CORTEX 183 (2025) 167–182

Available online at www.sciencedirect.com

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Journal homepage: www.elsevier.com/locate/cortex

Research Report

Increase in slow frequency and decrease in alpha and beta power during post-learning rest predict long-term memory success

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ARTICLE INFO

Article history:
Received 8 January 2024
Reviewed 23 April 2024
Revised 26 August 2024
Accepted 11 November 2024
Action editor Veena Kumari
Published online 2 December 2024

Keywords:
Wakeful rest
Memory formation
Reencounter
Cortical activity

ABSTRACT

Formation of episodic memories is linked to cortico–hippocampal interactions during learning, practice, and post-learning rest, although the role of cortical activity itself in such processes remains elusive. Behaviorally, long-term retention of episodic memories has been shown to be aided by several different practice strategies involving memory reencounters, such as repeated retrieval and repeated study. In a two-session resting state electroencephalography (EEG) experiment, using data from 68 participants, we investigated the electrophysiological predictors of long-term memory success in situations where such reencounters occurred after learning. Participants learned word pairs which were subsequently practiced either by cued recall or repeated studying in a between-subjects design. Participants' cortical activity was recorded before learning (baseline) and after practice during 15-min resting periods. Long-term memory retention after a 7-day period was measured. To assess cortical activity, we analyzed the change in spectral power from the pre-learning baseline to the post-practice resting state recordings. From baseline to post-practice, changes in alpha and beta power were negatively, while slow frequency power change was positively associated with long-term memory performance, regardless of practice strategy. These results are in line with previous observations pointing to the role of specific frequency bands in memory formation and extend them to situations where memory reencounters occur after learning. Our results also highlight that the effectiveness

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https://doi.org/10.1016/j.cortex.2024.11.012
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of practice by repeated testing seems to be independent from the beneficial neural mechanisms mirrored by EEG frequency power changes.
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1. Introduction

1.1. *Memory reencounters and long-term retention of episodic memories*

There is overwhelming evidence that reencountering events can alter their retention in long-term memory (Ebbinghaus, 1913; McClelland, McNaughton, & O'Reilly, 1995). Behavioral studies have demonstrated that intentional restudying (Racsmány, Szőllősi, & Marián, 2020; Zhang & Hupbach, 2020), repeated testing (Karpicke & Aue, 2015; Roediger & Butler, 2011) as well as reactivation by several different types of cues (Hu, Cheng, Chiu, & Paller, 2020) can aid long-term memory performance for a wide variety of materials. Although compelling behavioral demonstrations of this phenomenon exist involving memory reactivation during sleep using cues (in this case, visual or auditory stimuli aiding the access to memory items; Bendor & Wilson, 2012; Rasch, Büchel, Gais, & Born, 2007), offline periods are not the only situation where such reactivations or, in a broader sense, memory reencounters can occur.

In fact, in everyday life, previously encoded memories are typically reencountered during wakeful periods throughout the day (Johnson, Scharf, Verceles, & Westlake, 2019). An ordinary example of such online reencounter is learning a recipe from a cookbook. When making a certain dish for the first time, we carefully read the list of ingredients, and may attempt to memorize them for future use, with more or less success. This can be considered an episodic, associative learning situation, where the ingredient items are associated to, for example, the name of the dish. When attempting to prepare the dish the next time, we may try to recall the ingredient items on our own, using the name of the dish as a cue, or alternatively, go back to the cookbook and re-read the list. Both can be considered practice events involving reencounters with previously studied material, either involving the effortful retrieval of items, or encountering them via repeatedly reading the to-be-remembered material. Of these two, which constitute two of the most often used strategies, repeated retrieval is more efficient in terms of long-term memory retention, as demonstrated by several behavioral studies (e.g., Bangert-Drowns, Kulik, Kulik, & Morgan, 1991; Karpicke & Roediger, 2008; Racsmány, Szőllősi, & Bencze, 2018; Wheeler, Ewers, & Buonanno, 2003). This well-established advantage of retesting is termed the testing effect (for an overview, see e.g., Racsmány & Szőllősi, 2022; Karpicke, 2017). The benefits of repeated retest practice have been attributed to the strengthening of recollection-related processes by electrophysiological studies (e.g., Bai, Bridger, Zimmer, & Mecklinger, 2015; Bencze, Szőllősi, Németh, & Racsmány, 2022; Spitzer, Hanslmayr, Opitz, Mecklinger, & Bäuml, 2008), and further neuroimaging evidence points to the involvement of hippocampal areas (e.g., Jonker, Dimsdale-Zucker, Ritchey, Clarke, & Ranganath, 2018; Wiklund-Hörnqvist et al., 2021; Wing, Marsh, & Cabeza, 2013) as well as cortical regions associated with semantic processing (Van den Broek, Takashima, Segers, Fernández, & Verhoeven, 2013; Wing et al., 2013; Wirebring et al., 2015; for a review see Van den Broek et al., 2016). Interestingly, some of these studies reported that the facilitating effects of repeated retrieval on memory retention seems to at least partially rely on neural processes associated with (re)encoding (Bridge & Paller, 2012; Liu, Tan, & Reder, 2018; Wing et al., 2013), while recent works proposed the role of retrieval as a form of online, rapid consolidation in long-term memory facilitation (Antony, Ferreira, Norman, & Wimber, 2017; see also: Antony & Paller, 2018; Brodt et al., 2016; Wiklund-Hörnquist et al., 2021).

The neural basis of episodic learning and reencounter-based practice strategies has been discussed using several frameworks. The most widely accepted frameworks involve bidirectional connections between the hippocampus and cortical areas such as the prefrontal cortex (PFC) and the posterior parietal cortex (PPC) (see Addis & McAndrews, 2006; Brassen, Weber-Fahr, Sommer, Lehmbeck, & Braus, 2006; Churchwell & Kesner, 2011). At encoding, the PFC is involved in forming inter-item associations and organizing the to-be-learned material, while parietal areas are involved in forming rapid, feature-specific representations (Blumenfeld, Parks, Yonelinas, & Ranganath, 2011; Brodt et al., 2016). The hippocampus and the surrounding parahippocampal areas are involved in binding item details and binding items to contexts (Ranganath, 2010; Squire, 1992). Later on, during a timescale of hours, days or even possibly years (Nadel, Samsonovich, Ryan, & Moscovitch, 2000), the integration of new memories into an existing network of representations involves higher level cortical areas and their interactions with the hippocampus (Diekelmann & Born, 2010; Frankland & Bontempi, 2005; Robin & Moscovitch, 2017). Competing views exist on whether this process results in memory traces becoming independent of the hippocampus and reliant solely on cortical areas, or if the hippocampus remains needed for retrieval in the long term (Kitamura et al., 2017; Nadel et al., 2000; Sekeres, Moscovitch, & Winocur, 2017; Squire, 1984).

After learning, subsequent encounters with encoded memories seem to elicit changes in the neural network associated with item storage (Hashimoto, Umeda, & Kojima, 2011; Keresztes, Kaiser, Kovács, & Racsmány, 2014; Kuhl, Dudukovic, Kahn, & Wagner, 2007; Xue et al., 2011). Reencounters may result in neural replay, which entails the reactivation of neuronal circuits in the hippocampus and certain cortical areas (also the thalamus and striatum) that were active during the encoding of a previous online experience, theoretically aiding the distribution of hippocampal memory traces to the cortical neuronal network (Carr, Jadhav, & Frank, 2011; Peigneux et al., 2004; Ribeiro & Nicolelis, 2004; but see

Nadel et al., 2000 for a competing view). The functioning of different cortical areas during memory reencounters has not been studied extensively, but the existing data show that repeatedly retrieving items upon cues elicits a deactivation of frontal cortical regions such as the PFC (Wirebring et al., 2015; Kuhl et al., 2007), which might also happen in the case of repeated studying to some extent. This pattern suggests that repeated encounters decrease the load on control mechanisms necessary for either retrieving an item or for further encoding (see also Pajkossy, Szőllősi, & Racsmány, 2019). The PPC on the other hand, seems to show increased activity when repeatedly encountering the same episodic material in a spatial learning task, while its connectivity with the initially active hippocampus decreases over repeated encounters (Brodt et al., 2016).

1.2. *Electrophysiological indicators of successful memory consolidation*

With regards to EEG signatures of successful memory formation and consolidation, sleep following learning is a widely studied research topic (Diekelmann & Born, 2010; Diekelmann, Wilhelm, & Born, 2009; Walker & Stickgold, 2004). A long line of studies investigating the relationship between post-encoding sleep and declarative memory consolidation reported that certain characteristics of slow-wave sleep (Gais & Born, 2004; Maquet, 2001), including increased sleep spindle activity (e.g., Cox, Hofman, & Talamini, 2012; Mednick et al., 2013; Schabus et al., 2004) and slow wave power (.1–4 Hz; e.g., Lau, Tucker, & Fishbein, 2010; Holz et al., 2012) as well as specifically slow oscillation power (<1–1.5 Hz; Marshall, Helgadóttir, Mölle, & Born, 2006; Ngo, Martinetz, Born, & Mölle, 2013) showed a positive relationship with memory retention (see e.g., Schreiner & Staudigl, 2020). Recently, wakeful rest following learning has also gained attention as a platform for memory strengthening (Martini & Sachse, 2020; Wamsley, 2019), since there is evidence that sleep and rest have common features that allow for, or actively aid, memory stabilization (Deuker et al., 2013; Gais & Born, 2004; Jadhav, Kemere, German, & Frank, 2012). Brokaw and colleagues found that during a rest period following a session of learning and subsequent initial recall of auditory verbal material, a reduction of alpha power was associated with an improved performance on a later, final retrieval test (Brokaw et al., 2016). Since in this study, the negative relationship between alpha power and memory performance was present in both the resting and the active wakefulness condition, the authors argued that this might be a consequence of some kind of trait-like/general association between alpha activity and memory stabilizing processes. It is debated whether this correlation truly mirrors a trait-like association between individual cortical activity characteristics and memory functioning or a task-specific effect resulting from changes elicited by learning itself, although other research has also found support for a trait-like association (Huang et al., 2023). Brokaw et al. (2016) also found that an increase in slow oscillation during post-learning rest was positively associated with final memory performance. Importantly, this result is in line with previous findings on the relationship between slow oscillation increase and memory performance. Several studies have found that, for example, the boosting of slow oscillation during post-learning sleep enhances memory retention (Marshall et al., 2006; Ngo et al., 2013). Other research has shown that slow wave sleep during a short daytime nap is beneficial for protection from subsequent interference and long-term retention (Alger, Lau, & Fishbein, 2012), and slow-wave (.5–4 Hz) power is regulated in an experience-dependent manner and correlates with acquired memory (Miyamoto, Hirai, & Murayama, 2017). The prevailing explanation to this relationship is that slow waves play a role in synchronizing cortico–hippocampal interactions, specifically with regards to hippocampal sharp-wave ripples and sleep spindles (Clemens et al., 2007, 2011; Wamsley, 2022), which are associated with memory reactivation that is thought to play a key role in system level memory consolidation mechanisms (Berkers et al., 2018; Gisquet-Verrier & Riccio, 2012).

More recently, several studies have indicated that awake rest and sleep might share characteristics working in favor of the stabilization of memories. Some studies have even proposed that advantages in memory performance caused by awake rest are indistinguishable from those caused by sleep (Wang et al., 2021). Data also shows that spontaneous reactivation of recent memories occurs not only during sleep but awake periods (Karlsson & Frank, 2009; Oudiette, Antony, Creery, & Paller, 2013), and that sharp wave ripples associated with reactivation can also be observed in awake rest (Clemens et al., 2011). Certain neurochemical features of sleep that aid memory stabilization are also replicated during rest, such as decreased acetylcholine levels, as demonstrated in animal studies (e.g., Marrosu et al., 1995).

Overall, the emerging pattern of results suggests that when cortical EEG is assessed during post-learning rest, a decrease in alpha and beta, while an increase in slow frequency power reliably predicts future memory performance. Relatedly, data based on event related EEG recording shows that both successful memory encoding (e.g., Hanslmayr, Staresina, & Bowman, 2016; Sederberg, Kahana, Howard, Donner, & Madsen, 2003) as well as reactivation during retrieval (e.g., Michelmann, Bowman, & Hanslmayr, 2016; Waldhauser, Braun, & Hanslmayr, 2016) is associated with decreased alpha and beta synchronization.

1.3. *Study objectives*

In everyday life, learning is most often followed by some kind of repeated encounter with the studied material, such as in the form of trying to access the memory trace upon a cue, or going back to the material in an attempt to memorize it again. The behavioral aspects of such reencounters have been extensively studied (Rowland, 2014) and possible neural underpinnings of why repeated testing affects memory traces differently from repeated studying have been proposed (e.g., Liu, Liang, Li, & Reder, 2014; Van den Broek et al., 2013). In the present study, we aimed to combine this framework of practice effects on long memory and that of off-line memory consolidation, which also has considerable literature, especially using electroencephalography. At the overlap of these approaches, we carried out this study to examine how changes in electrophysiological measures as a result of a

combined learning and practice session can predict long-term memory performance. Moreover, to assess possible differences in how repeated testing and repeated study might alter the electrophysiological signature of successful memory formation, we devised an experimental paradigm based on that most often used to study the testing effect. We measured resting state brain activity before and after the learning-and-practice session to examine how changes from pre-learning to post-practice resting state cortical activity can predict memory after a one-week delay. Our main goal was to identify a possible overall pattern of EEG features that predict memory performance in an experimental design closely mimicking real-life situations. Also, while as a novel addition, one of our aims was to investigate possible differences in the EEG signature of the two practice strategies, we will consider both retrieving an item based on a cue (repeated retrieval) and being exposed to both cue and target item again (repeated encoding) under the umbrella term *memory reencounter*. Overall, we expected that long-term memory success would be associated with a decrease in alpha and an increase in slow oscillation power, measured as power change from pre-to post-learning rest periods. Additionally, we aimed to tap potential differences between the two reencounter types with regards to resting EEG patterns.

2. Materials and methods

2.1. Participants

We used G-Power (version 3.1.9.2.; Faul, Erdfelder, Lang, & Buchner, 2007) to calculate the required sample size. Based on pilot results ($n = 16$) we calculated the required sample size focusing on the effect of repeated testing practice in comparison to repeated study practice on final recall. Examining the difference between two independent group means (Retest group: $n = 8$, $M = 60.1\%$, $SD = 18.4$; Restudy group: $n = 8$, $M = 46.2\%$, $SD = 18.6$) we used an effect size value of Cohen $d = .75$, an alpha error probability of .05, and a power of .80. According to the results of this calculation, the required sample size was a minimum of $n = 58$. Expecting some dropout, we recruited 68 undergraduate students as participants. (Finally, we analyzed the data of 61 participants, as described below.) Participants whose data were used for the effect size calculation were also included in the sample.

The data of three participants were excluded from the analyses due to an extremely low level of memory performance (recall rate of less than 10% in the final test phase of the memory task). Four additional participants were excluded from the final analysis due to their EEG recording being too noisy for spectral analysis. Therefore, we analyzed the data of 61 participants, who were randomly assigned to either the Retest ($n = 30$, 8 men; age: 18–27 years, $M = 21.0$, $SD = 2.2$) or the Restudy practice group ($n = 31$, 7 men; age: 19–26 years, $M = 21.2$, $SD = 1.8$). To reduce between-subjects variance in sleepiness/alertness during the experiment, participants were asked not to consume alcohol or caffeine (for details, see Lumley, Roehrs, Asker, Zorick, & Roth, 1987; Pasman, Boessen, Donner, Clabbers, & Boorsma, 2017) in the 24-h period preceding the experiment, and to sleep according to their usual daily rhythm. Applicants with psychiatric or chronic neurological illnesses were not allowed to take part in the experiment. All exclusion criteria were established prior to data analysis.

Participants received course credit for participation and gave written informed consent at both sessions of the experiment. The study was approved by the United Ethical Review Committee for Research in Psychology, Hungary. The work described was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans.

2.2. Memory task

2.2.1. Initial learning

Stimuli were 36 Swahili-Hungarian word pairs translated from Nelson and Dunlosky (1994) that were randomly paired for each participant (the Hungarian stimulus set was also used in the studies of Marián, Szőllősi, & Racsmány, 2018 as well as of Racsmány et al., 2020). In an initial learning phase, participants were presented with all 36 pairs (5000 msec each with 500 msec inter-stimulus intervals [ISIs]) in random order for 5 consecutive cycles on a computer screen. The rationale for using 5 consecutive learning cycles was to improve recall success, since the multitude of learning cycles was necessary to achieve a sufficiently high rate of successful recall (Racsmány et al., 2020; for overviews, see e.g., Karpicke, Lehman, & Aue, 2014; Karpicke & Smith, 2012). Before each learning cycle participants were instructed to memorize the word pairs as well as they could. After reading the instruction, participants proceeded to the next learning cycle by pressing the Space bar. All word pairs were presented in each cycle. There was no systematic delay between the learning cycles.

The initial learning phase was followed by a 5-min delay to increase difficulty of retrieval at the first practice cycle and consequently the long-term effectiveness of retrieval practice (see e.g., Bjork & Bjork, 1992). The delay included an arithmetic distractor task during which participants solved a list of paper-and-pencil exercises (additions, subtractions, multiplications, and divisions) in any order they felt comfortable with, without using a calculator. The aim of this task was to preclude rote rehearsal during the delay. After the 5-min delay, the practice phase followed.

2.2.2. Practice (reencounter) phase

For the Retest group, the practice phase consisted of 5 cycles of associative recall trials for all initially studied word pairs. Participants were presented with the Swahili words and were required to recall their Hungarian counterparts. Participants' task was to press the Space bar as soon as they had the appropriate Hungarian word in mind, which allowed the experimenter to record recall reaction times (for previous application of this procedure, see Marián et al., 2018; Racsmány et al., 2018). After pressing the Space bar, they were allowed to type the Hungarian word. From the onset of the Swahili cue word, participants had a response window of 8000 msec to complete a word pair. Stimuli were present for the full 8000 msec regardless of whether participants gave an answer. The response window was followed by a 500 msec ISI. In each of the 5 cycles, all 36 word pairs were tested in random

order, and there was no systematic delay between the cycles. Participants proceeded to the subsequent practice cycle by pressing the Space bar.

For the Restudy group, the practice phase also consisted of 5 cycles, but instead of a recall task, all word pairs were presented again for additional studying. Word pairs were presented in each cycle in random order for 8000 msec each, with an ISI of 500 msec.

2.2.3. *Final test*

Following a seven-day retention period, participants' memory for all word pairs was tested once in an associative recall test identical to the practice cycles of the Retest group. The second experimental session took place at the same time of day as the first session.

2.3. *EEG recording*

Resting state EEG was recorded during the first session of the experiment immediately before the initial learning phase (baseline recording) and approximately 10 min after the practice phase (post-practice recording). Both recording sessions lasted 15 min. The 10-min delay between the practice phase and the EEG recording was filled with a distractor task that involved completing online questionnaires for an unrelated study about emotion regulation and body awareness. During both resting periods participants were instructed to relax but not to fall asleep, which was ensured by the experimenter instructing them through a speaker to open or close their eyes approximately once every minute. We deemed this a necessary technique, and a better alternative to fully open eyes rest, as the latter could have introduced an increased, unwanted variance in eye-movement as a result of patients scanning the room they were in during the rest periods. This mixed method served as the best compromise for maintaining wakefulness and decreasing eye-movement artifacts, while providing minimal external stimuli.

For the EEG recording, we used gold-coated Ag/AgCl EEG electrodes that were fixed using EC2 Grass electrode Cream (Grass Technologies, Natus Manufacturing Ltd., Galway, Ireland). We used 9 scalp electrodes (F3, F4, Fz, C3, C4, Cz, P3, P4, Pz), fitted according to the standard 10–20 electrode system (Jasper, 1958) in addition to (bipolar) electrooculographic (EOG) and electrocardiographic (ECG) electrodes. We used equidistantly placed electrodes on and around the midline between the frontal and parietal regions, as quiet rest recordings on the occipital and temporal electrodes can be contaminated by artifacts originating from muscles of the neck and around the ears. Although we expected changes in alpha power, which is usually peaking over occipital electrodes, posteriorly located alpha power is always largely captured by parietal recordings as well (Barry, Clarke, Johnstone, Magee, & Rushby, 2007; Lehmann, 1971; Tenke, Kayser, Abraham, Alvarenga, & Bruder, 2015). Scalp EEG electrodes were referred to the average of the mastoid (A1, A2) electrodes. We kept the impedance of all electrodes below 10 kΩ. For recording the electrophysiological data, we used Micromed SD LTM 32 Bs (Micromed S.p.A., Mogliano Veneto, Italy) and SystemPLUS 1.02.1098 software (Micromed Srl, Rome, Italy). Signals were collected, prefiltered (.30–1500 Hz; 40 dB/decade anti-aliasing hardware input filter), amplified, and digitized with 4096 Hz/channel sampling rate with 16-bit resolution. Thereafter, the digitized and filtered time series were downsampled at 512 Hz.

2.4. *Procedure*

The experimental procedure is illustrated in Fig. 1. Upon arrival to the first experimental session, participants signed an informed consent and filled out a questionnaire to assess subjective sleep quality, containing the Groningen Sleep Quality Scale and two additional items. The Groningen Sleep Quality Scale contains 14 yes/no items on subjective sleep quality (Mejiman, de Vries-Griever, & de Vries, 1988; Hungarian version: Simor, Köteles, Bódizs, & Bárdos, 2009). A total score of higher than 6 indicates disturbed sleep quality (Weil, 2004). Additionally, participants filled out two supplementary items: a 9-point Likert scale assessing the quality of sleep ("How did you sleep last night?") and a 10-point Likert scale concerning sleepiness ("How well rested do you feel now?") (previously used in Blaskovich, Reichardt, Gombos, Spoormaker, & Simor, 2020). Participants were also asked about how much they slept (in hours) the night before the first experimental session.

Subsequently, EEG electrodes were fitted for the electrophysiological recordings during the resting periods. The baseline resting phase was followed by the initial learning and practice phases. Subsequently, after the 10-min distractor task, the post-practice rest period with EEG recording took place. Once the rest period had elapsed, participants were

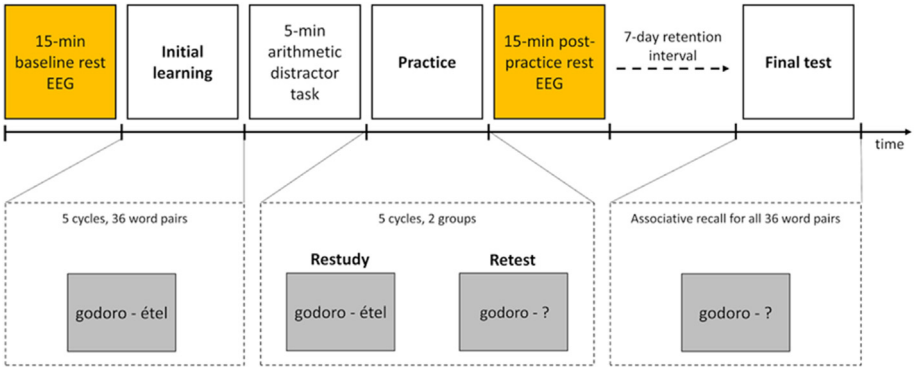

Fig. 1 – Summary of the experimental design and procedure.

asked to return 7 days later for an unrelated experiment (finally, no unrelated experiment was actually performed). The reason for deceiving participants was to preclude further individual rehearsal of the learned material. After this 7-day delay the second experimental session took place, comprising solely of a surprise associative recall test (final test phase of the experiment). No EEG recording was performed at the second experimental session.

2.5. Statistical analysis

2.5.1. Sleep characteristics

Sleep characteristics were compared between the groups to verify no difference between the two. For this purpose, we conducted a list of independent *t*-tests on hours of sleep the night before the first experimental session, on total score of the Groningen Sleep Quality Scale, and on the single-item scores of subjective sleep quality and sleepiness scales.

2.5.2. Behavioral analysis

To assess participants' performance during retest practice, we compared recall rates and reaction times between the six practice cycles in the retest group by conducting repeated measures analyses of variance (ANOVAs) with six levels, followed by contrast analyses with the last (sixth) practice cycle as a reference point. We used Greenhouse-Geisser correction to adjust for the lack of sphericity for the ANOVAs. To investigate whether the two reencounter types (Retest versus Restudy) led to different memory performance on the final test, we conducted two-tailed Welch *t*-tests to compare recall rates (percentage of words recalled), as well as reaction times (time elapsed between the onset of the Swahili word and pressing the Space bar) at final test in the two practice groups. Statistical analyses were conducted with an alpha level of $p = .05$ in RStudio version 1.4.1103 (RStudio Team, 2020).

2.5.3. Electrophysiological analysis: pre-processing and spectral analysis

Analysis of the EEG data was performed using the FieldTrip toolbox for EEG/MEG-analysis (Oostenveld, Fries, Maris, & Schoffelen, 2011) in the Matlab programming environment (MathWorks, Natick, MA, USA). The data was bandpass filtered offline removing frequencies below .5 Hz and above 48 Hz with an additional 50 Hz notch filter to remove noise from powerlines. Eye-movement related artifacts (eye movements, and blinks) were removed by independent component analysis (ICA; Ghahremani, Makeig, Jung, Bell, & Sejnowski, 1996). The EEG data was divided into 4-sec segments and all segments containing technical or movement-related artifacts were excluded using visual artifact-rejection.

Spectral analysis via Fast Fourier Transformation was applied to all artifact-free segments using Hanning-tapers and no segment overlaps. Absolute power for both baseline and post-practice resting periods was calculated with $\mu V^2/.25$ Hz resolution. In order to quantify the relative changes in spectral power after the practice sessions, the post-practice data was baseline-corrected by dividing the spectral power values of each .25 Hz bin of the post-practice data by its corresponding, bin-wise pre-practice spectral power data. We will refer to this baseline-corrected value as spectral power change. The bin-wise spectral power change values were averaged for the specific frequency bands of interest including the slow oscillation (.5–1 Hz), delta (1–4 Hz), theta (4–7 Hz), alpha (8–12 Hz) and beta (13–35 Hz) frequency bands.

2.5.4. Electrophysiological analysis: statistical analysis of spectral EEG data

To analyze the relationship between spectral power change and long-term memory performance (recall rate at final test) and whether this relationship is affected by the type of reencounter, we conducted hierarchical multiple regression analyses. In regression Model 1, we included Reencounter type (Restudy versus Retest) and Spectral power change as explanatory variables, and the Recall rate of the final test as the dependent variable. In Model 2 we used the interaction between Reencounter type and Spectral power change as the explanatory variable and the Recall rate of the final test as the dependent variable. To measure if the model with the interaction would explain the pattern of the final recall performance better compared to the first model, we report the R^2 change between the two models and the *p*-value of the within-subject ANOVA comparing the two models. We conducted the two regression models using the spectral power change values of three electrode clusters on the frontal (F3, Fz, F4), central (C3, Cz, C4) and parietal (P3, Pz, P4) regions of the scalp in the slow oscillation, delta, theta, alpha and beta frequency bands, separately. To account for Type I error for the separate regression models and model comparisons run for the three electrode clusters, we report Bonferroni corrected *p*-values.

3. Results

3.1. Sleep characteristics

Sleep characteristics were compared between the groups; for descriptive statistics, see Table 1. As expected, we found no significant group difference in hours of sleep the night before the first experimental session, $t(59) = .500$, $p = .619$, $d = .128$, in total score of the Groningen Sleep Quality Scale, $t(59) = .766$, $p = .447$, $d = .199$, and in the single-item scores of subjective sleep quality, $t(59) = .684$, $p = .497$, $d = .178$, and sleepiness, $t(59) = .114$, $p = .910$, $d = .030$.

3.2. Behavioral results

For the behavioral results (recall success and reaction times of correct responses), see Fig. 2. During the practice phase of the

Table 1 – Sleep characteristics in the two experimental groups separately.

	Restudy group	Retest group
Hours of sleep	7.6 (.2)	7.7 (.2)
Groningen sleep quality scale	3.0 (.5)	2.5 (.4)
Single item on subjective sleep quality	6.9 (.2)	7.1 (.2)
Single item on subjective sleepiness	6.7 (.3)	6.7 (.4)

Note(s). The values represent the means (with standard errors of the means in parentheses).

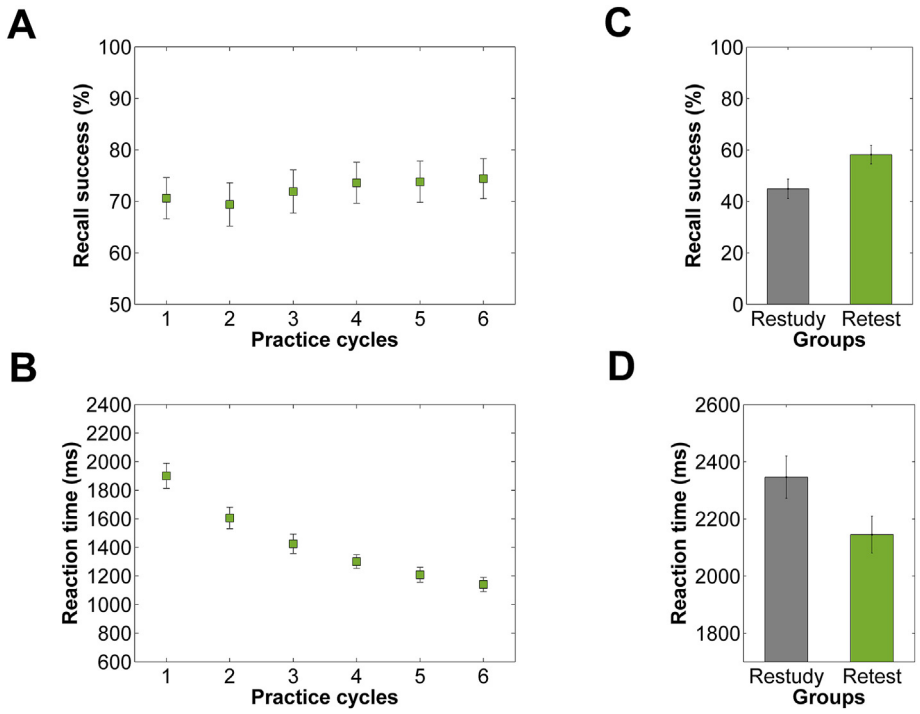

Fig. 2 – Behavioral results during practice and on the final test. *Note(s)*. Recall success ('A') and reaction times ('B') in the practice phase (only the Retest group has data in this phase). Recall success ('C') and reaction times ('D') on the final test in the two groups (Restudy and Retest) separately. (Error bars represent the standard error of the mean.)

retest group, we found a significant effect of Practice cycle on recall rate, $F(3.42, 99.22) = 11.035$, $p < .001$, $\eta^2_p = .276$ (Fig. 2a). Further contrast analyses showed that recall rate was higher in the last practice cycle than in Cycle 1, $F(1, 29) = 19.661$, $p < .001$, $\eta^2_p = .404$, Cycle 2, $F(1, 29) = 29.719$, $p < .001$, $\eta^2_p = .506$, and Cycle 3, $F(1, 29) = 10.296$, $p = .003$, $\eta^2_p = .262$. There was no significant difference between the recall rates of the last practice cycle and Cycle 4, $F(1, 29) = 1.634$, $p = .211$, $\eta^2_p = .053$, or Cycle 5, $F(1, 29) = 1.299$, $p = .264$, $\eta^2_p = .043$. We found a significant effect of Practice cycle on reaction time as well, $F(3.17, 92.03) = 58.677$, $p < .001$, $\eta^2_p = .669$ (Fig. 2b). Further contrast analysis revealed that participants responded faster in the last practice cycle than in all previous practice cycles, Cycle 1, $F(1, 29) = 125.995$, $p < .001$, $\eta^2_p = .813$, Cycle 2, $F(1, 29) = 87.075$, $p < .001$, $\eta^2_p = .750$, Cycle 3, $F(1, 29) = 29.051$, $p < .001$, $\eta^2_p = .500$, Cycle 4, $F(1, 29) = 18.824$, $p < .001$, $\eta^2_p = .394$, and Cycle 5, $F(1, 29) = 4.379$, $p = .045$, $\eta^2_p = .131$. This increasing recall rate and decreasing reaction time throughout practice showed the same pattern to previous studies using a similar experimental design (Marián et al., 2018; Racsmány et al., 2018).

With regards to recall rate at final test, the Retest group outperformed the Restudy group, recalling significantly more words (Fig. 2c), $t(58.99) = 2.548$, $p = .013$, $d = .652$, indicating a significant testing effect. In addition, the Retest group recalled correct answers significantly faster than the Restudy group at the final test (Fig. 2d), $t(58.34) = 2.031$, $p = .047$, $d = .519$. In sum, practice by repeated testing led to better recall rate and faster reaction times on the final test compared to practice by repeated studying, indicating the long-term facilitating effect of testing compared to repeated studying.

3.3. *Electrophysiological results*

The results of the regression models and model comparisons are reported in Table 1, the effects of the parameter estimates are described below. The comparison of Model 1 (model containing the effects of Power change and Reencounter type as predictors) and Model 2 (model containing the interaction between Power change and Reencounter type) revealed no significant predictive benefit of Model 2 in any of the cases (see Table 1). Therefore, we describe the effects of the parameter estimates for only Model 1, in cases when the regression model reached significance. Significant relationships between Power change and Final test recall rate are illustrated in Fig. 3.

In the *slow oscillation* frequency band, we found a significant regression model for the parietal electrode cluster (see Table 1a). Retested items were associated with higher Final test recall rate compared to restudied items, $\beta = .147$, $t(58) = 2.854$, $p = .006$, and, more importantly, larger Power change (power increase) was a significant predictor for a higher recall rate in the final test, $\beta = .272$, $t(58) = 2.029$, $p = .047$.

In the *alpha* frequency band, our results showed significant regression models in both the frontal and the central electrode clusters (see Table 1d). On the frontal electrode sites the effect of Reencounter type was significant, $\beta = .134$, $t(58) = 2.617$, $p = .011$, and a larger Power change (power decrease) was predictive to a lower recall rate in the final test, $\beta = -.183$, $t(58) = 2.035$, $p = .046$. On the central electrode cluster we only found a significant effect of Reencounter type, $\beta = .139$, $t(58) = 2.685$, $p = .009$. Power change did not show a significant association with Final test recall rate on its own, $\beta = .202$, $t(58) = 1.593$, $p = .117$.

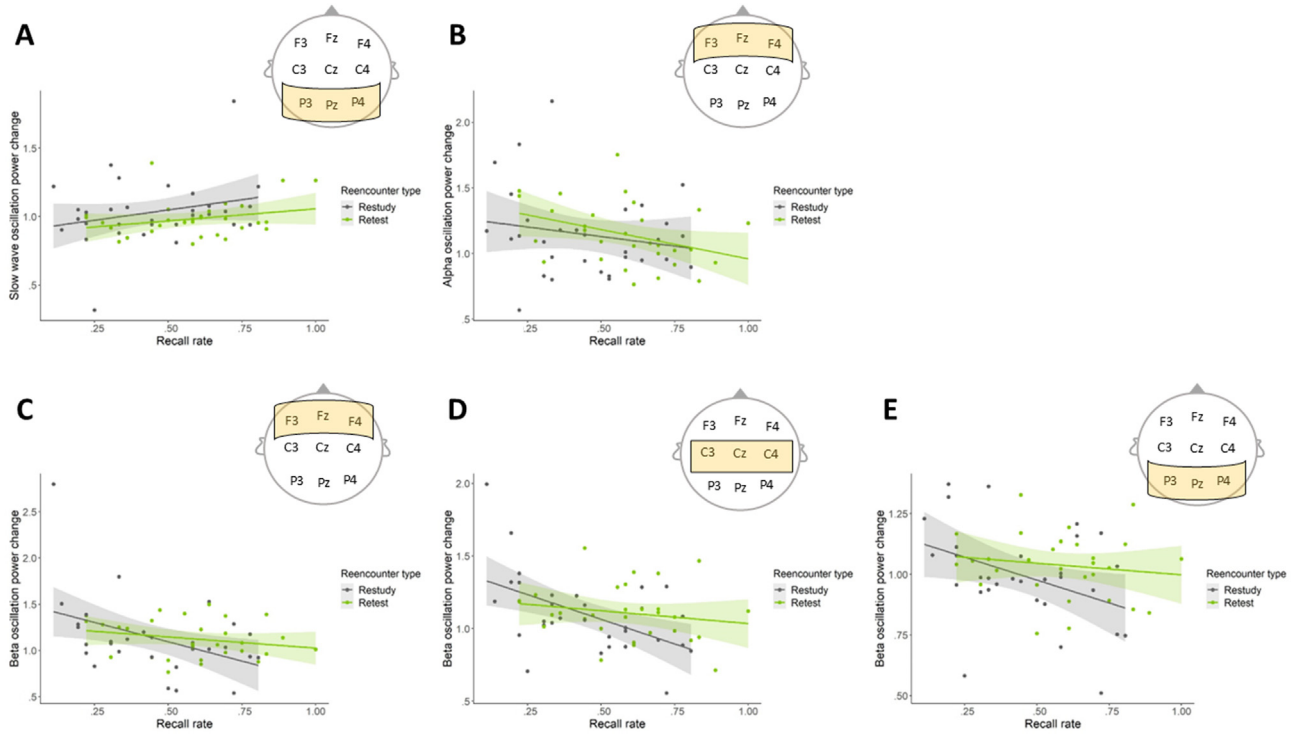

Fig. 3 – Significant relationships between power change and recall success on the final test in the two groups (Restudy and Retest) separately. *Note(s)*. 'A': slow oscillation (parietal cluster); 'B': alpha frequency band (frontal cluster); 'C', 'D', and 'E': beta frequency band (clusters frontal, central, and parietal, respectively).

In the *beta* frequency band Model 1 was significant on all electrode sites (see Table 1e). On the frontal electrode sites there was a significant effect of Reencounter type, $\beta = .131$, $t(58) = 2.649$, $p = .010$, and we found that larger Power change (power decrease) predicted a lower recall rate on the final test, $\beta = -.223$, $t(58) = 2.864$, $p = .006$. Similarly, on the central electrode cluster our results showed a significant effect of Reencounter type, $\beta = .137$, $t(58) = 2.797$, $p = .007$, and a negative association between Power change and Recall rate on the final test, $\beta = -.332$, $t(58) = 3.168$, $p = .003$. On the parietal electrode sites we found the same pattern with a significant effect of reencounter type, $\beta = .148$, $t(58) = 2.907$, $p = .005$, and larger Power change predicting a lower recall rate on the final test, $\beta = -.347$, $t(58) = 2.323$, $p = .024$. In the rest of the analyzed frequency bands and electrode clusters, the regression model was not significant (all $ps > .05$).

In sum, spectral power change in the slow oscillation band on the parietal electrode sites was positively associated with recall performance on the final test. Both frontal spectral power change in the alpha frequency band, and power change on the whole scalp in the beta frequency band were negatively associated with later recall performance.

4. Discussion

There is an emerging body of research concerning the effects of post-learning wakeful rest on memory retention (see Martini & Sachse, 2020; Wamsley, 2019). However, there have only been a handful of studies that investigated the neural processes behind the memory facilitating effects of rest by measuring changes in resting-state EEG. The aim of the present study was to investigate the relationship between brain oscillations measured during wakeful rest following a learning event and long-term memory success. To more closely follow real-life learning situations, we used an experimental design where in addition to the initial encoding event, participants reencountered the material by repeated encoding or repeated retrieval before a post-practice wakeful resting period.

4.1. *Slow frequency power change and long-term retention*

Our first main result showed that the increase of parietal slow frequency power from pre-learning to post-practice wakeful rest predicted long-term memory success. Slow oscillations are one of the main neurophysiological signals of slow-wave sleep that originate in the neocortex and are strongly associated with the memory stabilizing effects of sleep (Born, Rasch, & Gais, 2006). The alternating hyperpolarized and depolarized neural states ("down-states" and "up-states") of slow oscillations are suggested to coordinate memory reactivation during sleep in interaction with thalamo-cortical spindles and hippocampal sharp-wave ripples (Born & Wilhelm, 2012; Diekelmann & Born, 2010). This synchronization of thalamocortical spindles and hippocampal sharp-wave ripples is a putative mechanism for memory consolidation, enabling information transfer between the hippocampus and the neocortex during sleep (Born et al., 2006; Born & Wilhelm, 2012; Khodagholy, Gelinas, & Buzsáki, 2017; Peigneux et al., 2004). Moreover, the role of slow oscillations in memory

consolidation is further supported by findings indicating that stimulation of slow oscillations during sleep via transcranial stimulation (Marshall et al., 2006) or auditory stimulation (Ngo et al., 2013) facilitates sleep-dependent memory consolidation.

In recent years, increasing evidence has demonstrated the functional and neurophysiological similarities between sleep and quiet rest in association with memory consolidation (e.g., Brokaw et al., 2016; Craig, Ottaway, & Dewar, 2018; Dewar, Alber, Butler, Cowan, & Della Sala, 2012; Murphy, Stickgold, Parr, Callahan, & Wamsley, 2018; Wang et al., 2021). There is a growing number of behavioral findings showing the benefits of post-learning wakeful rest on memory retention that are comparable to the memory stabilizing effects of sleep (Brokaw et al., 2016; Craig et al., 2018; Dewar et al., 2012), even when directly contrasted with brief periods of sleep (Gottselig et al., 2004; Tucker, Humiston, Summer, & Wamsley, 2020; Wang et al., 2021). Additionally, there are striking parallels between the neurophysiological features of wakeful rest and the characteristics of sleep that are thought to be related to memory consolidation. Wakeful rest is characterized by slower EEG rhythms compared to active wakefulness, with an increased level of alpha and theta frequencies (Volavka, Matoušek, & Roubíček, 1967). More importantly, in both sleep and wakeful rest sharp-wave ripples are present in the hippocampus (Carr et al., 2011; Ego-Stengel & Wilson, 2010; Hasselmo & McGaughy, 2004; Jadhav et al., 2012).

More support for this parallel comes from a previous study of Brokaw et al. (2016) who investigated the electrophysiological correlates of wakeful rest and found a relationship between slow oscillation and memory retention. The authors reported similar results to those of the present study. Specifically, they found that post-learning slow oscillation was positively associated with memory performance following a delay lasting a couple of minutes. It is important to note, that while Brokaw et al. (2016) reported the strongest association between memory performance and slow frequency power at frontal and central electrodes, our results showed a positive relationship between memory retention and slow power change in the parietal electrode cluster. Even though a large number of studies highlighted the dominantly frontal activity of slow oscillations in NREM sleep (e.g., Riedner, Hulse, Murphy, Ferrarelli, & Tononi, 2011; Van Someren, Van Der Werf, Roelfsema, Mansvelder, & da Silva, 2011; Werth, Achermann, & Borbély, 1996; see), there is an emerging body of research describing the role of local, region-specific sleep oscillations in the consolidation of specific types of memory (Huber, Felice Ghilardi, Massimini, & Tononi, 2004; Menicucci et al., 2020; for reviews, see Geva-Sagiv & Nir, 2019; Siclari & Tononi, 2017). Relatedly, recent studies described a memory systems transition between the hippocampus and the posterior parietal cortex over repeated rehearsal (in the form of both relearning and recall) (Brodt et al., 2016; Himmer, Schönauer, Heib, Schabus, & Gais, 2019; also see Zhuang et al., 2022), which may be further stabilized by sleep (Himmer et al., 2019). Therefore, it could be speculated that the parietal distribution of the slow frequency effect in the present study may reflect the involvement of posterior parietal areas due to the increased number of reencounters compared to the one learning and one retrieval event in the study of Brokaw et al. (2016).

Our findings also extend the research of Brokaw et al. (2016) by showing that increased slow oscillation during wakeful rest is not only associated with memory retention on the scale of minutes, but this association is present even after one week, demonstrating a long-lasting effect. Accordingly, previous behavioral studies corroborate the presence of long-lasting benefits of resting on memory performance (e.g., Craig, Dewar, Della Sala, & Wolbers, 2015; Dewar et al., 2012). Additionally, we present evidence that this relationship is maintained in a situation where the initial learning event is followed by the reencounter of the material in two different practice conditions before rest. It is important to note that these reencounter events presumably involve reactivation processes as well. Specifically, both restudying (Xue et al., 2011) and retesting (e.g., Wirebring et al., 2015; Keresztes et al., 2014) of previously learned information have been shown to involve the reactivation of neural patterns related to encoding. It is nevertheless of note that our study was methodologically different from, for example, the work of Brokaw et al. (2016) in several ways. Brokaw et al. (2016) used a short story as the material to be remembered, participants only recalled the material once before the electrophysiological measures were taken during rest, and their memory performance was assessed immediately after this 15-min period. In contrast, in our study, subjects learned word pairs, had the opportunity to practice them in multiple cycles and their memory success was assessed after a week-long retention period. The nature of material, and the arrangement and timing of the memory test in our experiment was based on prior studies applying a similar approach, which have yielded robust results in research investigating post-learning practice effects (Bencze et al., 2022; Butler, 2010; Pajkossy et al., 2019; Racsmány et al., 2018; Roediger & Karpicke, 2006). The use of such an experimental paradigm in conjunction with a resting state EEG protocol that examines pre-to post-learning electrophysiological changes provides a framework for interpretation that is indeed different from ones typically assessing EEG signatures of post-learning consolidation (e.g., Gais & Born, 2004; Wang et al., 2021), while at the same time allowing for a perspective that has unique advantages, including the ecological validity of investigating a combined learning and practice episode.

4.2. *Alpha and beta power change and long-term retention*

In addition to the relationship between slow oscillation and memory retention, we found negative associations between the change of frontal alpha and widespread beta power from pre-learning to post-practice rest and long-term memory success. In line with our findings, there is a number of event-related EEG studies describing a common decrease of post-stimulus alpha and beta spectral power relative to a pre-stimulus baseline during both memory encoding (Long, Burke, & Kahana, 2014; Sederberg et al., 2007) and retrieval (Michelmann et al., 2016; Waldhauser et al., 2016; also see Hanslmayr, Staudigl, & Fellner, 2012; Hanslmayr et al., 2016 for reviews). This apparent decrease in concurrent alpha and beta power at successful encoding seems to be present in both incidental (Fellner et al., 2019) and intentional learning

situations (Sederberg et al., 2007), further corroborating the robustness of this effect. In case of successful encoding, simultaneous reduction of alpha and beta amplitudes was suggested to reflect the activation of cortical areas related to the processing of task-relevant information (Fellner et al., 2019; Griffiths et al., 2019; Hanslmayr, Spitzer, & Bäuml, 2009; see; Hanslmayr et al., 2012). For example, in case of verbal stimuli, previous studies found a decrease in alpha/beta power that was present most prominently in frontal regions (Hanslmayr et al., 2011; Long et al., 2014), while this effect showed a more posterior distribution for visual materials (Noh, Herzmann, Curran, & de Sa, 2014). In agreement with this pattern, the results of the present study using verbal stimuli showed a change in frontal alpha amplitude that points to a similar topographic pattern. Authors have suggested different explanations to these observed effects, with some proposing a gating model related to alpha desynchronization, where power decrease mirrors a functional inhibition gating the processing of irrelevant stimuli (Jensen & Mazaheri, 2010), while additional findings of simultaneous decrease in alpha and beta power imply that beta oscillations may have a similar association with inhibition (e.g., Waldhauser, Johansson, & Hanslmayr, 2012; Zanto & Gazzaley, 2009; see also Lundquist et al., 2024; Miller, Lundqvist, & Bastos, 2018). Another line of studies proposed a relationship between alpha (Vogelsang, Gruber, Bergström, Ranganath, & Simons, 2018) and beta (Kielar, Panamsky, Links, & Meltzer, 2015) power decrease (as well as their simultaneous desynchronization, see e.g., Fellner, Bäuml, & Hanslmayr, 2013; Hanslmayr et al., 2009) and semantic processing.

Studies focusing on memory retrieval linked the decrease of cortical alpha/beta activity to the reactivation of encoded material that also showed stimulus-specific topographical distribution. In a study involving the vivid episodic retrieval of auditory and visual memory items associated to word cues, the authors found a marked decrease in alpha power during the successful retrieval of items in both domains (Michelmann et al., 2016). This decrease was strongest in frontal and parietal areas, but showed a wide topography. Decreases of alpha/beta power at retrieval have also been observed in areas in the visual cortex, corresponding to the area where the visual stimuli had been encoded (Waldhauser et al., 2016), suggesting that the site where alpha/beta power decreases occur at retrieval is highly specific to stimuli, and highlighting the relationship between alpha/beta desynchronization and stimulus reactivation.

The relationship between post learning resting alpha/beta power and memory consolidation has only been described sparsely in previous studies, showing contrasting results. While a study examining spatial memory found an increase of alpha and beta power during post-training rest and no relation to test performance (Murphy et al., 2018), another study using verbal material reported a negative relationship between post-learning resting alpha oscillation and memory retention (Brokaw et al., 2016). Brokaw et al. (2016) found that this relationship was present in both the resting and the active wakefulness condition of their experiment, and interpreted the connection between alpha spectral power and memory as a trait-like association. Our results regarding resting alpha oscillation showed a similar pattern, however, while Brokaw and colleagues investigated the effects related to post-learning spectral power specifically, in the present study we analyzed power change compared to the participants' own pre-learning spectral power. Therefore, we can assume changes in participants' electrophysiological signals from pre-learning to post-practice are related to processes promoted by the encoding (and reencounter) of the material, and they are less likely to reflect a trait-like relationship between alpha/beta power and memory performance.

Crucially, the observed negative association between frontal alpha power and memory retention is in line with our research group's previous findings related to the role of the dorsolateral PFC in memory consolidation. Marián et al. (2018) using an experimental design similar to the present experiment reported that long-term retrieval of previously reencountered material was negatively affected by excitatory anodal transcranial direct current stimulation of the dorsolateral PFC applied in the reencounter phase. The changes elicited by prefrontal stimulation, and their effect on memory could be related to our current findings on alpha power, considering that amplified cortical alpha power was previously suggested as a possible mechanism involved with excitatory anodal stimulation and its effect on memory performance, as there is evidence that anodal stimulation, besides lowering neuronal firing thresholds, might induce (8–13 Hz) alpha oscillations as assessed by EEG (Dong, Wang, & Chen, 2020; Spitoni, Di Russo, Cimmino, Bozzacchi, & Pizzamiglio, 2013; Zaehle, Sandmann, Thorne, Jäncke, & Herrmann, 2011).

Regarding our behavioral data, the results showed better long-term memory performance and lower reaction times in the group that practiced the material via retesting compared to the restudy group. In other words, our results replicated the testing effect (Karpicke, 2017; Karpicke & Roediger, 2008) showing comparable effects sizes to studies investigating the effects of different practice strategies using within-subjects designs (Marián et al., 2018; Racsmány et al., 2018). Importantly, we controlled for possible demographic differences between the two practice groups, as well as factors such as subjective sleep quality that might impact consolidation-related processes. We also observed behavioral changes characteristic to repeated test practice (see Racsmány et al., 2018): we found increasing recall success and decreasing reaction times between retest practice rounds.

It is crucial to emphasize that we found that long-term memory performance was not dependent on the interaction of the observed electrophysiological changes and the two reencounter conditions, as revealed by a multiple regression analysis. The regression model that included the interaction between the power change measures and the two practice strategies showed no significant advantage over the model that treated these factors separately, meaning the predictive value of power change measures was not dependent on practice strategy. The presence of these behavioral effects, together with the lack of spectral power differences between reencounter types, suggests that even though we found resting-related neural changes that mirror neural processes aiding long-term retention, these changes do not seem to mediate the long-term beneficial effects of repeated retrieval. This result can partially be interpreted within a framework

proposed by Antony et al. (2017), who suggest that during retrieval practice, the act of retrieval itself serves as a way of rapid (on-line) consolidation. This process can be viewed as independent from the post-practice off-line consolidation during rest (although they might share some characteristics) that provides the beneficial environment and mechanisms mirrored in the EEG patterns observed in the present study. Based on this consideration, while retrieval practice might provide a fast, on-line form of stabilization for items that are tested and recalled, post-learning rest stabilizes all intentionally memorized items, regardless of practice condition.

Additionally, the lack of difference between practice strategies with regards to the association between the EEG changes and memory performance might also be attributed to the length of the retention interval used in our study. Even though it has been previously described that sleep-related consolidation may benefit restudied information more compared to retested material (Bäuml, Holterman, & Abel, 2014), recent findings demonstrated that this benefit disappears following longer, 24-h or one-week retention intervals (Abel et al., 2019; Antony & Paller, 2018; Mak & Gaskell, 2023). These results in conjunction with our present electrophysiological findings are in accordance with the bifurcation model of the testing effect (Kornell, Bjork, & Garcia, 2011). This account proposes that restudying strengthens memories to the same moderate degree, while during retesting successfully retrieved memories are strongly reinforced with no benefit to failed retrievals. Importantly, the strength of each item is decreasing at the same rate with time due to memory decay, and some eventually fall below the retrieval threshold. Considering this framework, the positive effects of sleep/rest would not be apparent after a short delay for retested information already strengthened by practice, while weaker, restudied memories would be strengthened by sleep (see e.g., Antony & Paller, 2018; Bäuml et al., 2014). In contrast, the memory decay following longer retention intervals could reveal similar benefits of sleep for both restudied and retested material (Abel et al., 2019). Based on these considerations, we could speculate that our results showing a similar association between post-learning resting EEG changes and memory performance for both restudied and retested items may reflect similar consolidation processes benefitting long term retention in case of both types of reencounter. Relatedly, although the benefits of sleep-dependent consolidation are more apparent for weak memories (e.g., Cairney, Lindsay, Sobczak, Paller, & Gaskell, 2016; Schapiro, McDevitt, Rogers, Mednick, & Norman, 2018), there is evidence that consolidation enhances stronger memories as well in case of increased retrieval demands, implying that post-learning sleep may strengthen both stronger and weaker memories (Petzka, Charest, Balanos, & Staresina, 2021).

Altogether, while it is clear that repeated retrieval has robust long-term behavioral advantages compared to repeated studying, our results are in agreement with earlier findings demonstrating that these forms of memory reencounters share neural features in service of long-term retention (Marián et al., 2018; Racsmány et al., 2018; Racsmány & Szőllősi, 2022; Szőllősi et al., 2017) and this might be the reason for the apparent lack of interaction between practice strategies and the observed electrophysiological measures.

5. Summary and conclusion

Our findings show that power change measures in the alpha, beta and slow frequency bands predict long-term memory performance when practice involving memory reencounters occurs following learning. From baseline to post-practice wakeful rest, alpha and beta change values are negatively, whereas slow frequency power change is positively associated with long-term memory performance. Crucially, this association seems to be independent from the form of practice that takes place after learning. One interesting future avenue in the vein of the current experiment would be to establish a non-learning control group (i.e., a group where participants are not subjected to a learning task between the two resting periods, but perform a non-learning control task), and examine how certain EEG frequency power changes differ between the learning and the control group. Although the lack of such a control group might be seen as a limitation of our study, since one of the main goals of the current experiment was to examine possible differences between the electrophysiological markers of different practice types, the inclusion of such a control group was outside the focus of the current study. However, such a modification in a future experiment could provide additional insight into the precise nature of EEG patterns related to long-term memory success. One additional limitation of our study is the lack of occipital leads in the electrode montage. While this methodological aspect of our study was implemented to reduce potential contamination of the EEG signal by muscle-related artifacts resulting from a horizontal resting position, future studies could achieve a more comprehensive assessment of alpha power during resting state with the inclusion of occipital electrode sites. Importantly, our results are in line with previous findings pointing to the role of frequency-specific cortical activities in memory formation and extend them to situations where memory reencounters occur after learning—such as in real life learning situations.

CRediT authorship contribution statement

Dorottya Bencze: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Miklós Marián:** Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Ágnes Szőllősi:** Writing – original draft, Methodology. **Péter Simor:** Writing – review & editing, Methodology, Conceptualization. **Mihály Racsmány:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

Open practices

The study in this article has earned Open Data, and Open Materials for transparent practices. The data, and materials are available at: https://osf.io/6asf4/.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgement

This work was supported by the Hungarian Brain Research Program 3.0 Research Grant (grant number NAP2022-I-2/2022) and by the Ministry of Innovation and Technology of Hungary from the National Research, Development and Innovation Fund (grant numbers NKFIH K146237, NKFIH FK142945). PS and ÁS were supported by the Bolyai János Scholarship of the Hungarian Academy of Sciences. Study data is archived at https://osf.io/6asf4/. No part of the study procedures or analysis was pre-registered prior to the research being conducted. We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

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