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Effects of sleep deprivation on cortical activation during directed attention in the absence and presence of visual stimuli

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ABSTRACT

Sleep deprivation (SD) can give rise to faltering attention but the mechanics underlying this remain uncertain. Using a covert attention task that required attention to a peripheral target location, we compared the effects of attention and SD on baseline activity prior to visual stimulation as well as on stimulus-evoked activity. Volunteers were studied after a night of normal sleep (RW) and a night of SD. Baseline signal elevations evoked by preparatory attention in the absence of visual stimulation were attenuated within rFEF, rIPS (sparing SEF) and all retinotopically mapped visual areas during SD, indicative of impaired endogenous attention. In response to visual stimuli, attention modulated activation in higher cortical areas and extrastriate cortex (hV4, ventral occipital areas) after RW. SD attenuated rFEF, rIPS, V3a and VO stimulus-evoked activation by attention was not affected by SD unlike for the preparatory period, suggesting a reduced number, but still functional circuits during SD. Deficits in endogenous attention in SD dominate in the preparatory period, whereas changes in stimulus-related activation arise from an interaction between compromised fronto-parietal top-down control of attention and reduced sensitivity of extrastriate visual cortex to top-down or bottom-up inputs.

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Introduction

Faltering attention in the setting of sleep deprivation (SD) contributes to transient cognitive failures (Lim and Dinges, 2010) that can lead to serious traffic, industrial and medical accidents (Mitler et al., 1988; Dinges, 1995; Barger et al., 2006; Philip and Akerstedt, 2006). The reduced ability to direct limited mental resources to process salient information at a given moment can take several forms, specifically the impairment of sustained (Doran et al., 2003; Mander et al., 2008; Chee et al., 2009), selective (Horowitz et al., 2003; Mander et al., 2008; Chee et al., 2001). Lim et al., 2010) or divided attention (Drummond et al., 2001). Behavioral impairment in SD can manifest in reduced performance accuracy, slower responses, greater variability in response time and an increase in non-responses (Doran et al., 2001; Lim and Dinges, 2010).

Reduced performance accuracy (Chuah and Chee, 2008; Tomasi et al., 2009; Chee and Tan, 2010), increased non-responses (Chuah and Chee, 2008) and delayed responding (Chee et al., 2008; Chee and Tan, 2010) have been correlated with reduced activation in brain regions

that show task-related activity, especially in fronto-parietal regions that bias sensory processing in visual cortex to task-relevant stimuli (Kastner et al., 1999; Hopfinger et al., 2000).

In addition to modulating stimulus-related activation, attention may bias sensory cortical activation in the period preceding target appearance. Such baseline shifts in neural activity have been demonstrated using single-cell recordings in monkey visual cortex (Luck et al., 1997) as well as event related potentials (Grent-'t-Jong and Woldorff, 2007) and fMRI (Sapir et al., 2005; Sylvester et al., 2006; Stokes et al., 2009) in humans. Of interest, subjects cued to a specified location show sustained baseline shifts in fMRI signals within retinotopically organized areas in the absence of visual stimulation (Kastner et al., 1999; Sapir et al., 2005; Sylvester et al., 2006; Silver et al., 2007). Hence, observing sleep deprivation induced, state-dependent differences in baseline shifts could allow us to unambiguously infer altered endogenous attention. We hypothesized that we would find evidence for attenuated endogenous attention in the form of reduced baseline shifts during the preparatory period after the cue but before stimulus onset. In contrast, altered stimulus-related responses to attended targets at a peripheral location can result from changes in both bottom-up influences on attention and endogenous attention. The contribution of such bottom-up effects on stimulus-related responses may nevertheless be discerned by examining state differences in responses to unattended peripheral stimuli. Along this



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line of reasoning we predicted that SD would reduce visual cortex responses to both attended and non-attended targets.

An additional issue of interest is whether lowered visual cortical responses to stimuli in sleep deprived persons primarily originate from attenuated biasing signals arising from the fronto-parietal cortex (Chee et al., 2008; Chee and Tan, 2010) or if this is also due to reduced sensitivity of visual cortex to sensory stimuli. The latter could possibly arise from use-dependent effects accompanying sustained wakefulness (Pigarev et al., 1997; Krueger et al., 2008; Vyazovskiy et al., 2011) – the converse of enhanced excitability of visual cortex induced by light-deprivation (Boroojerdi et al., 2000).

To resolve these questions, volunteers were studied twice with fMRI, once following a normal night of sleep and once following 24 h of SD. In one condition, volunteers were cued to covertly direct attention to a peripheral location, in anticipation of targets that appeared after variable periods (Kastner et al., 1999). In another condition, targets were not preceded by a cue and were not attended to. To evaluate the effects of SD on neural activation associated with preparatory attention and visually-evoked activity, we contrasted the magnitude of baseline shift and attentional modulation of stimulus-related activity across task-condition and state in fronto-parietal regions mediating attentional control and retinotopically mapped visual cortex.

Materials and methods

Participants

Twelve volunteers (5 men, mean age 26.4 years, range 22– 31 years) participated in the study after giving informed consent and fulfilling the recruitment criteria. Participants had to: (1) be righthanded, (2) be between 18 and 35 years of age, (3) report sleeping 6.5 h or more each night on a regular basis (4) not be on any longterm medication, (5) have no symptoms suggestive of a sleep disorder and (6) have no history of any psychiatric or neurologic disorders.

Participants' sleep habits were monitored throughout the twoweek duration of the study using motion-sensing by wrist actigraphy. Only persons who kept a regular sleep schedule (slept>6.5 h at night; went to sleep no later than 1:00 AM; woke up no later than 9:00 AM) for the week prior to each fMRI scanning session underwent scanning. All participants indicated that they did not smoke, consume any medications, stimulants, caffeine or alcohol for at least 24 h prior to scanning.

Study procedure

Participants visited the laboratory three times — for a practice session, a rested wakefulness (RW) session and a sleep deprivation (SD) session. During the practice session, they were assessed for MR compatibility and were briefed before practicing the experimental task in the scanner. There were 10 practice runs and participants were given feedback on their performance accuracy after each run. Eye movements were observed using an in scanner eye-camera (Resonance Technology, Los Angeles, USA), and each volunteer was evaluated for the ability to maintain fixation and to covertly attend and respond to the targets as described below. At the end of the practice session, qualifying participants were given an actigraph (Actiwatch, Philips Respironics, USA). They were also issued sleep diaries in which they were to record the onset and offset of all sleep bouts.

Brain imaging was conducted on the second and third visits. The order of these scanning sessions was counterbalanced across participants. The first session took place approximately one week after the practice session to ensure that regular sleep times were adhered to. The two scanning sessions were separated by one week to minimize residual effects of sleep curtailment on cognitive performance in participants whose SD session preceded the RW session (Van Dongen et al., 2003).

Scanning commenced at about 8:00 AM in the RW session and at about 6:00 AM after a night of total sleep deprivation for the SD session. These times were chosen as they represent the typical start time of a regular workday and the time when vigilance hits a nadir after a night of sleep deprivation (Doran et al., 2001; Graw et al., 2004).

During the SD session, participants arrived at the laboratory by 7:00 PM and were under the constant supervision of a research assistant. Retinotopic mapping scans were performed at 8:00 PM. From 9:00 PM to 6:00 AM, participants spent the first 12 min of each hour completing the Psychomotor Vigilance Task (Dinges et al., 1997; Doran et al., 2001) and rating their subjective sleepiness using the Karolinska Sleepiness Scale. At other times, participants were allowed to engage in non-strenuous activities such as reading and watching movies. Use of caffeine in any form and smoking was strictly prohibited.

Experimental stimuli

There were three types of trials – 'attend', 'non-attend' and 'catch' sharing an identical temporal structure (Fig. 1). Visual stimuli appeared in the 'attend' and 'non-attend' trials and consisted of a set of 10 successively appearing displays. Each display contained a complex image presented in the left upper quadrant comprised of an array of 4 colorful patterns, each $2^{\circ} \times 2^{\circ}$ in size. A target pattern appeared in the right lower quadrant of the complex image at random, up to 5 times within the sequence. The target pattern was presented at 6 degrees eccentricity from a central fixation cross. To reduce learning effects, 5 different targets were used in the 10 runs that constituted each scanning session.

These visual stimuli were presented using a set of MR-compatible LCD goggles (Resonance Technology, Los Angeles, USA). Participants responded to targets by pressing a button with their right index finger. An eye-camera was used to continuously monitor eyelid closures and maintenance of fixation. Participants were prompted through the intercom system if they failed to respond to two consecutive targets.

All trials shared the same temporal structure $-a 6, 8 \text{ or } 10 \text{ s pre-stimulus period where baseline shifts were expected in 'attend' but not 'non-attend' trials, followed by a 10 s period when the sequence of complex images appeared, followed by 18 or 20 s of fixation (Fig. 1). The effect of endogenous attention on visual cortex activation was assessed during the prestimulus 'preparatory attention' period. The effect of attention on stimulus-related activation was assessed when the series of complex images was presented. Each imaging session involved 10 experimental runs, each 6 minutes long. Each run comprised 10 trials, 5 'attend' trials, 4 'non-attend' trials and 1 'catch' trial.$

In 'attend' trials participants were cued to covertly attend to the target location by a centrally presented arrow that pointed to the left upper quadrant. The sequence of complex images containing the target pattern(s) appeared after a delay of 6, 8, or 10s.

'Non-attend' trials, were similar to 'attend' trials except that the sequence of complex images was not preceded by a cue. Participants maintained fixation and were not required to respond. In 'Catch' trials, a cue appeared and was followed by 28 s of fixation i.e. the sequence of complex images did not appear.

Retinotopic mapping

Polar angle and eccentricity mapping were conducted using procedures described previously (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997; Warnking et al., 2002; Arcaro et al., 2009) and are described only briefly here.

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