



Research paper

Anxiety moderates the effect of sleep on selective forgetting

Risto Halonen^a, Tommi Makkonen^b, Liisa Kuula^{a,c}, Anu-Katriina Pesonen^{a,*}^a SleepWell Research Program, Faculty of Medicine, P.O. Box 9, FI-00014, University of Helsinki, Finland^b Department of Psychology and Logopedics, Faculty of Medicine, P.O. Box 9, FI-00014, University of Helsinki, Finland^c Medical Faculty, University of Oulu, Aapistie 5, FI-90220 Oulu, Finland¹

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ABSTRACT

While anxiety predisposes to distressing memories, the role of sleep in maintaining or attenuating unwanted memories has been understudied. This study aims to fill this knowledge gap by examining sleep-driven selective memory consolidation using a directed forgetting (DF) paradigm. DF refers to the intentional suppression of certain memories during encoding, and it is usually observed in both anxious and non-anxious individuals during wakefulness. While sleep potentially enhances DF, it is unclear how anxiety interacts with sleep.

The sample ($N = 58$) was divided into low- and high-anxiety subgroups based on self-reported symptoms (GAD-7). The participants encoded to memory 120 face images (neutral/fearful). According to item-method DF, each image was instantly followed by Remember (R) or Forget (F) cue. Memory retrievals took place immediately, after a daytime nap in the sleep laboratory, and after two days. DF effect denoted the difference between R-cued and F-cued image recognition success.

Overall, relative to F-cued, R-cued images were better recognized. This DF effect was moderated by anxiety and sleep: in low-anxiety individuals only, the magnitude of the DF effect increased significantly over the nap. This increase was associated with sleep spindle density. Event-related potential amplitudes at encoding associated with the DF effect at the immediate retrieval, but not at the later assessments.

Sleep-related memory processing may be altered in individuals with elevated anxiety, making it harder to differentiate important from irrelevant information. This mechanism may contribute to the persistence of unwanted memories in anxiety. Understanding how sleep interacts with anxiety can open novel intervention possibilities.

1. Introduction

Anxiety is associated with increased attention to threat-related stimuli (Bar-Haim et al., 2007). This bias is suggested to stem from stimulus-driven processing of emotions, instead of using attentional control consisting of inhibition and shifting of attention (Eysenck et al., 2007). Such biases may have downstream effects on memory, for example, anxiety is often characterized by distressing intrusive memories (Marks et al., 2018). However, the evidence on anxiety-related memory processing is mostly concentrated on studies conducted during wakefulness (Herrera et al., 2017). As recently acquired memories are either strengthened or attenuated during sleep, the question of how anxiety interacts with sleep in moderating recent memories becomes highly relevant.

Specific brain activity patterns contribute to offline memory processing. For example, during non-rapid eye movement sleep (NREM), sleep spindles facilitate the reactivation and consolidation of recent memories (Klinzing et al., 2019), especially related declarative memory content. Emotional memories, on the other hand, have been observed to be modulated by the amount and quality of REM-sleep (van der Helm and Walker, 2011). Memory processing over sleep is allegedly selective, such that memories tagged as *salient* during encoding are preferentially consolidated (Chen et al., 2024), and non-salient memory items become forgotten. However, sleep-specific effects on selective memory consolidation remain inconclusive, as the hypothesis has been supported by only some of the existing experimental studies (Davidson et al., 2021).

Very few studies have examined sleep-related memory consolidation in people suffering from anxiety. One study showed higher Generalized

* Corresponding author.

E-mail addresses: risto.halonen@helsinki.fi (R. Halonen), tommi.makkonen@helsinki.fi (T. Makkonen), liisa.kuula@helsinki.fi (L. Kuula), anukatriina.pesonen@helsinki.fi (A.-K. Pesonen).¹ Present address.<https://doi.org/10.1016/j.jad.2025.119562>

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Anxiety Disorder-7 (GAD-7) (Spitzer et al., 2006) scores to associate with lower sleep spindle density and lower delayed memory performance (Halonen et al., 2023), suggesting impaired offline consolidation in anxious individuals. Given sleep's potency in selective memory strengthening and downscaling, it becomes important to question whether anxiety moderates selective memory processing during sleep, thus possibly contributing to the persistence of unwanted memories.

Active forgetting is an essential mechanism of adaptive emotional processing, as forgetting enables an individual to dismiss irrelevant information or information that impairs emotional adaptation (Nørby, 2015). Forgetting can be experimentally tested. Directed forgetting (DF) refers to a method aiming at attentional suppression of very recently presented stimuli (Fawcett and Taylor, 2008). In item-method DF, a cue to either remember (R) or forget (F) follows the stimulus, e.g. an image. Typically, DF paradigms result in better memory retrieval of R-cued, relative to F-cued, items (i.e. DF effect) (Pevie et al., 2023). Research among individuals with anxiety indicates functional, albeit slightly impaired, DF (Pevie et al., 2023). However, a recent study showed anxiety to enhance DF towards negative material (Pakkan et al., 2024).

The majority of DF research has been conducted over short memory retention interval, i.e. a delay not containing sleep. One of the existing sleep studies found that DF effect in free recall for words was better after sleep than wake (Saletin et al., 2011), and another report noted sleep-enhanced DF, but only for negative, not neutral, material (Alger et al., 2019). In these studies, sleep spindle density predicted positively DF effect after sleep. However, other studies found sleep-related DF effects limited or nonexistent (Rauchs et al., 2011; Scullin et al., 2017). Studies examining sleep-related DF in anxious individuals are lacking. Further studies on the topic are warranted to investigate whether individuals with anxiety able to forget if encouraged to do so, and whether sleep contributes to this process.

This study investigated whether sleep and self-reported anxiety interacted on selective forgetting. We applied DF paradigm as it offers strong experimental control and captures both memory strengthening and intentional forgetting. These two processes are central to sleep-related memory consolidation and may underlie a key feature of anxiety: difficulty in suppressing unwanted memories. A recognition memory task using neutral and fearful face images was administered. Retrieval performance was assessed three times: briefly following encoding, after a nap, and after two days. Of specific interest was whether sleep-related consolidation modulates DF effect across time, and whether the modulation is affected by anxiety. We expected to find an overall DF effect that is enhanced after the nap, but only in low-anxiety individuals. This is due to compromised sleep consolidation in anxious participants. The influence of facial expression was explored: while emotional content decreases the DF effect (Hall et al., 2021), anxiety may reverse this effect (Corenblum and Goernert, 2023; Pakkan et al., 2024).

Event-related potentials (ERPs) (Luck, 2014) were measured to investigate how brain dynamics at the R-/F-cue presentation predicted DF over repeated memory assessments. Evidence indicates that R- and F-cues elicit differing neural responses (Brandt et al., 2013; Gallant and Dyson, 2016; Yang et al., 2012) which in some cases have predicted behavioral DF effect (Hauswald et al., 2011; Paz-Caballero et al., 2004). However, specific ERP signatures for DF have not been identified.

2. Methods

2.1. Participants

The initial sample consisted of 59 young adults (mean age 22.4 y, SD = 0.54; 42 females, 17 males, four disclosed 'other' as their gender). The participants were invited from the SleepHelsinki! cohort (<https://clinicaltrials.gov/ct2/show/NCT02964598>) for which we had longitudinal data. To ensure representative variability in anxiety symptoms, we oversampled the recruitment among those who had reported elevated

anxiety during the 2018 follow-up. Compensation of €75 food delivery voucher was provided to all participants. Measurements were performed in February–August 2022. None of the participants met the exclusion criteria (diagnosed sleep disorders or major neurological conditions impairing the study tasks). Several participants were medicated for anxiety, we therefore considered medication use part of the phenomenon, not an exclusion criterion.

All participants provided written informed consents prior to participation. The study protocol was approved by the Helsinki University Hospital Ethics Committee (HUS/1390/2019), and all components of the study were conducted in accordance with the Declaration of Helsinki and its later amendments.

2.2. Study flow

Prior to participation, participants filled e-questionnaires regarding background information and physical and mental well-being. Participants were asked their highest achieved educational degree (1 = elementary school; 2 = upper secondary school; 3 = undergraduate degree; 4 = graduate degree; 5 = licentiate degree; 6 = doctoral degree), and their experienced stress level during the past week (1–4; 'not at all–a lot'). Anxiety was reported with GAD-7 (Spitzer et al., 2006) and depression with BDI (Beck et al., 1996). The sample was divided into low and high GAD-7 subgroups based on mild anxiety threshold (≥ 5 points).

On the study morning, participants were instructed to wake up 1–2 h before their typical waking time and to abstain from caffeine after their morning coffee, except for an immediate morning coffee. The study started at 1 pm, followed by oral briefing and polysomnography (PSG) installation. Next, participants underwent memory encoding (mean = 2.03 pm, SD = 18 min), followed by the first memory retrieval (MR1) after 5 min. Participants had then a 2-hour napping opportunity. After awakening, the second memory retrieval (MR2) took place (mean = 4.42 pm, SD = 21 min). The final memory retrieval (MR3) was administered two days later (mean = 11.10 am, SD = 136 min).

2.3. Memory material and task

The face recognition task consisted of 240 images obtained from the Chicago Face Database 3.0 (Ma et al., 2015) and the Umeå Face Database (Samuelsson et al., 2012) with permission, representing neutral or fearful expressions. Face size and background color were matched. 120 target and 120 sham images were divided into three sets of 40, i.e. immediate, post-nap and delayed recognition test (MR1–3, respectively). Each set contained equal numbers of neutral and fearful faces, and female and male faces. People in the images were either self-identified white (80 %) or black (20 %) individuals.

During encoding, participants were instructed to attend to the target images, displayed on a 24" computer screen. Each image was presented for 3000 ms, followed immediately by a Finnish version of the DF cue to remember ('R' = Remember) or to forget ('F' = Forget). The cue (height 85 mm; blue for R and orange for F) was visible for 1500 ms, followed by a fixation cross for 1000 ms before the next image. The R- and F-cues were presented in a random order. An equal number of each cue was combined with neutral and fearful faces.

During each retrieval, participants used number keys (1–5) to indicate their confidence in recognizing the image from encoding (1 – not very confident; 5 – totally confident), and 0 in case of no recognition, irrespective of the cue. The image remained visible until the participant responded. MR1 and MR2 were conducted in the laboratory, and MR3 was conducted over a remote online session (Zoom) with the participants' own device.

Hit and false alarm rates, i.e. z-transformed proportions of correctly/incorrectly recognized (responding 1–5) target/sham pictures of all target images, respectively, were calculated separately for both cues (Remember/Forget), emotions (neutral/fear) and each memory retrieval. Category-wise recognition accuracies (d') were obtained by

subtracting false alarm rates from hit rates. *DF effect* was calculated by subtracting F-cued *d'* rate from the respective R-cued *d'*. *DF change* denoted the change of *DF effect* between two consecutive retrievals, e.g. (MR2 *DF effect*)–(MR1 *DF effect*). As we found the starting level of *DF effect* (e.g. in MR1) to have a major impact on the subsequent *DF change* (e.g. between MR1 and MR2) we partialled out the starting level from the change variable (Vickers and Altman, 2001). Due to technical issues, data were lost on one participant in MR2, and on two participants in MR3.

2.4. Polysomnography and sleep spindle analysis

PSG recordings were performed with an EEG set and software by Brain Products (Brain Vision LLC, <https://brainvision.com>), including EasyCap Standard 128Ch cap, two actiCAP snap 32-channel active electrode bundles, an actiCHamp Plus amplifier, and a ground electrode at Fpz. Electro-oculograms (EOGs) and electromyograms (EMGs) were measured with electrodes from one of the EEG bundles: EMG was attached to the right upper back trapezius muscle, EOG1 to the right cheek, and EOG2 was kept in the cap above the left eye. Sampling rate was 1000 Hz. The online reference electrode was FCz. The sleep recording of one participant was lost due to disconnected ground electrode. We scored the PSG data into N1, N2, N3, REM sleep and wake, according to the AASM 2.6 (American Academy of Sleep Medicine, <https://aasm.org/>).

Sleep spindle detection included N2 and N3 sleep stages ('NREM') and frontal (F3, Fz, F4), central (C3, Cz, C4) and parietal (P3, Pz, P4) channels, using the reference FCz. The detection was performed using an in-house toolbox (SleepPlugin, v 1.013b, implemented by the second author) with an algorithm described by Ferrarelli et al. (2007). The EEG signals were digitally band-passed and filtered offline at 0.5–35 Hz (Hamming windowed sinc zero-phase FIR filter; cut-off –6 dB). Next, the pre-processed data were band-pass filtered (order 2816) in the 12–16 Hz frequency range. The channel-wise detection threshold values for spindle peak amplitudes were then calculated. Fluctuations exceeding six times the mean of the absolute amplitude of the filtered signal were considered spindles. The putative spindle's amplitude was required to stay above two times the mean channel amplitude for 250 ms in both directions from the peak maximum. The maximum spindle duration was set at 3.0 s. To prevent false alarms, the signal amplitude between spindles was required to stay under the lower threshold for 78.1 ms, (the approximate duration of one sine period at 13 Hz). Spindle-like bursts with amplitude that exceeded the channel-wise mean spindle amplitude by 3 standard deviations (SD) were removed. Sleep spindle data from two participants was lost due to signal quality issues. Spindle densities were calculated by dividing the number of spindles by NREM sleep minutes. Finally, we averaged lateral electrode values to frontal, central and parietal densities.

Memory association was investigated with total sleep time (TST) in minutes, NREM (N2 + N3) minutes, REM sleep existence as a dichotomous variable (as 44 % did not have REM sleep during the nap), and spindle densities in frontal, central and parietal derivations.

2.5. Event-related potentials

Frontal, central and parietal channels were included in the ERP analysis. The raw EEG data were preprocessed using EEGLAB software version 2023.0 (Delorme and Makeig, 2004) and an in-house toolbox (CBRUplugin, subversion 27.7.2023, implemented by the second author) running in MATLAB R2022b (Mathworks Inc., USA). Continuous data were band-pass filtered (FIR 0.5–45 Hz; 6 dB cut-off frequencies 0.25 Hz and 50.625 Hz, respectively) and cropped to only contain EEG recorded during memory encoding. Next, the data were visually inspected for artifactual channels (mean 0.94, max 4 per participant; one participant with ten artifactual channels was excluded). ICA decomposition (runica) was run excluding the artifactual channels.

ICA components regarding eye movements, muscle movement, channel and line noise were inspected participant-wise and removed according to individualized likelihood. Labelling was done using ICLabel v.1.5 (Pion-Tonachini et al., 2019). After this, bad channels were interpolated. Due to poor contacts in mastoids in several participants, we referenced the data against the average of all EEG electrodes. Finally, the data were segmented to epochs containing –300–1500 ms relative to the DF cue presentation. Baseline correction was applied using the –300–0 ms pre-stimulus interval. ERPs were laterally averaged to frontal, central and parietal regions. ERP data on 5 participants was lost due to a technical issue.

Sample-wise R- and F-cued ERP amplitudes were compared across the epoch using repeated-measures ANOVA (80 ms temporal smoothing) and corrected with False Discovery Rate (FDR) (Benjamini and Hochberg, 1995) ($q = 0.01$). As specific DF ERP signatures remain unsettled - latencies ranging 200–850 ms have been reported (Brandt et al., 2013; Paz-Caballero et al., 2004; Yang et al., 2012), behavioral DF associations were examined across the whole epoch (0–1500 ms) using a partially overlapping moving window approach. First, we computed R- vs. F-cued amplitude differences (DF-ERP) in 50 ms segments (amplitudes deviating $\pm 3SD$ were trimmed). A 200 ms window was composed of four consecutive segments, and it advanced in 50 ms steps. The windows were centered at 100–1400 ms post-cue.

2.6. Statistics

Statistical analyses were conducted with SPSS Statistics for Windows, version 29.0 (IBM) with $\alpha = 0.05$. The *d'* distributions (for MR1–3 and R- and F-cued items, and their change scores) and continuous independent variables were examined for outliers (deviating >3 SD from the sample mean) and for violations of residuals' normality (visually and with Kolmogorov-Smirnov test). The equality of variances and covariance matrices between the GAD-7 subgroups was tested with Levene's and Box's test, respectively. In preliminary analyses, we examined whether DF scores associated with age and gender (Pearson's correlation and linear regression, respectively), and whether spindle densities correlated with MR1 *DF effect*. Comparison of age, education, questionnaire scores and sleep parameters between GAD-7 subgroups was conducted with one-way ANOVA or Mann-Whitney test depending on distribution.

To examine the difference and time patterns of R- and F-cued *d'*s, we applied repeated-measures ANOVA with three levels of time (MR1–3), two levels of cue (Remember/Forget) and two levels of facial expression (fearful/neutral). The interaction between DF patterns and GAD-7 scores was tested by including GAD-7 as the independent variable (as continuous or 2-class categorical subgroup variable). A similar model was applied for the confidence ratings for positive recognitions to test whether DF cue affected confidence ratings, and whether GAD-7 subgroup had a main effect, 'time' interaction or 'time \times DF effect' interaction on the ratings. Repeated-measures ANOVA on MR1–3 *DF effect* was used to test the main effect and time interaction of 200-ms DF-ERP windows. Significant windows were tested for GAD-7 subgroup differences, i.e. one-way ANOVA (categorical) or Spearman's correlation (continuous), and DF-ERP interaction with repeated-measures ANOVA.

Following the hypothesis that sleep-related consolidation would induce post-nap DF differences, linear regression was used to test the influence of sleep parameters (TST, NREM minutes, REM sleep existence and spindle densities) on DF change: DF change (between MR1–MR2 and MR2–MR3) as the dependent, and sleep parameter as the independent variable. Moderation by GAD-7 score was tested with 'GAD-7 \times sleep parameter' interaction.

Significant interactions were followed-up with within- (DF) or between- (GAD-7) subjects *t*-tests (Bonferroni-corrected). Interaction tests and subgroup-wise linear regression tests concerning sleep parameters were corrected using FDR ($q = 0.05$; across six tests). FDR correction was also applied on DF-ERP windows' main effects, and on the follow-up

Pearson’s correlation analyses regarding significant time interaction windows ($q = 0.05$; across $3 \times < \# \text{ of significant windows} >$ tests). Gender was used as a covariate regarding over-nap DF change scores. Because only four participants reported ‘other’ for gender, a separate group was not formed to avoid unstable estimates. Instead, multiple imputation was applied, and pooled effects were examined across ten iterations.

No a priori power analyses were conducted. Sensitivity analysis with G*Power 3.1.9.2 (Faul et al., 2007) showed a reliably detectable effect size of $f = 0.30$ (medium; calculated ‘as in SPSS’) for interaction and within- and between-factors in a 2×3 mixed ANOVA ($N = 56$, two-tailed $\alpha = 0.05$, power = 0.8). For bivariate correlations ($N = 51$; with ERP data), medium effect size of $r \geq 0.38$ was required (two-tailed $\alpha = 0.05$, power = 0.8).

3. Results

3.1. Sample characteristics

The Low and High GAD-7 subgroups did not differ in age, education level or sleep parameters (all $p \geq .14$). Gender distribution was different between the subgroups ($\chi^2 p = .009$), and participants using psychiatric medication (mostly SSRI) were 4/33 in the Low and 12/24 in the High anxiety subgroup; $\chi^2 p = .004$. High GAD-7 subgroup displayed significantly higher scores in GAD-7 and BDI scores, and in the previous week’s stress level rating (all $p < .001$). See Table 1.

Females had higher DF change between MR1 and MR2 [$t(1,56) = 1.963, R^2 = 0.068, p = .050$]. Age did not correlate significantly with the outcome variables ($p \geq .074$). Sleep spindle densities did not correlate with MR1 DF effect ($p \geq .693$).

3.2. Remember-cued images recognized better than forget-cued images

Time had a significant main effect on d' [$F(2,110) = 28.803, p < .001$], such that d' in MR1 ($M = 1.406, SE = 0.063$) was higher than in MR2 ($M = 1.166, SE = 0.067$) and MR3 ($M = 0.976, SE = 0.061$) retrievals (both $p < .001$). MR2 was higher than MR3 ($p = .018$). There was a significant main effect of DF effect [$F(1,55) = 8.151, p = .006$], and ‘time \times DF effect’ interaction [$F(2,110) = 4.794, p = .010$]. The overall (mean) d' in R-cued images ($M = 1.232, SE = 0.058$) was higher than in F-cued images ($M = 1.134, SE = 0.057$). Follow-up examination of the ‘time \times DF effect’ showed that R-cued image d' was significantly higher than F-cued image d' in MR1 ($M = 1.475, SE = 0.070$ and $M = 1.337, SE = 0.067$, respectively; $p = .037$) and MR2 ($M = 1.255, SE =$

0.073 and $M = 1.078, SE = 0.069$, respectively; $p = .001$). No significant difference was found in MR3 ($M = 0.966, SE = 0.065$ and $M = 0.986, SE = 0.069, p = 1.000$, Bonferroni-corrected). See Fig. 1A. Facial expression did not significantly interact with DF effect [$F(1,55) = 0.128, p = .722$] or with ‘time \times DF effect’ [$F(2,110) = 1.160, p = .317$]. R- and F-cued images did not elicit significantly different confidence ratings [main effect $F(1,55) = 3.641, p = .062$; time interaction $F(2,110) = 0.985, p = .389$].

3.3. Low GAD-7 score associates with successful directed forgetting

The interaction ‘GAD-7 subgroup \times DF effect’ was significant [$F(1,54) = 5.910, p = .018$; Continuous GAD-7 $F(1,54) = 3.371, p = .072$]. Follow-up within-subgroup examination showed that the Low GAD-7 subgroup had significantly higher R-cued ($M = 1.216, SE = 0.079$), relative to F-cued ($M = 1.043, SE = 0.077$), mean d' ($p < .001$), whereas no DF effect was found in High GAD-7 subgroup ($M = 1.256, SE = 0.085$ and $M = 1.239, SE = 0.082$, respectively; $p = 1.000$) (Fig. 1B). The subgroups did not differ in R-cued ($p = 1.000$) or F-cued ($p = .164$) d' scores. The interaction ‘time \times DF effect \times GAD-7 subgroup’ was significant using continuous GAD-7 score [Greenhouse-Geisser epsilon = 0.844; $F(1.977, 108) = 3.097, p = .050$; categorical $F(2,108) = 2.596, p = .079$].

The interaction(s) prompted to examine retrieval-wise DF effects between GAD-7 subgroups. We found that the GAD-7 subgroups differed in MR2 ($p = .009$; $p = .027$ gender controlled), but not in MR1 or MR2 (all $p \geq .741$). Also, continuous GAD-7 score associated with MR2 (Spearman’s $r = -0.330, p = .036$) but not with MR1 or MR3 (both $p = 1.000$). Accordingly, the DF change between MR1 and MR2 differed significantly between GAD-7 subgroups ($p = .004$; $p = .018$ gender controlled; continuous GAD-7 Spearman’s $r = -0.343, p = .016$), but no difference was found regarding the MR2–MR3 change ($p = .508$; continuous GAD $p = 1.000$). Fig. 1C–D illustrate R- and F-cued d' in Low and High GAD-7 subgroups, respectively.

The interaction ‘DF effect \times emotion \times GAD-7 subgroup’ was not significant [$F(1,54) = 0.287, p = .594$; Continuous GAD-7 $F(1,54) = 3.869, p = .054$] nor was it significant when adding time to the interaction [$F(2,108) = 0.401, p = .670$; Continuous GAD-7 $F(2,108) = 0.417, p = .660$], indicating that facial expression did not affect the DF differently between the GAD-7 subgroups. Confidence ratings were not associated with GAD-7 subgroup as a main effect [$F(1,54) = 0.786, p = .379$], two-way ‘time \times GAD-7’ [$F(1,54) = 1.318, p = .256$] nor three-way ‘time \times DF effect \times GAD-7’ [$F(2,108) = 1.041, p = .357$] interaction.

3.4. Sleep spindles were associated with directed forgetting in low anxiety

Significant ‘time’ interactions in the whole sample were investigated according to the hypothesis that sleep parameters would contribute to DF change across time. First, regarding over-nap change (MR1–2), TST [$t(2,55) = 0.325, R^2 = 0.002, p = .745$], NREM minutes [$t(2,55) = -0.150, R^2 = 0.001, p = .881$] and REM sleep existence [$t(2,55) = 1.044, R^2 = 0.018, p = .296$] were not associated with outcome. Regarding spindle densities in frontal, central and parietal derivations, none remained significant after FDR correction [$t(2,53) = 1.297, R^2 = 0.052, p = .194$; $t(2,53) = 1.670, R^2 = 0.071, p = .095$; and $t(53) = 2.030, R^2 = 0.092, p = .042$, respectively]. Concerning over-delay (MR2–3) DF change, none of the sleep parameters were significant (all $p \geq .304$).

Next, we examined the interaction between GAD-7 scores and sleep parameters on MR1–2 DF change. TST [$t(4,53) = -0.357, R^2 = 0.002, p = .721$; continuous GAD-7 $t(4,53) = -0.890, R^2 = 0.012, p = .373$], NREM minutes [$t(4,53) = -0.554, R^2 = 0.005, p = .580$; continuous GAD-7 $t(4,53) = -0.908, R^2 = 0.013, p = .364$], and REM sleep existence [$t(4,53) = 1.636, R^2 = 0.039, p = .102$; continuous GAD-7 $t(4,53) = 0.863, R^2 = 0.011, p = .388$] did not interact with GAD-7 scores on the

Table 1
Sample characteristics and sleep parameters.

	Low GAD-7 ($n = 33$; 18 F, 14 M, 1 O)		High GAD-7 ($n = 26$; 21 F, 2 M, 3 O)		p
	Mean	SD	Mean	SD	
Age	22.4	0.6	22.4	0.5	.70 ^a
Education	2.1	0.5	2.1	0.3	.67 ^b
Stress level	1.4	0.9	2.8	0.8	<.001 ^b
GAD-7	1.3	1.4	8.5	3.5	<.001 ^b
BDI	3.7	4.4	16.5	11.8	<.001 ^b
TST (min)	89.3	21.8	81.7	32.6	.64 ^b
N1 (min)	8.4	4.3	6.7	4.5	.06 ^b
N2 (min)	43.7	14.9	39.4	17.1	.32 ^a
N3 (min)	27.3	16.7	28.7	19.4	.77 ^a
REM (min)	10.0	12.9	6.9	7.7	.57 ^b
Spindle density F	3.2	0.9	3.3	0.6	.51 ^a
Spindle density C	2.6	0.8	2.6	0.6	.91 ^a
Spindle density P	2.4	0.8	2.3	0.6	.45 ^a

GAD-7: General Anxiety Disorder 7 questionnaire. BDI: Beck Depression Inventory. TST: Total sleep time. REM: Rapid eye movement sleep. N1–3: Non-REM sleep stage 1–3. F: frontal. C: central. P: parietal.

^a One-way ANOVA.

^b Mann-Whitney U test.

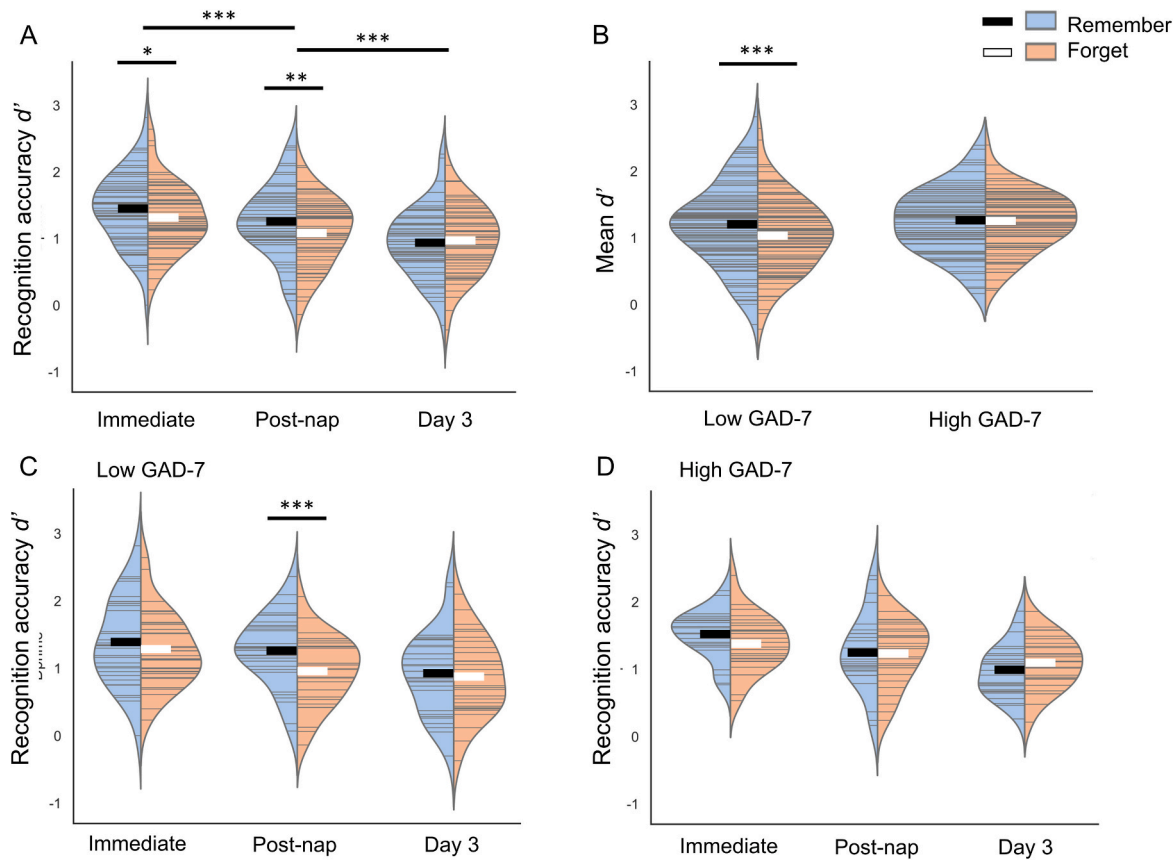


Fig. 1. Directed forgetting and anxiety. Remember-cued images are better retrieved than Forget-cued images at immediate ($p = .037$) and post-nap ($p = .001$) retrievals (A). On average, remember-cued images are better retrieved in the Low GAD-7 subgroup ($p < .001$) but not in the High anxiety subgroup (B). In the Low GAD-7 subgroup, the Remember/Forget difference was significant in post-nap retrieval ($p < .001$) but not in the immediate or Day 3 retrievals (C). No Remember/Forget differences were found in any retrieval in the High anxiety subgroup (D). Black/white bars: mean d' of Remember/Forget cues. *** $p < .001$; ** $p < .01$; * $p < .05$.

over-nap DF change. Spindle density revealed significant interactions with GAD-7 subgroup regarding frontal [$t(4,51) = -2.276, R^2 = 0.072, p = .023$; continuous GAD-7 $t(4,51) = -1.854, R^2 = 0.048, p = .063$] central [$t(4,51) = -2.818, R^2 = 0.105, p = .005$; continuous GAD-7 t

(4,51) = $-2.465, R^2 = 0.080, p = .014$] and parietal [$t(4,51) = -2.776, R^2 = 0.101, p = .006$; continuous GAD-7 $t(4,51) = -2.512, R^2 = 0.084, p = .012$] derivations. This indicated that the associations between spindle densities and over-nap DF change differed significantly between

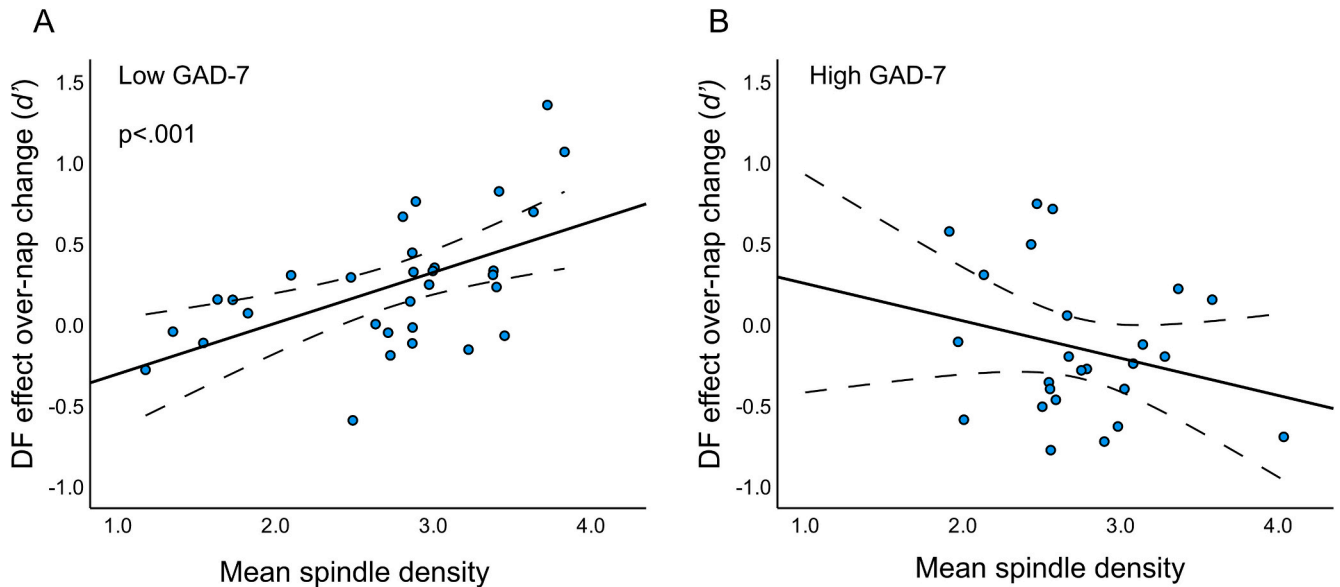


Fig. 2. Directed forgetting (DF) effect over-nap change (in d') and sleep spindle density. Averaged spindle density (over frontal, central and parietal derivations) associated significantly with DF change in the Low GAD-7 (A), but not the High GAD-7 (B), subgroup.

the GAD-7 subgroups. Follow-up within-subgroup analyses showed that spindle densities (frontal, central and parietal) associated positively with over-nap DF change in the Low GAD-7 subgroup [$t(2,28) = 2.647$, $R^2 = 0.220$, $p = .008$; $t(2,28) = 3.396$, $R^2 = 0.309$, $p < .001$; and $t(2,28) = 3.491$, $R^2 = 0.319$, $p < .001$, respectively], but not in the High GAD-7 subgroup (all $p \geq .278$). Fig. 2A–B illustrates the association between spindle density (averaged across derivations) and over-nap DF change for Low and High GAD-7 subgroups, respectively [$t(2,28) = 3.416$, $R^2 = 0.310$, $p < .001$ and $t(2,22) = -1.119$, $R^2 = 0.050$, $p = .263$].

We explored whether the greater over-nap DF change in the Low GAD-7 subgroup was more related to better preserved R-cued images or, more effectively forgotten F-cued images. The subgroups did not differ regarding over-nap change in either F-cued [$t(2,55) = 0.322$, $R^2 = 0.002$, $p = .747$] or R-cued [$t(2,55) = -1.906$, $R^2 = 0.064$, $p = .057$] d 's. Sleep spindle densities did not associate significantly with R-cued nor F-cued over-nap change in either Low (all $p \geq .224$ and $\geq .184$, respectively) or High GAD-7 subgroup (all $p \geq .620$ and $\geq .795$).

Due to substantial overlap between GAD-7 and BDI scores ($r = 0.733$, $p < .001$), we examined how BDI scores related to over-nap DF change. First, over-nap DF change did not differ according to BDI subgroup

(below/at least 10 points; $p = .877$). Second, including both GAD-7 and BDI subgroups and their interactions with averaged spindle density in the regression model showed that only 'GAD-7 \times spindle density' was significant on over-nap DF change [$t(6,49) = -2.298$, $R^2 = 0.070$, $p = .022$], while 'BDI \times spindle density' was not [$t(6,49) = 0.026$, $R^2 = 0.000$, $p = .979$].

3.5. ERPs predicted directed forgetting

Post-cue ERPs elicited by the R- and F-cues differed significantly ($p < .01$ after FDR correction) in frontal (200–231, 490–572 and 1095–1485 ms), central (280–480 and 1368–1488 ms) and parietal (175–448 and 1175–1408 ms) (Fig. 3A–C) regions.

There were no significant main effects regarding frontal ($p = .051$), central (all $p \geq .271$) or parietal ($p \geq .063$) DF-ERPs on overall (across MR1–3) DF effect (Fig. 3A–C). However, 'time \times frontal DF-ERP' interactions were nominally significant regarding time windows centered at 450 and 500 ms [$F(2,92) = 4.226$, $p = .018$ and $F(2,90) = 3.379$, $p = .038$, respectively], and 1000 ms [$F(2,90) = 3.100$, $p = .050$]. In parietal ERPs, significant 'time \times DF-ERP' interactions were found in time

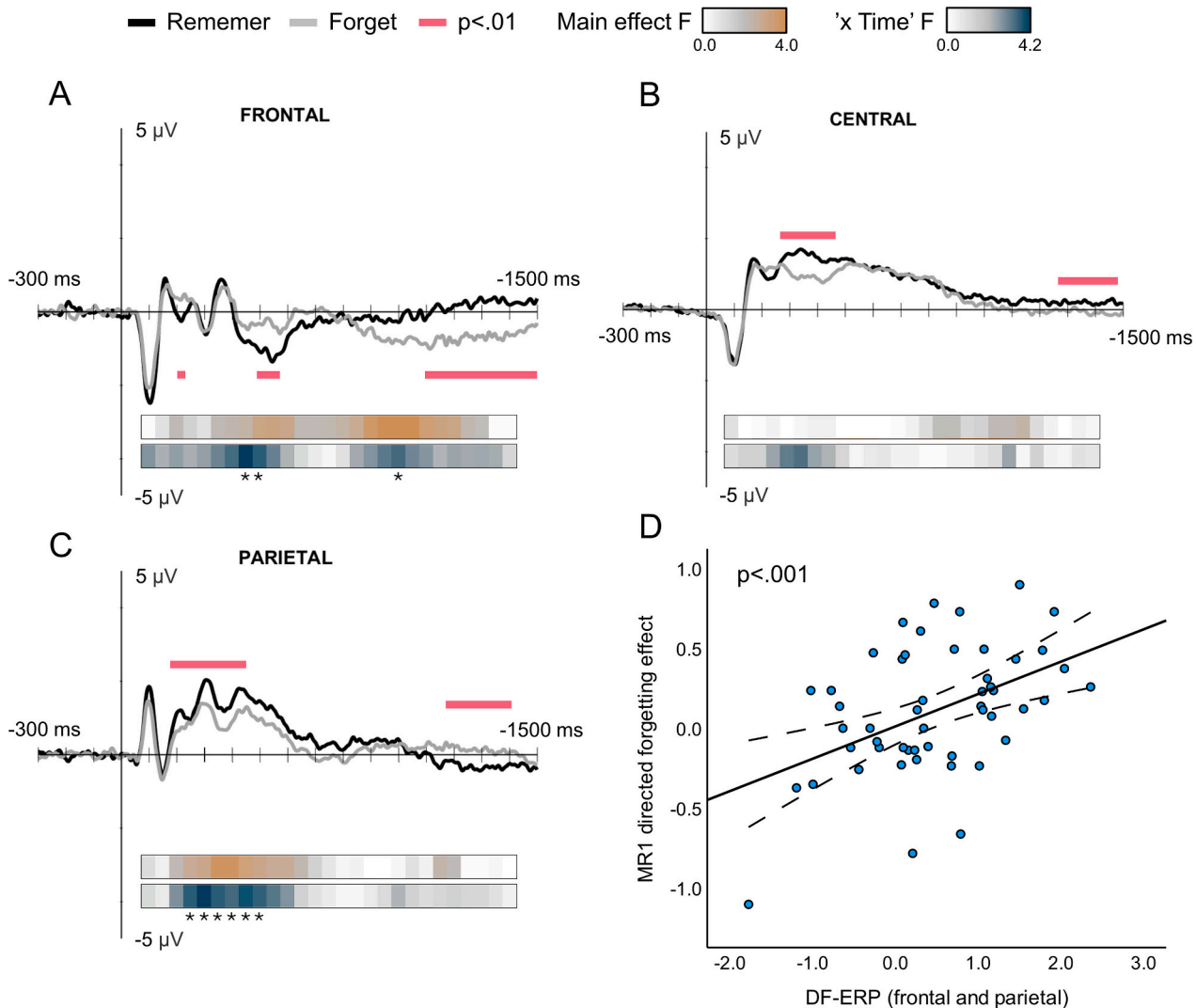


Fig. 3. Event-related potentials (ERP) and directed forgetting. Remember- and Forget-cues (black and gray lines, respectively) elicited significantly different (red lines; $p < .01$, FDR-corrected) amplitudes at frontal (A), central (B) and parietal (C) areas. Upper white-gray-orange bars represent DF-ERP windows' main effect F-value on overall DF effect. Lower white-gray-blue bars represent 'Time \times ERP' interaction strength F-value on DF effect. Significant ($p < .05$) time windows are marked with asterisks. Averaged over frontal (inverted) and parietal regions, the ERP difference between R- and F-cues (DF-ERP) across significant time windows associated positively with DF effect at the immediate retrieval (MR1) (D). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

windows centered at 250–500 ms [$F(2,92)$ values = 3.168–4.199, $p \leq .047$]. Central DF-ERPs did not yield significant interactions (all $p \geq .056$). See Fig. 3A–C. Follow-up correlation tests between DF-ERPs and MR1–3 DF effect showed that frontal DF-ERPs were significantly associated with MR1 DF effect concerning 450–500 ms windows ($r \leq -0.397$, $p \leq .004$), but the later (at 1000 ms) associations did not remain significant after FDR correction regarding any retrieval. Parietal DF-ERPs were positively associated with MR1 DF effect across 250–500 ms ($r = 0.348$ – 0.431 , $p \leq .012$). Fig. 3D illustrates the association of combined frontal (inverted for polarity) and parietal DF-ERPs on MR1 DF effect. None of these DF-ERPs associated with DF change across MR1–2 (all $p \leq .305$) or MR2–3 (all $p \leq .286$).

Low and High GAD-7 subgroups did not differ in the significant DF-ERP windows (all $p \geq .524$). The interactions between GAD-7 subgroup and DF-ERPs, or three-way interactions ‘GAD-7 \times DF-ERP \times time’, on the behavioral DF effect were not significant regarding frontal ($p = .347$ and 0.787 , respectively) or parietal ($p = .683$ and 0.440) ranges (clustered over significant windows).

4. Discussion

We studied how anxiety interacts with directed forgetting across a daytime nap. Compared with individuals with high anxiety, we found that low-anxiety individuals retrieved more faces tagged with ‘remember’ than with ‘forget’. Importantly, this DF effect was enhanced across sleep only in low-anxiety individuals, and the extent of this change was positively associated with sleep spindle density. The results suggest that sleep-related memory processing may be altered in individuals with elevated anxiety such that differentiation between important and irrelevant information becomes more difficult.

While the observed DF effect aligns with prior research (Hall et al., 2021), we found that anxiety degraded the effect more strongly than outlined in earlier studies (Pevie et al., 2023). The key factor may be sleep. The current results indicate an interaction between sleep-related memory processing and anxiety, whereby sleep-filled delay produced differentiation between R- and F-cued images in low-anxiety individuals only. This DF enhancement was robustly associated with sleep spindles. In DF context, spindles may consolidate salient (R-cued) memories (Chen et al., 2024) and/or suppressed non-salient (F-cued) ones (Cairney et al., 2014). However, our results did not clearly indicate whether sleep spindles specifically enhanced the salient or suppressed the non-salient memories, as the differentiation was not statistically significant when inspected separately. We suggest that both mechanisms may have contributed, as it has been reported that sleep spindles can simultaneously support the strengthening of to-be-remembered memories at the expense of to-be-forgotten ones, indicating a dual mechanism of selective consolidation (Saletin et al., 2011).

In sum, relative to non-anxious individuals, anxious persons may be less efficient in differentiating already encoded memories, regardless of the attached motivation or instruction. While this effect was associated with sleep spindle activity in our study, it does not preclude the possibility that other mechanisms operating at wakefulness would also be relevant. One study found anxious participants relatively impaired in suppressing memories in a think/no-think paradigm during wakefulness (Marzi et al., 2014). However, memory retention was administered without a long delay in that study, and further research disentangling the contributions of sleep and wakefulness is warranted.

ERPs at cue presentation complemented behavioral results. We observed amplitude differences between R- and F-cues in all the examined scalp regions at roughly 200–600 ms and at ~ 1100 ms onwards. These cue-tied ERP differences partially overlapped behavioral effects: the parietal and frontal ERPs at 250–500 and 450–500 ms, respectively, predicted DF at the immediate retrieval. These findings align with previous studies (Paz-Caballero et al., 2004; Yang et al., 2012), and likely reflect the P3 component that contributes to attentional processing and memory encoding (Azizian and Polich, 2007). The frontal ERP

resembles the result of Hauswald et al. (2011) and presumably represents active inhibitory control mechanisms engaged to suppress processing of to-be-forgotten items (Ye et al., 2019). The ERP difference at longer latencies did not correlate with behavioral outcome. ERPs at encoding did not associate with any post-nap DF effects, complementing earlier research describing mainly short-term effects. Additionally, anxiety did not associate with the DF-relevant ERPs, or their contribution to behavioral outcome. These observations emphasize the role of sleep-related offline processing as the potential mechanism of impaired DF in anxiety.

One distinction emerged between our results and some previous reports. Facial expression (fearful or neutral) did not interact with the DF cue, contrasting earlier evidence suggesting decreased DF effect towards emotional material in general (Hall et al., 2021). However, the main effect of this emotional bias may have been diluted in our anxiety-dense sample, as negative items are more effectively suppressed, or avoided, in individuals with elevated anxiety (Corenblum and Goernert, 2023; Pakkan et al., 2024). The lack of ‘anxiety \times DF’ interactions may reflect insufficient statistical power, or limited negative arousal induced by facial images relative to e.g. emotional scenes (Wangelin et al., 2012).

A strength of our study is the repeated paradigm that elucidates intended memory suppression in anxiety. While anxious individuals often succeed in DF (Corenblum and Goernert, 2023; Pevie et al., 2023), the ability to suppress already-encoded memories seems impaired (Catarino et al., 2015; Marzi et al., 2014). We showed that sleep-related processing may contribute to this phenomenon. However, there are several limitations. First, lacking a waking control precludes determining whether anxiety-related differences in the DF pattern were specifically attributable to sleep. It is possible that a retention interval during wakefulness could yield comparable results, albeit through different underlying mechanisms. Second, half of the participants with elevated GAD-7 score had psychiatric medication (mainly SSRIs), the impact of which on the results is not discernible. Reportedly, antidepressants do not influence cognitive control (Rosenblat et al., 2015). Also, our findings carry ecological validity such that individuals with anxiety are often medicated, and self-reported symptoms reflect current status. Third, using average reference instead of mastoids in the ERP analysis limits comparability with the literature, particularly regarding polarity and amplitude. However, direct comparability was subsidiary, as we primarily focused on whether amplitude differences were associated with DF across time. Finally, GAD-7 and BDI scores correlated strongly in this sample. Our auxiliary analyses did not show a depression-DF interaction, suggesting that anxiety was more consequential regarding the over-nap DF change.

5. Conclusions

Our study extended the literature regarding memory processing in anxiety. While DF is not strongly determined by trait anxiety in the short-term, sleep-related memory consolidation may differentiate to-be-remembered and to-be-forgotten memories more effectively in individuals with low, compared to high, anxiety. This can contribute to later intrusions of unwanted memories in anxious individuals. Understanding the role of sleep in anxiety persistence is crucial for developing effective interventions.

CRedit authorship contribution statement

Risto Halonen: Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Tommi Makkonen:** Writing – review & editing, Software. **Liisa Kuula:** Writing – review & editing, Conceptualization. **Anu-Katriina Pesonen:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors of this manuscript have nothing to declare.

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