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ORIGINAL ARTICLE

Targeted memory reactivation during sleep influences social bias as a function of slow-oscillation phase and delta power

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Abstract

To understand how memories are reactivated and consolidated during sleep, experimenters have employed the unobtrusive re-presentation of memory cues from a variety of pre-sleep learning tasks. Using this procedure, known as targeted memory reactivation (TMR), we previously found that reactivation of counter-social-bias training during post-training sleep could selectively enhance training effects in reducing unintentional social biases. Here, we describe re-analyses of electroencephalographic (EEG) data from this previous study to characterize neurophysiological correlates of TMR-induced bias reduction. We found that TMR benefits in bias reduction were associated with (a) the timing of memory-related cue presentation relative to the 0.1–1.5 Hz slow-oscillation phase and (b) cue-elicited EEG power within the 1–4 Hz delta range. Although cue delivery was at a fixed rate in this study and not contingent on the slow-oscillation phase, cues were found to be clustered in slow-oscillation upstates for those participants with stronger TMR benefits. Similarly, higher cue-elicited delta power 250–1000 ms after cue onset was also linked with larger TMR benefits. These electrophysiological results substantiate the claim that memory reactivation altered social bias in the original study, while also informing neural explanations of these benefits. Future research should consider these sleep physiology parameters in relation to TMR applications and to memory reactivation in general.

KEYWORDS

EEG, memory consolidation, slow-oscillation phase, slow-wave sleep, targeted memory reactivation

1 | INTRODUCTION

Spontaneous memory reactivation during post-encoding sleep contributes to enduring memories (Diekelmann & Born, 2010; Dudai, 2012; Klinzing et al., 2019; Paller et al., 2020; Rasch & Born, 2013; Stickgold & Walker, 2013). Intriguingly, reactivation can also be initiated and guided exogenously via unobtrusive delivery of memory-related sensory cues; targeted memory reactivation (TMR) can thus be used to promote memory consolidation during sleep (Antony et al., 2012; Cellini & Capuozzo, 2018; Feld & Diekelmann, 2020; Lewis & Bendor, 2019; Oudiette & Paller, 2013; Paller et al., 2021; Rasch et al., 2007; Rudoy et al., 2009; Schouten et al., 2017; for a meta-analysis of TMR, see Hu et al., 2020). Furthermore, certain types of memory modification could ultimately benefit psychological well-being and are useful beyond their impact on memory performance (Feld & Diekelmann, 2020;

Paller, 2017; Paller et al., 2021). In particular, TMR may hold promise for modifying unwanted habits and biases. However, the ultimate usefulness of TMR could depend on first developing a better understanding of relevant neural mechanisms operative in driving successful reactivation and consolidation during sleep.

Implicit social bias is recognized as an aspect of habit memory and as a critical aspect of social cognition, as well as a contributor to social inequality. Even when people do not endorse racial prejudice and gender biases when directly asked, biases can be evident in their behavior and in measures provided by the Implicit Association Test and the Evaluative Priming Task (Gawronski & De Houwer, 2014; Greenwald & Lai, 2020). These indirect tests are designed to assess the associative strength between social groups (e.g., racial minority) and attributes (e.g., good/bad) without participants' reflection on these evaluative processes (Gawronski & De Houwer, 2014). Given the prevalence of unintentional social biases, it is important to study how implicit biases can be changed (Dasgupta, 2013; Lai et al., 2013). While mounting evidence suggests that biases can be reduced when people engage in counter-stereotypical thinking, training benefits seem to be short-lived (Lai et al., 2016). The benefits may be transient because long-standing habits tend to predominate and because small effects of counter-bias training decay over time. However, training benefits may solidify, as with learning in general, if training is followed by repeated reactivation and consolidation during sleep.

In our prior study, TMR to reactivate counter-bias training during post-training sleep produced relative bias-reduction benefits both immediately and in additional testing after a one-week delay (Hu, Antony et al., 2015). There is reason to be confident that the TMR method can promote memory consolidation, given our recent meta-analysis of such effects across 91 studies (Hu et al., 2020), showing a significant TMR effect (Hedges' $g = 0.27–0.32$) when administered during non-rapid eye movement (NREM) sleep. However, there was also ample heterogeneity of effect sizes across studies and the effect size tends to be small-to-moderate. With respect to TMR for social bias, only two studies have been published to date, our initial study (Hu, Antony et al., 2015) and one replication study where TMR benefits were not observed (Humiston & Wamsley, 2019). On the one hand, a divergence in TMR effect size between these two studies is unclear at present. One possibility is that, given a small-to-moderate effect size overall (Cordi & Rasch, 2021a; Hu et al., 2020), such effects could be difficult to detect with a small sample size (Cordi & Rasch, 2021a), and that better studies are needed with larger sample sizes. On the other hand, we reasoned that insights could still be provided by examining associations between neural responses to memory cues presented during sleep and subsequent behavioral effects in our original study.

Recent evidence of TMR and sleep-based memory consolidation suggests that TMR effects can be predicted by slow-wave and spindle-related activity (Antony et al., 2012, 2018; Batterink et al., 2016; Cairney et al., 2014, 2018; Cox et al., 2014; Hauner et al., 2013; Laventure et al., 2016; Schreiner et al., 2015, 2018; Schreiner & Rasch, 2015). These data fit well with current accounts of sleep-based memory consolidation, which propose that successful memory consolidation relies on the coupling between neocortical slow-waves and thalamo-cortical spindles (Mölle et al., 2002; Mölle & Born, 2011). Intriguingly, the timing between spindles and slow-waves appears to be critical during consolidation: spindles during slow-wave upstates would theoretically promote cortical plasticity that allows hippocampal-neocortical interactions. Via this hippocampal-neocortical dialogue and with concurrent hippocampal ripples that carry specific memory information, memories can gradually be consolidated and become long-lasting (Klinzing et al., 2019; Staresina et al., 2015). Supporting the importance of the timing of slow waves and spindles in memory consolidation, prior evidence suggests that the timing of TMR cues relative to slow waves and spindles is instrumental in successful TMR benefits (Antony et al., 2018; Batterink et al., 2016; Göldi et al., 2019).

Building on these findings, we hypothesized that in our experiment (Hu, Antony et al., 2015), cue-related slow-wave (0.1–4 Hz) and spindle (12–16 Hz) activity could be important for TMR to reduce social biases. Alternatively, if effects on social bias were spurious in the first place, then such associations with sleep physiology would not be expected. To test our hypotheses, we categorized participants into high versus low benefits groups based on the median split of TMR-induced bias reductions. We next compared cue-related EEG activity between these two groups of participants, focusing on (1) timing of memory cues relative to slow waves, and particularly to slow-oscillation phase; and (2) cue-elicited EEG activity that may distinguish between high- versus low-benefit groups. In addition to these between-group analyses, we also conducted correlational analyses involving EEG activity and TMR-induced bias reduction across all participants.

2 | METHOD

2.1 | Participants

Data from 28 participants (age: mean ± *SD*, 22 ± 4 years, 13 female, 15 male) were included in the analyses. Data were collected as reported by Hu et al. (2015), wherein

counter-bias training to reduce unintentional social bias was followed by TMR during an afternoon nap. Only participants who received more than 80 cues during sleep were included, to ensure a good signal-to-noise ratio for EEG analyses. Ten additional participants were not included due to missing EEG files ($n = 6$), fewer than 80 cues presented during slow-wave sleep ($n = 2$, who received 39 and 22 cues, respectively), or missing stimulus triggers in the EEG data ($n = 2$).

2.2 | Experimental procedures

Participants completed the following seven steps of the procedure: (1) a seven-block, 200-trial implicit association test (IAT) to assess baseline racial and gender implicit biases; (2) counter-racial-bias and counter-gender-bias training with auditory cues; (3) post-training/pre-nap IATs to assess immediate counter-bias training effect; (4) sound-cue retrieval task to strengthen sound-training associations; (5) a 90-min nap with TMR; (6) post-nap IATs to assess TMR's immediate effect, and (7) 1-week delayed IATs.

Participants completed a racial bias IAT (white and black male faces, pleasant and unpleasant words) and a gender bias IAT (white male and female faces, science- and humanities-related words), the order of which was counterbalanced across participants. The IAT follows a standard 7-block, 200-trials setup (Greenwald et al., 2003). Participants used two response keys ("E" key for the left index finger; "I" key for the right index finger) for stimulus categorization. In block 1 (20 trials), participants completed a simple categorization task, wherein they categorized good ("E") and bad ("I") attribute words (for gender IAT, these are science and art words). In block 2 (20 trials), participants categorized White ("E") and Black ("I") male faces (for gender IAT, these are White male and female faces). In blocks 3 and 4 (20 and 40 trials respectively), participants completed a combined categorization task, wherein they pressed one button ("E") for either White or good words (for gender IAT, male or science words) and the other button ("I") for Black or bad words (for gender IAT, female or art words). In block 5 (40 trials), participants completed a reversed simple categorization block, wherein they pressed "I" for White faces and "E" for Black faces (for gender IAT, White male and female faces). In blocks 6 and 7 (20 and 40 trials respectively), participants again completed a combined categorization task, wherein they pressed one button ("E") for either Black face or good words (for gender IAT, female face or science words) and the other button ("I") for White face or bad words (for gender IAT, male face or art words). Via such key-stimuli mapping, the IAT contained bias-congruent blocks (e.g., when Black faces and bad words shared one button, or when female faces and art words shared one button; 60 trials) and bias-incongruent blocks (when Black faces and good words shared one button, or when female faces and science words shared one button; 60 trials). On each trial, a single stimulus was presented centrally until a correct response was registered (onset 150 ms after prior response). If an incorrect response was registered, an error feedback symbol "X" was presented on the screen until participants gave the correct response. Participants were instructed to make a categorization response as quickly and accurately as possible.

Following baseline IATs, participants completed two counter-bias training tasks, with each task containing 360 trials (see Figure 1a). During the task, participants made speeded button presses (within 1 s) to 180 counter-stereotypical face-word pairings (i.e., black face+pleasant word pairing; female face+science-related word pairing), while they withheld button presses for the remaining 180

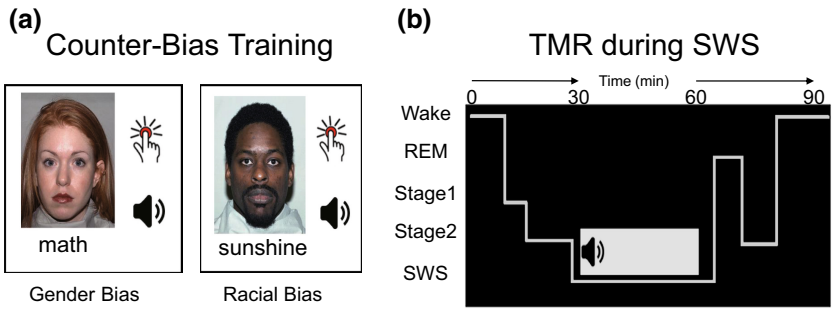

FIGURE 1 (a) Counter-bias training with sound cues. Participants pressed a button in response to counter-stereotypical face-word pairings within 1 s. upon a correct and timely button press, participants heard a distinctive sound (one for gender bias and another for race bias). Participants next completed a sound-cue retrieval task to further strengthen sound-training associations. (b) Nap and TMR. When participants showed signs of slow-wave sleep, one of the two sounds was repeatedly played to sleeping participants every 5 s (1-s sound duration, 4-s inter-stimulus-interval). Sounds were played with a low intensity to avoid arousal (figure adapted from Hu, Antony et al., 2015).

face-word trials (black face+unpleasant word; female face+humanities word). Following correct button presses to counter-stereotypical pairings, participants heard a 1-s sound cue to establish mental associations between sound cues and counter-bias training. Two sounds were created from frequency-modulated pure tones, with each sound paired with counter-racial-bias training or with counter-gender-bias training, respectively. The sound-training associations were counterbalanced across participants. To assess training effectiveness, participants next completed the racial and gender bias IATs again as post-training/pre-nap IATs. Words and faces used in these IATs were different from the baseline IATs.

Right before participants slept, they engaged in a sound-cue-retrieval task to further reinforce the association between sounds and counter-bias training. Each trial started with one of the two sounds from the counter-bias training. Participants were presented with either a White female face or a Black male face on the left side of the monitor, while a science word and a pleasant word were presented on the upper-right and lower-right side of the monitor (location of words randomized across trials). Participants were required to use a mouse to drag the face to its corresponding word to create a counter-bias pair in accordance with the sound that was presented. Participants completed 120 trials in total.

For the TMR administration, participants took a nap with scalp-recorded EEG. During the entire nap period, we played constant white noise [38–40 dB SPL]. When participants showed stable slow-wave sleep (SWS), one of the two auditory cues was presented (embedded at roughly the same intensity as the white noise) to reactivate the corresponding counter-bias memories. Auditory tones and their corresponding reactivation categories were nearly counterbalanced across participants in our sample, with 13 receiving the tone reactivating counter-race-bias and 15 receiving the tone reactivating counter-gender-bias. Each cue lasted 1 s, with an inter-stimulus interval of 4 s. Cueing was halted whenever recordings showed signs of arousal or when participants were no longer in SWS or N2 sleep. Participants were awakened after ~90 min or allowed more time to sleep if they were still in SWS. After waking up, participants took a 10-min break, followed by post-nap IATs that were the same as the pre-nap IATs.

2.3 | Behavioral data analyses

IAT effects are typically calculated as *D* scores (Greenwald et al., 2003), considering (1) mean and standard deviation (*SD*) of reaction times (RTs), (2) response accuracies from congruent (blocks 3,4) and incongruent (blocks 6,7) blocks. Here, we adopted a *D* score variant used in our previous IAT research (Hu, Bergström et al., 2015), the D_{600} score, wherein we adopted a 600-ms penalty for incorrect responses. This D_{600} score was calculated as follows: First, we deleted trials with RTs shorter than 300 ms or longer than 3 s (<1%). Second, we calculated averaged RTs (correct responses only) for congruent and for incongruent blocks, separately. Third, we calculated an inclusive *SD* using all correct trials from congruent and incongruent blocks combined. Fourth, we replaced incorrect responses with the averaged RT associated with that particular block plus a 600-ms penalty. Fifth, we calculated the averaged RTs for congruent and incongruent blocks including RTs of incorrect responses with the error penalties. Sixth, we calculated the RT differences as RT_incongruent minus RT_congruent from step five. Seventh, this difference was divided by inclusive *SD* obtained from step three. A larger D_{600} score indicates a stronger implicit social bias. Using this D_{600} score, we calculated TMR cueing benefits = (pre-nap IAT D_{600} minus post-nap IAT D_{600} for cued bias) minus (pre-nap IAT D_{600} minus post-nap IAT D_{600} for uncued bias). A higher score for this metric indicated a greater reduction for cued than uncued biases, corresponding to more successful reactivation of counter-bias training during sleep.

Participants were segregated into two groups, high- versus low-benefit, based on a median split of this TMR cueing benefit score. In the high-benefit group ($n = 14$), 8 participants received the tone reactivating counter-gender bias and 6 participants received the tone reactivating counter-racial bias. In the low-benefit group ($n = 14$), 7 participants received the tone reactivating counter-gender bias and 7 participants received the tone reactivating counter-racial bias.

2.4 | EEG recording and preprocessing

EEG was recorded using 21 electrodes (NeuroScan Synamps). Two additional electrodes were placed, one below the left eye and the other next to the right eye, for recording the vertical and horizontal EOG; and one additional electrode was placed on the chin to record EMG. Continuous EEG was recorded from International 10–20 locations Fpz, Fz, Cz, Pz, Oz, Fp1/2, F3/4, F7/8, C3/4, P3/4, T3/4, T5/6, and O1/2, amplified with a bandpass of 0.1–200 Hz at a 500-Hz sampling rate. Data were re-referenced offline to the average of left and right mastoids. We used MNE-Python for EEG preprocessing (Gramfort et al., 2013). Sleep stages were formally identified offline using the standard American Academy of Sleep Medicine Manual (Iber et al., 2007).

Raw EEG data were preprocessed as follows. First, EEG data were filtered with a band-pass of 0.1–40 Hz.

Second, some of the most lateral and anterior frontal scalp recording channels (F7/8, T3/4, T5/6, Fp1/2, FPz) were removed due to excessive artifacts (e.g., bad channels) and because TMR studies have typically focused on frontal/central/parietal electrodes for electrophysiological analyses. Third, continuous EEG data were segmented into 5-s epochs beginning 2 s prior to cue onset [−2 s to 3 s]. Fourth, epochs containing excessive artifacts were removed by visual inspection (Mean ± *SD*, 5 ± 6 per participant), Lastly, segmented EEG epochs were downsampled to 200 Hz. For analyses, we used Numpy (Harris et al., 2020); for phase-related statistics and plots, we used Pingouin (Vallat, 2018).

2.4.1 | Cue-related slow-wave phase analyses

We focused on the slow-oscillation band and the delta-frequency band to provide a detailed picture of their roles in TMR and in memory consolidation (see Kim et al., 2019). Filtered, segmented data were low-pass filtered to 1.5 Hz, producing the 0.1–1.5 Hz slow-oscillation band (Dasilva et al., 2021), or bandpass filtered between 1.5–4 Hz, producing the delta band (Kim et al., 2019). We applied Hilbert transformation to extract the instantaneous phase angle at the onset of an auditory cue. We used the Rayleigh Z test to determine whether cue onset timing followed a non-uniform (H1, alternative hypothesis) or a uniform distribution (H0, null hypothesis). These phase analyses were performed at Fz in accordance with previous research (Batterink et al., 2016; Heib et al., 2013). MNE-Python and custom Python scripts were used to conduct phase analysis.

2.4.2 | Cue-elicited event-related potential and time-frequency EEG analyses

We first compared event-related potentials (ERPs) between the two subgroups. Preprocessed EEG segments were baseline-corrected using the −1.5 – 0 s pre-stimulus interval. We used the −1.5 to 2.5 s epochs to match the timing of time-frequency results. Epochs were then averaged to obtain ERPs. To extract cue-elicited time-frequency EEG activity, we applied continuous wavelet transformation with variance cycles (3 cycle in length at 1 Hz, increasing linearly along with frequency to 15 cycles at 30 Hz) to calculate the power of each frequency band. After time-frequency transformation, epochs were cropped into −1.5 to 2.5 s epochs to eliminate edge artifacts, followed by baseline correction using the interval from −1.5 to −0.2 s. Time-frequency results were conducted on Cz based on a recent TMR study (Schechtman et al., 2021). Time-frequency analysis was conducted in MNE-Python.

3 | RESULTS

3.1 | TMR behavioral benefits

We first quantified the extent to which the differential change in bias for the TMR benefit was larger in the high- than in the low-benefit group (Mean ± *SE*, High: 0.792 ± 0.118; Low: −0.178 ± 0.09; independent sample *t*-test, $t(26) = 6.51$, $p < .001$, 95% CI [0.66, 1.28], Cohen's $d = 2.46$, Figure 2a). This difference was expected given the median-split procedure for creating the two groups.

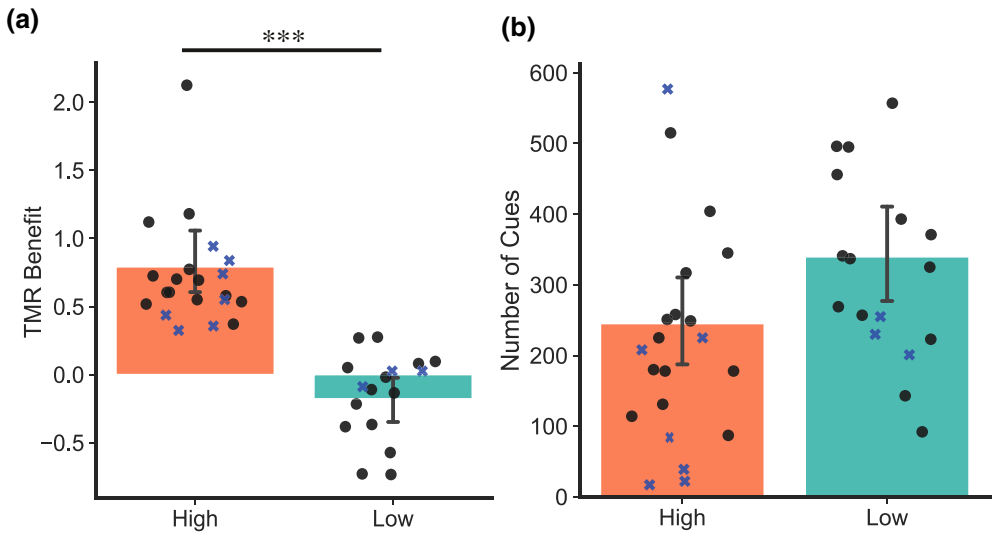

FIGURE 2 (a) TMR benefit and (b) the number of cues played in the high-benefit (high) and low-benefit (low) groups, defined by the magnitude of TMR benefit. TMR benefit scores and the number of cues from excluded participants ($n = 10$) are displayed with blue × symbols (note that the means and *SE* values were computed without these 10 participants).

Data from sleep-staging data are shown in Table 1. There was significantly less SWS in the high-benefit group than in the low-benefit group. Given that cues were played during SWS, the high-benefit group tended to receive fewer cues than the low TMR benefit group (245 ± 30 and 340 ± 35, respectively, $t(26) = 1.96$, $p = .060$, 95%CI [−193.38, 4.38], Cohen's $d = 0.74$, Figure 2b). Correlational analyses across all participants showed that neither SWS duration ($r(28) = -.28$, $p = .150$) nor number of cues ($r(28) = -.21$, $p = .152$) were significantly related to the TMR benefit. Based on these patterns of group differences, we can rule out the idea that stronger TMR benefits in the high-benefit group can be explained by a greater number of cues played or longer periods spent in SWS.

3.2 | TMR benefits were associated with a preferred phase angle of slow oscillation

To assess the relationship between TMR benefits and the phase of slow oscillations associated with cue onsets, we first assessed the slow-oscillation phases associated with cue onset at Fz in each participant. Given that our TMR cueing protocol was open-loop and thus not contingent upon EEG activity, it can be expected that for most participants, the cue onset phases would be randomly distributed within each participant. Indeed, we found that only 3 out of 14 participants in the high-benefit group, and 2 out of 14 participants in the low-benefit group had significantly non-uniform distributions (for phase distribution at a participant level, see Figure S2).

We next tested at a trial-level, whether the two groups showed different cue-onset phase distribution patterns related to slow-oscillation activity. To this end, we extracted the phase of cue onset for each trial, and collapsed this trial-level phase information across participants within each group. We found that the phase of cue onset showed a significant non-uniform distribution in the high-benefit group, preferentially clustering around 76° ($Z(3432) = 7.45$, $p < .001$, Rayleigh Z test, Figure 3a). In contrast, phases of cue onset were not significantly clustered in the low-benefit group ($Z(4755) = 0.41$, $p = .662$, Rayleigh Z test, Figure 3b). Given the different numbers of trials in the two groups, we next used re-sampling to control the influence of unequal trial numbers on phase calculation and clustering strength. In the low-benefit group, we randomly selected 3432 out of 4755 trials with replacements to match the number of trials in the high-benefit group, and calculated the phase clustering via Rayleigh Z tests. We repeated this re-sampling procedure 5000 times to create Rayleigh Z distributions for low-benefit groups (see Figure 3c). Regarding the high-benefit group, we repeated the same procedure (sampling 3432 out of 3432 with replacement) to create Rayleigh Z distributions for the high-benefit group (Figure 3c). Visual inspection of Figure 3c suggests that only the high-benefit group showed significant clustering and that the high-benefit group showed stronger clustering strength (i.e., higher Rayleigh Zs) than the low-benefit group. We next used the permutation test to statistically confirm this difference: we shuffled the labels of Rayleigh Zs from high- and low-benefit groups obtained in Figure 3c, and calculated a difference score between simulated "high" versus "low" groups. This procedure was repeated 5000 times to create a null distribution with 5000 difference scores. Comparing the empirical high- versus low-benefit group Rayleigh Zs difference against this null distribution revealed that the high- versus low-benefit group difference was highly significant ($p < .001$, Figure 3d). Together, these results suggest that with a matching number of trials, cue onset phases in the high-benefit group showed significant clustering in the 0.1–1.5 slow oscillation band; while cue onset phases in the low-benefit group showed random distributions. Moreover, the clustering strengths in the high-benefit group were significantly higher than that in the low-benefit group.

3.3 | TMR benefits were associated with cue-elicited delta power

Whereas the results above show that cue timing relative to ongoing slow oscillations was associated with the

TABLE 1 Sleep stages (in min, mean ± *SE*) in high- and low-benefit groups

Sleep stage	High-benefit group ($n = 14$)	Low-benefit group ($n = 14$)	*p*-value
Wake	23.04 ± 5.03 (min)	18.93 ± 4.34 (min)	.54
N1	7.29 ± 0.88 (min)	7.29 ± 1.89 (min)	1
N2	27.21 ± 2.61 (min)	24.57 ± 2.64 (min)	.48
N3	22.21 ± 2.74 (min)	34.29 ± 4.75 (min)	.04*
REM	6.18 ± 1.54 (min)	4.75 ± 1.59 (min)	.52
Total sleep time	62.89 ± 4.48 (min)	70.89 ± 5.01 (min)	.24
Total time	85.93 ± 1.99 (min)	89.82 ± 2.93 (min)	.28

*$p < .05$.

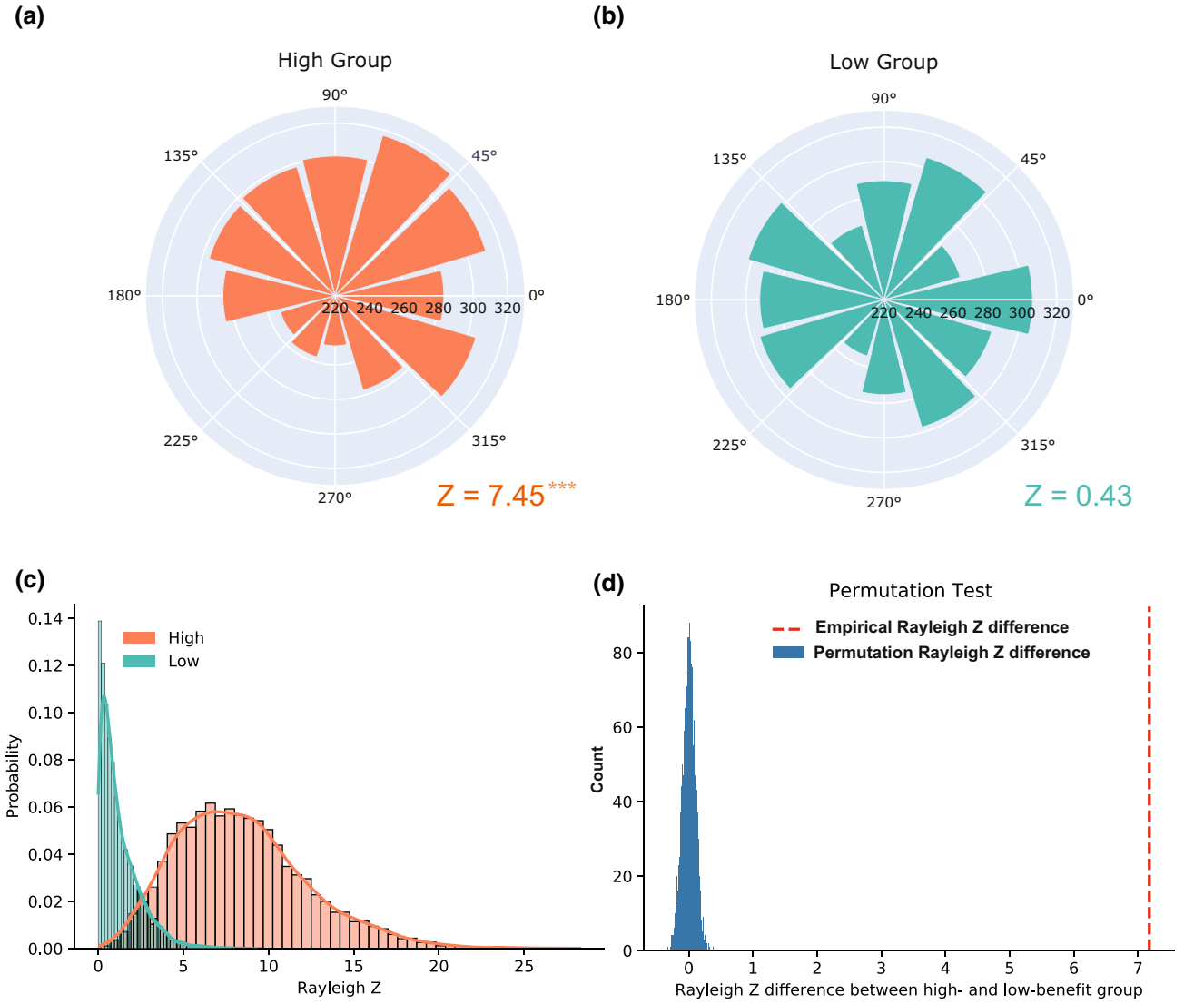

FIGURE 3 (a and b) Distributions of cue onset time in relation to 0.1–1.5 Hz slow-oscillation phase measured at Fz, collapsing trials across all participants from the high- and low-benefit groups, separately. Note that this analysis matched the trial numbers between these two groups. (c) A re-sampling with replacement procedure was repeated 5000 times to create Rayleigh Z distributions for high- and low-benefit groups, separately. (d) A permutation test was conducted to statistically confirm the difference between the Rayleigh Z distributions of high- versus low-benefit groups, which revealed that the empirical Rayleigh Z difference was highly significantly larger than the permutation Rayleigh Z difference ($p < .001$). *** denoted $p < .001$.

magnitude of TMR benefits, it would also be informative to know the role of cue-elicited EEG activity in influencing TMR benefits. Accordingly, we computed cue-elicited ERPs and time-frequency EEG responses. A non-parametric permutation test was conducted on ERPs across time points at Cz between the high- and low-benefit groups. No significant results were observed (cluster $ps > .86$, Figure S2), suggesting that ERPs were not significantly different between groups.

For time-frequency analyses, we focused on preselected electrode Cz in accordance with a recent TMR study (Schechtman et al., 2021). First, we performed a non-parametric cluster-based permutation test across time points and frequencies collapsing across all participants. This analysis identified significant clusters modulated by auditory cueing during sleep (delta-theta (1–9 Hz) cluster: cluster $p = .001$, sigma cluster (15–20 Hz): cluster $p = .037$). We further divided the delta-theta clusters into delta (1–4 Hz) and theta (4–9 Hz) separately to clarify the specific role of frequency bands in social bias reduction (Canales-Johnson et al., 2020; Legendre et al., 2022; Lehmann et al., 2016). Next, based on these three identified clusters, we compared EEG power from each cluster between high- and low-benefit groups. As shown in Figure 4a, results appeared to differ between the two groups in the delta (1–4 Hz) band during 250–1000 ms post cue onset ($t(26) = 2.35$, $p = .027$). In contrast, the between-group differences were not significant for the

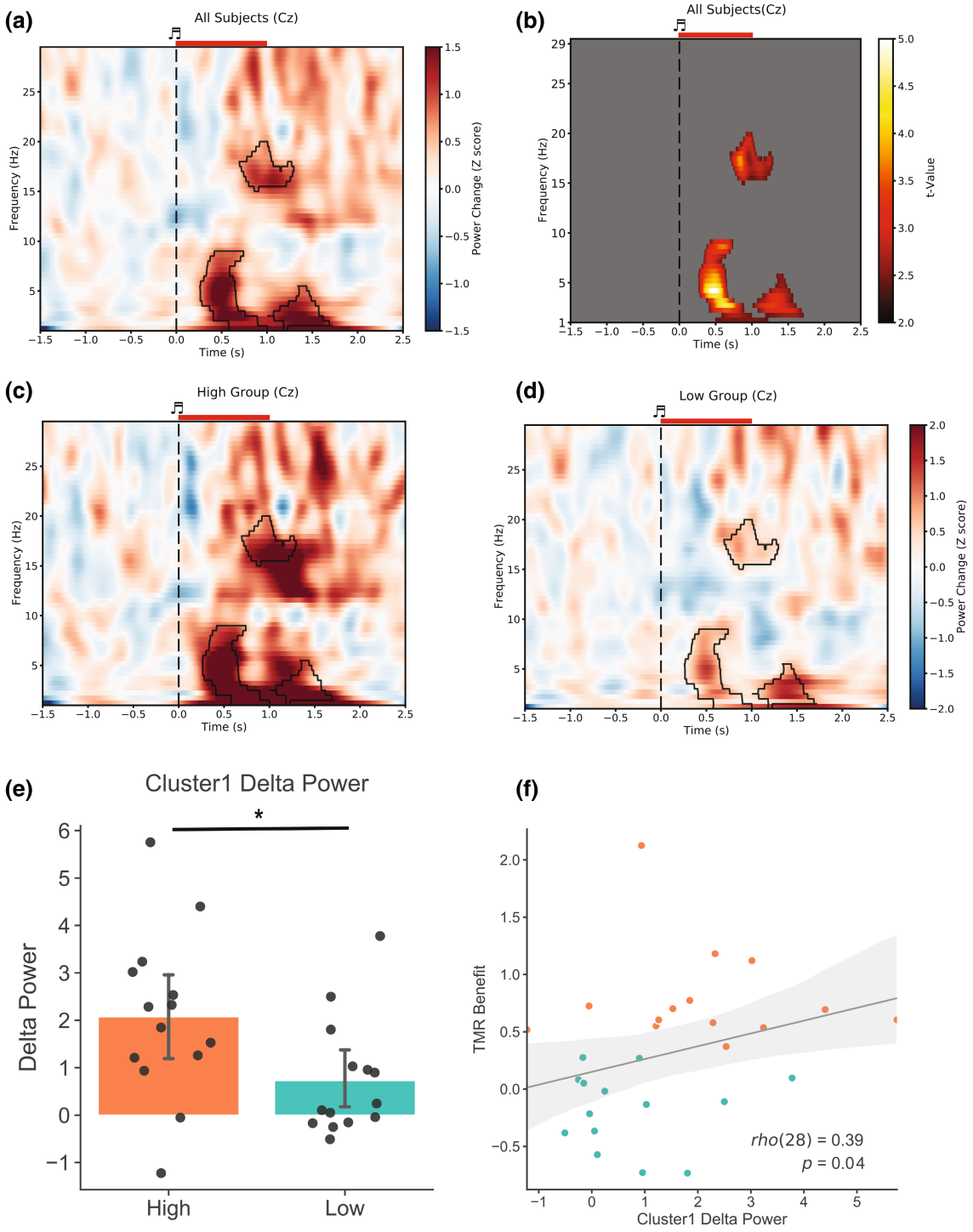

FIGURE 4 Electrophysiological differences between high-benefit and low-benefit groups. (a) A time-frequency raw power map across all participants. (b) Map of *t*-values for clusters modulated by auditory cues during sleep across all participants using a cluster-based permutation test on time-frequency data. Results revealed cluster 1 delta and theta power (~0–1000 ms), cluster 2 delta power (~1000–2000 ms), and cluster 3 sigma-beta power (~800–1400 ms). See Figure S1 for time-frequency results from all electrodes. The vertical line at time 0 ms represents cue onset, with the red line representing the duration of the sound (1000 ms). (c and d) time-frequency plots for high-benefit and low-benefit groups, with significant clusters highlighted, the color bars were the same in (c) and (d). (e) power difference between delta (~0–1000 ms, taken from the significant cluster). (f) Spearman correlation coefficient between cue-elicited delta power and the TMR benefit.

250–1000 ms theta (4–9 Hz) band ($t(26) = 1.30$, $p = .205$), nor for 1000–2000 ms delta (1–4 Hz) band ($t(26) = 0.74$, $p = .467$), nor for 800–1400 ms sigma-beta (15–20 Hz) band ($t(26) = 1.46$, $p = .155$). In addition to between-group comparisons, we conducted correlation analyses between TMR benefits and delta, theta, and sigma power from each

cluster across all participants. For delta power in cluster1 within the ~250–1000 ms time window, we found a significant correlation between cue-elicit delta power and TMR benefits ($rho(28) = 0.39$, $p = .042$). We did not observe significant correlations in cluster1 theta ($rho(28) = 0.25$, $p = .202$), cluster2 delta ($rho(28) = .07$, $p = .736$), and cluster 3 sigma-beta ($rho(28) = .16$, $p = .404$).

4 | DISCUSSION

What physiological events are associated with successful TMR-induced bias reduction during sleep? We addressed this question using data from a prior study in which targeted memory reactivation (TMR) was used following training to combat unintentional social biases (Hu, Antony et al., 2015). We found that larger TMR benefits in bias reduction emerged when memory cues (1) clustered toward the slow-oscillation upstate, and (2) elicited power increases in the delta EEG band. These results complement recent evidence concerning neural mechanisms of memory reactivation, particularly findings that demonstrated the importance of optimal slow-oscillation phase and cue-elicited delta power in memory reactivation and consolidation (Ai et al., 2018; Batterink et al., 2016; Batterink & Paller, 2017; Schreiner et al., 2015).

Our study is not the first to link TMR effects with preferential timing of cues to slow-oscillation phases (Batterink et al., 2016; Göldi et al. (2019; Ngo & Staresina, 2022). This clustering may have occurred here due to chance factors in this subset of individuals with respect to when cues were presented or instead to specific factors related to the generation of slow waves. Following previous TMR research (e.g., Creery et al., 2015; Rudoy et al., 2009), auditory cues in our study were delivered every 5 s (0.2 Hz) during SWS. Perhaps this rhythm entrained EEG oscillations in some participants, influencing slow-oscillation phase and delta power changes. Indeed, a recent study suggests that open-loop auditory stimulation can induce slow-oscillation amplitude changes (Huwiler et al., 2022).

Batterink et al. (2016) first reported that TMR benefits were predicted by slow-oscillation phase at the time of cueing: cues played during one particular interval of the slow-wave cycle (180–270°) led to less forgetting of cued items than did cues played during other phases. Subsequently, employing closed-loop stimulation to directly manipulate the timing of cues, Göldi et al. (2019) reported that memory cues delivered at the beginning of slow-oscillation upstates (but not downstates) yielded memory benefits as well as memory-related differences in theta and spindle-band EEG responses (Göldi et al., 2019). Similarly, we found stronger TMR effects when cues clustered during the upstate of 0.1–1.5 Hz slow oscillations (i.e., ~75° at the frontal region). Discrepancies in phase values between our results and those of Batterink et al. (2016) may be due to different TMR procedures. Batterink et al. (2016) used 25 unique sounds to reactivate 25 unique item memories, whereas our study used one auditory tone to reactivate training-related memories; much less processing may have been needed for sound categorization in the present study. Moreover, our results suggest that not only does slow-oscillation phase matter when a single sound is presented (as in Batterink et al., 2016), but also the preferred phase angle over many repetitions of the same sound appears to influence TMR benefits. Despite these differences, it is noteworthy that both the study by Batterink et al. and our study showed that TMR effects were stronger when cues incidentally occurred during an optimal phase of slow-oscillation activity. While future research is warranted to further establish the causal role of cue-onset timing and subsequent TMR benefits, extant findings consistently suggest that the timing of cues relative to slow oscillations is important for effective TMR (Göldi et al., 2019; Ngo et al., 2013; Ngo & Staresina, 2022). Indeed, one important prediction of the active systems consolidation account is that memory consolidation is more effective when memories are reactivated during the slow-oscillation upstate (Klinzing et al., 2019; Rasch & Born, 2013).

Other characteristics of sleep such as SWS duration have also been implicated in memory improvements in spatial memory, skill acquisition, fear extinction, and preference change (Ai et al., 2018; Antony et al., 2012; Cairney et al., 2014; Hauner et al., 2013; Oudiette et al., 2013; but see Cordi & Rasch, 2021b). Our results extend previous research by suggesting that cue-elicited delta power within the first 1000 ms post-cue contributed to the reactivation of recent counter-bias training, resulting in further weakening of long-standing biases. These findings, taken together, corroborate previous TMR findings and emphasize the critical role of slow oscillations and delta-band neural activity in memory reactivation and consolidation (Ai et al., 2018; Antony et al., 2012; Rudoy et al., 2009; Schreiner et al., 2015).

In addition to slow oscillations and delta activity, spindle-related activity (e.g., spindle density, power) has also been implicated in prior studies of TMR-induced memory consolidation (Antony et al., 2018; Cairney et al., 2018; Creery et al., 2015). Specifically, Cairney et al. (2018) reported that cue-elicited spindle activity carried category-level memory information at the time of reactivation, which was then associated with memory performance after sleep. In the present study, although auditory cues modulated sigma activity relative to pre-cue

baselines, sigma activity was not associated with TMR benefits.

One motivation for the current investigation was to understand whether there are specific neural characteristics that differentiate strong versus weak TMR benefits in bias reduction. While meta-analytical evidence of TMR convincingly suggests that memories can be selectively targeted and improved during SWS, the effect sizes of individual studies vary significantly (Hu et al., 2020). In the context of bias reduction, two studies were published, both conducted using a within-subject manipulation and auditory TMR during an afternoon nap, with the first reporting a significant TMR effect and the second reporting a null effect (Hu, Antony et al., 2015; Humiston & Wamsley, 2019). One possible explanation for this divergence in effect size across studies would emphasize the small size of an underlying effect, such that real effects are sometimes missed when small sample sizes are used. An alternative possibility is that memory reactivation does not change bias reduction and that the Hu, Antony et al., (2015) results are spurious, but the present findings of systematic relationships with sleep physiology cast doubt on that alternative. It is also possible that cues sometimes may not successfully reactivate corresponding memories due to factors not yet understood. In addition to the present and previous findings on preferential slow-wave phase and EEG power, sleep disruptions and arousal due to auditory cueing are also factors shown to be detrimental to memory benefits (Göldi & Rasch, 2019; Whitmore et al., 2022). Future research is warranted, preferably with closed-loop cue delivery that targets certain phase angles (see Göldi et al., 2019), to provide causal evidence on the relationship between these neural characteristics and TMR benefits.

Research with the method of targeted memory reactivation opens exciting new avenues for manipulating offline memory processing during sleep and for understanding how fundamental aspects of sleep influence memory storage. At a mechanistic level, what are the neural mechanisms that contribute to reactivation-induced behavioral benefits? The present approach provided some insights. We found that for TMR to be effective in weakening existing social biases, both cue timing relative to slow-oscillation phase and cue-elicited EEG power in the delta band is important. Together, these results contribute to our understanding of the optimal brain activity that can support memory reactivation during sleep and its behavioral benefits after sleep.

AUTHOR CONTRIBUTIONS

Tao Xia: Formal analysis; methodology; project administration; writing – original draft; writing – review and editing. **James W. Antony:** Writing – review and editing. **Ken A. Paller:** Writing – review and editing. **Xiaoqing Hu:** Conceptualization; funding acquisition; resources; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST

Nothing declared.

DATA AVAILABILITY STATEMENT

Pre-processed data and the code used for analysis are available at the open science framework (OSF: osf.io/s3yt4/).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1.

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