

Stability of neural encoding moderates the contribution of sleep and repeated testing to memory consolidation

Daniel Baena^a, Jose L. Cantero^{a,b}, Mercedes Atienza^{a,b,*}

^a *Laboratory of Functional Neuroscience, Universidad Pablo de Olavide, Seville 41013, Spain*

^b *CIBERNED, Network Center for Biomedical Research in Neurodegenerative Diseases, Spain*

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ABSTRACT

There is evidence suggesting that online consolidation during retrieval-mediated learning interacts with offline consolidation during subsequent sleep to transform memory. Here we investigate whether this interaction persists when retrieval-mediated learning follows post-training sleep and whether the direction of this interaction is conditioned by the quality of encoding resulting from manipulation of the amount of sleep on the previous night. The quality of encoding was determined by computing the degree of similarity between EEG-activity patterns across restudy of face pairs in two groups of young participants, one who slept the last 4 h of the pre-training night, and another who slept 8 h. The offline consolidation was assessed by computing the degree of coupling between slow oscillations (SOs) and spindles (SPs) during post-training sleep, while the online consolidation was evaluated by determining the degree of similarity between EEG-activity patterns recorded during the study phase and during repeated recognition of either the same face pair (i.e., specific similarity) or face pairs sharing sex and profession (i.e., categorical similarity) to evaluate differentiation and generalization, respectively. The study and recognition phases were separated by a night of normal sleep duration. Mixed-effects models revealed that the stability of neural encoding moderated the relationship between sleep- and retrieval-mediated consolidation processes over left frontal regions. For memories showing lower encoding stability, the enhanced SO-SP coupling was associated with increased reinstatement of category-specific encoding-related activity at the expense of content-specific activity, whilst the opposite occurred for memories showing greater encoding stability. Overall, these results suggest that offline consolidation during post-training sleep interacts with online consolidation during retrieval the next day to favor the reorganization of memory contents, by increasing specificity of stronger memories and generalization of the weaker ones.

1. Introduction

Systems consolidation is a complex process whereby repeated reactivation of recently acquired memories becomes integrated into general knowledge structures, often at the expense of specificity loss. These transformations, which improve long-term retention, are thought to occur during active retrieval (Ferreira et al., 2019; Karlsson Wirebring et al., 2015; Karpicke et al., 2017; Rickard & Pan, 2018; Roediger & Karpicke, 2006), resting awake periods (Oudiette et al., 2013; Tambini et al., 2017; Wamsley, 2019) and sleep (Abel et al., 2013; Born & Wilhelm, 2012; Gais et al., 2007; Hanert et al., 2017; Rasch & Born, 2013;

Takashima et al., 2009), although the underlying neural mechanisms remain poorly understood.

According to cognitive (Carpenter, 2009; Pyc & Rawson, 2010) and neurobiological theories of retrieval-mediated learning (Antony et al., 2017), active retrieval during memory acquisition benefits its rapid stabilization and integration with older memories via the co-activation of semantically related information. The co-activation of a memory network through repeated testing not only strengthens episode-unique information leading to increased specificity but also seems to be central in promoting generalized knowledge that can be transferred to a wide variety of situations (Ferreira et al., 2019). Similarly,

Abbreviations: ASR, Acute Sleep Restriction; NSD, Normal Sleep Duration; ROI, region of interest; SOs, Slow Oscillations; SPs, Spindles; STPS_{E3-E4}, Spatio-Temporal Pattern Similarity between 3rd and 4th repetition at encoding; STPS_{E4-R}, Spatio-Temporal Pattern Similarity between 4th repetition at encoding and 2nd, 3rd and 4th repetition at retrieval.

* Corresponding author at: Laboratory of Functional Neuroscience, Pablo de Olavide University, Ctra. de Utrera, Km 1, 41013 Seville, Spain.

E-mail address: matirui@upo.es (M. Atienza).

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neurobiological theories on systems consolidation postulate that the offline reactivation of recently acquired memories during sleep, either spontaneously or by presenting cues associated with the encoding of the event, leads to the formation of schematic versions of detailed representations initially encoded in the hippocampus that are subsequently transferred to the neocortex, facilitating their integration into existing knowledge schemas (Alvarez & Squire, 1994; Frankland & Bontempi, 2005; Lewis & Durrant, 2011; McClelland et al., 1995; Nadel & Moscovitch, 1997; Robin & Moscovitch, 2017; Squire, 2004; Winocur & Moscovitch, 2011).

To our knowledge, only one study to date has provided compelling evidence that retrieval-mediated learning and post-training sleep interact to facilitate long-term memory consolidation (Himmer et al., 2019). The authors of this study showed that post-training sleep is required to stabilize cortical reorganization of memory triggered by repetitive testing during memory acquisition. This idea is further supported by recent evidence that memory consolidation, specifically semantisation of episodic memory, is triggered by retrieval-mediated learning, but is enhanced if retrieval occurs after a period of two days (Lifanov et al., 2021). However, it is unknown whether this interaction persists when the order of the consolidation processes is reverted (i.e., when repeated testing is applied after post-training sleep); and whether the direction of this relationship is determined by the quality of prior encoding, as much evidence suggests that offline consolidation during sleep primarily prioritizes weaker memories (Baena et al., 2020; Cairney et al., 2016; Creery et al., 2015; Denis et al., 2020, 2021; Diekelmann et al., 2010; Djonlagic et al., 2009; Drosopoulos et al., 2007; Dumay, 2016; Kuriyama et al., 2004; McDevitt et al., 2015; Peters et al., 2007; Petzka et al., 2021; Schapiro et al., 2017; Sio et al., 2013; van de Ven et al., 2016; Walker et al., 2020).

In a previous study, we showed that restricting the pre-training sleep to the last 4 h of the night reduced stability of EEG-activity patterns throughout the restudy of stimuli relative to a group of participants that slept 8 h (Baena et al., 2020). After a full night of recovery sleep, the sleep-restricted group showed longer-lasting reinstatement of content-specific encoding-related activity during the first recognition test compared to controls, which was crucial to achieving equivalent performance (Baena et al., 2020). Interestingly, the increased coupling between slow oscillations (SOs) and spindles (SPs) in post-training sleep, which has been proposed as a key mechanism of overnight memory consolidation (Batterink et al., 2016; Helfrich et al., 2018; Jiang et al., 2019a, 2019b; Latchoumane et al., 2017; Maingret et al., 2016; Mölle et al., 2009; 2011; Muehlroth et al., 2019; Niknazar et al., 2015; Schreiner et al., 2021; Staresina et al., 2015; Zhang et al., 2018), was associated with reduced stability of neural encoding and also with prolonged reinstatement of episode-unique encoding-related activity during the recognition task the following morning, supporting the idea that weakly encoded memories are prioritized for consolidation during sleep (Baena et al., 2020).

In the present study, we are using part of the dataset analyzed in the prior survey (Baena et al., 2020) to determine whether the impact of sleep restriction on the stability of neural encoding moderates the relationship between sleep- and retrieval-mediated consolidation processes. For the sake of consistency across studies, we relied on the same original measure of neural stability across restudy of stimuli and on the same measure of coupling between SOs and SPs during N3 of post-training sleep (Baena et al., 2020). However, while our previous study was focused on reinstatement of content-specific encoding-related activity during the first recognition test; the present study seeks to assess the extent to which the degree of neural stability during encoding and the associated changes in SO-SP coupling during subsequent sleep accounts for variability in reinstatement of both content-specific and category-specific encoding-related activity patterns across multiple recognition tests. This approach allows us to determine if differentiation (i.e., encoding-retrieval specific similarity) and generalization outcomes (i.e., encoding-retrieval categorical similarity) triggered by offline

consolidation during sleep and online consolidation during active retrieval the next morning are conditioned by the quality of encoding.

We hypothesize that sleep- and retrieval-mediated consolidation processes will contribute to transform different aspects of memory representations depending on the stability of neural encoding. If acute sleep restriction on the pre-training night impairs the ability to consistently reactivate networks associated with detailed aspects of memory across restudy of face pairs (Baena et al., 2020), it is likely that post-training sleep will tend to reactivate those aspects that are common to memories to a greater extent than characteristic details of a particular memory. Subsequently, during the recognition task, these more global aspects are more likely to be reactivated to a greater extent with each test, which should translate into an increase in categorical similarity that would facilitate the integration of memories belonging to the same semantic category (i.e., semantic generalization). The moderating role of encoding stability on the relationship between post-training sleep and retrieval processes in promoting generalization in favor of differentiation is expected to be particularly evident in the group subjected to sleep restriction on the night before memory acquisition, because this group showed less stable encoding-related activity patterns over repeated presentations than the group that slept 8 h (Baena et al., 2020). Conversely, if a memory representation has been strongly encoded during the study phase, repeated recognition of that memory the next day is expected to enhance reinstatement of both categorical and episode-unique representations, regardless of the degree of coupling between SOs and SPs the previous night. This hypothesis is supported by evidence that sleep has little effect on the consolidation of strong memories (e.g., Bäuml et al., 2014; Denis et al., 2020, 2021), whereas retrieval-mediated learning tends to consolidate both specific and more abstract and generalized information (Ferreira et al., 2019).

2. Material and methods

2.1. Participants

Twenty-seven University students gave written informed consent to participate in the study. One participant was excluded from the analysis due to an insufficient number of trials across repeated testing. The final sample consisted of 26 participants [age 21.7 ± 2.7 (mean \pm SD), range 18–27 yr, 14 females] with normal or corrected-to-normal vision, regular sleep habits confirmed by sleep-diaries, and no history of neurological and/or psychiatric diseases. Participants were instructed to abstain from drugs, alcohol, and caffeine, and to refrain from napping for the week before the first experimental session until the experiment was finished. Participants were randomly assigned to either the normal sleep duration group (NSD = 12) or the acute sleep restriction group (ASR = 14). This research was approved by the Ethical Committee for Human Research at the Pablo de Olavide University according to the principles outlined in the Declaration of Helsinki.

2.2. Stimuli and experimental design

The stimuli and experimental protocol used in the present study have been described in detail elsewhere (Alberca-Reina et al., 2014, 2015; Baena et al., 2020). Briefly, the stimuli consisted of pairs of famous people's faces (gray-scale oval faces) obtained from pictures of celebrities whose professions were actor, singer, or TV host/newsreader. A schematic representation of the memory task is shown in Fig. 1A–B. The task included a training session in the evening (6:30 PM) after participants slept in the laboratory for either 8 h (12:00–8:00 AM; NSD group) or the last 4 h of the previous night (4:00–8:00 AM; ASR group); and a testing session (12:00 PM) after a full night's sleep in the laboratory. The experimental protocol is illustrated in Fig. 1C and described in detail in the [Supplementary Material](#).

During the training session (Fig. 1A), participants were presented with 48 pairs of faces corresponding to different celebrities of the same

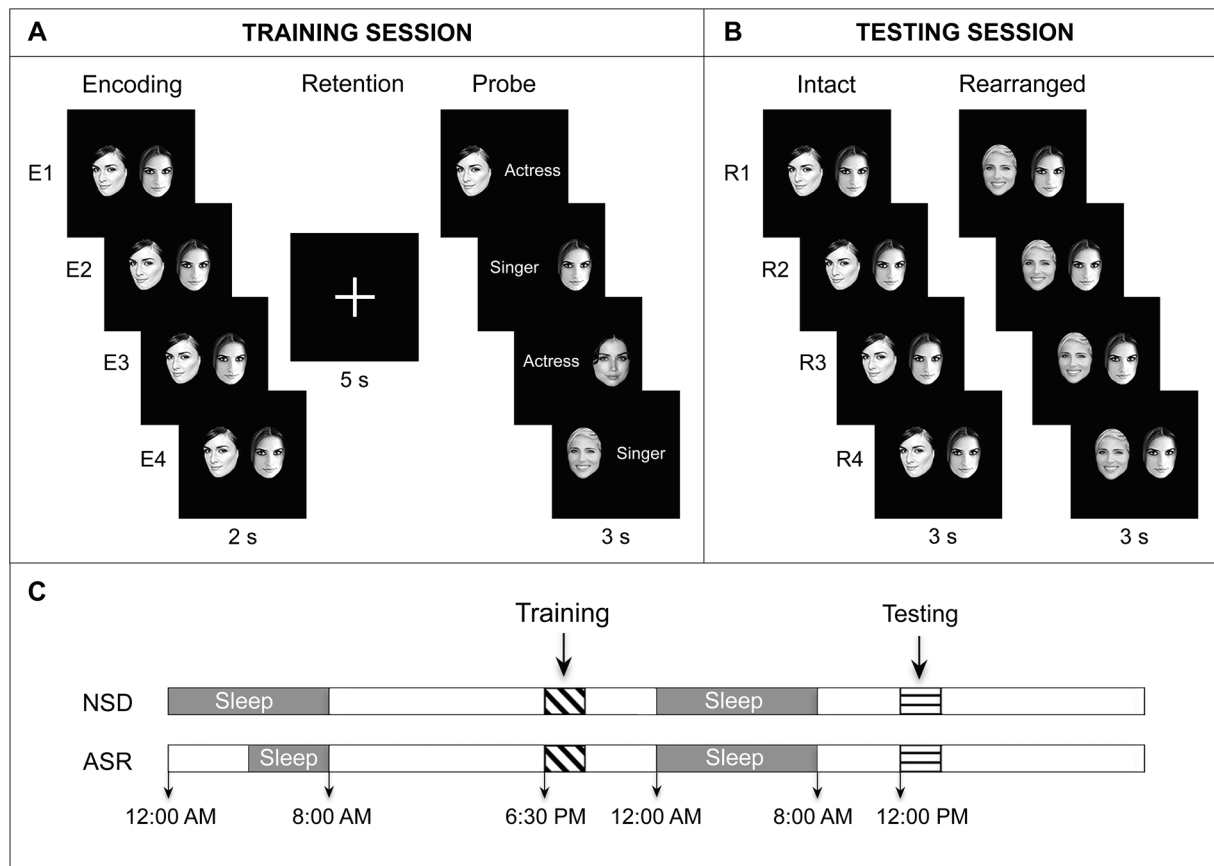


Fig. 1. Overview of the memory task and experimental protocol. (A) During the training session, participants were presented with face-face associative pairs for 2 s. Faces always corresponded to celebrities. In the trial example, faces of two famous actresses (semantically congruent professions), Paz Vega and Penélope Cruz, were shown together. After a retention period of 5 s, participants were asked to indicate if the profession and face corresponded with the faces they had previously encountered in that particular location. This association was presented 4 times (E1, E2, E3, E4). (B) During the testing session, participants performed a recognition task where they should indicate whether or not they had seen that particular combination of faces in the prior evening. In the intact condition, Paz Vega and Penélope Cruz were presented together, while in the rearranged condition Penélope Cruz was presented with Elsa Pataky (like in the example) and Paz Vega with Ana de Armas. Each combination of faces (intact and rearranged) was also presented 4 times (R1, R2, R3, R4) in alternant blocks. (C) Two groups of participants were trained in the evening (6:30 PM) following a night of either normal sleep duration (NSD; from 12:00 AM to 8:00 AM) or acute sleep restriction (ASR; from 4:00 AM to 8:00 AM) in the sleep laboratory. EEG was continuously recorded during sleep in the two consecutive nights as well as during the training and testing session.

sex, half of them with the same profession (i.e., semantically congruent) and the other half with a different profession (i.e., semantically incongruent). The procedure for the selection of famous faces is described in detail in the [Supplementary Material](#). Face pairs were presented in 2 consecutive blocks (24 pairs per block) that were repeated 4 times. The order of face pairs within each block was randomized. The trial began with a cross on the center of the screen for 2 s, followed by a face pair for another 2 s (encoding period), and by a retention period of 5 s during which participants retained faces, their location, and profession while fixating on a cross that appeared in the center of the screen. The trial finished with a probe stimulus for 3 s including a face and a word referring to a particular profession. Participants were asked to indicate via button press whether the face and profession presented on the left and right side corresponded to the study face that appeared in that particular position during the encoding period. The probe, and consequently the response, changed across the four repetitions of the face pair. In order to enhance sleep-dependent consolidation, participants were informed that memory for face-face associations would be evaluated the next morning (Alger et al., 2019; Bennion et al., 2016; Merhav et al., 2015; Rauchs et al., 2011; Saletin et al., 2011; van Dongen et al., 2012; Wilhelm et al., 2011). The task used during the training phase was initially designed to assess the effect of semantic congruence on memory (Alberca-Reina et al., 2014, 2015). This is why celebrities may or may not share a profession. Unfortunately, we do not have a sufficient

number of trials to evaluate the effect of semantic congruence on neural memory stability. However, there are advantages to keeping this variable in the current protocol. On the one hand, it allowed us to maintain attention of participants in a rather monotonous task and, on the other hand, it allowed us to establish more specific categories when assessing categorical similarity, as will be discussed below (see [Section 2.4](#)).

During the testing session ([Fig. 1B](#)), all faces were presented both coupled with the same face as in the training session (intact condition) and recombined with a different face (rearranged condition), while controlling that the rearrangement maintained the left–right relationship, sex, and semantic context (same or different profession) of the study phase. As in the training session, each face pair (intact and rearranged) was repeated 4 times in alternating blocks without feedback. Participants were asked to respond via button press as fast and accurately as possible as to whether or not the two faces had been presented together during the training session in the prior evening.

2.3. EEG data acquisition and preprocessing

EEG data from 59 scalp electrodes (Grass, USA) positioned according to the extended International 10–20 system were recorded at a sampling rate of 250 Hz during the training and testing session, as well as while sleeping in the laboratory both in the pre- and post-training night. Additional electrodes were placed to record vertical and horizontal eye

movements and to monitor submental muscle tone. Signals referenced to linked mastoids were amplified (BrainAmp MR, Brain Vision®) and bandpass-filtered between 0.1 and 100 Hz.

EEG data acquired during the 3rd and 4th repetition of face pairs during the training session and the 2nd, 3rd, and 4th repetition of face pairs during the testing session was preprocessed following the same procedure described previously (Baena et al., 2020). First, independent component analysis (ICA) as implemented in the BrainVision Analyzer software v.1.05 (Brain ProductsV® GmbH) was applied to remove eye movements, blinks, and muscle artifacts. Next, continuous EEG recordings were divided into epochs of 1300 ms, ranging from -300 ms to 1000 ms post stimulus onset. The remaining noisy EEG epochs were removed manually. Artifact-free epochs were transformed into the common average reference and band-pass filtered (0.5–30 Hz) using a finite impulse response based on Kaiser's window. The pre-stimulus interval (-300 to -100 ms) was used for baseline removal procedure.

2.4. Spatiotemporal EEG pattern similarity analysis

In the present study, we only analyzed face pairs that were subsequently remembered. We computed the degree of spatiotemporal pattern similarity (STPS) across repetitions of the same face pair as a measure of the stability of content-specific encoding activity. Here, we only used the STPS computed between EEG-activity patterns associated with the 3rd and 4th repetition (hereafter STPS_{E3-E4}) because we previously showed that differences between both groups only became evident after the 4th repetition (Baena et al., 2020). Importantly, we also demonstrated that the stability of content-specific encoding activity was greater for remembered than for forgotten face pairs (a detailed description of these results was included in the [Supplementary Material](#)). This finding is consistent with previous studies showing an association between greater stability of activation patterns across repeated study and successful memory encoding (LaRocque et al., 2013; Lu et al., 2015; Visser et al., 2013; Xiao et al., 2016; Xue et al., 2010; Zheng et al., 2018).

To assess STPS, we implemented the approach described in previous studies (Baena et al., 2020; Lu et al., 2015; Sols et al., 2017). Before computing STPS, scalp EEG electrodes were grouped into six regions of interest (ROIs). To obtain more stable spatial patterns, the electrodes in the border of two ROIs were included in both ROIs (ROI 1 [left frontal]: Fpz, Fp1, AFz, AF3, AF7, Fz, F1, F3, F5, F7, FCz, FC1, FC3, FC5, FT7; ROI 3 [left central]: FCz, FC1, FC3, FC5, FT7, Cz, C1, C3, C5, T7, CPz, CP1, Cp3, CP5, TP7; ROI 5 [left parietal]: CPz, CP1, Cp3, CP5, TP7, Pz, P1, P3, P5, P7, POz, PO3, PO7, Oz, O1; and the homologous electrodes for the ROIs 2, 4, and 6 in the right hemisphere). For each correctly remembered face pair, we constructed spatiotemporal vectors including the mean EEG voltage from one of the six ROIs, and a sliding window of 200 ms (50 time points, from 0 to 1000 ms post-stimulus onset) in time steps of one time point as representative of spatial and temporal features, respectively. The temporal data was finally grouped into 20 ms bins, resulting in 40 time points.

To evaluate reinstatement of encoding-related EEG-activity patterns, we computed encoding-retrieval similarity (hereafter STPS_{E4-R}) via Pearson correlation between EEG patterns associated with the 4th repetition during the training session and EEG patterns produced by the 2nd, 3rd, and 4th repetition during the testing session. For this analysis, we only included EEG epochs associated with face pairs presented as in the training session (intact condition). To address reinstatement of activation patterns shared by categorically related memories (i.e., categorical STPS_{E4-R}), similarity analysis was applied to spatiotemporal vectors of different face pairs sharing sex, profession, and semantic congruence condition; whereas for evaluating reinstatement of activation patterns associated with episodic details (i.e., specific STPS_{E4-R}), similarity analysis was applied to spatiotemporal vectors of the same face pairs. The resulting correlations were transformed into Fisher's z before performing group statistics. Fig. 2 shows a schematic version of

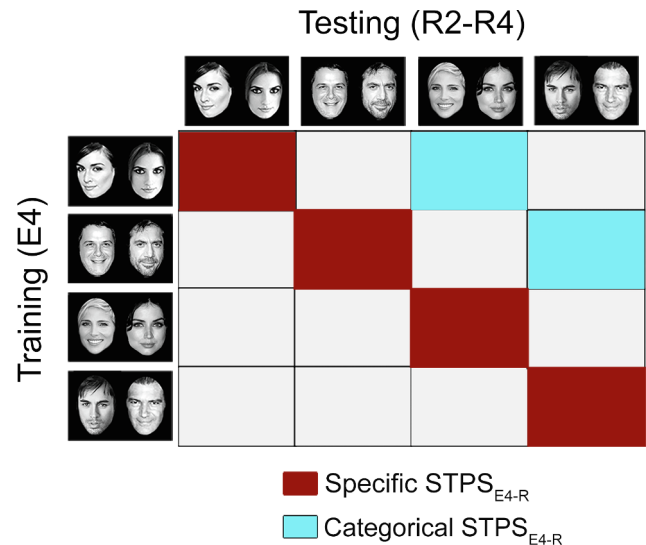


Fig. 2. Encoding-retrieval similarity (STPS_{E4-R}) across repeated testing. For STPS_{E4-R}, Pearson correlation was computed between EEG patterns associated with the 4th restudied association during the training phase (E4) and EEG patterns associated with every repeated test (R2, R3, R4) during the recognition task performed the next morning. These analyses were applied to associations correctly recognized during the testing session. The red boxes refer to similarity computed between EEG patterns associated with identical face pairs (specific STPS_{E4-R}), while the blue ones refer to similarity computed between EEG patterns produced by face-face associations of the same category (i.e., same sex, profession, and semantic congruence condition; categorical STPS_{E4-R}). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the procedure employed to compute categorical and specific similarity between encoding and retrieval sessions.

2.5. Coupling between SPs and SOs

As we were mainly interested in evaluating the contribution of the temporal grouping of SPs by the SO upstate to memory consolidation, and SOs are mainly observed during N3 sleep, both SOs and SPs were identified during N3 sleep of the post-training night. For this, post-training sleep recordings were scored manually in individual 30-s epochs according to the guidelines of the American Academy of Sleep Medicine (Iber et al., 2007).

SOs were automatically identified in frontocentral electrodes (F3, F1, Fz, F2, F4, FC1, FC2, Cz) using a standard detection method (Mölle et al., 2002). As the performance of automated SP-detection algorithms seems to be quite poor when compared to human experts and non-experts (Warby et al., 2014), we applied a semi-automatic method based on a visual identification performed by an expert technician. In the present study, we focused on the analysis of fast SPs (13–16 Hz) based on their consistent association with memory consolidation processes (Fogel & Smith, 2011; Rasch & Born, 2013) and their strong phase synchronization with the depolarizing upstate of SOs (Coppieters 't Wallant et al., 2016; Mölle et al., 2011; Staresina et al., 2015). To this aim, we first performed a manual identification based on visual inspection of SPs on a few electrodes (F3, F4, C3, Cz, C4, P3, Pz, P4, O1, O2) followed by an automatic analysis (Mölle et al., 2002). In line with previous studies comparing automated SP detection with expert manual SP scoring (Ray et al., 2015), start and end markers were manually placed in the EEG location that showed maximum amplitude if the SP fulfilled the following criteria: (i) duration varying between 0.5 and 3 s; (ii) minimum amplitude of 15 μ V; (iii) fusiform morphology; and (iv) minimum inter-SP interval of 1 s (Urakami et al., 2012). To reduce the number of false positives, the time window established by manual markers was

used for the automatic identification of SPs. Although fast SPs are more evident over centroparietal regions as opposed to the more frontocentral expression of slow SPs (Andrillon et al., 2011; Cox et al., 2017), evidence has shown that fast SPs are modulated by the SOs even at sites where they are less prominent (Cox et al., 2018), and that not only centroparietal but also frontocentral fast SPs can be a key determinant of offline memory consolidation (Baena et al., 2020; Cairney et al., 2018; Mander et al., 2017). Building on this evidence, the automatic identification of SPs was performed at anterior and posterior electrodes (F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8).

The SO-SP coupling was determined using the approach developed by Mölle and colleagues (Möller et al., 2002). Briefly, event correlation histograms of fast SPs were referenced to the negative half-wave peaks of the SOs using 6 s windows with 3 s offsets and a bin size of 48 ms. For SP counts, SP peaks and troughs, SPs were computed from all EEG electrodes used for their identification. SP counts in each time bin were divided by the number of SOs and then divided by the bin width to obtain the event rate per second (Hz). The resulting signal was baseline corrected after applying mean centering to each EEG electrode. The values corresponding to the bins representing the highest portion of the upstate were averaged for subsequent analyses.

2.6. Statistical analysis

Linear mixed models were applied to adequately handling the correlation between repeated measurements on the same subject (Gueorguieva & Krystal, 2004). Moreover, this statistical approach allows for random intercepts across participants and across time in the case of STPS, which, in turn, reduces the variance of fixed effect estimates (Clark & Linzer, 2015).

To assess whether the quality of encoding and subsequent consolidation processes during sleep moderated changes in neural memory reactivation and recognition task performance as a result of repeated testing, we started with a model that included only the intercept, then added the main predictors, and finally the double, triple and quadruple interactions. Models were specified using the *lme4* package (Bates et al., 2015) in R (R Core Team, 2016) via restricted maximum likelihood estimation. These models were statistically compared to each other using the ANOVA function. The null hypothesis for the different predictors added to successively complex models was rejected if the ANOVA revealed a significant improvement of the model's fit to the data, which implies a significant increase in variance.

For each model, we reported the estimates, confidence intervals (95%), and approximate p-values of fixed terms based on the t-statistics and using the normal distribution function. We further report the Akaike's information criterion (AIC), the number of observations, the marginal R^2 (variance of the fixed effects), conditional R^2 (Ω_0^2 , variance of the fixed and random effects), and the intraclass correlation coefficient (ICC) (Nakagawa et al., 2017). The F tests are based on the Satterthwaite's approximation to degrees of freedom (Kuznetsova et al., 2017).

3. Results

3.1. Recognition memory performance

For the recognition task, we analyzed reaction time (RT) to hits, performance sensitivity (d') and decision criterion (C) based on signal detection theory (Harvey, 1992). On a preliminary basis, we specified an intercept model with participants as random factor. This served as the null baseline model on which the two subsequent models were built upon. Next, we specified a two-step mixed effect model. In the first step, we added group (NSD, ASR) and repeated retrieval (R1, R2, R3, R4) as

main fixed predictors, while in the second step, we added the two-way interaction term.

Results derived from the two-step mixed effects model for RT, d' and C are shown in Tables 1–3, respectively. The model including the two main predictors (i.e., group and repeated testing) provided a better fit to the data than the intercept-only model for both RT ($\chi^2(4) = 83.6$, $p < 10^{-15}$) and decision criterion C ($\chi^2(4) = 78.2$, $p < 10^{-15}$), as did the model including the two-way interaction term when compared to the model including main predictors, but only for the decision criterion C ($\chi^2(3) = 8.97$, $p = 0.03$). No model fit improvement was found for the sensitivity measure d' , indicating that the null hypothesis was not rejected for either the main or interaction effect.

Fig. 3A illustrates the progressive decrease of RT throughout repetitive tests for correctly recognized intact face pairs ($F_{3,78} = 49.9$, $p < 10^{-15}$). This analysis showed a reduction of RT from R1 to R2 (estimate = -18.34 , $p < 0.001$) and from R2 to R3 (estimate = -16.6 , $p = 0.001$), but not additional gain was found from R3 to R4 (estimate = -5.93 , $p = 0.2$). The model failed to reject the null hypothesis for the main effect of group (Table 1, model 1) and for the repeated testing \times group interaction (Table 1, model 2). These results suggest that repeated testing facilitates the generalizability of memory regardless of sleep duration in the night before memory acquisition. Indeed, the more generalizable a mnemonic representation is, the less detail it tends to provide and the faster the decisions it elicits (Redish & Mizumori, 2015). Nevertheless, the shortening of RT with repetition could also result from improvements in motor, rather than cognitive, response as a result of repeated practice. As the two hypotheses are not mutually exclusive, the analysis of neural correlates may help to determine whether the generalization hypothesis is confirmed (see Section 3.3).

Fig. 3B and C illustrates changes in sensitivity and decision criterion based on d' and C indexes, respectively. Neither manipulation of pre-training sleep (Table 2, model 1), nor repeated testing (Table 2, model 1), nor the interaction term (Table 2, model 2) affected d' scores. On the contrary, the mixed-effects model for the decision criterion C yielded a main effect of repeated testing ($F_{3,78} = 45.6$, $p < 10^{-15}$; Table 3, model 1), as well as a repeated testing \times group interaction ($F_{3,78} = 3.2$, $p = 0.029$; Table 3, model 2). As illustrated in Fig. 3C, the ASR group showed a bias to say "new" in response to intact face-face associative pairs relative to the NSD group after R3 (estimate = 0.9 , $p = 0.008$) and R4 (estimate = 0.92 , $p = 0.007$) when compared to R1 (Table 3, model 2), but no group differences were found when compared to R2. The results indicate that even though both groups were equally accurate during recognition, the ASR group was more conservative in their decision making than the NSD group.

3.2. Effect of sleep restriction on STPS_{E3-E4}, macrostructure and microstructure of post-training sleep, and degree of SO-SP coupling

Group differences in the STPS_{E3-E4} as well as in the macrostructure and microstructure of sleep were previously reported (Baena et al., 2020) but they have also been summarized in the Supplementary Material. Fig. S1 further illustrates the effect of sleep restriction in the pre-training night on SO-SP coupling during post-training sleep.

3.3. Regression of STPS_{E3-E4}, SO-SP coupling, repeated testing, and ROI on STPS_{E4-R}

To assess the relationship between stability of neural encoding (i.e., STPS_{E3-E4}), SO-SP coupling, reinstatement of encoding-related activity patterns across repeated testing during the recognition task, and ROI, a four-step mixed effects model was specified for both categorical and specific STPS_{E4-R}, with participants and time (i.e., 40 time points across which STPS_{E3-E4} and STPS_{E4-R} were computed) as nested random intercepts. The four main predictors were added in the first step, whereas the two-, three- and four-way interactions were sequentially added in

Table 1
Mixed-effects regression of repeated testing and group on RT.

Predictors	Model 1			Model 2		
	Estimates	CI	p	Estimates	CI	p
(Intercept)	322.81	307.99–337.64	<0.001	325.20	309.84–340.56	<0.001
R2	–18.34	–25–67–11.02	<0.001	–21.87	–31.73–12.01	<0.001
R3	–33.68	–41.01–26.36	<0.001	–38.03	–47.88–28.17	<0.001
R4	–42.29	–49.62–34.97	<0.001	–43.96	–53.82–34.10	<0.001
Group	–7.71	–28.50–13.09	0.467	–12.87	–35.49–9.74	0.265
R2*Group				7.64	–6.87–22.15	0.302
R3*Group				9.41	–5.10–23.92	0.204
R4*Group				3.61	–10.90–18.12	0.626
<i>Random Effects</i>						
AIC	922.20			926.28		
σ^2	181.48			177.07		
$\tau_{00,Participant}$	681.97			683.07		
N _{Participant}	26			26		
ICC _{Participant}	0.79			0.79		
Observations	104			104		
R^2/Ω_0^2	0.242 / 0.841			0.245 / 0.845		

Reference category for repeated testing (R1) / Reference category for group (NSD).

Abbreviations: AIC, Akaike's information criterion; CI, confidence interval; ICC, intraclass correlation coefficient.

Table 2
Mixed-effects regression of repeated testing and group on d'

Predictors	Model 1			Model 2		
	Estimates	CI	p	Estimates	CI	p
(Intercept)	–0.02	–0.51–0.46	0.922	–0.12	–0.64–0.39	0.639
R2	0.07	–0.27–0.42	0.671	0.20	–0.26–0.66	0.397
R3	0.11	–0.23–0.45	0.532	0.23	–0.24–0.69	0.336
R4	–0.06	–0.40–0.28	0.742	0.10	–0.36–0.56	0.675
Group	–0.02	–0.66–0.62	0.961	0.20	–0.56–0.97	0.606
R2*Group				–0.27	–0.95–0.41	0.432
R3*Group				–0.26	–0.94–0.43	0.462
R4*Group				–0.34	–1.02–0.34	0.330
<i>Random Effects</i>						
AIC	262.16			268.06		
σ^2	0.40			0.39		
$\tau_{00,Participant}$	0.59			0.59		
N _{Participant}	26			26		
ICC _{Participant}	0.60			0.60		
Observations	104			104		
R^2/Ω_0^2	0.004 / 0.601			0.009 / 0.606		

Reference category for repeated testing (R1) / Reference category for group (NSD).

Abbreviations: AIC, Akaike's information criterion; CI, confidence interval; ICC, intraclass correlation coefficient.

subsequent steps.

Results from model 1 to model 4 for categorical and specific STPS_{E4-R} were shown in Tables S1 and S2, respectively (Supplementary Material). The addition of the four-way interaction term (i.e., model 4) provided a better model fit in comparison with the three-way interaction terms (i.e., model 3) for both categorical ($\chi^2(10) = 28.7$, $p < 0.001$) and specific STPS_{E4-R} ($\chi^2(10) = 247.5$, $p < 10^{-15}$).

Results derived from model 4 are illustrated in Fig. 4. For memories showing smaller STPS_{E3-E4} (i.e., lower stability of neural encoding), repeated testing reverted from negative (R2 and R3) to positive (R4) the association between SO-SP coupling and categorical STPS_{E4-R} (Fig. 4, top panel), particularly in ROI 1 (left frontal) when compared to ROI 5 (left parietal) (estimate = 1.02, $p < 0.001$), where the same pattern of results was observed for memories showing greater STPS_{E3-E4} (i.e., greater stability of neural encoding). The opposite pattern of results was observed for the association between SO-SP coupling and specific STPS_{E4-R} (Fig. 4, bottom panel), especially in ROI 1 (left frontal) when compared to ROI 4 (right central) (estimate = –2.61, $p < 0.001$). These results indicate that offline consolidation processes operating during post-training sleep interact with online consolidation processes during

retrieval the next morning to favor reactivation of the categorical aspects of weaker memories to the detriment of the more specific aspects, promoting the generalizability of such traces at the expense of differentiation. The opposite was observed for memories that showed a more stable neural pattern during encoding. There was a greater likelihood of differentiation to the detriment of integration with other memories.

Next, we evaluated whether the association between STPS_{E3-E4}, SO-SP coupling, and STPS_{E4-R} (either categorical or specific) across repeated testing during the recognition task was stronger in the ASR group compared to the NSD group. For sake of clarity, and to avoid the inclusion of a five-way interaction term, we restricted the analysis to data from ROI 1 (left frontal), where this relationship was most evident. Tables S3 and S4 included in the Supplementary Material show results from model 1 to model 4 for categorical and specific STPS_{E4-R}, respectively. The inclusion of a four-way interaction term (i.e., model 4) provided a better model fit in comparison with the three-way interaction terms (i.e., model 3) for both categorical ($\chi^2(4) = 21.9$, $p = 0.0002$) and specific STPS_{E4-R} ($\chi^2(4) = 72.8$, $p < 10^{-15}$).

Fig. 5 plots the regression of STPS_{E3-E4} and SO-SP coupling on categorical and specific STPS_{E4-R} across repeated testing at one standard

Table 3
Mixed-effects regression of repeated testing and group on C.

Predictors	Model 1			Model 2		
	Estimates	CI	p	Estimates	CI	p
(Intercept)	-1.37	-1.67--1.07	<0.001	-1.10	-1.45--0.75	<0.001
R2	1.62	1.27-1.98	<0.001	1.37	0.91-1.82	<0.001
R3	1.60	1.25-1.95	<0.001	1.18	0.73-1.64	<0.001
R4	1.59	1.24-1.94	<0.001	1.16	0.71-1.62	<0.001
Group	0.37	0.06-0.67	0.018	-0.23	-0.74-0.28	0.384
R2*Group				0.56	-0.11-1.23	0.102
R3*Group				0.90	0.23-1.57	0.008
R4*Group				0.92	0.25-1.59	0.007
Random Effects						
AIC	230			227		
σ^2	0.42			0.38		
$\tau_{00,Participant}$	0.05			0.06		
N Participant	26			26		
ICC Participant	0.60			0.60		
Observations	104			104		
R^2/Ω_0^2	0.524 / 0.574			0.559 / 0.620		

Reference category for repeated testing (R1) / Reference category for group (NSD).

Abbreviations: AIC, Akaike's information criterion; CI, confidence interval; ICC, intraclass correlation coefficient.

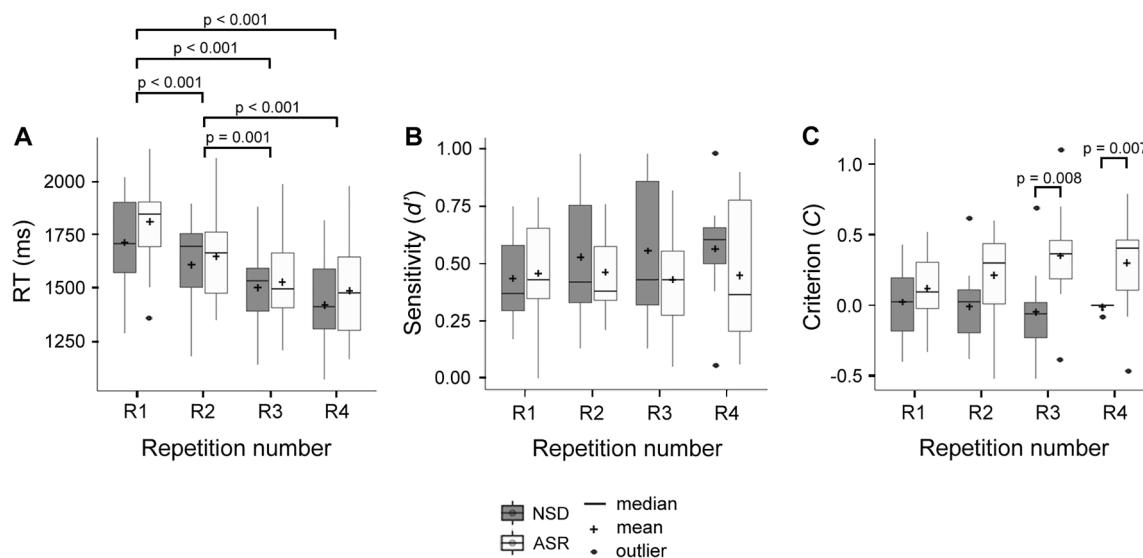


Fig. 3. Effect of sleep restriction and repeated testing on different indices of memory recognition. Box plots of RT for hits (A), sensitivity d' index (B), and decision criterion C (C) for each group (NSD and ASR) and repeated test. Horizontal lines are medians, crosses are means, boxes show the interquartile range representing 50% of the cases, and whisker bars extend to 1.5 times the interquartile range. Black circles represent the value of outliers. P-values for the repeated test factor are shown in A, while C shows the results of post hoc tests for the interaction. Neither main effects nor interaction were found in B.

deviation below and above the mean of $STPS_{E3-E4}$ for the NSD and ASR group. Relative to the NSD group, the ASR group showed a stronger positive association of SO-SP coupling with categorical $STPS_{E4-R}$ from R3 to R4 for memories with smaller $STPS_{E3-E4}$ (estimate = -1.08 , $p = 0.003$), which was paralleled by a negative association with specific $STPS_{E4-R}$ (estimate = -3.12 , $p < 0.001$). These results are consistent with evidence that sleep favors weaker memories over stronger ones, as the moderating effect of encoding quality on the interaction between post-training sleep and repeated testing during the recognition task was more marked in the ASR group than in the NSD group.

4. Discussion

Although there is increasing evidence highlighting the role of the interaction between the quality of encoding (Baena et al., 2020; Cairney et al., 2016; Creery et al., 2015; Denis et al., 2020, 2021; Diekelmann et al., 2010; Djonlagic et al., 2009; Drosopoulos et al., 2007; Dumay,

2016; Kuriyama et al., 2004; McDevitt et al., 2015; Peters et al., 2007; Petzka et al., 2021; Schapiro et al., 2017; Sio et al., 2013; van de Ven et al., 2016; Walker et al., 2020) or retrieval-mediated learning (Antony & Paller, 2018; Antony et al., 2017; Bäuml et al., 2014; Cowan et al., 2020; Ferreira et al., 2019; Himmer et al., 2019; Lifanov et al., 2021; Mazza et al., 2016) and subsequent sleep in transforming memory, to date no study has evaluated how these three processes are related in contributing to memory reorganization.

Our results showed that offline consolidation during post-training sleep interacts with online consolidation during repeated recognition of face pairs the next day to increase generalization (i.e., reinstatement of category-specific encoding activity in frontal regions) of memories showing lower stability of neural encoding to the detriment of differentiation (i.e., reinstatement of content-specific encoding activity in the same regions), whilst the opposite was true for memories showing greater neural stability during encoding. The moderating role of encoding stability became even more evident in the group of

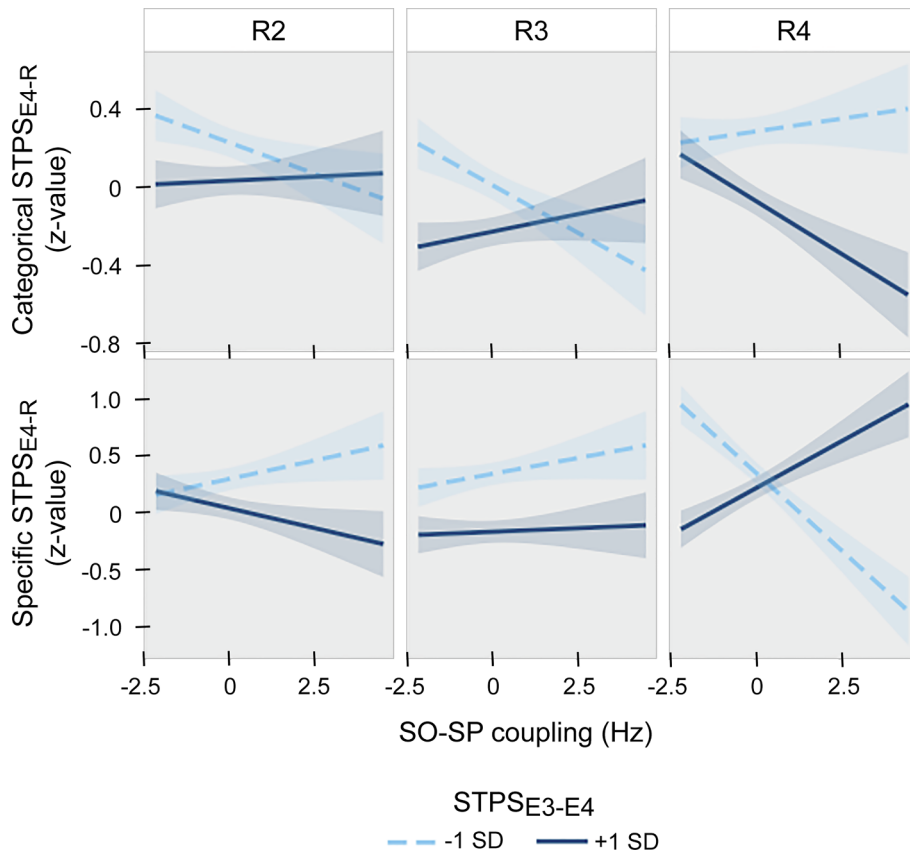


Fig. 4. Relationship between $STPS_{E3-E4}$ and SO-SP coupling on categorical and specific $STPS_{E4-R}$ across repeated testing. Association of SO-SP coupling with both categorical and specific $STPS_{E4-R}$ at one standard deviation (SD) below and above the mean of $STPS_{E3-E4}$ in the left frontal ROI for every repeated test, where the four-way interaction term was most evident. The shaded areas reflect the confidence bands (95%) for the fitted values.

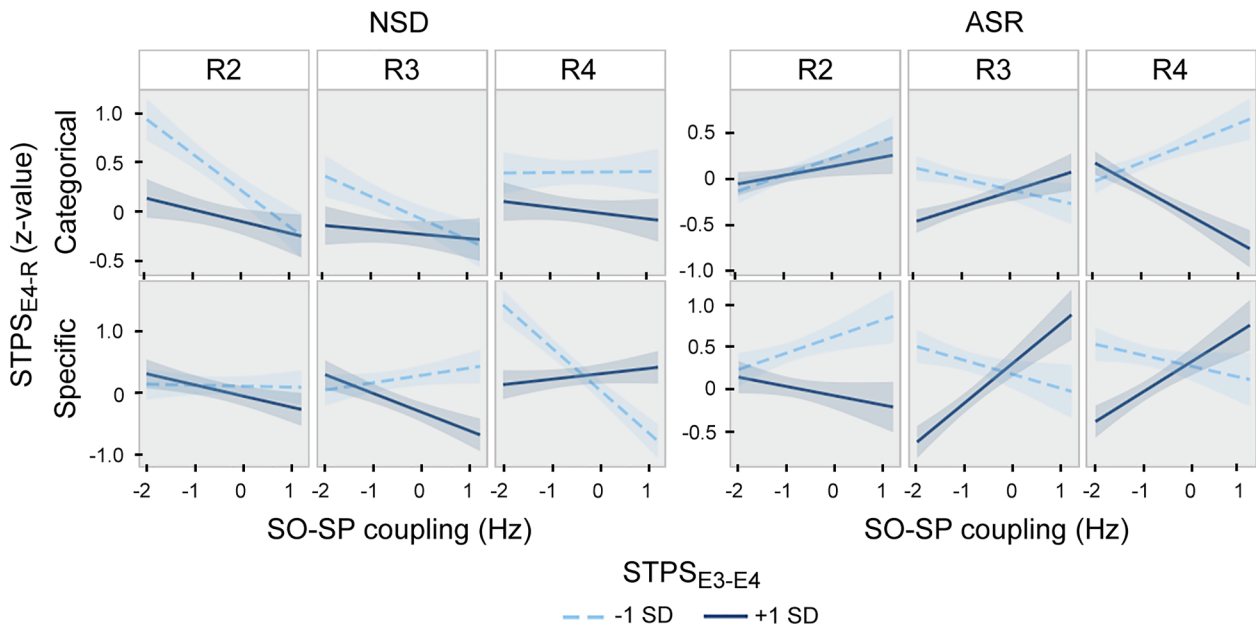


Fig. 5. Relationship between $STPS_{E3-E4}$ and SO-SP coupling on categorical and specific $STPS_{E4-R}$ across repeated testing for the NSD and ASR group. Association of SO-SP coupling with both categorical and specific $STPS_{E4-R}$ at one standard deviation (SD) below and above the mean of $STPS_{E3-E4}$ in the left frontal ROI for every repeated test, for the NSD and ASR group, separately. The shaded areas reflect the confidence bands (95%) for the fitted values.

participants that was submitted to sleep restriction the night before memory acquisition, supporting the notion that weakly encoded memories are prioritized for subsequent sleep consolidation and testing-

induced generalization.

The present results are consistent with previous results that have related the SP density during overnight sleep to enhanced category-

specific pattern similarity in the prefrontal cortex the next day while restudying information learned prior to sleep (Cowan et al., 2020). These findings extended the role of SPs from purely stabilizing recently acquired memory traces, to one that also involves promoting enduring neural changes associated with the restructuring of memory representations. Likewise, results of the current study suggest that SPs nested into the upstate of SOs may be critical in supporting not only the sleep-dependent reorganization of memory traces during sleep (Batterink et al., 2016; Helfrich et al., 2018; Jiang et al., 2019a, 2019b; Latchoumane et al., 2017; Maingret et al., 2016; Mölle et al., 2009, 2011; Muehlroth et al., 2019; Niknazar et al., 2015; Schreiner et al., 2021; Staresina et al., 2015; Zhang et al., 2018), especially of those that were weakly encoded (Denis et al., 2021), but also in shaping the future restructuring of neural memory representations reactivated by complete reminders during intentional retrieval the next morning. The fact that the interaction effect is restricted to the left frontal lobe is consistent with previous evidence linking the prefrontal cortex, particularly its ventromedial portion, to sleep-dependent consolidation processes (Sekeris et al., 2018; Sterpenich et al., 2007, 2009; Takashima et al., 2006, 2007, 2009) and to integration mechanisms in the service of generalization in episodic memory (Bowman & Zeithamova, 2018; Cowan et al., 2020; Xu et al., 2012).

In the present study, the sleep-retrieval interplay promoted specificity of strong memories (i.e., memories showing greater stability of neural encoding) and generalization of weak memories (i.e., memories showing lower stability of neural encoding). The latter result was further supported by the growing conservative trend shown by the sleep restriction group across repeated tests relative to controls. The shift in the decision criterion might be promoted by reactivation of memory traces decreasingly specific, which, in turn, might have been contributed to reduce neural excitability in cortical regions that are crucial for memory discrimination (Muckli & Petro, 2017). In line with this hypothesis, there is evidence that changes introduced in sensory encoding, through either modification of task parameters or optogenetic stimulation of primary sensory areas, may alter the decision criterion without affecting discriminability (Jin & Glickfeld, 2019), adding support to results of the present study.

It is generally accepted that reactivation during intentional retrieval induces a transient and labile state (Sara, 2000a, 2000b) during which the memory trace can be disrupted, deleted, or updated and integrated with other overlapped memory traces (McKenzie & Eichenbaum, 2011; Nadel et al., 2012). Our results are in line with the idea that instability induced by intentional retrieval is a gateway to generalization (Robertson, 2018), especially for those memories whose specific details could not be properly encoded in long-term memory. This does not mean that strong memories are not generalized over time, but rather that poorly encoded memories may be at greater risk of overgeneralization, which could be problematic in certain circumstances like threat learning conditions (Starita et al., 2019), anxiety (Lissek et al., 2014), depression and eating disorders (Thew et al., 2017).

Our findings are consistent with previous evidence suggesting that sleep consolidation processes interact with retrieval processes to transform memory traces (Antony & Paller, 2018; Antony et al., 2017; Bäuml et al., 2014; Cowan et al., 2020; Ferreira et al., 2019; Himmer et al., 2019; Lifanov et al., 2021; Mazza et al., 2016). Nevertheless, our study incorporated important methodological changes that make results hardly comparable. In addition to manipulating the amount of sleep in the pre-training night to interfere with subsequent encoding, repeated testing, rather than restudy (Cowan et al., 2020) or relearning (Mazza et al., 2016), was introduced after post-training sleep, and not during the study phase as in prior studies (Antony & Paller, 2018; Himmer et al., 2019); and instead of comparing changes in brain responses after sleep and wakefulness (Himmer et al., 2019), we evaluated the correlation of SO-SP coupling during overnight sleep with changes in pattern similarity between encoding and retrieval across multiple repeated tests. Taken together, these results suggest that the particular contribution of

sleep and retrieval processes to memory consolidation depends on whether repeated testing precedes or follows sleep. While previous results indicate that sleep is necessary for stabilization and maintenance of transformations triggered by retrieval practice during the prior wakefulness (Himmer et al., 2019), our findings show that consolidation processes during sleep interact with processes taking place during subsequent retrieval to balance the trade-off between specificity and generalization depending on whether more or fewer details were encoded during the study phase before sleep.

This research is subject to several limitations that warrant further consideration. The stability of neural encoding was manipulated by restricting sleep the night before; and memory was addressed after a full night's sleep by presenting a complete reminder of the episodic event through the simplest form of testing. Given that sleep benefit seems to be highly dependent on the way that encoding strength is manipulated (Denis et al., 2020, 2021) and on the testing conditions (Petzka et al., 2021), our results may not be generalizable beyond the context of this study. The small number of participants per group heightens this limitation. The study was further limited by the lack of a test to measure recognition memory immediately after training. It is therefore difficult to determine whether memories showing smaller neural stability across encoding trials were also remembered worse than memories showing greater neural stability at the end of the study phase or whether post-training sleep was linked to memory improvements in those participants who were submitted to sleep restriction before memory acquisition. Nevertheless, the inclusion of such a test may also be an important confounding factor because whilst some studies support the view that immediate retrieval test following learning enhances the sleep benefit (Schoch et al., 2017) others found the opposite (Antony & Paller, 2018; Bäuml et al., 2014). Results of the present study suggest that these discrepancies might be accounted for by the quality of encoding. Finally, we considered the reinstatement of category-specific encoding activity as a neural index of generalization but we did not measure performance transfer of knowledge. This is probably the reason why no group differences in performance were found across repeated tests. Additionally, it would also have been desirable that part of the associations presented in the training phase had been repeatedly restudied during the recognition phase. This condition would have allowed us to identify more precisely the neural changes associated with online consolidation during retrieval.

With all the above-mentioned limitations in mind, future studies should include neural and behavioral measures of memory stability during encoding as well as measures of the reactivation of encoding-induced patterns associated with repeated restudy and repeated retrieval together with appropriate behavioral indices of memory transfer within different timescales to determine the neural and behavioral correlates of the representational reorganization favored by the interplay between sleep- and retrieval-mediated consolidation processes.

5. Conclusion

The present study provided novel evidence that the coordination of SOs and SPs not only is important for memory consolidation during sleep (Batterink et al., 2016; Denis et al., 2021; Helfrich et al., 2018; Jiang et al., 2019a, 2019b; Latchoumane et al., 2017; Maingret et al., 2016; Mölle et al., 2009, 2011; Muehlroth et al., 2019; Niknazar et al., 2015; Staresina et al., 2015; Zhang et al., 2018), but also for development of additional reorganization of memory traces triggered by repeated testing during intentional retrieval. Importantly, the study revealed that the restructuring of memory traces provoked by the interaction between post-training sleep and subsequent retrieval-mediated consolidation processes is moderated by the stability of neural encoding, which, in turn, is modulated, among other factors, by the amount of sleep in the pre-training night.

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CRedit authorship contribution statement

Daniel Baena: Conceptualization, Methodology, Software, Investigation, Formal analysis, Visualization, Writing – original draft. **Jose L. Cantero:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **Mercedes Atienza:** Conceptualization, Methodology, Formal analysis, Visualization, Supervision, Writing – review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.nlm.2021.107529>.

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