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RESEARCH ARTICLE

A daytime nap with REM sleep is linked to enhanced generalization of emotional stimuli

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Summary

How memory representations are shaped during and after their encoding is a central question in the study of human memory. Recognition responses to stimuli that are similar to those observed previously can hint at the fidelity of the memories or point to processes of generalization at the expense of precise memory representations. Experimental studies utilizing this approach showed that emotions and sleep both influence these responses. Sleep, and more specifically rapid eye movement sleep, is assumed to facilitate the generalization of emotional memories. We studied mnemonic discrimination by the emotional variant of the Mnemonic Separation Task in participants ($N = 113$) who spent a daytime nap between learning and testing compared with another group that spent an equivalent time awake between the two sessions. Our findings indicate that the discrimination of similar but previously not seen items from previously seen ones is enhanced in case of negative compared with neutral and positive stimuli. Moreover, whereas the sleep and the wake groups did not differ in memory performance, participants entering rapid eye movement sleep exhibited increased generalization of emotional memories. Our findings indicate that entering into rapid eye movement sleep during a daytime nap shapes emotional memories in a way that enhances recognition at the expense of detailed memory representations.

KEYWORDS
daytime nap, generalization, memory consolidation, Mnemonic Separation Task, rapid eye movement sleep

1 | INTRODUCTION

Good memory is often conceptualized as accurate and detailed; however, generalization creating overlapping memory representations is also an integral feature of memory processing (Asok et al., 2019; Stickgold & Walker, 2013). Generalization depends on a neurocognitive process called pattern completion (Hunsaker & Kesner, 2013; Keresztes et al., 2018; Rolls, 2013), which enables the matching of incoming information with memory representations that overlap partially with the new input. On the flipside, a computation named pattern separation distinguishes incoming information from stored representations (Norman & O'Reilly, 2003). These processes are implemented by the hippocampus, as the microstructure of this region enables the formation of an auto-association network capable of performing such comparison processes (Cayco-Gajic & Silver, 2019; McNaughton & Morris, 1987).

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The Mnemonic Similarity Task (MST) is a widely used measure to assess the behavioural outcomes of pattern completion and separation (Stark et al., 2019). The MST is a modified object recognition task in which "lures" (i.e. novel but visually similar pictures to the previously presented pictures) are shown in the test phase along with "foil" pictures (not similar to the previously presented ones). Lures identified as "similar" or erroneously as "old" items yield to higher lure discrimination (LD) and generalization (GN) scores, respectively (Stark et al., 2019; Yassa & Stark, 2011). Since these behavioural measures are influenced by the fidelity of memory representations, which in turn is impacted by post-encoding memory processes, intervening time intervals between encoding and retrieval are of major interest.

Sleep is assumed to play a key role in memory reprocessing (Diekelmann & Born, 2010; Rasch & Born, 2013) and, more specifically, in mnemonic generalization (Lerner et al., 2021; Walker & Stickgold, 2010). Nonetheless, a recent experiment with the MST indicated that post-encoding nighttime sleep facilitated LD compared with a wake control condition (Doxey et al., 2018). Likewise, another study found that daytime sleep stabilized discrimination performance, especially for lures that were more different from the originally presented pictures (Hanert et al., 2017). Interestingly, a reverse pattern was found for highly similar lures, as sleep enhanced the generalization of these stimuli. These results may suggest that the behavioural measures of the MST depend on the level of similarity between previously presented and lure stimuli in the case of neutral stimuli. Moreover, sleep is a highly heterogeneous process, therefore inconsistent findings might also owe to the fact that different stages of sleep influence generalization and discrimination independently.

Post-encoding memory processes are profoundly modulated by emotions (McGaugh, 2018). Several studies observed that LD was enhanced in the case of emotionally salient material compared with neutral items (Cellini, 2023; Segal et al., 2012; Szőllősi et al., 2022; Szőllősi & Racsmány, 2020), and such increased discrimination was related to subjective (Szőllősi & Racsmány, 2020) and physiological measures of increased arousal (Segal et al., 2012). In contrast, another study observed the opposite: relatively reduced LD in the case of emotional material, which bias was even strengthened after a 24-hr-long delay, suggesting that emotionally charged memories especially in the long term are biased towards generalization (Leal et al., 2014). Nevertheless, the extent of generalization and the specific contribution of sleep on memory integration were not yet systematically examined.

Studies focusing on the processing of emotional memories indicate that generalization occurs during the rapid eye movement (REM) stage (Lerner et al., 2021; Sterpenich et al., 2014; Stickgold & Walker, 2013). For instance, memory reactivation by auditory cues facilitated the generalization of memory representations when the cues were presented during REM sleep (Sterpenich et al., 2014). Additionally, REM sleep seems to impair the recall of specific emotional memories while enhancing the recognition of threat signals, indicating a shift toward enhanced generalization (Lerner et al., 2021). In sum, while emotions may facilitate memory encoding, resulting in more detailed memory representations, sleep, and particularly REM sleep, appear to interact with these highly detailed emotional memories reducing their distinctiveness and increasing generalization. Here, we applied the emotional variant of the MST (Szőllőssi & Racsmány, 2020) and examined mnemonic discrimination 2 hr after encoding in participants that spent a daytime nap between learning and testing compared with another group that spent an equivalent time awake between the two sessions. We hypothesized that a daytime nap including REM sleep would facilitate the generalization (indicating pattern completion) of emotionally charged memories. Our study fills a hole in the current literature as it is the first one to assess the effect of a daytime nap on behavioural measures of the MST using polysomnography.

2 | METHODS

2.1 | Participants

Participants were university students from Eötvös Loránd University, and received partial course credits for participation. Participants reported no prior neuropsychiatric diagnoses or sleep disturbances, no use of mind-altering substances in the days before the experiment, and had normal or corrected to normal vision. The participants were not informed about the goal of the experiment before the completion of the tasks, but they were debriefed after. The task was completed by 121 participants. A total of nine exclusions left 112 participants in the final sample (age: 21.1 ± 3.1 years; 89 females), split randomly into a napping ($n = 55$; age: 21.1 ± 1.8 years; 46 females) and a wake group ($n = 57$; 21.1 ± 3.8 years; 43 females). Exclusions were made due to an abundance (over 40%) of missed responses ($n = 4$), inability to fall asleep in the nap group ($n = 3$) and technical problems concerning polysomnography ($n = 2$). Although we collected data regarding sleep the night before participation, we did not have to exclude anyone due to severe sleep restriction (average sleep time in hours the night before participation: 7.1 ± 1.3). The groups did not differ significantly in reported subjective sleep duration before task participation. Polysomnography was carried out in the napping group, and the staging of sleep served as the basis for distinguishing between those participants who entered REM sleep ($n = 19$) and those who did not ($n = 36$). Informed consent was obtained from all participants, and the procedures were approved by the United Ethical Review Committee for Research in Psychology, Hungary.

2.2 | Experimental design

Experimental sessions were carried out between 12:00 hours and 16:00 hours. We used the emotional variant of the MST, which was previously validated in other studies (Szőllősi et al., 2022; Szőllősi & Racsmány, 2020). The task, described in the next section, consists of a study phase and a test phase. After the study phase, participants in the wake group could return to their daily activities outside the lab in the upcoming 2 hr, while members of the napping group were

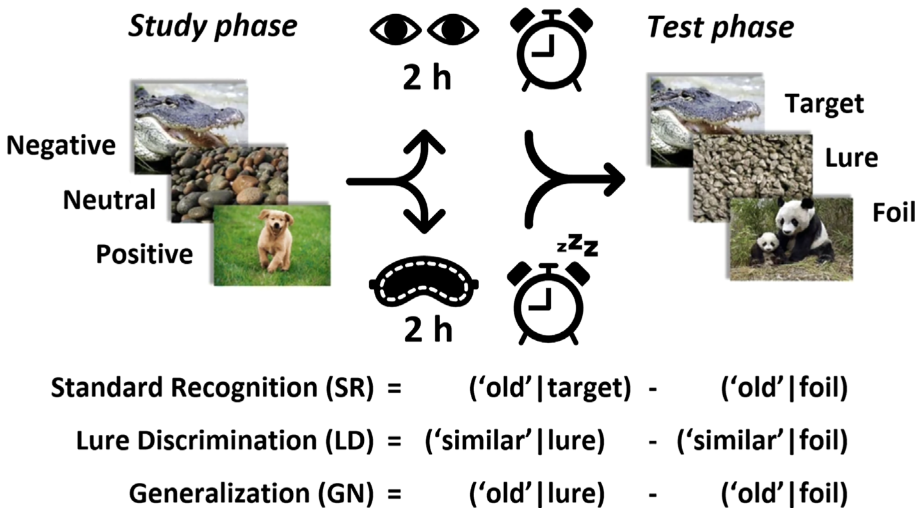

FIGURE 1 The study consisted of a study phase where participants viewed and rated pictures according to their emotional valence followed by a 2-hr-long delay, which some participants spent awake and some spent asleep. Daytime naps were monitored with sleep electroencephalography (EEG). After this delay, participants completed the test phase where previously presented pictures (targets) were intermixed with stimuli similar to previously presented pictures (lures) and entirely novel pictures (foils). Outcome measures including standard recognition (SR), lure discrimination (LD) and generalization (GN) were quantified as indicated in the figure.

provided the opportunity to spend a daytime nap (monitored with sleep electroencephalography [EEG]) for a maximum of 2 hr in our sleep laboratory. After this delay, all participants completed the test phase of the MST.

2.3 | Experimental task

The emotional variant of the MST presents 156 pictures (52 negative, 52 neutral, 52 positive) in the study phase preceded by 10 practice trials (emojis). In the study phase, the participants were asked to indicate the emotional valence of the stimuli by pressing a key on the keyboard (1: negative–9: positive). The stimuli were presented for a total of 2500 ms, with 500 ms inter-stimulus interval (ISI). The test phase consisted of a total of 234 trials. Out of these trials: 78 were targets (pictures presented during the study phase: 26 negative; 26 neutral; 26 positive); 78 were lures (pictures visually similar to the ones presented during the study phase: 26 negative; 26 neutral; 26 positive); and 78 were foils (pictures not resembling those presented during the study phase: 26 negative; 26 neutral; 26 positive). The stimuli were presented for 2500 ms with an ISI of 500 ms. The participants indicated with a keypress if the stimulus presented was already seen during the study phase ("old" response), was similar to a stimulus presented in the study phase ("similar" response) or was completely new ("new" response). Key assignments were the following: F = old, H = similar, and K = new. Based on the responses during the test phase we calculated standard recognition (SR), LD and GN scores. SR was calculated for all valence categories separately by calculating the rate of old responses to target stimuli ("old" | target) and subtracting the rate of old responses to foils ("old" | foil). LD and GN were calculated in a similar way: LD = ("similar" | lure) − ("similar" | foil); GN = ("old" | lure) − ("old" | foil). The experimental design of the study is summarized in Figure 1.

2.4 | Polysomnography

After arriving in the laboratory, participants of the sleep group were fitted with nine EEG electrodes (F3, F4, Fz, C3, C4, Cz, P3, P4, Pz) in accord with the 10–20 electrode placement system. Bipolar electrooculography (EOG), electromyography and electrocardiography electrodes were also used to measure eye- and muscle-related movements and heart rate during sleep. Gold-coated Ag/AgCl EEG cup electrodes were fixed with EC2 Grass Electrode Cream (Grass Technologies, Natus Manufacturing, Galway, Ireland) and referred to the mathematically linked mastoid (A1, A2) electrodes. Impedances were kept below 8 kΩ. The data were recorded with Micromed SD LTM 32 Bs (Micromed S.p.A., Mogliano Veneto, Italy) and System-PLUS 1.02.1098 software (Micromed Srl, Roma, Italy). Signals were digitized with 16-bit resolution with 512 Hz sampling rate. We scored the sleep stages during the nap by conventional criteria (Berry et al., 2012). The scoring was performed by trained experts. We used total sleep time and REM sleep duration in further analyses. We also calculated the spectral power of the EOG channel during REM sleep between 0.5 and 2.5 Hz by Fast Fourier Transformation on Hanning-tapered 4-s-long windows. This was done to yield a variable strongly related to eye movements during REM sleep. We also used a manual detection method for eye movements, which yielded the absolute number and density of eye movements during REM sleep (the ratio of seconds with eye movements of the full time spent in REM sleep). We found strong correlations (between 0.7 and 0.8) with the ratio of eye

TABLE 1 Sleep macrostructure data for the REM group and the NREM group.

	REM group	NREM group	Independent samples *t*-test			
Sleep dur. (min)	94.6 ± 10.1	60.3 ± 25.1	$t_{54} = 7.17$	$p < 0.01$	$d = 1.61$	CI[0.97, 2.26]
Sleep eff. (%)	81.5 ± 10.1	57.0 ± 19.7	$t_{54} = 6.08$	$p < 0.01$	$d = 1.43$	CI[0.80, 2.06]
Sleep lat. (min)	9.9 ± 8.1	13.9 ± 9.0	$t_{54} = -1.65$	$p = 0.11$	$d = -0.45$	CI[−1.03, 0.12]
WASO (min)	12.3 ± 10.4	30.4 ± 14.8	$t_{54} = -5.29$	$p < 0.01$	$d = -1.35$	CI[−1.97, −0.73]
Stage 1 dur. (min)	16.2 ± 12.3	17.2 ± 14.5	$t_{54} = -0.26$	$p = 0.80$	$d = -0.06$	CI[−0.64, 0.50]
Stage 2 dur. (min)	32.8 ± 12.2	23.3 ± 12.6	$t_{54} = 2.72$	$p < 0.01$	$d = 0.76$	CI[0.17, 1.35]
SWS dur. (min)	26.1 ± 17.9	19.8 ± 19.4	$t_{54} = 1.21$	$p = 0.24$	$d = 0.33$	CI[−0.24, 0.91]

Note: The two groups not only differ in the presence of REM sleep, but also in sleep efficiency, wakefulness after sleep onset (WASO), overall sleep duration and the length of the NREM2 phase.

Abbreviations: NREM, non-rapid eye movement; REM, rapid eye movement; SWS, slow wave sleep; WASO, wakefulness after sleep onset.

movements in the 0.5–1.75-Hz frequency range of the EOG power spectra, and used the cumulated power of these frequencies for further analyses as a measure of REM density. We hypothesized that REM sleep duration and REM density as indicators of REM pressure would accentuate the behavioural effects we expected in the group entering into REM sleep.

2.5 | Statistical analyses

We analysed the valence responses given during the study phase to ensure that the emotional valence of the stimulus material was perceived as intended by our sample. This was done with an analysis of variance (ANOVA) model using the valence category of pictures as a within-subjects factor (VALENCE: negative versus neutral versus positive) and the grouping as a between-subjects factor (GROUP: nap versus wake). The model also contained an interaction term between these factors (GROUP × VALENCE). We also used ANOVA models to compare SR, LD and GN for differently valenced picture categories (VALENCE: negative versus neutral versus positive) between the napping and wake groups (GROUP: nap versus wake) in the test phase.

The polysomnographic recordings were staged visually using standardized criteria (Berry et al., 2012), and the appearance of REM sleep in the recordings served as the basis for further division of the sleep group. A total of 19 participants entered REM sleep, the mean and standard deviation of time (minutes) spent in REM was 19.4 ± 10.9 (min: 1.7; max: 40). In order to examine the influence of REM sleep on memory performance, we repeated the above-mentioned ANOVA models with this between-subjects factor (GROUP: wake versus non-rapid eye movement [NREM] versus REM). We also conducted an ANCOVA with total sleep duration and Stage 2 duration as covariates to control for the influence of sleep architecture differentiating the NREM and REM groups.

Finally, we calculated emotional bias (EB) scores for GN, LD and SR by subtracting the appropriate score for neutral stimuli from the score for negative and positive stimuli (e.g. to calculate EB for GN, we used the formulas: $EB_{neg} = GN_{neg} - GN_{neu}$; $EB_{pos} = GN_{pos} - GN_{neu}$). We correlated these variables within the REM group with variables related to sleep.

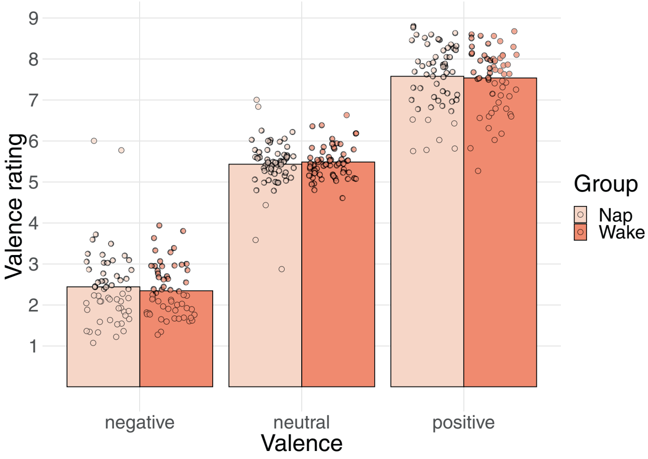

FIGURE 2 Subjective valence ratings (1: most negative; 9: most positive) for the pictures presented during the study phase. Bars represent mean values for the groups, and circles stand for the individual mean ratings for the different valence categories.

3 | RESULTS

3.1 | Sleep quality and macrostructure

Measures of sleep architecture of the participants in the sleep group are summarized in Table 1. Participants entering into REM sleep spent significantly more time asleep and less time awake after falling asleep. In addition, they also spent more time in Stage 2 sleep, compared with participants who fell asleep, but did not reach the REM phase.

The previous night's sleep quality as assessed by subjective sleep duration the night before the experiment was not different across the groups Wake versus Sleep (GROUP: $F_{1110} = 0.07$, $p = 0.79$, $\eta^2G < 0.01$) and Wake versus NREM versus REM (GROUP: $F_{2109} = 0.03$, $p = 0.97$, $\eta^2G < 0.01$).

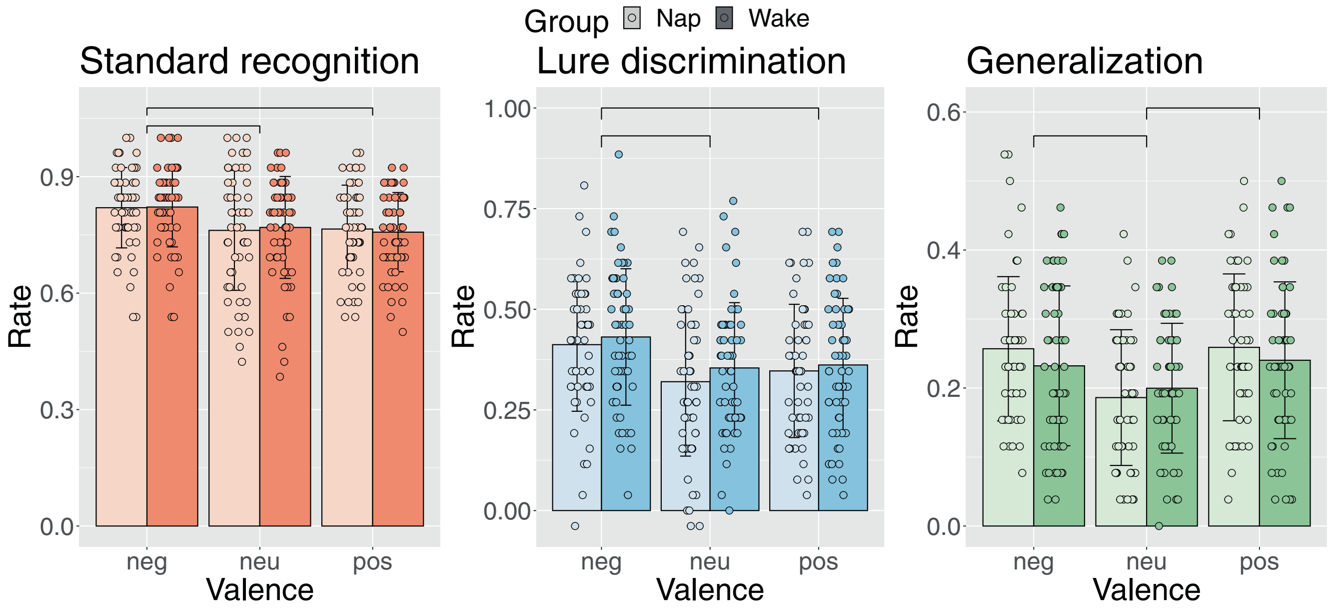

FIGURE 3 Standard recognition (SR), lure discrimination (LD) and generalization (GN) during the test phase for the nap and the wake groups by stimulus valence (neg = negative; neu = neutral; pos = positive). Bars represent the mean and error bars show the standard deviation. Circles represent the individual scores. Significance lines show statistically significant differences between valence categories. SR and LD were enhanced for negative images compared with neutral and positive ones, whereas GN was superior for both negative and positive images compared with neutrals. The daytime sleep and wake groups showed no differences in performance.

3.2 | Wake versus sleep group contrasts

The ANOVA on the valence ratings (Figure 2) showed no main effect for group membership (GROUP: $F_{1110} = 0.28$, $p = 0.60$, $\eta^2G < 0.01$), but showed a main effect of picture valence (VALENCE: $F_{2220} = 1280.18$, $p < 0.01$, $\eta^2G = 0.90$). The model did not indicate an interaction effect (GROUP × VALENCE: $F_{2220} = 0.28$, $p = 0.76$, $\eta^2G < 0.01$). This finding indicates that valence ratings aligned with the valence categories of the images, and were similar across the groups.

Next, we performed ANOVA models predicting SR, LD and GN from group membership (Wake versus Sleep) and valence (Positive, Negative and Neutral). The ANOVA model on SR scores (Figure 3) showed no difference between groups (GROUP: $F_{1110} < 0.01$, $p = 0.93$, $\eta^2G < 0.01$), but a significant difference for the valence factor (VALENCE: $F_{2220} = 16.61$, $p < 0.01$, $\eta^2G = 0.05$), indicating relatively higher recognition performance for negative pictures compared with neutral ($t_{110} = 4.49$, $p < 0.01$, Cohen's $d = 0.44$, CI[0.24, 0.65]) and positive pictures ($t_{110} = 5.78$, $p < 0.01$, Cohen's $d = 0.56$, CI [0.36, 0.77]). The interaction term in this model was not significant (GROUP × VALENCE: $F_{2220} = 0.35$, $p = 0.71$, $\eta^2G < 0.01$).

The ANOVA model for LD (Figure 3) showed that there was no group level difference in "similar" responses to lures (GROUP: $F_{1110} = 0.81$, $p = 0.37$, $\eta^2G < 0.01$). The valence of the pictures, however, produced a significant effect (VALENCE: $F_{2220} = 17.81$, $p < 0.01$, $\eta^2G = 0.04$) due to higher LD in case of negative pictures as compared with neutral ($t_{110} = 5.70$, $p < 0.01$, Cohen's $d = 0.49$, CI[0.31, 0.67]) and positive ones ($t_{110} = 4.35$, $p < 0.01$, Cohen's $d = 0.40$, CI [0.21, 0.58]). There was no significant interaction between the two factors (GROUP × VALENCE: $F_{2220} = 0.23$, $p = 0.79$, $\eta^2G < 0.01$).

The ANOVA model on GN scores (Figure 3) suggested that group membership had no effect on these responses (GROUP: $F_{1110} = 0.39$, $p = 0.53$, $\eta^2G < 0.01$), while stimulus valence did have an effect (VALENCE: $F_{2220} = 16.06$, $p < 0.01$, $\eta^2G = 0.06$), reflecting higher values for negative versus neutral ($t_{110} = 4.66$, $p < 0.01$, Cohen's $d = 0.51$, CI[0.27, 0.74]) and positive versus neutral items ($t_{110} = 5.97$, $p < 0.01$, Cohen's $d = 0.56$, CI[0.36, 0.75]). The interaction term was not significant in this model either (GROUP × VALENCE: $F_{2220} = 1.93$, $p = 0.15$, $\eta^2G < 0.01$).

In sum, valence in the wake and the sleep groups showed no differences with respect to the measures of the MST task, but the emotional valence of the images did exert an influence on mnemonic discrimination and generalization. More specifically, negative images were more accurately recognized and identified as lures than neutral and positive images, whereas generalization (i.e. the false identification of lure images as previously seen images) was more pronounced in case of both negative and positive images compared with neutrals.

3.3 | Wake versus NREM versus REM group contrasts

In addition, we performed separate ANOVAs for three groups, splitting the sleep group into NREM and REM groups. The ANOVA models including the NREM versus REM versus WAKE contrast (Figure 4)

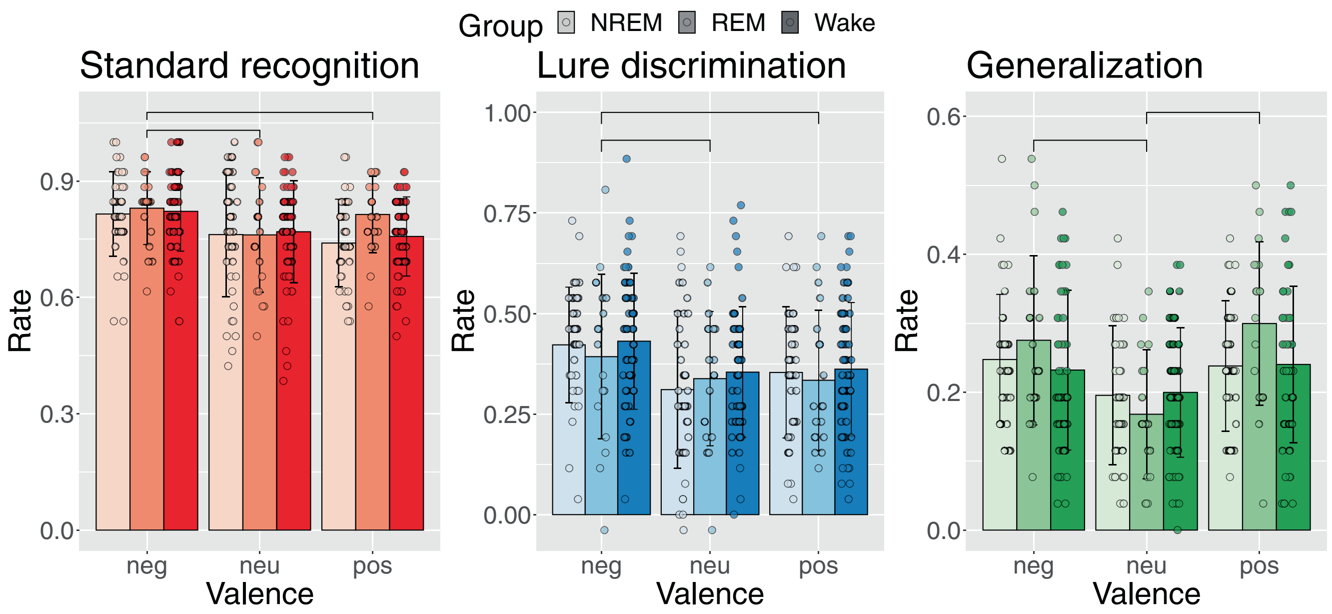

FIGURE 4 Standard recognition (SR) rate, lure discrimination (LD) rate and generalization (GN) rate during the test phase for the non-rapid eye movement (NREM), rapid eye movement (REM) and the wake groups by stimulus valence (neg = negative; neu = neutral; pos = positive). Bars represent the mean and error bars show the standard deviation. Circles represent the individual scores. Significance lines show statistically significant differences between valence categories. Generalization of negative and positive images compared with neutral ones was relatively enhanced in the REM group, compared with the nap without REM (NREM) group and the wake group.

yielded the following results. There was no difference for SR scores on the group level (GROUP: $F_{2109} = 0.66$, $p = 0.52$, $\eta^2G < 0.01$), only the valence factor showed a significant difference (VALENCE: $F_{2218} = 16.81$, $p < 0.01$, $\eta^2G = 0.05$). No significant interaction was observed in this model (GROUP × VALENCE: $F_{4218} = 1.33$, $p = 0.26$, $\eta^2G < 0.01$).

The ANOVA model for LD showed that there was no group level difference in "similar" responses to lures (GROUP: $F_{2109} = 0.41$, $p = 0.67$, $\eta^2G < 0.01$). The valence of the pictures produced a significant effect (VALENCE: $F_{2218} = 17.79$, $p < 0.01$, $\eta^2G = 0.04$), and there was no significant interaction between the two factors (GROUP × VALENCE: $F_{4218} = 0.56$, $p = 0.69$, $\eta^2G < 0.01$).

The ANOVA model on GN scores suggested that group membership had no effect on these responses (GROUP: $F_{2109} = 0.64$, $p = 0.53$, $\eta^2G < 0.01$), while stimulus valence did have an effect (VALENCE: $F_{2218} = 16.40$, $p < 0.01$, $\eta^2G = 0.06$). The interaction term, however, was significant in this model (GROUP × VALENCE: $F_{4218} = 2.65$, $p < 0.03$, $\eta^2G = 0.02$). Parsing out this interaction revealed that generalization was significantly higher for negatively and positively valenced pictures than for neutral stimuli in the REM group only ($t_{18} = 4.66$, $p < 0.01$, Cohen's $d = 0.51$, CI[0.27, 0.74]; $t_{18} = 5.97$, $p < 0.01$, Cohen's $d = 0.56$, CI[0.36, 0.75], respectively). Because differences in the group entering REM sleep might stem from other macrostructural discrepancies, we performed an additional analysis of covariance (ANCOVA) in which sleep latency, wakefulness after sleep onset (WASO), sleep duration and Stage 2 duration were entered as covariates in the model. The ANCOVA model showed that the occurrence of REM sleep influenced GN scores for emotional stimuli regardless of these covariates (GROUP: $F_{2105} = 1.92$, $p = 0.15$, $\eta^2G = 0.02$; VALENCE: $F_{2218} = 16.40$, $p < 0.01$, $\eta^2G = 0.06$; GROUP × VALENCE: $F_{4218} = 2.65$, $p = 0.03$, $\eta^2G = 0.02$; Covariates: sleep latency: $F_{1105} = 0.04$, $p = 0.83$, $\eta^2G < 0.01$; WASO: $F_{1105} < 0.01$, $p = 0.95$, $\eta^2G < 0.01$; total sleep duration: $F_{1105} = 0.09$, $p = 0.76$, $\eta^2G < 0.01$; S2 duration: $F_{1105} = 0.56$, $p = 0.46$, $\eta^2G < 0.01$). In sum, whereas falling asleep per se did not appear to influence performance in the MST task compared with an equivalent period spent awake, participants entering REM sleep during their daytime nap exhibited relatively increased generalization of emotional memories compared with neutral ones.

3.4 | REM and EB

We performed Pearson correlations between negative and positive EB scores and REM-related variables (REM duration, REM 0.5–1.75 Hz EOG spectral power, REM density). Correlation coefficients and statistical results are summarized in the Supplementary Materials. Negative EB for SR positively correlated with the duration of REM sleep and the absolute number of rapid eye movements. None of the other correlations was significant (all $p > 0.05$).

4 | DISCUSSION

In this study, we examined the influence of a daytime, post-encoding nap as compared with wakefulness on LD and GN of neutral and emotionally toned stimuli. More specifically, we examined if daytime naps with and without a period of REM sleep showed distinct associations with discrimination and generalization as assessed by the emotional variant of the MST.

Our findings indicate that LD, that is the discrimination of similar but previously not seen items from previously seen ones is enhanced in case of negative compared with neutral and positive stimuli. These results are in line with the findings of previous studies using the emotional variant of the MST (Szőllősi et al., 2022; Szőllősi & Racsmány, 2020). On the other hand, memory generalization was enhanced for both negative and positive items compared with neutral images. The sleep group did not differ in SR performance, mnemonic discrimination or generalization from the wake control group; however, the subgroup entering REM sleep showed a distinct pattern of memory performance. Whereas recognition and mnemonic discrimination were not different across the Wake, NREM and REM groups, we observed relatively enhanced generalization for negative and positive emotional items compared with neutral ones in the group of participants that entered REM sleep. Enhanced generalization for emotional items in the REM subgroup was observed regardless of differences in sleep architectural measures (e.g. sleep duration, WASO, Stage 2 duration), which differentiated the REM from the NREM subgroup.

Our results showing increased mnemonic discrimination for negative items are in line with a recent study that observed increased LD in case of negative images (compared with neutral and positive ones) immediately after encoding (Szőllősi & Racsmány, 2020), and extend these findings indicating that more precise memory representations for negatively toned images are maintained after a 2-hr-long delay.

Several studies examining the effect of sleep on mnemonic discrimination showed that LD performance is better after a full night sleep than after an equivalent time spent awake (Cellini, 2023; Doxey et al., 2018; Hanert et al., 2017). These results suggest that sleep protects the details of memory representations. Yet other studies using only a daytime nap did not show similar results (Cellini et al., 2020; Davidson et al., 2021), leading to the idea that this effect plays out on a longer timescale. Our results align with the general consensus based on these studies: a daytime nap has no observable effect on LD.

Studies using the emotional variant of the MST showed that sleep affects arousing stimuli in a different way (Cellini, 2023; Leal et al., 2014). An experiment utilizing a 24-hr delay between study and test showed that discrimination performance for emotional stimuli decreases after a full night of sleep (Leal et al., 2014). A similar study replicated these results but also showed that LD is better for negatively valenced stimuli after sleep than after an equivalent time spent in wakefulness (Cellini, 2023). It is also important to mention that immediate testing with the emotional variant of the MST consistently results in better LD performance for emotional stimuli, especially negative stimuli (Szőllősi et al., 2022; Szőllősi & Racsmány, 2020). This leads to the question of why a daytime nap shifts performance in the other direction, namely generalization.

Previous studies utilizing a daytime nap used non-emotional stimuli in the MST (Cellini et al., 2020; Davidson et al., 2021). One of the studies showed no effect of a daytime nap on MST performance (Davidson et al., 2021). This study used pictures of everyday objects in the stimulus pool, which constitutes the most important point of departure from the design used in our study. However, it is also worth mentioning that the control group spent the time before testing in quiet rest (Davidson et al., 2021). This may explain inconsistency with other results as it has recently been argued that memory processes classically associated with sleep may also occur during wake, when outside stimulation is minimal (Wamsley, 2022). Thus, a possible explanation for the findings in this study is that the control group also managed to consolidate the study material in quiet rest to a similar degree as participants in the napping group. The other study examined the effect of a short nap on the MST with delayed testing, meaning that half of the stimuli presented before the nap were tested after (Cellini et al., 2020). This study did not show any effect of sleep on the behavioural variables measured, but it also used non-emotional stimuli.

Based on this brief review of relevant studies, we speculate that short sleep time alters emotional memories in a specific manner, namely it fails to consolidate them to a degree that could support LD, and thus GN becomes more pronounced, provided that the participants complete a full sleep cycle entering REM sleep. Thus, in our study, REM sleep may have promoted the generalization of emotional memories, in accordance with previous studies pointing to such an effect (Lerner et al., 2021; Sterpenich et al., 2014).

Nevertheless, the duration of REM sleep was positively associated with the negative EB for SR, suggesting that longer times spent in REM sleep are linked to more precise emotional memory representations for negative items. Our correlative findings should not be taken at face value; however, they fit into the views regarding the role of REM sleep in memory processing (Boyce et al., 2017; Diekelmann & Born, 2010), more specifically with the sequential consolidation hypothesis, which proposes that newly encoded, hippocampus-dependent memories become embedded in cortical networks during slow-wave sleep and the strengthening of these neural representations occurs during REM sleep (Diekelmann & Born, 2010; Giuditta et al., 1995).

Our findings are in line with studies showing that brain regions involved in emotional processing are active during REM sleep (Braun et al., 1997; Maquet et al., 1996), as well as with those showing a particular role of REM sleep in emotional memory processing (Boyce et al., 2017; Genzel et al., 2015). Animal studies indicate that optogenetic silencing of inhibitory neurons in the medial septum during REM results in deficits in the recognition of freshly encountered novel objects and degrades fear association (Boyce et al., 2016). A more recent study showed that somatodendritic decoupling in prefrontal cortical pyramidal neurons during REM sleep influences performance on aversive conditioning (Aime et al., 2022). Suppression of dendritic activity results in worse, while somatic release of inhibition results in better discrimination performance.

There is also a line of evidence linking REM and memory processing through dopaminergic activity (Lima, 2013; Perogamvros & Schwartz, 2012). A recent study even showed that dopamine release in the amygdala of mice during sleep initiates the REM phase (Hasegawa et al., 2022). Dopamine is also known to be involved in memory processing, specifically it is thought that it tags synapses for later consolidation serving as a basis for long-term memory (Redondo & Morris, 2011). Based on these observations, it can be concluded that dopaminergic neurotransmission is an elementary neurobiological feature of REM sleep, which likely plays a role in memory processing taking place in this state. This process could explain that certain parts of memory representations become more strengthened while others are left behind resulting in memories that lose detail. Such representations are thought to drive generalization during the MST (Stark et al., 2019).

However, there are several studies suggesting that there are also active processes contributing to forgetting (Anderson & Hulbert, 2021). Forgetting has also been linked to REM sleep, by a study that showed that the activation of a population of hypothalamic neurons (melanin-concentrating hormone producing neurons) in this sleep stage decreases memory performance in a fear conditioning paradigm (Izawa et al., 2019). Interestingly, a recent preprint reported a finding in which the targeted reactivation of emotional memories during REM sleep resulted in decreased recognition performance (Yuksel et al., 2023). These studies support the idea that the memory processes during REM sleep are complex and can contribute to forgetting in an active manner.

Even though our results align well with those in the wider neuroscientific literature on the memory processes taking place during REM sleep, our study has some limitations that should be acknowledged. First, the NREM and REM groups are imbalanced stemming from differences between our participants in the ability to enter into REM sleep during a daytime nap. Sleeping in a novel environment, under unfamiliar conditions and equipped with polysomnography may provoke sleep fragmentation and arousals, similar to the first-night effect (Agnew Jr et al., 1966), limiting the ability to enter into REM sleep. Future studies may apply morning naps or longer nap time intervals, allowing more participants reaching REM sleep.

It should also be mentioned that recent results highlighted the possibility that relative deprivation from incoming sensory information also influences post-encoding memory processes (Wamsley, 2022). This limitation could be overcome through the inclusion of a quiet resting group in future studies. Finally, it is also worth mentioning that the sample of our study mainly consists of females; however, we did not collect data regarding their menstrual phase and the usage of contraceptives. Although our main result holds if males are removed from the sample, the possible confounding effect of hormonal states on emotional memory generalization should be further explored.

In conclusion, our study showed that participants reaching REM sleep during a daytime nap give significantly more recognition responses to emotional stimuli that are only similar to what they originally viewed. This suggests that REM supports the generalization of emotional memories. Future studies should aim to reveal what processes decide which parts of a memory representation are kept and which are erased. This line of inquiry has obvious relevance for the treatment of mental disorders like post-traumatic stress disorder or major depression, but also a more general usefulness in training and education.

INFORMED CONSENT

Informed consent was obtained from all participants, and the procedures were approved by the United Ethical Review Committee for Research in Psychology, Hungary.

AUTHOR CONTRIBUTIONS

Richárd Reichardt: Conceptualization; investigation; writing – original draft; writing – review and editing; methodology; formal analysis. **Anna Király:** Methodology; investigation; formal analysis. **Ágnes Szőllősi:** Conceptualization; methodology; formal analysis; supervision; writing – original draft; writing – review and editing; investigation. **Mihály Racsmány:** Conceptualization; methodology; supervision; writing – original draft; writing – review and editing; investigation. **Péter Simor:** Conceptualization; investigation; writing – original draft; writing – review and editing; supervision; methodology.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in OSF at https://osf.io/euhb5/.

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SUPPORTING INFORMATION

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

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