Daytime experiences shape neural activity and dream content in the sleeping brain

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Learning-related brain activity patterns are replayed during sleep, and memories of recent experiences appear in our dreams. The connection between these phenomena, however, remains unclear. We investigated whether memory reinstatement during sleep contributes to dreaming. Participants listened to audiobooks before falling asleep. We could determine which audiobook they had studied based on dream reports collected during the night. Audiobook content was also reinstated at the neural level, in high-density EEG recordings. Brain activity during rapid eye movement sleep, particularly in the high-frequency beta range, carried information about the audiobook and simultaneously benefitted memory retention. Crucially, when the learning condition was manifest in neural activity, it also emerged in dreams. Reprocessing of daytime experiences during sleep thus shapes our brain activity, our dreams, and our memories.

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Introduction

Sleep is an active state during which the brain processes new experiences in service of long-term memory storage (1–3). Dreams let us relive aspects of daytime experience (4, 5), and neuronal replay during sleep strengthens and transforms recent memories (6–9). It has been proposed that the fragments of daytime episodes that resurface in dreams could reflect the neural reactivation of those experiences (5, 10, 11). Whether the integration of memories into dreams depends on their neural reactivation and is thus instrumental to memory consolidation, however, remains elusive.

Converging evidence demonstrates spontaneous reactivation of newly encoded memories in the sleeping brain (8). Such experience-dependent reactivations have been observed in both animals and humans. In rodents, neural activity patterns in the hippocampus and neocortex during NREM (non-rapid eye movement) sleep (9, 12) and REM sleep (13, 14) reflect pre-sleep experience. Similarly, spontaneous human brain activity in both REM (15) and NREM sleep (8, 16, 17) reflects previously encoded information and benefits later memory performance. Furthermore, externally inducing reactivation of a previous memory task by auditory or olfactory cues during sleep boosts memory retention in REM and NREM sleep (18–20). Interestingly, these findings parallel evidence showing learning-related events resurfacing in dreams (4). It has been shown that extensive daytime activities, like playing Tetris for several hours, influence hypnagogic imagery at sleep onset (21). Another study observed that the content of sentences presented in an intensive study session before sleep was incorporated more often into dreams than that of other sentences (22). Dreaming of a learning task, such as navigating a virtual maze, can also improve participants' performance in later memory tests (23, 24). Although these findings have led to the proposal that memory reprocessing during dreams could support memory consolidation during sleep, the questions of how neural reactivation of learning content is associated with our dreaming experience and how this benefits memory consolidation, remain open.

We devised an experimental paradigm to investigate whether daytime experiences are reactivated during sleep, both in neural activity and in dreaming. Participants were presented with one of four different audiobooks while falling asleep (**Fig. 1A**). This systematic manipulation of pre-sleep experience was aimed at introducing dissociable brain activity as well as dreams during the ensuing sleep period. After sleeping for one 90-min sleep cycle, the participants were awoken to report their dreams and retrieve the previously presented audiobook content (**Fig. 1A**). This procedure was repeated multiple times during the night, with high-density EEG recorded throughout the experiment. We predicted that the narrative of the audiobooks should not only shape brain activity, but also the content of the dreams our participants experienced during sleep. We thus used pattern analyses to investigate whether spontaneous electrical brain activity during sleep holds information about the content of the recently encoded audiobook narratives (**Fig. 1B**), and had blind raters judge, based on the dream reports alone, which audiobook the participants had encoded before going to sleep (**Fig. 1C**). Crucially, if neural reactivation shapes the content of our dreams, we should observe a stronger neural processing signal in those participants who dreamt of the audiobook.

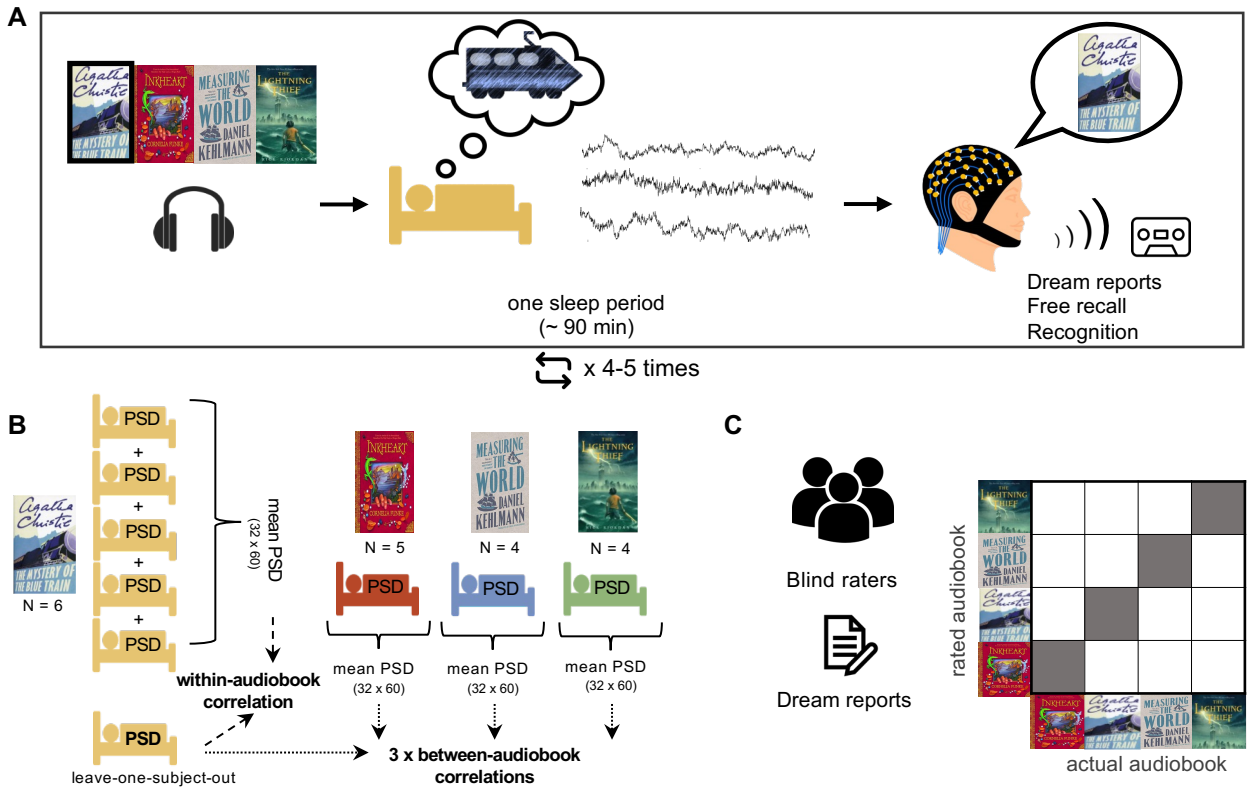

Fig. 1. Experimental procedure. A. During encoding, participants were presented with one of four audiobooks (e.g., The Mystery of the Blue Train by Agatha Christie). While participants fell asleep, EEG was recorded using active electrode 128-channel EEG. After 90 min of sleep, participants were awoken. First, they were asked for their dreams. Next, they then had to freely recall the audiobook content they had listened to while falling asleep. Finally, they indicated which sections of the audiobook they recognized. The whole procedure was repeated up to five times over the night. **B.** We assessed representational similarity between participants using power spectral density (PSD) within and between audiobook conditions in a leave-one-subject-out approach. The within-audiobook correlation was calculated as the Spearman correlation between the average sleep PSD (dimensions: 32 channel x 60 Hz) of one individual and the average PSDs of all remaining participants in the same audiobook condition. The between-audiobook correlations were computed between the average PSD of the left-out subject and the averaged PSDs of all participants in each other audiobook condition, respectively. Results of all subjects were averaged for all possible within- and between-audiobook correlations. Finally, we computed corr as the difference between within- and between-condition correlations. A higher corr indicates higher similarity of neural activity between subjects in the same audiobook condition and is a measure for audiobook reinstatement in sleep EEG. **C.** We also assessed whether the specific content of an audiobook is reprocessed in subsequent dreams: three blind raters were presented with isolated, anonymized dream reports and asked to judge which audiobook each participant had listened to before this dream.

Daytime experiences shape dream content during sleep

Our first prediction was that the narrative of an audiobook should shape the content of ensuing dreams. To assess whether the specific narrative of an audiobook is reactivated in dreams, three independent and blind human raters were asked to judge which audiobook each participant had listened to before having a particular dream. The blind raters were able to determine which audiobook the participants had listened to before sleep with above-chance-level accuracy based solely on their dream reports. We found significant concordance between the rated book and the actual audiobook participants had listened to ($\kappa = 0.107$, $z = 2.29$, $P = 0.02$, interrater agreement = 32.9%, (**Fig. 2**). We went on to test whether dreams collected after awakenings from REM and NREM sleep equally carried experience-driven information. Notably, it was REM dreams in particular that contained information about the previous audiobook. Raters were able to determine the correct audiobook based on dream reports collected after REM sleep awakenings ($\kappa = 0.343$, $z = 2.88$, $P = 0.003$, interrater agreement = 54.2%, **Fig. S1A**). However, they were unable to do so above chance level based on dream reports collected after NREM sleep awakenings ($\kappa = 0.08$, $z = 1.43$, $P = 0.154$, interrater agreement = 31.5%, **Fig. S1B**). Daytime experiences thus impact our dreams during later sleep.

Daytime experiences shape neural activity during sleep

Next, to test whether our experiences also shape neural activity in the sleeping brain, we investigated whether spontaneous electrical brain activity during sleep holds information about the previously played audiobook. For this, we assumed, based on previous findings, that brain activity that is influenced by similar experience will have similar features (8, 25). We therefore extracted the spatial pattern of brain oscillatory activity in different frequency bands (power spectral density, PSD) from sleep EEG, for REM and NREM, respectively. Correlating brain activity patterns between participants in a representational similarity analysis (RSA, **Fig. 1B**), we found that during REM sleep, brain activity was more similar between participants if they had listened to the same audiobooks than if they had listened to different books

(Δcorr = 0.063). Calculating permutation statistics by performing the same analyses with the effect of the audiobook removed by shuffling the condition labels across participants confirmed that the previous experience systematically shaped brain activity during REM sleep (Δcorr = 0.063, $P = 0.039$, **Fig. 3A**). We did not find similar evidence of memory reprocessing in NREM sleep (Δcorr = -0.052, $P = 0.785$, **Fig. 3A**). To test the robustness of our findings, we repeated all analyses with two variant approaches to RSA data processing, confirming the results (**Fig. S2**, **Fig. S3**). Information about previous learning content can thus be detected in sleep, demonstrating that daytime experiences are reinstated at the neural level.

Higher frequency EEG activity reflects memory reinstatement during REM sleep

To find out which aspects of the neural signal contribute to memory reactivation in REM sleep, we performed a frequency-of-interest (FOI) analysis on EEG activity in different frequency bands. We removed all audiobook condition information from specific EEG frequencies in the power spectrum between 0.05 and 30 Hz, by randomly re-assigning these parts of the signal between participants. If this procedure significantly lowers similarities between participants who listened to the same audiobook, the respective frequency band contains information about the narrative content and thus reflects the processing of the audiobook during sleep. Our results show that high-frequency beta activity (18–30 Hz) is critically involved in reprocessing of audiobook content during REM sleep ($P = 0.006$, **Fig. 3B**). We further confirmed this finding by performing RSA analyses on brain activity from the FOI range only. Again, only activity in the 18–30 Hz beta band contained information about the previously presented audiobook (**Fig. S4**). We thus suggest that high-frequency brain activity could serve as a neural fingerprint of memory reinstatement in human REM sleep.

Linking neural reinstatement and memory

Finally, to examine whether memory processing during sleep is associated with retention of the audiobook content, we correlated free recall and recognition performance for passages from the audiobook with EEG beta activity (18–30 Hz). Beta activity was positively correlated both with free recall performance ($r = 0.55$, $P = 0.01$) and recognition memory ($r = 0.45$, $P = 0.04$, **Fig. 3C**), indicating that activation in the beta frequency band during REM sleep benefits offline memory consolidation, such that the content of a complex narrative can be retained better over time.

Linking neural reinstatement and dreams

If neural reactivation shapes the content of our dreams, we should observe a stronger neural reinstatement signal in participants who dreamt of the audiobook. To test this hypothesis, we compared the neural reactivation strength between participants whose dreams contained information about the audiobook condition and participants whose dreams did not

Fig. 2. Classified dream content and neural reinstatement. Confusion matrix of actual vs. rated audiobook. Blind raters were able to judge with better than chance accuracy which audiobook the participants had listened to before sleep based on the dream reports. ($\kappa = 0.107$, $z = 2.29$, $P = 0.02$, interrater agreement = 32.9%, based on 149 dream ratings).

reflect the audiobook. Besides assigning the likeliest audiobook to a dream report, dream raters also quantified the amount of information in participants' dreams pertaining to the audiobook (see Methods). Based on this score, we identified dream incorporators and dream non-incorporators. As predicted, we observe a higher neural reactivation signal in participants who dreamt of the audiobook ($t_{16} = 2.4$, $P = 0.03$, Cohen's $d = 1.10$, **Fig. 4**). The content of our dreams is thus at least partially linked to experience-related neural activity, demonstrating that daytime experiences effectively shape both our brain activity and cognitive activity during sleep.

Discussion

Brain activity patterns of REM sleep held information about which audiobook our participants had listened to before falling asleep. Although most recent studies focused on memory reactivation in NREM sleep, previous studies provide noteworthy evidence of spontaneous reactivation of learning experiences also during REM sleep (8, 13, 15, 30, 31). In the rat hippocampus, neuronal firing patterns observed during path running are replayed in subsequent REM sleep(13). Similarly, the distribution of cerebral activity during REM sleep was found to be modified by previous learning experience in humans (15). However, the memory function of REM sleep has been understudied compared to NREM sleep (1) and as a result, evidence for reactivation of memories during REM sleep is scarce. Interestingly, a recent study in mice suggests that rapid eye movements during REM sleep may be accompanied by cognitive processes such as concordant

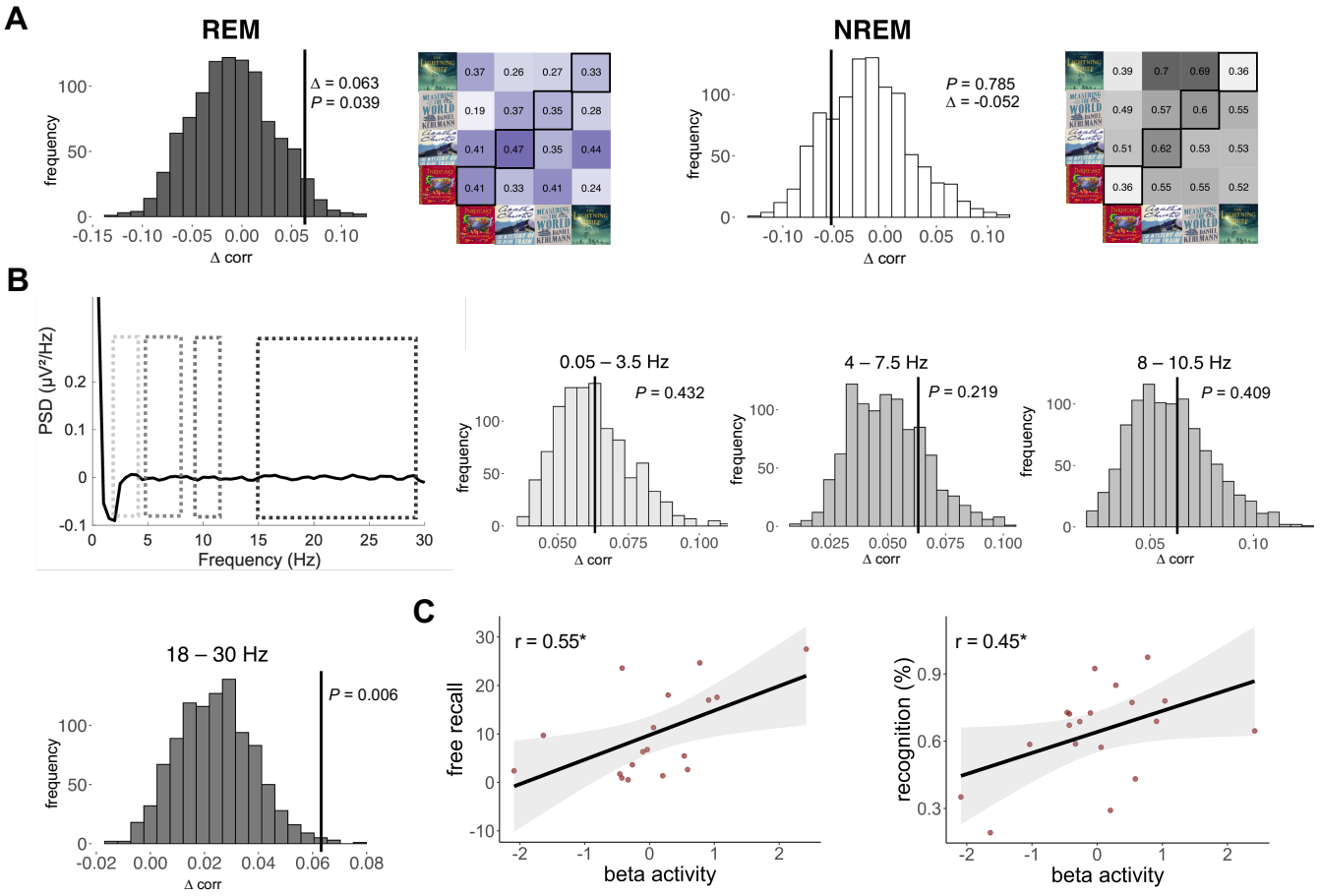

Fig. 3. PRISMA flow diagram of the literature search, screening, and inclusion processes; It has previously been shown that brain activity patterns induced by stimulation are similar across subjects (8, 25). Neural reinstatement is therefore measured as a higher similarity of brain activity in sleep in participants listening to the same audiobooks before sleep as compared to participants listening to different audiobooks (difference in Fisher's z transformed correlations, Δcorr). Histograms: permutation distributions of within-between differences (Δcorr); vertical lines: observed within-between differences. **A.** Brain activity during REM sleep but not NREM sleep was informative about which audiobook participants listened to before sleep: participants who listened to the same audiobook had more similar REM activity patterns than participants who listened to different audiobooks (Δcorr = 0.063, $P < 0.039$). The representational similarity matrices for REM and NREM show within-audiobook (diagonal) and between-audiobook (off-diagonal) correlation values (REM: within-audiobook correlation $M = 0.398$, between-audiobook correlation $M = 0.334$; NREM: within-audiobook correlation $M = 0.491$, between-audiobook correlation $M = 0.554$). **B.** To assess the contribution of the different EEG frequency bands to memory processing in REM sleep, we shuffled the frequency ranges of interest between participants, thus removing the association with the audiobook condition from these parts of the data while keeping the correct condition labels intact for all other frequency ranges. If informativeness is removed from REM sleep beta activity (18–30 Hz), the audiobook condition can no longer be discerned equally well from sleep EEG ($P < 0.006$). Neural reinstatement is thus strongest in REM-sleep high-frequency beta activity. Note that permutation distributions for searchlight analyses are not centered on 0 because brain activity in other frequency ranges may also hold partial information about audiobook content. The observed Δcorr remains constant at the value reported above (Δcorr = 0.063). **C.** Higher beta activity (18–30 Hz) in REM sleep correlated with better memory recall and retrieval after sleep. $^*p < 0.05$.

changes in perceived heading direction, which may reflect the generation of related dreaming experiences (32). Studies further support the idea that REM sleep has a functional role in sleep-related neuronal plasticity. Direct evidence for this assumption has accumulated over the past years, e.g., showing that REM sleep does not only prune a subset of newly formed spines in primary motor cortex but simultaneously strengthens others, dependent on calcium spikes on apical dendrites during REM sleep (33) and that neural reactivation in REM sleep might be related to regulating synaptic plasticity (33, 34).

As mentioned above, most studies investigating memory consolidation during sleep have focused on the role of NREM sleep. We now show that daytime experiences like listening to a complex narrative are reprocessed during REM sleep and that this reprocessing benefits memory retention. We thus add to existing evidence that also REM sleep has a significant role in offline memory processing. Our results agree with very early behavioral studies suggesting REM sleep actively facilitates memory consolidation (35, 36). This idea is supported by reports of increased REM sleep density after periods of learning (37), and of a positive association of post-learning REM sleep with performance outcomes (38, 39). Whether memories are processed during NREM or REM sleep may depend on the type of learning task. Particularly complex learning material may benefit from processing in REM sleep (36, 40). Moreover, recall of learning material with similar complexity to ours (short stories) was impaired by REM sleep deprivation (36). However, the function of REM sleep for memory is still far from being understood (e.g., for studies linking REM sleep and forgetting see (41, 42)). Our results

provide clear evidence that REM sleep is involved in both the processing and the consolidation of complex declarative learning content.

While we could find neural reinstatement of daytime events in REM sleep, we did not detect significant reprocessing of memories during NREM sleep. Oscillatory activity in NREM sleep is more variable than in REM sleep (e.g., spindles, slow oscillations, mixed theta rhythms in NREM sleep), and firing behavior of neurons differs greatly between these sleep stages (13). This variability could potentially have prohibited equally efficient detection of learning-related activity in NREM compared with in REM sleep. Indeed, a previous study using a similar approach as we applied here was also better at decoding memory content from REM sleep than from NREM sleep (8).

Particularly higher frequency oscillatory activity in the beta frequency range carried information about the previously presented material. Moreover, the amount of activation in the beta frequency band during REM sleep predicted post-sleep memory recall and recognition performance. These results align with previous studies investigating the role of beta activity in cognition including memory encoding, memory search, and also dream recall (43–48). Beta activity reaches its maximum across the night during REM sleep (49) and increases when participants are able to report the content of their dreams (43). Our results assign an active role of REM sleep beta activity in memory processing, indicating that it could serve as a neural fingerprint of memory reinstatement in humans. That REM sleep beta is also elevated during dreaming (43) suggests a tight interrelation between REM sleep memory functions and the cognitive experiences that accompany it. We suggest that in the present study, REM sleep beta activity reflects the reactivation of memory content across brain regions that store information relating to the studied narratives.

Our findings demonstrate that daytime events concurrently influence our brain activity during sleep and the content of our dreams. Learning material that was reinstated in REM sleep brain activity was also integrated into the narratives of dreams. We thus provide evidence that memory processing during sleep shapes the content of our dreams. Our study raises further questions about the memory sources of dreaming: in which form are life events recapitulated and interpreted by the sleeping brain? Does dreaming itself have a functional role in memory processing? Our results suggest an intricate interplay among our waking experiences, memory reactivation, dream content, and memory storage. Unraveling the neurophysiology of dreaming and its interaction with memory functions can give insights into how memories are reprocessed during sleep and will shed light on the mechanisms that govern the emergence of conscious experience in the sleeping brain.

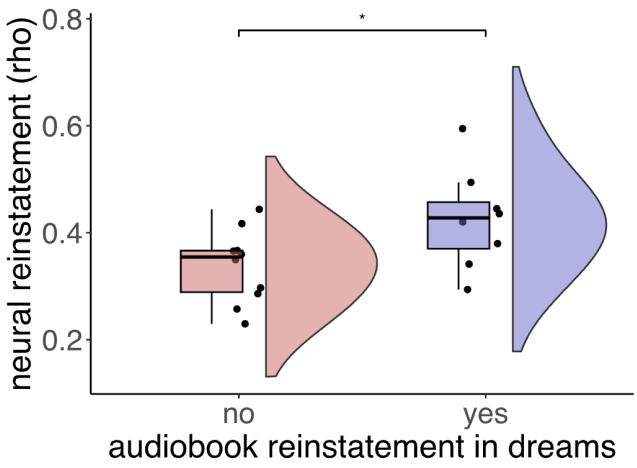

Fig. 4. Classified dream content and neural reinstatement. A two-sample t-test revealed that the amount of neural reactivation was higher in participants who had incorporated audiobook information into their dreams. $^{*}p < 0.05$

Materials and Methods

Subjects

20 participants (10 male) aged 20 – 30 years (25.5 ± 2.7) completed the study. They were healthy, nonsmokers, and did not ingest any alcohol, caffeine or medication other than oral contraceptives on the days of the experiment. The participants reported sleeping between 6 and 10 hours per night, had a regular circadian rhythm, and were neither extreme morning nor evening chronotypes, as measured by the Munich Chronotype Questionnaire. They had no shift work or long-distance flights during the six weeks preceding the experiment and did not have any sleep-related pathology. All participants were right-handed, confirmed by the Edinburgh Handedness Questionnaire. The experiment was approved by the local ethics committee (Department of Psychology, Ludwig-Maximilians-Universität München). Informed consent was obtained from all subjects.

Stimulus Material and Experimental Design

All participants visited the sleep laboratory twice, once for an adaptation night to become familiar with the experimental procedure and environment (i.e., wearing an EEG cap), and again for the night of the main experiment. On the experimental night, participants fell asleep while listening to one of four randomly assigned audiobooks: Inkheart by Cornelia Funke, The Mystery of the Blue Train by Agatha Christie, Measuring the World by Daniel Kehlmann, or Percy Jackson and the Olympians: The Lightning Thief by Rick Riordan. Participants had not read the book or listened to the audiobook prior to the experiment. Participants were instructed to remember the content of the audiobook. The audiobook was turned off once they reached consolidated stage 2 sleep. Participants were awoken multiple times during the night, approximately every 90 minutes, to answer questions regarding their cognitive experiences during sleep (i.e. dreaming) and about the content of the audiobook passage they had listened

to. After these tests, they continued listening to the same audiobook while falling asleep again. Each participant was awoken up to five times. One participant had to be excluded because due to a technical problem we had no information about audiobook timing. Two participants finished their audiobook before the experimental night was over. They later continued listening to a different audiobook. Data from the two affected awakenings was excluded. All other data from a total of 67 awakenings from 19 participants entered the analysis (**Fig. S5**). Further details about the experimental procedure can be found in **Fig. 1**.

Dreaming and Cognitive Measures

After each 90-min sleep cycle, participants were awoken and reported their cognitive experience (i.e., dreaming) in a standardized dream recall procedure. They were asked up to three times what was going through their minds immediately before waking up. If the participants were able to remember any dream, we instructed them that they should proceed to give a detailed report on who participated in the dream, where the dream was set, and what happened in the dream. We recorded their full dream report, asking up to three times "Can you recall more?" We then proceeded to inquire further details regarding the dream content with a custom questionnaire: Who had been part of the dream? Where had the dream taken place? What happened in the dream? What was the perspective of the dream? Did the participant experience any emotions while dreaming? What would they name as the central element of their dream? After reporting their dreams, participants also had to retrieve the audiobook content. They were first asked to freely recall what they remembered from the audiobook passage they had listened to before falling asleep, giving as much detail as possible. To test audiobook recognition memory, they were then aurally presented with parts of the audiobook passage they had listened to previously and asked to indicate whether they still remembered having listened to it earlier. The whole questioning procedure was recorded on tape.

Behavioral Data Analyses

Dream reports

To analyze the content of the dreams, three blind and independent raters received the dream reports in a randomized order. They were asked to indicate which audiobook participants had encoded and to rate how much information about the audiobook they detected in the dream report, as a measure of decision confidence (0 = guessed, 1 = gut feeling, 2 = implicit indication, 3 = explicit indication). To compare the rated and actual audiobook, we assessed Cohen's Kappa in 149 available dream ratings (150 values from 50 reported dreams, one missing rating).

Audiobook dream reinstatement score

From the ratings on how much information about the audiobook the scorers detected in the dream reports, we computed a separate audiobook dream reinstatement score. If a rater was able to correctly identify the audiobook, their information score was multiplied by 1, otherwise by -1. Scores higher than zero thus reflect that information pertaining to the audiobook was incorporated into the dream, allowing correct judgements, with higher scores indicating more direct evidence for incorporation, whereas scores of zero and lower mean that no information about the previously listened audiobook was present in the dream report such that the condition was judged incorrectly. For statistical analyses, we averaged these dream reinstatement scores across all raters and all awakenings per individual. We then divided participants into dream incorporators (average value above zero) and dream non-incorporators (average value below zero). A subject-level dream reinstatement score was necessary to relate dream incorporation to participant-specific neural reinstatement scores (see Relation of neural reinstatement and reinstatement in dreaming).

Cognitive Measures

Audiobook recognition was computed as the percentage of the audiobook passage remembered that was listened to while awake. Free recall was computed by dividing the number of recalled words by the time that participants had listened to the audiobook while awake. For further analyses, we separately averaged recall and recognition values across sleep awakenings for each participant.

EEG Recording

Sleep EEG was recorded using an active 128 channel Ag/AgCl-electrode system (BrainAmp MR with ActiCap, Brain Products, Gilching, Germany) with a 1 kHz sampling frequency and a high-pass filter of 0.1 Hz. Electrodes were positioned according to the extended international 10–20 electrode system. For sleep scoring, recordings were split into 30-s epochs and sleep stages were determined on electrodes C3/C4 according to standard rules by two independent raters. Discrepant ratings were decided by a third rater. Average sleep durations are reported in Table S1.

EEG Analyses

EEG data were split into 4-s trials. Artefact rejection was done in a semiautomatic process using custom MATLAB 2021a (MathWorks) scripts. To compute the spectral power, we performed Fourier transformation using the Welch method by averaging over 10 Hamming windows of 2-s length with %95 overlap, resulting in smooth power spectra with a final data resolution of 0.5 Hz. We then removed channels with bad recording quality and interpolated them using EEGLAB. To test whether memories of complex narratives are reactivated in sleep and whether this reactivation is related to participants' dreaming experience, we analyzed neural similarity of brain activity patterns during the time be-

fore we woke participants from their sleep. The last 250 trials before awakening entered these analyses, corresponding to the last 16.7 minutes of sleep where the reported dreams were most likely to have occurred. We thus ensured that an equal number of epochs per subject entered the representational similarity analysis (RSA). Following a previously published procedure to detect spontaneous memory processing in sleep (8), we averaged power spectra across electrodes within a radius of approximately 3 cm around 32 evenly spread locations of the extended 10–20 system to reduce the dimensionality of the data and to increase the signal-to-noise ratio. To remove amplitude differences between channels, spectra of all channels were then separately normalized between zero and one, which also removes between-subject variability unrelated to the experimental intervention. At the final stage, we applied a spectral sharpening filter to remove the baseline power spectrum by subtracting a moving average of six neighboring frequency bins (window size: 3 Hz) from the signal. This was done to emphasize signal differences (8). We then calculated an average PSD of each participant across all sleep segments of the night, separately for REM and NREM sleep, to maximize signal-to-noise ratio. Data between 0.5–30 Hz entered the final analyses (8).

Representational Similarity Analysis (RSA)

In the present study, we tested whether spontaneous electrical brain activity during sleep holds information about the content of a recently encountered narrative. We employed representational similarity analysis (RSA), a multivariate pattern analysis method that allows comparing how different experimental conditions shape neural activity patterns by assessing the distinctiveness of brain responses across multiple data features (50). We used PSD features for similarity calculation because these can integrate information across time and do not depend on specific temporal events. If memory for the story that participants encoded while listening to the audiobook is reactivated during sleep, the narrative should shape brain activity patterns in the sleeping brain, and we should be able to detect information about the narrated content in recordings of electrical brain activity. It can be assumed that brain activity patterns induced by stimulation are similar across subjects (8, 25). We thus hypothesized that brain activity patterns of participants who listened to the same audiobook would be more similar than brain activity pattern of participants who listened to a different audiobook.

Leave-one-subject-out RSA

We employed a leave-one-subject-out (LOO) approach for the RSA, correlating brain activity patterns of one participant with the average activity pattern of all other participants who listened to either the same or a different audiobook. This approach gives us a measure of how well an individual's brain activity patterns conform to the estimated template of brain activity reflecting audiobook reprocessing and can serve as a measure of individual reinstatement strength. We first removed the PSD of one individual (left-out subject) from one audiobook category and averaged the remaining subjects' PSDs within that audiobook category (**Fig. 2B**). To compute the within-audiobook correlation, we calculated the correlation between the PSD of the left-out subject and the average PSD of all other subjects within that category. The between-audiobook correlations were computed between the PSD of the left-out subject and the averaged PSD of participants in the three other audiobook categories, separately, as shown in Fig 2B. This procedure was repeated for each of the participants. The correlations were implemented using a non-parametric Spearman's correlation (ρ) across the PSD values (1-30 Hz, 0.5 Hz resolution) for all 32 electrode locations ($n = 32 \times 60$), separately for NREM (stages S2, S3, and S4) and REM sleep. We then converted the correlation values to a normal distribution using the inverse hyperbolic tangent (Fisher's z-transform) and quantified the amount of audiobook-specific neural processing during sleep by contrasting the average within-audiobook correlations with the average between-audiobook correlations. Positive within-between correlation differences (Δcorr) indicate audiobook reprocessing during sleep.

Pairwise RSA

In an additional analysis, we re-ran the RSA using the more traditional pairwise correlation approach. Here, we calculated pairwise non-parametric Spearman's correlations between the average PSDs of all individuals across 32 electrodes, again separately for NREM and REM sleep. We then converted the rho values to a normal distribution using the inverse hyperbolic tangent and averaged all within-audiobook condition correlations, as well as all between audiobook condition correlations that were obtained, to again calculate the within-between difference measure.

Permutation testing

To test for statistical significance of the within-between similarity differences, permutation tests were computed separately for all reported analyses. Audiobook labels were shuffled randomly between participants to remove information about audiobook conditions. Then, the exact analysis as reported above was repeated 1000 times, resulting in 1000 average within-between similarity differences that provide the permutation distribution of results when no information about the audiobook is present in the data. The p-value was then computed as the number of averaged within-between differences generated by randomly labeled data that were greater than or equal to the size of the observed average of within-between differences from the correctly labeled data, divided by the number of random permutations and the observed difference ($n + 1$).

Searchlight analyses for frequency bands of interest (FOI)

We assessed the contribution of different oscillatory frequencies to memory reprocessing during REM sleep by removing

information about the audiobook condition from specific frequency bands and testing its effect on signal similarity differences in the RSA described above. This was done by randomly swapping the features of interest between conditions. We randomly shuffled the data only regarding the FOI, to test whether this significantly decreases informative content. To achieve this, we randomly reassigned the parts of the PSD corresponding to the FOIs between participants, leaving the remaining data structure intact and maintaining correct audiobook labelling for all other frequency bands (delta: 0.5–3.5 Hz, theta: 4–7.5 Hz, alpha: 8–10.5 Hz, beta: 18–30 Hz). An advantage of this procedure is that the number of features and the overall data structure are kept constant for all analyses, regardless of the widths of the frequency bands. This procedure was completed 1000 times for each FOI. If the observed within-between similarity difference exceeds 95% of the values in the randomization distribution obtained by shuffling data in the FOI, the respective frequency band can be assumed to hold crucial information about the audiobook and thus significantly contributes to memory processing in sleep. As a control analysis, we also ran a LOO RSA on data within the FOI only, with a reduced number of features that consequently varied between FOIs. This type of analysis regards a limited number of features only, without controlling for the overall structure and dependencies in the data to be analyzed. Results of this supplementary analysis align with the FOI results reported in the main manuscript and are displayed in **Fig. 3**.

Correlation of neural activity with behavioral performance

To examine whether EEG activity that reflects audiobook reprocessing during sleep is associated with retention of the content of the audiobook after sleep, we further correlated beta activity with recall and recognition measures. To obtain a measure of beta activity, we averaged the PSD in the beta frequency range (18–30 Hz) for each participant. We then correlated these values with the individual average recognition and recall performance throughout the night.

Relation of neural reinstatement and reinstatement in dreaming

To relate the strength of neural reinstatement with the incorporation auf audiobook material into dreams, we calculated a neural reinstatement score for each of the participants. This score was quantified by how similar their brain activity during REM sleep was to the activity template gained from the average activity of the other participants in the same audiobook condition (see Leave-one-subject-out RSA). We then compared whether participants who incorporated audiobook information in their dreams showed higher neural reinstatement scores than participants who did not dream of the audiobook.

Data availability statement

The raw data and computer code necessary to understand and assess the conclusions of the study can be downloaded from the Open Science Framework platform (https://osf.io/2bkus/).

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Supplementary Material

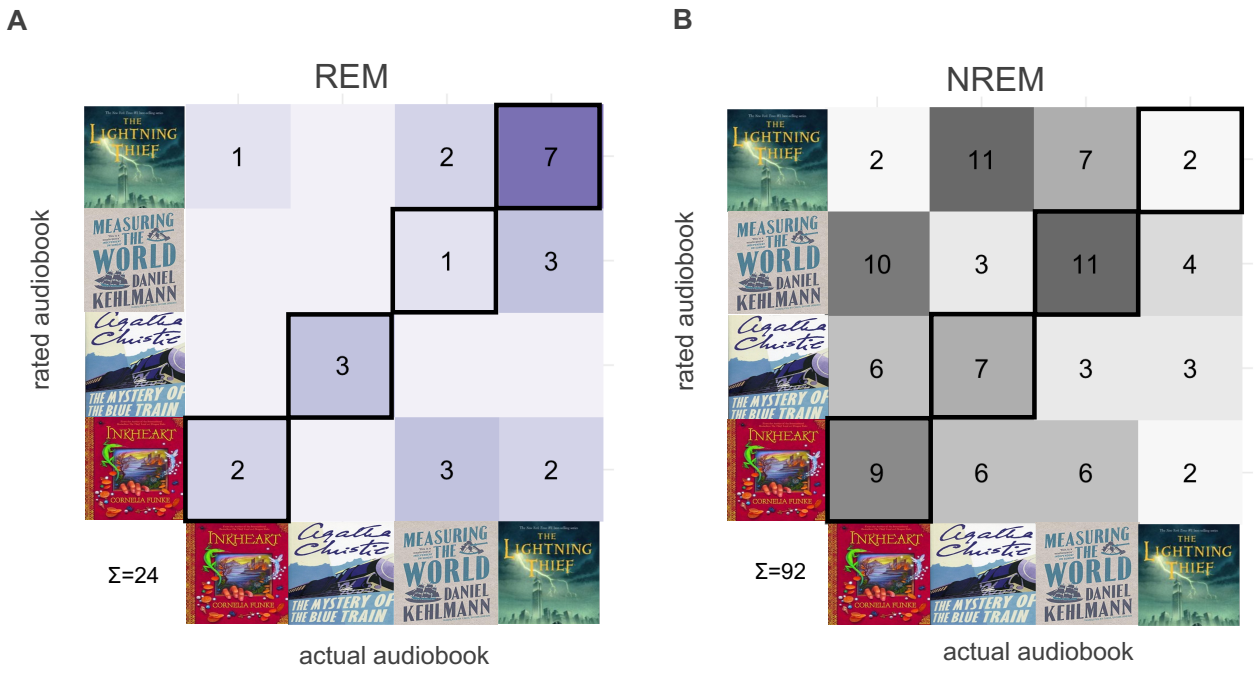

Fig. S1. Classified dream content separately for REM and NREM sleep Cohen's Kappa was used to compare the rated and actual audiobooks, separately for REM and NREM sleep. We observe that the blind raters were able to judge which audiobook participants encoded based on the content of subsequent dreams when the participants were awoken in **A.** REM sleep ($\kappa = 0.343$, $z = 2.88$, $P = 0.003$, % agree = 54.2), but not in **B.** NREM sleep (stages S2, S3, S4; $\kappa = 0.08$, $z = 1.43$, $P = 0.154$, % agree = 31.5). Note that some participants were awoken from S1 sleep ($k = 15$) or were already awake ($k = 18$) when we entered the sleep chambers to record dream reports such that the combined number of REM sleep and NREM sleep dream ratings is lower than the available total of $k = 149$ dream ratings reported in Fig. 2.

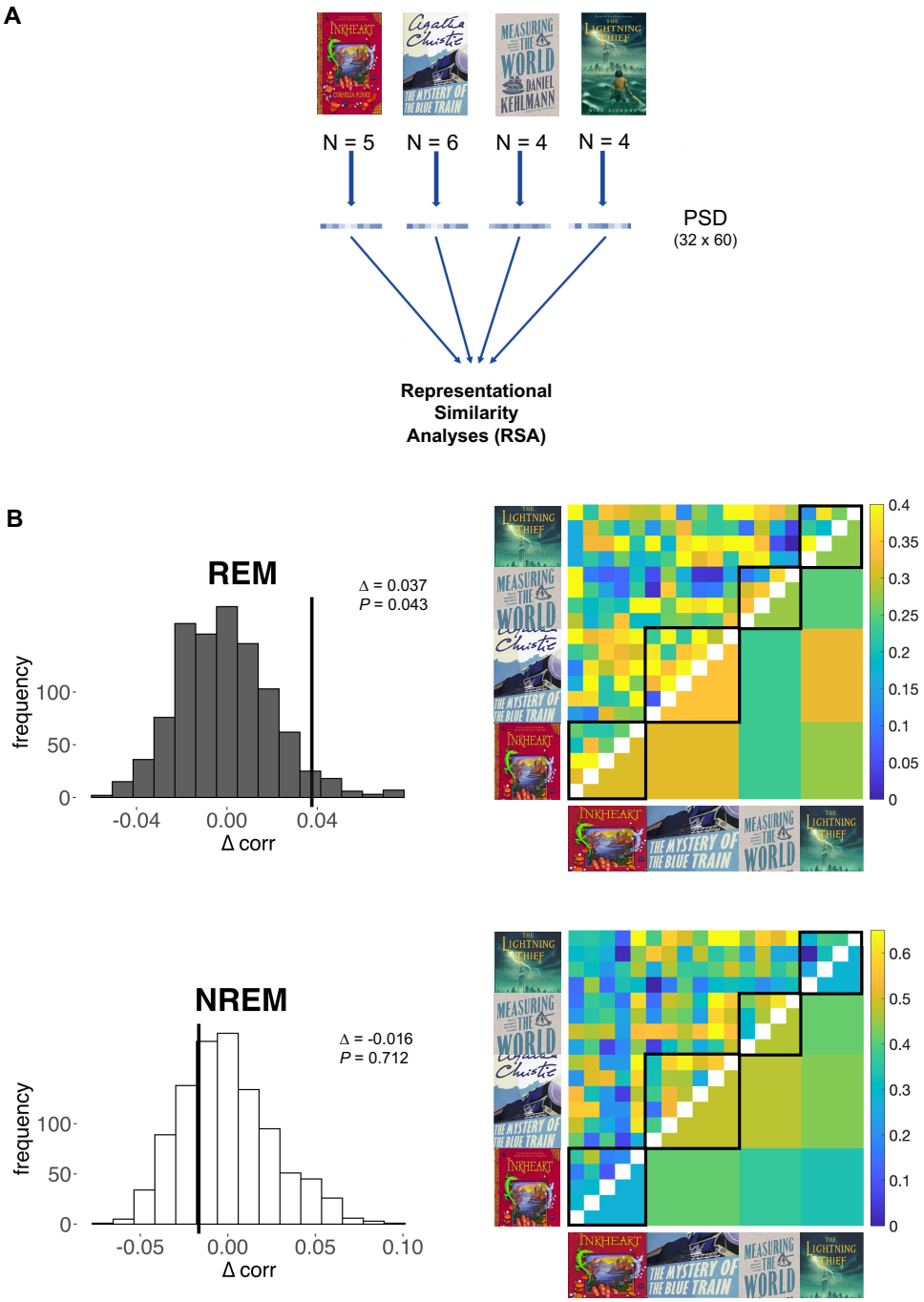

Fig. S2. Neural reinstatement using pairwise instead of LOO representational similarity analyses. A. We calculated a non-parametric Spearman's correlation between power spectral density values (PSD, dimensions: 32 channel x 60 Hz) of individuals. We then converted the obtained rho values to a normal distribution using Fisher's inverse hyperbolic tangent transform. **B.** RSA results for REM and NREM sleep. We converted correlation values (rho) to a normal distribution using the Fisher inverse hyperbolic tangent transformation. The histograms represent the permutation distribution of within-between differences for randomly relabeled data (x-axis; Δcorr). Representational similarity matrices are displayed to the right. Upper triangle: entries on the diagonal of the similarity matrix denoted by black lines represent pairwise within-audiobook correlations, off-diagonal entries show pairwise between-audiobook correlations. Lower triangle: average within (diagonal) and between (off-diagonal) correlation values for each audiobook condition. REM: within-audiobook correlation $M = 0.312$, between-audiobook correlation $M = 0.275$; NREM: within-audiobook correlation $M = 0.393$, between-audiobook correlation $M = 0.409$.

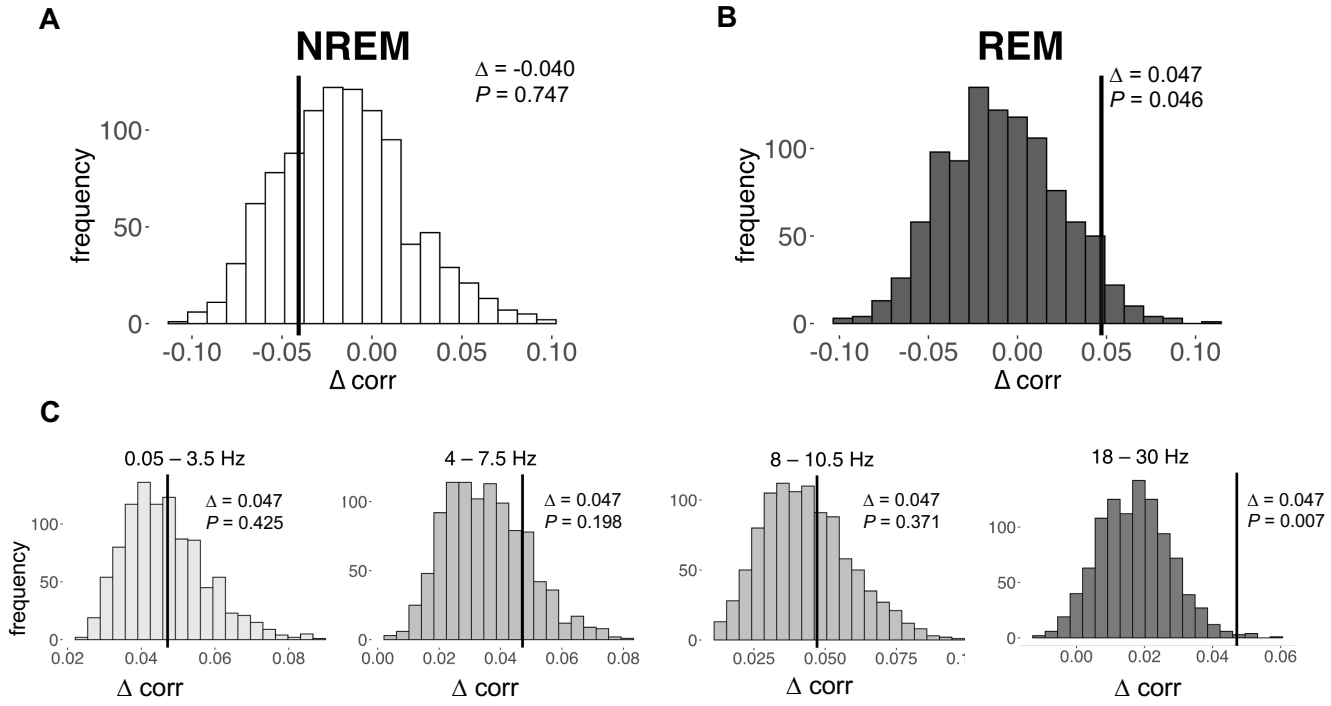

Fig. S3. Neural reinstatement using whole brain EEG with all 128 individual channels instead of 32 averaged channels. The histograms represent the permutation distribution of within-between differences for randomly relabeled data (x-axis; Δcorr) computed using the leave-one-subject-out representational similarity analysis approach, separately for **A.** NREM(Δcorr = -0.040, $P = 0.747$) and **B.** REM sleep (Δcorr = -0.040, $P = 0.047$). **C.** To assess the contribution of the different oscillatory activity to memory processing in REM sleep, we shuffled power spectral density (PSD) patterns between participants in specific frequency bands, thus removing audiobook information from these parts of the data while keeping the correct audiobook labels intact for all other frequency bands. The vertical black lines indicate the observed Δcorr for REM sleep with all frequency ranges intact. REM sleep beta activity (18–30 Hz) contributes significantly to neural reinstatement.

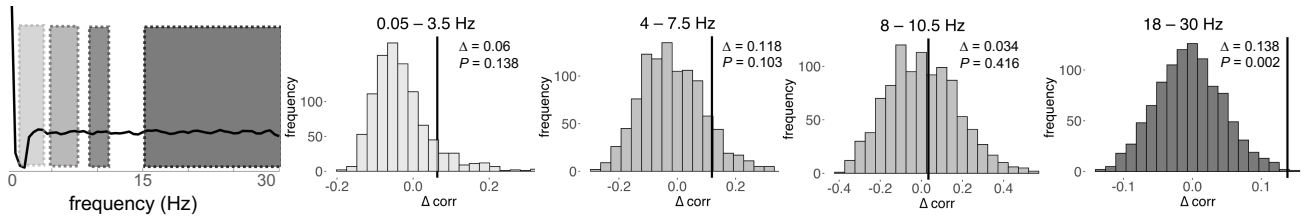

Fig. S4. The contribution of individual frequency bands to neural reinstatement. Only data in individual frequency bands was included in this analysis. The histograms represent the permutation distribution of random within-between differences (x-axis; Δcorr), while the black line indicates the observed differences. To assess the contribution of the different frequencies to RSA during REM sleep, we shuffled individuals' frequency bands (delta: 0.5–3.5 Hz, theta: 4–7.5 Hz, alpha: 8–10.5 Hz, beta: 18–30 Hz, frequency of interest (FOI); shown in dot line). Only beta frequency (18–30 Hz) contributes significantly to the neural reinstatement.

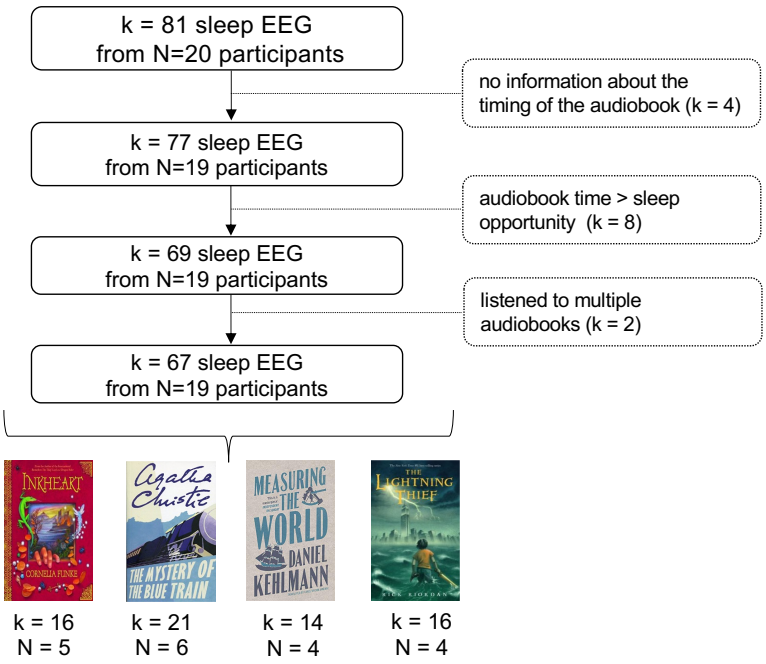

Fig. S5. Flow chart visualizing the selection process of dataset. k: number of sleep periods, N: number of participants.

Table S1. Averaged sleep data in minutes (mean ± SD)

	time to fall a sleep	S1	S2	S3	S4	REM	TST
SP 1	21 ± 18.8	7.1 ± 4.6	19.6 ± 13.7	11.7 ± 6.7	25.9 ± 24	9.7 ± 0.8	73.9 ± 7.8
SP 2	20.1 ± 18.2	8.2 ± 4.5	34.8 ± 15.6	10.7 ± 7.7	9.6 ± 9.8	16.8 ± 18.1	80 ± 11
SP 3	21.3 ± 13.8	18 ± 33.5	46.7 ± 20.7	8.3 ± 5.7	9.4 ± 5	23.6 ± 14.7	106 ± 15.6
SP 4	14.8 ± 10.8	9.9 ± 6.3	39.7 ± 22	10.6 ± 10.2	7.8 ± 7.6	31.4 ± 17.1	99.5 ± 14.7
SP 5	9 ± 9.5	5.3 ± 3.3	12.7 ± 10.8	8.9*	20.5*	38 ± 26.9	85.5 ± 13

*SP = Sleep Period, TST = Total Sleep Time, *note that only one participant reached S3/S4 in the 5th sleep segment.*