The relationship between sleep, dreaming and memory in light of psychophysiological investigations

FINAL REPORT

[Az alvás, az álmodás és az emlékezeti funkciók összefüggéseinek pszichofiziológai vizsgálata

NKFI PD 115432 Szakmai Záróbeszámoló]

Our project included the investigation of different topics that belong to the field sleep and memory research, more specifically to the cognitive neuroscience of sleep. In these studies, we applied questionnaires, behavioral paradigms, and neuroscientific tools to provide a more integrative view of the psychophysiological aspects of sleep and dreaming in healthy and pathological conditions. We believe that our findings opened new research perspectives and enriched our current knowledge of the specific subfields. Below, we provide a detailed description of our findings, their scientific impact and potential, separately for all the research studies that we conducted within the frames of the NKFI PD 115432 grant, and finally we summarize the results and possible future directions of our project.

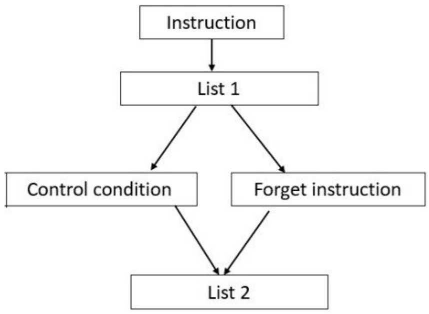
1. The influence of sleep in directed forgetting

Published paper: *Blaskovich, B., Szőllősi, Á., Gombos, F., Racsmány, M.,* ***Simor, P.*** *(2017). The benefit of directed forgetting persists after a daytime nap: the role of spindles and REM sleep in the consolidation of relevant memories. SLEEP, 40, 3. doi:10.1093/sleep/zsw076.*

Summary:

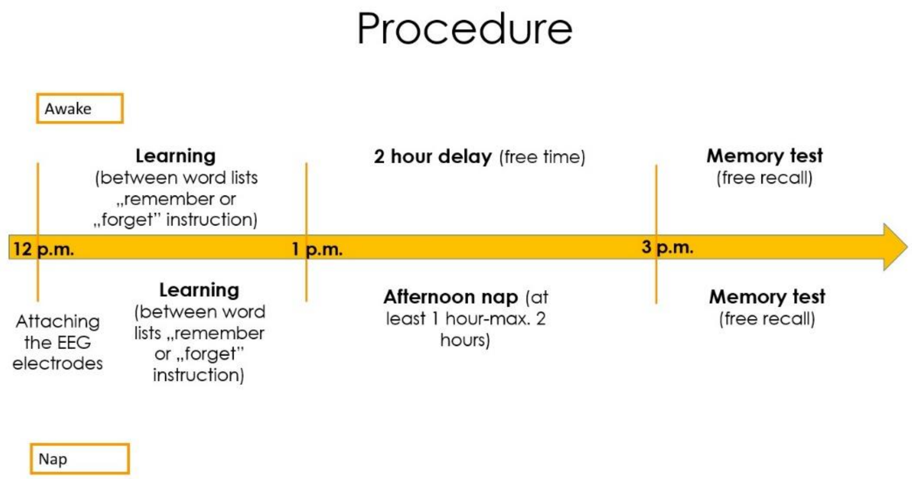
In this study, we investigated the effect of a directed forgetting instruction on memory retention after a 2-hour delay involving a daytime nap or an equivalent amount of time spent awake. According to earlier studies [1–4] sleep – nocturnal or afternoon nap – compared to the same amount of wake selectively enhance memories with future relevance. This selective enhancement is strongly correlated with sleep specific electroencephalographic (EEG) oscillations (slow wave activity [1–4Hz], sleep spindles [13–16Hz oscillations][5]). In sharp contrast with these findings and assumptions, in a pioneering study – with more than 300 participants – this difference between the retention of relevant and irrelevant memories disappeared after a good night's sleep[6]. In order to clarify some of the inconsistencies in previous studies and to improve the methodological shortcomings of the research in directed forgetting, our aim was to examine of the relationship between sleep and memory consolidation and the examination of differences in the consolidation of relevant and irrelevant memories. We aimed to manipulate the future relevance of newly acquired memory elements and with this manipulation to investigate the effects of daytime nap on memory consolidation. Our main questions were as follows: Does sleep play an active role in memory consolidation? Is there a difference between the consolidation of relevant and irrelevant memories?

We examined the associations between sleep-specific oscillations and the retention of relevant and irrelevant study materials. We applied a list-method directed forgetting paradigm manipulating the perceived relevance of previously encoded lists of words. Participants (112 healthy individuals, 44 men; Mage = 21.4 years, SD = 2.4) were randomly assigned to either a nap or an awake group, and to a remember or a forget subgroup. The remember and the forget subgroups were both instructed to study two consecutive lists of words, although, the forget subgroup was manipulated (with a simulated computer crash) to forget the first list and memorize only the second one.



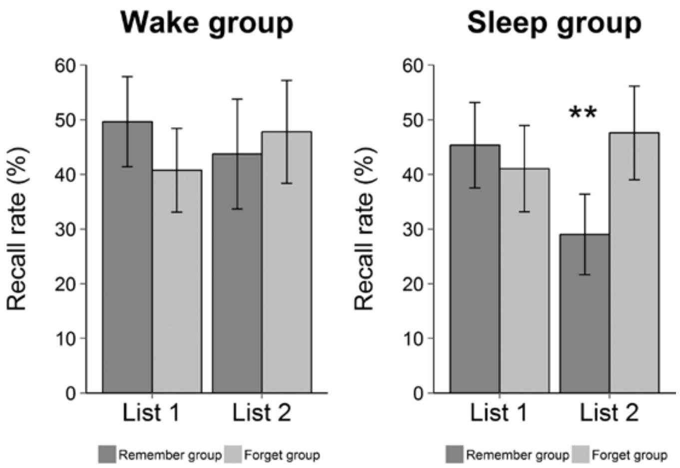
The basic procedure of the directed forgetting paradigm. Control condition creates the "remember" group and the Forget instruction creates the "forget" group.

After the study phase the participants of the wake group could return to their daily activities outside the lab. During this period they were asked not to repeat or recall the learned words. Following a 2-hour delay they came back to the lab and were tested on their memory performance (free recall of List 1 and then recall of List 2 orally). Before the recall of the lists participants of the forget subgroup were informed about the simulated program crash and were asked to recall both study lists, irrespective of the prior instruction to forget the first list. All of the participants were asked to recall List 1 first and then List 2. In the sleep group, the procedure had the following order: (1) the attachment of the electrodes, (2) study phase (similar to the wake group), (3) opportunity to spend a maximum of 2-hour long nap in the sleep laboratory (during which EEG activities were registered), and finally (4) the recall phase (free recall, similar to the wake group). See an illustration of the procedure below:



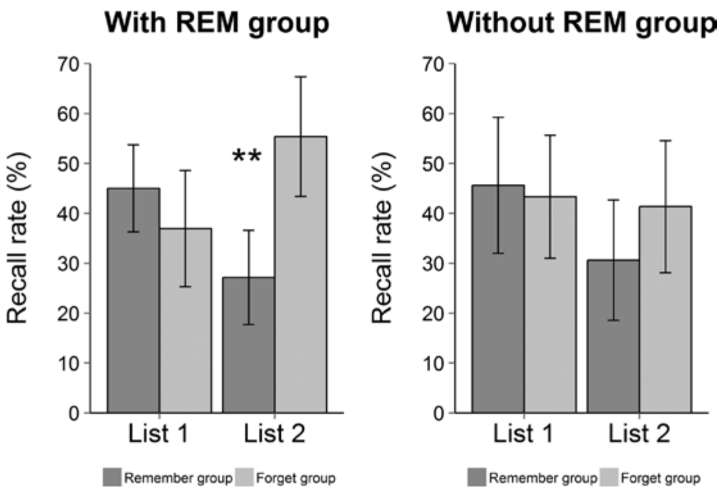
The procedure of our research. The experimental "steps" in the awake group is presented above and in the nap group below the arrow.

Neural activity during the naps were monitored by EEG. 9 electrodes (F3, F4, Fz, C3, C4, Cz, P3, P4, Pz) were used to observe activity on the scalp, EOG and EMG electrodes were used to detect eye and muscle movement. A significant directed forgetting effect emerged after a 2-hour delay both in the awake and sleep conditions; however, the effect was more pronounced within the sleep group:



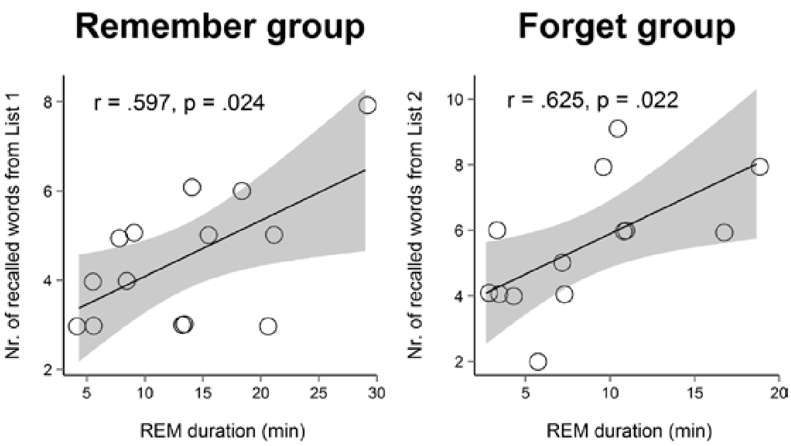
The average word recall after a two-hour delay spent either awake or asleep. Error bars represent 95% confidence intervals. Asterisks represent significance (p) of independent samples t tests: **$p < .001$.

Furthermore, the benefit of directed forgetting, that is, relatively enhanced recall of relevant words in the forget group, was evidenced only in those participants that reached rapid eye movement (REM) phase:



The amount of recalled words (%) from List 1 and List 2 within the sleep group, of those participants who reached both NREM and REM phase (With REM group), and of those who only slept in NREM state (Without REM group). Dark gray bars represent the performance of the remember subgroup and light gray bars the performance of the forget subgroup, within each groups. Significant three-way interaction between the recall of the two lists (List 1 and List 2), the instruction (forget or remember), and REM phase (with REM or without REM) emerged. As visualized, the directed forgetting effect was mainly due to the benefit of directed forgetting—better recall for List 2 in the forget than in the remember subgroup—within the with REM group only. Error bars *represent 95% confidence intervals. Asterisks represent significance (p) of independent samples t tests: **p < .001. NREM = non-rapid eye movement; REM = rapid eye movement.*

In addition, non-rapid eye movement (NREM) sigma power was correlated with memory performance for the relevant (second) list, and sleep spindle amplitude was associated with the retention of both lists. REM duration correlated with recall performance for the relevant (second) list within the forget subgroup, and with recall performance for the first list within the remember subgroup:



The association between the number of recalled words from List 1 and REM duration (min) within the remember group (on the left), and the association between the number of recalled words from List 2 and REM duration (min) within the forget subgroup (on the right). p values indicate significance values before FDR correction. FDR = false discovery rate; REM = rapid eye movement.

In sum, a directed forgetting effect persisted after a 2-hour delay spent awake or asleep. We conclude that spindle-related activity and subsequent REM sleep might selectively facilitate the processing of memories that are considered to be relevant for the future.

To the best of our knowledge, this is the first research to investigate the influence of sleep on list-based directed forgetting with the help of precise electro-physiological measurements. Furthermore, this high amount of participants (n = 112) is extremely rare in the field of sleep research. In conclusion, our results are unique and outstanding in their own field and they could play a determinative role in the further investigation of the interaction between sleep and memory. We have presented our findings in several (6) conferences and published the above study in a prestigious international journal (Sleep, D1).

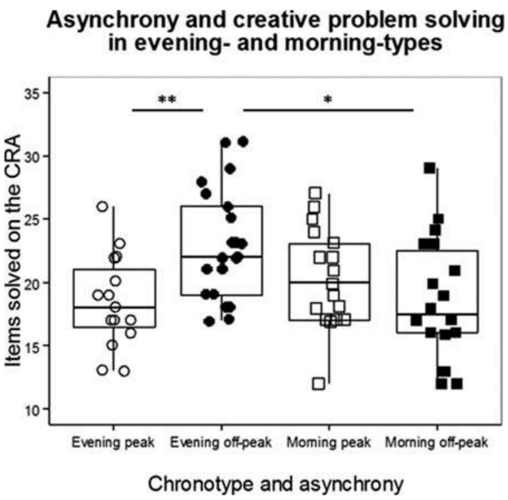
2. Chronotype, asynchrony and cognition

As the questionnaire-based screening of the potential research participants that are later invited to the laboratory required the collection of large databases including a wide variety of psychometric and demographic data, our database allowed us to investigate other interesting topics in relation to sleep and cognition. Three ancillary projects emerged from the collection of such precious databases. The first focused on the relationship between chronotype, daytime effects and problem-solving. The study was performed and published during the period of the research grant.

Published paper: ***Simor, P.*** *and Polner, B. (2017). Differential influence of asynchrony in early and late chronotypes on convergent thinking. Chronobiology International, 34, 1, 118–128. http://dx.doi.org/10.1080/07420528.2016.1246454.*

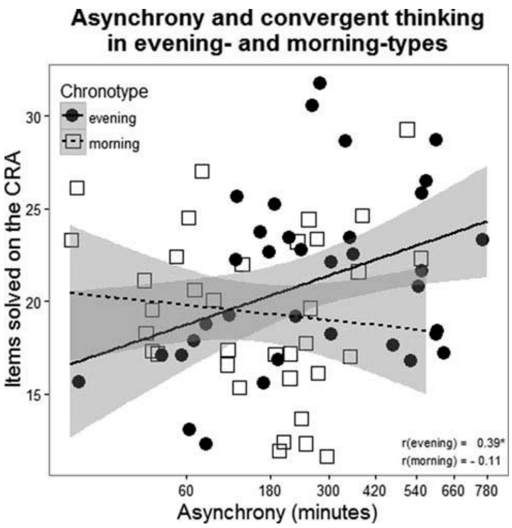
Summary:
Eveningness preference (late chronotype) was previously associated with different personality dimensions and thinking styles that were linked to creativity, suggesting that evening-type individuals tend to be more creative than the morning-types. Nevertheless, empirical data on the association between chronotype and creative performance is scarce and inconclusive. Moreover, cognitive processes related to creative thinking are influenced by other factors such as sleep and the time of testing. Therefore, our aim was to examine convergent and divergent thinking abilities in late and early chronotypes, taking into consideration the influence of asynchrony (optimal versus nonoptimal testing times) and sleep quality.

We analyzed the data of 36 evening-type and 36 morning-type young, healthy adults who completed the Compound Remote Associates (CRAs) as a convergent and the Just suppose subtest of the Torrance Tests of Creative Thinking as a divergent thinking task within a time interval that did (n = 32) or did not (n = 40) overlap with their individually defined peak times. Chronotype was not directly associated with creative performance, but in case of the convergent thinking task, an interaction between chronotype and asynchrony emerged. As the figure below indicates, late chronotypes who completed the test at subjectively nonoptimal times showed better performance than late chronotypes tested during their "peak" and early chronotypes tested at their peak or off-peak times:



Performance on the Compound Remote Associates task as a function of chronotype and subjectively optimal and non-optimal testing times.

Although insomniac symptoms predicted lower scores in the convergent thinking task, the interaction between chronotype and asynchrony was independent of the effects of sleep quality or the general testing time. Moreover asynchrony (as defined by the difference between subjectively defined optimal times and the time of testing in the experiment) positively correlated (r = 0.39, p = 0.02) with task performance within the evening group, whereas no such association was evidenced within the morning-types (r = −0.11, p = 0.5).



The association between asynchrony and performance in the Compound Remote Associates (CRA) Task within morning and evening-types.

Divergent thinking was not predicted by chronotype, asynchrony or their interaction. Our findings indicate that asynchrony might have a beneficial influence on convergent thinking, especially in late chronotypes. This study is the first to show the influence of chronotype and asynchrony on convergent thinking. Nevertheless, given the paucity of research on the complex relationship between chronotype, time of testing and creativity, these preliminary results have to be followed by further investigations.

3. **Insomniac symptoms, cognitive functioning and the link between creativity and schizotypal traits.**

The second ancillary study that was based on the large database collected for subsequent polysomnographic measurements examined the links between schizotypal traits and creativity taking into account different confounders that were not thoroughly considered in previous studies. The findings were presented at a Hungarian conference (in the annual congress of the Hungarian Psychological Association) and were published in an international journal.

Published paper: *Polner, B.,* ***Simor, P.****, Kéri, Sz. Insomnia and intellect mask the positive link between schizotypal traits and creativity.* PeerJ. *17;6:e5615. doi: 10.7717/peerj.5615.*

Summary:
Schizotypy is a set of personality traits that resemble the signs and symptoms of schizophrenia in the general population, and it is associated with various subclinical mental health problems, including sleep disturbances. Additionally, dimensions of schizotypy show specific but weak associations with creativity. Given that creativity demands cognitive control and mental health, and that sleep disturbances negatively impact cognitive control, we predicted that positive, impulsive and disorganized schizotypy will demonstrate stronger associations with indicators of creativity, if the effect of mental health, insomnia, and intellect are statistically controlled. University students (N = 182) took part in the study. Schizotypy was assessed with the shortened Oxford-Liverpool Inventory of Feelings and Experiences (sO-LIFE). Creative

achievements were measured with the Creative Achievement Questionnaire (CAQ), divergent thinking was assessed with the `Just suppose' task, and remote association problem solving was tested with Compound Remote Associate (CRA) problems. Mental health was assessed with the 12-item version of the General Health Questionnaire (GHQ-12), and insomnia was examined with the Athens Insomnia Scale (AIS). Verbal short-term memory was measured with the forward digit span task, and intellect was assessed with the Rational-Experiential Inventory (REI). Multiple linear regressions were performed to examine the relationship between creativity and schizotypy. Indicators of creativity were the dependent variables. In the first block, dimensions of schizotypy, age, gender and smoking were entered, and in the second block, the models were extended with mental health, insomnia, verbal short-term memory, and intellect. Positive schizotypy positively predicted real-life creative achievements, independently from the positive effect of intellect. Follow-up analyses revealed that positive schizotypy predicted creative achievements in art, while higher disorganized schizotypy was associated with creative achievements in science (when intellect was controlled for). Furthermore, disorganized schizotypy positively predicted remote association problem solving performance, if insomnia and verbal short-term memory were statistically controlled. No dimension of schizotypy was significantly associated with divergent thinking. In line with previous findings, positive schizotypy predicted real-life creative achievements. The positive effects of disorganized schizotypy might be explained in terms of the simultaneous involvement of enhanced semantic priming and cognitive control in problem solving. We speculate that the lack of associations between divergent thinking and schizotypy might be related to instruction effects. Our study underscores the relevance of sleep impairment to the psychosis-spectrum, and refines our knowledge about the adaptive aspects of schizotypy in the general population.

4. Eveningness, sleep quality, nightmares and daytime affect in Obsessive Compulsive Disorder

The third study that emerged from questionnaire-based data collection focused on the relationship between circadian preference, sleep quality and negative affect in psychiatric inpatients. The principal aim of the data collection was to assess the same scales and questionnaires that we used among the healthy population in a sample of psychiatric patients diagnosed with and mood and anxiety disorders. The relatively large number of OCD (Obsessive-compulsive Disorder) patients in our sample allowed us to perform a separate study in which we examined the associations between eveningness, sleep quality and daytime symptoms in a group of OCD patients and a mixed psychiatric group with anxiety and mood disorders.

Published paper: ***Simor, P.***, *Harsányi, A., Csigó, K., Miklós G., Demeter, G. (2018). Eveningness is associated with poor sleep quality and negative affect in obsessive–compulsive disorder.* Journal of Behavioral Addictions*, 7(1):10-20,* *doi: 10.1556/2006.7.2018.07.*

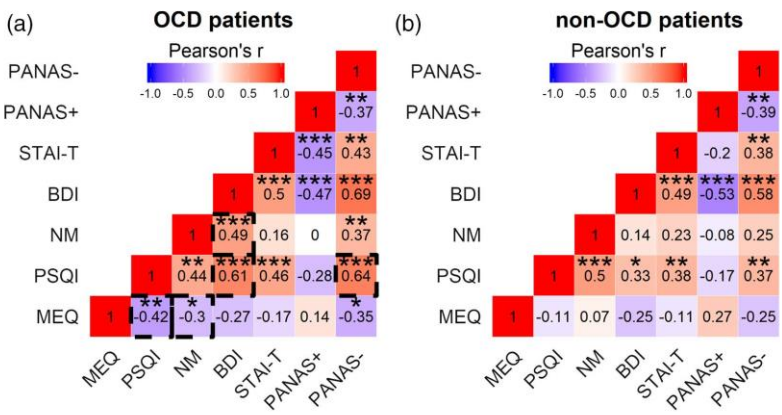
Summary:
Obsessive–compulsive disorder (OCD) is characterized by intrusive thoughts and repetitive behaviors that severely encumber daily functioning. OCD patients seem to exhibit sleep disturbances, especially delayed bedtimes that reflect disrupted circadian rhythmicity. Morningness–eveningness is a fundamental factor reflecting individual variations in diurnal

preferences related to sleep and waking activities. Eveningness reflecting a delayed sleep–wake timing has repeatedly been associated with sleep problems and negative affect (NA). Therefore, the aim of this study was to examine the associations between morningness–eveningness, sleep complaints, and symptom severity in OCD patients and compared with a mixed psychiatric control group. The data of 49 OCD and 49 mixed psychiatric inpatients (with unipolar depression and anxiety disorders) were analyzed:

	OCD Group N = 49	Non-OCD Group N = 49	Test Statistics	P value (adjusted)
Sex	34 males, 15 females	9 males, 40 females	$Chi^2 = 25.9$	< 0.001
Age	32.23 (9.34)	46.73 (14.31)	t = 5.89	<0.001
Education (years)	13.67 (2.7)	13.29 (3.2)	t = - 0.62	0.60
SSRI	N = 26	N = 29	$Chi^2 = 0.37$	0.60
Atypical antidepressant	N = 19	N = 20	$Chi^2 = 0.43$	0.80
Benzodiazepine	N = 24	N = 40	$Chi^2 = 11.53$	0.004
Mental illness (Duration in years)	14.48 (10.35)	17.55 (11.67)	t = 1.35	0.29
Psychotropic medication (Duration in years)	4.21 (6.55)	8.04 (10.21)	t = 2.11	0.07
Smoking	N = 10	N = 18	$Chi^2 = 2.99$	0.21

Demographic and clinical data of OCD and non-OCD psychiatric inpatients. Means and Standard deviation are shown in case of continuous variables.

Patients completed questionnaires regarding morningness–eveningness, sleep quality, nightmare frequency, depression, anxiety, and affective states. Obsessive and compulsive symptom severity was also assessed within the OCD group by clinician-rated scales. Eveningness preference was associated with impaired sleep quality and higher NA in OCD patients. In addition, impaired sleep quality showed a moderate correlation with anxiety and strong correlations with depressive symptoms and NA. Interestingly, in the mixed psychiatric group, eveningness was not linked to NA, and sleep quality also showed weaker associations with depressive symptoms and NA.



*Pearson's correlation coefficients between the examined variables in the OCD and non-OCD group. Dashed squares indicate significantly different correlation values between the two groups. *p < .05. **p < .01. ***p < .001. Correlation coefficients above .33 remained significant after FDR correction*

Within the OCD group, eveningness preference was predictive of poorer sleep quality regardless the influence of depressive symptoms. Our findings suggest that eveningness and sleep complaints are predictive of affective dysfunctions, and should be carefully considered in the evaluation and treatment of OCD patients.

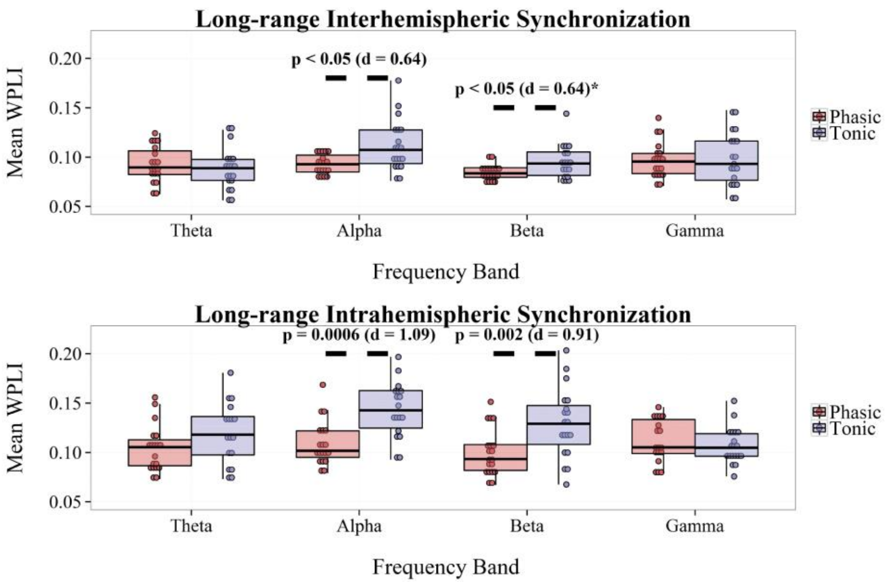
5. The heterogeneity of REM sleep: Large-scale EEG synchronization in phasic and tonic microstates

In this study we examined the short and long-range synchronization of EEG oscillations during phasic and tonic REM periods in healthy controls. This work will serve as the basis of our further analyses focusing on the sleep neurophysiology of nightmare sufferers.

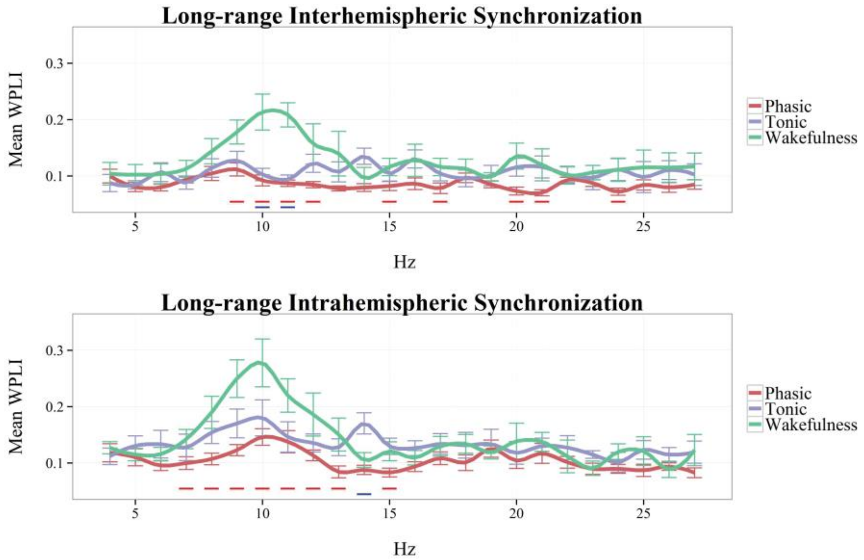
Published paper: ***Simor, P.**, Gombos, F., Blaskovich, B., Bódizs, R. (2018). Long-range alpha/beta and short-range gamma EEG synchronization distinguishes phasic and tonic REM periods.* SLEEP, *41(3). doi: 10.1093/sleep/zsx210.*

Summary:

Rapid eye movement (REM) sleep is characterized by the alternation of two markedly different microstates, phasic and tonic REM. These periods differ in awakening and arousal thresholds, sensory processing, and spontaneous cortical oscillations. Previous studies indicate that although in phasic REM, cortical activity is independent of the external environment, attentional functions and sensory processing are partially maintained during tonic periods. Large-scale synchronization of oscillatory activity, especially in the α- and β-frequency ranges, can accurately distinguish different states of vigilance and cognitive processes of enhanced alertness and attention. Therefore, we examined long-range inter- and intrahemispheric as well as short-range electroencephalographic synchronization during phasic and tonic REM periods quantified by the weighted phase lag index. Based on the nocturnal polysomnographic data of 19 healthy adult participants, we showed that long-range inter- and intrahemispheric α and β synchrony was enhanced in tonic REM states in contrast to phasic ones, and resembled α and β synchronization of resting wakefulness.



Long-range interhemispheric and intrahemispheric WPLI in phasic and tonic REM periods in different frequency bands.



Inter- and intrahemispheric WPLI in phasic REM, tonic REM, and resting wakefulness, between 4 and 27 Hz (1 Hz resolution). The linegraph (smoothed for visualization) depicts the mean values of 12 participants in each frequency bin. Vertical lines indicate standard errors. Blue horizontal lines correspond to statistically significant differences between tonic REM and wakefulness.

On the other hand, short-range synchronization within the γ-frequency range was higher in phasic compared with tonic periods. Increased short-range synchrony might reflect local and inwardly driven sensorimotor activity during phasic REM periods, whereas enhanced long-range synchrony might index frontoparietal activity that reinstates environmental alertness after phasic REM periods. Our findings contribute to the understanding of the complex and heterogeneous nature of REM sleep, and help to lay the bases for the analyses of REM microstates in sleep disorders and psychiatric conditions.

6. Hyperarousal and PTSD-like symptoms in Nightmare disorder

We have collected the polysomnographic data of 22 Nightmare Sufferers and 22 Healthy controls. Participants spent two consecutive nights in our sleep laboratory, completed psychometric tests in advance, and were assessed by a protocol examining subjective and physiological reactions (skin conductance and heart rate) in response to emotional stimuli (IAPS pictures). Salivary samples were collected each night, at 4-time points: before going to sleep, and three times after awakening to measure the cortisol awakening response. By now, we have finished data collection and some of the analyses, and we are currently preparing two papers for publication. Nevertheless, we a considerable amount of psychophysiological data remains to be analyzed in the upcoming weeks. We have presented the preliminary results of these analyses in a Hungarian (in the annual congress of the Hungarian Psychological Association) and two international conferences (European Congress of Clinical Neurophysiology, 2017; Congress of European Sleep Research Society, 2018).

<u>Conference abstracts:</u>

Simor, P., Blaskovich, B., Reicher, V., Reichard, R. REM – Dreaming – Emotions: The *neurophysiology of nightmare disorder, Clinical Neurophysiology, Volume 128, Issue 9, 2017,* Page e233, ISSN 1388-2457, https://doi.org/10.1016/j.clinph.2017.07.180.

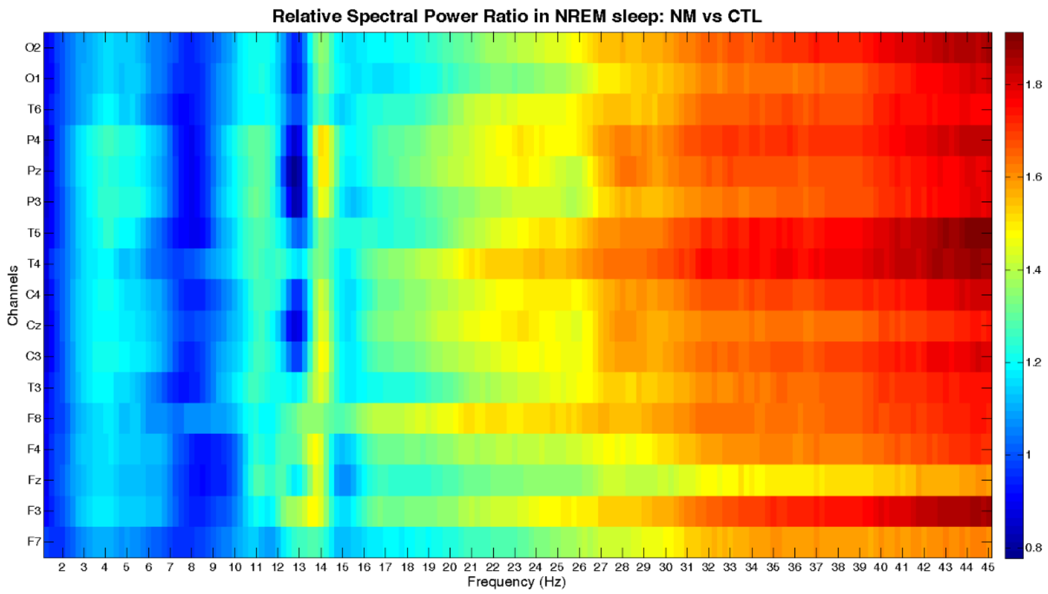
Blaskovich, B. Reichardt, R., Reicher, V., van der Wijk, G., Király, A., Szegőfi Á., **Simor, P.** PTSD-like symptoms, morning affect, and intrusive memories in nightmare disorder. Journal of Sleep Research, Vol.27/S1, page 102., 2018.

Summary:
Nightmares are intense and highly unpleasant mental experiences that occur usually – but not exclusively – during late-night Rapid Eye Movement (REM) sleep and often provoke abrupt awakenings. The most influential model of nightmare disorder was introduced by Levin and Nielsen (2007). One of the main assumptions of the model is that nightmares reflect unsuccessful fear-extinction processes during (REM) sleep due to a dysfunctional brain network comprising fronto-limbic structures. Consequently, amygdalar over-activation and inefficient (prefrontal) inhibition lead to the emotional intensification of dreaming and hyperarousal during sleep. Nevertheless, sleep quality and emotional regulation in nightmare sufferers were mainly examined by questionnaire-based studies. We have performed a quantitative EEG analyses based on the polysomnographic data of young (non-ptsd) nightmare sufferers and matched controls. In line with previous findings[7,8], we found that nightmare sufferers are characterized by reduced Slow Wave Sleep (SWS), however, no other parameters of sleep architecture differentiated the two groups:

Sleep parameters	**Control group (N=22)**		**Nightmare group (N=22)**		**Wilcoxon signed rank test (B-H corrected)**	
	Mean	SD	Mean	SD	z value	p value
Sleep duration (min)	440.17	41.82	439.32	38.19	235	.88
Relative wake duration (%)	6.06	5.62	7.38	4.51	176	.33
Sleep efficiency (%)	93.93	5.62	92.62	4.51	308	.33
WASO after first sleep (min)	17.52	20.4	23.31	19.31	185	.4
Relative NonREM duration (%)	74.85	3.63	74.25	4.32	254	.86
Relative REM duration (%)	25.15	3.63	25.75	4.32	230	.79
Relative S3 duration (%)	**25.89**	**3.56**	**21.78**	**4.51**	**370**	**.03***
REM latency from first sleep (min)	94.98	37.52	101.03	46.01	225	.86

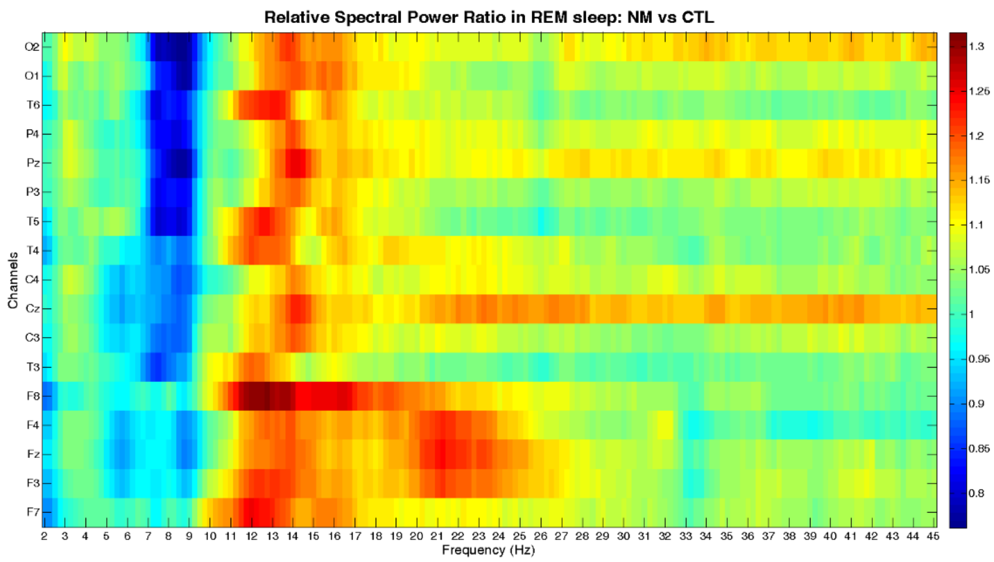
WASO: Wake after sleep onset; B-H: Benjamini-Hochberg correction

Furthermore, NMs' NREM sleep was characterized by reduced low frequency and increased high frequency power, reflecting impaired sleep regulation and increased hyperarousal during NREM sleep:



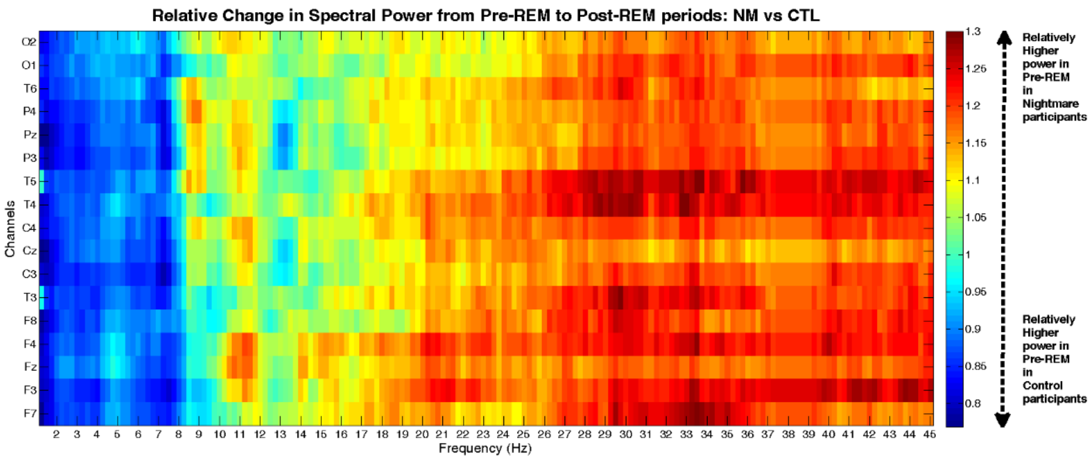
Bin-wise spectral power ratio (NM / CTLs) in NFREM sleep. Statistical analyses of bin-wise power spectra contrasting NMs and CTLs showed significantly decreased low frequency oscillations (1.25-2 Hz, and 3-7 Hz) and increased high frequency activity in NMs (16-46 Hz) compared to CTLs.

In case of REM sleep, NMs showed relatively reduced frontal low frequency power, reduced theta power, and increased high-alpha power compared to CTLs. This finding partly replicated our earlier findings[7], and suggests that wake-like alpha intrusions characterize the REM periods of NMs.



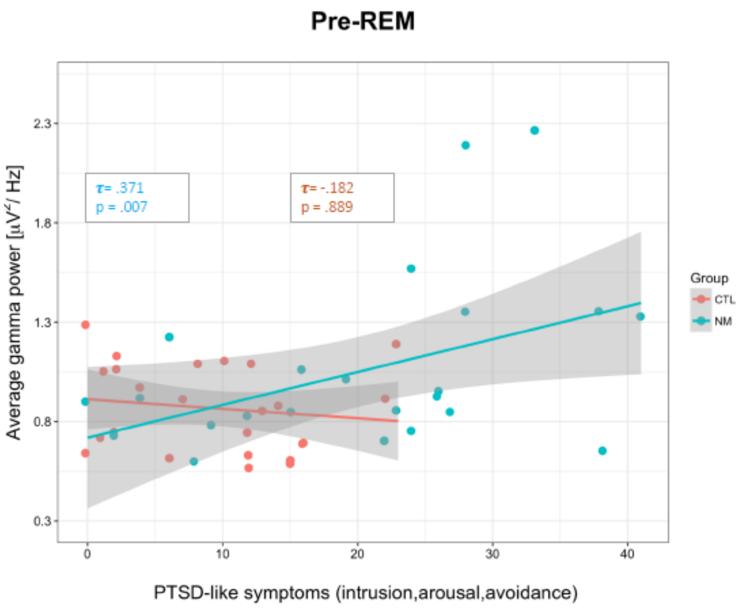
Bin-wise spectral power ratio (NM / CTLs) in REM sleep. Statistical analyses of bin-wise power spectra contrasting NMs and CTLs showed significantly decreased low frequency and theta oscillations (1.25-2 Hz, and 7-9 Hz), and increased high-alpha (12-16 Hz) activity in NMs compared to CTLs.

Furthermore, reduced low-frequency oscillations and increased high-frequency activity were evidenced in nightmare sufferers specifically during NREM to REM transitions.



Pre-REM vs. Post-REM periods in NMs vs. CTLs. NMs showed decreased low frequency power (1-8 Hz), and increased high-frequency power during pre-REM periods compared to post-REM periods.

Our analyses indicated that homeostatic sleep pressure (as indexed by low-frequency activity) is reduced in NMs during NREM-REM transitions, whereas hyperarousal (as indexed by high-frequency power) is relatively increased in NMs during NREM-REM transitions. Interestingly, post-REM periods showed no significant differences across NMs and CTLs, suggesting that after the end of REM periods, oscillatory activity is normalized in NMs. Furthermore, high-frequency gamma power in pre-REM periods was positively associated with PTSD-like symptoms in NMs, whereas no such associations emerged among CTLs:



The associations between average gamma power in Pre-REM periods and PTSD-like symptoms in nightmare sufferers (NM) and matched controls (CTL).

We conclude that hyperarpusal in NMs exhibits a dynamic pattern during sleep, showing high levels during NREM sleep and during NREM-REM transitions, but diminishes after REM periods. Moreover, hyperarousal during NREM sleep, especially during NREM-REM transitions is associated with PTSD-like symptoms in NMs, and suggests that it is a biological marker of the severity of the sleep disorder. We may speculate that increased gamma and beta frequency together with decreased delta activity during NREM and pre-REM suggests disturbed sleep regulation processes resulting in increased alertness towards the environment. Heightened external and internal information processing during sleep could result in perceptually vivid, realistic and emotionally absorbing dream images.

Our upcoming analyses will examine emotional reactivity, emotional habituation and emotional regulation after sleep in a group of NMs (N = 18) and healthy controls (N = 18). We measured emotional reactivity by subjective ratings of valence and arousal in response to negative and neutral IAPS pictures, as well as by physiological activity including skin conductance and heart rate. These analyses will empirically test the influential model of Levin and Nielsen[9].

Furthermore, we plan to analyze spectral power as well as large-scale synchronization in NMs and CTLs during phasic and tonic microstates (see Study 5 above.)

In sum, we believe that we have accomplished the main goals that we set in our research project. Although we still need to analyze a considerable amount of data that we have collected during the grant period, several interesting and even to some extent serendipitous results emerged from our studies that contribute to the field of sleep, dreaming and memory research and raise novel questions that we plan to explore in the future.

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