recognition memory contrasting with the finding of superior recognition of attended houses in the well-rested state. These results provide evidence for co-encoding of distracting information with targets into memory when one is sleep deprived.

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Introduction

Given limited time to analyze a cluttered scene, it quickly becomes evident that remarkable as the visual system is, it has finite processing capacity. Such capacity limits can be revealed in controlled settings through experiments evaluating visual search, visual short-term memory capacity or the attentional blink (Marois and Ivanoff, 2005). The results of goal-directed visual searches performed under time constraints can be improved by being selective about what we attend to and by suppressing task-irrelevant distractors (Dux and Marois, 2008). Realizing such 'focus' can benefit the identification of threatening persons, objects or medically significant image features.

In real life, security screening, baggage threat detection and emergency radiological diagnosis involve complex visual environments that are often carried out by fatigued and sleep-deprived persons. Contrastingly, investigations into visual attention have largely focused on relatively well-rested individuals (Kastner and Ungerleider, 2000). Filling the gap, functional imaging studies of attention in sleep-deprived persons (Drummond et al., 2005; Tomasi et al., 2009; Tucker et al., 2011a) have demonstrated that lateral fronto-parietal cortices, which are responsible for the biasing of attention or cognitive control, showed attenuated activation (Chee and Tan, 2010; Chee et al., 2008, 2011). Accompanying the lowered biasing signals is reduced ventral

visual cortex activity (Chee et al., 2010; Lim et al., 2010) whose shift across states correlates with behavioral performance decline (Chee and Chuah, 2008; Chee and Tan, 2010), contributing to our understanding of the mechanisms underlying altered behavior in sleep-deprived persons.

Relevant to the present study, the downstream effects of eroded top down control of selective attention include reduced visual cortex activation in a visual-category specific manner. Examining how selectively attending to faces or place scenes differentially influences maximal parahippocampal place area (PPA) activation across states has enabled the detection of loss of selectivity of attention as well as reduced perceptual processing capacity following SD. Selectivity is evidenced by the differential activation of PPA for attended and ignored place pictures when viewing pictures containing a mixture of places and faces. In contrast, examining activation in the fronto-parietal areas in this setting does not help discern loss of selectivity nor does this activity distinguish between the enhancement of targets and the suppression of distractors. Signals relating to target enhancement or distractor suppression are both top-down signals generated by fronto-parietal regions and can contribute to differential activation of the PPA in response to attended places/ignored faces relative to attended faces/ignored places.

Early studies of selective attention focused on the top-down enhancement or facilitation of relevant target information (Gazzaley et al., 2005b; Kastner and Ungerleider, 2000) but subsequent investigations have revealed that irrelevant spatial locations, features or objects are not simply passively ignored, they are also actively suppressed (Neumann and DeSchepper, 1991; Reynolds and Chelazzi, 2004;

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Wegener et al., 2008). The behavioral advantage of selective attention may thus arise from reduced interference from irrelevant information at early stages of visual processing (Rutman et al., 2010). Although it is well established that selective attention can be impaired following a night of total SD, it is not known if target enhancement and suppression are equally affected or if the latter is more severely depressed.

Although some contrary views have emerged (Tucker et al., 2011b), most behavioral studies on healthy cognitive aging have shown loss of cognitive inhibition to be a core cognitive deficit perhaps second only to the decline in speed of processing (Hasher and Zacks, 1988; Salthouse, 2000). Recent functional imaging studies (Gazzaley et al., 2005a, 2008; Zanto and Gazzaley, 2009) suggest that enhancement and suppression represent at least two, partially dissociable neural mechanisms that can account for performance decline associated with cognitive aging. Compared to their younger counterparts, healthy older adults show lower suppression of task-irrelevant distractors despite having relatively intact enhancement of task-relevant stimuli (Gazzaley et al., 2005a).

In keeping with investigations showing similarities between functional deficits in cognitive aging and sleep deprivation (Harrison et al., 2000), we predicted the existence of dissociable effects of SD on brain activation involving preserved enhancement of attended objects and impaired suppression of distractors. To test this hypothesis, we presented participants with a stream of spatially superimposed house and face images (O'Craven et al., 1999; Yi and Chun, 2005), instructing them to selectively attend to either faces or houses. Enhancement and suppression of houses as a function of attention or inhibition were assessed relative to the activation elicited by the passive viewing of similar superimposed face/house pictures. To ensure that altered suppression of irrelevant distracters was not masked by inter-individual variation in tolerance to sleep deprivation, each volunteer was studied twice, once following a night of adequate sleep and again after a night of total sleep deprivation.

Materials and methods

Participants

Twenty-two healthy right-handed participants (mean age 20 ± 1.3 years; 11 females) took part in this study. All participants provided informed consent, in compliance with a protocol approved by the National University of Singapore Institutional Review Board. They were selected from respondents of a web-based questionnaire who: (1) were right-handed, (2) had regular sleeping habits, (3) slept no less than 6.5 hours/night, (4) were not on any long-term medications, (5) had no symptoms of, or history of sleep disorders, (6) had no history of psychiatric or neurologic disorders and (7) drank less than 3 caffeinated drinks per day.

The sleeping pattern of each participant was monitored throughout the entire duration of the study and only those whose actigraphy data indicated habitual good sleep (i.e. sleeping no later than 12:30 AM and waking no later than 9:00 AM) were recruited following informed consent. All participants indicated that they did not smoke, consume any medication, stimulants, caffeine or alcohol for at least 24 hours prior to scanning.

Study procedure

Participants made three visits to the laboratory. The first was a briefing session during which they were informed about the study protocol and requirements. Suitable volunteers also practiced one run of the study task. At the end of this session, the participants were given a wrist actigraph (Actiwatch, Philips Respironics, USA) to wear throughout the study to verify regular and adequate sleeping patterns.

Each participant was scanned twice, once during rested wakefulness (RW) and once following SD. The order of the scans was counterbalanced across participants, and the sessions were separated by approximately 1 week to minimize residual effects of sleep deprivation on cognition for participants who underwent the SD session first.

RW scans took place at 8:00 AM. For the SD session, participants arrived at the laboratory at 6:00 PM, after staying awake the whole day without napping. They were subsequently monitored in the laboratory. SD scans took place at 6:00 AM the next day. During the SD session, participants were allowed to engage in non-strenuous activities such as reading, watching videos and conversing. Vigorous physical activity prior to the scans was not permitted. Every hour throughout the study night, participants performed a short battery of psychometric tests comprising of Psychomotor Vigilance Task (Dinges et al., 1997), a Likert-type rating scale (0–10) of motivation, fatigue and mood and Karolinska Sleepiness Scale (Åkerstedt and Gillberg, 1990).

Experimental design

The experiment investigated how SD influences top-down enhancement and suppression of activation in ventral visual cortex. The task stimuli were grayscale images of faces, houses and superimposed house-face images ($8° \times 8°$). The images were not repeated and
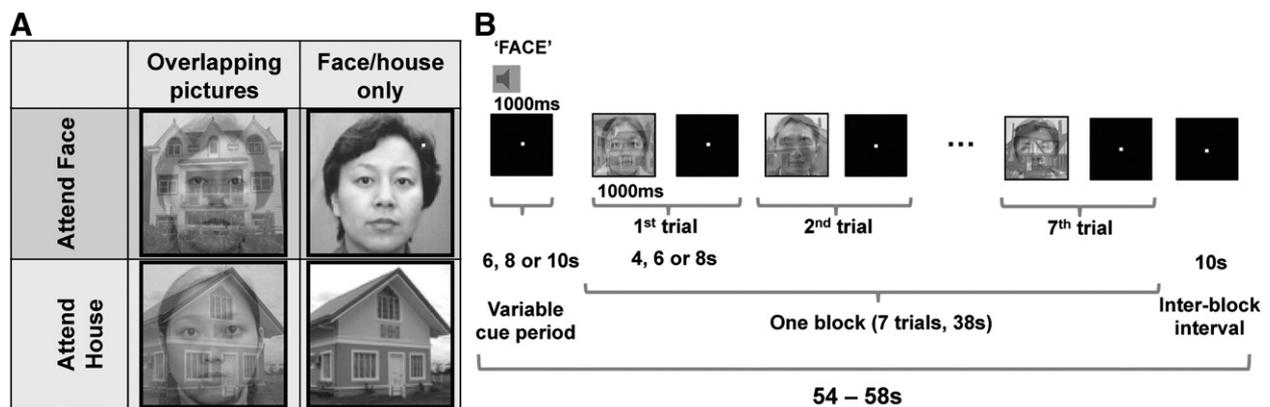

Fig. 1. Schematic of the experimental design. (A) Examples of each of the four task conditions: attend face (AF), attend face ignore house (AFIH), attend house (AH), and attend house ignore face (AHIF). Passive viewing condition (CTRL) is not shown. (B) Example of one task block. The five conditions were blocked in randomized order within each run. Each block was preceded by an auditory cue, informing participants to attend to house, face or to passively view the pictures.

the pairing of face and house images was randomized across different participants and sessions. There were five conditions, attend face (AF, individual face images), attend face ignore house (AFIH, superimposed house-face images), attend house (AH, individual house images), attend house ignore face (AHIF, superimposed house-face images) and passive viewing (CTRL, superimposed house-face images) (Fig. 1A).

Prior to each experimental run, participants memorized a face target and a house target. This was followed by a short recognition test to ensure participants remembered the targets. This procedure preceded functional imaging.

The functional imaging section of each experimental session (RW, SD) comprised ten runs. Each run comprised trials belonging to one of the 5 task conditions. These in turn were organized into five randomized blocks. Participants had to detect if a target was present during each trial. Prior to each block, a 1 s auditory cue instructed the participants to either: attend to house pictures (AH and AHIF), attend to face pictures (AF and AFIH), or passively view the images (CTRL). There were seven trials in each block, each picture was shown for 1 s, followed by fixation such that the duration of each trial was 4, 6 or 8 s (Fig. 1B). Each block lasted between 54 and 58 s (depending on the length of the cue period). Each run lasted 252 s and the total duration of the entire fMRI experiment excluding the 2–3 minute breaks between each run, was 42 minutes.

Participants viewed task stimuli using MR-compatible LCD goggles (Nordic Neurolab, Bergen, Norway) and responded with a button box held in the right hand. An eye camera was used to continuously monitor for eye closures. Participants were prompted through the intercom system whenever they failed to respond to two consecutive trials to ensure that they did not fall asleep for a sustained interval.

A self-paced post-experiment recognition task was administered outside the scanner following the imaging experiment, in both RW and SD sessions. Participants viewed 200 house pictures in each session, of which 100 were old and 100 were novel. The 100 old house images include 8 that were target houses and 23 non-target house images from each of the other 4 conditions. All stimuli were randomly ordered and the participants were instructed to give a confidence judgment about whether each stimulus was old or new: 1—definitely new; 2—probably new; 3—probably old; 4—definitely old. The post-experiment recognition index for each condition was calculated for each participant by subtracting the rating of the novel house stimuli from the mean familiarity rating of the house images for each of the other conditions (Clapp and Gazzaley, 2010; Rutman et al., 2010).

Imaging parameters

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 degrees, 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 the purpose of image display in Talairach space, an additional high-resolution anatomical reference image was acquired 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: $1.0 \times 1.0 \times 1.0$ mm).

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
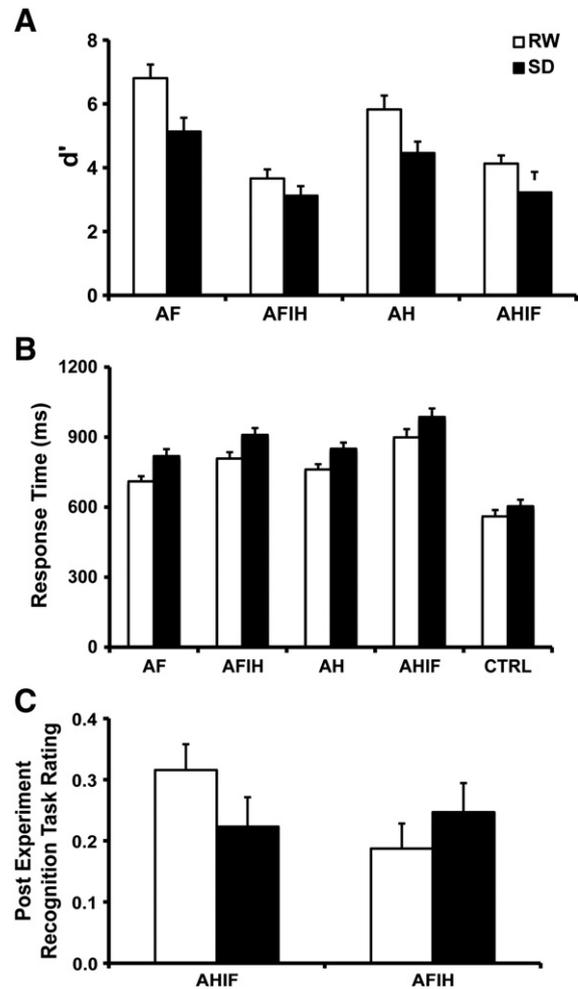

Fig. 2. Behavioral results. (A) Target detection performance during RW and SD in each condition. There were significant main effects of state ($F_{1,21} = 23.1$, $p < 0.001$) and interfering distractors ($F_{1,21} = 73.1$, $p < 0.001$). (B) Main effect of state on response time ($F_{1,21} = 20.0$, $p < 0.001$). The presence of interfering distractors ($F_{1,21} = 144.6$, $p < 0.001$) resulted in slower responses. (C) Post-experiment recognition indices. When well rested, participants recognized interfering distractor houses significantly less than attended houses ($t_{21} = 2.56$, $p < 0.05$), while after SD, the difference disappeared ($t_{21} < 1$, n.s.). Error bars indicate standard error.

attributable to slice acquisition order were adjusted using trilinear and sinc interpolation. Gaussian filtering was applied in the spatial domain 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 using a general linear model with eight predictors of interest and three nuisance predictors. The predictors of interest comprised one for each condition (face cue, house cue, control cue, AF, AFIH, AH, AHIF, CTRL), in both RW and SD states. The nuisance predictors comprised incorrect trials, missed trials and trials where targets were present. Only correctly rejected trials where the target was absent were used for further analysis. Each predictor was created by convolving relevant trials with a canonical double gamma hemodynamic response function.

The PPA was defined in each individual using the contrast of AH versus AF conditions in each state. Fifteen functional voxels ($3 \times 3 \times 3$ mm each) from each side of the brain with the maximum $PE_{AH} - PE_{AF}$ (PE: parameter estimate) values were defined as the PPA region of interest.

To assess the top-down modulation effect in the functionally determined ROI, normalized modulation indices were computed as follows

Enhancement Index

$$RW : (AHIF_{RW} - CTRL_{RW})/(CTRL_{RW} + CTRL_{SD})$$
$$SD : (AHIF_{SD} - CTRL_{SD})/(CTRL_{RW} + CTRL_{SD})$$

Suppression Index

$$RW : (AFIH_{RW} - CTRL_{RW})/(CTRL_{RW} + CTRL_{SD})$$
$$SD : (AFIH_{SD} - CTRL_{SD})/(CTRL_{RW} + CTRL_{SD})$$

In accord with the hypothesis that selective attention results in the enhancement of attended items and the suppression of distractors, selectivity of activation in the PPA would be evidenced by a positive value for the enhancement index and a negative value for the suppression index (Gazzaley et al., 2005b). Attention related enhancement of activation and distractor inhibition related suppression of activation relative to passive viewing can be assessed without including the denominator. However, doing so accounts for shifts in overall activation magnitude across states and provides more robust measures of the aforesaid constructs.

Results

Behavioral results

d' was used to evaluate target detection of each participant. $d' = Z(\text{hit rate}) - Z(\text{false alarm rate})$ where Z is the inverse of the cumulative Guassian distribution. Sleep deprivation reduced d' of target detection ($F_{1,21} = 23.1$, $p < 0.001$; Fig. 2A) and slowed responses ($F_{1,21} = 20.0$, $p < 0.001$; Fig. 2B). There was also a main effect of distraction on both d' of target detection ($F_{1,21} = 73.1$, $p < 0.001$) and response time ($F_{1,21} = 144.6$, $p < 0.001$). Although, participants were overall slower to respond to houses ($F_{1,21} = 59.9$, $p < 0.001$), target detection performance was comparable for houses and faces ($F_{1,21} = 2.0$, n.s.). There was no state by condition interaction.

There was a significant state by attention effect on scores for correctly recognized, attended houses (AHIF condition) and ignored houses (AFIH condition, $F_{1,21} = 3.91$, $p = 0.05$; Fig. 2C). A post-hoc paired t-test indicated that when well rested, participants achieved higher scores for attended houses (AHIF) than for ignored houses (AFIH condition, $t_{21} = 3.48$, $p < 0.01$). Contrastingly, after SD the two ratings were not significantly different ($t_{21} < 1$, n.s.) suggesting that SD rendered participants less able to suppress incidental encoding of house distractors. This asymmetry in recognition memory was not evident for faces even in the RW state, possibly because faces are less clearly discriminable than house pictures.

Imaging findings

There was a clear main effect of task ($F_{1,21} = 446.8$, $p < 0.001$) on PPA activation. Activation was highest when houses were attended and interfering faces were absent. The different combinations of factors resulted in graded levels of activation: AH > AHIF > CTRL > AFIH > AF (Fig. 3B). This gradation of activation is expected from the biased competition model of attention. An attended target object presented without competing distractors is expected to show the highest level of activation in visual cortex followed by an attended object together with a distractor. In turn, the deployment of attention to houses
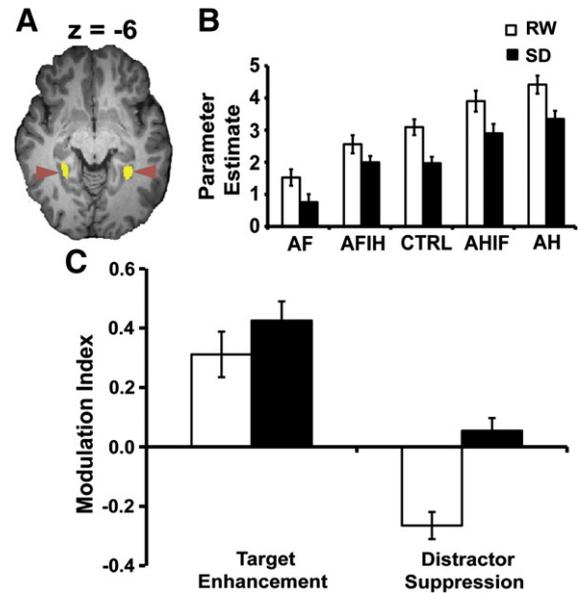

Fig. 3. Activation and modulation effects in PPA. (A) Group activation map showing the PPA ($z = -6$; $p < 10^{-6}$, uncorrected). Note that the figure is only for illustrative purposes as the PPA used for analysis was defined separately for each individual (Average Talairach Coordinates, left PPA: -30, -46, -6; right PPA: 26, -45, -5). (B) Activation in the PPA corresponding to different task conditions in each of the two states. Main effects of state ($F_{1,21} = 11.7$, $p < 0.01$) and task ($F_{1,21} = 446.8$, $p < 0.001$) are present. (C) Enhancement and suppression indices during RW and SD. Suppression ($t_{21} = -2.75$, $p < 0.05$) was significantly attenuated following SD while enhancement was relatively preserved.

(mixed with faces) results in higher PPA activation relative to unattended (passively viewed) houses in the control condition. Attending to faces in the AFIH condition would be expected to result in suppression of PPA activation and the least PPA activation can be expected when only faces were shown. The finding that activation to attended targets was reduced by a distractor is reminiscent of the results of animal electrophysiological studies (Reynolds and Desimone, 2003).

There was a main effect of state on PPA activation ($F_{1,21} = 11.7$, $p < 0.01$). Activation was lower following sleep deprivation in each of the task conditions. Critically, post-hoc comparisons showed that after a normal night of sleep, attending to houses when distracted by faces (AHIF) elicited higher PPA activation than passively viewing similar superimposed pictures (CTRL) condition ($t_{21} > 4.9$, $p < 0.001$). Contrastingly, reflecting distractor suppression, the AFIH condition elicited PPA activation that was lower than the passive viewing condition ($t_{21} < -5.0$, $p < 0.001$). After one night of sleep deprivation, attending to houses still elicited a higher PPA activation ($t_{21} > 4.8$, $p < 0.001$), while the difference in PPA activation between the AFIH and passive view conditions was no longer significant ($t_{21} < 1$, n.s.).

Normalized enhancement and suppression indices within the PPA were used as an indication of attentional modulation. In both RW and SD, attention to houses enhanced PPA activation (RW: $t_{21} > 4.7$, $p < 0.001$; SD: $t_{21} > 3.8$, $p < 0.001$). The extent of this modulatory effect was not significantly different across states ($t_{21} < 1$, n.s.; Fig. 3C). In contrast, modulation of PPA activation reflecting distractor suppression was only significant when the participants were well rested (RW: $t_{21} < -4.2$, $p < 0.001$; SD: $t_{21} < 1$, n.s.) and was significantly reduced following SD ($t_{21} < -2.75$, $p < 0.05$; Fig. 3C).

Using a whole brain analysis, sleep deprivation was found to reduce intraparietal sulcus (IPS) activation ($F_{1,21} = 9.4$, $p < 0.01$; Fig. 4A distractor). Trials with interfering face–house stimuli (AFIH and AHIF conditions) were more difficult to process than face only (AF) and house only (AH) trials. Consequently there was a main effect of task condition on IPS activation ($F_{1,21} = 43.3$, $p < 0.001$; Fig. 4B). However, in contrast to the PPA, we did not find a state by condition interaction in the IPS. We speculate that this is a result of being unable to
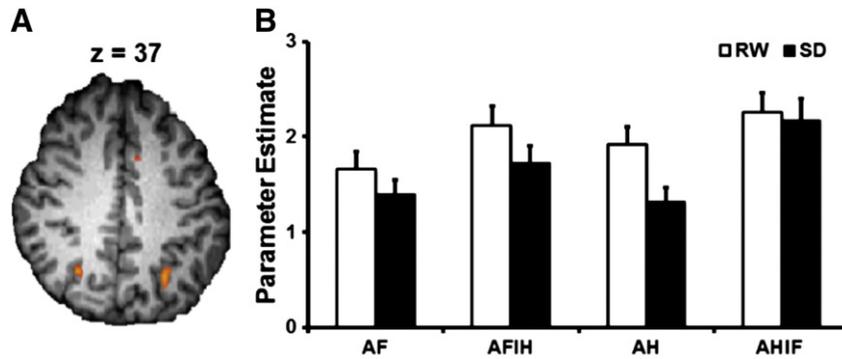
Fig. 4. Intraparietal sulcus (IPS) activation across task and state. (A) Group activation map thresholded at $p < 10^{-6}$, uncorrected. Note that the activation map is only for illustrative purposes as the IPS used for analysis was defined separately for each individual. (B) There are significant main effects of state ($F_{1,21} = 9.4$, $p < 0.01$) and task ($F_{1,21} = 43.3$, $p < 0.001$) for IPS activation (average Talairach coordinates, left IPS: −30, −55, −41; right IPS: 27, −52, 41).

dissociate the effects of SD on sustained attention, target enhancement and distractor suppression in the different conditions. We note that prior work has also reported activation data from only the ventral visual cortex where the state by condition interaction is dissociable (Gazzaley et al., 2005b).

Discussion

We found that sleep deprivation produced dissociable effects on suppression and enhancement of PPA activation in response to ignoring or attending house pictures that were superimposed on face pictures. During SD, there was reduced distractor suppression indexed by lowered PPA activation relative to the passive viewing condition. Contrastingly, target enhancement indexed by elevated PPA activation was intact. A by-product of reduced distractor suppression was relatively increased recognition of irrelevant house distractors following sleep deprivation. We hypothesize that this is a result of the opposing effects of reduction in perceptual processing capacity and an erosion of cognitive control of attention.

Sleep deprivation impairs distractor suppression

While selective attention has been found to be impaired following SD (Chee et al., 2010; Lim et al., 2010; Tomasi et al., 2009) a finer grained study to determine if these deficits reflect failure to increase activation related to relevant information, or impaired suppression of distractions/task-irrelevant information has not been undertaken till presently. Despite the fact that SD was associated with reduction in PPA activation across all conditions, only a deficit in suppression of cortical activity was observed. Contrastingly, enhancement of PPA activation to task-relevant stimuli was preserved. These observations parallel those reported in studies of cognitive aging (Gazzaley et al., 2005a; Lustig et al., 2007).

By keeping sensory input constant and manipulating the object of attention, target facilitation and distractor suppression were unequivocally dissociated because attention to houses obligates the suppression of the superimposed face distractors and vice versa. This provides a sterner test of distractor suppression compared to experiments where task-relevant and task-irrelevant stimuli are sequentially presented or alternated (Chee et al., 2010; Clapp and Gazzaley, 2010; Clapp et al., 2010; Gazzaley et al., 2005b). In these studies, actively suppressing task-irrelevant items would be advantageous but not obligatory.

Distractor suppression requires the maintenance of task goals and can be thought of as an executive function. Loss of top-down control of attention in sleep deprived persons may be impaired, resulting in increased head turns towards peripheral distracting events (Anderson and Horne, 2006). Increased distraction can impair working

memory in older adults, and correlates with poorer performance accuracy (Clapp and Gazzaley, 2010).

Impaired cognitive control and lowered visual perceptual processing capacity following sleep deprivation may exert opposing effects on distractor processing

The present results may appear contrary to a prior finding that SD lowers visual perceptual processing capacity. In that study, peripherally positioned task-irrelevant distractor houses elicited weaker repetition suppression when the centrally attended faces were perceptually harder to discriminate (Kong et al., 2011). Reduced repetition suppression served as a proxy for the extent to which a stimulus was processed. Hence this result suggests preserved inhibition of irrelevant distractor houses during SD.

Lavie's load theory of selective attention (Lavie, 2005; Lavie et al., 2004) posits that task-irrelevant peripheral distractors are processed automatically whenever there are available processing resources. Increasing perceptual difficulty of the central task would then leave less processing resources for peripheral targets. A reduction in total processing capacity, such as that induced by sleep deprivation could also be expected to lower peripheral distractor processing under conditions of high central task load, provided available resources continue to be concentrated on central task-relevant stimuli.

Critically, the effects of cognitive work-load on distractor processing depend on the type of mental processes that are loaded (Lavie, 2005; Lavie et al., 2004). Apart from the perceptual selective attention mechanism that processes information until perceptual capacity is exhausted, another cognitive control mechanism appears to maintain task goals and reduce distraction. In contrast to increasing perceptual load, increasing demands on cognitive control by incrementing working memory can result in greater processing of distractors (De Fockert et al., 2001; Yi and Chun, 2005). This may result from a diminution of cognitive resources supporting the maintenance of task goals - a form of failure of executive function.

A parsimonious reconciliation of the seemingly disparate findings across our studies is that while reduced perceptual capacity might attenuate the processing of peripheral distractors in the previous experiment, decreased capacity to engage cognitive control when distractor suppression is obligatory, resulted in the present findings.

Loss of distractor suppression and increased co-encoding of targets and distractors

Following SD, when attention was not well constrained to task-relevant stimuli, distractor houses showed comparable, familiarity-based recognition compared to attended houses, despite the overall level of house recognition being lower than for attended houses in the well-rested state.

Comparable observations have been reported with healthy elderly participants who evidence deficits in distractor suppression (Gazzaley et al., 2005a, 2008; Kim et al., 2007; Rowe et al., 2006; Schmitz et al., 2010). For example, Clapp and Gazzaley (2010) showed that while elderly showed poorer working memory for target items, they remembered the interfering stimuli significantly better than their younger counterparts. Thus, inefficient suppression of distractors in both sleep-deprived and elderly participants appears to result in greater processing and co-encoding of distractors into memory together with target items (Schmitz et al., 2010).

The upshot of these findings is that while normally not preferred, a deficit in distractor suppression could have adaptive value under conditions of impoverished overall processing capacity. For example someone who is overly engrossed in (selectively attending) a cell phone conversation while crossing a road after being sleep deprived, might be sufficiently distracted so as to detect an oncoming vehicle that might have otherwise gone unnoticed in the well-rested state.

Acknowledgments

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