Sleep Medicine 14 (2013) 1112–1122

Contents lists available at ScienceDirect

Sleep Medicine

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

Original Article

How we fall asleep: regional and temporal differences in electroencephalographic synchronization at sleep onset

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ARTICLE INFO

Article history:
Received 4 February 2013
Received in revised form 15 May 2013
Accepted 21 May 2013
Available online 23 August 2013

Keywords:
Sleep onset
Theta oscillations
Occipital cortex
Anteroposterior changes
Oscillatory activity
EEG analysis
BOSC

ABSTRACT

Objectives: We hypothesized that the brain shows specific and predictable patterns of spatial and temporal differences during sleep onset (SO) reflecting a temporal uncoupling of electrical activity between different cortical regions and a dissociated wakelike and sleeplike electrocortical activity in different cortical areas.

Methods: We analyzed full-scalp electroencephalographic (EEG) recordings of 40 healthy subjects to investigate spatial and temporal changes of EEG activity across the wake-sleep transition. We quantified EEG sleep recordings by a fast Fourier transform (FFT) algorithm and by a better oscillation (BOSC) detection method to the EEG signals, which measured oscillatory activity within a signal containing a nonrhythmic portion.

Results: The most representative spatial change at SO is the frontalization of slow-wave activity (SWA), while the θ activity, which mostly shares a similar temporal and spatial pattern with SWA, exhibits a temporo-occipital diffusion. The time course of these oscillations confirms that the changes of the dominant waves coexist with topographic changes. The waking occipital prevalence of α oscillations is progressively replaced by an occipital prevalence of θ oscillations. On the other hand, more anterior areas show a wide synchronization pattern mainly expressed by slow waves just below 4 Hz and by spindle oscillations.

Conclusions: The whole pattern of results confirms that the centrofrontal areas showed an earlier synchronization (i.e., they fall asleep first). This finding implies a coexistence of wakelike and sleeplike electrical activity during sleep in different cortical areas. It also implies that the process of progressive brain disconnection from the external world as we fall asleep does not necessarily affect primary and higher-order cortices at the same time.

1. Introduction

A growing body of evidence strongly supports the notion that sleep is a local and use-dependent process. Multichannel electroencephalographic (EEG) recordings in humans indicate that practically every sleep phenomenon from sleep onset (SO) to the awakening is strictly local in nature [1]. Extensive regional differences have been documented at SO [2–5], across all-night nonrapid eye movement (NREM) and rapid eye movement (REM) sleep [6] and on awakening [7,8]. Similarly every sleep EEG rhythm occurs locally: slow oscillations (<1 Hz), slow waves (0.5–4 Hz), and sleep spindles (12–15 Hz) are local phenomena, as revealed by simultaneous EEG recordings of the scalp, intracerebral EEG recording [9], and unit firing in multiple brain regions of neurosurgical patients [10]. Additionally, θ (5–7 Hz) and α (8–11 Hz) oscillations in scalp recordings likewise are predominantly local [11].

In the spatial acceptation of the local sleep notion, we focused on the existence of topographic, frequency-specific EEG differences, which were stable within sleep states and within individuals. This interpretation encompasses phenomena such as the frontal prevalence of low-frequency oscillations during both NREM and REM sleep [6], explained by homeostatic sleep regulating processes that preferentially involve those neuronal populations which mostly have been activated during wakefulness [1], or like the individual centroparietal profile of the EEG activity in the 8- to 16-Hz frequency range during NREM sleep [12].

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http://dx.doi.org/10.1016/j.sleep.2013.05.021

Undoubtedly the transitions between states of vigilance and in particular SO are a privileged scenario in which local sleep processes do occur. EEG and corticographic recordings suggest that SO is characterized by massive regional brain heterogeneity. Low-frequency EEG activity is prominent at the more anterior areas, and >8 Hz frequencies are prevalent at the occipital regions during presleep wakefulness [4]. Then the α activity (8–12 Hz) spreads toward anterior areas, and the progressive synchronization of the EEG during NREM sleep is expressed by an increased centrofrontal prominence of low-frequency activity and by centroparietal maxima of the σ activity (12–14 Hz) [4]. Scalp observations have been supported by electrocorticographic recordings of epileptic patients undergoing presurgical assessment [13].

This orchestrated series of cortical changes seems to dynamically involve different areas and different EEG frequencies. As recently demonstrated in drug-resistant epileptic patients, widespread cortical territories can maintain an activated pattern for several minutes after the thalamic [14] and the hippocampal deactivation [15]. Interestingly, the thalamocortical delay in SO is highly variable between individuals and cortical projections, ranging from few seconds to more than 10 min [14]. Such temporal uncoupling of electrical activity between different cortical regions may result in the coexistence of wakelike and sleeplike electrical activity during sleep of different cortical areas [9].

Our study aimed to describe the local (cortical) specific patterns of EEG activity during SO. In particular, we analyzed full-scalp EEG recordings in a large sample of normal subjects to investigate spatial and temporal changes across the wakefulness to sleep transition. These local EEG changes during SO have been analyzed and quantified by a consolidated algorithm based on fast Fourier transform (FFT) algorithm and by a better oscillation (BOSC) detection method for the first time [11,16–18]. Therefore, we performed a single-Hz FFT investigation of spatial EEG changes at SO without any a priori assumption regarding the definition, the frequency-range, and the functional meaning of each EEG band. Then we assessed the temporal dynamics (time courses) of the classic EEG frequency bands before and after SO. Finally we investigated the changes across the wake-sleep transition by detecting EEG oscillations and then we analyzed their topographic differences and time courses.

2. Methods

2.1. Participants

Forty right-handed healthy subjects (20 men and 20 women) ages 18–29 years (mean age, 23.8 ± 2.88 years) were selected from a university student population. The inclusion criteria were normal sleep duration and schedule (habitual sleep time, 12:00 am–8:00 am ±1 h); no daytime nap habits; no excessive daytime sleepiness; and no other sleep, medical, neurologic, or psychiatric disorders, as assessed by a 1-week sleep log and by a clinical interview. Participants were required to avoid napping throughout the experiment; compliance was controlled by actigraphic recordings (AMI Mini Motionlogger).

All subjects gave their written informed consent. The study was approved by the Institutional Ethics Committee of the Department of Psychology of "Sapienza" University of Rome and was conducted in accordance with the Declaration of Helsinki.

2.2. Procedure

A dataset of a previous study was analyzed [19]. The sleep recordings were scheduled in the first night (adaptation), in the second night (baseline sleep), and in the fourth night (recovery sleep after 40 h of sleep deprivation). For the purposes of our study, only the second undisturbed baseline sleep night after the adaptation to laboratory sleep was considered.

Sleep recordings were performed in a soundproof temperature-controlled room. The subjects' sleep was undisturbed and started at midnight and ended after 7.5 h of accumulated sleep, as visually observed online by expert sleep researchers.

2.3. Polysomnographic recordings

An Esaote Biomedica VEGA 24 polygraph was used for polysomnographic (PSG) recordings. EEG signals were analogically filtered (high-pass filter at 0.50 Hz and antialiasing low-pass filter at 30 Hz [−30 dB/octave]). The 19 unipolar EEG derivations of the international 10–20 system (Fp1, Fp2, F7, F8, F3, F4, Fz, C3, C4, Cz, P3, P4, Pz, T3, T4, T5, T6, O1, O2) were recorded from scalp electrodes with averaged mastoid reference. The submental electromyogram (EMG) was recorded with a time constant of 0.03 s. Bipolar horizontal eye movements were recorded with a time constant of 1 second. The bipolar horizontal electrooculogram (EOG) was recorded from electrodes placed approximately 1 cm from the medial and lateral canthi of the dominant eye. Impedance of these electrodes was kept below 5 K Ohm.

2.4. Data analysis

2.4.1. PSG and quantitative analysis of EEG signals

Central EEG derivation (Cz), EMG, and EOG were used to visually score sleep stages in 12-second epochs, according to the standard criteria [20]. PSG measures provided a clear picture of a normal night sleep of adapted subjects (Table 1). It should be noted that sleep latency was characterized by a considerable variability between subjects (standard deviation, 11.43 min).

The polygraphic signals (19 EEG channels, EOG, and EMG) were converted online from analog to digital with a sampling rate of 128 Hz and stored on the disk of a personal computer. We investigated the 0.50- to 25.00-Hz frequency range, computing power spectra by a FFT routine for 4-second periodograms. Spectra from three consecutive 4-second epochs were averaged to allow alignment with the visual scoring of sleep stages, based on 12-second epochs. EEG topography was evaluated by comparing the 5-minute presleep vs. postsleep intervals. Ocular and muscle artifacts were carefully excluded offline by visual inspection. Due to the intrinsic characteristics of the presleep stage, the percentage of rejected 12-second epochs was higher in these 5-minute intervals (41.2% ± 16.4%) than in the postsleep intervals (21.0% ± 16.0%). Individual time series of EEG power values were aligned as a function of the first epoch of sleep defined on the basis of the appearance of the first k-complex or sleep spindle. In fact it has been previously demonstrated that the first epoch of stage 2 sleep represents an unequivocal hallmark for the beginning of sleep [21,22].

Data analysis was mostly performed with the software package MATLAB (The Math Works, Inc., MA, USA) and its signal analysis and statistics toolbox.

2.4.2. Single-Hz EEG topography

Before statistical analyses, the data were reduced to a 1-Hz bin width by collapsing four adjacent 0.25-Hz bins. The only exception was the 0.50- to 1.00-Hz bin, for which two adjacent 0.25-Hz bins were collapsed. The bins were referred to and plotted by the center frequency included in our study (e.g., the 2-Hz bin referred to the averaged values of the following bins: 2.00, 2.25, 2.50, and 2.75 Hz).

EEG power values for each 1-Hz frequency bin were considered as dependent measures and compared by paired t tests in the 5-minute intervals preceding and succeeding SO. Values were log