Biological Psychology 91 (2012) 150–155

Contents lists available at SciVerse ScienceDirect

Biological Psychology

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

Consolidation of temporal order in episodic memories

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ARTICLE INFO

Article history:
Received 16 November 2011
Accepted 31 May 2012
Available online 13 June 2012

Keywords:
Temporal order
NREM/REM cycles
Sleep spindles
EEG
Sleep deprivation
Memory consolidation

ABSTRACT

Even though it is known that sleep benefits declarative memory consolidation, the role of sleep in the storage of temporal sequences has rarely been examined. Thus we explored the influence of sleep on temporal order in an episodic memory task followed by sleep or sleep deprivation. Thirty-four healthy subjects (17 men) aged between 19 and 28 years participated in the randomized, counterbalanced, between-subject design. Parameters of interests were NREM/REM cycles, spindle activity and spindle-related EEG power spectra. Participants of both groups (sleep group/sleep deprivation group) performed retrieval in the evening, morning and three days after the learning night. Results revealed that performance in temporal order memory significantly deteriorated over three days only in sleep deprived participants. Furthermore our data showed a positive relationship between the ratios of the (i) first NREM/REM cycle with more REM being associated with delayed temporal order recall. Most interestingly, data additionally indicated that (ii) memory enhancers in the sleep group show more fast spindle related alpha power at frontal electrode sites possibly indicating access to a yet to be consolidated memory trace. We suggest that distinct sleep mechanisms subserve different aspects of episodic memory and are jointly involved in sleep-dependent memory consolidation.

1. Introduction

The different functions of sleep have not yet been completely understood although some kind of involvement in memory consolidation seems to be widely accepted (for review see Diekelmann and Born, 2010). More specifically, sleep has been proven to enhance hippocampus dependent temporal sequence memory in rats (Fortin et al., 2002). In humans there is to date only one study which demonstrates that sleep in comparison to wakefulness strengthens the original temporal sequence structure of a memory trace (Drosopoulos et al., 2007). In that study subjects were asked to learn triplets of words presented one after the other. Later, recall was tested by presenting word by word and asking which one came after the other. Sleep was found to enhance word recall, but only when students were asked to reproduce the learned words in the original forward direction (cueing with A and B and asking for B and C, respectively). Still debated, however, are the exact mechanisms which underlie the transformation of newly learned information into more stable forms during sleep.

Different sleep stages are assumed to be crucial for different types of memory. One of the main hypotheses, the "dual process theory", assumes that a specific sleep stage is characteristic for a specific memory type. Slow wave sleep (SWS) supports declarative memory consolidation whereas rapid eye movement (REM) sleep does so for procedural memories (Gais and Born, 2004; Maquet, 2001; Plihal and Born, 1997, 1999). The "sequential hypothesis" on the other hand, proposes that the alternation of sleep stages in cycles supports effective memory re-processing (Ficca and Salzarulo, 2004; Giuditta et al., 1995). This idea of complementary functions of SWS and REM sleep for successful memory consolidation was revived by Diekelmann and Born (2010) who suggested an essential role of SWS for system consolidation which is complemented by synaptic consolidation taking place during REM sleep. However, data directly supporting this latter hypothesis is still incomplete.

Neuronal replay during both SWS (Nadasdy et al., 1999; Wilson and McNaughton, 1994) and REM sleep (Poe et al., 2000), as usually observed in animal studies, seems to underlie the beneficial effect of sleep over wakefulness with regard to memory consolidation. Specifically, hippocampal replay during the night but also during quiet restfulness following spatial learning is a well-documented phenomenon (Frank et al., 2011; Zugaro and Girardeau, 2011).

Concerning memory relevant sleep features during the night, most empirical evidence is present for individual slow waves (Mölle et al., 2002), sharp wave ripples (Buzsaki, 1984; Mölle et al., 2009) and sleep spindles (Clemens et al., 2005; Fogel and Smith, 2006; Schabus et al., 2004). Here, the fast spindle type (>13 Hz) appears to be more relevant for sleep-dependent memory

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0301-0511
http://dx.doi.org/10.1016/j.biopsycho.2012.05.012

consolidation, specifically for motor memory formation (Morin et al., 2008; Tamaki et al., 2009). Additionally sleep spindles have been found to be significantly related to general cognitive abilities or "intelligence" (Bodizs et al., 2005; Fogel et al., 2007; Schabus et al., 2006).

In contrast to the idea of memory consolidation in sleep, EEG specific alpha oscillations seem to play an important role for successful memory reactivation during waking (Klimesch et al., 2006). In light of this data and the finding that sleep spindles are temporally linked to hippocampal reactivation (Siapas and Wilson, 1998) the question arises if alpha might not also play a crucial role during nightly "replay" or spindle occurrence.

In summary, given the well investigated role of sleep in memory consolidation surprisingly little is known about sleep effects on temporal order in episodic memories. In this study we therefore focused on the effect of sleep on (emotional) episodic stories using a sleep group and a sleep deprivation group. As it is well known that SWS enhances declarative memory consolidation and REM sleep is specifically beneficial for emotional content, an overall advantage in memory performance was expected for the sleep group. In the analyses we further focused on fine-grained investigation of non-REM (NREM)/REM cycles, and sleep spindle related oscillatory EEG changes. As will be shown, no one single sleep stage or mechanism appears to support sleep-dependent temporal order consolidation in our task, but rather the orderly interplay of NREM/REM cycles and spindle-related α-oscillations.

2. Materials and methods

2.1. Subjects

34 volunteers (17 women) with a mean age of 23.5 years (SD: 1.76; range: 19–28) participated in the study. All subjects were students, non-smokers, right-handed and had no severe organic or mental illness. They were regular sleepers and reported no sleep (PSQI < 5, Buysse et al., 1989) or mood disorder (SAS < 36, Zung, 1971; SDS < 40, Zung, 1965). Participants were randomly assigned to a sleep ($n = 16$) or a sleep deprivation group ($n = 18$).

All participants underwent an initial psychometric examination including the D-MEQ (Horne and Ostberg, 1976) for discriminating between evening and morning types, the FPI-R (Freiburger Personality Inventory Revised) (Fahrenberg et al., 2001) for personality assessment, as well as the APM (Advanced Progressive Matrices) (Raven et al., 1998) and the WMS-R (Working Memory Scale Revised) (Wechsler, 1987) for assessing general cognitive and memory abilities, respectively. Furthermore, subjects reported their medical history and their usual sleep habits. Subjects assigned to the sleep group started with an adaptation night preceding the experimental learning night. To control for constant sleep–wake rhythms before and during the experimental period, participants had to fill in sleep diaries and report their nightly dreams. Before study participation all subjects signed an informed consent form.

2.2. Study design

Both groups had to learn 8 different memory sequences in the experimental night. Each sequence consisted of 12 pictures. After the encoding sessions subjects were tested for the temporal order of the pictures. Only after this first retrieval subjects were told to which group they would be assigned (sleep or sleep deprivation). Subjects in the sleep group went to bed 15–30 min after encoding and stayed in bed for the next 8 h. Subjects in the sleep deprivation group had to stay awake the whole night (8 h) and the following day. The Psychomotor Vigilance Test (Wilkinson and Houghton, 1982) was carried out every hour (8 times) during the night (Hoedlmoser et al., 2011). In between the tests, subjects were allowed to play cards and drink water or tea but it was forbidden to eat or drink caffeine containing beverages or turn on normal lights. Room temperature was constantly kept at 20–22 °C and lights were dimmed to a maximum of 10 lx.

Subjects in both groups were retested with the temporal order task tested in the morning (15–30 min after 8 h of sleep or deprivation). The last retrieval test was then done in the morning three days after the experimental night (72 h after the second, morning retrieval). Additionally a classic recognition task was performed on day three.

2.3. Memory tasks

To explore the episodic memory strength (i.e., temporal order) we implemented a modification of a sequence learning task already used by Kumaran and Maguire (2006). Therefore faces and objects were selected as stimuli (48 grayscale front-facing photographs of unfamiliar male and female faces obtained from the Stirling database http://pisc.psych.stir.ac.uk/ as well as 48 grayscale photographs of objects obtained from the software HEMERA Photo Objects©). All subjects were required to learn 8 sequences of pictures in total, consisting of 6 faces and 6 objects in each sequence. To control for the mnemonic strategies used, subjects were given a standardized instruction which requested them to create a personal story for each sequence in which they were personally involved. The goal then would be to simply remember the order of the 12 pictures. After a demonstration period using two semantically similar sequences (hobby–garden, hobby–car) four different types of themes (holiday, illness, crime and profession) were presented for episodic encoding.

One encoding phase included two sequences for a given theme (e.g. holiday–summer and holiday–winter). Each sequence was presented twice over the course of one encoding phase, with a retrieval test of sequential memory at the end of each encoding block. Each encoding phase started with a context-specific cue displayed for 3500 ms: 'Learn: Sequence 1: Holiday/Summer'. Next, in a sequence encoding block lasting 42 s in total, 6 faces and 6 objects were presented one after another, each for the duration of 3500 ms, in the center of the screen on a black background. After this, a central fixation cross was displayed for 8000 ms followed by a further cue (displayed for 3500 ms) indicating that a retrieval block would shortly occur: 'Test: order of faces and objects'.

Each retrieval block consisted of three trials: in each trial, four pictures were presented side by side in random positions. Thus, over the course of three trials constituting the sequence retrieval block, all 12 pictures that were presented in the preceding encoding block were seen again. The array of four pictures was then displayed for 6000 ms during which subjects were required to determine the relative order in which the pictures appeared in the preceding sequence. After those 6000 ms subjects were requested by the cue 'Now respond!' to order the pictures by using the numerical keys 1–4 (max. respond time was set to 12,000 ms).

The temporal order of pictures indicated by subjects using the keypad was scored as follows: each face or object was awarded one point if in the correct position in the sequence relative to each other picture in turn. Therefore subjects could get a maximum of 6 points for one trial and 18 points for a complete sequence. If the correct order was e.g. A C D B and the subject correctly pressed that order, he/she got 3 points for A, 2 points for C and 1 point for D (cf. Kumaran and Maguire, 2006).

In addition a recognition test was conducted on day 3. This test comprised twice 96 pictures, with an equal number of previously seen and unseen faces/objects. Subjects were required by button press to indicate whether the face/object was new or old and how certain they were about their judgment (1–3) (cf. Supplementary Table 1).

2.4. EEG recordings

The electroencephalogram (EEG) was recorded utilizing Synamps EEG amplifiers (NeuroScan Inc., El Paso, TX). All signals were filtered (0.10 Hz high-pass filter; 70 Hz low-pass filter; 50 Hz notch filter) and digitized online with 500 Hz sampling rate. 23 EEG channels (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1, Oz, O2, as well as A1 and A2 for later re-referencing), 1 bipolar vertical electrooculogram (EOG) channel to control for eye artifacts, 1 bipolar submental electromyogram (EMG) channel, 1 bipolar electrocardiogram (ECG) channel and 1 bipolar respiratory channel (chest wall movements) were placed. Electrodes were attached according to the international electrode (10-20) placement-system. During adaption nights, polysomnography (PSG) recording included 8 EEG, 4 EOG, 1 bipolar ECG, 3 unipolar EMG (submental and left/right tibialis), and 4 respiratory channels (nasal airflow, chest and abdominal wall movements, oxygen saturation). Sleep was automatically scored and visually checked according to standard criteria (Rechtschaffen and Kales, 1968) by the Siesta Group.

2.5. Sleep cycles

Sleep cycles were analyzed using Matlab 7.0.1 built scripts using the criteria from Mazzoni et al. (1999) specifying that NREM and REM sleep has to be longer than 2 min in order to be scored as a cycle. A NREM/REM cycle was defined as sequence of NREM and REM sleep not interrupted by a waking period longer than 2 min. REM epochs shorter than 2 min were included in the previous sleep stage. Similarly, a sequence of NREM stages interrupted by a period of wakefulness longer than 2 min was not considered part of a NREM/REM cycle. In addition we required a NREM/REM cycle to be longer than 30 min. To obtain changes over the night, we calculated a NREM/REM ratio for the first, second and last cycles as these data were present across all subjects.

2.6. Sleep spindles

Sleep spindles were detected automatically using the frontal (F3/F4) and central (C3/C4) electrodes, re-referenced to contralateral mastoids. Spindle detection was based on the following criteria: (1) 11–15-Hz band-pass filtering, (2) amplitude > 25 μV, (3) duration > 0.5 s, and (4) controlling for muscle (30–40 Hz) and/or alpha (8–12 Hz) artifacts (for details refer to Anderer et al., 2005). Concerning band-pass filtering, spindles were divided into a slow range (including spindles from 11 to