PhD thesis

Connections between sleep, memory and the hippocampus as revealed by low frequency EEG patterns

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1. Introduction

There is no doubt that one of the best known and the most studied hippocampal electrophysiologic activity pattern is the phenomenon of hippocampal theta or hippocampal rhythmic slow activity (RSA) [1]. At the same time with the discovery of REM state the researchers are not only faced with the two kinds of sleep (NREM and REM), but also with a paradox: one of the two kinds of sleep - namely REM sleep - is accompanied by electrophyisiologic activity patterns characteristic for wakefulness. Such kind of wakeful-like electrophysiological activity pattern is the hippocampal RSA, which can be recorded during exploratory behavior and REM sleep in most of the mammalian species [2]. The frequency of hippocampal RSA varies between 4-9 Hz. The mechanism of the formation of hippocampal RSA was studied at the level of single cell studies, and it is proven that it plays a crucial role in the consolidation of new memory traces [3]. Due to the role of the hippocampal RSA in memory processes and its place in the sleep-wakefulness cycle, it became a cornerstone of the theories focusing on memory consolidation and the debate around the function of REM sleep [4]. For these reasons it is of fundamental importance to decide wether hippocampal RSA exists in humans. The majority of the experiments were performed on rodents and to a lesser extent on cats and dogs. Similar experiments performed on primates and those few sporadic and controversial data which is available regarding humans do not make it possible to answer the question [5].

Sleep and the hippocampus are two issues which were both related to the problem of memory processes. Based on the available experimental data it is statable that sleep has a favourable influence on the process of memory consolidation, and the hippocampus has a crucial role in this effect. The connection between sleep, memory and the hippocampus is regarded as an acute effect, which means that there is a positive influence of the sleep-dependent hippocampal activity on the process of memory consolidation [6]. The possibility that this relationship could be a trait-like one has not been studied yet. As like regarding different traits and features humans of course differ from each other in their mnemonic effectiveness.

2. Aims

One of the aims of my study is to describe the low-frequency activity patterns of the human hippocampus during different sleep-waking states. In this regard, drifting away from the routine methods, I used monopolar derivation with the reference point being far from the hippocampus. This technic was found to be effective in animal studies regarding hippocampal theta and I supposed that conformity with such methodological requirments would produce more consequent results than human studies have ever performed until now. On the other hand I tried to change the routine of semi-quantitative reports based on a small number of subjects, and I also aimed for gathering statistically relevant data. The above requirements have not been fulfilled simultaneously in human hippocampal electrocorticography studies performed until now.

The other aim of my study is to correlate the sleep-wake dependent individual hippocampal activity patterns with memory performances in order to detect possible trait-like relationships. So the question is whether individual differences in memory performances are related to the individual differences in hippocampal activity patterns.

3. Methods

Study 1.

Twelve epileptic patients participated in the study. Their presurgical evaluation included long-term video EEG monitoring completed with foramen ovale electrodes.

Foramen ovale electrodes are special, flexible wires, which are introduced through the foramen ovales into the cisterna ambiens during general anaesthesia. They register from 4 points (which are 5 mm apart from each other) of the left and the right parahippocampal gyrus respectively. During video-EEG monitoring which lasted 3-12 days depending on clinical situation these electrodes were completed with additional scalp electrodes of the 10-20 system, submental electromiography, as well as vertical and horizontal electrooculography. Foramen ovale and temporolateral scalp electrodes were referred to the Cz point of the vertex. In two patients contralateral mastoid references and in three patients earlobe references were also available. I scored sleep stages according to Rechtschaffen and Kales criteria, after which I differentiated 6 sleep waking states as follows: waking-eyes open, waking-eyes closed, light NREM sleep (sleep stage 2), deep NREM sleep (sleep stage 3 and 4), tonic REM sleep (REM sleep periods without eye movements), and phasic REM sleep (REM sleep periods accompanied by eye movement bursts). From all of these sleep-waking states I have selected 30-100 4 second long epochs, free from artefacts and epileptic spikes. The epochs were analysed by fast Fourier transformation, and average spectral power values characterizing the sleep-waking states were calculated. Every patient had average spectral values for each of their foramen ovale (4 left and 4 right) and temporolateral (T3 and T4) electrodes. The input of statistical analysis consisted of the relative spectral power of the 0.00-1.25 Hz, 1.50-3.00 Hz, 3.25-4.50 Hz, 4.75-

6.25 Hz, 6.50-7.75 Hz and 8.00-9.50 Hz frequency bands. I used one-way ANOVA for the state effect in the case of each frequency band. After it sleep-waking states were analysed by contrast analysis as a comparison of waking versus other, NREM sleep versus other and REM sleep versus other, for each frequency band. This was followed by the post-hoc Sceffé test.

Study 2.

Analysis was based on thirteen foramen ovale recordings. All the thirteen patients were right-handed. Memory tests were parts of the preoperative examination and had preceded video-EEG monitoring by several weeks. The testing of verbal memory was done with the 10 Words Trial, which consists of the immediate and delayed recall of 10 auditorily presented common Hungarian words. Visual memory was quantified by the immediate and delayed recall performance in the Rey-Osterrieth Complex Figure Test. The method of quantitative EEG analysis were the same as in study 1, with one exception: in study 2 I used both the absolute and relative power values. During statistical analysis I calculated Pearson correlation coefficients between the memory performances and the quantified EEG measures. Age, years of intractable seizures, and hippocampal sclerosis were controlled by partial correlation coefficients.

4. Results

Study 1.

Visual examination of the activity patterns

In the waking-eyes open condition slow and fast components appeared mixed in the foramen ovale recordings. Rhythmic activity was not observable. This activity resembled the temporolateral EEG, but contained somewhat more slow components and of course it had higher amplitude. In the waking-eyes closed state alpha activity was present in the foramen ovale electrodes, but it was characterized by very high interindividual variability. Otherwise this state was also characterized by more slow components in the foramen ovale recordings than in the temporolateral scalp leads.

In light slow-wave sleep (NREM stage 2) foramen ovale and scalp EEG patterns were similar. These were characterized by the appearance of sleep spindles, high-voltage K-complex-like activity and more slow components compared to the waking state. Sleep spindles appeared in earlobe and/or mastoid referred leads too, so they could not be entirely attributed to the vertex reference.

During deep slow-wave sleep (stage 3 and 4 NREM) foramen ovale recorded and temporolateral scalp recorded activities showed a great similarity as well. On both of the temporal surfaces (medial and lateral) this state was dominated by a slow, lesser than 1 Hz, high-voltage EEG pattern, sometimes mixed with 1-4 Hz delta activity. The descending phase of the high-voltage <1 Hz oscillation was frequently superimposed by sleep spindles, and sometimes this superposition showed rhythmic recurrence.

Tonic and phasic REM sleep periods were characterized by a strikingly marked dissociation between the temporomedially and temporolaterally observable electrophysiologic activity patterns. While in the temporolateral scalp EEG the well-known low-voltage, desynchronized activity appeared, most of the foramen ovale electrodes were characterized by visually observable, striking, rhythmic slow activity belonging to the delta band (Fig. 1.). This activity was continuous during the whole REM periods and appeared in the tonic and phasic REM sleep periods as well. In some of the patients this slow activity became more pronuonced during the phasic REM periods, but in others this was not the case. Moreover some of the cases showed the contrary, i.e. more striking slow waves during tonic REM sleep. Slow oscillation did not differ between the epileptic seizure focus and the contralateral foramen ovale recordings, even in the case of unambiguous unilateral temporal lobe epilepsy. At the same time this slow oscillation was outlined not only with vertex reference, but also with contralateral mastoid reference (2 patients) and earlobe reference (3 patients) in every case when these reference points were available. This excludes the possibility that this slow wave is generated in the reference point. Moreover in the case of vertex reference the slow oscillation appeared with remarkably higher amplitude, which suggests that the oscillation in question is generated near the foramen ovale electrodes. In bipolar montages in turn, the slow oscillation during REM sleep was not outlined, which let us conclude that it involves large parts of the hippocampus simultaneously.

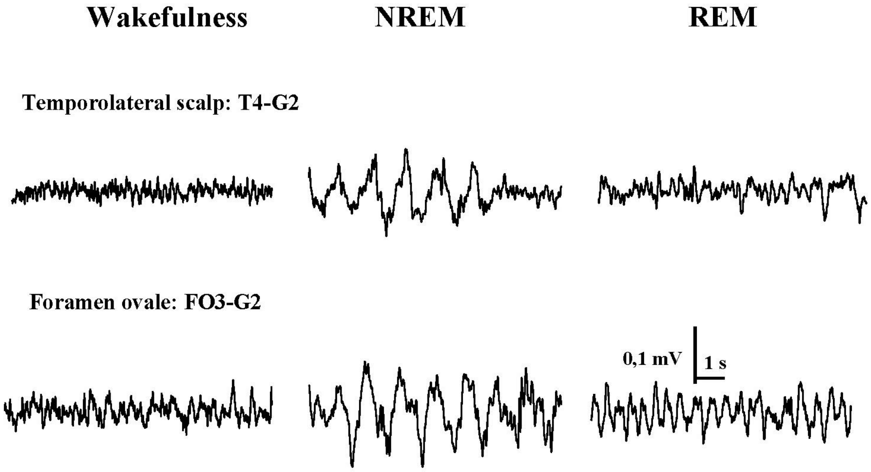

Figure 1. Activity patterns recorded during wakefulness, NREM sleep and REM sleep respectively

Quantitative analysis of the activity patterns

Average spectral power functions showed two prominent tendencies in the foramen ovale registered activity. One is the 0.75-1.00 Hz activity, dominating deep slow-wave sleep, but was present in light slow-wave sleep too. The other is the 1.50-3.00 Hz activity emerging in tonic and phasic REM sleep. Thus NREM and REM sleep diferred from each other from the point of view of the dominant frequencies. All the other frequency bands were much less characteristic. Statistical comparison of the relative power values confirmed the regular association between the 1.50-3.00 Hz activity and REM sleep, while the 0.00-1.25 Hz activity dominated NREM sleep. As measured with the foramen ovale electrodes these two subdivisions of the delta range seem to have a reciprocal relationship in NREM and REM sleep. Relative power values of the frequency bands above 3.25 Hz were significantly lower in deep NREM sleep as compared to other sleep-waking states' corresponding frequency bands' relative power values.

Apart from this the most prominent activity in the waking-eyes open condition was the 8.00-9.50 Hz one.

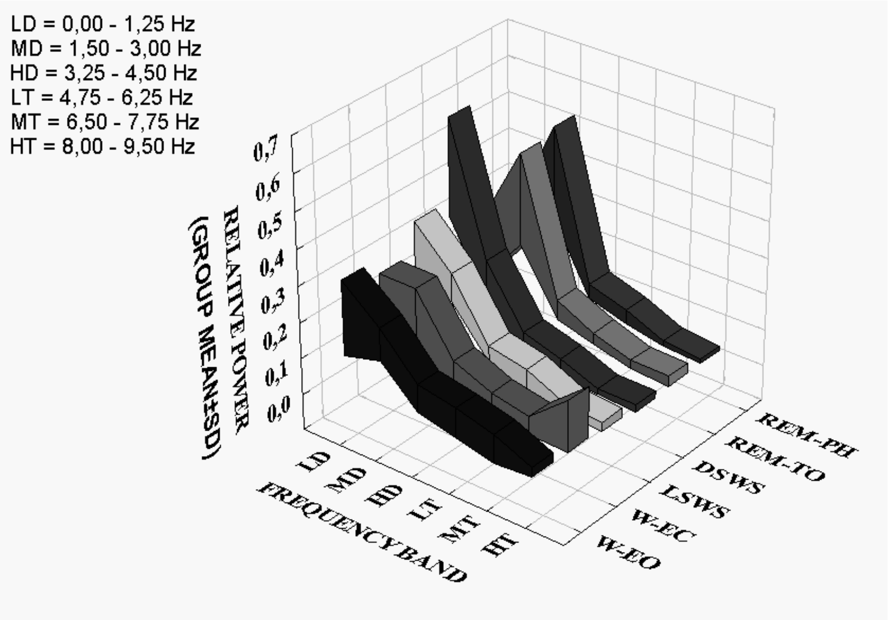

Figure 2. Group mean of the foramen ovale foramen ovale derived average spectral power and their standard deviations sharply differentiate between the characteristic frequencies for NREM and REM sleep. W-EO - waking eyes open; W-EC - waking eyes closed; LSWS - light slow wave sleep; DSWS - deep slow wave sleep; REM-TO - tonic REM periods; REM-PH - phasic REM periods.

Only one of the two above mentioned striking spectral peaks - the ~ 1 Hz peak in deep NREM sleep - appeared in the activity patterns recorded with the temporolateral scalp electrodes. The 1.50-3.00 Hz activity during REM sleep was not outlined as an independent spectral peak. In spite of this there is some statistical evidence supporting the statement that even in the temporolateral channels the 1.50-3.00 Hz activity is more pronounced in REM sleep than in other sleep-waking states.

Study 2.

Absolute power values of the EEG did not correlate with memory. In turn relative power values correlated significantly with memory at a number of contacting points. The correlations between the deep NREM sleep 0.00-1.25 Hz relative power and visual memory performances were the highest. While along the posterior-anterior axis of the hippocampal formation a linear increase of correlations was observed correlations pertaining to the right sided foramen ovale channels were higher than those pertaining to the left sided channels. The correlations with short-term memory values were higher than those with long-term values, yet both of them reached the level of statistical significance. Age, years of intractable seizures and hippocampal sclerosis did not affect the correlations.

An other relationship exists between the phasic REM sleep 0.00-1.25 Hz relative power and verbal learning ability. This relationship was outlined only in the left sided foramen ovale recordings. Age, years of intractable seizures and hippocampal sclerosis did not affect the relationship. 0.00-1.25 Hz activity in REM sleep usually consisted of scattered, non-rhythmic 1 Hz waves. As proved by the statistical comparison with all foramen ovale electrodes as statistical units this activity was somewhat higher in phasic than in tonic REM sleep (in Study 1. this difference was not visible with the 1 electrode/subject analysis).

The third relationship was observed between the visual memory retention values and the mentioned phasic REM sleep 0.00-1.25 Hz relative power. Correlations were significant only from the left sided foramen ovale recordings. Age and years of intractable seizures did not affect the correlations, but the statistical control of hippocampal sclerosis reduced them substantially.

Table 1. Correlations between sleep-dependent, low frequency activities and memory performances; number of + signs express the number of channels which showed significant correlation with memory (maximum 4).

	0.00-1.25 Hz – deep NREM sleep		0.00-1.25 Hz phasic REM sleep	
Memory/Laterality	Left	right	left	right
Visual memory – short term	++	++++		
Visual memory – long term	+	++++		
Verbal learning ability			+++	
Vizuális memory – retention			++	

The general property of the frequency bands above 1.50 Hz is that their relative power measured during deep NREM correlates negatively with visual memory. The statistical control of age, years of intractable seizures and hippocampal sclerosis reduced the correlations below the level of statistical significance.

The 0.00-1.25 Hz relative power of the EEG registered during deep NREM sleep in the temporolateral leads correlated positively with visual memory. This correlation is similar to that of the foramen ovale recordings with one exception: the temporolateral scalp EEG did not show a clear-cut sign of laterality and the left and the right correlations were both significant.

5. Discussion

According to my results, hippocampal RSA can be recorded during REM sleep in humans, just like in other mammals. The rhythmicity, synchrony, state-specificity, and spreading over other cortical areas are comparable to those of rodents' REM sleep-related theta. However its frequency is lower, therefore it belongs to the delta and not to the theta band (it is of 1.50-3.00 Hz). Conforming the requirments detailed in the introduction (monopolar derivation, a distant reference point, sufficient number of subjects, state specific analysis of REM sleep) led to more consequent results than most of the studies had performed until now.

Primitive, subcortical (brainstem, hypothalamic) structures take a part in the regulation of human REM sleep. This is supported by modern brain imaging studies as well [7]. It may be presumed, that the REM sleep hippocampal activity is more influenced by subcortical inputs than the waking hippocampal activity. This could be a reason for the fact that the human hippocampal RSA, which is detectable only in special circumstances or even not detectable at all, becomes dominant in REM sleep, or – according to an early result – appears during posterior hypothalamic stimulation [8].

Based on my result, the available data in the scientific literature can be reinterpreted from the point of view of changes in delta activity. Several other studies reported the dominance of delta activity though the majority of the authors sorted their results according to the presence or absence of theta activity. The possible reason for this is the lack of rhythmic components in the waking hippocampal activity patterns, which made the authors determine the frequencies on the basis of the animal results. Even in the studies reporting the lack of hippocampal theta, delta activity is often changed just as we would predict based on our results [9].

The other important result of study 1. is the exclusive dominance of the frequency band 0.00-1.25 Hz in deep NREM sleep. This is caused by a 0.75-1.00 Hz rhythmic activity, which is also observable on the scalp and corresponds to the slow, lesser than 1 Hz cortical oscillation characteristic for NREM sleep. Recently animal and human studies proved that the lesser than 1 Hz oscillation is different from the delta activity characteristic for NREM sleep [10]. Since we do not have human data about the presence of the lesser than 1 Hz oscillation on the mediotemporal surface (parahippocampal-hippocampal structures), my observation is the first evidence for the appearance of this oscillation in the above cortical areas during NREM sleep.

Only one of the two above mentioned rhythmic activities – the lesser than 1 Hz activity in deep NREM sleep – correlated with memory. The relative spectral power of this activity correlated positively with visual memory performances. In accordance with the material-specific cerebral lateralization of memory correlations predominated over the right mediotemporal surface. There was no clear-cut sign of laterality on the temporolateral surface which means that right- and left side EEG both correlated with visual memory. It may be presumed that the intensity of the lesser than 1 Hz activity in deep NREM sleep is related to the functional capacity of the cortical structures. The other accented rhythmic activity, the REM sleep-related 1.50-3.00 Hz slow activity, did not show any trait-like correlation with the examined memory performances.

Yet one of the non-rhythmic elements of the parahippocampal-hippocampal activity correlated with memory too. This was the lesser than 1.25 Hz activity registered during REM periods accompanied by eye movements, which correlated with verbal learning ability. The material-specific cerebral lateralization of memory also prevailed here, as in the case of verbal stimuli I have found significant correlations from the left sided foramen ovale recordings only. The lesser than 1.25 Hz activity during tonic and phasic REM sleep consisted of transient, non-rhythmic activity with irregular morphology of about 1 Hz frequency, which differed from the rhythmic 1 Hz frequency in NREM sleep. I postulate that this elements lacking rhythmicity are the expressions of the ponto-geniculo-occipital (PGO) bursts interrupting 1.50-3.00 Hz activity and signify the „permeability” of the mediotemporal structures by PGO bursts.

6. Summary

1. Hippocampal RSA can be recorded during human REM sleep.

2. Hippocampal RSA characterizing human REM sleep corresponds to the delta and not to the theta band (it is of 1.50-3.00 Hz).
3. As over the neocortical regions, synchronized, lesser than 1 Hz activity appears over the parahippocampal-hippocampal structures during deep NREM sleep.
4. The right-sided, lesser than 1 Hz activity registered over the parahippocampal-hippocampal structures during deep NREM sleep correlates positively with short- and long term visual memory.
5. Both right and left sided temporolateral, lesser than 1 Hz activity registered during NREM sleep correlates positively with visual memory performances.
6. The left-sided 0.00-1.25 Hz activity registered over the parahippocampal-hippocampal structures during phasic REM sleep correlates positively with verbal learning ability.

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