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Research Report

Similarity of brain activity patterns during learning and subsequent resting state predicts memory consolidation

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ABSTRACT

Spontaneous reactivation of brain activity from learning to a subsequent off-line period has been implicated as a neural mechanism underlying memory consolidation. However, similarities in brain activity may also emerge as a result of individual, trait-like characteristics. Here, we introduced a novel approach for analyzing continuous electroencephalography (EEG) data to investigate learning-induced changes as well as trait-like characteristics in brain activity underlying memory consolidation. Thirty-one healthy young adults performed a learning task, and their performance was retested after a short (~1 h) delay. Consolidation of two distinct types of information (serial-order and probability) embedded in the task were tested to reveal similarities in functional networks that uniquely predict the changes in the respective memory performance. EEG was recorded during learning and pre- and post-learning rest periods. To investigate brain activity associated with consolidation, we quantified similarities in EEG functional connectivity between learning and pre-learning rest (baseline similarity) and learning and post-learning rest (post-learning similarity). While comparable patterns of these two could indicate trait-like similarities, changes from baseline to post-learning similarity could indicate learning-induced changes, possibly spontaneous reactivation. Higher learning-induced changes in

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alpha frequency connectivity (8.5–9.5 Hz) were associated with better consolidation of serial-order information, particularly for long-range connections across central and parietal sites. The consolidation of probability information was associated with learning-induced changes in delta frequency connectivity (2.5–3 Hz) specifically for more local, short-range connections. Furthermore, there was a substantial overlap between the baseline and post-learning similarities and their associations with consolidation performance, suggesting robust (trait-like) differences in functional connectivity networks underlying memory processes.

1. Introduction

What makes us remember? Successful long-term memory performance depends on consolidation: a process that stabilizes encoded memory representations (McGaugh, 2000). For consolidation, the behavioral, cognitive, and neural states in the first few hours following the learning episode are critical (as shown predominantly in animal studies, McGaugh & Izquierdo, 2000). In humans, one systems-level mechanism occurring during this crucial time period is the reactivation of the brain activity related to the learning episode (Hermans et al., 2017; Peigneux et al., 2006; Tambini, Berners-Lee, & Davachi, 2017). Further, the patterns of brain activity that reappear during the off-line period following learning predict memory consolidation (Rasch & Born, 2007). However, to what extent this result reflects learning-induced changes or stable individual characteristics present over resting and learning periods remains unclear. Here, we aimed to fill this gap by examining how learning-induced changes (possibly reactivation) and trait-like individual characteristics of neural patterns captured by electroencephalography (EEG) support memory consolidation.

Post-learning reactivation (more specifically, replay) of memory traces has been widely studied in rodents using invasive neurophysiological techniques (Diba & Buzsáki, 2007; Foster & Wilson, 2006; Louie & Wilson, 2001; Nádasdy, Hirase, Czurkó, Csicsvari, & Buzsáki, 1999; Skaggs & McNaughton, 1996; for a recent review, see Tingley & Peyrache, 2020). However, translating the fine-scaled spatial and temporal resolution of these invasive neurophysiological recordings to non-invasive techniques used in human research is challenging. The first studies on spontaneous reactivation in humans focused on sleep and used non-invasive neuroimaging techniques, such as positron emission tomography or functional magnetic resonance imaging (fMRI, Maquet et al., 2000; Peigneux et al., 2004). Due to the lower spatial and especially temporal resolution compared to animal research, reactivation in these human studies was defined differently, by higher similarity of brain activity patterns during learning and post-learning periods compared to pre-learning (for a review, see Tambini & Davachi, 2019). For instance, using fMRI, Peigneux et al. (2006) investigated the modulation of brain activity during active wakefulness as a result of declarative or procedural learning (which were tested in separate sessions weeks apart). They examined changes in brain activity from pre-learning to post-learning active wake periods, immediately after learning and subsequently, following a 30 min rest. Their findings revealed distinct post-learning changes in brain activity for declarative and procedural learning. In the case of procedural memory, there was an initial decrease in brain activity in learning-related areas (e.g., the motor cortex and the basal ganglia) that was followed by a delayed increase, possibly indicating extended consolidation processes. Notably, these changes in brain activity following learning correlated with memory performance.

To capture the temporal information crucial for cognitive processes (and demonstrated in animal studies), recent studies applied neurophysiological techniques, such as magnetoencephalography (MEG) and electrocorticography (ECoG), to study reactivation (or more specifically, replay) in humans (Buch, Claudino, Quentin, Bönstrup, & Cohen, 2021; Liu, Dolan, Kurth-Nelson, & Behrens, 2019; Michelmann, Staresina, Bowman, & Hanslmayr, 2019; Vaz, Wittig, Inati, & Zaghloul, 2020; Wimmer, Liu, Vehar, Behrens, & Dolan, 2020). However, scalp EEG studies of reactivation during post-learning awake rest periods in humans are still scarce (Moisello et al., 2013; Murphy, Stickgold, Parr, Callahan, & Wamsley, 2018). Moisello et al. (2013) investigated changes in brain activity following a declarative sequence learning task. Using event-related EEG data, they identified learning-related spectral power changes by comparing brain activity during the learning to that of a non-learning control task. Declarative sequence learning was associated with activity in the theta and alpha bands, over frontal and right occipito-parietal areas. Comparing a short (3 min) pre- and post-learning rest, they revealed a significant change in alpha power following learning over a right occipito-parietal area, partially overlapping with the area relevant for learning. These changes in the resting EEG were correlated with the task-related brain activity but not with the memory performance. The lack of association between learning-induced changes in resting brain activity and memory performance might be due to the short duration of the post-learning rest (cf. Peigneux et al., 2006, demonstrating relevant changes in brain activity over a 30 min rest period for procedural learning) or because spectral power may not be a sensitive measure of learning-induced changes (Fell, Ludowig, Rosburg, Axmacher, & Elger, 2008).

The reason for the relative scarcity of EEG reactivation studies could be that the precise cellular mechanisms that contribute to specific features of EEG are largely unknown (Cohen, 2017). Nevertheless, it is important to highlight that reactivation should manifest at the level of scalp EEG signal for several reasons. First, there is evidence of a direct

connection between the microscopic (single unit activity) and macroscopic level (EEG, MEG, local field potential) of brain dynamics (Jacobs, Kahana, Ekstrom, & Fried, 2007; Mazzoni, Whittingstall, Brunel, Logothetis, & Panzeri, 2010; Whittingstall & Logothetis, 2009). It has been shown that coupling mechanisms in the EEG signal can provide information regarding the spiking activity of neurons (Whittingstall & Logothetis, 2009). Second and relatedly, this is in line with the role of oscillations integrating anatomically distributed processing and facilitating neuronal communication suggested by Buzsáki and Draguhn (2004). It has been suggested that phase synchronization is the mechanism through which neural assemblies communicate with each other to create the flexible and anatomically distant connections that underlie cognition (Fries, 2005, 2015; Womelsdorf et al., 2007). Third, it has been shown that an experience-specific pattern of firing correlations persists both in wakefulness or sleep following learning, therefore reactivation can be observed on longer timescales (Hoffman & Mcnaughton, 2002; Kudrimoti, Barnes, & McNaughton, 1999; Tambini & Davachi, 2013; Wilson & McNaughton, 1994). Lastly, animal studies have shown that reactivation also occurs in the cerebral cortex (Peyrache, Khamassi, Benchenane, Wiener, & Battaglia, 2009; Qin, McNaughton, Skaggs, & Barnes, 1997; Ribeiro et al., 2004; Rothschild, Eban, & Frank, 2017), suggesting that it can be studied with scalp EEG. These findings highlight the plausibility of measuring reactivation via phase synchronization in scalp EEG data in humans because reactivation should manifest in changes in the neural coupling in the cerebral cortex over longer time periods.

Phase synchronization in EEG has been shown to be important for several cognitive mechanisms (Sauseng & Klimesch, 2008; Varela, Lachaux, Rodriguez, & Martinerie, 2001), particularly for memory processes (Axmacher, Mormann, Fernández, Elger, & Fell, 2006; Fell & Axmacher, 2011). Notably, phase synchronization in the medial temporal lobe was proven to be a superior predictor of memory performance compared to other EEG measures, such as event-related potential and spectral power measures (Fell et al., 2008). It has also been shown that spontaneous replays in humans coincide with specific cortical resting state networks that are characterized by brain-wide phase synchronization (Higgins et al., 2021). Thus, in the current study, we investigated learning-induced changes by comparing functional networks emerging from phase synchronization measured via scalp EEG in healthy young adults. We followed a data-driven approach and did not define frequency ranges or brain areas of interest a priori. Rather, we aimed to reveal patterns in both the frequency and topography of functional networks that emerge both during learning and post-learning rest.

However, similarities in functional networks during learning and subsequent rest do not exclusively emerge as a function of reactivation (or other learning-induced changes); they may occur due to trait-like individual characteristics in brain activity. For instance, Smit, Stam, Posthuma, Boomsma, and De Geus (2008) showed that individual differences in resting state EEG functional connectivity are largely hereditary. Furthermore, several studies using fMRI provided evidence that resting state (intrinsic) connectivity predicts memory performance (Touroutoglou, Andreano, Barrett, & Dickerson, 2015; Wang, LaViolette, et al., 2010; Wang, Negreira, et al., 2010; Wig et al., 2008). Moreover, substantial intraindividual similarity between functional connectivity networks during resting state and task has been observed (Cole, Ito, Bassett, & Schultz, 2016; Satterthwaite, Xia, & Bassett, 2018). Gratton et al. (2018), studying fMRI functional networks, concluded that these networks are dominated by stable individual factors rather than cognitive content. Despite the growing recognition of trait-like individual differences in functional networks, human reactivation studies have predominantly focused on learning-induced changes alone and have not examined how trait-like individual differences contribute to cognitive performance.

In our study, to disentangle learning-induced changes and trait-like characteristics, we compared the similarity of functional connectivity between learning and both pre- and post-learning rest. If the similarity between learning and pre-learning rest is comparable to the similarity between learning and post-learning rest, the similarities likely emerge due to trait-like individual characteristics in brain activity. In contrast, higher similarity of learning and post-learning rest compared to pre-learning rest is indicative of learning-induced changes (possibly reactivation, as defined in fMRI studies, see Tambini & Davachi, 2019). Nevertheless, changes in functional networks from pre- to post-learning rest might also emerge for instance as a function of time-of-day effects or fatigue throughout an extended experimental protocol. To ensure that the learning-induced changes in brain activity are relevant for memory consolidation and thus potentially reflect reactivation, we focused specifically on those functional network similarities that were significantly associated with memory performance.

We used a procedural memory task with an alternating sequence that enabled us to present two types of regularities (serial-order and probability) within the same visual information stream (Nemeth, Janacsek, & Fiser, 2013). This design has higher ecological validity because in real life we are usually exposed to different types of information simultaneously. Studies have shown that learning serial-order and probability-based (also referred to as rule-based and statistical) regularities exhibit different characteristics at the behavioral and neural levels (Conway, 2020; Howard, Jr. & Howard, 1997; Maheu, Meyniel, & Dehaene, 2022; Nemeth et al., 2013; Quentin et al., 2021; Simor et al., 2019; Takács et al., 2021). At the behavioral level, the acquisition of probability information (also known as statistical learning) typically occurs incidentally and relatively rapidly (Kóbor et al., 2018; Simor et al., 2019). Conversely, the acquisition of serial-order information (also referred to as rule-based or sequence learning) can occur both incidentally or intentionally, and it exhibits a slower, gradual improvement over time (Horvath, Torok, Pesthy, Nemeth, & Janacsek, 2021; Howard et al., 2004; Howard, Jr. & Howard, 1997; Kóbor et al., 2018; Simor et al., 2019; Szegedi-Hallgató et al., 2017). On the neural level, statistical and serial-order learning have different electrophysiological characteristics, demonstrated by event-related potentials during learning (Kóbor et al., 2018; Takács et al., 2021) and neural oscillations during consolidation (Simor et al., 2019). As a synthesis from studies investigating the neural correlates of statistical and serial-order learning, Conway (2020) suggested

that statistical learning is based on experience-driven gradual tuning of cortical networks that is instantiated over multiple, hierarchically embedded networks, involving particularly the sensory areas. In contrast, serial-order learning requires top-down modulatory control mechanisms, therefore it exhibits a greater reliance on the prefrontal cortex and related fronto-parietal networks. Overall, examining the consolidation of different types of information simultaneously enabled us to reveal similarities in functional networks that uniquely predict the changes in the respective memory performance.

Importantly, procedural memory consolidation might take one of two distinct forms: off-line improvement or stabilization of memories (Robertson, Pascual-Leone, & Miall, 2004). For certain types of procedural memory, particularly explicit processes, extended periods of time or sleep might be necessary for off-line improvements to occur (Robertson, Pascual-Leone, & Press, 2004). In this study, given the relatively short time for consolidation (~1 h) and based on previous findings showing no off-line improvements for a consolidation period of similar duration using similar tasks (Peigneux et al., 2006; Simor et al., 2019), we expect the retention of statistical and serial-order knowledge over the post-learning rest period, potentially reflecting the stabilization of the acquired knowledge. Notably, previous studies demonstrated that procedural memory consolidation can be supported by 15–30 min (or less) of wakeful rest (Humiston & Wamsley, 2018; Quentin et al., 2021; Wang et al., 2021). Accordingly, spontaneous reactivation has been proven to occur in these shorter post-learning rest periods (similar to sleep) highlighting a possible neural mechanism to support these relatively rapid consolidation processes (for a review, see Wamsley, 2022). Thus, it is plausible that our study captures early system consolidation processes underlying the initial stabilization of procedural memory for two separate processes, namely statistical and serial-order learning.

In summary, the primary aim of the current study was to investigate the learning-induced changes in EEG functional connectivity that support procedural memory performance. To capture learning-induced changes, we employed a novel analysis technique, computing the Euclidean distance of phase synchronization networks using continuous EEG data. Secondly, we tested the specificity of these learning-induced changes to the type of learning by using a procedural learning task with two types of regularities. We hypothesized that distinct neural networks support the simultaneous memory consolidation of serial-order versus probability information. Lastly, we explored the stable functional connections emerging across learning and rest to examine trait-like individual differences and their associations with memory performance.

2. Materials and methods

2.1. Participants

Thirty-four participants (11 males, M_{age} = 21.82 ± 2.11) with normal or corrected-to-normal vision were included in the study. Participants were selected from a pool of undergraduate students from the Eötvös Loránd University in Budapest. The selection procedure was based on the completion of an online questionnaire assessing mental and physical health status. Respondents reporting no current or prior chronic somatic, psychiatric, or neurological disorders or regular consumption of drugs (other than contraceptives) were selected. In addition, individuals reporting occurrences of any kind of extreme life event (e.g., accident) during the last three months that might have had an impact on their mood, affect, and daily rhythms were excluded.

Individuals falling asleep during the post-learning rest (N = 2) were excluded from the analyses. Furthermore, one additional participant was excluded based on extreme behavioral performance (more than 3 interquartile ranges from the median in the average serial-order learning performance during the learning period). Therefore, the final sample consisted of 31 participants (9 males, M_{age} = 21.81 ± 2.10). This sample size was deemed sufficient to investigate learning-induced changes and their associations with memory performance based on prior studies: Previous EEG studies demonstrated robust learning-induced changes with 13–21 participants (Moisello et al., 2013; Murphy et al., 2018) and significant associations between EEG phase synchronization and procedural memory performance with 28 participants (Tóth et al., 2017). Data from twenty-six of these participants were included in a previous publication (Simor et al., 2019). All participants provided written informed consent before enrollment and received course credits for taking part in the experiment. The study was approved by the research ethics committee of the Eötvös Loránd University, Budapest, Hungary (201410) and was conducted in accordance with the Declaration of Helsinki.

2.2. Task

Behavioral performance was measured by the cued version of the Alternating Serial Reaction Time (ASRT) task (Fig. 1, Nemeth et al., 2013), which has been shown to have good reliability (Farkas, Krajcsi, Janacsek, & Nemeth, 2023). In this task, a stimulus (picture of a dog's head or a penguin) appeared in one of four horizontally arranged empty circles on the screen, and participants had to respond by pressing the corresponding button of a response box. Stimuli were presented until the participant responded, on a 19″ LCD screen at a viewing distance of 100 cm. The response-to-stimulus interval was set to 250 msec (i.e., the stimulus appeared approximately 250 msec after the response for the preceding stimulus). Participants were instructed to respond as fast and accurately as they could.

The task was presented in blocks of 85 stimuli. A block started with five random stimuli for practice purposes, followed by an 8-element alternating sequence that was repeated ten times. The alternating sequence was composed of fixed sequence and random elements (e.g., 2-R-4-R-3-R-1-R, where each number represents one of the four circles on the screen and "R" represents a randomly selected circle out of the four possible ones, Fig. 1B). Participants were informed about the underlying structure, and their attention was drawn to the alternation of sequence and random elements cued by different visual cues. In our case, a picture of a dog always corresponded to the fixed sequence elements, and a picture of

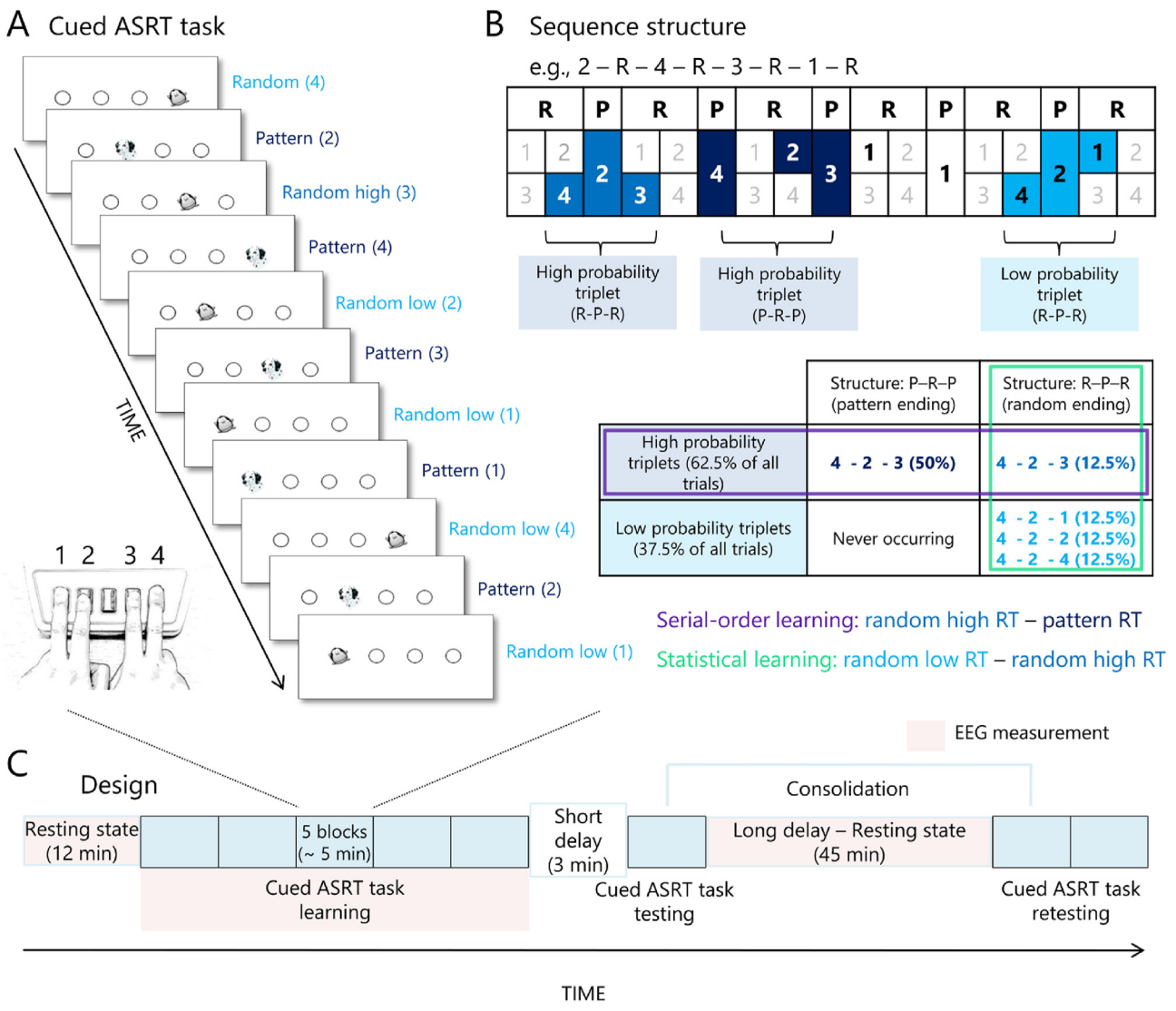

Fig. 1 – The cued version of the Alternating Serial Reaction Time (ASRT) task. A) The appearance of the task. In this task, stimuli appeared on the screen in one of four empty circles and participants had to press button box keys corresponding to the location of the stimuli. Stimuli were presented according to an alternating sequence with fixed and random elements. Fixed elements were marked with a picture of a dog, whereas random ones with a picture of a penguin. The location of stimuli during the sequence trials always followed a fixed sequence (e.g., 2-4-3-1 in the given example, where numbers correspond to the four locations on the screen), therefore runs of three consecutive elements (triplets) that ended with sequence elements occurred with high probability (*pattern* trials). Random trials included 1) trials that appeared in an order that was identical to the sequence, therefore they constituted triplets with high probability (*random high* trials) and 2) any other random trials that consequently occurred with low probability (*random low* trials). B) The same example stimuli stream as in panel A is shown (expressed as numbers corresponding to the location of the stimuli), illustrating the sequence structure and triplets constituting each trial type in the top table. The 'observed' position of the stimulus is depicted in bold and in case of the random elements, the other possible but non-observed positions are faded. We determined for each stimulus whether it was the last element of a pattern, random high (i.e., high probability triplets, marked with dark blue color), or random low triplet (i.e., low probability triplet, marked with light blue color) in a sliding window manner. We assessed *serial-order learning* (purple box in the bottom table) by comparing the responses to pattern trials (which are always high probability triplets) with responses to random high probability trials. *Statistical learning* (green box in the bottom table) was quantified as the difference between responses to those random elements that were the last elements of a high probability triplet versus those that were the last of a low probability triplet. C) The design of the experiment. First, participants were asked to rest with their eyes open and then closed for 6 min each (*pre-learning rest*). Then, after a short practice, the learning period of the ASRT followed that consisted of 25 task blocks. To eliminate the fatigue effect and ensure more accurate behavioral consolidation indices, we inserted a short break of 3 min before the testing period of the ASRT, which consisted of five blocks. After the testing period, there was a 45 min rest period, when participants were sitting with their eyes open and closed in 5 min turns (*post-learning rest*). Finally, there was a retesting period that comprised ten

a penguin indicated random elements (Fig. 1A). Participants were instructed to find the hidden sequence defined by the dog to improve their performance. At the end of each block, participants received feedback on their overall accuracy and reaction time, completed a sequence report, and had a 10–20 sec rest before starting a new block. Sequence reports consisted of the participants typing in the regularities of the fixed elements (cued by the dog) they noticed using the same response buttons they used during the task blocks. By the end of the task, all participants reported the correct sequence. On average, participants gained explicit knowledge of the sequence after the fourth block ($M = 4.10$, $SD = 5.95$), and 84% of participants reported the correct sequence during the first five blocks.

There are six unique sequence permutations of the four possible ASRT sequence elements (1,2,3,4, noting that the starting element of a sequence does not matter as the sequence is continuously presented). For each participant, one of these six unique permutations was selected in a pseudo-random manner, so that the six different sequences were used equally often across participants.

The task consisted of a total of 42 blocks (Fig. 1C). The first two blocks of the task served practice purposes to enable the participants to get familiar with the stimuli and the response box. During this practice period, all stimuli appeared randomly. Participants then completed 25 blocks of the ASRT task during the *learning period*. This was followed by a short (3 min) break to minimize the fatigue effect that typically emerges after extended practice (Rickard, Cai, Rieth, Jones, & Ard, 2008; Rieth, Cai, McDevitt, & Mednick, 2010). After the break, participants were tested on the ASRT task for five additional blocks that constituted the *testing period*. Subsequently, participants spent an approximately 45 min long offline period resting. Finally, they completed ten additional blocks of the ASRT task (*retesting period*). The learning period lasted approximately 30 min, the testing period 5 min, and the retesting period 10 min.

The alternating sequence of the ASRT task formed a sequence structure in which some runs of three consecutive elements (henceforth referred to as triplets) were more probable than others. The more probable triplets were those that formed the sequence (such as 2-X-4, 4-X-3, 3-X-1, and 1-X-2, where X indicates any middle element of the triplet in the above example sequence 2-R-4-R-3-R-1-R). In these triplets, the first and third elements could either be a fixed sequence or random stimuli (they constituted 62.5% of all trials). The less probable triplets (e.g., the triplets 4-X-1, 4-X-2, or 4-X-4) occurred less likely since the first and third elements could only be random stimuli (each of these triplets occurred in 12.5% of all trials, altogether 37.5%). The former triplet types were termed as high probability triplets, whereas the latter types were termed as low probability triplets (Fig. 1B). As a result of the ASRT sequence structure, the high probability triplets were five times more predictable than the low probability ones on the level of individual triplets.

To calculate learning indices, each stimulus was categorized as the third element of either a high or a low probability triplet. Note that in this way, we determined the probability of each triplet throughout the task in a sliding window manner (i.e., one stimulus was the last element of a triplet, but also the middle and the first element of the consecutive triplets). Moreover, trials were differentiated by whether the stimulus belonged to the fixed sequence or random elements (i.e., dog and penguin cues). Thus, the task consisted of three trial types: (1) elements that belonged to the fixed sequence and therefore appeared as the last element of a high probability triplet, called *pattern* trials; (2) random elements that appeared as the last element of a high probability triplet, called *random high* trials; and (3) any other random elements that consequently appeared as the last element of a low probability triplet, called *random low* trials (see the example in Fig. 1B).

To disentangle the two key learning processes underlying the performance on the cued ASRT task, we differentiated serial-order and statistical learning (Fig. 1B). Serial-order learning was measured by the difference in reaction times (RTs) between random high and pattern trials (that is, the average RTs for random high trials minus the average RTs for pattern trials so that a higher value corresponds to better learning). These trials shared the same statistical properties (both corresponded to the third element of high probability triplets) but had different sequential properties (i.e., fixed *vs* random element). Thus, greater serial-order learning was determined as faster responses to pattern versus random high trials. Statistical learning was measured by the difference in RTs between random low and random high trials (that is, the average RTs for random low trials minus the average RTs for random high trials so that a higher value corresponds to better learning). These trials shared the same sequential properties (both were random) but differed in statistical properties (i.e., they corresponded to the third element of a high or a low probability triplet). Thus, greater statistical learning was determined as faster responses to random high compared to random low trials. In sum, serial-order learning quantified the acquisition of the deterministic rule of the sequential pattern, whereas statistical learning captured purely probability-based learning (Maheu et al., 2022; Nemeth et al., 2013).

2.3. Experimental design

On the day of the experiment, participants arrived at the laboratory at 10.00 AM. First, an EEG cap with 64 electrodes was fitted by two assistants with impedances set under 10 kΩ. Then, participants were asked to rest with their eyes open and then closed for 6 min each as a baseline EEG recording (*pre-learning rest*, Fig. 1C). Testing with the task started around 11.30 AM and took place in a quiet room equipped with a computer screen, a response box and an EEG recording device. After listening to the instructions, participants completed two blocks of the ASRT task with only random stimuli to get familiar with the stimuli and the response box. This was

additional ASRT blocks. Behavioral consolidation indices were calculated as the difference in the performance between the beginning of the retesting period and the testing period (five blocks of each). EEG activity was measured during the pre-learning rest, the learning period of the ASRT, and the post-learning rest.

followed by the *learning period* of the cued ASRT task. To eliminate the effect of fatigue that may have built up during performing the task for about 25 min (Rickard et al., 2008; Rieth et al., 2010) and therefore to ensure more accurate behavioral measures, a short break of 3 min was introduced during which the EEG impedances were reset under 10 kΩ. After this short delay, the *testing period* of the ASRT followed. After the testing period, participants completed a ~45 min rest period, during which they sat in a dimly lit room, facing toward an empty wall (*post-learning rest*). During this rest period, to prevent participants from falling asleep, they were instructed to open and close their eyes periodically (approximately every 5 min). Furthermore, their EEG activity was monitored online, and at signs of sleepiness (alpha disappearance and theta increase) participants were instructed to open their eyes and/or make movements. After this resting period, impedances were again reset under 10 kΩ. Finally, a *retesting period* of the ASRT task followed. Behavioral consolidation indices were calculated as the difference in performance between the beginning of the retesting period and the testing period. EEG activity was measured during the pre-learning rest, the learning period of the ASRT task and the post-learning rest.

2.4. EEG recording

EEG activity was measured using a 64-channel recording system (BrainAmp amplifier and BrainVision Recorder software, BrainProducts GmbH, Gilching, Germany). The Ag/AgCl sintered ring electrodes were mounted in an electrode cap (EasyCap GmbH, Herrsching, Germany) on the scalp according to the 10% equidistant system. During acquisition, electrodes were referenced to a scalp electrode placed between the Fz and Cz electrodes (FCz). Horizontal and vertical eye movements were monitored by two EOG channels. Further, three EMG electrodes were placed on the chin and one ECG electrode on the chest to record muscle and cardiac activity respectively. All electrode contact impedances were kept below 10 kΩ. EEG data were recorded at a sampling rate of 500 Hz, and band-pass filtered between .3 and 70 Hz.

2.5. Data analysis

2.5.1. Behavioral data

For the analysis of the cued ASRT, we followed procedures outlined in previous studies (Howard, Jr. & Howard, 1997; Nemeth et al., 2013; Simor et al., 2019; Song, Howard, & Howard, 2007). These statistical analyses were carried out with the Statistical Package for the Social Sciences Version 22 (IBM SPSS Statistics). First, the blocks of the task were collapsed into epochs of five blocks to facilitate data processing and to increase statistical power. The first epoch contained blocks 1–5, the second epoch contained blocks 6–10, etc. We calculated median reaction times (RTs) for correct responses only, separately for pattern, random high and random low trials, and for each epoch. Two kinds of low probability triplets were eliminated: repetitions of a single element (e.g., 2-2-2, 3-3-3) and triplets beginning and ending with the same element (e.g., 2-1-2, 3-4-3) as individuals often show pre-existing response tendencies to such triplets (Howard et al., 2004). Thus, we eliminated these triplets to ensure that differences between high versus low probability triplets emerged due to learning and not because of pre-existing response tendencies.

Overall performance trajectory. To evaluate performance changes in RTs due to learning throughout the entire task, we conducted a repeated-measures analysis of variance (ANOVA) on RTs with EPOCH (1–8) and TRIAL TYPE (pattern, random high, random low) as within-subject factors. Greenhouse-Geisser epsilon (e) correction (Greenhouse & Geisser, 1959) was used to adjust for a lack of sphericity when necessary. Post-hoc comparisons were performed using Fisher's LSD test. Then, we computed a serial-order and a statistical learning score for each epoch. The serial-order learning score was calculated as the RTs for random high trials minus the RTs for pattern trials. The statistical learning score was calculated as the RTs for random low trials minus the RTs for random high trials. In both cases, higher learning scores indicated better learning.

Consolidation. To examine off-line changes occurring between the testing and retesting periods, we used a repeated-measures ANOVA on the learning scores, with EPOCH (6–7, the only epoch of the testing period and the first epoch of the retesting period) and LEARNING TYPE (serial-order learning, statistical learning) as within-subject factors. For the ANOVAs, original df values and corrected *p* values (if applicable) are reported together with partial eta-squared (η_p^2) as the measure of effect size. Next, to be able to identify associations between brain activity patterns and memory performance, we computed consolidation indices: off-line changes in serial-order and statistical learning were defined as the difference between the learning scores at the beginning of the retesting period (epoch 7) minus the learning scores in the testing period (epoch 6; Fig. 1C). A positive value indicated an improvement in learning performance during the off-line period. For all subsequent analyses between brain activity and memory performance, we used these consolidation indices.

2.5.2. EEG data

Preprocessing and further analysis (Fig. 2A) of the EEG data were performed in MATLAB (version R2017b, The Mathworks, Inc, Natick, MA) using the EEGLAB (14_0_0b version, Delorme & Makeig, 2004) and the Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) toolboxes. The following steps were executed for EEG data recorded during the pre-learning rest, the learning period of the ASRT and the post-learning rest.

First, non-EEG channels (two mastoids, two EOG, one ECG, and three EMG channels) were excluded, therefore all preprocessing steps and analyses were completed on the remaining 56 EEG channels (referenced to the FCz channel). Next, data were off-line band-pass filtered (.5–45 Hz) using Hamming windowed finite-impulse-response filter. Then, high amplitude artifacts (body movements, sweating, and temporary electrode malfunction) and the periods between the blocks of the task during the learning period were visually rejected. Subsequently, to identify (horizontal and vertical) eye-movement artifacts, we ran the extended infomax algorithm of independent component analysis (Lee, Girolami, & Sejnowski, 1999) via EEGLAB (option: runica, 'extended'). ICA components constituting eye-movement artifacts were

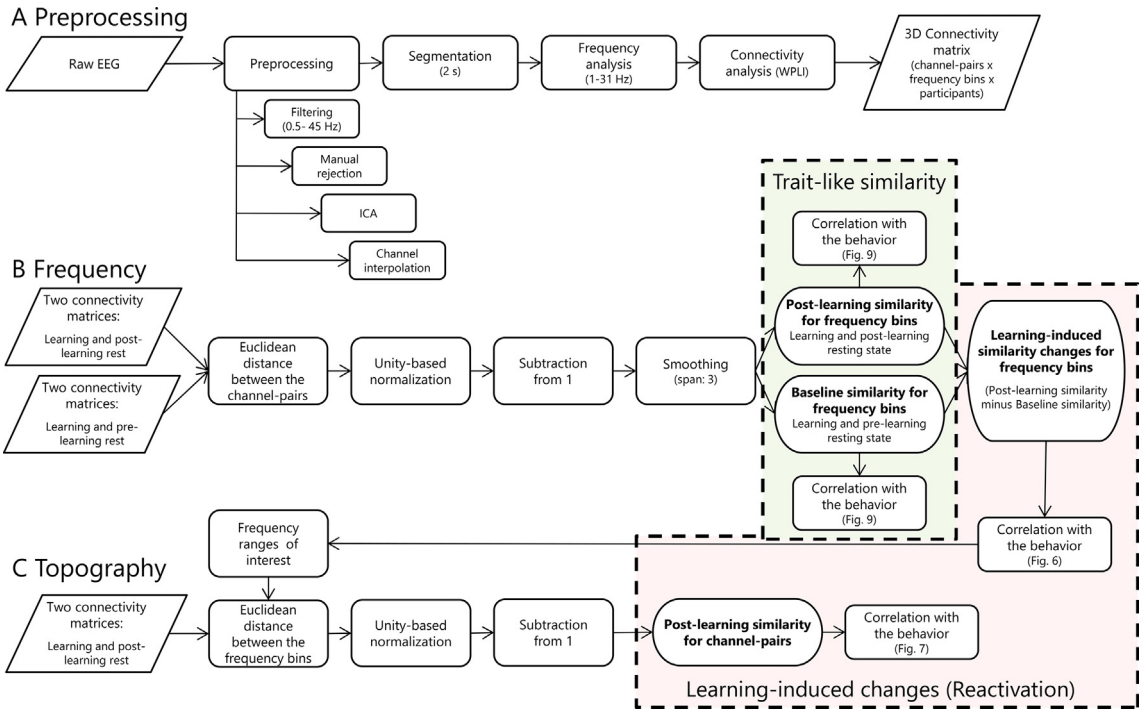

Fig. 2 – Steps of the analysis of EEG data. A) Following preprocessing (filtering, manual rejection of large body movements, ICA removal of eye movements and optionally channel interpolation), connectivity matrices were calculated from the raw EEG data for the pre-learning rest, the learning period of the ASRT and the post-learning rest, resulting in 3D connectivity matrices for these three periods with channel pairs, frequency bins and participants as dimensions. B) Comparing two connectivity matrices at a time (learning and post-learning rest or learning and pre-learning rest), we computed the similarity of functional connectivity during these different periods (henceforth referred to as Post-learning and Baseline similarity, respectively) for frequency bins between 1 and 31 Hz. We calculated the Euclidean distance between all channel pairs for each frequency bin. Then, we normalized these values to shift the scale to the range of 0–1 and subtracted them from 1 to indicate similarity rather than distance, with higher values indicating greater similarity. Finally, we smoothed these similarity values, applying a moving average filter with a span of 3. Then, we performed correlation analyses between the consolidation indices and these Post-learning and Baseline similarity values for frequency bins, which could reveal trait-like associations between behavior and similarity of neural patterns. To reveal learning-induced changes (possibly reactivation) in similarity, we subtracted the Baseline similarity values from the Post-learning similarity values, with larger values indicating greater similarity between the learning period and post-learning rest than between the learning period and pre-learning rest. We identified frequency ranges of interest for further analysis based on the correlations that these similarity difference values showed with the consolidation indices for consecutive frequency bins. C) As a second step, we computed Euclidean distance between the identified frequency bins of the learning and post-learning rest connectivity matrices, which we transformed again to similarity values by normalization and subtraction from 1. This resulted in Post-learning similarity values for each channel pair within the frequency ranges of interest. Finally, we contrasted these Post-learning similarity values for channel pairs with behavior to investigate the topographical patterns of the associations revealed in the frequency domain. With the steps outlined in B) and C), we aimed to differentiate trait-like (light green box) and learning-induced (light orange box) associations between memory consolidation and the similarity of functional connectivity across different periods (see main text for details).

removed via visual inspection of their time series, topographical distribution and frequency contents. A maximum of six independent components (out of 56 components produced by the algorithm) per participant were removed. Finally, if needed, bad channels were interpolated for a maximum of four bad channels per participant.

After artifact rejection, non-overlapping epochs of 2000 msec duration were extracted from the continuous EEG recording. This data segmentation yielded $M = 319.77$, $SD = 33.30$, $M = 707.94$, $SD = 67.43$, $M = 988.74$, $SD = 269.92$ epochs for the pre-learning rest, learning, and post-learning rest, respectively. Due to more body movement artifacts during the post-learning rest, proportionally more data from this period had to be removed. Note that the EEG during the learning period was segmented regardless of the onsets of stimuli (i.e., epochs had random timing relative to trials) and

during the resting states, it was segmented regardless of eyes open or closed periods. To compute power spectral density, Hann taper was first applied to the two-second long, artifact-free EEG segments. Then, for each participant and channel, power spectral density was computed for each .5 Hz frequency bin between 1 and 31 Hz with the Fast Fourier Transform (FFT) algorithm as implemented in Fieldtrip.

Functional connectivity was calculated between all channel pairs by measuring phase synchronization using the Weighted Phase Lag Index (WPLI) as implemented in Fieldtrip (ft_connectivityanalysis function, 'wpli' option). Phase Lag Index (PLI) was introduced by Stam, Nolte, and Daffertshofer (2007), and it reflects the consistency by which one signal is phase leading or phase lagging with respect to another signal. PLI has been shown to be sensitive in detecting dynamic changes of phase relationships between different brain areas and to be insensitive to the effect of volume conduction (effect of common sources of the EEG signal), as well as to be (largely) independent of the reference electrode (Stam et al., 2007). PLI attenuates the volume conduction effect by disregarding phase lags of zero or π (as these phase differences suggest two electrodes are picking up signal from the same source). The WPLI is a modified version of PLI that weights phase angle differences around .5 and 1.5 π more than those around zero and π, which makes the method more robust against volume conduction (Vinck, Oostenveld, Van Wingerden, Battaglia, & Pennartz, 2011). Note that the Fieldtrip function results in WPLI values between −1 and 1, with both −1 and 1 indicating higher synchronization. As WPLI is a non-directed functional connectivity measure, we used the absolute WPLI values as the measure of the strength of the interaction. Thus, the final WPLI values in our analyses fall between 0 and 1, with higher values indicating stronger synchronization.

The mentioned steps resulted in three 3D connectivity matrices, separately for the pre-learning rest, the learning period of the ASRT task and the post-learning rest (Fig. 2A). The dimensions in these matrices were channel pairs, frequency bins and participants. To measure similarity between the brain activity recorded at different periods, we calculated Euclidean distance between these connectivity matrices (Fig. 2BC).

2.5.3. *Associations between behavior and similarity in EEG functional connectivity across different periods*

To reveal associations between the behavioral indices of consolidation and brain activity, we first computed similarity between functional connectivity measured during the learning period and the pre-learning rest, and the learning period and the post-learning rest separately (henceforth referred to as *Baseline* and *Post-learning similarity*, respectively). We computed two types of similarity: 1) for frequency (Fig. 2B) and 2) for channel pairs (Fig. 2C). As a data-driven approach, we identified frequencies associated with the behavioral indices of consolidation first. Then, we explored relevant topographical patterns in the identified frequency ranges based on the channel pair similarity.

Frequency of learning-induced changes. To reveal possible reactivation of neural patterns after learning, we aimed to find frequencies 1) where the Post-learning similarity is different from the Baseline similarity, presumably reflecting learning-induced changes, and 2) where this similarity difference is linked to memory performance. We calculated the Baseline and Post-learning similarity values for frequency bins from 1 to 31 Hz as follows: We computed Euclidean distance between all channel pair connectivity values of the learning period and the pre-and post-learning rest respectively, separately for each participant and frequency bin. The formula of the Euclidean distance for frequency bins is:

$$d_{sf}(A,B) = \sqrt{\sum_{c=1}^{1540} \left(A_{scf} - B_{scf}\right)^2}$$

where A and B denote the studied two connectivity matrices and the index variables *s*, *c* and *f* indicate participant, channel pair and frequency bin, respectively.

Then, we transformed these distance values into similarity values by unity-based normalization (linear transformation to shift the scale to the range of 0–1 using the minimum and the maximum values of the data to define the range) and subtracted these values from 1. As a final step, we smoothed this data over the frequency dimension using a moving average filter with a span of 3. In this way, we obtained a similarity value for each participant and each frequency bin, separately for Baseline and Post-learning similarity (Fig. 2B). The similarity values fell between 0 and 1, where higher values indicated greater similarity. We then calculated the *Learning-induced similarity change* values by subtracting the Baseline similarity values from the Post-learning similarity values, where higher values indicated greater similarity between learning and post-learning rest compared to learning and pre-learning rest. These Learning-induced similarity change values reflected the changes in the resting state functional connectivity values that appear after the learning episode compared to the pre-learning resting state. Finally, to detect associations with behavioral measures, we computed Spearman correlations between the Learning-induced similarity change values and the two consolidation indices (consolidation of serial-order and statistical knowledge) for each frequency bin (Fig. 2B). We identified candidate oscillatory frequencies based on clusters of neighboring frequency bins showing similar, significant associations with the same consolidation index.

Controlling for multiple comparisons. To account for the problem of multiple comparisons, we ran a nonparametric cluster-based permutation correction for the correlations between the consolidation indices and the Learning-induced similarity change values (Cohen, 2014). Our aim was to find neighboring frequency bins (frequency ranges) that showed similar associations between behavior and brain activity, indicating plausible oscillatory activity relevant for consolidation. The emergence of clusters of frequency bins that display similar associations can indicate true effects. Thus, we accounted for the multiple comparison problem on the cluster level. We created test statistics under the null hypothesis of no association by randomly shuffling the behavioral index for 1000 iterations and calculating correlations between these shuffled behavioral measure and the original Learning-induced similarity change values. We then created clusters for the cluster-based correction by thresholding the original and the iteration maps by a *p*-value of .025 based on the standardized Z-values of null-hypothesis test statistics (pre-

cluster threshold) and using the Matlab function 'bwconncomp' to identify clusters in each thresholded map. This yielded a distribution of the largest pre-cluster suprathreshold clusters that can be expected under the null hypothesis. As a final step, we compared the suprathreshold clusters in the original statistical values to the 95 percentile (for an alpha level of .05 corresponding to statistical significance) of the distribution of the largest clusters under the null hypothesis.

Topography of learning-induced changes. To reveal topographical patterns in the functional connections in the identified frequency ranges of interest, we computed similarity values for channel pairs (Fig. 2C). The frequency ranges of interest were identified based on the correlations between the behavioral consolidation indices and the Learning-induced similarity change values (see the 'Frequency of learning-induced changes' paragraph above). For these frequency ranges of interest, we calculated the Euclidean distance between all relevant frequency bin connectivity values in the learning period and the post-learning rest, for each participant and channel pair separately. The formula of the Euclidean distance for channel pairs is:

$$d_{sc}(A,B) = \sqrt{\sum_{f=x}^{f} \left(A_{scf} - B_{scf}\right)^2}$$

where A and B denote the studied two connectivity matrices and the index variables *s*, *c* and *f* indicate participant, channel pair and frequency bin, respectively. As there are multiple frequency ranges where we compute the distance for the channel pairs, *x* denotes the lowest frequency in each of these frequency ranges.

Again, to yield similarity values, we used unity-based normalization and subtracted the Euclidean distance values from 1. To obtain the topography of functional connections relevant to memory consolidation within the frequency ranges of interest, we computed Spearman correlations separately for each channel pair similarity value and the two consolidation indices. Note that for these channel pair correlations, we used the Post-learning similarity rather than the Learning-induced similarity change values because we computed the channel pair similarity only in the frequency ranges where this change has been accounted for. Also, as our aim was to identify topographical patterns in functional connections (rather than identifying specific connections more reliably), we did not correct for multiple comparisons in these correlation analyses. For the same purpose, we differentiated positive and negative correlations in all analyses that targeted the exploration of topographical patterns in relevant functional connections.

Patterns in topography. To identify patterns in the topography of functional connections in the relevant frequency ranges, we first aimed to investigate how the range of the connections (short- or long-range) is associated with consolidation performance. We analyzed the associations between the distances of the electrodes in the channel pairs and the correlation coefficients that were obtained between the Post-learning similarity values of those respective channel pairs and the consolidation indices. Importantly, we investigated these associations separately for the consolidation of serial-order versus statistical knowledge, for those respective frequency ranges where they showed significant associations with the EEG similarity values. To include all (positive and negative) associations in this analysis, we used the absolute values of the correlation coefficients. To test whether the distances between the electrodes in the channel pairs were associated with the strength of their correlation with the consolidation performance, we computed Spearman correlations. Next, we aimed to investigate whether differences in associations due to distance are present both for positive and negative correlations. Therefore, we differentiated between positive and negative correlations and computed Spearman correlations again separately for serial-order and statistical consolidation in the relevant frequency ranges identified in the previous analyses.

Separating the mixed resting state to eyes open and eyes closed periods. To control for potential confounding factors as a result of analyzing a mixed resting state (e.g., varying proportions of eyes closed and eyes open periods in the pre- and post-learning rest), we separated the resting state data into eyes open and eyes closed only periods. These eyes open and eyes closed periods were preprocessed and Baseline and Post-learning similarity as well as the Learning-induced similarity changes were computed for each of these conditions as described in section '2.5.2. EEG data' and Fig. 2. Note that these separately preprocessed eyes open and eyes closed periods might include slightly different time periods compared to the mixed resting state. Next, the same correlation analyses between Learning-induced similarity changes in the frequency domain measured during eyes open and eyes closed resting state only and the consolidation measures were conducted as described in the 'Frequency of learning-induced changes' paragraph of the '2.5.3. Associations between behavior and similarity in EEG functional connectivity across different periods' section. Finally, in the identified frequency ranges of interest, the same correlation analyses were computed between the Post-learning similarity values for channel pairs and consolidation measures as described in the 'Topography of learning-induced changes' paragraph of the '2.5.3. Associations between behavior and similarity in EEG functional connectivity across different periods' section.

Trait-like similarity. Finally, to contrast trait-like and learning-induced similarities, we compared the Baseline and the Post-learning similarity values (rather than their difference, the Learning-induced similarity change values) for frequency bins and their associations with behavioral indices of consolidation. If the Baseline and Post-learning similarity values and their associations with memory consolidation are comparable, the similarities likely emerge due to trait-like characteristics in brain activity. This is in contrast with higher Post-learning than Baseline similarity values that are indicative of learning-induced changes. We computed Spearman correlations (similar to the correlations described in the 'Frequency of learning-induced changes' paragraph of the '2.5.3. Associations between behavior and similarity in EEG functional connectivity across different periods' section) between the consolidation indices and the Baseline and Post-learning similarity values respectively for the frequency bins between 1 and 31 Hz. For these analyses, we again ran a nonparametric cluster-based permutation correction (described in the 'Controlling for multiple comparisons' paragraph of the '2.5.3. Associations between behavior and

similarity in EEG functional connectivity across different periods' section). Finally, to compare the strength of the correlations for each frequency bin separately for serial-order and statistical consolidation that the Baseline and Post-learning similarities exhibited with the consolidation indices, we transformed the correlations to Z-scores using Fisher's r-to-Z formula (DeCoster, 2007).

Controlling for the influence of functional connectivity of a specific period. It is possible that the correlations emerging between the similarity/learning-induced similarity change values for frequency bins and the consolidation indices were dominated by the functional connectivity of one of the periods of learning or pre-/post-learning rest. To exclude this possibility, we again computed Spearman correlations between the consolidation indices and the functional connectivity measures averaged for the frequency bins between 1 and 31 Hz separately for the pre-learning rest, learning and post-learning rest. For these analyses, we again ran a nonparametric cluster-based permutation correction (described in the 'Controlling for multiple comparisons' paragraph of the '2.5.3. Associations between behavior and similarity in EEG functional connectivity across different periods' section).

3. Results

3.1. Behavioral data

3.1.1. Overall performance trajectory

To evaluate performance changes in RTs due to learning throughout the entire task, we conducted a repeated-measures ANOVA on RTs with EPOCH (1–8) and TRIAL TYPE (pattern, random high, random low) as within-subject factors. This ANOVA showed that irrespective of trial type, RTs significantly decreased across epochs (main effect of EPOCH: $F_{7,210} = 80.748$, $p < .0001$, $\eta_p^2 = .73$), indicating increasingly faster RTs due to practice (Fig. 3A). Furthermore, participants showed significant serial-order and statistical learning (main effect of TRIAL TYPE: $F_{2,60} = 25.065$, $p < .0001$, $\eta_p^2 = .45$): they responded faster to pattern compared to random high trials ($p < .0001$), and faster to random high compared to random low trials ($p < .0001$). The EPOCH × TRIAL TYPE interaction was also significant ($F_{14,420} = 4.689$, $p = .003$, $\eta_p^2 = .14$), indicating different learning trajectories for the three trial types (see Fig. 3A). Although participants became faster for all trial types with practice, responses to pattern trials showed greater gains in comparison to both random high and random low trials: average RTs of pattern trials decreased from 355.65 to 253.98 msec ($p < .0001$), of random high trials from 376.95 to 320.52 msec ($p < .0001$), and of random low trials from 392.07 to 349.87 msec ($p < .0001$). The speed-up in responses to pattern trials was significantly larger than that to random high trials ($t_{30} = 2.72$, $p = .011$), indicating increasing serial-order learning as the task progressed. The speed-up in responses to random high compared to random low trials was also significantly larger ($t_{30} = 2.07$, $p = .047$), indicating increasing statistical learning as the task progressed.

3.1.2. Consolidation of serial-order and statistical knowledge

To evaluate the changes in the memory performance during the off-line period that followed the learning, we computed learning scores for serial-order and statistical knowledge separately (for details see the '2.5.1. Behavioral data' section). Then, we conducted a repeated-measures ANOVA on the

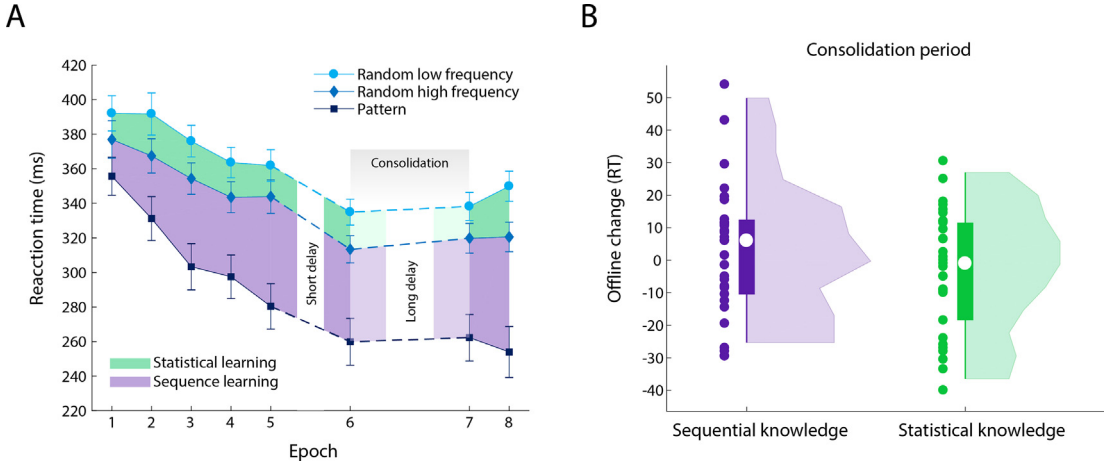

Fig. 3 – Performance in the ASRT task. A) Performance during the learning (epochs 1–5), testing (epoch 6) and retesting (epochs 7–8) periods. Median reaction times (RTs) across participants are shown for pattern (dark blue line with square symbols), random high (medium blue line with rhombus symbols), and random low (light blue line with circle symbols) trials in each epoch. Error bars denote the standard error of the mean (SEM). The difference of RTs for pattern and random high trials indicates serial-order learning (purple shading). The difference in RTs for random high and random low trials indicates statistical learning (green shading). B) Off-line changes in serial-order knowledge (purple) and statistical knowledge (green). Off-line changes were calculated as the learning scores of epoch 7 minus the learning scores of epoch 6. The plot shows the rotated probability density of these indices, the dots indicate individual data points, the bars represent data between the first and third quartiles, and the white circles within the bars show the medians.

learning scores, with EPOCH (6–7, the only epoch of the testing period and the first epoch of the retesting period) and LEARNING TYPE (serial-order learning, statistical learning) as within-subject factors. This ANOVA showed that participants exhibited overall higher scores in serial-order than in statistical knowledge (main effect of LEARNING TYPE: $F_{1,30} = 6.284$, $p = .018$, $\eta_p^2 = .17$). However, learning scores (regardless of learning type) were stable from the testing period to the first retesting epoch (main effect of EPOCH: $F_{1,30} = .064$, $p = .802$, $\eta_p^2 = .002$). Furthermore, the off-line changes (consolidation) of serial-order and statistical knowledge did not appear to be different (EPOCH × LEARNING TYPE interaction: $F_{1,30} = 1.356$, $p = .253$, $\eta_p^2 = .043$), suggesting retention of both types of knowledge in the off-line period. For further analyses, we computed consolidation indices separately for serial-order and statistical knowledge (see '2.5.1. Behavioral data' section). Notably, the variance of the consolidation indices appeared to be sufficient for subsequent analyses investigating associations between brain activity and memory consolidation performance (Fig. 3B).

3.2. *EEG data*

Both spectral power and functional connectivity analyses showed higher synchrony in the alpha frequency in the pre- and post-learning rest periods compared to the learning period (Fig. 4).

3.3. *Associations between behavior and similarity in EEG functional connectivity across different periods*

3.3.1. *Frequency-wise similarity analysis*

We computed similarity between the functional connectivity of the learning period and pre-learning rest (Baseline similarity) and the learning period and post-learning rest (Post-learning similarity) for frequencies 1–31 Hz (see Fig. 2 and section '2.5.3. Associations between behavior and similarity in EEG functional connectivity across different periods'). These Baseline and Post-learning similarity values computed for frequency bins exhibited similar patterns (Fig. 5A): They both showed on average high similarity (closer to the maximum value of 1) and a steep fall in similarity in the alpha frequency range. This drop in the similarities in the alpha frequency is expected, given the marked differences between alpha synchronization (both in spectral power and phase synchronization, Fig. 4) during learning and the pre-/post-learning resting states. To reveal changes in the resting state functional connectivity values that appear after the learning episode, we calculated Learning-induced similarity change values (the difference between the Baseline and Post-learning similarities, see also Fig. 2B). While the mean of the Learning-induced similarity change values across participants were around 0 for all frequencies, the individual differences (Fig. 5B) enabled us to compute correlations between the behavioral indices of memory consolidation and these Learning-induced change values. As we aimed to reveal associations between memory consolidation and brain activity, we focused on similarities that correlated with behavior, not the emergence of similarities per se.

3.3.2. *Frequency of learning-induced changes*

To identify the oscillatory frequencies where the Learning-induced similarity change values were associated with the behavioral indices of consolidation, we computed correlation coefficients (Fig. 6A). Consolidation of serial-order knowledge showed a significant positive correlation with the Learning-induced similarity change in the alpha frequency range (for the 8.5–9.5 Hz bins, all $rs > .43$, Fig. 6B). In contrast, consolidation of statistical knowledge was positively associated with the Learning-induced similarity change in the delta frequency (for the 2.5 and 3 Hz bins, all $rs > .42$, Fig. 6C). The sizes of these clusters did not exceed the cluster threshold based on the

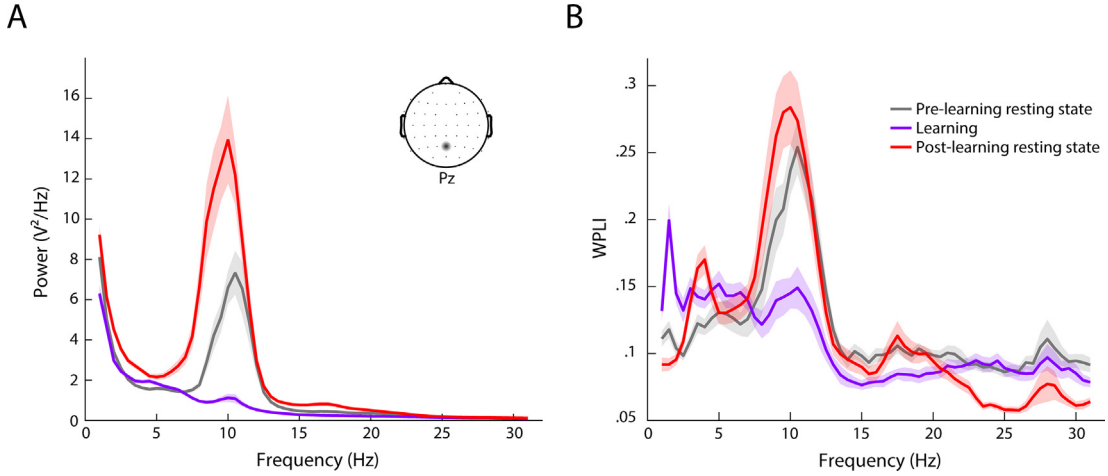

Fig. 4 – A) Example of spectral power in one channel (Pz) and B) mean connectivity (across all channels) measured by the Weighted Phase Lag Index (WPLI) for frequency bins between 1 and 31 Hz for the pre-learning rest (gray), ASRT learning (purple), and post-learning rest (red) periods. The solid lines indicate the mean across participants and the shaded error bars indicate SEM.

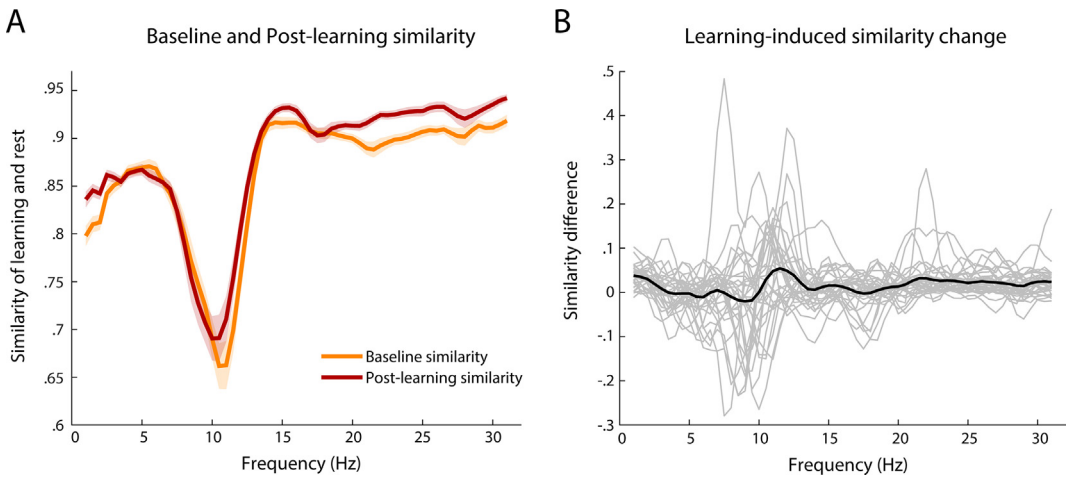

Fig. 5 – A) Similarity between connectivity matrices of the learning period and the pre-learning rest (Baseline similarity), and the learning period and the post-learning rest (Post-learning similarity) for frequency bins. Baseline and Post-learning similarity exhibited similar patterns. The solid lines indicate the mean and the shaded error bars indicate the SEM for Baseline (orange) and Post-learning (burgundy) similarity. B) Learning-induced similarity change was calculated as the Post-learning similarity values minus Baseline similarity values, with larger values indicating greater similarity between the learning period and post-learning rest than between the learning period and pre-learning rest. Thinner gray lines represent each participant, while the thicker black line indicates the mean averaged across all participants.

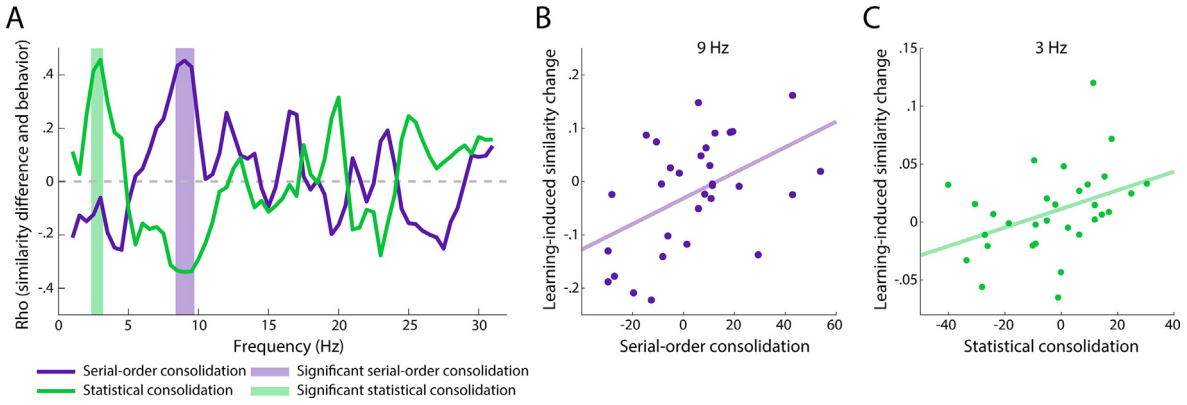

Fig. 6 – A) Correlation (Spearman Rho) between the behavioral indices of consolidation and the Learning-induced similarity change values (the difference between the Baseline and Post-learning similarity). Purple and green lines indicate associations with serial-order and statistical consolidation, respectively. The shading denotes the significant ($p < .05$, uncorrected) correlations. B) Positive correlation between the Learning-induced similarity change value at 9 Hz and the consolidation of serial-order knowledge. C) Positive correlation between the Learning-induced similarity change value at 3 Hz and the consolidation of statistical knowledge. On B) and C), the dots represent individual data points for each participant and the lines are linear trendlines.

permutation testing (with the threshold being 5 frequency bins for both serial-order and statistical consolidation). Nevertheless, the original significance levels ($p = .015$, .010 and .016 for serial-order consolidation at the frequency bins of 8.5, 9 and 9.5, and $p = .020$ and .098 for statistical consolidation at the frequency bins of 2.5 and 3) and the similar associations between neighboring frequency bins suggest that these clusters may be interpreted as meaningful. Specifically, these results suggest that the more similar the functional connections between the learning period and post-learning rest were compared to the learning period and the pre-learning rest in the alpha and delta frequencies, the better the consolidation was for serial-order and statistical knowledge, respectively.

3.3.3. *Topography of learning-induced changes*

Next, we aimed to reveal patterns in the topography of functional connections that were present both during learning and post-learning rest and could indicate reactivation (see Fig. 2C and section '2.5.3. Associations between behavior and similarity in EEG functional connectivity across different

periods'). We computed channel pair similarities within the frequency ranges where the Learning-induced similarity change values showed significant associations with the consolidation indices (alpha and delta). As we showed that higher Post-learning similarity compared to Baseline similarity in these frequency ranges is positively associated with memory consolidation, it is conceivable that Post-learning channel pair similarities in these frequency ranges are indicative of learning-induced changes (possibly spontaneous reactivation). To find channel pairs where the similarity is associated with the consolidation indices, we computed correlations: 1) correlation between channel pair similarity in the alpha frequency range (8.5–9.5 Hz) and the consolidation of serial-order knowledge, and 2) correlation between channel pair similarity in the delta frequency range (2.5–3 Hz) and the consolidation of statistical knowledge. Consolidation of serial-order knowledge showed significant positive correlations with channel pair similarity in the alpha frequency range over the whole brain, particularly at centro-parietal channel pairs (Fig. 7A). In contrast, the consolidation of statistical knowledge mainly exhibited significant negative correlations with channel pair similarity in the delta frequency over the whole brain, particularly over posterior and lateral sites (Fig. 7B).

3.3.4. *Patterns in topography*

Next, we aimed to explore patterns in the correlations between channel pair similarities and memory consolidation. More specifically, we tested whether the strength of the associations between the channel pair similarities and the consolidation indices vary as a function of the topographical distance of the functional connections (i.e., short *vs* long range connections). Importantly, we investigated these associations separately for the consolidation of serial-order and statistical knowledge, for the respective frequency ranges where they showed significant associations with the similarity values. Note that we included all correlation coefficients in subsequent analyses, not only the significant ones depicted in Fig. 7A and B.

The correlation coefficients between serial-order consolidation and the channel pair similarity values in the alpha frequency range showed a significant positive correlation with the distance of the electrodes in the channel pairs ($r = .22$, $p < .001$) indicating that longer range connections in the alpha frequency were more relevant for the consolidation of serial-order knowledge. When considering the direction of correlations (positive or negative correlation coefficients), we found that only the positive correlations were significantly associated with the distance of the electrodes ($r = .22$, $p < .001$, negative correlations: $r = -.08$, $p = .324$). Thus, the stronger associations between the consolidation of serial-order knowledge and longer range connections in the alpha frequency were led by positive correlation coefficients (Fig. 7C).

The correlation coefficients between statistical consolidation and the channel pair similarity values in the delta frequency range exhibited a significant negative correlation with the distance of the electrodes in the channel pairs ($r = -.09$, $p < .001$) indicating that shorter range connections in the delta frequency were more relevant for the consolidation of statistical knowledge. When considering the direction of correlations (positive or negative correlation coefficients), we found that only negative correlations were significantly associated with the distance of the electrodes ($r = .16$, $p < .001$, positive correlations: $r = .02$, $p = .724$). Thus, the stronger associations between the consolidation of statistical knowledge and shorter range connections in the delta frequency were led by negative correlation coefficients (Fig. 7D).

3.3.5. *Separating the mixed resting state into eyes open and eyes closed periods*

The eyes open and eyes closed resting states displayed different synchronization patterns (as indicated by WPLI) pronounced especially in the alpha frequency range, where the average connectivity was greater for both pre- and post-learning rest for the eyes closed compared to the eyes open periods (Fig. S1A and B). Accordingly, Baseline and Post-learning similarities also presented differently, albeit a general drop in similarities in the alpha frequency was observed both in the case of eyes open and eyes closed resting periods (Fig. S1C and D). Importantly, the variance in the Learning-induced similarity change values across participants was sufficient to compute correlations with the behavioral indices of memory consolidation for both eyes open and eyes closed rest periods (Fig. S1E and F).

To test whether the eyes open and closed rest periods separately exhibit similar associations with the behavioral indices of consolidation as the mixed resting state, we first computed correlation coefficients between these Learning-induced similarity change values and the consolidation indices. Similar to the results with the mixed resting state, the consolidation of serial-order knowledge showed a significant positive correlation with the Learning-induced similarity change in the alpha frequency range (for the 8.5–9.5 Hz bins) for the eyes closed resting periods (Fig. 8A). Again, the size of this cluster did not exceed the cluster threshold based on the permutation testing (with the threshold being 5 frequency bins). In contrast, consolidation of statistical knowledge was positively although not significantly associated with the Learning-induced similarity change in the delta frequency (for the 2.5 and 3 Hz bins) in the eyes open resting periods (Fig. 8B).

Exploring the topographic patterns of these associations, the Post-learning similarity values for channel-pairs in the alpha frequency range showed similar significant positive correlations with serial-order consolidation over the whole brain, particularly at centro-parietal channel pairs in the eyes closed periods as in the mixed resting state (Fig. S2A). Post-learning similarity values for channel-pairs in the delta frequency range also showed similar significant negative correlations with statistical consolidation over the whole brain, particularly over posterior and lateral sites in the eyes open periods as in the mixed resting state (Fig. S2B).

These results indicate that the findings using the mixed resting state are not a result of artifacts caused by EEG non-stationarity or varying proportions of eyes open and eyes closed periods, as the same associations were present when taking eyes open only or eyes closed only periods of the resting states. The results also highlight that the association between serial-order consolidation and Learning-induced changes in the alpha frequency is driven by the eyes closed rest periods, whereas the association between statistical

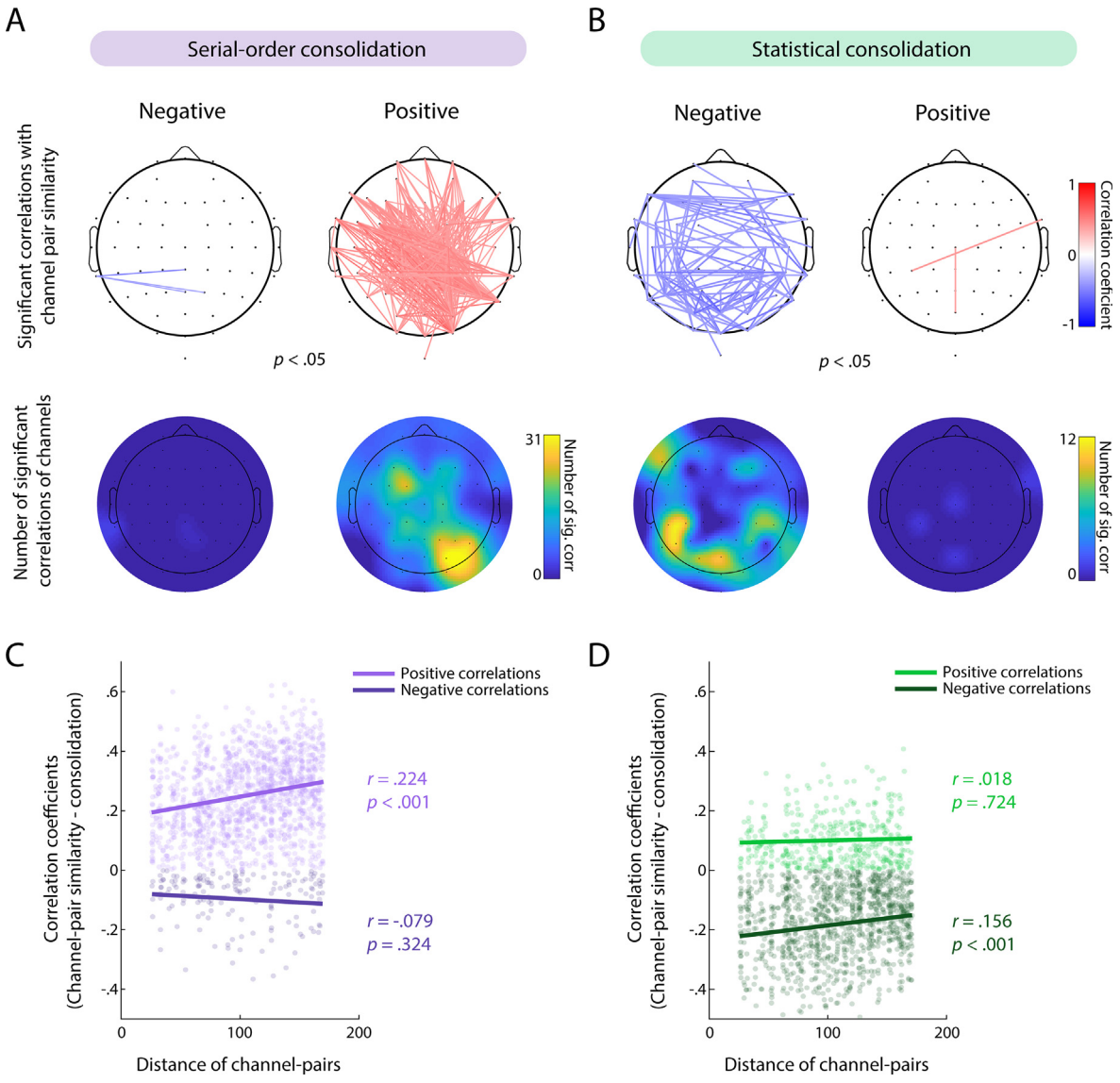

Fig. 7 – A) Topography of significant correlations between the consolidation of serial-order knowledge and Post-learning similarity for channel pairs in the (8.5–9.5 Hz) alpha frequency range. B) Topography of significant correlations between the consolidation of statistical knowledge and Post-learning similarity for channel pairs in the (2.5–3 Hz) delta frequency range. In the upper panel, significant ($p < .05$, uncorrected) positive and negative correlations are shown. In the lower panel, for each channel, the number of significant correlations in which the given channel appears is shown separately for positive and negative associations. C–D) Strength of the correlations between the Post-learning channel pair similarity values and the behavioral indices of consolidation as a function of the distance between the electrodes (Euclidean distance of the Cartesian coordinates of the electrodes) of the channel pairs. C) For the consolidation of serial-order knowledge (purple), associations with the Post-learning similarity values in the alpha frequency range are shown. D) For the consolidation of statistical knowledge (green), associations with the Post-learning similarity values in the delta frequency range are shown. Linear trendlines for the distance of the electrodes in the channel pairs and the correlation strength of the similarities of those channel pairs with the consolidation indices of serial-order (C) and statistical (D) knowledge are shown, separately for positive (lighter color) and negative (darker color) correlations. The dots indicate individual correlation coefficients for each channel pair. Serial-order consolidation exhibited a stronger positive association with longer-range connections, whereas statistical consolidation exhibited a stronger negative association with shorter range connections. Note that this analysis is conducted using all correlation coefficients, not only the significant ones depicted in A & B.

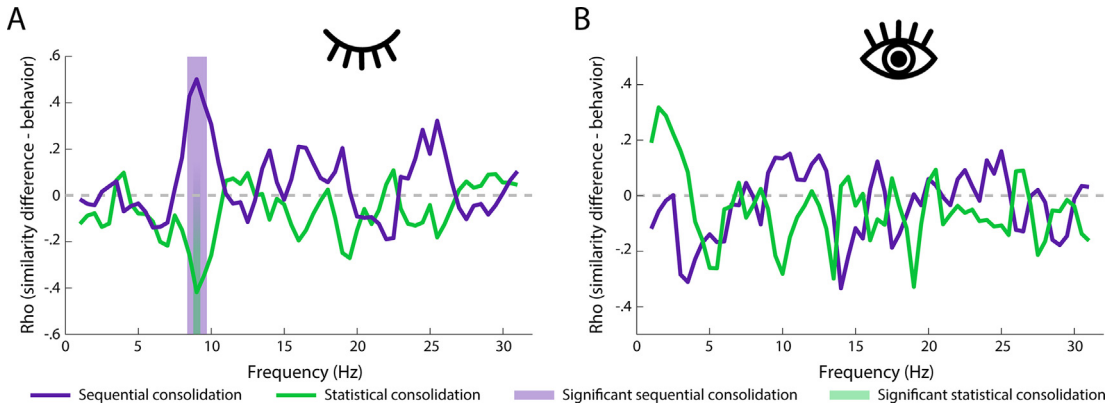

Fig. 8 – Correlation coefficients (Spearman Rhos) between the behavioral indices of consolidation and the Learning-induced similarity change values (difference between the Baseline and Post-learning similarity) for eyes closed A) and eyes open B) periods. Purple and green lines indicate associations with serial-order and statistical consolidation, respectively. The shading denotes the significant ($p < .05$, uncorrected) correlations.

consolidation and Learning-induced changes in the delta frequency was stronger in the eyes open rest periods.

3.3.6. Trait-like associations between behavior and similarity in EEG functional connectivity across different periods

To disentangle learning-induced versus trait-like similarities, we compared Baseline and Post-learning similarity for frequency bins and their associations with the consolidation indices. If the Baseline similarity (that is, the similarity of functional connectivity during learning and pre-learning rest) and its relation to memory consolidation is comparable to Post-learning similarity (that is, the similarity of functional connectivity during learning and post-learning rest), the resemblance may have emerged from stable individual characteristics in brain activity. Fig. 5A shows similar patterns for Baseline and Post-learning similarity computed for frequency bins. To compare the associations of Baseline and Post-learning similarity, we conducted the same correlation analyses with the consolidation indices for these similarity values as we computed for the Learning-induced similarity change values in the 'Frequency of learning-induced changes' paragraph of section '2.5.3. Associations between behavior and similarity in EEG functional connectivity across different periods'. The consolidation of serial-order knowledge showed a significant positive correlation in the alpha frequency range (for the 9.5–10.5 Hz bins) with Post-learning similarity (Fig. 9A). Similar to the results of the Learning-induced similarity change values, the size of this cluster did not exceed the cluster threshold (7 frequency bins) based on the permutation testing. The pattern of the associations of the consolidation of serial-order knowledge with the Baseline and the Post-learning similarity measures was similar, however, the effects were weaker and not significant for the Baseline similarity in the alpha frequency range (Fig. 9A). The

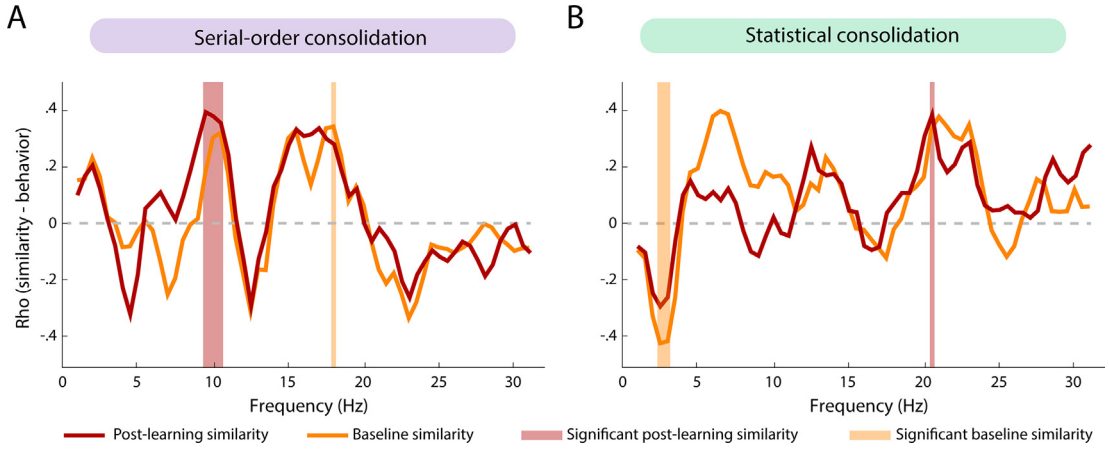

Fig. 9 – Correlation coefficients (Spearman Rhos) of Baseline (orange) and Post-learning (burgundy) similarity and the consolidation indices of serial-order (A) and statistical (B) knowledge. The patterns of the associations of the consolidation of serial-order and statistical knowledge were similar over the Baseline and the Post-learning similarity measures. The shading denotes significant ($p < .05$, uncorrected) correlations.

statistical comparison of the correlations between serial-order consolidation and the Baseline and Post-learning similarity values revealed significant differences in the alpha frequency range (9 Hz: $Z = 2.23$, $p = .025$, 9.5 Hz: $Z = 2.20$, $p = .028$). The remaining 59 correlations (out of 61) of the consolidation of serial-order knowledge were not significantly different for the Baseline and Post-learning similarity values (all $ps > .07$). The consolidation of statistical knowledge showed a significant negative correlation in the delta frequency range (2.5–3 Hz) with the Baseline similarity values (Fig. 9B). Similar to the results of the Learning-induced similarity change values, the sizes of the clusters in this analysis did not exceed the cluster threshold (7 frequency bins) based on the permutation testing. Again, the pattern of the associations of the consolidation of statistical knowledge with the Baseline and the Post-learning similarity measures was similar, however, the effects were weaker and not significant for the Post-learning similarity in the delta frequency range (Fig. 9B). The statistical comparison of the correlations between statistical consolidation and the Baseline and Post-learning similarity values did not reveal significant differences in the delta frequency range (1–4 Hz, all $ps > .15$), however significantly different correlations emerged in the lower alpha frequency range (7.5–9.5 Hz, all $ps < .05$). The remaining 56 correlations (out of 61) between statistical consolidation and the Baseline and Post-learning similarity values were not significantly different (all $ps > .07$). The similar pattern of the Baseline and Post-learning similarity per se (Fig. 5) and the similar patterns of their associations with the consolidation indices (Fig. 9) suggest that trait-like associations exist between the brain activity during different periods and memory consolidation.

Besides the trait-like associations, these analyses also unraveled the dynamics of the associations of the Learning-induced similarity changes in more detail: The positive correlation between the Learning-induced similarity change values and memory consolidation (Fig. 6) occurred for different reasons in alpha and delta frequency. In the alpha frequency, both the Baseline and the Post-learning similarity values showed positive correlations with the consolidation of serial-order knowledge, however, it was stronger for the Post-learning similarity. In contrast, in the delta frequency, both the Baseline and the Post-learning similarity values showed negative correlations with the consolidation of statistical knowledge, however, it was weaker for the Post-learning similarity.

3.3.7. *Controlling for the influence of functional connectivity of a specific period*

Importantly, the associations between the consolidation indices and similarity/learning-induced similarity change values were not led by the functional connectivity of the learning (or pre- or post-learning rest) period, as the correlation of the consolidation indices with these functional connectivity values showed different patterns from the similarity/learning-induced similarity change values (Fig. 10 cf. Fig. 6A, Fig. 9). The sizes of the clusters emerging from the correlations with these connectivity matrices did not reach the threshold (5, 7 and 6 frequency bins for Pre-learning rest, Learning and Post-learning rest connectivity, respectively, both for serial-order and statistical consolidation) based on the permutation testing.

4. Discussion

Our results showed that higher similarity in functional connectivity patterns between learning and post-learning rest compared to pre-learning rest (termed Learning-induced similarity change) in the alpha frequency range (8.5–9.5 Hz) is predictive of the consolidation of serial-order knowledge. At the same time, Learning-induced similarity change in the delta frequency range (2.5–3 Hz) was positively associated with the consolidation of statistical (probability-based) knowledge. The topographical analyses within these frequency ranges highlighted the involvement of long-range centro-parietal connections in the consolidation of serial-order knowledge and shorter-range connections in the consolidation of statistical knowledge.

Beyond these learning-induced changes, we also compared the similarity matrices themselves and their associations with memory consolidation to explore trait-like similarities. Similarities in functional connectivity of learning and post-learning rest (Post-learning similarity) and learning and pre-learning rest (Baseline similarity) exhibited similar patterns, and showed comparable associations with the consolidation indices, indicating the existence of trait-like resemblance.

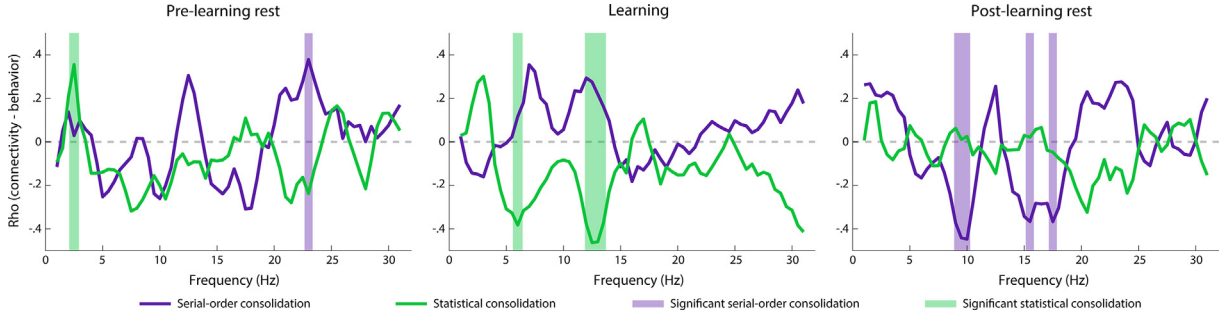

Fig. 10 – Correlation coefficients (Spearman Rhos) between behavioral indices of consolidation and EEG functional connectivity measured as the Weighted Phase Lag Index (WPLI) during pre-learning resting state (left), learning (middle) and post-learning resting state (right). Purple and green lines indicate associations with the consolidation of serial-order and statistical knowledge, respectively. The shading denotes significant ($p < .05$, uncorrected) correlations.

Furthermore, these comparisons shed light on two different dynamics underlying the positive correlations between the Learning-induced similarity change values and the consolidation indices: In case of serial-order knowledge, better consolidation was associated with the strengthening of a positive correlation (beneficial effect) between the similarity values and the consolidation index from Baseline to Post-learning similarity, whereas in case of statistical knowledge, better consolidation was associated with the weakening of a negative correlation (detrimental effect).

Our results suggest that learning-induced changes in alpha synchronization are associated with the consolidation of serial-order (but not probability) information (Fig. 6). How did alpha synchronization change over the different periods and what part of these changes were relevant for memory consolidation? Concerning the former, alpha synchronization was higher during both resting states than during learning and was higher during post-learning rest than during the pre-learning rest (Fig. 4). Similar to our study, Murphy et al. (2018) showed higher synchrony (albeit measured by spectral power rather than phase synchronization) in alpha frequency during post-learning rest compared to pre-learning rest. Importantly, this was only true when there was a learning episode involved between the two resting states (not when other cognitive tasks were completed). Concerning the relevant changes in alpha synchronization, the beneficial (higher) similarity between learning and post-learning rest could occur due to a smaller increase in (and thus relatively lower) alpha synchronization during post-learning rest (as alpha synchronization is lower during learning than the resting state periods, see Fig. 4B). In accordance with this, the correlation of the functional connectivity of learning and post-learning rest with memory consolidation showed that higher connectivity in the alpha frequency of post-learning rest negatively correlates with the consolidation of serial-order knowledge (Fig. 10). Thus, the associations with the similarity (Fig. 6) are most likely led by relatively lower alpha synchronization during the post-learning rest. This is in line with the study of Brokaw et al. (2016), which showed that greater alpha synchronization (again indexed by spectral power rather than phase synchronization) during rest following a declarative learning task was negatively correlated with subsequent recall performance. In other words, higher alpha synchronization was detrimental during the post-learning rest period for memory retention. Altogether, these results suggest that alpha synchronization increases after learning, but individuals showing a smaller increase in alpha synchronization have better memory consolidation.

Importantly, similarity in functional networks can occur not only due to generally higher or lower synchronization but also dynamics in synchronization that are present during different periods. The functional role of the alpha rhythm [i.e., excitatory (Palva & Palva, 2007) or inhibitory (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007)] seems to depend on phase dynamics (Palva & Palva, 2011), firing modes (Peterson & Voytek, 2017) and behavioral states (Alamia & VanRullen, 2019). Thus, similarity in alpha synchronization during learning and subsequent resting state could reflect reactivated or maintained brain dynamics in some of these additional factors (e.g., phase dynamics, firing modes).

Why learning-induced changes relevant for the consolidation of serial-order information were found in alpha frequency? Von Stein and Sarnthein (2000) suggested that the longer the range of the cortical connections, the slower the oscillatory frequency is through which they synchronize; that is, alpha as a relatively slow oscillation has been proposed to have a large-scale integrative function. Based on the tasks that involve higher alpha synchronization (e.g., mental imagery, working memory, resting state), they suggested that greater alpha synchronization reflects internal mental activity and may be responsible for top-down cognitive processes. Top-down here refers to the flow of information processing: For top-down processes, the sensory processing is influenced by higher-order cognition, i.e., it is model-dependent/hypothesis-driven, whereas for bottom-up processes, sensory processing is driven by the stimuli, i.e., it is model-free. In support of the role of alpha in top-down processing, it has been shown that alpha propagates from higher- to lower-order cortex and from cortex to thalamus (Halgren et al., 2019), providing a circuit for top-down processes. Our results are in line with the findings that show the role of alpha in top-down processes as we demonstrated that synchronization in alpha frequency is important for serial-order memory consolidation, which in our study was a top-down, attention-demanding process, whereas it did not show association with statistical learning, which is a bottom-up, stimulus-driven process (Nemeth et al., 2013). The topographical distribution of relevant phase synchronization in alpha frequency (Fig. 7) is also consistent with the integrative/top-down function of alpha oscillation in serial-order memory consolidation: Based on the channel pair similarity correlations in alpha frequency, our results indicate that long-range, centro-parietal connections are important for this type of memory. This is also in line with previous studies investigating the neural background of serial-order learning that seems to at least partially rely on fronto-parietal networks (Doyon et al., 2009; Sakai et al., 1998).

In contrast to the consolidation of serial-order knowledge, the consolidation of statistical knowledge showed associations with the learning-induced changes in the delta frequency range. However, this change was a weakening detrimental effect, i.e., decreasing adverse association between the consolidation of statistical knowledge and similarity from Baseline to Post-learning similarity. Why learning-induced changes relevant for the consolidation of probability information were found in delta frequency? Delta oscillation during cognitive tasks has been proposed to play a role in inhibiting interferences that may affect task performance (Harmony, 2013). Together with the topography of connections that correlated (negatively) with statistical learning, this suggests that the inhibition of the left, in particular parietal sites is beneficial for statistical memory. This is in line with studies showing that the right hemisphere is important for statistical learning (Janacsek, Ambrus, Paulus, Antal, & Nemeth, 2015; Roser, Fiser, Aslin, & Gazzaniga, 2011; Shaqiri & Anderson, 2013).

The learning-induced changes assessed in our study could emerge partly due to reactivation. However, the definition of

reactivation should be understood broadly in our study, as the similarities discussed here could occur as a result of reactivation of the memory traces per se, the reactivation of the overall learning experience, or the reactivation of the cognitive set in general during the learning episode.

Lastly, our results draw attention to the great overlap of active functional networks during a task and preceding/subsequent resting states. This inherent overlap has practical and theoretical implications. On the practical level, a larger sample size might be necessary to study learning-induced changes as the differences in functional networks from pre- to post-learning rest are small compared to the overall similarities. On the theoretical level, similarities during different behavioral states have been largely neglected in previous studies investigating reactivation (as reactivation is traditionally defined by the unique overlap between the learning and the post-learning off-line period). However, the functional brain networks that are present during other behavioral states might also be important for memory consolidation. We argue that not only reoccurring, but also stable, trait-like brain networks are important for cognitive performance, particularly for memory consolidation. For example, studies have shown that there is little difference between functional connectivity networks during resting state and a task measured via fMRI (Cole et al., 2016; Satterthwaite et al., 2018). Gratton et al. (2018) concluded that functional networks are dominated by stable individual factors, not cognitive content. Our results are in line with these fMRI results and demonstrate that these trait-like, stable networks can also be captured by EEG and support memory consolidation.

While our results alone cannot reveal the precise mechanism through which stable functional networks contribute to cognitive performance, we speculate that a possible mechanism could be the existence of preparatory networks in the brain that can be recruited during a cognitive task. This 'pre-activation' mechanism could be the functional network analog of a similar phenomenon: the preplay (Dragoi & Tonegawa, 2011, 2013; Silva, Feng, & Foster, 2015). In the case of a preplay, a specific sequential neuronal firing that is revealed during learning and subsequently during replay occurs before the learning episode itself. Dragoi and Tonegawa (2011) proposed that the role of preplay is to facilitate future learning by providing neural sequences naturally present in the neural network to be utilized during a learning experience to store new memory traces. Similarly, in the case of functional connectivity, 'preactivation' could manifest as a pre-existing functional network that would serve as a building block for functional networks to emerge during learning and that could subsequently be strengthened by reactivation (or other consolidation mechanisms). Nevertheless, further studies are warranted to reveal whether such supportive preparatory networks exist.

4.1. *Limitations*

The sizes of the clusters that we revealed in the frequency-wise comparisons did not reach the threshold computed by permutation testing. This implies that these clusters could have occurred by chance. It is important to note, however, that our method to reach that threshold is more conservative, as we compared the distribution of the largest cluster sizes occurring under the null hypothesis in opposition to the distribution of all cluster sizes occurring. Furthermore, we corrected only for the size of the clusters, not considering the effect sizes in those clusters which could further influence the results. Lastly, we set the pre-cluster threshold to a standard value (rather than fitting it arbitrarily to our data), which is important as the value of the pre-cluster threshold strongly influences the results of this correction. Therefore, the inference from our results should take into account the conservative parameters used in our analyses. We argue that the natural clustering in our data and the large effect sizes (especially for brain-behavior correlations) observed in the original comparisons provided sufficient evidence to interpret our results as meaningful. Nevertheless, our results should be treated with caution until further replication.

Another limitation of our study is that the post-learning rest is necessarily different from the pre-learning rest as it occurs later in time. Differences in brain activity from pre- to post-learning rest may be influenced by factors such as fatigue, sleepiness, relaxation, or time-of-day effects. However, our results are primarily based on the associations between brain activity and memory performance, and it is unlikely that these factors account for such correlations, even if they do affect brain activity.

Finally, our results in the alpha frequency could be influenced by participants falling asleep during our long post-learning period. Falling asleep diminishes alpha synchronization which seemed beneficial according to our results as well as sleep could benefit memory consolidation. We believe, however, that this could not be the case, as two experienced sleep-scorers verified participants staying awake during the post-learning rest. The two participants who did enter Stage 1 sleep were excluded from the analyses. Nevertheless, we cannot rule out the effects of local or microsleeps (Hung et al., 2013; Vyazovskiy et al., 2011).

4.2. *Conclusions*

Our results show that learning-induced changes in resting functional networks after learning differentially predict memory consolidation of serial-order and probability information acquired simultaneously: Learning-induced changes in alpha synchronization were associated with the consolidation of serial-order, whereas learning-induced changes in delta synchronization were associated with the consolidation of probability information. Long-range functional connections in the alpha frequency seem to be important for the consolidation of serial-order knowledge, potentially due to the involvement of top-down processes in this type of learning, requiring the synchronization of distant brain areas. In contrast, consolidation of statistical (probability-based) knowledge seems to rely on local synchronization, potentially due to the involvement of bottom-up, stimulus-driven processes that are less dependent on long-range synchronization. Finally, patterns of similarities between learning and pre- and post-learning rest (and their associations with consolidation performance) showed great overlap. This implies that in parallel with reoccurring brain dynamics, pre-existing or maintained networks are also important for cognitive performance,

particularly for memory consolidation. Lastly, our study provided a framework for studying memory consolidation in its complexity, incorporating the simultaneous consolidation of different information as well as the influence of learning-induced changes and stable characteristics of brain activity.

Data and code availability statement

The data and code that support the findings of this study are openly available on OSF at https://osf.io/j36s4/.

Other statements

No part of the study procedures or analyses was preregistered 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.

Open practices

The study in this article has earned Open Data and Open Materials badges for transparent practices. The data and materials are available at: https://osf.io/j36s4/.

CRediT authorship contribution statement

Zsófia Zavecz: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Karolina Janacsek:** Writing – review & editing, Software, Methodology, Conceptualization. **Peter Simor:** Writing – review & editing, Methodology, Conceptualization. **Michael X. Cohen:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Dezso Nemeth:** Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2024.07.008.

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