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Sleep Less, Think Worse: The Effect of Sleep Deprivation on Working Memory☆

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Sleep deprivation is increasingly common and poses serious problems for optimal cognitive functioning. Here we review the empirical literature on the consequences of sleep loss for working memory. The bulk of the research suggests that sleep is essential for working memory. Sleep deprivation inhibits general attentional and mnemonic abilities and influences neural activation in frontal and parietal cortices, areas critical for working memory. Decreases in task performance are typically accompanied by decreased activation in task-relevant areas under conditions of sleep deprivation. However, there is some evidence that deprivation can lead to increases in activation as a compensatory mechanism allowing for maintained performance. We conclude by discussing what is known about the remediation of these impairments through the use of caffeine and other stimulants.

Keywords: Sleep deprivation, Working memory, Sleep restriction

Experts in sleep medicine recommend that adults obtain an average of at least 7 h of sleep per night for optimal health (Watson et al., 2015). Meanwhile, average sleep duration has decreased dramatically over the past fifty years (Bixler, 2009) and Americans are increasingly likely to maintain a chronic state of sleep debt (i.e., averaging 6 or fewer hours per night; Ford, Cunningham, & Croft, 2015). This is worrisome, in part because both total sleep deprivation (total sleep loss for 24 h or more) and partial sleep restriction (obtaining less than 7 h of sleep on multiple consecutive nights) are associated with a wide range of physiological and cognitive deficits. The physiological effects include impairments in immune function (Cohen, Doyle, Alper, Janicki-Deverts, & Turner, 2009; Prather et al., 2012) cardiovascular health (Meier-Ewert et al., 2004; Wang, Xi, Liu, Zhang, & Fu, 2012), and glucose metabolism (Spiegel, Leproult, & Van Cauter, 1999; Spiegel, Tasali, Penev, & Van Cauter, 2004), to name a few (see Alvarez & Ayas, 2004; Copinschi, 2005; Gallicchio & Kalesan, 2009; Knutson, Spiegel, Penev, & Van Cauter, 2007; Mullington, Haack, Toth, Serrador, & Meier-Ewert, 2009; Patel & Hu, 2008, for reviews). Here, we summarize what is known about the cognitive consequences of sleep deprivation, with an emphasis on working memory.

Sleep deprivation produces wide-ranging impairments in cognitive function, among which are deficits in executive function and attention (e.g., Durmer & Dinges, 2005; Harrison & Horne, 2000). Sleep deprivation increases response times and produces more errors in tasks that require sustained attention, especially under time pressure and as task duration lengthens (Alhola & Polo-Kantola, 2007; Lim & Dinges, 2010). Furthermore, individuals who are sleep deprived have difficulty learning new information and acquiring new skills, and they are less likely to revise and adapt their strategies in response to failures (e.g., Wimmer, Hoffman, Bonato, & Moffitt, 1992). Instead, they tend to perseverate on failed strategies (Harrison & Horne, 1999) and neglect behaviors that they deem nonessential or peripheral. Finally, impulsivity increases and inhibitory ability decreases (Harrison & Horne, 1998a). Taken together, the bulk of the literature makes it clear that adequate sleep is absolutely essential for cognitive functioning.

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Given that working memory (WM) is critical to optimal cognitive functioning, it is important to understand the specific WM deficits that are associated with sleep deprivation. To briefly summarize, WM is traditionally understood to have four interrelated components (Baddeley, 2000; Baddeley & Hitch, 1974): a "phonological loop" (for processing acoustic and auditory information), a "visuospatial sketchpad" (for rehearsing visual and spatial information), an "episodic buffer" (for combining various kinds of information into an integrated whole), and a "central executive" which presides over each of the other components. Executive control, specifically, is linked to sustained attentional abilities, sometimes referred to as vigilance.

Working memory performance and its related cognitive operations are typically measured by tasks designed to tap various aspects of memory and attention, including (but not limited to) digit span and word list recall tasks (Quigley, Green, Morgan, Idzikowski, & King, 2000), the N-back task (Choo, Lee, Venkatraman, Sheu, & Chee, 2005), Sternberg-type verbal working memory tasks (Mu, Mishory, et al., 2005; Mu, Nahas, et al., 2005), random generation tasks (Heuer, Kohlisch, & Klein, 2005), the Flanker task (Tsai, Young, Hsieh, & Lee, 2005), and the psychomotor vigilance test (Van Dongen, Baynard, Maislin, & Dinges, 2004). Across hundreds of studies using these and other measures, sleep deprivation has been linked to slowed reaction times in simple attention tasks (Karakorpi et al., 2006), decreased auditory vigilance and visuospatial attention (Bocca & Denise, 2006; Johnsen, Laberg, Eid, & Hugdahl, 2002), and impaired verbal working memory (Chee et al., 2006; Karakorpi et al., 2006). Sleep deprivation has been shown to compromise performance on tasks in terms of both speed and accuracy. For instance, it may simply slow a person's ability to accurately complete a task (Chee & Choo, 2004; De Gennaro, Ferrara, Curcio, & Bertini, 2001) or compromise accuracy (but not speed; Gosselin, De Koninck, & Campbell, 2005; Kim et al., 2001), or impair both speed and accuracy (Smith, McEvoy, & Gevins, 2002; Yeniad et al., 2013). Thus, sleep deprivation impairs all facets of working memory.

A succinct summary and comparison of the effects of sleep deprivation across tasks is no easy feat, in part because studies vary considerably in terms of sample characteristics, experimental controls, and the duration of sleep deprivation or sleep restriction, to name a few. To illustrate, a number of studies have compared the performance of rested participants to participants who had endured anywhere between 21 h of sleep deprivation (Smith et al., 2002) to upwards of 75 h (Magill et al., 2003). Still others have merely restricted the sleep of participants, as in a study that compared performance in participants who slept either 3, 5, 7 or 9 h every night for a week (Belenky et al., 2003).

Across studies, one general finding is that several nights of sleep restriction results in similar performance impairments as one (or more) nights of total sleep deprivation. For example, one ambitious study compared attention and working memory performance following 14 days of restricted sleep (either 4 or 6 h per night) with performance after either 1, 2, or 3 nights of total sleep deprivation (Van Dongen, Maislin, Mullington, & Dinges, 2003). Participants who endured 3 nights of total sleep deprivation showed significantly worse performance on all tasks than any other group. However, the authors also found a dose response curve in the sleep restricted groups. Participants who obtained only 4 h of sleep per night for 14 days showed levels of impairment roughly equivalent to participants who had endured two nights of total sleep deprivation whereas participants who obtained 6 h of sleep per night for 14 days exhibited impairment on par with those who had endured just one night of total sleep deprivation. An implication of these findings is that the deleterious effects of chronic sleep restriction accumulate over time, eventually matching the more immediate effects of total sleep deprivation. That said, because there are relatively few studies comparing the effects of sleep restriction with the effects of total sleep deprivation, the precise relationship between the amount of sleep loss and the degree of cognitive impairment remains somewhat unclear. It seems, for instance, that sudden total sleep loss may be marginally more deleterious than the same amount of sleep lost gradually over a period of time, though the cognitive consequences of partial and/or chronic deprivation are serious in themselves.

Across these and other studies, extended wakefulness affects a number of cognitive operations, but seems to wreak particular havoc on sustained attention and vigilance, as well as working memory. A key concern emerging from these patterns of findings has to do with the relatively similar, albeit slightly smaller effects of chronic partial sleep deprivation. Of note, although total sleep deprivation can occur in the general population, chronic partial sleep deprivation closely mirrors the kind of sleep loss that is increasingly common in today's society. This is significant because of the profound real-world costs associated with the loss of these cognitive functions across a variety of high stakes domains. Whether this loss involves the speed with which a professional may complete an important task, or their ability to complete it accurately (or both), these findings warrant significant concern. Unfortunately, there have been significant challenges in summarizing across this vast literature due to a striking heterogeneity of study characteristics and methodologies. Further systematic comparisons of the relative impact of chronic and acute sleep loss are needed, ideally using a variety of methods in a variety of contexts and real-world situations.

How does sleep deprivation produce these deficits? One view suggests that sleep deprivation impairs performance by generally inhibiting the ability to sustain attention and alertness, especially in tasks that do not demand a high level of concentration and vigilant attention (see Durmer & Dinges, 2005; Pilcher, Band, Odle-Dusseau, & Muth, 2007). In part, this view is supported by research suggesting that simple attentional tasks are most strongly compromised by sleep deprivation, whereas more complex and intrinsically engaging tasks are less affected (e.g., Lim & Dinges, 2010). Furthermore, sleep deprivation causes "microsleeps," or brief, fleeting lapses in brain activity that appear to resemble patterns of activity observed during normal sleep (Priest, Brichard, Aubert, Liistro, & Rodenstein, 2001). Microsleeps can explain some of the functional declines among sleep-deprived participants. However, there is also evidence that impairment occurs even in the periods of time between these lapses (e.g., Dorrian, Rogers, & Dinges, 2005). One key factor that seems to contribute to performance

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