Neurobiology of Learning and Memory 121 (2015) 72–79

Contents lists available at ScienceDirect

Neurobiology of Learning and Memory

journal homepage: www.elsevier.com/locate/ynlme

Role of sleep for encoding of emotional memory

Kosuke Kaida [a,*], Kazuhisa Niki [a], Jan Born [b]

[a] Human Technology Research Institute, National Institute of Advanced Industrial Science and Technology (AIST), Tsukuba, Ibaraki, Japan
[b] Institute of Medical Psychology and Behavioral Neurobiology, University of Tuebingen, Tuebingen, Germany

ARTICLE INFO

Article history:
Received 4 February 2015
Revised 13 April 2015
Accepted 13 April 2015
Available online 21 April 2015

Keywords:
Sleep
Emotion
Memory encoding

ABSTRACT

Total sleep deprivation (TSD) has been consistently found to impair encoding of information during ensuing wakefulness, probably through suppressing NonREM (non-rapid eye movement) sleep. However, a possible contribution of missing REM sleep to this encoding impairment after TSD has so far not been systematically examined in humans, although such contribution might be suspected in particular for emotional information. Here, in two separate experiments in young healthy men, we compared effects of TSD and of selective REM sleep deprivation (REMD), relative to respective control conditions of undisturbed sleep, on the subsequent encoding of neutral and emotional pictures. The pictures were presented in conjunction with colored frames to also assess related source memory. REMD was achieved by tones presented contingently upon initial signs of REM sleep. Encoding capabilities were examined in the evening (18:00 h) after the experimental nights, by a picture recognition test right after encoding. TSD significantly decreased both the rate of correctly recognized pictures and of recalled frames associated with the pictures. The TSD effect was robust and translated into an impaired long term memory formation, as it was likewise observed on a second recognition testing one week after the encoding phase. Contrary to our expectation, REMD did not affect encoding in general, or particularly of emotional pictures. Also, REMD did not affect valence ratings of the encoded pictures. However, like TSD, REMD distinctly impaired vigilance at the time of encoding. Altogether, these findings indicate an importance of NonREM rather than REM sleep for the encoding of information that is independent of the emotionality of the materials.

1. Introduction

The ability to encode episodic memory information deteriorates after total sleep deprivation (TSD) (Drummond et al., 2000; Polzella, 1975; Walker & van der Helm, 2009). This effect has been attributed to the loss of non-rapid eye movement sleep (NonREM) rather than REM sleep during TSD before learning, and specifically to functions of slow waves (0.5–4 Hz) and spindles (12–16 Hz) characterizing the electroencephalogram (EEG) during NonREM sleep stage 2 and slow wave sleep (SWS) (Mander, Santhanam, Saletin, & Walker, 2011; Van Der Werf et al., 2009). Thus, suppressing slow waves during sleep prior to learning impaired subsequent encoding of pictures of landscapes and buildings (Van Der Werf et al., 2009) whereas enhancing slow waves by electrical stimulation improved subsequent encoding of such stimuli (Antonenko, Diekelmann, Olsen, Born, & Molle, 2013). Also, numbers of spindles during sleep were found to be positively correlated to post-sleep encoding capabilities (face-name associations, (Mander et al., 2011)). On a conceptual level, the benefiting influence of NonREM and SWS has been linked to the <1 Hz slow oscillation as a neurophysiological correlate underlying EEG slow wave activity, in the framework of the "synaptic homeostasis hypothesis" (Tononi & Cirelli, 2003, 2014). This hypothesis assumes that synaptic strength in cortical and hippocampal neural networks globally increases with the encoding of information in wakefulness, and that with prolonged wakefulness these synaptic networks become saturated and, thus, exhibit a reduced capacity to encode further information. Sleep, in particular the slow oscillations of SWS, drive a global re-normalization of synaptic strength and, thus, allows for encoding capacities to be recovered.

While the contribution of SWS to recovering encoding capabilities appears to be well-established, there are hints that REM sleep might also play a role in this process. For example, in rats, decreases in hippocampal neuronal activity across triads of NonREM–REM–NonREM periods correlated positively with the amount of theta activity during the intervening REM sleep period,

* Corresponding author at: Human Technology Research Institute, National Institute of Advanced Industrial Science and Technology (AIST), Tsukuba Central 6-11, 1-1-1, Higashi, Tsukuba, Ibaraki 305-8566, Japan.
E-mail address: kaida-kosuke@umin.ac.jp (K. Kaida).

http://dx.doi.org/10.1016/j.nlm.2015.04.002
1074-7427/

suggesting that REM sleep down-scales synaptic connectivity in hippocampal networks (Born & Feld, 2012; Grosmark, Mizuseki, Pastalkova, Diba, & Buzsaki, 2012). Also, deprivation of REM sleep compromises subsequent synaptic long-term potentiation in the rat hippocampus (Kim, Mahmoud, & Grover, 2005; Lopez et al., 2008; Ravassard et al., 2015). In particular, REM sleep might affect encoding of emotional stimuli. REM sleep is known to play an important role in the processing of emotional memory (Payne, Chambers, & Kensinger, 2012; Wagner, Gais, & Born, 2001; Walker & van der Helm, 2009; Werner, Schabus, Blechert, Kolodyazhniy, & Wilhelm, 2015). Humans after selective REM sleep deprivation showed an increased reactivity of emotional brain regions to threatening stimuli (Rosales-Lagarde et al., 2012). On the other hand, the ability to recognize affective facial stimuli was found to be attenuated after a REM-rich sleep (Gujar, McDonald, Nishida, & Walker, 2011). Collectively, these findings suggest an additional contribution of REM sleep to encoding particularly of emotional stimuli. Surprisingly, studies directly comparing the effects of TSD and selective REM sleep deprivation (REMD) to dissociate REM and NonREM-sleep related effects on encoding during ensuing wakefulness are scarce, and to the best of our knowledge, there is no study additionally controlling for the emotionality of the stimuli.

Here, in two separate experiments we compared effects of TSD and REMD, relative to undisturbed sleep, on the subsequent encoding of neutral and emotional pictures. The pictures were presented in conjunction with colored frames to also assess related source memory. Encoding capabilities were examined by a picture recognition test right after encoding. In order to assess whether changes in encoding translate into corresponding long-term memory changes, an additional recognition test was performed one week later. We expected that TSD would generally impair encoding whereas REMD would selectively affect encoding of emotional pictures.

2. Methods

2.1. Subjects

Sixteen male subjects participated in the TSD study and 19 different men in the REMD study. Two subjects of the TSD study (because they fell asleep during learning after total sleep deprivation) and one subject of the REMD study (outlier regarding recognition performance, i.e., >3 SD from the mean) were excluded from analyses. Consequently, the final samples included 14 men (21.4 ± 1.65 yrs) in the TSD study and 18 men (22.0 ± 2.09 yrs) in the REMD study. According to standardized interviews performed before the experiment proper, the participants had no current physical or mental health problems, did not suffer from any sleep disturbances, did not use any medication, were non-smokers, and had not engaged in any shift work or traveled to a different time zone within three months before the experiments. Subjects were asked to abstain from food and beverages containing caffeine and alcohol after 18:00 h on the day prior to, and throughout the experimental sessions. The experimental protocol was reviewed and approved by the Ethics Committee for Research Involving Humans at the National Institute of Advanced Industrial Science and Technology (AIST), Japan, according to the principles expressed in the Declaration of Helsinki. All subjects gave written informed consent prior to participating in the study.

2.2. Procedure

In both studies (TSD and REMD), each subject took part in a preparatory session, in which he was familiarized with the experimental procedures and tasks, and two experimental conditions, i.e., a total sleep deprivation (TSD) condition and a control (Cont) condition in the TSD study, and a selective REM sleep deprivation condition (REMD) and a Cont condition in the REMD study (Fig. 1A). The studies were conducted according to a within-subject crossover design with the order of conditions balanced across subjects. The subject's two experimental conditions were separated by an interval of at least seven days.

In the TSD condition subjects stayed awake at home for about 34 h, i.e., from 8:00 h till 18:10 h the next day, when the learning phase started at the laboratory. Subject were free to choose any procedure to keep themselves awake. However, they should refrain from watching highly emotional movies (horror, action, etc.) and from any drinks containing caffeine or alcohol. In the Cont condition of the TSD study, subjects slept at their usual time at home to report to the lab at 18:00 h for the learning phase. Subjects recorded their sleep times using a sleep diary. Adherence to the sleep deprivation protocol and reported sleep time, respectively, were confirmed using actigraphy (Actiwatch 2, Philips/Respironics, Inc.). Five subjects did not meet the TSD criteria and dropped out. For all subject included in the present sample, actigraphy data indicated the absence of any sleep-like resting state longer than 1.0 min during the period of total sleep deprivation. Self-reports indicated that subjects took rather different measures to keep themselves awake, such as taking a bath, chatting with friends, and watching movies.

In the REMD study, nocturnal sleep was recorded in the sleep laboratory in sound attenuated and temperature and light controlled conditions. Subjects were familiarized to the experimental sleep conditions by spending an adaptation night in the laboratory including standard polysomnography performed between 23:15 h (lights off) and 7:00 h. In the REMD condition, REM sleep was prevented by tones (5 types of alarm tones, maxim 80 dB SPL, at ear level) presented via speakers contingently upon initial somnopolygraphical signs of REM sleep (diminished muscle tone, EEG theta activity, REMs, etc.). In the Cont condition no tones were presented. In both conditions, subjects left the lab in the morning and followed their daily activities. Napping was not allowed. They returned to the lab for the learning phase starting at 18:10 h. Self-report and actigraphy (no sleep-like rest state >1.0 min) confirmed that subjects did not nap during the day, although these measures cannot exclude that very short periods of sleep occurred.

In the learning phase of both experiments (taking place on Day 1 after the sleep manipulation), subjects first filled in several questionnaires and performed on the Psychomotor Vigilance Test (PVT) to assess vigilance. Then, the picture learning task was performed to assess encoding of neutral and emotional stimuli. For exploratory purposes, memory for the learnt pictures was not only measured immediately after learning but also one weeks later (Day 8) at the same time of the day.

2.3. Picture learning task

The picture learning task was adapted from Groch, Wilhelm, Diekelmann, and Born (2013) where it was proved to be sensitive to the consolidating effects of sleep on memory (Groch et al., 2013). Briefly, a total of 180 pictures (60 negative, 60 neutral, 60 positive, taken from the International Affective Picture System – IAPS (Lang, Greenwald, Bradley, & Hamm, 1993) were presented on a screen in random order. Each picture trail started with the presentation of a fixation cross (1500 ms), then a colored frame (red, green, blue, yellow) was presented (1500 ms) and then the frame disappeared and the picture was presented for 500 ms (Fig. 1B). The next trial started 2500–2750 ms later. After every 60 pictures a short break was introduced. Subjects were instructed to memorize the pictures and the associated frame color. The colored frame was added to the task to increase hippocampal memory processing load (Staresina & Davachi, 2009).