Brain Research Bulletin 82 (2010) 118–123

Contents lists available at ScienceDirect

Brain Research Bulletin

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

Research report

The effects of morning training on night sleep: A behavioral and EEG study

Sara Määttä[a,b], Eric Landsness[a], Simone Sarasso[a], Fabio Ferrarelli[a], Florinda Ferreri[a,b,c], M. Felice Ghilardi[d,*], Giulio Tononi[a,*,1]

[a] Department of Psychiatry, University of Wisconsin, Madison, WI, USA
[b] Department of Clinical Neurophysiology, Kuopio University Hospital and University of Kuopio, Kuopio, Finland
[c] Department of Neurology, University Campus Biomedico, Rome, Italy
[d] Department of Physiology, Pharmacology and Neuroscience, CUNY Medical School, 138 Convent Ave, New York, NY 10031, USA

ARTICLE INFO

Article history:
Received 23 December 2009
Accepted 12 January 2010
Available online 25 January 2010

Keywords:
Learning
Memory
Consolidation
Motor learning
SWA

ABSTRACT

The consolidation of memories in a variety of learning processes benefits from post-training sleep, and recent work has suggested a role for sleep slow wave activity (SWA). Previous studies using a visuomotor learning task showed a local increase in sleep SWA in right parietal cortex, which was correlated with post-sleep performance enhancement. In these as in most similar studies, learning took place in the evening, shortly before sleep. Thus, it is currently unknown whether learning a task in the morning, followed by the usual daily activities, would also result in a local increase in sleep SWA during the night, and in a correlated enhancement in performance the next day. To answer this question, a group of subjects performed a visuomotor learning task in the morning and was retested the following morning. Whole night sleep was recorded with high-density EEG. We found an increase of SWA over the right posterior parietal areas that was most evident during the second sleep cycle. Performance improved significantly the following morning, and the improvement was positively correlated with the SWA increase in the second sleep cycle. These results suggest that training-induced changes in sleep SWA and post-sleep improvements do not depend upon the time interval between original training and sleep.

1. Introduction

Many behavioral studies have shown that performance in a variety of tasks improves following sleep [2,10,18,22,42–45]. Moreover, sleep deprivation impairs learning memory formation and inhibits plastic processes such as long-term potentiation [27,47]. For at least some learning tasks, sleep-dependent improvement relies on sleep slow wave activity (SWA, the EEG power during NREM sleep between 0.5 Hz and 4.5 Hz) [1,12,20,26,28,30,36], which reflects slow oscillations in the membrane potential of cortical neurons [35]. Sleep SWA is homeostatically regulated, generally increasing with the time spent awake, and decreasing with the time spent asleep [4,6]. Recent evidence indicates that sleep SWA is also regulated locally, and that changes in SWA may be related to synaptic plasticity. Specifically, procedures leading to local strengthening of synapses in wakefulness induce a local increment in SWA during sleep [18,7,16,19]. Conversely, behavioral or instrumental manipulations leading to synaptic depression in specific brain region produce a local decrease in SWA [7,17,19]. These findings suggest a direct link between the synaptic plasticity triggered by waking activities and the homeostatic regulation of sleep.

So far, studies investigating the role of sleep SWA in learning and memory in humans have placed the initial learning session shortly before sleep. This choice has the advantage of minimizing potential interference caused by subsequent waking activities and maximizing the chance of detecting learning-induced changes in brain activity during subsequent sleep. On the other hand, if sleep SWA plays an important role in learning and memory, it should be possible to document local changes in sleep SWA following learning, and such changes should be correlated with performance improvement the next day, irrespective of other daily activities. To evaluate this possibility, we took advantage of an implicit visuomotor learning task that showed sleep-dependent improvements related to a local change in sleep SWA [18]. Specifically, subjects who engaged in a rotation adaptation task in the evening before sleep showed a local increase in sleep SWA over the right posterior parietal region during the first 30 min of NREM sleep. Moreover, the next day subjects' performance improved in a way that was correlated with the amount of SWA during the first sleep cycle. The present work repeats the paradigm employed in the previous study. However, subjects performed the rotation adaptation task in the morning, and were left free to pursue their routine activities dur-

---

[*] Corresponding authors. Tel.: +1 212 650 7487.
E-mail addresses: lice.mg79@gmail.com (M.F. Ghilardi), gtononi@wisc.edu (G. Tononi).
[1] Contact address: University of Wisconsin/Madison, Department of Psychiatry, 6001 Research Park Blvd., Madison, WI 53719, USA. Tel: +1 608 263 6063; fax: +1 608 265 2953.

0361-9230/$ – see front matter © 2010 Elsevier Inc. All rights reserved.
doi:10.1016/j.brainresbull.2010.01.006

ing the day. We then used high-density EEG to record sleep activity patterns with sufficient topographic resolution for the entire night, and not just the first hour. We asked whether morning training also triggered local changes in sleep SWA over the right posterior parietal area, and whether there would be a correlated enhancement in performance the next day.

2. Materials and methods

2.1. Subjects and study design

Fourteen subjects (age = 20–38 years, mean: 28.4 years, eight men) were studied. Participants were right-handed, healthy, and had no history of psychiatric or neurological diseases or sleep disorders, as assessed in a preliminary screening visit. All subjects signed an informed consent form before participating in the study which was approved by the ethical committees of the participant institutions.

All subjects were tested in two sessions, separated by at least 1 week:

(1) *Learning session*: in the morning, around 9 am, they were trained in a visuomotor adaptation task [18,13,15,25] for about 1 h. Thereafter, they left the laboratory to pursue their usual daily activities. Twelve hours later, around 9 pm, they returned to the sleep lab, where EEG activity was recorded during undisturbed sleep. The following morning, 30 min after waking up, they were retested.

(2) *Control session*: after a day of usual activities, subjects arrived in the sleep lab about 1 h before their habitual bedtime and EEG during sleep was recorded for the entire night.

The order of the two sessions was randomized. Subjects were instructed to maintain their usual sleep–wake schedule for at least 1 week before the sessions. During the 2 days of testing, they were required to go to sleep and to wake up at their habitual times. In addition, they were to abstain from daytime napping; wrist actigraphic recordings (Actiwatch 64, MiniMitter; Bend, Oregon) were used to ascertain that none of the subjects napped during the day.

2.2. Motor task and analysis

The motor task has been described in detail elsewhere [18,13,15,25]. Briefly, subjects moved a handheld cursor on a digitizing tablet. An opaque shield prevented them from seeing their arm and hand at all times. They were instructed to execute out-and-back movements from a central starting point to one of eight radially-arranged targets (distance of 4.2 cm), which appeared randomly on a computer screen together with the cursor position. Unbeknownst to the subjects, the direction of cursor movement on the screen was progressively rotated counterclockwise or clockwise relative to the hand movement by a total of 60° in four incremental steps of 15°. Each step comprised three blocks of 90 movements, for a total of 1080 movements. To prevent fatigue, trial blocks were separated by 1–2 min resting periods.

For each movement, we computed several kinematic parameters as reported previously [13], including amplitude of peak velocity, reaction time, directional error at the peak velocity and movement duration. Adaptation at the end of training was measured as the decrease in percentage of the directional error at the peak velocity in a separate block [18,15,25]. Improvement at retest was computed as the difference in adaptation between the training and the testing sessions.

2.3. EEG recordings and analysis

EEG was recorded with a 256-channel EEG amplifier (Electrical Geodesic, Inc., Eugene, OR), sampled at 500 Hz and referenced to Cz. Electrode impedances were set below 50 kO. Offline, the EEG was down sampled to 128 Hz, band-pass filtered between 0.5 Hz and 50 Hz, and average-referenced after rejection of bad channels and epochs.

Sleep EEG was recorded for the entire night. For the analysis, sleep stages were visually scored in 20-s epochs according to standard criteria [32]. Matlab (The MathWorks, Natick, MA) and public license toolbox EEGLAB were used for data analysis. For a quantitative analysis of sleep EEG, we performed a spectral analysis of consecutive 20-s epochs (power spectral density estimate calculated applying a Welch's average modified periodgram with a Hanning window, based on averages of five consecutive 4-s epochs) for all included channels after visual and semiautomatic artifact removal based on the power in 0.75–4.5 Hz and 20–40 Hz bands [18]. Power spectra were calculated for NREM sleep, and the power of the two main EEG rhythms of NREM sleep, namely SWA (1–4.5 Hz) and sleep spindles (12–15 Hz) were used for analysis.

To assess significant topographic differences in sleep EEG power between the conditions, we applied statistical nonparametric mapping using a suprathreshold cluster analysis for multiple comparisons [18,31]. For all other comparisons, *t*-tests, appropriate designs of the analysis of variance (ANOVA), and post hoc tests (Tukey's HSD) were applied to determine the sources of the significant effects. Kinematic measures were correlated (Pearson) with EEG power density values for individual electrodes and for the mean of all scalp electrodes for each frequency bin. Statistical analyses were computed with Matlab and SPSS for Windows 17 statistical program.

3. Results

3.1. Morning learning is followed by performance enhancement after a night of sleep

During the training in the morning, subjects adapted their movements to the imposed rotation of 60° by progressively decreasing the mean directional error and its variance across each successive incremental step of 15°. As shown in Fig. 1, the decrements of mean directional error across blocks and steps were significant (block: $F(2,167) = 18.93$, $p < 0.0001$; step: $F(3,167) = 35.70$, $p < 0.0001$; block × step: $F(6,167) = 0.11$, $p = 0.99$). As previously reported, with the exception of the first 15° step, the directional error at the end of each step was progressively higher than the corresponding baseline values. At the last block of the 60° step, there was a residual error of approximately 10°, which was significantly greater than the baseline mean directional error (2.95°, Fig. 1, $F(1,28) = 40.63$, $p \leq 0.0001$). On the other hand, reaction time, movement duration and peak acceleration at the end of the training were not different from baseline (Fig. 2). After training, the degree of learning achieved was tested in a separate movement block. On average, subjects showed an adaptation of 55.31% (Fig. 1). These results are similar to those we previously reported for different groups of subjects with adaptation rates ranging from 50% to 60% [18,25].

We have previously shown that performance in this visuomotor adaptation task improves after a night of sleep [18]. As expected, upon retesting the next morning, adaptation significantly improved by 11.6 ± 0.9% (mean ± SE, $p < 0.0001$) an effect of similar magnitude as that observed when the training was performed just before going to sleep (11.3% [18]). In addition, as in previous works, this effect was specific for directional error, as there were no significant changes after sleep in either reaction time, movement duration or peak velocity compared to the training session.

3.2. Morning learning leads to local SWA increase during sleep

High-density EEG was recorded during sleep both 12 h after the motor learning task and in the control session, after usual daily activities. All subjects had at least three complete sleep cycles in both sessions, which did not differ in sleep latency, total

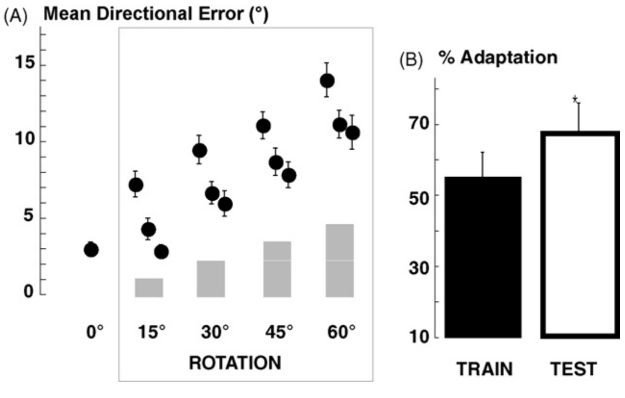

Fig. 1. Performance improves after sleep. (A) Learning curves for the rotation adaptation task in the morning training. The mean directional error for each block of movements is plotted. Points are means across subjects and bars represent standard errors ($n = 14$). (B) Percentage of adaptation achieved in the morning, after training, and the next day, at test.