



Learning and sleep-dependent consolidation of spatial and procedural memories are unaltered in young men under a fixed short sleep schedule



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ABSTRACT

Objective: To investigate if a fixed short sleep schedule impairs one of the main functions of sleep, which is to consolidate newly learned memories.

Methods: Sixteen young men participated in two experimental conditions, each of which lasted for 3 consecutive days and nights in our laboratory: a short sleep schedule (4.25-h sleep opportunity per night) versus a normal sleep schedule (8.5 h per night). In the evening after two experimental nights, participants learned locations of 15 card pairs (spatial memory task) and a procedural finger tapping sequence task. Post-sleep retrieval of both memory tasks was tested the next morning.

Results: The short sleep schedule, compared with the normal sleep schedule, considerably altered sleep characteristics, e.g. the proportion of time in slow-wave sleep increased across the three experimental nights. In contrast, neither learning in the evening of day 2, nor subsequent overnight memory consolidation (i.e. concerning the change in memory performance between pre-sleep learning on day 2 and post-sleep retrieval on day 3) differed between the normal and short sleep schedule conditions.

Conclusions: Our findings suggest that learning in the evening and subsequent sleep-dependent consolidation of procedural and spatial memories are unaltered in young men living under a fixed short sleep schedule. Future studies are warranted to validate our findings in other groups (e.g. adolescents and older subjects) and after more prolonged chronic sleep loss paradigms.

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1. Introduction

Converging evidence from independent laboratories has demonstrated that sleep facilitates the transfer of newly acquired information from temporary to long-term memory storage sites in the human brain (Durrant, Cairney, McDermott, & Lewis, 2015; Maurer et al., 2015; Rasch, Büchel, Gais, & Born, 2007; Rihm & Rasch, 2015; Walker, Brakefield, Hobson, & Stickgold, 2003). This concerns hippocampus-dependent (also called declarative) memories, including spatial (Moroni et al., 2014; Rasch et al., 2007; Talamini, Nieuwenhuis, Takashima, & Jensen, 2008) and semantic information (Lin & Yang, 2014; Ngo, Martinetz, Born, & Mölle, 2013; Tamminen, Lambon Ralph, & Lewis, 2013). Sleep-dependent consolidation of declarative memories mainly takes place during slow-wave sleep (SWS) (Rasch & Born, 2013), a sleep stage that predominates during the first 2–3 h after sleep onset.

Another memory type that is strengthened during sleep is procedural memory, such as coordinated motor movements (e.g. playing a piano piece). The consolidation of procedural memories is believed to benefit mostly from rapid-eye movement (REM) sleep, which predominates during the second half of a typical nocturnal sleep period (Fischer, Hallschmid, Elsner, & Born, 2002; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Mandai, Guerrien, Sockeel, Dujardin, & Leconte, 1989); however, there is also some evidence to the contrary (Rasch, Pommer, Diekelmann, & Born, 2009).

Given that an increasing number of adults on a daily basis in our 24/7-culture sleep less than 7 h per night (Ford, Cunningham, & Croft, 2015), an obvious research question is: to what extent does the memory consolidation-enhancing effect of nocturnal sleep depend on its duration? At first glance, the answer seems to be a non-linear relationship. Previous studies have for instance demonstrated that information encoded during wakefulness is equally well consolidated after just a few hours of nocturnal sleep (i.e. <5 h) as it is after an entire night of sleep (i.e. ≥7 h; Cedernaes, Rångtell et al., 2015; Tucker & Fishbein, 2009). However, a common

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experimental denominator of these studies is that their participants were not sleep-deprived at the time of learning, i.e. prior to the sleep retention interval, but rather in the night(s) that were allowed to elapse after initial learning. While these experiments undoubtedly have advanced our understanding of how sleep duration in the post-learning night affect memory consolidation, they have not conclusively addressed if this memory consolidation process is affected by preceding exposure to nightly recurring short sleep duration, as opposed to curtailed sleep duration only during the post-learning night(s).

Against this background, we sought to investigate whether learning and subsequent sleep-dependent memory consolidation are altered in young men following a three-day long fixed short vs. normal sleep schedule. To this aim, a procedural memory task and a spatial memory task were used. Both tasks have previously been shown to be reliable measures of sleep-dependent memory consolidation in humans (as shown by e.g. Rasch et al., 2007 and 2009).

Previous studies have demonstrated that nocturnal short sleep duration impairs a variety of cognitive functions the next day, such as general attention and working memory function (Fernandez-Mendoza et al., 2010; Lim & Dinges, 2010), encoding, retention and retrieval of hippocampus-dependent memories (Drummond et al., 2000; Harrison & Horne, 2000; Yoo, Hu, Gujar, Jolesz, & Walker, 2007), and encoding of information that cannot be integrated with prior conceptual knowledge (Alberca-Reina, Cantero, & Atienza, 2014). Thus, we hypothesized that living under a fixed short sleep schedule for two consecutive nights would impair participants' ability to learn new information during evening hours (i.e. prior to the sleep retention interval during the third night) and attenuate their ability to consolidate these newly acquired memories during subsequent nocturnal sleep.

2. Methods

2.1. Participants

Sixteen normal-weight (BMI <25 kg/m²) men were included in the present study (mean age \pm SD, 22.9 \pm 2.7 years). Subjects were of general good health and free from psychiatric conditions and medications, as indicated by an anamnestic interview conducted by a physician (J.C.). One week prior to each experimental sleep schedule condition, subjects filled out a sleep diary. Average self-reported sleep duration (7–9 h per night) – calculated from participants' sleep diaries – did not differ between the sleep schedule conditions (short vs. normal sleep schedule condition, $p = 0.38$, as determined by a paired t test). Within one week prior to the first experimental session, participants partook in an adaptation night that served to habituate them to our laboratory settings. The study was conducted in accordance with the Helsinki Declaration and was approved by the Regional Ethical Review Board in Uppsala (EPN 2014/242/1). Subjects received financial reimbursement for their participation.

2.2. Study design and procedure

According to a balanced crossover design, all subjects participated in two experimental conditions, each of which lasted three consecutive days and nights in our sleep laboratories at Uppsala University (see Fig. 1 for an experimental scheme, as well as for the order of experimental sessions and memory task versions across subjects). In one of the conditions (normal sleep schedule condition), subjects had an 8.5-h sleep opportunity between 2230 h (time when room ceiling lights were switched off) and 0700 h (time when room ceiling lights were switched on). In the

other condition (short sleep schedule condition), they were allowed to sleep 4.25 h each night, i.e. between 0245 h (low-intensity room lights were on between 2230 h and 0245 h in the short sleep schedule condition; at 0245 h all remaining room lights were switched off) and 0700 h (time when room ceiling lights were switched on). Before room lights were switched off prior to each experimental night, subjects were told that they could sleep until 0700 h the next morning; however, they were not free to do other activities once lights were switched off in the experimental room (e.g. reading). Experimental sessions were scheduled approximately 5 weeks apart.

Sleep was recorded by use of Embla A10 recorders (Flaga hf, Reykjavik, Iceland). Seven channels were recorded (4 EEG, 2 EOG, and 1 submental EMG). EEG signals were derived from C3, C4, Fp1, Fp2 and referenced to the contralateral mastoid. Sleep was subsequently scored by an experienced scorer (J.E.B.) after high-pass (0.3 Hz) and low-pass (35 Hz) filtering with the Somnologica software (Version. 3.3.2) (Silber et al., 2007). Daytime naps were not allowed, and subjects were constantly monitored by the experimenters. During each experimental session, subjects were provided with standardized meals (breakfast, lunch, dinner), but participants were only offered water to drink. When awake, subjects were engaged in sedentary activities such as reading books and magazines, or playing board games with experimenters, and they were allowed to watch movies and use electronic devices until 2000 h in the evening.

In the evening of the second day (i.e. after either two nights of full sleep or short sleep; \sim 2130 h), subjects learned a 2-D object location task and a procedural finger-tapping task (description can be found below). Performance on both memory tasks has previously been shown to benefit from sleep (Rasch et al., 2007, 2009). Note that upon awakening, cognitive performance is typically transiently impaired, in a state of grogginess known as sleep inertia (Tassi & Muzet, 2000). With this in mind, memory retrieval after the post-learning night was scheduled to occur about one hour after awakening to minimize possible confounding effects of sleep inertia (\sim 0810 h).

Self-reported sleepiness was measured by means of a 100-mm visual analogue scale (with 0 representing “not tired at all” and 100-mm representing “very tired”) at the following time points: at \sim 1930 h on the second day, i.e. prior to the post-learning night and at \sim 0800 h on the third day, i.e. immediately before the post-sleep recall procedure.

2.3. 2-D object location task

This hippocampus-dependent computerized memory task has been utilized for instance to investigate the influence of odor-cued memory reactivation during sleep (Rasch et al., 2007). It consists of 15 colored card pairs (e.g. animals). Each of the 30 possible spatial locations is displayed on a computer screen as a gray square (each depicting the back side of each of the 30 cards); each square geometrically ordered in a checkerboard fashion (5 \times 6 matrix).

In the present study, at learning (i.e. at \sim 2130 h in the evening of experimental day 2), one card of each pair was presented for 1 s. Then, both cards were displayed for 3 s. Following an inter-stimulus interval of another 3 s, the next pair was presented in the same manner, until all 15 card pairs had been presented, after which the presentation was repeated; however the presentation order was different between the two presentations. After encoding, recall of card pair locations was tested using a cued-recall procedure; i.e. one card of each pair was presented, and the subject had to indicate the location of the second card with a computer mouse. After the subject had indicated the decided location of the second card, visual feedback was given by presenting the second card at the correct location for 2 s, independent of whether the

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